Fig. 2   The MEKRE93 pathway. A. Expression patterns of Krüppel homolog 1 (Kr-h1), E93 and Broad complex (BR-C) in hemimetabolan insects (*Blattella germanica*). B. Expression patterns of Kr-h1, E93 and BR-C in holometabolan insects (*Tribolium castaneum*). C. The MEKRE93 pathway in hemimetabolan and holometabolan species. See the text for additional information and sources.

interactions, and additionally discovered that BR-C and Kr-h1 are reciprocally activated. In sharp contrast, and as shown mainly by the group of Riddiford in the decade of 1990, BR-C triggers the formation of the pupal stage in holometabolan species, where JH inhibits the expression of *BR-C* during larval stages and stimulates *BR-C* expression after pupal commitment (Fig. 2B). In 2019, Chafino and co-workers showed that E93 is involved in triggering the pupal stage, as it promotes *BR-C* expression in *T. castaneum*. The whole data indicates that the MEKRE93 pathway is conserved in the holometabolan species, which added the E93/BR-C interaction loop to the ancestral (hemimetabolan) pathway during the evolutionary transition from hemimetaboly to holometaboly (Fig. 2C).

Disclosure of interest   The author declares that he has no competing interest.

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Evolution of aposematism and mimicry in butterflies: Causes, consequences and paradoxes

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Insects represent valuable food for many predators, and as such they have evolved a large panel of anti-predator adaptations. While deceptive adaptations such as camouflage and masquerade rest on avoiding detection by predators, aposematism relies on advertising chemical defenses with conspicuous warning signals, such as colorful patterns. Because the efficiency of a warning signal increases with its own local abundance, multiple aposematic prey exposed to the same predators benefit from converging on the same warning signal, a phenomenon originally observed by Henri Bates and Alfred Wallace and later understood and formalized by the German naturalist Fritz Müller [1] and called Müllerian mimicry. Convergence in warning signal is therefore due to positive frequency-dependent selection, leading to a 'strength in numbers' effect. Species sharing the same warning are said to be co-mimetic and interact mutualistically (i.e. individuals from either species benefit from the presence of individuals of co-mimetic species), and form mimicry rings.

Müllerian mimicry exists in a variety of organisms, including frogs, wasps, millipedes and beetles, but it has been best studied in butterflies (Fig. 1). Two neotropical butterfly clades have attracted considerable attention: the genus *Heliconius* (43 species) and the tribe Ithomiini (393 species).

Here, I review recent genetic and ecological results on *Heliconius* and Ithomiini butterflies that advance our knowledge on the proximal and ultimate drivers of mimicry, and on the evolutionary and ecological consequences of mimicry in terms of speciation, genetic architecture and ecological niche evolution. I also present recent results that help us understanding two apparent paradoxes: the embarrassing diversity of mimicry patterns despite strong selection for convergence, and the evolution of transparent wing patterns in aposematic butterflies, where conspicuous signals are supposed to be favored.
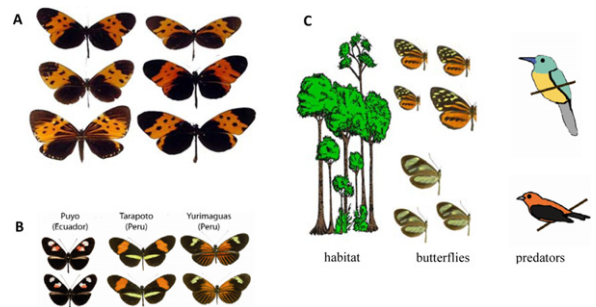
Fig. 1   A. A common mimicry ring in the Andean foothills. Left column, from top to bottom: *Hypothyris mansuetus* (Nymphalidae: Ithomiini), *Hyposcada anchiala* (Nymphalidae: Ithomiini), *Chetone* sp. (Erebidae: Arctiinae). Right column, from top to bottom: *Mechanitis messenoides* (Nymphalidae: Ithomiini), *Heliconius numata* (Nymphalidae: Heliconiini), *Melinaea mothone* (Nymphalidae: Ithomiini). Photo credit: Mathieu Joron. B. Co-mimetic subspecies of *Heliconius melpomene* (top) and *H. erato* (bottom) in three different regions of their common range, showing geographic variation in wing colour pattern. Photo credit: Jim Mallet. C. An illustration of microhabitat segregation of predators and mimicry rings. Illustration credits: Nicolas Chazot (trees) and Marianne Elias (birds); photo credits: Keith Willmott.

Selection on convergent wing colour pattern among mimetic butterflies is obviously strong, as illustrated by the striking similarity among distantly related species (Fig. 1A). Such convergent selection is expected to reduce warning signal diversity. Yet, diversity in warning signals is pervasive, at several geographical scales (Fig. 1B,C). Is this diversity transient, or is it stable? If so, what maintains it? Convergence in warning signal is driven by local predation pressure. Therefore, prey exposed to different communities of predators are not expected to converge on the same warning signal, as shown by theoretical models. In practice, geographical subspecies of mimetic butterflies, which occur in different regions, are exposed to different suites of predators and often harbour different colour patterns (Fig. 1B). At a much smaller scale, it has been shown that predators are segregated by microhabitat locally (for instance, some live in the canopy while other occupy the understorey), such that distinct mimicry rings can be maintained in different microhabitats (Fig. 1C). Therefore, mimicry diversity at various ecological scales can be maintained due to predator segregation [2].

Mimicry is also believed to be a driver of speciation. Indeed, in species harbouring multiple subspecies with distinct colour patterns (Fig. 1B), hybrids between subspecies typically have a recombinant, non-mimetic colour pattern, and suffer increased predation. Colour pattern is also often used as a mating cue such that mimetic butterflies mate assortatively, a likely consequence of selection against non-mimetic hybrids (reinforcement). Therefore, shifts in mimicry pattern causes both post- and pre-mating reproductive isolation, and, ultimately, speciation [2]. Mimicry may therefore be one of the factors explaining the high diversity of Müllerian mimetic butterflies. Mimicry raises the question of how convergent phenotypes are produced in different species. Are the same genes involved? Comparative analyses of genomic architectures controlling mimicry patterns in *Heliconius* reveal that homologous chromosomal regions, the "wing patterning toolkit" control much of mimicry variations in most species [2]. Some of the genes involved have now been characterized, and include the transcription factor *optix*, the morphogen *WntA*, the cell-cycle regulator *cortex* and the transcription factor *Aristaless1*. Mimicry between *Heliconius* lineages has occurred through parallel evolution (independent recruitment of the same genes), except in a few cases where there is evidence for adaptive introgression of wing pattern genes [2]. Mimicry can also incur strong selection on the genetic architecture of genes controlling colour pattern variation, as has been shown in the species *H. numata*. This species is unusual in that it is polymorphic within populations. Unlike other *Heliconius* species that embrace multiple species with distinct colour patterns, crosses between individuals harbouring different colour patterns that co-occur in *H. numata* never produce offspring with intermediate colour pattern. Instead, offspring look like either of their parents. Recent genetic and behavioural studies have shown that all variation is controlled at a single locus containing tightly linked genes (i.e. a supergene), and that different colour patterns correspond to different supergene haplotypes, which are characterized by different inversions of chromosome fragments within the supergene. Therefore, recombination between morphs is strongly reduced. Moreover, there is a strict series of dominance among morphs that co-occur. Both mechanisms prevent the formation of intermediate colour pattern, and have likely evolved as a response to selection against individuals with such intermediate, non-mimetic colour patterns [2].

Selection incurred by mimicry can also affect multiple ecological dimensions. Indeed, mimicry rings are segregated by microhabitat and habitat, and theoretical work and phylogenetic comparative analyses on Ithomiini butterflies have shown that the association between mimicry and (micro)habitat is adaptive, i.e. it is not due to shared ancestry, but most likely to selection for convergence on both colour pattern and ecological niche [2]. Moreover, since larval hostplants are also likely segregated ecologically, co-mimetic species tend to use the same hostplant more often than expected at random. Therefore,

mimicry, a kind of mutualistic interaction, drives convergence along multiple ecological dimensions, not only colour pattern. Finally, although the efficiency and memorability of a warning signal increases with its conspicuousness, the vast majority of Ithomiini species are transparent to some degrees, although all of them have conspicuous pattern elements (Fig. 2). Why has transparency evolved in aposematic butterflies? Bird vision modelling and detectability and palatability tests with bird predators have shown that transparent species are less detectable than opaque species; yet, they are no less unpalatable, and in fact they may even be more unpalatable [3]. Transparent species probably make the best of both worlds: they suffer less attacks from naïve predators because they are less often detected and, if they are detected by an 'educated' predator, they are not attacked because they are recognized as unpalatable. However, all else being equal, the predator learning process is expected to take longer with transparent than with opaque butterflies. Since increased unpalatability increases predator learning rate, we hypothesize that transparency can only evolve in highly unpalatable lineages, where it is less costly in terms of predator learning, which is consistent with the observation that all transparent species studied thus far are highly unpalatable.

In conclusion, Müllerian mimicry is a compelling example of the power of natural selection, where the evolution of defences against predators drives the evolution of conspicuous warning signals, which in turn drives convergence in those signals. Evolutionary implications of mimicry go well beyond warning signal convergence, since mimicry also affects the evolution of the ecological niche at various scales, and the genetic architecture of warning signals. The apparent paradox of the maintenance of mimicry diversity is now well understood, but the origin of diversity in the first place is still puzzling, since new warning signal are initially rare and should be selected against. However complex cognitive strategies of predators, such as the optimal sampling strategy, may protect rare warning signals, thereby enabling them to increase in frequency until they are common enough to be recognized and avoided by a large number of predators, and may be part of the explanation of the origin of diversity.

Finally, another apparent paradox, the evolution of transparent wing colour patterns in aposematic butterflies is also now understood. Yet, transparent wings, which entail a reduction in membrane coverage by scales and a reduction in wing pigmentation, may incur costs in terms of thermoregulation and hydrophobicity, which remain to be explored.

Fig. 2   *Pagyris cymothoe*, a species with transparent wings harbouring some conspicuously coloured pattern elements, and less detectable than opaque relatives. Photo credits: Marianne Elias.

Disclosure of interest　　The author declares that she has no competing interest.

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Session III. Social insects and other

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Supergene, sex and sociality

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Intraspecific variability in social organization is common, yet the underlying causes are rarely known. I will show that the existence of two divergent forms of social organization in six ant species is under the control of a pair of heteromorphic chromosomes that have many of the key properties of sex chromosomes. In particular, this social chromosome contains a large (13 megabases) region in which recombination is completely suppressed via three large inversions (Fig. 1). These findings highlight how genomic rearrangements can maintain divergent adaptive social phenotypes involving many genes acting together by locally limiting recombination.
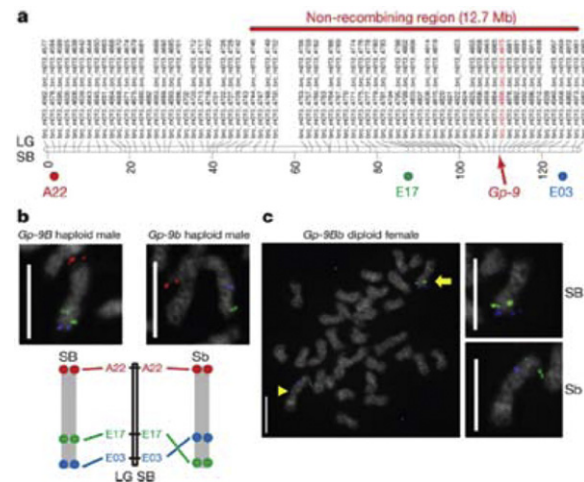
Fig. 1　Fine scale mapping and BAC-FISH analysis of social chromosome.

Disclosure of interest　　The author declares that he has no competing interest.

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Termites: Soil engineers for ecological engineering

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This communication assesses advances in our knowledge of the beneficial influences of termites on ecosystem functioning and services. Termites are amongst the main macroinvertebrate decomposers in arid and semi-arid environments and exert additional impacts through the creation of biostructures (mounds, galleries, sheetings, etc.) with different soil physical and chemical properties. Unfortunately, the positive 'or bright' role of termites is often overshadowed by their dark side, i.e. their status as pests threatening agriculture in the tropics (635 vs. 164 articles referenced in WoS with termites and either pest or ecosystem engineer as keywords. Source: WoS, April 2019). Termite impacts on soil properties and water dynamics can be differentiated at four different scales: (i) at the landscape scale, where termites act as heterogeneity drivers; (ii) at the soil profile scale, where termites act as soil bioturbators; (iii) at the aggregate scale, where they act as aggregate reorganizers; (iv) and last, at the clay mineral scale, where they can act as weathering agents [1].

In this communication, two examples of ecosystem services provided by termites are given.

The first describes the positive impact of termites on water infiltration and nutrient guidance at small scale through the production of foraging galleries in soil [2] and how this activity can be used to improve agro-ecosystem functioning in arid and semi-arid environments [3].

The second example deals with the construction of mounds and sheeting by termites in "natural" environments [4] and how these "patches of biodiversity and fertility" can be used in the lower Mekong Basin to reduce food insecurity and to provide a better access to health [5] (Fig. 1).

Finally, the perception of termite mounds in Southern Indian rural environments (Fig. 2) is discussed and used as example of the cultural services that can be provided by termites in some circumstances. The story of Valmiki, the author of the Ramayana, is explained and used as a parable for highlighting the interconnection between the "bright" and "dark" sides of termites, and more generally that to get the bright we also need the dark.