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RESEARCH

Using ecological niche modeling to model invasion risk of hornets (Hymenoptera: Vespidae) in Iran

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Background: Among the 22 species in the *Vespa* genus, five have successfully established populations outside their native ranges, while four others have been recorded either in natural habitats or during border inspections in various countries. This study aims to assess the potential threat posed by 12 hornet species—*Vespa crabro, Vespa mandarinia, Vespa simillima, Vespa velutina, Vespa affinis, Vespa analis, Vespa basalis, Vespa bicolor, Vespa ducalis, Vespa dybowskii, Vespa soror,* and *Vespa tropica*—within the geographical and ecological context of Iran, an arid Middle Eastern country. Using ecological niche modeling, we analyzed species occurrence data alongside climatic variables with minimal correlation to predict the potential distribution of these hornets across Iran. The mobility-oriented parity method was applied to identify areas where strict extrapolation is relevant for these species. Additionally, we generated a habitat suitability map for *Apis mellifera* (honey bee) using ecological niche modeling and compared the spatial overlap between the predicted risk maps for the hornets and the honey bee habitat suitability map, employing Schoener's *D* metric.
Results: The results revealed two key findings. First, a significant portion of Iran exhibits climatic dissimilarity compared to the native habitats of certain hornet species. Second, the spatial overlap analysis showed varying degrees of overlap between *A. mellifera* habitats and the potential distributions of different hornet species. Notably, *V. mandarinia* and *V. crabro* demonstrated the highest overlap values ($D = 0.68$), suggesting that these hornets could share substantial habitat preferences or ecological roles with honey bees in Iran.
Conclusions: Although most regions of Iran appear less suitable for hornet invasions, caution is warranted in the northern areas, where trade and exchanges could serve as pathways for *Vespa* hornet introductions. These findings highlight the importance of targeted monitoring and preventative measures in these high-risk regions.

Keywords: ecological niche modeling, hornets, invasive species, Iran, mobility-oriented parity

Introduction

The economic value of animal pollination as an ecosystem service in global agriculture ranges from $195 billion to $387 billion (Porto et al. 2020). Additionally, it is estimated that pollinators play a direct role in supplying up to 40% of the essential nutrients in the human diet (Eilers et al. 2011). Insect pollination alone contributes to 9.5% of the total economic worth of agricultural products that are directly consumed by humans (Gallai et al. 2009). Research conducted by Rodger et al. (2021) has demonstrated that a reduction in pollinators can result in a 50% decrease in seed-based reproduction for approximately one-third of flowering plants, indicating that a substantial number of flowering plants rely entirely on pollinators for seed production.

Pollinating insects encompass various groups such as moths, butterflies, bumblebees, honey bees, solitary bees, and hoverflies. Among these, bees hold particular importance as they are accountable for pollinating approximately 35% of the world's food production (Elias et al. 2017). Bees, categorized as ectothermic creatures, exhibit a significant reliance on the temperature of their habitat for their functioning. Honeybees and bumblebees are known to visit over 90% of global food crops (Doyle et al. 2020). Nevertheless, hornets can pose significant threats to these bee

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species, especially honeybees. Hornets belonging to the *Vespa* genus (Hymenoptera: Vespidae) are easily recognizable predators that form moderate to large annual colonies of eusocial insects. Several aspects of their biology contribute to their effective colonization of habitats in regions where they are not native (Rahimi and Jung 2024a). Multiple Vespa species have ventured beyond their natural ranges, invading nonnative regions. In doing so, they have the potential to disrupt local ecosystems by impacting biodiversity and interfering with pollination systems, a phenomenon observed in various invasive species of social wasps, such as the yellow jackets in the *Vespula* genus (Otis et al. 2023).

One of the most notorious invasive insect species is the hornet, such as *Vespa velutina*, which has successfully invaded regions like Europe, South Korea, and Japan (Otis et al. 2023; Rahimi et al. 2022; Rahimi and Jung 2024a). This invasive hornet species has had a highly detrimental impact on local ecosystems, particularly honeybee colonies in these areas (Laurino et al. 2020). For example, in Europe, *V. velutina* causes losses between 18% and 50% of beehives (Zhu et al. 2020). The annual economic loss of hornets to the beekeeping industry in Korea is also estimated at 100–170 billion Korean won (Jung and Cho 2015). They have the potential to inflict significant harm on bee colonies, as a cluster of 10 to 20 *Vespa mandarinia* workers have been documented as capable of decimating a bee colony with a population ranging from 10,000 to 30,000 bees (Matsuura and Yamane 1990).

While invasive species are usually constrained by their ability to disperse and find suitable new habitats, vespid hornets stand out due to their remarkable invasive achievements and impressive dispersal capabilities (Otis et al. 2023). The genus Vespa comprises a total of 22 hornet species, all of which are found in various regions of Asia (Archer 2012; Rahimi and Jung 2024a). Only two species, *Vespa crabro* Linnaeus and *Vespa orientalis* Linnaeus, naturally extend their ranges into Europe. None of these species are native to the Americas. However, in recent times, numerous hornet species have been identified in regions far from their native habitats. Among them, at least five species have successfully established non-native populations. This phenomenon underscores the potential ecological impacts associated with the expansion of hornet species beyond their original ranges (Otis et al. 2023).

The tendency of species to retain aspects of their fundamental niche over time is called niche conservatism (NC) (Wiens and Graham 2005). If species' fundamental niches are conserved, species will only be able to invade regions that have a climate similar to that of their native range (Tirozzi et al. 2022). Given climatic NC, the distribution of species in their native ranges may predict where they can successfully invade and subsequently spread (Bock et al. 2017; Wiens et al. 2010). For biogeographic hypotheses, a key idea is that climatically unsuitable conditions can limit geographic ranges when there is NC, and such conditions can potentially be identified and tested using species distribution models (SDMs) (Strubbe et al. 2013). For example, a hypothesis of climatic NC predicts that invasive species will spread primarily in regions that are climatically similar to their native range (Wiens et al. 2010).

Ecological niche models (ENM) have been employed to forecast the potential range of other Vespa species (Alaniz et al. 2021; Barbet-Massin et al. 2013; Barbet-Massin et al. 2018; Bessa et al. 2016; Herrera et al. 2023; Keeling et al. 2017; Moo-Llanes 2021; Nuñez-Penichet et al. 2021; Zhu et al. 2020). For example, Nuñez-Penichet et al. (2021) found that regions highly suitable for *V. mandarinia* align extensively with states where honey production is most prominent, as well as areas with the greatest species diversity of Bombus and Melipona. Alaniz et al. (2021) also assessed the potential expansion of *V. mandarinia* in the United States and evaluated its potential consequences on honey bee colonies. They found that *V. mandarinia* could pose a threat to approximately 95,216 ± 5,551 honey bee colonies, risking an estimated income loss of $11.9 million for hive-derived products and $101.8 million for bee-pollinated crop production. Barbet-Massin et al. (2018) successfully addressed the question of whether SDMs can accurately predict the expansion of invasive species. Their specific case study provides evidence that *V. velutina* is not yet in equilibrium with its surroundings within the European regions it has invaded.

Iran has been identified as home to a variety of pollinating bees across different regions. Among these, *Apis florea* and *Apis mellifera meda* are noteworthy species with wide distributions. *A. florea* is predominantly found in the southern regions of Iran, while *Apis mellifera meda* is indigenous to Iran and boasts the highest distribution among all bee species in the country (Rahimi and Mirmoayedi 2013; Rahimi et al. 2021a). The economic significance of bee-mediated pollination for Iran's agricultural products was substantial, estimated at approximately $6.59 billion in 2005–2006. Of this, $5.72 billion was attributed to honeybees, while $0.87 billion was attributed to wild bees (Sanjerehei 2014). It is estimated that pollinators play a role in the pollination of 25% of Iran's total agricultural output (Rahimi et al. 2021b; Sanjerehei 2014). Iran is home to two indigenous hornet species, *V. orientalis,* and *V. crabro*. *V. orientalis* is distributed across nearly the entire country, except for the northern coastal areas. In contrast, *V. crabro* is limited to the northern regions along the Caspian coastline (Bagriacik and Samin 2011; Ebrahimi and Carpenter 2012; Vaziritabar and Esmaeilzade 2018). Therefore, the arrival of other hornets in Iran poses a significant potential threat to both the environment and the economy in Iran. In this study, we employ ENM to identify suitable habitats for this species in Iran.

Materials and Methods

Natural geography of Iran

Iran's ecological landscape is categorized into three distinct phytogeographical regions (Fig. 1) as identified by Talebi et al. (2014): the Euxino-Hyrcanian region, the Saharo-Sindian region, and the Irano-Turanian region. Furthermore, ecologists have classified Iran's forests into three ecological zones, namely the Caspian or Hyrcanian zone, the Khalijo-Omanian zone, and the Iranian-Turanian zone. These are further subdivided into the Zagros mountainous zone and the central plateau zone. Here, we provide a brief overview of these five ecological regions in Iran, as depicted in Figure 1.

Table 1 presents an overview of the extent and distribution of Iran's natural resources. As per the data in this table, approximately 81% of Iran's land area is occupied by various natural features, including forests, deserts, rangeland, and bushes. Notably, rangelands account for nearly half of the country's land area, with a significant portion characterized as poor quality. Deserts encompass roughly 20% of Iran's territory, predominantly situated in the central, eastern, and southeastern regions, primarily within the Irano-Turanian ecological region.

Iran's hornets

Two species of hornets are present in Iran: *V. orientalis Linnaeus*, 1771, has a widespread distribution in most parts of Iran, except for the Caspian coast in northern Iran, but *V. crabro Linnaeus*, 1758, is present only on the Caspian coast (north of Iran). Both of these species are native to Iran, and there have been no recorded findings of non-native hornet species in Iran to date (Bagriacik and Samin

Table 1 Area and proportion of natural resources in Iran (Talebi et al. 2014)

Natural resources	Area (ha)	Proportion (%)
Natural forest	13,364,010	8.10
Man-made forest	946,546	0.57
Bush and woodland	2,723,756	1.65
Rangeland	84,960,321	51.60
Desert	32,863,972	19.94
Total	134,884,365	81.85

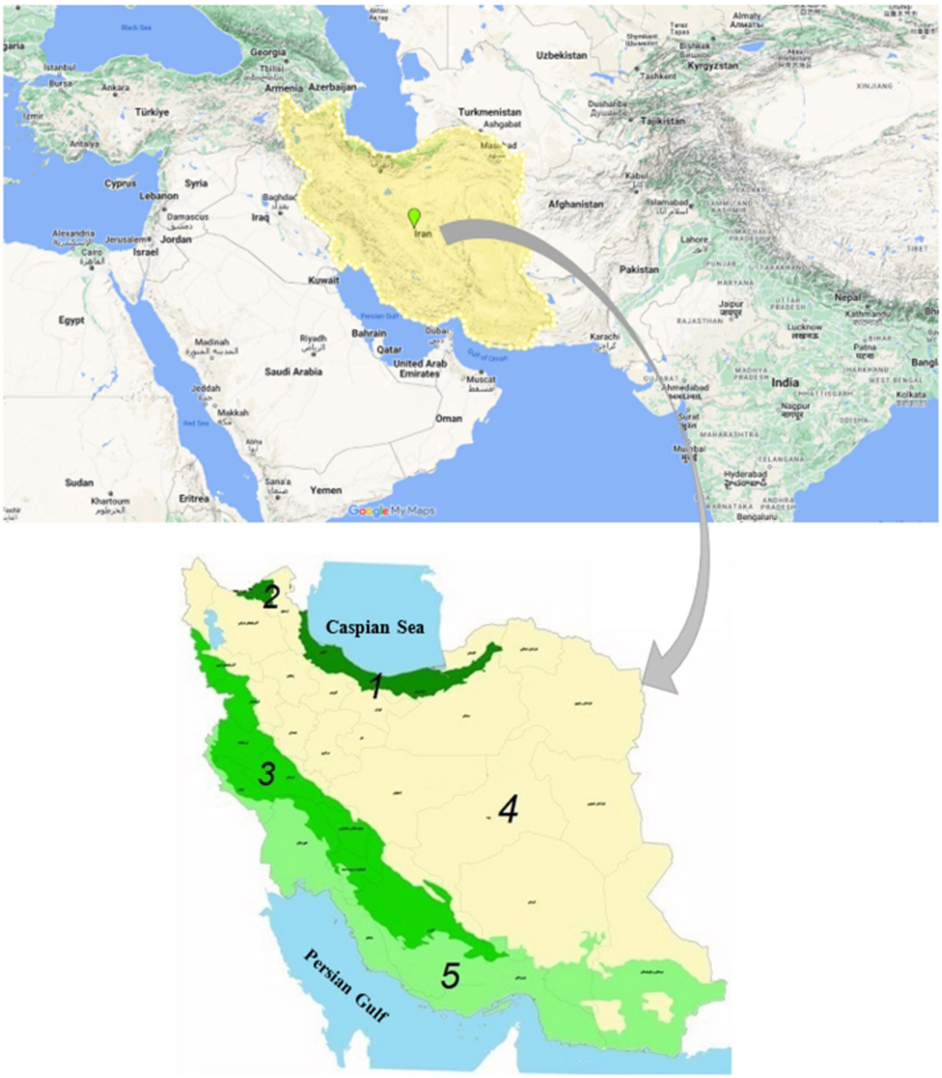

Fig. 1 Phytogeographical regions of Iran. Euxino-Hyrcanian: 1 Caspian (Hyrcanian), 2 Arasbaran; Irano-Turanian: 3 Zagros, 4 Steppic central plateau, 5 Saharo-Sindian.

2011; Ebrahimi and Carpenter 2012; Vaziritabar and Esmaeilzade 2018).

Ecological niche modeling

Occurrence data

The species selected for niche overlap analysis in this study include *V. crabro, V. mandarinia, Vespa simillima, V. velutina, Vespa affinis, Vespa analis, Vespa basalis*, *Vespa bicolor, Vespa ducalis, Vespa dybowskii, Vespa soror,* and *Vespa tropica*. We obtained the presence data of these species from the Global Biodiversity Information Facility (GBIF) website (www.gbif.org). To enhance data accuracy, a thorough examination of presence points was conducted to eliminate duplicate entries and records falling outside the study area boundary. Moreover, to mitigate potential biases arising from the clustering or overrepresentation of specific areas in the presence of data, spatial thinning was employed using the spThin package (Aiello-Lammens et al. 2015). The spatial thinning distance was set at 10 km, a choice based on the scale or pixel size of the predictor layers in the model. This decision was made to ensure that the spatial thinning distance was equal to or greater than the scale to effectively reduce any spatial autocorrelation (Rodríguez-Aguilar et al. 2023). The 'rgbif' package (Chamberlain et al. 2022) was utilized to filter the records located in the ocean. To assess the potential invasion risk of hornets and compare it with the distribution of honeybees, we conducted the same procedures as described above for *Apis mellifera* in Iran.

Environmental variables

Bioclimatic layers as predictor variables also were downloaded from the WorldClim database (www.worldclim.org). The Bioclimatic data in the WorldClim database includes 11 temperature variables and 8 precipitation variables, which have a spatial resolution of approximately 4 km. These 19 variables often have a high correlation with each other and therefore it is not recommended to use all these variables in species distribution modeling. For this purpose, we used the usdm (Naimi 2023) package to exclude the highly correlated variables from the set through a stepwise procedure based on variance inflation factor. The remaining variables include Mean Diurnal Range (Bio 2), Temperature Seasonality (Bio 4), Mean Temperature of Wettest Quarter (Bio 8), Mean Temperature of Driest Quarter (Bio 9), Precipitation Seasonality (Bio15), and Precipitation of Coldest Quarter (Bio 19).

In this study, we employed the SDM package (Naimi and Araujo 2018) within the R software environment to model the distribution of *A. mellifera* in Iran. Specifically, we utilized the MaxEnt model to generate a habitat suitability map, drawing upon both presence data and climatic information. To enhance our modeling efforts, we generated 10,000 pseudo-absence points to complement the presence points when applying the MaxEnt model (Rahimi and Jung 2024b).

Extrapolation modeling

Williams et al. (2007) pointed out that the availability of data can hinder the extrapolation to unfamiliar environments. This limitation arises from the fact that the species' niche may not be entirely captured or represented in the available data. Depending on the direction of environmental changes, certain aspects of the species' niche that have not been observed in the existing data may become relevant or newly significant. The advancement of techniques for handling uncertainty has not kept pace with the widespread use of SDMs (Mesgaran et al. 2014). Recently, several valuable approaches have been proposed to detect and visually represent new environmental conditions (Elith et al. 2010; Mesgaran et al. 2014; Owens et al. 2013). New environmental conditions can be classified into two categories: 1. For a specific individual variable, the values may fall outside the range covered during training, which is referred to as univariate or strict extrapolation. 2. Certain areas in the environmental space may lie within the range of individual variables but constitute new combinations of predictors, known as multivariate or combinational extrapolation (Zurell et al. 2012).

To manage this risk and identify analogous environments, we can employ three different approaches by comparing native and invaded ranges: a) Analysis of multivariate environmental similarity surface (MESS) (Elith et al. 2010), which provides a measure of how environmentally similar each location is to the median of the most dissimilar variable. b) Mobility-oriented parity (MOP) (Owens et al. 2013), a method that pinpoints areas of strict extrapolation and quantifies the environmental similarity between the calibrated and projected regions. c) Extrapolation detection (ExDet) (Mesgaran et al. 2014), a technique that detects similarities or novel environmental conditions between native and invaded areas.

In this study, we employed MOP analysis because the MESS tool identifies extrapolation or 'dissimilar' points based solely on the ranges of individual (univariate) predictors. It does not consider the correlation structure, which means it doesn't account for new multivariate combinations of the various covariates that might be included in the model.

Strict extrapolation occurs when the environmental conditions in the area of interest (new areas) fall completely outside the range of conditions observed in the reference or calibration area (original area). A MOP value of 0 for a specific location (or grid cell) in the area of interest indicates that at least one environmental variable at that location lies entirely outside the range observed in the reference area. This suggests the presence of novel environmental conditions that the model has not encountered before. As a result, predictions for these areas are highly uncertain and potentially unreliable due to the absence of prior data on these conditions. On the other hand, a MOP value of 1 indicates that the environmental conditions at a specific location in the area of interest are identical to those found in the reference area. In such cases, the model has already been trained on these conditions, allowing it to make predictions with a higher degree of confidence. Therefore, predictions in these regions are more dependable as they are based on familiar environmental conditions (Qiao et al. 2019; Rahimi et al. 2024; Velazco et al. 2024).

To perform this task, we will need to use the NicheToolBox (ntbox) R package (Osorio-Olvera et al. 2020). The mop function in this package requires two types of raster stacks: 1. 'M_stack': that is a RasterStack (bioclimatic variables) containing variables that represent the calibration area (hornets range). In the context of ENM, this typically means the region where we have species occurrence data and environmental variables that are used to train the model. 2. 'G_stack': This is another RasterStack (bioclimatic variables) containing variables that represent the areas or scenarios to which our ENM models will be transferred (Iran). To establish the calibration area, we must account for a zone surrounding the hornets' presence locations. As an illustration, these hornets are known to inhabit areas up to 100 km (Moo-Llanes 2021) from their occurrence points, but in this case, we've opted for a 50 km buffer around each point and masked the bioclimatic variables in ArcGIS software. Our analysis encompasses all recorded instances of hornet presence, both within their natural habitats and regions outside their native range.

Quantitative spatial overlap between hornets and honey bees

We employed Schoener's *D* metric (Schoener 1968; Warren et al. 2008) as a non-binary measure to quantify the overlap degree of predicted risk maps of hornets and honey bees in Iran. Using the *calc.niche.overlap* function in the ENMeval R package (Kass et al. 2021), we calculated spatial overlap between all hornets and honey bees pairs across Iran. The *D* statistic ranges from 0 to 1, where 0 indicates no spatial overlap between two species, and 1 represents complete overlap (Equation 1).

$$D\,(p_x, p_y) = 1\text{-}\ 1/2\ \Sigma\left|p_{x,\,i\,\text{-}}\ p_{y,\,i}\right| \qquad (1)$$

Which *pX, i* (or *pY, i*) denotes the probability assigned by the SDMs for species *X* (or *Y*) to cell *i*.

Model assessment

To evaluate the performance of the results obtained from the MaxEnt model for *A. mellifera*, we used two statistics of true skill statistic (TSS) and the area under the ROC curve (AUC). The range of AUC values between 0.7–0.9 is considered acceptable, and values above 0.9 are considered excellent results, which means that the model has estimated a very good prediction. TSS values are between –1 and +1, where 1 indicates complete and correct prediction, while values between 0.4 and 0.6 indicate moderate prediction. We used 10 runs of subsampling replications to evaluate the model and considered 70% of the presence data as training data and the remaining 30% as a test. The value range of the climate suitability maps is between 0 and 1, where the number 1 represents the maximum suitability.

Results

Model assessment

Table 2 shows the results of model validation metrics for different families based on statistics of AUC and TSS. To measure the values of these statistics, the output of all studied species in different families was evaluated, and for each family, the average AUC and TSS values of all species were reported. According to this table, the value of AUC for all families is between 0.91 and 0.95, which indicates that the results of the models are excellent. According to the TSS test, our results also fall within the perfect prediction range.

Extrapolation maps

As noted earlier, MOP analysis enables the comparison of environmental conditions between a reference set (South Asia) and an area of interest (Iran). The primary goal of MOP analysis is to identify non-analogous conditions in the area of interest relative to the reference set and to quantitatively evaluate the degree of dissimilarity in these conditions. This approach helps identify potential habitats where hornets could establish successfully based on their original habitat preferences. Predictions for areas with high values of MOP are more reliable due to strong data support from the model. However, low MOP values do not necessarily indicate that an area is unsuitable; instead, they highlight increased uncertainty, making invasion outcomes less predictable.

Figure 2 presents the maps illustrating the risk of hornet invasion in Iran. In these maps, the blue regions with values near zero indicate areas with low climatic suitability for hornets. Conversely, the brighter colors represent higher values, signifying a more favorable climate for these spe-

Table 2 Model validation metrics including TSS and AUC for *Apis mellifera*

Name	AUC	TSS
Apis mellifera	0.97	0.82

TSS: true skill statistic; AUC: area under the ROC curve.

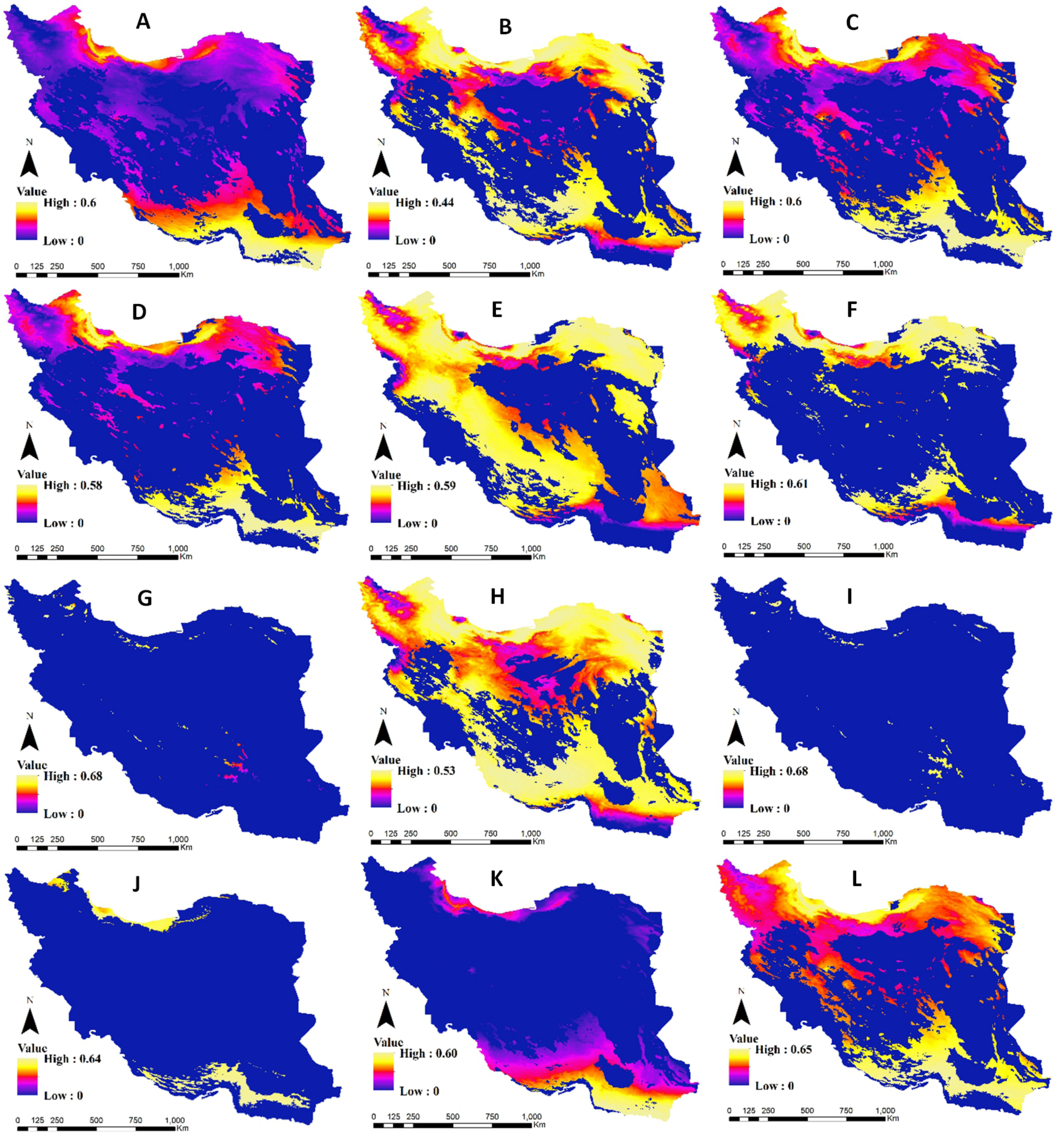

Fig. 2 Extrapolation maps of hornets. (A) *Vespa affinis,* (B) *Vespa analis,* (C) *Vespa basalis,* (D) *Vespa bicolor,* (E) *Vespa crabro,* (F) *Vespa ducalis,* (G) *Vespa dybowskii,* (H) *Vespa mandarinia,* (I) *Vespa similima,* (J) *Vespa soror,* (K) *Vespa tropica,* (L) *Vespa velutina.*

cies. A brief examination of these maps reveals two notable observations. Firstly, for certain hornet species, a significant portion of Iran exhibits a dissimilar climate compared to their native habitats. Secondly, none of the cells in the maps have values exceeding 0.7 for any of the species. Specifically, the distribution of *V. affinis* appears limited to small regions in the northern and southern parts of Iran. This distribution pattern is also observed in several other species, including *V. basalis*, *V. bicolor*, *V. ducalis*, *V. dybowskii*, *V. similima*, *V. soror*, and *V. tropica*. However, some species such as *V. Analis*, *V. crabro*, *V. mandarinia*, and *V. velutina* show a capacity to occupy more extensive areas within Iran.

Spatial overlap between hornets and honey bees

The spatial overlap analysis between *A. mellifera* (honey bee) and various hornet species shows varying degrees of overlaps. The strongest overlap values are observed with *V. mandarinia* (0.68) and *V. crabro* (0.68), indicating that these hornets may share significant habitat preferences or ecological roles with honey bees in Iran. This suggests that both species may utilize similar climatic niches or inhabit comparable environments, potentially leading to competition. Moderate overlap is seen with *V. affinis* (0.55), *V. analis* (0.53), and *V. velutina* (0.52), which implies that these hornets also share some climatic niche with honey bees but to a lesser extent than the two strongest overlaps. In contrast, *V. tropica* (0.42) and *V. basalis* (0.49) show lower levels of overlap, suggesting that while they might occupy some similar habitats, they are more likely to be specialized in different ecological niches. The minimal overlaps with *V. dybowskii* (0.01), *V. simillima* (0.01), and *V. soror* (0.05) indicate that these hornets have distinct ecological preferences, and their interactions with honey bees in Iran may be limited. Overall, these findings highlight the varying degrees of spatial overlap and potential competition between honey bees and hornets, with the strongest competition likely occurring between *A. mellifera* and *V. mandarinia* or *V. crabro*, while minimal competition occurs with species like *V. dybowskii* and *V. simillima*.

Potential competition between hornets

Based on the spatial overlap matrix (Fig. 3), the hornet species that exhibit the highest ecological overlap with each other are *V. analis* and *V. basalis*, which show the strongest overlap of 0.88. This high overlap suggests that these two species may share highly similar ecological niches in Iran, and their interactions could result in significant competition, especially for resources like floral resources or nesting sites. Another pair with considerable overlap is *V. basalis* and *V. bicolor*, with an overlap of 0.76, indicating that they likely compete for similar ecological resources. Additionally, *V. crabro* and *V. mandarinia* show a moderate overlap of 0.69, which suggests potential competition for shared resources, particularly in areas with limited floral resources or suitable nesting sites. *V. analis* and *V. affinis* show a high overlap of 0.74, further supporting the idea that these species share similar ecological preferences and may compete for similar resources in areas where they coexist. Finally, *V. basalis* and *V. mandarinia* also show a significant overlap of 0.75, indicating that these two species may face competition in overlapping habitats, particularly for food resources. Overall, the species with the highest overlap, particularly *V. analis* and *V. basalis*, are likely to experience intense competition, and their distributions may be constrained by resource limitations.

Cumulative risk of hornets for honey bees in Iran

Figure 4 presents both the composite risk map for hornets' invasion and the climatic suitability map for *A. mellifera* in Iran. The hornet risk map is constructed by summing or overlaying all the individual hornet maps from the

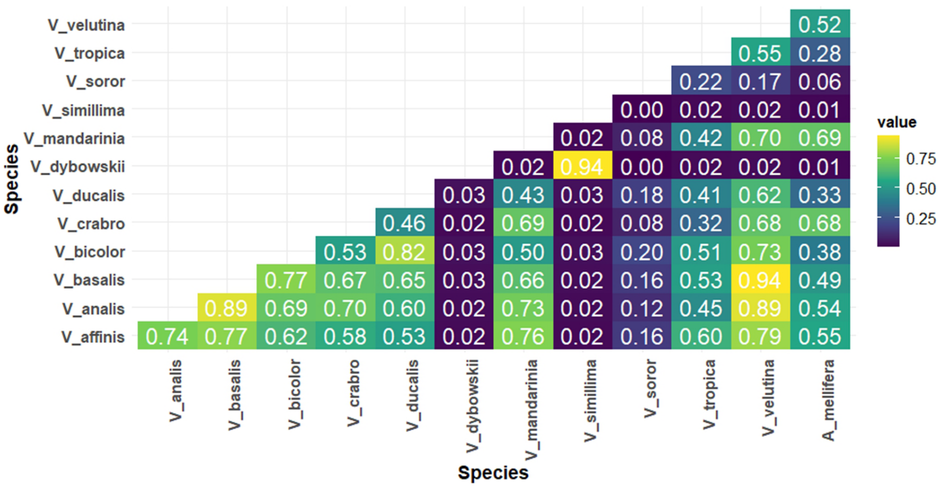

Fig. 3 Schoener's *D* statistic for pairs of hornets and honeybees in Iran.

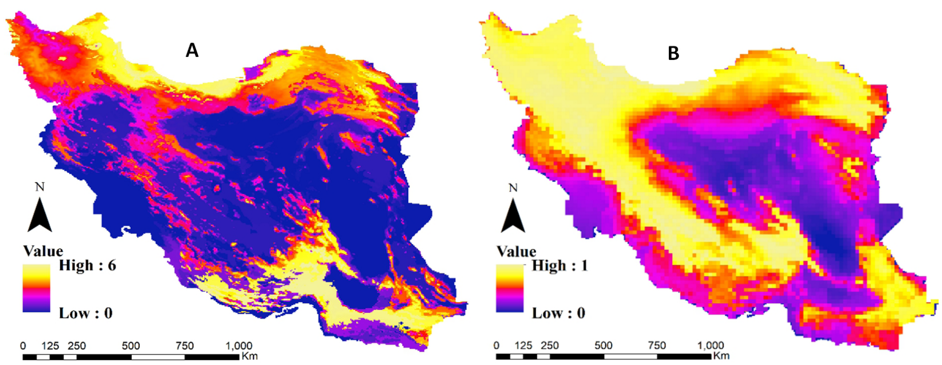

Fig. 4 Risk composite map of hornets (A) and climatic suability map of *Apis mellifera* (B) in Iran.

previous figure. The scale for this section ranges from 0 to 6, with 0 indicating that the cell is unsuitable for any hornet species, while 6 signifies that the cell offers a favorable climate for multiple hornet species. The suitability map for honey bees was generated using SDMs and the MaxEnt algorithm. This map reveals that, except for Iran's central regions, the majority of the country provides favorable climatic conditions for *A. mellifera*. In contrast, the hornet risk map indicates that only certain parts of southern and northern Iran are suitable for these species' presence and potential invasion. Consequently, it can be inferred that Iran's risk of hornet attacks falls within the low to moderate range.

Discussion

Our findings indicate that hornets have limited potential to inhabit specific areas in both the northern and southern regions of Iran. It's important to note that even in these regions, the climatic suitability for hornets is not exceptionally high (close to 1). Iran is home to two hornet species, namely *V. crabro* in the northern regions and *V. orientalis* throughout the country except for the Caspian coast in northern Iran. Given that *V. orientalis* has a broad distribution covering most of Iran, we opted not to model this species. However, given the restricted range of *V. crabro*, we sought to investigate whether this species could potentially inhabit regions across Iran.

V. orientalis is a prevalent hornet species and the sole inhabitant of dry landscapes (Perrard et al. 2013). This species has effectively colonized Spain as an introduced non-native species (Perrard et al. 2013). On the other hand, the natural habitat of *V. crabro* spans temperate Eurasia, encompassing regions from Japan and far Eastern Russia to Europe, the UK, the Iberian Peninsula, and most of Italy (Archer 1992). There have been two successful expansions of *V. crabro* beyond its native range. The first expansion occurred in the United States, starting around 1840 near port facilities in New York City. Secondly, in 2010, *V. crabro* was detected on the island of Sardinia, Italy (Otis et al. 2023). *V. crabro* is a versatile predator (Cini et al. 2018) and, as of current reports, it has not been associated with significant environmental impacts in either its native or introduced ranges. We discovered that *V. crabro* has the potential to inhabit regions beyond its known distribution in Iran. However, due to limited research on hornets in Iran, we lack sufficient data to determine the extent to which this species may occupy these additional areas.

V. mandarinia also showed a wide extrapolation in Iran. This species' native habitat spans from Hokkaido, Japan, and Primorsky Krai, Russia, reaching southward to Hong Kong, and then extending westward along the southern fringes of the Himalayas into northern India (Fig. 5). Within its natural range in Asia, it holds the distinction of being the most significant predator of honey bees (Otis et al. 2023). In Asia, which is recognized as the hub of hornet evolution (Matsuura and Yamane 1990), native honey bee species such as *Apis cerana* or *Apis dorsata* have developed effective defenses to safeguard their colonies against hornet threats (Abrol 2006). Conversely, introduced European honey bees, particularly *A. mellifera*, have displayed comparatively less efficient defense strategies (Jung and Cho 2015). In its natural habitat, *V. mandarinia* targets various bee species, some of which have evolved sophisticated defense mechanisms to counter these assaults (Fujiwara et al. 2016). In the context of extrapolation analysis, some studies have predicted the potential invasion of *V. mandarinia* in the United States and Canada (Alaniz et al. 2021; Moo-Llanes 2021; Nuñez-Penichet et al. 2021; Zhu et al. 2020). These models exhibit a relatively close consensus regarding the suitable region for *V. mandarinia*, particularly in the Pacific Northwest region where the species was initially discovered.

Nevertheless, some studies have focused on species distribution modeling of hornets, such as *V. velutina*, to forecast the potential invasion of this species into other regions globally. For instance, Villemant et al. (2011) employed ensemble models to predict the invasion risk *V. velutina* across Europe and other continents. They found that the most suitable area in Europe expands into adjacent countries, predominantly along the Atlantic coast, the Mediterranean coast, and the southern shores of the Black and Caspian Seas. We also found that northern parts of Iran along the Caspian Sea can be suitable habitats for *V. velutina* (Fig. 4). Barbet-Massin et al. (2013) also aimed to assess the potential impact of climate change on invasion risk of *V. velutina*, they extended the models to project future scenarios up to 2100. They found that climate change is likely to elevate invasion risk in the United States, except for areas along the Eastern coast. Nonetheless, our results indicated a significant decrease in invasion risk for certain hornet species in Asia. However, it's important to note that adaptability to climatic conditions is just one facet influencing the invasion risk of hornets. Other crucial factors include interspecific hierarchies, competition for prey resources, temporal overlap in seasonal phenology, competition for nesting sites, aggressiveness, and body size (Kwon and Choi 2020; Lioy et al. 2022, 2023).

Others have conducted niche overlap analyses comparing native and non-native ranges of hornets to determine if this species exhibit NC. For example, Barbet-Massin et al. (2018) tried to determine whether *V. velutina* has reached equilibrium in its invaded range in Europe. To do this, they compared the climatic niche that the species occupied during the initial phase of its invasion (from 2004 to 2010) with the niche it currently occupies based on more recent data from 2011 to 2015. Their analysis revealed a signifi-

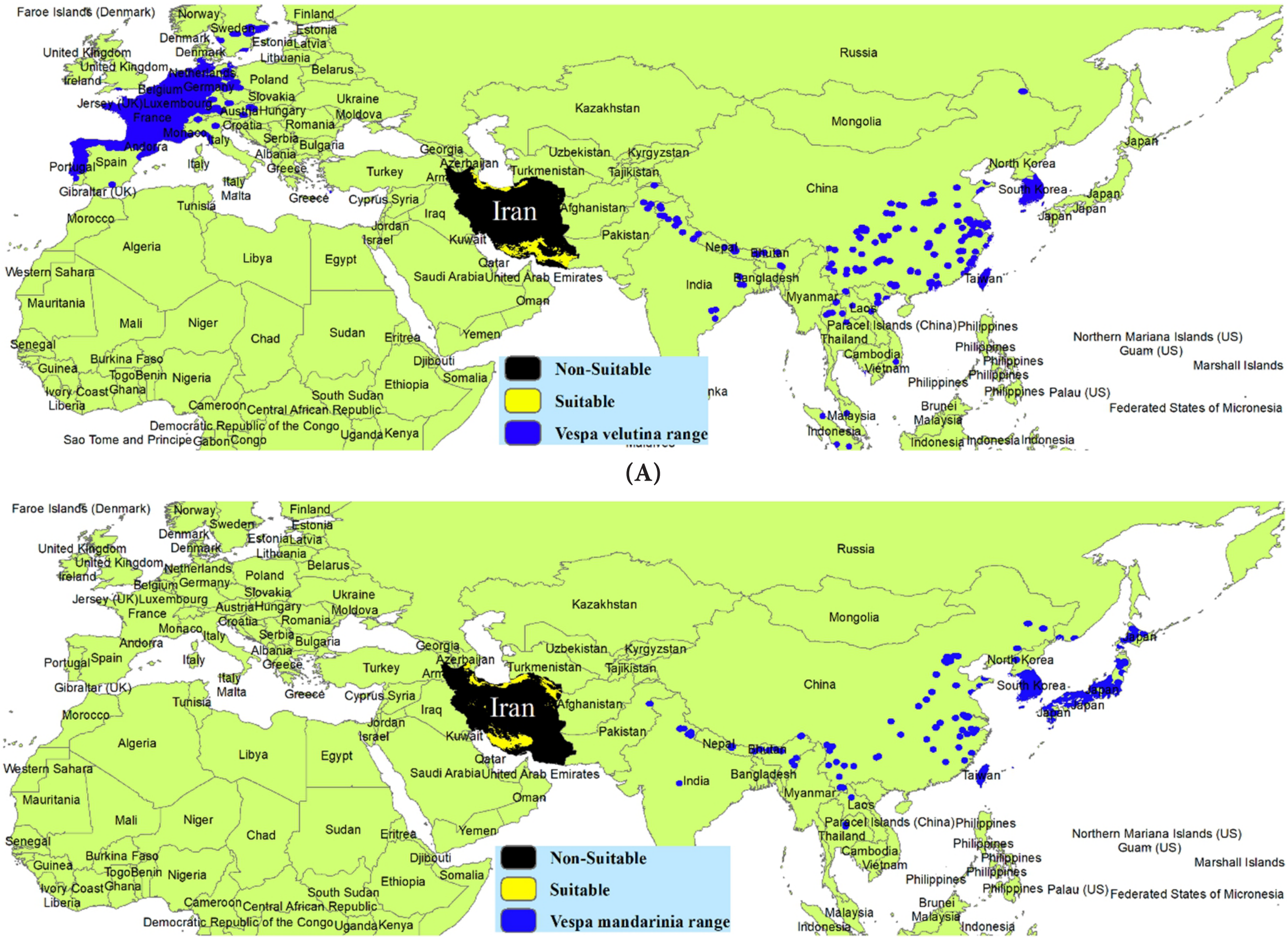

Fig. 5 Global distribution maps of (A) *Vespa velutina* and (B) *Vespa mandarinia*. Suitable and non-suitable areas in Iran for each species is colored in yellow and black respectively.

cant difference in the climatic niche occupied by *V. velutina* between the periods 2004–2010 and 2011–2015. Statistical tests confirmed that while the niches were similar, they were not equivalent. The fact that the niches were not equivalent implies that during the period from 2011 to 2015, *V. velutina* occupied a portion of its climatic niche that was not utilized between 2004 and 2010. This suggests that as of 2010, the species had not yet reached a state of equilibrium with its European environment, indicating ongoing adaptation and expansion. However, our findings indicated that even if *V. velutina* were to be introduced in Iran, it would likely only establish populations in the northern and southern regions of the country, which already exhibit low climatic suitability for this species.

V. velutina has demonstrated considerable success as an invader, showing nest densities in certain regions of Europe ranging from 5–6 nests/km2, and exceeding 12 nests/km2 in a single urban setting (Carvalho et al. 2020). Given the successful establishment of *V. velutina* in Western Europe, it presents the potential to occupy the northern regions of Iran through accidental introductions or transportation via shipments of fruits and vegetables. Therefore, a word of caution is essential in these northern areas, where trade and exchanges may serve as a conduit for a potential invasion by Vespa hornets. Monitoring and stringent measures should be considered to prevent the unintentional introduction and spread of this species, especially in areas prone to international commerce and exchange, as such pathways could inadvertently facilitate the invasion of Vespa hornets into these regions.

Lioy et al. (2023) also assessed the extent of niche overlap between *V. velutina* and two native hornets found in Europe, namely *V. crabro* and *V. orientalis*. The results indicate that the niches of both native species exhibit partial overlap with the niche of the invasive species, as evidenced by Schoener's *D* values of 0.43 for *V. crabro* and 0.28 for *V. orientalis.* However, these findings also reveal distinctions among the niches. *V. crabro* seems better adapted to cold and dry environmental conditions compared to the invasive species, while *V. orientalis* appears to be more suited for arid climates. These distinctions may confer a competitive advantage to the native species in regions with lower environmental suitability for *V. velutina*, particularly if the invasive species continues its spread and reaches all areas predicted to be suitable in Europe and the Mediterranean basin.

Conclusions

Multiple records of nine Vespa species occurring well beyond their native ranges (Otis et al. 2023) provide compelling evidence that hornets have been widely introduced to non-native regions due to human activities. Most hornets are generalist predators with a broad range of habitats, displaying significant adaptability in their behavior as eusocial insects. Additionally, their large size and potent stings make them formidable competitors in various environments. Predictive modeling of potential habitat for hornet species has been performed specifically for *V. velutina*, *V. orientalis*, and *V. mandarinia*. However, the limited availability of georeferenced location data for certain hornet species may hinder the efficacy of climate-based modeling when considering the potential ranges for these less common hornet species. Nonetheless, our endeavor aimed to forecast the invasion potential of 12 hornet species in Iran, with the belief that such studies are necessary for the broader Middle East region. Our findings suggest that Iran exhibits a relatively low to moderate susceptibility to hornet invasions. Given the diverse climatic conditions in Iran, certain regions within the country are indeed conducive to hornet presence.

Abbreviations

NC: Niche conservatism
SDM: Species distribution model
ENM: Ecological niche model
MESS: Multivariate environmental similarity surface
MOP: Mobility-oriented parity
TSS: True skill statistic
AUC: Area under the ROC curve

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Authors' contributions

ER has written the paper and has done the modeling part of the analysis. CJ has reviewed the paper and interpreted the results and final edition. All authors have read and agreed to the published version of the manuscript.

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Availability of data and materials

The datasets used and/or analyzed in the current study are available from the corresponding author on reasonable request.

Conflict of interest

The authors declare that they have no conflict of interest.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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