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Review

The invasive hornet *Vespa velutina*: distribution, impacts and management options

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Abstract: The Asian yellow-legged hornet *Vespa velutina* is an invasive alien species introduced and widespread in several countries of Europe and Asia. Its diffusion generates relevant environmental and socio-economic impacts. Environmental impacts include threats to the native insect biodiversity and the pollination ecosystem services. Socio-economic impacts include threats to the apiculture sector, economic consequences for the adoption of management strategies, social concern and health issues. Different options were developed and adopted for (i) preventing the introduction of *V. velutina*, (ii) early detecting its presence, (iii) eradicating populations at the initial stage of invasion or (iv) controlling populations for limiting and mitigating its impacts. The aim of this review was to provide an updated overview about the distribution, impacts and options for managing *V. velutina* populations, through a literature review of the published academic documents. Moreover, this study highlights that some topics received little attention (impacts of *V. velutina* on the biodiversity, on the pollination ecosystem services, on the economy) or require further research efforts (effective control methods for *V. velutina*); therefore, future research should be directed towards filling these gaps of knowledge.

Keywords: yellow-legged hornet, wasps, spread, monitoring, eradication, control, pests

1. Introduction

Invasive alien species are a serious threat to biodiversity and human activities [1] whose accumulation in the last centuries shows no sign of saturation for most of the introduced taxa [2]. Among insects, social wasps and hornets proved to be successful invaders, with 34 species introduced worldwide until 2010 and, among these, at least seven recorded as invasive species [3]. One of the introduced invasive species is *Vespa velutina* Lepeletier, 1836 (Hymenoptera: Vespidae), a hornet introduced in Europe, South Korea and Japan whose spread poses concern for the conservation of insect biodiversity, pollination ecosystem services as well as human activities, economies and health [4, 5]. From its introduction onwards, the knowledge about the species continually increased, with yearly new information on the biology, ecology, population dynamics and impacts of the species as well as on the techniques for monitoring its presence or controlling its spread (Fig. 1) [6, 7]. Therefore, the aim of this review is to provide an up-to-date summary of the knowledge about the distribution of *V. velutina*, its impacts, and the options for limiting its spread, with a brief insight into its biology and life cycle.

2. Review Methodology

The literature review was performed by searching a defined combination of words in the title, abstract and keywords of the documents indexed in three online databases (Scopus, Web of Science and CAB Direct). The searching string adopted for this purpose considered the following keywords: *Vespa velutina*, *Vespa velutina nigrithorax*, Asian yellow-legged hornet, Asian hornet. An overall number of 328 unique documents were found in the period 1975–2021, both considering indexed documents and references cited within them. Of these, 28 documents were excluded since unconnected to the species of interest. The remaining 300 documents were analysed for evaluating the covered research topics and their spatial distribution at the global level. For this purpose, each record was classified on the basis of the continent in which the research was conducted and the covered topics: (1) distribution, (2) Species Distribution Models or spread modalities, (3) impacts on biodiversity, (4) impacts on ecosystem services, (5) impacts on apiculture, (6) impacts on human health, (7) impacts on the economy, (8) positive effects, (9) monitoring, (10) eradication, (11) control, (12) genetic, (13) viruses and parasites, (14) biology, (15) taxonomy, (16) reviews on the species and (17) other topics not covered by the previous categories (Fig. 1). Of the analysed documents, 19 were in languages other than English and 30 did not have accessible full text. Finally, based on their relevance, 140 documents were selected for the preparation of this review.

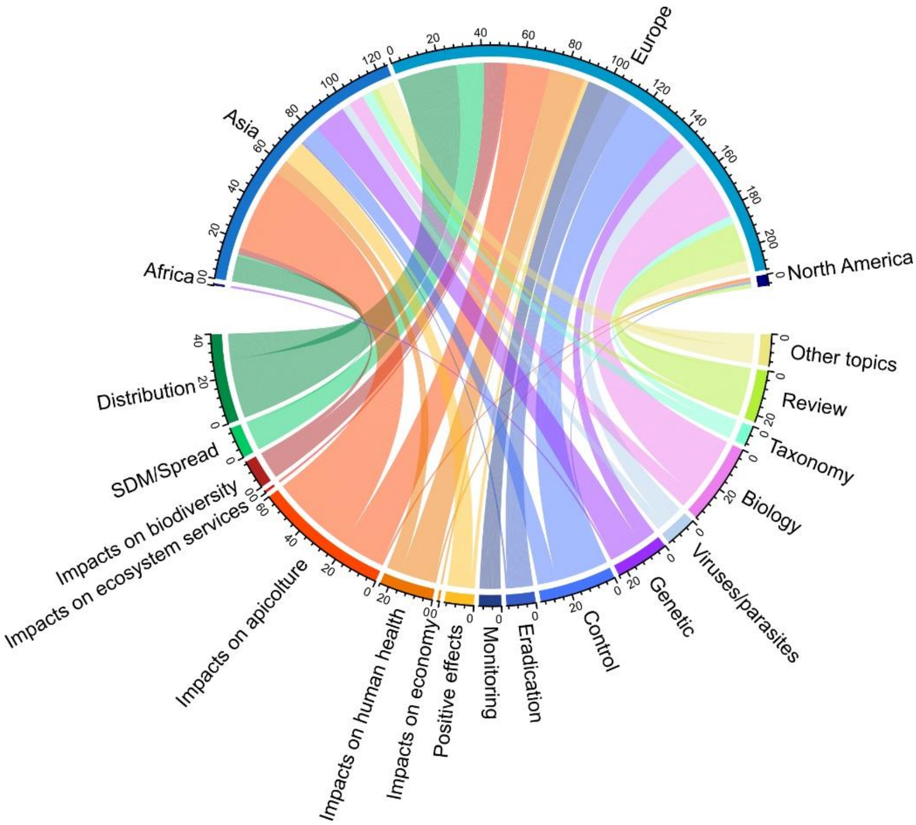

Figure 1 Research topics concerning *V. velutina* covered in the literature in the period 1975–2021 in relation to the continent in which the research was conducted.

3. Biology and life cycle

Morphological identification

The subspecies introduced in Europe and other countries of Asia where the species is not native, *Vespa velutina nigrithorax* (du Buysson, 1905) [8–11], is characterised by a dark-brown almost black thorax. The abdomen of the females, which is composed of six apparent tergites that correspond to the II-VII gastral terga (the first morphological segment, the propodeum, is fused with the thorax), is characterised by three tergites almost black with a yellow margin at the end (II-IV) and a tergum (V) almost yellow. The legs are dark, except for the tarsi that are yellow. The dorsal and ventral parts of the antennae are respectively black and dark-brown (Fig. 2a) [12, 13]. The absence of the sting and longer antennae allows to discriminate males from workers and queens. Although individual weight increases throughout the year, body weight provides an indication for caste differentiation between workers (mean ± SD of wet weight ranges from 188.8 ± 44.9 mg in June to 386.4 ± 88.3 mg in November) from queens (from 624 ± 15.2 mg in September to 721.3 ± 73.2 mg in November) [14].

Life cycle

As for the other social wasps, the life cycle of a colony of *V. velutina* could be divided into four different phases: the foundation, the worker, the reproductive and the intermediate phase [13]. During spring, mated queens that survive the winter begin the foundation of the initial nest, of small size, composed of a single comb and used by the queen to layer the eggs of the first workers [4, 5]. The length of the development stages was estimated in 48.1 days (13 days for the eggs, 15.8 days for the larvae and 19.3 days for the sealed brood) [13]. During the worker phase (Fig. 2b), the emerged workers will then contribute to the development of the colony, by enlarging the nest, recovering proteins for feeding the brood, protecting the colony from enemies, and contributing to cleaning and ventilation [4, 5, 15]. The reproductive phase starts with the emergence of males that generally occurs from early September on, about 15 days before the emergence of gynes (potential reproductive females). Reproductive castes reached their maximum numbers in November

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(mean number of gynes: 191 ± 195.7), and most of them left the colony before the end of this month [14]. During winter, the colony gradually collapses, although in Spain nests recovered in January still contained live specimens including gynes [16]. Winter active colonies were also observed in Italy (Lioy S., pers. comm.).

The dimensions of the colony vary throughout the year: the number of combs increases up to a mean of eight combs in December; and the total number of individuals produced in a year by the colonies increases up to a mean of 6151 individuals in November, with a maximum value of 13,340 individuals. The initial nest built by the queen could be relocated by the workers during the annual life cycle of the colony. A study conducted in France observed the shape and dimension of the first comb in 49 nests of *V. velutina*, and about 70% were considered relocated colonies [14]. When a colony is relocated, it is commonly named secondary nest, to distinguish it from the primary nest built by the queen and enlarged by the workers. The distinction between primary and secondary nest could only be performed by the internal morphological analysis of the structure of the nest, and not from the size of the nest or the time of the year. Indeed, primary nests are characterised by a first comb of irregular structure, with the embryo comb still visible at its centre, while secondary nests by a first comb of regular shape [14].

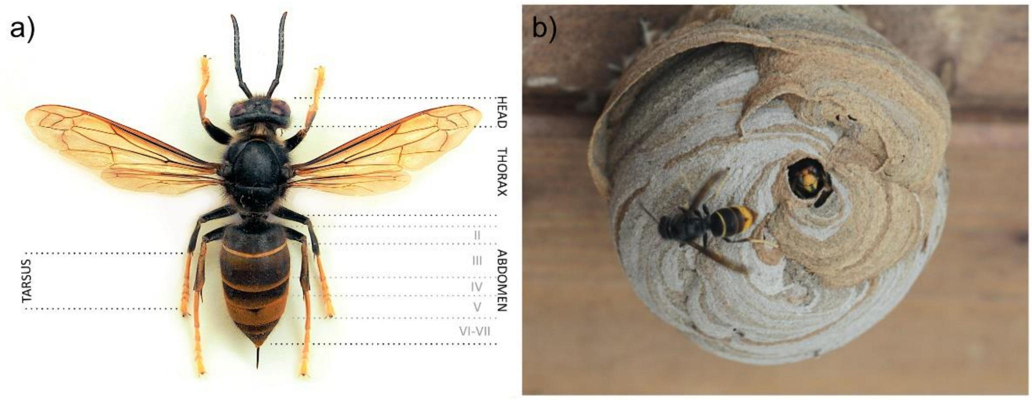

Figure 2 (a) Female specimen of *V. velutina nigrithorax* from Italy, with an indication of the main morphological parts that allow species identification (photo by S. Lioy). (b) Nest of the species observed in June (photo by M. Porporato).

4. Distribution

Native range

Vespa velutina is native to south-east Asia and occurs in Afghanistan, Bangladesh, Bhutan, China, Hong Kong, India, Indonesia, Laos, Malaysia, Myanmar, Nepal, Pakistan, Taiwan, Thailand and Vietnam (Fig. 3) [13, 18–23]. The species presents 12 colour subspecies across its native range, four on the mainland (*auraria*, *variana*, *divergens* and *nigrithorax*, the latter introduced in Europe, South Korea and Japan) and eight on islands (*flavitarsus*, *karyni*, *velutina*, *ardens*, *sumbana*, *floresiana*, *timorensis* and *celebensis*) [13]. Some authors [19, 24] recognised the subspecies *pruthii* as distinct subspecies, while others suggested to treat it as a synonym of *auraria* due to their minor colour differences and their range overlap [13].

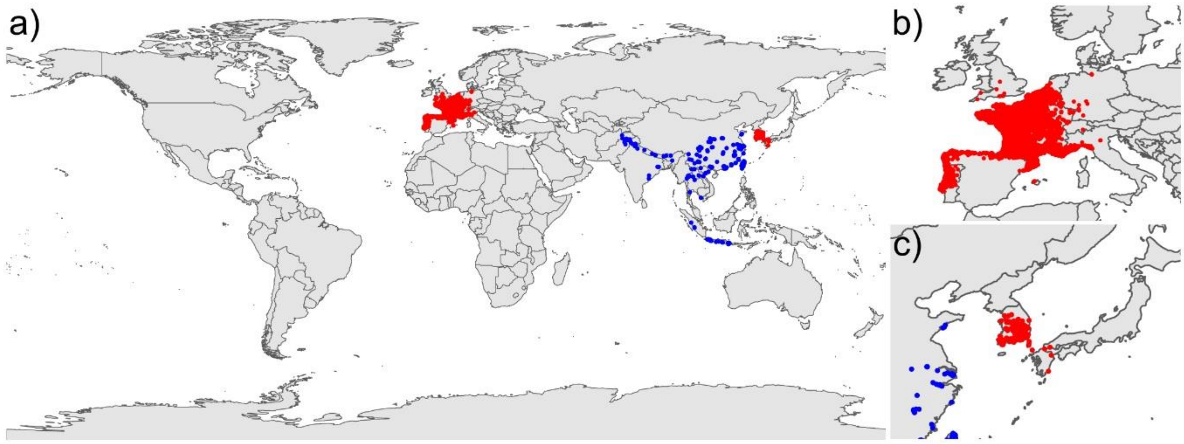

Figure 3 (a) Worldwide observations of *V. velutina* in its native range (blue) and in the areas of introduction (red). (b) Details of the alien range in Europe. (c) Details of the alien range in Asia. Records of *V. velutina* were obtained by aggregating data collected by the authors of this review with observations derived from GBIF [17] and from the literature.

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Alien range in Europe

V. velutina was accidentally introduced to Europe in 2004, probably through boat transport of horticultural products from an area between the Chinese provinces of Zhejiang and Jiangsu [4, 9, 25]. Following the introduction, which occurred in south-west France, the species spread across various European countries, with the French population acting as a source of diffusion or a source for new introductions [26]. The observed spread of *V. velutina* in Europe was impressively fast, probably due to a diffusion process that encompassed natural dispersal and human-mediated transportation [27–30], which in some cases (i.e. Portugal) has been correlated with the motorway traffic [31]. Hereafter, a summary of the evolution of *V. velutina* colonisation across European countries.

France. Detected for the first time in the department of Lot-et-Garonne in 2004 [4, 32], in the following years the species started to spread in the neighbouring departments [33] colonising an area of 190,000 km^2 by 2010 [34], 360,000 km^2 by 2012 [35] and mostly all the country by 2017 [29]. The estimated spread rate observed in France was 78 km/year [29]. In an area of western France (Andernos-les-Bains), nest density increased in the period 2007–2014 up to 4.81 nests/km^2 (considering both urban and non-urban areas) [36], and up to 10.23–12.26 nests/km^2 considering only urban areas [36, 37].

Spain. Detected for the first time in 2010 in an area close to the border with France, in Guipuzcoa and Navarra provinces [38–40], the species continued to spread westwards and eastwards until reaching in 2012 Galicia [41] and Catalonia, respectively [42]. *V. velutina* was also observed in the Balearic Island of Mallorca in 2015 [43], but here the species has been declared eradicated after some years of management [44].

Portugal. Detected in the Minho province in 2011 [45], in the following years *V. velutina* expanded its range southwards at an estimated spread rate of 37–45 km/year [31, 46], and by 2020, 62% of the mainland Portugal was colonised [46]. Urban nest density was estimated at the local scale in 5.4 ± 3.3 nests/km^2 [46].

Belgium. The species was firstly observed in 2011 in Wallonia [47] but the first nests were reported only in 2016 and 2017 in Wallonia and Flanders, respectively. In the following years, the population spread rapidly from west to east [48].

Italy. *V. velutina* was firstly spotted in 2012 in the Liguria region, in an area close to the motorway [49], while the first colonies were detected in 2013 in both Liguria and Piedmont [50]. In the following years, the species spread along the coastline of Liguria, increasing the colonised area from 205 km^2 in 2013 to 930 km^2 in 2015 at an estimated spread rate of 18.3 ± 3.3 km/year, reaching densities of 2.9–3.5 nests/km^2 (considering both urban and woodland areas) [27]. In 2016 and 2017, the species was observed in two areas at several hundred kilometres from the main invaded range, respectively in Veneto and in an area between Tuscany and eastern Liguria, but only in the latter case *V. velutina* established viable populations [5]. In years 2020–2021 a new outbreak was also reported in Lombardy (Lioy S., pers. comm.). Genetic studies confirmed that Italian populations most likely derived from the eastern spread of the species from France [51].

Germany. The species started to colonise the south-western part of Germany in 2014 [52]. In 2019, *V. velutina* was observed in Hamburg, several hundred kilometres of distance from other colonised areas [53]. The introduction in northern Germany probably occurred by the long-distance transportation of the species from the European population rather than a new introduction from Asia [54].

UK. *V. velutina* was firstly observed in 2016 in Tetbury [55], and in the following years, few nests were periodically located in various localities in southern England [56]. Based on their geographic distribution and on microsatellite analyses, it is supposed that all UK colonies found up to 2019 were derived from separate introductions from the European population, since none of the discovered nests were directly descended from nests of the previous years found in the UK [56]. The species has also been present in the Channel Islands since 2016, due to the natural spread or the introduction of the species from France [11].

Other countries in Europe. Recently, *V. velutina* continued to spread in Europe and it was observed in other countries such as the Netherlands, Switzerland [5], and Luxemburg [57]. Moreover, a single specimen was reported from Ireland [58].

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Alien range in Asia

Besides the European alien range, *V. velutina* has established expanding population also in two other Asian countries.

South Korea. The species was firstly discovered in 2003 in the city of Busan [12]. From the site of introduction, the species spread northwards at a rate of 10–20 km per year [59]. Independent introductions probably helped *V. velutina* to spread into South Korea [60].

Japan. *V. velutina* was spotted for the first time in 2012 on Tsushima Island [61, 62], and afterwards on Kyushu Island in 2015 [63] and Iki Island in 2017 [11, 64]. The genetic similarity of the individuals from the Japanese and South Korean populations suggests that *V. velutina* in Japan originated from a second event of introduction from the population in South Korea [10, 11].

Risk of invasion in other countries

After its introduction and initial spread, several studies investigated the potential invasion risk of the species, mostly based on the assessment of the climatic suitability [25, 65] or by a combination of multiple factors (e.g. climatic and habitat variables) [66, 67]. Most of the continents are characterised by temperate and subtropical areas with suitable climatic conditions for *V. velutina*, including the eastern part of North America, Europe, East Asia, and small areas in South America, South Africa and Australia [25, 65]. In Europe, many countries along the northern Mediterranean and Atlantic coasts, including wide areas of the UK [68] as well as coastal areas of the Balkan Peninsula and Turkey, exhibited a high probability of being invaded [69], and the observed spread in years 2011–2015 confirms the accuracy of the predictions made with data from the early stage of the invasion [70]. Furthermore, climate change could contribute to further increase the invasion risk, particularly in the northern hemisphere [71].

5. Impacts

Environmental impacts

The presence of *Vespa velutina* outside its native range is posing a concern due to the multiple impacts that the species could generate on native biodiversity. This could occur by the combination of different mechanisms: predation, competition and alteration of the pollination ecosystem service [4, 5].

The species preys upon other insects for feeding the brood, acting as a generalist predator [15, 34, 72, 73]. The analysis of its diet in an invaded area of France revealed that a single colony could prey upon at least 159 different species (11 orders and 43 families of insects, three families of spiders and four families of vertebrates), consuming about 11.32 kg of insect biomass in one season. Among insects, the mostly consumed preys are Hymenoptera (60.1%), particularly honey bees (38.1%) and social wasps (19.7%), followed by Diptera (29.9%) and other less frequent groups such as Lepidoptera, Hemiptera, Coleoptera, Mecoptera and Orthoptera [72]. The food spectrum could differ in relation to the habitat that surround *V. velutina* colonies, with a higher proportion of social wasps and flies in woodlands (respectively 28.3% and 31.5%) than in urban areas (7.8% and 17.2%), and a higher presence of bees in the latter (66.6% in urban areas and 33.4% in woodlands) [34].

Another impact mechanism to be considered is the competition, which may occur between *V. velutina* and those species with a similar ecological niche, namely, other wasps and hornets. Different mechanisms may generate competition, such as the overlap in the trophic niche between the invasive and the native species [74], the overlap in the seasonal phenology [75], or higher performance of the invasive species in terms of reproductive potential [76], boldness/exploration scores [77] and aggressiveness scores over smaller species [78]. Reproductive interference has also been observed in Japan between *V. velutina* and the native *V. simillima*, with 43% of native queen species inseminated by males of the invasive species and, of these, 28% having only sperms of *V. velutina* [79]. Moreover, a negative correlation in the abundances of *V. velutina* and three other native Vespa species of Japan (*V. simillima xanthoptera*, *V. analis* and *V. mandarinia japonica*) suggest a possible negative effect posed by the presence of the invasive species due to competition and/or predation [80].

Despite its importance, the impact of *V. velutina* on pollination has rarely been analysed. An observational study conducted in Spain demonstrated, for the first time, that the presence of the invasive hornet could induce changes in the foraging behaviour of several groups of pollinators (honey bees, bumblebees, small hymenopterans and syrphids) due to its preying behaviour on flowers, thus affecting the abundance of pollinators and their flower visitation frequency. This could generate an indirect effect on the quantity of pollen deposited on stigmas of a wild plant, *Mentha suaveolens* [81].

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Socio-economic impacts

Besides the environmental issues, the presence of *V. velutina* generates several not neglectable socio-economic impacts such as consequences for the beekeeping sector, management costs and health issues.

Honey bees are among the most insects preyed by *V. velutina* [15, 34, 72, 73]. This could be related to the olfactory attraction produced by honey bee colony odours (pollen and honey) and pheromones (geraniol, the honey bee aggregation pheromone) that may signal a high density of prey [82] or due to a combination of visual and olfactory cues that attract the species [83]. *V. velutina* prey on honey bees mostly by hovering in front of the hive for catching the returning bees [84]. Once a honey bee is caught, the hornet removes all the less protein portions of the insect, keeping only the thorax that is brought back to the colony for feeding the larvae [15]. Individuals of *V. velutina* are able to revisit the apiary more time during the day, suggesting a learning behaviour that could benefit the foraging performance [85]. Predation pressure on honey bees increases during the season (in France from July to October) according to the increase in the population of *V. velutina* colonies [84]. Moreover, predation pressure could vary in relation to environmental conditions such as temperature, humidity or wind speed [86]. The predation success increases in relation to the number of chasing hornets, with peaks around nine hornets per hive [84]. The overall observed predation success in South Korea was 80%, with peaks up to 96% in September [87]. This intensive predation activity is a source of oxidative stress in honey bees [88] and generates foraging paralysis that, in turn, could increase the homing failure of returning honey bees due to higher predation success of the hornets [89]. With time, the predation pressure could generate the collapse of honey bee colonies due to a reduction of the population and of the stocks of honey and pollen used by the honey bees for surviving the winter [5].

Unlike colonies of *Apis cerana*, which occur in sympatry with *V. velutina*, colonies of *Apis mellifera* are more susceptible to its predation pressure due to (i) a lower performance or absence of defensive behaviour, such as the heat balling [90, 91] and the wing shimmering [92, 93], (ii) the inability to eavesdrop the alarm pheromone of the hornet [94, 95], (iii) the lower number of guard bees at hive entrance [92] and (iv) the lower speed rate adopted by *A. mellifera* for entering inside the hive [92]. In fact, the hawking success of *V. velutina* is three times higher for *A. mellifera* foragers than that for *A. cerana* [92]. Concerning defensive behaviour, several studies have investigated the heat balling behaviour, in which honey bee workers respond to hornets' attacks by forming a ball of bees around the hornet with which they manage to kill the threat owing to the increase in both core-temperature and carbon dioxide concentration [90, 91]. Workers of *A. cerana* are better reacting with the heat balling behaviour to *V. velutina* attacks, due to a greater number of individuals engaged in this behaviour (32.2 ± 3.2 workers for *A. cerana* and 22.7 ± 3.1 workers for *A. mellifera*) and a higher core temperature reached by the ball (45.6 ± 0.1°C for *A. cerana* and 44.3 ± 0.2°C for *A. mellifera*) [90].

Besides the direct impacts on the beekeeping sector, the presence of *V. velutina* in invaded countries also generates massive economic costs for developing management practices, particularly those related to the implementation of nest destruction activities. It has been estimated that control activities performed in France between the years 2006–2015 cost about €23 million and, if the species continues to spread colonising all the areas predicted to be suitable, yearly cost could reach €29.5 million in three invaded countries of Europe (France, Italy and UK) and €31.4 million in two invaded countries of Asia (South Korea and Japan) [96].

As in the other eusocial wasps, workers of *V. velutina* tend to defend their colony in case the insects feel threatened, becoming a potential source of danger for people. Defensive behaviours could occur when people approach within three metres from the nest and could last as long as the distance is not increased to a few tens of metres, despite in some cases, few hornets could still attack up to 300 m [97]. Defensive behaviours are more frequent towards aggressors dressed in dark colours [98]. After stings, a series of reactions of different severity could occur, from allergic to toxic reactions that could lead to anaphylaxis and multiple organ failures [99–101] that in some cases could lead to fatal events [102, 103]. Moreover, ocular lesions could occur due to the projection of venom into the eyes of people: 29 cases were reported in France until 2019, and 80% of these were associated with occupational exposure due to nest destruction activities [104]. However, determining whether the presence of *V. velutina* causes a general increase in Hymenoptera stings is not always straightforward, also because in most cases, it is impossible to determinate the responsible species. A review of the data registered in the French Poison Control Centers highlighted the absence of a correlation between the increase in *V. velutina* populations and the number of Hymenoptera stings during the initial phase of invasion [105]. However, a study conducted in Spain reported that *V. velutina* has become one of the common cause of anaphylaxis [103], while an analysis of cases and emergency calls in South Korea demonstrated that *V. velutina* became one of the most prevalent sources of issues as the species was more widespread in the country and abundant in urban areas [106]. Furthermore, the global increase in temperature due to climate change could increase the areas of suitability for *V. velutina* [71], increasing thus the risks for humans in relation to a greater diffusion and abundance of Hymenoptera in the environment [107].

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Potential positive effects

Despite the many negative impacts associated with the presence of *V. velutina*, some studies highlighted that the species might generate benefits or positive effects (Fig. 1). For example, studies conducted in the native range showed that the species could contribute to pollination [108, 109] and seed dispersal [110, 111], or could be exploited as a food resource by humans [112, 113]. Recent studies from the invaded range highlighted that the abundance of *V. velutina* might be considered as a promising alternative source of chitin [114], while the antimicrobial proprieties of their nests might be used against pathogenic bacteria [115]. Moreover, *V. velutina* venom could be extracted and used for several purposes. For example, it can be used for treating allergy and/or anaphylaxis through immunotherapy [116], for obtaining peptides for the development of new antioxidants and antimicrobial agents [117, 118], or for obtaining anti-inflammatory compounds [119].

6. Management options

Tackling the spread of invasive alien species requires the adoption of different strategies based on the stage of invasion and the objectives to be achieved. Generally, the options to be considered for this purpose could be divided into four categories: (i) prevention, (ii) early detection, (iii) eradication and (iv) control [120]. These options are also suggested for managing *Vespa velutina* introductions and spread [5].

Prevention

Preventing new introductions of *V. velutina* queens is hardly feasible due to the number of drivers and pathways with which the species could be transported, such as contaminant of plants, wood, nursery or habitat material, or as hitchhikers on containers, boats or vehicles [121, 122]. However, including *V. velutina* in regulation's "black lists" as occurred in Europe (where the species is designated as invasive alien species of Union concern in all European countries; EU No 1143/2014, Reg. EU No 1141/2016) or in Japan (designated under the invasive alien species act) [64] could help to prevent new introductions of the species besides to adopt eradication/control measures. In fact, listing *V. velutina* as a species capable of generating massive impacts foresees the adoption of transportation restrictions, and action plans on the pathways of introductions and other related measures for raising awareness in people and stakeholders that may contribute to prevent new introductions.

Early detection

In countries or areas not yet colonised by *V. velutina*, surveillance strategies could contribute to early detecting the arrival of the species for attempt an eradication of the populations at early stages of invasions. For example, a monitoring strategy was established in Italy in 2007, several years earlier than the appearance of the species in the country, allowing to intercept a first specimen in 2012 [49] and detecting the first hornets and nests in the following year [50]. Surveillance strategies mostly adopted for monitoring the presence of *V. velutina* encompass (i) citizen science monitoring schemes and (ii) the engagement of relevant stakeholders such as the beekeepers, for monitoring the presence of *V. velutina* through monitoring traps and observations in apiaries [5, 7].

Citizen science projects were specifically developed for monitoring *V. velutina* in several countries worldwide [7] including, as non-exhaustive examples, Belgium [48], France [67], Italy [30], Luxembourg [57], Portugal [46, 123], Spain [44] and the UK [124]. The collection of reports through citizens could be based on website solutions, smartphone applications or hybrid systems [7]. Moreover, citizen science monitoring schemes could focus on detecting several wasp species simultaneously, such as the system developed in Sardinia (Italy) for monitoring the spread of *V. crabro* and detecting the arrival of *V. velutina* [125]. Additionally, the engagement of non-experts does not negatively affect the reliability of the collected data [123].

Beekeepers and beekeeper associations have been engaged in monitoring the presence of *V. velutina* mostly by organising local networks by using monitoring traps [49, 126, 127] or by reporting observations of nests and adults in the environment and near apiaries [5], the latter in relation to the attractiveness exerted by honey bees [82, 83]. Monitoring traps, either commercial or handmade, are nowadays unselective for *V. velutina* since the target species represent about 1% of all trapped insects [126, 127]. Although automatic detection systems are not widely adopted, the direct observation of hornets in apiaries could eventually be supported by automatic systems for the recognition of the species [128], particularly at the early stage of invasion when the number of hornets preying on honey bees is restrained, which implies a low probability of observing the species by the beekeepers.

Finally, rapid molecular methods have been developed for the in-field and laboratory identification of the species [129]. These tools would be useful for the determination of the species from damaged/incomplete specimens or immature life stages when morphological analysis is not feasible.

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Eradication

Once locally established in a new area, *V. velutina* could be eradicated by detecting and removing all the present nests, ideally before the reproductive phase of the colonies. The observation of multiple hornets preying in apiaries or feeding on flowers is an indicator of the presence of a colony, most likely within 1 km of distance [130]. Once discovered, colonies of *V. velutina* could be dissected and analysed for assessing their reproductive output and understanding if the next generation of queens was produced and dispersed into the surrounding environment [56]. Follow-up monitoring in the subsequent years should then be performed for confirm eradication, by establishing monitoring areas in the environment around the removed colonies with an extension that considers the dispersal capability of the species [30]. Successful examples of eradication are the cases from Mallorca Island (Spain) [44] and the different incursions managed in the UK [56].

Different techniques for improving colony detectability could be adopted for eradication. Techniques could be divided into (i) methods for tracking the flight of *V. velutina* foragers back to their colonies and (ii) methods for spotting *V. velutina* nests. Effective tracking methods currently adopted for tracking *V. velutina* encompass the following techniques.

– Harmonic radar tracking: hornets are trapped in apiaries, equipped with a passive (without battery) lightweight transponder (~15 mg) and tracked with a radar system [131–133] either in flat or complex environments characterised by a different degree of obstacles and slopes [134].

– Radio tracking: hornets are trapped, equipped with an active transmitter (~150–312 mg) and tracked manually in complex environments with a tracking receiver [135].

– Visual tracking and triangulation of flying directions: hornets are attracted by multiple baited food stations, followed on sight, and finally, the colonies are discovered by triangulating the flying directions [44].

A network of unmanned aerial vehicles (UAVs) has also been proposed as a tracking method for tagged hornets [136] but, to the best of our knowledge, experimental confirmations are currently lacking.

In addition to the tracking methods, other techniques for improving the probabilities of spotting *V. velutina* colonies could be adopted, particularly when nests are covered or masked by leaves. These techniques rely on the use of thermal imaging cameras to detect nest position, either with an operator acting from the ground [137] or with cameras mounted on drones for an aerial survey [138].

Control

Since no control method, taken individually, allows an effective control of the species, the control of *V. velutina* populations currently relies on a series of measures to limit or mitigate its environmental and socio-economic impacts [5, 64]. Due to their eusociality, an effective control of social insects should mainly target the colony rather than individuals [64]. For this reason, despite the associated costs [96], long-term nest destruction strategies are one of the most adopted techniques for both limiting the impacts of *V. velutina* and providing an answer to the requests of citizens asking for nests' removal [5, 37, 139]. Nest destruction is commonly performed by introducing insecticides, such as pyrethroids, directly inside the nests [5, 64, 139]. Steam injection has also been proposed as an alternative green control method for destroying *V. velutina* colonies [140].

A complementary method to nest destruction, often adopted in the invaded areas for reducing the number of individuals, is the use of traps for trapping queens or other castes [139]. Spring queen trapping is one of the most popular adopted techniques; however, its effectiveness is questionable since (i) few surviving queens can establish colonies able to produce hundreds of new reproductive individuals [37] and (ii) the available traps are not selective (on average, the number of *V. velutina* trapped is 1% of the overall number of insects caught in the traps). Trapping workers also appear ineffective since colonies are composed by several hundreds of individuals that could compensate for the losses [64]. Moreover, several studies have suggested possible side effects of trapping on native entomofauna, also toward those species or groups that are less affected by *V. velutina* predation, such as *V. crabro*, Lepidoptera or Coleoptera. Therefore, further research is requested for improving trapping methods [37, 126, 127, 141, 142].

Toxic baits are among the methods examined for the control of *V. velutina* [64, 139]. The approach relies on the behaviour of workers to collect proteins to feed the larvae, a behaviour that can be exploited to convey toxic substances to the colonies. However, the use of insecticides or insect growth regulators (IGRs) severely limits their use due to the potential negative effects on non-target species, the potential dissemination of substances in the environment (since nest position is unknown), together with legislation restrictions and the lack of specific information on their application to *V. velutina* [64, 139].

Different methods have also been developed by the beekeepers and adopted to mitigate the impact on honey bees, such as hive muzzles [139, 143, 144] and electric harps [139]. Muzzles prevent the hornets from getting close to the hives,

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reducing the stress of bees and their foraging paralysis [144, 145]. Electric harps are capable of electrocuting hornets without affecting the bees [139].

Other potential control methods have been suggested in the literature, such as the biocontrol through predators or parasites. These methods currently appear unsuitable for a large-scale control of *V. velutina* and therefore not covered within this review.

7. Conclusions

This review provides an update on the distribution, impacts and options currently available for managing *V. velutina* populations in the invaded countries. The observed spread from the early 2000s demonstrates that the species could rapidly increase its range, helped by multiple introductions due to human-mediated transportation. In the invaded range, *V. velutina* could generate massive impacts on the environment (biodiversity and pollination service) and the society (beekeepers, public administrations, public health). Several options and strategies could be adopted to prevent or mitigate *V. velutina* effects: including *V. velutina* in actionable lists (as already performed in Europe and other invaded countries of Asia); early detect new introductions by engaging citizens and stakeholders (i.e. beekeepers) in monitoring *V. velutina* presence; attempt eradication at the early stage of invasion, thanks also to the new technologies developed for locating nests; control *V. velutina* populations preferring strategies for targeting the colonies (e.g. nest removal). Additionally, the literature review highlighted that some topics received little attention or required further research efforts. For example, the impacts of *V. velutina* on the native entomofauna, on the pollination ecosystem services, and on the economy were investigated to a lesser extent than the impacts towards honey bees. Moreover, no control method, taken individually, allows to effectively interrupt the spread and impact of the species; therefore, further research is still needed to fill these gaps of knowledge.

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