11 Estimating the Potential Range Expansion and Environmental Impact of the Invasive Bee-Hawking Hornet, *Vespa velutina nigrithorax*

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ABSTRACT

*Vespa velutina nigrithorax*, an Asian bee-hawking hornet, was unintentionally introduced in southwestern France before 2004 and is currently spreading widely across the country. By modeling the climatic suitability of the yellow-legged hornet at a global scale using various niche models, we estimated the potential invasion risk of this invasive species across the world, with a focus on Europe. We used eight different modeling techniques within an ensemble forecast framework to show that the invasion success in southwestern France could have been predicted using data from the native Asian range of the species. We further used data from both the native and invaded ranges (including a recently established population in Korea) to better predict the potential invasion range across all continents. Results are discussed in terms of the interest of ecological niche modeling for invasion biology, realized niche of the invasive wasp, potential threats to native entomofauna, and economic impacts of this new predator. Particular attention is paid to beekeeping activities that are nowadays already threatened by a wide panel of adversary factors. However, as far as we know, the true impact of the alien hornet on colony losses and on honey production has not yet been evaluated in France or in its area of origin. Regions at risk hold the highest densities of beehives in Europe, which could suffer from the potential predation of the putative invading hornet of both honey bees and wild pollinators. Furthermore, the impacts of *V. velutina* on pollinators must be quickly investigated, as they might well have more durable consequences than the already publicly known nuisance to apiculture.

KEYWORDS

Beekeeping, Invasive species, Native range, Niche modeling, Social Hymenoptera, Vespidae

11.1 INTRODUCTION

Honey bees are essential pollinators of crops [1,2]. In Europe, important pollinator declines have been reported, which jeopardize pollination services in agricultural ecosystems and have great economic impacts [3–6]. The recent accidental introduction of the yellow-legged Asian bee-hawking hornet, *Vespa velutina*, into Europe represents a new threat to beekeeping activities. The hornet was unintentionally introduced in southwestern France before 2004 and since then has rapidly spread, covering about half of the country by 2011. Its arrival in northern Spain was also reported in 2010 and in Portugal and Belgium in 2011 [7–9]. Being a bee-hawking predator, this species has been noticed by the French population since 2007. Considered
as a dangerous stinging insect and a major threat to domestic bees, its expansion could challenge the economic viability of beekeeping and affect pollination services. Therefore, modeling the potential invasion extent of the invasive hornet appeared necessary to predict regions at risk and, hence, to help with planning future surveys of invasion range expansion and possible dedicated protection measures. The invasion progression currently observed matched with the predictions assessed using climatic suitability models [9]. We detail here the history of invasion and the biological cycle of the invasive wasp, its realized niche, and its potential range expansion in the world. We discuss the potential economic impacts of this new predator to beekeeping activities, which are nowadays already threatened by a wide panel of adversary factors [4,5,10–15].

11.2 HISTORY AND ORIGIN OF THE INVASION

The establishment of *Vespa velutina* in France represents the first successful invasion of an exotic social wasp into Europe [16]. Twenty other species have been introduced in various countries around the world, 12 of which were established in the Americas [17]. The potential for vespid wasps to gain assisted passage from humans is high as fertilized queens of many species seek sheltered locations to undergo diapause. Such shelters are often found in human goods, which may then be transported to new locations all around the world [17].

The yellow-legged hornet was recorded for the first time in Aquitaine in 2005 [18] but locally collected data suggested that hibernating founder queens could have been imported from China before 2004 through the horticultural trade [19]. This hornet has also established itself in Korea in the 2000s, where its spread remains very limited [20,21] compared to France. A key difference, however, is that Korea has six other hornet species that may compete with the alien species, whereas France has only one, the native European hornet *Vespa crabro* [9]. Moreover, one of the Korean hornets (*V. mandarinia*) is not only a fierce predator of social wasps and bees but also the most dominant when competing for food with other hornet species [22]. *Vespa crabro* is larger but has less populous colonies than *V. velutina*, and its nesting sites are different. While it has a similar prey spectrum, it does not mainly focus its attacks on social Hymenoptera as *V. velutina* does [23,24] and is considered in Europe as a mild predator of honey bees [25].

Asia is the center of evolutionary diversification of hornets [22]; 20 of the 22 known *Vespa* species are naturally restricted to Asia and Oceania and two others expanded westwards: the Oriental hornet *Vespa orientalis* reached the Mediterranean basin, where it is also known as a fear predator of honey bees [26,27], while the European hornet occupied the whole of Eurasia. So far, *V. crabro* is the only hornet species acclimatized in the United States after it was released in the nineteenth century to control forest caterpillar outbreaks [28]. Since then, it does not seem to have caused any particular damage [17].

*V. velutina*, which comprises 12 color variants in its natural area of distribution, is distributed from north Afghanistan to Bhutan, eastern China, Indochina, and Indonesia [29,30]. The French invasive lineage that belongs, as the Korean ones [20], to the black brown variant *nigrithorax* (Figure 11.1a), is restricted to
FIGURE 11.1  (See color insert.) (a) Adult worker and nest of *Vespa velutina nigrithorax*. (b) Heat-balling behavior of *Apis cerana* on *Vespa velutina auraria* (Nepal).
the temperate parts of this area: from West Bengal (India) and Bhutan to north-eastern China [19]. Molecular comparisons between native and invasive populations of *Vespa velutina* are in course to test the hypotheses of a Chinese origin and of the potential pathway modalities of its introduction in France. The analysis of the microsatellite allelic frequencies has evidenced a strong consanguinity among the invasive population, which may indicate a single introduction of one or more queens [31].

### 11.3 Life Cycle

Apart from reported damages on hives, little was known about *Vespa velutina* in its native range [32–34]. Studies performed since 2007 in France greatly improved the knowledge on the biology of this species [7,9,24,35,36]. Like many social wasps, *Vespa velutina* produces annual colonies, initiated by a single queen. Each fertilized foundress builds a primary nest in spring (February–April), earlier than that of *Vespa crabro* (April–May). She takes care of its brood until the first batch of adult workers emerges and takes over the work of enlarging the nest and feeding larvae, leaving the queen to focus on egg-laying activity. Thus, the colony initiated by a single individual develops by producing up to 15,000 individuals through the season (from April to November). In autumn, a nest may include up to 2,000 workers that rear more than 1,000 future queens and drones. The sexual offspring leave the nest in late autumn, generally after the death of the mother queen, and take part in mating flights. After reproductive swarming, the colony, composed only of remaining workers, males, and brood, decline to finally pass on before midwinter. Thus, a colony never survives more than 1 year, and the only survivors are the future foundresses that seek winter shelters to hibernate. This efficient life cycle initiated by only one individual makes social insects, such as hornets, redoubtable invaders [17].

The primary nest is generally founded in a sheltered place (hive, hut, hole in a wall, roof edge, bramble, etc.); however, as for many other hornet species [22], when the environment becomes adverse or the primary site too narrow for the growing nest, the colony relocates after building a secondary nest in a more open and higher location—mainly tree tops [9,36]. Initially spheroid, the nest often becomes ovoid at the end of the season, reaching on average 40–60 cm in diameter, while the largest nests may attain about 1 m in height and 80 cm in diameter. *Vespa velutina* nests are easy to distinguish from nests of all other European social wasps by their narrow entrance always open at the lateral side of the envelope (Figure 11.1). After the death of the colony in winter, the empty nest may remain more or less undamaged in place during several weeks or months.

### 11.4 Predation Behavior

Like other hornet species, *Vespa velutina* is a generalist predator that attacks a wide range of arthropod preys. It may also tear out flesh pellets from vertebrate dead bodies, as well as from fish and shrimp in open markets [9,36]. The hornet generally attacks its prey in flight and immediately hangs on to a support, keeps the prey’s thorax, which contains the nutritious flight muscles, and discards the rest. The flesh
pellet is then brought to the nest to feed larvae with proteins, while adults only consume sweet liquids and an energetic protein-rich liquid regurgitated by larvae [22]. Workers transport sweet liquids (sap exuding from trunks, honeydew, nectar, flesh of ripe fruit, etc.) in their crop to feed their fellows remaining in the nest by trophallaxis, including the queen and future foundresses.

### 11.4.1 Prey Spectrum

Observations made in French agricultural and natural areas showed that honey bees and social wasps may represent more than two-thirds of the preys captured by a colony, while flies (mainly hover flies, flesh and carrion flies) account for most of the rest of its diet. Other arthropods only represent a small fraction of preys, but they contrariwise belong to a wide variety of insects and spiders [35,36]. Our observations in Asian countries where the yellow-legged hornet is common showed that this predator focuses its attacks on feeding sources that provide insects more or less continuously along the day, like beehives and yellow jacket nests, carcasses and herds flown by flies, or honey flowers sought by pollinators [37]. In France, for example, umbels are such honey flowers that provide, in large number, pollinator preys (notably hover flies) to hornets. The predation impact of *Vespa velutina* on local entomofauna rapidly increases during summer with the size of the colony, and it reaches its maximum in October when workers feed the sexual brood [38]. The invasive hornet impact on the diversity and biomass of the invertebrate fauna in the invaded region is still under study [38].

### 11.4.2 Predation on Honey Bees

In the French territory, *Vespa velutina* multiplication was likely favored by the dense and wide occurrence of the European honey bee, which is one of its main preys. However, while it represents generally more than 70% of its diet in urbanized areas with poorly diversified entomofauna, it is much less captured (about 30%) in agricultural or natural and forestry sites where many other preys are available [24,35,36].

In Asia, many hornet species hunt honey bees but only several of them focus their attacks on hives. Apart from the giant hornet *Vespa mandarinia*, which attacks hives in groups, other species including *Vespa velutina* are bee-hawking hornets that predate bees individually, waiting for returning foraging bees in front of hives [22] or catching them when foraging in the field [39]. *Vespa velutina* is considered as a fierce enemy of honey bee colonies in Kashmir, India, Nepal [40], and China [41], as well as in Korea [21], countries where several other hornet species may hover at the same time in front of hives. Nevertheless, no real quantification of the impact of these hornets is available in the literature. Ken et al. [42] reported that 20%–30% of a colony of the Eastern honey bee *Apis cerana* might succumb to the predation of *Vespa velutina* in China, while losses appeared even greater for introduced European honey bees. In the presence of bee-hawking hornets, the cessation of forager activity and the consecutive stop of honey storage in the beehive are the main factors that impact the winter survival of honey bee colonies [43].
11.4.3 Honey Bee Defense Strategy

Having faced their hornet predators for long, native Asian honey bees have developed efficient strategies to defend their colonies. For example, when attacked by *Vespa mandarinia* or the yellow hornet *Vespa simillima*, the Eastern bee *Apis cerana* and the dwarf bee *Apis florea* form a ball of workers around the intruder and kill it by heat stroke [41,44] (Figure 11.1b). Similarly, *Apis mellifera cypria* in Cyprus forms a ball to kill the Oriental hornet, although the underlying killing mechanism (asphyxia) is different [26]. Observations made in the field in France showed that *Apis mellifera mellifera* is able to withstand the attack of this new predator [27,43]. However, several decades after its introduction in Asia, the European honey bee became able to display the same balling and killing behavior as *Apis cerana* although with less efficiency [41,45].

11.5 Current Invasion Range Expansion

Figure 11.2 shows the invasion progress of the alien hornet from 2004 to 2011. Since 2006, the monitoring of *Vespa velutina* presence in France is made by individual public warning through an online biodiversity database held by the MNHN [46]. The web page dedicated to *Vespa velutina* provides general information on the invasive hornet and the species with which it can be confused. Articles, fact sheets, and a slideshow are also downloadable [46]. Even if data are incomplete, notably for

![Annual distribution of *Vespa velutina* in Europe.](Figure 11.2)
In the first 2 years of observation (in addition to the still uncompleted 2010 and 2011 recordings), it is clear that the yellow-legged hornet rapidly spread out during this short period with a range expansion at around 100 km per year [7]. A few nests have also been recorded more than 200 km away from the invasion front [7], suggesting accidental human transport or migration of foundresses as reported for *Vespa crabro* by Mulhauser and Vernier [47]. First experiments showed that *Vespa velutina* foundresses can fly about 30 km in one day [36].

The first two nests were reported by a bonsai producer in Lot-et-Garonne (southwestern French counties) in 2004 [19]. Then the number of recorded nests gradually increased to reach 1,637 in 32 counties in 2009 [7,9]. The precise number of nests recorded in 2010 and 2011 is still unknown due to ongoing verification processes of public observations. In fact, misidentifications of adults and nests, mainly with representatives of other vespid species, lead to almost 30% of wrong records. The potential extent map obtained from modeling (see thereafter) would have been strongly overvalued with these incorrect records [35].

Nevertheless in 2011, already acquired records showed that the presence of the yellow-legged hornet already covered 50 French counties, corresponding to 270,000 km² of invaded area [8]. Moreover, the invasive hornet has now reached neighboring countries: Spain in 2010 [48,49] and Portugal and Belgium in 2011 [8,50].

The habitat of more than 4,000 nests correctly georeferenced between 2007 and 2009 was determined from the CORINE Land Cover database [51]. A nest distribution analysis showed that about 49% were located in urban or periurban areas, 43% in farmlands, 7% in woodlands, and 1% in wetlands. However, we must also consider that public warning is not homogeneous and that record frequency also depends on the opening of the environment, the nests being more likely visible and easily located in urbanized and open territories than in forests and closed nonurbanized environments [35,36].

### 11.6 InvasIon RIsK ModelIng

Impacts on domestic bees and native insect communities could locally challenge beekeeping economics and affect pollination services. Thus, modeling the potential invasion extent of the yellow-legged hornet around the world appeared necessary to predict regions at risk and, hence, to help with planning future surveys of potentially invaded areas and possible dedicated control measures, a prerequisite for replacing the reactive nature of current solutions with a proactive, predictive approach.

#### 11.6.1 Models

To predict the potential invasion risk by *Vespa velutina*, we used ecological niche modeling to infer suitable distribution ranges. Combining presence data of the taxon and bioclimatic variables allows modeling the species niche, while further projecting this niche geographically provides worldwide predictions of distribution suitability. For introduced invasive species, the presence data should include locations
Estimating the Range Expansion and Impact of *Vespa velutina* from both native and invaded ranges, and niche modeling tools are best multiplied than combined in an ensemble forecast framework. We used eight climatic variables for the niche modeling, extracted from the BIOCLIM database as five arc-minute grids (http://www.worldclim.org/ [52]). We considered the annual mean temperature, the temperature seasonality, the maximum temperature of the warmest month, the minimum temperature of the coldest month, the annual precipitation, the precipitation of the wettest month, the precipitation of the driest month, and the precipitation seasonality (coefficient of variation). Climatic variables are supposed to be the main contributors to species niche delimitation at large scales [53], and these variables have previously been used for insect niche modeling [54]. Temperature and precipitation seasonality are computed as the standard deviations of the monthly values. The use of climatic variables only assumes that current range limits are mainly driven by climate, which is a reasonable assumption at such a continental scale.

Climatic suitability was modeled by running eight different niche-based modeling techniques using the BIOMOD platform [55]. These models are (1) generalized linear model (GLM); (2) generalized additive model (GAM); (3) classification tree analysis (CTA), a classification method running a 50-fold cross-validation to select the best trade-off between the number of leaves of the tree and the explained deviance; (4) artificial neural networks (ANNs), a machine learning method, with the mean of three runs used to provide predictions and projections, as each simulation gives slightly different results; (5) multivariate adaptive regression splines (MARS); (6) mixture discriminant analysis (MDA), a classification method that uses MARS function for the regression part of the model; (7) generalized boosting model (GBM), a machine learning method that combines a boosting algorithm and a regression tree algorithm to construct an “ensemble” of trees; and (8) random forest (RF), a machine learning method that is a combination of tree predictors such that each tree depends on the values of a random vector sampled independently and with the same distribution for all trees in the forest. In order to evaluate the predictive performance of a species distribution model, we used a random subset of 70% of the data to calibrate every model and the remaining 30% for the evaluation. Models were evaluated using a receiver operating characteristic (ROC) curve and the area under the curve (AUC; [56]). We replicated the data splitting five times and calculated the average AUC of the cross-validations, which gives a more robust estimate of the predictive performance of each model. The final calibration of every model for making predictions uses 100% of the data available.

Presence data concerned only the variant *Vespa velutina nigrithorax*, with the French and Korean localities considered as nonnative. Two biases occurred in the presence data and necessitated a dedicated treatment: (1) records from the invaded range were by far more numerous (n ~ 1,700) than records from the native range (n = 69) and (2) the species range is still expanding in France, with more presence records close to the introduction center; so we randomly draw two localities per administrative county to avoid potential overweighting of historical invaded sites. At the time of the modeling exercise (end of 2010), the hornet occurred in 39 French counties and the random selection of at most 2 records per county resulted in a subset of 69 records—the same sample size as available for the native range. The final
In Silico Bees

11.6.2 Potential Range Expansion

The consensus map obtained from the models showed that *Vespa velutina nigri-thorax* could successfully invade many other parts of the world since the scenario of introduction through international trade that occurred in France could well be repeated [9].

Results emphasized that the area of invasion is globally discriminated from most of the Asian area of origin by its higher levels of precipitations during the driest month of the year—this represents an extension of the realized niche of the native grounds. Many countries of Western Europe exhibited a high probability of being invaded with a higher risk along the Atlantic and northern Mediterranean coasts. Coastal areas of the Balkan Peninsula, Turkey, and Near East also appeared suitable and could potentially be colonized later. All these European areas could well be reached by the still expanding French introduced population. Reduced invasion risks only concern dryer European southern regions (Figure 11.3). If accidentally introduced, the invasive hornet could also acclimatize in many other parts of the world (Figure 11.4), notably regions already invaded by *Vespula germanica*, with which it shares a similar climatic niche [9]. This yellow jacket is widely distributed in Eurasia and was (as the European *Vespula vulgaris*) unintentionally but successfully introduced in many regions of the world during the past decades; as well as being widespread, these two wasps have become significant pests in most countries they have invaded [17].

![Figure 11.3](See color insert.) Predicted potential invasion risk of *V. v. nigri-thorax* in Europe, based on ensemble forecast models using eight climatic data from WorldClim. The suitability probability is increasing from dark blue to red. (From Villemant, C. et al., *Biol. Conserv.*, 144, 2142, 2011.)
More than 200
100 – 200
75 – 100
50 – 75
25 – 49
0 – 24
Without data

FIGURE 11.4  (See color insert.) Predicted potential invasion risk of *V. v. nigrithorax* in the world, based on ensemble forecast models using eight climatic data from WorldClim. The suitability probability is increasing from dark blue to red. (From Villemant, C. et al., *Biol. Conserv.*, 144, 2142, 2011.)

11.6.3  **Invasion Risks and Beekeeping Activity in Europe**

When comparing the map of invasion risks (Figure 11.3) with the density of managed honey bee colonies in Europe and Turkey (Figure 11.5a [57,58]), we can notice that many European countries, and notably the Balkan area, combine a high level of beekeeping activity with a high risk of *Vespa velutina* acclimatization. Though ranking fourth in Europe with more than one million registered hives [59], France does not show as a whole a high level of beehive density due to the extent of its agricultural lands. However, when considering the previous ratio at the regional level (Figure 11.5b [59,60]), it appears that—in addition to the whole southwest of France—the Rhone valley, Corsica, and Alsace gather the greatest managed beehive

FIGURE 11.5  Ratio between the number of registered (or estimated) managed hives and the surface of agricultural land (beehive number per 10 km²) in (a) Europe and Turkey and (b) the French regions. Data (2007 for land surface, 2008 for beehives) from FAO agricultural resources [59]. For countries from which official data are lacking in FAOSTAT, estimated data are from the Apiservices database [60]. Beehive numbers in France (2004) are from the Gem-Oniflhor (2005) report [58] and land surface data from the 2000’s French agricultural survey [57].
numbers with the highest risks of *Vespa velutina* arrival. Moreover in Spain, which counts the greatest number of beehives (more than 2.5 million in 2008) in Europe, recently underwent the arrival of the bee-hawking hornet in the Basque country, colonizing from the French invasive population. In 2011, the invasive hornet also reached the north of Portugal. In our models, both Basque country and northern Portugal faced a high risk of invasion. On the other hand, the potential expansion of *Vespa velutina* could be constrained by the presence of a congeneric competitor [61] in countries like Albania, Greece, and Turkey, where it would face *Vespa orientalis*, another active bee-hawking hornet [26,27]. Indeed, it seems that the success of the invasion in France, explained by the ongoing colonization of new realized climatic niches, might well have been favored by a release from congeneric competition [62].

11.7 POTENTIAL CONSEQUENCES OF THE INVASION

Due to the size and the increasing number of its colonies, as well as the duration of its period of activity, the yellow-legged hornet is able to remove a considerable biomass of arthropods, so that vulnerable prey species may become threatened [36], as observed in southern countries invaded by European yellow jackets. In New Zealand, for example, the amount of preys killed by *Vespula vulgaris* and *V. germanica* has been considered to be similar to that consumed by the entire local insectivorous bird fauna [63]. However, while consuming a large variety of preys, the ecological and economic consequences of the spread of the invasive hornet would be particularly strong through its impact on honey bees and other pollinators. Such a potential impact must however be carefully assessed by comparison of faunas of the same areas before and after invasion [64]. Being able to predict the risk of acclimatization of *Vespa velutina* in a given region will thus greatly help with planning where to survey prey populations in a before/after invasion design in order to provide insights into a wide variety of impacts associated with such invasions.

11.7.1 IMPACT ON BEEKEEPING

For several decades, American and European managed honey bees have been in decline, though information for Europe remains patchy and localized [3,5,11]. In France, colony numbers are greater today when compared to 1961 populations, but have constantly decreased after reaching a peak in 2000 [65]. A wide panel of adversary factors, such as pests and diseases, pesticides, and loss of forage or beekeeping practices, are involved in this phenomenon throughout Europe [4,12–15]. The invasion of the yellow-legged hornet adds to this long list a new protagonist that will undoubtedly focus its attack on weakened bee colonies. Its damages on honey bee colonies are well established in the native range [39,45] and could be amplified in the invaded ranges. Even if the predation pressure may not be detrimental, at least bee behavior is modified; attacked hives spend more resources to face hornet attacks than to store reserves and produce honey. This could challenge the survival of the hive, especially during the winter, but also (as a direct or indirect consequence) the activity of honey production itself. Beekeepers could abandon this activity if their hives do not produce enough honey to ensure reasonable incomes. This would represent a direct loss
in free pollination services provided by the honey producers. This loss in services is associated with an economic cost, which can be estimated as the costs of funding the maintenance of the hives or of artificially pollinating crops. However, as far as we know, the true impact of the alien hornet on colony losses and honey production has not yet been evaluated in France or in its area of origin.

11.7.2 Threat to Local Entomofauna

If actively preyed, locally rare species may be endangered by the presence of the invasive hornet. Ongoing studies on the species prey spectrum comprise barcode referencing of the preys [38]. Indeed, visually determining the preys is very often challenging, as only insect thorax pieces are brought back to the nest. Consequently, barcoding is of great interest as a tool for better describing the prey spectrum. In addition, comparing these results to barcoded reference collections will allow an easy detection of rare or endangered species preyed by *Vespa velutina*.

In Europe, populations of social wasps should notably be impacted by *Vespa velutina*, as yellow jackets may represent a third of its prey spectrum. Moreover, the European hornet, whose colonies are three times smaller than those of *Vespa velutina* [66], may be threatened when competing for food with the huge colonies of its invasive congener. Further studies, however, are required to assess the prey overlap between the two species [36].

On the other hand, thoughtless reactions of the French public facing *Vespa velutina* invasion appeared to be more deleterious to the entomofauna than the pest problem itself. Uncontrolled mass trappings performed every year in France, in and outside the invaded area, by beekeepers and general public kill a huge number of nontarget insects [67,68], while uncontrolled nest destructions have a side effect by their greater impact on social vespid populations than in the past.

11.7.3 Threat to Pollination Services

Pollinators play a key role in most wild plant communities and agroecosystems [2,5,11,69]. A recent review by Potts et al. [6] reminds us that the value of insect pollination to European agriculture is estimated to be worth ~€22 billion per year [2] with 84% of European crop varieties being dependent, at least in part, on insect pollinators [70]; wildflowers being also highly dependent on insects for their reproduction, with an estimated 78%–94% of flowering species relying on biotic pollination [71]. Furthermore, the persistence of a plant community can be affected by a loss of diversity of its pollinating fauna. Thus, the functional diversity of plant–pollinator networks may be critical for the functioning of ecosystems and should be carefully protected [72,73]. By predating various taxonomic groups of pollinators, such as Apidae and Syrphidae especially, *Vespa velutina* is already interfering with native plant–pollinator networks. These impacts must soon be investigated, as they might well have more durable consequences than the already publicly known consequences on apiculture.

Furthermore, hoverflies are not only efficient pollinators but many of them are also natural predators of aphids in their larval state and thus play an important role in reducing these agricultural pests [74].
11.7.4 IMPACT ON HUMANS

Bees and social wasps have a well-known and painful sting that can occasionally cause a life-threatening allergic reaction, but death from such envenomation remains a rare event. Multiple stings that generally result from an accidental nest disturbance are even rare. Moreover, with supportive care, most nonallergic victims should be able to survive attacks from hundreds of wasps [75]. In France, there is concern from the general public when the enormous nests of *Vespa velutina* are discovered after leaf fall, often hanging from tree crowns at tens of meters above the ground [7]. As the species is common in urbanized areas, there is potential for an increase in the likelihood of humans being stung and a consequent increasing risk of allergic reactions [36]. However, the high location of most of the nests limits the risk of colony disturbance, and so far the rate of Hymenoptera stings appears not to have increased in regions colonized by the yellow-legged hornet [76].

11.8 CONTROL

When they happen to shelter in goods that get shipped, hibernating wasp foundresses have indeed a relatively low probability of being detected with standard protocols used for custom inspection [77]. On the other hand, as quoted by Thomas [78] for invasive yellow jackets in New Zealand, mass destruction of hornet foundress queens in spring seems to have virtually no effect on nest density in the following summer months [17,36,63,78,79], while side effects on nontarget species may be important [68]. The best control measure is to kill off a colony by spraying permethrin inside the nest after dark, when foraging activities cease. The nest is then removed and burned. However, nests are often difficult to locate before leaf fall, when sexual progeny is already produced [36]. While it is impossible to stop or slow the natural spread of the invasive hornet, the unique possibility is to use specific baited mass traps to protect hives from very fierce hornet attacks. The development of such specific traps is still under investigation [80], while it is too late now to consider any efficient global eradication methods for this bee-hawking hornet. Efforts have now to be made to slow down the range expansion and to mitigate the impacts on domestic and wild pollinators, with priorities defined from the modeled invasion risk across Europe.

11.9 CONCLUSION

Social wasps represent a particularly destructive and successful group of invasive invertebrates. Their sociality, including a number of unique mechanisms enhancing survival and reproduction, is certainly the key factor that substantially contributes to their success as invaders [81]. Their main general advantage may be the flexibility arising from having both individual and colony responses. This confers upon them a remarkable efficiency to compete and exploit food sources, buffering against environmental changes. They develop populous colonies with an effective predator defense and produce numerous foundresses that provide large dispersal capacity [81,82].
Given the potential economic and biological impacts of the invasive yellow-legged hornet, ongoing developments are focusing on better understanding the invasion dynamics by developing modeling approaches to predict the rate of range expansion, which is necessary for a temporal risk assessment and the further implementation of effective management strategies [83,84].

Furthermore, it would be of great interest to investigate the perturbations *Vespa velutina* might engender to the complete pollinator community. Theoretical approaches could be used, modeling theoretical mutualistic networks of plants and pollinators and applying an orientated change in the structure of the plant–pollinator network (mimicking depredation by the hornet on some of the pollinator agents). Results would help to understand how these changes might modify stability properties and architecture of the whole mutualistic network.

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