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Mapping Risk of Nipah Virus Transmission from Bats to Humans in Thailand

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Abstract

Nipah virus (NiV) is a zoonotic virus that can pose a serious threat to human and livestock health. Old-world fruit bats (*Pteropus spp.*) are the natural reservoir hosts for NiV, and *Pteropus lylei*, Lyle's flying fox, is an important host of NiV in mainland Southeast Asia. NiV can be transmitted from bats to humans directly via bat-contaminated foods (i.e., date palm sap or fruit) or indirectly via livestock or other intermediate animal hosts. Here we construct risk maps for NiV spillover and transmission by combining ecological niche models for the *P. lylei* bat reservoir with other spatial data related to direct or indirect NiV transmission (livestock density, foodborne sources including fruit production, and human population). We predict the current and future (2050 and 2070) distribution of *P. lylei* across Thailand, Cambodia, and Vietnam. Our best-fit model predicted that central and western regions of Thailand and small areas in Cambodia are currently the most suitable habitats for *P. lylei*. However, due to climate change, the species range is predicted to expand to include lower northern, northeastern, eastern, and upper southern

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Thailand and almost all of Cambodia and lower southern Vietnam. This expansion will create additional risk areas for human infection from *P. lylei* in Thailand. Our combined predictive risk maps showed that central Thailand, inhabited by 2.3 million people, is considered highly suitable for the zoonotic transmission of NiV from *P. lylei*. These current and future NiV transmission risk maps can be used to prioritize sites for active virus surveillance and developing awareness and prevention programs to reduce the risk of NiV spillover and spread in Thailand.

Keywords

Climate change; Ecological niche model; Emerging infectious disease; Lyle's flying fox; *Pteropus lylei*

Introduction

Nipah virus (NiV) encephalitis is an emerging infectious disease that is a significant threat to public health in the Asia–Pacific region, including countries where the virus has already emerged and infected people: Bangladesh, India, Malaysia, the Philippines, and Singapore (Ang et al., 2018; Ambat et al., 2019; Sharma et al., 2019; Hauser et al., 2021). NiV diversity in bats and human is split between two genetic clades the Malaysia (NiV-MY) and Bangladesh (NiV-BD) strains (Rota and Lo 2012), and these strains exhibit potential differences in pathogenicity (DeBuysscher et al. 2013). There have been more than 634 cases of NiV reported in people from 1998 to 2021 (Skowron et al. 2022), including some short chains of human-to-human infection following spillover. NiV-MY was first discovered as an outbreak in pigs and humans in peninsular Malaysia and Singapore in 1998–1999. The virus caused encephalitis, with a 39% fatality rate among human cases in Malaysia (Chua 2003). Since 2001, in western and northwestern Bangladesh and the area bordering India, NiV-BD transmission from bats to humans has frequently been reported; limited chains of subsequent human-to-human transmission have been observed (Luby et al. 2009b). NiV-BD outbreaks are associated with significantly higher case fatality rates (43–100%) than are NiV-MY outbreaks (Hsu et al. 2004; Chadha et al. 2006; Gurley et al. 2007).

Fruit bats of the genus *Pteropus* have been identified as a natural reservoir of NiV-MY and NiV-BD, and in Thailand, *Pteropus lylei* (Lyle's flying fox) serves as the primary natural NiV host (Wacharapluesadee et al. 2005; 2013; 2016). *P. lylei* is a member of the fruit bat family (Chiroptera: Pteropodidae); it is found in Cambodia, Thailand, and Vietnam (Bumrungsri et al. 2008; IUCN 2021). *P. lylei* is known to occur in lower central, western, and eastern Thailand, and about 30 roosting sites have been surveyed with a total population of 75,016 (Chaiyes et al. 2017). In Thailand and Cambodia, *P. lylei* travels distances of 2–23 and 6.88–105 km, respectively, from day roosts to foraging areas (Weber et al. 2015; Choden et al. 2019). *P. lylei* is an important reservoir of NiV, particularly in Thailand and Cambodia (Reynes et al. 2005; Wacharapluesadee et al. 2005; 2010). Wacharapluesadee et al. (2010), reporting on the prevalence of NiV among *P. lylei* in Thailand, found a seasonal pattern of viral shedding in seven of 30 bat roosting sites, and evidence of both the NiV-MY and NiV-BD strains present. All NiV surveillance sites (Wacharapluesadee et al. 2010),

representing 36% of the total bat population in Thailand, were located within Buddhist temples found near densely residential areas (Chaiyes et al. 2017; Duengkae et al. 2019).

Spatial modeling approaches and risk mapping can be a valuable tools to predict zoonotic disease transmission (Ostfeld et al. 2005) and determine the distribution of suitable habitats for host reservoirs (Hahn et al. 2014a). Ecological niche modeling (ENM) approaches establish a relationship between occurrence records and environmental variables and can be used to predict the habitat suitability for a target species or vector (Peterson 2006; 2014; Peterson et al. 2011). ENM is a theoretical framework that considers biotic interactions (B), environmental conditions (A), and mobility (M) to understand species distributions (i.e., the BAM diagram; Soberón and Peterson 2005). ENM has been used to produce risk maps of potential NiV transmission to humans by Daszak et al. (2013), Hahn et al. (2014b), Peterson (2015), Walsh (2015), and Deka and Morshed (2018). However, previous research involving the mapping of NiV transmission from *P. lylei* has been based on expert opinions comprising a potential surface analysis approach in Thailand (Thanapongtharm et al. 2015). A more complete picture of the entire extent of *P. lylei* distribution and ecological requirements is needed to assess the pathways to zoonotic spillover, thus substantially improving the ability to predict or prevent spillover events (Plowright et al. 2017).

Thailand has a confluence of potential risk factors for NiV disease outbreaks to occur as NiV has relatively high prevalence in *P. lylei*, and the NiV-BD is dominant and is known to directly transmit to humans (Wacharapluesadee et al. 2021). Almost all of the known *P. lylei* populations are found in close proximity to human communities including highly urban areas like Bangkok (Chaiyes et al. 2017), and there is an abundance of pig and livestock farming in the foraging zone of *P. lylei*. In addition to direct transmission from flying foxes to humans, NiV transmission from flying foxes to livestock or via foodborne sources is also possible.

Livestock or foodborne infection of NiV to humans has occurred on multiple occasions (Luby et al. 2006, 2009a; Chattu et al. 2018). Thus, NiV transmission from flying foxes to humans is clearly possible in Thailand and understanding this risk requires improved models to evaluate spatial risk of spillover via different mechanisms and transmission routes.

Here we construct improved risk maps for NiV spillover and transmission for a critical, populated areas of mainland Southeast Asia. Our study has two primary objectives: (1) to evaluate the ecological niche of NiV based on the *P. lylei* reservoir host occurrence across Thailand, Cambodia, and Vietnam; (2) to quantify possible spatial risk zones of NiV transmission in Thailand via exposure routes from (i) bats to livestock to humans, (ii) bats to humans via indirect foodborne transmission, and (iii) directly from bats to humans.

Methods

Study Area

Models were run across two different scales, regionally (including the entire spatial distribution of *P. lylei*) and only within Thailand. First, a niche model for *P. lylei* was trained using data from an area encompassing Thailand and Cambodia, approximately 159,200 km²

(8–16°N, 98–108°E), to include the potential range of climatic conditions under which the species occurs (Fig. 1). Second, for NiV, risk was mapped in an area of approximately 97,759 km² (10–15°N, 98–103°E), including 25 provinces in the western, central (including the capital and largest city, Bangkok), and eastern regions of Thailand (approximately 20% of Thailand's total land area).

Reservoir Host Occurrence Data

We obtained 48 occurrence records corresponding to all known roosting sites of *P. lylei* (Supplementary Table 1). Thirty locations were from Thailand (Chaiyes et al. 2017), 14 locations were from Cambodia, and four locations were from Vietnam (Ravon et al. 2014; Chaiyes et al. 2020). The occurrence records were filtered to reduce the effects of sampling biases, enabling better estimation of niche characteristics (Fourcade et al. 2014). To reduce the inherent geographic biases associated with collection data, we removed occurrence data that were within 10 km of each other (Boria et al. 2014). We used the Geographic Distance Matrix Generator version 1.2.3 to calculate the geographic distance between each pair of occurrence data points (Ersts, 2021). For each cluster of occurrence records less than 10 km apart, we determined the minimum number of records that could be retained. There were 33 occurrence records after filtering; these were used to analyze the ecological niche model (see Fig. 1 and Supplementary Table 1). We randomly split the occurrence dataset into two subsets, with 75% used for calibration and 25% used for evaluation during model calibration (Fig. 1).

Environmental Data

We used global bioclimatic variables from the WorldClim2 (Fick and Hijmans, 2017) dataset with the same spatial resolution (approximately 1 km²) in GeoTiff format (Supplementary Table 2) for the ecological niche of *P. lylei*. The bioclimatic variables represented current climates (averaged for 1950–2000), and estimates for the two future time periods of 2050 and 2070 were used as transfer layers. Future scenario layers were obtained for the representative concentration pathway (RCP) 4.5 and 8.5 scenarios using CMIP5 general circulation models (MPI-ESM-LR). The performance and suitability of these modeled data across Southeast Asia regions has been previously evaluated (McSweeney et al. 2015). We excluded four data layers with artifactual values that were expressed as abrupt and unrealistic climatic changes between neighboring pixels (i.e., 8, 9, 18, and 19: Escobar et al. 2014).

Ecological Niche Modeling

To model the ecological niche of *P. lylei*, we used the maximum entropy algorithm (Maxent; Phillips et al. 2006) using Maxent 3.4.1 software (Phillips et al. 2018). The kuenm package (Cobos et al. 2019) in R 3.5.1 (R Core Team 2018) was used to select the model used to estimate the ecological niche at a regional scale.

Model Calibration—To obtain an acceptable model performance, model calibration areas should encompass the areas into which species can disperse (i.e., areas that can be colonized by a species or that are accessible to a species for periodic movement) (**M**: Soberón and Peterson 2005; Barve et al. 2011). We calibrated an ecological niche model based on species

access via their dispersal potential, **M** (Poo-Muñoz et al. 2014; Cooper and Soberón 2018). We delineated **M** as the average distance between the recorded occurrences of *P. lylei* and generated a buffer of 870 km around known *P. lylei* occurrences in Thailand, Cambodia, and Vietnam (Fig. 1). Then, we clipped 15 bioclimatic variables of the current and future climate were clipped to the corresponding extent of **M**.

In total, 527 candidate models were built under 29 combinations of linear, quadratic, product, threshold, and hinge response types, with 17 regularization multiplier values (0.1, 0.2, 0.3...1, 2, 3, 4, 5, 6, 8, and 10). The evaluated candidate model performance was based on the significance of a partial receiver operating characteristic (ROC) with 500 iterations; 50% of the data were used for bootstrapping (Peterson et al. 2008). A 5% training presence threshold was used to evaluate omissions (Peterson et al. 2011), and the Akaike information criterion corrected for small sample sizes (AICc) was used to evaluate model complexity (Hurvich and Tsai 1989). The selected models from among those determined to be significant were low-omission candidate models with minimum delta AICc units (see the complete detail of model evaluation results in Supplementary Table 3 and Supplementary Material 2).

Final Models—We created the final models using the selected parameter settings and model performance. The models were then applied to Thailand, Cambodia, and Vietnam; the extent of **M** was considered under current conditions and based on the two future climate scenarios of 2050 and 2070. The mobility-oriented parity metric (MOP) was used to analyze the degree of novelty of climate conditions under all future climate scenarios (2 RCPs × 2 time periods) relative to present-day conditions in the calibration area as per Owens et al. (2013).

Mapping Potential NiV Spillover Risk Areas Based on Host Distribution and Various Transmission Pathways

We developed specific spatial models based on NiV transmission risk factors (i.e., *P. lylei*, presence, spillover via livestock, spillover via foodborne sources like fruit orchards, and human population density) to broadly assess the potential risk of NiV transmission. Data regarding the four NiV transmission factors were obtained as follows:

1. *P. lylei*: *P. lylei* is strongly associated with the occurrence of NiV because the species is a key reservoir for the virus (Reynes et al. 2005; Wacharapluesadee et al. 2005; 2010; 2021). Ecological niche models have been widely used to describe the geography of disease transmission risk (Peterson 2014). The suitability of reservoir host habitats was used as a predictor of NiV risk (Hahn et al. 2014b; Walsh 2015).
2. Livestock: Direct contact with infected livestock (pigs, goats, and cattle) has been identified as an important mode of NiV transmission to humans (Luby et al. 2009a). Pigs specifically have served as an amplifying host in the initial emergence of NiV in Malaysia (CDC, 1999; Chua et al. 1999; Mohd Nor et al. 2000). Other data from Bangladesh suggest that other livestock species (cattle and goats) were also previously infected with NiV (Chowdhury et al. 2014). In

the Philippines, horses were the intermediate reservoir for human NiV infection (Ching et al. 2014). Therefore, we used livestock data (e.g., pigs, cattle, and horse farm boundaries and locations from the land use types of each sub district), which were provided in vector format by the Thailand Land Development Department in 2016 (Supplementary Fig. 1A).

3. Foodborne sources: It is likely that humans have been infected via consumption of fruit contaminated with bat saliva (Luby et al. 2006; Chattu et al. 2018). The survival time of NiV in fruit pulp and fruit juices varies depending on the type of fruit and its pH (Fogarty et al. 2008). We used data from a detailed study mapping the foraging patterns of *P. lylei* in Thailand, and included spatial layers for 11 of the 34 most common plant species (Weber et al. 2015). The 11 types of *P. lylei* food provided a foodborne transfer route for NiV from *P. lylei* to humans; the food data were classified by the Thailand Land Development Department in 2016 (Supplementary Fig. 1B). Mango (*Mangifera indica*), banana (*Musa* sp.), tamarind (*Tamarindus indica*), earleaf acacia (*Acacia auriculiformis*), cashew (*Anacardium occidentale*), eucalyptus (*Eucalyptus* sp.), sapodilla (*Manilkara zapota*), Manila tamarind (*Pithecellobium dulce*), common guava (*Psidium guajava*), santol (*Sandoricum koetjape*), and Malabar plum (*Syzygium jambos*) were used as food by *P. lylei*, including the fruits, leaves, and flowers of these plants (Supplementary Fig. 1B).
4. Humans: Human population density and village locations have been associated with NiV spillover risk (Hahn et al. 2014a; b). We used village boundaries provided in vector format by the Thailand Land Development Department in 2016 (Supplementary Fig. 1C). The human density map in these 1 × 1-km pixels in 2018 was calculated using data from the National Statistical Office of Thailand (Supplementary Fig. 1C).

Risk maps for potential zoonotic spillover of NiV from *P. lylei* were created by overlapping human population density (people per km²) with the suitability of reservoir hosts and the spatial distribution of various transmission pathways of NiV (Fig. 2). First, we developed current suitability maps for the *P. lylei* reservoir host across Thailand, Cambodia, and Vietnam based on the ecological niche model (see the ENM section above). We then used the boundary of Thailand to mask the potential present suitability of *P. lylei*. This surface showed the areas suitable for *P. lylei* reservoir host occupancy, which was used as a predictor of NiV risk. The potential NiV risk in Thailand was reclassified into three categories (low, medium, and high) to represent the different levels of risk using the Jenks natural breaks classification method, with classes based on natural groupings inherent in the values of the data (Jenks 1967). We then quantified the possible spatial risk areas in Thailand for NiV transmission from (i) bats to livestock to humans, (ii) bats to humans via indirect foodborne transmission, and (iii) directly from bats to humans to humans. The spatial risk maps of the potential zoonotic spillover via each transmission pathway of NiV from *P. lylei* in Thailand were then determined by masking the area of livestock, foodborne sources, and village boundaries in ArcGIS (see above). Final outputs were produced by selecting the high transmission risk areas via pathways of NiV spillover from *P. lylei* to livestock,

by foodborne sources, and by humans, then overlaying population density (people/km²) according to sub districts of Thailand where the presence of NiV was considered likely.

RESULTS

Ecological Niche Modeling

Annual mean temperature (Bio1; importance 56.9%) was the climate variable that had the greatest importance in our *P. Iylei* ecological niche model. The minimum temperature of the coldest month (Bio6; importance 9.5%), mean temperature of the warmest quarter (Bio10; importance 6.9%), mean temperature of coldest quarter (Bio11; importance 6.5%), and temperature seasonality (standard deviation \times 100) (Bio4; importance 6.2%) were also retained as environmental predictors (Table 1).

The climate variables under present conditions were used to determine the suitability levels of the current geographic distribution of *P. Iylei* in Thailand, Cambodia, and Vietnam (Fig. 3). Areas of high suitability for *P. Iylei* were restricted to central, some eastern, and western regions of Thailand (15 provinces including Bangkok, the capital of Thailand), and the flat plain around Tonle Sap Lake of Cambodia (five provinces including Phnom Penh, the capital of Cambodia), with suitability declining toward the estuary of the Mekong river in southern Vietnam.

Area of future (2050 and 2070) habitat suitability for *P. Iylei* were conducted by considering two different emission scenarios (RCP 4.5 and RCP 8.5). Our distribution models indicated a marked expansion of the species range as a result of climate change: particularly suitable areas for *P. Iylei* included lower northern, northeastern, eastern, and upper southern Thailand; almost all of Cambodia; and lower southern Vietnam (Fig. 4A–D). Future areas of *P. Iylei* habitat suitability increased over time in both Thailand and Cambodia (Fig. 4A–D, dark green). The MOP results indicated broad areas of high-risk extrapolation for *P. Iylei* in all transfer scenarios (Fig. 4E–H); light blue values represent high-risk extrapolation areas and dark blue values represent levels of similarity between the calibration area and the different future conditions (2050 and 2070) under the RCP scenarios used in the projections.

Mapping the Potential for NiV Spillover from *P. Iylei*

The central-western region of Thailand was an area with high suitability for *P. Iylei* occurrence (high = 38,904 km², medium = 24,432 km², low = 38,904 km²; Fig. 5). A risk map based on habitat suitability for *P. Iylei* combined with land use layers for various transmission pathway of NiV (e.g., from *P. Iylei* to livestock, then to humans) identified high-risk areas covering a total human population of 244,640 in 22 provinces, 127 districts, and 670 sub districts (1522 km², 57% of the total livestock area); these areas were largely in the upper central, western, and eastern regions of the country (Fig. 6A). The high-risk areas for the transmission of NiV from *P. Iylei* via foodborne sources to humans covered a total human population of 718,982; these areas were distributed in 23 provinces, 165 districts, and 1071 sub districts in the upper and western, central and eastern areas (11,844 km², 35% of the total foodborne source areas; Fig. 6B). High-risk areas for the direct transmission of NiV from *P. Iylei* to humans were identified in areas with a high human population density

(approximate total population of 2,244,636); the areas were concentrated in 23 provinces, 197 districts, and 1336 sub districts in central and eastern areas of Thailand (20,055 km², 68% of the total village area; Fig. 6C). Furthermore, we found that a total population of 227,582 in 22 provinces, 126 districts, and 687 sub districts was at a high risk of the combination of all three routes of NiV transmission (Fig. 6D and Supplementary Table 4).

Discussion

This study mapped the risk of Nipah virus transmission from bats to humans through the intersection of suitable habitat for the *P. lylei* bat reservoir and spatial data for other risk factors related to specific transmission pathways for NiV. We show that the current and future areas of NiV spillover risk from *P. lylei* in Thailand, Cambodia, and Vietnam are extensive and will increase over time under various climate change scenarios.

The climatic variable that best explained the ecological niche for *P. lylei* was the annual mean temperature. This finding is supported in nature by a strong correlation between the annual number of *P. lylei* deaths and the mean ambient temperature (Hengjan et al. 2018). An estimated 29% of anomalous bat mortality is caused by warming; 49% of such mortality is caused by the El Nino/Southern Oscillation (Thirumalai et al. 2017). Hengjan et al. (2018) reported that the highest number of *P. lylei* deaths occurred during March and April, which is the period with the highest temperature in Thailand. This is similar to the effects of temperature extremes on Australian flying foxes in Australia, where bioclimatic variables are likely drivers of the spatial patterns of Hendra virus spillover from *P. alecto* and *P. conspicillatus* into horses, then humans (Welbergen et al. 2008; Martin et al. 2016). Regular population surveys for *P. lylei* in Thailand, Cambodia, and Vietnam will be critical to validate our model of this species' occurrence and project range expansion in 2050 and beyond. Our ENMs and risk map can be used to prioritize regions for future pandemic preparedness (i.e., increased and targeted human and animal surveillance for NiV), but also to understand the potential conservation impact of bat dieoffs in the context of future climatic changes.

Our findings support the results of previous studies that have used ENM to demonstrate a much broader regional and countrywide risk for potential NiV outbreaks. Hahn et al. (2014b), Peterson (2015), Walsh (2015), and Deka and Morshed (2018) developed ecological niche models based on human populations and *Pteropus* roosting sites in South and Southeast Asia. Daszak et al. (2013) used an ensemble modeling approach to predict the impacts of climate change on the potential distribution of henipavirus hosts across the world. In contrast, Thanapongtharm et al. (2015) employed a landscape variable approach across central Thailand based on *P. lylei* roosting sites; they used a potential surface analysis application to map the current NiV risk areas. Our broad-scale analysis, strengthened by data from our research team's *P. lylei* roosting survey data, was in broadly in concordance with findings by Daszak et al. (2013), Hahn et al. (2014b), Peterson (2015), and Deka and Morshed (2018). However, we added sub-analyses of spatial risk through a mechanistic understanding of various NiV transmission pathways. Targeting transmission pathways between reservoir hosts and humans is an effective prevention and control strategy for zoonotic emerging infectious diseases that has the benefit of moving beyond disease-specific

prevention approaches (Loh et al. 2015). Our study adds to this important base of knowledge using a more detailed analysis to identify the potential NiV spillover risk under three different routes of transmission in Thailand. These analyses identified high-risk areas that were suitable for NiV transmission from *P. lylei* to humans: (i) indirectly via livestock—primarily in a small area around upper central and eastern Thailand with a low human population density; (ii) indirectly via foodborne sources—primarily in a large area of western and eastern Thailand, with medium levels of population density; and (iii) directly to humans in a large metropolitan area in central Thailand with high human population density. Our analysis provides insights into which NiV transmission pathways are important in Thailand and where variable drivers of emerging infectious diseases are present. Thus, our findings can facilitate more targeted prevention measures, surveillance efforts at a sub-national and sub-province level, and development of early warning systems.

In Thailand, livestock and orchard fruit products are in high demand in the domestic and export markets (International Trade Centre, 2020). Smallholder agriculture systems and free-range livestock are possible risk factors for disease transmission through contact between animals and humans. NiV has been shown to infect livestock, including pigs, cattle, and goats (Luby et al. 2009a). We demonstrated that the overlap of livestock, orchards, and the centers of human communities varied across the study area (Fig. S1A–C). In Thailand, traditional pig farms and cattle farms are interspersed among orchards that grow a variety of fruit crops. These farms normally have fruit trees around the animal pens, and the seasonal activity of *P. lylei* in these locations has been reported by Weber et al. (2015). In Malaysia, farms served as the zoonotic transmission route for NiV emergence through pigs as an intermediate host (Field et al. 2001). NiV-BD transmission from bats to humans has occurred through the consumption of contaminated date palm sap by *P. medius* (formerly named *P. giganteus*) (Luby et al. 2006). We found that 22 provinces, 126 districts, and 687 sub districts were potential high-risk contact zones for NiV transmission via the combined *P. lylei*, livestock, foodborne, and human population routes; these locations should be prioritized for NiV surveillance.

One potential limitation of our study was that we only used the locations of *P. lylei* roosting sites to indicate their presence, whereas NiV spillovers can occur in locations where flying foxes forage or visit. There may be a spatial difference between areas used by flying foxes as roosting sites and areas where NiV is transmitted to livestock or becomes foodborne and then transfers to humans, as suggested in Malaysia, Bangladesh, and India (Field et al. 2001; Chua et al. 2002; Luby et al. 2006; Chattu et al. 2018). We considered dispersal distance in our ENM using the best available data from GPS tracking (Weber et al. 2015), but future efforts should consider long-distance or long-term bat movement, more detailed knowledge of foraging behavior (Giles et al. 2018), and the potential interactions between humans and bats to improve regional risk mapping efforts.

In summary, our study used ecological niche models to identify the current and future range of *P. lylei*, a key bat reservoir host species for NiV, in Thailand, Cambodia, and Vietnam. We overlaid habitat suitability maps with high-resolution, in-country data from Thailand to identify potential sites for NiV spillover based on three different transmission pathways. Together, these data will help to improve our understanding of the ecological influences

on NiV presence and transmission. The risk maps produced in this study will also provide an important baseline for guiding active NiV surveillance and can be used to shape policy decisions for surveillance, depending on the primary transmission pathway in each region. Our analyses and research approach can inform NiV awareness and prevention programs aimed at reducing disease outbreaks and their associated economic losses across Southeast Asia and beyond.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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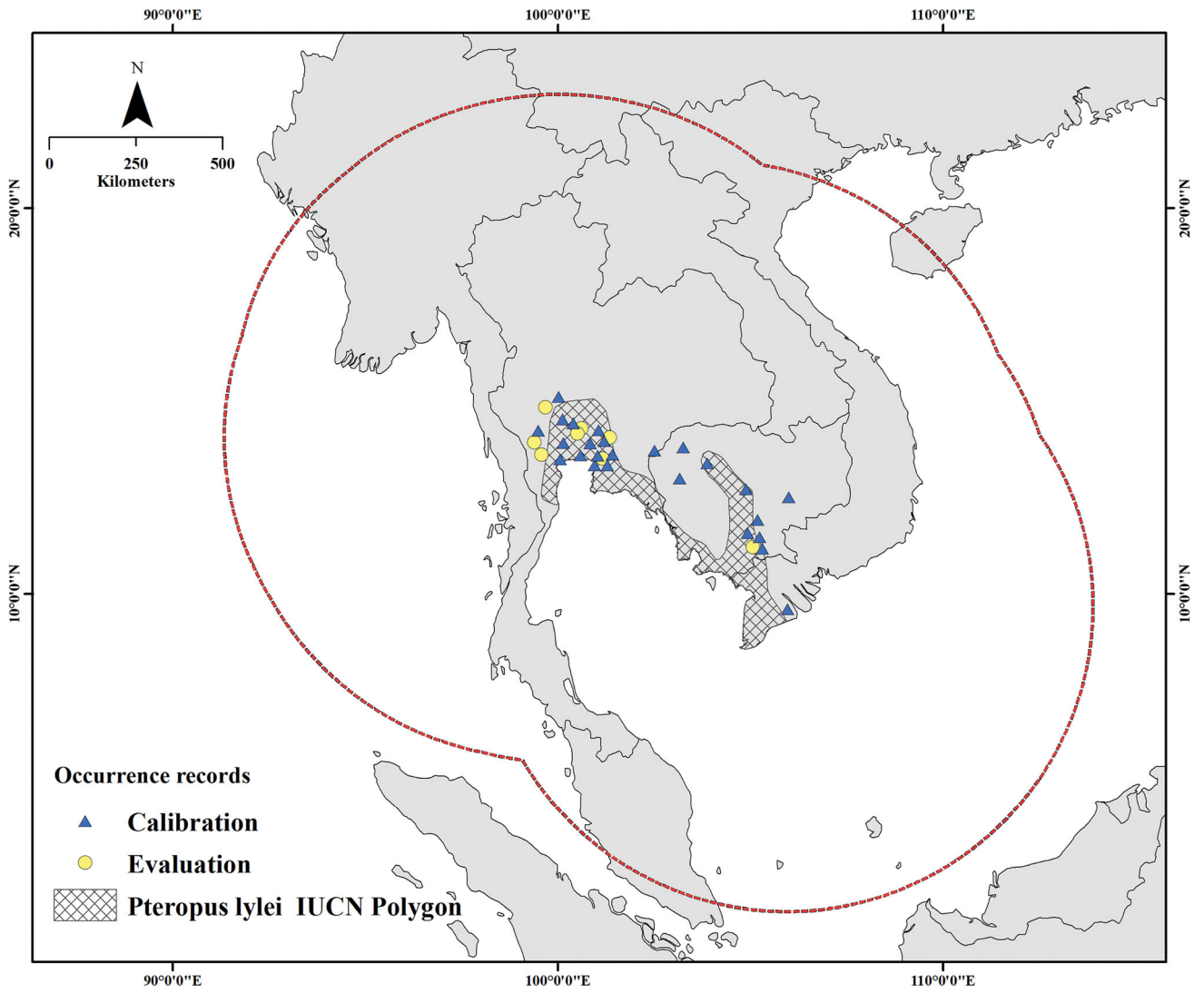


Figure 1.
Locations of *Pteropus lylei* roosting sites used to fit the model.

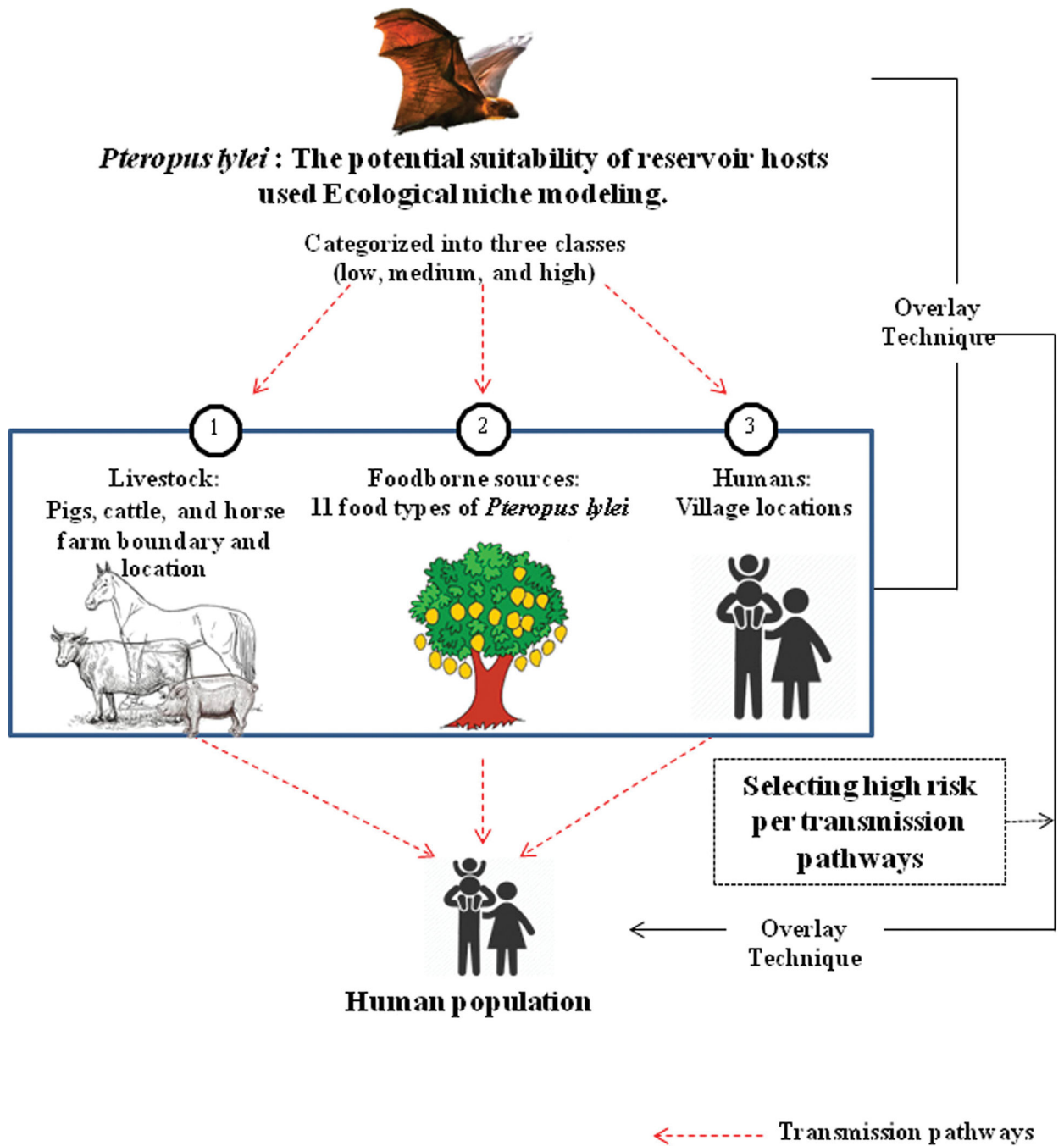


Figure 2.
Conceptual framework of the study.

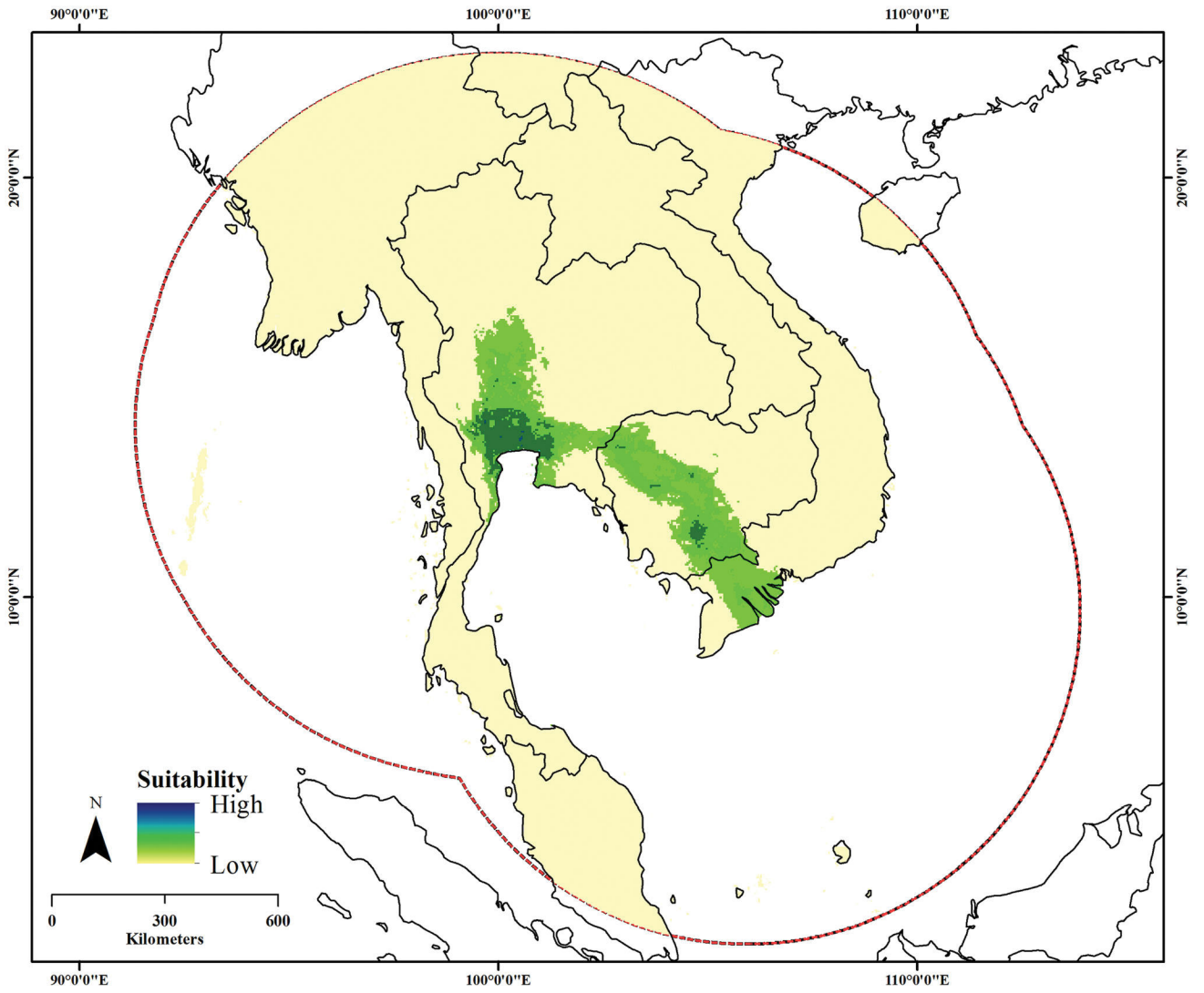


Figure 3. Potential suitability revealed by ecological niche modeling of the geographic area currently occupied by *Pteropus lylei* in Thailand, Cambodia, and Vietnam.

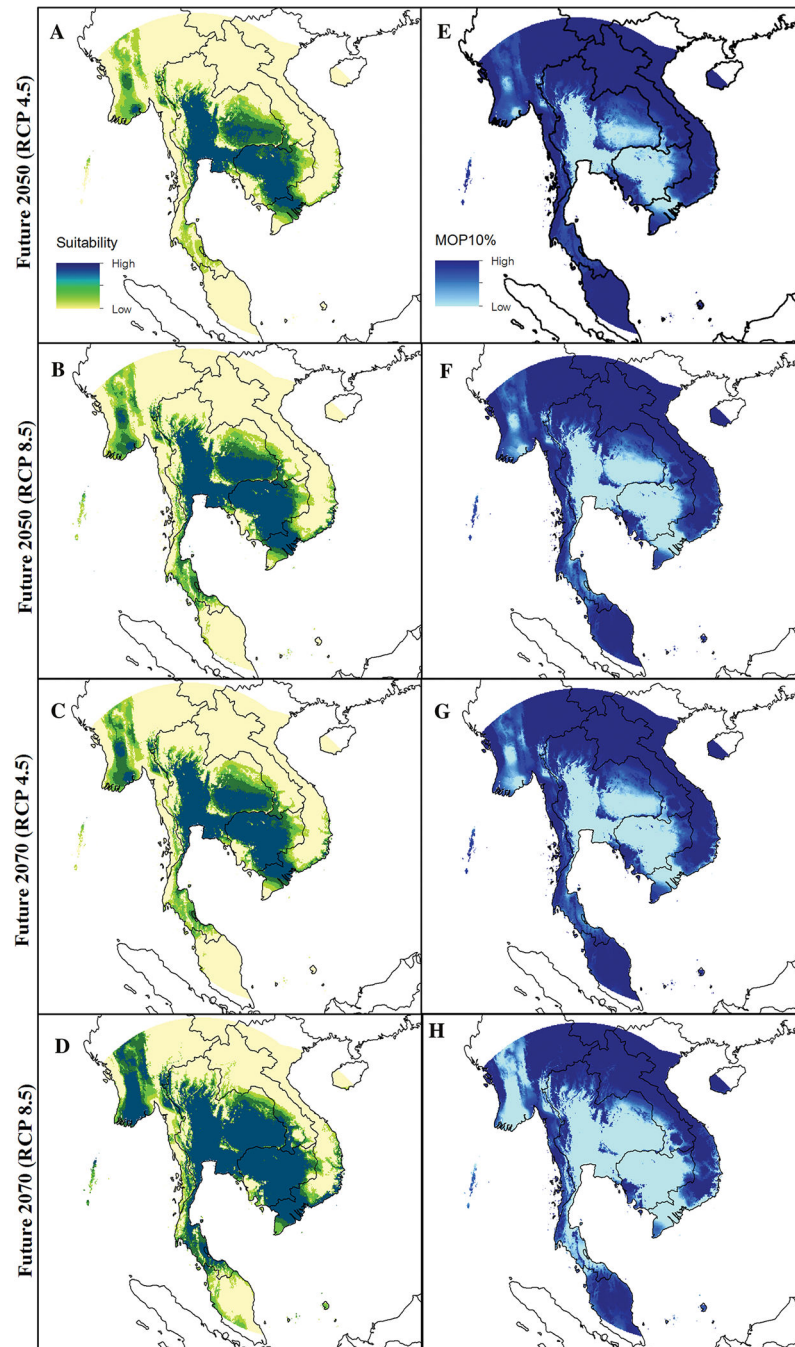


Figure 4. Predicted future climatic suitability for *Pteropus lylei* asc reservoir hosts of NiV (A–D) and the results of a MOP analysis for extrapolating risk from the calibration area under current conditions to the whole study area under future conditions (E–H).

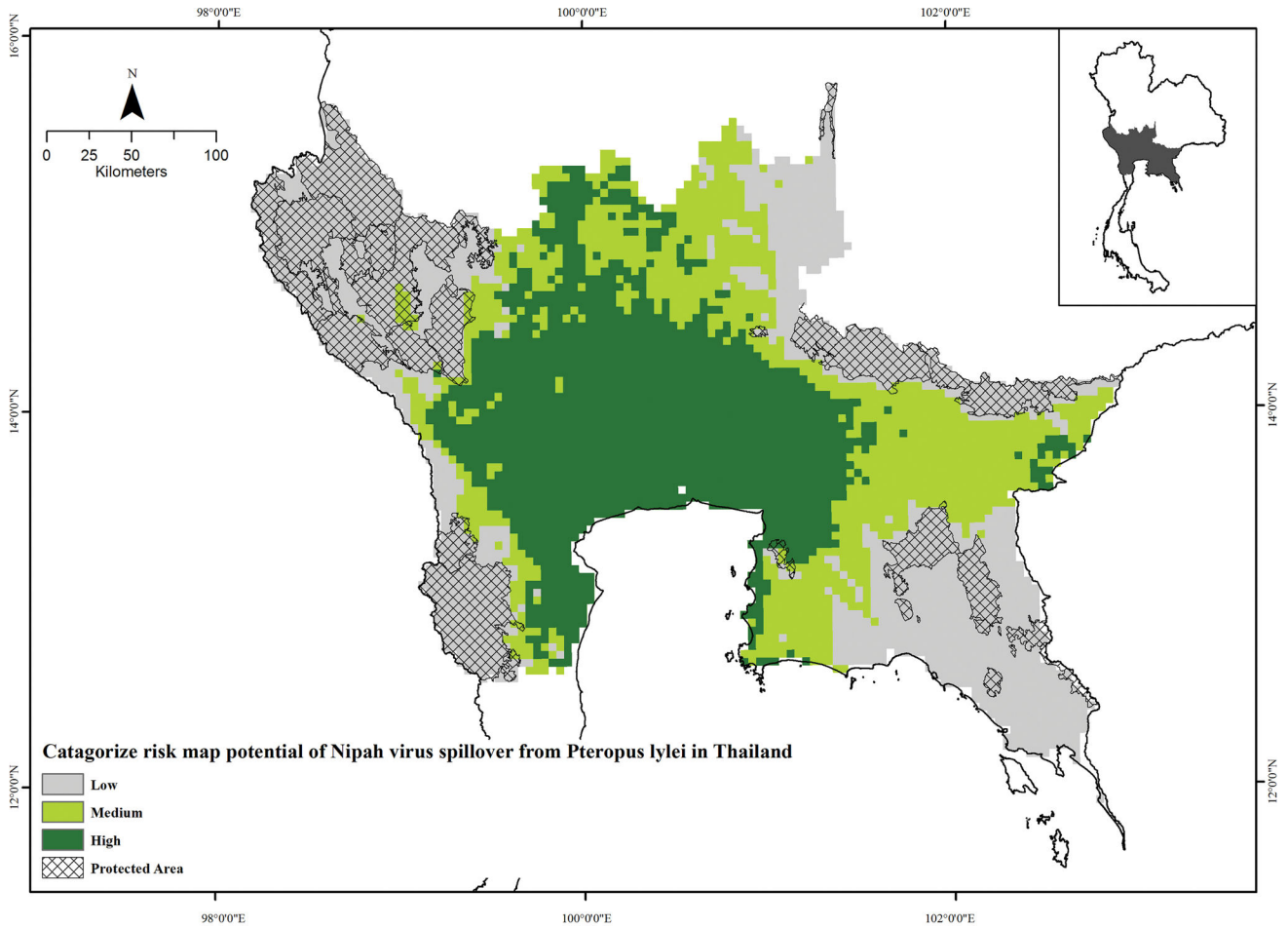


Figure 5. Map of Nipah virus spillover risk (high, medium, low) from *Pteropus lylei* reservoir hosts in Thailand. Protected areas denoted with hatching.

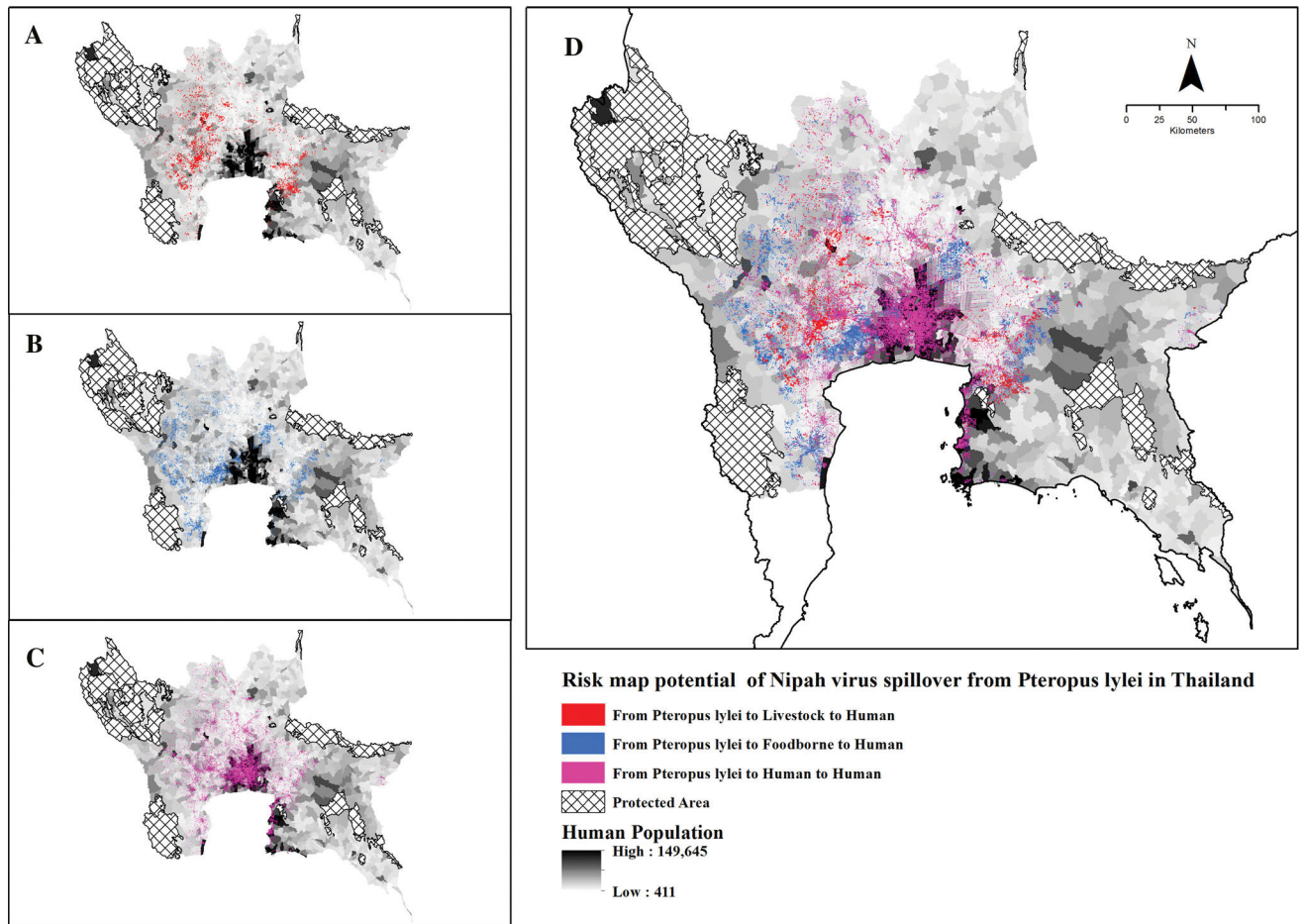


Figure 6. Risk map based on transmission routes for Nipah virus in Thailand from *Pteropus lylei* to livestock (A), via foodborne sources (B), and including human-to-human transmission (C).

Percentage (> 1%) Contributions and Sample Average Contribution of Variables Used in the Ecological Niche Model for *Pteropus lylei* Reservoir Host Distribution in Thailand, Cambodia, and Vietnam.

Table 1.

Variable	Percentage contribution	Sample average (\pm sd)
Annual mean temperature	56.9	27.80 (\pm 0.26) $^{\circ}$ C
Minimum temperature of coldest month	9.5	29.45 (\pm 0.31) $^{\circ}$ C
Mean temperature of warmest quarter	6.9	20.07 (\pm 1.05) $^{\circ}$ C
Mean temperature of coldest quarter	6.5	141.13 (\pm 18.16)
Temperature seasonality (standard deviation \times 100)	6.2	25.91 (\pm 0.42) $^{\circ}$ C
Annual precipitation	4.6	1,255.93 (\pm 214.06) mm
Maximum temperature of warmest month	3.6	35.07 (\pm 0.92) $^{\circ}$ C
Precipitation of wettest quarter	1.8	14.99 (\pm 1.87) $^{\circ}$ C