Asexual but not clonal: Evolutionary processes in populations with automictic reproduction
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Supplementary Information

1 Genetic configurations following Prophase I

In this section, the expected proportions of genetic configurations following prophase I will be derived for two linked biallelic loci. Let us denote the two loci by A and B and the centromere by C. Gene order will be assumed to be CAB. There are seven distinct configurations of alleles that can arise prior to the first meiotic division:

1 : $A_1B_1 \lor A_1B_1 \land A_2B_2 \lor A_2B_2$
2 : $A_1B_1 \lor A_1B_2 \land A_2B_1 \lor A_2B_1$
3 : $A_1B_1 \lor A_1B_2 \land A_2B_1 \lor A_2B_2$
4 : $A_1B_1 \lor A_2B_1 \land A_2B_1 \lor A_2B_2$
5 : $A_1B_1 \lor A_2B_2 \land A_1B_1 \lor A_2B_2$
6 : $A_1B_1 \lor A_2B_2 \land A_1B_2 \lor A_2B_1$
7 : $A_1B_2 \lor A_2B_1 \land A_1B_2 \lor A_2B_1$

In this notation, $A_1$ and $A_2$ are placeholders for alleles at locus A that can either be different (e.g., $A_1 = A$ and $A_2 = a$) or identical (e.g., $A_1 = A_2 = a$). Likewise, $B_1$ and $B_2$ are placeholders for alleles at locus B. Each pair of these placeholders represents alleles on the same chromatid, and the $\lor$ symbol indicates the two chromatids that are joined to the same centromere and that will hence be found in the same product of meiotic division I.

State 1 is the initial configuration prior to any crossovers, but crossovers can induce switches between these configurations. For example, a crossover between the centromer and locus A will induce a switch from state 1 to state 5, whereas a crossover between A and B will induce a switch from state 1 to state 3. More generally, we can express switches induced by a single crossover between C and A by the following transition matrix:

$$Q_{CA} = \begin{pmatrix}
0 & 0 & 0 & 0 & 1 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 1 \\
0 & 0 & 0 & 1/2 & 1/2 & 0 & 0 \\
0 & 0 & 1/2 & 1/2 & 0 & 0 & 0 \\
1/2 & 0 & 0 & 0 & 1/2 & 0 & 0 \\
0 & 0 & 1/2 & 0 & 0 & 1/2 & 0 \\
0 & 1/2 & 0 & 0 & 0 & 0 & 1/2 \\
\end{pmatrix}$$

Here, rows indicate the initial state and columns the new state achieved by a crossover. Similarly, we can write down the matrix describing transitions arising from crossovers between loci A and B: switches induced by a single crossover between C and A by the following

...
transition matrix:

\[
Q_{AB} = \begin{pmatrix}
0 & 0 & 1 & 0 & 0 & 0 & 0 \\
0 & 0 & 1 & 0 & 0 & 0 & 0 \\
1/4 & 1/4 & 1/2 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 1/4 & 1/2 & 1/4 \\
0 & 0 & 0 & 1/2 & 0 & 1/2 & 0 \\
0 & 0 & 0 & 1/2 & 1/4 & 0 & 1/4 \\
0 & 0 & 0 & 1/2 & 0 & 1/2 & 0
\end{pmatrix}
\]

(2)

Figure S1 illustrates these two transition matrices.

When there are multiple crossovers, the probability distribution for the final genetic state can be obtained by multiplying the matrices \(Q_{CA}\) and \(Q_{AB}\). The order in which crossovers occur is irrelevant, as is also mathematically evident by the fact that \(Q_{CA}Q_{AB} = Q_{AB}Q_{CA}\). Thus, when there are \(n\) crossovers between \(C\) and \(A\) and \(m\) crossovers between \(A\) and \(B\), the total transition matrix is given by \(Q_{CA}^nQ_{AB}^m\). Evaluating this matrix and extracting its first row (since the initial state is always state 1), we arrive at the expected fractions of genotype configurations. When \(m \geq 1\) (at least one crossover between \(A\) and \(B\)), this yields

\[
\hat{q}_{n,m} = \begin{pmatrix}
(1 - 2f_n)(1 - f_m) \\
(1 - 2f_n)(1 - f_m) \\
2(1 - 2f_n)f_m \\
2f_nf_m \\
f_n(1 - 2f_m) \\
2f_nf_m \\
f_n(1 - 2f_m)
\end{pmatrix},
\]

(3)

where the placeholders \(f_n\) and \(f_m\) are defined as

\[
f_i = \frac{1}{3} \left(1 - \left(-\frac{1}{2}\right)^i\right).
\]

(4)

When \(m = 0\) (no crossovers between \(A\) and \(B\)), we have

\[
\hat{q}_{n,m} = \begin{pmatrix}
1 - 2f_n \\
0 \\
0 \\
0 \\
2f_n \\
0 \\
0
\end{pmatrix}.
\]

(5)

Next, we can assume that the numbers of crossovers between \(C\) and \(A\) and between \(A\) and \(B\) follow two independent Poisson distributions, with expected values \(\bar{n}\) and \(\bar{m}\), respectively.
Under this assumption, the expected distribution of genotypic state becomes

$$\tilde{q}_{i,m} = \sum_{i,j=0}^{\infty} \Pr\{n = i, m = j\} \tilde{q}_{i,j} = \sum_{i,j=0}^{\infty} \frac{n! e^{-\bar{m}} \bar{m}^i e^{-\bar{m}}}{i! j!} \tilde{q}_{i,j} = \left(\begin{array}{c} \frac{1}{2} h_i (h_m + e^{-\bar{m}}) \\ \frac{1}{2} h_i (h_m - e^{-\bar{m}}) \\ 2 h_i g_m \\ 2 g_n g_m \\ g_i (h_m + e^{-\bar{m}}) \\ 2 g_n g_m \\ g_i (h_m - e^{-\bar{m}}) \end{array}\right), \quad (6)$$

where

$$g_i = \frac{1}{3} (1 - e^{-3i/2}) \quad \text{and} \quad h_i = \frac{1}{3} (1 + 2e^{-3i/2}). \quad (7)$$

Note that the probability of arriving in states 4 and 6 is always identical. Applying the fusion rules of automixis (see Table 1 in main text) and exploiting the relationships $h_i = 2 - g_i$ and $g_i + g_j - 3g_ig_j = g_{i+j}$, we can now calculate the expected fraction of offspring produced by a dually heterozygous mother that are homozygous at either locus (independent of the state at the other locus), or at both loci simultaneously. For central fusion automixis, these quantities compute to

$$\gamma_i^{CF} = \frac{1}{2} ((\tilde{q}_{\bar{m},\bar{m}})_4 + (\tilde{q}_{\bar{m},\bar{m}})_5 + (\tilde{q}_{\bar{m},\bar{m}})_6 + (\tilde{q}_{\bar{m},\bar{m}})_7) = g_{\bar{m}} = \frac{1}{3} (1 - e^{-3\bar{m}/2}) \quad (8)$$

$$\gamma_i^{CF} = \frac{1}{2} ((\tilde{q}_{\bar{m},\bar{m}})_3 + (\tilde{q}_{\bar{m},\bar{m}})_5 + (\tilde{q}_{\bar{m},\bar{m}})_6 + (\tilde{q}_{\bar{m},\bar{m}})_7) = g_{\bar{m}+\bar{m}} = \frac{1}{3} (1 - e^{-3(\bar{m}+\bar{m})/2}) \quad (9)$$

$$\gamma_i^{CF} = \frac{1}{2} ((\tilde{q}_{\bar{m},\bar{m}})_5 + (\tilde{q}_{\bar{m},\bar{m}})_7) = g_i h_{\bar{m}} = \frac{1}{9} (1 - e^{-3\bar{m}/2}) (1 + 2e^{-3\bar{m}/2}). \quad (10)$$

For terminal fusion automixis, we obtain

$$\gamma_i^{TF} = (\tilde{q}_{\bar{m},\bar{m}})_1 + (\tilde{q}_{\bar{m},\bar{m}})_2 + (\tilde{q}_{\bar{m},\bar{m}})_3 = h_{\bar{m}} = \frac{1}{3} (1 - e^{-3\bar{m}/2}) \quad (11)$$

$$\gamma_i^{TF} = (\tilde{q}_{\bar{m},\bar{m}})_1 + (\tilde{q}_{\bar{m},\bar{m}})_2 + (\tilde{q}_{\bar{m},\bar{m}})_4 = h_{\bar{m}+\bar{m}} = \frac{1}{3} (1 - e^{-3(\bar{m}+\bar{m})/2}) \quad (12)$$

$$\gamma_i^{TF} = (\tilde{q}_{\bar{m},\bar{m}})_1 + (\tilde{q}_{\bar{m},\bar{m}})_2 = h_i h_{\bar{m}} = \frac{1}{9} (1 + 2e^{-3\bar{m}/2}) (1 + 2e^{-3\bar{m}/2}). \quad (13)$$

Finally, note that from $\tilde{q}_{i,m}$ we can also calculate the fraction of recombinant gametes that would be produced in the absence of automixis as

$$\left(\tilde{q}_{\bar{m},\bar{m}})_2 + \frac{1}{2} (\tilde{q}_{\bar{m},\bar{m}})_3 + \frac{1}{2} (\tilde{q}_{\bar{m},\bar{m}})_4 + \frac{1}{2} (\tilde{q}_{\bar{m},\bar{m}})_6 + (\tilde{q}_{\bar{m},\bar{m}})_7 = \frac{1 - e^{-\bar{m}}}{2}. \quad (14)$$

After converting from mean crossover number to genetic distance $d$ in Morgans (i.e., replacing $\bar{m}$ by $2d$) this recovers the inverse of Haldane’s (1919) mapping function and thus demonstrates the consistency of the approach taken here with standard genetics.
2 Neutral genetic variation in automictic populations

As described in the main text, the model is based on seven possible outcomes that can arise when two individuals are sampled from the population:


Here, letters denote any alleles that are identical. Given a certain probability distribution $p(t) = (p_1(t),...,p_7(t))$ for these seven states, we can now ask how this distribution will change under the influence of random genetic drift, mutation, and automixis (or gene conversion).

Each of these evolutionary forces can be described by a matrix so that left multiplication of $p(t)$ with that matrix yields the new probability vector after one generation. For random genetic drift, the matrix will be denoted by $D$ and is given by

$$D = \begin{pmatrix}
1 & 0 & 0 & 0 & 0 & 0 & 0 \\
\frac{1}{2N} & 1 - \frac{1}{N} & 0 & 0 & \frac{1}{2N} & 0 & 0 \\
\frac{1}{2N} & 0 & 1 - \frac{1}{N} & 0 & \frac{1}{2N} & 0 & 0 \\
\frac{1}{2N} & 0 & 0 & 1 - \frac{1}{N} & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 1 & 0 & 0 \\
0 & 0 & 0 & 0 & \frac{1}{N} & 1 - \frac{1}{N} & 0 \\
0 & 0 & 0 & 0 & \frac{1}{N} & 0 & 1 - \frac{1}{N}
\end{pmatrix}$$

For example, under random genetic drift the probability of sampling a homozygous individual and a heterozygous individual sharing one allele with the homozygous individual (state 2) is reduced by a factor $(1 - 1/N)$ because with probability $1/N$ the two individuals will have the same mother, giving rise to either two identical homo- or heterozygotes (states 1 and 5, respectively).

Through automixis or gene conversion, heterozygotes are converted to homozygotes with probability $\gamma$. This can be expressed in the following matrix $A$:

$$A = \begin{pmatrix}
1 & 0 & 0 & 0 & 0 & 0 & 0 \\
\gamma/2 & 1 - \gamma & 0 & \gamma/2 & 0 & 0 & 0 \\
0 & 0 & 1 - \gamma & \gamma & 0 & 0 & 0 \\
0 & 0 & 0 & 1 & 0 & 0 & 0 \\
\gamma^2/2 & 2\gamma(1 - \gamma) & 0 & \gamma^2/2 & (1 - \gamma)^2 & 0 & 0 \\
\gamma^2/4 & \gamma(1 - \gamma) & \gamma(1 - \gamma) & 3\gamma^2/4 & (1 - \gamma)^2 & 0 & 0 \\
0 & 0 & 2\gamma(1 - \gamma) & \gamma^2 & 0 & 0 & (1 - \gamma)^2
\end{pmatrix}$$

For example, after one generation of automixis a sample configuration of two identical heterozygotes (state 5) can give rise to either two identical homozygotes (state 1), one homo- and one heterozygote with shared allele (state 2), two different homozygotes (state 4) or again two identical heterozygotes (state 5). Finally, the mutation matrix $M$ is given by

$$M = \begin{pmatrix}
1 - 4\mu & 4\mu & 0 & 0 & 0 & 0 & 0 \\
0 & 1 - 3\mu & \mu & 0 & 0 & 2\mu & 0 \\
0 & 0 & 1 - 2\mu & 0 & 0 & 0 & 2\mu \\
0 & 0 & 0 & 1 - 4\mu & 4\mu & 0 & 0 \\
0 & 0 & 0 & 0 & 1 - 4\mu & 4\mu & 0 \\
0 & 0 & 0 & 0 & 0 & 1 - 2\mu & 2\mu \\
0 & 0 & 0 & 0 & 0 & 0 & 1
\end{pmatrix}$$
This assumes that the mutation rate is sufficiently low so that more than one mutation event in a pair of genotypes within one generation can be ignored. Combining all three evolutionary events in a single generation and in the order mutation-automixis-drift gives the total probability transition matrix

\[
T = \text{MAD} = \begin{pmatrix}
\frac{N−2\mu(N\gamma+\bar{N})}{2N} & \frac{4\mu\bar{N}}{N} & 0 & 0 & 2\mu\gamma\bar{N} & 0 & 0 \\
\frac{1+N\gamma−\mu(2\gamma+\gamma(3−\gamma)\bar{N})}{2N} & \frac{\mu\bar{N}(1+\gamma)}{N} & \frac{\gamma(1−\mu(1−3\gamma))\bar{N}}{2N} & (1+2\mu)\gamma & 2\mu\gamma^2 \bar{N} & 0 \\
\frac{1+\gamma−2\mu\gamma}{2N} & 0 & \frac{\gamma(1−2\mu(1−2\gamma)\bar{N})}{N} & \frac{\gamma(1−2\mu(1−2\gamma)\bar{N})}{N} & (1+2\mu)\gamma & 0 \\
\frac{1−2\mu\gamma}{N} & 0 & \frac{4\mu\gamma\bar{N}}{N} & (1−4\mu\gamma)\bar{N} & 2\mu\gamma & 0 \\
\frac{\gamma(2+\gamma(1−2\mu)\bar{N})}{2N} & 2\gamma(1−2\mu)\bar{N} & \frac{4\mu\gamma\bar{N}}{N} & (1+2\mu)^2 \gamma^2 \bar{N} & \frac{\gamma(N−(\gamma+4\mu\gamma)\bar{N})}{N} & 4\mu\gamma^2 \bar{N} \\
\frac{\gamma(4+\gamma(1−2\mu)\bar{N})}{4N} & \frac{\gamma(1−2\mu)\bar{N}}{N} & \frac{\gamma(1+2\mu)\bar{N}}{N} & (3+2\mu)^2 \gamma^2 \bar{N} & \frac{\gamma}{N} & (1−2\mu)^2 \gamma^2 \bar{N} \\
0 & \frac{4\gamma\bar{N}}{N} & \frac{\gamma^2 \bar{N}}{N} & \frac{\gamma}{N} & 0 & \frac{\gamma^2 \bar{N}}{N}
\end{pmatrix}
\]

Here, the helper parameters \( \bar{\gamma} := 1 − \gamma \) and \( \bar{N} := N − 1 \) have been used to shorten the formulae. The matrix \( T \) defines a Markov chain for the change in the probability distribution \( p(t) \) through time \( t \in \{0, 1, 2, \ldots\} \),

\[
p_t = p_0^T T^t,
\]

where \( p_0 \) is the initial probability distribution of the sampling states.

Since the Markov chain defined by \( T \) is irreducible and aperiodic, there exists a unique stationary distribution \( \hat{p} \) to which the probability distribution converges independently of the initial distribution \( p_0 \) (Karlin & Taylor 1975). To find this stationary distribution, an eigendecomposition of the matrix \( T \) was performed. \( T \) has the five eigenvalues

\[
\lambda_1 = 1, \quad \lambda_2 = \frac{(1−2\mu)(N−1)}{N}, \quad \lambda_3 = (1−2\mu)(1−\gamma), \\
\lambda_4 = \frac{(1−3\mu)(1−\gamma)(N−1)}{N}, \quad \lambda_5 = \frac{(1−4\mu)(1−\gamma)^2(N−1)}{N},
\]

with \( \lambda_5 \) having multiplicity 3. \( T \) has eight corresponding, linearly independent eigenvectors \( v_1, \ldots, v_8 \), of which \( v_1 = (1, 1, \ldots, 1)^T \) (other eigenvectors not shown). After defining \( \Lambda := \text{diag}(\lambda_1, \ldots, \lambda_5, \lambda_5, \lambda_5) \) and \( G := (v_1, \ldots, v_8) \), we have \( T = G\Lambda G^{-1} \). Since all eigenvalues except \( \lambda_1 \) are < 1 and \( v_1 = (1, 1, \ldots, 1)^T \), this leads to

\[
\lim_{t \to \infty} T^t = G \left( \lim_{t \to \infty} \Lambda^t \right) G^{-1} = G \begin{pmatrix}
1 & 0 & \cdots & 0 \\
0 & 0 & \cdots & 0 \\
\vdots & \vdots & \ddots & 0 \\
0 & 0 & \cdots & 0
\end{pmatrix} G^{-1} = \begin{pmatrix}
1 & 0 & \cdots & 0 \\
1 & 0 & \cdots & 0 \\
\vdots & \vdots & \ddots & 0 \\
1 & 0 & 0 & 0
\end{pmatrix}
\]

Thus, the stationary distribution \( \hat{p} \) is given by the first row of \( G^{-1} \):

\[
\hat{p} = \frac{1}{A} \begin{pmatrix}
\gamma[1−\bar{N}^2\bar{\gamma}^3(1−\mu)(1−2\mu)(1−3\mu) + B − C] \\
4\bar{N}\bar{\gamma}\mu[(2−\gamma)(1+\bar{N}\bar{\gamma})−(8−3N(2−\gamma)−3\gamma)\bar{\gamma}\mu−2\bar{N}(4−\gamma)\bar{\gamma}\mu^2] \\
8\bar{N}\bar{\gamma}^2\mu^2[N^2(2−\gamma)(\gamma+3\bar{\gamma}\mu)+N(2−8\mu−(5−13\mu−(2−5\mu)))−\gamma^2(1−2\mu)] \\
\bar{N}\bar{\gamma}^2\mu[2N^2(2(2−2\bar{\gamma}\mu)(\gamma+3\bar{\gamma}\mu)+D−\bar{\gamma}^2(1−\mu(5−6\mu))] \\
2\bar{\gamma}\mu(1+2\bar{N}\bar{\mu})(\bar{\gamma}+N\bar{\gamma}+3\bar{N}\bar{\gamma}\mu) \\
8\bar{N}\bar{\gamma}^3\mu^2[\bar{\gamma}+N\gamma+\bar{N}(3−\gamma)\mu] \\
16\bar{N}^2\bar{\gamma}^3\mu^3(1−2\bar{\gamma}+N\gamma+3\bar{N}\bar{\gamma}\mu).
\end{pmatrix}
\]
Here, the following helper variables were used in addition to \( \bar{\gamma} \) and \( \tilde{N} \):

\[
A = (1 + 2\tilde{N}\mu)(\gamma + 2\bar{\gamma}\mu)(\bar{\gamma} + N\gamma + 3\tilde{N}\bar{\gamma}\mu)[1 - 2\gamma + 2N\gamma - \tilde{N}\gamma^2 + 4\tilde{N}\bar{\gamma}^2\mu]
\]

\[
B = \tilde{N}[\mu(5 + 6\tilde{N}\mu) + \gamma(3 + 8(N - 2)\mu - (25\tilde{N} + 2)\mu^2 + 6\tilde{N}\mu^3)]
\]

\[
C = \tilde{N}\gamma^2(3 - \mu(17 - 4(7 - 3\mu)\mu - 2N(1 - \mu(7 - 3\mu(5 - 2\mu)))))
\]

\[
D = N[4 - 7\gamma + 3\gamma^2 - \bar{\gamma}^2\mu(15 - 18\mu)].
\]

Considering a few special cases may be helpful to illustrate this stationary distribution and to confirm intuitive expectations.

**Case 1**: \( \mu = 0, \gamma > 0 \). In this case, heterozygotes are steadily converted to homozygotes but no new heterozygotes are produced by mutation. Thus, we expect all individuals to eventually become identical and homozygous, and indeed \( \hat{p} = (1, 0, 0, 0, 0, 0, 0)^T \).

**Case 2**: \( \gamma = 0, \mu > 0 \). This means reproduction is strictly clonal and therefore we expect all homozygotes to disappear from the population. In line with this, we obtain

\[
\hat{p} = \left(0, 0, 0, 0, \frac{1}{1 + 4\mu\tilde{N}}, \frac{4\mu\tilde{N}}{(1 + 2\mu\tilde{N})(1 + 4\mu\tilde{N})}, \frac{8\mu^2\tilde{N}^2}{(1 + 2\mu\tilde{N})(1 + 4\mu\tilde{N})}\right)^T,
\]

where again \( \tilde{N} = N - 1 \approx N \). The value for \( \hat{p}_5 \) (probability of sampling two identical heterozygotes) is analogous to the classic result in population genetics that the equilibrium homozygosity in sexual (or asexual haploid) populations under mutation-drift balance is equal to \( F = 1/(1 + 4\mu N) \). Here, the twofold higher per-locus mutation rate in asexual diploids compared to a haploid locus in sexuals is exactly offset by the twofold difference in the number of chromosomes or individuals. The probability that two individuals are different is distributed across states 6 and 7.

### 3 Simulating neutral genetic variation

In order to confirm the analytical predictions regarding the different statistics describing genetic diversity under mutation, drift and automixis, extensive individual-based simulations were performed. Here, a population of fixed size \( N = 1000 \) was considered. Individuals were diploid and their allelic state at each locus was given by a number ranging from 1 to \( 10^6 \). In each generation, mutations occurred with probability \( \mu \) at each locus, converting the allelic state to a new, randomly drawn number. (The large number of possible alleles ensured that every mutation produced a new allele not already segregating within the population.) Following mutation, individuals reproduced zygotes by automixis, i.e. heterozygote mothers produced each of the two possible homozygous zygotes with probability \( \gamma/2 \). Finally, random genetic drift was implemented by random sampling \( N \) new females with replacement from the zygotes. To simulate the data shown in Figs. 2 and S2, the populations were initialised with randomly chosen alleles for each individual. Following a burn-in period of \( 10^5 \) generations, every 1000 generations and during a total of \( 10^6 \) generations, samples of 500 pairs of individuals were randomly drawn from the population. Each sample was then classified as one of the seven states defined at the beginning of the previous section, and the average fraction of samples falling into one of these states was recorded. From these states, the different statistics (\( H_I, H_T, F_{IT}, \) and \( H_G \)) were then calculated. Ten of these replicate simulations were performed and results averaged.
4 A two-locus model for evolution in automictic populations

In this section, the two-locus/two-alleles model that was used in the main text (sections on "Associative Overdominance" and "Spread of beneficial mutations") is derived. This is a recursion equation model of an infinitely large or finite population reproducing in discrete, non-overlapping generations and involving four steps: (1) starting from juveniles, selection operates to give rise to reproducing, adult individuals, (2) mutations arise in the germ line of these individuals, (3) eggs are produced through automixis, and (4) random genetic drift affects the fraction of eggs that develop into a new generation of juveniles. Before describing these four steps in detail, for convenience of notation let us number the ten possible genotypes as follows:

1: aabb    2: aaBb    3: aaBB    4: Aabb    5: AaBb
6: AaBb    7: AaBB    8: AAbb    9: AABb    10: AABB

1. Selection. Let \( p \) be the vector of juvenile genotype frequencies before selection, in the above order. Assuming selection coefficients \( s_A \) and \( s_B \) at these loci, dominance coefficients \( h_A \) and \( h_B \), and multiplicative effects across loci (no epistasis), selection then changes these frequencies to

\[
p^{(s)} = \frac{p \odot w}{pw}, \tag{19}
\]

where the vector \( w \) of relative fitness values is given by

\[
w = \begin{pmatrix}
    1 \\
    1 + h_B s_B \\
    1 + s_B \\
    1 + h_A s_A \\
    (1 + h_A s_A) (1 + h_B s_B) \\
    (1 + h_A s_A) (1 + h_B s_B) \\
    (1 + h_A s_A) (1 + s_B) \\
    (1 + s_A) (1 + h_B s_B) \\
    (1 + s_A) (1 + s_B)
\end{pmatrix}
\]

In the numerator in Eq.19, \( \odot \) denotes the Hadamard product (element-wise multiplication), whereas the denominator is a scalar product.

2. Mutation. Mutations are assumed to occur at the same rate \( \mu \) at the two loci, and mutations are acquired independently at the two homologous chromosomes and the two loci. With these assumptions, the genotype frequencies after mutation can be expressed as

\[
p^{(m)} = Mp^{(s)}. \tag{20}
\]
Here, the matrix $M$ is defined such that $M_{ij}$ is the fraction of genotype $i$ arising through mutation from genotype $j$. This yields

$$M = \begin{pmatrix} \tilde{\mu}^4 & \mu \tilde{\mu}^3 & \mu^2 \tilde{\mu}^2 & \mu^3 \tilde{\mu} & \mu^2 \mu \tilde{\mu} & \mu^3 \mu \tilde{\mu} & \mu^2 \mu^2 \tilde{\mu} & \mu^3 \mu^2 \tilde{\mu} & \mu^4 \\ 2\mu^4 & \mu^3 + \tilde{\mu} & \mu^2 \tilde{\mu} & \mu^3 \mu & \mu^2 \mu \tilde{\mu} & \mu^3 \mu^2 \tilde{\mu} & \mu^2 \mu^2 \mu \tilde{\mu} & \mu^3 \mu^2 \mu^2 \tilde{\mu} & \mu^4 \\ \mu^2 \tilde{\mu} & \mu^3 \tilde{\mu} & \mu^2 \mu \tilde{\mu} & \mu^3 \mu^2 \tilde{\mu} & \mu^2 \mu^2 \mu \tilde{\mu} & \mu^3 \mu^2 \mu^2 \mu \tilde{\mu} & \mu^2 \mu^2 \mu^2 \mu \tilde{\mu} & \mu^3 \mu^2 \mu^2 \mu^2 \mu \tilde{\mu} & \mu^4 \\ \mu^3 \tilde{\mu} & \mu^2 \mu \tilde{\mu} & \mu^3 \mu \tilde{\mu} & \mu^2 \mu^2 \mu \tilde{\mu} & \mu^3 \mu^2 \mu \tilde{\mu} & \mu^2 \mu^2 \mu^2 \mu \tilde{\mu} & \mu^3 \mu^2 \mu^2 \mu^2 \mu \tilde{\mu} & \mu^4 \\ \mu^4 & \mu^3 \mu \tilde{\mu} & \mu^2 \mu^2 \mu \tilde{\mu} & \mu^3 \mu^2 \mu^2 \mu \tilde{\mu} & \mu^4 \\ \end{pmatrix},$$

with placeholders $\mu := 1 - \mu$ and $\nu := \mu^2 + \tilde{\mu}^2$.

3. Automixis. Offspring production through automixis can also be expressed by matrix multiplication,

$$p^{(n)} = A p^{(s)}.$$

The elements $A_{ij}$ in the matrix $A$ give the fractions of offspring with genotype $i$ produced by a mother with genotype $j$, for a given mode of automixis and mean crossover numbers $\bar{n}$ and $\bar{m}$. The matrices $A$ can be derived from the results in section 1. Using the same placeholders $g_i$ and $h_i$ as in section 1 (Eq. 7) these matrices are given by:

$$A_{\text{CentralFusion}} = \begin{pmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \frac{g_n + \bar{n}}{2} & 1 - \bar{n} & \frac{g_{\bar{n} + \bar{n}}}{2} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ \frac{g_{\bar{n}}}{4} & 0 & 0 & 0 & \frac{g_{\bar{n}}}{2} & 0 & 0 & 0 & 0 \\ g_{\bar{n}} h_{\bar{n}} & g_{\bar{n}} h_{\bar{n}} & g_{\bar{n}} h_{\bar{n}} & g_{\bar{n}} h_{\bar{n}} & g_{\bar{n}} h_{\bar{n}} & g_{\bar{n}} h_{\bar{n}} & g_{\bar{n}} h_{\bar{n}} & g_{\bar{n}} h_{\bar{n}} & g_{\bar{n}} h_{\bar{n}} \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \frac{(1-g_n)(1-g_{\bar{n}}-e^{-\bar{m}})}{2} & \frac{(1-g_n)(1-g_{\bar{n}}-e^{-\bar{m}})}{2} & \frac{(1-g_n)(1-g_{\bar{n}}-e^{-\bar{m}})}{2} & \frac{(1-g_n)(1-g_{\bar{n}}-e^{-\bar{m}})}{2} & \frac{(1-g_n)(1-g_{\bar{n}}-e^{-\bar{m}})}{2} & \frac{(1-g_n)(1-g_{\bar{n}}-e^{-\bar{m}})}{2} & \frac{(1-g_n)(1-g_{\bar{n}}-e^{-\bar{m}})}{2} & \frac{(1-g_n)(1-g_{\bar{n}}-e^{-\bar{m}})}{2} & \frac{(1-g_n)(1-g_{\bar{n}}-e^{-\bar{m}})}{2} \\ 0 & 1 - g_{\bar{n}} & 0 & 0 & \frac{g_{\bar{n}}}{2} & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 - g_{\bar{n}} & \frac{g_{\bar{n}} + \bar{n}}{2} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \end{pmatrix}.$$
\[
A_{\text{TerminalFusion}} = \begin{pmatrix}
\frac{1}{2} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
\frac{1}{2} - h_{\bar{m} + \bar{n}} & \frac{1}{2} & h_{\bar{m} + \bar{n}} & 0 & 0 & 0 \\
0 & 0 & 1 & 0 & 0 & 0 \\
h_{\bar{n}} & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
\end{pmatrix},
\]

\[
A_{\text{GameteDuplication}} = \begin{pmatrix}
1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
\end{pmatrix},
\]

4. Random genetic drift. When finite populations were assumed, a drift step was added by sampling individual numbers from a multinomial distribution. Specifically, for given population size \(N\), the genotype frequencies after drift were distributed according to

\[
p^{(d)} \sim \frac{\text{Multinomial}(N, p^{(a)})}{N}.
\]

This completes the life cycle.