

## Recursion Equations

In each generation we census the genotype frequencies in male and female haploids before haploid selection, e.g., sperm/pollen and eggs/ovules. Before haploid selection, the frequency of X-bearing male and female haploids are given by  $X_i^m$  and  $X_i^f$  and the frequency of Y-bearing haploids is given by  $Y_i^m$  where the index  $i$  specifies genotypes  $MA$ ,  $Ma$ ,  $mA$ , and  $ma$ . Selection then occurs among male haploids according to the **A** locus allele,  $k$ , carried by individuals with genotype  $i$ . Assuming that the fraction of X-bearing haploids produced by males is  $f$ , the genotype frequencies after haploid selection are  $X_i^{m,s} = fw_k X_i^m / \bar{w}_H$  and  $Y_i^{m,s} = (1-f)w_k Y_i^m / \bar{w}_H$ , where  $\bar{w}_H = \sum_{i=1}^4 fw_k X_i^m + (1-f)w_k Y_i^m$  is the mean fitness of male haploids. Random mating then occurs between gametes to produce diploid females with genotype  $ij$  at frequency  $x_{ij} = X_i^f X_j^{m,s}$  and diploid males at frequency  $y_{ij} = X_i^f Y_j^{m,s}$ . In females, individuals with genotype  $ij$  are equivalent to those with genotype  $ji$ . For simplicity we denote the frequency of genotype  $ij$  in females to the average of these frequencies,  $x_{ij} = (X_i^f X_j^{m,s} + X_j^f X_i^{m,s})/2$ . Note that the sex ratio before diploid selection depends both on the production of X-bearing haploids by fathers ( $f$ ) and on haploid selection ( $w_k$ ). However,  $f$  does not enter into any results, indicating that the main force driving recombination evolution is not to balance the current sex ratio.

**Table S.1. Fitness of different genotypes.**

Genotype	$A$	$a$	$AA$	$Aa$	$aa$
Fitness in males	$w_A$	$w_a$	$w_{AA}^m$	$w_{Aa}^m$	$w_{aa}^m$
Fitness in females	1	1	$w_{AA}^f$	$w_{Aa}^f$	$w_{aa}^f$

**Table S.2. Marginal fitnesses of YA and Xa haplotypes**

$\bar{w}_{YA}^m$	$= (w_A(p_X f w_{AA}^f + (1-p_X f)w_{Aa}^f))$
$\bar{w}_{Xa}^{mat,m}$	$= p_Y m w_A w_{Aa}^m + (1-p_Y m)w_a w_{aa}^m$
$\bar{w}_{Xa}^{pat,f}$	$= p_X f w_a w_{Aa}^f + (1-p_X f)w_a w_{aa}^f$
$\bar{w}_{Xa}^{mat,f}$	$= p_X m w_A w_{Aa}^f + (1-p_X m)w_a w_{aa}^f$

Selection among diploids then occurs according to the diploid genotype at the **A** locus,  $k$ , for an individual of type  $ij$  (see Table S.1). The diploid frequencies after selection are given by  $x_{ij}^s = w_k^f x_{ij} / \bar{w}^f$  in females and  $y_{ij}^s = w_k^m y_{ij} / \bar{w}^m$  in males, where  $\bar{w}^f = \sum_{i=1}^4 \sum_{j=1}^4 w_k^f x_{ij}$  and  $\bar{w}^m = \sum_{i=1}^4 \sum_{j=1}^4 w_k^m y_{ij}$  are the mean fitnesses of females and males, respectively. Finally, these diploids undergo meiosis to produce the next generation. The haplotype frequencies in the next generation of eggs/ovules is given by:

$$X_{MA}^{f'} = \left( \sum_{j=1}^4 x_{1j}^s \right) - R_f(x_{14}^s - x_{23}^s) \quad (\text{S.1a})$$

$$X_{Ma}^{f'} = \left( \sum_{j=1}^4 x_{2j}^s \right) + R_f(x_{14}^s - x_{23}^s) \quad (\text{S.1b})$$

$$X_{mA}^{f'} = \left( \sum_{j=1}^4 x_{3j}^s \right) + R_f(x_{14}^s - x_{23}^s) \quad (\text{S.1c})$$

$$X_{ma}^{f'} = \left( \sum_{j=1}^4 x_{4j}^s \right) - R_f(x_{14}^s - x_{23}^s) \quad (\text{S.1d})$$

which only involve the recombination rate between the **A** locus and the **M** locus in females ( $R_f$ ). In males, recombination between the SDR and the **A** locus or the **M** also affects the frequencies of haplotypes produced. The frequency of haplotypes among X-bearing sperm/pollen (before haploid selection) in the next generation are given by

$$\begin{aligned} X_{MA}^{m'} &= \left( \sum_{j=1}^4 y_{1j}^s \right) - r_{MM}(y_{12}^s - y_{21}^s) \\ &\quad - (R_m + r_{Mm} - 2\chi)(y_{13}^s - y_{31}^s) - (R_m + r_{Mm} - \chi)y_{14}^s \\ &\quad + (r_{Mm} - \chi)y_{41}^s + \chi y_{23}^s + (r_{Mm} - \chi)y_{32}^s \end{aligned} \quad (\text{S.2a})$$

$$X_{Ma}^{m'} = \left( \sum_{j=1}^4 y_{2j}^s \right) - r_{MM}(y_{21}^s - y_{12}^s) - (R_m + r_{Mm} - 2\chi)(y_{24}^s - y_{42}^s) - (R_m + r_{Mm} - \chi)y_{23}^s + (r_{Mm} - \chi)y_{32}^s + \chi y_{14}^s + (r_{Mm} - \chi)y_{41}^s \quad (\text{S.2b})$$

$$X_{mA}^{m'} = \left( \sum_{j=1}^4 y_{3j}^s \right) - r_{mm}(y_{34}^s - y_{43}^s) - (R_m + r_{Mm} - 2\chi)(y_{31}^s - y_{13}^s) - (R_m + r_{Mm} - \chi)y_{32}^s + (r_{Mm} - \chi)y_{23}^s + \chi y_{41}^s + (r_{Mm} - \chi)y_{14}^s \quad (\text{S.2c})$$

$$X_{ma}^{m'} = \left( \sum_{j=1}^4 y_{4j}^s \right) - r_{mm}(y_{43}^s - y_{34}^s) - (R_m + r_{Mm} - 2\chi)(y_{42}^s - y_{24}^s) - (R_m + r_{Mm} - \chi)y_{41}^s + (r_{Mm} - \chi)y_{14}^s + \chi y_{32}^s + (r_{Mm} - \chi)y_{23}^s \quad (\text{S.2d})$$

and the frequencies of Y-bearing sperm/pollen haplotypes (before haploid selection) are given by

$$Y_{MA}^{m'} = \left( \sum_{j=1}^4 y_{1j}^s \right) - r_{MM}(y_{21}^s - y_{12}^s) - (R_m + r_{Mm} - 2\chi)(y_{31}^s - y_{13}^s) - (R_m + r_{Mm} - \chi)y_{41}^s + (r_{Mm} - \chi)y_{14}^s + \chi y_{32}^s + (r_{Mm} - \chi)y_{23}^s \quad (\text{S.3a})$$

$$Y_{Ma}^{m'} = \left( \sum_{j=1}^4 y_{2j}^s \right) - r_{MM}(y_{12}^s - y_{21}^s) - (R_m + r_{Mm} - 2\chi)(y_{42}^s - y_{24}^s) - (R_m + r_{Mm} - \chi)y_{32}^s + (r_{Mm} - \chi)y_{23}^s + \chi y_{41}^s + (r_{Mm} - \chi)y_{14}^s \quad (\text{S.3b})$$

$$Y_{mA}^{m'} = \left( \sum_{j=1}^4 y_{3j}^s \right) - r_{mm}(y_{43}^s - y_{34}^s) - (R_m + r_{Mm} - 2\chi)(y_{13}^s - y_{31}^s) - (R_m + r_{Mm} - \chi)y_{23}^s + (r_{Mm} - \chi)y_{32}^s + \chi y_{14}^s + (r_{Mm} - \chi)y_{41}^s \quad (\text{S.3c})$$

$$Y_{ma}^{m'} = \left( \sum_{j=1}^4 y_{4j}^s \right) - r_{mm}(y_{34}^s - y_{43}^s) - (R_m + r_{Mm} - 2\chi)(y_{24}^s - y_{42}^s) - (R_m + r_{Mm} - \chi)y_{14}^s + (r_{Mm} - \chi)y_{41}^s + \chi y_{23}^s + (r_{Mm} - \chi)y_{32}^s \quad (\text{S.3d})$$

### Invasion of recombination modifiers

Invasion of modifiers that create a strong linkage between the X and *a* allele is determined by the largest solution to the characteristic polynomial

$$\lambda_{Xa}^2 - \lambda_{Xa}\bar{w}_{Xa}^{mat,f}/\bar{w}^f - (\bar{w}_{Xa}^{pat,f}/\bar{w}^f)(\bar{w}_{Xa}^{mat,m}/\bar{w}^m) = 0. \quad (\text{S.4})$$

This can be solved for  $\lambda_{Xa}$  if we assume that the selected locus is initially loosely linked to the SDR ( $r_{MM}$ ) and that there are no sex differences in selection ( $w_{ij}^m = w_{ij}^f = w_{ij}$ ). The equilibrium frequency of the *A* allele when maintained at a polymorphic equilibrium by selection is then

$$\hat{p}_{Xm} = \hat{p}_{Ym} = \hat{p}_{Xf} = \frac{2w_a w_{aa} - w_{Aa}(w_A + w_a)}{2(w_A(w_{AA} - w_{Aa}) + w_a(w_{aa} - w_{Aa}))}. \quad (\text{S.5})$$

This equilibrium is valid and stable when

$$\begin{aligned} w_{Aa}(w_A + w_a) &> 2w_A w_{AA} \text{ and} \\ w_{Aa}(w_A + w_a) &> 2w_a w_{aa}. \end{aligned} \quad (\text{S.6})$$

Therefore, a polymorphism can be maintained either if there is heterozygote advantage in diploids ( $w_{Aa} > w_{aa}$  and  $w_{Aa} > w_{AA}$ ) or if there is antagonistic selection between haploids and diploids (e.g.,  $w_A > w_a$  and  $w_{aa} > w_{Aa} > w_{AA}$ ) or a combination of both (Immler et al. 2012).

After this equilibrium is reached, the invasion of a modifier that brings the  $A$  allele into linkage with the  $Y$  is given by

$$\lambda_{YA} = 1 + \frac{(w_A - w_a)w_{Aa}(w_A + w_a)(w_{Aa}(w_A + w_a) - 2w_{AA}w_A)}{(w_A + w_a)(w_{Aa}^2(w_A + w_a)^2 - 4w_Aw_{AA}w_a w_{Aa})}, \quad (\text{S.7})$$

where  $\lambda_{YA} > 1$  indicates that the modifier increases in frequency. Given that a polymorphism at the  $\mathbf{A}$  locus is initially stable (conditions S.6 are met) the sign of  $\lambda_{YA} - 1$  depends on the sign of  $w_A - w_a$ . That is, modifiers that bring the allele favoured in haploids (e.g.,  $A$  when  $w_A > w_a$ ) into tight linkage with the  $Y$  will spread.

Similarly, condition 2 for the invasion of modifiers that bring the  $a$  allele into tight linkage with the  $X$  chromosome is satisfied if

$$\frac{(w_A - w_a)w_{Aa}(w_A + w_a)(w_{Aa}(w_A + w_a) - 2w_{AA}w_A)}{2(w_A + w_a)(w_{Aa}(w_A + w_a) - w_Aw_{AA} - w_a w_{Aa})} > 0, \quad (\text{S.8})$$

which requires  $w_A > w_a$ , given that conditions S.6 are met. These results indicate that recombination modifiers invade if they bring the  $X$  into tight linkage with the allele that is less fit during haploid selection, even without the weak selection assumptions in equation 4 and without sex differences in selection in the diploid phase.

In the main text and above, we consider the invasion of recombination suppressors that bring the  $a$  allele into tight linkage with the  $X$  when the  $\mathbf{A}$  locus is initially loosely linked to the SDR ( $r_{MM} = 1/2$ ) such that  $\hat{p}_{Xm} = \hat{p}_{Ym}$ . Here, we consider cases where  $r_{MM} < 1/2$  and define the difference in the frequency of the  $A$  allele between  $X$ - and  $Y$ -bearing pollen/sperm as  $\delta_{XY} = \hat{p}_{Ym} - \hat{p}_{Xm}$ . We assume that selection is weak relative to recombination such that  $\delta$ ,  $\delta_{XY}$ , and  $\delta_H$  are all small (of order  $\epsilon^2$ ). Invasion is then given by

$$\lambda'_{Xa} = \lambda_{Xa} \left( 1 - (1 - 2r_{MM})(3 + 2w_{Aa}^f/\bar{w}^f) \right) + \frac{w_{Aa}^f \delta_{XY}}{3\bar{w}^f} \quad (\text{S.9})$$

Under the conditions where  $\lambda_{Xa} > 1$ , we would expect that the  $a$  allele is associated with the  $X$  such that  $\delta_{XY} < 0$ . Thus, S.9 indicates that selection in favour of modifiers that suppress recombination is less strong when  $r_{MM} < 1/2$  ( $\lambda'_{Xa} < \lambda_{Xa}$ ), in which case intralocus conflicts are initially partially resolved by reduced recombination.

### Invasion of Modifiers That Increase Recombination from an Initially Low Level

We consider a population in which linkage is tight between the  $\mathbf{A}$  locus and the SDR ( $r_{MM}$  is of order  $\epsilon$ , where the  $M$  allele is initially fixed). Recombination has no effect if the  $\mathbf{A}$  locus is fixed for one allele, we therefore focus on the five equilibria that maintain both  $A$  and  $a$  alleles, of which four are given to leading order by:

$$\begin{aligned} (A) \quad & \hat{p}_{Ym} = 0, \quad \hat{p}_{Xf} = \frac{\alpha}{\alpha + \beta}, \quad \hat{p}_{Xm} = \frac{w_{Aa}^m \alpha}{w_{Aa}^m \alpha + w_{aa}^m \beta} \\ (A') \quad & \hat{p}_{Ym} = 1, \quad \hat{p}_{Xf} = 1 - \frac{\alpha'}{\alpha' + \beta'}, \quad \hat{p}_{Xm} = 1 - \frac{w_{Aa}^m \alpha'}{w_{Aa}^m \alpha' + w_{aa}^m \beta'} \\ (B) \quad & \hat{p}_{Ym} = 0, \quad \hat{p}_{Xf} = 1, \quad \hat{p}_{Xm} = 1 \\ (B') \quad & \hat{p}_{Ym} = 1, \quad \hat{p}_{Xf} = 0, \quad \hat{p}_{Xm} = 0 \\ & \alpha = w_{Aa}^f (w_{aa}^m w_a + w_{Aa}^m w_A) - 2w_{Aa}^f w_{aa}^m w_a \\ & \alpha' = w_{Aa}^f (w_{AA}^m w_A + w_{Aa}^m w_a) - 2w_{Aa}^f w_{AA}^m w_A \\ & \beta = w_{Aa}^f (w_{aa}^m w_a + w_{Aa}^m w_A) - 2w_{Aa}^f w_{AA}^m w_A \\ & \beta' = w_{Aa}^f (w_{AA}^m w_A + w_{Aa}^m w_a) - 2w_{Aa}^f w_{AA}^m w_a \end{aligned}$$

A fifth equilibrium ( $C$ ) also exists where  $A$  is present at an intermediate frequency on the  $Y$  chromosome ( $0 < \hat{p}_Y < 1$ ). However, equilibrium ( $C$ ) is never locally stable when  $r_{MM} \approx 0$  and is therefore not considered further. Thus, the  $Y$  can either be fixed for the  $a$  allele (equilibria  $A$  and  $B$ ) or the  $A$  allele (equilibria  $A'$  and  $B'$ ). The  $X$  chromosome can then either be polymorphic (equilibria  $A$  and  $A'$ ) or fixed for the alternative allele (equilibria  $B$  and  $B'$ ). Since equilibria ( $A$ ) and ( $B$ ) are equivalent to equilibria ( $A'$ ) and ( $B'$ ) with the labelling of  $A$  and  $a$  alleles interchanged, we discuss only equilibria ( $A'$ ) and ( $B'$ ), in which the  $YA$  haplotype is favoured (as in the previous section), without loss of generality.

We next calculate when ( $A'$ ) and ( $B'$ ) are locally stable for  $r_{MM} = 0$ . According to the ‘small parameter theory’ (Karlin and McGregor 1972a;b), these stability properties are unaffected by small amounts of recombination between the SDR and  $\mathbf{A}$  locus, although equilibrium frequencies may be slightly altered. For the  $A$  allele to be stably fixed on the  $Y$  requires that  $\bar{w}_{YA}^m > \bar{w}_{Ya}^m$ , where the marginal fitnesses of  $YA$  and  $Ya$  haplotypes are  $\bar{w}_{YA}^m$  (as above) and  $\bar{w}_{Ya}^m = w_{Aa}^m p_{Xf} + w_{aa}^m (1 - p_{Xf})$ , respectively. Substituting  $\hat{p}_{Xf}$  from above, fixation of the  $A$  allele on the  $Y$  requires that  $\gamma_i > 0$  where  $\gamma_{(A')} = w_A (w_{Aa}^m \alpha' + w_{AA}^m \beta') - w_a (w_{aa}^m \alpha' + w_{Aa}^m \beta')$  for equilibrium ( $A'$ ) and  $\gamma_{(B')} = w_{Aa}^m w_A - w_{aa}^m w_a$  for equilibrium ( $B'$ ). Stability of a polymorphism on the  $X$  chromosome (equilibrium  $A'$ ) further requires that  $\alpha' > 0$  and  $\beta' > 0$ . Fixation of the  $a$  allele on the  $X$  (equilibrium  $B'$ ) is

mutually exclusive with  $(A')$  and requires that  $\beta' < 0$ . We will assume that these conditions are met such that population has reached a stable equilibrium at the  $\mathbf{A}$  locus when considering evolution at the modifier locus.

To consider recombination rate evolution, we evaluate whether a mutant allele,  $m$ , can invade if it modifies the recombination rate between  $\mathbf{A}$  and the SDR by a small amount ( $|r_{mm} - r_{MM}|$  and  $|r_{Mm} - r_{MM}|$  are of order  $\epsilon$ ). As above, we use the leading eigenvalue,  $\lambda$ , from a local stability analysis to evaluate the spread of a rare mutant modifier, where now  $\lambda_i$  determines invasion into a population at equilibrium  $i$ . Firstly, because stability of equilibrium  $(A')$  requires that  $\alpha' > 0$  and  $\beta' > 0$  and all fitnesses must be non-negative, we can define the following series of  $\kappa$  terms, which must be positive when  $(A')$  is locally stable.

$$\begin{aligned}\kappa_1 &= w_{aa}^f \alpha' + w_{Aa}^f \beta' \\ \kappa_2 &= w_{Aa}^f \alpha' + w_{AA}^f \beta' \\ \kappa_3 &= w_{Aa}^m \alpha' + w_{AA}^m \beta' \\ \kappa_4 &= w_{aa}^f \alpha' + w_{AA}^f \beta' \\ \kappa_5 &= w_{Aa}^m w_a + w_{AA}^m w_A \\ \kappa_6 &= w_{Aa}^m w_a w_{AA}^m w_A \\ \kappa_7 &= w_{aa}^f w_{Aa}^m w_a \alpha' + w_{AA}^f w_{AA}^m w_A \beta' \\ \kappa_8 &= w_{aa}^m \alpha' \alpha' + 2w_{Aa}^m \alpha' \beta' + w_{AA}^m \beta' \beta' \\ \kappa_9 &= w_{Aa}^m w_a \alpha' + w_{AA}^m w_A \beta' \\ \kappa_{10} &= w_{Aa}^f \kappa_9 + 2\kappa_6 \kappa_4 / \kappa_5\end{aligned}$$

These are useful in determining the magnitude of  $\lambda_{(A')}$ , which determines invasion of modifiers and is given by

$$\lambda_{(A')} = 1 + (r_{Mm} - r_{MM}) \frac{w_{Aa}^m \alpha' K_1}{w_a R_m (w_{aa}^m \alpha' + w_{AA}^m \beta') K_2} \quad (\text{S.10})$$

where we neglect terms of order  $\epsilon^2$  and higher and  $K_2$  is strictly positive,

$$\begin{aligned}K_2 &= R_f 2w_{Aa}^f \kappa_3 \kappa_5 (\alpha' + \beta') \kappa_{10} + R_f R_m w_{Aa}^m w_{AA}^m 2w_a w_A K_3 \kappa_3 \kappa_4 / \kappa_5 \\ &\quad + R_m w_{Aa}^m w_{AA}^m (1 - 2R_f) (w_a \beta' \kappa_1 (2w_{AA}^m w_A \kappa_2 + \kappa_{10}) + w_A \alpha' \kappa_2 (2w_{Aa}^m w_a \kappa_1 + \kappa_{10}))\end{aligned}$$

such that  $\lambda_{(A')} > 1$  if and only if  $(r_{Mm} - r_{MM}) K_1 > 0$ , where

$$\begin{aligned}K_1 &= - (1 - 2R_f) R_m \gamma_{(A')} \kappa_1 \kappa_2 \kappa_6 - R_m R_f \gamma_{(A')} \kappa_4 \kappa_6 (\kappa_7 / \kappa_5 + w_{Aa}^f (\alpha' + \beta') / 2) \\ &\quad - R_f \gamma_{(A')} w_{Aa}^f w_a \kappa_1 \kappa_3 \kappa_5 \\ &\quad + R_f w_{Aa}^f w_{AA}^m (\gamma_{(A')} \alpha' + R_m w_a \kappa_8) ((w_{Aa}^m - w_{AA}^m) w_a w_A \kappa_4 + (w_A - w_a) w_{Aa}^f \kappa_5 (\alpha' + \beta') / 2)\end{aligned}$$

Modifiers that increase recombination ( $r_{Mm} - r_{MM} > 0$ ) therefore only spread if  $K_1 > 0$ . Only the last term of  $K_1$  can be positive, and this term can only be positive if either  $w_{Aa}^m > w_{AA}^m$  or  $w_A > w_a$ . Thus, for increased recombination to be favoured by selection ( $K_1 > 0$ ), heterozygous males must be more fit than males homozygous for the allele fixed on the Y and/or the allele fixed on the Y must be favoured during haploid selection. Since the  $A$  allele is fixed on the Y,  $w_{Aa}^m > w_{AA}^m$  implies that X chromosomes bearing the  $a$  allele are favoured during selection in males. If a polymorphism is maintained on the X (equilibrium  $A'$ ), counter-selection must favour the  $A$  allele during haploid selection and/or selection in females when  $w_{Aa}^m > w_{AA}^m$ . In addition, when linkage between the modifier locus and the selected locus is tight (at least in females,  $R_f = 0$ ),  $K_1$  is always negative and increased recombination is never favoured.

We next consider the invasion of a recombination modifier into a population at equilibrium  $(B')$ . Local stability of this equilibrium requires that  $(-\beta') > 0$  and  $\gamma_{(B')} > 0$ . Ignoring terms of order  $\epsilon^2$  and higher,

$$\lambda_{(B')} = 1 + \frac{(r_{Mm} - r_{MM}) K_4}{4(\gamma_{(B')} + R_m w_{aa}^m w_a)((-\beta') + w_{Aa}^f (R_f w_{Aa}^m w_a + R_m w_{AA}^m w_A (1 - R_f)))}$$

where

$$\begin{aligned}K_4 &= -2\gamma_{(B')} (-\beta') - (2R_f + R_m (1 - R_f)) w_{Aa}^f w_{AA}^m w_A \gamma_{(B')} \\ &\quad - R_m (-\beta') w_{aa}^m w_a \\ &\quad + R_f (w_A - w_a) w_{Aa}^f w_{AA}^m (2\gamma_{(B')} + R_m w_{aa}^m w_a) \\ &\quad + R_f R_m (w_{Aa}^m - w_{AA}^m) w_{Aa}^f w_{AA}^m w_a w_A\end{aligned}$$

Therefore  $\lambda_{(B')} > 1$  if and only if  $(r_{Mm} - r_{MM}) K_4 > 0$ . The only terms in  $K_4$  that can be positive again involve the factors  $(w_A - w_a)$  and  $(w_{Aa}^m - w_{AA}^m)$ , such that either  $w_{Aa}^m > w_{AA}^m$  or  $w_a > w_A$  are again necessary (but not sufficient) conditions for the invasion of modifiers that increase recombination.

Finally, we re-write the condition  $K_4 > 0$  to obtain

$$w_{aa}^f < w_{Aa}^f (1 - \gamma_{(B')}) R_f (2 - R_m) R_m - \gamma_{(B')} (w_{Aa}^m - w_{AA}^m) K_5 + (w_A - w_a) K_6 / K_7 \quad (\text{S.11})$$

where the following terms are positive

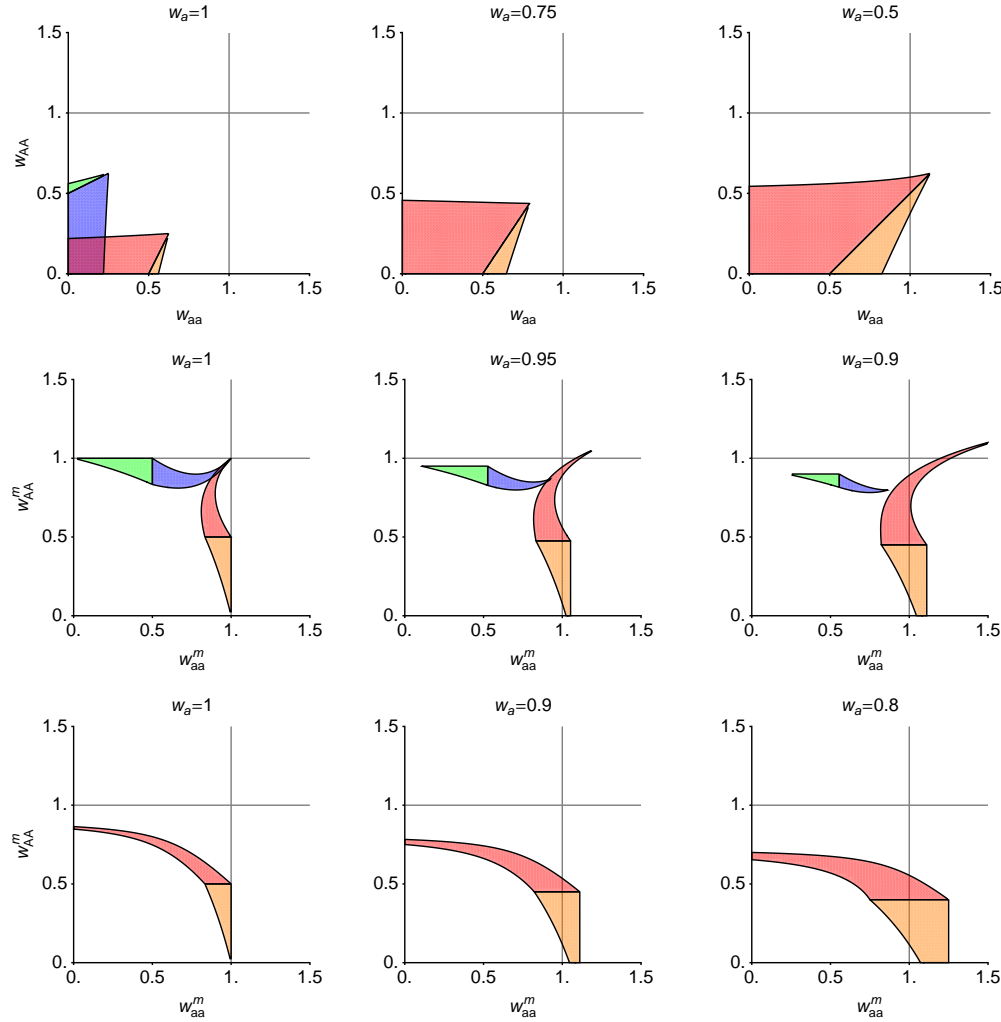
$$\begin{aligned} K_5 &= (1 - R_f)(2\gamma_{(B')}(1 - R_m) + R_m w_{Aa}^m w_a) / w_{Aa}^m \\ K_6 &= (R_f R_m w_A w_{Aa}^m + (w_{AA}^m(1 - R_f) + R_f w_{Aa}^m)(2\gamma_{(B')}(1 - R_m) + w_{Aa}^m w_A R_m)) \\ K_7 &= 4\gamma_{(B')} + 2w_{aa}^m w_a R_m \end{aligned}$$

Thus, if haploid selection favours the  $A$  allele, then condition **S.11** can be met whether selection among diploid females favours allele  $A$  or  $a$  ( $w_{aa}^f < w_{Aa}^f$  or  $w_{aa}^f > w_{Aa}^f$ ). However, if haploid selection favours the  $a$  allele ( $w_a > w_A$ ), the evolution of increased recombination requires that  $w_{Aa}^m > w_{AA}^m$  (see above), and equation **S.11** shows that selection must favour the  $A$  allele during selection in females ( $w_{aa}^f < w_{Aa}^f$ ). Thus, increased recombination is only favoured if the  $A$  allele is favoured during selection in females ( $w_{aa}^f < w_{Aa}^f$ ) and/or the  $A$  allele is favoured during haploid selection ( $w_A > w_a$ ). Only under these conditions is it possible for recombination between the  $XA$  and  $Ya$  to produce  $XA$  gametes that are favoured over the short term (in daughters and/or gametes/gametophytes, respectively).

One might not expect selection to favour  $XA$  haplotypes because an  $A$  allele on an average  $X$  background should either have the same fitness as an  $a$  allele (when a polymorphism is maintained, equilibrium  $A'$ ) or lower fitness (when  $A$  is fixed, equilibrium  $B'$ ). However, an  $XA$  haplotype created by recombination in males is found in a male haploid (pollen or sperm), not on an average  $X$  background (which is weighted across  $X$ -bearing male sperm/pollen and female eggs/ovules). Increased recombination does not evolve if  $R_f$  and  $R_m$  are small because the modifier remains linked to the haplotypes it creates, which will eventually be found on all backgrounds. However, when  $R_f$  and  $R_m$  are sufficiently large, modifiers that increase recombination can gain a transient fitness advantage.  $XA$  pollen/sperm haplotypes can gain a transient fitness advantage during haploid selection and/or selection in females. The evolution of increased recombination is only consistent with this form of selection.

## References

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**Fig. S.1.** Selection can favour increased recombination between the sex-determining region (SDR) and a selected locus that is closely linked ( $r_{ij} \approx 0$ ), even when selection in males is not overdominant. Coloured regions show where increased recombination is favoured in a population at equilibrium ( $A$ ) in blue, ( $B$ ) in green, ( $A'$ ) in red, and ( $B'$ ) in orange. Since this model is symmetrical, red/orange regions can be exchanged with blue/green regions if the labelling of  $A$  and  $a$  alleles is switched. Across columns we vary the fitness of  $a$ -bearing haploids relative to the  $A$ -bearing haploids ( $w_A = 1$ ). Grey lines show the fitness of heterozygous diploids  $w_{ij}^k = 1$ . In the first row, there are no differences in selection between male and female diploids ( $w_{ij}^f = w_{ij}^m = w_{ij}$ ), where  $w_{aa}$  and  $w_{AA}$  are varied along the x and y axes, respectively. As haploid selection becomes stronger, increased recombination can evolve with weaker overdominance in diploids and also with ploidally antagonistic selection ( $w_{aa} > 1 > w_{AA}$ ). In the second and third rows, we consider sex differences in selection, where  $w_{aa}^m$  and  $w_{AA}^m$  are varied along the x and y axes ( $w_{aa}^m = 1$ ). In the second row, where selection in females is overdominant ( $w_{AA}^f = 0.75$ ,  $w_{Aa}^f = 1$ ,  $w_{aa}^f = 0.75$ ), increased recombination can be favoured when selection is directional (or underdominant) in males and haploid selection is moderately strong. In the third row, selection favours the  $A$  allele in females ( $w_{AA}^f = 1.05$ ,  $w_{Aa}^f = 1$ ,  $w_{aa}^f = 0.75$ ) and increased recombination can also be favoured with sexually antagonistic selection ( $w_{AA}^m < 1 < w_{aa}^m$ ). For this plot, we assume that the modifier of recombination is unlinked ( $R_f = R_m = 1/2$ ).