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The origin, genomics and evolution of female-limited polymorphisms

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There is a growing interest in the genomic and developmental basis of discrete or multimodal phenotypes governed by genetic polymorphisms. Recent research has uncovered the genomic basis of such polymorphisms and their maintenance through balancing selection such as negative frequency-dependent selection (NFDS). Such polymorphisms often originate through structural genomic changes or through mutations in regulatory genes. Historically, researchers focused on male-limited polymorphisms and intrasexual competition as drivers of NFDS. However, an increasing number of female-limited polymorphisms are being discovered, with sexual conflict, social selection or natural selection maintaining such polymorphisms. Still, significant gaps in our understanding of female-limited polymorphisms linger, partly as a historical legacy of a male-centric research focus on conspicuous male phenotypes. We review and synthesize female-limited polymorphisms, their maintenance, genetic architecture, genomic basis, developmental origin, microevolutionary dynamics and macroevolutionary diversification. Animals with female-limited polymorphisms include invertebrates (e.g. bedbugs, butterflies, damselflies and fruit flies) but also vertebrates (e.g. birds, mammals and reptiles). By highlighting female-limited polymorphisms, we draw attention to the unique sex-specific selection pressures on females distinguishing them from male-limited polymorphisms. Finally, wee present a conceptual model aimed to explain the origin and evolution of female-limited polymorphisms and outline future research avenues in this emerging field.

This article is part of the theme issue 'Exploring negative frequency dependent selection across levels: from genetics to ecology and back again'.

1. Introduction

The evolution of phenotypic diversity has fascinated biologists for a long time. How and why did this enormous diversity we see evolve, and what are its ecological consequences? Historically this phenotypic variation has been attributed to niche differences and divergent patterns of natural or sexual selection between species that inhabit different physical or biotic environments [1,2]. However, striking phenotypic variation is also common within species [3]. Such adaptive, intraspecific phenotypic variation can be found between sexes (sexual dimorphism), can be expressed as discrete morphs shared between the sexes [4], or may be found only within only one sex (male-limited [5,6] and female-limited polymorphisms [7–9]).

Sexual dimorphism is the most well-understood form of intraspecific phenotypic variation. Sexual dimorphism is driven by sex-specific selection that favours different phenotypes or trait combinations in males and females, owing to different sex-specific fitness optima [10,11]. Sexual dimorphism can evolve from ecological resource competition [3], such as when males and females exploit different ecological niches [12,13], and can be advantageous for populations overall owing to reduced ecological competition between the sexes [14]. However, sex-specific selection can also cause intralocus sexual conflict [15–18], which raises questions about the mechanisms that maintain sexual dimorphism through time [19].

Another form of intraspecific phenotypic variation is the stable co-occurrence of two or more discrete or multimodal heritable phenotypes (morphs) within one or both of the sexes [7,20–24]. When morphs have a genetic basis (governed by allelic variation at one or more loci) they are classified as *polymorphisms*, as opposed to purely environmentally induced phenotypes, so-called *polyphenisms* [25–27]. In this review, we focus on heritable (genetic) polymorphisms. Interested readers can find extensive reviews on polyphenisms governed by diet and other environmental factors elsewhere [27,28].

Recently, Mank [23] defined *sex-specific morphs* as discrete phenotypes differing in many disparate traits, expressed in only one sex. Just like the sexes, such sex-specific morphs often differ along several phenotypic traits [29]. Such traits include gene expression profiles [23,30], hormone levels [31,32], immune function [33], body size [34,35], body shape [36], fine-scale morphology [37–40], temperature tolerance [41], colouration [42] and mating behaviours [35,43–45]. How do these multi-trait differences remain correlated within morphs? Such trait differences raise questions about the underlying genomic architectures and selection pressures that preserve morph differences against the eroding force of recombination [29,46]. Explanations for such morph differences include regulatory genes of major effect with widespread pleiotropic effects such as genes for steroid hormones in vertebrates [5,31,32], correlational selection for different trait combinations [29,46], a genetic architecture arising from inversion polymorphisms, physical linkage or supergenes [6,36,47,48] or a combination of these factors. Morph differences can also arise from polygenic architectures, such as threshold characters [49].

One fascinating question is the evolutionary maintenance of polymorphisms. Specifically, why does directional selection not reduce variation to a single morph over time, and why are morphs not lost by genetic drift? Sex-specific morphs have traditionally been studied in males and in relation to male competition for mates [23]. Once established, such male-limited polymorphisms are thought to be maintained by negative frequency-dependent sexual selection (NFDS), a form of balancing selection in which each male type has a fitness advantage when rare [43,45].

Polymorphisms that are limited to expression in females (female-limited polymorphisms) have historically received comparatively little attention [50] compared with male-limited phenotypic polymorphisms (figure 1). Female-limited polymorphisms occur in several insect groups, including fruit flies [51,52], beetles [40], damselflies [48], butterflies [53] and bedbugs [37,54], but have also been found in vertebrates like lizards [55–59] and birds [60–62] (electronic supplementary material, table S1; figure 2). Female-limited phenotypic polymorphisms could arise under strong female–female competition over resources for reproduction, or to avoid male mating harassment [63], for example females mimicking conspecific males. In many female polymorphic species, although not all, one female morph is phenotypically similar to males [7,8,51,52,60] (figure 1). As with male polymorphisms, the maintenance of female polymorphisms is often owing to various forms of balancing selection [48,64], including negative frequency-dependent selection (NFDS), which is widespread in both plants and animals [65–68]. Female-limited polymorphisms therefore raise interesting questions about the causes and form of selection on females, and require a broader research programme beyond the traditional male-centric programme, with its focus on male–male competition over females [34,36,45,69,70].

Here, we review the rapidly growing evidence for female-limited polymorphisms in the animal kingdom. We broadly define polymorphisms as the long-term co-existence of two or more heritable (genetic) forms within a species where the frequency of the morphs can clearly not be explained by recurrent mutations, following the classical definition by ecological geneticist E.B. Ford [20,71]. Female-limited polymorphisms are a subset of the broader class of sex-specific polymorphisms [23]. We first provide a brief overview with some illustrative examples (figure 1). We then discuss the ecological and social causes of the sex-specific selection pressures on female polymorphisms and how ecology and natural selection can interact with social or sexual selection and sexual conflict [11,41,72–75]. Next, we discuss the genomic and developmental basis of female-limited polymorphisms, including the roles of sex chromosomes, linkage, gene reusage and regulatory genes of major effects [51,76,77]. We discuss the fates and consequences of female-limited polymorphisms on macroevolutionary time scales, the role of long-term balancing selection and the possible role of introgressive hybridization [8,48,78]. We finish this review by presenting a conceptual model aimed to explain both the origin and maintenance of female-limited polymorphisms.

We focus on genomic and phylogenetic approaches, and our point of departure is population genetic theory for the maintenance of genetic polymorphisms through balancing selection [64]. We do not discuss the extensive behavioural ecology literature on alternative reproductive tactics in the game-theoretical tradition which was recently reviewed elsewhere [63]. Our general message is that although female-limited polymorphisms have historically been overlooked [50], they are actually more common than male-limited polymorphisms in some animal groups [7,9,60,79,80] (figures 1 and 2). Research on female-limited polymorphism can therefore provide new general insights into the evolution of balanced polymorphisms and balancing selection [64].

2. Diversity of female-limited polymorphisms

Female-limited polymorphisms have now been documented in a wide variety of taxa (figures 1 and 2, electronic supplementary material, table S1). Most of these have not yet been studied in detail, and our list of taxa will almost certainly grow over time. In one recent example, a female-limited plumage polymorphism in white-necked jacobin (*Florisuga mellivora*) hummingbirds

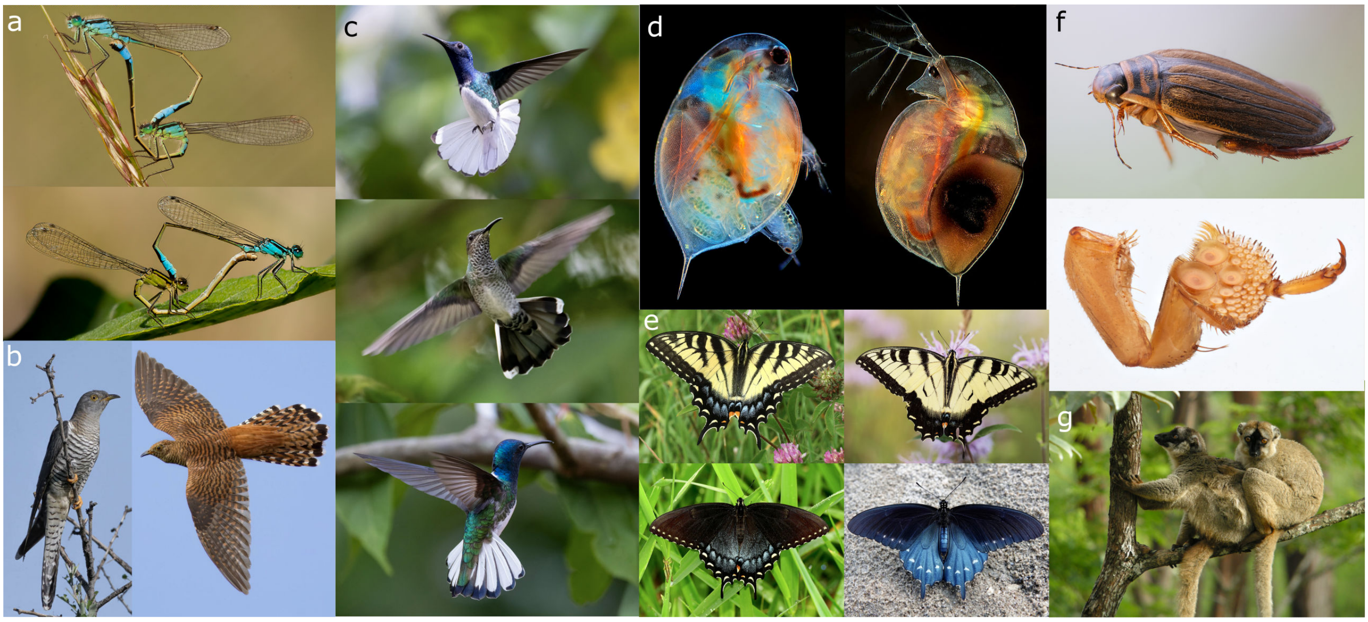

Figure 1. Diversity of female-limited polymorphisms in the animal kingdom. (a) Female colour polymorphism reducing male mating harassment in the damselfly genus *Ischnura* ('forktail damselflies'). (a) The evolutionarilyderived andromorph female of the common bluetail damselfly (*Ischnura elegans*) mating with a male (top). Bottom: another male mating with one of the two heteromorph females in this species. (b) Andromorph female (left) of the common cuckoo (*Cuculus canorus*) and the rufous female morph (right) is one of several avian examples of female plumage dichromatism. (c) Female colour polymorphism reduces social aggression in a hummingbird. Female plumage dichromatism in the white-necked jacobin (*Florisuga mellivora*); male (top), heteromorph female (middle) and andromorph female (bottom). (d) Some water fleas (genus *Daphnia*) have reproductive polymorphisms, where some females reproduce via cyclical parthenogenesis where they alternate between the production of sexual (right) and asexual eggs, while others reproduce exclusively asexually (left). (e) Female-limited Batesian mimicry in eastern tiger swallowtail (*Papilio glaucus*). Non-mimic female morph (top-left) resembles the males (top-right). Mimetic females (bottom-left) mimic the toxic pipevine swallowtail (*Battus philenor*; bottom-right). (f) Many species of diving beetles (Coleoptera: Dytiscidae) have polymorphic females that have either a smooth elytra or a rough, convoluted elytra structure sometimes with extended setae (top), that may reduce the clasping ability of males' front tarsal suction cups (bottom) during copulation attempts. (g) Some animal groups have female polymorphisms that are hidden to the human eye. Female brown lemurs (*Eulemur flavifrons*) have di- or trichromatic vision, creating differences in foraging under varying light conditions. Image credits: Photo credits: (a) Erik I. Svensson; (b) Macaulay Library left: ML617175231, right: ML621998799; (c) Macaulay Library, top: ML633356554, centre: ML628536787, bottom: ML632529357; (d) Marek Miś; (e) top left: Wikimedia Commons (PDM), top right: National Park Service—N. Lewis, bottom left: Wikimedia Commons (PDM), bottom right: NJ Carpenter; (f) top: Lars L. Iversen, bottom: Aslak Kappel Hansen; (g) Frank Vassen.

was first described in a small museum journal in 1950 [81], but this was not confirmed until more than 70 years later [61], showing that even published examples can lie largely unnoticed for decades. This lag partly reflects historical research biases, which might have often favoured male subjects [82], but could also reflect a general bias in ecology towards visual and highly conspicuous (male) display traits in terrestrial vertebrates. Traditionally, ornamentation in females was viewed as either anomalous or simply as a correlated response to sexual selection on males [83], yet this perspective has begun to change in the past 25 years [84–86]. Recent attention to females is surely one reason for the growing number of described female-limited polymorphisms (figures 1 and 2; electronic supplementary material, table S1).

Although female-limited polymorphisms were historically thought to be less common compared with male-limited polymorphisms [50], this also depends on the definition of polymorphism. In some animal groups, it is actually the opposite: female polymorphisms are more common than are male polymorphisms [8,9,60,87]. The most obvious polymorphisms to humans are those that are easily identifiable by human vision, such as colour polymorphisms. Female-limited polymorphisms could also involve non-body traits like egg colour, which is uniquely expressed by females and not by males. For example, in some species of brood parasitic birds, different female strains (or 'gentes') produce eggs of different colours that mimic the eggs of different hosts, enabling them to more efficiently parasitize these hosts [88–90].

Many female-specific traits are involved in offspring production. For example, social insects can produce split sex ratios, in which some females produce daughters, while others produce sons [91]. This is also the case in the fungus gnat *Bradysia coprophila* [92]. In social insect colonies, the number of queens is sometimes polymorphic [93]. Life history traits, behaviour and offspring sex ratios have also been shown to differ between females carrying different genotypes at the sex chromosome in several rodents with non-canonical sex determination systems [94,95]. In several invertebrates, there exist reproductive polymorphisms, where females reproduce either via parthenogenesis or via other reproductive modes (usually facultative or cyclical parthenogenesis) [96,96–98].

Female-limited polymorphisms can sometimes be difficult to detect, such as those involving the sensory system—for example, polymorphisms expressed in the colour vision of most New World monkeys (Platyrrhini) and some lemurs (Strepsirrhini) [99,100]. In contrast to most mammals, which have dichromatic vision, and catarrhines (apes and Old World monkeys), which exhibit routine trichromacy, female New World monkeys and some lemurs can have either di- or trichromatic vision owing to a polymorphism of their medium/long-wavelength sensitive opsin gene [99,100] (figure 2). These examples from

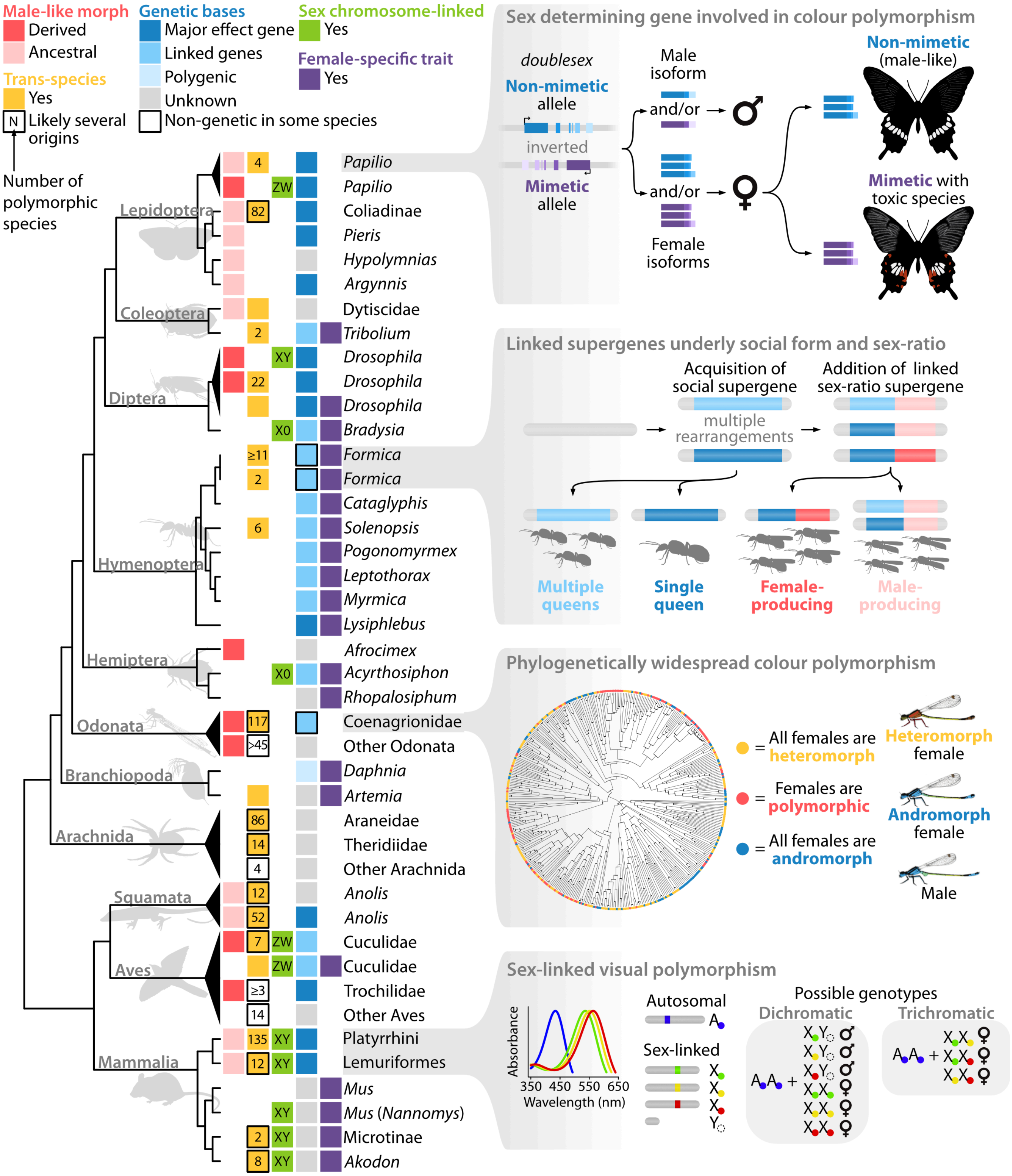

Figure 2. Widespread phylogenetic distributions of female-limited polymorphisms. Cladogram with arbitrary branch lengths depicting the relationship between the included taxa. Squares next to the cladogram illustrate (from left to right): **1**. The presence of a male-like morph and whether it is ancestral or derived. **2**. Whether the polymorphic is shared in two or more related species (number indicated in the square; polymorphisms that probably have multiple origins are indicated with a black border). **3**. Genetic basis: whether the trait is linked to the sex chromosome (sex determination system indicated in the square). **4**. whether the trait is female-specific, i.e. that males do not have the possibility to exhibit it (e.g. offspring production or female-specific castes). Right panel: four selected examples of female-limited polymorphisms illustrating the variation in the type of traits, genetic architectures and phylogenetic distribution. Additional information with references to the published literature can be found in electronic supplementary material, table S1. Silhouettes from Phylopic.org.

visual systems broaden the concept of polymorphisms and serve to remind us how alternative sensory modalities and traits other than colour polymorphisms may have been overlooked.

3. Ecological causes of polymorphism maintenance

Our knowledge about the ecological origin and behavioural consequences of female-limited polymorphisms is still limited, with some notable exceptions. Here, we discuss the ecological causes of polymorphism maintenance in the few organismal groups where a more extensive body of published research is available. Ecological factors that have been identified as sources of sex-specific selection on females include mating harassment and sexual conflict, abiotic factors like temperature, social selection and resource competition.

(a) Male mating harassment and sexual conflict

Male mating harassment of females and the resulting sexual conflict have been shown or suggested to maintain female-limited polymorphisms in several animal groups, including damselflies [9,65], diving beetles [40,101], bed bugs [37,54], cuckoos [62] and *Anolis*-lizards [58]. One well-studied group are damselflies (Odonata: Zygoptera), where female-limited colour polymorphisms are common. In the family Coenagrionidae ('pond damselflies'), such polymorphisms have evolved independently >40 times, and 28% of all species are polymorphic [9]. In the genus *Ischnura* ('forktail damselflies'), which is nested within this large damselfly family, polymorphisms have evolved up to 5 times [8]. The genus *Ischnura* has been especially well-studied in Europe [44,65,102–104], North America [105–107] and Japan [66,108]. The ancestral state was inferred to be sexual dimorphism with female monomorphism, i.e. a single female phenotype differing from males in colouration, typically denoted *heteromorph* [8]. However, at deeper phylogenetic nodes, this ancestral reconstruction is more uncertain owing to rapid evolution and high turnover of female colour polymorphisms, with frequent gains and losses of morphs [9].

From the ancestral state of heteromorph females, male-like females—here denoted *andromorphs*—evolved several times independently and were subsequently maintained as trans-species polymorphisms [78] that are currently shared between closely related species [8,48]. Genomic data have revealed a signature of long-term balancing selection, suggesting that NFDS has maintained these polymorphisms over millions of years and across species [48]. Although most polymorphic species in *Ischnura* have two female morphs (one heteromorph and one andromorph), one clade has evolved a third morph, a new heteromorph [8,102–104,109].

Morphs within a given sex can exploit the sensory biases of the other sex in an adaptive way through intersexual mimicry [43,110]. Intersexual mimicry has now been implicated in either males or females and in several different animal groups [35,45,111–113], with damselflies being one such example [105]. These female polymorphisms have been suggested to be maintained by NFDS arising from male mating harassment and sexual conflict, with andromorph females having an advantage through intersexual mimicry when rare [44,65–67,105,107,114]. Empirical support for frequency-dependent female fitness has been directly demonstrated or strongly inferred in several field and experimental studies [44,65,67,114–116], although other researchers have questioned this [117] and even claimed that such female morphs could be selectively neutral [118,119]. Nevertheless, molecular and genomic studies have decisively rejected this hypothesis of selective neutrality and have revealed the signatures of selection on these polymorphisms [48,120–122].

Male-like female morphs have been suggested to benefit from reduced detrimental and excessive mating attempts, presumably because their male-like appearance functions as intersexual mimicry [44,105,123]. Empirical support for this male mimicry hypothesis comes from lower male attention towards, and lower mating rates of, andromorph females compared with heteromorph females [44]. However, relative mating rates of andro- versus heteromorphs has also been shown to be density-dependent [44,102,104,124]. Recent comparative phylogenetic studies have shown that andromorphs are evolutionarily derived and arose from an ancestral state of heteromorphs and sexual dimorphism [8,9]. This supports the male mimicry hypothesis, since before male mimicry can evolve, there must (by definition) already exist an ancestral female morph (a heteromorph) that is not a male mimic [8].

Fincke [125] proposed an alternative frequency-dependent model for the maintenance of female-limited polymorphisms: the learnt mate recognition hypothesis. She suggested that mate-searching males develop a search image for common female morphs [125]. Males are assumed to harass common female morphs disproportionately, giving a fitness advantage to rare female morphs [125]. Plastic shifts in male search images were thus suggested to maintain female polymorphisms by NFDS. This proposed mechanism is similar to how predator learning generates apostatic selection on common prey phenotypes leading to NFDS [126,127]. The learnt mate recognition hypothesis therefore gives a central role to plasticity in the responses of antagonists (harassing males) in maintaining female-limited polymorphism and shows how plasticity and genetics interact in enemy–victim interactions. Behavioural and mechanistic studies provide some empirical support to the learnt mate recognition hypothesis, as mate preferences in damselflies and other insects are learnt and can change plastically in response to pre-mating interactions [44,115,128–132]. For example, in the common bluetail damselfly (*Ischnura elegans*), male opsin gene expression profiles, which are important in male colour vision, change plastically and partly predictably in relation to local frequencies of andromorph females [133].

The male mimicry and the learnt mate recognition hypotheses are certainly not mutually exclusive [41]. Both models require NFDS or some other form of balancing selection such as overdominance [64,134] to maintain polymorphisms over the long term. However, the learnt mate recognition hypothesis does not require a male-like female morph, nor does it uniquely predict that the male mimic should be in low frequency to function effectively in intersexual mimicry. Male mimicry alone without NFDS would require either a trade-off between natural and sexual selection, or mimicry being beneficial under some environmental contexts (e.g. at high density) while disadvantageous under other environmental contexts (e.g. low density). Trade-offs alone, without NFDS or some other form of balancing selection, are, however, unlikely to maintain stable polymorphisms in the long run [7,64], contrary to the claims by some authors [104].

Other insect groups with female-limited polymorphisms that are likely to be maintained by sexual conflict are diving beetles (Dytiscidae) [38–40,101,135] and bed bugs (Cimicidae) [37,54]. In these insect groups, females vary with respect to morphological (structural) traits, rather than colour, namely elytral structure (diving beetles) and copulatory organs (bed bugs), respectively. In diving beetles, females occur in two morphs: with a smooth or rough (granulated) elytra [38,40]. Biomechanical analyses of the adhesive force of male suction cups (which are attached to females during mating) are lower on the rough female morph, suggesting that female elytral roughness is a sexually antagonistic trait that reduces male mating harassment [38]. Males differ in their fine-scale morphology of their suction cups, with some male phenotypes being more adapted to attach to one of the morphs, resulting in assortative mating between male and female mating traits [40]. Such assortative mating promotes the formation of distinct genotypic and phenotypic clusters in males and females, and a highly dynamic intraspecific arms race driven by sexual conflict [40,101,136].

(b) The role of abiotic factors

Male mating harassment is certainly not the only selection pressure operating on female-limited polymorphisms. Sexual conflict is often also modulated by other environmental and demographic factors, such as sex ratios and population densities [137–139], environmental complexity and habitat structure [140,141], latitude [9] and ambient temperatures [41,142,143]. Lower temperatures have been shown to differentially benefit certain female morphs that differ in their tolerance to abiotic factors in both damselflies [41] and diving beetles [142]. Differential environmental tolerance of some morphs will generate environmental stochasticity that in turn can interfere with the more deterministic process of NFDS [144]. The interplay between the frequency-dependent conservative force of NFDS that prevents the loss of polymorphisms and opposes population divergence, and the frequency-independent effects of abiotic environmental factors can generate predictable evolutionary dynamics [144]. Such interplays between NFDS and abiotic factors can also affect the probability of evolutionary rescue [145].

(c) Social selection and resource competition

Not all female-limited polymorphisms have evolved primarily because of sexual conflict, even if they currently reduce mating harassment [80]. In hummingbirds (family Trochilidae), female-limited plumage colour polymorphisms with male-coloured females have evolved multiple times [60]. A recent phylogenetic comparative study estimated several independent evolutionary origins of such female-limited colour polymorphisms across the hummingbird clade and suggested that the ancestor was sexually dimorphic with monomorphic females [60]. This is similar to the situation in damselflies, where the ancestral state has been inferred to be monomorphic females differing from males (heteromorphic females) [8,9]. The comparative hummingbird study also suggested that neither intralocus sexual conflict, pleiotropy or other non-adaptive hypotheses could explain the origin and maintenance of these polymorphisms [60].

Field studies of the white-necked jacobin hummingbirds in Central America (figure 1c) revealed that andromorph females had higher access to feeders, probably because they suffered less from aggressive interference by both conspecific and heterospecific competitors, compared with heteromorph females [61,111]. Falk *et al*. argued that this female-limited plumage polymorphism is maintained by resource competition, rather than by sexual conflict, with andromorph females having an advantage in male mimicry owing to reduced aggression during interference competition [61,111]. Interestingly, both female morphs start out in early ontogeny in a male-like plumage, which is then progressively lost in the heteromorph females (80% of all mature females) as they reach adulthood [61]. This is a remarkable phenotypic convergence with female damselflies (*Ischnura elegans*) where all female morphs also start out with a male-like blue colour pattern on the abdomen, which is then gradually lost as the heteromorph females become sexually mature [123].

(d) Predation and other interspecific interactions

In swallowtail butterflies (genus *Papilio*), female Batesian mimetic polymorphism is common, with multiple independent evolutionary origins [146]. There are two or several female morphs mimicking the wing colour patterns of one or several unpalatable co-existing species [7,79,147]. The primary selective pressure explaining the maintenance of female polymorphisms and Batesian mimicry in *Papilio* butterflies is thought to be predator-mediated selection by birds on ovipositing females [7,79,146]. Some female morphs in *Papilio* are Batesian mimics of unpalatable species and these morphs are thought be favoured by NFDS through reduced predation [7,146]. However, reproductive interference between different species (the model and the mimic), female mate preferences (for non-mimetic males) [147,148] and male mating harassment of females could still play a role, even if these female polymorphisms did not primarily evolve because of sexual conflict [80,147]. Male *Papilio* butterflies are usually monomorphic [147] and the ancestral female morph is usually a male-like phenotype [146]. This contrasts strikingly with both damselflies [8,9] and hummingbirds [60], where male-like female morphs are derived, rather than ancestral.

Other systems where predation and interspecific interactions have been suggested to maintain female-limited polymorphisms include the back pattern dorsal polymorphism in brown anole lizards (*Anolis sagrei*) [55]. Finally, in brood parasitic birds and their hosts, both hosts and parasites have evolved egg colour polymorphisms in response to these antagonistic interspecific interactions in ongoing coevolutionary arms races [149].

4. Antagonistic selection, recombination suppression, supergenes and overdominance

When traits that benefit one sex are costly or harmful to the other sex, sexually antagonistic selection can give rise to intralocus conflict [15,150]. Such intralocus conflict can be resolved via the evolution of sex-limited phenotypic expression of autosomal loci [10], or through the evolution of sex-linkage [151] with different consequences for the heterogametic and homogametic sexes [152]. Intralocus conflict is not restricted to the two sexes, but could also operate when there are two or more morphs within either or both sexes [17,18]. The sex-linked colour morph locus on the W-chromosome in cuckoos that is only carried by females (figure 1b,c) [153] might suggest that intralocus sexual conflict was resolved via translocation, or that the conflict was never present from the beginning (assuming the locus first arose on the W-chromosome in these birds).

Evaluating the empirical support for these different evolutionary scenarios would require estimating the genomic location of the causal genes in outgroup species. The traditional theoretical assumption of the ancestral state in the evolution of sexual dimorphism is that novel mutations have equal phenotypic expression in males and females [10]. This assumption could be questioned as there are also plausible scenarios where sex-limited expression of new mutations was present already when they originated [154]. Partial expression of the morph locus in males (but with consequences that we have not yet discovered) remains another plausible scenario ripe for investigation.

Female-limited polymorphism can originate from structural rearrangements, followed by recombination suppression that can lead to the accumulation of duplications, transposable elements (TEs) and deleterious mutations within the inversion or nascent morph locus [48,134,155,156]. Genomic regions including loci for multiple traits encoded by several different genes have been called ‘supergenes’ [47,156–158]. Gutiérrez-Valencia *et al.* defined supergenes as *‘genomic regions with sets of tightly linked loci that control multi-trait polymorphisms under balancing selection’* [159]. Other historical definitions of supergenes come from Dobzhansky [160] (‘*coadapted combinations of several or many genes locked in inverted sections of chromosomes and therefore inherited as single units*’) and more recently Thompson & Jiggins [47] (‘*A genetic architecture involving multiple linked functional genetic elements that allows switching between discrete, complex phenotypes maintained in a stable local polymorphism*’).

The accumulation of slightly deleterious mutations in supergenes with reduced recombination can subsequently have consequences for the long-term maintenance of the polymorphisms [157]. Non-recombining haplotypes will increasingly appear in homozygote state as they increase in frequency in the population [134]. The mutation load at the morph locus will then be masked when such deleterious recessive mutations are kept at low frequency, but the fitness costs will become increasingly expressed as these mutations increase in frequency [134]. This results in an ‘internal’ form of NFDS arising from associative overdominance, where certain morphs have high fitness when being rare as heterozygotes, but where their fitness decreases as they increase in frequency and express the previously hidden mutation load [134,155–157,159,161]. This mechanism seems to play a part in the maintenance of colour polymorphisms on supergenes in *Helioconus* butterflies [134] but has not yet been detected in any system of female-limited polymorphisms, to our knowledge.

5. Genomic and developmental basis

(a) The role of sex chromosomes and autosomes

Early hypotheses for the genomic basis of female-limited polymorphism focused on the proximate role of female-specific sex chromosomes. Some taxa with female-limited polymorphisms have female heterogamety (e.g. ZW sex chromosomes), such as butterflies and birds [162]. The W chromosome, being unique to females in these groups, seems like a straightforward candidate that could harbour alleles governing female-limited polymorphisms without any pleiotropic effects on males. However, both foundational work using classic genetic tools like breeding experiments [163] and recent genomic research reveal a more diverse and complex genetic landscape than initially anticipated, with autosomal inheritance being more common than sex-linked inheritance [53,59,76,164,165]. The empirical support for sex chromosomes playing a major part in the origin and evolution of female-limited polymorphisms is therefore modest.

In addition, W chromosomes are often gene-poor and subject to rapid evolutionary turnover [166], limiting their potential general role in explaining widespread female-limited polymorphisms. However, in both common and oriental cuckoos (genus *Cuculus*), female plumage dichromatism (figure 1b) is strongly associated with content in the female restricted genome (either the W chromosome or the mitochondria) and this trans-species polymorphism has been maintained by balancing selection across speciation events [153].

Female-limited polymorphisms also exist in species with XY sex determination systems, and sometimes sex chromosomes are involved here too. For example, abdominal colouration in *Drosophila erecta* - a polymorphism that has been maintained by long-term balancing selection [51] - is associated with alleles located on the X-chromosome. Another example is the dichromatism–trichromatism in New World primates, which is caused by the presence of multiple alleles located on the X chromosome [167]. With these two exceptions of sex-linkage, most female polymorphisms investigated so far are encoded by one or several autosomal loci, with sex-limited phenotypic expression. For example, early crossings and laboratory rearing experiments on multiple European and North American damselfly species of the genus *Ischnura* revealed a Mendelian genetic basis for female colour polymorphisms and an autosomal morph locus with female-limited phenotypic expression [103,109,168–170]. This was later confirmed by genomic studies revealing a trans-species polymorphism that is at least 5 Myr old [48]. In the trimorphic species *I. elegans*, the three female colour morphs arise owing to a single autosomal locus located within a region of reduced recombination on chromosome 13 [48]. This polymorphism emerged from a sexually dimorphic ancestor with only heteromorphic females, whereafter structural genomic changes gave rise to a new andromorph female [48]. Subsequently, a third female morph arose through ectopic recombination back into the ancestral haplotype [48].

(b) Genes of major effect and regulatory evolution

Genes of major effect have been shown to play a key role in some female-limited polymorphisms [78]. For example, the *Alba* polymorphism in the butterfly genus *Colias*, where females exhibit either orange or white wings owing to a reallocation of metabolic resources, is controlled by a dominant autosomal locus [53]. Here a TE insertion is acting as a *cis*-regulatory element (CRE) of the *BarH-1* gene [53,165]. Knockout experiments demonstrated the specificity of this CRE. While *BarH-1* knockout affects eye development in both sexes, a CRE knockout only impacted wing colour in *Alba* females, with no effect in males or orange females. TEs and sex- and tissue-specific CREs could thus mediate almost instantaneous ('saltational') evolutionary origin of sex-specificity with minimal impact on the male phenotype [53,171].

Another central theme in female-limited polymorphisms is regulatory evolution. Wing patterning polymorphisms, such as Batesian mimicry in the butterfly genus *Hypolimnas*, have been associated with TE insertions within the regulatory region of core developmental genes [172]. In *Hypolimnas misippus*, a TE insertion appears to have disrupted a preexisting CRE, resulting in a derived dominant allele and the return of an ancestral female form [172].

(c) Transcription factors, epistasis and endocrine regulation

The *doublesex* (*dsx*) gene, a key component of the insect sex determination pathway, seems to have frequently been involved in female-limited polymorphisms. A key role of *doublesex* is well-established in several species of *Papilio* butterflies, where different *dsx* alleles control distinct mimetic forms [76,164]. *dsx* and other genes in the *dmrt* family are particularly interesting because these transcription factors regulate both sexual dimorphism and govern intrasexual phenotypic variation [77,173]. Presumably, the expression of *dsx* and other genes within the *dmrt* family can be modulated to produce novel phenotypes within either sex by co-opting the pathway governing the development of sexual dimorphism [30,76,77]. Indeed, *dsx* has been associated with the development of female-limited forms in the tropical bluetail damselfly *Ischnura senegalensis* [174].

In fruit flies of the *Drosophila montium* group, another transcription factor gives rise to female-limited polymorphism: the gene *pdm3* is a hotspot for the recurrent evolution and multiple origins of male-like females [52]. Intronic mutations and structural variants within the *pdm3* gene are implicated in three independent evolutionary origins of female-limited colour polymorphisms [52]. Female-limited phenotypic expression of autosomal loci implies some epistatic interaction with female-restricted factors or pathways. Rather than through sex-linked inheritance [175], female-limited phenotypic expression is more often achieved by autosomal loci integrating various signals from the female-specific physiological and developmental internal environment. This includes hormonal cues, as demonstrated by oestrogen's role in the dorsal back pattern polymorphism in the brown anole lizard females [59]. In this lizard, the female-limited dorsal pattern is governed by the autosomal gene *CCDC170*, where female-limited phenotypes develop through co-expression between this locus and the nearby oestrogen receptor-1 (*ESR1*) gene [59]. In other lizards, such as side-blotched lizards (*Uta stansburiana*), both male and female colour polymorphisms may develop through differences in steroid hormone levels that are known to have multiple and pleiotropic effects on behaviours, reproductive traits, immune function, maternal effects and dorsal colour patterns [29,33,176]. In the damselfly *I. elegans*, although the colour morph locus is a single gene of major effect [48], hundreds of downstream genes are differentially expressed between female morphs during ontogeny and sexual maturation, revealing extensive pleiotropic effects of this morph locus [30].

Epistatic interactions involving hormones ensure that the polymorphic phenotype is expressed only in females, even when the primary genetic determinants are autosomal. While *Dsx* and other sex-limited transcription factors have so far only been directly associated with a handful of sex-limited polymorphisms, they might be involved in many other polymorphisms where the causal genes are located on the autosomes. In fact, *in silico* predictions of TF binding sites in *Colias* butterflies did detect the potential presence of *dsx* binding sites in the *Alba* allele in butterflies [53]. An interesting question is whether the more common occurrence of female-limited polymorphisms compared with male-limited polymorphisms in some taxa (e.g. butterflies and damselflies) is owing to the relative ease with which female-restricted trans-acting factors are co-opted in these taxa compared with male-limited factors.

6. Macroevolutionary history

Some female-limited polymorphisms are ancient and trans-specific; that is, they are found in two or more related species [8,78,153,177] (figure 2). The persistence of trans-species polymorphisms is an indication of strong balancing selection, such as NFDS, that operates over long evolutionary timescales [78]. Nonetheless, evolutionary loss of female-limited polymorphisms happens and can be caused by genetic drift such as when balancing selection becomes inefficient and when genetically effective population size (N_e) decreases [178].

The large number of trans-species polymorphisms and the patchy distribution of monomorphic and polymorphic species on phylogenies [9,60,179] could in principle be explained by three mechanisms that are not mutually exclusive : repeated losses, introgression or multiple independent origins (parallel evolution). In *Colias* butterflies, comparative phylogenetic and genomic studies strongly suggest a polymorphic ancestor followed by multiple losses, resulting in multiple monomorphic tip species [53,179]. By contrast, comparative phylogenetic studies in hummingbirds and damselflies have found strong empirical support for multiple independent origins, rather than repeated losses [8,9,60].

Repeated losses of the polymorphism are interesting because many of these female-limited polymorphisms are known to be under balancing selection within populations [51,53,67,153,177], which would prevent or at least delay their loss [64]. If

NFDS favouring rare or novel phenotypes is strong, adaptive introgression of novel morphs into a new species would become more likely. NFDS can also lead to the evolution of an oligogenic architecture (e.g. a major effect locus) from an ancestral state of a polygenic architecture, according to some theoretical models [180]. Signatures of introgression have been found at the loci underlying some polymorphic species [53,181] but not in other systems [153,177]. We do not yet know how common introgression is in explaining the phylogenetic distribution of female-limited polymorphisms.

Female-limited polymorphisms can have wide-ranging impacts across different temporal evolutionary scales. For example, they can alleviate the demographic costs of sexual conflict [137,138,182] by decreasing male mating harassment and increasing female fitness, thereby reducing population extinction risk [114]. Female-limited polymorphisms can also potentially influence macroevolutionary dynamics, such as speciation and extinction rates. Indeed, both colour polymorphic birds [21] and lizards [183] have accelerated speciation rates and/or net diversification rates compared with monomorphic taxa within these clades. As a cautionary note, estimating extinction rates from molecular phylogenies alone has been a subject of considerable controversy [184,185]. Theory suggests that runaway processes driven by sexual conflict (such as in diving beetles [40]) can either increase the rate of population divergence and elevate speciation rates between allopatric populations [186] or, alternatively, fuel balancing selection such as NFDS, which would constrain population divergence and speciation [40,65,101,136]. Female-limited polymorphisms could also stabilize population divergence, increase population fitness and reduce extinction risk [40,65,67,114].

Female-limited polymorphism can potentially evolve from ancestral states where morphs were expressed in both males and females but where the polymorphism was subsequently lost in one sex, by genetic drift or selection. There are many examples where the same polymorphism (e.g. in colour) is expressed in both sexes, e.g. white-throated sparrows (*Zonotrichia albicollis*) [4] and side-blotched lizards (*U. stansburiana*) [18,45,187]. Among 82 species of *Anolis* lizards that have polymorphism in dewlap colour, 12 cases were female-limited, 41 male-limited and 29 shared polymorphisms [87,188]. In spiders, 104 out of the 133 colour polymorphic species are female-limited, 26 are shared and only 3 are male-limited polymorphisms [87]. Many of these occurrences might represent independent origins, but at least some of these might have a common origin, with different sex-specific losses in different lineages. Estimating the ecological factors that favour evolutionary transitions to and from sex-limited phenotypic expression should be an important goal for future research.

7. Conceptual model for the origin of female-limited polymorphisms

Our overview has revealed that multiple and different selection pressures, such as NFDS [68] or other forms of balancing selection [48,64], can maintain such polymorphisms. NFDS can arise from male mating harassment [44,65,67,114], social selection and resource competition [60,61,111] and visual predators that promote and maintain female-limited polymorphisms [55] and mimicry [7,79,146]. The genomic basis of female-limited polymorphisms obviously varies between different systems. Chromosomal inversions, gene duplications, TEs and recombination suppression play key roles in some cases [48,53], whereas in other cases regulatory genes of major effect such as *dsx* [76] and *pdm3* [52] have been identified.

Considering this genomic and ecological diversity, is it possible to formulate a general model for the evolutionary origin and maintenance of female-limited polymorphisms? We believe that this is possible, taking the concept of the adaptive landscape [189,190] as our point of departure (figure 3). When there are two or more female morphs within a population these can be conceptualized as occupying different adaptive peaks on a complex multi-peaked fitness surface (figure 3). Here we discuss three scenarios in which new fitness peaks may appear and become occupied by different female morphs.

In the first scenario, we envision an ancestral state with one male and one female adaptive peak, whereafter a new adaptive peak or social niche opens to females (figure 3A). Such a new adaptive peak can emerge, for example, if male mating harassment intensifies and sexual conflict reduces the fitness of the ancestral female phenotype. This would open for a gene of major effect or a regulatory gene like *dsx* or *pdm3* that would produce a novel male-like female morph almost instantaneously. The novel female morph would then climb upwards towards the novel male mimicry peak close to the male phenotype, followed by the evolution modifier loci of minor effect that fine-tune such intersexual mimicry (figure 3A). Through ‘cross-sexual transfer’, such a peak shift would require little change in the genome [28,193]. Andromorph females could thereby arise through a small genetic change causing a major phenotypic change simply by co-opting the sex-differentiation pathway (figure 3A). Subsequent modifications by genes of minor effect can improve male mimicry further (figure 3A). New female morphs can subsequently emerge, for example through ectopic recombination between existing morphs enabling the occupation of additional adaptive peaks (figure 3A).

A second scenario is represented by the mimicry polymorphisms in *Papilio* butterflies [146]. Here, the original female phenotype was closer to the male phenotype and the ancestral state was sexual monomorphism [146]. Intense predation on ovipositing females gave rise to several new adaptive peaks, by which novel female morphs started to mimic co-occurring model species and achieved fitness benefits through Batesian mimicry (figure 3B). In this scenario, simple genetic changes [76] also gave rise to novel female phenotypes that were able to occupy novel adaptive peaks, thereby presumably disrupting predator search images and reducing mortality during ovipositioning (figure 3B).

A third scenario are female polymorphisms where none of the female morphs are male-like, or where females are more variable than males overall (figure 3C). This scenario might apply to colour polymorphisms in spiders where female-limited polymorphisms are more common than male-limited polymorphisms [87,194] and to colour polymorphisms in *Anolis* lizards [188]. In these systems, polymorphic signals are highly evolutionarily labile, with rapid transitions between female-limited, male-limited and shared polymorphisms (figure 3C). This can happen when the number and identity of colour-encoding loci shift over short time scales within species [195].

While in scenarios 1 and 2 genetic constraints might limit the number of niches available, in the third scenario such constraints are lower and there are many more potential adaptive peaks that subsequently become occupied. Populations and

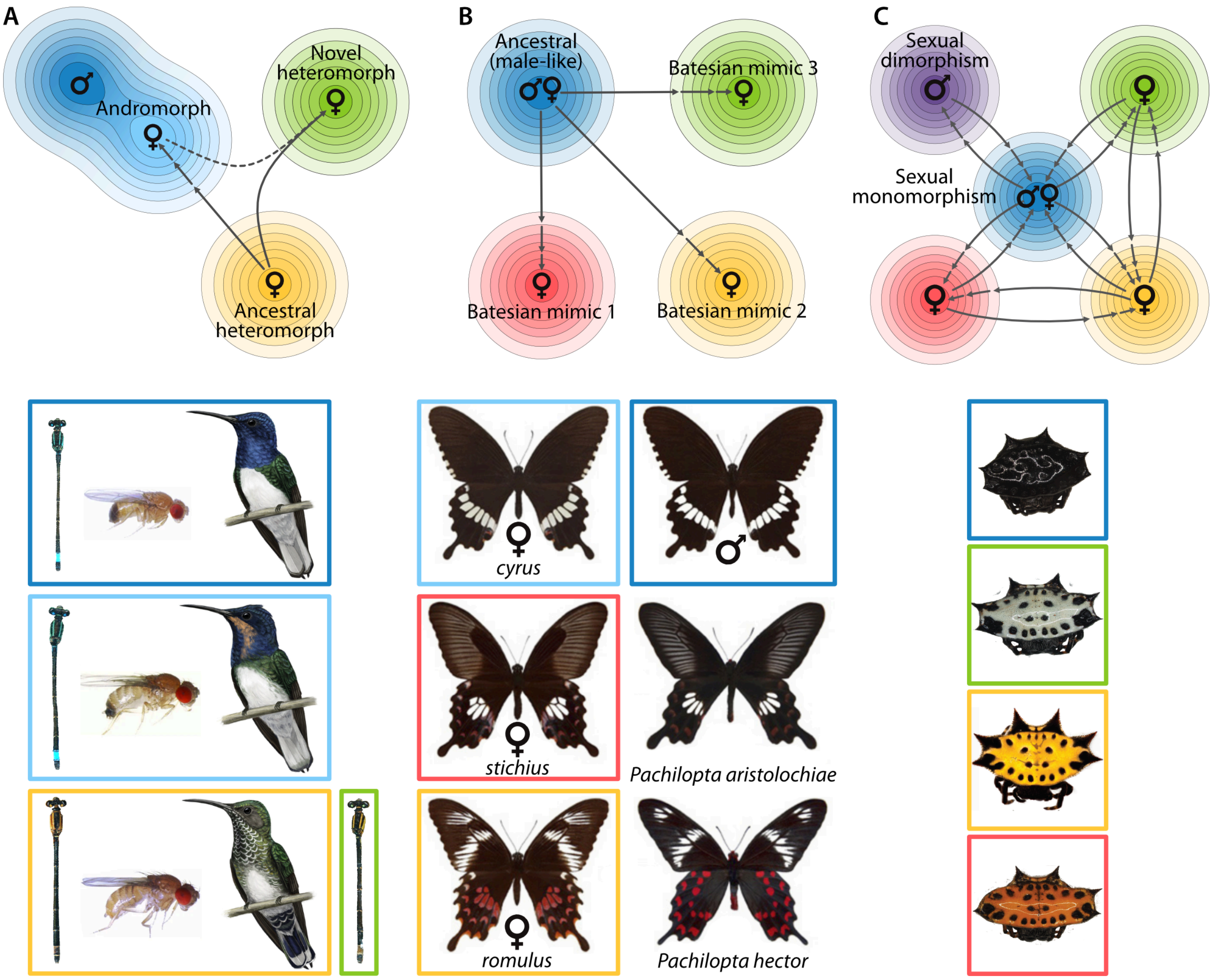

Figure 3. Graphical model for the evolution of female-limited polymorphism from different ancestral states. The model is built on the framework of the adaptive landscape [190] with multiple adaptive fitness peaks, corresponding to both the two sexes and different morphs within females. (A) Origin of female polymorphism from an ancestral state of sexual dimorphism, with a single female differing in phenotype (e.g. colouration) from males, here termed 'heteromorph'. Because of male mating harassment on females, like in damselflies [44], or competition for resources leading to social selection, like in hummingbirds [61], a new adaptive peak in the fitness landscape opens up, where male-like females gain fitness benefits owing to the reduction in sexual or social harassment. A gene of major effect that increases female similarity to males can then permit the occupation of this new adaptive peak (shown as long arrow from the ancestral female adaptive peak), followed by subsequent refinements of male mimicry through smaller steps and genes of minor effects (shown as progressively shorter arrows). This scenario is similar to the hypothesized evolutionary origins of interspecific Batesian and Müllerian mimicry [191] and the general recognition that genes of major effect can and do play important roles in the early stages of adaptive evolution [192]. The new peak can be reached by, for example, a chromosomal inversion reducing recombination, followed by the progressive evolution of a 'supergene' [48]. Subsequently, new morphs can emerge through ectopic recombination between the two already existing female morphs, which has happened in *Ischnura* damselflies [48]. This scenario is applicable to damselflies, hummingbirds and *Drosophila* flies [51,52] (illustrated below A), which all have male-like female morphs co-existing with heteromorph females. (B) Alternative scenario for the evolution of female-limited polymorphism from an ancestral state where females look like males (sexual monomorphism) and where females subsequently diversify into two or more morphs by mimicking sympatric toxic species (Batesian mimicry). This scenario captures the evolutionary dynamics of *Papilio* butterflies (illustrated below figure), where males are typically monomorphic, whereas females are polymorphic and mimic several different, more or less unrelated model species [79,146,147]. New female morphs (mimics) could emerge rapidly through mutations in regulatory genes of major effect [52,76]. (C) A third highly dynamic scenario with multiple male and female morphs where some morphs are sex-limited and others are shared between morphs. Such a situation may occur in spiders, where female-limited polymorphisms are more common than male-limited polymorphisms [87].

species may inhabit several such adaptive peaks while leaving many remaining open niches available, potentially leading to rapidly shifting population states. In this third scenario, the number of morphs may be more important than the actual morph identity, meaning that fine-tuning phenotypic mechanisms might be less common. Our conceptual framework here is general and can be applied to sex-limited polymorphisms within either females, males or both sexes.

8. Conclusions

Here, we have reviewed the increasing number of discovered systems where female-limited polymorphisms have been documented, across several orders and classes of animals (figure 2). Females experience unique sex-specific selection pressures caused by male mating harassment, owing either to vulnerability during oviposition or to targeted exclusion from resources. It is therefore not surprising that female polymorphisms have evolved in response to these and other sex-specific selection pressures. When female-limited polymorphisms involve intersexual or Batesian mimicry, the relative fitness of the different morphs should become frequency-dependent because mimics would sooner or later be detected by the antagonists via learning. When predators, competitors or harassing males rely on learning, rare deceptive phenotypes could persist over long evolutionary time scales owing to NFDS. Over macroevolutionary time scales, female-limited polymorphism may either be stably maintained or evolve rapidly, contributing to fast diversification of lineages. However, the causal links between signaler–response systems and the macroevolutionary consequences of female-limited polymorphism remain largely unknown. Further work should investigate how learning from antagonists (harassing males or predators) interacts with sex-limited polymorphisms in driving macroevolutionary trends.

The origin of female-limited polymorphism will also depend on the evolvability of traits and the origin of selectable variation. Specifically, how do novel female morphs arise, genetically and developmentally? Discrete phenotypic variation in females often originates from genomic structural variants, which can facilitate inheritance of co-adapted loci owing to suppressed recombination (figure 2). For instance, the structural variant responsible for the female-limited polymorphism in the damselfly genus *Ischnura* is caused by a locus on a chromosome with suppressed recombination with multiple regulatory regions that might coordinate different expression pathways across the genome [48]. Similar genomic architectures have been documented in male-limited polymorphisms with intersexual mimicry [110]. The ability to evolve such a master switch 'morph locus' probably exhibits some genomic contingency, with some lineages being constrained in their ability to generate novel morphs.

The evolution of discrete morphs within a sex requires that alternative downstream pathways be available to facilitate adaptive alternative output states. Future genomic and developmental research should focus on the capacity to evolve a master switch and the ability to express multiple and complex downstream pathways. Lineages that already express some form of discrete phenotypic variation (e.g. sexual dimorphism) could be 'pre-adapted' to evolve female-limited polymorphisms. Targeted investigation on developmental pathways (for instance, *Ischnura* damselflies and hummingbirds that both transition late in life from male-like to female-like forms) should increase our understanding of the mechanisms that facilitate or constrain sex-limited discrete variation. The role of developmental plasticity and cross-sexual transfer [28,193] in the origin of male-like females and male mimicry is largely unknown, yet it might have played a significant part in some female polymorphic systems [123]. By co-opting sex-differentiation and sex determination pathways governed by transcription factors like *dsx* [76], *dmrt* [173] and *pdm3* [52], female-limited polymorphisms with male-like females can rapidly evolve by simple genetic changes in key regulatory loci. Finally, experimental and mechanistic investigations of the expression of female-limited morph loci in males could be carried out in some model organisms like *Drosophila*, which have functional genetic resources that are unavailable in other systems [51,52].

The role of developmental plasticity in the origin female-limited polymorphisms is largely unknown. Schwander & Leimar [196] called for comparative studies where genetic polymorphisms and plastic polyphenisms are mapped onto phylogenies to infer ancestral states and character transitions between genetic polymorphisms and polyphenisms. For example, plastic polyphenisms could become stabilized against environmental perturbations following genetic assimilation of an ancestral genetic polymorphism [27,28,196]. More than a decade after Schwander's and Leimar's call for such comparative studies, little such research has been carried out, to our knowledge. One possible explanation for this lack of studies can be the difficulty of inferring ancestral character states on phylogenies for rapidly evolving traits [197].

Promising study systems where these questions could be addressed are within the insect order Odonata (dragonflies and damselflies), where heritable female-limited colour polymorphisms are widespread across phylogenies [9,198] and where age-related ontogenetic colour variation is also common [123,199]. Plastic colour variation expressed by females early in ontogeny [123,199] could potentially later give rise to adult female morphs through genetic assimilation [28]. Another promising study system could be the common blue butterfly (*Polyommatus icarus*), where females vary in wing colour from brown to entirely blue—the latter being very similar to males, which are also entirely blue [200]. The amount of blue on female wings has a genetic component but it is also influenced by thermal plasticity: larvae that are exposed to cold temperatures develop into blue-winged adult females [200]. Since blue wing colouration has both a plastic and a genetic component and varies geographically [200], different populations and geographic regions could be in different transitional stages between plasticity and genetic assimilation.

A key question is the importance of male mimicry (andromorph females) in some female-limited polymorphic systems. Have andromorph females specifically adapted to appear as males, or have they simply co-opted a pre-existing available pathway (i.e. gene pathway reuse [201])? Tracing down the downstream pathways from previously described morph loci using whole genome co-expression and proteomic networks could elucidate the extent to which the molecular basis of male-like female phenotypes is shared or novel, with respect to the model male. While pathways shared between the sexes do not necessarily resolve this question, novel pathways by which females would produce male-like phenotypes would imply adaptive convergence and strengthen the case for intersexual mimicry. Investigations of such mechanistic pathways should advance our general understanding of the developmental basis of intra- and intersexual diversity across the entire animal kingdom [23].

The maintenance of multiple female morphs takes place within specific biogeographic contexts, with larger ranges and more discrete and heterogeneous environments potentially favouring higher phenotypic variation within a sex [8]. This might explain some spider radiations on island archipelagos, where genomic architecture interacts with population structure across heterogeneous selection landscapes to produce polymorphisms that diverge between islands [202]. To elucidate the roles of biogeography and evolutionary history, further work should investigate the evolution of female polymorphism using explicitly process-based biogeographic and phylogenetic methods, incorporating the roles of ecological opportunity, habitat stability and genomic architecture. How genetic and phenotypic variation within species scale up and shape broad biogeographic pattern and the diversity of female-limited polymorphisms is largely unexplored.

Polymorphic females may avoid detection by predators [79], gain access to resources [61,111] or escape excessive mating harassment from conspecific males [44,114]. However, many other forms of female polymorphism may involve less conspicuous traits, for example different sensory modalities (figure 1), differing maternal investment or adaptive allocation of maternal effects [176]. We encourage further research on female-limited polymorphisms in maternal allocation and maternal effects, because these could offer exciting new avenues to generate evolutionary novelty through maternal–offspring coevolution and imprinting [203].

Finally, rapid technological development and the proliferation of ʼomics data could reveal new female-limited polymorphisms and increase our understanding of their evolutionary dynamics across time scales, from individuals to populations and to species and across adaptive and non-adaptive radiations. New female-limited polymorphisms are likely to be discovered in the future, particularly because more sophisticated clustering algorithms will enable us to identify and classify multimodal phenotypes using tools that overcome limitations of human cognitive biases, including our limited colour vision.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. Additional data are provided in Supplementary Material [204].

Declaration of AI use. We used Deep Seek and Chat GPT to obtain code to visualize the fitness landscapes in figure 3. Figures were later modified and refined using Adobe Illustrator.

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