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Assessing invasion risks and potential impacts of greater banded hornet across the United States

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Abstract

Invasions by hornets have occurred worldwide, threatening crops, native species, and honey bees. For emerging invasive hornets, habitat suitability models can estimate their potential distribution, rate of spread, and impacts. Recently, the greater banded hornet (*Vespa tropica*) was detected in Guam, where it poses a threat to honey bees, although an understanding of potential habitat suitability and spread of this species is lacking. Here we used habitat distribution models to assess habitat suitability for the greater banded hornet. We also estimated potential risks at US ports by assessing the overlap between suitable hornet habitats and human ports of entry. We identified diurnal range, isothermality, and maximum temperature of the warmest month as key factors that mediate the suitability of the greater banded hornet worldwide. While the greater banded hornet occupies a small realized climatic niche in Guam, it has the potential to expand into parts of the Pacific Northwest US and Hawaiian Islands. Our model suggests that the risk of invasion varies across ports of entry, with Atlantic ports potentially more susceptible than Pacific ones. Because of its potential to cause ecological harm, our study underscores the need to eradicate the greater banded hornet in Guam and implement biosecurity risk assessments in other vulnerable areas.

KEYWORDS
bees, hornets, invasion, NicheA, risk mapping, species distribution model

1 | INTRODUCTION

Invasions by hornet species have become increasingly common in recent years, primarily because of accidental introductions (Lioy et al., 2022; Otis et al., 2023; Takeuchi et al., 2017). Long-distance movement of hornet gynes in trans-oceanic shipments has facilitated invasions, while shorter-range expansion results from natural spread and local human transit (Otis et al., 2023). In addition to the risk hornets pose to native ecosystems and crops, hornets are effective predators of honey bees, and workers from several species actively prefer to attack honey bee hives over other prey items (Bista et al., 2020; Cappa et al., 2021). For example, the invasion of *Vespa velutina* in Europe and Japan has severely threatened commercial beekeeping as well as native social wasps (Takeuchi et al., 2017). Mitigating the risk of hornet invasions worldwide requires an integration between field monitoring and models to guide detection and eradication programs.

Greater banded hornet (*Vespa tropica*) is an emerging global threat that has been linked to the collapse of honey bee colonies (Ranabhat & Tamrakar, 2008). Greater banded hornet robs honey to meet the nutritional needs of its adults and larvae, killing honey bee guards until the hive is abandoned (Tan et al., 2013). Greater banded hornet also commonly attacks paper wasp nests. Greater banded hornet is native to Asia, including China, India, Japan, Singapore, and the Philippines, but in 2016 was observed outside its native range for the first time in Guam, USA (Rosario et al., 2016). The introduction of greater banded hornet outside its native range has raised concerns because of its potential to spread further across the islands of the Atlantic Ocean and its potential impact on honey bees and humans. However, effective biosecurity risk assessment of greater banded hornet and prediction of impacts requires a clearer understanding of its habitat suitability and potential spread into suitable regions.

Establishment of an invasive species is most likely when the environments of the native range and the introduction site are similar (Zhu et al., 2023). Habitat suitability models can be used to create geographical maps indicating environmental suitability (Porfirio et al., 2014). These models assess correlations between the distribution of a species and environmental conditions, enabling predictions of its potential range beyond known observed locations. The increasing use of habitat suitability models is because of the availability of georeferenced species records (e.g., Global Biodiversity Information Facility, gbif.com) and environmental data (e.g., Fick & Hijmans, 2017; Gomes et al., 2018), along with simple model interfaces (Keeling et al., 2017; Naimi & Araújo, 2016). However, modelling habitat suitability for the greater banded hornet is difficult because key ecological information, including physiology, dispersal capacity, detailed nesting ecology, climatic tolerances, and reliable presence and absence data, is still largely undocumented (Otis et al., 2023).

The recent introduction of the greater banded hornet in Guam shows a strategy is needed to mitigate spread and future invasions. Here, we first built models to assess habitat suitability of the greater banded hornet. Second, we identified overlap between greater banded hornet habitat and ports of entry to estimate risks at ports in the United States. Third, we assessed the niche breadth of the greater banded hornet in multidimensional space to compare native and invasive ranges. These analyses were based on global occurrence data for the greater banded hornet, allowing us to assess the potential for the greater banded hornet to spread into new regions beyond Guam. Next, we assessed where habitat conditions in ports overlapped with suitable habitat to estimate areas where new invasions might occur, which allowed us to estimate potential impacts of invasions into new areas. Our study reveals the potential for the greater banded hornet to spread and can guide detection, eradication, and containment programs.

2 | MATERIALS AND METHODS

2.1 | Species records and bioclimatic variables

We compiled 1439 records for greater banded hornet from databases, accessed 1 July 2025 (Global Biodiversity Information Facility, GBIF.org, https://doi.org/10.15468/dl.bp9dyy), Web of Science (https://www.webofscience.com/wos/woscc/basic-search), Google Scholar (https://scholar.google.com/), and published articles (Figures 1a and S1, Supporting Information). We then removed duplicates and erroneous records and enforced a 100 km distance between the records to reduce bias with the *sp*Thin package (Aiello-Lammens et al., 2015). Greater banded hornet might occur in climatic conditions similar to other invasive *Vespa* species (Nuñez-Penichet et al., 2021; Zhu et al., 2020). Its close relative, the yellow-legged hornet (*Vespa velutina*), spreads up to ~100 km per year in Europe and establishes nests more than 200 km beyond the invasion front (Robinet et al., 2017; Rome et al., 2012; Villemant et al., 2011). Although dispersal data for *V. tropica* are lacking, its comparable body size, flight capacity, and colony organization suggest similar potential. We therefore applied 100 km as a conservative and biologically grounded upper bound that also maintains spatial independence in our modelling framework. This filtering resulted in 260 global occurrence records for model calibration and evaluation. Nineteen bioclimatic variables for 1981–2010 were downloaded from CHELSA Bioclim (v. 2.1) which are primarily based on monthly precipitation and temperature records (Karger et al., 2017).

We developed models at a spatial resolution of 2.5 arc min (~5 km at the equator) to match the reliable scale of global climate data. For projections in Guam and Hawaii, we applied a finer resolution of 30 arc sec (~1 km) to enhance the spatial precision of

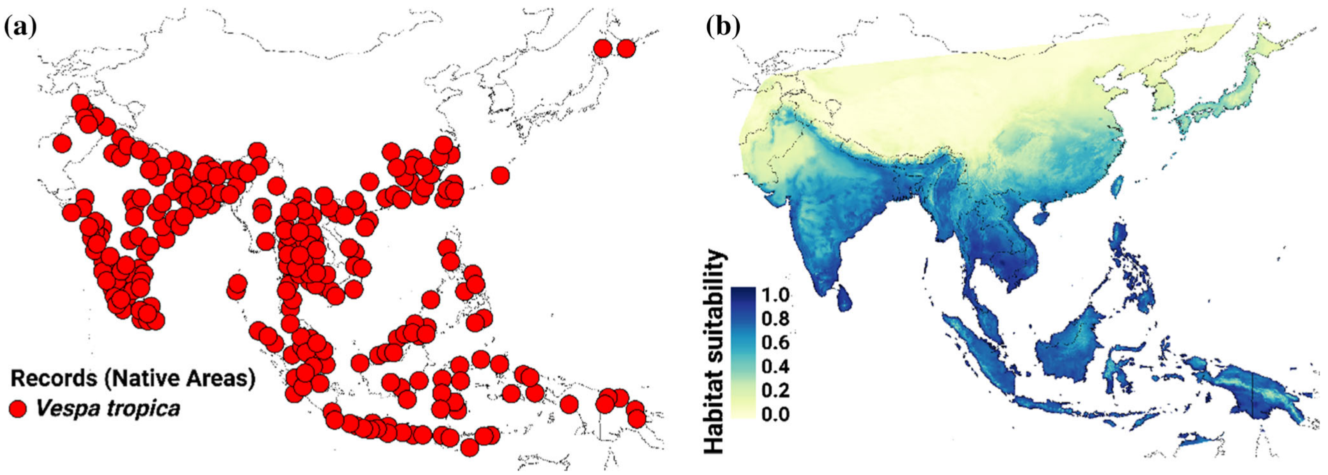

FIGURE 1 (a) Occurrence records of *Vespa tropica* in its native range, obtained from the Global Biodiversity Information Facility, the Centre for Agriculture and Bioscience International, and published articles (see Data S1). (b) Predicted habitat suitability of *Vespa tropica* in the known distribution area based on the ensemble model.

predictions. We acknowledge that potential spatial artifacts in some bioclimatic layers exhibit interpolation discontinuities in certain regions like the Amazon and the Sahara inherently affecting predictions in these areas (Booth, 2022; Escobar et al., 2014). Hence, we excluded mean temperature of wettest quarter, mean temperature of driest quarter, precipitation of warmest quarter, and precipitation of coldest quarter prior to the analysis, which have been demonstrated to have such discontinuities. To avoid autocorrelation among bioclimatic variables (Naimi et al., 2011), we used the *vifcor* function in the *sdm* package (Naimi & Araújo, 2016) with a threshold of 0.7, yielding five variables: (i) mean diurnal range, (ii) isothermality, (iii) maximum temperature of warmest month, (iv) precipitation of the wettest month, and (v) precipitation seasonality.

2.2 | Habitat suitability models

Ensemble models incorporate variability among different techniques used to model habitat suitability for a species (Kotu, 2019). We built an ensemble from six individual habitat suitability models: (i) maximum entropy, (ii) random forest, (iii) multivariate adaptive regression splines, (iv) boosted regression trees, (v) generalized additive model, and (vi) generalized linear model. The maximum entropy approach is a machine learning algorithm (Phillips et al., 2017), while random forests use an ensemble of decision trees (Breiman, 2001; Liaw & Wiener, 2002). The multivariate adaptive regression spline approach is often used to handle nonlinearities (Friedman, 1991), while generalized additive and linear models are often used to fit species–environment relationships (Li & Wang, 2013). Finally, boosted regression trees are a machine learning approach that combines boosting and regression trees (Elith et al., 2008).

Habitat suitability models were built with global records (Figure S1). We defined the study region by creating a minimum convex polygon around records using the *Wallace2* package (Kass et al., 2023). To address overfitting and enhance transferability of the MaxEnt model, we fine-tuned the feature classes and β regularization multipliers using SDMtune (Vignali et al., 2020). The MaxEnt model provides five features: linear (L), quadratic (Q), hinge (H), product (P), and threshold (T). We set the regularization multiplier between 0.5 and 5, increasing by 0.25 with each run, and adopted nine feature classes (L, Q, H, LQ, QH, LQH, LQP, QHP, and LQHP). We then tested all possible combinations of feature classes and regularization multipliers (Vignali et al., 2020). We selected the optimal parameterisation using the corrected Akaike information criterion (AICc): the model with $\Delta\text{AICc} = 0$ was considered the best, and models with $\Delta\text{AICc} < 2$ were deemed to have substantial empirical support (Phillips et al., 2017). In this study, we considered FC of *qh* and an *RM* of 2.25. Then, we set the replicates to 10 and used bootstrapping (Naimi & Araújo, 2016). We split the records into training (70%) and testing (30%) datasets.

To optimize models, we selected 10,000 points and 265 background points for the Maxent and non-maxent models, respectively (Barber et al., 2022; Rausell-Moreno et al., 2025). We then built each model using the *sdm* package (Naimi & Araújo, 2016) and created an ensemble global model based on the mean predictions. We also created a presence and absence map using maximum sensitivity plus specificity threshold (Max (se + sp): Maxent = 0.51 and non-maxent models = 0.50), which maximizes the True Skilled Statistics. Next, we predicted habitat suitability in the Hawaiian Islands, Guam, and the Pacific Northwest (PNW) US; the greater banded hornet has an established population on Guam that is threatening bees and pollination there. For Hawaii and PNW, they are both in the Pacific, sharing certain environmental conditions with Guam. We conducted a Spearman correlation (Schober et al., 2018) to assess similarity between prediction uncertainty and mean habitat suitability of the greater banded hornet, as well as similarity among modelling algorithms. To determine variation among modelling algorithms, we calculated pixel-wise variations across the individual models. To compare habitat suitability in Guam, Hawaii, and PNW, we calculated their suitability values. Then the relative contribution of each variable on model outputs was obtained using the getVarImp function in the *sdm* package (Naimi & Araújo, 2016). All analyses were performed in R v. 4.3.3 (R Core Team, 2024).

We assessed model performance with the area under the receiver operating characteristic curve (AUC) and true skill statistics (TSS). AUC measures show how well models distinguish between presence and absence records (Jiménez-Valverde, 2012). In contrast, TSS is more effective for imbalanced datasets and provides a single summary statistic (Allouche et al., 2006). AUC and TSS values of 1 are considered excellent, while values above 0.7 for AUC and 0.5 for TSS are generally regarded as acceptable (Allouche et al., 2006; Çorbacıoğlu & Aksel, 2023).

2.3 | Realized niche analysis

Using minimum volume ellipsoids (MVEs), which represent niches in three dimensions, we compared the climate space occupied by greater banded hornet in native (Asia) and invasive (Guam) ranges using a three-dimensional principal component based on important bioclimatic variables. First, we split species data from the native (Asia: 1389 records) and invaded (Guam: 50 records) ranges. Then, we performed PCA analysis to select key climatic variables (mean diurnal range, isothermality, maximum temperature of warmest month, precipitation of the wettest month, precipitation seasonality). This enabled us to select variables for the background cloud, which are required for the construction of MVEs (Qiao et al., 2016). To construct MVEs, we visualized realized niches using Niche Analyst (v. 3.0) (Qiao et al., 2016).

2.4 | Port-based risk assessment

Mated, diapausing hornet females (gynes) can be transported in transoceanic shipments, and ports handling international cargo from many countries pose high invasion risk (Otis et al., 2023; Ruiz-Utrilla et al., 2024; Smith-Pardo et al., 2020). To assess potential risks of introductions, we used data on ports in 2020 from the US Army Corps of Engineers (2023). To determine port suitability, we created a 100 km buffer zone around American ports and then extracted habitat

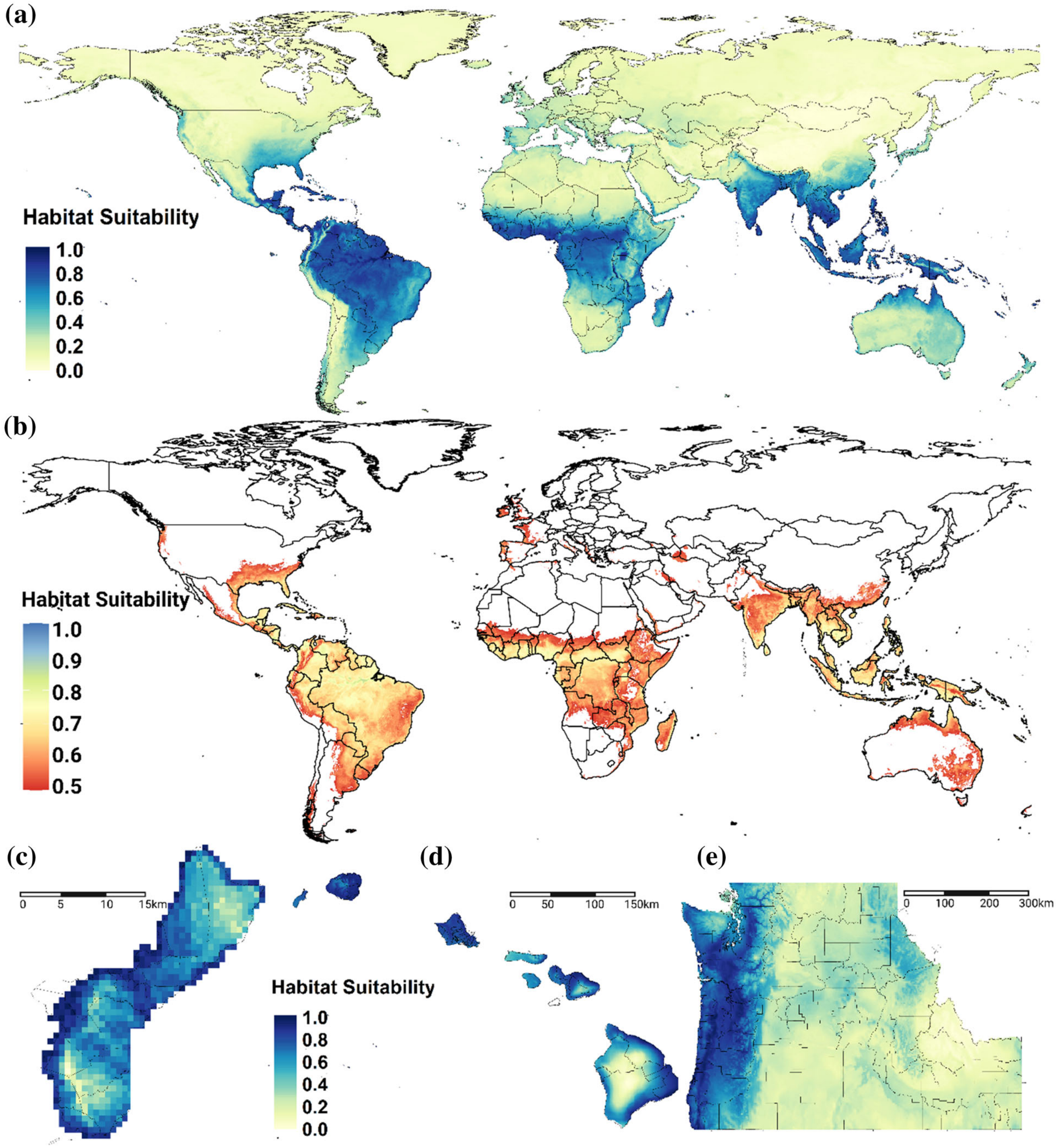

FIGURE 2 Habitat suitability of *Vespa tropica* based on the ensemble model, showing (a) global predictions, (b) presence verses absence based on maximum sensitivity plus specificity threshold (Max (se + sp.: Maxent = 0.51 and non-maxent models = 0.50), (c) Guam, (d) Hawaii, and (e) the Pacific Northwest US.

suitability values within this buffer using the *exactextractr* package (Baston, 2024). This distance assumes that the hornet will be able to disperse within these areas if exposed at the port. We calculated the *weighted suitability* of ports as: $\log_{10}$ (habitat suitability within 100 km) $\times$ $\log_{10}$(tonnage). We then calculated *normalized weighted suitability* of each port as: $\frac{\text{Weighted suitability}}{\text{Max (weighted suitability)}}$. We summarized risks at port of entry using the *sf*, *ggplot2*, *terra*, *dplyr*, and packages in R (Hijmans, 2025; Pebesma, 2018; Wickham, 2016; Wickham et al., 2023).

3 | RESULTS

3.1 | Model development, evaluation, and prediction

Each model had acceptable performance, although results varied across algorithms and the ensemble model (Tables S1–S3). We found high habitat suitability of the ensemble model in native areas (Figure 1b). Analysis of variable importance showed that mean diurnal range, isothermality,

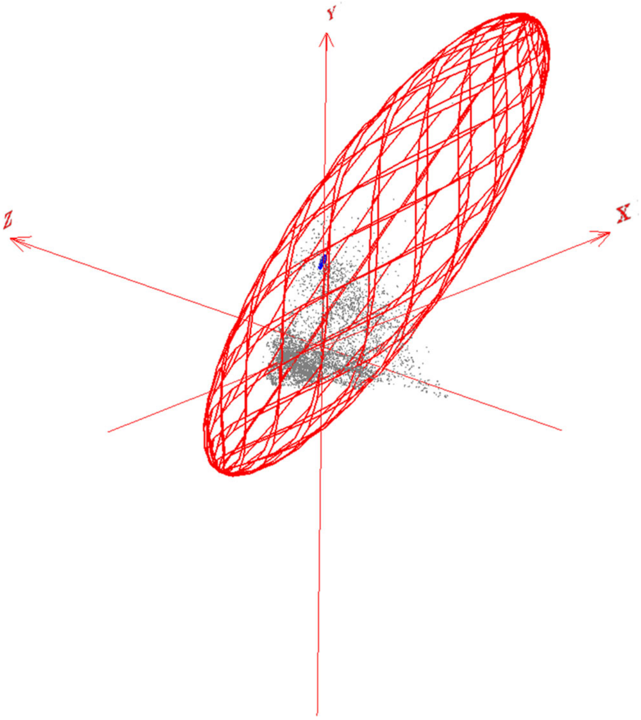

FIGURE 3 Fundamental niche analysis of *Vespa tropica*. Overlapping ellipsoids of *V. tropica* in (a) native area (red) and Guam (blue) suggest similar conditions. The cluster of grey dots depicts the first three principal components obtained from the most important variables that affect the distribution of the hornet. The X, Y, and X represent PC1, PC2, and PC3, respectively.

and maximum temperature of the warmest month were the most influential variables (Table S4). By projecting the ensemble model globally, areas with high predicted suitability include Brazil, Colombia, and Venezuela in the Americas; Ghana, Cote D'Ivoire, Nigeria, Benin, and Togo in Africa; India in Asia; and Australia and Papua New Guinea in Oceania (Figures 2a and S2). Guam had high habitat suitability (Figures 2b and S3 and Table S5), only certain Hawaiian Islands were likely suitable for hornets (Figures 2c and S4 and Table S5), and the Pacific Northwest US had relatively low habitat suitability throughout (Figures 2d and S5 and Table S5). However, areas with high suitability had greater prediction uncertainty than lower suitability areas (Figures S6–S8).

3.2 | Niche analysis

We found that the first three principal components explained approximately 90% of the variation in the five bioclimatic variables (see section 2.1). The realized niche of the greater banded hornet in its native regions is considerably broader than in the invaded Guam (Figure 3). However, both native and invasive populations occupy similar environmental conditions, suggesting that the climate niche was conserved during its invasion, and the greater banded hornet could establish a widespread distribution to other regions without containment measures.

3.3 | Port-based risk assessment

The highest risk ports in the United States are primarily located in the South and Pacific regions, while ports with low suitability for the hornet are mainly situated in the Midwest and Northeast (Figure 4a). Ports with high activity levels, measured by tonnage, are concentrated in the South, West, and Northeast (Figure 4b). The port-based risk assessment identifies high-risk ports of entry with high weighted suitability mainly in the South and Pacific regions (Figure 4c).

4 | DISCUSSION

Our six habitat suitability models and the ensemble for greater banded hornet produced predictions consistent with its known distribution in native and invaded areas (Rosario et al., 2016). Our niche analysis validated the findings, underscoring the robustness of predictions. While ensemble methods are commonly favored for habitat suitability analysis because they minimize effects of outliers and allow for the generality of predictions to be tested, optimized individual models can sometimes outperform them (Hao et al., 2020; Harris et al., 2024). However, we found small variation among our six models and the ensemble, and all aligned with the known distribution of greater banded hornet. Our study shows that examining diverse model performance can provide considerable insight into invasion dynamics (Araújo & New, 2007; Marmion et al., 2009; Murray, 2018).

Our results confirm that Guam, where the greater banded hornet is known to occur (Rosario et al., 2016), and exerts substantial predation pressure on honey bees (Rosario et al., 2025), has extremely suitable habitat throughout. As the main management tactic on Guam is nest removal (Otis et al., 2023), our maps identify localities where hornets may be located. However, the Hawaiian Islands did not have uniformity in habitat suitability, with each island having areas with varying suitability. Furthermore, the broader Pacific Northwest US shows low suitability for the greater banded hornet, suggesting invasions may be mainly limited to the Hawaiian Islands. Beyond the United States, many countries outside the known distribution areas in the Americas, Africa, Europe, Asia, and Oceania have suitable habitats. Overall, mean diurnal range, isothermality, and maximum temperature of the warmest month were identified as the most important environmental variables affecting the greater banded hornet. This demonstrates the critical influence of temperature on the survival and activity of the greater banded hornet (Otis et al., 2023; Ruiz-Cristi et al., 2020). Field studies also show that variation in seasonal temperatures across regions can significantly affect the incidence of the greater banded hornet (Singha et al., 2023).

Our habitat suitability models were complemented by an analysis showing ports in states such as the Pacific and Southern regions are hotspots for greater banded hornet entry into the United States. Such findings underscore the need for regular and thorough inspections at these ports of entry to prevent and mitigate invasions. Prioritizing these locations for increased surveillance and control measures may reduce the risk of invasive hornet species while providing a basis for

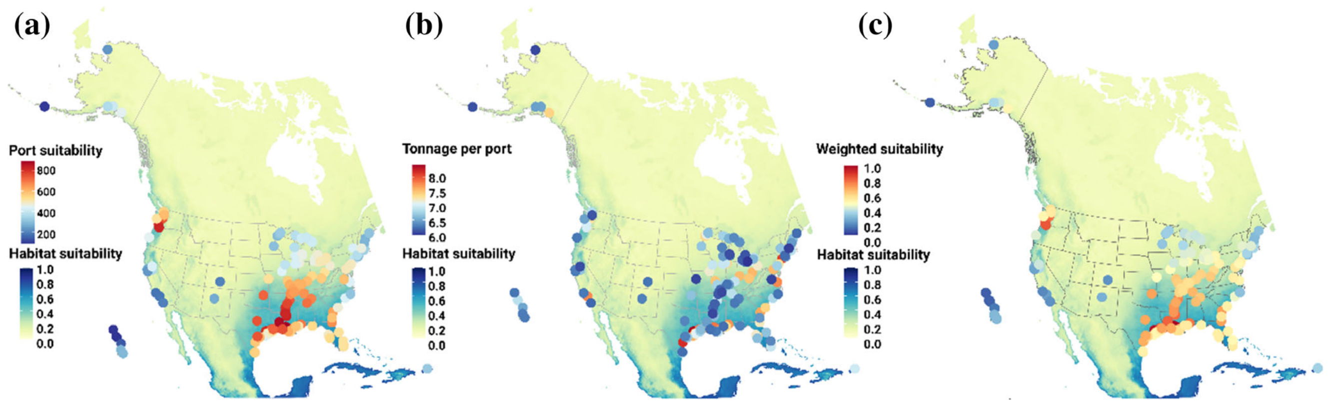

FIGURE 4 Port-based risk assessment in the United States ports for introduction of *V. tropica* based on the ensemble model. (a) Port habitat suitability considering a 100 km buffer zone around the ports. (b) Tons per port. (c) Predicted habitat suitability with the weighted suitability of the port.

regulatory decisions. Moreover, the high habitat suitability for greater banded hornet in Guam suggests the need for containment measures to avoid spread to the Hawaiian Islands. Further spread of the greater banded hornet could have severe repercussions on pollination services because honey bees lack effective defences (Arca et al., 2014). Hence, invasions could threaten the estimated $200+ million a year in pollination benefits https://cms.ctahr.hawaii.edu/pollinators.

While our study predicts locations that are suitable for greater banded hornet, the ultimate distribution of this species will be affected by many factors. For example, the spread of hornets into new areas depends on their dispersal capacity, their ability to adapt to environmental conditions, and interactions with native species (Mooney & Cleland, 2001; Santana et al., 2017). Further, models often assume unlimited dispersal that does not reflect real-world constraints (Engler & Guisan, 2009; Wisz et al., 2013), and habitat suitability models overlook the potential for rapid evolutionary responses to new environments (Urban et al., 2016). While predicting evolutionary responses of hornets to new environments is challenging, our study provides useful information for containment and early detection measures against greater banded hornet. Our climatic layers reflect the 1981–2010 baseline, and 15-year data may produce some variations in suitability patterns. Future work that uses time-explicit climatologies will help refine these predictions. Additionally, our models rely on macroclimatic variables derived from global datasets, yet microclimatic variation such as canopy shading, near-ground temperature, humidity, and thermal buffering by vegetation can strongly influence hornet habitat use. These fine-scale processes are typically unresolved in broad-scale models and may lead to localized differences between predicted and realized suitability. Similar microclimatic responses have been reported across diverse insect groups. For example, the sap-feeding African citrus psyllid (*Trioza erytreae*) is more abundant on shaded foliage than on sun-exposed foliage (Aidoo et al., 2019).

Our ensemble models identified several high-risk regions for greater banded hornet establishment, including Guam, parts of Hawaii, and the Pacific Northwest, where environmental conditions are highly suitable and trade-related introduction pressure is substantial. Notably, the areas predicted as highly suitable align closely with all known occurrences, underscoring the reliability of the ensemble approach. These findings highlight the need for continued containment in Guam, where populations are already established and habitat suitability is high, and they point to additional regions where proactive surveillance may be warranted. More broadly, our results reinforce growing evidence that habitat suitability models provide credible and repeatable forecasts that support invasion risk assessment and management (Harris et al., 2024; Sofaer et al., 2019). Such models can also help evaluate risks to sensitive species, including honey bees, by identifying areas where their ranges may overlap with emerging invasive hornet threats.

5 | CONCLUSION

Our study has defined habitat suitability for the greater banded hornet worldwide and across the United States. Guam, where the species is already established, and Hawaii, which is highly suitable but not yet invaded, serve as case studies illustrating how the hornet can occupy distinct climatic niches in different regions; however, these examples represent only a small fraction of the much broader niche space identified in our global models. Consequently, the species could pose an invasion risk across multiple continents if introduced, underscoring the need for proactive surveillance and strengthened biosecurity in climatically suitable areas. The risk of establishment varies by entry point, with Atlantic ports appearing more vulnerable than those in the Pacific. Given the ecological impacts this species can cause, our findings highlight the urgency of eradicating the greater banded hornet in Guam and preventing its spread to other regions.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

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