

Estimating global invasion risk of *Vespa affinis* with variable environmental scenarios

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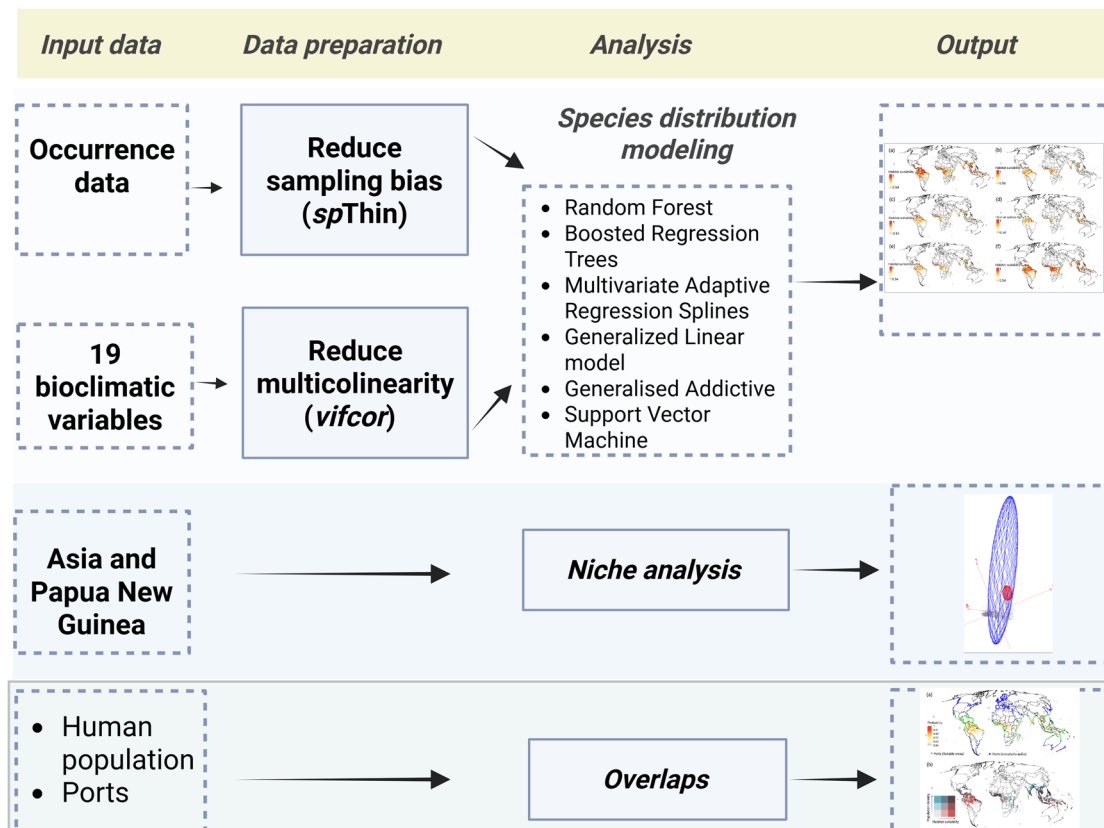
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Human activities are reshaping ecosystems worldwide, facilitating the spread of invasive insect species beyond their native ranges. The lesser banded hornet *Vespa affinis* Linnaeus (Vespidae:Vespa), a known predator of honeybees, poses risks to public health and apiculture outside its native range. However, whether suitable habitats for *V. affinis* overlap with human population hotspots and international ports are poorly understood. Here, we used an ensemble modeling approach to assess the probability of *V. affinis* establishment and invasion risks. Specifically, we considered global habitat suitability for this species under baseline (current) conditions (1970–2000) and in 2081–2100 (2090s) under the socioeconomic pathway (ssp585) scenario. Our models suggest that suitable areas for *V. affinis* will increase by over ~21% from now (2.06×10^7 km²) to the 2090s (2.49×10^7 km²). High-risk international ports are mainly concentrated in Africa, Southeast Asia, the Caribbean, and central parts of the Americas. Our findings also suggest there is high likelihood for human–hornet interactions and public health concerns in South and Southeast Asia, West Africa, and northern South America. These findings provide key insights into the hornet’s potential distribution and risk areas supporting targeted monitoring efforts and the development of biosecurity strategies to mitigate its spread.

Keywords: ensemble model, biogeography, hornets, honey bees, public health

Graphical abstract



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Introduction

Human activities, such as global trade and travel, are major drivers of biological invasions, enabling species to bypass natural barriers and establish in new regions (Hulme 2021). Although much invasion biology research is reactive, it is also key to proactively identify species that may become invasive and project their risk (Sales et al. 2019, Finch et al. 2021). Such approaches are particularly important for groups with a history of becoming invasive such as hornets (Zhu et al. 2020, Taylor et al. 2024). Identifying regions suitable for species establishment is important for targeted monitoring, biosecurity risk assessment, and development of management strategies should invasions occur (Sales et al. 2019, Finch et al. 2021). In introduced areas, environmental conditions affect species establishment and spread, and projecting distributions under current and future scenarios is further important to assess where an invader may establish (Finch et al. 2021).

Recent invasions of several hornet species have been driven by increased human transport and trade between countries with areas having similar climatic conditions and available nesting and foraging resources (Zhu et al. 2020, Lima et al. 2022, Taylor et al. 2024). These same drivers are relevant for the lesser banded hornet (*Vespa affinis* L), a predator of honeybees that threatens apiculture and public health (Kimsey and Carpenter 2012, Kularatne et al. 2014). *Vespa affinis* is native to Asia, from India to the Bismarck Archipelago, and occurs across tropical and subtropical Asia (Kimsey and Carpenter 2012, Gunasekara et al. 2019, Bequaert 2025). Beyond its native range, *V. affinis* has been detected in New Zealand and California, USA, but there is no evidence of sustained populations (Kimsey and Carpenter 2012, Smith-Pardo et al. 2020). Such limited evidence of establishment to date may reflect limited surveillance, low propagule pressure, and environmental mismatch with the fundamental niche of the hornet. Yet, *V. affinis* exhibits broad ecological flexibility, foraging on diverse resources such as nectar, fruits, tree sap, and insect prey. Additionally, *V. affinis* can nest in a variety of natural and anthropogenic substrates, consistent with traits associated with adaptive capacity in hornets and within its Asian range (Smith-Pardo et al. 2020).

As with all invasive species, defining suitable habitats for the establishment of *V. affinis* is essential for early detection, targeted monitoring, and management. Accordingly, it is essential to project suitable areas for *V. affinis* under current and future environmental scenarios while also mapping human–hornet overlap. This will provide insights to safeguard agriculture, public health, and biosecurity while aiding in deployment of resources for hornet monitoring and mitigation (Gallardo et al. 2024). Species distribution modeling of *V. affinis* could help identify suitable geographic areas, allowing researchers to predict where the species might spread beyond their current range (Aidoo et al. 2023). A newer species distribution modeling approach, ensemble modeling, integrates multiple algorithms to improve prediction accuracy by balancing the strengths of individual models and could be used for *V. affinis* (Harris et al. 2024).

In this study, we addressed 4 complementary objectives. First, we assessed the current distribution and environmental niche of *V. affinis*. Second, we tested whether predictive habitat suitability models could accurately identify regions with high future potential for *V. affinis* establishment. Third, we assessed how environmental variability into the future might affect

habitat suitability for *V. affinis* over the next 75 years. Fourth, we assessed spatial and socio-environmental implications of potential range shifts, including overlaps with ports, and human population density. By addressing these research goals, our study provides a framework for future monitoring and eradication of *V. affinis* in invaded regions. More broadly, we show how linking models with a risk management framework can be used to estimate impacts of future invasive species.

Materials and Methods

Species Data

To assess the known distribution of *V. affinis*, occurrence records were obtained from the Global Biodiversity Information Facility (<https://www.gbif.org/species/1311357>) (11 January 2026) and scientific literature. A total of 1534 records were initially retrieved from the hornet's known distribution range. We filtered records by removing duplicates, records with erroneous or lacking coordinates, and records sharing the same grid cells. We also applied a 50 km thinning distance between observations using the “*spThin*” package in R (Aiello-Lammens et al. 2015), reducing the dataset to 285 unique records for simulations (Fig. 1a). This distance was enforced to reduce spatial autocorrelation and sampling bias, ensuring that records were spatially independent and evenly distributed. This prevents overrepresentation of densely sampled regions and improves the robustness and generalizability of model predictions (Steen et al. 2021).

Environmental Data

To relate occurrence data of *V. affinis* to environmental conditions, 19 bioclimatic variables were obtained from the WorldClim database based on monthly temperatures and precipitations averaged over 1970–2000 (current) (baseline) (Table S1) (Fick and Hijmans 2017). We excluded 4 variables (mean temperature of the wettest quarter, mean temperature of the driest quarter, and precipitation of the warmest and coldest quarters) that can lead to discontinuities within interpolated environmental scenario surfaces (Escobar et al. 2014, Booth 2022). To reduce multicollinearity among the 15 remaining environmental variables, we defined the study region using a minimum convex polygon around the occurrence records with a 6-degree buffer (Kass et al. 2023). The variance inflation factor was assessed using the *Vifcor* function ($th=0.7$) in the *usdm* package in R (Naimi and Araújo 2016), resulting in selection of 5 key variables for species distribution models: mean diurnal temperature range, temperature seasonality, maximum temperature of the warmest month, precipitation of the wettest month, and precipitation of the driest month (Table S1).

Future suitability was projected using 6 CMIP6 general circulation models (GCMs): MRI-ESM2-0, BCC-CSM2-MR, CNRM-CM6-1, EC-Earth3-Veg, IPSL-CM6A-LR, and MIROC6 (Fick and Hijmans 2017, Tatebe et al. 2019, Meinshausen et al. 2020). These models were selected to represent a range of climate sensitivities and structural differences within CMIP6. Although individual GCMs may exhibit regional biases, using a multimodel ensemble allows intermodel uncertainty to be captured and reduces reliance on any single model. These data were applied to project the potential distribution of *V. affinis* for the late-century period (2081–2100: 2090s) for Socioeconomic pathway 585 (SSP 585). We

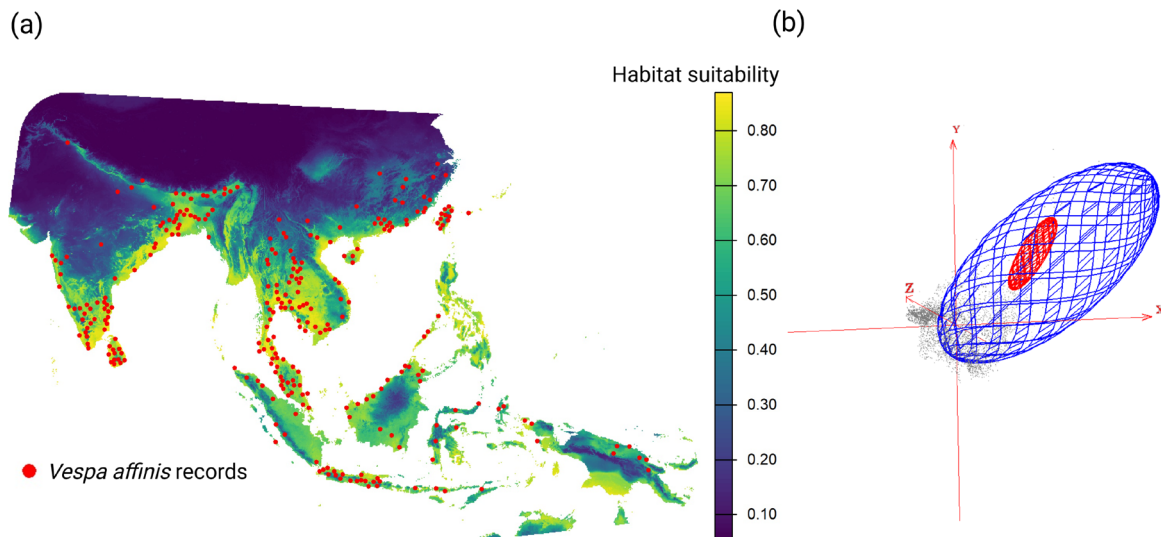


Fig. 1. Global distribution and niche analysis of *Vespa affinis*: (a) native and invaded records, and (b) minimum volume ellipsoids represent presence of *Vespa affinis* in environmental space. Overlapping ellipsoids indicate similar conditions in Asia (blue) and Papua New Guinea (red).

selected SSP585 as a stress-test scenario to evaluate upper-bound exposure and invasion risk under extreme warming, which is particularly relevant for early warning, biosecurity planning, and identifying worst-case spatial hotspots in a global analysis. Next, mean suitability across the 6 GCMs was calculated to represent the central tendency of projected invasion risk, whereas model agreement was quantified by summing thresholded binary projections, with higher values indicating stronger consensus among models.

Realized Niche Simulation

We assessed the environmental conditions of *V. affinis* in Asia and Papua New Guinea where it has naturalized using minimum volume ellipsoids. This analysis evaluates regional niche differentiation rather than a native versus non-native comparison. To achieve this, we constructed a 3-dimensional space derived from the first 3 principal components, which summarized 87% of the variations in the 4 original bioclimatic variables using the Niche Analyst (Qiao et al. 2016). This approach captures most of the information present in the environmental variables. Then, we plotted occurrence records of *V. affinis* from Asia and Papua New Guinea in environmental space to visualize their positions and environmental spread.

Species Distribution and Risk Modeling

The habitat suitability for *V. affinis* at a global scale was assessed by building an ensemble model with the *sdm* package in R (Naimi and Araújo 2016). Ensemble models are superior for prediction tasks compared to individual models as they integrate multiple algorithms, reducing model-specific bias and improving robustness (Marmion et al. 2009). Herein, we implemented an ensemble model approach combining 6 widely used habitat suitability models: (i) boosted regression trees, (ii) generalized additive model, (iii) generalized linear model, (iv) multivariate adaptive regression splines, (v) random forest, and (vi) support vector machine. Model training used 70% of the dataset, with 30% for testing.

A background-to-presence ratio of around 1:1 is enough to optimize habitat suitability models (Rausell-Moreno et al.

2025). Herein, 286 pseudo-absence points were randomly generated to optimize our model predictive performance, and simulations were run with 10 replicates. Bootstrapping was employed for model building, and suitability predictions were generated using a weighted ensemble approach. We created a binary habitat suitability map using a threshold of maximum sensitivity plus specificity [Max(se+sp) = 0.54]. Model performance was evaluated using the area under the curve (AUC) and the true skill statistic (TSS), with thresholds for acceptable performance of AUC > 0.7 and TSS > 0.4 (Allouche et al. 2006, Mandrekar 2010). All analyses were performed in R statistical software (version 4.4.1: 2024).

In native and invaded areas, *V. affinis* can attack humans in residential areas and threatens apiculture and pollination. Hence, we overlaid our predictions with human population density data (CIESIN 2017) to identify areas at risk for damaging outcomes of invasions. Additionally, Otis et al. (2023) showed a common pathway for hornet spread is through the transport gynes via shipping goods. Hence, we obtained international port locations from the Natural Earth Ports dataset (1:10 m cultural vector layer: <https://www.naturalearthdata.com/downloads/10m-cultural-vectors/>). Port-level climatic suitability was assessed by combining binary outputs with a 100 km buffer analysis around each global port. Ensemble suitability rasters (current and future scenarios), and mean suitability was calculated within each buffer as the proportion of suitable area. Ports were then ranked based on the empirical distribution of these buffer-level mean suitability values and classified into 4 risk categories: low (0–25), intermediate (25–50), high (50–75), and very high (75–100 percentile). Due to unavailability of these data in the future, we used the current data as a proxy for future prediction comparisons.

Results

Realized Niche Comparisons

By plotting the first 3 principal components in a 3-dimensional space, we were able to compare the niche overlap between populations from Asia and Papua New Guinea (Fig. 1b). We found overlap between the ecological niches of the 2

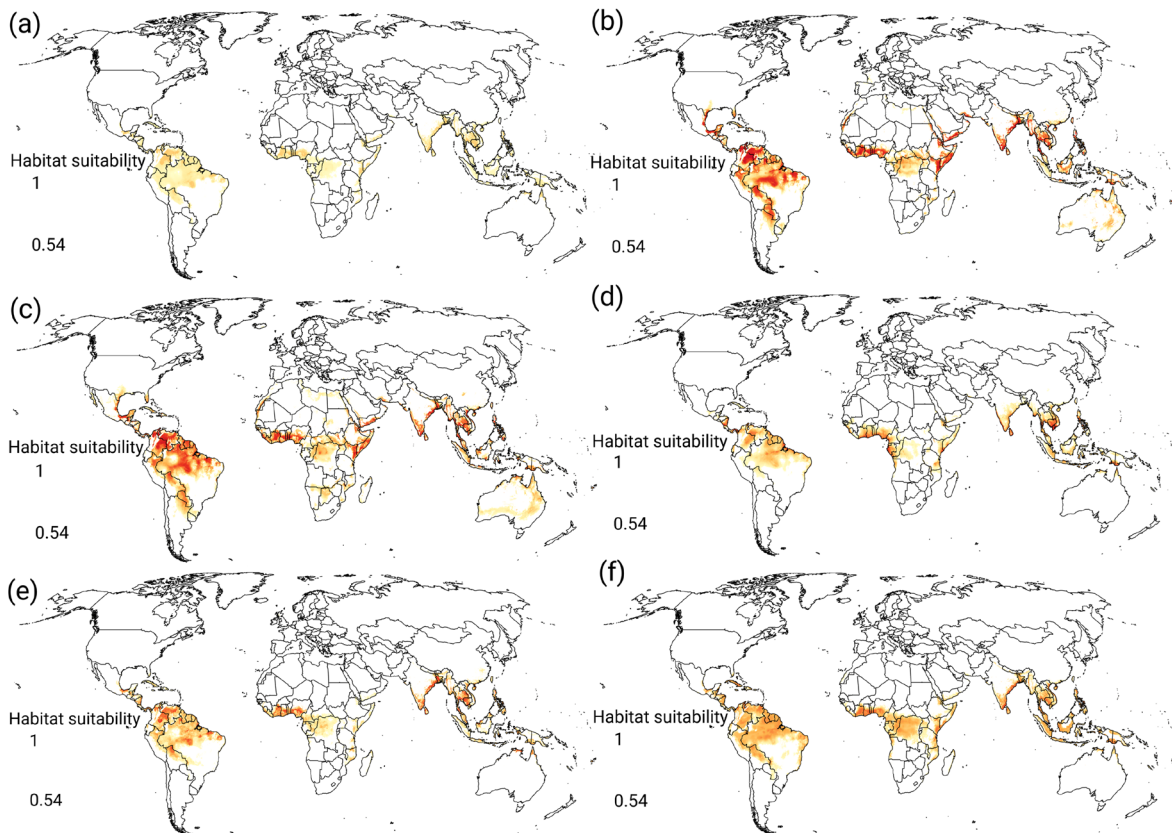


Fig. 2. Predicted habitat suitability for *Vespa affinis* with (a) boosted regression trees, (b) generalized additive model, (c) multivariate adaptive regression splines, (d) generalized linear model, (e) random forest, and (f) support vector machines, using a binary threshold of 0.54.

populations based on their ellipsoid volumes, suggesting environmental niche space was conserved. Furthermore, we show that the population in Papua New Guinea has the potential to expand its range, potentially occupying areas currently inhabited by the hornet within its Asian distribution.

Model Performance

We assessed the probability of *V. affinis* presence using an ensemble modeling approach, and all 6 of our modeling techniques showed good predictive performances (Table S2; Fig. 2a–f). Among the 6 models, the random forest model achieved the highest AUC and TSS values of 0.94 and 0.78, respectively. In contrast, the generalized linear model had the lowest performance, with AUC and TSS values of 0.82 and 0.55, respectively. These results indicate that various species distribution modeling approaches can effectively simulate the global distributions of *V. affinis*. The correlation (Fig. S1), variance (Fig. S2), and combined variance–correlation analysis (Fig. S3) together reveal the level of agreement and divergence among modeling algorithms in predicting the habitat suitability of *V. affinis*. Moreover, response curves which show how *V. affinis* responds to each bioclimatic variable are illustrated in Fig. S4. We found no single trend across all models highlighting how each algorithm interprets environmental variables uniquely.

Global Habitat Suitability

Our analysis identified many environmentally suitable habitats for *V. affinis* beyond its known distribution, particularly in parts of the Americas, Asia, and Africa (Fig. 3a). These baseline suitable areas covered about 2.06×10^7 km² of global area. In

Africa, high suitability was detected in western, central, and eastern regions, while in South America, suitable areas were identified in the northwest and southern regions. The most suitable areas in parts of the Americas include Brazil, Peru, Colombia, Venezuela, Nicaragua, Costa Rica, Honduras, and Bolivia. In the United States, suitable habitats were primarily found in the southern regions.

From the present to the 2090s, the probability of *V. affinis* presence is projected to increase from 2.06×10^7 to 2.49×10^7 km² (Fig. 3b). Habitat shifts, including expansion and contraction, were primarily observed in the Americas, Asia, and Africa, with this trend continuing through the 2090s (Fig. 3c). Additionally, parts of Europe are expected to have low suitability for *V. affinis* in the future compared to the other continents. The Americas consistently had the highest habitat suitability values, followed by Africa and Asia (Fig. 4a and b). In contrast, Europe and Oceania showed relatively low suitability across all scenarios and periods. High agreement among projections occurred across the tropical belt, including the Amazon Basin, Central Africa, and South/Southeast Asia. Agreement declined toward range edges, where projections diverged (Fig. S5). Core regions therefore show high confidence, whereas peripheral areas indicate greater uncertainty. However, areas predicted to be highly suitable were accompanied by slightly higher prediction uncertainty (Figs S6 and S7).

Port Risks and Human Population Impacts

Several major international ports fall within the very high percentile of environmental suitability for *V. affinis*, particularly along the coasts of Southeast Asia, West Africa, and South and

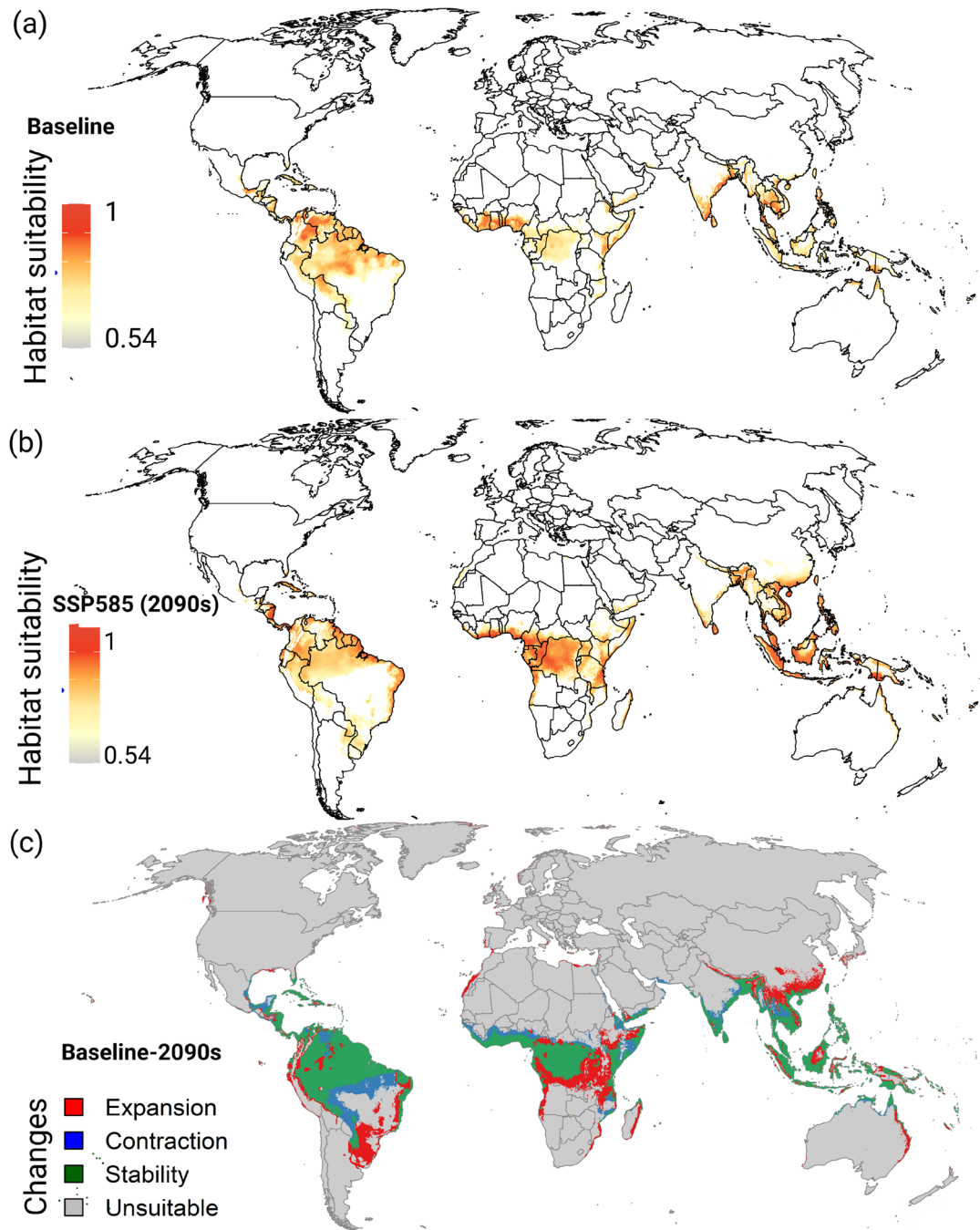


Fig. 3. Projected current and future habitat suitability for *Vespa affinis*. (a) Baseline (current: 1970-2000) habitat suitability map with suitability > 0.54. (b) Projected habitat suitability for the 2090s (ssp585:2081-2100). (c) Spatial changes in suitability from baseline to future, with red indicates suitable habitat expansion, blue contraction, green stable suitability, and gray unsuitable in both periods.

Central America (Fig. 5a). Under current conditions, a high proportion of ports in these regions are classified within the high and very high suitability percentiles, indicating a high likelihood of hornet establishment following introduction at these entry points. Our overlay assessment show that densely populated regions near coastal ports, including parts of India, Indonesia, and West Africa, fall within zones where the hornet could become established (Fig. 5b). Similarly, future projections of *V. affinis* suitability show a marked expansion across tropical and subtropical regions, especially along coastal zones with major ports. Notably, many of these areas overlap with regions

that currently have ports and high human populations (Fig. 6a and b). These areas cover West and East Africa, Southeast Asia, and northeastern South America.

Discussion

Invasive hornets pose a major threat to agriculture, biodiversity, and beekeeping, and the detection of many hornet species outside their native range has also greatly increased recently (Husemann et al. 2020, O'Shea-Wheller et al. 2023). Given the threats *V. affinis* and other hornets present to human and

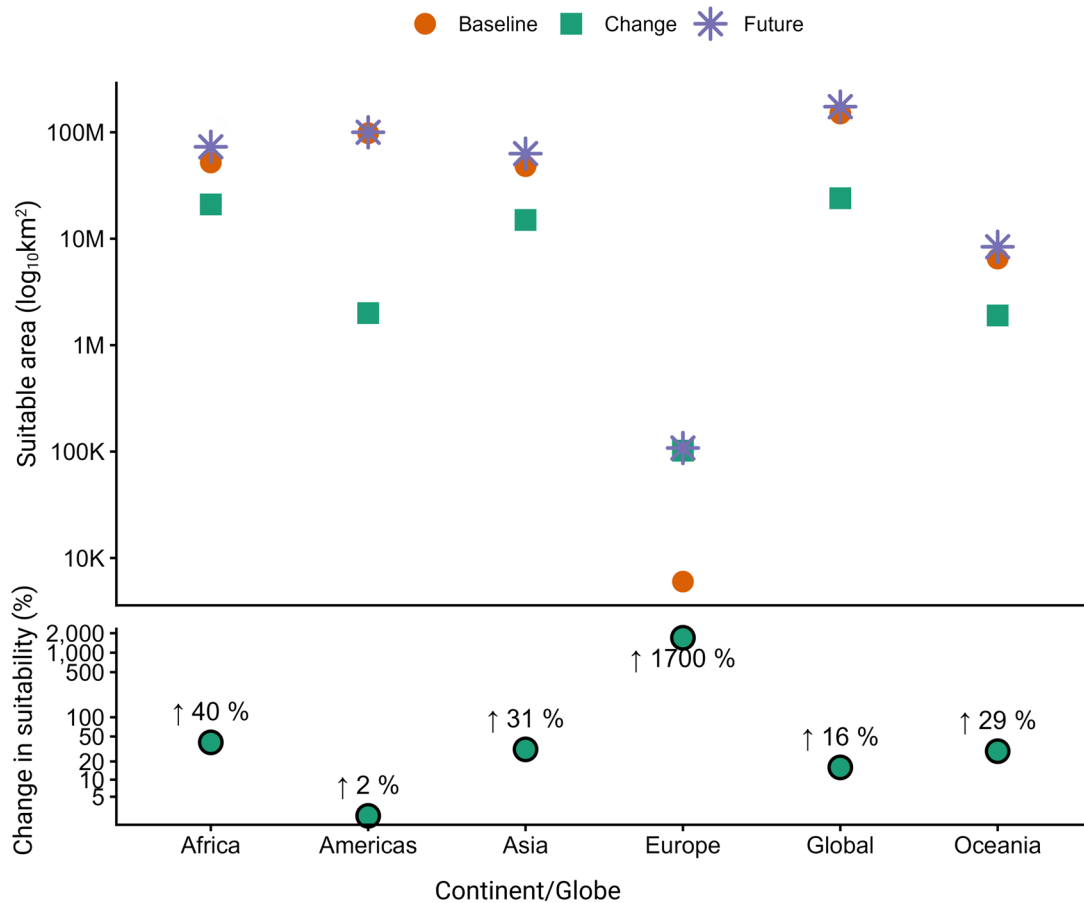


Fig. 4. Changes in projected habitat suitability for *Vespa affinis* in future climates. (a) Total area (log₁₀ km²) of suitable habitat at baseline (current: 1970-2000) (orange circles), future (ssp585: 2081-2100) (gray asterisk), and absolute change (green squares). (b) Percent increase in suitable habitat areas per region.

bee health, predicting their global spread and monitoring these predictions is essential. This study employed an ensemble modeling approach to assess global habitat suitability for *V. affinis*. Ensemble modeling integrates multiple models to capture the central tendency, improving predictive accuracy and robustness by leveraging the strengths of different techniques (Thuiller et al. 2009, Naimi and Araújo 2016). While all of our models showed good predictive performance (Allouche et al. 2006, Mandrekar 2010), comparing among them may be useful for understanding variance in potential invasion outcomes.

Our predictions align with the current distribution of *V. affinis* while identifying potential range expansion. Specifically, we found high habitat suitability in West, Central, and East Africa, parts of South and North America, and the northern fringes of Australia. *Vespa affinis* has been reported in the United States, Australia and New Zealand, but no further records have been obtained (Harris and Patrick 1997, Smith-Pardo et al. 2020). In the United States, although *V. affinis* was reported in California, our model predicts relatively low habitat suitability in this state, and this may be more due to its coastal proximity than suitability; invasions into other more suitable areas may be more likely to establish. We found that *V. affinis* is most likely in environments with warm, humid environments with high precipitation, low diurnal temperature variability, and relatively stable annual temperature regimes. Such findings confirm why the hornet is widely distributed in

tropical and subtropical regions (Archer 2012). We found high suitability for the hornet in China, Iran, India, and Brazil, which each have high agricultural pollination needs (Lautenbach et al. 2012, Rahimi and Jung 2025).

Hornets such as *V. affinis* can directly attack native and managed pollinators or alter their foraging behavior, leading to reduced activity, spatial displacement, and local declines in the abundance of wild and managed pollinators (Rome et al. 2013, Tan et al. 2007, O'Shea-Wheller et al. 2023). These effects can cascade in agricultural systems by reducing pollination efficiency and crop visitation rates, with consequences for regions that rely heavily on insect-mediated pollination for food production and yield stability (Klein et al. 2007). Beyond implications for pollination services, our spatial projections have relevance for apiculture and honey production systems. Our projections highlight regions in South and Southeast Asia, West Africa, and South America where *V. affinis* suitability overlaps major beekeeping areas (Boncristiani et al. 2021, Guerin et al. 2025). These are regions where targeted surveillance, apiary-level protection, and early intervention may be most effective in mitigating economic impacts on beekeepers.

The projected expansion of suitable habitat for *V. affinis* in Asia, Africa, and the Americas presents serious concerns for human safety. This hornet is known for its aggressive behavior and painful stings, which can lead to severe allergic reactions and, in some cases, fatalities (Kularatne et al. 2014). The hornet is predicted to have a high probability of occurrence in

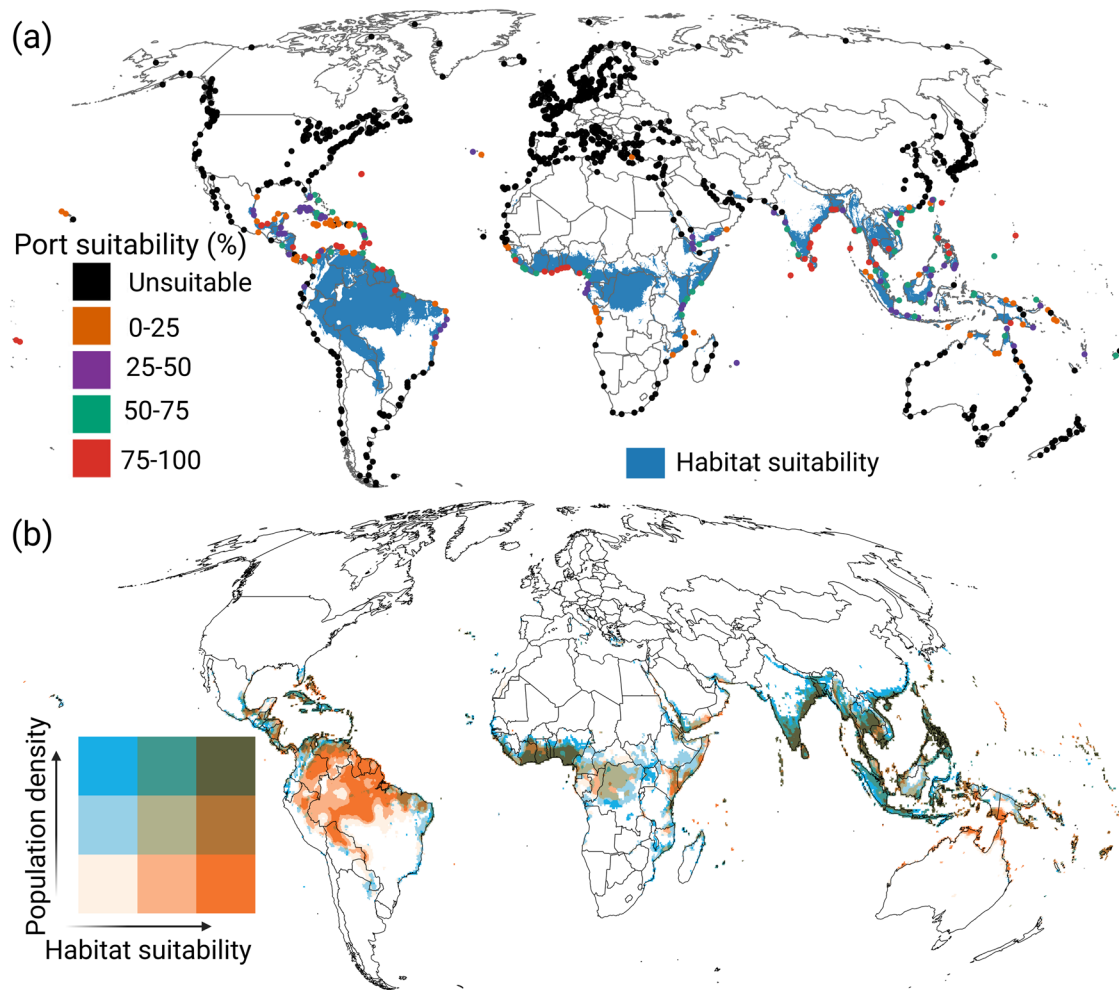


Fig. 5. Baseline (1970-2000: current) predictions of suitable habitat of *Vespa affinis* overlapping with ports and human population density. (a) Thresholded habitat suitability map for *V. affinis* (suitable areas shown in blue; unsuitable/transparent elsewhere) overlaid with global ports classified into 4 relative risk categories based on the percentile distribution of mean suitability within 100 km buffers: low (0–25th percentile), intermediate (25–50th percentile), high (50–75th percentile), and very high (75–100th percentile). (b) Bivariate map illustrating the overlap of suitable habitat with human population density. Darker red zones mark populated areas with high suitability.

residential and densely populated areas, a pattern that is consistent with the present study (Rahmawati et al. 2023). This likely reflects the availability of nesting substrates in built structures, supplemental food resources, irrigated vegetation, and favorable urban microclimatic conditions that buffer temperature and moisture extremes. Its growing potential to establish in new areas increases the likelihood of human-hornet conflict, especially in densely populated regions. However, given the limited information on *V. affinis* establishment outside its native range, our findings can help guide targeted monitoring and eradication efforts to prevent its establishment (Zhu et al. 2020).

To assess the potential impact of environmental change on *V. affinis* distribution, we incorporated projections from 6 GCMs dataset. Our findings indicate that suitable habitats will expand over time, with currently suitable areas becoming even more suitable. The Americas, Asia, and Africa exhibited notable increases in habitat suitability, suggesting an elevated risk of *V. affinis* invasion and establishment in the future. This highlights the urgency of implementing proactive surveillance, early detection, and robust management strategies to mitigate potential impacts. In Asia and Oceania, where *V. affinis* is already found, containment efforts should be strengthened, particularly in

residential and urban areas where the hornet is increasingly observed (Rahmawati et al. 2023). In contrast, Europe currently exhibits relatively low suitability and has no reported populations of *V. affinis*, and strict biosecurity measures are unlikely needed.

While our models predict habitat suitability for *V. affinis*, certain ecological and biological factors influencing its establishment were not incorporated. Propagule pressure, the number and frequency of introductions, plays a role in invasion success, but was not accounted for. Furthermore, while our model employed global environmental data, it did not capture microclimatic variability that could create local refugia and potentially support *V. affinis* in areas predicted as unsuitable. Additionally, factors such as dispersal ability, competition with native species, and interactions with natural enemies could affect *V. affinis* establishment. Although *V. affinis* has been sighted in the United States, its spread remains limited, potentially due to these factors or invasion-related lags that our models do not capture (Lockwood et al. 2005). Our future environmental projections also assumed niche stability, which may not hold true for a highly adaptive species like *V. affinis*. To improve accuracy, models could incorporate variables such as nesting habitat availability and phenology. Finally, as predictions can vary among

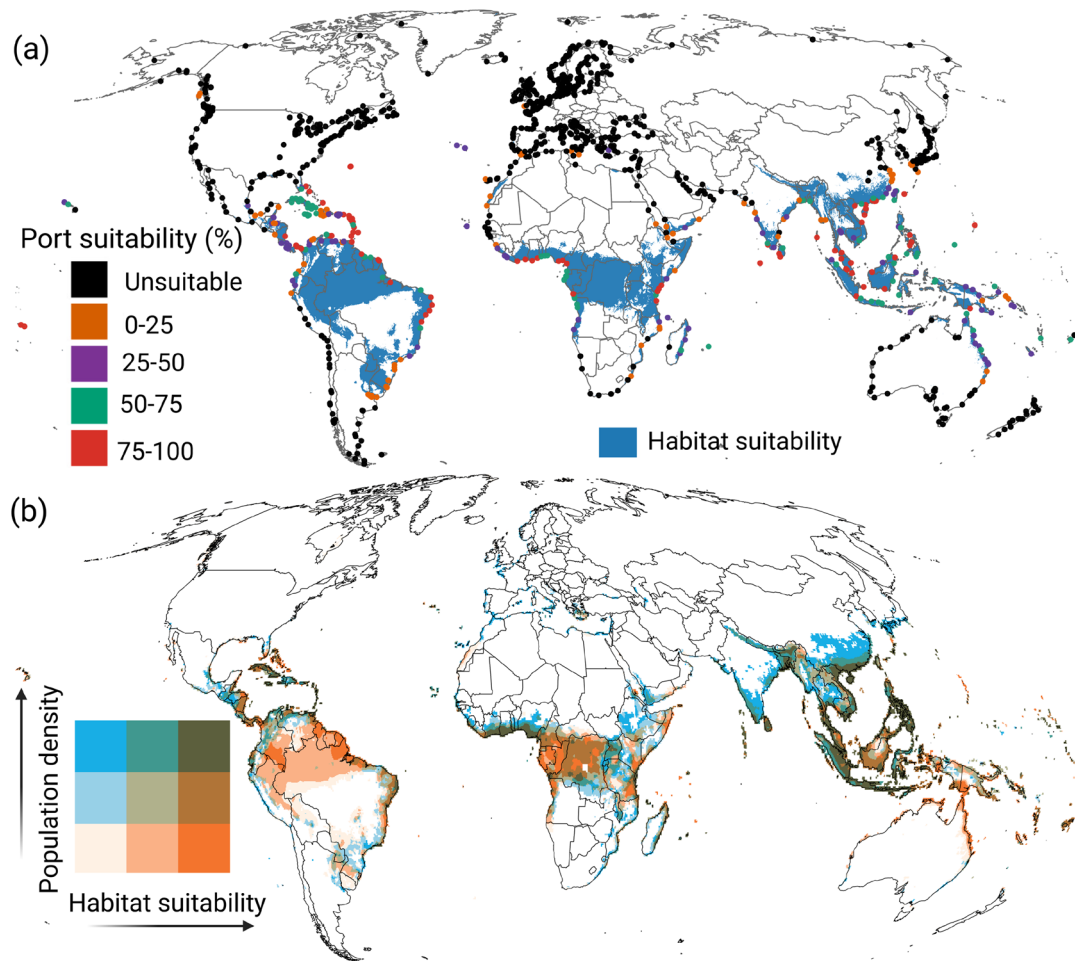


Fig. 6. Future (ssp585:2081-2100) predictions of suitable habitat of *Vespa affinis* overlapping global ports and human population density. (a) Thresholded habitat suitability map for *V. affinis* under future climate scenarios overlaid with global ports classified into 4 relative risk categories low (0–25th percentile), intermediate (25–50th percentile), high (50–75th percentile), and very high (75–100th percentile) within 100 km buffers. (b) Bivariate map illustrating the overlap of suitable habitat with human population density. Darker red zones mark populated areas with high suitability.

CMIP6 models, our projections represent only 6 plausible environmental outcomes and should be interpreted with recognition of intergenerational circulation model uncertainty.

Despite the limitations of models, our projections provide valuable insights into future habitat suitability, which can guide the deployment of monitoring traps and optimize surveillance efforts. Identifying suitable habitats beyond the hornet's known distribution, particularly in Africa and the Americas, shows the need for early intervention. We found major ports within the high and very high suitability percentiles, suggesting that the convergence of suitable habitat and high trade connectivity may amplify propagule pressure and increase the likelihood of *V. affinis* establishment and spread (Beaury et al. 2020, Epanchin-Niell et al. 2021, Hulme 2021, Costello et al. 2022). As habitat suitability is projected to increase through 2100, these insights are crucial for scientists studying hornet distribution and can inform the development of effective management strategies to prevent future invasions.

Author Contributions

Owusu F. Aidoo (Conceptualization [lead], Formal analysis [lead], Methodology [equal], Writing—original draft [lead]), Gengping Zhu (Conceptualization [supporting], Resources [supporting],

Supervision [supporting], Writing—review & editing [equal]), and David W. Crowder (Conceptualization [equal], Resources [lead], Supervision [lead], Writing—review & editing [lead])

Supplementary Material

Supplementary material is available at *Annals of the Entomological Society of America* online.

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Conflicts of Interest

The authors declare no conflict of interest.

Data Availability

The data is available upon a reasonable request.

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