

Deterministic analysis of a diploid two-locus continent-island model in discrete time

```
In[1]:= Needs["PlotLegends`"]
```

```
General::obspkg :
```

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

Monomorphic continent

We first study the case where the continent is fixed for the continent haplotype $A_2 B_2$, i.e. $c[i] = 0$ for $i \neq 4$ and $c[i] = 1$ for $i = 4$. In terms of allele frequencies, this means that $p_c = 0$, $q_c = 0$, where p_c and q_c are the frequencies of A_1 and B_1 on the continent, respectively.

```
In[2]:= ruleMonomorphContin := {pC -> 0, qC -> 0}
```

Remarks

- In the main text and the supporting information, we use m_B , m_C and m^* for the critical migration rates $m_{\text{crit},2}$, $m_{\text{crit},3}$ and $m_{\text{crit},5}$ used in this Mathematica Notebook, respectively.
- We are thankful to Ada Akerman (personal communication) for sharing an unpublished manuscript relevant for the analyses performed here. We refer to this manuscript as A2010.

Recursion equations

We focus on a specific fitness scheme, assuming that allelic effects interact additively both within and across loci. There is no epistasis and no dominance. We derive this from a more general parametrisation that allows for dominance.

■ Additive fitnesses with dominance

The matrix of relative fitnesses of the 16 possible two-locus genotypes, with deme-dependent coefficients of selection and dominance.

■ Relative fitness matrix

```
In[3]:= wDom[n_] :=
```

```
{ {1 + a[n] + b[n], 1 + a[n] + b[n] σ[n], 1 + b[n] + a[n] τ[n], 1 + b[n] σ[n] + a[n] τ[n]},  
  {1 + a[n] + b[n] σ[n], 1 + a[n] - b[n], 1 + b[n] σ[n] + a[n] τ[n], 1 - b[n] + a[n] τ[n]},  
  {1 + b[n] + a[n] τ[n], 1 + b[n] σ[n] + a[n] τ[n], 1 - a[n] + b[n], 1 - a[n] + b[n] σ[n]},  
  {1 + b[n] σ[n] + a[n] τ[n], 1 - b[n] + a[n] τ[n], 1 - a[n] + b[n] σ[n], 1 - a[n] - b[n]} }
```

```
wDom[1] // MatrixForm
```

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

For the case of epistasis, see Mathematica Notebook '120822_twoLocusContinentIslandDiscrete.nb' (internal use only).

■ Additive fitness scheme

■ Relative fitness matrix

```
In[4]:= assumeNoDom[n_] := {σ[n] → 0, τ[n] → 0};
```

```
In[5]:= wAdd[n_] := wDom[n] /. assumeNoDom[n]
```

```
wAdd[1] // MatrixForm
```

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

We simplify the notation to what is necessary for the time being, focussing on deme 1 (the island) only.

```
In[6]:= assumeOneDeme[x_[n_]] := {x[n] → x}
```

```
wAdd[1]
```

```
{ {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]} }
```

```
In[7]:= w := wAdd[1] /. assumeOneDeme[b[1]] /. assumeOneDeme[a[1]]
```

```
w // MatrixForm
```

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

■ Marginal and mean fitnesses

```
In[8]:= (* i: gamete *)
```

```
wMarg[i_] := Sum[w[[i, j]] * x[j], {j, 1, 4}]
```

```
w1 = wMarg[1]
```

```
(1 + a + b) x[1] + (1 + a) x[2] + (1 + b) x[3] + x[4]
```

```
w2 = wMarg[2]
```

```
(1 + a) x[1] + (1 + a - b) x[2] + x[3] + (1 - b) x[4]
```

```
In[9]:= wMean := Sum[wMarg[i] x[i], {i, 1, 4}]
```

```
wMean
```

```
x[1] ((1 + a + b) x[1] + (1 + a) x[2] + (1 + b) x[3] + x[4]) +  
  x[3] ((1 + b) x[1] + x[2] + (1 - a + b) x[3] + (1 - a) x[4]) +  
  x[2] ((1 + a) x[1] + (1 + a - b) x[2] + x[3] + (1 - b) x[4]) +  
  x[4] (x[1] + (1 - b) x[2] + (1 - a) x[3] + (1 - a - b) x[4])
```

```
In[10]:= simplGamNot[i_] := x[i] → ToExpression[ToString[x] <> ToString[i]]
```

```
wbar = wMean /. Table[simplGamNot[i], {i, 1, 4}]
```

```
x1 ((1 + a + b) x1 + (1 + a) x2 + (1 + b) x3 + x4) + x3 ((1 + b) x1 + x2 + (1 - a + b) x3 + (1 - a) x4) +  
  x2 ((1 + a) x1 + (1 + a - b) x2 + x3 + (1 - b) x4) + x4 (x1 + (1 - b) x2 + (1 - a) x3 + (1 - a - b) x4)
```

■ Migration matrix

```
In[11]:= M := {1 - m[1], m[1]}
```

■ Helper variables

```
In[12]:= δ := {1, -1, -1, 1} (* Recombination *)
```

```
μ := {0, 0, 1, 1} (* Migration *)
```

■ Recursions

■ Relationship between gamete frequencies and allele frequencies and linkage disequilibrium

```
In[14]:= (* Linkage disequilibrium *)
LD := x[1] x[4] - x[2] x[3]
(* Allele frequency of A1 *)
P := {x[1] + x[2]}
(* Allele frequency of B1 *)
Q := {x[1] + x[3]}
```

```
In[17]:= (* Transformation from haplotype frequencies to allele frequencies and LD *)
toAlFreqRule := {x[1] → p q + DD, x[2] → p (1 - q) - DD, x[3] → (1 - p) q - DD,
  x[4] → (1 - p) (1 - q) + DD, c[1] → 0, c[2] → 0, c[3] → qC, c[4] → 1 - qC}
```

■ Recursion equations in terms of haplotype frequencies

w // MatrixForm

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

```
In[18]:= (* i: gamete *)
recHap[i_] := M[[1]] * (x[i] * wMarg[i] - δ[[i]] * r * LD * w[[1, 4]]) / wMean + μ[[i]] * M[[2]] * c[i]
recHap[#] & /@ {1, 2, 3, 4} // MatrixForm
```

$$\begin{pmatrix} \frac{(1-m[1]) (x[1] ((1+a+b) x[1] + (1+a) x[2] + (1+b) x[3] + x[4]) - r (-x[2] : \\ x[1] ((1+a+b) x[1] + (1+a) x[2] + (1+b) x[3] + x[4]) + x[3] ((1+b) x[1] + x[2] + (1-a+b) x[3] + (1-a) x[4]) + x[2] ((1+a) x[1] + (1+a-b) \\ (1-m[1]) (x[2] ((1+a) x[1] + (1+a-b) x[2] + x[3] + (1-b) x[4]) + r (-x[2] : \\ x[1] ((1+a+b) x[1] + (1+a) x[2] + (1+b) x[3] + x[4]) + x[3] ((1+b) x[1] + x[2] + (1-a+b) x[3] + (1-a) x[4]) + x[2] ((1+a) x[1] + (1+a-b) \\ (1-m[1]) (x[3] ((1+b) x[1] + x[2] + (1-a+b) x[3] + (1-a) x[4]) + r \\ x[1] ((1+a+b) x[1] + (1+a) x[2] + (1+b) x[3] + x[4]) + x[3] ((1+b) x[1] + x[2] + (1-a+b) x[3] + (1-a) x[4]) + x[2] ((1+a) x[1] + \\ (1-m[1]) (x[4] (x[1] + (1-b) x[2] + (1-a) x[3] + (1-a-b) x[4]) - r \\ x[1] ((1+a+b) x[1] + (1+a) x[2] + (1+b) x[3] + x[4]) + x[3] ((1+b) x[1] + x[2] + (1-a+b) x[3] + (1-a) x[4]) + x[2] ((1+a) x[1] + \end{pmatrix}$$

The constant c[i] above denotes the constant frequency of haplotype i on the continent.

Comparison to A2010 suggests this implementation is correct.

■ Recursion equations in terms of allele frequencies and linkage disequilibrium

```
In[19]:= simplMigNot[n_] := {m[n] → m}
```

```
In[20]:= recP := recHap[1] + recHap[2] /. toAlFreqRule /. simplMigNot[1] // FullSimplify
recQ := recHap[1] + recHap[3] /. toAlFreqRule /. simplMigNot[1] // FullSimplify
recD := recHap[1] * recHap[4] - recHap[2] * recHap[3] /. toAlFreqRule /. simplMigNot[1] //
  FullSimplify
recPQD := {recP, recQ, recD}
```

recP

$$- \frac{(-1+m) (p + a p^2 + b (DD + p (-1 + 2 q)))}{1 + a (-1 + 2 p) + b (-1 + 2 q)}$$

recQ

$$- \frac{(-1+m) (q + b q^2 + a (DD + (-1 + 2 p) q))}{1 + a (-1 + 2 p) + b (-1 + 2 q)} + m qC$$

recD

$$\begin{aligned} & - \left((-1+m) \left(a b DD^2 (-1+m) + p q \left(a^2 m p (-1+2 p) + m (1+b q) (1+b (-1+2 q)) + \right. \right. \right. \\ & \quad \left. \left. \left. a (m (-1+3 p) + b (-1+m+p-2 m p + q - 2 m q - p q + 5 m p q)) \right) \right) - \right. \\ & \quad \left. m p (1-b+a (-1+2 p) + 2 b q) (1+a p + b (-1+2 q)) qC + DD (1+a^2 p (-1+p+m p) - r + \right. \\ & \quad \left. a (-1+b m (-q+qC) + p (2+m (1+b (-1+4 q - 2 qC)) - 2 r) + r) + b (-1+b (1+m) q^2 + \right. \\ & \quad \left. (-1+b) m qC + q (2-b+m-2 b m qC - 2 r) + r) \right) / (1+a (-1+2 p) + b (-1+2 q))^2 \end{aligned}$$

recPQD

$$\left\{ -\frac{(-1+m)(p+a p^2+b(DD+p(-1+2q)))}{1+a(-1+2p)+b(-1+2q)}, -\frac{(-1+m)(q+b q^2+a(DD+(-1+2p)q))}{1+a(-1+2p)+b(-1+2q)} + m q C, \right. \\ \left. -\left((-1+m)\left(a b D D^2(-1+m)+p q\left(a^2 m p(-1+2p)+m(1+b q)(1+b(-1+2q))+ \right. \right. \right. \right. \\ \left. \left. \left. a(m(-1+3p)+b(-1+m+p-2mp+q-2mq-pq+5mpq))\right) - \right. \right. \\ \left. \left. m p(1-b+a(-1+2p)+2b q)(1+a p+b(-1+2q)) q C+D D\left(1+a^2 p(-1+p+m p)-r+ \right. \right. \right. \\ \left. \left. \left. a(-1+b m(-q+q C)+p(2+m(1+b(-1+4 q-2 q C))-2 r)+r)+b(-1+b(1+m) q^2+ \right. \right. \right. \\ \left. \left. \left. (-1+b) m q C+q(2-b+m-2 b m q C-2 r)+r\right)\right)\right) / (1+a(-1+2 p)+b(-1+2 q))^2 \left. \right\}$$

Again, the above recursion equations were checked against A2010.

Jacobian matrix

```
In[24]:= J := Table[Table[D[recPQD[[j]] /. ruleMonomorphContin, i] // FullSimplify, {i, {p, q, DD}}],
  {j, {1, 2, 3}}]
J // MatrixForm
```

$$\begin{pmatrix} \dots \\ -\frac{(-1+m)(mq(-1+b-2bq)^2(1+bq)+a^3(DD-2DDmp+2m(-1+p)p(-1+2p)q)+a^2(-4bDD^2(-1+m)+q(m+6m(-1+p)p+b(1-q+m(-1+2q+2p)q) \dots}{(1+a(-1+2p)+b(-1+2q))^2} \end{pmatrix}$$

Global assumptions and rules

The following global assumptions apply (on top of the assumption of no dominance and no epistasis):

- Fitnesses must be non-negative, hence $0 < a$, $0 < b$, $a + b < 1$.
- Selection on the B locus is at least as strong as selection on the A locus, hence $a < b$.
- To be biologically meaningful, the migration rate m must fulfil $0 < m < 1$.
- The recombination rate r must be positive and its maximum is $\frac{1}{2}$, hence $0 < r \leq 0.5$.

```
In[25]:= assumeGlobal := {0 < a < b < 1, a + b < 1, 0 < m < 1, 0 < r <= .5}
smallForcesRule := {a -> a e, b -> b e, m -> v e, r -> rho e}
rescaleSmallForcesRule := {a -> a/e, b -> b/e, v -> m/e, rho -> r/e}
```

Equilibria – existence, properties, stability

■ Monomorphic equilibria

- E_I : Only the island haplotype $A_1 B_1$ is present on the island (no migration)

This implies that there is no migration, $m = 0$.

The linkage disequilibrium is 0.

$$LD /. \{x[1] \rightarrow 1, x[2] \rightarrow 0, x[3] \rightarrow 0, x[4] \rightarrow 0\}$$

0

Hence, in terms of p , q and D , we have

```
In[28]:= assumeEI := {p -> 1, q -> 1, DD -> 0, m -> 0}
```

```
pEI = recP /. ruleMonomorphContin /. assumeEI // FullSimplify
```

1

```

qEI = recQ /. ruleMonomorphContin /. assumeEI // FullSimplify
1
DEI = recD /. ruleMonomorphContin /. assumeEI // FullSimplify
0
EI = {pEI, qEI, DEI}
{1, 1, 0}

```

Eigenvalues of the Jacobian, evaluated at E_I .

```
In[29]:= JEI := J /. assumeEI // FullSimplify
```

```
JEI // MatrixForm
```

$$\begin{pmatrix} \frac{1+b}{1+a+b} & 0 & \frac{b}{1+a+b} \\ 0 & \frac{1+a}{1+a+b} & \frac{a}{1+a+b} \\ 0 & 0 & \frac{1-r}{1+a+b} \end{pmatrix}$$

```
In[30]:= evalsEI = Eigenvalues[JEI] // FullSimplify
```

```
Out[30]= {
```

$$\left\{ \frac{1+a}{1+a+b}, \frac{1+b}{1+a+b}, \frac{1-r}{1+a+b} \right\}$$

All eigenvalues are always positive. The second eigenvalue is always the leading one, and it is always smaller than 1. Hence, the equilibrium E_I is asymptotically stable for $m = 0$.

- E_C : Only the continent haplotype $A_2 B_2$ is present on the island

The linkage disequilibrium is 0 in this case:

```
LD /. {x[1] -> 0, x[2] -> 0, x[3] -> 0, x[4] -> 1}
0
```

Hence, in terms of p , q and D , we have

```
In[31]:= assumeEC := {p -> 0, q -> 0, DD -> 0}
```

```

pEC = recP /. ruleMonomorphContin /. assumeEC // FullSimplify
0
qEC = recQ /. ruleMonomorphContin /. assumeEC // FullSimplify
0
DEC = recD /. ruleMonomorphContin /. assumeEC // FullSimplify
0
EC = {pEC, qEC, DEC}
{0, 0, 0}

```

Eigenvalues of the Jacobian, evaluated at E_C .

```
In[32]:= JEC := J /. assumeEC // FullSimplify
```

```
JEC // MatrixForm
```

$$\begin{pmatrix} -\frac{(-1+b)(-1+m)}{-1+a+b} & 0 & \frac{b(-1+m)}{-1+a+b} \\ 0 & -\frac{(-1+a)(-1+m)}{-1+a+b} & \frac{a(-1+m)}{-1+a+b} \\ 0 & 0 & -\frac{(-1+m)(-1+r)}{-1+a+b} \end{pmatrix}$$

```
In[33]:= evalsEC = Eigenvalues[JEC] // FullSimplify
```

```
Out[33]= {
```

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

The denominators of all eigenvalues are always negative, because we require $a + b < 1$ for all fitnesses to be non-negative. Moreover, the products in the numerator of all eigenvalues are always positive, since $a, b, m, r < 1$. From this, we conclude that all eigenvalues are always non-negative.

```
Simplify[Reduce[(-1 + a) (-1 + m) > (-1 + b) (-1 + m)], Assumptions -> assumeGlobal]
```

```
True
```

We further see that the second eigenvalue can never be the largest (since $a < b$), which implies that either the first or the third eigenvalue is the leading eigenvalue λ_0 . In the case of $a < r$, the first eigenvalue is the leading eigenvalue; in the case of $a > r$, the third is the leading one, and if $a = r$, the first and the third eigenvalue are both equal and the leading eigenvalues.

```
condStabEC1 = Simplify[Reduce[evalsEC[[1]] < 1 && evalsEC[[2]] < 1 && evalsEC[[3]] < 1, m, Reals], Assumptions -> assumeGlobal]
```

```
(m > b + a m && a < r) || (m + r > a + b + m r && r ≤ a)
```

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

```
{ {m -> -a - b + r / -1 + r} }
```

Thus, we need to distinguish two cases.

- Case $a < r$: strong recombination relative to selection on the A locus. Then, E_C is stable if and only if $m > m_{\text{crit},2} = \frac{b}{1-a} > m_{\text{crit},3} = \frac{a+b-r}{1-r}$.
- Case $a \geq r$: weak recombination relative to selection on the A locus. Then, E_C is stable if and only if $m > m_{\text{crit},3} = \frac{a+b-r}{1-r} > m_{\text{crit},2} = \frac{b}{1-a}$. Note that if $a = r$, we have $m_{\text{crit},2} = m_{\text{crit},3}$.

```
mCrit3
```

```
a + b - r / 1 - r
```

If one of the two sets of conditions is fulfilled, E_C is stable in the two-locus model. In any case, E_C is stable if and only if m is larger than a critical value.

Next, we test when the equilibrium E_C is non-hyperbolic. This is the case if (the real part of) at least one eigenvalue is equal to 1. In such cases, the stability of the equilibrium cannot be determined based on the Jacobian (higher-order derivatives are necessary). Parameter combinations for which $\lambda = 1$ holds deserve attention, because the equilibrium may change its stability properties, or enter or leave the state space.

```
In[34]:= nonHyperBoLEC = Simplify[Solve[evalsEC[[1]] == 1 || evalsEC[[2]] == 1 || evalsEC[[3]] == 1, m], Assumptions -> assumeGlobal]
```

```
Out[34]:= { {m -> -b / -1 + a}, {m -> -a / -1 + b}, {m -> a + b - r / 1 - r} }
```

We may therefore define three critical values of m :

```
In[35]:= mCrit1Rule := nonHyperBoLEC[[2]]; mCrit2Rule := nonHyperBoLEC[[1]]; mCrit3Rule := nonHyperBoLEC[[3]]
```

```
In[37]:= mCrit1 = m /. mCrit1Rule
```

```
Out[37]:= -a / -1 + b
```

```
In[38]:= mCrit2 = m /. mCrit2Rule
```

```
Out[38]:= -b / -1 + a
```

```
In[39]:= mCrit3 = m /. mCrit3Rule
```

```
Out[39]:= a + b - r / 1 - r
```

For these to be biologically meaningful (between 0 and 1), we require:

```
Simplify[0 < mCrit1 < 1, Assumptions -> assumeGlobal]
```

```
True
```

```
Simplify[0 < mCrit2 < 1, Assumptions → assumeGlobal]
True
Simplify[0 < mCrit3 < 1, Assumptions → assumeGlobal]
r < a + b
```

That is, given our global assumptions, $m_{\text{crit},1}$ and $m_{\text{crit},2}$ are always biologically valid, whereas $m_{\text{crit},3}$ is biologically valid if and only if $r < a + b$, i.e. if recombination is weak relative to selection at both loci.

Assuming $b > a$ as we do throughout, we may distinguish three subcases (recall from above that $m_{\text{crit},1} < m_{\text{crit},2}$ holds always):

```
Simplify[Reduce[mCrit1 < mCrit3], Assumptions → Flatten[{assumeGlobal, {b > a > r}}]]
True
```

1. $b > a$

1.1. If $r > b > a$, there holds $m_{\text{crit},2} > m_{\text{crit},1} > m_{\text{crit},3}$

1.2. If $b > r > a$, there holds $m_{\text{crit},2} > m_{\text{crit},3} > m_{\text{crit},1}$

1.3. If $b > a > r$, there holds $m_{\text{crit},3} > m_{\text{crit},2} > m_{\text{crit},1}$

■ Perturbation of eigenvalues of the Jacobian of E_1 at $m = 0$

We recall that if $m = 0$, and if A_1 and B_1 are both initially present, $E_1 = \{1, 1, 0\}$ is globally attracting (see above). We are interested in the the eigenvalues of the Jacobian evaluated at E_B as m is perturbed by a small amount from 0, i.e. in the case where $m > 0$, but small.

First, we realise that if $m = 0$, the eigenvalues become

```
evalsEBLim1 = FullSimplify[evalsEB /. m → 0, Assumptions → assumeGlobal]
{
   $\frac{-1 + a}{-1 + a - b}$ ,  $\frac{1 + b}{1 - a + b}$ ,  $\frac{-1 + r}{-1 + a - b}$ 
}
```

and that the second one is larger than 1 independently of m . Therefore, as m increases from 0, E_B starts out unstable.

```
FullSimplify[Map[Reduce[# < 1] &, evalsEBLim1], Assumptions → assumeGlobal]
{True, False, True}
```

```
evalsEBPert1 =
```

```
FullSimplify[Map[Series[#, {m, 0, 1}] &, evalsEB], Assumptions → assumeGlobal] // Normal
{
   $\frac{-1 + a}{-1 + a - b} + \frac{(-1 + a + 2b)m}{-1 + a - b}$ ,  $\frac{1 + b}{1 - a + b} + \frac{m(r + b r - a(b + 2r))}{(-1 + a - b)(b + r)}$ ,
   $\frac{-1 + r}{-1 + a - b} + \frac{m(-ab + b^2 + b r + (-1 + r)r)}{(-1 + a - b)(b + r)}$ 
}
```

```
FullSimplify[Map[Reduce[# < 1] &, evalsEBPert1], Assumptions → assumeGlobal]
```

```
{a + 2b == 1 || m < b + a m + 2 b m, a (b + b m + r + 2 m r) < (1 + b) m r,
 a b + r == b^2 + b r + r^2 || (a - b) b (1 + m) + (a + m - b (2 + m)) r < (1 + m) r^2}
```

We focus on the second element of the list above, which corresponds to the largest eigenvalue of E_B with $m = 0$.

```
FullSimplify[Reduce[a (b + b m + r + 2 m r) < (1 + b) m r && m < mCrit5, m],
  Assumptions → assumeGlobal]
False
```

We conclude that as m is slightly perturbed away from 0 into the positive range, the previously dominant eigenvalue > 1 increases further, implying that E_B stays unstable as m is perturbed away from 0 by a small amount.

■ Marginal one-locus equilibria

■ E_A : One-locus polymorphism at the A locus

This equilibrium is given by $E_A = \{p_A, 0, 0\}$, where we exclude the special case of $p_A = 0$ that corresponds to E_C . Notice that in A2010 p_4 is used instead of p_A . Solving the recursion equations under these restrictions, we have

In[40]:= `soleA = Solve[{recP /. ruleMonomorphContin /. {q -> 0, DD -> 0}} == p, p]`

Out[40]:= $\left\{ \{p \rightarrow 0\}, \left\{ p \rightarrow \frac{a - m + b m}{a (1 + m)} \right\} \right\}$

In[41]:= `pEA = p /. soleA[[2]]`

Out[41]=
$$\frac{a - m + b m}{a (1 + m)}$$

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

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

This is in agreement with equation (20) in A2010.

In[42]:= `assumeEA = {p -> pEA, q -> 0, DD -> 0}`

Out[42]= $\left\{ p \rightarrow \frac{a - m + b m}{a (1 + m)}, q \rightarrow 0, DD \rightarrow 0 \right\}$

In[43]:= `qEA = recQ /. ruleMonomorphContin /. assumeEA`

Out[43]= 0

In[44]:= `DEA = recD /. ruleMonomorphContin /. assumeEA`

Out[44]= 0

For $m \rightarrow 0$, $p_A \rightarrow 1$.

`pEA /. m -> 0`

1

We define

In[45]:= `EA = {pEA, qEA, DEA}`

Out[45]= $\left\{ \frac{a - m + b m}{a (1 + m)}, 0, 0 \right\}$

Eigenvalues of the Jacobian, evaluated at E_A .

`JEA = J /. assumeEA // FullSimplify;`

`JEA // MatrixForm`

$$\begin{pmatrix} \frac{-1+b+2 a m+(-1+b) m^2}{(1+a-b) (-1+m)} & \frac{2 b m (a+(-1+b) m)}{a (1+a-b) (-1+m)} & \frac{b (1+m)}{1+a-b} \\ 0 & \frac{1+a-(1+a-2 b) m}{1+a-b} & \frac{a (1+m)}{1+a-b} \\ 0 & \frac{m (a+(-1+b) m)}{a (1+m)} & \frac{(1+m) (-1+r)}{-1-a+b} \end{pmatrix}$$

`evalsEA = Eigenvalues[JEA] // FullSimplify`

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

`Solve[evalsEA[[1]] == 1, m]`

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

`Solve[evalsEA[[2]] == 1, m]`

$$\left\{ \{m \rightarrow -1\}, \left\{ m \rightarrow \frac{b(a-b+r)}{-ab+b^2+r+ar-2br} \right\} \right\}$$

`Solve[evalsEA[[3]] == 1, m]`

$$\left\{ \{m \rightarrow -1\}, \left\{ m \rightarrow \frac{b(a-b+r)}{-ab+b^2+r+ar-2br} \right\} \right\}$$

From the above, we see that E_A is not hyperbolic if $m = \frac{a}{1-b} = m_{\text{crit},1}$ and if $m = \frac{b(a-b+r)}{-ab+b^2+r+ar-2br} = \frac{b(a-b+r)}{(b-r)(b-a)+r(1-b)} := m_{\text{crit},4}$.

$$\text{In[46]:= } m_{\text{Crit4}} := \frac{b(a-b+r)}{(b-r)(b-a)+r(1-b)};$$

If $m = m_{\text{crit},1}$, we have $E_A = E_C$.

`EA /. {m -> mCrit1} // FullSimplify`

$$\{0, 0, 0\}$$

If $m = m_{\text{crit},4}$, we have $p_A = \frac{(b-a)(b-r)}{ar}$. Given $b > a$, this p_A is in the biologically valid state space if $b > r \neq 0$, which corresponds to the above subcases 1.2 and 1.3.

`EA /. {m -> mCrit4} // FullSimplify`

$$\left\{ -\frac{(a-b)(b-r)}{ar}, 0, 0 \right\}$$

Since we require $b > r$, the denominator of $m_{\text{crit},4}$ is positive. Moreover, the numerator is positive only if $b < a + r$. See A2010 (p. 9) for further discussion of this equilibrium and a perturbation analysis (which we do not need here).

■ E_B : One-locus polymorphism at the B locus

This equilibrium is given by $E_B = \{0, q_B, 0\}$, where we exclude the special case of $q_B = 0$ that corresponds to E_C . Notice that in A2010 q_B is used instead of q_B . Solving the recursion equations under these restrictions, we have

`In[47]:= soleB = Solve[{recQ /. ruleMonomorphContin /. {p -> 0, DD -> 0}] == q, q]`

$$\text{Out[47]= } \left\{ \{q \rightarrow 0\}, \left\{ q \rightarrow \frac{b-m+a m}{b(1+m)} \right\} \right\}$$

`In[48]:= qEB = q /. soleB[[2]]`

$$\text{Out[48]= } \frac{b-m+a m}{b(1+m)}$$

This is in agreement with equation (22) in A2010.

`In[49]:= assumeEB = {p -> 0, q -> qEB, DD -> 0}`

$$\text{Out[49]= } \left\{ p \rightarrow 0, q \rightarrow \frac{b-m+a m}{b(1+m)}, DD \rightarrow 0 \right\}$$

`In[50]:= pEB = recP /. ruleMonomorphContin /. assumeEB`

`Out[50]= 0`

`In[51]:= DEB = recD /. ruleMonomorphContin /. assumeEB`

`Out[51]= 0`

For $m \rightarrow 0$, $q_B \rightarrow 1$, i.e. E_B merges with E_I .

`qEB /. m -> 0`

1

We define

In[52]:= **EB = {pEB, qEB, DEB}**

$$\text{Out[52]} = \left\{ 0, \frac{b - m + a m}{b (1 + m)}, 0 \right\}$$

FullSimplify[Reduce[0 < qEB < 1, m], Assumptions → assumeGlobal]

$$m < b + a m$$

Thus, E_B represents a biologically valid one-locus polymorphism if and only if $m < m_{\text{crit},2} = \frac{b}{1-a}$.

Eigenvalues of the Jacobian, evaluated at E_B :

In[53]:= **JEB = J /. assumeEB // FullSimplify;**

In[54]:= **JEB // MatrixForm**

Out[54]//MatrixForm=

$$\begin{pmatrix} \frac{1+b-(1-2a+b)m}{1-a+b} & 0 & \frac{b(1+m)}{1-a+b} \\ -\frac{2am(b+(-1+a)m)}{(-1+a-b)b(-1+m)} & \frac{1-2bm+m^2-a(1+m^2)}{(-1+a-b)(-1+m)} & \frac{a(1+m)}{1-a+b} \\ \frac{m(b+(-1+a)m)}{b(1+m)} & 0 & \frac{(1+m)(-1+r)}{-1+a-b} \end{pmatrix}$$

In[55]:= **evalsEB = Eigenvalues[JEB] // FullSimplify**

$$\text{Out[55]} = \left\{ \frac{1 - 2bm + m^2 - a(1 + m^2)}{(-1 + a - b)(-1 + m)}, \frac{1}{2(-1 + a - b)} \right. \\ \left. \left(-2 - b + r + m(-2a + b + r) - \sqrt{1 + m} \sqrt{b^2(1 + m) - 2b(-1 + m)r + r(r + m(-4 + 4a + r))} \right), \right. \\ \left. \frac{1}{2(-1 + a - b)} \right. \\ \left. \left(-2 - b + r + m(-2a + b + r) + \sqrt{1 + m} \sqrt{b^2(1 + m) - 2b(-1 + m)r + r(r + m(-4 + 4a + r))} \right) \right\}$$

The third eigenvalue is always smaller than the second one. However, any of these eigenvalues can have an absolute real part larger than one.

Equilibrium E_B is not hyperbolic (and may therefore change equilibrium properties or enter/leave the state space) if at least one of the eigenvalues is 1:

Solve[evalsEB[[1]] == 1, m]

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

Solve[evalsEB[[2]] == 1, m]

$$\left\{ \{m \rightarrow -1\}, \left\{ m \rightarrow \frac{-a^2 + ab + ar}{a^2 - ab + r - 2ar + br} \right\} \right\}$$

Solve[evalsEB[[3]] == 1, m]

$$\left\{ \{m \rightarrow -1\}, \left\{ m \rightarrow \frac{-a^2 + ab + ar}{a^2 - ab + r - 2ar + br} \right\} \right\}$$

From the above, we see that E_B is not hyperbolic if $m = \frac{b}{1-a} = m_{\text{crit},2}$ and if $m = \frac{a(b-a+r)}{a^2-ab+r-2ar+br} = \frac{a(b-a+r)}{(a-b)(a-r)+r(1-a)} := m_{\text{crit},5}$. Recall that E_B exists if and only if $m < m_{\text{crit},2}$.

In[56]:= **mCrit5 := $\frac{a(b-a+r)}{(a-r)(a-b)+r(1-a)}$;**

If $m = m_{\text{crit},2}$, we have $E_B = E_C$.

EB /. {m → mCrit2} // FullSimplify

$$\{0, 0, 0\}$$

If $m = m_{\text{crit},5}$, we have $q_B = \frac{(a-b)(a-r)}{br}$. Given $b > a$, this q_B is in the biologically valid state space if $a < r$, b , which corresponds to

subcases 1.1 and 1.2 above.

EB /. {m → mCrit5} // FullSimplify

$$\left\{ 0, \frac{(a-b)(a-r)}{br}, 0 \right\}$$

In[57]= **qEBmCrit5 :=**
$$\frac{(a-b)(a-r)}{br}$$

If we require $r > a$ (and therefore that $\left\{ 0, \frac{(a-b)(a-r)}{br}, 0 \right\}$ is a biologically valid one-locus equilibrium and non-hyperbolic), the denominator of $m_{\text{crit},5}$ is positive. Moreover, the numerator is always positive for $r > a$. We suspect that E_B bifurcates at $m = m_{\text{crit},5}$, giving rise to a fully polymorphic (internal) equilibrium E_{\pm} that may or may not be asymptotically stable. We perform a perturbation analysis of $E_B = \{p_B, q_B, D_B\} = \left\{ 0, \frac{(a-b)(a-r)}{br}, 0 \right\}$ where the migration rate m slightly deviates from $m_{\text{crit},5}$ and is given by $m = m_{\text{crit},5} - \zeta \nu$, with $\zeta > 0$ small, and ν a constant.

■ Perturbation of E_B : approximation of an internal equilibrium E_{\pm}

We perform a perturbation analysis of E_B assuming that m is close to but smaller than $m_{\text{crit},5} < m_{\text{crit},2}$. We assume $m = m_{\text{crit},5} - \zeta \nu$ with $\zeta > 0$ but small and ν a positive constant. We also assume that linkage disequilibrium D is of order ζ . Note that this is not a regular perturbation analysis, because for $\zeta = 0$, the marginal equilibrium E_B is not hyperbolic.

EB

$$\left\{ 0, \frac{b-m+a m}{b(1+m)}, 0 \right\}$$

qEB

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

In[58]= **rulePerturb2 := {m → mCrit5 - ζ ν}**

recP /. ruleMonomorphContin

$$\frac{(-1+m)(p+a p^2+b(DD+p(-1+2q)))}{1+a(-1+2p)+b(-1+2q)}$$

recQ /. ruleMonomorphContin

$$\frac{(-1+m)(q+b q^2+a(DD+(-1+2p)q))}{1+a(-1+2p)+b(-1+2q)}$$

recD /. ruleMonomorphContin

$$\begin{aligned} & - \left((-1+m) \left(a b D D^2 (-1+m) + p q \left(a^2 m p (-1+2p) + m(1+bq)(1+b(-1+2q)) + \right. \right. \right. \\ & \quad \left. \left. \left. a(m(-1+3p)+b(-1+m+p-2mp+q-2mq-pq+5mpq)) \right) + \right. \right. \\ & \quad \left. \left. DD(1+a^2p(-1+p+mp)-r+b(-1+b(1+m)q^2+q(2-b+m-2r)+r) + \right. \right. \\ & \quad \left. \left. \left. a(-1-bmq+p(2+m(1+b(-1+4q))-2r)+r) \right) \right) \right) / (1+a(-1+2p)+b(-1+2q))^2 \end{aligned}$$

recP /. ruleMonomorphContin /. rulePerturb2 // FullSimplify

$$\frac{(p+a p^2+b(DD+p(-1+2q))) \left(-1 + \frac{a(-a+b+r)}{a^2+r+br-a(b+2r)} - \zeta \nu \right)}{1+a(-1+2p)+b(-1+2q)}$$

recQ /. ruleMonomorphContin /. rulePerturb2 // FullSimplify

$$\frac{(q+b q^2+a(DD+(-1+2p)q)) \left(-1 + \frac{a(-a+b+r)}{a^2+r+br-a(b+2r)} - \zeta \nu \right)}{1+a(-1+2p)+b(-1+2q)}$$

```
recD /. ruleMonomorphContin /. rulePerturb2 // FullSimplify
```

$$\begin{aligned}
& - \left(\left(-1 + \frac{a(-a+b+r)}{a^2+r+br-a(b+2r)} - \zeta v \right) \left(abDD^2 \left(-1 + \frac{a(-a+b+r)}{a^2+r+br-a(b+2r)} - \zeta v \right) \right. \right. \\
& \quad \left. \left. + DD \left(1 - r + a^2 p \left(-1 + \frac{(1-a+b)pr}{a^2+r+br-a(b+2r)} - p\zeta v \right) \right) \right. \right. \\
& \quad \left. \left. + b \left(-1 + r + bq^2 \left(1 + \frac{a(-a+b+r)}{a^2+r+br-a(b+2r)} - \zeta v \right) + q \left(2 - b - 2r + \right. \right. \right. \right. \\
& \quad \left. \left. \left. \frac{a(-a+b+r)}{a^2+r+br-a(b+2r)} - \zeta v \right) \right) \right) + a \left(-1 + r - bq \left(\frac{a(-a+b+r)}{a^2+r+br-a(b+2r)} - \zeta v \right) \right) + \\
& \quad \left. p \left(2 - 2r + (1+b(-1+4q)) \left(\frac{a(-a+b+r)}{a^2+r+br-a(b+2r)} - \zeta v \right) \right) \right) \right) + \\
& \quad pq \left(a^2 p (-1+2p) \left(\frac{a(-a+b+r)}{a^2+r+br-a(b+2r)} - \zeta v \right) + (1+bq)(1+b(-1+2q)) \right. \\
& \quad \left. \left(\frac{a(-a+b+r)}{a^2+r+br-a(b+2r)} - \zeta v \right) - \right. \\
& \quad \left. \left(a \left((1+b)r(b(-1+p)(-1+q) + (-1+b+3p-2bp+b(-2+5p)q)\zeta v \right) + \right. \right. \\
& \quad \left. \left. a \left(b - 2b^2 - 3bp + 3b^2p + 3b^2q - 6b^2pq + r - 3br - 3pr + 4bpr + \right. \right. \right. \\
& \quad \left. \left. \left. 4bqr - 7bpqr - (-1+b+3p-2bp+b(-2+5p)q)(b+2r)\zeta v \right) + \right. \right. \\
& \quad \left. \left. a^2 \left((-1+3p)(1+\zeta v) + b(2-3p-3q+6pq+(1-2p-2q+5pq)\zeta v) \right) \right) \right) \right) / \\
& \quad \left. \left(a^2 + r + br - a(b+2r) \right) \right) \Big/ (1 + a(-1+2p) + b(-1+2q))^2
\end{aligned}$$

```
In[59]:= pSer := p0 + p1 \xi (**p2 \xi^2*);
```

```
In[60]:= qSer := q0 + q1 \xi (**q2 \xi^2*);
```

```
In[61]:= DDSer := D0 + D1 \xi (**D2 \xi^2*);
```

```
p - recP /. ruleMonomorphContin /. rulePerturb2 /. {p -> pSer} /. {q -> qSer} /. {DD -> DDSer};
(* Remove ';' to display *)
```

```
In[62]:= Clear[f1]
```

```
f1[\xi_] :=
```

```
Evaluate[p - recP /. ruleMonomorphContin /. rulePerturb2 /. {p -> pSer} /. {q -> qSer} /.
{DD -> DDSer}]
```

```
q - recQ /. ruleMonomorphContin /. rulePerturb2 /. {q -> qSer} /. {p -> pSer} /. {DD -> DDSer};
(* Remove ';' to display *)
```

```
In[64]:= Clear[f2]
```

```
f2[\xi_] :=
```

```
Evaluate[q - recQ /. ruleMonomorphContin /. rulePerturb2 /. {q -> qSer} /. {p -> pSer} /.
{DD -> DDSer}]
```

```
DD - recD /. ruleMonomorphContin /. rulePerturb2 /. {DD -> DDSer} /. {p -> pSer} /.
{q -> qSer}; (* Remove ';' to display *)
```

```
In[66]:= Clear[f3]
```

```
f3[\xi_] :=
```

```
Evaluate[DD - recD /. ruleMonomorphContin /. rulePerturb2 /. {DD -> DDSer} /. {p -> pSer} /.
{q -> qSer}]
```

Taylor series to the three functions above:

```
Series[f1[\xi], {\xi, 0, 2}] // Simplify; (* Remove ';' to display *)
```

```
Series[f2[\xi], {\xi, 0, 2}] // Simplify; (* Remove ';' to display *)
```

```
Series[f3[\xi], {\xi, 0, 2}] // Simplify; (* Remove ';' to display *)
```

qEBmCrit5

$$\frac{(a-b)(a-r)}{br}$$

We consider the zeroth order term and check if by plugging in the equilibrium E_B at $m_{\text{crit},5}$ we obtain zero.

qEBmCrit5

$$\frac{(a-b)(a-r)}{br}$$

```
SeriesCoefficient[f1[ξ], {ξ, 0, 0}] /. {p0 → 0, q0 → qEBmCrit5, D0 → 0}
SeriesCoefficient[f2[ξ], {ξ, 0, 0}] /. {p0 → 0, q0 → qEBmCrit5, D0 → 0} // FullSimplify
SeriesCoefficient[f3[ξ], {ξ, 0, 0}] /. {p0 → 0, q0 → qEBmCrit5, D0 → 0} // FullSimplify
0
0
0
```

We can now consider the coefficients of the second-order terms appearing in the approximations to $f_1(\zeta)$, $f_2(\zeta)$ and $f_3(\zeta)$, after plugging in the zeroth-order terms (the equilibrium E_B).

```
SeriesCoefficient[f1[ξ], {ξ, 0, 1}] /. {p0 → 0, q0 → qEBmCrit5, D0 → 0} // FullSimplify
SeriesCoefficient[f2[ξ], {ξ, 0, 1}] /. {p0 → 0, q0 → qEBmCrit5, D0 → 0} // FullSimplify
SeriesCoefficient[f3[ξ], {ξ, 0, 1}] /. {p0 → 0, q0 → qEBmCrit5, D0 → 0} // FullSimplify
```

$$\frac{-a^2 p_1 + a b p_1 - b D_1 r}{a^2 + r + b r - a (b + 2 r)}$$

$$\frac{(-(-1+a-b)(a-b)q_1(a-r)r^2 + 1/b(a r(-2a^2(a-b)^2 p_1 + 2a(a-b)(2a p_1 - b(D_1 + p_1))r - (b(1-3a+b)D_1 + 2a(a-b)p_1)r^2) - (a-b)(a-r)(a^2 + r + b r - a(b+2r))^2 v)}{(r(2a^2 - 2ab + r - 3ar + br)(a^2 + r + b r - a(b+2r)))}$$

$$\frac{(a-r)(-a+b+r)(-a^2 p_1 + a b p_1 - b D_1 r)}{b r (a^2 + r + b r - a (b + 2 r))}$$

We are interested in p_1 and q_1 such that the two coefficients above are equal to 0, which amounts to solving a two-dimensional system of equations. In fact, the first coefficient is independent of q_1 .

$$p1Sol = \text{Solve}\left[\frac{-a^2 p_1 + a b p_1 - b D_1 r}{a^2 + r + b r - a (b + 2 r)} = 0, p_1\right]$$

$$\left\{\left\{p_1 \rightarrow -\frac{b D_1 r}{a (a - b)}\right\}\right\}$$

$$D1Sol = \text{Solve}\left[\frac{(a-r)(-a+b+r)(-a^2 p_1 + a b p_1 - b D_1 r)}{b r (a^2 + r + b r - a (b + 2 r))} = 0, D_1\right] // \text{FullSimplify}$$

$$\left\{\left\{D_1 \rightarrow \frac{a(-a+b)p_1}{b r}\right\}\right\}$$

q1Sol =

$$\text{FullSimplify}\left[\text{Solve}\left[\frac{(-(-1+a-b)(a-b)q_1(a-r)r^2 + 1/b(a r(-2a^2(a-b)^2 p_1 + 2a(a-b)(2a p_1 - b(D_1 + p_1))r - (b(1-3a+b)D_1 + 2a(a-b)p_1)r^2) - (a-b)(a-r)(a^2 + r + b r - a(b+2r))^2 v)}{(r(2a^2 - 2ab + r - 3ar + br)(a^2 + r + b r - a(b+2r)))} = 0 /. p1Sol, q1\right]\right]$$

$$\left\{\left\{q_1 \rightarrow \frac{a D_1 r (-1 - a + b + 2 r)}{(-1 + a - b)(a - b)(a - r)} + \frac{(a^2 + r + b r - a (b + 2 r))^2 v}{b (1 - a + b) r^2}\right\}\right\}$$

We develop $f_1(\zeta)$ into a Taylor series up to second order of ζ , plugging in what we know about p_0 , q_0 and D_0 .

```

f1Series2 =
  Normal[Series[f1[ξ], {ξ, 0, 2}] /. {p0 → 0, q0 → qEBmCrit5, D0 → 0}] // FullSimplify
- (ξ (2 a4 (p1 + p1 ξ v) + r2 (b D1 (1 + b - 2 b q1 ξ) + (1 + b) (p1 + b (D1 + p1)) ξ v) +
  a r (-b (p1 + b (2 D1 + p1) + 3 D1 r) - p1 (p1 + b (2 D1 + p1 + 2 q1)) r ξ -
  (b (b D1 + 3 (1 + b) p1) + 2 (b D1 + 2 (1 + b) p1) r) ξ v) -
  a3 p1 (4 b (1 + ξ v) + r (3 + 2 p1 ξ + 6 ξ v)) + a2 (2 b2 (p1 + p1 ξ v) +
  b r (2 (D1 + p1 (2 + p1 ξ)) + (D1 + 9 p1) ξ v) + p1 r (1 + p1 r ξ + (3 + 4 r) ξ v))) /
  ((2 a2 - 2 a b + r - 3 a r + b r) (a2 + r + b r - a (b + 2 r)))

```

We also develop $f_2(\zeta)$ into a Taylor series up to first order of ζ in an analogous way.

```

f2Series1 =
  Normal[Series[f2[ξ], {ξ, 0, 1}] /. {p0 → 0, q0 → qEBmCrit5, D0 → 0}] // FullSimplify
- (ξ (a6 v + a5 (2 p1 r - 3 b v - 5 r v) +
  a r2 (b (b (1 + b) q1 + (D1 + b D1 + q1 + 2 b q1) r) - (1 + b) (b + 3 b2 + r + 5 b r) v) +
  a3 (r (2 b2 p1 + b (2 D1 + 6 p1 + q1) r + 2 p1 r2) - (b3 + b (4 + 11 b) r + 6 (1 + 3 b) r2 + 4 r3) v) +
  a4 (-4 p1 r (b + r) + (3 b2 + 13 b r + 2 r (1 + 4 r)) v) +
  a2 r (-b r (q1 + 2 b (D1 + p1 + q1) + (3 D1 + 2 p1 + q1) r) +
  (3 b3 + r + 4 r2 + 2 b r (5 + 4 r) + b2 (2 + 13 r)) v) + b (1 + b) r3 (v + b (-q1 + v))) /
  (b r (2 a2 - 2 a b + r - 3 a r + b r) (a2 + r + b r - a (b + 2 r)))

```

Now, we plug our solution for D_1 into the term for $f_1(\zeta)$ [to second order of ζ] and into the term for $f_2(\zeta)$ [to first order of ζ].

```

T1 = {f1Series2, f2Series1} /. D1Sol // FullSimplify
{{{p1 ξ2 (a r (2 b (-a + b) q1 + ((1 - a + b) p1 + 2 b q1) r) - (a2 + r + b r - a (b + 2 r))2 v)} /
  ((2 a2 - 2 a b + r - 3 a r + b r) (a2 + r + b r - a (b + 2 r))),
  - ((a - b) ξ (r2 (-a3 p1 + b (1 + b) q1 r - a b q1 (1 + b + r) + a2 (b q1 + p1 (-1 + b + 2 r))) +
  (a - r) (a2 + r + b r - a (b + 2 r))2 v)} /
  (b r (2 a2 - 2 a b + r - 3 a r + b r) (a2 + r + b r - a (b + 2 r)))}}

```

We have got two equations [approximations to $f_1(\zeta)$ and $f_2(\zeta)$] in p_1 and q_1 that we now equate to (0, 0) and solve for p_1 and q_1 .

```

sol1 = Solve[T1 == 0, {p1, q1}] // FullSimplify

```

$$\left\{ \left\{ p_1 \rightarrow 0, q_1 \rightarrow \frac{(a^2 + r + b r - a (b + 2 r))^2 v}{b (1 - a + b) r^2} \right\}, \right. \\ \left. \left\{ p_1 \rightarrow \frac{(a - r) (a^2 + r + b r - a (b + 2 r))^2 v}{a r^2 (a (1 + a - b) - (1 + a + b) r)}, q_1 \rightarrow \frac{(a^2 + r + b r - a (b + 2 r))^2 v}{b r (a (-1 - a + b) + (1 + a + b) r)} \right\} \right\}$$

The first solution corresponds to the perturbed marginal equilibrium E_B and the second solution corresponds to the fully polymorphic (internal) equilibrium E_{\pm} that enters the state space via E_B at $m = m_{\text{crit},5}$. We find the first-order term of the linkage disequilibrium maintained at E_{\pm} by plugging p_1 into 'D1Sol'.

```

D1Sol

```

$$\left\{ \left\{ D_1 \rightarrow \frac{a (-a + b) p_1}{b r} \right\} \right\}$$

```

D1Sol2 = D1Sol /. sol1[[2]] // FullSimplify

```

$$\left\{ \left\{ D_1 \rightarrow \frac{(a - b) (a - r) (a^2 + r + b r - a (b + 2 r))^2 v}{b r^3 (a (-1 - a + b) + (1 + a + b) r)} \right\} \right\}$$

```

pSer

```

```

p0 + p1 ξ

```

```

qSer

```

```

q0 + q1 ξ

```

DDSer

D0 + D1 ζ

Overall, we find for E_{\pm} :

EInternApprox1 =

$$\{ \text{pSer, qSer, DDSer} \} /. \text{p0} \rightarrow 0 /. \text{q0} \rightarrow \text{qEBmCrit5} /. \text{D0} \rightarrow 0 /. \text{sol1}[[2]] /. \text{D1Sol2}$$

$$\left\{ \left\{ \frac{(a-r) (a^2+r+br-a(b+2r))^2 \zeta v}{a r^2 (a(1+a-b) - (1+a+b)r)}, \frac{(a-b)(a-r)}{br} + \frac{(a^2+r+br-a(b+2r))^2 \zeta v}{br(a(-1-a+b) + (1+a+b)r)}, \right. \right.$$

$$\left. \left. \frac{(a-b)(a-r) (a^2+r+br-a(b+2r))^2 \zeta v}{br^3(a(-1-a+b) + (1+a+b)r)} \right\} \right\}$$

which can be rearranged to

EInternApprox =

$$\left\{ \frac{(a-r) (a(a-b) + r(1+b-2a))^2 \zeta v}{a r^2 (a(1+a-b) - (1+a+b)r)}, \frac{(a-b)(a-r)}{br} + \frac{(a(a-b) + r(1+b-2a))^2 \zeta v}{br(a(-1-a+b) + (1+a+b)r)}, \right.$$

$$\left. \frac{(a-b)(a-r) (a(a-b) + r(1+b-2a))^2 \zeta v}{br^3(a(-1-a+b) + (1+a+b)r)} \right\}$$

$$\left\{ \frac{(a-r) (a(a-b) + (1-2a+b)r)^2 \zeta v}{a r^2 (a(1+a-b) - (1+a+b)r)}, \right.$$

$$\left. \frac{(a-b)(a-r)}{br} + \frac{(a(a-b) + (1-2a+b)r)^2 \zeta v}{br(a(-1-a+b) + (1+a+b)r)}, \frac{(a-b)(a-r) (a(a-b) + (1-2a+b)r)^2 \zeta v}{br^3(a(-1-a+b) + (1+a+b)r)} \right\}$$

EInternApprox - EInternApprox1[[1]] // FullSimplify

{0, 0, 0}

■ Stability analysis of E_B

■ Preliminaries

Recall our global assumptions:

assumeGlobal

{0 < a < b < 1, a + b < 1, 0 < m < 1, 0 < r ≤ 0.5}

Throughout, we assume that $0 < a < b < 1$ and $a + b < 1$ and $0 < m < 1$ and $0 < r < \frac{1}{2}$. Consider the marginal one-locus migration-

selection equilibrium $E_B = \{0, \hat{q}_B, 0\}$, with $\hat{q}_B = \frac{b-m(1-a)}{b(1+m)}$. Denote by J_{E_B} the Jacobian matrix belonging to E_B under the two-locus

dynamics. As shown before, E_B is not hyperbolic if m is equal to either -1 (in which case E_B is not defined), $m_{\text{crit},2} = \frac{b}{1-a}$ or

$m_{\text{crit},5} = \frac{a(b-a+r)}{(a-b)(a-r)+(1-a)r}$. This is found by equating the eigenvalues of J_{E_B} to 1 and solving for m .

We distinguish the following four cases:

δ

{1, -1, -1, 1}

■ Case 1: $r = a$

Then

i) $m_{\text{crit},5} = m_{\text{crit},3} = m_{\text{crit},2} = \frac{b}{1-a}$, and

ii) E_B is never asymptotically stable when it is a biologically valid one-locus polymorphism and hyperbolic.

Moreover, we conjecture that whenever E_B exists and is unstable, there exists a fully-polymorphic (internal) equilibrium E_{\pm} that is asymptotically stable.

Proof:

i) Follows trivially from inserting $a = r$ into the expressions for $m_{\text{crit},5}$ and $m_{\text{crit},3}$.

mCrit5

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

mCrit5

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

**Series[mCrit5 /. {a → α ε, b → β ε, r → ρ ε}, {ε, 0, 1}] /.
{α → a / ε, β → b / ε, ρ → r / ε} // Normal**

$$a - \frac{a^2}{r} + \frac{ab}{r}$$

mCrit5 /. r → a

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

mCrit3

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

mCrit3 /. r → a

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

mCrit2

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

ii) E_B represents a biologically valid one-locus polymorphism if $0 < \hat{q}_B = \frac{b-m(1-a)}{b(1+m)} < 1$. The numerator is always smaller than the denominator, hence $\hat{q}_B < 1$. The denominator is always positive. Therefore, $0 < \hat{q}_B$ if and only if the numerator is positive. The numerator is positive if and only if $m < \frac{b}{1-a}$. Therefore, E_B represents a biologically valid one-locus polymorphism whenever $m < \frac{b}{1-a} = m_{\text{crit},2}$.

For $0 < m < m_{\text{crit},2}$, E_B is always hyperbolic. It remains to show that the leading eigenvalue of J_{E_B} is smaller than 1 always if $m < m_{\text{crit},2}$.

FullSimplify[evalsEB /. m → mCrit2, Assumptions → Flatten[{assumeGlobal, r == a}]]

$$\left\{1, 1, \frac{-1+b}{-1+r}\right\}$$

Since $r = a$, the third eigenvalue is smaller than 1 but positive. We know that for $0 < m < m_{\text{crit},2}$, none of the eigenvalues is equal to one. Therefore, to show that E_B is not stable for $0 < m < m_{\text{crit},2}$, it suffices to show that either the first or the second eigenvalue increases starting from 1 as m is decreased from $m_{\text{crit},2}$. We perturb the first and second eigenvalue at $m = m_{\text{crit},2} - \zeta \nu$, where $\zeta > 0$ but small and ν is a positive constant.

**FullSimplify[Normal[Series[evalsEB[[1 ;; 2]] /. m → mCrit2 - ζ ν, {ζ, 0, 1}]],
Assumptions → Flatten[{assumeGlobal}]]**

$$\left\{1 - \frac{(-1+a)\zeta\nu}{-1+a+b}, \left\{ \begin{array}{l} \frac{-1+b}{-1+a} + \frac{(a(b-2r)+r+b(-b+r))\zeta\nu}{(-1+a-b)(b-r)} \quad b < r \\ \frac{-1+r}{-1+a} + \frac{(ab+r(-1-b+r))\zeta\nu}{(-1+a-b)(b-r)} \quad \text{True} \end{array} \right. \right\}$$

If, in addition, we replace r by a :

**FullSimplify[Normal[Series[evalsEB[[1 ;; 2]] /. r → a /. m → mCrit2 - ζ ν, {ζ, 0, 1}]],
Assumptions → Flatten[{assumeGlobal}]]**

$$\left\{1 - \frac{(-1+a)\zeta\nu}{-1+a+b}, \frac{b+b^2+a^2(1-\zeta\nu)+a(-1-2b+\zeta\nu)}{(-1+a-b)(a-b)}\right\}$$

We have obtained the perturbed eigenvalues and now subtract 1 from them.


```
FullSimplify[% - 1]
```

$$\left\{ -\frac{(-1+a)\xi v}{-1+a+b}, -\frac{(-1+a)a\xi v}{(-1+a-b)(a-b)} \right\}$$

The first difference is always negative, meaning that the first eigenvalue decreases from 1 as m decreases from $m_{\text{crit},2}$. The second difference is always positive, meaning that the second eigenvalue increases from 1 as m decreases from $m_{\text{crit},2}$. Therefore, ii) is proven.

```
FullSimplify[Map[Reduce[#, >, %],
  Assumptions -> Flatten[{assumeGlobal, 0 < xi < 1, 0 < v}]]]
{False, True}
```

■ Case 2: $r < \frac{a(b-a)}{1-2a+b}$

We realise that $\frac{a(b-a)}{1-2a+b} = a \frac{b-a}{1-2a+b}$ is always larger than a , because $b-a < 1-2a+b \Leftrightarrow 0 < 1-a$ holds always given our assumptions. Therefore, case 2 implies $r < a$. Then

i) $0 < m_{\text{crit},2} < m_{\text{crit},3}$;

ii) $m_{\text{crit},5} < 0 < m_{\text{crit},2}$;

iii) E_B is never asymptotically stable when it is a biologically valid one-locus polymorphism and hyperbolic.

We conjecture that whenever E_B exists and is unstable, there exists a fully-polymorphic (internal) equilibrium E_{\pm} that is asymptotically stable.

Proof:

i) Recall from case 1 that $m_{\text{crit},3} = m_{\text{crit},2}$ if $r = a$. We start with the Ansatz $r = a - \epsilon \rho$, where $\epsilon > 0$ is small and ρ is a positive constant.

Plugging this into $m_{\text{crit},3} = \frac{a+b-r}{1-r}$ and expanding $m_{\text{crit},3}(\epsilon)$ around $\epsilon = 0$ up to first order in ϵ yields $m_{\text{crit},3} \approx m_{\text{crit},2} + \frac{1-a-b}{(1-a)^2} \rho \epsilon$. Because

$\frac{1-a-b}{(1-a)^2} > 0$ always, $m_{\text{crit},3} > m_{\text{crit},2}$ follows. Given our assumptions, $0 < m_{\text{crit},2}$ holds always, which is trivial to show.

```
In[68]:= rStar := a (b - a) / (1 - 2 a + b)
mCrit2
- b / (-1 + a)
mCrit3
(a + b - r) / (1 - r)
Series[mCrit3 /. r -> a - epsilon rho, {epsilon, 0, 1}]
- b / (-1 + a) - ((-1 + a + b) rho epsilon) / ((-1 + a)^2) + O[epsilon]^2
```

ii) $0 < m_{\text{crit},2} = \frac{b}{1-a}$ follows directly from our assumptions. Further, we note that $m_{\text{crit},5}$ is not defined for $r = \frac{a(b-a)}{1-2a+b}$. To show that $m_{\text{crit},5} = \frac{a(b-a+r)}{(a-b)(a-r)+(1-a)r} < 0$, it suffices to show that either the numerator is negative and the denominator strictly positive, or that the numerator is positive and the denominator strictly negative. We note that the numerator is always positive under our assumptions. Some algebra shows that the denominator is negative if and only if our condition $r < \frac{a(b-a)}{1-2a+b}$ is fulfilled. Hence ii) is proven.

```
mCrit5
a (-a + b + r) / ((a - b) (a - r) + (1 - a) r)
FullSimplify[Reduce[a (-a + b + r) > 0], Assumptions -> assumeGlobal]
True
FullSimplify[Reduce[(a - b) (a - r) + (1 - a) r < 0, r], Assumptions -> assumeGlobal]
a^2 + r + b r < a (b + 2 r)
```

`Solve[a2 + r + b r == a (b + 2 r), r]`

$$\left\{ \left\{ r \rightarrow \frac{a^2 - a b}{-1 + 2 a - b} \right\} \right\}$$

iii) We have already proven for case 1 that E_B is a biologically valid polymorphic one-locus equilibrium if and only if $m < m_{\text{crit},2}$ and we know that E_B is always hyperbolic for $0 < m < m_{\text{crit},2}$ given $m_{\text{crit},5} < 0$. E_B is hyperbolic if $m = m_{\text{crit},2}$. We show that at the absolute value of at least one eigenvalue of the Jacobian J_{E_B} is never smaller than 1 as m is between 0 and $m_{\text{crit},2}$.

`FullSimplify[evalsEB /. {m -> mCrit2}, Assumptions -> Flatten[{assumeGlobal}]]`

$$\left\{ 1, \frac{-2 + b + r - \text{Abs}[b - r]}{2(-1 + a)}, \frac{-2 + b + r + \text{Abs}[b - r]}{2(-1 + a)} \right\}$$

As we assume $r < \frac{a(b-a)}{1-2a+b} < a$, this simplifies to

`FullSimplify[evalsEB /. {m -> mCrit2}, Assumptions -> Flatten[{assumeGlobal, {r < a}}]]`

$$\left\{ 1, \frac{-1 + r}{-1 + a}, \frac{-1 + b}{-1 + a} \right\}$$

The second eigenvalue is always larger than 1.

`FullSimplify[evalsEB /. {m -> 0}, Assumptions -> Flatten[{assumeGlobal, {r < a}}]]`

$$\left\{ \frac{-1 + a}{-1 + a - b}, \frac{1 + b}{1 - a + b}, \frac{-1 + r}{-1 + a - b} \right\}$$

Perturbing the second eigenvalue the second eigenvalue at $m = m_{\text{crit},2}$, assuming $m = m_{\text{crit},2} - \epsilon \nu$, we find

`FullSimplify[Normal[Series[evalsEB[[2]] /. {m -> mCrit2 - \epsilon \nu}, {\epsilon, 0, 1}]], Assumptions -> Flatten[{assumeGlobal, {r < a}}]]`

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

`Coefficient[%, \epsilon]`

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

`FullSimplify[Reduce[% > 0],`

`Assumptions -> Flatten[{assumeGlobal, {r < a (b - a) / (1 - 2 a + b)}, {0 < \nu}}]]`

False

The second eigenvalue decreases from $\frac{1-r}{1-a} > 1$ as m decreases from $m_{\text{crit},2}$, and as m reaches 0, it is given by $\frac{1+b}{1-a+b} > 1$. As E_B is never hyperbolic for $0 < m < m_{\text{crit},2}$, it follows that the second eigenvalue must never take the value 1, and hence be larger than 1 throughout. This proves iii).

■ Case 3: $\frac{a(b-a)}{1-2a+b} < r < a$

Then

i) $0 < m_{\text{crit},5}$;

ii) $0 < m_{\text{crit},2} < m_{\text{crit},3}$;

iii) $0 < m_{\text{crit},2} < m_{\text{crit},5}$;

iv) If $m = m_{\text{crit},5}$, then $\hat{q}_B = \frac{(a-b)(a-r)}{b r} \notin (0, 1)$;

v) E_B is unstable whenever it is biologically valid and not hyperbolic.

The same conjecture as in case 2 applies.

Proof:

i) We note that $m_{\text{crit},5}$ is not defined for $r = \frac{a(b-a)}{1-2a+b}$. To show that $m_{\text{crit},5} = \frac{a(b-a+r)}{(a-b)(a-r)+(1-a)r} > 0$, it suffices to show that either both the numerator and the denominator are strictly positive, or that both the numerator and the denominator are strictly negative. We note that the numerator is always positive under our assumptions. Some algebra shows that the denominator is positive if and only if our condition $r > \frac{a(b-a)}{1-2a+b}$ is fulfilled. Hence i) is proven.

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

ii) This is true whenever $r < a$ and has already been proven for case 2.

```
mCrit2
mCrit3
- b
- 1 + a
a + b - r
1 - r
```

iii) We have already shown in i) that $0 < m_{\text{crit},5}$ whenever $r > \frac{a(b-a)}{1-2a+b}$, and it is trivial to show that $0 < m_{\text{crit},2}$. From case 1, we recall that $m_{\text{crit},5} = m_{\text{crit},2}$ if $r = a$. We perturb $m_{\text{crit},5}$ at $r = a$, using $r = a - \epsilon \rho$, where $\epsilon > 0$ is small and ρ is a positive constant.

```
mCrit5
a (-a + b + r)
(a - b) (a - r) + (1 - a) r
mCrit2
- b
- 1 + a
mCrit5
a (-a + b + r)
(a - b) (a - r) + (1 - a) r
FullSimplify[Normal[Series[mCrit5 /. {r → a - ε ρ}, {ε, 0, 1}]],
  Assumptions → Flatten[{assumeGlobal}]]
- (-1 + a) a b + (-1 + a - b) (a - b) ε ρ
(-1 + a)² a
Collect[%, ε]
- b
- 1 + a
+ (-1 + a - b) (a - b) ε ρ
(-1 + a)² a
```

It is easily seen that the first-order term of ϵ is always positive, implying that $m_{\text{crit},5} > m_{\text{crit},2} + C \epsilon$, where C is a positive constant, as long as ϵ is small.

A direct check using Mathematica confirms this:

```
FullSimplify[Reduce[0 < mCrit2 < mCrit5, r], Assumptions → assumeGlobal]
a (a - b)
- 1 + 2 a - b < r < a
```

We have proven iii)

iv) If $r < a$, the nominator of $\hat{q}_B = \frac{(a-b)(a-r)}{br}$ is negative, which means that \hat{q}_B is not biologically valid.

v) Identical to step iii) of the proof for case 2.

■ Case 4: $r > a$

Then

i) $m_{\text{crit},3} < m_{\text{crit},2}$ and $0 < m_{\text{crit},3}$ if $a < r < a + b$;

ii) $0 < m_{\text{crit},5} < m_{\text{crit},2}$;

iii) If $m = m_{\text{crit},5}$, then $\hat{q}_B = \frac{(a-b)(a-r)}{br} \in (0, 1)$;

iv) E_B is unstable if $0 < m < m_{\text{crit},5}$;

v) E_B is asymptotically stable if $m_{\text{crit},5} < m < m_{\text{crit},2}$.

We conjecture that if $m < m_{\text{crit},5}$, then a fully-polymorphic (internal) equilibrium exists and is asymptotically stable and globally attracting.

Proof:

i) Recall from case 1 that $m_{\text{crit},3} = m_{\text{crit},2}$ if $r = a$. We start with the Ansatz $r = a + \epsilon \rho$, where $\epsilon > 0$ is small and ρ is a positive constant.

Plugging this into $m_{\text{crit},3} = \frac{a+b-r}{1-r}$ and expanding $m_{\text{crit},3}(\epsilon)$ around $\epsilon = 0$ up to first order in ϵ yields $m_{\text{crit},3} \approx m_{\text{crit},2} - \frac{1-a-b}{(1-a)^2} \rho \epsilon$. Because $\frac{1-a-b}{(1-a)^2} > 0$ always, $m_{\text{crit},3} < m_{\text{crit},2}$ follows. Moreover, trivial algebra shows that $m_{\text{crit},3} > 0$ holds whenever $r < a + b$.

mCrit2

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

mCrit3

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

Series[mCrit3 /. r -> a + \epsilon \rho, {\epsilon, 0, 1}]

$$-\frac{b}{-1+a} + \frac{(-1+a+b)\rho\epsilon}{(-1+a)^2} + O[\epsilon]^2$$

FullSimplify[Reduce[mCrit3 > 0], Assumptions -> Flatten[{assumeGlobal, {a < r}}]]

$r < a + b$

ii) Recall that $m_{\text{crit},5} = m_{\text{crit},2} = \frac{b}{1-a}$ if $r = a$. We perturb $m_{\text{crit},5}$ at $r = a$, using $r = a + \epsilon \rho$, where $\epsilon > 0$ is small and ρ is a positive constant and find that for small ϵ , $m_{\text{crit},5} = m_{\text{crit},2} - C \epsilon$, where C is a positive constant. This means that $m_{\text{crit},5} < m_{\text{crit},2}$ for $r > a$. Moreover, for $r > a$, $m_{\text{crit},5}$ is positive because then both the numerator and denominator are both positive.

mCrit3

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

mCrit5

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

FullSimplify[Normal[Series[mCrit5 /. {r -> a + \epsilon \nu}, {\epsilon, 0, 1}]], Assumptions -> Flatten[{assumeGlobal}]]

$$-\frac{(-1+a)ab + (-1+a-b)(a-b)\epsilon\nu}{(-1+a)^2a}$$

Coefficient[%, \epsilon]

$$-\frac{(-1+a-b)(a-b)\nu}{(-1+a)^2a}$$

which is always negative under our assumptions, implying that for small ϵ , $m_{\text{crit},5} = m_{\text{crit},2} - C \epsilon$, where C is a positive constant.

FullSimplify[Reduce[0 < mCrit5], Assumptions -> Flatten[{assumeGlobal, r > a}]]

True

iii) Follows trivially from $r > a$, because then both the numerator and denominator of $\hat{q}_B = \frac{(a-b)(a-r)}{br} = \frac{(b-a)(r-a)}{br}$ are positive (implying $\hat{q}_B > 0$) and the numerator is smaller than the denominator (implying $\hat{q}_B < 1$).

iv)

```
FullSimplify[evalsEB /. m -> mCrit5, Assumptions -> Flatten[{assumeGlobal, r > a}]]
```

$$\left\{ \left(2 a^2 (a-b)^2 - 2 a (a-b) (-1+3 a-b) r + (1+a (-4+5 a-3 b) + b) r^2 \right) / \left((2 a^2 - 2 a b + r - 3 a r + b r) (a^2 + r + b r - a (b+2 r)) \right), 1, \frac{a^2 - a b + r - r^2}{a^2 + r + b r - a (b+2 r)} \right\}$$

The second eigenvalue is 1 if $m = m_{\text{crit},5}$. In order to show that E_B is unstable whenever $0 < m < m_{\text{crit},5}$, it suffices to show that the second eigenvalue increases from 1 as m is perturbed away from $m_{\text{crit},5}$, using the Ansatz $m = m_{\text{crit},5} - \epsilon \nu$, where $\epsilon > 0$ is small and ν is a positive constant.

```
FullSimplify[Normal[Series[evalsEB[[2]] /. m -> mCrit5 - \epsilon \nu, {\epsilon, 0, 1}]], Assumptions -> Flatten[{assumeGlobal, r > a}]]
```

$$\frac{a^2 (2 + \epsilon \nu) + (1 + b) (b + r + r \epsilon \nu) - a (2 + 3 b + r + (b + 2 r) \epsilon \nu)}{(-1 + a - b) (-2 a + b + r)}$$

```
Collect[%, \epsilon]
```

$$\frac{-2 a + 2 a^2 - 3 a b + b (1 + b) - a r + (1 + b) r}{(-1 + a - b) (-2 a + b + r)} \epsilon + \frac{(a^2 \nu + (1 + b) r \nu - a (b + 2 r) \nu)}{(-1 + a - b) (-2 a + b + r)}$$

```
FullSimplify[- \frac{-2 a + 2 a^2 - 3 a b + b (1 + b) - a r + (1 + b) r}{(-1 + a - b) (-2 a + b + r)}]
```

```
1
```

So, we find that the second eigenvalue takes the form $1 - C \epsilon$ as m decreases from $m_{\text{crit},5}$ and ϵ is small, where $C = \frac{a^2 + r + b r - a(b+2r)}{(1-a+b)(2a-b-r)} \nu$. It can be shown (see Mathematica code below) that $C < 0$ always under our assumptions, which means that the second eigenvalue increases from 1 as m decreases from $m_{\text{crit},5}$. This proves iv).

```
const1 = FullSimplify[ \frac{(a^2 \nu + (1 + b) r \nu - a (b + 2 r) \nu)}{(-1 + a - b) (-2 a + b + r)} ]
```

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

```
FullSimplify[Reduce[const1 < 0], Assumptions -> Flatten[{assumeGlobal, r > a, 0 < \nu}]]
```

```
True
```

v) We perturb the eigenvalues of the Jacobian J_{E_B} at m close to $m_{\text{crit},2}$ using the Ansatz $m = m_{\text{crit},2} - \epsilon \nu$ with $\epsilon > 0$ small and ν a positive constant, and we show that all eigenvalues have magnitudes smaller than 1 for $\epsilon > 0$.

The eigenvalues of J_{E_B} at $m = m_{\text{crit},2}$ are given by

```
FullSimplify[evalsEB /. m -> mCrit2, Assumptions -> Flatten[{assumeGlobal, r > a}]]
```

$$\left\{ 1, \frac{-2 + b + r - \text{Abs}[b - r]}{2 (-1 + a)}, \frac{-2 + b + r + \text{Abs}[b - r]}{2 (-1 + a)} \right\}$$

It is easily seen that the second and third eigenvalues are positive, but smaller than 1 always under the assumptions of $a < b$ and $a < r$. All we need to show is that the first eigenvalue decreases from 1 as we perturb m away from $m_{\text{crit},2}$ according to $m = m_{\text{crit},2} - \epsilon \nu$, where $\epsilon > 0$ is small and ν is a positive constant. We find that then, the second eigenvalue is given by $1 - C \epsilon$, where $C = \frac{(1-a)}{1-a-b} \nu > 0$ and hence decreasing for small but positive ϵ . It follows that E_B is asymptotically stable for $m_{\text{crit},5} < m < m_{\text{crit},2}$. Note that a fully-polymorphic (internal) equilibrium may nevertheless exist and it may even be locally asymptotically stable. However, invasion of A_1 via E_B is impossible as long as $m_{\text{crit},5} < m$.

```
FullSimplify[Normal[Series[evalsEB[[1]] /. m -> mCrit2 - \epsilon \nu, {\epsilon, 0, 1}]], Assumptions -> Flatten[{assumeGlobal}]]
```

$$1 - \frac{(-1 + a) \epsilon \nu}{-1 + a + b}$$

Coefficient[%, ϵ]

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

■ Comment on the conjectures

Above, we have stated a number of conjectures concerning existence and (global) stability of a fully-polymorphic internal equilibrium. We could not prove them in the discrete-time version of the model. Bürger and Akerman (2011; additive fitness) and Bank et al. (2012; epistasis) have proven them for the continuous-time version, which our model converges to if evolutionary forces are weak. In fact, it can be shown that there may be up to two fully-polymorphic (internal) equilibria, but only one of them is asymptotically stable. If there is only one internal equilibrium, it is asymptotically stable. The analogy to the continuous-time model and numerical explorations (not shown) suggest that, whenever the marginal one-locus equilibrium E_B is unstable under the two-locus dynamics, a fully-polymorphic internal equilibrium exists that is globally attracting and stable.

■ Comment on Cases 1 to 3 and simplification of the overall statement

The conditions that define Cases 1 to 3 can be simplified to the condition $r \leq a$. As the main result for these three cases is the same, namely that E_B is always unstable under the two-locus dynamics when it is a valid one-locus polymorphism, we can simplify our overall statement as follows:

If $r \leq a$, E_B is unstable under the two-locus dynamics whenever it is a polymorphic marginal one-locus equilibrium. If $r > a$, E_B is asymptotically stable under the two-locus dynamics if and only if $m_{\text{crit},5} < m < m_{\text{crit},2}$. Then, invasion of A_1 via E_B is excluded. If, in the case of $r > a$, it holds that $0 < m < m_{\text{crit},5}$, then E_B is unstable under the two-locus dynamics whenever it is a valid marginal one-locus equilibrium. Based on Bürger and Akerman's (2011) results, we conjecture that whenever E_B exists under the one-locus dynamics ($m < m_{\text{crit},2}$), but is unstable under the two-locus dynamics, an internal, fully polymorphic and asymptotically stable equilibrium exists. Note that in the paper we use m_B^* and m_B^{**} for $m_{\text{crit},2}$ and $m_{\text{crit},5}$, respectively.

Calculations referring to the stability of E_B

■ Recap and parallels to a continuous-time version of the model

mCrit2

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

mCrit3

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

mCrit5

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

Assuming weak evolutionary forces, the critical migration rates $m_{\text{crit},2}$, $m_{\text{crit},3}$, $m_{\text{crit},5}$ can be approximated as follows:

```
FullSimplify[Series[mCrit2 /. {a ->  $\alpha \epsilon$ , b ->  $\beta \epsilon$ , r ->  $\rho \epsilon$ }, { $\epsilon$ , 0, 1}]] /.
  { $\alpha \rightarrow a / \epsilon$ ,  $\beta \rightarrow b / \epsilon$ ,  $\rho \rightarrow r / \epsilon$ } // Normal // FullSimplify
```

b

```
FullSimplify[Series[mCrit3 /. {a ->  $\alpha \epsilon$ , b ->  $\beta \epsilon$ , r ->  $\rho \epsilon$ }, { $\epsilon$ , 0, 1}]] /.
  { $\alpha \rightarrow a / \epsilon$ ,  $\beta \rightarrow b / \epsilon$ ,  $\rho \rightarrow r / \epsilon$ } // Normal // FullSimplify
```

a + b - r

```
FullSimplify[Series[mCrit5 /. {a ->  $\alpha \epsilon$ , b ->  $\beta \epsilon$ , r ->  $\rho \epsilon$ }, { $\epsilon$ , 0, 1}]] /.
  { $\alpha \rightarrow a / \epsilon$ ,  $\beta \rightarrow b / \epsilon$ ,  $\rho \rightarrow r / \epsilon$ } // Normal // FullSimplify
```

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

As expected, these approximations correspond to the critical migration rates β , m_C and m_B found previously by Bürger and Akerman (2011) for the continuous-time version of this model.

```
FullSimplify[Reduce[0 < mCrit2 < 1], Assumptions → assumeGlobal]
```

```
True
```

Given our global assumptions, $0 < m_{\text{crit},2} < 1$ always holds.

```
mCrit5
```

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

```
FullSimplify[Reduce[a(-a+b+r) > 0], Assumptions → assumeGlobal]
```

```
True
```

```
FullSimplify[Reduce[(a-b)(a-r) + (1-a)r > 0], Assumptions → assumeGlobal]
```

$$a = r \mid \mid a(b+2r) < a^2 + r + br$$

The numerator of $m_{\text{crit},5}$ is always positive, but the denominator can be negative. Specifically, $m_{\text{crit},5}$ is negative if and only if $r < \frac{a(a-b)}{1-2a+b}$.

```
qEB /. m → mCrit3 // FullSimplify
```

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

```
FullSimplify[Reduce[0 <  $\frac{(-1+a+b)(a-r)}{b(1+a+b-2r)}$  < 1], Assumptions → assumeGlobal]
```

$$a < r < a+b$$

```
mCrit5 /. {r → a}
```

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

```
mCrit3 /. {r → a}
```

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

■ Case distinctions and numerical exploration of the characteristic polynomial

In the case of $r = a$, $m_{\text{crit},5} = m_{\text{crit},3} = m_{\text{crit},2} = \frac{b}{1-a} > 0$ holds.

```
FullSimplify[Reduce[mCrit5 > 0], Assumptions → assumeGlobal]
```

$$a \leq r \mid \mid a^2 + r + br > a(b+2r)$$

It is easy to see that $m_{\text{crit},5} \neq 0$ always under our assumptions.

```
FullSimplify[Reduce[mCrit5 == 0], Assumptions → assumeGlobal]
```

```
False
```

```
FullSimplify[Reduce[mCrit5 < 0], Assumptions → assumeGlobal]
```

$$a^2 + r + br < a(b+2r)$$

```
FullSimplify[Reduce[mCrit5 > 0], Assumptions → assumeGlobal]
```

$$a \leq r \mid \mid a^2 + r + br > a(b+2r)$$

```
FullSimplify[Reduce[mCrit5 == mCrit2], Assumptions → assumeGlobal]
```

$$a = r$$

```
FullSimplify[Reduce[mCrit5 < 0 < mCrit2], Assumptions → assumeGlobal]
```

$$a^2 + r + br < a(b+2r)$$

```
FullSimplify[Reduce[0 < mCrit2 < mCrit5, r], Assumptions → assumeGlobal]
```

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

In the case above, we already know that $m_{\text{crit},2} < m_{\text{crit},3}$.

```
mCrit3
mCrit5
```

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

```
FullSimplify[Reduce[0 < mCrit5 < 1],
```

```
Assumptions → Flatten[{{assumeGlobal,  $\frac{a(a-b)}{-1+2a-b} < r < a$ }}]]
```

$$2ab+3ar < 2a^2+r+br$$

```
qEBmCrit5
```

$$\frac{(a-b)(a-r)}{br}$$

```
FullSimplify[Reduce[0 < mCrit5 < mCrit2, r], Assumptions → assumeGlobal]
```

```
r > a
```

```
FullSimplify[Reduce[0 < mCrit3 < mCrit2, r], Assumptions → assumeGlobal]
```

```
r > a
```

```
EB /. {m → mCrit5} // FullSimplify
```

$$\left\{0, \frac{(a-b)(a-r)}{br}, 0\right\}$$

In summary, we recall that E_B exists (i.e. is a biologically valid polymorphic one-locus equilibrium) if and only if $m < m_{\text{crit},2}$, independently of $m_{\text{crit},5}$. Moreover, if $m = m_{\text{crit},2}$, $E_B = E_C = \{0, 0, 0\}$ and invasion of A_1 is impossible. Further, recall that either the first or second eigenvalue of the Jacobian belonging to E_B is the leading eigenvalue. We distinguish the following four cases and, for some of them, a number of subcases:

Case 1: $r = a \Rightarrow m_{\text{crit},5} = m_{\text{crit},2}$, which implies $0 < m_{\text{crit},2} = m_{\text{crit},5}$. Then, if $0 < m < m_{\text{crit},2} = m_{\text{crit},5}$, E_B exists and is unstable. In this case, we expect a fully polymorphic (internal) equilibrium E_+ to exist and to be asymptotically stable, which implies that A_1 can invade when the dynamical system is at E_B . If $m_{\text{crit},2} < m$, E_B does not exist. A fully polymorphic and (locally) stable equilibrium E_+ may still exist, but invasion of A_1 cannot happen by a single mutation at the A locus via E_B . If $m = m_{\text{crit},2} = m_{\text{crit},5}$, E_B coincides with E_C and invasion of A_1 is impossible via A_1 (although a fully polymorphic (stable) equilibrium E_+ may exist).

```
FullSimplify[evalsEB /. {r → a}, Assumptions → Flatten[{assumeGlobal, m < mCrit2}]]
```

$$\left\{ \frac{(1-2bm+m^2-a(1+m^2))}{((-1+a-b)(-1+m))}, \frac{1}{2(-1+a-b)} \left(-2+a+b(-1+m) - am - \sqrt{((1+m)((a+b)^2+(5a^2+b^2-2a(2+b))m)} \right), \frac{1}{2(-1+a-b)} \left(-2+a+b(-1+m) - am + \sqrt{((1+m)((a+b)^2+(5a^2+b^2-2a(2+b))m)} \right) \right\}$$

```
FullSimplify[Reduce[evalsEB[[1]] < 1 /. r → a],
Assumptions → Flatten[{assumeGlobal, m < mCrit2}]]
```

```
True
```

```
FullSimplify[Reduce[evalsEB[[2]] < 1 /. r → a],
Assumptions → Flatten[{assumeGlobal, m < mCrit2}]]
```

```
False
```


The second eigenvalue is larger than 1, which confirms that E_B is invadable if $m < m_{\text{crit},2} = m_{\text{crit},5}$.

Case 2: $r < \frac{a(b-a)}{1-2a+b} \Rightarrow m_{\text{crit},5} < 0 < m_{\text{crit},2}$. Then, if $0 < m < m_{\text{crit},2}$, E_B exists. Since $\frac{a(b-a)}{1-2a+b} < a$, $r < \frac{a(b-a)}{1-2a+b}$ implies $r < a < b$, which corresponds to case 1.3 from above (see analysis of E_C). In this case, we have $m_{\text{crit},3} > m_{\text{crit},2}$ and $m < m_{\text{crit},2}$ implies $m < m_{\text{crit},3}$. In this case, we expect a fully polymorphic equilibrium E_+ to exist and to be globally stable. Together, this implies that A_1 can invade. Otherwise (i.e. if $m_{\text{crit},2} \leq m$), E_B does not exist and therefore A_1 cannot invade.

```
FullSimplify[Reduce[mCrit5 < 0], Assumptions -> Flatten[{assumeGlobal, r <  $\frac{a(b-a)}{1-2a+b}$ }]]]
True
FullSimplify[Reduce[evalsEB[[1]] < 1],
  Assumptions -> Flatten[{assumeGlobal, m < mCrit2, r < a}]]
True
```

The evaluation of the following expression takes more than 10 minutes.

```
FullSimplify[Reduce[evalsEB[[2]] < 1],
  Assumptions -> Flatten[{assumeGlobal, m < mCrit2, r < a}]]
$Aborted
```

Instead, we investigate the characteristic polynomial.

```
In[69]:= charPolEB =
  FullSimplify[(-1)^3 CharacteristicPolynomial[JEB, λ], Assumptions -> assumeGlobal]
```

```
Out[69]= 
$$\frac{1}{(-1+a-b)^3 (-1+m)} \left( -1+a+2bm-m^2+am^2+(-1+a-b)(-1+m)\lambda \right. \\ \left. (1+b+2am-bm+abm-b^2m+a^2m^2-abm^2-r-br-2amr+m^2r- \right. \\ \left. 2am^2r+bm^2r+(1-a+b)(-2+b(-1+m)-2am+r+mr))\lambda + (1-a+b)^2\lambda^2 \right)$$

```

```
In[70]:= charPolEBRed = FullSimplify[charPolEB / (λ - evalsEB[[1]]), Assumptions -> assumeGlobal]
```

```
Out[70]= 
$$\frac{1}{(1-a+b)^2} \left( 1+b+2am-bm+abm-b^2m+a^2m^2-abm^2-r-br-2amr+m^2r- \right. \\ \left. 2am^2r+bm^2r+(1-a+b)(-2+b(-1+m)-2am+r+mr))\lambda + (1-a+b)^2\lambda^2 \right)$$

```

```
charPolEBRedRed =
  FullSimplify[charPolEBRed / (λ - evalsEB[[3]]), Assumptions -> assumeGlobal]
```

```

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

```

```
Collect[charPolEBRedRed, λ]
```

```

$$\frac{1}{2(-1+a-b)} \left( 2+b+2am-bm-(1+m)r + \sqrt{(1+m)(b^2(1+m)-2b(-1+m)r+r(r+m(-4+4a+r)))} \right) + \\ \frac{(-2+2a-2b)\lambda}{2(-1+a-b)}$$

```

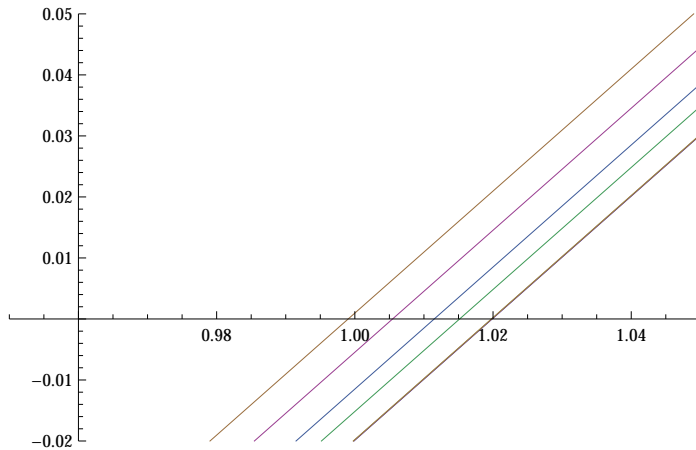
```
charPolEBRedRedFunc[a_, b_, m_, r_, λ_] := 
$$\frac{1}{2(-1+a-b)} \left( 2+b+2am-bm-(1+m)r + \sqrt{(1+m)(b^2(1+m)-2b(-1+m)r+r(r+m(-4+4a+r)))} \right) + \\ \frac{(-2+2a-2b)\lambda}{2(-1+a-b)}$$

```

```

paramRule := {a → 0.02, b → 0.04, m → 0.022, r → 0.01}
rVals := {0.0003, 0.0004, 0.0005, 0.01, 0.02, 0.05, 0.4}
  a (b - a)
  1 - 2 a + b /. paramRule
mCrit2 /. paramRule
mCrit5 /. {paramRule[[1]], paramRule[[2]], r → rVals[[7]]}
0.0004
0.0408163
0.021021
FullSimplify[Reduce[0 < mCrit5 < 1], Assumptions → assumeGlobal]
2 a ≤ r || 2 a2 + r + b r > 2 a b + 3 a r
Plot[{charPolEBRedRedFunc[a, b, m, rVals[[1]], λ] /. paramRule,
charPolEBRedRedFunc[a, b, m, rVals[[2]], λ] /. paramRule,
charPolEBRedRedFunc[a, b, m, rVals[[3]], λ] /. paramRule,
charPolEBRedRedFunc[a, b, m, rVals[[4]], λ] /. paramRule,
charPolEBRedRedFunc[a, b, m, rVals[[5]], λ] /. paramRule,
charPolEBRedRedFunc[a, b, m, rVals[[6]], λ] /. paramRule,
charPolEBRedRedFunc[a, b, m, rVals[[7]], λ] /. paramRule},
{λ, -2, 2}, PlotRange → {{0.95, 1.05}, {-0.02, 0.05}}]

```



Case 3: $\frac{a(b-a)}{1-2a+b} < r < a \Rightarrow 0 < m < m_{\text{crit},2} < \min(m_{\text{crit},3}, m_{\text{crit},5})$. Then, if $0 < m < m_{\text{crit},2}$, E_B exists, but is unstable because we have $m < m_{\text{crit},5}$. In this case, we expect a fully polymorphic equilibrium E_+ to exist and to be stable, which implies that A_1 can invade. If $m_{\text{crit},2} \leq m < \min(m_{\text{crit},3}, m_{\text{crit},5})$, E_B does not exist. A fully polymorphic and stable equilibrium E_+ may exist, but A_1 cannot invade via E_B .

```

mCrit3
  a + b - r
  1 - r
mCrit5
  a (-a + b + r)
  (a - b) (a - r) + (1 - a) r
FullSimplify[Reduce[mCrit2 < mCrit5],
Assumptions → Flatten[{{assumeGlobal,
  a (b - a)
  1 - 2 a + b < r < a}}]]]
True

```

```
FullSimplify[Reduce[mCrit2 < mCrit3],
  Assumptions → Flatten[{{assumeGlobal,  $\frac{a(b-a)}{1-2a+b} < r < a$ }}]]]
True
```

Case 4: $a < r \Rightarrow 0 < m_{\text{crit},5} < m_{\text{crit},2}$. Then, if $0 < m < m_5 < m_2$, E_B exists and is unstable. In this case, we expect a fully polymorphic equilibrium E_+ to exist and to be stable. On the other hand, if $0 < m = m_{\text{crit},5} < m_{\text{crit},2}$ then E_B exists but is not hyperbolic. At this point, we expect a fully polymorphic equilibrium E_+ to either enter the state space and immediately be stable, or to branch from and exchange stability with E_B . Last, if $0 < m_{\text{crit},5} < m < m_{\text{crit},2}$, E_B exists and is stable, such that A_1 cannot invade even in cases where a fully polymorphic locally stable equilibrium E_+ exists.

The fully polymorphic (internal) equilibria cannot be obtained analytically. Therefore, we cannot prove the conjectures formulated above (Cases 1 to 4). However, in a continuous-time version of the model we study here, one can obtain the internal equilibria and prove that the conjectures above hold (Bürger and Akerman 2011, Bank et al. 2012). Specifically, it can be shown that

As m increases from 0, an internal fully polymorphic equilibrium E_+ exists as long as m is smaller than a critical value. If m exceeds this critical value, E_+ may merge with E_B or with E_C or cease to exist (leave the state space). Moreover, as m increases from 0, the marginal one-locus polymorphism E_B exists as long as $m < m_{\text{crit},2}$ and merges with E_C if $m = m_{\text{crit},2}$.

As m decreases from 1, E_B enters the state space via E_C at $m = m_{\text{crit},2}$ and then bifurcates at $m = m_{\text{crit},5}$.

In summary, from our considerations here and by analogy to the continuous-time version of the model, the following statement about invasion of A_1 via E_B holds: Whenever E_B exists ($m < m_{\text{crit},2}$) and is unstable in the two-locus dynamics, there exists a fully polymorphic (internal) globally stable equilibrium E_+ and A_1 can invade when initially rare.

Polymorphic continent

We now study the case where the \mathcal{B} locus is polymorphic on the island, with allele B_1 at frequency q_c ($0 < q_c < 1$).

```
In[71]:= Needs["PlotLegends`"]
```

Recapitulation of dynamical equations

Recursion equations for p , q and D .

```
recPQD
```

$$\left\{ -\frac{(-1+m)(p+ap^2+b(DD+p(-1+2q)))}{1+a(-1+2p)+b(-1+2q)}, -\frac{(-1+m)(q+bq^2+a(DD+(-1+2p)q))}{1+a(-1+2p)+b(-1+2q)} + m q C, \right. \\ \left. -\left((-1+m)(abDD^2(-1+m)+pq(a^2mp(-1+2p)+m(1+bq)(1+b(-1+2q))+a(m(-1+3p)+b(-1+m+p-2mp+q-2mq-pq+5mpq))-mp(1-b+a(-1+2p)+2bq)(1+ap+b(-1+2q))qC+DD(1+a^2p(-1+p+mp))-r+a(-1+bm(-q+qC)+p(2+m(1+b(-1+4q-2qC))-2r)+r)+b(-1+b(1+m)q^2+(-1+b)mqC+q(2-b+m-2bmqC-2r)+r) \right) \right\} / (1+a(-1+2p)+b(-1+2q))^2$$

```
recPQD[[1]]
```

$$-\frac{(-1+m)(p+ap^2+b(DD+p(-1+2q)))}{1+a(-1+2p)+b(-1+2q)}$$

```
recPQD[[2]]
```

$$-\frac{(-1+m)(q+bq^2+a(DD+(-1+2p)q))}{1+a(-1+2p)+b(-1+2q)}+mqC$$

```
recPQD[[3]]
```

$$-\left((-1+m)\left(abDD^2(-1+m)+pq\left(a^2mp(-1+2p)+m(1+bq)(1+b(-1+2q))+a(m(-1+3p)+b(-1+m+p-2mp+q-2mq-pq+5mpq))\right)-mp(1-b+a(-1+2p)+2bq)(1+ap+b(-1+2q))qC+DD(1+a^2p(-1+p+mp))-r+a(-1+bm(-q+qC)+p(2+m(1+b(-1+4q-2qC))-2r)+r)+b(-1+b(1+m)q^2+(-1+b)mqC+q(2-b+m-2bmqC-2r)+r)\right)\right)/(1+a(-1+2p)+b(-1+2q))^2$$

```
recPQD /. {p -> 0, q -> 0, DD -> 0}
```

$$\{0, mqC, 0\}$$

Jacobian matrix

```
In[72]:= J1 := Table[Table[D[recPQD[[j]], i] // FullSimplify, {i, {p, q, DD}}], {j, {1, 2, 3}}
```

```
J1 // MatrixForm
```

$$\left(\begin{array}{ccc} -\frac{(-1+m)\left(a^3(DD-2DDmp+2m(-1+p)p(-1+2p)(q-qC))+m(-1+b-2bq)^2(q+bq^2+(-1+b)qC-2bqC)+a^2(-4bDD^2(-1+m)+q(m+6m(-1+p)p+2m(1+b(-1+2q)-2qC)+2r)+r)+b(-1+b(1+m)q^2+(-1+b)mqC+q(2-b+m-2bmqC-2r)+r)\right)}{(1+a(-1+2p)+b(-1+2q))^2} & & \end{array} \right)$$

```
J1 /. ruleMonomorphContin // MatrixForm
```

$$\left(\begin{array}{ccc} -\frac{(-1+m)\left(a^3(DD-2DDmp+2m(-1+p)p(-1+2p)q)+m(-1+b-2bq)^2(q+bq^2)+a^2(-4bDD^2(-1+m)+q(m+6m(-1+p)p+b(1-q+m(-1+2q+2p(2-2qC)+2r)+r)+b(-1+b(1+m)q^2+(-1+b)mqC+q(2-b+m-2bmqC-2r)+r)\right)}{(1+a(-1+2p)+b(-1+2q))^2} & & \end{array} \right)$$

Additional assumptions and rules

The global assumptions so far:

```
assumeGlobal
```

$$\{0 < a < b < 1, a + b < 1, 0 < m < 1, 0 < r \leq 0.5\}$$

Update the global assumptions:

```
In[73]:= assumeGlobal1 := {0 < m < 1, 0 < a < 1/2, a < b < 1 - a, 0 ≤ r ≤ 1/2, 0 < qC < 1}
```

Equilibria – existence, properties, stability

■ Monomorphic equilibria

- E_I : Only the island haplotype $A_1 B_1$ is present on the island (no migration)

This implies that there is no migration ($m = 0$) to start with.

The linkage disequilibrium is 0.

```
LD /. {x[1] -> 1, x[2] -> 0, x[3] -> 0, x[4] -> 0}
```

$$0$$

Hence, in terms of p , q and D , we have

```
In[74]:= assumeEI1 := {p → 1, q → 1, DD → 0, m → 0}
recP /. assumeEI1 // FullSimplify
1
recQ /. assumeEI1 // FullSimplify
1
recD /. assumeEI1 // FullSimplify
0
```

Eigenvalues of the Jacobian, evaluated at E_1 .

```
In[75]:= JEI1 := J1 /. assumeEI1 // FullSimplify
JEI1 // MatrixForm

$$\begin{pmatrix} \frac{1+b}{1+a+b} & 0 & \frac{b}{1+a+b} \\ 0 & \frac{1+a}{1+a+b} & \frac{a}{1+a+b} \\ 0 & 0 & \frac{1-r}{1+a+b} \end{pmatrix}$$

```

```
In[76]:= evalsEI1 = Eigenvalues[JEI1] // FullSimplify
```

```
Out[76]=  $\left\{ \frac{1+a}{1+a+b}, \frac{1+b}{1+a+b}, \frac{1-r}{1+a+b} \right\}$ 
```

The second eigenvalue is always the leading one, and it is always smaller than 1. Hence, the equilibrium E_1 is asymptotically stable for $m = 0$.

Nothing changed compared to the case of a monomorphic continent. This is not surprising, given that we assumed no migration ($m = 0$). However, as soon as migration is turned on ($m > 0$), the equilibrium E_1 cannot be stable anymore, since migration brings in continental haplotypes ($A_2 B_1, A_2 B_2$).

- E_C : Only the continent haplotype $A_2 B_2$ is present on the island

Since the B_1 allele is now continuously introduced by migration, gene flow can not swamp the island with the continental haplotype $A_2 B_2$. The monomorphic equilibrium $E_C = (0, 0, 0)$ leaves the state space as soon as $m > 0$ and B_1 is maintained at an intermediate frequency, as long as $0 < m < 1$.

```
In[77]:= myParams := {a → 0.02, b → 0.04, m → 0.03, r → 0.2, qC → 0.5}
```

```
In[78]:= mya = a /. myParams;
myb = b /. myParams;
mym = m /. myParams;
myr = r /. myParams;
myqc = qC /. myParams;
pInit = 0.;
qInit = 0.;
DInit = 0.;
```

```
In[86]:= tmax = 100;
```

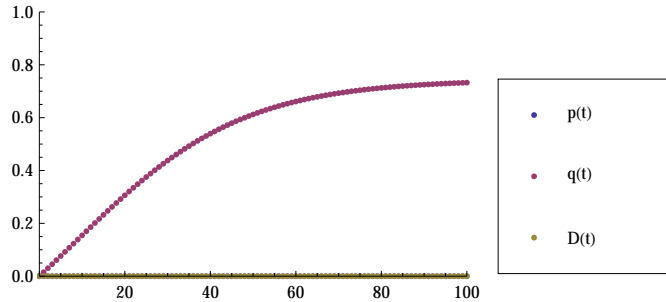
```
In[87]:= Clear[pp,qq,DDDD];
pp[a_,b_,m_,r_,qC_,0]=pInit;
pp[a_,b_,m_,r_,qC_,t_]:=pp[a,b,m,r,qC,t]=-((-1+m) (pp[a,b,m,r,qC,t-1]+a pp[a,b,m,r,qC,t]
qq[a_,b_,m_,r_,qC_,0]=qInit (*Evaluate[qEB1]*);
qq[a_,b_,m_,r_,qC_,t_]:=qq[a,b,m,r,qC,t]=-((-1+m) (qq[a,b,m,r,qC,t-1]+b qq[a,b,m,r,qC,t]
DDDD[a_,b_,m_,r_,qC_,0]=DInit;
DDDD[a_,b_,m_,r_,qC_,t_]:=DDDD[a,b,m,r,qC,t]=-((-1+m) (a b DDDD[a,b,m,r,qC,t-1]^2 (-1+m)
Clear[recPQDFunc];
recPQDFunc[a_,b_,m_,r_,qC_,t_]:={pp[a,b,m,r,qC,t],qq[a,b,m,r,qC,t],DDDD[a,b,m,r,qC,t]}
tablpp = Table[{t, pp[mya, myb, mym, myr, myqc, t]}, {t, 0, tmax}];
tablqq = Table[{t, qq[mya, myb, mym, myr, myqc, t]}, {t, 0, tmax}];
tablDDDD = Table[{t, DDDD[mya, myb, mym, myr, myqc, t]}, {t, 0, tmax}];
```

We expect the B_1 allele to approach the marginal one-locus selection-migration equilibrium (to be determined further below).

```
qEB1 /. {a -> mya, b -> myb, m -> mym, qC -> myqc}
```

```
0.744006
```

```
ListPlot[{tablpp, tablqq, tablDDDD}, PlotRange -> {{0, tmax}, {0., 1.}},  
PlotLegend -> {"p(t)", "q(t)", "D(t)"}, LegendPosition -> {1, -0.5}, LegendShadow -> None]
```



■ Marginal one-locus equilibria

We proceed directly to the equilibrium that is most relevant for our application:

■ E_B : One-locus polymorphism at the B locus

This equilibrium is given by $E_B = (0, \hat{q}_B, 0)$, where $\hat{q}_B > 0$, as B_1 alleles are introduced from the continent at a constant rate $m q_c$ (more precisely, a proportion $m q_c$ of resident alleles is replaced every generation by immigrants carrying the B_1 allele).

```
recQ
```

$$- \frac{(-1 + m) (q + b q^2 + a (DD + (-1 + 2 p) q))}{1 + a (-1 + 2 p) + b (-1 + 2 q)} + m qC$$

```
In[96]:= soleB1 = FullSimplify[Solve[{recQ /. {p -> 0, DD -> 0}} == q, q], Assumptions -> assumeGlobal1]
```

```
Out[96]=
```

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

Both solutions are candidates for the equilibrium frequency q_B . Next, we check under which conditions they are biologically valid, i.e. between 0 and 1. We are not interested in the non-generic cases of $q_B = 0$ and $q_B = 1$.

```
In[97]:= qEB1 = q /. soleB1[[1];  
qEB2 = q /. soleB1[[2];
```

```
condSolEB11 = FullSimplify[Reduce[0 < qEB1 < 1], Assumptions -> assumeGlobal1]
```

```
condSolEB12 = FullSimplify[Reduce[0 < qEB2 < 1], Assumptions -> assumeGlobal1]
```

```
True
```

```
False
```

Thus, the first solution is biologically valid, while the second is not in the state space.

```
qEB1
```

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

The frequency of B_1 at the marginal one-locus migration-selection equilibrium E_B is given by

$$\hat{q}_B = \frac{b - (1 - a) m + 2 b m q_c + \sqrt{R}}{2 b (m + 1)}$$

(1)

where

$$R = 4b(1-a-b)m(1+m)q_c + (b - (1-a)m + 2bm q_c)^2. \quad (2)$$

$$\text{Collect}[-4b(-1+a+b)m(1+m)q_c + (b + (-1+a)m + 2bm q_c)^2, \{a, b\}]$$

$$m^2 + a^2 m^2 + b(-2m - 4m^2 q_c + 4m(1+m)q_c) + b^2(1 + 4mq_c - 4m(1+m)q_c + 4m^2 q_c^2) + a(-2m^2 + b(2m + 4m^2 q_c - 4m(1+m)q_c))$$

$$\text{Collect}\left[\frac{am + 2bm q_c + b - m + R}{2b(m+1)}, \{m\}\right]$$

$$\frac{b - m + am + 2bm q_c + R}{2b(1+m)}$$

In[99]:= `assumeEB1 := {p → 0, q → qEB1, DD → 0}`

`recP /. assumeEB1`

`recD /. assumeEB1`

0

0

We define

In[100]:= `EB1 = {0, qEB1, 0}`

$$\text{Out[100]} = \left\{0, \frac{1}{2b(1+m)}\right.$$

$$\left. \left(b - m + am + 2bm q_c + \sqrt{-4b(-1+a+b)m(1+m)q_c + (b + (-1+a)m + 2bm q_c)^2}\right), 0\right\}$$

The eigenvalues of the Jacobian, evaluated at E_B :

In[101]:= `JEB1 = FullSimplify[J1 /. assumeEB1, Assumptions → assumeGlobal1];`

`MatrixForm[JEB1]`

$$\begin{pmatrix} \frac{b^2(-1+m) - (-1+a)(1+(-1+a)m) + abm(-1+2q_c) - a\sqrt{-4b(-1+a+b)m(1+m)q_c + (b+(-1+a)m+2bm q_c)^2}}{(-1+a)^2 - b^2} & 0 \\ -\frac{a(-1+m)\left(-b+m(-1+a+2b(-1+q_c)) + \sqrt{-4b(-1+a+b)m(1+m)q_c + (b+(-1+a)m+2bm q_c)^2}\right)\left(b-m+am+2bm q_c + \sqrt{-4b(-1+a+b)m(1+m)q_c + (b+(-1+a)m+2bm q_c)^2}\right)}{2b\left(1-a+bm(-1+2q_c) + \sqrt{-4b(-1+a+b)m(1+m)q_c + (b+(-1+a)m+2bm q_c)^2}\right)^2} & 0 \\ \frac{m\left(b-m+am-2b q_c + \sqrt{-4b(-1+a+b)m(1+m)q_c + (b+(-1+a)m+2bm q_c)^2}\right)}{2b(1+m)} & 0 \end{pmatrix}$$

`mCrit2 == m`

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

`MatrixForm[FullSimplify[JEB1 /. {qC → 0}, Assumptions → assumeGlobal1]]`

$$\begin{pmatrix} \begin{cases} \frac{-1+b+m-bm}{-1+a+b} & b+am < m \\ \frac{1+b-(1-2a+b)m}{1-a+b} & \text{True} \end{cases} & 0 & \frac{b(-1+m^2)}{-1+a+bm-\text{Abs}[b+(-1+a)m]} \\ \begin{cases} -\frac{2am(b+(-1+a)m)}{(-1+a-b)b(-1+m)} & b+am \geq m \\ 0 & \text{True} \end{cases} & \begin{cases} \frac{-1+a+m-am}{-1+a+b} & b+am < m \\ \frac{1-2bm+m^2-a(1+m^2)}{(-1+a-b)(-1+m)} & \text{True} \end{cases} & \frac{a(-1+m^2)}{-1+a+bm-\text{Abs}[b+(-1+a)m]} \\ \begin{cases} \frac{m(b+(-1+a)m)}{b(1+m)} & b+am \geq m \\ 0 & \text{True} \end{cases} & 0 & -\frac{(-1+m^2)(-1+x)}{-1+a+bm-\text{Abs}[b+(-1+a)m]} \end{pmatrix}$$

EB1 /. {qC → 0}

$$\left\{ 0, \frac{b - m + a m + \sqrt{(b + (-1 + a) m)^2}}{2 b (1 + m)}, 0 \right\}$$

FullSimplify[EB1 /. {qC → 0}, Assumptions → {assumeGlobal, m (1 - a) < b}]

$$\left\{ 0, \frac{b - m + a m}{b + b m}, 0 \right\}$$

The condition that appears here, $b + a m \geq m \iff m \leq \frac{b}{1-a} \equiv m_{\text{crit},2}$, is already known for the case of $q_c = 0$: if it holds, the marginal one-locus equilibrium (polymorphic B-locus) exists. Otherwise, there is only the monomorphic equilibrium E_C at which $q_B = 0$.

FullSimplify[J1 /. ruleMonomorphContin /. assumeEB1 /. {qC → 0},
Assumptions → (b + (-1 + a) m) > 0] // MatrixForm

$$\begin{pmatrix} \frac{1+b-(1-2a+b)m}{1-a+b} & 0 & \frac{b(1+m)}{1-a+b} \\ -\frac{2am(b+(-1+a)m)}{(-1+a-b)b(-1+m)} & \frac{1-2bm+m^2-a(1+m^2)}{(-1+a-b)(-1+m)} & \frac{a(1+m)}{1-a+b} \\ \frac{m(b+(-1+a)m)}{b(1+m)} & 0 & \frac{(1+m)(-1+r)}{-1+a-b} \end{pmatrix}$$

We identify a term that occurs repeatedly as a radicand (we call it R):

$$\text{In[102]= } R := 4 b (1-a-b) m (1+m) qC + (b - (1-a) m + 2 b m qC)^2$$

Given our global assumptions, R cannot be negative (see below). This is nice, because we then know that the entries in the Jacobian above are all real; the root terms are all positive. It also makes it easier to determine whether the Jacobian is non-negative.

FullSimplify[Reduce[R < 0], Assumptions → assumeGlobal]

False

JEB1[[2, 3]]

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

FullSimplify[Reduce[JEB1[[1, 3]] < 0], Assumptions → Flatten[{assumeGlobal, R > 0}]]

$$1 + \sqrt{(-(-1 + a)^2 + b^2) (-1 + m^2)} + b m (-1 + 2 qC) \leq a$$

FullSimplify[Reduce[JEB1[[2, 3]] < 0], Assumptions → Flatten[{assumeGlobal, R > 0}]]

False

FullSimplify[Reduce[JEB1[[3, 3]] < 0], Assumptions → Flatten[{assumeGlobal, R > 0}]]

False

FullSimplify[Reduce[JEB1[[3, 1]] < 0], Assumptions → Flatten[{assumeGlobal, R > 0}]]

False

FullSimplify[Reduce[JEB1[[2, 1]] < 0], Assumptions → Flatten[{assumeGlobal, R > 0}]]

$$a + \sqrt{(-(-1 + a)^2 + b^2) (-1 + m^2)} + b (m - 2 m qC) \leq 1 \quad || \quad m \geq b + a m$$

Here, we have found a relatively simple condition ($m \geq b + a m$) under which the Jacobian is expected to have at least one negative entry. To check this, we evaluate the Jacobian for a parameter combination that fulfills this condition.

JEB1 /. {a → 0.2, b → 0.4, m → 0.51, r → 0.1, qC → 0.2}

{{0.637969, 0, 0.295938}, {-0.039388, 0.5131, 0.147969}, {0.0652169, 0, 0.66586}}

Hence, we have the proof that the Jacobian above is not non-negative and, according to Otto and Day (2007, Box 8.2, p. 309ff), we cannot apply the method based on the Routh-Hurwitz conditions.

The eigenvalues can be found explicitly, but the following takes some time to evaluate.

(* Do not run this unless you want to wait for a long time. *)

evalsEB1 = FullSimplify[Eigenvalues[JEB1], Assumptions → assumeGlobal];

As the calculation above takes a long time, we hard-code it here:

```
In[103]:= evalsEB1 := { - ( (-1+m) ( 1+a^2 (1+m+m^2) + sqrt( (b+(-1+a) m)^2 - 4 b m (-1+a+b m) qC + 4 b^2 m^2 qC^2 - a ( 2+
```

```
Manipulate[Show[ContourPlot[evalsEB1Func[mya, myb, m, r, myqC],
```

```
{m, 0, mMax}, {r, 0, rMax}, Contours -> {-20, 1, 20},
```

```
ContourShading -> {Blue, RGBColor[0.9, 0.9, 0.9], RGBColor[0.75, 0.75, 0.75], Red},
```

```
PlotPoints -> 35, FrameLabel -> {"Migration rate m", "Recombination rate r"},
```

```
LabelStyle -> {Directive[FontSize -> 18], FontFamily -> "Helvetica"}],
```

```
Plot[rCritFunc[mya, myb, m, myqC], {m, 0, mMax}, PlotStyle -> Black]],
```

```
{{mya, 0.01}, 0, 0.5}, {{myb, 0.04}, 0, 0.5}, {{myqC, 0.}, 0, 1},
```

```
{{mMax, 0.08}, 0, 0.5}, {{rMax, 0.05}, 0, 0.5}]
```

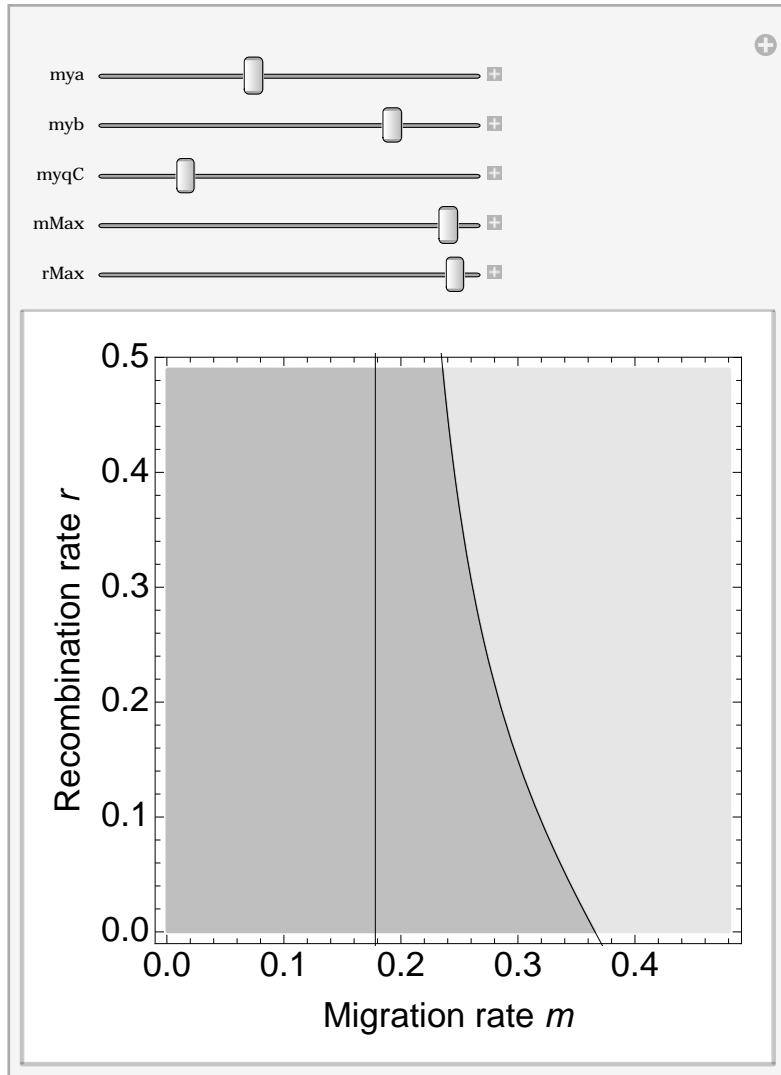
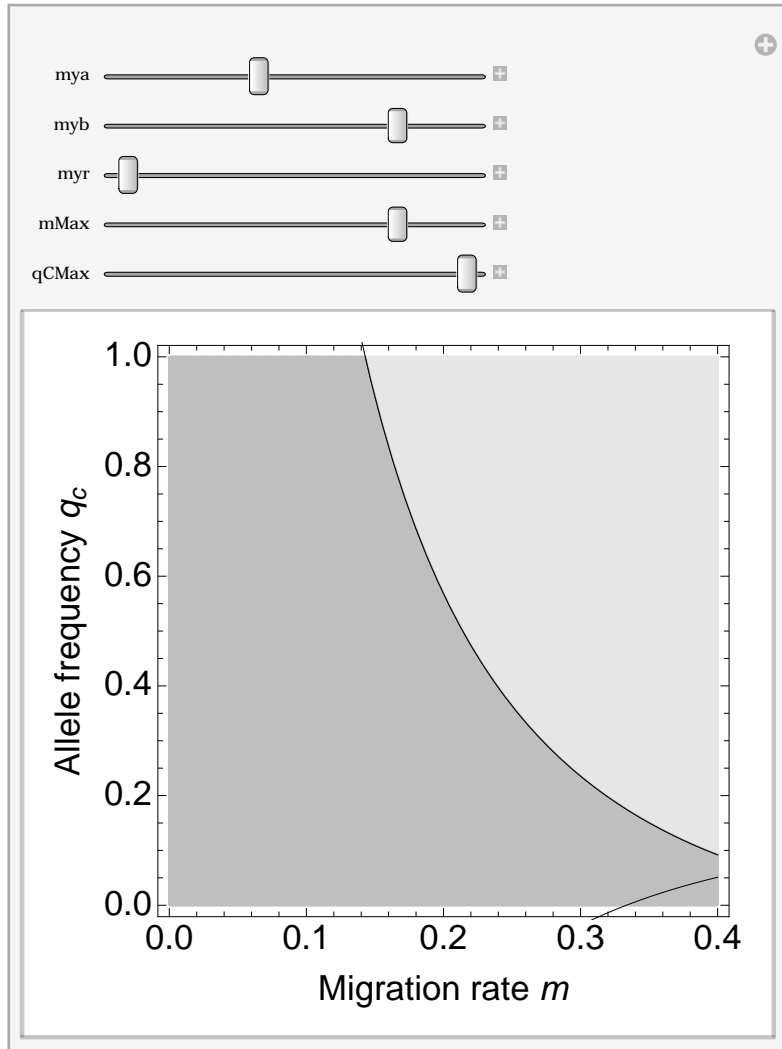


Figure: The dark grey area denotes the state space for which the marginal one-locus migration selection equilibrium E_B is unstable and A_1 can invade, while in the light grey area, E_B is asymptotically stable. The black lines show the candidate for the critical recombination rate, as derived and defined later. This function has a pole at a migration rate of approximately $m = a$. At and below this point, it seems likely that the critical recombination rate is 0.5.

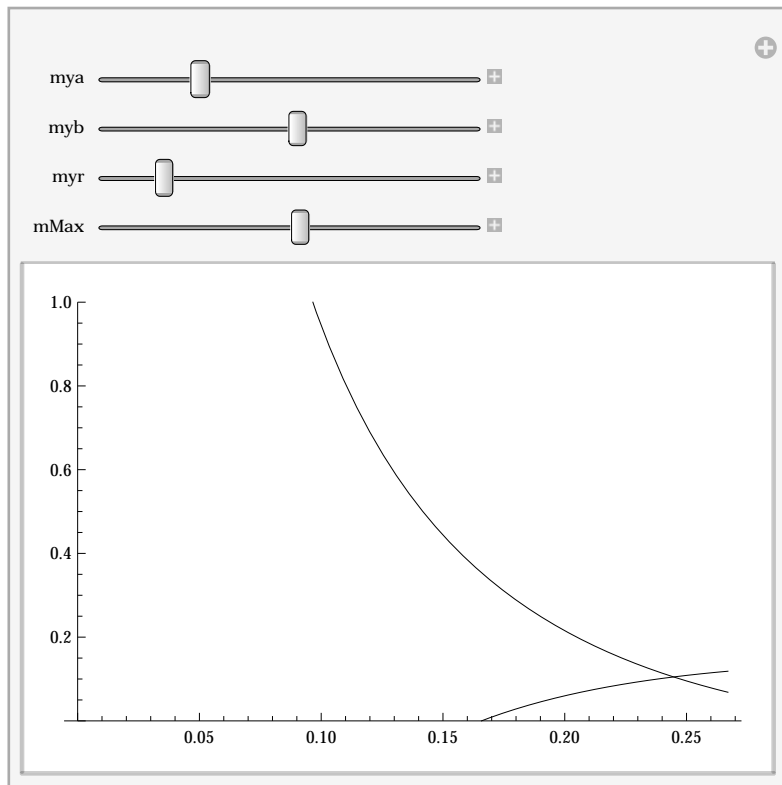
```

Manipulate[Show[ContourPlot[evalsEB1Func[mya, myb, m, myr, qC],
  {m, 0, mMax}, {qC, 0, qCMax}, Contours -> {-20, 1, 20},
  ContourShading -> {Blue, RGBColor[0.9, 0.9, 0.9], RGBColor[0.75, 0.75, 0.75], Red},
  PlotPoints -> 35, FrameLabel -> {"Migration rate  $m$ ", "Allele frequency  $q_c$ "},
  LabelStyle -> {Directive[FontSize -> 18], FontFamily -> "Helvetica"}],
  Plot[qCCritFunc[mya, myb, m, myr], {m, 0, mMax}, PlotStyle -> Black]],
  {{mya, 0.01}, 0, 0.5}, {{myb, 0.04}, 0, 0.5}, {{myr, 0.1}, 0, 5},
  {{mMax, 0.08}, 0, 0.5}, {{qCMax, 0.06}, 0, 1}]

```



```
Manipulate[Plot[qCCritFunc[mya, myb, m, myr], {m, 0, mMax},  
  PlotRange -> {Automatic, {0, 1}}, PlotStyle -> Black], {{mya, 0.01}, 0, 0.5},  
  {{myb, 0.04}, 0, 0.5}, {{myr, 0.1}, 0, 0.5}, {{mMax, 0.1}, 0, .5}]
```



In[104]:=

```

evalsEB1Func[a_, b_, m_, r_, qC_] := Module[{evals}, evals =
  { - ((-1 + m) (1 + a^2 (1 + m + m^2) + sqrt((b + (-1 + a) m)^2 - 4 b m (-1 + a + b m) qC + 4 b^2 m^2 qC^2) -
    a (2 + sqrt((b + (-1 + a) m)^2 - 4 b m (-1 + a + b m) qC + 4 b^2 m^2 qC^2) +
      2 m (1 + m + b (-1 + 2 qC))) + m (1 + m + b^2 (-1 + 4 m (-1 + qC) qC) +
      b (-1 + 2 qC) (2 + sqrt((b + (-1 + a) m)^2 - 4 b m (-1 + a + b m) qC + 4 b^2 m^2 qC^2)))) /
    (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))^2,
  1/2 ( (2/((-1 + a)^2 - b^2) - 1/((-1 + a)^2 - b^2) (-b^2 (-1 + m) + m + a^2 m +
    sqrt((b + (-1 + a) m)^2 - 4 b m (-1 + a + b m) qC + 4 b^2 m^2 qC^2) + a (2 + m (-2 + b - 2 b qC) +
    sqrt((b + (-1 + a) m)^2 - 4 b m (-1 + a + b m) qC + 4 b^2 m^2 qC^2) - r) + b m (-1 + 2 qC)
    (-1 + r) + r - sqrt((b + (-1 + a) m)^2 - 4 b m (-1 + a + b m) qC + 4 b^2 m^2 qC^2) r) -
    sqrt((( -1 + m)^2 (1 + m) (b^2 (1 + m) + 2 b m (-1 + 2 qC) r + r (2 sqrt((b + (-1 + a) m)^2 -
    4 b m (-1 + a + b m) qC + 4 b^2 m^2 qC^2) + r + m (-2 + 2 a + r)))) / (1 - a +
    b m (-1 + 2 qC) + sqrt((b + (-1 + a) m)^2 - 4 b m (-1 + a + b m) qC + 4 b^2 m^2 qC^2))^2) )},
  1/2 ( (2/((-1 + a)^2 - b^2) - 1/((-1 + a)^2 - b^2) (-b^2 (-1 + m) + m + a^2 m +
    sqrt((b + (-1 + a) m)^2 - 4 b m (-1 + a + b m) qC + 4 b^2 m^2 qC^2) + a (2 + m (-2 + b - 2 b qC) +
    sqrt((b + (-1 + a) m)^2 - 4 b m (-1 + a + b m) qC + 4 b^2 m^2 qC^2) - r) + b m (-1 + 2 qC)
    (-1 + r) + r - sqrt((b + (-1 + a) m)^2 - 4 b m (-1 + a + b m) qC + 4 b^2 m^2 qC^2) r) +
    sqrt((( -1 + m)^2 (1 + m) (b^2 (1 + m) + 2 b m (-1 + 2 qC) r + r (2 sqrt((b + (-1 + a) m)^2 - 4
    b m (-1 + a + b m) qC + 4 b^2 m^2 qC^2) + r + m (-2 + 2 a + r)))) / (1 - a + b m
    (-1 + 2 qC) + sqrt((b + (-1 + a) m)^2 - 4 b m (-1 + a + b m) qC + 4 b^2 m^2 qC^2))^2) )};
  Return[Max[Chop[Abs[evals]]]];
]

```

For the equilibrium to be stable, we require that the leading eigenvalue be between -1 and 1 . Simplifying this condition is impossible or takes a very long time with Mathematica, irrespectively of the reference parameter (below, not run).

```
FullSimplify[Reduce[-1 < evalsEB1[[1]] < 1 && -1 < evalsEB1[[2]] < 1 && -1 < evalsEB1[[3]] < 1], Assumptions -> assumeGlobal1]
```

\$Aborted

```
FullSimplify[Reduce[-1 < evalsEB1[[1]] < 1 && -1 < evalsEB1[[2]] < 1 && -1 < evalsEB1[[3]] < 1, m], Assumptions -> assumeGlobal1]
```

\$Aborted

```
FullSimplify[Reduce[-1 < evalsEB1[[1]] < 1 && -1 < evalsEB1[[2]] < 1 && -1 < evalsEB1[[3]] < 1, r], Assumptions -> assumeGlobal1]
```

\$Aborted

```
FullSimplify[Reduce[-1 < evalsEB1[[1]] < 1 && -1 < evalsEB1[[2]] < 1 && -1 < evalsEB1[[3]] < 1, qC], Assumptions -> assumeGlobal1]
```

\$Aborted

```
FullSimplify[Reduce[-1 < evalsEB1[[1]] < 1 && -1 < evalsEB1[[2]] < 1 && -1 < evalsEB1[[3]] < 1, a], Assumptions -> assumeGlobal1]
```

\$Aborted

```
FullSimplify[Reduce[-1 < evalsEB1[[1]] < 1 && -1 < evalsEB1[[2]] < 1 && -1 < evalsEB1[[3]] < 1, b], Assumptions -> assumeGlobal1]
```

\$Aborted

Instead, we focus on the characteristic polynomial. This looks ugly and the following takes several minutes to evaluate. Below, we multiply by $(-1)^n$ to make sure the coefficient of λ^n is positive. In the current case, $n = 3$.

```
charPolEB1 = FullSimplify[(-1)^3 * CharacteristicPolynomial[JEB1, λ];
```

This is the characteristic polynomial:

```
In[105]:= charPolEB1 := (m^6 (1+4 b^2 (-1+qC) qC) (1+b (-1+2 qC)-2 r)+a^3 ((-1+m)^2 m^2 (1+m^2)+(-1+m)^2 m (
```

Verification of the characteristic polynomial: The following must evaluate to 0 (which it does).

```
Simplify[charPolEB1 - (λ - evalsEB1[[1]]) (λ - evalsEB1[[2]]) (λ - evalsEB1[[3]]),
Assumptions -> assumeGlobal1]
```

0

To obtain a quadratic equation, we split the first eigenvalue off by dividing by $(\lambda - \lambda_1)$ [using the fundamental theorem of algebra]:

```
charPolEB1Red = FullSimplify[charPolEB1/(λ - evalsEB1[[1]])];
```

Again, this takes a long time and we hard-code this here:

```
In[106]:= charPolEB1Red := 1 / (2 ((-1+a)^2 - b^2)^2) (a^4 (m^2 + 2 m λ + 2 λ^2) + a (6 m - m sqrt((b + (-1+a) m)^2 - 4 b m (-1+a+b
```

The above should be a quadratic equation, bent upward. As a check, we plot it as a function of λ for some arbitrary (but instructive) parameter combinations:

```
In[107]:= charPolEB1RedFunc[a_, b_, m_, r_, qC_, λ_] := Evaluate[charPolEB1Red]
```

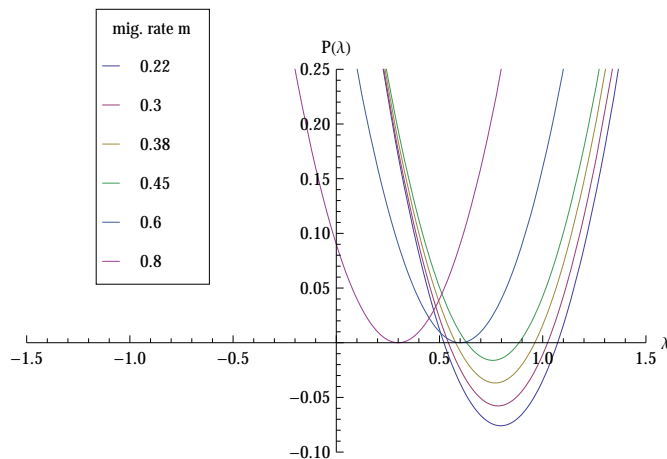
First with $q_c = 0$ and consider increasing migration rates:

```
In[108]:= paramRule1 := {a -> 0.2, b -> 0.4, m -> 0.22, r -> 0.4, qC -> 0.};
mVals := {0.22, 0.3, 0.38, 0.45, 0.6, 0.8}
```

Recall the critical values for m with respect to stability of the E_B in the case of $q_c = 0$:

```
{mCrit5, mCrit2}
% /. paramRule1
{ (a (-a + b + r) / ((a - b) (a - r) + (1 - a) r), -b / (-1 + a) }
{0.333333, 0.5}
```

```
Plot[{charPolEB1RedFunc[a, b, mVals[[1]], r, qC, λ] /. paramRule1,
charPolEB1RedFunc[a, b, mVals[[2]], r, qC, λ] /. paramRule1,
charPolEB1RedFunc[a, b, mVals[[3]], r, qC, λ] /. paramRule1,
charPolEB1RedFunc[a, b, mVals[[4]], r, qC, λ] /. paramRule1,
charPolEB1RedFunc[a, b, mVals[[5]], r, qC, λ] /. paramRule1,
charPolEB1RedFunc[a, b, mVals[[6]], r, qC, λ] /. paramRule1}, {λ, -2, 2},
AxesLabel -> {λ, "P(λ)"}, PlotRange -> {{-1.5, 1.5}, {-0.1, 0.25}}, PlotLegend -> mVals,
LegendPosition -> {-0.75, -0.1}, LegendShadow -> None, LegendLabel -> "mig. rate m"]
```

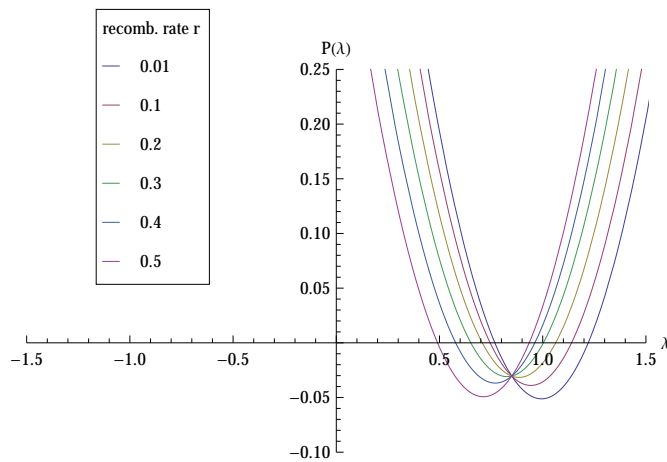


As expected from previous results, with $q_c = 0$, at least one root is > 1 (and E_B is unstable) as long as $m < m_{\text{crit},5}$. In this case, the fully polymorphic internal equilibrium is expected to be asymptotically stable and A_1 cannot invade. However, when $m_{\text{crit},5} < m < m_{\text{crit},2}$, the marginal one-locus equilibrium E_B is stable and invasion of A_1 is not possible (compare to A2010). If m increases further and reaches $m_{\text{crit},2}$, the marginal one-locus equilibrium E_B merges with the monomorphic equilibrium E_C at which the continent type $A_2 B_2$ is fixed.

Next, we keep $q_c = 0$, but now consider varying recombination rates. We expect that increasing r renders E_B stable and, on the other hand, makes it harder (eventually impossible) for A_1 to invade. To see this effect, we change m from 0.22 to 0.38:

```
paramRule1 := {a → 0.2, b → 0.4, m → 0.38, r → 0.4, qC → 0.};
rVals := {0.01, 0.1, 0.2, 0.3, 0.4, 0.5}

Plot[{charPolEB1RedFunc[a, b, m, rVals[[1]], qC, λ] /. paramRule1,
charPolEB1RedFunc[a, b, m, rVals[[2]], qC, λ] /. paramRule1,
charPolEB1RedFunc[a, b, m, rVals[[3]], qC, λ] /. paramRule1,
charPolEB1RedFunc[a, b, m, rVals[[4]], qC, λ] /. paramRule1,
charPolEB1RedFunc[a, b, m, rVals[[5]], qC, λ] /. paramRule1,
charPolEB1RedFunc[a, b, m, rVals[[6]], qC, λ] /. paramRule1}, {λ, -2, 2},
AxesLabel → {λ, "P(λ)"}, PlotRange → {{-1.5, 1.5}, {-0.1, 0.25}}, PlotLegend → rVals,
LegendPosition → {-0.75, -0.1}, LegendShadow → None, LegendLabel → "recomb. rate r"]
```

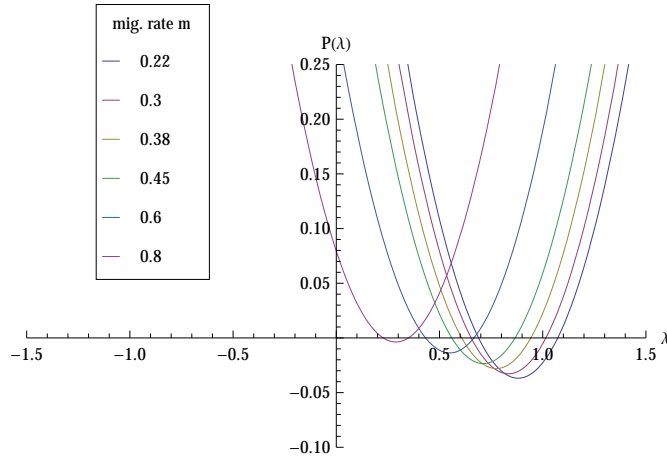


As expected, with increasing values of r , the equilibrium E_B becomes stable, meaning that A_1 cannot invade if $r > r_{\text{crit}}$. The critical recombination rate r_{crit} is still to be determined (see below).

Next, we set $q_c = 0.2$ and consider again increasing migration rates (keeping $r = 0.1$ constant):

```
paramRule2 := {a → 0.2, b → 0.4, m → 0.22, r → 0.1, qC → 0.2};
mVals := {0.22, 0.3, 0.38, 0.45, 0.6, 0.8}
```

```
Plot[{charPolEB1RedFunc[a, b, mVals[[1]], r, qc, λ] /. paramRule2,
charPolEB1RedFunc[a, b, mVals[[2]], r, qc, λ] /. paramRule2,
charPolEB1RedFunc[a, b, mVals[[3]], r, qc, λ] /. paramRule2,
charPolEB1RedFunc[a, b, mVals[[4]], r, qc, λ] /. paramRule2,
charPolEB1RedFunc[a, b, mVals[[5]], r, qc, λ] /. paramRule2,
charPolEB1RedFunc[a, b, mVals[[6]], r, qc, λ] /. paramRule2}, {λ, -2, 2},
AxesLabel → {λ, "P(λ)"}, PlotRange → {{-1.5, 1.5}, {-0.1, 0.25}}, PlotLegend → mVals,
LegendPosition → {-0.75, -0.1}, LegendShadow → None, LegendLabel → "mig. rate m"]
```

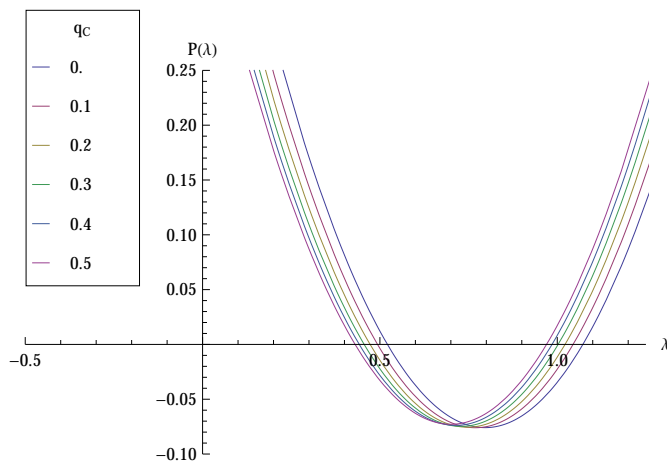


Again, for low migration rates, there is one root > 1 , indicating that E_B is unstable and A_1 can invade. Increasing m further, there is a critical migration rate (still to be determined) beyond which E_B is stable and A_1 cannot invade. However, in contrast to the case of $q_c = 0$, we now do not expect the equilibrium E_B to merge with the monomorphic equilibrium E_C , because some proportion of the immigrants also carries the B_1 allele.

Last, we consider the case of fixed r and m , but varying q_c .

```
paramRule3 := {a → 0.2, b → 0.4, m → 0.22, r → 0.4, qc → 0.2};
qcVals := Range[0, 0.5, 0.1]
```

```
Plot[{charPolEB1RedFunc[a, b, m, r, qcVals[[1]], λ] /. paramRule3,
charPolEB1RedFunc[a, b, m, r, qcVals[[2]], λ] /. paramRule3,
charPolEB1RedFunc[a, b, m, r, qcVals[[3]], λ] /. paramRule3,
charPolEB1RedFunc[a, b, m, r, qcVals[[4]], λ] /. paramRule3,
charPolEB1RedFunc[a, b, m, r, qcVals[[5]], λ] /. paramRule3,
charPolEB1RedFunc[a, b, m, r, qcVals[[6]], λ] /. paramRule3}, {λ, -2, 2},
AxesLabel → {λ, "P(λ)"}, PlotRange → {{-0.5, 1.25}, {-0.1, 0.25}}, PlotLegend → qcVals,
LegendPosition → {-0.95, -0.1}, LegendShadow → None, LegendLabel → "q_c"]
```



This shows how the value of q_c affects the stability of E_B for a choice of parameters. Increasing values of q_c makes it *harder* for A_1 to invade. At first glance, this seems counter-intuitive, because with $q_c > 0$ there is more of the good background allele B_1 on the island.

The critical value of q_c at which E_B changes from stable to unstable for increasing q_c still needs to be determined.

We have thus seen that m , r and q_c are of interest when considering the stability of E_B . Next, we attempt a more systematic analysis, still based on the characteristic polynomial. Our goal is to find conditions for stability of E_B in terms of m , r and q_c , or at least critical

values for these three parameters at which the equilibrium changes its properties (e.g. where it is not hyperbolic).

Conditions for stability of E_B :

E_B is stable if the both roots of the polynomial 'charPolEB1' are between -1 and 1 . This is the case if the following two conditions hold (we use $P(\lambda)$ for the polynomial):

- $P(-1) > 0 \wedge P(1) > 0$
- $P'(-1) < 0 \wedge P'(1) > 0$

where $P'(\tilde{\lambda})$ is the derivative $\frac{d}{d\lambda} P(\lambda)$ evaluated at $\lambda = \tilde{\lambda}$. In the following, we test each of these conditions separately.

Condition 1a: $P(-1) > 0$

We first note that there is another radicand that appears often in the characteristic polynomial. We find that this radicand is always positive given our global restrictions on the parameters.

```
In[110]:= R1 := (b + (-1 + a) m)^2 - 4 b m (-1 + a + b m) qC + 4 b^2 m^2 qC^2
FullSimplify[Reduce[R1 < 0], Assumptions -> assumeGlobal1]
False
FullSimplify[Reduce[(charPolEB1Red /. {lambda -> -1}) > 0],
Assumptions -> Flatten[{assumeGlobal1, Sqrt[R1] > 0}]]
$Aborted
FullSimplify[Reduce[(charPolEB1Red /. {lambda -> -1}) > 0, m],
Assumptions -> Flatten[{assumeGlobal1, Sqrt[R1] > 0}]]
$Aborted
FullSimplify[Reduce[(charPolEB1Red /. {lambda -> -1}) > 0, r],
Assumptions -> Flatten[{assumeGlobal1, Sqrt[R1] > 0}]]
$Aborted
FullSimplify[Reduce[(charPolEB1Red /. {lambda -> -1}) > 0, qC],
Assumptions -> Flatten[{assumeGlobal1, Sqrt[R1] > 0}]]
$Aborted
```

Condition 1b: $P(1) > 0$

```
FullSimplify[Reduce[(charPolEB1Red /. {lambda -> 1}) > 0],
Assumptions -> Flatten[{assumeGlobal1, Sqrt[R1] > 0}]]
$Aborted
FullSimplify[Reduce[(charPolEB1Red /. {lambda -> 1}) > 0, m],
Assumptions -> Flatten[{assumeGlobal1, Sqrt[R1] > 0}]]
$Aborted
FullSimplify[Reduce[(charPolEB1Red /. {lambda -> 1}) > 0, r],
Assumptions -> Flatten[{assumeGlobal1, Sqrt[R1] > 0}]]
$Aborted
FullSimplify[Reduce[(charPolEB1Red /. {lambda -> 1}) > 0, qC],
Assumptions -> Flatten[{assumeGlobal1, Sqrt[R1] > 0}]]
$Aborted
```

We note that none of the inequalities can be solved by Mathematica within reasonable time.

```
In[111]:= DcharPolEB1Red :=
Simplify[D[charPolEB1Red, lambda], Assumptions -> Flatten[{assumeGlobal1, Sqrt[R1] > 0}]]
```


DcharPolEB1Red

$$\frac{1}{1 - 2a + a^2 - b^2} \left(-2 + 2a + b^2 + m - 2am + a^2m + bm + abm - b^2m - \right. \\ \left. 2bmqC - 2abmqC + \sqrt{(b + (-1 + a)m)^2 - 4bm(-1 + a + bm)qC + 4b^2m^2qC^2} + \right. \\ \left. a\sqrt{(b + (-1 + a)m)^2 - 4bm(-1 + a + bm)qC + 4b^2m^2qC^2} + r - ar - bmr + 2bmqr - \right. \\ \left. \sqrt{(b + (-1 + a)m)^2 - 4bm(-1 + a + bm)qC + 4b^2m^2qC^2} r + 2\lambda - 4a\lambda + 2a^2\lambda - 2b^2\lambda \right)$$

Condition 2a: $P'(-1) < 0$

```
Simplify[Reduce[(DcharPolEB1Red /. {λ → -1}) < 0],
  Assumptions → Flatten[{assumeGlobal1, Sqrt[R1] > 0}]]
$Aborted

Simplify[Reduce[(DcharPolEB1Red /. {λ → -1}) < 0, m],
  Assumptions → Flatten[{assumeGlobal1, Sqrt[R1] > 0}]]
$Aborted

Simplify[Reduce[(DcharPolEB1Red /. {λ → -1}) < 0, r],
  Assumptions → Flatten[{assumeGlobal1, Sqrt[R1] > 0}]]
$Aborted

Simplify[Reduce[(DcharPolEB1Red /. {λ → -1}) < 0, qC],
  Assumptions → Flatten[{assumeGlobal1, Sqrt[R1] > 0}]]
$Aborted
```

Condition 2b: $P'(1) > 0$

```
Simplify[Reduce[(DcharPolEB1Red /. {λ → 1}) > 0],
  Assumptions → Flatten[{assumeGlobal1, Sqrt[R1] > 0}]]
$Aborted

Simplify[Reduce[(DcharPolEB1Red /. {λ → 1}) > 0, m],
  Assumptions → Flatten[{assumeGlobal1, Sqrt[R1] > 0}]]
$Aborted

Simplify[Reduce[(DcharPolEB1Red /. {λ → 1}) > 0, r],
  Assumptions → Flatten[{assumeGlobal1, Sqrt[R1] > 0}]]
$Aborted

Simplify[Reduce[(DcharPolEB1Red /. {λ → 1}) > 0, qC],
  Assumptions → Flatten[{assumeGlobal1, Sqrt[R1] > 0}]]
$Aborted
```

Since the steps above did not provide any progress, we try to split off the second eigenvalue from the second-order polynomial,

```
charPolEB1RedRed = FullSimplify[charPolEB1Red/(λ - evalsEB1[[2]]), Assumptions -> Flatten[{assumeGlobal1, Sqrt[R1] > 0}]];
```

The division above takes a long time, so we hard-code it below:

```
In[112]:= charPolEB1RedRed := (a^4 (m^2 + 2 m λ + 2 λ^2) + a (6 m - m sqrt((b + (-1 + a)m)^2 - 4 b m (-1 + a + b m) qC + 4 b^2 m^2 qC^2) + r - ar - bmr + 2bmqr - sqrt((b + (-1 + a)m)^2 - 4 b m (-1 + a + b m) qC + 4 b^2 m^2 qC^2) r + 2 λ - 4 a λ + 2 a^2 λ - 2 b^2 λ))

In[113]:= charPolEB1RedRedFunc[a_, b_, m_, r_, qC_, λ_] := Evaluate[charPolEB1RedRed]

paramRule2
{a → 0.2, b → 0.4, m → 0.22, r → 0.1, qC → 0.2}
```

```
charPolEB1RedRedFunc[a, b, m, r, qC, λ] /. paramRule2
```

$$\frac{1}{-0.689178 + \lambda} 2.17014 \left(0.0016 \left(0.0484 + 0.44 \lambda + 2 \lambda^2 \right) + \right. \\ 0.2 \left(1.27794 - 0.509845 \lambda - 2 \left(0.22 + 2 \lambda \right)^2 - 0.008448 \left(1.22 + 2 \lambda \right) + 4 \left(-0.9 + 3 \lambda \right) - \right. \\ \left. 0.2 \left(0.7084 + 3 \lambda \right) + 0.16 \left(4.13436 - 0.22 \left(4.11865 - 8 \lambda \right) + 0.2 \left(-2 + \lambda \right) - 8.63731 \lambda + 8 \lambda^2 \right) - \right. \\ \left. 0.0528 \left(0.310155 + 2 \lambda - 0.4 \left(0.22 + \lambda \right) \right) \right) + \\ 0.84 \left(0.0527366 - 2 \left(0.613212 - 0.84 \lambda \right) \left(-1 + \lambda \right) + \right. \\ \left. 0.22 \left(0.254923 + 0.16 \left(1 - 2 \lambda \right) + 2 \left(-0.9 + \lambda \right) + 0.24 \left(-2.48135 + 1.8 \lambda \right) \right) \right) + \\ 0.008 \left(-0.094864 + 2 \left(2.21865 - 4 \lambda \right) \lambda + 0.22 \left(2.11865 - 8 \lambda + 0.24 \left(1 + 2 \lambda \right) \right) - 0.04 \right. \\ \left. \left(-0.0895206 + 0.22 \left(5.78238 - 12 \lambda + 0.16 \left(-1 + 4 \lambda \right) - 0.24 \left(3.31865 - 2 \lambda - 0.2 \left(3 + \lambda \right) \right) \right) + \right. \\ \left. \left. 2 \left(-1.31865 + 0.1 \left(1.31865 - 2.68135 \lambda \right) + \lambda \left(6.31865 - 6 \lambda + 0.16 \left(-1 + 2 \lambda \right) \right) \right) \right) \right)$$

We repeat the graphical investigation of 'charPolEB1Red' for 'charPolEB1RedRed'.

First, we set $q_c = 0$ and consider increasing migration rates:

```
paramRule1 := {a → 0.2, b → 0.4, m → 0.22, r → 0.4, qC → 0.};
mVals := {0.22, 0.3, 0.38, 0.45, 0.6, 0.8}
```

Recall the critical values for m with respect to stability of the E_B in the case of $q_c = 0$:

```
paramRule1
```

```
{a → 0.2, b → 0.4, m → 0.22, r → 0.4, qC → 0.}
```

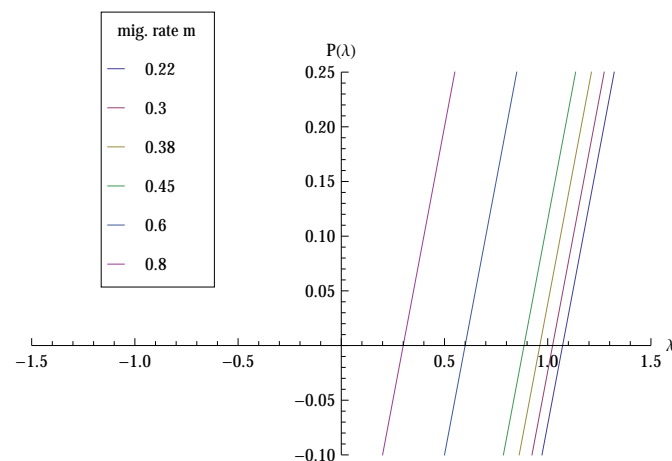
```
{mCrit5,  $\frac{b}{1-a}$ }
```

```
% /. paramRule1
```

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

```
{0.333333, 0.5}
```

```
Plot[{charPolEB1RedRedFunc[a, b, mVals[[1]], r, qC, λ] /. paramRule1,
charPolEB1RedRedFunc[a, b, mVals[[2]], r, qC, λ] /. paramRule1,
charPolEB1RedRedFunc[a, b, mVals[[3]], r, qC, λ] /. paramRule1,
charPolEB1RedRedFunc[a, b, mVals[[4]], r, qC, λ] /. paramRule1,
charPolEB1RedRedFunc[a, b, mVals[[5]], r, qC, λ] /. paramRule1,
charPolEB1RedRedFunc[a, b, mVals[[6]], r, qC, λ] /. paramRule1}, {λ, -2, 2},
AxesLabel → {λ, "P(λ)"}, PlotRange → {{-1.5, 1.5}, {-0.1, 0.25}}, PlotLegend → mVals,
LegendPosition → {-0.75, -0.1}, LegendShadow → None, LegendLabel → "mig. rate m"]
```

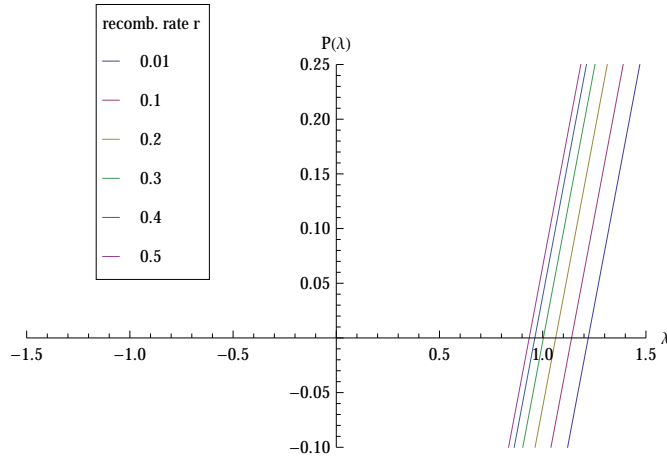


As expected, the root is > 1 (and E_B is unstable) as long as $m < m_{\text{crit},5}$, but when $m_{\text{crit},5} < m$ E_B is stable and A_1 cannot invade anymore.

Next, we consider $q_c = 0$ again, but varying recombination rates. We expect that increasing r makes E_B stable and, on the other hand, makes it harder for A_1 to invade. To see this effect, we change m from 0.22 to 0.38:

```
paramRule1 := {a → 0.2, b → 0.4, m → 0.38, r → 0.4, qC → 0.};
rVals := {0.01, 0.1, 0.2, 0.3, 0.4, 0.5}
```

```
Plot[{charPoleB1RedRedFunc[a, b, m, rVals[[1]], qC, λ] /. paramRule1,
charPoleB1RedRedFunc[a, b, m, rVals[[2]], qC, λ] /. paramRule1,
charPoleB1RedRedFunc[a, b, m, rVals[[3]], qC, λ] /. paramRule1,
charPoleB1RedRedFunc[a, b, m, rVals[[4]], qC, λ] /. paramRule1,
charPoleB1RedRedFunc[a, b, m, rVals[[5]], qC, λ] /. paramRule1,
charPoleB1RedRedFunc[a, b, m, rVals[[6]], qC, λ] /. paramRule1}, {λ, -2, 2},
AxesLabel → {λ, "P(λ)"}, PlotRange → {{-1.5, 1.5}, {-0.1, 0.25}}, PlotLegend → rVals,
LegendPosition → {-0.75, -0.1}, LegendShadow → None, LegendLabel → "recomb. rate r"]
```

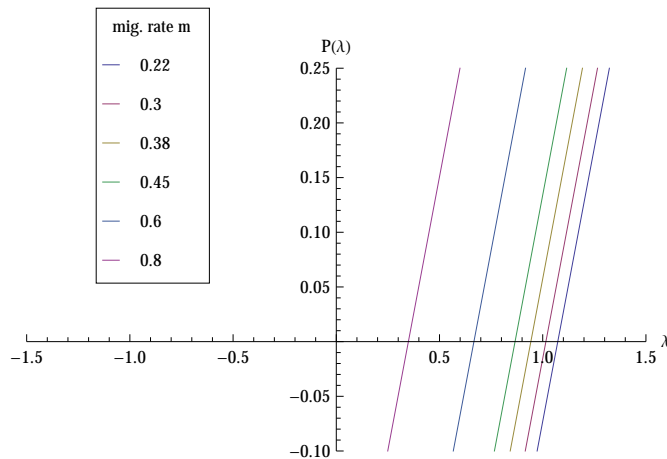


As expected, with increasing values of r , the equilibrium E_B becomes stable, meaning that A_1 cannot invade if $r > r_{\text{crit}}$.

Next, we set $q_c = 0.2 > 0$ and consider again increasing migration rates (having $r = 0.1$ constant):

```
paramRule2 := {a → 0.2, b → 0.4, m → 0.22, r → 0.1, qC → 0.2};
mVals := {0.22, 0.3, 0.38, 0.45, 0.6, 0.8}

Plot[{charPoleB1RedRedFunc[a, b, mVals[[1]], r, qC, λ] /. paramRule2,
charPoleB1RedRedFunc[a, b, mVals[[2]], r, qC, λ] /. paramRule2,
charPoleB1RedRedFunc[a, b, mVals[[3]], r, qC, λ] /. paramRule2,
charPoleB1RedRedFunc[a, b, mVals[[4]], r, qC, λ] /. paramRule2,
charPoleB1RedRedFunc[a, b, mVals[[5]], r, qC, λ] /. paramRule2,
charPoleB1RedRedFunc[a, b, mVals[[6]], r, qC, λ] /. paramRule2}, {λ, -2, 2},
AxesLabel → {λ, "P(λ)"}, PlotRange → {{-1.5, 1.5}, {-0.1, 0.25}}, PlotLegend → mVals,
LegendPosition → {-0.75, -0.1}, LegendShadow → None, LegendLabel → "mig. rate m"]
```

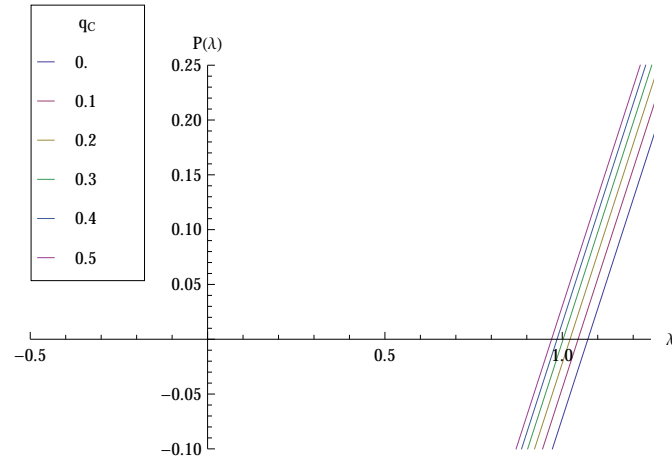


Again, increasing m turns E_B from unstable to stable and, at the same time, makes it impossible for A_1 to invade (increasing m much further does not result in absorption of E_B in E_C , compared to the case of $q_c = 0$, however).

Last, we consider the case of fixed r and m , but varying q_c .

```
paramRule3 := {a → 0.2, b → 0.4, m → 0.22, r → 0.4, qC → 0.2};
qcVals := Range[0, 0.5, 0.1]
```

```
Plot[{charPolEB1RedRedFunc[a, b, m, r, qcVals[[1]], λ] /. paramRule3,
charPolEB1RedRedFunc[a, b, m, r, qcVals[[2]], λ] /. paramRule3,
charPolEB1RedRedFunc[a, b, m, r, qcVals[[3]], λ] /. paramRule3,
charPolEB1RedRedFunc[a, b, m, r, qcVals[[4]], λ] /. paramRule3,
charPolEB1RedRedFunc[a, b, m, r, qcVals[[5]], λ] /. paramRule3,
charPolEB1RedRedFunc[a, b, m, r, qcVals[[6]], λ] /. paramRule3}, {λ, -2, 2},
AxesLabel → {λ, "P(λ)"}, PlotRange → {{-0.5, 1.25}, {-0.1, 0.25}}, PlotLegend → qcVals,
LegendPosition → {-0.95, -0.1}, LegendShadow → None, LegendLabel → "qc"]
```



With increasing q_c , the equilibrium E_B changes from unstable to stable. If q_c is beyond a critical value still to be determined, then A_1 cannot invade anymore.

'charPolEB1RedRed' contains the following radicand several times:

$$\text{In[114]:= R2 := \left(\left((-1+m)^2 (1+m) \left(b^2 (1+m) + 2 b m (-1+2 qC) r + r \left(2 \sqrt{(b+(-1+a) m)^2 - 4 b m (-1+a+b) m} qC \right. \right. \right. \right.$$

R2 /. {R1 → AA}

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

```
FullSimplify[Reduce[(R2 /. {R1 → AA}) < 0],
Assumptions → Flatten[{Sqrt[AA] > 0, assumeGlobal1}]]
```

\$Aborted

```
FullSimplify[Reduce[(charPolEB1RedRed /. {λ → -1}) < 0],
Assumptions → Flatten[{assumeGlobal1, Sqrt[R1] > 0}]]
```

```
FullSimplify[Reduce[(charPolEB1RedRed /. {λ → -1}) < 0, m],
Assumptions → Flatten[{assumeGlobal1, Sqrt[R1] > 0}]]
```

\$Aborted

```
FullSimplify[Reduce[(charPolEB1RedRed /. {λ → -1}) < 0, r],
Assumptions → Flatten[{assumeGlobal1, Sqrt[R1] > 0}]]
```

\$Aborted

```
FullSimplify[Reduce[(charPolEB1RedRed /. {λ → -1}) < 0, qC],
Assumptions → Flatten[{assumeGlobal1, Sqrt[R1] > 0}]]
```

\$Aborted

```
FullSimplify[Reduce[(charPolEB1RedRed /. {λ → 1}) > 0],
Assumptions → Flatten[{assumeGlobal1, Sqrt[R1] > 0}]]
```

\$Aborted

```
FullSimplify[Reduce[(charPolEB1RedRed /. {λ → 1}) > 0, m],
Assumptions → Flatten[{assumeGlobal1, Sqrt[R1] > 0}]]
```

\$Aborted

```
FullSimplify[Reduce[(charPolEB1RedRed /. {λ → 1}) > 0, r],
  Assumptions → Flatten[{assumeGlobal1, Sqrt[R1] > 0}]]
FullSimplify[Reduce[(charPolEB1RedRed /. {λ → 1}) > 0, qC],
  Assumptions → Flatten[{assumeGlobal1, Sqrt[R1] > 0}]]
```

It is not possible within reasonable time to assess whether/when R_2 is positive. Neither is it possible for Mathematica to find a sufficient condition for a root between -1 and 1 .

```
Simplify[(-1 + a)^2 m^2 - 2 (-1 + a) b m (-1 + 2 qC) + b^2 (1 + 4 m^2 (-1 + qC) qC) - R1]
0
mCrit5

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

```

Next, we approximate the characteristic polynomial of the second degree by a Taylor series expansion around $q_c = 0$, keeping terms up to the first order in q_c . We need to tell Mathematica that the radicand below is positive.

```
Simplify[Series[charPolEB1Red, {qC, 0, 1}]] // Normal
```

```
In[115]:= assumel := (b + (-1 + a) m)^2 > 0 && (b - m + a m)^2 > 0
```

```
In[116]:= charPolEB1RedSmallqC = FullSimplify[Series[charPolEB1Red, {qC, 0, 1}],
  Assumptions → Flatten[{assumel, assumeGlobal1}]] // Normal
```

```
Out[116]= 
$$\left[ \frac{1}{(1-a+b)^2} (1 + b + 2 a m - b m + a b m - b^2 m + a^2 m^2 - a b m^2 - r - b r - 2 a m r + m^2 r - 2 a m^2 r + b + a m \geq m \right.$$


$$\left. \begin{aligned} & b m^2 r + (1 - a + b) (-2 + b (-1 + m) - 2 a m + r + m r) \lambda + (1 - a + b)^2 \lambda^2 + \\ & (b m (1 + m) qC (-2 a^2 (m + \lambda) + (1 + b) (b (1 + m) - 2 r (m + \lambda) + 2 (-1 + r + \lambda)) + a \\ & (b (-1 + m + 2 \lambda) + 2 (-1 - m + r + 3 m r + r \lambda))) / ((1 - a + b)^2 (b + (-1 + a) m)) \\ & \frac{((-1+b) (-1+m) + (-1+a+b) \lambda) ((-1+m) (-1+r) + (-1+a+b) \lambda)}{(1-a+b)^2} + \text{True} \\ & (b (-1 + m) m qC (-(-1 + m) ((-1 + b) (2 + b - 2 r) + a (-2 + b + 2 r)) - \\ & 2 (-1 + a + b) (1 + a - r) \lambda) / ((-1 + a + b)^2 (b + (-1 + a) m)) \end{aligned} \right]$$

```

We try to obtain a critical value of m based on the approximate polynomial:

First, for the case of $b + a m \geq m \Leftrightarrow m \leq \frac{b}{1-a} \equiv m_{\text{crit},2}$:

For $q_c = 0$:

```
FullSimplify[Solve[(charPolEB1RedSmallqC[[1, 1, 1]] /. qC → 0 /. λ → 1) == 0, m],
  Assumptions → assumeGlobal1]
{{m → -1}, {m →  $\frac{a(-a + b + r)}{a^2 + r + b r - a(b + 2 r)}$ }}
```

The second solution is equal to $m_{\text{crit},5}$; the characteristic polynomial has collapsed to the one belonging to E_B in the case of $q_c = 0$.

For $q_c > 0$:

```
FullSimplify[Solve[(charPolEB1RedSmallqC[[1, 1, 1]] /. λ → 1) == 0, m],
Assumptions → assumeGlobal1]
```

$$\left\{ \{m \rightarrow -1\}, \right. \\ \left\{ m \rightarrow - \left(a^3 + b(1+b)(bqC+r) - a^2(1+2bqC+r) + a(b^2(-1+qC)+r+b(-1+2qC)(-1+2r)) + \right. \right. \\ \left. \sqrt{(-4ab(a-b-r)(a^3+ab(1+(-2+b)qC)+(1+b)(bqC(b-2r)-r) + \right. \\ \left. a(3+b+6bqC)r - a^2(1+b+2bqC+2r)) + (a^3+b(1+b)(bqC+r) - \right. \\ \left. a^2(1+2bqC+r) + a(b^2(-1+qC)+r+b(-1+2qC)(-1+2r)))^2} \right) / \\ \left. (2(a^3+ab(1+(-2+b)qC)+(1+b)(bqC(b-2r)-r) + a(3+b+6bqC)r - \right. \\ \left. a^2(1+b+2bqC+2r)) \right) \right\}, \\ \left\{ m \rightarrow - \left(a^3 + b(1+b)(bqC+r) - a^2(1+2bqC+r) + a(b^2(-1+qC)+r+b(-1+2qC)(-1+2r)) - \right. \right. \\ \left. \sqrt{(-4ab(a-b-r)(a^3+ab(1+(-2+b)qC)+(1+b)(bqC(b-2r)-r) + \right. \\ \left. a(3+b+6bqC)r - a^2(1+b+2bqC+2r)) + (a^3+b(1+b)(bqC+r) - \right. \\ \left. a^2(1+2bqC+r) + a(b^2(-1+qC)+r+b(-1+2qC)(-1+2r)))^2} \right) / \\ \left. (2(a^3+ab(1+(-2+b)qC)+(1+b)(bqC(b-2r)-r) + a(3+b+6bqC)r - \right. \\ \left. a^2(1+b+2bqC+2r)) \right) \right\} \left. \right\}$$

Second, for the case of $b + a m < m \Leftrightarrow m > \frac{b}{1-a} \equiv m_{\text{crit},2}$:

For $q_c = 0$:

```
FullSimplify[Solve[(charPolEB1RedSmallqC[[2]] /. qc → 0 /. λ → 1) == 0, m],
Assumptions → assumeGlobal1]
```

$$\left\{ \left\{ m \rightarrow -\frac{a}{-1+b} \right\}, \left\{ m \rightarrow \frac{a+b-r}{1-r} \right\} \right\}$$

These solutions are equal to $m_{\text{crit},1}$ and $m_{\text{crit},3}$ already known to be critical values at which the monomorphic equilibrium E_C is hyperbolic in the case of $q_c = 0$.

For $q_c > 0$:

```
Simplify[Solve[(charPolEB1RedSmallqC[[2]] /. λ → 1) == 0, m], Assumptions → assumeGlobal1]
```

```
$Aborted
```

Overall, the first row of 'charPolEB1RedSmallqC' applies under the condition that is necessary for E_B to be in the state space in the case of $q_c = 0$. Since E_B is also an equilibrium in the case of $q_c > 0$, the approximate characteristic polynomial in the first row of 'charPolEB1RedSmallqC' seems of interest here. On the other hand, the second row of 'charPolEB1RedSmallqC' applies under the condition that is necessary for E_B to have merged with E_C in the case of $q_c = 0$. Since E_C is no longer a fix point when $q_c > 0$, the approximate characteristic polynomial in the second row of 'charPolEB1RedSmallqC' is not of interest here. We therefore continue with the first row only:

```
In[117]:= mCrit6ApproxRule = FullSimplify[
  Solve[(charPolE1RedSmallqC[[1, 1, 1]] /. λ → 1) == 0, m], Assumptions → assumeGlobal1]
Out[117]= {{m → -1},
  {m → - (a^3 + b (1 + b) (b qC + r) - a^2 (1 + 2 b qC + r) + a (b^2 (-1 + qC) + r + b (-1 + 2 qC) (-1 + 2 r)) +
    sqrt((-4 a b (a - b - r) (a^3 + a b (1 + (-2 + b) qC) + (1 + b) (b qC (b - 2 r) - r) +
      a (3 + b + 6 b qC) r - a^2 (1 + b + 2 b qC + 2 r)) + (a^3 + b (1 + b) (b qC + r) -
      a^2 (1 + 2 b qC + r) + a (b^2 (-1 + qC) + r + b (-1 + 2 qC) (-1 + 2 r)))^2) /
    (2 (a^3 + a b (1 + (-2 + b) qC) + (1 + b) (b qC (b - 2 r) - r) + a (3 + b + 6 b qC) r -
      a^2 (1 + b + 2 b qC + 2 r)))},
  {m → - (a^3 + b (1 + b) (b qC + r) - a^2 (1 + 2 b qC + r) + a (b^2 (-1 + qC) + r + b (-1 + 2 qC) (-1 + 2 r)) -
    sqrt((-4 a b (a - b - r) (a^3 + a b (1 + (-2 + b) qC) + (1 + b) (b qC (b - 2 r) - r) +
      a (3 + b + 6 b qC) r - a^2 (1 + b + 2 b qC + 2 r)) + (a^3 + b (1 + b) (b qC + r) -
      a^2 (1 + 2 b qC + r) + a (b^2 (-1 + qC) + r + b (-1 + 2 qC) (-1 + 2 r)))^2) /
    (2 (a^3 + a b (1 + (-2 + b) qC) + (1 + b) (b qC (b - 2 r) - r) + a (3 + b + 6 b qC) r -
      a^2 (1 + b + 2 b qC + 2 r)))}}
Length[mCrit6ApproxRule]
3
```

We note that there is another radicand here and try to establish whether it is always positive.

```
In[118]:= R3 := (-4 a b (a - b - r) (a^3 + a b (1 + (-2 + b) qC) + (1 + b) (b qC (b - 2 r) - r) + a (3 + b + 6 b qC) r - a^2 (1 +
  Simplify[Reduce[R3 < 0], Assumptions → assumeGlobal1]
$Aborted
```

The second and third solution in 'mCrit6ApproxRule' are of interest. We assess if the coordinates of the marginal one-locus equilibrium $E_{B,1}$ are biologically valid when the critical values of m are assumed:

If we plug the critical values into the expression for the co-ordinates of $E_{B,1}$, as expected, complicated terms are obtained (below, not run). It seems impossible to judge whether/when these correspond to biologically feasible co-ordinates.

```
Simplify[EB1 /. mCrit6ApproxRule[[2]], Assumptions -> assumeGlobal1]
```

```
Simplify[EB1 /. mCrit6ApproxRule[[3]], Assumptions -> assumeGlobal1]
```

Next, we explore whether we obtain the previously known results in the case of $q_c = 0$.

```
In[119]:= mCrit6ApproxRuleqCZero =
  Simplify[mCrit6ApproxRule /. qC → 0, Assumptions → assumeGlobal1]
Out[119]= {{m → -1}, {m → {
  { -b / (-1+a) a < r
    a (-a+b+r) True
    a^2 + (1+b) r - a (b+2 r)
  }, {m → {
  { -b / (-1+a) a ≥ r
    a (-a+b+r) True
    a^2 + (1+b) r - a (b+2 r)
  }
  }
Simplify[mCrit6ApproxRuleqCZero, Assumptions → a < r]
{{m → -1}, {m → b / (1 - a)}, {m → a (-a + b + r) / (a^2 + (1 + b) r - a (b + 2 r))}}
Simplify[mCrit6ApproxRuleqCZero, Assumptions → a ≥ r]
{{m → -1}, {m → a (-a + b + r) / (a^2 + (1 + b) r - a (b + 2 r))}, {m → b / (1 - a)}}
mCrit5
a (-a + b + r)
(a - b) (a - r) + (1 - a) r
```

$$\text{Simplify}\left[\frac{a(-a+b+r)}{(a-b)(a-r)+(1-a)r} == \frac{a(-a+b+r)}{a^2+(1+b)r-a(b+2r)}\right]$$

True

The result above confirms, for $q_c = 0$, the two critical values we already know: $m_{\text{crit},2}$ and $m_{\text{crit},5}$.

We briefly recall when $m_{\text{crit},2}$ and $m_{\text{crit},5}$ are biologically valid:

$$\text{Simplify}\left[\text{Reduce}\left[0 < \frac{b}{1-a} < 1\right], \text{Assumptions} \rightarrow \text{assumeGlobal1}\right]$$

True

$$\text{FullSimplify}\left[\text{Reduce}\left[0 < m_{\text{crit},5} < 1, r\right], \text{Assumptions} \rightarrow \text{assumeGlobal1}\right]$$

$$(2b = 1 \ \&\& \ 3r > 2a) \ || \ (2a^2 + r + br > 2ab + 3ar \ \&\& \ 2b \neq 1)$$

$$\text{Solve}[m_{\text{crit},5} == 0, r]$$

$$\{\{r \rightarrow a - b\}\}$$

$$\text{Solve}[m_{\text{crit},5} == 1, r]$$

$$\left\{\left\{r \rightarrow \frac{2(a^2 - ab)}{-1 + 3a - b}\right\}\right\}$$

We also recall some further properties derived above for the case of a monomorphic continent:

- If $m = m_{\text{crit},2}$, we have $E_B = E_C$.
- If $m = m_{\text{crit},5}$, we have $q_B = \frac{(a-b)(a-r)}{br}$. Given $b > a$, this q_B is in the biologically relevant state space if $r > a \neq 0$
- Whenever $m_{\text{crit},5}$ is biologically meaningful, we have $0 < m_{\text{crit},5} \leq m_{\text{crit},2} < 1$. As m decreases from 1, we expect that E_B enters the state space via E_C at $m = m_{\text{crit},2}$ and then bifurcates at $m = m_{\text{crit},5}$, which one branch splitting of as the polymorphic internal equilibrium E_+ . According to Bürger and Akerman (2011), this applies only to a subcase of parameter combinations, however.

Rather than setting $q_c = 0$ as above, we now expand the more generic solutions for the critical values of m around $q_c = 0$ in order to obtain an approximation to the complicated critical values 'mCrit6ApproxRule':

$$\text{Simplify}[\text{Series}[m /. m_{\text{crit},6\text{ApproxRule}}, \{q_c, 0, 1\}], \text{Assumptions} \rightarrow \text{assumeGlobal1}] // \text{Normal} // \text{FullSimplify}$$

$$\left\{-1, \left\{\begin{array}{l} b \left(\frac{1}{1-a} + \frac{b q_c (-2a^2 + b(1+b-2r) + a(-2+b+4r))}{(-1+a)^2 (a-b)(a-r)} \right) \quad a < r \\ \frac{a(-a+b+r) \left(a^2 + r + br - \frac{b q_c (b+b^2-a(2+b-2r))r}{(a-b)(a-r)} - a(b+2r) \right)}{(a^2 + r + br - a(b+2r))^2} \quad \text{True} \end{array} \right.\right\}$$

$$\left\{\begin{array}{l} b \left(\frac{1}{1-a} + \frac{b q_c (-2a^2 + b(1+b-2r) + a(-2+b+4r))}{(-1+a)^2 (a-b)(a-r)} \right) \quad a \geq r \\ \frac{a(-a+b+r) \left(a^2 + r + br - \frac{b q_c (b+b^2-a(2+b-2r))r}{(a-b)(a-r)} - a(b+2r) \right)}{(a^2 + r + br - a(b+2r))^2} \quad \text{True} \end{array} \right\}$$

The above syntax means that, in the case of the second element of the output list, if $a < r$ is true, then the entry in the first row in the first column is the answer; otherwise, the entry in the second row in the first column is the answer.

We can simplify this as follows:

$$\text{In}[120]:= m_{\text{crit},6\text{ApproxSeries}} = \text{Simplify}[\text{Series}[m /. m_{\text{crit},6\text{ApproxRule}}, \{q_c, 0, 1\}], \text{Assumptions} \rightarrow \text{Flatten}[\{\text{assumeGlobal1}, a < r\}]] // \text{Normal} // \text{FullSimplify}$$

$$\text{Out}[120]= \left\{-1, b \left(\frac{1}{1-a} + \frac{b q_c (-2a^2 + b(1+b-2r) + a(-2+b+4r))}{(-1+a)^2 (a-b)(a-r)} \right), \frac{a(-a+b+r) \left(a^2 + r + br - \frac{b q_c (b+b^2-a(2+b-2r))r}{(a-b)(a-r)} - a(b+2r) \right)}{(a^2 + r + br - a(b+2r))^2} \right\}$$

Comment: A Taylor series expansion up to and including the second-order term of q_c does not seem to be computable within reasonable time.

Notice that these approximate critical values are twofold approximations: first, they are based on critical values obtained from an approximation of the characteristic polynomial that is valid for q_c close to 0. Second, they are first-order Taylor series approximations to these critical values, again assuming q_c close to 0.

In summary, there are three candidates for an approximations of the critical value of m . Surely, the first one ($m_{\text{crit},6} = -1$) is not biologically valid.

```
Simplify[Reduce[0 < mCrit6ApproxSeries[[2]],
  Assumptions -> Flatten[{assumeGlobal1, a < r}]]
$Aborted
```

If we set $q_c = 0$, do the approximations 'mCrit6ApproxRule' and 'mCrit6ApproxSeries' collapse to 'mCrit5'?

```
mCrit6ApproxRule[[2 ;; 3]]
```

$$\left\{ \left\{ m \rightarrow - \left(a^3 + b(1+b)(bqC+r) - a^2(1+2bqC+r) + a(b^2(-1+qC)+r+b(-1+2qC)(-1+2r)) + \sqrt{(-4ab(a-b-r)(a^3+ab(1+(-2+b)qC)+(1+b)(bqC(b-2r)-r)+a(3+b+6bqC)r-a^2(1+b+2bqC+2r))+(a^3+b(1+b)(bqC+r)-a^2(1+2bqC+r)+a(b^2(-1+qC)+r+b(-1+2qC)(-1+2r)))^2} \right) \right\} / \left(2(a^3+ab(1+(-2+b)qC)+(1+b)(bqC(b-2r)-r)+a(3+b+6bqC)r-a^2(1+b+2bqC+2r)) \right) \right\}, \\ \left\{ m \rightarrow - \left(a^3 + b(1+b)(bqC+r) - a^2(1+2bqC+r) + a(b^2(-1+qC)+r+b(-1+2qC)(-1+2r)) - \sqrt{(-4ab(a-b-r)(a^3+ab(1+(-2+b)qC)+(1+b)(bqC(b-2r)-r)+a(3+b+6bqC)r-a^2(1+b+2bqC+2r))+(a^3+b(1+b)(bqC+r)-a^2(1+2bqC+r)+a(b^2(-1+qC)+r+b(-1+2qC)(-1+2r)))^2} \right) \right\} / \left(2(a^3+ab(1+(-2+b)qC)+(1+b)(bqC(b-2r)-r)+a(3+b+6bqC)r-a^2(1+b+2bqC+2r)) \right) \right\} \right\}$$

```
mCrit6ApproxSeries[[2 ;; 3]]
```

$$\left\{ b \left(\frac{1}{1-a} + \frac{bqC(-2a^2+b(1+b-2r)+a(-2+b+4r))}{(-1+a)^2(a-b)(a-r)} \right), \right. \\ \left. \frac{a(-a+b+r) \left(a^2+r+br - \frac{bqC(b+b^2-a(2+b-2r))r}{(a-b)(a-r)} - a(b+2r) \right)}{(a^2+r+br-a(b+2r))^2} \right\}$$

Recall that for 'mCrit5' to be valid (i.e. associated with biologically meaningful fix point co-ordinates), we require $a < r$. With this assumption, the second entry of 'mCrit6ApproxRule' corresponds to $m_{\text{crit},2}$ and the third entry to $m_{\text{crit},5}$.

```
FullSimplify[(mCrit5 - m /. mCrit6ApproxRule[[2]]) /. qC -> 0,
  Assumptions -> Flatten[{assumeGlobal1, (-a + a^2 + b - 2ab + b^2)^2 > 0, (a - r)^2 > 0, a < r}]]
- \frac{(-1 + a - b)(a - b)(a - r)}{(-1 + a)(a^2 + r + br - a(b + 2r))}
```

The difference to ' $m_{\text{crit},2}$ ' is zero:

```
FullSimplify[\left( \frac{b}{1-a} - m /. mCrit6ApproxRule[[2]] \right) /. qC -> 0,
  Assumptions -> Flatten[{assumeGlobal1, (-a + a^2 + b - 2ab + b^2)^2 > 0, (a - r)^2 > 0, a < r}]]
```

0

For the third element, we expect the difference to ' $m_{\text{crit},5}$ ' to be zero:

```
FullSimplify[(mCrit5 - m /. mCrit6ApproxRule[[3]]) /. qC -> 0,
  Assumptions -> Flatten[{assumeGlobal1, (-a + a^2 + b - 2 a b + b^2)^2 > 0, (a - r)^2 > 0, a < r}]]]
0
```

The same expectations hold for the corresponding Taylor series approximations. The second entry of 'mCrit6ApproxSeries' corresponds to $m_{\text{crit},2}$ and the third entry to $m_{\text{crit},5}$.

```
FullSimplify[(mCrit5 - mCrit6ApproxSeries[[2]]) /. qC -> 0,
  Assumptions -> Flatten[{assumeGlobal1}]]]

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

```

But:

```
FullSimplify[( $\frac{b}{1-a}$  - mCrit6ApproxSeries[[2]]) /. qC -> 0,
  Assumptions -> Flatten[{assumeGlobal1}]]]
0
```

And

```
FullSimplify[(mCrit5 - mCrit6ApproxSeries[[3]]) /. qC -> 0,
  Assumptions -> Flatten[{assumeGlobal1}]]]
0
```

as expected.

```
In[121]:= R4:=(a-b)^2 (1-a+b)^2+8 a^2 b (1-a+b) qC+16 a^2 b^2 qC^2
FullSimplify[Series[m /. mCrit6ApproxRule[[2]], {r, Infinity, 0}],
  Assumptions -> Flatten[{assumeGlobal1}]]]

$$\left( a - a^2 + b - 2 a b + b^2 + 4 a b qC + \sqrt{(a - b)^2 (1 - a + b)^2 + 8 a^2 b (1 - a + b) qC + 16 a^2 b^2 qC^2} \right) /$$


$$(4 a^2 + 2 (1 + b) (1 + 2 b qC) - 2 a (3 + b + 6 b qC)) + O\left[\frac{1}{r}\right]^1$$

FullSimplify[% /. qC -> 0, Assumptions -> assumeGlobal1]

$$\frac{b}{1-a} + O\left[\frac{1}{r}\right]^1$$

FullSimplify[Series[m /. mCrit6ApproxRule[[3]], {r, Infinity, 0}],
  Assumptions -> Flatten[{assumeGlobal1}]]]
(2 a b) /

$$\left( a - a^2 + b - 2 a b + b^2 + 4 a b qC + \sqrt{(a - b)^2 (1 - a + b)^2 + 8 a^2 b (1 - a + b) qC + 16 a^2 b^2 qC^2} \right) + O\left[\frac{1}{r}\right]^1$$

FullSimplify[% /. {qC -> 0}, Assumptions -> assumeGlobal1]

$$\frac{a}{1-2a+b} + O\left[\frac{1}{r}\right]^1$$

Series[mCrit5, {r, Infinity, 0}]

$$\frac{a}{1-2a+b} + O\left[\frac{1}{r}\right]^1$$

```

These calculations suggest that the (approximate) critical values for m make sense, since they collapse to the right values in the marginal case of $q_c = 0$ when $r \rightarrow \infty$.

Next, we plug the approximate critical values of m into the co-ordinates of the marginal one-locus equilibrium and assess when the resulting co-ordinates are biologically relevant (i.e. in the state space).

mCrit6ApproxRule

$$\left\{ \{m \rightarrow -1\}, \right. \\ \left\{ m \rightarrow - \left(a^3 + b(1+b)(bqC+r) - a^2(1+2bqC+r) + a(b^2(-1+qC)+r+b(-1+2qC)(-1+2r)) \right) + \right. \\ \left. \sqrt{\left(-4ab(a-b-r)(a^3+ab(1+(-2+b)qC)+(1+b)(bqC(b-2r)-r) + \right. \right. \\ \left. \left. a(3+b+6bqC)r - a^2(1+b+2bqC+2r) \right) + (a^3+b(1+b)(bqC+r) - \right. \\ \left. \left. a^2(1+2bqC+r) + a(b^2(-1+qC)+r+b(-1+2qC)(-1+2r)) \right)^2 \right) \right\} / \\ \left(2(a^3+ab(1+(-2+b)qC)+(1+b)(bqC(b-2r)-r) + a(3+b+6bqC)r - \right. \\ \left. \left. a^2(1+b+2bqC+2r) \right) \right) \left. \right\}, \\ \left\{ m \rightarrow - \left(a^3 + b(1+b)(bqC+r) - a^2(1+2bqC+r) + a(b^2(-1+qC)+r+b(-1+2qC)(-1+2r)) \right) - \right. \\ \left. \sqrt{\left(-4ab(a-b-r)(a^3+ab(1+(-2+b)qC)+(1+b)(bqC(b-2r)-r) + \right. \right. \\ \left. \left. a(3+b+6bqC)r - a^2(1+b+2bqC+2r) \right) + (a^3+b(1+b)(bqC+r) - \right. \\ \left. \left. a^2(1+2bqC+r) + a(b^2(-1+qC)+r+b(-1+2qC)(-1+2r)) \right)^2 \right) \right\} / \\ \left(2(a^3+ab(1+(-2+b)qC)+(1+b)(bqC(b-2r)-r) + a(3+b+6bqC)r - \right. \\ \left. \left. a^2(1+b+2bqC+2r) \right) \right) \left. \right\}$$

Simplify[mCrit6ApproxRule /. {qC → 0}, Assumptions → Flatten[assumeGlobal1]]

$$\left\{ \{m \rightarrow -1\}, \left\{ m \rightarrow \left[\begin{array}{ll} -\frac{b}{-1+a} & a < r \\ \frac{a(-a+b+r)}{a^2+(1+b)r-a(b+2r)} & \text{True} \end{array} \right], \left\{ m \rightarrow \left[\begin{array}{ll} -\frac{b}{-1+a} & a \geq r \\ \frac{a(-a+b+r)}{a^2+(1+b)r-a(b+2r)} & \text{True} \end{array} \right] \right\} \right\}$$

mCrit6ApproxSeries

$$\left\{ -1, b \left(\frac{1}{1-a} + \frac{bqC(-2a^2+b(1+b-2r)+a(-2+b+4r))}{(-1+a)^2(a-b)(a-r)} \right), \right. \\ \left. \frac{a(-a+b+r) \left(a^2+r+br - \frac{bqC(b+b^2-a(2+b-2r))r}{(a-b)(a-r)} - a(b+2r) \right)}{(a^2+r+br-a(b+2r))^2} \right\}$$

Simplify[mCrit6ApproxSeries /. {qC → 0}, Assumptions → Flatten[assumeGlobal1]]

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

In[122]:= **qEB1CritMApprox =**

Simplify[qEB1 /. mCrit6ApproxRule[[2 ;; 3]], Assumptions → assumeGlobal1];

(* This returns a list with two equilibrium values q_B ;

the first one belongs to the approximate

critical value of m that corresponds to $m_{crit,2}$ for $q_c = 0$,

and the second one to the approximate critical value

of m that corresponds to $m_{crit,5}$ for $q_c = 0$. *)

Simplify[qEB1CritMApprox /. {qC → 0},

Flatten[{(a-b)^2(1-a+b)^2(a-r)^2 > 0, assumeGlobal1, a < r}]]

$$\left\{ 0, \frac{(a-b)(a-r)}{br} \right\}$$

The first entry belongs to the critical value $m_{crit,2}$ and, as expected, in that case the equilibrium E_B collapses to the monomorphic equilibrium E_C . The second entry belongs to the critical value $m_{crit,5}$ and is the expression for q_B we already know for the case of $q_c = 0$.

Working on the terms in 'qEB1CritMApprox' directly to obtain conditions for when they correspond to biologically valid allele frequencies is too complex. However, we may get an approximation to the equilibrium frequencies by expanding them around $q_c = 0$ in a Taylor series:

Reduce[qEB1CritMApprox < 0] (* Not run. *)

```

term1a = Simplify[Series[qEB1CritMAp[1] /. smallForcesRule, {ε, 0, 1}],
  Assumptions → assumeGlobal1];
term1b = Simplify[Series[qEB1CritMAp[2] /. smallForcesRule, {ε, 0, 1}],
  Assumptions → assumeGlobal1];
term2a = Simplify[term1a /. rescaleSmallForcesRule, assumeGlobal1];
term2b = Simplify[term1b /. rescaleSmallForcesRule, assumeGlobal1];
Simplify[Series[Normal[term2a], {qC, 0, 1}], Flatten[{assumeGlobal1}]]


$$\begin{cases} \text{ComplexInfinity } qC + O[qC]^2 & a < r \\ -\frac{a(-1+2b)(a-b-r)qC}{(a-b)(a-r)} + O[qC]^2 & a \geq r \\ \frac{(a-b)(a-r)}{br} + \frac{a(a-b-r)(2a-b-r)qC}{(a-b)(a-r)r} + O[qC]^2 & \text{True} \end{cases}$$


Simplify[Series[Normal[term2b], {qC, 0, 1}], Flatten[{assumeGlobal1}]]


$$\begin{cases} \text{ComplexInfinity } qC + O[qC]^2 & a \geq r \\ \frac{(a-b)(a-r)}{br} + \frac{a(a-b-r)(2a-b-r)qC}{(a-b)(a-r)r} + O[qC]^2 & \text{True} \end{cases}$$


```

These are rough approximations for q_B corresponding to the critical values $m_{\text{crit},2}$ and $m_{\text{crit},5}$, respectively, valid if all evolutionary forces are small and if q_c is close to zero. Recall that $a < r$ is the condition that must hold for the equilibrium E_B to be biologically valid when $m = m_{\text{crit},5}$ and $q_c = 0$. This would imply that

$$\frac{(a-b)(a-r)}{br} + \frac{a(a-b-r)(2a-b-r)qC}{(a-b)(a-r)r} + O[qC]^2$$

is of interest. It is supposed to denote a first order approximation to q_B around $q_c = 0$.

```
Exponent[charPolEB1Red /. {λ → 1}, r]
```

```
1
```

```
rCrit =
```

```
FullSimplify[Solve[(charPolEB1Red /. λ → 1) == 0, r]];
```

```
rCrit
```

$$\left\{ \left\{ r \rightarrow -\left(a^3 (2 - (-2 + m)m) + (-1 + b)(1 + b)m^2 \right. \right. \right. \\ \left. \left. \left(m + b(-1 + 2qC) + \sqrt{(b + (-1 + a)m)^2 - 4bm(-1 + a + bm)qC + 4b^2m^2qC^2} \right) \right. \right. \\ \left. \left. + a^2 \left(-2\sqrt{(b + (-1 + a)m)^2 - 4bm(-1 + a + bm)qC + 4b^2m^2qC^2} \right) \right. \right. \\ \left. \left. m \left(-4 + (-4 + m)m + b(-3 + (-3 + m)m)(-1 + 2qC) - \sqrt{(b + (-1 + a)m)^2 - 4bm(-1 + a + bm)qC + 4b^2m^2qC^2} \right) \right. \right. \\ \left. \left. + am \left(b^2(-1 + m(1 + m)(1 - 2qC)^2) \right. \right. \right. \\ \left. \left. \left. + 3\sqrt{(b + (-1 + a)m)^2 - 4bm(-1 + a + bm)qC + 4b^2m^2qC^2} \right) \right. \right. \\ \left. \left. m \left(3 + 2m + \sqrt{(b + (-1 + a)m)^2 - 4bm(-1 + a + bm)qC + 4b^2m^2qC^2} \right) \right. \right. \\ \left. \left. b(-1 + 2qC) \left(1 + \sqrt{(b + (-1 + a)m)^2 - 4bm(-1 + a + bm)qC + 4b^2m^2qC^2} \right) \right. \right. \\ \left. \left. \left. m \left(2 + 3m + \sqrt{(b + (-1 + a)m)^2 - 4bm(-1 + a + bm)qC + 4b^2m^2qC^2} \right) \right) \right) \right) \right\} / \\ \left(2(-1 + m) \left(-(-1 + b^2)m^2 + a^2(1 + 2m) - 2am(1 + m - bm + 2bmqC) \right) \right) \right\}$$

```
Sqrt[R] -  $\sqrt{(b + (-1 + a)m)^2 - 4bm(-1 + a + bm)qC + 4b^2m^2qC^2}$  // FullSimplify
```

```
0
```

```
rCritSimpl := - $\left( a^3 (2 - (-2 + m)m) + (-1 + b)(1 + b)m^2 \left( m + b(-1 + 2qC) + \sqrt{RR} \right) \right. \right. \right. \\ \left. \left. a^2 \left( -2\sqrt{RR} + m \left( -4 + (-4 + m)m + b(-3 + (-3 + m)m)(-1 + 2qC) - \sqrt{RR} \right) \right) \right. \right. \\ \left. \left. am \left( b^2(-1 + m(1 + m)(1 - 2qC)^2) + 3\sqrt{RR} + m \left( 3 + 2m + \sqrt{RR} \right) \right. \right. \right. \\ \left. \left. \left. b(-1 + 2qC) \left( 1 + \sqrt{RR} + m \left( 2 + 3m + \sqrt{RR} \right) \right) \right) \right) \right) / \\ \left( 2(-1 + m) \left( -(-1 + b^2)m^2 + a^2(1 + 2m) - 2am(1 + m - bm + 2bmqC) \right) \right)$ 
```

```
Collect[rCritSimpl, {a, b, m}]
```

$$\begin{aligned} & \left(-a^3 (2 - (-2 + m) m) - a^2 \left(m \left(-4 + (-4 + m) m + b (-3 + (-3 + m) m) (-1 + 2 qC) - \sqrt{RR} \right) - 2 \sqrt{RR} \right) - \right. \\ & \quad \left. (-1 + b) (1 + b) m^2 \left(m + b (-1 + 2 qC) + \sqrt{RR} \right) - a m \left(b^2 (-1 + m (1 + m) (1 - 2 qC)^2) + \right. \right. \\ & \quad \left. \left. m \left(3 + 2 m + \sqrt{RR} \right) + b (-1 + 2 qC) \left(1 + m \left(2 + 3 m + \sqrt{RR} \right) + \sqrt{RR} \right) + 3 \sqrt{RR} \right) \right) / \\ & \quad \left(2 (-1 + m) \left((1 - b^2) m^2 + a^2 (1 + 2 m) - 2 a m (1 + m - b m + 2 b m qC) \right) \right) \\ \text{rCritSimpl1} & := \left(a^3 (2 + (2 - m) m) - (1 - b) (1 + b) m^2 \left(m - b (1 - 2 qC) + \sqrt{RR} \right) \right. \\ & \quad \left. - a^2 \left(2 \sqrt{RR} + m \left(4 + (4 - m) m - b (3 + (3 - m) m) (1 - 2 qC) + \sqrt{RR} \right) \right) \right. \\ & \quad \left. - a m \left(b^2 (1 - m (1 + m) (1 - 2 qC)^2) - 3 \sqrt{RR} - \right. \right. \\ & \quad \left. \left. m \left(3 + 2 m + \sqrt{RR} \right) + b (1 - 2 qC) \left(1 + \sqrt{RR} + m \left(2 + 3 m + \sqrt{RR} \right) \right) \right) \right) / \\ & \quad \left(2 (1 - m) \left((1 - b^2) m^2 + a^2 (1 + 2 m) - 2 a m (1 + m - b m + 2 b m qC) \right) \right) \\ \text{rCritSimpl} - \text{rCritSimpl1} & // \text{Simplify} \end{aligned}$$

```
0
```

We define the following function of m that will be useful below:

$$\begin{aligned} \tilde{r}^*(m) &= \left(a^3 ((2 - m) m + 2) - a^2 \left(m \left(-b((3 - m) m + 3)(1 - 2 q_c) + (4 - m) m + \sqrt{R} + 4 \right) + 2 \sqrt{R} \right) - \right. \\ & \quad \left. a m \left(b^2 (1 - m(m + 1)(1 - 2 q_c)^2) + b(1 - 2 q_c) \left(m \left(3 m + \sqrt{R} + 2 \right) + \sqrt{R} + 1 \right) - m \left(2 m + \sqrt{R} + 3 \right) - 3 \sqrt{R} \right) - \right. \\ & \quad \left. (1 - b)(b + 1) m^2 \left(-b(1 - 2 q_c) + m + \sqrt{R} \right) \right) / \\ & \quad \left(2 (1 - m) (a^2 (2 m + 1) - 2 a m (2 b m q_c - b m + m + 1) + (1 - b^2) m^2) \right), \end{aligned} \quad (3)$$

where R is as defined above in eq. (1).

```
a m (b^2 (-1 + m (1 + m) (1 - 2 qC)^2) + 3 sqrt(RR) +
  m (3 + 2 m + sqrt(RR)) + b (-1 + 2 qC) (1 + sqrt(RR) + m (2 + 3 m + sqrt(RR))))
a m (b^2 (-1 + m (1 + m) (1 - 2 qC)^2) +
  m (3 + 2 m + sqrt(RR)) + b (-1 + 2 qC) (1 + m (2 + 3 m + sqrt(RR)) + sqrt(RR)) + 3 sqrt(RR))
Solve[r == 0 /. rCrit, m]
$Aborted
```

```
In[123]:=
```

```
rCritFunc[a_, b_, m_, qC_] :=
Chop[- (a^3 (2 - (-2 + m) m) + (-1 + b) (1 + b) m^2 (m + b (-1 + 2 qC) +
  sqrt((b + (-1 + a) m)^2 - 4 b m (-1 + a + b m) qC + 4 b^2 m^2 qC^2)) +
  a^2 (-2 sqrt((b + (-1 + a) m)^2 - 4 b m (-1 + a + b m) qC + 4 b^2 m^2 qC^2) +
  m (-4 + (-4 + m) m + b (-3 + (-3 + m) m) (-1 + 2 qC) -
  sqrt((b + (-1 + a) m)^2 - 4 b m (-1 + a + b m) qC + 4 b^2 m^2 qC^2))) +
  a m (b^2 (-1 + m (1 + m) (1 - 2 qC)^2) + 3 sqrt((b + (-1 + a) m)^2 - 4 b m (-1 + a + b m) qC + 4 b^2
  m^2 qC^2) + m (3 + 2 m + sqrt((b + (-1 + a) m)^2 - 4 b m (-1 + a + b m) qC + 4 b^2 m^2 qC^2))) +
  b (-1 + 2 qC) (1 + sqrt((b + (-1 + a) m)^2 - 4 b m (-1 + a + b m) qC + 4 b^2 m^2 qC^2) +
  m (2 + 3 m + sqrt((b + (-1 + a) m)^2 - 4 b m (-1 + a + b m) qC + 4 b^2 m^2 qC^2)))) /
(2 (-1 + m) (-(-1 + b^2) m^2 + a^2 (1 + 2 m) - 2 a m (1 + m - b m + 2 b m qC)))]
```

In[124]:=

```

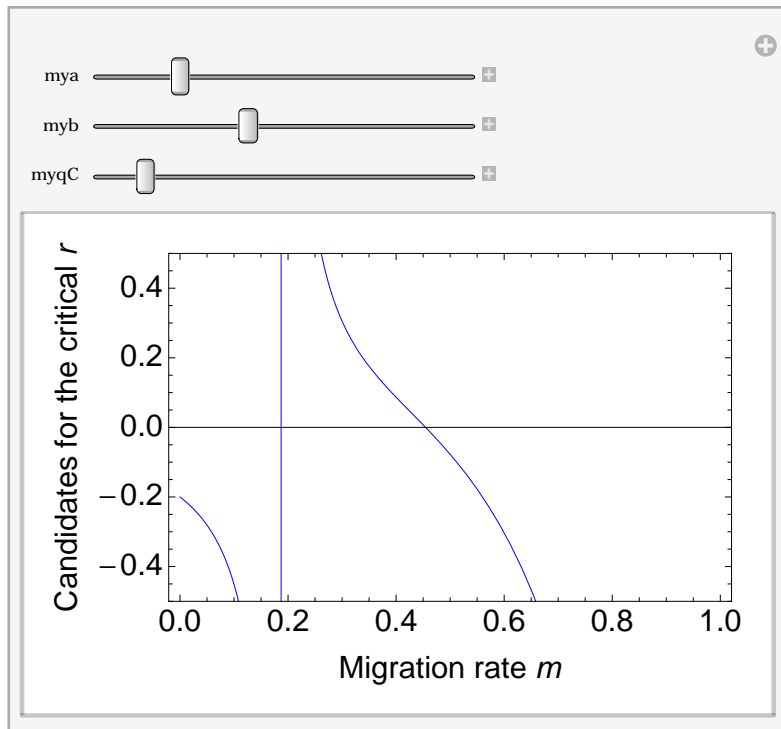
rCritFuncIgnoringPole[a_, b_, m_, qC_, rMax_] :=
Module[{rCrit, mCritSol, mm}, rCrit = Chop[-(a^3 (2 - (-2 + mm) mm) + (-1 + b) (1 + b) mm^2
  (mm + b (-1 + 2 qC) + sqrt((b + (-1 + a) mm)^2 - 4 b mm (-1 + a + b mm) qC + 4 b^2 mm^2 qC^2)) +
  a^2 (-2 sqrt((b + (-1 + a) mm)^2 - 4 b mm (-1 + a + b mm) qC + 4 b^2 mm^2 qC^2)) +
  mm (-4 + (-4 + mm) mm + b (-3 + (-3 + mm) mm) (-1 + 2 qC) -
  sqrt((b + (-1 + a) mm)^2 - 4 b mm (-1 + a + b mm) qC + 4 b^2 mm^2 qC^2))) +
  a mm (b^2 (-1 + mm (1 + mm) (1 - 2 qC)^2) + 3 sqrt((b + (-1 + a) mm)^2 - 4 b
  mm (-1 + a + b mm) qC + 4 b^2 mm^2 qC^2)) +
  mm (3 + 2 mm + sqrt((b + (-1 + a) mm)^2 - 4 b mm (-1 + a + b mm) qC + 4 b^2 mm^2 qC^2)) +
  b (-1 + 2 qC) (1 + sqrt((b + (-1 + a) mm)^2 - 4 b mm (-1 + a + b mm) qC + 4 b^2 mm^2 qC^2)) + mm
  (2 + 3 mm + sqrt((b + (-1 + a) mm)^2 - 4 b mm (-1 + a + b mm) qC + 4 b^2 mm^2 qC^2)))] /
(2 (-1 + mm) (-(-1 + b^2) mm^2 + a^2 (1 + 2 mm) - 2 a mm (1 + mm - b mm + 2 b mm qC)))]];
mCritSol = NSolve[rCrit == rMax, mm];
Return[If[m < mm /. mCritSol[[1]], 0.5, rCrit /. {mm -> m}]]
]

```

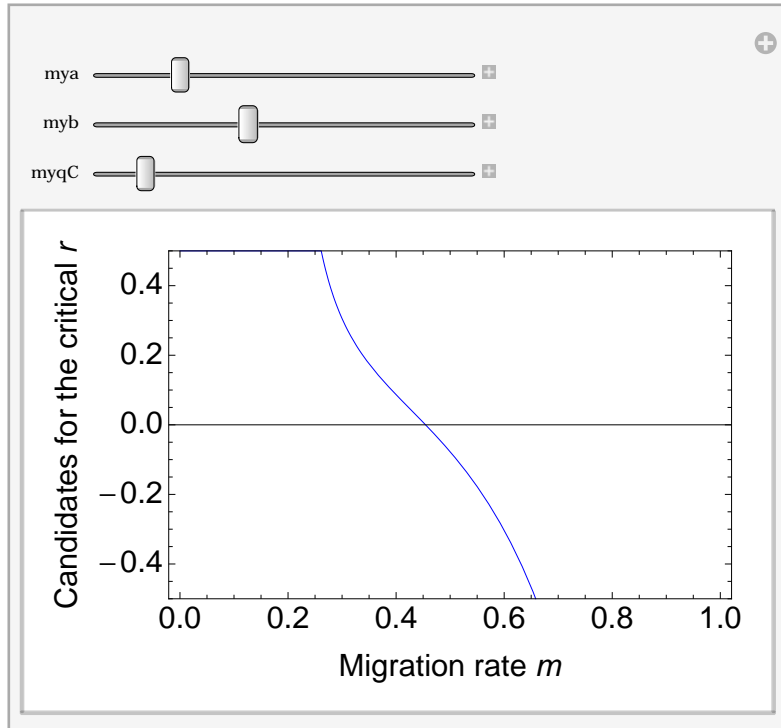
```

Manipulate[
Plot[rCritFunc[mya, myb, m, myqC], {m, 0, 1}, PlotRange -> {Automatic, {-0.5, 0.5}},
(*Epilog -> {Line[{{mya, 0}, {mya, 1}}], *} PlotStyle -> Blue, Frame -> True,
LabelStyle -> {Directive[FontSize -> 16], FontFamily -> "Helvetica"},
FrameLabel -> {"Migration rate m", "Candidates for the critical r"}],
{mya, 0.2}, 0, 1}, {{myb, 0.4}, 0, 1}, {{myqC, 0.1}, 0, 1}]

```



```
Manipulate[Plot[rCritFuncIgnoringPole[mya, myb, m, myqC, 0.5],
  {m, 0, 1}, PlotRange -> {Automatic, {-0.5, 0.5}},
  (*Epilog->{Line[{{mya, 0}, {mya, 1}}]}, *) PlotStyle -> Blue, Frame -> True,
  LabelStyle -> {Directive[FontSize -> 16], FontFamily -> "Helvetica"},
  FrameLabel -> {"Migration rate m", "Candidates for the critical r"}],
  {{mya, 0.2}, 0, 1}, {{myb, 0.4}, 0, 1}, {{myqC, 0.1}, 0, 1}]
```



We conjecture that the marginal one-locus migration-selection equilibrium E_B is unstable and A_1 can invade whenever $r < r^*$, where r^* is a critical migration rate defined as

$$r^* = \begin{cases} 0.5 & m \leq m_r \\ \tilde{r}^*(m) & \text{else,} \end{cases} \quad (4)$$

where m_r is the migration rate at which the function $\tilde{r}^*(m)$ has a pole. In practice, m_r is not easily determined, though.

Approximating the critical value of r , \tilde{r}^* , around $q_c = 0$ in a Taylor series:

```
FullSimplify[Series[r /. rCrit, {qC, 0, 1}], Assumptions -> Flatten[{assumeGlobal1}]]
```

$$\left\{ \begin{array}{l} \frac{a+b-m}{1-m} + \frac{b(-1+a+b)m(2a+b-2m+bm^2)qC}{(-1+m)(b+(-1+a)m)(a+(-1+b)m)} + O[qC]^2 \\ \frac{a(a-b)(1+m)}{a+2am-(1+b)m} + \frac{(-1+a-b)bm(1+m)(b(1+b)m+2a^2(1+m)-a(b+2(1+b)m))qC}{(b+(-1+a)m)(a+2am-(1+b)m)^2} + O[qC]^2 \end{array} \right. \begin{array}{l} b+a m < m \\ \text{True} \end{array}$$

In[125]:=

```
rCritFuncSmallqC[a_, b_, m_, qC_] := If[b + a m < m,
  Chop[
    
$$\frac{a+b-m}{1-m} + \frac{b(-1+a+b)m(2a+b-2m+bm^2)qC}{(-1+m)(b+(-1+a)m)(a+(-1+b)m)}$$
,
    Chop[
      
$$\frac{a(a-b)(1+m)}{a+2am-(1+b)m} + \frac{(-1+a-b)bm(1+m)(b(1+b)m+2a^2(1+m)-a(b+2(1+b)m))qC}{(b+(-1+a)m)(a+2am-(1+b)m)^2}$$

    ]
  ]]
```

The condition $b + a m < m$ is equivalent to $m > \frac{b}{1-a} = m_{\text{crit},2}$. Whenever it is true, the marginal one-locus equilibrium E_B does not exist in the case of a monomorphic continent. This means no B_1 allele is present on the island. However, this cannot occur in the case of a polymorphic continent. Therefore, both approximations above might be of interest.

```

Manipulate[Plot[{rCritFunc[mya, myb, m, myqC], rCritFuncSmallqC[mya, myb, m, myqC]},
  {m, 0, 1}, Epilog -> {Black, Dashed, Line[{{{\frac{myb}{1-myb}, 0}}, {\frac{myb}{1-myb}, 1}}]}},
  PlotRange -> {Automatic, {0, 0.5}}, PlotStyle -> {Blue, {Red, Thick, Dashed}},
  Frame -> True, LabelStyle -> {Directive[FontSize -> 16], FontFamily -> "Helvetica"},
  FrameLabel -> {"Migration rate m", "Candidates for the critical r"}],
  {{mya, 0.2}, 0, 1}, {{myb, 0.4}, 0, 1}, {{myqC, 0.1}, 0, 0.5}]

```

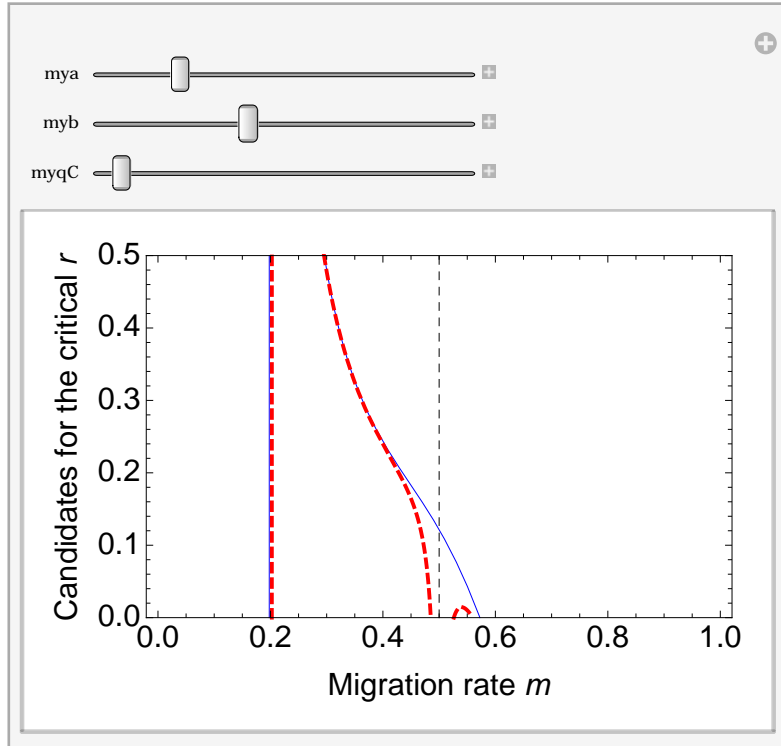


Figure: The red dashed line is the approximation to the blue line, valid for small q_c . For very small q_c , the approximation has an inconsistency at $m = m_{\text{crit},2} = \frac{b}{1-a}$, the critical migration rate above which E_B leaves the state space in the case of a monomorphic continent ($q_c = 0$). This makes the approximation not very useful, as the crucial feature of the dynamics with $q_c > 0$ is the fact that E_B does not leave the state space, independently of m .

Approximating the critical value of r , \tilde{r}^* , around $q_c = 1$ in a Taylor series:

```
FullSimplify[Series[r /. rCrit, {qC, 1, 1}], Assumptions -> Flatten[{assumeGlobal1}]]
```

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

In[126]:=

```

rCritFuncLargeqC[a_, b_, m_, qC_] :=
  Chop[
$$\frac{-a + b + m}{-1 + m} + \frac{(-1 + a - b) b m (2 a - 2 m - b (1 + m^2)) (qC - 1)}{(-1 + m) (b + m - a m) (-a + m + b m)}$$
]

```



```
Manipulate[Plot[{rCritFunc[mya, myb, m, myqC], rCritFuncLargeqC[mya, myb, m, myqC]},
  {m, 0, 1}, PlotRange -> {Automatic, {0, 0.5}}, PlotStyle -> {Blue, {Red, Thick, Dashed}},
  Frame -> True, LabelStyle -> {Directive[FontSize -> 16], FontFamily -> "Helvetica"},
  FrameLabel -> {"Migration rate m", "Candidates for the critical r"},
  {{mya, 0.2}, 0, 1}, {{myb, 0.4}, 0, 1}, {{myqC, 0.1}, 0, 0.5}]
```

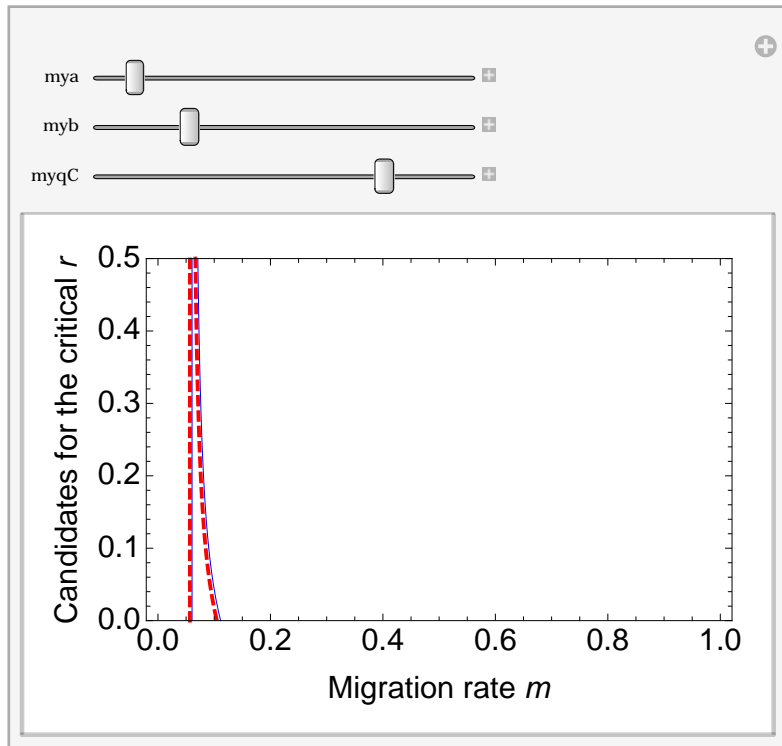


Figure: The red dashed line is the approximation to the blue line, valid for large q_c compared to a , b and m . The approximation is rather sensitive to violations of the assumption.

Finding a critical value of q_c :

```
Exponent[charPolEB1Red /. {λ -> 1}, qC]
```

2

`qCCrit = FullSimplify[Solve[(charPoleEB1Red /. λ → 1) == 0, qC]]`

$$\left\{ \left\{ qC \rightarrow \left(-2 a^3 (1+m) + \right. \right. \right.$$

$$\left. \left. \left(-1+b^2 \right) m \left(b+b m-2 r-\sqrt{b^2(1+m)^2+4 a r+4 m(-1+a+m(-1+r))} r \right) -2 a \right. \right.$$

$$\left. \left. \left(-b^2(1+m)+r-b m(1+m)(-1+2 r)+\sqrt{b^2(1+m)^2+4 a r+4 m(-1+a+m(-1+r))} r - \right. \right.$$

$$\left. \left. r \sqrt{b^2(1+m)^2+4 a r+4 m(-1+a+m(-1+r))} r + \right. \right.$$

$$\left. \left. m r \sqrt{b^2(1+m)^2+4 a r+4 m(-1+a+m(-1+r))} r + \right. \right.$$

$$\left. \left. m^2(-1+(3-2 r) r)+m(-1+2 r(1+r)) \right) + a^2(-2+6 r+ \right.$$

$$\left. \left. m \left(2 m-b(1+m)+6 r-2 m r+\sqrt{b^2(1+m)^2+4 a r+4 m(-1+a+m(-1+r))} r \right) \right) \right) \Bigg/$$

$$\left(2 b m(1+m)(-1+b^2-a(2+a-4 r)) \right) \Bigg\}, \left\{ qC \rightarrow \right.$$

$$\left(-2 a^3(1+m)+(-1+b^2) m \left(b+b m-2 r+\sqrt{b^2(1+m)^2+4 a r+4 m(-1+a+m(-1+r))} r \right) + \right.$$

$$\left. 2 a \left(m+b^2(1+m)-r+b m(1+m)(-1+2 r)+ \right. \right.$$

$$\left. \left. \sqrt{b^2(1+m)^2+4 a r+4 m(-1+a+m(-1+r))} r - \right. \right.$$

$$\left. \left. r \sqrt{b^2(1+m)^2+4 a r+4 m(-1+a+m(-1+r))} r + \right. \right.$$

$$\left. \left. m r \sqrt{b^2(1+m)^2+4 a r+4 m(-1+a+m(-1+r))} r + \right. \right.$$

$$\left. \left. m(-2 r(1+r)+m(-1+r)(-1+2 r)) \right) - a^2(2-6 r+ \right.$$

$$\left. \left. m \left(b-2 m+b m-6 r+2 m r+\sqrt{b^2(1+m)^2+4 a r+4 m(-1+a+m(-1+r))} r \right) \right) \right) \Bigg/$$

$$\left(2 b m(1+m)(-1+b^2-a(2+a-4 r)) \right) \Bigg\}$$

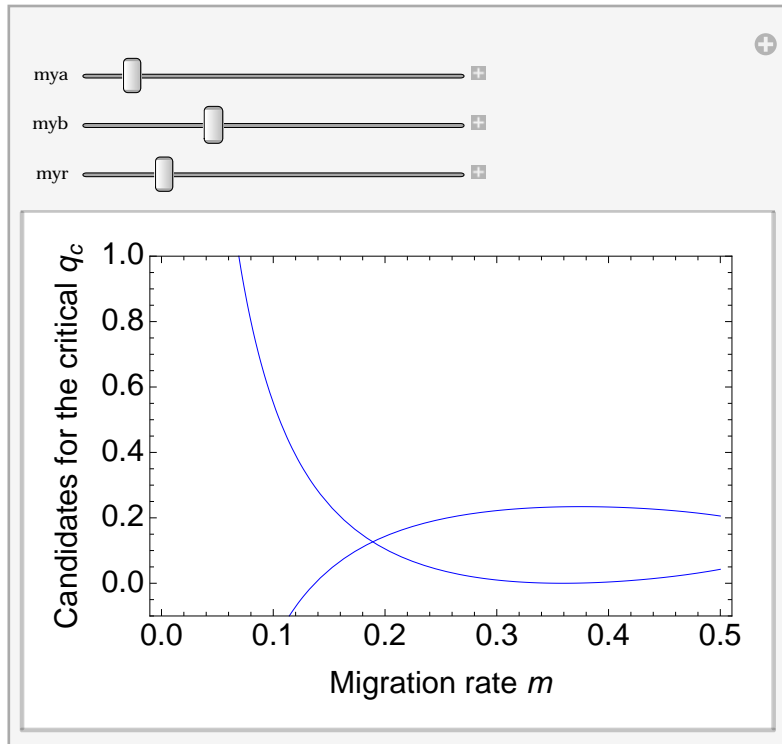
In[127]:=

```

qCCritFunc[a_, b_, m_, r_] := Chop[{{
  (-2 a^3 (1+m) +
  (-1+b^2) m (b+bm-2r - sqrt(b^2 (1+m)^2 + 4 a r + 4 m (-1+a+m (-1+r)) r) - 2 a
  (-b^2 (1+m) + r - bm (1+m) (-1+2r) + sqrt(b^2 (1+m)^2 + 4 a r + 4 m (-1+a+m (-1+r)) r -
  r sqrt(b^2 (1+m)^2 + 4 a r + 4 m (-1+a+m (-1+r)) r +
  m r sqrt(b^2 (1+m)^2 + 4 a r + 4 m (-1+a+m (-1+r)) r +
  m^2 (-1 + (3-2r) r) + m (-1+2r (1+r))) + a^2 (-2+6r+
  m (2m-b (1+m) + 6r-2mr + sqrt(b^2 (1+m)^2 + 4 a r + 4 m (-1+a+m (-1+r)) r))) /
  (2 b m (1+m) (-1+b^2 - a (2+a-4r))), (-2 a^3 (1+m) +
  (-1+b^2) m (b+bm-2r + sqrt(b^2 (1+m)^2 + 4 a r + 4 m (-1+a+m (-1+r)) r) +
  2 a (m+b^2 (1+m) - r + bm (1+m) (-1+2r) +
  sqrt(b^2 (1+m)^2 + 4 a r + 4 m (-1+a+m (-1+r)) r -
  r sqrt(b^2 (1+m)^2 + 4 a r + 4 m (-1+a+m (-1+r)) r +
  m r sqrt(b^2 (1+m)^2 + 4 a r + 4 m (-1+a+m (-1+r)) r +
  m (-2r (1+r) + m (-1+r) (-1+2r))) - a^2 (2-6r+
  m (b-2m+bm-6r+2mr + sqrt(b^2 (1+m)^2 + 4 a r + 4 m (-1+a+m (-1+r)) r))) /
  (2 b m (1+m) (-1+b^2 - a (2+a-4r)))}}]

```

```
Manipulate[Plot[qCCritFunc[mya, myb, m, myr], {m, 0, 0.5},
  PlotRange -> {Automatic, {-0.1, 1}}, PlotStyle -> {Blue}, Frame -> True,
  LabelStyle -> {Directive[FontSize -> 16], FontFamily -> "Helvetica"},
  FrameLabel -> {"Migration rate m", "Candidates for the critical q_c"}],
  {{mya, 0.2}, 0, 1}, {{myb, 0.4}, 0, 1}, {{myr, 0.1}, 0, 0.5}]
```



Approximating the critical value of q_c around $r = 0$ in a Taylor series:

```
FullSimplify[Series[qC /. qCCrit, {r, 0, 1}], Assumptions -> Flatten[{assumeGlobal1}]]
```

$$\left\{ \frac{a(a+b-m)}{b(1+a+b)m} - \frac{(-a+m+bm)(2a+b+ab+b^2-(1+b+a(a+b))m)r}{b^2(1+a+b)^2m(1+m)} + O[r]^2, \right. \\ \left. \frac{(-a+b)(a+(-1+b)m)}{b(-1-a+b)m} + \frac{(a+(-1+b)m)(b+m+a^2m-b(b+m)+a(-2+b-bm))r}{(1+a-b)^2b^2m(1+m)} + O[r]^2 \right\}$$

In[128]:=

```
qCCritFuncLowr[a_, b_, m_, r_] :=
Chop[
$$\left\{ \frac{a(a+b-m)}{b(1+a+b)m} - \frac{(-a+m+bm)(2a+b+ab+b^2-(1+b+a(a+b))m)r}{b^2(1+a+b)^2m(1+m)}, \right.$$


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


$$\left. \frac{(a+(-1+b)m)(b+m+a^2m-b(b+m)+a(-2+b-bm))r}{(1+a-b)^2b^2m(1+m)} \right\}]$$

```

```
Manipulate[Plot[{qCCritFunc[mya, myb, m, myr], qCCritFuncLowr[mya, myb, m, myr]},
  {m, 0, 0.5}, PlotRange -> {Automatic, {0, 1}}, PlotStyle -> {Blue, {Red, Thick, Dashed}},
  Frame -> True, LabelStyle -> {Directive[FontSize -> 16], FontFamily -> "Helvetica"},
  FrameLabel -> {"Migration rate m", "Candidates for the critical q_c"}],
  {{mya, 0.2}, 0, 1}, {{myb, 0.4}, 0, 1}, {{myr, 0.1}, 0, 0.5}]
```

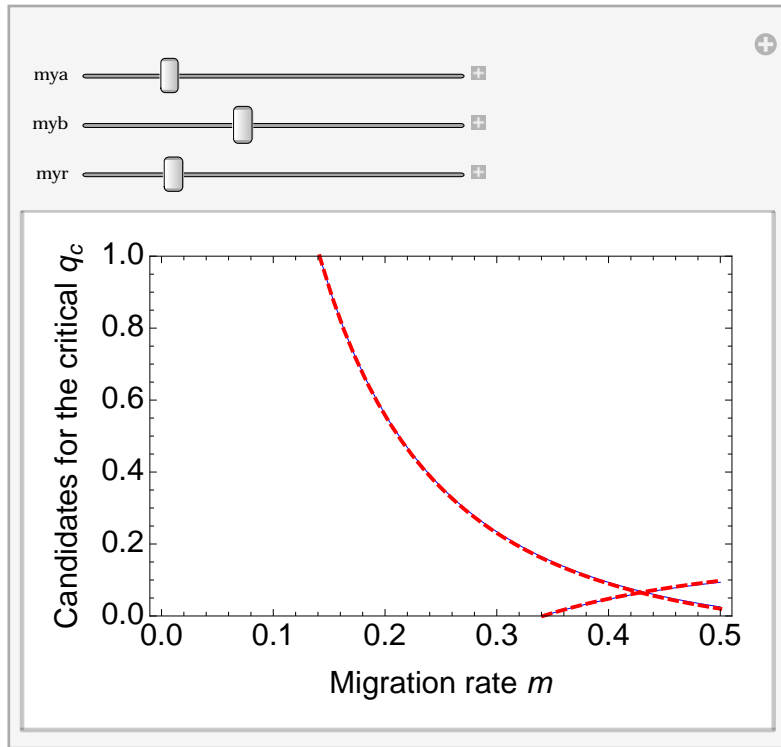


Figure: This approximation for low recombination rates (red dashed) seems very good, even for moderately large values of r . We note that there may be up to two critical values of q_c in the valid state space (between 0 and 1) at the same time.

Approximating the critical value of q_c around $r = 0.5$ in a Taylor series:

```
FullSimplify[Series[qC /. qCCrit, {r, 1/2, 1}], Assumptions -> Flatten[{assumeGlobal}]]
```

$$\left\{ \left(-2 a^3 (1+m) + (-1+b^2) m \left(-1+b+b m - \sqrt{2 a (1+m) + b^2 (1+m)^2 - m (2+m)} \right) - \right. \right. \\ \left. \left. a (1+m) \left(1 - 2 b^2 + \sqrt{2 a (1+m) + b^2 (1+m)^2 - m (2+m)} \right) + \right. \right. \\ \left. \left. a^2 \left(1+m \left(3+m - b (1+m) + \sqrt{2 a (1+m) + b^2 (1+m)^2 - m (2+m)} \right) \right) \right) \right\} / \\ \left(2 b (-1 - a^2 + b^2) m (1+m) + \right. \\ \left. \left(\left(-a^5 m (1+m) - (-1+b^2)^2 m \left(-m + \sqrt{2 a (1+m) + b^2 (1+m)^2 - m (2+m)} \right) - \right. \right. \right. \\ \left. \left. \left. a^3 (1+m) \left(-4 - m (3+m) + b^2 (1+m^2) + \sqrt{2 a (1+m) + b^2 (1+m)^2 - m (2+m)} + \right. \right. \right. \right. \\ \left. \left. \left. m \sqrt{2 a (1+m) + b^2 (1+m)^2 - m (2+m)} \right) + a (-1+b^2) (1+m) \left(b^2 (1+m+m^2) - \right. \right. \right. \\ \left. \left. \left. \sqrt{2 a (1+m) + b^2 (1+m)^2 - m (2+m)} - m \left(m + \sqrt{2 a (1+m) + b^2 (1+m)^2 - m (2+m)} \right) \right) \right) \right) + \\ a^4 \left(-1 + \sqrt{2 a (1+m) + b^2 (1+m)^2 - m (2+m)} + \right. \\ \left. m \left(-2 + \sqrt{2 a (1+m) + b^2 (1+m)^2 - m (2+m)} + m \sqrt{2 a (1+m) + b^2 (1+m)^2 - m (2+m)} \right) \right) \right) - \\ a^2 \left(1 + \sqrt{2 a (1+m) + b^2 (1+m)^2 - m (2+m)} + \right. \\ \left. m \left(m \left(5 + 2 m - \sqrt{2 a (1+m) + b^2 (1+m)^2 - m (2+m)} \right) + \right. \right.$$

$$\begin{aligned}
& 2 \left(3 + \sqrt{2 a (1+m) + b^2 (1+m)^2 - m (2+m)} \right) + \\
& b^2 \left(-3 + \sqrt{2 a (1+m) + b^2 (1+m)^2 - m (2+m)} + \right. \\
& \left. m \left(-8 + m \left(-5 - 2 m + \sqrt{2 a (1+m) + b^2 (1+m)^2 - m (2+m)} \right) \right) \right) \left(r - \frac{1}{2} \right) / \\
& \left(b (1+a^2 - b^2)^2 m (1+m) \sqrt{2 a (1+m) + b^2 (1+m)^2 - m (2+m)} \right) + \\
& o \left[r - \frac{1}{2} \right]^2, \\
& \left(-2 a^3 (1+m) + a (1+m) \left(-1 + 2 b^2 + \sqrt{2 a (1+m) + b^2 (1+m)^2 - m (2+m)} \right) + \right. \\
& \left. (-1 + b^2) m \left(-1 + b + b m + \sqrt{2 a (1+m) + b^2 (1+m)^2 - m (2+m)} \right) + \right. \\
& \left. a^2 \left(1 - m \left(-3 + b - m + b m + \sqrt{2 a (1+m) + b^2 (1+m)^2 - m (2+m)} \right) \right) \right) / \\
& \left(2 b (-1 - a^2 + b^2) m (1+m) \right) + \\
& \left(\left(a^5 m (1+m) - (-1 + b^2)^2 m \left(m + \sqrt{2 a (1+m) + b^2 (1+m)^2 - m (2+m)} \right) \right) - \right. \\
& \left. a (-1 + b^2) (1+m) \left(b^2 (1+m+m^2) + \sqrt{2 a (1+m) + b^2 (1+m)^2 - m (2+m)} + \right. \right. \\
& \left. \left. m \left(-m + \sqrt{2 a (1+m) + b^2 (1+m)^2 - m (2+m)} \right) \right) - a^3 (1+m) \left(4 - b^2 (1+m^2) + \right. \right. \\
& \left. \left. \sqrt{2 a (1+m) + b^2 (1+m)^2 - m (2+m)} + m \left(3 + m + \sqrt{2 a (1+m) + b^2 (1+m)^2 - m (2+m)} \right) \right) \right) + \\
& a^4 \left(1 + \sqrt{2 a (1+m) + b^2 (1+m)^2 - m (2+m)} + m \left(2 + \sqrt{2 a (1+m) + b^2 (1+m)^2 - m (2+m)} + \right. \right. \\
& \left. \left. m \sqrt{2 a (1+m) + b^2 (1+m)^2 - m (2+m)} \right) \right) - a^2 \\
& \left(-1 + \sqrt{2 a (1+m) + b^2 (1+m)^2 - m (2+m)} - m \left(6 - 2 \sqrt{2 a (1+m) + b^2 (1+m)^2 - m (2+m)} + \right. \right. \\
& \left. \left. m \left(5 + 2 m + \sqrt{2 a (1+m) + b^2 (1+m)^2 - m (2+m)} \right) \right) \right) + \\
& b^2 \left(3 + \sqrt{2 a (1+m) + b^2 (1+m)^2 - m (2+m)} + \right. \\
& \left. m \left(8 + m \left(5 + 2 m + \sqrt{2 a (1+m) + b^2 (1+m)^2 - m (2+m)} \right) \right) \right) \left(r - \frac{1}{2} \right) / \\
& \left(b (1+a^2 - b^2)^2 m (1+m) \sqrt{2 a (1+m) + b^2 (1+m)^2 - m (2+m)} \right) + \\
& o \left[r - \frac{1}{2} \right]^2 \}
\end{aligned}$$

Approximating the critical value of q_c around $r = \infty$ in a Taylor series (this means we assume selection and migration to be weak compared to recombination):

```
FullSimplify[Series[qC /. qCCrit, {r, ∞, 1}], Assumptions → Flatten[{assumeGlobal1}]]
```

$$\left\{ \frac{(a + (-1 + b) m) (a + 2 a m - (1 + b) m)}{4 a b m^2} + \frac{1}{16 a^2 b m^4 r} (a + (-1 + b) m) (a - (1 + b) m) (-a^2 + (1 + 2 (-1 + a) a - b^2) m^2) + O\left[\frac{1}{r}\right]^2, \frac{(-1 + m) r}{b (1 + m)} + \frac{2 (-1 + b) m^2 - a (1 + (-4 + m) m)}{4 b m^2} - \frac{1}{16 (b m^4) r} (1 + m) (-2 (-1 + b^2) m^3 + a^2 (-1 + m + m^2 + m^3) - 2 a m (-1 + m (2 + m))) + O\left[\frac{1}{r}\right]^2 \right\}$$

```
In[129]:=
```

$$\text{qCCritFuncHighr}[a_, b_, m_, r_] := \left\{ \frac{(a + (-1 + b) m) (a + 2 a m - (1 + b) m)}{4 a b m^2} + \frac{1}{16 a^2 b m^4 r} (a + (-1 + b) m) (a - (1 + b) m) (-a^2 + (1 + 2 (-1 + a) a - b^2) m^2), \frac{(-1 + m) r}{b (1 + m)} + \frac{2 (-1 + b) m^2 - a (1 + (-4 + m) m)}{4 b m^2} - \frac{1}{16 (b m^4) r} (1 + m) (-2 (-1 + b^2) m^3 + a^2 (-1 + m + m^2 + m^3) - 2 a m (-1 + m (2 + m))) \right\}$$

```
Manipulate[Plot[{qCCritFunc[mya, myb, m, myr], qCCritFuncHighr[mya, myb, m, myr]}, {m, 0, 0.5}, PlotRange → {Automatic, {0, 1}}, PlotStyle → {Blue, {Red, Thick, Dashed}}, Frame → True, LabelStyle → {Directive[FontSize → 16], FontFamily → "Helvetica"}, FrameLabel → {"Migration rate m", "Candidates for the critical q_c"}, {mya, 0.2}, 0, 1], {myb, 0.4}, 0, 1], {myr, 0.1}, 0, 0.5]
```

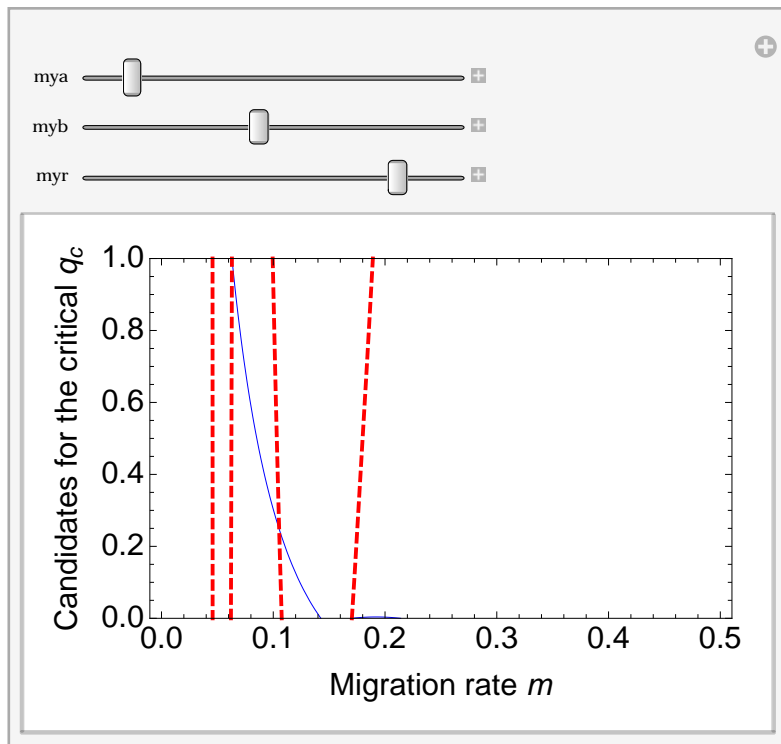


Figure: This approximation for high recombination rates is not useful at all.

Finding a critical value of m :

```

Exponent[charPolEB1Red /. {λ → 1}, r]
1
mCrit =
Simplify[Solve[(charPolEB1Red /. λ → 1) == 0, m], Assumptions → Flatten[{assumeGlobal1}]]
$Aborted

```

When is the first eigenvalue on the unit cycle?

```
FullSimplify[Solve[evalsEB1[[1]] == 1, m], Assumptions → Flatten[{assumeGlobal1}]]
```

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

```
FullSimplify[Solve[evalsEB1[[1]] == -1, m], Assumptions → Flatten[{assumeGlobal1}]]
```

\$Aborted

```
FullSimplify[Solve[evalsEB1[[1]] == 1, qC], Assumptions → Flatten[{assumeGlobal1}]]
```

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

```
FullSimplify[Solve[evalsEB1[[1]] == -1, qC], Assumptions → Flatten[{assumeGlobal1}]]
```

$$\left\{ \left\{ qC \rightarrow -\frac{1}{2 b (-3 + m) m} \left(-3 + \sqrt{-((-1 + a)^2 - b^2)}(-3 + m)(-1 + m)^3 + m - (-3 + m)(a + b m) \right) \right\}, \right. \\ \left. \left\{ qC \rightarrow \frac{1}{2 b (-3 + m) m} \left(3 + \sqrt{-((-1 + a)^2 - b^2)}(-3 + m)(-1 + m)^3 - m + (-3 + m)(a + b m) \right) \right\} \right\}$$

When is the second eigenvalue on the unit cycle?

```
FullSimplify[Solve[(evalsEB1[[2]] /. {qC → 0}) == 1, m],
Assumptions → Flatten[{assumeGlobal1, R1 > 0}]]
```

\$Aborted

```
FullSimplify[Solve[evalsEB1[[2]] == -1, m], Assumptions → Flatten[{assumeGlobal1, R1 > 0}]]
```

\$Aborted

```
FullSimplify[Solve[evalsEB1[[2]] == 1, qC], Assumptions → Flatten[{assumeGlobal1, R1 > 0}]]
```

\$Aborted

```
FullSimplify[Solve[evalsEB1[[2]] == -1, qC],
Assumptions → Flatten[{assumeGlobal1, R1 > 0}]]
```

\$Aborted

```
FullSimplify[Solve[evalsEB1[[2]] == 1, r], Assumptions → Flatten[{assumeGlobal1, R1 > 0}]]
```

\$Aborted

```
FullSimplify[Solve[evalsEB1[[2]] == -1, r], Assumptions → Flatten[{assumeGlobal1, R1 > 0}]]
```

\$Aborted

```
FullSimplify[Solve[(charPolEB1 /. {λ → -1}) == 0, r],
Assumptions → Flatten[{assumeGlobal1, R1 > 0}]]
```



```
FullSimplify[Solve[(charPolEB1 /. {λ → 1}) == 0, m],
  Assumptions → Flatten[{assumeGlobal1, R1 > 0}]]
```

```
$Aborted
```

```
Solve[(charPolEB1 /. {λ → 1}) == 0, m]
```

```
$Aborted
```

```
R1
```

$$(b + (-1 + a) m)^2 - 4 b m (-1 + a + b m) qC + 4 b^2 m^2 qC^2$$

```
R2
```

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

```
R1 == -4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2 // FullSimplify
```

```
True
```

```
R1
```

$$(b + (-1 + a) m)^2 - 4 b m (-1 + a + b m) qC + 4 b^2 m^2 qC^2$$

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

$$b (1 - a + b) (-1 + m) m qC == 0$$

```
Solve[b (1 - a + b) (-1 + m) m qC == 0, m]
```

```
{{m → 0}, {m → 1}}
```

Factor[charPolEB1Red /. λ → 1]

$$\frac{1}{2(-1+a-b)^2(-1+a+b)^2} \left(\begin{aligned} & 2a^2 - 4a^3 + 2a^4 + 4ab^2 - 2a^2b^2 - 2am + 6a^2m - 6a^3m + 2a^4m - bm - 3abm + a^2bm + 3a^3bm - \\ & b^2m + 4ab^2m - 3a^2b^2m + b^3m - 3ab^3m + b^4m + m^2 - 2am^2 + 2a^2m^2 - 2a^3m^2 + a^4m^2 + b^2m^2 - abm^2 - \\ & a^2bm^2 + a^3bm^2 - b^2m^2 + 4ab^2m^2 - a^2b^2m^2 - b^3m^2 - ab^3m^2 + 2bmqC + 6abmqC - 2a^2bmqC - \\ & 6a^3bmqC - 2b^3mqC + 6ab^3mqC - 2b^2mqC + 2abm^2qC + 2a^2bm^2qC - 2a^3bm^2qC - 4b^2m^2qC - \\ & 8ab^2m^2qC - 4a^2b^2m^2qC + 2b^3m^2qC + 2ab^3m^2qC + 4b^4m^2qC + 4b^2m^2qC^2 + 8ab^2m^2qC^2 + \\ & 4a^2b^2m^2qC^2 - 4b^4m^2qC^2 - 2a\sqrt{(b+(-1+a)m)^2 - 4bm(-1+a+bm)}qC + 4b^2m^2qC^2 + \\ & 2a^3\sqrt{(b+(-1+a)m)^2 - 4bm(-1+a+bm)}qC + 4b^2m^2qC^2 - \\ & 2ab^2\sqrt{(b+(-1+a)m)^2 - 4bm(-1+a+bm)}qC + 4b^2m^2qC^2 + \\ & m\sqrt{(b+(-1+a)m)^2 - 4bm(-1+a+bm)}qC + 4b^2m^2qC^2 - \\ & am\sqrt{(b+(-1+a)m)^2 - 4bm(-1+a+bm)}qC + 4b^2m^2qC^2 - \\ & a^2m\sqrt{(b+(-1+a)m)^2 - 4bm(-1+a+bm)}qC + 4b^2m^2qC^2 + \\ & a^3m\sqrt{(b+(-1+a)m)^2 - 4bm(-1+a+bm)}qC + 4b^2m^2qC^2 + \\ & bm\sqrt{(b+(-1+a)m)^2 - 4bm(-1+a+bm)}qC + 4b^2m^2qC^2 + \\ & 2abm\sqrt{(b+(-1+a)m)^2 - 4bm(-1+a+bm)}qC + 4b^2m^2qC^2 + \\ & a^2bm\sqrt{(b+(-1+a)m)^2 - 4bm(-1+a+bm)}qC + 4b^2m^2qC^2 - \\ & b^2m\sqrt{(b+(-1+a)m)^2 - 4bm(-1+a+bm)}qC + 4b^2m^2qC^2 - \\ & ab^2m\sqrt{(b+(-1+a)m)^2 - 4bm(-1+a+bm)}qC + 4b^2m^2qC^2 - \\ & b^3m\sqrt{(b+(-1+a)m)^2 - 4bm(-1+a+bm)}qC + 4b^2m^2qC^2 - \\ & 2bmqC\sqrt{(b+(-1+a)m)^2 - 4bm(-1+a+bm)}qC + 4b^2m^2qC^2 - \\ & 4abmqC\sqrt{(b+(-1+a)m)^2 - 4bm(-1+a+bm)}qC + 4b^2m^2qC^2 - \\ & 2a^2bmqC\sqrt{(b+(-1+a)m)^2 - 4bm(-1+a+bm)}qC + 4b^2m^2qC^2 + \\ & 2b^3mqC\sqrt{(b+(-1+a)m)^2 - 4bm(-1+a+bm)}qC + 4b^2m^2qC^2 - 2ar + 4a^2r - 2a^3r - \\ & 2ab^2r + 2mr - 6amr + 6a^2mr - 2a^3mr + 8abmr - 8a^2bmr - 2b^2mr + 2ab^2mr - \\ & 2a^2m^2r + 4a^2m^2r - 2a^3m^2r - 2b^2m^2r + 4abm^2r - 2a^2bm^2r - 2ab^2m^2r + 2b^3m^2r - \\ & 16abmqCr + 16a^2bmqCr + 4b^2mqCr - 8abm^2qCr + 4a^2bm^2qCr + 16ab^2m^2qCr - \\ & 4b^3m^2qCr - 16ab^2m^2qC^2r + 4a\sqrt{(b+(-1+a)m)^2 - 4bm(-1+a+bm)}qC + 4b^2m^2qC^2r - \\ & 4a^2\sqrt{(b+(-1+a)m)^2 - 4bm(-1+a+bm)}qC + 4b^2m^2qC^2r - \\ & 2m\sqrt{(b+(-1+a)m)^2 - 4bm(-1+a+bm)}qC + 4b^2m^2qC^2r + \\ & 4am\sqrt{(b+(-1+a)m)^2 - 4bm(-1+a+bm)}qC + 4b^2m^2qC^2r - \\ & 2a^2m\sqrt{(b+(-1+a)m)^2 - 4bm(-1+a+bm)}qC + 4b^2m^2qC^2r - \\ & 4abm\sqrt{(b+(-1+a)m)^2 - 4bm(-1+a+bm)}qC + 4b^2m^2qC^2r + \\ & 2b^2m\sqrt{(b+(-1+a)m)^2 - 4bm(-1+a+bm)}qC + 4b^2m^2qC^2r + \\ & 8abmqC\sqrt{(b+(-1+a)m)^2 - 4bm(-1+a+bm)}qC + 4b^2m^2qC^2r \end{aligned} \right)$$

Factor[charPolEB1]

$$\left(\begin{aligned} & -2 + 2a + 2m - 4am + 2a^2m + 5bm - 4abm + a^2bm + 3b^2m - ab^2m + m^2 + 3am^2 - 5a^2m^2 + a^3m^2 - \\ & 11bm^2 + 14abm^2 - 3a^2bm^2 - 8b^2m^2 + 4ab^2m^2 - 2b^3m^2 + 2m^3 - 6am^3 + 6a^2m^3 - 2a^3m^3 + \\ & 6bm^3 - 16abm^3 + 6a^2bm^3 + 8b^2m^3 - 8ab^2m^3 + 4b^3m^3 - 4m^4 + 8am^4 - 6a^2m^4 + 2a^3m^4 + \end{aligned} \right)$$

$$\begin{aligned}
& 8 a b m^4 - 8 a^2 b m^4 - 4 b^2 m^4 + 8 a b^2 m^4 - 2 b^3 m^4 - 2 a m^5 + 4 a^2 m^5 - 2 a^3 m^5 + b m^5 - 4 a b m^5 + \\
& 5 a^2 b m^5 + b^2 m^5 - 3 a b^2 m^5 + m^6 - a m^6 - a^2 m^6 + a^3 m^6 - b m^6 + 2 a b m^6 - a^2 b m^6 - 10 b m qC + \\
& 8 a b m qC - 2 a^2 b m qC + 22 b m^2 qC - 28 a b m^2 qC + 6 a^2 b m^2 qC + 16 b^2 m^2 qC - 8 a b^2 m^2 qC + \\
& 4 b^3 m^2 qC - 12 b m^3 qC + 32 a b m^3 qC - 12 a^2 b m^3 qC - 44 b^2 m^3 qC + 28 a b^2 m^3 qC - 12 b^3 m^3 qC - \\
& 16 a b m^4 qC + 16 a^2 b m^4 qC + 36 b^2 m^4 qC - 36 a b^2 m^4 qC + 16 b^3 m^4 qC - 2 b m^5 qC + 8 a b m^5 qC - \\
& 10 a^2 b m^5 qC - 4 b^2 m^5 qC + 20 a b^2 m^5 qC - 12 b^3 m^5 qC + 2 b m^6 qC - 4 a b m^6 qC + 2 a^2 b m^6 qC - \\
& 4 b^2 m^6 qC - 4 a b^2 m^6 qC + 4 b^3 m^6 qC - 16 b^2 m^2 qC^2 + 8 a b^2 m^2 qC^2 + 44 b^2 m^3 qC^2 - 28 a b^2 m^3 qC^2 + \\
& 12 b^3 m^3 qC^2 - 36 b^2 m^4 qC^2 + 36 a b^2 m^4 qC^2 - 36 b^3 m^4 qC^2 + 4 b^2 m^5 qC^2 - 20 a b^2 m^5 qC^2 + \\
& 36 b^3 m^5 qC^2 + 4 b^2 m^6 qC^2 + 4 a b^2 m^6 qC^2 - 12 b^3 m^6 qC^2 - 8 b^3 m^3 qC^3 + 24 b^3 m^4 qC^3 - \\
& 24 b^3 m^5 qC^3 + 8 b^3 m^6 qC^3 - 2 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} + \\
& 2 a \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} + \\
& 5 m \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} - \\
& 4 a m \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} + \\
& a^2 m \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} + \\
& 3 b m \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} - \\
& a b m \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} - \\
& 2 m^2 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} + \\
& 4 a m^2 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} - \\
& 2 a^2 m^2 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} - \\
& 8 b m^2 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} + \\
& 4 a b m^2 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} - \\
& 2 b^2 m^2 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} - \\
& 2 m^3 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} - \\
& 4 a m^3 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} + \\
& 2 a^2 m^3 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} + \\
& 6 b m^3 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} - \\
& 6 a b m^3 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} + \\
& 4 b^2 m^3 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} + \\
& 2 a m^4 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} - \\
& 2 a^2 m^4 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} + \\
& 4 a b m^4 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} - \\
& 2 b^2 m^4 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} + \\
& m^5 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} + \\
& a^2 m^5 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} - \\
& b m^5 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} - \\
& a b m^5 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} - \\
& 6 b m qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} + \\
& 2 a b m qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} + \\
& 16 b m^2 qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} - \\
& 8 a b m^2 qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} +
\end{aligned}$$

$$\begin{aligned}
& 4 b^2 m^2 qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} - \\
& 12 b m^3 qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} + \\
& 12 a b m^3 qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} - \\
& 12 b^2 m^3 qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} - \\
& 8 a b m^4 qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} + \\
& 12 b^2 m^4 qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} + \\
& 2 b m^5 qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} + \\
& 2 a b m^5 qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} - \\
& 4 b^2 m^5 qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} - \\
& 4 b^2 m^2 qC^2 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} + \\
& 12 b^2 m^3 qC^2 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} - \\
& 12 b^2 m^4 qC^2 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} + \\
& 4 b^2 m^5 qC^2 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} + 2 r - 2 a r - 2 m r + \\
& 4 a m r - 2 a^2 m r - 4 b m r + 2 a b m r - 2 b^2 m r - 2 m^2 r + 2 a^2 m^2 r + 8 b m^2 r - 8 a b m^2 r + 4 b^2 m^2 r + \\
& 4 a b m^3 r + 2 m^4 r - 2 a m^4 r - 8 b m^4 r + 8 a b m^4 r - 4 b^2 m^4 r + 2 m^5 r - 4 a m^5 r + 2 a^2 m^5 r + 4 b m^5 r - \\
& 6 a b m^5 r + 2 b^2 m^5 r - 2 m^6 r + 4 a m^6 r - 2 a^2 m^6 r + 8 b m qC r - 4 a b m qC r - 16 b m^2 qC r + \\
& 16 a b m^2 qC r - 8 b^2 m^2 qC r - 8 a b m^3 qC r + 16 b^2 m^3 qC r + 16 b m^4 qC r - 16 a b m^4 qC r - \\
& 8 b m^5 qC r + 12 a b m^5 qC r - 16 b^2 m^5 qC r + 8 b^2 m^6 qC r + 8 b^2 m^2 qC^2 r - 16 b^2 m^3 qC^2 r + \\
& 16 b^2 m^5 qC^2 r - 8 b^2 m^6 qC^2 r + 2 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} r - \\
& 2 a \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} r - \\
& 4 m \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} r + \\
& 2 a m \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} r - \\
& 2 b m \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} r + \\
& 4 b m^2 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} r + \\
& 4 m^3 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} r - \\
& 2 m^4 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} r + \\
& 2 a m^4 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} r - \\
& 4 b m^4 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} r - \\
& 2 a m^5 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} r + \\
& 2 b m^5 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} r + \\
& 4 b m qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} r - \\
& 8 b m^2 qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} r + \\
& 8 b m^4 qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} r - \\
& 4 b m^5 qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} r + 6 \lambda - 10 a \lambda + \\
& 4 a^2 \lambda + 4 b^2 \lambda - 2 a b^2 \lambda - 4 m \lambda + 10 a m \lambda - 8 a^2 m \lambda + 2 a^3 m \lambda - 23 b m \lambda + 28 a b m \lambda - 7 a^2 b m \lambda - \\
& 12 b^2 m \lambda + 6 a b^2 m \lambda - 3 b^3 m \lambda + m^2 \lambda - 11 a m^2 \lambda + 15 a^2 m^2 \lambda - 5 a^3 m^2 \lambda + 35 b m^2 \lambda - 54 a b m^2 \lambda + \\
& 19 a^2 b m^2 \lambda + 23 b^2 m^2 \lambda - 19 a b^2 m^2 \lambda + 9 b^3 m^2 \lambda - 11 m^3 \lambda + 29 a m^3 \lambda - 25 a^2 m^3 \lambda + 7 a^3 m^3 \lambda - \\
& 7 b m^3 \lambda + 34 a b m^3 \lambda - 23 a^2 b m^3 \lambda - 25 b^2 m^3 \lambda + 29 a b^2 m^3 \lambda - 9 b^3 m^3 \lambda + 5 m^4 \lambda - 15 a m^4 \lambda + \\
& 17 a^2 m^4 \lambda - 7 a^3 m^4 \lambda + b m^4 \lambda - 18 a b m^4 \lambda + 17 a^2 b m^4 \lambda + 9 b^2 m^4 \lambda - 15 a b^2 m^4 \lambda + 3 b^3 m^4 \lambda + \\
& 3 m^5 \lambda - 3 a m^5 \lambda - 3 a^2 m^5 \lambda + 3 a^3 m^5 \lambda - 6 b m^5 \lambda + 10 a b m^5 \lambda - 6 a^2 b m^5 \lambda + b^2 m^5 \lambda + a b^2 m^5 \lambda + \\
& 46 b m qC \lambda - 56 a b m qC \lambda + 14 a^2 b m qC \lambda + 6 b^3 m qC \lambda - 70 b m^2 qC \lambda + 108 a b m^2 qC \lambda - \\
& 38 a^2 b m^2 qC \lambda - 88 b^2 m^2 qC \lambda + 56 a b^2 m^2 qC \lambda - 18 b^3 m^2 qC \lambda + 14 b m^3 qC \lambda - 68 a b m^3 qC \lambda +
\end{aligned}$$

$$\begin{aligned}
& 46 a^2 b m^3 qC \lambda + 160 b^2 m^3 qC \lambda - 128 a b^2 m^3 qC \lambda + 42 b^3 m^3 qC \lambda - 2 b m^4 qC \lambda + 36 a b m^4 qC \lambda - \\
& 34 a^2 b m^4 qC \lambda - 56 b^2 m^4 qC \lambda + 88 a b^2 m^4 qC \lambda - 54 b^3 m^4 qC \lambda + 12 b m^5 qC \lambda - 20 a b m^5 qC \lambda + \\
& 12 a^2 b m^5 qC \lambda - 16 b^2 m^5 qC \lambda - 16 a b^2 m^5 qC \lambda + 24 b^3 m^5 qC \lambda + 88 b^2 m^2 qC^2 \lambda - 56 a b^2 m^2 qC^2 \lambda - \\
& 160 b^2 m^3 qC^2 \lambda + 128 a b^2 m^3 qC^2 \lambda - 72 b^3 m^3 qC^2 \lambda + 56 b^2 m^4 qC^2 \lambda - 88 a b^2 m^4 qC^2 \lambda + \\
& 144 b^3 m^4 qC^2 \lambda + 16 b^2 m^5 qC^2 \lambda + 16 a b^2 m^5 qC^2 \lambda - 72 b^3 m^5 qC^2 \lambda + 48 b^3 m^3 qC^3 \lambda - 96 b^3 m^4 qC^3 \lambda + \\
& 48 b^3 m^5 qC^3 \lambda + 10 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda - \\
& 10 a \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda + \\
& 2 a^2 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda - \\
& 13 m \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda + \\
& 18 a m \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda - \\
& 5 a^2 m \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda - \\
& 16 b m \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda + \\
& 8 a b m \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda - \\
& 3 b^2 m \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda - \\
& m^2 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda - \\
& 10 a m^2 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda + \\
& 7 a^2 m^2 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda + \\
& 28 b m^2 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda - \\
& 20 a b m^2 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda + \\
& 9 b^2 m^2 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda + \\
& m^3 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda + \\
& 6 a m^3 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda - \\
& 7 a^2 m^3 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda - \\
& 8 b m^3 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda + \\
& 16 a b m^3 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda - \\
& 9 b^2 m^3 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda + \\
& 3 m^4 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda - \\
& 4 a m^4 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda + \\
& 3 a^2 m^4 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda - \\
& 4 b m^4 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda - \\
& 4 a b m^4 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda + \\
& 3 b^2 m^4 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda + \\
& 32 b m qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda - \\
& 16 a b m qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda - \\
& 56 b m^2 qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda + \\
& 40 a b m^2 qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda - \\
& 24 b^2 m^2 qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda + \\
& 16 b m^3 qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda - \\
& 32 a b m^3 qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda +
\end{aligned}$$

$$\begin{aligned}
& 48 b^2 m^3 qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda + \\
& 8 b m^4 qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda + \\
& 8 a b m^4 qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda - \\
& 24 b^2 m^4 qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda + \\
& 24 b^2 m^2 qC^2 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda - \\
& 48 b^2 m^3 qC^2 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda + \\
& 24 b^2 m^4 qC^2 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda - 4 r \lambda + 6 a r \lambda - \\
& 2 a^2 r \lambda - 2 b^2 r \lambda + 2 m r \lambda - 4 a m r \lambda + 2 a^2 m r \lambda + 12 b m r \lambda - 10 a b m r \lambda + 4 b^2 m r \lambda + \\
& 2 m^2 r \lambda - 2 a^2 m^2 r \lambda - 12 b m^2 r \lambda + 12 a b m^2 r \lambda - 2 b^2 m^2 r \lambda + 2 m^3 r \lambda - 4 a m^3 r \lambda + 2 a^2 m^3 r \lambda - \\
& 12 b m^3 r \lambda + 8 a b m^3 r \lambda - 2 b^2 m^3 r \lambda + 2 m^4 r \lambda - 6 a m^4 r \lambda + 4 a^2 m^4 r \lambda + 12 b m^4 r \lambda - \\
& 12 a b m^4 r \lambda + 4 b^2 m^4 r \lambda - 4 m^5 r \lambda + 8 a m^5 r \lambda - 4 a^2 m^5 r \lambda + 2 a b m^5 r \lambda - 2 b^2 m^5 r \lambda - \\
& 24 b m qC r \lambda + 20 a b m qC r \lambda + 24 b m^2 qC r \lambda - 24 a b m^2 qC r \lambda + 24 b^2 m^2 qC r \lambda + 24 b m^3 qC r \lambda - \\
& 16 a b m^3 qC r \lambda - 24 b^2 m^3 qC r \lambda - 24 b m^4 qC r \lambda + 24 a b m^4 qC r \lambda - 24 b^2 m^4 qC r \lambda - \\
& 4 a b m^5 qC r \lambda + 24 b^2 m^5 qC r \lambda - 24 b^2 m^2 qC^2 r \lambda + 24 b^2 m^3 qC^2 r \lambda + 24 b^2 m^4 qC^2 r \lambda - \\
& 24 b^2 m^5 qC^2 r \lambda - 6 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} r \lambda + \\
& 4 a \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} r \lambda + \\
& 6 m \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} r \lambda - \\
& 6 a m \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} r \lambda + \\
& 6 b m \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} r \lambda + \\
& 6 m^2 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} r \lambda - \\
& 2 a m^2 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} r \lambda - \\
& 6 b m^2 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} r \lambda - \\
& 6 m^3 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} r \lambda + \\
& 6 a m^3 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} r \lambda - \\
& 6 b m^3 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} r \lambda - \\
& 2 a m^4 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} r \lambda + \\
& 6 b m^4 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} r \lambda - \\
& 12 b m qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} r \lambda + \\
& 12 b m^2 qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} r \lambda + \\
& 12 b m^3 qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} r \lambda - \\
& 12 b m^4 qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} r \lambda - \\
& 6 \lambda^2 + 14 a \lambda^2 - 10 a^2 \lambda^2 + 2 a^3 \lambda^2 - 10 b^2 \lambda^2 + 6 a b^2 \lambda^2 + 2 m \lambda^2 - 6 a m \lambda^2 + 6 a^2 m \lambda^2 - \\
& 2 a^3 m \lambda^2 + 36 b m \lambda^2 - 56 a b m \lambda^2 + 20 a^2 b m \lambda^2 + 10 b^2 m \lambda^2 - 10 a b^2 m \lambda^2 + 8 b^3 m \lambda^2 - \\
& 8 m^2 \lambda^2 + 24 a m^2 \lambda^2 - 24 a^2 m^2 \lambda^2 + 8 a^3 m^2 \lambda^2 - 26 b m^2 \lambda^2 + 52 a b m^2 \lambda^2 - 26 a^2 b m^2 \lambda^2 - \\
& 28 b^2 m^2 \lambda^2 + 28 a b^2 m^2 \lambda^2 - 10 b^3 m^2 \lambda^2 + 10 m^3 \lambda^2 - 30 a m^3 \lambda^2 + 30 a^2 m^3 \lambda^2 - 10 a^3 m^3 \lambda^2 - \\
& 16 a b m^3 \lambda^2 + 16 a^2 b m^3 \lambda^2 + 26 b^2 m^3 \lambda^2 - 26 a b^2 m^3 \lambda^2 + 4 b^3 m^3 \lambda^2 + 2 m^4 \lambda^2 - 2 a m^4 \lambda^2 - \\
& 2 a^2 m^4 \lambda^2 + 2 a^3 m^4 \lambda^2 - 10 b m^4 \lambda^2 + 20 a b m^4 \lambda^2 - 10 a^2 b m^4 \lambda^2 + 2 b^2 m^4 \lambda^2 + 2 a b^2 m^4 \lambda^2 - \\
& 2 b^3 m^4 \lambda^2 - 72 b m qC \lambda^2 + 112 a b m qC \lambda^2 - 40 a^2 b m qC \lambda^2 - 16 b^3 m qC \lambda^2 + 52 b m^2 qC \lambda^2 - \\
& 104 a b m^2 qC \lambda^2 + 52 a^2 b m^2 qC \lambda^2 + 160 b^2 m^2 qC \lambda^2 - 128 a b^2 m^2 qC \lambda^2 + 20 b^3 m^2 qC \lambda^2 + \\
& 32 a b m^3 qC \lambda^2 - 32 a^2 b m^3 qC \lambda^2 - 144 b^2 m^3 qC \lambda^2 + 144 a b^2 m^3 qC \lambda^2 - 56 b^3 m^3 qC \lambda^2 + \\
& 20 b m^4 qC \lambda^2 - 40 a b m^4 qC \lambda^2 + 20 a^2 b m^4 qC \lambda^2 - 16 b^2 m^4 qC \lambda^2 - 16 a b^2 m^4 qC \lambda^2 + \\
& 52 b^3 m^4 qC \lambda^2 - 160 b^2 m^2 qC^2 \lambda^2 + 128 a b^2 m^2 qC^2 \lambda^2 + 144 b^2 m^3 qC^2 \lambda^2 - 144 a b^2 m^3 qC^2 \lambda^2 + \\
& 144 b^3 m^3 qC^2 \lambda^2 + 16 b^2 m^4 qC^2 \lambda^2 + 16 a b^2 m^4 qC^2 \lambda^2 - 144 b^3 m^4 qC^2 \lambda^2 - 96 b^3 m^3 qC^3 \lambda^2 + \\
& 96 b^3 m^4 qC^3 \lambda^2 - 14 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda^2 +
\end{aligned}$$

$$\begin{aligned}
& 20 a \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda^2 - \\
& 6 a^2 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda^2 - \\
& 2 b^2 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda^2 + \\
& 8 m \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda^2 - \\
& 16 a m \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda^2 + \\
& 8 a^2 m \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda^2 + \\
& 28 b m \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda^2 - \\
& 20 a b m \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda^2 + \\
& 4 b^2 m \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda^2 + \\
& 2 m^2 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda^2 + \\
& 4 a m^2 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda^2 - \\
& 6 a^2 m^2 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda^2 - \\
& 24 b m^2 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda^2 + \\
& 24 a b m^2 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda^2 - \\
& 10 b^2 m^2 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda^2 + \\
& 4 m^3 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda^2 - \\
& 8 a m^3 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda^2 + \\
& 4 a^2 m^3 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda^2 - \\
& 4 b m^3 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda^2 - \\
& 4 a b m^3 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda^2 + \\
& 8 b^2 m^3 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda^2 - \\
& 56 b m qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda^2 + \\
& 40 a b m qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda^2 + \\
& 48 b m^2 qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda^2 - \\
& 48 a b m^2 qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda^2 + \\
& 48 b^2 m^2 qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda^2 + \\
& 8 b m^3 qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda^2 + \\
& 8 a b m^3 qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda^2 - \\
& 48 b^2 m^3 qC \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda^2 - \\
& 48 b^2 m^2 qC^2 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda^2 + \\
& 48 b^2 m^3 qC^2 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} \lambda^2 + 2 r \lambda^2 - \\
& 4 a r \lambda^2 + 2 a^2 r \lambda^2 + 2 b^2 r \lambda^2 - 8 b m r \lambda^2 + 8 a b m r \lambda^2 + 8 b m^3 r \lambda^2 - 8 a b m^3 r \lambda^2 - \\
& 2 m^4 r \lambda^2 + 4 a m^4 r \lambda^2 - 2 a^2 m^4 r \lambda^2 - 2 b^2 m^4 r \lambda^2 + 16 b m qC r \lambda^2 - 16 a b m qC r \lambda^2 - \\
& 16 b^2 m^2 qC r \lambda^2 - 16 b m^3 qC r \lambda^2 + 16 a b m^3 qC r \lambda^2 + 16 b^2 m^4 qC r \lambda^2 + 16 b^2 m^2 qC^2 r \lambda^2 - \\
& 16 b^2 m^4 qC^2 r \lambda^2 + 4 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} r \lambda^2 - \\
& 4 a \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} r \lambda^2 - \\
& 4 b m \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} r \lambda^2 - \\
& 4 m^2 \sqrt{-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2} r \lambda^2 +
\end{aligned}$$

$$\begin{aligned}
& 4 a m^2 \sqrt{-4 b (-1+a+b) m (1+m) qC + (b + (-1+a) m + 2 b m qC)^2} r \lambda^2 + \\
& 4 b m^3 \sqrt{-4 b (-1+a+b) m (1+m) qC + (b + (-1+a) m + 2 b m qC)^2} r \lambda^2 + \\
& 8 b m qC \sqrt{-4 b (-1+a+b) m (1+m) qC + (b + (-1+a) m + 2 b m qC)^2} r \lambda^2 - \\
& 8 b m^3 qC \sqrt{-4 b (-1+a+b) m (1+m) qC + (b + (-1+a) m + 2 b m qC)^2} r \lambda^2 + 2 \lambda^3 - 6 a \lambda^3 + \\
& 6 a^2 \lambda^3 - 2 a^3 \lambda^3 + 6 b^2 \lambda^3 - 6 a b^2 \lambda^3 - 18 b m \lambda^3 + 36 a b m \lambda^3 - 18 a^2 b m \lambda^3 - 6 b^3 m \lambda^3 + \\
& 6 m^2 \lambda^3 - 18 a m^2 \lambda^3 + 18 a^2 m^2 \lambda^3 - 6 a^3 m^2 \lambda^3 + 18 b^2 m^2 \lambda^3 - 18 a b^2 m^2 \lambda^3 - 6 b m^3 \lambda^3 + \\
& 12 a b m^3 \lambda^3 - 6 a^2 b m^3 \lambda^3 - 2 b^3 m^3 \lambda^3 + 36 b m qC \lambda^3 - 72 a b m qC \lambda^3 + 36 a^2 b m qC \lambda^3 + \\
& 12 b^3 m qC \lambda^3 - 96 b^2 m^2 qC \lambda^3 + 96 a b^2 m^2 qC \lambda^3 + 12 b m^3 qC \lambda^3 - 24 a b m^3 qC \lambda^3 + \\
& 12 a^2 b m^3 qC \lambda^3 + 36 b^3 m^3 qC \lambda^3 + 96 b^2 m^2 qC^2 \lambda^3 - 96 a b^2 m^2 qC^2 \lambda^3 - 96 b^3 m^3 qC^2 \lambda^3 + \\
& 64 b^3 m^3 qC^3 \lambda^3 + 6 \sqrt{-4 b (-1+a+b) m (1+m) qC + (b + (-1+a) m + 2 b m qC)^2} \lambda^3 - \\
& 12 a \sqrt{-4 b (-1+a+b) m (1+m) qC + (b + (-1+a) m + 2 b m qC)^2} \lambda^3 + \\
& 6 a^2 \sqrt{-4 b (-1+a+b) m (1+m) qC + (b + (-1+a) m + 2 b m qC)^2} \lambda^3 + \\
& 2 b^2 \sqrt{-4 b (-1+a+b) m (1+m) qC + (b + (-1+a) m + 2 b m qC)^2} \lambda^3 - \\
& 16 b m \sqrt{-4 b (-1+a+b) m (1+m) qC + (b + (-1+a) m + 2 b m qC)^2} \lambda^3 + \\
& 16 a b m \sqrt{-4 b (-1+a+b) m (1+m) qC + (b + (-1+a) m + 2 b m qC)^2} \lambda^3 + \\
& 2 m^2 \sqrt{-4 b (-1+a+b) m (1+m) qC + (b + (-1+a) m + 2 b m qC)^2} \lambda^3 - \\
& 4 a m^2 \sqrt{-4 b (-1+a+b) m (1+m) qC + (b + (-1+a) m + 2 b m qC)^2} \lambda^3 + \\
& 2 a^2 m^2 \sqrt{-4 b (-1+a+b) m (1+m) qC + (b + (-1+a) m + 2 b m qC)^2} \lambda^3 + \\
& 6 b^2 m^2 \sqrt{-4 b (-1+a+b) m (1+m) qC + (b + (-1+a) m + 2 b m qC)^2} \lambda^3 + \\
& 32 b m qC \sqrt{-4 b (-1+a+b) m (1+m) qC + (b + (-1+a) m + 2 b m qC)^2} \lambda^3 - \\
& 32 a b m qC \sqrt{-4 b (-1+a+b) m (1+m) qC + (b + (-1+a) m + 2 b m qC)^2} \lambda^3 - \\
& 32 b^2 m^2 qC \sqrt{-4 b (-1+a+b) m (1+m) qC + (b + (-1+a) m + 2 b m qC)^2} \lambda^3 + \\
& 32 b^2 m^2 qC^2 \sqrt{-4 b (-1+a+b) m (1+m) qC + (b + (-1+a) m + 2 b m qC)^2} \lambda^3 \Big) / \\
& \left(2 \left(1 - a - 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)^3 \right)
\end{aligned}$$

```

mGuess1 := m ->  $\frac{-b}{-1+a}$ ;
mGuess2 := m ->  $\frac{a(-a+b+r)}{(a-b)(a-r) + (1-a)r}$ ;
FullSimplify[(charPolEB1 /. mGuess2), Assumptions -> Flatten[{assumeGlobal1}]]
$Aborted
FullSimplify[(charPolEB1 /. mGuess1), Assumptions -> Flatten[{assumeGlobal1}]]
$Aborted

```

We assess the characteristic polynomial for the special case $q_c = 0$.

```
Factor[FullSimplify[charPolEB1 /. ruleMonomorphContin, Assumptions -> assumeGlobal1]]
```

$$\left\{ \begin{array}{ll}
\frac{1}{(-1+a+b)^3} ((-1+a)(-1+m) + (-1+a+b)\lambda) & b + a m < m \\
\frac{1}{(-1+a-b)^3 (-1+m)} (-1+a+2bm-m^2+am^2 + (-1+a-b)(-1+m)\lambda) & \text{True} \\
(1+b+2am-bm+abm-b^2m+a^2m^2-abm^2-r-br-2amr+m^2r- \\
2am^2r+bm^2r+(1-a+b)(-2+b(-1+m)-2am+r+mr)\lambda+(1-a+b)^2\lambda^2) &
\end{array} \right.$$

$$\text{Solve}\left[\left(\frac{1}{(-1+a+b)^3}((-1+a)(-1+m)+(-1+a+b)\lambda)\right.\right. \\ \left.\left.((-1+b)(-1+m)+(-1+a+b)\lambda)((-1+m)(-1+r)+(-1+a+b)\lambda)/\cdot\{\lambda\rightarrow 1\}\right)=0, m\right]$$

$$\left\{\left\{m\rightarrow -\frac{a}{-1+b}\right\}, \left\{m\rightarrow -\frac{b}{-1+a}\right\}, \left\{m\rightarrow \frac{-a-b+r}{-1+r}\right\}\right\}$$

We know these critical migration rates already. They occurred in the stability analysis of the equilibrium E_C in the case of $q_c = 0$.

$$\text{Solve}\left[\left(\frac{1}{(-1+a-b)^3(-1+m)}(-1+a+2bm-m^2+am^2+(-1+a-b)(-1+m)\lambda)\right.\right. \\ \left.\left.(1+b+2am-bm+abm-b^2m+a^2m^2-abm^2-r-br-2amr+m^2r-2am^2r+bm^2r+\right.\right. \\ \left.\left.(1-a+b)(-2+b(-1+m)-2am+r+mr)\lambda+(1-a+b)^2\lambda^2\right)/\cdot\{\lambda\rightarrow 1\}\right)=0, m\right]$$

$$\left\{\{m\rightarrow -1\}, \{m\rightarrow -1\}, \left\{m\rightarrow -\frac{b}{-1+a}\right\}, \left\{m\rightarrow \frac{-a^2+ab+ar}{a^2-ab+r-2ar+br}\right\}\right\}$$

Again, we already know these critical values (apart from the biologically non-relevant one $m = -1$). In particular, the fourth one is equal to 'mCrit5':

$$\text{mCrit5} == \frac{-a^2+ab+ar}{a^2-ab+r-2ar+br} // \text{FullSimplify}$$

True

Implementation of functions

Implementation of numerical iterations of (p, q, D) and plotting functions

■ Recursions

```
In[130]:= (* This works for t ≤ ~2000 on a Mac mini with 4GB. *)
recFuncSmallTimes::usage =
"recFuncSmallTimes[a, b, γ11, γ12, γ21, γ22, m, r, qC, p0, D0, t] iterates the
invasion dynamics of allele frequencies and linkage disequilibrium over
t generations with given parameters and initial values of p0 and D0 for
p and D. It is assumed that q starts at an initial value q0 equal to the
value attained at the marginal one-locus selection-migration equilibrium
if it exists or equal to zero otherwise. Returns the number of generations
simulated, the final values of p, q and D, and the full trajectories
of these. Importantly, this function should only be used for t ≤ ~2000
generations because it uses dynamic programming that is fast but requires
a lot of memory. For larger t, use 'recFuncLargTimes[]' instead. ";
recFuncSmallTimes[a_, b_, γ11_, γ12_, γ21_, γ22_, m_, r_, qC_, p0_, D0_, t_] :=
Module[{pp, qq, DDDD, q0},
Clear[pp, qq, DDDD];
q0 = If[m <  $\frac{b}{1-a}$ ,  $\frac{b-m+am}{b(1+m)}$ , 0];
pp[0] := p0;
qq[0] := q0;
DDDD[0] := D0;
```

```

pp[tt_] :=
  pp[tt] = - ((-1+m) (b (DD+p (-1+2 q)) + DD ((-1-2 DD+2 q) γ11+γ12-q γ12+DD (γ12+2
    γ21-γ22)) + p² (a+(-1+q) (-γ12+q (-2 γ11+γ12+2 γ21-γ22)+γ22)) -
    p (-1+γ12+q (-2 (-1+q) γ11+(-2+q) γ12)+2 DD ((-1+2 q) γ11+
    γ12-q γ12+γ21-2 q γ21+(-1+q) γ22))) /
  (1+a (-1+2 p)+b (-1+2 q)+2 (-DD (-1+2 p) (-γ11+2 q γ11+γ12-q γ12)+
    DD p (-1+2 q) γ21+DD² (-2 γ11+γ12+γ21)+
    p (-1+q) (-(-1+p) (2 q γ11+γ12-q γ12)+p q γ21)) - (DD+p (-1+q))² γ22) /.
  {p → pp[tt-1], q → qq[tt-1], DD → DDDD[tt-1]};

qq[tt_] :=
  qq[tt] = (q-a (-1+m) (DD+(-1+2 p) q)+a m (-1+2 p) qC+DD (-1-2 DD+2 p) γ11+
  q (b q+2 (DD-2 DD p+p (-1+p+q-p q)) γ11)+(DD+p (-1+q)) (DD+p q) γ21-
  m (DD (-1-2 DD+2 p) γ11+DD (DD-p) γ21+
  qC (-1+b+2 DD (γ11-2 p γ11-γ12+p (2 γ12+γ21-γ22))+DD²
  (4 γ11-2 (γ12+γ21)+γ22)+p (-2 (-1+p) γ12+p γ22)) +
  q² (b+p (2 (-1+p) (-1+2 qC) γ11+p γ21+qC (2 γ12-2 p γ12-2 p γ21+p γ22))) +
  q (1-2 b qC+2 DD ((-1+2 p) (-1+2 qC) γ11+p γ21+
  qC (γ12-2 p γ12-2 p γ21+p γ22))-p (2 (-1+p) (-1+2 qC) γ11+
  p γ21+qC (4 γ12-4 p γ12-2 p γ21+2 p γ22))) /
  (1+a (-1+2 p)+b (-1+2 q)+2 (-DD (-1+2 p) (-γ11+2 q γ11+γ12-q γ12)+
    DD p (-1+2 q) γ21+DD² (-2 γ11+γ12+γ21)+
    p (-1+q) (-(-1+p) (2 q γ11+γ12-q γ12)+p q γ21)) - (DD+p (-1+q))² γ22) /.
  {p → pp[tt-1], q → qq[tt-1], DD → DDDD[tt-1]};

DDDD[tt_] :=
  DDDD[tt] = ((1-m) ((DD (1+a p+b q-r-γ11+(q+r) γ11-p (-1+2 q) (γ11-γ21))+
    DD² (-γ11+γ21)+p q (1+a p+b q-(-1+q) ((-1+p) γ11-p γ21)))
  (m-m qC+((-1+m) (1+DD-p+a (-1+p) (DD+(-1+p) (-1+q))+
    b (DD+(-1+p) (-1+q)) (-1+q)-q+p q+DD p γ11+DD q γ11-
    p q γ11-2 DD p q γ11+p² q γ11+p q² γ11-p² q² γ11+DD r γ11-
    DD (r+γ11+DD γ11)+(DD+(-1+p) (-1+q)) (DD+p (-1+q)) γ12)) /
  (-1+a+b-2 a p-2 b q+2 (DD (-1+2 p) (-γ11+2 q γ11+γ12-q γ12)+
    DD² (2 γ11-γ12-γ21)+DD p (1-2 q) γ21+p (-1+q)
    ((-1+p) (2 q γ11+γ12-q γ12)-p q γ21)) + (DD+p (-1+q))² γ22) -
  (m qC - ((-1+m) (DD² γ11+(-1+p) q (1+a (-1+p)+b q+p (-1+q) γ11)+
    DD (1+a (-1+p)+b q-r+(-p-q+2 p q+r) γ11))) /
  (-1+a+b-2 a p-2 b q+2 (DD (-1+2 p) (-γ11+2 q γ11+γ12-q γ12)+
    DD² (2 γ11-γ12-γ21)+DD p (1-2 q) γ21+p (-1+q)
    ((-1+p) (2 q γ11+γ12-q γ12)-p q γ21)) + (DD+p (-1+q))² γ22)
  (-DD r (-1+γ11)-(DD+p (-1+q)) (1+a p+b (-1+q)-γ12+q ((-1+p) γ11+
    γ12-p (γ12+γ21-γ22))+p (γ12-γ22)+DD (γ11-γ12-γ21+γ22)))) /
  (1+a (-1+2 p)+b (-1+2 q)+2 (-DD (-1+2 p) (-γ11+2 q γ11+γ12-q γ12)+
    DD p (-1+2 q) γ21+DD² (-2 γ11+γ12+γ21)+
    p (-1+q) ((1-p) (2 q γ11+γ12-q γ12)+p q γ21)) - (DD+p (-1+q))² γ22) /.
  {p → pp[tt-1], q → qq[tt-1], DD → DDDD[tt-1]};

Return[{t, {pp[t], qq[t], DDDD[t]}}]
];

```

In[132]:= `recFuncLargeTimes::usage =`

"recFuncLargeTimes[a, b, γ11, γ12, γ21, γ22, m, r, qC, p0, D0, t] iterates the invasion dynamics of allele frequencies and linkage disequilibrium over t generations with given parameters and initial values of p0 and D0 for p and D. It is assumed that q starts at an initial value q0 equal to the value attained at the marginal one-locus selection-migration equilibrium if it exists or equal to zero otherwise. Returns the number of generations

simulated, the final values of p, q and D, and the full trajectories of these.";
 recFuncLargeTimes[a_, b_, γ_{11} _, γ_{12} _, γ_{21} _, γ_{22} _, m_, r_, qC_, p0_, D0_, t_] :=

Module[{pp, qq, DDDD, delta, res, n, q0},

(* Return the time in generations when the equilibrium is reached,
 the equilibrium values of {p,q,D},
 and the trajectories of p, q and D. Strictly speaking,
 we assume that the equilibrium has been reached if $(f_i[t] - f_i[t-1])/f_i[t-1] < \delta_i$
 holds for all functions f_i , where $\delta \in \mathbb{R}^+$ is a small positive
 tolerance determined by the system's numerical precision. *)

q0 = If[m < $\frac{b}{1-a}$, $\frac{b-m+a m}{b(1+m)}$, 0];

pp = Table[-9, {i, 0, t}];

qq = Table[-9, {i, 0, t}];

DDDD = Table[-9, {i, 0, t}];

delta[x_, n_] := If[Chop[x[n-1]] == 0,

Chop[x[n]] - Chop[x[n-1]], (Chop[x[n]] - Chop[x[n-1]]) / Chop[x[n-1]]];

pp[[1]] = p0;

qq[[1]] = q0;

DDDD[[1]] = D0;

pp[[2]] =

- ((-1+m) (b (DD+p (-1+2q)) + DD ((-1-2DD+2q) γ_{11} + γ_{12} - q γ_{12} + DD (γ_{12} + 2 γ_{21} - γ_{22})) + p² (a + (-1+q) (- γ_{12} + q (-2 γ_{11} + γ_{12} + 2 γ_{21} - γ_{22}) + γ_{22})) -
 p (-1 + γ_{12} + q (-2 (-1+q) γ_{11} + (-2+q) γ_{12}) + 2 DD ((-1+2q) γ_{11} +
 γ_{12} - q γ_{12} + γ_{21} - 2 q γ_{21} + (-1+q) γ_{22}))) / (1+a (-1+2p) +
 b (-1+2q) + 2 (-DD (-1+2p) (- γ_{11} + 2 q γ_{11} + γ_{12} - q γ_{12}) + DD p (-1+2q) γ_{21} +
 DD² (-2 γ_{11} + γ_{12} + γ_{21}) + p (-1+q) (-(-1+p) (2 q γ_{11} + γ_{12} - q γ_{12}) + p q γ_{21})) -
 (DD+p (-1+q))² γ_{22}) /. {p → pp[[1]], q → qq[[1]], DD → DDDD[[1]]};

qq[[2]] = (q - a (-1+m) (DD + (-1+2p) q) + a m (-1+2p) qC +

DD (-1-2DD+2p) γ_{11} + q (b q + 2 (DD - 2 DD p + p (-1+p+q-pq)) γ_{11}) +

(DD+p (-1+q)) (DD+p q) γ_{21} - m (DD (-1-2DD+2p) γ_{11} + DD (DD-p) γ_{21} +

qC (-1+b+2DD (γ_{11} - 2 p γ_{11} - γ_{12} + p (2 γ_{12} + γ_{21} - γ_{22})) +

DD² (4 γ_{11} - 2 (γ_{12} + γ_{21}) + γ_{22}) + p (-2 (-1+p) γ_{12} + p γ_{22})) +

q² (b+p (2 (-1+p) (-1+2qC) γ_{11} + p γ_{21} + qC (2 γ_{12} - 2 p γ_{12} - 2 p γ_{21} + p γ_{22}))) +

q (1-2bqC+2DD ((-1+2p) (-1+2qC) γ_{11} +

p γ_{21} + qC (γ_{12} - 2 p γ_{12} - 2 p γ_{21} + p γ_{22})) -

p (2 (-1+p) (-1+2qC) γ_{11} + p γ_{21} + qC (4 γ_{12} - 4 p γ_{12} - 2 p γ_{21} + 2 p γ_{22}))) /

(1+a (-1+2p) + b (-1+2q) + 2 (-DD (-1+2p) (- γ_{11} + 2 q γ_{11} + γ_{12} - q γ_{12}) +

DD p (-1+2q) γ_{21} + DD² (-2 γ_{11} + γ_{12} + γ_{21}) +

p (-1+q) (-(-1+p) (2 q γ_{11} + γ_{12} - q γ_{12}) + p q γ_{21})) -

(DD+p (-1+q))² γ_{22}) /. {p → pp[[1]], q → qq[[1]], DD → DDDD[[1]]};

DDDD[[2]] =

((1-m) ((DD (1+a p + b q - r - γ_{11} + (q+r) γ_{11} - p (-1+2q) (γ_{11} - γ_{21})) + DD² (- γ_{11} + γ_{21}) +
 p q (1+a p + b q - (-1+q) ((-1+p) γ_{11} - p γ_{21})))

(m - m qC + ((-1+m) (1+DD-p+a (-1+p) (DD+(-1+p) (-1+q)) +

b (DD+(-1+p) (-1+q)) (-1+q) - q + p q + DD p γ_{11} + DD q γ_{11} -

p q γ_{11} - 2 DD p q γ_{11} + p² q γ_{11} + p q² γ_{11} - p² q² γ_{11} + DD r γ_{11} -

DD (r + γ_{11} + DD γ_{11}) + (DD+(-1+p) (-1+q)) (DD+p (-1+q) γ_{12})) /

(-1+a+b-2a p - 2b q + 2 (DD (-1+2p) (- γ_{11} + 2 q γ_{11} + γ_{12} - q γ_{12}) +

DD² (2 γ_{11} - γ_{12} - γ_{21}) + DD p (1-2q) γ_{21} + p (-1+q)

((-1+p) (2 q γ_{11} + γ_{12} - q γ_{12}) - p q γ_{21})) + (DD+p (-1+q))² γ_{22})) -

(m qC - ((-1+m) (DD² γ_{11} + (-1+p) q (1+a (-1+p) + b q + p (-1+q) γ_{11}) +

$$\frac{\begin{aligned} & DD(1+a(-1+p)+bq-r+(-p-q+2pq+r)\gamma_{11}) \Big/ \\ & (-1+a+b-2ap-2bq+2(DD(-1+2p)(-\gamma_{11}+2q\gamma_{11}+\gamma_{12}-q\gamma_{12})+ \\ & DD^2(2\gamma_{11}-\gamma_{12}-\gamma_{21})+DDp(1-2q)\gamma_{21}+p(-1+q) \\ & ((-1+p)(2q\gamma_{11}+\gamma_{12}-q\gamma_{12})-pq\gamma_{21}))+(DD+p(-1+q))^2\gamma_{22}) \\ & (-DDr(-1+\gamma_{11})-(DD+p(-1+q))(1+ap+b(-1+q)-\gamma_{12}+q((-1+p)\gamma_{11}+ \\ & \gamma_{12}-p(\gamma_{12}+\gamma_{21}-\gamma_{22}))+p(\gamma_{12}-\gamma_{22})+DD(\gamma_{11}-\gamma_{12}-\gamma_{21}+\gamma_{22}))) \Big/ \\ & (1+a(-1+2p)+b(-1+2q)+2(-DD(-1+2p)(-\gamma_{11}+2q\gamma_{11}+\gamma_{12}-q\gamma_{12})+ \\ & DDp(-1+2q)\gamma_{21}+DD^2(-2\gamma_{11}+\gamma_{12}+\gamma_{21})+ \\ & p(-1+q)(-(-1+p)(2q\gamma_{11}+\gamma_{12}-q\gamma_{12})+pq\gamma_{21}))- \\ & (DD+p(-1+q))^2\gamma_{22}) \Big/ . \{p \rightarrow pp[[1]], q \rightarrow qq[[1]], DD \rightarrow DDDD[[\\ & 1]]\}; \end{aligned}}$$

n = 2;

While[And[Total[Boole[Chop[delta[#, n] // N] == 0 & /@ {pp, qq, DDDD}] < 3, n ≤ t],

n = n + 1;

pp[[n] =

$$\begin{aligned} & -((-1+m)(b(DD+p(-1+2q))+DD((-1-2DD+2q)\gamma_{11}+\gamma_{12}-q\gamma_{12}+DD(\gamma_{12}+2\gamma_{21}- \\ & \gamma_{22}))+p^2(a+(-1+q)(-\gamma_{12}+q(-2\gamma_{11}+\gamma_{12}+2\gamma_{21}-\gamma_{22}))+\gamma_{22}))- \\ & p(-1+\gamma_{12}+q(-2(-1+q)\gamma_{11}+(-2+q)\gamma_{12}))+2DD((-1+2q)\gamma_{11}+ \\ & \gamma_{12}-q\gamma_{12}+\gamma_{21}-2q\gamma_{21}+(-1+q)\gamma_{22}))) \Big/ (1+a(-1+2p)+ \\ & b(-1+2q)+2(-DD(-1+2p)(-\gamma_{11}+2q\gamma_{11}+\gamma_{12}-q\gamma_{12}))+DDp(-1+2q)\gamma_{21}+ \\ & DD^2(-2\gamma_{11}+\gamma_{12}+\gamma_{21}))+p(-1+q)(-(-1+p)(2q\gamma_{11}+\gamma_{12}-q\gamma_{12}))+pq\gamma_{21})) - \\ & (DD+p(-1+q))^2\gamma_{22}) \Big/ . \{p \rightarrow pp[[n-1]], q \rightarrow qq[[n-1]], DD \rightarrow DDDD[[n-1]]\}; \end{aligned}$$

$$\begin{aligned} qq[[n] = & (q-a(-1+m)(DD+(-1+2p)q)+am(-1+2p)qC + \\ & DD(-1-2DD+2p)\gamma_{11}+q(bq+2(DD-2DDp+p(-1+p+q-pq))\gamma_{11}+ \\ & (DD+p(-1+q))(DD+pq)\gamma_{21}-m(DD(-1-2DD+2p)\gamma_{11}+DD(DD-p)\gamma_{21}+ \\ & qC(-1+b+2DD(\gamma_{11}-2p\gamma_{11}-\gamma_{12}+p(2\gamma_{12}+\gamma_{21}-\gamma_{22}))+ \\ & DD^2(4\gamma_{11}-2(\gamma_{12}+\gamma_{21}))+\gamma_{22}))+p(-2(-1+p)\gamma_{12}+p\gamma_{22}))+ \\ & q^2(b+p(2(-1+p)(-1+2qC)\gamma_{11}+p\gamma_{21}+qC(2\gamma_{12}-2p\gamma_{12}-2p\gamma_{21}+p\gamma_{22}))) + \\ & q(1-2bqC+2DD((-1+2p)(-1+2qC)\gamma_{11}+ \\ & p\gamma_{21}+qC(\gamma_{12}-2p\gamma_{12}-2p\gamma_{21}+p\gamma_{22}))- \\ & p(2(-1+p)(-1+2qC)\gamma_{11}+p\gamma_{21}+qC(4\gamma_{12}-4p\gamma_{12}-2p\gamma_{21}+2p\gamma_{22})))) \Big/ \\ & (1+a(-1+2p)+b(-1+2q)+2(-DD(-1+2p)(-\gamma_{11}+2q\gamma_{11}+\gamma_{12}-q\gamma_{12}))+ \\ & DDp(-1+2q)\gamma_{21}+DD^2(-2\gamma_{11}+\gamma_{12}+\gamma_{21}))+ \\ & p(-1+q)(-(-1+p)(2q\gamma_{11}+\gamma_{12}-q\gamma_{12}))+pq\gamma_{21}))- (DD+p(-1+q))^2\gamma_{22}) \Big/ . \\ & \{p \rightarrow pp[[n-1]], q \rightarrow qq[[n-1]], DD \rightarrow DDDD[[n-1]]\}; \end{aligned}$$

DDDD[[n] =

$$\begin{aligned} & ((1-m)((DD(1+ap+bq-r-\gamma_{11}+(q+r)\gamma_{11}-p(-1+2q)(\gamma_{11}-\gamma_{21}))+DD^2(-\gamma_{11}+\gamma_{21}))+ \\ & pq(1+ap+bq-(-1+q)((-1+p)\gamma_{11}-p\gamma_{21}))) \\ & (m-mqC+((-1+m)(1+DD-p+a(-1+p)(DD+(-1+p)(-1+q))+ \\ & b(DD+(-1+p)(-1+q))(-1+q)-q+pq+DDp\gamma_{11}+DDq\gamma_{11}- \\ & pq\gamma_{11}-2DDpq\gamma_{11}+p^2q\gamma_{11}+p^2q^2\gamma_{11}-p^2q^2\gamma_{11}+DDr\gamma_{11}- \\ & DD(r+\gamma_{11}+DD\gamma_{11}))+DD+(-1+p)(-1+q)(DD+p(-1+q))\gamma_{12}))) \Big/ \\ & (-1+a+b-2ap-2bq+2(DD(-1+2p)(-\gamma_{11}+2q\gamma_{11}+\gamma_{12}-q\gamma_{12}))+ \\ & DD^2(2\gamma_{11}-\gamma_{12}-\gamma_{21}))+DDp(1-2q)\gamma_{21}+p(-1+q) \\ & ((-1+p)(2q\gamma_{11}+\gamma_{12}-q\gamma_{12})-pq\gamma_{21}))+ (DD+p(-1+q))^2\gamma_{22})) - \\ & (mqC-((-1+m)(DD^2\gamma_{11}+(-1+p)q(1+a(-1+p)+bq+p(-1+q)\gamma_{11}))+ \\ & DD(1+a(-1+p)+bq-r+(-p-q+2pq+r)\gamma_{11}))) \Big/ \\ & (-1+a+b-2ap-2bq+2(DD(-1+2p)(-\gamma_{11}+2q\gamma_{11}+\gamma_{12}-q\gamma_{12}))+ \\ & DD^2(2\gamma_{11}-\gamma_{12}-\gamma_{21}))+DDp(1-2q)\gamma_{21}+p(-1+q) \\ & ((-1+p)(2q\gamma_{11}+\gamma_{12}-q\gamma_{12})-pq\gamma_{21}))+ (DD+p(-1+q))^2\gamma_{22})) \\ & (-DDr(-1+\gamma_{11})-(DD+p(-1+q))(1+ap+b(-1+q)-\gamma_{12}+q((-1+p)\gamma_{11}+ \\ & \gamma_{12}-p(\gamma_{12}+\gamma_{21}-\gamma_{22}))+p(\gamma_{12}-\gamma_{22}))+DD(\gamma_{11}-\gamma_{12}-\gamma_{21}+\gamma_{22})))) \Big/ \end{aligned}$$

```

(1 + a (-1 + 2 p) + b (-1 + 2 q) + 2 (-DD (-1 + 2 p) (-γ11 + 2 q γ11 + γ12 - q γ12) +
  DD p (-1 + 2 q) γ21 + DD2 (-2 γ11 + γ12 + γ21) +
  p (-1 + q) (-(-1 + p) (2 q γ11 + γ12 - q γ12) + p q γ21)) -
  (DD + p (-1 + q))2 γ22) /. {p → pp[[n - 1]], q → qq[[n - 1]], DD → DDDD[
n - 1]];

];
Return[If[t ≤ 1, {t, Chop /@ {pp[[t + 1]], qq[[t + 1]], DDDD[[t + 1]]},
  {pp[[1 ;; t + 1]], qq[[1 ;; t + 1]], DDDD[[1 ;; t + 1]]},
  {n - 1, Chop /@ {pp[[n]], qq[[n]], DDDD[[n]]}, {pp[[1 ;; n]], qq[[1 ;; n]], DDDD[[1 ;; n]]}}]];
]

In[133]:= (* Works for tEnd - t0 < ~ 3000 on a Mac with 4GB RAM. *)
recursiveListSmallTimes::usage =
"recursiveListSmallTimes[a, b, γ11, γ12, γ21, γ22, m, r, qC, p0, q0, D0, t0,
End] iterates the invasion dynamics of allele frequencies and linkage
disequilibrium over tEnd - t0 generations with given parameters and initial
values of p0, q0 and D0 for p, q and D. Returns trajectories of p, q and
D between t0 and tEnd. Importantly, this function should only be used for
t ≤ ~3000 generations because it uses dynamic programming that is fast but
requires a lot of memory. For larger t, use 'recFuncLargTimes[]' instead. ";
recursiveListSmallTimes[a_, b_, γ11_, γ12_, γ21_, γ22_, m_, r_, qC_,
p0_, D0_, t0_, tEnd_] := Module[{pp, qq, DDDD, q0},
Clear[pp, qq, DDDD];
q0 = If[m <  $\frac{b}{1 - a}$ ,  $\frac{b - m + a}{b(1 + m)}$ , 0];
pp[0] := p0;
qq[0] := q0;
DDDD[0] := D0;
pp[tt_] :=
pp[tt] = -(((-1 + m) (b (DD + p (-1 + 2 q)) + DD ((-1 - 2 DD + 2 q) γ11 + γ12 - q γ12 + DD (γ12 + 2
  γ21 - γ22)) + p2 (a + (-1 + q) (-γ12 + q (-2 γ11 + γ12 + 2 γ21 - γ22) + γ22)) -
  p (-1 + γ12 + q (-2 (-1 + q) γ11 + (-2 + q) γ12) + 2 DD ((-1 + 2 q) γ11 +
  γ12 - q γ12 + γ21 - 2 q γ21 + (-1 + q) γ22)))) /
(1 + a (-1 + 2 p) + b (-1 + 2 q) + 2 (-DD (-1 + 2 p) (-γ11 + 2 q γ11 + γ12 - q γ12) +
  DD p (-1 + 2 q) γ21 + DD2 (-2 γ11 + γ12 + γ21) +
  p (-1 + q) (-(-1 + p) (2 q γ11 + γ12 - q γ12) + p q γ21)) - (DD + p (-1 + q))2 γ22) /.
{p → pp[tt - 1], q → qq[tt - 1], DD → DDDD[tt - 1]};

qq[tt_] :=
qq[tt] = (q - a (-1 + m) (DD + (-1 + 2 p) q) + a m (-1 + 2 p) qC + DD (-1 - 2 DD + 2 p) γ11 +
  q (b q + 2 (DD - 2 DD p + p (-1 + p + q - p q)) γ11) + (DD + p (-1 + q)) (DD + p q) γ21 -
  m (DD (-1 - 2 DD + 2 p) γ11 + DD (DD - p) γ21 +
  qC (-1 + b + 2 DD (γ11 - 2 p γ11 - γ12 + p (2 γ12 + γ21 - γ22)) + DD2
  (4 γ11 - 2 (γ12 + γ21) + γ22) + p (-2 (-1 + p) γ12 + p γ22)) +
  q2 (b + p (2 (-1 + p) (-1 + 2 qC) γ11 + p γ21 + qC (2 γ12 - 2 p γ12 - 2 p γ21 + p γ22))) +
  q (1 - 2 b qC + 2 DD ((-1 + 2 p) (-1 + 2 qC) γ11 + p γ21 +
  qC (γ12 - 2 p γ12 - 2 p γ21 + p γ22)) - p (2 (-1 + p) (-1 + 2 qC) γ11 +
  p γ21 + qC (4 γ12 - 4 p γ12 - 2 p γ21 + 2 p γ22)))) /
(1 + a (-1 + 2 p) + b (-1 + 2 q) + 2 (-DD (-1 + 2 p) (-γ11 + 2 q γ11 + γ12 - q γ12) +
  DD p (-1 + 2 q) γ21 + DD2 (-2 γ11 + γ12 + γ21) +
  p (-1 + q) (-(-1 + p) (2 q γ11 + γ12 - q γ12) + p q γ21)) - (DD + p (-1 + q))2 γ22) /.
{p → pp[tt - 1], q → qq[tt - 1], DD → DDDD[tt - 1]};

DDDD[tt_] :=
DDDD[tt] = ((1 - m) ((DD (1 + a p + b q - r - γ11 + (q + r) γ11 - p (-1 + 2 q) (γ11 - γ21)) +
  DD2 (-γ11 + γ21) + p q (1 + a p + b q - (-1 + q) ((-1 + p) γ11 - p γ21)))

```

$$\begin{aligned} & \left(m - m q C + \left((-1 + m) \left(1 + DD - p + a (-1 + p) (DD + (-1 + p) (-1 + q)) + \right. \right. \right. \\ & \quad b (DD + (-1 + p) (-1 + q)) (-1 + q) - q + p q + DD p \gamma_{11} + DD q \gamma_{11} - \\ & \quad p q \gamma_{11} - 2 DD p q \gamma_{11} + p^2 q \gamma_{11} + p q^2 \gamma_{11} - p^2 q^2 \gamma_{11} + DD r \gamma_{11} - \\ & \quad \left. \left. \left. DD (r + \gamma_{11} + DD \gamma_{11}) + (DD + (-1 + p) (-1 + q)) (DD + p (-1 + q)) \gamma_{12} \right) \right) \right) / \\ & \left(-1 + a + b - 2 a p - 2 b q + 2 (DD (-1 + 2 p) (-\gamma_{11} + 2 q \gamma_{11} + \gamma_{12} - q \gamma_{12}) + \right. \\ & \quad DD^2 (2 \gamma_{11} - \gamma_{12} - \gamma_{21}) + DD p (1 - 2 q) \gamma_{21} + p (-1 + q) \\ & \quad \left. \left((-1 + p) (2 q \gamma_{11} + \gamma_{12} - q \gamma_{12}) - p q \gamma_{21} \right) + (DD + p (-1 + q))^2 \gamma_{22} \right) - \\ & \left(m q C - \left((-1 + m) (DD^2 \gamma_{11} + (-1 + p) q (1 + a (-1 + p) + b q + p (-1 + q) \gamma_{11}) + \right. \right. \\ & \quad \left. \left. DD (1 + a (-1 + p) + b q - r + (-p - q + 2 p q + r) \gamma_{11}) \right) \right) / \\ & \left(-1 + a + b - 2 a p - 2 b q + 2 (DD (-1 + 2 p) (-\gamma_{11} + 2 q \gamma_{11} + \gamma_{12} - q \gamma_{12}) + \right. \\ & \quad DD^2 (2 \gamma_{11} - \gamma_{12} - \gamma_{21}) + DD p (1 - 2 q) \gamma_{21} + p (-1 + q) \\ & \quad \left. \left((-1 + p) (2 q \gamma_{11} + \gamma_{12} - q \gamma_{12}) - p q \gamma_{21} \right) + (DD + p (-1 + q))^2 \gamma_{22} \right) \\ & \left(-DD r (-1 + \gamma_{11}) - (DD + p (-1 + q)) (1 + a p + b (-1 + q) - \gamma_{12} + q ((-1 + p) \gamma_{11} + \right. \\ & \quad \left. \gamma_{12} - p (\gamma_{12} + \gamma_{21} - \gamma_{22})) + p (\gamma_{12} - \gamma_{22}) + DD (\gamma_{11} - \gamma_{12} - \gamma_{21} + \gamma_{22})) \right) \Big) / \\ & \left(1 + a (-1 + 2 p) + b (-1 + 2 q) + 2 (-DD (-1 + 2 p) (-\gamma_{11} + 2 q \gamma_{11} + \gamma_{12} - q \gamma_{12}) + \right. \\ & \quad DD p (-1 + 2 q) \gamma_{21} + DD^2 (-2 \gamma_{11} + \gamma_{12} + \gamma_{21}) + \\ & \quad \left. p (-1 + q) (-(-1 + p) (2 q \gamma_{11} + \gamma_{12} - q \gamma_{12}) + p q \gamma_{21}) - (DD + p (-1 + q))^2 \gamma_{22} \right) /. \\ & \{p \rightarrow pp[tt - 1], q \rightarrow qq[tt - 1], DD \rightarrow DDDD[tt - 1]\}; \end{aligned}$$

```
Return[{Table[pp[time], {time, t0, tEnd}],
Table[qq[time], {time, t0, tEnd}], Table[DDDD[time], {time, t0, tEnd}]}];
```

```
In[135]= mCrit2Func[a_, b_] :=  $\frac{b}{1 - a}$ 
```

```
In[136]= mCrit3Func[a_, b_, r_] :=  $\frac{a + b - r}{1 - r}$ 
```

```
In[137]= mCrit5Func[a_, b_, r_] :=  $\frac{a (b - a + r)}{(a - b) (a - r) + (1 - a) r}$ 
```

```
In[138]= rStarFunc[a_, b_] :=  $\frac{a (b - a)}{1 - 2 a + b}$ 
```

■ Plotting functions

```
In[139]= minMcritFunc[a_, b_, r_] := Module[{rStar, m2, m5},
```

```
  rStar =  $\frac{a (-a + b)}{1 - 2 a + b}$ ;
```

```
  m2 =  $\frac{b}{1 - a}$ ;
```

```
  m5 =  $\frac{a (-a + b + r)}{(a - b) (a - r) + (1 - a) r}$ ;
```

```
  Return[If[r < rStar, Max[m2, m5], Min[m2, m5]]]
```

```
]
```

```
In[140]= classifyEquilFunc[equil_List] := If[MatchQ[equil, {0, 0, 0}], "C",
  If[MatchQ[equil, {0, _Real, 0}], "B", If[MatchQ[equil, {_Real, _Real, 0}],
    "I", If[MatchQ[equil, {_Real, _Real, _Real}], "±", "Error"]]]]
```

```
In[141]= toNumericCodeFunc[char_] :=
  If[char == "C", 0, If[char == "B", 1, If[char == "I", 2, If[char == "±", 3, -9]]]
```

Plotting

```
In[142]:= figPath := "/Users/Simon/Documents/LocAdD/results/130526/stabilityEB/"
```

Stability of E_B and invasion of A_1

■ Additive fitnesses and monomorphic continent

■ Preliminaries

```
(* Parameter values *)
mya = 0.02;
myb = 0.04;
myg11 = 0;
myg12 = 0;
myg21 = 0;
myg22 = 0;
mym = 0.03;
myr = 0.01;
myqC = 0;

(* Initial values *)
p0 = 0.0001;
q0 = qEB /. {a → mya, b → myb, m → mym};
D0 = 0;
```

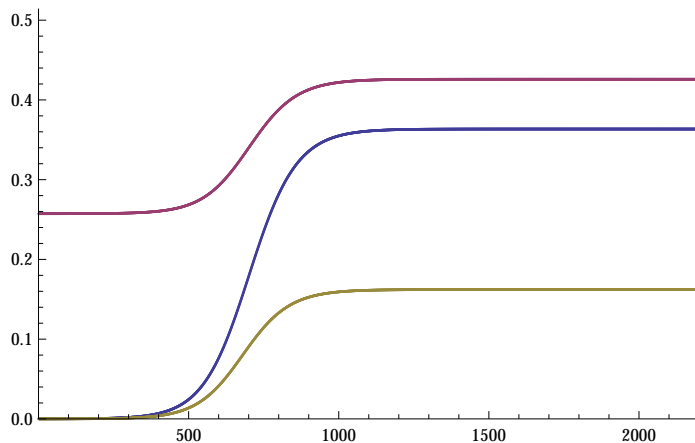
```
In[143]:= (* Times (start and end) *)
myt0 = 0;
myt1 = 1000000;
(* 3000 is about the maximum for which this works with 4GB of RAM. *)

(* Critical migration rates *)
{mCrit2, mCrit3, mCrit5} /. {a → mya, b → myb, m → mym, r → myr}
{0.0408163, 0.0505051, 0.0625}

(* Evaluation for 'arbitrary' times. Returns the number
of generations after which an equilibrium has been reached,
and the coordinates of the equilibrium {p,q,D}. *)
finalState = Block[{$RecursionLimit = Infinity},
  recFuncLargeTimes[mya, myb, myg11, myg12, myg21, myg22, mym, myr, myqC, p0, D0, myt1]];
finalState[[1 ;; 2]]

{2210, {0.363498, 0.425964, 0.162172}}

step = 20;
ListPlot[(*Part[# , 1 ;; Length[#] ;; step]&/@*) finalState[[3]],
  PlotRange → {{0, Length[finalState[[3, 1]]}, {0, 2 * q0}},
  PlotStyle → {PointSize[1 / 300], PointSize[1 / 300], PointSize[1 / 300]}]
```



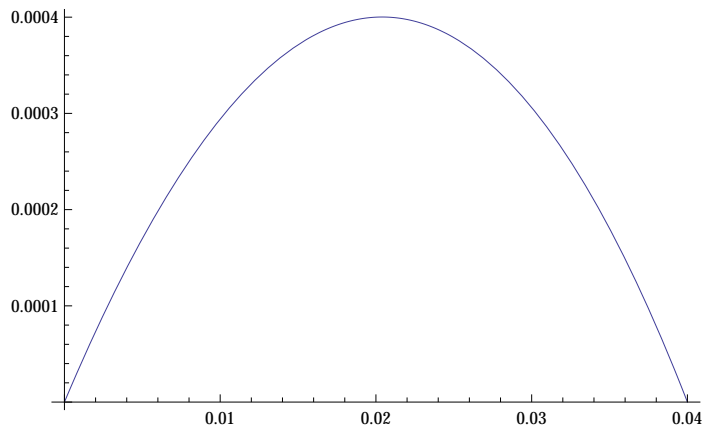
```
rStar
```

$$\frac{a(-a+b)}{1-2a+b}$$

```
rStar /. {a -> 0.02, b -> 0.04}
```

```
0.0004
```

```
Plot[rStarFunc[a, myb], {a, 0, myb}, PlotRange -> Full]
```



```
rStarFunc[mya, myb]
```

```
0.0004
```

```
myr
```

```
0.01
```

```
mCrit5 /. {a -> mya, b -> myb, r -> myr} // N
```

```
0.0625
```


■ Case 1: $a < \frac{b}{2}$

```
(* Parameter values *)
mya = 0.01;
myb = 0.04;
myg11 = 0;
myg12 = 0;
myg21 = 0;
myg22 = 0;
mym = 0.03;
myr = mya;
myqC = 0;
rmin = 0;
rmax = 0.05;
mmin = 0;
mmax = 0.08;
myMCrit2 = mCrit2 /. {a → mya, b → myb};
myMCrit3 = mCrit3 /. {a → mya, b → myb, r → 0.045};
myMCrit5 = mCrit5 /. {a → mya, b → myb, r → 0.045};
myRStar = rStar /. {a → mya, b → myb};
plot1 = Plot[{mCrit2Func[mya, myb], minMcritFunc[mya, myb, r],
  mCrit2Func[mya, myb], mCrit3Func[mya, myb, r], mCrit5Func[mya, myb, r]},
  {r, rmin, rmax}, PlotRange → {{rmin, rmax}, {mmin, mmax}}, AspectRatio → 1 / 1,
  Epilog → {{Dashed, Black, Line[{{rStarFunc[mya, myb], 0}, {rStarFunc[mya, myb], 1}}]},
  {Dashed, Black, Line[{{mya, 0}, {mya, 1}}]},
  {Text[Style["mB", Directive[FontSize → 16], FontFamily → "Helvetica"],
  {0.045, myMCrit2 + 0.005}], {Text[Style["mC", Directive[FontSize → 16],
  FontFamily → "Helvetica"], {0.045, myMCrit3 + 0.005}]},
  {Text[Style["m*", Directive[FontSize → 16], FontFamily → "Helvetica"],
  {0.045, myMCrit5 + 0.005}]}, {Text[Style[a, Directive[FontSize → 16],
  FontFamily → "Helvetica"], {mya + 0.0025, 0.07}]}, (*{PointSize[Small],
  Point[Flatten[Table[{{i, j}, {i, 0, 0.05, 0.0025}, {j, 0, 0.08, 0.0025}], 1]]}}, *)
  (*Frame→True, FrameLabel→{"Recombination rate r", "Migration rate m"},
  LabelStyle→{Directive[FontSize→16], FontFamily→"Helvetica"}, *)
  Frame → True, FrameLabel → {"", ""}, LabelStyle →
  {Directive[FontSize → 16], FontFamily → "Helvetica"},

  ImageSize → 3. {100, 100},

  PlotStyle → {{White, Thin}, {White, Thin},
  {Black, Dashed, Thick}, {Black, Dotted, Thick}, {Black, Thick}}, Filling →
  {1 → {Axis, RGBColor[0.9, 0.9, 0.9]}, 2 → {Axis, RGBColor[0.75, 0.75, 0.75]}},
  AxesLabel → {r, m}, AxesStyle → Directive[FontSize → 16]]
```



```

(* EC: continent haplotype fixed *)
pl1 = ListPlot[Pick[Flatten[coord1, 1], Map[# == "C" &, Flatten[pattern1]]],
  PlotMarkers → □, PlotStyle → Gray];

(* EB: marginal one-locus polymorphism at the B locus *)
pl2 = ListPlot[Pick[Flatten[coord1, 1], Map[# == "B" &, Flatten[pattern1]]],
  PlotMarkers → ○, PlotStyle → Gray];

(* EI: island haplotype fixed *)
pl3 = ListPlot[Pick[Flatten[coord1, 1], Map[# == "I" &, Flatten[pattern1]]], PlotMarkers → ★];

(* E±: fully-polymorphic equilibrium *)
pl4 = ListPlot[Pick[Flatten[coord1, 1], Map[# == "±" &, Flatten[pattern1]]],
  PlotMarkers → ●, PlotStyle → Gray];

plotStabilityEBMonom1 = Show[{plot1, pl1, pl2, pl4}]

```

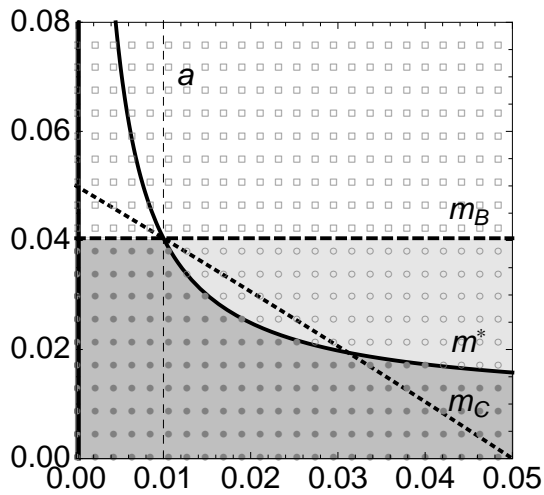


Figure 7: Critical migration rates determining the stability of the marginal one-locus equilibrium E_B and invasion of A_1 , as a function of the recombination rate. Dark grey: invasion of A_1 via the unstable marginal equilibrium E_B ; light grey: no invasion of A_1 , stable marginal equilibrium E_B ; white: no invasion, fixation of continental haplotype $A_2 B_2$ and realisation of equilibrium E_C . Numerical iterations of invasion dynamics were performed at coordinates indicated by grey symbols. Different symbols indicate which equilibrium is reached: ● E_{\pm} ; ○ E_B ; □ E_C . Initial values for iterations were $(p_0, q_0, D_0) = (0, \hat{q}_B, 0)$, where \hat{q}_B is the frequency of B_1 at the marginal one-locus migration-selection equilibrium. Iterations were stopped when changes in each coordinate from one time step to the next were smaller than the numerical precision. The thick, almost-vertical line close to $r=0$ belongs to the critical migration rate m^* . This curve crosses the r axis at $r^* = \frac{a(b-a)}{1-2a+b}$, which is denoted by a vertical dashed line that can hardly be seen. The second vertical dashed line corresponds to $r=a$. Selection coefficients are $a=0.01$, $b=0.04$.

Recall that $m_{\text{crit},2} = m_B$, $m_{\text{crit},3} = m_C$ and $m_{\text{crit},5} = m^*$.

```
figPath1 = figPath <> "stabilityEBMonomCont_1.eps";
```

```
Export[figPath1, plotStabilityEBMonom1, "EPS"]
```

```
/Users/Simon/Documents/LocAdD/results/130526/stabilityEB/stabilityEBMonomCont_1.eps
```

■ Case 2: $a = \frac{b}{2}$

```
(* Parameter values *)
mya = 0.02;
myb = 0.04;
myg11 = 0;
myg12 = 0;
myg21 = 0;
myg22 = 0;
mym = 0.03;
myr = mya;
myqC = 0;
rmin = 0;
rmax = 0.05;
mmin = 0;
mmax = 0.08;
myMCrit2 = mCrit2 /. {a → mya, b → myb};
myMCrit3 = mCrit3 /. {a → mya, b → myb, r → 0.045};
myMCrit5 = mCrit5 /. {a → mya, b → myb, r → 0.045};
myRStar = rStar /. {a → mya, b → myb};
plot2 = Plot[{mCrit2Func[mya, myb], minMcritFunc[mya, myb, r],
  mCrit2Func[mya, myb], mCrit3Func[mya, myb, r], mCrit5Func[mya, myb, r]},
  {r, rmin, rmax}, PlotRange → {{rmin, rmax}, {mmin, mmax}}, AspectRatio → 1 / 1,
  Epilog → {{Dashed, Black, Line[{rStarFunc[mya, myb], 0}, {rStarFunc[mya, myb], 1}]},
    {Dashed, Black, Line[{mya, 0}, {mya, 1}]},
    {Text[Style["mB", Directive[FontSize → 16], FontFamily → "Helvetica"],
      {0.045, myMCrit2 + 0.005}], {Text[Style["mC", Directive[FontSize → 16],
      FontFamily → "Helvetica"], {0.045, myMCrit3 + 0.005}]},
    {Text[Style["m*", Directive[FontSize → 16], FontFamily → "Helvetica"],
      {0.045, myMCrit5 + 0.005}], {Text[Style[a, Directive[FontSize → 16],
      FontFamily → "Helvetica"], {mya + 0.0025, 0.07}]}, (*{PointSize[Small],
      Point[Flatten[Table[{i, j}, {i, 0, 0.05, 0.0025}, {j, 0, 0.08, 0.0025}], 1]}*)},

  (*Frame→True, FrameLabel→{"Recombination rate r", "Migration rate m"},
  LabelStyle→{Directive[FontSize→16], FontFamily→"Helvetica"}, *)

  Frame → True, FrameLabel → {"", ""},
  LabelStyle → {Directive[FontSize → 16], FontFamily → "Helvetica"},

  ImageSize → 3. {100, 100},

  PlotStyle → {{White, Thin}, {White, Thin},
    {Black, Dashed, Thick}, {Black, Dotted, Thick}, {Black, Thick}},
  Filling → {1 → {Axis, RGBColor[0.9, 0.9, 0.9]}, 2 → {Axis, RGBColor[0.75, 0.75, 0.75]}},
  AxesLabel → {r, m}, AxesStyle → Directive[FontSize → 16]]
```



```

(* EC: continent haplotype fixed *)
pl1 = ListPlot[Pick[Flatten[coord2, 1], Map[# == "C" &, Flatten[pattern2]]],
  PlotMarkers → □, PlotStyle → Gray];

(* EB: marginal one-locus polymorphism at the B locus *)
pl2 = ListPlot[Pick[Flatten[coord2, 1], Map[# == "B" &, Flatten[pattern2]]],
  PlotMarkers → ○, PlotStyle → Gray];

(* EI: island haplotype fixed *)
pl3 = ListPlot[Pick[Flatten[coord2, 1], Map[# == "I" &, Flatten[pattern2]]], PlotMarkers → ★];

(* E±: fully-polymorphic equilibrium *)
pl4 = ListPlot[Pick[Flatten[coord2, 1], Map[# == "±" &, Flatten[pattern2]]],
  PlotMarkers → ●, PlotStyle → Gray];

plotStabilityEBMonom2 = Show[{plot2, pl1, pl2, pl4}]

```

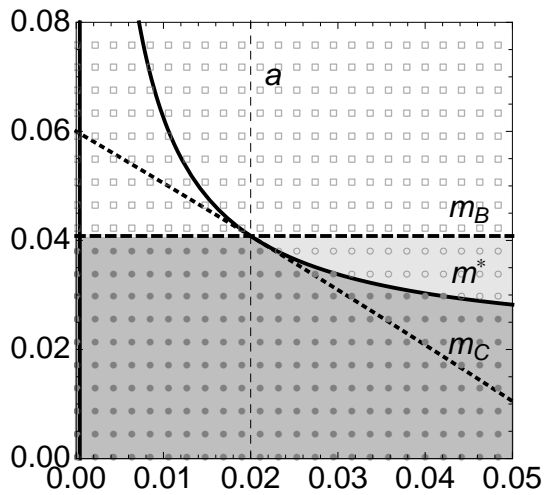


Figure 9: Critical migration rates determining the stability of the marginal one-locus equilibrium E_B and invasion of A_1 , as a function of the recombination rate. Dark grey: invasion of A_1 via the unstable marginal equilibrium E_B ; light grey: no invasion of A_1 , stable marginal equilibrium E_B ; white: no invasion, fixation of continental haplotype $A_2 B_2$ and realisation of equilibrium E_C . Numerical iterations of invasion dynamics were performed at coordinates indicated by grey symbols. Different symbols indicate which equilibrium is reached: ● E_{\pm} ; ○ E_B ; □ E_C . Initial values for iterations were $(p_0, q_0, D_0) = (0, \hat{q}_B, 0)$, where \hat{q}_B is the frequency of B_1 at the marginal one-locus migration-selection equilibrium. Iterations were stopped when changes in each coordinate from one time step to the next were smaller than the numerical precision. The thick, almost-vertical line close to $r=0$ belongs to the critical migration rate m^* . This curve crosses the r axis at $r^* = \frac{a(b-a)}{1-2a+b}$, which is denoted by a vertical dashed line that can hardly be seen. The second vertical dashed line corresponds to $r=a$. Selection coefficients are $a=0.02$, $b=0.04$.

Recall that $m_{\text{crit},2} = m_B$, $m_{\text{crit},3} = m_C$ and $m_{\text{crit},5} = m^*$.

```
figPath2 = figPath <> "stabilityEBMonomCont_2.eps";
```

```
Export[figPath2, plotStabilityEBMonom2, "EPS"]
```

```
/Users/Simon/Documents/LocAdD/results/130526/stabilityEB/stabilityEBMonomCont_2.eps
```

■ Case 3: $a > \frac{b}{2}$

```
(* Parameter values *)
mya = 0.03;
myb = 0.04;
myg11 = 0;
myg12 = 0;
myg21 = 0;
myg22 = 0;
mym = 0.03;
myr = mya;
myqC = 0;
rmin = 0;
rmax = 0.05;
mmin = 0;
mmax = 0.08;
myMCrit2 = mCrit2 /. {a → mya, b → myb};
myMCrit3 = mCrit3 /. {a → mya, b → myb, r → 0.045};
myMCrit5 = mCrit5 /. {a → mya, b → myb, r → 0.045};
myRStar = rStar /. {a → mya, b → myb};
plot3 = Plot[{mCrit2Func[mya, myb], minMcritFunc[mya, myb, r],
  mCrit2Func[mya, myb], mCrit3Func[mya, myb, r], mCrit5Func[mya, myb, r]},
  {r, rmin, rmax}, PlotRange → {{rmin, rmax}, {mmin, mmax}}, AspectRatio → 1 / 1,
  Epilog → {{Dashed, Black, Line[{rStarFunc[mya, myb], 0}, {rStarFunc[mya, myb], 1}]},
    {Dashed, Black, Line[{mya, 0}, {mya, 1}]},
    {Text[Style["mB", Directive[FontSize → 16], FontFamily → "Helvetica"],
      {0.045, myMCrit2 + 0.005}], {Text[Style["mC", Directive[FontSize → 16],
      FontFamily → "Helvetica"], {0.045, myMCrit3 - 0.003}]},
    {Text[Style["m*", Directive[FontSize → 16], FontFamily → "Helvetica"],
      {0.045, myMCrit5 - 0.003}], {Text[Style[a, Directive[FontSize → 16],
      FontFamily → "Helvetica"], {mya + 0.0025, 0.07}]}, (*{PointSize[Small],
      Point[Flatten[Table[{i, j}, {i, 0, 0.05, 0.0025}, {j, 0, 0.08, 0.0025}], 1]]}*)},

  (*Frame→True, FrameLabel→{"Recombination rate r", "Migration rate m"},
  LabelStyle→{Directive[FontSize→16], FontFamily→"Helvetica"}, *)

  Frame → True, FrameLabel → {"", ""},
  LabelStyle → {Directive[FontSize → 16], FontFamily → "Helvetica"},

  ImageSize → 3. {100, 100},

  PlotStyle → {{White, Thin}, {White, Thin},
    {Black, Dashed, Thick}, {Black, Dotted, Thick}, {Black, Thick}},
  Filling → {1 → {Axis, RGBColor[0.9, 0.9, 0.9]}, 2 → {Axis, RGBColor[0.75, 0.75, 0.75]}},
  AxesLabel → {r, m}, AxesStyle → Directive[FontSize → 16]

]
```



```

(* EC: continent haplotype fixed *)
pl1 = ListPlot[Pick[Flatten[coord3, 1], Map[# == "C" &, Flatten[pattern3]]],
  PlotMarkers → □, PlotStyle → Gray];

(* EB: marginal one-locus polymorphism at the B locus *)
pl2 = ListPlot[Pick[Flatten[coord3, 1], Map[# == "B" &, Flatten[pattern3]]],
  PlotMarkers → ○, PlotStyle → Gray];

(* EI: island haplotype fixed *)
pl3 = ListPlot[Pick[Flatten[coord3, 1], Map[# == "I" &, Flatten[pattern3]]], PlotMarkers → ★];

(* E±: fully-polymorphic equilibrium *)
pl4 = ListPlot[Pick[Flatten[coord3, 1], Map[# == "±" &, Flatten[pattern3]]],
  PlotMarkers → ●, PlotStyle → Gray];

plotStabilityEBMonom3 = Show[{plot3, pl1, pl2, pl4}]

```

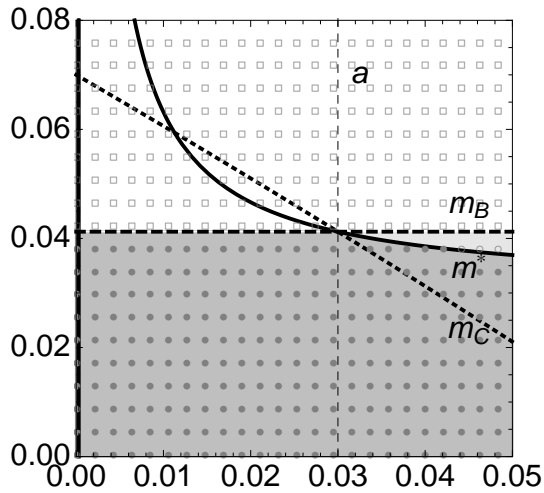


Figure 11: Critical migration rates determining the stability of the marginal one-locus equilibrium E_B and invasion of A_1 , as a function of the recombination rate. Dark grey: invasion of A_1 via the unstable marginal equilibrium E_B ; light grey: no invasion of A_1 , stable marginal equilibrium E_B ; white: no invasion, fixation of continental haplotype $A_2 B_2$ and realisation of equilibrium E_C . Numerical iterations of invasion dynamics were performed at coordinates indicated by grey symbols. Different symbols indicate which equilibrium is reached: ● E_{\pm} ; ○ E_B ; □ E_C . Initial values for iterations were $(p_0, q_0, D_0) = (0, \hat{q}_B, 0)$, where \hat{q}_B is the frequency of B_1 at the marginal one-locus migration-selection equilibrium. Iterations were stopped when changes in each coordinate from one time step to the next were smaller than the numerical precision. The thick, almost-vertical line close to $r=0$ belongs to the critical migration rate m^* . This curve crosses the r axis at $r^* = \frac{a(b-a)}{1-2a+b}$, which is denoted by a vertical dashed line that can hardly be seen. The second vertical dashed line corresponds to $r=a$. Selection coefficients are $a=0.03$, $b=0.04$.

Recall that $m_{\text{crit},2} = m_B$, $m_{\text{crit},3} = m_C$ and $m_{\text{crit},5} = m^*$.

```
figPath3 = figPath <> "stabilityEBMonomCont_3.eps";
```

```
Export[figPath3, plotStabilityEBMonom3, "EPS"]
```

```
/Users/Simon/Documents/LocAdD/results/130526/stabilityEB/stabilityEBMonomCont_3.eps
```

■ Combined plot

```

plotStabilityEBMonomComb = Labeled[GraphicsRow[
  MapThread[Labeled[#1, #2, {{Top, Left}}, LabelStyle -> {Directive[FontSize -> 22, Bold],
    FontFamily -> "Helvetica"}, FrameMargins -> {{-5, 0}, {-35, 0}}] &,
  {{plotStabilityEBMonom1, plotStabilityEBMonom2, plotStabilityEBMonom3},
  CharacterRange["A", "C"]}], ImageSize -> 3.6 {280, 90}, AspectRatio -> 0.45],
{"Recombination rate r", "Migration rate m"}, {Bottom, Left},
RotateLabel -> True,
LabelStyle -> {Directive[FontSize -> 24], FontFamily -> "Helvetica"},
FrameMargins -> {{0, 0}, {0, 0}}]

```

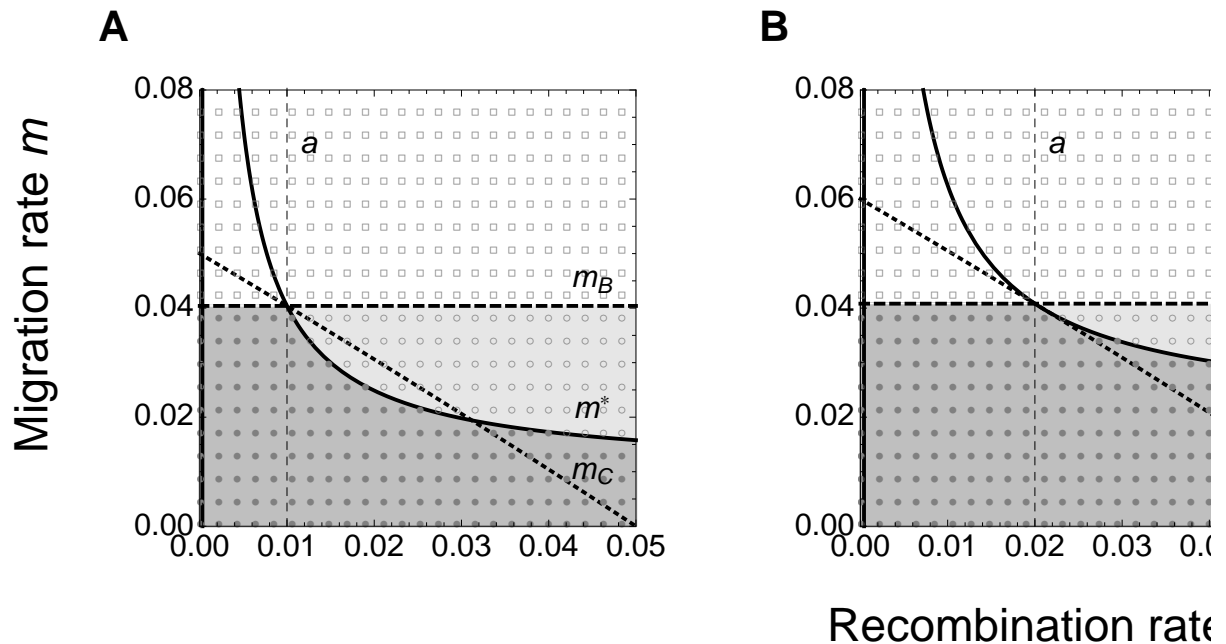


Figure 12: Critical migration rates determining the stability of the marginal one-locus equilibrium E_B and invasion of A_1 , as a function of the recombination rate. Dark grey: invasion of A_1 via the unstable marginal equilibrium E_B ; light grey: no invasion of A_1 , stable marginal equilibrium E_B ; white: no invasion, fixation of continental haplotype A_2 B_2 and realisation of equilibrium E_C . Numerical iterations of invasion dynamics were performed at coordinates indicated by grey symbols. Different symbols indicate which equilibrium is reached: \bullet E_1 ; \circ E_B ; \square E_C . Initial values for iterations were $\{p_0, q_0, D_0\} = \{0, \hat{q}_B, 0\}$, where \hat{q}_B is the frequency of B_1 at the marginal one-locus migration-selection equilibrium. Iterations were stopped when changes in each coordinate between successive time steps were smaller than the numerical precision. The thick, almost-vertical line close to $r=0$ belongs to the critical migration rate m^* . This curve crosses the r axis at $r^* = \frac{a(b-a)}{1-2a+b}$, which is denoted by a vertical dashed line that can hardly be seen. The second vertical dashed line corresponds to $r=a$. **A)** $a=0.01$, $b=0.04$. **B)** $a=0.02$, $b=0.04$. **C)** $a=0.03$, $b=0.04$.

```
figPath4 = figPath <> "stabilityEBMonomCont_comb.eps";
```

```
Export[figPath4, plotStabilityEBMonomComb, "EPS"]
```

```
/Users/Simon/Documents/LocAdD/results/130526/stabilityEB/stabilityEBMonomCont_comb.
eps
```

■ Arbitrary a for a given b

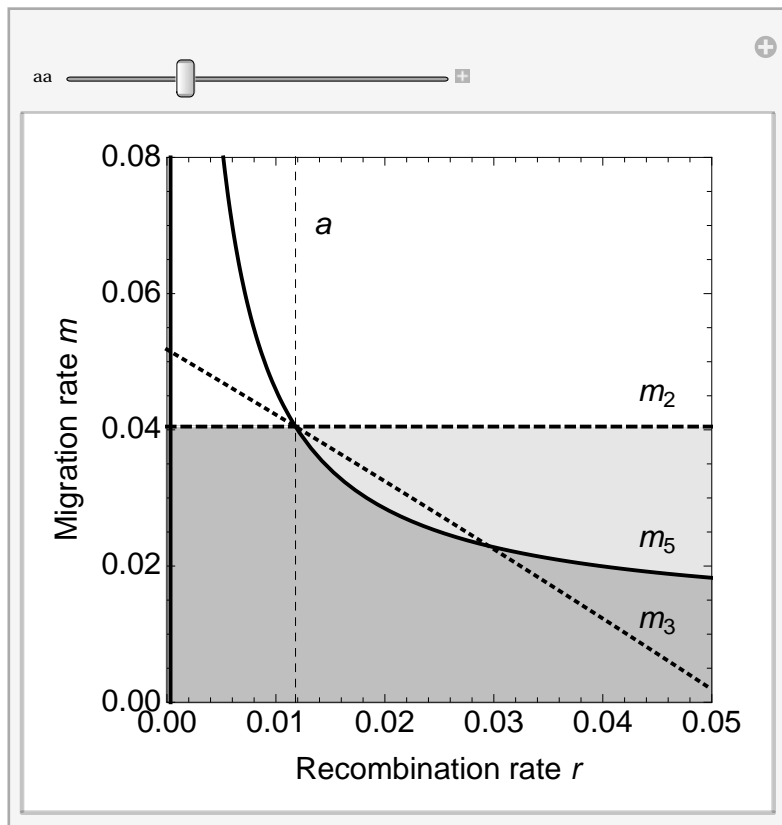
```

Manipulate[
  (* Parameter values *)
  (mya = 0.01;
  myb = 0.04;
  myg11 = 0;
  myg12 = 0;
  myg21 = 0;
  myg22 = 0;
  mym = 0.03;
  myr = mya;
  myqC = 0;
  rmin = 0;
  rmax = 0.05;
  mmin = 0;
  mmax = 0.08;
  myMCrit2 = mCrit2 /. {a → aa, b → myb};
  myMCrit3 = mCrit3 /. {a → aa, b → myb, r → 0.045};
  myMCrit5 = mCrit5 /. {a → aa, b → myb, r → 0.045};
  myRStar = rStar /. {a → aa, b → myb};
  Plot[{mCrit2Func[aa, myb], minMcritFunc[aa, myb, r],
    mCrit2Func[aa, myb], mCrit3Func[aa, myb, r], mCrit5Func[aa, myb, r]},
    {r, rmin, rmax}, PlotRange → {{rmin, rmax}, {mmin, mmax}}, AspectRatio → 1 / 1,
    Epilog → {{Dashed, Black, Line[{{rStarFunc[aa, myb], 0}, {rStarFunc[aa, myb], 1}]},
      {Dashed, Black, Line[{{aa, 0}, {aa, 1}]},
      {Text[Style["mB", Directive[FontSize → 16], FontFamily → "Helvetica"],
        {0.045, myMCrit2 + 0.005}], {Text[Style["mC", Directive[FontSize → 16],
        FontFamily → "Helvetica"], {0.045, myMCrit3 + 0.005}],
      {Text[Style["m*", Directive[FontSize → 16], FontFamily → "Helvetica"],
        {0.045, myMCrit5 + 0.005}], {Text[Style[a, Directive[FontSize → 16],
        FontFamily → "Helvetica"], {aa + 0.0025, 0.07}]}}},

    Frame → True, FrameLabel → {"Recombination rate r", "Migration rate m"},
    LabelStyle → {Directive[FontSize → 16], FontFamily → "Helvetica"},

    PlotStyle → {{White, Thin}, {White, Thin},
      {Black, Dashed, Thick}, {Black, Dotted, Thick}, {Black, Thick}}, Filling →
      {1 → {Axis, RGBColor[0.9, 0.9, 0.9]}, 2 → {Axis, RGBColor[0.75, 0.75, 0.75]}},
    AxesLabel → {r, m}, AxesStyle → Directive[FontSize → 16]],
  {{aa, mya}, 0, Min[myb, 1 - myb]}
]

```



\$Aborted

Recall that $m_{\text{crit},2} = m_B$, $m_{\text{crit},3} = m_C$ and $m_{\text{crit},5} = m^*$.

- Additive fitnesses and polymorphic continent

- Case 1: $a < \frac{b}{2}$ and $q_c = 0.01$

In[151]:= (* Initial values *)

p0 = 0.0001;

q0Polym = qEB1 /. {a → mya, b → myb, m → mym, qC → myqC};

D0 = 0;

```

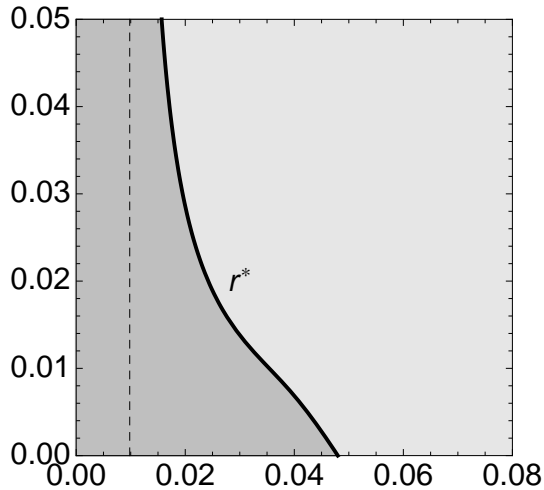
mya = 0.01;
myb = 0.04;
myg11 = 0;
myg12 = 0;
myg21 = 0;
myg22 = 0;
mym = 0.03;
myr = mya;
myqC = 0.01;
rmin = 0;
rmax = 0.05;
mmin = 0;
mmax = 0.08;
myMCrit2 = mCrit2 /. {a → mya, b → myb};
myMCrit3 = mCrit3 /. {a → mya, b → myb, r → 0.045};
myMCrit5 = mCrit5 /. {a → mya, b → myb, r → 0.045};
myRStar = rStar /. {a → mya, b → myb};
plot4 =
Plot[{1, rCritFuncIgnoringPole[mya, myb, m, myqC, rmax], rCritFunc[mya, myb, m, myqC]},
  {m, mmin, mmax}, PlotRange → {{mmin, mmax}, {rmin, rmax}}, AspectRatio → 1 / 1,
  Epilog → {Text[Style["r*", Directive[FontSize → 16],
    FontFamily → "Helvetica"], {0.03, 0.02}]},

  Frame → True, FrameLabel → {"", ""},
  LabelStyle → {Directive[FontSize → 16], FontFamily → "Helvetica"},

  ImageSize → 3. {100, 100},

  PlotStyle → {{White}, {Black, Thick}, {Black, Dashed}},
  Filling → {1 → {Axis, RGBColor[0.9, 0.9, 0.9]}, 2 → {Axis, RGBColor[0.75, 0.75, 0.75]}},
  AxesLabel → {r, m}, AxesStyle → Directive[FontSize → 16]]

```



```
In[154]:= coord4 = Table[{m, r}, {m, 0.0002, 0.0799, 0.0042}, {r, 0.0001, 0.0499, 0.0021}];
```

```

Timing[finalStateEncoded = Block[{$RecursionLimit = Infinity},
  vals4 = Table[recFuncLargeTimes[mya, myb, myg11, myg12, myg21, myg22, m, r, myqC,
    p0, D0, myt1][[2]], {m, 0.0002, 0.0799, 0.0042}, {r, 0.0001, 0.0499, 0.0021}]
]
];

```

The computation above takes about 24 minutes on a Mac mini 2.3 GHz Intel Core i5 with 4 GB of RAM. Below is a hard-coded version of the result.

```
In[155]:= vals4 = {{{0.9955997766412134`, 0.9958407348564504`, 0.004130636748916976`}, {0.994933945998
```



```

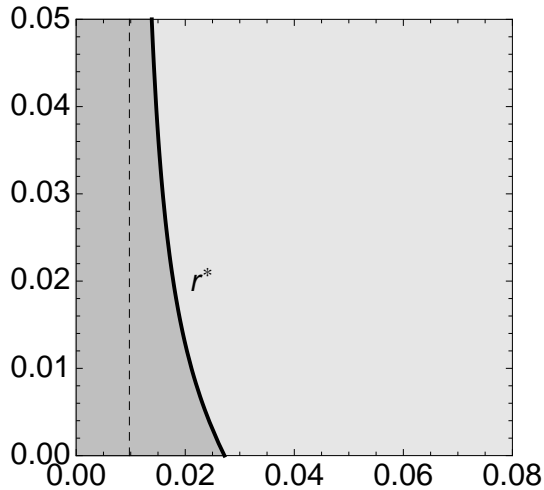
mya = 0.01;
myb = 0.04;
myg11 = 0;
myg12 = 0;
myg21 = 0;
myg22 = 0;
mym = 0.03;
myr = mya;
myqC = 0.2;
rmin = 0;
rmax = 0.05;
mmin = 0;
mmax = 0.08;
myMCrit2 = mCrit2 /. {a → mya, b → myb};
myMCrit3 = mCrit3 /. {a → mya, b → myb, r → 0.045};
myMCrit5 = mCrit5 /. {a → mya, b → myb, r → 0.045};
myRStar = rStar /. {a → mya, b → myb};
plot5 =
Plot[{1, rCritFuncIgnoringPole[mya, myb, m, myqC, rmax], rCritFunc[mya, myb, m, myqC]},
  {m, mmin, mmax}, PlotRange → {{mmin, mmax}, {rmin, rmax}}, AspectRatio → 1 / 1,
  Epilog → {Text[Style["r*", Directive[FontSize → 16],
    FontFamily → "Helvetica"], {0.023, 0.02}]},

  Frame → True, FrameLabel → {"", ""},
  LabelStyle → {Directive[FontSize → 16], FontFamily → "Helvetica"},

  ImageSize → 3. {100, 100},

  PlotStyle → {{White}, {Black, Thick}, {Black, Dashed}},
  Filling → {1 → {Axis, RGBColor[0.9, 0.9, 0.9]}, 2 → {Axis, RGBColor[0.75, 0.75, 0.75]}},
  AxesLabel → {r, m}, AxesStyle → Directive[FontSize → 16]]

```



```

In[156]:= coord5 = Table[{m, r}, {m, 0.0002, 0.0799, 0.0042}, {r, 0.0001, 0.0499, 0.0021}];

Timing[finalStateEncoded = Block[{$RecursionLimit = Infinity},
  vals5 = Table[recFuncLargeTimes[mya, myb, myg11, myg12, myg21, myg22, m, r, myqC,
    p0, D0, myt1][[2]], {m, 0.0002, 0.0799, 0.0042}, {r, 0.0001, 0.0499, 0.0021}]
  ]
];

```

The computation above takes about 24 minutes on a Mac mini 2.3 GHz Intel Core i5 with 4 GB of RAM. Below is a hard-coded version of the result.

```

In[157]:= vals5 = {{{0.9924147241897633`, 0.996638987852479`, 0.003327199873970181`}, {0.9918759314373

```



```

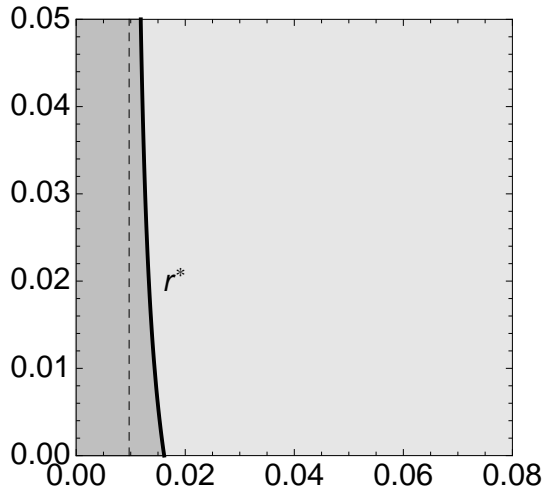
mya = 0.01;
myb = 0.04;
myg11 = 0;
myg12 = 0;
myg21 = 0;
myg22 = 0;
mym = 0.03;
myr = mya;
myqC = 0.5;
rmin = 0;
rmax = 0.05;
mmin = 0;
mmax = 0.08;
myMCrit2 = mCrit2 /. {a → mya, b → myb};
myMCrit3 = mCrit3 /. {a → mya, b → myb, r → 0.045};
myMCrit5 = mCrit5 /. {a → mya, b → myb, r → 0.045};
myRStar = rStar /. {a → mya, b → myb};
plot6 =
Plot[{1, rCritFuncIgnoringPole[mya, myb, m, myqC, rmax], rCritFunc[mya, myb, m, myqC]},
  {m, mmin, mmax}, PlotRange → {{mmin, mmax}, {rmin, rmax}}, AspectRatio → 1 / 1,
  Epilog → {Text[Style["r*", Directive[FontSize → 16],
    FontFamily → "Helvetica"], {0.018, 0.02}]}},

  Frame → True, FrameLabel → {"", ""},
  LabelStyle → {Directive[FontSize → 16], FontFamily → "Helvetica"},

  ImageSize → 3. {100, 100},

  PlotStyle → {{White}, {Black, Thick}, {Black, Dashed}},
  Filling → {1 → {Axis, RGBColor[0.9, 0.9, 0.9]}, 2 → {Axis, RGBColor[0.75, 0.75, 0.75]}},
  AxesLabel → {r, m}, AxesStyle → Directive[FontSize → 16]]

```



```

In[158]:= coord6 = Table[{m, r}, {m, 0.0002, 0.0799, 0.0042}, {r, 0.0001, 0.0499, 0.0021}];

Timing[finalStateEncoded = Block[{$RecursionLimit = Infinity},
  vals6 = Table[recFuncLargeTimes[mya, myb, myg11, myg12, myg21, myg22, m, r, myqC,
    p0, D0, myt1][[2]], {m, 0.0002, 0.0799, 0.0042}, {r, 0.0001, 0.0499, 0.0021}]
];

```

The computation above takes about 24 minutes on a Mac mini 2.3 GHz Intel Core i5 with 4 GB of RAM. Below is a hard-coded version of the result.

```

In[159]:= vals6 = {{{0.9873857333706446`, 0.9978993774642507`, 0.0020689523151086356`}, {0.98704825016

```



```

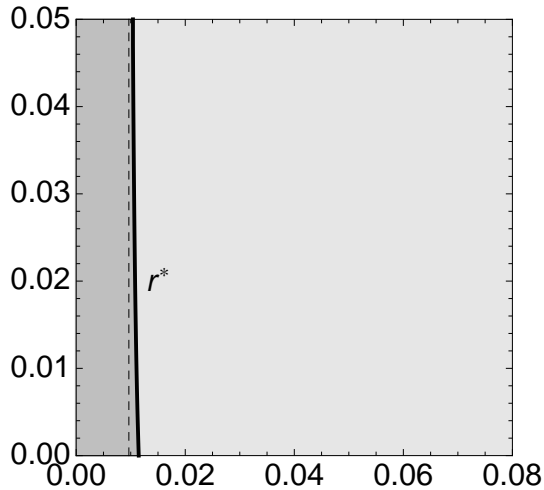
mya = 0.01;
myb = 0.04;
myg11 = 0;
myg12 = 0;
myg21 = 0;
myg22 = 0;
mym = 0.03;
myr = mya;
myqC = 0.8;
rmin = 0;
rmax = 0.05;
mmin = 0;
mmax = 0.08;
myMCrit2 = mCrit2 /. {a → mya, b → myb};
myMCrit3 = mCrit3 /. {a → mya, b → myb, r → 0.045};
myMCrit5 = mCrit5 /. {a → mya, b → myb, r → 0.045};
myRStar = rStar /. {a → mya, b → myb};
plot7 =
Plot[{1, rCritFuncIgnoringPole[mya, myb, m, myqC, rmax], rCritFunc[mya, myb, m, myqC]},
  {m, mmin, mmax}, PlotRange → {{mmin, mmax}, {rmin, rmax}}, AspectRatio → 1 / 1,
  Epilog → {Text[Style["r*", Directive[FontSize → 16],
    FontFamily → "Helvetica"], {0.015, 0.02}]},

  Frame → True, FrameLabel → {"", ""},
  LabelStyle → {Directive[FontSize → 16], FontFamily → "Helvetica"},

  ImageSize → 3. {100, 100},

  PlotStyle → {{White}, {Black, Thick}, {Black, Dashed}},
  Filling → {1 → {Axis, RGBColor[0.9, 0.9, 0.9]}, 2 → {Axis, RGBColor[0.75, 0.75, 0.75]}},
  AxesLabel → {r, m}, AxesStyle → Directive[FontSize → 16]]

```



```

In[160]:= coord7 = Table[{m, r}, {m, 0.0002, 0.0799, 0.0042}, {r, 0.0001, 0.0499, 0.0021}];

Timing[finalStateEncoded = Block[{$RecursionLimit = Infinity},
  vals7 = Table[recFuncLargeTimes[mya, myb, myg11, myg12, myg21, myg22, m, r, myqC,
    p0, D0, myt1][[2]], {m, 0.0002, 0.0799, 0.0042}, {r, 0.0001, 0.0499, 0.0021}]
  ]
];

```

The computation above takes about 24 minutes on a Mac mini 2.3 GHz Intel Core i5 with 4 GB of RAM. Below is a hard-coded version of the result.

```

In[161]:= vals7 = {{{0.9823567906084528`, 0.9991597550081732`, 0.0008233619642697345`}, {0.98222150241

```



```

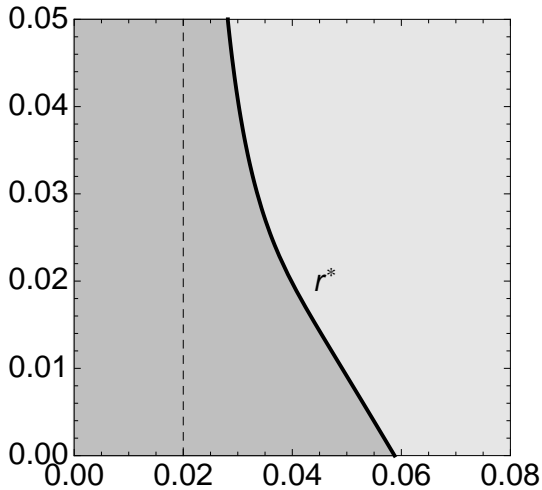
mya = 0.02;
myb = 0.04;
myg11 = 0;
myg12 = 0;
myg21 = 0;
myg22 = 0;
mym = 0.03;
myr = mya;
myqC = 0.01;
rmin = 0;
rmax = 0.05;
mmin = 0;
mmax = 0.08;
myMCrit2 = mCrit2 /. {a → mya, b → myb};
myMCrit3 = mCrit3 /. {a → mya, b → myb, r → 0.045};
myMCrit5 = mCrit5 /. {a → mya, b → myb, r → 0.045};
myRStar = rStar /. {a → mya, b → myb};
plot8 =
Plot[{1, rCritFuncIgnoringPole[mya, myb, m, myqC, rmax], rCritFunc[mya, myb, m, myqC]},
  {m, mmin, mmax}, PlotRange → {{mmin, mmax}, {rmin, rmax}}, AspectRatio → 1 / 1,
  Epilog → {Text[Style["r*", Directive[FontSize → 16],
    FontFamily → "Helvetica"], {0.046, 0.02}]}},

  Frame → True, FrameLabel → {"", ""},
  LabelStyle → {Directive[FontSize → 16], FontFamily → "Helvetica"},

  ImageSize → 3. {100, 100},

  PlotStyle → {{White}, {Black, Thick}, {Black, Dashed}},
  Filling → {1 → {Axis, RGBColor[0.9, 0.9, 0.9]}, 2 → {Axis, RGBColor[0.75, 0.75, 0.75]}},
  AxesLabel → {r, m}, AxesStyle → Directive[FontSize → 16]]

```



```

In[162]:= coord8 = Table[{m, r}, {m, 0.0002, 0.0799, 0.0042}, {r, 0.0001, 0.0499, 0.0021}];

Timing[finalStateEncoded = Block[{$RecursionLimit = Infinity},
  vals8 = Table[recFuncLargeTimes[mya, myb, myg11, myg12, myg21, myg22, m, r, myqC,
    p0, D0, myt1][[2]], {m, 0.0002, 0.0799, 0.0042}, {r, 0.0001, 0.0499, 0.0021}]
  ]
];

```

The computation above takes about 24 minutes on a Mac mini 2.3 GHz Intel Core i5 with 4 GB of RAM. Below is a hard-coded version of the result.

```

In[163]:= vals8 = {{{0.9963850991854859`, 0.9964997823060009`, 0.003478867509496358`}, {0.996149717787`

```



```

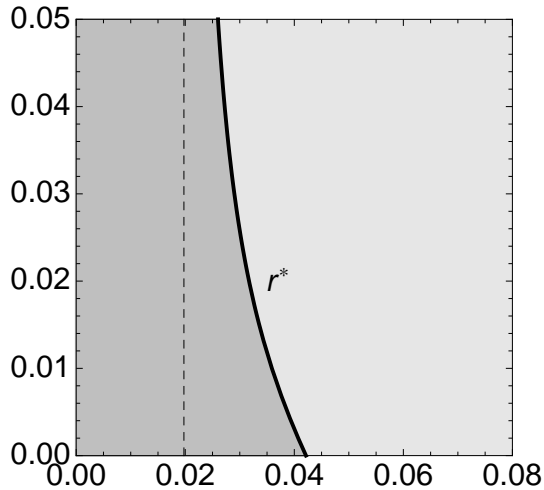
mya = 0.02;
myb = 0.04;
myg11 = 0;
myg12 = 0;
myg21 = 0;
myg22 = 0;
mym = 0.03;
myr = mya;
myqC = 0.2;
rmin = 0;
rmax = 0.05;
mmin = 0;
mmax = 0.08;
myMCrit2 = mCrit2 /. {a → mya, b → myb};
myMCrit3 = mCrit3 /. {a → mya, b → myb, r → 0.045};
myMCrit5 = mCrit5 /. {a → mya, b → myb, r → 0.045};
myRStar = rStar /. {a → mya, b → myb};
plot9 =
Plot[{1, rCritFuncIgnoringPole[mya, myb, m, myqC, rmax], rCritFunc[mya, myb, m, myqC]},
  {m, mmin, mmax}, PlotRange → {{mmin, mmax}, {rmin, rmax}}, AspectRatio → 1 / 1,
  Epilog → {Text[Style["r*", Directive[FontSize → 16],
    FontFamily → "Helvetica"], {0.037, 0.02}]}},

  Frame → True, FrameLabel → {"", ""},
  LabelStyle → {Directive[FontSize → 16], FontFamily → "Helvetica"},

  ImageSize → 3. {100, 100},

  PlotStyle → {{White}, {Black, Thick}, {Black, Dashed}},
  Filling → {1 → {Axis, RGBColor[0.9, 0.9, 0.9]}, 2 → {Axis, RGBColor[0.75, 0.75, 0.75]}},
  AxesLabel → {r, m}, AxesStyle → Directive[FontSize → 16]]

```



```
In[164]:= coord9 = Table[{m, r}, {m, 0.0002, 0.0799, 0.0042}, {r, 0.0001, 0.0499, 0.0021}];
```

```

Timing[finalStateEncoded = Block[{$RecursionLimit = Infinity},
  vals9 = Table[recFuncLargeTimes[mya, myb, myg11, myg12, myg21, myg22, m, r, myqC,
    p0, D0, myt1][[2]], {m, 0.0002, 0.0799, 0.0042}, {r, 0.0001, 0.0499, 0.0021}]
  ]
];

```

The computation above takes about 24 minutes on a Mac mini 2.3 GHz Intel Core i5 with 4 GB of RAM. Below is a hard-coded version of the result.

```
In[165]:= vals9 = {{{0.99504491855092`, 0.9971715472189118`, 0.002807418970236513`}, {0.99485448796827`
```



```

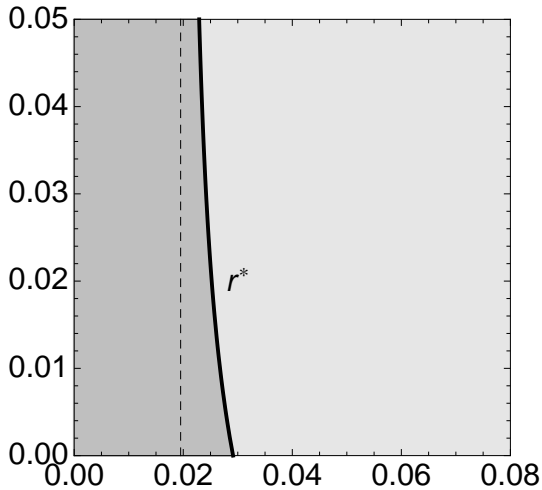
mya = 0.02;
myb = 0.04;
myg11 = 0;
myg12 = 0;
myg21 = 0;
myg22 = 0;
mym = 0.03;
myr = mya;
myqC = 0.5;
rmin = 0;
rmax = 0.05;
mmin = 0;
mmax = 0.08;
myMCrit2 = mCrit2 /. {a → mya, b → myb};
myMCrit3 = mCrit3 /. {a → mya, b → myb, r → 0.045};
myMCrit5 = mCrit5 /. {a → mya, b → myb, r → 0.045};
myRStar = rStar /. {a → mya, b → myb};
plot10 =
Plot[{1, rCritFuncIgnoringPole[mya, myb, m, myqC, rmax], rCritFunc[mya, myb, m, myqC]},
  {m, mmin, mmax}, PlotRange → {{mmin, mmax}, {rmin, rmax}}, AspectRatio → 1 / 1,
  Epilog → {Text[Style["r*", Directive[FontSize → 16],
    FontFamily → "Helvetica"], {0.03, 0.02}]},

  Frame → True, FrameLabel → {"", ""},
  LabelStyle → {Directive[FontSize → 16], FontFamily → "Helvetica"},

  ImageSize → 3. {100, 100},

  PlotStyle → {{White}, {Black, Thick}, {Black, Dashed}},
  Filling → {1 → {Axis, RGBColor[0.9, 0.9, 0.9]}, 2 → {Axis, RGBColor[0.75, 0.75, 0.75]}},
  AxesLabel → {r, m}, AxesStyle → Directive[FontSize → 16]]

```



```

In[166]:= coord10 = Table[{m, r}, {m, 0.0002, 0.0799, 0.0042}, {r, 0.0001, 0.0499, 0.0021}];

```

```

Timing[finalStateEncoded = Block[{$RecursionLimit = Infinity},
  vals10 = Table[recFuncLargeTimes[mya, myb, myg11, myg12, myg21, myg22, m, r, myqC,
    p0, D0, myt1][[2]], {m, 0.0002, 0.0799, 0.0042}, {r, 0.0001, 0.0499, 0.0021}]
  ]
];

```

The computation above takes about 24 minutes on a Mac mini 2.3 GHz Intel Core i5 with 4 GB of RAM. Below is a hard-coded version of the result.

```

In[167]:= vals10={{0.9929288552712007`,0.9982322228947664`,0.001750899629094998`},{0.99280961585

```

```

pattern10 = Map[classifyEquilFunc, vals10, {2}];
pattern10 // TableForm

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(* EB: marginal one-locus polymorphism at the B locus *)
pl2 = ListPlot[Pick[Flatten[coord10, 1], Map[# == "B" &, Flatten[pattern10]]],
  PlotMarkers → ○, PlotStyle → Gray];

(* Ei: fully-polymorphic equilibrium *)
pl4 = ListPlot[Pick[Flatten[coord10, 1], Map[# == "±" &, Flatten[pattern10]]],
  PlotMarkers → ●, PlotStyle → Gray];

plotStabilityEBPolym7 = Show[{plot10, pl2, pl4}]

```

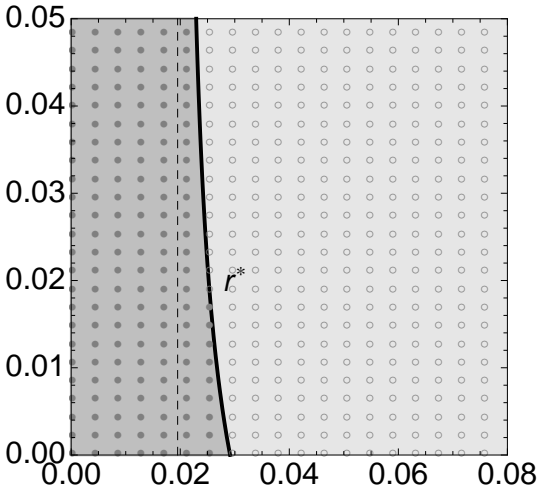


Figure 19: Critical recombination rate determining the stability of the marginal one-locus equilibrium E_B and invasion of A_1 for a polymorphic continent, as a function of the migration rate. Dark grey: invasion of A_1 via the unstable marginal equilibrium E_B ; light grey: no invasion of A_1 , stable marginal equilibrium E_B . Numerical iterations of invasion dynamics were performed at coordinates indicated by grey symbols. Different symbols indicate which equilibrium is reached: ● E_i ; ○ E_B . Initial values for iterations were $(p_0, q_0, D_0) = (0, \hat{q}_B, 0)$, where \hat{q}_B is the frequency of B_1 at the marginal one-locus migration-selection equilibrium. Iterations were stopped when changes in each coordinate from one time step to the next were smaller than the numerical precision. The vertical dashed line indicates the pole of the function $\tilde{r}(m)$. Parameters are $a = 0.02$, $b = 0.04$ and $q_c = 0.5$.

■ Case 8: $a = \frac{b}{2}$ and $q_c = 0.8$

```

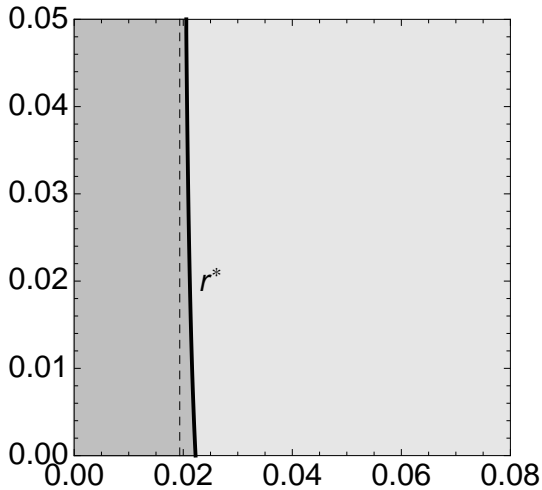
(* Initial values *)
p0 = 0.0001;
q0Polym = qEB1 /. {a → mya, b → myb, m → mym, qc → myqc};
D0 = 0;

```

```

mya = 0.02;
myb = 0.04;
myg11 = 0;
myg12 = 0;
myg21 = 0;
myg22 = 0;
mym = 0.03;
myr = mya;
myqC = 0.8;
rmin = 0;
rmax = 0.05;
mmin = 0;
mmax = 0.08;
myMCrit2 = mCrit2 /. {a → mya, b → myb};
myMCrit3 = mCrit3 /. {a → mya, b → myb, r → 0.045};
myMCrit5 = mCrit5 /. {a → mya, b → myb, r → 0.045};
myRStar = rStar /. {a → mya, b → myb};
plot11 =
Plot[{1, rCritFuncIgnoringPole[mya, myb, m, myqC, rmax], rCritFunc[mya, myb, m, myqC]},
  {m, mmin, mmax}, PlotRange → {{mmin, mmax}, {rmin, rmax}}, AspectRatio → 1 / 1,
  Epilog → {Text[Style["r*", Directive[FontSize → 16],
    FontFamily → "Helvetica"], {0.025, 0.02}],
  Frame → True, FrameLabel → {"", ""},
  LabelStyle → {Directive[FontSize → 16], FontFamily → "Helvetica"},
  ImageSize → 3. {100, 100},
  PlotStyle → {{White}, {Black, Thick}, {Black, Dashed}},
  Filling → {1 → {Axis, RGBColor[0.9, 0.9, 0.9]}, 2 → {Axis, RGBColor[0.75, 0.75, 0.75]}},
  AxesLabel → {r, m}, AxesStyle → Directive[FontSize → 16]]

```



```
In[168]:= coord11 = Table[{m, r}, {m, 0.0002, 0.0799, 0.0042}, {r, 0.0001, 0.0499, 0.0021}];
```

```

Timing[finalStateEncoded = Block[{$RecursionLimit = Infinity},
  vals11 = Table[recFuncLargeTimes[mya, myb, myg11, myg12, myg21, myg22, m, r, myqC,
    p0, D0, myt1][[2]], {m, 0.0002, 0.0799, 0.0042}, {r, 0.0001, 0.0499, 0.0021}]
  ]
];

```

The computation above takes about 24 minutes on a Mac mini 2.3 GHz Intel Core i5 with 4 GB of RAM. Below is a hard-coded version of the result.

```
In[169]:= vals11 = {{{0.9908128060462564`, 0.9992928915110391`, 0.0006988649805891363`}, {0.9907650222`
```

```

pattern11 = Map[classifyEquilFunc, vals11, {2}];
pattern11 // TableForm

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(* EB: marginal one-locus polymorphism at the B locus *)
pl2 = ListPlot[Pick[Flatten[coord11, 1], Map[# == "B" &, Flatten[pattern11]]],
  PlotMarkers → ○, PlotStyle → Gray];

(* Ei: fully-polymorphic equilibrium *)
pl4 = ListPlot[Pick[Flatten[coord11, 1], Map[# == "±" &, Flatten[pattern11]]],
  PlotMarkers → ●, PlotStyle → Gray];

plotStabilityEBPolym8 = Show[{plot11, pl2, pl4}]

```

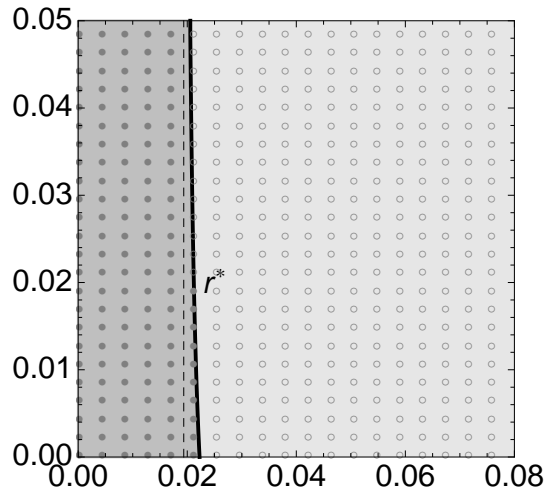


Figure 20: Critical recombination rate determining the stability of the marginal one-locus equilibrium E_B and invasion of A_1 for a polymorphic continent, as a function of the migration rate. Dark grey: invasion of A_1 via the unstable marginal equilibrium E_B ; light grey: no invasion of A_1 , stable marginal equilibrium E_B . Numerical iterations of invasion dynamics were performed at coordinates indicated by grey symbols. Different symbols indicate which equilibrium is reached: ● E_i ; ○ E_B . Initial values for iterations were $(p_0, q_0, D_0) = (0, \hat{q}_B, 0)$, where \hat{q}_B is the frequency of B_1 at the marginal one-locus migration-selection equilibrium. Iterations were stopped when changes in each coordinate from one time step to the next were smaller than the numerical precision. The vertical dashed line indicates the pole of the function $\tilde{r}(m)$. Parameters are $a = 0.02$, $b = 0.04$ and $q_c = 0.8$.

■ Case 9: $a > \frac{b}{2}$ and $q_c = 0.01$

```

(* Initial values *)
p0 = 0.0001;
q0Polym = qEB1 /. {a → mya, b → myb, m → mym, qc → myqc};
D0 = 0;

```

```

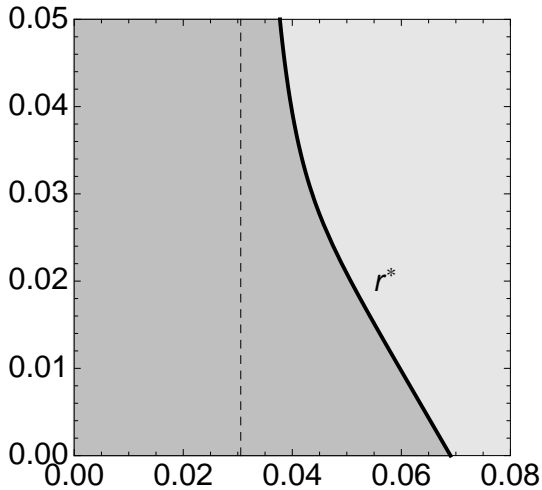
mya = 0.03;
myb = 0.04;
myg11 = 0;
myg12 = 0;
myg21 = 0;
myg22 = 0;
mym = 0.03;
myr = mya;
myqC = 0.01;
rmin = 0;
rmax = 0.05;
mmin = 0;
mmax = 0.08;
myMCrit2 = mCrit2 /. {a → mya, b → myb};
myMCrit3 = mCrit3 /. {a → mya, b → myb, r → 0.045};
myMCrit5 = mCrit5 /. {a → mya, b → myb, r → 0.045};
myRStar = rStar /. {a → mya, b → myb};
plot12 =
Plot[{1, rCritFuncIgnoringPole[mya, myb, m, myqC, rmax], rCritFunc[mya, myb, m, myqC]},
  {m, mmin, mmax}, PlotRange → {{mmin, mmax}, {rmin, rmax}}, AspectRatio → 1 / 1,
  Epilog → {Text[Style["r*", Directive[FontSize → 16],
    FontFamily → "Helvetica"], {0.057, 0.02}]}},

  Frame → True, FrameLabel → {"", ""},
  LabelStyle → {Directive[FontSize → 16], FontFamily → "Helvetica"},

  ImageSize → 3. {100, 100},

  PlotStyle → {{White}, {Black, Thick}, {Black, Dashed}},
  Filling → {1 → {Axis, RGBColor[0.9, 0.9, 0.9]}, 2 → {Axis, RGBColor[0.75, 0.75, 0.75]}},
  AxesLabel → {r, m}, AxesStyle → Directive[FontSize → 16]]

```



```

In[170]:= coord12 = Table[{m, r}, {m, 0.0002, 0.0799, 0.0042}, {r, 0.0001, 0.0499, 0.0021}];

```

```

Timing[finalStateEncoded = Block[{$RecursionLimit = Infinity},
  vals12 = Table[recFuncLargeTimes[mya, myb, myg11, myg12, myg21, myg22, m, r, myqC,
    p0, D0, myt1][[2]], {m, 0.0002, 0.0799, 0.0042}, {r, 0.0001, 0.0499, 0.0021}]
  ]
];

```

The computation above takes about 24 minutes on a Mac mini 2.3 GHz Intel Core i5 with 4 GB of RAM. Below is a hard-coded version of the result.

```

In[171]:= vals12 = {{{0.9968969614989158`, 0.9969707949293976`, 0.003012274587233875`}, {0.99677987332

```

```

pattern12 = Map[classifyEquilFunc, vals12, {2}];
pattern12 // TableForm

```

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±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±
±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±
±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±
±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±
±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±
±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±
±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±
±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±
±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±
±	±	±	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
±	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B

```

(* EB: marginal one-locus polymorphism at the B locus *)
pl2 = ListPlot[Pick[Flatten[coord12, 1], Map[# == "B" &, Flatten[pattern12]]],
  PlotMarkers -> o, PlotStyle -> Gray];

(* Ei: fully-polymorphic equilibrium *)
pl4 = ListPlot[Pick[Flatten[coord12, 1], Map[# == "±" &, Flatten[pattern12]]],
  PlotMarkers -> •, PlotStyle -> Gray];
plotStabilityEBPolym9 = Show[{plot12, pl2, pl4}]

```

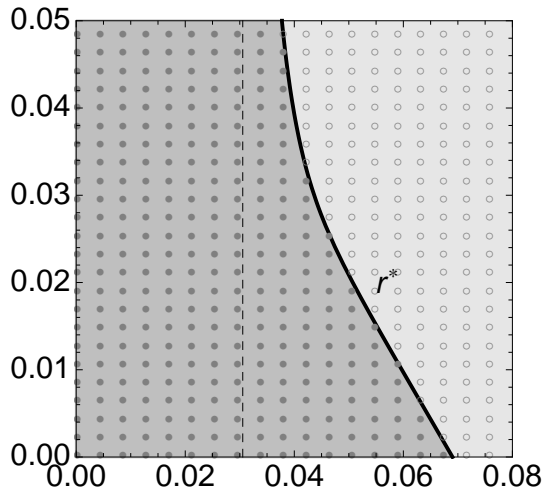


Figure 21: Critical recombination rate determining the stability of the marginal one-locus equilibrium E_B and invasion of A_1 for a polymorphic continent, as a function of the migration rate. Dark grey: invasion of A_1 via the unstable marginal equilibrium E_B ; light grey: no invasion of A_1 , stable marginal equilibrium E_B . Numerical iterations of invasion dynamics where performed at coordinates indicated by grey symbols. Different symbols indicate which equilibrium is reached: \bullet E_i ; \circ E_B . Initial values for iterations were $(p_0, q_0, D_0) = (0, \hat{q}_B, 0)$, where \hat{q}_B is the frequency of B_1 at the marginal one-locus migration-selection equilibrium. Iterations were stopped when changes in each coordinate from one time step to the next were smaller than the numerical precision. The vertical dashed line indicates the pole of the function $\tilde{r}(m)$. Parameters are $a = 0.03$, $b = 0.04$ and $q_c = 0.01$.

- Case 10: $a > \frac{b}{2}$ and $q_c = 0.2$

```

(* Initial values *)
p0 = 0.0001;
q0Polym = qEB1 /. {a -> mya, b -> myb, m -> mym, qc -> myqc};
D0 = 0;

```

```

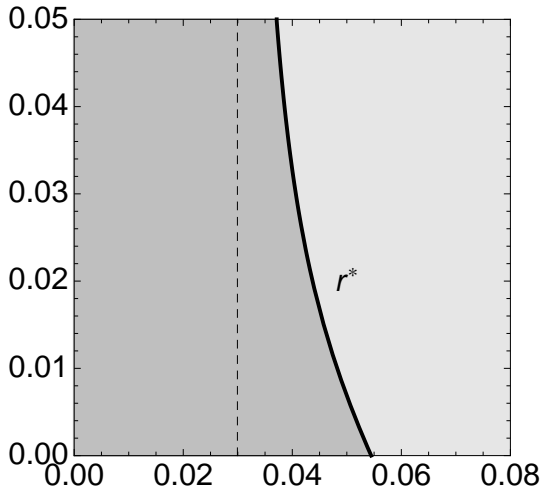
mya = 0.03;
myb = 0.04;
myg11 = 0;
myg12 = 0;
myg21 = 0;
myg22 = 0;
mym = 0.03;
myr = mya;
myqC = 0.2;
rmin = 0;
rmax = 0.05;
mmin = 0;
mmax = 0.08;
myMCrit2 = mCrit2 /. {a → mya, b → myb};
myMCrit3 = mCrit3 /. {a → mya, b → myb, r → 0.045};
myMCrit5 = mCrit5 /. {a → mya, b → myb, r → 0.045};
myRStar = rStar /. {a → mya, b → myb};
plot13 =
Plot[{1, rCritFuncIgnoringPole[mya, myb, m, myqC, rmax], rCritFunc[mya, myb, m, myqC]},
  {m, mmin, mmax}, PlotRange → {{mmin, mmax}, {rmin, rmax}}, AspectRatio → 1 / 1,
  Epilog → {Text[Style["r*", Directive[FontSize → 16],
    FontFamily → "Helvetica"], {0.05, 0.02}]},

  Frame → True, FrameLabel → {"", ""},
  LabelStyle → {Directive[FontSize → 16], FontFamily → "Helvetica"},

  ImageSize → 3. {100, 100},

  PlotStyle → {{White}, {Black, Thick}, {Black, Dashed}},
  Filling → {1 → {Axis, RGBColor[0.9, 0.9, 0.9]}, 2 → {Axis, RGBColor[0.75, 0.75, 0.75]}},
  AxesLabel → {r, m}, AxesStyle → Directive[FontSize → 16]]

```



```

In[172]:= coord13 = Table[{m, r}, {m, 0.0002, 0.0799, 0.0042}, {r, 0.0001, 0.0499, 0.0021}];

```

```

Timing[finalStateEncoded = Block[{$RecursionLimit = Infinity},
  vals13 = Table[recFuncLargeTimes[mya, myb, myg11, myg12, myg21, myg22, m, r, myqC,
    p0, D0, myt1][[2]], {m, 0.0002, 0.0799, 0.0042}, {r, 0.0001, 0.0499, 0.0021}]
  ]
];

```

The computation above takes about 24 minutes on a Mac mini 2.3 GHz Intel Core i5 with 4 GB of RAM. Below is a hard-coded version of the result.

```

In[173]:= vals13={{0.9961237386100369`,0.997552161312273`,0.0024322695141881967`},{0.99602902586:

```



```

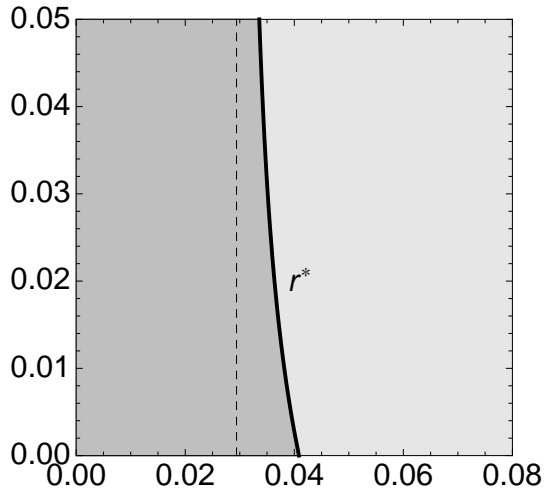
mya = 0.03;
myb = 0.04;
myg11 = 0;
myg12 = 0;
myg21 = 0;
myg22 = 0;
mym = 0.03;
myr = mya;
myqC = 0.5;
rmin = 0;
rmax = 0.05;
mmin = 0;
mmax = 0.08;
myMCrit2 = mCrit2 /. {a → mya, b → myb};
myMCrit3 = mCrit3 /. {a → mya, b → myb, r → 0.045};
myMCrit5 = mCrit5 /. {a → mya, b → myb, r → 0.045};
myRStar = rStar /. {a → mya, b → myb};
plot14 =
Plot[{1, rCritFuncIgnoringPole[mya, myb, m, myqC, rmax], rCritFunc[mya, myb, m, myqC]},
  {m, mmin, mmax}, PlotRange → {{mmin, mmax}, {rmin, rmax}}, AspectRatio → 1 / 1,
  Epilog → {Text[Style["r*", Directive[FontSize → 16],
    FontFamily → "Helvetica"], {0.041, 0.02}]}},

  Frame → True, FrameLabel → {"", ""},
  LabelStyle → {Directive[FontSize → 16], FontFamily → "Helvetica"},

  ImageSize → 3. {100, 100},

  PlotStyle → {{White}, {Black, Thick}, {Black, Dashed}},
  Filling → {1 → {Axis, RGBColor[0.9, 0.9, 0.9]}, 2 → {Axis, RGBColor[0.75, 0.75, 0.75]}},
  AxesLabel → {r, m}, AxesStyle → Directive[FontSize → 16]]

```



```

In[174]:= coord14 = Table[{m, r}, {m, 0.0002, 0.0799, 0.0042}, {r, 0.0001, 0.0499, 0.0021}];

```

```

Timing[finalStateEncoded = Block[{$RecursionLimit = Infinity},
  vals14 = Table[recFuncLargeTimes[mya, myb, myg11, myg12, myg21, myg22, m, r, myqC,
    p0, D0, myt1][[2]], {m, 0.0002, 0.0799, 0.0042}, {r, 0.0001, 0.0499, 0.0021}]
  ]
];

```

The computation above takes about 24 minutes on a Mac mini 2.3 GHz Intel Core i5 with 4 GB of RAM. Below is a hard-coded version of the result.

```

In[175]:= vals14 = {{{0.9949028652735226`, 0.9984701045638185`, 0.001518301584557664`}, {0.99484357489

```



```

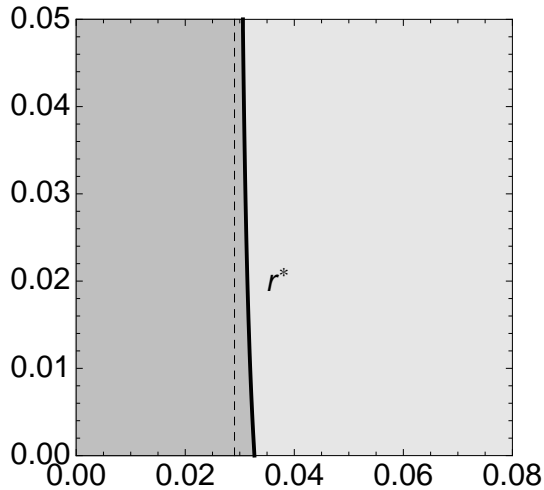
mya = 0.03;
myb = 0.04;
myg11 = 0;
myg12 = 0;
myg21 = 0;
myg22 = 0;
mym = 0.03;
myr = mya;
myqC = 0.8;
rmin = 0;
rmax = 0.05;
mmin = 0;
mmax = 0.08;
myMCrit2 = mCrit2 /. {a → mya, b → myb};
myMCrit3 = mCrit3 /. {a → mya, b → myb, r → 0.045};
myMCrit5 = mCrit5 /. {a → mya, b → myb, r → 0.045};
myRStar = rStar /. {a → mya, b → myb};
plot15 =
Plot[{1, rCritFuncIgnoringPole[mya, myb, m, myqC, rmax], rCritFunc[mya, myb, m, myqC]},
  {m, mmin, mmax}, PlotRange → {{mmin, mmax}, {rmin, rmax}}, AspectRatio → 1 / 1,
  Epilog → {Text[Style["r*", Directive[FontSize → 16],
    FontFamily → "Helvetica"], {0.037, 0.02}]},

  Frame → True, FrameLabel → {"", ""},
  LabelStyle → {Directive[FontSize → 16], FontFamily → "Helvetica"},

  ImageSize → 3. {100, 100},

  PlotStyle → {{White}, {Black, Thick}, {Black, Dashed}},
  Filling → {1 → {Axis, RGBColor[0.9, 0.9, 0.9]}, 2 → {Axis, RGBColor[0.75, 0.75, 0.75]}},
  AxesLabel → {r, m}, AxesStyle → Directive[FontSize → 16]]

```



```

In[176]:= coord15 = Table[{m, r}, {m, 0.0002, 0.0799, 0.0042}, {r, 0.0001, 0.0499, 0.0021}];

Timing[finalStateEncoded = Block[{$RecursionLimit = Infinity},
  vals15 = Table[recFuncLargeTimes[mya, myb, myg11, myg12, myg21, myg22, m, r, myqC,
    p0, D0, myt1][[2]], {m, 0.0002, 0.0799, 0.0042}, {r, 0.0001, 0.0499, 0.0021}]
  ]
];
$Aborted

```

The computation above takes about 24 minutes on a Mac mini 2.3 GHz Intel Core i5 with 4 GB of RAM. Below is a hard-coded version of the result.

```

In[177]:= vals15={{0.9936819978977282^`,0.9993880433229645^`,0.0006065738963986862^`},{0.9936582438:
pattern15 = Map[classifyEquilFunc, vals15, {2}];
pattern15 // TableForm

```

±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±
±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±
±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±
±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±
±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±
±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±
±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±
B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B

```

(* EB: marginal one-locus polymorphism at the B locus *)
pl2 = ListPlot[Pick[Flatten[coord15, 1], Map[# == "B" &, Flatten[pattern15]]],
  PlotMarkers -> o, PlotStyle -> Gray];
(* E±: fully-polymorphic equilibrium *)
pl4 = ListPlot[Pick[Flatten[coord15, 1], Map[# == "±" &, Flatten[pattern15]]],
  PlotMarkers -> ●, PlotStyle -> Gray];
plotStabilityEBPolym12 = Show[{plot15, pl2, pl4}]

```

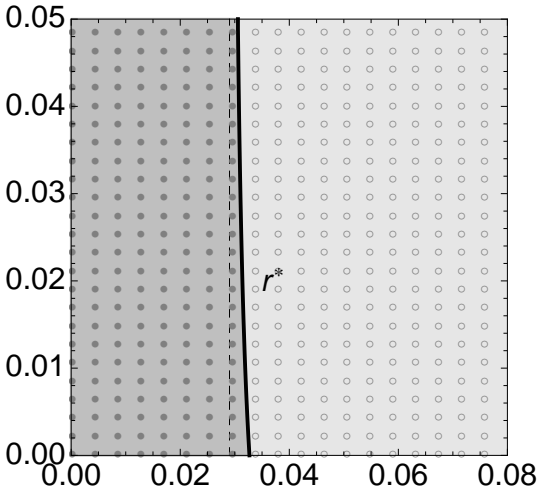
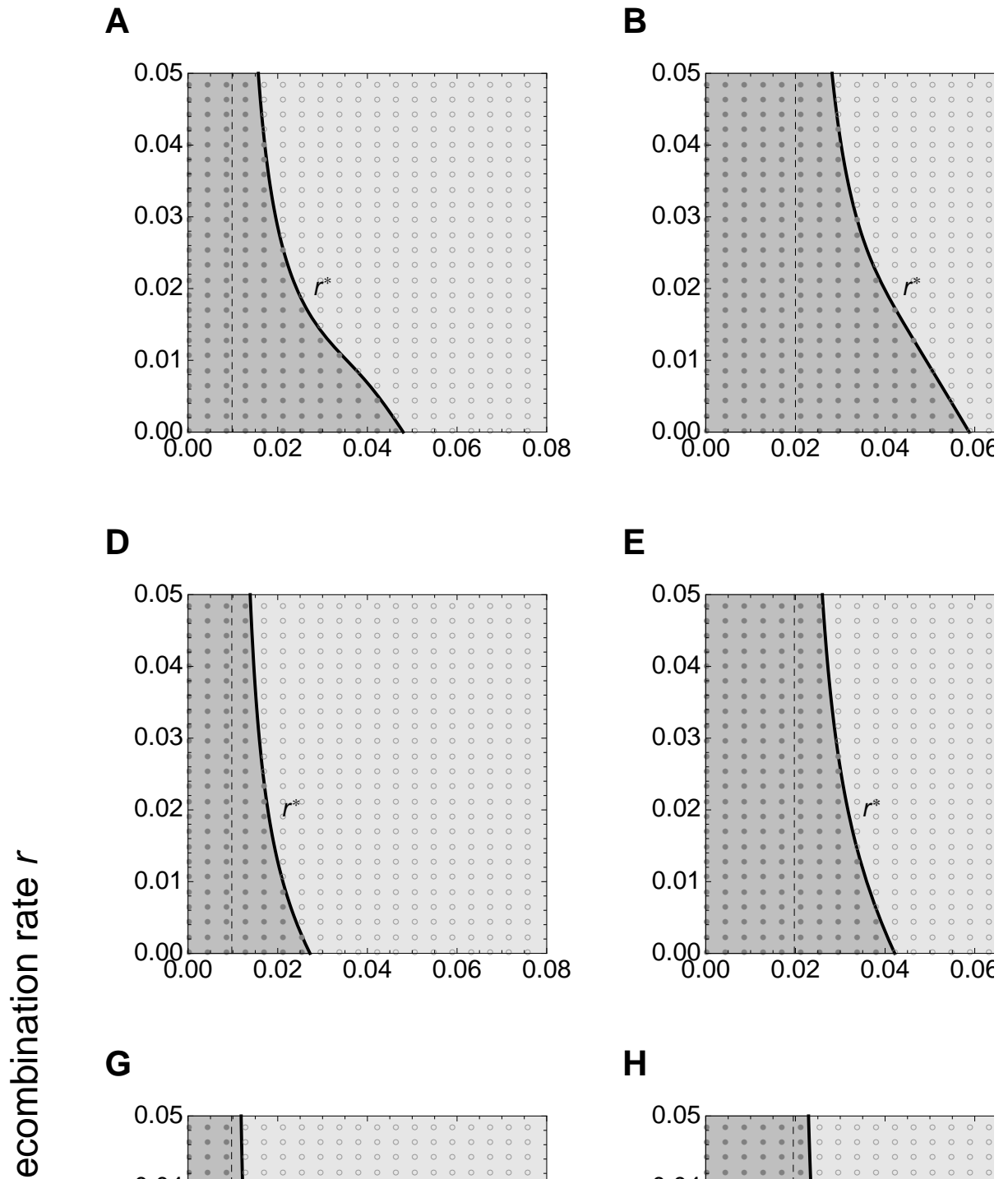


Figure 24: Critical recombination rate determining the stability of the marginal one-locus equilibrium E_B and invasion of A_1 for a polymorphic continent, as a function of the migration rate. Dark grey: invasion of A_1 via the unstable marginal equilibrium E_B ; light grey: no invasion of A_1 , stable marginal equilibrium E_B . Numerical iterations of invasion dynamics were performed at coordinates indicated by grey symbols. Different symbols indicate which equilibrium is reached: \bullet : E_{\pm} ; \circ : E_B . Initial values for iterations were $(p_0, q_0, D_0) = (0, \hat{q}_B, 0)$, where \hat{q}_B is the frequency of B_1 at the marginal one-locus migration-selection equilibrium. Iterations were stopped when changes in each coordinate from one time step to the next were smaller than the numerical precision. The vertical dashed line indicates the pole of the function $\vec{r}^*(m)$. Parameters are $a = 0.03$, $b = 0.04$ and $q_c = 0.8$.

■ Combined plot

```

plotStabilityEBPolymComb =
  Labeled[GraphicsGrid[Partition[MapThread[Labeled[#1, #2, {{Top, Left}},
    LabelStyle -> {Directive[FontSize -> 22, Bold], FontFamily -> "Helvetica"},
    FrameMargins -> {{-5, 0}, {-35, 0}}] &,
    {{plotStabilityEBPolym1, plotStabilityEBPolym5, plotStabilityEBPolym9,
    plotStabilityEBPolym2, plotStabilityEBPolym6, plotStabilityEBPolym10,
    plotStabilityEBPolym3, plotStabilityEBPolym7, plotStabilityEBPolym11,
    plotStabilityEBPolym4, plotStabilityEBPolym8, plotStabilityEBPolym12},
    CharacterRange["A", "L"]}], 3], ImageSize -> 3.6 {280, 360}, AspectRatio -> 1.5],
  {"Migration rate m", "Recombination rate r"}, {Bottom, Left}, RotateLabel -> True,
  LabelStyle -> {Directive[FontSize -> 24], FontFamily -> "Helvetica"},
  FrameMargins -> {{0, 0}, {15, 0}}]
  
```



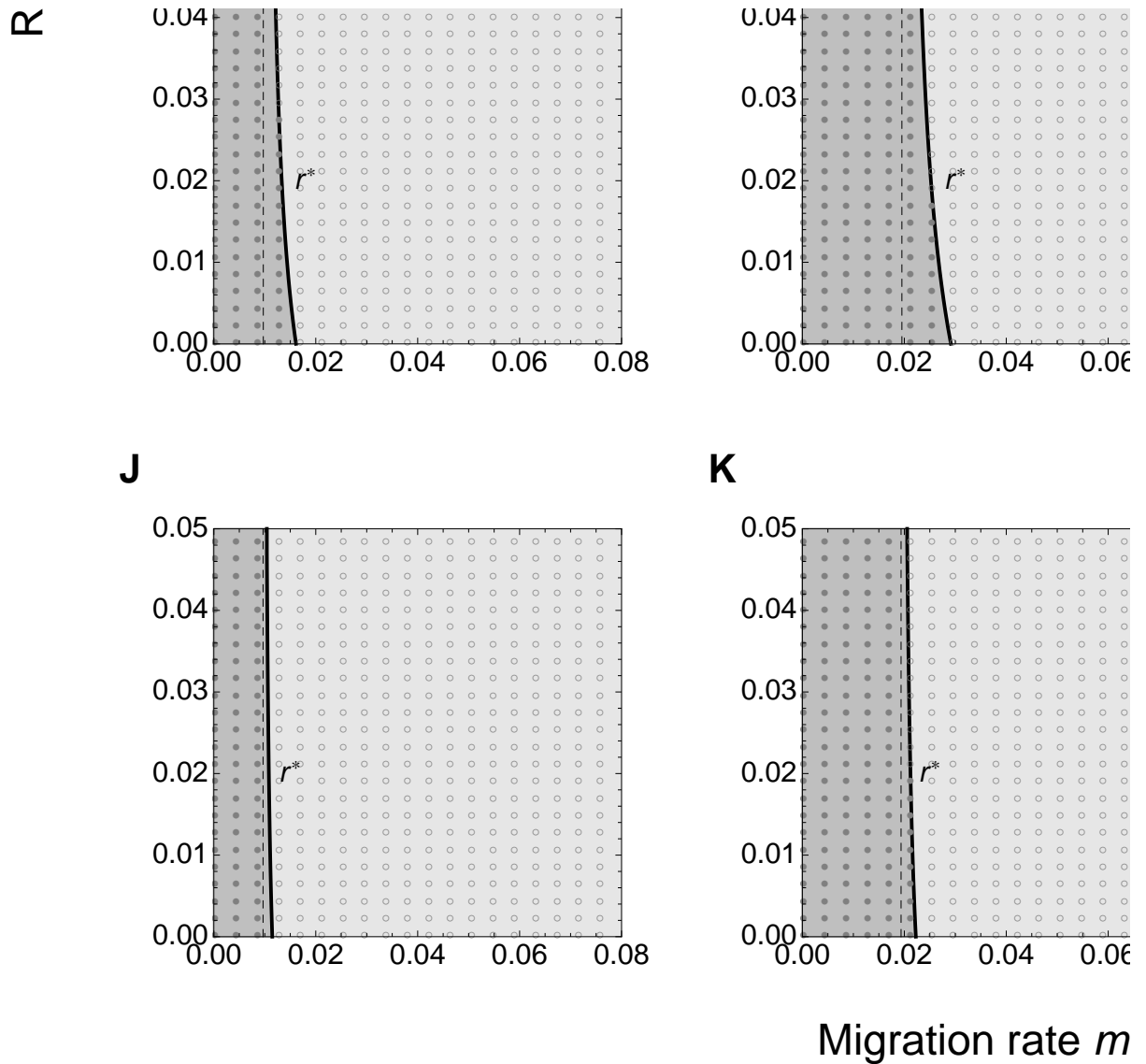


Figure 25: Critical recombination rate determining the stability of the marginal one-locus equilibrium E_B and invasion of A_1 for a polymorphic continent, as a function of the migration rate. Dark grey: invasion of A_1 via the unstable marginal equilibrium E_B ; light grey: no invasion of A_1 , stable marginal equilibrium E_B . Numerical iterations of invasion dynamics were performed at coordinates indicated by grey symbols. Different symbols indicate which equilibrium is reached: \bullet E_+ ; \circ E_B . Initial values for iterations were $\{\rho_0, q_0, D_0\} = \{0, \hat{q}_B, 0\}$, where \hat{q}_B is the frequency of B_1 at the marginal one-locus migration-selection equilibrium. Iterations were stopped when changes in each coordinate between successive time steps were smaller than the numerical precision. The vertical dashed line indicates the pole of the function $\vec{r}(m)$. In the left column (A), (D), (G), (J)), the selection coefficients are $a=0.01, b=0.04$ ($a < b/2$), in the middle column (B), (E), (H), (K)) they are $a=0.02, b=0.04$ ($a = b/2$), and in the right column (C), (F), (I), (L)) they are $a=0.03, b=0.04$ ($a > b/2$). From top to bottom, the continental frequency of B_1 increases and takes values of $q_c = 0.01$ (A) – (C)), $q_c = 0.2$ (D) – (F)), $q_c = 0.5$ (G) – (I)) and $q_c = 0.8$ (J) – (L)).

`figPath`

`/Users/Simon/Documents/LocAdD/results/130526/stabilityEB/`

`figPath5 = figPath <> "stabilityEBPolymCont_comb.eps";`

`Export[figPath5, plotStabilityEBPolymComb, "EPS"]`

`/Users/Simon/Documents/LocAdD/results/130526/stabilityEB/stabilityEBPolymCont_comb.
eps`