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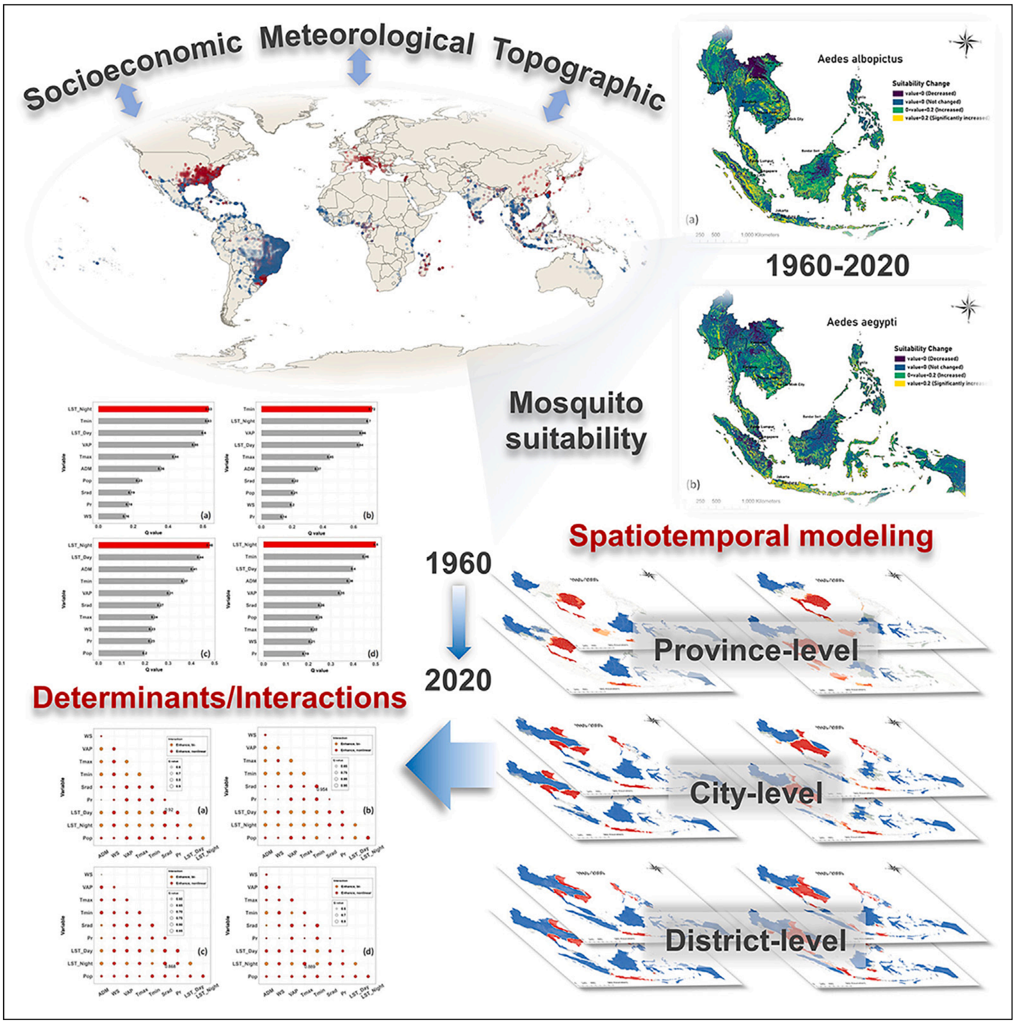

Weitao Hou, Yuxuan Zhou, Wei Luo, Lin Wang, Mei-Po Kwan, Alex R. Cook

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Highlights

Developed a high-resolution (500 m) mosquito distribution map for Southeast Asia

Revealed significant increases in mosquito suitability in most cities over 60 years

Identified a shift in high mosquito suitability areas from coastal to inland regions

Nighttime land surface temperature as a key factor in mosquito distribution changes

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Mapping environmental suitability changes for arbovirus mosquitoes in Southeast Asia: 1960–2020

Weitao Hou,[1,7,8,9] Yuxuan Zhou,[2,3,9] Wei Luo,[3,4,9,10,*] Lin Wang,[5] Mei-Po Kwan,[6] and Alex R. Cook[4]

SUMMARY

Spatial epidemiology recognizes the impact of environmental factors on human infectious diseases through disease vectors. The expansion of *Aedes aegypti* and *Aedes albopictus* raises concerns about health risks due to their changing distribution. However, current mosquito mapping methods have low spatial resolution and limited focus on long-term trends and factors. This study develops a high-resolution framework (500 m) to map mosquito distribution in Southeast Asia from 1960 to 2020. It includes a species distribution model, a spatial autocorrelation model, and a geographical detector model. The study produces Southeast Asia's first 500 m resolution map of mosquito suitability, revealing significant increases in mosquito suitability in most cities over the past 60 years. The analysis indicates a shift in high-suitability areas from coastal to inland regions, with nighttime land surface temperature playing a key role. These findings are crucial for regional risk assessments and mitigation strategies related to vector-borne diseases.

INTRODUCTION

The interaction between the environment and infectious disease vectors can perpetuate and expand the transmission scope of diseases, thereby increasing people's vulnerability and presenting a significant public health concern.[1] Spatial epidemiology, when studying infectious diseases, discerns their spatial distributions and investigates the intricate relationship between vector exposure to environmental variables and the etiology of diseases.[2] *Aedes albopictus* and *Aedes aegypti*, the primary vectors for several infectious diseases, including dengue virus and chikungunya virus, play a pivotal role in the transmission dynamics of these viruses.[3,4] Southeast Asia is a critically affected region impacted by the *Aedes* mosquito, with dengue fever alone resulting in over three million reported cases and more than 5,000 fatalities annually.[5,6] Therefore, mapping and estimating changes in the "environmental suitability" for these mosquito species in Southeast Asia is of great value and importance, as it can provide insights into helping mitigate the transmission of mosquito-borne diseases such as dengue and reduce the associated health burden in the region.

The environmental determinants influencing the suitability of *Aedes* mosquito species are typically categorized into three main groups: meteorological, socioeconomic, and topographic.[7,8] A substantial body of evidence underscores the pivotal role of meteorological factors, such as temperature, in shaping the suitability of *Aedes* mosquito habitats.[8–11] Environments conducive to high suitability for mosquitoes can directly impact mosquito populations by shortening the incubation period of mosquito larvae and extending the lifespan of adult mosquitoes.[12–14] Elevated meteorological suitability conditions correspondingly result in an increased mosquito biting rate, thereby enhancing the prospects of mosquito-borne virus transmission.[15–17] Conversely, socioeconomic factors, such as urbanization, give rise to complex thermal dynamics and contribute to expanding human populations, often resulting in suboptimal sanitation and public services.[18] These conditions, in turn, increase the availability of larval habitats, thus accelerating the developmental rates of mosquito larvae.[19,20] Consequently, these factors bring mosquitoes closer to human populations, augmenting the potential for mosquito-borne epidemics.[18,21] Regarding topographic factors, while their influence on elevating mosquito suitability has yet to be comprehensively evaluated, studies suggest that terrain characteristics can constrain disease geographical dispersion by restricting the availability of mosquito habitats, particularly in elevated areas inaccessible to mosquitoes.[22]

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The term "environmental suitability" concerning *Aedes* species has been widely employed in studies to assess the propensity of these species for mosquito-borne virus transmission to humans.[23] Currently, two principal modeling approaches are utilized to evaluate environmental suitability for *Aedes aegypti* and *Aedes albopictus*, which indicate disease transmission potential: mechanistic modeling and statistical modeling.[24,25] Mechanistic modeling focuses on identifying a specific range of temperature that accurately delineates the suitability for the development of mosquitoes and the transmission of the mosquito-borne virus to humans.[26] On the other hand, statistical modeling, particularly through the lens of species distribution models, assesses the probability of vector species occurrence within particular environmental settings, indicating the suitability level for mosquito-borne disease transmission in those specific areas.[27] It is acknowledged that mechanistic modeling falls short of incorporating socioeconomic factors comprehensively and faces challenges in unraveling the physiological links between virus transmission and factors other than temperature.[24] Consequently, statistical modeling emerges as the primary choice for large-scale assessments of disease transmission suitability.[24,28]

A range of studies has used statistical modeling to understand the distribution of mosquito suitability at diverse geographical scales and regions. Machine learning methods, such as random forest, are particularly effective in assessing the non-linear relationships between species occurrence records and environmental conditions, making them a preferred choice over traditional statistical methods like generalized linear models.[29,30] At a global scale, Campbell et al.[31] applied maximum entropy models, integrating meteorological data, to elucidate the influence of climatic conditions on the distribution of *Aedes aegypti* and *Aedes albopictus*, achieving a spatial resolution of 18 km. Subsequently, Nsoesie et al.[3] and Dickens et al.[32] enhanced the spatial resolution to 4 km and expanded the analysis by integrating remote sensing data, such as vegetation indices and socioeconomic factors, including land use types. Kraemer et al.[33] further expanded the research by incorporating human movement data and employing boosted regression trees to scrutinize historical and future tendencies in the dispersion of *Aedes* mosquitoes, maintaining a resolution of 4 km.

Furthermore, advancing research endeavors to encompass regional and national dimensions is critical for pinpointing specific areas at heightened risk of mosquito-borne transmission.[29] Despite the predominant utilization of 4 km resolution at these scales, it is noteworthy that such resolutions predominantly facilitate the identification of overarching patterns and may not capture the diverse environmental conditions across different locales.[26] For instance, mapping efforts specific to the WHO Eastern Mediterranean Region incorporate local monitoring and surveillance data, which has revealed areas of high mosquito environmental suitability that differ significantly from those identified at the global level at the same 4 km resolution.[34] This trend is corroborated by additional studies conducted within Europe[35] and the Hong Kong Special Administrative Region.[10] There remains a need for higher resolution at regional and national levels, as high-resolution mapping facilitates a detailed examination of areas, thereby enabling the prioritization of locales with greater propensities for mosquito habitation.[10,21] Yin et al.[10] recently exemplified this advancement by achieving a 10 m resolution within a localized setting in the Hong Kong Special Administrative Region, which holds substantial promise for mosquito-borne diseases mitigation through the strategic placement of mosquito traps.

Based on the aforementioned discussion, we have identified several limitations in previous studies regarding the suitability of mapping mosquitoes. A primary concern is the questionable quality of the data utilized, casting doubts on the reliability of the results produced by current models.[24,29] Data sources like Worldclim.com present a challenging dilemma as they offer either high-resolution datasets confined to specific time frames (1970–2000) or extensive temporal coverage with a limited selection of meteorological variables, creating a mismatch between the availability of mosquito occurrence records and accessible data, which in turn raises questions about the precision of the models.[21] Moreover, real-world systems are intricate, but the existing work at the larger geographical scales (i.e., world or regional) tends to use coarse maps or only consider a specific range of impervious surfaces to represent urban land use conditions.[15,19] Such a simplified assumption has resulted in a low resolution of the mosquito suitability map (i.e., 4 km), which distorts the relationship between vector presence and environmental conditions within species distribution models.[24,36] Furthermore, despite existing studies on the distribution of mosquito environmental suitability, there is a gap in examining the spatiotemporal elements that influence this suitability.[28] The omission hinders the ability to discern trends and detect the critical factors of changes in suitability, ultimately impeding the provision of data-driven recommendations for targeted regional mosquito-borne disease management.[28,37]

Therefore, this study introduces a framework to create high-resolution maps (i.e., 500 m) and assess changes in environmental suitability for *Aedes* mosquitoes in Southeast Asia to address the aforementioned challenges. The framework consists of a species distribution model to evaluate mosquito environmental suitability, a spatial autocorrelation model for suitability hotspot identification and comparison, and a geographical detector model for factor exploration. We address historical data limitations and enhance data quality by utilizing comprehensive meteorological, socioeconomic, and topographic data from multiple sources on a cloud computing platform, covering the period from 1960 to 2020.

RESULTS

Mapping high-resolution environmental suitability changes

We employed a species distribution model to generate high-resolution suitability maps for 1960–2000 and 2001–2020. The resulting maps, displayed in Figures 1 and 2, use darker red hues to denote areas of higher mosquito suitability. Specifically, Figures 1A and 1B reveal extensive regions highly conducive to *Aedes albopictus* in Southeast Asia, predominantly along the coastal areas. Countries such as Malaysia and the Philippines exhibit notable high-suitability zones along their coastlines. Additionally, distinct pockets of high suitability are observable inland, particularly in Thailand and Myanmar.

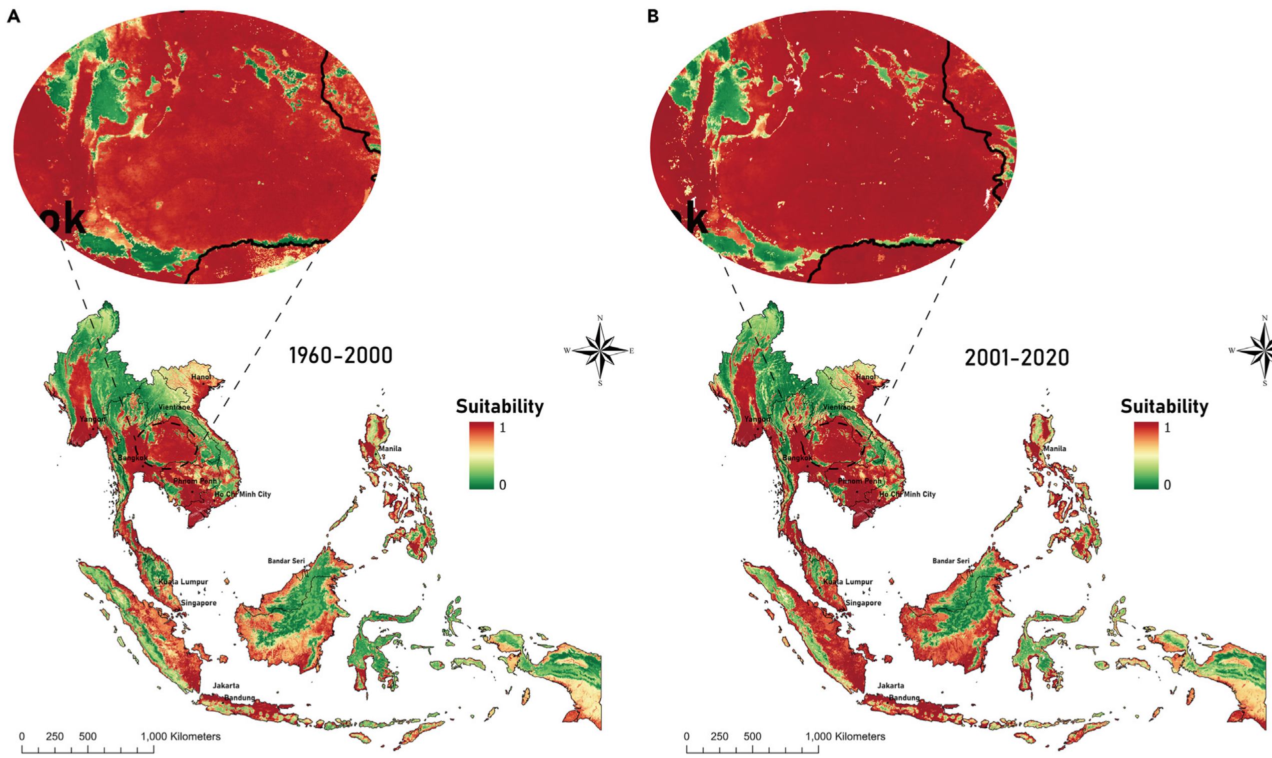

Figure 1. Environmental suitability for *Aedes albopictus* in Southeast Asia
Illustrating the suitability during 1960–2000 (A) and 2001–2020 (B).

The spatial pattern for *Aedes aegypti*, as shown in Figures 2A and 2B, shares similarities with that of *Aedes albopictus* but also presents crucial differences. Using specific regions in Thailand as an example, areas highly suitable for *Aedes aegypti* are observed on a smaller scale, appearing as discrete clusters as opposed to the extensive continuous zones typical of *Aedes albopictus* habitats in Figure 1. These areas of high suitability for *Aedes aegypti* are predominantly located within urban environments, such as the Bangkok metropolitan area in Thailand, Jakarta in Indonesia, and Phnom Penh in Cambodia. Additionally, the pattern of outward diffusion from these urban centers represents a notable observation that, to the best of our knowledge, has not been previously documented in the scientific literature.

Further analysis involves a pixel-level comparison of the suitability maps across the two time frames (Figures 3 and 4). Yellow regions in Figure 3 on these maps signify areas where suitability has significantly increased, with some regions experiencing changes exceeding 0.2 over the six decades. Both *Aedes albopictus* and *Aedes aegypti* show enhanced suitability across a large portion of Southeast Asia, with marked increases, particularly in Indonesia and Malaysia. Figure 4 analyzes the mean suitability changes over this period for districts within each Southeast Asian country. The results indicate widespread changes in mosquito distribution, suggesting an expansion in the affected areas. Notably, Singapore is the only country where 100% of districts show a decrease in *Aedes albopictus* suitability, with 80% also showing a decrease in *Aedes aegypti* suitability.

Model validation

The area under the receiver operating characteristic curve (AUC) obtained for both mosquito species and periods demonstrated excellent performance, with values surpassing 0.9 (Figure 5). Specifically, the accuracy for *Aedes albopictus* was 0.992 for 1960–2000 (Figure 5A) and 0.921 for 2001–2020 (Figure 5B). Regarding *Aedes aegypti*, the accuracy was 0.992 for 1960–2000 (Figure 5C) and 0.921 for 2001–2020 (Figure 5D). The mean absolute error for both species across the two periods does not exceed 0.2, and the root-mean-square error is not higher than 0.3 (Table S3). In conclusion, utilizing high-quality datasets and rigorous validation, our species distribution model provides reliable and accurate insights into the spatial distribution and changes of *Aedes aegypti* and *Aedes albopictus* in Southeast Asia.

Multi-scale spatiotemporal analyses

This study illustrates two spatiotemporal implications by harnessing high-resolution mapping results. Firstly, our attention is directed toward multi-scale hotspot identification and comparison. Secondly, we delve into multi-scale spatial analysis to detect underlying factors. These two case studies are the foundation for future research on multi-scale analyses of mosquito suitability based on high-resolution mapping.

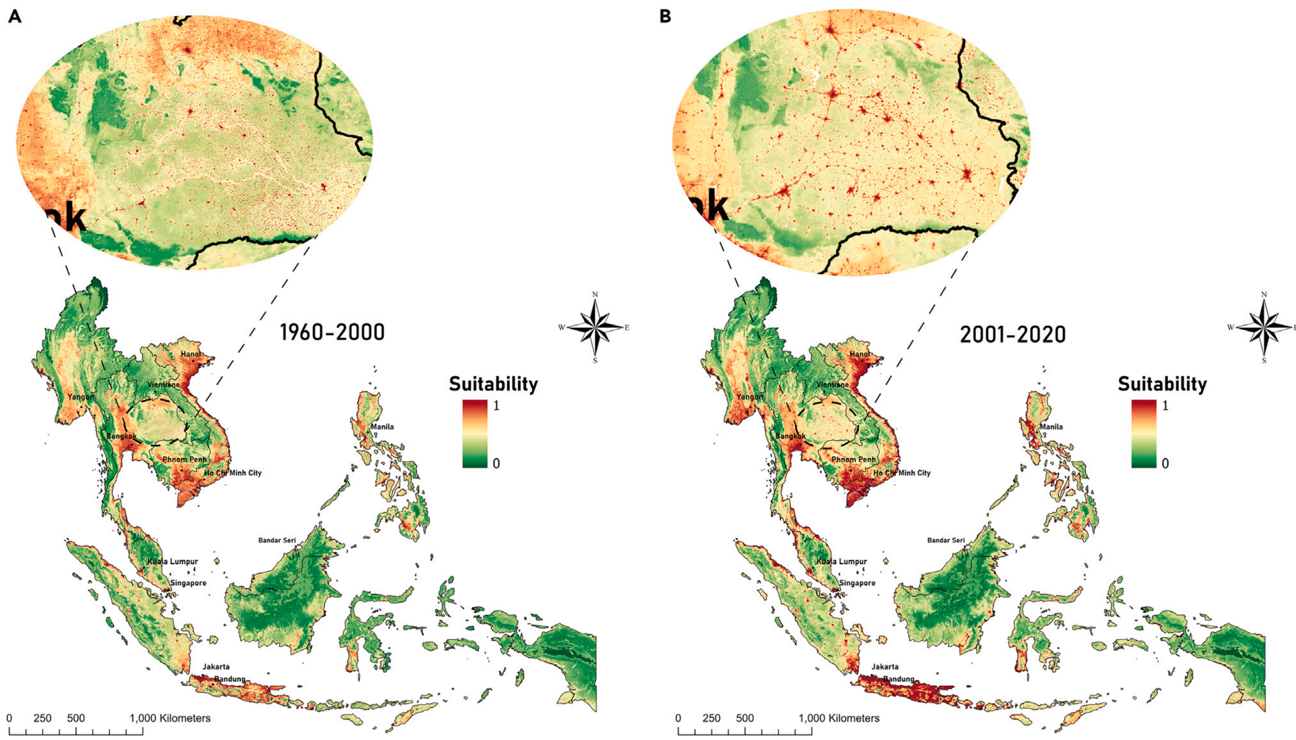

Figure 2. Environmental suitability for *Aedes aegypti* in Southeast Asia
Illustrating the suitability during 1960–2000 (A) and 2001–2020 (B).

Hotspot identification and comparison

This case study utilizes three administrative levels to analyze *Aedes albopictus* hotspot identification and comparison, illustrated in Figures 6, 7, and 8. Figure 6 details the hotspot identification across scales, while Figure 10 focuses on their comparison. At level 1 (provincial level), primary hotspots are identified in Cambodia, Malaysia, Indonesia, and the southern regions of Vietnam, Thailand, and Laos (Figure 6A). Refining to level 2 reveals an expansion of hotspot areas in Thailand and Indonesia, with the emergence of hotspots in the Philippines and Myanmar (Figure 6B). Further refinement to level 3 accentuates the contrast between hotspot and coldspot areas (Figure 6C). Comparative analysis of hotspot trends between 1960–2000 and 2001–2020 at level 1 shows expansion predominantly in Indonesia and Malaysia

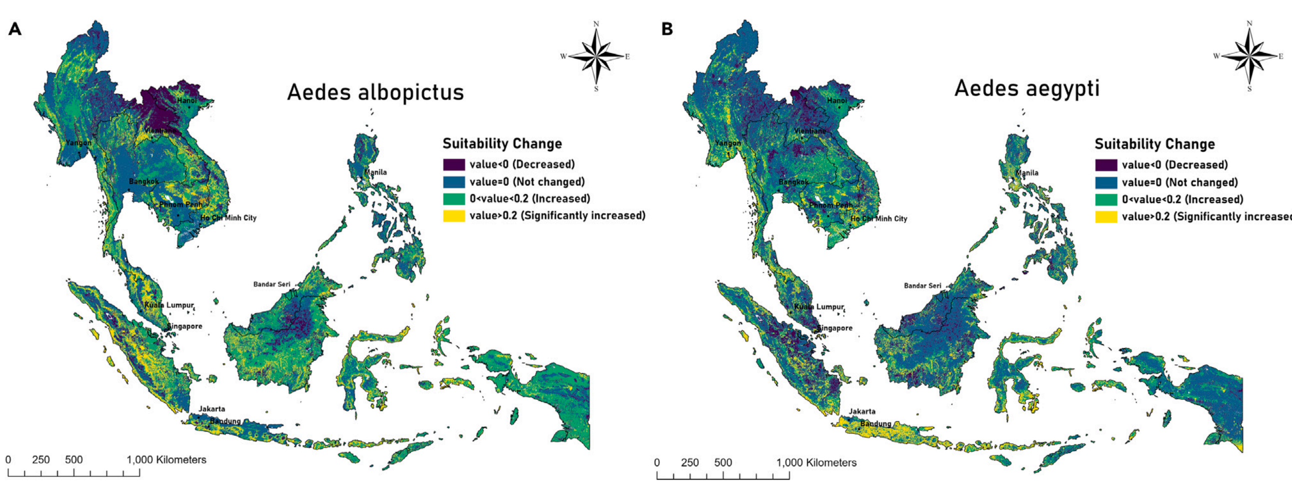

Figure 3. Changes in environmental suitability for mosquitoes in Southeast Asia
Depicting *Aedes albopictus* (A) and *Aedes aegypti* (B).

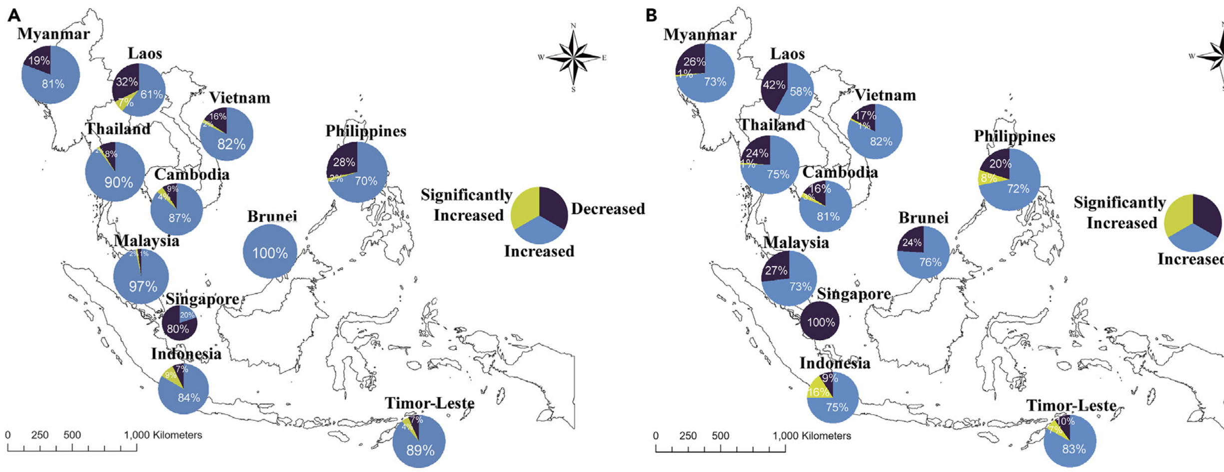

Figure 4. Proportion of the number of districts in each country with suitable changes for mosquitoes in Southeast Asia
(A) *Aedes albopictus* and (B) *Aedes aegypti*.

(Figure 8A). However, a more detailed trend emerges at level 3, where hotspots in Indonesia, the Philippines, and southern Thailand expand from coastal to inland regions. In contrast, Laos, Cambodia, and Vietnam shifted from inland to coastal areas (Figure 8C). This detailed approach provides a comprehensive understanding of the spatial dynamics of *Aedes albopictus* hotspots over time.

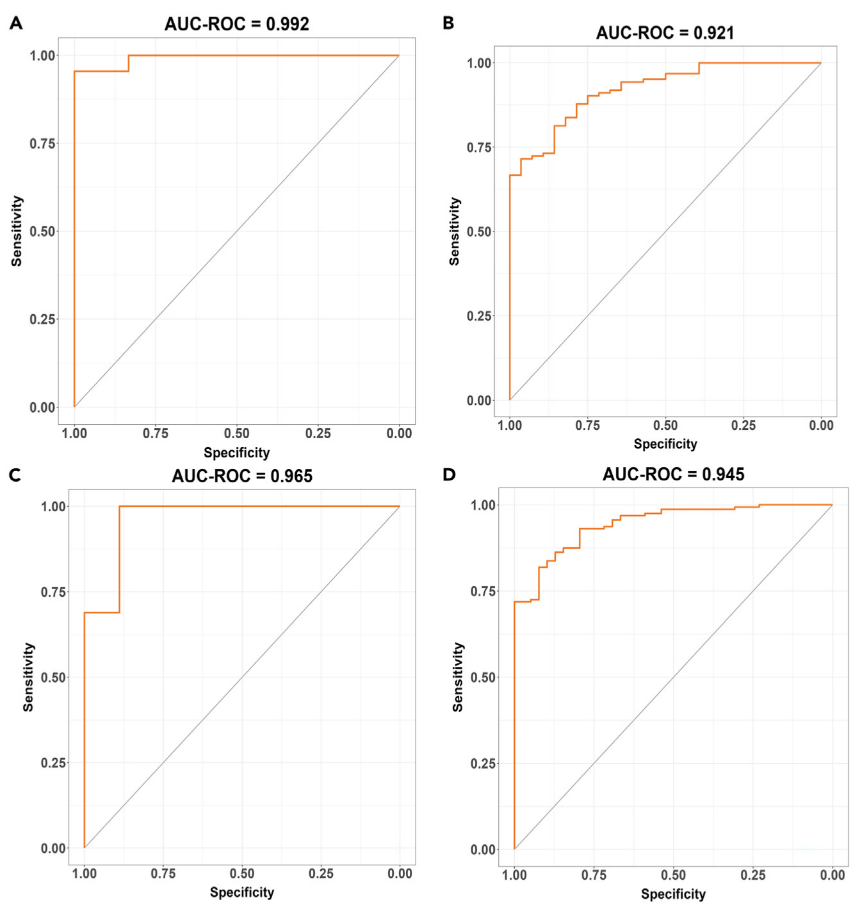

Figure 5. ROC-AUC curves for model validation
Evaluating the performance for *Aedes albopictus* in 1960–2000 (A) and 2001–2020 (B), and for *Aedes aegypti* in 1960–2000 (C) and 2001–2020 (D).

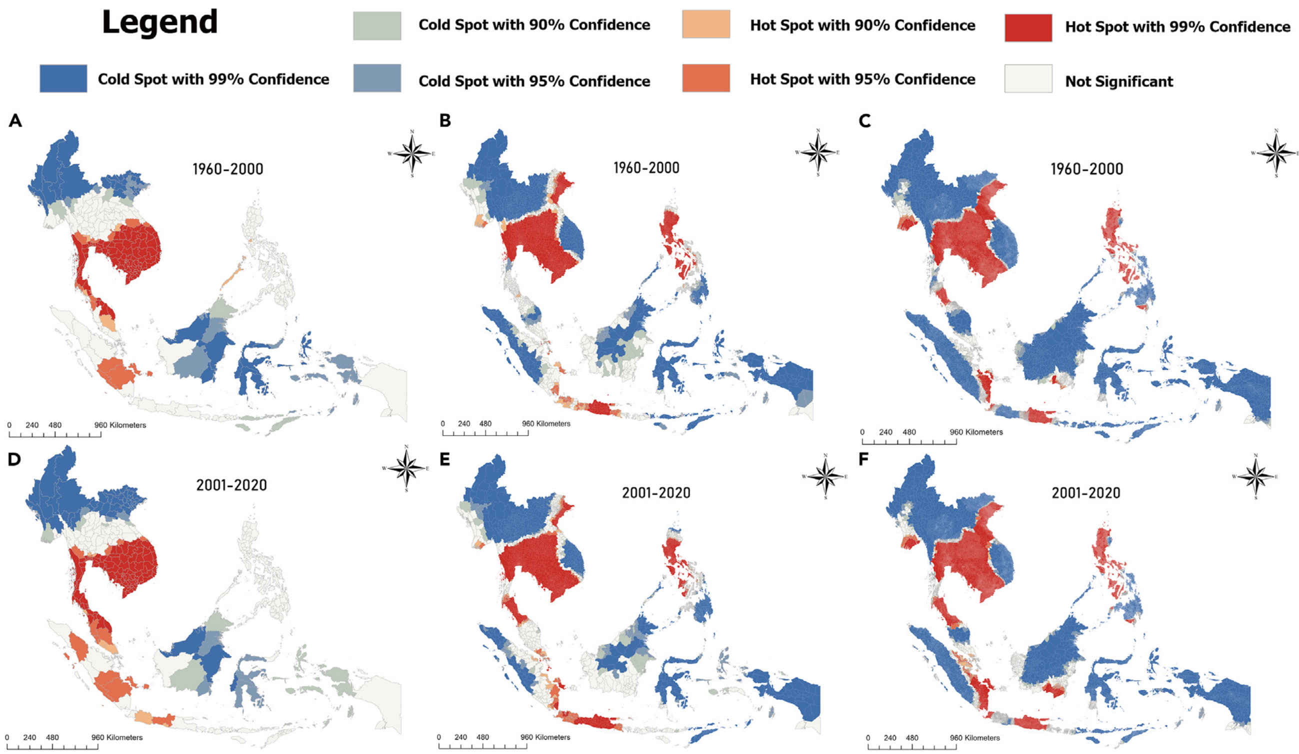

Figure 6. Hotspots for mosquito environmental suitability in Southeast Asia

Indicating *Aedes albopictus* hotspots in administrative regions (province level: A, C; city level: B, E; district level: C, F) during the periods 1960–2000 (A–C) and 2001–2020 (D–F).

For *Aedes aegypti*, the hotspot identification and comparison results showcase distinct patterns compared to *Aedes albopictus* (Figures 7, 8C, 8D, and 8F). At the level 1 administration, hotspot areas are primarily distributed in Cambodia, the southern regions of Vietnam, Thailand, and Laos (Figure 7A). However, when we refine the administrative level, hotspot areas become more concentrated in Cambodia, the northern and central regions of the Philippines, the southern regions of Indonesia and Thailand, and the eastern part of Vietnam (Figures 7B and 7C). In the hotspot comparison for *Aedes aegypti* between 1960–2000 and 2001–2020, finer administrative levels also provide more detailed insights into hotspot changes, revealing an expansion of hotspot areas from coastal regions and a reduction in the inland across countries in Southeast Asia (Figures 8D–8F).

Detecting underlying factors contributing to suitability variations

Our second study employed ten potential explanatory variables across three administrative levels to investigate spatial heterogeneity and changes in mosquito suitability in Southeast Asia. The variables included continuous environmental and socioeconomic conditions, with country region as a categorical variable. Due to administrative level constraints and minimal change over time, land use and topography were excluded.

Using a geographical detector-based approach comprising spatial-scale effect analysis, factor detector, and interaction detector, we first employed the geographical detector to ascertain the optimal analysis scale by evaluating the spatial effects of different administrative levels. This revealed varying impacts of meteorological and socioeconomic factors across spatial units (Figure 9), identifying administration level 1 (province level) as the optimal scale for assessing contributions to suitability changes.

In the next analysis phase, we used factor and interaction detectors to ascertain the suitability of single or multiple variable contributions to mosquitoes. The primary contributors were identified as land surface temperature, monthly minimum air temperature, and vapor pressure (Figure 10). For *Aedes albopictus*, nighttime land surface temperature initially dominated, later shifting toward minimum monthly temperature, with all variables showing an increasing trend in influence over time. Surface shortwave radiation's interaction with daytime land surface temperature was notably impactful, especially when combined with minimum temperature in the last two decades (Figures 11A and 11B).

For *Aedes aegypti*, the influence of nighttime land surface temperature consistently rose, with most meteorological variables' impacts intensifying, except for precipitation (Figures 10C and 10D). Socioeconomic factors like population showed a slight increase in influence, while the country region's effect decreased. Interaction detector analysis underscored land surface temperature's critical role, interacting with shortwave radiation and maximum temperature in different periods to account for a significant part of the suitability variation (Figures 11C and 11D).

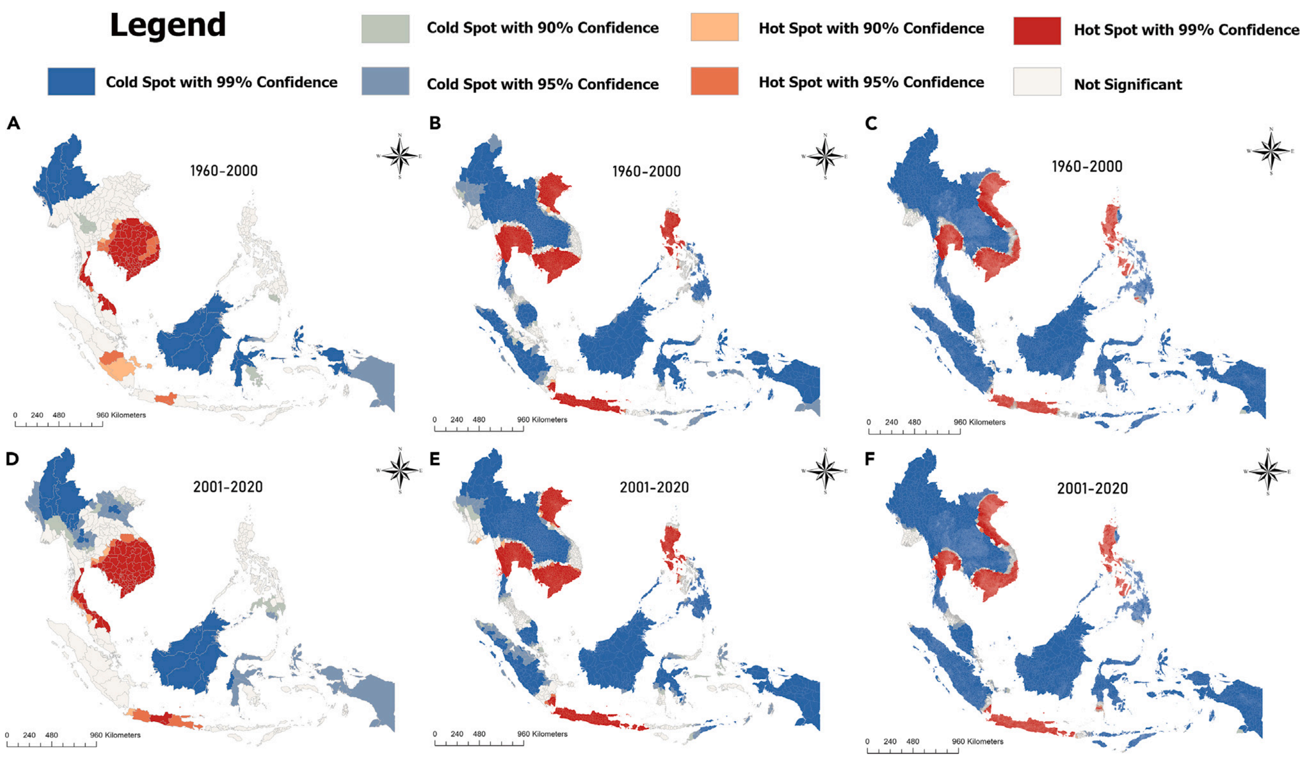

Figure 7. Hotspots for mosquito environmental suitability in Southeast Asia

Indicating *Aedes aegypti* hotspots in administrative regions (province level: A, C; city level: B, E; district level: C, F) during the periods 1960–2000 (A–C) and 2001–2020 (D–F).

DISCUSSION

It is imperative to accurately assess mosquito-borne risk by creating a continuous, long-term, and large-scale suitability map for *Aedes aegypti* and *Aedes albopictus*. However, this crucial task faces substantial challenges in Southeast Asia due to inadequate vector surveillance systems, particularly the absence of comprehensive mosquito surveillance repositories. Moreover, the lack of high-resolution data on micro-climatic and socioeconomic factors further complicates matters, resulting in the unavailability of 500 m resolution maps that can adequately capture the region's historical and current state of mosquito suitability.[24] To generate detailed mosquito suitability maps for 1960–2020, we merged over 38,000 *Aedes* occurrence records (17,661 *Aedes aegypti* and 20,739 *Aedes albopictus*) from 1960 to 2014. The training dataset comprises a high-resolution, long-term meteorological, socioeconomic, and topographic variables dataset. We employed the random forest model to assess mosquito suitability, enabling the evaluation of mosquito environmental suitability for six decades. Importantly, our model consistently yielded high accuracy under three criteria for *Aedes aegypti* and *Aedes albopictus* across the two specified periods. These attest to the reliability and robustness of the mosquito environmental suitability assessments conducted in this study. Furthermore, building upon the high-resolution suitability maps, we present two spatial-temporal applications: multi-scale hotspot identification and comparison and multi-scale geographical detection. These applications advance the analysis of mosquito suitability changes, offering valuable insights for health support planning, particularly in developing countries, and formulating effective mosquito-borne mitigation strategies.

Our high-resolution mapping differentiates the spatial patterns of *Aedes aegypti* and *Aedes albopictus*, highlighting their distinct habitat preferences. While previous maps have shown slight variation between these species' habitats in tropics and subtropics regions,[11,38,39] our analysis reveals a significant divergence. According to our results, *Aedes aegypti* primarily inhabits areas near human settlements, creating discrete clusters of suitable habitats that align with densely populated urban centers in Southeast Asia. In contrast, *Aedes albopictus* exhibits a more widespread distribution across various environments. *Aedes aegypti*'s preference for urban environments and its tendency to feed on humans result in a higher overlap with human populations, increasing the risk of mosquito-borne disease transmission.[17,20] On the other hand, *Aedes albopictus*, known for its adaptability, can thrive in rural and urban areas.[16,20] Given its adaptability, its presence in densely populated regions cannot be ignored, as it carries a substantial risk of transmitting diseases to humans. In summary, our study provides a nuanced understanding of the habitat preferences of these two critical mosquito-borne diseases vectors, emphasizing the importance of considering their distinct spatial distributions in disease prevention and control efforts.

Our research confirms previous findings, particularly about the environmental suitability of *Aedes albopictus* relative to *Aedes aegypti*. This reaffirms that *Aedes albopictus* not only shares a similar level of environmental suitability with *Aedes aegypti* but also sometimes surpasses it. Historically, research has often associated locations with sustained high mosquito-borne diseases such as dengue incidence and explosive

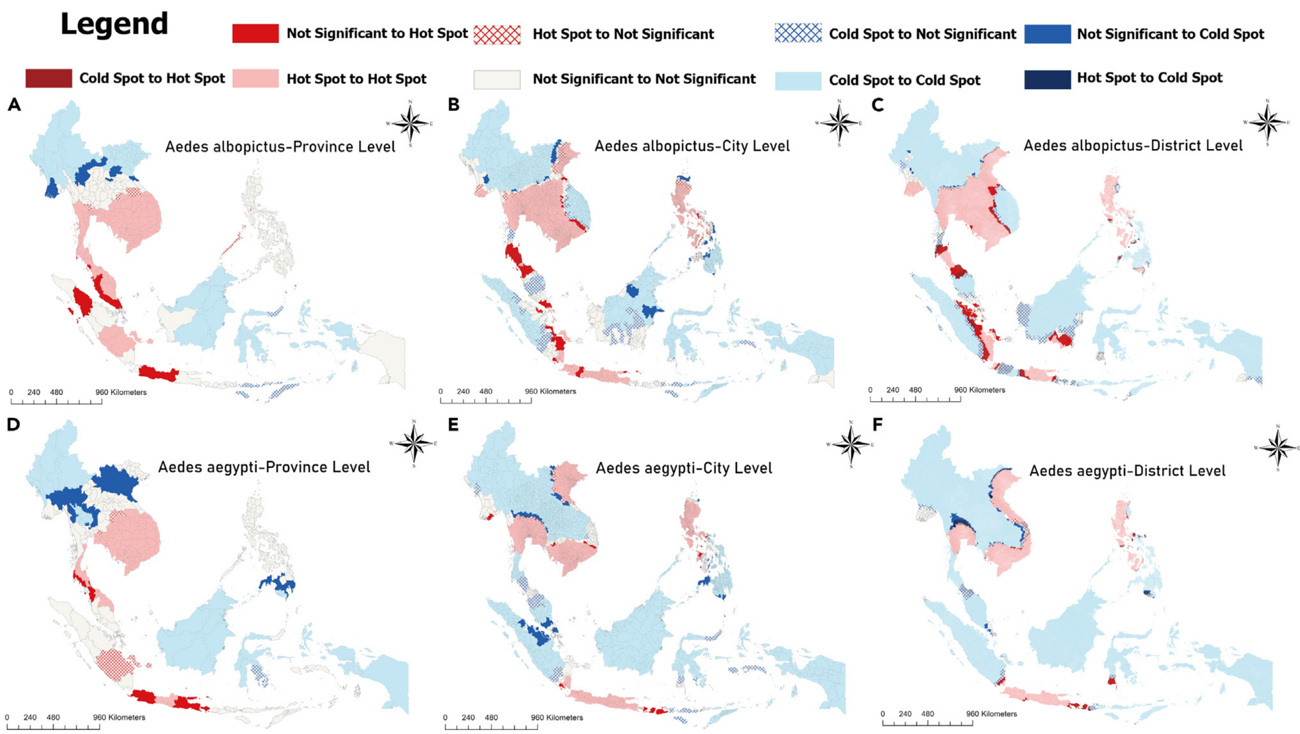

Figure 8. Hotspot comparison of mosquito environmental suitability in Southeast Asia

Results for *Aedes albopictus* are presented for administrative regions: province level (A), city level (B), and district level (C), while results for *Aedes aegypti* are displayed for province level (D), city level (E), and district level (F).

outbreaks with *Aedes aegypti* as the primary (if not the exclusive) vector.[4,40] This led to the prevailing notion that *Aedes aegypti* had a higher competence for disease transmission than *Aedes albopictus*. However, Brady et al.,[41] based on the examination of factors such as extrinsic incubation period and adult survival modeling, also revealed that even the highest temperature suitability values for *Aedes aegypti* were only marginally superior to those of *Aedes albopictus*. Our study not only corroborates Brady's findings by producing a suitability map that exhibits a broader range of highly suitable areas for *Aedes albopictus* compared to *Aedes aegypti* but also builds upon this by incorporating both meteorological and non-meteorological factors into our modeling and evaluation process. Furthermore, our research aligns with previous laboratory experiments that established *Aedes albopictus* as having a longer lifespan than *Aedes aegypti*.[42,43] This extended lifespan creates more suitable habitats for *Aedes albopictus* and increases the time available for them to become infectious and sustain their infectious state compared to *Aedes aegypti*. These findings strongly support that *Aedes albopictus* possesses a disease transmission potential equivalent to, if not greater, *Aedes aegypti*. Additionally, the changing suitability maps for *Aedes aegypti* and *Aedes albopictus* over the past six decades indicate that the suitability area for *Aedes albopictus* has expanded significantly more than that for *Aedes aegypti* (Figures 3 and 4). This expansion suggests that the regions suitable for *Aedes albopictus* are increasing in size. Given these insights, we propose that *Aedes albopictus* may emerge as a more efficient vector, even though the complete demonstration of risk from *Aedes albopictus* transmission awaits further research.

To harness the full potential of our high-resolution map, we present two distinct multi-scale analyses as case studies, which establish a comprehensive and cohesive framework for future research on mosquito suitability changes in Southeast Asia. Historically, investigations into changes in mosquito distribution across Southeast Asia have primarily focused on individual countries or single cities, often lacking the integration of analyses across multiple scales. This fragmented approach has hindered the development of a unified framework for understanding the region's expanding geographic patterns of mosquito distribution. Our research aims to address this gap by illustrating how multi-scale analyses can offer a more systematic and holistic approach. In our first case study, we demonstrate the application of multi-scale hotspot identification and comparison across three different administrative levels: province, city, and district. Notably, finer-scale analyses, especially at the district level, exhibit a greater capacity to elucidate suitability changes in Southeast Asia. Our findings reveal that hotspots of suitability for both *Aedes albopictus* and *Aedes aegypti* are expanding from coastal areas into the hinterlands. This expansion suggests a correlation with human activities influencing the spread of mosquito suitability.[30] However, our second case study, which delves into the spatial effect analysis at different scales using geographical detectors, presents a nuanced perspective. Here, we observe that the coarsest scale, namely administration level 1 (province level), exhibits the highest spatial effect in geographical detectors. This finding suggests that administration level 1 offers a more suitable scale for detecting the underlying factors driving dynamic changes in mosquito suitability across Southeast Asia and may have the best effects on disease control. Furthermore, our detector results highlight land surface temperature during nighttime as a key shared influence on the spatial heterogeneity of *Aedes aegypti* and *Aedes albopictus* suitability. This aligns with prior

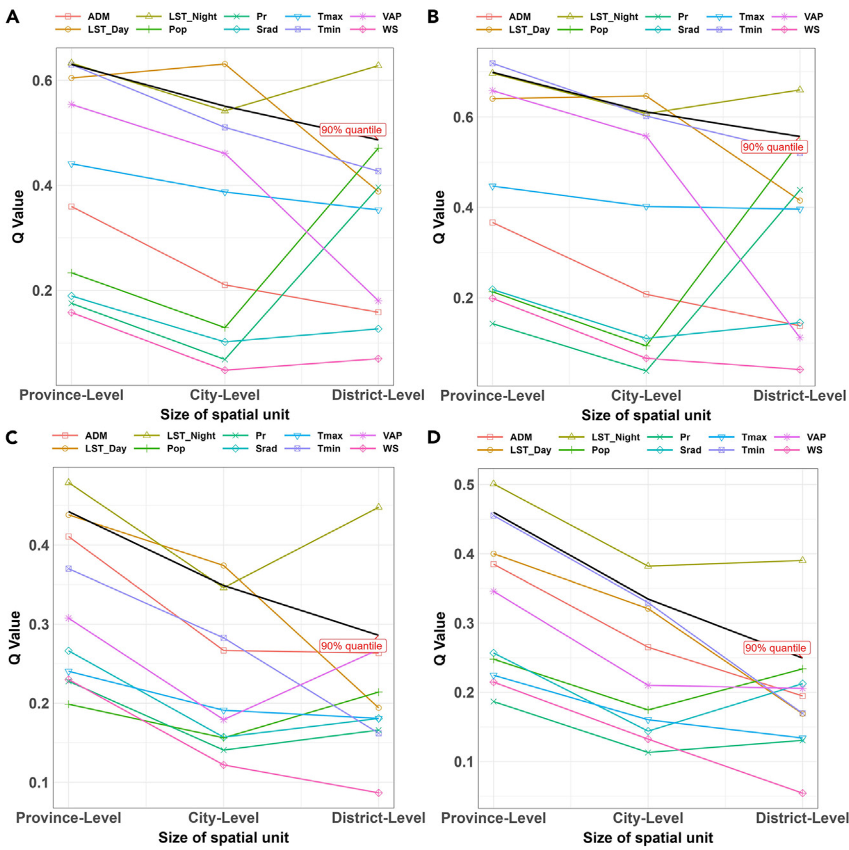

Figure 9. Differences in the Spatial effects of explanatory variables for Q values and the 90% quantile

(A) and (B) represent the analysis of *Aedes albopictus* suitability, while (C) and (D) depict the analysis of *Aedes aegypti* suitability (ADM: country; LST_Night: nighttime land surface temperature; Pr: monthly precipitation accumulation; Tmax: monthly maximum temperature; VAP: monthly vapor pressure; LST_Day: daytime land surface temperature; Pop: population; Srad: monthly surface downwelling shortwave radiation; WS: monthly wind speed at 10 m; Tmin: monthly minimum temperature).

research indicating that urban heat islands influence mosquito suitability.[44,45] Urban heat islands are known to increase the availability of mosquito habitats and expedite developmental rates. Additionally, our results suggest that El Niño events, which lead to rising land surface temperatures,[46] may indirectly impact mosquito suitability.

Limitations of the study

However, this study has limitations that warrant consideration in future research. Firstly, while the majority of our data possess a reasonable temporal resolution, encompassing the period from 1960 to 2020, it is essential to acknowledge that land cover and land surface temperature data were only available from 2001 to 2000, respectively. Our decision to utilize land cover data from 2001 and land surface temperature data from 2000 stems from a strategic compromise to glean insights into historical trends, given the limitations of available data. This methodology, though based on assumptions, aligns with common practices in risk mapping where direct historical data are scarce. For instance, studies using the WorldClim dataset for variables covering only 1970 to 2000 for bioclimatic are still considered valuable references despite not including the most current data, as they contribute to risk estimation insights.[29,34,38,47] Inspired by such precedents, we believe our dataset selection facilitates the estimation of long-term trends essential to our study's goals. Although this limitation is noteworthy as real-world changes over this four-decade span may introduce potential biases into our modeling, it does not undermine our study's overarching findings and conclusions. Our analysis aims to uncover broad patterns and trends, rather than detailing specific historical conditions. Secondly, mosquito suitability does not guarantee mosquito presence, and even when mosquitoes are present, their biting behavior influences human infection rates.[28,48] Thirdly, the incongruence between hotspot analysis and areas identified as highly suitable in the maps is acknowledged as a study limitation known as a modifiable areal unit problem because hotspots may be confined to specific locales within district settlements.[49] Additionally, while research has shown that socioeconomic factors substantially influence mosquito suitability, the precise drivers behind these influences remain somewhat ambiguous. In future endeavors, it becomes essential to establish a comprehensive microclimate and socioeconomic database with a vector surveillance repository conducive to long-term standardized analyses, particularly in developing countries where resources and data management can be challenging. Moreover, future directions should encompass causal analyses to elucidate

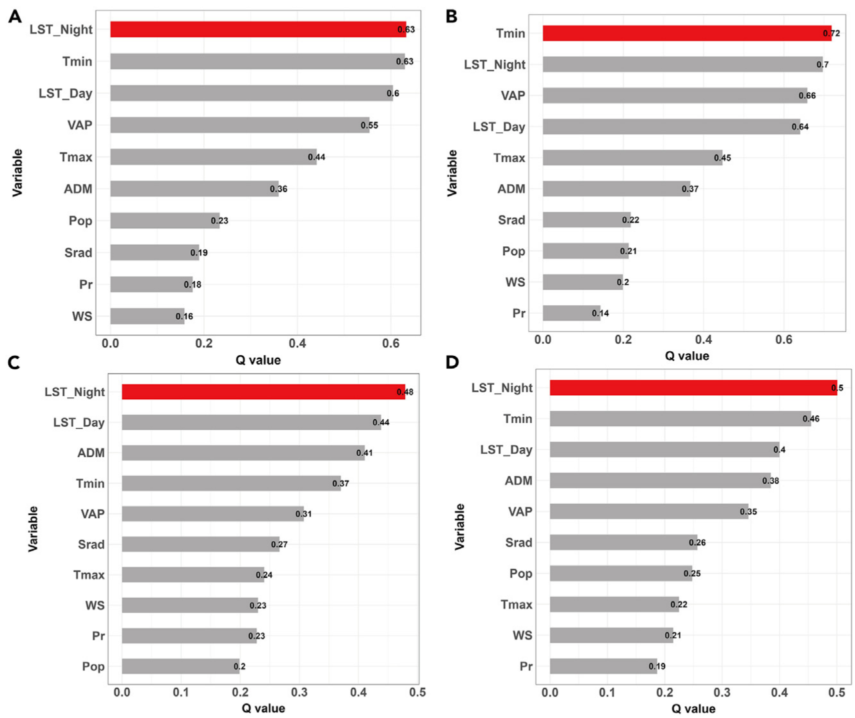

Figure 10. Explanatory variables exploration of suitability changes

The factor detector analyzes the impact of individual variables on suitability changes. Results for *Aedes albopictus* during the periods 1960–2000 (A) and 2001–2020 (B), and for *Aedes aegypti* during the periods 1960–2000 (C) and 2001–2020 (D) (ADM: country; LST_Night: nighttime land surface temperature; Pr: monthly precipitation accumulation; Tmax: monthly maximum temperature; VAP: monthly vapor pressure; LST_Day: daytime land surface temperature; Pop: population; Srad: monthly surface downwelling shortwave radiation; WS: monthly wind speed at 10 m; Tmin: monthly minimum temperature).

the relationship between mosquito suitability and human infection. This inquiry seeks to determine whether a highly suitable mosquito environment directly leads to disease outbreaks and, if so, which key factors drive this phenomenon. Furthermore, network analyses are essential for investigating the interactions between humans and mosquitoes in the propagation of mosquito-borne disease.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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  - Materials availability
  - Data and code availability
- METHOD DETAILS
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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.isci.2024.110498.

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AUTHOR CONTRIBUTIONS

W.H.: conceptualization, methodology, software, validation, formal analysis, investigation, data curation, writing – original draft, and visualization; Y.Z.: conceptualization, validation, formal analysis, investigation, and writing – original draft; W.L.: conceptualization, supervision,

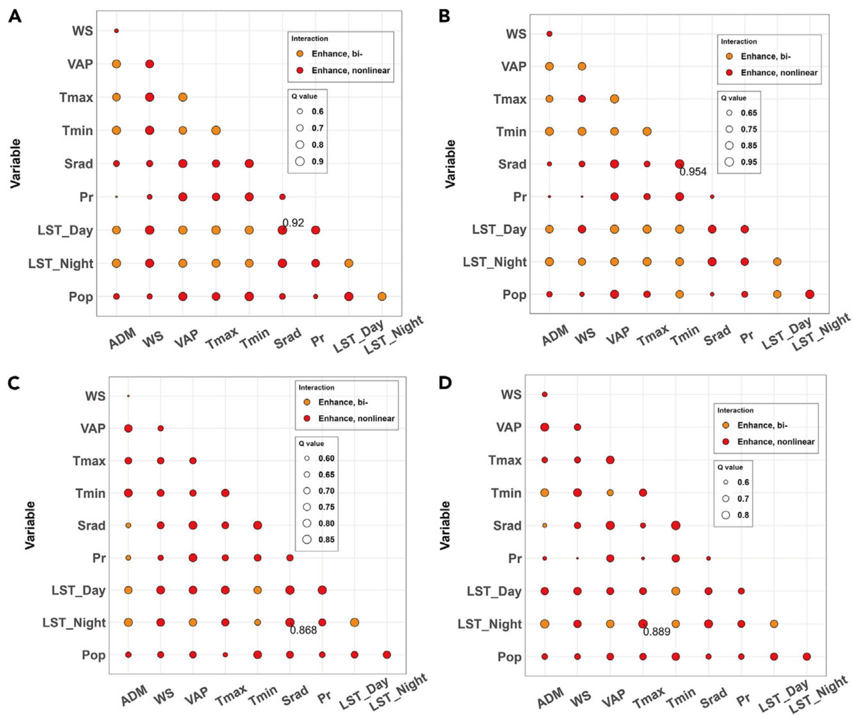

Figure 11. Exploration of explanatory variables in suitability changes

The interaction detector examines the influence of variable interactions on suitability changes. Results for *Aedes albopictus* for the periods 1960–2000 (A) and 2001–2020 (B) and for *Aedes aegypti* for the periods 1960–2000 (C) and 2001–2020 (D) (ADM: country; LST_Night: nighttime land surface temperature; Pr: monthly precipitation accumulation; Tmax: monthly maximum temperature; VAP: monthly vapor pressure; LST_Day: daytime land surface temperature; Pop: population; Srad: monthly surface downwelling shortwave radiation; WS: monthly wind speed at 10 m; Tmin: monthly minimum temperature).

funding acquisition, and writing – review and editing; L.W: writing – review and editing; M.-P.K.: writing – review and editing; A.R.C.: writing – review and editing.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Explanatory Variables	https://developers.google.com/earth-engine/datasets	
Mosquito Presence Dataset	https://datadryad.org/stash/dataset/doi:10.5061/dryad.47v3c	
Software and algorithms		
R and Javascript Codes	https://github.com/GeoSpatialX/SEA_Arbo_Env	

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Dr.Wei Luo (geowl@nus.edu.sg).

Materials availability

New datasets generated in this study have been deposited to the project public repository: https://github.com/GeoSpatialX/SEA_Arbo_Env.

Data and code availability

Analyses in this study were conducted using ArcGIS Pro (Version 3.2) and R. All the data is publicly available and has been detailed in the article and the key resources table. Codes used in this study can be accessed from the project public repository: https://github.com/GeoSpatialX/SEA_Arbo_Env.

Data

- Data have been deposited at https://github.com/GeoSpatialX/SEA_Arbo_Env and are publicly available as of the date of publication. Accession numbers are listed in the key resources table.

Code

- All original code has been deposited at: https://github.com/GeoSpatialX/SEA_Arbo_Env.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

METHOD DETAILS

Methods

Study area

Southeast Asia, located between the Indian and Pacific Oceans, comprises 11 countries across 4,340,700 km^2, with a total population of nearly 690 million in 2023. Southeast Asia is profoundly affected by mosquito-borne disease such as dengue, with alarming statistics showing over 3 million annual cases and more than five thousand deaths attributed to this disease.[5,6] Several factors contribute to this critical situation. Primarily, the region's climate is dominated by monsoonal patterns, characterized by warm temperatures and substantial rainfall, which are highly conducive to breeding *Aedes* mosquitoes.[5,50] Moreover, lower socio-economic conditions in the region contribute to an increase in potential mosquito breeding sites, such as slums with high populations and poor waste management, which contribute to making suitable habitats for larvae.[5,51] Given the socio-economic diversity across Southeast Asia, there is a critical need for localized analyses to understand mosquito distribution patterns concerning socio-economic factors.[51] Although previous high-resolution studies have primarily focused on individual Southeast Asian countries (e.g., Thailand), a comprehensive regional approach remains necessary.[26,52] Furthermore, the prevalent use of mechanistic modeling in these studies may not sufficiently account for the socio-economic complexities of the region, an essential aspect of understanding disease transmission patterns.[24,53,54]

Data

Mosquito presence dataset. Our dataset consolidates records of two principal vectors, *Aedes albopictus* and *Aedes aegypti*, offering precise, georeferenced occurrences (i.e., mosquito presence records). Originating from diverse sources, including peer-reviewed publications like Kraemer et al.[25] and crowd-sourced platforms like "inaturalist.com," each source has its benefits and drawbacks. While peer-reviewed datasets provide high-quality, reliable data, they can be outdated due to lengthy publication processes.[36] On the other hand, contributions from individuals offer real-time updates but may lack reliability and representativeness.[36,37]

In our research, emphasizing the need for reliable training data for species distribution modeling, we utilized the peer-reviewed dataset from Kraemer et al.,[25] encompassing global records from 1960 to 2014 with a resolution of 5 kilometers. We integrated 80% of these records into our training set, reserving 20% from Southeast Asia for validation. To enhance timeliness and ensure validation credibility, we supplemented our data with records from the Global Biodiversity Information Facility (GBIF) spanning 2014 to 2020 within Southeast Asia.[55] Our consistency check using a Student's t-test between the Kraemer et al. (2015) and GBIF datasets from 2000 to 2014 revealed no significant differences ($P > 0.5$), affirming our validation approach. Moreover, we employed sampling correction processes by the *CoordinateCleaner* function in the R package *CoordinateCleaner* (version 2.0).[56] As a result, our training dataset encompasses 20,739 occurrence records for *Aedes albopictus* and 17,661 occurrence records for *Aedes aegypti* across a global scale. For the validation dataset specific to Southeast Asia, we identified 22 occurrence records for *Aedes albopictus* spanning the period from 1960 to 2000 and 124 occurrence records from 2001 to 2020. Similarly, for *Aedes aegypti*, we compiled 45 occurrence records from 1960 to 2000 and 162 occurrence records from 2001 to 2020.

Mosquito pseudo-absence dataset. The Kraemer et al.[25] training dataset is a presence-only compilation of mosquito occurrence records. Recent literature has highlighted the drawbacks of employing solely presence-only datasets in modeling, pointing out the potential for diminished accuracy and inaccurate distribution estimations.[57] To counteract these issues and bolster the model's validity and output value, we integrated pseudo-absence points generated through specific protocols to simulate non-occurrence locations of the mosquitos.

Applying the Third Law of Geography, asserting that similar conditions yield comparable target variable values,[58] we employed k-means clustering to segregate the global environment into two distinct strata. The first aligns closely with mosquito presence records, while the second, differing significantly, forms the basis for our pseudo-absence points. We equated the number of pseudo-absence and presence points globally to ensure balance and data integrity.[59] This approach led to a balanced dataset, blending presence and pseudo-absence mosquito data, thereby minimizing biases in our modeling process.

Meteorological conditions. Temperature, precipitation, and their interaction with humidity play crucial roles in determining the behavior and survival of *Aedes aegypti* and *Aedes albopictus* mosquitoes, influencing factors such as survival rates and biting rates.[41,60] Our analysis focuses on monthly accumulated precipitation, highest and lowest temperatures, and vapor pressure to capture the complex interplay between temperature and humidity.[15,28] Additionally, we integrate land surface temperatures to account for microclimates and urban heat islands,[8] including both daytime and nighttime temperatures, as well as monthly surface downwelling shortwave radiation and wind speed for a comprehensive assessment.[44,61] Our selection of variables is grounded in a comprehensive review of the literature from previous studies. These variables have been demonstrated to effectively represent suitability predictions.

We obtained meteorological data, excluding land surface temperature, spanning 1960 to 2020 from the *Climatology Lab*[62] and land surface temperature data from 2000 to 2020 from the MOD11A2 MODIS product.[63] All data are monthly averages at pixel-level resolution. The non-land surface temperature data covers 1960—2020, while land surface temperature data is available only for 2000-2020. All maps are resampled to a 500-meter resolution using the nearest neighbor method for uniformity. The nearest neighbor method preserves data integrity by assigning new pixel values from the nearest original pixels, which is ideal for high-resolution mapping.[22,64,65]

Socio-economic conditions. Socioeconomic conditions are pivotal in mosquito-borne disease transmission, exhibiting significant variation across different regions.[66] Multiple datasets, such as deprivation indices, exist to quantify these conditions.[67] However, these datasets often present challenges due to their limited applicability to broader research areas, such as climate change's impact on mosquitoes' environmental suitability.[28] One primary issue is the variability in the definitions within these indices, which complicates comparisons with results from other studies, even when indices seemly describe similar conditions.[15,24] Additionally, these datasets are constructed based on diverse standards and modeling techniques, making it difficult for researchers to apply them in predictive studies, such as projecting the effects of climate change on mosquito habitats due to challenges in replication and forecasting.[24,28]

In contrast, population and land use data have shown a high correlation with socioeconomic development and have been commonly utilized in previous research.[60,68] This consistency makes the results from these datasets more comparable with historical studies and facilitates easier reproduction and prediction for future research. Therefore, we selected these two data types to represent the socioeconomic variables in our analysis. For population data, we extracted figures from the Global Human Settlement for the years 1975-1990 at a 250m resolution and from Worldpop for data post-2000 at a 100m resolution, aggregating both to a 500m resolution using Google Earth Engine.[69,70] Our analysis utilizes the International Geosphere-Biosphere Programme's land-use categories. We use data representing the year 2001 to reflect changes spanning from 1960 to 2000, and we incorporate subsequent data from the next 20 years, provided by MODIS MCD12Q1 dataset at a 500m resolution.[71]

Topographic conditions. Topographic conditions encompass tangible geological attributes like slope and elevation. By incorporating these factors, we introduce an additional dimension of analysis that complements the more traditional weight-based approach. To glean insights from these dimensions, we turn to the Shuttle Radar Topography Mission (SRTM), a National Aeronautics and Space Administration (NASA) initiative that offers digital elevation data with a resolution of 30 meters.[72] This dataset forms the foundational source for generating slope and elevation data.

Framework for suitability assessment

This study develops a framework to generate high-resolution maps and quantify changes in mosquito environmental suitability. The framework includes three steps: machine learning techniques for mosquito environmental suitability estimation, machine learning model validation, and spatiotemporal implementation for multi-scale analysis. Figure S2 demonstrates how our model has been structured to create a framework to achieve precision and confidence in our species distribution modeling. We also highlighted the steps in carrying out spatiotemporal analyses for multi-scale investigations. Our primary aim is to illustrate the changes occurring before and during the 21st century, thereby elucidating the alterations in mosquito environmental suitability over time. Furthermore, we contend that the observed variations between these periods logically support our assessment and, importantly, offer a foundation for establishing baselines in climate change impact studies. This underscores the significance of utilizing extended periods of data rather than relying on single-year observations. We split the study periods into two segments: 1960—2000 and 2001—2020, which allows us to compare the variations of environmental suitability for two mosquito species before and during the 21st century.

Species distribution model for mosquito environmental suitability estimation. This study employs a species distribution model using machine learning to generate suitability maps for *Ae. aegypti* and *Ae. albopictus*. We choose the random Forest algorithm for suitability analysis due to its efficacy in handling complex geospatial data. This method synthesizes decisions from multiple decision trees, enhancing prediction accuracy and robustness against overfitting.[73] Such capabilities render it particularly apt for addressing the nonlinear relationships and complex interactions among environmental variables that influence mosquito suitability. Additionally, Random Forest effectively manages collinearity among predictors, ensuring reliable performance even when data variables exhibit high correlation.[30] Finally, its capacity to process large datasets with numerous input variables and provide consistent outcomes solidifies its role as a valuable tool for comprehensive geospatial analyses.[74] Leveraging the inherent capabilities of the Random Forest methodology, the model is implemented within the Google Earth Engine (GEE) platform.[75] We configured the model with 1,000 trees, using the square root of the variables per split, a minimum of 10 training sets for node creation, and bagging 0.5 fraction of inputs per tree, thereby optimizing for both robust performance and computational efficiency in one setup.[30,34] To enhance predictive accuracy and reduce uncertainty, a tenfold execution approach is employed. This involves running the model ten times and aggregating the results to obtain mean values for each 500m * 500m pixel.

Model validation. To assess our model's performance, we rely on the Area under the Receiver Operating Characteristics curve (AUC) as our performance metric. This selection is based on its proven ability to be independent of prevalence, rendering it an effective measure of a model's discriminatory ability for probabilistic models.[76,77] Within the AUC curve, the false positive rate occupies the "X" axis, while the true positive rate resides on the "Y" axis. A curve that aligns more closely with the "Y" axis signifies heightened precision in model predictions.[78] The true positive rate indicates the model's effectiveness in correctly predicting positive instances, while the false positive rate represents the proportion of negative instances that are incorrectly identified as positive.[77,78] A model's predictive precision is higher when its curve closely approaches the Y-axis, underscoring its capability to accurately distinguish between the presence and absence of a condition.[77] With values ranging from 0 to 1, a higher AUC value indicates superior model performance.[78] An AUC exceeding 0.8 suggests the model's potential to distinguish suitable from unsuitable areas for the species.[39] Additionally, we employ root mean square error (RMSE) and mean absolute error (MAE) to validate model performance, in accordance with methodologies outlined in relevant literature.[79] The equations for RMSE and MAE are defined as follows:

$$RMSE = \sqrt{\frac{1}{N}\sum\left(\widehat{Y}_m - Y_m\right)^2} \quad \text{(Equation 1)}$$

$$MAE = \frac{1}{N}\left|\widehat{Y}_m - Y_m\right| \quad \text{(Equation 2)}$$

In these equations, Y_m (where m=1,..., N) represents the actual observations of mosquito presence and pseudo-absence, with suitability equal to 1 indicating presence and suitability equal to 0 indicating pseudo-absence. $\widehat{Y}_m$ represents the predicted suitability. Lower values of RMSE or MAE indicate better model performance. We validate the 1960—2000 and 2001—2020 periods, thus confirming our model's utility for analysis and interpretation across these distinct temporal intervals. We utilized the *pROC* R package (version 1.18.0) for the AUC assessment and the *Metrics* R package (version 0.1.4) for the RMSE and MAE calculations.

Spatiotemporal implementation for multi-scale analysis. After generating high-resolution suitability maps for *Aedes aegypti* and *Aedes albopictus* spanning 1960—2000 and 2001—2020, we delve into a landscape of spatiotemporal exploration. Our high-resolution suitability maps broaden the scope for a wide range of spatiotemporal analyses, particularly in multi-scale investigations into changes in mosquito environmental suitability and their underlying factors. To further highlight the application prospect of our high-resolution maps, we illuminated two case studies that comprehensively demonstrate the spatiotemporal dynamics of mosquito environmental suitability changes across three administrative levels in Southeast Asia and the associations between meteorological and socioeconomic factors and suitability.

Multi-scale hotspot analysis (HSA). Our case study unfolds with a spatial autocorrelation model for multi-scale hotspot analysis (HSA) to identify mosquito suitability hotspots. HSA stands as a prevalent approach in public health risk assessment, aimed at pinpointing areas characterized by high values (hotspots) and low values (cold spots).[80] The process comprises two stages. The first entails hotspot identification using the *Getis-Ord Gi** statistic, which yields z-scores and p-values. Regions with elevated z-scores and low p-values are tagged as hotspots, while those with diminished z-scores and p-values signify cold spots. The subsequent stage encompasses hotspot comparison, unveiling areas that change the risk profile. Our HSA case study aims to unearth the most pivotal areas of suitability for *Aedes aegypti* and *Aedes albopictus* across Southeast Asia, unraveling shifts across 60 years. We utilized the *hotspot analysis* tools in *ArcGIS Pro* (version 3.2.0).

Multi-scale geographical detector (GD). Our second case study involves harnessing the Geographical Detector (GD) to unearth the underlying factors driving mosquito suitability variations. GD operates under the premise that if an explanatory variable significantly impacts a response variable, it should exhibit similar geographical distributions.[81] The GD framework, widely used for exploring connections between physical/socioeconomic factors and response variables like greenspace exposure and H1N1 flu incidence distribution, helps uncover the underlying drivers of mosquito environmental suitability changes.[81,82] We deploy factor geographical detectors and interaction detectors. Factor geographical detectors probe the spatial heterogeneity of mosquito environmental suitability, quantifying the relative importance of explanatory variables—both meteorological and non-meteorological—using Q values that range from 0 to 1. Elevated Q values signify a link between explanatory variables and spatial suitability heterogeneity, spotlighting the most influential factors shaping distribution. Complementing these efforts, interaction detectors bridge the gap left by factor detectors by examining how explanatory variables collectively impact the response variable. These interaction detectors juxtapose the Q values of two explanatory variables, revealing the interplay between these variables and the response. Building upon these insights, spatial effects are compared across different scales of analysis, unveiling the optimal spatial scale for future explorations of suitability heterogeneity.

We explored spatial heterogeneity and temporal shifts in mosquito environmental suitability within Southeast Asia by utilizing ten potential explanatory variables across three administrative levels. These variables encompassed a range of continuous environmental and socioeconomic factors, including country region as a categorical variable to minimize variable bias and control for unmodeled confounders.[83] Due to constraints at the administrative level and the negligible changes observed over time, variables such as land use and topography were not considered. The selected variables for our geographical detector analysis are detailed in Table S2. We focus on analyzing the Q value differences between the two periods, with changes in these variables indicating shifts in their contributions to the heterogeneity of mosquito suitability. We conducted spatial heterogeneity analysis using the geographical detector from the *GD* R package (version 1.1).