

Supplementary Information for ‘Asymmetric life-history trade-offs shape sex-biased longevity patterns’

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This supplement includes:

Supplementary Figure 1 Convergence of male and female life expectancies to evolutionary equilibria.

Supplementary Figure 2 Effects of mating efficiency on evolved life expectancies.

Supplementary Figure 3 Effect of union divorce rate on evolved life expectancy.

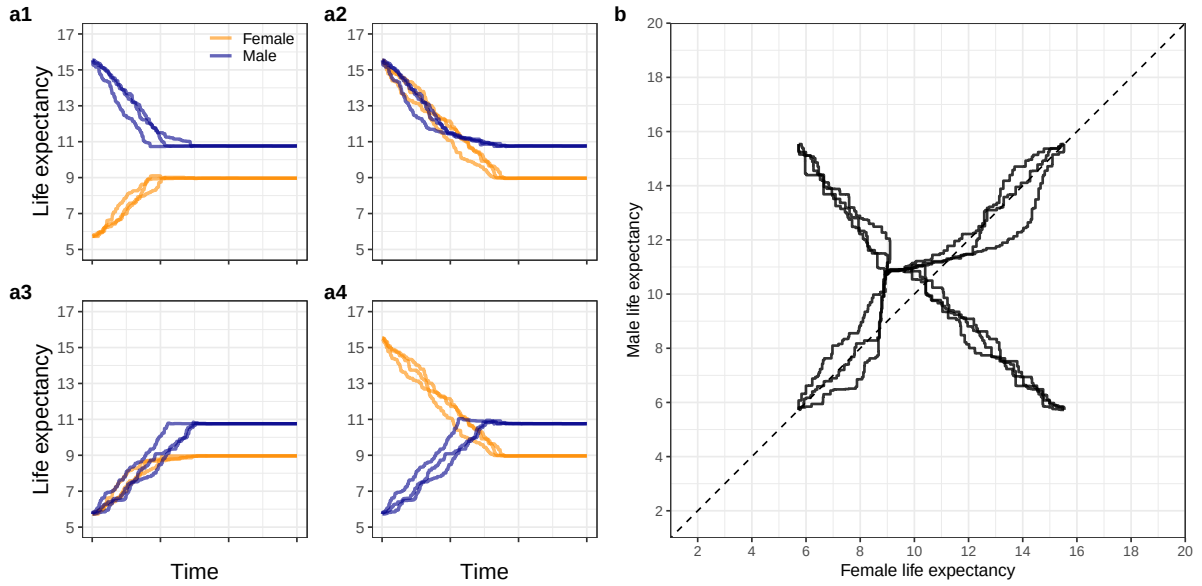
Supplementary Figure 4 Effect of bi-parental care on the evolution of sex differences in life expectancy.

Supplementary Figure 5 Life expectancy outcomes under density-dependent regulation acting on fecundity.

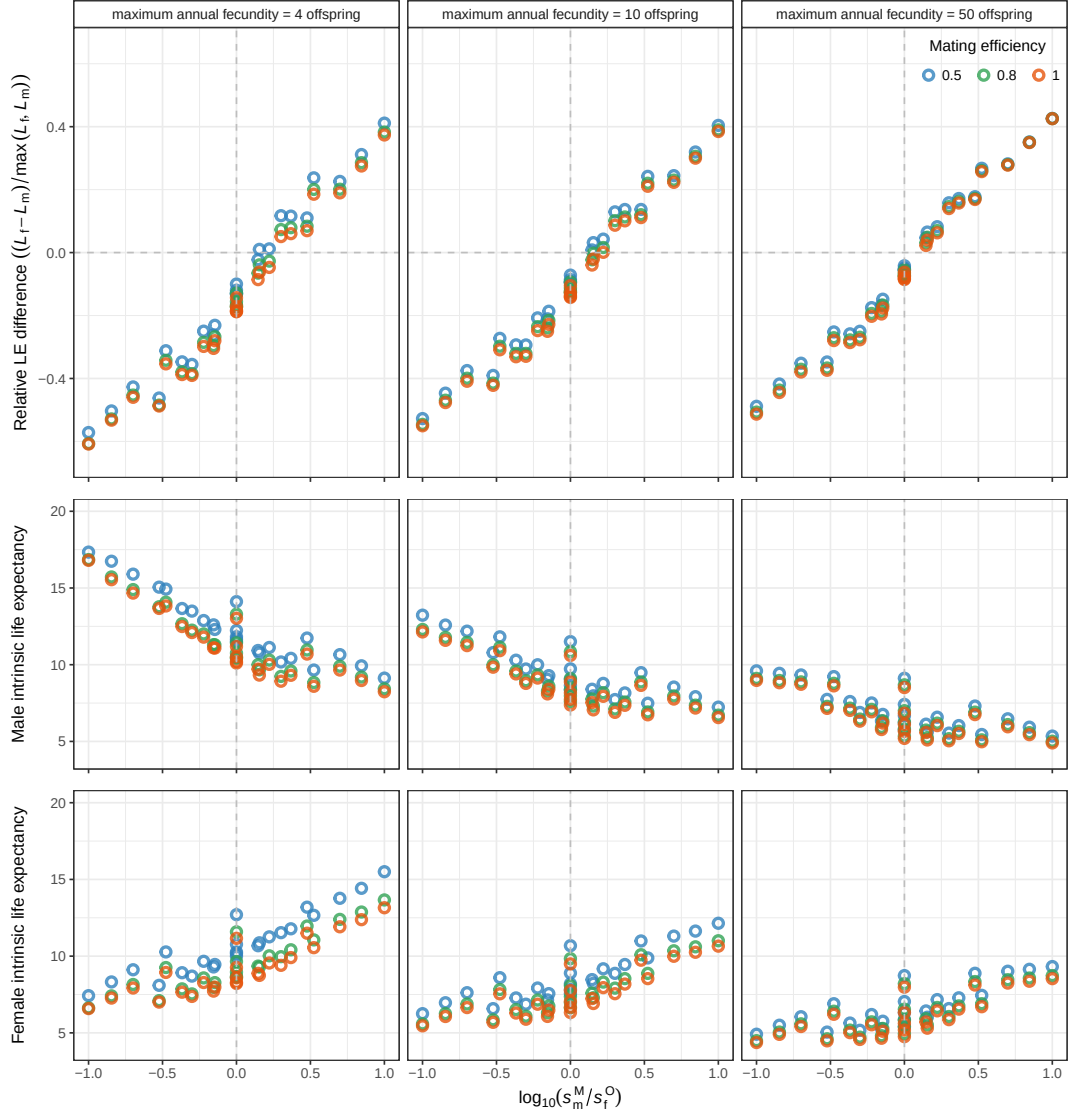
Supplementary Methods

References

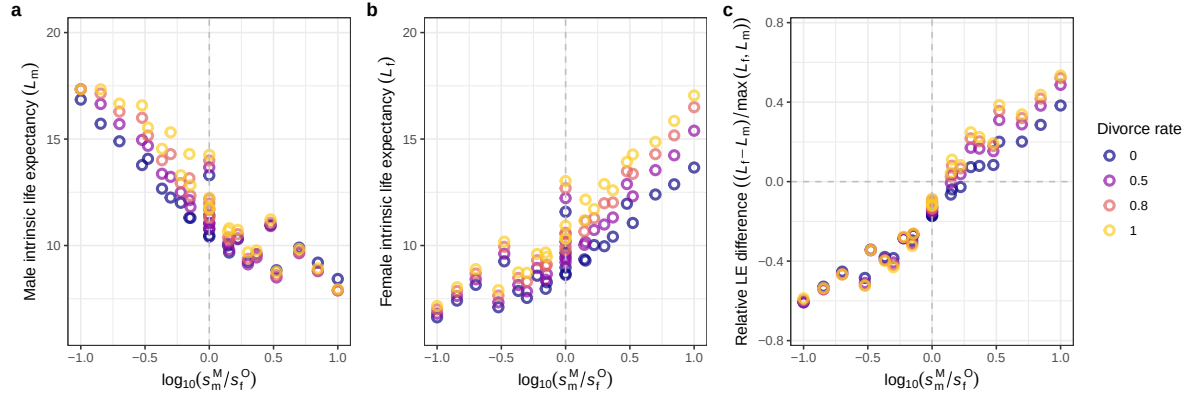
Supplementary Figures



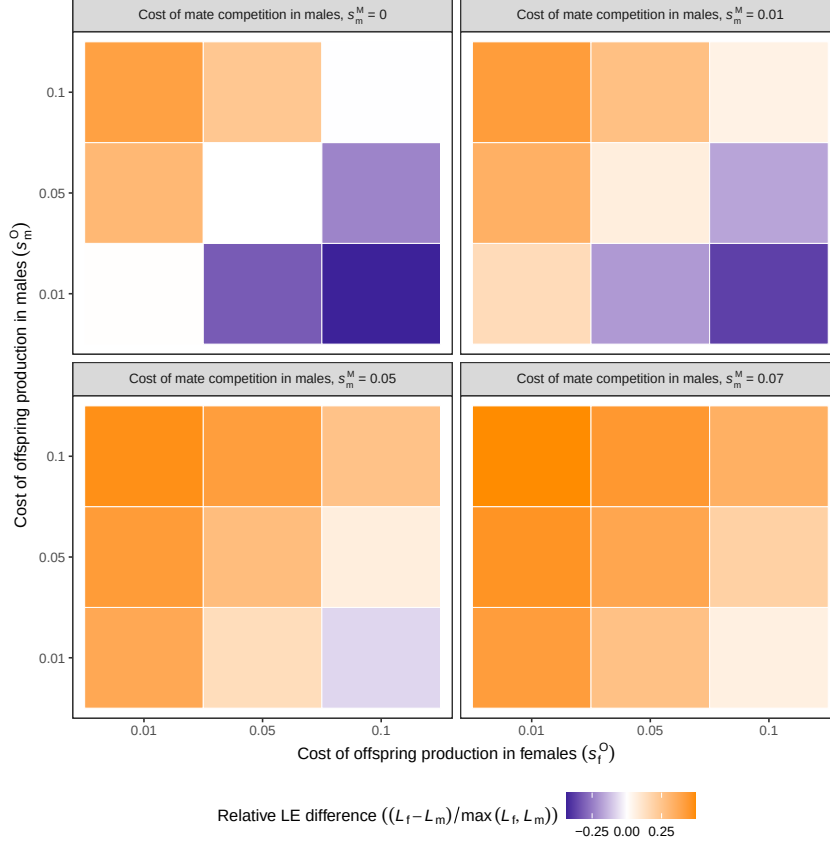
Supplementary Figure 1: Convergence of male and female life expectancies to evolutionary equilibria. Evolution of male and female life expectancies under the adaptive dynamics framework, showing convergence to evolutionary stable strategy (ESS) values from different initial conditions. At these equilibria, rare mutants with alternative life expectancies cannot invade. **a1-a4** Temporal trajectories of male and female life expectancies. **b** The same trajectories shown in phenotype space.



Supplementary Figure 2: Effects of mating efficiency on evolved life expectancies. Results under the minharmonic mating function allowing incomplete mating even under balanced sex ratios, parameterised by mating efficiency (η), the proportion of available individuals that form unions. We vary η to assess robustness of model predictions (main text uses $\eta = 0.8$). Conclusions are qualitatively robust, although higher mating efficiency slightly reduces life expectancy in both sexes. (*Top*) Relative adult intrinsic life expectancy difference, and the (*middle*) male and (*bottom*) female intrinsic life expectancies across combinations of relative trade-off strengths and maximum annual fecundity values (columns), with mating efficiency indicated by point colours. Figure conventions as in Fig. 3.



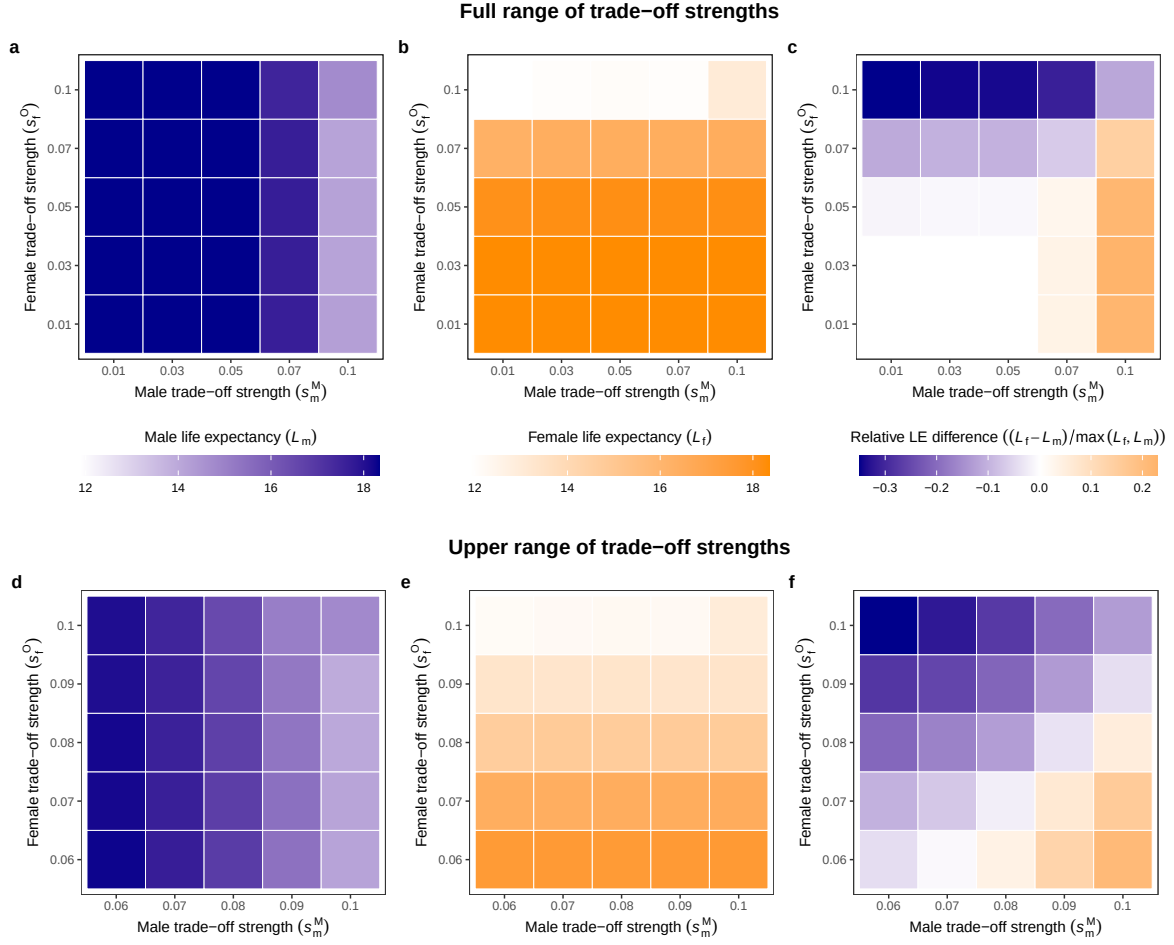
Supplementary Figure 3: Effect of union divorce rate on evolved life expectancy. **a** Male intrinsic life expectancy, **b** female intrinsic life expectancy, and **c** relative adult intrinsic life expectancy differences under various combinations of relative trade-off strengths in each sex, across varied union divorce rates. The divorce rate represents the annual probability of union dissolution, ranging from 0 (strict lifetime monogamy) to 1 (complete sequential monogamy). Results show that the main conclusions are robust to variation in divorce rate, although higher divorce rates increase life expectancy in both sexes, as individuals spend more time unmated in the singles pool – and effect mechanistically similar to reduced mating efficiency (Supplementary Fig. 2). Figure conventions as in Fig. 3.



Supplementary Figure 4: Effect of bi-parental care on the evolution of sex differences in life expectancy. Evolved relative life expectancy difference $((L_f - L_m) / \max(L_f, L_m))$ in a bi-parental care scenario ($w_f = 0.5$). Offspring production per union depends both on male and female life histories, such that the number of male (k_m) and female offspring (k_f) produced per union (assuming a primary sex ratio of 0.5) is:

$$k_m = k_f = \frac{1}{2}k \cdot e^{-[w_f s_f^O (M_f - 1) + (1 - w_f) s_m^O (M_m - 1)]} \quad (\text{S1})$$

where w_f determines the extent to which females bear the survival cost of offspring production ($w_f = 1$ corresponds to the baseline model with female-only care costs, whereas $w_f = 0.5$ represents bi-parental care). Within each heatmap, the survival-offspring production trade-off strengths for males and females (s_m^O and s_f^O) are varied, while across panels the male survival-mating trade-off strength (s_m^M) changes. Introducing bi-parental care increases the conditions under which females evolve longer life expectancies, because males incur costs from both mating effort and offspring production. When $s_m^M = 0$, the model is symmetric with respect to sex and the sex with the stronger offspring production trade-off evolves a shorter lifespan; increasing s_m^M shifts the bias toward longer female life expectancy.



Supplementary Figure 5: Life expectancy outcomes under density-dependent regulation acting on fecundity. Heatmaps show (a,d) male life expectancy, (b,e) female life expectancy, and (c,f) relative life expectancy difference $((L_f - L_m) / \max(L_f, L_m))$ as functions of male (s_m^M) and female (s_f^O) trade-off strengths. Here, density-dependent regulation acts on fecundity of mating unions rather than on age-independent survival. Top row shows the full parameter range used in the main manuscript (0.01 – 0.1), while the bottom row focuses on stronger trade-off strengths (0.06 – 0.1).

Our main conclusion – that males evolve longer life expectancies than females across a wider range of conditions – remains robust when density regulation acts on fecundity. Under weak trade-offs (top row), both sexes evolve towards the maximum age of onset of senescence (20, corresponding to a life expectancy of approximately 18). Weak trade-offs impose only small survival costs of reproduction, allowing higher population sizes, which in turn intensify density-dependent reductions in fecundity. Reduced fecundity per time step then selects for increased longevity (by allowing reproduction across more time steps), creating a feedback that drives both sexes towards the upper age limit and obscures underlying sex differences. With stronger trade-offs (bottom row), this saturation effect is alleviated and more realistic variation in life expectancy emerges. In this regime, males again evolve longer life expectancies than females across a wider range of trade-off strengths, consistent with results obtained when density regulation acts on survival.

Supplementary Methods

Details of baseline matrix model construction

Resident dynamics

Population vector

The model consists of a population of single males, single females, and monogamous unions (consisting of one male and one female), with each individual being of age class 1 to ω . The population state at time t can therefore be described by the following $\omega \times (2 + \omega)$ matrix:

$$\mathcal{N} = \begin{pmatrix} m_1 & f_1 & u_{11} & u_{12} & \cdots & u_{1\omega} \\ m_2 & f_2 & u_{21} & u_{22} & \cdots & u_{2\omega} \\ \vdots & & & \ddots & & \vdots \\ m_\omega & f_\omega & u_{\omega 1} & u_{\omega 2} & \cdots & u_{\omega\omega} \end{pmatrix}, \quad (\text{S2})$$

where m_x and f_x represent the number of males and females of age x , respectively, and u_{xy} represents the number of unions between females of age x and males of age y . This two-dimensional array is transformed into a population state vector using the vec operator, which stacks the columns on top of each other:

$$\tilde{\mathbf{n}}(t) = \text{vec}\mathcal{N}(t). \quad (\text{S3})$$

This population state vector consists of the following blocks:

$$\tilde{\mathbf{n}}(t) = \begin{pmatrix} \mathbf{m} \\ \mathbf{f} \\ \mathbf{u} \end{pmatrix} \quad (\text{S4})$$

where

$$\mathbf{u} = \begin{pmatrix} \mathbf{u}_1 \\ \vdots \\ \mathbf{u}_\omega \end{pmatrix} \quad (\text{S5})$$

and $\mathbf{u}_x$ contains all the unions with females of age x . Specifically, with the age classes explicit, the sub-vectors are given by:

$$\mathbf{m} = \begin{pmatrix} m_1 \\ m_2 \\ \vdots \\ m_\omega \end{pmatrix}, \quad (\text{S6})$$

$$\mathbf{f} = \begin{pmatrix} f_1 \\ f_2 \\ \vdots \\ f_\omega \end{pmatrix}, \quad (\text{S7})$$

$$\mathbf{u}_x = \begin{pmatrix} u_{x1} \\ u_{x2} \\ \vdots \\ u_{x\omega} \end{pmatrix}. \quad (\text{S8})$$

Projection matrix

Given the three blocks of the population vector (S4), the population projection matrix has following 3×3 structure:

$$\mathbf{A} = \begin{pmatrix} \mathbf{A}_{11} & \mathbf{A}_{12} & \mathbf{A}_{13} \\ \mathbf{A}_{21} & \mathbf{A}_{22} & \mathbf{A}_{23} \\ \mathbf{A}_{31} & \mathbf{A}_{32} & \mathbf{A}_{33} \end{pmatrix} \quad (\text{S9})$$

$$= \begin{pmatrix} \mathbf{U}_m(\mathbf{I}_\omega - \text{diag}(\mathbf{1}_{\omega^2}^\top \mathbf{M}_m)) & \mathbf{0} & \mathbf{F}_m + \mathbf{W}_m \\ \mathbf{0} & \mathbf{U}_f(\mathbf{I}_\omega - \text{diag}(\mathbf{1}_{\omega^2}^\top \mathbf{M}_f)) & \mathbf{F}_f + \mathbf{W}_f \\ \frac{1}{2}(\mathbf{I}_\omega \otimes \mathbf{U}_m) \mathbf{M}_m & \frac{1}{2}(\mathbf{U}_f \otimes \mathbf{I}_\omega) \mathbf{M}_f & \mathbf{U}_{\text{unions}} \end{pmatrix}, \quad (\text{S10})$$

where $\mathbf{U}_m$ and $\mathbf{U}_f$ describe the age-specific survival probabilities of males and females, respectively, and $\mathbf{M}_m$ and $\mathbf{M}_f$ contain the age-specific mating probabilities (i.e., transition into unions) respectively for males and females. $\mathbf{U}_{\text{unions}}$ contains the age-combination-specific survival rates of unions, $\mathbf{F}_m$ and $\mathbf{F}_f$ contain the reproductive rates of unions to produce sons and daughters, respectively, and $\mathbf{W}_m$ and $\mathbf{W}_f$ describe the widowing and divorce rates of unions to produce single male and females, respectively. There are four main processes that are described in the above 3×3 projection matrix: remaining as a single ($\mathbf{A}_{11}$ for single males and $\mathbf{A}_{22}$ for single females), singles transitioning to unions ($\mathbf{A}_{31}$ for males and $\mathbf{A}_{32}$ for females), remaining as a union ($\mathbf{A}_{33}$), and single production from unions through reproduction and widowing ($\mathbf{A}_{13}$ for males and $\mathbf{A}_{23}$ for females). Each process and its relevant sub-matrices are described in more detail below.

Remaining as a single

A single individual remains in this stage if they survive to the next age class and do not mate (transition to a union). That is, we multiply the survival probability of a given individual with one minus the probability that it mates.

Age-specific survival probabilities are described in matrix $\mathbf{U}_m$ for males and $\mathbf{U}_f$ for females. Considering an illustrative example of $\omega = 3$, these matrices will have the following structures:

$$\mathbf{U}_m = \begin{pmatrix} 0 & 0 & 0 \\ u_m(1) & 0 & 0 \\ 0 & u_m(2) & 0 \end{pmatrix}, \quad (\text{S11})$$

$$\mathbf{U}_f = \begin{pmatrix} 0 & 0 & 0 \\ u_f(1) & 0 & 0 \\ 0 & u_f(2) & 0 \end{pmatrix}, \quad (\text{S12})$$

where $u_i(x)$ gives the probability that an individual of sex i survives from age class x to age class $x + 1$:

$$u_i(x) = e^{-\int_x^{x+1} b e^{b(y-M_i)} dy}, \quad (\text{S13})$$

where b is the rate of increase of mortality with age and M_i is age at onset of senescence for individuals of sex i , and as such $b e^{b(x-M_i)}$ is the Gompertz hazard rate [1]. Note that individuals die when they reach the maximum age class ω , and thus $u_i(\omega) = 0$.

To calculate an individual's mating probability, we use a flexible, frequency-dependent *minharmonic mating function* [2]. We first calculate the size of the mating pool. The number of single males available to mate is given by:

$$m = \sum_{x=1}^{\omega} (\alpha_x u_m(x) m_x), \quad (\text{S14})$$

and likewise, the number of single available females is:

$$f = \sum_{x=1}^{\omega} (\alpha_x u_f(x) f_x), \quad (\text{S15})$$

where m_x and f_x are the numbers of single males and females in age class x , respectively. The term α_x represents the age-specific reduction in mating probability due to immaturity, modelled as:

$$\alpha_x = \frac{1}{1 + e^{g-hx}}, \quad (\text{S16})$$

where g and h determine the shape of this logistic maturation function. As age x increases, α_x approaches 1, describing a gradual transition from reproductive immaturity to maturity. The total size of the mating pool is:

$$N = m + f. \quad (\text{S17})$$

By summing over all age classes, we assume that mating is random with respect to age among individuals that are sufficiently mature to mate (as defined by equation (S16)). Following [2], the expected number of unions that form each time step is given by the minharmonic mating function:

$$U(f, m) = \begin{cases} \min(f, m) & \text{for } \frac{f}{N} \leq \eta - 0.5 \text{ and } \frac{f}{N} \geq 1.5 - \eta \\ \frac{\frac{f}{N} - N(\eta - 0.5)^2}{2(1 - \eta)} & \text{for } \eta - 0.5 \leq \frac{f}{N} \leq 1.5 - \eta \end{cases} \quad (\text{S18})$$

where η is the mating efficiency; the probability of mating at balanced operational sex ratios. For example, $\eta = 1$ means all available individuals form unions at balanced sex ratios, whereas $\eta = 0.8$ implies that only 80% of the mating pool does so, despite the balanced sex ratio. This mating function ensures that the number of unions formed is limited by the rarer sex under skewed sex ratios, and approximates the harmonic mean between sexes under balanced sex ratios. We can then use this to calculate the mating probabilities for specific union age combinations. For $\omega = 3$ age classes the male mating matrix has the structure:

$$\mathbf{M}_m = \begin{pmatrix} \mathbf{0} \\ \mathbf{M}_m^1 \\ \mathbf{M}_m^2 \end{pmatrix} \quad (\text{S19})$$

$$= \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \\ \frac{\alpha_1 e^{-s_m^M(M_m-1)} \alpha_1 f_1 u_f(1) U(f, m)}{f m} & 0 & 0 \\ 0 & \frac{\alpha_2 e^{-s_m^M(M_m-1)} \alpha_1 f_1 u_f(1) U(f, m)}{f m} & 0 \\ 0 & 0 & \frac{\alpha_3 e^{-s_m^M(M_m-1)} \alpha_1 f_1 u_f(1) U(f, m)}{f m} \\ \frac{\alpha_1 e^{-s_m^M(M_m-1)} \alpha_2 f_2 u_f(2) U(f, m)}{f m} & 0 & 0 \\ 0 & \frac{\alpha_2 e^{-s_m^M(M_m-1)} \alpha_2 f_2 u_f(2) U(f, m)}{f m} & 0 \\ 0 & 0 & \frac{\alpha_3 e^{-s_m^M(M_m-1)} \alpha_2 f_2 u_f(2) U(f, m)}{f m} \end{pmatrix}, \quad (\text{S20})$$

where $\mathbf{M}_m^1$ contains transitions of single males into unions with females that are currently age 1 but survive to age into age class 2. More generally for males aged y mating with females aged x :

$$\mathbf{M}_m^x = \frac{\alpha_x f_x u_f(x) U(f, m)}{f m} \sum_{y=1}^{\omega} (\mathbf{e}_y \otimes \mathbf{e}_y^T) \alpha_y e^{-s_m^M(M_m-1)}. \quad (\text{S21})$$

Similarly, for $\omega = 3$ age classes the female mating matrix has the structure:

$$\mathbf{M}_f = \begin{pmatrix} \mathbf{M}_f^1 \\ \mathbf{M}_f^2 \\ \mathbf{0} \end{pmatrix} \quad (\text{S22})$$

$$= \begin{pmatrix} \frac{\alpha_1 e^{-s_m^M(M_m-1)} \alpha_1 m_1 u_m(1) U(f, m)}{f m} & 0 & 0 \\ \frac{\alpha_2 e^{-s_m^M(M_m-1)} \alpha_1 m_2 u_m(2) U(f, m)}{f m} & 0 & 0 \\ \frac{\alpha_3 e^{-s_m^M(M_m-1)} \alpha_1 m_3 u_m(3) U(f, m)}{f m} & 0 & 0 \\ 0 & \frac{\alpha_1 e^{-s_m^M(M_m-1)} \alpha_2 m_1 u_m(1) U(f, m)}{f m} & 0 \\ 0 & \frac{\alpha_2 e^{-s_m^M(M_m-1)} \alpha_2 m_2 u_m(2) U(f, m)}{f m} & 0 \\ 0 & \frac{\alpha_3 e^{-s_m^M(M_m-1)} \alpha_2 m_3 u_m(3) U(f, m)}{f m} & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}, \quad (\text{S23})$$

where $\mathbf{M}_f^1$ contains transitions of single females into unions who are currently aged 1 but will survive and age into age class 2. More generally for females aged x mating with males aged y :

$$\mathbf{M}_f^x = \frac{\alpha_x U(f, m)}{f m} \sum_{y=1}^{\omega} (\mathbf{e}_y \otimes \mathbf{e}_x^\top) \alpha_y m_y u_m(y) e^{-s_m^M(M_m-1)}. \quad (\text{S24})$$

In summary, individuals stay single provided they survive and do not mate to form a union. The relevant elements of the projection matrix (equation (S9)) therefore take the form $\mathbf{A}_{11} = \mathbf{U}_m(\mathbf{I}_\omega - \text{diag}(\mathbf{1}_{\omega^2}^\top \mathbf{M}_m))$ for single males and $\mathbf{A}_{22} = \mathbf{U}_f(\mathbf{I}_\omega - \text{diag}(\mathbf{1}_{\omega^2}^\top \mathbf{M}_f))$ for single females, where $\mathbf{I}_\omega$ is an $\omega \times \omega$ identity matrix containing only zeroes except for 1s across the diagonal, and $\mathbf{1}_{\omega^2}^\top$ is $1 \times \omega^2$ row vector of 1s. The multiplication $\mathbf{1}_{\omega^2}^\top \mathbf{M}_i$ creates a vector with the column sums of the mating matrix for an individual of sex i , thus giving the total mating probability for each age class, and we use ‘diag()’ to produce a matrix with these probabilities across the diagonal. Since we want the probability that an individual *does not* mate, we need to calculate 1 minus the mating probability, which is achieved using $\mathbf{I}_\omega - \text{diag}(\mathbf{1}_{\omega^2}^\top \mathbf{M}_i)$. We can then multiply these “not-mating” probabilities with the age-specific survival probabilities in $\mathbf{U}_m$ or $\mathbf{U}_f$ to give the total probability that an individual stays as a single.

Singles transitioning to unions

Singles transition to unions provided that they survive and find a mate (i.e., we multiply the probability of survival with the probability of mating). The relevant elements of the projection matrix (equation (S9)) therefore take the form $\mathbf{A}_{31} = \frac{1}{2} (\mathbf{I}_\omega \otimes \mathbf{U}_m) \mathbf{M}_m$ for males and $\mathbf{A}_{32} = \frac{1}{2} (\mathbf{U}_f \otimes \mathbf{I}_\omega) \mathbf{M}_f$ for females, where $\mathbf{I}_\omega$ is an $\omega \times \omega$ identity matrix containing only zeroes except for 1s across the diagonal. Given the structure of the male mating probabilities within $\mathbf{M}_m$ (equation (S19)) where male age varies across the diagonal within each block, we use $(\mathbf{I}_\omega \otimes \mathbf{U}_m)$ to repeatedly place $\mathbf{U}_m$ across the diagonal of the resulting block matrix (such that male age varies across the diagonal within each block) before it can be multiplied with $\mathbf{M}_m$. Given the structure of female mating probabilities within $\mathbf{M}_f$ (equation (S22)) where female age varies between blocks, we use $(\mathbf{U}_f \otimes \mathbf{I}_\omega)$ to group each element of $\mathbf{U}_f$ and expand them into a block before moving to the next element (such that female age varies between blocks) before it is multiplied with $\mathbf{M}_f$. Finally, given that a single individual resident constitutes one half of a monogamous resident-resident union, the union formation rates in the projection matrix for each sex are multiplied by a factor of $\frac{1}{2}$.

Remaining as a union

Unions survive to the next time step, provided both the male and female members of them survive, and the unions does not dissolve due to divorce. In this case, we also wish to move both members of the union up one age class. We achieve this using a vec-permutation framework, in which we define

$$\mathbf{U}_{\text{unions}} = \mathbf{K}^\top \mathbf{U}_f \mathbf{K} \mathbf{U}_m (1 - d), \quad (\text{S25})$$

where d is the divorce rate, $\mathbf{K}$ is a vec-permutation matrix (see [3] for derivation), and for $\omega = 3$ age classes:

$$\mathbb{U}_m = \begin{pmatrix} \mathbf{U}_m & & \\ & \mathbf{U}_m & \\ & & \mathbf{U}_m \end{pmatrix} \quad (\text{S26})$$

$$\mathbb{U}_f = \begin{pmatrix} \mathbf{U}_f & & \\ & \mathbf{U}_f & \\ & & \mathbf{U}_f \end{pmatrix}. \quad (\text{S27})$$

In this way, (reading equation (S25) from right to left) we first consider the survival of males in each union, before re-arranging the population vector using $\mathbf{K}$ to then consider the survival of females, before using $\mathbf{K}^\top$ to return the population vector to its original structure. Another way to visualise this process

is by substituting equations (S26) and (S27) into equation (S25) to give the matrix structure:

$$\mathbf{K}^\top \mathbf{U}_f \mathbf{K} \mathbf{U}_m = \left(\begin{array}{ccc|ccc|} & & & & & & \\ \hline & 0 & 0 & 0 & & & \\ u_m(1)u_f(1) & & 0 & 0 & & & \\ 0 & u_m(2)u_f(1) & 0 & & & & \\ \hline & & & 0 & 0 & 0 & \\ & & & u_m(1)u_f(2) & 0 & 0 & \\ & & & 0 & u_m(2)u_f(2) & 0 & \end{array} \right), \quad (\text{S28})$$

where the empty blocks are all filled with zeroes. This matrix has the block structure of the survival part of a Leslie matrix, and in addition the two non-empty blocks are themselves Leslie matrices. The blocks move vectors of unions within a specific female age to the next female age class, and then within the blocks we move unions with a specific male age class to the next age class.

Single production from unions

Singles are produced from unions in two ways. First, unions can reproduce to create new single male and female individuals of age class 1. We describe this process in the fecundity matrices $\mathbf{F}_m$ and $\mathbf{F}_f$, respectively. Second, widowing can occur when one union member dies, and the remaining surviving partner is returned to the single population to potentially re-mate. Both surviving partners are returned to the singles populations if the union dissolves according to probability d . We describe these processes in the matrices $\mathbf{W}_m$ for widowed males and $\mathbf{W}_f$ for widowed females.

The fertility matrices $\mathbf{F}_m$ and $\mathbf{F}_f$ contain reproductive rates per union, which are the same for all combinations of parental ages. Offspring produced are of the first age class, and unions containing individuals of age 1 do not exist (mating to form a union is one time step before reproducing). So for $\omega = 3$:

$$\mathbf{F}_m = \left(\begin{array}{ccc|ccc} 0 & kre^{-s_f^O(M_f-1)} & kre^{-s_f^O(M_f-1)} & 0 & kre^{-s_f^O(M_f-1)} & kre^{-s_f^O(M_f-1)} \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \end{array} \right), \quad (\text{S29})$$

$$\mathbf{F}_f = \left(\begin{array}{ccc|ccc} 0 & k(1-r)e^{-s_f^O(M_f-1)} & k(1-r)e^{-s_f^O(M_f-1)} & 0 & k(1-r)e^{-s_f^O(M_f-1)} & k(1-r)e^{-s_f^O(M_f-1)} \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \end{array} \right), \quad (\text{S30})$$

where k is maximum annual union fecundity and r is the primary sex ratio (proportion of male offspring).

Males in unions return to the singles pool if they survive but their female partner does not, or if the union dissolves due to divorce (which requires both partners to survive). The matrix that produces single males from unions, for $\omega = 3$, has the structure:

$$\mathbf{W}_m = (\mathbf{W}_m(1) \mathbf{W}_m(2) \mathbf{W}_m(3)), \quad (\text{S31})$$

where $\mathbf{W}_m(x)$ contains the widowing and divorce rates of males in unions with females of age x :

$$\mathbf{W}_m(x) = \left(\begin{array}{ccc} 0 & 0 & 0 \\ u_m(1)(1 - u_f(x)) + du_m(1)u_f(x) & 0 & 0 \\ 0 & u_m(2)(1 - u_f(x)) + du_m(2)u_f(x) & 0 \end{array} \right), \quad (\text{S32})$$

but males of age 1 cannot be mated yet, and so there are no unions with age 1 males and therefore the first non-zero entry in this matrix will never get used, or will always act on a zero entry of the population vector. We can thus start the sum in the general formula for $\mathbf{W}_m(x)$ from $y = 2$:

$$\mathbf{W}_m(x) = (1 - u_f(x) + du_f(x)) \sum_{y=2}^{\omega-1} (\mathbf{e}_{y+1} \otimes \mathbf{e}_y^\top) u_m(y). \quad (\text{S33})$$

Similarly, females become widowed when they survive but their male partner does not. The matrix that produces single females from unions, for $\omega = 3$, has the structure:

$$\mathbf{W}_f = \begin{pmatrix} \mathbf{W}_f(1) & \mathbf{W}_f(2) & \mathbf{W}_f(3) \end{pmatrix}, \quad (\text{S34})$$

where $\mathbf{W}_f(x)$ contains the widowing rates of females of age x such that

$$\mathbf{W}_f(1) = \mathbf{0}, \quad (\text{S35})$$

$$\mathbf{W}_f(2) = \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & u_f(2)(1 - u_m(2)) + du_f(2)u_m(2) & u_f(2) \end{pmatrix}, \quad (\text{S36})$$

$$\mathbf{W}_f(3) = \mathbf{0}, \quad (\text{S37})$$

given that females aged 1 cannot be widowed as they cannot yet be mated, and females aged ω (3 in this example) are not widowed since they die themselves. More generally,

$$\mathbf{W}_f(x) = u_f(x) \sum_{y=1}^{\omega} (\mathbf{e}_{x+1} \otimes \mathbf{e}_y^T) (1 - u_m(y) + du_m(y)). \quad (\text{S38})$$

In summary, single males and females are produced from unions either as offspring or as widowed adults, such that $\mathbf{A}_{13} = \mathbf{F}_m + \mathbf{W}_m$ and $\mathbf{A}_{23} = \mathbf{F}_f + \mathbf{W}_f$ in the projection matrix (equation (S9)).

Mutant dynamics

Population vector

Unlike under resident dynamics, for the mutant population there are two types of union possible: resident females with mutant males, and mutant females with resident males [4]. Under an adaptive dynamics framework, we assume that the mutant is rare and thus that mutant-mutant unions have negligible effects on population dynamics, so mutant-mutant unions are not modelled here. Note that there is no projection of the mutant population vector in the model: mutant growth rate is calculated by evaluating the mutant projection matrix at the resident equilibrium population. We nevertheless show the explicit structure of the mutant population to aid understanding of the construction of the mutant projection matrix. The population vector has the structure:

$$\tilde{\mathbf{n}}^*(t) = \begin{pmatrix} \mathbf{m}^*(t) \\ \mathbf{f}^*(t) \\ \mathbf{u}_1 \\ \vdots \\ \mathbf{u}_\omega \\ \mathbf{u}_1^* \\ \vdots \\ \mathbf{u}_\omega^* \end{pmatrix}, \quad (\text{S39})$$

where $\mathbf{u}_x$ contains all the unions between resident females of age x with mutant males, and $\mathbf{u}_x^*$ contains all the unions between mutant females of age x with resident males. Specifically, with the age classes explicit, the sub-vectors are given by

$$\mathbf{m}^* = \begin{pmatrix} m_1^* \\ m_2^* \\ \vdots \\ m_\omega^* \end{pmatrix} \quad (\text{S40})$$

$$\mathbf{f}^* = \begin{pmatrix} f_1^* \\ f_2^* \\ \vdots \\ f_\omega^* \end{pmatrix} \quad (\text{S41})$$

$$\mathbf{u}_x = \begin{pmatrix} u_{x1*} \\ u_{x2*} \\ \vdots \\ u_{x\omega*} \end{pmatrix}. \quad (\text{S42})$$

$$\mathbf{u}_x^* = \begin{pmatrix} u_{x*1} \\ u_{x*2} \\ \vdots \\ u_{x*\omega} \end{pmatrix}, \quad (\text{S43})$$

where the $*$ indicates a mutant.

Projection matrix

Given the structure of the mutant population vector (equation (S39)), the mutant population projection matrix will have the structure:

$$\mathbf{A}^* = \begin{pmatrix} \mathbf{U}_{m*}(\mathbf{I}_\omega - \text{diag}(\mathbf{1}_{\omega^2}^\top \mathbf{M}_{m*})) & \mathbf{0} & \frac{1}{2}\mathbf{F}_{m*} + \mathbf{W}_{m*} & \frac{1}{2}\mathbf{F}_{m*}^* \\ \mathbf{0} & \mathbf{U}_{f*}(\mathbf{I}_\omega - \text{diag}(\mathbf{1}_{\omega^2}^\top \mathbf{M}_{f*})) & \frac{1}{2}\mathbf{F}_{f*} & \frac{1}{2}\mathbf{F}_{f*}^* + \mathbf{W}_{f*} \\ (\mathbf{I}_\omega \otimes \mathbf{U}_{m*}) \mathbf{M}_{m*} & \mathbf{0} & \mathbf{U}_{\text{unions}, fm*} & \mathbf{0} \\ \mathbf{0} & (\mathbf{U}_{f*} \otimes \mathbf{I}_\omega) \mathbf{M}_{f*} & \mathbf{0} & \mathbf{U}_{\text{unions}, f*m} \end{pmatrix}, \quad (\text{S44})$$

where $\mathbf{U}_{m*}$ and $\mathbf{U}_{f*}$ describe the age-specific survival probabilities of mutant males and females, respectively, and $\mathbf{M}_{m*}$ and $\mathbf{M}_{f*}$ contain the age-specific mating probabilities (i.e., transition into unions) respectively for mutant males and females with a resident of the opposite sex. $\mathbf{U}_{\text{unions}, fm*}$ and $\mathbf{U}_{\text{unions}, f*m}$ contain the age-combination-specific survival rates of the two union types. $\mathbf{F}_{m*}$ gives the reproductive rates of unions with resident females to produce mutant sons, and likewise $\mathbf{F}_{f*}^*$ for unions with mutant females to produce mutant daughters. Note that $\mathbf{W}_{m*}$ and $\mathbf{W}_{f*}$ describe the widowing and divorce rates of unions with a resident of the opposite sex to produce single mutant male and females, respectively.

Since we model sequentially alternating mutations of M_m and M_f , a mutation in the trait of one sex means mutants of the opposite sex are phenotypically residents (but still carry the mutation that can be passed on to offspring). More specifically, when M_m mutates to M_{m*} , mutant females still express the resident female M_f value, which is thus used in the calculations in the sub-matrices $\mathbf{U}_{f*}$, $\mathbf{W}_{f*}$, $\mathbf{F}_{f*}^*$, and $\mathbf{U}_{\text{unions}, f*m}$. Similarly, when M_f mutates to M_{f*} , mutant males still express the resident male M_m value, which is thus used in the calculations in the sub-matrices $\mathbf{U}_{m*}$, $\mathbf{M}_{m*}$, $\mathbf{M}_{f*}$, $\mathbf{W}_{m*}$, and $\mathbf{U}_{\text{unions}, fm*}$.

As with resident dynamics, we have four main processes described in this mutant 4×4 population projection matrix: remaining as a single ($\mathbf{A}_{11}^*$ for single mutant males and $\mathbf{A}_{22}^*$ for single mutant females), singles transitioning to unions ($\mathbf{A}_{31}^*$ for mutant males with a resident female, and $\mathbf{A}_{42}^*$ for mutant females with a resident male), remaining as a union ($\mathbf{A}_{33}^*$ for mutant males with a resident female, and $\mathbf{A}_{44}^*$ for mutant females with a resident male), and single production from unions ($\mathbf{A}_{13}^*$ for producing single mutant males and $\mathbf{A}_{24}^*$ for single mutant females). Each process and its relevant sub-matrices are described in more detail below.

Remaining as a single

As with residents, mutants remain single mutants provided they survive and do not mate. Therefore, this section of the mutant projection matrix has the same general structure of that for the residents. We define the survival matrices for mutants in the same structure:

$$\mathbf{U}_{m*} = \begin{pmatrix} 0 & 0 & 0 \\ u_{m*}(1) & 0 & 0 \\ 0 & u_{m*}(2) & 0 \end{pmatrix} \quad (\text{S45})$$

$$\mathbf{U}_{f*} = \begin{pmatrix} 0 & 0 & 0 \\ u_{f*}(1) & 0 & 0 \\ 0 & u_{f*}(2) & 0 \end{pmatrix}, \quad (\text{S46})$$

where $u_{i*}(x)$ is the probability that a mutant of sex i survives from age x to age $x + 1$. The survival probability $u_{i*}(x)$ is calculated in the same way as for residents (equation (S13)), but using the mutant ages of onset of senescence, M_{m*} and M_{f*} , instead of those of the residents.

The marriage matrices also take a similar structure as those for the resident population. Since we assume the mutants have a negligible effect on the resident population, we still define the mating pool as consisting of residents only (N in equation (S17); m in equation (S14); f in equation (S15)). We use these aspects of the resident mating pool to calculate the conditional value of $U(f, m)$ (equation (S18)). Similarly as for the residents, for $\omega = 3$ age classes the mutant male mating matrix has the structure:

$$\mathbf{M}_{m^*} = \begin{pmatrix} \mathbf{0} \\ \mathbf{M}_{m^*}^1 \\ \mathbf{M}_{m^*}^2 \end{pmatrix} \quad (\text{S47})$$

$$= \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \\ \hline \frac{\alpha_1 e^{-s_m^M (M_{m^*} - 1)} \alpha_1 f_1 u_f(1) U(f, m)}{f m} & 0 & 0 \\ 0 & \frac{\alpha_2 e^{-s_m^M (M_{m^*} - 1)} \alpha_1 f_1 u_f(1) U(f, m)}{f m} & 0 \\ 0 & 0 & \frac{\alpha_3 e^{-s_m^M (M_{m^*} - 1)} \alpha_1 f_1 u_f(1) U(f, m)}{f m} \\ \hline \frac{\alpha_1 e^{-s_m^M (M_{m^*} - 1)} \alpha_2 f_2 u_f(2) U(f, m)}{f m} & 0 & 0 \\ 0 & \frac{\alpha_2 e^{-s_m^M (M_{m^*} - 1)} \alpha_2 f_2 u_f(2) U(f, m)}{f m} & 0 \\ 0 & 0 & \frac{\alpha_3 e^{-s_m^M (M_{m^*} - 1)} \alpha_2 f_2 u_f(2) U(f, m)}{f m} \end{pmatrix}, \quad (\text{S48})$$

where $\mathbf{M}_{m^*}^1$ contains transitions of single males into unions with females that are currently age 1 but survive to age into age class 2. This is identical to the male mating matrix of the residents, only here we use M_{m^*} in the trade-off term instead of M_m . More generally for mutant males aged y mating with resident females aged x :

$$\mathbf{M}_{m^*}^x = \frac{\alpha_x f_x u_f(x) U(f, m)}{f m} \sum_{y=1}^{\omega} (\mathbf{e}_y \otimes \mathbf{e}_y^T) \alpha_y e^{-s_m^M (M_{m^*} - 1)}. \quad (\text{S49})$$

Since mutant females form unions with resident males, we use M_m in the trade-off term, and as such the mutant female mating matrix is identical to that of resident females (equation (S24); $\mathbf{M}_f = \mathbf{M}_{f^*}$).

Similarly to the residents, the relevant elements of the mutant projection matrix (equation (S44)) take the form $\mathbf{A}_{11} = \mathbf{U}_{m^*} (\mathbf{I}_{\omega} - \text{diag}(\mathbf{1}_{\omega_2}^T \mathbf{M}_{m^*}))$ for single mutant males and $\mathbf{A}_{22} = \mathbf{U}_{f^*} (\mathbf{I}_{\omega} - \text{diag}(\mathbf{1}_{\omega_2}^T \mathbf{M}_{f^*}))$ for single mutant females, since an individual stays single provided they survive and do not mate into a union (i.e., multiply the survival probability with one minus the mating probability).

Singles transitioning to unions

As with the residents, mutant singles also transition to unions provided that they survive and find a mate (i.e., we multiply the probability of survival with the probability of mating). The relevant elements of the projection matrix (equation (S44)) therefore take the form $\mathbf{A}_{31} = (\mathbf{I}_{\omega} \otimes \mathbf{U}_{m^*}) \mathbf{M}_{m^*}$ for mutant males and $\mathbf{A}_{42} = (\mathbf{U}_{f^*} \otimes \mathbf{I}_{\omega}) \mathbf{M}_{f^*}$ for mutant females. These terms are identical in structure as those for the residents, except we do not multiply by a factor of $\frac{1}{2}$ here since we are explicitly moving a single mutant individual into the union, not the resident partner.

Remaining as a union

Unions survive to the next time step, provided both partners within them survive and the union does not dissolve due to divorce. In this case, we also wish to move both partners up one age class. We achieve this in the same way as for residents (equation (S25)), but use M_{m^*} or M_{f^*} for the calculation of relevant survival probabilities. That is, we define

$$\mathbf{U}_{\text{unions}, fm^*} = \mathbf{K}^T \mathbf{U}_f \mathbf{K} \mathbf{U}_{m^*} (1 - d), \quad (\text{S50})$$

$$\mathbf{U}_{\text{unions}, f^* m} = \mathbf{K}^T \mathbf{U}_{f^*} \mathbf{K} \mathbf{U}_m (1 - d). \quad (\text{S51})$$

Single production from unions

As for with the resident population, mutant singles can also be produced from unions either as offspring through union reproduction, or as a widowed adult if the union partner does not survive or both partners survive but the union dissolves due to divorce. Since in mutant dynamics we only explicitly model the

production of mutant offspring, $\mathbf{F}_{m^*}$ describes the production of mutant males from a union of a resident female and mutant male, and $\mathbf{F}_{f^*}$ describes the production of mutant females from a union of a mutant female and resident male. For $\omega = 3$:

$$\mathbf{F}_{m^*} = \left(\begin{array}{c|cc} 0 & kre^{-s_f^O(M_f-1)} & kre^{-s_f^O(M_f-1)} \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{array} \middle| \begin{array}{c|cc} 0 & kre^{-s_f^O(M_f-1)} & kre^{-s_f^O(M_f-1)} \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{array} \right) \quad (\text{S52})$$

$$\mathbf{F}_{f^*} = \left(\begin{array}{c|cc} 0 & k(1-r)e^{-s_f^O(M_{f^*}-1)} & k(1-r)e^{-s_f^O(M_{f^*}-1)} \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{array} \middle| \begin{array}{c|cc} 0 & k(1-r)e^{-s_f^O(M_{f^*}-1)} & k(1-r)e^{-s_f^O(M_{f^*}-1)} \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{array} \right), \quad (\text{S53})$$

and note that since resident females are reproducing in unions of resident females and mutant males, $\mathbf{F}_{m^*} = \mathbf{F}_m$ (equation (S29)).

Widowing and divorce of mutants also works in the same way as for residents, only using M_{m^*} or M_{f^*} for the calculation of relevant survival probabilities. As such, the matrix that produces single mutant males from unions of resident females and mutant males, for $\omega = 3$, has the structure:

$$\mathbf{W}_{m^*} = \left(\mathbf{W}_{m^*}(1) \ \mathbf{W}_{m^*}(2) \ \mathbf{W}_{m^*}(3) \right), \quad (\text{S54})$$

where $\mathbf{W}_{m^*}(x)$ contains the widowing and divorce rates of mutant males in unions with resident females of age x :

$$\mathbf{W}_{m^*}(x) = (1 - u_f(x) + du_f(x)) \sum_{y=2}^{\omega-1} (\mathbf{e}_{y+1} \otimes \mathbf{e}_y^T) u_{m^*}(y). \quad (\text{S55})$$

Similarly, the matrix that produces single mutant females from unions of mutant females and resident males, for $\omega = 3$, has the structure:

$$\mathbf{W}_{f^*} = \left(\mathbf{W}_{f^*}(1) \ \mathbf{W}_{f^*}(2) \ \mathbf{W}_{f^*}(3) \right), \quad (\text{S56})$$

where $\mathbf{W}_{f^*}(x)$ contains the widowing and divorce rates of mutant females of age x such that

$$\mathbf{W}_{f^*}(x) = u_{f^*}(x) \sum_{y=1}^{\omega} (\mathbf{e}_{x+1} \otimes \mathbf{e}_y^T) (1 - u_m(y) + du_m(y)). \quad (\text{S57})$$

In summary, as with the residents, single mutant males and mutant females are produced from unions either as offspring or as widowed or divorced adults, such that $\mathbf{A}_{13}^* = \mathbf{F}_{m^*} + \mathbf{W}_{m^*}$ and $\mathbf{A}_{24}^* = \mathbf{F}_{f^*} + \mathbf{W}_{f^*}$ in the projection matrix (equation (S44)).

Details of group composition model extension construction

The population projection matrix for this model extension takes the form:

$$\mathbf{A} = \begin{pmatrix} \mathbf{S} & \mathbf{F} \\ \mathbf{M} & \mathbf{0} \end{pmatrix}, \quad (\text{S58})$$

where $\mathbf{S}$ contains probabilities single males and females surviving to the age class but not mating, $\mathbf{M}$ contains transitions of singles into mating groups, $\mathbf{F}$ governs reproduction by individuals in mating groups, and $\mathbf{0}$ is a zero block (individuals in mating groups immediately return to the singles pool after reproduction). Specifically, for $\omega = 3$ these blocks are:

$$\mathbf{A} = \left(\begin{array}{cccccc|cccccc} 0 & 0 & 0 & 0 & 0 & 0 & \frac{1}{2}n_{\text{f}}kre^{-s_{\text{f}}^{\text{O}}(M_{\text{f}}-1)} & \frac{1}{2}n_{\text{f}}kre^{-s_{\text{f}}^{\text{O}}(M_{\text{f}}-1)} & 0 & \frac{1}{2}kre^{-s_{\text{f}}^{\text{O}}(M_{\text{f}}-1)} & \frac{1}{2}kre^{-s_{\text{f}}^{\text{O}}(M_{\text{f}}-1)} \\ u_{\text{m}}(1) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & u_{\text{m}}(2) \cdot (1 - \frac{\alpha_2 U n_{\text{m}} e^{-s_{\text{m}}^{\text{M}}(M_{\text{m}}-1)}}{m}) & 0 & 0 & 0 & 0 & u_{\text{m}}(2) & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \frac{1}{2}n_{\text{f}}k(1-r)e^{-s_{\text{f}}^{\text{O}}(M_{\text{f}}-1)} & \frac{1}{2}n_{\text{f}}k(1-r)e^{-s_{\text{f}}^{\text{O}}(M_{\text{f}}-1)} & 0 & \frac{1}{2}k(1-r)e^{-s_{\text{f}}^{\text{O}}(M_{\text{f}}-1)} & \frac{1}{2}k(1-r)e^{-s_{\text{f}}^{\text{O}}(M_{\text{f}}-1)} \\ 0 & 0 & 0 & u_{\text{f}}(1) & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & u_{\text{f}}(2) \cdot (1 - \frac{\alpha_2 U n_{\text{f}} e^{-s_{\text{f}}^{\text{M}}(M_{\text{f}}-1)}}{f}) & 0 & 0 & 0 & 0 & u_{\text{f}}(2) & 0 \\ \hline 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & u_{\text{m}}(2) \cdot \frac{\alpha_2 U n_{\text{m}} e^{-s_{\text{m}}^{\text{M}}(M_{\text{m}}-1)}}{m} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & u_{\text{f}}(2) \cdot \frac{\alpha_2 U n_{\text{f}} e^{-s_{\text{f}}^{\text{M}}(M_{\text{f}}-1)}}{f} & 0 & 0 & 0 & 0 & 0 & 0 \end{array} \right), \quad (\text{S59})$$

where U represents the number of unions formed as defined by Equation 21 in the main text.

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