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Climate change–induced tropicalization of temperate ecosystems reshapes the global climatic context of zoonotic virus first detections

Attila J. Trájer[1]

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Abstract

The tropicalization of temperate ecosystems driven by climate change is reshaping global patterns of zoonotic viral disease emergence. This study investigates the climatic drivers of emergences and evaluates how future climate change can alter their climatic suitability. Latitudinal analyses reveal a bimodal distribution of emergence sites, with a dominant peak near the equator and a secondary concentration in mid-latitudes. The highest emergence rates occur within the Intertropical Convergence Zone and decline toward the subtropics. Global hotspots are consistently concentrated in the core tropics. Climatic characterization shows that 80.5% of first detection sites occur in regions with mean annual temperatures above 18 °C, predominantly within tropical climate zones, especially tropical savannas. Ensemble learning identifies isothermality and the mean diurnal range as the strongest predictors of zoonotic virus emergence. Future projections under SSP2-4.5 and SSP3-7.0 scenarios indicate a progressive intensification and spatial reorganization of climatically suitable areas throughout the 21st century. High suitability remains centered in the tropics but is increasingly spreading into subtropical and temperate regions, especially under SSP3-7.0. By 2081–2100, many temperate areas see increased suitability, while parts of the tropical core stabilize or expand. Overall, the global risk landscape broadens and flattens, suggesting that future zoonotic viral emergence may become more spatially diffuse, with subtropical and temperate regions gaining importance alongside persistent tropical hotspots.

Keywords Tropicalization · Zoonotic diseases · Climate change · Latitudinal occurrence · Diversity

✉ Attila J. Trájer
trajer.attila@mk.uni-pannon.hu

[1] Sustainability Solutions Research Lab, University of Pannonia, Veszprém, Hungary

1 Introduction

Zoonotic virus-caused diseases represent an enormous global medical, social, and economic burden (Skowron et al. 2022; Di Bari et al. 2023), and it is estimated that at least 75% of emerging viral diseases have zoonotic origins (Leifels et al. 2022). The emergence of these pathogens is strongly linked to environmental modifications driven by the growing global human population, particularly those that increase contact between anthropogenic and wild environments (Mishra et al. 2021). Neglected tropical diseases, many of which are zoonotic, significantly hinder the achievement of sustainable development goals and social development in several parts of the world (WHO 2021), and they remain major contributors to disability, poverty, and economic instability (Ghosh and Begam 2021; Di Bari et al. 2023).

The emergence of novel viral pathogens is often associated with host switching and intrahost speciation processes (Brito et al. 2021). Nevertheless, the environmental factors that promote anthropozoonotic spillovers remain insufficiently understood and are the subject of ongoing investigation (Da Silva et al. 2021). Geographic and climatic conditions have a crucial influence on the distribution and ranges of zoonotic diseases, as exemplified by mosquito-borne infections such as chikungunya, Zika, and dengue fevers (Carreto et al. 2022). Arboviruses also show heterogenous regional patterns among mammals in the Neotropics (Garcia-Romero et al. 2023). Similarly, the distribution of pappataci fever serotypes follows a well-defined belt across the temperate and arid regions of Afro-Eurasia (Alkan et al. 2013), shaped largely by the ranges of competent sand fly vectors (Cruaud et al. 2021). The presence of henipaviruses likewise depends on the environmental suitability of their fruit bat hosts (Mougari et al. 2022).

The COVID-19 pandemic clearly demonstrated the limitations of our current ability to predict the geographic origin of novel zoonotic viruses. Other examples underscore this challenge. The Nipah virus outbreak in Malaysia (1998–1999), which arose through multiple host switches—from fruit bats to pigs, pigs to humans, and ultimately human-to-human transmission—was entirely unexpected (Loyinmi and Gbodogbe 2024). The emergence of MERS-CoV in Saudi Arabia in 2012 was similarly unanticipated. Its sporadic yet persistent outbreaks and unusually high mortality rate (~35%) distinguished it from other coronaviruses (Berber et al. 2021), and its transmission chain involved fruit bats as reservoirs, camels as intermediate hosts, and humans as final hosts (Al-Salihi and Khalaf 2021). Likewise, the sudden appearance of the Hendra virus in Australian horse stables in 1994—with high fatality rates in horses and humans, as well as airborne transmission potential—occurred without warning (Allen et al. 2025).

Although the climatic backgrounds of several zoonotic diseases have been investigated, comparatively little attention has been given to the environmental characteristics of the sites of the first emergence. Yet, from the viewpoint of risk assessment and primary prevention, identifying the types of environments where new zoonotic diseases are most likely to appear is of fundamental importance (Wille et al. 2021). Identifying regions with a high potential for the emergence of new zoonoses is critically important for human and animal health. Addressing the existing gap in our understanding of the climatic context of zoonotic virus emergencies, this study aims to examine the environmental characteristics of first-detection sites, with a special focus on the climatic conditions that shape regional patterns of zoonotic viral diversity.

In this study, the first known detection sites of zoonotic viruses were mapped, their long-term thermal and aridity characteristics were quantified, and each site was assigned a Köppen–Geiger climate class. Ensemble machine-learning approaches were applied to identify the climatic variables most strongly associated with the geographic distribution of initial virus detection sites. Variables describing thermal stability and relative temperature variability, such as isothermality (bio3) and mean diurnal range (bio2), emerged as the principal climatic factors of first zoonotic viral emergences. These associations were projected onto future climate scenarios to estimate how global suitability for zoonotic virus emergence may shift over the 21st century. By integrating virus-specific detection patterns, family-level differences, climate classifications, and predictive modelling, the main climatic drivers of emergence were identified, and potential climate-driven changes in global risk were highlighted to support more targeted surveillance and early-warning efforts. This analysis addresses the climatic background conditions associated with the geographic emergence of zoonotic viruses.

2 Materials and methods

2.1 Zoonotic virus data source

The first detection data of zoonotic viruses were obtained from the Centers for Disease Control and Prevention Arbovirus Catalog (CDC Arbovirus Catalog), which provides information on virus names, taxonomic families, and original source records. Virus family assignments were verified and updated using the NCBI Taxonomy Browser (Schoch et al. 2020). The resulting dataset includes georeferenced first-detection records for 525 zoonotic viruses. This dataset is necessarily indicative rather than exhaustive. It has been estimated that more than 10,000 virus species may be capable of infecting humans, with over 90% currently circulating undetected in wildlife reservoirs (Carlson et al. 2022). Consequently, the objective of this study was not to capture the full diversity of zoonotic viruses but to identify broad geographical and climatic patterns associated with their first recorded detection events. Accordingly, first-detection locations are treated as proxies for the initial documented emergence of zoonotic viruses, not as complete representations of their ecological or geographic ranges. When required, coordinates of first detection sites were refined by consulting original virus descriptions, epidemiological reports, and taxonomic or surveillance literature. Corrections were applied only when clear evidence supported a more accurate or internally consistent location. The most numerous zoonotic virus families represented in the database are Arenaviridae (13), Flaviviridae (66), Nairoviridae (32), Peribunyaviridae (158), Phenuiviridae (47), Rhabdoviridae (68), Sedoreoviridae (67), and Togaviridae (25). First detection sites for members of these virus families were analysed both collectively and separately. The complete list of taxa and associated metadata is provided in Supplementary Table S1.

2.2 Climatic data

Long-term climatic means were used because the objective was to identify the general climate regimes associated with the first zoonotic virus detections, rather than short-term

weather conditions in the year of discovery. Climatological normals provide a stable and comparable basis for such global analyses and better reflect the background climatic envelopes within which virus–host systems occur, rather than the specific meteorological conditions triggering individual spillover events (Quiner and Nakazawa 2017; Assefa et al. 2022). To ensure temporal consistency between virus discovery records and available climatic data, only virus occurrences that could be reliably associated with an appropriate climatological reference period were included in the climatic analyses. Although a total of 525 zoonotic viruses were examined, climatic variables could be assigned to 366 viruses (approximately 70% of all records), corresponding to the total temporal coverage (1960–2000) of the applied climate models.

Climatic data were obtained from the WorldClim Global Climate and Weather Dataset, using two reference periods: WorldClim v1.4 (1960–1990) (Hijmans et al. 2005) for virus first detections between 1960 and 1984, and WorldClim version 2.1 (Fick and Hijmans 2017) for both virus first detections between 1985 and 2000 and for modelling purposes. The temporal threshold separating the two reference periods was defined as 1985, corresponding to the midpoint of the overlapping periods. When discovery dates spanned multiple years, the median year was used to assign the appropriate climatological reference period. This approach ensures each virus record is matched with the most representative long-term climatic conditions at the time of first detection.

Climate change may alter conditions for zoonotic pathogens and vectors, facilitating disease emergence in new regions (Leal Filho et al. 2022), making global climate scenarios a suitable basis for assessing long-term shifts in climatic suitability. For future climatic conditions, the wc2.1_2.5m_bioc_CMCC-ESM2_SSP2-4.5 and SSP3-7.0 series—downscaled CMIP6 climate simulations (Lovato et al. 2022)—were used for the periods 2021–2040, 2041–2060, 2061–2080, and 2081–2100. All analyses employed a spatial resolution of 2.5 arc minutes. The Köppen climatic categories (Köppen 1923) were used as one of the bases for characterizing first virus observation sites. The classification followed the definitions of Kottek et al. (2006), and the georeferenced Köppen-Geiger map used in the analysis was obtained from Beck et al. (2018).

2.3 Aridity index

To characterize the humidity conditions of the first observation sites of zoonotic viruses, the Köppen Aridity Index (KAI) was applied using long-term climatic normals for the periods 1960–1990 and 1970–2000 (Köppen 1923, 2011), ensuring that each virus record was matched with the most representative reference period. This aridity-related metric is calculated by dividing mean annual precipitation (P_s) by the sum of the mean annual temperature (T_m) and a constant of 33 (Quan et al. 2013, 2014):

$$KAI = \frac{P_s}{T_m + 33}$$

where KAI ($mm°C^{-1}$) denotes the Köppen Aridity Index, P_s (mm) is mean annual precipitation, T_m (°C) is mean annual temperature, and 33 is a constant.

KAI values classify climates into five categories (Quan et al. 2013, 2014), including hyper-arid (<0.9), arid (0.9–5.7), semi-arid and dry semi-humid (5.7–13.6), semi-humid

(13.6–15.6), and humid (> 15.6) climatic regions. All types of the used climatic factors used in the analyses can be found in Supplementary Table S2.

2.4 Modelling and analytic methods

All analyses were conducted in the Python 3.10 (64-bit, Anaconda 3) environment using Spyder. The following Python modules were employed: pandas and numpy for data handling and numerical computations, rasterio for reading, sampling, and writing climatic raster layers, scipy.stats.gaussian_kde for statistical calculations, including the Boyce index, sklearn for Random Forest and Gradient Boosting classifiers, and xgboost for eXtreme Gradient Boosting models.

All known zoonotic virus first emergence sites were georeferenced by extracting their geographic coordinates from the original database. These coordinates were also used to sample climatic data and to generate spatially constrained random background points, ensuring that pseudo-absence locations were at least 300 km away from known occurrence sites to minimize spatial bias. Up to 5,000 random background points were generated globally, respecting minimum distances from occurrence sites. Points outside terrestrial areas (e.g., oceans or no-data cells) were excluded, ensuring ecologically meaningful pseudo-absences. Bioclimatic values (bio1–bio19) were extracted for all presence (1) and background (0) points, creating a combined dataset suitable for machine learning.

The dataset was split into training (80%) and test (20%) sets, and three machine learning models were trained: Random Forest, Gradient Boosting, and XGBoost. Ensemble predictions were calculated by averaging the probabilities from the three models.

Model performance was quantified using the Boyce index, a presence-only evaluation metric suitable for continuous suitability predictions, which evaluates how well the predicted environmental suitability corresponds to the distribution of known presence locations. This approach replaced traditional ROC-AUC and binary thresholding, offering a more robust evaluation for presence–background modelling, as these metrics are known to be sensitive to pseudo-absence selection and arbitrary thresholding decisions in presence–background frameworks.

Finally, global suitability rasters were generated block-wise, enabling memory-efficient predictions across large climatic datasets. Each raster cell received an ensemble probability value representing climatic suitability for zoonotic virus emergence. The Boyce index was calculated for both individual models and the ensemble, ensuring that predicted high-suitability areas were strongly associated with known occurrence sites. This framework allows future climate-based suitability projections to be generated using ensemble models, with probabilistic outputs reflecting the relative favourability of environmental conditions for zoonotic virus emergence and evaluated robustly through the Boyce index rather than arbitrary presence/absence thresholds.

The model was projected onto both a reference period (1970–2000) and future climatic periods (2021–2040, 2041–2060, 2061–2080, and 2081–2100) using downscaled CMIP6 bioclimatic projections from the WorldClim database. Future climate conditions were represented by the CMCC-ESM2 general circulation model under the SSP2-4.5 and SSP3-7.0 socioeconomic pathways, allowing assessment of climate-driven shifts in climatic suitability for zoonotic virus emergence. Smoothed trend lines were fitted to mean values within latitude bins for visualization purposes.

Several studies have explicitly modelled zoonotic risk or spillover processes (e.g. Carlson et al. 2019; Eby et al. 2023; Wang et al. 2024), whereas the present study focuses on climatic correlates of first documented detection events rather than on transmission dynamics or spillover mechanisms. Accordingly, the results should be interpreted as describing broad climatic suitability envelopes associated with detection patterns, not as direct estimates of zoonotic risk.

3 Results

3.1 Characterizations of global geographical distribution patterns

The distribution of absolute latitudes for the first detection sites is bimodal, with a primary peak near the equator and a secondary peak at mid-latitudes. The highest first emergence values occur within the intertropical convergence zone (~0–3° absolute latitude interval), followed by a rapid decline toward higher latitudes within the lower-middle trade wind belt (~3–30° absolute latitude interval). A pronounced local minimum appears around the tropics (~20–23° absolute latitude interval), while a secondary maximum occurs at the transition between the trade winds and westerlies (~26–30° absolute latitude interval), corresponding to the subtropical high zone and a mid-latitude diversity plateau. Only a few zoonotic viruses were first detected at higher (50°< absolute latitude) latitudes (Fig. 1a). Kernel density patterns of first observations of zoonotic viruses show a strong concentration near the equator. The global hotspot is in the Amazon and surrounding regions, including the Guiana Highlands, northern Andes, and Panama. A secondary center of first detection occurs in southern West Africa, northern Central Africa, and western East Africa. Tertiary regions include the United States, the Mediterranean to India, and northeastern Australia (Fig. 1b).

The primary center of diversity for first observations of Arenaviridae is the Amazon region, with western Central Africa representing a secondary center (Suppl. Fig. S1a). The primary diversity center of Flaviviridae extends from the United States through Central Africa to Southeast Asia, with West and Central Africa showing the highest concentration of early detections (Suppl. Fig. S1b). Nairoviridae shows a center of origin in Central and the northwestern part of Southern Asia (Suppl. Fig. S1c). Peribunyaviridae were mostly first detected in the Amazon region, with West and Central Africa serving as secondary centers (Suppl. Fig. S1d). The primary first detections of Phenuiviridae are the Amazon region, with secondary centers in West-Central Africa and the Mediterranean Region (Suppl. Fig. S1e). The distribution of first descriptions of Rhabdoviridae and Sedoreoviridae shows elongated pan-tropical patterns with its main centre in the Amazon region in the case of Sedoreoviridae and a bifocal distribution pattern in the Amazon region and Central Africa in the case of Rhabdoviridae (Suppl. Fig. S1f, g). For Togaviridae, the center of first observations is located in the northwestern part of South America (Suppl. Fig. S1h).

3.2 Climatic distribution patterns

Examining the first virus detection sites in the context of global thermal regimes, 0.8% occurred in the very cold areas (annual mean temperature < 0 °C), 6.85% in cold regions

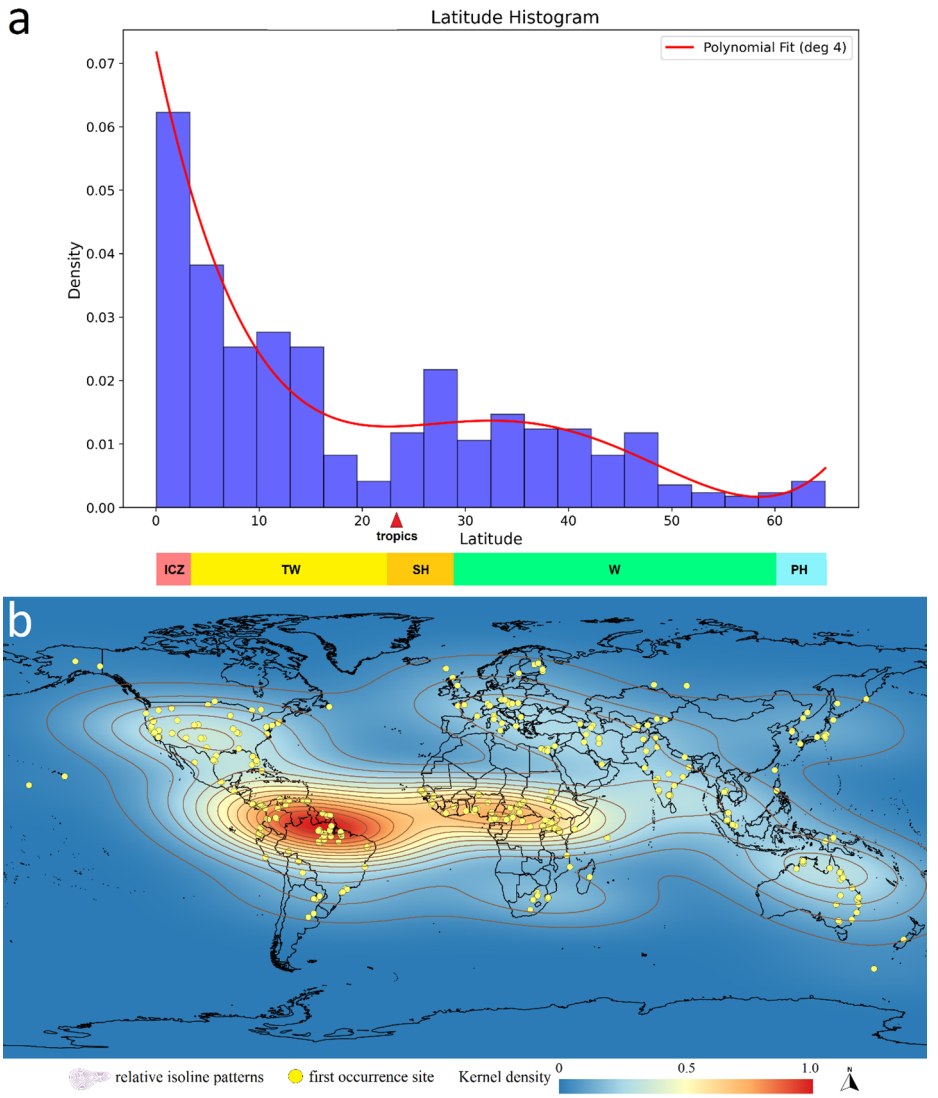

Fig. 1 The absolute latitudinal range of the first occurrences of zoonotic viruses (**a**) and the kernel density patterns of the first observations of all studied zoonotic viruses (**b**). ICZ: intertropical convergence zone, TW: zone of trade winds, SH: subtropical high zone, W: zone of westerlies, PH: polar high zone. Latitude values are absolute ones; density is in the 0 to 1 scale of all observations

(0–10 °C, with the coldest quarter > 0 °C), and 12% in temperate climate sites (10–18 °C, coldest quarter > 0 °C). The majority, 80.5%, were found in warm regions with an annual mean temperature > 18 °C (Fig. 2a).

Regarding aridity, 1.3% of first occurrences were in hyper-arid regions (KAI < 0.9 mm°C^{-1}), 4.4% in arid regions (KAI 0.9–5.7 mm°C^{-1}), 17.3% in semi-arid/dry semi-humid areas (KAI: 5.7–13.6 mm°C^{-1}), and 4.6% in semi-humid regions (KAI: 13.6–15.6 mm°C^{-1}). A majority, 72.4%, were detected in humid regions (KAI > 15.6 mm°C^{-1}) (Fig. 2b).

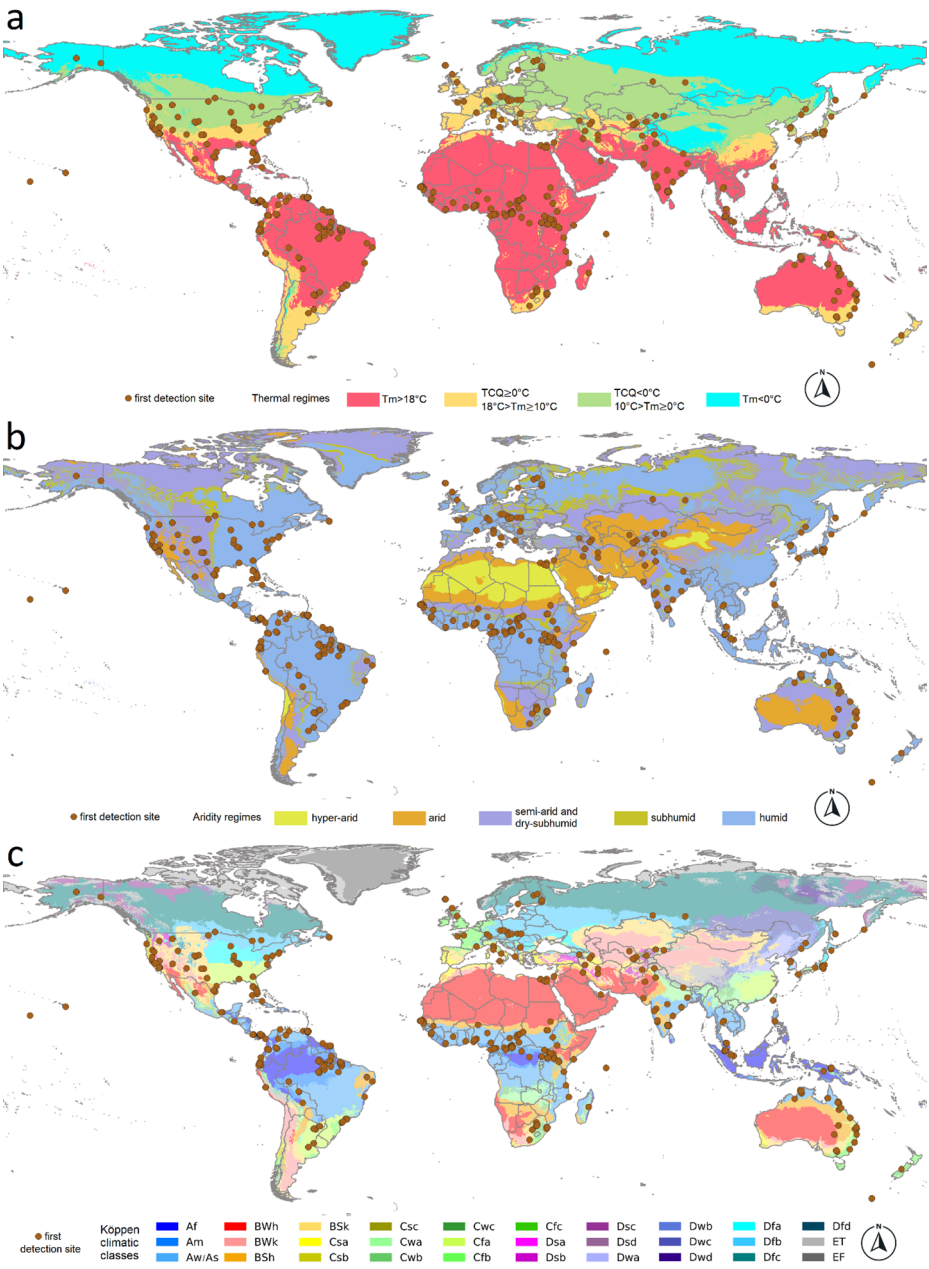

Fig. 2 The first occurrence of zoonotic virus detections plotted on the global thermal regime (**a**) and Köppen Aridity (**b**) patterns, and the distribution of zoonotic virus occurrences projected to the global Köppen-Geiger climatic map (**c**). Tm: annual mean temperature, TCQ: temperature of the coldest quarter. Köppen-Geiger climatic class abbreviations are in Supplementary Table S3

3.3 Köppen-Geiger climatic characterization results

Across virus families, tropical climates (Köppen A), particularly tropical savanna, were the most common environments of first observation. This general pattern applies to Arenaviridae, Flaviviridae, Nairoviridae, Peribunyaviridae, Phenuiviridae, Rhabdoviridae, Sedoreoviridae, and Togaviridae, although each family shows specific secondary tendencies toward arid or temperate climates. Arenaviridae viruses were mostly detected in warm and tropical climates, especially savanna climates. Flaviviridae were observed across multiple climate categories but most frequently in tropical savanna and other tropical climates. Nairoviridae were also most common in tropical savanna, though arid regions showed a notable presence. Peribunyaviridae were primarily tropical climates—especially tropical rainforests—with some arid and temperate occurrences. Phenuiviridae were likewise mainly tropical, distributed across rainforest, monsoon, and savanna types, with some arid detections. Rhabdoviridae were primarily tropical, with one-third of observations in tropical savanna. Sedoreoviridae were largely tropical savanna but also included arid, temperate, and continental sites. Togaviridae were common in tropical climates, with substantial representation in arid and temperate regions.

Figure 2c shows the distribution, while Fig. 3 presents pie charts of the first detection climate frequencies for the eight most abundant virus families and for the full virus dataset.

K-means clustering of Köppen-Geiger climate frequencies highlights clearer family-level differences. Nairoviridae form the most distinct cluster, with higher frequencies of BWh, BSk, Cwa, Dfc, and EF climates, indicating broader habitat occupancy, including arid, temperate, and cold regions. Peribunyaviridae also form a separate cluster due to their relatively higher representation of Csb, Dwb, and Dwc climates in the first detection sites. Arenaviridae and Togaviridae cluster together with higher proportions of Af, Aw/As, and Csa climates, while Phenuiviridae and Rhabdoviridae share relatively higher frequencies of Am, Cfa, Dsa, and Dsc climates. Flaviviridae and Sedoreoviridae show greater prevalence in BWk, BWk, BSh, Dwa, and Dsb climates, pointing to an affinity for arid and humid continental sites (Suppl. Fig. S2).

3.4 Relative importance of climatic predictors

Across all studied zoonotic virus species, the three machine-learning approaches consistently identify isothermality as the most influential climatic predictor of first occurrence sites (Fig. 4a). In the Gradient Boosting and Random Forest models, isothermality and mean diurnal range emerge as the most important variables. In contrast, the XGBoost model assigns the highest importance to isothermality, followed by the mean temperature of the coldest quarter, highlighting the central role of winter thermal constraints in shaping global first detections of zoonotic viruses.

The Random Forest model shows generally weaker contrasts in variable importance among virus families, yet broadly similar patterns are evident. The most influential predictors include mean diurnal range for Arenaviridae, Flaviviridae, Nairoviridae, Peribunyaviridae, and Sedoreoviridae (Fig. 4b, c, d, e, h); isothermality for Phenuiviridae (Fig. 4f) and Rhabdoviridae (Fig. 4g); and precipitation of the driest quarter for Togaviridae (Fig. 4i).

Family-specific Gradient Boosting results further emphasize the importance of mean diurnal range and isothermality constraints. Mean diurnal range is the most influential for

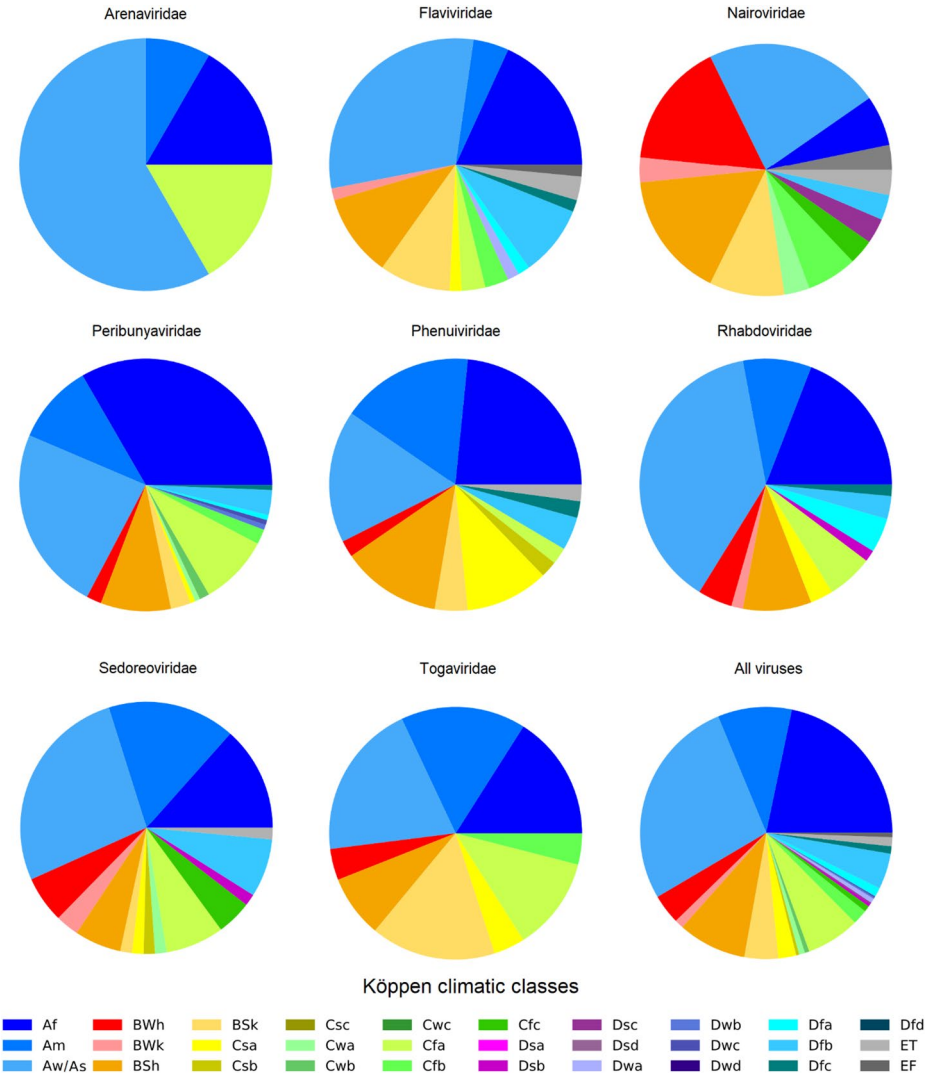

Fig. 3 The Köppen-Geiger climatic classes of eight zoonotic virus families and the total. Köppen-Geiger climatic class abbreviations are in Supplementary Table S3

Arenaviridae, Sedoreoviridae and Togaviridae (Fig. 4b, h, i), while isothermality ranks highest for Flaviviridae, Peribunyaviridae, and Rhabdoviridae (Fig. 4c, e, g). Mean temperature of the wettest quarter is the key predictor for Nairoviridae (Fig. 4d), and mean temperature of the coldest quarter is the key predictor for both Phenuiviridae (Fig. 4f).

3.5 Projected patterns

The global distribution of projected climate-based suitability for zoonotic virus emergence during the reference period 1970–2000 (Suppl. Fig. S3) exhibits clear and coherent spa-

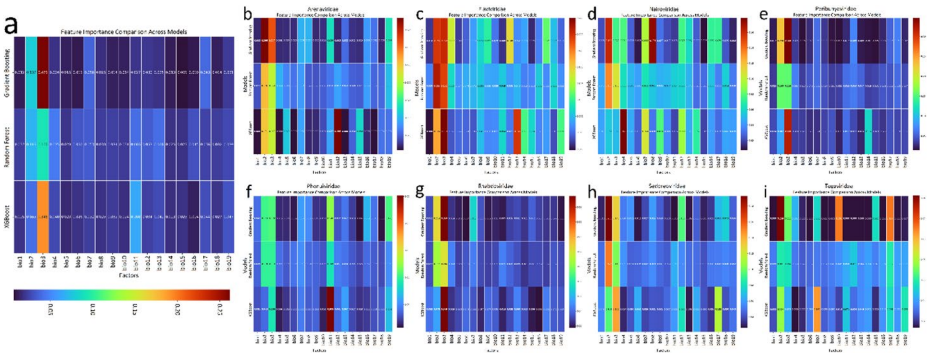

Fig. 4 Climatic factor importance for the emergence of all studied zoonotic viruses (**a**), Arenaviridae (**b**), Flaviviridae (**c**), Nairoviridae (**d**), Peribunyaviridae (**e**), Phenuiviridae (**f**), Rhabdoviridae (**g**), Sedoreoviridae (**h**), and Togaviridae (**i**) based on eXtreme Gradient Boosting (XGBoost), Random Forest, and Gradient Boosting models

tial patterns. High suitability values are concentrated primarily in tropical and subtropical regions, with peak suitability scores (0.90–1.00) occurring in equatorial zones such as the Amazon Basin, Central Africa, and Southeast Asia. These regions coincide with areas of biodiversity hotspots and frequent human-wildlife interaction In contrast, temperate regions—including much of North America, Europe, and northern China—display intermediate suitability values (approximately 0.59–0.79), while high-latitude regions in Canada, northern Europe, and Siberia show consistently low suitability (<0.59), reflecting climatic constraints on potential hosts and vectors. The Boyce index of the whole ensemble model was 0.933, while the individual models achieved even higher values: GBM, 0.988; RF, 1.000; and XGB, 0.988.

Future projections reveal clear temporal shifts in climatic suitability across the 21st century under both SSP2-4.5 and SSP3-7.0 scenarios (Fig. 5). The magnitude and spatial distribution of these changes relative to the 1970–2000 reference period are presented in Supplementary Figure S4, which depicts scenario-specific differences across successive future time slices. Because the two scenarios exhibit broadly similar spatial patterns but differ in magnitude, their results are discussed jointly. During the 2021–2040 period, areas of highest suitability (0.90≤) remain concentrated in equatorial South America, Central Africa, and Southeast Asia, closely resembling the reference-period pattern but showing a wider geographic range.

By 2041–2060, moderate increases in climatic suitability emerge in several subtropical and lower temperate regions, including parts of Central America, the Sahel, southern China, and eastern South America, while core tropical regions largely retain high suitability values. These trends become more pronounced during 2061–2080, with further intensification and spatial expansion of moderate-to-high suitability zones toward adjacent temperate regions, particularly under the SSP3-7.0 scenario.

By the end of the century (2081–2100), climatic suitability for zoonotic viral emergence is projected to increase markedly across many present-day temperate and cool regions, with several areas reaching high projected suitability levels, while parts of the current tropical core remain relatively stable or exhibit an increase in projected suitability. Moderate suitability classes (0.69–0.90) expand into previously marginal regions, including parts of the

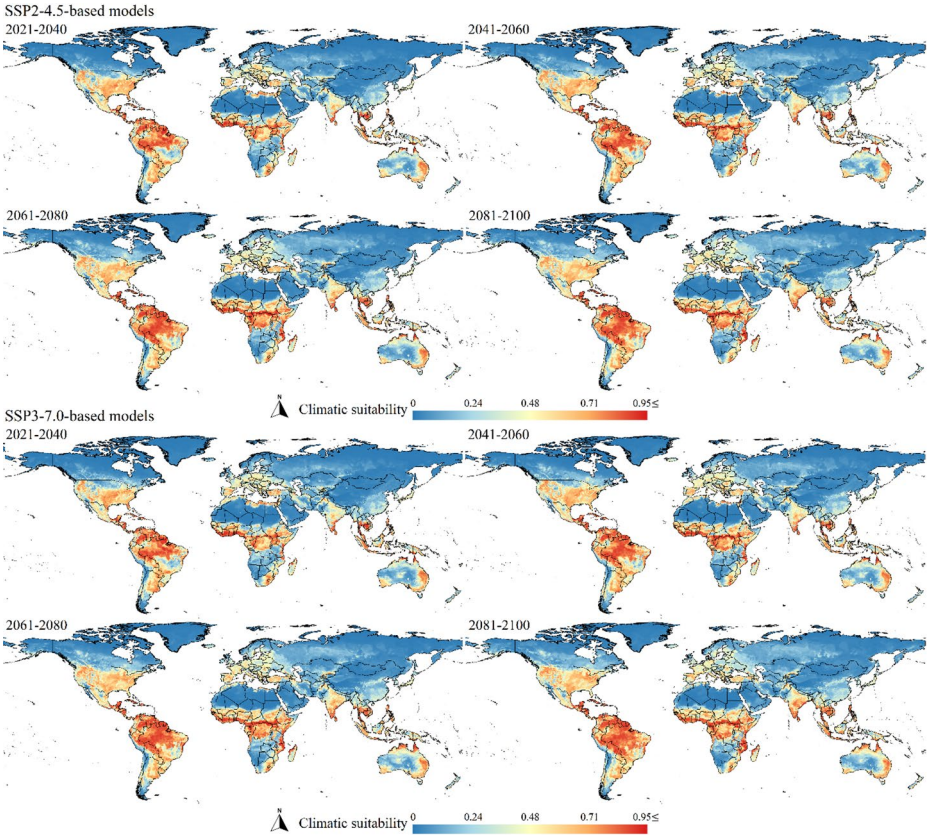

Fig. 5 Projected future global climatic suitability patterns of high-risk emergence of zoonotic viruses based on CMCC-ESM2_SSP2-4.5 and CMCC-ESM2_SSP3-7.0 scenarios

Mediterranean basin, East Asia, and southern South America. This pattern reflects increasing suitability at mid- and higher latitudes and outside the traditional tropical core, relative to historical tropical maxima, indicating a more spatially diffuse and latitude-dependent redistribution of emergence risk that occurs symmetrically across hemispheres.

The modelled climatic suitability values for the eight most abundant virus families were analysed across latitude using both normal and absolute latitude bins. As shown in Fig. 6a-d, the upper panels present the mean values and fitted curves along the conventional latitude scale (−90° to 90°; Fig. 6a-b), while the middle panels show the same data aggregated by absolute latitude (0°–90°; Fig. 6c-d). Climatic suitability generally peaks in the tropics and temperate zones and declines toward the poles, with minor local maxima and minima reflecting regional variability. Across future climate scenarios (SSP2-4.5 and SSP3-7.0), the model predicts a general increase in suitability values compared to the 1970–2000 baseline, particularly in mid-latitude regions. The similarity of the patterns in both normal and absolute latitude representations suggests that hemispheric asymmetry does not substantially affect the overall latitudinal trends in modelled climatic suitability of first viral emergences. Aggregated by Köppen climate groups, dry (B) and polar (E) zones exhibit minor changes (Fig. 6e–f). Overall, these projections indicate a broadening and more spatially diffuse risk

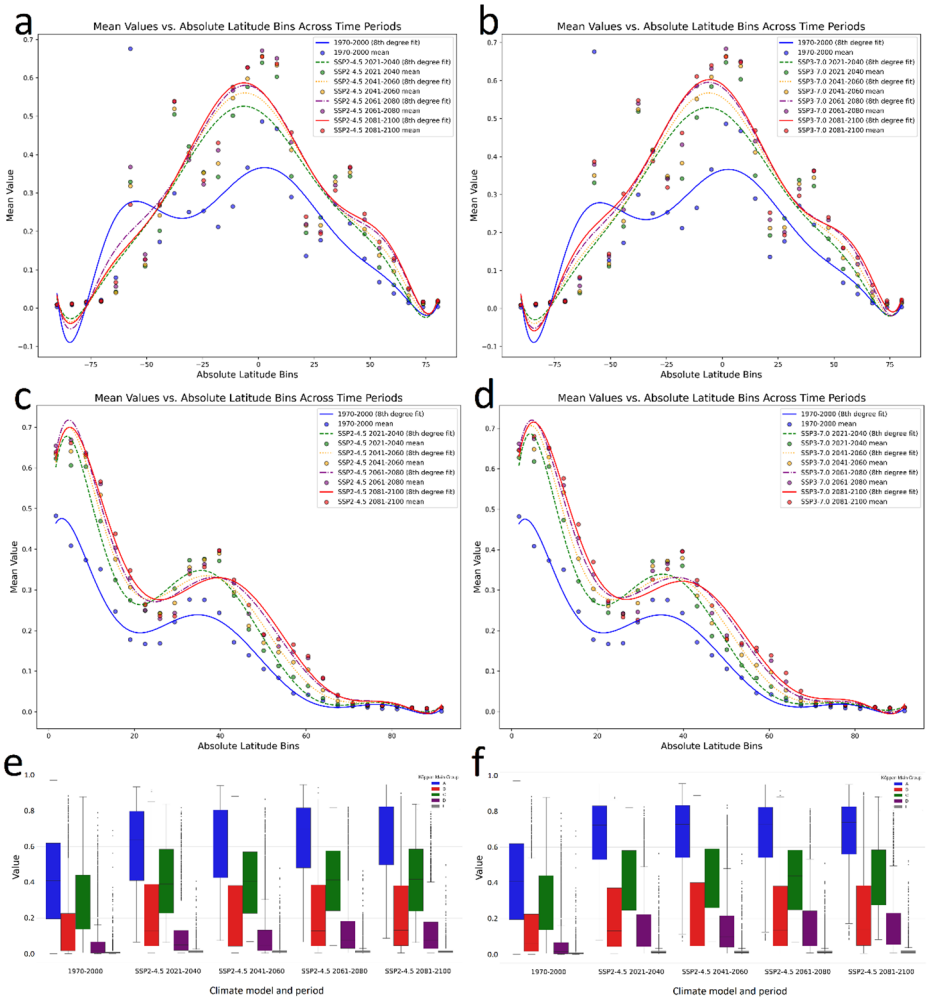

Fig. 6 Latitudinal and climate-zone–based patterns of modelled climatic suitability for zoonotic viral emergence under recent and future climate scenarios. Mean suitability values plotted against absolute latitude bins for 1970–2000 and four future periods (2021–2040, 2041–2060, 2061–2080, 2081–2100) under CMCC-ESM2_SSP2-4.5 (**a**) and CMCC-ESM2_SSP3-7.0 scenarios (**b**). Points show binned means and curves indicate smoothed latitudinal trends. The same relationships are expressed solely as functions of absolute latitude, highlighting latitudinal redistribution independent of hemisphere under SSP2-4.5 (**c**) and SSP3-7.0 (**d**). Climatic suitability values aggregated by reference-period Köppen main groups are given in the (**e**) and (**f**) panels. The Köppen-like main climate groups are tropical (**A**), arid (**B**), temperate (**C**), continental (**D**), and polar (**E**)

landscape, with temperate and continental areas gaining prominence alongside persistent tropical hotspots, particularly under the higher-emission SSP3-7.0 scenario.

Taken together, the modelled patterns indicate that areas classified as temperate and continental are likely to experience relatively higher climate-based suitability for zoonotic viral emergence in the future, while present-day tropical regions are projected to maintain stable or increased suitability. This suggests that future emergence risk may become increasingly

spatially diffuse, with growing importance of subtropical and temperate regions alongside persistent tropical hotspots.

4 Discussion

4.1 Latitudinal patterns and large-scale climatic drivers of first-detection patterns

The number of first detections of zoonotic viruses is strongly influenced by latitude and large-scale atmospheric circulation. The density of first observation sites generally declines from the equator towards the poles, with a local peak in the temperate zone and a subsequent minimum in the subarctic, closely reflecting global forest diversity gradients (Liang et al. 2022). These results highlight the importance of assessing which climatic factors most strongly drive the emergence of new zoonotic viral diseases. According to the results of this study.

Overall, the density patterns of first detection sites show an equatorial maximum, concentrated in warm regions (T_m > 18 °C) and humid to semi-humid territories (KAI > 13.6 mm°C^{-1}), consistent with most occurrences reported in Sect. 3.2. The ensemble learning models indicate that isothermality and mean diurnal range are key drivers of first-detection patterns. These results suggest that new zoonotic virus detections are associated with higher suitability in regions exhibiting stable thermal conditions with low diurnal and seasonal fluctuations. Equatorial regions, characterized by low interannual variability and persistently high temperatures, experience diurnal temperature fluctuations that often exceed seasonal changes (Kitayama et al. 2021). Rising temperatures can influence viral strain competition within hosts and affect viral genetic variability (Alcaide et al. 2021). In addition, several major reservoir host groups, such as megachiropteran bats, are largely restricted to tropical and warm subtropical regions (Ramanantsalama et al. 2022), reinforcing the strong tropical signal observed in first-detection patterns.

4.2 Latitudinal diversity gradients and biospheric context

The observed flattening of latitudinal diversity gradient (LDG) of first zoonotic viral emergencies aligns closely with the LDG of terrestrial vertebrate richness (Mannion et al. 2014). Although this study concerns the first observation sites rather than full viral distributions, zoonotic viruses co-evolve with animal hosts and vectors (de Angeli Dutra et al. 2022), making it reasonable to expect strong correlations between viral first-detection density and host diversity. This pattern reflects the baseline structure of the biosphere, as LDGs are known to flatten temporarily following major extinction events (Song et al. 2020), likely owing to the higher vulnerability of tropical ecosystems (Mannion 2020). Similar flattening or even higher-latitude diversity maxima have been documented in multiple marine and terrestrial taxa during specific geological intervals (Rose et al. 2011; Kröger 2018). A comparable flattening emerges when comparing reference periods with projected 21st-century high-risk emergence patterns.

4.3 Regional emergence hotspots and surveillance relevance

Model projections indicate that equatorial regions experience stable or an increase in projected climatic suitability, whereas higher suitability values also shift toward the Northern Hemisphere. This redistribution produces a more even latitudinal profile of climatic suitability rather than a simple poleward shift. Similar tendencies are observed in some virus families individually; for example, first detection sites of Nairoviridae peak predominantly in extra-tropical regions. Nevertheless, the overall latitudinal pattern of zoonotic virus first-detection density remains near-parabolic from equator to poles, consistent with general global biodiversity patterns (Mannion 2020). Lower Amazonia is identified as the most prominent global hotspot of first-detection density, with additional high-density regions in the Guianan Highlands, Orinoco Plains, and Northern Andes. These areas show elevated first-detection densities for several virus families, including Arenaviridae, Peribunyaviridae, Phenuiviridae, Sedoreoviridae, and Togaviridae. They are dominated by tropical rainforest (Köppen Af) and tropical monsoon (Köppen Am) climates and are recognized global biodiversity hotspots (Manes and Vale 2022).

Accelerating deforestation and landscape fragmentation in the Amazon since 2014–2015 (Beuchle et al. 2021; Ellwanger et al. 2022) have been shown to disrupt wildlife assemblages and ecological barriers relevant to pathogen transmission (Ellwanger et al. 2022). While these processes are not explicitly modelled in the present study, they provide important ecological context for interpreting regional patterns of climatic suitability. Accordingly, previous studies suggest that zoonotic virus spillover risk may be elevated in the Amazon region, independently of the climatic suitability patterns modelled in this study (Grillet and Vincenti-González 2024) (Grillet and Vincenti-González 2024). Warm subtropical-temperate transition zones also represent important regions of elevated climatic suitability and first-detection density, partly because they host large and growing human populations. Approximately 2.36 million people live between 22° and 36° N (Stevens et al. 2015; WorldPop. Population Counts 2000–2020), where even modest increases in climatic suitability may be of particular relevance for public health surveillance.

The emergence-density hotspots identified in this study partially overlap with the recognized global terrestrial biodiversity hotspots and the five major high-biodiversity wilderness areas (Schmitt 2007). Many also coincide with regions of high incidence of vector-borne diseases such as dengue and malaria (WHO 2024; Messina et al. 2019). This spatial correspondence is provided for contextual comparison only, as these epidemiological patterns are not explicitly modelled in this study, but it highlights the potential value of integrating climate-driven suitability models with epidemiological surveillance.

4.4 Implications under ongoing climate change

Mid-elevation and subtropical regions—including parts of the southern United States, the Mediterranean Basin, South Asia, and eastern Australia—form recurrent secondary hotspots for first detections. This pattern is consistent with the hypothesis that steep LDGs are a feature of 'icehouse' climates characterized by strong latitudinal thermal gradients (Fenton et al. 2016). Ongoing global warming somewhat flattens this gradient (Jones et al. 2019), facilitating the expansion of tropical-like conditions into higher latitudes and elevations (Uribe et al. 2023). Virus families whose emergence is strongly constrained by cold-season

temperatures—such as Sedoreoviridae and Rhabdoviridae—reflect this process particularly clearly.

The transition from an 'icehouse' to a more 'greenhouse' world is expected to promote the northward spread of zoonotic viruses and their hosts and vectors (Kulkarni et al. 2022). Climate change may expand tropical conditions while potentially narrowing the humid tropics (Uribe et al. 2023), though some studies predict little change in the 21st century (Berg and McColl 2021). Tropicalization of temperate ecosystems could allow tropical organisms, including hosts, vectors, and pathogens, to reach higher latitudes (Osland et al. 2021; Dash et al. 2021).

4.5 Climatic stability as a dominant constraint on family-specific emergence patterns

Differences in the kernel diversity patterns of the eight most species-rich families can be primarily interpreted through the lens of thermal stability, as the machine-learning models consistently identify isothermality and mean diurnal temperature range as the dominant climatic predictors of global first occurrence sites. This highlights that the balance between daily and seasonal temperature variability, rather than absolute thermal extremes, plays a central role in shaping the environmental suitability for zoonotic virus emergence, host persistence, and detection probability.

The spatial patterns observed for Flaviviridae remain closely linked to the broad geographic distribution of their potential hosts and vectors. The wide dispersion of first-occurrence sites reflects the global diversity of mosquito vectors —*Aedes* and *Culex* species (Soh and Aik 2021; Peinado et al. 2022)—as well as ixodid and argasid ticks (Lemasson et al. 2021; Sándor et al. 2021). Isothermality and mean diurnal range highlight that stable daily temperatures are key for vector survival, activity, viral replication, and host–vector contact. The heterogeneity in kernel density patterns reflects differences between thermally buffered tropical mosquito systems and extra-tropical tick systems, both operating in predictable thermal regimes.

The partial similarity between Flaviviridae and Togaviridae factor-importance profiles likely reflects their shared reliance on mosquito transmission cycles (Chase 2022), although the importance of precipitation during the driest quarter for Togaviridae emphasizes the additional role of moisture availability in regulating vector breeding habitats.

The global distribution of Phenuiviridae is characterized by a distinctive Mediterranean secondary hotspot, a pattern that aligns closely with the climatic sensitivity of their primary vectors, phlebotomine sand flies. Model results indicate that isothermality and the mean temperature of the coldest quarter jointly constrain first occurrence sites, suggesting that both thermal predictability and moderate winter conditions are essential for sustaining sand fly populations.

Sand flies are highly sensitive to temperature variability (Vivero-Gomez et al. 2024), and this sensitivity is reflected across their biogeographic lineages. Neotropical *Lutzomyia* species—vectors of viruses such as Alenquer and Chagres (Dehghani et al. 2021)— are strongly associated with humid tropical environments (Vivero-Gomez et al. 2024) characterized by low diurnal temperature variability, whereas Afro-Eurasian *Phlebotomus* species predominantly occupy thermally buffered Mediterranean climates shaped by Neogene-Quaternary geographical and paleoclimatic evolution (Cruaud et al. 2021).

First occurrence sites of Rhabdoviridae show a similarly strong association with isothermality, indicating convergence with Phenuiviridae in their dependence on stable thermal environments. This suggests that regions experiencing reduced temperature variability may provide increasingly favourable conditions for viral persistence and transmission, particularly where vector and host assemblages are already established. For Nairoviridae, the mean diurnal temperature range and the mean temperature of the wettest quarter emerge as the most influential climatic predictors. This pattern is consistent with the ecology of tick vectors, whose questing behaviour, survival, and host encounter rates are strongly regulated by short-term temperature fluctuations and moisture availability (Garrison et al. 2020). These findings underscore the importance of microclimatic conditions rather than broad-scale temperature gradients in shaping the emergence patterns of tick-borne viruses.

Rodent-associated virus families show distinct but coherent climatic responses. First observation sites of Arenaviridae are most strongly associated with mean diurnal temperature range, indicating that daily thermal variability plays a key role in structuring rodent activity, reproduction, and virus transmission dynamics. While precipitation remains an important background driver of rodent habitat suitability (Htwe et al. 2024), stable temperature regimes support year-round rodent population persistence, facilitate repeated host–host interactions, and promote viral survival in environmental reservoirs such as burrows and food caches (Zhang et al. 2024).

Similarly, Peribunyaviridae show a strong dependence on isothermality and mean diurnal range, reinforcing the importance of predictable thermal environments for rodent-borne (Yodjan 2022). Stable temperature regimes support year-round rodent population persistence, facilitate repeated host–host interactions, and promote viral survival in environmental reservoirs such as burrows and food caches (Zhang et al. 2024). Overall, the present results demonstrate that zoonotic virus emergence is tightly constrained by climatic stability at daily-to-seasonal scales. The dominance of isothermality and diurnal temperature dynamics across virus families highlights these factors as fundamental, yet often underappreciated, determinants of global first detection patterns, with important implications for anticipating future shifts in zoonotic risk under changing climate regimes.

4.6 Applicability, scope, and limitations of the framework

Although this framework was developed for zoonotic viruses, it can be readily applied to specific climate-sensitive pathogens, such as vector-borne diseases like dengue or malaria. Applying it to specific pathogens would require integrating key ecological and biological traits of both the pathogen and its vectors—such as host range, vector competence, and life-cycle constraints—into climate-based suitability models to capture species-specific risk patterns. For example, dengue risk projections could incorporate temperature-dependent mosquito development rates (Van Wyk et al. 2023), while malaria models might account for *Anopheles* vector distributions (Moffett et al. 2007). These findings highlight the need to prioritise targeted global surveillance in regions with high climate-driven suitability, particularly in tropical and subtropical areas, such as Southeast Asia, sub-Saharan Africa, and parts of South America, to strengthen early detection and preparedness for emerging pathogens.

Finally, it is important to emphasize the scope and limitations of the present framework. The analysis focuses on long-term climatic suitability derived from multi-decadal bio-

climatic variables and does not explicitly incorporate several well-established drivers of zoonotic emergence, including land-use change (da Silva Pessoa Vieira et al. 2022), host population dynamics and human–wildlife contact rates (Plowright et al. 2016), or short-term extreme climatic events (Fletcher et al. 2025). These factors are known to influence the timing and location of spillover events and outbreak dynamics (Eby et al. 2023; Wang et al. 2024), but they are difficult to integrate consistently at a global scale due to limited availability of harmonized historical data and incomplete metadata on virus detection circumstances. Consequently, the present results should be interpreted as describing broad climatic envelopes under which virus–host systems can persist, circulate, and be repeatedly detected, rather than predictors of individual spillover events.

5 Conclusion

The results demonstrate that first detections of zoonotic viruses are most strongly associated with warm climates (annual mean temperature > 18 °C), low thermal variability, and semi-humid to humid conditions typical of equatorial and subtropical regions. A secondary density maximum occurs near the subtropical high- pressure belts, reflecting the combined influence of climate, host ecology, and human exposure. The key climatic predictors identified closely mirror the ecological requirements of major hosts and vectors. Although clear general patterns exist, zoonotic virus families differ substantially in their climatic preferences and potential emergence regions, reflecting variation in host range and vector ecology. Future projections indicate a redistribution of climatic suitability rather than a simple poleward shift: suitability remains high in tropical regions but expands into subtropical and lower temperate zones. The ongoing poleward expansion suggests increasing climatic suitability for zoonotic virus emergence in temperate zones where host-pathogen interactions were previously limited. These patterns highlight the need for strengthened surveillance and public health preparedness and suggest that conservation efforts should prioritize regions where climate-driven shifts in suitability may alter wildlife distributions or disrupt host–vector–pathogen interactions, particularly in tropical hotspots and temperate areas projected to experience increasing suitability.

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Data availability The data supporting the findings of this study are available in the Supplementary Material. Publicly available datasets used in this study are cited and described in the Materials and Methods section. Further information is available from the corresponding author upon reasonable request.

Declarations

Ethics approval and consent to participate This study did not involve human participants, animals, or sensitive personal data. Therefore, ethics approval and consent to participate were not required.

Consent for publication Not applicable. This manuscript does not contain any individual person's data in any form.

Competing interests The author declares that there are no competing interests.

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