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

In[127]:=
```
Needs["PlotLegends`"] (* Needed for Mathematica versions below 9 *)
```

General::obspkg :
PlotLegends` is now obsolete. The legacy version being loaded may conflict with current Mathematica functionality. See the Compatibility Guide for updating information.

General fitness model

Set up and initialisation

- **Rules and definitions**

In[2]:=
```
ruleWeakForces := {a → α ϵ, b → β ϵ, m → μμ ϵ, r → ρ ϵ, γ11 → g11 ϵ, γ12 → g12 ϵ}
rescaleWeakForces := {α → a / ϵ, β → b / ϵ, μμ → m / ϵ, ρ → r / ϵ, g11 → γ11 / ϵ, g12 → γ12 / ϵ}
```

In[4]:=
```
ruleSimplifyNotation := x_[_] → x
```

- **Implementation of relative fitnesses and assumptions**

```
Clear[M, m]
```

In[5]:=
```
(** Relative fitnesses of genotypes **)
(* n=1,2 index of deme (for the time being, i.e. for the CI model, 2 is the continent a
(* i=1,2,3,4 index of haplotypes (gametes) *)
(* A, B the two loci with alleles A1, A2 and B1 and B2, respectively *)
(* We assume that there is no position effect, i.e. wij=wji, and w23=w14. *)
w23:=w14; w21:=w12; w31:=w13; w32:=w23;w41:=w14; w42:=w24; w43:=w34;
w[n_]:={{w11[n],w12[n],w13[n],w14[n]},{w21[n],w22[n],w23[n],w24[n]},{w31[n],w32[n],w33[

(* Marginal relative gamete fitnesses *)
wMarg[i_,n_]:=Sum[w[n][[i,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]→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 co
assumeCI:={x[1,2]→0,x[2,2]→0,x[3,2]→qC,x[4,2]→1-qC,m[2]→0,p[2]→0,q[2]→qC,LD[2]→0};(* C
(* Assume that the continent is monomorphic, i.e. that qC = x[4,2] = q[2] = 1. *)
assumeMonomorphContin:={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
assumeGenericMultiplicFitness[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 fitnes
assumeAdditiveMultiplicFitness[n_]:={
w11[n]→(1+a[n])*(1+b[n]),w12[n]→(1+a[n]),w13[n]→(1+b[n]),w14[n]→1,
w22[n]→(1+a[n])*(1-b[n]),w24[n]→(1-b[n]),
w33[n]→(1-a[n])*(1+b[n]), w34[n]→(1-a[n]),
w44[n]→(1-a[n])*(1-b[n])}
(* Additive fitness interactions between alleles within a gamete, multiplicative fitnes
assumeAdditiveMultiplicApproxFitness[n_]:={
w11[n]→(1+a[n]+b[n]),w12[n]→(1+a[n]),w13[n]→(1+b[n]),w14[n]→1,
w22[n]→(1+a[n]-b[n]),w24[n]→(1-b[n]),
w33[n]→(1-a[n]+b[n]), w34[n]→(1-a[n]),
w44[n]→(1-a[n]-b[n])}
(* Additive fitness interactions between alleles within a gamete, multiplicative fitnes
(* The interpretation of the coefficients of epistasis, γ, is as follows: γkl is the epi
assumeAdditiveMultiplicEpistaticFitness[n_]:={
w11[n]→(1+a[n])*(1+b[n]),w12[n]→(1+a[n])*(1-γ21[n]),w13[n]→(1+b[n]),w14[n]→(1-γ11[n]),
w22[n]→(1+a[n])*(1-b[n])*(1-γ22[n]),w24[n]→(1-b[n])*(1-γ12[n]),
w33[n]→(1-a[n])*(1+b[n]), w34[n]→(1-a[n]),
w44[n]→(1-a[n])*(1-b[n])}
(* Additive fitness interactions between alleles within a gamete, multiplicative fitnes
(* Details of epistasis are as in the previous case *)
assumeAdditiveMultiplicEpistaticApproxFitness[n_]:={
w11[n]→(1+a[n]+b[n]),w12[n]→(1+a[n]-γ21[n]),w13[n]→(1+b[n]),w14[n]→(1-γ11[n]),
w22[n]→(1+a[n]-b[n]-γ22[n]),w24[n]→(1-b[n]-γ12[n]),
w33[n]→(1-a[n]+b[n]), w34[n]→(1-a[n]),
w44[n]→(1-a[n]-b[n])}
```

■ Relative fitness matrices under specific assumptions

■ Fully generic regime

```
MatrixForm[w[1]]
```

$$\begin{pmatrix} w11[1] & w12[1] & w13[1] & w14[1] \\ w12[1] & w22[1] & w14[1] & w24[1] \\ w13[1] & w14[1] & w33[1] & w34[1] \\ w14[1] & w24[1] & w34[1] & w44[1] \end{pmatrix}$$

■ 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. $w_{ij,n} = v_{i,n} + v_{j,n}$, where i, j denote the gametes.
- Generic multiplicative: This means *generic* fitness interaction between alleles within a gamete, and *multiplicative* fitness interaction between gametes. $w_{ij,n} = v_{i,n}\, v_{j,n}$, 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_1A_1, A_1A_2, A_2A_2 from top to bottom, and the columns correspond to the B-locus configurations B_1B_1, B_1B_2, B_2B_2 from left to right.

$$w_n = \begin{pmatrix} w_{11,n} & w_{12,n} & w_{22,n} \\ w_{13,n} & w_{14,n} & w_{24,n} \\ w_{33,n} & w_{34,n} & w_{44,n} \end{pmatrix} = \begin{pmatrix} (a_n+1)(b_n+1) & a_n+1 & (a_n+1)(1-b_n) \\ b_n+1 & 1 & 1-b_n \\ (1-a_n)(b_n+1) & 1-a_n & (1-a_n)(1-b_n) \end{pmatrix} \tag{1}$$

- 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_1A_1, A_1A_2, A_2A_2 from top to bottom, and the columns correspond to the B-locus configurations B_1B_1, B_1B_2, B_2B_2 from left to right.

$$w_n = \begin{pmatrix} w_{11,n} & w_{12,n} & w_{22,n} \\ w_{13,n} & w_{14,n} & w_{24,n} \\ w_{33,n} & w_{34,n} & w_{44,n} \end{pmatrix} = \begin{pmatrix} a_n+b_n+1 & a_n+1 & a_n-b_n+1 \\ b_n+1 & 1 & 1-b_n \\ -a_n+b_n+1 & 1-a_n & -a_n-b_n+1 \end{pmatrix} \tag{2}$$

Checking the implementation:

```
MatrixForm[w[1]] /. assumeGenericAdditiveFitness[1]
```

$$\begin{pmatrix} 2\,v1[1] & v1[1]+v2[1] & v1[1]+v3[1] & v1[1]+v4[1] \\ v1[1]+v2[1] & 2\,v2[1] & v1[1]+v4[1] & 2\,v2[1] \\ v1[1]+v3[1] & v1[1]+v4[1] & 2\,v3[1] & v3[1]+v4[1] \\ v1[1]+v4[1] & 2\,v2[1] & v3[1]+v4[1] & 2\,v4[1] \end{pmatrix}$$

```
MatrixForm[w[1]] /. assumeGenericMultiplicFitness[1]
```

$$\begin{pmatrix} v1[1]^2 & v1[1]\,v2[1] & v1[1]\,v3[1] & v1[1]\,v4[1] \\ v1[1]\,v2[1] & v2[1]^2 & v1[1]\,v4[1] & v2[1]^2 \\ v1[1]\,v3[1] & v1[1]\,v4[1] & v3[1]^2 & v3[1]\,v4[1] \\ v1[1]\,v4[1] & v2[1]^2 & v3[1]\,v4[1] & v4[1]^2 \end{pmatrix}$$

```
MatrixForm[w[1]] /. assumeAdditiveMultiplicFitness[1]
```

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

```
MatrixForm[w[1]] /. assumeAdditiveMultiplicApproxFitness[1]
```

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

Migration matrix

```
MatrixForm[M]
```

$$\begin{pmatrix} 1-m[1] & m[1] \\ m[2] & 1-m[2] \end{pmatrix}$$

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 $x_{3,n} \approx q_n$ and $x_{4,n} \approx 1 - q_n$. Hence,

$$\begin{aligned} w_{1,n} &= w_{13,n}\, x_{3,n} + w_{14,n}\, x_{4,n} \approx w_{13,n}\, q_n + w_{14,n}(1 - q_n) \\ w_{2,n} &= w_{23,n}\, x_{3,n} + w_{24,n}\, x_{4,n} \approx w_{14,n}\, q_n + (1 - q_n) \end{aligned} \tag{3}$$

In[19]:=
```
(* In the following, an uppercase letter (A or B) denotes the locus which is polymorphi

(* Marginal fitnesses of types that will be followed in the branching process *)
wMargType[i_,n_]:=Sum[w[n][[i,j]]x[j,n],{j,3,4}](* Here, i is the index of the type of in
(* Mean relative fitness if A1 is absent (rare) *)
wMeanB[n_]:=Sum[w[n][[i,j]]*x[i,n]*x[j,n],{i,3,4},{j,3,4}]

(*!! Assumptions !!*)
(* The A1 allele is rare, so that x3=q1 and x4=1-q1 *)
assumeA1Rare[n_]:={x[3,n]→q[n], x[4,n]→1-q[n]}
```

Inspection of marginal fitnesses (check).

```
wMargType[1, 1] /. assumeA1Rare[1]
```

```
q[1] w13[1] + (1 - q[1]) w14[1]
```

```
wMargType[2, 1] /. 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 $(x_{1,n})^2 \approx x_{1,n}\, x_{2,n} \approx (x_{2,n})^2 \approx 0$, and $x_{3,n} \approx q_n$ and $x_{4,n} \approx 1 - q_n$. 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[22]:=
```
(* For simpler notation in the case of the continent-island model *)
r[A,B]:=r

(* Helper variable *)
δ={1,-1,-1,1};
(* Recursion of gamete frequencies under the full two-locus model *)
rec2LocFull[i_,n_]:=M[[n,1]]*(wMarg[i,1]*x[i,1]-δ[[i]]r[A,B]*w[1][[1,4]]*LD[1])/wbar[1]+M[[n,2

(*!! Assumptions !!*)
(* Ignore terms of order O(x_{i,n}x_{j,n}) , i = 1,2 *)
assumeSecOrderSmall[n_]:=Table[x[i,n]x[j,n]→0,{i,1,2},{j,1,2}]//Flatten
(* Approximate the overall mean fitness *)
assumeWMean[n_]:={wbar[n]→wMeanB[n]}

(* Rules for simplifying the notation *)
ruleSimplifyNotationCI:={m[1]→m,x[1,1]→x1,x[2,1]→x2,x[3,1]→x3,x[4,1]→x4,q[1]→q}
```

- 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.

```
(rec2LocFull[1, 1] /. assumeWMean[1] /. assumeWMean[2] /. assumeCI /.
          assumeMonomorphContin /. LDRule[1] // FullSimplify // Expand) /.
    assumeSecOrderSmall[1] /. assumeA1Rare[1] /. ruleSimplifyNotationCI // FullSimplify
```

$$\frac{(-1+m)\,(q\,x1\,w13[1]+((-1+q)\,(-1+r)\,x1+q\,r\,x2)\,w14[1])}{q\,(-q\,w33[1]+2\,(-1+q)\,w34[1])-(-1+q)^2\,w44[1]}$$

Approximate recursion equation for the gamete $A_1 B_2$ (x_2), obtained from applying the corresponding assumptions to the full equation and simplifying the notation.

```
(rec2LocFull[2, 1] /. assumeWMean[1] /. assumeWMean[2] /. assumeCI /.
          assumeMonomorphContin /. LDRule[1] // FullSimplify // Expand) /.
    assumeSecOrderSmall[1] /. assumeA1Rare[1] /. ruleSimplifyNotationCI // FullSimplify
```

$$((-1+m)\,(((-1+q)\,r\,x1+q\,(-1+r)\,x2)\,w14[1]+(-1+q)\,x2\,w24[1]))\Big/\left(q\,(q\,w33[1]-2\,(-1+q)\,w34[1])+(-1+q)^2\,w44[1]\right)$$

Rearranging the above manually, we can devise the following approximate recursion equations for the two types of interest ($A_1 B_1$ and $A_1 B_2$), assuming the continent-island model.

In[28]:=
```
(* Deterministic recursion equation for the change in frequency of the rare haplotypes
δδ={1,-1}; (* Helper *)
LDApprox[n_]:=LD[n]/.LDRule[n]/.assumeA1Rare[n]
rec2LocRareTypesCI[i_,n_]:=M[[n,1]](w[n][[i,3]]*x[i,n]*q+w[n][[i,4]]*x[i,n]*(1-q)-δδ[[i]]*r[A,B
```

```
LDApprox[1]
```

$$(1-q[1])\,x[1,1]-q[1]\,x[2,1]$$

```
ruleSimplifyNotationCI
```

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

```
rec2LocRareTypesCI[1, 1] /. ruleSimplifyNotationCI
```

$$((1-m)\,(q\,x1\,w13[1]+(1-q)\,x1\,w14[1]-r\,((1-q)\,x1-q\,x2)\,w14[1]))\,/\,wOverallMean[1]$$

```
rec2LocRareTypesCI[1, 1] /. assumeWMean[1] /. assumeA1Rare[1] /. ruleSimplifyNotationCI
```

$$((1-m)\,(q\,x1\,w13[1]+(1-q)\,x1\,w14[1]-r\,((1-q)\,x1-q\,x2)\,w14[1]))\,/\,wOverallMean[1]$$

```
rec2LocRareTypesCI[2, 1] /. ruleSimplifyNotationCI
```

$$((1-m)\,(q\,x2\,w14[1]+r\,((1-q)\,x1-q\,x2)\,w14[1]+(1-q)\,x2\,w24[1]))\,/\,wOverallMean[1]$$

```
rec2LocRareTypesCI[2, 1] /. assumeWMean[1] /. assumeA1Rare[1] /. ruleSimplifyNotationCI
```

$$((1-m)\,(q\,x2\,w14[1]+r\,((1-q)\,x1-q\,x2)\,w14[1]+(1-q)\,x2\,w24[1]))\,/\,wOverallMean[1]$$

■ Matrix form, mean matrix and eigenvalues

The determinisitic process may also be written in matrix form, where we use $\vec{x}^{\mathrm{T}}$ for the transpose of a matrix or vector:

$$\vec{x}_n^T(t+1) = \mathrm{G}_n\, \vec{x}_n^T(t) \tag{4}$$

with

$$\vec{x}_n^T(t) = \begin{pmatrix} x_{1,n}(t) \\ x_{2,n}(t) \end{pmatrix} \tag{5}$$

and

$$\begin{aligned} \mathrm{G}_n &= \begin{pmatrix} (1-m_n)\,(w_{13,n}\,q_n + w_{14,n}\,(1-q_n) - r\,w_{14}\,(1-q_n))/\overline{w}_n & (1-m_n)\,r\,w_{14,n}\,q_n/\overline{w}_n \\ (1-m_n)\,r\,w_{14,n}\,(1-q_n)/\overline{w}_n & (1-m_n)\,(w_{24,n}\,(1-q_n) + w_{23}\,q_n - r\,w_{14,n}\,q_n)/\overline{w}_n \end{pmatrix} \\ &= \begin{pmatrix} (1-m_n)\,(w_{1,n} - r\,w_{14,n}\,(1-q_n))/\overline{w}_n & (1-m_n)\,r\,w_{14,n}\,q_n/\overline{w}_n \\ (1-m_n)\,r\,w_{14,n}\,(1-q_n)/\overline{w}_n & (1-m_n)\,(w_{2,n} - r\,w_{14,n}\,q_n)/\overline{w}_n \end{pmatrix} \end{aligned} \tag{6}$$

where

$$\begin{aligned} w_{1,n} &= w_{13,n}\,q_n + (1-q_n)\,w_{14,n} \\ w_{2,n} &= w_{14,n}\,q_n + (1-q_n)\,w_{24,n}. \end{aligned} \tag{7}$$

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 $\mathrm{L} = \mathrm{G}_n^{\mathrm{T}}$ and we write $\vec{x}\,'(t+1) = \vec{x}\,(t)\,\mathrm{L}$ 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 λ_{ij} of L represents the expected number of j-type offspring produced by an i-type parent.

Equation (4) may now be written as

$$\vec{x}_n^T(t) = \mathrm{G}_n^t\, \vec{x}_n^T(0) \tag{8}$$

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 λ_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 ν_i (Greek nu) instead of λ_i for the eigenvalues, and v and u for the right and left eigenvectors, respectively. If we normalise so that $\vec{u}_i\,\vec{v}_i = 1$ ($i = 1,\ 2$), then we expand the matrix G^t in the spectral form

$$\mathrm{G}^t = {\lambda_1}^t\,\mathrm{G}_1 + {\lambda_2}^t\,\mathrm{G}_2, \tag{9}$$

where $\mathrm{G}_i = \vec{v}_i\,\vec{u}_i$. By inserting into eq. (8), we obtain

$$x_1(t) + x_2(t) = {\lambda_1}^t\left\{\mathbb{1}\,\mathrm{G}_1\,\vec{x}^T(0)\right\} + {\lambda_2}^t\left\{\mathbb{1}\,\mathrm{G}_2\,\vec{x}^T(0)\right\}, \tag{10}$$

where $\mathbb{1}$ is the row vector (1, 1). The frequency of the mutant (A_1) will eventually increase provided only that the maximum eigenvalue λ_1 is greater than 1.

Accordint 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 ($\lambda_1 \le 1$), the process is subcritical and the extinction probability is 1 (except for the degenerate case $\lambda_1 = 1$ and every individual produces *exactly* one offpring). 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, $\overline{w}$). 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).

In[31]:=
```
(* The mean matrix *)
G[n_]:={{M[[n,1]]*(w1[n]-r[A,B]*w[n][[1,4]]*(1-q[n]))/wbar[n],M[[n,1]]*r[A,B]*w[n][[1,4]]*q[n]/
(* Notice that the mean matrix *left-* multiplies the vector x! *)

G[1] /. ruleSimplifyNotationCI // MatrixForm
```

$$\begin{pmatrix} \frac{(1-m)\,(w1[1]-(1-q)\,r\,w14[1])}{wbar[1]} & \frac{(1-m)\,q\,r\,w14[1]}{wbar[1]} \\ \frac{(1-m)\,(1-q)\,r\,w14[1]}{wbar[1]} & \frac{(1-m)\,(-q\,r\,w14[1]+w2[1])}{wbar[1]} \end{pmatrix}$$

Inspection of eigenvalues.

```
G[1] /. {wbar[1] → wbar} /. ruleSimplifyNotationCI // MatrixForm
```

$$\begin{pmatrix} \frac{(1-m)\,(w1[1]-(1-q)\,r\,w14[1])}{wbar} & \frac{(1-m)\,q\,r\,w14[1]}{wbar} \\ \frac{(1-m)\,(1-q)\,r\,w14[1]}{wbar} & \frac{(1-m)\,(-q\,r\,w14[1]+w2[1])}{wbar} \end{pmatrix}$$

```
evaluesG :=
 Eigenvalues[G[1] /. {wbar[1] → wbar} /. ruleSimplifyNotationCI] // FullSimplify
evaluesG
```

$$\left\{-\frac{1}{2\,wbar}\,(-1+m)\,\left(w1[1]-r\,w14[1]+w2[1]+\sqrt{\left(w1[1]^2+r^2\,w14[1]^2+\right.\right.\right.$$
$$\left.\left.\left.w1[1]\,(2\,(-1+2\,q)\,r\,w14[1]-2\,w2[1])+2\,(1-2\,q)\,r\,w14[1]\,w2[1]+w2[1]^2\right)\right),$$
$$\frac{1}{2\,wbar}\,(-1+m)\,\left(-w1[1]+r\,w14[1]-w2[1]+\sqrt{\left(w1[1]^2+r^2\,w14[1]^2+\right.\right.$$
$$\left.\left.\left.w1[1]\,(2\,(-1+2\,q)\,r\,w14[1]-2\,w2[1])+2\,(1-2\,q)\,r\,w14[1]\,w2[1]+w2[1]^2\right)\right)\right\}$$

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 λ_1, we see that

```
evaluesG[[1]]
```

$$-\frac{1}{2\,wbar}\,(-1+m)$$
$$\left(w1[1]-r\,w14[1]+w2[1]+\sqrt{\left(w1[1]^2+r^2\,w14[1]^2+w1[1]\,(2\,(-1+2\,q)\,r\,w14[1]-2\,w2[1])+\right.\right.$$
$$\left.\left.2\,(1-2\,q)\,r\,w14[1]\,w2[1]+w2[1]^2\right)\right)$$

$$\lambda_1 > 1 \Rightarrow (1-m)\left(\sqrt{2\,(2\,q-1)\,r\,w_{14}\,(w_1-w_2)+r^2\,w_{14}^2+(w_1-w_2)^2}\;-r\,w_{14}+w_1+w_2\right) > 2\,\overline{w} \tag{11}$$

Rearranging the above manually, we obtain the inequlity

$$\begin{aligned} &\sqrt{\text{stuff}} > 2\,\frac{\overline{w}}{1-m}-w_1-w_2+r\,w_{14} \\ &\Rightarrow \text{stuff} > \left(2\,\frac{\overline{w}}{1-m}-w_1-w_2+r\,w_{14}\right)^2, \end{aligned} \tag{12}$$

where

$$\text{stuff} = (w_1-w_2)^2+2\,r\,w_{14}\,(2\,q-1)\,(w_1-w_2)+r^2\,{w_{14}}^2. \tag{13}$$

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

```
Expand[(w1 - w2)^2 + 2 r w14 (2 q - 1) (w1 - w2) + r^2 w14^2] - Expand[(2 wbar/(1 - m) - w1 - w2 + r w14)^2] > 0
```

$$4\,q\,r\,w1\,w14-4\,w1\,w2+4\,r\,w14\,w2-4\,q\,r\,w14\,w2+\frac{4\,w1\,wbar}{1-m}-\frac{4\,r\,w14\,wbar}{1-m}+\frac{4\,w2\,wbar}{1-m}-\frac{4\,wbar^2}{(1-m)^2}>0$$

Collecting terms in $r * w_{14}$, we obtain

```
Collect[4 q r w1 w14 - 4 w1 w2 + 4 r w14 w2 -
  4 q r w14 w2 + 4 w1 wbar/(1 - m) - 4 r w14 wbar/(1 - m) + 4 w2 wbar/(1 - m) - 4 wbar^2/(1 - m)^2 > 0, r * w14]
```

$$-4\,w1\,w2+\frac{4\,w1\,wbar}{1-m}+\frac{4\,w2\,wbar}{1-m}-\frac{4\,wbar^2}{(1-m)^2}+r\,w14\left(4\,q\,w1+4\,w2-4\,q\,w2-\frac{4\,wbar}{1-m}\right)>0$$

Dividing the whole equation by 4, shuffling terms without r onto the right and factorizing the resulting terms, we obtain

$$r\, w_{14}\left[\frac{\overline{w}}{1-m} - q\, w_1 - (1-q)\, w_2\right] < -\left(\frac{\overline{w}}{1-m} - w_1\right)\left(\frac{\overline{w}}{1-m} - w_2\right), \tag{14}$$

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

1. In cases where $\frac{\overline{w}}{1-m}$ lies between w_1 and w_2, *i.e.* when $(1-m)\, w_1 < \overline{w} < (1-m)\, w_2$ or when $(1-m)\, w_2 < \overline{w} < (1-m)\, w_1$, and if $\frac{\overline{w}}{1-m} > q\, w_1 + (1-q)\, w_2$, 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 $\mathcal{A}$ locus is sufficiently closely linked to the $\mathcal{B}$ locus*. This result was already obtained by Bodmer and Parsons (1962) for the case without migration.
2. If we assume $r > r_{00}$, with r_{00} a positive constant, it can be shown after some algebra that equation (14) implies $\frac{\overline{w}}{1-m} < w_1$ and $\frac{\overline{w}}{1-m} < w_2$. Therefore, if $r > r_{00}$, 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).

In[32]:=
```
conditionNonExtinction[n_]:=r w[n][[1,4]]( wbar[n]/(1-m[n])-q[n]*w1[n]-(1-q[n])*w2[n] )<-( wbar[n]/(1-m[n])-w
```

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 ρ. 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 α for a and β for b, and we let $\alpha < \beta$.

1. Diagram (a) applies if and only if

$$\beta \geq 2\,\alpha \text{ and } \rho < \alpha \quad (3.21\,\text{a})$$

or

$$\beta < 2\,\alpha \text{ and } \rho \leq \frac{1}{3}\,(\alpha+\beta). \quad (3.21\,\text{b})$$

2. Diagram (b) applies if and only if

$$\beta < 2\,\alpha \text{ and } \frac{1}{3}\,(\alpha+\beta) < \rho < \alpha. \quad (3.22)$$

3. Diagram (c) applies if and only if

$$\beta \geq 2\,\alpha \text{ and } \rho = \alpha. \quad (3.23)$$

4. Diagram (d) applies if and only if

$$\beta < 2\,\alpha \text{ and } \rho = \alpha. \quad (3.24)$$

5. Diagram (e) applies if and only if

$$\beta < 2\,\alpha \text{ and } \alpha < \rho \leq 3\,\beta - \alpha - 2\sqrt{2}\,\sqrt{\beta\,(\beta-\alpha)}\,. \quad (3.25)$$

6. Diagram (f) applies if and only if

$$\beta < 2\,\alpha \text{ and } 3\,\beta - \alpha - 2\sqrt{2}\,\sqrt{\beta\,(\beta-\alpha)} < \rho < 3\,\alpha - \beta. \quad (3.26)$$

7. Diagram (g) applies if and only if

$$\beta \geq 2\,\alpha \text{ and } \rho > \alpha \quad (3.27\,a)$$

or

$$\beta < 2\,\alpha \text{ and } \rho \geq 3\,\alpha - \beta. \quad (3.27\,b)$$

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. $\ll 1$).

Implementation

In[33]:=
```
mCritC::usage = "mCritC is the critical migration rate m_C characterising the properties
mCritC:=a+b-r
mCritA::usage = "mCritA is the critical migration rate m_A characterising the properties
mCritA:=b*(1-(b-a)/r)
mCritB::usage = "mCritB is the critical migration rate m_B characterising the properties
mCritB:=a*(1+(b-a)/r)
```

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 :
unstabilityEB[a_,b_,r_,m_]:=Module[{mb},
mb=a*(1+(b-a)/r);
Return[0<m<Min[mb,b]]]
```

In[43]:=
```
(* BA2011 stands for Bürger and Akerman (2011) *)
equilibriumConfig::usage="equilibriumConfig[α, β, ρ, m] returns the label (a-g) of the
equilibriumConfig[α_,β_,ρ_,m_]:=Module[{text,fig,comb,conditions,descriptions,paths},
conditions={
β ≥ 2*α && ρ < α,
β < 2*α && ρ ≤ 1/3*(α+β),
β < 2*α && 1/3*(α+β) < ρ < α,
β ≥ 2*α && ρ == α,
β < 2*α && ρ == α,
β < 2*α && α < ρ ≤ 3*β - α - 2*Sqrt[2]*Sqrt[β*(β-α)],
β < 2*α && 3*β - α - 2*Sqrt[2]*Sqrt[β*(β-α)] < ρ < 3*α - β,
β ≥ 2*α && ρ > α,
β < 2*α && ρ ≥ 3*α - β
};
descriptions={
"b ≥ 2a and r < a (3.21a); diagram (a) of Fig. 1 in BA2011 applies.",
"b < 2a and r ≤ 1/3(a + b) (3.21b); diagram (a) of Fig. 1 in BA2011 applies.",
"b < 2a and 1/3(a + b) < r < a (3.22); diagram (b) of Fig. 1 in BA2011 applies.",
"b ≥ 2a and r = a (3.23); diagram (c) of Fig. 1 in BA2011 applies.",
"b < 2a and r = a (3.24); diagram (d) of Fig. 1 in BA2011 applies.",
"b < 2 a and a < r ≤ 3b - a - 2Sqrt[2] Sqrt[b(b-a)] (3.25); diagram (e) of Fig. 1 in BA2011 ap
"b < 2a and 3b - a - 2Sqrt[2] Sqrt[b(b-a)] < r < 3a - b (3.26); diagram (f) of Fig. 1 in BA201
"b ≥ 2a and r > a (3.27a); diagram (g) of Fig. 1 in BA2011 applies.",
"b < 2a and r ≥ 3a - b (3.27b); diagram (g) of Fig. 1 in BA2011 applies."
};
paths=Table["Documents/LocAdD/doc/figures/bifurcationDiagramFig1"<>ToString[{a,a,b,c,d,
text=Which[conditions[[1]],descriptions[[1]],conditions[[2]],descriptions[[2]],conditions[[3]],de
fig=Import[Which[conditions[[1]],paths[[1]],conditions[[2]],paths[[2]],conditions[[3]],paths[[3]],c
res=Column[{text,fig}];
Return[res]
]
```

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 paremt by μ_{ij}.

```
MatrixForm[G[1]]
```

$$\begin{pmatrix} \frac{(1-m[1])\,(w1[1]-r\,(1-q[1])\,w14[1])}{wbar[1]} & \frac{r\,(1-m[1])\,q[1]\,w14[1]}{wbar[1]} \\ \frac{r\,(1-m[1])\,(1-q[1])\,w14[1]}{wbar[1]} & \frac{(1-m[1])\,(-r\,q[1]\,w14[1]+w2[1])}{wbar[1]} \end{pmatrix}$$

In[45]:=
```
μ[i_, j_, n_] := G[n][[j, i]] (* Notice the inverted order of indices! μij 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. *)
```

```
μ[1, 1, 1]
```

$$\frac{(1-m[1])\,(w1[1]-r\,(1-q[1])\,w14[1])}{wbar[1]}$$

```
μ[1, 2, 1]
```

$$\frac{r\,(1-m[1])\,(1-q[1])\,w14[1]}{wbar[1]}$$

```
μ[2, 1, 1]
```

$$\frac{r\,(1-m[1])\,q[1]\,w14[1]}{wbar[1]}$$

```
μ[2, 2, 1]
```

$$\frac{(1-m[1])\,(-r\,q[1]\,w14[1]+w2[1])}{wbar[1]}$$

In the manuscript, we use λ_{ij} instead of $\mu_{ij} = g_{ji}$, ($i,\ j \in \{1, 2\}$). 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 offpring 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

$$f_{ij}(s_j) = \sum_{k_j=0}^{\infty} P\left(X_{ij} = k_j\right) s_j^{k_j} = e^{-\mu_{ij}\,(1-s_j)}\ (i,\ j = 1,\ 2), \tag{15}$$

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

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

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

$$f_i(s_1,\ s_2) = \prod_{j=1}^{2} e^{-\mu_{ij}\,(1-s_j)} = e^{\sum_{j=1}^{2} -\mu_{ij}\,(1-s_j)} \tag{17}$$

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

- if $\lambda_1 \le 1$, 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 occured as an $A_1\,B_1$ ($A_1\,B_2$) gamete, then Q_1 and Q_2 are the smallest postitive solutions of

$$s_i = f_i(s_1,\ s_2)\ (i = 1,\ 2), \tag{18}$$

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

$$\begin{aligned} s_1 &= e^{-\mu_{11}\,(1-s_1)-\mu_{12}(1-s_2)} \\ s_2 &= e^{-\mu_{21}\,(1-s_1)-\mu_{22}(1-s_2)}. \end{aligned} \tag{19}$$

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.

In[46]:=
```
mCritApproxFunc::usage = "mCritApproxFunc[r, a, b] returns the critical migration rate
mCritApproxFunc[r_,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 (201
```

Critical recombination rate r_B as a function of the migration rate $m_{B,1}$ 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).

In[48]:=
```
rCritApproxFunc::usage = "rCritApproxFunc[m, a, b] returns the critical recombination r
rCritApproxFunc[m_,a_,b_]:=Module[{rcrit,res},
rcrit=a*(b-a)/(m-a); (* This is equation (4.15) of Bürger and Akerman (2011). *)
(* We assume that a ≤ b! This must not be violated by the arguments. *)
res=If[rcrit≥0.5,0.5,If[rcrit<0,0.0,rcrit]];
res=If[rcrit<0,0.0,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'.

In[50]:=
```
mCritFunc::usage = "mCritFunc[r, a, b] returns the critical migration rate m_inv for the
mCritFunc[r_,a_,b_]:=Module[{mcrit1,mcrit2,mcrit3,mcrit5,res},
mcrit1=a/(1-b);
mcrit2=b/(1-a); (* This is the critical value derived above, and also given in Akerman (201
mcrit3=(a+b-r)/(1-r); (* This is given in Akerman (2011); the continuous-time analog is m_c in B
mcrit5=(a*(b-a+r))/((a-b)*(a-r)+r*(1-a)); (* This is the equation after equation (22) in Akerman (201
(* res=If[mcrit5<0,Min[mcrit2],Min[mcrit2,mcrit5]]; *)
(* res=If[mcrit5<0,mcrit2,Max[Min[mcrit2,mcrit5],Max[mcrit1,mcrit5]]]; *)
res=If[r<a,mcrit2,If[a<r<b,mcrit5,Max[mcrit1,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 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.

In[52]:=
```
mCrit5 := 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 $m_{\text{crit},5}$, $a(b - a + r)$ 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:

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

$$a^2 + r + b\,r > a\,(b + 2\,r)$$

```
FullSimplify[Reduce[0 < mCrit5 < 1],
 Assumptions → {0 < r < 1 / 2, 0 < a < b < 1, a + b < 1, 0 < m < 1, a^2 + r + b r > a (b + 2 r)}]
```

$$2\,a \le r \;||\; 2\,a^2 + r + b\,r > 2\,a\,b + 3\,a\,r$$

In[53]:=
```
rCrit5Rule := FullSimplify[Solve[m == mCrit5, r],
  Assumptions → {0 < r < 1 / 2, 0 < a < b < 1, a + b < 1, 0 < m < 1}]
```

In[54]:=
```
rCrit5 := r /. rCrit5Rule
```

```
FullSimplify[Reduce[a * (a - b) * (1 + m) / (a + 2 * a * m - (1 + b) * m) ≤ 1 / 2, m],
 Assumptions -> {0 < r < 1 / 2, 0 < a < b < 1, a + b < 1, 0 < m < 1}]
```

$$m + b\,m < a + 2\,a\,m \;||\; m + b\,m + 2\,a^2\,(1 + m) \ge a\,(1 + 2\,m + 2\,b\,(1 + m))$$

```
Solve[m + b m == a + 2 a m, m]
```

$$\left\{\left\{m \to \frac{a}{1 - 2\,a + b}\right\}\right\}$$

```
Solve[m + b m + 2 a^2 (1 + m) == a (1 + 2 m + 2 b (1 + m)), m]
```

$$\left\{\left\{m \to \frac{a - 2\,a^2 + 2\,a\,b}{1 - 2\,a + 2\,a^2 + b - 2\,a\,b}\right\}\right\}$$

```
FullSimplify[Reduce[(a - 2 a^2 + 2 a b) / (1 - 2 a + 2 a^2 + b - 2 a b) > a / (1 - 2 a + b),
 Assumptions → {0 < r < 1 / 2, 0 < a < b < 1, a + b < 1, 0 < m < 1}]
```

```
True
```

```
FullSimplify[Reduce[(a - 2 a^2 + 2 a b) / (1 - 2 a + 2 a^2 + b - 2 a b) == a / (1 - 2 a + b),
 Assumptions → {0 < r < 1 / 2, 0 < m < 1}]
```

$$(1 + b \neq 0 \;\&\&\; (a == 0 \;||\; a == 1 + b)) \;||\; (a == b \;\&\&\; b \neq 1)$$

The first solution is always smaller than the second unless $a \ge b$, which is excluded by our assumptions. To see this, note that the numerator of the second solution is strictly larger then 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 $f_{r_{\text{crit}}}(m)$ of m is defined as follows:

$$f_{r_{\text{crit}}}(m) = \begin{cases} 0.5 & m \le m_{r_{\text{crit}}} \\ r_{\text{crit},5} & m > m_{r_{\text{crit}}} \end{cases} \tag{1}$$

where $m_{r_{\text{crit}}} = \frac{a-2a^2+2ab}{1-2a+2a^2+b-2ab}$ and $r_{\text{crit},5} = \frac{a(a-b)(1+m)}{a+2am-(1+b)m}$

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
rcrit5=(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. *)
mThresh=(a-2 a^2+2 a b)/(1-2 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 := 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 α. *)
mCrit2 := 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 β. *)
mCrit3 := (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 model

Here, we derive the marginal one-locus migration-selection equilibrium at locus $\mathcal{B}$. 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

In[60]:=
```
(* Marginal relative fitness of gamete i in deme n alleles at the B locus if A_1 is rare
wMargB[i_,n_]:=Sum[w[n][[i,j]]x[j,n],{j,3,4}] (* Here, i is the index of the B allele, i=

(* Recursion equation (selection followed by migration) for the allele frequencies at t
recB[i_,n_]:=M[[n,1]]wMargB[i,1]/wMeanB[1]*x[i,1]+M[[n,2]]wMargB[i,2]/wMeanB[2]*x[i,2] (* i

(*!! Assumptions !!*)
(* Generic fitness interaction between alleles within a gamete, additive fitness intera
assumeGenericAdditiveFitnessB[n_]:={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
assumeGenericMultiplicFitnessB[n_]:={w33[n]→v3[n]v3[n], w34[n]→v3[n]v4[n],w44[n]→v4[n]v
(* Additive fitness interactions between alleles within a gamete, multiplicative fitnes
assumeAdditiveMultiplicFitnessB[n_]:={w33[n]→(1-a[n])(1+b[n]), w34[n]→(1-a[n]),w44[n]→
(* Additive fitness interactions between alleles within a gamete, multiplicative fitnes
assumeAdditiveMultiplicApproxFitnessB[n_]:={w33[n]→(1-a[n]+b[n]), w34[n]→(1-a[n]),w44[r

wMargB[3, 1] /. assumeA1Rare[1]

q[1] w33[1] + (1 - q[1]) w34[1]

wMargB[4, 1] /. assumeA1Rare[1]

q[1] w34[1] + (1 - q[1]) w44[1]
```

■ 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 $x_{3,n} = q_n$ and $x_{4,n} = 1 - q_n$.

Generic relative fitnesses:

```
qEquil1BGeneric = Solve[
  (recB[3, 1] /. assumeCI /. assumeMonomorphContin /. assumeA1Rare[1] // FullSimplify) ==
   q[1], q[1]]
```

```
{{q[1] → 0}, {q[1] → (-w33[1] + m[1] w33[1] + 3 w34[1] - m[1] w34[1] - 2 w44[1] -
        √(-4 (-w33[1] + 2 w34[1] - w44[1]) (w34[1] - m[1] w34[1] - w44[1]) +
            (w33[1] - m[1] w33[1] - 3 w34[1] + m[1] w34[1] + 2 w44[1])^2)) /
     (2 (-w33[1] + 2 w34[1] - w44[1]))}, {q[1] →
    (-w33[1] + m[1] w33[1] + 3 w34[1] - m[1] w34[1] - 2 w44[1] +
        √(-4 (-w33[1] + 2 w34[1] - w44[1]) (w34[1] - m[1] w34[1] - w44[1]) +
            (w33[1] - m[1] w33[1] - 3 w34[1] + m[1] w34[1] + 2 w44[1])^2)) /
     (2 (-w33[1] + 2 w34[1] - w44[1]))}}
```

```
FullSimplify[
 Reduce[{0 < (q[1] /. qEquil1BGeneric[[2]]) && (q[1] /. qEquil1BGeneric[[2]]) < 1}, m[1]],
 Assumptions →
  {0 < m[1] < 1 && 0 < w33[1] && 0 < w34[1] && 0 < w44[1] && w33[1] > w34[1] > w44[1]}]
```

```
(m[1] w34[1] + w44[1] < w34[1] &&
    ((w33[1] + w44[1] > 2 w34[1] && 2 w34[1]^2 ≥ (w33[1] + w34[1]) w44[1]) ||
     w33[1] + w44[1] < 2 w34[1])) ||
 ((w33[1] + w34[1]) w44[1] > 2 w34[1]^2 && (-1 + m[1]) w33[1]^2 + (1 + m[1]) w34[1]^2 +
     2 √(w33[1] (w33[1] - 2 w34[1] + w44[1]) (-w34[1]^2 + w33[1] w44[1])) ≤
   2 w33[1] ((-1 + m[1]) w34[1] + w44[1]))
```

```
FullSimplify[
 Reduce[{0 < (q[1] /. qEquil1BGeneric[[3]]) && (q[1] /. qEquil1BGeneric[[3]]) < 1}, m[1]],
 Assumptions →
  {0 < m[1] < 1 && 0 < w33[1] && 0 < w34[1] && 0 < w44[1] && w33[1] > w34[1] > w44[1]}]
```

```
m[1] w34[1] + w44[1] > w34[1] && (-1 + m[1]) w33[1]^2 + (1 + m[1]) w34[1]^2 +
   2 √(w33[1] (w33[1] - 2 w34[1] + w44[1]) (-w34[1]^2 + w33[1] w44[1])) ≤
  2 w33[1] ((-1 + m[1]) w34[1] + w44[1]) && 2 w34[1]^2 < (w33[1] + w34[1]) w44[1]
```

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

```
qEquil1BGenericAdditive =
 Solve[(recB[3, 1] /. assumeCI /. assumeMonomorphContin /. assumeA1Rare[1] /.
       assumeGenericAdditiveFitnessB[1] // FullSimplify) == q[1], q[1]] // FullSimplify
```

$$\left\{\{q[1] \to 0\}, \left\{q[1] \to 1 + \frac{2\, m[1]\, v3[1]}{(1 + m[1])\, (-v3[1] + v4[1])}\right\}\right\}$$

Conditions for admissibility of the above equilibrium:

```
FullSimplify[Reduce[
  {0 < (q[1] /. qEquil1BGenericAdditive[[2]]) && (q[1] /. qEquil1BGenericAdditive[[2]]) < 1},
  m[1]], Assumptions → {0 < m[1] < 1 && v3[1] ≥ v4[1] > 0}]
```

```
v4[1] + m[1] (v3[1] + v4[1]) < v3[1]
```

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

$$m_1 < \frac{v_3 - v_4}{v_3 + v_4}. \tag{2}$$

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

```
qEquil1BGenericMultiplic =
 Solve[(recB[3, 1] /. assumeCI /. assumeMonomorphContin /. assumeA1Rare[1] /.
       assumeGenericMultiplicFitnessB[1] // FullSimplify) == q[1], q[1]] // FullSimplify
```

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

Conditions for admissibility of the above equilibrium:

```
FullSimplify[Reduce[{0 < (q[1] /. qEquil1BGenericMultiplic[[2]]) &&
     (q[1] /. qEquil1BGenericMultiplic[[2]]) < 1}, m[1]],
 Assumptions → {0 < m[1] < 1 && v3[1] ≥ v4[1] > 0}]
```

```
m[1] v3[1] + v4[1] < v3[1]
```

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

$$m_1 < \frac{v_3 - v_4}{v_3}. \tag{3}$$

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

```
qEquil1BAdditiveMultiplic =
 Solve[(recB[3, 1] /. assumeCI /. assumeMonomorphContin /. assumeA1Rare[1] /.
       assumeAdditiveMultiplicFitnessB[1] // FullSimplify) == q[1], q[1]]
```

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

Conditions for admissibility of the above equilibrium:

```
FullSimplify[Reduce[{0 < (q[1] /. qEquil1BAdditiveMultiplic[[2]]) &&
     (q[1] /. qEquil1BAdditiveMultiplic[[2]]) < 1}, m[1]],
 Assumptions → {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

$$m_1 < b_1 \tag{4}$$

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

In[66]:=
```
qEquil1BAdditiveMultiplicApprox =
 Solve[(recB[3, 1] /. assumeCI /. assumeMonomorphContin /. assumeA1Rare[1] /.
       assumeAdditiveMultiplicApproxFitnessB[1] // FullSimplify) == q[1], q[1]]
```

Out[66]=
$$\left\{\{q[1] \to 0\}, \left\{q[1] \to \frac{b[1] - m[1] + a[1]\ m[1]}{b[1]\ (1 + m[1])}\right\}\right\}$$

Conditions for admissibility of the above equilibrium:

```
FullSimplify[Reduce[{0 < (q[1] /. qEquil1BAdditiveMultiplicApprox[[2]]) &&
     (q[1] /. qEquil1BAdditiveMultiplicApprox[[2]]) < 1}, m[1]],
 Assumptions → {0 < m[1] < 1 && 0 < b[1] ≤ 1 && 0 < a[1] ≤ b[1]}]
```

```
(a[1] < 1 && m[1] < b[1] + a[1] m[1]) || a[1] == 1
```

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

$$m_1 < \frac{b_1}{1 - a_1}. \tag{5}$$

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_twoLocusContinentIslandDiscreteStochastic.nb

In[67]:=
```
pgf[i_, n_] := Exp[Sum[-μ[i, j, n] (1 - s[j]), {j, 2}]]
```

```
pgf[1, 1]
```

$$e^{-\frac{r\,(1-m[1])\,(1-q[1])\,(1-s[2])\,w14[1]}{wbar[1]}-\frac{(1-m[1])\,(1-s[1])\,(w1[1]-r\,(1-q[1])\,w14[1])}{wbar[1]}}$$

```
pgf[2, 1]
```

$$e^{-\frac{r\,(1-m[1])\,q[1]\,(1-s[1])\,w14[1]}{wbar[1]}-\frac{(1-m[1])\,(1-s[2])\,(-r\,q[1]\,w14[1]+w2[1])}{wbar[1]}}$$

Implementation for the following scheme of relative fitnesses:

```
w[1] /. assumeAdditiveMultiplicEpistaticApproxFitness[1] // MatrixForm
```

$$\begin{pmatrix} 1+a[1]+b[1] & 1+a[1]-\gamma 21[1] & 1+b[1] & 1-\gamma 11[1] \\ 1+a[1]-\gamma 21[1] & 1+a[1]-b[1]-\gamma 22[1] & 1-\gamma 11[1] & 1-b[1]-\gamma 12[1] \\ 1+b[1] & 1-\gamma 11[1] & 1-a[1]+b[1] & 1-a[1] \\ 1-\gamma 11[1] & 1-b[1]-\gamma 12[1] & 1-a[1] & 1-a[1]-b[1] \end{pmatrix}$$

For this scheme, the equilibrium allele frequency of B_1 in the marginal one-locus model (at selection-migration balance) is given by

```
q[1] /. qEquil1BAdditiveMultiplicApprox[[2]]
```

$$\frac{b[1]-m[1]+a[1]\,m[1]}{b[1]\,(1+m[1])}$$

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

a_1: Twice the additive selective advantage of A_1 compared to A_2 in deme 1 (island)
b_1: Twice the additive selective advantage of B_1 compared to B_2 in deme 1 (island)
γ_{kl1}: 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_1: The proportion of individuals in deme 1 (island) replaced every generation by imigrants from deme 2 (continent)
r: The recombination frequency between loci A and B.

Further ingedients needed for the implementation:

```
wMeanB[1] /. assumeAdditiveMultiplicEpistaticApproxFitness[1] /. assumeA1Rare[1] //
 FullSimplify
```

```
1 - a[1] + b[1] (-1 + 2 q[1])
```

```
wMargType[1, 1] /. assumeAdditiveMultiplicEpistaticApproxFitness[1] /. assumeA1Rare[1]
```

```
(1 + b[1]) q[1] + (1 - q[1]) (1 - γ11[1])
```

```
FullSimplify[%]
```

```
1 + b[1] q[1] + (-1 + q[1]) γ11[1]
```

```
wMargType[2, 1] /. assumeAdditiveMultiplicEpistaticApproxFitness[1] /. assumeA1Rare[1]
```

```
q[1] (1 - γ11[1]) + (1 - q[1]) (1 - b[1] - γ12[1])
```

```
FullSimplify[%]
```

```
1 + b[1] (-1 + q[1]) - q[1] γ11[1] + (-1 + q[1]) γ12[1]
```

```
w[1][[1, 4]] /. assumeAdditiveMultiplicEpistaticApproxFitness[1]
```

```
1 - γ11[1]
```

```
qEquil1BAdditiveMultiplicApprox[[2]]
```

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

In[68]:=
```
pgf1Add = pgf[1, 1] /. qEquil1BAdditiveMultiplicApprox[[2]] /. wbar[1] → wMeanB[1] /.
            assumeAdditiveMultiplicEpistaticApproxFitness[1] /. assumeA1Rare[1] /.
          w1[1] → wMargType[1, 1] /. assumeAdditiveMultiplicEpistaticApproxFitness[1] /.
        assumeA1Rare[1] /. {γ11[1] → 0, γ12[1] → 0, γ21[1] → 0, γ22[1] → 0} /.
      qEquil1BAdditiveMultiplicApprox[[2]] /. {a[1] → a, b[1] → b,
      m[1] → m, s[1] → s1, s[2] → s2} // FullSimplify
```

Out[68]=
$$e^{\frac{b^2\,(-1+s1)+(-1+a)\,m\,r\,(s1-s2)+b\,(-1+a\,m\,(-1+s1)+s1-m\,r\,s1+m\,r\,s2)}{b\,(1-a+b)}}$$

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

$$-b - b^2 - a\,b\,m + \left(b + b^2 + a\,b\,m + (-1 + a)\,m\,r - b\,m\,r\right) s1 + \left((1 - a)\,m\,r + b\,m\,r\right) s2$$

```
Factor[-b - b^2 - a b m]
```

$$-b\,(1 + b + a\,m)$$

```
Factor[b + b^2 + a b m + (-1 + a) m r - b m r]
```

$$b + b^2 + a\,b\,m - m\,r + a\,m\,r - b\,m\,r$$

In[69]:=
```
pgf2Add = pgf[2, 1] /. qEquil1BAdditiveMultiplicApprox[[2]] /. wbar[1] → wMeanB[1] /.
            assumeAdditiveMultiplicEpistaticApproxFitness[1] /. assumeA1Rare[1] /.
          w2[1] → wMargType[2, 1] /. assumeAdditiveMultiplicEpistaticApproxFitness[1] /.
        assumeA1Rare[1] /. {γ11[1] → 0, γ12[1] → 0, γ21[1] → 0, γ22[1] → 0} /.
      qEquil1BAdditiveMultiplicApprox[[2]] /. {a[1] → a, b[1] → b,
      m[1] → m, s[1] → s1, s[2] → s2} // FullSimplify
```

Out[69]=
$$e^{\frac{(-1+a)\,m\,r\,(s1-s2)+b^2\,(m-m\,s2)+b\,(-1+r\,s1+a\,m\,(-1+s2)+s2-r\,s2)}{b\,(1-a+b)}}$$

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

$$-b - a\,b\,m + b^2\,m + (b\,r + (-1 + a)\,m\,r)\,s1 + \left(b + a\,b\,m - b^2\,m - b\,r + (1 - a)\,m\,r\right) s2$$

```
Factor[-b - a b m + b^2 m]
```

$$b\,(-1 - a\,m + b\,m)$$

■ Implementation of numerical solution

```
(*Solve[pgf1Add==s1&&pgf2Add==s2,{s1,s2}]*)
```

In[70]:=
```
probEstablAMApproxFunc::usage = "probEstablAMApproxFunc[r, m1, a1, b1, γ111, γ121, γ211
probEstablAMApproxFunc[r_,m1_,a1_,b1_,γ111_,γ121_,γ211_,γ221_]:=Module[{qEq,wbar,w1,w2,
qEq=(b1-m1+a1*m1)/(b1*(1+m1)); (* Verified by equation (22) in Akerman (2011), subsecti
wbar=1-a1+b1*(-1+2*qEq);
w1=1+b1*qEq+(-1+qEq)*γ111;
w2=1+b1*(-1+qEq)-qEq*γ111+γ121*(-1+qEq);
w14=1-γ111;
(* Leading eigenvalue of the mean matrix *)
λ1=-1/(2 wbar)(-1+m1)*(w1-r*w14+w2+(w1^2+r^2*w14^2+w1*(2*(-1+2*qEq)*r*w14-2*w2)+2*(1-2*qEq)*r*
(* Probability generating functions *)
pgf1[s1_,s2_]:=Exp[-(r*(1-m1)*(1-qEq)*(1-s2)*w14)/wbar-((1-m1)*(1-s1)*(w1-r*(1-qEq)*w14))/wbar];
pgf2[s1_,s2_]:=Exp[-(r*(1-m1)*qEq*(1-s1)*w14)/wbar-((1-m1)*(1-s2)*(-r*qEq*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[{λ1,(1-q1),(1-q2),qEq*(1-q1)+(1-qEq)*(1-q2),qEq}/.qSol]
];

(* Rules for the specific model considered *)
rulesCI[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) /.
   assumeA1Rare[n] // FullSimplify

GAdditiveMultiplicEpistaticApprox[1] // MatrixForm
```

$$\begin{pmatrix} \frac{(-1+m[1])\,(1+b[1]\,q[1]-r\,(-1+q[1])\,(-1+\gamma 11[1])+(-1+q[1])\,\gamma 11[1])}{-1+a[1]+b[1]-2\,b[1]\,q[1]} & -\frac{r\,(-1+m[1])\,q[1]\,(-1+\gamma 11[1])}{-1+a[1]+b[1]-2\,b[1]\,q[1]} \\ \frac{r\,(-1+m[1])\,(-1+q[1])\,(-1+\gamma 11[1])}{-1+a[1]+b[1]-2\,b[1]\,q[1]} & \frac{(-1+m[1])\,(1+b[1]\,(-1+q[1])-\gamma 12[1]+q[1]\,(r\,(-1+\gamma 11[1])-\gamma 11}{-1+a[1]+b[1]-2\,b[1]\,q[1]} \end{pmatrix}$$

```
(* Eigenvalues[GAdditiveMultiplicEpistatic[1]]//FullSimplify *)
(* This takes some time to evaluate *)

assumeA1Rare[1]
```

$$\{x[3,\,1]\to q[1],\; x[4,\,1]\to 1-q[1]\}$$

Test of the above function probEstablAMApproxFunc[r_,m1_,a1_,b1_,γ111_,γ121_,γ211_,γ221_]:

```
Clear[myr, mym1, mya1, myb1, myγ111, myγ121, myγ211,
 myγ221, myqEq, mywbar, myw1, myw2, myw14, myλ1, mypgf1, mypgf2]

myr = 0.008;
mym1 = 0.015;
mya1 = 0.01;
myb1 = 0.02;
myγ111 = 0.;
myγ121 = 0.;
myγ211 = 0.;
myγ221 = 0.;
myqEq = (myb1 - mym1 + mya1 * mym1) / (myb1 * (1 + mym1));
mywbar = 1 - mya1 - myb1 * (1 - 2 * myqEq);
myw1 = 1 + myb1 myqEq + (-1 + myqEq) myγ111;
myw2 = 1 - myb1 * (1 - myqEq) - myqEq * myγ111 - myγ121 * (1 - myqEq);
myw14 = 1 - myγ111;
```

```
myλ1 = -1/(2 mywbar) (-1 + mym1)
    (myw1 - myr myw14 + myw2 + (myw1^2 + myr^2 myw14^2 + myw1 (2 (-1 + 2 myqEq) myr myw14 - 2 myw2) +
          2 (1 - 2 myqEq) myr myw14 myw2 + myw2^2)^(1/2));

mypgf1[s1_, s2_] := Exp[-(myr (1 - mym1) myqEq (1 - s2) myw14)/mywbar -
    1/mywbar (1 - mym1) (1 - s1) (myw1 - myr (1 - myqEq) myw14)];

mypgf2[s1_, s2_] := Exp[-(myr (1 - mym1) (1 - myqEq) (1 - s1) myw14)/mywbar -
    1/mywbar (1 - mym1) (1 - s2) (-myr myqEq myw14 + myw2)];

qSol = FindRoot[{mypgf1[q1, q2] == q1, mypgf2[q1, q2] == q2}, {q1, 0.5}, {q2, 0.5}];

{1 - q1, 1 - q2} /. qSol

{0.00976312, 0.00413608}

probEstablAMApproxFunc[myr, mym1, mya1, myb1, myγ111, myγ121, myγ211, myγ221]

{1.00478, 0.00993348, 0.00157342, 0.00369432, 0.253695}

myqEq * (1 - q1) + (1 - myqEq) * (1 - q2) /. qSol

0.00556363
```

End of test.

■ Explicit equilibrium frequency of B_1

```
Clear[qhat, w1, w2, wbar, b, m, a, γ11, γ12, γ21, γ22]
```

In[74]:=
```
assumParamRelationsAdditiveMultiplicApprox[n_]:={0<a[n]≤b[n]≤1&&0<m[n]<b[n]}
```

In[75]:=
```
qhatAMApprox = q[1] /. qEquil1BAdditiveMultiplicApprox⟦2⟧
```

Out[75]=
$$\frac{b[1]-m[1]+a[1]\,m[1]}{b[1]\,(1+m[1])}$$

■ Explicit fitnesses

In[76]:=
```
wbarAMApprox =
 wMeanB[1] /. assumeAdditiveMultiplicApproxFitness[1] /. assumeA1Rare[1] // FullSimplify
```

Out[76]=
$$1-a[1]+b[1]\,(-1+2\,q[1])$$

In[77]:=
```
w1AMApprox =
 wMargType[1, 1] /. assumeAdditiveMultiplicApproxFitness[1] /. assumeA1Rare[1] //
  FullSimplify
```

Out[77]=
$$1+b[1]\,q[1]$$

In[78]:=
```
w2AMApprox =
 wMargType[2, 1] /. assumeAdditiveMultiplicApproxFitness[1] /. assumeA1Rare[1] //
  FullSimplify
```

Out[78]=
$$1+b[1]\,(-1+q[1])$$

In[79]:=
```
w14AMApprox[n_] := 1
```

We evaluate the mean and marginal fitnesses at equilibrium.

```
w1AMApprox /. {q[1] → qhatAMApprox} // FullSimplify
```

$$\frac{1 + b[1] + a[1]\, m[1]}{1 + m[1]}$$

```
w2AMApprox /. {q[1] → qhatAMApprox} // FullSimplify
```

$$\frac{1 + (a[1] - b[1])\, m[1]}{1 + m[1]}$$

```
wbarAMApprox /. {q[1] → qhatAMApprox} // FullSimplify
```

$$\frac{(-1 + a[1] - b[1])\, (-1 + m[1])}{1 + m[1]}$$

■ Explicit mean matrix

The elements of the mean matrix for additive fitnesses:

```
G[1] /. ruleSimplifyNotationCI // MatrixForm
```

$$\begin{pmatrix} \frac{(1-m)\,(w1[1]-(1-q)\,r\,w14[1])}{wbar[1]} & \frac{(1-m)\,q\,r\,w14[1]}{wbar[1]} \\ \frac{(1-m)\,(1-q)\,r\,w14[1]}{wbar[1]} & \frac{(1-m)\,(-q\,r\,w14[1]+w2[1])}{wbar[1]} \end{pmatrix}$$

```
assumeAdditiveMultiplicApproxFitness[1]
```

$$\{w11[1] \to 1 + a[1] + b[1],\ w12[1] \to 1 + a[1],\ w13[1] \to 1 + b[1],\ w14[1] \to 1,\ w22[1] \to 1 + a[1] - b[1],\ w24[1] \to 1 - b[1],\ w33[1] \to 1 - a[1] + b[1],\ w34[1] \to 1 - a[1],\ w44[1] \to 1 - a[1] - b[1]\}$$

```
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] /. ruleSimplifyNotationCI /. {w1[1] → w1AMApprox, w2[1] → w2AMApprox, wbar[1] →
        wbarAMApprox} /. assumeAdditiveMultiplicApproxFitness[1] /.
    {q[1] → qhatAMApprox} /. {q → qhatAMApprox} /.
   ruleSimplifyNotationCI /. {a[1] → a, b[1] → b} // FullSimplify;
```

```
GAdd // MatrixForm
```

$$\begin{pmatrix} \frac{1+b+a\,m}{1-a+b} - \frac{m\,r}{b} & \frac{(b+(-1+a)\,m)\,r}{b\,(1-a+b)} \\ \frac{m\,r}{b} & \frac{b^2\,m+(-1+a)\,m\,r+b\,(-1-a\,m+r)}{(-1+a-b)\,b} \end{pmatrix}$$

```
GAdd /. {a → α ϵ, b → β ϵ, m → μ ϵ, r → ρ ϵ}
```

$$\left\{\left\{\frac{1 + \beta\,\epsilon + \alpha\,\epsilon^2\,\mu}{1 - \alpha\,\epsilon + \beta\,\epsilon} - \frac{\epsilon\,\mu\,\rho}{\beta},\ \frac{(\beta\,\epsilon + \epsilon\,(-1 + \alpha\,\epsilon)\,\mu)\,\rho}{\beta\,(1 - \alpha\,\epsilon + \beta\,\epsilon)}\right\},\ \left\{\frac{\epsilon\,\mu\,\rho}{\beta},\ \frac{\beta^2\,\epsilon^3\,\mu + \epsilon^2\,(-1 + \alpha\,\epsilon)\,\mu\,\rho + \beta\,\epsilon\,\left(-1 - \alpha\,\epsilon^2\,\mu + \epsilon\,\rho\right)}{\beta\,\epsilon\,(-1 + \alpha\,\epsilon - \beta\,\epsilon)}\right\}\right\}$$

```
GAddApprox = Series[{{{1 + β ϵ + α ϵ^2 μ)/(1 - α ϵ + β ϵ) - ϵ μ ρ/β, ((β ϵ + ϵ (-1 + α ϵ)) μ) ρ/(β (1 - α ϵ + β ϵ))},
      {ϵ μ ρ/β, (β^2 ϵ^3 μ + ϵ^2 (-1 + α ϵ) μ ρ + β ϵ (-1 - α ϵ^2 μ + ϵ ρ))/(β ϵ (-1 + α ϵ - β ϵ))}}, {ϵ, 0, 1}] /.
  {α → a/ϵ, β → b/ϵ, ρ → r/ϵ, μ → m/ϵ} // Normal;
```

```
GAddApprox // MatrixForm
```

$$\begin{pmatrix} 1 + a - \frac{m\,r}{b} & r - \frac{m\,r}{b} \\ \frac{m\,r}{b} & 1 + a - b - r + \frac{m\,r}{b} \end{pmatrix}$$

■ Explicit conditions for invasion

```
conditionNonExtinction[1]
```

$$r\, w14[1] \left(-q[1]\, w1[1] - (1-q[1])\, w2[1] + \frac{wbar[1]}{1-m[1]}\right) < \left(w1[1] - \frac{wbar[1]}{1-m[1]}\right)\left(-w2[1] + \frac{wbar[1]}{1-m[1]}\right)$$

```
conditionNonExtinctionAMApprox =
 conditionNonExtinction[1] /. {w14[1] → w14AMApprox[1], wbar[1] → wbarAMApprox,
     w1[1] → w1AMApprox, w2[1] → w2AMApprox} /. {q[1] → qhatAMApprox} // FullSimplify
```

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

We simplify the notation.

```
condNonExtAdd = conditionNonExtinctionAMApprox /. ruleSimplifyNotation
```

$$\frac{(-a + (1 - 2\,a + b)\, m)\, r}{1 + m} < a\,(-a + b)$$

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

```
FullSimplify[Reduce[condNonExtAdd, m],
 Assumptions → Flatten[{0 < a < b < 1, a + b < 1, 0 < m < 1, 0 < r < 1 / 2}]]
```

$$a^2 + r + b\,r < a\,(b + 2\,r) \;||\; a^2 + r + b\,r == a\,(b + 2\,r) \;||\; m < \frac{a\,(-a + b + r)}{a^2 + r + b\,r - a\,(b + 2\,r)}$$

```
mCrit1
```

$$\frac{a}{1 - b}$$

```
mCrit2
```

$$\frac{b}{1 - a}$$

```
mCrit5
```

$$\frac{a\,(-a + b + r)}{(a - b)\,(a - r) + (1 - a)\, r}$$

```
a (-a + b + r)/(a^2 + r + b r - a (b + 2 r)) - mCrit5 // Simplify
```

$$0$$

In terms of m, we recover the critical value $\frac{a(b-a+r)}{(a-b)(a-r)+(1-a)r}$ previously known as $m_{\text{crit},5}$, which was expected. Allele A_1 can invade if $m < m_{\text{crit},5}$. The condition $a^2 + r + b\,r < a(b + 2\,r)$ implies that $m_{\text{crit},5} < 0$, meaning that invasion is possible independently of the migration rate m. The condition $a^2 + r + b\,r == a(b + 2\,r)$ 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.

```
FullSimplify[Reduce[condNonExtAdd, r],
 Assumptions → Flatten[{0 < a < b < 1, a + b < 1, 0 < m < mCrit2, 0 < r < 1 / 2}]]
```

$$a + 2\,a\,m == m + b\,m \;||\; m + b\,m < a + 2\,a\,m \;||\; r < \frac{a\,(a - b)\,(1 + m)}{a + 2\,a\,m - (1 + b)\, m}$$

Again, the critical value $\frac{a(a-b)(1+m)}{a+2\,a\,m-(1+b)\,m}$ for the recombination rate is equal to the one previously established for the deterministic model, $r_{\text{rcit},5}$. 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.

```
Solve[m + b m == a + 2 a m, m]
```

$$\left\{\left\{m \to \frac{a}{1 - 2\,a + b}\right\}\right\}$$

```
Series[a (-a + b + r)/((a - b) (a - r) + (1 - a) r) /. {a → α ϵ, b → β ϵ, r → ρ ϵ}, {ϵ, 0, 1}] // Normal
```

$$\epsilon \left(\alpha - \frac{\alpha^2}{\rho} + \frac{\alpha\,\beta}{\rho}\right)$$

```
Solve[α - α^2/ρ + α β/ρ == μ, ρ] // FullSimplify
```

$$\left\{\left\{\rho \to \frac{\alpha\,(\alpha - \beta)}{\alpha - \mu}\right\}\right\}$$

Plots of numerical solutions

Helper rules

Replacement rule for explicit fitness matrices.

In[80]:=
```
ruleFitness:={a[1]→mya,b[1]→myb,γ11[1]→myγ11temp,γ12[1]→myγ12temp,γ21[1]→myγ21temp,γ22
```

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

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 $m_1 \geq a_1$. 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: $0 < a_1 \leq m_1 \leq b_1 < 1$.

$$0 < a_1 \leq m_1 \leq b_1 < 1 \tag{6}$$

```
Clear[myr, mym, mya, myb, myγ11temp, myγ12temp,
 myγ21temp, myγ22temp, myqEq, mywbar, myw1, myw2, myw14]
```

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

Weak evoutionary forces; migration rate $m = 0.022$

```
mym = 0.022;
mya = 0.02;
myb = 0.04;
myγ11temp = 0.;
myγ12temp = 0.;
myγ21temp = 0.;
myγ22temp = 0.;
```

```
ruleFitness
```

```
{a[1] → 0.02, b[1] → 0.04, γ11[1] → 0., γ12[1] → 0., γ21[1] → 0., γ22[1] → 0.}
```

```
wCompact[1] /. assumeAdditiveMultiplicEpistaticApproxFitness[1] /. 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 E_C.

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

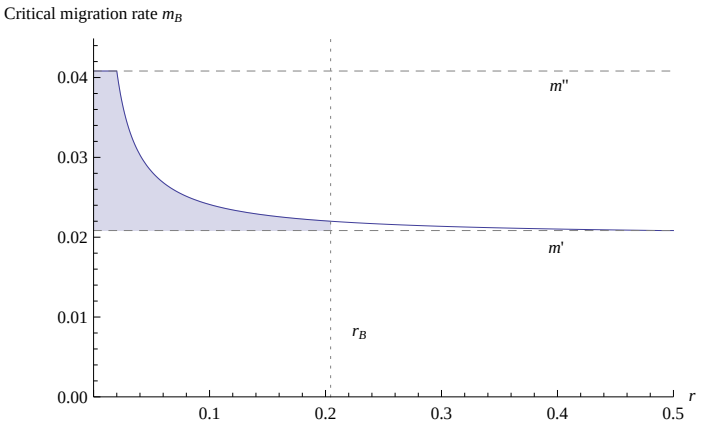
```
0.0208333
```

```
0.0408163
```

```
-0.181498
```

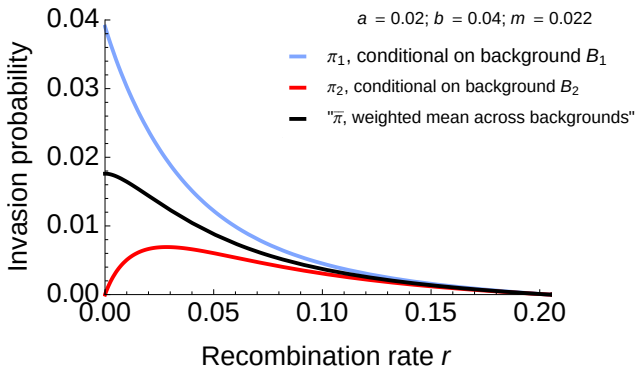
Critical value for the migration rate, $m_{B,1}$, as a function of r for the current parameter values.

```
Show[Plot[mCritFunc[r, mya, myb], {r, 0, 0.5}, PlotRange → {{0, 0.5}, {0, mc2 + 0.1 * mc2}},
  AxesLabel → {r, "Critical migration rate mB"}],
 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[ "rB", {.025 + rCrit, 0.2 * mc2}]],
 Graphics[{Gray, Dashed, Line[{{.0, mc1}, {.5, mc1}}]}],
 Graphics[Text[ "m'", {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 *)
```



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

```
plot1 =
 Show[Plot[{probEstablAMApproxFunc[r, mym, mya, myb, myγ11temp, myγ12temp, myγ21temp,
      myγ22temp][[2]], probEstablAMApproxFunc[r, mym, mya, myb, myγ11temp,
      myγ12temp, myγ21temp, myγ22temp][[3]], probEstablAMApproxFunc[r,
      mym, mya, myb, myγ11temp, myγ12temp, myγ21temp, myγ22temp][[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["π1, conditional on background B1", FontFamily → "Helvetica", 10],
     Style["π2, conditional on background B2", FontFamily → "Helvetica"],
     Style["π̄, 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 evoutionary forces; migration rate $m = 0.03$

```
mym = 0.03;
mya = 0.02;
myb = 0.04;
myγ11temp = 0.;
myγ12temp = 0.;
myγ21temp = 0.;
myγ22temp = 0.;
```

```
wCompact[1] /. assumeAdditiveMultiplicEpistaticApproxFitness[1] /. 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! *)
```

```
0.04
```

```
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.

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

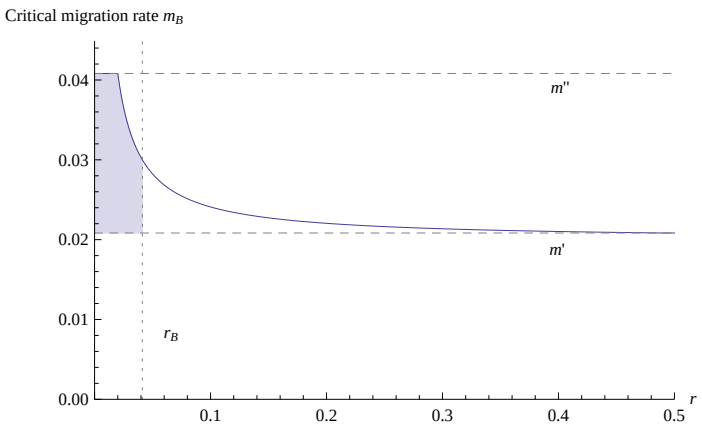
```
0.0208333
```

```
0.0408163
```

```
0.0196078
```

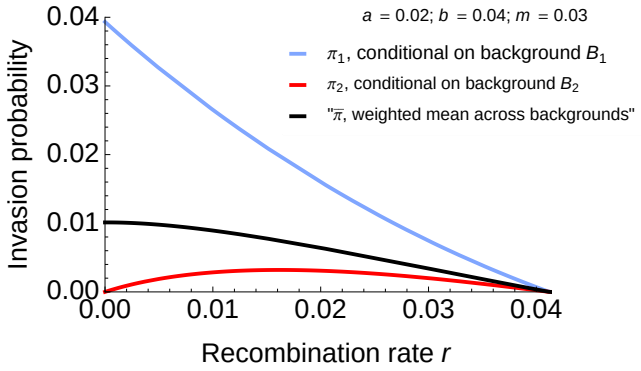
Critical value for the migration rate, $m_{B,1}$, as a function of r for the current parameter values.

```
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[ "r_B", {.025 + rCrit, 0.2 * mc2}]],
 Graphics[{Gray, Dashed, Line[{{.0, mc1}, {.5, mc1}}]}],
 Graphics[Text[ "m'", {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 *)
```



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

```
plot2 =
 Show[Plot[{probEstablAMApproxFunc[r, mym, mya, myb, myγ11temp, myγ12temp, myγ21temp,
       myγ22temp][[2]], probEstablAMApproxFunc[r, mym, mya, myb, myγ11temp,
       myγ12temp, myγ21temp, myγ22temp][[3]], probEstablAMApproxFunc[r,
       mym, mya, myb, myγ11temp, myγ12temp, myγ21temp, myγ22temp][[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["π_1, conditional on background B_1", FontFamily → "Helvetica", 10],
     Style["π_2, conditional on background B_2", FontFamily → "Helvetica"],
     Style["π̄, 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 evoutionary forces; migration rate $m = 0.038$

```
mym = 0.038;
mya = 0.02;
myb = 0.04;
myγ11temp = 0.;
myγ12temp = 0.;
myγ21temp = 0.;
myγ22temp = 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! *)
```

```
0.0222222
```

```
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. *)
```

```
0.0230667
```

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}
```

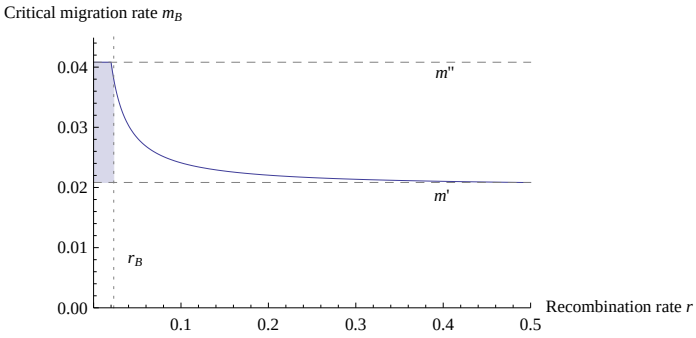
```
0.0208333
```

```
0.0408163
```

```
0.0378054
```

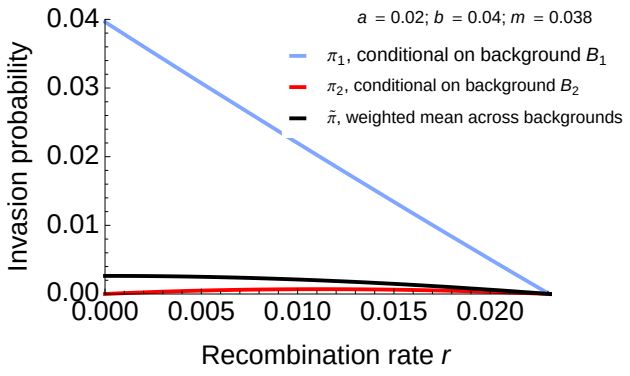
Critical value for the migration rate, $m_{B,1}$, as a function of r for the current parameter values.

```
Show[Plot[mCritFunc[r, mya, myb], {r, 0, 0.5}, PlotRange → {{0, 0.5}, {0, mc2 + 0.1 * mc2}},
  AxesLabel → {"Recombination rate 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, mc1}, {.5, mc1}}]}],
 Graphics[Text[ "m'", {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 *)
```



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

```
plot3 =
 Show[Plot[{probEstablAMApproxFunc[r, mym, mya, myb, myγ11temp, myγ12temp, myγ21temp,
      myγ22temp][[2]], probEstablAMApproxFunc[r, mym, mya, myb, myγ11temp,
      myγ12temp, myγ21temp, myγ22temp][[3]], probEstablAMApproxFunc[r,
      mym, mya, myb, myγ11temp, myγ12temp, myγ21temp, myγ22temp][[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["π_1, conditional on background B_1", FontFamily → "Helvetica", 10],
     Style["π_2, conditional on background B_2", FontFamily → "Helvetica"],
     Style["π̄, 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, recombination rate $r = 0.001$

```
myr = 0.001;
mya = 0.02;
myb = 0.04;
myγ11temp = 0.;
myγ12temp = 0.;
myγ21temp = 0.;
myγ22temp = 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! *)
```

```
0.04
```

```
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.

```
mc1
```

```
0.0208333
```

```
mCrit1
```

$$\frac{a}{1-b}$$

```
mc1 = mCrit1 /. {a → mya, b → myb}
mc2 = mCrit2 /. {a → mya, b → myb}
mc3 = mCrit3 /. {a → mya, b → myb, r → myr}
```

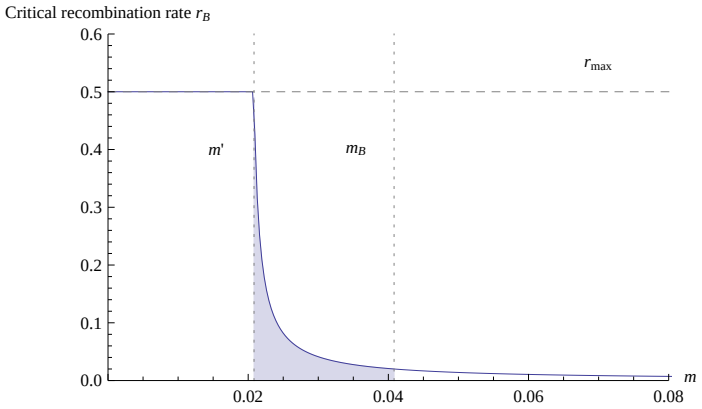
```
0.0208333
```

```
0.0408163
```

```
0.0590591
```

```
Show[Plot[rCritApproxFunc[m, mya, myb], {m, 0, 1}, PlotRange → {{0, 0.08}, {0, .6}},
    AxesLabel → {m1, "Critical recombination rate rB (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["a1", {.75 * mya, 0.8 * .5}]],
  Graphics[{Gray, Dotted, Line[{{mCritApprox, 0}, {mCritApprox, .6}}]}],
  Graphics[Text["mB,1", {mCritApprox - .25 * mya, 0.8 * .5}]],
  Graphics[{Gray, Dashed, Line[{{0, .5}, {1, .5}}]}],
  Graphics[Text["rmax", {.07, 1.1 * .5}]]](* This uses approximate critical values *);
```

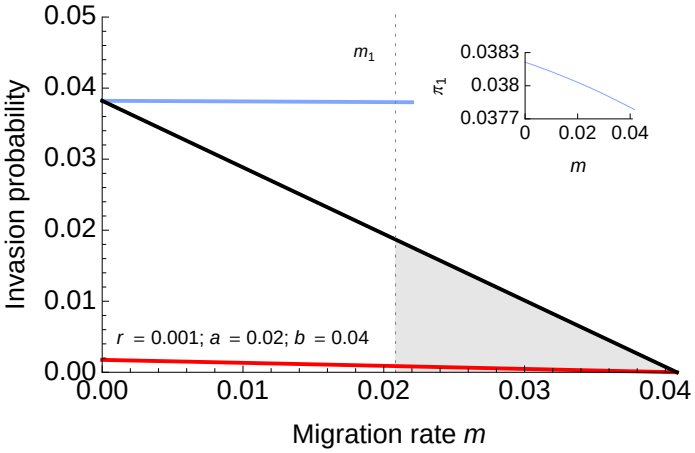
```
Show[Plot[rCritFunc[m, mya, myb], {m, 0, 1}, PlotRange → {{0, 0.08}, {0, .6}},
  AxesLabel → {m, "Critical recombination rate r_B"}],
 Plot[rCritFunc[m, mya, myb], {m, mc1, mCrit}, PlotRange → {{0, 0.08}, {0, 1}},
  PlotStyle → None, Filling → {1 → Axis}],
 Graphics[{Gray, Dotted, Line[{{mc1, 0}, {mc1, .6}}]}],
 Graphics[Text["m'", {.75 * mc1, 0.8 * .5}]],
 Graphics[{Gray, Dotted, Line[{{mCrit, 0}, {mCrit, .6}}]}],
 Graphics[Text["m_B", {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 *)
```



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

```
inset4 =
  Plot[{1, probEstablAMApproxFunc[myr, m, mya, myb, myγ11temp, myγ12temp, myγ21temp,
      myγ22temp][[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, "π1"},
   LabelStyle → {Directive[FontSize → 10], FontFamily → "Helvetica"},
   FrameTicks → {{0, 0.02, 0.04}, {0.0377, 0.0380, 0.0383}}];
```

```
plot4 =
 Show[Plot[probEstablAMApproxFunc[myr, m, mya, myb, myγ11temp, myγ12temp, myγ21temp,
     myγ22temp][[4]], {m, mc1, 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[{probEstablAMApproxFunc[myr, m, mya, myb, myγ11temp, myγ12temp,
     myγ21temp, myγ22temp][[2]], probEstablAMApproxFunc[myr, m,
     mya, myb, myγ11temp, myγ12temp, myγ21temp, myγ22temp][[3]],
   probEstablAMApproxFunc[myr, m, mya, myb, myγ11temp, myγ12temp, myγ21temp,
     myγ22temp][[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, 0.005}]],
  Graphics[{Gray, Dotted, Line[{{mc1, .0}, {mc1, 1.}}]}],
  Graphics[Text[Style["m1", FontFamily → "Helvetica"], {0.9 * mc1, 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 $r = 0.01$

```
myr = 0.01;
mya = 0.02;
myb = 0.04;
myγ11temp = 0.;
myγ12temp = 0.;
myγ21temp = 0.;
myγ22temp = 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! *)
```

```
0.04
```

```
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.

```
mc1 = mCrit1 /. {a → mya, b → myb}
mc2 = mCrit2 /. {a → mya, b → myb}
mc3 = mCrit3 /. {a → mya, b → myb, r → myr}
```

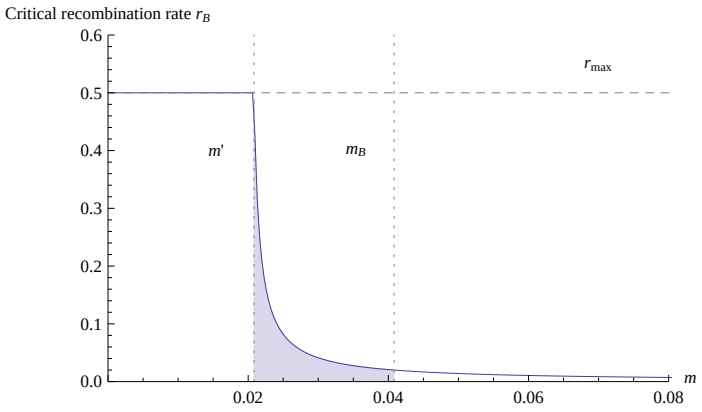
```
0.0208333
```

```
0.0408163
```

```
0.0505051
```

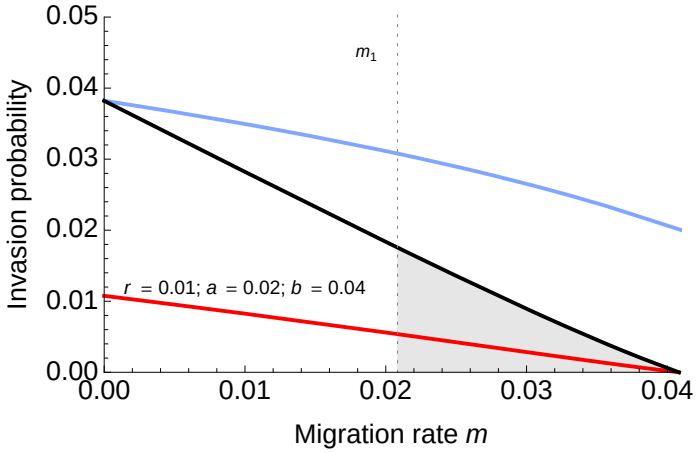
```
Show[Plot[rCritApproxFunc[m, mya, myb], {m, 0, 1}, PlotRange → {{0, 0.08}, {0, .6}},
    AxesLabel → {m1, "Critical recombination rate rB (approximate)"}],
  Plot[rCritApproxFunc[m, mya, myb], {m, 0, mCritApprox},
    PlotRange → {{mya, mCritApprox}, {0, .5}}, PlotStyle → None, Filling → {1 → Axis}],
  Graphics[{Gray, Dotted, Line[{{mya, 0}, {mya, .6}}]}],
  Graphics[Text["a1", {.75 * mya, 0.8 * .5}]],
  Graphics[{Gray, Dotted, Line[{{mCritApprox, 0}, {mCritApprox, .6}}]}],
  Graphics[Text["mB,1", {mCritApprox - .25 * mya, 0.8 * .5}]],
  Graphics[{Gray, Dashed, Line[{{0, .5}, {1, .5}}]}],
  Graphics[Text["rmax", {.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 rB"}],
 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[Text["m'", {.75 * mc1, 0.8 * .5}]],
 Graphics[{Gray, Dotted, Line[{{mCrit, 0}, {mCrit, .6}}]}],
 Graphics[Text["mB", {mCrit - .25 * mc1, 0.8 * .5}]],
 Graphics[{Gray, Dashed, Line[{{0, .5}, {1, .5}}]}],
 Graphics[Text["rmax", {.07, 1.1 * .5}]]] (* This uses exact critical values *)
```



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

```
plot5 =
 Show[Plot[probEstablAMApproxFunc[myr, m, mya, myb, myγ11temp, myγ12temp, myγ21temp,
     myγ22temp][[4]], {m, mc1, 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[{probEstablAMApproxFunc[myr, m, mya, myb, myγ11temp, myγ12temp,
     myγ21temp, myγ22temp][[2]], probEstablAMApproxFunc[myr, m,
     mya, myb, myγ11temp, myγ12temp, myγ21temp, myγ22temp][[3]],
   probEstablAMApproxFunc[myr, m, mya, myb, myγ11temp, myγ12temp, myγ21temp,
     myγ22temp][[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[{{mc1, .0}, {mc1, 1.}}]}],
  Graphics[Text[Style["m1", FontFamily → "Helvetica"], {0.9 * mc1, 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;
myγ11temp = 0.;
myγ12temp = 0.;
myγ21temp = 0.;
myγ22temp = 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! *)
```

```
0.04
```

```
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.

```
mc1 = mCrit1 /. {a → mya, b → myb}
mc2 = mCrit2 /. {a → mya, b → myb}
mc3 = mCrit3 /. {a → mya, b → myb, r → myr}
```

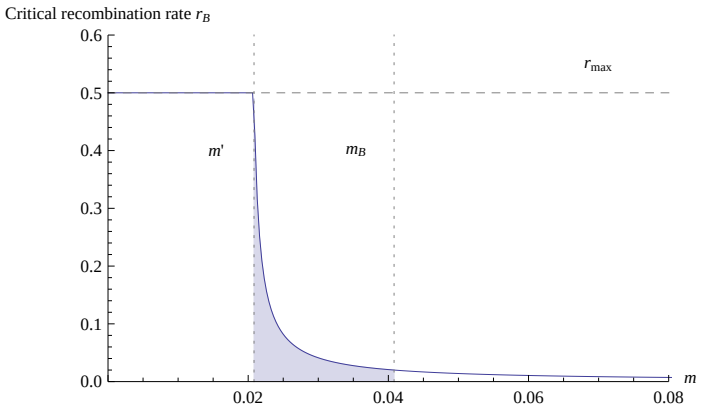
```
0.0208333
```

```
0.0408163
```

```
0.0408163
```

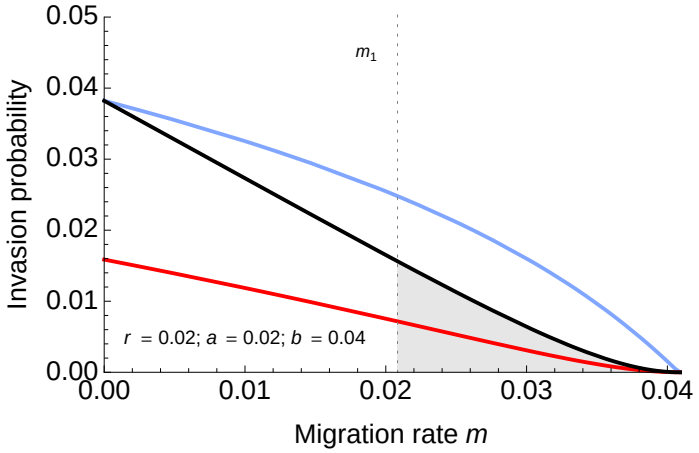
```
Show[Plot[rCritApproxFunc[m, mya, myb], {m, 0, 1}, PlotRange → {{0, 0.08}, {0, .6}},
    AxesLabel → {m1, "Critical recombination rate rB (approximate)"}],
  Plot[rCritApproxFunc[m, mya, myb], {m, 0, mCritApprox},
    PlotRange → {{mya, mCritApprox}, {0, .5}}, PlotStyle → None, Filling → {1 → Axis}],
  Graphics[{Gray, Dotted, Line[{{mya, 0}, {mya, .6}}]}],
  Graphics[Text["a1", {.75 * mya, 0.8 * .5}]],
  Graphics[{Gray, Dotted, Line[{{mCritApprox, 0}, {mCritApprox, .6}}]}],
  Graphics[Text["mB,1", {mCritApprox - .25 * mya, 0.8 * .5}]],
  Graphics[{Gray, Dashed, Line[{{0, .5}, {1, .5}}]}],
  Graphics[Text["rmax", {.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 rB"}],
 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[Text["m'", {.75 * mc1, 0.8 * .5}]],
 Graphics[{Gray, Dotted, Line[{{mCrit, 0}, {mCrit, .6}}]}],
 Graphics[Text["mB", {mCrit - .25 * mc1, 0.8 * .5}]],
 Graphics[{Gray, Dashed, Line[{{0, .5}, {1, .5}}]}],
 Graphics[Text["rmax", {.07, 1.1 * .5}]] (* This uses exact critical values *)
```



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

```
plot6 =
 Show[Plot[probEstablAMApproxFunc[myr, m, mya, myb, myγ11temp, myγ12temp, myγ21temp,
     myγ22temp][[4]], {m, mc1, 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[{probEstablAMApproxFunc[myr, m, mya, myb, myγ11temp, myγ12temp,
     myγ21temp, myγ22temp][[2]], probEstablAMApproxFunc[myr, m,
     mya, myb, myγ11temp, myγ12temp, myγ21temp, myγ22temp][[3]],
   probEstablAMApproxFunc[myr, m, mya, myb, myγ11temp, myγ12temp, myγ21temp,
     myγ22temp][[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, 0.005}]],
  Graphics[{Gray, Dotted, Line[{{mc1, .0}, {mc1, 1.}}]}],
  Graphics[Text[Style["m1", FontFamily → "Helvetica"], {0.9 * mc1, 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;
myγ11temp = 0.;
myγ12temp = 0.;
myγ21temp = 0.;
myγ22temp = 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! *)
```

```
0.022
```

```
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.

```
mc1 = mCrit1 /. {a → mya, b → myb}
mc2 = mCrit2 /. {a → mya, b → myb}
mc3 = mCrit3 /. {a → mya, b → myb, r → myr}
```

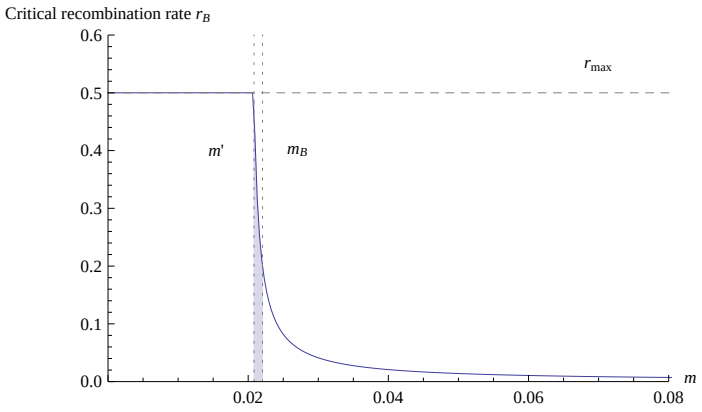
```
0.0208333
```

```
0.0408163
```

```
-0.175
```

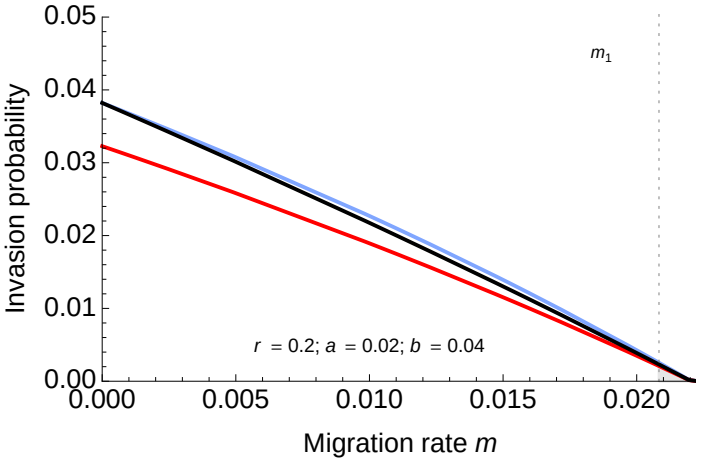
```
Show[Plot[rCritApproxFunc[m, mya, myb], {m, 0, 1}, PlotRange → {{0, 0.08}, {0, .6}},
    AxesLabel → {m1, "Critical recombination rate rB (approximate)"}],
  Plot[rCritApproxFunc[m, mya, myb], {m, 0, mCritApprox},
    PlotRange → {{mya, mCritApprox}, {0, .5}}, PlotStyle → None, Filling → {1 → Axis}],
  Graphics[{Gray, Dotted, Line[{{mya, 0}, {mya, .6}}]}],
  Graphics[Text["a1", {.75 * mya, 0.8 * .5}]],
  Graphics[{Gray, Dotted, Line[{{mCritApprox, 0}, {mCritApprox, .6}}]}],
  Graphics[Text["mB,1", {mCritApprox - .25 * mya, 0.8 * .5}]],
  Graphics[{Gray, Dashed, Line[{{0, .5}, {1, .5}}]}],
  Graphics[Text["rmax", {.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 rB"}],
 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[Text["m'", {.75 * mc1, 0.8 * .5}]],
 Graphics[{Gray, Dotted, Line[{{mCrit, 0}, {mCrit, .6}}]}],
 Graphics[Text["mB", {mCrit + .25 * mc1, 0.8 * .5}]],
 Graphics[{Gray, Dashed, Line[{{0, .5}, {1, .5}}]}],
 Graphics[Text["rmax", {.07, 1.1 * .5}]]] (* This uses exact critical values *)
```



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

```
plot7 =
 Show[Plot[probEstablAMApproxFunc[myr, m, mya, myb, myγ11temp, myγ12temp, myγ21temp,
     myγ22temp][[4]], {m, mc1, 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[{probEstablAMApproxFunc[myr, m, mya, myb, myγ11temp, myγ12temp,
     myγ21temp, myγ22temp][[2]], probEstablAMApproxFunc[myr, m,
     mya, myb, myγ11temp, myγ12temp, myγ21temp, myγ22temp][[3]],
   probEstablAMApproxFunc[myr, m, mya, myb, myγ11temp, myγ12temp, myγ21temp,
     myγ22temp][[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, 0.005}]],
  Graphics[{Gray, Dotted, Line[{{mc1, .0}, {mc1, 1.}}]}],
  Graphics[Text[Style["m1", FontFamily → "Helvetica"], {0.9 * mc1, 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 $r = 0.5$

```
myr = 0.5;
mya = 0.02;
myb = 0.04;
myγ11temp = 0.;
myγ12temp = 0.;
myγ21temp = 0.;
myγ22temp = 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! *)
```

```
0.0208
```

```
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. *)
```

```
0.0208333
```

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}
```

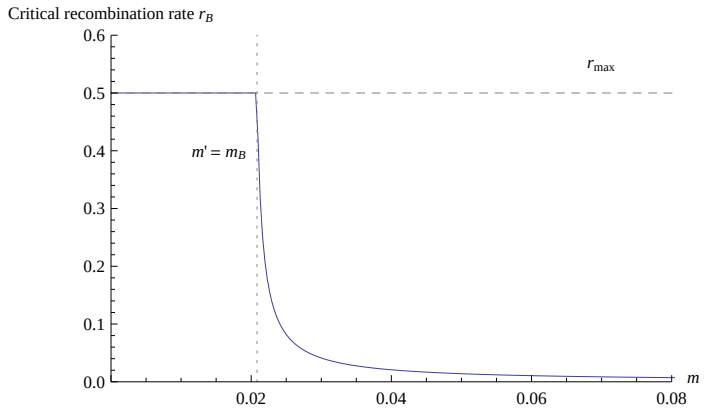
```
0.0208333
```

```
0.0408163
```

```
-0.88
```

```
Show[Plot[rCritApproxFunc[m, mya, myb], {m, 0, 1}, PlotRange → {{0, 0.08}, {0, .6}},
    AxesLabel → {m1, "Critical recombination rate rB (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["a1", {.75 * mya, 0.8 * .5}]],
  Graphics[{Gray, Dotted, Line[{{mCritApprox, 0}, {mCritApprox, .6}}]}],
  Graphics[Text["mB,1", {mCritApprox - .25 * mya, 0.8 * .5}]],
  Graphics[{Gray, Dashed, Line[{{0, .5}, {1, .5}}]}],
  Graphics[Text["rmax", {.07, 1.1 * .5}]](* This uses approximate critical values *);
```

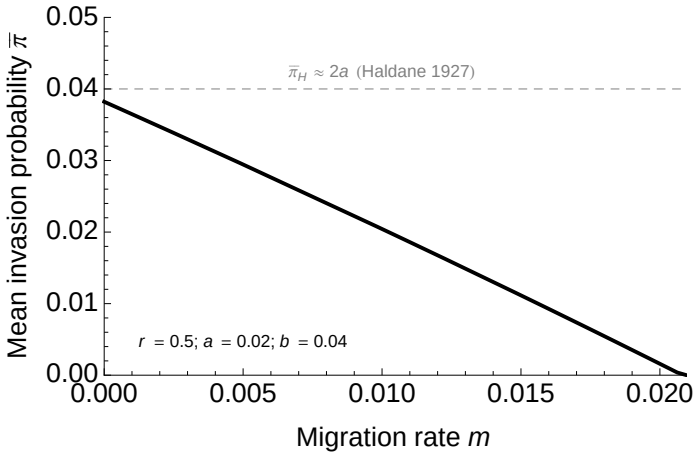
```
Show[Plot[rCritFunc[m, mya, myb], {m, 0, 1}, PlotRange → {{0, 0.08}, {0, .6}},
  AxesLabel → {m, "Critical recombination rate rB"}], (* Plot[rCritFunc[m,mya,myb],
  {m,mc1,mCrit},PlotRange→{{0,0.08},{0,1}},PlotStyle→None,Filling→{1→Axis}],*)
 Graphics[{Gray, Dotted, Line[{{mc1, 0}, {mc1, .6}}]}],
 Graphics[Text["m' = mB", {.75 * mc1, 0.8 * .5}]],
 (* Graphics[{Gray,Dotted,Line[{{mCrit,0},{mCrit,.6}}]}],
 Graphics[Text[ "mB",{mCrit+.25*mc1,0.8*.5}]],*)
 Graphics[{Gray, Dashed, Line[{{0, .5}, {1, .5}}]}],
 Graphics[Text["rmax", {.07, 1.1 * .5}]]] (* This uses exact critical values *)
```



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

In the following, we add for comparison Haldande's (1927) approximation $\bar{\pi}_H \approx 2\,a$. This should approximate our $\bar{\pi}$ for $m_1 \to 0$.

```
plot8 = Show[Plot[{probEstablAMApproxFunc[myr,
      m, mya, myb, myγ11temp, myγ12temp, myγ21temp, myγ22temp][[4]]},
   {m, 0, 1}, PlotRange → {{0, mCrit}, {0, .05}}, PlotStyle → {Black, Thick},
   Frame → True, FrameStyle → {{Black, Opacity[0]}, {Black, Opacity[0]}},
   FrameLabel → {"Migration rate m", "Mean invasion probability π̄"},
   LabelStyle → {Directive[FontSize → 14], FontFamily → "Helvetica"}],
  Graphics[Text[Style["r = " <> ToString[myr] <> "; a = " <> ToString[mya] <>
      "; b = " <> ToString[myb], FontFamily → "Helvetica"], {0.005, 0.005}]],
  Graphics[{Gray, Dashed, Line[{{.0, 2 * mya}, {1., 2 * mya}}]}],
  Graphics[{Gray, Text[Style["π̄H ≈ 2a (Haldane 1927)",
      FontFamily → "Helvetica"], {0.01, 2 * mya + 0.0025}]}]]
```



- Strong evoutionary forces; migration rate $m = 0.22$

```
mym = 0.22;
mya = 0.2;
myb = 0.4;
myγ11temp = 0.;
myγ12temp = 0.;
myγ21temp = 0.;
myγ22temp = 0.;
```

```
wCompact[1] /. assumeAdditiveMultiplicEpistaticApproxFitness[1] /. ruleFitness //
 MatrixForm
```

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

```
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! *)
```

```
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. *)
```

```
0.5
```

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}
```

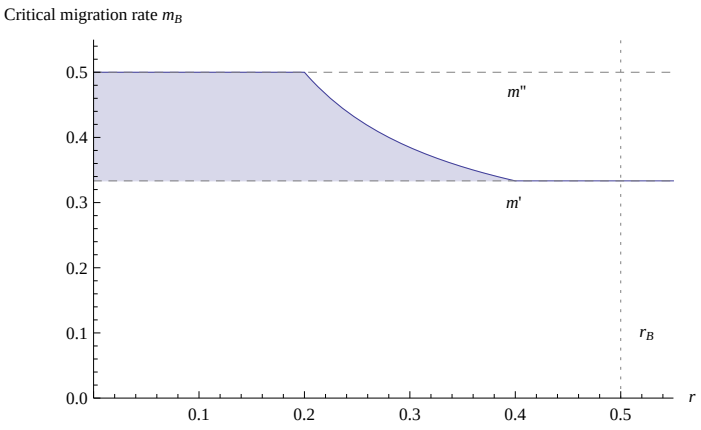
```
0.333333
```

```
0.5
```

```
0.2
```

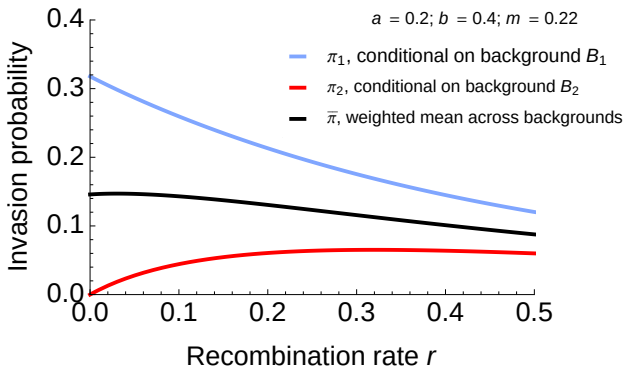
Critical value for the migration rate, $m_{B,1}$, as a function of r for the current parameter values.

```
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_B"}], 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[{{rCrit, 0}, {rCrit, mc2 + 0.1 + mc2}}]}],
 Graphics[Text[ "r_B", {.025 + rCrit, 0.2 * mc2}]],
 Graphics[{Gray, Dashed, Line[{{.0, mc1}, {1.1 * rCrit, mc1}}]}],
 Graphics[Text[ "m'", {0.4, 0.9 * mc1}]],
 Graphics[{Gray, Dashed, Line[{{.0, mc2}, {1.1 * rCrit, mc2}}]}],
 Graphics[Text["m''" , {0.4, mc2 - 0.1 * mc1}]]]
 (* This uses exact critical values *)
```

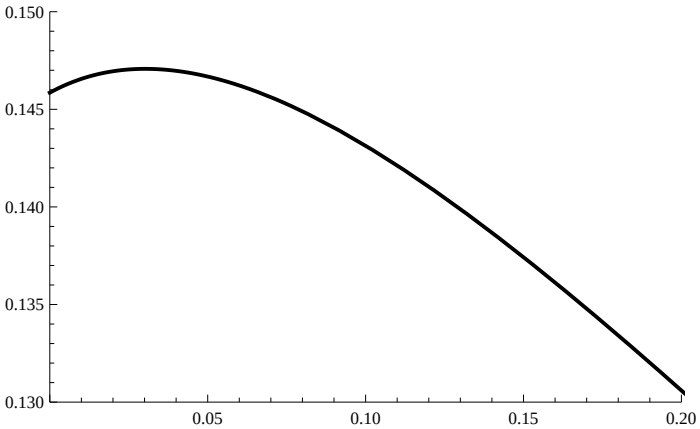


Recall: $m' = m_{\text{crit},1} = \frac{1-a}{b}$, $m'' = m_{\text{crit},2} = \frac{1-b}{a}$, and $m_B = m_{\text{crit},5} = \frac{a(b-a+r)}{(a-b)(a-r)+r(1-a)}$.

```
plot9 =
 Show[Plot[{probEstablAMApproxFunc[r, mym, mya, myb, myγ11temp, myγ12temp, myγ21temp,
       myγ22temp][[2]], probEstablAMApproxFunc[r, mym, mya, myb, myγ11temp,
       myγ12temp, myγ21temp, myγ22temp][[3]], probEstablAMApproxFunc[r,
       mym, mya, myb, myγ11temp, myγ12temp, myγ21temp, myγ22temp][[4]]},
   {r, 0, 0.5}, 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["π1, conditional on background B1", FontFamily → "Helvetica", 10],
     Style["π2, conditional on background B2", FontFamily → "Helvetica"],
     Style["π̄, 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"]]
 ]
```




```
Plot[probEstablAMApproxFunc[r, mym, mya, myb,
    myγ11temp, myγ12temp, myγ21temp, myγ22temp][[4]], {r, 0, 1 / 2},
 PlotRange → {{0, 0.2}, {0.13, 0.15}}, PlotStyle → {Black, Thick}]
```



- Strong evoutionary forces; migration rate $m = 0.3$

```
mym = 0.3;
mya = 0.2;
myb = 0.4;
myγ11temp = 0.;
myγ12temp = 0.;
myγ21temp = 0.;
myγ22temp = 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! *)
```

```
0.4
```

```
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. *)
```

```
0.5
```

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}
```

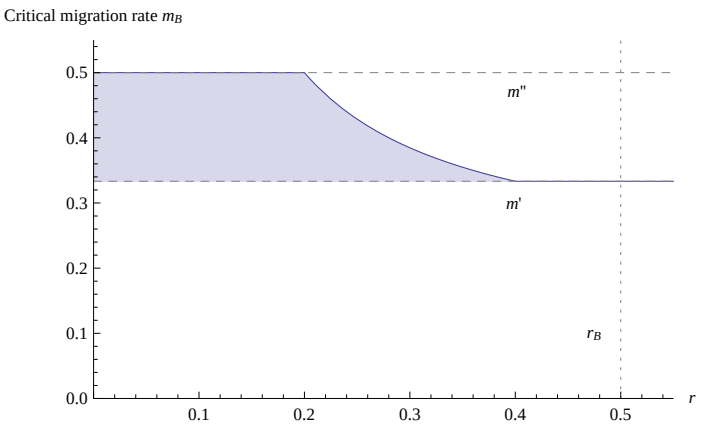
```
0.333333
```

```
0.5
```

```
0.2
```

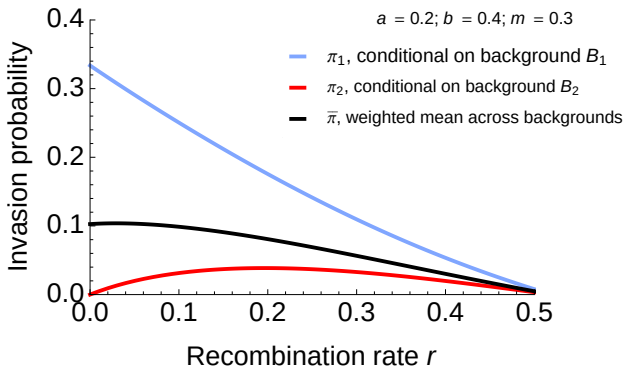
Critical value for the migration rate, $m_{B,1}$, as a function of r for the current parameter values.

```
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 mB"}], 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[{{rCrit, 0}, {rCrit, mc2 + 0.1 + mc2}}]}],
 Graphics[Text[ "rB", {rCrit - 0.025, 0.2 * mc2}]],
 Graphics[{Gray, Dashed, Line[{{.0, mc1}, {1.1 * rCrit, mc1}}]}],
 Graphics[Text[ "m'", {0.4, 0.9 * mc1}]],
 Graphics[{Gray, Dashed, Line[{{.0, mc2}, {1.1 * rCrit, mc2}}]}],
 Graphics[Text["m''" , {0.4, mc2 - 0.1 * mc1}]]]
 (* 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 $m_B = m_{\text{crit},5} = \frac{a(b-a+r)}{(a-b)(a-r)+r(1-a)}$.

```
plot10 =
 Show[Plot[{probEstablAMApproxFunc[r, mym, mya, myb, myγ11temp, myγ12temp, myγ21temp,
      myγ22temp][[2]], probEstablAMApproxFunc[r, mym, mya, myb, myγ11temp,
      myγ12temp, myγ21temp, myγ22temp][[3]], probEstablAMApproxFunc[r,
      mym, mya, myb, myγ11temp, myγ12temp, myγ21temp, myγ22temp][[4]]},
   {r, 0, 0.5}, 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["π1, conditional on background B1", FontFamily → "Helvetica", 10],
     Style["π2, conditional on background B2", FontFamily → "Helvetica"],
     Style["π̄, 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 evoutionary forces; migration rate $m = 0.38$

```
mym = 0.38;
mya = 0.2;
myb = 0.4;
myγ11temp = 0.;
myγ12temp = 0.;
myγ21temp = 0.;
myγ22temp = 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}
```

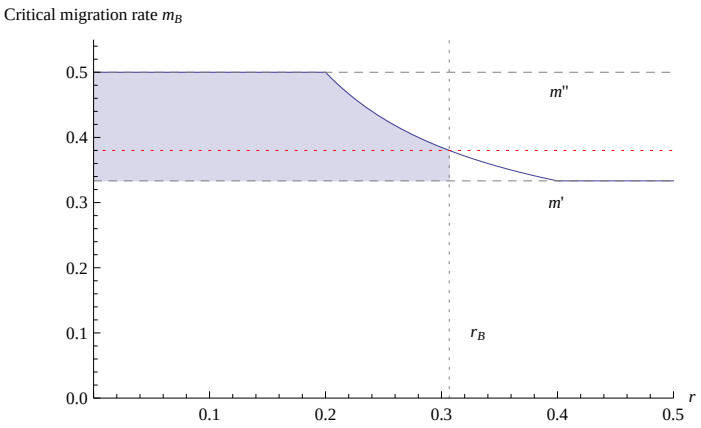
```
0.333333
```

```
0.5
```

```
0.423077
```

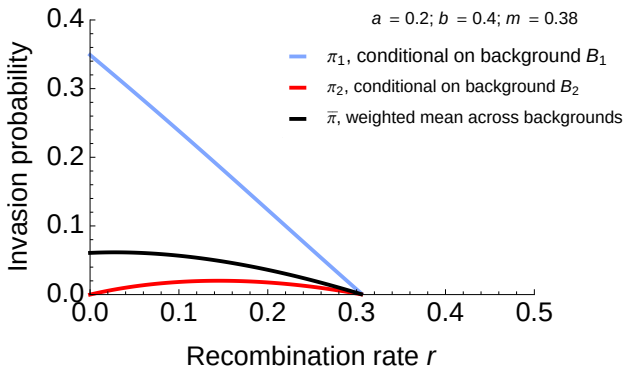
Critical value for the migration rate, $m_{B,1}$, as a function of r for the current parameter values.

```
Show[Plot[mCritFunc[r, mya, myb], {r, 0, 0.5}, PlotRange → {{0, 0.5}, {0, mc2 + 0.1 * mc2}},
  AxesLabel → {r, "Critical migration rate mB"}],
 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[ "rB", {.025 + rCrit, 0.2 * mc2}]],
 Graphics[{Gray, Dashed, Line[{{.0, mc1}, {.5, mc1}}]}],
 Graphics[Text[ "m'", {0.4, 0.9 * mc1}]],
 Graphics[{Gray, Dashed, Line[{{.0, mc2}, {.5, mc2}}]}],
 Graphics[Text["m''" , {0.4, mc2 - 0.1 * mc1}]],
 Graphics[{Red, Dotted, Line[{{0, mym}, {0.5, mym}}]}]]
 (* 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 $m_B = m_{\text{crit},5} = \frac{a(b-a+r)}{(a-b)(a-r)+r(1-a)}$.

```
plot11 =
 Show[Plot[{probEstablAMApproxFunc[r, mym, mya, myb, myγ11temp, myγ12temp, myγ21temp,
      myγ22temp][[2]], probEstablAMApproxFunc[r, mym, mya, myb, myγ11temp,
      myγ12temp, myγ21temp, myγ22temp][[3]], probEstablAMApproxFunc[r,
      mym, mya, myb, myγ11temp, myγ12temp, myγ21temp, myγ22temp][[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["π1, conditional on background B1", FontFamily → "Helvetica", 10],
     Style["π2, conditional on background B2", FontFamily → "Helvetica"],
     Style["π̄, 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, recombination rate $r = 0.01$

```
myr = 0.01;
mya = 0.2;
myb = 0.4;
myγ11temp = 0.;
myγ12temp = 0.;
myγ21temp = 0.;
myγ22temp = 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.

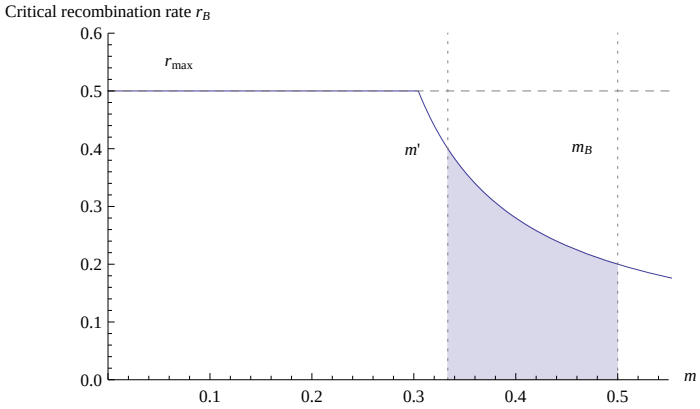
```
mc1 = mCrit1 /. {a → mya, b → myb}
mc2 = mCrit2 /. {a → mya, b → myb}
mc3 = mCrit3 /. {a → mya, b → myb, r → rCrit}
```

```
0.333333
```

```
0.5
```

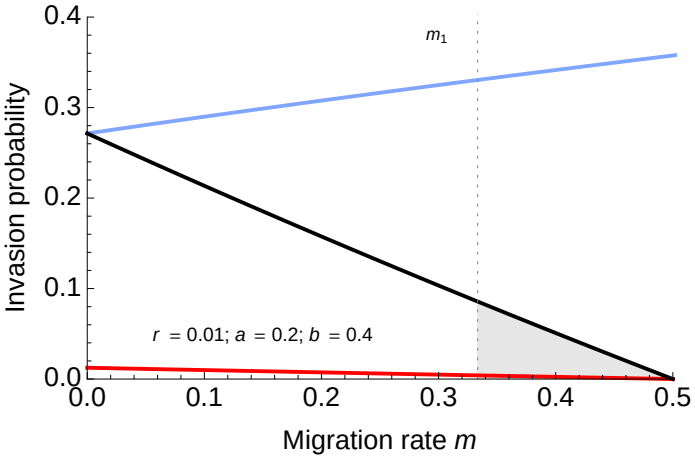
$$\frac{0.6 - \text{rCrit}}{1 - \text{rCrit}}$$

```
Show[Plot[rCritFunc[m, mya, myb], {m, 0, 1}, PlotRange → {{0, 1.1 * mCrit}, {0, .6}},
  AxesLabel → {m, "Critical recombination rate r_B"}],
 Plot[rCritFunc[m, mya, myb], {m, mc1, mCrit}, PlotRange → {{0, 1.1 * mCrit}, {0, .6}},
  PlotStyle → None, Filling → {1 → Axis}],
 Graphics[{Gray, Dotted, Line[{{mc1, 0}, {mc1, .6}}]}],
 Graphics[Text["m'", {.9 * mc1, 0.8 * .5}]],
 Graphics[{Gray, Dotted, Line[{{mCrit, 0}, {mCrit, .6}}]}],
 Graphics[Text["m_B", {mCrit - .1 * 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 *)
```



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

```
plot12 =
 Show[Plot[probEstablAMApproxFunc[myr, m, mya, myb, myγ11temp, myγ12temp, myγ21temp,
     myγ22temp][[4]], {m, mc1, 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, myγ11temp, myγ12temp,
     myγ21temp, myγ22temp][[2]], probEstablAMApproxFunc[myr, m,
     mya, myb, myγ11temp, myγ12temp, myγ21temp, myγ22temp][[3]],
   probEstablAMApproxFunc[myr, m, mya, myb, myγ11temp, myγ12temp, myγ21temp,
     myγ22temp][[4]]}, {m, 0, 1}, PlotRange → {{0, mCrit}, {0, 2 * mya}},
  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], {0.15, 0.05}]],
  Graphics[{Gray, Dotted, Line[{{mc1, .0}, {mc1, 1.}}]}],
  Graphics[Text[Style["m1", 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 $r = 0.07$

```
myr = 0.07;
mya = 0.2;
myb = 0.4;
myγ11temp = 0.;
myγ12temp = 0.;
myγ21temp = 0.;
myγ22temp = 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.

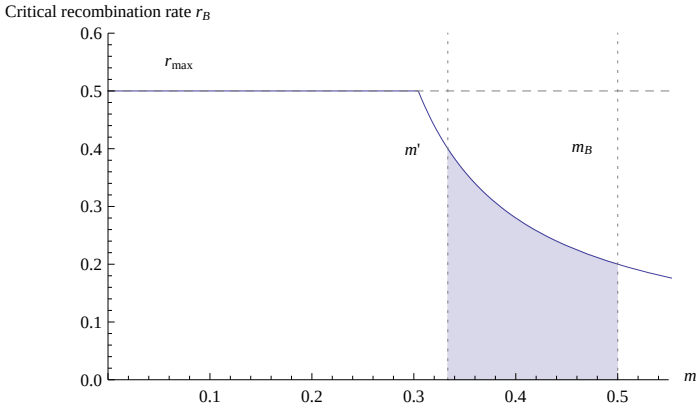
```
mc1 = mCrit1 /. {a → mya, b → myb}
mc2 = mCrit2 /. {a → mya, b → myb}
mc3 = mCrit3 /. {a → mya, b → myb, r → rCrit}
```

```
0.333333
```

```
0.5
```

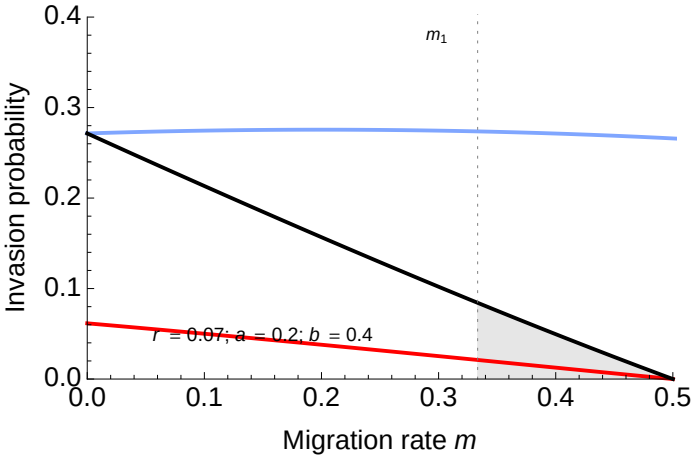
$$\frac{0.6 - \text{rCrit}}{1 - \text{rCrit}}$$

```
Show[Plot[rCritFunc[m, mya, myb], {m, 0, 1}, PlotRange → {{0, 1.1 * mCrit}, {0, .6}},
  AxesLabel → {m, "Critical recombination rate r_B"}],
 Plot[rCritFunc[m, mya, myb], {m, mc1, mCrit}, PlotRange → {{0, 1.1 * mCrit}, {0, .6}},
  PlotStyle → None, Filling → {1 → Axis}],
 Graphics[{Gray, Dotted, Line[{{mc1, 0}, {mc1, .6}}]}],
 Graphics[Text["m'", {.9 * mc1, 0.8 * .5}]],
 Graphics[{Gray, Dotted, Line[{{mCrit, 0}, {mCrit, .6}}]}],
 Graphics[Text["m_B", {mCrit - .1 * 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 *)
```



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

```
plot12 =
 Show[Plot[probEstablAMApproxFunc[myr, m, mya, myb, myγ11temp, myγ12temp, myγ21temp,
     myγ22temp][[4]], {m, mc1, 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, myγ11temp, myγ12temp,
     myγ21temp, myγ22temp][[2]], probEstablAMApproxFunc[myr, m,
     mya, myb, myγ11temp, myγ12temp, myγ21temp, myγ22temp][[3]],
   probEstablAMApproxFunc[myr, m, mya, myb, myγ11temp, myγ12temp, myγ21temp,
     myγ22temp][[4]]}, {m, 0, 1}, PlotRange → {{0, mCrit}, {0, 2 * mya}},
  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], {0.15, 0.05}]],
  Graphics[{Gray, Dotted, Line[{{mc1, .0}, {mc1, 1.}}]}],
  Graphics[Text[Style["m1", 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 $r = 0.1$

```
myr = 0.1;
mya = 0.2;
myb = 0.4;
myγ11temp = 0.;
myγ12temp = 0.;
myγ21temp = 0.;
myγ22temp = 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.

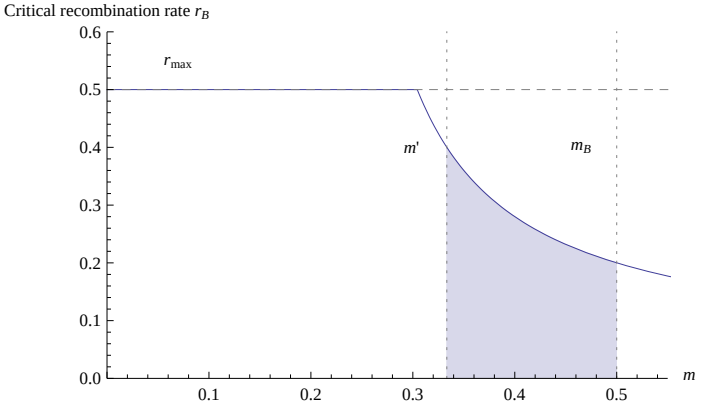
```
mc1 = mCrit1 /. {a → mya, b → myb}
mc2 = mCrit2 /. {a → mya, b → myb}
mc3 = mCrit3 /. {a → mya, b → myb, r → myr}
```

```
0.333333
```

```
0.5
```

```
0.555556
```

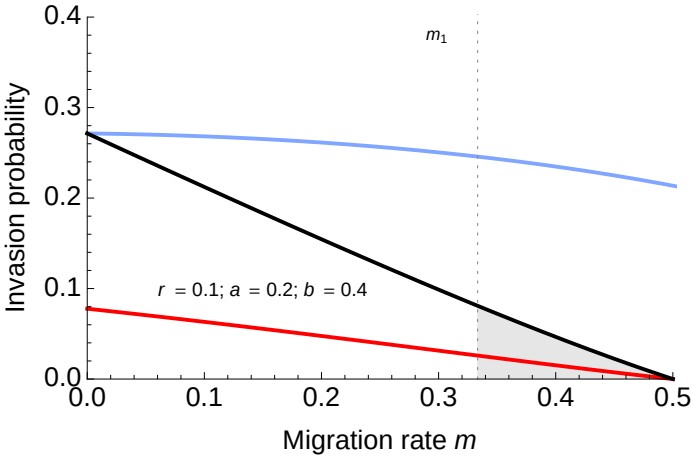
```
Show[Plot[rCritFunc[m, mya, myb], {m, 0, 1}, PlotRange → {{0, 1.1 * mCrit}, {0, .6}},
  AxesLabel → {m, "Critical recombination rate r_B"}],
 Plot[rCritFunc[m, mya, myb], {m, mc1, mCrit}, PlotRange → {{0, 1.1 * mCrit}, {0, .6}},
  PlotStyle → None, Filling → {1 → Axis}],
 Graphics[{Gray, Dotted, Line[{{mc1, 0}, {mc1, .6}}]}],
 Graphics[Text["m'", {.9 * mc1, 0.8 * .5}]],
 Graphics[{Gray, Dotted, Line[{{mCrit, 0}, {mCrit, .6}}]}],
 Graphics[Text["m_B", {mCrit - .1 * 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 *)
```



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

Read simulated values.

```
plot13 =
 Show[Plot[probEstablAMApproxFunc[myr, m, mya, myb, myγ11temp, myγ12temp, myγ21temp,
     myγ22temp][[4]], {m, mc1, 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, myγ11temp, myγ12temp,
     myγ21temp, myγ22temp][[2]], probEstablAMApproxFunc[myr, m,
     mya, myb, myγ11temp, myγ12temp, myγ21temp, myγ22temp][[3]],
   probEstablAMApproxFunc[myr, m, mya, myb, myγ11temp, myγ12temp, myγ21temp,
     myγ22temp][[4]]}, {m, 0, 1}, PlotRange → {{0, mCrit}, {0, 2 * mya}},
  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], {0.15, 0.1}]],
  Graphics[{Gray, Dotted, Line[{{mc1, .0}, {mc1, 1.}}]}],
  Graphics[Text[Style["m1", 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;
myγ11temp = 0.;
myγ12temp = 0.;
myγ21temp = 0.;
myγ22temp = 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.

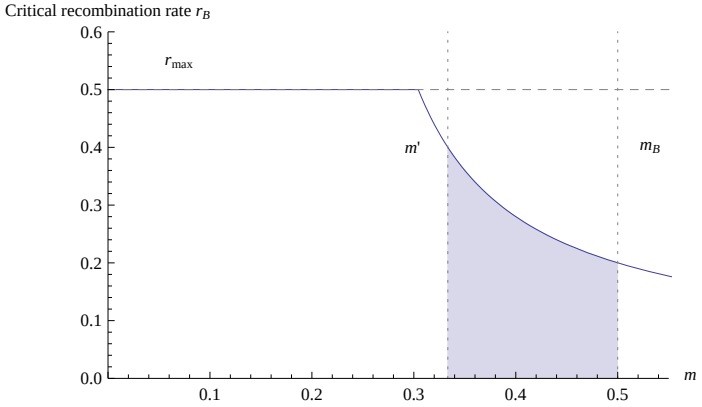
```
mc1 = mCrit1 /. {a → mya, b → myb}
mc2 = mCrit2 /. {a → mya, b → myb}
mc3 = mCrit3 /. {a → mya, b → myb, r → myr}
```

```
0.333333
```

```
0.5
```

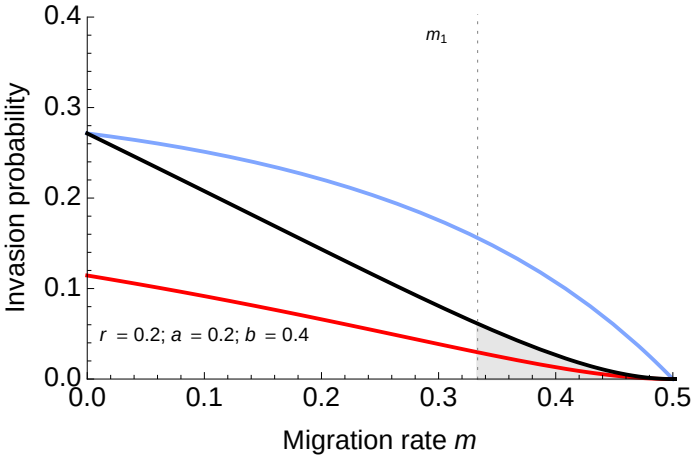
```
0.5
```

```
Show[Plot[rCritFunc[m, mya, myb], {m, 0, 1}, PlotRange → {{0, 1.1 * mCrit}, {0, .6}},
  AxesLabel → {m, "Critical recombination rate r_B"}],
 Plot[rCritFunc[m, mya, myb], {m, mc1, mCrit}, PlotRange → {{0, 1.1 * mCrit}, {0, 1}},
  PlotStyle → None, Filling → {1 → Axis}],
 Graphics[{Gray, Dotted, Line[{{mc1, 0}, {mc1, .6}}]}],
 Graphics[Text["m'", {.9 * mc1, 0.8 * .5}]],
 Graphics[{Gray, Dotted, Line[{{mCrit, 0}, {mCrit, .6}}]}],
 Graphics[Text["m_B", {mCrit + .1 * 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 *)
```



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

```
plot13 =
 Show[Plot[probEstablAMApproxFunc[myr, m, mya, myb, myγ11temp, myγ12temp, myγ21temp,
     myγ22temp][[4]], {m, mc1, 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, myγ11temp, myγ12temp,
     myγ21temp, myγ22temp][[2]], probEstablAMApproxFunc[myr, m,
     mya, myb, myγ11temp, myγ12temp, myγ21temp, myγ22temp][[3]],
   probEstablAMApproxFunc[myr, m, mya, myb, myγ11temp, myγ12temp, myγ21temp,
     myγ22temp][[4]]}, {m, 0, 1}, PlotRange → {{0, mCrit}, {0, 2 * mya}},
  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], {0.1, 0.05}]],
  Graphics[{Gray, Dotted, Line[{{mc1, .0}, {mc1, 1.}}]}],
  Graphics[Text[Style["m1", 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 $r = 0.5$

```
myr = 0.5;
mya = 0.2;
myb = 0.4;
myγ11temp = 0.;
myγ12temp = 0.;
myγ21temp = 0.;
myγ22temp = 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! *)
```

```
0.28
```

```
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.

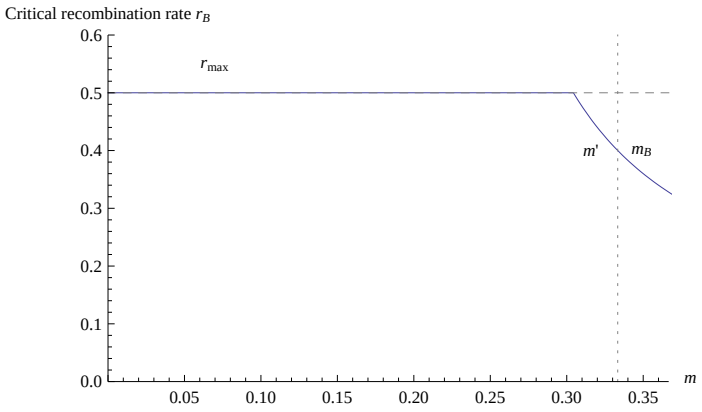
```
mc1 = mCrit1 /. {a → mya, b → myb}
mc2 = mCrit2 /. {a → mya, b → myb}
mc3 = mCrit3 /. {a → mya, b → myb, r → myr}
```

```
0.333333
```

```
0.5
```

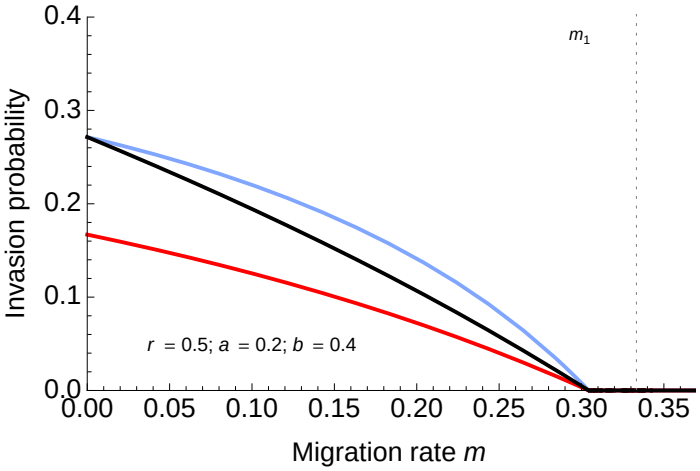
```
0.2
```

```
Show[Plot[rCritFunc[m, mya, myb], {m, 0, 1}, PlotRange → {{0, 1.1 * mCrit}, {0, .6}},
  AxesLabel → {m, "Critical recombination rate r_B"}], (* 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[Text["m'", {.95 * mc1, 0.8 * .5}]],
 Graphics[{Gray, Dotted, Line[{{mCrit, 0}, {mCrit, .6}}]}],
 Graphics[Text["m_B", {mCrit + .05 * 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 *)
```



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

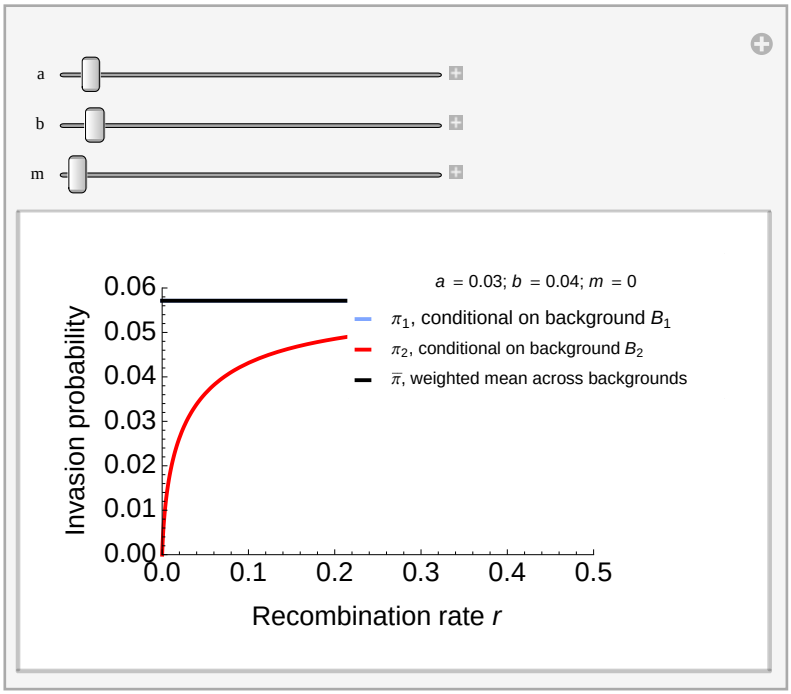
```
plot14 = Show[Plot[
    probEstablAMApproxFunc[myr, m, mya, myb, myγ11temp, myγ12temp, myγ21temp, myγ22temp][[
     4]], {m, mc1, 1}, PlotRange → {{0, 1.1 * mCrit}, {0, 2 * mya}}, PlotStyle → None,
    Filling → {1 → Axis}, FillingStyle → RGBColor[0.9, 0.9, 0.9, 1](*, Epilog→
     Inset[inset4,{0.0375,0.045},{0.04,0.0383} ,{0.021,0.021},Background→White] *)],
   Plot[{probEstablAMApproxFunc[myr, m, mya, myb, myγ11temp, myγ12temp,
       myγ21temp, myγ22temp][[2]], probEstablAMApproxFunc[myr, m,
       mya, myb, myγ11temp, myγ12temp, myγ21temp, myγ22temp][[3]],
     probEstablAMApproxFunc[myr, m, mya, myb, myγ11temp, myγ12temp, myγ21temp,
       myγ22temp][[4]]}, {m, 0, 1}, PlotRange → {{0, mCrit}, {0, 2 * mya}},
    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], {0.1, 0.05}]],
   Graphics[{Gray, Dotted, Line[{{mc1, .0}, {mc1, 1.}}]}],
   Graphics[Text[Style["m1", 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"}]
```



■ Plots for arbitrary parameter combinations

■ Invasion probability as a function of recombination rate

```
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 * rCritFunc[m, a, b]}, PlotRange → {{0, rCritFunc[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["π1, conditional on background B1", FontFamily → "Helvetica", 10],
     Style["π2, conditional on background B2", FontFamily → "Helvetica"],
     Style["π̄, weighted mean across backgrounds", FontFamily → "Helvetica"] },
   LegendPosition → {0, 0.19}, LegendSize → {1.3, 0.5}, LegendShadow → None,
   LegendTextSpace → 10, LegendBorderSpace → 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}]
```

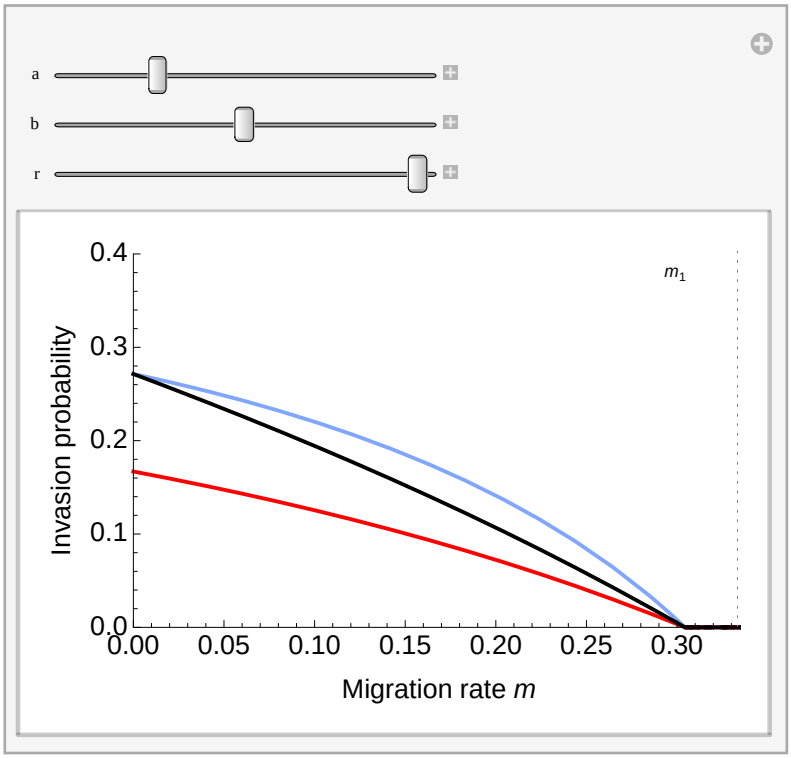


■ Invasion probability as a function of migration rate

```
mCrit1
```

$$\frac{a}{1-b}$$

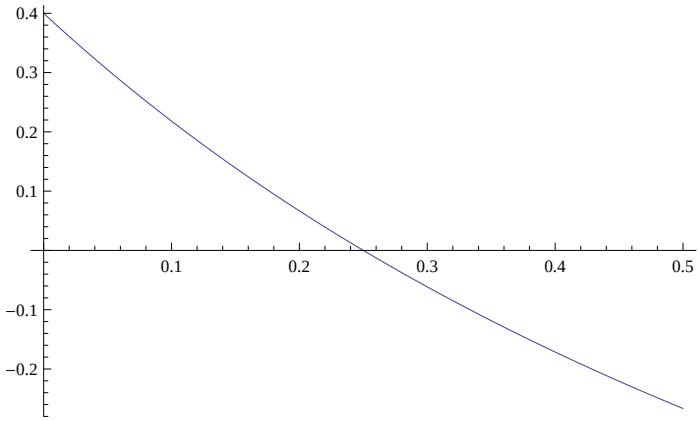
```
Manipulate[Show[Plot[probEstablAMApproxFunc[r, m, a, b, 0, 0, 0, 0][[4]],
    {m, a/(1 - b), 1}, PlotRange → {{0, mCritFunc[r, a, b]}, {0, 2 * a}}, PlotStyle → None,
    Filling → {1 → Axis}, FillingStyle → RGBColor[0.9, 0.9, 0.9, 1](*, Epilog→
     Inset[inset4,{0.0375,0.045},{0.04,0.0383} ,{0.021,0.021},Background→White] *)],
  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/(1 - b), .0}, {a/(1 - b), 1.}}]}],
  Graphics[Text[Style["m1", FontFamily → "Helvetica"], {0.9 * a/(1 - b), 0.95 * 2 * a}]],
  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, 0.8}, {{b, 0.4}, 0, 0.8}, {{r, 0.1}, 0, 0.5}]
```




```
b - m (1 - a) / (b (1 + m)) /. {a → 0.2, b → 0.4, r → 0.01, m → 0.}
```

```
0.4
```

```
Plot[b - m (1 - a) / (b (1 + m)) /. {a → 0.2, b → 0.4}, {m, 0, 0.5}]
```



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

In[82]:=
```
assumeNeutrality[n_]:={w33[n]→1, w34[n]→1,w44[n]→1}
```

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

```
recB[3, 1]
```

$$\frac{(1 - m[1])\, x[3, 1]\, (w33[1]\, x[3, 1] + w34[1]\, x[4, 1])}{w33[1]\, x[3, 1]^2 + 2\, w34[1]\, x[3, 1]\, x[4, 1] + w44[1]\, x[4, 1]^2} + \frac{m[1]\, x[3, 2]\, (w33[2]\, x[3, 2] + w34[2]\, x[4, 2])}{w33[2]\, x[3, 2]^2 + 2\, w34[2]\, x[3, 2]\, x[4, 2] + w44[2]\, x[4, 2]^2}$$

```
assumeCI
```

```
{x[1, 2] → 0, x[2, 2] → 0, x[3, 2] → qC,
 x[4, 2] → 1 - qC, m[2] → 0, p[2] → 0, q[2] → qC, LD[2] → 0}
```

```
recB[3, 1] /. assumeCI // FullSimplify
```

$$\frac{qC\, m[1]\, (qC\, (w33[2] - w34[2]) + w34[2])}{qC\, (qC\, w33[2] - 2\, (-1 + qC)\, w34[2]) + (-1 + qC)^2\, w44[2]} - \frac{(-1 + m[1])\, x[3, 1]\, (w33[1]\, x[3, 1] + w34[1]\, x[4, 1])}{w33[1]\, x[3, 1]^2 + x[4, 1]\, (2\, w34[1]\, x[3, 1] + w44[1]\, x[4, 1])}$$

```
assumeA1Rare[1]
```

```
{x[3, 1] → q[1], x[4, 1] → 1 - q[1]}
```

```
recB[3, 1] /. assumeCI /. assumeA1Rare[1] // FullSimplify
```

$$-\frac{((-1+m[1])\,q[1]\,(q[1]\,(w33[1]-w34[1])+w34[1]))\,/\,\left(2\,q[1]\,(w34[1]-w44[1])+w44[1]+q[1]^2\,(w33[1]-2\,w34[1]+w44[1])\right)+qC\,m[1]\,(qC\,(w33[2]-w34[2])+w34[2])}{qC\,(qC\,w33[2]-2\,(-1+qC)\,w34[2])+(-1+qC)^2\,w44[2]}$$

```
assumeNeutrality[2]
```

$$\{w33[2]\to 1,\ w34[2]\to 1,\ w44[2]\to 1\}$$

```
recB[3, 1] /. assumeCI /. assumeA1Rare[1] /. assumeNeutrality[2] // FullSimplify
```

$$qC\,m[1]-((-1+m[1])\,q[1]\,(q[1]\,(w33[1]-w34[1])+w34[1]))\,/\,\left(2\,q[1]\,(w34[1]-w44[1])+w44[1]+q[1]^2\,(w33[1]-2\,w34[1]+w44[1])\right)$$

Generic relative fitnesses:

```
qEquil1BGenericPolymCont =
 Solve[(recB[3, 1] /. assumeCI /. assumeA1Rare[1] /. assumeNeutrality[2] //
      FullSimplify) == q[1], q[1]] // Simplify
```

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

$$\Big\{\Big\{q[1]\to -\frac{1}{6\,(w33[1]-2\,w34[1]+w44[1])}\Big(-2\,((1+(-1+qC)\,m[1])\,w33[1]+(-3+m[1]-2\,qC\,m[1])\,w34[1]+(2+qC\,m[1])\,w44[1])+\frac{2\times 2^{1\,\ll 1\gg\,\ll 1\gg}\,(\ll 1\gg)}{(\ll 1\gg)^{1/3}}+2^{2/3}\left(-2\,w33[1]^3+\ll 114\gg+\sqrt{-4\,\ll 1\gg^3+\ll 1\gg^2}\right)^{1/3}\Big)\Big\},\ \Big\{q[1]\to -\frac{-4\,(\ll 1\gg)-\ll 1\gg+\ll 1\gg}{12\,(\ll 1\gg)}\Big\},\ \{q[1]\to -(-4\,((1+(-1+qC)\,m[1])\,w33[1]+(-3+m[1]-\ll 1\gg)\,\ll 1\gg+(2+qC\,m[1])\,w44[1])+\ll 1\gg\,\ll 1\gg\,\ll 1\gg)\,/\,(12\,(w33[1]-2\,w34[1]+w44[1])))\}\Big\}$$

Show Less | Show More | Show Full Output | Set Size Limit...

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]
```

$$\{w33[1]\to 2\,v3[1],\ w34[1]\to v3[1]+v4[1],\ w44[1]\to 2\,v4[1]\}$$

```
qEquil1BGenericAdditivePolymCont =
 Solve[(recB[3, 1] /. assumeCI /. assumeA1Rare[1] /. assumeNeutrality[2] /.
       assumeGenericAdditiveFitnessB[1] // FullSimplify) == q[1], q[1]] // FullSimplify
```

$$\Big\{\Big\{q[1]\to \Big((1+(-1+2\,qC)\,m[1])\,v3[1]-(1+m[1]+2\,qC\,m[1])\,v4[1]+\sqrt{\left(8\,qC\,m[1]\,(1+m[1])\,(v3[1]-v4[1])\,v4[1]+((1+(-1+2\,qC)\,m[1])\,v3[1]-(1+m[1]+2\,qC\,m[1])\,v4[1])^2\right)}\Big)\,/\,(2\,(1+m[1])\,(v3[1]-v4[1]))\Big\},\ \Big\{q[1]\to -\Big((-1+m[1]-2\,qC\,m[1])\,v3[1]+(1+m[1]+2\,qC\,m[1])\,v4[1]+\sqrt{\left(8\,qC\,m[1]\,(1+m[1])\,(v3[1]-v4[1])\,v4[1]+((1+(-1+2\,qC)\,m[1])\,v3[1]-(1+m[1]+2\,qC\,m[1])\,v4[1])^2\right)}\Big)\,/\,(2\,(1+m[1])\,(v3[1]-v4[1]))\Big\}\Big\}$$

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 :

```
FullSimplify[Reduce[{0 < (q[1] /. qEquil1BGenericAdditivePolymCont⟦1⟧) &&
     (q[1] /. qEquil1BGenericAdditivePolymCont⟦1⟧) < 1}, m[1]],
 Assumptions → {0 < m[1] < 1 && v3[1] ≥ 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 :

```
FullSimplify[Reduce[{0 < (q[1] /. qEquil1BGenericAdditivePolymCont⟦2⟧) &&
     (q[1] /. qEquil1BGenericAdditivePolymCont⟦2⟧) < 1}, m[1]],
 Assumptions → {0 < m[1] < 1 && v3[1] ≥ v4[1] > 0, 0 < qC < 1}]
```

```
False
```

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

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

```
qEquil1BGenericAdditivePolymCont⟦1⟧ /. ruleSimplifyNotationCI /. {x_[1] → x} //
 FullSimplify
```

$$\left\{q \to \frac{1}{2\,(1+m)\,(v3-v4)}\left((1+m\,(-1+2\,qC))\,v3-(1+m+2\,m\,qC)\,v4+\sqrt{8\,m\,(1+m)\,qC\,(v3-v4)\,v4+((-1+m-2\,m\,qC)\,v3+(1+m+2\,m\,qC)\,v4)^2}\right)\right\}$$

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

$v_3 > v_4$. (1)

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

```
qEquil1BGenericMultiplicPolymCont =
 Solve[(recB[3, 1] /. assumeCI /. assumeA1Rare[1] /. assumeNeutrality[2] /.
       assumeGenericMultiplicFitnessB[1] // FullSimplify) == q[1], q[1]] // FullSimplify
```

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

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 :

```
FullSimplify[Reduce[{0 < (q[1] /. qEquil1BGenericMultiplicPolymCont⟦1⟧) &&
     (q[1] /. qEquil1BGenericMultiplicPolymCont⟦1⟧) < 1}, m[1]],
 Assumptions → {0 < m[1] < 1 && v3[1] ≥ 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 :

```
FullSimplify[Reduce[{0 < (q[1] /. qEquil1BGenericMultiplicPolymCont⟦2⟧) &&
     (q[1] /. qEquil1BGenericMultiplicPolymCont⟦2⟧) < 1}, m[1]],
 Assumptions → {0 < m[1] < 1 && v3[1] ≥ v4[1] > 0, 0 < qC < 1}]
```

```
False
```

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

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

```
qEquil1BGenericMultiplicPolymCont[[1]] /. ruleSimplifyNotationCI /. {x_[1] → x} //
 FullSimplify
```

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

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

$v_3 > v_4$. (2)

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

```
qEquil1BAdditiveMultiplicPolymCont =
 Solve[(recB[3, 1] /. assumeCI /. assumeA1Rare[1] /. assumeNeutrality[2] /.
      assumeAdditiveMultiplicFitnessB[1] // FullSimplify) == q[1], q[1]]
```

$$\left\{\left\{q[1] \to \left(b[1]-m[1]+2\,qC\,b[1]\,m[1]-\sqrt{b[1]^2-2\,b[1]\,m[1]+4\,qC\,b[1]\,m[1]+m[1]^2-4\,qC\,b[1]^2\,m[1]^2+4\,qC^2\,b[1]^2\,m[1]^2}\right)\Big/(2\,(b[1]+b[1]\,m[1]))\right\},\left\{q[1] \to \left(b[1]-m[1]+2\,qC\,b[1]\,m[1]+\sqrt{b[1]^2-2\,b[1]\,m[1]+4\,qC\,b[1]\,m[1]+m[1]^2-4\,qC\,b[1]^2\,m[1]^2+4\,qC^2\,b[1]^2\,m[1]^2}\right)\Big/(2\,(b[1]+b[1]\,m[1]))\right\}\right\}$$

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 :

```
FullSimplify[Reduce[{0 < (q[1] /. qEquil1BAdditiveMultiplicPolymCont[[1]]) &&
    (q[1] /. qEquil1BAdditiveMultiplicPolymCont[[1]]) < 1}, m[1]],
 Assumptions → {0 < m[1] < 1 && 0 < b[1] < 1, 0 < qC < 1}]
```

```
False
```

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

Conditions for admissibility of the second equilibrium :

```
FullSimplify[Reduce[{0 < (q[1] /. qEquil1BAdditiveMultiplicPolymCont[[2]]) &&
    (q[1] /. qEquil1BAdditiveMultiplicPolymCont[[2]]) < 1}, m[1]],
 Assumptions → {0 < m[1] < 1 && 0 < b[1] < 1, 0 < qC < 1}]
```

```
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, for given, but variable parameter b.

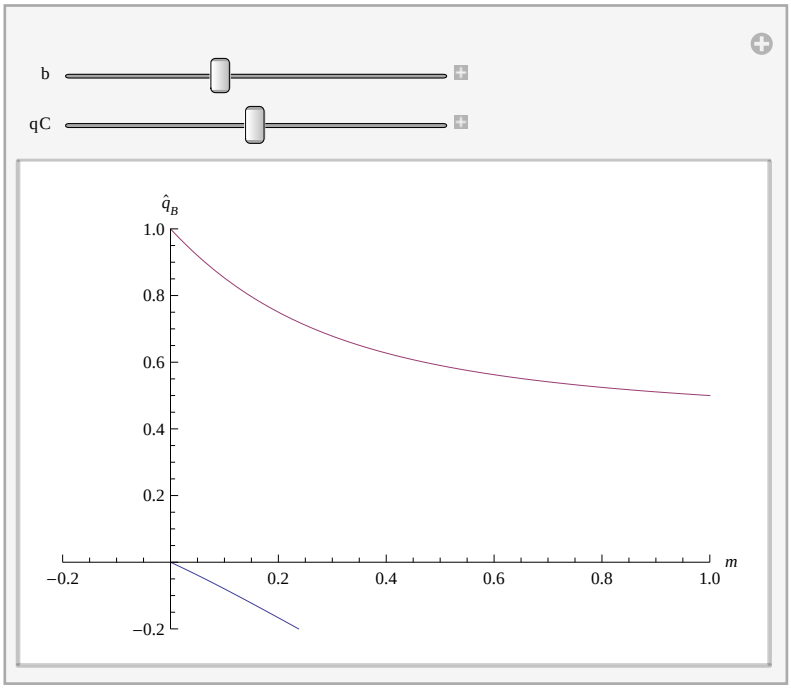
```
qEquil1BAdditiveMultiplicPolymCont /. ruleSimplifyNotationCI /. {x_[1] → x} //
 FullSimplify
```

$$\left\{\left\{q \to -\frac{1}{2\,b\,(1+m)}\left(m-b\,(1+2\,m\,qC)+\sqrt{m^2+2\,b\,m\,(-1+2\,qC)+b^2\left(1+4\,m^2\,(-1+qC)\,qC\right)}\right)\right\},\left\{q \to \frac{1}{2\,b\,(1+m)}\left(b-m+2\,b\,m\,qC+\sqrt{m^2+2\,b\,m\,(-1+2\,qC)+b^2\left(1+4\,m^2\,(-1+qC)\,qC\right)}\right)\right\}\right\}$$

In[83]:=
```
qEquil1BAdditiveMultiplicPolymContFunc1[b_, m_, qC_] :=
 -1/(2 b (1 + m)) (m - b (1 + 2 m qC) + Sqrt[m^2 + 2 b m (-1 + 2 qC) + b^2 (1 + 4 m^2 (-1 + qC) qC)])
```

In[84]:=
```
qEquil1BAdditiveMultiplicPolymContFunc2[b_, m_, qC_] :=
 1/(2 b (1 + m)) (b - m + 2 b m qC + Sqrt[m^2 + 2 b m (-1 + 2 qC) + b^2 (1 + 4 m^2 (-1 + qC) qC)])
```

```
qCmin = 0.;
qCmax = 1.;
Manipulate[
 Plot[{qEquil1BAdditiveMultiplicPolymContFunc1[b, m, qC],
   qEquil1BAdditiveMultiplicPolymContFunc2[b, m, qC]}, {m, 0, 1},
  PlotRange → {{-0.2, 1}, {-0.2, 1}}, AxesLabel → {m, "q̂B"}],
 {{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 Nobebook):

In[85]:=
```
qEquil1BAdditiveMultiplicApproxPolymCont =
 Solve[(recB[3, 1] /. assumeCI /. assumeA1Rare[1] /. assumeNeutrality[2] /.
      assumeAdditiveMultiplicApproxFitnessB[1] // FullSimplify) == q[1], q[1]]
```

Out[85]=
$$\left\{\left\{q[1] \to \frac{1}{2\,(-b[1]-b[1]\,m[1])}\left(-b[1]+m[1]-a[1]\,m[1]-2\,qC\,b[1]\,m[1]-\sqrt{\left(-4\,(-b[1]-b[1]\,m[1])\,(qC\,m[1]-qC\,a[1]\,m[1]-qC\,b[1]\,m[1])+(b[1]-m[1]+a[1]\,m[1]+2\,qC\,b[1]\,m[1])^2\right)}\right)\right\},\right.$$
$$\left.\left\{q[1] \to \frac{1}{2\,(-b[1]-b[1]\,m[1])}\left(-b[1]+m[1]-a[1]\,m[1]-2\,qC\,b[1]\,m[1]+\sqrt{\left(-4\,(-b[1]-b[1]\,m[1])\,(qC\,m[1]-qC\,a[1]\,m[1]-qC\,b[1]\,m[1])+(b[1]-m[1]+a[1]\,m[1]+2\,qC\,b[1]\,m[1])^2\right)}\right)\right\}\right\}$$

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 :

```
FullSimplify[Reduce[{0 < (q[1] /. qEquil1BAdditiveMultiplicApproxPolymCont[[1]]) &&
    (q[1] /. qEquil1BAdditiveMultiplicApproxPolymCont[[1]]) < 1}, m[1]],
 Assumptions → {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 :

```
FullSimplify[Reduce[{0 < (q[1] /. qEquil1BAdditiveMultiplicApproxPolymCont[[2]]) &&
    (q[1] /. qEquil1BAdditiveMultiplicApproxPolymCont[[2]]) < 1}, m[1]],
 Assumptions → {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*.

```
qEquil1BAdditiveMultiplicApproxPolymCont /. ruleSimplifyNotationCI /. {x_[1] → x} //
 FullSimplify
```

$$\left\{\left\{q \to \frac{1}{2\,b\,(1+m)}\left(b-m+a\,m+2\,b\,m\,qC+\sqrt{-4\,b\,(-1+a+b)\,m\,(1+m)\,qC+(b+(-1+a)\,m+2\,b\,m\,qC)^2}\right)\right\},\ \left\{q \to \frac{1}{2\,b\,(1+m)}\left(b-m+a\,m+2\,b\,m\,qC-\sqrt{-4\,b\,(-1+a+b)\,m\,(1+m)\,qC+(b+(-1+a)\,m+2\,b\,m\,qC)^2}\right)\right\}\right\}$$

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

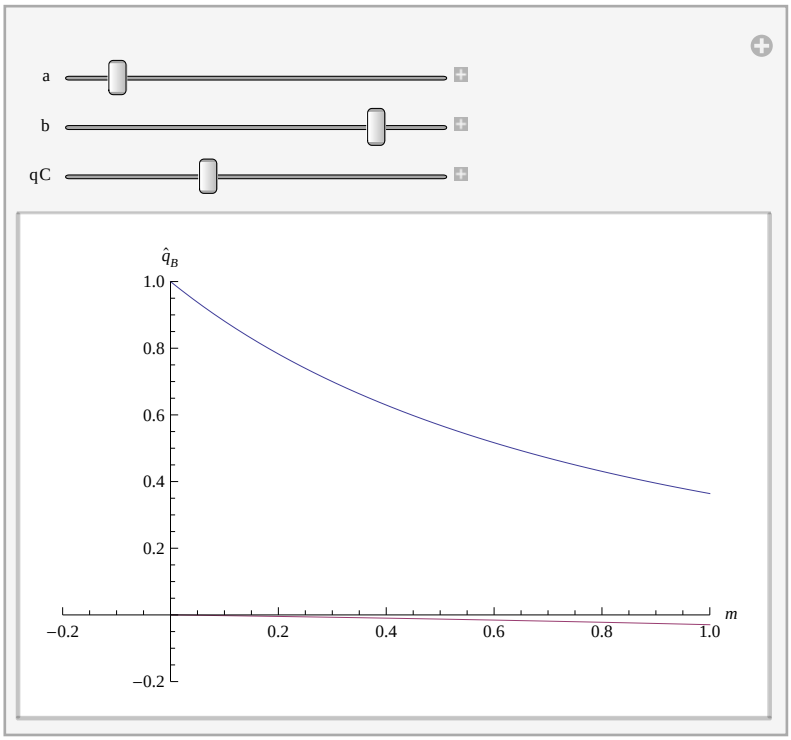
```
qEquil1BAdditiveMultiplicApproxPolymCont[[1]] /. ruleSimplifyNotationCI /. {x_[1] → x} //
 FullSimplify
```

$$\left\{q \to \frac{1}{2\,b\,(1+m)}\left(b-m+a\,m+2\,b\,m\,qC+\sqrt{-4\,b\,(-1+a+b)\,m\,(1+m)\,qC+(b+(-1+a)\,m+2\,b\,m\,qC)^2}\right)\right\}$$

In[86]:=
```
qEquil1BAdditiveMultiplicApproxPolymContFunc1[a_, b_, m_, qC_] :=
 1/(2 b (1 + m)) (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])
```

In[87]:=
```
qEquil1BAdditiveMultiplicApproxPolymContFunc2[a_, b_, m_, qC_] :=
 1/(2 b (1 + m)) (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])
```

```
qCmin = 0.;
qCmax = 1.;
Manipulate[
 Plot[{qEquil1BAdditiveMultiplicApproxPolymContFunc1[a, b, m, qC],
   qEquil1BAdditiveMultiplicApproxPolymContFunc2[a, b, m, qC]}, {m, 0, 1},
  PlotRange → {{-0.2, 1}, {-0.2, 1}}, AxesLabel → {m, "q̂B"}], {{a, 0.1}, 0., 1.},
 {{b, 0.4}, 0., 1.}, {{qC, 0.5}, qCmin, qCmax}]
```



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:

```
pgf[1, 1]
```

$$e^{-\frac{r\,(1-m[1])\,(1-q[1])\,(1-s[2])\,w14[1]}{wbar[1]}-\frac{(1-m[1])\,(1-s[1])\,(w1[1]-r\,(1-q[1])\,w14[1])}{wbar[1]}}$$

```
pgf[2, 1]
```

$$e^{-\frac{r\,(1-m[1])\,q[1]\,(1-s[1])\,w14[1]}{wbar[1]}-\frac{(1-m[1])\,(1-s[2])\,(-r\,q[1]\,w14[1]+w2[1])}{wbar[1]}}$$

```
assumeA1Rare[1]
```

```
{x[3, 1] → q[1], x[4, 1] → 1 - q[1]}
```

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

```
q[1] /. qEquil1BAdditiveMultiplicApproxPolymCont[[1]]
```

```
(-b[1] + m[1] - a[1] m[1] - 2 qC b[1] m[1] -
    √(-4 (-b[1] - b[1] m[1]) (qC m[1] - qC a[1] m[1] - qC b[1] m[1]) +
        (b[1] - m[1] + a[1] m[1] + 2 qC b[1] m[1])^2)) / (2 (-b[1] - b[1] m[1]))
```

```
wMeanB[1]
```

```
w33[1] x[3, 1]^2 + 2 w34[1] x[3, 1] x[4, 1] + w44[1] x[4, 1]^2
```

In[88]:=
```
pgf1PolymCont =
 pgf[1, 1] /. qEquil1BAdditiveMultiplicApproxPolymCont[[1]] /. wbar[1] → wMeanB[1] /.
          assumeAdditiveMultiplicEpistaticApproxFitness[1] /. assumeA1Rare[1] /.
        w1[1] → wMargType[1, 1] /. assumeAdditiveMultiplicEpistaticApproxFitness[1] /.
      assumeA1Rare[1] /. {γ11[1] → 0, γ12[1] → 0, γ21[1] → 0, γ22[1] → 0} /.
    qEquil1BAdditiveMultiplicApproxPolymCont[[1]] /.
   {a[1] → a, b[1] → b, m[1] → m, s[1] → s1, s[2] → s2} // FullSimplify
```

Out[88]=
$$e^{-\frac{(-1+m)\left(b^2(1+2mqC)(-1+s1)+\left((-1+a)m+\sqrt{-4b(-1+a+b)m(1+m)qC+(b+(-1+a)m+2bmqC)^2}\right)r(s1-s2)+b\left(-2-\sqrt{-4b(-1+a+b)m(1+m)qC+(b+(-1+a)m+2bmqC)^2}+2s1+\sqrt{-4b(-1+a+b)m(1+m}\right.\right.}{2b\left(1-a+bm(-1+2qC)+\sqrt{-4b(-1+a+b)m(1+m)qC+(b+(-1+a)m+2bmqC)^2}\right)}}$$

In[89]:=
```
R1Rule = R1 → Sqrt[-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2] ;
```

In[90]:=
```
pgf1PolymContShort = e^((1-m) (b^2 (1+2 m qC) (-1+s1)+((-1+a) m+R1) r (s1-s2)+b (-2-R1+2 s1+R1 s1-r s1+m (-1+a (-1+s1)+s1+2 (-1+qC) r (s1-s2))+r s2))/(2 b (1-a+b m (-1+2 qC)+R1)))
```

Out[90]=
$$e^{\frac{(1-m)\left(b^2(1+2mqC)(-1+s1)+r((-1+a)m+R1)(s1-s2)+b(-2-R1+2s1+R1s1-rs1+m(-1+a(-1+s1)+s1+2(-1+qC)r(s1-s2))+rs2)\right)}{2b(1-a+bm(-1+2qC)+R1)}}$$

```
pgf1PolymContShort - pgf1PolymCont /. R1Rule // FullSimplify
```

```
0
```

```
Collect[
  (1 - m) (b^2 (1 + 2 m qC) (-1 + s1) + ((-1 + a) m + R1) r (s1 - s2) + b (-2 - R1 + 2 s1 + R1 s1 - r s1 +
        m (-1 + a (-1 + s1) + s1 + 2 (-1 + qC) r (s1 - s2)) + r s2)), {s1, s2}]
```

```
(1 - m) (-2 b - b m - a b m - b^2 (1 + 2 m qC) - b R1) +
 (1 - m) (2 b + b m + a b m + b^2 (1 + 2 m qC) - b r + 2 b m (-1 + qC) r + b R1 + r ((-1 + a) m + R1)) s1 +
 (1 - m) (b r - 2 b m (-1 + qC) r - r ((-1 + a) m + R1)) s2
```

```
FullSimplify[(-2 b - b m - a b m - b^2 (1 + 2 m qC) - b R1)]
```

```
-b (2 + b + m + a m + 2 b m qC + R1)
```

```
FullSimplify[(2 b + b m + a b m + b^2 (1 + 2 m qC) - b r + 2 b m (-1 + qC) r + b R1 + r ((-1 + a) m + R1))]
```

```
b^2 (1 + 2 m qC) + r ((-1 + a) m + R1) + b (2 - r + m (1 + a + 2 (-1 + qC) r) + R1)
```

```
FullSimplify[(b r - 2 b m (-1 + qC) r - r ((-1 + a) m + R1))]
```

```
r (b + m - a m + 2 b m - 2 b m qC - R1)
```

```
pgf1PolymContDisplay =
```

$$e^{\frac{(1-m)\left(b^2(1+2mqC)+r(-(1-a)m+R1)+b(2-r+m(1+a-2(1-qC)r)+R1)\right)s1+(1-m)r(b+m-am+2bm-2bmqC-R1)s2-(1-m)b(2+b+m+am+2bmqC+R1)}{2b(1-a-bm(1-2qC)+R1)}}$$

$$e^{\frac{-b(1-m)(2+b+m+am+2bmqC+R1)+(1-m)\left(b^2(1+2mqC)+r((-1+a)m+R1)+b(2-r+m(1+a-2(1-qC)r)+R1)\right)s1+(1-m)r(b+m-am+2bm-2bmqC-R1)s2}{2b(1-a-bm(1-2qC)+R1)}}$$

```
pgf1PolymContDisplay - pgf1PolymContShort // FullSimplify
```

```
0
```

Check if this terms conincides with the one for the monomorphic continent if we set $q_C = 0$.

```
FullSimplify[pgf1PolymContDisplay /. R1Rule /. {qC → 0},
 Assumptions → Flatten[{assumeGeneral, m < mCrit2}]]
```

$$e^{-\frac{b^2(-1+s1)+(-1+a)mr(s1-s2)+b(-1+am(-1+s1)+s1-mrs1+mrs2)}{(-1+a-b)b}}$$

```
% - pgf1Add // Simplify
```

```
0
```

This seems fine.

In[91]:=
```
pgf2PolymCont =
 pgf[2, 1] /. qEquil1BAdditiveMultiplicApproxPolymCont[[1]] /. wbar[1] → wMeanB[1] /.
           assumeAdditiveMultiplicEpistaticApproxFitness[1] /. assumeA1Rare[1] /.
         w2[1] → wMargType[2, 1] /. assumeAdditiveMultiplicEpistaticApproxFitness[1] /.
       assumeA1Rare[1] /. {γ11[1] → 0, γ12[1] → 0, γ21[1] → 0, γ22[1] → 0} /.
     qEquil1BAdditiveMultiplicApproxPolymCont[[1]] /.
   {a[1] → a, b[1] → b, m[1] → m, s[1] → s1, s[2] → s2} // FullSimplify
```

Out[91]=
$$e^{-\frac{(-1+m)\left(\left((-1+a)\,m+\sqrt{-4\,b\,(-1+a+b)\,m\,(1+m)\,qC+(b+(-1+a)\,m+2\,b\,m\,qC)^2}\right)r\,(s1-s2)+b^2\,(-1+2\,m\,(-1+qC))\,(-1+s2)+b\left(r\,(s1-s2)+\left(2+\sqrt{-4\,b\,(-1+a+b)\,m\,(1+m)\,qC+(b+(-1+a)\,m+2\,b\,m\,qC)^2}\right)(-1+s2)+\right.\right.}{2\,b\left(1-a+b\,m\,(-1+2\,qC)+\sqrt{-4\,b\,(-1+a+b)\,m\,(1+m)\,qC+(b+(-1+a)\,m+2\,b\,m\,qC)^2}\right)}}$$

In[92]:=
```
pgf2PolymContShort = e^((1-m) ((-(1-a) m+R1) r (s1-s2)+b^2 (-1+2 m (-1+qC)) (-1+s2)+b (r (s1-s2)+(2+R1) (-1+s2)+m (-1+2 qC r (s1-s2)+a (-1+s2)+s2)))/(2 b (1-a-b m (1-2 qC)+R1)))
```

Out[92]=
$$e^{\frac{(1-m)\left(r\,((-1+a)\,m+R1)\,(s1-s2)+b^2\,(-1+2\,m\,(-1+qC))\,(-1+s2)+b\,(r\,(s1-s2)+(2+R1)\,(-1+s2)+m\,(-1+2\,qC\,r\,(s1-s2)+a\,(-1+s2)+s2))\right)}{2\,b\,(1-a-b\,m\,(1-2\,qC)+R1)}}$$

```
pgf2PolymContShort - pgf2PolymCont /. R1Rule // FullSimplify
```

```
0
```

```
Collect[(1 - m) ((-(1 - a) m + R1) r (s1 - s2) + b^2 (-1 + 2 m (-1 + qC)) (-1 + s2) +
     b (r (s1 - s2) + (2 + R1) (-1 + s2) + m (-1 + 2 qC r (s1 - s2) + a (-1 + s2) + s2))), {s1, s2}]
```

$$(1-m)\left(-2\,b-b\,m-a\,b\,m-b^2\,(-1+2\,m\,(-1+qC))-b\,R1\right)+$$
$$(1-m)\,(b\,r+2\,b\,m\,qC\,r+r\,((-1+a)\,m+R1))\,s1+$$
$$(1-m)\left(b\,m+a\,b\,m+b^2\,(-1+2\,m\,(-1+qC))-b\,r-2\,b\,m\,qC\,r+b\,(2+R1)-r\,((-1+a)\,m+R1)\right)s2$$

```
FullSimplify[(-2 b - b m - a b m - b^2 (-1 + 2 m (-1 + qC)) - b R1)]
```

$$-b\,(2+m+a\,m+b\,(-1+2\,m\,(-1+qC))+R1)$$

```
FullSimplify[(b r + 2 b m qC r + r ((-1 + a) m + R1))]
```

$$r\,(b+(-1+a)\,m+2\,b\,m\,qC+R1)$$

```
FullSimplify[
  (b m + a b m + b^2 (-1 + 2 m (-1 + qC)) - b r - 2 b m qC r + b (2 + R1) - r ((-1 + a) m + R1))]
```

$$b^2\,(-1+2\,m\,(-1+qC))-r\,((-1+a)\,m+R1)+b\,(2-r+m\,(1+a-2\,qC\,r)+R1)$$

```
pgf2PolymContDisplay =
 e^((1-m) (r (b-(1-a) m+2 b m qC+R1)) s1+(1-m) (-b^2 (1+2 m (1-qC))+r ((1-a) m-R1)+b (2-r+m (1+a-2 qC r)+R1)) s2+(1-m) (-b (2+m+a m-b (1+2 m (1-qC)))+R1))/(2 b (1-a-b m (1-2 qC)+R1))
```

$$e^{\frac{-b\,(1-m)\,(2+m+a\,m-b\,(1+2\,m\,(1-qC))+R1)+(1-m)\,r\,(b-(1-a)\,m+2\,b\,m\,qC+R1)\,s1+(1-m)\left(-b^2\,(1+2\,m\,(1-qC))+r\,((1-a)\,m-R1)+b\,(2-r+m\,(1+a-2\,qC\,r)+R1)\right)s2}{2\,b\,(1-a-b\,m\,(1-2\,qC)+R1)}}$$

```
pgf2PolymContDisplay - pgf2PolymContShort // FullSimplify
```

```
0
```

Check if this terms conincides with the one for the monomorphic continent if we set $q_C = 0$.

```
FullSimplify[pgf2PolymContDisplay /. R1Rule /. {qC → 0},
 Assumptions → Flatten[{assumeGeneral, m < mCrit2}]]
```

$$e^{-\frac{(-1+a)\,m\,r\,(s1-s2)+b^2\,(m-m\,s2)+b\,(-1+r\,s1+a\,m\,(-1+s2)+s2-r\,s2)}{(-1+a-b)\,b}}$$

```
% - pgf2Add // Simplify
```

```
0
```

This seems fine, too.

■ Implementation of numerical solution (polymorphic continent)

There is now an additional parameter q_c denoting the frequency of the B_1 allele on the continent.

Importantly, the parameter q_c enters only in the recursion equations for $x_3 = [A_2 B_1]$ and $x_4 = [A_2 B_2]$, but not in those for $x_1 = [A_1 B_1]$ and $x_2 = [A_1 B_2]$. 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, m1, a1, b1
probEstablAMApproxPolymContFunc[r_,m1_,a1_,b1_,γ111_,γ121_,γ211_,γ221_,qC_]:=Module[{qE
qEq= (b1-m1+a1*m1+2*b1*m1*qC+Sqrt[-4*b1*(-1+a1+b1)*m1*(1+m1)*qC+(b1+(-1+a1)*m1+2*b1*m1*qC)^2])/(2*b1*(1+m1));
wbar=1-a1+b1*(-1+2*qEq);
w1=1+b1*qEq+(-1+qEq)*γ111;
w2=1+b1*(-1+qEq)-qEq*γ111+γ121*(-1+qEq);
w14=1-γ111;
(* Leading eigenvalue of the mean matrix; Note that qc does *not* enter here! *)
λ1=-1/(2 wbar)(-1+m1)*(w1-r*w14+w2+(w1^2+r^2*w14^2+w1*(2*(-1+2*qEq)*r*w14-2*w2)+2*(1-2*qEq)*r*
(* Probability generating functions *)
pgf1[s1_,s2_]:=Exp[-(r*(1-m1)*(1-qEq)*(1-s2)*w14)/wbar-((1-m1)*(1-s1)*(w1-r*(1-qEq)*w14))/wbar];
pgf2[s1_,s2_]:=Exp[-(r*(1-m1)*qEq*(1-s1)*w14)/wbar-((1-m1)*(1-s2)*(-r*qEq*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[{λ1,(1-q1),(1-q2),qEq*(1-q1)+(1-qEq)*(1-q2),qEq}/.qSol]
];

(* Rules for the specific model considered *)
rulesCI[n_]:={wbar[n]→wMeanB[n],w1[n]→wMargType[1,n],w2[n]→wMargType[2,n],w14[n]→w[n][[
```

■ Explicit equilibrium frequency of B_1

In[96]:=
```
qhatAMApproxPolymCont = q[1] /. qEquil1BAdditiveMultiplicApproxPolymCont[[1]]
```

Out[96]=
$$\frac{1}{2\,(-b[1]-b[1]\,m[1])}\Big(-b[1]+m[1]-a[1]\,m[1]-2\,qC\,b[1]\,m[1]-\sqrt{\big(-4\,(-b[1]-b[1]\,m[1])\,(qC\,m[1]-qC\,a[1]\,m[1]-qC\,b[1]\,m[1])+(b[1]-m[1]+a[1]\,m[1]+2\,qC\,b[1]\,m[1])^2\big)}\Big)$$

■ Explicit fitnesses

```
wMeanB[1]
```

$$w33[1]\,x[3,1]^2+2\,w34[1]\,x[3,1]\,x[4,1]+w44[1]\,x[4,1]^2$$

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 previous ones here:

```
wbarAMApprox
```

$$1-a[1]+b[1]\,(-1+2\,q[1])$$

```
w1AMApprox
```

$$1-q[1]+(1+b[1])\,q[1]$$

```
w2AMApprox
```

$$(1-b[1])\,(1-q[1])+q[1]$$

```
w14AMApprox[1]
```

$$1$$

■ Explicit mean matrix

Remember the mean matrix and our assumptions about additive fitnesses:

```
G[1] /. ruleSimplifyNotationCI // MatrixForm
```

$$\begin{pmatrix} \frac{(1-m)\,(w1[1]-(1-q)\,r\,w14[1])}{wbar[1]} & \frac{(1-m)\,q\,r\,w14[1]}{wbar[1]} \\ \frac{(1-m)\,(1-q)\,r\,w14[1]}{wbar[1]} & \frac{(1-m)\,(-q\,r\,w14[1]+w2[1])}{wbar[1]} \end{pmatrix}$$

```
assumeAdditiveMultiplicApproxFitness[1]
```

```
{w11[1] → 1 + a[1] + b[1], w12[1] → 1 + a[1], w13[1] → 1 + b[1],
 w14[1] → 1, w22[1] → 1 + a[1] - b[1], w24[1] → 1 - b[1],
 w33[1] → 1 - a[1] + b[1], w34[1] → 1 - a[1], w44[1] → 1 - a[1] - b[1]}
```

```
ruleSimplifyNotationCI
```

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

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

```
qhatAMApproxPolymCont
```

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

```
GAddPolymCont =
  G[1] /. ruleSimplifyNotationCI /. {w1[1] → w1AMApprox, w2[1] → w2AMApprox,
        wbar[1] → wbarAMApprox} /. assumeAdditiveMultiplicApproxFitness[1] /.
    {q[1] → qhatAMApproxPolymCont} /. {q → qhatAMApproxPolymCont} /.
   ruleSimplifyNotationCI /. {x_[1] → x} // FullSimplify;
```

```
GAddPolymCont // MatrixForm
```

$$\begin{pmatrix} -\frac{(-1+m)\left(b^2\,(1+2\,m\,qC)+b\sqrt{-4\,b\,(-1+a+b)\,m\,(1+m)\,qC+(b+(-1+a)\,m+2\,b\,m\,qC)^2}+(-1+a)\,m\,r+\sqrt{-4\,b\,(-1+a+b)\,m\,(1+m)\,qC+(b+(-1+a)\,m+2\,b\,m\,qC}\right.}{2\,b\left(1-a+b\,m\,(-1+2\,qC)+\sqrt{-4\,b\,(-1+a+b)\,m\,(1+m)\,qC+(b+(-1+a)\,m+2\,b\,m\,qC)^2}\right)} & \\ \left.\frac{\left(-b+m\,(-1+a-2\,b\,(-1+qC))+\sqrt{-4\,b\,(-1+a+b)\,m\,(1+m)\,qC+(b+(-1+a)\,m+2\,b\,m\,qC)^2}\right)\,r}{2\,b\,(-1+a+b)}\right. & \end{pmatrix}$$

This is what we call λ_{11} in the main text:

```
Collect[GAddPolymCont[[1, 1]], r] /.
 {Sqrt[-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2] → R1}
```

$$-\frac{(-1+m)\,r\,(-b+(-1+a)\,m+2\,b\,m\,(-1+qC)+R1)}{2\,b\,(1-a+b\,m\,(-1+2\,qC)+R1)}-\frac{(-1+m)\left(2\,b+b\,m+a\,b\,m+b^2\,(1+2\,m\,qC)+b\,R1\right)}{2\,b\,(1-a+b\,m\,(-1+2\,qC)+R1)}$$

```
-((-1 + m) (2 b + b m + a b m + b^2 (1 + 2 m qC) + b R1))/(2 b (1 - a + b m (-1 + 2 qC) + R1)) // FullSimplify
```

$$\frac{(-1+m)\,(2+b+m+a\,m+2\,b\,m\,qC+R1)}{2\,(-1+a+b\,(m-2\,m\,qC)-R1)}$$

```
-((-1 + m) r (-b + (-1 + a) m + 2 b m (-1 + qC) + R1))/(2 b (1 - a + b m (-1 + 2 qC) + R1)) // FullSimplify
```

$$-\frac{(-1+m)\,r\,((-1+a)\,m+b\,(-1+2\,m\,(-1+qC))+R1)}{2\,b\,(1-a+b\,m\,(-1+2\,qC)+R1)}$$

This is what we call λ_{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] -> R1}
```

$$\frac{r\,(-b+m\,(-1+a-2\,b\,(-1+qC))+R1)}{2\,b\,(-1+a+b)}$$

```
FullSimplify[Collect[GAddPolymCont[[2, 1]], r] /. qC -> 0,
 Assumptions -> {0 < a < b < 1, 0 < m < 1, m < b / (1 - a)}]
```

$$\frac{m\,r}{b}$$

```
r (-b + m (-1 + a - 2 b (-1 + qC)) + R1) // FullSimplify
```

$$\frac{r\,(-b+m\,(-1+a-2\,b\,(-1+qC))+R1)}{2\,b\,(-1+a+b)}$$

This is what we call λ_{21} in the main text:

```
Collect[GAddPolymCont[[1, 2]], r] /.
 {Sqrt[-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2] -> R1}
```

$$\frac{r\,(b-m+a\,m-2\,b\,m\,qC+R1)}{2\,b\,(1-a+b)}$$

```
FullSimplify[Collect[GAddPolymCont[[1, 2]], r] /. qC -> 0,
 Assumptions -> {0 < a < b < 1, 0 < m < 1, m < b / (1 - a)}]
```

$$\frac{(b+(-1+a)\,m)\,r}{b\,(1-a+b)}$$

```
r (b - m + a m - 2 b m qC + Sqrt[R]) // FullSimplify
```

$$\frac{r\,\left(b-m+a\,m-2\,b\,m\,qC+\sqrt{R}\right)}{2\,b\,(1-a+b)}$$

This is what we call λ_{22} in the main text:

```
Collect[GAddPolymCont[[2, 2]], r] /.
 {Sqrt[-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2] -> R1}
```

$$-\frac{(-1+m)\,r\,(-b+(1-a)\,m-2\,b\,m\,qC-R1)}{2\,b\,(1-a+b\,m\,(-1+2\,qC)+R1)}-\frac{(-1+m)\,\left(2\,b+b\,m+a\,b\,m+b^2\,(-1+2\,m\,(-1+qC))+b\,R1\right)}{2\,b\,(1-a+b\,m\,(-1+2\,qC)+R1)}$$

```
-((-1 + m) r (-b + (1 - a) m - 2 b m qC - R1))/(2 b (1 - a + b m (-1 + 2 qC) + R1)) // FullSimplify
```

$$\frac{(-1+m)\,r\,(b+(-1+a)\,m+2\,b\,m\,qC+R1)}{2\,b\,(1-a+b\,m\,(-1+2\,qC)+R1)}$$

```
-((-1 + m) (2 b + b m + a b m + b^2 (-1 + 2 m (-1 + qC)) + b R1))/(2 b (1 - a + b m (-1 + 2 qC) + R1)) // FullSimplify
```

$$\frac{(-1+m)\,(2+m+a\,m+b\,(-1+2\,m\,(-1+qC))+R1)}{2\,(-1+a+b\,(m-2\,m\,qC)-R1)}$$

```
FullSimplify[Collect[GAddPolymCont[[2, 2]], r] /. qC -> 0,
 Assumptions -> {0 < a < b < 1, 0 ≤ m < b / (1 - a)}]
```

$$\frac{b^2\,m+(-1+a)\,m\,r+b\,(-1-a\,m+r)}{(-1+a-b)\,b}$$

```
Collect[(b^2 m + (-1 + a) m r + b (-1 - a m + r))/((-1 + a - b) b), r]
```

$$\frac{-b-a\,b\,m+b^2\,m}{(-1+a-b)\,b}+\frac{(b+(-1+a)\,m)\,r}{(-1+a-b)\,b}$$

```
FullSimplify[(-b - a b m + b^2 m)/((-1 + a - b) b)]
```

$$\frac{1+a\,m-b\,m}{1-a+b}$$

In[97]:=
```
EPolymCont := ((1 - m) (2 + b + m + a m + 2 b m qC + R1))/(2 (1 - a - b m (1 - 2 qC) + R1))

FPolymCont := -((1 - m) ((1 - a) m + b + 2 b m (1 - qC) - R1))/(2 b (1 - a - b m (1 - 2 qC) + R1))

GPolymCont := (b + m (1 - a - 2 b (1 - qC)) - R1)/(2 b (1 - a - b))

HPolymCont := (b - (1 - a) m - 2 b m qC + R1)/(2 b (1 - a + b))

IPolymCont := -((1 - m) (b - (1 - a) m + 2 b m qC + R1))/(2 b (1 - a - b m (1 - 2 qC) + R1))

JPolymCont := ((1 - m) (2 + m + a m - b (1 + 2 m (1 - qC)) + R1))/(2 (1 - a - b (m - 2 m qC) + R1))

tt1 = Exp[-λ11 (1 - s1) - λ12 (1 - s2)] /.
    {λ11 → GAddPolymCont[[1, 1]], λ12 → GAddPolymCont[[2, 1]]} /.
  Sqrt[-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2] → R1
```

$$e^{\frac{(-1+m)\left(b^2\,(1+2\,m\,qC)+(-1+a)\,m\,r+b\,(2-r+m\,(1+a+2\,(-1+qC)\,r))+b\,R1+r\,R1\right)\,(1-s1)}{2\,b\,(1-a+b\,m\,(-1+2\,qC)+R1)}-\frac{r\,(-b+m\,(-1+a-2\,b\,(-1+qC))+R1)\,(1-s2)}{2\,b\,(-1+a+b)}}$$

```
tt1 - pgf1PC[s1, s2] /. R1Rule // Simplify
```

0

```
tt2 = Exp[-λ21 (1 - s1) - λ22 (1 - s2)] /.
    {λ21 → GAddPolymCont[[1, 2]], λ22 → GAddPolymCont[[2, 2]]} /.
  Sqrt[-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2] → R1
```

$$e^{-\frac{r\,(b-m+a\,m-2\,b\,m\,qC+R1)\,(1-s1)}{2\,b\,(1-a+b)}+\frac{(-1+m)\left(b^2\,(-1+2\,m\,(-1+qC))-(-1+a)\,m\,r+b\,(2-r+m\,(1+a-2\,qC\,r))+b\,R1-r\,R1\right)\,(1-s2)}{2\,b\,(1-a+b\,m\,(-1+2\,qC)+R1)}}$$

```
tt2 - pgf2PC[s1, s2] /. R1Rule // Simplify
```

0

```
(Collect[GAddPolymCont[[1, 1]], r] /.
    {Sqrt[-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2] → R1}) -
  (EPolymCont + FPolymCont r) // Simplify
```

0

```
(Collect[GAddPolymCont[[2, 1]], r] /.
    {Sqrt[-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2] → R1}) -
  (GPolymCont r) // Simplify
```

0

```
(Collect[GAddPolymCont⟦1, 2⟧, r] /.
    {√(-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2) → R1}) -
  (HPolymCont r) // Simplify
```

```
0
```

```
(Collect[GAddPolymCont⟦2, 2⟧, r] /.
    {√(-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2) → R1}) -
  (JPolymCont + IPolymCont r) // Simplify
```

```
0
```

```
e^(-λ11 (1-s1)) e^(-λ12 (1-s2)) /. {λ11 → (EE + FF r), λ12 → (GG r)}
```

```
e^(-(EE+FF r) (1-s1)-GG r (1-s2))
```

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

```
-EE - FF r - GG r + (EE + FF r) s1 + GG r s2
```

```
e^(-λ21 (1-s1)) e^(-λ22 (1-s2)) /. {λ21 → (HH r), λ22 → (JJ + II r)}
```

```
e^(-HH r (1-s1)-(JJ+II r) (1-s2))
```

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

```
-JJ - HH r - II r + HH r s1 + (JJ + II r) s2
```

```
t1 = GAddPolymCont /. {a → α ϵ, b → β ϵ, m → μ ϵ, r → ρ ϵ, qC → ξC ϵ};
```

```
t1 // MatrixForm
```

$$\begin{pmatrix} -\dfrac{(-1+\epsilon\,\mu)\left(\beta^2\epsilon^2\left(1+2\,\epsilon^2\,\mu\,\xi C\right)+\beta\,\epsilon\sqrt{-4\,\beta\,\epsilon^3\,(-1+\alpha\,\epsilon+\beta\,\epsilon)\,\mu\,(1+\epsilon\,\mu)\,\xi C+\left(\beta\,\epsilon+\epsilon\,(-1+\alpha\,\epsilon)\,\mu+2\,\beta\,\epsilon^3\,\mu\,\xi C\right)^2}+\epsilon^2\,(-1+\alpha\,\epsilon)\,\mu\,\rho+\epsilon\sqrt{-4\,\beta\,\epsilon^3\,(-1+\alpha\,\epsilon+\beta\,\epsilon)\,\mu\,(1+\epsilon\,\mu)\,\xi C+\left(\beta\,\epsilon+\epsilon\,(-1+\alpha\,\epsilon)\,\mu+2\,\beta\,\epsilon^3\,\mu\,\xi C\right)^2}\right)}{2\,\beta\,\epsilon\left(1-\alpha\,\epsilon+\beta\,\epsilon^2\,\mu\,(-1+2\,\epsilon\,\xi C)+\sqrt{-4\,\beta\,\epsilon^3\,(-1+\alpha\,\epsilon+\beta\,\epsilon)\,\mu\,(1+\epsilon\,\mu)\,\xi C+\left(\beta\,\epsilon+\epsilon\right.}\right.} \\ \dfrac{\left(-\beta\,\epsilon+\epsilon\,\mu\,(-1+\alpha\,\epsilon-2\,\beta\,\epsilon\,(-1+\epsilon\,\xi C))+\sqrt{-4\,\beta\,\epsilon^3\,(-1+\alpha\,\epsilon+\beta\,\epsilon)\,\mu\,(1+\epsilon\,\mu)\,\xi C+\left(\beta\,\epsilon+\right.}\right.}{2\,\beta\,(-1+\alpha\,\epsilon+\beta\,\epsilon)} \end{pmatrix}$$

```
FullSimplify[
 Series[t1, {ϵ, 0, 1}] /. {α → a / ϵ, β → b / ϵ, ρ → r / ϵ, μ → m / ϵ, ξC → qC / ϵ} // Normal,
 Assumptions → {0 < a < b < 1, a + b < 1, 0 < m < 1}]
```

$$\left\{\left\{\begin{cases} 1+a+b-m-r & b<m \\ 1+a-\frac{m\,r}{b} & \text{True} \end{cases}\text{, }\begin{cases} r-\frac{m\,r}{b} & b\geq m \\ 0 & \text{True} \end{cases}\right\}\text{, }\left\{\begin{cases} r & b<m \\ \frac{m\,r}{b} & \text{True} \end{cases}\text{, }\begin{cases} 1+a-m & b<m \\ 1+a-b-r+\frac{m\,r}{b} & \text{True} \end{cases}\right\}\right\}$$

```
t2 = GAddPolymCont /. {a → α ϵ, b → β ϵ, m → μ ϵ, r → ρ ϵ};
```

```
t2 // MatrixForm
```

$$\begin{pmatrix} -\dfrac{(-1+\epsilon\,\mu)\left(\beta^2\epsilon^2\,(1+2\,qC\,\epsilon\,\mu)+\beta\,\epsilon\sqrt{-4\,qC\,\beta\,\epsilon^2\,(-1+\alpha\,\epsilon+\beta\,\epsilon)\,\mu\,(1+\epsilon\,\mu)+\left(\beta\,\epsilon+2\,qC\,\beta\,\epsilon^2\,\mu+\epsilon\,(-1+\alpha\,\epsilon)\,\mu\right)^2}+\epsilon^2\,(-1+\alpha\,\epsilon)\,\mu\,\rho+\epsilon\sqrt{-4\,qC\,\beta\,\epsilon^2\,(-1+\alpha\,\epsilon}\right.}{2\,\beta\,\epsilon\left(1-\alpha\,\epsilon+(-1+2\,qC)\,\beta\,\epsilon^2\,\mu+\sqrt{-4\,qC\,\beta\,\epsilon^2\,(-1+\alpha\,\epsilon+\beta\,\epsilon)\,\mu\,(1+\epsilon\,\mu)+\left(\beta\,\epsilon+2\,q\right.}\right.} \\ \dfrac{\left(-\beta\,\epsilon+\epsilon\,(-1+\alpha\,\epsilon-2\,(-1+qC)\,\beta\,\epsilon)\,\mu+\sqrt{-4\,qC\,\beta\,\epsilon^2\,(-1+\alpha\,\epsilon+\beta\,\epsilon)\,\mu\,(1+\epsilon\,\mu)+\left(\beta\,\epsilon+2\,C\right.}\right.}{2\,\beta\,(-1+\alpha\,\epsilon+\beta\,\epsilon)} \end{pmatrix}$$

```
GAddPolymContSmallForces =
  FullSimplify[Series[t2, {ϵ, 0, 1}] /. {α → a / ϵ, β → b / ϵ, ρ → r / ϵ, μ → m / ϵ} // Normal,
   Assumptions → {0 < a < b < 1, a + b < 1, 0 < m < 1}];
```

```
GAddPolymContSmallForces // MatrixForm
```

$$\begin{pmatrix} \frac{b^2+\left(-m+\sqrt{(b-m)^2+4\,b\,m\,qC}\right)r-b\left(-2-2\,a+m+\sqrt{(b-m)^2+4\,b\,m\,qC}+r\right)}{2\,b} & \frac{\left(b-m+\sqrt{(b-m)^2+4\,b\,m\,qC}\right)r}{2\,b} \\ \frac{\left(b+m-\sqrt{(b-m)^2+4\,b\,m\,qC}\right)r}{2\,b} & -\frac{b^2+\left(-m+\sqrt{(b-m)^2+4\,b\,m\,qC}\right)r+b\left(-2-2\,a+m+\sqrt{(b-m)^2+4\,b\,m\,qC}+r\right)}{2\,b} \end{pmatrix}$$

The R_1 that follows here is different from R_1 above!

```
FullSimplify[GAddPolymContSmallForces /. {(b - m)^2 + 4 b m qC → R1}] // MatrixForm
```

$$\begin{pmatrix} \frac{b^2+r\left(-m+\sqrt{R1}\right)-b\left(-2-2\,a+m+r+\sqrt{R1}\right)}{2\,b} & \frac{r\left(b-m+\sqrt{R1}\right)}{2\,b} \\ \frac{r\left(b+m-\sqrt{R1}\right)}{2\,b} & -\frac{b^2+r\left(-m+\sqrt{R1}\right)+b\left(-2-2\,a+m+r+\sqrt{R1}\right)}{2\,b} \end{pmatrix}$$

```
Collect[GAddPolymContSmallForces /. {(b - m)^2 + 4 b m qC → R1}, r] // MatrixForm
```

$$\begin{pmatrix} \frac{r\left(-b-m+\sqrt{R1}\right)}{2\,b}+\frac{2\,b+2\,a\,b+b^2-b\,m-b\sqrt{R1}}{2\,b} & \frac{r\left(b-m+\sqrt{R1}\right)}{2\,b} \\ \frac{r\left(b+m-\sqrt{R1}\right)}{2\,b} & -\frac{r\left(b-m+\sqrt{R1}\right)}{2\,b}-\frac{-2\,b-2\,a\,b+b^2+b\,m+b\sqrt{R1}}{2\,b} \end{pmatrix}$$

```
FullSimplify[r (-b - m + Sqrt[R1])/(2 b)]
```

$$-\frac{r\left(b+m-\sqrt{R1}\right)}{2\,b}$$

```
FullSimplify[(2 b + 2 a b + b^2 - b m - b Sqrt[R1])/(2 b)]
```

$$\frac{1}{2}\left(2+2\,a+b-m-\sqrt{R1}\right)$$

```
FullSimplify[-(r (b - m + Sqrt[R1])/(2 b))]
```

$$-\frac{r\left(b-m+\sqrt{R1}\right)}{2\,b}$$

```
FullSimplify[-(-2 b - 2 a b + b^2 + b m + b Sqrt[R1])/(2 b)]
```

$$\frac{1}{2}\left(2+2\,a-b-m-\sqrt{R1}\right)$$

This assumes small evolutionary forces ($a,\ b,\ m,\ r$) but does not restrict the frequency q_C of B_1on the continent.

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

```
w1AMApprox /. {q[1] → qhatAMApproxPolymCont} /. {x_[1] → x} // FullSimplify
```

$$\frac{1}{2\,(1+m)}\left(2+b+m+a\,m+2\,b\,m\,qC+\sqrt{-4\,b\,(-1+a+b)\,m\,(1+m)\,qC+(b+(-1+a)\,m+2\,b\,m\,qC)^2}\right)$$

```
w2AMApprox /. {q[1] → qhatAMApproxPolymCont} /. {x_[1] → x} // FullSimplify
```

$$\frac{1}{2\,(1+m)}\left(2+m+a\,m+b\,(-1+2\,m\,(-1+qC))+\sqrt{-4\,b\,(-1+a+b)\,m\,(1+m)\,qC+(b+(-1+a)\,m+2\,b\,m\,qC)^2}\right)$$

```
wbarAMApprox /. {q[1] → qhatAMApproxPolymCont} /. {x_[1] → x} // FullSimplify
```

$$\frac{1}{1+m}\left(1-a+b\,m\,(-1+2\,qC)+\sqrt{-4\,b\,(-1+a+b)\,m\,(1+m)\,qC+(b+(-1+a)\,m+2\,b\,m\,qC)^2}\right)$$

■ Explicit conditions for invasion

Recall the generic condition for invasion:

```
conditionNonExtinction[1]
```

$$r\,w14[1]\left(-q[1]\,w1[1]-(1-q[1])\,w2[1]+\frac{wbar[1]}{1-m[1]}\right)<\left(w1[1]-\frac{wbar[1]}{1-m[1]}\right)\left(-w2[1]+\frac{wbar[1]}{1-m[1]}\right)$$

```
conditionNonExtinctionAMApproxPolymCont = FullSimplify[
  conditionNonExtinction[1] /. {w14[1] → w14AMApprox[1], wbar[1] → wbarAMApprox,
      w1[1] → w1AMApprox, w2[1] → w2AMApprox} /. {q[1] → qhatAMApproxPolymCont} /.
   {x_[1] → x}, Assumptions → {0 < a < b < 1, a + b < 1, 0 < m < 1, 0 < qC < 1}]
```

$$\frac{1}{4\,(-1+m)^2}\left(-2\,a-b+m+a\,m+2\,b\,m\,qC+\sqrt{-4\,b\,(-1+a+b)\,m\,(1+m)\,qC+(b+(-1+a)\,m+2\,b\,m\,qC)^2}\right)\left(-2\,a+b+m+a\,m-2\,b\,m+2\,b\,m\,qC+\sqrt{-4\,b\,(-1+a+b)\,m\,(1+m)\,qC+(b+(-1+a)\,m+2\,b\,m\,qC)^2}\right)<\frac{1}{-1+m^2}\left(a\,(-1+(-1+m)\,m)+m\,(1+b\,m\,(-1+2\,qC))+m\sqrt{-4\,b\,(-1+a+b)\,m\,(1+m)\,qC+(b+(-1+a)\,m+2\,b\,m\,qC)^2}\right)r$$

```
rSolInv = FullSimplify[Solve[1/(4 (-1 + m)^2)
      (-2 a - b + m + a m + 2 b m qC + √(-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2))
      (-2 a + b + m + a m - 2 b m + 2 b m qC +
        √(-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2)) ==
     1/(-1 + m^2) (a (-1 + (-1 + m) m) + m (1 + b m (-1 + 2 qC)) +
        m √(-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2)) r, r],
  Assumptions → {0 < a < b < 1, a + b < 1, 0 < m < 1, 0 < r ≤ 1/2}]
```

$$\left\{\left\{r\to\left((1+m)\left(-2\,a-b+m+a\,m+2\,b\,m\,qC+\sqrt{-4\,b\,(-1+a+b)\,m\,(1+m)\,qC+(b+(-1+a)\,m+2\,b\,m\,qC)^2}\right)\left(-2\,a+b+m+a\,m-2\,b\,m+2\,b\,m\,qC+\sqrt{-4\,b\,(-1+a+b)\,m\,(1+m)\,qC+(b+(-1+a)\,m+2\,b\,m\,qC)^2}\right)\right)\Big/\left(4\,(-1+m)\left(a\,(-1+(-1+m)\,m)+m\,(1+b\,m\,(-1+2\,qC))+m\sqrt{-4\,b\,(-1+a+b)\,m\,(1+m)\,qC+(b+(-1+a)\,m+2\,b\,m\,qC)^2}\right)\right)\right\}\right\}$$

```
(* The critical r from the deterministic model *)
rcrit = (1 + m)/(2 (1 - m)) (a^2 (2 - 2 m + m^2) - a m (2 - b (3 - m) (1 - 2 qC)) +
      m (m - b (1 + m) (1 - 2 qC) + b^2 (1 - 4 m (1 - qC) qC)) + (m (1 - b + 2 b qC) - a (2 - m)) R) /
    (a (1 + m - m^2) - m (1 - b m + 2 b m qC + R)) /.
  R → √((b - (1 - a) m)^2 + 4 b m (1 - a - b m) qC + 4 b^2 m^2 qC^2) ;
r - rcrit /. rSolInv // Simplify
```

$$\{0\}$$

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.

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

$Aborted

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

$Aborted

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

$Aborted

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

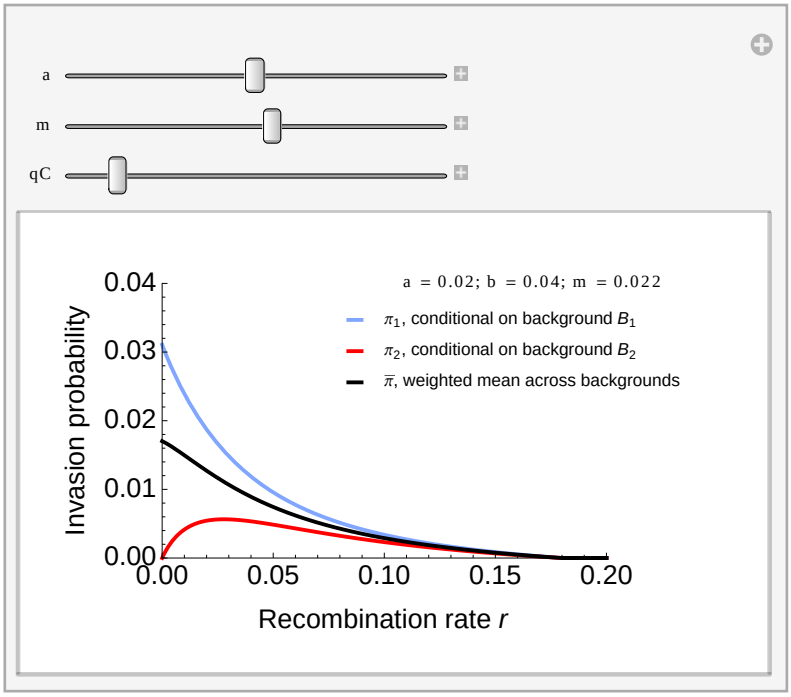
$Aborted

Plots of numerical solutions

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

In[103]:=
```
myb1 = 0.04;
myγ111 = 0.;
myγ121 = 0.;
myγ211 = 0.;
myγ221 = 0.;
rMax1 = 0.2;
```

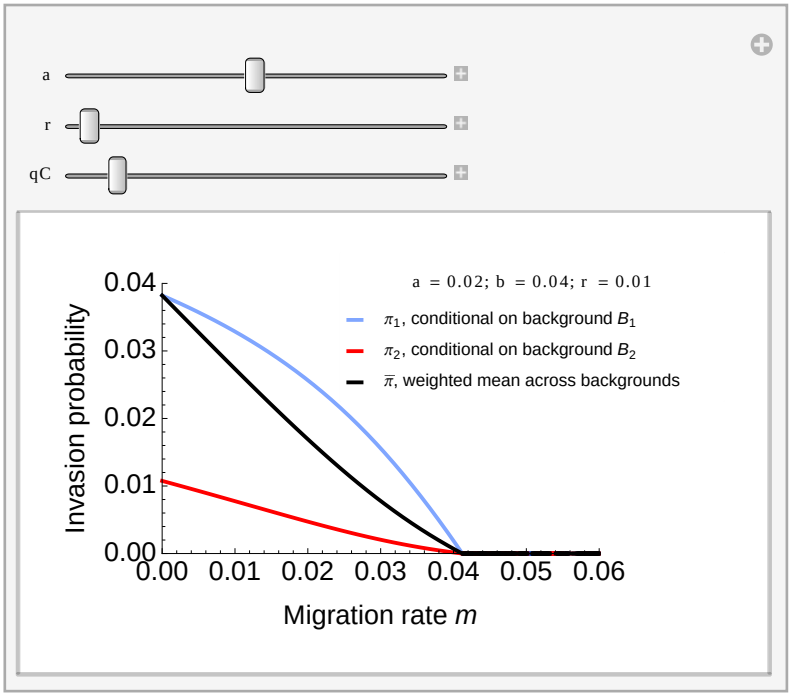
```
Manipulate[
 Show[Plot[{probEstablAMApproxPolymContFunc[r, m, a, myb1, myγ111, myγ121, myγ211,
       myγ221, qC][[2]], probEstablAMApproxPolymContFunc[
       r, m, a, myb1, myγ111, myγ121, myγ211, myγ221, qC][[3]],
     probEstablAMApproxPolymContFunc[r, m, a, myb1, myγ111, myγ121, myγ211, myγ221, 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["π1, conditional on background B1", FontFamily → "Helvetica"],
     Style["π2, conditional on background B2", FontFamily → "Helvetica"],
     Style["π̄, 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 → "Helvtica"]]
 ],
 {{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;
myγ112 = 0.;
myγ122 = 0.;
myγ212 = 0.;
myγ222 = 0.;
mMax2 = 0.06;
```

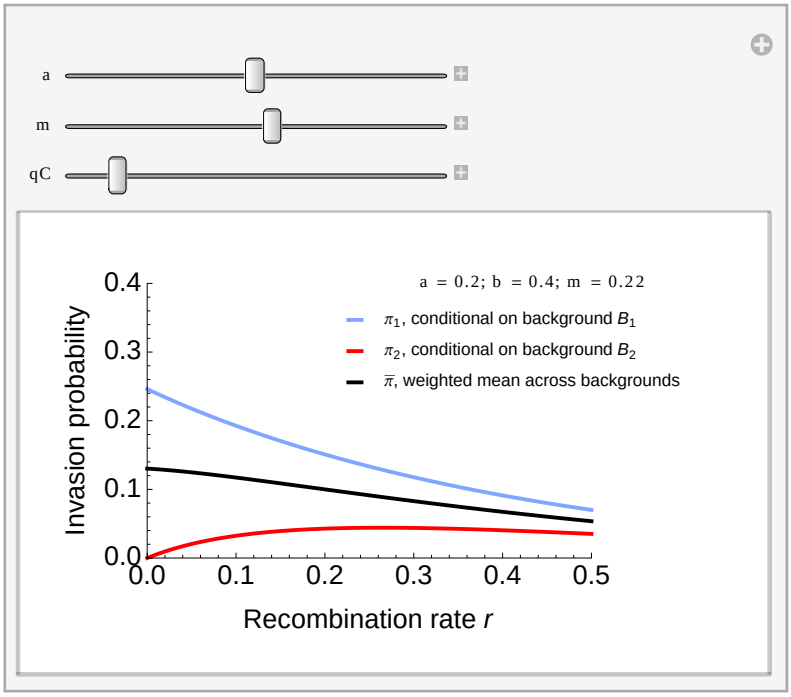
```
Manipulate[
 Show[Plot[{probEstablAMApproxPolymContFunc[r, m, a, myb2, myγ112, myγ122, myγ212,
       myγ222, qC][[2]], probEstablAMApproxPolymContFunc[
       r, m, a, myb2, myγ112, myγ122, myγ212, myγ222, qC][[3]],
     probEstablAMApproxPolymContFunc[r, m, a, myb2, myγ112, myγ122, myγ212, myγ222, 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["π1, conditional on background B1", FontFamily → "Helvetica"],
     Style["π2, conditional on background B2", FontFamily → "Helvetica"],
     Style["π̄, 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 → "Helvtica"]]
 ],
 {{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

In[115]:=
```
myb3 = 0.4;
myγ113 = 0.;
myγ123 = 0.;
myγ213 = 0.;
myγ223 = 0.;
rMax3 = 0.5;
```

```
Manipulate[
 Show[Plot[{probEstablAMApproxPolymContFunc[r, m, a, myb3, myγ113, myγ123, myγ213,
       myγ223, qC][[2]], probEstablAMApproxPolymContFunc[
       r, m, a, myb3, myγ113, myγ123, myγ213, myγ223, qC][[3]],
     probEstablAMApproxPolymContFunc[r, m, a, myb3, myγ113, myγ123, myγ213, myγ223, 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["π1, conditional on background B1", FontFamily → "Helvetica"],
     Style["π2, conditional on background B2", FontFamily → "Helvetica"],
     Style["π̄, 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[myb3] <> "; m = " <> ToString[m], FontFamily → "Helvtica"]]
 ],
 {{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

In[121]:=
```
myb4 = 0.4;
myγ114 = 0.;
myγ124 = 0.;
myγ214 = 0.;
myγ224 = 0.;
mMax4 = 0.6;
```

```
Manipulate[
 Show[Plot[{probEstablAMApproxPolymContFunc[r, m, a, myb4, myγ114, myγ124, myγ214,
       myγ224, qC][[2]], probEstablAMApproxPolymContFunc[
       r, m, a, myb4, myγ114, myγ124, myγ214, myγ224, qC][[3]],
    probEstablAMApproxPolymContFunc[r, m, a, myb4, myγ114, myγ124, myγ214, myγ224, 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["π1, conditional on background B1", FontFamily → "Helvetica"],
     Style["π2, conditional on background B2", FontFamily → "Helvetica"],
     Style["π̄, 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[myb4] <> "; r = " <> ToString[r], FontFamily → "Helvtica"]]
 ],
 {{a, 0.2}, 0., myb4}, {{r, 0.1}, 0., 0.5}, {{qC, 0.1}, 0., 1.}]
```