Branching-process approximation of the invasion probability of a weakly beneficial mutation linked to an established polymorphism at migration-selection balance

General fitness model

Set up and initialisation

- Rules and definitions

\begin{verbatim}
In[2]:= ruleWeakForces := 
{a \rightarrow a \epsilon, b \rightarrow b \epsilon, m \rightarrow \mu \mu \epsilon, r \rightarrow \rho \epsilon, \gamma_{11} \rightarrow \gamma_{11} \epsilon, \gamma_{12} \rightarrow \gamma_{12} \epsilon}

rescaleWeakForces := 
{a \rightarrow a / \epsilon, b \rightarrow b / \epsilon, \mu \mu \rightarrow \mu \mu / \epsilon, \rho \rightarrow \rho / \epsilon, \gamma_{11} \rightarrow \gamma_{11} / \epsilon, \gamma_{12} \rightarrow \gamma_{12} / \epsilon}

In[4]:= ruleSimplifyNotation := x_[_] \rightarrow x
\end{verbatim}

- Implementation of relative fitnesses and assumptions

Clear[M, m]
(** Relative fitnesses of genotypes **) 
(* n=1,2 index of deme (for the time being, i.e. for the CI model, 2 is the continent as *)
(* i=1,2,3 index of haplotypes (gametes) *)
(* A, B the two loci with alleles A_1, A_2 and B_1 and B_2, respectively *)
(* We assume that there is no position effect, i.e. w_{ij}=w_{ji}, and w_{23}=w_{14}. *)
w_{23}=w_{14}; w_{21}=w_{12}; w_{31}=w_{13}; w_{32}=w_{23}; w_{41}=w_{14}; w_{42}=w_{24}; w_{43}=w_{34};
w[n_\_]=\{(w11[n],w12[n],w13[n],w14[n]),(w21[n],w22[n],w23[n],w24[n]),(w31[n],w32[n],w33[n],w34[n])\}

(* Marginal relative gamete fitnesses *)
wMarg[i\_\_, n\_] := Sum[w[n][1, j]*x[j, n], {j, 1, 4}]

(* Mean relative fitness *)
wMean[n\_\_] := Sum[wMarg[i\_, n\_]*x[i, n], {i, 1, 4}]

(* Migration matrix *)
M=((1-m[1],m[1]),(m[2],1-m[2]));

(* Linkage disequilibrium *)
LDRule[n\_\_] := {LD[n] \rightarrow x[1,n]x[4,n]-x[2,n]x[3,n]}

(*!! Assumptions !!*)
(* Continent-island context (still allowing for the B-locus to be polymorphic on the coi*)
(* Assume that the continent is monomorphic, i.e. that qC = x[4,2] = q[2] = 1. *)
assumeMonomorphicContin:=qc=0;
assumeGenericAdditiveFitness[n\_\_]:=\{
w11[n]-v1[n]+v1[n],w12[n]-v1[n]+v2[n],w13[n]-v1[n]+v3[n],w14[n]-v1[n]+v4[n],
w22[n]-v2[n]+v2[n],w24[n]-v2[n]+v2[n],
w33[n]-v3[n]+v3[n], w34[n]-v3[n]+v4[n],
w44[n]-v4[n]+v4[n]\}

(* Generic fitness interaction between alleles within a gamete, multiplicative fitness*)
assumeGenericMultiplicativeFitness[n\_\_]:=\{
w11[n]-v1[n]+v1[n],w12[n]-v1[n]+v2[n],w13[n]-v1[n]+v3[n],w14[n]-v1[n]+v4[n],
w22[n]-v2[n]+v2[n],w24[n]-v2[n]+v2[n],
w33[n]-v3[n]+v3[n], w34[n]-v3[n]+v4[n],
w44[n]-v4[n]+v4[n]\}

(* Additive fitness interactions between alleles within a gamete, multiplicative fitness*)
assumeAdditiveMultiplicativeFitness[n\_\_]:=\{
w11[n]-\rightarrow(a+a[n])*\rightarrow(b+n)],w12[n]-\rightarrow(a+a[n]),w13[n]-\rightarrow(1+b[n]),w14[n]=1,
w22[n]-\rightarrow(a+n)*\rightarrow(1-b[n]),w24[n]=\rightarrow(1-b[n]),
w33[n]-\rightarrow(1-a[n])*\rightarrow(1+b[n]), w34[n]-\rightarrow(1-a[n]),
w44[n]-\rightarrow(1-a[n])+\rightarrow(1-b[n])\}

(* Additive fitness interactions between alleles within a gamete, multiplicative fitness*)
assumeAdditiveMultiplicativeApproxFitness[n\_\_]:=\{
w11[n]-\rightarrow(a+a[n]+b[n]],w12[n]-\rightarrow(a+a[n]),w13[n]-\rightarrow(1+b[n]),w14[n]=1,
w22[n]-\rightarrow(a+n)-b[n]),w24[n]=\rightarrow(1-b[n]),
w33[n]-\rightarrow(1-a+n)+b[n]), w34[n]-\rightarrow(1-a[n],
w44[n]=\rightarrow(1-a[n])-\rightarrow(1-b[n])\}

(* Additive fitness interactions between alleles within a gamete, multiplicative fitness*)
(* The interpretation of the coefficients of epistasis, \gamma, is as follows: \gamma_{kl} is the epi*)
assumeAdditiveMultiplicativeEpistaticFitness[n\_\_]:=\{
w11[n]-\rightarrow(a+a[n]+b[n]),w12[n]-\rightarrow(a+a[n])*(\rightarrow(1+21[n])),w13[n]=\rightarrow(1+b[n]),w14[n]=\rightarrow(1-\gamma_{1}[n]),
w22[n]=\rightarrow(a+a[n]+a+b[n]),w24[n]=\rightarrow(1-b[n]+(1+\gamma_{22}[n]),
w33[n]=\rightarrow(a+a[n])+\rightarrow(1-b[n]+(1+\gamma_{22}[n]), w34[n]=\rightarrow(1-a[n]),
w44[n]=\rightarrow(1-a[n]+(1-b[n])\}

(* Additive fitness interactions between alleles within a gamete, multiplicative fitness*)
(* Details of epistasis are as in the previous case *)
assumeAdditiveMultiplicativeEpistaticApproxFitness[n\_\_]:=\{
w11[n]=\rightarrow(a+a[n]+b[n]),w12[n]=\rightarrow(a+a[n]-21[n]),w13[n]=\rightarrow(1+b[n]),w14[n]=\rightarrow(1-\gamma_{1}[n]),
w22[n]=\rightarrow(1-a[n]-b[n]-22[n]),w24[n]=\rightarrow(1-b[n]-\gamma_{12}[n]),
w33[n]=\rightarrow(a+a[n]+b[n]), w34[n]=\rightarrow(1-a[n],
w44[n]=\rightarrow(1-a[n])-\rightarrow(1-b[n])\}
Relative fitness matrices under specific assumptions

**Fully generic regime**

\[
\text{MatrixForm}[w[1]] = \begin{pmatrix}
\end{pmatrix}
\]

**Regimes without epistasis**

Below, we introduce the following specific schemes of relative fitness (the subscript \( n \) denotes the deme; \( n = 1 \) applied for the island deme):

- **Generic additive:** This means generic fitness interaction between alleles within a gamete, and additive fitness interaction between gametes. \( w_{ij,n} = v_{ij} + v_{j,n} \), where \( i, j \) denote the gametes.

- **Generic multiplicative:** This means generic fitness interaction between alleles within a gamete, and multiplicative fitness interaction between gametes. \( w_{ij,n} = v_{ij} v_{j,n} \), where \( i, j \) denote the gametes.

- **Additive multiplicative:** This means additive fitness interaction between alleles within a gamete, and multiplicative fitness interaction between gametes. In the following matrix, the rows correspond to the A-locus configurations \( A_1 A_1, A_1 A_2, A_2 A_2 \) from top to bottom, and the columns correspond to the B-locus configurations \( B_1 B_1, B_1 B_2, B_2 B_2 \) from left to right.

\[
w_{\text{a}} = \begin{pmatrix}
w_{11,n} & w_{12,n} & w_{13,n} & w_{14,n} \\
w_{12,n} & w_{22,n} & w_{14,n} & w_{24,n} \\
w_{13,n} & w_{14,n} & w_{33,n} & w_{34,n} \\
w_{14,n} & w_{24,n} & w_{34,n} & w_{44,n}
\end{pmatrix} = \begin{pmatrix}
(a_n + 1)(b_n + 1) & a_n + 1 & (a_n + 1)(1 - b_n) & b_n + 1 \\
1 & 1 & 1 & 1
\end{pmatrix}
\]

(1)

- **Additive multiplicative approximated (or, simply ‘Additive’):** This means additive fitness interaction between alleles within a gamete, and multiplicative fitness interaction between gametes. In addition, we assume that selection is weak, so that higher order and interaction terms of the selection coefficients can be ignored. In the following matrix, the rows correspond to the A-locus configurations \( A_1 A_1, A_1 A_2, A_2 A_2 \) from top to bottom, and the columns correspond to the B-locus configurations \( B_1 B_1, B_1 B_2, B_2 B_2 \) from left to right.

\[
w_{\text{a}} = \begin{pmatrix}
w_{11,n} & w_{12,n} & w_{13,n} & w_{14,n} \\
w_{12,n} & w_{22,n} & w_{14,n} & w_{24,n} \\
w_{13,n} & w_{14,n} & w_{33,n} & w_{34,n} \\
w_{14,n} & w_{24,n} & w_{34,n} & w_{44,n}
\end{pmatrix} = \begin{pmatrix}
a_n + b_n + 1 & a_n + 1 & a_n - b_n + 1 & b_n + 1 \\
1 & 1 & 1 & 1
\end{pmatrix}
\]

(2)

Checking the implementation:

\[
\text{MatrixForm}[w[1]] // \text{assumeGenericAdditiveFitness}[1]
\]

\[
\begin{pmatrix}
\end{pmatrix}
\]

\[
\text{MatrixForm}[w[1]] // \text{assumeGenericMultiplicFitness}[1]
\]

\[
\begin{pmatrix}
\end{pmatrix}
\]

\[
\text{MatrixForm}[w[1]] // \text{assumeAdditiveMultiplicFitness}[1]
\]

\[
\begin{pmatrix}
(1 + a[1]) (1 + b[1]) & 1 + a[1] & 1 + b[1] & 1 \\
1 + a[1] & (1 + a[1]) (1 - b[1]) & 1 & 1 - b[1] \\
1 + b[1] & 1 & (1 - a[1]) (1 + b[1]) & 1 - a[1] \\
1 & 1 - b[1] & 1 - a[1] & (1 - a[1]) (1 - b[1])
\end{pmatrix}
\]

\[
\text{MatrixForm}[w[1]] // \text{assumeAdditiveMultiplicApproxFitness}[1]
\]

\[
\begin{pmatrix}
\end{pmatrix}
\]
- Migration matrix

MatrixForm[M]

\[
\begin{pmatrix}
1 - m[1] & m[1] \\
\end{pmatrix}
\]

Deterministic analysis

- Assuming a rare mutant and a constant resident population

**Preliminaries**

This part follows Ewens (1967) closely, but uses notation and conventions introduced by Bürger (2000) and Bürger and Akerman (2011). We build the deterministic model that describes the dynamics of the two haplotypes of interest, \( A_1 B_1 \) (\( x_1 \)) and \( A_1 B_2 \) (\( x_2 \)) when they are rare. We call the first type '1' and the second 'type 2'.

In the following, we define the marginal fitnesses of type 1 and 2. *Marginal* means that we account for the fact that, in diploids, each type can occur in combination with two possible other haplotypes, namely with \( A_2 B_1 \) or \( A_2 B_2 \). These two are present in the deme \( n \) at frequencies \( x_{3,n} \) and \( x_{4,n} \), respectively. Assuming that \( A_1 \) is rare, we make the approximations \( x_{3,n} \approx q_0 \) and \( x_{4,n} \approx 1 - q_0 \). Hence,

\[
\begin{align*}
\w_{1,n} &= w_{13,n} x_{3,n} + w_{14,n} x_{4,n} \\
\w_{2,n} &= w_{23,n} x_{3,n} + w_{24,n} x_{4,n}
\end{align*}
\]

(3)

In the following, an uppercase letter (A or B) denotes the locus which is polymorphic.

- Marginal fitnesses of types that will be followed in the branching process (*)

\[
\text{wMargType}[i_\_ , n\_] := \text{Sum}[\text{w}[n][i, j] x[j,n], \{j, 3, 4\}]
\]

(* Here, \( i \) is the index of the type of in

(* Mean relative fitness if \( A_1 \) is absent (rare) *)

\[
\text{wMeanB}[n\_] := \text{Sum}[\text{w}[n][i, j] * x[i,n] * x[j,n], \{i, 3, 4\}, \{j, 3, 4\}]
\]

(*!! Assumptions !!*)

(* The \( A_1 \) allele is rare, so that \( x_3 = q_0 \) and \( x_4 = 1 - q_0 \) *)

\[
\text{assumeA1Rare}[n\_] := (x[3,n] \rightarrow q[n], x[4,n] \rightarrow 1 - q[n])
\]

Inspection of marginal fitnesses (check).

\[
\text{wMargType}[1, 1] /\_ /\_ /\_ /\_ /\_ \text{assumeA1Rare}[1]
\]

\[
\]

\[
\text{wMargType}[2, 1] /\_ /\_ /\_ /\_ /\_ \text{assumeA1Rare}[1]
\]

\[
q[1] w14[1] + (1 - q[1]) w24[1]
\]

- Recursion equation for frequency of the two rare gametes (types 1 and 2)

The general notation for the recombination rate between loci X and Y is \( r_{XY} \). With two loci only, we use the short hand \( r = r_{AB} \).

The deterministic recursion equation for the rare haplotypes \( (A_1 B_1, A_1 B_2) \) in the diploid case is obtained from the full system of recursion equations and then from assuming \( x_{1,n} \) and \( x_{2,n} \) are small, such that \( (x_{1,n})^2 \approx x_{1,n} x_{2,n} = (x_{2,n})^2 \approx 0 \), and \( x_{3,n} = q_0 \) and \( x_{4,n} \approx 1 - q_0 \). For the moment, we only consider the continent-island model, but the recursion equations below are more general (valid for the two-deme model). To obtain the equations for the continent-island model, we have to apply the continent-island assumptions, which yields simpler expressions.

Further, we assume that, although present at low frequencies, the haplotypes \( A_1 B_1 \) and \( A_1 B_2 \) do not contribute to the mean relative fitness of the population.
In[28]:= (* For simpler notation in the case of the continent-island model *)

\[ \mathbf{r}[A, B] := r \]

(* Helper variable *)
\[ \delta = (1, -1, -1, 1); \]

(* Recursion of gamete frequencies under the full two-locus model *)
\[ \text{rec2LocFull}[i_\_, n_\_] := \text{M}[n, 1] \ast (\text{wMarg}[i, 1] \ast \text{x}[i, 1] - \delta[i] \ast \mathbf{r}[A, B] \ast \text{w}[1][1, 4] \ast \text{LD}[1]) \ast \text{wbar}[1] + \mathbf{M}[n, 2] \]

(*!! Assumptions !!*)

(* Ignore terms of order O(\(x_i \ast x_j\), i = 1, 2 *)
\[ \text{assumeSecOrderSmall}[n_] := \text{Table}[\text{x}[i, n] \text{x}[j, n] \to 0, (i, 1, 2), (j, 1, 2)] \]

(* Approximate the overall mean fitness *)
\[ \text{assumeWMean}[n_] := (\text{wbar}[n] \to \text{wMean}[n]) \]

(* Rules for simplifying the notation *)
\[ \text{ruleSimplifyNotationCI} := (\text{m}[1] \to \text{m}, \text{x}[1, 1] \to \text{x}1, \text{x}[2, 1] \to \text{x}2, \text{x}[3, 1] \to \text{x}3, \text{x}[4, 1] \to \text{x}4, \text{q}[1] \to \text{q}) \]

\[ \text{In[29]} \]

**Inspection of terms**

Approximate recursion equation for the gamete \(A_1 B_1\) \((x_1)\), obtained from applying the corresponding assumptions to the full equation and simplifying the notation.

\[ \text{LDApprox}[n_] := \text{LD}[n]/\text{LDRule}[n]/\text{assumeAllRare}[n] \]
\[ \text{rec2LocRareTypesCI}[i_\_, n_\_] := \text{M}[n, 1] \text{w}[n][1] \ast \text{x}[i, n] \ast \text{q} \ast \text{w}[n][1, 4] \ast \text{x}[i, n] \ast (1-q) \ast \delta[i] \ast \mathbf{r}[A, B] \]
\[ \text{LDApprox}[1] \]
\[ (1-q[1]) \text{x}[1, 1] - q[1] \text{x}[2, 1] \]

\[ \text{ruleSimplifyNotationCI} \]
\[ \{\text{m}[1] \to \text{m}, \text{x}[1, 1] \to \text{x}1, \text{x}[2, 1] \to \text{x}2, \text{x}[3, 1] \to \text{x}3, \text{x}[4, 1] \to \text{x}4, \text{q}[1] \to \text{q}\} \]

\[ \text{rec2LocRareTypesCI}[1, 1] /\text{. ruleSimplifyNotationCI} \]
\[ ((1-m) \text{q}[1] \text{x}[1, 1] \ast (1-q) \text{x}[1, 1] \text{w}[1][1] - \text{r} \ast ((1-q) \text{x}[1, 1] \text{w}[1][1] \ast \text{LD}[1])) \ast \text{wOverallMean}[1] \]

\[ \text{rec2LocRareTypesCI}[1, 1] /\text{. assumeWMean}[1] /\text{. assumeAllRare}[1] /\text{. ruleSimplifyNotationCI} \]
\[ ((1-m) \text{q}[1] \text{x}[1, 1] \ast (1-q) \text{x}[1, 1] \text{w}[1][1] - \text{r} \ast ((1-q) \text{x}[1, 1] \text{w}[1][1] \ast \text{LD}[1])) \ast \text{wOverallMean}[1] \]

\[ \text{rec2LocRareTypesCI}[2, 1] /\text{. ruleSimplifyNotationCI} \]
\[ ((1-m) \text{q}[2] \text{w}[1][1] \ast \text{r} \ast ((1-q) \text{x}[1, 1] \text{w}[1][1] \ast (1-q) \text{x}[2, 1] \text{w}[1][1] \ast \text{LD}[1])) \ast \text{wOverallMean}[1] \]

\[ \text{rec2LocRareTypesCI}[2, 1] /\text{. assumeWMean}[1] /\text{. assumeAllRare}[1] /\text{. ruleSimplifyNotationCI} \]
\[ ((1-m) \text{q}[2] \text{w}[1][1] \ast \text{r} \ast ((1-q) \text{x}[1, 1] \text{w}[1][1] \ast (1-q) \text{x}[2, 1] \text{w}[1][1] \ast \text{LD}[1])) \ast \text{wOverallMean}[1] \]
Matrix form, mean matrix and eigenvalues

The deterministic process may also be written in matrix form, where we use $\tilde{X}$ for the transpose of a matrix or vector:

$$x_{G}^{T}(t + 1) = G_{x}x_{G}^{T}(t)$$

with

$$x_{G}^{T}(t) = \left(\begin{array}{c} x_{1,n}(t) \\ x_{2,n}(t) \end{array}\right)$$

and

$$G_{x} = \left(\begin{array}{ccc} (1 - m_{0})(w_{13,n} q_{a} + w_{14,n}(1 - q_{a}) - r w_{14}(1 - q_{a})/w_{n}) & (1 - m_{0}) r w_{14,n} q_{a}/w_{n} \\ (1 - m_{0}) r w_{14,n}(1 - q_{a})/w_{n} & (1 - m_{0})(w_{24,n}(1 - q_{a}) + w_{23} q_{a} - r w_{14,n} q_{a})/w_{n} \end{array}\right)$$

where

$$w_{1,n} = w_{13,n} q_{a} + (1 - q_{a}) w_{14,n}$$

$$w_{2,n} = w_{14,n} q_{a} + (1 - q_{a}) w_{24,n}.$$  

These are the marginal relative fitnesses of the two types ‘wMargType[n]’ defined above. Notice that in the manuscript and in other Mathematica Notebooks, we use $L = G_{x}^{T}$ and we write $X^{T}(t + 1) = X(t) L$ instead of (4), but the two are equivalent. The notation with the matrix $G$ is consistent with the one used by Ewens (1967).

Specifically, the entry $g_{ij}$ of $G$ (i and j being the row and column indices, respectively) represents the expected number of i-type offspring produced by a j-type parent, whereas the entry $\lambda_{ij}$ of $L$ represents the expected number of j-type offspring produced by an i-type parent.

Equation (4) may now be written as

$$x_{G}^{T}(t) = G_{x}x_{G}^{T}(0)$$

For the next steps, we follow Ewens (1967) and drop the index $n$, since for the moment, we assume $n = 1$ (continent-island model, island = deme 1). Let $\lambda_{i} (i = 1, 2)$ be the eigenvalues of $G$, $\vec{v}_{i}$ the corresponding right eigenvectors (column vectors), and $\vec{u}_{i}$ the corresponding left eigenvectors (row vectors). In the manuscript and in other Mathematica Notebooks, we use $\gamma_{i}$ (Greek nu) instead of $\lambda_{i}$ for the eigenvalues, and $\vec{v}$ and $\vec{u}$ for the right and left eigenvectors, respectively. If we normalise so that $\vec{v}_{i} \vec{v}_{\ast} = 1 (i = 1, 2)$, then we expand the matrix $G$ in the spectral form

$$G' = \lambda_{1}^{\ast} G_{1} + \lambda_{2}^{\ast} G_{2},$$

where $G_{i} = \vec{v}_{i} \vec{u}_{i}^{\ast}$. By inserting into eq. (8), we obtain

$$x_{1}(t) + x_{2}(t) = \lambda_{1}^{\ast} \left(\begin{array}{c} x_{G_{1}}^{T}(0) \\ x_{G_{2}}^{T}(0) \end{array}\right) + \lambda_{2}^{\ast} \left(\begin{array}{c} x_{G_{1}}^{T}(0) \\ x_{G_{2}}^{T}(0) \end{array}\right),$$

where $I$ is the row vector $(1, 1)$. The frequency of the mutant ($\lambda_{1}$) will eventually increase provided only that the maximum eigenvalue $\lambda_{1}$ is greater than 1.

According to the theory of multi-type branching processes, the above requirement ($\lambda_{1} > 1$) corresponds to the condition that must be fulfilled such that the extinction probability of the process is $< 1$, i.e. such that the multi-type branching process is supercritical. Otherwise ($\lambda_{1} \leq 1$), the process is subcritical and the extinction probability is 1 (except for the degenerate case $\lambda_{1} = 1$ and every individual produces exactly one offspring). We call $G$ the ‘mean matrix’.

In the following, we obtain the mean matrix for the continent-island case and determine its eigenvalues. We do so first for generic fitnesses ($w_{1}, w_{2}, \bar{w}$). Later, we apply various assumptions about the relative fitnesses (see definitions above). These results will later be taken up in the stochastic treatment (see below).

```
ln[31]:= (* The mean matrix *)
(* Notice that the mean matrix *left-* multiplies the vector x' *)
G[1] /. ruleSimplifyNotationCI // MatrixForm
```

Inspection of eigenvalues.
G[1] /. \{wbar[1] \to wbar\} /. ruleSimplifyNotationCI // MatrixForm

\[
\begin{pmatrix}
(1-m) w[1] & (1-q) r \times w[1] & (1-m) q \times w[1]4[1] \\
(1-m) q \times w[1] & (1-m) w[1] & (1-m) \times (-q + q \times w[1]4[1]) \\
\end{pmatrix}
\]

evaluesG :=

evaluesG

\[
\left\{-\frac{1}{2 \times wbar} (-1 + m) \left(w[1] - r \times w[14] + w[2] + \sqrt{(w[1])^2 + r^2 (w[14])^2}\right),
\frac{1}{2 \times wbar} (-1 + m) \left(-w[1] + r \times w[14] - w[2] + \sqrt{(w[1])^2 + r^2 (w[14])^2}\right)
\right\}
\]

As expected, these eigenvalues are the same as those obtained by Ewens (1967) for the case without migration, up to the factor \((1-m)\). Note that they are valid for a monomorphic as well as a polymorphic continent, and that the fitnesses are completely general so far.

Next, we find the conditions under which \(\lambda_1 > 1\). From inspection of the term representing \(\lambda_1\), we see that

evaluesG[1]

\[
\frac{1}{2 \times wbar} (-1 + m) \left(w[1] - r \times w[14] + w[2] + \sqrt{(w[1])^2 + r^2 (w[14])^2}\right) > (1-m) \left(2(w[14] - w[2]) + r^2 (w[14])^2 - r \times w[14] + w[1] + w[2]\right) > 2 \times w \quad (11)
\]

Rearranging the above manually, we obtain the inequality

\[
\sqrt{\text{stuf}f} > 2 \frac{w}{1 - m} - w[1] - w[2] - r \times w[14]
\]

\[
\Rightarrow \text{stuf}f > \left(2 \frac{w}{1 - m} - w[1] - w[2] - r \times w[14]\right)^2 ,
\]

where

\[
\text{stuf}f = (w[1] - w[2])^2 + 2 r \times w[14](w[1] - w[2]) + r^2 (w[14])^2 .
\]

Expanding all terms, on both sides, and simplifying, we obtain

\[
\]

\[
4 q \times r \times w[14] - 4 w[14] - 4 r \times w[14] - 4 q \times r \times w[14] + \frac{4 w[14] \times \text{wbar}}{1 - m} - \frac{4 r \times w[14] \times \text{wbar}}{1 - m} - \frac{4 w[2] \times \text{wbar}}{1 - m} - \frac{4 \times \text{wbar}^2}{(1 - m)^2} > 0
\]

Collecting terms in \(r \times w[14]\), we obtain

\[
\text{Collect}\left[ 4 q \times r \times w[14] - 4 w[1] - 4 r \times w[14] - 4 q \times r \times w[14] - \frac{4 w[14] \times \text{wbar}}{1 - m} - \frac{4 r \times w[14] \times \text{wbar}}{1 - m} - \frac{4 w[2] \times \text{wbar}}{1 - m} - \frac{4 \times \text{wbar}^2}{(1 - m)^2} > 0, r \times w[14]\right]
\]

\[
-4 w[2] + \frac{4 w[14] \times \text{wbar}}{1 - m} - \frac{4 r \times w[14] \times \text{wbar}}{1 - m} - \frac{4 w[2] \times \text{wbar}}{1 - m} + r \times w[14] \left(4 q \times w[1] + 4 w[2] - 4 q \times w[2] - \frac{4 \times \text{wbar}}{1 - m}\right) > 0
\]

Dividing the whole equation by 4, shuffling terms without \(r\) onto the right and factorizing the resulting terms, we obtain
In[32]:= \[\text{conditionNonExtinction}[n_\_]:=}\text{r}[\text{w}][1,4]\left(\frac{\text{wbar}[n]}{1-m[n]}-q[n]*\text{w1}[n]-(1-q[n])*\text{w2}[n]\right)\leq \frac{\text{wbar}[n]}{1-m[n]} - w\right]

Option: One could go on here and derive general results parallel to those in Ewens (1967), but for the continent-island model instead of a panmictic isolated population.

**Classification according to the continuous-time version of the deterministic model**

**Determination of parameter regime (class of bifurcation diagrams according to Bürger and Akerman (2011))**

The purpose of this subsubsection is to implement tests for the conditions for

- Existence of the marginal one-locus equilibrium $E_B$ (see also next subsection)
- Stability of $E_B$

according to Bürger and Akerman (2011) for given values of $a$, $b$, and $m$. Moreover, we will define a function that determines the class of bifurcation diagrams and the parameter regime (equations 3.21 to 3.27 in Bürger and Akerman (2011)), given $a$, $b$, $m$ and $\rho$. These equations are part of their Theorem 2, refer to their Figure 1 (diagrams (a) to (g)) and are as follows:

In the following, we use $\alpha$ for $a$ and $\beta$ for $b$, and we let $\alpha < \beta$.

1. Diagram (a) applies if and only if
   $\beta \geq 2 \alpha$ and $\rho < \alpha$ \hspace{1cm} (3.21 a)
   or
   $\beta < 2 \alpha$ and $\rho \leq \frac{1}{3} (\alpha + \beta)$. \hspace{1cm} (3.21 b)

2. Diagram (b) applies if and only if
   $\beta < 2 \alpha$ and $\rho \leq \frac{1}{3} (\alpha + \beta) < \rho < \alpha$. \hspace{1cm} (3.22)

3. Diagram (c) applies if and only if
   $\beta \geq 2 \alpha$ and $\rho = \alpha$. \hspace{1cm} (3.23)

4. Diagram (d) applies if and only if
   $\beta < 2 \alpha$ and $\rho = \alpha$. \hspace{1cm} (3.24)

which is equivalent to Ewens’ (1967) equation (15) if, in his equation, $\text{w}$ is replaced by our $\frac{\text{w}}{1-m}$. In analogy to Ewens (1967), we may draw two important conclusions from equation (14):

1. In cases where $\frac{\text{w}}{1-m}$ lies between $w_1$ and $w_2$, i.e. when $(1-m)w_1 < \frac{\text{w}}{1-m} < (1-m)w_2$ or when
   $(1-m)w_2 < \frac{\text{w}}{1-m} < (1-m)w_1$, and if $\frac{\text{w}}{1-m} > q w_1 + (1-q) w_2$, condition (14) assumes the form $r < r_0$, where $r_0$ is a positive constant. Thus, there will be cases where the frequency of $A_1$ will increase (i.e. where $\lambda_1 > 1$) only if $r < r_0$, i.e. if the $A$ locus is sufficiently closely linked to the $B$ locus. This result was already obtained by Bodmer and Parsons (1962) for the case without migration.

2. If we assume $r > r_0$, with $r_0$ a positive constant, it can be shown after some algebra that equation (14) implies $\frac{\text{w}}{1-m} < w_1$ and $\frac{\text{w}}{1-m} < w_2$. Therefore, if $r > r_0$, there is no case where decreased linkage is necessary for $A_1$ to increase in frequency.

As a comment (already made by Ewens 1967), notice that the above statements will also hold true in the stochastic case. However, there may be cases in the stochastic setting where decreased linkage is more favourable to survival probability than tight linkage (this does not mean that survival probability is zero as $r \to 0$, though).
5. Diagram (e) applies if and only if

\[ \beta < 2 \alpha \text{ and } \alpha < \rho \leq 3 \beta - \alpha - 2 \sqrt{2} \sqrt{\beta (\beta - \alpha)} \] (3.25)

6. Diagram (f) applies if and only if

\[ \beta < 2 \alpha \text{ and } 3 \beta - \alpha - 2 \sqrt{2} \sqrt{\beta (\beta - \alpha)} < \rho < 3 \alpha - \beta \] (3.26)

7. Diagram (g) applies if and only if

\[ \beta \geq 2 \alpha \text{ and } \rho > \alpha \] (3.27 a)

or

\[ \beta < 2 \alpha \text{ and } \rho \geq 3 \alpha - \beta \] (3.27 b)

It is important to remember that the conditions above apply to the continuous-time version of the model. Hence, for the discrete-time version discussed here, they only provide approximate conditions. The approximations are good as long as the evolutionary forces are weak (i.e. \( \epsilon \ll 1 \)).

### Implementation

```mathematica
In[33]:= mCritC::usage = "mCritC is the critical migration rate \( m_C \) characterising the properties of the model."
mCritC::usage = "\( m_C \) characterising the properties of the model."
mCritA::usage = "mCritA is the critical migration rate \( m_A \) characterising the properties of the model."
mCritB::usage = "mCritB is the critical migration rate \( m_B \) characterising the properties of the model."

In[39]:= existenceEB::usage = "existenceEB[b_, m_] returns 'True' if the equilibrium \( E_B \) exists."];
existenceEB[b_, m_]:=Return[0<m<b]

In[41]:= unstabilityEB::usage = "unstabilityEB[a, b, r, m] returns 'True' if the equilibrium \( E_B \) is unstable."];
unstabilityEB[a_, b_, r_, m_]:=Module[{mb},
  mb=a\( 1+\frac{b-a}{r} \);
  Return[0<m<\text{Min}[mb,b]]
]```
Stochastic analysis (multi-type branching process)

Formulation in terms of probability generating functions

For the stochastic treatment, we are interested in the expected number of offspring of each type produced by an i-type parent. These expectations are given by the mean matrix $G^T = L = \begin{pmatrix} \mu_{11} & \mu_{12} \\ \mu_{21} & \mu_{22} \end{pmatrix}$. Denote the expected number of j-type offspring produced by an i-type parent by $\mu_{ij}$.

\[
\text{MatrixForm}[G[1]]
\]

\[
\begin{pmatrix}
\mu_{11} & \mu_{12} \\
\mu_{21} & \mu_{22}
\end{pmatrix}
\]

\[
\mu_{ij} = G[i][j] \quad \text{(* Notice the inverted order of indices! $\mu_{ij}$ is the number of offspring of type j produced by a parent of type i. On the other hand, $G[i][j]$ is the number of offspring of type i produced by a parent of type j. In both cases, i is the index for the rows and j is the index for the columns. *)}
\]
\[ \mu[1, 1, 1] \]
\[
(1 - m[1]) \frac{(w1[1] - r (1 - q[1]) w14[1])}{wbar[1]}
\]
\[ \mu[1, 2, 1] \]
\[
r (1 - m[1]) (1 - q[1]) w14[1] \]
\[ wbar[1] \]
\[ \mu[2, 1, 1] \]
\[
r (1 - m[1]) q[1] w14[1] \]
\[ wbar[1] \]
\[ \mu[2, 2, 1] \]
\[
(1 - m[1]) (-r q[1] w14[1] + w2[1]) \]
\[ wbar[1] \]

In the manuscript, we use \( \lambda_{ij} \) instead of \( \mu_{ij} = g_{ij} \) (\( i, j \in \{1, 2\} \)). We assume that the number of offspring of each type produced by a parent of a given type follows a Poisson distribution, and that the distribution is independent for each type. The latter is a crucial assumption and may not be justified in organisms that have a small number of offspring, so that the number of offspring of each type produced by a certain parent may well be (negatively) correlated! [However, offspring distributions other than the Poisson, e.g. the negative-binomial distribution suitable for organisms like humans, do not have probability generating functions (pgf) that are mathematically as tractable as that of the Poisson distribution.]

The pgfs belonging to the distribution of the number of offspring of type \( j \) produced by a single \( i \)-type parent are

\[ f_i(s) = \sum_{k=0}^{\infty} P(X_i = k) s^k = e^{-\mu_i(1-s)} (i, j = 1, 2), \] (15)

where the last equality holds due to the definition of the pgf for the Poisson distribution. Because we assume that the numbers of offspring of the different types produced by an \( i \)-type parent are independent, we have

\[ f_i(s_1, s_2) = \sum_{k_1=0}^{\infty} \sum_{k_2=0}^{\infty} P(X_{i1} = k_1, X_{i2} = k_2) s_1^{k_1} s_2^{k_2} = \prod_{j=1}^{2} \sum_{k_j=0}^{\infty} P(X_{ij} = k_j) s_j^{k_j} = \prod_{j=1}^{2} f_i(s_j), \] (16)

where the second equality holds because of the assumption of independent distributions of the different offspring types. Specifically, for the Poisson distribution of offspring number, we obtain

\[ f_i(s_1, s_2) = \prod_{j=1}^{2} e^{-\mu_j(1-s_j)} = e^{\sum_{j=1}^{2} -\mu_j(1-s_j)} \] (17)

Standard branching-process theory (e.g. Theorem 7.1 in Harris 1963) asserts the following:

- if \( \lambda_1 \leq 1 \), the probability of ultimate joint extinction of all types (of the \( A_1 \) mutation in our case) is 1. The multi-type branching process is called subcritical if \( \lambda_1 < 1 \) and critical if \( \lambda_1 = 1 \).
- if \( \lambda_1 > 1 \), and if we denote by \( Q_1 (Q_2) \) the probability of ultimate extinction of the \( A_1 \) mutant when the initial \( A_1 \) mutant occurred as an \( A_1 B_1 \) (\( A_1 B_2 \) ) gamete, then \( Q_1 \) and \( Q_2 \) are the smallest positive solutions of

\[ s_i = f_i(s_1, s_2) \ (i = 1, 2), \] (18)

or, in explicit terms, using the particular pgf belonging to the Poisson distribution,

\[ s_1 = e^{-\mu_1(1-s_1)+\mu_2(1-s_2)} \]
\[ s_2 = e^{-\mu_1(1-s_1)+\mu_2(1-s_2)}. \] (19)
Additive fitness model

Deterministic analysis

- Critical migration and recombination rates

In this subsection, we consider the additive fitness regime.

We first consider the critical values for \( m_1 \) and \( r \) obtained under the continuous-time model by Bürger and Akerman (2011), which provide an approximation to the critical values valid for the discrete-time version. Then, we consider the exact values for the discrete-time version, as partly described in Akerman (2011, technical report; see her equation for \( m_{\text{crit},5} \) just after her equation (22)).

- Continuous-time version (approximate critical values)

Critical migration rate \( m_{B,1} \) as a function of the recombination rate \( r \) and the selection coefficients. This function is an approximation, valid for weak evolutionary forces only. This is because we here consider a discrete-time model, whereas the approximation below was obtained under the continuous-time model.

```mathematica
In[48]:= mCritApproxFunc::usage = "mCritApproxFunc[r, a, b] returns the critical migration rate ;
mCritApproxFunc[m_\_\_\_, a_, b_] := Module[{mcrit}, 
mcrit = a*(1 - b - a)/r; (* This is equation (3.11) of Bürger and Akerman (2011). *) 
Return[Min[mcrit, b]]] (* This corresponds to equation (4.12) of Bürger and Akerman (2011). *)"
```

Critical migration rate \( m_{\text{crit}} \) as a function of the recombination rate \( r_{B,1} \) and the selection coefficients. This function is an approximation, valid for weak evolutionary forces only (again, it is valid for the continuous-time model, whereas here, we consider the discrete-time model).

```mathematica
In[49]:= rCritApproxFunc::usage = "rCritApproxFunc[m, a, b] returns the critical recombination r;
rCritApproxFunc[m, a, b] := Module[{rcrit, res}, 
rcrit = a*b/(b - a)/m; (* This is equation (4.15) of Bürger and Akerman (2011). *) 
(* We assume that a \( \leq \) b! This must not be violated by the arguments. *) 
res = If[rcrit > 0.5, 0.5, If[rcrit < 0, 0, rcrit]]; 
res = If[rcrit < 0, 0, rcrit]; 
Return[res]]"
```

- Discrete-time version (exact critical values)

Critical migration rate \( m_{B,1} \) as a function of the recombination rate \( r \) and the selection coefficients. This function is exact and corresponds to the equation after equation (22) in Akerman (2011). For a detailed analysis of the deterministic model in discrete time, see the Mathematica Notebook "2LocContIsland_Det_Discr.nb".

```mathematica
In[50]:= mCritFunc::usage = "mCritFunc[r, a, b] returns the critical migration rate \( m_{\text{crit}} \) for the;
mCritFunc[r, a, b] := Module[{mcrit1, mcrit2, mcrit3, mcrit5, res},
mcrit1 = a; 
mcrit2 = b; (* This is the critical value derived above, and also given in Akerman (2011). *) 
mcrit3 = a + b - r; (* This is given in Akerman (2011); the continuous-time analog is \( m_c \) in B Büger and Akerman, 2011. *) 
mcrit5 = (a - b)*r; (* This is the equation after equation (22) in Akerman (2011) *) 
(* res = If[mcrit5 < 0, Min[mcrit2, Min[mcrit2, mcrit5]], Max[mcrit1, mcrit3]]; *) 
(* res = If[rcrit < 0, mcrit2, Max[Min[mcrit2, mcrit5], Max[mcrit1, mcrit3]]]; *) 
res = If[r < a, mcrit2, If[a < r < b, mcrit5, Max[mcrit1, max[mcrit5]]]; 
Return[res]]"
```

Next, we construct a function of the migration rate \( m \) that gives the recombination rate below which \( A_1 \) can invade. For this purpose, we note that \( r < 0.5 \) must hold always. Setting \( m = m_{\text{crit},5} = f(r) \) and solving for \( r \) yields a function of \( m \) that intersects twice with \( r_{B,1} \) and that Critical recombination rate \( r_{B} \) as a function of the migration rate \( m_{B,1} \) and the selection coefficients. This function is exact and can be
derived from the equation for the critical migration rate \( m_{\text{crit},5} \) given in the equation after equation (22) in Akerman (2011) follows.

\[
\text{mCrit5} := \frac{a (b - a + r)}{(a-b) (a-r) + r (1-a)};
\]

(* Equation below equation (22) in Akerman (2011). This corresponds to the continuous-time analog \( m_b \) in Bürger and Akerman (2011) *)

The numerator of \( m_{\text{crit},5} \), \((b - a + r)\) is always positive under our assumptions of \(0 < a < b\) and \(0 < r < 0.5\). For \( m_{\text{crit},5} \) to be a valid migration rate, it is necessary that the denominator is positive:

\[
\text{FullSimplify}[\text{Reduce}[\{(a-b) (a-r) + r (1-a) > 0, r\}}, \text{Assumptions} \rightarrow \{(0 < r < 1/2, 0 < a < b, a+b < 1, 0 < m < 1)\}]
\]

\[
a^2 + r + b r > a (b + 2 r)
\]

\[
\text{FullSimplify}[\text{Reduce}[0 < \text{mCrit5} < 1], \text{Assumptions} \rightarrow \{(0 < r < 1/2, 0 < a < b, a+b < 1, 0 < m < 1)\}]
\]

\[
2 a \leq r | | 2 a^2 + r + b r > 2 a b + 3 a r
\]

\[
 \text{xCrit5Rule} := \text{FullSimplify}[[\text{Solve}[m = \text{mCrit5}, r], \text{Assumptions} \rightarrow \{(0 < r < 1/2, 0 < a < b, a+b < 1, 0 < m < 1)\}]
\]

\[
\text{xCrit5} := r \cdot \text{xCrit5Rule}
\]

\[
\text{FullSimplify}[\text{Reduce}\left\{\frac{a *(a-b)*(1+m)}{a+2*a+m-(1+b)*m} \leq \frac{1}{2}, m\right\}, \text{Assumptions} \rightarrow \{(0 < r < 1/2, 0 < a < b, a+b < 1, 0 < m < 1)\}]
\]

\[
m + b m < a + 2 a m | | m + b m + 2 a^2 (1+m) \geq a (1+2 m + 2 b (1+m))
\]

\[
\text{Solve}[m + b m = a + 2 a m, m]
\]

\[
\{\{m \rightarrow a \over 1-2 a+b\}\}
\]

\[
\text{Solve}[m + b m + 2 a^2 (1+m) = a (1+2 m + 2 b (1+m)), m]
\]

\[
\{\{m \rightarrow a - 2 a^2 + 2 a b \over 1-2 a+2 a^2+b-2 a b\}\}
\]

\[
\text{FullSimplify}[\text{Reduce}\left\{\frac{a - 2 a^2 + 2 a b}{1-2 a+2 a^2+b-2 a b} > \frac{a}{1-2 a+b}, \text{Assumptions} \rightarrow \{(0 < r < 1/2, 0 < a < b, a+b < 1, 0 < m < 1)\}\right\}]
\]

\[
\text{True}
\]

\[
\text{FullSimplify}[\text{Reduce}\left\{\frac{a - 2 a^2 + 2 a b}{1-2 a+2 a^2+b-2 a b} = \frac{a}{1-2 a+b}, \text{Assumptions} \rightarrow \{(0 < r < 1/2, 0 < m < 1)\}\right\}]
\]

\[
(1 + b \neq 0 \&\& (a = 0 | | a = 1 + b)) | | (a = b \&\& b \neq 1)
\]

The first solution is always smaller than the second unless \(a \geq b\), which is excluded by our assumptions. To see this, note that the numerator of the second solution is strictly larger than the numerator of the first solution, whereas the denominator of the second solution is strictly smaller than the denominator of the first solution. Therefore, whenever \( m < \frac{a-2a^2+2ab}{1-2a+2a^2+b-2ab} \) holds, \( r_{\text{crit},5} > 0.5 \) and our desired function must be truncated at 0.5.

In summary, our function \( f_{\text{lim}}(m) \) of \( m \) is defined as follows:

\[
f_{\text{lim}}(m) = \begin{cases} 
0.5 & m \leq m_{\text{crit}} \\
\frac{a - 2a^2 + 2ab}{1 - 2a + 2a^2 + b - 2ab} & m > m_{\text{crit}}
\end{cases}
\]

where \( m_{\text{crit}} = \frac{a - 2a^2 + 2ab}{1 - 2a + 2a^2 + b - 2ab} \) and \( r_{\text{crit},5} = \frac{a(b - a + r)}{(a-b)(a-r) + r(1-a)} \)
In[55]:= rCritFunc::usage = "rCritFunc[m, a, b] returns the critical recombination rate \( r_{crit} \) for
rCritFunc[m_, a_, b_] := Module[{rmax, rcrit5, mThresh, mm},
  rmax = 0.5; (* This is the maximum recombination rate that is biologically plausible in t
  \( r_{crit} = \frac{a*(a-b)*(1+m)}{a+2*a*m-(1+b)*m} \);
  (* This is obtained from solving \( m = m_{crit,5} = f(r) \) for \( r \). *)
  rcrit5 = a*(a-b)*(1+m)
  a+2*a*m-(1+b)*m
  mThresh = \frac{a-2}{a^2+b-2} a b
  (* If \( m \) is below this value, \( r \) is above 0.5. *)
  res = If[m > mThresh, rmax, rcrit5];
  Return[res];]

Critical values for the migration rate for the stability of the equilibrium \( E_C \).

In[57]:= mCrit1 := \frac{a}{1 - b}; (* Equation at the beginning of section 2.3

in Akerman (2011). The corresponding criterion in the continuous-
time version in Bürger and Akerman (2011) is \( a \). *)

mCrit2 := \frac{b}{1 - a}; (* Equation at the beginning of section 2.3 in

Akerman (2011). The corresponding criterion in the continuous-
time version in Bürger and Akerman (2011) is \( b \). *)

mCrit3 := \frac{a + b - r}{1 - r}; (* Equation at the beginning of section 2.3

in Akerman (2011). The corresponding criterion in the continuous-
time version in Bürger and Akerman (2011) is \( m_C \) given in their equation (3.4). *)

When plotting, and most likely in a future manuscript, mCrit1, mCrit2, mCrit3 and mCrit5 will be called \( m', m'', m_C \) and \( m_B \). It is then important to point out to the reader the difference between the discrete and the continuous-time versions (cf. Bürger and Akerman (2011)).

**Marginal one-locus equilibrium**

Here, we derive the marginal one-locus migration-selection equilibrium at locus \( \beta \). The assumption is that the \( A_1 \) allele has not yet occurred, such that there are only two haplotypes present, \( A_2 B_1 (x_3) \) and \( A_2 B_2 (x_4) \). In this case, \( x_3 = q_1 \) and \( x_4 = 1 - q_1 \), where \( q_1 \) is the frequency of the \( B_1 \) allele on the island (in deme 1).

**Definitions**

(*) Marginal relative fitness of gamete \( i \) in deme \( n \) alleles at the \( B \) locus if \( A_1 \) is rare

\[ w_{MargB[i,j,n]} := \text{Sum}[w[n][i,j]x[j,n],(j,3,4)] \] (* Here, \( i \) is the index of the \( B \) allele, \( i = 0 \) if \( A_1 \) is common in the deme \).

(*) Recursion equation (selection followed by migration) for the allele frequencies at \( t \):

\[ w_{MargB[i,j,n]} := M[n,1]w_{MargB[i,1]} + \text{wMeanB[1]*x[1,1]} + M[n,2]w_{MargB[i,2]} + \text{wMeanB[2]*x[1,2]} \] (* \( i = 1 \) for \( A_1 \) )

(*) Generic fitness interaction between alleles within a gamete, additive fitness interaction:

\[ w_{MargB[i,j,n]} := \text{w33[n]*v3[n]+v3[n], w34[n]*v3[n]+v4[n], w44[n]*v4[n]} \] (* Generic fitness interaction between alleles within a gamete, multiplicative fitness:

\[ w_{MargB[i,j,n]} := \text{w33[n]*v3[n]*v3[n], w34[n]*v3[n]*v4[n], w44[n]*v4[n]} \] (* Additive fitness interactions between alleles within a gamete, multiplicative fitness:

\[ w_{MargB[i,j,n]} := \text{w33[n]*(1-a[n])*(1-b[n]), w34[n]*(1-a[n]), w44[n]} \] (* Additive fitness interactions between alleles within a gamete, multiplicative fitness:

\[ w_{MargB[i,j,n]} := \text{w33[n]*(1-a[n]+b[n]), w34[n]*(1-a[n]), w44[n]} \] (* Additive fitness interactions between alleles within a gamete, multiplicative fitness:

\[ w_{MargB[i,j,n]} := \text{w33[n]*(1-a[n]+b[n]), w34[n]*(1-a[n]), w44[n]} \]

**Frequency of the \( B_1 \) allele in deme 1 (island) at the migration-selection equilibrium**

For completeness, we also investigate in this paragraph other fitness schemes than the purely additive one.
Recall that \( x_{3n} = q_n \) and \( x_{4n} = 1 - q_n \).

Generic relative fitnesses:

\[
\text{qEquillIBGeneric} = \text{Solve[}
\{\text{recB}[3, 1] /. \text{assumeCI} /. \text{assumeMonomorphContin} /. \text{assumeAllRare[1] // FullSimplify} = q[1], q[1] \}
\]

\[
\text{FullSimplify[}
\text{Reduce[}\{0 < q[1] /. \text{qEquillIBGeneric[2]} \&\& (q[1] /. \text{qEquillIBGeneric[2]} < 1), m[1], \text{Assumptions} \rightarrow \{0 < m[1] < 1 \&\& 0 < w33[1] \&\& 0 < w44[1] \&\& w33[1] > w34[1] > w44[1]\} \]
\]

Generic interactions between alleles within a haplotype, additive fitness interactions across haplotypes:

\[
\text{qEquillIBGenericAdditive} = \text{Solve[}\{\text{recB}[3, 1] /. \text{assumeCI} /. \text{assumeMonomorphContin} /. \text{assumeAllRare[1] /. assumeGenericAdditiveFitnessB[1] // FullSimplify} = q[1], q[1] \} \}
\{q[1] \rightarrow 0\}, \{q[1] \rightarrow 1 + \frac{2 m[1] v3[1]}{(1 + m[1]) (-v3[1] + v4[1])}\} \}
\]

Conditions for admissibility of the above equilibrium:

\[
\text{FullSimplify[Reduce[}
\{0 < q[1] /. \text{qEquillIBGenericAdditive[2]} \&\& (q[1] /. \text{qEquillIBGenericAdditive[2]} < 1), m[1], \text{Assumptions} \rightarrow \{0 < m[1] < 1 \&\& v3[1] > v4[1] > 0\} \}
\]

Or, equivalently, for \( q \) to be admissible and describe a polymorphic equilibrium, we require

\[
m_1 < \frac{v_3 - v_4}{v_3 + v_4}\]

Generic interactions between alleles within a haplotype, multiplicative fitness interactions across haplotypes:
For \( q \) to be admissible and describe a polymorphic equilibrium, we require

\[ m_1 < b_1 \]

Additive interactions between alleles within a haplotype, multiplicative fitness interactions across haplotypes:

\[
q_{\text{Equil1BAdditiveMultiplic}} = \text{Solve}[\{\text{recB}[3,1] /\text{. assumeCI} / \text{. assumeMonomorphContin} / \text{. assumeAlRare}[1] / \text{. assumeAdditiveMultiplicFitnessB}[[1] / \text{FullSimplify}) = q[1], q[1]]
\]

\[
\left\{ \left\{ q[1] \to 0 \right\}, \left\{ q[1] \to 1 + \frac{m[1]}{v3[1] + v4[1]} \right\} \right\}
\]

Conditions for admissibility of the above equilibrium:

\[
\text{FullSimplify}[\text{Reduce}[[0 < (q[1] / \text{qEquil1BAdditiveMultiplic}[2]) \&\& (q[1] / \text{qEquil1BAdditiveMultiplic}[2]) < 1), m[1]], \text{Assumptions} \to \{0 < m[1] < 1 \&\& v3[1] < v4[1] > 0\}]
\]


Or, equivalently, for \( \hat{q} \) to be admissible and describe a polymorphic equilibrium, we require

\[
m_1 < \frac{v_3 - v_4}{v_3}.
\]

Additive interactions between alleles within a haplotype, multiplicative fitness interactions across haplotypes:

\[
q_{\text{Equil1BAdditiveMultiplicApprox}} = \text{Solve}[\{\text{recB}[3,1] /\text{. assumeCI} / \text{. assumeMonomorphContin} / \text{. assumeAlRare}[1] / \text{. assumeAdditiveMultiplicFitnessApproxB}[[1] / \text{FullSimplify}) = q[1], q[1]]
\]

\[
\left\{ \left\{ q[1] \to 0 \right\}, \left\{ q[1] \to 1 + \frac{b[1] - m[1]}{b[1] (1 + m[1])} \right\} \right\}
\]

Conditions for admissibility of the above equilibrium:

\[
\text{FullSimplify}[\text{Reduce}[[0 < (q[1] / \text{qEquil1BAdditiveMultiplicApprox}[2]) \&\& (q[1] / \text{qEquil1BAdditiveMultiplicApprox}[2]) < 1), m[1]], \text{Assumptions} \to \{0 < m[1] < 1 \&\& 0 < b[1] < 1\}]
\]

\[ b[1] > m[1] \]

For \( \hat{q} \) to be admissible and describe a polymorphic equilibrium, we require

\[
m_1 < b_1
\]

Additive interactions between alleles within a haplotype, multiplicative fitness interactions across haplotypes, and weak allelic effects (called ‘additive’ in the rest of the Notebook):

\[
q_{\text{Equil1BAdditiveMultiplicApprox}} = \text{Solve}[\{\text{recB}[3,1] /\text{. assumeCI} / \text{. assumeMonomorphContin} / \text{. assumeAlRare}[1] / \text{. assumeAdditiveMultiplicApproxFitnessB}[[1] / \text{FullSimplify}) = q[1], q[1]]
\]

\[
\left\{ \left\{ q[1] \to 0 \right\}, \left\{ q[1] \to 1 + \frac{a[1] m[1]}{b[1] (1 + m[1])} \right\} \right\}
\]

Conditions for admissibility of the above equilibrium:

\[
\text{FullSimplify}[\text{Reduce}[[0 < (q[1] / \text{qEquil1BAdditiveMultiplicApprox}[2]) \&\& (q[1] / \text{qEquil1BAdditiveMultiplicApprox}[2]) < 1), m[1]], \text{Assumptions} \to \{0 < m[1] < 1 \&\& 0 < a[1] < b[1] \}]
\]

\[ a[1] < b[1] \]

For \( \hat{q} \) to be admissible and describe a polymorphic equilibrium, we require (as long as \( a_1 < 1 \)):

\[
m_1 < \frac{b_1}{1 - a_1}
\]

A comparison to Akerman (2011), second equation in subsection 2.3 (Strong migration), verifies this result.
Stochastic analysis (multi-type branching process)

- Explicit probability generating functions

Remark: For an analogous implementation for multiplicative fitnesses, see the Mathematica Notebook 120309_twoLocusContinentIslandDiscrStochastic.nb

\[ p_{\text{gf}}[l_, n_] := \text{Exp}\left[\sum_{j=1}^{n} -\mu[i, j, n] (1 - s[j])\right] \]

\[ \text{pgf}[1, 1] \]

\[ \text{pgf}[2, 1] \]

Implementation for the following scheme of relative fitnesses:

\[ w[1] / . \text{assumeAdditiveMultiplicEpistaticApproxFitness}[1] // \text{MatrixForm} \]

\[ q[1] / . \text{qEquilibriumAdditiveMultiplicApproxFitness}[2] \]

The function that finds a numerical solution for the probability of establishment should take the following parameters:

- \( a_i \): Twice the additive selective advantage of \( A_i \) compared to \( A_j \) in deme 1 (island)
- \( b_i \): Twice the additive selective advantage of \( B_i \) compared to \( B_j \) in deme 1 (island)
- \( \gamma_{kl} \): The epistatic coefficient if there are \( k \) epistatic interactions present at the first locus and \( l \) at the second in deme 1, where \( k, l = 1, 2 \)
- \( m_i \): The proportion of individuals in deme 1 (island) replaced every generation by immigrants from deme 2 (continent)
- \( r \): The recombination frequency between loci A and B.

Further ingredients needed for the implementation:

\[ w\text{MeanB}[1] / . \text{assumeAdditiveMultiplicEpistaticApproxFitness}[1] / . \text{assumeAlRare}[1] // \text{FullSimplify} \]

\[ \text{wMargType}[1, 1] / . \text{assumeAdditiveMultiplicEpistaticApproxFitness}[1] / . \text{assumeAlRare}[1] \]

\[ \text{FullSimplify}[] \]

\[ \text{wMargType}[2, 1] / . \text{assumeAdditiveMultiplicEpistaticApproxFitness}[1] / . \text{assumeAlRare}[1] \]

\[ \text{FullSimplify}[] \]

\[ \text{w}[1][1, 4] / . \text{assumeAdditiveMultiplicEpistaticApproxFitness}[1] \]

\[ 1 - \gamma_{11[1]} \]
\[ q_{\text{EquillBAdditiveMultiplicApprox}[2]} \]
\[
\{ q[1] \to \frac{b[1] - m[1] + a[1] m[1]}{b[1] (1 + m[1])} \}
\]

```
   assumeAdditiveMultiplicEpistaticApproxFitness[1] /.
   assumeAlRare[1] /.
   w[1] \to wMargType[1, 1] /.
   assumeAdditiveMultiplicEpistaticApproxFitness[1] /.
   assumeAlRare[1] /.
   (\gamma[1][1] \to 0, \gamma[12][1] \to 0, \gamma[21][1] \to 0, \gamma[22][1] \to 0) /.
   (a[1] \to a, b[1] \to b,
   m[1] \to m, s[1] \to s_1, s[2] \to s_2) // FullSimplify
```

```
Out[68]=
\[ e^{\frac{b^2 (1 + s_1) + (-1 + a) m r (s_1 - s_2) + b (-1 + a m (-1 + s_1 + s_1 - m r s_1 + m r s_2))}{(s_1, s_2)}} \]
```

```
   assumeAdditiveMultiplicEpistaticApproxFitness[1] /.
   assumeAlRare[1] /.
   w[2] \to wMargType[2, 1] /.
   assumeAdditiveMultiplicEpistaticApproxFitness[1] /.
   assumeAlRare[1] /.
   (\gamma[1][1] \to 0, \gamma[12][1] \to 0, \gamma[21][1] \to 0, \gamma[22][1] \to 0) /.
   (a[1] \to a, b[1] \to b,
   m[1] \to m, s[1] \to s_1, s[2] \to s_2) // FullSimplify
```

```
Out[69]=
\[ e^{\frac{(-1 + a) m r (s_1 - s_2) + b^2 (m - m s_2) + b (-1 + r s_1 + a m (-1 + s_2) + s_2 - r s_2))}{(s_1, s_2)}} \]
```

```
In[70]:= Collect[\[\frac{b^2 (1 + s_1) + (-1 + a) m r (s_1 - s_2) + b (-1 + a m (-1 + s_1 + s_1 - m r s_1 + m r s_2))}{(s_1, s_2)}\] - b - b^2 - a b m + (b + b^2 + a b m + (-1 + a) m r - b m r) s_1 + ((1 - a) m r + b m r) s_2] // FullSimplify
```

```
Out[70]=
\[ \frac{b^2 (1 + s_1) + (-1 + a) m r (s_1 - s_2) + b (-1 + a m (-1 + s_1 + s_1 - m r s_1 + m r s_2))}{(s_1, s_2)} \]
```

**Implementation of numerical solution**

\((*\text{Solve}[\text{pgf1Add}=s1&&\text{pgf2Add}=s2,\{s1,s2\}]*\)
In[70]:= probEstablamApproxFunc::usage = "probEstablamApproxFunc[r, m1, a1, b1, y111, y121, y211
probEstablamApproxFunc[r_, m1_, a1_, b1_, y111_, y121_, y211_] := Module[{
(qEq, wbar, w1, w2, qEq=(b1-m1+a1m1)/(b1*(1+m1)); (* Verified by equation (22) in Akerman (2011), subsecti
wbar=1-a1-b1*(-1+2*qEq);
w1=1+b1+qEq*(1-qEq)*y111;
w2=1+b1*(-1+qEq)*y111+y121*(-1+qEq);
w1d=1-y111;
(* Leading eigenvalue of the mean matrix *)
λ1= -1 
* (1+qEq)*y111+y121*(-1+qEq);
(* Probability generating functions *)
pgf1[s1_,s2_]:=Exp[(r*(1-m1)*qEq*(1-s1)+w14*(1-m1)*(1-s1)+(w1-r*(1-qEq)*w14)]
pgf2[s1_,s2_]:=Exp[-r*(1-m1)*qEq*(1-s1)+w14*(1-m1)*(1-s2)+(-r*qEq+w14+w2)]
qSol=FindRoot[{pgf1[q1,q2]=q1,pgf2[q1,q2]=q2},{q1,0.5},{q2,0.5}];
(* Return the probability of establishment, 1-q *)
Return[(λ1,(1-q1),(1-q2),qEq*(1-q1)*(1-q2),qEq/.qSol]
];
(* Rules for the specific model considered *)
rulesCl[n_]:=(wbar[n]+wMeanB[n],w1[n]+wMargType[1,n],w2[n]+wMargType[2,n],w14[n]+w[n]]
];
In[73]:= GAdditiveMultiplicEpistaticApprox[n_]:= (G[n] /. rulesCI[n] /. assumeAdditiveMultiplicEpistaticApproxFitness[n] // Expand) /. assumeAllRare[n] // FullSimplify
GAdditiveMultiplicEpistaticApprox[1] // MatrixForm
(* This takes some time to evaluate *)
assumeAlRare[1]
{x[3,1] -> q[1], x[4,1] -> 1-q[1]}
Test of the above function probEstablamApproxFunc[r_,m1_,a1_,b1_,y111_,y121_,y211_,y221_]:

Clear[myr, myml, myal, myb1, myy111, myy121, myy211,
myy221, myEq, mywbar, myw1, myw2, myw14, myal, mypgf1, mypgf2]
myr = 0.008;
myml = 0.015;
myal = 0.01;
myb1 = 0.02;
myy111 = 0.;
myy121 = 0.;
myy211 = 0.;
myy221 = 0.;
myy221 = 0.;
myEq = (myb1 - myml + myal * myml) / (myb1 * (1 + myml));
mywbar = 1 - myal - myb1 * (1 - 2 * myEq);
myw1 = 1 + myb1 myEq + (-1 + myEq) myy111;
myw2 = 1 + myb1 * (1 - myEq) - myEq * myy111 - myy121 * (1 - myEq);
myw14 = 1 - myy111;
my\alpha_1 = - \frac{1}{2} \frac{(-1 + my\alpha_1)}{my\betabar} \left( myw1 - myr myw14 + myw2 + \left( myw1^2 + myr^2 myw14^2 + myw1 \left( 2 (-1 + 2 myEq) myr myw14 - 2 myw2 \right) + \right. \left. 2 \left( 1 - 2 myEq \right) myr myw14 myw2 + myw2^2 \right)^{1/2} \right);

mypgf1[s1_, s2_] := \text{Exp} \left[ \frac{myr (1 - my\alpha_1) myEq (1 - s2) myw14}{my\betabar} \right. \\
\left. \frac{1}{my\betabar} \frac{(1 - my\alpha_1) (1 - s1) (myw1 - myr (1 - myEq) myw14)}{myw14} \right];

mypgf2[s1_, s2_] := \text{Exp} \left[ \frac{myr (1 - my\alpha_1) (1 - myEq) (1 - s1) myw14}{my\betabar} \right. \\
\left. \frac{1}{my\betabar} \frac{(1 - my\alpha_1) (1 - s2) (-myr myEq myw14 + myw2)}{myw14} \right];

qSol = \text{FindRoot}[(mypgf1[q1, q2] = q1, mypgf2[q1, q2] = q2), \{q1, 0.5\}, \{q2, 0.5\}];
\{1 - q1, 1 - q2\} /. qSol
\{0.00976312, 0.00413608\}

\text{probEstABLAMApproxFunc}[myr, my\alpha_1, my\alpha_1, myr11, myr111, myr121, myr211, myr221]
\{1.00478, 0.00993348, 0.00157342, 0.00369432, 0.253695\}

myEq \ast (1 - q1) + (1 - myEq) \ast (1 - q2) /. qSol
0.00556363

- Explicit equilibrium frequency of $B_1$

\text{Clear}[qhat, w1, w2, wbar, b, m, a, \gamma11, \gamma12, \gamma21, \gamma22]

\text{assumParamRelationsAdditiveMultiplicApproxFtn} = \{0 < a[n] < b[n] \leq m[n] < b[n]\}

\text{qhatAMApprox} = q[1] /. \text{qEquillBAAdditiveMultiplicApproxFtn}[2]

\text{b[1]} = \frac{m[1] + a[1] m[1]}{b[1] (1 + m[1])}

- Explicit fitnesses

\text{wbarAMApprox} = w\text{MeanB}[1] /. \text{assumeAdditiveMultiplicApproxFtn}[1] /. \text{assumeA1Rare}[1] // \text{FullSimplify}

\text{w1AMApprox} = w\text{MargType}[1, 1] /. \text{assumeAdditiveMultiplicApproxFtn}[1] /. \text{assumeA1Rare}[1] // \text{FullSimplify}

\text{w2AMApprox} = w\text{MargType}[2, 1] /. \text{assumeAdditiveMultiplicApproxFtn}[1] /. \text{assumeA1Rare}[1] // \text{FullSimplify}

\text{w14AMApprox}[n_] := 1

We evaluate the mean and marginal fitnesses at equilibrium.
\[ w1AMApprox /. \{ q[1] \to \text{qhatAMApprox} \} \] // FullSimplify
\[
1 + m[1]
\]

\[ w2AMApprox /. \{ q[1] \to \text{qhatAMApprox} \} \] // FullSimplify
\[
1 + (a[1] - b[1]) m[1] \\
1 + m[1]
\]

\[ \text{wbarAMApprox} /. \{ q[1] \to \text{qhatAMApprox} \} \] // FullSimplify
\[
(-1 + a[1] - b[1]) (-1 + m[1]) \\
1 + m[1]
\]

- **Explicit mean matrix**

The elements of the mean matrix for additive fitnesses:

\[
G[1] /. \text{ruleSimplifyNotationCI} \] // MatrixForm
\[
\begin{pmatrix}
\end{pmatrix}
\]

\[ \text{assumeAdditiveMultiplicativeApproxFitness[1]} \]
\[
\]

\[ \text{ruleSimplifyNotationCI} \]
\[
\{ m[1] \to m, x[1, 1] \to x1, x[2, 1] \to x2, x[3, 1] \to x3, x[4, 1] \to x4, q[1] \to q \}
\]

\[ GAdd = G[1] /. \text{ruleSimplifyNotationCI} /. \{ w[1]1[1] \to \text{w1AMApprox}, w[2]1[1] \to \text{w2AMApprox}, \text{wbar[1]} \to \text{wbarAMApprox} \} /. \text{assumeAdditiveMultiplicativeApproxFitness[1]} /. \{ q[1] \to \text{qhatAMApprox} \} /. \text{ruleSimplifyNotationCI} /. \{ a[1] \to a, b[1] \to b \} \] // FullSimplify;

\[ \text{GAdd} \] // MatrixForm
\[
\begin{pmatrix}
\frac{1 + b + a m}{1 - a + b} & \frac{m r}{b} & \frac{(b + (1-a) m) r}{b(1-a-b)} \\
\frac{m r}{b} & \frac{b^2 m (-1 + a) m + r (-1 - a + r)}{(-1 - a - b) b}
\end{pmatrix}
\]

\[ \text{GAdd} /. \{ a \to a e, b \to \beta e, m \to \mu e, r \to \rho e \}
\]
\[
\begin{pmatrix}
\frac{1 + e \beta + e^2 \mu - \mu \rho}{\beta}, & \frac{(\beta e + e (-1 + a e) \mu) \rho}{\beta (1 - a e + \beta e)} \\
\frac{e \mu \rho}{\beta}, & \frac{\beta^2 e^3 \mu + e^2 (-1 + a e) \mu \rho + \beta e (-1 - a e^2 \mu + e \rho)}{\beta e (-1 + a \ e - \beta e)}
\end{pmatrix}
\]

\[ \text{GAddApprox} = \text{Series} \left[ \left\{ \frac{1 + e \beta + e^2 \mu - \mu \rho}{\beta}, \frac{(\beta e + e (-1 + a e) \mu) \rho}{\beta (1 - a e + \beta e)} \right\}, \{ e, 0, 1 \} \right] \] /. \{ a \to a / e, \beta \to b / e, \rho \to r / e, \mu \to m / e \} // Normal;

\[ \text{GAddApprox} \] // MatrixForm
\[
\begin{pmatrix}
\frac{1 + a}{b} - \frac{m r}{b} & \frac{r - \frac{m r}{b}}{b} \\
\frac{\frac{n r}{b}}{b} & \frac{1 + a - b - r + \frac{m r}{b}}{b}
\end{pmatrix}
\]
Explicit conditions for invasion

\[
\text{conditionNonExtinction}[1] = \frac{\text{w1}[4] \left(-q[1] \text{w1}[1] - (1 - q[1]) \text{w2}[1] + \frac{\text{wbar}[1]}{1 - \text{m}[1]}\right) < \left(\text{w1}[1] - \frac{\text{wbar}[1]}{1 - \text{m}[1]}\right) \left(-\text{w2}[1] + \frac{\text{wbar}[1]}{1 - \text{m}[1]}\right)}{\text{w1}[1] - \frac{\text{wbar}[1]}{1 - \text{m}[1]}}
\]

\[
\text{conditionNonExtinctionAMApprox} = \text{conditionNonExtinction}[1] / \text{. (w1[4] \rightarrow \text{w1}[4] \text{AMApprox}[1], \text{wbar}[1] \rightarrow \text{wbar}[\text{AMApprox}], w1[1] \rightarrow w1[1 \text{AMApprox}, w2[1] \rightarrow w2[1 \text{AMApprox}] / . (q[1] \rightarrow qhat[\text{AMApprox}) // \text{FullSimplify}}
\]

\[
\frac{r \left(-a[1] + (1 - 2 a[1] + b[1]) m[1]\right)}{1 + m[1]} < a[1] \left(-a[1] + b[1]\right)
\]

We simplify the notation.

\[
\text{condNonExtAdd} = \text{conditionNonExtinctionAMApprox} / . \text{ruleSimplifyNotation}
\]

\[
\frac{-a + (1 - 2 a + b) m}{1 + m} < a (-a + b)
\]

We want to express this condition in terms of \(m\) and \(r\) to obtain critical values of these two parameters.

\[
\text{FullSimplify[Reduce[condNonExtAdd, m], Assumptions -> Flatten[\{0 < a < b < 1, a + b < 1, 0 < m < 1, 0 < r < 1/2\}]}
\]

\[
a^2 + r + br < a (b + 2 r) \quad | \quad a^2 + r + br = a (b + 2 r) \quad | \quad m < \frac{a (-a + b + r)}{a^2 + r + br - a (b + 2 r)}
\]

\[
m\text{Crit1}
\]

\[
\frac{a}{1 - b}
\]

\[
m\text{Crit2}
\]

\[
\frac{b}{1 - a}
\]

\[
m\text{Crit5}
\]

\[
\frac{(a - b) (a - r) + (1 - a) r}{a (-a + b + r)}
\]

\[
\frac{a^2 + r + br - a (b + 2 r)}{a^2 + r + br - a (b + 2 r)} - m\text{Crit5} // \text{Simplify}
\]

\[
0
\]

In terms of \(m\), we recover the critical value \(\frac{a b}{(a-b)(a-r)+(1-a)r}\) previously known as \(m_{\text{crit,5}}\), which was expected. Allele \(A_1\) can invade if \(m < m_{\text{crit,5}}\). The condition \(a^2 + r + br < a(b + 2r)\) implies that \(m_{\text{crit,5}} < 0\), meaning that invasion is possible independently of the migration rate \(m\). The condition \(a^2 + r + br = a(b + 2 r)\) denotes the degenerate case where \(m_{\text{crit,5}}\) is not defined, because its denominator is zero. In that case, invasion is also independent of \(m\).

We now ask about the condition in terms of the recombination rate.

\[
\text{FullSimplify[Reduce[condNonExtAdd, r], Assumptions -> Flatten[\{0 < a < b < 1, a + b < 1, 0 < m < m\text{Crit2}, 0 < r < 1/2\}]}
\]

\[
a + 2 a m = m + b m \quad | \quad m + b m < a + 2 a m \quad | \quad r < \frac{a (a - b) (1 + m)}{a + 2 a m - (1 + b) m}
\]

Again, the critical value \(\frac{a b}{a + 2 a m - (1 + b) m}\) for the recombination rate is equal to the one previously established for the deterministic model, \(r_{\text{crit,5}}\). The conditions \(a + 2 a m = m + b m\) and \(m + b m < a + 2 a m\) correspond to the cases where \(r_{\text{crit,5}}\) is not defined because its denominator is zero or where \(r_{\text{crit,5}}\) is negative, respectively. In both of these cases, the invasion criterion is independent
of $r$.

\[
\text{Solve}[m + b m = a + 2 a m, m]
\]

\[
\left\{\{m \rightarrow \frac{a}{1 - 2 a + b}\}\right\}
\]

\[
\text{Series}\left[\frac{a (-a + b + r)}{(a - b) (a - r) + (1 - a) r}\right] / . \{a \rightarrow a \epsilon, b \rightarrow b \epsilon, r \rightarrow \rho \epsilon\}, \{\epsilon, 0, 1\}\] // Normal
\]

\[
\epsilon \left(\frac{a - a^2}{\rho} + \frac{a \beta}{\rho}\right)
\]

\[
\text{Solve}\left[a - \frac{a^2}{\rho} + \frac{a \beta}{\rho} = \mu, \rho\right] // \text{FullSimplify}
\]

\[
\left\{\{\rho \rightarrow \frac{a (a - \beta)}{a - \mu}\}\right\}
\]

**Plots**

- **Helper rules**

Replacement rule for explicit fitness matrices.

```mathematica
```

The more compact 3x3 relative fitness matrix (showing no redundant combinations).

```mathematica
In[81]:= wCompact[n_] := ((w11[n], w12[n], w22[n]), (w13[n], w14[n], w24[n]), (w33[n], w34[n], w44[n]))
```

- **Plots for various parameter combinations ('regimes')**

- **Preliminaries**

Recall that the interesting case is $m_1 > a_1$. In this case, the $A_1$ mutant could never invade in a one-locus system. Combining with the other conditions, we have the following restriction for $m_1$: $0 < a_1 \leq m_1 \leq b_1 < 1$.

\[
0 < a_1 \leq m_1 \leq b_1 < 1
\]

```mathematica
Clear[myr, my, mya, myb, myy1temp, myy2temp,
     myy21temp, myy22temp, myyEq, myybar, myy1, myy2, myy14]
```

We first consider weak evolutionary forces, so that the approximate critical values are appropriate.

- **Weak evolutionary forces; migration rate $m = 0.022$**

```mathematica
mym = 0.022;
my = 0.02;
myb = 0.04;
mym1temp = 0.;
mym2temp = 0.;
mym21temp = 0.;
mym22temp = 0.;
rulFitness
wCompact[1] /. \text{assumeAdditiveMultiplicativeEpistaticApproxFitness[1]} /. \text{ruleFitness} //
MatrixForm
```

\[
\begin{pmatrix}
1.06 & 1.02 & 0.98 \\
1.04 & 1. & 0.96 \\
1.02 & 0.98 & 0.94
\end{pmatrix}
\]
rcritapprox = rCritApproxFunc[mym, mya, myb]
(* r must be lower than this critical value;
the value is a good approximation under the discrete-
time model only if evolutionary forces are weak! *)

0.2

rcrit = rCritFunc[mym, mya, myb] (* r must be lower than this critical value;
this value is exact under the discrete-time version of the model. *)

0.2044

Critical values for the migration rate for the stability of the equilibrium Ec.

mc1 = mCrit1 /. {a -> mya, b -> myb}
mc2 = mCrit2 /. {a -> mya, b -> myb}
mc3 = mCrit3 /. {a -> mya, b -> myb, r -> rCrit}

0.0208333

0.0408163

-0.181498

Critical value for the migration rate, m_b, as a function of r for the current parameter values.

Show[Plot[mCritFunc[r, mya, myb], {r, 0, 0.5}, PlotRange -> {{0, 0.5}, {0, mc2 + 0.1 + mc2}},
AxesLabel -> {r, "Critical migration rate m_b"}],
Plot[{mCritFunc[r, mya, myb], {r, 0, rCrit}},
PlotRange -> {{0, 0.5}, {0, mc2 + 0.1 + mc2}}, PlotStyle -> None, Filling -> {1 + mc1},
Graphics[{Gray, Dotted, Line[{{rCrit, 0}, {rCrit, mc2 + 0.1 + mc2}}]}],
Graphics[Text["r_b", {.025 + rCrit, 0.2 + mc2}]],
Graphics[{Gray, Dashed, Line[{{0.0, mc1}, {.5, mc1}}]}],
Graphics[Text["m'", {0.4, 0.9 + mc1}]],
Graphics[{Gray, Dashed, Line[{{0.0, mc2}, {.5, mc2}}]}],
Graphics[Text["m''", {0.4, mc2 - 0.1 + mc1}]]] (* This uses exact critical values *)

Recall: $m' = m_{crit,1} = \frac{1-a}{b}$, $m'' = m_{crit,2} = \frac{1-b}{a}$, and $m_b = m_{crit,5} = \frac{a(b-a+1)}{(a-b)(a-r)+(1-a)}$. 
plot1 = Show[Plot[{probEstablAMApproxFunc[r, mym, mya, myb, myy11temp, myy12temp, myy21temp, myy22temp][2], probEstablAMApproxFunc[r, mym, mya, myb, myy11temp, myy12temp, myy21temp, myy22temp][3], probEstablAMApproxFunc[r, mym, mya, myb, myy11temp, myy12temp, myy21temp, myy22temp][4]}, {r, 0, 0.5}, PlotRange -> {{0, rCrit}, {0, 2*mya}}, PlotStyle -> {{RGBColor[0.0, 0.3, 1, 0.5], Thick}, {Red, Thick}, {Black, Thick}}, Frame -> True, FrameStyle -> {{Black, Opacity[0]}, {Black, Opacity[0]}}, FrameLabel -> ("Recombination rate r", "Invasion probability"), LabelStyle -> (Directive[FontSize -> 14], FontFamily -> "Helvetica"), PlotLegend -> {Style["r_1, conditional on background B_1", FontFamily -> "Helvetica", 10], Style["r_2, conditional on background B_2", FontFamily -> "Helvetica"], Style["\(\bar{r}\), weighted mean across backgrounds", FontFamily -> "Helvetica"], LegendPosition -> (-0.05, 0.175), LegendSize -> {1.3, 0.5}, LegendShadow -> None, LegendTextSpace -> 10, LegendBorderSpace -> Automatic, LegendBorder -> None, LegendLabelSpace -> 1.8, LegendLabel -> Style["a = " <> ToString[mya] <> "; b = " <> ToString[myb] <> "; m = " <> ToString[mym], FontFamily -> "Helvetica"]}

- Weak evolutionary forces; migration rate \(m = 0.03\)

mym = 0.03;
mya = 0.02;
myb = 0.04;
myy11temp = 0.;
myy12temp = 0.;
myy21temp = 0.;
myy22temp = 0.;


\[
\begin{pmatrix}
1.06 & 1.02 & 0.98 \\
1.04 & 1.0 & 0.96 \\
1.02 & 0.98 & 0.94 \\
\end{pmatrix}
\]

rCritApprox = rCritApproxFunc[mym, mya, myb]
(* \(r\) must be lower than this critical value; the value is a good approximation under the discrete-time model only if evolutionary forces are weak! *)

0.04

rCrit = rCritFunc[mym, mya, myb] (* \(r\) must be lower than this critical value; this value is exact under the discrete-time version of the model. *)

0.0412

Critical values for the migration rate for the stability of the equilibrium \(E_C\).
Critical value for the migration rate, $m_{B,1}$, as a function of $r$ for the current parameter values.

Show[Plot[mCritFunc[r, mya, myb], {r, 0, 0.5}, PlotRange -> {{0, 0.5}, {0, mc2 + 0.1 + mc2}}, AxesLabel -> {r, "Critical migration rate $m_B$"}],
Plot[mCritFunc[r, mya, myb], {r, 0, rCrit},
PlotRange -> {{0, 0.5}, {0, mc2 + 0.1 + mc2}}, PlotStyle -> None, Filling -> {1 -> mc1},
Graphics[{Gray, Dotted, Line[{{rCrit, 0}, (rCrit, mc2 + 0.1 + mc2)}]},
Graphics[{Text["$x_B$", {.025 + rCrit, 0.2 + mc2}],
Graphics[{Gray, Dashed, Line[{{.0, mc1}, (.5, mc2)}]},
Graphics[{Text["$m_{crit}$", {0.4, 0.9 + mc1}]},
Graphics[{Gray, Dashed, Line[{{0, mc2}, {.5, mc2}}]},
Graphics[{Text["$m'$", {0.4, mc2 - 0.1 + mc1}]]}>(* This uses exact critical values *)

Critical migration rate $m_B$

Recall: $m' = m_{crit1} = \frac{1-a}{b}$, $m'' = m_{crit2} = \frac{1-b}{a}$, and $m_B = m_{crit5} = \frac{a(b-a+b)}{(a-b)(a+b+1-a)}$

plot2 =
Show[Plot[{probEstableMAproxFunc[r, mym, mya, myb, myy1temp, myy2temp, myy21temp, myy212temp, myy212temp, myy22temp][2], probEstableMAproxFunc[r, mym, mya, myb, myy1temp, myy11temp, myy12temp, myy21temp, myy22temp][3], probEstableMAproxFunc[r, mym, mya, myb, myy1temp, myy11temp, myy12temp, myy21temp, myy22temp][4]},
{r, 0, 0.5}, PlotRange -> {{0, rCrit}, {0, 2 + mya}},
PlotStyle -> {{RGBColor[0, 0.3, 1, 0.5], Thick}, {Red, Thick}, {Black, Thick}},
Frame -> True, FrameStyle -> {{Black, Opacity[0]}, {Black, Opacity[0]}},
FrameLabel -> {"Recombination rate $r$", "Invasion probability"},
LabelStyle -> {Directive[FontSize -> 14], FontFamily -> "Helvetica"}, PlotLegend ->
{Style["$m_{1}$, conditional on background $B_1$", FontFamily -> "Helvetica"], 10],
Style["$m_{2}$, conditional on background $B_2$", FontFamily -> "Helvetica"],
Style["$m_{3}$, weighted mean across backgrounds", FontFamily -> "Helvetica"],
LegendPosition -> (-0.05, 0.175), LegendSize -> {1.3, 0.5}, LegendShadow -> None,
LegendTextSpace -> 10, LegendBorderSpace -> Automatic,
LegendBorder -> None, LegendLabelSpace -> 1.8,
LegendLabel -> Style["a = " <> ToString[mya] <> "; b = " <> ToString[myb] <> "; m = " <> ToString[mym], FontFamily -> "Helvetica"]]
- Weak evolutionary forces; migration rate $m = 0.038$

```math
\begin{align*}
\text{mym} &= 0.038; \\
\text{mya} &= 0.02; \\
\text{myb} &= 0.04; \\
\text{myy11temp} &= 0.; \\
\text{myy12temp} &= 0.; \\
\text{myy21temp} &= 0.; \\
\text{myy22temp} &= 0.; \\
\text{rcritapprox} &= \text{rcritapproxfunc}[\text{mym}, \text{mya}, \text{myb}] \\
& \quad \text{(r must be lower than this critical value;} \\
& \quad \text{the value is a good approximation under the discrete-} \\
& \quad \text{time model only if evolutionary forces are weak! *)} \\
0.0222222
\end{align*}
```

```math
\begin{align*}
\text{rcrit} &= \text{rcritfunc}[\text{mym}, \text{mya}, \text{myb}] \quad \text{(r must be lower than this critical value;} \\
& \quad \text{this value is exact under the discrete-time version of the model. *)} \\
0.0230667
\end{align*}
```

Critical values for the migration rate for the stability of the equilibrium $E_C$.

```math
\begin{align*}
\text{mc1} &= \text{mcrit1} / (a \rightarrow \text{mya}, b \rightarrow \text{myb}) \\
\text{mc2} &= \text{mcrit2} / (a \rightarrow \text{mya}, b \rightarrow \text{myb}) \\
\text{mc3} &= \text{mcrit3} / (a \rightarrow \text{mya}, b \rightarrow \text{myb}, r \rightarrow \text{rcrit}) \\
0.0208333 \\
0.0408163 \\
0.0378054
\end{align*}
```

Critical value for the migration rate, $m_{B1}$, as a function of $r$ for the current parameter values.
Show[Plot[mCritFunc[r, mya, myb], {r, 0, 0.5}, PlotRange -> {{0, 0.5}, {0, mc2 + 0.1 + mc2}}, AxesLabel -> "Recombination rate r", "Critical migration rate m"]],
Plot[mCritFunc[r, mya, myb], {r, 0, rCrit}, PlotRange -> {{0, 0.5}, {0, mc2 + 0.1 + mc2}}, PlotStyle -> None, Filling -> {1 -> mc1}, Graphics[{Gray, Dotted, Line[{{rCrit, 0}, {rCrit, mc2 + 0.1 + mc2}}]}], Graphics[{Text["r_a", {.025 + rCrit, 0.2 + mc2}]}], Graphics[{Gray, Dashed, Line[{{0.0, mc1}, {0.5, mc1}}]}], Graphics[{Text["m", {0.4, 0.9 + mc1}]}], Graphics[{Gray, Dashed, Line[{{0.0, mc2}, {0.5, mc2}}]}], Graphics[{Text["m'", {0.4, mc2 - 0.1 + mc1}]}] (* This uses exact critical values *)

Recall: $m^* = m_{col,1} = \frac{1-a}{b}$, $m^+ = m_{col,2} = \frac{1-b}{a}$, and $m_B = m_{col,5} = \frac{b}{a+b}$.
- Weak evolutionary forces, recombination rate \( r = 0.001 \)

\[
\begin{align*}
\text{myr} &= 0.001; \\
\text{mya} &= 0.02; \\
\text{myb} &= 0.04; \\
\text{myy11temp} &= 0.; \\
\text{myy12temp} &= 0.; \\
\text{myy21temp} &= 0.; \\
\text{myy22temp} &= 0.; \\
\text{mCritApprox} &= \text{Min}[\text{mCritApproxFunc}[\text{myr}, \text{mya}, \text{myb}], \text{myb}] \\
\text{(} \ast \text{ m must be lower than the (approximate) critical value and lower than } \text{b}; \text{ however, this criterion is valid for the continuous-time version and provides a good approximation to the discrete-time version only if evolutionary forces are weak! } \ast \text{)} \\
0.04 \\
\text{mCrit} &= \text{mCritFunc}[\text{myr}, \text{mya}, \text{myb}] \text{ (} \ast \text{ m must be lower than this critical value; this value is exact under the discrete-time version of the model. } \ast \text{)} \\
0.0408163 \\
\text{Critical values for the migration rate for the stability of the equilibrium } E_C. \\
\end{align*}
\]

\[
\begin{align*}
\text{mCl} &= 0.0208333 \\
\text{mCrit1} \\
a \frac{1}{1 - b} \\
\text{mCl} &= \text{mCrit1} . \{a \rightarrow \text{mya}, b \rightarrow \text{myb}\} \\
\text{mCl2} &= \text{mCrit2} . \{a \rightarrow \text{mya}, b \rightarrow \text{myb}\} \\
\text{mCl3} &= \text{mCrit3} . \{a \rightarrow \text{mya}, b \rightarrow \text{myb}, r \rightarrow \text{myr}\} \\
0.0208333 \\
0.0408163 \\
0.0590591 \\
\text{Show}[\text{Plot}[\text{rCritApproxFunc}[\text{m}, \text{mya}, \text{myb}], \{\text{m}, 0, 1\}, \text{PlotRange} \rightarrow \{(0, 0.08), (0, .6)\}, \text{AxesLabel} \rightarrow \{\text{m}, \text{"Critical recombination rate } r_b \text{ (approximate)"}\}], \\
\text{Plot}[\text{rCritApproxFunc}[\text{m}, \text{mya}, \text{myb}], \{\text{m}, 0, \text{mCritApprox}\}, \text{PlotRange} \rightarrow \{(\text{mya}, \text{mCritApprox}), \{0, .5\}\}, \text{PlotStyle} \rightarrow \text{None}, \text{Filling} \rightarrow \{1 \rightarrow \text{Axis}\}], \\
\text{Graphics}[\text{Gray, Dotted, Line}[\{(\text{mya}, 0), (\text{mya}, .6)\}]], \\
\text{Graphics}[\text{Text}[\text{"a1", \{.75 * \text{mya}, 0.8 * .5\}}]], \\
\text{Graphics}[\text{Gray, Dotted, Line}[\{(\text{mCritApprox}, 0), (\text{mCritApprox}, .6)\}]], \\
\text{Graphics}[\text{Text}[\text{"mClip", \{\text{mCritApprox} - .25 * \text{mya}, 0.8 * .5\}}]], \\
\text{Graphics}[\text{Gray, Dashed, Line}[\{(0, .5), (1, .5)\}]], \\
\text{Graphics}[\text{Text}[\text{"rmax", \{.07, 1.1 * .5\}}])(\ast \text{ This uses approximate critical values } \ast);
Show[Plot[rCritFunc[m, mya, myb], {m, 0, 1}, PlotRange -> {{0, 0.08}, {0, .6}}, AxesLabel -> {m, "Critical recombination rate r_c"}], Plot[rCritFunc[m, mya, myb], {m, mc1, mCrit}, PlotRange -> {{0, 0.08}, {0, 1}}, PlotStyle -> None, Filling -> {1 -> Axis}], Graphics[{{Gray, Dotted, Line[{{mc1, 0}, (mc1, .6)}]}}, Graphics[{{Gray, Dotted, Line[{{mCrit, 0}, (mCrit, .6)}]}}, Graphics[Text["m'"], {.75 * mc1, 0.8 * .5}], Graphics[{{Gray, Dotted, Line[{{0, 0.5}, (1, .5)}]}}, Graphics[Text["m''", {(mCrit - .25 * mc1, 0.8 * .5)}]}, Graphics[{{Gray, Dashed, Line[{{0, .5}, (1, .5)}]}}, Graphics[Text["r_{max}"], {.07, 1.1 * .5}]] (* This uses exact critical values *)

Critical recombination rate r_c

Recall: m' = m_{crit,1} = \frac{1-a}{b}, m'' = m_{crit,2} = \frac{1-b}{a}, and m_y = m_{crit,5} = \frac{a(b-a+b)}{(a-b)(a+b)+(1-a)}.

inset4 = Plot[{1, probEstabLMApproxFunc[myr, m, mya, myb, myy1temp, myy2temp, myy22temp][2]}, {m, 0, 1}, PlotRange -> {{0, mCrit}, (0.0377, 0.0383)}, PlotStyle -> {None, {RGBColor[0, 0.3, 1, 0.5]}}, Frame -> True, FrameStyle -> {{Black, Opacity[0]}, {Black, Opacity[0]}}, FrameLabel -> {m, "x_1"}, LabelStyle -> Directive[FontSize -> 10, FontFamily -> "Helvetica"], FrameTicks -> {{0, 0.02, 0.04}, {0.0377, 0.0380, 0.0383}}];
Weak evolutionary forces, recombination rate $r = 0.01$

- $myr = 0.01$
- $mya = 0.02$
- $myb = 0.04$
- $myy11temp = 0.$
- $myy12temp = 0.$
- $myy21temp = 0.$
- $myy22temp = 0.$

$mCritApprox = \text{Min}[\text{mCritApproxFunc}[myr, mya, myb], myb]$

(* m must be lower than the (approximate) critical value and lower than $b_1$;
however, this criterion is valid for the continuous-time version and provides a good approximation to the discrete-time version only if evolutionary forces are weak! *)

0.04

$mCrit = \text{mCritFunc}[myr, mya, myb] (* m must be lower than this critical value; this value is exact under the discrete-time version of the model. *)

0.0408163

Critical values for the migration rate for the stability of the equilibrium $E_C$. 

mcl = mCrit1 /. {a -> mya, b -> myb}
imc2 = mCrit2 /. {a -> mya, b -> myb}
imc3 = mCrit3 /. {a -> mya, b -> myb, r -> myr}

0.0208333
0.0408163
0.0505051

Show[Plot[rCritApproxFunc[m, mya, myb], {m, 0, 1}, PlotRange -> {{0, 0.08}, {0, .6}},
AxesLabel -> {m, "Critical recombination rate \( r_b \) (approximate)"}],
Plot[rCritApproxFunc[m, mya, myb], {m, 0, mCritApprox},
PlotRange -> {{mya, mCritApprox}, {0, .5}}, PlotStyle -> None, Filling -> {1 -> Axis},
Graphics[{Gray, Dotted, Line[{{mya, 0}, {mya, .6}}]}],
Graphics[Text["a_1", {.75 * mya, 0.8 * .5}]],
Graphics[{Gray, Dotted, Line[{{mCritApprox, 0}, {mCritApprox, .6}}]}],
Graphics[Text["m_0,1", {mCritApprox - .25 * mya, 0.8 * .5}]],
Graphics[{Gray, Dashed, Line[{{0, .5}, (1, .5)}]}],
Graphics[Text["r_{max}", {.07, 1.1 * .5}]] (* This uses approximate critical values *)];

Show[Plot[rCritFunc[m, mya, myb], {m, 0, 1}, PlotRange -> {{0, 0.08}, {0, .6}},
AxesLabel -> {m, "Critical recombination rate \( r_b \)"}],
Plot[rCritFunc[m, mya, myb], {m, mcl, mCrit}, PlotRange -> {{0, 0.08}, {0, 1}},
PlotStyle -> None, Filling -> {1 -> Axis},
Graphics[{Gray, Dotted, Line[{{mcl, 0}, {mcl, .6}}]}],
Graphics[Text["m'", {.75 * mcl, 0.8 * .5}]],
Graphics[{Gray, Dotted, Line[{{mCrit, 0}, {mCrit, .6}}]}],
Graphics[Text["m_b", {mCrit - .25 * mcl, 0.8 * .5}]],
Graphics[{Gray, Dashed, Line[{{0, .5}, (1, .5)}]}],
Graphics[Text["r_{max}^\prime", {.07, 1.1 * .5}]] (* This uses exact critical values *)]

Recall: \( m' = m_{\text{crit.1}} = \frac{1-a}{b} \), \( m'' = m_{\text{crit.2}} = \frac{1-b}{a} \), and \( m_B = m_{\text{crit.5}} = \frac{a(b-a+1)}{(a-b)(a-r)(1-a)} \)
plot5 = Show[Plot[probEstablishAMAPproxFunc[myr, m, mya, myb, myy1temp, myy2temp, myy2temp][4], {m, mcl, 1}, PlotRange -> {{0, mCrit}, {0, .05}}, PlotStyle -> None, Filling -> {1 -> Axis}, FillingStyle -> RGBColor[0.9, 0.9, 0.9, 1] (*, Epilog->Inset[[inset4, (0.0375, 0.045), {0.04, 0.0383}, {0.021, 0.021}, Background -> White] *)], Plot[{probEstablishAMAPproxFunc[myr, m, mya, myb, myy1temp, myy2temp, myy2temp][2], probEstablishAMAPproxFunc[myr, m, mya, myb, myy1temp, myy2temp, myy2temp][3], probEstablishAMAPproxFunc[myr, m, mya, myb, myy1temp, myy2temp, myy2temp][4]}], {m, 0, 1}, PlotRange -> {{0, mCrit}, {0, .05}}], PlotStyle -> {{RGBColor[0, 0.3, 1, 0.5], Thick}, {Red, Thick}, {Black, Thick}}], Graphics[Text[Style["r = " <> ToString[myr] <> "; a = " <> ToString[mya] <> "; b = " <> ToString[myb], FontFamily -> "Helvetica", FontSize -> 10], {0.01, 0.012}], Graphics[{Gray, Dotted, Line[{{mcl, .0}, {mcl, 1.}}]}], Graphics[Text[Style["m", FontFamily -> "Helvetica"], {0.9*mcl, 0.045}]], Frame -> True, FrameStyle -> {{Black, Opacity[0]}, {Black, Opacity[0]}}, FrameLabel -> {"Migration rate \(m\)", "Invasion probability"}, LabelStyle -> {Directive[FontSize -> 14], FontFamily -> "Helvetica"}]

- Weak evolutionary forces, recombination rate \(r = 0.02\)

myr = 0.02;
mya = 0.02;
myb = 0.04;
myy1temp = 0.;
myy2temp = 0.;
myy2temp = 0.;

mCritApprox = Min[mCritApproxFunc[myr, mya, myb], myb]
(* m must be lower than the (approximate) critical value and lower than \(b_1\);
however, this criterion is valid for the continuous-time version and provides a good approximation to the discrete-time version only if evolutionary forces are weak! *)

0.04

mCrit = mCritFunc[myr, mya, myb] (* m must be lower than this critical value;
this value is exact under the discrete-time version of the model. *)

0.0408163

Critical values for the migration rate for the stability of the equilibrium \(E_C\).
Recall: 
\[ m' = m_{\text{crit}, 1} = \frac{1-a}{b}, \quad m'' = m_{\text{crit}, 2} = \frac{1-b}{a}, \quad \text{and} \quad m_B = m_{\text{crit}, 5} = \frac{a(b-a+1)}{(a+b)(a-b)+(1-a)} \]
plot6 = 
Show[Plot[probEstablAMApproxFunc[myr, m, mya, myb, myy1temp, myy2temp, myy22temp][4], 
{m, mcl, 1}, PlotRange -> {{0, mCrit}, {0, 0.05}}, PlotStyle -> 
{Filling -> (1 -> Axis), FillingStyle -> RGBColor[0.9, 0.9, 0.9, 1] (*, Epilog-> 
Inset[inset4, (0.0375, 0.045), {0.04, 0.0383}, {0.021, 0.021}, Background -> White]*)}, 
Plot[probEstablAMApproxFunc[myr, m, 
mya, myb, myy1temp, myy2temp, myy22temp][2], probEstablAMApproxFunc[myr, m, 
mya, myb, myy1temp, myy2temp, myy22temp][3], 
probEstablAMApproxFunc[myr, m, mya, myb, myy1temp, myy2temp, myy22temp][4]], 
{m, 0, 1}, PlotRange -> {{0, mCrit}, {0, 0.05}}], 
PlotStyle -> {{RGBColor[0.3, 0.3, 0.5], Thick}, {Red, Thick}, {Black, Thick}}], 
Graphics[Text[Style[r = " <> ToString[myr] <> "; a = " <> ToString[mya] <> "; b = " <> 
ToString[myb], FontFamily -> "Helvetica", FontSize -> 10, {0.01, 0.005}]], 
Graphics[{Gray, Dotted, Line[{{mcl, .0}, (mcl, 1.)}]}]], 
Graphics[Text[Style[m = "-fontFamily -> "Helvetica", FontSize -> 10, {0.9 * mcl, 0.045}]], 
Frame -> True, FrameStyle -> {{Black, Opacity[0]}, {Black, Opacity[0]}}, 
FrameLabel -> {"Migration rate m", "Invasion probability"}, 
LabelStyle -> {Directive[FontSize -> 14], FontFamily -> "Helvetica"]}

- Weak evolutionary forces, recombination rate \( r = 0.1 \)

myr = 0.1; 
mya = 0.02; 
myb = 0.04; 
myy1temp = 0.; 
myy2temp = 0.; 
myy22temp = 0.; 

mCritApprox = Min[mCritApproxFunc[myr, mya, myb], myb] 
(* \( m \) must be lower than the (approximate) critical value and lower than \( b_1 \); 
however, this criterion is valid for the continuous- 
time version and provides a good approximation to the discrete-
time version only if evolutionary forces are weak! *)

0.022

mCrit = mCritFunc[myr, mya, myb] (* \( m \) must be lower than this critical value; 
this value is exact under the discrete-time version of the model. *)

0.0220441

Critical values for the migration rate for the stability of the equilibrium \( E_C \).
m1 = mCrit1 /. \{a \to mya, b \to myb\}

m2 = mCrit2 /. \{a \to mya, b \to myb\}

m3 = mCrit3 /. \{a \to mya, b \to myb, r \to myr\}

0.0208333

0.0408163

-0.175

Show[Plot[rCritApproxFunc[m, mya, myb], \{m, 0, 1\},\n  PlotRange \to \{(0, 0.08), (0, .6)\},\n  AxesLabel \to \{m, \"Critical recombination rate \(r_m\) (approximate)\}\}],\n  Plot[rCritApproxFunc[m, mya, myb], \{m, 0, mCritApprox\},\n  PlotRange \to \{(mya, mCritApprox), (0, .5)\}, PlotStyle \to None, Filling \to \{1 \to Axis\}],\n  Graphics[\{Gray, Dotted, Line[\{(mya, 0), (mya, .6)\}\}],\n  Graphics[Text[\"a_1\", (0.75 * mya, 0.8 * .5)]]],\n  Graphics[Gray, Dotted, Line[\{(mCritApprox, 0), (mCritApprox, .6)\}]]],\n  Graphics[Text[\"m_{b,1}\", \{(mCritApprox, .75 * mya, 0.8 * .5)\}],\n  Graphics[Gray, Dashed, Line[\{(0, .5), (1, .5)\}]]],\n  Graphics[Text[\"r_{max}\", (0.07, 1.1 * .5)\}]] (* This uses approximate critical values *)

Show[Plot[rCritFunc[m, mya, myb], \{m, 0, 1\},\n  PlotRange \to \{(0, 0.08), (0, .6)\},\n  AxesLabel \to \{m, \"Critical recombination rate \(r_m\)\}\}],\n  Plot[rCritFunc[m, mya, myb], \{m, m1, mCrit\},\n  PlotRange \to \{(0, 0.08), (0, 1)\},\n  PlotStyle \to None, Filling \to \{1 \to Axis\}],\n  Graphics[\{Gray, Dotted, Line[\{(m1, 0), (m1, .6)\}\}],\n  Graphics[Text[\"m_{c,1}\", (0.75 * m1, 0.8 * .5)]]],\n  Graphics[Gray, Dotted, Line[\{(mCrit, 0), (mCrit, .6)\}]]],\n  Graphics[Text[\"m_{b}\", \{(mCrit + .25 * m1, 0.8 * .5)\}],\n  Graphics[Gray, Dashed, Line[\{(0, .5), (1, .5)\}]]],\n  Graphics[Text[\"r_{max}\", (0.07, 1.1 * .5)\}]] (* This uses exact critical values *)

Recall: \(m' = m_{\text{crit,1}} = \frac{1-a}{b}\), \(m'' = m_{\text{crit,2}} = \frac{1-b}{a}\), and \(m_b = m_{\text{crit,5}} = \frac{a(b-a+1)}{(a-b)(a-r) + (1-a)}\).
Weak evolutionary forces, recombination rate \( r = 0.5 \)

\[
\begin{align*}
\text{myr} & = 0.5; \\
\text{mya} & = 0.02; \\
\text{myb} & = 0.04; \\
\text{myy1ltemp} & = 0.; \\
\text{myy12temp} & = 0.; \\
\text{myy21temp} & = 0.; \\
\text{myy22temp} & = 0.;
\end{align*}
\]

\( m\text{CritApprox} = \min[m\text{CritApproxFunc}[\text{myr}, \text{mya}, \text{myb}], \text{myb}] \)

(* \( m \) must be lower than the (approximate) critical value and lower than \( b_1 \);
however, this criterion is valid for the continuous-time version and provides a good approximation to the discrete-time version only if evolutionary forces are weak! *)

0.0208

\( m\text{Crit} = m\text{CritFunc}[\text{myr}, \text{mya}, \text{myb}] \) (* \( m \) must be lower than this critical value; 
this value is exact under the discrete-time version of the model. *)

0.0208333

Critical values for the migration rate for the stability of the equilibrium \( E_c \).
mc1 = mCrit1 /. {a -> mya, b -> myb}
mc2 = mCrit2 /. {a -> mya, b -> myb}
mc3 = mCrit3 /. {a -> mya, b -> myb, r -> myr}
0.0208333
0.0408163
-0.88
Show[Plot[rCritApproxFunc[m, mya, myb], {m, 0, 1}, PlotRange -> {{0, 0.08}, {0, .6}},
AxesLabel -> {m, "Critical recombination rate \( r_b \) (approximate)"}],
Plot[rCritApproxFunc[m, mya, myb], {m, 0, mCritApprox},
PlotRange -> {{mya, mCritApprox}, {0, .5}}, PlotStyle -> None, Filling -> {1 -> Axis},
Graphics[{Gray, Dotted, Line[{{mya, 0}, {mya, .6}}]}],
Graphics[Text["\( a_1 \), \{.75 * mya, 0.8 * .5\}]],
Graphics[{Gray, Dotted, Line[{{mCritApprox, 0}, {mCritApprox, .6}}]}],
Graphics[Text["\( m_b \_1 \), \{mCritApprox - .25 * mya, 0.8 * .5\}]],
Graphics[{Gray, Dashed, Line[{{0, .5}, (1, .5)}]}],
Graphics[Text["\( \max r \), \{.07, 1.1 * .5\}]"] (* This uses approximate critical values *)
Show[Plot[rCritFunc[m, mya, myb], {m, 0, 1}, PlotRange -> {{0, 0.08}, {0, .6}},
AxesLabel -> {m, "Critical recombination rate \( r_b \)"}], (* Plot[rCritFunc[m,mya,myb],
{m,mcl,mCrit},PlotRange->({0,0.08},{0,1}),PlotStyle=,None,Filling=1Axis],*)
Graphics[{Gray, Dotted, Line[{{mcl, 0}, {mcl, .6}}]}],
Graphics[Text["\( m' = m_b \), \{.75 * mcl, 0.8 * .5\}]],
(* Graphics[{Gray, Dotted, Line[{{mCrit,0},{mCrit,.6}}]}],
Graphics[Text["\( m_b \),\{mCrit+.25*mcl,0.8*0.5\}],*)
Graphics[{Gray, Dashed, Line[{{0, .5}, (1, .5)}]}],
Graphics[Text["\( \max r \), \{.07, 1.1 * .5\}]"] (* This uses exact critical values *)

Recall: \( m' = m\_\text{crit,1} = \frac{1-a}{b}, m'' = m\_\text{crit,2} = \frac{1-b}{a}, \) and \( m_B = m\_\text{crit,5} = \frac{a(b-a)(a-1)(1-a)}{(a-b)(a-v)+1(a-\pi)} \).

In the following, we add for comparison Haldane’s (1927) approximation \( \pi_H = 2a \). This should approximate our \( \pi \) for \( m_1 \to 0 \).
Strong evolutionary forces; migration rate \( m = 0.22 \)

\[
\begin{align*}
mym &= 0.22; \\
mya &= 0.2; \\
myb &= 0.4; \\
myy11temp &= 0.; \\
myy12temp &= 0.; \\
myy21temp &= 0.; \\
myy22temp &= 0.;
\end{align*}
\]

\( \text{wCompact}[1] \) /. \text{assumeAdditiveMultiplicEpistaticApproxFitness}[1] /. \text{ruleFitness} // \text{MatrixForm}

\[
\begin{pmatrix}
1.6 & 1.2 & 0.8 \\
1.4 & 1. & 0.6 \\
1.2 & 0.8 & 0.4
\end{pmatrix}
\]

\( r_{\text{CritApprox}} = r_{\text{CritApproxFunc}}[\text{mym}, \text{mya}, \text{myb}] \)

\( * r \) must be lower than this critical value; the value is a good approximation under the discrete-time model only if evolutionary forces are weak! 

2.

\( r_{\text{Crit}} = r_{\text{CritFunc}}[\text{mym}, \text{mya}, \text{myb}] \) \( * r \) must be lower than this critical value; this value is exact under the discrete-time version of the model.

0.5

Critical values for the migration rate for the stability of the equilibrium \( E_c \).

\[
\begin{align*}
m\text{c1} &= \text{mCrit1} /. \{ \text{a} \rightarrow \text{mya}, \text{b} \rightarrow \text{myb} \} \\
m\text{c2} &= \text{mCrit2} /. \{ \text{a} \rightarrow \text{mya}, \text{b} \rightarrow \text{myb} \} \\
m\text{c3} &= \text{mCrit3} /. \{ \text{a} \rightarrow \text{mya}, \text{b} \rightarrow \text{myb}, r \rightarrow \text{rCrit} \}
\end{align*}
\]

0.333333

0.5

0.2
Critical value for the migration rate, \( m_{B,1} \), as a function of \( r \) for the current parameter values.

\[
\text{Show[Plot[mCritFunc[r, mya, myb], \{r, 0, 1.1 \times rCrit\}, PlotRange \rightarrow \{(0, 1.1 \times rCrit), (0, mc2 + 0.1 \times mc2)\}, AxesLabel \rightarrow \{r, "Critical migration rate m_B"\}, Plot\{mCritFunc[r, mya, myb]\}, \{r, 0, 1.1 \times rCrit\}, PlotRange \rightarrow \{(0, 1.1 \times rCrit), (0, mc2 + 0.1 \times mc2)\}, PlotStyle \rightarrow \text{None}, Filling \rightarrow \{1 \rightarrow mc1\}, Graphics\{\text{Gray, Dotted, Line\{\{rCrit, 0\}, \{rCrit, mc2 + 0.1 \times mc2\}\}\}, Graphics\{\text{Text\{"r_B\", \{0.025 \times rCrit, 0.2 \times mc2\}\}\}, Graphics\{\text{Gray, Dashed, Line\{\{.0, mc1\}, \{1.1 \times rCrit, mc1\}\}\}, Graphics\{\text{Text\{"m'\", \{0.4, 0.9 \times mc1\}\}\}, Graphics\{\text{Gray, Dashed, Line\{\{.0, mc2\}, \{1.1 \times rCrit, mc2\}\}\}, Graphics\{\text{Text\{"m''\", \{0.4, mc2 - 0.1 \times mc1\}\}\}\}}\)
\]
\]

\text{(This uses exact critical values *)}

Recall: \( m' = m_{\text{crit,1}} = \frac{1-a}{b}, m'' = m_{\text{crit,2}} = \frac{1-b}{a}, \text{and } m_B = m_{\text{crit,5}} = \frac{a(b-a-r)}{(a-b)(a-r) + (1-a)} \).
plot9 = Show[Plot[{probEstablAMApproxFunc[r, mym, mya, myb, myy1temp, myy12temp, myy21temp, myy22temp][2], probEstablAMApproxFunc[r, mym, mya, myb, myy1temp, myy12temp, myy21temp, myy22temp][3], probEstablAMApproxFunc[r, mym, mya, myb, myy1temp, myy12temp, myy21temp, myy22temp][4]}, {r, 0, 0.5}, PlotRange -> {{0, 0.5}, {0, 2 * mya}}, PlotStyle -> {RGBColor[0.3, 1, 0.5], Thick}, {Red, Thick}, {Black, Thick}], Frame -> True, FrameStyle -> {{Black, Opacity[0]}, {Black, Opacity[0]}}, FrameLabel -> {"Recombination rate r", "Invasion probability"}, LegendBorder -> {Automatic}, LegendTextSpace -> 0.05, LegendPosition -> {0.05, 0.175}, LegendSize -> {1.3, 0.5}, LegendShadow -> None, LegendBorderSpace -> Automatic, LegendBorder -> None, LegendLabelSpace -> 1.8, LegendLabel -> Style["a = " <> ToString[mym] <> "; b = " <> ToString[myb] <> "; m = " <> ToString[mmy], FontFamily -> "Helvetica"]};

Plot[probEstablAMApproxFunc[r, mym, mya, myb, myy1temp, myy12temp, myy21temp, myy22temp][4], {r, 0, 1/2}, PlotRange -> {{0, 0.2}, {0.13, 0.15}}, PlotStyle -> {Black, Thick}]

- Strong evolutionary forces; migration rate \( m = 0.3 \)

mym = 0.3;
mya = 0.2;
myb = 0.4;
myy1temp = 0.;
myy12temp = 0.;
myy21temp = 0.;
myy22temp = 0.;
Recall: $m' = m_{crit,1} = \frac{1-a}{b}$, $m'' = m_{crit,2} = \frac{1-b}{a}$, and $m_b = m_{crit,5} = \frac{a(b-a+c)}{(a-b)(a+c)(1-a)}$. 

Critical values for the migration rate for the stability of the equilibrium $E_c$.

```
m1 = mCrit1 /. {a -> mya, b -> myb}
m2 = mCrit2 /. {a -> mya, b -> myb}
m3 = mCrit3 /. {a -> mya, b -> myb, r -> rCrit}
0.333333
0.5
0.2
```

Critical value for the migration rate, $m_{b,1}$, as a function of $r$ for the current parameter values.

```
Show[Plot[mCritFunc[r, mya, myb], {r, 0, 1.1*rCrit},
      PlotRange -> {{0, 1.1*rCrit}, {0, mc2 + 0.1*mc2}},
      AxesLabel -> {r, "Critical migration rate $m$"}],
      Plot[{mCritFunc[r, mya, myb]},
           {r, 0, 1.1*rCrit}, PlotRange -> {{0, 1.1*rCrit}, {0, mc2 + 0.1*mc2}},
           PlotStyle -> None, Filling -> {1 -> mc1}],
      Graphics[{Gray, Dotted, Line[{0, {rCrit, mc2 + 0.1*mc2}]}]},
      Graphics[{Gray, Dashed, Line[{0, {rCrit, mc2 + 0.1*mc2}]}]},
      Graphics[{Text["\(r_b\)", {rCrit - 0.025, 0.2*mc2}]}],
      Graphics[{Text["\(m'\)", {0.4, 0.9*mc1}]}],
      Graphics[{Text["\(m''\)", {0.4, mc2 - 0.1*mc1}]}]]
(* This uses exact critical values *)
```

Critical migration rate $m_b$
plot10 = Show[Plot[probEstablAMApproxFunc[r, mym, mya, myb, myy11temp, myy12temp, myy21temp, myy22temp][2], probEstablAMApproxFunc[r, mym, mya, myb, myy11temp, myy12temp, myy21temp, myy22temp][3], probEstablAMApproxFunc[r, mym, mya, myb, myy11temp, myy12temp, myy21temp, myy22temp][4]], {r, 0, 0.5}, PlotRange -> {{0, 0.5}, {0, 2 + mya}}, PlotStyle -> {RGBColor[0.3, 0.3, 1, 0.5], Thick}, {Red, Thick}, {Black, Thick}], Frame -> True, FrameStyle -> {{Black, Opacity[0]}, {Black, Opacity[0]}}, FrameLabel -> {"Recombination rate \( r \)\), "Invasion probability"}, LabelStyle -> {Directive[FontSize -> 14], FontFamily -> "Helvetica"}, PlotLegend -> {Style["\( m_1 \), conditional on background \( B_1 \)\], FontFamily -> "Helvetica", 10], Style["\( m_2 \), conditional on background \( B_2 \)\], FontFamily -> "Helvetica"], Style["\( \bar{m} \), weighted mean across backgrounds\], FontFamily -> "Helvetica"}], LegendPosition -> {-0.05, 0.175}, LegendSize -> {1.3, 0.5}, LegendShadow -> None, LegendTextSpace -> 10, LegendBorderSpace -> Automatic, LegendBorder -> None, LegendLabelSpace -> 1.8, LegendLabel -> Style["a = " <> ToString[mya] <> ", b = " <> ToString[myb] <> ", m = " <> ToString[mym], FontFamily -> "Helvetica"]

**Strong evolutionary forces; migration rate \( m = 0.38 \)**

mym = 0.38;
mya = 0.2;
myb = 0.4;
myy11temp = 0.0;
myy12temp = 0.0;
myy21temp = 0.0;
myy22temp = 0.0;

rCritApprox = rCritApproxFunc[mym, mya, myb]
(* \( r \) must be lower than this critical value;
the value is a good approximation under the discrete-time model only if evolutionary forces are weak! *)

0.222222

rCrit = rCritFunc[mym, mya, myb] (* \( r \) must be lower than this critical value;
this value is exact under the discrete-time version of the model. *)

0.306667

Critical values for the migration rate for the stability of the equilibrium \( E_C \).

mc1 = mCrit1 /. {a -> mya, b -> myb}
mc2 = mCrit2 /. {a -> mya, b -> myb}
mc3 = mCrit3 /. {a -> mya, b -> myb, r -> rCrit}

0.333333
0.5
0.423077
Critical value for the migration rate, $m_{B,1}$, as a function of $r$ for the current parameter values.

```math
Show[Plot[mCritFunc[r, mya, myb], {r, 0, 0.5}, PlotRange -> {{0, 0.5}, {0, mc2 + 0.1*mc2}}, AxesLabel -> {r, "Critical migration rate $m_B$"}],
Plot[mCritFunc[r, mya, myb], {r, 0, rCrit},
PlotRange -> {{0, 0.5}, {0, mc2 + 0.1*mc2}}, PlotStyle -> None, Filling -> {1 -> mc1},
Graphics[{Gray, Dotted, Line[{{rCrit, 0}, {rCrit, mc2 + 0.1*mc2}}]}],
Graphics[{Gray, Dashed, Line[{{.0, mc1}, {.5, mc1}}]}],
Graphics[Text["$r_B$", {.025 + rCrit, 0.2*mc2}]],
Graphics[Text[="$m'$", {0.4, 0.9*mc1}]],
Graphics[Text[="$m''$", {0.4, mc2 - 0.1*mc1}]],
Graphics[Text[="$m_{B}$", {0.5, mym}]]]
(* This uses exact critical values *)
```

Recall: $m' = m_{crit,1} = \frac{1-a}{b}$, $m'' = m_{crit,2} = \frac{1-b}{a}$, and $m_B = m_{crit,5} = \frac{a(b-a+1)}{(a-b)(a-r)+(1-a)}$. 

![Graph](image_url)
plot11 = 
Show[Plot[{probEstablAMApproxFunc[r, myr, mya, myb, myy1temp, myy2temp, myy12temp, myy22temp][2], probEstablAMApproxFunc[r, mym, mya, myb, myy1temp, myy12temp, myy21temp, myy22temp][3], probEstablAMApproxFunc[r, mym, mya, myb, myy1temp, myy12temp, myy21temp, myy22temp][4]}, 
{r, 0, 0.305}, PlotRange -> {{0, 0.5}, {0, 2*mya}}, 
PlotStyle -> {{RGBColor[0, 0.3, 1, 0.5], Thick}, {Red, Thick}, {Black, Thick}}, 
Frame -> True, FrameStyle -> {{Black, Opacity[0]}, {Black, Opacity[0]}}, 
FrameLabel -> {"Recombination rate r", "Invasion probability"}, 
LabelStyle -> {Directive[Fontsize -> 14], FontFamily -> "Helvetica"}, PlotLegend -> 
{Style["\[chi\]1, conditional on background B1", FontFamily -> "Helvetica", 10], 
Style["\[chi\]2, conditional on background B2", FontFamily -> "Helvetica"], 
Style["\[chi\], weighted mean across backgrounds", FontFamily -> "Helvetica"], 
LegendPosition -> {-0.05, 0.175}, LegendSize -> {1.3, 0.5}, LegendShadow -> None, 
LegendTextSpace -> 10, LegendBorderSpace -> Automatic, 
LegendBorder -> None, LegendLabelSpace -> 1.8, 
LegendLabel -> Style["a = " <> ToString[mya] <> "; b = " <> ToString[myb] <> "; m = " <> ToString[mym], FontFamily -> "Helvetica"], 

\[chi\]r = 0.2; b = 0.4; m = 0.38

- Strong evolutionary forces, recombination rate r = 0.01

myr = 0.01; 
mya = 0.2; 
myb = 0.4; 
myy1temp = 0.; 
myy12temp = 0.; 
myy21temp = 0.; 
myy22temp = 0.; 
mCritApprox = Min[mCritApproxFunc[myr, mya, myb], myb] (* m must be lower than the (approximate) critical value and lower than b1; however, this criterion is valid for the continuous-time version and provides a good approximation to the discrete-time version only if evolutionary forces are weak! *)

0.4

mCrit = mCritFunc[myr, mya, myb] (* m must be lower than this critical value; this value is exact under the discrete-time version of the model. *)

0.5

Critical values for the migration rate for the stability of the equilibrium $E_C$. 
Recall: $m' = m_{\text{crit}, 1} = \frac{1-a}{b}$, $m'' = m_{\text{crit}, 2} = \frac{1-b}{a}$, and $m_B = m_{\text{crit}, 5} = \frac{a(b-a+r)}{(a-b)(a+b)(1-a)}$. 

Critical recombination rate $r_B$
Strong evolutionary forces, recombination rate \( r = 0.07 \)

```math
\begin{align*}
\text{myr} &= 0.07; \\
\text{mya} &= 0.2; \\
\text{myb} &= 0.4; \\
\text{myy1ltemp} &= 0.; \\
\text{myy12temp} &= 0.; \\
\text{myy2ltemp} &= 0.; \\
\text{myy22temp} &= 0.; \\
\text{mCritApprox} &= \text{Min}[\text{mCritApproxFunc}[\text{myr}, \text{mya}, \text{myb}], \text{myb}] \\
& \quad (* m \text{ must be lower than the (approximate) critical value and lower than } b_1; \\
& \text{however, this criterion is valid for the continuous-time version and provides a good approximation to the discrete-time version only if evolutionary forces are weak! } *)
\end{align*}
```

```math
\begin{align*}
\text{mCrit} &= \text{mCritFunc}[\text{myr}, \text{mya}, \text{myb}] (* m \text{ must be lower than this critical value;}
& \text{this value is exact under the discrete-time version of the model. } *)
\end{align*}
```

0.4

0.5

Critical values for the migration rate for the stability of the equilibrium \( E_C \).
Recall: \( m' = m_{\text{crit},1} = \frac{1-a}{b} \), \( m'' = m_{\text{crit},2} = \frac{1-b}{a} \), and \( m_B = m_{\text{crit},5} = \frac{a(b-a+r)}{(a-b)(a-r)+(1-a)} \).
Strong evolutionary forces, recombination rate $r = 0.1$

myr = 0.1;
mya = 0.2;
myb = 0.4;
myy1temp = 0.;
myy2temp = 0.;
myy2temp = 0.;
mCritApprox = Min[mCritApproxFunc[myr, mya, myb], myb]
(* m must be lower than the (approximate) critical value and lower than b1; however, this criterion is valid for the continuous-time version and provides a good approximation to the discrete-time version only if evolutionary forces are weak! *)

0.4

mCrit = mCritFunc[myr, mya, myb] (* m must be lower than this critical value; this value is exact under the discrete-time version of the model. *)

0.5

Critical values for the migration rate for the stability of the equilibrium $E_C$. 
Recall: \( m' = m_{\text{crit,1}} = \frac{1-a}{b}, \) \( m'' = m_{\text{crit,2}} = \frac{1-b}{a}, \) and \( m_B = m_{\text{crit,5}} = \frac{a(b-a+\alpha)}{\alpha-b(a+\gamma+1-\alpha)}. \)

Read simulated values.
plot13=
Show[Plot[probEstablAMApproxFunc[myr, m, mya, myb, myy1temp, myy2temp, myy22temp][4], {m, mcl, 1}, PlotRange -> {{0, mCrit}, {0, 2*mya}}, PlotStyle -> None, Filling -> {1 -> Axis}, FillingStyle -> RGBColor[0.9, 0.9, 0.9, 1](*, Epilog-> Inset[inset4, (0.0375, 0.045), (0.04, 0.0383) , (0.021, 0.021), Background -> White] *)],
Plot[{probEstablAMApproxFunc[myr, m, mya, myb, myy1temp, myy2temp, myy22temp][2], probEstablAMApproxFunc[myr, m, mya, myb, myy1temp, myy2temp, myy22temp][3],
probEstablAMApproxFunc[myr, m, mya, myb, myy1temp, myy2temp, myy22temp][4]}, {m, 0, 1}, PlotRange -> {{0, mCrit}, {0, 2*mya}},
PlotStyle -> {{RGBColor[0.0, 0.3, 1, 0.5], Thick}, {Red, Thick}, {Black, Thick}}],
Graphics[Text[Style["r = " <> ToString[myr] <> "; a = " <> ToString[mya] <> "; b = " <>
ToString[myb], FontFamily -> "Helvetica", FontSize -> 10], {0.15, 0.1}]],
Graphics[{Gray, Dotted, Line[{{mc1, 0}, (mc1, 1.1)}]}],
Graphics[Text[Style["m", FontFamily -> "Helvetica"], {0.9*mc1, 0.95 + 2*mya}]],
Frame -> True, FrameStyle -> {{Black, Opacity[0]}, {Black, Opacity[0]}},
FrameLabel -> {"Migration rate m", "Invasion probability"},
LabelStyle -> {Directive[FontSize -> 14], FontFamily -> "Helvetica"}]

Strong evolutionary forces, recombination rate $r = 0.2$

myr = 0.2;
mya = 0.2;
myb = 0.4;
myy1temp = 0.;
myy2temp = 0.;
myy22temp = 0.;

mCritApprox = Min[mCritApproxFunc[myr, mya, myb], myb]
(* m must be lower than the (approximate) critical value and lower than $b_1$;
however, this criterion is valid for the continuous-
time version and provides a good approximation to the discrete-
time version only if evolutionary forces are weak! *)

0.4

mCrit = mCritFunc[myr, mya, myb] (* m must be lower than this critical value;
this value is exact under the discrete-time version of the model. *)

0.5

Critical values for the migration rate for the stability of the equilibrium $E_C$. 
Recall: \( m' = m_{\text{crit},1} = \frac{1-a}{b}, \quad m'' = m_{\text{crit},2} = \frac{1-b}{a}, \quad \text{and} \quad m_{\text{B}} = m_{\text{crit},5} = \frac{a(b-a+b)}{(a-b)(a-b)+(1-a)}. \)
Strong evolutionary forces, recombination rate $r = 0.5$

myr = 0.5;
mya = 0.2;
myb = 0.4;
myy1temp = 0.;
myy12temp = 0.;
myy21temp = 0.;
myy22temp = 0.;

mCritApprox = Min[mCritApproxFunc[myr, mya, myb], myb];
(* m must be lower than the (approximate) critical value and lower than $b_1$; however, this criterion is valid for the continuous-time version and provides a good approximation to the discrete-time version only if evolutionary forces are weak! *)

0.28

mCrit = mCritFunc[myr, mya, myb];
(* m must be lower than this critical value; this value is exact under the discrete-time version of the model. *)

0.333333

Critical values for the migration rate for the stability of the equilibrium $E_c$. 
m1 = mCrit1 /. {a -> mya, b -> myb}
m2 = mCrit2 /. {a -> mya, b -> myb}
m3 = mCrit3 /. {a -> mya, b -> myb, r -> myr}

0.333333

0.5

0.2

Show[Plot[rCritFunc[m, mya, myb], {m, 0, 1}, PlotRange -> {{0, 1.1 mCrit}, {0, 0.6}}, AxesLabel -> {m, "Critical recombination rate rB"}], (* Plot[rCritFunc[m, mya, myb], {m, mcl, mCrit}, PlotRange -> {{0, 0.08}, {0, 1}}, PlotStyle -> None, Filling -> {1 -> Axis}]], Graphics[{Gray, Dotted, Line[{{mcl, 0}, {mcl, 0.6}}]}], Graphics[{Text["m'", {.95 mcl, 0.8 * .5}]}], Graphics[{Gray, Dotted, Line[{{mCrit, 0}, {mCrit, 0.6}}]}], Graphics[{Text["mg", {mCrit + .05 mcl, 0.8 * .5}]}], Graphics[{Gray, Dashed, Line[{{0, .5}, {1, .5}}]}], Graphics[{Text["rmax", {.07, 1.1 * .5}]}], (* This uses exact critical values *)

Recall: 

\[ m' = m_{\text{crit,1}} = \frac{1-a}{b}, \quad m'' = m_{\text{crit,2}} = \frac{1-b}{a}, \quad \text{and} \quad m_B = m_{\text{crit,5}} = \frac{a(b-a+b)}{(a-b)(a-r)+(1-a)}. \]
plot14 = Show[{Plot[
    probEstablAMApproxFunc[myr, m, mya, myb, myy11temp, myy12temp, myy21temp, myy22temp][4],
    {m, mcl, 1}, PlotRange -> {{0, 1.1 + mCrit}, {0, 2 + mya}}, PlotStyle -> None,
    Filling -> {1 -> Axis}, FillingStyle -> RGBColor[0.9, 0.9, 0.9],
    Epilog -> Inset[Inset[0.045, 0.045], {0.04, 0.0383}, {0.021, 0.021}, Background -> White],
    Plot[probEstablAMApproxFunc[myr, m, mya, myb, myy11temp, myy12temp, myy21temp, myy22temp][2],
    PlotStyle -> {{RGBColor[0, 0.3, 1, 0.5], Thick}, {Red, Thick}, {Black, Thick}},
    PlotRange -> {0, mCrit}, {0, 2 + mya}},
    PlotStyle -> {{RGBColor[0.9, 0.3, 1, 0.5], Thick}, {Red, Thick}, {Black, Thick}},
    Graphics[Text[Style["r = " <> ToString[myr] <> "; a = " <> ToString[mya] <> "; b = " <>
    ToString[myb], FontFamily -> "Helvetica", FontSize -> 10, {0.1, 0.05}]],
    Graphics[{Gray, Dotted, Line[{{mcl, 0}, {mcl, 1.}}]}],
    Graphics[Text[Style["m_1", FontFamily -> "Helvetica"], {0.9 * mcl, 0.95 + 2 * mya}],
    Frame -> True, FrameStyle -> {{Black, Opacity[0]}, {Black, Opacity[0]}},
    FrameLabel -> {"Migration rate m", "Invasion probability"},
    LabelStyle -> {Directive[FontSize -> 14], FontFamily -> "Helvetica"}]}];
**Plots for arbitrary parameter combinations**

**Invasion probability as a function of recombination rate**

```math
Manipulate[
    Show[Plot[{
        probEstablAMApproxFunc[r, m, a, b, 0, 0, 0, 0][2],
        probEstablAMApproxFunc[r, m, a, b, 0, 0, 0, 0][3],
        probEstablAMApproxFunc[r, m, a, b, 0, 0, 0, 0][4]],
    {r, 0, 1.1 + rsCritFunc[m, a, b]}, PlotRange -> {{0, rsCritFunc[m, a, b]}, (0, 2 + a)},
    PlotStyle -> {{RGBColor[0, 0.3, 1, 0.5], Thick}, {Red, Thick}, {Black, Thick}},
    Frame -> True, FrameStyle -> {{Black, Opacity[0]}, {Black, Opacity[0]}},
    FrameLabel -> ("Recombination rate r", "Invasion probability"),
    LabelStyle -> (Directive[FontSize -> 14, FontFamily -> "Helvetica"],
    PlotLegend -> {Style["\(p_1\), conditional on background \(B_1\)"],
        FontFamily -> "Helvetica", 10],
    Style["\(p_2\), conditional on background \(B_2\)"],
        FontFamily -> "Helvetica"],
    Style["\(\bar{p}\), weighted mean across backgrounds"],
        FontFamily -> "Helvetica"}],
    LegendPosition -> (0, 0.19), LegendSize -> (1.3, 0.5),
    LegendShadow -> None, LegendTextSpace -> 1.3, LegendBorderStyle -> Automatic,
    LegendBorder -> None, LegendLabelSpace -> 1.8, LegendLabel -> Style["a = " <> ToString[a] <> "; b = " <> ToString[b] <> "; m = " <> ToString[m],
        FontFamily -> "Helvetica"]], {(a, 0.03), 0, 0.8}, {{b, 0.04}, 0, 0.8}, {{m, 0.032}, 0, 1}]
```

**Invasion probability as a function of migration rate**

```
mCrit1
```

```
a = 1 - b
```
Manipulate[Show[Plot[probEstablAMApproxFunc[r, m, a, b, 0, 0, 0, 0][4],
{m, a, m}, PlotRange -> {{0, mCritFunc[r, a, b]], {0, 2 * a}}, PlotStyle -> None,
Filling -> {1 -> Axis}, FillingStyle -> RGBColor[0.9, 0.9, 0.9, 1][*], Epilog->
Inset[inset4, (0.0375, 0.045), (0.04, 0.021), Background -> White] +]
Plot[{probEstablAMApproxFunc[r, m, a, b, 0, 0, 0, 0][2],
probEstablAMApproxFunc[r, m, a, b, 0, 0, 0, 0][3],
probEstablAMApproxFunc[r, m, a, b, 0, 0, 0, 0][4]},
{m, 0, 1}, PlotRange -> {{0, mCritFunc[r, a, b]], {0, 2 * a}},
PlotStyle -> {{RGBColor[0, 0.3, 1, 0.5], Thick}, (Red, Thick), (Black, Thick)}],
Graphics[{Gray, Dotted, Line[{{a, 0}, {a, 1 - b}}]},
Graphics[Text[Style["m = ", FontFamily -> "Helvetica"], {0.9 * a, 0.95 * 2 * a}], 1 - b],
Frame -> True, FrameStyle -> {{Black, Opacity[0]}, (Black, Opacity[0])},
FrameLabel -> {"Migration rate m", "Invasion probability"},
LabelStyle -> {Directive[FontSize -> 14], FontFamily -> "Helvetica"},
{(a, 0.2), 0.0, 0.8}, {(b, 0.4), 0, 0.8}, {(r, 0.1), 0, 0.5}]

\[ \frac{b - m (1 - a)}{(b (1 + m)) / . {a \rightarrow 0.2, b \rightarrow 0.4, r \rightarrow 0.01, m \rightarrow 0.} = 0.4 \]
Polymorphic continent

Deterministic analysis (Polymorphic continent)

- Marginal one-locus model
  Note that we exclude the cases of \( q_C = 0 \) and \( q_C = 1 \) here. The former is equivalent to the case of the monomorphic continent, and the latter corresponds to the trivial case in which the island will always become monomorphic with the island type.

- Definitions

\[
\text{assumeNeutrality}[n_\_] := \{w33[n] \to 1, w34[n] \to 1, w44[n] \to 1\}
\]

- Frequency of the \( B_1 \) allele in deme 1 (island) at the migration-selection equilibrium

\[
\]

\[
\text{assumeCI}[\{x[1, 2] \to 0, x[2, 2] \to 0, x[3, 2] \to qC, x[4, 2] \to 1 - qC, m[2] \to 0, p[2] \to 0, q[2] \to qC, LD[2] \to 0\}]
\]

\[
\text{recB}[3, 1] / . \text{assumeCI} // \text{FullSimplify}
\]

\[
\text{assumeAIRare}[1]
\]

\[
\{x[3, 1] \to q[1], x[4, 1] \to 1 - q[1]\}
\]
recB[3, 1] /. assumeCI /. assumeAllRare[1] // FullSimplify

- ((-1 + m[1]) q[1] (q[1] (w33[1] - w34[1]) + w34[1])) / 
  qC m[1] (qC (w33[2] - w34[2]) + w34[2])

qC (qC w33[2] - 2 (-1 + qC) w34[2]) + (-1 + qC)^2 w44[2]

assumeNeutral[2]


qC m[1] - ((-1 + m[1]) q[1] (q[1] (w33[1] - w34[1]) + w34[1])) / 

Generic relative fitnesses:

qEquilibriumGenericPolymCont = 

A very large output was generated. Here is a sample of it:

{[q[1] -> 
  1 - 6 (w33[1] - 2 w34[1] + w44[1])^2 ((1 + (-1 + qC) m[1]) w33[1] + (-3 + m[1] + 2 qC m[1]) w34[1] + 
    (2 + qC m[1]) w44[1]) + 
  2/3 (-2 w33[1]^3 + <<114>> + 
    Sqrt[4 <<1>>^3 + <<1>>^2]) 1/3, 
  q[1] -> 
  (-4 (-1 + qC m[1]) w33[1] + (-3 + m[1] - <<1>> <<1>> + (2 + qC m[1]) w44[1]) + 
    <<1>> <<1>> / (12 (w33[1] - 2 w34[1] + w44[1]))
}

We do not investigate this case further, but switch to a number of more specific fitness schemes.

Generic interactions between alleles within a haplotype, additive fitness interactions across haplotypes:

assumeGenericAdditiveFitnessB[1]


qEquilibriumGenericAdditivePolymCont = 
  assumeGenericAdditiveFitnessB[1] // FullSimplify} = q[1], q[1]] // FullSimplify

{{q[1] -> 
  (1 + (-1 + 2 qC) m[1]) v3[1] - 
    (1 + m[1] + 2 qC m[1]) v4[1] + 
    (1 + m[1] + 2 qC m[1]) v3[1] - 
    (1 + m[1] + 2 qC m[1]) v4[1] + 
    (1 + m[1] + 2 qC m[1]) v3[1] - (1 + m[1] + 2 qC m[1]) v4[1])^2 / 
  (2 (1 + m[1]) (v3[1] - v4[1]))}, 
  q[1] -> 
  (-1 + m[1] - 2 qC m[1]) v3[1] + 
  (1 + m[1] + 2 qC m[1]) v4[1] + 
    (1 + (-1 + 2 qC) m[1]) v3[1] - (1 + m[1] + 2 qC m[1]) v4[1])^2 / 
  (2 (1 + m[1]) (v3[1] - v4[1]))}

There are two solutions, and we need to establish which of them can be biologically valid and under which conditions.

Conditions for admissibility of the first equilibrium:

...
Hence, the first solution is a biologically valid equilibrium whenever allele $B_1$ has a higher fitness on the island than allele $B_2$, which is corresponds to the scenario we are interested in.

Conditions for admissibility of the second equilibrium:

\[
\]

\[v3[1] > v4[1]\]

The second solution is never a biologically valid equilibrium, given our assumptions.

We define in this case $\hat{q}$ as:

\[
qEquillBGenericAdditivePolymCont[1] / . \text{ruleSimplifyNotationCI} / . \{x_[1] \rightarrow x\} / \text{FullSimplify}
\]

\[
\left\{ q \rightarrow \frac{1}{2 (1 + m)} \left( (1 + m) (1 + 2 qC) v3[1] - (1 + m + 2 m qC) v4[1] + \sqrt{8 m (1 + m) qC (v3[1] - v4[1]) v4[1] + \left( (-1 + m - 2 m qC) v3[1] - (1 + m + 2 m qC) v4[1]\right)^2}}\right\}
\]

To summarise, $\hat{q}$ is a biologically admissible polymorphic one-locus equilibrium if

\[v3 > v4\]

(I)

Generic interactions between alleles within a haplotype, multiplicative fitness interactions across haplotypes:

\[
\]

\[
\left\{ \{ q[1] \rightarrow \frac{1}{2 (v3[1] - v4[1])} \left( (1 + qC m[1]) v3[1] - (1 + qC m[1]) v4[1] + \sqrt{4 qC m[1] (v3[1] - v4[1]) v4[1] + \left( (1 + qC m[1]) v3[1] - (1 + qC m[1]) v4[1]\right)^2}}\right\},
\]

\[
\left\{ q[1] \rightarrow \frac{1}{2 (v3[1] - v4[1])} \left( (-1 + qC m[1]) v3[1] + (1 + qC m[1]) v4[1] + \sqrt{4 qC m[1] (v3[1] - v4[1]) v4[1] + \left( (1 + qC m[1]) v3[1] - (1 + qC m[1]) v4[1]\right)^2}}\right\}\}
\]

There are two solutions, and we need to establish which of them can be biologically valid and under which conditions.

Conditions for admissibility of the first equilibrium:

\[
\text{FullSimplify[Reduce}\{0 < (q[1] / . qEquillBGenericMultiplicPolymCont[1]) \&\& (q[1] / . qEquillBGenericMultiplicPolymCont[1] < 1), m[1]\}, \text{Assumptions} \rightarrow \{0 < m[1] < 1 \&\& v3[1] \leq v4[1] > 0, 0 < qC < 1\}]
\]

\[v3[1] > v4[1]\]

Hence, the first solution is a biologically valid equilibrium whenever allele $B_1$ has a higher fitness on the island than allele $B_2$, which is corresponds to the scenario we are interested in.

Conditions for admissibility of the second equilibrium:

\[
\]

\[\text{False}\]

The second solution is never a biologically valid equilibrium, given our assumptions.
We define in this case \( \hat{q} \) as:

\[
\text{qEquillBGenericMultiplicPolymCont[1]} / . \text{ruleSimplifyNotationCI} / . (x_\{1\} \rightarrow x) / \\
\text{FullSimplify}
\]

\[
\left\{ q \rightarrow \frac{1}{2 (v_3 - v_4)} \left( (1 + m (-1 + qC)) v_3 - (1 + m qC) v_4 + \sqrt{4 m qC (v_3 - v_4) v_4 + ((1 + m (-1 + qC)) v_3 - (1 + m qC) v_4)^2} \right) \right\}
\]

To summarise, \( \hat{q} \) is a biologically admissible polymorphic one-locus equilibrium if

\[ v_3 > v_4. \]

Additive interactions between alleles within a haplotype, multiplicative fitness interactions across haplotypes:

\[
\text{qEquillBAdditiveMultiplicPolymCont} = \\
\text{Solve}[(\text{recB[3, 1] / . \text{assumeCI} / . \text{assumeARare[1] / . \text{assumeNeutrality[2]} / . \text{assumeAdditiveMultiplicFitnessB[1] / \text{FullSimplify} = q[1], q[1]}])} \\
\left\{ \left\{ q[1] \rightarrow \frac{1}{2 (b_1) m[1]} - \sqrt{2 b_1 m[1] + 4 qC b[1] m[1] + m[1]^2 - 4 qC b[1]^2 m[1]^2 + 4 qC^2 b[1]^2 m[1]^2} \right\} / \\
(2 (b[1] + b_1 m[1])) \right\}, \left\{ q[1] \rightarrow \frac{1}{2 (b_1 - m[1])} \right\}]
\]

There are two solutions, and we need to establish which of them can be biologically valid and under which conditions.

Conditions for admissibility of the first equilibrium:

\[
\text{FullSimplify}[\text{Reduce}[(0 < q[1] / . \text{qEquillBAdditiveMultiplicPolymCont[1]} \&\& (q[1] / . \text{qEquillBAdditiveMultiplicPolymCont[1]} < 1), m[1]], \\
\text{Assumptions} \rightarrow \{0 < m[1] < 1 \&\& 0 < b[1] < 1, 0 < qC < 1\}] \\
\text{False}
\]

The first solution is never a biologically valid one-locus polymorphism.

Conditions for admissibility of the second equilibrium:

\[
\text{Assumptions} \rightarrow \{0 < m[1] < 1 \&\& 0 < b[1] < 1, 0 < qC < 1\}] \\
\text{True}
\]

The second solution is always a biologically valid one-locus polymorphism, given our assumptions.

We illustrate this by plotting the two solutions as a function of \( m \), given, but variable parameter \( b \).

\[
\text{qEquillBAdditiveMultiplicPolymCont} / . \text{ruleSimplifyNotationCI} / . (x_\{1\} \rightarrow x) / \\
\text{FullSimplify}
\]

\[
\left\{ \left\{ q \rightarrow \frac{1}{2 b (1 + m)} \left( m - b (1 + 2 m qC) + \sqrt{m^2 + 2 b m (-1 + 2 qC) + b^2 \left( 1 + 4 m^2 (-1 + qC) qC \right)} \right) \right\}, \right.
\left. \left\{ q \rightarrow \frac{1}{2 b (1 + m)} \left( b - m + 2 b m qC + \sqrt{m^2 + 2 b m (-1 + 2 qC) + b^2 \left( 1 + 4 m^2 (-1 + qC) qC \right)} \right) \right\} \right\}
\]

\[\text{In[83]}\]

\[
\text{qEquillBAdditiveMultiplicPolymContFunc1[b_, m_, qC_] := -} \\
\frac{1}{2 b (1 + m)} \left( m - b (1 + 2 m qC) + \sqrt{m^2 + 2 b m (-1 + 2 qC) + b^2 \left( 1 + 4 m^2 (-1 + qC) qC \right)} \right)
\]

\[\text{In[84]}\]

\[
\text{qEquillBAdditiveMultiplicPolymContFunc2[b_, m_, qC_] := } \\
\frac{1}{2 b (1 + m)} \left( b - m + 2 b m qC + \sqrt{m^2 + 2 b m (-1 + 2 qC) + b^2 \left( 1 + 4 m^2 (-1 + qC) qC \right)} \right)
\]
\text{qCmin} = 0.;
qCmax = 1.;
Manipulate[
  Plot[{qEquiliBAdditiveMultiplicPolymContFunc1[b, m, qC],
    qEquiliBAdditiveMultiplicPolymContFunc2[b, m, qC]}, {m, 0, 1},
  PlotRange \rightarrow \{(-0.2, 1), (-0.2, 1), AxesLabel \rightarrow \{m, "\text{qB}\"\}\},
  {{b, 0.4}, 0., 1}, {{qC, 0.5}, qCmin, qCmax}]

The red curve corresponds to the second solution and always corresponds to a biologically one-locus equilibrium as long as our assumptions are fulfilled, whereas the second solution is always zero or negative (blue curve).

Additive interactions between alleles within a haplotype, multiplicative fitness interactions across haplotypes, and weak allelic effects (called ‘additive’ in the rest of the Notebook):

\text{qEquiliBAdditiveMultiplicApproxPolymCont} =
\text{assumeAdditiveMultiplicApproxFitnessB[1] // FullSimplify} = \text{q[1], q[1]}}

\text{Out[85]=}

There are two solutions, and we need to establish which of them can be biologically valid and under which conditions.

Conditions for admissibility of the first equilibrium:

\text{FullSimplify[Reduce[\{0 < (q[1]) /. qEquiliBAdditiveMultiplicApproxPolymCont[1]\} \&
  Assumptions \rightarrow \{0 < m[1] < 1 \&\& 0 < a[1] < b[1] < 1, a[1] + b[1] < 1, 0 < qC < 1\}]}

True

The first solution is always a biologically valid one-locus polymorphism, given our assumptions.
Conditions for admissibility of the second equilibrium:

\[ \text{FullSimplify}[\text{Reduce}[\{0 < (q[1] / q[1]) \&\& (q[1] / q[1]) < 1\}, m[1]], \text{Assumptions} \rightarrow \{0 < m[1] < 1 \&\& 0 < a[1] < b[1] < 1, a[1] + b[1] < 1, 0 < qC < 1\}] \]

False

The second solution is never a biologically valid one-locus polymorphism, given our assumptions.

We illustrate this by plotting the two solutions as a function of \(m\), for given, but variable parameter \(b\).

\[ \text{FullSimplify} \left[ \{ \{q \rightarrow \frac{1}{2 b (1 + m)} \left( b - m + a m + 2 b m qC + \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \right) \}, \{q \rightarrow \frac{1}{2 b (1 + m)} \left( b - m + a m + 2 b m qC - \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \right) \} \right] \]

We define this case \(\tilde{q}\) as

\[ \text{FullSimplify} \left[ \{ \{q \rightarrow \frac{1}{2 b (1 + m)} \left( b - m + a m + 2 b m qC + \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \right) \} \right] \]

\[ \text{FullSimplify} \left[ \{ \{q \rightarrow \frac{1}{2 b (1 + m)} \left( b - m + a m + 2 b m qC - \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \right) \} \right] \]

\[ \text{FullSimplify} \left[ \{ \{q \rightarrow \frac{1}{2 b (1 + m)} \left( b - m + a m + 2 b m qC + \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \right) \} \right] \]

\[ \text{FullSimplify} \left[ \{ \{q \rightarrow \frac{1}{2 b (1 + m)} \left( b - m + a m + 2 b m qC - \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \right) \} \right] \]
\[ q_{\text{Cmin}} = 0; \]
\[ q_{\text{Cmax}} = 1. ; \]
\[ \text{Manipulate[} \]
\[ \text{Plot[Evaluate[} \{q_{\text{EquilibriumAdditiveMultiplicApproxPolymContFunc1}}[a, b, m, qC], \]
\[ \text{q_{EquilibriumAdditiveMultiplicApproxPolymContFunc2}}[a, b, m, qC] \}, \{m, 0, 1\}, \]
\[ \text{PlotRange} \to \{(0.2, 1), (0.2, 1)\}, \text{AxesLabel} \to \{m, "q_{\text{Cbar}}"\}, \{\{a, 0.1\}, 0., 1.\}, \{\{b, 0.4\}, 0., 1.\}, \{\{qC, 0.5\}, q_{\text{Cmin}}, q_{\text{Cmax}}\}] \]

Importantly, with a polymorphic continent, existence of a biologically valid one-locus polymorphism is independent of the migration rate \( m \) as long as \( 0 < m < 1 \) holds. We note that there seems to exist only one biologically valid one-locus equilibrium as long as we require \( a + b < 1 \), which is the condition for non-negative relative fitnesses.

**Stochastic analysis (multi-type branching process)**

- **Explicit probability generating functions**

Recall the generic probability generating functions:

\[ \text{pgf}[1, 1] \]
\[ \text{pgf}[2, 1] \]
\[ \text{assumeA1Rare}[1] \]
\[ \{x[3, 1] \to q[1], x[4, 1] \to 1 - q[1]\} \]

The frequency of \( B_1 \) at the marginal one-locus migration-selection equilibrium:

\[ q[1] / . \text{q_{EquilibriumAdditiveMultiplicApproxPolymContFunc1}[1]} \]
\begin{align*}
\text{pgf1PolymCont} & = \text{pgf[1, 1] / . qEquill1AdditiveMultiplicApproxPolymCont[1] / . wbar[1] \to \text{wMeanB[1] / . assumeAdditiveMultiplicEpistaticApproxPolymCont[1] / . assumeAdditiveMultiplicEpistaticApproxFitness[1] / . assumeAllRare[1] / . w1[1] \to \text{wArgType[1, 1] / . assumeAdditiveMultiplicEpistaticApproxPolymCont[1] / . assumeAdditiveMultiplicEpistaticApproxFitness[1] / . g[1][1] \to 0, g[12][1] \to 0, g[21][1] \to 0, g[22][1] \to 0 / . qEquill1AdditiveMultiplicApproxPolymCont[1] / . a[1] \to a, b[1] \to b, m[1] \to m, s[1] \to s1, s[2] \to s2} / \text{FullSimplify}
\end{align*}

\begin{align*}
\text{pgf1PolymContShort} & = e \\
\text{pgf1PolymContShort} - \text{pgf1PolymCont} / . \text{RlRule} / \text{FullSimplify}
\end{align*}

\begin{align*}
\text{Collect} & \left[ 1-m \right] \left[ b^2 \left( 1+2 \text{m qC} \right) \left( -1+s1 \right) + \left( -1+a \right) \text{m + R1} \right] \left[ s1-s2 \right] + b \left( -2-R1+2 s1+R1 s1-r s1+ m \right) \left( -1+a \right) \left( -1+s1 \right) + s1 \left( -1+a \right) m+R1) + s1 \left( -1+a \right) \left( -1+s1 \right) + r s2) \right] + \left\{ s1, s2 \right\}
\end{align*}

\begin{align*}
\text{FullSimplify} & \left[ -2 b-b m-a b m-b^2 \left( 1+2 \text{m qC} \right) \right] - b \left( 2+b m+a m+2 b m \text{qC}+R1 \right)
\end{align*}

\begin{align*}
\text{FullSimplify} & \left[ 2 b+b m+a b m+b^2 \left( 1+2 \text{m qC} \right) - b r+2 b m \left( -1+\text{qC} \right) r+b R1+r \left( \left( -1+a \right) m+R1 \right) \right] \left( -1+a \right) \left( -1+qC \right) + R1)
\end{align*}

\begin{align*}
\text{FullSimplify} & \left[ b r-2 b m \left( -1+\text{qC} \right) r-\left( -1+a \right) m+R1)) \right] \left( -1+a \right) m+R1)
\end{align*}

\begin{align*}
\text{pgf1PolymContDisplay} & = \left( 1-m \right) \left[ b^2 \left( 1+2 \text{qC} \right) -1 \right] \left[ -1+\text{a m}+R1) \right] \text{a} \to \text{a m}} \text{b m m b m qC - R1}
\end{align*}

\begin{align*}
\text{Check if this terms coincides with the one for the monomorphic continent if we set qC = 0.}
\end{align*}

\begin{align*}
\text{FullSimplify} & \left[ \text{pgf1PolymContDisplay} / . \text{RlRule} / \{ \text{qC} \to 0, \text{Assumptions} \to \text{Flatten}[\{\text{assumeGeneral, m < mCrit2}\}] \right] \\
\text{FullSimplify} & \left[ \text{pgf1Add} / \text{Simplify} \right]
\end{align*}
This seems fine.

In[91] := pgf2PolymCont =

Collect[(1 - m) (Sqrt[2 - 2 m] (-(1 + m) + 2 b Sqrt[-1 + m] - Sqrt[-1 + m] b + b (-1 + m) - Sqrt[-1 + m] b))
(1 - m) (-(1 - a) m + Rl) r (s1 - s2) + b^2 (-(1 + m) (-1 + qC)) (-1 + s2) + 
b (r (s1 - s2) + (2 + Rl) (-1 + s2) + m (-1 + 2 qC r (s1 - s2) + a (-1 + s2) + s2)), {s1, s2}]

Collect[(1 - m) (-2 b - b m - a b m - b^2 (-1 + 2 m (-1 + qC)) - b Rl) + 
(1 - m) (b r + 2 b m qC r + r (-1 + a) m + Rl)) s1 + 
(1 - m) (b m + a b m + b^2 (-1 + 2 m (-1 + qC))) - b r - 2 b m qC r + b (2 + Rl) - r (-1 + a) m + Rl]

FullSimplify[(1 - m) (-2 b - b m - a b m - b^2 (-1 + 2 m (-1 + qC)) - b Rl)]

FullSimplify[(b r + b m qC r + r ((-1 + a) m + Rl))]

FullSimplify[(b r + b m qC r + r ((-1 + a) m + Rl))]

Collect[(1 - m) (b m + a b m + b^2 (-1 + 2 m (-1 + qC))) - b r - 2 b m qC r + b (2 + Rl) - r (-1 + a) m + Rl)]

FullSimplify[(b m + a b m + b^2 (-1 + 2 m (-1 + qC))) - b r - 2 b m qC r + b (2 + Rl) - r (-1 + a) m + Rl)]

Check if this terms coincides with the one for the monomorphic continent if we set qC = 0.

FullSimplify[pgf2PolymContDisplay /. RlRule /. (qC → 0), 
Assumptions → Flatten[{assumeGeneral, m < mMcrit2}]]
Importantly, the parameter $q$, enters only in the recursion equations for $x_1 = [A_1 B_1]$ and $x_2 = [A_2 B_2]$, but not in those for $x_3 = [A_3 B_3]$, and $x_4 = [A_4 B_4]$. As a consequence, the mean matrix is not affected, because it only concerns the dynamics of $x_1$ and $x_2$. What is affected, though, is the frequency of $B_1$ on the island at the marginal one-locus migration-selection equilibrium.

```
In[93]:= probEstablAMApproxPolymContFunc::usage = "probEstablAMApproxPolymContFunc[r, ml, al, bl probEstablAMApproxPolymContFunc[r, ml, al, bl, y111, y121, y211, y221, qC] := Module[{qE

\[\begin{align*}
qE &= \frac{-b1 + m1 + 2b1 + m1 + qC + \sqrt{4b1 + (-1 + a1 + b1) m1 + (1 + m1) qC + (b1 + (-1 + a1) m1 + 2b1 + m1 + qC)^2}}{2b1 + (1 + m1)}
\end{align*}\]

wbar = 1 - a1 + b1 + (-1 + 2 qE);

w1 = 1 + b1 + qE + (-1 + qE) + y111;

w2 = 1 + b1 + (-1 + qE) - qE + y111 + y121 + (-1 + qE);

w4 = 1 - y111;

(* Leading eigenvalue of the mean matrix; Note that qE does not enter here! *)

A1 = -1 + m1 + (w1 - w14 + w2 + w1^2 + r^2 + w14^2 + w1 (2 (-1 + qE) r + w14 - 2 w2) + 2 (-m1 + 2 qE) r + 2 wbar

(* Probability generating functions *)

pgf1[s1_, s2_] := Exp[-r (m1 + (1 - qE) + (1 - s2)) w14 - (1 - m1) (1 - s1) (w1 - r (1 - qE) w14) wbar]

pgf2[s1_, s2_] := Exp[-r (m1 + qE) (1 - s1) w14 - (1 - m1) (1 - s2) (-r + qE w14 + w2) wbar]

qSol = FindRoot[{pgf1[q1, q2] == q1, pgf2[q1, q2] == q2}, {q1, 0.5}, {q2, 0.5}];

(* Return the probability of establishment, 1-q *)

Return[{A1, (1 - q1), (1 - q2), qE + (1 - q1) + (1 - q2) qE / qSol}];

(* Rules for the specific model considered *)

```

- **Explicit equilibrium frequency of $B_1$**

```

Out[96]= 1

\[\begin{align*}
&= \frac{1}{1 + \sqrt{\frac{-4 (-b1 + b1 m1) (qC m1 - qC a1 m1 + qC b1 m1) + (b1 - m1 + a1 m1 + 2 qC b1 m1)^2}}{2 (-b1 + b1 m1)}}
\end{align*}\]
```

- **Explicit fitnesses**

```
In[97]:= WMeanB[1]


```

Note that the following expressions for mean and marginal fitnesses are identical to ‘wbarAMApprox’. The difference will exclusively be in $q$, for which we will later insert the frequency of $B_1$ on the island at the marginal one-locus migration-selection equilibrium. We therefore do not assign new variables, but just restate the ones here:

```
wbarAMApprox
1 - a1 + b1 (-1 + 2 q[1])
w1AMApprox
1 - q[1] + (1 + b1) q[1]
w2AMApprox
(1 - b1) (1 - q[1]) + q[1]
w4AMApprox[1]
```

1
Explicit mean matrix

Remember the mean matrix and our assertions about additive fitnesses:

$$G[1] \ / . \ \text{ruleSimplifyNotationCI} / / \ \text{MatrixForm}$$

\[
\begin{pmatrix}
(1-m) \cdot (w[1] \cdot (1-q) \cdot r_{w4}[1]) & (1-m) \cdot q \cdot r_{w4}[1] \\
\text{wbar}[1] & \text{wbar}[1]
\end{pmatrix}
\begin{pmatrix}
(1-m) \cdot (1-q) \cdot r_{w4}[1] \\
\text{wbar}[1]
\end{pmatrix}
\]

\text{assumeAdditiveMultiplicApproxFitness[1]}

\{w[1][1] \rightarrow 1 + a[1] + b[1], w[1][2] \rightarrow 1 + a[1], w[1][3] \rightarrow 1 + b[1],
\ w[1][4] \rightarrow 1, w[2][1] \rightarrow 1 + a[1] + b[1], w[2][4] \rightarrow 1 - b[1],
\ w[3][1] \rightarrow 1 - a[1] + b[1], w[3][4] \rightarrow 1 - a[1], w[4][1] \rightarrow 1 - a[1] - b[1]\}

\text{ruleSimplifyNotationCI}

\{m[1] \rightarrow m, x[1, 1] \rightarrow x1, x[2, 1] \rightarrow x2, x[3, 1] \rightarrow x3, x[4, 1] \rightarrow x4, q[1] \rightarrow q\}

We now substitute specific formulas for 'wbar' and 'q':

$$\text{qhatAMApproxPolymCont}$$

\[
\frac{1}{2 \cdot (-b[1] - b[1] \cdot m[1])} \cdot \left\{ (-b[1] + m[1] - a[1] \cdot m[1] - 2 \cdot qC \cdot b[1] \cdot m[1]) - \sqrt{-4 \cdot (-b[1] - b[1] \cdot m[1]) \cdot (qC \cdot m[1] - qC \cdot a[1] \cdot m[1] - qC \cdot b[1] \cdot m[1]) + \left\{ (b[1] - m[1] + a[1] \cdot m[1] + 2 \cdot qC \cdot b[1] \cdot m[1])^2 \right\}}
\]

$$\text{GAddPolymCont} =$$

$$G[1] \ / . \ \text{ruleSimplifyNotationCI} / . \ \{w[1][1] \rightarrow w[1] \cdot \text{AMApprox}, w[2][1] \rightarrow w[2] \cdot \text{AMApprox},
\ w[bar][1] \rightarrow \text{wbar} \cdot \text{AMApprox} / . \ \text{assumeAdditiveMultiplicApproxFitness[1] / .}
\ (q[1] \rightarrow \text{qhatAMApproxPolymCont} / . \ (q \rightarrow \text{qhatAMApproxPolymCont}) / .
\ \text{ruleSimplifyNotationCI} / . \ (x[1]_1 \rightarrow x) / / \text{FullSimplify;}$$

$$\text{GAddPolymCont} / / \ \text{MatrixForm}$$

\[
\begin{pmatrix}
\frac{1}{2 \cdot (-b[1] - b[1] \cdot m[1])} \cdot \left\{ (-b[1] + m[1] - a[1] \cdot m[1] - 2 \cdot qC \cdot b[1] \cdot m[1]) - \sqrt{-4 \cdot (-b[1] - b[1] \cdot m[1]) \cdot (qC \cdot m[1] - qC \cdot a[1] \cdot m[1] - qC \cdot b[1] \cdot m[1]) + \left\{ (b[1] - m[1] + a[1] \cdot m[1] + 2 \cdot qC \cdot b[1] \cdot m[1])^2 \right\}}
\end{pmatrix}
\]

This is what we call \( \lambda_{11} \) in the main text:

$$\text{Collect} \{ \text{GAddPolymCont}[[1, 1]], x \} / .
\left\{ \sqrt{-4 \cdot b \cdot (-1 + a + b) \cdot m \cdot (1 + m) \cdot qC \cdot (b + (-1 + a) \cdot m + 2 \cdot b \cdot m \cdot qC)^2} \rightarrow R1 \right\}$$

\[
\begin{pmatrix}
-1 + m \cdot x \cdot (-b + (-1 + a) \cdot m + 2 \cdot b \cdot m \cdot (-1 + qC) + R1) \\
\end{pmatrix}
\]

\[
\begin{pmatrix}
2 \cdot b \cdot (1 - a + b \cdot m) \cdot (-1 + 2 \cdot qC) + R1 \\
\end{pmatrix}
\]

\[
\begin{pmatrix}
2 \cdot b \cdot (1 - a + b \cdot m) \cdot (-1 + 2 \cdot qC) + R1 \\
\end{pmatrix}
\]

\[
\begin{pmatrix}
2 \cdot b \cdot (1 - a + b \cdot m) \cdot (-1 + 2 \cdot qC) + R1 \\
\end{pmatrix}
\]

\[
\begin{pmatrix}
2 \cdot b \cdot (1 - a + b \cdot m) \cdot (-1 + 2 \cdot qC) + R1 \\
\end{pmatrix}
\]

This is what we call \( \lambda_{12} \) in the main text:
Collect[GAddPolymCont[2, 1], r] /.
\[\sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \rightarrow R1\]
\[r (-b + m (-1 + a + b)) + R1\]
\[2 b (-1 + a + b)\]
\[\text{FullSimplify}[\text{Collect}[\text{GAddPolymCont}[2, 1], r]] / . \ qC \rightarrow 0,\]
Assumptions \rightarrow \{0 < a < b < 1, 0 < m < 1, m < b / (1 - a)\}
\[m r \]
\[b\]
\[r (-b + m (-1 + a + b) (-1 + qC)) + R1\]
\[2 b (-1 + a + b)\]
This is what we call \(b_1\) in the main text:
\[\text{Collect}[\text{GAddPolymCont}[1, 2], r] /.
\[\sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \rightarrow R1\]
\[r (b - m + a m - 2 b m qC + R1)\]
\[2 b (1 - a + b)\]
\[\text{FullSimplify}[\text{Collect}[\text{GAddPolymCont}[1, 2], r]] / . \ qC \rightarrow 0,\]
Assumptions \rightarrow \{0 < a < b < 1, 0 < m < 1, m < b / (1 - a)\}
\[(b + (-1 + a) m) r \]
\[b (1 - a + b)\]
\[r \left| b + (-1 + a) m - 2 b m qC + \sqrt{R1} \right|\]
\[2 b (1 - a + b)\]
This is what we call \(b_2\) in the main text:
\[\text{Collect}[\text{GAddPolymCont}[2, 2], r] /.
\[\sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \rightarrow R1\]
\[(-1 + m) r (-b + (1 - a) m - 2 b m qC - R1)\]
\[2 b (1 - a + b m (-1 + 2 qC) + R1)\]
\[\text{FullSimplify}[\text{Collect}[\text{GAddPolymCont}[2, 2], r]] / . \ qC \rightarrow 0,\]
Assumptions \rightarrow \{0 < a < b < 1, 0 < m < 1, m < b / (1 - a)\}
\[(-1 + m) (b + (1 - a) m + 2 b m qC + R1)\]
\[2 b (1 - a + b m (-1 + 2 qC) + R1)\]
\[\text{FullSimplify}[\text{Collect}[\text{GAddPolymCont}[2, 2], r]] / . \ qC \rightarrow 0,\]
Assumptions \rightarrow \{0 < a < b < 1, 0 < m < 1, m < b / (1 - a)\}
\[b^2 m + (-1 + a) m r + b (-1 - a m + R1)\]
\[(-1 + a - b) b\]
\[\text{Collect}\left[\frac{b^2 m + (-1 + a) m r + b (-1 - a m + r)}{(-1 + a - b) b}, r\right] \]
\[\frac{-b - a b m + b^2 m}{(-1 + a - b) b} \]
\[-(b + (-1 + a) m) r \]
\[\text{FullSimplify}\left[\frac{-b - a b m + b^2 m}{(-1 + a - b) b}\right] \]
\[\frac{1 + a m - b m}{1 - a + b} \]
\[\text{b[27]} := \text{EPolymCont} := \frac{(1 - m) (2 + b + a m + 2 b m q C + R1)}{2 (1 - a - b m (1 - 2 q C) + R1)} \]
\[\text{FPolymCont} := \frac{(1 - m) ((1 - a) m + b + 2 b m (1 - q C) - R1)}{2 b (1 - a - b m (1 - 2 q C) + R1)} \]
\[\text{GPolymCont} := \frac{b + m (1 - a - 2 b (1 - q C)) - R1}{2 b (1 - a - b)} \]
\[\text{HPolymCont} := \frac{b - (1 - a) m - 2 b m q C + R1}{2 b (1 - a + b)} \]
\[\text{IPolymCont} := \frac{(1 - m) (b - (1 - a) m + 2 b m q C + R1)}{2 b (1 - a - b m (1 - 2 q C) + R1)} \]
\[\text{JPolymCont} := \frac{(1 - m) (2 + m + a m - b (1 + 2 m (1 - q C)) + R1)}{2 (1 - a - b (m - 2 m q C) + R1)} \]
\[\text{tt1} := \text{Exp}[-\lambda 11 (1 - s_1) - \lambda 12 (1 - s_2)] /.
\{\lambda 11 \to \text{GAddPolymCont}[1, 1], \lambda 12 \to \text{GAddPolymCont}[2, 1]\} \]
\[\sqrt{-4 b (-1 + a + b) m (1 + m) q C + (b + (-1 + a) m + 2 b m q C)^2} \to R1 \]
\[\text{tt1} - \text{pgf1PC}[s_1, s_2] / . \text{RIRule} / \text{Simplify} \]
\[0 \]
\[\text{tt2} := \text{Exp}[-\lambda 21 (1 - s_1) - \lambda 22 (1 - s_2)] /.
\{\lambda 21 \to \text{GAddPolymCont}[1, 2], \lambda 22 \to \text{GAddPolymCont}[2, 2]\} \]
\[\sqrt{-4 b (-1 + a + b) m (1 + m) q C + (b + (-1 + a) m + 2 b m q C)^2} \to R1 \]
\[\text{tt2} - \text{pgf2PC}[s_1, s_2] / . \text{RIRule} / \text{Simplify} \]
\[0 \]
\[\text{Collect}[\text{GAddPolymCont}[1, 1], r] /.
\[\left\{\sqrt{-4 b (-1 + a + b) m (1 + m) q C + (b + (-1 + a) m + 2 b m q C)^2} \to R1\right\} -
\left(\text{EPolymCont} + \text{FPolymCont}\right) / \text{Simplify} \]
\[0 \]
\[\text{Collect}[\text{GAddPolymCont}[2, 1], r] /.
\[\left\{\sqrt{-4 b (-1 + a + b) m (1 + m) q C + (b + (-1 + a) m + 2 b m q C)^2} \to R1\right\} -
\left(\text{GPolymCont}\right) / \text{Simplify} \]
\[0 \]
\( \text{Collect}[\text{GAddPolymCont}[1, 2], r] /.
\) \( \left\{ \sqrt{-4 \, b \, (-1 + a + b) \, m \, (1 + m) \, qC \, + \, (b \, + \, (-1 + a) \, m \, + \, 2 \, b \, m \, qC)^2} \, \rightarrow \, R1 \right\} \)

\( \text{HPolymCont} \) // Simplify

0

\( \text{Collect}[\text{GAddPolymCont}[2, 2], r] /.
\) \( \left\{ \sqrt{-4 \, b \, (-1 + a + b) \, m \, (1 + m) \, qC \, + \, (b \, + \, (-1 + a) \, m \, + \, 2 \, b \, m \, qC)^2} \, \rightarrow \, R1 \right\} \)

\( \text{JPolyCont} + \text{IPolyCont} \) // Simplify

0

\( e^{-\lambda 11} (1-s1) \, e^{-\lambda 12} (1-s2) /.
\) \( \left\{ \lambda 11 \rightarrow (\text{EE} + \text{FF} \, r), \, \lambda 12 \rightarrow (\text{GG} \, r) \right\} \)

\( e^{-\lambda 21} (1-s1) \, e^{-\lambda 22} (1-s2) /.
\) \( \left\{ \lambda 21 \rightarrow (\text{HH} \, r), \, \lambda 22 \rightarrow (\text{JJ} + \text{II} \, r) \right\} \)

\( \text{Collect}[-(\text{EE} + \text{FF} \, r) \, (1-s1) - \text{GG} \, r \, (1-s2), \, \{s1, \, s2\}] \)

\(-\text{EE} + \text{FF} \, r \, - \, \text{GG} \, r \, + \, (\text{EE} + \text{FF} \, r) \, s1 + \text{GG} \, r \, s2 \)

\( e^{-\lambda 21} (1-s1) \, e^{-\lambda 22} (1-s2) /.
\) \( \left\{ \lambda 21 \rightarrow (\text{HH} \, r), \, \lambda 22 \rightarrow (\text{JJ} + \text{II} \, r) \right\} \)

\( \text{Collect}[-\text{HH} \, r \, (1-s1) - (\text{JJ} + \text{II} \, r) \, (1-s2), \, \{s1, \, s2\}] \)

\(-\text{JJ} - \text{HH} \, r \, - \, \text{II} \, r \, + \, \text{HH} \, r \, s1 + (\text{JJ} + \text{II} \, r) \, s2 \)

t1 = \text{GAddPolymCont} / (a \rightarrow \alpha \, e, \, b \rightarrow \beta \, e, \, m \rightarrow \mu \, e, \, r \rightarrow \rho \, e, \, qC \rightarrow \xi \, e);

t1 // \text{MatrixForm}

\text{FullSimplify[}
\text{Series[t1, \{e, 0, 1\}] / (a \rightarrow \alpha \, e, \, \beta \rightarrow \beta \, e, \, \rho \rightarrow r \, / \, e, \, \mu \rightarrow m \, / \, e, \, \xi \rightarrow qC \, / \, e) // Normal, 
\text{Assumptions \rightarrow \{0 < a < b < 1, \, a + b < 1, \, 0 < m < 1\}}]

\text{t2 = GAddPolymCont} / (a \rightarrow \alpha \, e, \, b \rightarrow \beta \, e, \, m \rightarrow \mu \, e, \, r \rightarrow \rho \, e);

t2 // \text{MatrixForm}

\text{GAddPolymContSmallForces =}
\text{FullSimplify[Series[t2, \{e, 0, 1\}] / (a \rightarrow \alpha \, e, \, \beta \rightarrow \beta \, e, \, \rho \rightarrow r \, / \, e, \, \mu \rightarrow m \, / \, e) // Normal, 
\text{Assumptions \rightarrow \{0 < a < b < 1, \, a + b < 1, \, 0 < m < 1\}}]:
We evaluate the assumptions here.

\[
\text{FullSimplify}\left[\text{GAddPolymContSmallForces} / \{ (b - m)^2 + 4 b m q C \to R1 \}\right] / \text{MatrixForm}
\]

\[
\begin{pmatrix}
\frac{b^2 r \left[ -m \sqrt{R1} \right] - b \left[ -2 a + m + \sqrt{R1} \right]}{2 b} & \frac{r \left[ b - m \sqrt{R1} \right]}{2 b} \\
\frac{r \left[ b - m \sqrt{R1} \right]}{2 b} & \frac{b^2 r \left[ -m \sqrt{R1} \right] - b \left[ -2 a + m + \sqrt{R1} \right]}{2 b}
\end{pmatrix}
\]

Collect\left[\text{GAddPolymContSmallForces} / \{ (b - m)^2 + 4 b m q C \to R1 \}, r \right] / \text{MatrixForm}

\[
\begin{pmatrix}
\frac{r \left[ b - m \sqrt{R1} \right]}{2 b} + \frac{2 b^2 a b + b^2 - b m - b \sqrt{R1}}{2 b} & \frac{r \left[ b - m \sqrt{R1} \right]}{2 b} \\
\frac{r \left[ b - m \sqrt{R1} \right]}{2 b} & \frac{r \left[ b - m \sqrt{R1} \right]}{2 b} + \frac{2 b^2 a b + b^2 - b m - b \sqrt{R1}}{2 b}
\end{pmatrix}
\]

\[
\text{FullSimplify}\left[\frac{r \left[ b - m \sqrt{R1} \right]}{2 b} \right]
\]

\[
\text{FullSimplify}\left[\frac{2 b + 2 a b + b^2 - b m - b \sqrt{R1}}{2 b} \right]
\]

\[
\frac{1}{2} \left[ 2 a + b - m - \sqrt{R1} \right]
\]

\[
\text{FullSimplify}\left[\frac{r \left[ b - m \sqrt{R1} \right]}{2 b} \right]
\]

\[
\text{FullSimplify}\left[\frac{-2 b - 2 a b + b^2 + b m + b \sqrt{R1}}{2 b} \right]
\]

\[
\frac{1}{2} \left[ 2 a + b - m - \sqrt{R1} \right]
\]

This assumes small evolutionary forces \((a, b, m, r)\) but does not restrict the frequency \(q_C\) of \(B_1\) on the continent.

We evaluate the mean evolutionary and marginal fitnesses at the one-locus migration-selection equilibrium.

\[
\text{w1AMApprox} / . \{ q[1] \to qhatAMApproxPolymCont \} / . \{ x_[1] \to x \} / \text{FullSimplify}
\]

\[
\frac{1}{2 (1 + m)} \left[ 2 + b + m + a m + 2 b m q C + \sqrt{-4 b \left( b - m + a \right) m \left( 1 + m \right) q C + \left( b + \left( b - m + a \right) m + 2 b m q C \right)^2} \right]
\]

\[
\text{w2AMApprox} / . \{ q[1] \to qhatAMApproxPolymCont \} / . \{ x_[1] \to x \} / \text{FullSimplify}
\]

\[
\frac{1}{2 (1 + m)} \left[ 2 + m + a m + b \left( b - m + a \right) m + \sqrt{-4 b \left( b - m + a \right) m \left( 1 + m \right) q C + \left( b + \left( b - m + a \right) m + 2 b m q C \right)^2} \right]
\]
\[
\frac{1}{1 + m} \left[ 1 - a + b m (1 + m) q C + \sqrt{-4 b (-1 + a + b) m (1 + m) q C + (b + (-1 + a) m + 2 b m q C)^2} \right]
\]

**Explicit conditions for invasion**

Recall the generic condition for invasion:

\[
\text{conditionNonExtinction}[1] = \frac{w14[1] - (1 - q[1]) w2[1] + \frac{\text{wbar}[1]}{1 - m[1]} - \frac{w2[1]}{1 - m[1]} - \frac{\text{wbar}[1]}{1 - m[1]}}{2 (1 - m)^2}
\]

\[
\begin{align*}
\text{conditionNonExtinction} \text{AMApproxPolymCont} &= \text{FullSimplify}[
\text{conditionNonExtinction}[1] \rightarrow \text{w14AMApprox}[1], \text{wbar}[1] \rightarrow \text{wbarAMApprox,}
\text{w1}[1] \rightarrow \text{w1AMApprox, w2}[1] \rightarrow \text{w2AMApprox}].
\end{align*}
\]

As expected according to a Theorem by Haccou et al. (2005), the invasion condition obtained based on the mean matrix is the same as the one obtained from a corresponding deterministic model.
We want to express the condition in terms of $m$, $q_C$, or $r$. However, this takes more than 2 hours on a Mac mini with 2.3 GHz Intel Core i5 with 4 GB of RAM.

```math
condMAdditiveMultiplicAMApproxPolymContM = FullSimplify[Refine[Reduce[(conditionNonExtinctionAMApproxPolymCont), m], Assumptions -> {0 < a < b < 1, a + b < 1, 0 < m < 1, 0 < qC < 1, 0 < r <= 1/2}]]
```

$\text{Aborted}$

```math
condMAdditiveMultiplicAMApproxPolymContQC = FullSimplify[Refine[Reduce[(conditionNonExtinctionAMApproxPolymCont), qC], Assumptions -> {0 < a < b < 1, a + b < 1, 0 < m < 1, 0 < qC < 1, 0 < r <= 1/2}]]
```

$\text{Aborted}$

```math
condMAdditiveMultiplicAMApproxPolymContR = FullSimplify[Refine[Reduce[(conditionNonExtinctionAMApproxPolymCont), r], Assumptions -> {0 < a < b < 1, a + b < 1, 0 < m < 1, 0 < qC < 1, 0 < r <= 1/2}]]
```

$\text{Aborted}$

Simplify[Refine[Reduce[(conditionNonExtinctionAMApproxPolymCont), r], Assumptions -> {0 < a < b < 1, a + b < 1, 0 < m < 1, 0 < qC < 1, 0 < r <= 1/2}]]

$\text{Aborted}$

### Plots of numerical solutions

- Plots for various parameter combinations (‘regimes’)
- Invasion probabilities as a function of recombination rate $r$, weak evolutionary forces

```math
In[103]:= myb1 = 0.04;
myy111 = 0.;
myy121 = 0.;
myy211 = 0.;
myy221 = 0.;
rMax1 = 0.2;
```
Manipulate[
  Show[Plot[{probEstablAMApproxPolymContFunc[r, m, a, myb1, myy111, myy121, myy211, myy221, qC][2],
    probEstablAMApproxPolymContFunc[r, m, a, myb1, myy111, myy121, myy211, myy221, qC][3],
    probEstablAMApproxPolymContFunc[r, m, a, myb1, myy111, myy121, myy211, myy221, qC][4],
    {r, 0, rMax1}, PlotRange -> {{0, rMax1}, (0, 2*a)},
    PlotStyle -> {{RGBColor[0, 0.3, 1, 0.5], Thick}, {Red, Thick}, {Black, Thick}},
    Frame -> True, FrameStyle -> {{Black, Opacity[0]}, {Black, Opacity[0]}},
    FrameLabel -> ("Recombination rate r", "Invasion probability"),
    LabelStyle -> (Directive[FontSize -> 14, FontFamily -> "Helvetica"],
    PlotLegend -> {Style["\(\pi_1\), conditional on background \(B_1\)"], FontFamily -> "Helvetica"],
    Style["\(\pi_2\), conditional on background \(B_2\)"], FontFamily -> "Helvetica"],
    Style["\(\bar{\pi}\), weighted mean across backgrounds"], FontFamily -> "Helvetica"}],
    LegendPosition -> (-0.05, 0.175), LegendSize -> {1.3, 0.5}, LegendShadow -> None,
    LegendTextSpace -> 10, LegendBorderSpace -> Automatic, LegendBorder -> None,
    LegendLabelSpace -> 1.8, LegendLabel -> Style["a = " <> ToString[a] <> "; b = " <>
    ToString[myb1] <> "; m = " <> ToString[m], FontFamily -> "Helvetica"]
    ],
    {{a, 0.02}, 0., myb1}, {{m, 0.022}, 0., myb1}, {{qC, 0.1}, 0., 1.}]

- Invasion probabilities as a function of migration rate \(m\), weak evolutionary forces

In[109] :=
myb2 = 0.04;
myy112 = 0.;
myy122 = 0.;
myy212 = 0.;
myy222 = 0.;
nMax2 = 0.06;
Manipulate[
    Show[Plot[{probEstablAMApproxPolymContFunc[r, m, a, myb2, myy112, myy122, myy212, myy222, qC][2], probEstablAMApproxPolymContFunc[r, m, a, myb2, myy112, myy122, myy212, myy222, qC][4]}, {m, 0, mMax2}, PlotRange -> {{0, mMax2}, {0, 2 + a}}, PlotStyle -> {{RGBColor[0, 0.3, 1, 0.5], Thick}, {Red, Thick}, {Black, Thick}}, Frame -> True, FrameStyle -> {{Black, Opacity[0]}, {Black, Opacity[0]}}, FrameLabel -> ({"Migration rate m", "Invasion probability"}), LabelStyle -> {Directive[FontSize -> 14], FontFamily -> "Helvetica"}, PlotLegend -> {Style["\(p_1\), conditional on background \(B_1\)", FontFamily -> "Helvetica"], Style["\(p_2\), conditional on background \(B_2\)", FontFamily -> "Helvetica"], Style["\(\bar{\pi}\), weighted mean across backgrounds", FontFamily -> "Helvetica"], LegendPosition -> {-0.05, 0.175}, LegendSize -> {1.3, 0.5}, LegendShadow -> None, LegendTextSpace -> 10, LegendBorderSpace -> Automatic, LegendBorder -> None, LegendLabelSpace -> 1.8, LegendLabel -> Style["a = " <> ToString[a] <> "; b = " <> ToString[myb2] <> "; \(r = \) " <> ToString[r], FontFamily -> "Helvetica"]}, {{a, 0.02}, 0., myb2}, {{r, 0.01}, 0., 0.5}, {{qC, 0.1}, 0., 1.}]

Invasion probabilities as a function of recombination rate \(r\), strong evolutionary forces

\begin{align*}
\text{In[115]} := \quad & \text{myb3 = 0.4; } \\
& \text{myy113 = 0.; } \\
& \text{myy123 = 0.; } \\
& \text{myy213 = 0.; } \\
& \text{myy223 = 0.; } \\
& \text{rMax3 = 0.5; }
\end{align*}
Manipulate[
  Show[Plot[{probEstablAMApproxPolymContFunc[r, m, a, myb3, myy113, myy123, myy213, myy223, qC][2], probEstablAMApproxPolymContFunc[
    r, m, a, myb3, myy113, myy123, myy213, myy223, qC][3],
    probEstablAMApproxPolymContFunc[r, m, a, myb3, myy113, myy123, myy213, myy223, qC][4]}, {r, 0, rMax3}, PlotRange -> {{0, rMax3}, {0, 2 + a}},
  PlotStyle -> {{RGBColor[0, 0.3, 1, 0.5], Thick}, {Red, Thick}, {Black, Thick}},
  Frame -> True, FrameStyle -> {{Black, Opacity[0]}, {Black, Opacity[0]}},
  FrameLabel -> "(Recombination rate r", "Invasion probability")],
  LabelStyle -> Directive[FontSize -> 14, FontFamily -> "Helvetica"],
  PlotLegend -> {Style["\(\pi_1\), conditional on background \(B_1\)" , FontFamily -> "Helvetica"],
  Style["\(\pi_2\), conditional on background \(B_2\)" , FontFamily -> "Helvetica"],
  Style["\(\pi\), weighted mean across backgrounds" , FontFamily -> "Helvetica"],
  LegendPosition -> {-0.05, 0.175}, LegendSize -> {1.3, 0.5}, LegendShadow -> None,
  LegendTextStyle -> 10, LegendBorderSpace -> Automatic, LegendBorder -> None,
  LegendLabelSpace -> 1.8, LegendLabel -> Style["a = " <> ToString[a] <> "; b = " <>
  ToString[myb3] <> "; m = " <> ToString[m], FontFamily -> "Helvetica"]
},
{{a, 0.2}, 0., myb3}, {{m, 0.22}, 0., myb3}, {{qC, 0.1}, 0., 1.}]

- Invasion probabilities as a function of migration rate \(m\), strong evolutionary forces

\begin{align*}
\text{myb4} &= 0.4; \\
\text{myy114} &= 0.; \\
\text{myy124} &= 0.; \\
\text{myy214} &= 0.; \\
\text{myy224} &= 0.; \\
\text{rMax4} &= 0.6;
\end{align*}
Manipulate[
  Show[Plot[{probEstablAMApproxPolymContFunc[r, m, a, myb4, myy114, myy124, myy214, myy224, qC][2], probEstablAMApproxPolymContFunc[r, m, a, myb4, myy114, myy124, myy214, myy224, qC][3], probEstablAMApproxPolymContFunc[r, m, a, myb4, myy114, myy124, myy214, myy224, qC][4]}, {m, 0, mMax4}, PlotRange -> {{0, mMax4}, {0, 2 + a}}, PlotStyle -> {{RGBColor[0, 0.3, 1, 0.5], Thick}, {Red, Thick}, {Black, Thick}}, Frame -> True, FrameStyle -> {{Black, Opacity[0]}, {Black, Opacity[0]}}, FrameLabel -> ("Migration rate m", "Invasion probability"), LabelStyle -> Directive[FontSize -> 14, FontFamily -> "Helvetica"], PlotLegend -> {Style["\(\pi_1\) conditional on background \(B_1\)\), FontFamily -> "Helvetica"], Style["\(\pi_2\) conditional on background \(B_2\)\), FontFamily -> "Helvetica"], Style["\(\bar{\pi}\) weighted mean across backgrounds\), FontFamily -> "Helvetica"}], LegendPosition -> (-0.05, 0.175), LegendSize -> {1.3, 0.5}, LegendShadow -> None, LegendTextSpace -> 1.8, LegendLabel -> Style["a = " <> ToString[a] <> "; b = " <> ToString[myb4] <> "; r = " <> ToString[r], FontFamily -> "Helvetica"]], {{a, 0.2}, 0., myb4}, {{r, 0.1}, 0., 0.5}, {{qC, 0.1}, 0., 1.}]
}