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ORIGINAL RESEARCH

Risk of Asian hornet invasion in Mexico: a proposal for invasive species risk assessment from a spatial perspective

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Abstract

Biological invasions need to be assessed as spatial processes, incorporating information on introduction sites, environmental suitability, dispersal parameters and negative impacts. The above allows us to develop risk maps, which are an important tool to determine the probability and consequences of an invasion in each area. In this study, we developed species niche-based distribution models for *Vespa mandarinia* and *V. velutina*, exotic species recently discovered in North America, being *V. velutina* a recognized invasive alien species that has caused enormous economic impacts in Europe. Species niche-based distribution models were used as a base map to determine the risk of establishment in conjunction with information related to the introduction, economic and biodiversity risk. The models developed in this study show environmental suitability for the establishment of these species in tropical and subtropical locations of North America. In Mexico, more than 50% of the ports are at high risk especially those located in the Gulf of Mexico. The biodiversity impact risk map for *V. mandarinia* shows that 57 protected areas are in regions with some risk of invasion and the *V. velutina* analysis shows 49 protected areas at potential risk. By implementing comprehensive surveillance and monitoring programs, integrating early detection and rapid response strategy and leveraging geographic information systems, Mexico can take proactive measures to mitigate the potential impacts of invasive species. These efforts will be crucial in protecting biodiversity, preserving ecosystems and safeguarding the country's economy from the negative consequences associated with invasive species.

Keywords Ecological niche models · Alien invasive species · Economic impacts · Biodiversity impacts · Introduction pathways

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Introduction

Biological invasions, along with climate change and land use change have been identified as one of the global terrestrial biodiversity loss drivers (Knapp et al. 2017; Pyšek et al. 2020). Invasive insects produce negative impacts on biodiversity, human health, and agriculture, with enormous economic losses. Impacts mainly occurred throughout biotic interactions such as predation, herbivory (Dueñas et al. 2018; Snyder and Evans 2006; Thomson 2004), and hybridization with native species (Jensen et al. 2005). In terms of biodiversity conservation and agricultural biosecurity, the introduction of Invasive Alien Species (IAS), such as hornets, bark beetles, among others, has significantly contributed to biodiversity loss and crop losses, exerting negative impacts on structure and function of ecosystems, as well as food security, leading to a reduction in food supply (Dueñas et al. 2018; Mack et al. 2000, IPBES 2023).

Exotic invertebrates have been introduced through various pathways; however, there is a strong association with accidental means, such as contaminated goods because of global trade (Hulme 2009). For example, *Vespa velutina*, named Asian hornet, was introduced to France in 2004, probably in the commodities (López et al. 2011). Currently, *V. velutina* has been established in Belgium, Spain, Portugal, Italy, Germany, and Great Britain (CABI 2022; Villemant et al. 2011) and a new report in August 2023 indicates its presence in Savannah, Georgia, USA (Georgia Department of Agriculture 2023). Another accidentally introduced hornet is *Vespa mandarinia* (Asian giant hornet) (EPPO 2022). It was detected in September 2019 in Nanaimo, Vancouver Island, Canada (BC Ministry of Agriculture 2019). Additional specimens have been captured in 2020 and 2021 (Washington State Department of Agriculture 2022). In South America, *Vespa orientalis* was reported in Chile in 2018, and the identification was confirmed in 2020 with the capture of 36 individuals (Ríos et al. 2020). In Mexico, *V. orientalis* was observed on Cozumel Island in 1998 (Dvořák 2006), although there is currently no evidence of its presence or establishment in the country (CONABIO 2021; Sánchez et al. 2019). However, overall, these introductions underscore the critical importance of addressing biosecurity and preventing the spread of invasive species to protect ecosystems and agriculture.

Countries activate their alert systems primarily due to the protein-feeding behavior of hornets, such as *V. orientalis*, which negatively impacts beekeeping by preying on bees and wasps. This direct predation results in both biodiversity and economic losses (Thomson 2004). Additionally, countries incur the cost of implementing mitigation and control strategies to address the hornet problem (Lee 2010). For instance, the economic impact for control strategies of *V. velutina* invasion in Europe, could achieve 13.2 million USD in France, 9.9 million USD in Italy and 9.5 million USD in Great Britain (Barbet-Massin et al. 2020) and the impact on beekeeping could be around 5–30% or even more (Monceau et al. 2014). Additionally, it has been documented that *V. mandarinia* is capable of preying on a substantial number of bees, estimated between 5,000 and 25,000 within a span of six hours (Matsuura and Sakagami 1973). In Japan, according to the Ministry of Agriculture, the apiculture industry has experienced losses estimated at around 10–20% annual in the number of hives (Matsuura and Yamane 1990).

Given the accidental introduction of *Vespa* species worldwide, the confirmed presence of *V. mandarinia* and *V. velutina* in the USA and the economic and biodiversity impacts caused by these species, important efforts have been made to assess their potential impacts.

Research on *V. mandarinia* has focused on its global invasive potential (Zhu et al. 2020), by estimating potential distribution, dispersion and impacts in North America (Alaniz et al. 2021; Nuñez-Penichet et al. 2021). In the case of *V. velutina*, research has been directed toward understanding its invasion potential and economic impacts in Europe (Barbet-Massin et al. 2020; Ibáñez-Justicia and Loomans 2011; Monceau et al. 2014), biodiversity impacts (Rojas-Nossa and Calviño-Cancela 2020), control techniques (Rome et al. 2011), and potential distribution worldwide (Villemant et al. 2011).

One of the most widely used approaches to predict species suitability is niche-based species distribution models, which involves correlating species occurrences with environmental variables to find suitable areas where the species could persist (Peterson et al. 2011). Ecological niche models (ENM) are represented in the environmental space. This approach aims to recreate either the fundamental niche (N_F) or the effective niche (EF). The N_F is defined as the range of environmental conditions that a species can tolerate according to its fitness, while the effective niche represents the actual environmental conditions that a species is known to inhabit (Soberon and Arroyo-Pena 2017). Some studies suggest that N_F is often under-represented because it only provides the existent portion of species niche (Peterson et al. 2011), resulting in limitations in geographic transference. Therefore, for a more comprehensive understanding of potential risks posed by certain species to a given region, it is advisable to include closely related species (Castaño-Quintero et al. 2020). By incorporating data from related species, a broader spectrum of suitable habitats can be identified, providing a more nuanced perspective on areas vulnerable to invasion. This approach enhances the accuracy and applicability of risk assessments, allowing for better-informed management and conservation strategies.

Niche-based species distribution models assist in surveillance efforts to predict negative impacts, thereby enhancing the potential for early detection and rapid response (EDRR), and formulating strategies for managing biological invasions (Venette 2015). Hulme (2009) underscores the importance of integrating multiple factors—such as invasion probability, entry points, climate suitability, habitat availability, and dispersion parameters—into risk likelihood maps to comprehend biological invasions as spatial processes. These maps are crucial for evaluating invasion probabilities and consequences within a specific area (Secretariat of the International Plant Protection Convention 2007; Venette et al. 2010). Typically, risk maps focus on one component of the invasive process, such as establishment or spread risk, though the goal is to assess the probability and consequences of a biological invasion and its variation in a given area (Venette 2015). In Mexico, the emphasis has been on likelihood of establishment. For instance, the National Forest Commission (CONAFOR) has created early alert and risk evaluation maps for exotic ambrosia beetle species, using ENM, land use, vegetation variables, and establishing risk levels (CONAFOR 2022). Another institution, CONABIO, conducts risk assessments using various methodologies tailored to Mexico (CONABIO 2022), occasionally incorporating species distribution models (SDM).

In this study, we undertake the characterization of the environmental space by modeling the ecological niche of two invasive Asian hornets, *V. mandarinia* and *V. velutina*. Our primary objective was to predict the geographical areas that may be vulnerable to the introduction of these species in North America, with a particular focus on Mexico. To achieve this, we initially compared the ecological niches of *V. mandarinia* and *V. velutina* to assess their similarity, providing a comprehensive understanding of species suitability across the study area. Subsequently, we generated potential distribution maps, which were then reclassified to develop species-specific likelihood risk maps for Mexico. For the species-specific likelihood risk map we include the estimation of establishment through potential distribution models, an analysis of the likelihood of introduction, and an evaluation of potential impacts on apiculture and native species.

Methods

Our methods comprise two main steps. First, we evaluate niche similarity between *V. mandarina* and *V. velutina.* In the second step, we create variables regarding suitable areas for both species' establishment and regions prone to hornet introduction, considering biodiversity and economic impact. These variables were integrated to develop species-specific likelihood risk maps for Mexico (Fig. 1). Subsequent sections will offer a comprehensive description of our employed methods.

Ecological niche modeling

We collected species occurrence data for *V. mandarinia* and *V. velutina* from GBIF (GBIF 2020a, 2022b). Specifically, for *V. mandarinia*, we used occurrence records from its native range, encompassing the countries Bhutan, China, India, Japan, Nepal, Russia, and South Korea (Kumar and Srinivasan 2010). For *V. velutina*, our data compilation also included occurrences from its native range (China, Indonesia, Laos, Pakistan, and Thailand) as well as areas where it has invaded, such as Belgium, France, Portugal, and Spain (CABI 2022). Details regarding the cleaning process for occurrence records are provided in Supplementary Material.

For climatic variables we used Worldclim version 2.1 (Fick and Hijmans 2017) at spatial resolution, roughly 1 km². To reduce variable correlation, we applied a Spearman's test, excluding variables with a correlation coefficient ≥ 0.8 using the correlation_finder function from the ntbox package (Osorio-Olvera et al. 2020). The final set of climate variables for both species was: mean diurnal range (Bio 2), isothermality (Bio 3), mean temperature of the warmest quarter (Bio 10), annual precipitation (Bio 12), precipitation of the driest month (Bio 14), and precipitation seasonality (Bio 15). Details regarding the selection of climate variables are also provided in Supplementary Material.

To address the under-represented N_F for *V. mandarina*, wherein current occurrence records may not fully capture its complete range, we applied the ecological niche conservatism hypothesis. This hypothesis suggests that closely related species share identical or similar fundamental niches, regardless of their geographic distribution. Consequently, by leveraging this principle, ecological niches can be considered complementary, aiding in the reconstruction of a more precise representation of the fundamental niche (Castaño-Quintero et al. 2020). Therefore, we first assess if *V. mandarina* and *V. velutina* exhibit niche similarity. If so, we also model *V. velutina.* This approach assists in obtaining a more comprehensive representation of the areas that could harbor climate conditions suitable for the establishment of this invasive species. To evaluate niche similarity in a tridimensional space, we used both species occurrence records with the Niche Analyst software (Qiao et al. 2016).

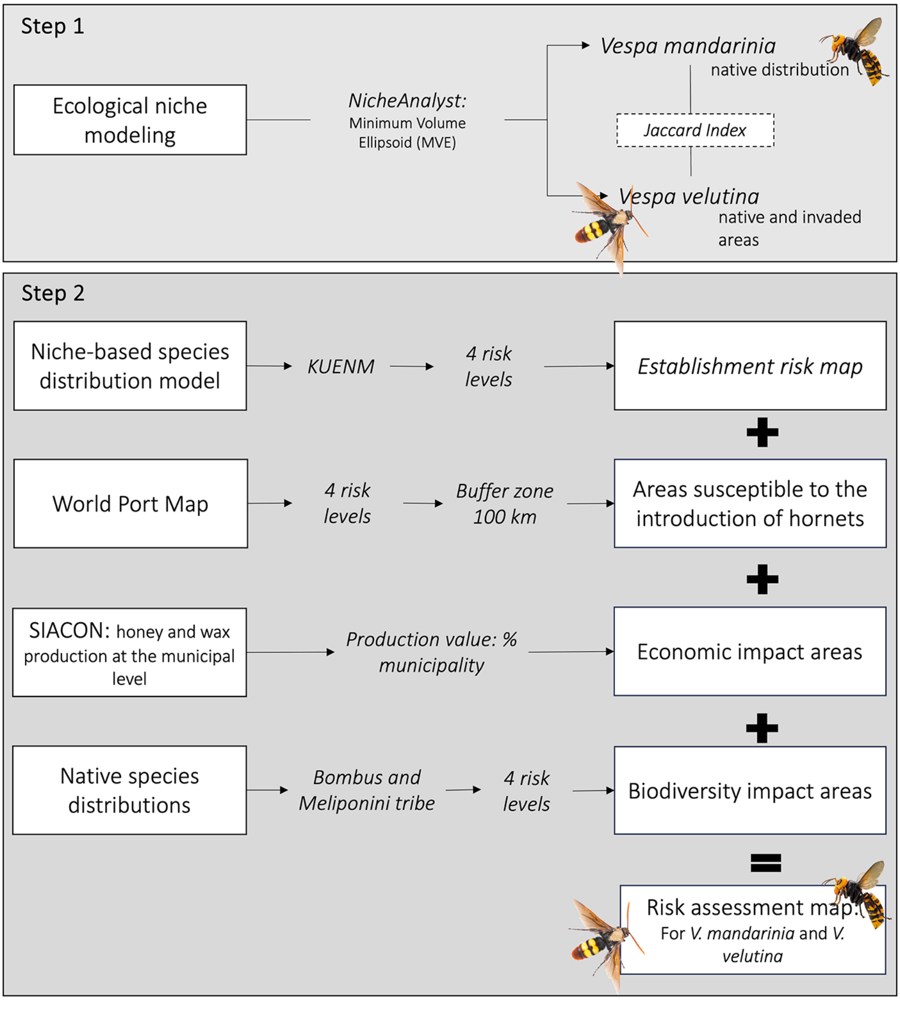

Fig. 1 Schematic representation of the methods used in our spatial risk assessment

For *V. mandarinia*, we developed a minimum volume ellipsoid (MVE) using occurrences from its native distribution (Supplementary material). In the case of *V. velutina*, the data was partitioned into the native and invaded areas (Fig. 1). We used 807,345 background points, which represent the environmental characteristics available to the species (Qiao et al. 2016). Because we used the same variables for the *V. mandarinia* and *V. velutina* models, the background points include the same six variables with a worldwide extension. Furthermore, we calculated the Jaccard Index to determine the degree of niche similarity (Escobar et al. 2015). The Jaccard Index values range from 0 to 1, with 0 indicating no similarity and 1 denoting complete similarity between species. The formula used for the calculation was:

$$V0 = \frac{V1 \cap V2}{V1 \cup V2}$$

V0 = Overlay Volume.
V1 = First ellipsoid volume.
V2 = Second ellipsoid volume.

Niche-based species distribution model

We used an ecoregion layer to define the calibration area (M area sensu Soberón and Peterson 2005). Each ecoregion was selected if at least one occurrence fell within its boundaries (Olson et al. 2001). For *V. mandarinia*, only records from its native distribution were included since its recent introduction in North America and because of the limited evidence of its establishment and dispersal (Supplementary Material). In contrast, for *V. velutina*, both native and exotic occurrences were considered, acknowledging that this species has successfully progressed through each step of the invasion process (Blackburn et al. 2011).

During calibration, our aim was to select the most suitable parameter combination to accurately represent the species' niche distribution and achieve the highest data fit (Peterson et al. 2008). To achieve this, we employed the kuenm package (Cobos et al. 2019) within the R work environment (R Core Team 2020). Kuenm uses Maxent (Phillips et al. 2006) to create models and identifies those with high performance and low complexity. We made 10 replicates by bootstrapping occurrence records, and used Maxent cloglog output. We explored combinations of all available feature classes and examined 13 values of the beta multiplier, ranging from 0.1 to 1 in increments of 0.1, and from 2 to 6 in increments of 2. Changing the beta multiplier aids in preventing overfitting or reducing the discriminatory capacity, thereby mitigating the risk of underestimation or overestimation of areas (Radosavljevic and Anderson 2014). Subsequently, kuenm facilitated an evaluation process to identify the best models based on criteria such as Partial Area Under the ROC Curve (pROC) values (Peterson et al. 2008), omission values ≤ 5%, and delta AICc values ≤ 2. We then projected the best models to North America and Central America, using clamping, free extrapolation, and no-extrapolation options. Different extrapolation settings can significantly influence the outcomes. When clamping is used, the model is restricted by the surrounding environments within the calibration area. In contrast, free extrapolation allows the model to follow the trend of values in the calibrated area, thereby enabling projections into environmentally distinct regions. In the case of no extrapolation, the model refrains from assigning suitability if the environment differs from the calibrated area (Cobos et al. 2019).

Since we only generated potential distribution models for native species in Mexico and had spatially explicit information on honey and wax production in the same country, the risk map was exclusively estimated for Mexico. Final models were evaluated using the kuenm_feval function with default parameters (Cobos et al. 2019). Additionally, we conducted analyses using the ExDet tool to assess novel environmental conditions. The ExDet tool identifies non-analog conditions where there is a risk of model extrapolation, providing a measure of uncertainty for new environments. Unlike other tools like MESS, available in the Maxent interface, ExDet considers both univariate ranges and combinations of covariates, providing a more comprehensive measure of uncertainty for new environments. Given that potential distribution models operate in a multivariate space, ExDet offers the opportunity to assess novel covariate combinations (Mesgaran et al. 2014).

Likelihood of establishment risk map

Finally, we reclassified the distribution models in four levels, where the minimum value to determine risk establishment was set using the threshold of the minimum training presence (MTP), which means pixels below MTP value are considered as sites with no risk. For the other three levels, we calculated the 25th, 50th, and 75th percentile of the training presence values, and were considered as sites with low risk, medium risk, and high risk, respectively. It is important to note that the MTP has been commonly used in prediction maps for IAS (Jarnevich and Reynolds 2011; Jarnevich and Young 2015).

Spatial variables

We considered four main variables, to create a spatial perspective of Mexico's risk of *Vespa* invasion, these were: (I) likelihood of establishment (previously described), (II) susceptible areas to the introduction of hornets, (III) biodiversity impact areas and (IV) economic impact areas. Each variable is spatially explicit; thus, we report a map for each. Here we describe how each variable was estimated and used.

Susceptible areas to the introduction of hornets

Susceptible areas to the introduction of hornets encompass regions such as ports, harbors, roads, and densely populated areas. There is empirical support for the introduction of *Vespa* species through ports (Smith-Pardo et al. 2020). To evaluate the associated likelihood of risk across various ports in Mexico, we used the World Port Index layer (National Geospatial-Intelligence Agency 2019). The Mexican Port System is integrated with 117 ports (Diario Oficial de la Federación 2021), however, the layer used for this analysis only has 30 ports, representing the most significant ones in the country.

For the classification of each port, we gathered information from the websites of the maritime safety information web page (National Geospatial- Intelligence Agency 2019). Various factors were considered in determining the risk classification, including port type (local and international), cargo type and countries visited (Table A2. in Supplementary material). A buffer zone of 100 km was generated around each port. We chose this distance based on the maximum dispersal distance of *V. mandarinia* within a day (Tripodi and Hardin 2020) and the dispersal velocity of *V. velutina* in its invaded range which is between 75 and 112 km per year (Robinet et al. 2017). By incorporating this buffer zone, we aimed to capture the potential range of influence and dispersal from the ports, considering the movement patterns of the hornet species. Finally, we summed the species likelihood establishment and the port buffer, resulting in the identification of areas susceptible to the introduction of each species. This integrated approach considers both the inherent risk associated with species establishment and the proximity to ports, which serve as potential pathways for the accidental introduction of these invasive species.

Biodiversity impact areas

The *Vespa* genus primarily feeds on carbohydrates from *Quercus sp*. for adults, while larval feeding relies on protein obtained from insects and spiders (Matsuura and Sakagami 1973; Matsuura and Yamane 1990). Recent eDNA research in nests from the U.S.A (an introduced area) indicates that *V. mandarinia* can feed on 36 taxa from 23 different families, with Hymenoptera species being the most common prey (Wilson et al. 2023).

To identify biodiverse areas potentially affected by *Vespa*, we employed distribution models of native Hymenopteran species, specifically from the *Bombus* genus and Meliponini tribe. The distribution models for *Bombus* were obtained from CONABIO (Table A1). For the Meliponini tribe, we conducted distribution models using the Maxent algorithm in its standalone software. We selected species based on Ayala's (1999) review, modeling only those with over 20 occurrences, downloaded from (CONABIO 2020). To evaluate each model, we used pROC via the Niche toolbox in R (Osorio-Olvera et al. 2020), considering models with a pROC value ≥ 0.75.

Subsequently, we transformed each model into binary maps using the 10-percentile training presence threshold. This threshold was chosen to mitigate the uncertainty of outlier presence points and eliminate areas of low suitability (Ahmadi et al. 2020). To obtain the potential richness map, we added the binary maps for *Bombus* and Meliponini using SDM Toolbox v2.4 of ArcMap 10.4 (Brown et al. 2017). This map was classified into four levels suggesting a potential impact on *Bombus* and Meliponini diversity. We used a quantile distribution to establish these levels which were assigned as follows: null impact = 0, low impact = 1, medium impact = 2, and high impact = 3, based on quantile values.

To determine the biodiversity impact areas, we combined the establishment risk of each hornet species with the potential richness of native hymenopteran. This integration allowed us to identify areas where the presence of the hornets could potentially impact native biodiversity. Furthermore, we incorporated a map of natural protected areas in Mexico from (CONANP 2022a) to assess if any of these critical sites for biodiversity conservation and ecosystem services are at potential risk from the invasion of these hornets. This integration provides valuable insights into the potential overlap between hornet invasion risk and protected areas, aiding in the identification of priority areas for conservation efforts.

Economic impact areas

The economic impact assessment relied on data from the Agri-food Information System (SIACON) for the year 2021, specifically municipal honey and wax production information (SADER 2021). Key fields from SIACON included production (measured in tons or thousands of liters), the average price per kilogram, and production value (measured in thousands of Mexican pesos). To evaluate the economic impact of beekeeping at the municipal level, we combined honey and wax production values and calculated the percentage relative to the total state-level production (Norderud et al. 2021).

In Mexico, areas with the highest bee production generally show profitability ranging from 19 to 38 cents for every Mexican peso invested (Magaña Magaña and Leyva Morales 2011). To identify areas with potential economic impact, we reclassified this map to depict levels of exposure to the risk of invasion by *Vespa* species. Municipalities were categorized as follows: those with a production percentage of 0% were designated as having null exposure, municipalities with production percentages ranging from 0.1 to 5% were classified as low-exposure areas, those with production percentages from 5.1 to 18.9% were categorized as medium-exposure areas, and municipalities with production percentages exceeding 19% were deemed high-exposure areas. This classification helps pinpoint areas where the economic impact of beekeeping is significant and potentially vulnerable.

We also integrated the likelihood of establishment risk map and apiarian production for each species. The potential final economic loss was calculated using two loss percentages: 5% and 30%, reflecting different levels of severity. These percentages were selected based on reported economic impact for *V. velutina* in invaded areas (ranging from 5 to 30%) (Monceau et al. 2014), and for *V. mandarinia* in its native distribution (ranging from 10 to 20%) (Matsuura and Yamane 1990). The resulting potential economic loss was expressed in monetary terms, aiming to provide a more realistic estimate considering that the economic repercussions of these species do not encompass 100% of the resources.

Results

Ecological niche modeling

The extent of niche overlap between *V. velutina* and *V. mandarinia* is extensive. When examining the minimum volume ellipsoids (MVE) in their respective native distribution, it becomes apparent that the niche of *V. velutina* (MVE = 24) is larger than that of *V. mandarinia* (MVE = 15.80; Fig. 2a). However, when comparing the niches of these species in their exotic distributional areas, *V. velutina* niche is smaller (MVE of 2.13) than to the niches of both species in their native ranges (Fig. 2b and **c**). Also, the similarity of the niches of *V. mandarinia* and *V. velutina* in their native areas is moderate (Jaccard index = 0.48, Fig. 2a). It is important to note that for *V. mandarinia* the native distribution represents the realized niche since no population has been established outside of Asia so far. Conversely, when considering environmental data from native and invasive distribution of *V. velutina*, the similarity decreases (Jaccard index = 0.33, Fig. 2d).

Overall, these findings suggest that *V. velutina* exhibits a larger niche in its native range compared to *V. mandarinia*. Additionally, the invasive distribution of *V. velutina* reveals a smaller niche size, indicating potential differences in ecological preferences and adaptive capabilities between the two species.

Potential distribution model

A total of 1,333 models were parameterized, however, for each parametrization, one model received the best values for the mentioned criteria (pROC = 0, omission = 0.055 and delta AICc = 0). The final criteria are shown in Table 1. The final models were used to estimate the potential distribution for both species in North America and Central America (projection area was 19,069,000 km2, Fig. A1). The final evaluation of the models yielded pROC ratio values greater than 1.4 for all three models, indicating that the models are better than a randomly generated model (Table 2).

For *Vespa mandarinia* suitability was found in eastern Canada and the United States (southeastern, northeastern and central-eastern regions), except for the no-extrapolation

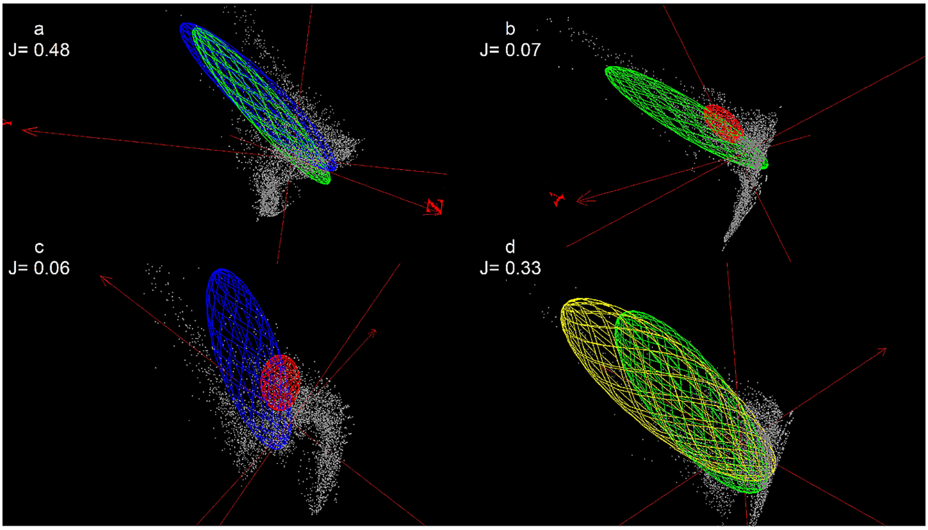

Fig. 2 Ecological niche of *Vespa mandarinia* and *V. velutina*. The green ellipsoid represents the realized niche of *V. mandarinia*. The red ellipsoid represents the environmental space occupied by *V. velutina* in the invaded area in Europe, while the blue ellipsoid represents the native area. The yellow ellipsoid represents the realized niche of *V. velutina* (native area + invaded area). The cloud of gray dots represents the environmental data. a.- Realized niche of *V. mandarinia* and environmental space of native area of *V. velutina*; b.- Realized niche of *V. mandarinia* and environmental space of invaded area of *V. velutina*; c.- Environmental space of native and invaded area of *V. velutina*; d.- Realized niche of both species

Table 1 Criteria used for the potential distribution models of the species *Vespa mandarinia* and *V. velutina*. Summary of the criteria used for the three final models for *Vespa* species. Features column shows the types of base functions that were used in each model:l = linear; q = quadratic; h = hinge ; p = product

Model	Features	Beta regularizer value	Number of environmental variables	Calibration occurrences	Evaluation occurrences
V. mandarinia	lq	0.1	6	126	56
V. mandarinia	lqh	2	7	126	56
V. velutina	lqp	0.2	6	64	28

Table 2 Final evaluation for the potential distribution models of the species *Vespa mandarinia* and *V. velutina*

Model	Mean AUC ratio	Partial ROC	Omission rate at 5%
V. mandarinia (6 variables)	1.74	0	0.036
V. mandarinia (7 variables)	1.72	0	0.072
V. velutina (6 variables)	1.45	0	0.035

scenario, which contains an area of low suitability (Fig. A1d, h). In the regions of British Columbia and Washington, where the species has been observed since 2019, suitability values were intermediate. Conversely, in Mexico, the suitability scores are low, particularly in the Gulf of Mexico and the southeast of the country. The suitability scores in Central America were found to be like those observed in Mexico (Fig. A1a-h).

The distribution of *V. velutina* exhibits contrasting patterns across extrapolation scenarios. The extrapolation model (Fig. A1i) predicts intermediate to high suitability (ranging from 0.4 to 0.7) for both North America and Central America. In contrast, when applying extrapolation-clamping, the model indicates high suitability for Canada and the United States, while suitability values in Mexico are low to intermediate. Notably, these values are greater than 0.1, particularly in the states near the Gulf of Mexico. These suitability patterns in Mexico align closely with those obtained for *V. mandarinia* (Fig. A1k). In the absence of an extrapolation, no suitability sites are identified as suitable within the extrapolation areas across North America (Fig. A1l).

Likelihood of establishment risk map

The establishment sites map for *V. mandarinia* show that extrapolation and extrapolation-clamping encompass a larger geographic area. The model predicts likelihood of establishments sites in eastern regions of Canada and the United States, specifically in the southeast, northeast and central east region. In Mexico, the Gulf of Mexico exhibits a low-risk category, while the remaining parts of the country are considered to have no risk.

For *V. velutina* extrapolation scenario indicates a low to intermediate likelihood of establishment across the entire area, while when using extrapolation-clamping, the risk categories vary from low to intermediate for most of the territory of Canada and the United States. In Mexico, the Gulf Coast is characterized by a low likelihood. Finally, the no-extrapolation scenario does not predict any likelihood of establishment throughout the entire area (Fig. A2). Given the similarity observed between the potential distribution models of both *V. mandarinia* and *V. velutina* using extrapolation-clamping scenario, also considering the conservatism hypothesis, the following analyses were performed using the distribution maps derived from this scenario.

Furthermore, with the analysis of climate novelty we identify the presence of type 1 novelty for both species, which identifies areas with at least one environmental variable outside of the data range. In the case of *V. mandarinia*, the affected sites are primarily located in the eastern United States and western regions of Mexico and the United States. The climate variables involved were precipitation seasonality and isothermality. For *V. velutina*, the variables were isothermality in most of the area and the mean temperature of the warmest Quarter in the south of Mexico and Central America (Fig. A4).

Susceptible areas to the introduction of hornets

We identified a total of 16 ports, out of 30, with a high likelihood for the introducing *Vespa* species due to their connection with international ports, linking with over 100 countries worldwide. These ports handle cargoes such as ores, agricultural products and containers, which pose a significant likelihood for the introduction of *Vespa* species. Furthermore, there were six ports classified as having medium likelihood, primarily associated with tourism services. This category poses a potential risk because tourists are an important pathway for introduction (CBD 2014). Furthermore, there is evidence indicating that *V. mandarinia* may have been introduced to North America for human consumption, as this species is used in traditional medicine and as a food source (Tripodi and Hardin 2020). Regarding the port San Marcos Island, located in the state of Baja California, we used a precautionary principle and classify it as a medium risk likelihood due to a lack of information regarding shipments or countries visited by ships. Morro Redondo Port in Baja California, which receives and transports salt shipments, was identified as a potential accidental pathway introduction due to its connection with Asia, although salt itself is not a resource for these species. Lastly, eight ports were classified as low risk likelihood. These ports primarily serve local activities such as fishing boats, embarkation of passengers to platforms and floating vessels (Fig. 3; Table A2).

For *V. mandarinia*, there are 18 ports near potential establishment sites. Ports that represent the highest risk likelihood are in the Gulf of Mexico, they are Altamira, Tuxpan, Tampico, Veracruz and Progreso. For *V. velutina* there are 20 ports near potential establishment sites with the highest risk likelihood in the Gulf of Mexico and the Pacific coast, they are Altamira, Tuxpan, Tampico, Veracruz, Guaymas, Ensenada and Rosarito.

Economic impact areas

In Mexico, according to data from the Ministry of Agriculture and Rural Development (SADER 2021), honey production was 2,819,774,450 MXN (139,042,132.64 USD). Municipalities with higher production were Champotón, Holpechén, Campeche (Campeche), Jamay (Jalisco) and Felipe Carrillo Puerto (Quintana Roo) with a production equivalent of 12.5% of the total. Furthermore, the production of wax has a value of 115,554,260 MXN (5,697,941.81 USD), municipalities with higher production were Champotón (Campeche), Jamay (Jalisco), Felipe Carrillo Puerto (Quintana Roo) and Coatepec (Veracruz) with a production value of 15% of the total. The value of honey and beeswax in Mexico was 2,935,328,710 MXN (144,740,074.45 USD) (Fig. 4).

If *V. mandarinia* is introduced in Mexico and affects the potential areas of honey and beeswax production, the economic impact is estimated to be approximately 1,552,347,020

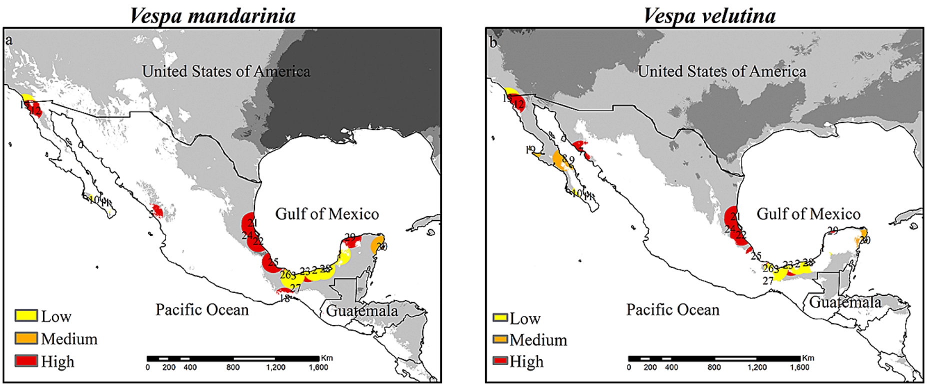

Fig. 3 Susceptible areas to the introduction of hornets. a) Classification of the risk of the introduction of Asian hornet species for the ports of Mexico with a buffer of 100 km. The maps represent the locations with risk of introduction in Mexico for the *Vespa* species. The gray area represents the map of the establishment risk of each species. The port names are: (1) Campeche, (2) Frontera, (3) Nanchital, (4) Puerto Vallarta, (5) Mazatlan, (6) Topolobampo, (7) Guaymas, (8) Santa Rosalia, (9) Isla San Marcos, (10) San Juan de la Costa, 11) La Paz, 12) Ensenada, 13) Rosarito, 14) Acapulco, 15) Lazaro Cardenas, 16) Manzanillo, 17) Puerto Madero, 18) Salina Cruz, 19) Puerto Morro Redondo, 20) Pichilingue, 21) Altamira, 22) Tuxpan, 23) Dos Bocas Terminal, 24) Tampico, 25) Veracruz, 26) Coatzacoalcos, 27) Minatitlan, 28) Ciudad del Carmen, 29) Progreso, 30) San Miguel De Cozumel

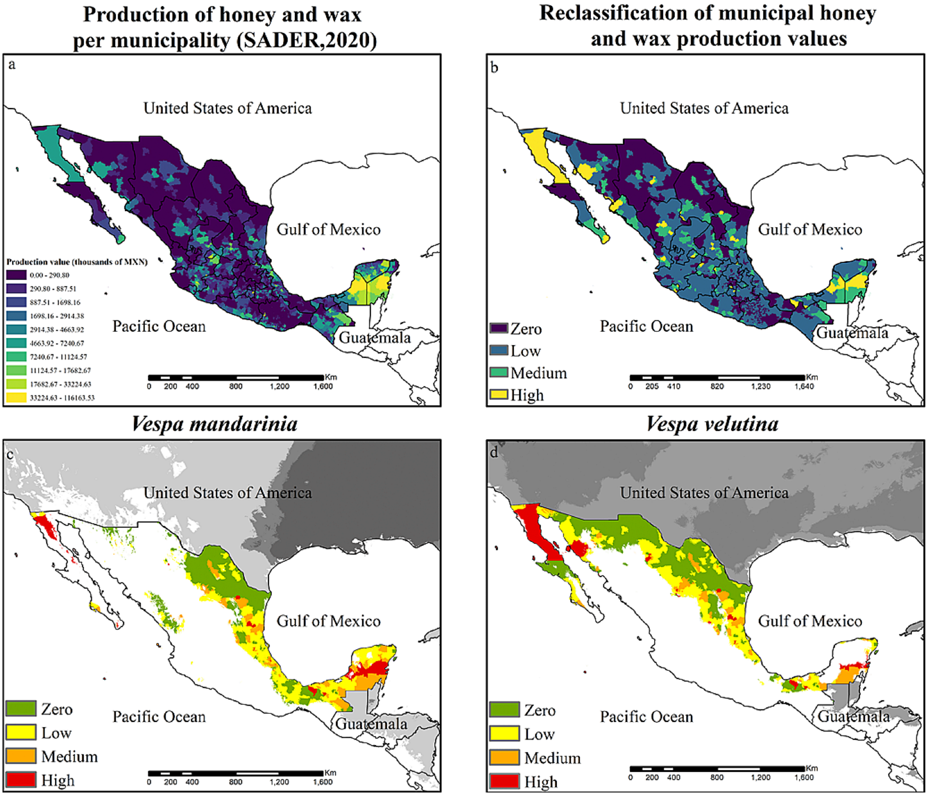

Fig. 4 Potential economic impact areas before the potential introduction and establishment of *V. mandarinia* and *V. velutina*. **a**) Value of honey and wax production in 2021 at the municipal level (data from the SIACON). **b**) Reclassification of municipal honey and wax production values, municipalities with a state production percentage of 0 are classified as no exposure, municipalities with a state average production of 0.1–5% are areas with low exposure, 5.1–18.9% have a medium exposure and above 19% are municipalities with high exposure to risk. **c**) Potential economic risks for the scenario of *V. mandarinia* establishment. **d**) Potential economic risks for the scenario of V. *velutina* establishment. The gray area represents the map of the likelihood of establishment of each species

MXN (76,545,711.04 USD). This represents 53% of the total production at potential risk. The states more vulnerable to this risk are Campeche, Quintana Roo, Veracruz, Chiapas and Baja California (Fig. 4). For *V. velutina*, the potential impact could be of 1,024,672,280 MXN (50,526,246.54 USD), accounting for approximately 35% of total production. The states at more potential risk are Baja California and Campeche.

The final potential economic loss, considering a conservative scenario (10% of economic loss) is approximately 155,234,702 MXN (7,654,571.10 USD) and 102,467,228 MXN (5,052,624.65 USD) for *V. mandarinia* and *V. velutina*, respectively. In the worst-case scenario (30% of loss), the impact could have a cost of 465,704,106 MXN (22,963,713.31 USD) for *V. mandarinia* and 307,401,684 MXN (15,157,873.96 USD) for *V. velutina*.

Biodiversity impact areas

For Meliponini, the areas of high richness are in the south of the country, in the states of Campeche, Chiapas, Guerrero, Oaxaca, Quintana Roo, Veracruz and Yucatán. The richness map of *Bombus* (obtained with information downloaded from CONABIO, Table A1) shows that Chiapas, Estado de México, Guerrero, Morelos, Michoacán and Oaxaca are the states with the highest richness.

In the scenario of the introduction and establishment of *V. mandarina*, the biodiversity area that could be impacted is estimated to be 357,149 km^2. This area is primarily located in the eastern and southeastern of Mexico. Within this area, the high-impact area covers 22,105 km^2, the medium impact level spans 102,590 km^2 and the low-impact area of 232,454 km^2. For *V. velutina*, the potentially impacted biodiversity areas cover approximately 187,562 km^2, primarily concentrated in the southeast of Mexico. Within this, the high-impact area spans 40,018 km^2, the medium-impact area covers 59,400 km^2, and the low-impact area encompasses about 88,144 km2. (Fig. 5).

The species that are at risk in the potential scenario of the introduction of *V. mandarinia* are *Cephalotrigona zexmeniae*, *Melipona beechei*, *Nannotrigona perilampoides, Partamona bilineata*, *Scaptotrigona pectoralis*, *Trigona (Trigona) fulviventris* and *Trigona*

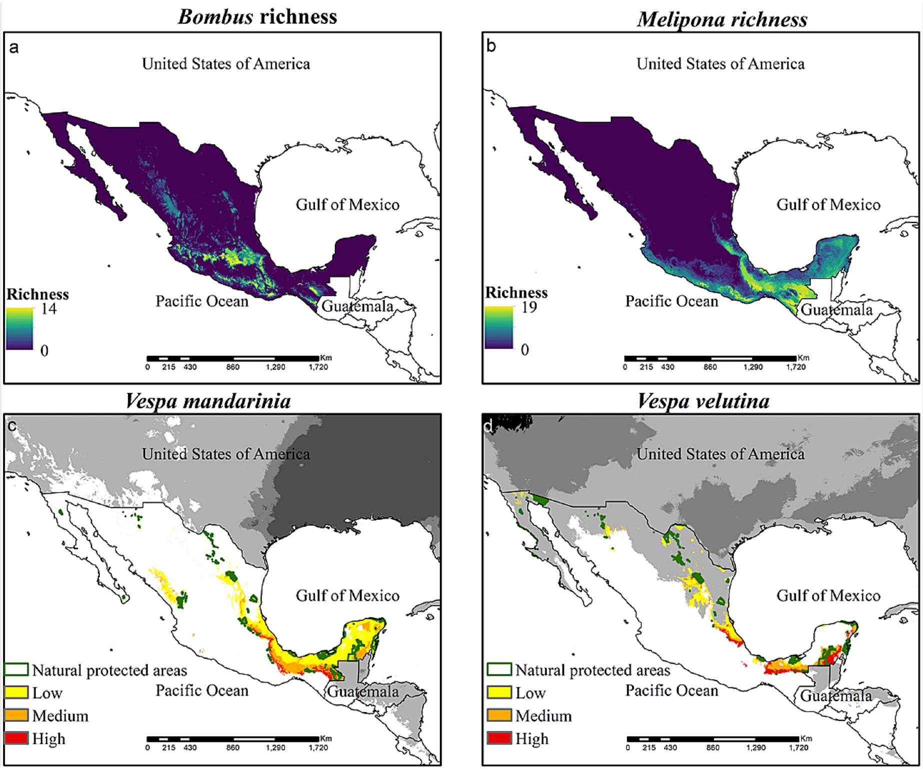

Fig. 5 Biodiversity impact areas. **a**) Richness of native *Bombus* species; **b**) Richness of native Meliponini tribe species; **c**) Biodiversity impact areas in the potential establishment of *V. mandarinia*; **d**) Biodiversity impact areas in the potential establishment of *V. velutina.* The green polygons in **c** and **d** represent natural protected areas and the gray area represents the map of the establishment risk of each species

(Trigona) fuscipennis. Similarly, in the case of the introduction of *V. velutina* species at risk include *C. zexmeniae*, *M. fasciata*, *N. perilampoides*, *S. mexicana*, *S. pectoralis*, Trigona (Trigona) *fulviventris*, *Trigona (Frieseomelitta) nigra* and *Trigona (Trigona) corvina*.

According to the biodiversity impact, the potential invasion risk of *V. mandarinia* overlaps with 57 protected areas (37,463 km^2). Among these are notable sites such as the Flora and Fauna Protected Area Laguna de Términos as well as the Biosphere Reserves of Montes Azules, Sian Ka´an and Calakmul. Similarly, the biodiversity impact map for *V. velutina* reveals that 49 protected areas spanning a total area of 29,367 km^2, have a potential risk of invasion. These areas would be the Flora and Fauna Protected Area Laguna de Términos and the Biosphere Reserves of Sian Ka´an, Calakmul and El Pinacate y Gran Desierto de Altar. Unfortunately, these protected areas represent 50% of the total protected areas at risk, where the Biosphere Reserves and the Protected Areas for Flora and Fauna would bear the most significant impact if either *V. mandarinia* or *V. velutina* were to establish successfully in the country (Table 3).

Risk assessment map

The integrated risk assessment map, considering potential establishment areas, areas susceptible to hornet introduction and economic and biodiversity impact areas, reveals that the highest-risk area where *V. mandarinia* could have a significant impact covers approximately 131,220 km^2, accounting for 6.7% of the total area of the country. This area is predominantly located in the states of Tabasco, Veracruz, Campeche, Yucatán and Quintana Roo (Fig. 6). In the case of *V. velutina*, the highest-risk areas encompass approximately 58,948 km^2, representing 3% of the total national area. The states of Tabasco and Veracruz are identified as high-risk areas for *V. velutina* invasion.

Discussion

Our analyses focus on a likelihood risk assessment for the introduction of species *V. mandarinia* and *V. velutina*. The findings suggest that *V. velutina* has a larger niche in its native range compared to *V. mandarinia*. However, in their exotic distributional areas, *V. velutina's* niche is smaller, which justifies the inclusion of the correctly characterized species niche in the potential invaded area. The spatial risk assessment for Mexico identifies potential

Table 3 Categories and extent of protected natural areas at risk of invasion by *V. mandarinia* and *V. velutina*

	Vespa mandarinia		Vespa velutina	
Protected natural area management category	**Number of areas**	**Area at risk (km^2)**	**Number of areas**	**Area at risk (km^2)**
Parque Nacional (PN)	13	1,723.5	6	1,293.8
Reserva de la Biosfera (RB)	21	24,539	18	17,767
Área de Protección de Flora y Fauna (APFF)	15	7,006	19	7,664.5
Área de Protección de los Recursos Naturales (APRN)	4	4,113	3	2,625.1
Santuario (SAN)	1	0.4	1	0.4
Monumentos Naturales (MN)	3	80.6	2	15.8
Total	57	37,463	49	29,367

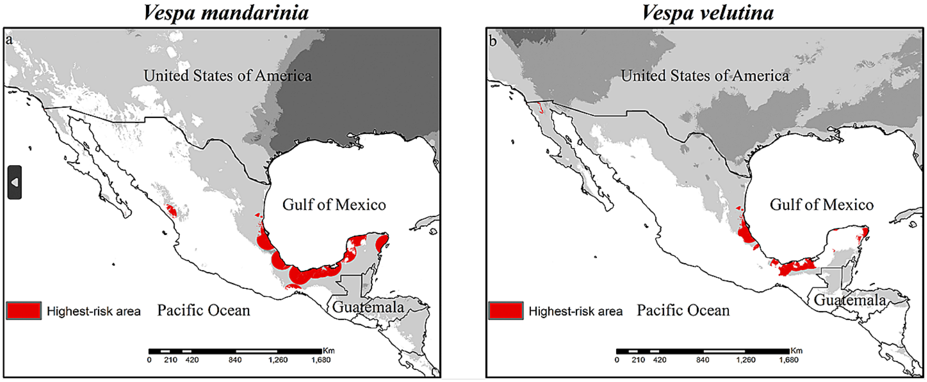

Fig. 6 Risk assessment maps of **a**) *V. mandarinia* and **b**) *V. velutina*. The gray area represents the map of the establishment risk of each species

high-risk areas for both species, with *V. mandarinia* posing a significant impact in Tabasco, Veracruz, Campeche, Yucatán and Quintana Roo, while *V. velutina* poses a potential high risk in Tabasco and Veracruz. Economic impact analysis reveals potential losses in honey and beeswax production for both species, with *V. mandarinia* posing a higher economic risk (Thomson 2004). Biodiversity impact areas indicate that the introduction of these species could affect certain native species and protected areas.

The *Vespa* genus has 22 species with shared morphological and genetic traits (Perrard et al. 2013). In this study, we reconstructed ecological niches using only native distribution data, revealing strong similarity. However, when including data from invaded areas, similarity diminishes. This is because species crossing geographical barriers or translocated encounter novel environments not found in their native range, which complement their niche (Broennimann and Guisan 2008). Other research also indicates that models based solely on native distribution data may not fully represent the underlying niche (Castaño-Quintero et al. 2020; Qiao et al. 2017). The "splitting" approach, using separate models (Smith et al. 2019), has been effective in understanding *V. velutina's* niche in its invaded European region. It also highlights that the environmental range in the invaded area is smaller than the native range, aligning with findings in the ecological niche of biological invasions (Liu et al. 2020).

This research aligns with others in predicting *V. mandarinia* invasion risk, particularly in the northeast and southeast of the United States (Alaniz et al. 2021), southern and northeastern Mexico (Moo-Llanes 2021; Nuñez-Penichet et al. 2021; Zhu et al. 2020). The potential establishment of *V. velutina* in North America mirrors predictions by Villemant et al. (2011) for the USA. In Mexico, our study suggests a more cautious outlook for species establishment, differing from Villemant et al. (2011) due to methodological variations. While ensemble forecasting in Biomod for invasive species distribution prediction is limited (Hao et al. 2019), the extensive use of Maxent consistently demonstrates strong predictability (Jarnevich and Young 2015).

Evidence shows that *Vespa* has been repeatedly introduced to North America, with several species intercepted ~ 50 times in ports of the United States, including *V. bellicosa, V. crabro, V. orientalis, V. mandarinia, and V. tropica* (Smith-Pardo et al. 2020). This highlights the ongoing likelihood of introductions and the need for effective measures to prevent the establishment of these invasive hornets. A similar proposal emphasizes the importance of considering information of port classification, which has shown to be relevant in evaluating the likelihood of introduction and establishment. Evidence from other arthropod introductions supports the significance of incorporating such data (Norderud et al. 2021). In Mexico, more than 50% of the ports represent a high risk, especially those that are in the Gulf of Mexico, in this sense it is essential that surveillance authorities strengthen their strategies for interception of *V. mandarinia* and *V. velutina* and other *Vespa* species. Actions such as training for the correct identification of these species are essential for the prevention and early management of an introduction (Smith-Pardo et al. 2020).

The potential risk of natural dispersion for *V. mandarinia* has been assessed in its introduction area in the United States. The findings indicate that the species has a high dispersal potential, like that of *V. velutina*. Consequently, if no efforts are made to halt the invasion, *V. mandarinia* could potentially invade the western part of North America (Zhu et al. 2020). Natural dispersion can play a significant role in the spread of invasive species. An example of this is the case of the exotic dung beetle *Digitonthopagus gazella*, which was intentionally introduced to certain regions in the United States in 1970. Within ten years, it had already reached northeastern Mexico and it has since invaded various countries in the Americas, including Argentina (Kohlmann 1994; Bohle-Álvarez et al. 2009). This demonstrates how introduced species can naturally disperse and establish populations in new areas. Nuñez-Penichet et al. (2021), who researched the potential distribution of *V. mandarinia* in the United States, also mention that the species could potentially follow a direct route from the northwest Pacific region to the east coast, which borders Mexico. This raises concerns about the possibility of the species crossing geopolitical borders and invading the country.

The economic impact of invasive species encompasses various costs, including control, survey, detection, management, and eradication. However, such information is often unavailable and underestimated (Diagne et al. 2021). In the context of Asian hornet invasions, there are both direct and indirect economic losses to consider. Direct losses, as highlighted in this study, can result from the invasion itself. Additionally, there are indirect losses associated with the decline in pollination services provided by *Apis mellifera* (honey bees) and species of the *Bombus* and *Melipona* genera in Mexico's agri-food sector. Particularly, crops like fruits, nuts, and seeds, which generate significant income of 5.1 billion Mexican pesos, could be at risk (Ibarra-Zapata et al. 2022). The economic risk is further heightened by the potential threat of Asian hornets to native species that hold both cultural and economic importance in México. For instance, the *M. beechei, known* as "Xunaan-Kaab" or royal bee, has been used in rituals related to honey production for centuries (ECOSUR et al. 2018; Guzman et al. 2011). Similarly, *S. mexicana* known as "Pisilnek-mej" or Congo bee, is culturally significant.

Native bees play a vital role as pollinators for wild and cultivated plants, facing existing threats like agrochemicals and diseases (Bacab-Pérez and Canto 2020). The introduction of predatory species would further stress them. This study shows potential overlap of *V. mandarinia* and *V. velutina* establishment areas with native Meliponini tribe and *Bombus* genus distribution. *Vespa* species' impact on biodiversity extends beyond native bees, affecting various arthropods due to their opportunistic foraging (Monceau et al. 2014). Considering *V. mandarinia* preys on 36 species across different taxonomic groups (Wilson et al. 2023), the research potentially underestimates biodiversity impact. Wilson et al. (2023) also note *V.*

mandarinia's adaptable nature, preying on different species in Washington, U.S. compared to its native range.

The National Biodiversity Information System reports about 5,174 arthropod species in federal natural protected areas overlapping with *V. mandarinia's* establishment risk, with 286 of them IUCN-threatened (CONABIO 2023). Protected areas in Mexico operate under diverse categories, each with distinct conservation goals and allowed activities. Biosphere Reserves, most susceptible to Asian hornet introduction, focus on safeguarding endemic, threatened, and endangered species. Productive activities like beekeeping are permitted in buffer zones, determined at their designation (CONANP 2022b). Hence, potential Asian hornet invasion could significantly impact biodiversity and the economy, notably in Biosphere Reserves like Sian Ka'an and Calakmul where such activities occur (CONABIO and AECID 2011; SEMARNAT and CONANP 2014; Villanueva and Collí 1996).

Potential high-risk areas for the introduction of *Vespa* species in Mexico, particularly concentrated in the southern region, underscore the urgent need for prioritized surveillance efforts. EDRRS before the arrival of Asian hornets is crucial. These proactive measures, supplemented by further research validating our findings, are imperative. It's worth noting that Mexico's spatial assessments often lack necessary data not only for evaluating invasive species likelihood of establishment, but also for assessing potential introduction pathways and impacts. This data deficiency significantly heightens the risk of invasive species proliferation within the country. Here, geographic information systems, coupled with environmental and publicly available biological data, enable an effective risk assessment. These endeavors are essential for biodiversity protection, ecosystem preservation, and shielding the economy from invasive species' negative repercussions.

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Declarations

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Statement During the preparation of this work the author(s) used OpenAI (https://chat.openai.com) in order to improve readability and language. After using this tool, the author(s) reviewed and edited the content as needed and took full responsibility for the content of the publication.

References

EPPO (2022) Vespa mandarinia. EPPO Global Database. https://gd.eppo.int/taxon/VESPMA. Accessed 23 February 2024

Ahmadi M, Farhadinia MS, Cushman SA, Hemami MR, Nezami Balouchi B, Jowkar H, Macdonald DW (2020) Species and space: a combined gap analysis to guide management planning of conservation areas. Landsc Ecol. https://doi.org/10.1007/s10980-020-01033-5

Alaniz AJ, Carvajal MA, Vergara PM (2021) Giants are coming? Predicting the potential spread and impacts of the giant Asian hornet (*Vespa Mandarinia*, Hymenoptera: Vespidae) in the USA. Pest Manag Sci. https://doi.org/10.1002/ps.6063

Ayala R (1999) Revisión De las abejas sin aguijón de México. Folia Entomol Mex 106:1–123

Bacab-Pérez AI, Canto A (2020) La abeja melipona en la cultura maya. Desde el herbario CICY. https://www.cicy.mx/Documentos/CICY/Desde_Herbario/2020/2020-07-23-Bacab-Canto-La-abeja-melipona.pdf. Accessed 23 February 2024

Barbet-Massin M, Salles JM, Courchamp F (2020) The economic cost of control of the invasive yellow-legged Asian hornet. NeoBiota. https://doi.org/10.3897/neobiota.55.38550

Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JRU, Richardson DM (2011) A proposed unified framework for biological invasions. Trends Ecol Evol. https://doi.org/10.1016/j.tree.2011.03.023

Bohle-Álvarez MC, Damborsky M, Bar ME, Ocampo F (2009) Registros Y distribución De La Especie afroasiática *Digitonthophagus gazella* (Coleoptera: Scarabaeidae: Scarabaeinae) en Argentina. Rev Soc Entomol Argent 68:373–376

British Columbia Ministry of Agriculture (2019) Three Asian giant hornets found in Nanaimo. BC Gov News. https://news.gov.bc.ca/releases/2019AGRI0102-001759. Accessed 23 February 2024

Broennimann O, Guisan A (2008) Predicting current and future biological invasions: both native and invaded ranges matter. Biol Lett. https://doi.org/10.1098/rsbl.2008.0254

Brown JL, Bennett JR, French CM (2017) SDMtoolbox 2.0: the next generation Python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. https://doi.org/10.7717/peerj.4095. PeerJ

CABI (2022) *Vespa velutina* (Asian hornet). Invasive Species Compendium CAB International. https://www.cabi.org/isc/datasheet/109164. Accessed 23 February 2024

Castaño-Quintero S, Escobar-Luján J, Osorio-Olvera L, Peterson AT, Chiappa-Carrara X, Martínez-Meyer E, Yañez-Arenas C (2020) Supraspecific units in correlative niche modeling improves the prediction of geographic potential of biological invasions. PeerJ. https://doi.org/10.7717/peerj.10454

CBD (2014) Pathways of Introduction of invasive species, their prioritization and management. Convention on Biological Diversity. https://www.cbd.int/doc/meetings/sbstta/sbstta-18/official/sbstta-18-09-add1-en.pdf. Accessed 23 February 2024

Cobos ME, Peterson AT, Barve N, Osorio-Olvera L (2019) Kuenm: an R package for detailed development of ecological niche models using Maxent. https://doi.org/10.7717/peerj.6281. PeerJ

CONABIO AECID (2011) Plan rector para promover una denominación de origen de mieles de la Península De Yucatán. Comisión Nacional Para El Conocimiento Y Uso De La Biodiversidad. Agencia Española de Cooperación Internacional para el Desarrollo, Mexico

CONABIO (2020) Sistema Nacional de Información sobre Biodiversidad. Registros de ejemplares. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. https://www.snib.mx/. Accessed 23 February 2024

CONABIO (2021) Sistema Nacional de Información sobre Biodiversidad. Registros de ejemplares. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. https://www.snib.mx/. Accessed 23 February 2024

CONABIO (2023) Sistema Nacional de Información sobre Biodiversidad. Registros de ejemplares. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. https://www.snib.mx/. Accessed 23 February 2024
CONABIO (2022) Sistema de información sobre especies invasoras. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. https://www.biodiversidad.gob.mx/especies/Invasoras. Accessed 23 February 2024
CONAFOR (2022) Alerta temprana y evaluación de riesgo para escarabajos ambrosiales exóticos. Comisión Nacional Forestal. http://sivicoff.cnf.gob.mx/ContenidoPublico/01 Avisos Publicos/mapas de alerta temprana/AMBROSIALES/2022/Mapas Riesgo Escarabajos Ambrosiales Abril-Junio 2022.pdf. Accessed 23 February 2024
CONANP (2022b) Áreas naturales protegidas decretadas. Comisión Nacional para las Áreas Naturales Protegidas. http://sig.conanp.gob.mx/website/pagsig/datos_anp.htm. Accessed 23 February 2024
CONANP (2022a) Información espacial de las áreas naturales protegidas. Comisión Nacional para las Áreas Naturales Protegidas. http://sig.conanp.gob.mx/website/pagsig/info_shape.htm. Accessed 23 February 2024
R Core Team (2020) *R*: A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.r-project.org/. Accessed 23 February 2024
Diagne C, Leroy B, Vaissière AC, Gozlan RE, Roiz D, Jarić I, Salles JM, Bradshaw CJA, Courchamp F (2021) High and rising economic costs of biological invasions worldwide. Nature. https://doi.org/10.1038/s41586-021-03405-6
Diario Oficial de la Federación (2021) Reglas de operación del programa apoyos para el desarrollo forestal sustentable. https://www.conafor.gob.mx/apoyos//docs/adjuntos/5e53ee80881ddea8af544ee25945b2f9.pdf. Accessed 23 February 2024
Dueñas MA, Ruffhead HJ, Wakefield NH, Roberts PD, Hemming DJ, Diaz-Soltero H (2018) The role played by invasive species in interactions with endangered and threatened species in the United States: a systematic review. Biodivers Conserv. https://doi.org/10.1007/s10531-018-1595-x
Dvořák L (2006) Oriental hornet *Vespa Orientalis* Linnaeus, 1771 found in Mexico. Ent Probl 36:80
ECOSUR CONABIO, GEF (2018) Mieles mesoamericacas. https://www.ecosur.mx/mieles/miel-de-melipona/. Accessed 23 February 2024
Escobar LE, Ryan SJ, Stewart-Ibarra AM, Finkelstein JL, King CA, Qiao H, Polhemus ME (2015) A global map of suitability for coastal *Vibrio cholerae* under current and future climate conditions. Acta Trop. https://doi.org/10.1016/j.actatropica.2015.05.028
Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int J Climatol. https://doi.org/10.1002/joc.5086
GBIF (2022b) Occurrence Download. The Global Biodiversity Information Facility. https://doi.org/10.15468/DL.KBD5AA
GBIF (2020a) GBIF Occurrence Download. The Global Biodiversity Information Facility https://doi.org/10.15468/dl.t4zfjk
Georgia Department of Agriculture (2023) Yellow-Legged hornet. https://agr.georgia.gov/yellow-legged-hornet. Accessed 23 February 2024
Guzmán M, Balboa C, Vandame R, Albores ML, González-Acereto J (2011) Manejo de las abejas nativas sin aguijón en México: *Melipona beecheii* y *Scaptotrigona mexicana*. El Colegio de la Frontera Sur, Mexico
Hao T, Elith J, Guillera-Arroita G, Lahoz-Monfort JJ (2019) A review of evidence about use and performance of species distribution modeling ensembles like BIOMOD. https://doi.org/10.1111/ddi.12892. Divers Distrib
Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. J Appl Ecol. https://doi.org/10.1111/j.1365-2664.2008.01600.x
Ibáñez-Justicia A, Loomans AJM (2011) Mapping the potential occurrence of an invasive species by using CLIMEX: case of the Asian hornet (*Vespa Velutina Nigrithorax*) in the Netherlands. Proc Neth Entomol Soc Meet 22:39–46
Ibarra-Zapata E, Aguirre-Salado CA, Miranda-Aragón L, Loredo-Osti C, Escoto-Rodríguez M, Ramírez F (2022) Mapeo de una posible amenaza para el sector agrícola mexicano: avispón gigante asiático *Vespa mandarinia* (Smith 1852) (Hymenoptera: Vespidae). Rev Soc Entomol Argent 81:1–18
IPBES, Summary for Policymakers of the Thematic Assessment Report on Invasive Alien Species and their Control of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Roy HE, Pauchard A, Stoett P, Renard Truong T, Bacher S, Galil BS, Hulme PE, Ikeda T, Sankaran KV, McGeoch MA, Meyerson LA, Nuñez MA, Ordonez A, Rahlao SJ, Schwindt E, Seebens H, Sheppard AW, Vandvik V (eds)(2023) IPBES secretariat, Germany. https://doi.org/10.5281/zenodo.7430692

Jarnevich CS, Reynolds LV (2011) Challenges of predicting the potential distribution of a slow-spreading invader: a habitat suitability map for an invasive riparian tree. Biol Invasions. https://doi.org/10.1007/s10530-010-9798-4

Jarnevich CS, Young NE (2015) Using the Maxent program for species distribution modelling to assess invasion risk. In: Venette RC (ed) Pest risk modelling and mapping for invasive alien species. CAB International, USDA, United States, pp 65–81

Jensen AB, Palmer KA, Boomsma JJ, Pedersen BV (2005) Varying degrees of *Apis mellifera ligustica* introgression in protected populations of the black honeybee, *Apis mellifera mellifera*, in northwest Europe. Mol Ecol 14:93–10

Knapp S, Schweiger O, Kraberg A, Asmus H, Asmus R, Brey T, Frickenhaus S, Gutt J, Kühn I, Liess M, Musche M, Pörtner HO, Seppelt R, Klotz S, Krause G (2017) Do drivers of biodiversity change differ in importance across marine and terrestrial systems- Or is it just different research communities' perspectives? https://doi.org/10.1016/j.scitotenv.2016.09.002. Sci Total Environ

Kohlmann B (1994) A preliminary study of the invasion and dispersal of *Digitonthophagus gazella* (Fabricius, 1787) in Mexico (Coleoptera: Scarabaeidae: Scarabaeinae). Acta Zool Mex 61:5–42

Kumar PG, Srinivasan G (2010) Taxonomic studies of hornet wasps (Hymenoptera: Vespidae) *Vespa* Linnaeus of India. Rec Zool Surv India 110:57–80

Lee JXQ (2010) Notes on *Vespa Analis* and *Vespa mandarinia* (Hymenoptera, Vespidae) in Hong Kong and a key to all *Vespa* species known from the SAR. Hong Kong Entomol Bull 2:31–33

Liu C, Wolter C, Xian W, Jeschke JM (2020) Most invasive species largely conserve their climatic niche. PNAS. https://doi.org/10.1073/pnas.2004289117

López S, González M, Goldarazena A (2011) *Vespa Velutina* Lepeletier, 1836 (Hymenoptera: Vespidae): first records in Iberian Peninsula. EPPO. https://doi.org/10.1111/j.1365-2338.2011.02513.x

Mack RN, Simberloff D, Lonsdale WM, Evans HC, Clout MN, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences and control. Ecol Appl. https://doi.org/10.1890/1051-0761(2000)010[0689:BICEGC]2.0.CO;2

Magaña-Magaña MA, Leyva-Morales CE (2011) Costos y rentabilidad del proceso de producción apícola en México. Contaduría y Administración. https://doi.org/10.22201/fca.24488410e.2011.421

Matsuura M, Sakagami S (1973) A bionomic sketch of the giant hornet, *Vespa mandarinia*, a serious pest for Japanese apiculture. Jour Fac Sci Hokkaido Univ 19:125–162

Matsuura M, Yamane S (1990) Biology of Vespine wasps. Springer, Germany

Mesgaran MB, Cousens RD, Webber BL (2014) Here be dragons: a tool for quantifying novelty due to covariate range and correlation change when projecting species distribution models. Divers Distrib. https://doi.org/10.1111/ddi.12209

Monceau K, Bonnard O, Thiéry D (2014) *Vespa Velutina*: a new invasive predator of honeybees in Europe. J Pest Sci. https://doi.org/10.1007/s10340-013-0537-3

Moo-Llanes DA (2021) Inferring distributional shifts of Asian giant hornet *Vespa Mandarinia* Smith in climate change scenarios. Neotrop Entomol. https://doi.org/10.1007/s13744-020-00840-4

National Geospatial Intelligence Agency (2019) World Port Index. National Geospatial Intelligence Agency https://msi.nga.mil/api/publications/download?key=16694622/SFH00000/Pub150bk.pdf&type=view. Accessed 23 February 2024

Norderud ED, Powell SL, Peterson RKD (2021) Risk assessment for the establishment of *Vespa mandarinia* (Hymenoptera: Vespidae) in the Pacific northwest, United States. J Insect Sci. https://doi.org/10.1093/jisesa/ieab052

Nuñez-Penichet C, Osorio-Olvera L, Gonzalez VH, Cobos ME, Jiménez L, DeRaad DA, Alkishe A, Contreras-Díaz RG, Nava-Bolaños A, Utsumi K, Ashraf U, Adeboje A, Peterson AT, Soberon J (2021) Geographic potential of the world's largest hornet, *Vespa mandarinia* Smith (Hymenoptera: Vespidae), worldwide and particularly in North America. PeerJ. https://doi.org/10.7717/peerj.10690

Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC, D'Amico JA, Itoua I, Strand HE, Morrison JC, Loucks CJ, Allnutt TF, Ricketts TH, Kura Y, Lamoreux JF, Wettengel WW, Hedao P, Kassem KR (2001) Terrestrial ecoregions of the world: A new map of life on Earth. BioScience. https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2

Osorio-Olvera L, Lira-Noriega A, Soberón J, Peterson AT, Falconi M, Contreras-Díaz RG, Martínez-Meyer E, Barve V, Barve N (2020) Ntbox: an r package with graphical user interface for modeling and evaluating multidimensional ecological niches. Methods Ecol Evol. https://doi.org/10.1111/2041-210X.13452

Perrard A, Pickett KM, Villemant C, Kojima JI, Carpenter J (2013) Phylogeny of hornets: a total evidence approach (Hymenoptera, Vespidae, Vespinae, *Vespa*). J Hymenopt Res. https://doi.org/10.3897/JHR.32.4685

Peterson AT, Papeş M, Soberón J (2008) Rethinking receiver operating characteristic analysis applications in ecological niche modeling. Ecol Model. https://doi.org/10.1016/j.ecolmodel.2007.11.008

Peterson AT, Soberón J, Pearson RG, Anderson RP, Martínez-Meyer E, Nakamura M, Araújo MB (2011) Ecological niches and geographic distributions. Princeton University Press, United States
Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecol Model. https://doi.org/10.1016/j.ecolmodel.2005.03.026
Pyšek P, Hulme PE, Simberloff D, Bacher S, Blackburn TM, Carlton JT, Dawson W, Essl F, Foxcroft LC, Genovesi P, Jeschke JM, Kühn I, Liebhold AM, Mandrak NE, Meyerson LA, Pauchard A, Pergl J, Roy HE, Seebens H, van Kleunen M, Vilà M, Wingfield MJ, Richardson DM (2020) Scientists' warning on invasive alien species. Biol Rev. https://doi.org/10.1111/brv.12627
Qiao H, Peterson AT, Campbell LP, Soberón J, Ji L, Escobar LE (2016) NicheA: creating virtual species and ecological niches in multivariate environmental scenarios. Ecography. https://doi.org/10.1111/ecog.01961
Qiao H, Escobar LE, Peterson TA (2017) Accessible areas in ecological niche comparisons of invasive species: recognized but still overlooked. Sci Rep. https://doi.org/10.1038/s41598-017-01313-2
Radosavljevic A, Anderson RP (2014) Making better Maxent models of species distributions: complexity, overfitting and evaluation. J Biogeogr. https://doi.org/10.1111/jbi.12227
Ríos M, Barrera-Medina R, Contreras JM (2020) Primer reporte del género *Vespa* Linnaeus (Hymenoptera: Vespidae: Vespinae) en Chile. https://doi.org/10.35249/rche.46.2.20.14. Rev Chil Entomol
Robinet C, Suppo C, Darrouzet E (2017) Rapid spread of the invasive yellow-legged hornet in France: the role of human-mediated dispersal and the effects of control measures. J Appl Ecol. https://doi.org/10.1111/1365-2664.12724
Rojas-Nossa SV, Calviño-Cancela M (2020) The invasive hornet *Vespa Velutina* affects pollination of a wild plant through changes in abundance and behaviour of floral visitors. Biol Invasions. https://doi.org/10.1007/s10530-020-02275-9
Rome R, Perrard A, Muller F, Villemant C (2011) Monitoring and control modalities of a honeybee predator, the yellow-legged hornet Vespa Velutina Nigrithorax (Hymenoptera- Vespidae). Aliens: Invasive Species Bull 31:7–15
SADER (2021) Sistema de Información Agroalimentaria de Consulta (SIACON-NG). https://www.gob.mx/siap/prensa/sistema-de-informacion-agroalimentaria-de-consulta-siacon. Accessed 23 February 2024
Sánchez I, Fajardo C, Castro M (2019) Primeras Citas Del avispón oriental *Vespa orientalis* Linnaeus 1771 (Hymenoptera: Vespidae) para Andalucía (España). Rev Soc Gad Hist Nat 13:11–14
Secretariat of the International Plant Protection Convention (2007) Framework for pest risk analysis. Secretariat of the International Plant Protection Convention https://www.ippc.int/static/media/files/publication/en/2016/01/ISPM_02_2007_En_2015-12-22_PostCPM10_InkAmReformatted.pdf. Accessed 23 February 2024
SEMARNAT CONANP (2014) Programa De manejo complejo Sian Ka´an: reserva de la biosfera Sian Ka´an, área de protección de flora y fauna Uaymil Y reserva de la biosfera arrecifes de Sian Ka´an. SEMARNAT, Mexico
Smith AB, Godsoe W, Rodríguez-Sánchez F, Wang HH, Warren D (2019) Niche estimation above and below the species level. Trends Ecol Evol. https://doi.org/10.1016/j.tree.2018.10.012
Smith-Pardo AH, Carpenter JM, Kimsey L (2020) The diversity of hornets in the genus Vespa (Hymenoptera: Vespidae; Vespinae), their importance and interceptions in the United States. Insect Syst Divers. https://doi.org/10.1093/isd/ixaa006
Snyder WE, Evans EW (2006) Ecological effects of invasive arthropod generalist predators. Annu Rev Ecol Evol Syst. https://doi.org/10.1146/annurev.ecolsys.37.091305.110107
Soberon J, Arroyo-Pena B (2017) Are fundamental niches larger than the realized? Testing a 50-year-old prediction by Hutchinson. PLoS ONE. https://doi.org/10.1371/journal.pone.0175138
Soberon J, Peterson AT (2005) Interpretation of models of fundamental ecological niches and species' distributional areas. Biodivers Inf. https://doi.org/10.17161/bi.v2i0.4
Thomson D (2004) Competitive interactions between the invasive European honeybee and native bumble bees. Ecology. https://doi.org/10.1890/02-0626
Tripodi A, Hardin T (2020) New pest response guidelines *Vespa mandarinia*. USDA. https://cms.agr.wa.gov/WSDAKentico/Documents/PP/PestProgram/Vespa_mandarinia_NPRG_10Feb2020-(002).pdf. Accessed 23 February 2024
Venette RC (2015) The challenge of modelling and mapping the future distribution and impact of invasive alien species. In: Venette RC (ed) Pest risk modelling and mapping for invasive alien species. CAB International, USDA, United States, pp 1–17
Venette RC, Kriticos DJ, Magarey RD, Koch FH, Baker RHA, Worner SP, Gomez-Raboteaux N, McKenney DW, Dobesberger EJ, Yemshanov D, De Barro PJ, Hutchison WD, Fowler G, Kalaris TM, Pedlar J (2010) Pest risk maps for invasive alien species: a roadmap for improvement. https://doi.org/10.1525/bio.2010.60.5.5. BioScience

Villanueva R, Collí W (1996) La apicultura en la península de Yucatán, México, y sus perspectivas. Folia Entomol Mex 97:55–70
Villemant C, Barbet-Massin M, Perrard A, Muller F, Gargominy O, Jiguet F, Rome Q (2011) Predicting the invasion risk by the alien bee-hawking yellow-legged hornet *Vespa Velutina Nigrithorax* across Europe and other continents with niche models. Biol Conserv. https://doi.org/10.1016/j.biocon.2011.04.009
Washington State Department of Agriculture (2022) Report Asian giant hornet sightings. Washington State Department of Agriculture. https://agr.wa.gov/departments/insects-pests-and-weeds/insects/hornets. Accessed 23 February 2024
Wilson T, Looney C, Tembrock LR, Dickerson S, Orr J, Gilligan TM, Wildung M (2023) Insights into the prey of *Vespa mandarinia* (Hymenoptera: Vespidae) in Washington state, obtained from metabarcoding of larval feces. Front Insect Sci. https://doi.org/10.3389/finsc.2023.1134781
Zhu G, Illan JG, Looney C, Crowder DW (2020) Assessing the ecological niche and invasion potential of the Asian giant hornet. PNAS. https://doi.org/10.1073/pnas.2011441117

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