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# Müllerian mimicry among bees and wasps: a review of current knowledge and future avenues of research

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## ABSTRACT

Many bees and stinging wasps, or aculeates, exhibit striking colour patterns or conspicuous coloration, such as black and yellow stripes. Such coloration is often interpreted as an aposematic signal advertising aculeate defences: the venomous sting. Aposematism can lead to Müllerian mimicry, the convergence of signals among different species unpalatable to predators. Müllerian mimicry has been extensively studied, notably on Neotropical butterflies and poison frogs. However, although a very high number of aculeate species harbour putative aposematic signals, aculeates are under-represented in mimicry studies. Here, we review the literature on mimicry rings that include bee and stinging wasp species. We report over a hundred described mimicry rings, involving a thousand species that belong to 19 aculeate families. These mimicry rings are found all throughout the world. Most importantly, we identify remaining knowledge gaps and unanswered questions related to the study of Müllerian mimicry in aculeates. Some of these questions are specific to aculeate models, such as the impact of sociality and of sexual dimorphism in defence levels on mimicry dynamics. Our review shows that aculeates may be one of the most diverse groups of organisms engaging in Müllerian mimicry and that the diversity of aculeate Müllerian mimetic interactions is currently under-explored. Thus, aculeates represent a new and major model system to study the evolution of Müllerian mimicry. Finally, aculeates are important pollinators and the global decline of pollinating insects raises considerable concern. In this context, a better understanding of the impact of Müllerian mimicry on aculeate communities may help design strategies for pollinator conservation, thereby providing future directions for evolutionary research.

*Key words:* Müllerian mimicry, bees, wasps, community ecology, aposematism, mimicry rings.

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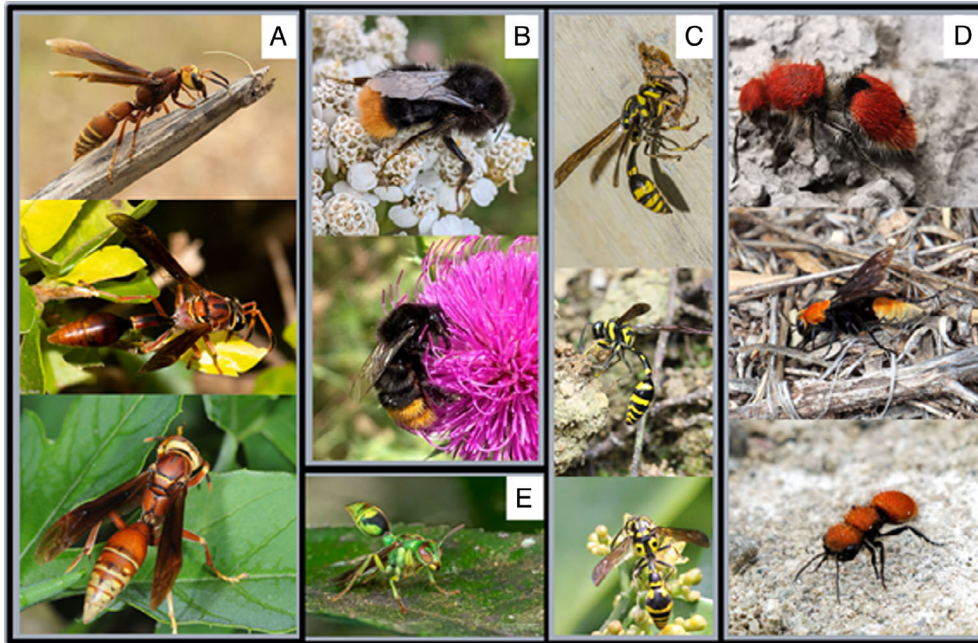
## I. INTRODUCTION

Many bees and stinging wasps (Hymenoptera: Apocrita, Aculeata) exhibit striking colour patterns or conspicuous coloration (Fig. 1), such as their infamous black and yellow or red stripes (Poulton, 1890; Cott, 1940; Plowright & Owen, 1980). These colorations have been explained by some authors as adaptations for thermoregulation (Stiles, 1979; Opler, 1981; Badejo *et al.*, 2020; Wilson *et al.*, 2020) or crypsis (Table 1; Williams, 2007; Wilson *et al.*, 2020). Most frequently, however, given that females possess a venomous sting, the contrasted coloration of these insects has been interpreted as being aposematic (Table 1), i.e. a warning signal advertising unpalatability to putative predators (Williams, 2007; Hines & Williams, 2012).

Predation by birds or predatory arthropods can place strong selective pressures on flying insects (e.g. Holmes, Schultz & Nothnagle, 1979; Tiitsaar, Kaasik & Teder, 2013). After having experienced the pain or the distasteful venom of a stinging hymenopteran, predators tend to avoid that prey, and generalise their aversion to prey with similar aposematic coloration (Poulton, 1890; Ruxton, Speed & Sherratt, 2004). Some predators have an innate tendency to avoid prey displaying certain signals (Schuler & Hesse, 1985; Lindström, Alatalo & Mappes, 1999). Because predator learning often entails the death of some aposematic prey individuals, aposematic colorations are under positive frequency-dependent selection: the more frequent a coloration pattern is in the environment, the

more advantageous it is for individuals harbouring this pattern because the probability of encounter with a naive predator diminishes. This positive frequency-dependent selection induces convergence (independently evolved similarity) of aposematic colorations among species exposed to the same suite of predators, a phenomenon called Müllerian mimicry (Müller, 1879; Table 1). Aposematism can also drive the evolution of Batesian mimicry (Bates, 1862), where individuals from an undefended species (the mimic) benefit from the protection provided by a defended species (the model). While Müllerian mimetic interactions are mutualistic (Sherratt, 2008), Batesian mimicry is detrimental to the model prey because it slows down predator learning, thereby increasing the individual probability that the model prey will be killed by a predator (Table 1). Prey species harbouring similar aposematic colour patterns are said to form a mimicry ring (Table 1).

Batesian and Müllerian mimicry were first described in butterflies (Bates, 1862; Müller, 1879), and most mimicry studies have used lepidopteran systems (Sherratt, 2008). Recently, other taxa have increasingly become the focus of mimicry studies, notably Hymenoptera [e.g. velvet ants (Wilson *et al.*, 2015), bumble bees (Ezray *et al.*, 2019)]. Batesian mimicry with bees and stinging wasps as protective models has been the focus of many studies (e.g. Howarth, Edmunds & Gilbert, 2004; Golding *et al.*, 2005; Hassall, Billington & Sherratt, 2019). Batesian mimics include stingless Hymenoptera species such as sawflies (Vilhelmsen, 2019),



**Fig. 1.** Examples of some members of known mimicry rings among bees and wasps. From top to bottom: (A) *Polistes cavaypita* ring: *Montezumia ferruginea*, *Zeta argillaceum*, *Polistes cavaypita* (Vespidae) (Garcete-Barrett, 1999), from Paraguay, the first two are solitary; (B) Red-tailed black bumblebees: *Bombus (Thoracobombus) ruderarius*, *Bombus (Melanobombus) lapidarius* (Apidae) (Plowright & Owen 1980), from England, both are eusocial and not closely related; (C) Eumenine – Philippines ring: *Pareumenes quadrispinosus*, *Phimenes flavopictus*, *Pseumenes depressus* (Vespidae) (Nugroho *et al.*, 2020), from Java, all are solitary; (D) Mutillid – Western ring: *Dasyntilla erythrina*, *Psorthaspis portiae*, *Pseudomethoca anthracina* (Mutillidae) (Wilson *et al.*, 2015; Rodriguez *et al.*, 2014), from western North-America, all are solitary; (E) A member of the ‘apple-green’ ring *Ropalidia sp.* (Pauly *et al.*, 2003), from Madagascar, this is a eusocial Vespidae but the ring contains various families including solitary species. Image A–D were taken from the iNaturalist platform, photograph credits (top to bottom): (A) mendezcla7, Ísis Medri, Andrea Aristides Cocucci; (B) Denis X., Dag Terje Filip Endresen; (C) Vijay Anand Ismavel, Agnes Trekker, Agnes Trekker; (D) Gabriel Alejandro Pérez Villazana, Noreen Baker, Andrew Newmark; (E) Nick Bay.

chalcidoid wasps (Garcete-Barrett, 1999; Pauly, Vago & Wahis, 2003) and ichneumonid wasps (Evans, 1968; West-Eberhard, Carpenter & Hanson, 1995), as well as other insect orders such as Lepidoptera (Poulton, 1897), Diptera (Myers, 1935; Brower, Van Zandt Brower & Westcott, 1960), Coleoptera (Linsley, 1959; Silberglied & Eisner, 1969; Lanteri & Del Rio, 2005), Hemiptera (Elkins, 1969), Orthoptera (Poulton, 1890), Neuroptera (Opler, 1981), Mantodea (Svenson & Rodrigues, 2019) and even some non-insect arthropods such as spiders (Nentwig, 1985). While the profusion and diversity of mimics of bees and stinging wasps suggests an important protective value of their aposematic colorations, Müllerian mimicry among bees and stinging wasp species has attracted far less interest than Batesian mimicry. Recent studies are starting to explore Müllerian mimicry in such species at a large scale (e.g. Pekar *et al.*, 2017; Wilson *et al.*, 2018), suggesting that mimicry is an important phenomenon in their evolution. As a highly diversified group, with around 53,000 species (Grimaldi & Engel, 2005; Aguiar *et al.*, 2013), bees and stinging wasps provide an unparalleled opportunity for studying the evolution of aposematism and Müllerian mimicry. A recent contribution discussed several aspects of mimicry in aculeates, but only focused on the two best-studied taxa, velvet ants and

bumblebees, leaving aside the potential incidence of mimicry in the tens of thousands of other species of bees and wasps (Willadsen, 2022).

Increasing our understanding of Müllerian mimicry among bees and wasps might bring insights on the current decline in pollinators (Potts *et al.*, 2010). Bees act as major pollinators, and wasps also play an important role in plant pollination (Rader *et al.*, 2016). While there are substantial research efforts on pollinator conservation (IPBES, 2016), we know very little about the implications of Müllerian mimicry, as a mutualistic interaction among pollinators, on the current fate of pollinator populations. Theoretical work, however, has suggested that mutualistic interactions are key to species coexistence and biodiversity (Bastolla *et al.*, 2009).

Our aim herein is to review the literature on Müllerian mimicry in bees and stinging wasps, and to propose directions for future research. Specifically, our objectives are to identify (i) what has been studied, (ii) what still needs to be investigated, and (iii) how several features of this group such as sexual dimorphism in defence levels and sociality impact the evolution of Müllerian mimicry in bees and stinging wasps. Bees and stinging wasps belong to the hymenopteran clade Aculeata [*sensu* Sharkey *et al.* (2012) and Peters *et al.* (2017)]

Table 1. Definitions of general terms referring to different adaptive resemblances used in this review [after Quicke (2017) and Briolat *et al.* (2019)].

Concept	Definition
Aposematism	Term originally coined by Poulton (1890) referring to the association of a conspicuous or salient, strikingly different from the background, warning signal with a mechanism of defence.
Automimicry	Batesian mimicry within a given species where some members lack defences. In aculeates, automimicry occurs between males and females of the same species. Automimicry tends to slow down predator avoidance learning.
Batesian mimicry	Named after Henry Walter Bates' work (Bates, 1862), it describes anti-predator mimicry adopted by a palatable potential prey mimicking an unpalatable one. Beneficial only for the palatable species, it disadvantages the unpalatable one by antagonistic indirect interaction.
Crypsis	When an organism has a similar appearance to its background, making it less detectable.
Masquerade	Introduced by Endler (1981), to designate an organism resembling an object that is detectable but of little interest to its predator, prey or host.
Mimicry ring	A group of individuals from at least two species that co-occur to some extent and share a warning signal (honest or dishonest).
Müllerian mimicry	Named after Fritz Müller's work (Müller 1879), it describes a resemblance between equally or near equally unpalatable, aposematic prey, which dilutes the cost of predator learning across those species. Beneficial for both prey species by mutualistic indirect interaction. Although theoretically there can be a whole spectrum of interactions between classical Müllerian (i.e. mutualistic) and classical Batesian (i.e. parasitic) mimicry (Speed & Turner, 1999; Ruxton <i>et al.</i> , 2004; Sherratt, 2008), this review focuses on these two classical categories (Anderson & de Jager, 2020; Briolat <i>et al.</i> , 2019).

together with ants (Formicidae). In this review we exclude ants because they depart from the other aposematic aculeate families with respect to behaviour and locomotion, as only winged breeding individuals are able to fly, and they do so over a very restricted period. Thus, we considered that they may share few predators with other aculeates and therefore likely are under independent mimicry dynamics. The remaining Aculeata includes 35 families (Peters *et al.*, 2017; Sann *et al.*, 2018). For simplicity, in the following sections we use the term 'aculeates' to refer only to bees and stinging wasps.

This review focuses on aculeate Müllerian mimicry, although we do mention several studies on Batesian mimicry to illustrate some of the understudied aspects of aculeate aposematism in a Müllerian mimicry context. We first review studies showing that aculeates exhibit the prerequisites for

the evolution of Müllerian mimicry. We then undertake a comprehensive review of the literature to list the described instances of Müllerian mimicry involving aculeates, the distribution and composition of aculeate mimicry rings, and the methodology as well as questions used in these studies. In particular, we review the traits under potential selection for convergence that have been studied, whether the hypothesis of evolutionary convergence was tested and whether predators were taken into account in the mimicry analysis. Finally, we review various factors likely to affect the dynamics of mimicry and how they were considered in the studies. Some of these factors, such as sociality and sexual dimorphism in defence mechanisms, are specific to aculeates and their relevance in mimetic systems is discussed.

## II. PREDATION AS A SELECTIVE PRESSURE

Since mimicry results from selective pressures incurred by predators on aposematic signals, we first review evidence that aculeate insects are potential prey and that their phenotype can be considered aposematic, a prerequisite for the evolution of Müllerian mimicry.

### (1) Are aculeates under predation pressure?

Many studies have shown that aculeates represent potential prey to a wide range of insectivorous organisms including mammals, birds (Davies & Green, 1976), lizards (Sexton, 1964; Punzo, 2003), frogs (Cott, 1932; Bull, 2005), dragonflies (Wright, 1944; Needham, 1945), spiders (Dukas & Morse, 2003) and even other aculeates (Rome *et al.*, 2021). Evidence comes from direct observations in the field (e.g. Knight *et al.*, 2005), experimental setups (e.g. Kauppinen & Mappes, 2003), and from gut content analyses (e.g. Cott, 1932).

### (2) Are aculeate defence mechanisms efficient at repelling predators?

Aposematism implies that species have anti-predator defence mechanisms. Aculeate females share two defences: a weaponized ovipositor, or 'aculeus', able to inflict painful stings, and a venom that can be injected during the sting (Baumann *et al.*, 2018). Several studies have shown that aculeate prey are not appealing to most predators, unlike other insects of the same size (Cott, 1932; Bull, 2005; Punzo, 2003). Although some predators are known to be able to circumvent their defences (Davies, 1977; Best & Pfaffenberger, 1987; Manley & Sherbrooke, 2001), rejection of aculeate prey by predators has been observed in multiple cases (e.g. Davies & Green, 1976), and seems to be the rule rather than the exception. Prey rejection by predators has been linked to their venomous sting (e.g. Van Zandt Brower & Brower, 1962), although this has been debated for some predators such as birds (Mostler, 1935;

Gilbert, 2004). Rejection was also related to other aspects such as distastefulness of the female abdomen, possibly due to the venom gland (Evans & Waldbauer, 1982), or to difficulty in prey handling (Mostler, 1935).

The level of defence can vary among and within aculeate species (Schmidt, 2019), and the response varies among predators (Lane, 1957; Barnett, Ringhofer & Suzuki, 2020). For example, some *Odynerus* (Vespidae) stings are not particularly painful for humans but appear efficient against some avian predators (Lane, 1957). This emphasises the importance of the structure of the predator community in shaping Müllerian mimicry. Although defended prey are usually unpalatable to insectivores, predators may attack and consume unfamiliar prey when alternative food is scarce and/or when informed about their potential toxicity, depending on the perceived defence intensity (Poulton, 1887; Speed, 1993; Sherratt, 2011; Aubier & Sherratt, 2015, 2020).

### (3) Can predators learn to avoid aculeate-like prey?

Aculeate defence mechanisms are efficient at repelling predators. Some studies suggest that this avoidance might be partly related to an innate aversion in some predators including birds (Davies, 1977), dragonflies (O'Donnell, 1996; Kauppinen & Mappes, 2003) and spiders (Myers, 1935). In these studies, while avoidance of aculeates was clearly demonstrated, an active learning process by predators was not shown. Predator learning of the aculeate warning signal was nonetheless demonstrated in other studies (Poulton, 1887; Mostler, 1935). Experiments on various groups of predators have supported the hypothesis that predators can learn to avoid aculeates [birds (Davies & Green, 1976; Evans & Waldbauer, 1982), toads and frogs (Cott, 1932; Brower *et al.*, 1960; Van Zandt Brower & Brower, 1962, 1965), lizards and mammals (Sexton, 1964; Gall *et al.*, 2018)]. For example, 10 vertebrate species belonging to a range of groups (birds, lizards, mole, shrew and toads) were shown to avoid velvet ants (Mutillidae) almost entirely (Gall *et al.*, 2018). The authors also proved that three lizard species (*Aspidoscelis tigris*, *Gambelia wislizenii* and *Uta stansburiana*) that co-occur with eight velvet ant species involved in two distinct mimicry rings searched for those prey and attacked them significantly less after having experienced the sting. A similar pattern was found for nocturnal mammals: velvet ants and spider wasps were the least frequent item in the diet of the grey shrew *Notiosorex crawfordi* (Punzo, 2003). This aversion was also found to extend to non-aculeate mimics and even aculeate-like dummies (e.g. Van Zandt Brower & Brower, 1962, Kauppinen & Mappes, 2003). These predators were therefore able to generalise the painful experience to new potential prey.

To summarise, there is a large community of naive predators that potentially predate aculeates; at least some aculeates are unpalatable to some predators; and some of these predators can generalise their avoidance to prey with a similar appearance. Aculeates therefore meet the prerequisites for the evolution of Müllerian mimicry.

## III. METHODS OF LITERATURE REVIEW

In order to synthesise existing knowledge on aculeate Müllerian mimicry, we performed several literature searches complemented by other studies known to the authors. Literature searches were performed with ISI *Web of Science* and last updated on 20th May 2021, with the options 'all databases' and 'all years'. Two searches were performed in the topics field, focusing either on mimicry in general (including Batesian mimicry), [TOPIC: ("mimicry" OR "mimetic") OR "aposemati\*"] AND (("aculeat\*" OR "bee") OR "wasp") OR "hornet") NOT ("orchid" OR "floral") or specifically on Müllerian mimicry [TOPIC: ("müllerian mimicry" OR "aposemati\*") AND (("aculeat\*" OR "bee") OR "wasp") OR "hornet") NOT ("orchid" OR "floral")], with both searches excluding cases of orchid mimicry. The first search yielded 736 papers and the second search 72, all of which were included in the results of the first search. Studies on ant mimicry ( $N = 242$ ) were discarded since they were out of the scope of this study (see Section I). We then screened these 494 titles and abstracts, excluding studies that did not explicitly address Müllerian mimicry rings ( $N = 475$ ), resulting in only 19 relevant references. Some Müllerian mimicry rings are described in papers focusing mainly on other aspects, such as Batesian mimicry, so we complemented our search results with references known to us that were not found by our search string, and with relevant references cited within the extracted papers. The final list included 44 studies (see online Supporting Information, Tables S1 and S2).

For each selected paper, we identified the mimicry rings described and recorded the geographical scale of the study, the species involved, how the similarity between species was quantified, on which traits, and whether sociality, sexual dimorphism, abundance, phenology, predators and phylogeny were taken into account in defining these mimicry rings. Here, we considered as 'social', taxa that exhibit reproductive division of labour, cooperative brood care and overlap of generations (Danforth, Minckley & Neff, 2019). We considered two mimicry rings in different studies as the same when they were explicitly referred to as the same ring, or when all of the species of one of the rings was included in the other study. When available, we used the mimicry ring names provided by the authors and added the taxon name when necessary. When no name was provided, we used a name based on the main feature mentioned in the study for this ring, either a geographic area, a pattern description or a main species. We used the R packages *ggplot2* (Wickham, 2016) and *igraph* (Csardi & Nepusz, 2006) to produce the figures.

## IV. MÜLLERIAN MIMICRY RINGS AMONG ACULEATES

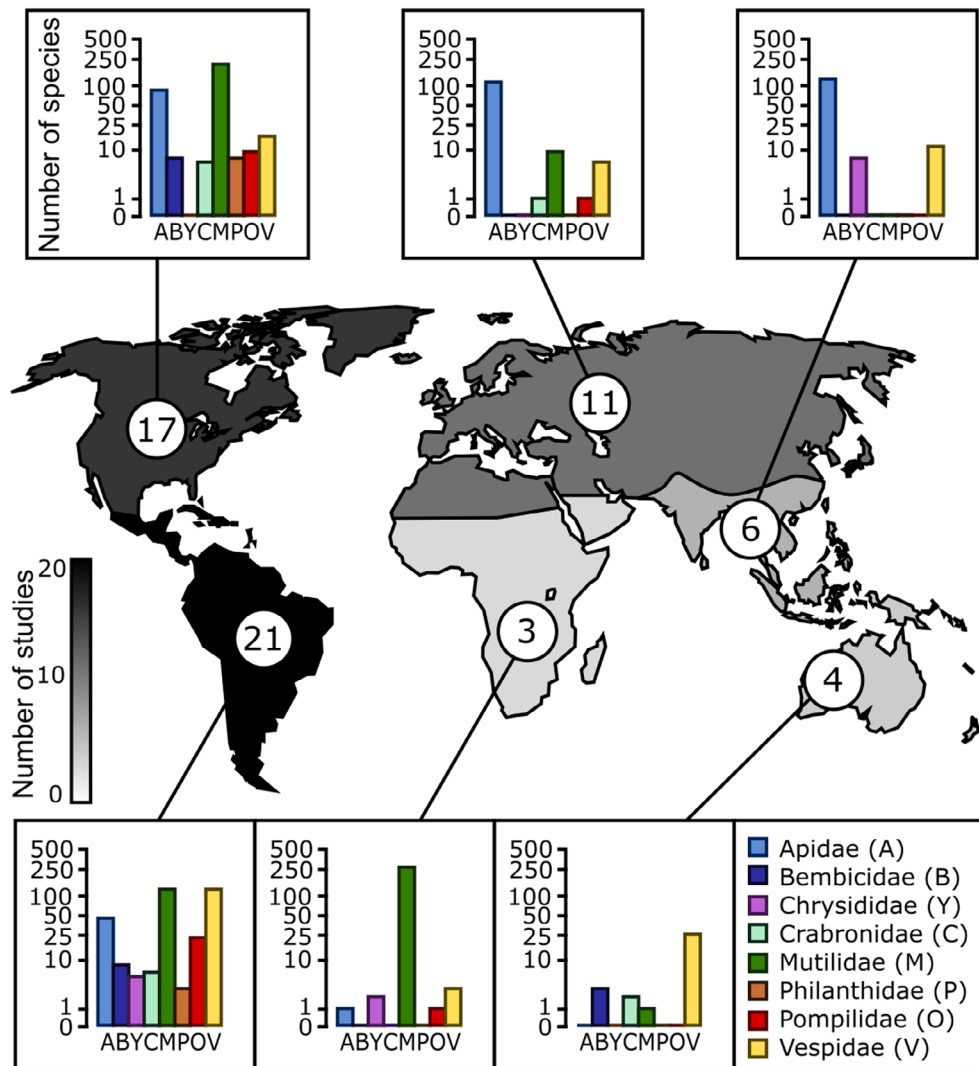
### (1) Are there multiple mimicry rings among aculeates?

Aculeates are widely known for aposematic signals such as black and yellow stripes or black with a red abdomen

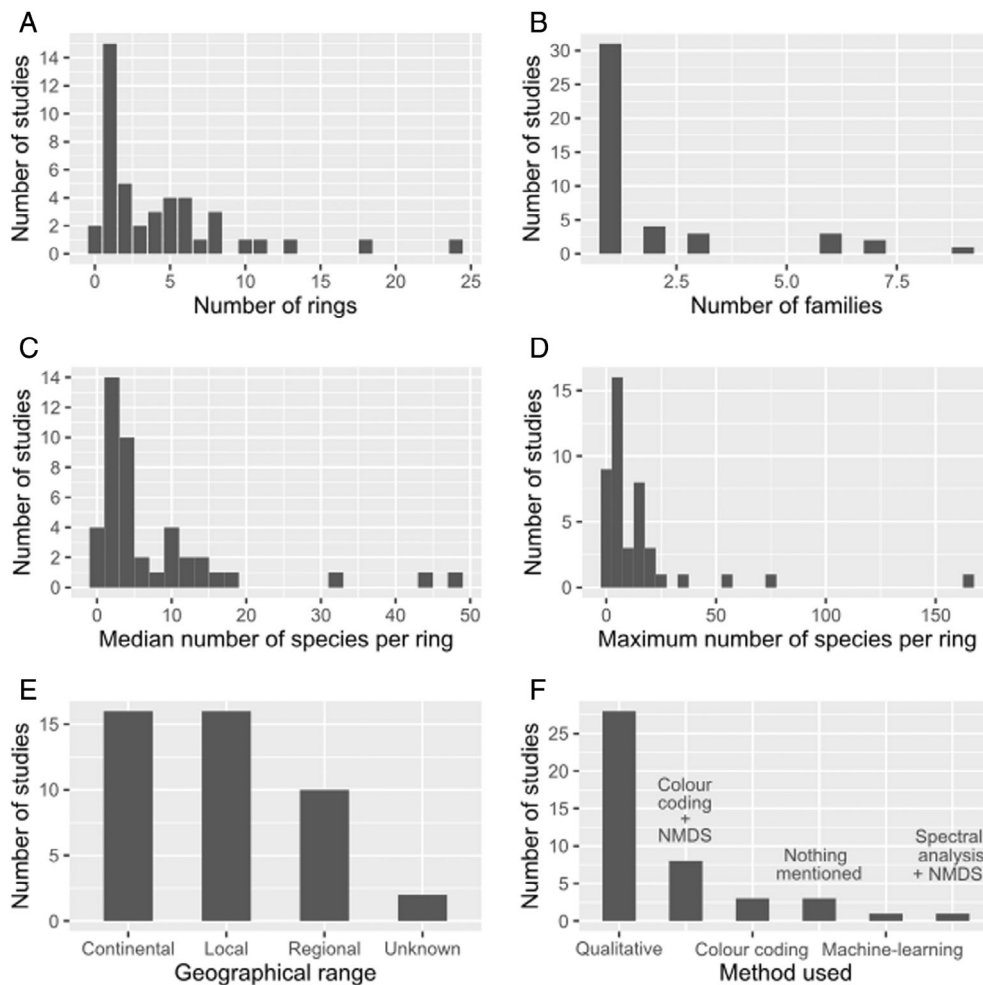
coloration in the northern hemisphere, but there are many other signals across this taxon. In the studies we identified, mimicry rings were described from almost all regions of the globe (Fig. 2). Those studies collectively reported a total of 150 recognised or ‘potential’ mimicry rings, defined on the basis of human perception. Two studies addressed Müllerian mimicry in aculeates without describing the species composition of the ring. We found 14 references that described at least one ring that was the same as a mimicry ring from another study. Twenty-one of the 150 mimicry rings were revised in later studies. Fifteen of the studies focused on a single ring (Fig. 3A), i.e. on a single aposematic signal. These 15 studies focused either on a single species, and restricted their description to the mimicry ring of this species (e.g. Garcete-Barrett, 2014), or on unusual signals such as the ‘apple green’ colour of various aculeate families in

Madagascar (Pauly *et al.*, 2003). We therefore highlight that studies are restricted to a subset of the aculeate community, rather than investigating the local monomorphism expected for Müllerian mimicry (Müller, 1879). Knowledge of aculeate mimicry rings appears scattered among studies focusing on other aspects of aculeate biology and diversity, and is therefore incomplete with the true number of aculeate mimicry rings likely to exceed the 150 recorded here.

The maximum number of species per mimicry ring was 177 (mean = 14.45, median = 4, mode = 2; Fig. 3C,D). Considering the diversity of aculeates and the fact that predator-driven selection applies to an entire prey community, it seems unlikely that most mimicry rings only extend to two species. Therefore, mimicry ring sizes (Fig. 3C,D) are likely underestimated for the majority of described rings due to limited taxonomic or geographic study scale.



**Fig. 2.** Geographical distribution of studies on aculeate mimicry rings included in our data set. For each biogeographical zone, shades of grey and numbers inside the biogeographical regions represent the number of studies located for that region (13 studies covered several biogeographical areas). Barplots represent the number of species per taxonomic family included in these studies. Only the eight best-studied families are shown.



**Fig. 3.** Barplots of the information extracted from the 44 reviewed papers (data available in Table S1). Method used: Qualitative, verbal description; Colour-coding, numerical or categorical description of different body parts compared for each species; NMDS, non-metric dimensional scaling; Nothing mentioned, no description other than ‘mimicry’; machine-learning, estimation of the dissimilarity between pattern templates using a deep convolutional neural network; Spectral analysis, comparison of the reflectance profiles of the coloration using a spectrometer.

## (2) Are mimicry studies biased towards ‘dangerous’ species?

Some aculeates are better defended against predation than others. Social species and those with potent stings are more likely to impact their predators negatively. Thus, it may be the case that mimicry studies have focused more on social species, from Vespidae, Apidae and Halictidae, or on species known for their painful sting (e.g. Pompilidae and Mutillidae; Schmidt, 2019).

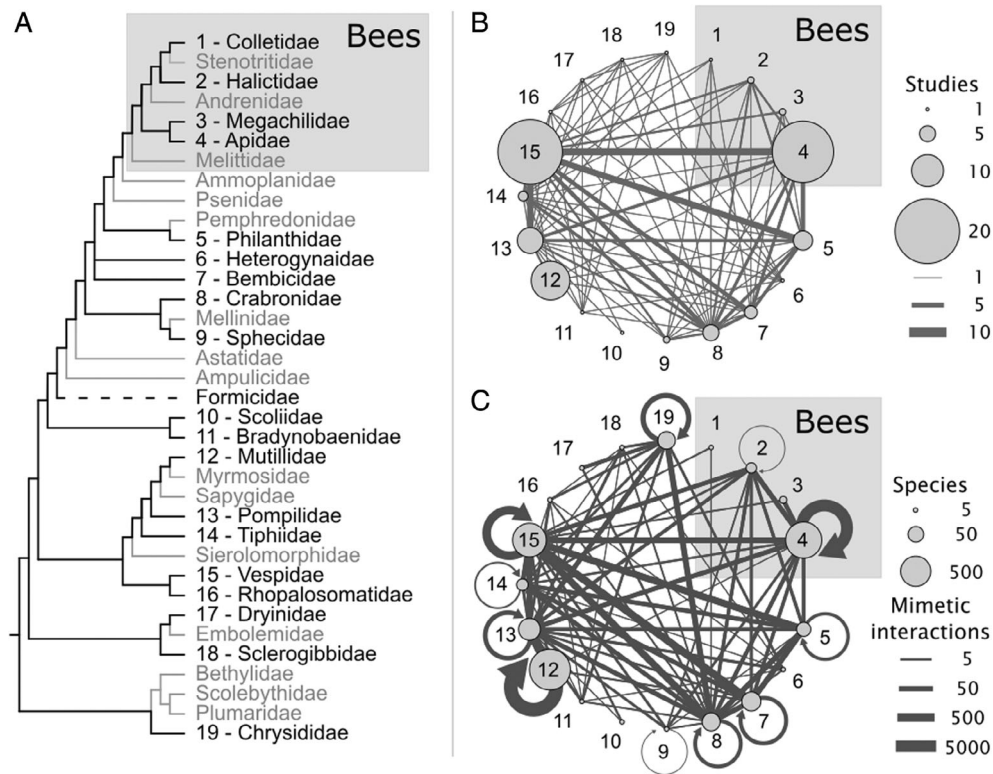
To date, at least 1089 species of bees and stinging wasps, belonging to 218 genera from 19 families (Tables S1 and S2; Fig. 4A), have been reported as part of Müllerian mimicry rings. This is a diverse but small proportion of the 53,000 known species of bees and aculeate wasps (Grimaldi & Engel, 2005; Aguiar *et al.*, 2013). This figure increases to 1150 when including subspecies, colour forms or hybrids. An accurate number is difficult to determine due to incomplete species identification in several studies. More precisely, we found records for 1025 species, 62 taxa

identified to the genus level or higher rank, two genera mentioned as belonging to mimicry rings with no mention of the exact number of species involved, 58 additional subspecies, varieties or colour forms and three hybrids (Table S3). As the large majority of studies used species as the taxonomic unit, we use the term ‘species’ below to designate any of the 1150 taxa with recorded involvement in a mimicry ring, including those studied at supra-specific or a subspecies level [see Doré *et al.* (2022) for discussion of the taxonomy unit problem in mimicry studies].

A total of 401 species (34.87%) were recorded in at least two studies with most of these from Mutillidae (299 species). We found a high level of polymorphism, with 190 species (16.52%) belonging to multiple rings, either in sympatry or not. Most of these (133 species) were bumblebees (genus *Bombus*).

The best-studied families (Fig. 4) were the Mutillidae (the velvet ants, 587 species), Apidae (bees and bumblebees, 300 species) mostly from the tribe Bombini, and Vespidae





**Fig. 4.** (A) Aculeate phylogeny [after Peters *et al.* (2017) and Sann *et al.* (2018)]. Taxa included in the 44 reviewed papers are in black, other taxa are in grey; numbers identify the corresponding nodes in B and C. (B, C) Network representation of the mimicry rings of the aculeate families included in the reviewed studies. Node size corresponds to the number of studies including this family (B), or to the number of species described as mimetic in the family (C). Link thickness corresponds to the number of studies suggesting a mimetic interaction between these families (B), or to the number of pairs of co-mimetic species between these families.

(wasps and hornets, 190 species) mostly from the subfamilies Eumeninae and Polistinae. Mimicry rings could include species from multiple aculeate families (up to nine; Fig. 4B), although the numbers of co-mimetic species from each family varied. It is noteworthy that bumblebee mimicry rings rarely included other aculeates (Apidae loop in Fig. 4B,C). However, the extent of aculeate taxonomic diversity in mimicry rings is probably underestimated (Fig. 4A): 31 studies out of 44 focused on a single aculeate family (Fig. 3B), and many aculeate families are under-represented or absent in the reviewed studies (Fig. 4). It was surprising to find that so few studies included Halictidae, as this family contains social, brightly coloured species, and has a number of species equivalent to the most represented families in this review.

### (3) Do bees and stinging wasps interact mutualistically through Müllerian mimicry?

Wasps are potential predators of bees (e.g. Spradbery, 1973), but they may also benefit bees by reducing their predation through Müllerian mimicry. To explore this, we determined how many studies reported mimicry between bees and stinging wasps, and whether these mimetic resemblances were restricted to certain bee groups. Out of the 13 studies that focused on more than one family, seven reported a mimicry

ring including at least one bee and one wasp (Ducke, 1909; Kasperek, 2019; Nicholson, 1927; Pauly *et al.*, 2003; Smith-Pardo, 2005; Waldbauer, Sternburg & Maier, 1977; West-Eberhard *et al.*, 1995). These rings involved four of the seven bee families (Apidae, Coletidae, Halictidae, Megachilidae), and eight stinging wasp families (Bembicidae, Crabronidae, Mutillidae, Philanthidae, Pompilidae, Sphecidae, Tiphidae, Vespidae). This suggests that mimicry between bees and stinging wasps evolved multiple times and is not anecdotal.

### (4) Have mimicry studies focused on specific geographic areas?

Studies included in this review reported mimicry rings from every continent except Antarctica. Their spatial scales were heterogeneous, from a few square kilometres to continental scale (Fig. 3E). Seven studies included mimicry rings from different continents. Most studies were carried out in North and South America (17 and 21 studies, respectively, Fig. 2). Only three studies focused on Afrotropical fauna but they included almost twice as many species as studies from the Palearctic. The Australasian and Indo-Malayan areas were also poorly investigated. Considering the distribution of bee diversity (Orr *et al.*, 2021), the low number of mimicry rings

studied in areas such as the Afrotropics, Australasia or even the Mediterranean region is more likely to reflect a bias in the geographical or taxonomic scope of research than a limitation of aculeate mimicry.

### (5) How were aculeate mimicry rings tested?

The most common method used to attribute species to a mimicry ring was the qualitative description of colour patterns (Table S1; Fig. 3F). Studies that included the largest number of species, most of which were published in the past 10 years, often used non-metric multidimensional scaling (NMDS) on morphological characters and colour coding (Fig. 3F and Table S1). The way such colour-coding data are analysed (qualitative and semi-quantitative data) differs among studies.

One study used a spectral analysis approach to model predator perception of these insects (Fig. 3F; Wilson *et al.*, 2020). All other studies reported similarities in appearance based on human perception, one study based on machine-learning used templates drawn by the researchers (Ezray *et al.*, 2019). Since predators are the drivers of mimicry, their perception will be a crucial aspect of defining a mimicry ring. Experiments on pigeons suggested that human visual perception is an accurate approximation of avian vision for insect classification (Dittrich *et al.* 1993; Bain *et al.*, 2007), so the mimicry rings described in the studies included here are likely to be biologically relevant. However, some exceptions were found, with wasp mimics classified as different from wasps by humans but almost identical by the birds. These differences may arise due to different perception abilities such as the ability to see ultraviolet (UV) colours in birds, but also to different cognitive abilities (Bain *et al.*, 2007), to physiological state such as hunger (Lindström *et al.*, 2004) or to the degree of unpalatability of the prey (Lindström, Alatalo & Mappes, 1997). Such generalisation by predators in natural conditions suggests that the size of mimicry rings described in aculeate studies could be underestimated.

If we define mimicry as the convergence of traits among different species under selective pressures due to predation, it becomes important to test whether resemblance among species is due to convergent evolution, rather than shared ancestry, using phylogenetic comparative methods.

In aculeates, seven of the 44 studies formally investigated phylogenetic relationships between Müllerian co-mimics (e.g. Smith-Pardo, 2005; Rodriguez *et al.*, 2014; Pekar *et al.*, 2017), representing only 100 out of the 1025 aculeate species studied in the context of mimicry. These were mostly bumblebees (Hines & Williams, 2012; Ezray *et al.*, 2019) and velvet ants (Wilson *et al.*, 2012).

Different methods were applied to assess convergence when analysing aculeate mimicry rings: genetic distance (Hines & Williams, 2012), distance correlations (Ezray *et al.*, 2019), Bayesian tip-association tests (Wilson *et al.*, 2012), permutation and phylogenetic principal component analysis (Rodriguez *et al.*, 2014), phylogenetic generalised least

squares (Pekar *et al.*, 2017), ancestral state reconstruction (Wilson *et al.*, 2020) and mapping of colour patterns onto the phylogeny (Smith-Pardo, 2005; Wilson *et al.*, 2020).

Convergence has been formally rejected for only one described mimicry ring: the ‘Eastern ring’ of the North American velvet ants (Wilson *et al.*, 2012). Species of this ring have a particular colour pattern, black and orange-reddish with silver setae, most likely due to common ancestry. Quantitative methods to test for convergence have been developed only relatively recently (Stayton, 2015a,b; Speed & Arbuckle, 2017), perhaps explaining why testing of convergence is poorly represented in the aculeate mimicry literature. Since more accurate phylogenies and molecular data are becoming increasingly available, these new methods represent a promising tool to disentangle the phylogenetic and ecological components of known aculeate mimicry rings.

## V. PREDATORS DRIVING MIMICRY IN ACULEATES

In the context of Müllerian mimicry, information about potential predators is important because they act as selective agents and may determine the strength of selection for a specific signal or form in a given habitat.

Eighteen of the 44 studies coupled their description or study of mimicry rings with predator identification. Putative predators were primarily lizards (Wilson *et al.*, 2012, 2015, 2018, 2020; Rodriguez *et al.*, 2014; Pan, Williams & Wilson, 2017; Ezray *et al.*, 2019), but also birds (Nicholson, 1927; Waldbauer & Sheldon, 1971; Waldbauer *et al.*, 1977; Plowright & Owen, 1980; West-Eberhard *et al.*, 1995; Hines & Williams, 2012; Pekar *et al.*, 2017; Ezray *et al.*, 2019), spiders (Pekar *et al.*, 2017; Ezray *et al.*, 2019), amphibians (Ezray *et al.*, 2019; Rodriguez *et al.*, 2014), mammals (Pauly *et al.*, 2003; Rodriguez *et al.*, 2014; Evans & West-Eberhard, 1970), dragonflies (O’Donnell & Joyce, 1999; Gilbert, 2004), robber flies (Ezray *et al.*, 2019; Evans & West-Eberhard, 1970; Gilbert, 2004), antlions (Evans & West-Eberhard, 1970) and wasps (Evans & West-Eberhard, 1970; Gilbert, 2004). Most of these studies used literature reports or indirect methods such as distribution data to identify potential predators driving the formation of a mimicry ring (e.g. Pan *et al.*, 2017). These studies identified potential predator assemblages in areas where a prey mimicry ring has been identified. Inference of predation was refined by using dietary preferences and spatio-temporal co-occurrence into account. However, different sexes and life stages of a predator species can have different ecologies and dietary habits, which could affect the validity of such methods (Best & Pfaffenberger, 1987; Punzo, 2003).

Among the 44 studies, only one study employed a direct approach to predator identification (Pekar *et al.*, 2017), on a mimicry ring in Australia consisting of one velvet ant species and several ant, bug and spider species. The authors used a combination of barcoding of gut content and faeces from

local predators and direct predation experiments to identify three predatory guilds (spiders, lizards and birds) for the local insect community. The results of these analyses confirmed the aversion of predators to members of the mimicry ring. More studies of this kind are needed to confirm and to understand the dynamics of other known mimicry rings.

Studies on predation are also important for other aspects of aculeate ecology. For example, it has been shown in multiple studies that predation can have a strong negative effect on flower visitations and time spent by pollinators on flowers (Knight *et al.*, 2005; Romero, Antiqueira & Koricheva, 2011). Since most aculeate species are pollinators (Kevan & Baker, 1983), it will be of interest to understand how aculeate species are affected by predation at the community level, and the role of Müllerian mimicry in protecting these communities from predation.

## VI. CONVERGENT TRAITS IN BEES AND WASPS

Several features are involved in detection and learning by a predator (Poulton, 1890; Heikertinger, 1921; Mostler, 1935; Hauglund, Hagen & Lampe, 2006). Among these features, conspicuous coloration such as contrasting colour patterns (e.g. black and yellow stripes) are likely to be the most important (Théry & Gomez, 2010). However, a focus on conspicuous coloration introduces a bias in the literature: other prey attributes, such as body shape or behaviour, are often overlooked (de Solan & Aubier, 2019). These other attributes also may have various non-warning functions (Hauglund *et al.*, 2006) and are therefore under other selective pressures. However, they may also be under selection for convergence among mimetic species, since they participate in overall resemblance (de Solan & Aubier, 2019). Below, we review how different traits involved in aculeate Müllerian mimicry, including but not restricted to coloration, have been assessed in the studies included in our analyses.

### (1) Conspicuous coloration

An organism can be conspicuous either because its coloration is strikingly different from the background, or because of strong internal contrasts. In aculeates, most species have at least some black or brown markings on their bodies. When referring to aposematic coloration, most authors refer to the other colours that contrast with these dark pigments. A distinction between coloration-based and pattern-based (i.e. the ways colours are arranged across the body) signals is also important for studies on aculeates. There is no opposition between coloration-based and pattern-based mimicry (Brodie Jr, 1993), but it introduces heterogeneity in comparisons and might blur proper interpretation of similarities (Badejo *et al.*, 2020). For instance, in a black-and-yellow striped pattern, the yellow colour increased the aversion of naive avian predators whereas the stripes increased their learning speed (Hauglund *et al.*, 2006).

### (a) Does mimicry rely on colours alone?

Seven of the 44 selected papers addressed colour-based signals of aculeate co-mimics, together with behaviour or general aspect (Gabritschevsky, 1926; Evans, 1968; Wheeler, 1983; Garcete-Barrett, 1999; Pauly *et al.*, 2003; Lanteri & Del Rio, 2005; Smith-Pardo, 2005). In these studies, mimicry was proposed without formal testing or critical evaluation. Colorations were succinctly described, sometimes with a discussion on pigmentation, such as the ‘apple green’ colour found in various Vespidae of Madagascar (Pauly *et al.*, 2003; Fig. 1E). Several studies on aposematism in a range of insects concluded that colour matters more than pattern (Aronsson & Gamberale-Stille, 2008; Finkbeiner, Briscoe & Reed, 2014; Rönkä *et al.*, 2018), including for aculeate-like models (Hauglund *et al.*, 2006). Regarding aculeate Müllerian mimicry, colour has been studied less often as a signalling trait compared to pattern.

### (b) Does mimicry rely on colour patterns?

Most mimicry rings that included aculeate species have been established on the basis of colour patterns, with 36 out of 44 studies referring to colour patterns.

Even when species share the same colours, the way those colours are distributed over the body may vary among species. For example, the ‘Texan mutillid’ ring has a black head and mesosoma, and a reddish to orange metasoma, whereas the ‘Western mutillid’ ring (Fig. 1D) has dense reddish dorsal setae and contrasting black setae on the legs, petiole and apex of the metasoma (Wilson *et al.*, 2012). The presence of contrasting colour patterns on the whole or parts of the body can be found within many different bee and wasp families, including Apidae (e.g. Plowright & Owen, 1980; Hines & Williams, 2012; Ezray *et al.*, 2019), Vespidae (e.g. van der Vecht, 1961; Garcete-Barrett, 2014), Mutillidae (e.g. Wilson *et al.*, 2015, 2018), Pompilidae (West-Eberhard *et al.*, 1995; Rodriguez *et al.*, 2014), Chrysididae (Mora & Hanson, 2019), Sphecidae (West-Eberhard *et al.*, 1995; Nicholson, 1927), and others such as Philanthidae, Bembicidae and Crabronidae (Nicholson, 1927; Waldbauer & Sheldon, 1971; Waldbauer *et al.*, 1977). Thus, patterns involving contrasting or bright colours are common in aculeates and are usually recognised as aposematic signals (Poulton, 1887). However, they are extremely diverse, ranging from simple alternating black and reddish bands such as the ‘Pepsis-like’ ring from South America (Evans, 1968) to complex multicolour patterns such as the ‘Tropical ring’ of velvet ants and spider wasps (Rodriguez *et al.*, 2014).

### (2) Morphology and shape

In addition to coloration, aculeates exhibit a large diversity in the shape of body parts (e.g. legs, wings, mesosoma, metasoma) or overall appearance. Even with similar colours, a bumblebee, a spider wasp, or a solitary bee of the same size may not appear visually similar to a predator if the general aspect (i.e. the overall appearance perceived by an observer) differs. Although morphology and shape are striking components of

prey phenotypes, quantitative protocols to study and compare aculeate co-mimics with respect to these are very rare. A global approach was used in one study on aculeates to define mimetic pairs with dipteran Batesian mimics using a machine-learning approach (Hassall *et al.*, 2019), with mimetic pairs found to be similar for either human or avian subjects.

In our literature survey, only 12 of the 44 studies took body shape and morphological elements into account when defining mimetic interactions. One explanation for the scarcity of analytical studies on body shape could be that it is often implicitly considered in visual-appearance-based methodologies (Evans, 1968; Smith-Pardo, 2005), without any quantitative evaluation. Another reason could be that many studies that did not discuss body shape in aculeate co-mimics focused on closely related species with restricted body shape variation (e.g. Garcete-Barrett, 2014; Nugroho, Lupiyaningdyah & Kojima, 2020).

### (3) Sound

Like many insects, aculeates produce recognisable sounds when attacked by predators, such as buzzing, vibrations or stridulation (Kirchner & Röscher, 1999; Quicke, 2017). None of the mimicry rings described in the included studies invoked sound as a convergent trait among aculeate species, although this is theoretically possible and was suggested for Batesian mimics of aculeates (Evans & West-Eberhard, 1970).

Acoustic signals may be perceived by predators as a warning of chemically defended prey or as reinforcement of another aposematic signal. Experiments artificially preventing mutillids or their Batesian mimics from stridulating increased their risk of predation in laboratory conditions, demonstrating that predators can react to ‘acoustic aposematism’ (Masters, 1979; Pekar, Garcia & Bulbert, 2020). However, another experiment showed that a bumblebee sound did not affect the learning speed of chicks to avoid unpalatable food (Siddall & Marples, 2011), suggesting that ‘acoustic aposematism’ requires further study.

Aposematic sounds could be under selection for convergence in mimetic systems, but acoustic mimicry has rarely been rigorously tested (Aubret & Mangin, 2014; Moore & Hassall, 2016). Bee buzzing mimicry has been debated with regard to their harmless Batesian mimics (Myers, 1935; Van Zandt Brower & Brower, 1965; Rashed *et al.*, 2009; Skowron Volponi *et al.*, 2021). In aculeates, the aposematic potential of acoustic signals is still too poorly studied to draw general conclusions about its efficiency and role in reducing predation. However, if, as documented above, acoustic mimicry is found among aculeates and their Batesian mimics, we could also expect it to be present among Müllerian aculeate mimics. Acoustic mimicry raises the additional challenge of quantifying such signals as perceived by potential predators in a comparative framework.

### (4) Behaviour

Similarity in behaviour between aculeate co-mimics was mentioned in 10 of the 44 studies (Evans, 1968; Evans & West-Eberhard, 1970; Thorp, Horning & Dunning, 1983;

Nentwig, 1985; Yanega, 1994; West-Eberhard *et al.*, 1995; Dejean, Corbara & Lachaud, 1998; Garcete-Barrett, 1999; Gilbert, 2004; Pan *et al.*, 2017). These similarities included flight style (Evans, 1968), areas visited in the environment (Yanega, 1994; Dejean *et al.*, 1998), and locomotion (Nentwig, 1985; Pan *et al.*, 2017), but most references only mentioned a similarity in behaviour with little detail. Behavioural mimicry remains therefore largely unstudied in aculeates.

When a prey moves in a given habitat, its movements are not random. Unlike crypsis, a particular behaviour can be visually conspicuous and could act as an aposematic signal (Skowron Volponi *et al.*, 2018). Bees and wasps can fly in very characteristic ways, notably regarding trajectory straightness, speed, directional changes and height (Skowron Volponi *et al.*, 2018). Such behavioural cues are likely to play a role in detection and attack decisions by predators. In aculeates, flight patterns and resting poses could be selected as cues by predation pressures, but such convergence remains to be studied.

### (5) Multimodal signalling

As discussed in Sections VI.1–4, aposematism and mimicry could involve multiple traits in aculeates, from morphology to behaviour, and multimodal signalling is therefore likely. For example, behavioural mimicry is unlikely to evolve unless it is associated with another warning signal, such as coloration or general aspect (Penney *et al.*, 2014). Multiple signals are probably present simultaneously in many cases (Sexton, 1964; Best & Pfaffenberger, 1987; Punzo, 2003), and seven studies took at least two of these components into account when describing their mimicry rings, mostly general aspect with coloration or colour patterns.

There might be a selective advantage to multicomponent deceptive signals over single-component signals (Skelhorn, Halpin & Rowe, 2016). Experimental approaches to aposematism, including those with aculeate models (e.g. Kauppinen & Mappes, 2003; Taylor *et al.*, 2017), have attempted to disentangle the respective roles of shape, size, pattern and colour in warning signals. Kauppinen & Mappes (2003) suggested that avoidance by dragonflies was due to the presence of a contrasted coloration with a weak effect of body shape or colour type. By contrast, humans seem to rely mostly on shape to distinguish immobile insects and less on size or colour patterns (Taylor *et al.*, 2017). Another trait not discussed above, odour, was also tested and refuted as a potential signal (Kauppinen & Mappes, 2003). However, we still need comparative studies specifically designed to investigate Müllerian mimicry in aculeates that disentangle all the traits involved in signalling.

To conclude, most studies on aculeate Müllerian mimicry used colour patterns to identify the mimicry rings, but other attributes could also be under positive frequency-dependent selection within these mimicry rings. Few studies mentioned these other traits when addressing aculeate Müllerian mimicry, and we currently lack formal tests of convergence of these traits. Further studies on aculeate mimicry that go

beyond coloration and include shape, size, sound and behavioural aspects of aculeate similarity are therefore needed.

## VII. OTHER FACTORS AFFECTING MIMICRY IN ACULEATES

Müllerian mimicry requires shared predators, but its dynamics also depend on other factors. Below, we discuss some of these factors, how they could impact Müllerian mimicry in aculeates and how they were tackled in the studies reviewed herein.

### (1) Mimetic fidelity

Mimetic fidelity is the degree of similarity between co-mimics, as perceived by their predators. When co-mimetic species have only a weak resemblance, mimicry is said to be imperfect (Kikuchi & Pfennig, 2013). The less co-mimics resemble one another, the less they share the aposematic signal, and the more they will suffer the cost of predator education. Although several studies have addressed mimetic fidelity of Batesian mimics towards aculeate models (e.g. Penney *et al.*, 2011), to our knowledge, no study has quantified mimetic fidelity among bees or wasps to evaluate its impact on mimicry ring structure and evolution.

Yet, mimetic fidelity potentially has a strong impact on the fitness of co-mimics depending on how much predators generalise their phenotypes (Penney *et al.*, 2011; Iserbyt *et al.*, 2011). Indeed, if predators can discriminate phenotypes that differ only slightly, they may not be fooled by an imperfect mimic. By contrast, if they discriminate less well, selection on close resemblance may be relaxed. Imperfect mimicry can be maintained by selection if alternative edible prey occur as a source of energy (Poulton, 1890; Sherratt, 2003).

Mimetic fidelity may be enhanced when the predator itself is part of the mimicry ring, for example, in aculeates, wasps can be visual predators of other aculeates. Social wasps were reported as the main driver behind high-fidelity mimicry of a Batesian mimic, a day-flying moth, masquerading as a wasp, its own predator (Boppré, Vane-Wright & Wickler, 2017). In this case, the moth benefits both from masquerading as its predator, as wasps tend to avoid conspecific individuals, and from mimicking its predator as seen by other predators. This high-fidelity convergence is likely induced by strong selection because wasps may be better at visually identifying conspecifics than other organisms. Similar striking masquerades were also found between cleptoparasite aculeates and their bee hosts (Williams, 2008; Kasperek, 2019). In the case of aculeate mimicry, models and mimics could therefore share both a mimicry ring and a prey–predator or a host–parasite relationship. Three studies noted host–parasite similarities in a context of aculeate Müllerian mimicry (Plowright & Owen, 1980; Williams, 2008; Kasperek, 2019)

but this topic has yet to be explored concerning predation within a mimicry ring and its potential effects on mimetic fidelity.

### (2) Different levels of defence

Unpalatability comprises venom toxicity, pain, a bad taste, unpleasant internal buzzing and hard cuticular parts (Rettenmeyer, 1970; Quicke, 2017). Aculeate females in a given mimicry ring might not be equally defended. Although qualitative differences in unpalatability have been reported within the reviewed mimicry rings (e.g. Spradbery, 1973; Waldbauer & Cowan, 1985; O'Donnell & Joyce, 1999; Pauly *et al.*, 2003; Smith-Pardo, 2005), only one study quantified this variation (Pekar *et al.*, 2017). In this study, unpalatability was defined as the sum of the traits linked to unpalatability, i.e. sting length, number and length of spines, size of mandibles, cuticle thickness, size of the poison/pygidial gland, and whether the species performed communal attacks. Although this study focused mostly on ants and included only a single other aculeate, it showed that there was considerable variation in unpalatability among species but not among rings, and that most species were moderately unpalatable.

Pain is a major component of aculeate defences (Schmidt, Blum & Overal, 1980; Starr, 1985; Schmidt, 2004, 2019), and is likely important for predator learning. Although studying pain is not straightforward, in part due to the difficulty of objectively quantifying ‘pain’, we believe that such research will yield novel material for mimicry theory and testing.

Effective unpalatability depends on both prey defences and predator sensitivity to these defences (Wallace, 1882; see also e.g. Dixey, 1919; Nicholson, 1927; Brower *et al.*, 1968). This variability will have major consequences on selection because a defended prey can still be attacked if it is profitable – which is related to the net gain of energy (Aubier, Joron & Sherratt, 2017; Aubier & Sherratt, 2020). Depending on the population size and predators’ hunger and experience, unequally defended co-mimics can have either a mutualistic (Rowland *et al.*, 2007) or a parasitic relationship (Rowland *et al.*, 2010), the latter being termed ‘quasi-Batesian’ mimicry (Speed, 1999). The relative contributions of ‘less defended’ aculeate species to their mimicry rings and their potential impact on ring structure remain unknown. This effect of degree of defence will also be impacted by the presence of harmless individuals within a species: the stingless males.

### (3) The impact of stingless haploid males on mimicry

In all aculeate species, males are haploid and lack the sting and venom gland, the main defence mechanism derived from ovipositor structures. Therefore, aculeate males act not as Müllerian mimics but as Batesian ones (Table 1), both among and within species.

Males that resemble their own females are called ‘automimetic’. Automimicry (Table 1) is Batesian mimicry

within a species, where some undefended individuals (males in the case of aculeates) benefit from a warning signal associated with defences of other individuals (here, females), at the cost of reducing the signal efficiency. In aculeates, automimicry was first reported for bumblebees (Stiles, 1979). More recently, automimicry was addressed in an evolutionary perspective for carpenter bees, albeit not under the prism of Müllerian mimicry *per se* (Blaimer, Mawdsley & Brady, 2018). There is a benefit to automimetic male bees and wasps in co-mimetic species because this decreases their risk of predation (Stiles, 1979). Automimicry prevalence has remained largely overlooked, and male automimicry was mentioned in only seven of the 44 studies (Evans & West-Eberhard, 1970; Waldbauer & Sheldon, 1971; Waldbauer *et al.*, 1977; Plowright & Owen, 1980; Thorp *et al.*, 1983; Wilson *et al.*, 2012, 2015).

Automimicry may also be extended to behaviour: while lacking a sting, some aculeate males exhibit a pseudo-stinging behaviour when caught (Evans, 1968; Rothschild, 1984; Stubblefield & Seger, 1994). Males can move their abdomen in a motion that is very similar to a stinging female in action (Giannotti, 2004; Quicke, 2017). Furthermore, sting-like genitalia are known in some wasp males [*Myzinum quinquecinctum* tiphiid wasp (Quicke, 2017) and *Anterhynchium gibbifrons* mason wasp (Sugiura & Tsujii, 2022)], which could accentuate mimicry of the stinging behaviour. Pseudo-stinging behaviour was shown to be an effective anti-predator defence when genitalia have sting-like structures (Sugiura & Tsujii, 2022).

When males do not mimic females of their own species, but instead resemble stinging females from another species (special cases of sexual dimorphism), this is referred to as dual mimicry (Evans, 1968). Among the reviewed studies, dual mimicry was only highlighted in spider wasps [Evans (1968); see also Day (1984) on male polymorphism]. Sexual dimorphism may be widespread among bees and wasps (Blaimer *et al.*, 2018) but we do not know how common it is. Interestingly, Evans (1968) suggested that micro-habitat segregation between the sexes in the genus *Chirodamus* may explain colour dimorphism, as males remain above the ground in a habitat dominated by similarly coloured social wasps, whereas females forage on the ground with other orange-winged solitary females.

A potential consequence of the absence of defence in males and their Batesian interaction with females of their own or different species is that males tend to be more variable in coloration than females (e.g. Thorp *et al.*, 1983). This could be caused by negative frequency-dependent selection, as often observed for colour patterns of Batesian mimics, which is expected to drive polymorphism (Ruxton *et al.*, 2004; Shine, Brown & Goiran, 2022). In addition, in species where males have shorter lifespans than females, selection on males might be relaxed compared to that on females.

Haplo-diploid sex determination in aculeates, where recessive alleles are always expressed in males, but not in heterozygous females, could potentially impact the dynamics of

mimicry. Dominance has been shown to maintain warning pattern polymorphism and to favour rare alleles under certain circumstances in Müllerian systems (Llaurens, Billiard & Joron, 2013). The consequences of sex-dependent dominance patterns due to haplo-diploidy in combination with the absence of defences in males on the evolution of mimicry has been investigated using theoretical modelling (Boutin *et al.*, 2022), but remains to be explored more widely empirically.

#### (4) Body size

Fourteen studies mentioned a similarity in body size when defining mimicry rings (Evans, 1968; Waldbauer & Sheldon, 1971; Waldbauer *et al.*, 1977; Dressler, 1979; West-Eberhard *et al.*, 1995; Dejean *et al.*, 1998; O'Donnell & Joyce, 1999; Gilbert, 2004; Lanteri & Del Rio, 2005; Garcete-Barrett, 2014; Perrard *et al.*, 2014; Pekar *et al.*, 2017; Kasperek, 2019; Hlaváček *et al.*, 2022) but only one study quantified body size to define their mimicry ring (Pekar *et al.*, 2017).

Prey body size is known to affect prey choice by predators, with predators preferring larger prey within the limits of their handling capacities (Kasperek & Joern, 1993). Body size may therefore impact mimicry by affecting the community of predators involved, the attractiveness of the species and the level of defence they need (Smith, Halpin & Rowe, 2016). A small bee is unlikely to be confused with its 10 times larger relatives even though they have similar colours and shape, since at least some predators are able to discriminate palatable prey based on size (Marples, 1993).

Bees and wasps exhibit a large diversity of body sizes, sometimes even within a given species (see Section VII.7 for caste differentiation in social species). Thus, body size could be an important parameter shaping mimetic interactions within an aculeate community. However, this remains untested. Mimicry accuracy increased with body size in velvet ants, suggesting that patterns are more distinguishable on larger prey (Wilson *et al.*, 2013; also discussed in Penney *et al.*, 2011). Pekar *et al.* (2017) included body size in their analyses, but only to control for size in coloration assessment or to correlate size with defence traits.

We expect that mimicry is more likely to occur between species of similar sizes and that larger prey present a more conspicuous warning signal than smaller ones (Pembury Smith & Ruxton, 2021). Furthermore, small-bodied prey are likely to benefit more from possessing toxins than larger ones, which would need a much larger amount of toxins to reach an equivalent level of defence (Smith *et al.*, 2016). Evolutionary shifts in the mimicry model can be associated with differences in body size, as was shown for net-winged beetles (Motyka, Kampova & Bocak, 2018). It was also suggested in social Vespidae, where larger queens of some species mimic different species compared with their smaller workers (Perrard *et al.*, 2014). We hope that the influence of body size on Müllerian mimicry within aculeates will be explored in the near future.

### (5) Abundance

Since the origins of Müllerian mimicry theory, quantitative models implementing species abundances have been developed (Müller, 1879; Mallet & Joron, 1999; Joron & Iwasa, 2005). As Müllerian mimics converge under positive frequency-dependent selection, the more abundant an aposematic signal is, the more the *per capita* mortality rate of individuals harbouring this signal decreases. Prey abundance could also enhance signal effectiveness, as predators will be constantly reminded of it (Speed, 1993). Twenty studies from those included herein considered this aspect of mimicry among aculeates. Most only mentioned that some members of the mimicry ring were common, but two used abundance in the description of the mimicry ring to disentangle numerical and noxious components of protection (O'Donnell & Joyce, 1999), or implemented species density in a model explaining colour polymorphism by temporal effects in bumblebees (Plowright & Owen, 1980). Model abundance was also used as an argument to categorise two bees (*Neocorynura rufa* and *N. panamensis*, Halictidae) as Batesian mimics of other bee and wasp species, even though they also possess a sting and very likely venom (Smith-Pardo, 2005). This classification may be discussed since abundance (numerical protection) and toxicity (chemical protection) are to be considered jointly (Briolat *et al.*, 2019).

There are few data assessing the relative abundances of the species forming known mimicry rings (Kikuchi *et al.*, 2021). Abundance data are still largely absent in the aculeate literature. Appreciating the quantitative nature of Müllerian mimicry processes would allow a far better understanding of mimicry dynamics.

### (6) Phenology

Convergence on a given colour pattern and the emergence of a mimicry ring will depend on patterns of co-occurrence in space and time, as well as on the predator community present. It has long been recognised that phenological mismatch between co-mimics is critical for predator education (Silberglied & Eisner, 1969; Waldbauer & Sheldon, 1971; Waldbauer *et al.*, 1977; Evans & Waldbauer, 1982; Gilbert, 2004; Hassall *et al.*, 2019; Svenson & Rodrigues, 2019; Hlaváček *et al.*, 2022). Phenology can influence the fitness of co-mimics, especially when more or less unpalatable species form a mimicry ring, because education of predators depends on the temporal sequence of the encounter with unpalatable prey. Out of the 44 studies, 11 provided information on phenological dynamics, mostly in bumblebees (Waldbauer & Sheldon, 1971; Waldbauer *et al.*, 1977; Dressler, 1979; Plowright & Owen, 1980; Owen & Plowright, 1988; O'Donnell & Joyce, 1999; Pauly *et al.*, 2003; Gilbert, 2004; Williams, 2008; Hines & Williams, 2012; Hlaváček *et al.*, 2022).

Phenology affects co-occurrence, which is generally implicit within studies (e.g. Silberglied & Eisner, 1969; Pauly *et al.*, 2003; Martin *et al.*, 2010; Hines & Williams, 2012).

For field-based studies, individuals are usually collected on the same dates, but this may not be true for large studies and may not account for intra-annual or seasonal dynamics of the ring (see Mappes *et al.*, 2014) where the benefit of aposematism decreases during the season. The earlier a species appears in a season or a predator life cycle, the more it will suffer from naive predation. Within a mimicry ring, late species therefore benefit from more protection than earlier ones, a phenomenon coined 'serial mimicry' (Plowright & Owen, 1980). In our 44 studies, one study discussed how serial mimicry combined with automimicry could select for temporal polymorphism in a bumblebee species (Plowright & Owen, 1980). In this species, early specimens benefit from a black signal already exposed to predators, until the early emergence of males of the black co-mimics, which counter-select the black signal in favour of the red one, which has not yet been learned by predators.

The impact of phenology on the fitness of co-mimics will also be related to the spatial range and lifespan of their predators. Such information can be hard to obtain from field studies because it requires multiple long-term studies with time-consuming captures. While it might still be unrealistic to attempt an integration of phenological information into mimicry ring definition, with attention to this knowledge gap, this may be possible in the future.

### (7) Sociality

In our results, 29 out of the 44 studies included social species. However, few studies included data on social castes in mimicry ring delimitation (Waldbauer & Sheldon, 1971; Waldbauer *et al.*, 1977; Williams, 2007, 2008; Hines & Williams, 2012; Perrard *et al.*, 2014), and only two discussed the link between sociality and aposematism (O'Donnell & Joyce, 1999; Perrard *et al.*, 2014). O'Donnell & Joyce (1999) suggested that social wasps of the genus *Agelaia* (Vespidae) should be considered as mimetic models for two morphs of *Mischocyttarus mastigophorus* (Vespidae) because the colonies of the former are much larger, abundant and aggressively defended (Wenzel, 1992). Perrard *et al.* (2014) raised the hypothesis that caste colour polymorphism of several wasp species could be linked to mimicry of local species of different sizes. However, these two hypotheses were not tested.

We found that a third (34%) of all co-mimics were social species, while social species represent around 6% of aculeate bee and wasp taxa worldwide (Batra, 1984; Archer, 2012). This suggests that the prevalence of mimicry among bees and wasps tends to be higher in social species. It could also reflect a study bias towards social species that are more abundant or more appealing as research subjects than solitary ones.

Links between sociality and aposematism have been studied for social-like behaviours, such as gregariousness, where density is also increased. It has been shown that aposematism can promote the evolution of gregariousness in butterflies (Sillén-Tullberg, 1988; Tullberg & Hunter, 1996), and may even facilitate transitions to solitary living

(Wang *et al.*, 2021). The effect of eusociality (i.e. reproductive division of labour, cooperative brood care and overlap of generations) on aposematism and mimicry raises several hypotheses that have yet to be supported by empirical evidence: (i) sociality could enhance predator learning by increasing the aggressiveness and local abundance of signal carriers (Spradbery, 1973; Breed, Guzmán-Novoa & Hunt, 2004); (ii) new aposematic signals establish more easily if exhibited by social species due to the presence of multiple, sterile individuals that act on predator education more efficiently than solitary species; (iii) the possible influence of size on mimicry could drive the evolution of colour caste dimorphism (Perrard *et al.*, 2014).

The factors discussed in this section are likely to be interlinked: for example, caste polymorphism and phenology (Hines & Williams, 2012) or sociality and size or morphology (Wheeler, 1991; Harvell, 1994; O'Donnell, 1998). While we lack data for how these factors independently or jointly affect Müllerian mimicry in aculeates, studies that address these aspects in an integrated way are much needed.

## VIII. CONCLUSIONS

(1) Aculeates are one of the largest taxonomic groups involved in Müllerian mimicry. We identified 1150 species or subspecies putatively involved in Müllerian mimicry in the literature. Considering the gaps found in the literature, this number is likely a strong underestimate of the actual number of aculeate species with mimetic interactions. Although Müllerian mimicry among aculeates has long been acknowledged, relatively few comprehensive studies and descriptions of mimicry rings are available. Some parts of the world, such as the Mediterranean region, seem understudied. The protective value of bees or wasps' aposematic signalling might be more widespread and common than current studies suggest.

(2) Various predator taxa attack and learn to avoid aculeate Müllerian mimics. However, studies documenting predation are often independent of mimicry ring delimitation. Aposematic signals and cues in mimicry depend on the receiver's perception. Therefore, different predators, with different vision models, might lead to the evolution of different mimicry rings. We advocate that empirical findings on mimicry rings should be related to their actual predator communities. We need more experimental studies to investigate the drivers of the 150 aculeate mimicry rings currently recognised around the world.

(3) There are multiple traits for which bees and wasps converge under predation pressures. The best studied in the Müllerian mimicry literature are colour patterns and general aspect. Behaviour mimicry, sound aposematism and multi-modal signalling are reported for aculeates and appear important in a mimetic context but are understudied in the reviewed literature. We also highlight a lack of testing for convergence between co-mimetic species. Considering that

sharing a given aposematic signal might be due to common ancestry, convergence (*sensu lato*) should be tested using phylogenies when studying aculeate mimicry.

(4) In comparison to well-studied Müllerian mimetic taxa, e.g. toxic neotropical butterflies such as the genus *Heliconius* or the tribe Ithomiini, crucial factors that have a significant impact on mimicry ring evolution and dynamics, such as body size, species abundance, phenology, imperfect mimicry or sociality, are not well documented for aculeate co-mimics. The impact of such parameters on the dynamics of mimicry should be tested using both experimental data and theoretical models. The case of males is also interesting regarding aculeates: males do not sting and can be considered as Batesian mimics or automimics (when there is no sexual dimorphism), which is likely to impact predator learning and reduce the overall protection of aposematism. Hymenopteran males – both in social and solitary species – are haploid, and recessive alleles should always be expressed in males. This constitutes an intriguing and unexplored context for future studies on genetic variation in mimetic systems.

(5) Bees and wasps represent useful potential models in aposematism and Müllerian mimicry research, and therefore for the entire field of evolutionary biology since they provide a compelling example of natural selection. With only 44 studies addressing this phenomenon, with only a thousand out of the tens of thousands of known species in the group, aculeate mimicry research appears still in its infancy. It seems very likely that many more aculeate mimetic systems will be uncovered in the near future, and attention should be drawn to more comprehensive approaches. Finally, since many aculeate species are pollinators, experiencing a now well-recognised global decline (Zattara & Aizen, 2021), this research could shed light on a potentially overlooked additional threat, the loss of co-mimetic species.

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## XI. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Table S1.** Details of the studies included in our review.

**Table S2.** Details of taxa and their putative mimicry rings found in the studies included in our review.

**Table S3.** Detailed list of taxa in the database.

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