

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/343863420>

Giants are coming? Predicting the potential spread and impacts of the giant Asian hornet (*Vespa mandarinia*, Hymenoptera:Vespidae) in the United States

Article in *Pest Management Science* · August 2020

DOI: 10.1002/ps.6063

CITATIONS

17

READS

2,523

3 authors, including:



Alberto J Alaniz

University of Santiago, Chile

63 PUBLICATIONS 269 CITATIONS

[SEE PROFILE](#)



Mario A Carvajal

Pontificia Universidad Católica de Chile

23 PUBLICATIONS 125 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



Spatial Epidemiological modeling of infectious diseases [View project](#)



IUCN Red List of Ecosystems (RLE) assessment for Chile [View project](#)

Giants are coming? Predicting the potential spread and impacts of the giant Asian hornet (*Vespa mandarinia*, Hymenoptera:Vespidae) in the USA

Alberto J Alaniz,^{a,b,c*} Mario A Carvajal^{a,b} and Pablo M Vergara^a



Abstract

BACKGROUND: Biological invasions are a global concern in agriculture, food production and biodiversity. Among the invasive species, some hornets are known to have serious effects on honey bees, as found during the invasion of *Vespa velutina* in Europe. The recent findings of *Vespa mandarinia* individuals in Washington state in the west coast of the USA have raised alarm in the whole country. Here we estimate the potential spread of *V. mandarinia* in the USA, analyzing its potential impacts on honey bee colonies, economic losses in the honey bee industry and bee-pollinated croplands.

RESULTS: We found that *V. mandarinia* could colonize Washington and Oregon states in the west coast and a significant proportion of the east coast. If this species spread across the country, it could threaten $95\,216 \pm 5551$ honey bee colonies, threatening an estimated income of US\$11.9 and 101.8 million for hive derived products and bee-pollinated crops production, respectively, while colonizing 60 837.8 km² of bee-pollinated croplands.

CONCLUSION: Our results suggest that *V. mandarinia* will have serious effects in the USA, raising the need for prompt monitoring actions and planning at different administrative levels to avoid its potential spread.

© 2020 Society of Chemical Industry

Supporting information may be found in the online version of this article.

1 INTRODUCTION

Biological invasions are one of the main problems of the 21st century for biodiversity and food production arising from pest introduction in different countries.^{1,2} Invasive species have detrimental effects on the newly colonized areas, such as impoverishment of local species assemblages in terrestrial and aquatic ecosystems,^{3,4} as well as the decline of key insects providing herbivore control and pollination services, such as ladybirds, butterflies and bees.^{5–7} In this sense, invasive hornets and wasps are particularly problematic due to the effects they have on local bee assemblages as well as the possible negative human health implications derived from stings and their allergenic effects.^{8,9} In Europe the accidental introduction of the yellow-legged or Asian hornet (*Vespa velutina* Lepeletier¹⁰) has had serious consequences for honey bees (*Apis mellifera* Linnaeus¹¹), affecting their foraging activity and survival probability.^{12–15} Hornets of the *Vespa* genus are known to have serious negative effects on honey bee colonies, hunting foragers while attacking their hives.^{14–17} These gregarious hornets live in social groups founded by queens that can generate colonies in human-modified zones such as agricultural or urban landscapes.¹⁸ In Europe the yellow-legged hornet population experienced a rapid spread across the entire continent, colonizing France in 2004, Spain in 2010, Belgium and Portugal in 2011, Italy in 2013, Germany in 2014, the UK in 2016 and the Netherlands in 2017.^{12,14} The actions taken to control *V. velutina* in Europe have been expensive and inefficient, with yearly control costs reaching US\$13.9 million, US\$10.5 million and US\$10 million in France, Italy

and the UK, respectively.¹² Some studies suggest that such control costs may be much higher in zones where *V. velutina* is not present yet, amounting to US\$31.4 million for the USA.¹²

The recent finding of the Giant Asian Hornet (*Vespa mandarinia* Smith¹⁹) in the USA, a social species of the same genus as *V. velutina*, has raised an alarm in the country.^{20,21} This insect is the largest hornet worldwide known to prey on several native and economically important species, such as honey bees.²² The foraging of *V. mandarinia* individuals is coordinated by pheromones, which they use to mark honey bee hives as food sources.¹⁷ In their native range, *Apis cerana* Fabricius²³ (a sympatric species) cope with the predatory pressure of *V. mandarinia* by generating a mass defensive action against the hornets, which are captured by defending bees that increase their thorax temperature to kill the engulfed hornet by heat.²⁴ Although this defensive behavior

* Correspondence to: AJ Alaniz, Enrique Kirberg Baltiansky No. 03, Estación Central, Santiago, Chile. E-mail: alberto.alaniz@usach.cl

^a Departamento de Gestión Agraria, Facultad Tecnológica, Universidad de Santiago de Chile, Santiago, Chile

^b Ecogeografía, Centro de Estudios en Ecología Espacial y Medio Ambiente, Santiago, Chile

^c Departamento de Ingeniería Geográfica, Facultad de Ingeniería, Universidad de Santiago de Chile, Santiago, Chile

against predator wasps has been argued for European honey bees evidencing recent adaptative responses to attacks,^{24,25} a potential strategy to reduce the impact of *V. mandarinia* on honey bees should consider the similarity in habitat and ecological niche requirements between both species. The abundance of *V. mandarinia* is positively associated with amounts of green spaces in urban landscapes, suggesting that the control of their populations should be focused on urban green areas.²⁶ On the other hand, *V. mandarinia* has been described as a species highly sensitive to heat and extreme climate conditions, and negatively associated with high temperatures, as found in other invasive hornets.²⁷

The recent report of *V. mandarinia* in the USA raises the challenge of implementing a predictive assessment of its potential spread and effects on the environment and the economy. The strong association of *V. mandarinia* presence and environmental factors found in its native range suggest the ecological niche modeling (ENM) technique is an appropriate method to evaluate its potential global and regional distribution while identifying environmental variables explaining these patterns.^{12,27–31} Here we aim to quantify the potential distribution of *V. mandarinia* in the USA, evaluating the number of honey bee hives under threat as well as the potential costs and the amount of agricultural land potentially being invaded by this species.

2 MATERIALS AND METHODS

As our main approach we used **ENM based on the MaxEnt algorithm**, which combines spatially explicit occurrences of the target species and a set of environmental predictor variables to estimate the habitat suitability of the species.³² The ENM approach is useful for estimating the environmental niche requirement of a species and projecting these requirements into new zones or throughout time, considering the niche conservatism and niche-biotope duality as main principles.^{33–36} This approach is useful to predict potential invadable areas before the introduction of a species, and it is also useful to assess the extrapolation level generated by the model in these new areas.^{37,38} Here we predicted the environmentally suitable areas for *V. mandarinia* in the USA, considering the native distribution zone in Asia as the main source of the introduced individuals.

2.1 Data source

The occurrence dataset was collected from the Global Biodiversity Information Facility (GBIF) database and previously published studies,^{18,22,26,39–44} compiling an initial database of 275 occurrences for the native area (Table S1).⁴⁵ We considered only records including geographical coordinates and deleted duplicated occurrences. On the other hand, the initial environmental predictor set included climatic and vegetation variables, and human modification index, considering the results of previous studies for *V. velutina*^{12,27–31} and *V. mandarinia*²⁶ (Table S2). Climatic variables consisted of the 19 bioclimatic variables from WorldClim v2.0 plus.⁴⁶ Vegetation variables were calculated using the MODIS satellite vegetation indices, generating a median of all the 16-day images since the year 2000. We included (i) the normalized difference water index (NDWI), which is linked to the liquid water content in the vegetation canopy; (ii) the enhanced vegetation index (EVI), related to the chlorophyll content of the vegetation; (iii) the yearly net primary productivity (NPP), which measures plant growth per year in kilograms of carbon per square meter per year ($\text{kg C/m}^2/\text{year}^{-1}$); and (iv) the vegetation continuous field (VCF), which is the canopy closure expressed as a

percentage. We also included the human modification index,⁴⁷ which corresponds to an estimation of the human-induced environmental modification, including human settlement, agriculture, transportation, electrical infrastructure, and mining and energy production.⁴⁷ All the variables had 1 km² of pixel resolution, and the vegetation variables were processed in the cloud-based Google Earth Engine platform.⁴⁸

2.2 Modeling procedure

First, we reduced the spatial autocorrelation of occurrence by applying a spatial rarefaction using SDMTtoolbox in a Geographic Information System (GIS), a process that selected and maintained points having more than 5 km between them.⁴⁹ Then we generated an initial exploratory model considering the 25 environmental variables and the nonautocorrelated occurrence dataset, using MaxEnt v3.4.1, and ran it using a 10-fold cross-validation technique.^{50,51} As a result we obtained the percentage contribution and permutation importance as measures of variable importance, additionally calculating Spearman's correlation between pairs of variables. Then, to avoid potential overfitting and multicollinearity, we selected the variables with highest importance to the exploratory model and with less than 0.7 of Spearman's correlation. Finally, we generated a model considering a 10-fold cross-validation technique that included the nonautocorrelated occurrences and the selected variables from the exploratory model. This model was generated to the complete Asia (native range of the species) and projected into the USA considering niche conservatism and niche-biotope duality.⁵² As invasive species are not in environmental equilibrium in the colonized zones, our results could represent a conservative estimation of potential invadable range in the USA.³³ As a metric to evaluate the model's extrapolation in the invadable zone, we calculated the mean multivariate environmental similarity surfaces (MESS) from the 10 replicates.³⁷ This analysis allowed us to identify the level of uncertainty of the predicted invadable range on the USA.

2.3 Threatened honey bee colonies

To determine the number of threatened colonies we used data from the National Agricultural Statistics Services of the USA (<https://quickstats.nass.usda.gov/results/98D6C754-2F7A-319C-95FE-CB8F673A140E>) which reports the number of colonies per county in which the honey was harvested or stocks were stored, considering producers with more than five colonies. We generated a layer of the total number of colonies, assuming a homogeneous density of colonies within each county due to the nonavailability of a georeferenced national cadaster of colonies. We used the predicted suitability as a proxy of potential abundance of *V. mandarinia* in the invadable zone,^{53,54} estimating the average suitability per county. We then used the layer of average suitability per county (from 0 to 1) as a proxy to the impact level of *V. mandarinia* over hives using a similar methodology to that proposed by Alaniz *et al.*⁵⁵ for biological control, considering suitability as a proxy of *V. mandarinia* potential abundance.^{56,57} We multiplied the map of suitability per county by the layer with the total number of colonies per county, obtaining an estimate of the number of threatened colonies. Additionally, as a measure of uncertainty we used the standard deviation of the suitability map, which was also multiplied by the number of colonies. All the probabilities under the 10th percentile of training of suitability values were considered nonsignificant and were therefore not included in the analysis.

2.4 Potential economic losses for hive products

To estimate the potential economic losses for hive products, we used the income registered for 2017 per county from the National Agricultural Statistics Services (NASS) of the USA (<https://quickstats.nass.usda.gov/results/98D6C754-2F7A-319C-95FE-CB8F673A140E>). We applied the same procedure used for the number of threatened colonies to estimate the potential economic losses derived from hive products, using the suitability map as a proxy for the potential impact derived from *V. mandarinia* potential abundance. Additionally, as a measure of uncertainty we also used the standard deviation of the suitability map.

2.5 Threatened bee-pollinated croplands

Considering that *V. mandarinia* is a strong predator of honey bees, which are widely used for pollination, we quantified the potentially affected croplands area and the threatened income derived from these crops.

To estimate the area of bee-pollinated croplands potentially affected we combined the suitability map of *V. mandarinia* and a map of cropland types for 2019 from NASS. First, we reclassified the significant suitability values for *V. mandarinia* in the USA into three categories, low, medium and high, as a proxy for the potential damage based on the potential abundance of *V. mandarinia*. We excluded the probabilities under the 10th percentile of training of suitability values and considered equal intervals as thresholds for the three categories. Then, we overlapped the map of suitability levels with the croplands map, quantifying the area per level, cropland type and county. The complete list of included croplands and additional data is shown in Table S3. We excluded from this analysis self-pollinated and wind-pollinated crops.

We also estimated a 'threatened income' as the income generated by each bee-pollinated cropland that is under threat due to the potential colonization of *V. mandarinia*. This was estimated by using the total income data per cropland type and state from NASS and the suitability map of *V. mandarinia*. We only included

crop types identified in the cropland map for 2019 from NASS. First, we divided the total income of each cropland type by the specific area for each state, obtaining an estimate of the income per square kilometer. For the cases where income was not reported in the database, we assumed the median from the income per square kilometer among the other states or counties for each crop type. Then, aiming to quantify the threatened income from the potentially invadable area by *V. mandarinia*, we reclassified the suitability map of *V. mandarinia* into a binary presence-absence map (1 = presence, 0 = absence), considering the 10th percentile of suitability as the threshold. Finally, the map of *V. mandarinia* presence-absence was overlapped with each cropland type, calculating the potentially affected area and the threatened income.

3 RESULTS

3.1 Potential spread

The model reached a good performance, with an average AUC test of 0.975 ± 0.008 , while the MESS analysis showed a low level of extrapolation of the predicted suitability in the USA (Figs S1 and S2). The variables that reached the most important contribution corresponded to precipitation in the driest month (bio14), human modification index, primary productivity and annual precipitation (bio12), with 51.7%, 12.1%, 9.9% and 9.5%, respectively (Table S4). The high suitability was reached with 50 mm of precipitation in the driest month, while the human modification index was positively correlated with suitability (Fig. S4). The suitability related to temperature of the warmest quarter showed a strong decrease above 20 °C, while the temperature seasonality reached a peak at four standard deviations. The suitability increased with the percentage of canopy cover, while the normalized differential water index presented a Gaussian pattern with a peak at -0.05 (Fig. S4).

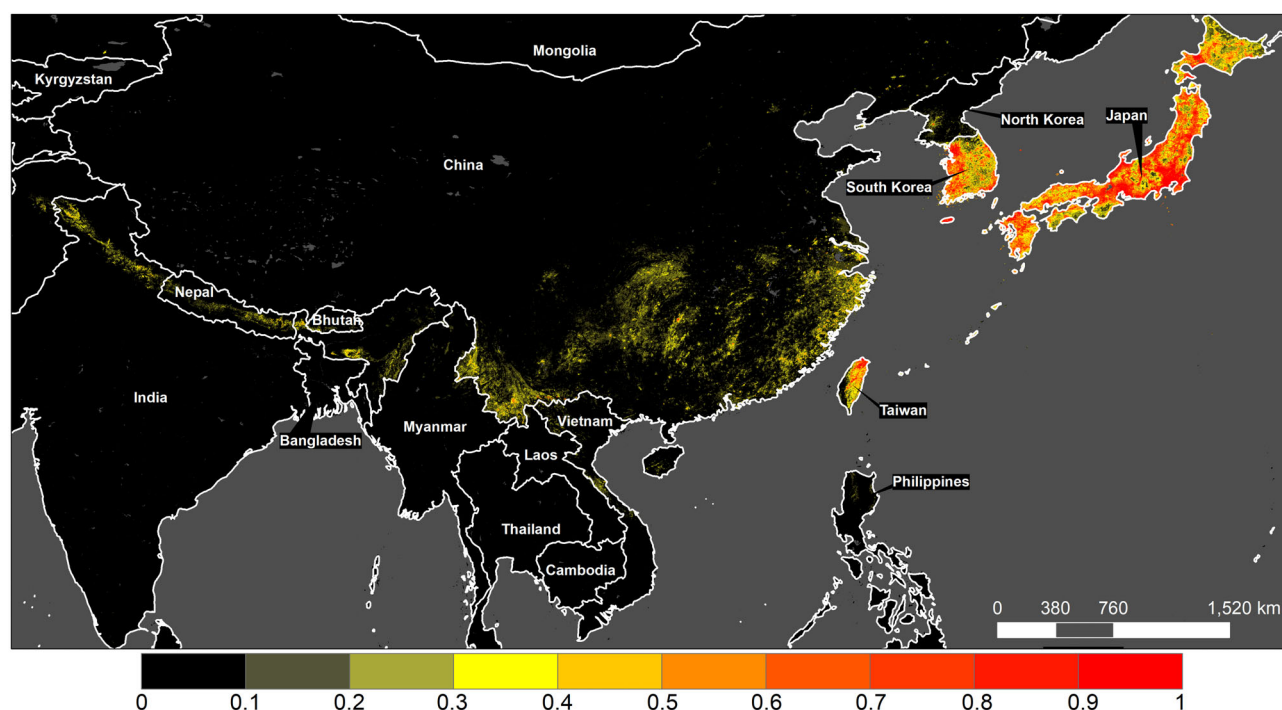


Figure 1. Estimated suitability for *V. mandarinia* in its native range (Asia). Low suitability is shown in black, while the highest suitability is presented in red.

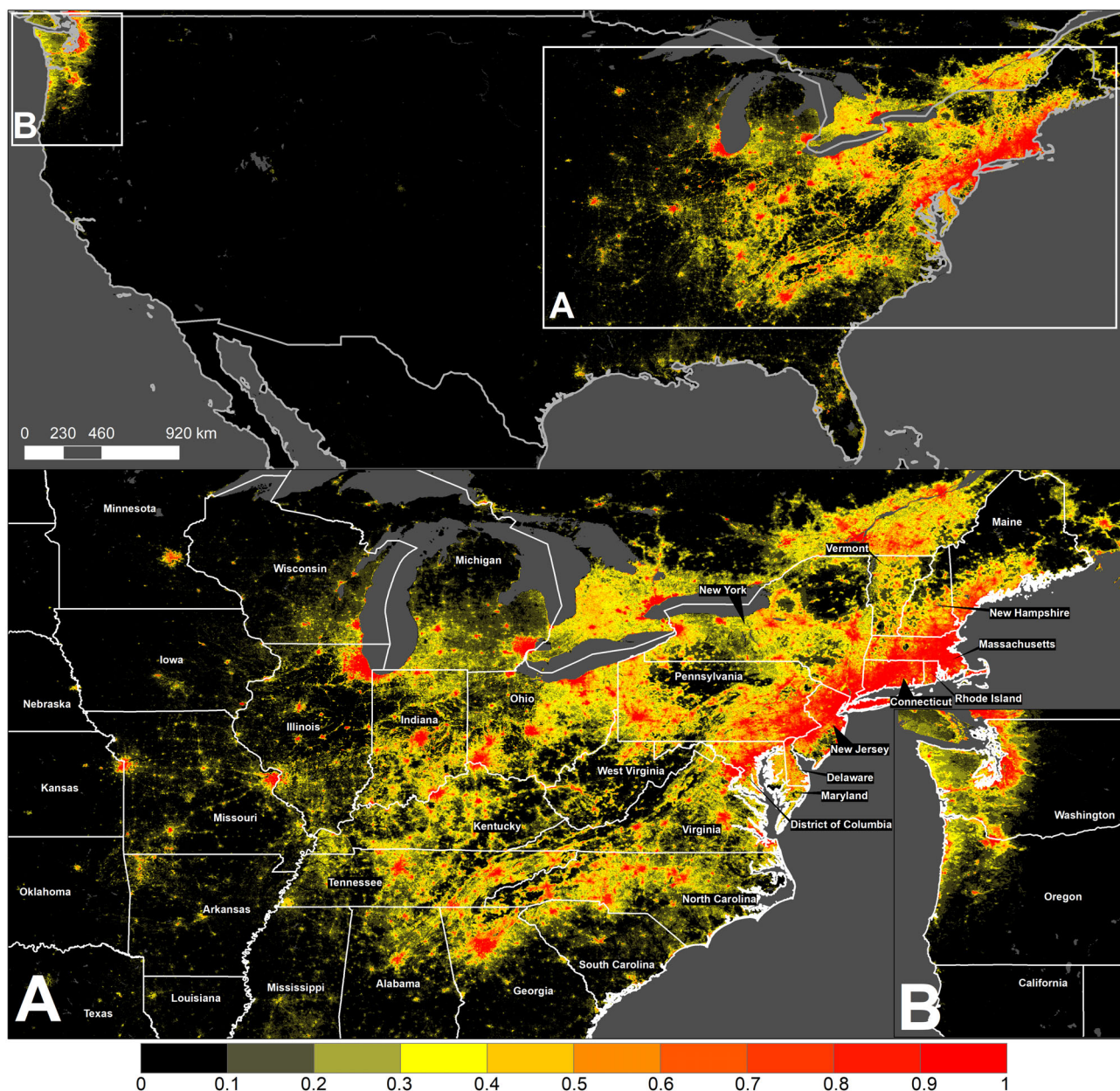


Figure 2. Projected suitability in the USA, with two highlighted areas showing the east coast (A) and the west coast (B). The suitability scale in the lower part shows values from low (black) to high (red).

The species in its native range is mainly distributed in Japan, South Korea, Taiwan and coastal China, and it is also present in the mountainous zone of the Himalayas in Butan, Nepal, and India (Figs 1 and S3). In the USA the highest suitability values are concentrated in the east coast and in the northwestern coast zones (Fig. 2). In the east coast the highest suitability is concentrated from the states of Maine to Virginia, with high suitability also from Pennsylvania to Illinois (Fig. 2(A)). In the western coast zone, the higher suitability values are concentrated in the states of Washington and Oregon, and in northern California.

3.2 Threatened colonies

A total of $95\,216 \pm 5551$ honey bee colonies is under threat if the species colonizes the invadable zones in the whole USA (Figs 3 and 4). In the west coast, Washington has 4568 ± 299 threatened

colonies, while Oregon has 1065 ± 72 , representing 11.0% and 1.8% of their total colonies (Figs 3(A) and 4(A)). In the east coast the states with more threatened colonies are New York, Pennsylvania and North Carolina, with $11\,193 \pm 655$, $10\,388 \pm 541$ and 6886 ± 455 , respectively (Figs 3(B) and 4(A)). In seven states, Connecticut, Rhode Island, Massachusetts, New Jersey, Delaware, Maryland and New Hampshire, more than 50% of the honey bee colonies are under threat (Tables S5 and S6).

3.3 Hive products potential losses

If this species invades all the suitable areas, the potential economic losses from hive-derived products could reach US $\$11.98 \pm 0.64$ million per year. In the west coast, the states of Washington and Oregon could reach economic losses of US $\$0.2 \pm 0.02$ million and US $\$0.07 \pm 0.005$ million, respectively

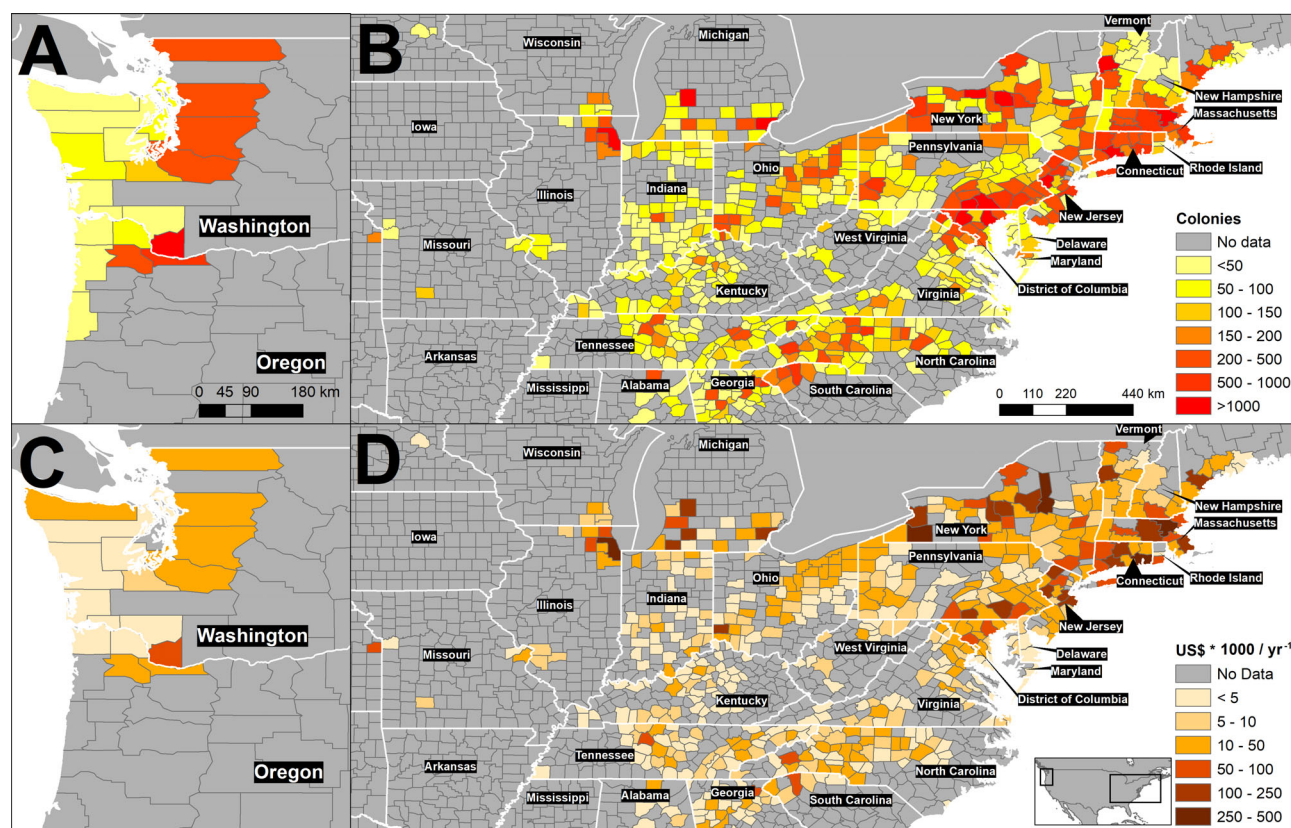


Figure 3. The upper maps show the estimated number of honeybee colonies affected in the west (A) and east (B) coasts. The lower maps correspond to the estimated economic losses in thousands of dollars (US\$×1000 per year) from honeybee derived products in the west (C) and east (D) coasts.

(Figs 3(C) and 4(B)). On the east coast the potentially worst affected states correspond to New York, Massachusetts and Pennsylvania, with US\$2.32 ± 0.14 million, US\$1.21 ± 0.02 million and US\$1.09 ± 0.06 million losses, respectively (Figs 3(D) and 4(B)). Seven states could have more than 50% of their income derived from honey bees under threat, Massachusetts, Connecticut, Rhode Island, New Jersey, Delaware, Maryland and New Hampshire. Data for all counties and states are shown in Tables S5 and S6.

3.4 Threatened bee-pollinated croplands

The total national area of threatened bee-pollinated croplands was 60 837.8 km², consisting of 3385.1, 29 813.0 and 27 639.8 km² under high, medium and low threat levels, respectively (Table S7). The largest area under a high threat level is the east coast, mainly the states of Massachusetts, Connecticut and New York, with 793.9, 578.6 and 372.3 km², respectively (Fig. 5 and Table S7). On the west coast, Washington state has 26.9 km², 400.6 km² and 118.5 km² under high, medium and low threat levels, respectively. In the same area Oregon has 12.7 km², 44.2 km² and 14.3 km² under high, medium and low threat levels, respectively. The complete list of states is shown in Table S7. We also identified that alfalfa/hay, apples, grapes and tobacco are the crops with the largest threatened areas of 58 484.1, 522.9, 468.5 and 432.9 km², respectively (Table S8).

The potential threatened income associated with bee-pollinated croplands reached US\$101.8 million per year (Tables S7 and S8). Among the states with the largest amount of threatened income are North Carolina, New Jersey and Virginia, with US\$19.8, US\$18.5 and US\$12.8 million per year (Fig. 5). In relation to the bee-

pollinated crops we found that cotton, alfalfa/hay, blueberries, and tobacco have the highest threatened incomes of US\$26.4, US\$21.6, US\$16.6 and US\$11.0 million, respectively (Table S9).

4 DISCUSSION

4.1 Model results and assumptions

The recent findings of individuals in Washington state and southern British Columbia (Canada)²⁰ have raised the alarm in these zones. Here we predict that these zones are environmentally suitable for hornets and thus represent a potential zone for initiating their spread across North America. ENM techniques allowed the spread of invasive species after their recent arrival to be predicted with a good level of accuracy, hence we recommend focusing the control actions in these zones.^{38,51} However, we also recommend careful interpretation of our results because the actual economic cost and number of affected colonies will depend on some variables not included in or predicted by our approach. Quantifying the relationship between mortality rate of honey bees and hornet colony densities in the colonized zones will be highly determinant to assessing the economic losses after colonization. Although we cannot quantify the actual proportion of affected colonies or losses, our results provide an initial baseline before the colonization under a worst-case scenario generating a potential overestimation of risk. However, the actual risk could vary on a local scale depending on management actions and how the effects of hornet density change with the apiary size. In relation to management, the survey data from NASS does not consider the movement of colonies among counties for pollination, causing an underestimation when colonies are moved to high-risk zones

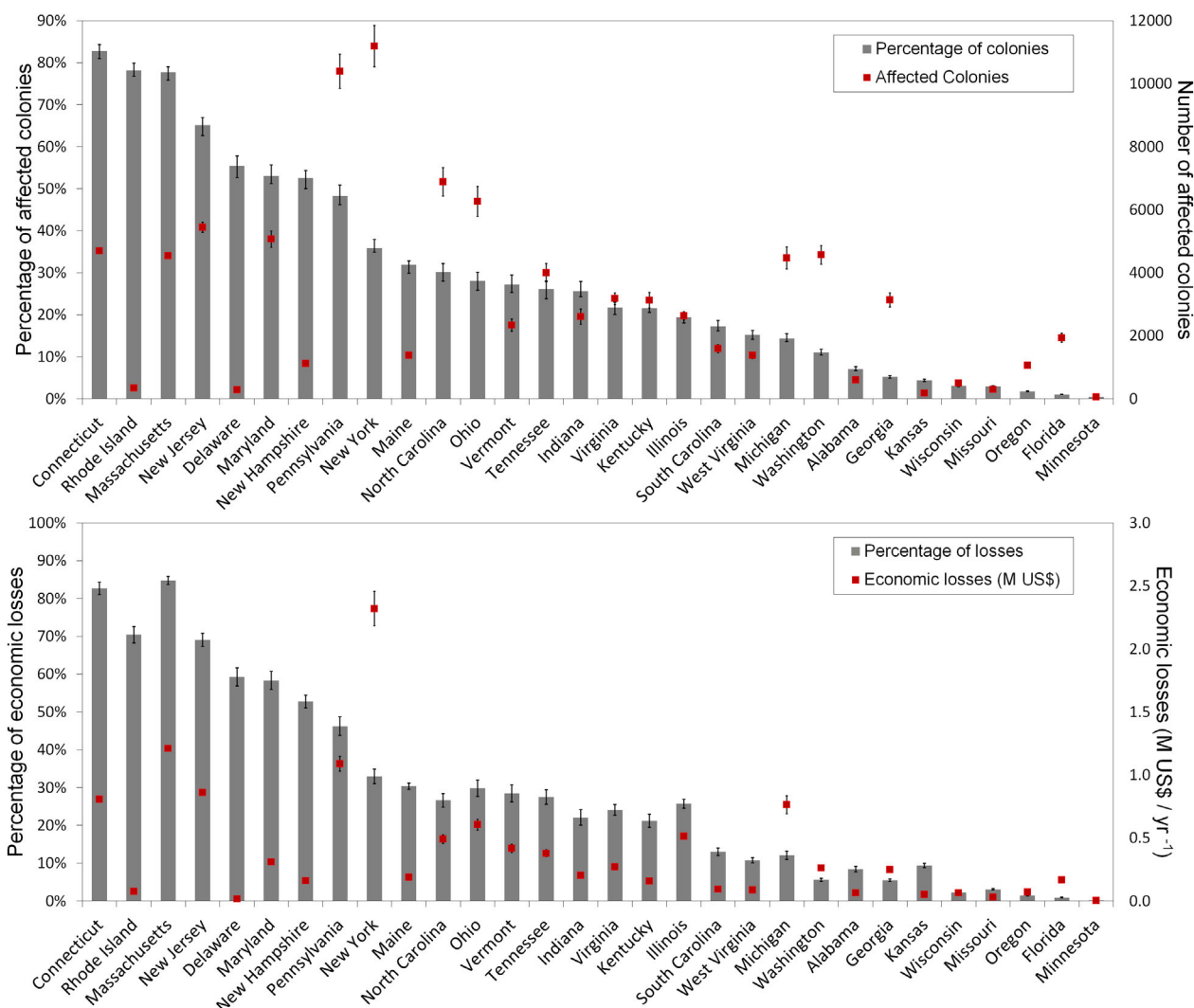


Figure 4. The upper graph shows the percentage of affected colonies per state (gray bars) and the number of affected colonies (red points). The lower graph shows the percentage of economic losses in relation to the total income derived from the honeybee industry (gray bars) and the amount of loss in thousands of US dollars.

but also an overestimation when colonies are moved to low-risk zones. In relation to apiary size, in Asia, local-scale studies have evidenced a lower impact of hornets as apiary size increases due to the large number of defensive individuals in the colony.^{17,58} Additionally, studies have identified that chemically induced behavioral changes could generate adaptative responses to the attacks of hornets by honey bees, which are very hard to predict in a large-scale model as presented here.^{16,22} These variables were not included in our estimations due to the lack of fine-scale spatially explicit information about apiary size for the complete country. However, we suggest that further studies should simulate bee-hornet interaction on a local scale to reduce the uncertainty in loss estimations. Other more mechanistic approaches could also be used to estimate the potential spread, establishment and interaction zones, as addressed in Europe for *V. velutina* in previous studies.^{28,59} We suggest that new studies with different approaches should test the congruence of their results with our findings, reducing the uncertainty for practitioners and decision makers. Additionally, we suggest developing new studies for other zones of the world where this species could colonize in the future.

Our results show that the east coast is highly suitable for the establishment and spread of *V. mandarinia*, a zone where this species has not been recorded yet, making it necessary to implement preventive actions to avoid a possible invasion. The environmental suitability for *V. mandarinia* was highly associated with medium precipitation in the driest quarter and high annual precipitation. Desert ecosystems could be an important dispersal barrier that prevent spread across the inner zone of the country. Another variable that was important for *V. mandarinia* was the net primary productivity, a result consistent with the findings of Azmy *et al.*,¹⁹ who found that in its native range the abundance of *V. mandarinia* is positively associated with the vegetation index in urban landscapes. In addition, the positive relationship of human influence with suitability values suggests that disturbed habitats and human-mediated dispersal benefits this species, as found in previous studies for similar species.^{13,28,60} For canopy cover, a similar result was found by Azmy *et al.*²⁶ in urban environments in China, where the quality of green areas benefited the abundance of *V. mandarinia*. The relationship between suitability and the temperatures of warmest and driest quarter suggest a

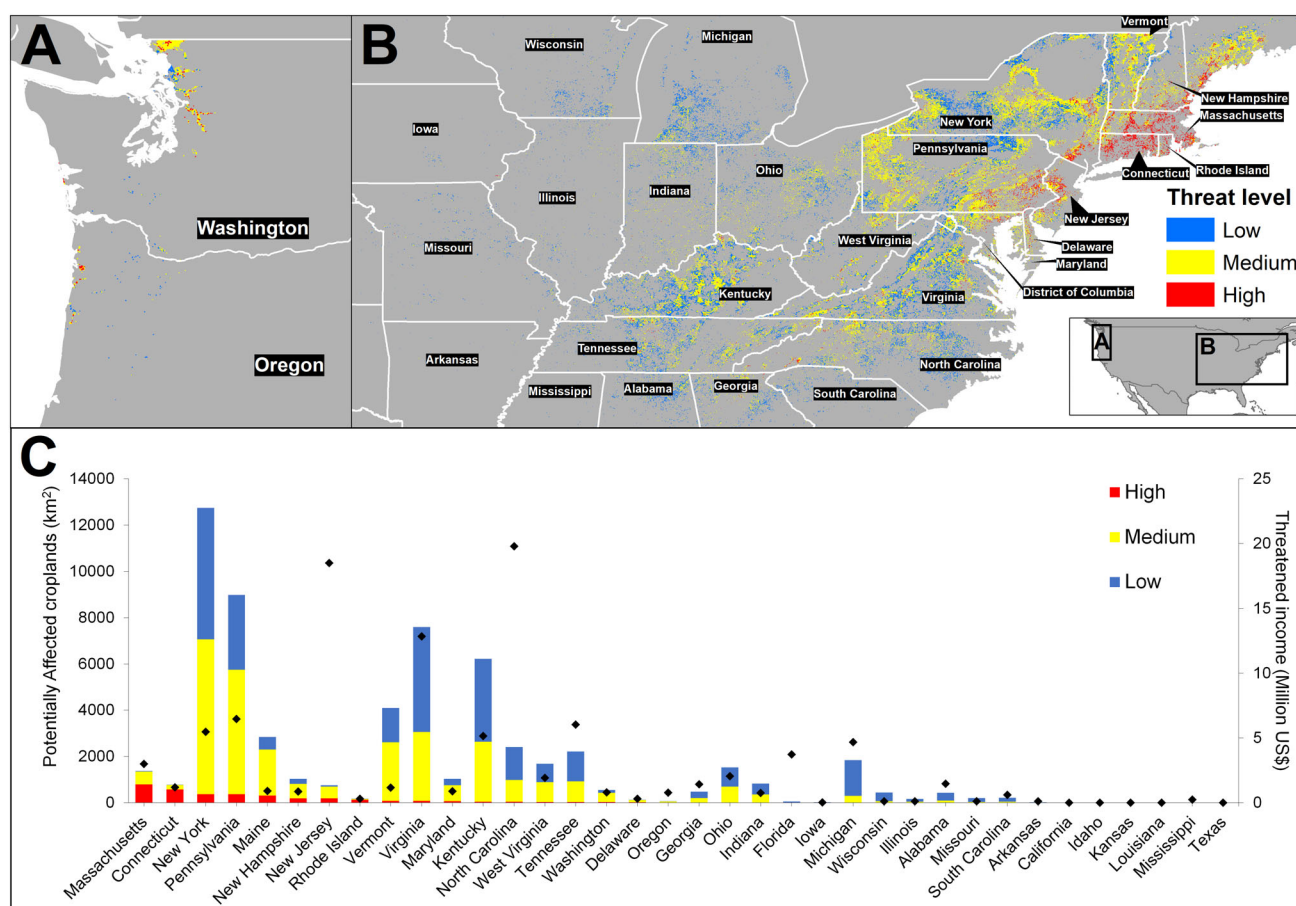


Figure 5. Map of the bee pollinated croplands potentially affected by *V. mandarinia* in the west coast (A) and east coast (B) of the USA. (C) The areas of bee-pollinated croplands and the threatened income per level of threat and estate.

dependency of this species on temperate climates, which could prevent its expansion to drier zones.

4.2 Potential effects and control

Honey bee predation is the main economic effect associated with the invasion of hornet species, and represents a serious threat to crop pollination and the manufacture of honey bee-derived products.^{12,14,16} In Europe, the yellow-legged hornet has resulted in serious costs associated with the loss of honey bee colonies, reduction of honey bees for crop pollination and control actions.^{12,13,15} A strategy to reduce outcomes associated with sampling and monitoring of invasive species would involve the implementation of citizen science programs.^{61,62} These programs are very useful when the species that we need to identify is conspicuous, as *V. mandarinia*. In fact, a successful program was implemented for *Vespa crabro* Linnaeus¹¹ in Italy.⁶¹ Another important issue is associated with economic help programs for small and medium honey bee owners, who can suffer significant losses. In this regard we provide a spatially explicit tool for decision making by state- and county-level governments. This information may help local governments to identify the potential costs incurred by not controlling this invasive species, allowing them to plan their budgets in case of potential negative effects. We identified that the potential effects of this species may represent an important threat to honey bee colonies across the country, as well as economic losses for this industry. This is of

particular concern, since the yield of several bee-pollinated crops is highly influenced by bee pollination.⁶³ Additionally, international agreements demand certain fruit caliber and quality, which are also highly influenced by effective pollination, thus a depletion of bee colonies could seriously affect agricultural production.

Radio-tracking to identify and destroy hornet nests prior to a potential generalized spread across the country has been stated by Kennedy *et al.*⁶⁴ as potentially useful for *V. mandarinia* monitoring programs the recently colonized USA. On the other hand, applying control measures is also necessary, as stated by Turchi and Derijard,⁶⁵ who provide a series of physical and biological measures to control *V. velutina* in Europe. A recent document from the US Department of Agriculture (USDA) proposed highly relevant pest response guidelines to control *V. mandarinia* populations.²¹ The document suggests lethal and passive traps, as well as a series of effective pesticides against *V. mandarinia* and control actions at different scales.²¹ The economic cost of control measures of invasive species only in Europe reaches around US \$13.4 billion per year, and in relation to *V. velutina* the cost may reach US\$13.3 million per year just in France. Here we have estimated an annual projected loss of US\$113.7 million per year. However, the costs associated with control actions not included in our study may eventually increase these amounts significantly (i.e. c. US\$26 million as estimated by Barbet-Massin *et al.*¹² for *V. velutina*). In addition to the economic losses and the negative

effect on honey bees, *V. velutina* raises concerns for public health derived from human allergic reactions to its stings.⁶⁶

We believe that our maps and statistics will contribute to the response and planning against this species, providing a spatially explicit basis for an administrative level assessment of specific indicators. We recommend that the maps and statistics presented here are used alongside the recent pest response guidelines from the USDA,²¹ allowing the promotion and structure of national and subnational strong control strategies with a clear spatial dimension of the potential consequences.

ACKNOWLEDGEMENTS

Pablo M. Vergara was funded by FONDECYT under project 1180978. Alberto J. Alaniz and Mario A. Carvajal were supported by CONICYT-PFCHA/ Doctorado Nacional 2020-21201496 and 2020-21201494, respectively.

SUPPORTING INFORMATION

Supporting information may be found in the online version of this article.

REFERENCES

- Núñez MA and Pauchard A, Biological invasions in developing and developed countries: does one model fit all? *Biol Invasions* **12**: 707–714 (2010).
- Perrings C, Dehnen-Schmutz K, Touza J and Williamson M, How to manage biological invasions under globalization. *Trends Ecol Evol* **20**:212–215 (2005).
- Gallardo B, Clavero M, Sánchez MI and Vilà M, Global ecological impacts of invasive species in aquatic ecosystems. *Glob Chang Biol* **22**:151–163 (2016).
- Early R, Bradley BA, Dukes JS, Lawler JJ, Olden JD, Blumenthal DM *et al.*, Global threats from invasive alien species in the twenty-first century and national response capacities. *Nat Commun* **7** (2016).
- Aizen MA, Smith-Ramírez C, Morales CL, Vieli L, Sáez A, Barahona-Segovia RM *et al.*, Coordinated species importation policies are needed to reduce serious invasions globally: the case of alien bumblebees in South America. *J Appl Ecol* **56**:100–106 (2019).
- Roy HE, Adriaens T, Isaac NJB, Kenis M, Onkelinx T, Martin GS *et al.*, Invasive alien predator causes rapid declines of native European ladybirds. *Divers Distrib* **18**:717–725 (2012).
- Baker AM and Potter DA, Invasive paper wasp turns urban pollinator gardens into ecological traps for monarch butterfly larvae. *Sci Rep* **10**:9553 (2020).
- Beggs JR, Brockerhoff EG, Corley JC, Kenis M, Masciocchi M, Muller F *et al.*, Ecological effects and management of invasive alien Vespidae. *BioControl* **56**:505–526 (2011).
- Clapperton BK, Alspach PA, Moller H and Matheson AG, The impact of common and German wasps (Hymenoptera: Vespidae) on the New Zealand beekeeping industry. *N Z J Zool* **16**:325–332 (1989).
- Lepeletier de Saint-Fargeau A, *Histoire naturelle des insectes. Hyménoptères*. Roret, Paris (1836).
- Linnaeus C, *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Impensis Direct, Laurentii Salvii, Holmiae (1758).
- Barbet-Massin M, Salles J-M and Courchamp F, The economic cost of control of the invasive yellow-legged Asian hornet. *NeoBiota* **55**: 11–25 (2020).
- Monceau K, Bonnard O and Thiéry D, *Vespa velutina*: a new invasive predator of honeybees in Europe. *J Pest Sci* **87**:1–16 (2014).
- Requier F, Rome Q, Chiron G, Decante D, Marion S, Menard M *et al.*, Predation of the invasive Asian hornet affects foraging activity and survival probability of honey bees in Western Europe. *J Pest Sci* **92**: 567–578 (2019).
- Laurino D, Liroy S, Carisio L, Manino A and Porporato M, *Vespa velutina*: an alien driver of honey bee colony losses. *Diversity* **12**:1–15 (2020).
- Tan K, Dong S, Li X, Liu X, Wang C, Li J *et al.*, Honey bee inhibitory signaling is tuned to threat severity and can act as a colony alarm signal. *PLoS Biol* **14**:e1002423 (2016).
- Ono M, Igarashi T, Ohno E and Sasaki M, Unusual thermal defence by a honeybee against mass attack by hornets. *Nature* **377**:334–336 (1995).
- Yoshimoto J, Kakutani T and Nishida T, Do battles lead to coexistence? Role of interference competition in structuring the insect community on fermented tree sap. *Ecol Entomol* **32**:552–558 (2007).
- Smith F, Descriptions of some new and apparently undescribed species of hymenopterous Insects from North China, collected by Robert Fortune. *Trans R Entomol Soc London* **5**:33–44 (1852).
- Gill C, Jack C and Lucky A, *Vespa mandarinia* Smith (1852) (Insecta: Hymenoptera: Vespidae). *EDIS* **2020**:5 (2020).
- (USDA) New Pest Response Guidelines *Vespa mandarinia* Asian giant hornet (2020). [https://cms.agr.wa.gov/WSDAKentico/Documents/PP-PestProgram/Vespa_mandarinia_NPRG_10Feb2020-\(002\).pdf](https://cms.agr.wa.gov/WSDAKentico/Documents/PP-PestProgram/Vespa_mandarinia_NPRG_10Feb2020-(002).pdf).
- McClenaghan B, Schlaf M, Geddes M, Mazza J, Pitman G, McCallum K *et al.*, Behavioral responses of honey bees, *Apis cerana* and *Apis mellifera*, to *Vespa mandarinia* marking and alarm pheromones. *J Apic Res* **58**:141–148 (2019).
- Fabricius JC, *Entomologia systematica emendata et aucta*. Christ. Gottl. Proft, Hafniae (1793).
- Abrol DP, Defensive behaviour of *Apis cerana* F. against predatory wasps. *J Apic Sci* **50**:39–46 (2006).
- Hosono S, Nakamura J and Ono M, European honeybee defense against Japanese yellow hornet using heat generation by bee-balling behavior. *Entomol Sci* **20**:163–167 (2017).
- Azmy MM, Hosaka T and Numata S, Responses of four hornet species to levels of urban greenness in Nagoya city, Japan: implications for ecosystem disservices of urban green spaces. *Urban For Urban Green* **18**:117–125 (2016).
- Bessa AS, Carvalho J, Gomes A and Santarém F, Climate and land-use drivers of invasion: predicting the expansion of *Vespa velutina nigrithorax* into the Iberian Peninsula. *Insect Conserv Divers* **9**:27–37 (2016).
- Robinet C, Darrouzet E and Suppo C, Spread modelling: a suitable tool to explore the role of human-mediated dispersal in the range expansion of the yellow-legged hornet in Europe. *Int J Pest Manag* **65**: 258–267 (2019).
- Villemant C, Barbet-Massin M, Perrard A, Muller F, Gargominy O, Jiguet F *et al.*, 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* **144**:2142–2150 (2011).
- Barbet-Massin M, Rome Q, Muller F, Perrard A, Villemant C and Jiguet F, Climate change increases the risk of invasion by the yellow-legged hornet. *Biol Conserv* **157**:4–10 (2013).
- Fournier A, Barbet-Massin M, Rome Q and Courchamp F, Predicting species distribution combining multi-scale drivers. *Glob Ecol Conserv* **12**:215–226 (2017).
- Elith J and Leathwick JR, Species distribution models: ecological explanation and prediction across space and time. *Annu Rev Ecol Syst* **40**:677–697 (2009).
- Gallien L, Douzet R, Pratte S, Zimmermann NE and Thuiller W, Invasive species distribution models – how violating the equilibrium assumption can create new insights. *Glob Ecol Biogeogr* **21**:1126–1136 (2012).
- Broennimann O and Guisan A, Predicting current and future biological invasions: both native and invaded ranges matter. *Biol Lett* **4**: 585–589 (2008).
- Broennimann O, Treier UA, Müller-Schärer H, Thuiller W, Peterson AT and Guisan A, Evidence of climatic niche shift during biological invasion. *Ecol Lett* **10**:701–709 (2007).
- Peterson AT and Soberón J, Species distribution modeling and ecological niche modeling: getting the concepts right. *Nat Conserv* **10**: 102–107 (2012).
- Elith J, Kearney M and Phillips S, The art of modelling range-shifting species. *Methods Ecol Evol* **1**:330–342 (2010).
- Alaniz AJ, Soares AO, Vergara PM, Azevedo EB and Grez AA, The failed invasion of *Harmonia axyridis* in the Azores, Portugal: Climatic restriction or wrong population origin?. *Insect Sci* (2020). <http://dx.doi.org/10.1111/1744-7917.12756>.

- 39 Liu AZ, Kress WJ, Wang H and Li DZ, Insect pollination of *Musella* (Musaceae), a monotypic genus endemic to Yunnan, China. *Plant Syst Evol* **235**:135–146 (2002).
- 40 Fujiwara A, Sasaki M and Washitani I, First report on the emergency dance of *Apis cerana japonica*, which induces odorous plant material collection in response to *Vespa mandarinia japonica* scouting. *Entomol Sci* **21**:93–96 (2018).
- 41 Kim WM, Kim SY and Song W, Microhabitat characteristics affecting the occurrence and diversity of queen hornets (genus *Vespa*) in an urban green area. *Landsc Ecol Eng* **16**:173–186 (2020).
- 42 Makino S, Kawashima M and Kosaka H, First record of occurrence of *Xenos moutoni* (Strepsiptera; Stylopidae), an important parasite of hornets (Hymenoptera: Vespidae: *Vespa*), in Korea. *J Asia Pac Entomol* **14**:137–139 (2011).
- 43 Suenami S, Konishi Nobu M and Miyazaki R, Community analysis of gut microbiota in hornets, the largest eusocial wasps, *Vespa mandarinia* and *V. simillima*. *Sci Rep* **9**:1–13 (2019).
- 44 Yoshimoto J, Interspecific variation in competitor avoidance and foraging success in sap-attracted insects. *Eur J Entomol* **106**:529–533 (2009).
- 45 GBIF.org, GBIF Occurrence, GBIF.org, 2020.
- 46 Fick SE and Hijmans RJ, WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int J Climatol* **37**:4302–4315 (2017).
- 47 Kennedy CM, Oakleaf JR, Theobald DM, Baruch-Mordo S and Kiesecker J, Managing the middle: a shift in conservation priorities based on the global human modification gradient. *Glob Chang Biol* **25**:811–826 (2019).
- 48 Gorelick N, Hancher M, Dixon M, Ilyushchenko S, Thau D and Moore R, Google Earth Engine: planetary-scale geospatial analysis for everyone. *Remote Sens Environ* **202**:18–27 (2017).
- 49 Brown JL, SDMtoolbox: a python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *Methods Ecol Evol* **5**:694–700 (2014).
- 50 Carvajal MA, Alaniz AJ, Smith-Ramírez C and Sieving KE, Assessing habitat loss and fragmentation and their effects on population viability of forest specialist birds: linking biogeographical and population approaches. *Divers Distrib* **24**:820–830 (2018).
- 51 Carvajal MA, Alaniz AJ, Núñez-Hidalgo I and González-Céspedes C, Spatial global assessment of the pest *Bagrada hilaris* (Burmeister) (Heteroptera: Pentatomidae): current and future scenarios. *Pest Manag Sci* **75**:809–820 (2019).
- 52 Wiens JJ, Ackerly DD, Allen AP, Anacker BL, Buckley LB, Cornell HV *et al.*, Niche conservatism as an emerging principle in ecology and conservation biology. *Ecol Lett* **13**:1310–1324 (2010).
- 53 West AM, Kumar S, Brown CS, Stohlgren TJ and Bromberg J, Field validation of an invasive species Maxent model. *Ecol Inform* **36**:126–134 (2016).
- 54 Searcy CA and Shaffer HB, Field validation supports novel niche modeling strategies in a cryptic endangered amphibian. *Ecography* **37**: 983–992 (2014).
- 55 Alaniz AJ, Núñez-Hidalgo I, Carvajal MA, Alvarenga TM, Gómez-Cantillana P and Vergara PM, Current and future spatial assessment of biological control as a mechanism to reduce economic losses and carbon emissions: the case of *Solanum sisymbriifolium* in Africa. *Pest Manag Sci* **76**:2395–2405 (2020).
- 56 VanDerWal J, Shoo LP, Johnson CN and Williams SE, Abundance and the environmental niche: environmental suitability estimated from niche models predicts the upper limit of local abundance. *Am Nat* **174**:282–291 (2009).
- 57 Martínez-Meyer E, Díaz-Porras D, Peterson AT and Yanez-Arenas C, Ecological niche structure and rangewide abundance patterns of species. *Biol Lett* **9**:20120637–20120637 (2012).
- 58 Sugahara M, Nishimura Y and Sakamoto F, Differences in heat sensitivity between Japanese honeybees and hornets under high carbon dioxide and humidity conditions inside bee balls. *Zoolog Sci* **29**: 30–36 (2012).
- 59 Keeling MJ, Franklin DN, Datta S, Brown MA and Budge GE, Predicting the spread of the Asian hornet (*Vespa velutina*) following its incursion into Great Britain. *Sci Rep* **7**:1–7 (2017).
- 60 Robinet C, Suppo C and Darrouzet E, 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* **54**:205–215 (2017).
- 61 Pusceddu M, Floris I, Mannu R, Cocco A and Satta A, Using verified citizen science as a tool for monitoring the European hornet (*Vespa crabro*) in the Island of Sardinia (Italy). *NeoBiota* **50**:97–108 (2019).
- 62 Comont RF and Ashbrook K, Evaluating promotional approaches for citizen science biological recording: bumblebees as a group versus *Harmonia axyridis* as a flagship for ladybirds. *BioControl*. **62**: 309–318 (2016).
- 63 Stein K, Coulibaly D, Stenchly K, Goetze D, Porembski S, Lindner A *et al.*, Bee pollination increases yield quantity and quality of cash crops in Burkina Faso, West Africa. *Sci Rep* **7**:17691 (2017).
- 64 Kennedy PJ, Ford SM, Poidatz J, Thiéry D and Osborne JL, Searching for nests of the invasive Asian hornet (*Vespa velutina*) using radio-telemetry. *Commun Biol* **1**:88 (2018).
- 65 Turchi L and Derijard B, Options for the biological and physical control of *Vespa velutina nigrithorax* (Hym.: Vespidae) in Europe: a review. *J Appl Entomol* **142**:553–562 (2018).
- 66 de Haro L, Labadie M, Chanseau P, Cabot C, Blanc-Brisset I and Penouil F, Medical consequences of the Asian black hornet (*Vespa velutina*) invasion in Southwestern France. *Toxicon* **55**:650–652 (2010).