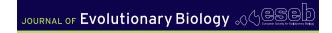
REVIEW



Ecology and the evolution of sex chromosomes

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Abstract

Sex chromosomes are common features of animal genomes, often carrying a sex determination gene responsible for initiating the development of sexually dimorphic traits. The specific chromosome that serves as the sex chromosome differs across taxa as a result of fusions between sex chromosomes and autosomes, along with sex chromosome turnover-autosomes becoming sex chromosomes and sex chromosomes 'reverting' back to autosomes. In addition, the types of genes on sex chromosomes frequently differ from the autosomes, and genes on sex chromosomes often evolve faster than autosomal genes. Sex-specific selection pressures, such as sexual antagonism and sexual selection, are hypothesized to be responsible for sex chromosome turnovers, the unique gene content of sex chromosomes and the accelerated evolutionary rates of genes on sex chromosomes. Sex-specific selection has pronounced effects on sex chromosomes because their sex-biased inheritance can tilt the balance of selection in favour of one sex. Despite the general consensus that sexspecific selection affects sex chromosome evolution, most population genetic models are agnostic as to the specific sources of these sex-specific selection pressures, and many of the details about the effects of sex-specific selection remain unresolved. Here, I review the evidence that ecological factors, including variable selection across heterogeneous environments and conflicts between sexual and natural selection, can be important determinants of sex-specific selection pressures that shape sex chromosome evolution. I also explain how studying the ecology of sex chromosome evolution can help us understand important and unresolved aspects of both sex chromosome evolution and sex-specific selection.

KEYWORDS

pigmentation, predation, sex determination, sexual antagonism, sexual selection, thermal adaptation

1 | INTRODUCTION

Sex chromosomes are found in many eukaryotic genomes (Beukeboom & Perrin, 2014). Sex can be determined in many different ways, including the presence of an allele that initiates either male or female sexual development, the dosage of a sex-determining gene, heterozygosity of a sex-determining locus, genetic interactions across multiple loci, an environmental cue (e.g. egg incubation temperature) or a combination of genetic and environmental factors (Bachtrog et al., 2014). When sex is determined by genotype, a

sex-determining locus can be found on a sex chromosome, but not all species with genetic sex determination have sex chromosome.

Most animal sex chromosome systems generally fall into one of two categories. In XY systems, such as in mammals and *Drosophila* (Graves, 1995; Salz & Erickson, 2010), males are heterogametic (XY) and females are homogametic (XX). In ZW systems, such as in Lepidoptera and birds (Sahara et al., 2012; Zhou et al., 2014), females are heterogametic (ZW) and males are homogametic (ZZ). In these systems, sex can be determined by a single locus on the Y or W chromosome, an X or Z chromosome locus with dosage-sensitive effects,

or some other mechanism (Bachtrog et al., 2014; Beukeboom & Perrin, 2014). However, the dichotomy between XY and ZW systems belies additional complexities across sex chromosome (Furman et al., 2020). For example, old or established sex chromosome systems often have highly differentiated X and Y (or Z and W) chromosomes, as a result of sex-specific selection pressures that push the two sex chromosomes in diverging evolutionary trajectories (Charlesworth, 1991; Charlesworth et al., 2005). By contrast, some sex chromosome pairs are homomorphic—with very little divergence between X and Y, or Z and W—which is often, but not always, a hallmark of 'young' sex chromosomes (Kamiya et al., 2012; Son & Meisel, 2021; Stöck et al., 2011; Wright et al., 2017).

Most research on the evolution of sex chromosomes is focused on two key areas (Abbott et al., 2017). First, there is a large body of work on how new sex chromosomes arise from autosomes and how established sex chromosomes revert to autosomes. These large-scale changes include sex chromosome turnovers (autosomes becoming sex chromosomes and vice versa), as well as fusions between sex chromosomes and autosomes that create neo-sex chromosomes, described in more detail below (e.g. Pennell et al., 2015; van Doorn, 2014; Vicoso & Bachtrog, 2015). Second, there is a comparable amount of research on how the evolutionary trajectories of sex chromosomes differ from the autosomes, including differences in rates of evolution and unique gene content of sex chromosomes (e.g. Bachtrog, 2013; Meisel & Connallon, 2013; Vicoso & Charlesworth, 2006).

Sex chromosome turnovers, neo-sex chromosomes and unique aspects of sex chromosome evolution have been hypothesized to result from sex-specific selection pressures, which differentially affect sex chromosomes and autosomes (Bachtrog, 2006; Charlesworth & Charlesworth, 1980; Hurst et al., 2015; Rice, 1987; van Doorn & Kirkpatrick, 2007). For example, sex differences in the ploidy of sex chromosomes can cause the variance in fitness to differ between males or females for traits controlled by genes on an X or Z chromosome (James, 1973; Reinhold & Enggvist, 2013). In addition, biased transmission via males or females can allow for selection pressures in one sex to be the predominant selective force shaping sex chromosome evolution (Charlesworth et al., 1987; Rice, 1984). These sex-specific effects can be especially important if they are sexually antagonistic, that is in opposite directions in males and females (Blackmon & Brandvain, 2017; Rowe et al., 2018; van Doorn & Kirkpatrick, 2007, 2010). Because sex-specific selection pressures can disproportionately affect genes on sex chromosomes, contrasts between sex chromosomes and autosomes have been a valuable approach for studying the causes and consequences of sex-specific selection.

Most population genetic models are agnostic as to the specific sources of sex-specific selection pressures that affect sex chromosome evolution. In the past decade, considerable attention has been given to how sex chromosome evolution is affected by intragenomic conflicts that act on intra- or intercellular traits, such as sex ratio distorters, selfish genetic elements and germline endosymbionts (e.g. Bachtrog, 2020; Cocquet et al., 2012; Cordaux et al., 2011;

Helleu et al., 2019; Meiklejohn & Tao, 2010; Roy, 2018; Yoshida & Kitano, 2012). Other recent work has addressed the effects of ploidy, dosage compensation and meiotic segregation on sex chromosome evolution (e.g. Abbott et al., 2020; Bachtrog et al., 2010; Blackmon & Demuth, 2015; Hurst et al., 2015; Meisel et al., 2012; Meisel & Connallon, 2013; Vicoso & Charlesworth, 2006). This work has moved the study of sex chromosome evolution forward, but there are still multiple unresolved questions about the effects of sex-specific selection on sex chromosome evolution.

Here, I describe how considering ecological factors that affect sex-specific selection pressures can improve our understanding of sex chromosome evolution. These ecological factors include differences between the sexes in how they use their natural environment (Shine, 1989), conflicts between sexual and natural selection (Zuk & Kolluru, 1998) and variation in the environment across the species range (Delcourt et al., 2009; Delph et al., 2011). In addition to improving our understanding of sex chromosome evolution, I also explain how considering the ecology of sex chromosome evolution can help us understand the causes and effects of sex-specific selection pressures more generally.

2 | SEX-SPECIFIC SELECTION AND THE EVOLUTION OF SEX CHROMOSOMES

Sex-specific selection pressures are thought to be important for many aspects of genome evolution, and in particular the evolution of sex chromosomes. Sex-specific selection can involve selection operating in only one sex (sex-limited selection), selection in the same direction but with different strengths in each sex (sexually concordant selection), or selection in different directions between the sexes (sexually antagonistic selection). The effects of sex-specific selection on sex chromosome evolution are often reversed depending on whether a species has an XY or ZW system because the heterogametic and homogametic sexes are reversed, and there are additional important differences in how sex-specific selection affects XY and ZW systems (Mank et al., 2014). Nonetheless, many of the same principles apply to both XY and ZW systems.

Sexual antagonism is a specific type of sex-specific selection that has received considerable attention and is thought to be important for sex chromosome evolution. Sexually antagonistic selection, or intersexual conflict, refers to the phenomenon whereby males and females have different fitness optima for genotypes or traits (Figure 1), and it is conventionally divided into two categories (Arnqvist & Rowe, 2013; Schenkel et al., 2018). First, intralocus sexual antagonism arises when males and females differ in which genotype (at a single locus) maximizes fitness (Bonduriansky & Chenoweth, 2009; Lande, 1980). Intralocus conflicts can be especially pronounced in adults (Chippindale et al., 2001), where males and females are likely to have different phenotypic optima (Figure 1). Second, interlocus sexual conflicts occur when an allele of one gene expressed in one sex has antagonistic effects on the other sex (Rice & Holland, 1997). Interlocus conflicts may be an important aspect

of sexual selection, where alleles that increase mating success in one sex could reduce the fitness of the other sex (Arnqvist & Rowe, 1995). Both intralocus and interlocus sexual antagonism can

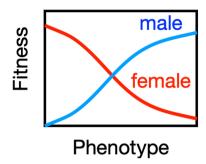


FIGURE 1 Example of sexually antagonistic phenotypic variation. The fitness of males (blue) and females (red) is shown for a continuum of phenotypic values. Phenotypes that maximize female fitness are deleterious to males, and phenotypes that maximize male fitness are costly to females.

be important for the evolution of sex chromosomes, but not to the exclusion of other (non-antagonistic) forms of sex-specific selection (Charlesworth et al., 1987; Otto, 2014).

Sex-specific selection pressures are thought to contribute to sex chromosome turnover and the establishment of neo-sex chromosomes (Charlesworth & Charlesworth, 1978, 1980; van Doorn, 2014). A neo-sex chromosome is created by a fusion between an autosome and one of the sex chromosomes (Figure 2). Neo-sex chromosomes have been observed across many different animal taxa (Steinemann, 1982; Castillo et al., 2010; Pennell et al., 2015). Y-autosome fusions, in particular, are expected to be favoured to invade a population if the autosome carries a male-beneficial allele (Charlesworth & Charlesworth, 1980), or female-beneficial allele for a W-autosome fusion. This is because the sex-limited inheritance of a sex-beneficial allele (following the fusion to the Y or W chromosome) can resolve a sexual conflict if the allele is deleterious when expressed in the other sex (Figure 2). Despite this theoretical prediction, empirical evidence that sexual conflict is a driving force in

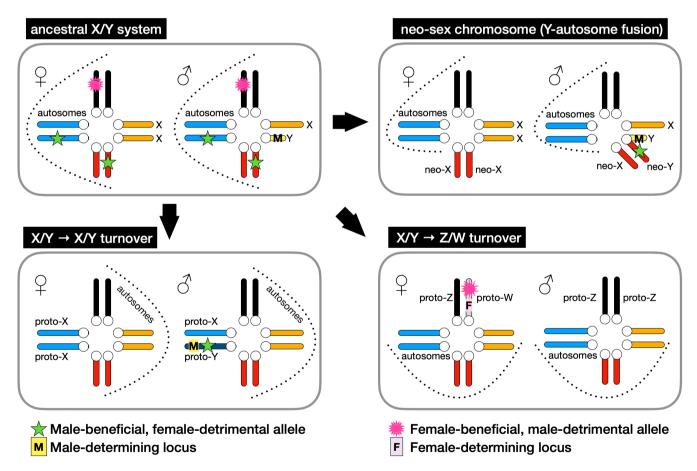


FIGURE 2 Sex chromosome turnovers and neo-sex chromosomes can resolve intralocus sexual antagonism. In the examples shown here, the ancestral karyotype has a sex chromosome pair along with three autosomal pairs of chromosomes (top left). In the ancestral karyotype, a male-determining locus (M) is found on the Y chromosome, male-beneficial sexually antagonistic alleles (green stars) are found on two autosomes, and a female-beneficial sexually antagonistic allele is found on another autosome. Neo-sex chromosomes can be created when an autosome (red) fuses to the Y chromosome (top right). An autosome can be converted into a proto-X/Y or Z/W chromosome when it acquires a new male (M)- or female (F)-determining locus (bottom), with the ancestral sex chromosome reverting to an autosome. The creation of neo- and proto-sex chromosomes can resolve a sexual conflict by allowing a sexually antagonistic allele to be inherited only by the sex in which it is beneficial.

the fixation of neo-sex chromosomes is remarkably weak (Pennell et al., 2015; Wright et al., 2016).

A sex chromosome turnover involves a chromosome transitioning from a sex chromosome to an autosome and vice versa (Bull, 1983; Vicoso, 2019). Sex chromosome turnovers can involve an XY system evolving into another XY, a ZW evolving into a different ZW, an XY to ZW transition, or a ZW to XY turnover (Figure 2). For example, in a species with an XY system, an autosome can become a proto-X/proto-Y chromosome pair with the acquisition of a maledetermining locus (e.g. Keating et al., 2022). The ancestral X and/ or Y chromosome can subsequently revert to an autosome, as has been observed in Drosophila (Carvalho & Clark, 2005; Larracuente et al., 2010; Vicoso & Bachtrog, 2013). Alternatively, an XY system can evolve into a ZW system if an autosome acquires a femaledetermining allele, and the ancestral X and/or Y chromosome can revert to an autosome (e.g. Roberts et al., 2009). An existing ZW system can similarly transition to a different ZW system or evolve into an XY system. Lastly, sometimes only one of the two sex chromosomes experiences a turnover (i.e. a new Y chromosome replaces the existing Y, but the X chromosome remains the same), which can be especially difficult to detect (Meisel, 2020).

Sexually antagonistic selection is thought to increase the probability of a sex chromosome turnover because Y- or W-linkage of a sexually antagonistic allele can resolve the intersexual conflict (van Doorn & Kirkpatrick, 2007, 2010). However, there are few examples in which there is evidence that sexually antagonism was responsible for a sex chromosome turnover (Roberts et al., 2009), in part because it is challenging to tease apart the causes of a turnover from the subsequent effects of sex-linkage following the turnover (Mank et al., 2014). Below, I describe how considering ecological factors that affect sex-specific selection could help us to better understand the causes of sex chromosome turnovers, as well as the invasion and fixation of neo-sex chromosomes.

Sex-specific selection pressures are also thought to explain gene content differences between sex chromosomes and autosomes, as well as different evolutionary rates of sex chromosome genes relative to autosomal genes. For example, many, but not all, Y (or W) chromosomes have male (female)-limited inheritance and little to no recombination with their X (or Z) chromosome partner along some or all of their length (Charlesworth, 1991; Furman et al., 2020; Rice, 1996a). Suppressed X-Y (or Z-W) recombination may be favoured to maintain tight genetic linkage between a male (female)-determining locus and male (female)-beneficial alleles on the Y (W) chromosome (Charlesworth, 2017; Ponnikas et al., 2018), although sexually antagonistic selection is not necessarily required for the evolution of suppressed recombination (Ironside, 2010; Jeffries et al., 2021; Lenormand & Roze, 2022; Olito et al., 2022). Regardless of the cause, suppressed X-Y (or Z-W) recombination favours the fixation of male (female)-beneficial alleles on the Y (W) chromosome, and promotes the degeneration of the Y (W) chromosome via a combination of Muller's ratchet and genetic hitchhiking (Bachtrog, 2013; Charlesworth et al., 2005; Charlesworth & Charlesworth, 2000). Experiments in Drosophila have indeed

demonstrated that male-limited inheritance allows male-beneficial, female-detrimental sexually antagonistic alleles to accumulate on Y chromosomes (Prasad et al., 2007; Rice, 1996b, 1998; Zhou & Bachtrog, 2012). Below, I describe how considering the extent to which the male-beneficial effects depend on ecological contexts can contribute to our understanding of Y chromosome evolution.

The sexually asymmetrical inheritance of X and Z chromosomes may also favour the accumulation of alleles with sex-specific fitness effects. X chromosomes are carried by females 2/3 of the time and are haploid (hemizygous) in males, whereas Z chromosomes are preferentially transmitted by males and hemizygous in females. These factors may favour the invasion and fixation of recessive male-beneficial or dominant female-beneficial X-linked mutations. and vice versa for Z chromosomes (Charlesworth et al., 1987; Orr & Betancourt, 2001; Rice, 1984). The dominance of fitness effects and genetic architecture of adaptation may further affect the maintenance of sexually antagonistic polymorphisms or fixation of sexually antagonistic alleles on X or Z chromosomes in a way that differs from the autosomes (Connallon et al., 2012; Fry, 2010; Patten & Haig, 2009; Ruzicka & Connallon, 2020). However, although there is some evidence that X-linked (or Z-linked) genes evolve faster than autosomal genes (i.e. faster-X effects) because selection in hemizygous males (females) favours the fixation of recessive beneficial alleles, there are multiple examples where there is not faster-X evolution (Charlesworth et al., 2018; Meisel & Connallon, 2013). In addition, the evidence for differences in the frequencies of sexually antagonistic alleles on the X chromosome and autosomes is mixed (Gibson et al., 2002; Ruzicka et al., 2019), and testing for excess Xlinkage of sexually antagonistic alleles can easily be biased by methodological artefacts (Ruzicka & Connallon, 2020). Below, I discuss how considering ecological factors that affect sex-specific selection could improve our understanding of the unique evolutionary dynamics of sex chromosomes.

3 | THE ECOLOGY OF SEX-SPECIFIC SELECTION AND SEXUAL ANTAGONISM

Before discussing how ecological factors affect the evolution of sex chromosomes, I will review some of the evidence that sex-specific selection pressures can depend on the environment that organisms experience. This is important to consider in the light of sex chromosome evolution because so many aspects of sex chromosome evolution depend on sex-specific selection pressures (see above). I will focus on both sexually antagonistic and sexually selected traits, noting that these are not mutually exclusive evolutionary forces. Sexual selection involves a specific class of sex-specific or sexually dimorphic traits that are involved in the competitive access to mates (Jones, 2016).

Sex-specific selection pressures can arise from differences in how males and females use their environment (including niche partitioning or different dietary strategies), which could be a selective force in favour of sexual dimorphism (Shine, 1989; Slatkin, 1984). For

example, Selander (1966) observed sexual dimorphism in size and foraging behaviour in two woodpecker species, suggesting sex differences in niche utilization. Similarly, in carpet pythons (Morelia spilota), females have larger heads and consume larger prey than males (Pearson et al., 2002). Sex differences in niche utilization could potentially arise from sex differences in parental care, which could limit the foraging or hunting capacity of one sex (Kernaléguen et al., 2015). Importantly, sex differences in niche utilization could create sexually antagonistic selection pressures. The resulting sexual conflict could favour a sex chromosome turnover or neo-sex chromosome, and it could differentially affect the fixation of sexually antagonistic alleles on the sex chromosomes and autosomes.

Sex-specific selection pressures can also differ across ecological habitats within a species' range (Connallon, Débarre, & Li, 2018; Rhen & Crews, 2002). In the dioecious plant *Silene latifolia*, for instance, intralocus sexual conflict for leaf area depends on water availability in the environment, which can vary across populations (Delph et al., 2011). Similarly, in *Drosophila serrata*, whether genetic variation has sexually antagonistic fitness effects, and the extent of those effects, depends on the diet on which the flies are raised (Delcourt et al., 2009; Punzalan et al., 2014. These types of genotype-by-environment (GxE) interactions could be especially important for sexual selection (Hunt & Hosken, 2014; Ingleby et al., 2010). One such example comes from the lesser waxmoth, *Achroia grisella*, where GxE interactions affect multiple male signal characters, as well as female choice for those signals (Jia et al., 2000; Rodríguez & Greenfield, 2003; Danielson-François et al., 2006).

Theory also predicts that sexually antagonistic selection should decrease in more extreme environments, variable conditions or near the limits of the species range (Connallon, 2015; Lande, 1980). This prediction is supported by data from some natural and experimental populations (Berger et al., 2014; De Lisle et al., 2018; Holman & Jacomb, 2017; Martinossi-Allibert et al., 2018). However, the clinal distribution of traits in Drosophila melanogaster is concordant between males and females, suggesting that sex-specific selection pressures do not differ across the species range (Lasne et al., 2018). Therefore, although sex-specific selection pressures frequently vary across habitats and environments, the pattern is not universal. Contrasts between sex chromosomes and autosomes could be a useful approach to test hypotheses about how ecological factors affect sexual conflict because of the different predictions about the polymorphism and fixation of sexually antagonistic alleles on the sex chromosomes and autosomes (Rice, 1984; Charlesworth et al., 1987; Connallon et al., 2012).

Pathogens are an especially intriguing ecological factor that could affect sex-specific selection pressures. Exposure to pathogens depends on the ecological environment (Ostfeld et al., 2010), and there are sex differences in immune responses to infections (Belmonte et al., 2019; Klein & Flanagan, 2016). These sex differences could be a cause of sexual conflict, or they could be explained by the resolution of historical conflict. One specific cause of intersexual conflicts may be the effect of mating on the induction of the female immune system (Morrow & Innocenti, 2012), which provides

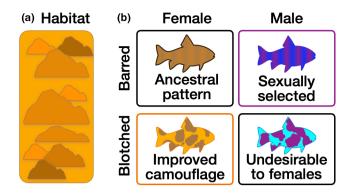


FIGURE 3 Example of sexual conflict over a sexually selected male trait and camouflage in females. (a) Lake Malawi cichlids recently colonized a mottled rock habitat. (b) The ancestral females typically have a drab brown 'barred' pigmentation pattern (top left). Males have a purple and blue barred pattern that is important for mate recognition and attraction (top right). A mutation that produces an orange blotched phenotype may improve female camouflage in the new habitat (bottom left). However, this blotched pattern decreases the mating success of males (bottom right). The blotched pattern can be female-limited because it is genetically linked to a female-determining locus on a new W chromosome. Modified from Roberts et al. (2009).

an interface between disease ecology and sexual selection. In addition, mate choice based on disease resistance has been hypothesized to explain some aspects of sexually selected traits (Hamilton & Zuk, 1982).

Interactions between sexually selected traits and environments can have additional consequences for the evolution of secondary sexual characteristics. Sexually selected traits can be costly, such as when they attract predators (Reznick et al., 1996; Zuk & Kolluru, 1998). Different pigmentation patterns, for instance, may be favoured in males and females if one pattern is sexually selected in males whereas the other provides camouflage to females, creating an intersexual conflict (Figure 3). Moreover, pigmentation patterns that provide camouflage from predators can depend on specific aspects of the natural environment (Cott, 1940; Endler, 1978), suggesting that sexual conflicts over pigmentation can vary across environments.

Sexual selection can also inhibit or promote local adaptation, depending on the extent of migration across populations and strength of selection within populations (Servedio & Boughman, 2017). Of particular relevance here is work in *D. melanogaster* that found sexual selection can impede adaptation (Arbuthnott & Rundle, 2012; Chenoweth et al., 2015; Hollis & Houle, 2011), possibly because intersexual conflict interferes with natural selection purging deleterious alleles. However, the relationship between sexual and natural selection is more complicated than one simply impeding the other (Rowe & Rundle, 2021), and additional work is needed to evaluate the extent to which sexual selection impedes adaptation to specific environments. Contrasts between sex chromosomes and autosomes could be a promising approach for testing whether sexual selection

affects the response to natural selection because there may be different expectations for the fixation of sex-linked and autosomal alleles.

The work described above demonstrates that ecological factors can affect sex-specific selection pressures, yet the extent of those effects remains unresolved. Because sex chromosome evolution is affected by sex-specific selection, it stands to reason that some aspects of sex chromosome evolution will depend on the natural environment in which organisms live. Below, I review the evidence from both population genetic theory and empirical studies that sex chromosome evolution is affected by ecology. I further explain how considering the ecology of sex chromosome evolution can help address unresolved questions about sex chromosome evolution and sex-specific selection more generally.

4 | THE ECOLOGY OF SEX CHROMOSOME TURNOVERS

Sex chromosome turnover has long been recognized to be affected by ecological factors, specifically when the sex determination pathway is sensitive to temperature. In many reptiles and other vertebrates, sex can be determined by the incubation temperature of eggs (Valenzuela & Lance, 2004). Temperature-dependent sex determination can be selectively favoured under certain thermal regimes, such as when sex-specific fitness depends on environmental conditions (Charnov & Bull, 1977; Janzen & Phillips, 2006). However, temperature-dependent systems are also capable of evolving into genotypic sex chromosome systems with sex chromosomes (Sarre et al., 2004). Evolutionary transitions from temperature-dependent to heritable (i.e. genotypic or sex chromosome) sex determination can be favoured if the thermal environment that determines each sex is not well aligned with the environment that maximizes sex-specific fitness (Bullmer & Bull, 1982).

Sex determination systems with sex chromosomes can also be sensitive to temperature in ways that are not necessarily well adapted to the environment. Sexual development is malleable, and sex determination pathways can produce a single sex, regardless of genotype, in specific environments, such as above or below threshold temperatures (Sarre et al., 2004). The Australian bearded dragon, Pogona vitticeps, for example, has a ZW sex chromosome system (ZZ males and ZW females), but at high temperatures, ZZ embryos develop into fertile 'sex-reversed' females (Shine et al., 2002; Ezaz et al., 2005; Radder et al., 2008). Therefore, above the threshold temperature, only females are produced, regardless of sex chromosome genotype. This thermal sensitivity can create scenarios where fluctuations in temperatures over breeding seasons can drive a transition from genotypic to temperature-dependent sex determination by a stochastic (i.e. non-adaptive) process (Holleley et al., 2015). Moreover, if only females are produced above a threshold temperature (regardless of sex chromosome genotype), as annual temperatures rise, there is a possibility that no males will be produced in a population, creating the potential for extinction (Boyle et al., 2014;

TABLE 1 Ecological factors that affected sex chromosome turnover

Temperature override of genetic sex determination in the Australian bearded dragon, *Pogona vitticeps* (Holleley et al., 2015)

Lake Malawi cichlid W chromosome with a female-determining locus linked to an allele that improves female camouflage but negatively affects male courtship display (Roberts et al., 2009)

Holleley et al., 2015). In general, this fluidity between genotypic and temperature-dependent sex determination provides a direct link between thermal ecology and sex chromosome evolution (Table 1).

Other examples demonstrate how ecological factors can select for sex chromosome turnover independent of direct effects on the sex determination pathway itself. For example, pigmentation, specifically sexual dichromatism, is a phenotype with environmentdependent fitness effects that also contributes to sex chromosome evolution in teleost fish. Many sex chromosome turnovers, neo-sex chromosomes and polygenic sex determination systems have been documented in teleosts (Mank & Avise, 2009; Pennell et al., 2015; Sember et al., 2021). Intriguingly, sexually dimorphic pigmentation in fish is often controlled by genes on the sex chromosomes (Kottler & Schartl, 2018). As described above, pigmentation patterns can be under opposing selection in males and females if pigmentation affects both sexual selection and camouflage from predators (Figure 3). It is therefore not surprising that intersexual conflicts over sexually selected and camouflaging pigmentation may be important for sex chromosome turnover in teleosts.

Intralocus sexual conflict appears to have favoured at least one sex chromosome turnover amongst cichlid fish in Lake Malawi (Roberts et al., 2009). In these fish, bright, barred pigmentation is favoured in males because it increases mate recognition (Van Oppen et al., 1998), but a blotched coloration pattern improves female camouflage against the rock substrate of the lakes they inhabit (Figure 3). This created a conflict between natural selection in females (for predation avoidance) and sexual selection in males, which was resolved when a female-determining allele arose that is genetically linked to the allele that determines the female-advantageous blotched colour pattern (Parnell & Streelman, 2013; Roberts et al., 2009). This is a clear example of an ecological selection pressure (camouflage for predator avoidance) driving the evolutionary turnover of a sex chromosome system (Table 1). I describe additional possible examples in the Future Directions section, below.

5 | ECOLOGY AND Y-LINKED POLYMORPHISMS

Y chromosomes frequently have a gene content that differs from the autosomes and X chromosomes. Notably, Y chromosomes are often enriched for genes that are testis expressed and encode proteins essential for spermatogenesis or other aspects of male fertility (Hafezi et al., 2020; Hughes & Rozen, 2012; Rice, 1996a). In *Drosophila* species, for example, Y chromosomes can harbour alleles

with large effects on male fertility and fitness, despite having very few genes (Carvalho et al., 2009; Chippindale & Rice, 2001). Rohmer et al. (2004) showed that the effects of *D. melanogaster* Y chromosome genotypes on male fertility can depend on temperature (Table 2), but it is not yet determined whether other fitness effects of *Drosophila* Y-linked alleles depend on ecological factors. Below, I describe other taxa where there are clear relationships between the phenotypic and fitness effects of Y-linked alleles across different natural environments.

Poeciliid fishes are classic models for the evolution of sex chromosomes and sex determination (Schultheis et al., 2009; Volff & Schartl, 2001), and there are multiple examples of Y-linked alleles that affect pigmentation in ecologically relevant ways (Table 2). For example, loci controlling colour polymorphisms in *Poecilia spp.* are often Y-linked (Winge, 1927; Houde, 1992; Lindholm & Breden, 2002; Lindholm et al., 2004; Morris et al., 2018). In addition, mate choice in the guppy, *Poecilia reticulata*, depends on male colour patterns (Houde, 1987). If colour patterns have male-specific fitness benefits (i.e. via sexual selection), Y-linkage of those alleles could be favoured because they limit the trait to males. However, many of the alleles for individual male ornaments do not map to the guppy Y chromosome, suggesting that the Y chromosome may act more as a modifier of male ornaments rather than controlling individual ornaments (Morris et al., 2020).

Consideration of the ecology of *Poecilia spp.* has been informative for the causes and effects of sexual selection, and this system has been useful for resolving questions about Y chromosome evolution. Notably, male guppies from high predation environments tend to be less colourful than those from locations with lower predation (Endler, 1980; Magurran, 2005), and colour traits are less likely to be Y-linked in guppy populations that are adapted to low predation environments (Gordon et al., 2012, 2017). These associations between Y-linked pigmentation and predation risk are both consistent with trade-offs between sexual selection and predator avoidance (Endler, 1995; Godin & McDonough, 2003), which is informative for the effect of sexual antagonism on Y chromosome evolution.

The benefits of sexual selected pigmentation traits and selection for predator avoidance can also be frequency-dependent. For example, rare colour morphs in *P. reticulata* can be favoured,

TABLE 2 Ecological effects of Y-linked alleles

Y chromosome genotype modulates the effect of heat stress on male fertility in *D. melanogaster* (Rohmer et al., 2004)

Guppy Y chromosome affects pigmentation phenotype under sexual selection but also associated with predation risk (Gordon et al., 2012, 2017)

Swordtail fish Y-linked allele affects sexually selected pigmentation (Kingston et al., 2003)

Y-linked allele in a mosquitofish with temperature-dependent effects on melanization that is involved in mate signalling and predator avoidance (Angus, 1989; Horth, 2004, 2006; Horth et al., 2013)

Y chromosome of seed beetle affects response to selection on male body size (Kaufmann et al., 2021).

possibly because predators are more likely to capture the more common morph as a result of selective search strategies (Olendorf et al., 2006). *Poecilia parae* also has multiple male colour morphs that are determined by Y-linked genetic variation (Sandkam et al., 2021). Rare colour morphs of *P. parae* are preferred by females (Lindholm et al., 2004), suggesting that the polymorphism may be maintained by frequency-dependent sexual selection. Moreover, males deploy different mating strategies (e.g. sneakers, courters) depending on their colour morph, suggesting that tradeoffs across alternative mating strategies may further contribute to the maintenance of the polymorphism (Hurtado-Gonzales & Uy, 2009). The Y-linkage of alleles in *P. parae* demonstrates how studying sex chromosome evolution can contribute to our understanding of the complex interplay between sexual and natural selection.

Xiphophorus is another genus of poeciliid fish that is a classic model for the evolution of sex chromosomes and sexual conflict. For example, Xiphophorus maculatus has a polygenic sex determination system that is thought to be maintained by sex-specific or sexually antagonistic selection—females carrying a W chromosome have higher fitness than XX females, whereas XY males have higher fitness than YY males (Orzack et al., 1980). In addition, pigmentation patterns are frequently Y-linked in Xiphophorus spp. (Zimmerer & Kallman, 1988), and the pigmentation affects both sexual selection and predator avoidance (Table 2). In the pygmy swordtail, Xiphophorus pygmaeus, a polymorphic Y-linked locus, controls body colour, with both blue and gold males found in natural populations (Baer et al., 1995; Kallman, 1989). Females from populations with few predators prefer blue males, but females from high predation risk populations have no colour preference (Kingston et al., 2003). This is consistent with sexual selection (female choice) being weaker in populations with more risk of predators because of trade-offs between sexual and natural selection (Zuk, 1992). The examples from Xiphophorus therefore provide additional evidence for opposing effects of sexual selection and predator avoidance, which can be informative for the sex-specific selection pressures affecting sex chromosome evolution.

Sex linkage of pigmentation alleles is observed in other fish, as well. For example, there is a Y-linked melanism allele in the eastern mosquitofish, Gambusia holbrooki, and the penetrance of the allele depends on temperature (Angus, 1989; Horth, 2006). Non-melanic mosquitofish males are preferred by females, possibly because the melanism resembles a parasitic infection (Horth et al., 2013). However, melanic males have an advantage in the presence of predators (Horth, 2004), suggesting an environmentdependent selective advantage that could maintain genetic variation at this sexually selected Y-linked locus (Table 2). There is also a Y-linked colour allele in the Japanese rice fish, Oryzias latipes (Aida, 1921), a member of a genus with multiple sex chromosome turnovers (Takehana et al., 2014; Myosho et al., 2015). Future work could test whether these Y-linked alleles have ecologically relevant fitness effects, which could be informative for trade-offs between sexual and natural selection. In addition, rice fishes may be a promising model system to test whether there is a relationship between pigmentation, ecological factors (e.g. predation) and sex chromosome turnovers.

Body size is another phenotype that can be affected by Y chromosome genotypes, which could be informative for the interplay between ecological factors, sex-specific selection, and sex chromosome evolution. Sexual size dimorphism is ubiquitous across animals, with size differences evolving under the influence of sexual selection, ecological factors and developmental constraints (Abouheif & Fairbairn, 1997; Blanckenhorn, 2005; Hedrick & Temeles, 1989; Janicke & Fromonteil, 2021). Effects of sex chromosomes on sexual size dimorphisms have been documented in multiple animal species. For example, differences in adult male size and age at sexual maturity in a population of Xiphophorus nigrensis swordtail fish are controlled by genetic variation at a Ylinked locus (Lampert et al., 2010). Females prefer large males, and small males often employ a 'sneaker' strategy to mate with females (Zimmerer & Kallman, 1989). Although it is possible that large and small males have equal fitness (Ryan et al., 1992), there may also be undescribed ecological factors that favour or differentially affect one morph in specific environments, which could be revealed by comparisons of Y chromosome genotypes. Ecological effects on size dimorphisms have been observed in one population of P. reticulata guppies, where GxE interactions affect male body size (the environmental variable manipulated was food amount), with some of the alleles for body size mapping to the Y chromosome (Hughes et al., 2005). Moreover, alleles associated with phenotypic and behavioural divergence, including body size, between sympatric stickleback species in the Gasterosteus aculeatus complex are located on the ancestral- and neo-sex chromosomes (Kitano et al., 2009; Yoshida et al., 2014). Lastly, Kaufmann et al. (2021) selected sexual size dimorphism in a seed beetle (Callosobruchus maculatus) for ten generations in the laboratory, and they found that the small Y chromosome had a disproportionate effect on male body size (Table 2). Determining whether Y-linked body size alleles in fish, insects, or other animals have context-dependent fitness effects across ecological habitats would be informative for how sex-specific selection affects sex chromosome evolution and could also reveal new insights into opposing effects of sexual and natural selection.

6 | CLINAL SEX CHROMOSOMES AND SEX-SPECIFIC LOCAL ADAPTATION

Geographic clines, with a gradient in selection pressures along a species' range (Endler, 1977; Huxley, 1938), are especially informative for sex-specific selection pressures that differ across environments. Theory predicts that the evolution of sexually selected traits can be affected by clinal variation in natural selection (Day, 2000; Lande, 1982). Owen (1986) additionally showed that sex-specific selection along a cline can create differences in the frequencies of X-linked alleles between males and females. Lasne et al. (2017)

TABLE 3 Sex chromosome clines and sex-linked locally adapted alleles

Wing melanization in *Colias philodice eriphyle* varies across populations and depends on W-linked genetic variation (Ellers & Boggs, 2002)

Alleles associated with cold tolerance and climate are enriched on the *Drosophila montana* X chromosome (Wiberg et al., 2021)

Frequency of clinal neo-sex chromosome in *D. americana* is associated with minimum winter temperatures (McAllister et al., 2008)

Temperature-dependent fitness effects maintain a cline of house fly proto-Y chromosome (Delclos et al., 2021)

X-linked gene expression divergence in females is elevated across populations of *Drosophila serrata* (Allen et al., 2017)

further demonstrated that X-linked genes should contribute more to local adaptation than autosomal genes, especially if migration is male-biased. Selection within local environments is also predicted to increase the rate of fixation of chromosomal inversions on the X chromosome relative to the autosomes (Connallon, Olito, et al., 2018), a phenomenon that has been observed in *Drosophila* (Bhutkar et al., 2008).

Despite the theoretical predictions described above, empirical tests of disproportionate sex chromosome effects on clinal variation and local adaptation have produced mixed results (Table 3). Lasne et al. (2019) failed to find evidence that the D. melanogaster X chromosome contributes meaningfully to clinal variation in multiple traits, although they did not consider sex-specific phenotypic effects. By contrast, wing melanization in the butterfly Colias philodice eriphyle increases with elevation and depends largely on W-linked genetic variation (Ellers & Boggs, 2002). In addition, there is an enrichment of X-linked alleles associated with divergence in cold tolerance and climatic variables across populations of Drosophila montana (Wiberg et al., 2021). Moreover, a polymorphic neo-sex chromosome in Drosophila americana is distributed along a latitudinal cline, and the frequency across populations is best predicted by the minimum winter temperature (McAllister et al., 2008).

One of the clearest examples of a clinal sex chromosome polymorphism with environment-dependent fitness effects comes from the house fly, *Musca domestica* (Table 3). House fly has a multifactorial sex determination system, with a male-determining gene that is frequently found on one of two different proto-Y chromosomes (Hamm et al., 2015; Meisel et al., 2017; Sharma et al., 2017; Son & Meisel, 2021). One of these male-determining proto-Y chromosomes is most common at northern latitudes, and the other is predominantly found at southern latitudes (Denholm et al., 1986; Hamm et al., 2005; Kozielska et al., 2008; Tomita & Wada, 1989). As predicted by their clinal distributions, the frequencies of these two proto-Y chromosomes are associated with temperature variation across populations (Feldmeyer et al., 2008). Moreover, the northern proto-Y chromosome confers greater cold tolerance and preference for colder temperatures, whereas the southern proto-Y

confers heat tolerance and preference for warmer temperatures (Delclos et al., 2021). These patterns suggest that the polymorphism is maintained by temperature-dependent fitness effects of the proto-Y chromosomes, but it is not yet resolved if these effects are sex-specific.

Sexually dimorphic gene expression may be an especially promising phenotype to study across environments in order to test for differences in local adaptation between sex chromosomes and autosomes (Ingleby et al., 2014). There is evidence that the expression levels of X-linked genes evolve faster than autosomal genes, which could possibly be explained by sex-specific selection pressures (Brawand et al., 2011; Kayserili et al., 2012; Meisel et al., 2012). It is not clear, however, whether this faster-X evolution of gene expression is caused by selection on ecologically relevant phenotypes. In the house fly example described above, transcriptome-wide gene expression analysis has identified candidate genes whose temperature-dependent expression differences between proto-Y chromosome genotypes may be responsible for the phenotypes under selection (Adhikari et al., 2021). In addition, across populations of D. serrata, X-linked gene expression divergence in females is elevated, relative to the autosomes (Table 3), suggesting that the X chromosome may disproportionately contribute to female-specific local adaptation (Allen et al., 2017). Further work is needed to evaluate whether sex chromosomes disproportionately contribute to local adaptation more generally, if those contributions depend on whether the alleles under selection have sex-specific fitness effects, and the extent to which those fitness effects depend on differential gene expression. Work to address these open questions would be informative for how sex-specific selection affects sex chromosome evolution, and the extent to which sexual conflict differs across environments.

7 | FUTURE DIRECTIONS

I have explained how ecological factors can favour sex chromosome turnovers (Table 1), including a clear example where the sexspecific selection pressure has been identified (Roberts et al., 2009). There are also multiple examples where sex-linked alleles disproportionately contribute to ecologically relevant phenotypes and local adaptation (Tables 2 and 3), as predicted by some population genetics theory (Connallon, Olito, et al., 2018; Lasne et al., 2017; Owen, 1986). These theoretical predictions and empirical results demonstrate how consideration of ecological factors can inform our understanding of sex chromosome evolution, and also how studying the ecology of sex chromosome evolution can help us to understand the causes and effects of sex-specific selection pressures. However, each of these phenomena is illustrated by a small number of examples, and future work investigating the ecology of sex chromosome evolution will help us better understand both sex chromosome evolution and sex-specific selection. Below, I describe specific questions and model systems for studying the ecology of sex chromosome evolution.

7.1 | Pigmentation and sex chromosome turnover

Examining conflicts over pigmentation that attracts both mates and predators is likely to be the most promising way forward to investigate how ecological factors affect sex chromosome turnover. The example of cichlid fish pigmentation clearly demonstrates how a sexual conflict over sexually selected male pigmentation and female camouflage can be resolved by a sex chromosome turnover that limits inheritance of one allele to the sex in which it is beneficial (Roberts et al., 2009). In addition, the poeciliid fish Y chromosome polymorphisms are a classic model for sexually selected male-limited pigmentation (Kingston et al., 2003; Gordon et al., 2012, 2017). Continuing work in both the cichlid and poeciliid systems is likely to reveal more examples of sex-specific and ecologically dependent selection pressures that shape sex chromosome turnover, and sex chromosome evolution more broadly.

Cichlids are an especially promising system for future work because of the high rate of both sex chromosome turnover and ecological adaptation that has happened in a very short period of time (El Taher et al., 2021; Ronco et al., 2021). There has been extensive sex chromosome turnover during the evolution of cichlids from Lake Malawi, Lake Tanganyika, and other East African lakes (El Taher et al., 2021; Gammerdinger & Kocher, 2018). Closely related cichlid species often differ in which linkage group is the sex chromosome, and some species have polygenic sex determination systems with multiple chromosomes carrying sex-determining loci (Böhne et al., 2019; Roberts et al., 2016; Ser et al., 2010). Cichlid fish are also one of the best examples of an adaptive radiation giving rise to many new species in a short period of time, possibly as a result of niche specialization for a diversity of ecological habitats (Ronco et al., 2021). Sex chromosomes are thought to have a large effect on speciation because they may be more likely to harbour loci for reproductive isolation (Payseur et al., 2018), providing a link between sex chromosome turnover and speciation in cichlid fish (El Taher et al., 2021). Moreover, alleles responsible for colour variation in cichlids are often sex-linked (Lande et al., 2001), suggesting that sexual conflicts over camouflage and mate attraction at pigmentation loci could be partially responsible for both sex chromosome turnover and speciation in cichlid fish. This is notable because it ties together ecological factors that promote speciation with ecological factors that favour sex chromosome turnover. Niche specialization in cichlids would therefore be a well-suited model system for further investigations into the effects of ecological adaptation on sex chromosome turnover or vice versa (Parnell & Streelman, 2013). This research could additionally be integrated with work on other sexual dimorphisms in cichlids to address questions related to sex differences in niche utilization (Ronco et al., 2019). Future work could also examine whether sex-linked loci are disproportionately involved in ecological adaptation or speciation in cichlids, addressing questions about the role sex chromosomes play in local adaptation.

Cichlids are also well suited for investigating whether and why specific chromosomes are more likely to become sex chromosomes. When sex chromosome turnovers are common, the same linkage group can become the sex chromosome in multiple evolutionary lineages. There has indeed been repeated recruitment of the same chromosome to be an X-Y or Z-W chromosome across cichlids, with rates of sex chromosome re-use exceeding random expectations (Böhne et al., 2019; El Taher et al., 2021; Feller et al., 2021; Gammerdinger & Kocher, 2018). There are at least two explanations for the same chromosome repeatedly being recruited to be a sex chromosome in multiple evolutionary lineages (Furman & Evans, 2016; O'Meally et al., 2012). First, the chromosomes that ultimately transition to sex chromosomes may be enriched for genes that can mutate into sex-determining alleles, such as Sox9 in Oryzias rice fishes (Takehana et al., 2007, 2014; Myosho et al., 2015). Alternatively, some chromosomes may be more likely to harbour sexually antagonistic alleles whose conflicts can be resolved by Y- or W-linkage, for example genes involved in pigmentation that have dual roles in camouflage and mate attraction. Additional work could distinguish between these explanations by further testing whether genes affecting ecologically relevant phenotypes (e.g. pigmentation traits) in cichlids are disproportionately found on sex chromosomes (Lande et al., 2001).

Sexual dichromatism is extensive across animals, raising the possibility that conflicts between sexual selection and predator avoidance may be important for sex chromosome turnover in other taxa. Of note here are the sexually dichromatic fish beyond cichlids and poeciliids (Miller et al., 2021). There is also extensive sexual dichromatism in frogs (Bell & Zamudio, 2012). Frogs, like fish, have experienced very high rates of sex chromosome turnover during their evolution (Jeffries et al., 2018; Ma & Veltsos, 2021). However, unlike fish, no clear links have been identified between pigmentation, ecology and sex chromosome evolution in frogs. Frogs may therefore represent a promising, untapped system to investigate how intersexual conflicts over sexual selection and ecological adaptation promote sex chromosome turnover.

7.2 | Local adaptation and clinal variation involving sex chromosomes

There have been multiple proposed connections between sex chromosomes, local adaptation and geographic clines. I described examples where variation in ecological factors (e.g. temperature) across a species range creates heterogeneous selection pressures that maintain sex-linked polymorphisms (Table 3). In addition, there are theoretical predictions that multiple classes of mutations (e.g. amino acid substitutions, chromosomal inversions) should reach fixation on the sex chromosomes more quickly or more often than on the autosomes (Rice, 1984; Charlesworth et al., 1987; Connallon et al., 2012), some of which predict that local adaptation could affect the rate of sex chromosome evolution (Connallon, Olito, et al., 2018). Future work should evaluate how variation in temperature, humidity, nutritional resources or other ecological factors affects sex-linked alleles and sex chromosome inversions relative to autosomes for reasons described below.

Investigating how ecological factors affect selection of sex chromosome inversions could help us to understand why there is suppressed recombination between X and Y (or Z and W) chromosomes. Inversions on the Y (or W) chromosome suppress recombination with the X (or Z) chromosome, but there is debate as to whether these inversions are favoured because of sexually antagonistic selection (Charlesworth, 2017; Ironside, 2010; Jeffries et al., 2021; Lenormand & Roze, 2022; Olito et al., 2022; Ponnikas et al., 2018). One promising route forward to help resolve this debate is by examining how ecological factors affect selection on sex chromosome and autosomal inversions. For example, testing whether there are sex-specific ecological factors that maintain clines of sex chromosome inversion polymorphisms in Drosophila and other animals (e.g. Balanyà et al., 2003; Coluzzi et al., 2002; Hooper et al., 2019; Neafsey et al., 2010; Simões & Pascual, 2018; Sturtevant & Dobzhansky, 1936) could address questions about how sex-specific selection differentially affects sex chromosome and autosomal inversions. Similarly, investigating how ecological factors affect sexual conflict on Y or W chromosomes (Tables 2 and 3) could help resolve questions about causal relationships between Y/W inversions and sexually antagonistic alleles. This work would be valuable for evaluating the extent to which sexual antagonism favours the fixations of sex chromosome inversions, as opposed to sexually antagonistic alleles reaching fixation on existing inversions (Mank et al., 2014).

More generally, the field should continue to test the prediction that sex-specific selection and local adaptation involves sex-linked alleles more than autosomal variants (Connallon, Olito, et al., 2018; Lasne et al., 2017; Owen, 1986). Previous empirical studies of natural populations have revealed mixed support for this prediction (Lasne et al., 2018, 2019. Wiberg et al., 2021. One possible explanation for the mixed evidence is that sex-specific fitness effects were not always considered in previous experiments. Specifically, GxE interactions that depend on sex (i.e. GxSxE effects) may be important for sexual selection and the evolution of sexual dimorphism (Ingleby et al., 2010; Delph et al., 2011). Given the importance of sex-specific selection on sex chromosome evolution, it is likely worth considering sex-specific phenotypic and fitness effects in any study of the relationship between sex chromosomes and local adaptation. However, it is also worth noting that not all sexually selected traits depend on the environment (e.g. Arbuthnott & Rundle, 2014), and it is not clear the extent to which sexual selection varies across environments. Future work could address these open questions by comparing the effects of environmental conditions on sexually selected traits that map to either the sex chromosomes or autosomes to test whether GxE or GxSxE interactions are more common for autosomal or sexlinked sexually selected traits. This work would address fundamental questions about how environmental variation affects sex-specific selection, in addition to testing theoretical predictions about sex chromosome evolution.

Insect cuticular hydrocarbons (CHCs) are well suited for investigating whether sex-linked alleles are disproportionately involved in local adaptation. Insect CHCs are essential for desiccation resistance, but they are also sexually dimorphic and important for

mate recognition (Chung & Carroll, 2015). This dual role in natural and sexual selection means that the genes responsible for CHC production can harbour alleles that have sexually antagonistic effects (Blows, 2002; Chenoweth & Blows, 2005; Chung et al., 2014; Rusuwa et al., 2022), similar to the pigmentation patterns in fish described above. There is also evidence for local adaptation and clinal distributions of CHC profiles in Drosophila (Chenoweth & Blows, 2008; Frentiu & Chenoweth, 2010), and sex differences additionally vary across populations (Chenoweth et al., 2008; Etges & Ahrens, 2001). X-linked alleles can disproportionately affect sexually dimorphic CHC profiles in Drosophila (Chenoweth et al., 2008; Chenoweth & Blows, 2003), but it is not yet known whether the sexspecific effects of X-linked alleles differ across populations or along clines. Future work could examine whether sex-specific differences in CHC profiles across populations are disproportionately affected by X-linked alleles, addressing fundamental questions about sex chromosome evolution, sexual selection and sexual conflict.

Two additional phenotypes that are promising candidates for studying how sex-linked alleles affect local adaptation are body size and immune response to infection. Body size evolution is affected by both sexually antagonistic selection and ecological factors that vary across latitudes Cox et al., 2003; Blanckenhorn et al., 2006; Fairbairn et al., 2007). Pathogen exposure also varies across environments (Ostfeld et al., 2010), which could create heterogeneous selection pressures across populations. In addition, there are sex differences in immune responses (Belmonte et al., 2019; Klein & Flanagan, 2016), suggesting that there are sex-specific selection pressures on the immune system, such as post-mating induction of the female immune system (Morrow & Innocenti, 2012). Notably, the D. melanogaster X chromosome is depauperate in genes encoding antimicrobial peptides (Hill-Burns & Clark, 2009), which could be explained by sex-specific selection pressures (Meisel et al., 2022). Future work could investigate whether sex-linked body size or immune alleles have context-dependent fitness effects across ecological habitats. A complementary approach could investigate whether sex-linked alleles disproportionately have sex-specific or sexually dimorphic effects on clinal variation or local adaptation of body size phenotypes or immune responses. Each of these lines of inquiry would address important and unresolved questions about how sexspecific selection affects sex chromosome evolution, as well as how sexual conflict depends on ecology.

Lastly, ecological effects of Y-linked genetic variation have not been broadly considered beyond a few limited examples, such as Y-linked pigmentation alleles in fish (Table 2) and thermal traits in house fly (Table 3). There is substantial evidence that Y-linked alleles have other important fitness effects, such as Y chromosome genotypes that affect male fertility in *Drosophila* (Chippindale & Rice, 2001; Clark, 1990). Y-linked variation in *D. melanogaster* also affects genome-wide gene expression, immune response to infection and aging (Brown et al., 2020; Griffin et al., 2015; Lemos et al., 2008, 2010), which is suggestive of important epistatic interactions between Y-linked alleles and the rest of the genome. Indeed, there is evidence for co-adaptation between Y-linked and autosomal

genotypes in D. melanogaster (Lund-Hansen et al., 2021). Moreover, the phenotypic effects of Y-linked alleles can depend on both social and environmental contexts, including temperature (Rohmer et al., 2004; Dean et al., 2015). Notably, the deleterious effects of high temperature on male fertility in Drosophila depend on Y chromosome genotype, and Y chromosomes from tropical populations are more robust to heat stress than temperate Y chromosomes (Rohmer et al., 2004). Future work investigating how ecological factors affect additional phenotypic and fitness effects of Y-linked alleles in Drosophila would be a well-suited model system to address how environmental variation modulates sex-specific selection pressures and how sex-specific selection shapes Y chromosome evolution. In other animals where generating Y chromosome replacement lines is not feasible, contrasting how environmental gradients in natural populations affect Y-linked, X-linked and autosomal variants could address similar questions.

8 | CONCLUSIONS

Sex chromosome evolution is greatly affected by sex-specific selection pressures, and I have described multiple examples wherein those sex-specific selection pressures depend on ecological factors. These examples illustrate how ecological factors can create intersexual conflicts favouring sex chromosome turnover (Table 1), and also how sex-linked alleles affect local adaptation or clinal variation (Tables 2 and 3). However, these examples are limited, and multiple open questions remain about how ecology affects sex chromosome evolution. For instance, future work is needed to test whether sex chromosomes play a disproportionate role in local adaptation, and whether those effects are limited to sex-specific or sexually antagonistic traits. X-autosome contrasts of alleles responsible for local adaptation are informative about the sex-specific selection pressures affecting sex chromosome evolution; they also serve as a model for studying the causes and effects of sex-specific selection more generally, addressing fundamental questions at the intersection of ecological adaptation and sexual dimorphism. In addition, although sexual conflict arising from ecological factors can promote sex chromosome turnover (e.g. Roberts et al., 2009), it is not clear whether ecologically relevant selection pressures are a common factor in sex chromosome turnover. Addressing this question could help disentangle the causes of sex chromosome turnover from the subsequent effects of sex-linkage following a turnover event (Mank et al., 2014). These should be motivating questions for researchers interested in ecology and the evolution of sex chromosomes going forward.

AUTHOR CONTRIBUTIONS

Richard Meisel: Conceptualization (lead); visualization (lead); writing – original draft (lead); writing – review and editing (lead).

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CONFLICT OF INTEREST

The author has no conflict of interest to declare.

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