Veterinary Medicine and Science

WILEY

REVIEW OPEN ACCESS

Other

Influence of Host and Landscape-Associated Factors in the Infection and Transmission of Pathogens: The Case of Directly Transmitted Virus in Mammals

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Received: 5 July 2024 | **Revised:** 19 November 2024 | **Accepted:** 29 November 2024

Funding: This work was supported by Consejo Nacional de Humanidades, Ciencia y Tecnología (CONAHCyT) (Grant number: 49790).

Keywords: climate features | direct transmission | host traits | landscape | mammal | virus

ABSTRACT

Background: Among pathogens associated with mammals, numerous viruses with a direct transmission route impact human, domestic and wild species health. Host and landscape factors affect viral infection and transmission dynamics of these viruses, along with barriers to host dispersal and gene exchange. However, studies show biases toward certain locations, hosts and detected pathogens, with regional variations in similar host–virus associations.

Methods: Using a systematic review, in two electronic repositories for articles published until December 2022, we analysed the available information on host- and landscape-associated factors influencing the infection and transmission of directly transmitted viruses in mammals.

Results: In the analysis, about 50% of papers examined either host traits, landscape composition or configuration measures, while approximately 24% combined host and landscape-associated factors. Additionally, approximately 17% of the articles included climatic data and 30% integrated factors related to anthropogenic impact, as these variables have a role in host density, distribution and virus persistence. The most significant and frequent host traits used as predictor variables were sex, age, body weight, host density and species identity. Land cover was the most evaluated landscape attribute, while some explored configuration variables like edge density and fragmentation indexes. Finally, temperature, precipitation and features such as human population density and human footprint index were also typically measured and found impactful.

Conclusion: Given the many contributions host- and landscape-related factors have in pathogen dynamics, this systematic study contributes to a better knowledge of host–virus dynamics and the identification of variables and gaps that can be used for disease prevention.

1 | Introduction

Understanding the patterns and factors driving pathogen infection and transmission in host–virus interactions is crucial to mitigate the impact infectious diseases have on human and animal populations. Within host-virus interactions, hosts are considered a habitat 'patch' that possesses different biological and functional traits that play an important role in defining host exposure, susceptibility and suitability to pathogens (Huang, Halliday, and Becker 2023). This means these traits can act as

https://doi.org/10.1002/vms3.70160

Summary

- We summarize host- and landscape-associated factors influencing the infection and transmission of directly transmitted mammalian viruses.
- Key host traits included sex, age and body mass. Whereas studies considering landscape-associated factors focused primarily on land cover composition. Climatic features and anthropogenic variables were also analysed.
- Detected bias and gaps towards geographical regions and host–virus systems in this review highlight local studies importance. Systematic reviews can aid these studies by identifying significant variables for future studies, enhancing understanding of disease transmission and emergence.

filters determining host–virus associations, as well as the host's ability to transmit and spread these agents (Fountain-Jones et al. 2017a; Veitch, Bowman, and Schulte-Hostedde 2020).

For example, in some species of rodents and carnivores, the expression of certain genes associated with the immune system (e.g., TLR-4, TLR-7, TNF-α and Mx2) provokes variations in infection susceptibility and viral loads discarded by infected individuals (Guivier et al. 2011; Heni et al. 2020; Zhao et al. 2015). Likewise, in some species of rodents, carnivores and bats, it has been described that male individuals can drive the transmission and dispersal of viruses under experimental or natural conditions (Cornwall et al. 2021; Erazo et al. 2021; Streicker et al. 2016), due to the presentation of agonistic behaviours and a greater dispersion capacity for reproductive or territorial purposes, favouring virus exposure, transmission and spatial spread (Schmid et al. 2018; Streicker et al. 2016).

Landscape factors associated with the host's habitat also played an important role in shaping host–virus interactions. Landscape attributes such as land cover type, land use, edge density and patch density influence host abundance, richness and contact rates between other hosts and vectors (Dorigo, Boscutti, and Sigura 2021; Gras et al. 2018, Linard et al. 2007; Okanga et al. 2013; Regolin et al. 2020). Which consequently affects virus infection probability, transmission, dispersal and evolution (Fountain-Jones et al. 2017a; Gras et al. 2018; Hahn et al. 2014; Wheeler, Waller, and Biek 2010; Zeng et al. 2021).

Among pathogens associated with mammals, viruses present rapid mutation rates that generate genetic structures that can be compared at small spatial and temporal scales and be associated with heterogeneous landscapes, recent changes in host populations and anthropogenic perturbations (e.g., highways, urban settlements) (Biek et al. 2007; Kozakiewicz et al. 2020). Therefore, they are often used as models in studies to understand and analyse the effects of host traits and landscape attributes on pathogen infection (Schmid et al. 2018), transmission (Biek et al. 2007) and spread (Kozakiewicz et al. 2020).

In this paper, we consider direct-transmitted viruses (DTV), those viruses that can be mainly transmitted by direct contact with infected individuals, body fluids and droplets but also through contact with carcasses, environments and food contaminated with faecal matter or urine (Milotic et al. 2020). For these viruses, it is expected that their infection and transmission are influenced by host distribution, movement and contacts across the landscape (Lee et al. 2012). Moreover, barriers to host dispersal and gene exchange also could facilitate potentially viral spread (Talbot et al. 2012).

Mammals are considered important hosts for DTV of zoonotic and animal health importance (Epstein et al. 2006; Khalil et al. 2014). On one side, it seems to be a positive relationship between their species richness and the number of zoonotic viruses they harbour (Mollentze and Streicker 2020). On the other hand, it is not ruled out that biological traits (Plourde et al. 2017), physiological traits (Kunz and Fenton 2003), or close evolutionary relationships with domestic animals and humans (Peeters and Delaporte 2012) may have a role in the emergence of zoonotic viruses in this host group.

Additionally, in the face of anthropogenic modifications in wild environments, some mammalian species can modify their behaviour and use interfaces with a mixture of forested areas, pastures and human settlements, increasing potential contacts between humans, domestic and wild animals (Gonçalves, Fischer, and Dirzo 2017; McKinney 2019), which may also favour the emergence of infectious diseases (Han et al. 2015).

According to the latter, various approaches have been employed to investigate the influence of host- and landscape-associated factors in DTV disease dynamics. These include landscape epidemiology approaches which aim to comprehend the role of landscape connectivity in interactions among susceptible and infectious individuals (Langlois et al. 2001), as well as understanding how biotic and abiotic conditions affect the geographical distribution of diseases (Dion, VanSchalkwyk, and Lambin 2011; Yan et al. 2007). Moreover, the integration of landscape genetics approaches, has been used to identify landscape features influencing pathogen infection spread and simulate transmission risk across the landscape (Barton et al. 2010; Fountain-Jones et al. 2017; Rees et al. 2008; Streicker et al. 2012). Consequently, different factors related to host biological traits and landscape features have been linked with infection risk, transmission and spread of DTV viruses in different mammal species including humans.

However, this information leans towards specific pathogens and presents a geographical bias. Furthermore, mixed patterns have been found for infection risks (Hernández et al. 2020; Prist et al. 2017), transmission (Kozakiewicz et al. 2020) and spread (Barton et al. 2010) in similar host–virus associations examined in different geographical regions. We performed a systematic review to summarize the factors related to host and landscape attributes influencing the infection and transmission of DTV in mammal hosts. Upon surveying the literature: (1) we identified the most common factors and mechanisms driving these relationships among the different mammal orders and (2) we highlighted understudied variables and gaps that need to be assessed in approaches analysing patterns and factors driving pathogen dynamics in host–virus interactions.

2 | Material and Methods

A literature review was performed under the question: What factors associated with host and landscape attributes influence the infection and transmission of DTV in mammals?. A search was performed from August to December of 2022 using the PRISMA strategy and the following text strings: virus NOT (plant virus OR plant pathogen OR plant parasite) AND (host traits OR landscape) AND (transmission OR prevalence OR infection OR risk OR spread) in ISI Web of Knowledge (Biological Abstracts, Core Collection) and (((virus AND NOT plant AND virus OR plant AND pathogen OR plant AND parasite) AND host traits OR landscape AND transmission OR prevalence OR infection OR risk OR spread)) in Scopus.

The title and abstracts of each study were subsequently screened to determine if they met the following inclusion criteria: (i) not repeated works, (ii) studies in mammal hosts and (iii) studies related to DTV. Based on screening criteria, 604 studies were chosen for evaluation and posterior inclusion in the review.

We classified research articles according to mammal host group (e.g., rodent, carnivore, ungulate), detected virus, detection method (e.g., serology, molecular detection and virus isolation), studied host traits and landscape attributes and the effect these attributes had on virus infection or transmission. We classified landscape attributes in composition (e.g., land cover, percentage of vegetation cover), configuration (edge density, patch density, mean patch size) and other features (e.g., elevation, slope, presence of barriers). We also recorded climatic and human impact variables (e.g., temperature, human population density) considered in the selected studies.

We excluded most of the studies where serologic analyses were made, as the presence of antibodies is evidence of host exposure, whether the host is infected or not (Gilbert et al. 2013). Nonetheless, hantavirus studies in rodents where enzyme-linked immunosorbent assays (ELISA) were applied were conserved. Hantavirus generates a persistent and chronic infection in these hosts; hence the presence of antibodies is considered a reliable indicator of hantavirus infection (Botten et al. 2002; Clay et al. 2009). Likewise, studies detecting rabies virus through direct fluorescent antibody (DFA) and those detecting feline immunodeficiency virus (FIV) by ELISA and then confirming it using Western blot techniques were kept in our database as these tests are considered benchmark tests for their diagnosis (Frankenfeld et al. 2019; Patrick et al. 2019).

3 | Results

Our search identified 12,737 studies, of which 140 research articles met the criteria of inclusion in the review following evaluation (Figure 1). The majority of studies included in this review were conducted in America (40.7%), followed by Europe (22.8%) and, to a lesser extent, Asia (15.7%), Africa (12.8%) and Oceania (2.8%). A smaller proportion of papers were made with data from several countries (5.7%). In America, research papers were mainly located in the USA (56.1%), with a smaller proportion conducted in North American countries such as Canada and Mexico (5.7%), as well as Central and South American countries (i.e., Brazil, Chile, Argentina, Panama) (36.8%). In Europe, studies were mainly carried out in Sweden (21.7%), followed by Belgium, France and the United Kingdom (15.6%). In Asia, China (31.8%) accounted for the highest number of studies, while in Africa many studies were located in Tanzania (22.2%).

The most frequently detected viral agents were hantavirus (31.4%), rabies virus (19.2%), FIV (12.1%), morbillivirus (5%), henipavirus (5%), coronavirus (4.2%) and ebolavirus (3.5%). The most studied hosts were carnivores (31.4%), rodents (28.5%), humans (19.2%), bats (10%) and ungulates (7.1%). While hosts like horses (2.8%) or rabbits (1%) were less frequently studied (Figure 2).

Twenty-four papers consider only host traits, whereas 26 studies consider landscape features, and 33 combine variables related to both factors. Among bats, carnivores, humans, rodents and ungulate hosts, sex (24.2%) and age (16.4%) were the most frequently and significantly studied biological traits. Whereas features like host density (19.2%), species identity (10%) and body weight or body condition (6.4%), as well as population structure measures (10%), were variables of importance in some of these host groups (Table 1). Studies related to rabbits and horses included significant host features such as host density and abundance measures (Table 1; Figure 3).

Land cover, land use and percentage of vegetation cover were the most usual variables of importance analysed in research papers involving almost all the host groups (45.7%), followed by elevation (18.5%). Other significant landscape attributes were sampling location (7.1%), the presence and distance to roads or bodies of water (10%), along with landscape configuration measures (10.0%) (Table 1). Research papers also included climatic variables; among the most common and important were precipitation (23%) and temperature (23%). To a lesser extent, other articles considered abiotic variables such as humidity (9.2%), soil characteristics (2.8%) and season (12.4%) (Table 1). Furthermore, the articles included variables associated with human impact and activities (e.g., human population density, human footprint index, hunting, urbanisation) (24.2%) (Table 1; Figure 3).

4 | Discussion

Through a systematic review, we found that studies regarding host and landscape-associated factors influencing the infection and transmission of DTV present bias towards geographic locations, detected viruses, and hosts. Geographically, there is a concentration of studies in countries that have developed and conducted wildlife surveillance programs for a long time (e.g., USA, Belgium) (Morner et al. 2002). Conversely, lesser papers were made in regions with higher potential zoonotic disease risk due to their high mammal biodiversity (i.e., Neotropical, African, Guineo–Congolian) (Allen et al. 2017; Dunn et al. 2010). One possible explanation for this is that, unlike more developed countries, countries in these regions often derived fewer resources to the study of diseases in wildlife (Morner et al. 2002).

The most frequently detected viruses in this review were the rabies virus, hantavirus, FIV, morbillivirus, coronavirus and

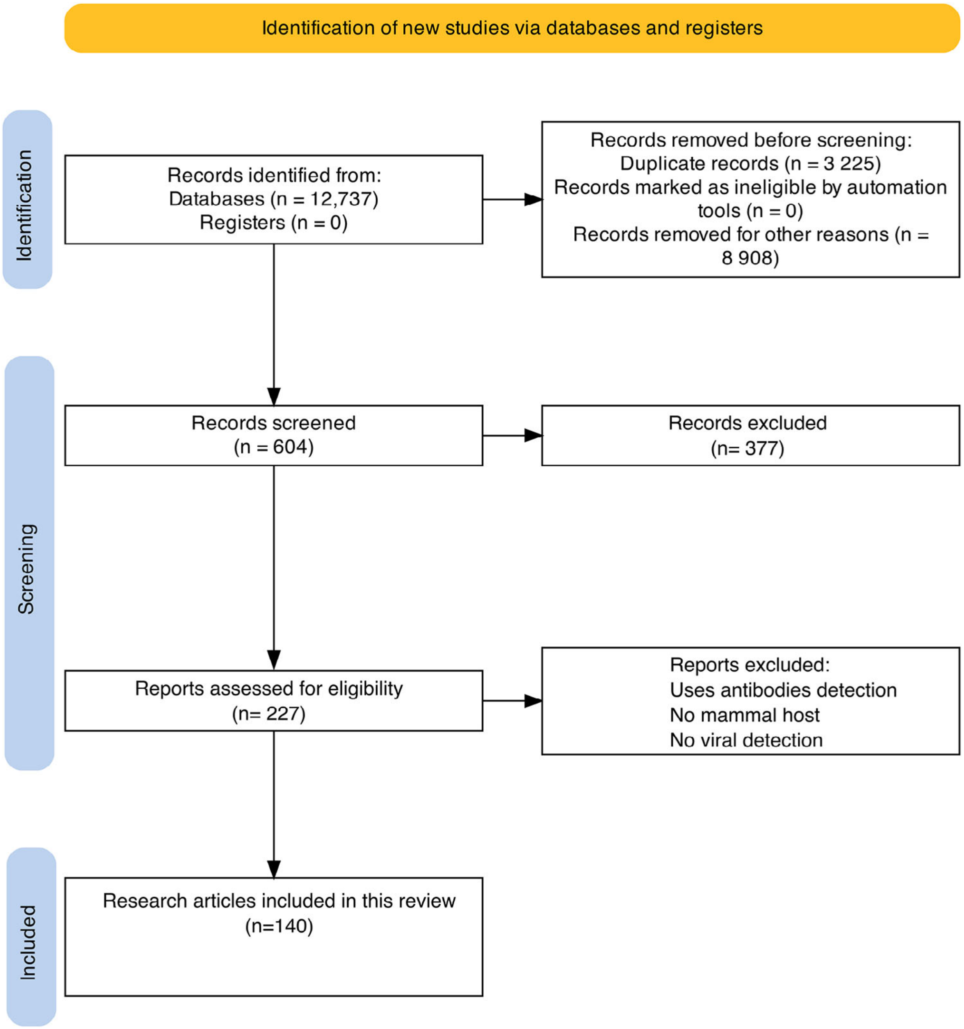

FIGURE 1 | PRISMA flow diagram for the systematic review carried out in this paper. This figure was created using the Shiny app PRISMA2020 (Haddaway et al. 2022).

henipavirus. Rabies is an important zoonosis that has also seriously affected mammal populations (Jackson 2016; Stuchin et al. 2018); likewise, hantavirus, coronavirus and henipavirus are causes of zoonotic disease and have rodents and bats as natural reservoirs (Halpin et al. 2011; Li et al. 2005). Whereas morbillivirus englobes pathogens of public health, economic and wildlife conservation importance (Kamel and El-Sayed 2019; Karki, Rajak, and Singh 2022). Finally, FIV, a well-suited model to infer the influence of host and landscape factors on pathogen direct transmission (Kozakiewicz et al. 2023), was also frequently selected within the reviewed papers.

Among the most commonly studied hosts were rodents, carnivores, humans and ungulates. Rodents and bats are taxonomic groups of interest in infectious disease studies. These mammals present life histories and physiological traits (e.g., early age to sexual maturity, larger litter size, flight capacity). Which have been associated with their pathogen reservoir status (Han et al. 2015; Plourde et al. 2017). Furthermore, some rodent and bat species can establish themselves in the proximities of human settlements and livestock productions, facilitating contact between them and humans or domestic animals (Bordes et al. 2017; Hahn et al. 2014), which could have led to the origin of important zoonotic pathogens like Hantavirus, Lassa fever and Nipah virus (Han, Kramer, and Drake 2016; Epstein et al. 2022; Recht, Schuenemann, and Sánchez-Villagra 2020).

Carnivores and ungulates not only play a critical role in ecosystem processes (Murray, Webster, and Bump 2013; Ripple et al. 2014), but they are also involved in multi-host systems in which viral diseases are introduced by domestic animals and can be maintained in wildlife populations (Trebbien et al. 2014; Weaver et al. 2013). Thus, determining the role wild carnivore and ungulate hosts have in the circulation and maintenance of viral pathogens is vital to establishing preventive and mitigation measures against infectious diseases in wild and domestic animal populations (Belsare and Gompper 2015).

We identified distinct patterns for host- and landscape-associated factors driving pathogen infection and transmission in similar host–viral associations. For example, in Asian and South American countries, rodents sampled in land covers such as agricultural fields presented higher hantavirus infection, unlike in European studies where rodents in conserved forests presented higher prevalence values (Prist et al. 2016). FIV transmission and infection in South American carnivores seem to be occurring

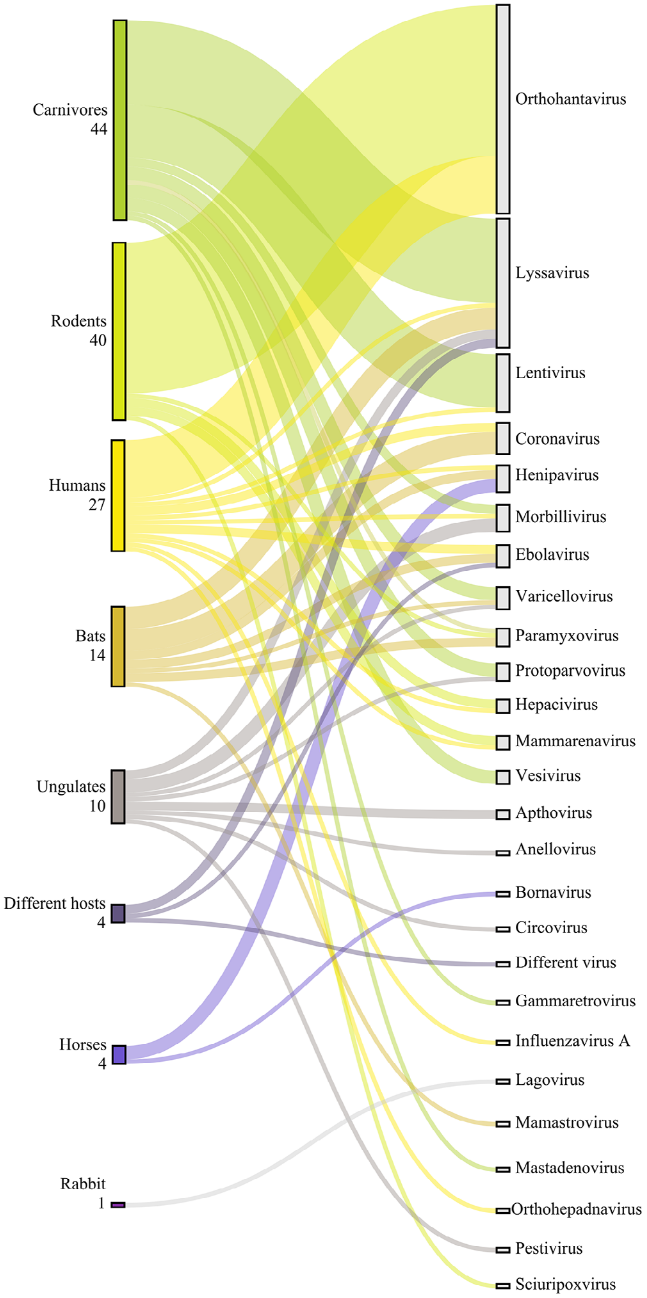

FIGURE 2 | Sankey diagram for the distribution of studies by host order and viral genus. The number denotes the number of observations recorded per host.

in peri-urban and fragmented landscapes, whereas in North America, transmission events are more likely to occur in areas with a higher amount of natural vegetation cover and away from human settlements (Fountain-Jones et al. 2017a).

These mixed patterns could reflect the different habitat preferences host species have, for instance, *Myodes glareolus*, the main hantavirus reservoir in Europe. This mammal is found in forested and wooded areas (Weber de Melo et al. 2015), whereas species such as *Akodon montensis* and *Calomys tener* (important hosts of hantavirus in Brazil) are considered habitat generalists, being greatly abundant on agricultural sites (Gheler-Costa et al. 2022).

The detection of FIV in guiñas (*Leopardus guigna)* ranging in human-perturbed landscapes of Chile could be a result of *L. guigna*'s capacity to tolerate habitat loss caused by human activities and predate poultry living in rural settlements (Gálvez 2015). Whereas pumas and lynxes living in northern latitudes tend to avoid areas with human activity (Reed et al. 2017), resulting in a higher prevalence of FIV in locations with more native vegetation cover. This suggests that similar hosts can differ in their morphological, biological and ecological traits, as well as their responses to environmental change, which could generate a variety of patterns in host–pathogen dynamics (Hammond et al. 2019; Raghwani et al. 2023).

Regarding the intrinsic host attributes included in the analysis and linked to the infection and transmission of viral agents. Sex and age were significant traits evaluated in bats (Moreira et al. 2021), rodents (Schmid et al. 2018), carnivores (Kraberger et al. 2020), ungulates (Righi et al. 2022) and humans (Aaby 1992).

Males may present a higher infection probability owing to their involvement in aggressive encounters (Steinmann and Priotto 2011) and greater dispersion capacity, for reproductive or territorial purposes, which could favour virus exposure, transmission and spatial spread (Schmid et al. 2018; Streicker et al. 2016). While, in females, physiologic processes like gestation could facilitate viral infection, due to a decrease in immune response to allow offspring development, this has been described in temporal associations between viral prevalence and birth pulses among bat species (Plowright et al. 2008; Peel et al. 2014).

Younger individuals could present a lower infection probability than adults due to the presence of maternal antibodies (Stone 2016). However, once that immunity is lost, these individuals represent susceptible individuals who can drive the transmission and maintenance of viral agents (Hayman 2015). Although older individuals might experience more opportunities for viral, younger individuals may also face increased exposure, as they travel greater distances seeking to establish a territory (Deter et al. 2008). Other less frequently analysed host traits included body weight or body mass (in rodents and bats) and population structure measures (in carnivores, rodents and lagomorphs). Larger body weights are associated with older age (Heroldová et al. 2010; Seltmann et al. 2017), thus greater exposure to viral agents (Polop et al. 2018).

Likewise, different studies show a positive trend between a higher host density and a higher viral prevalence and transmission in rodents (Boone et al. 2002), carnivores (Sidorov, Sidorova, and Poleshchuk 2010), ungulates (Zhang et al. 2022), and humans (Redding et al. 2016), due to a higher probability of contacts between susceptible and infectious individuals (Schuchert et al. 2014, Zhang et al. 2022).

However, studies in carnivores show that even when host density is lower than necessary to sustain viral transmission, the dispersal of infected hosts from one habitat patch to another, where other subpopulations are found, can maintain virus presence (Moran et al. 2021).

In this context, the distribution and mobility of host populations, along with their connectivity through host dispersal

TABLE 1 | Important host, climate and landscape features influencing infection and transmission of directly transmitted virus in mammals.

Factor type	Factor	Host	Effect	Virus	Reference
Host trait	Host density	Humans	• High human population density was associated with an increased risk of zoonotic transmission	Hantavirus, Arenavirus, Ebolavirus	Zhu et al. (2023); Redding et al. (2016); Olivero et al. (2020)
		Rodents, carnivores, ungulates, horses, rabbits	• Population density is positively associated with infection risk and transmission	Hantavirus, Hepacivirus, FMDV, PPRV, Rabies virus, Henipavirus, EBHSV	Munsey et al. (2021); Schmid et al. (2018); Voutilainen et al. (2012); Abdrakhmanov et al. (2022); Sokos et al. (2018); Wheeler et al. (2008)
	Body size/condition	Rodents	• Infection risk increased with body mass	Hantavirus	Salvador et al. (2011); Griffiths et al. (2022); Clay et al. (2009)
		Bats	• Infection risk increased with lower body condition	Astrovirus	Seltmann et al. (2017)
	Sexual features	Rodents, carnivores	• Males presented a higher infection probability than females	Hantavirus, Hepacivirus, FeLV	Salvador et al. (2011); Schmid et al. (2018); Sacristán et al. (2021); Pontier et al. (1998)
		Bats	• Mating strategy and birth pulses were determinant factors associated with viral prevalence	Adenovirus, Ebolavirus	Rossetto et al. (2020); Hranac et al. (2019)
	Age	Rodents, carnivores, bats	• Older individuals had a higher probability of infection and could drive transmission • Younger individuals presented both higher and reduced odds of infection	Hantavirus, Hepacivirus, Rabies virus, Protoparvovirus, FIV, CDV Coronavirus, Herpesvirus	Schmid et al. (2018); Gheler-Costa (2022); Sacristán et al. (2021); Carver et al. (2016); Gilbertson et al. (2022); Marescot et al. (2018); Moreira Marrero et al. (2021)
	Genetic features	Rodents, carnivores, ungulates, rabbits	• Expression of certain genes was associated with viral infection • Host relatedness positively associated with viral prevalence • Host high genetic diversity and low genetic isolation was associated with viral infection	Hantavirus, Hepacivirus, Bovine viral diarrhea, FIV	Guivier et al. (2011, 2014); Heni et al. (2020); Fountain-Jones et al. (2017b)
	Species identity	Rodents, carnivores, ungulates, bats	• Species identity associated to virus prevalence	Hantavirus, Herpesvirus, Coronavirus, Astrovirus, Torque virus, Rabies virus	Griffiths et al. (2022); Moreira Marrero et al. (2021); Seltmann et al. (2017); Righi et al. (2022); Zhang et al. (2009)
	Diet	Bats	• Insectivore, frugivorous and hematophagous diet were features of importance in positive individuals • Diet breadth was features of importance in positive individuals	Henipavirus, Herpesvirus, Ebolavirus	Escobar et al. (2015); Plowright et al. (2019); Schmidt et al. (2019)
	Morphologic features	Bats	• Adult body length and forearm length were features of importance in positive individuals	Henipavirus	Plowright et al. (2019)

(Continues)

TABLE 1 | (Continued)

Factor type	Factor	Host	Effect	Virus	Reference
Landscape attributes	Land cover	Humans, rodents, carnivores, bats, ungulates, horses	• Croplands, pasture, plantations, urban and residential areas were positively associated with viral infection, as well as conserved forests	Hantavirus, Torque virus, Borna virus, PPRV, Henipavirus, Mammarenavirus	Faust et al. (2023); Morand et al. (2015, 2019); Voutilainen et al. (2012); Langlois et al. (2001); Zeng et al. (2021); Redding et al. (2016); Recuenco et al. (2008)
	Landscape configuration	Rodents, carnivores, humans, ungulates	• Different measures related to fragmentation (i.e., edge density, index of landscape configuration, number of patches, contagion index, landscape division index, patch density, number of patches) were positively associated with virus infection	Hantavirus, Rabies virus, Coronavirus, Ebolavirus, PPRV, Henipavirus	Morand et al. (2015); Langlois et al. (2001); Linard et al. (2007); Raghavan et al. (2016); Rulli et al. (2017); Hahn et al. (2014); Ye and Qiu (2021)
	Elevation	Rodents, carnivores, ungulates, rabbits	• Positive individuals and transmission occurred at lower altitudes	Hantavirus, Rabies virus, PPRV, EBHSV, CDV	Carella et al. (2022); Dellicour et al. (2016, 2017); Recuenco et al. (2008); Sokos et al. (2018)
	Barriers	Carnivores, ungulates, rabbits	• Rivers and roads pose an obstacle for viral infection and transmission • Water channels could facilitate viral transmission • Higher prevalence found in near road networks	Rabies virus, FIV, PPRV, EBHSV	Barton et al. (2010); Laenen et al. (2016); Recuenco et al. (2008); Lee et al. (2012); Sokos et al. (2018)
	Soil features	Rodents, humans	• Soil type and moistures were related with virus persistence in the environment and consequently infection risks	Hantavirus	Yan et al. (2007); Linard et al. (2007)
Climatic features	Temperature	Humans, rodents, carnivores, ungulates, horses	• Both positive and negative associations with infection risks	Hantavirus, Mammarenavirus, Rabies virus, PPRV, Henipavirus, Borna virus, Influenza virus	Faust et al. (2023); Xiao et al. (2018); Ren et al. (2010); Raghavan et al. (2016); Encarnação et al. (2013); Zhang et al. (2022)
	Precipitation	Humans, bats, horses	• Both positive and negative associations with infection risks.	Hantavirus, Mammarenavirus, Henipavirus, Borna virus	Xiao et al. (2018); Redding et al. (2016); Encarnação et al. (2013); Martin et al. (2018); Zhang et al. (2022)
	Humidity	Humans	• Low humidity conditions were positively associated with infection risks	Influenza virus	Ren et al. (2010)
	Season	Bats, horses	• Both positive and negative associations with infection risks	Rabies virus, Henipavirus, Astrovirus	Lane et al. (2022); McFarlane, Becker, and Field (2011); Seltmann et al. (2017)

(Continues)

TABLE 1 | (Continued)

Factor type	Factor	Host	Effect	Virus	Reference
Other features	Species diversity	rodents, bats	• Changes in species diversity were associated with virus prevalence	Hantavirus, Henipavirus	Ecke et al. (2017); Voutilainen et al. (2012); Clay et al. (2009)
	Parasite coinfection	Rodents, bats	• Coinfection with helminth positively associated with virus infection	Hantavirus, Coronavirus	Salvador et al. (2011); Seltmann et al. (2017)
	Human activities	Humans, horses, ungulates carnivores	• Human footprint index positively associated with spillover risks • Human population density was a feature of importance in spillover and infection risks • Hunting season negatively associated with virus infection	Henipavirus, PPRV, FMDV, FIV, Rabies virus	Abdrakhmanov et al. (2022); Faust et al. (2023); Walsh (2015); Fountain-Jones et al. (2022); Dellicour et al. (2017); Zeng et al. (2021); Munsey et al. (2021)

Abbreviations: CDV, canine distemper virus; EBHSV, European Brown Hare Syndrome Virus; FeLV, feline leukaemia virus; FFV, feline foamy virus; FIV, feline immunodeficiency virus; FMDV, foot and mouth disease virus; PPRV, peste des petits ruminants.

(metapopulation dynamics) across the landscape, could enhance virus spread and persistence (Gilligan 2002). Furthermore, hosts exhibit different preferences for habitat types according to resource availability (F. Ecke, Löfgren, and Sörlin 2002, May et al. 2008), resulting in non-uniform population densities and consequently variable pathogen prevalence (Andreo et al. 2012). By integrating host density information and population structure measures, it becomes possible to better comprehend the influence host population variability, connectivity and barriers to gene flow have in virus infection (Salvador et al. 2011), transmission (Fountain-Jones et al. 2017) and spread (Nadin-Davies et al. 2010).

These intrinsic traits influence contact rates and infectious periods. Additionally, they fluctuate within the same host species. Hence, identifying the contribution of population individuals in virus infection and transmission associated with their biological traits can enhance the detection of individuals with greater transmission capacity and determine effective control measures (Hearst et al. 2023). Additionally, a few papers focused on rodents and bats used host species identity and diversity measures as predictor variables for virus infection (Ecke et al. 2017; Schmid et al. 2018).

Species identity congregates intrinsic attributes (e.g., physiology, behaviour, habitat specialisation) that influence host contact rates, host susceptibility and competence. According to this, host populations may play different roles in pathogen epidemiology (Caron et al. 2015). For instance, minks (*Neovison vison*) and otters (*Lontra canadensis*) have been suggested as maintenance hosts in multi-host disease systems affecting wild carnivores, such as feline panleukopenia virus and Aleutian mink disease virus (Canuti et al. 2020). Likewise, *N. vison* might be an intermediate host to spread Avian influenza A viruses (Zhao et al. 2019). Therefore, recognizing the role hosts have in multi-host disease systems is crucial to efficiently developing preventive measures against infectious diseases (Paull et al. 2012).

Diversity measures in their different components (e.g., alpha-diversity, beta-diversity) were also considered predictor variables in some studies (Milholland et al. 2017; Schmid et al. 2018). In multi-host systems, evidence suggests diversity in host communities influences infection risk and transmission due to variations in host encounter probabilities (Schmid et al. 2018; Ecke et al. 2017). Communities with greater diversity may present fewer encounters among competent hosts (dilution effect). This has been recorded across multi-host systems such as hantavirus (Khalil et al. 2016) and may be present in other directly transmitted viruses.

Within the landscape attributes, land cover was the most frequent predictor variable for several host groups registered in our systematic research. Habitat selection made by key hosts in either conserved (Linard et al. 2007) or perturbed landscapes (de Brito et al. 2020) has an impact on infection risk (Viel et al. 2011) and transmission of viral agents (Escobar and Peterson 2013). Furthermore, other landscape composition measures, such as the percentage of vegetation cover habitat, seem to have an indirect effect on virus prevalence due to the presence of microclimatic conditions and the amount of preferred habitat that influence virus survival, persistence and host density (Davis et al. 2019; Razzauti et al. 2021).

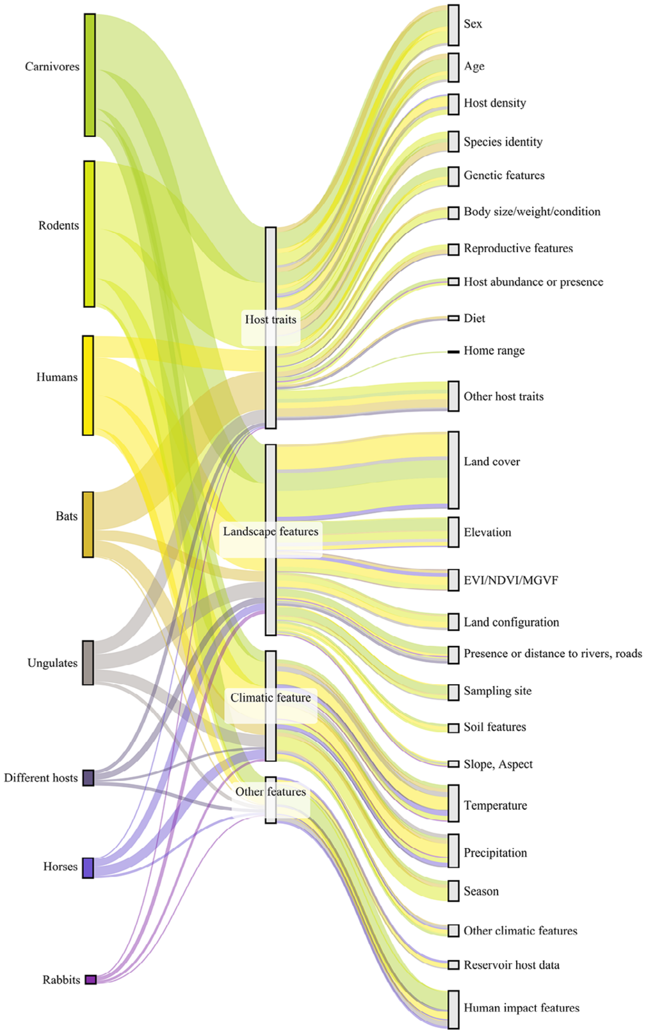

FIGURE 3 | Sankey diagram for the distribution of host landscape attributes among the papers in the systematic review.

Landscape configuration measures were included as predictor variables in thirteen articles, in which patch density, total edge length, largest path index and number of patches were used to analyse the effect of habitat fragmentation on virus–host associations such as hantavirus prevalence in rodents (Morand et al. 2015; Razzauti et al. 2017), rabies outbreaks occurrence in ungulates (Botto Nuñez et al. 2020), and the risk of Nipah virus spillover in humans (Hahn et al. 2014).

Habitat fragmentation happens when contiguous natural habitats are transformed into smaller and isolated habitat remnants surrounded by a matrix of human-modified landscapes (Arroyo-Rodríguez and Mandujano 2009; Loh 2019). Fragmentation alters the richness and abundance of host assemblages; this response seems to vary across geographic regions and hosts (Adjapong et al. 2022; Estrada-Villegas, Meyer, and Kalko 2010; Puettker, Meyer-Lucht, and Sommer 2008; Struebig et al. 2008).

Different rodent and bat species seem to be resilient and modify their movement patterns across the habitat when facing fragmentation (Diffendorfer, Gaines, and Holt 1995; Romero-Nava, León-Paniagua, and Ortega 2014). Furthermore, they can establish near or in human settlements and take advantage of the alternative resources human presence offers, congregating and thriving at these sites (Mendoza et al. 2024; Hahn et al. 2014), which could result in high prevalence, transmission and spillover risk of viral agents (Khalil et al. 2014; Hahn et al. 2014).

When assessing the response of species to landscape composition and configuration, it is important to consider that this response is scale-dependent (Galán-Acedo et al. 2018). This means that there is a spatial extent where the relationship between species response (e.g., abundance, density, richness) and landscape composition and configuration has a stronger influence or can be recognized (Jackson and Fahrig 2015). Therefore, integrating a multi-scale approach can be useful in determining the effects of landscape composition and configuration on virus epidemiology in different hosts; however, this approach was only used in one of the papers analysed in this review (Langlois et al. 2001).

Embedded in landscape features, the presence of rivers, highways, terrain slopes or elevation could represent natural or artificial barriers. These barriers can impede host movement and contact and could limit viral transmission and spread (Smith et al. 2002; Streicker et al. 2016). However, in carnivore studies, transmission events could occur even between separated populations; a possible explanation for this is that short contacts between individuals can still be sufficient for transmission (Lee et al. 2012). Moreover, the use of rudimentary roads for host dispersal across their habitat facilitates viral spread (Fountain-Jones et al. 2021) and viral traits such as low virulence and long incubation periods (Barton et al. 2010, Maestas 2014).

In studies directed at rodents and humans, elevation was measured to characterize the location of refugia and potential risk sites with an increased hantavirus prevalence and spillover risk (Zhang et al. 2009; Xiao et al. 2018). Similarly, this feature was used to establish risk areas for peste des petits ruminants in ungulates (Zeng et al. 2021). While for bats, it was used to model the spread of rabies (Benavides, Valderrama, and Streicker 2016).

The effects of climate features and phenomena were also considered in a small percentage of the selected studies (17%). Temperature and precipitation were the most common variables included; less frequent variables were humidity and season. These features can favour pathogen infection and transmission, generating a suitable environment for pathogen persistence (Linard et al. 2007; Zeimes et al. 2015). Additionally, they modulate resource availability and host behaviour (Raghavan et al. 2016), which are important drivers of host distribution, density and contact with other hosts (Faust et al. 2022).

Currently, most landscapes include covers with anthropogeneic perturbations, which generate the loss of native vegetation, fragmentation and variation in matrix permeability (land cover between habitat patches) (Tscharntke et al. 2012). These processes influence the richness (Brady et al. 2011), abundance (Willig et al. 2007) and movement (Pozo-Montuy, Serio-Silva, and Bonilla-Sánchez 2011) of mammal species (Presley et al. 2019).

Several of the articles included in this review incorporated variables like human population density and factors related to anthropogenic impact, such as the presence of human settlements, livestock production, human footprint index, and wildlife disease management strategies (i.e., vaccination) (Davis et al. 2019; Dellicour, Rose, and Pybus 2016; Faust et al. 2023). These variables can give an insight into how anthropogenetc perturbations and preventive strategies can indirectly shape viral transmission and increase the risk of spillover events by generating demographic changes in the wildlife population (Fountain-Jones et al. 2021) and contacts between wildlife, domestic animals and humans (Kraberger et al. 2020; Morand et al. 2019; Zeng et al. 2021).

Although many of the mammal hosts of importance in zoonotic and economically burdensome diseases were frequently studied (i.e., rodents, carnivores, ungulates). Other mammal hosts serving as reservoirs of viruses that represent a risk to public and animal health remained poorly studied (Gong et al. 2024). Additionally, investigation efforts have leaned toward specific host–virus systems (e.g., rodent-hantavirus in Europe, rodent-arenavirus in Asia), leaving aside similar systems in other geographical regions.

The few records we found showed mixed patterns suggesting that findings in one region may not be applicable in another. This highlights the necessity of generating local studies, particularly in regions with high mammal diversity and scarce investment in wildlife pathogen studies (i.e., Neotropical, African, Guineo–Congolian) (Heesterbeek et al. 2015). In this sense, we believe the development of effective mitigation strategies against disease threats can greatly benefit from using tools such as predictive models (Becker et al. 2022; Mull et al. 2022) that could integrate the highlighted host traits and environmental features in work such as this (e.g., longevity, body mass, land cover) to first identify and monitor wildlife hosts and subsequently describe patterns of infectious disease dynamics that are surging in these regions.

Regarding the factors influencing DTV infection and transmission, our results indicate a categorisation into four distinct groups: host biological traits, landscape features, abiotic factors and anthropogenic factors. Most studies included in this review focused on variables within one of these categories. Twenty-four percent of the studies integrated host and landscape-associated factors, while twelve percent examined host biological traits, landscape features and abiotic factors. Finally, only 6.4% consider variables related to all four categories.

This indicates constraints in our understanding of DTV disease dynamics, as the variables do not operate isolated within the context of the disease dynamics (Botto Nuñez et al. 2020). Integrative approaches that account for host biological traits, landscape features and abiotic and anthropogenic factors should be implemented in future studies to enhance understanding of their direct and indirect effects on DTV dynamics and to develop effective mitigation measures for the associated diseases.

Finally, we would like to highlight that the research papers included in our systematic review approached the influence of host and landscape-associated factors in viral infection and transmission across different ecological scales: among hosts of the same species (Guivier et al. 2011; Khalil et al. 2014; Marescot et al. 2018) and in multi-host–pathogen interactions (Kraberger et al. 2020; Lewis et al. 2017). Both approximations carry great significance in the understanding of host-pathogen dynamics (Fountain-Jones et al. 2017a) and should be considered to better comprehend cross-transmission risks in wildlife–human–livestock interfaces (Hahn et al. 2014).

5 | Conclusion

This systematic review suggests multiple directions for future research that may improve our comprehension and management of DTV disease dynamics. It is crucial to highlight the insufficient research in geographic areas characterized by high mammalian biodiversity, including the Neotropical, African, and Guineo–Congolian regions, which exhibit elevated zoonotic risks due to species density and inadequate funding for wildlife surveillance initiatives. Local studies in these regions would facilitate the identification of specific infection and transmission patterns, thereby aiding the development of mitigation strategies in resource-limited areas. Infection and transmission of DTV are influenced by host biological traits, landscape features, abiotic factors and anthropogenic factors. Most of the studies have examined factors in isolation; it is essential to implement more integrative approaches that concurrently account for host biological traits, landscape features and both abiotic and anthropogenic factors. These approaches would improve our understanding of the complex interactions among these factors and their direct and indirect effects on viral transmission dynamics, thereby aiding the development of more effective control measures across diverse ecological systems. Furthermore, incorporating multi-scale studies that evaluate the effects of landscape composition and configuration on viral epidemiology, especially concerning host population movement and environmental factors across different spatial scales, may uncover patterns not apparent in single-scale studies. This may enhance predictions related to disease dissemination and is essential for comprehending cross-transmission risks at the interfaces between wildlife, humans and livestock.

Author Contributions

María del Carmen Villalobos-Segura: Conceptualization (equal); data curation (lead); formal analysis (lead); investigation (lead); methodology (equal); writing-original draft preparation (lead). Oscar Rico-Chávez: Concentualization (equal); methodology (equal); writing-review and editing (equal). Andrea Chaves: Conceptualization (equal); methodology (equal); writing-review and editing (equal) . Gerardo Suzán: Conceptualization (equal); writing-review and editing (equal).

Acknowledgements

The authors would like to thank the Posgrado en Ciencias de la Producción de la Salud Animal program of UNAM and the Consejo Nacional de Humanidades, Ciencias y Tecnologías (CONAHCyT) for the Doctorate's Scholarship granted to M.V.-S. (Grant number: 49790).

Conflicts of Interest

The authors declare no conflicts of interest.

Ethics Statement

The authors have nothing to report.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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