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Global economic trade and climate change influence stinging social wasp distribution and appropriate venom immunotherapy

Abstract: Social wasps (Hymenoptera: Vespidae) constitute an important group of predatory insects that are particularly well-suited for transportation beyond their native habitats into new environments through commercial trade, a phenomenon that is strongly influenced by climate change. As they are predominantly predators dominating numerous natural food chains of insects, these alien species can exert serious and devastating impacts on the native entomological fauna of the new habitats they invade. Additionally, because species belonging to the subfamilies Polistinae and Vespinae possess potent stings for defending their colonies, invasive social wasps represent a public health concern due to the wide range of allergic reactions they can elicit in humans. In this paper, we review the principal invasions of social wasps into novel habitats around the world and highlight the need for efficient immunotherapies to address the allergological risks posed by alien species. We detail the recent invasion of the Asian *Vespa velutina nigrithorax* in Europe, where the native *Vespa crabro* is found, as well as the increasing presence of *Vespa orientalis* in northern Tuscany, Italy. We discuss the optimal immunotherapy required in cases of human stinging incidents and describe how this relates to the phylogenetic distance between the three species.

Riassunto: Il commercio globale e i cambiamenti climatici influenzano la distribuzione delle vespe sociali e l'immunoterapia con il veleno. La globalizzazione dell'economia ed i cambiamenti climatici stanno influenzando la distribuzione delle vespe sociali e di conseguenza la scelta del veleno per l'immunoterapia specifica. Le vespe sociali (Hymenoptera: Vespidae) costituiscono un importante gruppo di insetti particolarmente adatti a essere trasportati dal loro habitat originario in nuovi territori attraverso gli scambi commerciali e i cambiamenti climatici favoriscono questo fenomeno. Essendo prevalentemente predatrici, queste specie aliene possono esercitare impatti gravi e devastanti sulla fauna entomologica autoctona nei territori che stanno invadendo. Inoltre, poiché le specie appartenenti alle sottofamiglie Polistinae e Vespinae possiedono potenti pungiglioni per difendere le loro colonie, le vespe sociali invasive rappresentano un problema di salute pubblica a causa delle reazioni allergiche che possono provocare nell'uomo. In questo articolo passiamo in rassegna le principali invasioni di vespe sociali in nuovi territori e sottolineiamo la necessità di avere a disposizione delle immunoterapie efficaci per affrontare le reazioni allergiche causate da queste specie aliene. Descriviamo in dettaglio la recente invasione dell'asiatica *Vespa velutina nigrithorax* in Europa, dove è presente l'autoctona *Vespa crabro*, nonché la crescente presenza di *Vespa orientalis* nell'Italia centro settentrionale. In base ai rapporti filogenetici di queste specie appartenenti al genere *Vespa* valutiamo la scelta del veleno per l'immunoterapia specifica nei pazienti con reazioni allergiche gravi alle punture di questi insetti.

Key words: Social wasps, allergy, global trades, climate changes, venom immunotherapy.

INTRODUCTION

Climate change and globalization are consequences of human activities known to have significant impacts on global ecology and human life. The observable increases in temperature, alterations to precipitation patterns, elevated CO₂ levels, deforestation, polar ice melting, and air pollution are influencing global ecosystems at various complex levels. Many insect species have exhibited a clear reduction in biodiversity, while others have experienced an increase in biomass associated with a shift in their distribution patterns and, consequently, competition with native species (Heshmati, 2021). Particularly noteworthy is the economic importance of the altered distribution and stability of allergenic animal species,

including venomous insects, which has been widely affected (Turillazzi & Turillazzi, 2017), potentially impacting human health risks. Insects have long been recognized as vectors of important human diseases, but they can also cause various types of allergies. Among these insects, the Hymenoptera constitute a large group of more than two hundred thousand species, of which the suborder Apocrita (containing the Aculeata) is represented by a conspicuous number of species equipped with venom-producing glands and a sting to deliver the venom, used for predation and colony defence. Social Aculeata, together with termites, encompass relatively few species but account for over half of insect biomass (Holldobler & Wilson, 2009).

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Eusociality is defined by three fundamental characteristics: i) immature broods are reared collectively by adults in colonies; ii) there is an overlap of various generations of individuals; iii) there is a reproductive division of labour with some individuals reproducing and sterile individuals assisting in reproduction (Wilson & Hölldobler, 2005). These insects are mainly found in the families Formicidae (ants), Apidae (social bees), and Vespidae (social wasps), where colonies can range from a limited number of adults to millions of members and, in some cases, can have complex nest architecture. All these insects have been shown to defend their colonies with venom and stings. Aculeate Hymenoptera, particularly the social ones, can cause serious toxic and allergic reactions in humans, with the allergic response varying in severity. Toxic reactions are due to the irritating and toxic action of the venom and occur following several stings (usually more than 50) and although very rarely, they can also be fatal; these reactions are dose-dependent, and the different components of the venom can damage the skin, muscles, blood cells and nervous system. There is an increased vascular permeability, which can lead to vascular depletion and irreversible shock; peptides can induce lysis of blood and muscle cells with tubular necrosis and renal failure. Among the enzymatic components, phospholipase can act through a direct cytotoxic mechanism or as a cytolytic indirectly through plasma lipoproteins; hyaluronidase acts directly in the connective tissue of the skin, opening the passage for other components of the venom, such as peptides. Among the peptides, melittin interacts with the cell membranes of erythrocytes, platelets, and mast cells with increased potassium leakage and subsequent cytolysis, while MCD-peptide and mastoparan C have a degranulating action on mast cells (Severino *et al.*, 2006). In toxic reactions, death can occur, according to the described actions, after a few days, while in severe systemic allergic reactions, death can occur even after a few minutes. Allergic reactions, IgE mediated, presuppose the presence of specific IgE towards the venom of the insect responsible for the sting. A sting may result in normal local reactions, large local reactions (defined as swelling exceeding a diameter of 10 cm lasting more than 24 hours), cutaneous systemic reactions (hives, angioedema, flush), or anaphylaxis (with hypotension, dizziness, dyspnea, or throat symptoms) (Bilò *et al.*, 2005). Venom-specific immunotherapy (VIT) is able to prevent systemic reactions in sensitized subjects. The degree of clinical effi-

cacy is approximately 98% for patients allergic to Vespidae venom and slightly lower for subjects allergic to bee venom. VIT is able to induce changes in some mechanisms of the allergic reaction: in the initial build-up phase of VIT, an increase in specific IgG and desensitization of mast cells and basophils was demonstrated, while in the maintenance phase a cytokine shift with reduction of interleukin (IL)-4 and IL-5 production and increase of interferon- γ , reduction of adhesion molecules, including *ICAM-1*, down-regulation of the lymphocyte stimulating molecule *CTLA-4*, reduction of mast cell activation and basophils (Demšar Luzar *et al.*, 2021). A correct allergy diagnosis represents the main foundation on which the choice of the venom for the most appropriate specific VIT for the patient is based and is decisive for the effectiveness of the therapy itself. Identification of the insect is important to establish the diagnosis, prescribe therapy and educate the patient to avoid future stings (Golden *et al.*, 2011). It is therefore important that the allergist is aware of the hymenopteran species present in the area: native and new alien species.

The appearance of alien allergenic insects in new habitats or territories has been shown to be mainly caused by commercial trade, but recently, climate change has also contributed to the ease with which alien species acclimatize in new areas, thereby influencing the distribution ranges of native species. For example, an increase in the number of nests of social Vespidae in urban areas has been documented in Australia, Chile, and Korea (Kasper *et al.*, 2008; Estay & Lima, 2010). This is due to temperature increases caused by the destruction of forests and parks surrounding cities, while an increase in allergic reactions to yellowjackets was reported in Alaska by Demain *et al.* (2009) for many of the same reasons. Similarly, a rise in allergic reactions to vespid stings following an increase in the number of nests after the nuclear disaster in Fukushima has been observed. This resulted from the massive desertion of the city by residents and, therefore, the lack of regular maintenance and removal of wasp nests prior to the disaster (Ozaki *et al.*, 2017).

Mathematical models that analyse and predict the dynamics of distribution ranges for various invasive species are essential for forecasting the appearance and likelihood of survival of alien species in each country. This allows nations to be prepared to address new public health challenges. A pertinent real example is the first record of the invasive fire ant *Solenopsis invicta*

Buren 1972 in Italy (Menchetti *et al.*, 2023) which had been predicted by previous analyses (Morrison *et al.*, 2004). Here, we will focus our attention on the effects of global trade and climate change on social wasps of the Vespidae.

SOCIAL WASPS

Three out of the six subfamilies in the family Vespidae contain eusocial species. The eusocial characteristics arose independently in the subfamily Stenogastrinae and in the two subfamilies Polistinae and Vespinae (Piekarski *et al.*, 2018). The latter two subfamilies are particularly noteworthy for their ability to deliver potent stings to humans, which can trigger significant allergic reactions to their venom. In a 2011 paper, Beggs *et al.* (2011) published a comprehensive table listing 23 eusocial Vespidae species that have been introduced to various parts of the world beyond their original range and have become established as invasive species (causing substantial negative impacts on local environments). Since then, other species have likely joined this group. Social wasps possess a high invasive capacity because the founding of new colonies typically involves a single queen, which can easily be transported through commercial trade (Spradbery & Maywald, 1992; Otis *et al.*, 2023).

POLISTINAE

The Polistinae subfamily encompasses 958 species and is particularly well-represented in tropical environments of both the Old and New Worlds. In South America, there are 25 endemic genera on the continent, but information regarding the movements and allergenic importance of the species is scarce. Nonetheless, the venom of some species has been investigated by various authors, particularly that of *Polybia paulista* Ihering 1896 (dos Santos *et al.*, 2010; Jacomini *et al.*, 2014; Perez-Riverol *et al.*, 2018). Species belonging to other genera have also been studied, such as *Agelaia pallipes* Olivier 1992 (Galvao *et al.*, 2006; Perez-Riverol *et al.*, 2018), *Protonectarina sylveirae* (de Saussure 1854) (Brigatte *et al.*, 2011), and *Apoica pallens* (Fabricius 1804) (Mendonça *et al.*, 2020). For the time being, all these genera appear to be strictly confined to South America due to their adaptation to forest environments and their generally swarm-founding colony

establishment. However, in the presence of warmer temperatures, they could potentially expand to other territories. Other genera of tropical Polistinae have been poorly studied in terms of their venom characteristics, although some may pose a risk to plantation workers [e.g., *Polybioides tabidus* (Fabricius 1791) in Cameroon and *Polybioides raphigastra* (de Saussure 1854) in Malaysia; S. Turillazzi, personal communication]. Notably, one genus of Polistine wasps, *Polistes Latreille 1802*, represents an important subject for the study of allergy given the physiological and behavioural characteristics of its species.

Polistes

Polistes represent a genus (with more than 200 species) of relatively common paper wasps distributed globally and forming annual colonies, both in temperate and tropical regions, with a maximum of a few hundred adults. They construct nests composed of a single, unenclosed comb, and queens and workers differ primarily in behaviour. From a systematic perspective, various subgenera have been recognized (Carpenter, 1996a; Arévalo *et al.*, 2004), with species living in temperate regions of the Old World belonging especially to the subgenus *Polistes s.s.*. Beggs *et al.* (2011) report 14 species of *Polistes* as introduced and invasive in non-native areas, with three species being particularly noteworthy for their impact on new environments.

Polistes olivaceus

Polistes olivaceus (De Geer 1773) is a tropical species belonging to the subgenus *Gyrostoma* Kirby and Spence 1828 (Carpenter, 1996b). It is native to India and has colonized at least 18 separate countries, primarily islands of the Indian and Pacific Oceans, as well as parts of Australia and New Zealand (Harris, 1979). Information on allergic reactions to the sting of this wasp is lacking, but recently, a case of anaphylaxis resulting from the consumption of larvae of this species has been reported on Réunion Island (Maillot *et al.*, 2023).

Polistes chinensis antennalis

Polistes chinensis antennalis Perez 1905 was introduced in New Zealand in 1979 from Southeast Asia. It spread rapidly and had a significant impact on the entomological fauna it used as prey. It is now competing with two other introduced congeneric species, *P. hu-*

milis (Fabricius 1781) (Clapperton *et al.*, 1996) and *P. dominula* (Christ 1791) (Howse, 2021). Interestingly, *Polistes chinensis antennalis* can adapt to different climates by altering its nest-building activities (Hozumi *et al.*, 2015). Another *Polistes* species that caused significant changes in the insect fauna after its introduction (in 1988) to the Galapagos Islands is *P. versicolor* (Olivier 1791), which is common throughout South America (Parent *et al.*, 2020) and poses problems for insectivorous birds on the islands (Causton *et al.*, 2006).

Polistes dominula

Polistes dominula is probably the most studied species of the genus *Polistes*. It has established populations in various countries far removed from its original range in Southern Europe. In Europe, its range is expanding northward. A recent study by German researchers (Höcherl & Tautz, 2015) highlights that the species is expanding in Germany and other countries of Central and Northern Europe (Baltic countries). This expansion is due to the species' nest-founding behaviour, which preferentially occurs in natural and anthropogenic cavities, and the number of foundresses, which can participate in nest construction (usually varying between 2 and 5) (Pardi, 1942). The study by Kovac *et al.* (2017) on this species, compared with another species native to the Mediterranean Basin, *P. gallicus* (Linneus 1767), concludes that differences in thermal tolerance of foundress females could be responsible for the successful northward distribution of *P. dominula*. This species was introduced into the USA in the late 1970s (Hathaway, 1981) and, probably followed by other introductions, can now be found in various states and even in Southern Canada (Liebert *et al.*, 2006). Currently, it is also present in other parts of the world, having been introduced into Western Australia and South America (Liebert *et al.*, 2006; Buck *et al.*, 2008), New Zealand (McGruddy *et al.*, 2021), Argentina (Sackmann *et al.*, 2003), and South Africa (Van Zyl, 2016; Roets *et al.*, 2019).

The size and habits of social wasp species differ to some extent, but one of the most important differences lies in their venom composition. It has been established that VIT performed with the venom of American *Polistes* is sometimes ineffective in treating patients allergic to European species (personal experience of ST). This evidently depends on differences in the main components of the venom (Pantera *et al.*, 2003). On the other hand, it has been demonstrated that

the venom of at least two European species (*P. dominula* and *P. gallicus*) is sufficient for diagnosis and, therefore, in the therapy of European patients (Severino *et al.*, 2006).

Given the difficulty in performing an efficient VIT with the venom of different subgenera, the possibility of introducing American species in Europe and their subsequent potential spread across the continent could create public health issues. However, this incident has been officially reported only once, when a nest of *Polistes major major* Palisot de Beauvois 1818 (subgenus *Aphanilopterus* Meunier 1888) was found in Northern Spain in 2013 (Castro *et al.*, 2013). No other cases of introduction have been reported since then.

VESPINAE

In species of the subfamily Vespinae (comprising 69 described species), wasps form colonies that can reach impressive sizes. Their nests are enveloped and composed of multiple combs. This subfamily includes four genera: *Vespula Thomson* 1869, *Dolichovespula* (Blutgen 1943), *Vespa Linneus* 1758, and *Provespa Ashmead* 1903, but the genera *Vespula* and *Vespa* are most significant when concerning health issues.

Vespula

This genus encompasses 23 described species that construct massive nests and form colonies where queens differ from workers in their larger size and activities. Colonies are founded by fertilized queens, which build multi-comb nests in underground cavities. Three species are particularly notable for their tendency to be introduced into new countries and habitats through commercial trade, owing to the overwintering of queens in shipments of furniture and plants. Their spread into new areas is then facilitated by their capacity to adapt to various climatic conditions and the absence of specific predators, competitors, and parasites (Lester & Beggs, 2019).

Within the genus *Vespula*, two species originating from Europe have established themselves outside their native range to become pests: the German wasp or yellowjacket [*Vespula germanica* (Fabricius 1793)] and the common wasp (*Vespula vulgaris* Linneus 1758). *V. germanica* has been introduced to various non-European countries, including the USA, South America, South Africa, Australia, New Zealand,

and various Atlantic islands. The first record in North America dates to 1891 (Edwards, 1976); in South America, it was first introduced in Chile in the 1970s (Castro *et al.*, 2013) and then invaded Argentina around 1980, likely spread by human trade (Masciocchi & Corley, 2013). It was also introduced in South Africa around 1972 (Whitehead & Prins, 1975) and is present in the Western Cape province (Veldtman *et al.*, 2021), with a high likelihood of further range expansion. In New Zealand, it appeared in 1945 (Thomas, 1960) and then spread to Australia around 1959 (Spradbery & Maywald, 1992). A similar situation was demonstrated by the other European invasive *Vespula vulgaris*. This species was introduced in Australia, probably around the same time as *V. germanica*, and later in the 1970s (Donovan, 1984) in New Zealand, where it competed with *V. germanica* in exploiting the honeydew produced by tree parasites in beech forests. Lester *et al.* (2017) compared the density dependence of this species in its native and invaded ranges and concluded that wasp abundance in both ranges depends mainly on the number of queens that survived the winter and spring weather conditions. In Chile, Estay and Lima (2010) found that El Niño and SAM can also influence the survivorship of founding queens, while the favourable climatic conditions found in Australia and New Zealand can promote the formation of perennial colonies of *V. germanica* with the construction of giant nests (Greene, 1991; Goodisman *et al.*, 2001).

Vespula pensylvanica de Saussure is native to Western North America and was introduced to the Hawaiian Islands around 1919 (Carpenter, 2008), likely due to the presence of queens in a shipment of Christmas trees from North America (Hollingsworth *et al.*, 2009). Its impact on the endemic insect and arthropod fauna was substantial, partly because Hawaii lacks native eusocial Hymenoptera (Wilson & Holway, 2010).

Vespa

The species belonging to the genus *Vespa* are defined as hornets and have the largest size of all social wasps. They construct large nests in natural or artificial cavities or aerial nests in trees and shrubs. The nests have a multi-layered envelope and various superimposed combs. Colonies can contain thousands of adult individuals and immature larvae and are predominantly founded by single-fertilized queens. In

this genus, there are important species that contribute to both public health and economic problems (especially for apiculture). There are 22 described species in this genus, but 6 of them are particularly invasive: these six species have been found outside their original range (in Southeast Asia): *V. crabro*, *V. orientalis* Linneus 1771, *V. tropica* (Linneus 1758, *V. bicolor* Fabricius 1787, *V. mandarinia* Smith 1852, and *V. velutina* Lepelletier 1836. A recent paper by Otis *et al.* (2023) analysed the invasive potentials of hornets and presented complete information on these six species. From an evolutionary standpoint, the phylogenetic distances of these six species and their membership in three different clades can be seen in the cladogram for the genus *Vespa* (Perrard *et al.*, 2013) to highlight (Fig. 1).

Vespa crabro, the European hornet, has colonized all of Eurasia. It is mainly a forest species and builds its nests in hollow trees or artificial structures, forming colonies with several hundred adults. It preys exclusively on insects, including other smaller social wasps such as *Vespula* and *Polistes*. It is not overly aggressive, and its sting can be treated with a commercially available, specific VIT. This wasp was imported into the USA around 1840 (Shaw & Weidhaas, 1956) to limit infestations of forest caterpillars and has since expanded its range, now being present in Eastern States and Southern Canada (Landolt *et al.*, 2010).

Vespa orientalis, unlike *Vespa crabro*, is a scavenger hornet, feeding on nectar, fruit, insects, and carrion (Smith-Pardo *et al.*, 2020). It is broadening its range towards Mediterranean countries, moving northward in Italy, France (Gereys *et al.*, 2021), Romania (Zachi & Ruicănescu, 2021), and Spain (Castro & del Pico 2021). It has reached central and North-East Italy (Graziani & Cinferoni, 2021; Zucca *et al.*, 2024) and was also introduced in central Chile (Werenkraut *et al.*, 2022).

Vespa tropica, native to Southeast Asia, Indonesia, the Philippines, and New Guinea, was introduced on the Pacific Island of Guam, where it causes great environmental damage (Otis *et al.*, 2023).

Vespa bicolor was introduced in Taiwan around 2009 (Sung *et al.*, 2014) and has spread across the entire island. It has also been found in Spain since 2019 (Castro, 2019) and can now be considered at least locally established. It preys on honeybees and belongs to the same clade as *V. velutina* (Fig. 1).

Vespa mandarinia is the largest of all social

wasps, reaching a length of about 5.5 cm in queens. Its range extends from Northern India to Japan, and it can cause severe health problems for humans (Yanagawa *et al.*, 2007). It can be considered a forest species (Kim *et al.*, 2020), and its attacks on European honeybees can be devastating, resulting in the destruction of entire beehives. Since 2019, specimens and colonies of this wasp have been found in Canada (Vancouver and British Columbia) and Northwestern USA (Washington state) (Looney *et al.*, 2023), but there have been no official reports of further findings since then, suggesting a population decline.

Vespa velutina nigrithorax Du Buysson 1905 represents a new economic and health emergency in Europe. It originates from Southeast Asia and exhibits various subspecies. In 2004, a queen of the subspecies *nigrithorax*, present in the northern part of the species' original distribution range, was accidentally introduced into a plant nursery near Bordeaux, France (Haxaire *et al.*, 2006; Villemant *et al.*, 2006). From there it rapidly spread to many other countries in Western Europe (Spain, Portugal, Belgium, the Netherlands, Switzerland, England, and Italy) (Piekarski *et al.*, 2018). The nest of this species is

usually built on trees or shrubs and reaches a considerable size (Monceau *et al.*, 2014), while the queen is typically multiply mated (Arca *et al.*, 2015). Its impact on apiculture is particularly significant, and as in other countries (*e.g.*, France), in Italy, a national project has been established to monitor the expansion of hornet distribution with the contribution of beekeepers. In Tuscany, the invasion of *Vespa velutina* from the northwest has coincided with the invasion of *Vespa orientalis* from the south. These two species overlap with the “native” *Vespa crabro* in the same territories. Carisio *et al.* (2022) studied the potential competition between *V. velutina* and *V. crabro* and compared the abundance of the two wasp species between two nearby invaded/uninvaded areas. The study suggested a lack of negative effects on the native species by the invasive wasp. On the other hand, Liroy *et al.* (2023), reporting the presence of all three species in the same territories, remark that the slight differences in the climatic and trophic niches of the native species (*V. crabro* and *V. orientalis*) could potentially limit the southward expansion of the alien species. Due to its particular biological and behavioural characteristics (large colonies and strong ag-

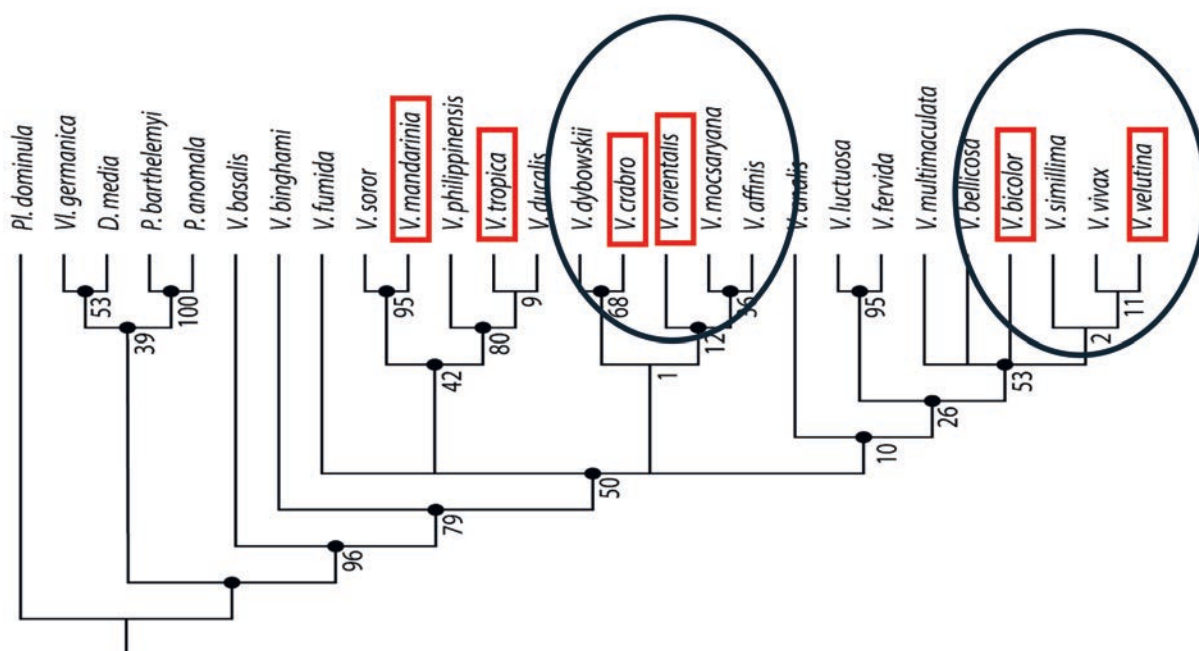


Fig. 1. The phylogenetic cladogram of the species of the genus *Vespa* (redrawn from Perrard *et al.*, 2013). Phylogenetic distances between the most invasive species can be appreciated.

gressiveness), *Vespa velutina nigrithorax* poses some health problems. Up to now, there have been various fatal casualties in Europe (Spain 6, France 5) (Feás, 2021) (due to allergic reactions to toxins and allergens contained in the venom. Using the whole venom of *V. velutina*, Monsalve *et al.* (2020), have purified the phospholipase (named Vesp v 1), as well as the antigen 5 (Vesp v 5), while two hyaluronidase isoforms have been found (Vesp v 2A and Vesp v 2B). This study showed the highest similarity of the Asian hornet venom components with those of the *Vespa* and *Vespula* species, in comparison with those of the *Polistes* species. As there is currently no specific available VIT for *V. velutina*, *Vespula* spp. VIT may be a valid option for patients allergic to this wasp and, when available, VIT with *Vespa crabro* venom may be even more effective (Bilò *et al.*, 2023).

FUTURE STRATEGIES

As the number of reported cases of anaphylaxis due to *V. velutina* has exponentially increased, and the fact that it currently represents three-quarters of new cases involving Hymenoptera anaphylaxis in northern Spain, it is desirable to have *V. velutina* venom available for diagnostic and therapeutic use (Vidal *et al.*, 2021; Vidal, 2022). This is also suggested by the higher phylogenetic distance between this species and the pair composed by *V. crabro* and *V. orientalis* (Fig. 1).

CONCLUSIONS

Climate change and globalization can influence the geographical distribution patterns of many insect species. In the case of Hymenoptera, these fac-

tors have repercussions on environmental, economic, and medical aspects. Various species of stinging ants, bees, and wasps with allergenic potential have invaded new territories, and predictive models foresee an increasing tendency for such invasions in the near future. Specific recognition patterns of sensitization for venom must be developed to counteract allergic reactions to the stings of these new species with appropriate immunotherapies. The recent invasion of Western Europe by the Asian *Vespa velutina nigrithorax* and the progression northward of *Vespa orientalis* into Italy are examples that present important challenges for the treatment of severe allergies.

Note: While we were correcting the proofs of the present paper we received a report from Sanchez *et al.* who found another species of the genus *Vespa* (*V. soror* du Buysson 1905) in insect traps in Northern Spain.

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CONTRIBUTIONS

ST and FT conceptualized the biological problems, and MS conceptualized the medical problem. ST, FT and MS wrote the paper.

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