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Müllerian Mimicry and pollinators decline

Paul Chatelain

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École doctorale 227

Sciences de la Nature et de l'Homme : écologie et évolution

Thèse de doctorat en Sciences de l'Evolution

Mimétisme mullérien et déclin de pollinisateurs

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*La souffrance enfante les songes
Comme une ruche ses abeilles*

Louis Aragon, *Les Poètes*

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This is it!

Et voilà, cette thèse se termine ! Ou presque ! Ou déjà ! Ou encore ! En tous les cas j'ai à cœur d'adresser ici mes remerciements à toutes celles et ceux qui l'ont rendue possible, qui m'ont accompagné ou suivi dans cette aventure. Merci à tous !

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General Introduction

« Si au total la capacité de piquer est utile à la communauté sociale, elle remplira toutes les conditions requises par la sélection naturelle, même si elle cause la mort d'un petit nombre de ses membres »

Charles Darwin, *L'Origine des espèces*, 1859

0.1 Adaptive coloration in Hymenoptera

Bees, bumblebees, wasps, hornets, velvet ants and many other aculeate hymenoptera are diverse, colorful, and diversely colored animals, exhibiting a range of colors varying from metallic blue to bright and contrasting yellow or red bands/stripes (Figure 0.1). Colors in hymenoptera, like in other insects, are produced through reflection of sunlight in various ways. Colorations can be either pigmentary or structural or both; and borne by the cuticle, or hair (Chapman & Chapman, 1998). Different pigments in different concentrations produce different colors on body parts: mainly melanin (black to red), pterins (yellow), purines (orange to reddish). Colors in insects have multiple integrative functions, such as body protection, signaling and physiology (Badejo *et al.*, 2020).

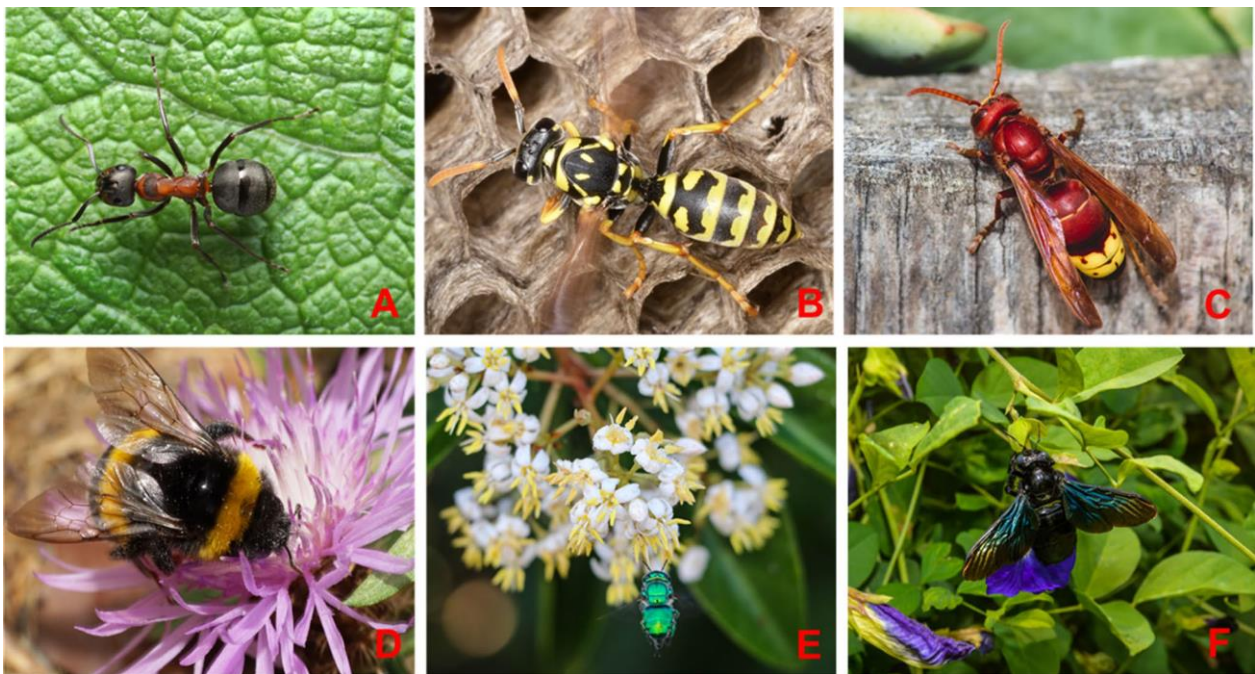


Figure 0.1. Diversity and types of colorations in various aculeate species (from Badejo *et al.* 2020). **A** melanin based coloration of *Formica rufa*; photo ©Andrey Pavlov. **B** Melanin and pterin in *Polistes dominula*; photo ©Andrey Pavlov. **C** Melanin-, purine-, pteridine-based pigment coloration of *Vespa orientalis*; photo ©Tennessee Witney **D** Melanin- and pterine- based hair colors in *Bombus lucorum*; photo ©Sergey. **E** Structural green coloration in *Euglossa dilemma*; photo ©Laurel A Egan. **F** Blue pigment and structural cuticular coloration of *Xylocopa sp.*; photo ©YuRi Photolife

Like in many insects and also vertebrates, Hymenoptera colorations have been considered under numerous adaptive hypotheses (due to natural or sexual selection). Crypsis, for instance, is the ability for a potential prey to avoid predation by remaining undetected in the environment. Williams examined some bumblebees' (Apidae) colorations which might (by disruptive effect) prevent detection by predators in their environment (Williams, 2007). He suggested there might be a match between the color of the ground and of workers, making the position of the nest less detectable by predators. Another type of protection against predators, masquerade (where prey is well detected but recognized as another unappealing object), has been reported in desert velvet ants (Mutillidae), which mimic a fruit of creosote bush (Wilson *et al.*, 2020). In social wasps, conspecific recognition may also drive color pattern variation but rather on the head of these insects (Cappa, Beani & Cervo, 2016; Boppré, Vane-Wright & Wickler, 2017). Similarly, paper wasps' males with more black on the face and larger yellow spots on the abdomen are more likely to be chosen by queens for reproduction (Souza *et al.*, 2014). Because insects are ectotherms, thermoregulation has been frequently invoked as a driver of colorations (*e.g.* Stiles, 1979; Pereboom & Biesmeijer, 2003; Williams, 2007; Plotkin *et al.*, 2009; Badejo, Skaldina & Sorvari, 2018; Lopez *et al.*, 2021), darker forms (*i.e.* with higher proportions of black pigments) being better adapted to cold environments as light is better absorbed, resulting in faster heating of the body.

Finally, aposematism is the most common explanation in the literature (*e.g.* Cott, 1940; Plowright & Owen, 1980; Wilson *et al.*, 2012; Hines *et al.*, 2017; Blaimer, Mawdsley & Brady, 2018; Willadsen, 2022). Aposematism (Poulton, 1890) is the association of a conspicuous warning signal (typically contrasting coloration) with a mechanism of defense (typically a chemical defense). It is precisely where our present work begins.

0.2 From Aposematism to Mimicry

What are exactly these defense mechanisms in bees and wasps? The unfortunate knows: with only a very few exceptions, aculeate females possess a venomous and painful sting. This sting has evolved as a modification of the ovipositor. It has defensive and hunting functions (for hunting wasps). Sting induces pain to a potential predator and/or can be also used to penetrate and paralyze potential prey. The morphology of the sting apparatus is composed of several mobile valves which make it retractable and efficient in tissues penetration and injection (Figure 0.2).

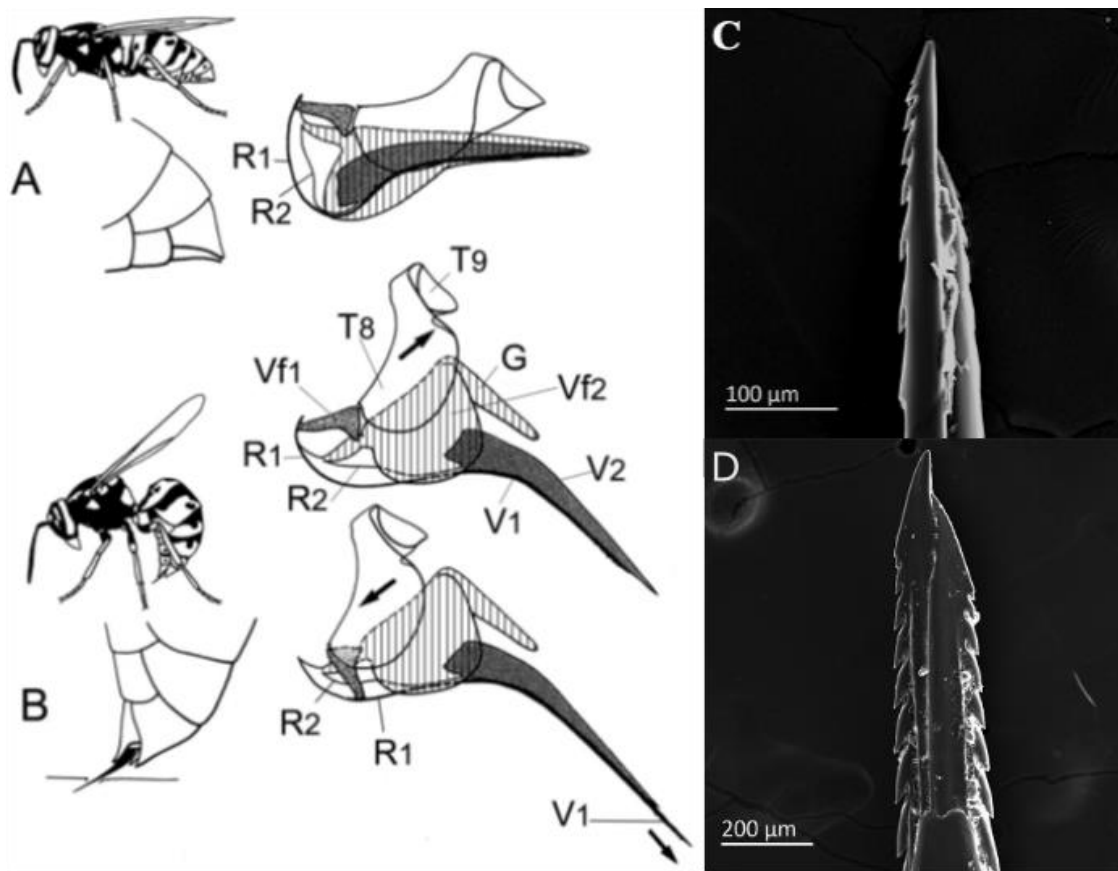


Figure 0.2. Aculeates' sting apparatus morphology, moving from A to B in action (after Akre *et al.*, 1981, in Villemant & Casevitz-Weulersse, 2015), G: gonostyle; T8-T9: last tergites; R1-R2: ramus; V1: lancet; V2: stylet; Vf1-Vf2: valvifera; C-D scanning electron microscope image of respectively: *Apis mellifera* and *Vespa mandarinia* (from Baumann *et al.*, 2018).

Aculeate females vary in many defensive traits, such as venom quantities and composition (Pekar *et al.*, 2017), sting length (Sadler, Pitts & Wilson, Joseph S., 2018), structure and also composition (Polidori, Garcia & Nieves-Aldrey, 2013; Polidori *et al.*, 2020; Jorge *et al.*, 2017; Baumann *et al.*, 2018). Indeed, the sting apparatus in itself, as some mouth parts, can be armed with barbs and/or enriched in metals, such as Zn, Fe, Mn, Ti, Cu, which most likely increases the hardness and physical pain (Figure 0.2.C-D).

Chemical pain is induced by venom injection. Venoms in Hymenoptera have also multiple functions (primary or secondary) and can be composed of many components, the effects of which are not always correlated (Sadler *et al.*, 2018; Schmidt, 2019; Ronchetti & Polidori, 2020). The functions of venom injection can be involved non-exclusively either in defense against attackers/predators, like in social or solitary bees (Aculeata, Anthophila), or in predation, like in spider wasps (Aculeata, Pompilidae), where adults paralyze/kill their prey to feed the larvae (Dashevsky *et al.*, 2023). There is a large variation of venom composition among aculeate families even within a single genus, and components implied in inducing pain may differ (Jensen *et al.*, 2021). There might be convergence for pain inducing components. Some of them are relatively constant, however, and have specific effects, all known to induce pain (Piek, 2013). Despite the fact that posttranslational modifications of venom proteins can be numerous and complex, it has been shown that most of the known venom peptides from aculeate hymenoptera are derived from a gene superfamily - called 'aculeatoxins' - (Robinson *et al.*, 2018). For example, a recent study identified two kinds of peptides as responsible of pain in velvet ants stinging: Dk5 and Dk13, composed of 25-29 residues (amino-acids), that interact with cell membranes and increase ion conductivity (Ca²⁺) and pain signaling (Jensen *et al.*, 2021). Although the mode of action of

aculeate toxins may differ among groups, depending on peptide chemical identity and structure (Walker *et al.*, 2018), they definitely induce pain in the end (dos Santos-Pinto *et al.*, 2018). For further reading on aculeate venoms see comprehensive reviews: Lee, Baek & Yoon, 2016; Konno, Kazuma & Nihei, 2016; dos Santos-Pinto *et al.*, 2018. We can briefly summarize that aculeate venoms are complex and diverse, among and within groups, and have multiple functions one of which is principally inducing chemical pain, which may have evolved through parallel pathways.

It is well demonstrated that warning signals (signals for all the above defenses) are selected, through predation pressure, as reliable in indicating a defense mechanism (Sherratt & Beatty, 2003; Chouteau, Arias & Joron, 2016). When a naïve predator attacks a defended prey it might get stung and after a learning process will avoid the bearers of the aposematic signal, having associated the signal with the unpleasant experience of the stinging. Learning speed depends on hunger levels and prey profitability and availability in the habitat (Sherratt, 2003; Aubier & Sherratt, 2020). Species in sympatry, either in space or time or both, with a given predator community, share the load of predator education and are in proportion better protected from predation (reduced *per capita* mortality rate) when they resemble to the forms the predator has already learned to avoid. In this way, species can converge toward an aposematic signal under predator selective pressure, and form what is called a “mimicry ring” (Sherratt, 2008). The indirect interactions that result between prey individuals at the community scale range along a spectrum between mutualism and antagonism, depending on levels of defense or palatability (Figure 0.3). These interactions are classically categorized as Batesian mimicry (antagonistic), when undefended (i.e. palatable) ‘mimics’ resemble to defended (i.e. unpalatable) ‘models’, acting as parasites for the models, and Müllerian mimicry (mutualistic), when co-mimics are unpalatable, which benefits to all individuals forming the mimicry rings, i.e. the aposematic signal is under frequency-dependent selection (Ruxton,

Sherratt & Speed, 2004). In such rings, defended but unequally defended co-mimics have also sometimes been categorized as “quasi-Batesian mimicry” (Speed, 1999; Speed & Turner, 1999).

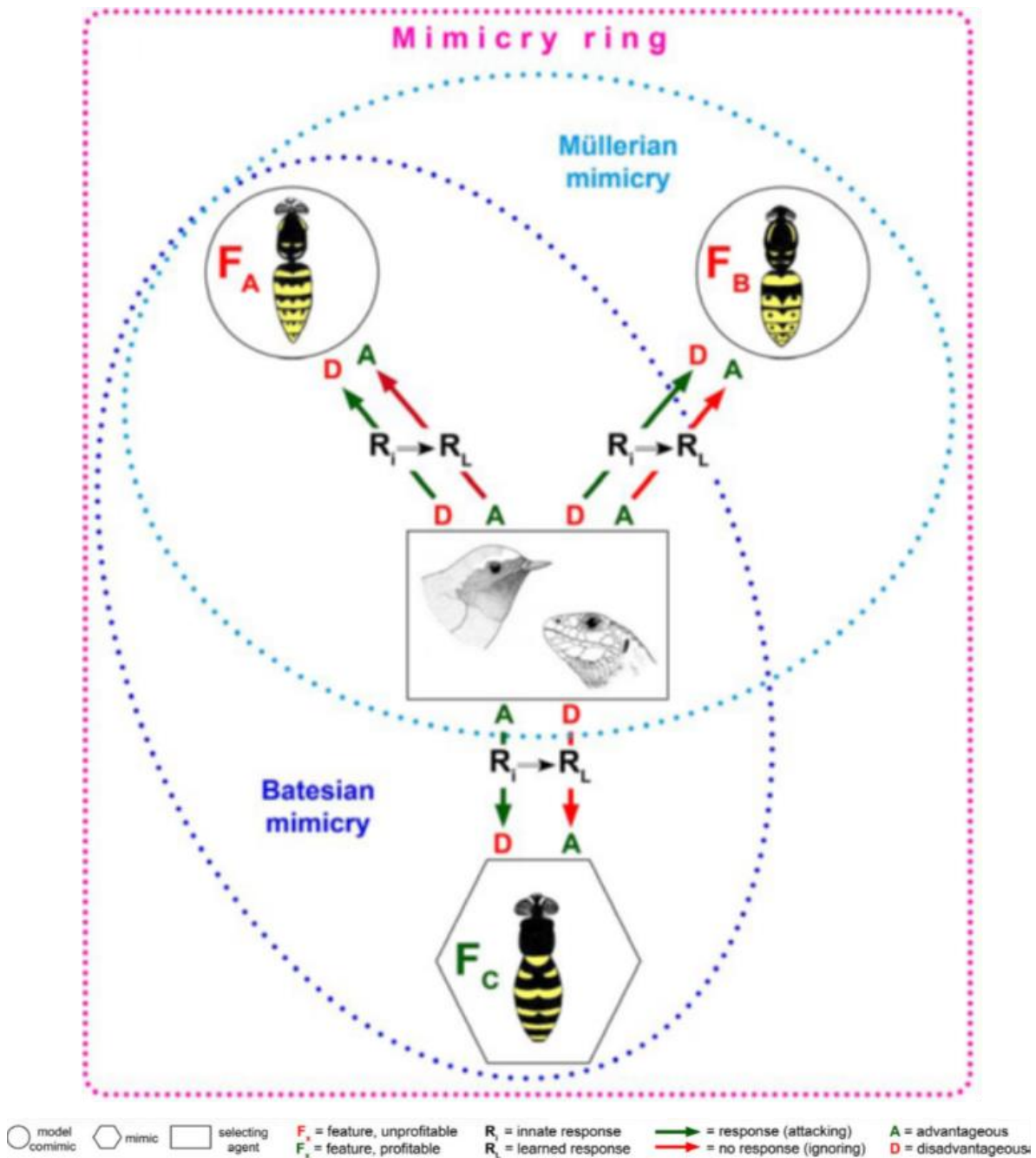


Figure 0.3. Schematic representation of Batesian and Müllerian mimicry (after Boppré *et al.*, 2017). The yellow jacket pattern is represented by two putative vespid wasp species and one hoverfly species.

Bees and wasps are mimicked by a large diversity of species among distant taxa (Figure 0.4). The extent of resemblance, shown in Figure 0.4, is sometimes striking and provides an insight of how widespread and protective it is to “look like a” wasp (or a bee). It is important to note here that convergence is only due to predator perception of similarity, and what can appear as strikingly similar or dissimilar may be biased by “human eye” (see discussion in Chapter 2). My PhD will not focus on Batesian mimicry but only on Müllerian mimicry, even if both are intrinsically linked in natural communities. Multiple Müllerian mimicry rings have been described among aculeates and are fully reviewed in Chapter 1.



Figure 0.4. Phenotypes diversity among ‘non bees and wasps’ mimics. A, *Coenopychus pulcher* (Araneae, Corinnidae), ©Thilina Hettiarachi; B, *Climacellia brunnea* (Neuroptera, Mantispidae), ©Katja Schulz; C, *Volucella bombylans* (Diptera, Syrphidae), ©nevwright; D, *Scaphura nigra* (Orthoptera, Tettigoniidae), ©luciakaju; E, *Clytus arietis* (Coleoptera, Cerambycidae), ©ruebezahl; F, *Pseudosphex laticincta* (Lepidoptera, Erebidae), ©Hannes Freitag.

Bees and stinging wasps belong to the Hymenoptera clade called Aculeata, which includes 36 families (Sharkey *et al.*, 2012; Peters *et al.*, 2017; Sann *et al.*, 2018). The clade originated during the Jurassic ca. 190 Mya ago (Peters *et al.*, 2017) and comprises about 53 000 extent species (Grimaldi *et al.*, 2005; Aguiar *et al.*, 2013). Aculeata are highly diversified and some traits, such as eusociality for instance, evolved multiple times independently (Figure 0.5). Therefore they exhibit a large diversity of traits, behavior or habitats. We will further review (Chapter 1) aculeate traits or characteristics that make them a perfect model to study mimetic systems. Species belonging to a same mimicry ring, sharing the same aspect and color pattern, might have independently evolved similar color patterns, sometimes over a very long time: more than ten million years in some velvet ants for example (Wilson *et al.*, 2020), even more with their spider wasps co-mimics (Rodriguez *et al.*, 2014), and very likely more in Müllerian rings with larger taxonomic scale such as the ‘Black body - black wings with white tips’ ring from Costa Rica, comprising vespids and bembicids, described by West-Eberhard (West-Eberhard, Carpenter & Hanson, 1995). Only phylogenies (Figure 0.5) can enable a proper test for such convergences in order to reject or not the hypothesis that a same aposematic pattern is shared due to common ancestry (Chapter 2).

0.3 From the origins to modern issues: a glimpse into the history of mimicry research

Let us now examine the historical framework of Batesian and Müllerian theory in mimicry, as an introduction to the core hypothesis of this thesis. Henry Walter Bates proposed the term mimicry in 1862, and this was the first « transformist » explanation of this kind of resemblance (Bates, 1862), see Box 1. Bates noticed butterflies predators' leftovers in Amazonia (i.e. broken wings separated from their body) which seemed to belong to the unpalatable "Heliconidae" family (sensu Bates; today tribes Heliconiini and Ithomiini both belong to the family Nymphalidae) but were in fact not "Heliconids" and belonged to a different but palatable family (Pieridae). He first supposed that "Heliconids" colorations signaling bad taste and smell (i.e. aposematism) explained why they are not predated upon by potential avian predators, and did not occur in predators' leftovers. However a second observation triggers his wondering: "*Leptalis*", a genus of palatable Pieridae (today *Patia*), looks very much alike "*Ithomia*", another genus of unpalatable Nymphalidae (today *Thyridia*). He then describes 7 mimics and 6 models (Figure 0.6 right) and also lists 10 genera in which he is aware of various species that mimic a single species of "Heliconids".



Figure 0.6. First historical cases of Müllerian (left) and Batesian (right) mimicry in Amazonian butterflies. Left panel: up, *Lycorea ilione* (©Adrian Hoskins); down, *Methona megisto* (©Almir Cândido de Almeida). Right panel (from Bates, 1862): up, *Patia orise* (palatable); down, *Thyridia psidii* (unpalatable). These four species were studied by Müller and Bates, respectively.

Within the same locality, he observed intraspecific polymorphism for palatable mimics, but palatable variants resembling the local aposematic model were more abundant and may therefore have better survived; he noted that this variation seems to only affect the Batesian mimics. This indirect proof of natural selection is integrated in Darwin's 4th edition of the *Origin*. Bates also described resembling defended models (which were to be explained by Fritz Müller) but chose to exclude them from his beautiful plates as those cases were, according to him, too few in comparison with Batesian mimics (which turned out to be false), could not fit in his theory, and he might have attributed those cases to common ancestry rather than convergence. A few years later, Fritz Müller proposed in 1879 the first mathematical model in evolution (Figure 0.7) based on naïve predator learning on n attacked individuals in the population (Müller, 1879). Following this model, equally

unpalatable species (*Lycorea ilione* and *Methona megisto*, Figure 0.6) benefit from mimicry, and the rarer species should be more favored (in terms of abundance ratios). Müller explained:

“For instance, let us suppose that in a given region during one summer 1200 butterflies of a distasteful species have to be destroyed before it becomes recognised as such, and that in this region there exist 2000 individuals of one (A) and 10,000 of another (B) distasteful species. If they are quite different each species will lose 1200 individuals; but if they are deceptively alike, then this loss will be divided among them in proportion to their numbers, the first (A) will lose 200, and the second (B) 1000. The former (A) accordingly gains 1000 (or 50 per cent) of the total loss, and the latter (B) only 200 (or 2 per cent.) of this number. Thus, whilst the relative number of the two species is in the ratio 1 : 5 the advantage derived by those possessing the resemblance is 25 : 1”
(Müller, 1879)

+ Let a_1 and a_2 be the numbers of two distasteful species of butterflies in some definite district during one summer, and let n be the number of individuals of a distinct species which are destroyed in the course of a summer before its distastefulness is generally known. If both species are totally dissimilar, then each loses n individuals. If, however, they are indistinguishably similar, then the first loses $\frac{a_1 n}{a_1 + a_2}$, and the second $\frac{a_2 n}{a_1 + a_2}$. The absolute gain by resemblance is therefore for the first species $n - \frac{a_1 n}{a_1 + a_2} = \frac{a_2 n}{a_1 + a_2}$; and in a similar manner for the second, $\frac{a_1 n}{a_1 + a_2}$. This absolute gain, compared with the occurrence of the species, gives for the first, $\mathbf{l}_1 = \frac{a_2 n}{a_1 (a_1 + a_2)}$, and for the second species, $\mathbf{l}_2 = \frac{a_1 n}{a_2 (a_1 + a_2)}$, whence follows the proportion, $\mathbf{l}_1 : \mathbf{l}_2 = a_2^2 : a_1^2$.

Figure 0.7. The first model in evolutionary ecology, published as a footnote by Müller in 1879.

In 1989, positive frequency-dependent selection was empirically demonstrated by Mallet and Barton with marked-recaptured data, still on Neotropical butterflies species (Mallet & Barton, 1989), showing that novel morphs had significantly lower survival rates than local ones. Under such selection, we should expect convergence in warning signals among defended species. However, this is not what was observed in many mimetic communities. Mimetic diversity maintenance, i.e. diversity of aposematic signals in a given community, was to be explained, especially in the perspective of spatiotemporal heterogeneity or microhabitat segregation (Joron & Mallet, 1998; Elias *et al.*, 2008; Gompert, Willmott & Elias, 2011). And indeed, microhabitats partitioning was only recently empirically demonstrated in Neotropical butterflies mimetic communities (Willmott *et al.*, 2017). Predator community as a selective force also depends on many parameters, such as predator psychology and perceptual abilities, that may impact the resulting diversity in warning signals, and other adaptive advantages in colors may meddle (Briolat *et al.*, 2019).

One century and a half later, mimicry is still a major topic in evolutionary ecology and continues to fascinate researchers around the world. We hope this thesis will bring some fresh news and help to better understand the importance of mimetic systems in nature, using bees and wasps as a key model.

Box 1. The Imperfect coexistence between Batesian and Müllerian explanation

Mimicry is an exemplary case of what Jean Gayon called “la stratégie de corroboration indirecte” in his major work *Darwin et l'après-Darwin* (Gayon, 1992).

He explains: 1) mimicry is the first empirical evidence for the hypothesis of natural selection, not discovered yet in the first edition of *The Origin of species* (Darwin, 1859), which shows that Darwinian theory was already overtaking Darwin's own work ; 2) Darwin termed facts of mimicry as « special difficulties » for natural selection theory and forces one to see natural selection as a work hypothesis on a specific empirical problem (e.g. no derivation toward biological philosophy) ; 3) It emerges as both an empirical confirmation of natural selection and a new field of research with its own original problems ; 4) the hypothesis is freed from the “artificial selection” context where it lies in 1859.

Alfred Russell Wallace immediately adopted Müller's proposition while Bates did not (Wallace, 1882; Poulton, 1897). Both Müller and Bates refuted the mere resemblance by common descent. However, because of predator learning, Müller's model is in total contradiction with the Lamarckian view of inheritance, which might have been too strict for Bates at the time (Gayon, 1992). Gayon concludes that, even if both grounded on natural selection, to think Batesian and Müllerian mimicry altogether (e.g. explaining why Batesian mimics did not go extinct), science needed a ‘quantitative ecology’ framework (e.g. population dynamics). This was not yet the case.

0.4 Co-extinctions cascades in pollinators communities

Extinctions at local scale can be due to multiple non-mutually exclusive factors, such as competition, environmental factors (including anthropogenic), or stochastic effects in small populations. Inter- and intraspecific competition has raised much attention in the study of species coexistence in diverse communities (Chesson, 2000; Barabás, Michalska-Smith & Allesina, 2016). The impact of such factors on ecological dynamics is a concerning issue, especially in the context of climate change (Cahill *et al.*, 2013; Doré *et al.*, 2022). Moreover, the interdependence in the interactions context might determine how the loss of some species may impact local abundances of other species in the community (Knight *et al.*, 2005). When a species depends upon another, the extinction of the first might result in the loss of the last. This is called co-extinction, or in our context, local co-extinction. Co-extinctions between butterflies and their specific host plants have

been reported in the tropics and are expected to increase exponentially (Koh, Sodhi & Brook, 2004b; Koh *et al.*, 2004a).

Even if differently structured (Thébault & Fontaine, 2010), mutualistic and antagonistic networks are strongly linked. Positive interactions such as plant-pollinator interactions may shape community composition in space (Duffy & Johnson, 2017). In a meta-analysis, Knight *et al.* (Figure 0.8) found that predators preying on insect pollinators, butterflies or bees for instance, had strong negative indirect effect on flowering plants (Knight *et al.*, 2006). Incidentally, bees and wasps are major pollinators and insect predators in natural communities. Indeed, adult bees feed on nectar and collect pollen for their brood. In parallel, non-parasitoid stinging wasps hunt other insects and generally also visit flowers (Brock, Cini & Sumner, 2021).

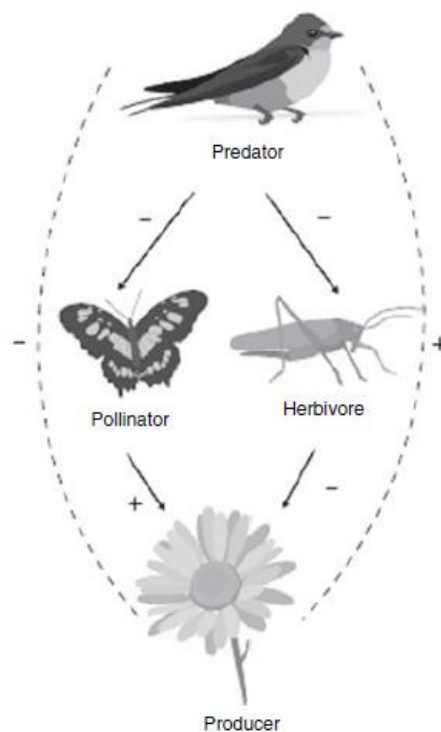


Figure 0.8. A trophic cascade including: a predator (insect feeding bird), herbivore (grasshopper), pollinator (butterfly) and producer (flowering plant). Solid and dotted lines indicate direct and indirect effects respectively (from Knight *et al.* 2006).

As we have seen, mutualistic networks are likely to be impacted by co-extinction cascades (Dunn *et al.*, 2009; Toby Kiers *et al.*, 2010). This is precisely in such a context that Müllerian mimicry intervenes in a pollinator community. In a Müllerian mimicry ring (a ring formed by bees and wasps species for example), the distribution of numerical (abundances) and chemical protection (noxiousness or toxicity) among co-mimetic species determine the protection's degree of the aposematic signal, by providing a better protection to larger mimicry rings (Ruxton *et al.*, 2004). Therefore, a drastic loss in local abundances might entail a co-extinction cascade. Intra-ring et inter-ring competition might also be an important factor affecting such co-extinction risks (Alexandrou *et al.*, 2011; Boussens-Dumon & Llaurens, 2021). Thus, we hypothesize that mimicry rings' effective defense (i.e. size and/or unpalatability) may explain observed differences in decline between species within a pollinator community. And our prediction would be that species from well defended rings are more likely to be found through time, and lesser defended rings would undergo more co-extinctions.

0.5 Main objectives

Müllerian mimicry was first described and theorized in Lepidoptera, and as such the large majority of mimicry studies have focused on this insect order. Yet, as colorful and unpalatable (stinging) insects, bees and stinging wasps are also experiencing Müllerian mimicry. With nearly 50 000 species, bees and stinging wasps probably represent the most diverse group of aposematic and mimetic prey on Earth. Furthermore, the profusion and diversity of distantly related harmless mimics of these insects (Figure 0.4) testifies of the efficacy of their aposematic colorations as a protection against predators. In addition, contrasting with mimetic butterflies, beetles or poison frogs, these insects also present unique traits that could impact mimicry dynamics, such as

haplodiploidy and sociality. Finally, as many bees and stinging wasps are major pollinators, understanding their community dynamics is of utmost importance given the extent of the current pollination crisis. Indeed, Müllerian mimicry is likely a strong driver of community structure, and the loss of one species could lead to cascading extinctions on co-mimetic species.

In order to address the above issues, we first established a state of the art of research on mimicry in bees and stinging wasps, by conducting an extensive review of existing studies that document Müllerian mimicry among bees and stinging wasps (Chapter 1). More specifically, in chapter one we examine the various reasons that make aculeates a key model for mimicry studies. Then, we study a whole aculeate community from South Corsica (France, Mediterranean region), by quantifying mimetic resemblance and convergence to evaluate if our empirical community is partitioned in potential mimicry rings (Chapter 2). Finally, we test our prediction, both with theoretical and empirical approaches (on a one century timespan): do better defended rings in the Corsican community tend to better survive throughout time? (Chapter 3). This is to our knowledge the first empirical attempt to attest for temporal turnover in mimicry rings at community scale and among aculeates.

0.6 References

Aguiar, A.P., Deans, A.R., Engel, M.S., Forshage, M., Huber, J.T., Jennings, J.T., Johnson, N.F., Lelej, A.S., Longino, J.T., Lohrmann, V., Mikó, I., Ohl, M., Rasmussen, C., Taeger, A. & Yu, D.S.K. (2013) Order Hymenoptera. In: Zhang, Z.-Q. (Ed.) *Animal Biodiversity: An Outline of Higher-level Classification and Survey of Taxonomic Richness* (Addenda 2013). *Zootaxa* **3703**, 51-62-51–62.

- Akre, R., Greene, A., MacDonald, J., Landolt, P. & Davis, H. (1981) The Yellowjackets of America North of Mexico. *A*, 1–102.
- Alexandrou, M.A., Oliveira, C., Maillard, M., McGill, R.A.R., Newton, J., Creer, S. & Taylor, M.I. (2011) Competition and phylogeny determine community structure in Müllerian co-mimics. *Nature* **469**, 84–90.
- Aubier, T.G. & Sherratt, T.N. (2020) State-dependent decision-making by predators and its consequences for mimicry. *The American Naturalist*.
- Badejo, O., Skaldina, O., Gilev, A. & Sorvari, J. (2020) Benefits of insect colours: a review from social insect studies. *Oecologia*, 1–14.
- Badejo, O., Skaldina, O. & Sorvari, J. (2018) Spatial and Temporal Variation in Thermal Melanism in the Aposematic Common Wasp (*Vespula vulgaris*) in Northern Europe. *Annales Zoologici Fennici* **55**, 67–78. Finnish Zoological and Botanical Publishing Board.
- Barabás, G., Michalska-Smith, M.J. & Allesina, S. (2016) The Effect of Intra- and Interspecific Competition on Coexistence in Multispecies Communities. *The American Naturalist*. University of Chicago Press Chicago, IL.
- Bates, H.W. (1862) Contributions to an Insect Fauna of the Amazon Valley. Lepidoptera: Heliconidae. *Transactions of the Linnean Society of London* **23**, 495–566.
- Baumann, K., Vicenzi, E.P., Lam, T., Douglas, J., Arbuckle, K., Cribb, B., Brady, S.G. & Fry, B.G. (2018) Harden up: metal acquisition in the weaponized ovipositors of aculeate hymenoptera. *Zoomorphology* **137**, 389–406.

- Blaimer, B.B., Mawdsley, J.R. & Brady, S.G. (2018) Multiple origins of sexual dichromatism and aposematism within large carpenter bees. *Evolution* **72**, 1874–1889.
- Boppré, M., Vane-Wright, R.I. & Wickler, W. (2017) A hypothesis to explain accuracy of wasp resemblances. *Ecology and Evolution* **7**, 73–81.
- Boussens-Dumon, G. & Llaurens, V. (2021) Sex, competition and mimicry: an eco-evolutionary model reveals unexpected impacts of ecological interactions on the evolution of phenotypes in sympatry. *Oikos* **130**, 2028–2039.
- Briolat, E.S., Burdfield-Steel, E.R., Paul, S.C., Rönkä, K., Seymoure, B.M., Stankowich, T. & Stuckert, A.M.M. (2019) Diversity in warning coloration: selective paradox or the norm? *Biological Reviews* **94**, 388–414.
- Brock, R.E., Cini, A. & Sumner, S. (2021) Ecosystem services provided by aculeate wasps. *Biological Reviews* **96**, 1645–1675.
- Cahill, A.E., Aiello-Lammens, M.E., Fisher-Reid, M.C., Hua, X., Karanewsky, C.J., Yeong Ryu, H., Sbeglia, G.C., Spagnolo, F., Waldron, J.B., Warsi, O. & Wiens, J.J. (2013) How does climate change cause extinction? *Proceedings of the Royal Society B: Biological Sciences* **280**, 20121890. Royal Society.
- Cappa, F., Beani, L. & Cervo, R. (2016) The importance of being yellow: visual over chemical cues in gender recognition in a social wasp. *Behavioral Ecology* **27**, 1182–1189.
- Chapman, R.F. & Chapman, R.F. (1998) *The Insects: Structure and Function*. Cambridge University Press.

- Chesson, P. (2000) Mechanisms of Maintenance of Species Diversity. *Annual Review of Ecology and Systematics* **31**, 343–366.
- Chouteau, M., Arias, M. & Joron, M. (2016) Warning signals are under positive frequency-dependent selection in nature. *PNAS* **113**, 2164–2169.
- Cott, H.B. (1940) *Adaptive Coloration in Animals*. Methuen and Company, London.
- Dashevsky, D., Baumann, K., Undheim, E.A.B., Nouwens, A., Ikonopoulou, M.P., Schmidt, J.O., Ge, L., Kwok, H.F., Rodriguez, J. & Fry, B.G. (2023) Functional and Proteomic Insights into Aculeata Venoms. *Toxins* **15**, 224. Multidisciplinary Digital Publishing Institute.
- Doré, M., Willmott, K., Leroy, B., Chazot, N., Mallet, J., Freitas, A.V.L., Hall, J.P.W., Lamas, G., Dasmahapatra, K.K., Fontaine, C. & Elias, M. (2022) Anthropogenic pressures coincide with Neotropical biodiversity hotspots in a flagship butterfly group. *Diversity and Distributions* **28**, 2912–2930.
- Duffy, K.J. & Johnson, S.D. (2017) Specialized mutualisms may constrain the geographical distribution of flowering plants. *Proceedings of the Royal Society B: Biological Sciences* **284**, 20171841. Royal Society.
- Dunn, R.R., Harris, N.C., Colwell, R.K., Koh, L.P. & Sodhi, N.S. (2009) The sixth mass coextinction: are most endangered species parasites and mutualists? *Proceedings of the Royal Society B: Biological Sciences* **276**, 3037–3045. Royal Society.

- Elias, M., Gompert, Z., Jiggins, C. & Willmott, K. (2008) Mutualistic Interactions Drive Ecological Niche Convergence in a Diverse Butterfly Community. *PLOS Biology* **6**, e300. Public Library of Science.
- Gompert, Z., Willmott, K. & Elias, M. (2011) Heterogeneity in predator micro-habitat use and the maintenance of Müllerian mimetic diversity. *Journal of Theoretical Biology* **281**, 39–46.
- Grimaldi, D., Engel, M.S., Engel, M.S. & Engel, S.C. and P.M.S. (2005) *Evolution of the Insects*. Cambridge University Press.
- Hines, H.M., Witkowski, P., Wilson, J.S. & Wakamatsu, K. (2017) Melanic variation underlies aposematic color variation in two hymenopteran mimicry systems. *PLoS ONE* **12**, 1–17.
- Jensen, T., Walker, A.A., Nguyen, S.H., Jin, A.-H., Deuis, J.R., Vetter, I., King, G.F., Schmidt, J.O. & Robinson, S.D. (2021) Venom chemistry underlying the painful stings of velvet ants (Hymenoptera: Mutillidae). *Cellular and Molecular Life Sciences*.
- Jorge, A., Polidori, C., Garcia-Guinea, J. & Nieves-Aldrey, J.L. (2017) Spectral cathodoluminescence analysis of hymenopteran mandibles with different levels of zinc enrichment in their teeth. *Arthropod Structure and Development* **46**, 39–48.
- Joron, M. & Mallet, J. (1998) Diversity in mimicry: paradox or paradigm? *Trends in Ecology and Evolution* **13**, 461–466.
- Knight, T.M., Chase, J.M., Hillebrand, H. & Holt, R.D. (2006) Predation on mutualists can reduce the strength of trophic cascades. *Ecology Letters* **9**, 1173–1178.

- Knight, T.M., McCoy, M.W., Chase, J.M., McCoy, K.A. & Holt, R.D. (2005) Trophic cascades across ecosystems. *Nature* **437**, 880–883. Nature Publishing Group.
- Koh, L.P., Dunn, R.R., Sodhi, N.S., Colwell, R.K., Proctor, H.C. & Smith, V.S. (2004a) Species Coextinctions and the Biodiversity Crisis. *Science* **305**, 1632–1634. American Association for the Advancement of Science.
- Koh, L.P., Sodhi, N.S. & Brook, B.W. (2004b) Co-Extinctions of Tropical Butterflies and their Hostplants. *Biotropica* **36**, 272–274.
- Konno, K., Kazuma, K. & Nihei, K. (2016) Peptide Toxins in Solitary Wasp Venoms. *Toxins* **8**, 114. Multidisciplinary Digital Publishing Institute.
- Lee, S.H., Baek, J.H. & Yoon, A. (2016) Differential Properties of Venom Peptides and Proteins in Solitary vs. Social Hunting Wasps. *Toxins* **8**, 1–29.
- Lopez, V.M., Azevedo Tosta, T.A., da Silva, G.G., Bartholomay, P.R., Williams, K.A. & Ferreira, R.G. (2021) Color lightness of velvet ants (Hymenoptera: Mutillidae) follows an environmental gradient. *Journal of Thermal Biology*, 103030.
- Mallet, J. & Barton, N.H. (1989) Strong natural selection in a warning-color hybrid zone. *Evolution* **43**, 421–431.
- Müller, F. (1879) Ituna and Thyridia: a remarkable case of mimicry in butterflies. *Transactions of the Entomological Society of London*, 20–29.

- Pekar, S., Petrakova, L., Bulbert, M.W., Whiting, M.J. & Herberstein, M.E. (2017) The golden mimicry complex uses a wide spectrum of defence to deter a community of predators. *eLife*, 1–25.
- Pereboom, J. & Biesmeijer, J. (2003) Thermal constraints for stingless bee foragers: the importance of body size and coloration. *Oecologia* **137**, 42–50.
- Peters, R.S., Krogmann, L., Mayer, C., Donath, A., Gunkel, S., Meusemann, K., Kozlov, A., Podsiadlowski, L., Petersen, M., Lanfear, R., Diez, P.A., Heraty, J., Kjer, K.M., Klopstein, S., Meier, R., et al. (2017) Evolutionary History of the Hymenoptera. *Current Biology* **27**, 1013–1018.
- Piek, T. (2013) *Venoms of the Hymenoptera: Biochemical, Pharmacological and Behavioural Aspects*. Elsevier.
- Plotkin, M., Volynchik, S., Ermakov, N.Y., Benyamini, A., Boiko, Y., Bergman, D.J. & Ishay, J.S. (2009) Xanthopterin in the Oriental Hornet (*Vespa orientalis*): Light Absorbance Is Increased with Maturation of Yellow Pigment Granules. *Photochemistry and Photobiology* **85**, 955–961.
- Plowright, R.C. & Owen, R.E. (1980) The Evolutionary Significance of Bumble Bee Color Patterns: A Mimetic Interpretation. *Evolution* **34**, 622–637.
- Polidori, C., Garcia, A.J. & Nieves-Aldrey, J.L. (2013) Breaking up the Wall: Metal-Enrichment in Ovipositors, but Not in Mandibles, Co-Varies with Substrate Hardness in Gall-Wasps and Their Associates. *PLoS ONE* **8**, 1–13.

- Polidori, C., Jorge, A., Keller, A., Ornos, C., Tormos, J., Asis, J.D. & Nieves-Aldrey, J.L. (2020) Strong phylogenetic constraint on transition metal incorporation in the mandibles of the hyper-diverse Hymenoptera (Insecta). *Organisms Diversity and Evolution*, 1–16.
- Poulton, E.B. (1890) *The colours of animals: their meaning and use, especially considered in the case of insects*. D. Appelton and Company.
- Robinson, S.D., Mueller, A., Clayton, D., Starobova, H., Hamilton, B.R., Payne, R.J., Vetter, I., King, G.F. & Undheim, E.A.B. (2018) A comprehensive portrait of the venom of the giant red bull ant, *Myrmecia gulosa*, reveals a hyperdiverse hymenopteran toxin gene family. *Science Advances* **4**, eaau4640. American Association for the Advancement of Science.
- Rodriguez, J., Pitts, J.P., Von Dohlen, C.D. & Wilson, J.S. (2014) Müllerian Mimicry as a Result of Codivergence between Velvet Ants and Spider Wasps. *PLoS ONE* **9**, 1–7.
- Ronchetti, F. & Polidori, C. (2020) A sting affair: A global quantitative exploration of bee, wasp and ant hosts of velvet ants. *PLoS ONE*, 1–26.
- Ruxton, G.D., Sherratt, T.N. & Speed, M.P. (2004) *Avoiding attack: the evolutionary ecology of crypsis, warning signals and mimicry* Oxford University Press. London.
- Sadler, E.A., Pitts, J.P. & Wilson, Joseph S. (2018) Stinging wasps (Hymenoptera: Aculeata), which species have the longest sting? *PeerJ*, 1–15.
- Sann, M., Niehuis, O., Peters, R.S., Mayer, C., Kozlov, A., Podsiadlowski, L., Bank, S., Meusemann, K., Misof, B., Bleidorn, C. & Ohl, M. (2018) Phylogenomic analysis of Apoidea sheds new light on the sister group of bees. *BMC Evolutionary Biology* **18**, 1–15.

- dos Santos-Pinto, J.R.A., Perez-Riverol, A., Lasa, A.M. & Palma, M.S. (2018) Diversity of peptidic and proteinaceous toxins from social Hymenoptera venoms. *Toxicon* **148**, 172–196.
- Schmidt, J.O. (2019) Pain and Lethality Induced by Insect Stings: An Exploratory and Correlational Study. *Toxins* **11**, 1–14.
- Sharkey, M.J., Carpenter, J.M., Vilhelmsen, L., Heraty, J., Liljeblad, J., Dowling, A.P.G., Schulmeister, S., Murray, D., Deans, A.R., Ronquist, F., Krogmann, L. & Wheeler, W.C. (2012) Phylogenetic relationships among superfamilies of Hymenoptera. *Cladistics* **28**, 80–112.
- Sherratt, T.N. (2003) State-dependent risk-taking by predators in systems with defended prey. *Oikos* **103**, 93–100.
- Sherratt, T.N. (2008) The evolution of Müllerian mimicry. *Naturwissenschaften* **95**, 681–695.
- Sherratt, T.N. & Beatty, C.D. (2003) The Evolution of Warning Signals as Reliable Indicators of Prey Defense. *The American Naturalist* **162**, 377–389.
- Souza, A.R. de, Júnior, C.A.M., Nascimento, F.S. do & Lino-Neto, J. (2014) Sexy Faces in a Male Paper Wasp. *PLOS ONE* **9**, e98172. Public Library of Science.
- Speed, M.P. (1999) Batesian, quasi-Batesian or Müllerian mimicry? Theory and data in mimicry research. *Evolutionary Ecology* **13**, 755–776.
- Speed, M.P. & Turner, J.R.G. (1999) Learning and memory in mimicry: II. Do we understand the mimicry spectrum? *Biological Journal of the Linnean Society* **67**, 281–312.

- Stiles, E.W. (1979) Evolution of Color Pattern and Pubescence Characteristics in Male Bumblebees: Automimicry vs. Thermoregulation. *Evolution* **33**, 941–957.
- Thébaud, E. & Fontaine, C. (2010) Stability of Ecological Communities and the Architecture of Mutualistic and Trophic Networks. *Science* **329**, 853–856. American Association for the Advancement of Science.
- Toby Kiers, E., Palmer, T.M., Ives, A.R., Bruno, J.F. & Bronstein, J.L. (2010) Mutualisms in a changing world: an evolutionary perspective. *Ecology Letters* **13**, 1459–1474.
- Villemant, C. & Casevitz-Weulersse, J. (2015) Insectes Hyménoptères. In *La Fonction venimeuse* pp. 115–156. Lavoisier.
- Walker, A.A., Robinson, S.D., Yeates, D.K., Jin, J., Baumann, K., Dobson, J., Fry, B.G. & King, G.F. (2018) Entomo-venomics: The evolution, biology and biochemistry of insect venoms. *Toxicon* **154**, 15–27.
- West-Eberhard, M.J., Carpenter, J.M. & Hanson, P.E. (1995) The vespid wasps (Vespidae). In *The Hymenoptera of Costa Rica* pp. 561–587 Oxford Science Publications. Oxford.
- Willadsen, P.C. (2022) Aculeate Hymenopterans as Aposematic and Mimetic Models. *Frontiers in Ecology and Evolution* **10**.
- Williams, P. (2007) The distribution of bumblebee colour patterns worldwide: possible significance for thermoregulation, crypsis, and warning mimicry. *Biological Journal of the Linnean Society* **92**, 97–118.

Willmott, K.R., Robinson Willmott, J.C., Elias, M. & Jiggins, C.D. (2017) Maintaining mimicry diversity: optimal warning colour patterns differ among microhabitats in Amazonian clearwing butterflies. *Proceedings of the Royal Society B: Biological Sciences* **284**, 20170744. Royal Society.

Wilson, J.S., Sidwell, J.S., Forister, M.L., Williams, K.A. & Pitts, J.P. (2020) Thistledown velvet ants in the Desert Mimicry Ring and the evolution of white coloration: Müllerian mimicry, camouflage and thermal ecology. *Biology Letters* **16**, 1–6.

Wilson, J.S., Williams, K.A., Forister, M.L., Von Dohlen, C.D. & Pitts, J.P. (2012) Repeated evolution in overlapping mimicry rings among North American velvet ants. *Nature Communications* **3**, 1–7.

Chapter 1

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

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As we have seen in the introduction, Müllerian mimicry provides protection to prey through indirect mutualistic interactions. However, Müllerian mimicry in bees and stinging wasps remains largely understudied and we lack a global picture of the extent of the mimicry phenomenon in these insects. The aim of the present chapter is to first establish a state of the art of research on mimicry in bees and stinging wasps, and by doing so to identify directions for future research.

In this chapter we conduct an extensive review of existing studies that document Müllerian mimicry among bees and stinging wasps (see abstract). I led, conducted and analyzed all present data and results.

Supplementary material (Tables S1-S3) can be found online:

<https://onlinelibrary.wiley.com/doi/full/10.1111/brv.12955>

« Le mimétisme est essentiellement énigmatique, aussi a-t-il donné lieu à d'innombrables controverses. Les arguments échangés, aussi frappants, aussi ingénieux qu'ils soient, donnent cependant une curieuse impression de monotonie. »

Roger Caillois, *Méduse et Cie*, 1960

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.

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 generalize 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), 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)] 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* (Vespididae) stings are not particularly painful for humans but appear efficient against some avian predators (Lane, 1957). This emphasizes 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 and 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, Van Zandt Brower & Westcott, 1960; Van Zandt Brower & Brower, 1962, 1965), lizards and mammals (Sexton, 1964; Gall *et al.*, 2018)]. For example, ten 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 generalize the painful experience to new potential prey.

To summarize, there is a large community of naive predators that potentially predate aculeates; at least some aculeates are able to prove unpalatable to some predators; and some of these predators can generalize 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 synthesize 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 recognized 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, Vago & Wahis, 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.

(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 (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. 4A-C). 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, Vago & Wahis, 2003; Smith-Pardo, 2005; Waldbauer, Sternburg & Maier, 1977; West-Eberhard, Carpenter & Hanson, 1995). These rings involved four of the seven bee families (Apidae, Colettidae, Halictidae, Megachilidae), and eight stinging wasp families (Bembicidae, Crabronidae, Mutillidae, Philanthidae, Pompilidae, Sphecidae, Tiphiidae, 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 Palaearctic. 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 generalization 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 a hundred 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 generalized 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, Sternburg & Maier, 1977; Plowright & Owen, 1980; West-Eberhard, Carpenter & Hanson, 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, Vago & Wahis, 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, Williams & Wilson, 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, Hagen & Lampe, 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, Hagen & Lampe, 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, Vago & Wahis, 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, Vago & Wahis, 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, Hagen & Lampe, 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, Carpenter & Hanson, 1995; Rodriguez *et al.*, 2014), Chrysididae (Mora & Hanson, 2019), Sphecidae (West-Eberhard, Carpenter & Hanson, 1995; Nicholson, 1927), and others such as Philanthidae, Bembicidae and Crabronidae (Nicholson, 1927; Waldbauer & Sheldon, 1971; Waldbauer, Sternburg & Maier, 1977). Thus, patterns involving contrasting or bright colours are common in aculeates and are usually recognized 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, Billington & Sherratt, 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 recognizable sounds when attacked by predators, such as buzzing, vibrations or stridulation (Kirchner & Röschard, 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, Carpenter & Hanson, 1995; Dejean, Corbara & Lachaud, 1998; Garcete-Barrett, 1999; Gilbert, 2004; Pan, Williams & Wilson, 2017). These similarities included flight style (Evans, 1968), areas visited

in the environment (Yanega, 1994; Dejean *et al.*, 1998), and locomotion (Nentwig, 1985; Pan, Williams & Wilson, 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 signaling 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 generalize 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 the 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, Vago & Wahis, 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, Sternburg & Maier, 1977; Plowright & Owen, 1980; Thorp, Horning & Dunning, 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 proved 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, Horning & Dunning, 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, Speed & Sherratt, 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, Sternburg & Maier, 1977; Dressler, 1979; West-Eberhard, Carpenter & Hanson, 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 (Kaspari & 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 (Marple, 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, Halpin & Rowe, 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 categorized 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 recognized that phenological mismatch between co-mimics is critical for predator education (Silberglied & Eisner, 1969; Waldbauer & Sheldon, 1971; Waldbauer, Sternburg & Maier, 1977; Evans & Waldbauer, 1982; Gilbert, 2004; Hassall, Billington & Sherratt, 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, Sternburg & Maier, 1977; Dressler, 1979; Plowright & Owen, 1980; Owen & Plowright, 1988; O'Donnell & Joyce, 1999; Pauly, Vago & Wahis, 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, Vago & Wahis, 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 lifecycle, 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 predator, until the early emergence of males of the black co-mimics, which counter-select the black signal in favour of the red one, which had 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, Sternburg & Maier, 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: (1) sociality could enhance predator learning by increasing the aggressiveness and local abundance of signal carriers (Spradbery, 1973; Breed, Guzmán-Novoa & Hunt, 2004); (2) 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; (3) 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 recognized 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 multimodal 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-recognized 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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X. REFERENCES

References identified with an asterisk (*) are cited only within the supporting information.

- AGUIAR, A.P., DEANS, A.R., ENGEL, M.S., FORSHAGE, M., HUBER, J.T., JENNINGS, J.T., JOHNSON, N.F., LELEJ, A.S., LONGINO, J.T., LOHRMANN, V., MIKÓ, I., OHL, M., RASMUSSEN, C., TAEGER, A. & YU, D.S.K. (2013). Order Hymenoptera. In: Zhang, Z.-Q. (Ed.) *Animal Biodiversity: An Outline of Higher-level Classification and Survey of Taxonomic Richness* (Addenda 2013). *Zootaxa* **3703**, 51–62.
- ANDERSON, B. & DE JAGER, M.L. (2020). Natural selection in mimicry. *Biological Reviews* **95**, 291–304.
- ARCHER, M.E. (2012). *Vespine wasps of the world: behaviour, ecology and taxonomy of the Vespinae*. Siri Scientific Press. Manchester.
- ARONSSON, M. & GAMBERALE-STILLE, G. (2008). Domestic chicks primarily attend to colour, not pattern, when learning an aposematic coloration. *Animal Behaviour* **75**, 417–423.
- AUBIER, T.G., JORON, M. & SHERRATT, T.N. (2017). Mimicry among unequally defended prey should be mutualistic when predators sample optimally. *The American Naturalist* **189**, 267–282.

- AUBIER, T.G. & SHERRATT, T.N. (2015). Diversity in Müllerian mimicry: The optimal predator sampling strategy explains both local and regional polymorphism in prey. *Evolution* **69**, 2831–2845.
- AUBIER, T.G. & SHERRATT, T.N. (2020). State-dependent decision-making by predators and its consequences for mimicry. *The American Naturalist* **196**, 127–144.
- AUBRET, F. & MANGIN, A. (2014). The snake hiss: potential acoustic mimicry in a viper–colubrid complex. *Biological Journal of the Linnean Society* **113**, 1107–1114.
- BADEJO, O., SKALDINA, O., GILEV, A. & SORVARI, J. (2020). Benefits of insect colours: a review from social insect studies. *Oecologia* **194**, 27–40.
- BAIN, R.S., RASHED, A., COWPER, V.J., GILBERT, F.S. & SHERRATT, T.N. (2007). The key mimetic features of hoverflies through avian eyes. *Proceedings of the Royal Society B: Biological Sciences* **274**, 1949–1954.
- BARNETT, C.R.A., RINGHOFER, M. & SUZUKI, T.N. (2020). Differences in predatory behavior among three bird species when attacking chemically defended and undefended prey. *Journal of Ethology* **39**, 29–37.
- BASTOLLA, U., FORTUNA, M. A., PASCUAL-GARCÍA, A., FERRERA, A., LUQUE, B., & BASCOMPTE, J. (2009). The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature* **458**, 1018–1020.
- BATES, H.W. (1862). Contributions to an Insect Fauna of the Amazon Valley. Lepidoptera: Heliconidae. *Transactions of the Linnean Society of London* **23**, 495–566.
- BATRA, S.W.T. (1984). Solitary Bees. *Scientific American* **250**, 120–127.

- BAUMANN, K., VICENZI, E.P., LAM, T., DOUGLAS, J., ARBUCKLE, K., CRIBB, B., BRADY, S.G. & FRY, B.G. (2018). Harden up: metal acquisition in the weaponized ovipositors of aculeate hymenoptera. *Zoomorphology* **137**, 389–406.
- BEST, T.L. & PFAFFENBERGER, G.S. (1987). Age and sexual variation in the diet of collared Lizards (*Crotaphytus collaris*). *The Southwestern Naturalist* **32**, 415–426.
- BLAIMER, B.B., MAWDSLEY, J.R. & BRADY, S.G. (2018). Multiple origins of sexual dichromatism and aposematism within large carpenter bees. *Evolution* **72**, 1874–1889.
- BOPPRÉ, M., VANE-WRIGHT, R.I. & WICKLER, W. (2017). A hypothesis to explain accuracy of wasp resemblances. *Ecology and Evolution* **7**, 73–81.
- BOUTIN, M., COSTA, M., FONTAINE, C., PERRARD, A. & LLAURENS, V. (2022). Influence of sex-limited mimicry on extinction risk in Aculeata: a theoretical approach. *bioRxiv*.
- BREED, M.D., GUZMÁN-NOVOA, E. & HUNT, G.J. 3 (2004). Defensive behavior of honey bees: Organization, Genetics, and Comparisons with Other Bees. *Annual Review of Entomology* **49**, 271–298.
- BRIOLAT, E.S., BURDFIELD-STEEL, E.R., PAUL, S.C., RÖNKÄ, K., SEYMOURE, B.M., STANKOWICH, T. & STUCKERT, A.M.M. (2019). Diversity in warning coloration: selective paradox or the norm? *Biological Reviews* **94**, 388–414.
- BRODIE JR, E.D. (1993). Differential avoidance of coral snake banded patterns by free-ranging avian predators in Costa Rica. *Evolution* **47**, 227–235.
- BROWER, L.P., RYERSON, W.N., COPPINGER, L.L. & GLAZIER, S.C. (1968). Ecological Chemistry and the Palatability Spectrum. *Science* **161**, 1349–1351.

- BROWER, L.P., VAN ZANDT BROWER, J. & WESTCOTT, P.W. (1960). Experimental studies of mimicry. 5. The reactions of toads (*Bufo terrestris*) to bumblebees (*Bombus americanorum*) and their robberfly mimics (*Mallophora bomboides*), with a discussion of aggressive mimicry. *The American Naturalist* **94**, 343–355.
- BULL, E.L. (2005). Ecology of the Columbia Spotted Frog in Northeastern Oregon.
- COTT, H.B. (1932). On the Ecology of Tree-Frogs in the Lower Zambesi Valley, with special reference to Predatory Habits considered in relation to the Theory of Warning Colours and Mimicry. *Proceedings of the Zoological Society of London* **1932**, 1–76.
- COTT, H.B. (1940). *Adaptive Coloration in Animals*. Methuen and Company, London.
- CSARDI, G. & NEPUSZ, T. (2006). The igraph software package for complex network research. *InterJournal, Complex Systems* **1695**, 1–9.
- DANFORTH, B.N., MINCKLEY, R.L. & NEFF, J.L. (2019). *The solitary bees: biology, evolution, conservation*. Princeton University Press.
- DAVIES, N.B. (1977). Prey selection and the search strategy of the spotted flycatcher (*Muscicapa striata*): a field study on optimal foraging. *Animal Behaviour* **25**, 1016–1033.
- DAVIES, N.B. & GREEN, R.E. (1976). The development and ecological significance of feeding techniques in the reed warbler (*Acrocephalus scirpaceus*). *Animal Behaviour* **24**, 213–229.
- DAY, M.C. (1984). Male polymorphism in some Old World species of *Cryptocheilus* Panzer (Hymenoptera: Pompilidae). *Zoological Journal of the Linnean Society* **79**, 83–101.
- DE SOLAN, T. & AUBIER, T.G. (2019). The Evolutionary Importance of Cues in Protective Mimicry. *Frontiers in Ecology and Evolution* **7**, 1–5.

- DEJEAN, A., CORBARA, B. & LACHAUD, J.-P. (1998). The anti-predator strategies of *Parachartergus apicalis* (Vespidae: Polistinae). *Sociobiology* **32**, 477–487.
- DITTRICH, W., GILBERT, F., GREEN, P., MCGREGOR, P. & GREWCOCK, D. (1993). Imperfect mimicry: A pigeon's perspective. *Proceedings of the Royal Society of London Series B. Biological Sciences* **251**, 195–200.
- DIXEY, F.A. (1919). The geographical factor in mimicry. In *Presidential Address* pp. 199–207 Report of the British Association for the Advancement of Science. London.
- DORÉ, M., WILLMOTT, K., LEROY, B., CHAZOT, N., MALLET, J., FREITAS, A.V.L., HALL, J.P.W., LAMAS, G., DASMAHAPATRA, K.K., FONTAINE, C. & ELIAS, M. (2022). Anthropogenic pressures coincide with Neotropical biodiversity hotspots in a flagship butterfly group. *Diversity and Distributions* **28**, 2912–2930.
- DRESSLER, R.L. (1979). *Eulaema bombiformis*, *E. meriana*, and Mullerian Mimicry in Related Species (Hymenoptera: Apidea). *Biotropica* **11**, 144–151.
- DUCKE, A. (1909). *Odyneropsis* Schrottky, genre d'Abeilles parasites mimétiques [Hym.]. *Bulletin de la Société entomologique de France* **14**, 306–309.
- DUKAS, R. & MORSE, D.H. (2003). Crab spiders affect flower visitation by bees. *Oikos* **101**, 157–163.
- ELKINS, J.C. (1969). A New Genus of Hemipteran Wasp Mimics (Reduviidae, Harpactorinae). *Journal of the Kansas Entomological Society* **42**, 456–461.
- ENDLER, J.A. (1981). An overview of the relationships between mimicry and crypsis. *Biological Journal of the Linnean Society* **16**, 25–31.

- EVANS, H.E. (1968). Studies on Neotropical Pompilidae (Hymenoptera). IV. Examples of dual sex-limited mimicry in *Chirodamus*. *Psyche* **75**, 1–23.
- EVANS, D.L. & WALDBAUER, G.P. (1982). Behavior of Adult and Naive Birds when Presented with a Bumblebee and its Mimic. *Zeitschrift für Tierpsychologie* **59**, 247–259.
- EVANS, H.E. & WEST-EBERHARD, M.J. (1970). *The Wasps*. University of Michigan Press, Ann Arbor, Michigan, 265 pp.
- EZRAY, B.D., WHAM, D.C., HILL, C.E. & HINES, H.M. (2019). Unsupervised machine learning reveals mimicry complexes in bumblebees occur along a perceptual continuum. *Proceedings of the Royal Society B* **286**, 20191501.
- FINKBEINER, S.D., BRISCOE, A.D. & REED, R.D. (2014). Warning signals are seductive: Relative contributions of color and pattern to predator avoidance and mate attraction in Heliconius butterflies. *Evolution* **68**, 3410–3420.
- *GABRITSCHESKY, E. (1924). Farbenpolymorphismus und Vererbung mimetischer Varietäten der Fliege *Volucella bombylans* und anderer “hummelähnlicher” Zweiflügler. *Induktive Abstammungs und Vererbungslehre* **32**, 321–353.
- GABRITSCHESKY, E. (1926). Convergence of coloration between American pilose flies and bumblebees (*Bombus*). *The Biological Bulletin* **51**, 269–286.
- GALL, B.G., SPIVEY, K.L., CHAPMAN, T.L., DELPH, R.J., BRODIE JR, E.D. & WILSON, J.S. (2018). The indestructible insect: Velvet ants from across the United States avoid predation by representatives from all major tetrapod clades. *Ecology and Evolution* **8**, 5852–5862.
- GARCETE-BARRETT, B. (1999). *Guía ilustrada de las avispas sociales del Paraguay (Hymenoptera: Vespidae: Polistinae)*. Natural Museum, London.

- GARCETE-BARRETT, B. (2014). *Stenonartonia tekoraava* sp. nov. (Hymenoptera: Vespidae: Eumeninae), a new member of a typical Amazonian mimicry ring. *Zootaxa* **3860**, 097–100.
- GIANNOTTI, E. (2004). Male behavior in colonies of the social wasp *Polistes lanio* (Hymenoptera, Vespidae). *Sociobiology* **43**, 551–555.
- GILBERT, F. (2004). The evolution of imperfect mimicry. In *Symposium-Royal Entomological Society of London* **22**, 231 pp.
- GOLDING, Y., ENNOS, R., SULLIVAN, M. & EDMUNDS, M. (2005). Hoverfly mimicry deceives humans. *Journal of Zoology* **266**, 395–399. Cambridge University Press.
- GRIMALDI, D. & ENGEL, M.S. (2005). *Evolution of the Insects*. Cambridge University Press.
- HARVELL, C.D. (1994). The Evolution of Polymorphism in Colonial Invertebrates and Social Insects. *The Quarterly Review of Biology* **69**, 155–185.
- HASSALL, C., BILLINGTON, J. & SHERRATT, T.N. (2019). Climate-induced phenological shifts in a Batesian mimicry complex. *PNAS* **16**, 929–933.
- HAUGLUND, K., HAGEN, S.B. & LAMPE, H.M. (2006). Responses of domestic chicks (*Gallus gallus domesticus*) to multimodal aposematic signals. *Behavioral Ecology* **17**, 392–398.
- HEIKERTINGER, F. (1921). Die Wespenmimikry oder Sphekoidie. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien* **70**, 316–385.
- HINES, H.M. & WILLIAMS, P.H. (2012). Mimetic colour pattern evolution in the highly polymorphic *Bombus trifasciatus* (Hymenoptera: Apidae) species complex and its comimics. *Zoological Journal of the Linnean Society* **166**, 805–826.

- HLAVÁČEK, A., DAŇKOVÁ, K., BENDA, D., BOGUSCH, P. & HADRAVA, J. (2022). Batesian-Müllerian mimicry ring around the Oriental hornet (*Vespa orientalis*). *Journal of Hymenoptera Research*, **92**, 211–228.
- HOLMES, R.T., SCHULTZ, J.C. & NOTHNAGLE, P. (1979). Bird Predation on Forest Insects: An Enclosure Experiment. *Science* **206**, 462–463.
- HOWARTH, B., EDMUNDS, M. & GILBERT, F. (2004). Does the Abundance of Hoverfly (syrphidae) Mimics Depend on the Numbers of Their Hymenopteran Models? *Evolution* **58**, 367–375.
- IPBES (2016). The assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on pollinators, pollination and food production. Potts, S.G., Imperatriz-Fonseca, V.L. & Ngo, H.T. (eds). Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, Bonn, Germany. 552 pages. <https://doi.org/10.5281/zenodo.3402856>
- ISERBYT, A., BOTS, J., VAN DONGEN, S., TING, J.J., VAN GOSSUM, H. & SHERRATT, T.N. (2011). Frequency-dependent variation in mimetic fidelity in an intraspecific mimicry system. *Proceedings of the Royal Society B: Biological Sciences* **278**, 3116–3122.
- JORON, M. & IWASA, Y. (2005). The evolution of a Müllerian mimic in a spatially distributed community. *Journal of Theoretical Biology* **237**, 87–103.
- KASPAREK, M. (2019). Bees in the genus *Rhodanthidium*: A review and identification guide. *Entomofauna supplement* **24**, 1–132.
- KASPARI, M. & JOERN, A. (1993). Prey Choice by Three Insectivorous Grassland Birds: Reevaluating Opportunism. *Oikos* **68**, 414–430.

- KAUPPINEN, J. & MAPPES, J. (2003). Why are wasps so intimidating: field experiments on hunting dragonflies (Odonata: *Aeshna grandis*). *Animal Behaviour* **66**, 505–511.
- KEVAN, P.G. & BAKER, H.G. (1983). Insects as Flower Visitors and Pollinators. *Annual Review of Entomology* **28**, 407–453.
- KIKUCHI, D.W. & PFENNIG, D.W. (2013). Imperfect Mimicry and the Limits of Natural Selection. *The Quarterly Review of Biology* **88**, 297–315.
- KIKUCHI, D.W., HERBERSTEIN, M.E., BARFIELD, M., HOLT, R.D. & MAPPES, J. (2021). Why aren't warning signals everywhere? On the prevalence of aposematism and mimicry in communities. *Biological Reviews* **96**, 2446–2460.
- KIRCHNER, W.H. & RÖSCHARD, J. (1999). Hissing in bumblebees: an interspecific defence signal. *Insectes sociaux* **46**, 239–243.
- KNIGHT, T.M., MCCOY, M.W., CHASE, J.M., MCCOY, K.A. & HOLT, R.D. (2005). Trophic cascades across ecosystems. *Nature* **437**, 880–883.
- LANE, C. (1957). Preliminary note on insects eaten and rejected by a tame Shama (*Kittacincla malabarica* Gm.), with the suggestion that in certain species of butterflies and moths females are less palatable than males. *Entomologist's Monthly Magazine* **93**, 172–179.
- LANTERI, A.A. & DEL RIO, M.G. (2005). Taxonomy of the monotypic genus *Trichaptus* Pascoe (Coleoptera: Curculionidae: Entiminae), a potential weevil mimic of Mutillidae. *The Coleopterists Bulletin* **58**, 111–118.
- LINDSTRÖM, L., ALATALO, R.V. AND MAPPES, J. (1997). Imperfect Batesian mimicry—the effects of the frequency and the distastefulness of the model. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **264**, 149–153.

- LINDSTRÖM, L., ALATALO, R.V. AND MAPPES, J. (1999). Reactions of hand-reared and wild-caught predators toward warningly colored, gregarious, and conspicuous prey. *Behavioral Ecology* **10**, 317–322.
- LINDSTRÖM, L., ALATALO, R.V., LYYTINEN, A. AND MAPPES, J. (2004). The effect of alternative prey on the dynamics of imperfect Batesian and Müllerian mimics. *Evolution* **58**, 1294–1302.
- LINSLEY, E.G. (1959). Mimetic Form and Coloration in the Cerambycidae (Coleoptera). *Annals of the Entomological Society of America* **52**, 125–131.
- LLAURENS, V., BILLIARD, S. & JORON, M. (2013). The effect of dominance on polymorphism in Müllerian mimicry. *Journal of Theoretical Biology* **337**, 101–110.
- MALLET, J. & JORON, M. (1999). Evolution of Diversity in Warning Color and Mimicry: Polymorphisms, Shifting Balance, and Speciation. *Annual Review of Ecology and Systematics* **30**, 201–233.
- MANLEY, D.G. & SHERBROOKE, W.C. (2001). Predation on velvet ants (Hymenoptera: Mutillidae) by Texas horned lizards (*Phrynosoma cornutum*). *The Southwestern Naturalist* **46**, 221–222.
- MAPPES, J., KOKKO, H., OJALA, K. & LINDSTRÖM, L. (2014). Seasonal changes in predator community switch the direction of selection for prey defences. *Nature Communications* **5**, 1–7.
- MARPLES, N.M. (1993). Do wild birds use size to distinguish palatable and unpalatable prey types? *Animal Behaviour* **46**, 347–354.
- MARTIN, S.J., CARRUTHERS, J.M., WILLIAMS, P.H. & DRIJFHOUT, F.P. (2010). Host Specific Social Parasites (*Psithyrus*) Indicate Chemical Recognition System in Bumblebees. *Journal of Chemical Ecology* **36**, 855–863.

- MASTERS, W.M. (1979). Insect Disturbance Stridulation: Its Defensive Role. *Behavioral Ecology and Sociobiology* **5**, 187–200.
- MOORE, C.D. & HASSALL, C. (2016). A bee or not a bee: an experimental test of acoustic mimicry by hoverflies. *Behavioral Ecology* **27**, 1767–1774.
- MORA, R. & HANSON, P.E. (2019). Widespread occurrence of black-orange-black color pattern in Hymenoptera. *Journal of Insect Science* **19**, 1–12.
- MOSTLER, G. (1935). Beobachtungen zur frage der wespenmimikry. *Zeitschrift für Morphologie und Ökologie der Tiere* **29**, 381–454.
- MOTYKA, M., KAMPOVA, L. & BOCAK, L. (2018). Phylogeny and evolution of Müllerian mimicry in aposematic *Dilophotes*: evidence for advergence and size-constraints in evolution of mimetic sexual dimorphism. *Scientific Reports* **8**, 1–10.
- MÜLLER, F. (1879). *Ituna* and *Thyridia*: a remarkable case of mimicry in butterflies. *Transactions of the Entomological Society of London*, 20–29.
- MYERS, J.G. (1935). Experiments with spiders and the bee-like *Eristalis tenax* Linn. *Proceedings of the Royal Entomological Society London* **9**, 93–95.
- NEEDHAM, J.G. (1945). Notes on some dragonflies of southwest peninsular Florida. *Bulletin of the Brooklyn Entomological Society* **40**, 104–110.
- NENTWIG, W. (1985). A mimicry complex between Mutillid wasps (Hymenoptera: Mutillidae) and spiders (Araneae). *Studies on Neotropical Fauna and Environment* **20**, 113–116.
- NICHOLSON, A.J. (1927). A new theory of mimicry in insects. *The Australian Zoologist* **5**, 10–101.

- NUGROHO, H., LUPIYANINGDYAH, P. & KOJIMA, J. (2020). Review of the potter wasps (Hymenoptera: Vespidae, Eumeninae) with a petiolate metasoma from Indonesian Archipelago. *BIO Web of Conferences* **19**, 1–12.
- O'DONNELL, S. (1996). Dragonflies (*Gynacantha nervosa* Rambur) avoid wasps (*Polybia aequatorialis* Zavattari and *Mischocyttarus* sp.) as prey. *Journal of Insect Behavior* **9**, 159–162.
- O'DONNELL, S. (1998). Reproductive caste determination in eusocial wasps (Hymenoptera: Vespidae). *Annual Review of Entomology* **43**, 323–346.
- O'DONNELL, S. & JOYCE, F.J. (1999). Dual mimicry in the dimorphic eusocial wasp *Mischocyttarus mastigophorus* Richards (Hymenoptera: Vespidae). *Biological Journal of the Linnean Society* **66**, 501–514.
- OPLER, P.A. (1981). Polymorphic Mimicry of Polistine Wasps by a Neotropical Neuropteran. *Biotropica* **13**, 165–176.
- ORR, M.C., HUGHES, A.C., CHESTERS, D., PICKERING, J., ZHU, C.-D. & ASCHER, J.S. (2021). Global Patterns and Drivers of Bee Distribution. *Current Biology* **31**, 451–458
- OWEN, R.E. & PLOWRIGHT, R.C. (1988). Inheritance of metasomal pile colour variation in the bumble bee *Bombus rufocinctus* Cresson (Hymenoptera: Apidae). *Canadian Journal of Zoology* **66**, 1172–1178.
- PAN, A.D., WILLIAMS, K.A. & WILSON, J.S. (2017). Are diurnal iguanian lizards the evolutionary drivers of New World female velvet ant (Hymenoptera: Mutillidae) Müllerian mimicry rings? *Biological Journal of the Linnean Society* **120**, 436–447.
- PAULY, A., VAGO, J.-L. & WAHIS, R. (2003). La couleur vert pomme chez les Hyménoptères de Madagascar (Vespidae, Apidae, Pompilidae, Leucospidae). *Annales du Musée Royal de l'Afrique Centrale (Zoologie)* **291**, 91–98.

- PEKAR, S., GARCIA, L.F. & BULBERT, M.W. (2020). Spiders mimic the acoustic signalling of mutillid wasps to avoid predation: startle signalling or Batesian mimicry? *Animal Behaviour* **170**, 157–166.
- PEKAR, S., PETRAKOVA, L., BULBERT, M.W., WHITING, M.J. & HERBERSTEIN, M.E. (2017). The golden mimicry complex uses a wide spectrum of defence to deter a community of predators. *eLife* **6**, e22089.
- PEMBURY SMITH, M.Q.R. & RUXTON, G.D. (2021). Size-dependent predation risk in cryptic prey. *Journal of Ethology* **39**, 191–198.
- PENNEY, H.D., HASSALL, C., SKEVINGTON, J.H., ABBOTT, K.R. & SHERRATT, T.N. (2011). A comparative analysis of the evolution of imperfect mimicry. *Nature* **483**, 461–466.
- PENNEY, H.D., HASSALL, C., SKEVINGTON, J.H., LAMBORN, B. & SHERRATT, T.N. (2014). The Relationship between Morphological and Behavioral Mimicry in Hover Flies (Diptera: Syrphidae). *The American Naturalist* **183**, 281–289.
- PERRARD, A., ARCA, M., ROME, Q., MULLER, F., TAN, J., BISTA, S., NUGROHO, H., BAUDOIN, R., BAYLAC, M., SILVAIN, J.-F., CARPENTER, J.M. & VILLEMANT, C. (2014). Geographic Variation of Melanisation Patterns in a Hornet Species: Genetic Differences, Climatic Pressures or Aposematic Constraints? *PLoS ONE* **9**, 1–16.
- PETERS, R.S., KROGMANN, L., MAYER, C., DONATH, A., GUNKEL, S., MEUSEMANN, K., KOZLOV, A., PODSIADLOWSKI, L., PETERSEN, M., LANFEAR, R., DIEZ, P.A., HERATY, J., KJER, K.M., KLOPFSTEIN, S., MEIER, R., *et al.* (2017). Evolutionary History of the Hymenoptera. *Current Biology* **27**, 1013–1018.
- PLOWRIGHT, R.C. & OWEN, R.E. (1980). The Evolutionary Significance of Bumble Bee Color Patterns: A Mimetic Interpretation. *Evolution* **34**, 622–637.

- POTTS, S.G., BIESMEIJER, J.C., KREMEN, C., NEUMANN, P., SCHWEIGER, O., & KUNIN, W.E. (2010). Global pollinator declines: trends, impacts and drivers. *Trends in ecology & evolution* **25**, 345–353.
- POULTON, E.B. (1887). The Experimental Proof of the Protective Value of Colour and Markings in Insects in reference to their Vertebrate Enemies. *Proceedings of the Zoological Society of London* **55**, 191–274.
- POULTON, E.B. (1890). *The colours of animals: their meaning and use, especially considered in the case of insects*. D. Appelton and Company.
- POULTON, E.B. (1897). Mimicry in Butterflies and Moths. *Nature* **57**, 1–4.
- *PRYS-JONES, O.E. & CORBET, S.A. (1991). Bumblebees. *Naturalists' handbook series* **6**.
- PUNZO, F. (2003). Observations on the diet composition of the gray shrew *Notiosorex crawfordi* (Insectivora), including interactions with large arthropods. *The Texas Journal of Science* **55**, 75–86.
- QUICKE, D.L.J. (2017). *Mimicry, crypsis, masquerade and other adaptive resemblances*. John Wiley and Sons.
- RADER, R., BARTOMEUS, I., GARIBALDI, L.A., GARRATT, M.P., HOWLETT, B.G., WINFREE, R., CUNNINGHAM, S.A., MAYFIELD, M.M., ARTHUR, A.D., ANDERSSON, G.K. AND BOMMARCO, R. (2016). Non-bee insects are important contributors to global crop pollination. *Proceedings of the National Academy of Sciences* **113**, 146–151.
- RASHED, A., KHAN, M.I., DAWSON, J.W., YACK, J.E. & SHERRATT, T.N. (2009). Do hoverflies (Diptera: Syrphidae) sound like the Hymenoptera they morphologically resemble? *Behavioral Ecology* **20**, 396–402.
- RETTENMEYER, C.W. (1970). Insect Mimicry. *Annual Review of Entomology* **15**, 43–74.

- RODRIGUEZ, J., PITTS, J.P., VON DOHLEN, C.D. & WILSON, J.S. (2014). Müllerian Mimicry as a Result of Codivergence between Velvet Ants and Spider Wasps. *PLoS ONE* **9**, 1–7.
- ROME, Q., PERRARD, A., MULLER, F., FONTAINE, C., QUILES, A., ZUCCON, D. & VILLEMANT, C. (2021). Not just honeybees: predatory habits of *Vespa velutina* (Hymenoptera: Vespidae) in France. *Annales de la Société entomologique de France (N.S.)* **57**, 1–11. Taylor & Francis.
- ROMERO, G.Q., ANTIQUEIRA, P.A.P. & KORICHEVA, J. (2011). A Meta-Analysis of Predation Risk Effects on Pollinator Behaviour. *PLoS ONE* **6**, 1–9.
- RÖNKÄ, K., DE PASQUAL, C., MAPPES, J., GORDON, S. & ROJAS, B. (2018). Colour alone matters: no predator generalization among morphs of an aposematic moth. *Animal Behaviour* **135**, 153–163.
- ROTHSCHILD, M. (1984). Aide memoire mimicry. *Ecological Entomology* **9**, 311–319.
- ROWLAND, H.M., IHALAINEN, E., LINDSTRÖM, L., MAPPES, J. & SPEED, M.P. (2007). Co-mimics have a mutualistic relationship despite unequal defences. *Nature* **448**, 64–68.
- ROWLAND, H.M., MAPPES, J., RUXTON, G.D. & SPEED, M.P. (2010). Mimicry between unequally defended prey can be parasitic: evidence for quasi-Batesian mimicry. *Ecology Letters* **13**, 1494–1502.
- RUXTON, G.D., SPEED, M.P. & SHERRATT, T.N. (2004). Evasive mimicry: when (if ever) could mimicry based on difficulty of capture evolve? *Proceedings of the Royal Society of London B* **271**, 2135–2142.
- SANN, M., NIEHUIS, O., PETERS, R.S., MAYER, C., KOZLOV, A., PODSIADLOWSKI, L., BANK, S., MEUSEMANN, K., MISOF, B., BLEIDORN, C. & OHL, M. (2018). Phylogenomic analysis of Apoidea sheds new light on the sister group of bees. *BMC Evolutionary Biology* **18**, 1–15.

- SCHMIDT, J.O. (2004). Venom and the Good Life in Tarantula Hawks (Hymenoptera: Pompilidae): How to Eat, Not be Eaten, and Live Long. *Journal of the Kansas Entomological Society* **77**, 402–413.
- SCHMIDT, J.O. (2019). Pain and Lethality Induced by Insect Stings: An Exploratory and Correlational Study. *Toxins* **11**, 1–14.
- SCHMIDT, J.O., BLUM, M.S. & OVERAL, W.L. (1980). Comparative lethality of venoms from stinging hymenoptera. *Toxicon* **18**, 469–474.
- SCHULER, W. & HESSE, E. (1985). On the function of warning coloration: a black and yellow pattern inhibits prey-attack by naive domestic chicks. *Behavioral Ecology and Sociobiology* **16**, 249–255.
- *SELIS, M. (2018). Description of the first endemic *Polistes* Latreille, 1802 from Sulawesi (Hymenoptera: Vespidae: Polistinae). *Zootaxa* **4508**, 435–438.
- SEXTON, O.J. (1964). Differential predation by the lizard, *Anolis carolinensis*, upon unicoloured and polycholoured insects after an interval of no contact. *Animal Behaviour* **12**, 101–110.
- SHARKEY, M.J., CARPENTER, J.M., VILHELMSSEN, L., HERATY, J., LILJEBLAD, J., DOWLING, A.P.G., SCHULMEISTER, S., MURRAY, D., DEANS, A.R., RONQUIST, F., KROGMANN, L. & WHEELER, W.C. (2012). Phylogenetic relationships among superfamilies of Hymenoptera. *Cladistics* **28**, 80–112.
- SHERRATT, T.N. (2003). State-dependent risk-taking by predators in systems with defended prey. *Oikos* **103**, 93–100.
- SHERRATT, T.N. (2008). The evolution of Müllerian mimicry. *Naturwissenschaften* **95**, 681–695.
- SHERRATT, T.N. (2011). The optimal sampling strategy for unfamiliar prey. *Evolution* **65**, 2014–2025.
- SHINE, R., BROWN, G.P. & GOIRAN, C. (2022). Frequency-dependent Batesian mimicry maintains colour polymorphism in a sea snake population. *Scientific Reports* **12**, 1–9.

- SIDDALL, E.C. & MARPLES, N.M. (2011). Hear no evil: The effect of auditory warning signals on avian innate avoidance, learned avoidance and memory. *Current Zoology* **57**, 197–207.
- SILBERGLIED, R.E. & EISNER, T. (1969). Mimicry of Hymenoptera by Beetles with Unconventional Flight. *Science* **163**, 486–488.
- SILLÉN-TULLBERG, B. (1988). Evolution of gregariousness in aposematic butterfly larvae: a phylogenetic analysis. *Evolution* **42**, 293–305.
- SKELHORN, J., HALPIN, C.G. & ROWE, C. (2016). Learning about aposematic prey. *Behavioral Ecology* **27**, 955–964.
- SKOWRON VOLPONI, M.A., MCLEAN, D.J., VOLPONI, P. & DUDLEY, R. (2018). Moving like a model: mimicry of hymenopteran flight trajectories by clearwing moths of Southeast Asian rainforests. *Biology Letters* **14**, 1–6.
- SKOWRON VOLPONI, M., CASACCI, L.P., VOLPONI, P. & BARBERO, F. (2021). Southeast Asian clearwing moths buzz like their model bees. *Frontiers in Zoology* **18**, 1–10.
- SMITH, K.E., HALPIN, C.G. & ROWE, C. (2016). The benefits of being toxic to deter predators depends on prey body size. *Behavioral Ecology* **27**, 1650–1655.
- SMITH-PARDO, A.H. (2005). Systematics and mimicry of the genus *Neocorynura*: an example of two species from Central America (Hymenoptera: Halictidae). *Acta zoologica cracoviensia* **48**, 11–21.
- SPEED, M.P. (1993). Muellierian mimicry and the psychology of predation. *Animal Behaviour* **45**, 571–580.
- SPEED, M.P. (1999). Batesian, quasi-Batesian or Müllerian mimicry? Theory and data in mimicry research. *Evolutionary Ecology* **13**, 755–776.

- SPEED, M.P. & ARBUCKLE, K. (2017). Quantification provides a conceptual basis for convergent evolution. *Biological Reviews* **92**, 815–829.
- SPEED, M.P. & TURNER, J.R.G. (1999). Learning and memory in mimicry: II. Do we understand the mimicry spectrum? *Biological Journal of the Linnean Society* **67**, 281–312.
- SPRADBERY, J.P. (1973). *Wasps. An account of the biology and natural history of social and solitary wasps, with particular reference to those of the British Isles*. University of Washington Press.
- STARR, C.K. (1985). A simple pain scale for field comparison of hymenopteran stings. *Journal of Entomological Sciences* **20**, 225–232.
- STAYTON, C.T. (2015a). The definition, recognition, and interpretation of convergent evolution, and two new measures for quantifying and assessing the significance of convergence. *Evolution* **69**, 2140–2153.
- STAYTON, C.T. (2015b). What does convergent evolution mean? The interpretation of convergence and its implications in the search for limits to evolution. *Interface Focus* **5**, 1–8.
- STILES, E.W. (1979). Evolution of Color Pattern and Pubescence Characteristics in Male Bumblebees: Automimicry vs. Thermoregulation. *Evolution* **33**, 941–957.
- STUBBLEFIELD, J.W. & SEGER, J. (1994). Sexual dimorphism in the Hymenoptera. In Short, R.V. & Balaban, E. (Eds) *The Differences Between the Sexes*, pp. 71–103, Cambridge University Press.
- SUGIURA, S. & TSUJII, M. (2022). Male wasp genitalia as an anti-predator defense. *Current Biology* **32**, 1325–1337.

- SVENSON, G.J. & RODRIGUES, H.M. (2019). A novel form of wasp mimicry in a new species of praying mantis from the Amazon rainforest, *Vespamantoida wherleyi* gen. nov. sp. nov. (Mantodea, Mantoididae). *PeerJ* **7**, e7886.
- TAYLOR, C.H., WARRIN, J., GILBERT, F. & READER, T. (2017). Which traits do observers use to distinguish Batesian mimics from their models? *Behavioral Ecology* **28**, 460–470.
- THÉRY, M. & GOMEZ, D. (2010). Insect Colours and Visual Appearance in the Eyes of Their Predators. In *Advances in Insect Physiology* **38**, 267–353.
- THORP, R.W., HORNING, D.S.JR. & DUNNING, L.L. (1983). *Bumble bees and cuckoo bumble bees of California (Hymenoptera, Apidae)*. University of California Press. Los Angeles.
- TIITSAAR, A., KAASIK, A., TEDER, T. (2013). The effects of seasonally variable dragonfly predation on butterfly assemblages. *Ecology* **94**, 200–207.
- TULLBERG, B. S. & HUNTER, A. F. (1996). Evolution of larval gregariousness in relation to repellent defences and warning coloration in tree-feeding Macrolepidoptera: a phylogenetic analysis based on independent contrasts. *Biological Journal of the Linnean Society* **57**, 253–276.
- VAN DER VECHT, J. (1961). Evolution in a group of Indo-Australian *Eumenes* (Hymenoptera, Eumenidae). *Evolution* **15**, 468–477.
- VAN ZANDT BROWER, J. & BROWER, L.P. (1962). Experimental studies of mimicry. 6. The reaction of toads (*Bufo terrestris*) to honeybees (*Apis mellifera*) and their dronefly mimics (*Eristalis vinetorum*). *The American Naturalist* **96**, 297–307.
- VAN ZANDT BROWER, J. & BROWER, L.P. (1965). Experimental studies of mimicry. 8. Further investigations of honeybees (*Apis mellifera*) and their dronefly mimics (*Eristalis* spp.). *The American Naturalist* **99**, 173–187.

- VILHELMOSEN, L. (2019). Giant sawflies and their kin: morphological phylogeny of Cimbicidae (Hymenoptera). *Systematic Entomology* **44**, 103–127.
- WALDBAUER, G.P. & COWAN, D.P. (1985). Defensive stinging and Müllerian mimicry among Eumenid wasps (Hymenoptera: Vespoidea: Eumenidae). *The American Midland Naturalist* **113**, 198–199.
- WALDBAUER, G.P. & SHELDON, J.K. (1971). Phenological relationships of some Aculeate Hymenoptera, their Dipteran mimics, and insectivorous birds. *Evolution* **25**, 371–382.
- WALDBAUER, G.P., STERNBURG, J.G. & MAIER, C.T. (1977). Phenological relationships of wasps, bumblebees, their mimics, and insectivorous birds in an Illinois sand area. *Ecology* **58**, 583–591.
- WALLACE, A.R. (1882). Dr. Fritz Müller on some difficult cases of mimicry. *Nature* **26**, 86–87.
- WANG, L., CORNELL, S.J., SPEED, M.P. & ARBUCKLE, K. (2021). Coevolution of group-living and aposematism in caterpillars: warning colouration may facilitate the evolution from group-living to solitary habits. *BMC Ecology and Evolution* **21**, 1–9.
- WENZEL, J.W. (1992). Extreme queen-worker dimorphism in *Ropalidia ignobilis*, a small-colony wasp (Hymenoptera: Vespidae). *Insectes sociaux* **39**, 31–43.
- WEST-EBERHARD, M.J., CARPENTER, J.M. & HANSON, P.E. (1995). The vespid wasps (Vespidae). In Hanson, P.E. & Gauld, I.D. (Eds.) *The Hymenoptera of Costa Rica*, pp. 561–587, Oxford Science Publications. Oxford.
- WHEELER, D.E. (1991). The Developmental Basis of Worker Caste Polymorphism in Ants. *The American Naturalist* **138**, 1218–1238.
- WHEELER, G.C. (1983). A mutillid mimic of an ant (Hymenoptera: Mutillidae and Formicidae). *Entomological News* **94**, 143–144.

- WICKHAM, H. (2016). *ggplot2: elegant graphics for data analysis*. Springer-Verlag New York.
- WILLADSEN, P.C. (2022). Aculeate Hymenopterans as aposematic and mimetic models. *Frontiers in Ecology and Evolution* **10**, 827319.
- WILLIAMS, P. (2007). The distribution of bumblebee colour patterns worldwide: possible significance for thermoregulation, crypsis, and warning mimicry. *Biological Journal of the Linnean Society* **92**, 97–118.
- WILLIAMS, P.H. (2008). Do the parasitic *Psithyrus* resemble their host bumblebees in colour pattern? *Apidologie* **39**, 637–649.
- WILSON, J.S., JAHNER, J.P., FORISTER, M.L., SHEEHAN, E.S., WILLIAMS, K.A. & PITTS, J.P. (2015). North American velvet ants form one of the world's largest known Müllerian mimicry complexes. *Current Biology* **25**, R704–R706.
- WILSON, J.S., JAHNER, J.P., WILLIAMS, K.A. & FORISTER, M.L. (2013). Ecological and evolutionary processes drive the origin and maintenance of imperfect mimicry. *PLOS ONE* **8**, e61610.
- *WILSON, J.S., PAN, A.D., ALVAREZ, S.I. & CARRIL, O.M. (2022). Assessing Müllerian mimicry in North American bumble bees using human perception. *Scientific Reports* **12**, 17604.
- WILSON, J.S., PAN, A.D., LIMB, E.S. & WILLIAMS, K.A. (2018). Comparison of African and North American velvet ant mimicry complexes: another example of Africa as the 'odd man out'. *PLoS ONE* **13**, 1–15.
- WILSON, J.S., SIDWELL, J.S., FORISTER, M.L., WILLIAMS, K.A. & PITTS, J.P. (2020). Thistledown velvet ants in the Desert Mimicry Ring and the evolution of white coloration: Müllerian mimicry, camouflage and thermal ecology. *Biology Letters* **16**, 1–6.

WILSON, J.S., WILLIAMS, K.A., FORISTER, M.L., VON DOHLEN, C.D. & PITTS, J.P. (2012). Repeated evolution in overlapping mimicry rings among North American velvet ants. *Nature Communications* **3**, 1–7.

WRIGHT, M. (1944). Some random observations on dragonfly habits with notes on their predaceousness on bees. *Journal of the Tennessee Academy of Science* **19**, 295–301.

YANEGA, D. (1994). Arboreal, ant-mimicking Mutillid wasps, *Pappognatha*; parasites of neotropical *Euglossa* (Hymenoptera: Mutillidae and Apidae). *Biotropica* **26**, 465–468.

ZATTARA, E.E. & AIZEN, M.A. (2021). Worldwide occurrence records suggest a global decline in bee species richness. *One Earth* **4**, 114–123.

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 44 references included in our review.

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

Table S3. Detailed list of taxa in our database.

FIGURES

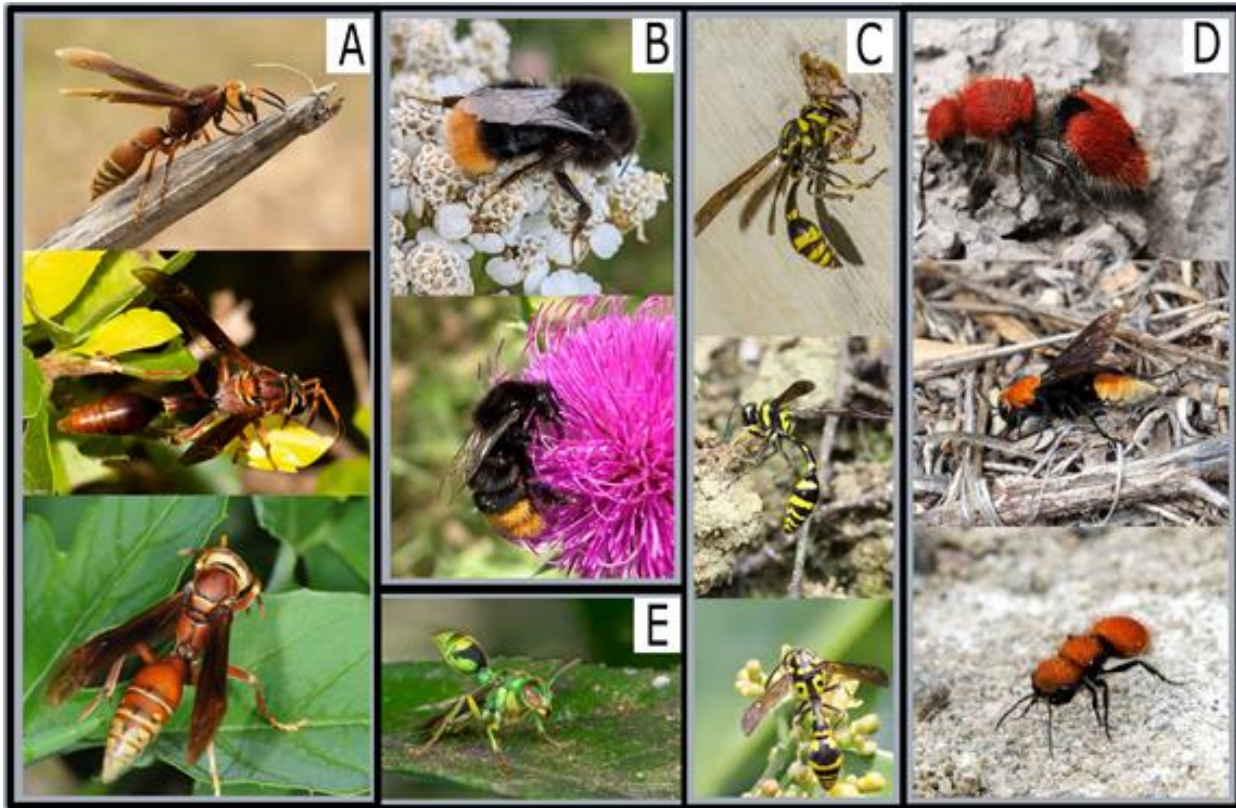


Fig. 1. Examples of some members of known mimicy rings among bees and wasps. From top to bottom: (A) *Polistes cavapyta* ring: *Montezumia ferruginea*, *Zeta argillaceum*, *Polistes cavapyta* (Vespidae) (Garcete-Barett, 1999), from Paraguay, the first two are solitary, (B) Red-tailed black bumblebees: *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: *Dasymutilla 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, Vago & Wahis, 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](https://www.inaturalist.org/) platform, photographs credits (top to bottom): (A) mendezcla7, Ísis Medri, Andrea Arístides 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.

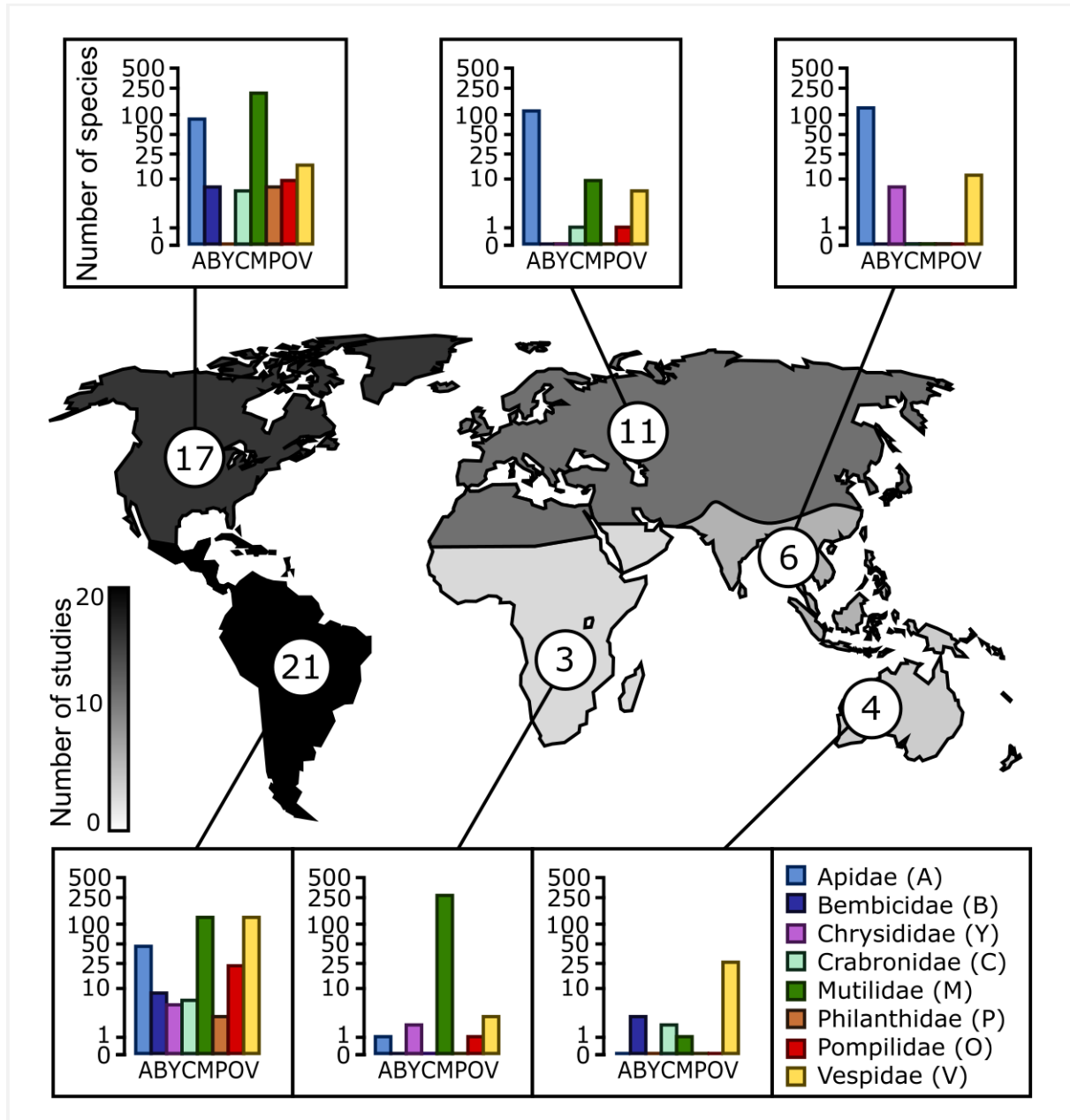


Fig. 2. Geographical distribution of studies on aculeate mimicry rings included in our data set. For each biogeographical zone, shades of grey and numbers inside the biogeographical regions represent the number of studies located for that region (13 studies covered several biogeographical areas). Barplots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

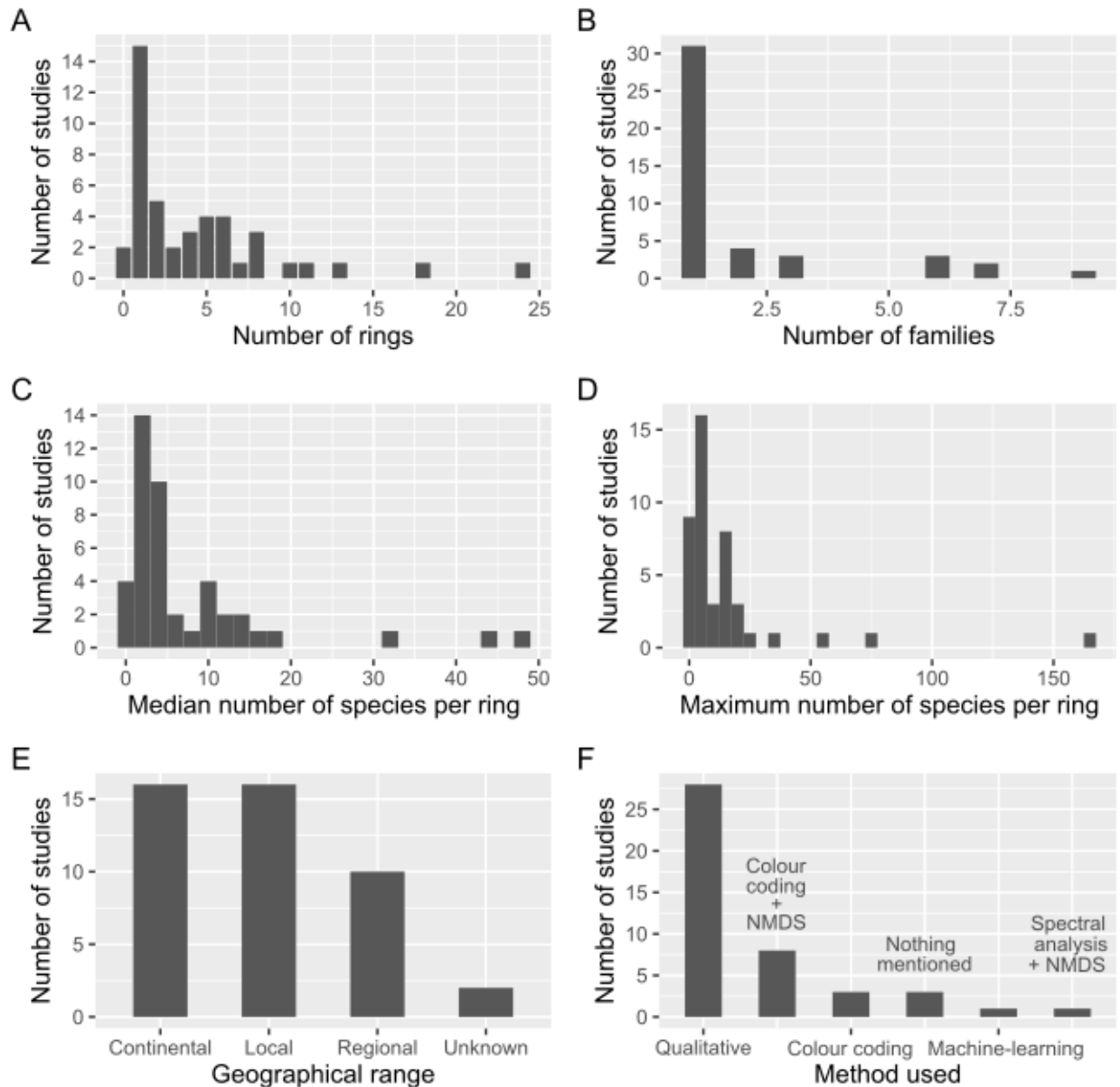


Fig. 3. Barplots of the information extracted from the reviewed 44 papers (data available in Table S1). Method used: Qualitative, verbal description; Colour-coding, numerical or categorical description of different body parts compared for each species; NMDS, non-metric dimensional scaling; Nothing mentioned, 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.

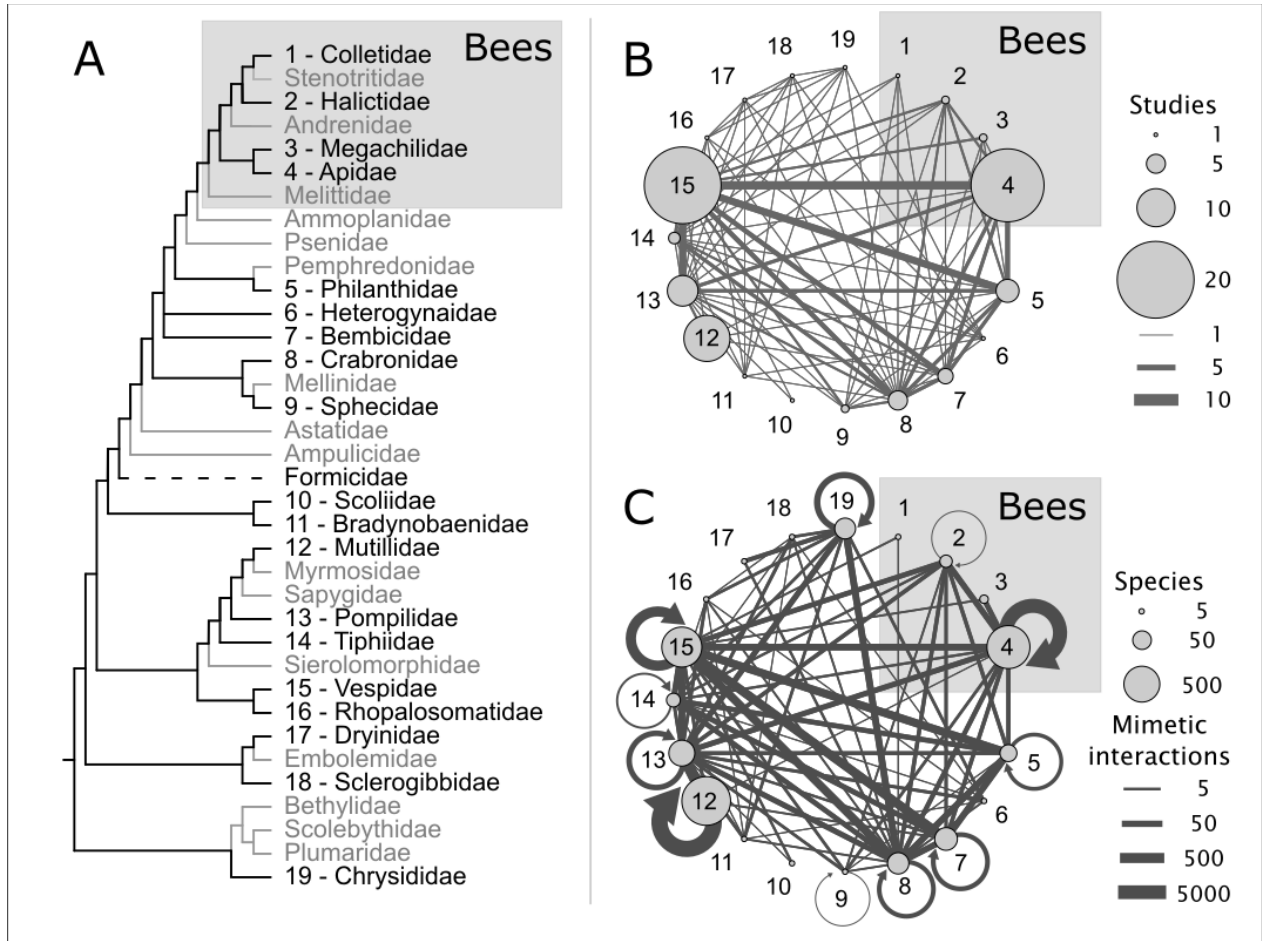


Fig. 4. (A) Aculeate phylogeny [after Peters *et al.* (2017) and Sann *et al.* (2018)]. Taxa included in the 44 reviewed papers are in black, other taxa are in grey; numbers identify the corresponding nodes in B and C. (B, C) Network representation of the mimicry rings of the aculeate families included 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.

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 form 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, 2019; Briolat <i>et al.</i> , 2019).

Chapter 2

Characterization of a hymenopteran Müllerian mimetic community from South Corsica (France): a quantitative approach of convergent color patterns at community level

In collaboration with: Yann Le Poul, Paul Zaharias, Frida Sanchez-Garrido, Romain Le Divelec, Colin Fontaine, Isabelle Dajoz, Marianne Elias and Adrien Perrard

We have seen in the previous chapter that: aculeates are one of the largest taxonomical group involved in Müllerian mimicry. However, our review highlights recurrent gaps of knowledge: i) some parts of the world, such as the Mediterranean area, seem understudied, ii) phylogeny is seldom integrated to test for convergence between putative co-mimetic species. In this chapter we studied an entire aculeate community from South Corsica (France, Mediterranean region) and took the above gaps into consideration. The aim of the present chapter is to quantify mimetic resemblance among individuals and establish putative mimicry rings at community scale, in order to evaluate mimicry occurrence and prevalence and estimate the extent of convergence.

In this study, I did not participate in: the collection of specimens (field data from 2017) and their identifications, the development and run of Yann Le Poul's method (section 2.2.2.3.a). I acquired all image data (from specimen selection and curation to image-preprocessing and analyses) and molecular sequences (protocols, DNA extractions, PCRs, assembly analyses), led and participated to alignments and phylogeny reconstruction procedure (with Paul Zaharias) and did the statistical analyses.

2.1 Introduction

Aposematism is a cornerstone phenomenon of adaptive coloration in nature and as such it receives considerable attention from evolutionary biologists (Briolat *et al.*, 2019; Kikuchi *et al.*, 2021). Aposematism is involved in prey-predator interactions, which are major components of interaction networks. Predation can incur positive frequency-dependent selection, leading preys to convergent evolution toward a common warning signal or color pattern, a phenomenon called Müllerian mimicry. Therefore, Müllerian Mimicry, which benefits to all co-occurring individuals that share the aposematic signal, may involve a substantial number of species in a community (Motyka *et al.*, 2021) even at small scale (Willmott *et al.*, 2017).

Aculeata (Hymenoptera, Apocrita) comprise numerous aposematic species involved in many different mimicry rings around the world, and is one of the largest known clades engaged in mimicry (see Chapter 1). Some aculeate mimicry rings, such as the Pan-African velvet-ants ring, comprise at least 165 species (Wilson *et al.*, 2018). This underlies their potential significant importance in the ecological processes that structure communities. Quite surprisingly, in comparison to North and South America, very few aculeate mimicry rings have been described in Europe. Five studies described mimicry rings in bumble bees (Plowright & Owen, 1980; Williams, 2007, 2008) as well as among hornets and a few aculeate species (Kasperek, 2019; Hlaváček *et al.*, 2022). Three velvet-ant rings are also known from North Africa (Wilson *et al.*, 2018). This is unexpectedly low given that several of the main bee diversity hotspots are in the Mediterranean region (Orr *et al.*, 2021). Many mimicry studies may be taxonomically biased, for instance focusing on a single family, whereas mimicry processes happen at the community scale. The goal of this study is to document and characterize aculeate mimicry rings in the Mediterranean site, South Corsica. Here, we quantify colorations and color patterns to infer putative mimicry rings, and test

whether resemblance between species is the result of convergent evolution rather than shared ancestry. The original community we study here comprises 20 different aculeate families and is located in South Corsica (France, Mediterranean region), distributed in eight localities near Bonifacio.

Whether warning or aposematic signals rely on coloration (or color patterns) *per se* has been debated in the literature (Brodie Jr, 1993; Badejo *et al.*, 2020). It has been shown experimentally, using domestic chicks preying on aculeate, that both color alone and pattern can promote predator avoidance, separately or in synergy (Hauglund, Hagen & Lampe, 2006). However, some authors insisted on the fact that color alone sometimes matters more than pattern in warning signals (Aronsson & Gamberale-Stille, 2008; Finkbeiner, Briscoe & Reed, 2014; Rönkä *et al.*, 2018). In this present study we will try to disentangle colors and patterns with appropriate methods.

Many methods have been developed throughout the last twenty years to quantitatively describe and compare color patterns. These methods focus on various aspects and/or elements of color patterns (such as conspicuousness, salience, contrasts and adjacency or other details of pattern geometry, regularities; see (Chan, Stevens & Todd, 2019)), which themselves depend on the biological questions and hypotheses at stake (Kelly *et al.*, 2021). As Van den Berg *et al.* stated in a recent publication: “*Colour adjacency analysis focuses on pattern geometry, whereas visual contrast analysis is designed to investigate colour, pattern and luminance simultaneously (Endler & Mielke, 2005). This is important because spatial, chromatic and achromatic properties of colour patterns and visual scenes can interact to promote or suppress functional components of pattern conspicuousness such as its saliency, vividness, memorability and detectability*” (van den Berg *et al.*, 2019). It is also important to note that some authors advocate for a quantification “as it is perceived” by the receiver (Pike, 2011). Some of the available methods are directly compatible

with predator vision (Troschianko & Stevens, 2015; Maia *et al.*, 2019; van den Berg *et al.*, 2019), however they require to know which predators are the effective selective forces in the habitat. Despite this methodological diversity, going from color patterns analysis to mimetic similarity analysis is another step forward, and drastically restrains the list of existing methods that can be applied to mimicry. Most aculeate mimicry rings were established with qualitative descriptions, synthetic and subjective observations, and ordination methods on color coding (see Chapter 1). In this study, we used three image analysis methods, two inspired from the Color Pattern Modelling (CPM) method (Le Poul, 2014) for quantification of the color pattern, and a third one for global color comparison. We then used clustering methods to define similarity groups.

Phylogenetic relationships are essential in understanding the evolutionary history involved in the ecological processes that structure communities (Webb *et al.*, 2002), especially in the context of mimicry (Elias *et al.*, 2008; Motyka, Kampova & Bocak, Ladislav, 2018). For instance, if co-mimetic species belong to the same genus and if that genus is monophyletic, the hypothesis of inherited aposematic color pattern cannot be refuted and common ancestry, as opposed to convergence, may solely explain similarity (Rodriguez *et al.*, 2014; Pekar *et al.*, 2017). In the present study we reconstruct the community's phylogeny to test for convergence within mimicry rings.

We hypothesize that color patterns are structured in discrete entities, and we investigate the phylogenetic structure of such entities (i.e. overdispersion, clustering, or random distribution), which may be under the selective pressure exerted by predators or under other non-mutually exclusive selective pressures. We test this hypothesis on 1066 specimens representing 388 aculeate species (83 genera of 18 families). In this study we aim to quantify variations in colors and color patterns of bees and wasps species (both males and females) in a pollinator community from South

Corsica (France), classify phenotypes into discrete categories, quantify and test for convergence within each category in order to assess putative mimicry rings. This study aims to answer the following questions: *i*) are there multiple mimicry rings co-existing in a community of aculeates? (i.e. is there resemblance between co-occurring species in the community?), *ii*) is there evidence for convergence in aposematic signal among co-mimetic species?

2.2 Material and Methods

2.2.1 Protocol and set-up

2.2.1.1 Dataset and pinned insects challenges

We use a dataset from South Corsica (Bonifacio, France). Charles Ferton was a famous hymenopteran collector from the late nineteenth century, and his collection (owned by the Muséum national d'Histoire naturelle in Paris) covers all Europe in various proportion (from Canaries islands to Caucasian mountains). Ferton's collection mostly comprises specimens from North Africa (e.g. Algeria), Corsica and continental France. We focused on localities near Bonifacio (a subsample of the Corsican collection) to make a consistent comparison with data from the exact same localities sampled in 2017.

Pinned insects provide many challenging issues for standardized image analysis. Color Pattern Modelling (CPM) was originally conceived for butterflies (Le Poul, 2014), which have (more or less) flat wings displayed in a very standardized way and on which reflections do not generally occur. Unfortunately, in the case of Hymenoptera, color patterns on body parts are displayed in 3 dimensions and some patterns or parts of patterns can be hidden depending on how the specimen was pinned and displayed. Another difficulty is the shiny cuticle (most of specimens are not dull

or hairy), which can cause reflections (i.e. white pixels) and hide parts of the actual color pattern. Shadows are also problematic for image registration (extraction from background). Finally, old or dry specimens are quite fragile and even simple manipulations such as labels removal should be limited (which is why spreading specimens anew was not doable) and limit time for manipulation. Here we only focused on a single dorsal view of the metasoma (abdominal segments posterior to the first), leaving aside the mesosoma (thorax + first abdominal segments) or other body parts because of their orientation and specimens' display.

2.2.1.2 Specimen selection

In order to select specimens, for color pattern analysis, both in the 2017 dataset and the Fertton collection, all specimens were checked by the first author. No species were excluded a priori. Only types would not be touched with the exception of *Arachnospila holomelas*, EY23378 (which was the only specimen available for this species). When it occurred, intra-specific variation was considered (and within each sex) for all species and variants were included in the analysis. We selected a maximum of three individuals per sex and species. Specimens were selected according to the following criteria: i) proper conservation both in terms of colors and body shape, ii) a visible pattern (not covered by legs or wings – for some recent and soft material, when specimens were large enough, we pushed aside wings), and iii) a display that allowed photography of metasoma (tergites or metasomal piles can overlap and bias the potential color pattern). For the 2017 dataset, as specimens were not yet registered in the MNHN collections, and inventory numbers and tagged labels were attributed. List of all photographed specimens are given in Appendix 2.1.

2.2.1.3 Set-up and protocol

After removing all labels, the pinned specimen was displayed on background and oriented toward the flattest position of metasoma's dorsal view. Then background and specimen were manually

lifted up or down using a lab jack stand, so that the specimen is at the same distance from the camera than the scale (Figure 2.1).

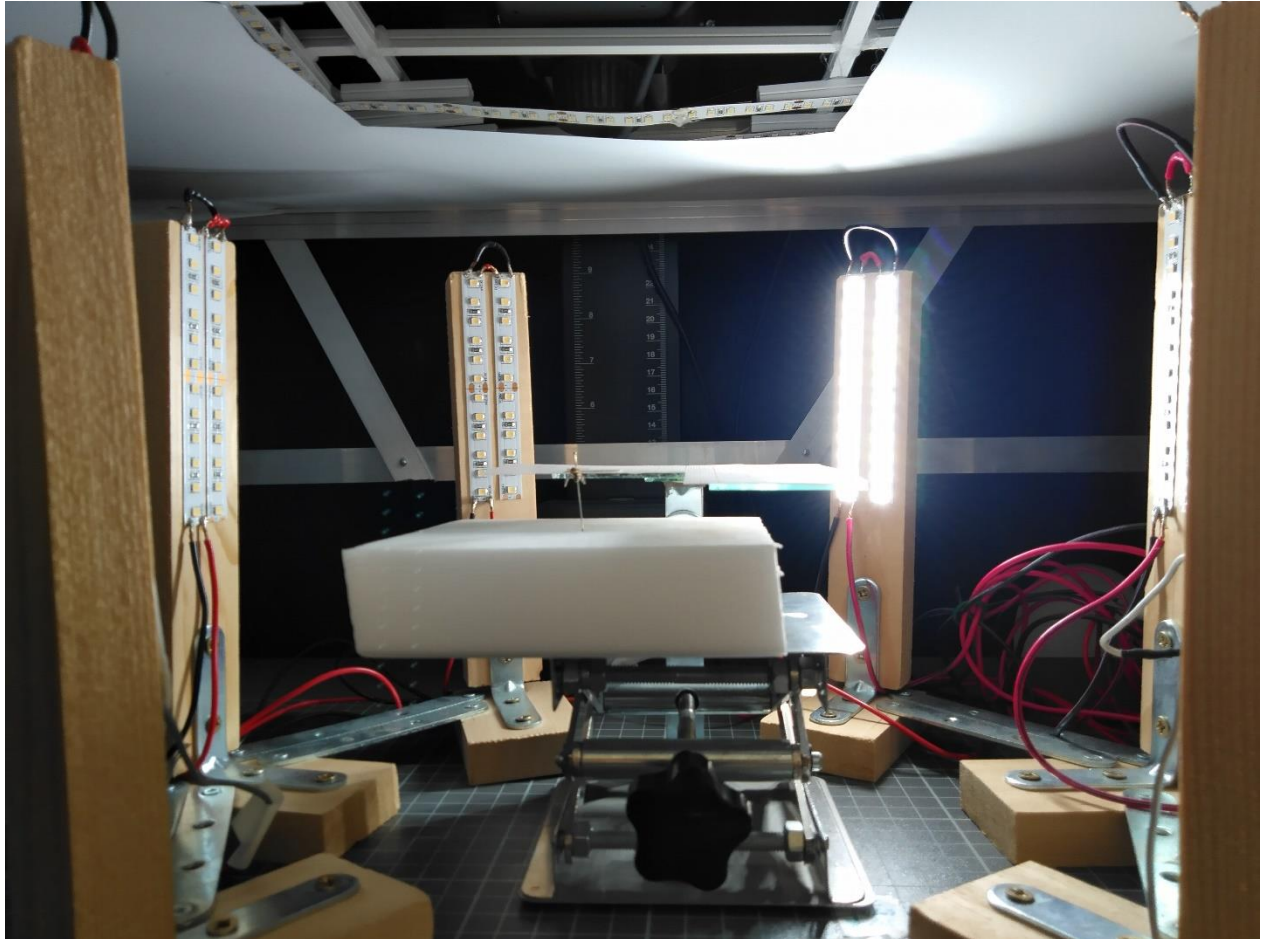


Figure 2.1. Set-up for standardized images (see text for explanation).

Photos were taken in standardized conditions in a dark chamber. We used a Nikon D90 DSLR camera with the Micro-NIKKOR 60mm f/2.8G IF-ED AF-S ED lens. The camera was set at a distance of 44 cm from the background. Lights consisted of 6 vertical props of high color rendering led lights. Each prop maintained one pair of led bands. In order to be free of reflections (unwanted white pixels), each of the six props was successively turned on and a photo taken. Then each batch of 6 images were combined under Matlab (script in Appendix 2.2), by selecting the 4th darkest

pixel value for each pixel on the 6 aligned images. The value of 4 is set-up-dependent and was found optimally by trial and error, so that image registration was correctly run and reflection-free.

2.2.1.4 Photo parameters and pre-processing

Raw images were then converted to TIFF images with a white balance using LZW compression. Parameters were set manually and systematically for all photos: opening was set to f/4 and closing speed to 1/80 s. No special corrections were added. Images were then clipped manually with GIMP to extract abdomen and scale. We generated a dataset of 1067 images (610 from 2017 and 457 from Fertón's collection). All images will be versed to the MNHN collection database.

2.2.2 Image analyses and quantification of mimetic resemblance

2.2.2.1 CPM segmentation and color clustering

Segmentation and color clustering were performed with the CPM method (Le Poul, 2014). Abdomen outlines are automatically detected against the white background and extracted using watershed transformation. A color was automatically attributed (see palette, segmented histogram, color map) to each pixel of homogenously-colored patch, using RGB threshold. All abdomen segmentations and color patches attributions were then checked individually (Figure 2.2).

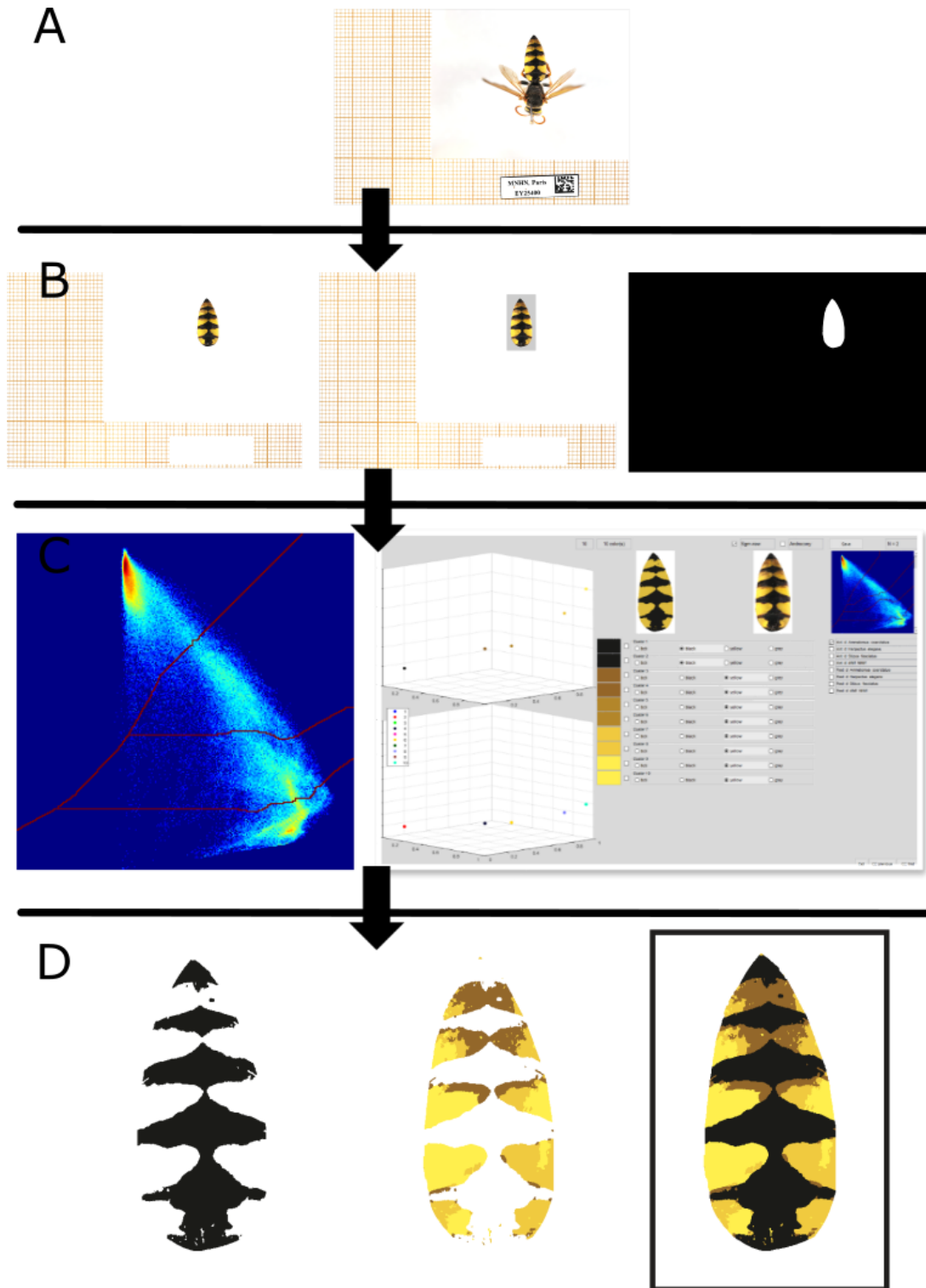


Figure 2.2. Overview of image processing, extraction and color clustering in *Stizus fasciatus* (MNHN inventory code EY25400), a large Bembecidae species (“Crabronid” wasps). **A:** original dorsal view image with scale. **B:** from left to right, manually cropped abdomen, automatically detected and extracted from background. **C:** left panel is watershed gradient for color clustering, right panel view of the CPM interface to reduce color to predefined categories (see text). **D:** separated and combined resulting color layers.

The number of colors was then reduced to correspond to basic colors composing aculeate patterns. These colors were chosen for the analysis after visually checking all images. We estimated two possible colors set: 1) a maximal one (Figure 2.3), and 2) a simplified one included in 1). This step is comparable to color coding by defining homolog colors among all the color variations in the dataset.

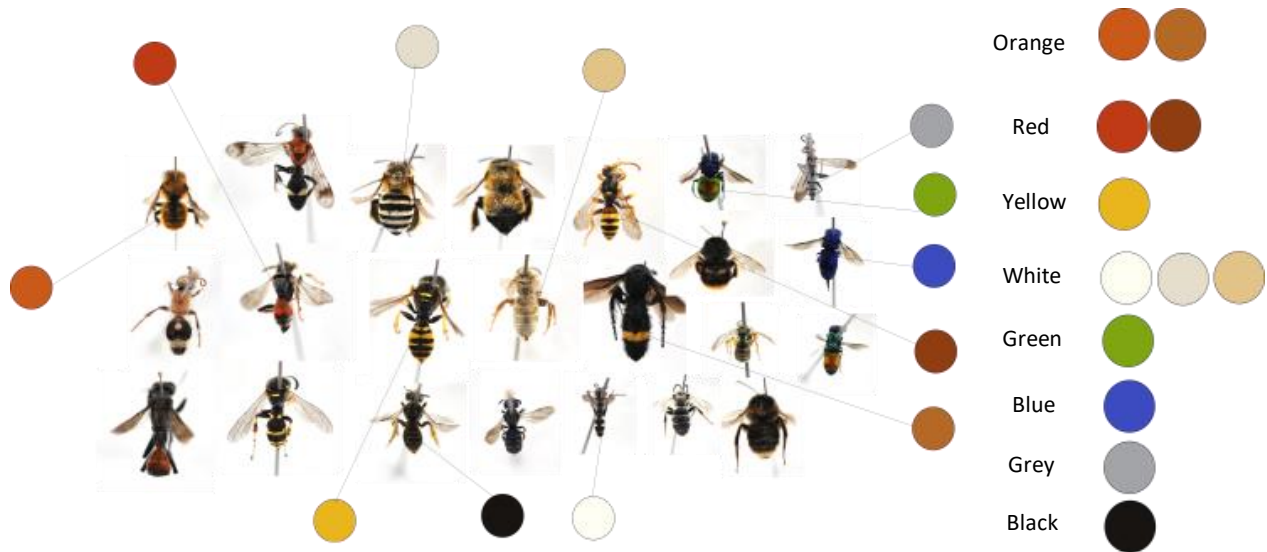


Figure 2.3. An overview of diversity in colorations in our dataset (sizes are not scaled here). Sampled pixel RGB values are illustrated. Right panel: color palette used for colors reduction. For instance, various shades of white are arbitrarily considered by the user as “white”.

2.2.2.2 Quantification and comparison of overall colorations only

To quantify similarity in colorations we used the {colordistance} R package (Weller & Westneat, 2019). This method extracts colors by color clustering: pixels are binned into color categories in a given color space, here the CIE Lab space. We chose histogram binning method. Then the method performs pairwise comparisons of histograms, yielding a distance matrix for a given metric. We chose the Earth mover’s distance (EMD) (Rubner, Tomasi & Guibas, 2000) to measure the color

distance between each pair. This metric scores the minimum cost of transforming one histogram distribution into another from the pairwise comparison.

$$EMD(P, Q) = \frac{\sum_{i=1}^m \sum_{j=1}^n d_{ij} f_{ij}}{\sum_{i=1}^m \sum_{j=1}^n f_{ij}}$$

Where P and Q are two images, with m and n clusters respectively, d is the distance in the space between clusters p_i and q_j , f the “flow” that minimizes the overall cost. This metric takes into account both size and location (i.e. color in a given color space) of the clusters.

For comparison purpose we transformed the resulting distance matrix into a non-metric multidimensional scaling with the isoMDS() function from the {MASS} R package, visualized in its two first components.

2.2.2.3 Quantification and comparison of color patterns

(a) Standardized Patterns algorithm

The original CPM method seemed not particularly adapted to symmetrical objects or patterns, therefore we used a different procedure to quantify variation in color patterns. Segmented and color clustered abdomens were aligned using a novel and original procedure, conceived and coded in Python by Yann Le Poul (unpublished). This procedure can be basically summarized as follows:

An ellipse is fitted on the abdomen’s median axis (i.e. the axis of bilateral symmetry), right and left lines starting and ending at each edge of this direction (outline) are then optimized to fit the abdomen, the resulting shape is normalized by size so that all objects will be comparable, and slight deformations due to specimen conformation or orientation are also normalized via an optimization.

In this way, images are aligned by definition (Figure 2.4).

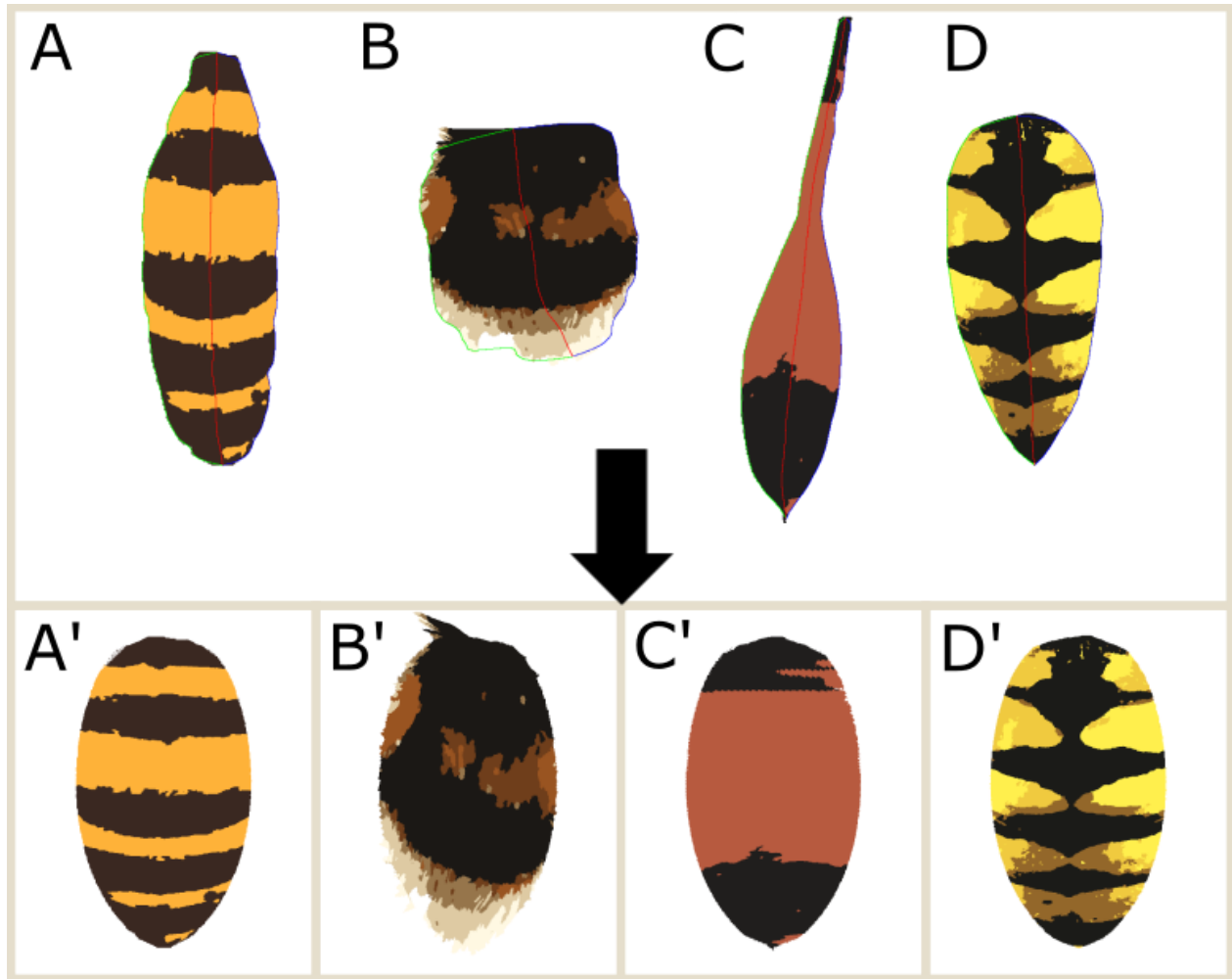


Figure 2.4. Illustration of Standardized patterns procedure. A-D are the color clustered objects, explain. A'-D' are the aligned objects. A, *Gorytes sulcifrons* (EY17112); B, *Bombus terrestris* (EY22720); C, *Ammophila heydeni* (EY16518); D, *Stizus fasciatus* (EY25400).

A phenotypic space based on a binary Principle Component Analysis was then built. Each pixel in common was used as an independent variable (coded as 0s and 1s for each distinct color as in the original CPM procedure).

(b) Recolorize + Patternize workflow

Quantification of similarity in color patterns was also done with an alternative approach to Standardized patterns following the Recolorize (Weller *et al.*, 2022) + Patternize (Van Belleghem *et al.*, 2018) workflow.

First, in order to align all images, to get a proper pixel-to-pixel comparison (positional homology), we used the `alignReg()` function in the `{patternize}` R package (Van Belleghem *et al.*, 2018). This function aligns all images using automated registration with a single target image from the dataset, applying affine transformations. Unfortunately, RGB thresholds and landmarks registrations (Van Belleghem *et al.*, 2018) were not feasible with our image data.

Once aligned, Raster bricks were converted to image arrays compatible with the `{recolorize}` R package (Weller *et al.*, 2022) to perform colors reduction, in order to get standardized (i.e. homogeneous) colors throughout all aligned images. Sets for color clustering were identical to those described in section 2.2.2.4. The resulting color palette (6 clustered color categories) was then applied to “*re-colorize*” aligned images.

We ran a multicolor principal component analysis (`patPCA()` function, not published in the original `patternize` package, available on this [GitHub](#)). This analysis is similar to the previous approach (CPM and standardized patterns): aligned pixels are treated as independent variables, coded as 0s and 1s for each distinct color.

2.2.3 Assessment and attribution of mimicry rings

2.2.3.1 Testing clusters

We used Gaussian Mixture Models (GMM) on all phenotypic spaces (PCoA or distance matrices) to assign each point (i.e. individual or pattern) to a potential mimicry ring. We ran the `Mclust()`

function from {mclust} R package (Scrucca *et al.*, 2016), testing for a number of potential clusters (G=1 to G=9). This maximum was defined by default given our diversity. The smallest set with the lowest BIC was retained as potential mimicry rings partition for the rest of the analysis.

PCoA components that contained less than 5% of variance were not considered: Colordistance (2 axes), Standardized patterns (3 axes, 65% of variance retained), Patternize (2 axes, 38.9% of variance retained).

In the GMM each point is necessarily attributed to a cluster, which may result in cluster containing highly different phenotypes and not representing realistic mimicry rings. To assess for statistical significance of those groupings we performed a perMANOVA using clusters as groups.

Similarity between classifications from the three independent methods was computed with a quantitative version of Jaccard's similarity index (vegdist() function from the {vegan} R package Oksanen *et al.*, 2016), and visualized with a neighbor joining tree. This index (d_{jk}) quantifies the

number of species shared by each pair of cluster: $d_{jk} = \frac{2 \times \frac{\sum_i |x_{ij} - x_{ik}|}{\sum_i (x_{ij} + x_{ik})}}{1 + \frac{\sum_i |x_{ij} - x_{ik}|}{\sum_i (x_{ij} + x_{ik})}}$; where x_{ij} and x_{ik} are the

number of individuals, belonging to species i , shared by clusters j and k respectively; d_{jk} varies between 0 and 1.

2.2.3.2 Molecular phylogeny of the community

(a) DNA dataset

Many sequences were already available from published sources and downloaded from NCBI GenBank (Appendix 2.3). We only selected genes with the highest number of available sequences in databases for our taxonomic sample (Aculeata, ants excluded). Data comprise one mitochondrial gene, cytochrome c oxidase subunit (COI, DNA barcode fragment, 658 bp), and four nuclear genes

(Table 2.1), three of which being coding genes: elongation factor-1 α (EF-1 α , ~1000 bp), wingless (Wnt1, ~400 bp), long-wave rhodopsin (Lwrh, ~800 bp), and 28S non-coding (28S, ~800 bp). When several sequences were available for a given species, we preferred those of similar length to the rest of our sequences. Many of our species did not have any available published sequences. Then new sequences were generated for this study to complete the dataset, to a minimum genus scale. Protocols are detailed in Appendix 2.4.

Table 2.1. Loci and respective primer sequences used for the community phylogeny.

Locus	Primer	Reference	Sequence	Sequence Length
Rhodopsin	OpsinFor	Danforth <i>et al.</i> , 2004	AATTGCTATTAYGARACNTGGGT	23
	OpsinRev	Danforth <i>et al.</i> , 2004	ATATGGAGTCCANGCCATRAACCA	24
Wingless	Lepwg2a	Danforth <i>et al.</i> , 2004	ACTCGCARCACCARTGGAATGTRCA	25
	beewgFor	Danforth <i>et al.</i> , 2004	TGCCANGTSAAGACCTGYTGGATGAG	26
EF1a	F2-rev1	Danforth, Sauquet & Packer, 1999	AATCAGCAGCACCTTTAGGTGG	22
	HaF2For1	Danforth, Sauquet & Packer, 1999	GGGYAAAGGWCCTTCAARTATGC	24
COI	LCO	Folmer <i>et al.</i> , 1994	GGTCAACAAATCATAAAGATATTGG	25
	HCO	Folmer <i>et al.</i> , 1994	TAAACTTCAGGGTGACCAAAAAATCA	26
28S	Rev28SVesp	Hines <i>et al.</i> , 2007	GGAACCAGCTACTAGATGG	19
	For28SVesp	Hines <i>et al.</i> , 2007	AGAGAGAGTTCAAGAGTACGTG	22

We obtained a total of 151 new sequences (65 for 28S, 54 for COI and 32 for wingless) that will be submitted to GenBank. The total dataset comprises 263 in-group species (533 sequences) concatenated in a 3891 bp length matrix (see (b) and (c)). Four outgroup species, only represented

by the COI, were added to the matrix: *Gyrinus marinus* (Coleoptera, Gyrinidae), *Tenthredo koehleri* (Hymenoptera, Tenthredinidae), *Hyposoter annulipes* (Hymenoptera, Ichneumonidae), and *Brachymeria femorata* (Hymenoptera, Chalcididae).

(b) Alignments

Sequences of Rhodopsin and EF1a were extracted from NCBI as CDS. If a sequence had no annotation, it was aligned on aligned CDS and non-coding parts were trimmed when representing less than 50 percent of samples. Coding sequences were aligned on nucleotides with the G-INS-i algorithm in MAFFT (<https://mafft.cbrc.jp/alignment/software/algorithms/algorithms.html>). Sequences were then unaligned and translated in amino-acid sequences, realigned with G-INS-I, and translated back to nucleotides (insertions should be codons). 28S was treated similarly (except for amino-acids) but with the E-INS-i algorithm. We used AliView software version 1.8 parametrized with MAFFT options.

(c) Phylogenetic analysis

A preliminary Maximum Likelihood tree was built to check for doubtful sequences. Three sequences of 28S were discarded: *Dasylabris_maura*, *Smicromyrme_viduata* and *Ronisia_brutia*. We used IQ-TREE 2.2.0 with command: “iqtree2 -nt AUTO -s <alignement> -b 100”. The 5 partitioned alignments were concatenated with AMAS (<https://github.com/marekborowiec/AMAS>) with command “concat”.

For the phylogenetic analyses, substitution models were estimated on the concatenated matrix with ModelFinder tool in IQ-TREE and trees were estimated with RAxML-ng: “iqtree2 -nt AUTO -s

<matrice> -spp <partition> -m MF -cmax 15”; “raxml-ng --all --msa <matrice> --model <partition.best_scheme> --bs-trees 100”.

Nodes constraints. We built a reference tree (190/263 taxa) after (Peters *et al.*, 2017), to constrain relationships between all genera, and to create a node for each genus (assumed monophyletic). We then ran RAxML with the command: “raxml-ng --all --msa <matrice> --model <partition.best_scheme> --bs-trees 100 --tree-constraint <reftree-using-Peters.tre>”.

The phylogeny in Peters *et al.* (2017) is a high rank taxonomic level phylogeny. Consequently, no sequences were available for 167 species that occurred in the phenotypic analysis. Those supplementary species were added in the phylogeny and placed following their taxonomy, using the `add.species.to.genus()` and `drop.tip()` functions from {ape} R package (Paradis, Claude & Strimmer, 2004): e.g. *Amegilla magnilabris* was branched at midpoint with *Amegilla quadrifasciata*, already in the phylogeny. To do so, phylogeny was forced to be ultrametric by extending all the external edges to match the external edge with the longest branch length (function `force.ultrametric()` in {phytools} R package).

2.2.3.3 Quantification of convergence

To quantify convergence within each potential mimicry ring we calculated the Mean Phylogenetic Distance (MPD) between comimetic species: computed as the average pairwise distance for all pairs of species within each mimicry ring. Convergence events are expected to result in overdispersion on the phylogeny, while phylogenetic clustering corresponds to conservatism. Therefore, MPD was compared to a null model by randomly reshuffling taxa labels (999 randomizations) via the `ses.mpd()` function from {picante} R package (Kembel *et al.*, 2010). Standardized effect sizes was calculated as follows: (observed MPD – Mean Null MPD) / Standard Null Deviation. Positive values indicate that phylogenetic distances among co-occurring species

are larger than expected under the null model, whereas negative values indicate that phylogenetic distances among co-occurring species are smaller than expected under the null model. We accept a risk $\alpha = 5\%$ for statistical significance.

2.3 Results

2.3.1 Community phylogeny

A total of 151 new sequences (65 28S, 54 COI and 32 wingless) were generated for this study and will be submitted to GenBank. Phylogeny is presented in Figure 2.5. Note that, despite imposed constraints, there are a few unexpected results in our phylogeny. Indeed, the members of the Astatidae family (sensu (Sann *et al.*, 2018)) are found sister to all Bembecidae, while they should branch more basally. The digger wasp (sphecid) genus *Palmodes* is included in the Pemphredonidae clade which is also unexpected.

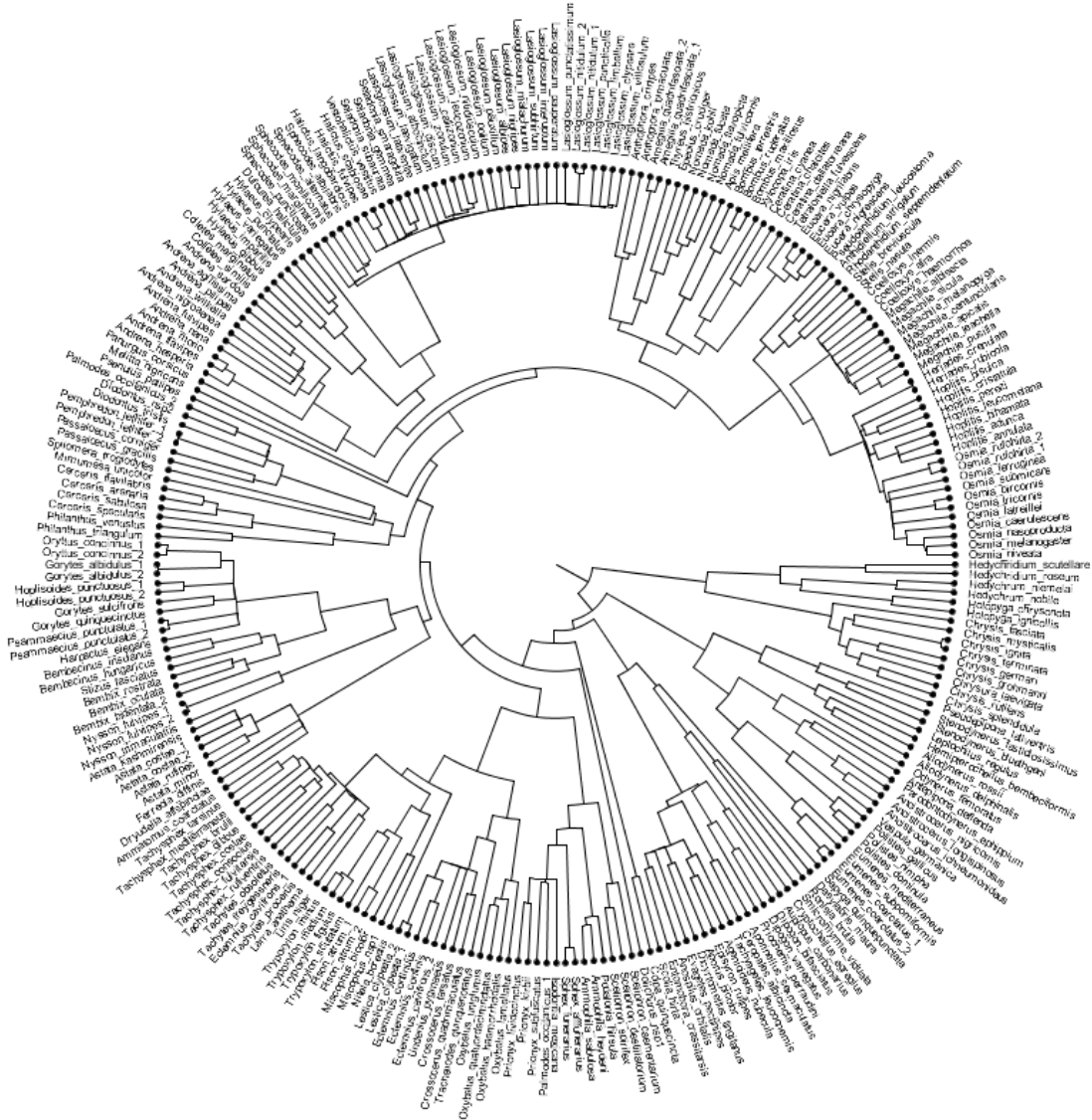


Figure 2.5. Maximum Likelihood tree of the community phylogeny using 5 molecular markers (259 species). Outgroups are not shown: *Gyrinus marinus* (Coleoptera, Gyrinidae), *Tenthredo koehleri* (Hymenoptera, Tenthredinidae), *Hyposoter annulipes* (Hymenoptera, Ichneumonidae), and *Brachymeria femorata* (Hymenoptera, Chalcididae).

2.3.2 Mimicry rings defined on colors only with the Colordistance method

Distances in colorations between individuals are summarized in the form of a Neighbor-Joining tree in Figure 2.6. When transformed into a PCoA space, the GMM analysis fits ellipsoid with varying volumes, shapes and orientation (Table 2.2). This suggests that potential mimicry rings based on coloration differ in variance, smaller ellipsoids comprising less variation. The GMM analysis yields a total amount of 7 clusters summarized in Table 2.2. Cluster 1 (color) corresponds to the “whole-black” individuals, cluster 2 “whole-grey” individuals, cluster 3 “metallic” individuals, cluster 4 “black and red” individuals, cluster 5 “black and yellow” and “black and orange” individuals, cluster 6 comprises various color patterns, and cluster 7 is a small group of “black and yellow” species.

Table 2.2. Gaussian Mixture Models for each image analysis and PERMANOVA on classifications. VVV: ellipsoidal, varying volume, shape, and orientation; EVV: ellipsoidal, equal volume; VVI: diagonal, varying volume and shape. Number of permutations: 999.

Method	Gaussian finite model	# clusters (#individuals)	# components retained	log-Likelihood	BI C	n	d	Perm anov a R ²	F value	p-value
Colordistance	VVV	7 (262,153,61,157,145,220,35)	2	-5395,399	-11075,35	1043	41	0,09416	107,17	<<0,01
Standard patterns	EVV	6 (11,721,62,120,68,40)	3	-5623,251	-10872,31	1042	54	0,42521	754,5	<<0,01
Patternize	VVI	5 (184,134,376,205,133)	2	-9457,7	-19081,94	1043	24	0,03966	42,539	<<0,01

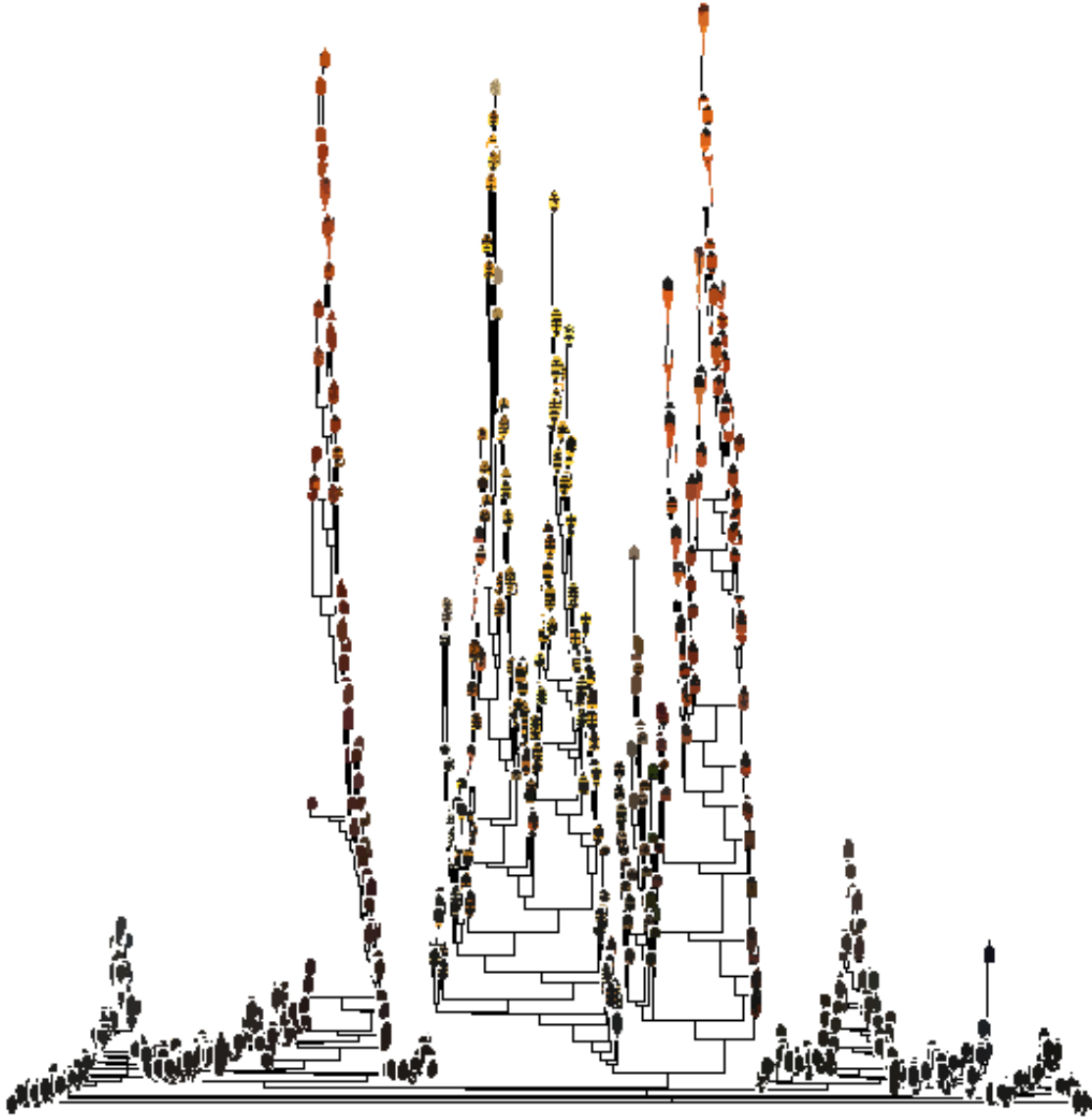


Figure 2.6. Neighbor Joining tree visualization of EMD distances between each pair of images, using CIELab colorspace. The more similar the tips are, the smaller the branches are. Similarity follows the order of branching.

2.3.3 Mimicry rings defined on color patterns

(a) Standardized patterns

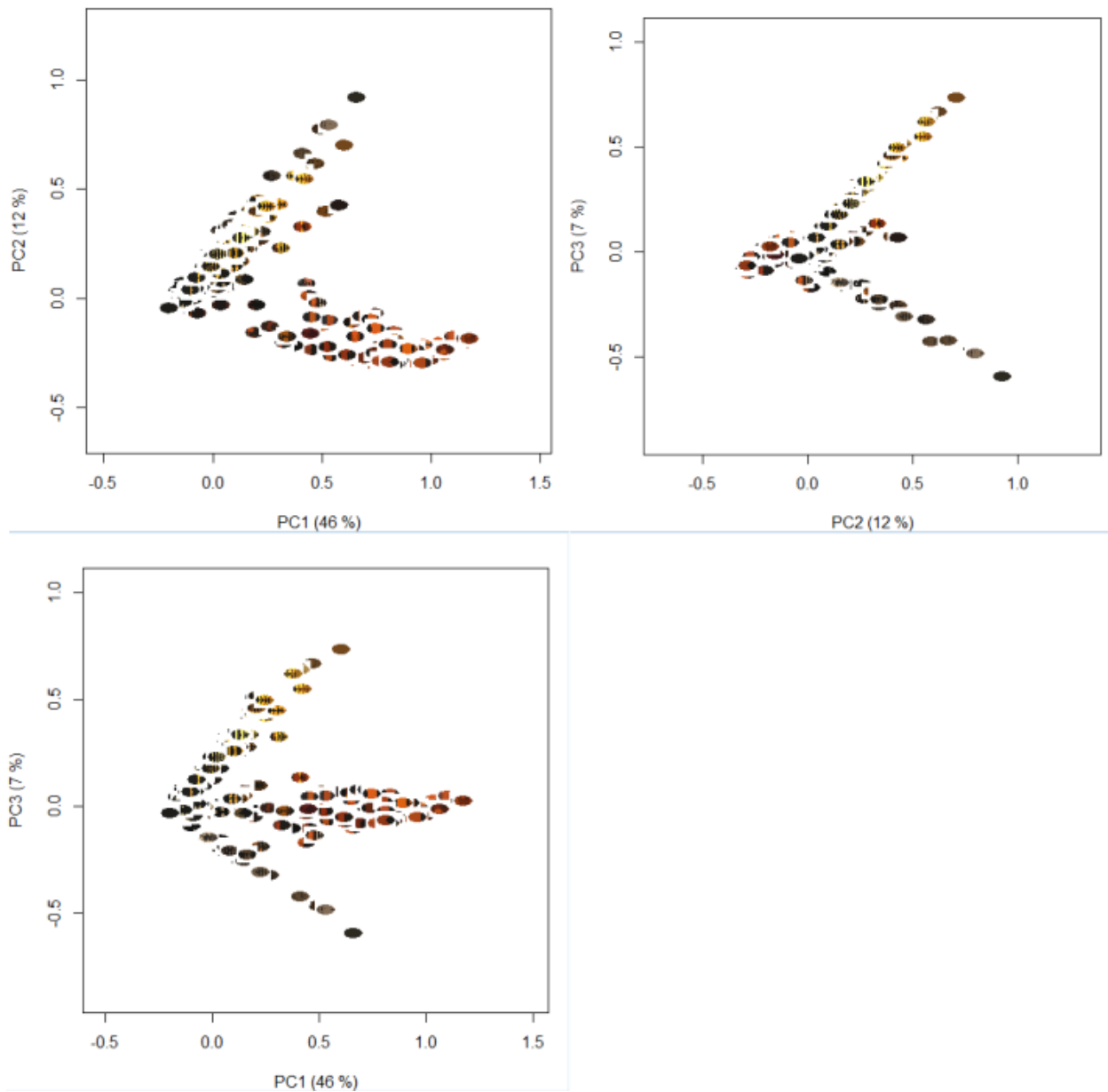


Figure 2.7. PCA space of standardized patterns. Each point (here image) is an individual and each pixel within the same color category (aligned patterns) is an independent variable. Components that contain less than 5% of variance are not considered.

For standardized patterns, the first PCA component (46% of variation) allows to separate whole black individuals from banded or striped ones. The second and third components appear as color axes. The GMM analysis for standardized patterns yields a total of 6 clusters with equal ellipsoidal

volumes summarized in Table 2.2 and Figure 2.8. Since abdomens are aligned and standardized, the axes do not capture any variation in shape.

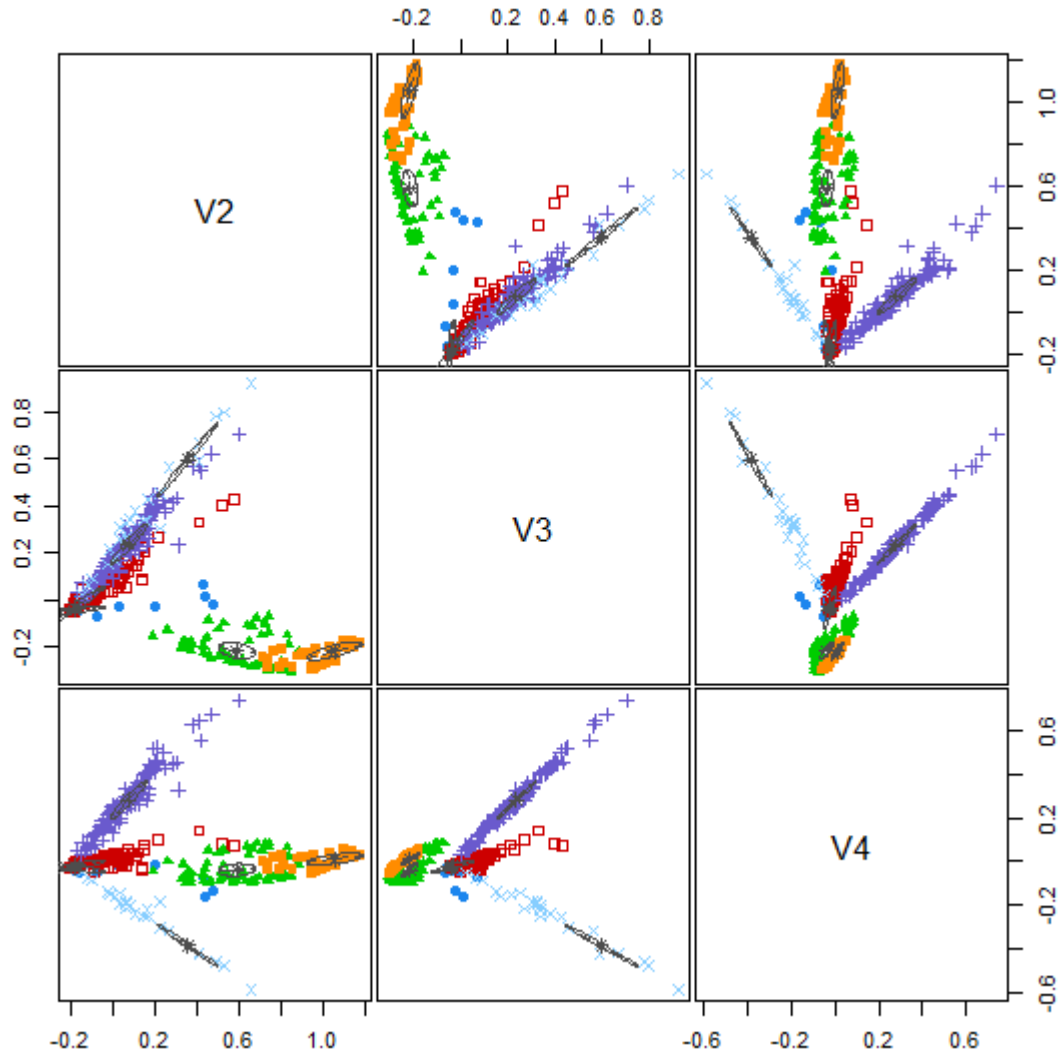


Figure 2.8. GMM classification in the PCA space for standardized patterns. V2-V4 are the first three components of the PCA. Colors correspond to distinct clusters.

(b) Recolorize + Patternize

The analysis yields a total amount of 5 clusters of varying volumes and shapes, shown in Table 2.2 and Figure 2.9. The first component (31% of variation) also separates whole black patterns from

banded and striped ones. With this analysis long and petiolate abdomens are separated from oval ones on PC2 (7.9% of variation), either with yellow or red colorations.

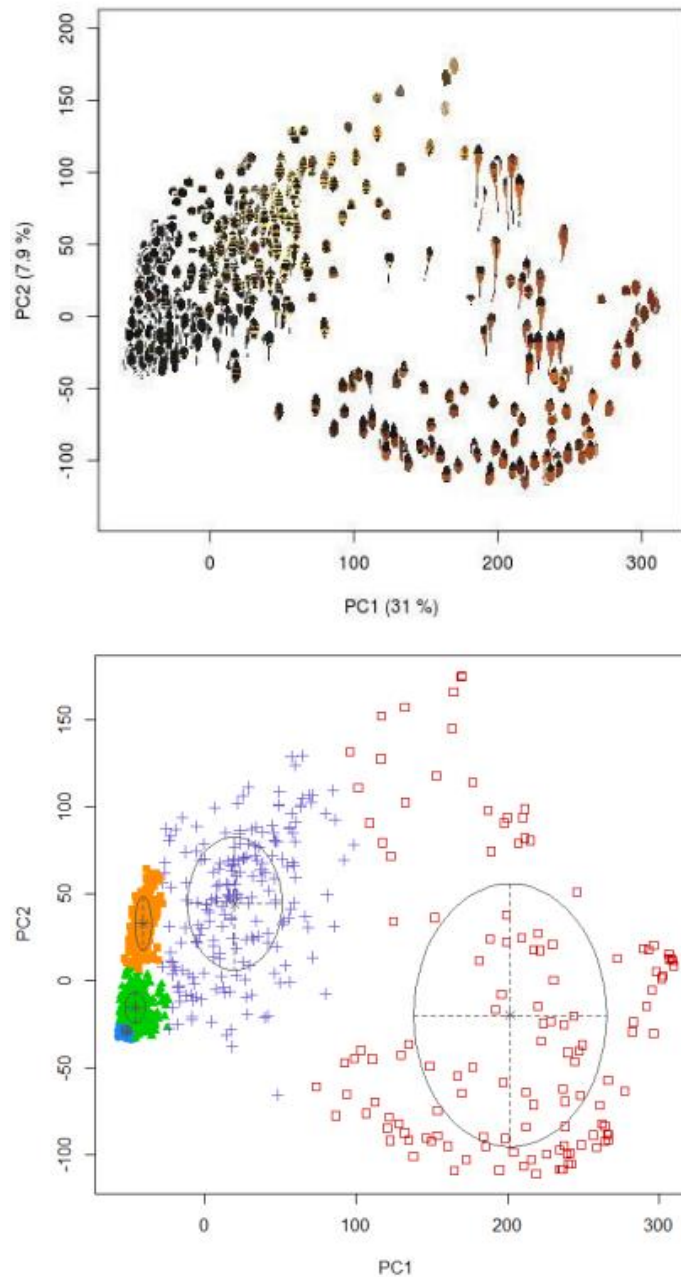


Figure 2.9. PCA space (top) and GMM classification (bottom) from the recolorize+patternize analysis. Each point is an individual ($n = 1033$), images are not original abdomens but the result from the CPM pre-analysis (color clustered images).

2.3.4 Do the different methods yield similar clusters?

Species composition of putative mimicry rings shows variation among methods (Figures 2.8-2.9). Overall, rings defined with either methods (colors only or color patterns) overlap (Figure 2.10). The clusters Patternize 2, Colordistance 4, and Standard 3 and 5, are very similar in composition (Figure 2.10). We may assume they correspond to “the” same mimicry ring (and Standard 3 being an instance of Standard 5). We observe the same result for the clusters Patternize 4, Standard 4 and Colordistance 5 and 7. The grouping of the three methods in the neighbor joining tree suggests that independent mimicry rings are consistent in their composition.

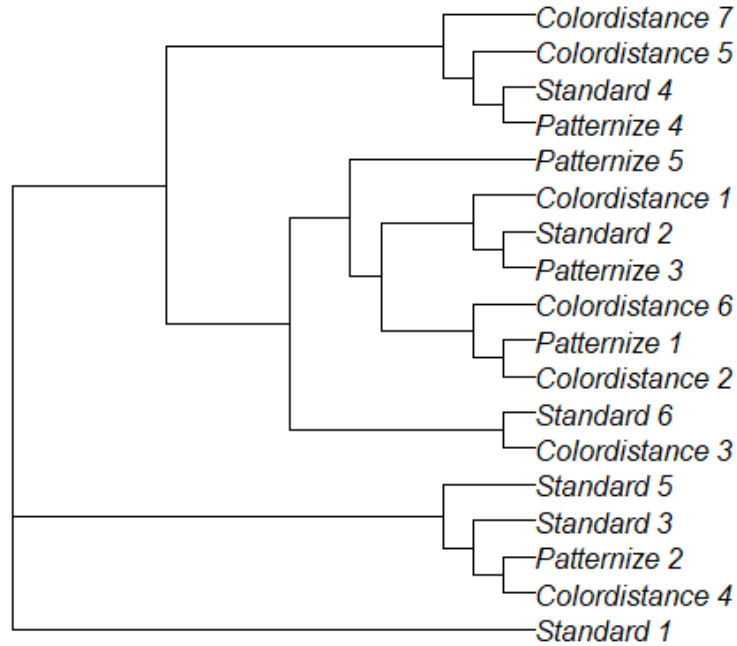


Figure 2.10. Neighbor joining tree on quantitative Jaccard similarity index between each pair of putative mimicry rings. Similarity follows the order of branching.

2.3.5 Is there convergence for colors and patterns?

The method we used allows to discriminate phylogenetic clustering from overdispersion of mimicry rings among the community phylogeny, the latter suggesting evolutionary convergence.

Only the ring 3 from Colordistance and the ring 5 from Standardized patterns are convergent (Table 2.3). In each method, 2 putative mimicry rings are phylogenetically clustered, except for Patternize where three rings are clustered. The main pattern here is random distribution among the phylogeny.

Therefore we observe a mix between potentially convergent aposematic signals and phylogenetically conserved ones.

Table 2.3. Results of Mean Phylogenetic Distance simulations for each putative mimicry ring obtained with GMM. Mean observed distance (Mpd obs) is compared (Mpd obs z) to 999 randomizations (Mpd rand mean), p-values are given for clustering (original p) and overdispersion (1-p). Phylogenetically clustered rings are highlighted in blue, overdispersed in green.

Mimicry ring	#taxa	Mpd obs	Mpd rand mean	Mpd rand sd	Mpd obs z	P for clustering	P for overdispersion
Colordistance1	106	0,9427	1,0021	0,0090	-6,5586	0.001	0.999
Colordistance2	80	0,9837	1,0015	0,0109	-1,6348	0.059	0.941
Colordistance3	26	1,0354	1,0023	0,0218	1,5182	0.957	0.043
Colordistance4	59	1,0053	1,0020	0,0139	0,2416	0.589	0.411
Colordistance5	56	1,0128	1,0021	0,0144	0,7353	0.766	0.234
Colordistance6	106	0,9642	1,0016	0,0091	-4,1195	0.001	0.999
Colordistance7	14	0,9740	1,0027	0,0301	-0,9524	0.169	0.831
Patternize1	103	0,9652	1,0043	0,0096	-4,0557	0.001	0.999
Patternize2	51	1,0103	1,0043	0,0150	0,4038	0.649	0.351
Patternize3	176	0,9840	1,0044	0,0061	-3,3748	0.002	0.998
Patternize4	92	1,0026	1,0048	0,0102	-0,2094	0.401	0.599
Patternize5	88	0,9458	1,0041	0,0105	-5,5259	0.001	0.999
Standardized patterns1	7	0,9697	1,0050	0,0473	-0,7480	0.201	0.799
Standardized patterns2	265	0,9904	1,0044	0,0034	-4,0825	0.001	0.999
Standardized patterns3	29	1,0051	1,0045	0,0205	0,0307	0.487	0.513
Standardized patterns4	51	1,0089	1,0039	0,0150	0,3350	0.601	0.399
Standardized patterns5	30	1,0386	1,0043	0,0206	1,6582	0.97	0.03
Standardized patterns6	18	0,8567	1,0055	0,0271	-5,4962	0.001	0.999

2.4 Discussion

The present study is the first application to bees and wasps mimicry in the Mediterranean region, at community scale, of such quantitative methods for analyzing colors and patterns.

We identified 5 to 7 putative mimicry rings in this Corsican community. The identified clusters are based on colors and/or patterns but independently of how predators may perceive them. For instance, color patterns within the same cluster might not be perceived as ‘the same’ by a predator, and color patterns belonging to different clusters might also not be discriminated by predator. To attempt to quantify mimetic similarity through perception, deep learning have been implemented (Ezray *et al.*, 2019; Wham, Ezray & Hines, 2019; Wilson *et al.*, 2022), but they do not capture perception of real predators. Idealistically, only experiments with real predators and natural prey may attest for mimicry. Predators are indeed able to generalize an aposematic signal, to a certain extent (Páez *et al.*, 2021; Linke *et al.*, 2022). Some authors have argued that color alone has a greater influence on predator recognition than pattern (Finkbeiner *et al.*, 2014; Rönkä *et al.*, 2018), while others advocated for the opposite (Hauglund *et al.*, 2006) or showed a clear discrimination between quite similar color patterns (Chouteau, Arias & Joron, 2016; Arias *et al.*, 2016, 2020). We cannot conclude here whether mimicry relies on coloration only or on color pattern. We can only say that it yields different results but quite similar in composition if we focus on shared species (and individuals). Colordistance method is simpler in its conceptualization, fast and straightforward. It only informs on similarity in colors composition, not geometry or other aspects of color patterns. However it also recovers images that are similar in patterns. Patternize with no landmark data raises issues in managing the white background which is interdependent with size and shape. None of these two methods consider differences in sizes and shape. The Standardized patterns method has the advantage of being fast and simple: pattern are reduced to one dimension

along the median axis (but relevant for a band succession pattern), which allows to separate variables of shape (outline coordinates on the median axis, not exploited here) and variable of colors in the analysis (contrarily to patternize). It has however a major drawback: the largest color patches will have a higher weight compared to smallest ones (in terms of number of pixels), similarly to landmark approaches. However predators might also be impacted by such differences.

The relatively high number of putative mimicry rings recovered in each method is not surprising given the variation of colors and shapes in our dataset (Figure 2.3). This is also in agreement with the results of other studies targeting relatively comparable regional scales. For instance, (van der Vecht, 1961) described five different mimicry rings in vespid species from the same Australasian islands. In the same family, but with many more species involved, (Garcete-Barrett, 1999) described 18 distinct mimicry ring in Paraguay. Still focusing on a single family, but at a much wider scale (global), (Williams, 2007) described 24 mimicry rings among bumblebees. For comparison: in Neotropical butterflies, among 15 communities distributed along an elevational gradient, Chazot et al. found a total of 25 mimicry rings collectively comprising 155 species (Chazot *et al.*, 2014). A different point of view also emerged, recently applied for bumblebee mimetic complexes (Ezray *et al.*, 2019), seeing mimicry rings as a perceptual continuum rather than artificial categories, therefore the number and composition of such groups might not be relevant.

Our community phylogeny will not be further discussed here. Taxonomic sampling and community composition did not perfectly match, therefore a more comprehensive phylogeny must be produced in the future. However, when the mimicry rings identified in this study are phylogenetically overdispersed, this may indicate substantial convergence, which suggests that multiple aposematic signals (shared by each group) are under natural selection incurred by unidentified predators.

Nonetheless, phylogenetically random or clustered mimicry rings does not rule out the possibility that at least some similar phenotypes have evolved through convergent evolution. We observed a mix of potentially convergent and potentially non-convergent mimicry rings, which has already been demonstrated in American velvet ants (Wilson *et al.*, 2012). This was also attested in Neotropical butterflies (Le Poul, 2014; Chazot *et al.*, 2014; Doré *et al.*, 2023). The relative advantage of shared color pattern remains, even in non-convergent patterns: all conspecifics or co-mimetic species do participate to predator education, which does not refute mimicry. For instance, in the Eastern mimicry ring of velvet-ants from North American, the color pattern ‘black and orange-reddish with silver setae’ is not randomly distributed across the phylogeny and therefore likely due to common ancestry (Wilson *et al.*, 2012). However, phylogeny seems to be an important factor constraining or structuring mimetic resemblance. This suggests that various selective regime for strong resemblance may be at play: in the case of strong selection on close resemblance, phylogeny is not expected to drive variation in forms and color patterns. Therefore, the 5-7 mimicry rings (i.e. aposematic signals) might not be under equivalent selective pressures. The evolutionary emergence of aposematic signals or conspicuous colorations are complex. It has been shown that North American desert velvet ants, closely resembling a fruit of creosote bush with fluffy white hairs, occurred million years before such bushes became widespread in the environment (Wilson *et al.*, 2020). The white coloration of these aculeates evolved from aposematic coloration and not toward camouflage, as it was previously considered, but rather as a thermal adaptation to desert environment. Moreover, the evolutionary transition from camouflage to aposematism tends to occur in intermediate forms, hiding a ‘facultative’ aposematic signal (Loeffler-Henry, Kang & Sherratt, 2023).

To conclude, this study characterized a diverse community of aculeate species, partitioned in different mimicry rings. A more careful comparison of the various mimicry rings identified here, with different methods, must be conducted in the future. We hope the present work constitutes a first step toward a larger knowledge of mimetic communities in bees and wasps.

2.5 References

ARIAS, M., DAVEY, J.W., MARTIN, S., JIGGINS, C.D., NADEAU, N., JORON, M. & LLAURENS, V.

(2020) How do predators generalize warning signals in simple and complex prey communities? Insights from a videogame. *Proceedings of the Royal Society B* **287**, 0962–8452.

ARIAS, M., LE POUL, Y., CHOUTEAU, M., BOISSEAU, R., ROSSER, N., THÉRY, M. & LLAURENS, V.

(2016) Crossing fitness valleys: empirical estimation of a fitness landscape associated with polymorphic mimicry. *Proceedings of the Royal Society B: Biological Sciences* **283**, 20160391. Royal Society.

ARONSSON, M. & GAMBERALE-STILLE, G. (2008) Domestic chicks primarily attend to colour, not pattern, when learning an aposematic coloration. *Animal Behaviour* **75**, 417–423.

BADEJO, O., SKALDINA, O., GILEV, A. & SORVARI, J. (2020) Benefits of insect colours: a review from social insect studies. *Oecologia*, 1–14.

VAN DEN BERG, C.P., TROSCIANKO, J., ENDLER, J.A., MARSHALL, N.J. & CHENEY, K.L. (2019) Quantitative Colour Pattern Analysis (QCPA): A Comprehensive Framework for the Analysis of Colour Patterns in Nature. *bioRxiv*, 1–37.

- BRIOLAT, E.S., BURDFIELD-STEEL, E.R., PAUL, S.C., RÖNKÄ, K., SEYMOURE, B.M., STANKOWICH, T. & STUCKERT, A.M.M. (2019) Diversity in warning coloration: selective paradox or the norm? *Biological Reviews* **94**, 388–414.
- BRODIE JR, E.D. (1993) DIFFERENTIAL AVOIDANCE OF CORAL SNAKE BANDED PATTERNS BY FREE-RANGING AVIAN PREDATORS IN COSTA RICA. *Evolution* **47**, 227–235.
- CHAN, I.Z., STEVENS, M. & TODD, P.A. (2019) PAT-GEOM: A software package for the analysis of animal patterns. *Methods in Ecology and Evolution* **10**, 591–600.
- CHAZOT, N., WILLMOTT, K.R., SANTACRUZ ENDARA, P.G., TOPOROV, A., HILL, R.I., JIGGINS, C.D. & ELIAS, M. (2014) Mutualistic Mimicry and Filtering by Altitude Shape the Structure of Andean Butterfly Communities. *The American Naturalist* **183**, 26–39. The University of Chicago Press.
- CHOUTEAU, M., ARIAS, M. & JORON, M. (2016) Warning signals are under positive frequencydependent selection in nature. *PNAS* **113**, 2164–2169.
- DANFORTH, B.N., BRADY, S.G., SIPES, S.D. & PEARSON, A. (2004) Single-Copy Nuclear Genes Recover Cretaceous-Age Divergences in Bees. *Systematic Biology* **53**, 309–326.
- DANFORTH, B.N., SAUQUET, H. & PACKER, L. (1999) Phylogeny of the Bee Genus *Halictus* (Hymenoptera: Halictidae) Based on Parsimony and Likelihood Analyses of Nuclear EF-1a Sequence Data. *Molecular Phylogenetics and Evolution* **13**, 605–618.

- DORÉ, M., WILLMOTT, K., LAVERGNE, S., CHAZOT, N., FREITAS, A.V.L., FONTAINE, C. & ELIAS, M. (2023) Mutualistic interactions shape global spatial congruence and climatic niche evolution in Neotropical mimetic butterflies. *Ecology Letters* **26**, 843–857.
- ELIAS, M., GOMPERT, Z., JIGGINS, C. & WILLMOTT, K. (2008) Mutualistic Interactions Drive Ecological Niche Convergence in a Diverse Butterfly Community. *PLOS Biology* **6**, e300. Public Library of Science.
- EZRAY, B.D., WHAM, D.C., HILL, C.E. & HINES, H.M. (2019) Unsupervised machine learning reveals mimicry complexes in bumblebees occur along a perceptual continuum. *Proceedings of the Royal Society B* **286**, 20191501.
- FINKBEINER, S.D., BRISCOE, A.D. & REED, R.D. (2014) Warning signals are seductive: Relative contributions of color and pattern to predator avoidance and mate attraction in *Heliconius* butterflies. *Evolution* **68**, 3410–3420.
- FOLMER, O., BLACK, M., HOEH, W., LUTZ, R. & VRIJENHOEK, R. (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* **3**, 294–299.
- GARCETE-BARRETT, B. (1999) *Guía ilustrada de las avispas sociales del Paraguay (Hymenoptera: Vespidae: Polistinae)*. Natural Museum, London.
- HAUGLUND, K., HAGEN, S.B. & LAMPE, H.M. (2006) Responses of domestic chicks (*Gallus gallus domesticus*) to multimodal aposematic signals. *Behavioral Ecology* **17**, 392–398.
- HINES, H.M., HUNT, J.H., O'CONNOR, T.K., GILLESPIE, J.J. & CAMERON, S.A. (2007) Multigene phylogeny reveals eusociality evolved twice in vespidae wasps. *PNAS* **104**, 3295–3299.

- HLAVÁČEK, A., DAŇKOVÁ, K., BENDA, D., BOGUSCH, P. & HADRAVA, J. (2022) Batesian-Müllerian mimicry ring around the Oriental hornet (*Vespa orientalis*). *Journal of Hymenoptera Research* **92**, 211–228. Pensoft Publishers.
- KASPAREK, M. (2019) *Bees in the genus Rhodanthidium: A review and identification guide*. Entomofauna. Ansfelden.
- KELLY, M.B.J., MCLEAN, D.J., WILD, Z.K. & HERBERSTEIN, M.E. (2021) Measuring mimicry: methods for quantifying visual similarity. *Animal Behaviour* **178**, 115–126.
- KEMBEL, S.W., COWAN, P.D., HELMUS, M.R., CORNWELL, W.K., MORLON, H., ACKERLY, D.D., BLOMBERG, S.P. & WEBB, C.O. (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* **26**, 1463–1464.
- KIKUCHI, D.W., HERBERSTEIN, M.E., BARFIELD, M., HOLT, R.D. & MAPPE, J. (2021) Why aren't warning signals everywhere? On the prevalence of aposematism and mimicry in communities. *Biological Reviews* **n/a**.
- LE POUL, Y. (2014) Selection for mimicry in butterflies: Quantitative approaches on colour pattern resemblance and diversity. Doctorat, MUSEUM NATIONAL D'HISTOIRE NATURELLE, Paris.
- LINKE, D., ELIAS, M., KLEČKOVÁ, I., MAPPE, J. & MATOS-MARAVÍ, P. (2022) Shape of Evasive Prey Can Be an Important Cue That Triggers Learning in Avian Predators. *Frontiers in Ecology and Evolution* **10**.

- LOEFFLER-HENRY, K., KANG, C. & SHERRATT, T.N. (2023) Evolutionary transitions from camouflage to aposematism: Hidden signals play a pivotal role. *Science* **379**, 1136–1140. American Association for the Advancement of Science.
- MAIA, R., GRUSON, H., ENDLER, J.A. & WHITE, T.E. (2019) pavo 2: New tools for the spectral and spatial analysis of colour in R. *Methods in Ecology and Evolution* **4**, 906–913.
- MOTYKA, M., KAMPOVA, L. & BOCAK, LADISLAV (2018) Phylogeny and evolution of Müllerian mimicry in aposematic Dilophotes: evidence for advergence and size-constraints in evolution of mimetic sexual dimorphism. *Scientific Reports* **8**, 1–10.
- MOTYKA, M., KUSY, D., MASEK, M., BOCEK, M., LI, Y., BILKOVA, R., KAPITÁN, J., YAGI, T. & BOCAK, L. (2021) Conspicuousness, phylogenetic structure, and origins of Müllerian mimicry in 4000 lycid beetles from all zoogeographic regions. *Scientific Reports* **11**, 5961. Nature Publishing Group.
- OKSANEN, J., BLANCHET, G., KINDT, R., LEGENDRE, P., MINCHIN, P., O'HARA, R., SIMPSON, G., SOLYMOS, P., STEVENS, H. & WAGNER, H. (2016) Vegan: Community Ecology Package. *R package* version 2.3-5.
- ORR, M.C., HUGHES, A.C., CHESTERS, D., PICKERING, J., ZHU, C.-D. & ASCHER, J.S. (2021) Global Patterns and Drivers of Bee Distribution. *Current Biology* **31**, 451-458.e4.
- PÁEZ, E., VALKONEN, J.K., WILLMOTT, K.R., MATOS-MARAVÍ, P., ELIAS, M. & MAPPES, J. (2021) Hard to catch: experimental evidence supports evasive mimicry. *Proceedings of the Royal Society B: Biological Sciences* **288**, 20203052. Royal Society.

- PARADIS, E., CLAUDE, J. & STRIMMER, K. (2004) APE: Analyses of Phylogenetics and Evolution in R language. *Bioinformatics* **20**, 289–290.
- PEKAR, S., PETRAKOVA, L., BULBERT, M.W., WHITING, M.J. & HERBERSTEIN, M.E. (2017) The golden mimicry complex uses a wide spectrum of defence to deter a community of predators. *eLife*, 1–25.
- PETERS, R.S., KROGMANN, L., MAYER, C., DONATH, A., GUNKEL, S., MEUSEMANN, K., KOZLOV, A., PODSIADLOWSKI, L., PETERSEN, M., LANFEAR, R., DIEZ, P.A., HERATY, J., KJER, K.M., KLOPFSTEIN, S., MEIER, R., ET AL. (2017) Evolutionary History of the Hymenoptera. *Current Biology* **27**, 1013–1018.
- PIKE, T.W. (2011) Using digital cameras to investigate animal colouration: estimating sensor sensitivity functions. *Behavioral Ecology and Sociobiology* **65**, 849–858.
- PLOWRIGHT, R.C. & OWEN, R.E. (1980) The Evolutionary Significance of Bumble Bee Color Patterns: A Mimetic Interpretation. *Evolution* **34**, 622–637.
- RODRIGUEZ, J., PITTS, J.P., VON DOHLEN, C.D. & WILSON, J.S. (2014) Müllerian Mimicry as a Result of Codivergence between Velvet Ants and Spider Wasps. *PLoS ONE* **9**, 1–7.
- RÖNKÄ, K., DE PASQUAL, C., MAPPES, J., GORDON, S. & ROJAS, B. (2018) Colour alone matters: no predator generalization among morphs of an aposematic moth. *Animal Behaviour* **135**, 153–163.
- RUBNER, Y., TOMASI, C. & GUIBAS, L.J. (2000) The Earth Mover's Distance as a Metric for Image Retrieval. *International Journal of Computer Vision* **40**, 99–121.

- SANN, M., NIEHUIS, O., PETERS, R.S., MAYER, C., KOZLOV, A., PODSIADLOWSKI, L., BANK, S., MEUSEMANN, K., MISOF, B., BLEIDORN, C. & OHL, M. (2018) Phylogenomic analysis of Apoidea sheds new light on the sister group of bees. *BMC Evolutionary Biology* **18**, 1–15.
- SCRUCCA, L., FOP, M., MURPHY, T.B. & RAFTERY, A.E. (2016) mclust 5: Clustering, Classification and Density Estimation Using Gaussian Finite Mixture Models. *The R Journal* **8**, 289–317.
- TROSCIANKO, J. & STEVENS, M. (2015) Image calibration and analysis toolbox – a free software suite for objectively measuring reflectance, colour and pattern. *Methods in Ecology and Evolution* **6**, 1320–1331.
- VAN BELLEGHEM, S.M., PAPA, R., ORTIZ-ZUAZAGA, H., HENDRICKX, F., JIGGINS, C.D., MCMILLAN, W.O. & COUTERMAN, B.A. (2018) patternize: An R package for quantifying colour pattern variation. *Methods in Ecology and Evolution* **9**, 390–398.
- VAN DER VECHT, J. (1961) Evolution in a group of Indo-Australian Eumenes (Hymenoptera, Eumenidae). *Evolution* **15**, 468–477.
- WEBB, C.O., ACKERLY, D.D., MCPEEK, M.A. & DONOGHUE, M.J. (2002) Phylogenies and community ecology. *Annual Review of Ecology, Evolution, and Systematics* **33**, 475–505.
- WELLER, H.I., VAN BELLEGHEM, S.M., HILLER, A.E. & LORD, N.P. (2022) recolorize: improved color segmentation of digital images (for people with other things to do). *bioRxiv*, 1–24.
- WELLER, H.I. & WESTNEAT, M.W. (2019) Quantitative color profiling of digital images with earth mover’s distance using the R package colordistance. *PeerJ* **7**, 1–31.

- WHAM, D.C., EZRAY, B.D. & HINES, H.M. (2019) Measuring Perceptual Distance of Organismal Color Pattern using the Features of Deep Neural Networks. *bioRxiv*, 1–37.
- WILLIAMS, P. (2007) The distribution of bumblebee colour patterns worldwide: possible significance for thermoregulation, crypsis, and warning mimicry. *Biological Journal of the Linnean Society* **92**, 97–118.
- WILLIAMS, P.H. (2008) Do the parasitic Psithyrus resemble their host bumblebees in colour pattern? *Apidologie* **39**, 637–649.
- WILLMOTT, K.R., ROBINSON WILLMOTT, J.C., ELIAS, M. & JIGGINS, C.D. (2017) Maintaining mimicry diversity: optimal warning colour patterns differ among microhabitats in Amazonian clearwing butterflies. *Proceedings of the Royal Society B: Biological Sciences* **284**, 20170744. Royal Society.
- WILSON, J.S., PAN, A.D., ALVAREZ, S.I. & CARRIL, O.M. (2022) Assessing Müllerian mimicry in North American bumble bees using human perception. *Scientific Reports* **12**, 17604. Nature Publishing Group.
- WILSON, J.S., PAN, A.D., LIMB, E.S. & WILLIAMS, K.A. (2018) Comparison of African and North American velvet ant mimicry complexes: Another example of Africa as the 'odd man out'. *PLoS ONE* **13**, 1–15.
- WILSON, J.S., SIDWELL, J.S., FORISTER, M.L., WILLIAMS, K.A. & PITTS, J.P. (2020) Thistledown velvet ants in the Desert Mimicry Ring and the evolution of white coloration: Müllerian mimicry, camouflage and thermal ecology. *Biology Letters* **16**, 1–6.

WILSON, J.S., WILLIAMS, K.A., FORISTER, M.L., VON DOHLEN, C.D. & PITTS, J.P. (2012) Repeated evolution in overlapping mimicry rings among North American velvet ants. *Nature Communications* **3**, 1–7.

Chapter 3

Do mutualistic interactions enhance species persistence in a diverse Hymenoptera community in South Corsica?

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Several Müllerian mimicry rings were evidenced from chapter two in our Corsican community. They all vary in the number of species they comprise, and potentially in abundance, habitat use and chemical defense. In this chapter we investigate, both with a theoretical and an empirical approach, how better defended rings tend to better survive through time, on a one century timespan. The aim of the present chapter is to quantify and attest for temporal turnover in mimicry rings at community scale (species in sympatry), in order to evaluate mimicry protective value in bees and wasps. In the first part of this study, we use a mathematical model to estimate population dynamics of co-mimetic and non-mimetic species in sympatry. We tested the effect of parameters such as unpalatability, mimicry ring species richness and abundance and competition on the extinction risks. We aimed to evaluate a potential link between Müllerian mimicry and bees and wasps decline. In a second part we confront our hypotheses with empirical data based on the mimicry rings established in Chapter 2.

In this study, I initiated and co-wrote the model with Violaine Llaurens and Adrien Perrard. The modelling work was entirely conducted by Maxime Boutin (Master 1 internship) and his results are summarize here. Regarding the empirical study, we used the dataset presented in chapter 2, and I performed the statistical analysis.

« L'aigle dévore le moineau, le loup dévore les marmottes, mais les aigles et les loups s'aident entre eux pour chasser, et les moineaux et les marmottes se solidarisent si bien contre les animaux de proie que les maladroits seuls se laissent pincer. En toute société animale, la solidarité est une loi (un fait général) de la nature, infiniment plus importante que cette lutte pour l'existence dont les bourgeois nous chantent la vertu sur tous les refrains, afin de mieux nous abrutir.

Quand nous étudions le monde animal et que nous cherchons à nous rendre compte de la lutte pour l'existence soutenue par chaque être vivant contre les circonstances adverses et contre ses ennemis, nous constatons que plus le principe de solidarité égalitaire est développé dans une société animale et passé à l'état d'habitude, - plus elle a de chances de survivre et de sortir triomphante de la lutte contre les intempéries et contre ses ennemis. »

Pierre Kropotkine, 1889, *La Morale anarchiste*

3.1 Introduction

Müllerian mimicry entails positive frequency or density dependence selection on aposematic signals [“increase in the population growth rate with increasing local frequency or density of heterospecifics or conspecifics” harboring similar aposematic signals (Aubier, 2020)]. Such selection is incurred by predators, and indirectly favors the coexistence of similar-looking species. As we have seen in the previous chapters, aposematic species in sympatry can form a mimicry ring and share the load of predator education, resulting in a lower per capita mortality. A form of positive density-dependence that reduces predation (Müllerian mimicry typically) can favor species coexistence (and therefore not necessarily imply species exclusion): it has been shown theoretically that the kind of interactions or density-dependency such as Müllerian mimicry may maintain species-rich communities (Gross, 2008; Aubier, 2020).

Because mimicry selects for convergence in aposematic signals, one might expect mimetic communities to consist in a single or a small number of mimicry rings. Yet, mimetic communities often comprise multiple mimicry rings (Elias *et al.*, 2008; Alexandrou *et al.*, 2011; Willmott *et al.*, 2017). This may be due to relaxed selection pressure (Mallet & Joron, 1999), but also to heterogeneity in predation pressure (Gompert, Willmott & Elias, 2011), which allows the maintenance of different mimicry rings in different areas or microhabitats occupied by different suites of predators, as shown in butterflies (Willmott *et al.*, 2017). Indeed, mutualistic interactions enhance ecological similarity because this favors fine-scale co-occurrence (Elias *et al.*, 2008; Gompert *et al.*, 2011; Doré *et al.*, 2023). Co-occurrence of species within the same areas and microhabitats may increase competition for resources (Elias *et al.*, 2008; Willmott *et al.*, 2017), although this is not necessarily the case if co-mimetic species partition their resources (Alexandrou *et al.*, 2011;

Aubier & Elias, 2020). Competition for resources entails negative density-dependent selection, which is a major driver of species exclusion.

Individuals from species belonging to the same mimicry ring interact mutualistically and collectively benefit from increased protection against predation, with tight co-evolution between co-mimetic species (Willmott & Mallet, 2004; Elias *et al.*, 2008; Doré *et al.*, 2023). The downside is that because those species are interdependent, the local extinction of one species may weaken the entire mimicry ring and lead to co-extinction cascades. Larger mimicry rings (i.e. those that comprise more individuals, which can be achieved both through the number of species and species' abundance) will likely be more robust to such cascading extinctions. Other factors, such as the level of defenses and competition among co-mimics may also have an impact on species co-existence and extinction risks. Yet, no theoretical or empirical studies have addressed this question.

Aculeate mimetic communities represent an excellent system to investigate the occurrence and extent of cascading extinctions, because those communities are highly diverse (see Chapter 1). Some empirical studies on Müllerian mimicry in aculeates focus on a large taxonomic scale: 6 (West-Eberhard, Carpenter & Hanson, 1995) sometimes 7 (Smith-Pardo, 2005) distinct families have been described in a single mimicry ring. However, in order to conduct such empirical studies, communities must be surveyed during a consistent amount of time and on clearly identified localities. This study grounds on an empirical dataset that fills all such requirements: an explicit and complete aculeate community in the region of Bonifacio (South Corsica, France), which has been sampled in the exact same localities in the beginning of the late century and more recently in 2017. Indeed, Charles Ferton, a French entomologist from the late nineteenth century that lived in Bonifacio (South Corsica, France), thoroughly collected aculeate specimens (ants excluded) that might represent a comprehensive sampling of aculeate communities present at the time. His

exceptional historical collection, deposited in the Muséum national d'Histoire naturelle (MNHN) of Paris, was recently fully revised and localities from the region of Bonifacio were resampled a century after Ferton's initial collections.

In this study, we aim to elucidate whether mutualistic interactions may enhance species persistence in a diverse hymenopteran community (from South Corsica). More precisely, we aim to 1) theoretically test the impact of mimicry ring size, unpalatability and intra-ring competition on co-extinctions, and 2) test whether species in larger mimicry rings tend to persist more through time.

3.2 Material & methods

3.2.1 Theoretical community and hypotheses

In order to study the effect of Müllerian mimicry on ring composition and population dynamics, we propose a mathematical model inspired by the work of Joron and Iwasa (2005). The main goal of the model is to explore the conditions, and the extent to which co-extinction cascades occur in a mimicry context. We first check whether, given our model (see below), mimicry limits local extinction. If so, abundance and species richness of mimicry rings may influence their sensitivity to perturbation: species of larger or abundant rings may be more resilient. In parallel, higher levels of defense may also positively impact such resilience. Finally, we explore how competition may mitigate intra-ring resilience to perturbation, since co-mimetic species (which are therefore co-occurring) may undergo higher competition for resources than between other mimicry rings.

Mathematical model. We consider a mimetic community of 10 species, distributed in 2 mimicry rings A and B. Each mimicry ring contains a single, distinct, aposematic signal. All 10 species are chemically defended. Environment, predator community and predation rate are constant in time.

Let us consider the following model:

$$\frac{dN_k}{dt} = r_k N_k \left(1 - \frac{N_k + \sum_{k \neq j} c_{kj} N_j}{K} \right) - \frac{p_k}{1 + \lambda_k N_k + \sum_{k \neq i} \lambda_i N_i m_{ki}} N_k - \delta_k N_k$$

Variables and parameters are listed in Table 3.1. N_k represents the size of population of species k . Birth of new individuals in the population is modeled by $r_k N_k$, where r_k is the birth rate of species k , modulated by competition with any other species j with competition coefficient c_{kj} and carrying capacity K . The mortality rate is split into two components: p_k and δ_k , representing mortality due to predation and to other factors, respectively. We followed Joron and Iwasa (2005) by dividing p by $1 + \sum \lambda_i m_{ki} N_i$ in order to model positive density-dependence due to the protection conferred by the mimicry ring they belong to (Joron & Iwasa, 2005). Predator learning depends on chemical defense ($0 < \lambda_i < 1$), numerical protection (N_i) and co-mimics' similarity (m_{ki} ; 0, 1).

Table 3.1. Parameters and variables of the model. Ranges are given in the right column (see text for explanation).

<i>Symbol</i>	<i>Description</i>	<i>Range</i>
N_k	Population size of species k	$0 \leq N_k$
r_k	Birth rate of k	$0 \leq r_k$
c_{kj}	Competition coefficient between species k et j	$0 \leq c_{kj}$
N_j	Population size of species j	$0 \leq N_j$
K	Carrying capacity	$0 < K$
p_k	Mortality rate due to predation on species k	$0 \leq p_k$
λ_k	Degree of unpalatability of species k	$0 \leq \lambda_k$
λ_i	Degree of unpalatability of co-mimetic species i	$0 \leq \lambda_i$
N_i	Population size of co-mimetic species i	$0 \leq N_i$
m_{ki}	Degree of similarity between species k et i	$m_{ki} = 0$ or 1
δ_k	Mortality rate not due to predation on species k	$0 \leq \delta_k \leq 1$

Programmation and simulations. Simulations were coded with Python version 3.9 (Van Rossum & Drake, Python 3 Reference Manual, 2009) under PyCharm environment (*version 2020.3.3, build 203.7148.72*). We used matrix representation to simulate the 10 population dynamics in a single step (Appendix 3.1). Python libraries are listed in Table 3.2.

Table 3.2. List of Python’s libraries used in the code.

<i>Name</i>	<i>Use and references</i>
NumPy	Generates matrices (Harris <i>et al.</i> , 2020)
Random	Generates pseudo-random numbers (Van Rossum, 2020)
Matplotlib.pyplot	2D graphics (Hunter, 2007)
Matplotlib.ticker	Graphic tools (Hunter, 2007)
Seaborn	Heatmap graphics (Waskom, 2021)

3.2.1.1 Initial conditions and perturbations

For the whole community and each species, we fixed the following parameters: $N=25$, $r=1.1$, $\delta=0.05$, $\lambda=0.001$, $c=0.1$. These values were set empirically in order to observe consistent variations. Co-mimics similarity was considered binary and set as $m = 1$ within a ring and $m = 0$ between rings. We assumed local extinction if $N < 2$.

Except for question *i*) (see below) we applied a perturbation to the community in order to evaluate co-extinction risks. First, we calculated equilibrium population size for each species. Equilibrium was considered reached when $|\frac{dN_k}{dt}| \leq 0.0001$. Then a perturbation was applied to a single species: δ raised to 0.7 from t_0 to t_{20} . The new equilibrium was then calculated.

3.2.1.2 Tested predictions and parameters' values

With the above model and assumptions we tested five different predictions (only predictions ii. and iii. are empirically tested):

i) Mimicry limits local extinction

We ran 5000 simulations on a five-species community, where r was randomly sampled at each generation. We compared situations where $m=0$ (no mimicry, i.e. all species have a distinct aposematic signal) and $m=1$ (with a single aposematic signal).

ii) Richer rings are less sensitive to perturbations

We increased the number of species of mimicry ring A from 1 to 5 (the remaining being in ring B). We then looked in final states whether all A species have survived, or only the perturbed species go extinct, or the whole co-mimetic species go extinct.

iii) More abundant rings are less sensitive to perturbation

Species population sizes were calculated before and after the perturbation. To study the effect of ring abundance on resilience to perturbation, the values of r were drawn randomly for each simulation, resulting in variable population sizes at equilibrium. We ran 100 simulations 0.01 for values of p incremented by 0.01 units, from 0 to 1.5. Results were examined in the same way as for prediction *ii*).

iv) Levels of defense impact resilience to perturbation

In ring A we raised λ values from 0.001 to 0.005, while λ was fixed to 0.001 in ring B. Results were examined in the same way as for prediction *ii*).

v) Competition can mitigate intra-ring resilience to perturbation

We increased c values in species from the same mimicry rings, from 0.1 to 0.5, for the two A species and the eight B species. Results were examined in the same way as for prediction *ii*).

3.2.2 Empirical community and prediction

In our dataset, true abundances during Ferton's time are unknown, we only have the abundances of the 2017 dataset. Assuming that abundant species in 2017 were already abundant a century ago, our empirical prediction is that species belonging to a mimicry ring (Müllerian mimetic relationship) with at least one abundant species at present, will tend to persist through time. The rationale is that the higher numerical protection conferred by abundant co-mimetic species benefits, and to a higher degree, to all the species involved in such mutualistic interactions (i.e. sharing the same mimicry ring).

We tested 1) the correlation between the proportion of persistent species (i.e. the number of species in both centuries divided by ring size at Ferton's time) and the abundance of commonest species in 2017, and between 2) the proportion of persistent species and ring size (i.e. ring species richness) from Ferton. In this analysis, we use species richness as a proxy for total ring abundance (i.e. true numerical protection). To ensure that this assumption is correct we used a linear model and tested the relative contributions of within-ring common species abundances and richness to total abundance: *Total abundance ~ Ring size + Common species abundance*.

Study sites and protocol. This study uses the same empirical community as in chapter 2, from South Corsica. A total of 7 sites were sampled in 2017, all being also covered by Ferton's collection (1-3 stations each), spanning a range of habitats such as maquis, shrublands and grasslands (Table 3.3). Specimens from the 2017 dataset were collected following standardized protocols: insects were collected by pan traps and sweep netting transects. Three pan traps (white, yellow and blue) were set in each site and emptied every two weeks, between March and November 2017. Two

transects of 25 meters long were sampled in each site, by two independent collectors, in the morning and in the afternoon, every month during this period.

Table 3.3. Site coordinates (WGS 84) and habitats (from Alexandre Cornuel-Willermoz unpublished data).

<i>Station</i>	<i>Site</i>	<i>Latitude</i>	<i>Longitude</i>	<i>Habitat</i>
1A	Santa Manza	41.414531	9.237372	Maquis
1B		41.414325	9.237643	Maquis
2A	Route de Santa Manza	41.400568	9.216798	Maquis, mesoxerophilous grassland
2B		41.400355	9.214525	Grassland, hedgerows
3A	Saint Julien	41.390343	9.180577	Fallow
3B		41.389786	9.179714	Fallow
4A	Bocca di Valle	41.378785	9.178601	Grassland, low shrubland
4B		41.378538	9.178807	Maquis
5A	Pertusato	41.368864	9.181344	Shrubland
5B		41.370934	9.181357	Maquis
5C		41.371996	9.181751	Maquis
6A	Bonifacio centre	41.387842	9.157838	Shrubland
6B		41.386439	9.155151	Shrubland
7A	Mont de la Trinité	41.403898	9.120824	Maquis, rocks
7B		41.403416	9.120351	Shrubland

Dataset preparation. Our empirical dataset from South Corsica (Bonifacio, France) comprised 19751 individuals (7682 from 2017 and 12069 from Ferton’s collection) belonging to 572 species distributed in 21 aculeate families. Differences between ancient (early 20th century) and recent diversity (early 21st century) are summarized in figure 3.0.

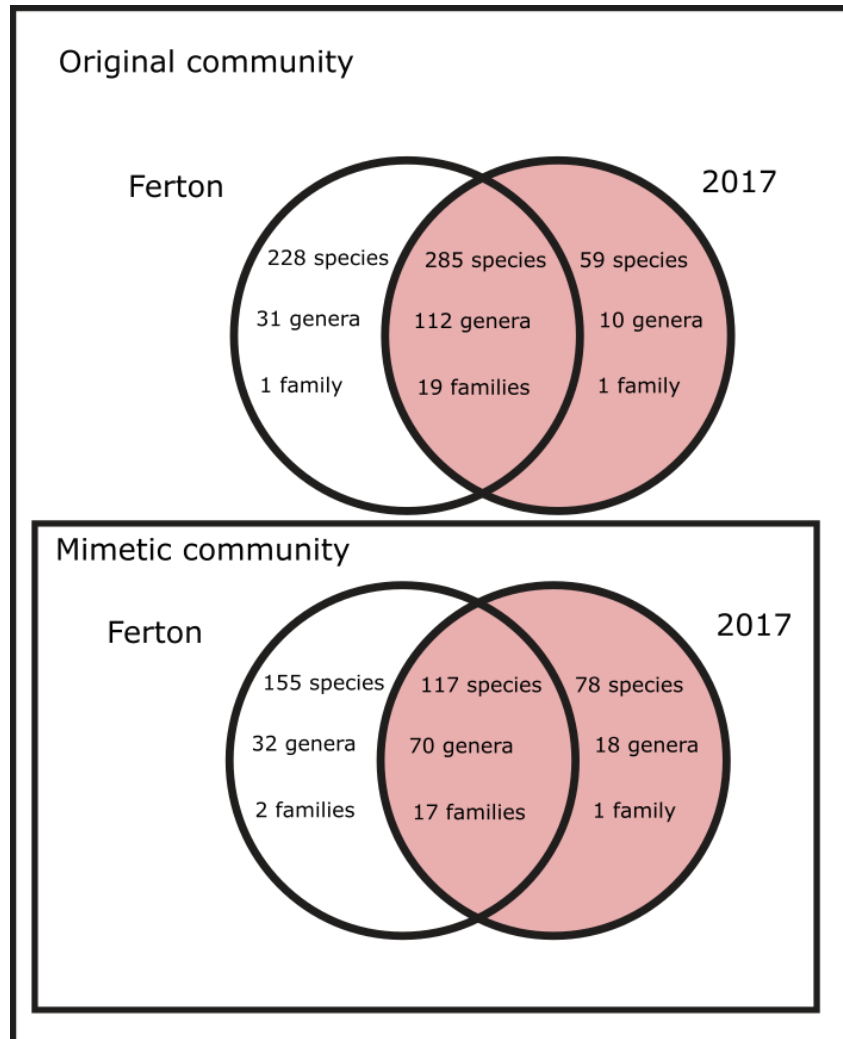


Figure 3.0. Venn diagrams representing the original (all species) and mimetic (only species studied in chapter 2) community composition. Left/white circle: Ferton’s collection; right/red circle: 2017 dataset.

We focus on the mimetic community dataset (Figure 3.0), that resulted from the classification obtained with the Colordistance method (see Chapter 2). The original community corresponds to the entire Bonifacio community, unfortunately specimens' display was not always suitable for image analysis, which limited the number of exploitable specimens and species in our analysis. From the Colordistance classification we discarded individuals from their original mimicry ring when classification uncertainty was larger than 25%. A total of 170 specimens (17% of the 2017 images) were excluded from potential mimicry rings. Image analysis and clustering was only run on a subset sample (selected individuals, see Chapter 2). Attribution of each remaining individual to a given mimicry ring was done by generalizing within the species that had been characterized in Chapter 2. When multiple rings were represented in a species, unattributed specimens were excluded from our dataset. Males and females were not split by default, and when sexual dimorphism occurred no attribution was made.

Only the 2017's dataset had reliable abundances (standardized protocol). The distribution of abundances can be summarized as follows: mean=22.2; median=5; mode=1, maximum=720; standard error= 62.015. In order to establish which species may be considered as "abundant species" (i.e. with a better numerical protection) we used a cut-off criterion with a conventional threshold of 10% of the distribution. This yields a threshold value of 49 individuals for a species to be considered abundant (i.e. 34/344 abundant species), which is reasonable considering abundances distribution in the community (Appendix 3.2).

3.3 Results

3.3.1 Theoretical community

i. Does mimicry limit local extinction?

We tested the effect of mimicry (occurrence of a convergent aposematic signal in the community) on local extinction risk, by comparing a non-mimetic community with a mimetic community. All of the 5000 simulations showed a total number of individuals higher in the mimetic case (Figure 3.1a), with a mean gain of 40 percent of individuals. In the non-mimetic community, the number of species at equilibrium ranges from 1 to 5 with a mean of 4.18 species (Figure 3.1b) whereas this figure raises to 5 in all simulations for the mimetic community which differ significantly (t test value = -81,371; df = 4999; p-value < 2,2e-16). This confirms that a shared aposematic signal among multiple species has a protective effect on co-mimetic species.

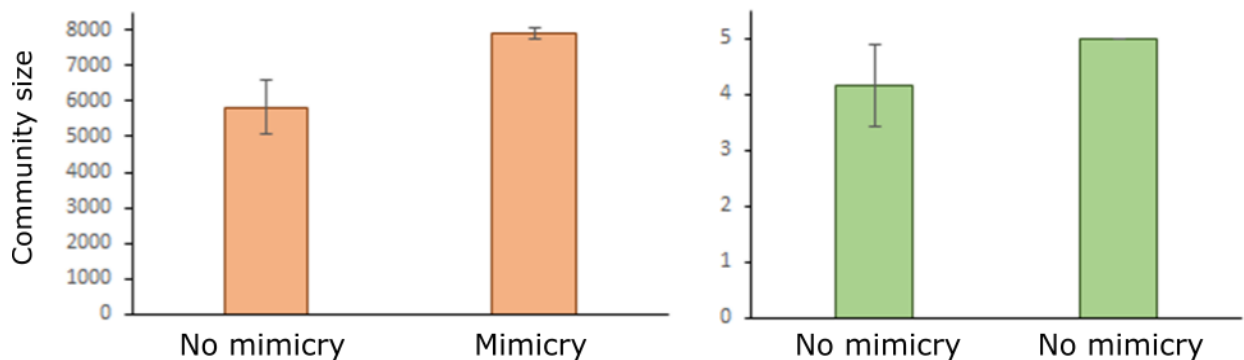


Figure 3.1. Final sizes of the community in abundances (left panel, in red) and species richness (right panel, in green), at equilibrium. A 5 species community simulated 5000 times, with random sampling of r each time. Dynamics calculated each time without ($m = 0$) and with mimicry ring ($m = 1$).

ii. Are richest rings less sensitive to perturbations?

We predicted that extinction and co-extinction risks will decrease as intra-ring species richness increases. We found that when species richness increases in the smaller ring, extinctions occur as high predation rates continue to increase (Figure 3.2). Co-extinction risk is reduced when intra-ring richness is higher, as the perturbed species is better maintained.

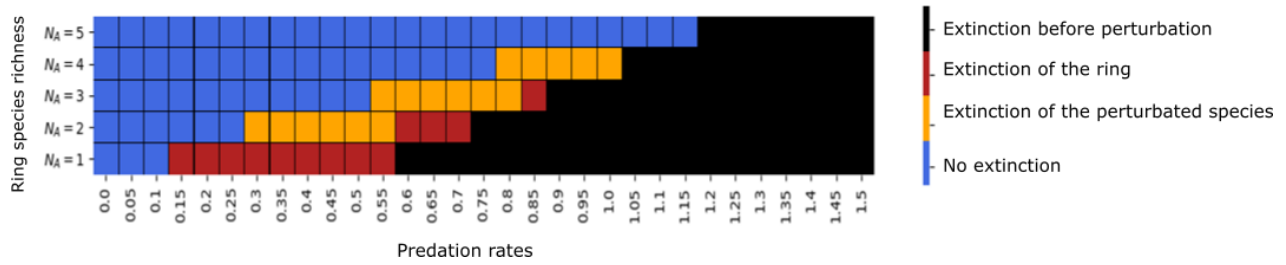


Figure 3.2. Final state of mimicry ring A, species richness as a function of predation rate; in blue all species persist, in orange the perturbed species goes extinct, in red the whole mimicry ring goes extinct, in black predation incurs extinction before first equilibrium.

iii. Are more abundant rings less sensitive to perturbation?

Increase in abundance within the rings leads to an increase in the number of simulations where all species were maintained (Figure 3.3). Abundance seems also to be a factor limiting the extinction risk of the perturbed species, and therefore limiting co-extinction risks.

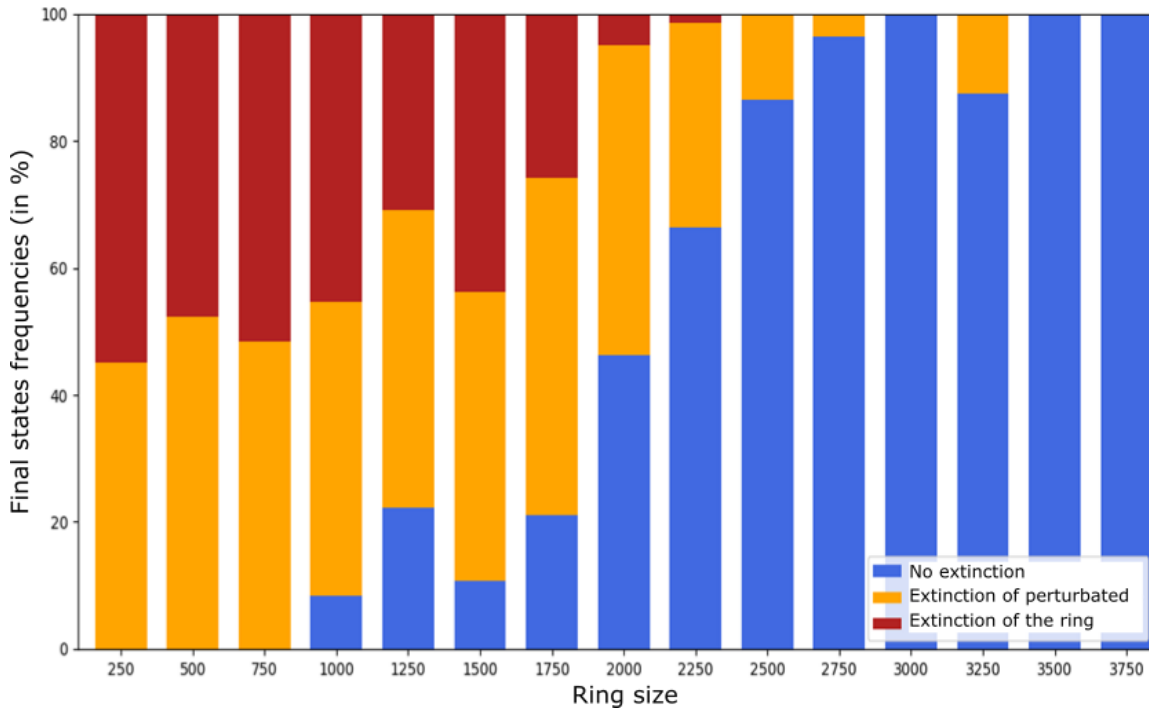


Figure 3.3. Final state of a mimicry ring with 2 species, as a function of ring size, for various predation rates (100 simulations each 0.01 step from 0 to 1.5). In blue all species persist, in orange the perturbed species goes extinct, in red the whole mimicry ring goes extinct.

iv. Do levels of defenses impact resilience to perturbations?

As expected, in the smaller rings, increase in unpalatability (or noxiousness) has a similar effect as species richness on extinction risk (Figure 3.4), and limits co-extinction risks. Over a given threshold of λ , the only observed outcome is maintenance of all co-mimetic species.

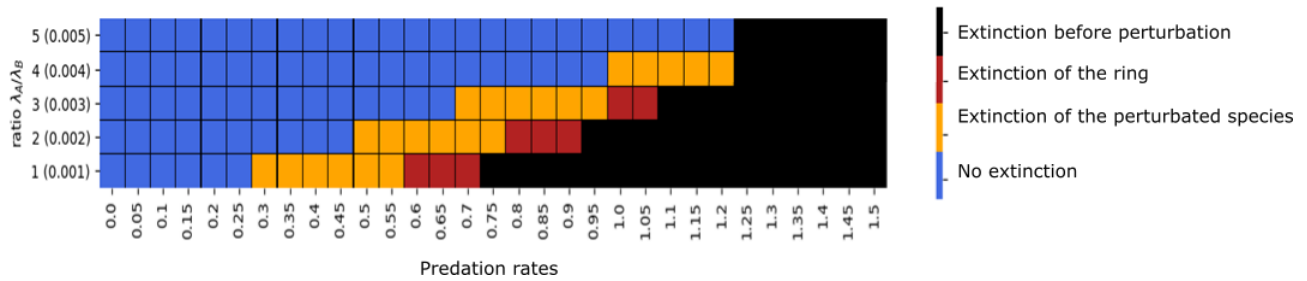


Figure 3.4. Final state of mimicry ring A as a function of predation rate and degree of unpalatability. In blue all species persist, in orange the perturbed species goes extinct, in red the whole mimicry ring goes extinct, in black predation incurs extinction before first equilibrium.

v. How does competition mitigate intra-ring resilience to perturbations?

First, increase in intra-ring competition reduces extinction risk in the smaller ring. This is because intra-ring competition affects more the larger ring, and thus reduces inter-ring competition for the smaller ring (Figure 3.5). Over a given threshold intra-ring competition is too high and increases extinction risk of the perturbed species. There are however no more co-extinctions when a species disappears, as competition pressures on the co-mimics are relaxed.

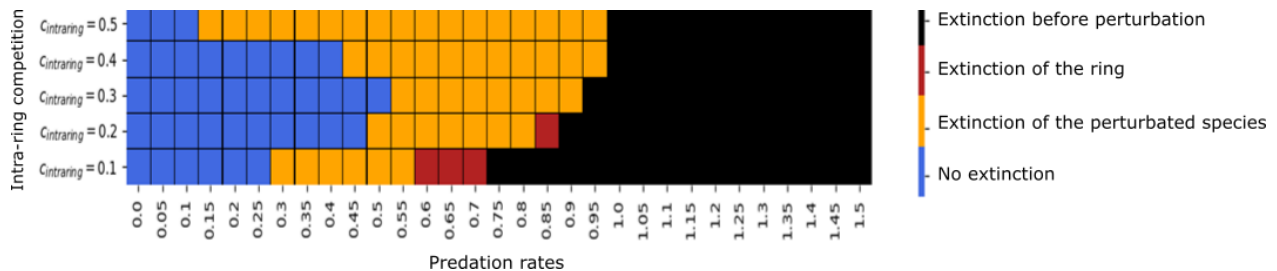


Figure 3.5. Final state of mimicry ring A as a function of predation rate and intra-ring-competition; in blue all species persist, in orange the perturbed species goes extinct, in red the whole mimicry ring goes extinct, in black predation incurs extinction before first equilibrium.

3.3.2 Empirical community

3.3.2.1 Is mimicry rings' total abundance driven by species richness or highest abundances?

Results for the linear model are presented in Table 3.4. Both factors significantly contribute to total abundances (Table 3.4). Common species abundance and species richness (i.e. ring size) may be, relatively to our sample, good proxies for total abundances.

Table 3.4. Anova table of the linear model (type III). Formula: Total abundance ~ Ring size*Common species abundance; Residuals = 1453; df = 3.

<i>Coefficients</i>	<i>Sum of Squares</i>	<i>Df</i>	<i>F value</i>	<i>P-value</i>
<i>Intercept</i>	208	1	0.4295	0.558992
<i>Ring size</i>	21440	1	44.2751	0.006918
<i>Common species abundance</i>	53942	1	111.3912	0.001817
<i>Interaction</i>	4436	1	9.1596	0.056468

In our community (Table 3.5), abundance and species richness in each ring are highly correlated (Spearman's $r = 0.8108$; p -value = 0.0269). Correlation between total abundance and the abundance of common species is also very high (Spearman's $r = 1$; p -value $\ll 0.01$).

3.3.2.2 Do mutualistic interactions enhance species persistence?

If ring size is a good proxy for ring abundance, we would expect, if our prediction is right, a highest proportion of persisting species (i.e. proportion of species found both in the present and in the past) associated with more numerically protected rings. There is no significant relationship between proportion of persisting species and the proportion of abundant co-mimetic species (Spearman's r

= 0.6429; p-value = 0.1194). We also obtain a non-significant relationship when we use Ferton's species richness as a proxy (Spearman's $r = -0.1429$; p-value = 0.7599). The null hypothesis in which mimicry ring abundance, or its proxy, has no effect on co-mimetic species persistence cannot be rejected. Our prediction seems not to be fully confirmed by our data. However, the proportion of persisting species is weakly and positively correlated to the variable "contribution of abundant species" (Spearman's $r = 0.75$; p-value = 0.0522). This might eventually suggest that mimicry rings with abundant species having a highest degree of dominance in 2017, count a higher proportion of persisting species.

Table 3.5. Diversity measures on the empirical mimetic dataset. 'Ring sizes' represent species richness. *Proportion of persisting species = Number of species in both centuries / Ring size Ferton*; *Proportion of abundant species = Number of abundant species / Ring size total*; *Contribution of abundant species = Abundance of abundant species / Abundance tot.*

<i>Ring id</i>	<i>1</i>	<i>2</i>	<i>4</i>	<i>5</i>	<i>6</i>	<i>7</i>	<i>3</i>
<i>Ring size total Ferton+2017</i>	123	85	67	65	122	14	34
<i>Number of species in both centuries</i>	38	12	26	18	18	3	3
<i>Ring size Ferton</i>	72	59	55	40	87	5	32
<i>Ring size 2017</i>	89	38	38	43	53	12	5
<i>Proportion of persisting species</i>	0,5278	0,2034	0,4727	0,45	0,2069	0,6	0,0938
<i>Number of abundant species in 2017</i>	26	9	4	11	15	2	0
<i>Proportion of abundant species</i>	0,2114	0,1059	0,0597	0,1692	0,1230	0,1429	0
<i>Abundance tot 2017</i>	1583	143	510	441	234	42	8
<i>Abundance of abundant species in 2017</i>	1202	12	279	254	27	6	NA
<i>Contribution of abundant species</i>	0,7593	0,0839	0,5471	0,5760	0,1154	0,1429	NA

3.4 Discussion

Our study is original in two aspects: 1) we provide the first application of a theoretical model to Aculeate Müllerian community (except Boutin *et al.*, 2022), 2) it is the first empirical and theoretical test of our main hypothesis at community scale in aculeates: do mutualistic interactions enhance species persistence? This question illuminates the interplay between pollinator decline and mimetic interactions. Our theoretical model shows that decline within mimicry rings seems to be limited by total species richness, the number of individuals involved in mimicry, and degree of unpalatability (i.e. the richer/abundant/unpalatable the ring is the more resilient it is). Intra-ring competition also appears to increase co-extinction risk. These preliminary theoretical results show the effect of the above parameters on local extinction and co-extinction risks. All of these assumptions were already expected under the Müllerian theory of mimicry (Müller, 1879; Sherratt, 2008).

As expected, an aposematic signal shared by multiple species has a protective effect on co-mimetic species. We explored this prediction in our theoretical approach by comparing a mimetic community and a ‘non-mimetic’ community (Figure 3.1). This suggests that Müllerian mimicry limits local extinction, at least in theory, but defining a ‘non-mimetic’ community seems less reasonable in practice with our empirical dataset.

Our theoretical model shows that richest rings are less sensitive to perturbation: co-extinction risk is reduced when intra-ring richness is higher (Figure 3.2). We observed the same relationship for abundant rings in our model (Figure 3.3): when abundances increase within a ring, all-species-persistence is the more frequent outcome. Moreover, we found in our empirical dataset that both species richness and abundance may contribute to total abundances in each ring. In Neotropical mimetic butterflies, communities harboring the largest mimicry rings, which, according to our

findings, are expected to be better protected against co-extinction cascades, are also those with the highest diversity, and therefore represent targets for conservation plans (Doré *et al.*, 2022).

It is widely recognized that there is a spectrum in palatability and chemical defenses (Brower *et al.*, 1968). There is a large variation, among bee and wasp species, in venom composition and effects (e.g. pain, paralysis) on potential predators or attackers (dos Santos-Pinto *et al.*, 2018; Schmidt, 2019; see also General Introduction). Thus, levels of defenses within and among our seven mimicry rings may differ greatly. In this study we theoretically show that levels of defenses impact resilience to perturbation: over a given threshold of unpalatability, the only observed outcome is maintenance of all co-mimetic species (Figure 3.4). Unfortunately, empirical data on chemical protection were not directly available in our empirical dataset.

Competition can also mitigate intra-ring resilience to perturbation. Our results (Figure 3.5) show that over a given threshold, intra-ring competition increases extinction risk for the perturbed species, even though in smaller rings, it decreases it. However no more co-extinctions occur when a species disappears, for competition pressure on the co-mimics is relaxed. Once again, we lack data to infer competition in our empirical analysis. Moreover we did not include any intra-specific competition in this study, only inter-specific competition within mimicry rings.

Our mathematical model has some major drawbacks that, for a matter of time and time for calculation we could not immediately correct, but these drawbacks should be corrected in the future. We chose a value of 1 for time step in a discrete approach for simulation (see material and methods), which might be a bit high considering the model complexity, and generate a coarse linear approximation. A solution might be to choose a smaller value or to use Runge Kutta methods to solve such compromise (Conde *et al.*, 2017). We also chose a value of 2 individuals as a threshold for extinction, since 0 is never reached. However, this value is also arbitrarily high and does not

per se correspond to a number of individuals but rather to a certain amount of individuals. Because the variable is continuous, a very small value (i.e. acceptable as a threshold for extinction) would be closer to 0.01. Species richness and abundance are interdependent factors, therefore disentangling their effects might be tricky, and our theoretical results are limited in such purpose. For the same reasons, the competition coefficient should be varying instead of the r parameter (which is also huge with a value of 1.1). Finally, this model assumes that for a similar total density, predators will still sample prey at the same rate. This has been criticized both in theory and empirically (Mallet & Barton, 1989; Lindström *et al.*, 2001; Beatty, Beirinckx & Sherratt, 2004).

As seen in the previous chapters, we do not directly consider Batesian mimics here. In a diverse community such as ours, multiple rings may co-occur, even without Batesian mimics occurrence: it has even been shown that, under a certain threshold, as Batesian mimics increase, the number of mimicry rings will decrease (Franks & Noble, 2004). However, hymenopteran males are in fact Batesian mimics of females and sexual dimorphism is directly linked to Batesian mimicry and could be studied with our data in the future. In perspective, Boutin *et al.* recently wrote a paper (which I could not co-author) with a modified version of this first model, now submitted to *PCI Evol Biol* (Boutin *et al.*, 2022). This paper investigates sex-limited mimicry in aculeates with similar issues and questions, and shows that the positive effects on species coexistence also depend on sex ratios. Indeed, the more undefended males occur in the population, the higher the extinction probability will be. It enhances our present understanding since co-extinction will occur when females are less abundant or less defended.

To conclude, all the empirical results presented in this study rely on too few replicates (here only seven rings in a community considered as one). We therefore suggest that data should be analyzed in a different way: partitioned by collecting site (seven distinct localities). Even if we can still

consider it as a unique mimetic community, each sampling site being a replicate ($n = 49$). Unfortunately this was not possible during the analysis because of too scarce information in Ferton's dataset. However, despite lack of statistical significance, our empirical findings exhibit a noteworthy pattern: a large temporal turnover in the mimetic community. Overall, 155 species which occurred in the community in the early 20th century (Ferton's collection), did not occur in 2017, or may have gone locally extinct. We cannot of course attest for local extinction since we only have a two-point comparison and do not include temporal variation. Multiple biotic and abiotic factors have likely changed during the late century in this region (although precise environmental data concerning Ferton's time might be difficult to obtain). However, whatever the factors, mimicry rings do persist, as a dynamical equilibrium. This might suggest that rings change in their species composition but persist at the community scale since they confer a protection against predation to such mutualistic species. For now we are not aware of other data or protocols in the literature that might help to discuss such patterns in a mimetic context.

More work needs to be done to understand more precisely the effects of species richness, abundances, unpalatability and competition on mimetic systems (within and among mimicry rings) in the context of co-extinction cascades, both in theory and in the field. However, these preliminary results tend to indicate that mutualistic interactions may enhance species persistence in a diverse Hymenoptera community.

3.5 References

ALEXANDROU, M.A., OLIVEIRA, C., MAILLARD, M., MCGILL, R.A.R., NEWTON, J., CREER, S. & TAYLOR, M.I. (2011) Competition and phylogeny determine community structure in Müllerian co-mimics. *Nature* **469**, 84–90.

- AUBIER, T.G. (2020) Positive density dependence acting on mortality can help maintain species-rich communities. *eLife*, 1–18.
- AUBIER, T.G. & ELIAS, M. (2020) Positive and negative interactions jointly determine the structure of Müllerian mimetic communities. *Oikos*.
- BEATTY, C.D., BEIRINCKX, K. & SHERRATT, T.N. (2004) The evolution of müllerian mimicry in multispecies communities. *Nature* **431**, 63–66. Nature Publishing Group.
- BOUTIN, M., COSTA, M., FONTAINE, C., PERRARD, A. & LLAURENS, V. (2022) Influence of sex-limited mimicry on extinction risk in Aculeata: a theoretical approach. bioRxiv. <https://www.biorxiv.org/content/10.1101/2022.10.21.513153v1> [accessed 11 May 2023].
- BROWER, L.P., RYERSON, W.N., COPPINGER, L.L. & GLAZIER, S.C. (1968) Ecological Chemistry and the Palatability Spectrum. *Science* **161**, 1349–1351.
- CONDE, S., GOTTLIEB, S., GRANT, Z.J. & SHADID, J.N. (2017) Implicit and Implicit–Explicit Strong Stability Preserving Runge–Kutta Methods with High Linear Order. *Journal of Scientific Computing* **73**, 667–690.
- DORÉ, M., WILLMOTT, K., LAVERGNE, S., CHAZOT, N., FREITAS, A.V.L., FONTAINE, C. & ELIAS, M. (2023) Mutualistic interactions shape global spatial congruence and climatic niche evolution in Neotropical mimetic butterflies. *Ecology Letters* **26**, 843–857.
- DORÉ, M., WILLMOTT, K., LEROY, B., CHAZOT, N., MALLET, J., FREITAS, A.V.L., HALL, J.P.W., LAMAS, G., DASMAHAPATRA, K.K., FONTAINE, C. & ELIAS, M. (2022) Anthropogenic pressures coincide with Neotropical biodiversity hotspots in a flagship butterfly group. *Diversity and Distributions* **28**, 2912–2930.

- ELIAS, M., GOMPERT, Z., JIGGINS, C. & WILLMOTT, K. (2008) Mutualistic Interactions Drive Ecological Niche Convergence in a Diverse Butterfly Community. *PLOS Biology* **6**, e300. Public Library of Science.
- FRANKS, D.W. & NOBLE, J. (2004) Batesian Mimics Influence Mimicry Ring Evolution. *Proceedings: Biological Sciences* **271**, 191–196.
- GOMPERT, Z., WILLMOTT, K. & ELIAS, M. (2011) Heterogeneity in predator micro-habitat use and the maintenance of Müllerian mimetic diversity. *Journal of Theoretical Biology* **281**, 39–46.
- GROSS, K. (2008) Positive interactions among competitors can produce species-rich communities. *Ecology Letters* **11**, 929–936.
- HARRIS, C.R., MILLMAN, K.J., VAN DER WALT, S.J., GOMMERS, R., VIRTANEN, P., COURNAPEAU, D., WIESER, E., TAYLOR, J., BERG, S., SMITH, N.J., KERN, R., PICUS, M., HOYER, S., VAN KERKWIJK, M.H., BRETT, M., ET AL. (2020) Array programming with NumPy. *Nature* **585**, 357–362. Nature Publishing Group.
- HUNTER, J.D. (2007) Matplotlib: A 2D Graphics Environment. *Computing in Science & Engineering* **9**, 90–95. IEEE Computer Society.
- JORON, M. & IWASA, Y. (2005) The evolution of a Müllerian mimic in a spatially distributed community. *Journal of Theoretical Biology* **237**, 87–103.
- LINDSTRÖM, L., ALATALO, R.V., LYYTINEN, A. & MAPPES, J. (2001) Strong antiapostatic selection against novel rare aposematic prey. *Proceedings of the National Academy of Sciences* **98**, 9181–9184. Proceedings of the National Academy of Sciences.

- MALLET, J. & BARTON, N.H. (1989) Strong Natural Selection in a Warning-Color Hybrid Zone. *Evolution* **43**, 421–431.
- MALLET, J. & JORON, M. (1999) Evolution of Diversity in Warning Color and Mimicry: Polymorphisms, Shifting Balance, and Speciation. *Annual Review of Ecology and Systematics* **30**, 201–233.
- MÜLLER, F. (1879) Ituna and Thyridia: a remarkable case of mimicry in butterflies. *Transactions of the Entomological Society of London*, 20–29.
- DOS SANTOS-PINTO, J.R.A., PEREZ-RIVEROL, A., LASA, A.M. & PALMA, M.S. (2018) Diversity of peptidic and proteinaceous toxins from social Hymenoptera venoms. *Toxicon* **148**, 172–196.
- SCHMIDT, J.O. (2019) Pain and Lethality Induced by Insect Stings: An Exploratory and Correlational Study. *Toxins* **11**, 1–14.
- SHERRATT, T.N. (2008) The evolution of Müllerian mimicry. *Naturwissenschaften* **95**, 681–695.
- SMITH-PARDO, A.H. (2005) Systematics and mimicry of the genus *Neocorynura*: an example of two species from Central America (Hymenoptera: Halictidae). *Acta zoologica cracoviensia* **48B**, 11–21.
- VAN ROSSUM, G. (2020) The Python Library Reference, Release 3.8.2. *Python Software Foundation*.
- WASKOM, M.L. (2021) seaborn: statistical data visualization. *Journal of Open Source Software* **6**, 3021.

WEST-EBERHARD, M.J., CARPENTER, J.M. & HANSON, P.E. (1995) The vespid wasps (Vespidae).
In *The Hymenoptera of Costa Rica* pp. 561–587 Oxford Science Publications. Oxford.

WILLMOTT, K.R. & MALLET, J. (2004) Correlations between adult mimicry and larval host plants
in ithomiine butterflies. *Proceedings of the Royal Society of London. Series B: Biological
Sciences* **271**, S266–S269. Royal Society.

WILLMOTT, K.R., ROBINSON WILLMOTT, J.C., ELIAS, M. & JIGGINS, C.D. (2017) Maintaining
mimicry diversity: optimal warning colour patterns differ among microhabitats in
Amazonian clearwing butterflies. *Proceedings of the Royal Society B: Biological Sciences*
284, 20170744. Royal Society.

General summary and perspectives

Our PhD work is, to our knowledge, the first empirical attempt to attest for temporal turnover in mimicry rings at community scale and among aculeates. Overall, we demonstrated that such a study is feasible. Three main conclusions may be of interest:

4.1 Bees and stinging wasps are a major but overlooked model for Müllerian mimicry studies

In this thesis, we established that aculeates are a key and suitable model for research on mimicry, by conducting an extensive review on 1150 aculeate species described in the literature as involved in 150 mimicry rings around the world. However, natural predators' perception, the complex and multimodal aspect of their aposematic signal, and other aculeate characteristics that may influence mimicry, are poorly understood. In order to get a better picture of their protective value, it would be interesting to integrate to our findings, as much information as possible about other (non-aculeate) co-mimetic taxa, such as many hoverflies and moths, reported as closely resembling to these models.

4.2 Müllerian Mimicry is an important component of our diverse hymenopteran community from South Corsica

In this work, we studied a whole aculeate community from South Corsica (France, Mediterranean region), by quantifying mimetic resemblance and convergence. We found that the community was indeed partitioned in multiple mimicry rings, each one comprising many species with a large diversity in colorations, color patterns and body shapes. This suggested that mimicry is a significant component of such communities' structure. Yet, only a few of them were the result of signal convergence among species. Unfortunately, only the specimens' abdomens could be integrated in this study, because of display issues. Abdomens may be a reasonable proxy for cues forming the aposematic signal (e.g. largest body part, likely visible in motion), however both thorax and

abdomens may either co-vary or form distinct elements of color patterns detectable by predators. Moreover, their variations in shape still need to be added to our analysis.

4.3 Müllerian mimicry might enhance species persistence in a diverse Hymenoptera community

Our prediction was confirmed theoretically but not empirically (in the span of a century). The hypothesis that better defended rings in the Corsican community tend to better survive throughout time, is inconclusive with the information at hand. However, we do observe a large temporal turnover in community composition while mimicry rings persist through time. This is an intriguing result which needs a more careful focus in a future study, and may eventually be compared to independent datasets.

4.4 Perspectives

Despite these preliminary steps toward a better understanding of Müllerian mimicry implication in natural communities experiencing a global decline, other aspects partly at hand (but not studied during this PhD), might provide insightful perspectives:

- In this study, variation in body size was not studied. Since some predators are able to discriminate prey on size, lengths should be measured on each specimen in order to test if mimicry occur between species of similar sizes.
- Many aculeate species in our community are engaged in direct antagonistic interactions (e.g. parasitic, predation). For instance, wasp genera such as *Evagetes* are known kleptoparasites of other genera such as *Anoplius* or *Arachnospila*; *Nysson* can parasitize *Psammaecius*. These relationships are also common in bees ('cuckoo bees'): *Coelioxys* can parasitize *Megachile*; *Nomada* parasitize members of the Andrenidae family; *Stelis* can parasitize

Anthidium and related genera. Parasitic interactions might impact the community dynamics, lowering the effects of mutualistic protection. All of these genera occur in our mimicry rings and it could be interesting to test the prevalence of parasitism in mimicry rings: do they tend to share a same aposematic signal with their hosts?

- Since sociality could enhance predator learning and drive the emergence of novel morphs or aposematic signals, our data may reveal the prevalence of social species in mimicry rings at the community level.
- The occurrence of sexually dimorphic species among mimicry rings could also be studied based on our dataset.
- Finally, species that appear earlier in the season suffer more attacks because there are more naive predators. Within a mimicry ring, individuals flying later benefit from increased protection. Phenology patterns within mimicry rings were not studied here. However, the study of how abundances (i.e. numerical protection) vary during the season could be initiated with such data because we do possess information on their emergence.

Supplementary Material

Appendix 2.1

List of all photographed specimens in image analyses. NumInv is the inventory number for hymenoptera collections from the MNHN.

Famille	Genre	Espèce	Sous.espèce	Sexe	NumInv	Projet
Megachilidae	Megachile	argentata	schmiedeknehti	F	EY34080	2017
Megachilidae	Megachile	argentata	schmiedeknehti	F	EY34031	2017
Megachilidae	Megachile	argentata	schmiedeknehti	F	EY34126	2017
Crabronidae	Tachysphex	rufiventris		F	EY25397	2017
Crabronidae	Tachysphex	rufiventris		F	EY34181	2017
Crabronidae	Tachysphex	rufiventris		F	EY34180	2017
Andrenidae	Andrena	sardoa		F	EY25441	2017
Andrenidae	Andrena	sardoa		F	EY34178	2017
Andrenidae	Andrena	sardoa		F	EY34179	2017
Crabronidae	Bembix	bidentata		F	EY25433	2017
Crabronidae	Bembix	bidentata		F	EY34177	2017
Crabronidae	Bembix	bidentata		F	EY34176	2017
Ampulicidae	Dolichurus	nsp1		M	EY34225	2017
Ampulicidae	Dolichurus	nsp2		M	EY34206	2017
Ampulicidae	Dolichurus	nsp2		M	EY34210	2017
Andrenidae	Andrena	cinerea		F	EY34167	2017
Andrenidae	Andrena	cinerea		F	EY34214	2017
Andrenidae	Andrena	cinerea		F	EY34222	2017
Andrenidae	Andrena	cinerea		M	EY34219	2017
Andrenidae	Andrena	cinerea		M	EY34220	2017
Andrenidae	Andrena	cinerea		M	EY34159	2017
Andrenidae	Andrena	fabrella		M	EY34218	2017
Andrenidae	Andrena	fabrella		F	EY34175	2017
Andrenidae	Andrena	fabrella		F	EY34164	2017
Andrenidae	Andrena	fabrella		M	EY34221	2017
Andrenidae	Andrena	flavipes		F	EY25436	2017
Andrenidae	Andrena	flavipes		F	EY34162	2017
Andrenidae	Andrena	flavipes		M	EY34160	2017
Andrenidae	Andrena	flavipes		F	EY34213	2017
Andrenidae	Andrena	flavipes		M	EY34171	2017
Andrenidae	Andrena	flavipes		M	EY34209	2017
Andrenidae	Andrena	hesperia		F	EY34156	2017
Andrenidae	Andrena	hesperia		F	EY34165	2017
Andrenidae	Andrena	hesperia		M	EY34217	2017
Andrenidae	Andrena	lepida		F	EY34530	2017

Andrenidae	Andrena	miegiella		M	EY34173	2017
Andrenidae	Andrena	miegiella		M	EY34207	2017
Andrenidae	Andrena	morio		F	EY34168	2017
Andrenidae	Andrena	morio		M	EY34224	2017
Andrenidae	Andrena	morio		M	EY25439	2017
Andrenidae	Andrena	morio		M	EY34079	2017
Andrenidae	Andrena	morio		F	EY34208	2017
Andrenidae	Andrena	nigroaenea	corsa	F	EY34081	2017
Andrenidae	Andrena	nigroaenea	corsa	F	EY34127	2017
Andrenidae	Andrena	nigroolivacea		F	EY34216	2017
Andrenidae	Andrena	nigroolivacea		F	EY34161	2017
Andrenidae	Andrena	pilipes	iliensis	F	EY34579	2017
Andrenidae	Andrena	pilipes	iliensis	F	EY34476	2017
Andrenidae	Andrena	pilipes	iliensis	F	EY25434	2017
Andrenidae	Andrena	pilipes	iliensis	M	EY34532	2017
Andrenidae	Andrena	pilipes	iliensis	M	EY34577	2017
Andrenidae	Andrena	pilipes	iliensis	M	EY34681	2017
Andrenidae	Andrena	sardoa		M	EY34128	2017
Andrenidae	Andrena	sardoa		M	EY34027	2017
Andrenidae	Andrena	sardoa		M	EY34029	2017
Andrenidae	Andrena	aff. croceiventris		F	EY34211	2017
Andrenidae	Andrena	aff. croceiventris		F	EY34163	2017
Andrenidae	Andrena	aff. croceiventris		M	EY34172	2017
Andrenidae	Andrena	aff. croceiventris		M	EY34170	2017
Andrenidae	Andrena	aff. croceiventris		M	EY34212	2017
Andrenidae	Andrena	aff. croceiventris		F	EY34157	2017
Andrenidae	Andrena	vulpecula		F	EY34682	2017
Andrenidae	Andrena	vulpecula		F	EY34477	2017
Andrenidae	Andrena	vulpecula		F	EY34676	2017
Andrenidae	Andrena	vulpecula		M	EY34529	2017
Andrenidae	Andrena	vulpecula		M	EY34583	2017
Andrenidae	Andrena	vulpecula		M	EY34628	2017
Andrenidae	Panurgus	corsicus		F	EY25387	2017
Andrenidae	Panurgus	corsicus		M	EY34677	2017
Andrenidae	Panurgus	corsicus		F	EY34626	2017
Andrenidae	Panurgus	corsicus		F	EY34631	2017
Andrenidae	Panurgus	corsicus		M	EY34580	2017
Andrenidae	Panurgus	corsicus		M	EY34627	2017
Apidae	Amegilla	quadrifasciata		M	EY33826	2017
Apidae	Amegilla	quadrifasciata		F	EY25431	2017
Apidae	Amegilla	quadrifasciata		M	EY33779	2017

Apidae	Amegilla	talaris		M	EY33928	2017
Apidae	Anthophora	canescens	luticincta	M	EY33828	2017
Apidae	Anthophora	crinipes		M	EY33930	2017
Apidae	Anthophora	crinipes		M	EY34011	2017
Apidae	Anthophora	crinipes		M	EY33781	2017
Apidae	Anthophora	dispar		F	EY33829	2017
Apidae	Anthophora	nigrovittata		F	EY33830	2017
Apidae	Anthophora	sichelii		M	EY33884	2017
Apidae	Anthophora	sichelii		M	EY33926	2017
Apidae	Anthophora	sichelii		M	EY34075	2017
Apidae	Anthophora	sichelii		F	EY33730	2017
Apidae	Anthophora	sichelii		F	EY33727	2017
Apidae	Anthophora	sichelii		F	EY33732	2017
Apidae	Apis	mellifera		F	EY33773	2017
Apidae	Apis	mellifera		F	EY33823	2017
Apidae	Apis	mellifera		F	EY33821	2017
Apidae	Bombus	runderatus	corsicola	M	EY33834	2017
Apidae	Bombus	runderatus	corsicola	M	EY33833	2017
Apidae	Bombus	runderatus	corsicola	M	EY33880	2017
Apidae	Bombus	xanthopus		F	EY33872	2017
Apidae	Bombus	xanthopus		F	EY33971	2017
Apidae	Bombus	xanthopus		F	EY33871	2017
Apidae	Bombus	xanthopus		M	EY33877	2017
Apidae	Bombus	xanthopus		M	EY33783	2017
Apidae	Bombus	xanthopus		M	EY33734	2017
Apidae	Ceratina	cyanea		F	EY33883	2017
Apidae	Ceratina	cyanea		M	EY33934	2017
Apidae	Ceratina	cyanea		F	EY33731	2017
Apidae	Ceratina	cyanea		M	EY33933	2017
Apidae	Ceratina	cyanea		M	EY33728	2017
Apidae	Ceratina	cyanea		F	EY33881	2017
Apidae	Epeolus	cruciger		M	EY33878	2017
Apidae	Epeolus	compar		F	EY33726	2017
Apidae	Eucera	nigrescens		M	EY34070	2017
Apidae	Eucera	nigrescens		M	EY34065	2017
Apidae	Eucera	nigrescens		F	EY34071	2017
Apidae	Eucera	nigrescens		M	EY34020	2017
Apidae	Eucera	nigrescens		M	EY34021	2017
Apidae	Eucera	nigrescens		F	EY33780	2017
Apidae	Eucera	nigrescens		F	EY33929	2017
Apidae	Eucera	nigrifacies		M	EY33927	2017

Apidae	Eucera	nigrifacies		M	EY33876	2017
Apidae	Eucera	nigrifacies		M	EY33827	2017
Apidae	Eucera	nigrifacies		F	EY33879	2017
Apidae	Eucera	nigrifacies		F	EY33777	2017
Apidae	Eucera	nigrifacies		F	EY34119	2017
Apidae	Eucera	nigrilabris		F	EY34064	2017
Apidae	Eucera	nigrilabris		F	EY33778	2017
Apidae	Eucera	nigrilabris		F	EY33931	2017
Apidae	Nomada	flavopicta		M	EY33882	2017
Apidae	Nomada	fucata		M	EY33729	2017
Apidae	Nomada	fucata		M	EY33784	2017
Apidae	Nomada	fucata		M	EY33832	2017
Apidae	Nomada	fulvicornis		F	EY33772	2017
Apidae	Nomada	kohli		M	EY33825	2017
Apidae	Nomada	kohli		M	EY33775	2017
Apidae	Nomada	kohli		M	EY33824	2017
Apidae	Nomada	numida	manni	M	EY33972	2017
Apidae	Nomada	numida	manni	F	EY33975	2017
Apidae	Nomada	numida	manni	F	EY33875	2017
Apidae	Tetraloniella	fulvescens		M	EY33831	2017
Apidae	Tetraloniella	fulvescens		M	EY25440	2017
Apidae	Tetraloniella	fulvescens		M	EY33776	2017
Apidae	Tetraloniella	fulvescens		F	EY33782	2017
Apidae	Tetraloniella	julliani		M	EY33932	2017
Apidae	Thyreus	histrionicus	picaron	M	EY33923	2017
Apidae	Thyreus	histrionicus	picaron	F	EY33922	2017
Apidae	Xylocopa	iris	iris	M	EY33873	2017
Apidae	Xylocopa	iris	iris	M	EY33973	2017
Apidae	Xylocopa	iris	iris	F	EY34077	2017
Apidae	Xylocopa	iris	iris	F	EY34030	2017
Apidae	Xylocopa	iris	iris	F	EY34130	2017
Chrysididae	Chrysis	comta		M	EY34634	2017
Chrysididae	Chrysis	fasciata		F	EY34585	2017
Chrysididae	Chrysis	gribodoi		M	EY34535	2017
Chrysididae	Chrysis	melaensis		M	EY34485	2017
Chrysididae	Chrysis	mysticalis	simii	M	EY34685	2017
Chrysididae	Chrysis	splendidula		M	EY34684	2017
Chrysididae	Chrysis	tristicula		F	EY34584	2017
Chrysididae	Chrysura	laevigata		F	EY34534	2017
Chrysididae	Hedychridium	chloropygum		F	EY34633	2017
Chrysididae	Hedychridium	scutellare		F	EY25437	2017

Chrysididae	Hedychrum	niemelai		F	EY34526	2017
Chrysididae	Holopyga	jurinei sensu Linsenmeyer		M	EY34629	2017
Chrysididae	Holopyga	jurinei sensu Linsenmeyer		M	EY34630	2017
Chrysididae	Holopyga	sardoa		M	EY34581	2017
Chrysididae	Pseudochrysis	incrassata		F	EY34578	2017
Chrysididae	Pseudochrysis	incrassata		F	EY34484	2017
Colletidae	Colletes	marginatus		F	EY33751	2017
Colletidae	Colletes	similis		M	EY33905	2017
Colletidae	Colletes	similis		M	EY33851	2017
Colletidae	Colletes	similis		M	EY33857	2017
Colletidae	Colletes	similis		F	EY33758	2017
Colletidae	Colletes	similis		F	EY33958	2017
Colletidae	Colletes	similis		F	EY33904	2017
Colletidae	Hylaeus	clypearis		F	EY34152	2017
Colletidae	Hylaeus	clypearis		M	EY34158	2017
Colletidae	Hylaeus	clypearis		F	EY34104	2017
Colletidae	Hylaeus	clypearis		M	EY34205	2017
Colletidae	Hylaeus	clypearis		F	EY34102	2017
Colletidae	Hylaeus	clypearis		M	EY34155	2017
Colletidae	Hylaeus	deceptorius		F	EY33753	2017
Colletidae	Hylaeus	deceptorius		F	EY33902	2017
Colletidae	Hylaeus	deceptorius		F	EY33852	2017
Colletidae	Hylaeus	euryscapus		M	EY34223	2017
Colletidae	Hylaeus	gibbus		M	EY33807	2017
Colletidae	Hylaeus	gibbus		F	EY33954	2017
Colletidae	Hylaeus	imparilis		M	EY33801	2017
Colletidae	Hylaeus	imparilis		F	EY33754	2017
Colletidae	Hylaeus	imparilis		M	EY33756	2017
Colletidae	Hylaeus	punctatus		M	EY33750	2017
Colletidae	Hylaeus	punctatus		M	EY33806	2017
Colletidae	Hylaeus	punctatus		F	EY33906	2017
Colletidae	Hylaeus	punctatus		M	EY33804	2017
Colletidae	Hylaeus	taeniolatus		F	EY33956	2017
Colletidae	Hylaeus	taeniolatus		M	EY33800	2017
Colletidae	Hylaeus	taeniolatus		M	EY33953	2017
Colletidae	Hylaeus	taeniolatus		M	EY33951	2017
Colletidae	Hylaeus	taeniolatus		F	EY33908	2017
Colletidae	Hylaeus	taeniolatus		F	EY33805	2017
Colletidae	Hylaeus	variegatus		M	EY33856	2017
Colletidae	Hylaeus	variegatus		M	EY33901	2017
Bembicidae	Ammatomus	coarctatus		M	EY34149	2017

Bembicidae	Ammatomus	coarctatus		F	EY25381	2017
Astatidae	Astata	costae		M	EY34099	2017
Astatidae	Astata	picea		F	EY34148	2017
Astatidae	Astata	picea		M	EY34198	2017
Astatidae	Astata	picea		F	EY34044	2017
Astatidae	Astata	rufipes	rufipes	M	EY34049	2017
Bembicidae	Bembix	bidentata		M	EY34037	2017
Bembicidae	Bembix	bidentata		M	EY34032	2017
Bembicidae	Bembix	bidentata		M	EY33983	2017
Bembicidae	Bembix	oculata		F	EY34036	2017
Bembicidae	Bembix	oculata		F	EY34041	2017
Bembicidae	Bembix	oculata		M	EY33990	2017
Bembicidae	Bembix	oculata		F	EY33991	2017
Philanthidae	Cerceris	flavilabris		F	EY34082	2017
Philanthidae	Cerceris	flavilabris		F	EY33977	2017
Philanthidae	Cerceris	flavilabris		M	EY34132	2017
Philanthidae	Cerceris	flavilabris		M	EY34085	2017
Philanthidae	Cerceris	flavilabris		M	EY34184	2017
Philanthidae	Cerceris	flavilabris		F	EY34136	2017
Philanthidae	Cerceris	corsica		F	EY34185	2017
Philanthidae	Cerceris	corsica		F	EY33979	2017
Philanthidae	Cerceris	corsica		M	EY34183	2017
Philanthidae	Cerceris	corsica		M	EY34086	2017
Philanthidae	Cerceris	corsica		M	EY34135	2017
Philanthidae	Cerceris	corsica		F	EY34133	2017
Philanthidae	Cerceris	fertoni		F	EY34134	2017
Philanthidae	Cerceris	fertoni		M	EY34141	2017
Philanthidae	Cerceris	fertoni		M	EY34188	2017
Philanthidae	Cerceris	sabulosa		F	EY34138	2017
Philanthidae	Cerceris	sabulosa		M	EY34087	2017
Philanthidae	Cerceris	sabulosa		M	EY34187	2017
Philanthidae	Cerceris	sabulosa		F	EY34140	2017
Philanthidae	Cerceris	specularis		M	EY34189	2017
Philanthidae	Cerceris	specularis		M	EY34190	2017
Crabronidae	Crossocerus	elongatulus		F	EY34174	2017
Crabronidae	Crossocerus	tarsatus		M	EY34166	2017
Crabronidae	Diodontus	nsp2		F	EY34048	2017
Crabronidae	Diodontus	nsp2		F	EY34098	2017
Crabronidae	Diodontus	nsp2		F	EY25385	2017
Crabronidae	Diodontus	nsp2		M	EY34199	2017
Crabronidae	Diodontus	nsp2		M	EY34197	2017

Crabronidae	Dryudella	aff. spinolae		M	EY25438	2017
Crabronidae	Ectemnius	cavifrons		F	EY25388	2017
Crabronidae	Ectemnius	aff. confinis		M	EY34200	2017
Bembicidae	Gorytes	albidulus		M	EY34047	2017
Bembicidae	Harpactus	elegans		F	EY25383	2017
Bembicidae	Harpactus	elegans		F	EY34150	2017
Bembicidae	Harpactus	leucurus		F	EY34193	2017
Bembicidae	Hoplisoides	punctuosus		M	EY34003	2017
Bembicidae	Hoplisoides	punctuosus		M	EY33998	2017
Crabronidae	Lestica	clypeata		M	EY25442	2017
Crabronidae	Nitela	nsp		M	EY34060	2017
Crabronidae	Nitela	nsp		F	EY34109	2017
Crabronidae	Nitela	nsp		M	EY34008	2017
Bembicidae	Nysson	fulvipes		M	EY25443	2017
Bembicidae	Nysson	trimaculatus		F	EY33997	2017
Crabronidae	Oryttus	concinus		F	EY25385	2017
Crabronidae	Oryttus	concinus		M	EY34002	2017
Crabronidae	Oxybelus	haemorrhoidalis	haemorrhoidalis	M	EY34057	2017
Pemphredonidae	Passaloecus	gracilis		F	EY34110	2017
Pemphredonidae	Passaloecus	gracilis		F	EY25401	2017
Pemphredonidae	Passaloecus	gracilis		M	EY34105	2017
Pemphredonidae	Passaloecus	gracilis		F	EY34009	2017
Pemphredonidae	Passaloecus	gracilis		M	EY34125	2017
Pemphredonidae	Passaloecus	nsp		M	EY34108	2017
Pemphredonidae	Passaloecus	nsp		F	EY34005	2017
Pemphredonidae	Pemphredon	lethifer		F	EY34090	2017
Pemphredonidae	Pemphredon	lethifer		M	EY34139	2017
Pemphredonidae	Pemphredon	lethifer		F	EY25451	2017
Pemphredonidae	Pemphredon	lethifer		M	EY34089	2017
Pemphredonidae	Pemphredon	lethifer		M	EY34137	2017
Pemphredonidae	Pemphredon	lethifer		F	EY34088	2017
Philanthidae	Philanthus	triangulum		F	EY34191	2017
Philanthidae	Philanthus	triangulum		F	EY34091	2017
Philanthidae	Philanthus	triangulum		F	EY33984	2017
Philanthidae	Philanthus	triangulum		M	EY33988	2017
Philanthidae	Philanthus	triangulum		M	EY33989	2017
Philanthidae	Philanthus	triangulum		M	EY33985	2017
Crabronidae	Pison	atrum		M	EY34107	2017
Crabronidae	Pison	atrum		F	EY25393	2017
Crabronidae	Pison	atrum		M	EY34106	2017
Crabronidae	Pison	atrum		M	EY34058	2017

Crabronidae	Pison	atrum		F	EY34169	2017
Crabronidae	Pison	atrum		F	EY34055	2017
Bembicidae	Psammaecius	punctulatus		F	EY34000	2017
Bembicidae	Psammaecius	punctulatus		F	EY25450	2017
Pemphredonidae	Spilomena	troglodytes		F	EY25448	2017
Bembicidae	Stizus	fasciatus		F	EY25400	2017
Crabronidae	Tachysphex	brullii		F	EY34053	2017
Crabronidae	Tachysphex	brullii		F	EY34004	2017
Crabronidae	Tachysphex	brullii		M	EY34001	2017
Crabronidae	Tachysphex	brullii		F	EY34203	2017
Crabronidae	Tachysphex	costae		F	EY34201	2017
Crabronidae	Tachysphex	gibbus		F	EY34103	2017
Crabronidae	Tachysphex	rufiventralis		M	EY34151	2017
Crabronidae	Tachysphex	rufiventralis		F	EY34153	2017
Crabronidae	Tachysphex	rufiventralis		F	EY34635	2017
Crabronidae	Tachysphex	rufiventralis		M	EY34052	2017
Crabronidae	Tachysphex	rufiventralis		M	EY33999	2017
Crabronidae	Tachysphex	rufiventris		M	EY34051	2017
Crabronidae	Tachysphex	rufiventris		M	EY34202	2017
Crabronidae	Tachysphex	rufiventris		M	EY34101	2017
Crabronidae	Tachysphex	tarsinus		M	EY34204	2017
Crabronidae	Tachysphex	tarsinus		F	EY34154	2017
Crabronidae	Tachysphex	tarsinus		M	EY34054	2017
Crabronidae	Tachytes	procerus		M	EY25447	2017
Crabronidae	Tracheliodes	quinqenotatus		F	EY25392	2017
Crabronidae	Tracheliodes	quinqenotatus		F	EY34038	2017
Crabronidae	Tracheliodes	quinqenotatus		M	EY34040	2017
Crabronidae	Tracheliodes	quinqenotatus		F	EY34039	2017
Crabronidae	Tracheliodes	quinqenotatus		M	EY33986	2017
Crabronidae	Tracheliodes	quinqenotatus		M	EY33987	2017
Crabronidae	Trypoxylon	figulus		F	EY34059	2017
Crabronidae	Trypoxylon	medium		M	EY34007	2017
Crabronidae	Trypoxylon	minus		F	EY34006	2017
Crabronidae	Trypoxylon	minus		F	EY34056	2017
Halictidae	Halictus	brunnescens		M	EY34723	2017
Halictidae	Halictus	fulvipes		F	EY34622	2017
Halictidae	Halictus	langobardicus		F	EY34624	2017
Halictidae	Halictus	scabiosae		M	EY34725	2017
Halictidae	Halictus	scabiosae		F	EY34675	2017
Halictidae	Halictus	scabiosae		M	EY34724	2017
Halictidae	Halictus	scabiosae		F	EY34673	2017

Halictidae	Halictus	scabiosae		F	EY34623	2017
Halictidae	Lasioglossum	albocinctum		M	EY33767	2017
Halictidae	Lasioglossum	albocinctum		F	EY33915	2017
Halictidae	Lasioglossum	albocinctum		F	EY33965	2017
Halictidae	Lasioglossum	albocinctum		F	EY33814	2017
Halictidae	Lasioglossum	bimaculatum		F	EY33920	2017
Halictidae	Lasioglossum	bimaculatum		F	EY33862	2017
Halictidae	Lasioglossum	bimaculatum		F	EY33819	2017
Halictidae	Lasioglossum	interruptum		F	EY33766	2017
Halictidae	Lasioglossum	interruptum		F	EY33962	2017
Halictidae	Lasioglossum	lativentre		F	EY34483	2017
Halictidae	Lasioglossum	leucozonium		M	EY33818	2017
Halictidae	Lasioglossum	leucozonium		F	EY33868	2017
Halictidae	Lasioglossum	limbellum		F	EY33812	2017
Halictidae	Lasioglossum	malachurum		M	EY34525	2017
Halictidae	Lasioglossum	malachurum		F	EY33815	2017
Halictidae	Lasioglossum	malachurum		F	EY33770	2017
Halictidae	Lasioglossum	malachurum		F	EY33970	2017
Halictidae	Lasioglossum	nigripes		F	EY34478	2017
Halictidae	Lasioglossum	nitidulum	hammi	F	EY25445	2017
Halictidae	Lasioglossum	nitidulum	hammi	F	EY34482	2017
Halictidae	Lasioglossum	nitidulum	hammi	F	EY34481	2017
Halictidae	Lasioglossum	pauperatum		M	EY34523	2017
Halictidae	Lasioglossum	pauillum		F	EY34576	2017
Halictidae	Lasioglossum	pauillum		F	EY34480	2017
Halictidae	Lasioglossum	prasinum	haemorrhoidale	M	EY33820	2017
Halictidae	Lasioglossum	prasinum	haemorrhoidale	F	EY33916	2017
Halictidae	Lasioglossum	prasinum	haemorrhoidale	F	EY33919	2017
Halictidae	Lasioglossum	prasinum	haemorrhoidale	F	EY33866	2017
Halictidae	Lasioglossum	punctatissimum		F	EY34678	2017
Halictidae	Lasioglossum	punctatissimum		F	EY33867	2017
Halictidae	Lasioglossum	puncticolle		M	EY34524	2017
Halictidae	Lasioglossum	puncticolle		F	EY33912	2017
Halictidae	Lasioglossum	puncticolle		M	EY33861	2017
Halictidae	Lasioglossum	puncticolle		F	EY33765	2017
Halictidae	Lasioglossum	puncticolle		F	EY33762	2017
Halictidae	Lasioglossum	transitorium	planulum	M	EY34575	2017
Halictidae	Lasioglossum	transitorium	planulum	M	EY34680	2017
Halictidae	Lasioglossum	transitorium	planulum	M	EY34582	2017
Halictidae	Lasioglossum	transitorium	planulum	F	EY34573	2017
Halictidae	Lasioglossum	transitorium	planulum	F	EY34674	2017

Halictidae	Lasioglossum	transitorium	planulum	F	EY34722	2017
Halictidae	Lasioglossum	villosulum		F	EY34672	2017
Halictidae	Lasioglossum	villosulum		M	EY34574	2017
Halictidae	Seladonia	gemmea		F	EY34572	2017
Halictidae	Seladonia	gemmea		F	EY34625	2017
Halictidae	Seladonia	gemmea		F	EY34522	2017
Halictidae	Seladonia	smaragdula		M	EY34679	2017
Halictidae	Seladonia	smaragdula		F	EY34479	2017
Halictidae	Seladonia	smaragdula s.str		F	EY34527	2017
Halictidae	Seladonia	smaragdula s.str		F	EY34533	2017
Halictidae	Seladonia	subaurata	corsa	F	EY34528	2017
Halictidae	Seladonia	subaurata	corsa	F	EY34531	2017
Halictidae	Seladonia	subaurata	corsa	F	EY34632	2017
Halictidae	Seladonia	subaurata	corsa	M	EY34683	2017
Halictidae	Sphecodes	alternatus		F	EY33822	2017
Halictidae	Sphecodes	puncticeps		M	EY33974	2017
Halictidae	Sphecodes	puncticeps		M	EY33874	2017
Halictidae	Sphecodes	puncticeps		M	EY33925	2017
Halictidae	Vestitohalictus	vestitus		M	EY25394	2017
Megachilidae	Anthidiellum	strigatum		F	EY34122	2017
Megachilidae	Anthidiellum	strigatum		M	EY34018	2017
Megachilidae	Anthidiellum	strigatum		M	EY34118	2017
Megachilidae	Anthidiellum	strigatum		F	EY34062	2017
Megachilidae	Anthidiellum	strigatum		M	EY34113	2017
Megachilidae	Anthidiellum	strigatum		M	EY34072	2017
Megachilidae	Coelioxys	afra		M	EY33921	2017
Megachilidae	Coelioxys	afra		F	EY33733	2017
Megachilidae	Heriades	crenulata		M	EY34117	2017
Megachilidae	Heriades	crenulata		F	EY34120	2017
Megachilidae	Heriades	crenulata		F	EY34125	2017
Megachilidae	Heriades	crenulata		M	EY34013	2017
Megachilidae	Heriades	crenulata		M	EY34069	2017
Megachilidae	Heriades	crenulata		F	EY34024	2017
Megachilidae	Heriades	rubicola		F	EY34016	2017
Megachilidae	Heriades	rubicola		M	EY34115	2017
Megachilidae	Heriades	rubicola		F	EY34066	2017
Megachilidae	Hoplitis	annulata	corsaria	M	EY33793	2017
Megachilidae	Hoplitis	annulata	corsaria	M	EY33889	2017
Megachilidae	Hoplitis	annulata	corsaria	M	EY33749	2017
Megachilidae	Hoplitis	bihamata		M	EY33888	2017
Megachilidae	Hoplitis	bisulca		F	EY33787	2017

Megachilidae	Hoplitis	bisulca		F	EY33796	2017
Megachilidae	Hoplitis	bisulca		M	EY33937	2017
Megachilidae	Hoplitis	bisulca		M	EY33886	2017
Megachilidae	Hoplitis	bisulca		M	EY33839	2017
Megachilidae	Hoplitis	crisatula		M	EY33893	2017
Megachilidae	Hoplitis	fasciculata		F	EY33798	2017
Megachilidae	Hoplitis	fasciculata		M	EY33846	2017
Megachilidae	Megachile	albisecta		M	EY33737	2017
Megachilidae	Megachile	albisecta		F	EY33847	2017
Megachilidae	Megachile	albisecta		M	EY33894	2017
Megachilidae	Megachile	albisecta		M	EY33738	2017
Megachilidae	Megachile	argentata	schmiedeknechti	M	EY33789	2017
Megachilidae	Megachile	argentata	schmiedeknechti	M	EY33745	2017
Megachilidae	Megachile	argentata	schmiedeknechti	M	EY33790	2017
Megachilidae	Megachile	centuncularis		M	EY33771	2017
Megachilidae	Megachile	leachella	fassoria	M	EY33844	2017
Megachilidae	Megachile	pusilla		M	EY33938	2017
Megachilidae	Megachile	pusilla		M	EY33799	2017
Megachilidae	Megachile	melanopyga		M	EY33924	2017
Megachilidae	Megachile	melanopyga		M	EY33774	2017
Megachilidae	Megachile	melanopyga		M	EY33935	2017
Megachilidae	Megachile	sicula	corsica	M	EY33899	2017
Megachilidae	Megachile	sicula	corsica	M	EY33848	2017
Megachilidae	Megachile	sicula	corsica	M	EY33948	2017
Megachilidae	Megachile	sicula	corsica	F	EY33748	2017
Megachilidae	Megachile	sicula	corsica	F	EY33895	2017
Megachilidae	Megachile	sicula	corsica	F	EY33885	2017
Megachilidae	Osmia	bicornis		M	EY33797	2017
Megachilidae	Osmia	bicornis		M	EY33743	2017
Megachilidae	Osmia	bicornis		M	EY33843	2017
Megachilidae	Osmia	caerulescens	caerulescens	F	EY33890	2017
Megachilidae	Osmia	caerulescens	caerulescens	F	EY33849	2017
Megachilidae	Osmia	caerulescens	caerulescens	M	EY33791	2017
Megachilidae	Osmia	caerulescens	caerulescens	M	EY33947	2017
Megachilidae	Osmia	caerulescens	caerulescens	F	EY33747	2017
Megachilidae	Osmia	ferruginea	igneopurpurea	M	EY33897	2017
Megachilidae	Osmia	ferruginea	igneopurpurea	F	EY33788	2017
Megachilidae	Osmia	latreillei		M	EY33936	2017
Megachilidae	Osmia	latreillei		M	EY33838	2017
Megachilidae	Osmia	latreillei		M	EY33845	2017
Megachilidae	Osmia	melanogaster		M	EY33898	2017

Megachilidae	Osmia	nasoproducta		F	EY25391	2017
Megachilidae	Osmia	niveata	albiscopa	F	EY33944	2017
Megachilidae	Osmia	niveata	albiscopa	M	EY33836	2017
Megachilidae	Osmia	niveata	albiscopa	M	EY33835	2017
Megachilidae	Osmia	rufohirta		M	EY33739	2017
Megachilidae	Osmia	rufohirta		F	EY25398	2017
Megachilidae	Osmia	rufohirta		F	EY33735	2017
Megachilidae	Osmia	rufohirta		F	EY33891	2017
Megachilidae	Osmia	rufohirta		M	EY33892	2017
Megachilidae	Osmia	rufohirta		M	EY33740	2017
Megachilidae	Osmia	scutellaris		M	EY33842	2017
Megachilidae	Osmia	signata	signata	F	EY33940	2017
Megachilidae	Osmia	submicans	submicans	M	EY33794	2017
Megachilidae	Osmia	submicans	submicans	M	EY33736	2017
Megachilidae	Osmia	submicans	submicans	M	EY33943	2017
Megachilidae	Osmia	tricornis		M	EY33746	2017
Megachilidae	Osmia	tricornis		M	EY33896	2017
Megachilidae	Rhodanthidium	septemdentatum		M	EY34067	2017
Megachilidae	Rhodanthidium	septemdentatum		M	EY34061	2017
Megachilidae	Rhodanthidium	septemdentatum		F	EY34078	2017
Megachilidae	Rhodanthidium	septemdentatum		F	EY34131	2017
Megachilidae	Rhodanthidium	septemdentatum		M	EY34074	2017
Mutillidae	Dasylabris	maura	carinulata	M	EY33887	2017
Mutillidae	Dasylabris	maura	carinulata	F	EY25455	2017
Mutillidae	Dasylabris	maura	carinulata	M	EY33744	2017
Mutillidae	Dasylabris	maura	carinulata	F	EY33945	2017
Mutillidae	Dasylabris	maura	carinulata	F	EY33949	2017
Mutillidae	Ronisia	brutia		F	EY25405	2017
Mutillidae	Ronisia	ghilianii		F	EY33795	2017
Mutillidae	Smicromyrme	ausonia		M	EY33742	2017
Mutillidae	Smicromyrme	perisii		M	EY33941	2017
Mutillidae	Smicromyrme	perisii		M	EY33792	2017
Mutillidae	Smicromyrme	viduata		F	EY25407	2017
Mutillidae	Smicromyrme	viduata		M	EY33841	2017
Mutillidae	Smicromyrme	viduata		F	EY33837	2017
Mutillidae	Smicromyrme	viduata		F	EY33785	2017
Pompilidae	Agenioideus	sericeus		M	EY34026	2017
Pompilidae	Anospilus	orbitalis	luctiger	M	EY34129	2017
Pompilidae	Anospilus	orbitalis	luctiger	F	EY25464	2017
Pompilidae	Anospilus	orbitalis	luctiger	M	EY33981	2017
Pompilidae	Anospilus	orbitalis	luctiger	F	EY34028	2017

Pompilidae	Anospilus	orbitalis	luctiger	F	EY34076	2017
Pompilidae	Anospilus	orbitalis	luctiger	M	EY33976	2017
Pompilidae	Aporinellus	sexmaculatus	sexmaculatus	F	EY25457	2017
Pompilidae	Aporinellus	sexmaculatus	sexmaculatus	F	EY34186	2017
Pompilidae	Aporus	bicolor	fulviventris	F	EY34182	2017
Pompilidae	Aporus	bicolor	fulviventris	F	EY34083	2017
Pompilidae	Aporus	bicolor	fulviventris	F	EY33978	2017
Pompilidae	Arachnospila	holomelas	dissona	M	EY34019	2017
Pompilidae	Auplopus	carbonarius	carbonarius	F	EY25458	2017
Pompilidae	Auplopus	carbonarius	carbonarius	F	EY34084	2017
Pompilidae	Ceropales	albicincta	albicincta	F	EY25453	2017
Pompilidae	Cryptocheilus	egregius		F	EY34114	2017
Pompilidae	Cryptocheilus	octomaculatus		F	EY34012	2017
Pompilidae	Entomobora	crassitarsis	damryi	F	EY34023	2017
Pompilidae	Entomobora	crassitarsis	damryi	F	EY25460	2017
Pompilidae	Entomobora	crassitarsis	damryi	F	EY34017	2017
Pompilidae	Entomobora	plicata		M	EY34063	2017
Pompilidae	Episyron	capiticrassum		F	EY34022	2017
Pompilidae	Episyron	rufipes	sardous	F	EY34025	2017
Pompilidae	Evagetes	siculus		F	EY34015	2017
Pompilidae	Evagetes	siculus		F	EY34116	2017
Pompilidae	Pompilus	cinereus		F	EY33980	2017
Pompilidae	Priocnemis	abdominalis		F	EY34121	2017
Pompilidae	Priocnemis	perraudini		F	EY25452	2017
Pompilidae	Priocnemis	perraudini		F	EY34014	2017
Scoliidae	Colpa	quinquecincta		F	EY25465	2017
Scoliidae	Colpa	quinquecincta		M	EY33757	2017
Scoliidae	Colpa	quinquecincta		M	EY33952	2017
Scoliidae	Colpa	quinquecincta		M	EY33909	2017
Scoliidae	Colpa	quinquecincta		F	EY33854	2017
Scoliidae	Colpa	quinquecincta		F	EY33752	2017
Scoliidae	Colpa	sexmaculata		F	EY33907	2017
Scoliidae	Scolia	hirta	unifasciata	F	EY25461	2017
Scoliidae	Scolia	hirta	unifasciata	M	EY33859	2017
Scoliidae	Scolia	hirta	unifasciata	F	EY33910	2017
Scoliidae	Scolia	hirta	unifasciata	M	EY33810	2017
Scoliidae	Scolia	hirta	unifasciata	F	EY33760	2017
Scoliidae	Scolia	hirta	unifasciata	M	EY33960	2017
Scoliidae	Scolia	maculata	flavifrons	F	EY33860	2017
Scoliidae	Scolia	maculata	flavifrons	F	EY33959	2017
Scoliidae	Scolia	maculata	flavifrons	F	EY33809	2017

Scoliidae	Scolia	sexmaculata		M	EY33969	2017
Scoliidae	Scolia	sexmaculata		M	EY33917	2017
Scoliidae	Scolia	sexmaculata		F	EY33768	2017
Scoliidae	Scolia	sexmaculata		M	EY33761	2017
Scoliidae	Scolia	sexmaculata		F	EY33918	2017
Sphecidae	Ammophila	heydeni f1		F	EY33982	2017
Sphecidae	Ammophila	heydeni f1		F	EY34035	2017
Sphecidae	Ammophila	heydeni f1		M	EY34033	2017
Sphecidae	Ammophila	heydeni f1		M	EY34034	2017
Sphecidae	Ammophila	heydeni f1		F	EY34145	2017
Sphecidae	Ammophila	heydeni f2 rubriventris		M	EY34042	2017
Sphecidae	Ammophila	heydeni f2 rubriventris		M	EY34143	2017
Sphecidae	Ammophila	heydeni f2 rubriventris		M	EY33992	2017
Sphecidae	Isodontia	mexicana		M	EY33993	2017
Sphecidae	Isodontia	mexicana		F	EY34196	2017
Sphecidae	Isodontia	mexicana		F	EY34194	2017
Sphecidae	Isodontia	mexicana		M	EY34146	2017
Sphecidae	Isodontia	mexicana		F	EY34043	2017
Sphecidae	Isodontia	mexicana		M	EY34094	2017
Sphecidae	Palmodes	occitanicus		M	EY33996	2017
Sphecidae	Palmodes	occitanicus		F	EY25413	2017
Sphecidae	Podalonia	hirsuta	mervensis	F	EY34093	2017
Sphecidae	Podalonia	hirsuta	mervensis	F	EY33995	2017
Sphecidae	Podalonia	hirsuta	mervensis	F	EY34142	2017
Sphecidae	Podalonia	hirsuta	mervensis	M	EY34046	2017
Sphecidae	Podalonia	hirsuta	mervensis	M	EY34192	2017
Sphecidae	Podalonia	hirsuta	mervensis	M	EY33994	2017
Sphecidae	Prionyx	kirbii		F	EY34092	2017
Sphecidae	Prionyx	kirbii		M	EY34096	2017
Sphecidae	Prionyx	kirbii		M	EY34045	2017
Sphecidae	Prionyx	kirbii		M	EY34195	2017
Sphecidae	Prionyx	lividocinctus		F	EY34147	2017
Sphecidae	Prionyx	subfuscatus		F	EY34095	2017
Sphecidae	Prionyx	subfuscatus		F	EY34097	2017
Sphecidae	Sceliphron	caementarium		F	EY34123	2017
Sphecidae	Sceliphron	caementarium		F	EY34068	2017
Sphecidae	Sceliphron	caementarium		M	EY34112	2017
Sphecidae	Sceliphron	caementarium		M	EY34111	2017
Sphecidae	Sceliphron	caementarium		F	EY34073	2017
Sphecidae	Sceliphron	caementarium		M	EY34124	2017
Sphecidae	Sphex	aff. funerarius		F	EY25414	2017

Sphecidae	Sphex	aff. funerarius		M	EY34144	2017
Sphecidae	Sphex	aff. funerarius		M	EY34050	2017
Sphecidae	Sphex	aff. funerarius		F	EY34100	2017
Tiphiidae	Meria	dorsalis		F	EY33939	2017
Tiphiidae	Meria	dorsalis		F	EY25409	2017
Tiphiidae	Meria	tripunctata		F	EY33942	2017
Tiphiidae	Meria	tripunctata		F	EY33741	2017
Tiphiidae	Meria	tripunctata/dorsalis		M	EY33786	2017
Tiphiidae	Meria	tripunctata/dorsalis		M	EY33946	2017
Tiphiidae	Meria	tripunctata/dorsalis		M	EY33840	2017
Tiphiidae	Tiphia	nsp		M	EY33950	2017
Tiphiidae	Tiphia	nsp		M	EY33900	2017
Tiphiidae	Tiphia	nsp		F	EY33850	2017
Vespidae	Allodynerus	delphinalis		M	EY33963	2017
Vespidae	Ancistrocerus	biphaleratus	triphaleratus	F	EY33759	2017
Vespidae	Ancistrocerus	biphaleratus	triphaleratus	M	EY33769	2017
Vespidae	Ancistrocerus	longispinosus	gazelloides	F	EY33811	2017
Vespidae	Ancistrocerus	longispinosus	gazelloides	F	EY33869	2017
Vespidae	Ancistrocerus	longispinosus	gazelloides	M	EY33865	2017
Vespidae	Ancistrocerus	longispinosus	gazelloides	F	EY25459	2017
Vespidae	Ancistrocerus	longispinosus	gazelloides	M	EY33961	2017
Vespidae	Ancistrocerus	longispinosus	gazelloides	M	EY33763	2017
Vespidae	Ancistrocerus	renimaculata		M	EY33964	2017
Vespidae	Eumenes	coarctatus	coarctatus	M	EY33913	2017
Vespidae	Eumenes	coarctatus	coarctatus	F	EY33914	2017
Vespidae	Eumenes	coarctatus	coarctatus	F	EY25412	2017
Vespidae	Eumenes	coarctatus	coarctatus	M	EY33813	2017
Vespidae	Eumenes	coarctatus	coarctatus	M	EY33870	2017
Vespidae	Eumenes	coarctatus	coarctatus	F	EY33966	2017
Vespidae	Eumenes	dubius	dubius	F	EY33911	2017
Vespidae	Eumenes	dubius	dubius	F	EY33764	2017
Vespidae	Eumenes	mediterraneus		M	EY33816	2017
Vespidae	Eumenes	mediterraneus		M	EY33863	2017
Vespidae	Eumenes	sardous		M	EY33817	2017
Vespidae	Odynerus	reniformis		F	EY33968	2017
Vespidae	Polistes	dominula		F	EY33755	2017
Vespidae	Polistes	dominula		F	EY33802	2017
Vespidae	Polistes	dominula		M	EY33903	2017
Vespidae	Polistes	dominula		F	EY33957	2017
Vespidae	Polistes	dominula		M	EY33803	2017
Vespidae	Polistes	dominula		M	EY33808	2017

Vespidae	Polistes	gallicus		F	EY33853	2017
Vespidae	Polistes	gallicus		F	EY33955	2017
Vespidae	Polistes	gallicus		F	EY33855	2017
Vespidae	Polistes	nimpha		F	EY33858	2017
Vespidae	Stenodynerus	fastidiosissimus	laborans	F	EY33967	2017
Vespidae	Vespula	germanica		F	EY33864	2017
Andrenidae	Andrena	aff. wilkella		F	EY13266	Ferton
Andrenidae	Andrena	aff. wilkella		F	EY16931	Ferton
Andrenidae	Andrena	aff. wilkella		M	EY27185	Ferton
Andrenidae	Andrena	aff. wilkella		F	EY28057	Ferton
Andrenidae	Andrena	agilissima		F	EY11643	Ferton
Andrenidae	Andrena	agilissima		F	EY11710	Ferton
Andrenidae	Andrena	agilissima		M	EY13388	Ferton
Andrenidae	Andrena	agilissima		F	EY13690	Ferton
Andrenidae	Andrena	agilissima		M	EY13785	Ferton
Andrenidae	Andrena	agilissima		M	EY14190	Ferton
Andrenidae	Andrena	didonia		F	EY29046	Ferton
Andrenidae	Andrena	didonia		F	EY29047	Ferton
Andrenidae	Andrena	didonia		F	EY29601	Ferton
Andrenidae	Andrena	impunctata		F	EY13091	Ferton
Andrenidae	Andrena	mucida		M	EY13539	Ferton
Andrenidae	Andrena	mucida		F	EY13651	Ferton
Andrenidae	Andrena	mucida		M	EY14348	Ferton
Andrenidae	Andrena	mucida		F	EY14651	Ferton
Andrenidae	Andrena	mucida		F	EY16306	Ferton
Andrenidae	Andrena	mucida		M	EY17120	Ferton
Andrenidae	Andrena	nana		F	EY14262	Ferton
Andrenidae	Andrena	nana		M	EY16809	Ferton
Andrenidae	Andrena	nana		F	EY16845	Ferton
Andrenidae	Andrena	nana		F	EY16851	Ferton
Andrenidae	Andrena	puella		F	EY13451	Ferton
Andrenidae	Andrena	savignyi		M	EY12844	Ferton
Andrenidae	Andrena	savignyi		F	EY15064	Ferton
Andrenidae	Andrena	savignyi		F	EY15065	Ferton
Andrenidae	Andrena	savignyi		M	EY16509	Ferton
Andrenidae	Andrena	savignyi		M	EY16510	Ferton
Apidae	Amegilla	albigena		M	EY24897	Ferton
Apidae	Amegilla	garrula		F	EY24887	Ferton
Apidae	Amegilla	garrula		F	EY24888	Ferton
Apidae	Amegilla	magnilabris		F	EY24892	Ferton
Apidae	Amegilla	magnilabris		F	EY24893	Ferton

Apidae	Amegilla	magnilabris		F	EY24894	Ferton
Apidae	Amegilla	quadrifasciata		M	EY24909	Ferton
Apidae	Amegilla	quadrifasciata		F	EY24916	Ferton
Apidae	Amegilla	quadrifasciata		F	EY24921	Ferton
Apidae	Amegilla	quadrifasciata		F	EY24925	Ferton
Apidae	Anthophora	bimaculata		F	EY25068	Ferton
Apidae	Anthophora	bimaculata		M	EY25069	Ferton
Apidae	Anthophora	bimaculata		M	EY25070	Ferton
Apidae	Anthophora	salviae		M	EY25132	Ferton
Apidae	Anthophora	salviae		M	EY25134	Ferton
Apidae	Anthophora	salviae		M	EY25151	Ferton
Apidae	Anthophora	salviae		F	EY25158	Ferton
Apidae	Anthophora	salviae		F	EY25159	Ferton
Apidae	Anthophora	salviae		F	EY25167	Ferton
Apidae	Bombus	terrestris			EY22716	Ferton
Apidae	Bombus	terrestris			EY22720	Ferton
Apidae	Bombus	terrestris			EY22721	Ferton
Apidae	Bombus	vestalis	perezi		EY22661	Ferton
Apidae	Ceratina	callosa		M	EY27411	Ferton
Apidae	Ceratina	callosa		M	EY28935	Ferton
Apidae	Ceratina	chalcites		F	EY15707	Ferton
Apidae	Ceratina	dallator		F	EY13205	Ferton
Apidae	Eucera	chrysopyga		F	EY12547	Ferton
Apidae	Eucera	chrysopyga		M	EY14686	Ferton
Apidae	Eucera	chrysopyga		M	EY26578	Ferton
Apidae	Eucera	chrysopyga		F	EY26703	Ferton
Apidae	Eucera	chrysopyga		F	EY27383	Ferton
Apidae	Eucera	chrysopyga		F	EY27384	Ferton
Apidae	Nomada	basalis		M	EY27666	Ferton
Apidae	Nomada	insignipes		F	EY15559	Ferton
Apidae	Tetraloniella	sp		F	EY26454	Ferton
Astatidae	Astata	gallica		M	EY14098	Ferton
Astatidae	Astata	gallica		M	EY14099	Ferton
Astatidae	Astata	gallica		F	EY16502	Ferton
Astatidae	Astata	gallica		M	EY17161	Ferton
Astatidae	Astata	gallica		F	EY29544	Ferton
Astatidae	Astata	gallica		F	EY29548	Ferton
Astatidae	Astata	kashmirensis		M	EY27816	Ferton
Astatidae	Astata	kashmirensis		F	EY29562	Ferton
Astatidae	Astata	minor		M	EY14232	Ferton
Astatidae	Astata	minor		M	EY16906	Ferton

Astatidae	Astata	minor		F	EY17054	Ferton
Astatidae	Astata	minor		M	EY17065	Ferton
Bembicidae	Bembecinus	hungaricus		F	EY29528	Ferton
Bembicidae	Bembecinus	insulanus		F	EY29523	Ferton
Bembicidae	Bembecinus	insulanus		M	EY29525	Ferton
Bembicidae	Bembecinus	insulanus		F	EY29527	Ferton
Bembicidae	Bembix	rostrata		M	EY26997	Ferton
Bembicidae	Bembix	rostrata		M	EY29496	Ferton
Bembicidae	Bembix	rostrata		F	EY29497	Ferton
Bembicidae	Bembix	rostrata		F	EY29498	Ferton
Bembicidae	Bembix	rostrata		M	EY29500	Ferton
Bembicidae	Bembix	rostrata		F	EY29507	Ferton
Bembicidae	Gorytes	quinquecinctus		M	EY16130	Ferton
Bembicidae	Gorytes	quinquecinctus		F	EY29937	Ferton
Bembicidae	Gorytes	quinquecinctus		F	EY29938	Ferton
Bembicidae	Gorytes	quinquecinctus		F	EY29940	Ferton
Bembicidae	Gorytes	quinquecinctus		M	EY29942	Ferton
Bembicidae	Gorytes	sulcifrons		M	EY11770	Ferton
Bembicidae	Gorytes	sulcifrons		M	EY12401	Ferton
Bembicidae	Gorytes	sulcifrons		F	EY16661	Ferton
Bembicidae	Gorytes	sulcifrons		F	EY17057	Ferton
Bembicidae	Gorytes	sulcifrons		M	EY17112	Ferton
Bembicidae	Gorytes	sulcifrons		F	EY17160	Ferton
Bembicidae	Harpactus	fertoni		M	EY29905	Ferton
Bembicidae	Harpactus	fertoni		F	EY29907	Ferton
Bembicidae	Nysson	nsp		F	EY16897	Ferton
Bembicidae	Nysson	nsp		F	EY16900	Ferton
Bembicidae	Nysson	nsp		F	EY29962	Ferton
Bembicidae	Nysson	nsp		M	EY29967	Ferton
Chrysididae	Chrysis	cf. corusca		F	EY32272	Ferton
Chrysididae	Chrysis	cf. insperata		F	EY32284	Ferton
Chrysididae	Chrysis	germari	calviensis	M	EY27442	Ferton
Chrysididae	Chrysis	germari	calviensis	F	EY29792	Ferton
Chrysididae	Chrysis	germari	calviensis	M	EY31491	Ferton
Chrysididae	Chrysis	grohmanni	subaequalis	F	EY29787	Ferton
Chrysididae	Chrysis	maderi		F	EY15090	Ferton
Chrysididae	Chrysis	maderi		F	EY27025	Ferton
Chrysididae	Chrysis	maderi		F	EY29833	Ferton
Chrysididae	Chrysis	pulcherrima		M	EY32278	Ferton
Chrysididae	Chrysis	ragusae		M	EY28534	Ferton
Chrysididae	Chrysis	rutilans		F	EY32281	Ferton

Chrysididae	Chrysis	rutilans		F	EY32283	Ferton
Chrysididae	Chrysis	subsnuata	laevifallax	M	EY17056	Ferton
Chrysididae	Chrysis	subsnuata	laevifallax	F	EY29837	Ferton
Chrysididae	Chrysis	terminata		F	EY15804	Ferton
Chrysididae	Elampus	spina		F	EY15300	Ferton
Chrysididae	Elampus	spina		M	EY29830	Ferton
Chrysididae	Elampus	spina		M	EY29831	Ferton
Chrysididae	Hedychridium	jucundum		F	EY31468	Ferton
Chrysididae	Hedychridium	roseum		M	EY15840	Ferton
Chrysididae	Hedychridium	sculpturatum		M	EY15581	Ferton
Chrysididae	Hedychridium	wolffi		F	EY27879	Ferton
Chrysididae	Hedychrum	longicolle		F	EY29829	Ferton
Chrysididae	Hedychrum	longicolle		F	EY32310	Ferton
Chrysididae	Hedychrum	nobile		F	EY32319	Ferton
Chrysididae	Holopyga	cf. generosa		M	EY15729	Ferton
Chrysididae	Holopyga	chrysonota	sensu Linsmeyer	M	EY15731	Ferton
Chrysididae	Holopyga	chrysonota	sensu Linsmeyer	M	EY29810	Ferton
Chrysididae	Holopyga	ignicolis	sensu Linsmeyer	M	EY27521	Ferton
Chrysididae	Holopyga	jurinei	sensu Linsmeyer	M	EY17039	Ferton
Chrysididae	Holopyga	jurinei	sensu Linsmeyer	F	EY18845	Ferton
Chrysididae	Holopyga	jurinei	sensu Linsmeyer	M	EY27542	Ferton
Chrysididae	Pseudomalus	cf. auratus		F	EY32300	Ferton
Chrysididae	Pseudomalus	cf. triangulifer		M	EY15204	Ferton
Chrysididae	Stilbum	calens		F	EY32301	Ferton
Colletidae	Hylaeus	soror		F	EY12754	Ferton
Colletidae	Hylaeus	soror		F	EY12791	Ferton
Colletidae	Hylaeus	soror		F	EY12792	Ferton
Colletidae	Hylaeus	subhyalinatus		F	EY13745	Ferton
Colletidae	Hylaeus	subhyalinatus		F	EY15254	Ferton
Crabronidae	Crossocerus	aff. elongatulus		F	EY29142	Ferton
Crabronidae	Crossocerus	quadrimaculatus		F	EY29241	Ferton
Crabronidae	Crossocerus	quadrimaculatus		F	EY29242	Ferton
Crabronidae	Crossocerus	quadrimaculatus		M	EY29243	Ferton
Crabronidae	Crossocerus	quadrimaculatus		F	EY29362	Ferton
Crabronidae	Crossocerus	varus		F	EY29238	Ferton
Crabronidae	Diodontus	tristis		F	EY16113	Ferton
Crabronidae	Diodontus	tristis		F	EY16115	Ferton
Crabronidae	Ectemnius	continuus		F	EY29144	Ferton
Crabronidae	Ectemnius	continuus		F	EY29193	Ferton
Crabronidae	Ectemnius	continuus		M	EY29377	Ferton
Crabronidae	Ectemnius	hypsoae		F	EY29357	Ferton

Crabronidae	Ectemnius	hypsaе		F	EY29358	Ferton
Crabronidae	Ectemnius	hypsaе		M	EY29369	Ferton
Crabronidae	Ectemnius	hypsaе		F	EY29370	Ferton
Crabronidae	Ectemnius	hypsaе		M	EY29374	Ferton
Crabronidae	Entomognathus	aff. brevis		M	EY12076	Ferton
Crabronidae	Entomognathus	aff. brevis		M	EY15516	Ferton
Crabronidae	Larra	anathema		F	EY24408	Ferton
Crabronidae	Larra	anathema		M	EY27223	Ferton
Crabronidae	Larra	anathema		M	EY27525	Ferton
Crabronidae	Larra	anathema		F	EY29485	Ferton
Crabronidae	Larra	anathema		F	EY29486	Ferton
Crabronidae	Lindenius	pygmaeus	armatus	F	EY29413	Ferton
Crabronidae	Mimumesa	unicolor		F	EY28001	Ferton
Crabronidae	Miscophus	bonifaciensis		M	EY12010	Ferton
Crabronidae	Miscophus	bonifaciensis		F	EY12852	Ferton
Crabronidae	Miscophus	bonifaciensis		M	EY14261	Ferton
Crabronidae	Miscophus	bonifaciensis		F	EY14329	Ferton
Crabronidae	Miscophus	bonifaciensis		F	EY14702	Ferton
Crabronidae	Miscophus	bonifaciensis		M	EY16481	Ferton
Crabronidae	Oxybelus	lamellatus	andalusialus	F	EY29786	Ferton
Crabronidae	Oxybelus	quatuordecimnotatus		F	EY29160	Ferton
Crabronidae	Oxybelus	quatuordecimnotatus		M	EY29185	Ferton
Crabronidae	Oxybelus	quatuordecimnotatus		F	EY29333	Ferton
Crabronidae	Oxybelus	quatuordecimnotatus		M	EY29403	Ferton
Crabronidae	Oxybelus	quatuordecimnotatus		M	EY29414	Ferton
Crabronidae	Oxybelus	quatuordecimnotatus		F	EY29773	Ferton
Crabronidae	Oxybelus	uniglumis		F	EY29745	Ferton
Crabronidae	Solierella	seabrai	corsa	F	EY12484	Ferton
Crabronidae	Solierella	seabrai	corsa	F	EY15629	Ferton
Crabronidae	Solierella	seabrai	corsa	M	EY17008	Ferton
Crabronidae	Solierella	seabrai	corsa	F	EY27994	Ferton
Crabronidae	Solierella	seabrai	corsa	M	EY28713	Ferton
Crabronidae	Tachysphex	aff. nitidior		M	EY11906	Ferton
Crabronidae	Tachysphex	aff. nitidior		M	EY12149	Ferton
Crabronidae	Tachysphex	aff. nitidior		M	EY17151	Ferton
Crabronidae	Tachysphex	aff. nitidior		F	EY27519	Ferton
Crabronidae	Tachysphex	aff. nitidior		F	EY29434	Ferton
Crabronidae	Tachysphex	aff. nitidior		F	EY29455	Ferton
Crabronidae	Tachysphex	cf. dimidiatus		M	EY27549	Ferton
Crabronidae	Tachysphex	cf. dimidiatus		F	EY27774	Ferton
Crabronidae	Tachysphex	consocius		F	EY16982	Ferton

Crabronidae	Tachysphex	consocius		F	EY18837	Ferton
Crabronidae	Tachysphex	consocius		M	EY18848	Ferton
Crabronidae	Tachysphex	fulvitaris		M	EY11991	Ferton
Crabronidae	Tachysphex	fulvitaris		M	EY12168	Ferton
Crabronidae	Tachysphex	fulvitaris		M	EY23821	Ferton
Crabronidae	Tachysphex	mediterraneus		M	EY23794	Ferton
Crabronidae	Tachysphex	mediterraneus		F	EY29437	Ferton
Crabronidae	Tachysphex	mediterraneus		F	EY29440	Ferton
Crabronidae	Tachysphex	mediterraneus		M	EY29442	Ferton
Crabronidae	Tachysphex	mediterraneus		F	EY29443	Ferton
Crabronidae	Tachytes	freygessneri		M	EY27754	Ferton
Crabronidae	Tachytes	freygessneri		M	EY29466	Ferton
Crabronidae	Tachytes	obsoletus	occidentalis	M	EY15338	Ferton
Crabronidae	Tachytes	obsoletus	occidentalis	F	EY15756	Ferton
Crabronidae	Tachytes	obsoletus	occidentalis	M	EY15769	Ferton
Crabronidae	Tachytes	obsoletus	occidentalis	M	EY15775	Ferton
Crabronidae	Trypoxylon	nsp		F	EY15059	Ferton
Halictidae	Dufourea	halictula		F	EY31377	Ferton
Halictidae	Lasioglossum	albipes		F	EY30731	Ferton
Halictidae	Lasioglossum	callizonium		F	EY30877	Ferton
Halictidae	Lasioglossum	clypeare		F	EY27887	Ferton
Halictidae	Lasioglossum	corsicanum		F	EY24359	Ferton
Halictidae	Lasioglossum	discum	discum	M	EY24287	Ferton
Halictidae	Lasioglossum	laevigatum		M	EY30419	Ferton
Halictidae	Lasioglossum	mesosclurum		F	EY16089	Ferton
Halictidae	Lasioglossum	mesosclurum		F	EY16099	Ferton
Halictidae	Lasioglossum	nitidiusculum		F	EY28583	Ferton
Halictidae	Lasioglossum	politum		M	EY29643	Ferton
Halictidae	Lasioglossum	politum		F	EY30433	Ferton
Halictidae	Lasioglossum	quadrisignatum		F	EY30819	Ferton
Halictidae	Lasioglossum	subhirtum		F	EY12446	Ferton
Halictidae	Lasioglossum	tarsatum		F	EY16292	Ferton
Halictidae	Lasioglossum	tarsatum		F	EY16293	Ferton
Halictidae	Lasioglossum	tarsatum		F	EY16297	Ferton
Halictidae	Lasioglossum	tarsatum		F	EY26586	Ferton
Halictidae	Lasioglossum	tarsatum		F	EY28511	Ferton
Halictidae	Nomiapis	bispinosa	albocincta	F	EY14544	Ferton
Halictidae	Nomioides	minutissimum		M	EY15993	Ferton
Halictidae	Nomioides	minutissimum		F	EY16610	Ferton
Halictidae	Nomioides	minutissimum		F	EY16612	Ferton
Halictidae	Nomioides	minutissimum		M	EY16676	Ferton

Halictidae	Nomioides	minutissimum		F	EY26779	Ferton
Halictidae	Nomioides	minutissimum		M	EY26782	Ferton
Halictidae	Rophites	quinquespinosa		M	EY31383	Ferton
Halictidae	Rophites	quinquespinosa		F	EY31384	Ferton
Halictidae	Seladonia	confusa	perkinsi	M	EY30407	Ferton
Halictidae	Seladonia	seladonia		M	EY16015	Ferton
Halictidae	Seladonia	seladonia		F	EY16020	Ferton
Halictidae	Seladonia	seladonia		M	EY16021	Ferton
Halictidae	Sphecodes	albilabris		M	EY18924	Ferton
Halictidae	Sphecodes	albilabris		F	EY28114	Ferton
Halictidae	Sphecodes	grp marginatus		F	EY11720	Ferton
Halictidae	Sphecodes	grp marginatus		F	EY13779	Ferton
Halictidae	Sphecodes	grp marginatus		F	EY14653	Ferton
Halictidae	Sphecodes	marginatus		F	EY12354	Ferton
Halictidae	Sphecodes	monilicornis		F	EY26740	Ferton
Halictidae	Vestitohalictus	pollinosus	cyrnosardicus	F	EY26609	Ferton
Halictidae	Vestitohalictus	pollinosus	cyrnosardicus	M	EY26620	Ferton
Halictidae	Vestitohalictus	pollinosus	cyrnosardicus	F	EY26637	Ferton
Halictidae	Vestitohalictus	pollinosus	cyrnosardicus	F	EY26647	Ferton
Megachilidae	Coelioxys	acanthura		M	EY14514	Ferton
Megachilidae	Coelioxys	acanthura		F	EY31357	Ferton
Megachilidae	Coelioxys	haemorrhoea		F	EY25632	Ferton
Megachilidae	Coelioxys	haemorrhoea		F	EY31409	Ferton
Megachilidae	Dioxys	cinctus		M	EY27224	Ferton
Megachilidae	Dioxys	cinctus		M	EY28696	Ferton
Megachilidae	Hoplitis	acuticornis		F	EY31386	Ferton
Megachilidae	Hoplitis	aff. adunca		F	EY16618	Ferton
Megachilidae	Hoplitis	aff. adunca		F	EY16632	Ferton
Megachilidae	Hoplitis	aff. adunca		M	EY26410	Ferton
Megachilidae	Hoplitis	aff. adunca		M	EY26471	Ferton
Megachilidae	Hoplitis	aff. adunca		M	EY26486	Ferton
Megachilidae	Hoplitis	aff. adunca		F	EY29103	Ferton
Megachilidae	Hoplitis	leucomelana		F	EY13893	Ferton
Megachilidae	Hoplitis	leucomelana		F	EY15585	Ferton
Megachilidae	Hoplitis	leucomelana		M	EY15616	Ferton
Megachilidae	Hoplitis	perezi		F	EY16979	Ferton
Megachilidae	Hoplitis	perezi		F	EY27378	Ferton
Megachilidae	Hoplitis	perezi		M	EY27381	Ferton
Megachilidae	Hoplitis	perezi		M	EY27382	Ferton
Megachilidae	Hoplitis	perezi		M	EY27436	Ferton
Megachilidae	Hoplitis	perezi		F	EY28295	Ferton

Megachilidae	Megachile	apicalis		F	EY18833	Ferton
Megachilidae	Megachile	apicalis		M	EY27034	Ferton
Megachilidae	Megachile	apicalis		F	EY27771	Ferton
Megachilidae	Megachile	apicalis		M	EY28119	Ferton
Megachilidae	Megachile	apicalis		M	EY28129	Ferton
Megachilidae	Megachile	apicalis		F	EY28873	Ferton
Megachilidae	Osmia	erythrogastra		M	EY23926	Ferton
Megachilidae	Osmia	erythrogastra		F	EY23928	Ferton
Megachilidae	Osmia	erythrogastra		M	EY23932	Ferton
Megachilidae	Osmia	erythrogastra		F	EY23933	Ferton
Megachilidae	Osmia	erythrogastra		F	EY23935	Ferton
Megachilidae	Pseudoanthidium	leucostoma		F	EY24151	Ferton
Megachilidae	Pseudoanthidium	leucostoma		M	EY24155	Ferton
Megachilidae	Pseudoanthidium	leucostoma		F	EY30898	Ferton
Megachilidae	Stelis	nasuta		M	EY26356	Ferton
Megachilidae	Stelis	nasuta		F	EY33485	Ferton
Melittidae	Melitta	nigricans		M	EY12280	Ferton
Melittidae	Melitta	nigricans		M	EY12858	Ferton
Melittidae	Melitta	nigricans		M	EY12859	Ferton
Mutillidae	Artiotilla	biguttata		F	EY27395	Ferton
Mutillidae	Artiotilla	biguttata		M	EY27560	Ferton
Mutillidae	Blakeius	chiesii		F	EY14026	Ferton
Mutillidae	Blakeius	chiesii		F	EY27627	Ferton
Mutillidae	Blakeius	chiesii		F	EY31721	Ferton
Mutillidae	Cystomutilla	ruficeps		M	EY29134	Ferton
Mutillidae	Cystomutilla	ruficeps		F	EY32226	Ferton
Mutillidae	Cystomutilla	ruficeps		F	EY32227	Ferton
Mutillidae	Mutilla	quinquemaculata		F	EY31554	Ferton
Mutillidae	Mutilla	quinquemaculata		F	EY31558	Ferton
Mutillidae	Mutilla	quinquemaculata		F	EY32241	Ferton
Mutillidae	Mutilla	viduata		F	EY31595	Ferton
Mutillidae	Mutilla	viduata		M	EY31599	Ferton
Mutillidae	Mutilla	viduata		M	EY31602	Ferton
Mutillidae	Mutilla	viduata		M	EY31604	Ferton
Mutillidae	Mutilla	viduata		F	EY32234	Ferton
Mutillidae	Mutilla	viduata		F	EY32236	Ferton
Mutillidae	Myrmilla	capitata		F	EY31700	Ferton
Mutillidae	Myrmilla	capitata		F	EY31705	Ferton
Mutillidae	Myrmilla	capitata		M	EY31710	Ferton
Mutillidae	Myrmilla	capitata		M	EY31711	Ferton
Mutillidae	Myrmilla	capitata		M	EY32229	Ferton

Mutillidae	Myrmilla	capitata		F	EY32230	Ferton
Mutillidae	Myrmilla	erythrocephala		M	EY12913	Ferton
Mutillidae	Myrmilla	erythrocephala		F	EY14730	Ferton
Mutillidae	Myrmilla	erythrocephala		F	EY15295	Ferton
Mutillidae	Myrmilla	erythrocephala		F	EY15701	Ferton
Mutillidae	Myrmilla	erythrocephala		M	EY31713	Ferton
Mutillidae	Myrmilla	erythrocephala		M	EY31714	Ferton
Mutillidae	Smicromyrme	punctata		F	EY31622	Ferton
Mutillidae	Smicromyrme	punctata		F	EY31623	Ferton
Mutillidae	Smicromyrme	ruficollis	ceresae	F	EY31564	Ferton
Mutillidae	Smicromyrme	ruficollis	ceresae	F	EY31565	Ferton
Mutillidae	Smicromyrme	ruficollis	ceresae	F	EY31566	Ferton
Mutillidae	Smicromyrme	ruficollis	ceresae	M	EY31576	Ferton
Mutillidae	Smicromyrme	ruficollis	ceresae	M	EY31579	Ferton
Mutillidae	Smicromyrme	ruficollis	ceresae	M	EY31580	Ferton
Mutillidae	Smicromyrme	sericeiceps		F	EY15243	Ferton
Mutillidae	Smicromyrme	sicana		F	EY14208	Ferton
Mutillidae	Smicromyrme (Ast)	pusilla		F	EY31574	Ferton
Mutillidae	Smicromyrme (Ast)	sp3		F	EY31620	Ferton
Mutillidae	Smicromyrme (Ast)	sp3		F	EY31621	Ferton
Mutillidae	Smicromyrme (Ph)	sp1		F	EY11739	Ferton
Mutillidae	Smicromyrme (Ph)	sp1		F	EY15266	Ferton
Mutillidae	Smicromyrme (Ph)	sp2		F	EY31615	Ferton
Mutillidae	Smicromyrme (Ph)	subcornata		F	EY31572	Ferton
Mutillidae	Smicromyrme (Ph)	subcornata		F	EY32270	Ferton
Mutillidae	Stenomutilla	argentata	cirnea	F	EY31508	Ferton
Mutillidae	Stenomutilla	argentata	cirnea	F	EY31511	Ferton
Mutillidae	Stenomutilla	argentata	cirnea	F	EY31517	Ferton
Mutillidae	Stenomutilla	argentata	cirnea	M	EY31522	Ferton
Mutillidae	Stenomutilla	argentata	cirnea	M	EY31525	Ferton
Mutillidae	Stenomutilla	argentata	cirnea	M	EY31527	Ferton
Philanthidae	Cerceris	arenaria		F	EY29647	Ferton
Philanthidae	Cerceris	arenaria		F	EY29648	Ferton
Philanthidae	Philanthus	venustus		M	EY27588	Ferton
Philanthidae	Philanthus	venustus		M	EY29405	Ferton
Pompilidae	Agenioideus	ciliatus		F	EY23374	Ferton
Pompilidae	Agenioideus	ciliatus		F	EY23375	Ferton
Pompilidae	Agenioideus	ciliatus		F	EY24538	Ferton
Pompilidae	Agenioideus	ruficeps	nigriculus	F	EY24543	Ferton
Pompilidae	Agenioideus	ruficeps	nigriculus	F	EY24544	Ferton
Pompilidae	Agenioideus	ruficeps	nigriculus	F	EY24547	Ferton

Pompilidae	Anoplius	infuscatus	simii	M	EY22853	Ferton
Pompilidae	Anoplius	infuscatus	simii	M	EY22857	Ferton
Pompilidae	Anoplius	samariensis		F	EY24382	Ferton
Pompilidae	Arachnospila	tyrrhena		F	EY23379	Ferton
Pompilidae	Arachnospila	tyrrhena		F	EY23380	Ferton
Pompilidae	Arachnospila	tyrrhena		F	EY23384	Ferton
Pompilidae	Arachnospila	tyrrhena		M	EY23388	Ferton
Pompilidae	Arachnospila	tyrrhena		M	EY23389	Ferton
Pompilidae	Arachnospila	tyrrhena		M	EY23392	Ferton
Pompilidae	Batozonellus	lacerticida		M	EY23484	Ferton
Pompilidae	Batozonellus	lacerticida		M	EY23488	Ferton
Pompilidae	Batozonellus	lacerticida		F	EY23490	Ferton
Pompilidae	Batozonellus	lacerticida		M	EY23493	Ferton
Pompilidae	Batozonellus	lacerticida		F	EY23496	Ferton
Pompilidae	Ceropales	maculata		M	EY15958	Ferton
Pompilidae	Ceropales	maculata		M	EY23500	Ferton
Pompilidae	Ceropales	maculata		M	EY23502	Ferton
Pompilidae	Ceropales	maculata		F	EY23504	Ferton
Pompilidae	Ceropales	maculata		F	EY23507	Ferton
Pompilidae	Ceropales	maculata		M	EY27562	Ferton
Pompilidae	Cryptocheilus	variabilis	nigripes	M	EY23541	Ferton
Pompilidae	Cryptocheilus	variabilis	nigripes	F	EY23543	Ferton
Pompilidae	Cryptocheilus	variabilis	nigripes	F	EY23545	Ferton
Pompilidae	Cryptocheilus	variabilis	nigripes	F	EY23547	Ferton
Pompilidae	Cryptocheilus	variabilis	nigripes	M	EY23548	Ferton
Pompilidae	Cryptocheilus	variabilis	nigripes	M	EY28886	Ferton
Pompilidae	Cryptocheilus	versicolor		M	EY23552	Ferton
Pompilidae	Dipogon	bifasciatus		F	EY18940	Ferton
Pompilidae	Eoferreola	manticata		F	EY23650	Ferton
Pompilidae	Eoferreola	manticata		F	EY23651	Ferton
Pompilidae	Eoferreola	manticata		F	EY23653	Ferton
Pompilidae	Episyrus	arrogans		F	EY16875	Ferton
Pompilidae	Episyrus	gallicus		F	EY24537	Ferton
Pompilidae	Evagetes	elongatus		F	EY22797	Ferton
Pompilidae	Evagetes	elongatus		F	EY22798	Ferton
Pompilidae	Homonotus	niger		F	EY22874	Ferton
Pompilidae	Microphadnus	pumilus		F	EY22885	Ferton
Pompilidae	Microphadnus	pumilus		F	EY22886	Ferton
Pompilidae	Microphadnus	pumilus		M	EY22887	Ferton
Sapygidae	Sapyga	quinquepunctata		F	EY27476	Ferton
Sapygidae	Sapyga	quinquepunctata		F	EY27727	Ferton

Scoliidae	Colpa	interrupta		M	EY11926	Ferton
Scoliidae	Colpa	interrupta		M	EY11927	Ferton
Sphecidae	Ammophila	heydeni		M	EY11782	Ferton
Sphecidae	Ammophila	heydeni		F	EY11949	Ferton
Sphecidae	Ammophila	heydeni		F	EY12030	Ferton
Sphecidae	Ammophila	heydeni		M	EY12043	Ferton
Sphecidae	Ammophila	heydeni		M	EY12172	Ferton
Sphecidae	Ammophila	heydeni		F	EY16518	Ferton
Sphecidae	Ammophila	rubriventris		F	EY24601	Ferton
Sphecidae	Ammophila	rubriventris		F	EY24602	Ferton
Sphecidae	Ammophila	rubriventris		M	EY26479	Ferton
Sphecidae	Ammophila	rubriventris		F	EY27215	Ferton
Sphecidae	Ammophila	sabulosa		M	EY15510	Ferton
Sphecidae	Sceliphron	destillatorium		F	EY11895	Ferton
Sphecidae	Sceliphron	destillatorium		M	EY14319	Ferton
Sphecidae	Sceliphron	destillatorium		M	EY15703	Ferton
Sphecidae	Sceliphron	destillatorium		M	EY15705	Ferton
Sphecidae	Sceliphron	spirifex		F	EY27984	Ferton
Sphecidae	Sceliphron	spirifex		F	EY32248	Ferton
Vespidae	Alastor	atropos		M	EY29733	Ferton
Vespidae	Alastor	atropos		F	EY29734	Ferton
Vespidae	Ancistrocerus	ichneumonideus		F	EY16389	Ferton
Vespidae	Eumenes	aff. aemilianus		M	EY27164	Ferton
Vespidae	Eumenes	subpomiformis		F	EY26759	Ferton
Vespidae	Eumenes	subpomiformis		M	EY27103	Ferton
Vespidae	Eumenes	subpomiformis		F	EY29743	Ferton
Vespidae	Euodynerus	wilhelmi		F	EY15743	Ferton
Vespidae	Stenodynerus	vergesi		M	EY29705	Ferton
Vespidae	Stenodynerus	vergesi		M	EY29730	Ferton
Apidae	Eucera	vulpes		F	EY11684	Ferton
Apidae	Eucera	vulpes		F	EY11781	Ferton
Apidae	Eucera	vulpes		M	EY13640	Ferton
Apidae	Eucera	vulpes		M	EY13825	Ferton
Apidae	Eucera	vulpes		M	EY14392	Ferton
Apidae	Eucera	vulpes		F	EY16132	Ferton
Apidae	Melecta	leucorhyncha	taormina	M	EY14191	Ferton
Megachilidae	Coelioxys	inermis		F	EY14545	Ferton
Megachilidae	Coelioxys	inermis		M	EY14940	Ferton
Megachilidae	Coelioxys	inermis		M	EY16094	Ferton
Megachilidae	Coelioxys	inermis		M	EY17164	Ferton
Megachilidae	Coelioxys	inermis		F	EY28523	Ferton

Pompilidae	Priocnemis	vachali		F	EY22778	Ferton
Pompilidae	Priocnemis	vachali		F	EY22779	Ferton
Pompilidae	Priocnemis	vachali		F	EY22780	Ferton
Pompilidae	Priocnemis	vachali		F	EY22781	Ferton
Pompilidae	Priocnemis	vachali		M	EY22782	Ferton
Vespidae	Stenodynerus	bluethgeni		M	EY29714	Ferton
Vespidae	Stenodynerus	bluethgeni		M	EY29715	Ferton
Apidae	Amegilla	sp2		F	EY29861	Ferton
Apidae	Anthophora	nigrocincta		F	EY24864	Ferton
Apidae	Bombus	maxillosus		F	EY22606	Ferton
Apidae	Bombus	maxillosus		F	EY22607	Ferton
Apidae	Bombus	renardi		F	EY22505	Ferton
Crabronidae	Miscophus	bicolor		M	EY18781	Ferton
Crabronidae	Tachysphex	aff. strigosus		F	EY23820	Ferton
Crabronidae	Tachysphex	aff. strigosus		F	EY28077	Ferton
Crabronidae	Tachysphex	aff. strigosus		F	EY29436	Ferton
Crabronidae	Tachysphex	aff. strigosus		F	EY28412	Ferton
Crabronidae	Trypoxylon	latilobatum		F	EY18921	Ferton
Halictidae	Lasioglossum	zonulum		F	EY30383	Ferton
Halictidae	Lasioglossum	minutissimum		F	EY28248	Ferton
Vespidae	Ancistrocerus	nigricornis		M	EY26891	Ferton
Pemphredonidae	Passaloecus	corniger		F	EY15633	Ferton
Chrysididae	Chrysis	ignita	bischoffi	F	EY27697	Ferton
Chrysididae	Chrysis	ignita	bischoffi	F	EY28231	Ferton
Chrysididae	Holopyga	miranda		F	EY32302	Ferton

Appendix 2.2

Matlab script for image combination (coded by Yann Le Poul and Adrien Perrard). See Chapter 2 for explanation.

```
%% initialization
clear

ImFolder='E:\photos\Paul\2017_original_tiff\';
ImFolder2='E:\photos\Paul\2017_combin\';
ImType = 'tif';% files extension

ListF = fList(ImFolder,ImType);
```



```

ListF2 = ListF;
for e=1:length(ListF)
    StrLF = strsplit(ListF{e},'_');
    ListF2{e} = StrLF{1};
end

ListF3 = unique(ListF2)
%% read images from folder
for j=1:length(ListF3)
    tic
    StrC = strcmp(ListF2,ListF3{j});
    ListF4 = ListF(StrC);
    I = imread([ ImFolder , ListF4{1} ]);
    s1 = size(I,1); %% pixels en y
    s2 = size(I,2); %% pixels en x
    A = zeros(s1,s2,3,length(ListF4),'uint16');
    A(:,:,1) = I;
    fixed=rgb2gray(I);
    for e=2:length(ListF4)%ImFolder2 %ok<NOPTS>
        I = imread([ ImFolder , ListF4{e} ]);
        moving=rgb2gray(I);
        tform= imregcorr(moving,fixed);
        Rfixed = imref2d(size(fixed));
        movingReg = imwarp(I,tform,'OutputView',Rfixed);
        %% test avec taille inférieure
        %I2 = imresize(I,[s1 s2]);
        A(:,:,e) = movingReg;
    end
    B = zeros(s1,s2,3,'uint16');
    for l=1:3
        for i=1:s1
            for ii=1:s2
                a = sort(A(i,ii,:));
                B(i,ii,l) = a(4);
            end
        end
    end
end
end

```

```

filename = [ImFolder2,ListF3{j}','-d.tif' ];
B = im2uint8(B);
imwrite(B, filename,'Compression','lzw');

toc

end

```

Appendix 2.3

Presence/absence (1/0) of a nucleotide sequence in our community phylogeny for all selected markers and species. Coverage are given in the last column and row. Missing data represent 60% of the matrix.

Genus_species	COI	28S	EF1a	Wingless	Rhodopsin	Total
<i>Agenioideus_nubecula</i>	0	1	0	0	0	20%
<i>Allodynerus_delphinalis</i>	1	0	0	0	0	20%
<i>Allodynerus_rossii</i>	1	1	0	0	0	40%
<i>Amegilla_quadrifasciata</i>	1	0	0	0	0	20%
<i>Ammatomus_coarctatus</i>	1	1	0	1	0	60%
<i>Ammophila_heydeni</i>	1	0	1	0	1	60%
<i>Ammophila_sabulosa</i>	1	0	1	0	1	60%
<i>Ancistrocerus_ichneumonideus</i>	1	0	0	0	0	20%
<i>Ancistrocerus_longispinosus</i>	1	1	0	1	0	60%
<i>Ancistrocerus_nigricornis</i>	0	1	0	0	0	20%
<i>Andrena_agilissima</i>	1	0	0	0	0	20%
<i>Andrena_flavipes</i>	0	1	0	1	0	40%
<i>Andrena_fulvipes</i>	1	0	0	0	0	20%
<i>Andrena_hesperia</i>	1	1	0	1	0	60%
<i>Andrena_morio</i>	0	1	0	1	0	40%
<i>Andrena_nana</i>	1	0	0	0	0	20%
<i>Andrena_nigroaenea</i>	1	0	0	0	1	40%
<i>Andrena_pilipes</i>	1	1	0	0	0	40%
<i>Andrena_wilkella</i>	1	0	1	0	0	40%
<i>Andrena_sardoa</i>	0	1	0	0	0	20%
<i>Anospilus_orbitalis</i>	1	1	0	1	0	60%
<i>Antepipona_deflenda</i>	1	1	0	0	0	40%
<i>Anthidiellum_strigatum</i>	1	1	1	0	1	80%
<i>Anthophora_bimaculata</i>	1	0	0	1	0	40%
<i>Anthophora_crinipes</i>	1	0	0	0	0	20%
<i>Apis_mellifera</i>	1	1	1	1	1	100%

<i>Aporinellus_sexmaculatus</i>	1	1	0	1	1	80%
<i>Aporus_bicolor</i>	0	1	1	1	1	80%
<i>Astata_costae</i>	1	1	0	0	0	40%
<i>Astata_kashmirensis</i>	1	0	0	0	0	20%
<i>Astata_minor</i>	1	0	0	0	0	20%
<i>Astata_rufipes</i>	1	0	0	0	0	20%
<i>Auplopus_carbonarius</i>	1	0	0	0	0	20%
<i>Bembecinus_hungaricus</i>	1	0	0	0	0	20%
<i>Bembecinus_insulanus</i>	1	0	0	0	0	20%
<i>Bembix_bidentata</i>	1	1	0	0	0	40%
<i>Bembix_oculata</i>	1	0	0	0	0	20%
<i>Bembix_rostrata</i>	1	0	0	0	0	20%
<i>Bombus_maxillosus</i>	0	0	0	0	1	20%
<i>Bombus_ruderatus</i>	1	0	1	0	1	60%
<i>Bombus_terrestris</i>	1	1	1	0	1	80%
<i>Brachymeria_femorata</i>	1	0	0	0	0	20%
<i>Ceratina_chalcites</i>	0	0	1	0	0	20%
<i>Ceratina_cyanea</i>	1	1	1	1	1	100%
<i>Ceratina_dallatorreana</i>	1	0	0	0	0	20%
<i>Cerceris_arenaria</i>	1	0	1	0	1	60%
<i>Cerceris_flavilabris</i>	1	0	0	0	0	20%
<i>Cerceris_sabulosa</i>	1	0	1	0	1	60%
<i>Cerceris_specularis</i>	1	0	0	0	0	20%
<i>Ceropales_albicincta</i>	1	1	0	0	0	40%
<i>Chrysis_fasciata</i>	1	0	0	0	0	20%
<i>Chrysis_germari</i>	1	0	0	0	0	20%
<i>Chrysis_grohmanni</i>	1	0	0	0	0	20%
<i>Chrysis_ignita</i>	1	1	0	0	0	40%
<i>Chrysis_mysticalis</i>	1	0	0	0	0	20%
<i>Chrysis_rutilans</i>	1	0	0	0	0	20%
<i>Chrysis_splendidula</i>	1	0	0	0	0	20%
<i>Chrysis_terminata</i>	1	1	0	0	0	40%
<i>Chrysura_laevigata</i>	1	0	0	0	0	20%
<i>Coelioxys_afra</i>	1	1	1	0	1	80%
<i>Coelioxys_haemorrhoea</i>	1	0	0	0	0	20%
<i>Coelioxys_inermis</i>	1	0	0	0	0	20%
<i>Colletes_marginatus</i>	1	0	0	0	0	20%
<i>Colletes_similis</i>	1	1	0	0	0	40%
<i>Colpa_quinquecincta</i>	1	0	0	0	0	20%
<i>Crossocerus_quadrimaculatus</i>	1	0	0	0	0	20%
<i>Crossocerus_tarsatus</i>	1	0	0	0	0	20%

Cryptocheilus_egregius	1	1	0	0	0	40%
Dasylabris_maura	0	1	0	0	0	20%
Dicyrtomellus_tingitanus	1	1	0	1	0	60%
Diodontus_nsp2	1	1	0	0	0	40%
Diodontus_tristis	1	0	0	0	0	20%
Dipogon_bifasciatus	1	0	0	0	0	20%
Dipogon_variegatus	1	0	0	0	0	20%
Dolichurus_nsp1	0	1	0	0	0	20%
Dryudella_affspinolae	1	1	0	0	0	40%
Dufourea_halictula	1	0	0	0	0	20%
Ectemnius_cavifrons	1	0	0	0	0	20%
Ectemnius_confinis	1	0	0	0	0	20%
Ectemnius_continuus	1	0	0	0	0	20%
Entomobora_crassitarsis	1	1	1	0	0	60%
Epeolus_cruciger	1	1	1	1	1	100%
Episyron_rufipes	1	1	0	1	0	60%
Eucera_chrysopyga	1	0	0	0	0	20%
Eucera_nigrescens	1	0	0	0	1	40%
Eucera_nigrilabris	1	1	0	0	1	60%
Eucera_vulpes	0	1	0	0	1	40%
Eumenes_coarctatus	1	0	0	0	0	20%
Eumenes_mediterraneus	1	0	0	0	0	20%
Eumenes_subpomiformis	1	0	0	0	0	20%
Evagetes_pectinipes	1	1	0	0	0	40%
Ferreola_diffinis	1	1	0	0	0	40%
Gorytes_albidulus	1	1	0	1	0	60%
Gorytes_quinquecinctus	1	0	0	0	0	20%
Gorytes_sulcifrons	1	0	0	0	0	20%
Gyrinus_marinus	1	0	0	0	0	20%
Halictus_fulvipes	1	0	1	1	1	80%
Halictus_langobardicus	1	0	0	0	0	20%
Halictus_scabiosae	1	0	1	1	1	80%
Harpactus_elegans	1	0	0	0	0	20%
Hedychridium_roseum	1	0	0	0	0	20%
Hedychridium_scutellare	1	1	0	1	0	60%
Hedychrum_niemelai	1	0	0	0	0	20%
Hedychrum_nobile	1	0	0	0	0	20%
Hemipterocheilus_bembeciformis	1	1	0	0	0	40%
Heriades_crenulata	1	0	0	0	0	20%
Heriades_rubicola	1	0	0	0	0	20%
Holopyga_chrysonota	1	0	0	0	0	20%

Holopyga_ignicolis	1	0	0	0	0	20%
Hoplisoides_punctuosus	1	1	0	1	0	60%
Hoplitis_adunca	1	1	1	0	1	80%
Hoplitis_annulata	1	0	1	0	1	60%
Hoplitis_bihamata	0	0	1	0	1	40%
Hoplitis_bisulca	1	0	1	0	1	60%
Hoplitis_cristatula	1	0	1	0	1	60%
Hoplitis_leucomelana	1	0	0	0	1	40%
Hoplitis_perezi	1	0	0	0	1	40%
Hylaeus_clypearis	1	0	0	0	0	20%
Hylaeus_gibbus	1	0	0	0	0	20%
Hylaeus_impairilis	1	0	0	0	0	20%
Hylaeus_punctatus	1	1	1	1	1	100%
Hylaeus_variegatus	1	0	0	0	1	40%
Hyposoter_annulipes	1	0	0	0	0	20%
Isodontia_mexicana	1	1	1	0	1	80%
Larra_anathema	1	0	0	0	0	20%
Lasioglossum_albipes	1	0	0	1	1	60%
Lasioglossum_albocinctum	1	0	1	0	0	40%
Lasioglossum_callizonium	1	0	0	1	1	60%
Lasioglossum_clypeare	1	0	0	0	0	20%
Lasioglossum_discum	1	0	0	1	1	60%
Lasioglossum_interruptum	1	0	1	1	1	80%
Lasioglossum_laevigatum	1	0	0	1	1	60%
Lasioglossum_lativentre	1	0	0	0	0	20%
Lasioglossum_leucozonium	1	0	1	1	1	80%
Lasioglossum_limbellum	1	0	1	1	1	80%
Lasioglossum_malachurum	1	0	0	1	1	60%
Lasioglossum_nigripes	1	0	1	1	1	80%
Lasioglossum_nitidiusculum	1	0	0	0	0	20%
Lasioglossum_nitidulum	1	0	0	0	0	20%
Lasioglossum_pauperatum	1	0	0	0	0	20%
Lasioglossum_pauxillum	1	0	1	1	1	80%
Lasioglossum_politum	1	0	0	1	1	60%
Lasioglossum_punctatissimum	1	0	0	0	0	20%
Lasioglossum_puncticolle	1	0	1	1	1	80%
Lasioglossum_subhirtum	1	0	0	0	0	20%
Lasioglossum_villosulum	1	0	1	1	1	80%
Lasioglossum_zonulum	1	1	0	1	1	80%
Leptochilus_regulus	1	1	0	0	0	40%
Lestica_clypeata	1	0	0	0	0	20%

Lindenius_pygmaeus	1	0	0	0	0	20%
Liris_niger	1	1	0	1	0	60%
Megachile_albisecta	1	1	1	0	1	80%
Megachile_apicalis	1	0	0	0	0	20%
Megachile_centuncularis	1	0	0	0	0	20%
Megachile_leachella	1	0	0	0	1	40%
Megachile_melanopyga	1	1	1	0	1	80%
Megachile_pusilla	1	0	0	0	1	40%
Megachile_sicula	1	0	0	0	0	20%
Melitta_nigricans	1	0	1	1	1	80%
Mimumesa_unicolor	1	0	0	0	0	20%
Miscophus_bicolor	1	0	0	0	0	20%
Miscophus_nsp1	1	1	0	1	0	60%
Nitela_borealis	1	1	0	0	0	40%
Nomada_flavopicta	1	0	0	0	0	20%
Nomada_fucata	1	0	1	0	0	40%
Nomada_fulvicornis	1	0	0	0	1	40%
Nomada_kohli	1	0	0	0	0	20%
Nysson_fulvipes	1	0	0	0	0	20%
Nysson_trimaculatus	1	0	0	0	0	20%
Odynerus_femoratus	1	1	0	0	0	40%
Oryttus_concinnus	1	0	0	0	0	20%
Osmia_bircornis	1	0	0	1	0	40%
Osmia_caerulescens	1	0	1	0	1	60%
Osmia_ferruginea	1	0	1	1	1	80%
Osmia_latreillei	1	0	0	0	0	20%
Osmia_melanogaster	1	0	0	0	0	20%
Osmia_nasoproducta	1	1	0	0	0	40%
Osmia_niveata	1	0	1	0	1	60%
Osmia_rufohirta	1	0	0	0	0	20%
Osmia_submicans	1	0	0	0	0	20%
Osmia_tricornis	1	0	1	1	1	80%
Oxybelus_haemorrhoidalis	1	0	0	0	0	20%
Oxybelus_lamellatus	1	0	0	0	0	20%
Oxybelus_quatuordecimnotatus	1	0	0	0	0	20%
Oxybelus_uniglumis	1	0	0	0	0	20%
Palmodes_occitanicus	1	0	0	0	0	20%
Panurgus_corsicus	1	1	0	1	0	60%
Parodontodynerus_ephippium	1	1	0	0	0	40%
Passaloecus_corniger	1	0	0	0	0	20%
Passaloecus_gracilis	1	1	0	0	0	40%

<i>Pemphredon lethifer</i>	1	0	0	0	0	20%
<i>Philanthus triangulum</i>	1	1	1	1	1	100%
<i>Philanthus venustus</i>	1	1	0	0	1	60%
<i>Pison atrum</i>	1	0	0	0	0	20%
<i>Podalonia hirsuta</i>	1	0	1	0	1	60%
<i>Polistes dominula</i>	1	0	0	0	0	20%
<i>Polistes gallicus</i>	1	1	0	0	0	40%
<i>Polistes nimpha</i>	1	1	1	0	0	60%
<i>Priocnemis perraudini</i>	0	1	0	0	0	20%
<i>Prionyx kirbii</i>	1	0	1	0	1	60%
<i>Prionyx lividocinctus</i>	1	0	0	0	0	20%
<i>Prionyx subfuscatus</i>	1	0	0	0	0	20%
<i>Psammaecius punctulatus</i>	1	0	0	0	0	20%
<i>Psenulus pallipes</i>	0	1	0	1	0	40%
<i>Pseudepipona lativentris</i>	1	1	0	0	0	40%
<i>Pseudoanthidium leucostoma</i>	0	1	0	1	0	40%
<i>Rhodanthidium septemdentatum</i>	1	1	1	0	1	80%
<i>Ronisia brutia</i>	0	1	0	0	0	20%
<i>Sapyga quinquepunctata</i>	1	0	0	0	0	20%
<i>Sceliphron caementarium</i>	1	0	1	1	1	80%
<i>Sceliphron destillatorium</i>	1	0	0	0	0	20%
<i>Sceliphron spirifex</i>	1	0	0	0	0	20%
<i>Scolia hirta</i>	1	1	0	0	1	60%
<i>Smicromyrme viduata</i>	0	1	0	1	0	40%
<i>Seladonia gemmea</i>	1	0	1	1	1	80%
<i>Seladonia smaragdula</i>	1	0	0	1	0	40%
<i>Seladonia subaurata</i>	1	0	1	1	1	80%
<i>Sphecodes albilabris</i>	1	0	0	1	1	60%
<i>Sphecodes alternatus</i>	1	1	1	1	1	100%
<i>Sphecodes marginatus</i>	1	1	0	1	0	60%
<i>Sphecodes monilicornis</i>	1	1	0	1	1	80%
<i>Sphecodes puncticeps</i>	1	1	1	1	1	100%
<i>Sphex afffunerarius</i>	1	1	0	1	0	60%
<i>Sphex funerarius</i>	1	1	0	0	0	40%
<i>Spilomena troglodytes</i>	0	1	0	0	0	20%
<i>Stelis breviscula</i>	0	1	0	0	0	20%
<i>Stelis nasuta</i>	1	1	0	0	0	40%
<i>Stenodynerus bluethgeni</i>	1	0	0	0	0	20%
<i>Stenodynerus fastidiosissimus</i>	1	1	0	0	0	40%
<i>Stizus fasciatus</i>	1	1	0	1	0	60%
<i>Tachyagetes leucocnemis</i>	0	1	0	0	0	20%

Tachysphex_brullii	1	0	0	0	0	20%
Tachysphex_consocius	1	0	0	0	0	20%
Tachysphex_costae	1	0	0	0	0	20%
Tachysphex_fulvitaris	1	0	0	0	0	20%
Tachysphex_gibbus	1	0	0	0	0	20%
Tachysphex_mediterraneus	1	0	0	0	0	20%
Tachysphex_rufiventris	1	1	0	1	0	60%
Tachysphex_tarsinus	1	0	0	0	0	20%
Tachytes_freygessneris	1	0	0	0	0	20%
Tachytes_obsoletus	1	0	0	0	0	20%
Tachytes_procerus	1	1	0	1	0	60%
Tenthredo_koehlerii	1	0	0	0	0	20%
Tetraloniella_fulvescens	1	1	0	1	0	60%
Thyreus_histrionicus	1	0	0	0	0	20%
Tracheliodes_quinquenotatus	1	0	0	0	0	20%
Trypoxylon_figulus	1	0	0	0	0	20%
Trypoxylon_medium	1	0	0	0	0	20%
Trypoxylon_minus	1	0	0	0	0	20%
Trypoxylon_scutatum	1	1	0	0	0	40%
Vespula_germanica	0	1	1	1	0	60%
Vestohalictus_vestitus	1	1	0	1	0	60%
Xylocopa_iris	1	1	1	1	1	100%
Total	92%	35%	21%	25%	27%	

Appendix 2.4

Protocols used for amplification:

COI: ~628 bp

primers designed by Folmer et al. (1994)

LCO 5' GGT CAA CAA ATC ATA AAG ATA TTG G 3'

HCO 5' TAA ACT TCA GGG TGA CCA AAA AAT CA 3'

Initial: 180s denaturation at 95°C. 40 cycles of denaturation at 95°C for 30s, annealing at 50°C for 60s, and extension at 72°C for 90s. A 600s extension period following the final cycle at 72°C.

Mix PCR for 1 unit:

12.94 microL H2O milliQ

2 Buffer10x

1.5 MgCl 25mM

1 DMSO

1 BSA 1mg/mL
0.8 dNTP 6.6mM
0.32 F 1/10
0.32 R 1/10
0.12 Taq 5unit/microL

28S: ~1000 bp

For28SVesp	5' AGAGAGAGTTCAAGAGTACGTG 3'	Hines et al. 2007
Rev28SVesp	5' GGAACCAGCTACTAGATGG 3'	Hines et al. 2007

Initial: 240s denaturation at 94°C. 10 cycles of denaturation at 94°C for 30s, annealing at 46°C for 30s, and extension at 72°C for 30s. 25 cycles of denaturation at 94°C for 30s, annealing at 52°C for 30s, and extension at 65°C for 30s. A 600s extension period following the final cycle at 65°C.

Mix PCR for 1 unit:

12.94 microL H2O milliQ
2 Buffer10x
1.5 MgCl 25mM
1 DMSO
1 BSA 1mg/mL
0.8 dNTP 6.6mM
0.32 F 1/10
0.32 R 1/10
0.12 Taq 5unit/microL

Rhodopsin: ~700 bp

primers from Danforth et al., 2004 = LWRhF and LWRhR of Mardulyn & Cameron, 1999

Opsin For 5' AAT TGC TAT TAY GAR ACN TGG GT 3'

Opsin Rev 5' ATA TGG AGT CCA NGC CAT RAA CCA 3'

Initial: 120s denaturation at 94°C. 60 cycles of denaturation at 94°C for 60s, annealing at 52°C for 60s, and extension at 68°C for 240s. A 600s extension period following the final cycle at 68°C.

Mix PCR (for 20 microL):

2 microL 10x TaqBuffer
1.5 microL MgCl₂
1 microL BSA (1 mg/ml)
1 microL DMSO
0.8 microL dNTPs 6.6 mM
0.4 microL of each primer (1/10)
0.2 microL Taq polymerase (5 U/microL)
2 microL DNA

10.7 microL H2O to complete

TaqBuffer 10x (added as 2.5 microL): Tris (pH 8.3) 10 mM, MgCl₂ 1.5 mM, KCl 50 mM, Gelatin 0.01%, NP-40 0.01%, TritonX 100 0.01%

Wnt1 (wingless): ~400 bp

beewgFor 5' TGCCANGTSAAGACCTGYTGGATGAG 3' Danforth et al. 2004

Lepwg2a 5' ACTCGCARCACCARTGGAATGTRCA 3' Danforth et al. 2004

Initial: 120s denaturation at 94°C. 60 cycles of denaturation at 94°C for 45s, annealing at 58°C for 45s, and extension at 68°C for 240s. A 600s extension period following the final cycle at 68°C.

Mix PCR (for 20 microL):

2 microL 10x TaqBuffer

1.5 microL MgCl₂

1 microL BSA (1 mg/ml)

1 microL DMSO

0.8 microL dNTPs 6.6 mM

0.4 microL of each primer (1/10)

0.2 microL Taq polymerase (5 U/microL)

2 microL DNA

10.7 microL H2O to complete

TaqBuffer 10x (added as 2.5 microL): Tris (pH 8.3) 10 mM, MgCl₂ 1.5 mM, KCl 50 mM, Gelatin 0.01%, NP-40 0.01%, TritonX 100 0.01%

EF1a: ~1100 bp

HaF2For1 5' GGGYAAAGGWCCTTCAARTATGC 3' Danforth et al. 1999

F2-rev1 5' AATCAGCAGCACCTTTAGGTGG 3' Danforth et al. 1999

Initial: 180s denaturation at 94°C. 60 cycles of denaturation at 94°C for 60s, annealing at 54°C for 60s, and extension at 68°C for 240s. A 600s extension period following the final cycle at 68°C.

Mix PCR (for 20 microL):

2 microL 10x TaqBuffer

1.5 microL MgCl₂

1 microL BSA (1 mg/ml)

1 microL DMSO

0.8 microL dNTPs 6.6 mM

0.4 microL of each primer (1/10)

0.2 microL Taq polymerase (5 U/microL)

2 microL DNA

10.7 microL H2O to complete

TaqBuffer 10x (added as 2.5 microL): Tris (pH 8.3) 10 mM, MgCl₂ 1.5 mM, KCl 50 mM, Gelatin 0.01%, NP-40 0.01%, TritonX 100 0.01%

Appendix 3.1

Python script for population dynamics of 10 mimetic species under perturbations (see Chapter 3).

```
"""
```

Descriptif : ce programme (codé par Maxime Boutin, 2021) est composé de 2 parties : tout d'abord le calcul des effectifs à l'équilibre pour les 10 populations, puis une perturbation est appliquée (augmentation du taux de mortalité "delta") sur une pop de chaque cercle mimétique afin de voir s'il y a une répercussion sur les autres pop. Les 10 populations sont réparties selon deux cercles mimétiques :

- cercle A -> pop 1 et pop 2 (2 populations)
- cercle B -> pop 3 à pop 10 (8 populations)

Paramètres :

- n -> matrice des effectifs initiaux (fixés à 25)
- r -> taux de reproduction (fixé à 1.1)
- c -> matrice des coefficients de compétition (1 pour intraspécifique, 0.1 pour interspécifique)
- K -> capacité de charge du milieu (fixée à 2500)
- p -> taux de prédation (fixé à 0.50)
- L -> degré de nocivité (fixé à 0.001)
- m -> matrice des taux de ressemblance entre 2 espèces (0 ou 1)
- d -> matrice des taux de mortalité hors-prédation (0.05, ou 0.7 pour la perturbation)

Version : 2 (24/02/2021)

```
"""
```

```
### importation des bibliothèques ###
```

```
import numpy as np # bibliothèque NumPy pour les matrices
```

```
import matplotlib.pyplot as plt # bibliothèque Matplotlib pour les plots
```

```
### définition des paramètres ###
```

```
n = np.array(10*[[25]], dtype="float32") # np.array permet de définir une matrice
```

```
r = 1.1
```

```
c = np.array([[1, 0.1, 0.1, 0.1, 0.1, 0.1, 0.1, 0.1, 0.1, 0.1],
```

```
             [0.1, 1, 0.1, 0.1, 0.1, 0.1, 0.1, 0.1, 0.1, 0.1],
```

```
             [0.1, 0.1, 1, 0.1, 0.1, 0.1, 0.1, 0.1, 0.1, 0.1],
```

```
             [0.1, 0.1, 0.1, 1, 0.1, 0.1, 0.1, 0.1, 0.1, 0.1],
```

```
             [0.1, 0.1, 0.1, 0.1, 1, 0.1, 0.1, 0.1, 0.1, 0.1],
```

```
             [0.1, 0.1, 0.1, 0.1, 0.1, 1, 0.1, 0.1, 0.1, 0.1],
```

```
             [0.1, 0.1, 0.1, 0.1, 0.1, 0.1, 1, 0.1, 0.1, 0.1],
```

```
             [0.1, 0.1, 0.1, 0.1, 0.1, 0.1, 0.1, 1, 0.1, 0.1],
```

```
             [0.1, 0.1, 0.1, 0.1, 0.1, 0.1, 0.1, 0.1, 1, 0.1],
```

```
             [0.1, 0.1, 0.1, 0.1, 0.1, 0.1, 0.1, 0.1, 0.1, 1]])
```

```
K = 2500.0
```

```

p = 0.50
L = 0.001
m = np.array([[1, 1, 0, 0, 0, 0, 0, 0, 0, 0],
              [1, 1, 0, 0, 0, 0, 0, 0, 0, 0],
              [0, 0, 1, 1, 1, 1, 1, 1, 1, 1],
              [0, 0, 1, 1, 1, 1, 1, 1, 1, 1],
              [0, 0, 1, 1, 1, 1, 1, 1, 1, 1],
              [0, 0, 1, 1, 1, 1, 1, 1, 1, 1],
              [0, 0, 1, 1, 1, 1, 1, 1, 1, 1],
              [0, 0, 1, 1, 1, 1, 1, 1, 1, 1],
              [0, 0, 1, 1, 1, 1, 1, 1, 1, 1],
              [0, 0, 1, 1, 1, 1, 1, 1, 1, 1]])
d = np.array([[0.05],[0.05],[0.05],[0.05],[0.05],[0.05],[0.05],[0.05],[0.05],[0.05]])

##### 1. CALCUL DES EQUILIBRES #####

n = np.array(10 * [[25]], dtype="float32")
for t in range(500): # t est incrémenté de 1 à chaque itération, de t=0 à (range(n-1))
    n += r * n * (1 - np.dot(c,n) / K) - (p / (1 + np.dot(m, L * n))) * n - d * n # np.dot(a,b) : produit matriciel a.b
    n[n<2]=0 # remplace tous les effectifs inférieurs à 2 par 0 (extinction)

##### 2. PERTURBATION #####

t = 0 # permet de réinitialiser la variable "temps"
x = [t] # enregistre toutes les valeurs de t (liste), pour tracer la courbe
save = n # enregistre tous les effectifs (matrice), pour tracer la courbe

for t in range(500):
    # applique la perturbation pour la pop1 et la pop10, de la génération 1 à la génération 20
    if t <= 20 and t>=1 : d = np.array([[0.7], [0.05], [0.05], [0.05], [0.05], [0.05], [0.05], [0.05], [0.05], [0.7]])
    else : d = np.array([[0.05],[0.05],[0.05],[0.05],[0.05],[0.05],[0.05],[0.05],[0.05],[0.05]])

    n += r * n * (1 - np.dot(c, n) / K) - (p / (1 + np.dot(m, L * n))) * n - d * n
    n[n < 2] = 0
    save = np.dstack((save, n)) # ajout de la matrice "n" à la matrice "save"
    x.append(t) # ajout de la valeur de t à la liste x

### réalisation des courbes pour les 10 populations ###

```

```

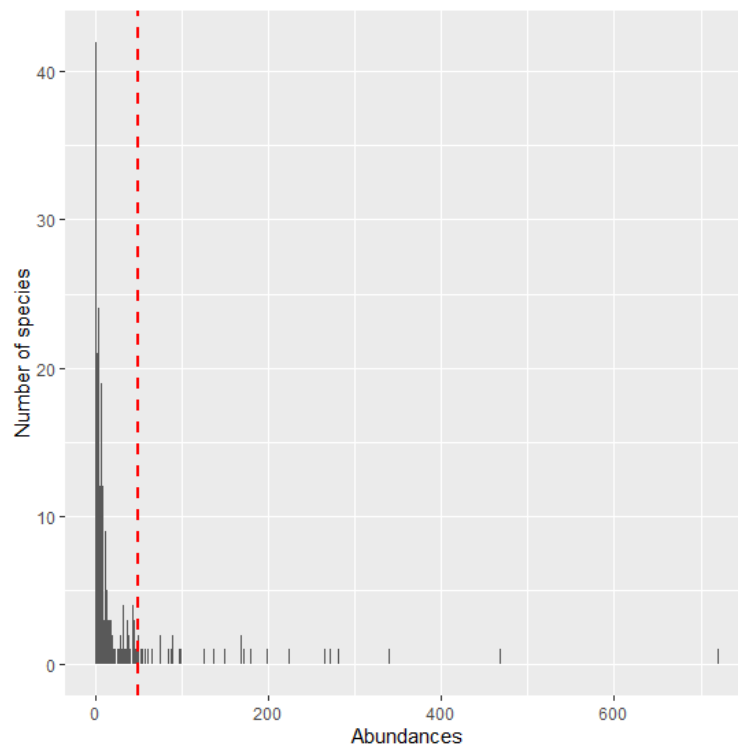
for u in range(10):
    plt.plot(x, save[u, 0], label="pop "+str(u+1))

### mise en forme de la fenêtre graphique ###
plt.axvline(x=1, color='grey', linestyle=':') # ligne verticale pour le début de la perturbation
plt.axvline(x=20, color='grey', linestyle=':') # ligne verticale pour la fin de la perturbation
plt.xlabel("Génération") # nomme l'axe des abscisses
plt.ylabel("Effectifs") # nomme l'axe des ordonnées
plt.legend() # permet d'afficher les légendes (indiquées par l'argument "label")
plt.title("Dynamique de 10 populations selon 2 cercles (2|8) suite à une perturbation \n r=1.1, p=0.5, c=0.1, K=2500, L=0.001, d=0.05")
plt.show() # ouvre la fenêtre graphique

```

Appendix 3.2

The graphic below shows abundances distribution in the 2017 dataset. Singleton species are not shown. The dashed red line indicate the 10% cut-off threshold ($x=49$ individuals).



Abstract

Many bees and stinging wasps (Aculeata) exhibit striking color patterns or conspicuous coloration. These colorations are often interpreted as an aposematic signal advertising aculeate defenses: the venomous sting. Under predators' selective pressure, signals may converge among unpalatable species, to the benefit of all individuals forming the Müllerian mimicry rings (i.e. indirect mutualistic interactions). By modifying the probabilities of local extinctions, global changes can modify species abundances and composition of pollinators' communities, depending on their mimicry ring. Therefore, we would expect that dominant mimetic species are better protected from predation and might better maintain through time. The aim of this thesis is to test if mimicry rings size can explain differences in decline between species in a pollinators' community from South Corsica (France), sampled twice in a century span. In the first chapter we establish a state of the art of research on mimicry in bees and stinging wasps, and identify directions for future research. In the second chapter we quantify mimetic resemblance among an entire aculeate community from South Corsica to establish its mimicry rings. A community-level phylogeny was reconstructed to attest similarities not due to common ancestry. We demonstrate convergent resemblance between co-occurring species in the community. In the third chapter we test if mutualistic interactions may enhance species persistence (i.e. species from numerically well protected rings tend to better survive through time). We first used a mathematical model to estimate population dynamics within the mimetic community testing the effect of parameters of interest on the extinction risks. Then, we confronted our hypothesis with empirical data based on mimicry rings from the Corsican community. Although we observe both theoretically and empirically a tendency that confirms our predictions, statistics are not conclusive and we propose some perspectives to elucidate the potential interplay between pollinators decline and mimetic interactions.

Keywords: [Mimicry rings, aposematism, hymenoptera, community ecology, co-extinctions]

Résumé

La plupart des espèces de guêpes et d'abeilles (Aculeata) ont des motifs colorés et des couleurs marquées. Ces colorations sont souvent interprétées comme un signal dit aposématique, traduisant leur moyen de défense qu'est l'aiguillon venimeux. Sous la pression de sélection des prédateurs, les individus d'espèces nocives peuvent converger pour un signal, qui bénéficie à chacun de ces individus formant un cercle mimétique dit mullérien (interactions mutualistes indirectes). En modifiant les probabilités d'extinctions locales, les changements globaux peuvent modifier les abondances des espèces et la composition des communautés de pollinisateurs, selon leur cercle mimétique. Par conséquent on s'attend à ce que les espèces mimétiques dominantes soient mieux protégées de la prédation et se maintiennent mieux au cours du temps. Le but de cette thèse est de tester si la taille des cercles mimétiques permet d'expliquer des différences de déclin observées entre les espèces d'une communauté de pollinisateurs dans le sud de la Corse (France), échantillonnée à deux reprises à un siècle d'intervalle. Dans le premier chapitre nous faisons un état de l'art des recherches sur le mimétisme chez les aculéates tout en identifiant des directions pour la recherche à venir. Dans le second chapitre nous quantifions la ressemblance entre espèces d'une communauté entière dans le sud de la Corse pour identifier des cercles mimétiques. Une phylogénie de la communauté est reconstruite afin de tester une ressemblance due à une ascendance commune. Nous démontrons une évolution phénotypique converge entre espèces en sympatrie dans la communauté. Dans le troisième chapitre nous nous demandons si ces interactions mutualistes peuvent augmenter la persistance des espèces (les espèces des cercles numériquement bien protégés survivent mieux au cours du temps). Dans un premier temps nous utilisons un modèle mathématique pour estimer la dynamique de population au sein de la communauté mimétique, en testant l'effet de paramètres d'intérêt sur les risques d'extinctions. Ensuite nous testons notre hypothèse sur les données empiriques de la communauté. Bien que l'on observe théoriquement et empiriquement une tendance qui confirme nos prédictions, les résultats ne sont pas concluants et nous proposons des perspectives pour élucider ce lien potentiel entre déclin de pollinisateurs et interactions mimétiques.

Mots clés : [Cercles mimétiques, aposématisme, hyménoptères, écologie des communautés, co-extinctions]