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Review

Hybridization, sex-specific genomic architecture and local adaptation

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While gene flow can reduce the potential for local adaptation, hybridization may conversely provide genetic variation that increases the potential for local adaptation. Hybridization may also affect adaptation through altering sexual dimorphism and sexual conflict, but this remains largely unstudied. Here, we discuss how hybridization may affect sexual dimorphism and conflict due to differential effects of hybridization on males and females, and then how this, in turn, may affect local adaptation. First, in species with heterochromatic sexes, the lower viability of the heterogametic sex in hybrids could shift the balance in sexual conflict. Second, sex-specific inheritance of the mitochondrial genome in hybrids may lead to cytonuclear mismatches, for example, in the form of 'mother's curse', with potential consequences for sex ratio and sex-specific expression. Third, sex-biased introgression and recombination may lead to sex-specific consequences of hybridization. Fourth, transgressive segregation of sexually antagonistic alleles could increase sexual dimorphism in hybrid populations. Sexual dimorphism can reduce sexual conflict and enhance intersexual niche partitioning, increasing the fitness of hybrids. Adaptive introgression of alleles reducing sexual conflict or enhancing intersexual niche partitioning may facilitate local adaptation, and could favour the colonization of novel habitats. We review these consequences of hybridization on sex differences and local adaptation, and discuss how their prevalence and importance could be tested empirically.

This article is part of the theme issue 'Linking local adaptation with the evolution of sex differences'.

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1. Introduction

Here we outline how hybridization, through its effects on sex-specific viability, sexual conflict and sexual dimorphism, can contribute to sex-specific local adaptation. Recent research has highlighted the importance of understanding sex-specific local adaptation [1]. Sometimes, sexual dimorphism evolves in the same way and for the same reasons as sympatric ecological divergence and speciation, namely to reduce competition for resources [2]. Ecological divergence and sexual dimorphism may evolve at once [3] to maximize niche packing (see Glossary) [2–4]. In addition to classical examples such as the extreme sexual dimorphism in the beaks of the Huia [5], evidence from a wide range of taxa (e.g. birds [6], reptiles [7] and fish [8]) suggests that sexual dimorphism and niche partitioning may be important mechanisms to decrease competition for food resources between males and females. Moreover, different reproductive roles may lead to different requirements on body size, habitat use or diet. While such niche division can be advantageous, the genetic correlation between the sexes may constrain the evolution of sexual

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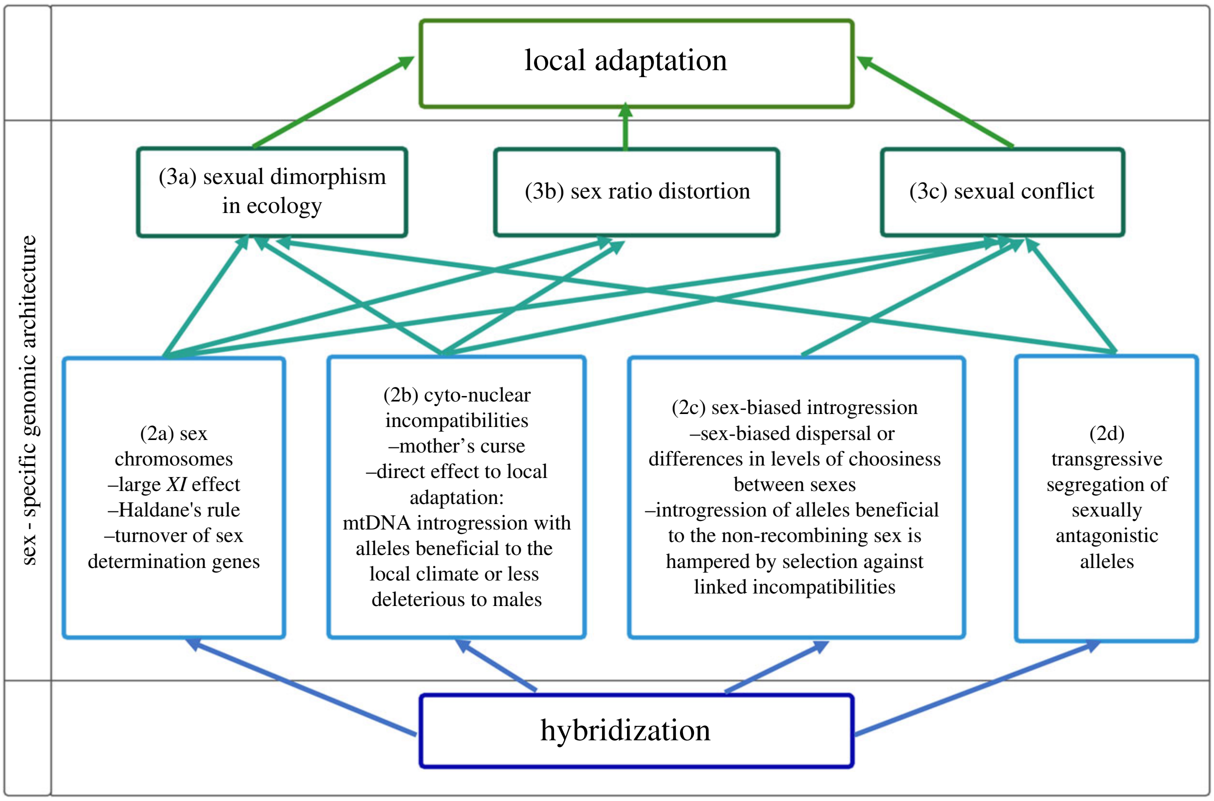

Figure 1. How hybridization may alter sex-specific local adaptation through its effects on sexual dimorphism, sex ratio and sexual conflict. This schematic illustrates the outline of the manuscript. In §2, we discuss how patterns resulting from hybridization may result in sexual dimorphism, sex-ratio distortion and affect sexual conflict. In §3, we address how resulting changes in sexual dimorphism, sex ratio and sexual conflict may affect local adaptation. (Online version in colour.)

dimorphism [9]. Unless resolved, selection towards different optima may result in both sexes residing away from their fitness peaks and hence sexual conflict [9].

Despite a long-standing research tradition investigating sex-specific viability and fitness effects of hybridization [10], and an increasing appreciation of the importance of mitonuclear co-adaptation for hybridizing taxa [11], the effects of these phenomena on the potential for local adaptation following hybridization remain largely unexplored. Sex-specific inheritance and recombination mechanisms could affect sexual dimorphism, interlocus sexual conflict (Glossary), sex-specific expression patterns or sex ratios in hybrids (figure 1), but this has never been the main focus of hybridization studies. Moreover, hybridization may reshuffle sexually antagonistic alleles leading to transgressive segregation [12], which may enhance sexual dimorphism in niche use. This could dampen intersexual competition and have important consequences for ecological niche breadth.

It is increasingly recognized that under certain conditions, hybridization may have a positive impact on local adaptation [13]. Traditionally, plant ecologists viewed hybridization as potentially beneficial to adaptive evolution [14,15], while zoologists viewed it mostly as a cause of maladaptive breakdown of isolating mechanisms [16]. Recent studies suggest that the tree of life is rather a net of life with frequent introgression events [13,17–19]. Currently, a plethora of examples of evolutionary consequences of hybridization, ranging from local extinction to speciation, are described [13]. While adaptation to novel niches by hybrid species with trait values that differ from those of both parent species is documented (e.g. in *Helianthus* sunflowers where hybrid species inhabit more extreme habitats compared with the parent species [20,21]), other consequences of hybridization for local adaptation are less understood [22]. In particular, we argue that there is a gap between the multitude of studies documenting sex-specific viability, sex-specific expression and sex-biased introgression in hybrid species and introgressed taxa, and the lack of studies of how these factors affect sexual dimorphism in ecological niche and local adaptation in these taxa. Here, we review how hybridization interacts with sex-specific inheritance and recombination mechanisms, their effects on hybrid fitness, sex-specific fitness, sex ratio and how this can lead to sexual dimorphism and/or alter the prospects for local adaptation (figure 1). Following the structure outlined in figure 1, we first present how sex-specific effects of hybridization may affect sexual dimorphism, sex ratios and sexual conflict in §2, then we outline how altered sexual dimorphism, sex ratios and sexual conflict may affect local adaptation in §3, and finally, we discuss ideas for how to test our novel predictions in §4. We identify exciting areas for future research and suggest analyses to elucidate effects of hybridization on the prospects of local adaptation.

2. How hybridization can affect sexual conflict, sex ratio and sexual dimorphism

(a) Interactions with sex chromosomes

Patterns of sex-specific inheritance related to differentiated sex chromosomes are long known. However, little is known of how these patterns may affect sexual conflict, sex ratio and sexual dimorphism, and here we outline how hybridization between species with heteromorphic sex chromosomes may influence these factors. In addition, we discuss how hybridization between species with different sex-determination genes can lead to sex-chromosome turnover and affect sexual conflict.

Almost a century ago Haldane [10] noted that 'when in the F_1 offspring of two different animal races one sex is absent, rare or sterile, that sex is the heterozygous sex' (Haldane's rule; Glossary). A closely related observation is the so-called 'large X(Z) effect' (Glossary), pertaining to the disproportionate contribution of the X/Z-chromosome in causing the reduced fitness of heterogametic hybrids [23]. The principal cause of both patterns is thought to be recessive alleles with deleterious effects in hybrids having a stronger impact on the heterogametic relative to the homogametic sex, due to hemizygous expression [24]. In taxa with well-differentiated sex chromosomes, Haldane's rule has shown to be close to universal, and heteromorphic sex chromosomes show reduced introgression on the X in XY (in mammals [25]; flies [26]) and the Z in ZW systems (Lepidoptera [27]; birds [28,29]).

While 'Haldane's rule' and the 'large X(Z) effect' both consider alleles with the same fitness effects in males and females, sex chromosomes are expected to accumulate disproportionate numbers of sexually antagonistic alleles. This follows from their sexually asymmetric inheritance resulting in the relative effect of male- and female-specific selection acting on the sex chromosomes becoming unbalanced [30]. Dominant alleles coding for sexually antagonistic traits that benefit the homogametic sex are expected to accumulate on the X chromosome in XY systems (female-benefitting alleles) and on the Z chromosome in ZW systems (male-benefitting alleles). This is because they spend two-thirds of their evolutionary time in the homogametic sex which has two copies of that sex chromosome. Recessive alleles that favour the heterogametic sex are expected to accumulate on the X chromosome in XY systems and on the Z chromosome in ZW systems because they are rarely exposed to antagonistic selection in the homogametic sex. Modifiers that lead to reduced gene expression in the sex with lower fitness or increased expression in the sex with higher fitness are expected to subsequently evolve and accumulate [31,32].

While these properties and patterns of sex-chromosome evolution have been extensively reviewed elsewhere [30,32,33], their implications for sex-specific local adaptation in hybrid populations remain poorly understood. The lower viability of the heterogametic sex may lead to biased sex ratios in hybrid populations in laboratory settings, e.g. in *Drosophila* [23], but also in the wild, e.g. in flycatcher hybrids [34]. Sex-linked gene regulation may become disrupted in hybrids resulting in abnormal gene expression. Male sterility due to disrupted sex-linked gene regulation has been observed, e.g. in *Drosophila* [35,36] and hybrids between *Mus musculus* and *M. domesticus* [37]. This may potentially cause sex-specific sterility, inviability or phenotypic differences influencing sexual dimorphism.

'Haldane's rule' and the 'large X(Z) effect' are less important in taxa with sex chromosomes that are not strongly differentiated and in taxa without reduced recombination rates in the sex-linked chromosome. In many taxa, genetic sex determination differs even between closely related species (e.g. in fishes [38–40], geckos [41] and *Drosophila* [42]). Hybridization between species with different sex-determining regions may result in biased sex ratios [38,43] and modified interactions between sex determination and sexually antagonistic alleles. Theoretical models suggest that selection against biased sex ratio or sexual conflict may lead to turnover of sex-determination genes [44–47] with some support from empirical studies, e.g. in frogs where the authors find introgression of sex chromosome due to selection against biased sex ratio [48], guppies [49] and cichlids [40,50,51]. If a sex determination or modifier gene of one species is more closely linked to sexually antagonistic genes than the sex determiners of the other species, it may introgress into the other species as a result of reduced sexual conflict. Sexually antagonistic alleles linked to the sex determiner may introgress in concert increasing the fitness in hybrids of both sexes. Hybridization between species with different sex determiners may also modify sexual dimorphism as has been shown for strawberry hybrids [52].

(b) Cytonuclear incompatibilities

It is increasingly clear that cytonuclear incompatibilities often affect hybrid fitness, but their effects on sex-specific survival, sexual antagonism and sexual dimorphism have rarely been discussed. Below we outline how such consequences may arise.

Cytonuclear incompatibilities arise as the mitochondrial genome encodes specific components of the oxidative phosphorylation system used for aerobic respiration [53], and there is hence strong selection for compatibility between the mitochondrial (mtDNA) and the nuclear (nuDNA) genome [11]. The mitochondrial genome is transmitted through the maternal lineage in most species [54]. Consequently, a male–female asymmetry in the fitness effects of mitochondrial mutations can arise [55] as mtDNA mutations that affect only males detrimentally will be less easily removed by natural selection than mutations that are also or only detrimental to females. The resulting accumulation of mutations that are disadvantageous to males but benign to females is coined 'mother's curse' (Glossary) [56]. This is supported by evidence for cytoplasmic variants beneficial to females being disadvantageous to males with consequences, e.g. disruption of production of cytochrome *c* oxidase [57,58]. Effects of mtDNA mutations in the form of male-biased fitness costs include reduced male fertility and increased rates of male ageing, e.g. in *Drosophila melanogaster* strains with introgressed mitochondria [55,59,60]. However, compensatory nuclear adaptations may evolve after a lag time [61]. Negative effects associated with disruption of co-evolved mitonuclear complexes, e.g. on ageing [60,62] and fertility [59,62], support the existence of such compensatory genetic variants. Cytonuclear incompatibilities arising from hybridization between diverged taxa are found in a range of taxa, e.g. in birds [63–65], carnivorous mice [66], flat worms [67] and plants [68,69]. Suboptimal respiration is one of the fitness costs to hybrids in flycatchers [64], carnivorous mice [66], voles [70] and chickadees [71], likely due to mitonuclear incompatibilities. Mitonuclear incompatibilities have also been shown to distort sex ratios, e.g. in experimental mitonuclear introgression lines of *D. pseudoobscura* [72]. In a recent modelling study, the authors found that strong selection on males or nonlinear fitness effects of mitochondria resulted in paternal leakage [73]. Consistent with this scenario, heteroplasmy found in hybrids across a wide range of taxa, including mussels [74], wheat [75], birds [63,65] and *Drosophila* [76] could potentially be due to selection for paternal leakage to counteract negative fitness effects of matrilinearily inherited mitochondria.

Interactions between mtDNA and nuDNA can lead to sex-specific global transcript responses [77]. In experimental trials in *D. melanogaster* mitochondrial polymorphism had major effects in males, modifying almost 10 per cent of nuclear transcripts. For most transcripts expression was upregulated in males, while effects on females were small. Expression differences were most pronounced in the testes and accessory glands [78], suggesting a cost to males and potentially reducing male ability for sexual coercion. Sex-specific expression alterations could either increase or decrease sexual dimorphism, contingent on whether the expression patterns of individuals with introgressed mitochondria are more similar among sexes or not. Finally, introgression of heterospecific mitochondrial variants could also have direct positive effects on population fitness. Introgressed mitochondria could replace mitochondrial genomes that have accumulated mutations with negative fitness effects, e.g. through genetic drift (e.g. due to Muller's ratchet [79]; see Glossary) as suggested in Llopart *et al*. [80]. Moreover, introgression of mitochondria with allelic variants that are well adapted to e.g. the local climate could improve population fitness. An example of this is the eastern yellow robin *Eopsaltria australis*, where mitochondrial DNA variants suited to coastal and inland climates covary with climate rather than nuclear genome origin, creating perpendicular axes of nuDNA and mtDNA differentiation [81].

Cytonuclear incompatibilities are also found in plants where chloroplast-driven incompatibilities cause reduced hybrid fitness [82,83], which can be remedied by biparental chloroplast inheritance, as found in *Campanulastrum americanum* where biparental inheritance leads to increased fitness of F_1 hybrids and recovery in the F_2 generation [84].

(c) Sex-biased introgression and meiotic drive

In this section, we discuss how sex-biased introgression and meiotic drive can affect patterns of sexual dimorphism, sexual conflict and sex ratio. Rates of introgression may differ between the sexes due to interspecific differences in mate preferences [85]. Additionally, sex-biased dispersal [86] may lead to increased introgression via the more dispersive sex. Unidirectional hybridization may thus contribute to differential introgression between sex-linked genes and biparentally inherited genes [87]. Reduced or no recombination in sex-limited chromosomes (Y or W) may additionally alter their introgression rates compared autosomes. In the absence of recombination, the combined effects of selection against introgression on multiple loci will lead to purging of entire introgressed sex chromosomes and as beneficial alleles cannot recombine away from incompatibilities, they cannot introgress [88]. Differential introgression of sex-linked genes and nuclear genes may alter sexual conflict.

In many species, one sex shows strongly reduced (heterochiasmy, e.g. some frogs, many fishes [89]) or no recombination (achiasmy, e.g. *Drosophila*, butterflies, copepods; see Glossary). We expect that in these species, alleles that are beneficial mostly to the non-recombining sex cannot introgress as easily as alleles beneficial to the recombining sex, thus potentially shifting the balance of sexual conflict. In addition, crosses between *Tigriopus* copepod populations suggest that if multiple loci on the same chromosome jointly cause Dobzhansky–Müller (DM) incompatibilities with other loci, they are most detrimental in backcrosses of the non-recombining sex (hybrid female, non-recombining, crossed with parental male) [90].

Finally, meiotic drive (Glossary) can manipulate the meiotic process to distort the allelic segregation away from expected Mendelian ratios [91]. The resulting reduced fecundity favours the evolution of drive suppressors [92], and the breaking-up of these associations may affect hybrid fertility and viability [91]. Avoidance of meiotic drive has been shown to drive female preference for larger eye-span, a sexually dimorphic ornament, in stalk-eyed flies *Teleopsis dalmanni* as short eye-span is coupled to the X-linked region causing the drive [93].

(d) Transgressive sorting of sexually antagonistic variation

Hybridization may reshuffle sexually antagonistic alleles [12], leading to transgressive segregation (Glossary) of phenotypic sex differences. This may, in turn, generate early generation hybrid populations with extreme sexual dimorphism (figure 2*a*). When sexually antagonistic alleles are fixed at different loci in the hybridizing species, hybrids could either eliminate all sources of sexual antagonism or fix sexually antagonistic alleles at several loci through recombination. The latter scenario could enable hybridizing species to evolve stronger sexual dimorphism. Sexual dimorphism may, in turn, increase the carrying capacity of hybrid populations through intersexual niche partitioning [94], and may even allow hybrid species to colonize habitats that are unsuitable for their parent species. Such transgression in terms of ecological niche is well documented in both *Helianthus* and *Cottus* [20,95], but it has yet to be investigated from a sexual dimorphism perspective. Strongly sexually dimorphic hybrid lineages may also be able to adapt to environments with otherwise constraining levels of sex-specific selection. For instance, Saino & Bernardi [96] found that the extent of sexual size dimorphism varied across a crow hybrid zone. Moreover, the sexual dimorphism was significantly correlated both to sex-specific selection on males and altitude [96].

3. How hybridization may affect local adaptation via alteration of sexual dimorphism, sex ratio and sexual conflict

In this section, we outline how effects of hybridization on sexual dimorphism, sex ratio and sexual conflict may affect local adaptation. While these three phenomena are interrelated, we present them separately as they have different implications for local adaptation.

(a) Effects of hybridization-altered sexual dimorphism on local adaptation

Here, we discuss how patterns of sexual dimorphism altered by hybridization may affect local adaptation. As explained above, hybridization may affect sexual dimorphism and could hence potentially increase the ability of males and females to exploit different niches, adding to other selection pressures and mechanisms that enable the sexes to use

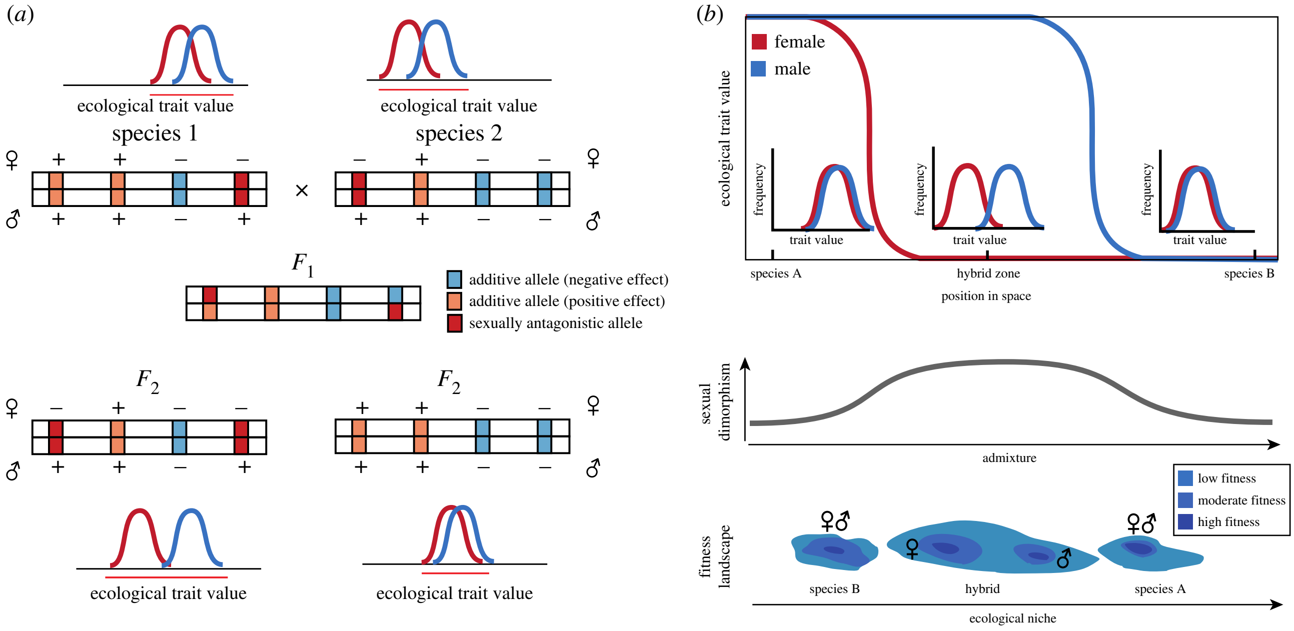

Figure 2. Mechanisms through which hybridization can enhance or reduce sexual dimorphism and, in turn, affect local adaptation. (*a*) Transgressive segregation of sexually antagonistic alleles which have become fixed at different loci in two hybridizing species. These are quantitative trait loci for a trait involved in niche use (e.g. beak shape in birds). After initial hybridization, recombination may lead to different phenotypic outcomes (females above and males below each locus) where sexual dimorphism is either enhanced (left lower panel) or dampened (right lower panel). This may, in turn, have consequences on intersexual niche partitioning and local adaptation. (*b*) Non-coincident geographical clines between sexes for ecological traits in a hybrid zone. In admixed populations, enhanced sexual dimorphism, due to sex-specific differences in geographical clines (upper panel), may promote the occupation of novel ecological niches. Parent species may be incapable of colonizing this novel ecological niche, not because of morphospace constraints, but simply as a result of decreased mean population fitness due to intersexual competition and costly gender load (lower panel).

different niches. Additionally, we argue that hybridization may affect the genetic architecture of traits in such a way that hybrid males and females reach their maximum intrinsic fitness at different levels of genome-wide admixture (for instance, at different points along a hybrid zone (figure 2), due to cytonuclear and/or sex-linked genetic incompatibilities). In hybrid zones, this may be reflected by non-coincident genomic clines (Glossary) for sex-specific genetic markers [97]. Along the hybrid zone, geographical clines of ecological traits may thus also become decoupled and displaced between males and females (figure 2*b*), especially if sex-biased genotype by environment interactions are directly affected by hybridization [98]. This could lead to a situation where sexual dimorphism increases in the centre of the hybrid zone, enhancing intersexual niche partitioning (Glossary) and mean population fitness, as both sexes then are better adapted to local conditions. For two species with weak sexual dimorphism and high gender load (Glossary), i.e. where the sexes have different optima but have not been able to develop sexual dimorphism to better match these optima, hybridization could thus potentially dampen sexual conflict through formation of hybrid lineages. Sexual conflict could partially or fully be resolved in hybrid lineages through transgressive sorting of variants that enable sexually sex-specific expression of traits (cf. [12]). Such sorting where variants underlying sexual dimorphism from both lineages are favoured and accumulate in a hybrid lineage would result in elevated mean population fitness, and could potentially allow for the colonization of habitats where parental species would not be able to survive (cf. [99]), although no empirical examples have yet been identified to our knowledge. Increased sexual dimorphism allows a population to explore a wider phenotypic space around the local fitness peak, potentially facilitating climbing alternative fitness peaks [100], increasing prospects for local adaptation.

Finally, the impact of hybridization on sexual dimorphism could be directly involved in range shift processes (Glossary) and species range dynamics. Theory predicts that sex-specific maladaptation should increase at range margins [1]. The probability for hybridization might also increase at range margins though. Fitness asymmetries between sexes and maladaptation could thus be reduced following interspecific gene flow, and improve the viability of range margin populations by alleviating gender load and increasing fitness of the maladapted sex through introgression of beneficial alleles.

(b) Sex-ratio distortion

Here, we introduce how sex-ratio distortions due to hybridization may facilitate or hamper local adaptation. Sex-specific viability following hybridization may result in skewed sex ratios. The operational sex ratio (OSR; Glossary) may affect intrasexual mating competition [101], but empirical evidence for an effect of OSR on mating competition is mixed [102] because skewed sex ratios might also increase the cost of mate guarding [103]. A recent meta-analysis concluded that there is compelling evidence that OSR predicts strength of sexual selection in males, but not females [104]. Sexual selection can both promote and inhibit local adaptation (reviewed in [105]). When sexual selection inhibits local adaptation, e.g. through pushing the population off the fitness optimum [106,107], a relaxation in sexual selection is likely to increase the prospects for local adaptation. Hence, altered OSR could potentially reduce sexual selection on males, enabling populations to match the ecological optimum closer in cases where sexual selection opposes natural selection.

Sex ratio is also important for the ability of populations to survive and adapt as the number of females in the population determines the reproductive output (e.g. [108]) and strongly biased sex ratios may lead to inbreeding depression as found, e.g. in the gypsy moth *Lymantria dispar* [109]. Biased sex ratios may hence also hamper local adaptation.

(c) Effects of hybridization on local adaptation via modulation of sexual conflict

A shift in the balance between male harming and female harming antagonistic variants can lead to sex-ratio distortion, which may impact local adaptation, as outlined above. In addition, a reduction of sexual conflict, e.g. due to introgression of a sex modifier increasing sex-linkage of a sexually antagonistic gene [44] or of a sex chromosome harbouring sexually antagonistic genes [99], may facilitate local adaptation by allowing for greater sexual dimorphism in ecology. Such sexual dimorphism could allow the sexes to better track their respective adaptive optima, and hence add to local adaptation of the population.

4. Testing for effects of hybridization on sex-specific local adaptation

Many of the interactions between hybridization and local adaptation via modulation of sex ratio, sexual dimorphism and sexual conflict, which we have proposed above, lack empirical examples and theoretical studies. In this section, we suggest approaches to study some of these interactions.

Sex-specific viability in early generation hybrids may result from the greater impact of deleterious recessive alleles on hybrids of the heterogametic sex, i.e. the faster X/Z theory and mitonuclear incompatibilities. This may lead to a biased sex ratio affecting sexual conflict and sex-specific adaptation as outlined above. Meta-analyses of sex ratios in young hybrid populations or in hybrid zones would allow testing of this hypothesis, especially given such data must have been already collected and should be available from the numerous field studies of hybrid zones published over the years. Another interesting comparison would be one of sex ratios between young hybrid taxa or hybrid swarms and old, stabilized hybrid taxa. Taking advantage of the fact that nucleotide diversity on the Y/W chromosome depends only on the effective population size of the heterogametic sex, while the nucleotide diversity of the other sex chromosome depends on effective population sizes of both sexes, it is possible to tentatively infer past sex ratios. Comparing the relative effective population sizes of the two heteromorphic sex chromosomes in hybrid taxa and parental taxa (where other factors affecting this ratio, such as mating systems should be very similar) could hence be informative of differences in sex-specific survival between these taxa. Sex-specific viability may affect local adaptation by relaxing sexual selection, and by increasing the probability of population persistence through female-skewed sex ratios (see above). To address whether these mechanisms take place in hybrid populations, it may be possible to compare the relative strength of sexual selection in hybrid taxa or hybrid zones with that of the parental taxa.

Several specific predictions can be made based on the current knowledge of mitonuclear incompatibilities. First, hybrids with foreign mitochondria are expected to have suboptimal respiration and a higher incidence of sterility. Moreover, when hybrid populations differ in parental contributions, e.g. as in the hybrid species Italian sparrow (*Passer italiae*, cf. [65]), populations with larger parts of their genomes matching the mitochondrial ancestry are expected to have a more well-functioning respiration. In addition, males are expected to be disproportionately affected by mitonuclear incompatibilities in species with XY systems where mitochondria are not selected to be compatible with the Y chromosome due to female inheritance. These predictions can be tested by comparing, e.g. cost of respiration or basal metabolic rate in the two sexes in young hybrid taxa and stabilized hybrid taxa [70]. Moreover, meta-studies addressing whether taxa with heterospecific introgressed mitochondria have obtained these from taxa adapted to the climate in their current distribution, e.g. as in the eastern yellow robin [81], could be interesting.

The consequences of hybridization on sexual dimorphism and local adaptation have been poorly studied, as much empirical work on hybridization often only considers one sex (e.g. [110]) or controls for sexual dimorphism at the phenotypic level (e.g. [96]) without making it a specific focus. However, we argue that our hypotheses warrant reanalyses of the data on hybrid zones and hybrid species. To understand how hybridization affects sexual dimorphism in ecological traits and niche partitioning, we suggest a more systematic investigation of whether sexual dimorphism is greater in hybrid species than in parent species. This would be predicted if transgressive sorting of sexually antagonistic alleles could increase beneficial dimorphism. Consistent testing of variation in sexual dimorphism across hybrid zones would also shed light on the effects of hybridization on sexual dimorphism. Another interesting possibility is to use hybrid zones as natural experiments, and test if genomic clines and geographical clines differ between sexes. If hybrid zone clines of ecological traits are shifted between the sexes, it implies that males and females have different ecological fitness optima (figure 2*b*).

In some taxa, clades with the strongest sexual dimorphism show particularly high rates of hybridization and turnover in sex-determination genes, potentially to reduce sexual conflict (e.g. in cichlids [40] and jumping spiders [111,112]). Investigating the role of introgression in sex chromosome turnover in these systems and performing meta-analyses investigating the generality of these findings would be a promising avenue. Little if anything is known about how the phenomena we have discussed above differ between early generation hybrids and stabilized hybrid taxa. Investigating this may give insights into the selection for compatibility of hybrid genomes [65,113] and the balance between selection for compatibility and selection for local adaptation [114]. We argue that the study of hybridization should move beyond classical approaches and also focus on the study of how hybridization and sex-specific selection pressures interact and affect, e.g. sexual dimorphism, sex differences in viability and sexual conflict. Much remains to be done to assess the generality of the impact of hybridization on local adaptation via modulation of sexual conflict, sex ratio and sexual dimorphism.

Data accessibility. This article has no additional data.

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Glossary

Achiasmy	Absence of recombination in one sex.
Dobzhansky–Müller incompatibilities	Genetic incompatibilities arising from fixation of alternative alleles at two or more loci in the parental species that if brought together in hybrids are incompatible and decrease fitness.
Gender load	The reduction of fitness resulting from sexual conflict.
Genomic cline	Analysis that compares allele or genotype frequencies of each locus to a genome-wide average.
Haldane's rule	If only one sex is inviable or sterile in a species hybrid, that sex is more likely to be the heterogametic sex.
Heterochiasmy	Differential recombination rates between sexes.
Interlocus sexual conflict	Displacement of the phenotypic optimum due to selection on the opposite sex, and by interactions between sexually antagonistic alleles at different loci.
Intersexual niche partitioning	The divergence in the niche space between the sexes.
Large X(Z) effect	Sex chromosomes (X or Z) have a disproportionate impact in adaptive evolution.
Meiotic drive	When a gene is passed to the offspring more frequently than expected due to manipulation of the meiotic process.
Mother's curse	Accumulation of mitochondrial mutations which are deleterious to males but not to females because, due to the matrilineal inheritance, they are less easily removed by selection than mutations that are also deleterious to females.
Muller's ratchet	Irreversible accumulation of deleterious mutations in the genomes of asexual populations.
Niche packing	The resulting narrower (i.e. more specialized) niches of species occurring in biologically diverse communities relative to similar species in less biologically diverse communities as a consequence of increased interspecific competition in diverse communities.
Operational sex ratio	The ratio of fertilizable females to sexually active males at any given time.
Range shift processes	The processes that might shift species' ranges, such as climatic factors, dispersal capacity and population persistence.
Transgressive segregation	Hybrid offspring trait values that fall outside the range of both parentals.

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