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Escuela de Ciencias Biológicas e Ingeniería

TÍTULO: An Overview of zoonotic chiropteran paramyxoviruses that cause respiratory infections in humans and their possible transmission causes.

Trabajo de integración curricular presentado como requisito para la obtención del título de Bióloga

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Dedication

This thesis is dedicated:

To my parents Carlos e Itsmenia, who have inspired me to fulfill my goals and objectives with their love and example.

To my siblings, for their support and encouragement at all times.

To Carlos L., who always believes in me and supports me absolutely.

Pamela Lisseth Suárez Paladines

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Resumen

Las actividades antropogénicas han causado graves estragos en la biodioversidad a nivel mundial. Estos impactos resultan en graves afectaciones para el ser humano, y en cuanto a salud pública, significan elevados costos monetarios. Los murciélagos son refugios naturales de paramyxovirus. Algunos son conocidos por el gran impacto que han tenido, principalmente en el continente Asiático. El virus Nipah y el virus Hendra son los paramyxovirus de quirópteros con más alcance hasta ahora. Sin embargo, han existido otros brotes, y debido a las prácticas humanas, no se descartan nuevos eventos zoonóticos. En Ecuador se practican muchas actividades que en otros lugares del mundo han sido "drivers" de zoonosis, lo que destaca la importancia de evaluar el contenido viral de los murciélagos en el país y los "drivers" que posiblemente puedan desencadenar nuevos eventos zoonóticos. En esta revisión bibliográfica, se describen brevemente la importancia ecológica de los murciélagos y las amenazas que enfrentan. También, se describen los brotes zoonóticos paramyxovirales de murciélagos alrededor del mundo, que han sido causantes de infecciones respiratorias. Además, se realiza una comparación de los paramyxovirus del mundo con los paramyxovirus en Ecuador, con un enfoque en los "drivers" de los brotes mundiales.

Palabras clave: paramyxovirus, zoonosis, murciélago, infección respiratoria

Abstract

Anthropogenic activities have wreaked serious havoc on biodiversity globally. These impacts result in grave harm to human beings, and in terms of public health, high monetary costs to society. Bats are natural refuges for paramyxoviruses. Some are known for the enormous impact they have had, mainly on the Asian continent. Nipah virus and Hendra virus are the most widespread chiropteran paramyxoviruses so far. However, there have been other outbreaks, and due to human practices, new zoonotic events are not ruled out. In Ecuador, many human practices that in other parts of the world have been drivers for zoonosis are commonplace. This highlights the importance of evaluating the viral content of bats in the country and the drivers that may trigger new zoonotic events. In this literature review, the ecological importance of bats and the threats they face are briefly described. In this context, paramyxoviral zoonotic outbreaks of bats worldwide are described, which have been the cause of respiratory infections. In addition, a comparison of paramyxoviruses in the world with paramyxoviruses in Ecuador is made, with a focus on the global drives of outbreaks.

Keywords: paramyxovirus, zoonoses, bat, respiratory infection

Contents

Resumen VII
Abstract VIII
List of Figures XI
List of Tables XII
Glossary XIII
Abbreviations XVI
1. Introduction 1
  1.1 Zoonotic Diseases 1
    1.1.1 Evolutionary stages leading to endemic human diseases 1
    1.1.2 Drivers for the appearance of zoonotic diseases 3
2. Problem Statement 5
  2.1 Objective 5
  2.2 Specific Objectives 5
3. Bats 6
  3.1 Diversity and taxonomy of bats 7
    3.1.1 Bats diversity in Neotropics 8
    3.1.2 Bats in Ecuador 12
    3.1.2.1 Historical importance of bats 12
    3.1.2.2 Bat diversity 13
    3.1.2.3 Bat ecology 26
  3.2 Ecological importance of bats 28
    3.2.1 Arthropod suppression 28
    3.2.1.1 Importance in agriculture-related to pests 29
    3.2.2 Pollination and seed dispersal 31
    3.2.2.1 Importance for agriculture 34
  3.3 Threats to Bat Biodiversity 36
    3.3.1 Deforestation 37
    3.3.1.1 Fragmentation 38
    3.3.1.2 Agriculture 41
    3.3.1.2.1 Exposure to pesticides 43
    3.3.2 Invasive species 44
    3.3.3 Climate change 45
    3.3.4 Legal and illegal hunting 48

3.3.5 Threats to roosting caves 49
3.3.6 Threats to bats and paramyxoviruses 50
3.3.7 Urbanization 51
3.3.8 Wind mills 52
4. Chiropteran paramyxoviruses and human respiratory infections in the world 56
4.1 Family Paramyxoviridae 57
4.1.1 Subfamily Orthoparamyxovirinae 61
4.1.1.1 Genus Respirovirus 61
4.1.1.1.1 Human parainfluenza virus (HPIV) 61
4.1.1.2 Genus Henipavirus 62
4.1.1.2.1 Hendra virus (HeV) 62
4.1.1.2.2 Nipah virus (NiV) 64
4.1.1.2.3 Ghana virus (GhV) 69
4.1.1.2.4 Cedar virus (CedV) 70
4.1.2 Subfamily Rubulavirinae 70
4.1.2.1 Genus Orthorubulavirus 70
4.1.2.1.1 Mumps virus (MuV) 70
4.1.2.1.2 Human parainfluenza virus 2 and 4 (HPIV-2, HPIV-4) 71
4.1.2.1.3 Porcine rubulavirus (PoRV) / La Piedad Michoacán México virus (LPMV) 71
4.1.2.2 Genus Pararubulavirus 72
4.1.2.2.1 Menangle virus (MenV) 73
4.1.2.2.2 Tioman virus (TioV) 74
4.1.2.2.3 Achimota virus (AchV) 75
4.1.2.2.4 Sosuga virus (SOSV) 76
5. Chiropteran paramyxoviruses and drivers of human respiratory infections in Ecuador 79
6. Conclusion and Outlooks 81
References 82

List of Figures

Figure 1. Habitats where individual bats are recorded. 7
Figure 2. Map of the transition zones / subregions of the Neotropical realm. 10
Figure 3. Habitats in the Neotropics where species bats have been observed............... 12
Figure 4. The number of bat species discovered in Ecuador until December 2020. 25
Figure 5. Conservation status of bats in the world. 37
Figure 6. Relationship between threats to species bats and agriculture at various scales. 42
Figure 7. Main threats to bats in relation to climate change... 47
Figure 8. Main threats to bats around the world... 51
Figure 9. Schematic diagram of a paramyxovirus virion structure in cross-section. 57
Figure 10. General Paramyxovirus genome structure (not to scale). 58
Figure 11. Phylogenetic tree of members of the family *Paramyxoviridae*.................... 60

List of Tables

Table 1. Evolutionary stages of spillover from animal pathogens to unique human pathogens. 2

Table 2. Native species of bats in Ecuador until December 2020. 15

Table 3. Species of bats not described or pending inclusion in Ecuador until 2020. 24

Table 4. Five endemic species of bats in Ecuador until 2020....................................... 25

Table 5. Some examples of the monetary benefit of bats in relation to pollination and seed dispersal. 36

Table 6. Bat paramyxoviruses causing possible respiratory infections in humans. 78

Table 7. Distribution of the bat families around the world. 79

Glossary

Adaptation: Behavior patterns or characteristics of an organism that suit it to its condition of existence. Under the theory of descendent with modification, adaptation is a derived feature of an organism that increases its reproductive and survival success by possession of that feature (1).

Aggregation: Anonymous assemblage of individuals at the same place. Bats in aggregations do not engage in cooperative or other affiliate social interactions and show no social bonds (2).

Alpha biodiversity: Local diversity of species. It is measured as the number of species per area or through another measure of diversity (3).

Animalivorous bat: Insectivorous and carnivorous bat (4).

Assemblage: A collection of plants and/or animals characteristically associated with a particular environment that can be used as an indicator of that environment (5).

Beta biodiversity: Level of species changes between habitats. It is measured as an index of similarity or rate of species turnover as a function of the area (3).

Bottleneck: A severe reduction in population size, often leading to a founder effect (5).

Clinical disease: Theoretical disease that is diagnosed (6). Clinical disease has recognizable clinical symptoms (7).

Colony: A grouping of individual species of the same species living closely together (1). All kinds of roosting associations of bats. Commonly, colony is used for females breeding communally in “maternity” colonies (2).

Community: An assemblage of species coexisting in a given area and interacting with each other through trophic and spatial relationships (1).

Direct transmission: Transmission of an infection from one individual to another (8).

Echolocation: The detection of an object by means of reflected sound. Bats, some cetaceans, and other animals use echo-location for purposes of orientation and the pursuit of prey (5).

Enzootic: Disease persistently at low incidence in an animal population. Analogous to endemic in humans (9).

Fitness: Measures how well a phenotype performs in terms of its ability to survive and reproduce (reproductive success) (10).

Gleaning bat: A bat taking prey from substrate (11).

Gregarious: Tending to form a group with individuals of the same species (12).

Group: Members of the same group interact more with one another than with the members of other groups. Bats that forage together have also been called groups (2).

Interference competition: During interference competition, two species interact physically by aggressively attempting to exclude one another from particular habitats (13).

Monophyly: State of grouping that contains all the descendants of a particular node in a phylogeny (14). A monophyletic group contains all descendants of a common ancestor (15).

Paraphyly: State of a grouping that contains some, but not all, of the descendants of a particular node in a phylogeny (14). A paraphyletic group contains some, but not all, of the descendants from a common ancestor (15).

Phenology: Timing of life cycle events (growth & reproduction), or series of events themselves, as they relate to seasonal events; natural phenomena that occur periodically (16).

Phylogenetic: Pertaining to the true pattern of relationship, usually expressed in the form of a binary branching tree, or phylogeny (14).

Population: Group of interacting individuals of same species in common spatial arrangement with potential for gene flow (16).

Spillover: Transmission of a pathogen from reservoir hosts to other species that generally do not sustain the pathogen (1).

Subclinic disease: An illness that is staying below the surface of clinical detection. A subclinical disease has no recognizable clinical findings. It is distinct from a clinical disease, which has signs and symptoms that can be recognized (17).

Sylvatic: Affecting, occurring in, or transmitted by wild animals (12).

Sympatric: Taxa, species, or population that occur together in the same geographical area within the dispersal range of one another (1).

Syncytium: A large cell-like structure formed by the joining together of two or more cells. The plural is syncytia (18).

Viral tropism: Viral tropism is the ability of a given virus to productively infect a particular cell (cellular tropism), tissue (tissue tropism) or host species (host tropism) (19).

Virion: An individual viral particle (1).

Virus: An infectious agent causing disease in all forms of organisms. A genetic element of DNA or RNA that can replicate only in cells. A virus has an extracellular state (1).

Zooanthroponosis: Any pathogen normally reservoired in humans that can be transmitted to other vertebrates (20).

Zoonosis: Human diseases caused by pathogens that proliferate within and are transmitted from nonhuman vertebrate animals (1). Also called anthropozoonosis (20).

Abbreviations

AchV: Achimota virus

AchV-1; AchPV1: Achimota virus 1

AchV-2; AchPV2: Achimota virus 2

AchV-3; AchPV3: Achimota virus 3

ATUs: Additional transcription units

BED: Blue eye disease

CedV: Cedar virus

CITES: Convention on International Trade in Endangered Species of Wild Fauna and Flora

F: fusion protein

G: glycoprotein

GhV: Ghana virus

GM: Genetically modified

H: Haemagglutinin

HeV: Hendra virus

HN: Haemagglutinin-neuraminidase protein

HPIV: Human parainfluenza virus

L: Large protein

LPMV: La Piedad Michoacán México virus

M: Matrix protein

MenV: Menangle virus

MojV: Mojiang virus

MPRV: Mapuera virus

MuV: Mumps virus

N: Nucleocapsid protein gen

NiV: Nipah virus

NiV-BD: NiV Bangladesh

NiV-MY: NiV Malaysia

nsNSV: Non-segmented Negative-Strand RNA Viruses

ORF: Open reading frames

P: Phosphoprotein

PoRV: Porcine rubulavirus

RBP: Receptor-binding protein

RdRp: RNA-directed RNA polymerase

RNP: Ribonucleoprotein

SARS: Severe acute respiratory syndrome

SH: Hydrophobic transmembrane protein

SOSV: Sosuga virus

TioV: Tioman virus

VRTI: Viral respiratory tract infections

1. Introduction

1.1 Zoonotic Diseases

Naturally, indirect or direct contact mediates the transmission of zoonotic diseases from animals to humans. Zoonotic diseases have always existed; however, during the last 30 years, infectious diseases in humans have increased, and of these, 70% are zoonotic. These infections are increasing because of human interactions with wildlife and changes in habitat, human behavior, as well as the environment. In particular, occurrences of zoonoses increase with close contact interactions, which can be through water, food, and the environment, and through contact with animals from distant geographic regions (21,22).

We can classify zoonotic diseases into different categories. Depending on the ecosystem in which the pathogens circulate zoonoses may be exoanthropic or synanthropic. Exoanthropic zoonoses occur outside human habitats in wild and feral animals, such as Lyme disease and wild animal rabies. Occasionally they may be found in urban environments. In contrast, synanthropic zoonoses cycle in urban or domestic animals, as in zoonotic ringworm or urban rabies (23).

1.1.1 Evolutionary stages leading to endemic human diseases

Their ability to spread to and among humans allow classifying transmissibility of zoonotic diseases into 5 stages. The spread of a pathogen that infects only animals corresponds to stage 1, and the spread of pathogens only among humans is stage 5. Two transitions between stages are less common. The first is the transition from stage 1 to stage 2, when a pathogen confined to animals infects humans for the first time. The second transition refers to a switch from stage 2 to 3 or 4, when a pathogen develops the ability to pass from human-to-human, rather than continuously cycling before disappearing. Some pathogenic microbes cannot reach stage 5; they get stuck at some previous stage. **Table 1** describes the 5 stages (24).

Table 1. Evolutionary stages of spillover from animal pathogens to unique human pathogens.

Stage	Description	Example	Ref
Stage 1	Microbes unique to animals. Not detected in humans.	Malarial plasmodia are mainly specific to a single host species or a related group, such as avian malaria, ungulate malaria, and lizard malaria.	(25–27)
Stage 2	Transmission of animal pathogens to humans under natural conditions ("primary infection"), but without human-to-human infection ("secondary infection").	Nipah, West Nile virus, anthrax.	(28–30)
Stage 3	Animal pathogens with the ability to cause occasional outbreaks in the human population through primary infection. Cycles of secondary transmission between humans are few.	Marburg virus, Ebola virus.	(31,32)
Stage 4	Cycle of natural (sylvatic; see glossary) infection in humans by an animal disease. Occasional human transmission is primarily from the animal, although there are also secondary transmission		

	between humans.		
Stage 4a	The sylvatic (see glossary) cycle is relevant (more than human-human direct transmission).	Chagas disease (secondary transmission approaches stage 4b), yellow fever.	(33,34)
Stage 4b	Sylvatic (see glossary) and direct transmission (see glossary) are important.	Dengue fever in Southeast Asia, and West Africa.	(35,36)
Stage 4c	Greatest spread between humans is of relevance. However, pathogens can cycle back to wild animals.	Human African Trypanosomiasis, cholera, typhus, influenza A.	(37–40)
Stage 5	A human only pathogen.	Syphilis, measles, falciparum malaria, smallpox.	(41–44)

Adapted from Wolfe et al., 2007.

1.1.2 Drivers for the appearance of zoonotic diseases

Zoonotic diseases appear due to several factors. Drivers include climate change, modern agricultural practices, human encroachment, habitat destruction, and pathogen genetics. Hunting and consumption of bush meat is a tradition in many cultures. The increase in these practices as well as trade facilitate the transmission of zoonotic diseases. For example, the pandemic caused by the Sars-CoV-2 virus likely originated from wild animals traded in a Chinese market. The probable natural host are bats (45).

Agricultural drivers are an essential factor. Modernization in agricultural practices, such as clearing of large areas for cultivation, and agricultural intensification affect biodiversity. Crops and livestock replace wild flora and fauna. In this way, transferring zoonotic diseases to new susceptible hosts is more probable (22).

Geoclimatic change is of great relevance in the epidemiology of zoonotic diseases. Vectors and changes in the dynamics of pathogenic reservoirs mediate the influence of climatic variations on zoonotic affections. The creation of new ecological niches for vectors result from climatic fluctuation, which alter the spatial and temporal distribution of diseases (46). This introduces pathogens to geographically distant, naïve populations or species in which they have not been found before, including humans (22). Any animal with the potential to transmit pathogens to humans is a vector, as for instance with rabies, which is one of the most deadly diseases. When a rabid animal such as a fox, dog, raccoon, bat, monkey, or skunk bites a human, the virus enters their body through saliva (23).

Understanding these drivers and evaluating the interactions between pathogens and hosts will allow the development of new mitigation strategies. Because of the impact on public health, the economy, and social welfare, it is important to understand that the appearance of a zoonotic disease which arise due to multifactorial effects and thus achieve timely and effective responses (22).

2. Problem Statement

The increase in human activity has caused an alteration of ecosystems throughout the world. These events represent grave damage to biodiversity with critical consequences for humans by way of worldwide zoonotic viral events (47). Paramyxoviruses are viruses that have co-evolved with several classes of animals. Bats harbor a large number of paramyxoviruses, and some of them have been determined to be zoonotic or potentially zoonotic (48). Some current drivers of bat population decline can affect humans as well (49–51). Public health issues, particularly respiratory infections, are of great concern. Around the world, millions of people contract respiratory infections, with mild or severe symptoms, often resulting in fatalities and representing millions of dollars annually in health related costs for entire nations (52,53). Since Ecuador harbors a great diversity of bats, the country has an immense potential to study the viral diversity that co-exists with bats and possible zoonotic drivers.

2.1 Objective

To review current information on the Paramyxoviridae family viruses, the probable causes of transmission to humans, and the regions where the virus outbreaks have occurred worldwide and in Ecuador, focusing on the viruses causing respiratory diseases in humans.

2.2 Specific Objectives

i. Describe patterns of diversity of bats in the world and Ecuador.
ii. To describe the ecosystem services provided by bats, emphasizing the monetary costs and benefits they represent to humans.
iii. To describe the threats faced by bats worldwide and in Ecuador.
iv. To describe the paramyxoviruses in chiropterans with zoonotic potential associated with respiratory infections in humans worldwide.
v. To compare the possible causes and drivers of bat to human viral transmission of paramyxovirus worldwide and in Ecuador, focusing on respiratory infections.

3. Bats

Bats are nocturnal mammals that belong to the order Chiroptera (means: hand-wing). It is one of the most diverse mammal orders worldwide, with more than 1,400 identified species (54). They are distributed around the globe, occupying different habitats, such as forests, wetlands, shrublands, rocky areas and savannas, except the Arctic, Antarctica, and high elevations (**Figure 1**) (55). Their diversity decreases as latitude increases and increases closer to the equator (54).

Chiropterans are the only mammals capable of continuous and active flight. They have wings formed by thin elastic membranes stretching between the digits of the hands, legs and tail. Due to ligaments in their feet, they do not need to expend energy to hang upside down. The bodyweight pulls on the ligaments, which flexes the claws, allowing them to adhere to a surface. Except for one family, all bats can create sounds with their larynx, and all have functional eyes (54).

Bats are the vertebrates that form the largest aggregations (see glossary). They live in groups (see glossary) or colonies (see glossary), which brings them fitness (see glossary) benefits when interacting with known individuals, such as increased vigilance, risk dilution or enhanced thermoregulation (54,56). Colossal colonies of millions of individuals are known scattered throughout the world. In general, they live in caves and tree cavities although they can live in other shelters such as artificial tunnels, mines, or basements as well as vegetation (54).

Bats vary greatly in body size, often related to the large number of ecological niches they occupy. The smallest bat, Kitti’s Hog-nosed bat, *Craseonycteris thonglongyai,* weighs 2g, whereas the Indian flying fox, *Pteropus giganteus,* can exceed 1600g. The feeding habits are different among species and include frugivory, hematophagy, piscivory, nectarivory, insectivory, and small vertebrates predation (54).

Berkovitz and Shellis, (2018) mention the duality of food, a hypothesis proposed by Gillette (1975), which explains the diet's diversity. According to this hypothesis, chiropterans were originally insectivores and began to feed on fruits and other foods as supplements to insects until these became specialized on them (57).

Bats use different mechanisms to find their food. Megachiropterans, or flying foxes, find their food by smell and specialized night vision. Microchiropterans, or small bats, use a sophisticated laryngeal and hearing mechanism called echolocation to find their prey. These chiropterans generate ultrasound pulses in their larynx and transmit them through their nose or mouth. The ears receive the echoes of the objects that surround the animal and are interpreted by the brain as spatial information (57). However, the eyesight of some Microchiropterans, such as Long-eared bats, *Plecotus auritus*, allows them to rely less on echolocation and prefer to detect visual cues than sonar cues in situations such as obstacle avoidance, long-distance orientation, detection of landmarks, and prey detection. In addition, studies in *Pipistrellus subflavus*, *Myotis sodalis*, *Phyllostomus hastatus*, *Carollia perspicillata*, *Anoura geoffroyi*, and *Desmodus rotundus* concluded that visual capabilities allow them to see well beyond the range of echolocation (58).

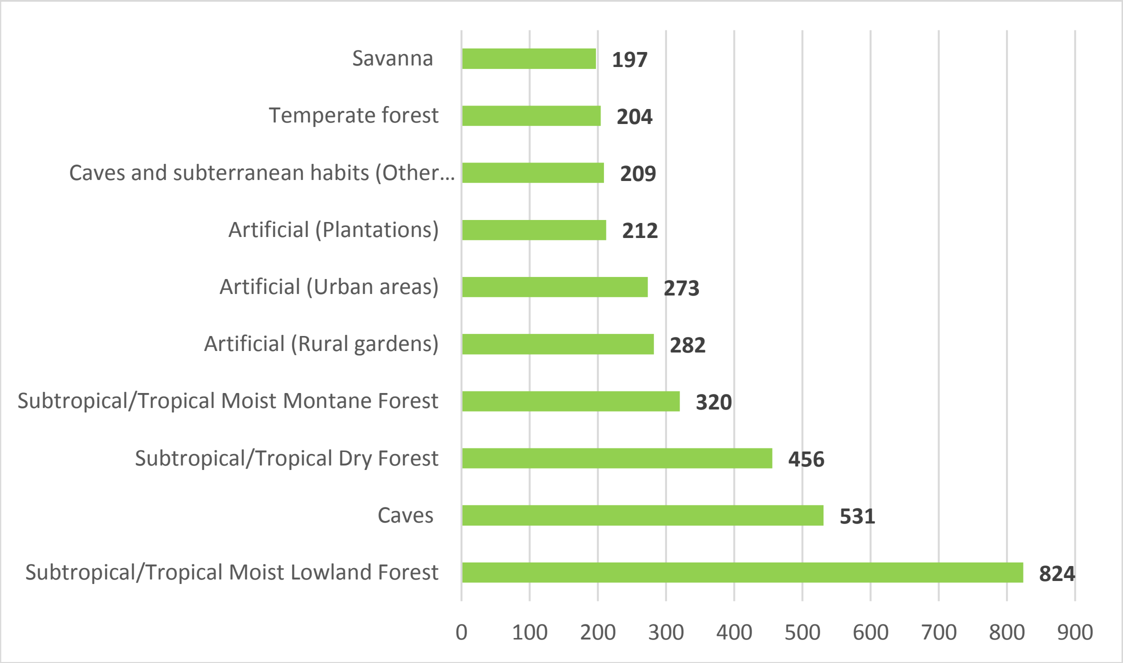

Figure 1. Habitats where individual bats are recorded.
Adapted from IUCN (International Union for Conservation of Nature), 2020.

3.1 Diversity and taxonomy of bats

Bats are the second most species-rich order of mammals. Of all the diversity of existing mammals, bats account for approximately 20%. It is estimated that there are 1,386 species of bats globally distributed in 227 genera and 21 families (59).

As mentioned earlier, bats were traditionally divided into two superordinal groups: megabats or Megachiropterans and microbats or Microchiropterans. Megabats are the giant bats, with a wingspan between 40-220 cm, while the wingspan of microbats varies between 22 and 135 cm (40). This latter group contains 20 families, while the giant bats contain only 1 family (61). This division was based on paleontological and morphological studies, considering also differences at the level of sensory perception (40).

The natural association of Microchiroptera bats (monophyly; see glossary) versus the unnatural association (paraphyly; see glossary) is of great interest to understand the evolution of laryngeal echolocation (see glossary). Microbat monophyly originates from morphological cladistics and postulates the evolution of echolocation in the common ancestor of living microbats. On the other hand, the Chiroptera paraphyly suggests the close relationship of the rhinolophoid microbats with the Pteropodidae megabats, more than with other microbats, from the molecular analysis. This classification is based on molecular studies and implies that echolocation evolved independently in different groups of microbats, or echolocation was lost in Old World frugivores after evolving into the common ancestor of Chiroptera (62).

These data were included in a new taxonomy divided into the suborders Yangochiroptera and Yinpterochiroptera. Yangochiroptera includes the superfamilies: Emballonuroidea (Emballonuridae and Nycteridae families), Noctilionoidea (Furipteridae, Mormoopidae, Mystacinidae, Myzopodidae, Noctilionidae, Phyllostomidae and Thyropteridae families), and Vespertilionoidea (Cistugidae, Miniopteridae, Molossidae, Natalidae and Vespertilionidae families). Yinpterochiroptera includes the family Pteropodidae and the subfamily Rhinolophoidea (Craseonycteridae, Hipposideridae, Megadermatidae, Rhinolophidae, Rhinonycteridae, and Rhinopomatidae families) (61).

3.1.1 Bats diversity in Neotropics

The Neotropical region is probably the most diverse in the world. At least 1,100 species of mammals, 1,700 amphibians and reptiles, and 3,000 birds have been described (63). Concerning flora, the Neotropics has more than 90,000 species, with more than 90% being angiosperms (64). The number of species of flora and fauna increases every year due to discoveries. Forty five % (281.2 million hectares) of the total hectares of the world's tropical forest are found in the Neotropics (65).

Taxonomic biogeographic analyzes in the Neotropics have inferred the origin of biota in the main Neotropical regions. Possibly, the Amazon is the main source of Neotropical biodiversity, providing > 2,800 lineages to other regions. Most of the dispersions occurred in Mesoamerica, followed by northern South America and the Chaco and Cerrado biomes (66).

Recently, researchers have redefined the Neotropics based on geographic distribution maps and phylogenetic analyzes (67). The Neotropical region corresponds to the tropical areas of the New World, including Central America, southern and central Mexico, most of America, and the Antilles. The Neotropical region includes the Chacoana, Brazilian and Antillean subregions. The Neotropical region of South America overlaps with the Andean region in the South American transition zone. The Neotropical region of Mexico overlaps with the Nearctic region in the Mexican transition zone **(Figure 2)** (68). Simultaneously, these transition zones belong to the Neotropical region and the Andean and Nearctic regions, respectively (68).

Numerous systems have been proposed to classify Neotropic forests. The most used are floristic, physiognomic (structural), and bioclimatic. The physiognomic classification is based on characteristics, such as stratum number (canopy, sub-canopy, understory), canopy height, percentage of deciduous species, number of growth forms, and variety of leaf forms. The advantage of this classification is that it does not depend on an inventory of tree species. The plant formations within this classification are Rain forest, seasonal forest, dry evergreen forest, montane forest, swamp forest, and seasonal lagoon or swamp. UNESCO uses descriptors to define vegetation formations as deciduous, deciduous-dry, evergreen, ombrophilous, and seasonal. Altitudinal bands are formed in the bioclimatic classification. These bands are basal or tropical, premontane, low montane, subalpine montane, alpine, and nival (69).

Figure 2. Map of the transition zones / subregions of the Neotropical realm. Adapted from Morrone, 2014.

Chiropterans are one of the two most ecological, phylogenetical, and taxonomically diverse groups of vertebrates. Around the world, the Neotropical region is the most diverse in bats due to the wide range of ecological niches they occupy and the diversity of food resources available (70). Bats represent more than 50% of the species of the mammalian fauna (71). A global analysis to understand the mechanisms of bat richness patterns in the tropics showed that species richness declined as water availability and temperature decreased. In contrast, bat richness patterns increased where the availability of water and the temperature were high. In mountains with humid and warm bases, the richness of the species decreases altitude. In contrast, the richness of the species shows peaks of biodiversity of medium elevation in mountains with arid bases. For most bats, abrupt weather changes, lower temperatures, lower productivity at high altitudes, and lower habitat complexity make highlands less profitable and sometimes unsuitable (72).

Neotropical rainforests make up the largest expanses of rainforests on the planet. The Neotropical rainforests can be divided into four regions: Amazon, Chocoan, Mesoamerican / Caribbean, and Atlantic / Paraná. All these regions combined are more extensive than any tropical rainforest ecosystem in the world. Among the best-known rainforests are the Atlantic rainforest, Darién in Panama, Amazon basin jungle, and the Choco jungle in Colombia, Panama, and Ecuador. Tropical rainforests receive annual rainfalls at least 2000 mm, occurring between 23 ° 27´N and 23 ° 27´S latitude. In terms of vegetation structure, tropical forests are stratified with distinct understory, middle level, canopy, and emergent layers. Canopy height is around 30 to 50 m, although emergent trees might rise above the canopy, reaching heights over 50 m. Located below 500 m, lowland rainforests comprise the largest expanse of rainforests in the Neotropics (73).

The Neotropical Montane Forest exhibits drastic variations in environmental conditions along the elevation gradient. The specialized traits in such environments promote isolation and speciation. Therefore, most endemic species in this ecosystem tend to be confined to small areas. The montane cloud forest in the Valle del Silencio (2500 masl) of the Cordillera de Talamanca, in Costa Rica, is a natural barrier between the Pacific and Caribbean coasts of Panama and Costa Rica, making the cloud forest a center of endemism. The species *Myotis oxyotus*, *Myotis keaysi*, and *Sturnira burtonlimi*, previously classified as Andean para-montanes, were identified. These bats share characteristics, such as the prevalence of the Phyllostomidae and Vespertilionidae families, reduced species richness, and an almost equal insectivores and frugivores presence, with other mountain bat guilds in the Neotropics (72).

The pre-montane tropical forests are located between 500 and 1700 m, whereas montane cloud forest occurs between 1200 and 1700 m. Species do not recognize these divisions but are limited by habitat. In this way, lowland, premontane, and montane forests have their own set of species but with great overlap. Combined, these regions have the highest levels of biodiversity on earth. For example, the alpha (local scale; see glossary) and beta (between sites; see glossary) plant diversity is high. It is estimated that in the Amazon basin alone, there are more than 50,000 plant species that make up a complex, stratified structure. High plant diversity allows animals to occupy an abundance of habitats. This is one of the many hypotheses that explain why the fauna of these tropical forests is the most diverse in the world (**Figure 3**) (55).

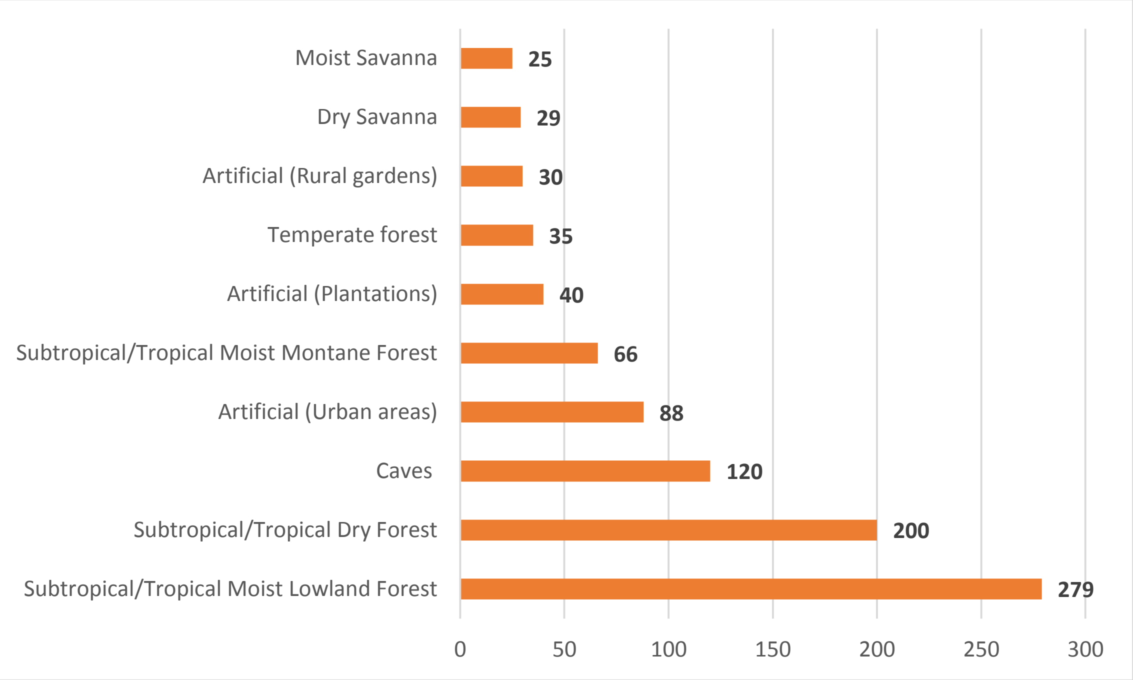

Figure 3. Habitats in the Neotropics where species bats have been observed. Adapted from IUCN (International Union for Conservation of Nature), 2020.

Continental South America comprises altitudes above 7000 m. In addition, it has considerable climatic, geological, geomorphological and hydrological diversity, and marked local and regional differences between flora and fauna (74). In general, the Amazon of Brazil and Guyana is one of the most diverse in Neotropical bats. Sampaio et al., (2003) sampled 72 species from 43 genera; out of 117 predicted bats species for the Amazon region. In South America, nine families have been registered. Phyllostomids are the most diverse and common cave bats of the Neotropics, especially in tropical and subtropical South America. Chiropterans represent 40% of the diversity of mammals in the Amazon region (70).

3.1.2 Bats in Ecuador

3.1.2.1 Historical importance of bats

The implementation of strategies for the conservation of bats implies transmitting their cultural and historical expression. Local knowledge about biodiversity has been useful in wildlife management; however, the perception of bats continues to be complex.

Therefore, it is necessary to analyze social, cultural, and historical aspects that help communities to recognize their natural resources as emblematic (75).

In Ecuador, bats had great cultural importance and significance in certain pre-Hispanic societies. The oldest evidence of the close bat-human relationship dates back to the end of the Early Formative period (3,400 to 1,500 BC). In the north of Manabí, it was founded the funerary remains of a woman and a bat skeleton. The period in question corresponds to the Valdivia phase. Bats probably played a role in shamanic rituals, in which the bat represents magical (drug induced) flight related to blood and fertility. Other findings have been recorded in the Chorrera culture (between Manabí, Santa Elena and Guayas), the Tumaco-La Tolita culture (north of Esmeraldas), Bahía and Jama-Coaque II (Manabí), the Tejar, Jambelí and Guangala cultures (all in the south, center and coast of Ecuador), Atacames-Balao and Manteño-Huancavilca cultures (coastal region). The Negativo del Carchi culture was the only one in the sierra region with evidence (in a gold breastplate) of human-bat interaction. The bat also represented masculinity and motherhood, and blood-sucking bats were probably associated with human rituals (76).

3.1.2.2 Bat diversity

Biodiversity in Ecuador is one of the richest on the planet and is favored by three factors, which are the influence of marine currents along the coast, the country's location in the equatorial zone, and the rise of the Andes. The presence of the Andes may be the most relevant factor in the richness of Neotropical species. The Andes are a geographical barrier that caused the isolation of populations (see glossary) in temperate and high Andean zones, such as in the eastern and western tropics and subtropics, facilitating the appearance of new species. Furthermore, due to its altitudinal range (up to 6263 m), the Andes allowed the formation of a great variety of ecosystems. The equatorial location of the country permits a tropical climate throughout the year. Weather is strongly influenced by marine currents and vegetation, resulting in the humid forests in the extreme north by the warm El Niño Current and dry forests in the south by the scarce rainfall caused by the cold Humboldt Current (77).

Burneo and Tirira, (2014), conducted an investigation of potential richness and distribution patterns of 81 species of bats in Ecuador. The areas with the greatest richness in the country are the central and northeastern foothills of the Andes. This diversity can be explained by the location of the zones along an altitude gradient, from tropical regions in the Amazonian plains to higher altitude subtropical and temperate forests. The colonization process in these areas has been prevented by the altitude variation and the geographical location (78). Changes produced by the rising of the Andes millions of years ago possibly promoted adaptation (see glossary) and ultimately endemism of bats. For example, the *Amorphochilus schnablii* bat is endemic to the coastal plain west of the Andes Mountains, with populations from northern Chile to southern Ecuador (79). In addition, regional endemism is high for bats in Ecuador, with 24% (of 125 species) of the country's bats confined to the western lowlands (80).

The areas of greatest relative richness in the central and northeastern foothills of the Andes are in the Machalilla National Park, the Cayapas-Mataje Mangrove Ecological Reserve, the Cofán-Bermejo Ecological Reserve (not much studied due to the presence of guerrilla groups), the Antisana Ecological Reserve, and the Sumaco-Napo Galeras National Park. Surprisingly, the Yasuní National Park reported a relatively low diversity (54 species of bats). Furthermore, only 5.6% of the mentioned areas are protected. Additionally, it was possible to identify priority areas for research (Southeastern tropics, Northern Andes, tropical dry forests) and conservation (Northwest of the Pichincha province, Pastaza, Morona Santiago, and Zamora Chinchipe) (78).

Ecosystem analyzes support the eastern low montane evergreen forests of the Andean foothills as ecosystems with the highest concentration of bats in the country. The altitudinal range ranges from 600 to 2900 m; and is 36% protected by the location of protected areas in this territory, such as the Cerro Plateado, Cofán-Bermejo, and Antisana ecological reserves, the El Quimi and El Cóndor biological reserves, the Llanganates, Cayambe-Coca, Podocarpus, Sumaco-Napo Galeras, and Sangay National Parks; and El Zarza Wildlife Refuge. On the other hand, the eastern lowland evergreen forests of the lower altitude ecosystems in the Amazon have only a 22% protected area. The Cuyabeno Wildlife Production Reserve, the Yasuní National Park, and small areas in the Cofán-Bermejo Ecological Reserve are in this area. The eastern piedmont evergreen forests have a protected area of 11%, included in the Cofán-Bermejo Ecological Reserve and the Sumaco-Napo Galeras, Cayambe-Coca, and Llanganates National Parks (78).

From the discovery of the first bat in Ecuador, in 1789, by the Jesuit priest Juan de Velasco to the present, several studies have contributed to the knowledge of the diversity of bats in the country (81). Currently, there are 196 species of bats discovered in Ecuador, which are distributed in 8 families, 14 subfamilies, and 63 genera (82). These species are divided in native species (**Table 2**), not described or pending inclusion (**Table 3**), and endemic species (**Table 4**) (82).

Table 2. Native species of bats in Ecuador until December 2020.

Species		Common name
Family Emballonuridae		Sac-winged Bats and Ghost Bats
Subfamily Emballonurinae		
Genus *Balantiopteryx*		
1.	*Balantiopteryx infusca*	Ecuadorian Sac-winged Bat
Genus *Centronycteris*		
2.	*Centronycteris centralis*	Central American Shaggy Bat
Genus *Cormura*		
3.	*Cormura brevirostris*	Chestnut Sac-winged Bat
Genus *Diclidurus*		
4.	*Diclidurus albus*	Common Ghost Bat
5.	*Diclidurus scutatus*	Lesser Ghost Bat
Genus *Peropteryx*		
6.	*Peropteryx kappleri*	Greater Dog-like Bat
7.	*Peropteryx leucoptera*	White-winged Dog-like Bat
8.	*Peropteryx macrotis*	Lesser Dog-like Bat
9.	*Peropteryx pallidoptera*	Pale-winged Dog-like Bat
Genus *Rhynchonycteris*		
10.	*Rhynchonycteris naso*	Proboscis Bat
Genus *Saccopteryx*		
11.	*Saccopteryx bilineata*	Greater Sac-winged Bat
12.	*Saccopteryx leptura*	Lesser Sac-winged Bat

	Family Phyllostomidae	**New World Leaf-nosed Bats**
	Subfamily Desmodontinae	Vampire Bats
Genus *Desmodus*		
13.	*Desmodus rotundus*	Common Vampire Bat
Genus *Diaemus*		
14.	*Diaemus youngii*	White-winged Vampire Bat
Genus *Diphylla*		
15.	*Diphylla ecaudata*	Hairy-legged Vampire Bat
	Subfamily Glossophaginae	Nectarivorous Bats
Genus *Anoura*		
16.	*Anoura aequatoris*	Ecuadorian Tailless Bat
17.	*Anoura caudifer*	Lesser Tailless Bat
18.	*Anoura cultrata*	Black Tailless Bat
19.	*Anoura fistulata*	Long-lipped Tailless Bat
20.	*Anoura geoffroyi*	Geoffroy’s Tailless Bat
21.	*Anoura peruana*	Peruvian Tailless Bat
Genus *Choeroniscus*		
22.	*Choeroniscus minor*	Lesser Long-tongued Bat
23.	*Choeroniscus periosus*	Greater Long-tongued Bat
Genus *Glossophaga*		
24.	*Glossophaga commissarisi*	Commissaris’ Long-tongued Bat
25.	*Glossophaga soricina*	Common Long-tongued Bat
Genus *Lichonycteris*		
26.	*Lichonycteris degener*	Pale Brown Long-nosed Bat

27.	*Lichonycteris obscura*	Dark Brown Long-nosed Bat
	Subfamily Lonchophyllinae	Nectar Bats
Genus *Hsunycteris*		
28.	*Hsunycteris cadenai*	Cadena’s Small Nectar Bat
29.	*Hsunycteris pattoni*	Patton’s Small Nectar Bat
30.	*Hsunycteris thomasi*	Thomas’s Small Nectar Bat
Genus *Lionycteris*		
31.	*Lionycteris spurrelli*	Chestnut Long-tongued Bat
Genus *Lonchophylla*		
32.	*Lonchophylla chocoana*	Chocoan Nectar Bat
33.	*Lonchophylla concava*	Central American Nectar Bat
34.	*Lonchophylla fornicata*	Pacific Forest Nectar Bat
35.	*Lonchophylla handleyi*	Handley’s Nectar Bat
36.	*Lonchophylla hesperia*	Western Nectar Bat
37.	*Lonchophylla orcesi*	Orcés’ Nectar Bat
38.	*Lonchophylla orienticollina*	Eastern Cordilleran Nectar Bat
39.	*Lonchophylla robusta*	Orange Nectar Bat
	Subfamily Micronycterinae	Little Big-eared Bats
Genus *Lampronycteris*		
40.	*Lampronycteris brachyotis*	Yellow-throated Bat
Genus *Micronycteris*		
41.	*Micronycteris giovanniae*	Giovanni’s Big-eared Bat
42.	*Micronycteris hirsuta*	Hairy Big-eared Bat
43.	*Micronycteris megalotis*	Little Big-eared Bat

44.	*Micronycteris minuta*	Tiny Big-eared Bat
45.	*Micronycteris schmidtorum*	Schmidts's Big-eared Bat
46.	*Micronycteris simmonsae*	Simmons' Big-eared Bat
	Subfamily Lonchorhininae	Sword-nosed Bats
Genus *Lonchorhina*		
47.	*Lonchorhina aurita*	Common Sword-nosed Bat
	Subfamily Phyllostominae	Leaf-nosed Bats and False Vampire Bats
Genus *Chrotopterus*		
48.	*Chrotopterus auritus*	Woolly False Vampire Bat
Genus *Gardnerycteris*		
49.	*Gardnerycteris crenulatum*	Striped Hairy-nosed Bat
50.	*Gardnerycteris keenani*	Pacific Striped Bat
Genus *Lophostoma*		
51.	*Lophostoma brasiliense*	Pygmy Round-eared Bat
52.	*Lophostoma carrikeri*	Carriker's Round-eared Bat
53.	*Lophostoma occidentale*	Western Round-eared Bat
54.	*Lophostoma silvicola*	White-throated Round-eared Bat
Genus *Macrophyllum*		
55.	*Macrophyllum macrophyllum*	Long-legged Bat
Genus *Phylloderma*		
56.	*Phylloderma stenops*	Pale-faced Bat
Genus *Phyllostomus*		
57.	*Phyllostomus discolor*	Pale Spear-nosed Bat
58.	*Phyllostomus elongatus*	Lesser Spear-nosed Bat
59.	*Phyllostomus hastatus*	Greater Spear-nosed Bat
Genus *Tonatia*		
60.	*Tonatia bakeri*	Baker's Stripe-headed Round-eared Bat
61.	*Tonatia maresi*	Mares' Stripe-headed Round- eared Bat
Genus *Trachops*		
62.	*Trachops cirrhosus*	Fringe-lipped Bat
Genus Vampyrum		

63.	*Vampyrum spectrum*	Spectral Bat
	Subfamily Glyphonycterinae	Graybeard bats and Niceforo's Bat
Genus *Glyphonycteris*		
64.	*Glyphonycteris daviesi*	Davies's Graybeard Bat
65.	*Glyphonycteris sylvestris*	Little Graybeard Bat
Genus *Trinycteris*		
66.	*Trinycteris nicefori*	Niceforo's Bat
	Subfamily Carolliinae	Short-tailed Bats
Genus *Carollia*		
67.	*Carollia brevicaudum*	Silky Short-tailed Bat
68.	*Carollia castanea*	Chestnut Short-tailed Bat
69.	*Carollia perspicillata*	Common Short-tailed Bat
	Subfamily Rhinophyllinae	Little Fruit Bats
Genus *Rhinophylla*		
70.	*Rhinophylla alethina*	Hairy Little Fruit Bat
71.	*Rhinophylla fischerae*	Fischer's Little Fruit Bat
72.	*Rhinophylla pumilio*	Dwarf Little Fruit Bat
	Subfamily Stenodermatinae	New World Fruit Bats
Genus *Sturnira*		
73.	*Sturnira aratathomasi*	Giant Yellow-shouldered Bat
74.	*Sturnira bakeri*	Baker's Yellow-shouldered Bat
75.	*Sturnira bidens*	Bidentate Yellow-shouldered Bat
76.	*Sturnira bogotensis*	Bogota Yellow-shouldered Bat
77.	*Sturnira erythromos*	Hairy Yellow-shouldered Bat
78.	*Sturnira giannae*	Gianna's Yellow-shouldered Bat
79.	*Sturnira koopmanhilli*	Chocoan Yellow-shouldered Bat
80.	*Sturnira ludovici*	Ludovic's Yellow-shouldered Bat
81.	*Sturnira luisi*	Luis's Yellow-shouldered Bat
82.	*Sturnira magna*	Greater Yellow-shouldered Bat
83.	*Sturnira nana*	Lesser Yellow-shouldered Bat
84.	*Sturnira oporaphilum*	Eastern Yellow-shouldered Bat
85.	*Sturnira perla*	Perla Yellow-shouldered Bat

86.	*Sturnira tildae*	Tilda's Yellow-shouldered Bat
Genus *Artibeus*		
87.	*Artibeus aequatorialis*	Ecuadorian Fruit-eating Bat
88.	*Artibeus concolor*	Brown Fruit-eating Bat
89.	*Artibeus fraterculus*	Fraternal Fruit-eating Bat
90.	*Artibeus lituratus*	Great Fruit-eating Bat
91.	*Artibeus obscurus*	Dark Fruit-eating Bat
92.	*Artibeus planirostris*	Flat-faced Fruit-eating Bat
93.	*Artibeus anderseni*	Andersen's Little Fruit-eating Bat
94.	*Artibeus glaucus*	Silver Little Fruit-eating Bat
95.	*Artibeus gnomus*	Dwarf Little Fruit-eating Bat
96.	*Artibeus ravus*	Yellowish Little Fruit-eating Bat
97.	*Artibeus rosenbergi*	Rosenberg's Little Fruit- eating Bat
Genus *Chiroderma*		
98.	*Chiroderma gorgasi*	Handley's Big-eyed Bat
99.	*Chiroderma salvini*	Salvin's Big-eyed Bat
100.	*Chiroderma trinitatum*	Little Big-eyed Bat
101.	*Chiroderma villosum*	Hairy Big-eyed Bat
Genus *Enchisthenes*		
102.	*Enchisthenes hartii*	Velvety Fruit-eating Bat
Genus *Mesophylla*		
103.	*Mesophylla macconnelli*	McConnell's Bat
Genus *Platyrrhinus*		
104.	*Platyrrhinus albericoi*	Alberico's Broad-nosed Bat
105.	*Platyrrhinus angustirostris*	Slender Broad-nosed Bat
106.	*Platyrrhinus brachycephalus*	Short-headed Broad-nosed Bat
107.	*Platyrrhinus dorsalis*	Thomas' Broad-nosed Bat
108.	*Platyrrhinus fusciventris*	Brown-bellied Broad-nosed Bat
109.	*Platyrrhinus helleri*	Heller's Broad-nosed Bat
110.	*Platyrrhinus incarum*	Incan Broad-nosed Bat
111.	*Platyrrhinus infuscus*	Buffy Broad-nosed Bat
112.	*Platyrrhinus ismaeli*	Ismael's Broad-nosed Bat
113.	*Platyrrhinus matapalensis*	Matapalo Broad-nosed Bat
114.	*Platyrrhinus nitelinea*	Western Broad-nosed Bat

115.	*Platyrrhinus umbratus*	Shadowy Broad-nosed Bat
116.	*Platyrrhinus vittatus*	Greater Broad-nosed Bat
Genus *Sphaeronycteris*		
117.	*Sphaeronycteris toxophyllum*	Visored Bat
Genus *Uroderma*		
118.	*Uroderma bilobatum*	Common Tent-making Bat
119.	*Uroderma convexum*	Pacific Tent-making Bat
120.	*Uroderma magnirostrum*	Brown Tent-making Bat
Genus *Vampyressa*		
121.	*Vampyressa melissa*	Peruvian Yellow-eared Bat
122.	*Vampyressa thyone*	Little Yellow-eared Bat
Genus *Vampyriscus*		
123.	*Vampyriscus bidens*	Bidentate Yellow-eared Bat
124.	*Vampyriscus nymphaea*	Striped Yellow-eared Bat
Genus *Vampyrodes*		
125.	*Vampyrodes caraccioli*	Caracciolo’s Stripe-faced Bat
126.	*Vampyrodes major*	Great Stripe-faced Bat
	Family Mormoopidae	**Leaf-chinned Bats and Mustached Bats**
Genus *Mormoops*		
127.	*Mormoops megalophylla*	Ghost-faced Bat
Genus *Pteronotus*		
128.	*Pteronotus rubiginosus*	Wagner’s Common Mustached Bat
	Family Noctilionidae	**Bulldog Bats**
Genus *Noctilio*		
129.	*Noctilio albiventris*	Lesser Bulldog Bat
130.	*Noctilio leporinus*	Greater Bulldog Bat
	Family Furipteridae	**Thumbless Bats**
Genus *Amorphochilus*		
131.	*Amorphochilus schnablii*	Smoky Bat
Genus *Furipterus*		
132.	*Furipterus horrens*	Thumbless Bat

Family Thyropteridae		Disk-winged Bats
Genus *Thyroptera*		
133.	*Thyroptera discifera*	Peters’ Disk-winged Bat
134.	*Thyroptera lavali*	LaVal’s Disk-winged Bat
135.	*Thyroptera tricolor*	Spix’s Disk-winged Bat

Family Molossidae		Free-tailed Bats
Subfamily Molossinae		
Genus *Cabreramops*		
136.	*Cabreramops aequatorianus*	Cabrera’s Free-tailed Bat
Genus *Cynomops*		
137.	*Cynomops greenhalli*	Greenhall’s Dog-faced Bat
138.	*Cynomops mastivus*	Thomas’ Dog-faced Bat
139.	*Cynomops tonkigui*	Waorani Dog-faced Bat
Genus *Eumops*		
140.	*Eumops auripendulus*	Black Bonneted Bat
141.	*Eumops hansae*	Sanborn’s Bonneted Bat
142.	*Eumops maurus*	Guianan Bonneted Bat
143.	*Eumops nanus*	Dwarf Bonneted Bat
144.	*Eumops perotis*	Greater Bonneted Bat
145.	*Eumops wilsoni*	Wilson’s Bonneted Bat
Genus *Molossops*		
146.	*Molossops temmincki*	Dwarf Dog-faced Bat
Genus *Molossus*		
147.	*Molossus coibensis*	Coiban Mastiff Bat
148.	*Molossus currentium*	Bonda Mastiff Bat
149.	*Molossus fentoni*	Fenton’s Mastiff Bat
150.	*Molossus molossus*	Common Mastiff Bat
151.	*Molossus rufus*	Black Mastiff Bat
Genus *Nyctinomops*		
152.	*Nyctinomops laticaudatus*	Broad-eared Free-tailed Bat
153.	*Nyctinomops macrotis*	Big Free-tailed Bat
Genus *Promops*		
154.	*Promops centralis*	Big Crested Mastiff Bat

155.	*Promops davisoni*	Davison’s Crested Mastiff Bat
Genus *Tadarida*		
156.	*Tadarida brasiliensis*	Brazilian Free-tailed Bat
	Family Vespertilionidae	**Vesper Bats**
	Subfamily Vespertilioninae	Vesper Bats
Genus *Eptesicus*		
157.	*Eptesicus andinus*	Little Black Serotine
158.	*Eptesicus brasiliensis*	Brazilian Serotine
159.	*Eptesicus chiriquinus*	Chiriquinan Serotine
160.	*Eptesicus furinalis*	Argentine Serotine
161.	*Eptesicus fuscus*	Big Brown Bat
162.	*Eptesicus innoxius*	Harmless Serotine
Genus *Histiotus*		
163.	*Histiotus humboldti*	Humboldt’s Big-eared Brown Bat
164.	*Histiotus montanus*	Small Big-eared Brown Bat
Genus *Lasiurus*		
165.	*Lasiurus blossevillii*	Southern Red Bat
166.	*Lasiurus ega*	Southern Yellow Bat
167.	*Lasiurus villosissimus*	South American Hoary Bat
Genus *Rhogeessa*		
168.	*Rhogeessa io*	Southern Little Yellow Bat
169.	*Rhogeessa velilla*	Ecuadorian Little Yellow Bat
	Subfamily Myotinae	Myotis Bats
Genus *Myotis*		
170.	*Myotis albescens*	Silver-tipped Myotis
171.	*Myotis armiensis*	Armien’s Myotis
172.	*Myotis caucensis*	Cauca Myotis
173.	*Myotis diminutus*	Diminutive Myotis
174.	*Myotis keaysi*	Hairy-legged Myotis
175.	*Myotis nigricans*	Black Myotis
176.	*Myotis oxyotus*	Montane Myotis
177.	*Myotis riparius*	Riparian Myotis
178.	*Myotis simus*	Velvety Myotis

Adapted from Tirira et al., 2020.

Table 3. Species of bats not described or pending inclusion in Ecuador until 2020.

	Species
	Family Phyllostominae
179.	*Carollia* unnamed sp., *Carollia castanea* Clado C
	Family Thyropteridae
180.	*Thyroptera* sp.
	Family Vespertilionidae
181.	*Myotis* Clade A
182.	*Myotis* Clade B
183.	*Myotis* Clade C
184.	*Myotis* cf. *nigricans* A
185.	*Myotis* cf. *nigricans* B
186.	*Myotis* sp. 2
187.	*Myotis* sp. 3
188.	*Myotis* sp. 4
189.	*Myotis* sp. 7
190.	*Myotis* sp. 8
191.	*Myotis* cf. *riparius* 1

Adapted from Tirira et al., 2020.

Table 4. Five endemic species of bats in Ecuador until 2020.

	Species	Common name
	Family Phyllostomidae	**New World Leaf-nosed Bats**
192.	*Lonchophylla orcesi*	Orcés' Nectar Bat
193.	*Micronycteris giovanniae*	Giovanni's Big-eared Bat
194.	*Micronycteris simmonsae*	Simmons' Big-eared Bat
195.	*Sturnira perla*	Perla Yellow-shouldered Bat
	Family Molossidae	**Free-tailed Bats**
196.	*Cabreramops aequatorianus*	Cabrera's Free-tailed Bat

Adapted from Tirira et al., 2020.

These results can be observed with more clarity in **Figure 4** (82).

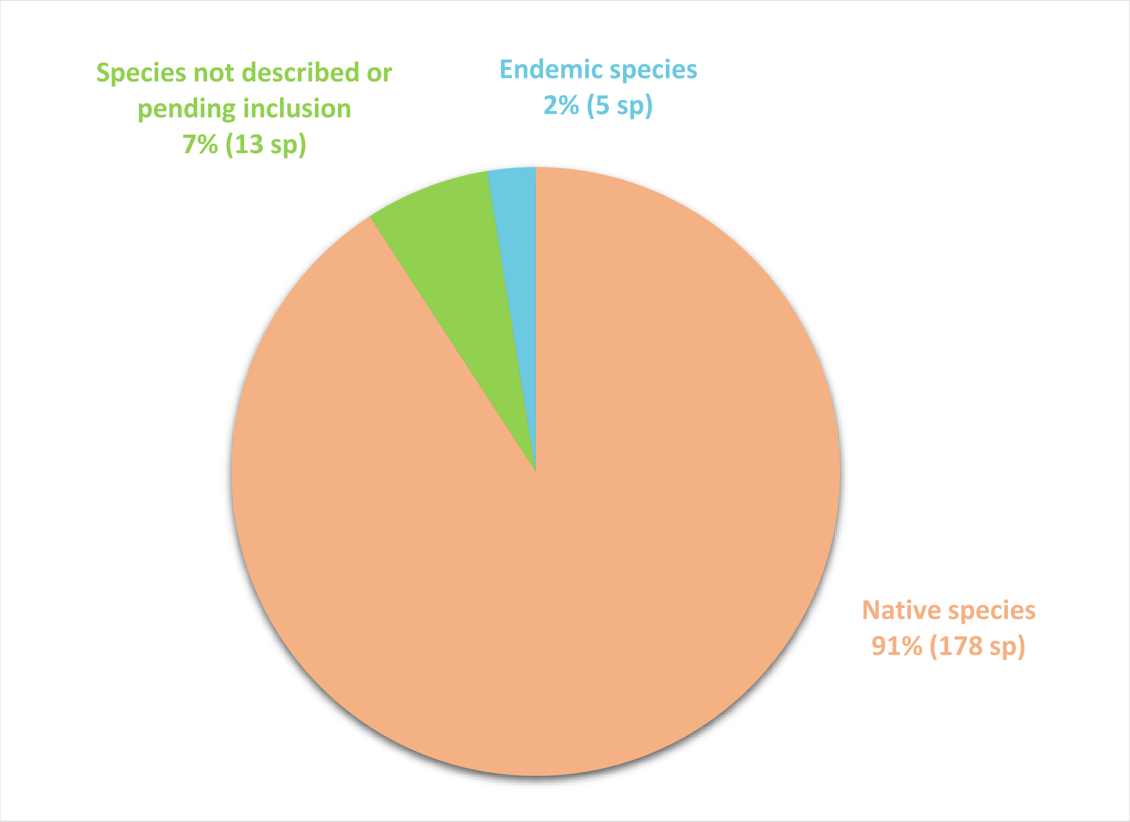

Figure 4. The number of bat species discovered in Ecuador until December 2020. Adapted from Tirira et al., 2020.

3.1.2.3 Bat ecology

As mentioned in the previous section, the areas with the greatest diversity in the country are the central and northeastern foothills of the Andes. Most colonization process in these areas has been prevented by the altitude variation and the geographical location (78). However, there is a loss of habitats and fragmentation that compromises the diversity and abundance of species. Therefore, it is relevant for conservation to study the effects that the habitat configurations produce in the ecology of the bats.

A study in the Andean foothills of Ecuador, in the province of Napo, evaluated the influence of the Borja-Sumaco highway on secondary forest, crops, and pastures. This area belongs to the bioclimatic region Montane Evergreen Forest, on the slopes of the Galeras mountain range. The families identified in grasslands were Phyllostomidae, Vespertilionidae, and Molossidae. In crops and secondary forests, a higher abundance of the Phyllostomidae, Stenodermatinae, and Carolliinae subfamilies were identified (83).

The vegetation structure contributes to determining the occurrence of abundance, diversity, and taxonomic compositions. The crops reported less richness and abundance of species, unlike the secondary forest. The analyzed grasslands showed similar values to the secondary forests, possibly because they contained some tree species similar to that of the secondary forest (83).

Of the identified species, half are considered common (*Anoura caudifer*, *Anoura geoffroyi*, *Myotis nigricans*, *Carollia brevicauda*, *Artibeus glaucus*, *Vampyressa thyone*, *Rhinophylla pumilio*). The highest number of common species were detected in the grasslands, followed by the secondary forest and the cultivation area. Probably, the reason for these results is due to the preferences of common species to fly on edges or clear landscapes (ease of movement) (83).

The secondary forest reported the most uncommon species and the rare species, probably, because the number of uncommon and rare species increases as the degree of conservation of ecosystems improves (83).

Another study documenting the effects of habitat disturbances in the Andean region is research in the Ceja Andina forests in the Carchi province. These forests are found within the Northern Andes, a vegetal formation corresponding to the transition zone between temperate forests and páramo. The Northern Andes belong to the tropical Andes ecoregion and hotspot. The study determined the diversity of mammals in the Guandera Ecological Reserve (RB Guandera) and forests near Jesús del Gran Poder (JG Poder), which are found in the upper Montane Evergreen Forest, also known as the Ceja Andina forest. The Guandera Ecological Reserve presents a better state of conservation, with continuous primary and secondary forests in recovery. Of seven species of bats, four were insectivores. This guild shows the existence of a forest few intervened. The forests near Jesús del Gran Poder are fragmented mainly by deforestation. In addition, there are no primary forests. The results in this area indicate a greater abundance of frugivores, a guild that shows greater alterations in the zones. This fact probably indicates the incidence of the edge effect between natural and intervened forests (84).

Forests in the west of the country are considered the most severely threatened forests in the world's ecosystems (85). The humid forest of the Ecuadorian coast contains 165 species of mammals, of which 85 belong to the Chiroptera order. Although the original vegetation cover has been diminished for the small and extensive agrosystems implementation, some bats have survived these ecological conditions. Thirty two % of the species living in the northwest of Ecuador were registered in these agrosystems. Most research report frugivores as the most abundant species in agricultural landscapes. However, this research reported the nectarivore *Glossophaga soricina* as the most abundant species, followed by the frugivore guild. Usually, frugivores and nectarivores are the most abundant guilds in natural forest patches surrounded by agricultural areas. The nectarivorous and frugivorous guilds are probably more accustomed to environmental degradation (86).

Usually, some shelters that bats use in natural habitats are cavities in trees. If the intervened forests with plantations have trees, some species of bats remain in these degraded environments. Some specialist species such as frugivores and nectarivores may be unable to occupy new habitats if these zones do not have the environmental requirements. However, the aerial insectivores guild has adapted to habitats with a minimum of environmental requirements. For example, the dominant habitat of the insectivore *Eptesicus innoxius* was the dry forest of Isla Santay and the seasonal floodplain evergreen forest, in the alluvial plain of Jama-Zapotillo, in the province of Guayas. With the degradation of habitats, bats have taken refuge in holes in the trunks and branches of dead trees (85).

3.2 Ecological importance of bats

Bats have been on Earth for over 53 million years (87), and they have diversified into over 1,300 species (88). This significant diversification has allowed them to occupy various ecosystems in which they provide important ecosystem functions. The rich diversity of diets, the elimination of pests (biocontrol), redistribution of nutrients and energy, seed dispersal, pollination, among other ecosystem services, are of great importance to humans. These benefits are often inadvertently gained, and if bat conservation continues neglected, the benefits will be lost or diminished, leading to devastating consequences for the stability of ecosystems (89).

3.2.1 Arthropod suppression

Two-thirds of bats are obligate or facultative insectivores. The species find their prey in dense (water and vegetation) and open forests, such as grasslands or even agricultural landscapes. There are several and not exclusive hunting methods. Gleaning bats (see glossary) can capture their prey from surfaces in chaotic environments, such as dense foliage. Aerial hawking bats pick up prey from the air with the webbing of their wing or tail. Bats that feed on flies hang from perches and wait for their prey. Trawling bats capture insects from the water surface using the membrane of their tails or with their legs (89).

The activity of insectivorous bats has a strong relation to the abundance of arthropods. Most of these bats consume Hemiptera (true bed bugs), Coleoptera (beetles), Homoptera (cicadas), Lepidoptera (moths), and/or Diptera (flies). Sometimes they also consume spiders and scorpions, although these prey are rare. Depending on the bat's size, the prey size varies between 1-50 mm. The amount of arthropods consumed depends on the season, the reproductive cycle, and the bat species. Bats feed at night and then return to their shelters to rest and nurse their young. Captive bats consume up to 25% of their body mass from insects per night. Some representative species are *Lasionycteris noctivagans, Lasiurus cinereus, Myotis lucifugus, M. thysanodes,* and *Eptesicus fuscus* (89).

The above estimates increase under natural conditions, perhaps because of higher energy demand. For example, at the peak of lactation, a female Brazilian free-tailed bat, *Tadarida brasiliensis,* can consume up to 70% of her body mass per night. A colony (see glossary) of this species (in maternity and weighing 12 g each animal) can consume up to 8.4 metric tons of insects per night. Another species with high energy demand is *Myotis lucifugus*. At the peak of lactation, a 7.9 g individual needs to consume 9.9 g of insects per night. They need over 100% of their body mass to compensate for the energy expenditure during the reproductive cycle (89). The studies mentioned above suggest the enormous capacity of bats to consume insects and their potential as arthropod suppressors (89).

3.2.1.1 Importance in agriculture-related to pests

Estimates in 2007 concluded that the value of bats to the agricultural industry as pest suppressants in the continental United States is US $ 22.9 billion / year. However, these values may be underestimated (90). The reason is that the number of species of bats that feed on agricultural pests is also underestimated. Previously, the identification of insectivorous bats prey was based on analysis of insect remains in the excrement of bats, which was an uncertain method. Current molecular methods, such as environmental DNA analyzes and DNA metabarcoding, has allowed more accurate and realistic identifications (91).

As already mentioned, Lepidoptera is one of the main arthropods consumed by bats. Many moths (Lepidoptera), which comprise one of the main crop pests in the world, have developed tympanal organs that allow them to detect the ultrasound emitted by a bat as it approaches and escapes predation. However, due to counter-evolutionary strategies such as stealth echolocation (see glossary), use of vision, and passive listening to sounds emitted by prey, bats are capable of catching tympanal moths. Some species of bats without such adaptations (see glossary) are less likely to catch tympanal moths. However, these bats feed on other insects in crops, where they produce ultrasound for prey detection that disturbs the feeding and reproductive behaviors of tympanal moths. That results in a reduction in the number of these moths in crop fields (91).

The concept “fear landscape” is a visual model that explains how prey alters habitat use in response to fear induced by predators and reduces the risk, real or perceived, of predation. In the bat-moth context, Russo et al., (2018) propose that the concept of “fear landscape” may be related to the “soundscape” concept. The last one refers to the sounds perceived and processed by an individual to collect information from the environment. Researchers argue that moths could experience “soundscapes of fear”, which implies sublethal effects on pests in agricultural lands thanks to the ultrasound emitted by bats (91).

Herbivorous insects or arthropods destroy between 25% and 50% of crops worldwide. In response to these threats, the use of synthetic pesticides has increased, but some of their effects are undesirable since they are related to the degradation of ecosystems, resistance to pesticides developed by pests, and risks to human health. Furthermore, beneficial invertebrates can also be eliminated by the indiscriminate action of pesticides. As a result, species that are not normally considered pests can become pests (89). These undesirable effects of pesticides, and the economic benefits that bats represent, have prompted North American farmers to install artificial shelters to attract insectivorous bats (92).

Ramírez-Fráncel et al., (2021) found 158 studies documenting the benefits of bats to agricultural production due to the consumption of pests. However, only 16 studies had been conducted in the Neotropical region. Almost half of these studies reported the suppression of pests (*Cricotopus bicinctus*, *Helicoverpa zea*, *Xyleborus ferrugineus*, *Spodoptera littoralis*, *Tetramorium caespitum*, *Chironomus aprilinus* and *Spodoptera frugiperda*) that affected the production of wheat, sorghum, cotton, tobacco, apples, barley, avocado, coffee, yam, corn, pine, and rice (93).

A novel study in corn provided information on the trophic effect of bats in row crops. Corn is grown on more than 150 million hectares worldwide and has enormous economic relevance. In particular, this study evaluated the abundance of larvae of the fall armyworm, *Helicoverpa zea*. These moths feed on leaves during their larval stages. Besides the direct impact produced by this pest, there are indirect ones as the herbivorous insect facilitating infection by *Fusarium graminear* and *Aspergillus flavus*, fungi that are harmful to crops. These fungi also produce carcinogenic mycotoxins such as fumonisins and aflatoxins that pose a health hazard to livestock. Additionally, the larvae lower the value of corn and cause enormous economic losses. Bats exert pressure on pests, starting a food chain that suppresses larval densities and, consequently, fungal growth, reinforcing the value of corn. Only in the cultivation of corn, the elimination of herbivory and concomitant suppression of fungi and toxic compounds by insectivorous bats has a value of over $1 billion worldwide (94).

Another study in Texas and South Carolina showed bats are also efficient pest killers on certain genetically modified (GM) crops. For example, simulations on transgenic cotton crops (with *Bacillus thuringiensis*) affected by *Helicoverpa zea* show that the impact of Brazilian free-tailed bats (*Tadarida brasiliensis*) for cotton production saves about $46 / ha. Furthermore, the studied model suggests it is possible to go from three insecticide sprays to one per season since bats keep the number of larvae below the acceptable threshold for applying an insecticide. In conventional non-transgenic cotton crops, bats save approximately US $86 / ha. Also, the use of insecticides decreases from four sprays to three in the presence of bats. These results show the importance of the Brazilian free-tailed bat for agriculture. Bats still have a positive impact on crop profitability, even with the pest reduction because of Bt toxins and the application of insecticides (95).

3.2.2 Pollination and seed dispersal

Pollination supports biodiversity and ecosystem functions. It also improves food production and food security. Pollination by bats has a significant influence as a reproductive strategy of flowering plants. Chiropteran pollination occurs at the pantropic level, encompassing approximately 67 plant families and 250 genera (96).

At the Neotropical level, the subfamilies of nectarivores Lonchophyllinae and Glossophaginae of the Phyllostomidae family stand out. Glossophaginae is an animal with short bodies, with a bodyweight of 7.5 to 30 g, and with long tongues in comparison to their size. Glossophagine bats can echolocate (see glossary) and hover when visiting flowers. Due to their body surface area, they are excellent for carrying pollen. This potential has caused a great dispersal of plants in tropical and subtropical zones (96,97).

The pollination of *Stenocereus queretaroensis* by the bat *Leptonycteris curasoae* in Mexico, is an example of pollination by Glossophaginae. *Stenocereus queretaroensis* is a columnar cactus in the Cactaceae family. Some biological traits of the flower of this columnar cactus support chiropterophilia, such as the opening time of the flower and the receptivity of the stigma. Besides, the production of nectar exhibited by *S. queretaroensis* is fundamental. This cactus reaches peak nectar production at midnight when *L. curasoae* frequently visit the plant. This bat was the most abundant species during the four years of study. Other species of chiropterans were rare. Bats presented two eating behaviors, the illegitimate and the legitimate. The illegitimate describes the exploratory visits by bats without touching the flowers. Contrary, the legitimate behavior has bats feeding on nectar or pollen by making contact with the anthers or stigma. In 93.8% of legitimate visits, the stigma contain the deposited pollen or the bat's hair attached to the pollen. The bat consumed pollen in the remaining 6.2% visits, always touching the stigma (98).

The tropical Andes is home to approximately 15% of all the world's angiosperms. This high level of floral biodiversity is closely related to pollinators. Because each pollinator exerts selective pressure on a particular group of plants, this ecosystem service influences different floral morphologies between plant species. Bats are large and warm-blooded animals; thus, they need large flowers with abundant nectar. Certain species of flowers are more attractive to bats. Species that bloom at night, with muted flowers and foul odors, are provocative to them. However, the most relevant feature is the opening of the corolla. Bats prefer swollen and wide apertures that facilitate snout entry (99).

The Bromeliaceae family of plants is one of the most diverse species in the Neotropics. Bromeliaceae make up more than 300 species distributed in 58 genera. Only in the Andes of Bolivian territory, bats pollinate 7% of 188 species of bromeliads. Bat-pollinated species of these plants are monophyletic (see glossary) (97).

A study carried out in Mexico on the epiphytic bromeliad *Tillandsia macropetala* Wawra concluded that the bat *Anoura geoffroyi* is an effective nocturnal pollinator. Contrarily, the diurnal pollinators only steal nectar. This plant has a nocturnal pollination system, and its distribution occupies the humid mountain forests. The floral characteristics are a light green corolla, green bracts, helical flowers, and twilight anthesis flowering. However, the most notable thing is that this plant does not have the floral characteristics preferred by chiropterans. *T. macropetala* does not have large, flared, or zygomorphic flowers, nor does it have a strong odor. Other plants have sulfur compounds, but this species lacks them. Besides, the nectar does not have an unpleasant odor as in other chiropteraphilous bromeliads, and the sugar concentration is low compared to the nectar of different flowering plants. The nectar has a sweet smell, and the sugar concentration is 10% below average. In addition, *A. geoffroyi* pollinates at least two bromeliads species, *Vriesea longiscapa* Ule and *Vriesea platynema* Gaudichaud, both distributed in Brazil (100).

Laurindo et al. (2020) mention that, in the Neotropics region, bats are essential for seed dispersal. In particular, 23 plants depend on bats for this ecosystemic service. The variation of morphological and ecological traits resulting from the frugivory of obligatory and opportunistic fruit bats can result in an increase in functional diversity in seed dispersal networks (101).

Seed dispersal influences the aptitude of the dispersed adult in parallel with their offspring. Also, it drives the gene flow of plants, affects ecosystem functions such as recolonization, the dynamics of plant populations, and the connectivity of landscapes. The dispersion characteristics determine the probability of survival of the plant. Moreover, the colonization in suitable sites for the completion of the plant life cycle, and the seed scape of negative biotic influence, including inter and intraspecific competition, mediates the seed dispersion. Seed dispersal is key to the recovery of fragmented habitats and the resilience of native ecosystems (102–104).

In evolution, seed dispersal and frugivory are the central paradigms of co-evolution. The interaction between organisms has a notable influence on evolution. For example, the olfactory ability of bats allows them to locate ripe fruit. Similarly, bats' wings and flight have allowed them to access resources that other mammals cannot. In addition, fruits also have acquired singular evolutionary characteristics, such as the bat fruit syndrome of some fruits. Attributes such as the pulpy nature, the dull greenish color, and the exposed fruit position describe this syndrome. This set of characteristics makes the fruits less attractive to daytime predators. By transporting the seeds of the fruits that bats eat, the chiropterans facilitate the gene flow between isolated plant populations (105).

Factors as the size and weight seed and the bats carrying capacity determine the seed dispersal success. Small bats feed on fruits with tiny seeds, which facilitate their ingestion and dispersal through defecation. The handling and processing of the fruit by the animal is also crucial. On the other hand, depending on the fruit size, bats shed the fruit and consume them in their feeders, or "in situ" (105).

One study showed the relationship between *Madhuca latifolia*, a tropical deciduous tree, and pteropodid bats. The flowers and fruits of *M. latifolia* have bat syndrome. Moreover, the study reported three sympatric (see glossary) bats species (*Pteropus giganteus*, *Cynopterus sphinx*, and *Rousettus leschenaultii*) in this tree. The presence of lactating and other pregnant females indicates that this tree species is integral for bat nutrition. Bats evaluate the quality of the fruit by floating. Through their olfactory faculties, they can differentiate a ripe fruit from an immature one. This ability helps them avoid consuming secondary metabolites that can be harmful. *P. giganteus* consumed fruits from the same tree, but if it competed for food, they would pluck the fruit and fly, causing seeds dispersion over great distances. Compared to the other species, *P. giganteus* processed more fruit due to the large size that individuals of this species reach. On the other hand, *R. leschenaultii* and *C. sphinx* are bats of medium and small size. These animals foraged for fruit in groups and then carried the fruit to their feeders. The feeding shelters of these bats are located at short distances, causing the dispersal of seeds of around 100 m (105).

Carollia perspicillata of the Phyllostomidae family, is a widespread species from the Neotropical region. This species consumes several fruit species, but its preferred species are the *Piper* genus of the Piperaceae family, with significant consumption of more than 60% of its diet. The mechanisms of dispersal observed include non-random defecation patterns. Probably, the bats perform the defecation during flight or earlier to decrease body mass. Bats are very faithful to the feeding roost in tree cavities, in lowland forests. The observed defecation patterns increase *Piper*'s likelihood of dispersal near feeding roosts. This influence of *C. perspicillata* on *Piper* is related to patterns of directed dispersal. The seeds, differentially deposited by the defecation of bats in certain sites, confer a fitness (see glossary) advantage to *Piper* compared to the sites chosen at random for defecation. Through this mechanism, plants are more likely to survive and reproduce (106).

In Ecuador, the benefits of bats in seed dispersal have also been observed. In the Wisu Biological station, there was a considerable dispersion of *Anthurium* sp. 1 (epiphyte), *Marcgravia helversiana* (hemiepiphyte), and *Clusia* sp. (primary forest tree) by *Carollia brevicauda* (insectivore and generalist frugivore) and *Sturnira magna* (frugivore). Although the captured species usually move through the lower parts of the forest, the plants' fruits were from higher strata and usually from the primary forest. In addition, it was reported the dispersion of *Piper* sp. by *Carollia castanea* (107).

3.2.2.1 Importance for agriculture

Pollination and seed dispersal are vital for the supply of human resources. According to evidence, food production is highly dependent on pollination. Pollinators improve the quality of the fruit and its economic value (108). Bats have an indefinite economic impact on the tropics in terms of pollination and seed dispersal (**Table 5**) (109–111). For example, in Southeast Asia, frugivorous and nectarivorous bats pollinate several economically important plant species in agroforestry. The pollination by bats represents between 80 and 100% of fruit production in crops (109).

A study carried out in Mexico quantified the value of pollination by bats of the genus *Leptonycteris* in the cultivation of pitaya (*Stenocereus queretaroensis*). This plant is of great commercial importance for the country; its use for fruit production dates back to pre-Hispanic times. In Mexico, 85% of cultivated plants depend on animal pollination, and concerning columnar cacti, 22 members of the genus *Stenocereus* depend on bats for pollination. In particular, *Leptonycteris yerbabuenae* and *Leptonycteris nivalis* are migratory bats with nectarivorous eating habits. The distributions of these bats species range from Central America to the southern United States. In this range, the chiropterans pollinate agaves and cacti. Bat pollination increased on average 35% in cultivar yield compared to wild cacti. In economics, bats contributed approximately 40% of pitaya growers' gross income. These plants also perform vital ecological functions providing water and nutrients to various animals in arid ecosystems (110).

Seed dispersal is also relevant in economic terms. *Vitellaria paradoxa* dominates shea butter production in Sub-Saharan Africa. This substance, obtained from fruit grain, is highly valued by the cosmetic industry. In continental Africa, this species supplies raw materials for 800,000 meter-ton-second per year production. Until 2007, this volume represented $115 million US dollars. The production of around 2.5 million meter-tonne-second represents a monetary value of $360 million US dollars. Five hundred million trees are needed to reach this level of productivity and economic output. These numbers illustrate the bat's economic value and its particular influence on this tree species (111).

Additionally, around 23% of products related to the Old World's tropical plants depend on the ecosystem services provided by Flying Foxes. On the African continent, pteropodid bats disperse fruit seeds of about 34% of economically important timber species. The importance of pteropodids in the seed dispersal of trees such as shea (*Butyrospermum parkii*) and margo (*Mangifera indica*) also has been observed (111).

At a global and local level, the economic value obtained from the pollination and dispersal of seeds by bats is subject to changes in the ecological conditions and supply and demand for products. For this reason, the monetary value can increase or decrease. The state of the habitat in terms of fragmentation, changes in land use, urbanization, and all the impacts resulting from anthropogenic activity mean that a constant recalculation of the bat's economic benefits is required.

Table 5. Some examples of the monetary benefit of bats in relation to pollination and seed dispersal.

Plant	Monetary benefit	Region/Country	Ref.
Pollination			
Durian and petari plants	$13 million/year	Thailand	(109)
Pitaya (*Stenocereus queretaroensis*)	$2,500 ha/year	Mexico	(110)
Seed dispersal			
Vitellaria Paradoxa	$360 million/ 2.5 million meter-tonne-second of production.	Continental Africa	(111)

3.3 Threats to Bat Biodiversity

Bats are among the most threatened mammals worldwide. In the world, about a quarter of bat species are in danger of extinction, and others are in danger of soon becoming endangered (**Figure 5**) (55).

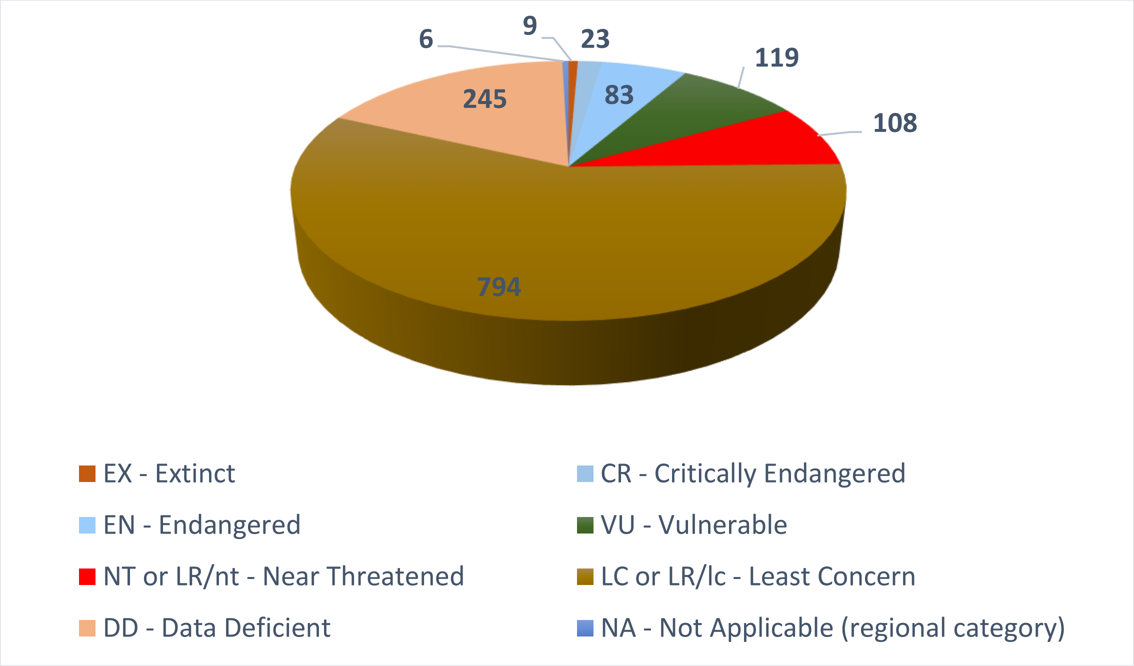

Figure 5. Conservation status of bats in the world.
Adapted from IUCN (International Union for Conservation of Nature), 2020.

3.3.1 Deforestation

The logging of tropical forests in Latin America reaches 2.5 million hectares. Livestock or agriculture are the main uses for the logged land. In these areas, conventional logging and clear-cut logging are the most destructive because they generate a decrease in biodiversity, soil compaction, increased fire risk, and reduced canopy cover. Although detrimental effects of selective logging are minor, it also affects the forest structure, biodiversity, nutrients, and soil (112,113). In addition, the loss of habitat caused by deforestation can modify migration paths and forest dynamics, affecting the species abundance (112).

Chiropterans' response to anthropogenic disturbances and selective logging has been extensively studied in the Neotropics. In response to logging, a decline in the richness and abundance of carnivorous and insectivorous phyllostomids was notorious. In contrast, nectarivorous and frugivorous phyllostomids increase in abundance after selective or conventional logging, in comparison to forests that have not been affected by logging (112).

Bat species have different responses to anthropogenic effects, depending on the differences in agility, life histories, nutritional characteristics, and other factors. In Mexico, deforestation has caused a dramatic reduction in tropical forests. A study in this country documented the loss of habitat due to deforestation and the decline in bat species. The richness of these mammals increase with the increase in forest cover. For example, the insectivorous mormoopid bats decrease in deforested areas. These bats feed best where vegetation is dense and insect abundances are high. Insects disappear in deforested areas (113).

Species that use tree trunks as shelter are also affected, for example, *Carollia perspicillata*. This species can also use corridors in deforested zones but will not explore open areas (113). The result of this research contrasts with other research in which the abundance of *C. perspicillata* in cultivated forests is higher (114). The reason for these differences in the bat responses is unknown. Another affected bat is the hematophagous *Desmodus rotundus*. This bat needs forested regions, even if the canopy is scarce (113).

As deforestation increases due to a growing demand for agricultural resources and an increasing human population, less destructive approaches for natural resources conservation policies in forests will be necessary.

3.3.1.1 Fragmentation

The loss of habitat and fragmentation are the main causes of biological diversity loss, mainly in tropical and subtropical ecosystems (71,115). Habitat fragmentation is continuous habitat alteration, creating a mosaic of isolated habitat fragments in a modified, usually uninhabitable landscape (116). The expansion of agriculture and urban areas are the main causes of deforestation and habitat fragmentation (117). Fragmentation has three qualitative effects. First, habitat patches cannot offer shelter, provide breeding sites or sustainably feed to maintain a viable population (see glossary). Second, the behavioral and physiological parameters of some animals limit their movement and dispersal between patches of habitat. If the species have large area needs, they could be at greater risk of local extinction. Third, microclimatic change, an increased parasitic or competitive pressure by invasive species at edges or clearings, and increased predation rates usually degrade the remaining habitat (116).

Human-induced changes in the landscape pattern mostly result in habitat fragmentation (116). Fragmented landscapes are dominated by small, irregular, and isolated patches of forest (<50 ha). Patches are very prone to edge effects, which are systematic changes in biotic and abiotic variables at the boundary between adjacent land-use types (118).

The case of the loss of the Amazon is an example of the fragmentation effects due to deforestation in 1980, which decreased forest cover more than habitat loss alone. Some studies have confused habitat loss per se, which is habitat fragmentation independent of area loss. Parameters such as isolation, fragment shape and number, matrix structure, number of habitat patches, and the appropriate amount of habitat all contribute to the overall effect of fragmentation (119).

In Neotropics, bats represent more than 50% of the species of mammalian fauna. At the assembly (see glossary) level, studies that have compared fragmented and continuous forests in terms of diversity, richness, and species composition are inconsistent and with few generalizations (71). The differences between the sites concerning the history of fragmentation and the structural contrast between the surrounding matrix and fragments complicate the detection of generalized patterns (118). The highly specific responses provided by bat fragmentation studies overlook the diversity metric applied at the assembly (see glossary) level (71).

At the population level (see glossary), studies that have documented abundance responses to fragmentation are highly assembly (see glossary) and species specific. For example, the abundance of some insectivores and gleaning animalivores (see glossary) bats decreases due to fragmentation, while the abundance of nectarivores and frugivores usually increases (118). For these reasons, research should focus on fragmentation in multi-scale assessments and on the mechanisms behind responses to this fragmentation by individual bat species (71).

Studies of trophic guilds in the Neotropics also show inconsistent and generalized responses. Since most studies focus on frugivores, studies remain uncertain in carnivores or arthropods (71). These types of studies are of great importance in terms of zoonotic potential. Research in Vampire bats *Desmodus rotundus*, one of the three vampire species of the Neotropics, found changes in the heterogeneity of the microbiota and some core bacteria of Proteobacteria, Epsilonbacteraeota, Tenericutes and Firmicutes, in a small fragment of a forest in Belize. It is well known that the microbiota regulates immunity and that vampire bats can be reservoirs for zoonotic pathogens. Therefore, this alteration of the microbiota possibly impacts host immunity and the transmission of pathogens between species (120).

Regarding the responses to landscape structure, studies suggest negative effects of habitat loss in many bat taxa (lower density or abundance). In contrast, the fragmentation effects per se are weaker, and the answers vary. Regarding the edge effects, the responses of bats have been scarcely studied. The little evidence in the Neotropics suggests that responses differ depending on the history of land use and the matrix. These responses are species and assembly (see glossary) specific. At the population level, two species of frugivores in the fragmented Atlantic Forest showed negative responses related to the density of the edges, while in the Amazon, six species of phyllostomids were positively related to the density of the edges. These discrepancies in responses are possibly due to differences in predominant land conversion patterns (118).

The Atlantic Forest is a highly deforested tropical forest that remains fragmented. Only about 7-16% of its original expansion remains, making it one of the most threatened forests. A simulation study determined whether habitat fragmentation could cause population subdivision of *Artibeus lituratus*, a Neotropic seed-dispersing bat. From the genetic structure, there was not much genetic differentiation or correlation between the geography of fragmented or continuous landscapes. Possibly, these results were obtained because *A. lituratus* is a generalist and relatively mobile species, delaying the reduction of connectivity in a fragmented habitat. However, these studies do not contradict the ample evidence that habitat fragmentation contributes to the extinction of species and populations (see glossary) worldwide, nor can they be generalized to other pollinators and seed dispersers of the Neotropics (115).

Human-driven habitat fragmentation is all over the planet. Understanding the effects of fragmentation is key to predicting and mitigating the effects that fragmentation modifications could have on species (115).

3.3.1.2 Agriculture

One of the main causes behind bat extinction is agriculture (**Figure 6**) (55). Bats have a diverse range of diets that have been affected by intensified agricultural practices, resulting in loss or degradation of food resource areas, such as the availability of prey, exposure to polluting compounds, and the reduction of survival through the loss of roosts (121). In addition, intensive agriculture and cattle ranching affects bat biodiversity by compromising ecosystem function (114).

In the Amazon, modification of the landscape for agricultural purposes is one of the most severe threats to biodiversity. In general, the conversion of forests to agricultural areas produces patches that divide and isolate populations. One consequence is alterations in the behavior of species and interspecific interactions (114).

A study in the closed canopy rainforest of the Amazonian rainforests evaluated the effects of conversion of forest to agriculture on bats. These effects were specific to the feeding guilds. For example, for frugivores, the species composition of the forest differed from that of the plantation. In particular, *Carollia perspicillata* was the most predominant species in the study area. The relative abundance was 50% higher in the agricultural zone than in the primary forest. In contrast, the abundance of other common species did not differ between forest and plantation. In the case of gleaning animalivores (see glossary), the species composition did differ but only in the dry season. In the forest, three species were dominant, while in plantation, two species were rare, and one doubled in abundance. The common species in that season in the forest was rare in the plantation. In contrast, two rare species in the forest were common in the plantation (114).

Therefore, although species persist on agricultural lands, their interaction with other species in their guild and their contributions to ecosystem functions may have differed highly at local level. In general, the abundance of bats was higher in agricultural areas and secondary forests than in the primary forest due to the increased abundance of fruit-eating nectarivorous bats. For frugivores, abundance differed regardless of the season. Consider that agricultural areas are typically close to human dwellings. Thus, a greater abundance of bats in agricultural areas and secondary forests may represent a greater risk of zoonotic transmission (114).

Monocultures or grasslands lacking structural complexity are more intensive than agroforestry systems. Agroforestry systems are more similar to authentic non-anthropogenic land uses because they incorporate woody perennials and trees into the agricultural landscape. This configuration means few effects on the abundance and activity of chiropterans (122).

The responses of bats to habitat changes due to agriculture vary among species. The echolocation (see glossary) mechanism or wing configuration influence habitat selection. For example, some bats can feed along forest edges, others can feed in dense forests, while others prefer to fly in open habitats. The perception that bats have a lower risk of extinction due to their ability to fly has not allowed a comprehensive assessment of tropical biodiversity and habitat fragmentation. However, several ecological aspects, such as their slow reproduction rate, and the high permanence in a given site, make them vulnerable to fragmentation and habitat loss. Capture studies in the tropics have shown reductions in species richness as lands turn to monocultures and pastures (121).

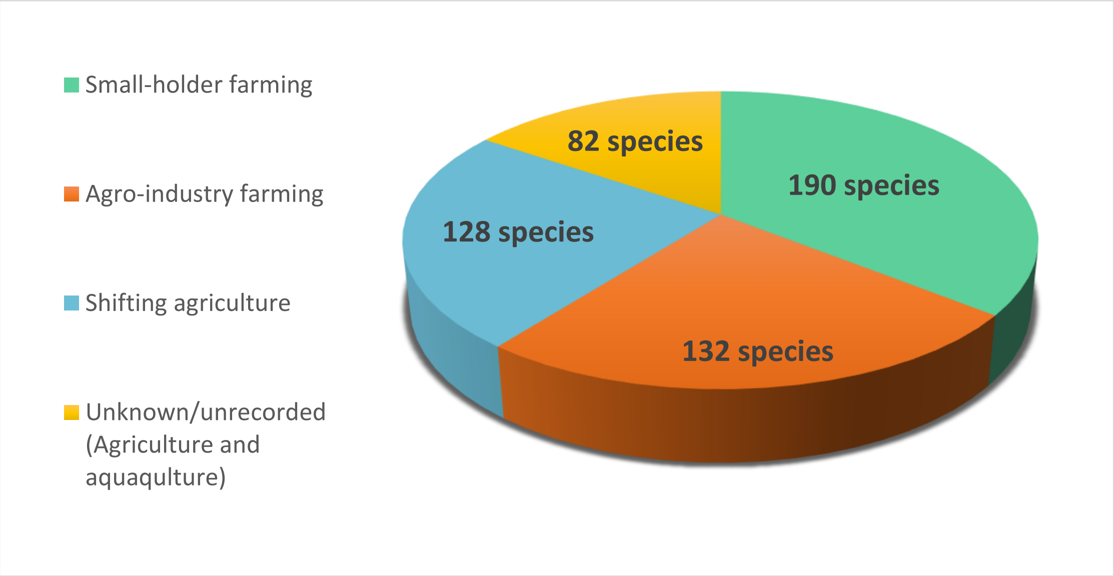

Figure 6. Relationship between threats to species bats and agriculture at various scales. Adapted from IUCN (International Union for Conservation of Nature), 2020.

3.3.1.2.1 Exposure to pesticides

Worldwide, the use of pesticides is predominant in the agricultural production model. According to van den Berg et al. (2020), 4 million tons of pesticides were used in 2016. The excessive use of these chemicals seriously threatens biodiversity and, therefore, the environmental services offered by ecosystems (123).

As seen above, bats contribute a wide variety of ecosystem services related to their diverse eating habits. However, bat populations have decreased due to the ingestion of water and food contaminated by pesticides, dermal contact, or inhalation, diminishing certain ecosystem services they provide (124).

The environmental problem derived from pesticides is a studied concern since the 1950s. The first works reported on the organochlorine pesticides, such as DDT, and their metabolites. This pesticide was used widely until the 1970s. After the ban of organochlorines in several countries, the use of other pesticides intensified. However, their effects on bats remained unknown until after 2010. The majority of studies about the impact of pesticides, have been conducted in temperate climates, such as European countries and the United States. Only 66 bat species (5% bat species in the world) have been studied in these regions. The insectivorous Vespertilionidae has been the most studied because of their broad distribution and great species richness. Also, these species are considered good models for the evaluation of environmental pollution due to their ecological and biological characteristics, which makes them more susceptible to exposure and bioaccumulation.

Bats have high metabolic rates, which makes them consume large amounts of prey. Continuous ingestion of food increases the chances of oral contamination. They are also animals located at a high level in the food chain, making them more vulnerable to bioaccumulation. Studies on bioaccumulation have yielded results mainly for organochlorine pesticides due to their persistence and bioaccumulation potential. Animals tend to store these lipophilic compounds in their adipose tissue. When fat is mobilized for hibernation or migration, lipophilic compounds can cause late effects. Studies have detected substances in bats' tissues and guano, such as pyrethroid, organophosphates, and carbamates. Fungicides (organochlorine and triazole groups) and insecticides (organochlorines, pyrethroids, neonicotinoids, spinosyns, organophosphates, and carbamates) are some compounds identified in bats. Herbicide exposure and its effects in bats have not yet been studied (124).

The effects of pesticides on bats can vary depending on their eating habits, metabolism, behavior, and foraging. In pollinating bats, sublethal and lethal effects have been reported in various parts of the world, although scientists have not yet studied the impacts in depth. Thus, little information is available about the pesticide contamination effects despite a few studies in some fruit bats species, such as phyllostomids and pteropodids. These bats can be good bioindicators of direct pesticide exposure on crops. In carnivorous, omnivorous, and blood-sucking bats, the impact of pesticides has not been evaluated (124).

There are few studies on the impact of pesticides in tropical regions despite being regions with large quantities of crops and great bat biodiversity. The study of exposure in these bats could yield substantive results pertinent to ecotoxicology due to ecological diversity of bats in the tropics.

3.3.2 Invasive species

Invasive predatory species are a grave threat to biodiversity worldwide and have had devastating impacts on endemic faunas. Although these impacts are not known in depth in bats because they are cryptic species hard to study, there are reports about several mammalian predators that feed on bats, such as rats, wild cats, and stoats (*Rattus* spp., *Felis catus*, and *Mustela erminea*, respectively) (125).

In particular, boat rats, *Rattus rattus*, are a significant threat to bats, especially those that live on oceanic islands. Predators are a common threat in these ecosystems. More than 200 threatened bat species have been documented in more than 50 island archipelagos where ships have facilitated the invasive rats' introduction. Additionally, invasive species threaten more than half of endemic islands. In New Zealand, boat rats have caused the extinction of *Mystacina robusta*, the greater short-tailed bat, and the population decline of *Chalinolobus tuberculatus*, the long-tailed bat (125,126).

The Rose-ringed Parakeet, *Psittacula krameri*, is a highly studied species. In Europe, this invasive bird is considered one of the 100 worst alien species, and probably, it is scattered around the world. This species has had considerable impacts on populations of other birds. However, it is also affecting the Hugger Noctulous bat population, *Nyctalus lasiopterus*, of the Vespertilionidae family. This species is the largest in Europe, and its conservation status is considered vulnerable. In southern Spain, *N. lasiopterus* had formed the largest known colony (see glossary) in Europe in an urban area, until 2003. Mainly, it used tree trunk cavities as shelters. In 2017, a new study revealed that invasive parakeets were competing with bats for cavities. The parakeets attacked the noctules with their beaks during the day. They inflicted damage to the wings, phalanges, and abdomen of the bats resulting in mass mortalities. Also, the birds made loud noises and drove the bats out of the cavities. The parakeets then occupied almost all of the shelters. In approximately 80% of the cases, the remaining mammals had no choice but to occupy the tree cavities in trees housing parakeet nests. This interference competition (see glossary) caused a significant reduction in the chiropteran population (127).

Bats had severe limitations to compensate for loss of cavities due to their slow reproduction rate. The social alteration caused by the displacement of bats can have consequences on their reproductive behavior. Additionally, parakeets attack other bat species in urban sites, such as *Nyctalus noctula* in the Netherlands, *Nyctalus leisleri* in Italy, and *Eptesicus isabellinus*, in Spain (127).

While artificial shelter construction can help a species affected by invasive species to recover, sometimes it is not enough. Control the growth of invasive species' populations and their effects on bat diversity with active monitoring programs can be an alternative. Other measures may be the controlled extermination of the invasive species. If there are no measures implemented, invasive species can drive vulnerable bats to extinction.

3.3.3 Climate change

Today, climate change is a worrying threat to biodiversity (**Figure 7**) (55). Floods, droughts, unusually hot and dry climates, increased natural disasters caused by typhoons and hurricanes, and other extreme events cause a change in distribution patterns and richness of biodiversity. The high mobility of bats may allow them to respond to these climate change events, altering their behaviors or occupying various habitats to protect themselves from the risk of extinction (128).

Climate change can alter reproductive, migratory, and survival behavior of bats. In addition, changes in flowering phenology (see glossary) by climate shifts can interrupt the availability of food for pollinating bats, affecting pollination and seed dispersal. These negative effects are likely to affect vulnerable bat species the most. Unfortunately, a quarter of the bat species in the world are in a state of vulnerability (128).

Island bats of tropical climates are vulnerable to cyclones and their devastating effects on the landscape. Due to this natural phenomenon and forest loss, it is possible to detect an 80 to 90% decline in the *Pteropus* spp. populations. Note that in the Pacific, temperatures are increasing, exceeding 42°C. These climatic conditions cause physiological stress that increases the mortality rate of Flying Foxes in Australia and Asia. The impacts of temperature on this species are easy to observe in colonies perched on trees. However, the same cannot apply to other bat species that are not in sight (128).

On the other hand, there is a relationship between the ability of bats to echolocate prey and the temperature change. Sound attenuation is a direct function of temperature and is more pronounced for high-frequency sound. Therefore, if ambient temperature increases produce an increase in atmospheric attenuation, and bats will detect prey at maximum distances but in minimal volumes. Global warming alters the acoustic properties of the habitat, leading to variations in the animal behavior sensory ecology. In this way, temperature changes could affect approximately 1000 species of bats that depend largely on echolocation (see glossary) to find their prey (129).

Depending on the calling frequency, the prey detection volume will increase or decrease. The crossover frequency refers to the frequency at which the prey detection volume will not change. If the bats call on a crossover frequency, they will lose detection volume. On the other hand, the species that call below the crossing frequency will gain prey detection volume. This species will benefit from climate change, whereas it represents a waste of energy for other bats searching a prey. These changes can cause alterations in the composition of the community (see glossary) and affect interspecific interactions, reproduction, and search success. Also, bats that live in cold, arid, and temperate regions will suffer more from these effects, while bats that live in areas with a tropical climate will be less affected due to the lower frequency of crossover in cold regions (129).

The active space by which a receiver detects the acoustic signal of an emitter depends on two factors, the process of transmitting the sound and the signal. The sounds emitted by many animals are adapted to the acoustic properties of the habitat to reduce the loss of sound transmission. In this way, changing the habitat conditions by temperature changes can alter the reception of echolocation (see glossary) sounds (129).

The impact on water availability is another effect of climate change on bats. In the southern Rocky Mountains of North America, warming occurs in the winter months at higher elevations. As the temperature increases due to global warming, the snowfall decreases. Consequently, the snow cover decreases as well. Similarly, rainfall in the summer months also decreases, which further limits the availability of water. In this way, water limitations impact organisms at lower elevations (130).

Bats are small in size but have a high area to volume ratio. This characteristic makes them susceptible to losing water through evaporation. Evaporative losses are likely to increase due to global warming, especially in the lactation period, as the milk produced by females contains ¾ parts of water (130). Therefore, climate change will have significant consequences on bat populations and reproductive outcomes.

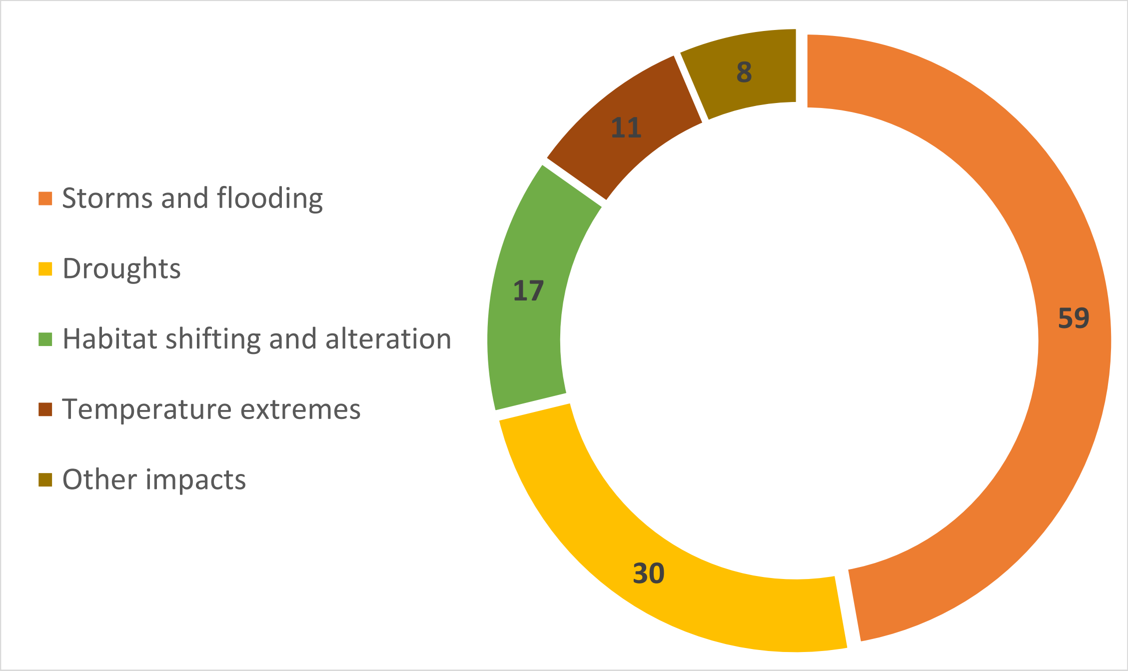

Figure 7. Main threats to bats in relation to climate change.
Adapted from IUCN (International Union for Conservation of Nature), 2020.

3.3.4 Legal and illegal hunting

Another activity that puts bats at risk is hunting. People hunt approximately 13% of the species (167 species) for medicinal or food purposes. In Africa (West and Central) and Asia (Southern) countries, bush meat is an extreme threat that puts bats at risk. The bats most affected by this activity are the Old World frugivores belonging to the Pteropodidae. People use approximately half of this family for medicine, sports hunting, and food. The most hunted species are those with the highest body mass, exceeding 100 g (128).

Although there is a greater awareness of the impact of bat hunting, there are few estimates on how this practice reduces populations. However, a few studies indicate extremely alarming catch rates. Only *Platyrrhinus* sp. (1 species), *Pteropus* spp. (65 species) and *Acerodon* spp. (5 species) are included in the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) that regulates trade. In addition, apart from exploitation of bats for consumption, there are other reasons why bats are killed intentionally, such as capture for tourist souvenirs or decoration, cultural beliefs that bats are evil, the fear of transmission of zoonotic diseases, reduction of damage to fruit crops, and eradication of bats from human structures. The risks for intentional killing to which bats are exposed vary depending on the existence of biodiversity protection laws, the cultural context, or the type of bat in an area (128).

The public perception of bats as sources of disease is skewed by misinformation and fear (131). In Central and South America, people implement various indiscriminate killing methods against vampire bats. These animals are exterminated because they can be vectors for the transmission of rabies in livestock. Entire roosts have been lost, with caves destroyed and other species killed that coexist with vampire bats. However, research on transmission dynamics has shown that killing does not reduce rabies transmission but can increase it in some cases (128). New hosts are recruited, increasing the likelihood of dispersal among infected bats, causing disease transmission to inexperienced bats (131).

3.3.5 Threats to roosting caves

Caves house a high diversity and enormous bat colonies for long periods, even increasing the temperatures higher than expected (74). Caves are more vulnerable than other ecosystems. Commonly, threats include urbanization, vandalism, sinkhole development, soil erosion. Concerning the water, there are groundwater contamination, over-extraction, and saline intrusion. There are also other types of threats to underground ecosystems, for example, excessive cave visits that also pose a dangerous threat. Other cave-dwelling animals also suffer the threats described above. However, bats are affected by unique threats, such as white-nose syndrome, which has killed more than 6 million individuals living in hibernating caves since 2006 (132).

Mexican free-tailed bats are good indicators of the severity of threats and the conservation status of Neotropic caves. These animals can form one of the highest concentrations in caves in the world. Shelters of this species have been affected by vandalism and human encroachment, particularly from exposure to DDT. This organochlorine pesticide is harmful to insectivorous bats since they can acquire high DDT loads in their diets (132).

The Neotropics hot caves experiment threats, which modify and damage the cave's structure. These activities include the extraction of guano as fertilizer or the extraction of construction material, such as limestone destined to cement production. In the Caribbean, where most of the hot caves have been found, people extract more than 2 million tons of limestone per year. Additionally, they produce more than 8 million tons of cement annually. Also, caves are used as a groundwater source and are affected by activities such as agricultural development (133).

Caves are not common in tropical South America (74). Currently, it is difficult to assess threats to populations in hot caves of continental South America, although there are a few records of these ecosystems. Similarly, global ecological population studies inhabiting these ecosystems are lacking, making it difficult to develop conservation measures focused on these species. However, several reasons point to the bat sensitivity to disturbances of the cave's geomorphology, affected by natural or human-caused erosion. These disturbances can cause an increase in airflow, which would lower temperatures, causing specialized bats to leave the caves. Also, the microclimate of the hot caves requires a minimum number of individuals. Natural and anthropogenic factors decrease the number of bats in hot cave colonies. However, deforestation is likely the most significant cause since it generates the loss of feeding areas. Consequently, the bat colony is threatened (134).

Studies of hot caves in the Caribbean indicate that 80% of caves with fossilized bat remains are currently ventilated and could not possibly support microclimates, even if the appropriate specialized bat species were present. On the other hand, studies in Cuba yielded results about the influence of guano in the caves. While more extracted guano in some hot caves, the temperature decreases more than in the caves where extraction was not allowed. Guano extraction affects the microclimate because of diminishing the heating that produces the guano decomposition (134).

3.3.6 Threats to bats and paramyxoviruses

Although bats are carriers of virulent human pathogens, there is not much evidence of clinical signs related to diseases or these pathogens in chiropterans, mainly for intracellular pathogens such as viruses. Due to the identification of antibodies, healthy bats are known to survive long-term infections. Viruses genetically detected in bats are very diverse and are often ancestral to viruses in other mammals and humans. These findings suggest the coevolution of viruses and bats. Studies in immunology have determined the immunotolerance of intracellular pathogens, lower tumor production, and longevity in bats. Probably, immunotolerance to viruses favors the establishment of infections (131).

The usually gregarious (see glossary) behavior of bats and high population densities increase the probability of virus transmission intra and inter-species. Additionally, the persistence of viral infections in bats and longevity can increase the likelihood of transmission. Large-scale movements can facilitate the exchange of new viruses and variants across continents. Bats have highly conserved cell receptors, facilitating viral transmission between mammals (131).

By hibernating, temperate-zone bats lower their body temperatures and reduce their metabolism and viral activity, reducing the likelihood of epizootic fadeout. During the flight, the high body temperature (approximately 38 ° C) and metabolism of bats select tolerant viruses to these febrile defense conditions. However, other mammals are incapable of this mechanism, so the viral infection in them is more lethal (131).

Few viruses affect bats. Infection with the rabies virus (Lyssavirus family) had a 40-90% mortality (depending on the species) in experimentally infected bats. However, under natural conditions, massive mortality has not been observed. Only the Lloviu virus of the Filoviridae family appears to be lethal in bats. The virus was detected in caves in Spain, causing a mass extinction in *Miniopterus schreibersii*, and it still has no zoonotic relevance. Interestingly, other bat species in the same caves were not affected. (131).

Apart from the threats described above, there are other threats that also seriously affect bats, such as recreational activities, mining and quarrying (**Figure 8**) (55).

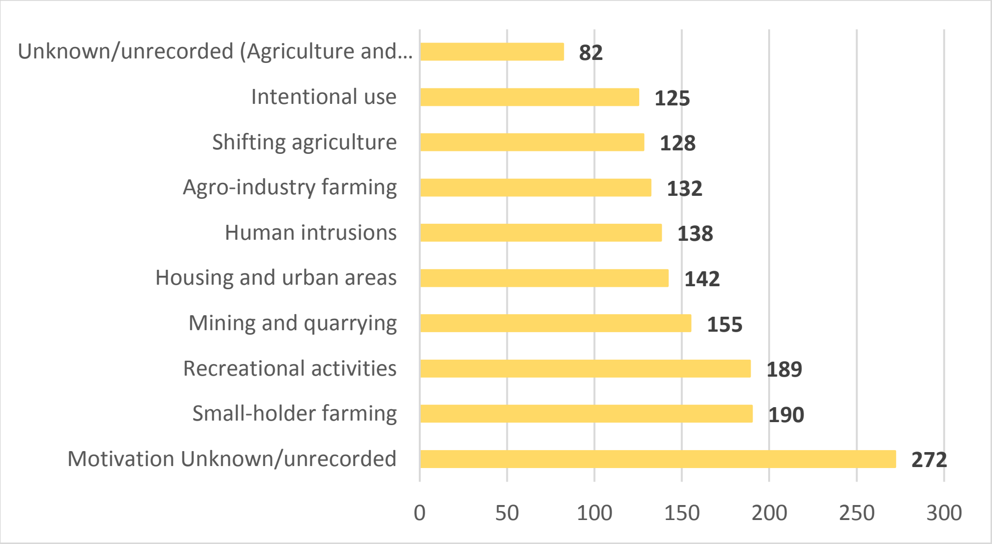

Figure 8. Main threats to bats around the world.
Adapted from IUCN (International Union for Conservation of Nature), 2020.

3.3.7 Urbanization

Urbanization plays a critical role in changing the ranges and distribution of species. The replacement of natural habitats with built-up structures is a tremendous driver affecting the survival of wildlife species. However, not only the effect of fragmenting and replacing habitats is remarkable. Acoustic, light, and chemical pollution are impacts of urbanization on bats (135).

Some bat species can avoid urban areas or tolerate urbanization. They can even take advantage of human settlements for their benefit by finding refuge. In species adapted to hot climates, urban refuges can favor distribution changes since they can act as heat islands. However, some bats, being specialists in specific habitats, have lost feeding and resting areas, which has affected many populations (135).

Urban sites can act as ecological traps for seemingly tolerant bats. First, urban areas can attract various bat species and expose them to opportunistic predators, such as opossums, dogs, cats, and seagulls. A study in Italy found that domestic cats exerted much stronger predation on bats in urban areas, where people kept cats outdoors. The cats captured primarily adult females. Also, owls take more bats in urban settlements, possibly due to the ease of access to non-wooded urban refuges where bats roost. Additionally, bats can get trapped in urban areas. Studies in Greece, Spain, and Italy have documented cases of mortality from *Tadarida teniotis*. There are records of up to 600 bats trapped in buildings, balconies, or patios in these cities. Besides, some building materials entangle bats or do not offer adequate support, especially to the young, making them vulnerable to starvation, dehydration, or being exposed to predators (51).

In addition to the risk factors mentioned above, there is the risk suffered by bats on roads. The risk of collisions with vehicles increases due to the roads, or there may be an indirect impact due to the behavioral fragmentation of feeding areas as bats avoid roads. This mainly affecting low-flying bats (51).

3.3.8 Wind mills

Wind energy is gaining popularity in various parts of the world in response to climate change. Wind farms are probably one of the most relevant strategies for renewable energy generation. Despite their energy benefits, wind power parks can have significant unfavorable effects on biodiversity. These effects include the degradation or loss of habitat, the barrier effect that limits mobility, and the displacement of shelters or feeding areas (136,137).

However, the proximate and most prominent causes for bat mortality in wind turbines are barotrauma and direct collision. The turbine blades act as an airfoil. Along the top of the blades is created a low-pressure region, as well as the spiraling vortex, with a low-pressure core, created at the tip tips of the blades. Bats that fly through the sudden change in pressure die from injury to the lungs and other organs. Barotrauma does not require bats to have direct contact with the turbines and is characterized by internal lesions of the abdominal and thoracic cavity, edema, pulmonary hemorrhage, blisters, congestion, and lung collapse, all of which are signs of lung injury (138).

Respiratory physiology and anatomy possibly determine the differences in bird and bat mortality from barotrauma. Bats have dead-end airflow, while birds have unidirectional airflow. These characteristics make the lungs of bats unable to withstand the drop in barometric pressure. Therefore, mortality is higher in bats than in birds, which can be exempt from suffering barotraumas (138).

Direct collision implies the direct contact of the bats with the blades of the turbines or with monopoles. Collisions are associated with severe lacerations and broken skulls, columns, or wings (138). The increase in the mortality rate in birds and bats due to the direct impact with wind turbines has been observed repeatedly, especially near aggregation (see glossary) sites. The mortality of bats varies between species and is highly dependent on the size of the population. Furthermore, energetic trade-offs in terms of sex are different among individuals in a population and determine the bats' flightpaths, which are different for males and females (139). On the other hand, bat activity during flight varies according to the speed of the winds. Chiropterans are most active at moderate or low speeds. For this reason, they are more vulnerable to wind turbines when wind speeds are low (139,140).

Several studies in the eastern North American continent have recorded mortality in 24 species of the 47 recorded in North America. In particular, bats that migrate long distances and perch in trees are the most vulnerable. Chiropterans belonging to the family Vespertilionidae, such as the eastern Red bat (*Lasiurus borealis*), the Silver-haired bat (*Lasionycteris noctivagans*), and the Gray bat (*Lasiurus cinereus*) account for more than 75% of deaths in wind turbines in the east of North America. In North America, estimates of bat mortality range from 600,000 to 949,000 per year. Surveys in Europe indicate that bat mortality rates associated with wind power plants are up to 41 bats per turbine per year, while in the United States the estimates are 70 bats per turbine per year. Also, forested areas are singled out as the areas with the highest mortality rates. Installations of wind turbines have increased since these estimates were made. The characteristics of the landscape, the season of the year, bat activity levels, and the atmospheric conditions could determine likelihood of bat mortality by turbine. In addition, preliminary studies determined that the bats' deaths are more elevated than those of birds (139,141,142). Various research suggests that bats are attracted to wind turbines. One study found that insects are attracted to light-colored turbines. Thus, bats are attracted to turbines as a food resource (143).

Additional studies suggest that wind installations close to ravines, wetlands, or hibernacles influence mortality. However, the percentage cover of grasslands surrounding the wind farms maintains an inverse relationship with mortality. In the United States, deaths occur mainly between July and October due to species migration. During migration, perched bats in grasslands are less abundant than bats in trees; consequently, there is a minimal collision, therefore, lower mortality. However, there are exceptions in grasslands surrounding large wind farms. On the other hand, there is a positive relationship between the size of the turbines and mortality (144).

Migration is a phenomenon that exposes bats to wind turbines. For this reason, migratory bats are exposed to bottleneck (see glossary) collisions (136,137). The Indiana bat *Myotis sodalis* is an endangered species. This species is found in the eastern and western United States and migrates seasonally. Wind turbines have undesirable effects on the dynamics of this species' metapopulations and connectivity due to the reduction of migratory routes. Also, the slow reproductive rate of bats contributes to the decline in populations. For this reason, the rapid recovery of the population is unlikely (145).

Simulations have shown that turbines have the potential to affect especially wintering populations. Probably, it is because the species make seasonal migrations due to winter, and turbines affect their migration routes (146). It is suggested that if a bat remains resident (does not migrate) is less likely to experience wind turbine mortality since mortality mainly occurs during migration (145).

Modeling approaches, hampered by the lack of standardized protocols for bat sampling around wind turbines, and the difficulty of identifying individual species due to the rapid decomposition of small-bodied individuals increases the challenge of determining the proximal and distal causes of bat mortality at wind turbines (145).

Studies on the impact of wind farms are scarce, not only in North America but in other countries. Besides, evaluating the vulnerable bat population's strength and their mortality is harsh. These studies are of great importance, however, especially in threatened species due to other anthropogenic causes. When evaluating the areas designated to install wind farms, it is crucial to consider migration routes or zones with higher bat populations (see glossary). Before wind farms are built, the vulnerability of bats should be evaluated so that undesirable effects can be minimized.

4. Chiropteran paramyxoviruses and human respiratory infections in the world

Viral respiratory tract infections (VRTIs) are among the most common worldwide and are of great public health importance. Viruses (see glossary) that cause human respiratory diseases affect various age groups and contribute to high percentages of mortality and morbidity. The illnesses can be mild or life-threatening. Note that VRTIs also include non-influenza infections. In fact, in the United States, approximately 500 million annual VRTIs are non-influenza, and the estimated cost of these diseases is $ 40 billion US (147).

Currently, the advancement of technology allows associating human respiratory diseases with several pathogens and their natural hosts. Many of these human pathogens have their natural reservoir in bats (147). Bats harbor a large number of viruses. Scientists from around the world have detected more than 170 viruses (148) distributed in 24 different families. Usually, these pathogens do not exert considerable effects on bats. The cause is probably due to their resistant immune system. However, due to the spillover (see glossary) potential, these pathogens can affect the health of other vertebrates such as fish, birds, reptiles, and mammals, including humans (149). Several species of chiropterans are natural reservoirs of zoonotic viruses. Some of these viruses include Hendra and Nipah paramyxoviruses, SARS coronaviruses, herpesviruses, papillomaviruses, filoviruses, lyssaviruses, among others (150).

Infection with some of these viruses in human populations can occur through direct or indirect contact. Direct transmission (see glossary) includes scratching, biting, touching the mucous membranes, or inhaling aerosols. Indirect contagion requires intermediate hosts such as pigs, horses, or cattle; or it can be through inhalation of pathogenic spores released in bat guano. Activities such as the wildlife trade and hunting for bushmeat increase the possibility of zoonoses (149).

Bats carry DNA and RNA viruses, but the literature suggests thus far that viruses causing diseases in other species are RNA viruses (151). This work focuses on zoonotic RNA viruses that cause human respiratory diseases belonging to the paramyxoviruses.

4.1 Family Paramyxoviridae

Paramyxoviruses belong to the mononegaviral order (152). These are enveloped non-segmented negative-strand RNA viruses (nsNSV) that replicate in the cytoplasm (153). Virions (see glossary) have a ribonucleoprotein (RNP) core containing the RNA genome. The RNA is protected by the viral nucleocapsid protein (N), the large protein (L), which includes the RNA-directed RNA polymerase (RdRp, with cap and capping methylation activities), and the polymerase-associated protein (P). The envelope of virion (see glossary) paramyxovirus has an unglycosylated inner membrane or matrix protein (M) and two membrane surface glycoprotein complexes. The binding complex is composed of the receptor-binding protein (RBP) (also designated as haemagglutinin-neuraminidase protein (HN), haemagglutinin (H), or glycoprotein (G)). The fusion complex includes the fusion protein (F) (**Figure 9)** (154). The binding and fusion complexes help the host infection. Fusion complex fuses their lipid membranes with the target host cell-plasma membrane; probably, due to receptor-induced conformational changes within the binding proteins complex, leading to the activation and folding of the fusion protein (155).

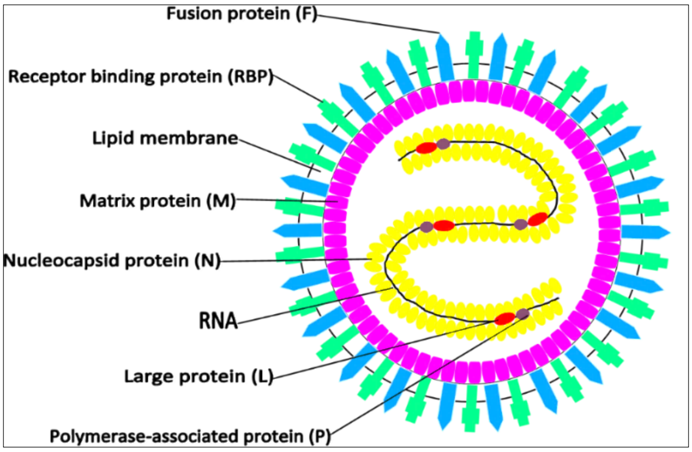

Figure 9. Schematic diagram of a paramyxovirus virion structure in cross-section. Adapted from Rima et al., 2019.

The genome ranges from 14 296–20 148 nt. Six structural proteins are expressed for the assembly of paramyxoviruses (**Figure 10**) (154). Some members have interspaces with additional transcription units (ATUs). The binding of the P/L protein complex to the promotor at the 3′-end of the RNA starts the genome transcription. For replication,

the negative-sense ribonucleoprotein (RNP) template is copied into an encapsidated positive-sense RNA. Subsequently, RNPs are transported to the cellular surface. Here, the matrix protein (or membrane, M) interacts with RNPs and the cytoplasmic tails of the fusion protein and binding protein. The matrix protein (M) is responsible for organizing the particle assembly through the interaction with membrane glycoproteins and protein N (154). However, some exceptions, such as rubulaviruses, contain an additional hydrophobic transmembrane protein (SH) (152).

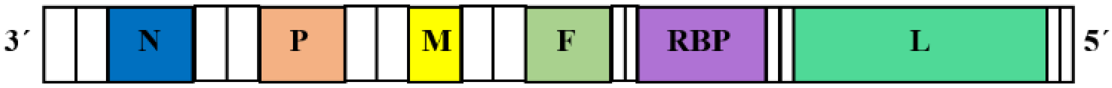

Figure 10. General Paramyxovirus genome structure (not to scale). "N": Nucleocapsid protein gen, "P": Phospho protein gen, "M": Matrix protein gen, "F": Fusion protein, "RBP": Ribosome-binding protein, "L": Large protein. Non-colored regions: untranslated regions in the mRNAs. Adapted from Rima et al., 2019.

In replication, the viral replicase complex is essential, and in some viruses, this is an assembly of cellular and viral proteins. The RNA-directed RNA polymerase (RdRp) is the catalytic subunit of the complex. RdRps are prone to errors, so viral RNA genomes are subject to alterations in RNA synthesis. During mRNA transcription, RdRp can sometimes add nucleotides without a template. These alterations generate transcripts with different qualities of the same gene, resulting in the accumulation of defective genomes at the time of replication. Furthermore, environmental factors (physical or chemical damage) can also affect viral genomes (156).

The "rule of six" is a mechanism that some non-segmented negative-strand RNA viruses have developed to overcome the aggressions they may suffer against their genomes (156). For the efficient replication process, the genomes must be of polyhexameric length (6n+0) or multiples of 6 nucleotides (28). Within the context of the N-nucleocapsid protein, the promoter sequences must be staggered with each N-protein monomer for RdRp to recognize the RNA sequences. If non-template nucleotide insertions are generated during replication, non-hexameric genomes disrupt the N-RNA phase in the promoter region. Consequently, mutant replication products could not act as templates in other rounds of replication (156).

These viruses have six open reading frames encoding structural genes, although some paramyxoviruses have additional open reading frames encoding non-structural genes. Some non-structural proteins' functions remain poorly understood, but many of them are involved in interfering with the host's immune system. The genera of paramyxoviruses that infect mammals are Henipavirus, Rubulavirus, Respirovirus, and Morbillivirus. Each genus contains both tropical animal and human viruses. Some recently reported paramyxoviruses are mammalian but do not belong to the aforementioned genera (28).

According to previous classifications, the Paramyxoviridae family had been divided into two subfamilies, Pneumovirinae and Paramyxovirinae (155). Currently, the Paramyxoviridae family is divided into four subfamilies based on amino acid sequence comparison of the L protein: Avulavirinae, Metaparamyxovirinae, Orthoparamyxovirinae, and Rubulavirinae. The family contains 78 species classified into 17 genera (157). Four of these genera are not assigned to any subfamily: Cynoglossusvirus, Hoplichthysvirus, and Scoliodonvirus (**Figure 11**) (154). The constant discovery of new viruses reveals a very high genetic diversity of Paramyxoviridae (157).

These subfamilies are relevant to human health. The morbidity and mortality from diseases caused by these viruses increase even in developed countries. Transmission occurs through direct contact or respiratory droplets, the last being the main route of transmission (158). Many of the viruses described in this chapter inhabit the African continent, reflecting the great diversity of paramyxoviruses on this mainland (159). The appearance of paramyxoviruses in this chapter is determined by chronological order, referring to the date of discovery.

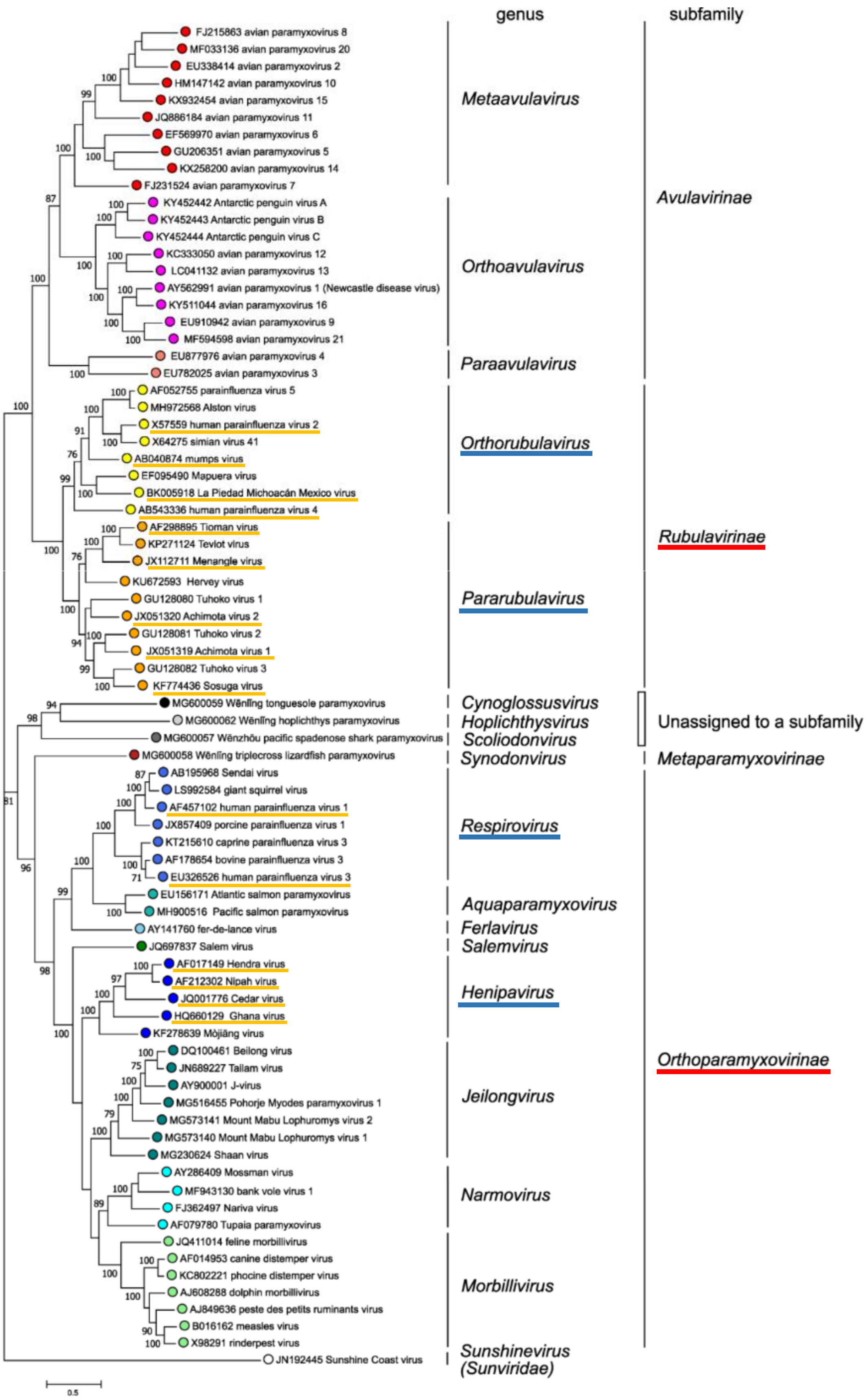

Figure 11. Phylogenetic tree of members of the family *Paramyxoviridae*. Paramyxoviruses mentioned in the text are highlighted. From Rima et al., 2019.

4.1.1 Subfamily Orthoparamyxovirinae

4.1.1.1 Genus Respirovirus

Members of this genus possess neuraminidase and hemagglutinin activities on the receptor-binding protein. Besides, they have six transcriptional elements. Regarding the relationship of the amino acid sequence in the genus, it varies depending on the proteins, although it is always greater within the genus than that of other genera. For example, the HPIV-1 N protein is approximately 88% similar to its murine counterpart, Sendai virus, while it is 63% similar to the HPIV-3 N protein (154).

4.1.1.1.1 Human parainfluenza virus (HPIV)

The discovery of HPIV dates back to the 1950s when it was isolated from infants with lower respiratory tract (LRT) disease. HPIV is very similar to the influenza virus due to some shared characteristics; however, it has been classified into a new family due to the different antigenic sites of HPIV and the poor growth in embryonated chicken eggs (160,161).

The virus is classified into four serotypes, which are HPIV-1, HPIV-2, HPIV-3, and HPIV-4. All human parainfluenza viruses share several characteristics, but each of them infects people of different ages, with distinct seasonality and symptoms. HPIV-3 is more associated with lower respiratory tract diseases, followed by HPIV-1 and 2 (162).

The human parainfluenza virus is of great relevance since it can cause infection in the upper and lower respiratory tract of elderly, immunosuppressed adults, and children. The common symptoms are croup, bronchiolitis, pneumonia, and colds. Seventeen percent of hospitalizations correspond to acute respiratory infections in children under five years of age. These infections are the leading causes of infant mortality and morbidity worldwide (163). HPIV infections are acquired by direct contact between people, via salivary drops (160). Infections with human parainfluenza viruses are frequent and prolonged. Some factors that predispose the infection are environmental toxins or smoke, malnutrition, vitamin A deficiency, and overcrowding (161).

In 1966, the first paramyxovirus, the parainfluenza virus, was isolated in fruit bats. This virus was isolated from *Rousettus leschenaulti* in India, and was classified as a Paramyxoviridae (164). The limited genomic information about the putative bat parainfluenza virus suggests that it could be homologous to the primate (ape parainfluenza virus) and human viruses. These findings suggest that HPIV-2 (orthorubulavirus) may be the ancestral virus of the clade and that zooanthroponosis (see glossary) probably occurred (165).

A study reported the possible transmission from bat-to-human due to the positive results in 10% of human sera analyzed, although cross-reactivity was considered (164). In addition, no significant studies are reporting the transmission of the virus from bat-to-human. Likely, HPIV infections in humans transmitted by bats have not been properly diagnosed since these animals are associated with various respiratory infections (165).

As described above, there is no clear link between the bat parainfluenza virus and human parainfluenza viruses. However, HPIV currently poses risks to human health. For this reason, it is considered within this section. More research and comprehensive analysis of viral genomes are needed, which will allow their phylogenetic origin to be determined.

4.1.1.2 Genus Henipavirus

Another relevant genus is Henipavirus. The discovery of this genus dates back to 1994, in Australia and Malaysia. Infections in humans, pigs, and horses were the cause of the first investigations on henipavirus. Until 2012, these viruses were the only biosecurity level 4 agents in the Paramyxoviridae. The mortality of humans and other animals varies between 40% and 100%, depending on the species and the geographical outbreak zone. These factors make them one of the deadliest groups of viruses infecting humans (166).

In the last 25 years, the records include five species, which are Nipah virus (NiV), Hendra virus (HeV) (these are emerging zoonotic RNA viruses), Mojiang virus (MojV), Ghana virus (GhV), and Cedar virus (CedV). These last three are the most recent. Henipaviruses have spread geographically out of Australia and Southeast Asia into Africa and Brazil, raising global health concerns (167).

4.1.1.2.1 Hendra virus (HeV)

In 1994, there was a report of several cases of infections in horses and people in the Brisbane suburb of Hendra (Queensland, Australia). The horses showed signs of acute respiratory disease, fever, and a high fatality rate. People who had close contact with them also developed a respiratory illness, and one of them died. The virus was isolated from an infected horse and was named Hendra virus (168–170). Transmission of this virus to people was rare. From 1994 to 2009, there was the contagion of seven people, of which four died. The cause of the infections was direct contact with the infected equines. Exposure of the mucosa to nasal or respiratory secretions, urine, and saliva of infected animals may be the mode of transmission of the virus (171). Australian authorities installed security protocols, and since 2009 there have been no human cases (172).

Despite protocols and an equine vaccine that went on the market in 2012, concern about infected horses persists. Due to the perception of non-contagion, which leads to minimizing the risks of infection, and the cost, vaccine acceptance is low in some areas. Thus, the contagion from an unvaccinated mare with Hendra virus in Scone, New South Wales, was reported in June 2019. In this region (Horse Capital of Australia), there are several properties of thoroughbred horses (173).

The current mortality rate in horses is approximately 80% and, in humans, 60%. However, the horses' mortality rate cannot be estimated accurately because equines are euthanized at the moment of HeV infection discovery. Besides, two asymptomatic dogs had neutralizing antibodies against the Hendra virus. The dogs were in direct contact with horses. In addition, experimental tests have reported the contagion of guinea pigs, pigs, hamsters, African green monkeys, ferrets, cats, dogs, and horses. In these experiments, the inoculation doses were high, which turns the animals into plausible hosts with possible transmission to humans (174).

HeV belongs to the Paramyxovirinae subfamily along with Nipah. The virus characterization was made in Vero cells (African green monkey), and it was possible to observe the formation of syncytia (see glossary). As in Nipah, Hendra's genetic material is RNA, an unsegmented negative strand. Hendra causes fatal encephalitis and pneumonia in horses and humans (175).

Flying Foxes, *Pteropus* spp., are the natural reservoir hosts for the Hendra virus. So far, serological studies identified antibodies in four species of Australian flying foxes, which are the black flying fox (*Pteropus alecto*), the spectacled flying fox (*Pteropus conspicillatus*), the gray-headed flying fox *(Pteropus poliocephalus*), and the small red

Flying Fox (*Pteropus scapulatus*). However, *P. alecto* and *P. conspicillatus* are the main reservoirs. Flying foxes are asymptomatic, but they are a potential source of infection for horses (176).

Flying foxes have spread to urban areas, especially in South Australia, where it is easier to get food. HeV is currently considered endemic to Queensland and northern New South Wales, Australia. Chiropterans live in these areas, from which the spillover of infectious events has occurred. There is no relationship between these events and any particular species of flying fox. On the other hand, some species inhabit the islands of Indonesia and Papua New Guinea. The concern of the spread of the Hendra virus to areas outside Australia arises because some non-Australians *Pteropus* spp. have been found to have neutralizing antibodies (177).

Horses are the spillover (see glossary) hosts. Although there is no evidence of bat-to-horse viral transmission, it possibly occurred through food or pasture contaminated with feces, urine and/or reproductive fluids of flying foxes. On the other hand, there is evidence of horse-to-horse transmission. For this contagion to occur, there must be direct contact with infectious fluids or secretions from horses. In contrast, there are no reports of direct transmission (see glossary) from bat-to-human of HeV. So far, no evidence of asymptomatic infections has been found. Also, cases of human-to-human transmission are unknown. The infection route to humans is through direct contact with infected horses (172).

Climatic variables can contribute to the risk of equine infection. HeV is sensitive to desiccation, high temperatures (22 °C), and changes in pH. Although temperature alone is not fundamental to the infection process, combined with other environmental factors can influence viral survival (178).

4.1.1.2.2 Nipah virus (NiV)

In 1998, the first cases of infection in pigs by an unknown pathogen were reported in Malaysia. The disease caused encephalitis in humans and neurological and respiratory symptoms in pigs (179). However, it was not until early 1999 that scientists named the pathogen the Nipah virus (NiV). The virus was isolated from the cerebrospinal fluid of a human with fatal encephalitis in Kampung Sungai Nipah, Malaysia (180).

NiV is a negative-sense single-stranded RNA virus and is very similar to other Paramyxoviridae viruses. Analyzes showed evidence of syncytia (see glossary) formation in the inoculated Vero cells. NiV lacks hemagglutinin and neuraminidase activities, contrary to other paramyxoviruses (181). The protein of the binding complex is the binding glycoprotein (G), which is responsible for binding to the ephrin-B2 and ephrin-B3 receptors on host cells (182). The ephrin (Eph) family is the largest receptor of tyrosine kinases. Ephrine-B2 is expressed in endothelial cells, neurons, smooth muscle, the spleen, and placental tissue, whereas Eph-B3 is expressed in lymphoid cells. In many species, the Eph-B2 and B3 sequences are conserved, which explains the broad tropism (see glossary) of NiV (183).

NiV maintains 80% genome similarity to HeV. Together with HeV, NiV has the longest genome in the family and a broader host range than other members of this family of viruses (180). Due to the requirements of high containment facilities (biosafety level 4), studies on NiV mechanisms are still lacking (181).

NiV has an extensive geographic range. There are records of outbreaks in people from India, Bangladesh, Malaysia, and Singapore (179). Until 1999, encephalitis affected 265 people in Malaysia, of whom 105 died. The death rate for humans reached 40% (184). Humans were infected by sick pigs, and the evidence of progressive infection was scant (179). The outbreaks have meant immense economic losses for Malaysia because over one million pigs had to be euthanized, which decreased trade (180).

Meanwhile, some traded pigs (carrying the virus) were slaughtered in Singapore, where 11 slaughterhouse workers contracted NiV infection. The patients presented neurological and respiratory symptoms and fever. These symptoms appeared two to three weeks after the importation and slaughter of the pigs. This incubation period is consistent with that of other Paramyxoviruses. The outbreak led Singapore to ban the importation of Malaysian pigs, meat derivatives, and other products. Until this day, the ban is in force (180).

Since 1999 no cases have been reported in Malaysia or Singapore. By contrast, since 2001, several cases have been reported in Bangladesh (almost every year) and India. In that same year, the first outbreak occurred in Meherpur, Bangladesh. The events were due to a new strain, independent of the NiV strain from Malaysia and Singapore. Until 2012, there were 209 NiV encephalitis human cases, reaching a mortality rate of 77%.

Additionally, on the India-Bangladesh border, there were two cases of NiV encephalitis between 2001 and 2007. In addition, outbreaks occurred in 2001, 2007, and 2018 in India. The latter occurred in the Kerala state, where there were 23 human cases (18 confirmed), of which 16 died. After this, no new cases or deaths were detected. In general, in Southeast Asia, the average fatality rate is 74.5% between 2001 and 2012. Note that in the Malaysia-Singapore outbreaks in 1998, transmission occurred from infected pigs, while there is the continuous transmission of NiV from bat-to-human and human-to-human in Bangladesh (184). In Malaysia, *Pteropus* were the natural hosts, and pigs were the mediating hosts for human infection (181).

In 2014, NiV cases were detected in humans and horses in the Philippines. The patients' symptoms were similar to those of influenza (5 people), encephalitis (11 people), and meningitis (1 person). Some people and horses died. These deaths led people to think that human infection was due to exposure to sick horses, horse meat consumption, or contact with their fluids. The mortality rate reached 82% for patients with water encephalitis, although overall, mortality was 53% (180). Also, there was evidence of human-to-human and horse-to-human transmission during the outbreak. In conclusion, as of June 2018, NiV affected humans from Bangladesh, India, the Philippines, Malaysia, and Singapore. In total, the virus has been responsible for the infection of 643 confirmed patients and a minimum of 380 deaths, which represents a mortality rate of 59% (181). India and Bangladesh have had the highest mortality rates, reaching 100% in some areas (179).

So far, two human disease-causing strains are known: NiV Bangladesh (NiV-BD) and NiV Malaysia (NiV-MY). In terms of function, the two strains are very similar. However, studies indicate increased pathogenicity of NiV-BD. In ferrets experimentally infected with NiV-BD, infection was faster, oral excretion was higher, and virus replication in the respiratory tract was higher than the Malaya strain. These are probably the causes of the differences between the reported cases in Bangladesh and India. In addition, the virus incubation period is shorter in these countries. The NiV Malaysia strain is the most likely the cause of the Philippines outbreak. There are differences in genome size between NiV Malaysia and NiV Bangladesh strains. The latter has six more nucleotides (18,252 nt) than NiV Malaysia (18,246 nt). The role of the increase in these six nucleotides in the viral pathogenicity and transmission is unknown (180).

There are approximately 60 species of flying foxes distributed throughout China, Asia, Australia, some African territories and islands of the Pacific. Some *Pteropus* spp. are the natural reservoir of NiV. In particular, the fruit bats *Pteropus hypomelanus* (small flying fox) and *Pteropus vampyrus* (large flying fox) are the main reservoirs of the virus (185), although *P. giganteus* also has been found to have antibodies against NiV. These bat inhabit the Indian Territory and some areas of Bangladesh where outbreaks have emerged. In countries that have not experienced NiV outbreaks, bats also have antibodies against NiV, as is the case of *P. lylei* in Cambodia. The NiV sequence obtained from this species is similar to NiV-MY (186).

A study from Zambia, southern Africa, reported several paramyxoviruses in *Eidolon helvum*, including the Nipah virus (187). In addition, antibodies against NiV were detected in the house bat *Scotophilus kuhlii* (3%), the lesser dog-faced fruit bat *Cynopterus brachyotis* (4%), and the cave bat *Eonycteris spelaea* (5%). Small frugivores and insectivores were sampled in secondary native vegetation, oil palm plantations, and residential areas. Domestic and hunting (wild boar) dogs there were sampled. The domestics showed a prevalence of antibodies of 46% (92 dogs analyzed in total), while in hunting dogs, no antibodies against NiV were reported (188).

This study also analyzed *Pteropus hypomelanus* and *P. vampyrus*. The prevalence of antibodies for these bats was 31% and 17%, respectively. Additionally, there were antibodies in *P. hypomelanus* on a Malaysian island. The geographical location of the island is far from the known sources of infection. These results indicate that the virus is found not only in Peninsular Malaysia but that it co-exists in other non-pteropid microchiropterans bats, in addition to frugivorous megachiropterans (188).

In Thailand, NiV antibodies were found in *P. lylei*, *P. vampyrus*, *P. hypomelanus*, and a non-pteropid. The analyzed sequence of NiV in *P. lylei* indicated more than one strain of the virus in the bat. In Indonesia, *P. vampyrus* showed evidence of infection with NiV or a similar virus. On the other hand, in China, Ghana, Papua New Guinea, and Madagascar, analyses on pteropids have shown anti-henipavirus antibodies. In Papua New Guinea, the Pteropodid *Dobsonia magna* showed antibodies against NiV (189), while in Madagascar, the analysis was carried out in three frugivores, *Rousettus madagascariensis*, *Eidolon dupreanum*, and *P. rufus*. As seen above, henipavirus circulation is not limited only to

Pteropus spp. but also affects other bats of the Pteropodidae family and micro-bats from all over the world (186).

It is not clear whether bats develop clinical symptoms from virus infection. Experimental studies on *Pteropus* from Bangladesh, Malaysia, Cambodia, and Thailand showed animal infection between 9 and 25% of studied animals. In the latter two countries, infections were detected only in bats, and there no human cases have been reported. Furthermore, NiV infection of flying foxes was also detected in Singapore, India, and the Philippines. Bat urine was the source for the virus isolation (181).

Biologists attempt to understand how infection occurred in Malaysian pigs. The clearing of forests (agricultural purposes), wildlife trade, and other factors enhance the viral exchange from wild animals to domesticated animals and humans. Soil burning for deforestation produces particles of organic carbon and sulfate in the haze. This activity reduces the light by 73-92% and alters the ecosystem, the jungles, and probably photosynthesis. In 1994 there was a decrease in photosynthesis, likely caused by a haze event in Malaysia. Consequently, the flowering and fruiting of fruit trees suffered condensation caused by smog, causing food shortages for bats. In the rainforests of Southeast Asia, the Amazon, and Africa, this is a threat caused by agricultural livestock activity. Additionally, the scarcity of food habitats and industrialization have led bats to migrate and live permanently in other refuges (185).

All the previously mentioned factors stimulated the migration of bats to areas inhabited by humans. People cultivate fruit trees on intensive pig farms in Peninsular Malaysia to generate additional income. The bats have found in these places a new refuge and feeding habitat. Possibly, the pigs fed on partially contaminated fruit eaten by bats, which fell into the pigsty (185).

According to Sharma et al. (2019), the Malaysian and Singaporean infections among pigs and humans occurred through the respiratory and oral routes. Furthermore, prolonged contact with infected pig tissues from abattoirs may be another route of NiV transmission (181). The case of Bangladesh is curious since the observed events were not due to transmission from pig-to-human in this area. This country is predominantly Muslim; unlike in India, pig farming is not practiced here. In Bangladesh, a common practice to collect the sap of the date palm for alcoholic beverage production or fresh consumption is through a superior cut in the bark of the palm tree. During the night, the sap oozes out and is collected in pots hanging on the trees. One study reported that *Pteropus* spp. feeds on the palm tree shaved bark contaminating the sap with urine, feces, or saliva. Subsequent research identified the consumption of fresh sap as the main route of NiV transmission (bat-to-human). Additionally, consumption of contaminated fruit (bats shed partially ingested fruit) and tree climbing by harvesters (probably on contaminated stems) are other risk factors (180).

Studies in animal models such as hamsters, cats, dogs, and ferrets indicate a NiV incubation period of less than 15 days in almost all cases, although in some, it may take up to 4 months or more. After infection, the virus spreads to different organs, including the cranial nerves employing the CNS. However, the most affected systems are the respiratory and central nervous system, in 62% and > 90% of cases, respectively. Unlike other viral encephalitis, NiV forms multinucleated syncytial (see glossary) giant endothelial cells. Infection symptoms can be highly variable, and the infected patients can be asymptomatic or have very severe symptoms. The cases in Bangladesh were not asymptomatic. In contrast, 17-25% of infections were silent in Singapore and Malaysia. The NiV encephalitis symptoms include pyrexia, headache, fever, vomiting, dizziness, reduced (or absent reflexes), and brain stem abnormalities. Respiratory symptoms include fever, cough, dyspnea, and common cold symptoms (181).

4.1.1.2.3 Ghana virus (GhV)

RNA Ghana virus (GhV) (formerly known as Kumasi) was also detected in 2009 in the straw-colored frugivore *Eidolon helvum* in Ghana. This African henipavirus maintains a close phylogenetic (see glossary) relationship with the Nipah and Hendra viruses. However, until 2019 the zoonotic potential of GhV was unknown (190). The species from which the virus was isolated is highly mobile, flying up to 2,500 km per year. For the same reason, studies in bats from continental Africa found anti-HNV antibodies in *E. helvum*, particularly in Ghana and the Gulf of Guinea. Besides, HNV sequences were present in the meat of fruit bats in the Republic of Congo (159).

4.1.1.2.4 Cedar virus (CedV)

CedV was isolated from the frugivore *Pteropus alecto* in Australia in 2012. Pathogenicity is almost absent in bats and other small animal infection models (167). Cedar virus also did not induce clinical signs in experimentally infected animals (131).

CedV is genetically related to HeV and NiV, although its relationship is less than between HeV and NiV. These last two do cause clinical diseases (see glossary) in small animal models. Despite the almost non-existent pathogenicity, CedV infection can probably occur in other hosts, such as horses (166).

4.1.2 Subfamily Rubulavirinae

4.1.2.1 Genus Orthorubulavirus

Members of this genus have hemagglutination and neuraminidase activities. Some members contain an additional transcriptional element between the receptor-binding protein (RBP complex or hemagglutinin-neuraminidase protein, HN) and the fusion protein (F). All members of this genus lack the non-structural ORF protein (C). As in pararubulaviruses, the P protein is smaller than that of morbilliviruses or respiroviruses. Some human viral pathogens are human parainfluenza 2 (HPIV-2) and MuV (154).

4.1.2.1.1 Mumps virus (MuV)

Hippocrates was the first to describe mumps in his first Book of Epidemics in the 5th century BC. However, it was not until 1930 that Johnson and Goodpasture demonstrated the viral etiology of this disease. They did it by fulfilling Koch's postulates. The spread of the disease between people in close contact suggests that its transmission route is through the respiratory tract by oral contact, inhalation, or droplets of secretions from infected people. Probably, the virus can infect the upper respiratory tract, although, until 2015, this has not been formally demonstrated (191).

The bats from which the virus was isolated are *Epomophorus* spp. In addition, the antigenic test confirmed the direct relationship between bat viruses and the human mumps virus (192).

4.1.2.1.2 Human parainfluenza virus 2 and 4 (HPIV-2, HPIV-4)

HPIV-4 was the last HPIV to be discovered (1959), creating the family of "parainfluenza viruses" (161). HPIV-4 subdivides into HPIV-4A and HPIV-4B. The one most associated with serious lower respiratory tract diseases is HPIV-3, followed by HPIV-1 and HPIV-2. Few studies associate serious illness with HPIV-4 (162).

As described for the respirovirus genus, there is no clear link between the bat parainfluenza virus and human parainfluenza viruses. However, a study suggested that HPIV-2 could be the ancestral virus of the clade (165).

4.1.2.1.3 Porcine rubulavirus (PoRV) / La Piedad Michoacán México virus (LPMV)

In the early 1980s, porcine rubulavirus (PoRV) was discovered in Mexico. Also known as La Piedad Michoacán México virus (LPMV), this pathogen was the cause of disease outbreaks in pigs in this country. The disease spread to other parts of Mexico but does not appear to have spread across border into other countries. The origin of the virus is unknown. Additionally, it is important to mention the Mapuera virus (MPRV) that was isolated in 1979 in Brazil from a fruit bat, although its pathogenic potential or range of hosts is unknown. Therefore, it has not been addressed further in this work (193).

The sequence of PoRV is known and very similar to the MPRV sequence. The organization and viral sequence indicate a close relationship between these two viruses. The coding region of the P gene of the two viruses has an ORF that overlaps the coding region of the P protein, similar to the ORF of the protein C in most Paramyxovirinae viruses, even though it is absent in other rubulaviruses. Consequently, it has been hypothesized that PoRV also has its origin in bats (193).

PoRV is the cause of blue eye disease (BED). Symptoms of PoRV infection include nerve and respiratory afflictions in pigs and piglets. Pregnant sows can abort or deliver mummified fetuses. Male pigs may become infertile and present epididymitis (inflammation of the epididymis) or orchitis (inflammation of the testis). Also, the infection can cause unilateral blue opacity cornea in 1% to 10% of cases (194).

Scientists identified this negative-sense RNA virus in La Piedad, Michoacán, Mexico, in pig farms. There are BED records only in Mexico, and there have been no reports of the disease in other countries. Furthermore, BED is an enzootic disease in the Midwest and central Mexico (193).

The seroprevalence of PoRV infection in pigs from Mexico ranges between 9% and 23.7%. The pigs' disease was diagnosed in at least 16 Mexican states. Antigenic variants were detected in unvaccinated pigs from the endemic region of Mexico (State of Mexico, Jalisco, Michoacán, and Guanajuato). It suggests that antigenic variants have spread to the swine population. Since the first outbreak in the 1980s, other sporadic epidemics have occurred, and specific sources are unknown; however, it is suggested that persistently infected pigs or subclinically infected pigs are the responsible sources of the outbreaks (195).

Rhogeessa parvula (Vespertilionidae) is a species of insectivorous chiropteran endemic to Mexico (196). A study determined antibodies against PoRV in a male bat of this species on the Mexican Central Pacific coast, even though it was the only positive of 108 samples analyzed from various species of bats in the area. Therefore, the authors suggested that bats do not play a fundamental role in the epidemiology of PoRV on the Mexican Central Pacific coast (197). However, other studies consider that bats may be the natural and original hosts of PoRV because fruit bats are considered natural hosts of MPRV and other related paramyxoviruses (TioV, MenV, HeV, NiV). PoRV isolates from bat tissues support this idea (195).

A study showed the prevalence of antibodies to PoRV and other viruses in seven veterinarians in Mexico. PoRV infection is endemic to the west-central and central areas where veterinarians worked. Veterinarians in this areas had been exposed to farms with infected pigs and presented muscle and joint pains, constipation, headache, fever, vomiting, diarrhoea, conjunctivitis, and nausea (198).

4.1.2.2 Genus Pararubulavirus

The RBP complex of these viruses probably lacks neuraminidase activity and hemagglutination. Members of this genus lack a non-structural ORF protein (C), and the P protein is smaller than that of morbilliviruses or respiroviruses. Many Pararubulaviruses are derived from bats. Some of the relevant human viruses in this classification are human parainfluenza viruses 2 and 4 and mumps virus (154).

4.1.2.2.1 Menangle virus (MenV)

In 1997, the Menangle virus (MenV) was isolated from stillborn piglets on a farm in New South Wales, Australia. MenV reduced the reproductive rate of live pigs, causing abortions or stillborn pigs with skeletal and brain malformations. Two humans in close contact with the infected pigs contracted an illness with symptoms of influenza (199,200). Serological evidence suggests that source of MenV in pigs was frugivorous bats, and for humans, infected pigs from the pigsty (201).

Some *Pteropus* species in other parts of Australia contain the MenV, which suggests that bats are the natural hosts for the virus. A *P. poliocephalus* population close to the infected pigpen had antibodies (201), as well as *P. conspicillatus*, *P. alecto* and *P. scapulatus*, the latter with a lower number of antibodies. Interestingly, it also has few antibodies against HenV (202).

Likely, the exposition of bats to the virus is due to their migratory behaviors, facilitating inter-colony mixing and the spread of pathogens. Considering the long-term exposure of bats to the virus, the risk of infection in pigs is low, as bat and pig populations have coexisted for three decades with no evidence of pig infection (201).

Following pig infection in New Wales, the virus was eradicated from all three infected pigs, and there is no evidence of new infections. However, the virus continues to coexist with and is endemic to frugivorous bats. Therefore, the infection risk is latent. This possibility increases as susceptible pigs replace the immune pigs. Likely, the transmission mode between pigs is by feces or urine rather than respiratory aerosols. Note that it is possible to shed some paramyxoviruses in the feces (201).

Kirkland et al., 2001 observed the rapid inactivation of MenV under normal environmental conditions, decreasing the persistence of the virus in the pigsty environment; that indicates that the spread of MenV from pig-to-pig is slow and requires pronounced and direct contact (201).

4.1.2.2.2 Tioman virus (TioV)

In 2001, a new virus called the Tioman virus (TioV) was isolated for the first time on Tioman Island, Malaysia. The virus was isolated from fruit bats, *Pteropus hypomelanus*. It is unknown whether it is a human pathogen (203). The virus is taxonomically associated with the Menangle virus (204).

A study between 2001 and 2002 showed serological evidence of infection with TioV in Tioman Island residents, although it is unknown if there were associated clinical manifestations. The infection cause is also unknown; however, two of three positive residents for TioV had eaten fruit partially ingested by bats, suggesting a possible route of direct bat-to-human transmission. On the other hand, susceptibility to TioV infection has been detected in experimental infection of pigs by the nasal/oral route or parental route, so it is imperative to determine the existence of an intermediate host for the amplification and transmission of TioV to humans, facilitating spillover (205).

Another study between 2003 and 2005 reported neutralizing antibodies against TioV in Pteropodid from Madagascar, specifically, in *Pteropus rufus* and *Rousettus madagascariensis*. These animals are hunted for bush meat. In addition, humans eat fruit from trees where bats have eaten (206). Likely, direct transmission (see glossary) of the virus from bat-to-human may occur, although at a minimum frequency (205).

Acerodon and *Pteropus* include about 70 bat species. In Indonesia, approximately one-third of the flying fox species can be found. The genera are *Acerodon* (3 species) and *Pteropus* (21 species). Much of the flying foxes are declining in Indonesia due to land conversion and hunting, pushing them to live within human limits (203).

There is evidence of TioV infection in *Pteropus vampyrus* in the island northeast of Flores, Indonesia. This bat population is very isolated, lacking gene flow with other island bats. The situation of this species is contrasting with the bats of western Indonesia. In this place, bats compete for refuge in human settlements, while *P. vampyrus* of the island northeast of Flores remains in a stable population, with more than 5000 individuals in one place. Detection of the virus in such an isolated population suggests that it was possibly endemic in the *P. vampyrus*, founder of the island's population, and the detection of the virus in Indonesia suggests that the virus is probably endemic in the genus *Pteropus*, even though there are doubts about its endemicity in the Pacific Islands and Australia (203).

Apart from Malaysia, Madagascar and Indonesia, bats infection with TioV has been reported from 6 countries: India (*Pteropus giganteus*), New Guinea (*Pteropus conspicillatus*), and Australia (*Pteropus poliocephalus*) (203).

While there are no reports of human respiratory illnesses, the virus is considered in this section because of the serological evidence of infection in various Malaysian residents. Biologists should consider these factors in future studies to determine the zoonotic scope and improve the diagnostic process.

4.1.2.2.3 Achimota virus (AchV)

African insectivorous and frugivorous bats contain several rubulaviruses (207). In 2009, two paramyxoviruses genomes, similar to henipavirus and mumps virus, were characterized. The paramyxoviruses were named Achimota virus 1 (AchV-1; AchPV1) and Achimota virus 2 (AchV-2; AchPV2). Both viruses were isolated from the Old World frugivore, *Eidolon helvum*, very common in sub-Saharan Africa. The clinical implications of these two paramyxoviruses are unknown; even so, it is worth highlighting the multiple opportunities for direct and indirect contact between humans and *E. helvum* in Accra, Ghana, and Muheza, Tanzania. Frequently, people hunt this chiropteran for consumption. On the other hand, colossal shelters (almost one million individuals) are often located in urban areas of the mentioned cities (164).

Sera from both febrile and healthy humans neutralized AchPV2 in a study in Ghana and Tanzania, which likely indicates the presence of neutralizing antibodies. In addition, previous AchPV2 infection was detected; however, no serum neutralized AchPV1. It could be evidence for the possible zoonotic spillover (see glossary) of AchPV2 (164).

Besides, a new Achimota virus, AchPV3, has been described. This virus was also isolated from *E. helvum* in Ghana. The zoonotic potential of other pararubulaviruses suggests that AchPV3 is a new potentially zoonotic virus. The viral genome is 15,600 bp, which makes it divisible by 6. AchPV3 also exhibits paramyxoviral characteristics such as syncytia (see glossary) formation (208). So far, there are no reports of respiratory diseases in humans due to achimota virus infection. However, to establish the consequences for human health, more research about the zoonotic potential of *E. helvum* is necessary.

4.1.2.2.4 Sosuga virus (SOSV)

The Sosuga virus (SOSV) was identified after a biologist who collected bats and rodents for his research in Uganda and South Sudan presented symptoms including oropharynx ulcerations, fever, and maculopapular rash, in 2012. The biologist did not report direct contact with bats. For this reason, the excretory mucosal pathway could be the mechanism for viral transmission. In subsequent studies, Egyptian rousette frugivorous bat, *Rousettus aegyptiacus* (Pteropodidae), presented the virus. It suggested that the origin of the virus was in bats (209).

Egyptian rousette bats experimentally inoculated with SOSV reported systemic infection, although the bats did not show significant clinical disease (see glossary) or disease-related mortality. In addition, there were also no fluctuations in weight, changes in food consumption or behavior, and body temperature remained in the normal range. However, slight changes were observed in the salivary glands and gastrointestinal tissues, characterized by a mild and segmental expansion of the lamina propria at the tip of the small intestine villi and loss of the brush border in overlying enterocytes. These signs of subclinical disease (see glossary) are consistent with reports of natural reservoirs and competent hosts (210).

The highest viral load of all tissues was observed in the small intestine, followed by the kidney and colon, which indicates that the systems of these organs are potential routes of viral transmission. Also, it suggests that mucosa contact with urogenital and excretory secretions from infected bats is a possible mechanism of viral transmission to humans and other animals. It was not possible to detect the viral permanence in the testes. It suggests that it is not transmitted sexually between bat-to-bat (210).

Python Cave is a tunnel open at both ends, 15 meters deep (m) and 12 m wide. The height of the interior varies from 3.5 to 5 m. Due to the space limitations of Python Cave, juveniles from the Egyptian rousette bats colony (see glossary) rest on the floor (211). The bats tend to defecate and urinate before and during flight, especially when disturbed. These airborne droplets of urine and feces are potentially infectious and rain down on juveniles. Also, these wastes fall into vegetation near bat refuges. This excretory-oral route can also mean a transmission route for humans and other animals near the roosts. In this case, direct contact among animals is not necessary for infection (210).

The virus also appears to spread orally, and possibly this is a common bat-to-bat transmission route. Egyptian rousette bats taste fruits for ripeness and spit out the pulp or drop the fruit. In addition, the Egyptian rousette live in large colonies, sometimes competing for space. Several records of aggressions between bats with bites and other reports of aggressive contact with other animals evidence the potential for transmission of zoonotic diseases (210).

A summary of the reviewed viruses causing respiratory infections is shown in **Table 6**. So far, there are no respiratory disease symptoms reported in humans. It is necessary to conduct more studies to determine the extent of the virus in humans and avoid misdiagnosis.

Table 6. Bat paramyxoviruses causing possible respiratory infections in humans.

Virus	Genus	Year	Geographical distribution	Bat source(s)	Spillover hosts	Evidence of human-to-human transmission	Ref.
Sosuga virus (SOSV)	Pararubulavirus	2012	Uganda	*Rousettus aegyptiacus*	Humans*	No	(209–211)
Achimota virus 1, 2 (AchV-1, AchPV-2)	Pararubulavirus	2009	Accra, Ghana Dar es Salaam / Muheza, Tanzania São Tomé and Principe	*Eidolon helvum*	Humans*	No	(28,164)
Ghanaian bat henipavirus (G H-M74a KV; GhV)	Henipavirus	2009	Ghana Cameroon	*Eidolon helvum*	Humans*	No	(28,159)
Bat Mumps virus (BMV; BMuV)	Orthorubulavirus	2009	Democratic Republic of Congo	*Epomophorus* spp.	Humans	Yes	(28)
Hendra virus (HeV)	Henipavirus	1994	Queesland/ New South Wales, Australia, Papua New Guinea	*Pteropus alecto,* *P. conspicillatus,* *P. poliocephalus,* *P. scapulatus*	Humans, dogs, horses	No	(28,168–172,174–177)
Menangle virus (MenV)	Pararubulavirus	1997	New South Wales, Australia	*P. poliocephalus,* *P. conspicillatus,* *P. alecto,* *P. scapulatus*	Humans, Pigs	No	(28,199–202)
Nipah virus (NiV)	Henipavirus	1998 (year of first case); 1999 (year of identification)	Bangladesh, India, Malaysia, Philippines, Papua New Guinea Singapore, Thailand.	*Pteropus* spp.; *Eidolon helvum,* *Eidolon dupreanum,* *Dobsonia magna,* *Scotophilus kuhli,* *Cynopterus brachyotis,* *Eonycteris spelaea,* *Rousettus madagascariensis*	Humans, pigs, horses	Yes	(179–181,186–188)
Porcine rubulavirus (PoRV)/La Piedad Michoacán México (LPMV)	Orthorubulavirus	1980s	México	*Rhogeessa parvula*	Humans, pigs	No	(193–195,198)
Human parainfluenza virus 1, 2, 3 (HPIV-1, HPIV-2, HPIV-3)**	Respirovirus	1950s (first case); 1966 (year of isolation)	India	*Rousettus leschenaulti*	Human	Yes	(160–165)

* Only patients with fever and other conditions were reported, not noting whether the disease was associated with a respiratory infection.

** There is no clear link between the bat parainfluenza virus and human parainfluenza viruses.

5. Chiropteran paramyxoviruses and drivers of human respiratory infections in Ecuador

In Ecuador, there are 8 families of bats, the Emballonuridae, Phyllostomidae, Mormoopidae, Noctilionidae, Furipteridae, Thyropteridae, Molossidae, and Vespertilionidae (82). Of all the bat families in Ecuador, only 3 (Vespertilionidae, Molossidae, and Emballonuridae) occur in both the New and Old World (**Table 7**) (212).

Table 7. Distribution of the bat families around the world.

Family	Distribution
Vespertilionidae, Molossidae and Emballonuridae	New and Old World.
Myzopodidae, Mystacinidae, Miniopteridae, Hipposideridae, Cistugidae, Pteropodidae, Rhinolophidae, Megadermatidae, Rhinopomatidae, Craseonycteridae, and Nycteridae	Only in the Old World.
Noctilionidae, Mormoopidae, Thyropteridae, Natalidae, Phyllostomidae and Furipteridae	Only in the New World.

Adapted from Moratelli and Calisher, 2015.

Almost all of the previously described paramyxovirus-linked bat species belong to families of Pteropodidae. The wide distribution of these bats in the Old World is broadly known (213,214). However, certain paramyxoviruses co-exist with the bats of the countries of the American continent (197).

A phyllostomid with a paramyxovirus has not been found in Ecuador. However, in French Guyana, the common vampire bat, *Desmodus rotundus*, and *Carollia perspicillata* have been associated with paramyxoviruses, similar to *Jeilongvirus* (215). This is a recently named genus and harbors viruses capable of infecting a wide range of hosts (157). Note that the mentioned bats are also found in Ecuador (82). For this reason, it is necessary to conduct additional studies in the country on the viral content in bats.

Comparing zoonotic events that cause respiratory infections in other parts of the world, it is possible to find several causes in common with Ecuador. The biodiversity of the

Ecuadorian Amazon is also affected by deforestation, pollution (especially pre-control), climate change, among others. For example, areas of the Esmeraldas and Imbabura provinces are vulnerable to deforestation related to African palm and eucalyptus logging, and littoral forests have been lost due to agricultural and livestock expansion. Other areas of the Pastaza province are concessioned to oil blocks, and areas of the Cordillera del Cóndor have been divided into mining blocks. In addition, the original Amazonian vegetation cover has been lost due to the expansion of the road system and deforestation (78).

As seen previously, these causes have been potential drivers for zoonotic outbreaks in other parts of the world. Considering that the same practices are also carried out in Ecuador, it is crucial to prevent zoonotic paramyxoviral events of chiropterans in the country. In addition, some closely related species of bats carrying diseases can be found in the country. For example, the bat-related to the La Piedad Michoacán Mexico (LPMV) paramyxovirus outbreak was *Rhogeessa parvula*. This chiropter is endemic to Mexico and belongs to the Vespertilionidae family (197). However, in Ecuador, there are other species of the same genus. This is the case of *Rhogeessa velilla* and *Rogheessa io* (82). Not much is known about its conservation status of *R. velilla* because of insufficient data (216). *Rhogeessa velilla* was originally thought to be a subspecies of *R. parvula* (217).

6. Conclusion and Outlooks

Currently, the planet undergoes changes that profoundly affect its biodiversity due to the rapid advance of anthropogenic activity worldwide. These phenomena also affect humans because anthropogenic activities cause the outbreak of zoonotic diseases. In particular, the impact of zoonotic diseases caused by different paramyxoviruses has been seen since the 1950s. These viruses have been the cause of respiratory infections in various parts of the world. The symptoms produced by these diseases can be mild to severe, even fatal. Also, zoonotic respiratory infections represent millions of dollars in public health costs annually for nations that have to deal with this problem.

There is a vast bat diversity worldwide with great ecological importance due to the ecosystem services they offer. These services represent high monetary benefits for humans. However, anthropogenic activities are a threat to bats, and these threats become drivers of zoonotic diseases.

Ecuador hosts a great diversity of bats. Therefore, genomic, transcriptomic, molecular, physiological, behavioral, and biological studies of bats are needed to investigate: 1) Ecuadorian bats as possible paramyxovirus reservoirs, 2) possible drivers of zoonotic events, and 3) respiratory diseases that zoonotic events can cause in humans and animals in Ecuador.

There is not much information on the interaction of bat-paramyxovirus, nor have studies been reported on zoonotic events caused by bats infected with paramyxoviruses in the country, therefore studies on these viruses are urgent given their zoonotic potential.

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