Analytical approximation of the invasion probability for a slightly-supercritical branching process

Here, we derive analytical approximations to the invasion probability for the continent-island model with two biallelic loci, where the focus is on a new beneficial mutation arising at one locus ($\mathcal{A}$), given that there is an established migration-selection equilibrium at the second locus ($\mathcal{B}$). The approximations assume that the corresponding branching process is slightly supercritical, *i.e.* that the leading eigenvalue of the mean matrix is $\nu_1 = 1 + \xi$, where ξ is small. The approach we take here is based on Theorem 5.6 in Haccou *et al.* (2005, pp. 127–128). In the following, we refer to this theorem as T5.6_HJV2005.

We first set up definitions – some previously derived in other *Mathematica* Notebooks – and then proceed with the applications to additive fitnesses for a monomorphic continent. We also consider the case in which locus $\mathcal{B}$ is polymorphic on the continent with allele B_1 segregating at constant frequency q_c. The approximations derived in the following are valid for weak evolutionary forces.

Set-up and initialisation

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.

Generic assumptions

In[2]:=
```
genericAssumpt := {0 < r, 0 < a < b < 1, a + b < 1, 0 < m < 1}
assumeMonomorphCont := {qC → 0}
```

Functions previously established

The following is taken from the *Mathematica* Notebook '2LocContIsland_Stoch_Discr.nb', where a derivation is also provided.

- Numerical solution to branching-process invasion probabilities (including polymorphic continent)

The following is taken from the *Mathematica* Notebook '2LocContIsland_Stoch_Discr.nb', where a derivation is also provided.

In[4]:=
```
probEstablAMApproxPolymContFunc::usage = "probEstablAMApproxPolymContFunc[r, m1, a1, b1
probEstablAMApproxPolymContFunc[r1_,m1_,a1_,b1_,γ111_,γ121_,γ211_,γ221_,qC_]:=Module[{q
r=r1;
qEq=(b1-m1+a1*m1+2*b1*m1*qC+Sqrt[-4*b1*(-1+a1+b1)*m1*(1+m1)*qC+(b1+(-1+a1)*m1+2*b1*m1*qC)^2])/(2*b1*(1+m1))
wbar=1-a1+b1*(-1+2*qEq);
w1=1+b1*qEq+(-1+qEq)*γ111;
w2=1+b1*(-1+qEq)-qEq*γ111+γ121*(-1+qEq);
w14=1-γ111;
(* Leading eigenvalue of the mean matrix; Note that q_C does *not* enter here! *)
λ1=-1/(2 wbar) (-1+m1)*(w1-r*w14+w2+(w1^2+r^2*w14^2+w1*(2*(-1+2*qEq)*r*w14-2*w2)+2*(1-2*qEq)*r*
(* Probability generating functions *)
pgf1[s1_,s2_]:=Exp[-(r*(1-m1)*(1-qEq)*(1-s2)*w14)/wbar-((1-m1)*(1-s1)*(w1-r*(1-qEq)*w14))/wbar];
pgf2[s1_,s2_]:=Exp[-(r*(1-m1)*qEq*(1-s1)*w14)/wbar-((1-m1)*(1-s2)*(-r*qEq*w14+w2))/wbar];
qSol=FindRoot[{pgf1[q1,q2]==q1,pgf2[q1,q2]==q2},{q1,0.5},{q2,0.5}];
(* Return the probability of establishment, 1-q *)
Return[{λ1,(1-q1),(1-q2),qEq*(1-q1)+(1-qEq)*(1-q2),qEq}/.qSol]
];
```

- Critical migration rate $m_{\text{crit},5}$ for the monomorphic case with additive fitnesses

In[6]:=
```
mCritFunc::usage = "mCritFunc[r, a, b] returns the critical migration rate m_inv for the
mCritFunc[r_,a_,b_]:=Module[{mcrit1,mcrit2,mcrit3,mcrit5,res},
mcrit1=a/(1-b);
mcrit2=b/(1-a); (* This is the critical value derived above, and also given in Akerman (201
mcrit3=(a+b-r)/(1-r); (* This is given in Akerman (2011); the continuous-time analog is m_C in B
mcrit5=(a*(b-a+r))/((a-b)*(a-r)+r*(1-a)); (* This is the equation after equation (22) in Akerman (201
(* res=If[mcrit5<0,Min[mcrit2],Min[mcrit2,mcrit5]]; *)
(* res=If[mcrit5<0,mcrit2,Max[Min[mcrit2,mcrit5],Max[mcrit1,mcrit5]]]; *)
res=If[r<a,mcrit2,If[a<r<b,mcrit5,Max[mcrit1,mcrit5]]];
Return[res]]
```

- Critical recombination rate for the monomorphic case with additive fitnesses

In[8]:=
```
rCritFunc::usage = "rCritFunc[m, a, b] returns the critical recombination rate r_crit for
rCritFunc[m_,a_,b_]:=Module[{rmax,rcrit5,mThresh,mm},
rmax=0.5; (* This is the maximum recombination rate that is biologically plausible in t
rcrit5=(a*(a-b)*(1+m))/(a+2*a*m-(1+b)*m); (* This is obtained from solving m = m_crit,5 = f(r) for r. *)
mThresh=(a-2 a^2+2 a b)/(1-2 a+2 a^2+b-2 a b); (* If m is below this value, r is above 0.5. *)
res=If[m≤mThresh,rmax,rcrit5];
Return[res];
]
```

Fitness and marginal fitness

The generic fitness matrix

```
In[10]:= Wgeneric =
           {{w11, w12, w13, w14}, {w21, w22, w23, w24}, {w31, w32, w33, w34}, {w41, w42, w43, w44}};
         MatrixForm[Wgeneric]
```

$$\begin{pmatrix} w11 & w12 & w13 & w14 \\ w21 & w22 & w23 & w24 \\ w31 & w32 & w33 & w34 \\ w41 & w42 & w43 & w44 \end{pmatrix}$$

Fitness equivalences

```
In[11]:= assumeNoPosEff :=
          {w21 → w12, w31 → w13, w41 → w14, w32 → w14, w42 → w24, w43 → w34, w23 → w14}
```

Fitness matrix assuming no position effects

```
In[12]:= W = Wgeneric /. assumeNoPosEff;
         MatrixForm[W]
```

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

Assume additive fitnesses

```
In[13]:= assumeAddFit := {w11 → 1 + a + b, w12 → 1 + a, w22 → 1 + a - b,
           w13 → 1 + b, w14 → 1, w24 → 1 - b, w33 → 1 - a + b, w34 → 1 - a, w44 → 1 - a - b}
In[14]:= Wadd = W /. assumeAddFit;
         MatrixForm[Wadd]
```

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

Assume epistasis on top of additive fitnesses

```
In[15]:= assumeAddEpiFit := {w11 → 1 + a + b, w12 → 1 + a - γ21, w22 → 1 + a - b - γ22, w13 → 1 + b,
           w14 → 1 - γ11, w24 → 1 - b - γ12, w33 → 1 - a + b, w34 → 1 - a, w44 → 1 - a - b}
In[16]:= WaddEpi = W /. assumeAddEpiFit;
         MatrixForm[WaddEpi]
```

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

Mean fitness of resident population

```
In[17]:= wbarRule := {wbar → qHatB^2 w33 + 2 qHatB (1 - qHatB) w34 + (1 - qHatB)^2 w44}
```

Marginal fitnesses of the haplotypes $A_1 B_1$ and $A_1 B_2$

```
In[18]:= w1Rule := {w1 → w13 qHatB + w14 (1 - qHatB)};
         w2Rule := {w2 → w24 (1 - qHatB) + w14 qHatB};
```

Factors in the dynamics

```
In[20]:= A := (1 - m) (w1 - (1 - qHatB) r w14) / wbar;
         B := (1 - m) r w14 qHatB / wbar;
         C := (1 - m) r w14 (1 - qHatB) / wbar;
         D := (1 - m) (w2 - qHatB r w14) / wbar;
```

▪ Frequency of B_1 at the marginal one-locus migration-selection equilibrium

Frequency of the B_1 allele at the marginal one-locus migration-selection equilibrium

In[24]:=
```
qHatBRule := qHatB → (b - m + a m)/(b + b m)
```

In[25]:=
```
qHatBPolymContRule := qHatB → 1/(2 b (1 + m))
  (b - m + a m + 2 b m qC + Sqrt[-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2])
```

In[26]:=
```
qHatBMonomorphCont = FullSimplify[qHatB /. qHatBRule /. assumeMonomorphCont,
   Assumptions → Flatten[{genericAssumpt, b + a m ≥ m}]]
```

Out[26]= $\frac{b - m + a\, m}{b + b\, m}$

In[27]:=
```
qHatBPolymorphCont = qHatB /. qHatBRule
```

Out[27]= $\frac{b - m + a\, m}{b + b\, m}$

In[28]:=
```
qHatBMonomorphContRule := qHatB → qHatBMonomorphCont
```

For a derivation of these equilibrium frequencies, see the *Mathematica* Notebook '2LocContIsland_Stoch_Discr.nb'.

Mean matrix (expected numbers of offspring)

Generic

The mean matrix of the offspring numbers

In[29]:=
```
L := {{λ11, λ12}, {λ21, λ22}}

MatrixForm[L]
```

$$\begin{pmatrix} \lambda 11 & \lambda 12 \\ \lambda 21 & \lambda 22 \end{pmatrix}$$

where λ_{ij} is the expected number of *j*-type offspring produced per generation by a single *i*-type parent.

Additive fitnesses without epistasis

Give the entries of L explicitly for additive fitnesses, as well as for additive fitnesses and epistasis.

In[30]:=
```
λ11add = 𝒜 /. w1Rule /. wbarRule /. qHatBRule /. assumeAddFit // FullSimplify;
λ12add = 𝒞 /. wbarRule /. qHatBRule /. assumeAddFit // FullSimplify;
λ21add = ℬ /. wbarRule /. qHatBRule /. assumeAddFit // FullSimplify;
λ22add = 𝒟 /. w2Rule /. wbarRule /. qHatBRule /. assumeAddFit // FullSimplify;

λ11add
λ12add
λ21add
λ22add
```

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

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

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

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

- Additive fitnesses and polymorphic continent

```
In[34]:= λ11addPolymCont =
    𝒜 /. w1Rule /. wbarRule /. qHatBPolymContRule /. assumeAddFit // FullSimplify;
  λ12addPolymCont = 𝒞 /. wbarRule /. qHatBPolymContRule /. assumeAddFit // FullSimplify;
  λ21addPolymCont = ℬ /. wbarRule /. qHatBPolymContRule /. assumeAddFit // FullSimplify;
  λ22addPolymCont =
    𝒟 /. w2Rule /. wbarRule /. qHatBPolymContRule /. assumeAddFit // FullSimplify;

  λ11addPolymCont
  λ12addPolymCont
  λ21addPolymCont
  λ22addPolymCont
```

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

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

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

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

- **Approximating the entries of the mean matrices**

- Transformation rules

Assume small evolutionary forces of same order, inlcuding the coefficients of epistasis, but not the continental frequency of B_1, q_c.

```
In[38]:= assumeSmallForces :=
   MapThread[#1 → #2 ϵ &, {{a, b, r, m, γ11, γ12, γ21, γ22}, {α, β, ρ, μ, g11, g12, g21, g22}}]
  backSubstSmallForces := MapThread[#1 → #2 / ϵ &,
    {{α, β, ρ, μ, g11, g12, g21, g22}, {a, b, r, m, γ11, γ12, γ21, γ22}}]
```

- Additive fitnesses

```
In[40]:= Clear[λ11addAx, λ12addAx, λ21addAx, λ22addAx]

In[41]:= MapThread[
    {#1 = Series[#2 /. assumeSmallForces, {ϵ, 0, 1}] /. backSubstSmallForces // Normal} &,
    {{λ11addAx, λ12addAx, λ21addAx, λ22addAx}, {λ11add, λ12add, λ21add, λ22add}}];

  {{λ11addAx, λ12addAx}, {λ21addAx, λ22addAx}} // MatrixForm
```

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

- Additive fitnesses and polymorphic continent

```
In[42]:= Clear[λ11addPolymContAx, λ12addPolymContAx, λ21addPolymContAx, λ22addPolymContAx]
```

```
In[43]:= MapThread[FullSimplify[{#1 =
            Series[#2 /. assumeSmallForces, {ϵ, 0, 1}] /. backSubstSmallForces // Normal}] &,
        {{λ11addPolymContAx, λ12addPolymContAx, λ21addPolymContAx, λ22addPolymContAx},
         {λ11addPolymCont, λ12addPolymCont, λ21addPolymCont, λ22addPolymCont}}];

genericAssumpt
```

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

```
FullSimplify[
  {{λ11addPolymContAx, λ12addPolymContAx}, {λ21addPolymContAx, λ22addPolymContAx}},
  Assumptions → Flatten[genericAssumpt]] // MatrixForm
```

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

Checking if we obtain the correct terms when setting $q_c = 0$:

```
FullSimplify[
  {{λ11addPolymContAx, λ12addPolymContAx}, {λ21addPolymContAx, λ22addPolymContAx}} /.
   qC → 0, Assumptions → Flatten[{genericAssumpt, m < b}]] // MatrixForm
```

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

Additive fitness

■ Mean matrix

```
Clear[u, v, v1, v2]

In[44]:= Ladd := {{λ11add, λ12add}, {λ21add, λ22add}}
         LaddAx := {{λ11addAx, λ12addAx}, {λ21addAx, λ22addAx}}
```

Rules for the assumptions we are going to make:

```
genericAssumpt
```

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

The mean matrix with additive fitnesses

```
MatrixForm[Ladd]
```

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

The mean matrix with additive fitnesses under the assumption that all evolutionary forces are weak:

```
assumeSmallForces
```

{a → α ϵ, b → β ϵ, r → ϵ ρ, m → ϵ μ, γ11 → g11 ϵ, γ12 → g12 ϵ, γ21 → g21 ϵ, γ22 → g22 ϵ}

```
MatrixForm[LaddAx]
```

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

Recall that the entry λ_{ij} of the mean matrix L denotes the expected number of *j*-type offspring produced per generation by a single *i*-type parent.

■ Exploration of eigenvalues

```
Eigenvalues[Ladd] // FullSimplify
```

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

```
FullSimplify[Reduce[(1 + m) (b^2 (1 + m) - 2 b (-1 + m) r + r (r + m (-4 + 4 a + r))) ≥ 0, m],
 Assumptions → Flatten[{genericAssumpt, {a + b < 1}}]]
```

$$(b-r)^2+4(-1+a)r \geq 0 \;||\; m+\frac{(b+r)^2}{(b-r)^2+4(-1+a)r} \leq 0$$

If the condition above is fulfilled, the first eigenvalue is larger than the second one. If the condition is not fulfilled, then the real parts of the two eigenvalues are equal.

Therefore, the first is the dominant eigenvalue.

In[46]:=
```
ν = FullSimplify[Eigenvalues[Ladd][[1]], Assumptions → genericAssumpt]
```

Out[46]=
$$-\frac{1}{2(-1+a-b)}\left(2+b-r-m(-2a+b+r)+\sqrt{\left((1+m)\left(b^2(1+m)-2b(-1+m)r+r(r+m(-4+4a+r))\right)\right)}\right)$$

```
FullSimplify[(1 + m) (b^2 (1 + m) - 2 b (-1 + m) r + r (r + m (-4 + 4 a + r)))]
```

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

For small evolutionary forces:

```
FullSimplify[Eigenvalues[LaddAx], Assumptions → genericAssumpt]
```

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

```
FullSimplify[Reduce[b^2 + 2 b r - 4 m r + r^2 ≥ 0], Assumptions → genericAssumpt]
```

$$m \leq \frac{(b+r)^2}{4r}$$

If $m \leq \frac{(b+r)^2}{4r}$, the radicand $R=(b+r)^2-4mr$ is positive (or zero in the case of equality) and the two eigenvalues are real. Then, the second eigenvalue is the dominant eigenvalue. If $m > \frac{(b+r)^2}{4r}$, the radicand R is negative and we have $\nu^{(1)}=\frac{1}{2}\left(2+2a-b-r-i\sqrt{-R}\right)$ and $\nu^{(2)}=\frac{1}{2}\left(2+2a-b-r+i\sqrt{-R}\right)$. The real parts are the same. We take the second eigenvalue as the dominant eigenvalue.

In[47]:=
```
νAx = Eigenvalues[LaddAx][[2]]
```

Out[47]=
$$\frac{2b+2ab-b^2-br+b\sqrt{b^2+2br-4mr+r^2}}{2b}$$

■ Identification of ξ

ν

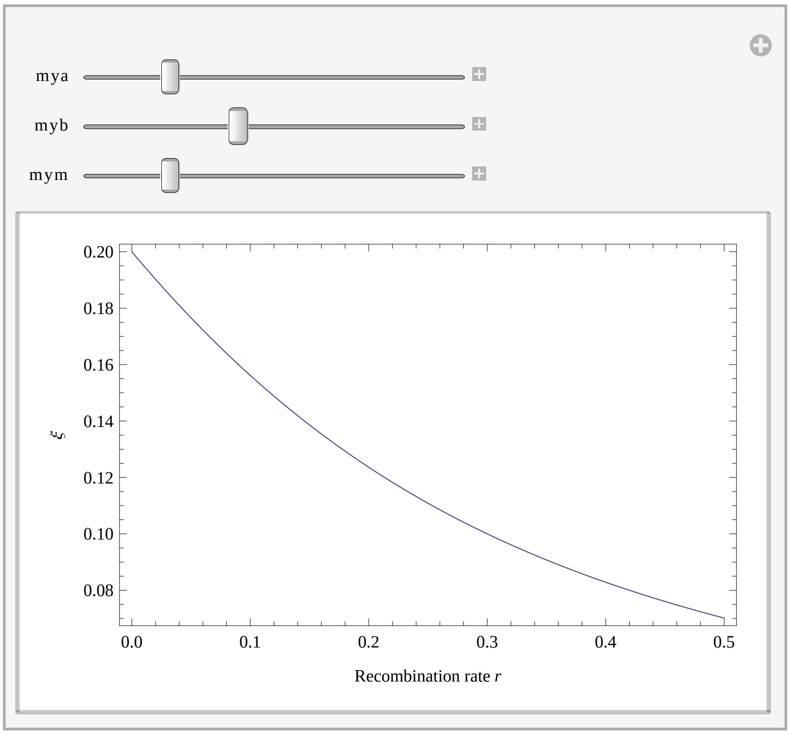
$$-\frac{1}{2\,(-1+a-b)}\left(2+b-r-m\,(-2\,a+b+r)+\sqrt{(1+m)\,\left(b^2\,(1+m)-2\,b\,(-1+m)\,r+r\,(r+m\,(-4+4\,a+r))\right)}\right)$$

In[48]:=
```
ξRule = FullSimplify[Solve[ν == 1 + ξ, ξ], Assumptions → genericAssumpt]
```

Out[48]=

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

```
Manipulate[Plot[ξAddFunc[mya, myb, mym, r], {r, 0, 0.5},
  Frame → True, FrameLabel → {"Recombination rate r", "ξ"}],
 {{mya, 0.2}, 0, 1}, {{myb, 0.4}, 0, 1}, {{mym, 0.2}, 0, 1}]
```



What is ξ if all forces are weak?

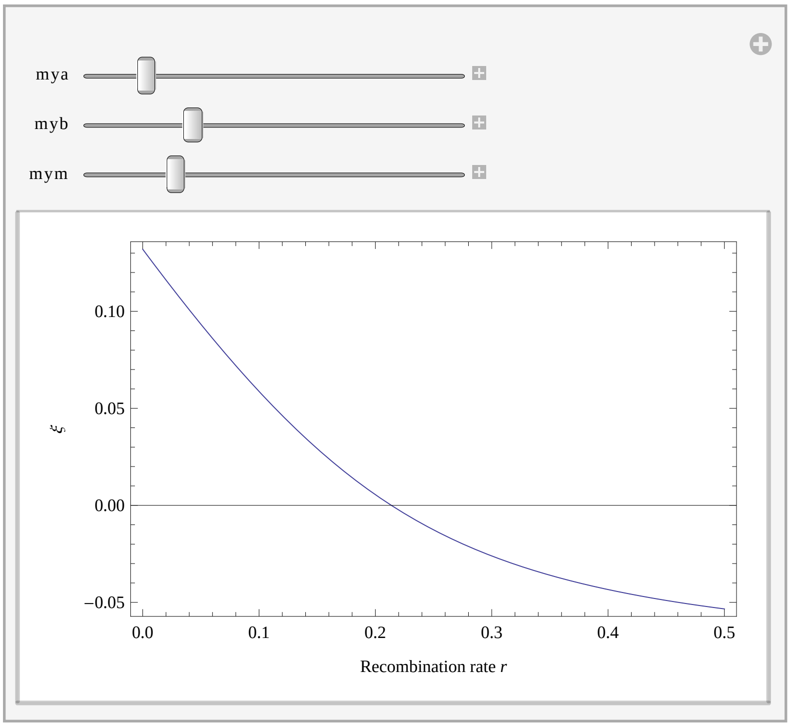
In[49]:=
```
assumeSmallForcesAdj = {a → α ϵ1, b → β ϵ1, r → ϵ1 ρ,
   m → ϵ1 μ, γ11 → g11 ϵ1, γ12 → g12 ϵ1, γ21 → g21 ϵ1, γ22 → g22 ϵ1};
```

In[50]:=
```
backSubstSmallForcesAdj =
  {α → a/ϵ1, β → b/ϵ1, ρ → r/ϵ1, μ → m/ϵ1, g11 → γ11/ϵ1, g12 → γ12/ϵ1, g21 → γ21/ϵ1, g22 → γ22/ϵ1};
```

```
Series[ξ /. ξRule /. assumeSmallForcesAdj, {ϵ1, 0, 1}] /.
  backSubstSmallForcesAdj // Normal
```

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

```
Manipulate[Plot[ξAddApproxFunc[mya, myb, mym, r],
  {r, 0, 0.5}, Frame → True, FrameLabel → {"Recombination rate r", "ξ"}],
 {{mya, 0.2}, 0, 1}, {{myb, 0.4}, 0, 1}, {{mym, 0.2}, 0, 1}]
```




```
νAx
```

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

```
Solve[νAx == 1 + ξ, ξ]
```

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

If we assume *m* small in addition:

```
FullSimplify[Series[1/2 (2 a - b - r + Sqrt[b^2 + 2 b r - 4 m r + r^2]), {m, 0, 1}],
  Assumptions → genericAssumpt] // Normal
```

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

If we assume *r* small in addition:

```
FullSimplify[Series[1/2 (2 a - b - r + Sqrt[b^2 + 2 b r - 4 m r + r^2]), {r, 0, 1}],
  Assumptions → genericAssumpt] // Normal
```

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

■ Eigenvectors and their normalisation

The right and left leading eigenvectors:

The first one is the leading eigenvector (belonging to the dominant eigenvalue).

In[51]:=
```
vDef = FullSimplify[Eigenvectors[Ladd][[1]], Assumptions → genericAssumpt]
```

Out[51]=
$$\left\{\left(b^2 (1+m)+2(-1+a)\, m\, r+ b\left(r-m\, r+\sqrt{(1+m)\left(b^2(1+m)-2b(-1+m)\,r+r\,(r+m(-4+4a+r))\right)}\right)\right)\Big/\left(2(b+(-1+a)\,m)\,r\right),\ 1\right\}$$

Recall: The left eigenvectors of a matrix A are obtained as the right eigenvectors of the transpose of A.

```
Eigensystem[Transpose[Ladd]] // FullSimplify
```

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

In[52]:=
```
uDef = FullSimplify[Eigenvectors[Transpose[Ladd]][[1]], Assumptions → genericAssumpt]
```

Out[52]=
$$\left\{-\left(b^2(1+m)+2(-1+a)\,m\,r+b\left(r-m\,r+\sqrt{(1+m)\left(b^2(1+m)-2b(-1+m)\,r+r\,(r+m(-4+4a+r))\right)}\right)\right)\Big/\left(2(-1+a-b)\,m\,r\right),\ 1\right\}$$

Get the normed eigenvectors.

In[53]:=
```
u = uDef / Total[uDef] // FullSimplify;
u // MatrixForm
```

$$\begin{pmatrix} \dfrac{b(1+m)-(1+m)\,r+\sqrt{(1+m)\left(b^2(1+m)-2b(-1+m)\,r+r\,(r+m(-4+4a+r))\right)}}{2b(1+m)} \\[2ex] \dfrac{2(1-a+b)\,m\,r}{b\left(b+r+m(b+r)+\sqrt{(1+m)\left(b^2(1+m)-2b(-1+m)\,r+r\,(r+m(-4+4a+r))\right)}\right)} \end{pmatrix}$$

In[54]:=
```
k = FullSimplify[Sum[u[[i]] vDef[[i]], {i, 1, 2}], Assumptions → genericAssumpt]
```

Out[54]=
$$\frac{1}{2(b+(-1+a)\,m)\,r}\left((b+r)^2+m\left((b-r)^2+4(-1+a)\,r\right)+b\sqrt{(1+m)\left(b^2(1+m)-2b(-1+m)\,r+r\,(r+m(-4+4a+r))\right)}-r\sqrt{(1+m)\left(b^2(1+m)-2b(-1+m)\,r+r\,(r+m(-4+4a+r))\right)}\right)$$

In[55]:=
```
v = FullSimplify[Table[vDef[[i]] / k, {i, 1, 2}], Assumptions → genericAssumpt]
```

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

```
uDef.Ladd == uDef * ν // FullSimplify
```

```
True
```

```
Ladd.vDef == vDef * ν // FullSimplify
```

```
True
```

```
u.Ladd == u * ν // FullSimplify
```

```
True
```

```
Ladd.v == v * ν // FullSimplify
```

```
True
```

The following is required according to T5.6_HJV2005, and we check that it holds.

```
Total[u] // FullSimplify
```

```
1
```

```
Sum[u⟦i⟧ v⟦i⟧, {i, 1, 2}] // FullSimplify
```

```
1
```

The limit matrix

The limit matrix (the evaluation immediately below takes some time, therefore we hard-code the definition below):

```
B = Sum[u⟦h⟧ * Sum[v⟦j⟧ Ladd⟦h, j⟧, {j, 1, 2}], {h, 1, 2}] +
    ν (ν - 1) Sum[u⟦j⟧ * v⟦j⟧^2, {j, 1, 2}] // FullSimplify;
```

$$B = \sum_{h=1}^{2} u_h \sum_{j=1}^{2} v_j \lambda_{hj} + \nu(\nu - 1) \sum_{j=1}^{2} u_j v_j^2 \tag{1}$$

where λ_{hj} is the entry in the hth row and jth column of the mean matrix L, u_k (v_k) is the kth entry of the left (right) eigenvector corresponding to the leading eigenvalue ν of L. Note the difference between ν (greek letter *nu* for the leading eigenvalue) and v (italic shape of latin letter v for the indexed entry of the right eigenvector $\vec{v}$ belonging to the leading eigenvalue ν).

```
In[56]:= B=-(2 m (b+(-1+a) m) r^2 (-2-b+r+m (-2 a+b+r)-√((1+m) (b^2 (1+m)-2 b (-1+m) r+r (r+m (-4+4
```

Check if the limit of B(ϵ) for small forces (scaling all parameters by ϵ and letting $\epsilon \to 0$) is positive (as is required according to T5.6_HJV2005):

```
In[57]:= BLim := Limit[B /. assumeSmallForces, ϵ → 0] // FullSimplify
```

```
BLim /. backSubstSmallForces /. {ϵ → 1} // FullSimplify
```

```
1
```

It is even equal to 1 (and this could in principle be seen already before re-scaling and setting $\epsilon = 0$).

```
ν
```

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

Letting Q_h be the extinction probability if the population starts with type h, T5.6_HJV2005 states that, as $\xi \to 0$, $Q_h = Q_h(\xi) \to 1$, and

$$\pi_h(\xi) = 1 - Q_h(\xi) = \frac{2(\nu(\xi) - 1)}{B(\xi)} v_h(\xi) + o(\xi). \tag{2}$$

Further, Haccou *et al.* (2005) state that, provided B(ϵ) → B(0) and also the eigenvector v(ϵ) → v (0) as $\epsilon \to 0$, one can conclude that

$$1 - Q_h(\xi) = \frac{2(\nu(\xi) - 1)}{B(0)} v_h(0) + o(\xi). \tag{3}$$

Note that in the manuscript and, sometimes, in other *Mathematica* Notebooks, we use s_i instead of Q_i.

Application

Analytical expressions without further approximation

The equilibrium frequency of allele B_1 (see *Mathematica* Notebook 2LocContIsland_Stoch_Discr.nb for a derivation):

```
qHatBRule
```

$$\text{qHatB} \to \frac{b - m + a\,m}{b + b\,m}$$

In[58]:=

```
π1 = (2 (ν - 1))/B v[[1]] // Simplify;
π2 = (2 (ν - 1))/B v[[2]];
πAv = qHatB * π1 + (1 - qHatB) * π2 /. qHatBRule;
```

Algebraic rearrangements

In[61]:=

```
R0Rule := R0 → Sqrt[(1 + m) (b^2 (1 + m) - 2 b (-1 + m) r + r (r + m (-4 + 4 a + r)))]
```

In[62]:=

```
mCrit5 := (a * (b - a + r))/((a - b) * (a - r) + r * (1 - a))
```

```
FullSimplify[Reduce[(1 + m) (b^2 (1 + m) - 2 b (-1 + m) r + r (r + m (-4 + 4 a + r))) ≥ 0],
 Assumptions → Flatten[{genericAssumpt, m < mCrit5}]]
```

True

We see that R_0 is non-negative whenever invasion is possible ($m < m_{\text{crit},5}$).

```
FullSimplify[π1 /. Sqrt[(1 + m) (b^2 (1 + m) - 2 b (-1 + m) r + r (r + m (-4 + 4 a + r)))] → R0,
 Assumptions → Flatten[{genericAssumpt, 0 ≤ R0}]]
```

$$-\Big(8\,b\,((1+m)\,(-2\,a+b+r)-R0)\,\Big((b+r)^2+m\,\big((b-r)^2+4\,(-1+a)\,r\big)+b\,R0-r\,R0\Big)\,\Big(b^2\,(1+m)+2\,(-1+a)\,m\,r+b\,(r-m\,r+R0)\Big)\Big)\Big/\Big((-1+a-b)$$
$$\Big(1/(b+r+m\,(b+r)+R0)\;\;16\,m\,(b+(-1+a)\,m)\,r^2\,(-2-b+r+m\,(-2\,a+b+r)-R0)$$
$$\Big((b+r)^2+m\,\big((b-r)^2+4\,(-1+a)\,r\big)+b\,R0-r\,R0\Big)-1/(1+m)\;\;4\,((1+m)\,(b-r)+R0)$$
$$\Big((b+r)^2+m\,\big((b-r)^2+4\,(-1+a)\,r\big)+b\,R0-r\,R0\Big)\,\Big(\frac{2\,m\,(b+(-1+a)\,m)\,r^2}{b}+$$
$$\Big(\frac{1+b+a\,m}{1-a+b}-\frac{m\,r}{b}\Big)\,\Big(b^2\,(1+m)+2\,(-1+a)\,m\,r+b\,(r-m\,r+R0)\Big)\Big)+$$
$$1\Big/(1-a+b)^2\,((1+m)\,(-2\,a+b+r)-R0)\,(2+b-r-m\,(-2\,a+b+r)+R0)$$
$$\Big(-\frac{16\,(-1+a-b)\,m\,(b+(-1+a)\,m)^2\,r^3}{b+r+m\,(b+r)+R0}+\frac{1}{1+m}$$
$$((1+m)\,(b-r)+R0)\,\Big(b^2\,(1+m)+2\,(-1+a)\,m\,r+b\,(r-m\,r+R0)\Big)^2\Big)\Big)\Big)$$

```
FullSimplify[π2 /. Sqrt[(1 + m) (b^2 (1 + m) - 2 b (-1 + m) r + r (r + m (-4 + 4 a + r)))] → R0,
 Assumptions → Flatten[{genericAssumpt, 0 ≤ R0}]]
```

$$
\begin{aligned}
&-\Big(16\,b\,(b+(-1+a)\,m)\,r\,((1+m)\,(-2\,a+b+r)-R0)\\
&\quad\big((b+r)^2+m\,\big((b-r)^2+4\,(-1+a)\,r\big)+b\,R0-r\,R0\big)\Big)\Big/\Big((-1+a-b)\\
&\quad\Big(1/(b+r+m\,(b+r)+R0)\;\;16\,m\,(b+(-1+a)\,m)\,r^2\,(-2-b+r+m\,(-2\,a+b+r)-R0)\\
&\qquad\big((b+r)^2+m\,\big((b-r)^2+4\,(-1+a)\,r\big)+b\,R0-r\,R0\big)-1/(1+m)\;\;4\,((1+m)\,(b-r)+R0)\\
&\qquad\big((b+r)^2+m\,\big((b-r)^2+4\,(-1+a)\,r\big)+b\,R0-r\,R0\big)\Big(\frac{2\,m\,(b+(-1+a)\,m)\,r^2}{b}+\\
&\qquad\quad\Big(\frac{1+b+a\,m}{1-a+b}-\frac{m\,r}{b}\Big)\big(b^2\,(1+m)+2\,(-1+a)\,m\,r+b\,(r-m\,r+R0)\big)\Big)+\\
&\qquad 1\big/(1-a+b)^2\,((1+m)\,(-2\,a+b+r)-R0)\,(2+b-r-m\,(-2\,a+b+r)+R0)\\
&\qquad\Big(-\frac{16\,(-1+a-b)\,m\,(b+(-1+a)\,m)^2\,r^3}{b+r+m\,(b+r)+R0}+\frac{1}{1+m}\\
&\qquad\quad((1+m)\,(b-r)+R0)\,\big(b^2\,(1+m)+2\,(-1+a)\,m\,r+b\,(r-m\,r+R0)\big)^2\Big)\Big)\Big)
\end{aligned}
$$

```
FullSimplify[πAv /. Sqrt[(1 + m) (b^2 (1 + m) - 2 b (-1 + m) r + r (r + m (-4 + 4 a + r)))] → R0,
 Assumptions → Flatten[{genericAssumpt, 0 ≤ R0}]]
```

$$
\begin{aligned}
&-\Big(8\,b\,(b+(-1+a)\,m)\,((1+m)\,(-2\,a+b+r)-R0)\,((1+m)\,(b+r)+R0)\\
&\quad\big((b+r)^2+m\,\big((b-r)^2+4\,(-1+a)\,r\big)+b\,R0-r\,R0\big)\Big)\Big/\Big((-1+a-b)\,(1+m)\\
&\quad\Big(\frac{1}{b+r+m\,(b+r)+R0}16\,m\,(b+(-1+a)\,m)\,r^2\,(-2-b+r+m\,(-2\,a+b+r)-R0)\\
&\qquad\big((b+r)^2+m\,\big((b-r)^2+4\,(-1+a)\,r\big)+b\,R0-r\,R0\big)-1/(1+m)\;\;4\,((1+m)\,(b-r)+R0)\\
&\qquad\big((b+r)^2+m\,\big((b-r)^2+4\,(-1+a)\,r\big)+b\,R0-r\,R0\big)\Big(\frac{2\,m\,(b+(-1+a)\,m)\,r^2}{b}+\\
&\qquad\quad\Big(\frac{1+b+a\,m}{1-a+b}-\frac{m\,r}{b}\Big)\big(b^2\,(1+m)+2\,(-1+a)\,m\,r+b\,(r-m\,r+R0)\big)\Big)+\\
&\qquad 1\big/(1-a+b)^2\,((1+m)\,(-2\,a+b+r)-R0)\,(2+b-r-m\,(-2\,a+b+r)+R0)\\
&\qquad\Big(-\frac{16\,(-1+a-b)\,m\,(b+(-1+a)\,m)^2\,r^3}{b+r+m\,(b+r)+R0}+\frac{1}{1+m}\\
&\qquad\quad((1+m)\,(b-r)+R0)\,\big(b^2\,(1+m)+2\,(-1+a)\,m\,r+b\,(r-m\,r+R0)\big)^2\Big)\Big)\Big)
\end{aligned}
$$

Testing the implementation of the plotting functions:

```
π1 - π1Func[a, b, m, r] // Simplify
```

0

```
π2 - π2Func[a, b, m, r] // Simplify
```

0

```
πAv - πAvFunc[a, b, m, r] // Simplify
```

0

- Assume weak evolutionary forces (up to first order of ϵ)

Inspection of π_1, π_2 and π_{Av} shows that these are big terms. Therefore we are going to approximate them by assuming weak evolutionary forces (the continental frequency q_c of B_1can be arbitrary, however)..

π1

$$\begin{aligned}
&\Big(\big(b+b\,m-2\,a\,(1+m)+r+m\,r-\sqrt{(1+m)\left(b^2\,(1+m)-2\,b\,(-1+m)\,r+r\,(r+m\,(-4+4\,a+r))\right)}\big)\\
&\quad\big(b^2\,(1+m)+2\,(-1+a)\,m\,r+\\
&\qquad b\,\big(r-m\,r+\sqrt{(1+m)\left(b^2\,(1+m)-2\,b\,(-1+m)\,r+r\,(r+m\,(-4+4\,a+r))\right)}\big)\big)\Big)\Big/\\
&\Big((-1+a-b)\,\big((b+r)^2+m\,\left((b-r)^2+4\,(-1+a)\,r\right)+\\
&\qquad b\,\sqrt{(1+m)\left(b^2\,(1+m)-2\,b\,(-1+m)\,r+r\,(r+m\,(-4+4\,a+r))\right)}-\\
&\qquad r\,\sqrt{(1+m)\left(b^2\,(1+m)-2\,b\,(-1+m)\,r+r\,(r+m\,(-4+4\,a+r))\right)}\big)\\
&\quad\Big(-\big(2\,m\,(b+(-1+a)\,m)\,r^2\,\big(-2-b+r+m\,(-2\,a+b+r)-\\
&\qquad\qquad\sqrt{(1+m)\left(b^2\,(1+m)-2\,b\,(-1+m)\,r+r\,(r+m\,(-4+4\,a+r))\right)}\big)\big)\Big/\\
&\qquad\big(b\,\big(b+r+m\,(b+r)+\sqrt{(1+m)\left(b^2\,(1+m)-2\,b\,(-1+m)\,r+r\,(r+m\,(-4+4\,a+r))\right)}\big)\\
&\qquad\quad\big((b+r)^2+m\,\left((b-r)^2+4\,(-1+a)\,r\right)+\\
&\qquad\qquad b\,\sqrt{(1+m)\left(b^2\,(1+m)-2\,b\,(-1+m)\,r+r\,(r+m\,(-4+4\,a+r))\right)}-\\
&\qquad\qquad r\,\sqrt{(1+m)\left(b^2\,(1+m)-2\,b\,(-1+m)\,r+r\,(r+m\,(-4+4\,a+r))\right)}\big)\big)+\\
&\qquad\Big(\big(b\,(1+m)-(1+m)\,r+\sqrt{(1+m)\left(b^2\,(1+m)-2\,b\,(-1+m)\,r+r\,(r+m\,(-4+4\,a+r))\right)}\big)\\
&\qquad\quad\Big(\frac{2\,m\,(b+(-1+a)\,m)\,r^2}{b}+\left(\frac{1+b+a\,m}{1-a+b}-\frac{m\,r}{b}\right)\,\big(b^2\,(1+m)+2\,(-1+a)\,m\,r+\\
&\qquad\qquad b\,\big(r-m\,r+\sqrt{(1+m)\left(b^2\,(1+m)-2\,b\,(-1+m)\,r+r\,(r+m\,(-4+4\,a+r))\right)}\big)\big)\Big)\Big)\Big/\\
&\qquad\big(2\,b\,(1+m)\,\big((b+r)^2+m\,\left((b-r)^2+4\,(-1+a)\,r\right)+\\
&\qquad\qquad b\,\sqrt{(1+m)\left(b^2\,(1+m)-2\,b\,(-1+m)\,r+r\,(r+m\,(-4+4\,a+r))\right)}-\\
&\qquad\qquad r\,\sqrt{(1+m)\left(b^2\,(1+m)-2\,b\,(-1+m)\,r+r\,(r+m\,(-4+4\,a+r))\right)}\big)\big)-\Big(\big(b-2\,a\,(1+m)+\\
&\qquad\qquad r+m\,(b+r)-\sqrt{(1+m)\left(b^2\,(1+m)-2\,b\,(-1+m)\,r+r\,(r+m\,(-4+4\,a+r))\right)}\big)\,\big(2+b-\\
&\qquad\qquad r-m\,(-2\,a+b+r)+\sqrt{(1+m)\left(b^2\,(1+m)-2\,b\,(-1+m)\,r+r\,(r+m\,(-4+4\,a+r))\right)}\big)\\
&\qquad\quad\Big(-\big(16\,(-1+a-b)\,m\,(b+(-1+a)\,m)^2\,r^3\big)\Big/\\
&\qquad\qquad\big(b+r+m\,(b+r)+\sqrt{(1+m)\left(b^2\,(1+m)-2\,b\,(-1+m)\,r+r\,(r+m\,(-4+4\,a+r))\right)}\big)+\\
&\qquad\qquad 1/(1+m)\,\big(b\,(1+m)-(1+m)\,r+\sqrt{(1+m)\left(b^2\,(1+m)-2\,b\,(-1+m)\,r+\right.}\\
&\qquad\qquad\qquad\overline{\left.r\,(r+m\,(-4+4\,a+r))\right)}\big)\,\big(b^2\,(1+m)+2\,(-1+a)\,m\,r+b\,\big(r-m\,r+\\
&\qquad\qquad\qquad\sqrt{(1+m)\left(b^2\,(1+m)-2\,b\,(-1+m)\,r+r\,(r+m\,(-4+4\,a+r))\right)}\big)\big)^2\Big)\Big)\Big/\\
&\qquad\Big(8\,b\,(1-a+b)^2\,\big((b+r)^2+m\,\left((b-r)^2+4\,(-1+a)\,r\right)+b\,\sqrt{(1+m)\right.}\\
&\qquad\qquad\overline{\left.\left(b^2\,(1+m)-2\,b\,(-1+m)\,r+r\,(r+m\,(-4+4\,a+r))\right)}-\\
&\qquad\qquad r\,\sqrt{(1+m)\left(b^2\,(1+m)-2\,b\,(-1+m)\,r+r\,(r+m\,(-4+4\,a+r))\right)}\big)^2\Big)\Big)\Big)
\end{aligned}$$

```
term1 = Series[π1 /. assumeSmallForces, {ϵ, 0, 1}] // Normal
```

$$\begin{aligned}
&\Big(\epsilon\,\left(2\,\alpha-\beta-\rho+\sqrt{\beta^2+2\,\beta\,\rho-4\,\mu\,\rho+\rho^2}\right)\\
&\quad\left(\beta+\rho+\sqrt{\beta^2+2\,\beta\,\rho-4\,\mu\,\rho+\rho^2}\right)\,\left(\beta^2+\beta\,\rho-2\,\mu\,\rho+\beta\,\sqrt{\beta^2+2\,\beta\,\rho-4\,\mu\,\rho+\rho^2}\right)\Big)\Big/\\
&\Big(2\,\Big(\beta^3+2\,\beta^2\,\rho-4\,\beta\,\mu\,\rho+\beta\,\rho^2+\beta^2\,\sqrt{\beta^2+2\,\beta\,\rho-4\,\mu\,\rho+\rho^2}+\\
&\qquad\beta\,\rho\,\sqrt{\beta^2+2\,\beta\,\rho-4\,\mu\,\rho+\rho^2}-2\,\mu\,\rho\,\sqrt{\beta^2+2\,\beta\,\rho-4\,\mu\,\rho+\rho^2}\Big)\Big)
\end{aligned}$$

The following results are approximations, based on the assumption that the branching process is slightly supercritical, *i.e.* the leading eigenvalue of the mean matrix is of the form $1 + \epsilon$ with small and positive. Moreover, to simplify the expressions, it was assumed that evolutionary forces are weak (the continental frequency q_c of B_1can be arbitrary, however).

Approximation to the invasion probability of A_1 conditional on occurrence on the beneficial background B_1.

```
π1Approx4 = FullSimplify[term1 /. backSubstSmallForces,
  Assumptions → Flatten[{genericAssumpt, ϵ > 0}]]
```

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

```
term2 = Series[π2 /. assumeSmallForces, {ϵ, 0, 1}] // Normal
```

$$-\left(\epsilon\,(\beta - \mu)\,\rho\left(-2\,\alpha + \beta + \rho - \sqrt{\beta^2 + 2\,\beta\,\rho - 4\,\mu\,\rho + \rho^2}\right)\left(\beta + \rho + \sqrt{\beta^2 + 2\,\beta\,\rho - 4\,\mu\,\rho + \rho^2}\right)\right)\Big/ \left(\beta^3 + 2\,\beta^2\,\rho - 4\,\beta\,\mu\,\rho + \beta\,\rho^2 + \beta^2\sqrt{\beta^2 + 2\,\beta\,\rho - 4\,\mu\,\rho + \rho^2} + \beta\,\rho\sqrt{\beta^2 + 2\,\beta\,\rho - 4\,\mu\,\rho + \rho^2} - 2\,\mu\,\rho\sqrt{\beta^2 + 2\,\beta\,\rho - 4\,\mu\,\rho + \rho^2}\right)$$

Approximation to the invasion probability of A_1 conditional on occurrence on the deleterious background B_2.

```
π2Approx4 = FullSimplify[term2 /. backSubstSmallForces,
  Assumptions → Flatten[{genericAssumpt, ϵ > 0}]]
```

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

Approximation to the weighted average invasion probability of A_1.

```
πAvApprox4 = FullSimplify[qHatB * π1Approx4 + (1 - qHatB) * π2Approx4 /. qHatBRule,
  Assumptions → Flatten[{genericAssumpt}]]
```

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

We simplify the above result:

```
simplπAvApprox4Temp =
 (2 a^2 m + m (b^2 - r - 2 m r - H + b (1 + r - H)) + a (b - 2 b m + r + H + 2 m (-1 + H))) / ((1 + m) H) //
  FullSimplify
```

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

```
simplπAvApprox4Temp1 =
 1/((1 + m) H) (a (b + r + H) - 2 m^2 r + m (2 a^2 - 2 a (1 + b - H) + (1 + b) (b - H) - r (1 - b)))
```

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

```
simplπAvApprox4Temp1 - simplπAvApprox4Temp // FullSimplify
```

0

```
In[63]:= HRule := H → Sqrt[b^2 + 2 b r + r (-4 m + r)]
```

```
simplπAvApprox4Temp1 - πAvApprox4 /. HRule // Simplify
```

0

- Assume weak evolutionary forces (up to second order of ϵ)

```
term12 = Series[π1 /. assumeSmallForces, {ϵ, 0, 2}] // Normal;
```

```
π1Approx5Raw = FullSimplify[term12 /. backSubstSmallForces,
  Assumptions → Flatten[{genericAssumpt, ϵ > 0}]]
```

$$\frac{1}{\left(b^2+2 b r+r (-4 m+r)\right)^{3/2}}\Bigg(m r \left(4 m^2 r-(b+r)^2 (2+2 b+r)+m r (8+3 b+5 r)+2 b^2 \sqrt{b^2+2 b r+r (-4 m+r)}+3 b r \sqrt{b^2+2 b r+r (-4 m+r)}-7 m r \sqrt{b^2+2 b r+r (-4 m+r)}+r^2 \sqrt{b^2+2 b r+r (-4 m+r)}\right)-$$
$$a^2 \left(b^3-(3 m-r) r \left(r+\sqrt{b^2+2 b r-4 m r+r^2}\right)+b^2 \left(3 r+\sqrt{b^2+2 b r-4 m r+r^2}\right)+b r \left(-m+3 r+2 \sqrt{b^2+2 b r-4 m r+r^2}\right)\right)+$$
$$a \Bigg(-b^4+b^3 \left(1+m-3 r-\sqrt{b^2+2 b r-4 m r+r^2}\right)+b^2 \left(-3 r^2+(1+m) \sqrt{b^2+2 b r-4 m r+r^2}+r \left(3+17 m-2 \sqrt{b^2+2 b r-4 m r+r^2}\right)\right)-b r \Bigg(6 m^2-2 \sqrt{b^2+2 b r-4 m r+r^2}+$$
$$m \left(4-23 r-6 \sqrt{b^2+2 b r-4 m r+r^2}\right)+r \left(-3+r+\sqrt{b^2+2 b r-4 m r+r^2}\right)\Bigg)+$$
$$r \Bigg(r \left(r+\sqrt{b^2+2 b r-4 m r+r^2}\right)-2 m^2 \left(15 r+2 \sqrt{b^2+2 b r-4 m r+r^2}\right)+$$
$$m \left(-4 \sqrt{b^2+2 b r-4 m r+r^2}+r \left(-4+7 r+3 \sqrt{b^2+2 b r-4 m r+r^2}\right)\right)\Bigg)\Bigg)\Bigg)$$

```
HRule
```

$$H \to \sqrt{b^2+2 b r+r (-4 m+r)}$$

```
1 / (b^2 + 2 b r + r (-4 m + r))^(3/2) - H^-3 /. HRule // Simplify
```

0

```
FullSimplify[Reduce[b^2 + 2 b r + r (-4 m + r) ≥ 0],
 Assumptions → Flatten[{genericAssumpt, m < mCrit5}]]
```

$$m \le \frac{(b+r)^2}{4 r}$$

The radicand of H can be negative or positive.

```
π1Approx5 =
 FullSimplify[π1Approx5Raw /. {√(b^2 + 2 b r + r (-4 m + r)) → H, √(b^2 + 2 b r - 4 m r + r^2) → H,
    1 / (b^2 + 2 b r + r (-4 m + r))^(3/2) → H^-3}, Assumptions → Flatten[{genericAssumpt}]]
```

$$\frac{1}{H^3}\Big(-a b^2 (b+H) (-1+a+b-m)-\Big(a b (-1+a+b) (3 b+2 H)-\left(-2 b^2 (1+b-H)+a^2 (b+3 H)+a (-4 H+b (-4+17 b+6 H))\right) m+2 a (3 b+2 H) m^2\Big) r+$$
$$\Big(-a (-1+a+b) (3 b+H)+\left(3 a^2+b (-4-5 b+3 H)+a (-4+23 b+3 H)\right) m+(8-30 a+3 b-7 H) m^2+4 m^3\Big) r^2+\left(-a (-1+a+b)+(-2+7 a-4 b+H) m+5 m^2\right) r^3-m r^4\Big)$$

```
Collect[π1Approx5, r]
```

$$-\frac{a\,b^2\,(b+H)\,(-1+a+b-m)}{H^3}+\frac{1}{H^3}\left(-a\,b\,(-1+a+b)\,(3\,b+2\,H)+\left(-2\,b^2\,(1+b-H)+a^2\,(b+3\,H)+a\,(-4\,H+b\,(-4+17\,b+6\,H))\right)m-2\,a\,(3\,b+2\,H)\,m^2\right)r+\frac{1}{H^3}\left(-a\,(-1+a+b)\,(3\,b+H)+\left(3\,a^2+b\,(-4-5\,b+3\,H)+a\,(-4+23\,b+3\,H)\right)m+(8-30\,a+3\,b-7\,H)\,m^2+4\,m^3\right)r^2+\frac{\left(-a\,(-1+a+b)+(-2+7\,a-4\,b+H)\,m+5\,m^2\right)r^3}{H^3}-\frac{m\,r^4}{H^3}$$

with H defined as follows:

```
HRule
```

$$H\to\sqrt{b^2+2\,b\,r+r\,(-4\,m+r)}$$

```
Collect[π1Approx5, m]
```

$$\frac{4\,m^3\,r^2}{H^3}+\frac{m^2\left(-2\,a\,(3\,b+2\,H)\,r+(8-30\,a+3\,b-7\,H)\,r^2+5\,r^3\right)}{H^3}+\frac{1}{H^3}\left(a\,b^2\,(b+H)-a^2\,b^2\,(b+H)-a\,b^3\,(b+H)-a\,b\,(-1+a+b)\,(3\,b+2\,H)\,r-a\,(-1+a+b)\,(3\,b+H)\,r^2-a\,(-1+a+b)\,r^3\right)+\frac{1}{H^3}\,m\left(a\,b^2\,(b+H)+\left(-2\,b^2\,(1+b-H)+a^2\,(b+3\,H)+a\,(-4\,H+b\,(-4+17\,b+6\,H))\right)r+\left(3\,a^2+b\,(-4-5\,b+3\,H)+a\,(-4+23\,b+3\,H)\right)r^2+(-2+7\,a-4\,b+H)\,r^3-r^4\right)$$

$$\mathbf{term1a}=\frac{b^2\,(b+H)\,T2}{H^3}+\frac{a\,b^2\,(b+H)\,m}{H^3}+\frac{1}{H^3}\left(b\,T2\,(3\,b+2\,H)+\left(-2\,b^2\,(1+b-H)+a^2\,(b+3\,H)+a\,(-4\,H+b\,(-4+17\,b+6\,H))\right)m-2\,a\,(3\,b+2\,H)\,m^2\right)r+\frac{1}{H^3}\left(T2\,(3\,b+H)+\left(3\,a^2+b\,(-4-5\,b+3\,H)+a\,(-4+23\,b+3\,H)\right)m+(8-30\,a+3\,b-7\,H)\,m^2+4\,m^3\right)r^2+\frac{\left(T2+(-2+7\,a-4\,b+H)\,m+5\,m^2\right)r^3}{H^3}-\frac{m\,r^4}{H^3}$$

$$\frac{a\,b^2\,(b+H)\,m}{H^3}-\frac{m\,r^4}{H^3}+\frac{b^2\,(b+H)\,T2}{H^3}+\frac{r^3\left((-2+7\,a-4\,b+H)\,m+5\,m^2+T2\right)}{H^3}+\frac{1}{H^3}\,r^2\left(\left(3\,a^2+b\,(-4-5\,b+3\,H)+a\,(-4+23\,b+3\,H)\right)m+(8-30\,a+3\,b-7\,H)\,m^2+4\,m^3+(3\,b+H)\,T2\right)+\frac{1}{H^3}\,r\left(\left(-2\,b^2\,(1+b-H)+a^2\,(b+3\,H)+a\,(-4\,H+b\,(-4+17\,b+6\,H))\right)m-2\,a\,(3\,b+2\,H)\,m^2+b\,(3\,b+2\,H)\,T2\right)$$

```
In[64]:= T2Rule := T2 → a (1 - a - b)
```

```
Collect[FullSimplify[term1a], r]
```

$$-\frac{m\,r^4}{H^3}+\frac{r^3\,(7\,a\,m-4\,b\,m+m\,(-2+H+5\,m)+T2)}{H^3}+\frac{1}{H^3}\,r^2\left(3\,a^2\,m-4\,b\,m+23\,a\,b\,m-5\,b^2\,m+3\,b\,H\,m+a\,(-4+3\,H-30\,m)\,m+3\,b\,m^2+m^2\,(8-7\,H+4\,m)+3\,b\,T2+H\,T2\right)+\frac{1}{H^3}\,r\left(-4\,a\,b\,m+a^2\,b\,m-2\,b^2\,m+17\,a\,b^2\,m-2\,b^3\,m+3\,a^2\,H\,m+6\,a\,b\,H\,m+2\,b^2\,H\,m-6\,a\,b\,m^2-4\,a\,H\,m\,(1+m)+3\,b^2\,T2+2\,b\,H\,T2\right)+\frac{a\,b^3\,m+a\,b^2\,H\,m+b^3\,T2+b^2\,H\,T2}{H^3}$$

```
% - π1Approx5 /. T2Rule /. HRule // FullSimplify
```

0

```
Collect[FullSimplify[term1a], m]
```

$$\frac{4 m^3 r^2}{H^3} + \frac{m^2 \left(-6 a b r - 4 a H r + 8 r^2 - 30 a r^2 + 3 b r^2 - 7 H r^2 + 5 r^3\right)}{H^3} + \frac{1}{H^3} m \left(a b^3 - 4 a b r - 2 b^3 r - 4 a H r + 6 a b H r + b^2 (-2 + 2 H - 5 r) r - 4 a r^2 - 4 b r^2 + 23 a b r^2 + 3 a H r^2 + 3 b H r^2 - 2 r^3 + 7 a r^3 - 4 b r^3 + H r^3 - r^4 + a b^2 (H + 17 r) + a^2 r (b + 3 (H + r))\right) + \frac{(b + r)^2 (b + H + r)\, T2}{H^3}$$

```
term22 = Series[π2 /. assumeSmallForces, {ϵ, 0, 2}] // Normal;
```

Approximation to the invasion probability of A_1 conditional on occurrence on the deleterious background B_2.

```
π2Approx5Raw = FullSimplify[term22 /. backSubstSmallForces,
  Assumptions → Flatten[{genericAssumpt, ϵ > 0}]]
```

$$\frac{1}{\left(b^2 + 2 b r + r (-4 m + r)\right)^{3/2}} \Big(b^5 + b^4 \left(1 + m + 4 r - \sqrt{b^2 + 2 b r - 4 m r + r^2}\right) + b^2 r \left(-6 m^2 - 2 \sqrt{b^2 + 2 b r - 4 m r + r^2} + r \left(3 + 4 r - 3 \sqrt{b^2 + 2 b r - 4 m r + r^2}\right) + 3 m \left(-2 - 5 r + \sqrt{b^2 + 2 b r - 4 m r + r^2}\right)\right) + m r^2 \left(4 m^2 + m \left(8 + 5 r - 7 \sqrt{b^2 + 2 b r - 4 m r + r^2}\right) + r \left(-2 - r + \sqrt{b^2 + 2 b r - 4 m r + r^2}\right)\right) - a^2 \left(-b^3 + b^2 \sqrt{b^2 + 2 b r - 4 m r + r^2} - (3 m - r) r \left(r + \sqrt{b^2 + 2 b r - 4 m r + r^2}\right) + b r \left(m + 2 r + \sqrt{b^2 + 2 b r - 4 m r + r^2}\right)\right) - b^3 \left(-6 r^2 + (1 + m) \sqrt{b^2 + 2 b r - 4 m r + r^2} + r \left(-3 + 4 m + 3 \sqrt{b^2 + 2 b r - 4 m r + r^2}\right)\right) + b r \left(-r (1 + r) \left(-r + \sqrt{b^2 + 2 b r - 4 m r + r^2}\right) + m^2 \left(11 r + 4 \sqrt{b^2 + 2 b r - 4 m r + r^2}\right) + m \left(4 \sqrt{b^2 + 2 b r - 4 m r + r^2} + r \left(-8 - 11 r + 8 \sqrt{b^2 + 2 b r - 4 m r + r^2}\right)\right)\right) + a \Big(-2 b^4 + b^3 \left(-1 - m - 6 r + 2 \sqrt{b^2 + 2 b r - 4 m r + r^2}\right) + b r \left(6 m^2 + r - 2 r^2 + 2 \sqrt{b^2 + 2 b r - 4 m r + r^2} + m \left(4 + 25 r - 4 \sqrt{b^2 + 2 b r - 4 m r + r^2}\right)\right) + b^2 \left(-6 r^2 + (1 + m) \sqrt{b^2 + 2 b r - 4 m r + r^2} + r \left(-1 + 9 m + 2 \sqrt{b^2 + 2 b r - 4 m r + r^2}\right)\right) + r \left(r \left(r + \sqrt{b^2 + 2 b r - 4 m r + r^2}\right) - 2 m^2 \left(15 r + 2 \sqrt{b^2 + 2 b r - 4 m r + r^2}\right) + m \left(-4 \sqrt{b^2 + 2 b r - 4 m r + r^2} + r \left(-4 + 7 r + 3 \sqrt{b^2 + 2 b r - 4 m r + r^2}\right)\right)\right)\Big)\Big)$$

```
π2Approx5 =
 FullSimplify[π2Approx5Raw /. {√(b² + 2 b r + r (-4 m + r)) → H, √(b² + 2 b r - 4 m r + r²) → H,
    1 / (b² + 2 b r + r (-4 m + r))^(3/2) → H^-3}, Assumptions → Flatten[{genericAssumpt}]]
```

$$
\begin{aligned}
&\frac{1}{H^3}\Big((a-b)\,b^2\,(b-H)\,(-1+a-b-m)-\big(a^2\,(-3\,H\,m+b\,(H+m))+\\
&\quad b\,\big(-4\,b^3-4\,H\,m\,(1+m)+b^2\,(-3+3\,H+4\,m)+b\,(H\,(2-3\,m)+6\,m\,(1+m))\big)+\\
&\quad a\,\big(6\,b^3+b^2\,(1-2\,H-9\,m)+4\,H\,m\,(1+m)-2\,b\,(H-2\,H\,m+m\,(2+3\,m))\big)\big)\,r+\\
&\quad \big(6\,b^3-a^2\,(2\,b+H-3\,m)+m^2\,(8-7\,H+4\,m)-3\,b^2\,(-1+H+5\,m)+\\
&\quad a\,\big(b-6\,b^2+H+(-4+25\,b+3\,H)\,m-30\,m^2\big)+b\,\big(-H+8\,(-1+H)\,m+11\,m^2\big)\big)\,r^2+\\
&\quad \big(a-a^2+b-2\,a\,b+4\,b^2-b\,H+(-2+7\,a-11\,b+H)\,m+5\,m^2\big)\,r^3+(b-m)\,r^4\Big)
\end{aligned}
$$

```
Collect[π2Approx5, r]
```

$$
\begin{aligned}
&\frac{(a-b)\,b^2\,(b-H)\,(-1+a-b-m)}{H^3}+\frac{1}{H^3}\Big(-a^2\,(-3\,H\,m+b\,(H+m))-\\
&\quad b\,\big(-4\,b^3-4\,H\,m\,(1+m)+b^2\,(-3+3\,H+4\,m)+b\,(H\,(2-3\,m)+6\,m\,(1+m))\big)-\\
&\quad a\,\big(6\,b^3+b^2\,(1-2\,H-9\,m)+4\,H\,m\,(1+m)-2\,b\,(H-2\,H\,m+m\,(2+3\,m))\big)\Big)\,r+\\
&\quad \frac{1}{H^3}\Big(6\,b^3-a^2\,(2\,b+H-3\,m)+m^2\,(8-7\,H+4\,m)-3\,b^2\,(-1+H+5\,m)+\\
&\quad a\,\big(b-6\,b^2+H+(-4+25\,b+3\,H)\,m-30\,m^2\big)+b\,\big(-H+8\,(-1+H)\,m+11\,m^2\big)\Big)\,r^2+\\
&\quad \frac{\big(a-a^2+b-2\,a\,b+4\,b^2-b\,H+(-2+7\,a-11\,b+H)\,m+5\,m^2\big)\,r^3}{H^3}+\\
&\quad \frac{(b-m)\,r^4}{H^3}
\end{aligned}
$$

with H defined as follows:

```
HRule
```

$$H\to\sqrt{b^2+2\,b\,r+r\,(-4\,m+r)}$$

Approximation to the weighted average invasion probability of A_1.

```
πAvApprox5 = FullSimplify[qHatB * π1Approx5 + (1 - qHatB) * π2Approx5 /. qHatBRule,
  Assumptions → Flatten[{genericAssumpt}]]
```

$$
\begin{aligned}
&\frac{1}{b\,H^3\,(1+m)}\Big((1-a+b)\,m\,\Big((a-b)\,b^2\,(b-H)\,(-1+a-b-m)-\big(a^2\,(-3\,H\,m+b\,(H+m))+\\
&\quad b\,\big(-4\,b^3-4\,H\,m\,(1+m)+b^2\,(-3+3\,H+4\,m)+b\,(H\,(2-3\,m)+6\,m\,(1+m))\big)+\\
&\quad a\,\big(6\,b^3+b^2\,(1-2\,H-9\,m)+4\,H\,m\,(1+m)-2\,b\,(H-2\,H\,m+m\,(2+3\,m))\big)\big)\,r+\\
&\quad \big(6\,b^3-a^2\,(2\,b+H-3\,m)+m^2\,(8-7\,H+4\,m)-3\,b^2\,(-1+H+5\,m)+\\
&\quad a\,\big(b-6\,b^2+H+(-4+25\,b+3\,H)\,m-30\,m^2\big)+b\,\big(-H+8\,(-1+H)\,m+11\,m^2\big)\big)\,r^2+\\
&\quad \big(a-a^2+b-2\,a\,b+4\,b^2-b\,H+(-2+7\,a-11\,b+H)\,m+5\,m^2\big)\,r^3+(b-m)\,r^4\Big)-\\
&\quad (b+(-1+a)\,m)\,\Big(a\,b^2\,(b+H)\,(-1+a+b-m)+\big(a\,b\,(-1+a+b)\,(3\,b+2\,H)-\\
&\quad \big(-2\,b^2\,(1+b-H)+a^2\,(b+3\,H)+a\,(-4\,H+b\,(-4+17\,b+6\,H))\big)\,m+2\,a\,(3\,b+2\,H)\,m^2\big)\,r+\\
&\quad \big(a\,(-1+a+b)\,(3\,b+H)+\big(-3\,a^2+a\,(4-23\,b-3\,H)+b\,(4+5\,b-3\,H)\big)\,m+\\
&\quad (-8+30\,a-3\,b+7\,H)\,m^2-4\,m^3\big)\,r^2+\big(a^2+a\,(-1+b-7\,m)+(2+4\,b-H-5\,m)\,m\big)\,r^3+m\,r^4\Big)\Big)
\end{aligned}
$$

```
Collect[πAvApprox5, r]
```

$$\frac{1}{b H^3 (1+m)} \Big((a-b) b^2 (1-a+b)(b-H)(-1+a-b-m)\, m + a b^2 (b+H)(-1+a+b-m)(-b-(-1+a)m)\Big) + \frac{1}{b H^3 (1+m)}\Big((-b-(-1+a)m)\Big(a b(-1+a+b)(3b+2H) - \big(-2b^2(1+b-H)+a^2(b+3H)+a(-4H+b(-4+17b+6H))\big)m + 2a(3b+2H)m^2\Big) + (-1+a-b)\, m \Big(a^2(-3Hm+b(H+m)) + b\big(-4b^3-4Hm(1+m)+b^2(-3+3H+4m)+b(H(2-3m)+6m(1+m))\big) + a\big(6b^3+b^2(1-2H-9m)+4Hm(1+m)-2b(H-2Hm+m(2+3m))\big)\Big)\Big)\, r + \frac{1}{b H^3 (1+m)}\Big((-b-(-1+a)m)\Big(a(-1+a+b)(3b+H) + \big(-3a^2+a(4-23b-3H)+b(4+5b-3H)\big)m + (-8+30a-3b+7H)m^2 - 4m^3\Big) + (1-a+b)\, m\Big(6b^3-a^2(2b+H-3m)+m^2(8-7H+4m)-3b^2(-1+H+5m) + a\big(b-6b^2+H+(-4+25b+3H)m-30m^2\big) + b\big(-H+8(-1+H)m+11m^2\big)\Big)\Big)\, r^2 + \frac{1}{b H^3 (1+m)}\Big((-b-(-1+a)m)\big(a^2+a(-1+b-7m)+(2+4b-H-5m)m\big) + (1-a+b)\, m\big(a-a^2+b-2ab+4b^2-bH+(-2+7a-11b+H)m+5m^2\big)\Big)\, r^3 + \frac{((1-a+b)(b-m)m + m(-b-(-1+a)m))\, r^4}{b H^3 (1+m)}$$

with H defined as follows:

```
HRule
```

$$H \to \sqrt{b^2 + 2 b r + r(-4m + r)}$$

Plots

- Invasion probability as a function of recombination rate r

In[113]:=
```
mya1 = 0.02;
myb1 = 0.04;
mym1 = 0.022;
myγ1111 = 0;
myγ1211 = 0;
myγ2111 = 0;
myγ2211 = 0;
myqC1 = 0;
parComb1 = {a → mya1, b → myb1, m → mym1, γ111 → myγ1111,
  γ121 → myγ1211, γ211 → myγ2111, γ221 → myγ2211, qC → myqC1}
```

Out[121]=
```
{a → 0.02, b → 0.04, m → 0.022, γ111 → 0, γ121 → 0, γ211 → 0, γ221 → 0, qC → 0}
```

Comparing to the numerical solution for fixed values of a, b and m:

```
Plot[{probEstablAMApproxPolymContFunc[r, mym1, mya1, myb1, myγ1111,
    myγ1211, myγ2111, myγ2211, myqC1][[2]], probEstablAMApproxPolymContFunc[
    r, mym1, mya1, myb1, myγ1111, myγ1211, myγ2111, myγ2211, myqC1][[3]],
  probEstablAMApproxPolymContFunc[r, mym1, mya1, myb1, myγ1111, myγ1211,
    myγ2111, myγ2211, myqC1][[4]], π1Func[a, b, m, r] /. parComb1,
  π2Func[a, b, m, r] /. parComb1, πAvFunc[a, b, m, r] /. parComb1,
  π1Approx4Func[a, b, m, r] /. parComb1, π2Approx4Func[a, b, m, r] /. parComb1,
  πAvApprox4Func[a, b, m, r] /. parComb1}, {r, 0, 0.5},
 PlotRange → {{0, rCritFunc[mym1, mya1, myb1]}, {0, 2.5 * mya1}}, PlotStyle →
  {{RGBColor[0, 0.3, 1, 0.5]}, {Red}, {Black}, {RGBColor[0, 0.3, 1, 0.5], DotDashed},
   {Red, DotDashed}, {Black, DotDashed}, {RGBColor[0, 0.3, 1, 0.5], Thick, Dashed},
   {Red, Thick, Dashed}, {Black, Thick, Dashed}},
 LabelStyle → {Directive[FontSize → 14], FontFamily → "Helvetica"},
 AxesLabel → {"Recombination rate r", "Invasion probability"},
 Frame → True, FrameStyle → {{Black, Opacity[0]}, {Black, Opacity[0]}},
 FrameLabel → {"Recombination rate r", "Invasion probability"}]
```

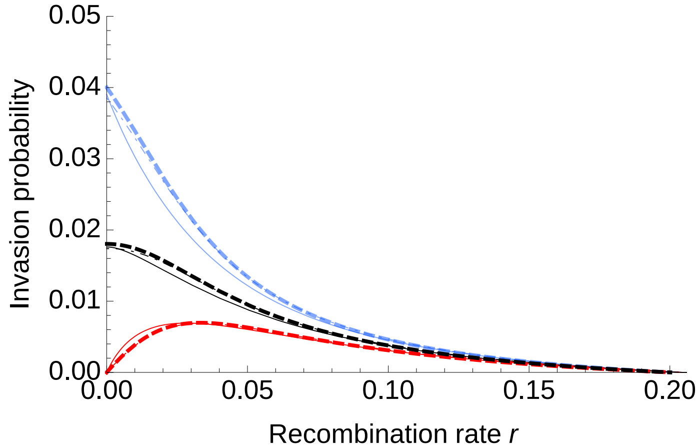


Figure 1: The invasion probability as a function of the recombination rate r for a monomorphic continent ($q_c = 0$) and additive fitness effects. Invasion probabilities are shown for A_1 occuring on the beneficial background B_1 (blue), on the deleterious background B_2 (red) and as a weighted average across backgrounds (black), where the weights are determinded by the frequency $\hat{q}_B$ of B_1 at the marginal one-locus migration-selection equilibrium. Analytical approximations assuming a slightly-supercritical branching process (thin dot-dashed lines) and, in addition, weak evolutionary forces (up to first order of ϵ; thick dashed lines) are compared to the exact numerical branching-process solution (thin solid lines). Parameter values are $a = 0.02$, $b = 0.04$, $m = 0.022$.

Comparing to the numerical solution for various values of a, b and m:

In[122]:=
```
Manipulate[
 Plot[{probEstablAMApproxPolymContFunc[
     r, m, a, b, myγ1111, myγ1211, myγ2111, myγ2211, myqC1]⟦2⟧,
   probEstablAMApproxPolymContFunc[r, m, a, b, myγ1111, myγ1211, myγ2111, myγ2211,
     myqC1]⟦3⟧, probEstablAMApproxPolymContFunc[r, m, a, b, myγ1111,
     myγ1211, myγ2111, myγ2211, myqC1]⟦4⟧, π1Func[a, b, m, r],
   π2Func[a, b, m, r], πAvFunc[a, b, m, r], π1Approx4Func[a, b, m, r],
   π2Approx4Func[a, b, m, r], πAvApprox4Func[a, b, m, r]}, {r, 0, 0.5},
  PlotRange → {{0, rCritFunc[m, a, b]}, {0, 2.5 * a}}, PlotStyle →
   {{RGBColor[0, 0.3, 1, 0.5]}, {Red}, {Black}, {RGBColor[0, 0.3, 1, 0.5], DotDashed},
    {Red, DotDashed}, {Black, DotDashed}, {RGBColor[0, 0.3, 1, 0.5], Thick, Dashed},
    {Red, Thick, Dashed}, {Black, Thick, Dashed}},
  LabelStyle → {Directive[FontSize → 14], FontFamily → "Helvetica"},
  AxesLabel → {"Recombination rate r", "Invasion probability"},
  Frame → True, FrameStyle → {{Black, Opacity[0]}, {Black, Opacity[0]}},
  FrameLabel → {"Recombination rate r", "Invasion probability"}],
 {{a, 0.03}, 0, 0.08}, {{b, 0.04}, 0, 0.08}, {{m, 0.032}, 0, 0.1}]
```

Out[122]=

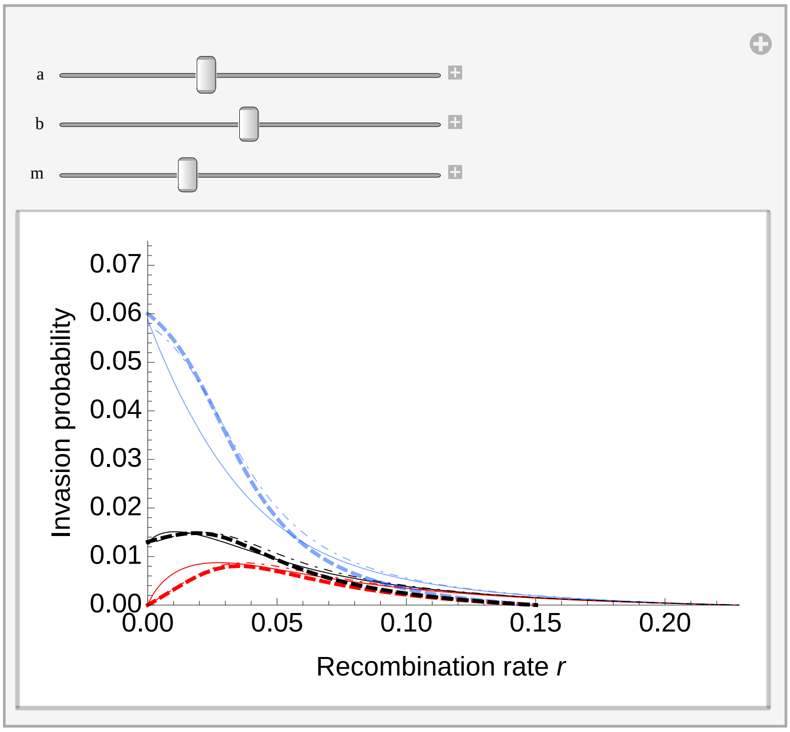


Figure: The invasion probability as a function of the recombination rate r for a monomorphic continent ($q_c = 0$) and additive fitness effects. Invasion probabilities are shown for A_1 occuring on the beneficial background B_1 (blue), on the deleterious background B_2 (red) and as a weighted average across backgrounds (black), where the weights are determined by the frequency $\hat{q}_B$ of B_1 at the marginal one-locus migration-selection equilibrium. Analytical approximations assuming a slightly-supercritical branching process (thin dot-dashed lines) and, in addition, weak evolutionary forces (up to first order of ϵ; thick dashed lines) are compared to the exact numerical branching-process solution (thin solid lines). Parameter values for a, b and m can be chosen arbitrarily from a range of values.

We note that the approximation up to first order of ϵ (thick dashed lines in the two previous plots) is good for the weighted average invasion probability (black) when r is small. For intermediate r, the approximation becomes rather poor and underestimates the invasion probability. For r growing further, though, the approximation becomes better again.

In the following, we use an approximation up to second order of ϵ instead and we observe that the error becomes smaller for large r. This comes at the cost of a slightly larger error for small r, however. As expected, this approximation is now much closer to the analytical expressions obtained assuming a slightly supercritical branching process without further restrictions on the strength of evolutionary forces (the thick dotted lines are almost identical to the thin dot-dashed lines in the figure below).

In[123]:=
```
Manipulate[
 Plot[{probEstablAMApproxPolymContFunc[
     r, m, a, b, myγ1111, myγ1211, myγ2111, myγ2211, myqC1][[2]],
   probEstablAMApproxPolymContFunc[r, m, a, b, myγ1111, myγ1211, myγ2111, myγ2211,
     myqC1][[3]], probEstablAMApproxPolymContFunc[r, m, a, b, myγ1111,
     myγ1211, myγ2111, myγ2211, myqC1][[4]], π1Func[a, b, m, r],
   π2Func[a, b, m, r], πAvFunc[a, b, m, r], π1Approx5Func[a, b, m, r],
   π2Approx5Func[a, b, m, r], πAvApprox5Func[a, b, m, r]}, {r, 0, 0.5},
  PlotRange → {{0, rCritFunc[m, a, b]}, {0, 2.5 * a}}, PlotStyle →
   {{RGBColor[0, 0.3, 1, 0.5]}, {Red}, {Black}, {RGBColor[0, 0.3, 1, 0.5], DotDashed},
    {Red, DotDashed}, {Black, DotDashed}, {RGBColor[0, 0.3, 1, 0.5], Thick, Dotted},
    {Red, Thick, Dotted}, {Black, Thick, Dotted}},
  LabelStyle → {Directive[FontSize → 14], FontFamily → "Helvetica"},
  AxesLabel → {"Recombination rate r", "Invasion probability"},
  Frame → True, FrameStyle → {{Black, Opacity[0]}, {Black, Opacity[0]}},
  FrameLabel → {"Recombination rate r", "Invasion probability"}],
 {{a, 0.03}, 0, 0.08}, {{b, 0.04}, 0, 0.08}, {{m, 0.032}, 0, 0.1}]
```

Out[123]=

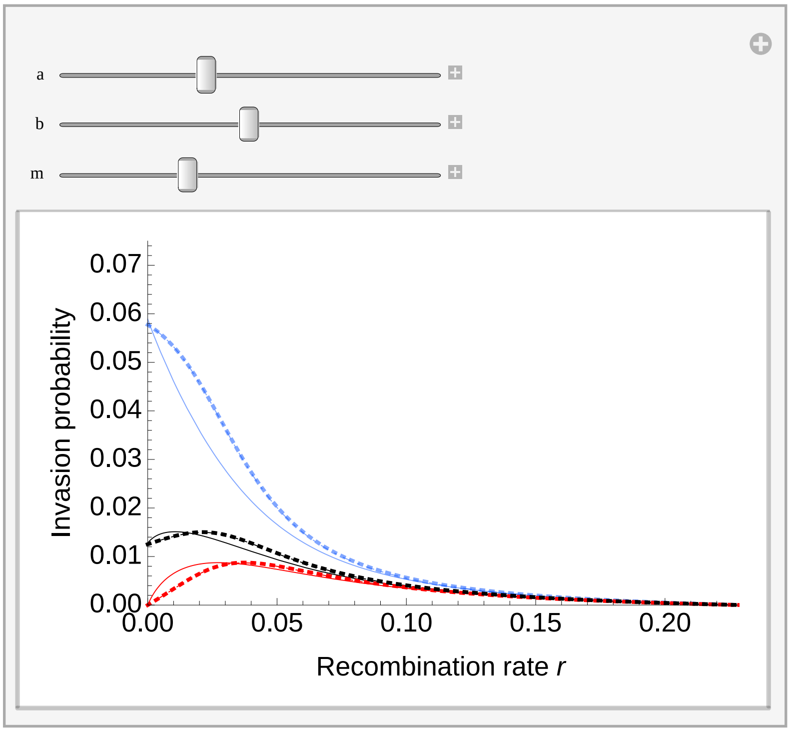


Figure: The invasion probability as a function of the recombination rate r for a monomorphic continent ($q_c = 0$) and additive fitness effects. Invasion probabilities are shown for A_1 occuring on the beneficial background B_1 (blue), on the deleterious background B_2 (red) and as a weighted average across backgrounds (black), where the weights are determined by the frequency $\hat{q}_B$ of B_1 at the marginal one-locus migration-selection equilibrium. Analytical approximations assuming a slightly-supercritical branching process (thin dot-dashed lines) and, in addition, weak evolutionary forces (up to second order of ϵ; thick dotted lines) are compared to the exact numerical branching-process solution (thin solid lines). Parameter values for a, b and m can be chosen arbitrarily from a range of values.

- Invasion probability as a function of migration rate m

In[74]:=
```
myr1 = 0.02;
parComb1a = {a → mya1, b → myb1, r → myr1, γ111 → myγ1111,
  γ121 → myγ1211, γ211 → myγ2111, γ221 → myγ2211, qC → myqC1}
```

Out[75]=
```
{a → 0.02, b → 0.04, r → 0.02, γ111 → 0, γ121 → 0, γ211 → 0, γ221 → 0, qC → 0}
```

Comparing to the numerical solution for fixed values of a, b and r:

```
Plot[{probEstablAMApproxPolymContFunc[myr1,
     m, mya1, myb1, myγ1111, myγ1211, myγ2111, myγ2211, myqC1][[2]],
   probEstablAMApproxPolymContFunc[myr1, m, mya1, myb1, myγ1111, myγ1211,
     myγ2111, myγ2211, myqC1][[3]], probEstablAMApproxPolymContFunc[
     myr1, m, mya1, myb1, myγ1111, myγ1211, myγ2111, myγ2211, myqC1][[4]],
   π1Func[a, b, m, r] /. parComb1a, π2Func[a, b, m, r] /. parComb1a,
   πAvFunc[a, b, m, r] /. parComb1a, π1Approx4Func[a, b, m, r] /. parComb1a,
   π2Approx4Func[a, b, m, r] /. parComb1a, πAvApprox4Func[a, b, m, r] /. parComb1a},
  {m, 0, 2 * mCritFunc[myr1, mya1, myb1]},
  PlotRange → {{0, (mCritFunc[myr1, mya1, myb1] /. parComb1a)}, {0, 2.5 * mya1}},
  PlotStyle → {{RGBColor[0, 0.3, 1, 0.5]}, {Red}, {Black},
    {RGBColor[0, 0.3, 1, 0.5], DotDashed}, {Red, DotDashed},
    {Black, DotDashed}, {RGBColor[0, 0.3, 1, 0.5], Thick, Dashed},
    {Red, Thick, Dashed}, {Black, Thick, Dashed}},
  LabelStyle → {Directive[FontSize → 14], FontFamily → "Helvetica"},
  AxesLabel → {"Migration rate m", "Invasion probability"},
  Frame → True, FrameStyle → {{Black, Opacity[0]}, {Black, Opacity[0]}},
  FrameLabel → {"Migration rate m", "Invasion probability"}]
```

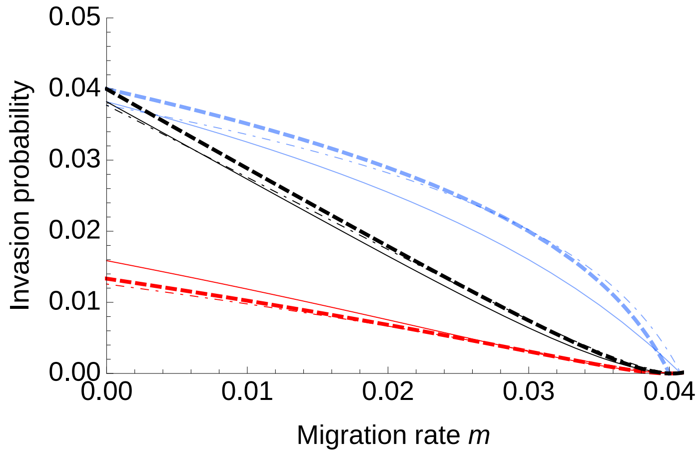


Figure 4: The invasion probability as a function of the migration rate m for a monomorphic continent ($q_c = 0$) and additive fitness effects. Invasion probabilities are shown for A_1 occuring on the beneficial background B_1 (blue), on the deleterious background B_2 (red) and as a weighted average across backgrounds (black), where the weights are determinded by the frequency $\hat{q}_B$ of B_1 at the marginal one-locus migration-selection equilibrium. Analytical approximations assuming a slightly-supercritical branching process (thin dot-dashed lines) and, in addition, weak evolutionary forces (up to first order of ϵ; thick dashed lines) are compared to the exact numerical branching-process solution (thin solid lines). Parameter values are $a = 0.02$, $b = 0.04$, $r = 0.02$.

Comparing to the numerical solution for various values of a, b and r:

In[124]:=
```
Manipulate[
 Plot[{probEstablAMApproxPolymContFunc[r, m, a, b, myγ1111,
     myγ1211, myγ2111, myγ2211, myqC1][[2]], probEstablAMApproxPolymContFunc[
     r, m, a, b, myγ1111, myγ1211, myγ2111, myγ2211, myqC1][[3]],
   probEstablAMApproxPolymContFunc[r, m, a, b, myγ1111, myγ1211, myγ2111,
     myγ2211, myqC1][[4]], π1Func[a, b, m, r], π2Func[a, b, m, r],
   πAvFunc[a, b, m, r], π1Approx4Func[a, b, m, r], π2Approx4Func[a, b, m, r],
   πAvApprox4Func[a, b, m, r]}, {m, 0, 2 * mCritFunc[r, a, b]},
  PlotRange → {{0, (mCritFunc[r, a, b])}, {0, 2.5 * a}}, PlotStyle →
   {{RGBColor[0, 0.3, 1, 0.5]}, {Red}, {Black}, {RGBColor[0, 0.3, 1, 0.5], DotDashed},
    {Red, DotDashed}, {Black, DotDashed}, {RGBColor[0, 0.3, 1, 0.5], Thick, Dashed},
    {Red, Thick, Dashed}, {Black, Thick, Dashed}},
  LabelStyle → {Directive[FontSize → 14], FontFamily → "Helvetica"},
  AxesLabel → {"Migration rate m", "Invasion probability"},
  Frame → True, FrameStyle → {{Black, Opacity[0]}, {Black, Opacity[0]}},
  FrameLabel → {"Migration rate m", "Invasion probability"}],
 {{a, 0.03}, 0, 0.08}, {{b, 0.04}, 0, 0.08}, {{r, 0.02}, 0, 0.1}]
```

Out[124]=

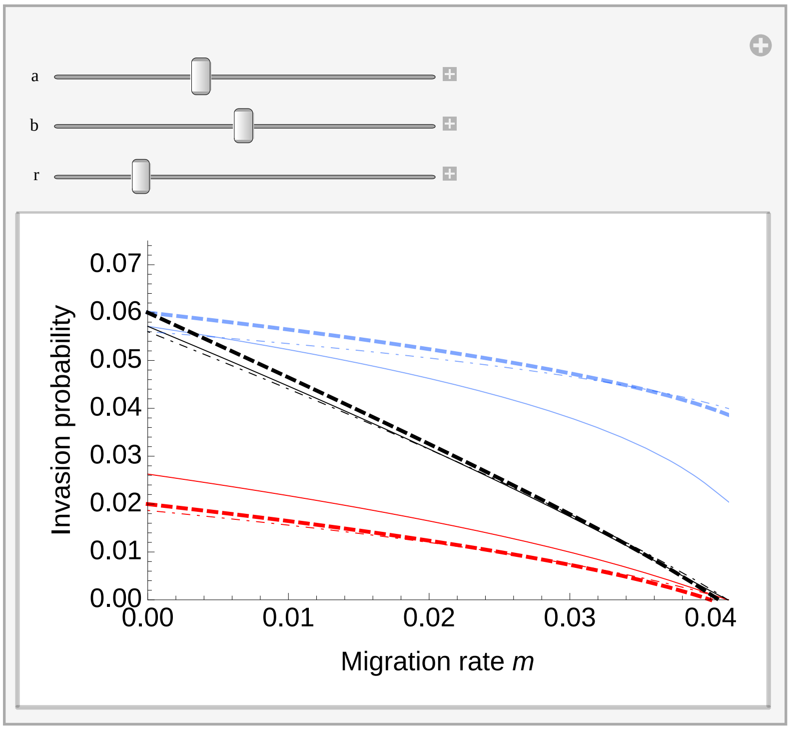


Figure: The invasion probability as a function of the migration rate m for a monomorphic continent ($q_c = 0$) and additive fitness effects. Invasion probabilities are shown for A_1 occuring on the beneficial background B_1 (blue), on the deleterious background B_2 (red) and as a weighted average across backgrounds (black), where the weights are determined by the frequency $\hat{q}_B$ of B_1 at the marginal one-locus migration-selection equilibrium. Analytical approximations assuming a slightly-supercritical branching process (thin dot-dashed lines) and, in addition, weak evolutionary forces (up to first order of ϵ; thick dashed lines) are compared to the exact numerical branching-process solution (thin solid lines). Parameter values for a, b and r can be chosen arbitrarily from a range of values.

We note that the approximation up to first order of ϵ (thick dashed lines in the two previous plots) is rather good for the weighted average invasion probability (black) when m is not too small. The approximation to the conditional invasion probabilities becomes worse as m increases; π_1 and π_2 tend to be over- and underestimated, respectively. These effects seem to become balanced out when the weighted average is taken. We suspect that taking a more exact approximation (up to second order of ϵ may help to reduce the error in the average invasion probability for small m.

In the following, we use an approximation up to second order of ϵ instead and we observe that the error in the average invasion probability (black) becomes smaller for small m. As expected, this approximation is now much closer to the analytical expressions obtained assuming a slightly supercritical branching process without further restrictions on the strength of evolutionary forces (the thick dotted lines are almost identical to the thin dot-dashed lines in the figure below).

In[125]:=
```
Manipulate[
 Plot[{probEstablAMApproxPolymContFunc[r, m, a, b, myγ1111,
     myγ1211, myγ2111, myγ2211, myqC1][[2]], probEstablAMApproxPolymContFunc[
     r, m, a, b, myγ1111, myγ1211, myγ2111, myγ2211, myqC1][[3]],
   probEstablAMApproxPolymContFunc[r, m, a, b, myγ1111, myγ1211, myγ2111,
     myγ2211, myqC1][[4]], π1Func[a, b, m, r], π2Func[a, b, m, r],
   πAvFunc[a, b, m, r], π1Approx5Func[a, b, m, r], π2Approx5Func[a, b, m, r],
   πAvApprox5Func[a, b, m, r]}, {m, 0, 2 * mCritFunc[r, a, b]},
  PlotRange → {{0, (mCritFunc[r, a, b])}, {0, 2.5 * a}}, PlotStyle →
   {{RGBColor[0, 0.3, 1, 0.5]}, {Red}, {Black}, {RGBColor[0, 0.3, 1, 0.5], DotDashed},
    {Red, DotDashed}, {Black, DotDashed}, {RGBColor[0, 0.3, 1, 0.5], Thick, Dotted},
    {Red, Thick, Dotted}, {Black, Thick, Dotted}},
  LabelStyle → {Directive[FontSize → 14], FontFamily → "Helvetica"},
  AxesLabel → {"Migration rate m", "Invasion probability"},
  Frame → True, FrameStyle → {{Black, Opacity[0]}, {Black, Opacity[0]}},
  FrameLabel → {"Migration rate m", "Invasion probability"}],
 {{a, 0.03}, 0, 0.08}, {{b, 0.04}, 0, 0.08}, {{r, 0.02}, 0, 0.1}]
```

Out[125]=

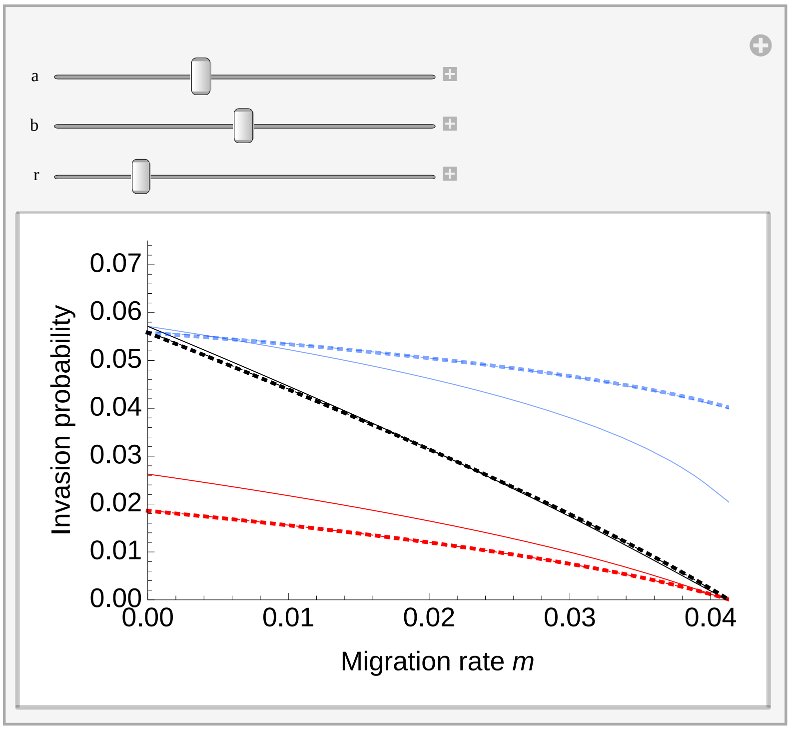


Figure: The invasion probability as a function of the migration rate m for a monomorphic continent ($q_c = 0$) and additive fitness effects. Invasion probabilities are shown for A_1 occuring on the beneficial background B_1 (blue), on the deleterious background B_2 (red) and as a weighted average across backgrounds (black), where the weights are determined by the frequency $\hat{q}_B$ of B_1 at the marginal one-locus migration-selection equilibrium. Analytical approximations assuming a slightly-supercritical branching process (thin dot-dashed lines) and, in addition, weak evolutionary forces (up to second order of ϵ; thick dotted lines) are compared to the exact numerical branching-process solution (thin solid lines). Parameter values for a, b and r can be chosen arbitrarily from a range of values.

Additive fitnesses and polymorphic continent

- **Mean matrix**

```
Clear[uPolymCont, vPolymCont]
```

In[76]:=
```
LaddPolymCont :=
  {{λ11addPolymCont, λ12addPolymCont}, {λ21addPolymCont, λ22addPolymCont}}
LaddPolymContAxRaw := {{λ11addPolymContAx, λ12addPolymContAx},
   {λ21addPolymContAx, λ22addPolymContAx}}
```

In[78]:=
```
LaddPolymContAx =
  FullSimplify[LaddPolymContAxRaw, Assumptions → Flatten[{genericAssumpt, 0 ≤ qC ≤ 1}]];
```

Rules for the assumptions we are going to make:

The mean matrix with additive fitnesses

```
MatrixForm[LaddPolymCont]
```

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

The mean matrix with additive fitnesses under the assumption that all evolutionary forces are small

```
assumeSmallForces
```

$\{a \to \alpha\,\epsilon,\ b \to \beta\,\epsilon,\ r \to \epsilon\,\rho,\ m \to \epsilon\,\mu,\ \gamma 11 \to g11\,\epsilon,\ \gamma 12 \to g12\,\epsilon,\ \gamma 21 \to g21\,\epsilon,\ \gamma 22 \to g22\,\epsilon\}$

```
MatrixForm[LaddPolymContAxRaw]
```

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

```
MatrixForm[LaddPolymContAx]
```

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

Exploration of eigenvalues

```
genericAssumpt
```

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

- Exact mean matrix

```
FullSimplify[Eigenvalues[LaddPolymCont], Assumptions → genericAssumpt]
```

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

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

The computation above takes a few minutes, which is why we have hard-coded the result here:

In[79]:=
```
evalLaddPolymCont1Func[a_, b_, m_, r_, qC_] :=
 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)])
```

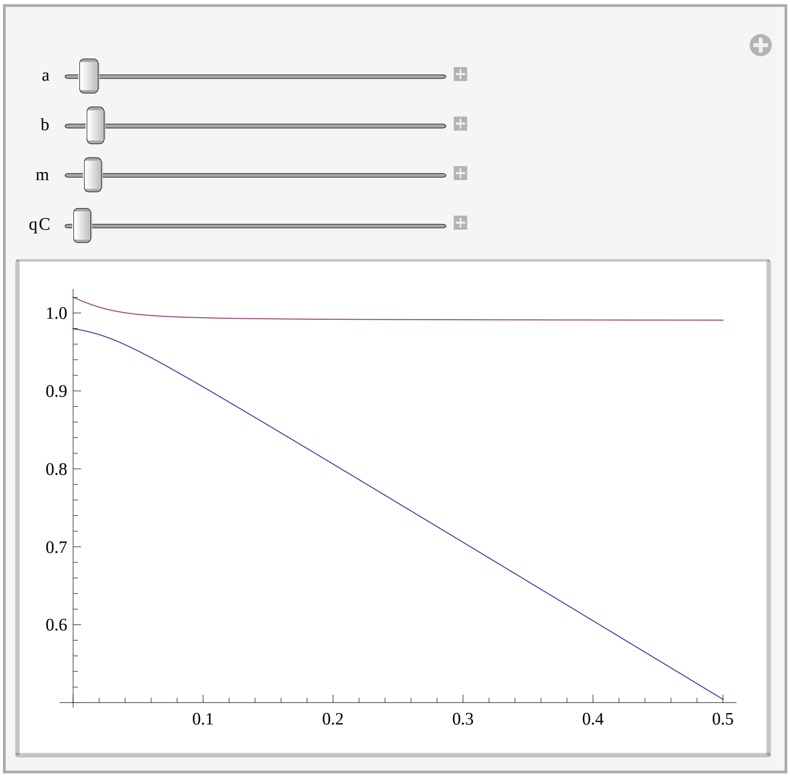
In[80]:=

$$\text{evalLaddPolymCont2Func}[a\_, b\_, m\_, r\_, qC\_] := \frac{1}{2}\left(\frac{2}{(-1+a)^2-b^2} - \frac{1}{(-1+a)^2-b^2}\left(-b^2(-1+m)+m+a^2 m+\sqrt{(b+(-1+a)m)^2-4\,b\,m\,(-1+a+b\,m)\,qC+4\,b^2 m^2 qC^2} + a\left(2+m\,(-2+b-2\,b\,qC)+\sqrt{\left((b+(-1+a)m)^2-4\,b\,m\,(-1+a+b\,m)\,qC+4\,b^2 m^2 qC^2\right)}-r\right) + b\,m\,(-1+2\,qC)\,(-1+r)+r-\sqrt{(b+(-1+a)m)^2-4\,b\,m\,(-1+a+b\,m)\,qC+4\,b^2 m^2 qC^2}\;r\right) + \sqrt{\left(\left((-1+m)^2(1+m)\left(b^2(1+m)+2\,b\,m\,(-1+2\,qC)\,r + r\left(2\sqrt{\left((b+(-1+a)m)^2-4\,b\,m\,(-1+a+b\,m)\,qC+4\,b^2 m^2 qC^2\right)}+r+m\,(-2+2\,a+r)\right)\right)\right) \Big/ \left(1-a+b\,m\,(-1+2\,qC)+\sqrt{\left((b+(-1+a)m)^2-4\,b\,m\,(-1+a+b\,m)\,qC+4\,b^2 m^2 qC^2\right)}\right)^2\right)}\right)$$

In[126]:=

```
Manipulate[
 Plot[{evalLaddPolymCont1Func[a, b, m, r, qC], evalLaddPolymCont2Func[a, b, m, r, qC]},
  {r, 0, 0.5}], {{a, 0.02}, 0, 1}, {{b, 0.04}, 0, 1}, {{m, 0.03}, 0, 1}, {{qC, 0}, 0, 1}
]
```

Out[126]=



Numerical exploration suggests that the second eigenvalue is the leading one.

If the condition above is fulfilled, the first eigenvalue is larger than the second one. If the condition is not fulfilled, then the real parts of the two eigenvalues are equal.

In[81]:=

```
νPolymCont =
 FullSimplify[Eigenvalues[LaddPolymCont][[2]], Assumptions → Flatten[{genericAssumpt}]]
```

Out[81]= $Aborted

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

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

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

$$\begin{aligned}&\frac{1}{2}\Bigg(\frac{2}{(-1+a)^2-b^2}-\\&\quad\frac{1}{(-1+a)^2-b^2}\Big(-b^2(-1+m)+m+a^2 m+\sqrt{(b+(-1+a)\,m)^2-4\,b\,m\,(-1+a+b\,m)\,qC+4\,b^2\,m^2\,qC^2}+\\&\qquad a\left(2+m\,(-2+b-2\,b\,qC)+\sqrt{(b+(-1+a)\,m)^2-4\,b\,m\,(-1+a+b\,m)\,qC+4\,b^2\,m^2\,qC^2}-r\right)+\\&\qquad b\,m\,(-1+2\,qC)\,(-1+r)+r-\sqrt{(b+(-1+a)\,m)^2-4\,b\,m\,(-1+a+b\,m)\,qC+4\,b^2\,m^2\,qC^2}\;r\Big)+\\&\quad\sqrt{\Big(\Big((-1+m)^2\,(1+m)\,\Big(b^2\,(1+m)+2\,b\,m\,(-1+2\,qC)\,r+}\\&\qquad\qquad r\left(2\sqrt{\left((b+(-1+a)\,m)^2-4\,b\,m\,(-1+a+b\,m)\,qC+4\,b^2\,m^2\,qC^2\right)}+r+m\,(-2+2\,a+r)\right)\Big)\Big)\Big/\\&\qquad\left(1-a+b\,m\,(-1+2\,qC)+\sqrt{(b+(-1+a)\,m)^2-4\,b\,m\,(-1+a+b\,m)\,qC+4\,b^2\,m^2\,qC^2}\right)^2\Big)\Bigg)\end{aligned}$$

$$\begin{aligned}&\frac{1}{2}\Bigg(\frac{2}{(-1+a)^2-b^2}-\\&\quad\frac{1}{(-1+a)^2-b^2}\Big(-b^2(-1+m)+m+a^2 m+\sqrt{(b+(-1+a)\,m)^2-4\,b\,m\,(-1+a+b\,m)\,qC+4\,b^2\,m^2\,qC^2}+\\&\qquad a\left(2+m\,(-2+b-2\,b\,qC)+\sqrt{(b+(-1+a)\,m)^2-4\,b\,m\,(-1+a+b\,m)\,qC+4\,b^2\,m^2\,qC^2}-r\right)+\\&\qquad b\,m\,(-1+2\,qC)\,(-1+r)+r-\sqrt{(b+(-1+a)\,m)^2-4\,b\,m\,(-1+a+b\,m)\,qC+4\,b^2\,m^2\,qC^2}\;r\Big)+\\&\quad\sqrt{\Big(\Big((-1+m)^2\,(1+m)\,\Big(b^2\,(1+m)+2\,b\,m\,(-1+2\,qC)\,r+}\\&\qquad\qquad r\left(2\sqrt{\left((b+(-1+a)\,m)^2-4\,b\,m\,(-1+a+b\,m)\,qC+4\,b^2\,m^2\,qC^2\right)}+r+m\,(-2+2\,a+r)\right)\Big)\Big)\Big/\\&\qquad\left(1-a+b\,m\,(-1+2\,qC)+\sqrt{(b+(-1+a)\,m)^2-4\,b\,m\,(-1+a+b\,m)\,qC+4\,b^2\,m^2\,qC^2}\right)^2\Big)\Bigg)\end{aligned}$$

$$\begin{aligned}&\frac{1}{2}\Bigg(\frac{2}{(-1+a)^2-b^2}-\\&\quad\frac{1}{(-1+a)^2-b^2}\Big(-b^2(-1+m)+m+a^2 m+\sqrt{(b+(-1+a)\,m)^2-4\,b\,m\,(-1+a+b\,m)\,qC+4\,b^2\,m^2\,qC^2}+\\&\qquad a\left(2+m\,(-2+b-2\,b\,qC)+\sqrt{(b+(-1+a)\,m)^2-4\,b\,m\,(-1+a+b\,m)\,qC+4\,b^2\,m^2\,qC^2}-r\right)+\\&\qquad b\,m\,(-1+2\,qC)\,(-1+r)+r-\sqrt{(b+(-1+a)\,m)^2-4\,b\,m\,(-1+a+b\,m)\,qC+4\,b^2\,m^2\,qC^2}\;r\Big)+\\&\quad\sqrt{\Big(\Big((-1+m)^2\,(1+m)\,\Big(b^2\,(1+m)+2\,b\,m\,(-1+2\,qC)\,r+}\\&\qquad\qquad r\left(2\sqrt{\left((b+(-1+a)\,m)^2-4\,b\,m\,(-1+a+b\,m)\,qC+4\,b^2\,m^2\,qC^2\right)}+r+m\,(-2+2\,a+r)\right)\Big)\Big)\Big/\\&\qquad\left(1-a+b\,m\,(-1+2\,qC)+\sqrt{(b+(-1+a)\,m)^2-4\,b\,m\,(-1+a+b\,m)\,qC+4\,b^2\,m^2\,qC^2}\right)^2\Big)\Bigg)\end{aligned}$$

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

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

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

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

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

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

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

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

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

$$\frac{1}{2}\left(\frac{2}{(-1+a)^2-b^2}-\frac{1}{(-1+a)^2-b^2}\left(-b^2(-1+m)+m+a^2 m+\sqrt{(b+(-1+a)m)^2-4bm(-1+a+bm)qC+4b^2m^2qC^2}+a\left(2+m(-2+b-2bqC)+\sqrt{(b+(-1+a)m)^2-4bm(-1+a+bm)qC+4b^2m^2qC^2}-r\right)+bm(-1+2qC)(-1+r)+r-\sqrt{(b+(-1+a)m)^2-4bm(-1+a+bm)qC+4b^2m^2qC^2}\;r\right)+\sqrt{\left(\left(\left((-1+m)^2(1+m)\left(b^2(1+m)+2bm(-1+2qC)r+r\left(2\sqrt{\left((b+(-1+a)m)^2-4bm(-1+a+bm)qC+4b^2m^2qC^2\right)}+r+m(-2+2a+r)\right)\right)\right)\right)\Big/\left(1-a+bm(-1+2qC)+\sqrt{(b+(-1+a)m)^2-4bm(-1+a+bm)qC+4b^2m^2qC^2}\right)^2\right)}\right)$$

- Approximate mean matrix

```
FullSimplify[Eigenvalues[LaddPolymContAx], Assumptions → genericAssumpt]
```

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

In[127]:= **evalLaddPolymContAx1Func[a_, b_, m_, r_, qC_] :=**

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

In[128]:= **evalLaddPolymContAx2Func[a_, b_, m_, r_, qC_] :=**

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

In[129]:= **Rad1 =** $b^2+r\left(-2m+2\sqrt{(b-m)^2+4bmqC}+r\right)$

Out[129]= $b^2+r\left(-2m+2\sqrt{(b-m)^2+4bmqC}+r\right)$

```
FullSimplify[Reduce[Rad1 > 0], Assumptions → Flatten[{genericAssumpt, 0 < qC < 1}]]
```

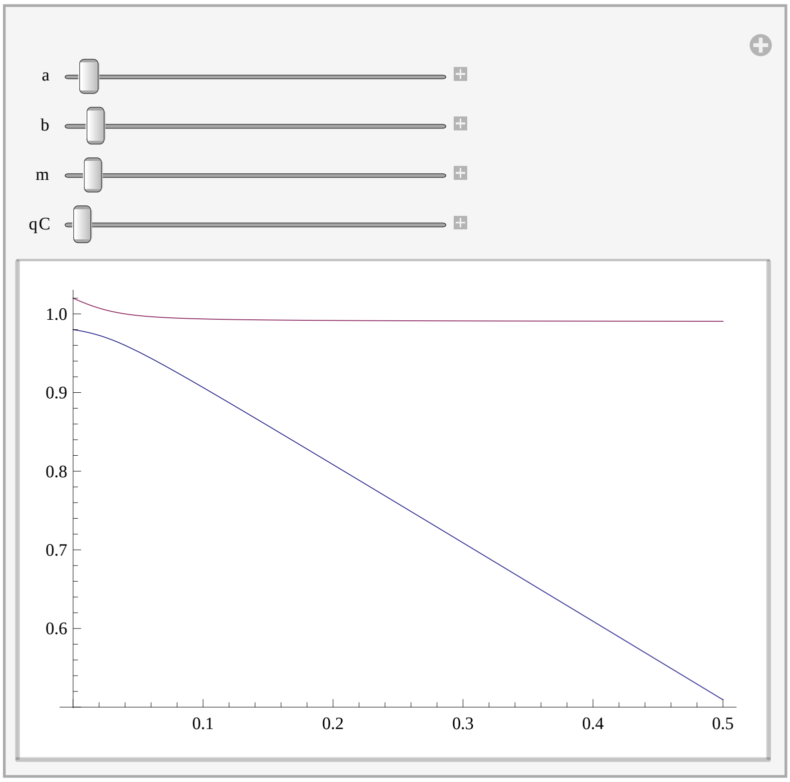
True

FullSimplify$\left[\textbf{Reduce}\left[2+2a-m-\sqrt{(b-m)^2+4bmqC}>0\right],\right.$
Assumptions → Flatten[{genericAssumpt, 0 < qC < 1}]]

$4bmqC<(2+2a-b)(2+2a+b-2m)$

In[130]:=
```
Manipulate[
 Plot[{evalLaddPolymContAx1Func[a, b, m, r, qC],
   evalLaddPolymContAx2Func[a, b, m, r, qC]}, {r, 0, 0.5}],
 {{a, 0.02}, 0, 1}, {{b, 0.04}, 0, 1}, {{m, 0.03}, 0, 1}, {{qC, 0}, 0, 1}
]
```

Out[130]=



Analytical results the plot above suggests that either the first and second approximate eigenvalue can be the leading one, depending on the parameter combinations. However, for weak forces, *i.e.* when the assumptions justifying the approximate eigenvalues is fulfilled, the second is the leading eigenvalue.

```
νPolymContAx = FullSimplify[Eigenvalues[LaddPolymContAx],
  Assumptions → Flatten[{genericAssumpt, 0 ≤ qC ≤ 1}]]
```

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

In the following, we work with the exact leading eigenvalue ν.

```
assumeSmallForces
```

$\{a \to \alpha\,\epsilon,\ b \to \beta\,\epsilon,\ r \to \epsilon\,\rho,\ m \to \epsilon\,\mu,\ \gamma 11 \to g11\,\epsilon,\ \gamma 12 \to g12\,\epsilon,\ \gamma 21 \to g21\,\epsilon,\ \gamma 22 \to g22\,\epsilon\}$

```
Limit[νPolymCont /. assumeSmallForces, ϵ → 0] // Simplify
```

1

The above two expressions are as it should be: $\nu(\epsilon) \to 1$ as $\epsilon \to 0$. This suggests we can apply T5.6_HJV2005.

■ Identification of ξ

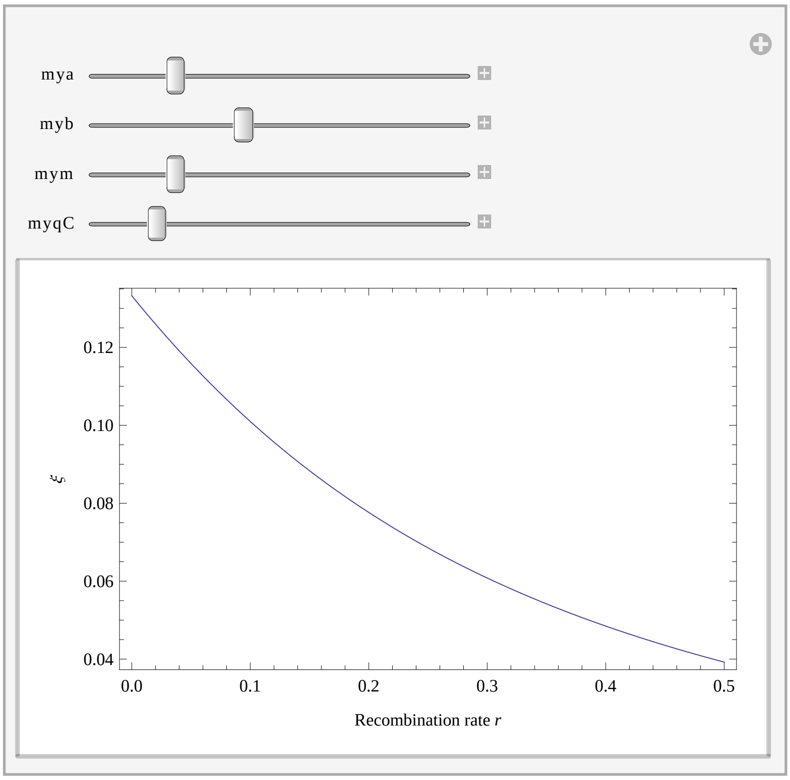
```
νPolymCont
```

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

```
ξPolymContRule =
 FullSimplify[Solve[νPolymCont == 1 + ξ, ξ], Assumptions → Flatten[{genericAssumpt}]]
```

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

```
Manipulate[Plot[ξAddPolymContFunc[mya, myb, mym, r, myqC],
  {r, 0, 0.5}, Frame → True, FrameLabel → {"Recombination rate r", "ξ"}],
 {{mya, 0.2}, 0, 1}, {{myb, 0.4}, 0, 1}, {{mym, 0.2}, 0, 1}, {{myqC, 0.2}, 0, 1}]
```



What is ξ if all forces are small?

```
assumeSmallForcesAdj = {a → α ϵ1, b → β ϵ1, r → ϵ1 ρ,
   m → ϵ1 μ, γ11 → g11 ϵ1, γ12 → g12 ϵ1, γ21 → g21 ϵ1, γ22 → g22 ϵ1};
backSubstSmallForcesAdj =
  {α → a/ϵ1, β → b/ϵ1, ρ → r/ϵ1, μ → m/ϵ1, g11 → γ11/ϵ1, g12 → γ12/ϵ1, g21 → γ21/ϵ1, g22 → γ22/ϵ1};
FullSimplify[Series[ξ /. ξPolymContRule /. assumeSmallForcesAdj, {ϵ1, 0, 1}] /.
   backSubstSmallForcesAdj // Normal, Assumptions → genericAssumpt]
```

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

```
νPolymContAx
```

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

```
Solve[νPolymContAx[[1]] == 1 + ξ, ξ]
```

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

If we assume m small in addition:

```
FullSimplify[Series[
    -1 + 1/2 (2 + 2 a - m - Sqrt[(b - m)^2 + 4 b m qC] - r - Sqrt[b^2 + r (-2 m + 2 Sqrt[(b - m)^2 + 4 b m qC] + r)]),
    {m, 0, 1}], Assumptions → genericAssumpt] // Normal
```

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

This was the ξ belonging to the first approximate eigenvalue.

```
Solve[vPolymContAx[[2]] == 1 + ξ, ξ]
```

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

If we assume *m* small in addition:

```
FullSimplify[Series[
    -1 + 1/2 (2 + 2 a - m - Sqrt[(b - m)^2 + 4 b m qC] - r + Sqrt[b^2 + r (-2 m + 2 Sqrt[(b - m)^2 + 4 b m qC] + r)]),
    {m, 0, 1}], Assumptions → genericAssumpt] // Normal
```

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

This was the ξ belonging to the second approximate eigenvalue.

■ Eigenvectors and their normalisation

The right and left leading eigenvectors:

The second one is the leading eigenvector (belonging to the dominant eigenvalue).

```
vPolymContDef =
  FullSimplify[Eigenvectors[LaddPolymCont][[2]], Assumptions → genericAssumpt];
```

Recall: The left eigenvectors of a matrix A are obtained as the right eigenvectors of the transpose of A.

```
FullSimplify[Eigensystem[Transpose[LaddPolymCont]], Assumptions → genericAssumpt]
```

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

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

```
            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) + √((b + (-1 + a) m)^2 - 4 b m (-1 + a + b m) qC + 4 b^2 m^2 qC^2))^2)}},
{{(-(-1 + m) ((-1 + a) m + √((b + (-1 + a) m)^2 - 4 b m (-1 + a + b m) qC + 4 b^2 m^2 qC^2)) r +
      b^2 (1 - m^2 + m (1 - 2 qC)
          √(((-1 + m)^2 (1 + m) (b^2 (1 + m) + 2 m (-1 + a - b + 2 b qC) r + 2 √((b + (-1 + a) m)^2 - 4 b
                      m (-1 + a + b m) qC + 4 b^2 m^2 qC^2) r + (1 + m) r^2)) / (1 - a + b m (-1 + 2 qC) +
                √((b + (-1 + a) m)^2 - 4 b m (-1 + a + b m) qC + 4 b^2 m^2 qC^2))^2)) +
      b (m (-1 + m + 2 qC - 2 m qC) r + (-1 + a - √((b + (-1 + a) m)^2 - 4 b m (-1 + a + b m)
                qC + 4 b^2 m^2 qC^2)) √(((-1 + m)^2 (1 + m) (b^2 (1 + m) + 2 b m (-1 + 2 qC) r +
                  r (2 √((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) +
                √((b + (-1 + a) m)^2 - 4 b m (-1 + a + b m) qC + 4 b^2 m^2 qC^2))^2))) / ((-1 + m)
      (-b + m (-1 + a + 2 b (-1 + qC)) + √((b + (-1 + a) m)^2 - 4 b m (-1 + a + b m) qC + 4 b^2 m^2 qC^2))
      r), 1},
  {-((-1 + m) ((-1 + a) m + √((b + (-1 + a) m)^2 - 4 b m (-1 + a + b m) qC + 4 b^2 m^2 qC^2)) r +
       b^2 (-1 + m^2 + m (1 - 2 qC)
           √(((-1 + m)^2 (1 + m) (b^2 (1 + m) + 2 m (-1 + a - b + 2 b qC) r + 2 √((b + (-1 + a) m)^2 -
                       4 b m (-1 + a + b m) qC + 4 b^2 m^2 qC^2) r + (1 + m) r^2)) / (1 - a + b m
                 (-1 + 2 qC) + √((b + (-1 + a) m)^2 - 4 b m (-1 + a + b m) qC + 4 b^2 m^2 qC^2))^2)) +
       b ((-1 + m) m (-1 + 2 qC) r + (-1 + a - √((b + (-1 + a) m)^2 - 4 b m (-1 + a + b m) qC +
                 4 b^2 m^2 qC^2)) √(((-1 + m)^2 (1 + m) (b^2 (1 + m) + 2 b m (-1 + 2 qC) r +
                   r (2 √((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) +
                 √((b + (-1 + a) m)^2 - 4 b m (-1 + a + b m) qC + 4 b^2 m^2 qC^2))^2))) / ((-1 + m)
       (-b + m (-1 + a + 2 b (-1 + qC)) + √((b + (-1 + a) m)^2 - 4 b m (-1 + a + b m) qC + 4 b^2 m^2 qC^2))
       r), 1}}}
```

```
uPolymContDef = FullSimplify[
   Eigenvectors[Transpose[LaddPolymCont]][[2]], Assumptions → genericAssumpt];
```

Get the normed eigenvectors.

```
uPolymCont = FullSimplify[uPolymContDef / Total[uPolymContDef],
   Assumptions → Flatten[{genericAssumpt}]];
```

```
uPolymCont // MatrixForm
```

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

```
kPolymCont = Simplify[
   Sum[uPolymCont⟦i⟧ vPolymContDef⟦i⟧, {i, 1, 2}], Assumptions → genericAssumpt];
vPolymCont = Simplify[
   Table[vPolymContDef⟦i⟧ / kPolymCont, {i, 1, 2}], Assumptions → genericAssumpt];
uPolymContDef.LaddPolymCont == uPolymContDef * νPolymCont // Simplify
```

```
True
```

```
LaddPolymCont.vPolymContDef == vPolymContDef * νPolymCont // Simplify
```

```
True
```

```
uPolymCont.LaddPolymCont == uPolymCont * νPolymCont // Simplify
```

```
True
```

```
LaddPolymCont.vPolymCont == vPolymCont * νPolymCont // Simplify
```

```
True
```

The following is required according to Haccou *et al.* (2005, p.127), and we check that it holds.

```
Total[uPolymCont] // FullSimplify
```

```
1
```

```
Sum[uPolymCont⟦i⟧ vPolymCont⟦i⟧, {i, 1, 2}] // Simplify
```

```
1
```

■ The limit matrix

The limit matrix (the evaluation immediately below takes some time, therefore we hard-code the definition below):

```
BPolymCont =
  Simplify[Sum[uPolymCont⟦h⟧ * Sum[vPolymCont⟦j⟧ LaddPolymCont⟦h, j⟧, {j, 1, 2}], {h, 1, 2}] +
    νPolymCont (νPolymCont - 1) Sum[uPolymCont⟦j⟧ * vPolymCont⟦j⟧^2, {j, 1, 2}],
   Assumptions → genericAssumpt];
```

```
$Aborted
```

```
BPolymCont = Sum[uPolymCont⟦h⟧ * Sum[vPolymCont⟦j⟧ LaddPolymCont⟦h, j⟧, {j, 1, 2}], {h, 1, 2}] +
  νPolymCont (νPolymCont - 1) Sum[uPolymCont⟦j⟧ * vPolymCont⟦j⟧^2, {j, 1, 2}]
```

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

```
<<1>>
```

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

$$\text{BPolymCont} = \frac{1}{2}\left(\frac{2}{(-1+a)^2-b^2}-\frac{1}{(-1+a)^2-b^2}\left(-b^2\ (-1+m)+m+a^2\ m+\sqrt{(b+(-1+a)\ m)^2-4\ b\ m\ (-1+a+b\ m}\right.\right.$$

This is analogous to equation (1), but for a polymorphic continent.

νPolymCont

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

Letting Q_h be the extinction probability if the population starts with type h, T5.6_HJV2005 states that, as $\xi \to 0$, $Q_h = Q_h(\xi) \to 1$, and

$$\pi_h(\xi) = 1 - Q_h(\xi) = \frac{2\,(\nu(\xi)-1)}{B(\xi)}\,v_h(\xi) + o(\xi). \tag{4}$$

Further, Haccou *et al.* (2005) state that, provided B(ξ) → B(0) and also the eigenvector v(ξ) → v (0) as $\xi \to 0$, one can conclude that

$$1 - Q_h(\xi) = \frac{2\,(\nu(\xi)-1)}{B\,(0)}\,v_h(0) + o(\xi). \tag{5}$$

Note that in the manuscript and, sometimes, in other *Mathematica* Notebooks, we use s_i instead of Q_i.

- **Application**
- Analytical expressions without further approximation

The equilibrium frequency of allele B_1 (see *Mathematica* Notebook 120309_twoLocusContinentIslandDiscreteStochastic.nb for a derivation):

qHatBPolymContRule

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

```
π1PolymCont = (2 (νPolymCont - 1) / BPolymCont) vPolymCont[[1]];
π2PolymCont = (2 (νPolymCont - 1) / BPolymCont) vPolymCont[[2]];
πAvPolymCont = qHatB * π1PolymCont + (1 - qHatB) * π2PolymCont /. qHatBPolymContRule;
```

assumeSmallForces

$\{a \to \alpha\,\epsilon,\ b \to \beta\,\epsilon,\ r \to \epsilon\,\rho,\ m \to \epsilon\,\mu,\ \gamma 11 \to g11\,\epsilon,\ \gamma 12 \to g12\,\epsilon,\ \gamma 21 \to g21\,\epsilon,\ \gamma 22 \to g22\,\epsilon\}$

backSubstSmallForces

$$\left\{\alpha \to \frac{a}{\epsilon},\ \beta \to \frac{b}{\epsilon},\ \rho \to \frac{r}{\epsilon},\ \mu \to \frac{m}{\epsilon},\ g11 \to \frac{\gamma 11}{\epsilon},\ g12 \to \frac{\gamma 12}{\epsilon},\ g21 \to \frac{\gamma 21}{\epsilon},\ g22 \to \frac{\gamma 22}{\epsilon}\right\}$$

- Algebraic rearrangements

```
R1Rule = R1 → √(-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2);

R1 - √((-1 + a)^2 m^2 - 2 (-1 + a) b m (-1 + 2 qC) + b^2 (1 + 4 m^2 (-1 + qC) qC)) /. R1Rule // Simplify
0

FullSimplify[Reduce[-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2 ≥ 0],
 Assumptions → Flatten[{genericAssumpt, 0 ≤ qC ≤ 1}]]
True

R2a = (-1 + m)^2 (1 + m) (b^2 (1 + m) + 2 b m (-1 + 2 qC) r + r (r + m (-2 + 2 a + r) + 2 R1));

FullSimplify[Reduce[R2a ≥ 0], Assumptions → Flatten[{genericAssumpt, 0 ≤ qC ≤ 1, 0 ≤ R2}]]
$Aborted

R2Rule = R2 → √(((-1 + m)^2 (1 + m) (b^2 (1 + m) + 2 b m (-1 + 2 qC) r + r (r + m (-2 + 2 a + r) + 2 R1))) /
      (1 - a + b m (-1 + 2 qC) + R1)^2);

(-1 + m)^2 (1 + m) (b^2 (1 + m) + 2 b m (-1 + 2 qC) r + r (r + m (-2 + 2 a + r) + 2 R1)) -
  ((-1 + m)^2 (1 + m) (b^2 (1 + m) + 2 b m (-1 + 2 qC) r + r (r + m (-2 + 2 a + r) + 2 R1))) // Simplify
0

(-1 + m)^2 (1 + m) (b^2 (1 + m) + 2 m (-1 + a - b + 2 b qC) r + (1 + m) r^2 + 2 r R1) -
  ((-1 + m)^2 (1 + m) (b^2 (1 + m) + 2 b m (-1 + 2 qC) r + r (r + m (-2 + 2 a + r) + 2 R1))) // Simplify
0

FullSimplify[Series[R1 /. R1Rule /. assumeSmallForces /. {qC → χC ϵ}, {ϵ, 0, 2}] /.
    backSubstSmallForces /. {χC → qC / ϵ},
  Assumptions → Flatten[{genericAssumpt, 0 ≤ qC ≤ 1}]] // Normal

(b + (-1 + a) m) Sign[b - m] + (2 b m qC Sign[b - m])/(b - m)

Simplify[π1PolymCont /. {√((b + (-1 + a) m)^2 - 4 b m (-1 + a + b m) qC + 4 b^2 m^2 qC^2) → R1,
     √(-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2) → R1,
     √((-1 + a)^2 m^2 - 2 (-1 + a) b m (-1 + 2 qC) + b^2 (1 + 4 m^2 (-1 + qC) qC)) → R1} /.
   {√(((-1 + m)^2 (1 + m) (b^2 (1 + m) + 2 b m (-1 + 2 qC) r + r (r + m (-2 + 2 a + r) + 2 R1))) /
        (1 - a + b m (-1 + 2 qC) + R1)^2) → R2,
    √(((-1 + m)^2 (1 + m) (b^2 (1 + m) + 2 m (-1 + a + b (-1 + 2 qC)) r + (1 + m) r^2 + 2 r R1)) /
        (1 - a + b m (-1 + 2 qC) + R1)^2) → R2,
    √(((-1 + m)^2 (1 + m) (b^2 (1 + m) + 2 m (-1 + a - b + 2 b qC) r + (1 + m) r^2 + 2 r R1)) /
        (1 - a + b m (-1 + 2 qC) + R1)^2) → R2,
    √(((-1 + m)^2 (1 + m) (b^2 (1 + m) + 2 b m (-1 + 2 qC) r + r (r + m (-2 + 2 a + r) + 2 R1))) /
        (1 - a - b m + 2 b m qC + R1)^2) → R2},
 Assumptions → Flatten[{genericAssumpt, 0 ≤ R1, 0 ≤ qC ≤ 1}]]
```

$$
\begin{aligned}
&(4 b^2 (-m - r + b m (-1 + 2 qC + r - 2 qC r) - R1 + r R1 + \\
&\quad a (2 + m (2 - b + 2 b qC) + r - R1 - 2 R2) + b^2 (1 + m - R2) + R2 + a^2 (-2 - m + R2)) \\
&\quad ((-1 + m) r ((-1 + a) m + R1) + b ((-1 + m) m (-1 + 2 qC) r + (-1 + a - R1) R2) + \\
&\quad b^2 (-1 + m^2 + m (R2 - 2 qC R2))) (r - m^2 r + (1 - a + R1) R2 + b (1 - m (m + R2 - 2 qC R2))) \\
&\quad ((-1 + m)^2 r^2 (-b + m (-1 + a + 2 b (-1 + qC)) + R1) - \\
&\quad ((-1 + m) r ((-1 + a) m + R1) + b (m^2 (-1 + 2 qC) r + m (r - 2 qC r) + (-1 + a - R1) R2) + \\
&\quad b^2 (-1 + m^2 + m (R2 - 2 qC R2)))^2 / (b + (-1 + a) m + 2 b m qC + R1))) / \\
&((1 - 2 a + a^2 - b^2) (b + (-1 + a) m + 2 b m qC + R1) (2 (-1 + m) r^2 (-b + m (-1 + a + 2 b (-1 + qC)) + R1) \\
&\quad (-((-1 + m)^2 (b^2 (-1 + 2 m (-1 + qC)) - r ((-1 + a) m + R1) + b (2 - r + m (1 + a - 2 qC r) + \\
&\quad R1))) / (1 - a + b m (-1 + 2 qC) + R1) + ((b + (-1 + a) m - 2 b m qC + R1) \\
&\quad ((-1 + m) r ((-1 + a) m + R1) + b ((-1 + m) m (-1 + 2 qC) r + (-1 + a - R1) R2) + \\
&\quad b^2 (-1 + m^2 + m (R2 - 2 qC R2)))) / ((1 - a + b) (b + (-1 + a) m + 2 b m qC + R1))) \\
&\quad ((-1 + m)^2 r^2 (-b + m (-1 + a + 2 b (-1 + qC)) + R1) - \\
&\quad ((-1 + m) r ((-1 + a) m + R1) + b (m^2 (-1 + 2 qC) r + m (r - 2 qC r) + (-1 + a - R1) R2) + \\
&\quad b^2 (-1 + m^2 + m (R2 - 2 qC R2)))^2 / (b + (-1 + a) m + 2 b m qC + R1)) + \\
&\quad 2 (-1 + m) ((1 - m) r ((-1 + a) m + R1) + b (m (-1 + m + 2 qC - 2 m qC) r + (1 - a + R1) R2) + \\
&\quad b^2 (1 - m (m + R2 - 2 qC R2))) \left(\frac{r^2 (-b + m (-1 + a - 2 b (-1 + qC)) + R1)}{-1 + a + b} - \right. \\
&\quad ((b^2 (1 + 2 m qC) + r ((-1 + a) m + R1) + b (2 - r + m (1 + a + 2 (-1 + qC) r) + R1)) \\
&\quad ((-1 + m) r ((-1 + a) m + R1) + b ((-1 + m) m (-1 + 2 qC) r + (-1 + a - R1) R2) + \\
&\quad b^2 (-1 + m^2 + m (R2 - 2 qC R2)))) / \\
&\quad \left. ((b + (-1 + a) m + 2 b m qC + R1) (1 - a + b m (-1 + 2 qC) + R1))\right) \\
&\quad ((-1 + m)^2 r^2 (-b + m (-1 + a + 2 b (-1 + qC)) + R1) - \\
&\quad ((-1 + m) r ((-1 + a) m + R1) + b (m^2 (-1 + 2 qC) r + m (r - 2 qC r) + (-1 + a - R1) R2) + \\
&\quad b^2 (-1 + m^2 + m (R2 - 2 qC R2)))^2 / (b + (-1 + a) m + 2 b m qC + R1)) + \\
&\quad 1 / (1 - 2 a + a^2 - b^2) b^2 \left(\frac{2}{(-1 + a)^2 - b^2} - \frac{1}{(-1 + a)^2 - b^2} (-b^2 (-1 + m) + m + a^2 m + \right. \\
&\quad \left. b m (-1 + 2 qC) (-1 + r) + r + R1 - r R1 + a (2 + m (-2 + b - 2 b qC) - r + R1)) + R2\right) \\
&\quad (-m - r + b m (-1 + 2 qC + r - 2 qC r) - R1 + r R1 + a (2 + m (2 - b + 2 b qC) + r - R1 - 2 R2) + \\
&\quad b^2 (1 + m - R2) + R2 + a^2 (-2 - m + R2)) \\
&\quad (r - m^2 r + (1 - a + R1) R2 + b (1 - m (m + R2 - 2 qC R2))) \\
&\quad ((-1 + m)^3 r^3 (-b + m (-1 + a + 2 b (-1 + qC)) + R1) - \\
&\quad ((-1 + m) r ((-1 + a) m + R1) + b (m^2 (-1 + 2 qC) r + m (r - 2 qC r) + (-1 + a - R1) R2) + \\
&\quad b^2 (-1 + m^2 + m (R2 - 2 qC R2)))^3 / (b + (-1 + a) m + 2 b m qC + R1)^2)))
\end{aligned}
$$

We know that the radicand of R_1 is always non-negative, which means that R_1 is real.

```
Simplify[π2PolymCont /. {√((b + (-1 + a) m)^2 - 4 b m (-1 + a + b m) qC + 4 b^2 m^2 qC^2) → R1,
    √(-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2) → R1,
    √((-1 + a)^2 m^2 - 2 (-1 + a) b m (-1 + 2 qC) + b^2 (1 + 4 m^2 (-1 + qC) qC)) → R1} /.
  {√(((-1 + m)^2 (1 + m) (b^2 (1 + m) + 2 b m (-1 + 2 qC) r + r (r + m (-2 + 2 a + r) + 2 R1))) /
        (1 - a + b m (-1 + 2 qC) + R1)^2) → R2,
    √(((-1 + m)^2 (1 + m) (b^2 (1 + m) + 2 m (-1 + a + b (-1 + 2 qC)) r + (1 + m) r^2 + 2 r R1)) /
        (1 - a + b m (-1 + 2 qC) + R1)^2) → R2,
    √(((-1 + m)^2 (1 + m) (b^2 (1 + m) + 2 m (-1 + a - b + 2 b qC) r + (1 + m) r^2 + 2 r R1)) /
        (1 - a + b m (-1 + 2 qC) + R1)^2) → R2,
    √(((-1 + m)^2 (1 + m) (b^2 (1 + m) + 2 b m (-1 + 2 qC) r + r (r + m (-2 + 2 a + r) + 2 R1))) /
        (1 - a - b m + 2 b m qC + R1)^2) → R2},
  Assumptions → Flatten[{genericAssumpt, 0 ≤ R1, 0 ≤ qC ≤ 1}]]
```

$$\Big(4 b^2 (-1+m) r \Big(-m - r + b m (-1 + 2 qC + r - 2 qC r) - R1 + r R1 + a (2 + m (2 - b + 2 b qC) + r - R1 - 2 R2) + b^2 (1 + m - R2) + R2 + a^2 (-2 - m + R2)\Big) \Big(r - m^2 r + (1 - a + R1) R2 + b (1 - m (m + R2 - 2 qC R2))\Big) \Big((-1+m)^2 r^2 (-b + m (-1 + a + 2 b (-1 + qC)) + R1) - \Big((-1+m) r ((-1+a) m + R1) + b \Big(m^2 (-1 + 2 qC) r + m (r - 2 qC r) + (-1 + a - R1) R2\Big) + b^2 \Big(-1 + m^2 + m (R2 - 2 qC R2)\Big)\Big)^2 \Big/ (b + (-1+a) m + 2 b m qC + R1)\Big)\Big) \Big/$$

$$\Bigg(\Big(1 - 2 a + a^2 - b^2\Big) \Bigg(2 (-1+m) r^2 (-b + m (-1 + a + 2 b (-1 + qC)) + R1) \Big(-\Big((-1+m)^2 \Big(b^2 (-1 + 2 m (-1 + qC)) - r ((-1+a) m + R1) + b (2 - r + m (1 + a - 2 qC r) + R1)\Big)\Big) \Big/ (1 - a + b m (-1 + 2 qC) + R1) + \Big((b + (-1+a) m - 2 b m qC + R1) \Big((-1+m) r ((-1+a) m + R1) + b ((-1+m) m (-1 + 2 qC) r + (-1 + a - R1) R2) + b^2 \Big(-1 + m^2 + m (R2 - 2 qC R2)\Big)\Big)\Big) \Big/ ((1 - a + b) (b + (-1+a) m + 2 b m qC + R1))\Big) \Big((-1+m)^2 r^2 (-b + m (-1 + a + 2 b (-1 + qC)) + R1) - \Big((-1+m) r ((-1+a) m + R1) + b \Big(m^2 (-1 + 2 qC) r + m (r - 2 qC r) + (-1 + a - R1) R2\Big) + b^2 \Big(-1 + m^2 + m (R2 - 2 qC R2)\Big)\Big)^2 \Big/ (b + (-1+a) m + 2 b m qC + R1)\Big) + 2 (-1+m) \Big((1-m) r ((-1+a) m + R1) + b (m (-1 + m + 2 qC - 2 m qC) r + (1 - a + R1) R2) + b^2 (1 - m (m + R2 - 2 qC R2))\Big) \Bigg(\frac{r^2 (-b + m (-1 + a - 2 b (-1 + qC)) + R1)}{-1 + a + b} - \Big(\Big(b^2 (1 + 2 m qC) + r ((-1+a) m + R1) + b (2 - r + m (1 + a + 2 (-1 + qC) r) + R1)\Big) \Big((-1+m) r ((-1+a) m + R1) + b ((-1+m) m (-1 + 2 qC) r + (-1 + a - R1) R2) + b^2 \Big(-1 + m^2 + m (R2 - 2 qC R2)\Big)\Big)\Big) \Big/ ((b + (-1+a) m + 2 b m qC + R1) (1 - a + b m (-1 + 2 qC) + R1))\Bigg) \Big((-1+m)^2 r^2 (-b + m (-1 + a + 2 b (-1 + qC)) + R1) - \Big((-1+m) r ((-1+a) m + R1) + b \Big(m^2 (-1 + 2 qC) r + m (r - 2 qC r) + (-1 + a - R1) R2\Big) + b^2 \Big(-1 + m^2 + m (R2 - 2 qC R2)\Big)\Big)^2 \Big/ (b + (-1+a) m + 2 b m qC + R1)\Big) + 1 \Big/ \Big(1 - 2 a + a^2 - b^2\Big) b^2 \Bigg(\frac{2}{(-1+a)^2 - b^2} - \frac{1}{(-1+a)^2 - b^2} \Big(-b^2 (-1+m) + m + a^2 m + b m (-1 + 2 qC) (-1 + r) + r + R1 - r R1 + a (2 + m (-2 + b - 2 b qC) - r + R1)\Big) + R2\Bigg) \Big(-m - r + b m (-1 + 2 qC + r - 2 qC r) - R1 + r R1 + a (2 + m (2 - b + 2 b qC) + r - R1 - 2 R2) + b^2 (1 + m - R2) + R2 + a^2 (-2 - m + R2)\Big) \Big(r - m^2 r + (1 - a + R1) R2 + b (1 - m (m + R2 - 2 qC R2))\Big) \Big((-1+m)^3 r^3 (-b + m (-1 + a + 2 b (-1 + qC)) + R1) - \Big((-1+m) r ((-1+a) m + R1) + b \Big(m^2 (-1 + 2 qC) r + m (r - 2 qC r) + (-1 + a - R1) R2\Big) + b^2 \Big(-1 + m^2 + m (R2 - 2 qC R2)\Big)\Big)^3 \Big/ (b + (-1+a) m + 2 b m qC + R1)^2\Big)\Bigg)\Bigg)$$

```
Simplify[πAvPolymCont /. {√((b + (-1 + a) m)^2 - 4 b m (-1 + a + b m) qC + 4 b^2 m^2 qC^2) → R1,
    √(-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2) → R1,
    √((-1 + a)^2 m^2 - 2 (-1 + a) b m (-1 + 2 qC) + b^2 (1 + 4 m^2 (-1 + qC) qC)) → R1} /.
  {√(((-1 + m)^2 (1 + m) (b^2 (1 + m) + 2 b m (-1 + 2 qC) r + r (r + m (-2 + 2 a + r) + 2 R1))) /
       (1 - a + b m (-1 + 2 qC) + R1)^2) → R2,
   √(((-1 + m)^2 (1 + m) (b^2 (1 + m) + 2 m (-1 + a + b (-1 + 2 qC)) r + (1 + m) r^2 + 2 r R1)) /
       (1 - a + b m (-1 + 2 qC) + R1)^2) → R2,
   √(((-1 + m)^2 (1 + m) (b^2 (1 + m) + 2 m (-1 + a - b + 2 b qC) r + (1 + m) r^2 + 2 r R1)) /
       (1 - a + b m (-1 + 2 qC) + R1)^2) → R2,
   √(((-1 + m)^2 (1 + m) (b^2 (1 + m) + 2 b m (-1 + 2 qC) r + r (r + m (-2 + 2 a + r) + 2 R1))) /
       (1 - a - b m + 2 b m qC + R1)^2) → R2},
 Assumptions → Flatten[{genericAssumpt, 0 ≤ R1, 0 ≤ qC ≤ 1}]]
```

```
(2 b^2 (-m - r + b m (-1 + 2 qC + r - 2 qC r) - R1 + r R1 +
      a (2 + m (2 - b + 2 b qC) + r - R1 - 2 R2) + b^2 (1 + m - R2) + R2 + a^2 (-2 - m + R2))
   ((-1 + m^2) r + (-1 + a - R1) R2 + b (-1 + m^2 + m (R2 - 2 qC R2)))
   (r - m^2 r + (1 - a + R1) R2 + b (1 - m (m + R2 - 2 qC R2)))
   ((-1 + m)^2 r^2 (-b + m (-1 + a + 2 b (-1 + qC)) + R1) -
     ((-1 + m) r ((-1 + a) m + R1) + b (m^2 (-1 + 2 qC) r + m (r - 2 qC r) + (-1 + a - R1) R2) +
         b^2 (-1 + m^2 + m (R2 - 2 qC R2)))^2 / (b + (-1 + a) m + 2 b m qC + R1))) /
 ((1 - 2 a + a^2 - b^2) (1 + m) (2 (-1 + m) r^2 (-b + m (-1 + a + 2 b (-1 + qC)) + R1)
       (-((-1 + m)^2 (b^2 (-1 + 2 m (-1 + qC)) - r ((-1 + a) m + R1) + b (2 - r + m (1 + a - 2 qC r) +
                R1))) / (1 - a + b m (-1 + 2 qC) + R1) + ((b + (-1 + a) m - 2 b m qC + R1)
            ((-1 + m) r ((-1 + a) m + R1) + b ((-1 + m) m (-1 + 2 qC) r + (-1 + a - R1) R2) +
             b^2 (-1 + m^2 + m (R2 - 2 qC R2)))) / ((1 - a + b) (b + (-1 + a) m + 2 b m qC + R1)))
       ((-1 + m)^2 r^2 (-b + m (-1 + a + 2 b (-1 + qC)) + R1) -
         ((-1 + m) r ((-1 + a) m + R1) + b (m^2 (-1 + 2 qC) r + m (r - 2 qC r) + (-1 + a - R1) R2) +
             b^2 (-1 + m^2 + m (R2 - 2 qC R2)))^2 / (b + (-1 + a) m + 2 b m qC + R1)) +
     2 (-1 + m) ((1 - m) r ((-1 + a) m + R1) + b (m (-1 + m + 2 qC - 2 m qC) r + (1 - a + R1) R2) +
         b^2 (1 - m (m + R2 - 2 qC R2))) ((r^2 (-b + m (-1 + a - 2 b (-1 + qC)) + R1)) / (-1 + a + b) -
         ((b^2 (1 + 2 m qC) + r ((-1 + a) m + R1) + b (2 - r + m (1 + a + 2 (-1 + qC) r) + R1))
            ((-1 + m) r ((-1 + a) m + R1) + b ((-1 + m) m (-1 + 2 qC) r + (-1 + a - R1) R2) +
              b^2 (-1 + m^2 + m (R2 - 2 qC R2)))) /
          ((b + (-1 + a) m + 2 b m qC + R1) (1 - a + b m (-1 + 2 qC) + R1)))
       ((-1 + m)^2 r^2 (-b + m (-1 + a + 2 b (-1 + qC)) + R1) -
         ((-1 + m) r ((-1 + a) m + R1) + b (m^2 (-1 + 2 qC) r + m (r - 2 qC r) + (-1 + a - R1) R2) +
             b^2 (-1 + m^2 + m (R2 - 2 qC R2)))^2 / (b + (-1 + a) m + 2 b m qC + R1)) +
     1 / (1 - 2 a + a^2 - b^2) b^2 (2 / ((-1 + a)^2 - b^2) - 1 / ((-1 + a)^2 - b^2) (-b^2 (-1 + m) + m + a^2 m +
             b m (-1 + 2 qC) (-1 + r) + r + R1 - r R1 + a (2 + m (-2 + b - 2 b qC) - r + R1)) + R2)
       (-m - r + b m (-1 + 2 qC + r - 2 qC r) - R1 + r R1 + a (2 + m (2 - b + 2 b qC) + r - R1 - 2 R2) +
         b^2 (1 + m - R2) + R2 + a^2 (-2 - m + R2))
       (r - m^2 r + (1 - a + R1) R2 + b (1 - m (m + R2 - 2 qC R2)))
       ((-1 + m)^3 r^3 (-b + m (-1 + a + 2 b (-1 + qC)) + R1) -
         ((-1 + m) r ((-1 + a) m + R1) + b (m^2 (-1 + 2 qC) r + m (r - 2 qC r) + (-1 + a - R1) R2) +
             b^2 (-1 + m^2 + m (R2 - 2 qC R2)))^3 / (b + (-1 + a) m + 2 b m qC + R1)^2)))
```

- Assume weak evolutionary forces (attempt without success)

Inspection of π_1, π_2 and π_{Av} shows that these are big terms. Therefore we are going to approximate them by assuming small evolutionary forces.

```
π1PolymCont /. assumeSmallForces /. {qC → χC ϵ};

Simplify[π1PolymCont /. assumeSmallForces /. {qC → χC ϵ}, Assumptions → genericAssumpt]

$Aborted
```

This takes more than an hour on a Mac mini 2.3 GHz Intel Core i5 with 4 GB RAM.

```
term1PolymCont =
 Series[π1PolymCont /. assumeSmallForces /. {qC → χC ϵ}, {ϵ, 0, 1}] // Normal
```

$Aborted

- Remark

At this point, we realise that analytical expressions become nasty, containing square roots of square roots and multiple divisions. This makes it difficult to take derivatives and approximate the expressions by Taylor Series expansion. As an alternative, we start with a mean matrix with approximate entries – rather than with the exact one – and then follow the steps in T5.6_HJV2005. This is done in the section that starts after the following paragraph with plots.

Additive fitness and polymorphic continent, approximate mean matrix

- **Preliminaries**

Recall the eigenvalues of the approximate mean matrix:

```
νPolymContAx
```

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

For small forces, the second eigenvalue is the leading one.

- **Identification of ξ**

```
νPolymContAx⟦2⟧
```

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

```
ξPolymContAxRule =
 FullSimplify[Solve[νPolymContAx⟦2⟧ == 1 + ξ, ξ], Assumptions → Flatten[{genericAssumpt}]]
```

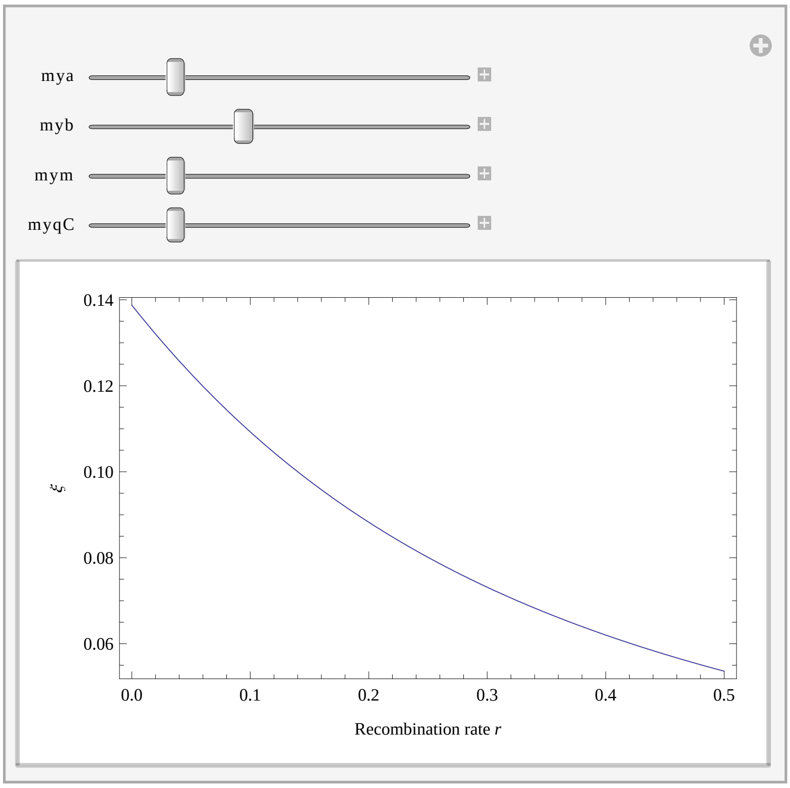
$$\left\{\left\{\xi\to a+\frac{1}{2}\left(-m-\sqrt{(b-m)^2+4\,b\,m\,qC}-r+\sqrt{b^2+r\left(-2\,m+2\sqrt{(b-m)^2+4\,b\,m\,qC}+r\right)}\right)\right\}\right\}$$

The branching process for a polymorphic continent and weak evolutionary forces is slightly supercritical if ξ is small, where

$$\xi \approx a-\frac{1}{2}\left[m+r+\sqrt{R'_3}-\sqrt{b^2-r\left(2\,m-r-2\sqrt{R'_3}\right)}\,\right], \tag{6}$$

where $R'_3=(b-m)^2+4\,b\,m\,q_c>0$.

```
Manipulate[Plot[ξAddPolymContApproxFunc[mya, myb, mym, r, myqC],
  {r, 0, 0.5}, Frame → True, FrameLabel → {"Recombination rate r", "ξ"}],
 {{mya, 0.2}, 0, 1}, {{myb, 0.4}, 0, 1}, {{mym, 0.2}, 0, 1}, {{myqC, 0.2}, 0, 1}]
```



■ Eigenvectors and their normalisation

The right and left leading eigenvectors:

The second one is the leading eigenvector (belonging to the dominant eigenvalue).

```
vPolymContAxDef = FullSimplify[Eigenvectors[LaddPolymContAx][[2]],
  Assumptions → Flatten[{genericAssumpt, 0 ≤ qC ≤ 1}]]
```

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Recall: The left eigenvectors of a matrix A are obtained as the right eigenvectors of the transpose of A.

```
FullSimplify[Eigensystem[Transpose[LaddPolymContAx]],
 Assumptions → Flatten[{genericAssumpt, 0 ≤ qC ≤ 1}]]
```

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

```
uPolymContAxDef = FullSimplify[Eigenvectors[Transpose[LaddPolymContAx]][[2]],
  Assumptions → Flatten[{genericAssumpt, 0 ≤ qC ≤ 1}]]
```

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

Get the normed eigenvectors.

```
uPolymContAx = FullSimplify[uPolymContAxDef / Total[uPolymContAxDef],
  Assumptions → Flatten[{genericAssumpt, 0 ≤ qC ≤ 1}]]
```

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

```
uPolymContAx // MatrixForm
```

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

```
kPolymContAx = FullSimplify[Sum[uPolymContAx[[i]] vPolymContAxDef[[i]], {i, 1, 2}],
  Assumptions → Flatten[{genericAssumpt, 0 ≤ qC ≤ 1}]]
```

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

```
vPolymContAx = FullSimplify[Table[vPolymContAxDef[[i]] / kPolymContAx, {i, 1, 2}],
  Assumptions → Flatten[{genericAssumpt, 0 ≤ qC ≤ 1}]]
```

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

```
Simplify[uPolymContAxDef.LaddPolymContAx == uPolymContAxDef * νPolymContAx⟦2⟧,
 Assumptions → Flatten[{genericAssumpt, 0 ≤ qC ≤ 1}]]
```

```
True
```

```
FullSimplify[LaddPolymContAx.vPolymContAxDef == vPolymContAxDef * νPolymContAx⟦2⟧,
 Assumptions → Flatten[{genericAssumpt, 0 ≤ qC ≤ 1}]]
```

```
True
```

```
FullSimplify[uPolymContAx.LaddPolymContAx == uPolymContAx * νPolymContAx⟦2⟧,
 Assumptions → Flatten[{genericAssumpt, 0 ≤ qC ≤ 1}]]
```

```
True
```

```
FullSimplify[LaddPolymContAx.vPolymContAx == vPolymContAx * νPolymContAx⟦2⟧,
 Assumptions → Flatten[{genericAssumpt, 0 ≤ qC ≤ 1}]]
```

```
True
```

The following is required according to Haccou *et al.* (2005, p.127), and we check that it holds.

```
Total[uPolymContAx] // FullSimplify
```

```
1
```

```
Sum[uPolymContAx⟦i⟧ vPolymContAx⟦i⟧, {i, 1, 2}] // Simplify
```

```
1
```

■ The limit matrix

The limit matrix (the evaluation immediately below takes some time, therefore we hard-code the definition below):

```
BPolymContAx = FullSimplify[
   Sum[uPolymContAx⟦h⟧ * Sum[vPolymContAx⟦j⟧ LaddPolymContAx⟦h, j⟧, {j, 1, 2}], {h, 1, 2}] +
```

```
  νPolymContAx⟦2⟧ (νPolymContAx⟦2⟧ - 1) Sum[uPolymContAx⟦j⟧ * vPolymContAx⟦j⟧^2, {j, 1, 2}],
 Assumptions → Flatten[{genericAssumpt, 0 ≤ qC ≤ 1}]];
```

$$\text{BPolymContAx} = -\left(\left(b-m+\sqrt{(b-m)^2+4\ b\ m\ qC}\right)\ r\ \left(b+r-\sqrt{b^2+r\ \left(-2\ m+2\ \sqrt{(b-m)^2+4\ b\ m\ qC}+r\right)}\right)\ \left(-\right.\right.$$

This is analogous to eq. (1), but for a monomorphic continent. In addition, the entries of the mean matrix L were approximated assuming weak evolutionary forces.

νPolymContAx⟦2⟧

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

Letting Q_h be the extinction probability if the population starts with type h, T5.6_HJV2005 states that, as $\xi \to 0$, $Q_h = Q_h(\xi) \to 1$, and

$$\pi_h(\xi) = 1 - Q_h(\xi) = \frac{2(\nu(\xi-1)}{B(\xi)}\, v_h(\xi) + o(\xi.$$

Further, Haccou *et al.* (2005) state that, provided B(ξ) → B(0) and also the eigenvector v(ϵ) → v (0) as $\xi \to 0$, one can conclude that

$$1 - Q_h(\xi) = \frac{2(\nu(\xi)-1)}{B(0)}\, v_h(0) + o(\xi.$$

Note that in the manuscript and, sometimes, in other *Mathematica* Notebooks, we use s_i instead of Q_i.

Application

Analytical expressions

The equilibrium frequency of allele B_1 (see *Mathematica* Notebook 2LocContIsland_Determ_Discr.nb for a derivation):

qHatBPolymContRule

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

```
FullSimplify[Series[qHatB /. qHatBPolymContRule /. assumeSmallForces, {ϵ, 0, 1}] /.
   backSubstSmallForces, Assumptions → Flatten[{genericAssumpt, 0 ≤ qC ≤ 1}]] // Normal
```

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

```
π1PolymContAx = Simplify[(2 (νPolymContAx⟦2⟧ - 1))/BPolymContAx vPolymContAx⟦1⟧,
   Assumptions → Flatten[{genericAssumpt, 0 ≤ qC ≤ 1}]];
π2PolymContAx = Simplify[(2 (νPolymContAx⟦2⟧ - 1))/BPolymContAx vPolymContAx⟦2⟧,
   Assumptions → Flatten[{genericAssumpt, 0 ≤ qC ≤ 1}]];
πAvPolymContAx = qHatB * π1PolymContAx + (1 - qHatB) * π2PolymContAx /.
   qHatBPolymContRule;
```

Algebraic rearrangement

Some simplification/rearrangement of these results:

R1Rule

$$\text{R1} \to \sqrt{-4\,b\,(-1+a+b)\,m\,(1+m)\,qC+(b+(-1+a)\,m+2\,b\,m\,qC)^2}$$

```
R3Rule := R3 → √((b – m)^2 + 4 b m qC)
R4Rule := R4 → √(b^2 + r (–2 m + r + 2 R3))
```

The following results are approximations, based on the assumption that the branching process is slightly supercritical, *i.e.* the leading eigenvalue of the mean matrix is of the form $1+\epsilon$ with small and positive. Moreover, to simplify the expressions, it was assumed that evolutionary forces are weak (the continental frequency q_c of B_1can be arbitrary, however).

Approximation to the invasion probability of A_1 conditional on occurrence on the beneficial background B_1:

```
π1PolymContAx /. {√((b – m)^2 + 4 b m qC) → R3} /. {√(b^2 + r (–2 m + r + 2 R3)) → R4} // FullSimplify
```

$$\Big(4\, b^2\, (2\, a - m - r - R3 + R4)\, \big(b^2 + r\, (-2\, m + r + 2\, R3 - R4) + b\, R4\big)\, (r\, (-m + R3) + b\, (b + R4))\Big) \Big/ \Big(-b\, r\, (b - m + R3)\, (b + r - R4)\, (-2 - 2\, a + m + r + R3 - R4)\, \big(b^2 + r\, (-2\, m + r + 2\, R3 - R4) + b\, R4\big) + (b - r + R4)\, \big(b^2 + r\, (-2\, m + r + 2\, R3 - R4) + b\, R4\big)\, \big(2\, m\, r^2\, (b - m - 2\, b\, qC + R3) + \big(b^2 + r\, (-m + R3) - b\, (-2 - 2\, a + m + r + R3)\big)\, (r\, (-m + R3) + b\, (b + R4))\big) + b\, (2 + 2\, a - m - r - R3 + R4)\, \left(a + \frac{1}{2}\, (-m - r - R3 + R4)\right) \big(r^2\, (b - m + R3)^2\, (b + r - R4) + (b - r + R4)\, (r\, (-m + R3) + b\, (b + R4))^2\big)\Big)$$

The approximate invasion probability of A_1, conditional on initial occurrence on the B_1 background and assuming weak evolutionary forces, is given by

$$\Big(4\, b^2\, (2\, a - m - r - R_3 + R_4)\, \big(b^2 + r\, (-2\, m + r + 2\, R_3 - R_4) + b\, R_4\big)\, (r\, (-m + R_3) + b\, (b + R_4))\Big) \Big/ \Big(-b\, r\, (b - m + R_3)\, (b + r - R_4)\, (-2 - 2\, a + m + r + R_3\, 3 - R_4)\, \big(b^2 + r\, (-2\, m + r + 2\, R_3 - R_4) + b\, R_4\big) + (b - r + R_4)\, \big(b^2 + r\, (-2\, m + r + 2\, R_3 - R_4) + b\, R_4\big)\, \big(2\, m\, r^2\, (b - m - 2\, b\, q_c + R_3) + \big(b^2 + r\, (-m + R_3) - b\, (-2 - 2\, a + m + r + R_3)\big)\, (r\, (-m + R_3) + b\, (b + R_4))\big) + b\, (2 + 2\, a - m - r - R_3 + R_4)\, \left(a + \frac{1}{2}\, (-m - r - R_3 + R_4)\right) \big(r^2\, (b - m + R_3)^2\, (b + r - R_4) + (b - r + R_4)\, (r\, (-m + R_3) + b\, (b + R_4))^2\big)\Big), \tag{7}$$

where $R_3 = \sqrt{(b-m)^2 + 4\, b\, m\, q_c}$ and $R_4 = \sqrt{b^2 - r\,(2\, m - r - 2\, R_3)}$.

Approximation to the invasion probability of A_1 conditional on occurrence on the deleterious background B_2:

```
π2PolymContAx /. {√((b – m)^2 + 4 b m qC) → R3} /. {√(b^2 + r (–2 m + r + 2 R3)) → R4} // FullSimplify
```

$$\Big(4\, b^2\, r\, (b - m + R3)\, (2\, a - m - r - R3 + R4)\, \big(b^2 + r\, (-2\, m + r + 2\, R3 - R4) + b\, R4\big)\Big) \Big/ \Big(-b\, r\, (b - m + R3)\, (b + r - R4)\, (-2 - 2\, a + m + r + R3 - R4)\, \big(b^2 + r\, (-2\, m + r + 2\, R3 - R4) + b\, R4\big) + (b - r + R4)\, \big(b^2 + r\, (-2\, m + r + 2\, R3 - R4) + b\, R4\big)\, \big(2\, m\, r^2\, (b - m - 2\, b\, qC + R3) + \big(b^2 + r\, (-m + R3) - b\, (-2 - 2\, a + m + r + R3)\big)\, (r\, (-m + R3) + b\, (b + R4))\big) + b\, (2 + 2\, a - m - r - R3 + R4)\, \left(a + \frac{1}{2}\, (-m - r - R3 + R4)\right) \big(r^2\, (b - m + R3)^2\, (b + r - R4) + (b - r + R4)\, (r\, (-m + R3) + b\, (b + R4))^2\big)\Big)$$

The approximate invasion probability of A_1, conditional on initial occurrence on the B_2 background and assuming weak evolutionary forces, is given by

$$\Big(4\, b^2\, r\, (b - m + R_3)\, (2\, a - m - r - R_3 + R_4)\, \big(b^2 + r\, (-2\, m + r + 2\, R_3 - R_4) + b\, R_4\big)\Big) \Big/$$

$$\Big(-b\,r\,(b-m+R_3)\,(b+r-R_4)\,(-2-2\,a+m+r+R_3-R_4)\left(b^2+r\,(-2\,m+r+2\,R_3-R_4)+b\,R_4\right)+ (b-r+R_4)\left(b^2+r\,(-2\,m+r+2\,R_3-R_4)+b\,R_4\right) \left(2\,m\,r^2\,(b-m-2\,b\,q_c+R_3)+\left(b^2+r\,(-m+R_3)-b\,(-2-2\,a+m+r+R_3)\right)(r\,(-m+R_3)+b\,(b+R_4))\right)+ b\,(2+2\,a-m-r-R_3+R_4)\left(a+\frac{1}{2}(-m-r-R_3+R_4)\right) \left(r^2\,(b-m+R_3)^2\,(b+r-R_4)+(b-r+R_4)\,(r\,(-m+R_3)+b\,(b+R_4))^2\right)\Big),$$

where $R_3=\sqrt{(b-m)^2+4\,b\,m\,q_c}$ and $R_4=\sqrt{b^2-r\,(2\,m-r-2\,R_3)}$, as above.

```
denom1 =
  (-b r (b - m + R3) (b + r - R4) (-2 - 2 a + m + r + R3 - R4) (b^2 + r (-2 m + r + 2 R3 - R4) + b R4) +
    (b - r + R4) (b^2 + r (-2 m + r + 2 R3 - R4) + b R4) (2 m r^2 (b - m - 2 b qC + R3) +
       (b^2 + r (-m + R3) - b (-2 - 2 a + m + r + R3)) (r (-m + R3) + b (b + R4))) +
    b (2 + 2 a - m - r - R3 + R4) (a + 1/2 (-m - r - R3 + R4))
     (r^2 (b - m + R3)^2 (b + r - R4) + (b - r + R4) (r (-m + R3) + b (b + R4))^2));

denom2 =
  (-b r (b - m + R3) (b + r - R4) (-2 - 2 a + m + r + R3 - R4) (b^2 + r (-2 m + r + 2 R3 - R4) + b R4) +
    (b - r + R4) (b^2 + r (-2 m + r + 2 R3 - R4) + b R4) (2 m r^2 (b - m - 2 b qC + R3) +
       (b^2 + r (-m + R3) - b (-2 - 2 a + m + r + R3)) (r (-m + R3) + b (b + R4))) +
    b (2 + 2 a - m - r - R3 + R4) (a + 1/2 (-m - r - R3 + R4))
     (r^2 (b - m + R3)^2 (b + r - R4) + (b - r + R4) (r (-m + R3) + b (b + R4))^2));

denom1 - denom2 // Simplify

0
```

We see that the denominator of the two expressions is the same.

```
num1 = (4 b^2 (2 a - m - r - R3 + R4) (b^2 + r (-2 m + r + 2 R3 - R4) + b R4) (r (-m + R3) + b (b + R4)));
num2 = (4 b^2 r (b - m + R3) (2 a - m - r - R3 + R4) (b^2 + r (-2 m + r + 2 R3 - R4) + b R4));
num1 + num2 // Simplify

4 b^2 (2 a - m - r - R3 + R4) (b^2 + r (-2 m + r + 2 R3 - R4) + b R4) (b^2 + 2 r (-m + R3) + b (r + R4))
```

Approximation to the weighted average invasion probability of A_1.

```
πAvPolymContAx /. {Sqrt[(b - m)^2 + 4 b m qC] → R3} /. {Sqrt[b^2 + r (-2 m + r + 2 R3)] → R4} /.
  {Sqrt[-4 b (-1 + a + b) m (1 + m) qC + (b + (-1 + a) m + 2 b m qC)^2] → R1} // FullSimplify
```

$$\Big(2 b^2 (2 a - m - r - R3 + R4) \left(b^2 + r (-2 m + r + 2 R3 - R4) + b R4\right) \left(b^2 (1 + 2 m qC) - r (m (1 + a + 2 m) + R1) + 2 (1 + m) r R3 + ((-1 + a) m + R1) R4 + b (r + R1 + R4 + m (-1 + a + 2 r - 2 qC r + 2 qC R4))\right)\Big) \Big/ \Big((1 + m) \Big(-b r (b - m + R3) (b + r - R4) (-2 - 2 a + m + r + R3 - R4) \left(b^2 + r (-2 m + r + 2 R3 - R4) + b R4\right) + (b - r + R4) \left(b^2 + r (-2 m + r + 2 R3 - R4) + b R4\right) \left(2 m r^2 (b - m - 2 b qC + R3) + \left(b^2 + r (-m + R3) - b (-2 - 2 a + m + r + R3)\right) (r (-m + R3) + b (b + R4))\right) + b (2 + 2 a - m - r - R3 + R4) \left(a + \frac{1}{2} (-m - r - R3 + R4)\right) \left(r^2 (b - m + R3)^2 (b + r - R4) + (b - r + R4) (r (-m + R3) + b (b + R4))^2\right)\Big)\Big)$$

The weighted average invasion probabiity of A_1 for weak evolutionary forces is given by

$$\Big(2 b^2 (2 a - m - r - R_3 + R_4) \left(b^2 + r (-2 m + r + 2 R_3 - R_4) + b R_4\right) \left(b^2 (1 + 2 m q_C) - r (m (1 + a + 2 m) + R_1) + 2 (1 + m) r R_3 + ((-1 + a) m + R_1) R_4 + b (r + R_1 + R_4 + m (-1 + a + 2 r - 2 q_C r + 2 q_C R_4))\right)\Big) \Big/ \Big((1 + m) \Big(-b r (b - m + R_3) (b + r - R_4) (-2 - 2 a + m + r + R_3 - R_4) \left(b^2 + r (-2 m + r + 2 R_3 - R_4) + b R_4\right) + (b - r + R_4) \left(b^2 + r (-2 m + r + 2 R_3 - R_4) + b R_4\right) \left(2 m r^2 (b - m - 2 b q_C + R_3) + \left(b^2 + r (-m + R_3) - b (-2 - 2 a + m + r + R_3)\right) (r (-m + R_3) + b (b + R_4))\right) + b (2 + 2 a - m - r - R_3 + R_4) \left(a + \frac{1}{2} (-m - r - R_3 + R_4)\right) \left(r^2 (b - m + R_3)^2 (b + r - R_4) + (b - r + R_4) (r (-m + R_3) + b (b + R_4))^2\right)\Big)\Big) \tag{9}$$

where R_3 and R_4 are as defined above and $R_1 = \sqrt{4 b (1 - a - b) m (1 + m) q_c + [b - (1 - a) m + 2 b m q_c]^2}$.

```
assumeSmallForces
```

{a → α ϵ, b → β ϵ, r → ϵ ρ, m → ϵ μ, γ11 → g11 ϵ, γ12 → g12 ϵ, γ21 → g21 ϵ, γ22 → g22 ϵ}

```
backSubstSmallForces
```

$\left\{\alpha \to \frac{a}{\epsilon},\ \beta \to \frac{b}{\epsilon},\ \rho \to \frac{r}{\epsilon},\ \mu \to \frac{m}{\epsilon},\ g11 \to \frac{\gamma 11}{\epsilon},\ g12 \to \frac{\gamma 12}{\epsilon},\ g21 \to \frac{\gamma 21}{\epsilon},\ g22 \to \frac{\gamma 22}{\epsilon}\right\}$

- **Plots**
- Invasion probability as a function of recombination rate r

In[131]:=
```
mya2 = 0.02;
myb2 = 0.04;
mym2 = 0.022;
myγ1112 = 0;
myγ1212 = 0;
myγ2112 = 0;
myγ2212 = 0;
myqC2 = 0.1;
parComb2 = {a → mya2, b → myb2, m → mym2, γ111 → myγ1112,
  γ121 → myγ1212, γ211 → myγ2112, γ221 → myγ2212, qC → myqC2}
```

Out[139]= {a → 0.02, b → 0.04, m → 0.022, γ111 → 0, γ121 → 0, γ211 → 0, γ221 → 0, qC → 0.1}

Comparing to the numerical solution for fixed values of a, b and m:

```
Plot[{probEstablAMApproxPolymContFunc[r,
    mym2, mya2, myb2, myγ1112, myγ1212, myγ2112, myγ2212, myqC2][[2]],
  probEstablAMApproxPolymContFunc[r, mym2, mya2, myb2, myγ1112, myγ1212,
    myγ2112, myγ2212, myqC2][[3]], probEstablAMApproxPolymContFunc[
    r, mym2, mya2, myb2, myγ1112, myγ1212, myγ2112, myγ2212, myqC2][[4]],
  π1PolymContFunc[a, b, m, r, qC] /. parComb2, π2PolymContFunc[a, b, m, r, qC] /. parComb2,
  πAvPolymContFunc[a, b, m, r, qC] /. parComb2,
  π1PolymContAxFunc[a, b, m, r, qC] /. parComb2,
  π2PolymContAxFunc[a, b, m, r, qC] /. parComb2,
  πAvPolymContAxFunc[a, b, m, r, qC] /. parComb2}, {r, 0, 0.5},
 PlotRange → {{0, (rCritFunc[mym2, mya2, myb2] /. parComb2)}, {0, 2.5 * mya2}},
 PlotStyle → {{RGBColor[0, 0.3, 1, 0.5]}, {Red}, {Black},
   {RGBColor[0, 0.3, 1, 0.5], DotDashed}, {Red, DotDashed},
   {Black, DotDashed}, {RGBColor[0, 0.3, 1, 0.5], Thick, Dashed},
   {Red, Thick, Dashed}, {Black, Thick, Dashed}},
 LabelStyle → {Directive[FontSize → 14], FontFamily → "Helvetica"},
 AxesLabel → {r, "Invasion probability"}, Frame → True,
 FrameStyle → {{Black, Opacity[0]}, {Black, Opacity[0]}},
 FrameLabel → {"Recombination rate r", "Invasion probability"}]
```

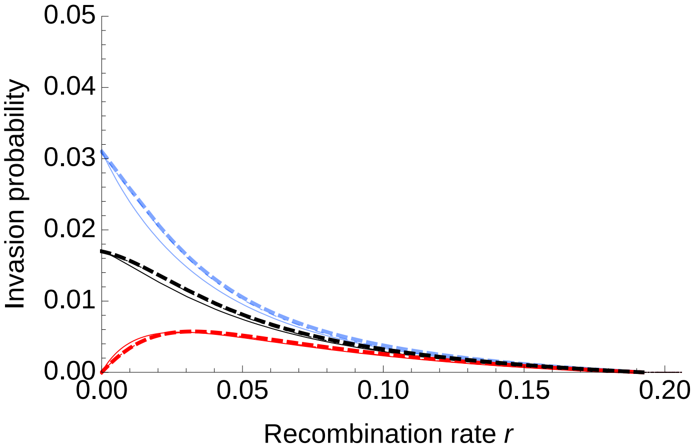


Figure 7: The invasion probability as a function of the recombination rate r for a polymorphic continent ($q_c = 0.1$) and additive fitness effects. Invasion probabilities are shown for A_1 occuring on the beneficial background B_1 (blue), on the deleterious background B_2 (red) and as a weighted average across backgrounds (black), where the weights are determinded by the frequency $\hat{q}_B$ of B_1 at the marginal one-locus migration-selection equilibrium. Analytical approximations assuming a slightly-supercritical branching process (thin dot-dashed lines) and, in addition, weak evolutionary forces (thick dashed lines) are compared to the exact numerical branching-process solution (thin solid lines). Other parameter values are $a = 0.02$, $b = 0.04$, $m = 0.022$ and $q_c = 0.1$.

Comparing to the numerical solution for various values of a, b and m:

In[140]:=
```
Manipulate[
 Plot[
  {probEstablAMApproxPolymContFunc[r, m, a, b, myγ1112, myγ1212, myγ2112, myγ2212, qC][[
    2]], probEstablAMApproxPolymContFunc[r, m, a,
     b, myγ1112, myγ1212, myγ2112, myγ2212, qC][[3]],
   probEstablAMApproxPolymContFunc[r, m, a, b, myγ1112, myγ1212, myγ2112, myγ2212, qC][[
    4]], π1PolymContFunc[a, b, m, r, qC], π2PolymContFunc[a, b, m, r, qC],
   πAvPolymContFunc[a, b, m, r, qC], π1PolymContAxFunc[a, b, m, r, qC],
   π2PolymContAxFunc[a, b, m, r, qC], πAvPolymContAxFunc[a, b, m, r, qC]},
  {r, 0, 0.5}, PlotRange → {{0, rCritFunc[m, a, b]}, {0, 2.5 * a}}, PlotStyle →
   {{RGBColor[0, 0.3, 1, 0.5]}, {Red}, {Black}, {RGBColor[0, 0.3, 1, 0.5], DotDashed},
    {Red, DotDashed}, {Black, DotDashed}, {RGBColor[0, 0.3, 1, 0.5], Thick, Dashed},
    {Red, Thick, Dashed}, {Black, Thick, Dashed}},
  LabelStyle → {Directive[FontSize → 14], FontFamily → "Helvetica"},
  AxesLabel → {r, "Invasion probability"}, Frame → True,
  FrameStyle → {{Black, Opacity[0]}, {Black, Opacity[0]}},
  FrameLabel → {"Recombination rate r", "Invasion probability"}],
 {{a, 0.03}, 0, 0.08}, {{b, 0.04}, 0, 0.08}, {{m, 0.032}, 0, 0.1}, {{qC, 0.1}, 0, 1}]
```

Out[140]=

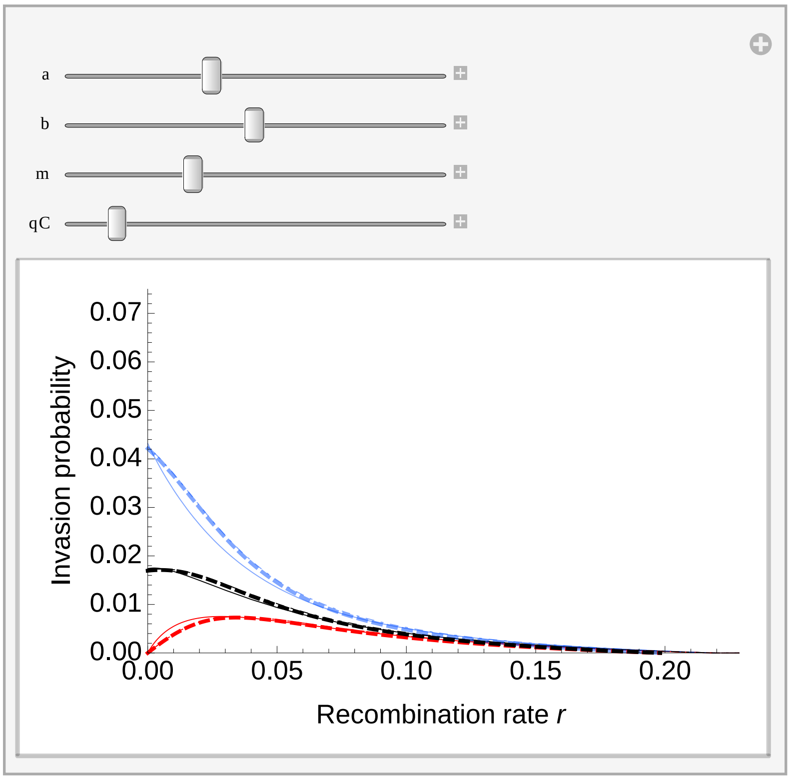


Figure: The invasion probability as a function of the recombination rate r for a polymorphic continent ($q_c > 0$) and additive fitness effects. Invasion probabilities are shown for A_1 occuring on the beneficial background B_1 (blue), on the deleterious background B_2 (red) and as a weighted average across backgrounds (black), where the weights are determinded by the frequency $\hat{q}_B$ of B_1 at the marginal one-locus migration-selection equilibrium. Analytical approximations assuming a slightly-supercritical branching process (thin dot-dashed lines) and, in addition, weak evolutionary forces (thick dashed lines) are compared to the exact numerical branching-process solution (thin solid lines). Parameter values for a, b , m and q_c can be chosen arbitrarily from a range of values.

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

```
myr2 = 0.02;
parComb2a = {a → mya2, b → myb2, r → myr2, γ111 → myγ1112,
  γ121 → myγ1212, γ211 → myγ2112, γ221 → myγ2212, qC → myqC2}
```

```
{a → 0.02, b → 0.04, r → 0.02, γ111 → 0, γ121 → 0, γ211 → 0, γ221 → 0, qC → 0.1}
```

Comparing to the numerical solution for fixed values of *a*, *b* and *r*:

```
Plot[{probEstablAMApproxPolymContFunc[myr2, m, mya2, myb2, myγ1112,
     myγ1212, myγ2112, myγ2212, myqC2][[2]], probEstablAMApproxPolymContFunc[
     myr2, m, mya2, myb2, myγ1112, myγ1212, myγ2112, myγ2212, myqC2][[3]],
   probEstablAMApproxPolymContFunc[myr2, m, mya2, myb2, myγ1112, myγ1212,
     myγ2112, myγ2212, myqC2][[4]], π1PolymContFunc[a, b, m, r, qC] /. parComb2a,
   π2PolymContFunc[a, b, m, r, qC] /. parComb2a, πAvPolymContFunc[a, b, m, r, qC] /.
    parComb2a, π1PolymContAxFunc[a, b, m, r, qC] /. parComb2a,
   π2PolymContAxFunc[a, b, m, r, qC] /. parComb2a,
   πAvPolymContAxFunc[a, b, m, r, qC] /. parComb2a},
  {m, 0, 2 * mCritFunc[myr2, mya2, myb2]},
  PlotRange → {{0, mCritFunc[myr2, mya2, myb2]}, {0, 2.5 * mya2}}, PlotStyle →
   {{RGBColor[0, 0.3, 1, 0.5]}, {Red}, {Black}, {RGBColor[0, 0.3, 1, 0.5], DotDashed},
    {Red, DotDashed}, {Black, DotDashed}, {RGBColor[0, 0.3, 1, 0.5], Thick, Dashed},
    {Red, Thick, Dashed}, {Black, Thick, Dashed}},
  LabelStyle → {Directive[FontSize → 14], FontFamily → "Helvetica"},
  AxesLabel → {m, "Invasion probability"}, Frame → True,
  FrameStyle → {{Black, Opacity[0]}, {Black, Opacity[0]}},
  FrameLabel → {"Migration rate m", "Invasion probability"}]
```

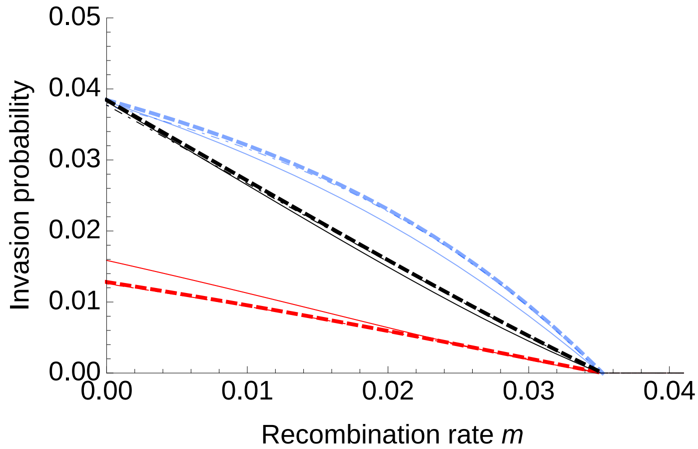


Figure 9: The invasion probability as a function of the migration rate m for a polymorphic continent ($q_c > 0$) and additive fitness effects. Invasion probabilities are shown for A_1 occuring on the beneficial background B_1 (blue), on the deleterious background B_2 (red) and as a weighted average across backgrounds (black), where the weights are determinded by the frequency $\hat{q}_B$ of B_1 at the marginal one-locus migration-selection equilibrium. Analytical approximations assuming a slightly-supercritical branching process (thin dot-dashed lines) and, in addition, weak evolutionary forces (up to first order of ϵ; thick dashed lines) are compared to the exact numerical branching-process solution (thin solid lines). Parameter values are $a = 0.02$, $b = 0.04$, $r = 0.02$ and $q_c = 0.1$.

Comparing to the numerical solution for various values of a, b and r:

In[141]:=
```
Manipulate[
 Plot[
  {probEstablAMApproxPolymContFunc[r, m, a, b, myγ1112, myγ1212, myγ2112, myγ2212, qC][[
    2]], probEstablAMApproxPolymContFunc[r, m, a, b, myγ1112, myγ1212, myγ2112,
     myγ2212, qC][[3]], probEstablAMApproxPolymContFunc[r, m, a, b, myγ1112,
     myγ1212, myγ2112, myγ2212, qC][[4]], π1PolymContFunc[a, b, m, r, qC],
   π2PolymContFunc[a, b, m, r, qC], πAvPolymContFunc[a, b, m, r, qC],
   π1PolymContAxFunc[a, b, m, r, qC], π2PolymContAxFunc[a, b, m, r, qC],
   πAvPolymContAxFunc[a, b, m, r, qC]}, {m, 0, 2 * mCritFunc[r, a, b]},
  PlotRange → {{0, 1.5 * mCritFunc[r, a, b]}, {0, 2.5 * a}}, PlotStyle →
   {{RGBColor[0, 0.3, 1, 0.5]}, {Red}, {Black}, {RGBColor[0, 0.3, 1, 0.5], DotDashed},
    {Red, DotDashed}, {Black, DotDashed}, {RGBColor[0, 0.3, 1, 0.5], Thick, Dashed},
    {Red, Thick, Dashed}, {Black, Thick, Dashed}},
  LabelStyle → {Directive[FontSize → 14], FontFamily → "Helvetica"},
  AxesLabel → {m, "Invasion probability"}, Frame → True,
  FrameStyle → {{Black, Opacity[0]}, {Black, Opacity[0]}},
  FrameLabel → {"Migration rate m", "Invasion probability"}],
 {{a, 0.03}, 0, 0.08}, {{b, 0.04}, 0, 0.08}, {{r, 0.01}, 0, 0.1}, {{qC, 0.1}, 0, 1}]
```

Out[141]=

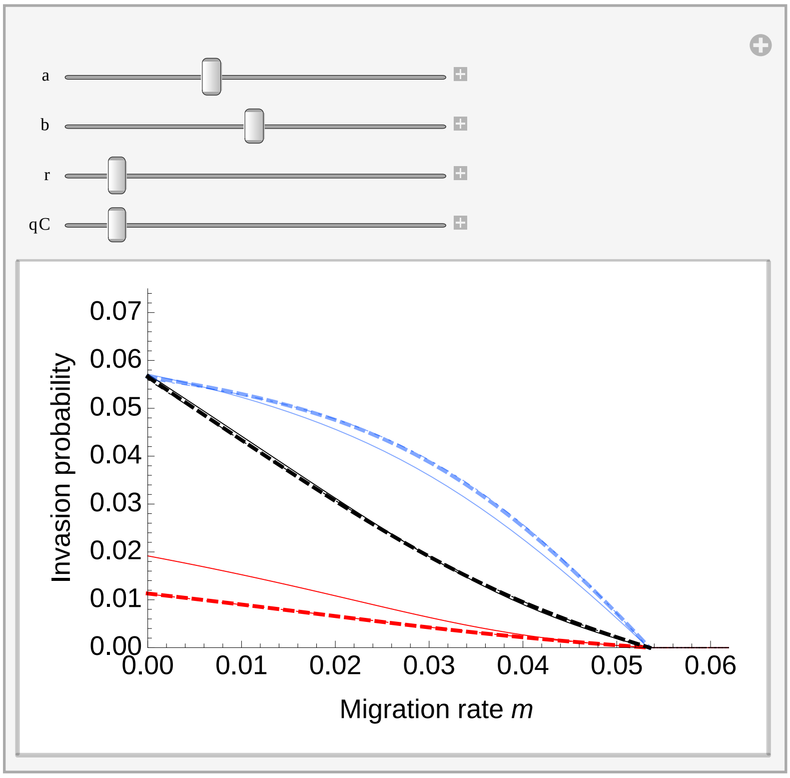


Figure: The invasion probability as a function of the migration rate m for a polymorphic continent ($q_c > 0$) and additive fitness effects. Invasion probabilities are shown for A_1 occuring on the beneficial background B_1 (blue), on the deleterious background B_2 (red) and as a weighted average across backgrounds (black), where the weights are determinded by the frequency $\hat{q}_B$ of B_1 at the marginal one-locus migration-selection equilibrium. Analytical approximations assuming a slightly-supercritical branching process (thin dot-dashed lines) and, in addition, weak evolutionary forces (up to first order of ϵ; thick dashed lines) are compared to the exact numerical branching-process solution (thin solid lines). Parameter values for a, b, r and q_c can be chosen arbitrarily from a range of values.

We note that the approximation up to first order of ϵ (thick dashed lines in the two previous plots) is rather good for the weighted average invasion probability (black) over the whole range of m. The approximation to the invasion probabilities conditional on A_1 occurring on B_1 (red) may be poor for small m.

Functions for plotting

Analytical approximations to invasion probabilities

- **Monomorphic continent, additive fitnesses**
- Application of T5.6_HJV2005 (slightly supercritical process) without further approximation

```
In[98]:= π1Func::usage="π1Func[a, b, m, r] a: selection coefficient in favour of A1; b: selectio
```

```
π1Func[a_,b_,m_,r_]:=-(8 b ((1+m) (-2 a+b+r)-√((1+m) (b^2 (1+m)-2 b (-1+m) r+r (r+m (-4+
```

```
In[100]:= π2Func::usage="π2Func[a, b, m, r] a: selection coefficient in favour of A1; b: selectio
```

```
π2Func[a_,b_,m_,r_]:=-(16 b (b+(-1+a) m) r ((1+m) (-2 a+b+r)-√((1+m) (b^2 (1+m)-2 b (-1+
```

```
In[102]:= πAvFunc::usage="πAvFunc[a, b, m, r] a: selection coefficient in favour of A1; b: select
```

```
πAvFunc[a_,b_,m_,r_]:=-(8 b (b+(-1+a) m) ((1+m) (-2 a+b+r)-√((1+m) (b^2 (1+m)-2 b (-1+m)
```

- Application of T5.6_HJV2005 (slightly supercritical process) assuming weak evolutionary forces (up to first order of ϵ)

```
In[104]:= π1Approx4Func::usage =
  "π1Approx4Func[a, b, m, r] a: selection coefficient in favour of A1; b: selection
    coefficient in favour of B1; m: migration rate; r: recombination rate";
```

$$\pi1Approx4Func[a\_, b\_, m\_, r\_] := \frac{-2 m r + a \left(b + r + \sqrt{b^2 + 2 b r - 4 m r + r^2}\right)}{\sqrt{b^2 + 2 b r + r (-4 m + r)}}$$

```
In[105]:= π2Approx4Func::usage =
  "π2Approx4Func[a, b, m, r] a: selection coefficient in favour of
    A1; b: selection coefficient in favour of B1; m: migration
    rate; r: recombination rate"; π2Approx4Func[a_, b_, m_, r_] :=
```

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

```
In[106]:= πAvApprox4Func::usage =
  "πAvApprox4Func[a, b, m, r] a: selection coefficient in favour
    of A1; b: selection coefficient in favour of B1; m: migration
    rate; r: recombination rate"; πAvApprox4Func[a_, b_, m_, r_] :=
```

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

- Application of T5.6_HJV2005 (slightly supercritical process) assuming weak evolutionary forces (up to second order of ϵ)

In[107]:=
```
π1Approx5Func::usage="π1Approx5Func[a, b, m, r] a: selection coefficient in favour of A
```
$$\pi 1Approx5Func[a\_,b\_,m\_,r\_]:=\frac{1}{\left(b^2+2\ b\ r+r\ (-4\ m+r)\right)^{3/2}}\left(m\ r\ \left(4\ m^2\ r-(b+r)^2\ (2+2\ b+r)+m\ r\ (8\right.\right.$$

In[109]:=
```
π2Approx5Func::usage = "π2Approx5Func[a, b, m, r] a: selection coefficient in favour of
```
$$\pi 2Approx5Func[a\_,b\_,m\_,r\_]:=\frac{1}{\left(b^2+2\ b\ r+r\ (-4\ m+r)\right)^{3/2}}\left(b^5+b^4\ \left(1+m+4\ r-\sqrt{b^2+2\ b\ r-4\ m\ r+r^2}\right)\right.$$

In[111]:=
```
πAvApprox5Func::usage = "πAvApprox5Func[a, b, m, r] a: selection coefficient in favour
```
$$\pi AvApprox5Func[a\_,b\_,m\_,r\_]:=\frac{1}{\left(b^2+2\ b\ r+r\ (-4\ m+r)\right)^{3/2}}\left(1/(b+b\ m)(b-m+a\ m)\ \left(m\ r\ \left(4\ m^2\ r-(b\right.\right.\right.$$

- **Polymorphic continent, additive fitnesses**

- Application of T5.6_HJV2005 (slightly supercritical process) without further approximation

In[86]:=
```
π1PolymContFunc::usage = "π1PolymContFunc[a, b, m, r, qC] a: selection coefficient in f
```
$$\pi 1PolymContFunc[a\_,b\_,m\_,r\_,qC\_]:=\left(4\ b^2\ \left(-m-\sqrt{-4\ b\ (-1+a+b)\ m\ (1+m)\ qC+(b+(-1+a)\ m+2\ b\right.\right.\right.$$

In[88]:=
```
π2PolymContFunc::usage = "π2PolymContFunc[a, b, m, r, qC] a: selection coefficient in f
```
$$\pi 2PolymContFunc[a\_,b\_,m\_,r\_,qC\_]:=\left(4\ b^2\ (-1+m)\ r\ \left(-m-\sqrt{-4\ b\ (-1+a+b)\ m\ (1+m)\ qC+(b+(-1+\right.\right.\right.$$

In[90]:=
```
πAvPolymContFunc::usage = "πAvPolymContFunc[a, b, m, r, qC] a: selection coefficient in
```
$$\pi AvPolymContFunc[a\_,b\_,m\_,r\_,qC\_]:=\left(2\ b^2\ \left(-m-\sqrt{-4\ b\ (-1+a+b)\ m\ (1+m)\ qC+(b+(-1+a)\ m+2\ b\right.\right.\right.$$

- Application of T5.6_HJV2005 (slightly supercritical process) assuming weak evolutionary forces (up to first order of ϵ)

In[92]:=
```
π1PolymContAxFunc::usage = "π1PolymContAxFunc[a, b, m, r, qC] a: selection coefficient
```
$$\pi 1PolymContAxFunc[a\_,b\_,m\_,r\_,qC\_]:=\left(4\ b^2\ \left(2\ a-m-\sqrt{(b-m)^2+4\ b\ m\ qC}-r+\sqrt{b^2+r\ \left(-2\ m+2\ \sqrt{(}\right.}\right.\right.$$

In[94]:=
```
π2PolymContAxFunc::usage = "π2PolymContAxFunc[a, b, m, r, qC] a: selection coefficient
```
$$\pi 2PolymContAxFunc[a\_,b\_,m\_,r\_,qC\_]:=\left(4\ b^2\ \left(b-m+\sqrt{(b-m)^2+4\ b\ m\ qC}\right)\ r\ \left(2\ a-m-\sqrt{(b-m)^2+4\ b}\right.\right.$$

In[96]:=
```
πAvPolymContAxFunc::usage = "πAvPolymContAxFunc[a, b, m, r, qC] a: selection coefficien
```
$$\pi AvPolymContAxFunc[a\_,b\_,m\_,r\_,qC\_]:=\left(2\ b^2\ \left(2\ a-m-\sqrt{(b-m)^2+4\ b\ m\ qC}-r+\sqrt{b^2+r\ \left(-2\ m+2\ \sqrt{}\right.}\right.\right.$$

Further functions

- **Identification of ξ to specify what slightly supercritical means**

- Monomorphic continent

In[82]:=

$$\xi\text{AddFunc}[a\_, b\_, m\_, r\_] := \frac{1}{2(-1+a-b)}\left(b-2a(1+m)+r+m(b+r)-\sqrt{(1+m)\left(b^2(1+m)-2b(-1+m)r+r(r+m(-4+4a+r))\right)}\right)$$

- Monomorphic continent, weak evolutionary forces

In[83]:=

$$\xi\text{AddApproxFunc}[a\_, b\_, m\_, r\_] := \frac{1}{2}\left(2a-b-r+\sqrt{b^2+2br-4mr+r^2}\right)$$

- Polymorphic continent

In[84]:=

$$\begin{aligned}\xi\text{AddPolymContFunc}[a\_, b\_, m\_, r\_, qC\_] := \frac{1}{2}\Bigg(&-2+\frac{2}{(-1+a)^2-b^2}-\\&\frac{1}{(-1+a)^2-b^2}\Big(-b^2(-1+m)+m+a^2m+\sqrt{(b+(-1+a)m)^2-4bm(-1+a+bm)qC+4b^2m^2qC^2}+\\&\quad a\left(2+m(-2+b-2bqC)+\sqrt{(b+(-1+a)m)^2-4bm(-1+a+bm)qC+4b^2m^2qC^2}-r\right)+\\&\quad bm(-1+2qC)(-1+r)+r-\sqrt{(b+(-1+a)m)^2-4bm(-1+a+bm)qC+4b^2m^2qC^2}\,r\Big)+\\&\sqrt{\Big((-1+m)^2(1+m)\Big(b^2(1+m)+2bm(-1+2qC)r+}\\&\quad\overline{r\left(2\sqrt{(b+(-1+a)m)^2-4bm(-1+a+bm)qC+4b^2m^2qC^2}+r+m(-2+2a+r)\right)\Big)\Big)\Big/}\\&\quad\overline{\left(1-a+bm(-1+2qC)+\sqrt{(b+(-1+a)m)^2-4bm(-1+a+bm)qC+4b^2m^2qC^2}\right)^2}\Bigg)\end{aligned}$$

- Polymorphic continent, weak evolutionary forces

In[85]:=

$$\xi\text{AddPolymContApproxFunc}[a\_, b\_, m\_, r\_, qC\_] := a+\frac{1}{2}\left(-m-\sqrt{(b-m)^2+4bm\,qC}-r+\sqrt{b^2+r\left(-2m+2\sqrt{(b-m)^2+4bm\,qC}+r\right)}\right)$$