Introduction

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Linking local adaptation with the evolution of sex differences

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Many conspicuous forms of evolutionary diversity occur within species. Two prominent examples include evolutionary divergence between populations differentially adapted to their local environments (local adaptation), and divergence between females and males in response to sex differences in selection (sexual dimorphism *sensu lato*). These two forms of diversity have inspired vibrant research programmes, yet these fields have largely developed in isolation from one another. Nevertheless, conceptual parallels between these research traditions are striking. Opportunities for local adaptation strike a balance between local selection, which promotes divergence, and gene flow—via dispersal and interbreeding between populations—which constrains it. Sex differences are similarly constrained by fundamental features of inheritance that mimic gene flow. Offspring of each sex inherit genes from same-sex and opposite-sex parents, leading to gene flow between each differentially selected half of the population, and raising the question of how sex differences arise and are maintained. This special issue synthesizes and extends emerging research at the interface between the research traditions of local adaptation and sex differences. Each field can promote understanding of the other, and interactions between local adaptation and sex differences can generate new empirical predictions about the evolutionary consequences of selection that varies across space, time, and between the sexes.

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

1. Introduction

Environmental conditions vary across species' ranges, generating selection for locally adapted phenotypes. Nevertheless, gene flow—caused by dispersal and interbreeding between individuals that were born in different regions of the range—opposes genetic differentiation between populations and constrains local adaptation [1,2]. This tension between adaptation and gene flow is central to several productive research topics in modern evolutionary biology, including the genetics of adaptation and speciation [3–5], the evolutionary ecology of species' range limits [6–9], the maintenance of genetic variation [10–12], the evolution of phenotypic plasticity [13] and the empirical study of natural selection and geographical clines in the wild [14–17].

The theory of local adaptation characteristically ignores a widespread feature of biology: sexual dimorphism. Yet many classical study species for local adaptation comprise separate sexes. Such species often display pronounced sex differences in selection and demography, which can directly impact the dynamics of sex-specific adaptation and population dynamics [18–20]. Likewise, relatively few studies focusing on sex differences and/or sexual selection are conducted with spatially varying environments in mind (e.g. [21–24]).

Recent empirical and theoretical research has begun to question and extend many standard assumptions underlying theories of local adaptation with gene

flow [22,25–27], and of sex-specific selection and adaptation in heterogeneous environments [23,24,28–31]. These studies reveal unexplored opportunities for research that merges the fields of spatial evolutionary ecology, sexual selection and sexual dimorphism.

There are at least two good reasons for merging studies of local adaptation with the evolution of sex differences. First, establishing conceptual connections between traditionally separated areas of study can enrich and broaden our understanding of each. For example, evolutionary predictions about the genetic basis of local adaptation with gene flow can generate novel predictions about the genetic basis of sex-specific adaptation and sexually antagonistic genetic variation [32,33] (see below). Secondly, predictions regarding single contexts of evolutionary change may break down, or change in interesting ways, when multiple contexts co-occur. Recent research shows that sex-specific selection and local adaptation can interact to drive evolutionary dynamics that are unique to the combination of processes (e.g. persistent sex asymmetries in geographical patterns of local adaptation and maladaptation across species' ranges; [30,31]).

Despite recent efforts to better integrate these two fields, several general questions remain largely unanswered, and indeed are rarely asked. How does environmental variation mediate selection on male and female traits? How do sex differences in selection impact extinction, species' range size evolution and ecological invasions? How do classical evolutionary concepts of hard and soft selection apply in species with separate sexes? How do interactions between sex and local selection shape the genetic architecture of local adaptation, and sex-specific patterns of genetic variance and covariance? In this special issue, we bring together a collection of papers that address these and related questions at the intersection between local adaptation and sex differences. The topics covered within the issue fall within four major themes, upon which we expand below:

— *Parallels between sex-specific adaptation and local adaptation with gene flow.* Processes that play out during the evolution of local adaptation and of sexual dimorphism bear many striking dynamical similarities with one another, with each field enriching our view of the other.
— *Sex differences and the genetic basis of local adaptation.* Females and males differ in both genomic architecture [34] and the intensity with which selection, migration, recombination, mutation, and genetic drift operate [35]. These fundamental sex differences shape the genetic basis of population and species divergence.
— *Ecological drivers of sex-specific phenotypic selection and sexual conflict.* Research over the past century has established the centrality of sexually divergent reproductive roles in the evolution of phenotypic sexual dimorphism [36,37]. The role of ecological context in promoting or constraining sex differences has only recently begun to receive the attention that it deserves.
— *Environmental variation and the evolution of reproductive systems.* Reproductive systems evolve in response to interactions between members each sex, their reproductive interests, and ecological conditions that affect mating and reproduction. Evolutionary diversity of reproductive systems is shaped by local environments in native and invasive species' ranges (e.g. [38–41]), providing an active arena for theoretical and empirical research.

2. Parallels between sex-specific adaptation and local adaptation with gene flow

Local adaptation hinges upon the balance between the strength of local selection, which promotes population divergence, and the magnitude of gene flow, which erodes it [2,42]. Weak gene flow allows for strong local adaptation and high genetic differentiation between populations, whereas high gene flow can severely limit such divergence. At best, local adaptation is hindered by this strong gene flow [43] (but see [44,45]). At worst, populations can be driven to extinction as a consequence of maladaptive gene flow [7,46].

In contexts of high gene flow, evolutionary scenarios of local adaptation bear striking similarities to scenarios of selection for sex differences [33,47]. Consider an extreme example of a haploid population, where individuals disperse randomly between a pair of habitat types ('habitat 1' and 'habitat 2'; figure 1, left), the direction of selection differs between habitats, and gene flow is very high (table 1). Local selection promotes genetic differentiation ($p_1 > p_t > p_2$, where p_t is the frequency of the focal allele before selection in generation t, and p_1 and p_2 are the frequencies in habitats 1 and 2 after selection; see figure 1), whereas gene flow erodes these differences, homogenizing allele frequencies between habitats following dispersal (i.e. both habitats have allele frequencies p_t and p_{t+1} in generations t and $t+1$, respectively). Sex differences in selection result in evolutionary dynamics that parallel the local adaptation scenario (figure 1, right). Selection promotes allele frequency differentiation between breeding females and males of the population ($q_f > q_t > q_m$; see figure 1), whereas the equal genetic contributions of each sex to reproduction equalize allele frequencies in female and male offspring ($q_{t+1} = (q_f + q_m)/2$; figure 1). In fact, the evolutionary dynamics of the two scenarios of selection become mathematically indistinguishable when adults from habitats 1 and 2 contribute equally to the production of offspring of the next generation ($c_1 = c_2 = \frac{1}{2}$, $s_1 = s_f$ and $s_2 = s_m$; figure 1 and table 1).

The dynamical similarities between scenarios of local adaptation and sex differences in selection provide an example of a wider range of parallels between the concepts. For example, over short evolutionary intervals, both scenarios can maintain stable genetic variation for fitness [10,47], stabilize linkage disequilibrium in the absence of epistasis [32,50], and select for tightly linked clusters of alleles that are exclusively beneficial within a given habitat or sex [48,51–54]. Both scenarios can also generate detectable signals of differential selection between populations or sexes (e.g. through F_{ST} analysis [55–58]). Over long evolutionary intervals, both scenarios can impact the evolution of genomic architecture, including the evolution of inversions, translocations and gene duplications [59–64], as well as the evolutionary modification of genetic dominance [65,66]. Most of the above scenarios involve simple, univariate patterns of selection (i.e. selection on single traits), providing an opportunity for future work in more complex, multivariate contexts of evolutionary change. Finally, scenarios of sex-specific selection and local adaptation can both favour the evolution of sex- or
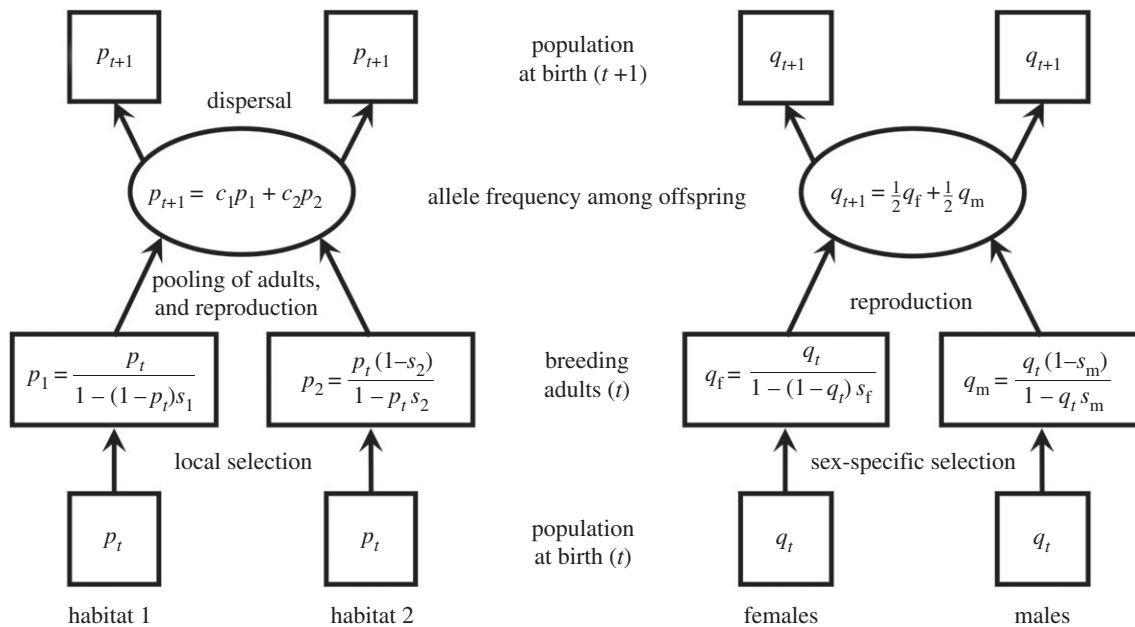
Figure 1. Parallels between scenarios of local adaptation with gene flow and of sex-specific adaptation. The left panel shows the life cycle of a haploid population evolving in response to local selection with high gene flow between habitats (e.g. [10,11]). Allele frequency differentiation between habitats fluctuates during the life cycle, with dispersal homogenizing the allele frequencies between habitats (p_t and p_{t+1} are equal between habitats), and local selection favouring differentiation between habitats ($p_1 > p_t > p_2$). The frequency of allele A in offspring of the next generation depends on the frequency in adults from each habitat (p_1, p_2) and the proportions of breeding adults from each habitat (c_1, c_2, where $c_2 = 1 - c_1$). The right panel shows the life cycle of a haploid population evolving in response to sexually antagonistic selection (e.g. [48,49]). Females and males make equal genetic contributions to offspring, which homogenizes the allele frequencies of female and male offspring of a given generation (q_t and q_{t+1} are equal between sexes). Sex differences in selection elevate the frequency of the A allele in breeding females and decrease the frequency of A in breeding males ($q_f > q_t > q_m$).

Table 1. Conflicting selection between habitats and sexes.

	allele A	allele a
local selection		
habitat 1 fitness	1	$1 - s_1$
habitat 2 fitness	$1 - s_2$	1
frequency in the population	p_t	$1 - p_t$
sex-specific selection		
female fitness	1	$1 - s_f$
male fitness	$1 - s_m$	1
frequency in the population	q_t	$1 - q_t$

environment-dependent phenotypic plasticity, which are widely observed in nature [13,18].

3. Sex differences and the genetic basis of local adaptation

Gene flow shapes genome-wide patterns of genetic divergence, leading to empirically detectable genetic bases underlying locally adapted phenotypes. For example, whereas gene flow erodes population divergence at loci contributing weakly to local adaptation or genetic incompatibilities between species, strong selection maintains sharp genetic differentiation at loci that contribute the most to traits or genetic systems under divergent selection. These loci are identifiable as outliers with sharp genetic clines across

hybrid zones (e.g. from studies of hybrid zones [67,68]), high F_{ST} between geographically diverged populations [55], or they may be enriched in genomic regions that suppress ancestral or ongoing gene flow [60,69].

There are several reasons why a view towards sex differences may be useful in research on the genetic basis of local adaptation. For example, sex differences in dispersal, genetic drift, and the strength of natural selection, can impact the chromosomal locations of loci contributing the most to local adaptation, as well as the statistical power to identify them as outliers (see [35,70]). For example, Camus *et al.* [71] reported strong effects of mitochondrial genetic backgrounds on local adaptation of *Drosophila melanogaster* to variable thermal conditions across eastern Australia. The mitochondrial genome is maternally inherited, is primarily responsive to selection in females, and contributes substantially to local adaptation in thermal tolerance, despite its small size relative to the nuclear genome. On the other hand, the lower effective population size of the mitochondrial genome should simultaneously elevate background levels of neutral divergence between populations, complicating interpretation of the evolutionary causes of geographical divergence of mitochondrial DNA. Recent theory suggests that similar considerations should also apply to X-linked genes: they exhibit female-biased transmission, are more responsive to selection than autosomal genes, are expected to disproportionately contribute to the evolution of local adaptation [70] and are more likely to fix inversions capturing locally adapted alleles [72] (this issue). However, X-linked genes also diverge more readily under genetic drift, which may mask population genetic signals (e.g. based on F_{ST}) of local adaptation involving the X chromosome (see [70,73]).

The genes and phenotypes that promote local adaptation may also differ between the sexes. Although most genes within a genome are expressed by both sexes, expression levels and phenotypic effects of mutations differ extensively between the sexes, allowing for sexual dimorphism in the genetic architecture of traits expressed by both (e.g. [74–77]). In addition, the way in which selection varies across a species' range may differ between the sexes, leading to differences in the direction or strength of local selection [23]. Although rare, studies of sex-specific genetic and phenotypic trait clines can shed light on processes of sex-specific selection and local adaptation. For example, Allen *et al.* [78,79] (this issue) show that male-biased genes in *Drosophila* exhibit more extensive clinal divergence than female-biased genes—a pattern consistent with sex differences in the intensity of local selection and/or lower pleiotropic constraints in male- relative to female-biased genes. Phenotypic body size clines show similar patterns [80], although interpretation of the body size data is complicated by potential effects of sexually dimorphic phenotypic plasticity [81] and additive genetic correlations between the sexes that may constrain geographical divergence of sexual dimorphism [82].

Combinations of sex-specific selection and sexually dimorphic genetic architecture can manifest in sexually dimorphic fitness consequences of dispersal, local adaptation and hybridization between populations or species [83,84]. In these contexts, Runemark *et al.* [83] (this issue) review and synthesize consequences of hybridization for the expression of sexual dimorphism, sexual conflict and the ecology of local adaptation. Svensson *et al.* [84] (this issue) review reciprocal transplant studies in local adaptation, and discuss the importance of recording sex-specific fitness consequences in future studies in this field. Although such studies are still rare, they can elucidate the role of sex differences in local adaptation, providing a strong impetus for further empirical attention.

4. Ecological drivers of sex-specific phenotypic selection and sexual conflict

Phenotypic sexual dimorphism can evolve in response to sexual selection or natural selection [18,19], although in practice, delineating the role of each in the evolution of sexual dimorphism is challenging (e.g. [85–87]). Selection for sexual dimorphism can potentially arise from different interactions between each sex and its environment, or from resource competition leading to ecological character displacement; both factors can drive the evolution of niche partitioning between the sexes [18,19]. Selander [88] suggested that the only reliable evidence for sexual dimorphism via niche partitioning is a sex-specific modification of trophic structures (e.g. mouthparts) beyond what would be expected from body size differences and the direction of sexual selection. However, these criteria could exclude many cases of ecologically based dimorphism, include spurious cases (e.g. dimorphic mouthparts that reflect sex-specific reproductive functions, such as digging nesting cavities or incubating eggs, rather than dimorphic diets), and have empirical difficulties in their application [85]. In some cases, sexual selection may initiate selection for sexual dimorphism, with ecological

factors secondarily influencing its magnitude, for example by placing upper limits on the benefits of expressing sexually selected traits, or by favouring elaboration of initially modest sex differences. For example, the evolution of dwarf male seadevils, which parasitically feed on females, may have evolved in response to the scarcity of food and mates within deep sea environments [89]. Forsman [90] (this issue) synthesizes two decades of pygmy grasshopper research to consider how interactions between each sex and its environment shape sex differences in coloration, thermotolerance and other ecologically relevant traits.

The net outcome of natural and sexual selection is that males and females have different trait optima defined by the ecological conditions in which they evolve. The sexes also share nearly identical genomes, constraining the potential rate of evolutionary divergence between female and male traits [18,75]. Although this genetic constraint promotes adaptation when the direction of selection is the same in each sex [91,92], it becomes maladaptive when selection is misaligned between the sexes, giving rise to intralocus sexual conflict [93,94]. Recent research has shown that the manifestation of intralocus sexual conflict is sensitive to environmental conditions [29,95–97] and the degree to which each sex is adapted to its environment [31,98–100]. For example, in well-adapted populations of *D. melanogaster*, high-fitness males sire unfit daughters (intralocus sexual conflict is present); in maladapted populations, high-fitness males sire high-fitness offspring of both sexes (intralocus sexual conflict is absent) [98]. Using a large dataset of field-estimated selection gradients, De Lisle *et al.* [101] (this issue) demonstrate that environmental stressors (measured using microclimatic data) are associated with patterns of sexually concordant selection, which weakens intralocus sexual conflict in environments that are more stressful, more variable, and closer to the edge of the species' range (consistent with theory [31,99]).

Another type of sexual conflict—interlocus sexual conflict—arises from direct, antagonistic interactions between the sexes, including male sexual coercion and female resistance to mating [37,102]. The intensity and consequences of interlocus sexual conflict for sex-specific phenotypic evolution also depend on ecological context. For example, experimental populations of *D. melanogaster* adapted faster to a novel food resource in spatially complex environments, where interlocus sexual conflict was relatively weak, than in spatially simple environments where interlocus conflict was strong [103–104]. In this issue, Perry & Rowe [105] review the diverse ways in which ecology can affect coevolution between males and females through interlocus sexual conflict. Using water striders as a model system, they show that population-specific elaboration of sexual armaments (traits associated with male coercion and female resistance) is associated with several ecological variables, including water acidity, temperature, seasonality and winter severity (see [106]), with harsh conditions providing an advantage to females in countering male coercion.

Not only do females and males respond differently to local conditions in their environments; they can, in turn, differentially impact selection in species with which they interact, providing a context for sexual dimorphism to shape coevolutionary dynamics. Pronounced sex differences in behaviour, physiology, morphology and immune responses expose

pathogens to drastically different selective environments in male and female hosts [107–109]. The adaptation of pathogens to female and male hosts may also intensify sex difference in selection on immunity [110]. In the water flea *Daphnia magna*, sex differences in morphology, physiology, and life-history influence potential for growth, performance, and transmission of a common pathogen, *Pasteuria ramosa* [111]. Hall & Mideo [111] (this issue) combine experimental data on infection and transmission of different strains of *Pasteuria ramosa* in hosts of each sex with an epidemiological model of pathogen virulence and transmission evolution. They show that performance (spore load), transmission and the dynamics of infection and evolution differ between pathogens infecting female versus male hosts. Pathogen evolutionary trajectories may therefore depend upon the sex with which they interact the most in nature—a scenario that is likely to differ between taxa and between different geographical populations of single species (e.g. pathogens tend to interact with females in facultatively sexual species versus both equally in obligately outcrossing taxa).

Finally, females and males differ in their spatial distributions and patterns of dispersal across their ranges [112]—an observation with implications for the manner in which each sex interfaces with environmental conditions that vary across space, as well as the evolutionary consequences of sex-biased dispersal for adaptation with gene flow (e.g. [35]). For example, sex-biased dispersal can shape the genetic architecture of local adaptation, since it mediates the effective strength of gene flow across different regions of the genome (e.g. male-biased dispersal facilitates responses of mitochondrial-encoded and X-linked genes to local selection, but dampens local adaption at Y-linked genes [70,71]). Unique responses of each sex to shared environmental conditions can also affect the expression and evolution of sex-biased dispersal and 'dispersal syndromes' (suites of traits that correlate with dispersal [113]). As Mishra *et al.* [114] show in this issue, nutrition levels shape ecologically plastic sex differences in dispersal syndromes for body size, desiccation resistance and exploratory behaviour traits. Yet these sex-specific syndromes are evolutionarily labile, and changed during the experimental evolution of dispersal (greater than 70 generations). Their results point to developmental and evolutionary mechanisms that can impact the expression of sex differences in dispersal behaviour.

5. Environmental variation and the evolution of reproductive systems

Variation in environmental conditions across native or invasive portions of a species' range can alter the economics of reproduction, including the fitness costs and benefits of different reproductive strategies and the arena in which mating competition and mate choice occurs. This provides wide scope for evolutionary divergence among subpopulations in the mode of reproduction and the nature of mating interactions between the sexes. At the most basic level, environmental variation provides an arena in which natural selection can favour the evolution and maintenance of sexual reproduction [115,116], with the details of environmental fluctuation determining the rate of sexual reproduction that evolves in a population. At a higher level, environmental variation provides an ecological context for direct and indirect selection on mating preferences, and the divergence of mating systems and species [23,24,117,118].

Individuals of many species can reproduce sexually with other individuals of the population, or individually through clonal reproduction, parthenogenesis, or self-fertilization [119–122]. The frequency with which these different reproductive tactics are employed can vary across the species' range, as evolved responses to local benefits and costs of sex and outcrossing (e.g. [38–41,123]). Geographical differences in the predictability of the environment can lead to variation across the species' range in the benefits of outcrossing, sex and recombination [124], potentially selecting for different rates of sex across habitats. Gerber & Kokko [125] (this issue) show that sex can be viewed as one of a class of bet-hedging strategies [126] for coping with environmental uncertainty. Dispersal, dormancy and sexual reproduction have bet-hedging attributes that partly complement one another, and in this context, theory predicts that the three traits (dispersal, dormancy and sex) exhibit tightly correlated coevolutionary patterns in simulated populations that evolve in spatially or temporally variable environments [125].

The role of males in selecting for or against sex can also change across a species' range. Individuals near range boundaries and those occupying recently invaded ranges may have difficulty finding suitable mates if local population densities are low, which can favour the evolution alternative modes of reproduction. The classic example is Baker's Rule (or Baker's Law), in which colonizing populations show higher capacity for selfing than their native-range populations (see [41,127]). Costs associated with males include the classic 'twofold' demographic cost of producing males [128], as well as indirect and direct costs to female fitness that arise from inter- and intralocus sexual conflict [105,129] (see above). Burke and Bondwith riansky [130] (this issue) consider the consequences of interlocus conflict on the evolution of facultative sex; they show that conflict favours the spread of facultative sex and influences the geographical distribution of asexual reproduction and the sex ratio. Intralocus sexual conflict is also expected to promote the spread of asexual reproduction [131]. On the other hand, mate preferences can help offset costs associated with intralocus conflict, particularly when females evolve preference for males that carry genes that benefit daughters. Theory suggests that such an outcome is possible, although not inevitable, in stable environments [132,133]. Li & Holman [134] (this issue) show that metapopulation structure and spatially variable environments promote the evolution of choice for female-beneficial alleles, particularly when selection is hard (also see [30]).

Finally, the mating system of the species can impact the evolutionary response to selection on males and females (or on male and female sex-functions in hermaphrodites). While the evolutionary trajectories in outcrossing populations are equally responsive to selection in each sex (e.g. [18,47]), self-fertilization can tip this balance, leading to a stronger response to selection through female than through male sex-functions (e.g. [54,135–137]). Olito *et al.* [138] (this issue) merge classical theories of environmental heterogeneity and sex-specific selection (e.g. [10,47]), to reveal further complexity in the interplay between sex-specific selection, self-fertilization and hermaphrodite mating systems.

6. Where to?

Studies of local adaptation and of sexual dimorphism each have rich histories within the field of evolutionary biology. The interaction between processes that promote evolutionary differentiation between populations and processes driving intersexual divergence provides a relatively untapped area for productive research that advances our understanding of adaptation, and the many ways in which environment and sex can mediate it. Closer links between these topics also provide an ideal opportunity for new collaborations between researchers with expertise in each context of evolutionary diversification.

The papers within this special issue highlight many outstanding research questions at the interface between sex differences and the geography of adaptation, each worthy of future attention. Among them, we highlight five sets of questions that remain largely unaddressed and provide good material for future exploration:

— How much do females and males 'agree' in the direction or intensity of selection for local adaptation, and how do sex differences in selection shape patterns of local adaptation across species' ranges [101]?
— How do different regions of a genome—including chromosomes with symmetric versus sex-biased patterns of inheritance—contribute to local adaptation with gene flow and the maintenance of species differences [70,73,139,140]?
— How do sex differences in selection, dispersal and environmental heterogeneity interact to facilitate the maintenance of genetic variation in fitness and life-history traits, and the evolution of mating systems [130,134,138]?
— To what extent do scenarios of local adaptation and the evolution of sex differences parallel one another [32,33,47]? To what extent do these scenarios, in combination, give rise to emergent evolutionary patterns that qualitatively differ from predictions of either scenario by itself [30,31]?
— Does sexual selection tend to reinforce or conflict with natural selection promoting local adaptation and/or species divergence [24]?

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