

Hybridization, sex specific genomic architecture and local adaptation

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Abstract:

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, 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 cyto-nuclear mismatches, for example in the form of “mother’s curse”, with potential consequences for sex-ratio and sex specific expression. Third, transgressive segregation of sexually antagonistic alleles could lead to greater sexual dimorphism in hybrid populations. These mechanisms 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.

Introduction

Recent research has highlighted the importance of understanding sex specific local adaptation [1]. Sexual dimorphism can evolve in the same way and for the same reasons as sympatric ecological divergence and speciation [2]. Sometimes, both 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 may be advantageous, the genetic correlation between the sexes may constrain the evolution of sexual dimorphism [9]. Unless resolved, selection towards different optima may result in both sexes residing away from their fitness peaks and hence sexual conflict [9].

In spite of a long-standing research tradition investigating sex-specific viability and fitness effects of hybridization [10], and an increasing appreciation of the importance of mito-nuclear 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 (Fig. S1), 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 break-down 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 which have trait values that differ from those of both parent species is documented [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 and the lack of studies of how these factors affect sexual dimorphism in ecological niche and local adaptation in hybrid species and introgressed 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 (Fig. S1). We identify exciting areas for future research and suggest analyses to elucidate effects of hybridization on the prospects of local adaptation.

1) How hybridization can affect sexual conflict, sex ratio and sexual dimorphism

1.1) Through interactions with sex chromosomes

Almost a century ago J. B. S. 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]. Haldane’s rule has shown to be close to universal in both XY and ZW systems, 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) because they spend two-thirds of their time in the homogametic sex, while recessive alleles that favour the heterogametic sex are expected to accumulate on the Z chromosome in ZW systems and on the X chromosome in XY 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 both in laboratory settings [23] and in wild 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 in e.g. *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.

In many taxa genetic sex determination is highly liable and differs even between closely related species (e.g. fishes [38], [39], geckos [40], and *Drosophila* [41]). Hybridization between species with different sex determining regions will result in biased sex ratios and modify interactions between sex determination and sexually antagonistic alleles. Selection against the biased sex ratio may lead to turnover of sex determination genes [42]. 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 readily introgress into the other species as a result of reduced sexual conflict [43]. Sexually antagonistic alleles linked to the sex determiner may introgress in concert increasing the fitness in hybrids of both sexes. For example, in guppies [44] and cichlids [39] sex chromosome turnover has been shown to occur through introgression of sex determination genes linked to sexually-antagonistic colour pattern genes.

1.2) Through cytonuclear incompatibilities

The mitochondrial genome encodes specific components of the oxidative phosphorylation system used for aerobic respiration [45], and there is hence strong selection for compatibility between the mitochondria and the nuclear genome [11]. The mitochondrial genome is transmitted through the maternal lineage in most species [46]. Consequently, a male-female asymmetry in the fitness effects of mitochondrial mutations can arise [47] as mtDNA mutations that affect only males detrimentally will not be subject to natural selection. The resulting accumulation of mutations that are disadvantageous to males but benign to females is coined “mother’s curse”(Glossary) [48]. This is supported by evidence for cytoplasmic variants beneficial to females being disadvantageous to males [49,50] due to mtDNA mutations with male-biased fitness costs e.g. [47,51,52]. However, compensatory nuclear adaptations may evolve after a lag time [53]. Negative effects associated with disruption of co-evolved mito-nuclear complexes e.g. on ageing [52,54] and fertility [51,54] 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. birds [55,56] [57], carnivorous mice [58] flat worms [59] and

plants [60,61]. Suboptimal respiration is one of the fitness costs to hybrids in flycatchers [56], carnivorous mice [58], voles [62], and chickadees [63], likely due to mito-nuclear incompatibilities. The findings of heteroplasmy in hybrids across a wide range of taxa, including mussels [64], wheat [65], birds [55,57] and *Drosophila* [66] could potentially be due to selection for paternal leakage to counteract negative fitness effects of matrilineally inherited mitochondria [67].

Interactions between mtDNA and nDNA can lead to sex-specific global transcript responses [68]. Sex specific expression alterations could either increase or decrease sexual dimorphism, contingent on whether the expression patterns of individuals with foreign mitochondria are more similar among sexes or not. Finally, introgression of heterospecific mitochondrial variants could also have direct positive effects on population fitness through replacing mutationally loaded genomes (e.g. due to Muller's ratchet [69]; see Glossary) as suggested in [70] and through introgression of mitochondria with allelic variants that are well adapted to e.g. the local climate c.f. [71].

Cyto-nuclear incompatibilities are also found in plants where chloroplast driven incompatibilities cause reduced hybrid fitness [72,73], which can be remedied by bi-parental chloroplast inheritance [74].

1.3) Through unidirectional hybridization, meiotic drive and sex-biased recombination rates

Rates of introgression may also differ between the sexes due to interspecific differences in mate preferences [75]. Additionally, sex-biased dispersal [76] may lead to increased hybridization in the dispersive sex. Unidirectional hybridization may thus contribute to differential introgression between sex-linked genes and bi-parentally inherited genes [77]. Reduced or no recombination in sex-linked markers may additionally alter their introgression rates compared to other genomic regions. In the absence of recombination, the combined effects of selection against introgression on multiple loci will lead to purging of entire introgressed chromosomes and as beneficial alleles cannot recombine away from incompatibilities, they cannot introgress [78]. Differential introgression of sex-linked genes and nuclear genes may alter sexual conflict. In many species recombination rates differ drastically between the sexes also at nuclear chromosomes, whereby in one sex recombination is either completely absent (achiasmy, e.g. *Drosophila*, *Bombyx*, *Gammarus*; see Glossary) or restricted to telomers (heterochiasmy, e.g. some frogs, many fishes [79]; see Glossary). 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. Finally, meiotic drive (Glossary) can manipulate the meiotic process to distort the allelic segregation away from expected Mendelian ratios [80]. The resulting reduced fecundity favors the evolution of drive suppressors [81], and the breaking-up of these associations may affect hybrid fertility and viability [80].

1.4) Through 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 (Fig. 1A). 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 [82], 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 hybrid species [20,83] 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, [84] 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 [84].

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

2.1) Effects of hybridization-altered sexual dimorphism on local adaptation

As explained above, hybridization may affect sexual dimorphism via transgressive segregation of sexually antagonistic alleles or sex specific modification of expression patterns. 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 due to cyto-nuclear and/or sex-linked genetic incompatibilities). In hybrid zones, this may be reflected by non-coincident genomic clines(Glossary) for sex-specific genetic markers [85]. Along the hybrid zone, geographical clines of ecological traits may thus also become decoupled and displaced between males and females (Fig. 1B), especially if sex-biased genotype by environment interactions are directly affected by hybridization [86]. 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. For two species with weak sexual dimorphism and high gender load (Glossary), hybridization could thus potentially dampen sexual conflict through formation of hybrid lineages where sexual conflict is partially or fully resolved. This would result in elevated mean population fitness, and could potentially allow for the colonization of harsh habitats where parent species would not be able to survive, c.f. [87]. Increased sexual dimorphism allows a population to explore a wider phenotypic space around the local fitness peak, potentially facilitating climbing alternative fitness peaks [88].

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 [87].

2.2) Sex ratio distortion

Sex specific viability may result in skewed sex ratios. The Operational sex ratio (OSR; Glossary) affects the mating competition of males and females in a population [89]. The empirical evidence for this pattern is mixed [90], with one confounding factor arising as skewed sex ratios might increase the cost of mate guarding [91]. A recent meta-analysis concluded that there is compelling evidence that OSR predicts strength of sexual selection in males, but not females [92]. Sexual selection can both promote and inhibit local adaptation (reviewed in [93]). When sexual selection inhibits local adaptation, e.g. through pushing the population off the fitness optimum [94,95] a relaxation in sexual selection is likely to increase the prospects for local adaptation.

Sex ratio is also important for the ability of populations to survive and adapt as the number of females in the population determine the reproductive output e.g. [96] and strongly biased sex ratios may lead to inbreeding depression e.g. [97].

2.3) 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 [42] or of a sex chromosome harbouring sexually antagonistic genes [87] may facilitate local adaptation by allowing for greater sexual dimorphism in ecology.

3) Testing for effects of hybridization on sex-specific local adaptation

Sex specific viability in early generation hybrids may result from the greater impact of deleterious recessive alleles on hybrids of the heterogametic sex, the faster X/Z theory and mitonuclear incompatibilities and 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 to test 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. Comparing effective population sizes of the two heteromorphic sex chromosomes in hybrid taxa and parental taxa could also be informative of past sex-specific survival. Sex specific viability may affect local adaptation through relaxing sexual selection, and through increasing the probability of population persistence through female skewed sex ratios (see above). To address whether these mechanisms take place in hybrid populations, estimating the relative strength of sexual selection in hybrid taxa or hybrid zones and compare that to the parental taxa is one possibility.

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 (c.f. [57]) the populations with larger parts of their genomes matching the mitochondria are expected to have a more well-functioning respiration. In addition, males are expected to be disproportionately affected by mitonuclear incompatibilities. These predictions can be tested through comparing e.g. cost of respiration or basal metabolic rate in the two sexes in young hybrid taxa and stabilized hybrid taxa [62]. Moreover, meta studies addressing whether taxa with heterospecific introgressed mitochondria have obtained these from taxa adapted to the climate in their current distribution (c.f. [71]) 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 consider one sex e.g. [98] or control for sexual dimorphism at the phenotypic level e.g. [84] 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 also 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 would enable increased 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 the hybrid zone clines of ecological traits are shifted between the sexes, it implies that in the centre of the hybrid zones, ecological fitness differs between males and females (Fig. 1b). In some taxa, the clades with strongest sexual dimorphism show high rates of turnover in sex determination potentially to reduce sexual conflict and high rates of hybridization (e.g. cichlids [39] and jumping spiders [99,100]. 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 above outlined phenomena differ between early generation hybrids and stabilized hybrid taxa. Investigating this might give insights into the selection for compatibility of hybrid genomes [57,101] and the balance between this and selection for local adaptation [102]. We argue that the study of hybridization should move beyond the classical approaches and also focus on the study of ecological effects affecting sexes differently, 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 sexual genetic architecture and its consequences on adaptive potential of hybrid lineages.

Glossary

Achiasmy: Absence of autosomal recombination in one sex.

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) play a disproportionate impact in adaptive evolution.

Meiotic drive: When a gene is passed to the offspring more than the expected due to manipulation of the meiotic process.

Mother's curse: Accumulation mutations deleterious to males but not females on the mitochondria as mtDNA mutations that affect only males will not be subject to natural selection.

Muller's ratchet: Irreversible accumulation of deleterious mutations in the genomes of asexual populations.

Niche packing: An approach to understanding the number of species and their relative abundance in dimensional niche space where the niches are packed.

Operational sex ratio (OSR): the ratio of fertilizable females to sexually active males at any given time.

Range shift processes: the processes that might shifts the range as climatic factors, dispersal capacity and population persistence.

Transgressive segregation: Progeny trait values that fall outside the range of both parents.

Competing interests

We declare no competing interests.

Authors' contributions

A.R. and F.E. conceived of the idea, AR wrote most of the paper and all other authors helped writing and preparing figures. All authors gave final approval for publication.

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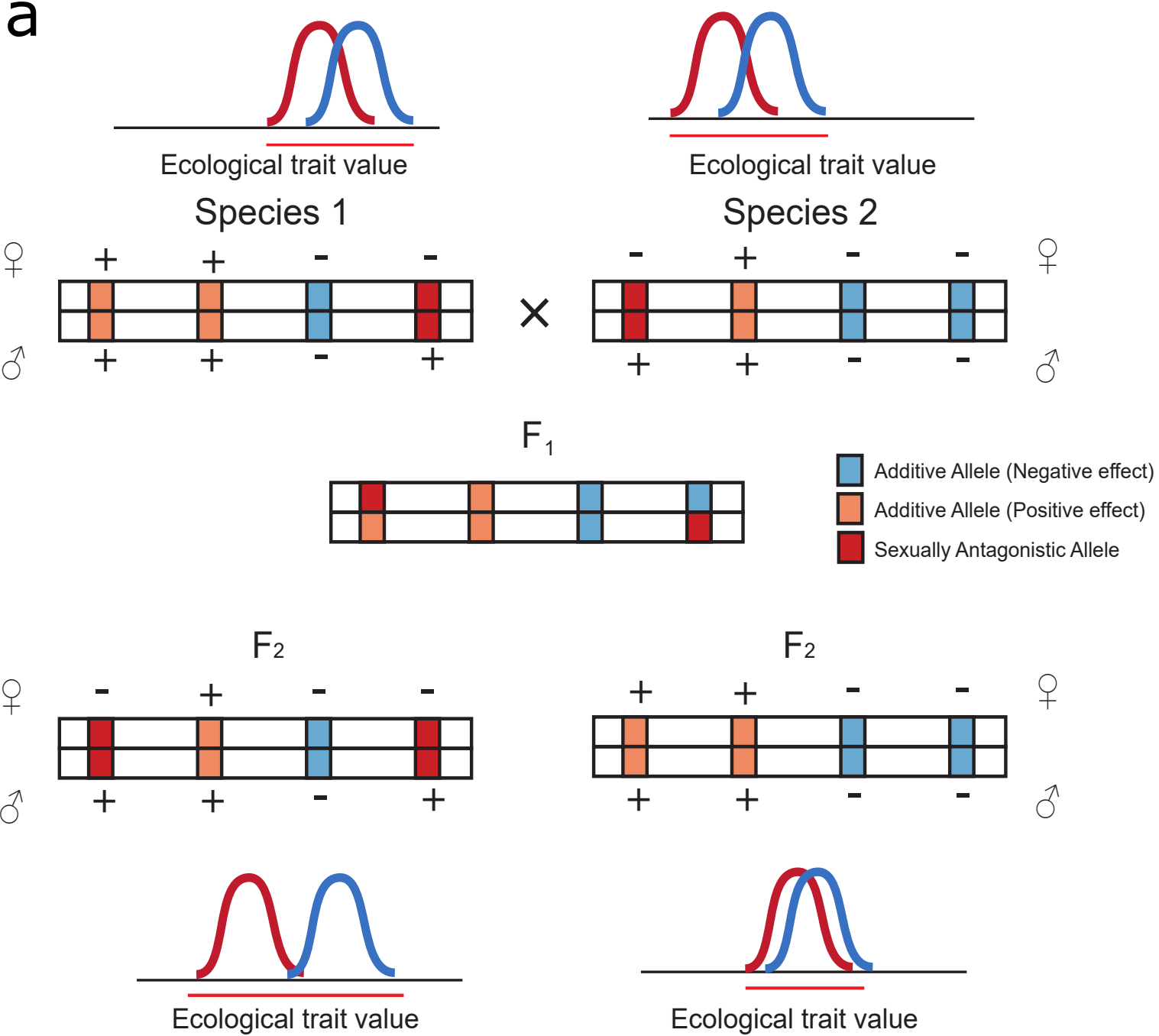
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Figure captions

Fig. 1. 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 loci are QTL 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 geographic 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).

a



b

