## Title

# Mapping the potential risk of coronavirus spillovers in a global hotspot

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## Abstract

Bats harbor approximately a third of known mammal viruses, including the recent coronaviruses SARS-CoV1 and SARS-CoV2 that likely spilled over in Asia. As spillover risk increases due to habitat loss and fragmentation, we identified potential zoonotic spillover and pandemic risk hotspots by combining landscape characteristics with the diversity of competent hosts, with horseshoe bats (genus *Rhinolophus*) used as proxies for zoonotic pathogen reservoir hosts. We estimated the risk of coronavirus emergence in South and Southeast Asia by integrating Rhinolophid species distributions, forest fragmentation, and human population density data. Two scenarios were considered: one using baseline forest cover data, and another incorporating new regional infrastructure which drives further fragmentation. Results showed that under both scenarios, spillover risk hotspots are concentrated in Indochina and southern China, where species richness and fragmentation are high, and where coronaviruses were previously detected in bat populations. Simulation of pandemic spread from the spillover risk hotspots using network models revealed risk hotspots clustered in Bangladesh and northeast India. These results highlight the vulnerability of human population centers and heightened risks from habitat fragmentation in Asia, especially given its history of recent coronavirus spillovers that became pandemics. Identifying hotspots emphasizes the need for a multidisciplinary approach to protect ecosystem integrity for public health, paving the way for improved predictive capabilities and targeted disease surveillance in at-risk regions.

## Keywords

zoonoses, emerging infectious diseases (EID), spillover risk, One Health, habitat fragmentation, ecological modeling, horseshoe bats

## Introduction

An estimated 60-75% of emerging infectious diseases for humans originate from zoonotic pathogens coming from wildlife (Jones et al., 2008; Taylor et al., 2001). Various taxa may be particularly likely to host zoonotic pathogens, with rodents, bats, and to some extent, carnivores well known for their capacity to host and transmit pathogens (Han et al., 2016; Olival et al., 2017; Z. Wu et al., 2021; Zhou et al., 2021). Effective zoonotic disease vectors are species that have high biological compatibility with pathogens, serving as reservoirs while also frequently interacting with target hosts either through their behaviors or due to habitat disturbances, thus facilitating transmission (Marquardt, 2004). The probability of spillover relates to two interconnected factors: firstly, changes in the interface between different animals, which alters the potential for wildlife to contract or spread pathogens, and secondly, stressors which may alter the vulnerability of animals to become sick or alter the rate of viral shedding (Keesing & Ostfeld, 2021; Plowright et al., 2015). Habitat loss and fragmentation do both by increasing potential interfaces for spillover, as well as increasing stress and likely rate of shedding. With increasing habitat loss and degradation, climate change, and exposure to various chemicals, zoonotic spillovers from wildlife may increase in the future, yet these patterns and risks depend on the hosts (Carlson et al., 2022; Rulli et al., 2017; Wilkinson et al., 2018). Habitat degradation resulting from activities such as deforestation, agricultural expansion, and urbanization can increase pathogen spillover risk by creating edges which increase interspecies contact and the transmission of zoonotic pathogens (Faust et al., 2018; Wilkinson et al., 2018). These edge regions serve as transition zones where wildlife, domestic animals, and humans come into closer contact, heightening the risk of spillover (Hassell et al., 2017). Increasing the interfaces creates more opportunities for potential competent hosts to come into contact and potentially exchange pathogens, while also elevating stress levels, and forcing them to travel further (and expend more energy to forage effectively) thus increasing the susceptibility to infection (Glidden et al., 2021). Understanding the potential for spillover requires knowing the interfaces where wildlife interacts with humans, livestock, and domestic animals, including how these connect to human population centers. Competent hosts are frequently commensal with humans, thus as areas are destroyed and degraded the probability of wild species harboring and spreading pathogens increases (Gibb et al., 2020; Kane et al., 2024; Keesing & Ostfeld, 2024).

Bats represent a prominent group of competent hosts which harbor a significantly higher percentage of zoonotic viruses compared to other mammals (Olival et al., 2017). This ability to host diverse viruses, often without showing symptoms, is likely due to the high metabolic costs (and associated ecophysiological pressures) associated with flight (Gorbunova et al., 2020; Irving et al., 2021; O'Shea et al., 2014). Spillover may occur either via direct human contact with bats (bat bites or consumption) or through exposure to intermediate hosts or food contaminated with bat saliva, urine and feces. A number of pathogens with reservoirs in bats have the potential to spill over into humans (Eby et al., 2023; Plowright et al., 2015; Wang & Anderson, 2019). These include viruses hosted by fruit bats (Pteropodidae), such as Hendra, Nipah, Marburg and possibly Ebola, which are associated with high human fatality rates. Understanding the ecology, and risks of pathogen spillover must reflect the distribution and ecophysiology of competent hosts, as these factors likely determine the patterns and risks of spillover. Thus, whilst Pteropids carry an array of pathogens, their ability to cover large distances and disperse across diverse environments will produce a very different pattern of risks to pathogens spread by species poorer at dispersing, or more limited to cluttered environments.

Different viruses have different hosts, and horseshoe (Rhinolophid) bats provide reservoirs of betacoronaviruses (Becker et al., 2022; W. Li et al., 2005) including SARS-CoV1 in 2003, SARS-CoV2 in the COVID-19 pandemic in 2019, and the MERS-CoV outbreak in the Middle East in 2012 (Letko et al., 2020; Zhou et al., 2020). There are a total of 118 described horseshoe bat species within the genus *Rhinolophus*, and are all distributed throughout the Old World (Csorba et al., 2003; Simmons & Cirranello, 2025). Rhinolophids are generally photophobic (restricted to dark conditions) and dependent on densely cluttered environments (typically forests), poor at dispersing due to their short, broad wing design, and use echolocation calls adapted for short-range prey detection among clutter (Wilson & Mittermeier, 2019). These characteristics indicate that fragmentation of forested habitats may have a disproportionate impact on Rhinolophids. The implications of fragmentation, such as heightened exposure to pesticides on fragment edges resulting from agriculture, may restrict movement, thus reducing resources and increasing ecophysiological stress, with photophobia further limiting the ability to move between patches (Kingston, 2013; Torquetti et al., 2021). Habitat alteration and fragmentation were found to be highly associated with increased ecophysiological stress and reduced the immunity of foliage-roosting bats, such as in *Rhinolophus trifoliatus* and *R, sedulus* (Seltmann et al., 2017). Forest edges interface with areas used by humans (especially for livestock) and likely represent hotspots for potential spillover, especially during times of natural ecophysiological stress such as during pregnancy (Montecino-Latorre et al., 2020; Rulli et al., 2021), yet how these risks vary over space and time requires further work.

Thus, understanding how landscape structure interfaces with species distributions, especially those of competent hosts for any given pathogen, may provide insights into where and even when the probability of spillover may occur. In previous outbreaks, the viruses are thought to have spilled over from bats to an intermediate host (e.g. horses for Hendra, pigs for Nipah, palm civets for SARS) that are closely associated with humans (Plowright et al., 2015). For example, in the case of Hendra, the loss of habitat due to deforestation coupled with periods of winter drought forced *Pteropus alecto* into horse pastures to forage, and this increase in stress in conjunction with increased interface with horses is specifically associated with spillover events (Eby et al., 2023). In South and Southeast Asia, higher spillover risk of Nipah virus from *Pteropus* fruit bats was predicted in areas with greater human footprint (Walsh, 2015), specifically in regions with higher human settlements and livestock or food sources for the bats (Chaiyes et al., 2022). Recent work on the origins of the betacoronaviruses SARS-CoV1 and SARS-CoV2 suggests these viruses have been circulating in *Rhinolophus* bat populations in China and Southeast Asia for thousands of years (Pekar et al., 2025) before emerging as a zoonotic disease. Currently, there are no well-documented cases of direct bat-to-human spillover infections of coronaviruses, and intermediate hosts are likely key to transmission to humans, thus understanding where they are at risk is the first potential step in the transmission chain (Ruiz-Aravena et al., 2022). In addition, human-mediated transport of wild and farmed animal trade likely accelerated the movement of viral lineages through intermediate hosts (Pekar et al., 2025; Zhao et al., 2024). Yet our understanding of these interacting elements of risk are limited, despite the critical role of bats as sources of a diverse variety of zoonoses.

A OneHealth approach emphasizes the interconnectedness of human, animal, and environmental health (Cunningham et al., 2017; Zinsstag et al., 2011). The use of this approach in detecting potential spillover risk in connection to ecological changes arising from human impacts on the environment has been increasing in recent decades (Eby et al., 2023; Jones et al., 2008; Rulli et al., 2017, 2021; Wilkinson et al., 2018). Regions such as Southeast and South Asia may be at particular risk due to the high rates of habitat loss coupled with high host diversity, and high human population densities (Allen et al., 2017; Jones et al., 2008; Morse et al., 2012; Olival et al., 2017; Rulli et al., 2021). Given the distribution of previous betacoronavirus pandemic outbreaks, it is a key region for further work to understand the risk of potential future spillover events. Furthermore, whilst studies have attempted to explore the risk of spillover from Southeast Asia, limited data on both habitat quality and species diversity may hamper the accuracy of such approaches (Sánchez et al., 2022). Planned infrastructure that may negatively impact wildlife in sensitive habitats are either being considered or already being constructed (Alamgir, Sloan, et al., 2019; Sloan et al., 2019), and these could create new interfaces for zoonotic spillover through further habitat fragmentation. Investigating locations of potential hotspots in Asia provides insights into the dynamics of virus emergence, allowing targeted action to counteract those risks.

Thus in this study, we assess the potential risk of betacoronavirus spillover arising from their most frequent reservoir host, the horseshoe bats (*Rhinolophus*), in South and Southeast Asia using a OneHealth approach. We explore potential pandemic spread scenarios incorporating planned infrastructure in the region. By understanding the landscape level risks of spillover, targeted approaches (i.e. conserving and reconnecting key habitats) can be applied in areas where risk is high, and activities such as mining and road-building be reduced, especially during time periods which may already be sensitive, such as during reproduction or climatic extremes.

## Materials and Methods

To locate areas with high potential for novel disease emergence arising from horseshoe bat richness and habitat fragmentation, we first generated maps that display both using the following methods. These approaches were based on Wilkinson et al. (2018) but adapted for the context of the South and Southeast Asian region, and for a more specific approach to coronaviruses.

### *Assessment of habitat fragmentation in Asia through analysis of remote sensing products*

Land-cover maps that exist typically overestimate the amount of forest in the region due to their overreliance on canopy cover as the sole metric to identify forest vs non-forest (e.g. Y. Liu et al., 2024; Sexton et al., 2013). This is especially obvious in Southeast Asia, where there is a significant coverage of rubber and palm oil plantations yet are not identified as separate land-cover classes in existing products (e.g. GLAD Land Cover) due to the challenge of distinguishing types of tree-cover using basic mapping approaches (Hughes, 2017). In addition, in drier climates in the region, natural forests may be both shorter and sparser (Murphy & Lugo, 1986), thus to accurately map forests and distinguish them from plantations, different thresholds must be set based on precipitation (Sexton et al., 2016). We therefore mapped remaining forest areas in tropical East Asia, which we defined as the region with tropical and subtropical climates spanning India in the northwest down to Papua New Guinea in the southeast (66° to 156° E longitude, -16° S to 36° N latitude; Figure S1) (Corlett, 2013, 2019). Using a combination of remotely sensed canopy height and modeled precipitation data following an approach used in B. V. Li et al. (2016) to accurately map forests across the same region. First, we obtained canopy height data from ETH Global Sentinel-2 10m Canopy Height data for 2020 covering the entire region. Data was downloaded through Google Earth Engine, after resampling from 10 m to 1 km (download date: 8 Aug 2023). We chose 1 km as the resolution as it corresponds closest to the highest available resolution for climate data (30", which is approx. 1 km at the equator). Annual precipitation data was obtained from CHELSA ver. 2.1 (download date: 6 Sep 2022).

Given the dependence of Rhinolophid bats on intact forest regions (Wilson & Mittermeier, 2019), we needed to delineate forest from non-forest in the region so that fragmentation could be assessed. Owing to the precipitation differences between dry deciduous and wetter forests, we separated the region between these two climate regions based on biomes delineated in the Ecoregions 2017 map (Dinerstein et al., 2017), and precipitation thresholds used in B. V. Li et al. (2016). We then applied the following criteria to classify forest pixels from the canopy height map:

1. Tropical areas with precipitation values ≥ 1800 mm/year and with canopy height ≥ 20 m were classified as forest;
2. Tropical areas with precipitation values < 1800 mm/year and with canopy height ≥ 25 m were classified as forest;
3. Temperate areas with precipitation values ≥ 600 mm/year and with canopy height ≥ 20 m were classified as forest

In order to mask out plantation areas that fall under the canopy height limits we set for each region, we used plantation map data obtained from the following sources. First, we primarily utilized data from the Spatial Database of Planted Trees (version 1.0, 2019) compiled by Global Forest Watch, which gathered and harmonized available land cover data (ca. 2003-2017) from relevant national government mapping agencies, non-governmental organizations, and independent researchers to categorize plantations of native or introduced species worldwide using supervised classification or manual delineation of satellite imagery (Harris et al., 2019, downloaded on 15 Aug 2023). We then supplemented this by generating a land-cover mask of all cropland and plantation areas in Thailand classified in Sritongchuay et al. (2019), and a study which classified rubber plantations in Yunnan Province in China for 2016 (Lapuz et al., 2021). All geoprocessing was performed in R version 4.0.5 using the raster ver.3.6.20 package.

Lastly, we conducted an area-adjusted pixel-based accuracy assessment on the forest map generated by creating a confusion matrix. From this matrix, we calculated the overall, user's, and producer's accuracy metrics for the forest and non-forest classes. To derive this, we randomly sampled points from the forest and non-forest classes on the map product. Each point was then visually assessed for its classification accuracy by comparing it with high-resolution (15 m) imagery obtained from ESRI World Imagery Wayback (version date: 2020-06-10) using ArcMap 10.4. The results were then compiled into a confusion matrix to quantify the classification performance. To assess the uncertainty associated with each estimation, we computed error-adjusted area estimations and confidence intervals for each class (Olofsson et al., 2013). The resulting forest map demonstrated an overall accuracy of 96.1%, with producer's accuracy for the classes ranging from 86.3 to 100%, and user's accuracy ranging from 78.0 to 98.0% (Table S1).

### ***Mapping Rhinolophid species richness in Asia***

We used Rhinolophid species richness as a metric for potential interactions between competent hosts in the forest fragments. We computed species richness by overlapping the suitable habitats for Rhinolophid bats, which were predicted using Maxent (Phillips et al., 2006), a widely used algorithm in modeling species distributions due to its generally good capability of predicting suitable habitats given a minimum number of species records (Pearson et al., 2006). Accurate maps based on recent data are essential for such work as alternate data sources (i.e. IUCN) are highly inaccurate (Hughes et al., 2021).

#### *Species points sources and processing*

Species occurrence points for bats from the Rhinolophidae family within the study region were obtained from the dataset used in Pekar et al. (2025), which is a combination of data from the Global Biodiversity Information Facility (GBIF.org, 2022, 2023), the DarkCideS database (Tanalgo et al., 2022), and field sampling. We also compiled additional points for Indonesia from multiple published datasets (see Supplementary S3). Taxonomic names were then updated using the Bats of the World database (batnames.org, accessed on 1 Oct 2023). A total of 7,885 data points across 59 Rhinolophid bat species were compiled.

To avoid spatial autocorrelation, a spatial thinning algorithm that retains one occurrence point per species for each grid cell at 30" resolution (0.008333°) was applied. Potentially invalid coordinates were also identified and removed using the clean_coordinates() function of the CoordinateCleaner package ver. 2.0.20 in R. Invalid points include those that might be outliers, within country capitals or country centroids, within research institutions and botanical gardens, or outside land masses. Outliers were identified using a quantile-based method, and were defined as points exceeding five times the interquartile range, ensuring that only the most extreme deviations were flagged. After cleaning, we retained species with more than 15 points for modeling, leaving the final number of species at 42.

### *Environmental predictors*

To predict the suitable habitat for each species, a combination of climatic, topographic, and biotic predictors important to bat ecology was selected based on previous regional bat distribution modeling studies (Hughes, 2017; Hughes et al., 2012; Pekar et al., 2025). For climate, we obtained bioclimatic variables from CHELSA version 2.1 (Karger et al., 2017), and a Global Aridity Index from the Global Aridity Index and Potential Evapo-Transpiration (ET0) Database v3 (Zomer et al., 2022). Rhinolophids are typically cave roosters (Wilson & Mittermeier, 2019), however, there is a lack of high-resolution global karst maps. We represented karst habitats by using a Depth to bedrock (R horizon) layer obtained from SoilGrids 2.0 (Hengl et al., 2017) similar to methods by Pekar et al. (2025), with the assumption that karst areas are in regions with shallow bedrock depths indicating possible exposed rock outcrops.

To represent vegetation cover, we used two layers. First, we obtained the ETH Global Canopy Height 2020 product, which estimated vegetation heights globally from remote sensing data (Lang et al., 2023). This is useful to differentiate between areas where vegetation is present, as Rhinolophids forage in areas with denser vegetation (Wilson & Mittermeier, 2019). Second, we used a Normalized Difference Vegetation Index (NDVI) layer obtained from the MOD13A2 V6.1 Terra product set released by MODIS (Didan, 2021) to represent vegetation productivity, which is a useful metric as it highlights resources available in the ecosystem (Hughes, 2017). Since this image satellite product is released every 16 days, we computed the mean NDVI for the year 2020 using all available imagery for that year. Both these vegetation layers were hosted, processed, and downloaded through Google Earth Engine Data Catalog (downloaded on 20 Sep 2023).

Foraging can take place above water and dense riparian vegetation can provide foraging areas for many species and is often maintained near waterways (Wilson & Mittermeier, 2019). We therefore produced a “distance from water bodies” layer, in which each grid cell’s distance to the nearest freshwater body was calculated using a freshwater bodies layer obtained from the MERIT Hydro

Global Hydrography dataset (Yamazaki et al., 2019, downloaded on 30 Aug 2023). We first processed the available freshwater bodies layer into binary (i.e. water body vs land), then computed the Euclidean distance of each land grid cell to the nearest water body cell. Processing for this was performed in ArcMap version 10.4.

All environmental predictors were then resampled to 30” resolution, stacked together, and checked for multicollinearity using Spearman’s rank correlation test. Predictors with Spearman’s r > 0.7 were removed from the model, and the following predictors were retained: mean annual temperature (Bio1), temperature annual range (Bio7), precipitation of wettest month (Bio13), precipitation seasonality (Bio15), aridity index, depth to bedrock, distance to water bodies, and vegetation height.

### *Maxent modeling*

Maxent was used to model suitable habitats of the Rhinolophid bat species. Prior to each species run, 10,000 background points were randomly generated from within a 500-km buffer region of the species’ occurrence points. The ENMEVal package ver. 2.0.4 was then used to test different combinations of feature classes (linear, quadratic, and hinge) and regularization multipliers (1 to 5), and the model with the lowest delta AIC score was selected as the most optimal and predicted to space to visualize suitable habitats (Kass et al., 2021). Model accuracy tests utilized the Area Under the Curve (AUC) and the True Skill Statistic (TSS; Allouche et al., 2006). All species models yielded good scores, with mean AUC score at 0.861, ranging from 0.780 to 0.951, while TSS scores were generally fair to good, with a mean of 0.534 and ranging from 0.278 to 0.875 (Table S3).

Each continuous species suitability map was then converted into a binary presence-and-absence map using the 10-percentile training threshold score for each species (Hughes et al., 2012). This threshold was chosen as it provides a more conservative and thus more targeted criterion during binary map conversion for species richness mapping (Radosavljevic & Anderson, 2014). As species distribution models only predict the distribution of the fundamental niche (i.e. the environmental space a species could occupy), other factors need to be encompassed in biogeographically complex regions, where the fundamental and realized niche may differ. In regions with complex geography and islands in particular, contemporary range will reflect not only current requirements, but also the barriers to species previous dispersal. Thus, after species ranges have been reclassified, masking was required to exclude biogeographic regions where the species does not occur.

To better reflect species biogeography, a biogeographic filter was created for each species. To create this filter, we split South and Southeast Asia into 19 biogeographic regions based on boundaries introduced in Corlett (2019), the Ecoregions 2017 map (Dinerstein et al., 2017), and major island groups (see Figure S1 for the map and list of regions). The continental region was separated on the basis of climate (i.e. subtropical vs. tropical vs. temperate) using the Ecoregions map, as well as known zoogeographic divisions, such as the Isthmus of Kra and the Kangar-Pattani Line (Hughes et al., 2011). Islands were also grouped on the basis of classic zoogeographic divisions, such as the Wallace's, Lydekker's, and Huxley's lines (Corlett, 2019), and island endemicity of our bat species obtained from Wilson & Mittermeier (2019). We then cross-referenced these regions with the IUCN mapped ranges of each species (IUCN, 2022) and the distribution points used for modeling. For each species, we listed all biogeographic regions with at least 30% of points, or 5 points (when total point number was below 20). For species with hundreds of points, we also looked at where remaining points fell to ensure no parts of the range were incorrectly excluded. The listed regions were then used to remove zones where the species was known not to be present (see Table S3 for the biogeographic zones listed for each species). Clipping was performed individually for each species binary map using ArcMap 10.4 to remove potentially suitable habitat (fundamental niche) outside the biogeographic range of the species. Lastly, the clipped rasters were summed to obtain species richness scores. All processing was performed using R ver. 4.0.5 unless otherwise specified.

### ***Mapping potential spillover risk hotspots***

To determine potential disease risk hotspots from the Rhinolophid bat populations in remaining habitat fragments, we used an approach from Wilkinson et al. (2018) called the estimated risk of infectious disease emergence, or eRIDE, index (Wilkinson et al., 2018). In this model, the potential disease risk is estimated based on the diversity of disease-causing species within a habitat patch. It directly correlates species diversity within habitat patches with exposure to human populations, quantified using the edges of the habitat fragments. The model assumes that the number of potential zoonotic agents within the habitat has a direct, linear relationship with fragment diversity, such that the total risk from novel pathogens is proportional to competent host diversity (i.e. host and pathogens) within each patch. In this case, we represented diversity using the viral populations hosted by the Rhinolophids in each patch. The model also assumes that the area where human populations come into contact with the habitat is represented by the perimeter of the patches. Thus, the more habitat fragment edges there are, the higher the risk becomes.

To compute eRIDE, we first identified the edge pixels of each fragment, then the focal sum of edge pixels within a 20 x 20 moving window was computed for each grid cell following Wilkinson et al. (2018). The eRIDE index of each cell was then computed as the product of its focal sum of edge pixels and bat species richness score. To identify which populations are at most risk from potential emerging infectious diseases, an estimated population at risk (PAR) index was computed as the product of each cell's eRIDE index and population density. The relative eRIDE and PAR percent scores for each country/territory were then computed as the sum of eRIDE or PAR for each country/territory divided by the total eRIDE or PAR value across the entire modeling region. To assess the categorical risk percentages for each location, the eRIDE and PAR (log) values were reclassified into five categories to represent the different levels of risk (low, moderately low, high, moderately high, highest risk). The thresholds were drawn from the respective geometric progression interval limits of the eRIDE and PAR (log) values across the whole region. Unconstrained individual population density data for 2020 for all Asian countries within our mapping domain was obtained from WorldPop (https://hub.worldpop.org/project/categories?id=18, downloaded on 11 July 2023).

***Pandemic risk mapping***

Potential pandemic hotspots were then identified using a network model of pandemic spread based on human density and connectivity (Wilkinson et al., 2018). First the PAR raster was aggregated from 1-km to 10-km resolution, then the pixel grid was converted into a network using 4-connectivity, with each grid cell representing nodes. Pandemic spread was assumed to likely travel faster between more densely populated places, thus the edge weights between adjacent pixels were computed as the inverse of the product of the population densities of each pixel.

The likelihood for pandemic spread between corresponding pixels $x$ and $y$ was then assessed by first determining the shortest distance $s(x, y)$ on the graph between the two nodes, which was computed using Djikstra's algorithm. The relative chance of pandemic spread $ps$ for any pixel $y$ was then computed as

$$ps(y) = \sum_{x} \mathrm{PAR}(x)s(x,y)$$

where the sum from all potential source pixels $x$ is obtained. The relative pandemic risk percent score and categorical risk percentages for each country/territory were then computed by applying the same formulae used to obtain relative and categorical eRIDE and PAR. The R packages raster ver. 3.6.20, tidygraph ver. 1.2.1 , and igraph ver. 1.2.6 were used for these analyses.

### *Increased fragmentation from existing and planned infrastructure scenario*

Existing and planned infrastructure are known to introduce further fragmentation to natural habitats (Laurance et al., 2009). To investigate the possible effect of adding infrastructure to spillover risk, the models were also run under a second scenario wherein existing and planned infrastructure are applied to mask the existing forest cover map. Existing infrastructure data (e.g. road and rail networks) for the entire region were obtained from OpenStreetMaps (downloaded on 29 March 2024). Planned infrastructure data were also downloaded from various sources for China, Indonesia, Malaysia, India, and Papua New Guinea (see Supplementary for complete list of sources). After processing these into rasters, the infrastructure layers were masked from the existing forest cover map using raster calculator. The models for eRIDE, PAR and pandemic spread were then run using the fragmented forest cover map. Changes in mean eRIDE, PAR index, and pandemic spread scores between baseline and new infrastructure scenarios within each country were tested for significance with Wilcoxon signed-rank tests using the stats package in R ver. 4.0.5 (R Core Team, 2021).

Fragmentation statistics for each country were computed for the two scenarios (baseline + new infrastructure) to determine fragment numbers and areas, as well as their respective geometric complexities, physical connectedness, and edge densities. The statistics measured include the: number of fragments, mean patch area, largest patch index, mean patch shape ratio, patch cohesion index, and edge density. These were all quantified using the landscapemetrics package ver. 1.5.4 in R.

## Results

### *Mapping potential spillover risk hotspots*

Based on relative estimated risk of disease emergence (eRIDE) indices computed across the whole region, the majority of the potential spillover risk hotspots are concentrated in China and Indochina (Myanmar, Laos, Vietnam, Cambodia and Thailand), which collectively account for almost threequarters (74.1%) of the total relative eRIDE (Figures 1a and 2a; Table S4). The highest risk areas are in the montane and forested regions of the countries of Indochina. Concerning individual country risks, Laos and Vietnam have over half of their land areas categorized as the highest eRIDE risk, at 56.5% and 51.3%, respectively (Figure 3; Table S5). For China, 12.0% of its modeled area is classified as the highest eRIDE risk, with most found in its southern areas adjacent to Indochina. India has 7.4% of its area classified as the highest eRIDE risk, and 42.5% of its land area is at moderately high eRIDE risk, particularly in its northeast region and the Western Ghats. In Bangladesh, 7.4% of its area is at highest eRIDE risk, while 70.9% of its land area is classified as moderately high risk. In the insular region, Indonesia has 10.8% of its land area categorized as moderately high eRIDE risk, concentrated in Sumatra and Kalimantan (Borneo), followed by Sulawesi and Papua (Figure 3; Table S5).

The spatial distribution of population-at-risk (PAR) indices resembles that of eRIDE, suggesting that the populations at risk are near the spillover risk hotspots (Figure 1). These hotspots are spatially concentrated in Nepal, northeast India, western Myanmar, Vietnam, and southern China (Figure 1b). Countries with the highest relative PAR scores (computed for across the entire region) are those with the largest populations. China registered the highest relative PAR score (29.6%), followed by India (21.2%), and Indonesia (13.5%) (Figure 2b; Table S4). Concerning individual country risks, Singapore recorded 86.1% of its population at the highest risk, followed by Sri Lanka (82.2%), Vietnam (76.0%), and Bangladesh (75.1%) (Figure 3; Table S6). Notably, India and China registered 46.5% and 36.5% of their large populations at the highest risk, respectively.

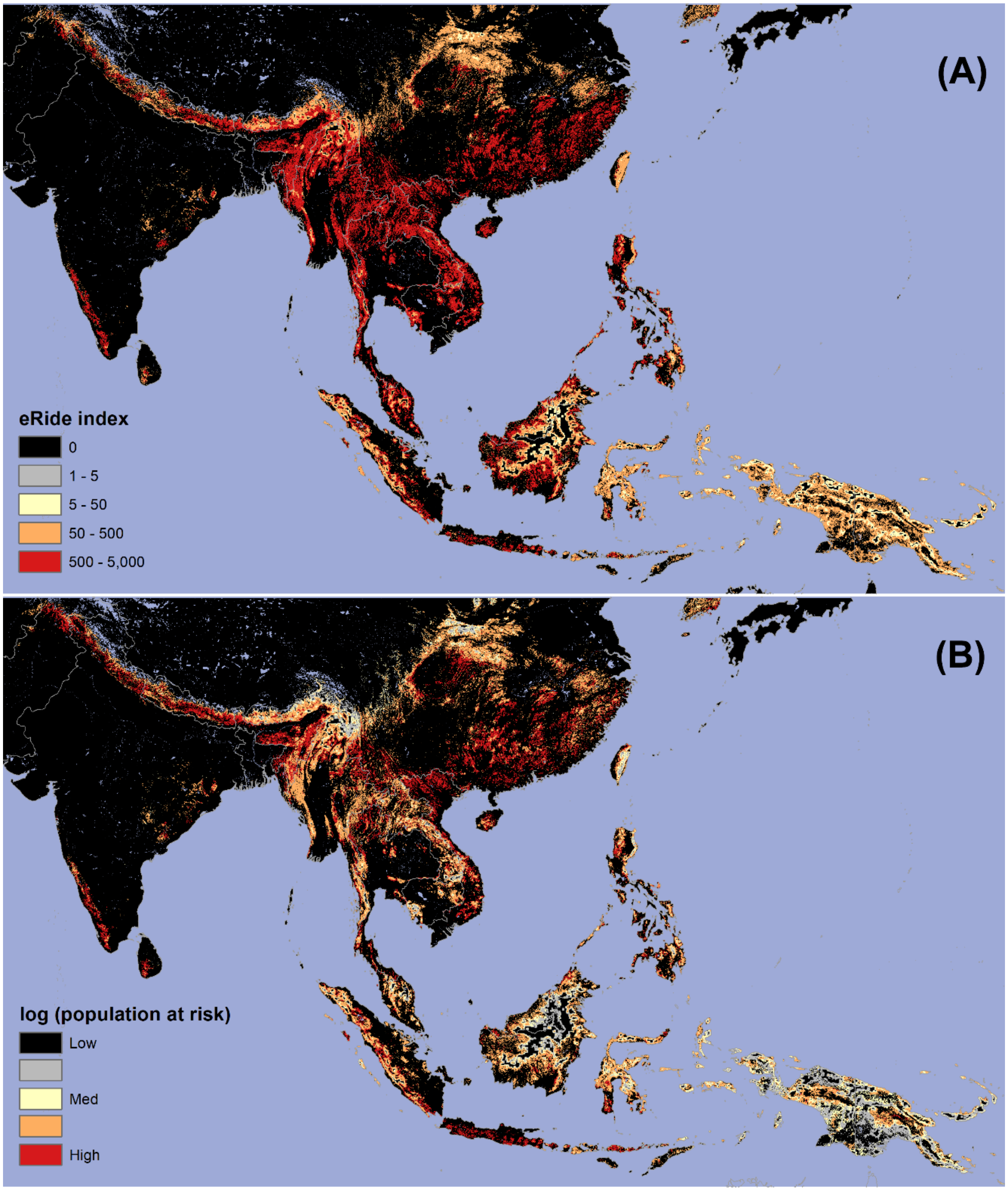

**Figure 1. Zoonotic Risk Hotspots in Rhinolophid Bats of Tropical East Asia.** Maps of tropical East Asia showing risk hotspots from zoonotic agents in Rhinolophid bats of tropical East Asia. Depicted here are (**A**) eRIDE and (**B**) Population at risk (PAR, log values displayed for clarity) scores. For both maps, discrete color bands follow a geometric scale.

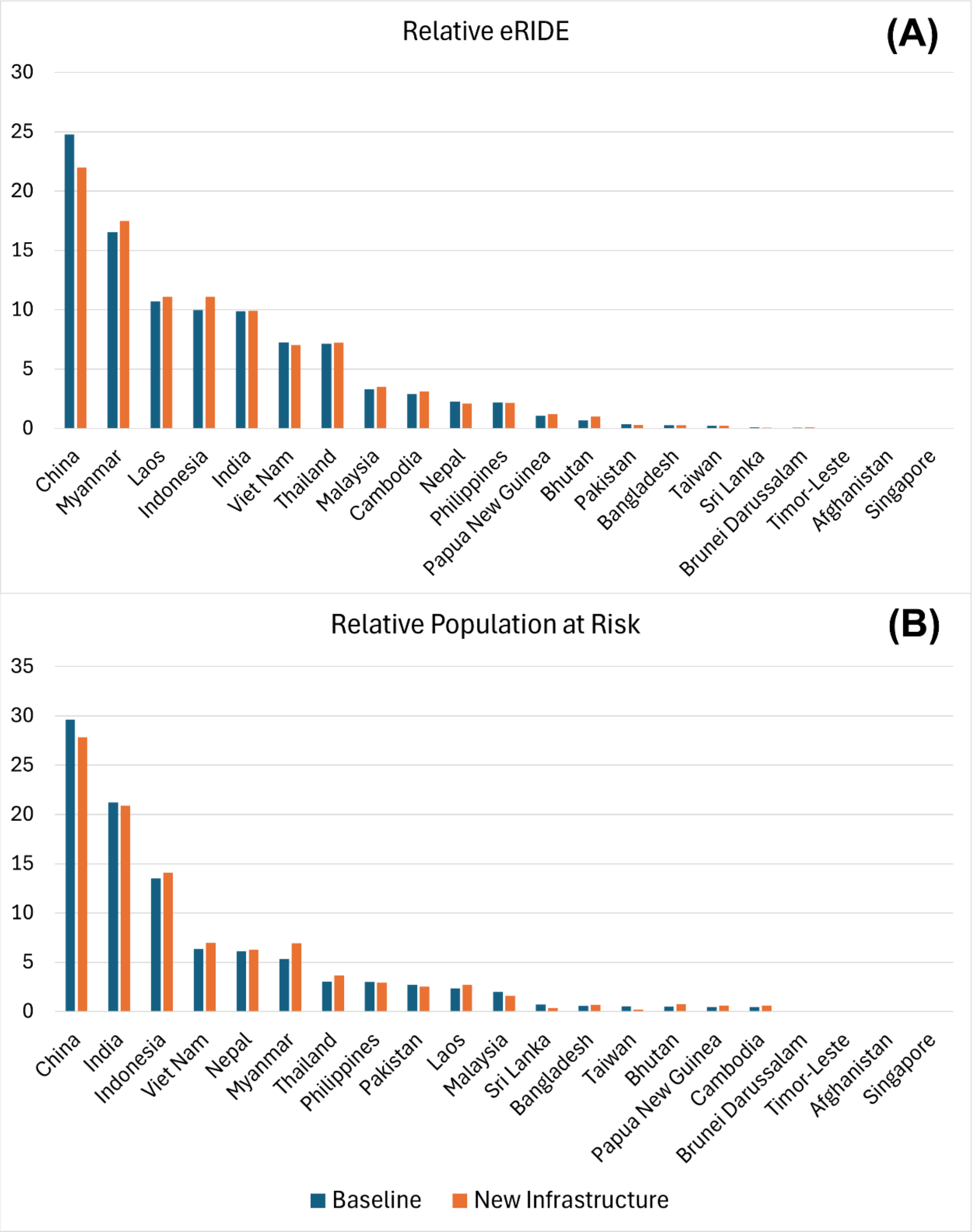

**Figure 2. Index rankings per country under baseline (blue) and new infrastructure (orange) scenarios.** Numbers displayed are the sums of all (**A**) eRIDE index and (**B**) PAR values within each country's boundaries as shown in Figure 1. Decreases are due to losses of small fragments due to the resolution of analysis.

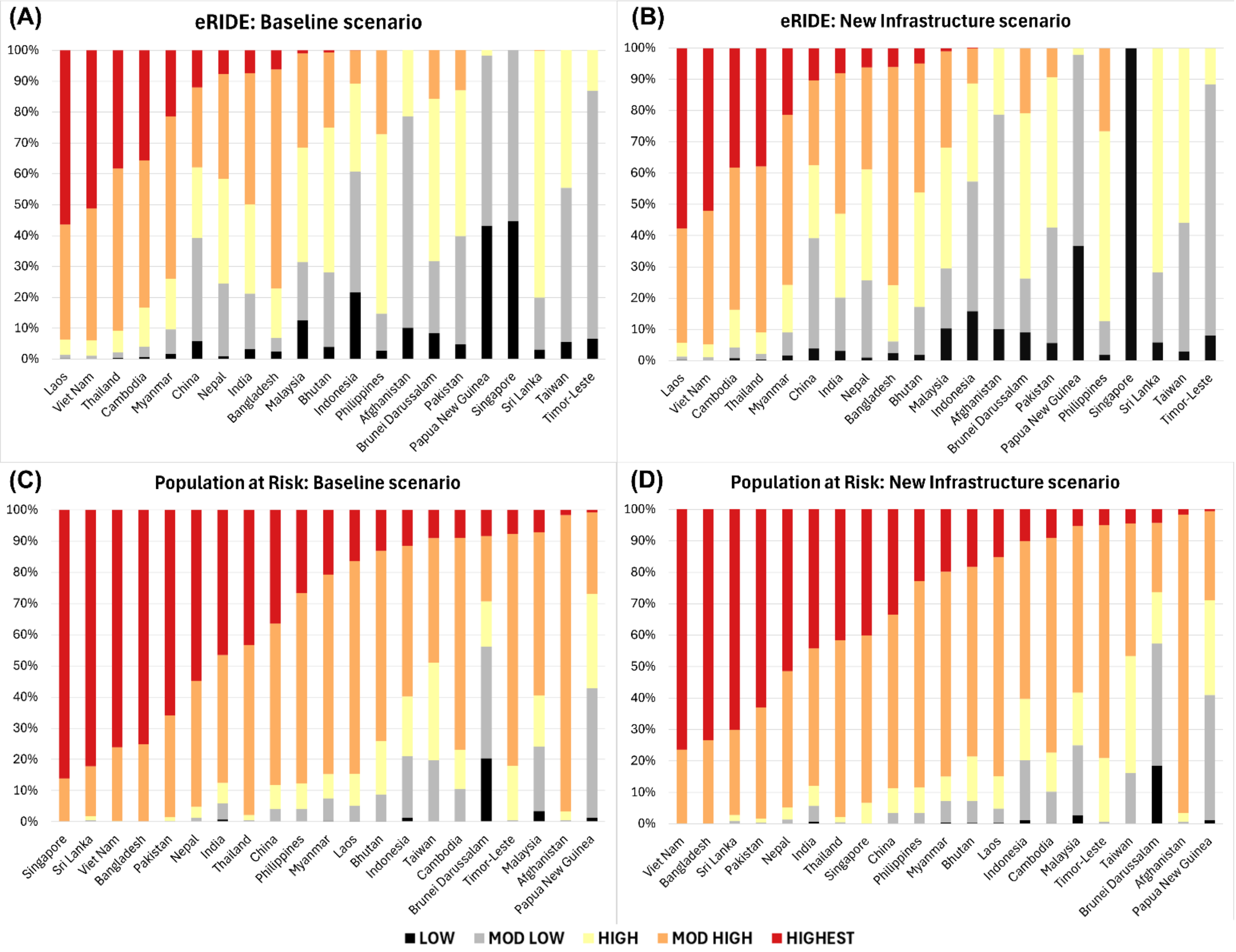

**Figure 3. Country Risk Class Distributions: Baseline vs. New Infrastructure Scenarios.** Stacked bar plots illustrating the distribution of risk classes per country in tropical East Asia, categorized by eRIDE and Population at Risk scores for baseline (**A, C**) and new infrastructure (**B, D**) scenarios. The color scheme denotes varying risk levels, with red indicating the highest risk category and black representing the lowest risk category.

***Pandemic risk mapping***

Pandemic spread modeling showed that the countries with highest pandemic risk are China, Bangladesh, and India (Figure 4). Specific areas in South Asia where pandemic risk is highest are in Bangladesh, India's north, northeast, and southern regions, and eastern Pakistan (Figure 4a). India and China have the highest relative pandemic risk scores, respectively garnering 47% and 30% out of a total possible 100% computed for the entire region (Figure 4b; Table S4). They are followed to a lesser extent by Bangladesh (5.5%) and Pakistan (5.4%), although they are notably smaller in terms of size than the previous two countries. In China, the surrounding coastal areas of the large Chinese cities of the Greater Bay Area (Guangzhou, Shenzhen, Hong Kong and Macau) and Shanghai are the highest pandemic risk areas. Pockets of high-risk areas also exist in cities in Myanmar, Thailand, Indonesia, Vietnam, Malaysia, and the Philippines.

Among all countries, Bangladesh recorded the largest percentages of highest (0.2%), moderately high (30.4%), and moderate (26.1%) at-risk areas for pandemic spread (Table S7). India follows, with 7.5% of its land area classified at moderate or moderately high risk for pandemic spread. Pakistan and China are next with 3.0% of their respective country areas recorded to be at high risk of pandemic spread. These results highlight that countries with higher population densities and are closest to high eRIDE and PAR areas are at most risk of a possible pandemic.

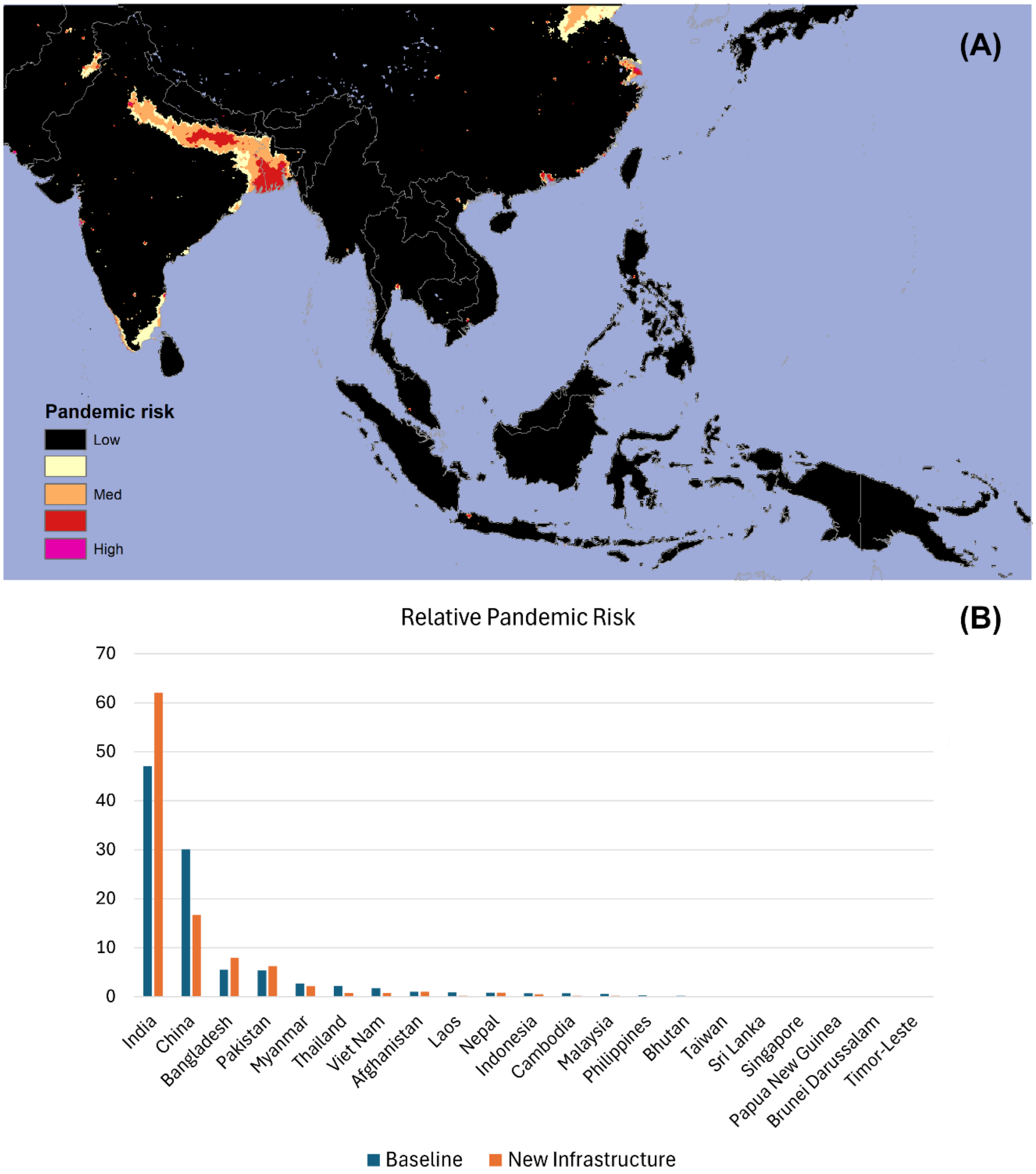

**Figure 4. Simulated Pandemic Risk from Zoonotic Agents in Rhinolophid Bats of Tropical East Asia.** Depicted here are the (**A**) map of pandemic risk areas under baseline scenario (discrete color bands in the legend follow an exponential scale), and (**B**) index rankings per country under baseline (blue) and new infrastructure (orange) scenarios, derived from the sum of pandemic risk scores within each country's borders.

### ***Increased fragmentation from existing and planned infrastructure scenario***

Introducing road networks over the habitat increased fragmentation generally across all countries when compared to baseline scenario values (Table S2). All countries/territories experienced a decrease in mean patch area and patch cohesion index values compared to baseline values, and all except Bangladesh had a decline in their largest patch index values. China ranked first in terms of highest habitat fragmentation across first (baseline) and second (baseline + new infrastructure) scenarios. The most dramatic change is from Papua New Guinea, which experienced a +335.1% increase in number of patches concurrently with a -83.1% decrease in mean patch area and a -48.9% decline in its largest patch index value.

The relative eRIDE index rankings in the second scenario remain mostly unchanged when compared to the baseline scenario, with only minor redistributions in values between countries (Figure 2a). However, there were significant ($p<0.005$) increases in mean eRIDE scores observed for Bhutan, Cambodia, Indonesia, and Papua New Guinea (Table S8). Hotspots in specific regions were further revealed by risk categorization and grid-wise spatial comparisons between the first and second scenarios (Figure 5; Table 1). In mainland Asia, the largest increases in combined high-risk areas were observed in Bhutan (+21.2%), followed by northeast India (+3.1%), western Myanmar (+1.8%) and Vietnam (+0.8%). In insular Asia, Taiwan observed a +11.4% increase in moderate risk areas, while Indonesia had a +5.8% increase in combined high-risk areas distributed among its islands of Kalimantan (Borneo), Sumatra, and Sulawesi. In Papua New Guinea, a +6.6% increase was observed. These hotspots occur in forest areas where existing and planned road networks are located (Figure 6).

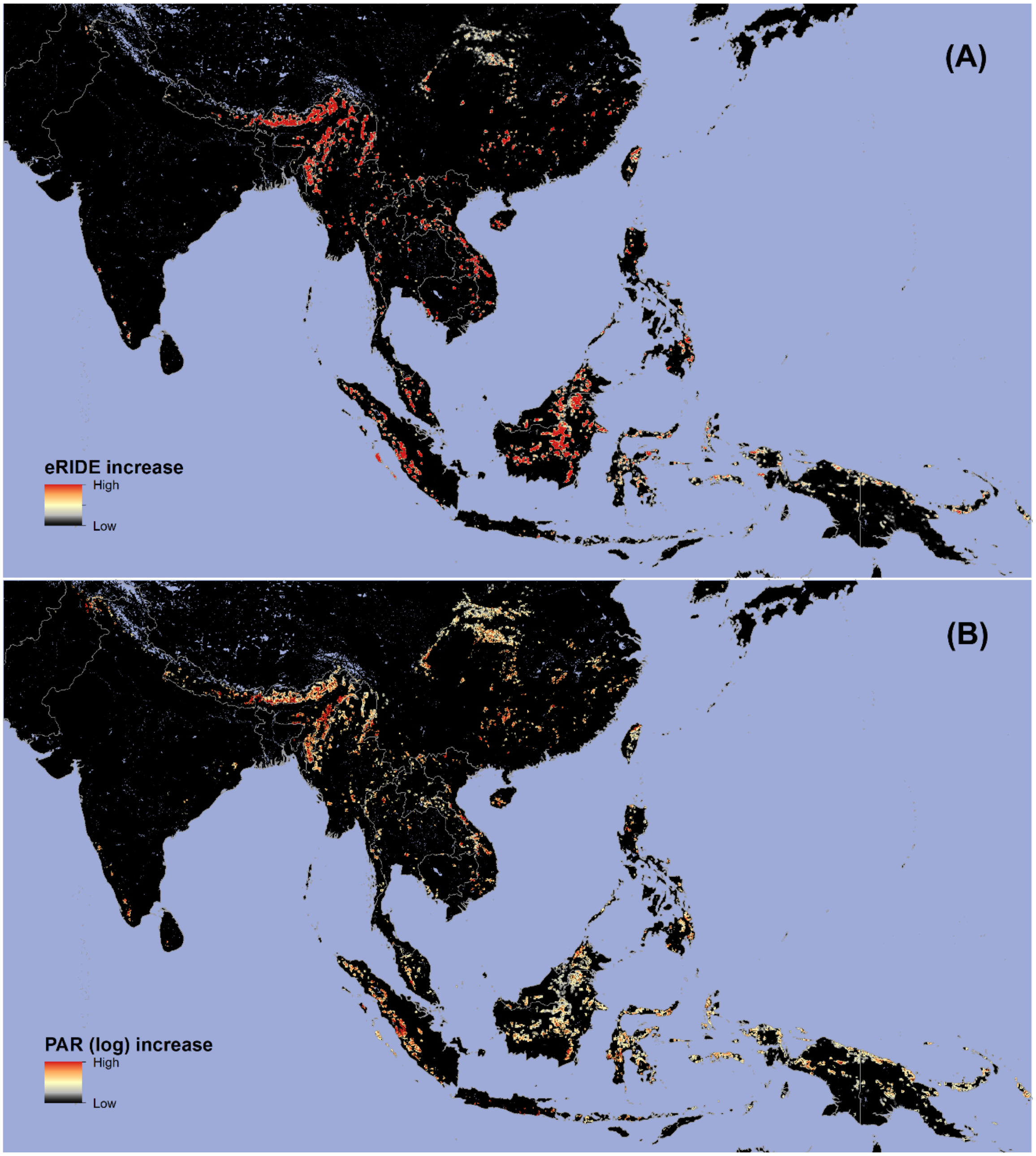

**Figure 5. Changes in eRIDE and PAR Scores in Tropical East Asia Under New Infrastructure Scenario.** Maps depicting increases in (**A**) eRIDE and (**B**) PAR (log) scores under the new infrastructure (NI) scenario. Change maps were computed by subtracting the values of the NI scenario from the baseline. Colors transition from black to red to indicate stronger increases.

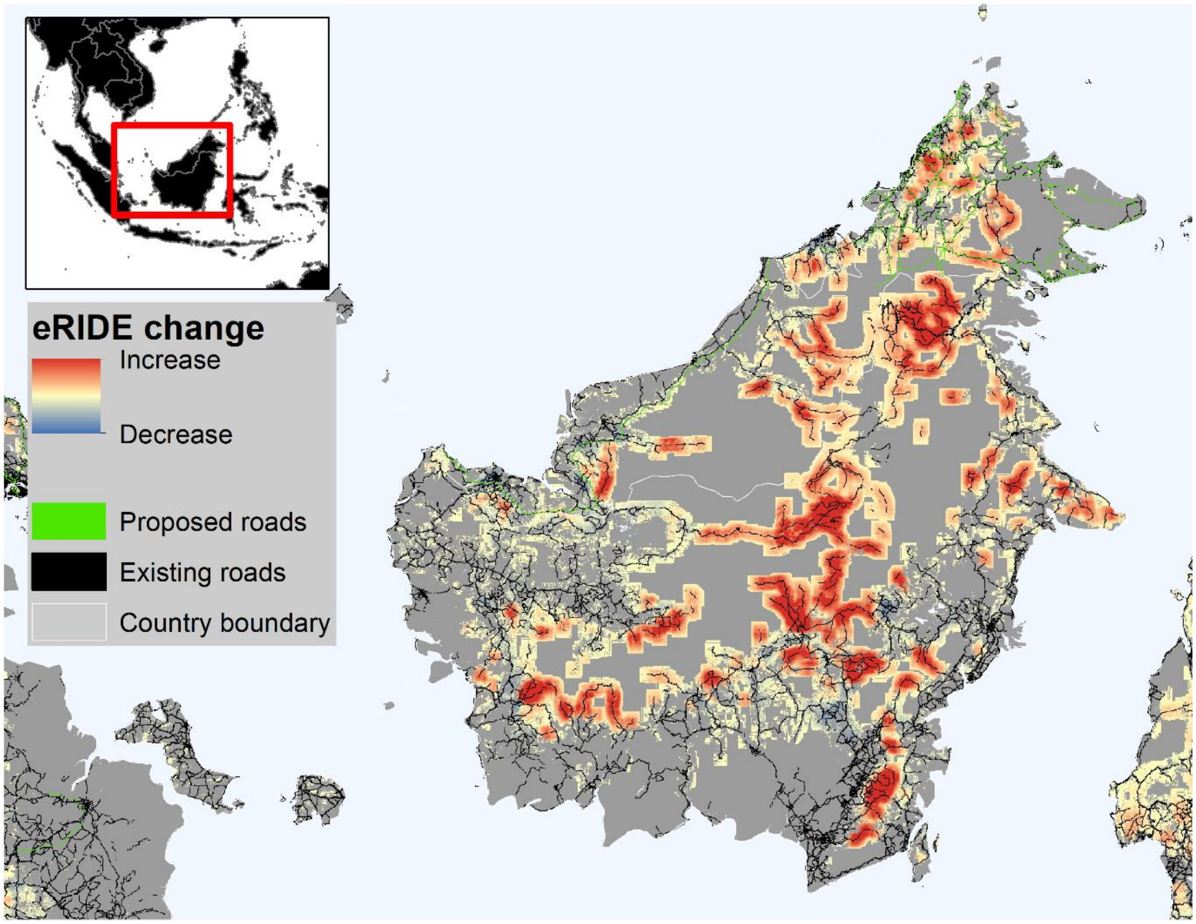

**Figure 6. Changes in eRIDE in Borneo Island.** Enlarged map of Borneo Island depicting changes in eRIDE values under the new infrastructure scenario. Increased eRIDE values are depicted here in yellows and reds, particularly along road networks (black and neon green lines), illustrating the potential impacts of infrastructure on tropical regions with intact forest habitats.

China, India, and Indonesia still maintained the highest relative PAR scores under the second scenario (Table S4). The relative PAR scores for Vietnam (+0.6%), Myanmar (+1.6%), Thailand (+0.7%), Nepal (+0.2%), Laos (+0.4%), Bhutan (+0.3%), Bangladesh (+0.1%), and Papua New Guinea (+0.1%) also increased under the second scenario, although these changes barely affected the rankings (Figure 2b; Table S4). Risk categorization and spatial comparison between the scenarios revealed strong increases in high PAR areas for Sri Lanka (+11.1%), Taiwan (+8.1%) and Bhutan (+5.1%). The hotspots observed in the spatial comparisons were supported by the risk categorization (Table 1), particularly along northeast India (+2.6%), western Myanmar (+1.1%), central China (+3.6%), and Indonesia (+2.2%) (Figure 5b). Central Vietnam (+0.3%), peninsular Malaysia (+2.7%), Papua New Guinea (+2.3%), and southern Philippines (+4.5%) also registered moderate upward shifts.

The changes in PAR distributions intensified the relative pandemic risk values for the South Asian countries of India, Bangladesh, and Pakistan, as these countries registered significant ($p<0.005$) increases in their mean and relative pandemic risk scores (Figure 4; Table S4; Table S8). India had a dramatic increase of +15%. China remained the second highest country at risk due to its huge land area. Spatially, the risk patterns in the map are similar to the baseline simulation, with the majority of the highest risk areas still concentrated in the north-northeast India-Bangladesh corridor, as well as in the greater Guangzhou and Shanghai areas of China (Supplementary Figure S3). Relative to their respective land areas, Bangladesh registered the highest increase in pandemic risk areas (+9.8%), followed by (+1.8%), Pakistan (+1.3%), and Nepal (+0.2%) (Table 3).

## Discussion

### *A OneHealth approach to spillover surveillance*

There is a growing realization of the importance of integrating OneHealth perspectives into landscape management (Meyer et al., 2024; Muylaert et al., 2023). New approaches which combine landscape parameters with the distribution of competent hosts can predict patterns of spillover risk. Here we demonstrate the use of a OneHealth approach to predict potential spillover and pandemic risk hotspots in tropical East Asia. Using the estimated risk of infectious disease emergence (eRIDE) and population-at-risk (PAR) indices, which are models that utilize the relationships between species richness, habitat fragmentation metrics and human population density in determining spillover hotspots, we found that Indochina and southern China are of highest risk for spillover in Asia due to their high Rhinolophid species richness alongside dense human populations. A subsequent pandemic spread network model we applied also revealed that South Asia, specifically Bangladesh and northeast India, has the highest risk for a pandemic once spillover occurs in the hotspots, or if infected wildlife is potentially transported to urban centers.

Using an approach that incorporates the biological, environmental, and human aspects of health is useful in establishing baseline knowledge on spillover potential hotspots, including distribution of competent hosts and natural interfaces for spillover without initially needing immunological or viral data. Spillovers into human populations require a virus to spill into humans (often via an intermediate host) and then spread from human-to-human, which is not only rare, but also is more likely to happen in areas where human populations have not acquired immunity (Epstein et al., 2020). Rates of SARS-related coronaviruses from

Southeast Asian bats have been previously examined, but such studies may not accurately capture species ranges or the landscape dynamics that should be considered (Sánchez et al., 2022). Localized spillovers potentially remain underreported due to factors such as the lack of human-to-human transmission, the presence of acquired immunity preventing case mortalities, or inadequate reporting and identification in rural areas (Wang & Anderson, 2019). This suggests that whilst existing studies on viral surveillance provide valuable insights, they may overlook potential spillover hotspots, as the bias in the data in these studies may not adequately represent where spillover events are likely to occur in the landscape. Thus, integrating species ecology and limitations into analysis is essential, as the ecology of vectors has profound implications for transmission pathways, or understanding how to manage and mitigate risk.

### *Direct use of competent hosts in modeling risk*

Understanding potential spillover locations in the landscape requires identifying interfaces between humans and competent hosts. Competent hosts such as rodents and birds act as reservoirs for pathogenic viruses and bacteria (Bordes et al., 2017; Kane et al., 2024; Neves et al., 2018). By focusing on the distribution of these competent hosts, we can pinpoint natural interfaces for spillover events. Rhinolophid bats, which are known reservoirs of coronaviruses related to SARS and COVID-19 (W. Li et al., 2005; Pekar et al., 2025; Zhou et al., 2021), were directly studied to look at their potential for zoonoses. Utilizing the eRIDE and PAR models, which are most effective in systems with defined edges such as forests (Wilkinson et al., 2018), we identified spillover hotspots where bat movement between forest fragments could lead to pathogen transmission to humans and other hosts.

The eRIDE (potential pathogen emergence) hotspots identified coincided with forested regions of high Rhinolophid species richness (Supplementary Figure S2) but also in areas with high fragmentation, aligning with previous studies mapping potential coronavirus host bat species in Southeast Asia (Muylaert et al., 2022; Sánchez et al., 2022), particularly in Southern China, eastern Myanmar, and northern Laos. Recent investigations have uncovered the presence of SARS-CoV-like coronaviruses in bats in these regions despite limited sampling (Sánchez et al., 2022; Zhou et al., 2020, 2021). The diverse Rhinolophid bat communities in these regions can facilitate interactions between species, potentially leading to the mixing of potential zoonotic viruses.  Given that individual bats can host multiple viruses concurrently and tend to roost in densely populated fragmented habitats (Latinne et al., 2024; Zhou et al., 2021), the risk of pathogen spillover to humans in these habitat edges are higher. However, further work is needed to better describe Rhinolophid species and their interactions across the region (Chornelia et al., 2022) to facilitate a clearer understanding of viral dynamics, especially in how they vary across space and time.

*Impact of population density in pandemic risk*

The high similarity between the high eRIDE and PAR hotspots demonstrates that populations in Asia are at proximity to high spillover risk exposure areas. This is in contrast with the original application of these models in Africa, which found that potential risk transmission areas (i.e. high eRIDE risk) are sparsely populated and distant from the high PAR areas, and thus highlighted the role of population centers in disease emergence and transmission (Wilkinson et al., 2018). Our use of the models in Asia provides a more localized context wherein the proximity of nearby population centers could mean that zoonotic diseases from Rhinolophids could possibly be transmitted from animal to people more rapidly. In Asia, there is steadily increasing population density in peri-urban areas where there are potential interactions between wildlife and domesticated animals and humans, therefore higher proximity between zoonotic systems (Alirol et al., 2011; Hassell et al., 2017; Vanwambeke et al., 2019). Migration of human populations or changing patterns of tourism can increase exposure of naïve human populations to pathogens, thus increasing chances for outbreak when spillover happens (Cascio et al., 2011; T. Wu et al., 2017). Furthermore, migrating human populations may drive wildlife trade, wildlife farming, and their associated risks of spillover (Goldstein et al., 2022; Zhu & Zhu, 2020).

In terms of pandemic spread post-spillover event, our network model results showed that the high-risk areas were aggregated around dense population centers, notably in eastern India and Bangladesh as well as the megacities in eastern (Shanghai) and southern (Guangdong) China. These further demonstrate the effect of population density and land transport networks in moving potentially zoonotic viruses from their sources as evidenced in the PAR hotspots, and akin to what has been observed in previous cases of zoonoses, such as for Marburg and Ebola in the African continent (Mbonye et al., 2012; Rulli et al., 2017; Wilkinson et al., 2018). For instance, the index case for the 2013 Ebola epidemic in West Africa was traced to a Guinean village already heavily modified by human activity, in contrast to earlier cases where initial spillover likely occurred in villages closer to core forest areas (Marí Saéz et al., 2015; Rulli et al., 2017). Similarly, the index case for a Marburg virus outbreak in 2012 in Uganda was attributed to a traveler who got infected upon returning from his hometown (Mbonye et al., 2012). eRIDE predictions are consistent with risk emergence hotspots with high spatial resolution for *Ebolavirus* in Africa, a region where spillover data for Ebola virus disease is more widely tracked (Wilkinson et al., 2018). This approach therefore provides a non-invasive and cost-efficient strategy to localize potential risk areas without resorting to lethal methods for pathogen detection in bats, a practice documented in previous studies (e.g. Dzikwi et al., 2010; Sasaki et al., 2012), and can be cross validated by field surveys, such as the use of tarpaulins to collect urine for testing in saves. The outcomes derived from our models can provide guidance for governmental organizations in the designated high-risk regions to formulate contingency measures in anticipation of potential recurrence of a coronavirus spillover event.

*Fragmentation increases spillover risk in Asia*

Increasing habitat fragmentation resulting from the development of road networks may increase spillover risks, as increased eRIDE and PAR scores were observed in forested areas of western Myanmar, Bhutan, Borneo, and New Guinea. High PAR scores in the northern portions of South Asia have particularly led to the high pandemic spread risk score of Bangladesh and India, given especially the high population density and connectivity of this area to both South and mainland Southeast Asia, where eRIDE hotspots are concentrated. Additionally, planned infrastructure in Bornean landscapes will fragment important landscapes and drive biodiversity declines (Alamgir, Campbell, et al., 2019; Sloan et al., 2019). The same patterns of decline are likely to be observed in Indonesian New Guinea, as development along the Trans-Papuan highway has already led to significant loss in forest areas, and subsequently, this region's remarkable biodiversity (Gaveau et al., 2021). Similar projections of loss were also found for Papua New Guinea stemming from the government's "Connect PNG 2020-2040" project, whose planned road networks traverse multiple critical biodiversity habitats and open up forests for rapid expansion of logging, mining, and plantation activities (Alamgir, Sloan, et al., 2019).

The loss of biodiversity from habitat fragmentation increases spillover risk, as decreasing habitat quality reduces species diversity and abundance, reversing the "dilution effect" that normally helps lower pathogen prevalence due to a higher number of susceptible host species (Keesing et al., 2006; Keesing & Ostfeld, 2021). This was demonstrated in a study on CoV prevalence in bat communities in Ghana, where higher CoV prevalence and infection likelihood were observed in communities with lower bat diversity resulting from disturbances in habitat structure, thus leading to increased exposure to diseases by humans or greater interface with potential generalist intermediate hosts (Meyer et al., 2024). This highlights the buffering effect of biodiversity, and proactive strategies to enhance habitat connectivity and extent must be implemented to maintain healthy wildlife populations and reduce the interfaces where spillover is most probable.

Pathogen spillover increases during land conversion, particularly at intermediate levels of habitat loss where there is a large population of competent hosts still present in core habitats alongside susceptible hosts in human-modified landscapes (Faust et al., 2018; Gibb et al., 2020). Intermediately fragmented areas contain higher numbers of competent hosts in the core habitats, leaving naïve populations exposed in the surrounding matrix (Goldberg et al., 2008; Walsh, 2013; Wilk-da-Silva et al., 2023). This scenario is evident in cases such as in Henipavirus outbreaks in Bangladesh and rabies incidences in cattle associated with deforestation and habitat fragmentation (Andrade et al., 2016; Epstein et al., 2020). This may be linked to high stress to wildlife populations as well as large interfaces between wildlife and humans, livestock or domestic animals. Therefore, addressing habitat fragmentation is crucial in regions like southwest China, known for high rates of coronavirus transmission risk and being a major habitat for bats identified as betacoronavirus reservoirs (Fan et al., 2019; Pekar et al., 2025), but where fragmentation of natural habitats is also high (Lapuz et al., 2021; J. Liu et al., 2019).

Maintaining the core of habitats is essential for reducing habitat perimeters and minimizing contact zones where disease transmissions can occur (Wilkinson et al., 2018). The growth of infrastructure and increasing edge density in these habitats will make these areas higher-risk zones for pandemic spread in neighboring regions. Preventing further fragmentation is crucial, as there are already observed shifts in global bat diversity due to climate change (Beyer et al., 2021), which could exacerbate viral transmission risk between species (Carlson et al., 2022). Furthermore, spillover risk is not static over time. Factors such as increasing extreme climate events, interacting with habitat loss and agricultural expansion, play a direct role in driving spillover events, like those seen in the case of Hendra (Becker et al., 2023) and Nipah viruses (Cimaroli, 2024; Martin et al., 2018). Recognizing and understanding these interconnected threats can facilitate actions to break the transmission chains (Eby et al., 2020). Maintaining intact habitats, especially in the face of multiple other stressors is clearly critical not only for maintaining biodiversity, but also to reduce the risk of spillover, and thus should be seen as a component of maintaining ecological security.

### *Summary, limitations, and next steps*

Our work demonstrates an application of the OneHealth paradigm in addressing the threat of zoonotic spillover events from Rhinolophid bats in Asia, a region identified as the epicenter of recent epidemics and pandemics, including the devastating global COVID-19 pandemic which has already claimed over 7 million lives worldwide (World Health Organization, 2025). By identifying hotspots and advocating for urgent implementation of mitigation measures, we emphasize the importance of a multidisciplinary and collaborative approach in safeguarding public health and ecosystem integrity. Our results suggest that there are high spillover risk hotspots concentrated in Indochina and Southern China, which could then propagate across the region, particularly affecting the densely populated areas of northern India and Bangladesh.

Given that Rhinolophid bats prefer to roost in forest habitats, the eRIDE model, which assumes linear, uniform contact occurs at the edge of habitats, is appropriate. However, further research would help add nuance into how this relationship changes across space and time. The eRIDE model also presents limitations as it does not incorporate abundance. However, some elements, such as estimating abundance are not possible without additional data. Whilst Maxent probabilistic layers are sometimes used as a proxy for population, there are various assumptions involved, so it is likely that given limited dispersal capacity and habitat requirements of many Rhinolophids, there is a correlation between diversity and population. However, too little data exists to explicitly include population in this work (which may also change over time), but future studies can benefit from including abundance data when available.

Whilst model validation is challenging due to the underreporting of coronavirus spillover events in Asia (Wang & Anderson, 2019) and the probable high levels of immunity in rural human populations, understanding the potential for spillover provides the means for targeting actions to stem the potential for spillover risk. Our findings can offer guidance for targeted resource allocation in epidemiological surveillance of identified high-risk areas, presenting a collaborative approach to result validation and mitigation of impacts on bat populations and viral disease transmission risks. Furthermore, frameworks like these can reflect the diverse species ecophysiology across different taxa, exemplified here by the Rhinolophids, and can also evaluate seasonal fluctuations (Eby et al., 2023). This proactive and cost-effective strategy can address potential sources of the issue preemptively, rather than reactively responding to spillover events.

The methods presented in our study can be further enhanced by including seasonality factors, especially when linked to seasonal biological phenomena such as pregnancy and hibernation, as well as land use and anthropogenic climate change dynamics in the models. While we ensured the temporal alignment of the data used in modeling as much as possible, more work will be needed to explore changes over time (e.g. seasonal changes). Additionally, the inclusion of wildlife farm locations, particularly those housing known competent hosts like small carnivores, can enhance the model's effectiveness. Wildlife farming for fur or consumption presents a major risk for potential zoonotic spillovers (Peacock & Barclay, 2023; Zhao et al., 2024). These activities may be linked to the trade and trafficking of wildlife, as evidenced by instances where raccoon dogs in Chinese markets are sometimes native (possibly wild-caught) rather than farmed species (Crits-Christoph et al., 2024). Future models of spillover risk that can incorporate these farms, and potential transmission chains would enhance planning and implementation of rigorous biosecurity monitoring measures. Given calls for further exploration of viruses with zoonotic potential, further work is clearly needed to understand the mechanistic basis of spillover, and how it varies over space and time (Carlson et al., 2025).

With regards to the pandemic spread network model, previous work using the same model captured the distribution of Ebola outbreaks in West Africa, highlighting the international nature of disease spread and mitigation (Wilkinson et al. 2018). In Asia, this might be most applicable to continental regions, given countries share adjacent borders and have higher cross-border traffic. The model's direct distance-based nature could be the reason why more high-risk hotspots for pandemic spread were observed in the mainland, and less so in the islands. Whilst transport links are not explicitly included in the spread model, their presence are captured by human population density data to some degree, as presence of humans implies the presence of transport networks. It is also important to note that naïve populations may also be susceptible, and thus insular regions may have higher susceptibility when infections arrive, and air and seaports have their own associated risks. Future work can more directly incorporate transport networks (especially air and seaports) in modeling disease spread from spillover risk hotspots to improve realism and better reflect the heterogenous nature of connectivity across borders.

Nevertheless, our work lays a foundation for future research that explores the integration of additional factors for enhanced predictive capabilities and tailored surveillance efforts in vulnerable regions. Furthermore, we highlight the vulnerability of human population centers across the region and the heightened risk accompanying infrastructural growth. Notably, SARS-CoV2 is only one of several betacoronaviruses which has emerged from Southeast Asia, with Rhinolophid bats as a probable source. Preventing future epidemics necessitates interventions to mitigate this risk, integrate OneHealth approaches into planning, and reduce interactions between stressed wildlife and potential intermediate species of bat-borne pathogens.

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Conceptualization: RSL, ACH
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Formal analysis: RSL
Data curation: RSL, ACH, AC
Visualization: RSL
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**Data availability:** The R codes used in modeling are posted at https://github.com/sedrickel/horseshoe_bats_spillover.