

The effective migration rate experienced by a neutral site linked to two loci at migration-selection balance

We assume two loci under selection (\mathcal{A} and \mathcal{B}) and a third neutral locus C , each with two alleles denoted by A_1 and A_2 , B_1 and B_2 , and C_1 and C_2 , respectively. Let the frequencies of alleles A_1 , A_2 , B_1 , B_2 , C_1 and C_2 be p , $1 - p$, q , $1 - q$, n and $1 - n$, respectively. We denote the recombination rate between locus i and j by r_{ij} and consider a continuous-time model, such that second-order terms of recombination rates can be ignored.

We first consider the case where the neutral locus lies between the selected loci, i.e. $\mathcal{A}-C-\mathcal{B}$. We denote the frequencies of the eight haplotypes $A_1 C_1 B_1$, $A_1 C_1 B_2$, $A_2 C_1 B_1$, $A_2 C_1 B_2$, $A_1 C_2 B_1$, $A_1 C_2 B_2$, $A_2 C_2 B_1$, and $A_2 C_2 B_2$ by y_1, \dots, y_8 , respectively. In this case, the recombination rate between locus \mathcal{A} and C is r_{AC} and the one between locus C and \mathcal{B} is r_{CB} . As mentioned, we ignore interaction terms, so that $r_{AB} = r_{AC} + r_{CB}$.

Later, we consider the case where the neutral locus lies to the right ($\mathcal{A}-\mathcal{B}-C$) or to the left ($C-\mathcal{A}-\mathcal{B}$) of the two selected loci.

As outlined by Bürger and Akerman (2011), the recursion equations due to selection and migration are immediately obtained from the two-locus migration-selection model (eq. 2.2 in Bürger and Akerman, 2011), because locus C is neutral.

In this context, we point out that equations (4.25) and (4.26) in Bürger and Akerman (2011) are wrong and need to be replaced by

Order of loci: $\mathcal{A}-C-\mathcal{B}$

Rules and assumptions

```
In[1]:= recScale := {r1 → ρ1 ε, r2 → ρ2 ε}
recBackScale := {ρ1 → r1 / ε, ρ2 → r2 / ε}

In[3]:= pDef := y1 + y2 + y5 + y6
qDef := y1 + y3 + y5 + y7
nDef := y1 + y2 + y3 + y4
DACDef := (y1 + y2) (y7 + y8) - (y5 + y6) (y3 + y4)
DCBDef := (y1 + y3) (y6 + y8) - (y2 + y4) (y5 + y7)
DABDef := (y1 + y5) (y4 + y8) - (y2 + y6) (y3 + y7)

In[9]:= DACBDef := y1 - p q n - p DCB - q DAC - n DAB /
{p → pDef, q → qDef, n → nDef, DCB → DCBDef, DAC → DACDef, DAB → DABDef}

In[10]:= gamToAllLD := {
y1 → p q n + p DCB + q DAC + n DAB + DACB,
y2 → p (1 - q) n - p DCB + (1 - q) DAC - n DAB - DACB,
y3 → (1 - p) q n + (1 - p) DCB - q DAC - n DAB - DACB,
y4 → (1 - p) (1 - q) n - (1 - p) DCB - (1 - q) DAC + n DAB + DACB,
y5 → p q (1 - n) - p DCB - q DAC + (1 - n) DAB - DACB,
y6 → p (1 - q) (1 - n) + p DCB - (1 - q) DAC - (1 - n) DAB + DACB,
y7 → (1 - p) q (1 - n) - (1 - p) DCB + q DAC - (1 - n) DAB + DACB,
y8 → (1 - p) (1 - q) (1 - n) + (1 - p) DCB + (1 - q) DAC + (1 - n) DAB - DACB
}
```

```
In[11]:= allToGam := {
  p → y1 + y2 + y5 + y6,
  (*1-p→y3+y4+y7+y8, *)
  q → y1 + y3 + y5 + y7,
  (*1-q→y2+y4+y6+y8, *)
  n → y1 + y2 + y3 + y4
}
```

Derivation of recursion equations

■ Relationships between LD coefficients, allele and gamete frequencies.

Before deriving the recursion equations, we recall some relationships between gamete frequencies, allele frequencies and linkage disequilibria:

The gamete frequencies of marginal two-locus models in terms of the gamete frequencies of the three-locus model:

$$x_1 := [A_1 B_1] = y_1 + y_5 \quad (1)$$

$$x_2 := [A_1 B_2] = y_2 + y_6 \quad (2)$$

$$x_3 := [A_2 B_1] = y_3 + y_7 \quad (3)$$

$$x_4 := [A_2 B_2] = y_4 + y_8 \quad (4)$$

$$x_5 := [A_1 C_1] = y_1 + y_2 \quad (5)$$

$$x_6 := [A_1 C_2] = y_5 + y_6 \quad (6)$$

$$x_7 := [A_2 C_1] = y_3 + y_4 \quad (7)$$

$$x_8 := [A_2 C_2] = y_7 + y_8 \quad (8)$$

$$x_9 := [C_1 B_1] = y_1 + y_3 \quad (9)$$

$$x_{10} := [C_1 B_2] = y_2 + y_4 \quad (10)$$

$$x_{11} := [C_2 B_1] = y_5 + y_7 \quad (11)$$

$$x_{12} := [C_2 B_2] = y_6 + y_8 \quad (12)$$

The allele frequencies in terms of the gamete frequencies:

$$p = x_1 + x_2 = y_1 + y_2 + y_5 + y_6 \quad (13)$$

$$1 - p = x_3 + x_4 = y_3 + y_4 + y_7 + y_8 \quad (14)$$

$$q = x_1 + x_3 = y_1 + y_3 + y_5 + y_7 \quad (15)$$

$$1 - q = x_2 + x_4 = y_2 + y_4 + y_6 + y_8 \quad (16)$$

$$n = y_1 + y_2 + y_3 + y_4 \quad (17)$$

$$1 - n = y_5 + y_6 + y_7 + y_8 \quad (18)$$

The two-way linkage disequilibria in terms of allele and gamete frequencies:

$$D_{AB} = x_1 - p q = (y_1 + y_5) - p q = x_1 x_4 - x_2 x_3 = (y_1 + y_5)(y_4 + y_8) - (y_2 + y_6)(y_3 + y_7) \quad (19)$$

$$D_{AC} = [A_1 C_1] - p n = (y_1 + y_2) - p n = (y_1 + y_2) - [(y_1 + y_2) + (y_5 + y_6)][(y_1 + y_2) + (y_3 + y_4)] = (y_1 + y_2)(y_7 + y_8) - (y_5 + y_6)(y_3 + y_4) = x_5 x_8 - x_6 x_7 \quad (20)$$

$$D_{CB} = [C_1 B_1] - q n = (y_1 + y_3) - q n = (y_1 + y_3) - [(y_1 + y_3) + (y_5 + y_7)][(y_1 + y_3) + (y_2 + y_4)] = (y_1 + y_3)(y_6 + y_8) - (y_2 + y_4)(y_5 + y_7) = x_9 x_{12} - x_{10} x_{11} \quad (21)$$

The three-way linkage disequilibrium in terms of gamete frequencies, allele frequencies and two-way linkage disequilibria:

$$D_{ACB} = y_1 - p q n - p D_{AB} - q D_{AC} - n D_{CB} = y_1 - p q n - p [(y_1 + y_3) - q n] - q [(y_1 + y_2) - p n] - n [(y_1 + y_5) - p q] \quad (22)$$

Some marginal two-locus gamete frequencies in terms of allele frequencies and two-way linkage disequilibria:

$$x_1 = p q + D_{AB} \quad (23)$$

$$x_2 = p(1 - q) - D_{AB} \quad (19)$$

$$x_3 = (1 - p)q - D_{AB} \quad (20)$$

$$x_4 = (1 - p)(1 - q) + D_{AB} \quad (21)$$

$$x_5 = p n + D_{AC} \quad (22)$$

$$x_6 = p(1 - n) - D_{AC} \quad (23)$$

$$x_7 = (1 - p)n - D_{AC} \quad (24)$$

$$x_8 = (1 - p)(1 - n) + D_{AC} \quad (25)$$

$$x_9 = n q + D_{CB} \quad (26)$$

$$x_{10} = n(1 - q) - D_{CB} \quad (27)$$

$$x_{11} = (1 - n)q - D_{CB} \quad (28)$$

$$x_{12} = (1 - n)(1 - q) + D_{CB} \quad (29)$$

The three-locus gamete frequencies in terms of allele frequencies and two-way linkage disequilibria:

$$y_1 = p q n + p D_{CB} + q D_{AC} + n D_{AB} + D_{ACB} \quad (30)$$

$$y_2 = p(1 - q)n - p D_{CB} + (1 - q)D_{AC} - n D_{AB} - D_{ACB} \quad (31)$$

$$y_3 = (1 - p)q n + (1 - p)D_{CB} - q D_{AC} - n D_{AB} - D_{ACB} \quad (32)$$

$$y_4 = (1 - p)(1 - q)n - (1 - p)D_{CB} - (1 - q)D_{AC} + n D_{AB} + D_{ACB} \quad (33)$$

$$y_5 = p q (1 - n) - p D_{CB} - q D_{AC} + (1 - n) D_{AB} - D_{ACB} \quad (34)$$

$$y_6 = p(1 - q)(1 - n) + p D_{CB} - (1 - q)D_{AC} - (1 - n)D_{AB} + D_{ACB} \quad (35)$$

$$y_7 = (1 - p)q(1 - n) - (1 - p)D_{CB} + q D_{AC} - (1 - n) D_{AB} + D_{ACB} \quad (36)$$

$$y_8 = (1 - p)(1 - q)(1 - n) + (1 - p)D_{CB} + (1 - q)D_{AC} + (1 - n)D_{AB} - D_{ACB} \quad (37)$$

The recursion equation for y_1 (gamete A₁ N₁ B₁) in discrete time:

■ Automatisation of construction of difference equations under recombination

```
In[12]:= gametesProduced[parent1_, parent2_, parentFreq1_, parentFreq2_] :=
Module[{tup, factors, pf1, pf2, freqDist, δ},
pf1 = parentFreq1;
pf2 = parentFreq2;
δ = 1;
factors = {1/2 (1 - r1) (1 - r2), 1/2 (1 - r1) r2, 1/2 r1 r2, 1/2 r1 (1 - r2),
1/2 r1 (1 - r2), 1/2 r1 r2, 1/2 (1 - r1) r2, 1/2 (1 - r1) (1 - r2)} * δ * pf1 * pf2;
tup = Tuples[Partition[Riffle[parent1, parent2], 2]];
freqDist = Table[Sum[factors[[i]], {i, Flatten[Position[tup, Union[tup][[i]]]]}], {i, Length[Union[tup]]}];
Return[{Union[tup], freqDist}];

]

In[13]:= gametes = {{A1, C1, B1}, {A1, C1, B2}, {A2, C1, B1},
{A2, C1, B2}, {A1, C2, B1}, {A1, C2, B2}, {A2, C2, B1}, {A2, C2, B2}};

Out[13]= {{A1, C1, B1}, {A1, C1, B2}, {A2, C1, B1}, {A2, C1, B2},
{A1, C2, B1}, {A1, C2, B2}, {A2, C2, B1}, {A2, C2, B2}}
```

```
In[14]:= matings = Flatten[
  Table[{gametes[[i]], gametes[[j]]}, {i, 1, Length[gametes]}, {j, 1, Length[gametes]}], 1]
Length[
%]

Out[14]= {{ {A1, C1, B1}, {A1, C1, B1}}, {{A1, C1, B1}, {A1, C1, B2}},
{{A1, C1, B1}, {A2, C1, B1}}, {{A1, C1, B1}, {A2, C1, B2}},
{{A1, C1, B1}, {A1, C2, B1}}, {{A1, C1, B1}, {A1, C2, B2}}, {{A1, C1, B1}, {A2, C2, B1}},
{{A1, C1, B1}, {A2, C2, B2}}, {{A1, C1, B2}, {A1, C1, B1}}, {{A1, C1, B2}, {A1, C1, B2}},
{{A1, C1, B2}, {A2, C1, B1}}, {{A1, C1, B2}, {A2, C1, B2}}, {{A1, C1, B2}, {A1, C2, B1}},
{{A1, C1, B2}, {A1, C2, B2}}, {{A1, C1, B2}, {A2, C2, B1}}, {{A1, C1, B2}, {A2, C2, B2}},
{{A2, C1, B1}, {A1, C1, B1}}, {{A2, C1, B1}, {A1, C1, B2}}, {{A2, C1, B1}, {A2, C1, B1}},
{{A2, C1, B1}, {A2, C1, B2}}, {{A2, C1, B2}, {A1, C1, B1}}, {{A2, C1, B2}, {A1, C2, B1}},
{{A2, C1, B2}, {A2, C2, B1}}, {{A2, C1, B2}, {A2, C1, B2}}, {{A2, C1, B2}, {A2, C1, B2}},
{{A2, C1, B2}, {A1, C2, B1}}, {{A2, C1, B2}, {A2, C2, B1}}, {{A2, C1, B2}, {A1, C1, B1}},
{{A2, C1, B2}, {A1, C1, B2}}, {{A2, C1, B2}, {A2, C1, B1}}, {{A2, C1, B2}, {A2, C1, B2}},
{{A2, C1, B2}, {A1, C2, B1}}, {{A2, C1, B2}, {A1, C2, B2}}, {{A2, C1, B2}, {A1, C1, B2}},
{{A2, C1, B2}, {A2, C2, B1}}, {{A2, C1, B2}, {A1, C2, B1}}, {{A2, C1, B2}, {A1, C2, B2}},
{{A1, C2, B1}, {A1, C2, B1}}, {{A1, C2, B1}, {A2, C2, B1}}, {{A1, C2, B1}, {A1, C2, B2}},
{{A1, C2, B1}, {A1, C2, B2}}, {{A1, C2, B1}, {A2, C2, B1}}, {{A1, C2, B1}, {A2, C2, B2}},
{{A1, C2, B2}, {A1, C2, B1}}, {{A1, C2, B2}, {A2, C2, B1}}, {{A1, C2, B2}, {A1, C2, B2}},
{{A1, C2, B2}, {A2, C2, B1}}, {{A1, C2, B2}, {A2, C2, B2}}, {{A1, C2, B2}, {A2, C2, B1}},
{{A1, C2, B2}, {A2, C2, B2}}, {{A1, C2, B2}, {A1, C2, B1}}, {{A1, C2, B2}, {A2, C2, B2}},
{{A1, C2, B2}, {A2, C2, B1}}, {{A1, C2, B2}, {A2, C2, B2}}, {{A1, C2, B2}, {A1, C2, B2}},
{{A1, C2, B2}, {A2, C2, B2}}, {{A1, C2, B2}, {A1, C2, B2}}, {{A1, C2, B2}, {A2, C2, B2}}}

Out[15]= 64

In[16]:= gameteFreqs = {y1, y2, y3, y4, y5, y6, y7, y8}

Out[16]= {y1, y2, y3, y4, y5, y6, y7, y8}

In[17]:= freqPairs = Flatten[Table[{gameteFreqs[[i]], gameteFreqs[[j]]},
{i, 1, Length[gameteFreqs]}, {j, 1, Length[gameteFreqs]}], 1]
% //
Length

Out[17]= {{y1, y1}, {y1, y2}, {y1, y3}, {y1, y4}, {y1, y5}, {y1, y6}, {y1, y7}, {y1, y8},
{y2, y1}, {y2, y2}, {y2, y3}, {y2, y4}, {y2, y5}, {y2, y6}, {y2, y7}, {y2, y8},
{y3, y1}, {y3, y2}, {y3, y3}, {y3, y4}, {y3, y5}, {y3, y6}, {y3, y7}, {y3, y8},
{y4, y1}, {y4, y2}, {y4, y3}, {y4, y4}, {y4, y5}, {y4, y6}, {y4, y7}, {y4, y8},
{y5, y1}, {y5, y2}, {y5, y3}, {y5, y4}, {y5, y5}, {y5, y6}, {y5, y7}, {y5, y8},
{y6, y1}, {y6, y2}, {y6, y3}, {y6, y4}, {y6, y5}, {y6, y6}, {y6, y7}, {y6, y8},
{y7, y1}, {y7, y2}, {y7, y3}, {y7, y4}, {y7, y5}, {y7, y6}, {y7, y7}, {y7, y8},
{y8, y1}, {y8, y2}, {y8, y3}, {y8, y4}, {y8, y5}, {y8, y6}, {y8, y7}, {y8, y8}]

Out[18]= 64

MapThread[gametesProduced[#, #1[[1]], #1[[2]], #2[[1]], #2[[2]]] &,
{matings[[1 ;; 2]], freqPairs[[1 ;; 2]]}] // TableForm

A1 C1 B1      (1 - r1) (1 - r2) y1^2 + r1 (1 - r2) y1^2 + (1 - r1) r2 y1^2 + r1 r2 y1^2
A1 C1 B1       $\frac{1}{2}$  (1 - r1) (1 - r2) y1 y2 +  $\frac{1}{2}$  r1 (1 - r2) y1 y2 +  $\frac{1}{2}$  (1 - r1) r2 y1 y2 +  $\frac{1}{2}$  r1 r2 y1 y2
A1 C1 B2       $\frac{1}{2}$  (1 - r1) (1 - r2) y1 y2 +  $\frac{1}{2}$  r1 (1 - r2) y1 y2 +  $\frac{1}{2}$  (1 - r1) r2 y1 y2 +  $\frac{1}{2}$  r1 r2 y1 y2

In[19]:= recSep = MapThread[gametesProduced[#, #1[[1]], #1[[2]], #2[[1]], #2[[2]]] &, {matings, freqPairs}];
TableForm[recSep]

Out[20]/TableForm=
A1 C1 B1      (1 - r1) (1 - r2) y1^2 + r1 (1 - r2) y1^2 + (1 - r1) r2 y1^2 + r1 r2 y1^2
A1 C1 B1       $\frac{1}{2}$  (1 - r1) (1 - r2) y1 y2 +  $\frac{1}{2}$  r1 (1 - r2) y1 y2 +  $\frac{1}{2}$  (1 - r1) r2 y1 y2 +  $\frac{1}{2}$  r1 r2 y1 y2
A1 C1 B2       $\frac{1}{2}$  (1 - r1) (1 - r2) y1 y2 +  $\frac{1}{2}$  r1 (1 - r2) y1 y2 +  $\frac{1}{2}$  (1 - r1) r2 y1 y2 +  $\frac{1}{2}$  r1 r2 y1 y2
A1 C1 B1       $\frac{1}{2}$  (1 - r1) (1 - r2) y1 y3 +  $\frac{1}{2}$  r1 (1 - r2) y1 y3 +  $\frac{1}{2}$  (1 - r1) r2 y1 y3 +  $\frac{1}{2}$  r1 r2 y1 y3
A2 C1 B1       $\frac{1}{2}$  (1 - r1) (1 - r2) y1 y3 +  $\frac{1}{2}$  r1 (1 - r2) y1 y3 +  $\frac{1}{2}$  (1 - r1) r2 y1 y3 +  $\frac{1}{2}$  r1 r2 y1 y3
```

$$\begin{aligned}
& \frac{1}{2} (1 - r1) (1 - r2) y1 y4 + \frac{1}{2} r1 r2 y1 y4 \\
& \frac{1}{2} r1 (1 - r2) y1 y4 + \frac{1}{2} (1 - r1) r2 y1 y4 \\
& \frac{1}{2} r1 (1 - r2) y1 y4 + \frac{1}{2} (1 - r1) r2 y1 y4 \\
& \frac{1}{2} (1 - r1) (1 - r2) y1 y4 + \frac{1}{2} r1 r2 y1 y4 \\
& \frac{1}{2} (1 - r1) (1 - r2) y1 y5 + \frac{1}{2} r1 (1 - r2) y1 y5 + \frac{1}{2} (1 - r1) r2 y1 y5 + \frac{1}{2} r1 r2 y1 y5 \\
& \frac{1}{2} (1 - r1) (1 - r2) y1 y5 + \frac{1}{2} r1 (1 - r2) y1 y5 + \frac{1}{2} (1 - r1) r2 y1 y5 + \frac{1}{2} r1 r2 y1 y5 \\
& \frac{1}{2} (1 - r1) (1 - r2) y1 y6 + \frac{1}{2} r1 (1 - r2) y1 y6 \\
& \frac{1}{2} (1 - r1) r2 y1 y6 + \frac{1}{2} r1 r2 y1 y6 \\
& \frac{1}{2} (1 - r1) r2 y1 y6 + \frac{1}{2} r1 r2 y1 y6 \\
& \frac{1}{2} (1 - r1) (1 - r2) y1 y6 + \frac{1}{2} r1 (1 - r2) y1 y6 \\
& \frac{1}{2} (1 - r1) (1 - r2) y1 y7 + \frac{1}{2} (1 - r1) r2 y1 y7 \\
& \frac{1}{2} r1 (1 - r2) y1 y7 + \frac{1}{2} r1 r2 y1 y7 \\
& \frac{1}{2} r1 (1 - r2) y1 y7 + \frac{1}{2} r1 r2 y1 y7 \\
& \frac{1}{2} (1 - r1) (1 - r2) y1 y7 + \frac{1}{2} (1 - r1) r2 y1 y7 \\
& \frac{1}{2} (1 - r1) (1 - r2) y1 y8 \\
& \frac{1}{2} (1 - r1) r2 y1 y8 \\
& \frac{1}{2} r1 r2 y1 y8 \\
& \frac{1}{2} r1 (1 - r2) y1 y8 \\
& \frac{1}{2} r1 (1 - r2) y1 y8 \\
& \frac{1}{2} r1 r2 y1 y8 \\
& \frac{1}{2} (1 - r1) r2 y1 y8 \\
& \frac{1}{2} (1 - r1) (1 - r2) y1 y8 \\
& \frac{1}{2} (1 - r1) (1 - r2) y1 y2 + \frac{1}{2} r1 (1 - r2) y1 y2 + \frac{1}{2} (1 - r1) r2 y1 y2 + \frac{1}{2} r1 r2 y1 y2 \\
& \frac{1}{2} (1 - r1) (1 - r2) y1 y2 + \frac{1}{2} r1 (1 - r2) y1 y2 + \frac{1}{2} (1 - r1) r2 y1 y2 + \frac{1}{2} r1 r2 y1 y2 \\
& A1 C1 B2 (1 - r1) (1 - r2) y2^2 + r1 (1 - r2) y2^2 + (1 - r1) r2 y2^2 + r1 r2 y2^2 \\
& \frac{1}{2} r1 (1 - r2) y2 y3 + \frac{1}{2} (1 - r1) r2 y2 y3 \\
& \frac{1}{2} (1 - r1) (1 - r2) y2 y3 + \frac{1}{2} r1 r2 y2 y3 \\
& \frac{1}{2} (1 - r1) (1 - r2) y2 y3 + \frac{1}{2} r1 r2 y2 y3 \\
& \frac{1}{2} r1 (1 - r2) y2 y3 + \frac{1}{2} (1 - r1) r2 y2 y3 \\
& A1 C1 B2 \frac{1}{2} (1 - r1) (1 - r2) y2 y4 + \frac{1}{2} r1 (1 - r2) y2 y4 + \frac{1}{2} (1 - r1) r2 y2 y4 + \frac{1}{2} r1 r2 y2 y4 \\
& A2 C1 B2 \frac{1}{2} (1 - r1) (1 - r2) y2 y4 + \frac{1}{2} r1 (1 - r2) y2 y4 + \frac{1}{2} (1 - r1) r2 y2 y4 + \frac{1}{2} r1 r2 y2 y4 \\
& \frac{1}{2} (1 - r1) r2 y2 y5 + \frac{1}{2} r1 r2 y2 y5 \\
& \frac{1}{2} (1 - r1) (1 - r2) y2 y5 + \frac{1}{2} r1 (1 - r2) y2 y5 \\
& \frac{1}{2} (1 - r1) (1 - r2) y2 y5 + \frac{1}{2} r1 (1 - r2) y2 y5 \\
& \frac{1}{2} (1 - r1) r2 y2 y5 + \frac{1}{2} r1 r2 y2 y5 \\
& A1 C1 B2 \frac{1}{2} (1 - r1) (1 - r2) y2 y6 + \frac{1}{2} r1 (1 - r2) y2 y6 + \frac{1}{2} (1 - r1) r2 y2 y6 + \frac{1}{2} r1 r2 y2 y6 \\
& A1 C2 B2 \frac{1}{2} (1 - r1) (1 - r2) y2 y6 + \frac{1}{2} r1 (1 - r2) y2 y6 + \frac{1}{2} (1 - r1) r2 y2 y6 + \frac{1}{2} r1 r2 y2 y6
\end{aligned}$$

$$\begin{aligned}
& \frac{1}{2} (1 - r1) r2 y2 y7 \\
A1 & C1 B1 \\
A1 & C1 B2 \\
A1 & C2 B1 \\
A1 & C2 B2 \\
A2 & C1 B1 \\
A2 & C1 B2 \\
A2 & C2 B1 \\
A2 & C2 B2 \\
& \frac{1}{2} (1 - r1) (1 - r2) y2 y7 \\
& \frac{1}{2} r1 (1 - r2) y2 y7 \\
& \frac{1}{2} r1 r2 y2 y7 \\
& \frac{1}{2} r1 r2 y2 y7 \\
& \frac{1}{2} r1 (1 - r2) y2 y7 \\
& \frac{1}{2} (1 - r1) (1 - r2) y2 y7 \\
& \frac{1}{2} (1 - r1) r2 y2 y7 \\
& \frac{1}{2} (1 - r1) (1 - r2) y2 y8 + \frac{1}{2} (1 - r1) r2 y2 y8 \\
A1 & C1 B2 \\
A1 & C2 B2 \\
A2 & C1 B2 \\
A2 & C2 B2 \\
& \frac{1}{2} r1 (1 - r2) y2 y8 + \frac{1}{2} r1 r2 y2 y8 \\
& \frac{1}{2} r1 (1 - r2) y2 y8 + \frac{1}{2} r1 r2 y2 y8 \\
& \frac{1}{2} (1 - r1) (1 - r2) y2 y8 + \frac{1}{2} (1 - r1) r2 y2 y8 \\
A1 & C1 B1 \\
A2 & C1 B1 \\
& \frac{1}{2} (1 - r1) (1 - r2) y1 y3 + \frac{1}{2} r1 (1 - r2) y1 y3 + \frac{1}{2} (1 - r1) r2 y1 y3 + \frac{1}{2} r1 r2 y1 y3 \\
& \frac{1}{2} (1 - r1) (1 - r2) y1 y3 + \frac{1}{2} r1 (1 - r2) y1 y3 + \frac{1}{2} (1 - r1) r2 y1 y3 + \frac{1}{2} r1 r2 y1 y3 \\
& \frac{1}{2} r1 (1 - r2) y2 y3 + \frac{1}{2} (1 - r1) r2 y2 y3 \\
A1 & C1 B1 \\
A1 & C1 B2 \\
A2 & C1 B1 \\
A2 & C1 B2 \\
& \frac{1}{2} (1 - r1) (1 - r2) y2 y3 + \frac{1}{2} r1 r2 y2 y3 \\
A2 & C1 B1 \\
A2 & C1 B2 \\
& \frac{1}{2} (1 - r1) (1 - r2) y2 y3 + \frac{1}{2} r1 r2 y2 y3 \\
& \frac{1}{2} r1 (1 - r2) y2 y3 + \frac{1}{2} (1 - r1) r2 y2 y3 \\
& (1 - r1) (1 - r2) y3^2 + r1 (1 - r2) y3^2 + (1 - r1) r2 y3^2 + r1 r2 y3^2 \\
A2 & C1 B1 \\
A2 & C1 B2 \\
& \frac{1}{2} (1 - r1) (1 - r2) y3 y4 + \frac{1}{2} r1 (1 - r2) y3 y4 + \frac{1}{2} (1 - r1) r2 y3 y4 + \frac{1}{2} r1 r2 y3 y4 \\
& \frac{1}{2} (1 - r1) (1 - r2) y3 y4 + \frac{1}{2} r1 (1 - r2) y3 y4 + \frac{1}{2} (1 - r1) r2 y3 y4 + \frac{1}{2} r1 r2 y3 y4 \\
& \frac{1}{2} r1 (1 - r2) y3 y5 + \frac{1}{2} r1 r2 y3 y5 \\
A1 & C1 B1 \\
A1 & C2 B1 \\
A2 & C1 B1 \\
A2 & C2 B1 \\
& \frac{1}{2} (1 - r1) (1 - r2) y3 y5 + \frac{1}{2} (1 - r1) r2 y3 y5 \\
& \frac{1}{2} (1 - r1) (1 - r2) y3 y5 + \frac{1}{2} (1 - r1) r2 y3 y5 \\
& \frac{1}{2} r1 (1 - r2) y3 y5 + \frac{1}{2} r1 r2 y3 y5 \\
& \frac{1}{2} r1 (1 - r2) y3 y6 \\
& \frac{1}{2} r1 r2 y3 y6 \\
A1 & C1 B1 \\
A1 & C1 B2 \\
A1 & C2 B1 \\
A1 & C2 B2 \\
A2 & C1 B1 \\
A2 & C1 B2 \\
A2 & C2 B1 \\
A2 & C2 B2 \\
& \frac{1}{2} (1 - r1) (1 - r2) y3 y6 \\
& \frac{1}{2} (1 - r1) r2 y3 y6 \\
& \frac{1}{2} (1 - r1) (1 - r2) y3 y6 \\
& \frac{1}{2} (1 - r1) (1 - r2) y3 y6 \\
& \frac{1}{2} (1 - r1) r2 y3 y6 \\
& \frac{1}{2} r1 r2 y3 y6 \\
& \frac{1}{2} r1 (1 - r2) y3 y6 \\
& \frac{1}{2} (1 - r1) (1 - r2) y3 y7 + \frac{1}{2} r1 (1 - r2) y3 y7 + \frac{1}{2} (1 - r1) r2 y3 y7 + \frac{1}{2} r1 r2 y3 y7 \\
A2 & C1 B1 \\
A2 & C2 B1 \\
& \frac{1}{2} (1 - r1) (1 - r2) y3 y7 + \frac{1}{2} r1 (1 - r2) y3 y7 + \frac{1}{2} (1 - r1) r2 y3 y7 + \frac{1}{2} r1 r2 y3 y7 \\
& \frac{1}{2} (1 - r1) (1 - r2) y3 y8 + \frac{1}{2} r1 (1 - r2) y3 y8 \\
& \frac{1}{2} (1 - r1) r2 y3 y8 + \frac{1}{2} r1 r2 y3 y8 \\
& \frac{1}{2} (1 - r1) r2 y3 y8 + \frac{1}{2} r1 r2 y3 y8 \\
& \frac{1}{2} (1 - r1) (1 - r2) y3 y8 + \frac{1}{2} r1 (1 - r2) y3 y8 \\
& \frac{1}{2} (1 - r1) (1 - r2) y1 y4 + \frac{1}{2} r1 r2 y1 y4 \\
& \frac{1}{2} r1 (1 - r2) y1 y4 + \frac{1}{2} (1 - r1) r2 y1 y4 \\
& \frac{1}{2} r1 (1 - r2) y1 y4 + \frac{1}{2} (1 - r1) r2 y1 y4 \\
& \frac{1}{2} (1 - r1) (1 - r2) y1 y4 + \frac{1}{2} r1 r2 y1 y4
\end{aligned}$$

$$\begin{aligned}
& \frac{1}{2} (1 - r1) (1 - r2) y2 y4 + \frac{1}{2} r1 (1 - r2) y2 y4 + \frac{1}{2} (1 - r1) r2 y2 y4 + \frac{1}{2} r1 r2 y2 y4 \\
& \frac{1}{2} (1 - r1) (1 - r2) y2 y4 + \frac{1}{2} r1 (1 - r2) y2 y4 + \frac{1}{2} (1 - r1) r2 y2 y4 + \frac{1}{2} r1 r2 y2 y4 \\
& \frac{1}{2} (1 - r1) (1 - r2) y3 y4 + \frac{1}{2} r1 (1 - r2) y3 y4 + \frac{1}{2} (1 - r1) r2 y3 y4 + \frac{1}{2} r1 r2 y3 y4 \\
& \frac{1}{2} (1 - r1) (1 - r2) y3 y4 + \frac{1}{2} r1 (1 - r2) y3 y4 + \frac{1}{2} (1 - r1) r2 y3 y4 + \frac{1}{2} r1 r2 y3 y4 \\
& A2 C1 B2 (1 - r1) (1 - r2) y4^2 + r1 (1 - r2) y4^2 + (1 - r1) r2 y4^2 + r1 r2 y4^2 \\
& \frac{1}{2} r1 r2 y4 y5 \\
& A1 C1 B1 \frac{1}{2} r1 (1 - r2) y4 y5 \\
& A1 C1 B2 \frac{1}{2} (1 - r1) (1 - r2) y4 y5 \\
& A1 C2 B1 \frac{1}{2} (1 - r1) r2 y4 y5 \\
& A2 C1 B1 \frac{1}{2} (1 - r1) r2 y4 y5 \\
& A2 C1 B2 \frac{1}{2} (1 - r1) (1 - r2) y4 y5 \\
& A2 C2 B1 \frac{1}{2} r1 (1 - r2) y4 y5 \\
& A2 C2 B2 \frac{1}{2} r1 r2 y4 y5 \\
& \frac{1}{2} r1 (1 - r2) y4 y6 + \frac{1}{2} r1 r2 y4 y6 \\
& A1 C1 B2 \frac{1}{2} (1 - r1) (1 - r2) y4 y6 + \frac{1}{2} (1 - r1) r2 y4 y6 \\
& A2 C1 B2 \frac{1}{2} (1 - r1) (1 - r2) y4 y6 + \frac{1}{2} (1 - r1) r2 y4 y6 \\
& A2 C2 B2 \frac{1}{2} r1 (1 - r2) y4 y6 + \frac{1}{2} r1 r2 y4 y6 \\
& A2 C1 B1 \frac{1}{2} (1 - r1) r2 y4 y7 + \frac{1}{2} r1 r2 y4 y7 \\
& A2 C1 B2 \frac{1}{2} (1 - r1) (1 - r2) y4 y7 + \frac{1}{2} r1 (1 - r2) y4 y7 \\
& A2 C2 B1 \frac{1}{2} (1 - r1) (1 - r2) y4 y7 + \frac{1}{2} r1 (1 - r2) y4 y7 \\
& A2 C2 B2 \frac{1}{2} (1 - r1) r2 y4 y7 + \frac{1}{2} r1 r2 y4 y7 \\
& A2 C1 B2 \frac{1}{2} (1 - r1) (1 - r2) y4 y8 + \frac{1}{2} r1 (1 - r2) y4 y8 + \frac{1}{2} (1 - r1) r2 y4 y8 + \frac{1}{2} r1 r2 y4 y8 \\
& A2 C2 B2 \frac{1}{2} (1 - r1) (1 - r2) y4 y8 + \frac{1}{2} r1 (1 - r2) y4 y8 + \frac{1}{2} (1 - r1) r2 y4 y8 + \frac{1}{2} r1 r2 y4 y8 \\
& A1 C1 B1 \frac{1}{2} (1 - r1) (1 - r2) y1 y5 + \frac{1}{2} r1 (1 - r2) y1 y5 + \frac{1}{2} (1 - r1) r2 y1 y5 + \frac{1}{2} r1 r2 y1 y5 \\
& A1 C2 B1 \frac{1}{2} (1 - r1) (1 - r2) y1 y5 + \frac{1}{2} r1 (1 - r2) y1 y5 + \frac{1}{2} (1 - r1) r2 y1 y5 + \frac{1}{2} r1 r2 y1 y5 \\
& A1 C1 B1 \frac{1}{2} (1 - r1) r2 y2 y5 + \frac{1}{2} r1 r2 y2 y5 \\
& A1 C1 B2 \frac{1}{2} (1 - r1) (1 - r2) y2 y5 + \frac{1}{2} r1 (1 - r2) y2 y5 \\
& A1 C2 B1 \frac{1}{2} (1 - r1) (1 - r2) y2 y5 + \frac{1}{2} r1 (1 - r2) y2 y5 \\
& A1 C2 B2 \frac{1}{2} (1 - r1) r2 y2 y5 + \frac{1}{2} r1 r2 y2 y5 \\
& A1 C1 B1 \frac{1}{2} r1 (1 - r2) y3 y5 + \frac{1}{2} r1 r2 y3 y5 \\
& A1 C1 B2 \frac{1}{2} (1 - r1) (1 - r2) y3 y5 + \frac{1}{2} (1 - r1) r2 y3 y5 \\
& A2 C1 B1 \frac{1}{2} (1 - r1) (1 - r2) y3 y5 + \frac{1}{2} (1 - r1) r2 y3 y5 \\
& A2 C2 B1 \frac{1}{2} r1 (1 - r2) y3 y5 + \frac{1}{2} r1 r2 y3 y5 \\
& A1 C1 B1 \frac{1}{2} r1 r2 y4 y5 \\
& A1 C1 B2 \frac{1}{2} (1 - r1) (1 - r2) y4 y5 \\
& A1 C2 B1 \frac{1}{2} (1 - r1) r2 y4 y5 \\
& A1 C2 B2 \frac{1}{2} (1 - r1) (1 - r2) y4 y5 \\
& A2 C1 B1 \frac{1}{2} (1 - r1) r2 y4 y5 \\
& A2 C1 B2 \frac{1}{2} (1 - r1) (1 - r2) y4 y5 \\
& A2 C2 B1 \frac{1}{2} r1 (1 - r2) y4 y5 \\
& A2 C2 B2 \frac{1}{2} r1 r2 y4 y5 \\
& A1 C2 B1 (1 - r1) (1 - r2) y5^2 + r1 (1 - r2) y5^2 + (1 - r1) r2 y5^2 + r1 r2 y5^2 \\
& A1 C2 B1 \frac{1}{2} (1 - r1) (1 - r2) y5 y6 + \frac{1}{2} r1 (1 - r2) y5 y6 + \frac{1}{2} (1 - r1) r2 y5 y6 + \frac{1}{2} r1 r2 y5 y6 \\
& A1 C2 B2 \frac{1}{2} (1 - r1) (1 - r2) y5 y6 + \frac{1}{2} r1 (1 - r2) y5 y6 + \frac{1}{2} (1 - r1) r2 y5 y6 + \frac{1}{2} r1 r2 y5 y6
\end{aligned}$$

$$\begin{aligned}
& \frac{1}{2} (1 - r1) (1 - r2) y5 y7 + \frac{1}{2} r1 (1 - r2) y5 y7 + \frac{1}{2} (1 - r1) r2 y5 y7 + \frac{1}{2} r1 r2 y5 y7 \\
& \frac{1}{2} (1 - r1) (1 - r2) y5 y7 + \frac{1}{2} r1 (1 - r2) y5 y7 + \frac{1}{2} (1 - r1) r2 y5 y7 + \frac{1}{2} r1 r2 y5 y7 \\
& \frac{1}{2} (1 - r1) (1 - r2) y5 y8 + \frac{1}{2} r1 r2 y5 y8 \\
& \frac{1}{2} r1 (1 - r2) y5 y8 + \frac{1}{2} (1 - r1) r2 y5 y8 \\
& \frac{1}{2} r1 (1 - r2) y5 y8 + \frac{1}{2} (1 - r1) r2 y5 y8 \\
& \frac{1}{2} (1 - r1) (1 - r2) y5 y8 + \frac{1}{2} r1 r2 y5 y8 \\
& \frac{1}{2} (1 - r1) (1 - r2) y1 y6 + \frac{1}{2} r1 (1 - r2) y1 y6 \\
& \frac{1}{2} (1 - r1) r2 y1 y6 + \frac{1}{2} r1 r2 y1 y6 \\
& \frac{1}{2} (1 - r1) r2 y1 y6 + \frac{1}{2} r1 r2 y1 y6 \\
& \frac{1}{2} (1 - r1) (1 - r2) y1 y6 + \frac{1}{2} r1 (1 - r2) y1 y6 \\
& \frac{1}{2} (1 - r1) (1 - r2) y2 y6 + \frac{1}{2} r1 (1 - r2) y2 y6 + \frac{1}{2} (1 - r1) r2 y2 y6 + \frac{1}{2} r1 r2 y2 y6 \\
& \frac{1}{2} (1 - r1) (1 - r2) y2 y6 + \frac{1}{2} r1 (1 - r2) y2 y6 + \frac{1}{2} (1 - r1) r2 y2 y6 + \frac{1}{2} r1 r2 y2 y6 \\
& \frac{1}{2} r1 (1 - r2) y3 y6 \\
& \frac{1}{2} r1 r2 y3 y6 \\
& \frac{1}{2} (1 - r1) r2 y3 y6 \\
& \frac{1}{2} (1 - r1) (1 - r2) y3 y6 \\
& \frac{1}{2} (1 - r1) (1 - r2) y3 y6 \\
& \frac{1}{2} r1 r2 y3 y6 \\
& \frac{1}{2} r1 (1 - r2) y3 y6 \\
& \frac{1}{2} r1 (1 - r2) y4 y6 + \frac{1}{2} r1 r2 y4 y6 \\
& \frac{1}{2} (1 - r1) (1 - r2) y4 y6 + \frac{1}{2} (1 - r1) r2 y4 y6 \\
& \frac{1}{2} (1 - r1) (1 - r2) y4 y6 + \frac{1}{2} (1 - r1) r2 y4 y6 \\
& \frac{1}{2} r1 (1 - r2) y4 y6 + \frac{1}{2} r1 r2 y4 y6 \\
& \frac{1}{2} (1 - r1) (1 - r2) y5 y6 + \frac{1}{2} r1 (1 - r2) y5 y6 + \frac{1}{2} (1 - r1) r2 y5 y6 + \frac{1}{2} r1 r2 y5 y6 \\
& \frac{1}{2} (1 - r1) (1 - r2) y5 y6 + \frac{1}{2} r1 (1 - r2) y5 y6 + \frac{1}{2} (1 - r1) r2 y5 y6 + \frac{1}{2} r1 r2 y5 y6 \\
& (1 - r1) (1 - r2) y6^2 + r1 (1 - r2) y6^2 + (1 - r1) r2 y6^2 + r1 r2 y6^2 \\
& \frac{1}{2} r1 (1 - r2) y6 y7 + \frac{1}{2} (1 - r1) r2 y6 y7 \\
& \frac{1}{2} (1 - r1) (1 - r2) y6 y7 + \frac{1}{2} r1 r2 y6 y7 \\
& \frac{1}{2} (1 - r1) (1 - r2) y6 y7 + \frac{1}{2} r1 r2 y6 y7 \\
& \frac{1}{2} r1 (1 - r2) y6 y7 + \frac{1}{2} (1 - r1) r2 y6 y7 \\
& \frac{1}{2} (1 - r1) (1 - r2) y6 y8 + \frac{1}{2} r1 (1 - r2) y6 y8 + \frac{1}{2} (1 - r1) r2 y6 y8 + \frac{1}{2} r1 r2 y6 y8 \\
& \frac{1}{2} (1 - r1) (1 - r2) y6 y8 + \frac{1}{2} r1 (1 - r2) y6 y8 + \frac{1}{2} (1 - r1) r2 y6 y8 + \frac{1}{2} r1 r2 y6 y8 \\
& \frac{1}{2} (1 - r1) (1 - r2) y1 y7 + \frac{1}{2} (1 - r1) r2 y1 y7 \\
& \frac{1}{2} r1 (1 - r2) y1 y7 + \frac{1}{2} r1 r2 y1 y7 \\
& \frac{1}{2} r1 (1 - r2) y1 y7 + \frac{1}{2} r1 r2 y1 y7 \\
& \frac{1}{2} (1 - r1) (1 - r2) y1 y7 + \frac{1}{2} (1 - r1) r2 y1 y7
\end{aligned}$$

$$\begin{aligned}
& \frac{1}{2} (1 - r1) r2 y2 y7 \\
A1 & C1 B1 \\
A1 & C1 B2 \\
A1 & C2 B1 \\
A1 & C2 B2 \\
A2 & C1 B1 \\
A2 & C1 B2 \\
A2 & C2 B1 \\
A2 & C2 B2 \\
& \frac{1}{2} (1 - r1) (1 - r2) y2 y7 \\
& \frac{1}{2} r1 (1 - r2) y2 y7 \\
& \frac{1}{2} r1 r2 y2 y7 \\
& \frac{1}{2} r1 r2 y2 y7 \\
& \frac{1}{2} r1 (1 - r2) y2 y7 \\
& \frac{1}{2} (1 - r1) (1 - r2) y2 y7 \\
& \frac{1}{2} (1 - r1) r2 y2 y7 \\
& \frac{1}{2} (1 - r1) (1 - r2) y3 y7 + \frac{1}{2} r1 (1 - r2) y3 y7 + \frac{1}{2} (1 - r1) r2 y3 y7 + \frac{1}{2} r1 r2 y3 y7 \\
A2 & C1 B1 \\
A2 & C2 B1 \\
& \frac{1}{2} (1 - r1) (1 - r2) y3 y7 + \frac{1}{2} r1 (1 - r2) y3 y7 + \frac{1}{2} (1 - r1) r2 y3 y7 + \frac{1}{2} r1 r2 y3 y7 \\
& \frac{1}{2} (1 - r1) r2 y4 y7 + \frac{1}{2} r1 r2 y4 y7 \\
A2 & C1 B2 \\
A2 & C2 B1 \\
& \frac{1}{2} (1 - r1) (1 - r2) y4 y7 + \frac{1}{2} r1 (1 - r2) y4 y7 \\
& \frac{1}{2} (1 - r1) (1 - r2) y4 y7 + \frac{1}{2} r1 (1 - r2) y4 y7 \\
& \frac{1}{2} (1 - r1) r2 y4 y7 + \frac{1}{2} r1 r2 y4 y7 \\
A1 & C2 B1 \\
A1 & C2 B2 \\
A2 & C2 B1 \\
A2 & C2 B2 \\
& \frac{1}{2} (1 - r1) (1 - r2) y5 y7 + \frac{1}{2} r1 (1 - r2) y5 y7 + \frac{1}{2} (1 - r1) r2 y5 y7 + \frac{1}{2} r1 r2 y5 y7 \\
A1 & C2 B1 \\
A1 & C2 B2 \\
& \frac{1}{2} (1 - r1) (1 - r2) y5 y7 + \frac{1}{2} r1 (1 - r2) y5 y7 + \frac{1}{2} (1 - r1) r2 y5 y7 + \frac{1}{2} r1 r2 y5 y7 \\
& \frac{1}{2} r1 (1 - r2) y6 y7 + \frac{1}{2} (1 - r1) r2 y6 y7 \\
A1 & C2 B1 \\
A1 & C2 B2 \\
A2 & C2 B1 \\
A2 & C2 B2 \\
& \frac{1}{2} (1 - r1) (1 - r2) y6 y7 + \frac{1}{2} r1 r2 y6 y7 \\
& \frac{1}{2} (1 - r1) (1 - r2) y6 y7 + \frac{1}{2} r1 r2 y6 y7 \\
& \frac{1}{2} r1 (1 - r2) y6 y7 + \frac{1}{2} (1 - r1) r2 y6 y7 \\
A2 & C2 B1 \\
& (1 - r1) (1 - r2) y7^2 + r1 (1 - r2) y7^2 + (1 - r1) r2 y7^2 + r1 r2 y7^2 \\
A2 & C2 B1 \\
A2 & C2 B2 \\
& \frac{1}{2} (1 - r1) (1 - r2) y7 y8 + \frac{1}{2} r1 (1 - r2) y7 y8 + \frac{1}{2} (1 - r1) r2 y7 y8 + \frac{1}{2} r1 r2 y7 y8 \\
& \frac{1}{2} (1 - r1) (1 - r2) y7 y8 + \frac{1}{2} r1 (1 - r2) y7 y8 + \frac{1}{2} (1 - r1) r2 y7 y8 + \frac{1}{2} r1 r2 y7 y8 \\
& \frac{1}{2} (1 - r1) (1 - r2) y1 y8 \\
& \frac{1}{2} (1 - r1) r2 y1 y8 \\
A1 & C1 B1 \\
A1 & C1 B2 \\
A1 & C2 B1 \\
A1 & C2 B2 \\
A2 & C1 B1 \\
A2 & C1 B2 \\
A2 & C2 B1 \\
A2 & C2 B2 \\
& \frac{1}{2} r1 r2 y1 y8 \\
& \frac{1}{2} r1 (1 - r2) y1 y8 \\
& \frac{1}{2} r1 (1 - r2) y1 y8 \\
& \frac{1}{2} r1 r2 y1 y8 \\
& \frac{1}{2} (1 - r1) r2 y1 y8 \\
& \frac{1}{2} (1 - r1) (1 - r2) y1 y8 \\
& \frac{1}{2} (1 - r1) (1 - r2) y2 y8 + \frac{1}{2} (1 - r1) r2 y2 y8 \\
A1 & C1 B2 \\
A1 & C2 B2 \\
A2 & C1 B2 \\
A2 & C2 B2 \\
& \frac{1}{2} r1 (1 - r2) y2 y8 + \frac{1}{2} r1 r2 y2 y8 \\
& \frac{1}{2} r1 (1 - r2) y2 y8 + \frac{1}{2} r1 r2 y2 y8 \\
& \frac{1}{2} (1 - r1) (1 - r2) y2 y8 + \frac{1}{2} (1 - r1) r2 y2 y8 \\
& \frac{1}{2} (1 - r1) (1 - r2) y3 y8 + \frac{1}{2} r1 (1 - r2) y3 y8 \\
A2 & C1 B1 \\
A2 & C1 B2 \\
A2 & C2 B1 \\
A2 & C2 B2 \\
& \frac{1}{2} (1 - r1) r2 y3 y8 + \frac{1}{2} r1 r2 y3 y8 \\
& \frac{1}{2} (1 - r1) r2 y3 y8 + \frac{1}{2} r1 r2 y3 y8 \\
& \frac{1}{2} (1 - r1) (1 - r2) y3 y8 + \frac{1}{2} r1 (1 - r2) y3 y8 \\
& \frac{1}{2} (1 - r1) (1 - r2) y4 y8 + \frac{1}{2} r1 (1 - r2) y4 y8 + \frac{1}{2} (1 - r1) r2 y4 y8 + \frac{1}{2} r1 r2 y4 y8 \\
A2 & C1 B2 \\
A2 & C2 B2 \\
& \frac{1}{2} (1 - r1) (1 - r2) y4 y8 + \frac{1}{2} r1 (1 - r2) y4 y8 + \frac{1}{2} (1 - r1) r2 y4 y8 + \frac{1}{2} r1 r2 y4 y8
\end{aligned}$$

```


$$\begin{aligned}
& \frac{1}{2} (1 - r1) (1 - r2) y5 y8 + \frac{1}{2} r1 r2 y5 y8 \\
A1 & C2 B1 \\
& \frac{1}{2} r1 (1 - r2) y5 y8 + \frac{1}{2} (1 - r1) r2 y5 y8 \\
A1 & C2 B2 \\
& \frac{1}{2} r1 (1 - r2) y5 y8 + \frac{1}{2} (1 - r1) r2 y5 y8 \\
A2 & C2 B1 \\
& \frac{1}{2} (1 - r1) (1 - r2) y5 y8 + \frac{1}{2} r1 r2 y5 y8 \\
& \frac{1}{2} (1 - r1) (1 - r2) y6 y8 + \frac{1}{2} r1 (1 - r2) y6 y8 + \frac{1}{2} (1 - r1) r2 y6 y8 + \frac{1}{2} r1 r2 y6 y8 \\
A2 & C2 B2 \\
& \frac{1}{2} (1 - r1) (1 - r2) y6 y8 + \frac{1}{2} r1 (1 - r2) y6 y8 + \frac{1}{2} (1 - r1) r2 y6 y8 + \frac{1}{2} r1 r2 y6 y8 \\
& \frac{1}{2} (1 - r1) (1 - r2) y7 y8 + \frac{1}{2} r1 (1 - r2) y7 y8 + \frac{1}{2} (1 - r1) r2 y7 y8 + \frac{1}{2} r1 r2 y7 y8 \\
A2 & C2 B1 \\
& \frac{1}{2} (1 - r1) (1 - r2) y7 y8 + \frac{1}{2} r1 (1 - r2) y7 y8 + \frac{1}{2} (1 - r1) r2 y7 y8 + \frac{1}{2} r1 r2 y7 y8 \\
A2 & C2 B2 \\
& (1 - r1) (1 - r2) y8^2 + r1 (1 - r2) y8^2 + (1 - r1) r2 y8^2 + r1 r2 y8^2 \\
\text{recSep}[[1, 1]] \\
\text{recSep}[[1, 2]] \\
\{\{A1, C1, B1\}\} \\
\{(1 - r1) (1 - r2) y1^2 + r1 (1 - r2) y1^2 + (1 - r1) r2 y1^2 + r1 r2 y1^2\} \\
\text{indices} = \text{Table}[\text{Position}[\text{recSep}[i, 1], \text{gametes}[2]], \{i, \text{Length}[\text{recSep}]\}] \\
\{\{\}, \{\{2\}\}, \{\}, \{\{2\}\}, \{\}, \{\{2\}\}, \{\}, \{\{2\}\}, \{\{1\}\}, \{\{2\}\}, \{\{1\}\}, \{\{2\}\}, \{\{1\}\}, \\
\{\{2\}\}, \{\{1\}\}, \{\}, \{\{2\}\}, \{\}, \{\}, \{\{2\}\}, \{\}, \{\}, \{\{2\}\}, \{\{1\}\}, \{\}, \{\}, \{\{2\}\}, \\
\{\{1\}\}, \{\}, \{\}, \{\}, \{\{2\}\}, \{\}, \{\{2\}\}, \{\}, \{\}, \{\{2\}\}, \{\{1\}\}, \{\{2\}\}, \{\{1\}\}, \{\}, \\
\{\}, \{\}, \{\}, \{\{2\}\}, \{\}, \{\}, \{\}, \{\}, \{\{2\}\}, \{\{1\}\}, \{\}, \{\}, \{\}, \{\}, \{\}, \{\}, \{\}, \{\}, \{\} \\
\text{Flatten}[\text{Table}[\text{Part}[\text{recSep}, i, 2] \text{Flatten}[\text{indices}[i]]], \{i, \text{Length}[\text{indices}]\}]] // \\
\text{Total} // \text{FullSimplify} \\
y2^2 + r1 (r2 y3 y6 + y4 (y5 - r2 y5 + y6)) + \\
y2 ((1 - r2 + r1 (-1 + 2 r2)) y3 + y4 + y5 - r2 y5 + y6 + (-1 + r1) ((-1 + r2) y7 - y8)) + \\
y1 (y2 + r2 (y4 + y6 + y8) + r1 (y4 - 2 r2 y4 - r2 y8))$$

```

```

In[21]:= sumPerOffspringGamete[gametes_, gameteIndex_, separateRecursions_] :=
Module[{indices, recSep, sum},
recSep = separateRecursions;
indices =
Table[Position[recSep[i, 1], gametes[gameteIndex]], {i, Length[recSep]}];
sum = Flatten[Table[Part[recSep, i, 2] \text{Flatten}[\text{indices}[i]]], {i, Length[indices]}] // Total;
Return[sum]
]

```

■ Differential equations under recombination

■ In terms of gamete frequencies

```

rec1 = sumPerOffspringGamete[gametes, 1, recSep] // FullSimplify \\
y1^2 + r2 y2 (y3 + y5 + y7) + r1 (r2 y4 y5 + y3 (y5 + y6 - r2 y6) + y2 (y3 - 2 r2 y3 - r2 y7)) + \\
y1 (y2 + y3 + (1 - r2 + r1 (-1 + 2 r2)) y4 + y5 + y6 - r2 y6 - (-1 + r1) (y7 + y8 - r2 y8))

```

The corresponding continuous-time differential equation:

```

y1D = FullSimplify[Series[rec1 - y1 /. recScale, {\epsilon, 0, 1}] /. recBackScale // Normal] \\
y1^2 + r1 y3 (y2 + y5 + y6) + r2 y2 (y3 + y5 + y7) + \\
y1 (-1 + y2 + y3 - (-1 + r1 + r2) y4 + y5 + y6 + y7 + y8 - r2 (y6 + y8) - r1 (y7 + y8)) \\
Collect[y1D, {r1, r2}] \\
-y1 + y1^2 + y1 y2 + y1 y3 + y1 y4 + y1 y5 + y1 y6 + y1 y7 + y1 y8 + \\
r2 (-y1 y4 + y2 (y3 + y5 + y7) - y1 (y6 + y8)) + r1 (-y1 y4 + y3 (y2 + y5 + y6) - y1 (y7 + y8)) \\
FullSimplify[(-y1 + y1^2 + y1 y2 + y1 y3 + y1 y4 + y1 y5 + y1 y6 + y1 y7 + y1 y8), \\
Assumptions \rightarrow {y8 = 1 - y1 - y2 - y3 - y4 - y5 - y6 - y7, y1 + y2 + y3 + y4 + y5 + y6 + y7 + y8 == 1}]

```

We note that 'y1D' can be simplified to

```
In[22]:= y1DotRec := -r1 (y1 (1 - p) - y3 p) - r2 (y1 (1 - q) - y2 q)

y1DotRec - y1D /. {p → y1 + y2 + y5 + y6, q → y1 + y3 + y5 + y7} //.
{y1 → 1 - (y2 + y3 + y4 + y5 + y6 + y7 + y8)} // Simplify
0

The following test term is from an independent derivation of Reinhard Bürger (personal communication).
```

```
testTerm1 := r2 (y[2] (y[3] + y[5] + y[7]) - y[1] (y[4] + y[6] + y[8])) +
r1 (y[3] (y[2] + y[5] + y[6]) - y[1] (y[4] + y[7] + y[8])) /.
{y[1] → y1, y[2] → y2, y[3] → y3, y[4] → y4, y[5] → y5, y[6] → y6, y[7] → y7, y[8] → y8}

r2 (-y1 y4 + y2 (y3 + y5 + y7) - y1 (y6 + y8)) +
r1 (-y1 y4 + y3 (y2 + y5 + y6) - y1 (y7 + y8)) - testTerm1 // Simplify
0

rec2 = sumPerOffspringGamete[gametes, 2, recSep] // FullSimplify

y2^2 + r1 (r2 y3 y6 + y4 (y5 - r2 y5 + y6)) +
y2 ((1 - r2 + r1 (-1 + 2 r2)) y3 + y4 + y5 - r2 y5 + y6 + (-1 + r1) ((-1 + r2) y7 - y8)) +
y1 (y2 + r2 (y4 + y6 + y8) + r1 (y4 - 2 r2 y4 - r2 y8))

y2D = FullSimplify[Series[rec2 - y2 /. recScale, {ε, 0, 1}] /. recBackScale // Normal]

y2^2 + r1 y4 (y1 + y5 + y6) + r2 y1 (y4 + y6 + y8) +
y2 (-1 + y1 - (-1 + r1 + r2) y3 + y4 + y5 + y6 + y7 - r2 (y5 + y7) + y8 - r1 (y7 + y8))

Collect[y2D, {r1, r2}]

-y2 + y1 y2 + y2^2 + y2 y3 + y2 y4 + y2 y5 + y2 y6 + y2 y7 + y2 y8 +
r2 (-y2 y3 - y2 (y5 + y7) + y1 (y4 + y6 + y8)) + r1 (-y2 y3 + y4 (y1 + y5 + y6) - y2 (y7 + y8))

FullSimplify[(-y2 + y1 y2 + y2^2 + y2 y3 + y2 y4 + y2 y5 + y2 y6 + y2 y7 + y2 y8),
Assumptions → {y8 = 1 - y1 - y2 - y3 - y4 - y5 - y6 - y7, y1 + y2 + y3 + y4 + y5 + y6 + y7 + y8 == 1}]
0
```

```
In[23]:= y2DotRec := -r1 (y2 (1 - p) - y4 p) - r2 (y2 q - y1 (1 - q))

y2DotRec - y2D /. {p → y1 + y2 + y5 + y6, q → y1 + y3 + y5 + y7} //.
{y1 → 1 - (y2 + y3 + y4 + y5 + y6 + y7 + y8)} // Simplify
0
```

The following test term is from an independent derivation of Reinhard Bürger (personal communication).

```
testTerm2 := r2 (-y[2] (y[3] + y[5] + y[7]) + y[1] (y[4] + y[6] + y[8])) +
r1 (y[4] (y[1] + y[5] + y[6]) - y[2] (y[3] + y[7] + y[8])) /.
{y[1] → y1, y[2] → y2, y[3] → y3, y[4] → y4, y[5] → y5, y[6] → y6, y[7] → y7, y[8] → y8}

r2 (-y2 y3 - y2 (y5 + y7) + y1 (y4 + y6 + y8)) +
r1 (-y2 y3 + y4 (y1 + y5 + y6) - y2 (y7 + y8)) - testTerm2 // Simplify
0

rec3 = sumPerOffspringGamete[gametes, 3, recSep] // FullSimplify

y3^2 + y3 y4 + y3 y5 - r1 y3 y5 + r2 y4 y5 - r1 r2 y4 y5 + y3 y6 - r1 y3 y6 - r2 y3 y6 +
r1 r2 y3 y6 + y3 y7 + r2 y4 y7 + y2 (y3 - r1 y3 - r2 y3 + 2 r1 r2 y3 + r1 r2 y7) +
y3 y8 - r2 y3 y8 + y1 (y3 + r2 y4 + r1 (y4 - 2 r2 y4 + y7 + y8 - r2 y8))

y3D = FullSimplify[Series[rec3 - y3 /. recScale, {ε, 0, 1}] /. recBackScale // Normal]

y3^2 + r2 y4 (y1 + y5 + y7) + r1 y1 (y4 + y7 + y8) +
y3 (-1 + y1 - (-1 + r1 + r2) y2 + y4 + y5 + y6 - r1 (y5 + y6) + y7 + y8 - r2 (y6 + y8))
```

```

Collect[y3D, {r1, r2}]

-y3 + y1 y3 + y2 y3 + y32 + y3 y4 + y3 y5 + y3 y6 + y3 y7 + y3 y8 +
r2 (-y2 y3 + y4 (y1 + y5 + y7) - y3 (y6 + y8)) + r1 (-y2 y3 - y3 (y5 + y6) + y1 (y4 + y7 + y8))

FullSimplify[(-y3 + y1 y3 + y2 y3 + y32 + y3 y4 + y3 y5 + y3 y6 + y3 y7 + y3 y8),
Assumptions → {y8 == 1 - y1 - y2 - y3 - y4 - y5 - y6 - y7, y1 + y2 + y3 + y4 + y5 + y6 + y7 + y8 == 1}]

0

In[24]:= y3DotRec := -r1 (y3 p - y1 (1 - p)) - r2 (y3 (1 - q) - y4 q)

y3DotRec - y3D /. {p → y1 + y2 + y5 + y6, q → y1 + y3 + y5 + y7} //.
{y1 → 1 - (y2 + y3 + y4 + y5 + y6 + y7 + y8)} // Simplify

0

```

The following test term is from an independent derivation of Reinhard Bürger (personal communication).

```

testTerm3 := r2 (y[4] (y[1] + y[5] + y[7]) - y[3] (y[2] + y[6] + y[8])) +
r1 (-y[3] (y[2] + y[5] + y[6]) + y[1] (y[4] + y[7] + y[8])) /.
{y[1] → y1, y[2] → y2, y[3] → y3, y[4] → y4, y[5] → y5, y[6] → y6, y[7] → y7, y[8] → y8}

r2 (-y2 y3 + y4 (y1 + y5 + y7) - y3 (y6 + y8)) +
r1 (-y2 y3 - y3 (y5 + y6) + y1 (y4 + y7 + y8)) - testTerm3 // Simplify

0

rec4 = sumPerOffspringGamete[gametes, 4, recSep] // FullSimplify

y4 (y1 + y2 + y3 + y4 + y5 + y6 + y7 + y8) + r2 (-y4 (y1 + y5 + y7) + y3 (y2 + y6 + y8)) +
r1 ((-1 + r2) y4 y5 - (r2 y3 + y4) y6 + y2 (y3 - 2 r2 y3 + y7 - r2 y7 + y8) + y1 (-y4 + 2 r2 y4 + r2 y8))

y4D = FullSimplify[Series[rec4 - y4 /. recScale, {ε, 0, 1}] /. recBackScale // Normal]

y4 (-1 + y1 + y2 + y3 + y4 + y5 + y6 + y7 + y8) +
r2 (-y4 (y1 + y5 + y7) + y3 (y2 + y6 + y8)) + r1 (-y4 (y1 + y5 + y6) + y2 (y3 + y7 + y8))

Collect[y4D, {r1, r2}]

y4 (-1 + y1 + y2 + y3 + y4 + y5 + y6 + y7 + y8) +
r2 (-y4 (y1 + y5 + y7) + y3 (y2 + y6 + y8)) + r1 (-y4 (y1 + y5 + y6) + y2 (y3 + y7 + y8))

FullSimplify[(y4 (-1 + y1 + y2 + y3 + y4 + y5 + y6 + y7 + y8)),
Assumptions → {y8 == 1 - y1 - y2 - y3 - y4 - y5 - y6 - y7, y1 + y2 + y3 + y4 + y5 + y6 + y7 + y8 == 1}]

0

In[25]:= y4DotRec := -r1 (y4 p - y2 (1 - p)) - r2 (y4 q - y3 (1 - q))

y4DotRec - y4D /. {p → y1 + y2 + y5 + y6, q → y1 + y3 + y5 + y7} //.
{y1 → 1 - (y2 + y3 + y4 + y5 + y6 + y7 + y8)} // Simplify

0

```

The following test term is from an independent derivation of Reinhard Bürger (personal communication).

```

testTerm4 := r2 (-y[4] (y[1] + y[5] + y[7]) + y[3] (y[2] + y[6] + y[8])) +
r1 (-y[4] (y[1] + y[5] + y[6]) + y[2] (y[3] + y[7] + y[8])) /.
{y[1] → y1, y[2] → y2, y[3] → y3, y[4] → y4, y[5] → y5, y[6] → y6, y[7] → y7, y[8] → y8}

r2 (-y4 (y1 + y5 + y7) + y3 (y2 + y6 + y8)) +
r1 (-y4 (y1 + y5 + y6) + y2 (y3 + y7 + y8)) - testTerm4 // Simplify

0

rec5 = sumPerOffspringGamete[gametes, 5, recSep] // FullSimplify

y3 y5 - r1 y3 y5 + y4 y5 - r1 y4 y5 - r2 y4 y5 + r1 r2 y4 y5 + y52 +
r2 y3 y6 - r1 r2 y3 y6 + y5 y6 + y5 y7 + r1 y6 y7 + r2 y6 y7 - 2 r1 r2 y6 y7 -
(-1 + r2) y2 (y5 + r1 y7) + (1 - r1 - r2 + 2 r1 r2) y5 y8 + y1 (y5 + r2 y6 + r1 y7 + r1 r2 y8)

```

```

y5D = FullSimplify[Series[rec5 - y5 /. recScale, {ε, 0, 1}] /. recBackScale // Normal]

y52 + r1 (y1 + y2 + y6) y7 + r2 y6 (y1 + y3 + y7) +
y5 (-1 + y1 + y2 - r2 y2 + y3 - r1 y3 + y4 + y6 + y7 + y8 - (r1 + r2) (y4 + y8))

Collect[y5D, {r1, r2}]

-y5 + y1 y5 + y2 y5 + y3 y5 + y4 y5 + y52 + y5 y6 + y5 y7 + y5 y8 +
r1 (-y3 y5 + (y1 + y2 + y6) y7 - y5 (y4 + y8)) + r2 (-y2 y5 + y6 (y1 + y3 + y7) - y5 (y4 + y8))

FullSimplify[(-y5 + y1 y5 + y2 y5 + y3 y5 + y4 y5 + y52 + y5 y6 + y5 y7 + y5 y8),
Assumptions → {y8 == 1 - y1 - y2 - y3 - y4 - y5 - y6 - y7, y1 + y2 + y3 + y4 + y5 + y6 + y7 + y8 == 1}]

0

In[26]:= y5DotRec := -r1 (y5 (1 - p) - y7 p) - r2 (y5 (1 - q) - y6 q)

y5DotRec - y5D /. {p → y1 + y2 + y5 + y6, q → y1 + y3 + y5 + y7} //.
{y1 → 1 - (y2 + y3 + y4 + y5 + y6 + y7 + y8)} // Simplify

0

The following test term is from an independent derivation of Reinhard Bürger (personal communication).

testTerm5 := r2 (y[6] (y[1] + y[3] + y[7]) - y[5] (y[2] + y[4] + y[8])) +
r1 ((y[1] + y[2] + y[6]) y[7] - y[5] (y[3] + y[4] + y[8])) /.
{y[1] → y1, y[2] → y2, y[3] → y3, y[4] → y4, y[5] → y5, y[6] → y6, y[7] → y7, y[8] → y8}

r1 (-y3 y5 + (y1 + y2 + y6) y7 - y5 (y4 + y8)) +
r2 (-y2 y5 + y6 (y1 + y3 + y7) - y5 (y4 + y8)) - testTerm5 // Simplify

0

rec6 = sumPerOffspringGamete[gametes, 6, recSep] // FullSimplify

y6 (y1 + y2 + y3 - r1 y3 + y4 + y5 + y6 + y7 - r1 (y4 + y7)) + (r1 (y1 + y2 + y5) + y6) y8 +
r2 (y4 (y5 - r1 y5) - y6 (y1 + y3 - r1 y3 + y7 - 2 r1 y7) + y2 (y5 + r1 y7) + (y5 - r1 (y1 + 2 y5)) y8)

y6D = FullSimplify[Series[rec6 - y6 /. recScale, {ε, 0, 1}] /. recBackScale // Normal]

y6 (-1 + y1 + y2 + y3 - r1 y3 + y4 + y5 + y6 + y7 - r1 (y4 + y7)) +
(r1 (y1 + y2 + y5) + y6) y8 + r2 (-y6 (y1 + y3 + y7) + y5 (y2 + y4 + y8))

Collect[y6D, {r1, r2}]

-y6 + y1 y6 + y2 y6 + y3 y6 + y4 y6 + y5 y6 + y62 + y6 y7 + y6 y8 +
r1 (-y3 y6 - y6 (y4 + y7) + (y1 + y2 + y5) y8) + r2 (-y6 (y1 + y3 + y7) + y5 (y2 + y4 + y8))

FullSimplify[-y6 + y1 y6 + y2 y6 + y3 y6 + y4 y6 + y5 y6 + y62 + y6 y7 + y6 y8,
Assumptions → {y8 == 1 - y1 - y2 - y3 - y4 - y5 - y6 - y7, y1 + y2 + y3 + y4 + y5 + y6 + y7 + y8 == 1}]

0

In[27]:= y6DotRec := -r1 (y6 (1 - p) - y8 p) - r2 (y6 q - y5 (1 - q))

y6DotRec - y6D /. {p → y1 + y2 + y5 + y6, q → y1 + y3 + y5 + y7} //.
{y1 → 1 - (y2 + y3 + y4 + y5 + y6 + y7 + y8)} // Simplify

0

```

The following test term is from an independent derivation of Reinhard Bürger (personal communication).

```

testTerm6 := -r1 y[6] (y[3] + y[4] + y[7]) + r1 (y[1] + y[2] + y[5]) y[8] +
r2 (-y[6] (y[1] + y[3] + y[7]) + y[5] (y[2] + y[4] + y[8])) /.
{y[1] → y1, y[2] → y2, y[3] → y3, y[4] → y4, y[5] → y5, y[6] → y6, y[7] → y7, y[8] → y8}

r1 (-y3 y6 - y6 (y4 + y7) + (y1 + y2 + y5) y8) +
r2 (-y6 (y1 + y3 + y7) + y5 (y2 + y4 + y8)) - testTerm6 // Simplify

0

```

```

rec7 = sumPerOffspringGamete[gametes, 7, recSep] // FullSimplify
y7 (y1 + y2 - r2 y2 + y3 + y4 + y5 + y6 - r2 (y4 + y6) + y7) + (r2 (y1 + y3 + y5) + y7) y8 +
r1 (y4 (y5 - r2 y5) + y3 (y5 + r2 y6) - (y1 + y2 - r2 y2 + y6 - 2 r2 y6) y7 + (y5 - r2 (y1 + 2 y5)) y8)
y7D = FullSimplify[Series[rec7 - y7 /. recScale, {ε, 0, 1}] /. recBackScale // Normal]
y7 (-1 + y1 + y2 - r2 y2 + y3 + y4 + y5 + y6 - r2 (y4 + y6) + y7) +
(r2 (y1 + y3 + y5) + y7) y8 + r1 (- (y1 + y2 + y6) y7 + y5 (y3 + y4 + y8))
Collect[y7D, {r1, r2}]
-y7 + y1 y7 + y2 y7 + y3 y7 + y4 y7 + y5 y7 + y6 y7 + y7^2 + y7 y8 +
r2 (-y2 y7 + (-y4 - y6) y7 + (y1 + y3 + y5) y8) + r1 (- (y1 + y2 + y6) y7 + y5 (y3 + y4 + y8))
FullSimplify[-y7 + y1 y7 + y2 y7 + y3 y7 + y4 y7 + y5 y7 + y6 y7 + y7^2 + y7 y8,
Assumptions → {y8 == 1 - y1 - y2 - y3 - y4 - y5 - y6 - y7, y1 + y2 + y3 + y4 + y5 + y6 + y7 + y8 == 1}]
0

In[28]:= y7DotRec := -r1 (y7 p - y5 (1 - p)) - r2 (y7 (1 - q) - y8 q)

y7DotRec - y7D /. {p → y1 + y2 + y5 + y6, q → y1 + y3 + y5 + y7} //.
{y1 → 1 - (y2 + y3 + y4 + y5 + y6 + y7 + y8)} // Simplify
0

```

The following test term is from an independent derivation of Reinhard Bürger (personal communication).

```

testTerm7 := -r2 (y[2] + y[4] + y[6]) y[7] + r2 (y[1] + y[3] + y[5]) y[8] +
r1 (- (y[1] + y[2] + y[6]) y[7] + y[5] (y[3] + y[4] + y[8])) /.
{y[1] → y1, y[2] → y2, y[3] → y3, y[4] → y4, y[5] → y5, y[6] → y6, y[7] → y7, y[8] → y8}
r2 (-y2 y7 + (-y4 - y6) y7 + (y1 + y3 + y5) y8) +
r1 (- (y1 + y2 + y6) y7 + y5 (y3 + y4 + y8)) - testTerm7 // Simplify
0

rec8 = sumPerOffspringGamete[gametes, 8, recSep] // FullSimplify
r2 (y2 + y4 + y6) y7 - r2 (y1 + y3 + y5) y8 + y8 (y1 + y2 + y3 + y4 + y5 + y6 + y7 + y8) +
r1 (y6 (y3 + y4 + y7) - (y1 + y2 + y5) y8 + r2 (-y2 y7 - y6 (y3 + 2 y7) + y1 y8 + y5 (y4 + 2 y8)))
y8D = FullSimplify[Series[rec8 - y8 /. recScale, {ε, 0, 1}] /. recBackScale // Normal]
r2 (y2 + y4 + y6) y7 + r1 y6 (y3 + y4 + y7) - r1 (y1 + y2 + y5) y8 -
r2 (y1 + y3 + y5) y8 + y8 (-1 + y1 + y2 + y3 + y4 + y5 + y6 + y7 + y8)
Collect[y8D, {r1, r2}]
y8 (-1 + y1 + y2 + y3 + y4 + y5 + y6 + y7 + y8) +
r1 (y6 (y3 + y4 + y7) + (-y1 - y2 - y5) y8) + r2 ((y2 + y4 + y6) y7 + (-y1 - y3 - y5) y8)
FullSimplify[y8 (-1 + y1 + y2 + y3 + y4 + y5 + y6 + y7 + y8),
Assumptions → {y8 == 1 - y1 - y2 - y3 - y4 - y5 - y6 - y7, y1 + y2 + y3 + y4 + y5 + y6 + y7 + y8 == 1}]
0

```

```

In[29]:= y8DotRec := -r1 (y8 p - y6 (1 - p)) - r2 (y8 q - y7 (1 - q))

y8DotRec - y8D /. {p → y1 + y2 + y5 + y6, q → y1 + y3 + y5 + y7} //.
{y1 → 1 - (y2 + y3 + y4 + y5 + y6 + y7 + y8)} // Simplify
0

```

The following test term is from an independent derivation of Reinhard Bürger (personal communication).

```

testTerm8 := r2 (y[2] + y[4] + y[6]) y[7] + r1 y[6] (y[3] + y[4] + y[7]) -
r1 (y[1] + y[2] + y[5]) y[8] - r2 (y[1] + y[3] + y[5]) y[8] /.
{y[1] → y1, y[2] → y2, y[3] → y3, y[4] → y4, y[5] → y5, y[6] → y6, y[7] → y7, y[8] → y8}

```

```
r1 (y6 (y3 + y4 + y7) + (-y1 - y2 - y5) y8) +
r2 ((y2 + y4 + y6) y7 + (-y1 - y3 - y5) y8) - testTerm8 // Simplify
0
```

Some further tests:

```
y1DotRec + y5DotRec // FullSimplify
r2 ((-1 + q) y1 - y5 + q (y2 + y5 + y6)) + r1 ((-1 + p) y1 - y5 + p (y3 + y5 + y7))
```

A bit of algebra confirms that this is equal to $(r_{AC} + r_{CB})(p q - y_1 - y_5) = -r_{AB} D_{AB}$, as expected from the marginal two-locus system.

```
y2DotRec + y6DotRec // FullSimplify
-r2 ((-1 + q) y1 - y5 + q (y2 + y5 + y6)) + r1 ((-1 + p) y2 - y6 + p (y4 + y6 + y8))
```

Again, some algebra confirms that this is equal to $(r_{AC} + r_{CB})(-p q + y_1 + y_5) = r_{AB} D_{AB}$, as expected from the marginal two-locus system. To see this, note that D_{AB} can also be defined as $-(y_2 + y_6) + p(1 - q)$.

```
y3DotRec + y7DotRec // FullSimplify
-r1 ((-1 + p) y1 - y5 + p (y3 + y5 + y7)) + r2 ((-1 + q) y3 - y7 + q (y4 + y7 + y8))
```

Noting that D_{AB} can also be defined as $-(y_3 + y_7) + (1 - p)q$, one can show that this is equal to $(r_{AC} + r_{CB})(-p q + y_1 + y_5) = r_{AB} D_{AB}$, as expected from the marginal two-locus system.

```
y4DotRec + y8DotRec // FullSimplify
-r1 ((-1 + p) y2 - y6 + p (y4 + y6 + y8)) - r2 ((-1 + q) y3 - y7 + q (y4 + y7 + y8))
```

which is equal to $(r_{AC} + r_{CB})(y_2 + y_6 - p(1 - q)) = -r_{AB} D_{AB}$, as expected from the marginal two-locus system.

■ In terms of allele frequencies and LD

```
allToGam
{p → y1 + y2 + y5 + y6, q → y1 + y3 + y5 + y7, n → y1 + y2 + y3 + y4}

DACPDefAlt := y1 - (y1 + y2 + y5 + y6) (y1 + y3 + y5 + y7) (y1 + y2 + y3 + y4) -
(y1 + y2 + y5 + y6) ((y1 + y3) (y6 + y8) - (y2 + y4) (y5 + y7)) -
(y1 + y3 + y5 + y7) ((y1 + y2) (y7 + y8) - (y5 + y6) (y3 + y4)) -
(y1 + y2 + y3 + y4) ((y1 + y5) (y4 + y8) - (y2 + y6) (y3 + y7))

DACPDefAlt - DACPDef
0

DACPDef // FullSimplify
y1 - (y1 + y2 + y3 + y4) (y1 + y2 + y5 + y6) (y1 + y3 + y5 + y7) -
(y1 + y2 + y3 + y4) (- (y2 + y6) (y3 + y7) + (y1 + y5) (y4 + y8)) -
(y1 + y2 + y5 + y6) (- (y2 + y4) (y5 + y7) + (y1 + y3) (y6 + y8)) -
(y1 + y3 + y5 + y7) (- (y3 + y4) (y5 + y6) + (y1 + y2) (y7 + y8))

DANB[1] // . {x_[i_], j_] → x[i]} /.
{y[1] → y1, y[2] → y2, y[3] → y3, y[4] → y4, y[5] → y5, y[6] → y6, y[7] → y7, y[8] → y8}
DANB[1]
```

```
In[30]:= pDotRec := D[pDef /. {y1 → y1[t], y2 → y2[t], y5 → y5[t], y6 → y6[t]}, t] /.
   {y1'[t] → y1DotRec, y2'[t] → y2DotRec, y5'[t] → y5DotRec, y6'[t] → y6DotRec} /.
   gamToAllLD // FullSimplify
qDotRec := D[qDef /. {y1 → y1[t], y3 → y3[t], y5 → y5[t], y7 → y7[t]}, t] /.
   {y1'[t] → y1DotRec, y3'[t] → y3DotRec, y5'[t] → y5DotRec, y7'[t] → y7DotRec} /.
   gamToAllLD // FullSimplify
nDotRec := D[nDef /. {y1 → y1[t], y2 → y2[t], y3 → y3[t], y4 → y4[t]}, t] /.
   {y1'[t] → y1DotRec, y2'[t] → y2DotRec, y3'[t] → y3DotRec, y4'[t] → y4DotRec} /.
   gamToAllLD // FullSimplify
DACDotRec := D[DACDef /. {y1 → y1[t], y2 → y2[t], y3 → y3[t],
   y4 → y4[t], y5 → y5[t], y6 → y6[t], y7 → y7[t], y8 → y8[t]}, t] /.
   {y1'[t] → y1DotRec, y2'[t] → y2DotRec, y3'[t] → y3DotRec, y4'[t] → y4DotRec,
   y5'[t] → y5DotRec, y6'[t] → y6DotRec, y7'[t] → y7DotRec, y8'[t] → y8DotRec} /.
   {x_[t] → x} /. gamToAllLD // FullSimplify
DCBDotRec := D[DCBDef /. {y1 → y1[t], y2 → y2[t], y3 → y3[t], y4 → y4[t],
   y5 → y5[t], y6 → y6[t], y7 → y7[t], y8 → y8[t]}, t] /.
   {y1'[t] → y1DotRec, y2'[t] → y2DotRec, y3'[t] → y3DotRec, y4'[t] → y4DotRec,
   y5'[t] → y5DotRec, y6'[t] → y6DotRec, y7'[t] → y7DotRec, y8'[t] → y8DotRec} /.
   {x_[t] → x} /. gamToAllLD // FullSimplify
DABDotRec := D[DABDef /. {y1 → y1[t], y2 → y2[t], y3 → y3[t], y4 → y4[t],
   y5 → y5[t], y6 → y6[t], y7 → y7[t], y8 → y8[t]}, t] /.
   {y1'[t] → y1DotRec, y2'[t] → y2DotRec, y3'[t] → y3DotRec, y4'[t] → y4DotRec,
   y5'[t] → y5DotRec, y6'[t] → y6DotRec, y7'[t] → y7DotRec, y8'[t] → y8DotRec} /.
   {x_[t] → x} /. gamToAllLD // FullSimplify
DACBDotRec := D[DACBDef /. {y1 → y1[t], y2 → y2[t], y3 → y3[t],
   y4 → y4[t], y5 → y5[t], y6 → y6[t], y7 → y7[t], y8 → y8[t]}, t] /.
   {y1'[t] → y1DotRec, y2'[t] → y2DotRec, y3'[t] → y3DotRec, y4'[t] → y4DotRec,
   y5'[t] → y5DotRec, y6'[t] → y6DotRec, y7'[t] → y7DotRec, y8'[t] → y8DotRec} /.
   {x_[t] → x} /. gamToAllLD // FullSimplify
{pDotRec, qDotRec, nDotRec, DACDotRec, DCBDotRec, DABDotRec, DACBDotRec} // TableForm
0
0
0
-DAC r1
-DCB r2
-DAB (r1 + r2)
-DACB (r1 + r2)

An independently derived test term (Reinhard Bürger, personal communication):
testTerm := y1 - (y1 + y2 + y3 + y4) (y1 + y2 + y5 + y6) (y1 + y3 + y5 + y7) -
(y1 + y2 + y3 + y4) ((-y2 - y6) (y3 + y7) + (y1 + y5) (y4 + y8)) -
(y1 + y2 + y5 + y6) ((-y2 - y4) (y5 + y7) + (y1 + y3) (y6 + y8)) -
(y1 + y3 + y5 + y7) ((-y3 - y4) (y5 + y6) + (y1 + y2) (y7 + y8))
DACBDef - testTerm // FullSimplify
0
testTerm
y1 - (y1 + y2 + y3 + y4) (y1 + y2 + y5 + y6) (y1 + y3 + y5 + y7) -
(y1 + y2 + y3 + y4) ((-y2 - y6) (y3 + y7) + (y1 + y5) (y4 + y8)) -
(y1 + y2 + y5 + y6) ((-y2 - y4) (y5 + y7) + (y1 + y3) (y6 + y8)) -
(y1 + y3 + y5 + y7) ((-y3 - y4) (y5 + y6) + (y1 + y2) (y7 + y8))

In[37]:= DACBRule := y1 - p q n - p (y1 + y3 - q n) - q (y1 + y2 - p n) - n (y1 + y5 - p q)
```

■ Differential equations under migration

■ In terms of gamete frequencies

```
In[38]:= 
y1DotMig := -m y1
y2DotMig := -m y2
y3DotMig := -m y3
y4DotMig := m (nC - y4)
y5DotMig := -m y5
y6DotMig := -m y6
y7DotMig := -m y7
y8DotMig := m (1 - nC - y8)

FullSimplify[y1DotMig + y2DotMig + y3DotMig + y4DotMig + y5DotMig + y6DotMig +
y7DotMig + y8DotMig, Assumptions -> {y1 + y2 + y3 + y4 + y5 + y6 + y7 + y8 == 1}]
0

FullSimplify[y1DotMig + y5DotMig /. {y2 + y4 + y6 + y8 -> x2 + x4} /.
{y3 + y4 + y7 + y8 -> x3 + x4}] /. {y1 + y5 -> x1}
-m x1

FullSimplify[y2DotMig + y6DotMig /. {y1 + y3 + y5 + y7 -> x1 + x3, y3 + y4 + y7 + y8 -> x3 + x4}] /.
{y2 + y6 -> x2}
-m x2

FullSimplify[y3DotMig + y7DotMig /. {y1 + y2 + y5 + y6 -> x1 + x2, y2 + y4 + y6 + y8 -> x2 + x4}] /.
{y3 + y7 -> x3}
-m x3

FullSimplify[y4DotMig + y8DotMig /. {y1 + y2 + y5 + y6 -> x1 + x2, y1 + y3 + y5 + y7 -> x1 + x3}] /.
{y4 + y8 -> x4}
-m (-1 + x4)

■ In terms of allele frequencies and LD
```

allToGam

{p → y1 + y2 + y5 + y6, q → y1 + y3 + y5 + y7, n → y1 + y2 + y3 + y4}

```
In[46]:= pDotMig := D[pDef /. {y1 → y1[t], y2 → y2[t], y5 → y5[t], y6 → y6[t]}, t] /.
   {y1'[t] → y1DotMig, y2'[t] → y2DotMig, y5'[t] → y5DotMig, y6'[t] → y6DotMig} /.
   gamToAllLD // FullSimplify
qDotMig := D[qDef /. {y1 → y1[t], y3 → y3[t], y5 → y5[t], y7 → y7[t]}, t] /.
   {y1'[t] → y1DotMig, y3'[t] → y3DotMig, y5'[t] → y5DotMig, y7'[t] → y7DotMig} /.
   gamToAllLD // FullSimplify
nDotMig := D[nDef /. {y1 → y1[t], y2 → y2[t], y3 → y3[t], y4 → y4[t]}, t] /.
   {y1'[t] → y1DotMig, y2'[t] → y2DotMig, y3'[t] → y3DotMig, y4'[t] → y4DotMig} /.
   gamToAllLD // FullSimplify
DACDotMig := D[DACDef /. {y1 → y1[t], y2 → y2[t], y3 → y3[t],
   y4 → y4[t], y5 → y5[t], y6 → y6[t], y7 → y7[t], y8 → y8[t]}, t] /.
   {y1'[t] → y1DotMig, y2'[t] → y2DotMig, y3'[t] → y3DotMig, y4'[t] → y4DotMig,
   y5'[t] → y5DotMig, y6'[t] → y6DotMig, y7'[t] → y7DotMig, y8'[t] → y8DotMig} /.
   {x_[t] → x} /. gamToAllLD // FullSimplify
DCBDotMig := D[DCBDef /. {y1 → y1[t], y2 → y2[t], y3 → y3[t], y4 → y4[t],
   y5 → y5[t], y6 → y6[t], y7 → y7[t], y8 → y8[t]}, t] /.
   {y1'[t] → y1DotMig, y2'[t] → y2DotMig, y3'[t] → y3DotMig, y4'[t] → y4DotMig,
   y5'[t] → y5DotMig, y6'[t] → y6DotMig, y7'[t] → y7DotMig, y8'[t] → y8DotMig} /.
   {x_[t] → x} /. gamToAllLD // FullSimplify
DABDotMig := D[DABDef /. {y1 → y1[t], y2 → y2[t], y3 → y3[t], y4 → y4[t],
   y5 → y5[t], y6 → y6[t], y7 → y7[t], y8 → y8[t]}, t] /.
   {y1'[t] → y1DotMig, y2'[t] → y2DotMig, y3'[t] → y3DotMig, y4'[t] → y4DotMig,
   y5'[t] → y5DotMig, y6'[t] → y6DotMig, y7'[t] → y7DotMig, y8'[t] → y8DotMig} /.
   {x_[t] → x} /. gamToAllLD // FullSimplify
DACPBDotMig := D[DACPBDDef /. {y1 → y1[t], y2 → y2[t], y3 → y3[t],
   y4 → y4[t], y5 → y5[t], y6 → y6[t], y7 → y7[t], y8 → y8[t]}, t] /.
   {y1'[t] → y1DotMig, y2'[t] → y2DotMig, y3'[t] → y3DotMig, y4'[t] → y4DotMig,
   y5'[t] → y5DotMig, y6'[t] → y6DotMig, y7'[t] → y7DotMig, y8'[t] → y8DotMig} /.
   {x_[t] → x} /. gamToAllLD // FullSimplify
```

Test of the pattern rule $x_{\cdot}[t] \rightarrow x$:

```
D[DACPBDDef /. {y1 → y1[t], y2 → y2[t], y3 → y3[t],
   y4 → y4[t], y5 → y5[t], y6 → y6[t], y7 → y7[t], y8 → y8[t]}, t] /.
   {y1'[t] → y1DotMig, y2'[t] → y2DotMig, y3'[t] → y3DotMig, y4'[t] → y4DotMig,
   y5'[t] → y5DotMig, y6'[t] → y6DotMig, y7'[t] → y7DotMig, y8'[t] → y8DotMig} /.
   ruleRemoveDummy /. gamToAllLD // FullSimplify
m (-DACPBD + DCB p + DAC q + (n - nC) (DAB - p q))
%- DACBDotMig // FullSimplify
0
In[53]:= ruleRemoveDummy := {y1[t] → y1, y2[t] → y2, y3[t] → y3,
   y4[t] → y4, y5[t] → y5, y6[t] → y6, y7[t] → y7, y8[t] → y8}
{pDotMig, qDotMig, nDotMig, DACDotMig, DCBDotMig, DABDotMig, DACPBDotMig} // TableForm
- m p
- m q
m (-n + nC)
- m (DAC + (-n + nC) p)
- m (DCB + (-n + nC) q)
-DAB m + m p q
m (-DACPBD + DCB p + DAC q + (n - nC) (DAB - p q))
```

■ Differential equations under selection

■ In terms of gamete frequencies

```
In[54]:= 
y1DotSel := y1 (a (y3 + y4 + y7 + y8) + b (y2 + y4 + y6 + y8))
y2DotSel := y2 (a (y3 + y4 + y7 + y8) - b (y1 + y3 + y5 + y7))
y3DotSel := y3 (-a (y1 + y2 + y5 + y6) + b (y2 + y4 + y6 + y8))
y4DotSel := y4 (-a (y1 + y2 + y5 + y6) - b (y1 + y3 + y5 + y7))

y5DotSel := y5 (a (y3 + y4 + y7 + y8) + b (y2 + y4 + y6 + y8))
y6DotSel := y6 (a (y3 + y4 + y7 + y8) - b (y1 + y3 + y5 + y7))
y7DotSel := y7 (-a (y1 + y2 + y5 + y6) + b (y2 + y4 + y6 + y8))
y8DotSel := y8 (-a (y1 + y2 + y5 + y6) - b (y1 + y3 + y5 + y7))

FullSimplify[y1DotSel + y5DotSel /. {y2 + y4 + y6 + y8 → x2 + x4} /.
{y3 + y4 + y7 + y8 → x3 + x4}] /. {y1 + y5 → x1}
x1 (b (x2 + x4) + a (x3 + x4))

FullSimplify[y2DotSel + y6DotSel /. {y1 + y3 + y5 + y7 → x1 + x3, y3 + y4 + y7 + y8 → x3 + x4}] /.
{y2 + y6 → x2}
x2 (-b (x1 + x3) + a (x3 + x4))

FullSimplify[y3DotSel + y7DotSel /. {y1 + y2 + y5 + y6 → x1 + x2, y2 + y4 + y6 + y8 → x2 + x4}] /.
{y3 + y7 → x3}
x3 (-a (x1 + x2) + b (x2 + x4))

FullSimplify[y4DotSel + y8DotSel /. {y1 + y2 + y5 + y6 → x1 + x2, y1 + y3 + y5 + y7 → x1 + x3}] /.
{y4 + y8 → x4}
- (a (x1 + x2) + b (x1 + x3)) x4
```

■ In terms of allele frequencies and LD

allToGam

{p → y1 + y2 + y5 + y6, q → y1 + y3 + y5 + y7, n → y1 + y2 + y3 + y4}

```
In[62]:= pDotSel := D[pDef /. {y1 → y1[t], y2 → y2[t], y5 → y5[t], y6 → y6[t]}, t] /.
   {y1'[t] → y1DotSel, y2'[t] → y2DotSel, y5'[t] → y5DotSel, y6'[t] → y6DotSel} /.
   gamToAllLD // FullSimplify
qDotSel := D[qDef /. {y1 → y1[t], y3 → y3[t], y5 → y5[t], y7 → y7[t]}, t] /.
   {y1'[t] → y1DotSel, y3'[t] → y3DotSel, y5'[t] → y5DotSel, y7'[t] → y7DotSel} /.
   gamToAllLD // FullSimplify
nDotSel := D[nDef /. {y1 → y1[t], y2 → y2[t], y3 → y3[t], y4 → y4[t]}, t] /.
   {y1'[t] → y1DotSel, y2'[t] → y2DotSel, y3'[t] → y3DotSel, y4'[t] → y4DotSel} /.
   gamToAllLD // FullSimplify
DACDotSel := D[DACDef /. {y1 → y1[t], y2 → y2[t], y3 → y3[t],
   y4 → y4[t], y5 → y5[t], y6 → y6[t], y7 → y7[t], y8 → y8[t]}, t] /.
   {y1'[t] → y1DotSel, y2'[t] → y2DotSel, y3'[t] → y3DotSel, y4'[t] → y4DotSel,
   y5'[t] → y5DotSel, y6'[t] → y6DotSel, y7'[t] → y7DotSel, y8'[t] → y8DotSel} /.
   {x_[t] → x} /. gamToAllLD // FullSimplify
DCBDotSel := D[DCBDef /. {y1 → y1[t], y2 → y2[t], y3 → y3[t], y4 → y4[t],
   y5 → y5[t], y6 → y6[t], y7 → y7[t], y8 → y8[t]}, t] /.
   {y1'[t] → y1DotSel, y2'[t] → y2DotSel, y3'[t] → y3DotSel, y4'[t] → y4DotSel,
   y5'[t] → y5DotSel, y6'[t] → y6DotSel, y7'[t] → y7DotSel, y8'[t] → y8DotSel} /.
   {x_[t] → x} /. gamToAllLD // FullSimplify
DABDotSel := D[DABDef /. {y1 → y1[t], y2 → y2[t], y3 → y3[t], y4 → y4[t],
   y5 → y5[t], y6 → y6[t], y7 → y7[t], y8 → y8[t]}, t] /.
   {y1'[t] → y1DotSel, y2'[t] → y2DotSel, y3'[t] → y3DotSel, y4'[t] → y4DotSel,
   y5'[t] → y5DotSel, y6'[t] → y6DotSel, y7'[t] → y7DotSel, y8'[t] → y8DotSel} /.
   {x_[t] → x} /. gamToAllLD // FullSimplify
DACBDotSel := D[DACBDef /. {y1 → y1[t], y2 → y2[t], y3 → y3[t],
   y4 → y4[t], y5 → y5[t], y6 → y6[t], y7 → y7[t], y8 → y8[t]}, t] /.
   {y1'[t] → y1DotSel, y2'[t] → y2DotSel, y3'[t] → y3DotSel, y4'[t] → y4DotSel,
   y5'[t] → y5DotSel, y6'[t] → y6DotSel, y7'[t] → y7DotSel, y8'[t] → y8DotSel} /.
   {x_[t] → x} /. gamToAllLD // FullSimplify

{pDotSel, qDotSel, nDotSel, DACDotSel, DCBDotSel, DABDotSel, DACBDotSel} // TableForm

b DAB - a (-1 + p) p
a DAB - b (-1 + q) q
a DAC + b DCB
b DACB + a (DAC - 2 DAC p)
a DACB + b DCB (1 - 2 q)
DAB (a + b - 2 a p - 2 b q)
a (-2 DAB DAC + DACB - 2 DACB p) + b (DACB - 2 DAB DCB - 2 DACB q)
```

■ Differential equations under selection, migration and recombination

■ Remark

As we are assuming continuous-time dynamics, interactions of selection, migration and recombinations are ignored and the order of the processes is irrelevant. Therefore, the overall differential equations are obtained by adding those for the single processes.

■ In terms of gamete frequencies

```
In[69]:= y1Dot := y1DotSel + y1DotMig + y1DotRec
y2Dot := y2DotSel + y2DotMig + y2DotRec
y3Dot := y3DotSel + y3DotMig + y3DotRec
y4Dot := y4DotSel + y4DotMig + y4DotRec

y5Dot := y5DotSel + y5DotMig + y5DotRec
y6Dot := y6DotSel + y6DotMig + y6DotRec
y7Dot := y7DotSel + y7DotMig + y7DotRec
y8Dot := y8DotSel + y8DotMig + y8DotRec

Simplify[y4DotSel + y4DotMig]

m (nC - y4) - y4 (a (y1 + y2 + y5 + y6) + b (y1 + y3 + y5 + y7))
```

```

{y1Dot, y2Dot, y3Dot, y4Dot, y5Dot, y6Dot, y7Dot, y8Dot} // Simplify // TableForm

-m y1 + r2 ((-1 + q) y1 + q y2) + r1 ((-1 + p) y1 + p y3) + y1 (b (y2 + y4 + y6 + y8) + a (y3 + y4 + y7 + y8)
-m y2 - r2 ((-1 + q) y1 + q y2) + r1 ((-1 + p) y2 + p y4) + y2 (-b (y1 + y3 + y5 + y7) + a (y3 + y4 + y7 + y8)
-m y3 - r1 ((-1 + p) y1 + p y3) + r2 ((-1 + q) y3 + q y4) + y3 (-a (y1 + y2 + y5 + y6) + b (y2 + y4 + y6 + y8)
m (nC - y4) - r1 ((-1 + p) y2 + p y4) - r2 ((-1 + q) y3 + q y4) + y4 (-a (y1 + y2 + y5 + y6) - b (y1 + y3 + y7 + y8)
-m y5 + r2 ((-1 + q) y5 + q y6) + r1 ((-1 + p) y5 + p y7) + y5 (b (y2 + y4 + y6 + y8) + a (y3 + y4 + y7 + y8)
-m y6 - r2 ((-1 + q) y5 + q y6) + r1 ((-1 + p) y6 + p y8) + y6 (-b (y1 + y3 + y5 + y7) + a (y3 + y4 + y7 + y8)
-m y7 - r1 ((-1 + p) y5 + p y7) + r2 ((-1 + q) y7 + q y8) + y7 (-a (y1 + y2 + y5 + y6) + b (y2 + y4 + y6 + y8)
(-a (y1 + y2 + y5 + y6) - b (y1 + y3 + y5 + y7)) y8 - m (-1 + nC + y8) - r1 ((-1 + p) y6 + p y8) - r2 ((-1 + q) y7 + q y8)

Map[Collect[#, {m, r1, r2}] &,
{y1Dot, y2Dot, y3Dot, y4Dot, y5Dot, y6Dot, y7Dot, y8Dot}] // TableForm

-m y1 + r2 ((-1 - q) y1 + q y2) + r1 ((-1 - p) y1 + p y3) + y1 (b (y2 + y4 + y6 + y8) + a (y3 + y4 + y7 + y8)
-m y2 + r2 ((1 - q) y1 - q y2) + r1 ((-1 - p) y2 + p y4) + y2 (-b (y1 + y3 + y5 + y7) + a (y3 + y4 + y7 + y8)
-m y3 + r1 ((1 - p) y1 - p y3) + r2 ((-1 - q) y3 + q y4) + y3 (-a (y1 + y2 + y5 + y6) + b (y2 + y4 + y6 + y8)
m (nC - y4) + r1 ((1 - p) y2 - p y4) + r2 ((1 - q) y3 - q y4) + y4 (-a (y1 + y2 + y5 + y6) - b (y1 + y3 + y5 + y7 + y8)
-m y5 + r2 ((-1 - q) y5 + q y6) + r1 ((-1 - p) y5 + p y7) + y5 (b (y2 + y4 + y6 + y8) + a (y3 + y4 + y7 + y8)
-m y6 + r2 ((1 - q) y5 - q y6) + r1 ((-1 - p) y6 + p y8) + y6 (-b (y1 + y3 + y5 + y7) + a (y3 + y4 + y7 + y8)
-m y7 + r1 ((1 - p) y5 - p y7) + r2 ((-1 - q) y7 + q y8) + y7 (-a (y1 + y2 + y5 + y6) + b (y2 + y4 + y6 + y8)
m (1 - nC - y8) + (-a (y1 + y2 + y5 + y6) - b (y1 + y3 + y5 + y7)) y8 + r1 ((1 - p) y6 - p y8) + r2 ((1 - q) y7 + q y8)

```

■ In terms of allele frequencies and LD

nDotMig

m (-n + nC)

nDotSel

a DAC + b DCB

```

In[77]:= pDot := pDotSel + pDotMig + pDotRec
qDot := qDotSel + qDotMig + qDotRec
nDot := nDotSel + nDotMig + nDotRec
DACDot := DACDotSel + DACDotMig + DACDotRec
DCBDot := DCBDotSel + DCBDotMig + DCBDotRec
DABDot := DABDotSel + DABDotMig + DABDotRec
DACPBDot := DACPBDotSel + DACPBDotMig + DACPBDotRec

```

```

{pDot, qDot, nDot, DACDot, DCBDot, DABDot, DACPBDot} // Simplify // TableForm

b DAB - (m + a (-1 + p)) p
a DAB - (m + b (-1 + q)) q
a DAC + b DCB + m (-n + nC)
b DACB + a (DAC - 2 DAC p) - m (DAC + (-n + nC) p) - DAC r1
a DACB + b DCB (1 - 2 q) - m (DCB + (-n + nC) q) - DCB r2
-DAB m + m p q + DAB (a + b - 2 a p - 2 b q) - DAB (r1 + r2)
a (-2 DAB DAC + DACB - 2 DACB p) + b (DACB - 2 DAB DCB - 2 DACB q) + m (-DACB + DCB p + DAC q + (n - nC)) (I
Collect[DACPBDot, {DAB, DAC, DCB, DACB}]

DAB (-2 a DAC - 2 b DCB + m (n - nC)) + DCB m p +
DAC m q - m (n - nC) p q + DACB (a + b - m - 2 a p - 2 b q - r1 - r2)
FullSimplify[(a + b - m - 2 a p - 2 b q - r1 - r2)]

a + b - m - 2 a p - 2 b q - r1 - r2

```

```

Map[Collect[#, {m, r1, r2}] &,
{pDot, qDot, nDot, DACDot, DCBDot, DABDot, DACBDot}] // TableForm

b DAB - m p - a (-1 + p) p
a DAB - m q - b (-1 + q) q
a DAC + b DCB + m (-n + nC)
b DACB + a (DAC - 2 DAC p) + m (-DAC - (-n + nC) p) - DAC r1
a DACB + b DCB (1 - 2 q) + m (-DCB - (-n + nC) q) - DCB r2
DAB (a + b - 2 a p - 2 b q) + m (-DAB + p q) - DAB r1 - DAB r2
a (-2 DAB DAC + DACB - 2 DACB p) + b (DACB - 2 DAB DCB - 2 DACB q) + m (-DACB + DCB p + DAC q + (n - nC)) (I)

```

These are the differential equations given by BA2011 for n , D_{AC} , D_{CB} and D_{ACB} , which are obviously different from those just above.

```

In[84]:= nDotTarget := m ((nC - n) (p + q - p q) - DAC (1 - q) - DCB (1 - p) + DACB) + a DAC + b DCB
DACDotTarget := -(r1 + m (1 - p + p q) - a (1 - 2 p)) DAC +
    m p (1 - p) DCB + m (nC - n) p DAB + (b - m p) DACB + m (nC - n) p (p + q - p q)
DCBDotTarget := -(r2 + m (1 - q + p q) - b (1 - 2 q)) DCB + m q (1 - q) DAC +
    m (nC - n) q DACB + (a - m q) DACB + m (nC - n) q (p + q - p q)
DACBDotTarget := m p q (nC - n) (p + q - p q) + m q (1 - (1 - q) p) DAC + m p (1 - (1 - p) q) DCB -
    m (nC - n) (p + q) DAB - (r1 + r2 + m (1 - p q) - a (1 - 2 p) - b (1 - 2 q)) DACB +
    m (nC - n) DAB2 + (m (1 - q) - 2 a) DAB DAC + (m (1 - p) - 2 b) DAB DCB - m DAB DACB

```

Internal equilibrium

■ Coordinates

We recall the differential equations:

```

In[88]:= diffEqs =
    Map[Collect[#, {m, r1, r2}] &, {pDot, qDot, DABDot, nDot, DACDot, DCBDot, DACBDot}];
diffEqs // TableForm

Out[89]//TableForm=
b DAB - m p - a (-1 + p) p
a DAB - m q - b (-1 + q) q
DAB (a + b - 2 a p - 2 b q) + m (-DAB + p q) - DAB r1 - DAB r2
a DAC + b DCB + m (-n + nC)
b DACB + a (DAC - 2 DAC p) + m (-DAC - (-n + nC) p) - DAC r1
a DACB + b DCB (1 - 2 q) + m (-DCB - (-n + nC) q) - DCB r2
a (-2 DAB DAC + DACB - 2 DACB p) + b (DACB - 2 DAB DCB - 2 DACB q) + m (-DACB + DCB p + DAC q + (n - nC)) (I)

In[90]:= diffEqsTarget = Map[Collect[#, {m, r1, r2}] &,
    {pDot, qDot, DABDot, nDotTarget, DACDotTarget, DCBDotTarget, DACBDotTarget}];
diffEqsTarget // TableForm

Out[91]//TableForm=
b DAB - m p - a (-1 + p) p
a DAB - m q - b (-1 + q) q
DAB (a + b - 2 a p - 2 b q) + m (-DAB + p q) - DAB r1 - DAB r2
a DAC + b DCB + m (DACB - DCB (1 - p) - DAC (1 - q) + (-n + nC) (p + q - p q))
b DACB + a DAC (1 - 2 p) + m (-DACB p + DAB (-n + nC) p + DCB (1 - p) p + (-n + nC) p (p + q - p q) - DAC (1 -
a DACB + b DCB (1 - 2 q) + m (-DACB q + DAB (-n + nC) q + DAC (1 - q) q + (-n + nC) q (p + q - p q) - DCB (1 -
- 2 a DAB DAC - 2 b DAB DCB + a DACB (1 - 2 p) + b DACB (1 - 2 q) + m (-DAB DACB + DAB2 (-n + nC) + DAB DCB

For testing purposes, we introduce equations independently derived by Reinhard Bürger (Mathematica Notebook 'Three_Loci_gen1.nb', personal communication):
```

```

In[92]:= testEqs := { - (-1 + p) p α + DAB β - p μ, DAB α - (-1 + q) q β - q μ,
    - DAB r1 - DAB r2 + DAB (1 - 2 p) α + DAB (1 - 2 q) β - DAB μ + p q μ,
    DAN α + DNB β + (-n + nC) μ, -DAN r1 + DAN (1 - 2 p) α + DANB β + (-DAN + (n - nC) p) μ,
    - DNB r2 + DANB α + (DNB - 2 DNB q) β - DNB μ + n q μ - nC q μ,
    - DANB r1 - DANB r2 + (-2 DAB DAN + DANB - 2 DANB p) α + (DANB - 2 DAB DANB - 2 DANB q) β -
        DANB μ + DAB n μ - DAB nC μ + DNB p μ + DAN q μ - n p q μ + nC p q μ} /.
    {α → a, β → b, μ → m, DANB → DACB, DAN → DAC, DNB → DCB}

diffEqs - testEqs // FullSimplify

```

```
{0, 0, 0, 0, 0, 0, 0}
```

which confirms the equations.

BA2011 (eq. 3.15) showed the coordinates of the internal stable equilibrium to be

$$\begin{aligned} \text{In[93]:= } & R1 := \sqrt{(a + b + r)^2 - 8 m (r1 + r2)} \\ \text{In[94]:= } & pEqBA := \frac{1}{8 a r} (b^2 - a^2 + 6 a r - r^2 - 4 m r + (a - b + r) R1) /. \{r \rightarrow r1 + r2\} \\ & qEqBA := \frac{1}{8 b r} (a^2 - b^2 + 6 b r - r^2 - 4 m r + (b - a + r) R1) /. \{r \rightarrow r1 + r2\} \\ & DABEqBA := \frac{1}{32 a b r^2} ((a - b - r) (a + b - r) (a - b + r) ((a + b + r) - R1) - \\ & \quad 4 m r (a^2 + b^2 + r^2 - 2 a b - 2 a r - 2 b r) - 8 m^2 r^2) /. \{r \rightarrow r1 + r2\} \\ & nEqBA := nC \\ & DACEqBA := 0 \\ & DCBEqBA := 0 \\ & DACBEqBA := 0 \end{aligned}$$

We have used the assumption that higher-order recombination terms can be ignored, and therefore $r = r_1 + r_2$.

$$\begin{aligned} \text{In[101]:= } & \text{ruleApplyEq} := \{p \rightarrow pEqBA, q \rightarrow qEqBA, n \rightarrow nEqBA, \\ & \quad DAB \rightarrow DABEqBA, DAC \rightarrow DACEqBA, DCB \rightarrow DCBEqBA, DACB \rightarrow DACBEqBA\} \end{aligned}$$

We have

$$\begin{aligned} & \text{diffEqs /. ruleApplyEq // FullSimplify} \\ & \{0, 0, 0, 0, 0, 0, 0\} \end{aligned}$$

which confirms that this is indeed an equilibrium. We omit the proof that this equilibrium is asymptotically stable (cf. Bürger and Akerman 2011). Instead, we directly proceed to the computation of the Jacobian matrix.

$$\begin{aligned} & \text{diffEqsTarget /. ruleApplyEq // FullSimplify} \\ & \{0, 0, 0, 0, 0, 0, 0\} \end{aligned}$$

The equations of BA2011 obviously also represent an equilibrium.

■ Jacobian matrix and effective migration rate

■ Generic

$$\begin{aligned} \text{In[102]:= } & J := \text{Map}[\text{Table}[D[\#, \{i\}], \{i, \{p, q, DAB, n, DAC, DCB, DACB\}\}] \&, \text{diffEqs}] \\ & J // \text{MatrixForm} \end{aligned}$$

$$\begin{pmatrix} -m - a (-1 + p) - a p & 0 & b \\ 0 & -m - b (-1 + q) - b q & a \\ -2 a DAB + m q & -2 b DAB + m p & a + b - m - 2 a p - 2 b q - r1 - r2 \\ 0 & 0 & 0 \\ -2 a DAC + m (n - nC) & 0 & 0 \\ 0 & -2 b DCB + m (n - nC) & 0 \\ -2 a DACB + m (DCB - (n - nC) q) & -2 b DACB + m (DAC - (n - nC) p) & -2 a DAC - 2 b DCB + m (n - nC) m (D \end{pmatrix}$$

As an intermediate step, we set n , D_{AC} , D_{CB} , and D_{ACB} to their equilibrium values n_c , 0, 0, and 0, respectively.

$$\begin{aligned} \text{In[104]:= } & JPrep = J /. \{n \rightarrow nC, DAC \rightarrow 0, DCB \rightarrow 0, DACB \rightarrow 0\} // \text{FullSimplify}; \\ & JPrep // \text{MatrixForm} \end{aligned}$$

$$\begin{pmatrix} a - m - 2 a p & 0 & b & 0 & 0 & 0 \\ 0 & b - m - 2 b q & a & 0 & 0 & 0 \\ -2 a DAB + m q & -2 b DAB + m p & a + b - m - 2 a p - 2 b q - r1 - r2 & 0 & 0 & 0 \\ 0 & 0 & 0 & -m & a & b \\ 0 & 0 & 0 & m p & a - m - 2 a p - r1 & 0 \\ 0 & 0 & 0 & m q & 0 & b - m - 2 a p - r1 \\ 0 & 0 & 0 & m (DAB - p q) & -2 a DAB + m q & -2 b DAB + m p \end{pmatrix}$$

Now we plug in the equilibrium coordinates into the generic matrix of first-order partial derivatives:

```
ruleApplyEq
```

$$\left\{ \begin{array}{l} p \rightarrow \frac{1}{8 a (r1 + r2)} \left(-a^2 + b^2 + 6 a (r1 + r2) - 4 m (r1 + r2) - (r1 + r2)^2 + (a - b + r1 + r2) \sqrt{-8 m (r1 + r2) + (a + b + r1 + r2)^2} \right), \\ q \rightarrow \frac{1}{8 b (r1 + r2)} \left(a^2 - b^2 + 6 b (r1 + r2) - 4 m (r1 + r2) - (r1 + r2)^2 + (-a + b + r1 + r2) \sqrt{-8 m (r1 + r2) + (a + b + r1 + r2)^2} \right), n \rightarrow nC, DAB \rightarrow \frac{1}{32 a b (r1 + r2)^2} \\ \left(-8 m^2 (r1 + r2)^2 - 4 m (r1 + r2) (a^2 - 2 a b + b^2 - 2 a (r1 + r2) - 2 b (r1 + r2) + (r1 + r2)^2) + (a - b - r1 - r2) (a + b - r1 - r2) (a - b + r1 + r2) \right. \\ \left. \left(a + b + r1 + r2 - \sqrt{-8 m (r1 + r2) + (a + b + r1 + r2)^2} \right) \right), DAC \rightarrow 0, DCB \rightarrow 0, DACB \rightarrow 0 \end{array} \right\}$$

```
In[106]:= JEqGeneric = JPrep /. ruleApplyEq // FullSimplify;
JEqGeneric // MatrixForm
```

Out[107]//MatrixForm=

$$\left(\begin{array}{c} a - m - \frac{-a^2 + b^2 + 6 a (r1 + r2) - 4 m (r1 + r2) - (r1 + r2)^2 + (a - b + r1 + r2)}{4 (r1 + r2)} \\ 0 \\ \frac{8 m^2 (r1 + r2)^2 + 4 m (r1 + r2) (a^2 + (-b + r1 + r2)^2 - 2 a (b + r1 + r2)) - (a - b - r1 - r2) (a + b - r1 - r2) (a - b + r1 + r2) \left(a + b + r1 + r2 - \sqrt{-8 m (r1 + r2) + (a + b + r1 + r2)^2} \right)}{16 b (r1 + r2)^2} \\ 0 \\ 0 \\ 0 \\ 0 \end{array} \right)$$

```
JEqGeneric[[4 ;; 7, 4 ;; 7]] // MatrixForm
```

$$\left(\begin{array}{c} m \left(-a^2 + b^2 + 6 a (r1 + r2) - (r1 + r2)^2 + (a - b + r1 + r2) \sqrt{-8 m (r1 + r2) + (a + b + r1 + r2)^2} \right) \left(a^2 - b^2 + 6 b (r1 + r2) - 4 m (r1 + r2) - (r1 + r2)^2 + (-a + b + r1 + r2) \sqrt{-8 m (r1 + r2) + (a + b + r1 + r2)^2} \right) \\ m \left(a^2 - b^2 + 6 b (r1 + r2) - 4 m (r1 + r2) - (r1 + r2)^2 + (-a + b + r1 + r2) \sqrt{-8 m (r1 + r2) + (a + b + r1 + r2)^2} \right) \left(-a^2 + b^2 + 6 a (r1 + r2) - 4 m (r1 + r2) - (r1 + r2)^2 + (a - b + r1 + r2) \sqrt{-8 m (r1 + r2) + (a + b + r1 + r2)^2} \right) \end{array} \right)$$

```
JEqGeneric[4 ;; 7, 4 ;; 7]
```

$$\begin{aligned}
& \left\{ \{-m, a, b, 0\}, \left\{ \frac{1}{8 a (r1 + r2)} m \left(-a^2 + b^2 + 6 a (r1 + r2) - \right. \right. \right. \\
& \quad 4 m (r1 + r2) - (r1 + r2)^2 + (a - b + r1 + r2) \sqrt{-8 m (r1 + r2) + (a + b + r1 + r2)^2} \left. \right), \\
& \quad a - m - r1 - \frac{1}{4 (r1 + r2)} \left(-a^2 + b^2 + 6 a (r1 + r2) - 4 m (r1 + r2) - (r1 + r2)^2 + \right. \\
& \quad \left. \left. \left. (a - b + r1 + r2) \sqrt{-8 m (r1 + r2) + (a + b + r1 + r2)^2} \right), 0, b \right\}, \\
& \left\{ \frac{1}{8 b (r1 + r2)} m \left(a^2 - b^2 + 6 b (r1 + r2) - 4 m (r1 + r2) - (r1 + r2)^2 + \right. \right. \\
& \quad \left. \left. (-a + b + r1 + r2) \sqrt{-8 m (r1 + r2) + (a + b + r1 + r2)^2} \right), 0, \right. \\
& \quad b - m - r2 - \frac{1}{4 (r1 + r2)} \left(a^2 - b^2 + 6 b (r1 + r2) - 4 m (r1 + r2) - (r1 + r2)^2 + \right. \\
& \quad \left. \left. (-a + b + r1 + r2) \sqrt{-8 m (r1 + r2) + (a + b + r1 + r2)^2} \right), a \right\}, \\
& \left\{ \frac{1}{64 a b (r1 + r2)^2} m \left(- \left(-a^2 + b^2 + 6 a (r1 + r2) - 4 m (r1 + r2) - (r1 + r2)^2 + \right. \right. \right. \\
& \quad \left. \left. (a - b + r1 + r2) \sqrt{-8 m (r1 + r2) + (a + b + r1 + r2)^2} \right) \left(a^2 - b^2 + 6 b (r1 + r2) - \right. \\
& \quad \left. \left. 4 m (r1 + r2) - (r1 + r2)^2 + (-a + b + r1 + r2) \sqrt{-8 m (r1 + r2) + (a + b + r1 + r2)^2} \right) + \right. \\
& \quad \left. 2 \left(-8 m^2 (r1 + r2)^2 - 4 m (r1 + r2) \left(a^2 + (-b + r1 + r2)^2 - 2 a (b + r1 + r2) \right) + \right. \right. \\
& \quad \left. \left. (a - b - r1 - r2) (a + b - r1 - r2) (a - b + r1 + r2) \right. \right. \\
& \quad \left. \left. \left(a + b + r1 + r2 - \sqrt{-8 m (r1 + r2) + (a + b + r1 + r2)^2} \right) \right) \right), \\
& \frac{1}{16 b (r1 + r2)^2} \left(8 m^2 (r1 + r2)^2 + 4 m (r1 + r2) \left(a^2 + (-b + r1 + r2)^2 - 2 a (b + r1 + r2) \right) - \right. \\
& \quad (a - b - r1 - r2) (a + b - r1 - r2) (a - b + r1 + r2) \\
& \quad \left. \left(a + b + r1 + r2 - \sqrt{-8 m (r1 + r2) + (a + b + r1 + r2)^2} \right) + 2 m (r1 + r2) \left(a^2 - b^2 + 6 b (r1 + r2) - \right. \right. \\
& \quad \left. \left. 4 m (r1 + r2) - (r1 + r2)^2 + (-a + b + r1 + r2) \sqrt{-8 m (r1 + r2) + (a + b + r1 + r2)^2} \right) \right), \\
& \frac{1}{16 a (r1 + r2)^2} \left(8 m^2 (r1 + r2)^2 + 4 m (r1 + r2) \left(a^2 + (-b + r1 + r2)^2 - 2 a (b + r1 + r2) \right) - \right. \\
& \quad (a - b - r1 - r2) (a + b - r1 - r2) (a - b + r1 + r2) \\
& \quad \left. \left(a + b + r1 + r2 - \sqrt{-8 m (r1 + r2) + (a + b + r1 + r2)^2} \right) + \right. \\
& \quad 2 m (r1 + r2) \left(-a^2 + b^2 + 6 a (r1 + r2) - 4 m (r1 + r2) - (r1 + r2)^2 + \right. \\
& \quad \left. \left. (a - b + r1 + r2) \sqrt{-8 m (r1 + r2) + (a + b + r1 + r2)^2} \right) \right), \\
& \frac{1}{2} \left(-a - b + 2 m - r1 - r2 - \sqrt{-8 m (r1 + r2) + (a + b + r1 + r2)^2} \right) \}
\end{aligned}$$

Now we proceed analogous to the previous steps, but starting from eqs. (4.25) and (4.26) in BA2011 for the differentials of n , D_{AC} , D_{CB} and D_{ACB} .

```
In[108]:= JTTarget := Map[Table[D[#, i], {i, {p, q, DAB, n, DAC, DCB, DACB}}]] &, diffEqsTarget]
JTTarget // MatrixForm

Out[109]//MatrixForm=

$$\begin{pmatrix} -m - a (-1 + p) - a p \\ 0 \\ -2 a DAB + m q \\ m (DCB + (-n + nC) (1 - q)) \\ -2 a DAC + m (-DACB + DAB (-n + nC) + DCB (1 - p) - DCB p + (-n + nC) p (1 - q) - DAC (-1 + m (-DCB q + (-n + nC) (1 - q) q) \\ -2 a DACB + m (-DAB DCB - DAB (-n + nC) + DACB q + DCB p q + (-n + nC) p (1 - q) q + DAC (-1 + q) q + DCB \end{pmatrix}$$


In[110]:= JPrepTarget = JTTarget /. {n → nC, DAC → 0, DCB → 0, DACB → 0} // FullSimplify;
JPrepTarget // TableForm

Out[111]//TableForm=


|                 |                 |                                     |                                      |
|-----------------|-----------------|-------------------------------------|--------------------------------------|
| a - m - 2 a p   | 0               | b                                   | 0                                    |
| 0               | b - m - 2 b q   | a                                   | 0                                    |
| - 2 a DAB + m q | - 2 b DAB + m p | a + b - m - 2 a p - 2 b q - r1 - r2 | 0                                    |
| 0               | 0               | 0                                   | m (p (-1 + q) - q)                   |
| 0               | 0               | 0                                   | - m p (DAB + p + q - p q)            |
| 0               | 0               | 0                                   | - m q (DAB + p + q - p q)            |
| 0               | 0               | 0                                   | - m (DAB + p (-1 + q) - q) (DAB - p) |



JPrep // TableForm



|               |               |                                     |         |                    |           |
|---------------|---------------|-------------------------------------|---------|--------------------|-----------|
| a - m - 2 a p | 0             | b                                   | 0       | 0                  | 0         |
| 0             | b - m - 2 b q | a                                   | 0       | 0                  | 0         |
| m q           | m p           | a + b - m - 2 a p - 2 b q - r1 - r2 | 0       | 0                  | 0         |
| 0             | 0             | 0                                   | - m     | a                  | b         |
| 0             | 0             | 0                                   | m p     | a - m - 2 a p - r1 | 0         |
| 0             | 0             | 0                                   | m q     | 0                  | b - m - 2 |
| 0             | 0             | 0                                   | - m p q | m q                | m p       |



JPrep - JPrepTarget // TableForm



|   |   |   |                               |                            |                            |
|---|---|---|-------------------------------|----------------------------|----------------------------|
| 0 | 0 | 0 | 0                             | 0                          | 0                          |
| 0 | 0 | 0 | 0                             | 0                          | 0                          |
| 0 | 0 | 0 | 0                             | 0                          | 0                          |
| 0 | 0 | 0 | - m - m (p (-1 + q) - q)      | - m (-1 + q)               | - m (-1 + p)               |
| 0 | 0 | 0 | m p + m p (p + q - p q)       | - m - m (-1 + p - p q)     | m (-1 + p) p               |
| 0 | 0 | 0 | m q + m q (p + q - p q)       | m (-1 + q) q               | - m - m (-1 + q - p q)     |
| 0 | 0 | 0 | - m p q + m p q (p + q - p q) | m q - m (1 + p (-1 + q)) q | m p - m p (1 + (-1 + p) q) |


```

We note that the two matrices differ. At least one must be wrong.

Now we plug in the equilibrium coordinates into the generic matrix of first-order partial derivatives:

```
JTarget /. ruleApplyEq // MatrixForm
```

$$\left(\begin{array}{l} -m = \frac{-a^2 + b^2 + 6a(r1+r2) - 4m(r1+r2) - (r1+r2)^2 + (a-b+r1+r2)\sqrt{-8m(r1+r2)+(a+b+r1+r2)^2}}{8(r1+r2)} - a \left(-1 + \frac{-a^2 - b^2 + 6b(r1+r2) - 4m(r1+r2) - (r1+r2)^2 + (-a+b+r1+r2)\sqrt{-8m(r1+r2)+(a+b+r1+r2)^2}}{8b(r1+r2)} \right) \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{array} \right)$$

■ Using the Ansatz $m_e = -\lambda_N = mz$

```
JEqGeneric // MatrixForm
```

$$\left(\begin{array}{l} \frac{1}{4} \left(-2a + r1 + r2 + \frac{(a-b)(a+b)}{r1+r2} - \sqrt{-8m(r1+r2)+(a+b+r1+r2)^2} - \frac{a\sqrt{}}{4} \right) \\ 0 \\ \frac{8m^2(r1+r2)^2 + 4m(r1+r2)(a^2 + (-b+r1+r2)^2 - 2a(b+r1+r2)) - (a-b-r1-r2)(a+b-r1-r2)(a-b+r1+r2)}{16b(r1+r2)^2} \\ 0 \\ 0 \\ 0 \\ 0 \end{array} \right)$$

```
Simplify[Series[Det[JTarget - x IdentityMatrix[7]] /. x → -m z], {m, 0, 1}], Assumptions → {a ≥ 0, b ≥ 0, r1 ≥ 0, r2 ≥ 0}] // Normal
```

$$\begin{aligned} & -abm(a(-1+2p)+b(-1+2q)+r1+r2)(a(-1+2p)(2DAB+(-1+2p)(-1+2q))+(-1+2q)(b(1+2DAB-2p-2q+4pq)+(-1+2p)(r1+r2))) \\ & (r1(r2(p+q-pq-z)+b(3q^2+p(-1+4q-3q^2)+q(-1+DAB-2z)+z))+a(r2(-3p^2(-1+q)-q+p(-1+DAB+4q-2z)+z)+b(DAB^2+q-3q^2-3p^2(1-4q+3q^2)+2DAB(pq-z)-z+2qz+p(1-7q+12q^2+2z-4qz)))) \end{aligned}$$

```

Simplify[Solve[% == 0, z]]

\{ \{ z \rightarrow (r1 (-b (p + q - DAB q - 4 p q - 3 q^2 + 3 p q^2) + (p + q - p q) r2) +
a (b (DAB^2 + 2 DAB p q - (-1 + 3 p) (p (-1 + q) - q) (-1 + 3 q)) -
(3 p^2 (-1 + q) + q - p (-1 + DAB + 4 q)) r2)) /
(r1 (b (-1 + 2 q) + r2) + a (b (1 + 2 DAB - 2 p - 2 q + 4 p q) + (-1 + 2 p) r2))) \} \}

```

This is obviously not the same as in Bürger and Akerman (2011, Eq. 4.30).

Applying the same Ansatz to the Jacobian obtained from the differential equations developed in this Mathematica Notebook yields the correct solution:

```

Simplify[Series[Det[JEqGeneric - x IdentityMatrix[7] /. x \rightarrow -m z], {m, 0, 1}],
Assumptions \rightarrow {a \geq 0, b \geq 0, r1 \geq 0, r2 \geq 0}] // Normal

a b m (a + b + r1 + r2)^2 (a (b + r2) z + r1 (r2 (-1 + z) + b z))

Simplify[Solve[% == 0, z]]

\{ \{ z \rightarrow \frac{r1 r2}{(a + r1) (b + r2)} \} \}

```

which is identical to eq. (4.30) in BA2011.

■ Assuming weak migration

The coordinates of the internal equilibrium under the assumption of weak migration, up to and including first-order terms of m , can be obtained from eq. (4.1) in BA2011.

```

In[112]:= pEqBAWeakMig = FullSimplify[Series[pEqBA, {m, 0, 1}] // Normal,
Assumptions \rightarrow {0 < a < b, 0 < m, 0 < r1, 0 < r2}];
qEqBAWeakMig = FullSimplify[Series[qEqBA, {m, 0, 1}] // Normal,
Assumptions \rightarrow {0 < a < b, 0 < m, 0 < r1, 0 < r2}];
DABEqBAWeakMig = FullSimplify[Series[DABEqBA, {m, 0, 1}] // Normal,
Assumptions \rightarrow {0 < a < b, 0 < m, 0 < r1, 0 < r2}];

{pEqBAWeakMig, qEqBAWeakMig, DABEqBAWeakMig} // TableForm


$$\begin{aligned} 1 - \frac{m(a+r1+r2)}{a(a+b+r1+r2)} \\ 1 - \frac{m(b+r1+r2)}{b(a+b+r1+r2)} \\ \frac{m}{a+b+r1+r2} \end{aligned}$$


```

Checking these against first-order terms w.r.t. m of Eq. (4.1) in BA2011:

```

1 - \frac{m}{a} \left(1 - \frac{b}{a+b+r}\right) - pEqBAWeakMig /. {r \rightarrow r1 + r2} // FullSimplify
0
1 - \frac{m}{b} \left(1 - \frac{a}{a+b+r}\right) - qEqBAWeakMig /. {r \rightarrow r1 + r2} // FullSimplify
0
\frac{m}{a+b+r} - DABEqBAWeakMig /. {r \rightarrow r1 + r2} // FullSimplify
0

```

```

In[115]:= ruleApplyEqWeakMig := {p \rightarrow pEqBAWeakMig, q \rightarrow qEqBAWeakMig,
n \rightarrow nC, DAB \rightarrow DABEqBAWeakMig, DAC \rightarrow 0, DCB \rightarrow 0, DACB \rightarrow 0}

ruleApplyEqWeakMig

\{p \rightarrow 1 - \frac{m (a + r1 + r2)}{a (a + b + r1 + r2)}, q \rightarrow 1 - \frac{m (b + r1 + r2)}{b (a + b + r1 + r2)},
n \rightarrow nC, DAB \rightarrow \frac{m}{a + b + r1 + r2}, DAC \rightarrow 0, DCB \rightarrow 0, DACB \rightarrow 0\}

```

JPrep // MatrixForm

$$\begin{pmatrix} a - m - 2ap & 0 & b & 0 & 0 & 0 \\ 0 & b - m - 2bq & a & 0 & 0 & 0 \\ -2aDAB + mq & -2bDAB + mp & a + b - m - 2ap - 2bq - r1 - r2 & 0 & 0 & 0 \\ 0 & 0 & 0 & -m & a & b \\ 0 & 0 & 0 & mp & a - m - 2ap - r1 & 0 \\ 0 & 0 & 0 & mq & 0 & b - m - 2 \\ 0 & 0 & 0 & m(DAB - pq) & -2aDAB + mq & -2bDA \end{pmatrix}$$

Now we see the block structure claimed in eq. (4.27) of BA2011.

```
In[116]:= JEQ = JPrep /. ruleApplyEqWeakMig // FullSimplify;
JEQ // MatrixForm
```

Out[117]//MatrixForm=

$$\begin{pmatrix} -a + m - \frac{2bm}{a+b+r1+r2} & 0 & b & 0 & 0 & 0 \\ 0 & -b + m - \frac{2am}{a+b+r1+r2} & a & 0 & 0 & 0 \\ \frac{m(-ab+(b-m)(b+r1+r2))}{b(a+b+r1+r2)} & m\left(1 - \frac{a(2b+m)+m(r1+r2)}{a(a+b+r1+r2)}\right) & -a - b + 3m - r1 - r2 - \frac{2(a+b)m}{a+b+r1+r2} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & m\left(1 - \frac{m}{a(\epsilon)}\right) & 0 & 0 \\ 0 & 0 & 0 & m\left(1 - \frac{m}{b(\epsilon)}\right) & 0 & 0 \\ 0 & 0 & 0 & m\left(\frac{m}{a+b+r1+r2} - \left(1 - \frac{m(a+r1)}{a(a+b+r1+r2)}\right)\right) & 0 & 0 \end{pmatrix}$$

The matrix above should correspond to the one given in Box 1 in BA2011, but it does not. For instance, the difference between the elements at the bottom right position is:

```
-a - b + 3m - r1 - r2 - \frac{2(a+b)m}{a+b+r1+r2} - \left(-a - b - r + 2m \frac{(a+b+2r)}{a+b+r}\right) /. {r \rightarrow r1+r2} // FullSimplify
-m
```

```
In[118]:= JEQTarget = JPrepTarget /. ruleApplyEqWeakMig // FullSimplify;
JEQTarget // MatrixForm
```

Out[119]//MatrixForm=

$$\begin{pmatrix} -a + m - \frac{2bm}{a+b+r1+r2} & 0 & b & 0 & 0 & 0 \\ 0 & -b + m - \frac{2am}{a+b+r1+r2} & a & 0 & 0 & 0 \\ \frac{m(-ab+(b-m)(b+r1+r2))}{b(a+b+r1+r2)} & m\left(1 - \frac{a(2b+m)+m(r1+r2)}{a(a+b+r1+r2)}\right) & -a - b + 3m - r1 - r2 - \frac{2(a+b)m}{a+b+r1+r2} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & -\frac{m(a^2 - m(r1+r2) + a(b-m+r1+r2))}{a(b-m+r1+r2)} & 0 & 0 \\ 0 & 0 & 0 & -\frac{m(-ab-(b-m)(b+r1+r2))}{a(b-m+r1+r2)} & 0 & 0 \\ 0 & 0 & 0 & -m\left(-1 + \frac{m(a^2 b + a(b+m)(b+r))}{a b (a+b+r1+r2)}\right) & 0 & 0 \end{pmatrix}$$

But the matrix above is also different from the one presented in Box 1 in BA2011.

```
JEq // MatrixForm
```

$$\begin{pmatrix} -a + m - \frac{2bm}{a+b+r1+r2} & 0 & b & & \\ 0 & -b + m - \frac{2am}{a+b+r1+r2} & a & & \\ \frac{m(-a+b+(b-m)(b+r1+r2))}{b(a+b+r1+r2)} & m\left(1 - \frac{a(2b+m)+m(r1+r2)}{a(a+b+r1+r2)}\right) & -a - b + 3m - r1 - r2 - \frac{2(a+b)m}{a+b+r1+r2} & & \\ 0 & 0 & 0 & - & \\ 0 & 0 & 0 & m\left(1 - \frac{m}{a}\right) & \\ 0 & 0 & 0 & m\left(1 - \frac{m}{b}\right) & \\ 0 & 0 & 0 & m\left(\frac{m}{a+b+r1+r2} - \left(1 - \frac{m(a+r1)}{a(a+b+r1+r2)}\right)\right) & \end{pmatrix}$$

```
In[120]:= JEqrN = JEqr[[{4, 5, 6, 7}, {4, 5, 6, 7}]];
JEqrN // MatrixForm
```

Out[121]/MatrixForm=

$$\begin{pmatrix} -m & a & b & & \\ m\left(1 - \frac{m(a+r1+r2)}{a(a+b+r1+r2)}\right) & -a + m - r1 - \frac{2bm}{a+b+r1+r2} & 0 & & \\ m\left(1 - \frac{m(b+r1+r2)}{b(a+b+r1+r2)}\right) & 0 & -b + m - r2 - \frac{2am}{a+b+r1+r2} & & \\ m\left(\frac{m}{a+b+r1+r2} - \left(1 - \frac{m(a+r1+r2)}{a(a+b+r1+r2)}\right)\right) & m\left(1 - \frac{m(b+r1+r2)}{b(a+b+r1+r2)}\right) & m\left(1 - \frac{a(2b+m)+m(r1+r2)}{a(a+b+r1+r2)}\right) & -a - & \end{pmatrix}$$

If we now assume that the migration rate m is weak, we obtain

```
In[122]:= JEqrNmSmall := Simplify[Normal[Series[JEqr, {m, 0, 1}]]];
JEqrNmSmall // MatrixForm
```

Out[123]/MatrixForm=

$$\begin{pmatrix} -a + m - \frac{2bm}{a+b+r1+r2} & 0 & b & 0 & 0 \\ 0 & -b + m - \frac{2am}{a+b+r1+r2} & a & 0 & 0 \\ \frac{m(-a+b+r1+r2)}{a+b+r1+r2} & m - \frac{2bm}{a+b+r1+r2} & -a - b - r1 - r2 + \frac{m(a+b+3(r1+r2))}{a+b+r1+r2} & 0 & 0 \\ 0 & 0 & 0 & -m & a \\ 0 & 0 & 0 & m - a + m - r1 - \frac{2bm}{a+b+r1+r2} & \\ 0 & 0 & 0 & m & 0 & -b + m \\ 0 & 0 & 0 & -m & \frac{m(-a+b+r1+r2)}{a+b+r1+r2} & m \end{pmatrix}$$

```
In[124]:= JEqrNmSmall := JEqrNmSmall[[4 ;; 7, 4 ;; 7]];
JEqrNmSmall // MatrixForm
```

Out[125]/MatrixForm=

$$\begin{pmatrix} -m & a & b & 0 & \\ m & -a + m - r1 - \frac{2bm}{a+b+r1+r2} & 0 & b & \\ m & 0 & -b + m - r2 - \frac{2am}{a+b+r1+r2} & a & \\ -m & \frac{m(-a+b+r1+r2)}{a+b+r1+r2} & m - \frac{2bm}{a+b+r1+r2} & -a - b - r1 - r2 + \frac{m(a+b+3(r1+r2))}{a+b+r1+r2} & \end{pmatrix}$$

This can alternatively be written as

```
JEqrNmSmallDispl := \{ {-m, a, b, 0}, \{m, -a - r1 + \frac{m(a-b+r)}{a+b+r}, 0, b\},
\{m, 0, -b - r2 + \frac{m(b-a+r)}{a+b+r}, a\}, \{-m, \frac{m(b-a+r)}{a+b+r}, \frac{m(a-b+r)}{a+b+r}, -a - b - r + \frac{m(a+b+3r)}{a+b+r}\} \}
JEqrNmSmallDispl - JEqrNmSmall /. {r \rightarrow r1 + r2} // Simplify
\{0, 0, 0, 0\}, \{0, 0, 0, 0\}, \{0, 0, 0, 0\}, \{0, 0, 0, 0\}
```

```
JEqNmSmallDispl // MatrixForm
```

$$\begin{pmatrix} -m & a & b & 0 \\ m & -a + \frac{m(a-b+r)}{a+b+r} - r1 & 0 & b \\ m & 0 & -b + \frac{m(-a+b+r)}{a+b+r} - r2 & a \\ -m & \frac{m(-a+b+r)}{a+b+r} & \frac{m(a-b+r)}{a+b+r} & -a - b - r + \frac{m(a+b+3r)}{a+b+r} \end{pmatrix}$$

```
In[126]:= JEqNTarget = JEQTarget[[4, 5, 6, 7], {4, 5, 6, 7}];  
JEqNTarget // MatrixForm
```

Out[127]//MatrixForm=

$$\begin{aligned} & -m + \frac{m^3 (a+r1+r2) (b+r1+r2)}{a b (a+b+r1+r2)^2} \\ & - \frac{m (a^2-m (r1+r2)+a (b-m+r1+r2)) (a^3 b-m^2 (r1+r2) (b+r1+r2)+a^2 b (2 b+m+2 (r1+r2))+a (b+r1+r2) (b^2-m^2+b (m+r1+r2)))}{a^2 b (a+b+r1+r2)^3} \\ & - \frac{m (-a b-(b-m) (b+r1+r2)) (-a^3 b+m^2 (r1+r2) (b+r1+r2)-a^2 b (2 b+m+2 (r1+r2))-a (b+r1+r2) (b^2-m^2+b (m+r1+r2)))}{a b^2 (a+b+r1+r2)^3} \\ & -m \left(-1 + \frac{m (a^2 b+a (b+m) (b+r1+r2)+m (r1+r2) (b+r1+r2))}{a b (a+b+r1+r2)^2} \right) \left(\frac{m}{a+b+r1+r2} - \left(1 - \frac{m (a+r1+r2)}{a (a+b+r1+r2)} \right) \left(1 - \frac{m (b+r1+r2)}{b (a+b+r1+r2)} \right) \right) m \left(1 - \right. \end{aligned}$$

Eigenvalues[JEqN] // Simplify

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

$$\begin{aligned} & \text{Root}\left[a^3 b m^3 + 2 a^2 b^2 m^3 + \dots + \text{Root}\left[a^3 + 3 a^2 b + 3 a b^2 + b^3 + 3 a^2 r1 + 6 a b r1 + 3 b^2 r1 + 3 a r1^2 + 3 b r1^2 + r1^3 + 3 a^2 r2 + 6 a b r2 + 3 b^2 r2 + 6 a r1 r2 + 6 b r1 r2 + 3 r1^2 r2 + 3 a r2^2 + 3 b r2^2 + 3 r1 r2^2 + r2^3\right]^{\frac{1}{4}}, 1\right], \\ & \text{Root}\left[a^3 b m^3 + 2 a^2 b^2 m^3 + \dots + \text{Root}\left[a^3 + 3 a^2 b + 3 a b^2 + b^3 + 3 a^2 r1 + 6 a b r1 + 3 b^2 r1 + 3 a r1^2 + 3 b r1^2 + r1^3 + 3 a^2 r2 + 6 a b r2 + 6 b r1 r2 + 3 r1^2 r2 + 3 a r2^2 + 3 b r2^2 + 3 r1 r2^2 + r2^3\right]^{\frac{1}{4}}, 2\right], \text{Root}\left[a^3 b m^3 + \dots + \text{Root}\left[a^3 + 3 a^2 b + 3 a b^2 + b^3 + \dots + 3 b r2^2 + 3 r1 r2^2 + r2^3\right]^{\frac{1}{4}}, 3\right], \\ & \text{Root}\left[a^3 b m^3 + 2 a^2 b^2 m^3 + \dots + \text{Root}\left[a^3 + 3 a^2 b + 3 a b^2 + b^3 + \dots + 3 b r2^2 + 3 r1 r2^2 + r2^3\right]^{\frac{1}{4}}, 4\right] \end{aligned}$$

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

Eigenvalues[JEqNTarget]

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

$$\begin{aligned} & \text{Root}\left[4 a^{10} b^3 m + \dots + \left(a^8 b^2 + 6 a^7 b^3 + 15 a^6 b^4 + 20 a^5 b^5 + 15 a^4 b^6 + 6 a^3 b^7 + a^2 b^8 + 6 a^7 b^2 r1 + 30 a^6 b^3 r1 + 60 a^5 b^4 r1 + 60 a^4 b^5 r1 + 30 a^3 b^6 r1 + 6 a^2 b^7 r1 + 15 a^6 b^2 r1^2 + 60 a^5 b^3 r1^2 + 90 a^4 b^4 r1^2 + 60 a^3 b^5 r1^2 + 15 a^2 b^6 r1^2 + 20 a^5 b^2 r1^3 + 60 a^4 b^3 r1^3 + 60 a^3 b^4 r1^3 + 20 a^2 b^5 r1^3 + 15 a^4 b^2 r1^4 + \dots + 60 a^3 b^2 r1^3 r2^2 + 60 a^2 b^3 r1^3 r2^2 + 15 a^2 b^2 r1^4 r2^2 + 20 a^5 b^2 r2^3 + 60 a^4 b^3 r2^3 + 60 a^3 b^4 r2^3 + 20 a^2 b^5 r2^3 + 60 a^4 b^2 r1 r2^3 + 120 a^3 b^3 r1 r2^3 + 60 a^2 b^4 r1 r2^3 + 60 a^3 b^2 r1^2 r2^3 + 60 a^2 b^3 r1^2 r2^3 + 20 a^2 b^2 r1^3 r2^3 + 15 a^4 b^2 r2^4 + 30 a^3 b^3 r2^4 + 15 a^2 b^4 r2^4 + 30 a^3 b^2 r1 r2^4 + 30 a^2 b^3 r1 r2^4 + 15 a^2 b^2 r1^2 r2^4 + 6 a^3 b^2 r2^5 + 6 a^2 b^3 r2^5 + 6 a^2 b^2 r1 r2^5 + a^2 b^2 r2^6\right]^{\frac{1}{4}}, 1\right], \text{Root}\left[\dots, 4\right] \end{aligned}$$

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

■ Using the Ansatz $m_e = -\lambda_N = m z$

JEq

$$\left\{ \left\{ -a + m - \frac{2 b m}{a + b + r1 + r2}, 0, b, 0, 0, 0, 0 \right\}, \left\{ 0, -b + m - \frac{2 a m}{a + b + r1 + r2}, a, 0, 0, 0, 0 \right\}, \right.$$

$$\left\{ \frac{m (-a b + (b - m) (b + r1 + r2))}{b (a + b + r1 + r2)}, m \left(1 - \frac{a (2 b + m) + m (r1 + r2)}{a (a + b + r1 + r2)} \right), \right.$$

$$\left. -a - b + 3 m - r1 - r2 - \frac{2 (a + b) m}{a + b + r1 + r2}, 0, 0, 0, 0 \right\}, \{0, 0, 0, -m, a, b, 0\},$$

$$\left\{ 0, 0, 0, m \left(1 - \frac{m (a + r1 + r2)}{a (a + b + r1 + r2)} \right), -a + m - r1 - \frac{2 b m}{a + b + r1 + r2}, 0, b \right\},$$

$$\left\{ 0, 0, 0, m \left(1 - \frac{m (b + r1 + r2)}{b (a + b + r1 + r2)} \right), 0, -b + m - r2 - \frac{2 a m}{a + b + r1 + r2}, a \right\},$$

$$\left\{ 0, 0, 0, m \left(\frac{m}{a + b + r1 + r2} - \left(1 - \frac{m (a + r1 + r2)}{a (a + b + r1 + r2)} \right) \left(1 - \frac{m (b + r1 + r2)}{b (a + b + r1 + r2)} \right) \right), \right.$$

$$\left. \frac{m (-a b + (b - m) (b + r1 + r2))}{b (a + b + r1 + r2)}, m \left(1 - \frac{a (2 b + m) + m (r1 + r2)}{a (a + b + r1 + r2)} \right), \right.$$

$$\left. -a - b + 3 m - r1 - r2 - \frac{2 (a + b) m}{a + b + r1 + r2} \right\}$$

$$\text{Simplify}[\text{Series}[\text{Det}[\text{JEqTarget} - x \text{IdentityMatrix}[7] /. x \rightarrow -m \frac{r1 r2}{(r1 + a) (r2 + b)}], \{m, 0, 1\}]]$$

$$a b (-a - b - r1 - r2) \left(a^2 b + a b^2 + a b r1 + a b r2 + (a + b + r1 + r2) (3 a b + 2 b r1 + 2 a r2) \right) m + O[m]^2$$

JEqTarget // TableForm

$-a + m - \frac{2 b m}{a+b+r1+r2}$	0	b	0
0	$-b + m - \frac{2 a m}{a+b+r1+r2}$	a	0
$\frac{m (-a b + (b - m) (b + r1 + r2))}{b (a + b + r1 + r2)}$	$m \left(1 - \frac{a (2 b + m) + m (r1 + r2)}{a (a + b + r1 + r2)} \right)$	$-a - b + 3 m - r1 - r2 - \frac{2 (a + b) m}{a + b + r1 + r2}$	0
0	0	0	$-m + \frac{m^3 (a + r1 + r2) (b + r1 + r2)}{a b (a + b + r1 + r2)}$
0	0	0	$- \frac{m (a^2 - m (r1 + r2) + a (b + r1 + r2))}{a b (a + b + r1 + r2)}$
0	0	0	$-m \left(-1 + \frac{m (a^2 b + a (b + r1 + r2))}{a b (a + b + r1 + r2)} \right)$

Dimensions[JEqTarget]

$$\{7, 7\}$$

$$\text{Simplify}[\text{Series}[\text{Det}[\text{JEqTarget} - x \text{IdentityMatrix}[7] /. x \rightarrow -m z], \{m, 0, 1\}]] // \text{Normal}$$

$$a b m (a + b + r1 + r2)^2 (a (b (-4 + z) + r2 (-2 + z)) + r1 (b (-2 + z) + r2 (-1 + z)))$$

Simplify[Solve[% == 0, z]]

$$\left\{ z \rightarrow \frac{(2 a + r1) (2 b + r2)}{(a + r1) (b + r2)} \right\}$$

This does not yield the same term as the one given in eq. (4.30) of BA2011, which suggests that the equations (4.25) and (4.26) in BA2011 are wrong.

Applying the same Ansatz to the Jacobian obtained from the differential equations developed in this Mathematica Notebook, however, yields the correct solution:

```

Simplify[Series[Det[(JEq /. ruleApplyEq) - x IdentityMatrix[7] /. x → -m z], {m, 0, 1}],
Assumptions → {a ≥ 0, b ≥ 0, r1 ≥ 0, r2 ≥ 0}] // Normal
a b m (a + b + r1 + r2)^2 (a (b + r2) z + r1 (r2 (-1 + z) + b z))

Simplify[Solve[% == 0, z]]
{z → r1 r2 / ((a + r1) (b + r2))}

```

which is identical to eq. (4.30) in BA2011.

We can also use the approximate J_N for small m :

```

Simplify[Series[Det[(JEqMSmall /. ruleApplyEq) - x IdentityMatrix[7] /. x → -m z],
{m, 0, 1}], Assumptions → {a ≥ 0, b ≥ 0, r1 ≥ 0, r2 ≥ 0}] // Normal
a b m (a + b + r1 + r2)^2 (a (b + r2) z + r1 (r2 (-1 + z) + b z))

Simplify[Solve[% == 0, z]]
{z → r1 r2 / ((a + r1) (b + r2))}

```

■ Starting directly from eq. (4.28) in BA2011

Next, we directly start with J_N given in Box 1 (eq. 4.28) of BA2011 and compute the eigenvalues.

```

In[128]:= JEqNBA2011 :=
{{{-m, a, b, m}, {m, -a - r1 + m (a - b + r) / (a + b + r), 0, b - m}, {m, 0, -b - r2 + m (b - a + r) / (a + b + r), a - m},
{-m, m (b - a + r) / (a + b + r), m (a - b + r) / (a + b + r), -a - b - r + 2 m (a + b + 2 r) / (a + b + r)}}} /. {r → r1 + r2}

JEqNBA2011 // MatrixForm

$$\begin{pmatrix} -m & a & b & m \\ m & -a - r1 + \frac{m(a-b+r)}{a+b+r} & 0 & b - m \\ m & 0 & -b - r2 + \frac{m(-a+b+r)}{a+b+r} & a - m \\ -m & \frac{m(-a+b+r)}{a+b+r} & \frac{m(a-b+r)}{a+b+r} & -a - b - r1 - r2 + \frac{2m(a+b+2(r1+r2))}{a+b+r} \end{pmatrix}$$


FullSimplify[Eigenvalues[JEqNBA2011], Assumptions → {0 < a < b, 0 < m, 0 < r}]
{Root[
a^4 b m^2 + 3 a^3 b^2 m^2 + 3 a^2 b^3 m^2 + a b^4 m^2 + a^3 m^4 - a^2 b m^4 - a b^2 m^4 + b^3 m^4 + 2 a^3 b m^2 r1 + 3 a^2 b^2 m^2 r1 - b^4 m^2 r1 - 2 a^2 b m^3 r1 + 2 b^3 m^3 r1 + 3 a^2 m^4 r1 - 6 a b m^4 r1 + 3 b^2 m^4 r1 - a^3 m^2 r1^2 - 3 a^2 b m^2 r1^2 - 6 a b^2 m^2 r1^2 - 4 b^3 m^2 r1^2 + 4 a b m^3 r1^2 + 8 b^2 m^3 r1^2 - a m^4 r1^2 - b m^4 r1^2 - 3 a^2 m^2 r1^3 - 8 a b m^2 r1^3 - 6 b^2 m^2 r1^3 + 4 a m^3 r1^3 + 10 b m^3 r1^3 - 3 m^4 r1^3 - 3 a m^2 r1^4 - 4 b m^2 r1^4 + 4 m^3 r1^4 - m^2 r1^5 - a^4 m^2 r2 + 3 a^2 b^2 m^2 r2 + 2 a b^3 m^2 r2 + 2 a^3 m^3 r2 - 2 a b^2 m^3 r2 + 3 a^2 m^4 r2 - 6 a b m^4 r2 + 3 b^2 m^4 r2 + a^4 m r1 r2 + 4 a^3 b m r1 r2 + 6 a^2 b^2 m r1 r2 + 4 a b^3 m r1 r2 + b^4 m r1 r2 - 6 a^3 m^2 r1 r2 - 12 a^2 b m^2 r1 r2 - 12 a b^2 m^2 r1 r2 - 6 b^3 m^2 r1 r2 + 8 a^2 m^3 r1 r2 + 8 a b m^3 r1 r2 + 8 b^2 m^3 r1 r2 - 2 a m^4 r1 r2 - 2 b m^4 r1 r2 + 4 a^3 m r1^2 r2 + 12 a^2 b m r1^2 r2 + 12 a b^2 m r1^2 r2 + 4 b^3 m r1^2 r2 - 17 a^2 m^2 r1^2 r2 - 34 a b m^2 r1^2 r2 - 20 b^2 m^2 r1^2 r2 + 18 a m^3 r1^2 r2 + 24 b m^3 r1^2 r2 - 9 m^4 r1^2 r2 + 6 a^2 m r1^3 r2 + 12 a b m r1^3 r2 + 6 b^2 m r1^3 r2 - 20 a m^2 r1^3 r2 - 22 b m^2 r1^3 r2 + 16 m^3 r1^3 r2 + 4 a m r1^4 r2 + 4 b m r1^4 r2 - 8 m^2 r1^4 r2 + m r1^5 r2 - 4 a^3 m^2 r2^2 - 6 a^2 b m^2 r2^2 - 3 a b^2 m^2 r2^2 - b^3 m^2 r2^2 + 8 a^2 m^3 r2^2 + 4 a b m^3 r2^2 - a m^4 r2^2 - b m^4 r2^2 + 4 a^3 m r1 r2^2 + 12 a^2 b m r1 r2^2 + 12 a b^2 m r1 r2^2 + 4 b^3 m r1 r2^2 - 20 a^2 m^2 r1 r2^2 - 34 a b m^2 r1 r2^2 - 17 b^2 m^2 r1 r2^2 + 24 a m^3 r1 r2^2 + 18 b m^3 r1 r2^2 - 9 m^4 r1 r2^2 + 12 a^2 b m r1^2 r2^2 + 24 a b m r1^2 r2^2 - 12 b^2 m r1^2 r2^2 - 35 a m^2 r1^2 r2^2 - 35 b m^2 r1^2 r2^2 + 24 m^3 r1^2 r2^2 + 12 a m r1^3 r2^2 + 12 b m r1^3 r2^2 - 19 m^2 r1^3 r2^2 + 4 m r1^4 r2^2 - 6 a^2 m^2 r2^3 - 8 a b m^2 r2^3 - 3 b^2 m^2 r2^3 + 10 a m^3 r2^3 + 4 b m^3 r2^3 - 3 m^4 r2^3 + 6 a^2 m r1 r2^3 + 12 a b m r1 r2^3 + 6 b^2 m r1 r2^3 - 22 a m^2 r1 r2^3 - 20 b m^2 r1 r2^3 + 16 m^3 r1 r2^3 + 12 a m r1^2 r2^3 + 12 b m r1^2 r2^3 - 19 m^2 r1^2 r2^3 + 6 m r1^3 r2^3 - 4 a m^2 r2^4 - 3 b m^2 r2^4 + 4 m^3 r2^4 + 4 a m r1 r2^4 + 4 b m r1 r2^4 - 8 m^2 r1 r2^4 + 4 m r1^2 r2^4 - m^2 r2^5 + m r1 r2^5 +

```

$$\begin{aligned}
& \left(a^5 b + 4 a^4 b^2 + 6 a^3 b^3 + 4 a^2 b^4 + a b^5 - a^4 b m - 3 a^3 b^2 m - 3 a^2 b^3 m - a b^4 m - 2 a^4 m^2 + 4 a^2 b^2 m^2 - \right. \\
& \quad 2 b^4 m^2 - a^3 m^3 + a^2 b m^3 + a b^2 m^3 - b^3 m^3 + 5 a^4 b r1 + 16 a^3 b^2 r1 + 18 a^2 b^3 r1 + 8 a b^4 r1 + b^5 r1 - \\
& \quad 8 a^3 b m r1 - 19 a^2 b^2 m r1 - 14 a b^3 m r1 - 3 b^4 m r1 - 6 a^3 m^2 r1 + 2 a^2 b m^2 r1 + 2 a b^2 m^2 r1 - \\
& \quad 6 b^3 m^2 r1 + 3 a^2 b^3 r1 + 2 a b m^3 r1 + 3 b^2 m^3 r1 + 10 a^3 b r1^2 + 24 a^2 b^2 r1^2 + 18 a b^3 r1^2 + \\
& \quad 4 b^4 r1^2 - 18 a^2 b m r1^2 - 29 a b^2 m r1^2 - 11 b^3 m r1^2 - 6 a^2 m^2 r1^2 + 4 a b m^2 r1^2 - 2 b^2 m^2 r1^2 + \\
& \quad 5 a m^3 r1^2 + 5 b m^3 r1^2 + 10 a^2 b r1^3 + 16 a b^2 r1^3 + 6 b^3 r1^3 - 16 a b m r1^3 - 13 b^2 m r1^3 - \\
& \quad 2 a m^2 r1^3 + 2 b m^2 r1^3 + m^3 r1^3 + 5 a b r1^4 + 4 b^2 r1^4 - 5 b m r1^4 + b r1^5 + a^5 r2 + 8 a^4 b r2 + \\
& \quad 18 a^3 b^2 r2 + 16 a^2 b^3 r2 + 5 a b^4 r2 - 3 a^4 m r2 - 14 a^3 b m r2 - 19 a^2 b^2 m r2 - 8 a b^3 m r2 - \\
& \quad 6 a^3 m^2 r2 + 2 a^2 b m^2 r2 + 2 a b^2 m^2 r2 - 6 b^3 m^2 r2 + 3 a^2 m^3 r2 + 2 a b m^3 r2 + 3 b^2 m^3 r2 + \\
& \quad 5 a^4 r1 r2 + 32 a^3 b r1 r2 + 54 a^2 b^2 r1 r2 + 32 a b^3 r1 r2 + 5 b^4 r1 r2 - 12 a^3 m r1 r2 - \\
& \quad 50 a^2 b m r1 r2 - 50 a b^2 m r1 r2 - 12 b^3 m r1 r2 - 8 a^2 m^2 r1 r2 + 8 a b m^2 r1 r2 - 8 b^2 m^2 r1 r2 + \\
& \quad 10 a m^3 r1 r2 + 10 b m^3 r1 r2 + 10 a^3 r1^2 r2 + 48 a^2 b r1^2 r2 + 54 a b^2 r1^2 r2 + 16 b^3 r1^2 r2 - \\
& \quad 18 a^2 m r1^2 r2 - 58 a b m r1^2 r2 - 31 b^2 m r1^2 r2 - 2 a m^2 r1^2 r2 + 2 b m^2 r1^2 r2 + 3 m^3 r1^2 r2 + \\
& \quad 10 a^2 r1^3 r2 + 32 a b r1^3 r2 + 18 b^2 r1^3 r2 - 12 a m r1^3 r2 - 22 b m r1^3 r2 + 5 a r1^4 r2 + \\
& \quad 8 b r1^4 r2 - 3 m r1^4 r2 + r1^5 r2 + 4 a^4 r2^2 + 18 a^3 b r2^2 + 24 a^2 b^2 r2^2 + 10 a b^3 r2^2 - \\
& \quad 11 a^3 m r2^2 - 29 a^2 b m r2^2 - 18 a b^2 m r2^2 - 2 a^2 m^2 r2^2 + 4 a b m^2 r2^2 - 6 b^2 m^2 r2^2 + \\
& \quad 5 a m^3 r2^2 + 5 b m^3 r2^2 + 16 a^3 r1 r2^2 + 54 a^2 b r1 r2^2 + 48 a b^2 r1 r2^2 + 10 b^3 r1 r2^2 - \\
& \quad 31 a^2 m r1 r2^2 - 58 a b m r1 r2^2 - 18 b^2 m r1 r2^2 + 2 a m^2 r1 r2^2 - 2 b m^2 r1 r2^2 + 3 m^3 r1 r2^2 + \\
& \quad 24 a^2 r1^2 r2^2 + 54 a b r1^2 r2^2 + 24 b^2 r1^2 r2^2 - 29 a m r1^2 r2^2 - 29 b m r1^2 r2^2 + 16 a r1^3 r2^2 + \\
& \quad 18 b r1^3 r2^2 - 9 m r1^3 r2^2 + 4 r1^4 r2^2 + 6 a^3 r2^3 + 16 a^2 b r2^3 + 10 a b^2 r2^3 - 13 a^2 m r2^3 - \\
& \quad 16 a b m r2^3 + 2 a m^2 r2^3 - 2 b m^2 r2^3 + m^3 r2^3 + 18 a^2 r1 r2^3 + 32 a b r1 r2^3 + 10 b^2 r1 r2^3 - \\
& \quad 22 a m r1 r2^3 - 12 b m r1 r2^3 + 18 a r1^2 r2^3 + 16 b r1^2 r2^3 - 9 m r1^2 r2^3 + 6 r1^3 r2^3 + 4 a^2 r2^4 + \\
& \quad 5 a b r2^4 - 5 a m r2^4 + 8 a r1 r2^4 + 5 b r1 r2^4 - 3 m r1 r2^4 + 4 r1^2 r2^4 + a r2^5 + r1 r2^5 \} \#1 + \\
& \left(a^5 + 6 a^4 b + 13 a^3 b^2 + 13 a^2 b^3 + 6 a b^4 + b^5 - a^4 m - 4 a^3 b m - 6 a^2 b^2 m - 4 a b^3 m - b^4 m - \right. \\
& \quad 2 a^3 m^2 - 2 a^2 b m^2 - 2 a b^2 m^2 - 2 b^3 m^2 + 5 a^4 r1 + 24 a^3 b r1 + 39 a^2 b^2 r1 + 26 a b^3 r1 + \\
& \quad 6 b^4 r1 - 8 a^3 m r1 - 26 a^2 b m r1 - 28 a b^2 m r1 - 10 b^3 m r1 - 2 a^2 m^2 r1 - 2 b^2 m^2 r1 + \\
& \quad 10 a^3 r1^2 + 36 a^2 b r1^2 + 39 a b^2 r1^2 + 13 b^3 r1^2 - 18 a^2 m r1^2 - 40 a b m r1^2 - 22 b^2 m r1^2 + \\
& \quad 6 a m^2 r1^2 + 6 b m^2 r1^2 + 10 a^2 r1^3 + 24 a b r1^3 + 13 b^2 r1^3 - 16 a m r1^3 - 18 b m r1^3 + \\
& \quad 6 m^2 r1^3 + 5 a r1^4 + 6 b r1^4 - 5 m r1^4 + r1^5 + 6 a^4 r2 + 26 a^3 b r2 + 39 a^2 b^2 r2 + 24 a b^3 r2 + \\
& \quad 5 b^4 r2 - 10 a^3 m r2 - 28 a^2 b m r2 - 26 a b^2 m r2 - 8 b^3 m r2 - 2 a^2 m^2 r2 - 2 b^2 m^2 r2 + \\
& \quad 24 a^3 r1 r2 + 78 a^2 b r1 r2 + 78 a b^2 r1 r2 + 24 b^3 r1 r2 - 40 a^2 m r1 r2 - 80 a b m r1 r2 - \\
& \quad 40 b^2 m r1 r2 + 12 a m^2 r1 r2 + 12 b m^2 r1 r2 + 36 a^2 r1^2 r2 + 78 a b r1^2 r2 + 39 b^2 r1^2 r2 - \\
& \quad 50 a m r1^2 r2 - 52 b m r1^2 r2 + 18 m^2 r1^2 r2 + 24 a r1^3 r2 + 26 b r1^3 r2 - 20 m r1^3 r2 + \\
& \quad 6 r1^4 r2 + 13 a^3 r2^2 + 39 a^2 b r2^2 + 36 a b^2 r2^2 + 10 b^3 r2^2 - 22 a^2 m r2^2 - 40 a b m r2^2 - \\
& \quad 18 b^2 m r2^2 + 6 a m^2 r2^2 + 6 b m^2 r2^2 + 39 a^2 r1 r2^2 + 78 a b r1 r2^2 + 36 b^2 r1 r2^2 - 52 a m r1 r2^2 - \\
& \quad 50 b m r1 r2^2 + 18 m^2 r1 r2^2 + 39 a r1^2 r2^2 + 39 b r1^2 r2^2 - 30 m r1^2 r2^2 + 13 r1^3 r2^2 + \\
& \quad 13 a^2 r2^3 + 24 a b r2^3 + 10 b^2 r2^3 - 18 a m r2^3 - 16 b m r2^3 + 6 m^2 r2^3 + 26 a r1 r2^3 + \\
& \quad 24 b r1 r2^3 - 20 m r1 r2^3 + 13 r1^2 r2^3 + 6 a r2^4 + 5 b r2^4 - 5 m r2^4 + 6 r1 r2^4 + r2^5 \} \#1^2 + \\
& \left(2 a^4 + 8 a^3 b + 12 a^2 b^2 + 8 a b^3 + 2 b^4 - a^3 m - 3 a^2 b m - 3 a b^2 m - b^3 m + 8 a^3 r1 + 24 a^2 b r1 + \right. \\
& \quad 24 a b^2 r1 + 8 b^3 r1 - 7 a^2 m r1 - 14 a b m r1 - 7 b^2 m r1 + 12 a^2 r1^2 + 24 a b r1^2 + 12 b^2 r1^2 - \\
& \quad 11 a m r1^2 - 11 b m r1^2 + 8 a r1^3 + 8 b r1^3 - 5 m r1^3 + 2 r1^4 + 8 a^3 r2 + 24 a^2 b r2 + \\
& \quad 24 a b^2 r2 + 8 b^3 r2 - 7 a^2 m r2 - 14 a b m r2 - 7 b^2 m r2 + 24 a^2 r1 r2 + 48 a b r1 r2 + \\
& \quad 24 b^2 r1 r2 - 22 a m r1 r2 - 22 b m r1 r2 + 24 a r1^2 r2 + 24 b r1^2 r2 - 15 m r1^2 r2 + \\
& \quad 8 r1^3 r2 + 12 a^2 r2^2 + 24 a b r2^2 + 12 b^2 r2^2 - 11 a m r2^2 - 11 b m r2^2 + 24 a r1 r2^2 + \\
& \quad 24 b r1 r2^2 - 15 m r1 r2^2 + 12 r1^2 r2^2 + 8 a r2^3 + 8 b r2^3 - 5 m r2^3 + 8 r1 r2^3 + 2 r2^4 \} \#1^3 + \\
& \left(a^3 + 3 a^2 b + 3 a b^2 + b^3 + 3 a^2 r1 + 6 a b r1 + 3 b^2 r1 + 3 a r1^2 + 3 b r1^2 + r1^3 + 3 a^2 r2 + 6 a b r2 + \right. \\
& \quad 3 b^2 r2 + 6 a r1 r2 + 6 b r1 r2 + 3 r1^2 r2 + 3 a r2^2 + 3 b r2^2 + 3 r1 r2^2 + r2^3 \} \#1^4 \&, 1], \\
& \text{Root}\left[a^4 b m^2 + 3 a^3 b^2 m^2 + 3 a^2 b^3 m^2 + a b^4 m^2 + a^3 m^4 - a^2 b m^4 - a b^2 m^4 + b^3 m^4 + \right. \\
& \quad 2 a^3 b m^2 r1 + 3 a^2 b^2 m^2 r1 - b^4 m^2 r1 - 2 a^2 b m^3 r1 + \\
& \quad 2 b^3 m^3 r1 + 3 a^2 m^4 r1 - 6 a b m^4 r1 + 3 b^2 m^4 r1 - a^3 m^2 r1^2 - \\
& \quad 3 a^2 b m^2 r1^2 - 6 a b^2 m^2 r1^2 - 4 b^3 m^2 r1^2 + 4 a b m^3 r1^2 + \\
& \quad 8 b^2 m^3 r1^2 - a m^4 r1^2 - b m^4 r1^2 - 3 a^2 m^2 r1^3 - 8 a b m^2 r1^3 - \\
& \quad 6 b^2 m^2 r1^3 + 4 a m^3 r1^3 + 10 b m^3 r1^3 - 3 m^4 r1^3 - 3 a m^2 r1^4 - \\
& \quad 4 b m^2 r1^4 + 4 m^3 r1^4 - m^2 r1^5 - a^4 m^2 r2 + 3 a^2 b^2 m^2 r2 + \\
& \quad 2 a b^3 m^2 r2 + 2 a^3 m^3 r2 - 2 a b^2 m^3 r2 + 3 a^2 m^4 r2 - 6 a b m^4 r2 + \\
& \quad 3 b^2 m^4 r2 + a^4 m r1 r2 + 4 a^3 b m r1 r2 + 6 a^2 b^2 m r1 r2 +
\end{aligned}$$

$$\begin{aligned}
& 4ab^3mr1r2 + b^4mr1r2 - 6a^3m^2r1r2 - 12a^2bm^2r1r2 - \\
& 12ab^2m^2r1r2 - 6b^3m^2r1r2 + 8a^2m^3r1r2 + 8abm^3r1r2 + \\
& 8b^2m^3r1r2 - 2am^4r1r2 - 2bm^4r1r2 + 4a^3mr1^2r2 + \\
& 12a^2bmr1^2r2 + 12ab^2mr1^2r2 + 4b^3mr1^2r2 - 17a^2m^2r1^2r2 - \\
& 34abm^2r1^2r2 - 20b^2m^2r1^2r2 + 18am^3r1^2r2 + 24bm^3r1^2r2 - \\
& 9m^4r1^2r2 + 6a^2mr1^3r2 + 12abmr1^3r2 + 6b^2mr1^3r2 - \\
& 20am^2r1^3r2 - 22bm^2r1^3r2 + 16m^3r1^3r2 + 4amr1^4r2 + \\
& 4bmr1^4r2 - 8m^2r1^4r2 + mr1^5r2 - 4a^3m^2r2^2 - 6a^2bm^2r2^2 - \\
& 3ab^2m^2r2^2 - b^3m^2r2^2 + 8a^2m^3r2^2 + 4abm^3r2^2 - am^4r2^2 - \\
& bm^4r2^2 + 4a^3mr1r2^2 + 12a^2bmr1r2^2 + 12ab^2mr1r2^2 + \\
& 4b^3mr1r2^2 - 20a^2m^2r1r2^2 - 34abm^2r1r2^2 - 17b^2m^2r1r2^2 + \\
& 24am^3r1r2^2 + 18bm^3r1r2^2 - 9m^4r1r2^2 + 12a^2mr1^2r2^2 + \\
& 24abmr1^2r2^2 + 12b^2mr1^2r2^2 - 35am^2r1^2r2^2 - \\
& 35bm^2r1^2r2^2 + 24m^3r1^2r2^2 + 12amr1^3r2^2 + 12bmr1^3r2^2 - \\
& 19m^2r1^3r2^2 + 4mr1^4r2^2 - 6a^2m^2r2^3 - 8abm^2r2^3 - \\
& 3b^2m^2r2^3 + 10am^3r2^3 + 4bm^3r2^3 - 3m^4r2^3 + 6a^2mr1r2^3 + \\
& 12abmr1r2^3 + 6b^2mr1r2^3 - 22am^2r1r2^3 - 20bm^2r1r2^3 + \\
& 16m^3r1r2^3 + 12amr1^2r2^3 + 12bmr1^2r2^3 - 19m^2r1^2r2^3 + \\
& 6mr1^3r2^3 - 4am^2r2^4 - 3bm^2r2^4 + 4m^3r2^4 + 4amr1r2^4 + \\
& 4bmr1r2^4 - 8m^2r1r2^4 + 4mr1^2r2^4 - m^2r2^5 + mr1r2^5 + \\
& (a^5b + 4a^4b^2 + 6a^3b^3 + 4a^2b^4 + ab^5 - a^4bm - 3a^3b^2m - 3a^2b^3m - ab^4m - 2a^4m^2 + 4a^2b^2m^2 - \\
& 2b^4m^2 - a^3m^3 + a^2bm^3 + ab^2m^3 - b^3m^3 + 5a^4br1 + 16a^3b^2r1 + 18a^2b^3r1 + 8ab^4r1 + b^5r1 - \\
& 8a^3bmr1 - 19a^2b^2mr1 - 14ab^3mr1 - 3b^4mr1 - 6a^3m^2r1 + 2a^2bm^2r1 + 2ab^2m^2r1 - \\
& 6b^3m^2r1 + 3a^2m^3r1 + 2abm^3r1 + 3b^2m^3r1 + 10a^3br1^2 + 24a^2b^2r1^2 + 18ab^3r1^2 + \\
& 4b^4r1^2 - 18a^2bmr1^2 - 29ab^2mr1^2 - 11b^3mr1^2 - 6a^2m^2r1^2 + 4abm^2r1^2 - 2b^2m^2r1^2 + \\
& 5am^3r1^2 + 5bm^3r1^2 + 10a^2br1^3 + 16ab^2r1^3 + 6b^3r1^3 - 16abmr1^3 - 13b^2mr1^3 - \\
& 2am^2r1^3 + 2bm^2r1^3 + m^3r1^3 + 5abr1^4 + 4b^2r1^4 - 5bmr1^4 + br1^5 + a^5r2 + 8a^4br2 + \\
& 18a^3b^2r2 + 16a^2b^3r2 + 5ab^4r2 - 3a^4mr2 - 14a^3bmr2 - 19a^2b^2mr2 - 8ab^3mr2 - \\
& 6a^3m^2r2 + 2a^2bm^2r2 + 2ab^2m^2r2 - 6b^3m^2r2 + 3a^2m^3r2 + 2abm^3r2 + 3b^2m^3r2 + \\
& 5a^4r1r2 + 32a^3br1r2 + 54a^2b^2r1r2 + 32ab^3r1r2 + 5b^4r1r2 - 12a^3mr1r2 - \\
& 50a^2bmr1r2 - 50ab^2mr1r2 - 12b^3mr1r2 - 8a^2m^2r1r2 + 8abm^2r1r2 - 8b^2m^2r1r2 + \\
& 10am^3r1r2 + 10bm^3r1r2 + 10a^3r1^2r2 + 48a^2br1^2r2 + 54ab^2r1^2r2 + 16b^3r1^2r2 - \\
& 18a^2mr1^2r2 - 58abmr1^2r2 - 31b^2mr1^2r2 - 2am^2r1^2r2 + 2bm^2r1^2r2 + 3m^3r1^2r2 + \\
& 10a^2r1^3r2 + 32abr1^3r2 + 18b^2r1^3r2 - 12amr1^3r2 - 22bmr1^3r2 + 5ar1^4r2 + \\
& 8br1^4r2 - 3mr1^4r2 + r1^5r2 + 4a^4r2^2 + 18a^3br2^2 + 24a^2b^2r2^2 + 10ab^3r2^2 - \\
& 11a^3mr2^2 - 29a^2bmr2^2 - 18ab^2mr2^2 - 2a^2m^2r2^2 + 4abm^2r2^2 - 6b^2m^2r2^2 + \\
& 5am^3r2^2 + 5bm^3r2^2 + 16a^3r1r2^2 + 54a^2br1r2^2 + 48ab^2r1r2^2 + 10b^3r1r2^2 - \\
& 31a^2mr1r2^2 - 58abmr1r2^2 - 18b^2mr1r2^2 + 2am^2r1r2^2 - 2bm^2r1r2^2 + 3m^3r1r2^2 + \\
& 24a^2r1^2r2^2 + 54abr1^2r2^2 + 24b^2r1^2r2^2 - 29amr1^2r2^2 - 29bmr1^2r2^2 + 16ar1^3r2^2 + \\
& 18br1^3r2^2 - 9mr1^3r2^2 + 4r1^4r2^2 + 6a^3r2^3 + 16a^2br2^3 + 10ab^2r2^3 - 13a^2mr2^3 - \\
& 16abmr2^3 + 2am^2r2^3 - 2bm^2r2^3 + m^3r2^3 + 18a^2r1r2^3 + 32abr1r2^3 + 10b^2r1r2^3 - \\
& 22amr1r2^3 - 12bmr1r2^3 + 18ar1^2r2^3 + 16br1^2r2^3 - 9mr1^2r2^3 + 6r1^3r2^3 + 4a^2r2^4 + \\
& 5abr2^4 - 5amr2^4 + 8ar1r2^4 + 5br1r2^4 - 3mr1r2^4 + 4r1^2r2^4 + ar2^5 + r1r2^5) \#1 + \\
& (a^5 + 6a^4b + 13a^3b^2 + 13a^2b^3 + 6ab^4 + b^5 - a^4m - 4a^3bm - 6a^2b^2m - 4ab^3m - b^4m - \\
& 2a^3m^2 - 2a^2bm^2 - 2ab^2m^2 - 2b^3m^2 + 5a^4r1 + 24a^3br1 + 39a^2b^2r1 + 26ab^3r1 + \\
& 6b^4r1 - 8a^3mr1 - 26a^2bmr1 - 28ab^2mr1 - 10b^3mr1 - 2a^2m^2r1 - 2b^2m^2r1 + \\
& 10a^3r1^2 + 36a^2br1^2 + 39ab^2r1^2 + 13b^3r1^2 - 18a^2mr1^2 - 40abmr1^2 - 22b^2mr1^2 + \\
& 6am^2r1^2 + 6bm^2r1^2 + 10a^2r1^3 + 24abr1^3 + 13b^2r1^3 - 16amr1^3 - 18bmr1^3 + \\
& 6m^2r1^3 + 5ar1^4 + 6br1^4 - 5mr1^4 + r1^5 + 6a^4r2 + 26ab^3r2 + 39a^2b^2r2 + 24ab^3r2 + \\
& 5b^4r2 - 10a^3mr2 - 28ab^2mr2 - 26ab^2mr2 - 8b^3mr2 - 2a^2m^2r2 - 2b^2m^2r2 + \\
& 24a^3r1r2 + 78a^2br1r2 + 78ab^2r1r2 + 24b^3r1r2 - 40a^2mr1r2 - 80abmr1r2 - \\
& 40b^2mr1r2 + 12am^2r1r2 + 12bm^2r1r2 + 36a^2r1^2r2 + 78abr1^2r2 + 39b^2r1^2r2 - \\
& 50amr1^2r2 - 52bmr1^2r2 + 18m^2r1^2r2 + 24ar1^3r2 + 26br1^3r2 - 20mr1^3r2 + \\
& 6r1^4r2 + 13a^3r2^2 + 39a^2br2^2 + 36ab^2r2^2 + 10b^3r2^2 - 22a^2mr2^2 - 40abmr2^2 - \\
& 18b^2mr2^2 + 6am^2r2^2 + 6bm^2r2^2 + 39a^2r1r2^2 + 78abr1r2^2 + 36b^2r1r2^2 - 52amr1r2^2 - \\
& 50bmr1r2^2 + 18m^2r1r2^2 + 39ar1^2r2^2 + 39br1^2r2^2 - 30mr1^2r2^2 + 13r1^3r2^2 + \\
& 13a^2r2^3 + 24abr2^3 + 10b^2r2^3 - 18amr2^3 - 16bmr2^3 + 6m^2r2^3 + 26ar1r2^3 +
\end{aligned}$$

$$\begin{aligned}
& 24 b r1 r2^3 - 20 m r1 r2^3 + 13 r1^2 r2^3 + 6 a r2^4 + 5 b r2^4 - 5 m r2^4 + 6 r1 r2^4 + r2^5 \} \#1^2 + \\
& (2 a^4 + 8 a^3 b + 12 a^2 b^2 + 8 a b^3 + 2 b^4 - a^3 m - 3 a^2 b m - 3 a b^2 m - b^3 m + 8 a^3 r1 + 24 a^2 b r1 + \\
& 24 a b^2 r1 + 8 b^3 r1 - 7 a^2 m r1 - 14 a b m r1 - 7 b^2 m r1 + 12 a^2 r1^2 + 24 a b r1^2 + 12 b^2 r1^2 - \\
& 11 a m r1^2 - 11 b m r1^2 + 8 a r1^3 + 8 b r1^3 - 5 m r1^3 + 2 r1^4 + 8 a^3 r2 + 24 a^2 b r2 + \\
& 24 a b^2 r2 + 8 b^3 r2 - 7 a^2 m r2 - 14 a b m r2 - 7 b^2 m r2 + 24 a^2 r1 r2 + 48 a b r1 r2 + \\
& 24 b^2 r1 r2 - 22 a m r1 r2 - 22 b m r1 r2 + 24 a r1^2 r2 + 24 b r1^2 r2 - 15 m r1^2 r2 + \\
& 8 r1^3 r2 + 12 a^2 r2^2 + 24 a b r2^2 + 12 b^2 r2^2 - 11 a m r2^2 - 11 b m r2^2 + 24 a r1 r2^2 + \\
& 24 b r1 r2^2 - 15 m r1 r2^2 + 12 r1^2 r2^2 + 8 a r2^3 + 8 b r2^3 - 5 m r2^3 + 8 r1 r2^3 + 2 r2^4) \#1^3 + \\
& (a^3 + 3 a^2 b + 3 a b^2 + b^3 + 3 a^2 r1 + 6 a b r1 + 3 b^2 r1 + 3 a r1^2 + 3 b r1^2 + r1^3 + 3 a^2 r2 + 6 a b r2 + \\
& 3 b^2 r2 + 6 a r1 r2 + 6 b r1 r2 + 3 r1^2 r2 + 3 a r2^2 + 3 b r2^2 + 3 r1 r2^2 + r2^3) \#1^4 \&, 2], \\
\text{Root} & [a^4 b m^2 + 3 a^3 b^2 m^2 + 3 a^2 b^3 m^2 + a b^4 m^2 + a^3 m^4 - a^2 b m^4 - a b^2 m^4 + b^3 m^4 + \\
& 2 a^3 b m^2 r1 + 3 a^2 b^2 m^2 r1 - b^4 m^2 r1 - 2 a^2 b m^3 r1 + \\
& 2 b^3 m^3 r1 + 3 a^2 m^4 r1 - 6 a b m^4 r1 + 3 b^2 m^4 r1 - a^3 m^2 r1^2 - \\
& 3 a^2 b m^2 r1^2 - 6 a b^2 m^2 r1^2 - 4 b^3 m^2 r1^2 + 4 a b m^3 r1^2 + \\
& 8 b^2 m^3 r1^2 - a m^4 r1^2 - b m^4 r1^2 - 3 a^2 m^2 r1^3 - 8 a b m^2 r1^3 - \\
& 6 b^2 m^2 r1^3 + 4 a m^3 r1^3 + 10 b m^3 r1^3 - 3 m^4 r1^3 - \\
& 3 a m^2 r1^4 - 4 b m^2 r1^4 + 4 m^3 r1^4 - m^2 r1^5 - a^4 m^2 r2 + \\
& 3 a^2 b^2 m^2 r2 + 2 a b^3 m^2 r2 + 2 a^3 m^3 r2 - 2 a b^2 m^3 r2 + \\
& 3 a^2 m^4 r2 - 6 a b m^4 r2 + 3 b^2 m^4 r2 + a^4 m r1 r2 + \\
& 4 a^3 b m r1 r2 + 6 a^2 b^2 m r1 r2 + 4 a b^3 m r1 r2 + b^4 m r1 r2 - \\
& 6 a^3 m^2 r1 r2 - 12 a^2 b m^2 r1 r2 - 12 a b^2 m^2 r1 r2 - \\
& 6 b^3 m^2 r1 r2 + 8 a^2 m^3 r1 r2 + 8 a b m^3 r1 r2 + 8 b^2 m^3 r1 r2 - \\
& 2 a m^4 r1 r2 - 2 b m^4 r1 r2 + 4 a^3 m r1^2 r2 + 12 a^2 b m r1^2 r2 + \\
& 12 a b^2 m r1^2 r2 + 4 b^3 m r1^2 r2 - 17 a^2 m^2 r1^2 r2 - \\
& 34 a b m^2 r1^2 r2 - 20 b^2 m^2 r1^2 r2 + 18 a m^3 r1^2 r2 + \\
& 24 b m^3 r1^2 r2 - 9 m^4 r1^2 r2 + 6 a^2 m r1^3 r2 + 12 a b m r1^3 r2 + \\
& 6 b^2 m r1^3 r2 - 20 a m^2 r1^3 r2 - 22 b m^2 r1^3 r2 + 16 m^3 r1^3 r2 + \\
& 4 a m r1^4 r2 + 4 b m r1^4 r2 - 8 m^2 r1^4 r2 + m r1^5 r2 - \\
& 4 a^3 m^2 r2^2 - 6 a^2 b m^2 r2^2 - 3 a b^2 m^2 r2^2 - b^3 m^2 r2^2 + \\
& 8 a^2 m^3 r2^2 + 4 a b m^3 r2^2 - a m^4 r2^2 - b m^4 r2^2 + 4 a^3 m r1 r2^2 + \\
& 12 a^2 b m r1 r2^2 + 12 a b^2 m r1 r2^2 + 4 b^3 m r1 r2^2 - \\
& 20 a^2 m^2 r1 r2^2 - 34 a b m^2 r1 r2^2 - 17 b^2 m^2 r1 r2^2 + \\
& 24 a m^3 r1 r2^2 + 18 b m^3 r1 r2^2 - 9 m^4 r1 r2^2 + 12 a^2 m r1^2 r2^2 + \\
& 24 a b m r1^2 r2^2 + 12 b^2 m r1^2 r2^2 - 35 a m^2 r1^2 r2^2 - \\
& 35 b m^2 r1^2 r2^2 + 24 m^3 r1^2 r2^2 + 12 a m r1^3 r2^2 + 12 b m r1^3 r2^2 - \\
& 19 m^2 r1^3 r2^2 + 4 m r1^4 r2^2 - 6 a^2 m^2 r2^3 - 8 a b m^2 r2^3 - \\
& 3 b^2 m^2 r2^3 + 10 a m^3 r2^3 + 4 b m^3 r2^3 - 3 m^4 r2^3 + 6 a^2 m r1 r2^3 + \\
& 12 a b m r1 r2^3 + 6 b^2 m r1 r2^3 - 22 a m^2 r1 r2^3 - 20 b m^2 r1 r2^3 + \\
& 16 m^3 r1 r2^3 + 12 a m r1^2 r2^3 + 12 b m r1^2 r2^3 - 19 m^2 r1^2 r2^3 + \\
& 6 m r1^3 r2^3 - 4 a m^2 r2^4 - 3 b m^2 r2^4 + 4 m^3 r2^4 + 4 a m r1 r2^4 + \\
& 4 b m r1 r2^4 - 8 m^2 r1 r2^4 + 4 m r1^2 r2^4 - m^2 r2^5 + m r1 r2^5 + \\
& (a^5 b + 4 a^4 b^2 + 6 a^3 b^3 + 4 a^2 b^4 + a b^5 - a^4 b m - 3 a^3 b^2 m - 3 a^2 b^3 m - a b^4 m - 2 a^4 m^2 + 4 a^2 b^2 m^2 - \\
& 2 b^4 m^2 - a^3 m^3 + a^2 b m^3 + a b^2 m^3 - b^3 m^3 + 5 a^4 b r1 + 16 a^3 b^2 r1 + 18 a^2 b^3 r1 + 8 a b^4 r1 + b^5 r1 - \\
& 8 a^3 b m r1 - 19 a^2 b^2 m r1 - 14 a b^3 m r1 - 3 b^4 m r1 - 6 a^3 m^2 r1 + 2 a^2 b m^2 r1 + 2 a b^2 m^2 r1 - \\
& 6 b^3 m^2 r1 + 3 a^2 m^3 r1 + 2 a b m^3 r1 + 3 b^2 m^3 r1 + 10 a^3 b r1^2 + 24 a^2 b^2 r1^2 + 18 a b^3 r1^2 + \\
& 4 b^4 r1^2 - 18 a^2 b m r1^2 - 29 a b^2 m r1^2 - 11 b^3 m r1^2 - 6 a^2 m^2 r1^2 + 4 a b m^2 r1^2 - 2 b^2 m^2 r1^2 + \\
& 5 a m^3 r1^2 + 5 b m^3 r1^2 + 10 a^2 b r1^3 + 16 a b^2 r1^3 + 6 b^3 r1^3 - 16 a b m r1^3 - 13 b^2 m r1^3 - \\
& 2 a m^2 r1^3 + 2 b m^2 r1^3 + m^3 r1^3 + 5 a b r1^4 + 4 b^2 r1^4 - 5 b m r1^4 + b r1^5 + a^5 r2 + 8 a^4 b r2 + \\
& 18 a^3 b^2 r2 + 16 a^2 b^3 r2 + 5 a b^4 r2 - 3 a^4 m r2 - 14 a^3 b m r2 - 19 a^2 b^2 m r2 - 8 a b^3 m r2 - \\
& 6 a^3 m^2 r2 + 2 a^2 b m^2 r2 + 2 a b^2 m^2 r2 - 6 b^3 m^2 r2 + 3 a^2 m^3 r2 + 2 a b m^3 r2 + 3 b^2 m^3 r2 + \\
& 5 a^4 r1 r2 + 32 a^3 b r1 r2 + 54 a^2 b^2 r1 r2 + 32 a b^3 r1 r2 + 5 b^4 r1 r2 - 12 a^3 m r1 r2 - \\
& 50 a^2 b m r1 r2 - 50 a b^2 m r1 r2 - 12 b^3 m r1 r2 - 8 a^2 m^2 r1 r2 + 8 a b m^2 r1 r2 - 8 b^2 m^2 r1 r2 + \\
& 10 a m^3 r1 r2 + 10 b m^3 r1 r2 + 10 a^3 r1^2 r2 + 48 a^2 b r1^2 r2 + 54 a b^2 r1^2 r2 + 16 b^3 r1^2 r2 - \\
& 18 a^2 m r1^2 r2 - 58 a b m r1^2 r2 - 31 b^2 m r1^2 r2 - 2 a m^2 r1^2 r2 + 2 b m^2 r1^2 r2 + 3 m^3 r1^2 r2 + \\
& 10 a^2 r1^3 r2 + 32 a b r1^3 r2 + 18 b^2 r1^3 r2 - 12 a m r1^3 r2 - 22 b m r1^3 r2 + 5 a r1^4 r2 + \\
& 8 b r1^4 r2 - 3 m r1^4 r2 + r1^5 r2 + 4 a^4 r2^2 + 18 a^3 b r2^2 + 24 a^2 b^2 r2^2 + 10 a b^3 r2^2 - \\
& 11 a^3 m r2^2 - 29 a^2 b m r2^2 - 18 a b^2 m r2^2 - 2 a^2 m^2 r2^2 + 4 a b m^2 r2^2 - 6 b^2 m^2 r2^2 +
\end{aligned}$$

$$\begin{aligned}
& 5 a m^3 r2^2 + 5 b m^3 r2^2 + 16 a^3 r1 r2^2 + 54 a^2 b r1 r2^2 + 48 a b^2 r1 r2^2 + 10 b^3 r1 r2^2 - \\
& 31 a^2 m r1 r2^2 - 58 a b m r1 r2^2 - 18 b^2 m r1 r2^2 + 2 a m^2 r1 r2^2 - 2 b m^2 r1 r2^2 + 3 m^3 r1 r2^2 + \\
& 24 a^2 r1^2 r2^2 + 54 a b r1^2 r2^2 + 24 b^2 r1^2 r2^2 - 29 a m r1^2 r2^2 - 29 b m r1^2 r2^2 + 16 a r1^3 r2^2 + \\
& 18 b r1^3 r2^2 - 9 m r1^3 r2^2 + 4 r1^4 r2^2 + 6 a^3 r2^3 + 16 a^2 b r2^3 + 10 a b^2 r2^3 - 13 a^2 m r2^3 - \\
& 16 a b m r2^3 + 2 a m^2 r2^3 - 2 b m^2 r2^3 + m^3 r2^3 + 18 a^2 r1 r2^3 + 32 a b r1 r2^3 + 10 b^2 r1 r2^3 - \\
& 22 a m r1 r2^3 - 12 b m r1 r2^3 + 18 a r1^2 r2^3 + 16 b r1^2 r2^3 - 9 m r1^2 r2^3 + 6 r1^3 r2^3 + 4 a^2 r2^4 + \\
& 5 a b r2^4 - 5 a m r2^4 + 8 a r1 r2^4 + 5 b r1 r2^4 - 3 m r1 r2^4 + 4 r1^2 r2^4 + a r2^5 + r1 r2^5) \#1 + \\
& (a^5 + 6 a^4 b + 13 a^3 b^2 + 13 a^2 b^3 + 6 a b^4 + b^5 - a^4 m - 4 a^3 b m - 6 a^2 b^2 m - 4 a b^3 m - b^4 m - \\
& 2 a^3 m^2 - 2 a^2 b m^2 - 2 a b^2 m^2 - 2 b^3 m^2 + 5 a^4 r1 + 24 a^3 b r1 + 39 a^2 b^2 r1 + 26 a b^3 r1 + \\
& 6 b^4 r1 - 8 a^3 m r1 - 26 a^2 b m r1 - 28 a b^2 m r1 - 10 b^3 m r1 - 2 a^2 m^2 r1 - 2 b^2 m^2 r1 + \\
& 10 a^3 r1^2 + 36 a^2 b r1^2 + 39 a b^2 r1^2 + 13 b^3 r1^2 - 18 a^2 m r1^2 - 40 a b m r1^2 - 22 b^2 m r1^2 + \\
& 6 a m^2 r1^2 + 6 b m^2 r1^2 + 10 a^2 r1^3 + 24 a b r1^3 + 13 b^2 r1^3 - 16 a m r1^3 - 18 b m r1^3 + \\
& 6 m^2 r1^3 + 5 a r1^4 + 6 b r1^4 - 5 m r1^4 + r1^5 + 6 a^4 r2 + 26 a^3 b r2 + 39 a^2 b^2 r2 + 24 a b^3 r2 + \\
& 5 b^4 r2 - 10 a^3 m r2 - 28 a^2 b m r2 - 26 a b^2 m r2 - 8 b^3 m r2 - 2 a^2 m^2 r2 - 2 b^2 m^2 r2 + \\
& 24 a^3 r1 r2 + 78 a^2 b r1 r2 + 78 a b^2 r1 r2 + 24 b^3 r1 r2 - 40 a^2 m r1 r2 - 80 a b m r1 r2 - \\
& 40 b^2 m r1 r2 + 12 a m^2 r1 r2 + 12 b m^2 r1 r2 + 36 a^2 r1^2 r2 + 78 a b r1^2 r2 + 39 b^2 r1^2 r2 - \\
& 50 a m r1^2 r2 - 52 b m r1^2 r2 + 18 m^2 r1^2 r2 + 24 a r1^3 r2 + 26 b r1^3 r2 - 20 m r1^3 r2 + \\
& 6 r1^4 r2 + 13 a^3 r2^2 + 39 a^2 b r2^2 + 36 a b^2 r2^2 + 10 b^3 r2^2 - 22 a^2 m r2^2 - 40 a b m r2^2 - \\
& 18 b^2 m r2^2 + 6 a m^2 r2^2 + 6 b m^2 r2^2 + 39 a^2 r1 r2^2 + 78 a b r1 r2^2 + 36 b^2 r1 r2^2 - 52 a m r1 r2^2 - \\
& 50 b m r1 r2^2 + 18 m^2 r1 r2^2 + 39 a r1^2 r2^2 + 39 b r1^2 r2^2 - 30 m r1^2 r2^2 + 13 r1^3 r2^2 + \\
& 13 a^2 r2^3 + 24 a b r2^3 + 10 b^2 r2^3 - 18 a m r2^3 - 16 b m r2^3 + 6 m^2 r2^3 + 26 a r1 r2^3 + \\
& 24 b r1 r2^3 - 20 m r1 r2^3 + 13 r1^2 r2^3 + 6 a r2^4 + 5 b r2^4 - 5 m r2^4 + 6 r1 r2^4 + r2^5) \#1^2 + \\
& (2 a^4 + 8 a^3 b + 12 a^2 b^2 + 8 a b^3 + 2 b^4 - a^3 m - 3 a^2 b m - 3 a b^2 m - b^3 m + 8 a^3 r1 + 24 a^2 b r1 + \\
& 24 a b^2 r1 + 8 b^3 r1 - 7 a^2 m r1 - 14 a b m r1 - 7 b^2 m r1 + 12 a^2 r1^2 + 24 a b r1^2 + 12 b^2 r1^2 - \\
& 11 a m r1^2 - 11 b m r1^2 + 8 a r1^3 + 8 b r1^3 - 5 m r1^3 + 2 r1^4 + 8 a^3 r2 + 24 a^2 b r2 + \\
& 24 a b^2 r2 + 8 b^3 r2 - 7 a^2 m r2 - 14 a b m r2 - 7 b^2 m r2 + 24 a^2 r1 r2 + 48 a b r1 r2 + \\
& 24 b^2 r1 r2 - 22 a m r1 r2 - 22 b m r1 r2 + 24 a r1^2 r2 + 24 b r1^2 r2 - 15 m r1^2 r2 + \\
& 8 r1^3 r2 + 12 a^2 r2^2 + 24 a b r2^2 + 12 b^2 r2^2 - 11 a m r2^2 - 11 b m r2^2 + 24 a r1 r2^2 + \\
& 24 b r1 r2^2 - 15 m r1 r2^2 + 12 r1^2 r2^2 + 8 a r2^3 + 8 b r2^3 - 5 m r2^3 + 8 r1 r2^3 + 2 r2^4) \#1^3 + \\
& (a^3 + 3 a^2 b + 3 a b^2 + b^3 + 3 a^2 r1 + 6 a b r1 + 3 b^2 r1 + 3 a r1^2 + 3 b r1^2 + r1^3 + 3 a^2 r2 + 6 a b r2 + \\
& 3 b^2 r2 + 6 a r1 r2 + 6 b r1 r2 + 3 r1^2 r2 + 3 a r2^2 + 3 b r2^2 + 3 r1 r2^2 + r2^3) \#1^4 &, 3], \\
\text{Root} & [a^4 b m^2 + 3 a^3 b^2 m^2 + 3 a^2 b^3 m^2 + a b^4 m^2 + a^3 m^4 - a^2 b m^4 - a b^2 m^4 + b^3 m^4 + \\
& 2 a^3 b m^2 r1 + 3 a^2 b^2 m^2 r1 - b^4 m^2 r1 - 2 a^2 b m^3 r1 + \\
& 2 b^3 m^3 r1 + 3 a^2 m^4 r1 - 6 a b m^4 r1 + 3 b^2 m^4 r1 - \\
& a^3 m^2 r1^2 - 3 a^2 b m^2 r1^2 - 6 a b^2 m^2 r1^2 - 4 b^3 m^2 r1^2 + \\
& 4 a b m^3 r1^2 + 8 b^2 m^3 r1^2 - a m^4 r1^2 - b m^4 r1^2 - \\
& 3 a^2 m^2 r1^3 - 8 a b m^2 r1^3 - 6 b^2 m^2 r1^3 + 4 a m^3 r1^3 + \\
& 10 b m^3 r1^3 - 3 m^4 r1^3 - 3 a m^2 r1^4 - 4 b m^2 r1^4 + \\
& 4 m^3 r1^4 - m^2 r1^5 - a^4 m^2 r2 + 3 a^2 b^2 m^2 r2 + 2 a b^3 m^2 r2 + \\
& 2 a^3 m^3 r2 - 2 a b^2 m^3 r2 + 3 a^2 m^4 r2 - 6 a b m^4 r2 + \\
& 3 b^2 m^4 r2 + a^4 m r1 r2 + 4 a^3 b m r1 r2 + 6 a^2 b^2 m r1 r2 + \\
& 4 a b^3 m r1 r2 + b^4 m r1 r2 - 6 a^3 m^2 r1 r2 - 12 a^2 b m^2 r1 r2 - \\
& 12 a b^2 m^2 r1 r2 - 6 b^3 m^2 r1 r2 + 8 a^2 m^3 r1 r2 + \\
& 8 a b m^3 r1 r2 + 8 b^2 m^3 r1 r2 - 2 a m^4 r1 r2 - 2 b m^4 r1 r2 + \\
& 4 a^3 m r1^2 r2 + 12 a^2 b m r1^2 r2 + 12 a b^2 m r1^2 r2 + \\
& 4 b^3 m r1^2 r2 - 17 a^2 m^2 r1^2 r2 - 34 a b m^2 r1^2 r2 - \\
& 20 b^2 m^2 r1^2 r2 + 18 a m^3 r1^2 r2 + 24 b m^3 r1^2 r2 - \\
& 9 m^4 r1^2 r2 + 6 a^2 m r1^3 r2 + 12 a b m r1^3 r2 + 6 b^2 m r1^3 r2 - \\
& 20 a m^2 r1^3 r2 - 22 b m^2 r1^3 r2 + 16 m^3 r1^3 r2 + 4 a m r1^4 r2 + \\
& 4 b m r1^4 r2 - 8 m^2 r1^4 r2 + m r1^5 r2 - 4 a^3 m^2 r2^2 - \\
& 6 a^2 b m^2 r2^2 - 3 a b^2 m^2 r2^2 - b^3 m^2 r2^2 + 8 a^2 m^3 r2^2 + \\
& 4 a b m^3 r2^2 - a m^4 r2^2 - b m^4 r2^2 + 4 a^3 m r1 r2^2 + \\
& 12 a^2 b m r1 r2^2 + 12 a b^2 m r1 r2^2 + 4 b^3 m r1 r2^2 - \\
& 20 a^2 m^2 r1 r2^2 - 34 a b m^2 r1 r2^2 - 17 b^2 m^2 r1 r2^2 + \\
& 24 a m^3 r1 r2^2 + 18 b m^3 r1 r2^2 - 9 m^4 r1 r2^2 + 12 a^2 m r1^2 r2^2 + \\
& 24 a b m r1^2 r2^2 + 12 b^2 m r1^2 r2^2 - 35 a m^2 r1^2 r2^2 -
\end{aligned}$$

$$\begin{aligned}
& 35 b m^2 r1^2 r2^2 + 24 m^3 r1^2 r2^2 + 12 a m r1^3 r2^2 + \\
& 12 b m r1^3 r2^2 - 19 m^2 r1^3 r2^2 + 4 m r1^4 r2^2 - 6 a^2 m^2 r2^3 - \\
& 8 a b m^2 r2^3 - 3 b^2 m^2 r2^3 + 10 a m^3 r2^3 + 4 b m^3 r2^3 - \\
& 3 m^4 r2^3 + 6 a^2 m r1 r2^3 + 12 a b m r1 r2^3 + 6 b^2 m r1 r2^3 - \\
& 22 a m^2 r1 r2^3 - 20 b m^2 r1 r2^3 + 16 m^3 r1 r2^3 + \\
& 12 a m r1^2 r2^3 + 12 b m r1^2 r2^3 - 19 m^2 r1^2 r2^3 + 6 m r1^3 r2^3 - \\
& 4 a m^2 r2^4 - 3 b m^2 r2^4 + 4 m^3 r2^4 + 4 a m r1 r2^4 + \\
& 4 b m r1 r2^4 - 8 m^2 r1 r2^4 + 4 m r1^2 r2^4 - m^2 r2^5 + m r1 r2^5 + \\
& (a^5 b + 4 a^4 b^2 + 6 a^3 b^3 + 4 a^2 b^4 + a b^5 - a^4 b m - 3 a^3 b^2 m - 3 a^2 b^3 m - a b^4 m - 2 a^4 m^2 + 4 a^2 b^2 m^2 - \\
& 2 b^4 m^2 - a^3 m^3 + a^2 b m^3 + a b^2 m^3 - b^3 m^3 + 5 a^4 b r1 + 16 a^3 b^2 r1 + 18 a^2 b^3 r1 + 8 a b^4 r1 + b^5 r1 - \\
& 8 a^3 b m r1 - 19 a^2 b^2 m r1 - 14 a b^3 m r1 - 3 b^4 m r1 - 6 a^3 m^2 r1 + 2 a^2 b m^2 r1 + 2 a b^2 m^2 r1 - \\
& 6 b^3 m^2 r1 + 3 a^2 m^3 r1 + 2 a b m^3 r1 + 3 b^2 m^3 r1 + 10 a^3 b r1^2 + 24 a^2 b^2 r1^2 + 18 a b^3 r1^2 + \\
& 4 b^4 r1^2 - 18 a^2 b m r1^2 - 29 a b^2 m r1^2 - 11 b^3 m r1^2 - 6 a^2 m^2 r1^2 + 4 a b m^2 r1^2 - 2 b^2 m^2 r1^2 + \\
& 5 a m^3 r1^2 + 5 b m^3 r1^2 + 10 a^2 b r1^3 + 16 a b^2 r1^3 + 6 b^3 r1^3 - 16 a b m r1^3 - 13 b^2 m r1^3 - \\
& 2 a m^2 r1^3 + 2 b m^2 r1^3 + m^3 r1^3 + 5 a b r1^4 + 4 b^2 r1^4 - 5 b m r1^4 + b r1^5 + a^5 r2 + 8 a^4 b r2 + \\
& 18 a^3 b^2 r2 + 16 a^2 b^3 r2 + 5 a b^4 r2 - 3 a^4 m r2 - 14 a^3 b m r2 - 19 a^2 b^2 m r2 - 8 a b^3 m r2 - \\
& 6 a^3 m^2 r2 + 2 a^2 b m^2 r2 + 2 a b^2 m^2 r2 - 6 b^3 m^2 r2 + 3 a^2 m^3 r2 + 2 a b m^3 r2 + 3 b^2 m^3 r2 + \\
& 5 a^4 r1 r2 + 32 a^3 b r1 r2 + 54 a^2 b^2 r1 r2 + 32 a b^3 r1 r2 + 5 b^4 r1 r2 - 12 a^3 m r1 r2 - \\
& 50 a^2 b m r1 r2 - 50 a b^2 m r1 r2 - 12 b^3 m r1 r2 - 8 a^2 m^2 r1 r2 + 8 a b m^2 r1 r2 - 8 b^2 m^2 r1 r2 + \\
& 10 a m^3 r1 r2 + 10 b m^3 r1 r2 + 10 a^3 r1^2 r2 + 48 a^2 b r1^2 r2 + 54 a b^2 r1^2 r2 + 16 b^3 r1^2 r2 - \\
& 18 a^2 m r1^2 r2 - 58 a b m r1^2 r2 - 31 b^2 m r1^2 r2 - 2 a m^2 r1^2 r2 + 2 b m^2 r1^2 r2 + 3 m^3 r1^2 r2 + \\
& 10 a^2 r1^3 r2 + 32 a b r1^3 r2 + 18 b^2 r1^3 r2 - 12 a m r1^3 r2 - 22 b m r1^3 r2 + 5 a r1^4 r2 + \\
& 8 b r1^4 r2 - 3 m r1^4 r2 + r1^5 r2 + 4 a^4 r2^2 + 18 a^3 b r2^2 + 24 a^2 b^2 r2^2 + 10 a b^3 r2^2 - \\
& 11 a^3 m r2^2 - 29 a^2 b m r2^2 - 18 a b^2 m r2^2 - 2 a^2 m^2 r2^2 + 4 a b m^2 r2^2 - 6 b^2 m^2 r2^2 + \\
& 5 a m^3 r2^2 + 5 b m^3 r2^2 + 16 a^3 r1 r2^2 + 54 a^2 b r1 r2^2 + 48 a b^2 r1 r2^2 + 10 b^3 r1 r2^2 - \\
& 31 a^2 m r1 r2^2 - 58 a b m r1 r2^2 - 18 b^2 m r1 r2^2 + 2 a m^2 r1 r2^2 - 2 b m^2 r1 r2^2 + 3 m^3 r1 r2^2 + \\
& 24 a^2 r1^2 r2^2 + 54 a b r1^2 r2^2 + 24 b^2 r1^2 r2^2 - 29 a m r1^2 r2^2 - 29 b m r1^2 r2^2 + 16 a r1^3 r2^2 + \\
& 18 b r1^3 r2^2 - 9 m r1^3 r2^2 + 4 r1^4 r2^2 + 6 a^3 r2^3 + 16 a^2 b r2^3 + 10 a b^2 r2^3 - 13 a^2 m r2^3 - \\
& 16 a b m r2^3 + 2 a m^2 r2^3 - 2 b m^2 r2^3 + m^3 r2^3 + 18 a^2 r1 r2^3 + 32 a b r1 r2^3 + 10 b^2 r1 r2^3 - \\
& 22 a m r1 r2^3 - 12 b m r1 r2^3 + 18 a r1^2 r2^3 + 16 b r1^2 r2^3 - 9 m r1^2 r2^3 + 6 r1^3 r2^3 + 4 a^2 r2^4 + \\
& 5 a b r2^4 - 5 a m r2^4 + 8 a r1 r2^4 + 5 b r1 r2^4 - 3 m r1 r2^4 + 4 r1^2 r2^4 + a r2^5 + r1 r2^5) \#1 + \\
& (a^5 + 6 a^4 b + 13 a^3 b^2 + 13 a^2 b^3 + 6 a b^4 + b^5 - a^4 m - 4 a^3 b m - 6 a^2 b^2 m - 4 a b^3 m - b^4 m - \\
& 2 a^3 m^2 - 2 a^2 b m^2 - 2 a b^2 m^2 - 2 b^3 m^2 + 5 a^4 r1 + 24 a^3 b r1 + 39 a^2 b^2 r1 + 26 a b^3 r1 + \\
& 6 b^4 r1 - 8 a^3 m r1 - 26 a^2 b m r1 - 28 a b^2 m r1 - 10 b^3 m r1 - 2 a^2 m^2 r1 - 2 b^2 m^2 r1 + \\
& 10 a^3 r1^2 + 36 a^2 b r1^2 + 39 a b^2 r1^2 + 13 b^3 r1^2 - 18 a^2 m r1^2 - 40 a b m r1^2 - 22 b^2 m r1^2 + \\
& 6 a m^2 r1^2 + 6 b m^2 r1^2 + 10 a^2 r1^3 + 24 a b r1^3 + 13 b^2 r1^3 - 16 a m r1^3 - 18 b m r1^3 + \\
& 6 m^2 r1^3 + 5 a r1^4 + 6 b r1^4 - 5 m r1^4 + r1^5 + 6 a^4 r2 + 26 a^3 b r2 + 39 a^2 b^2 r2 + 24 a b^3 r2 + \\
& 5 b^4 r2 - 10 a^3 m r2 - 28 a^2 b m r2 - 26 a b^2 m r2 - 8 b^3 m r2 - 2 a^2 m^2 r2 - 2 b^2 m^2 r2 + \\
& 24 a^3 r1 r2 + 78 a^2 b r1 r2 + 78 a b^2 r1 r2 + 24 b^3 r1 r2 - 40 a^2 m r1 r2 - 80 a b m r1 r2 - \\
& 40 b^2 m r1 r2 + 12 a m^2 r1 r2 + 12 b m^2 r1 r2 + 36 a^2 r1^2 r2 + 78 a b r1^2 r2 + 39 b^2 r1^2 r2 - \\
& 50 a m r1^2 r2 - 52 b m r1^2 r2 + 18 m^2 r1^2 r2 + 24 a r1^3 r2 + 26 b r1^3 r2 - 20 m r1^3 r2 + \\
& 6 r1^4 r2 + 13 a^3 r2^2 + 39 a^2 b r2^2 + 36 a b^2 r2^2 + 10 b^3 r2^2 - 22 a^2 m r2^2 - 40 a b m r2^2 - \\
& 18 b^2 m r2^2 + 6 a m^2 r2^2 + 6 b m^2 r2^2 + 39 a^2 r1 r2^2 + 78 a b r1 r2^2 + 36 b^2 r1 r2^2 - 52 a m r1 r2^2 - \\
& 50 b m r1 r2^2 + 18 m^2 r1 r2^2 + 39 a r1^2 r2^2 + 39 b r1^2 r2^2 - 30 m r1^2 r2^2 + 13 r1^3 r2^2 + \\
& 13 a^2 r2^3 + 24 a b r2^3 + 10 b^2 r2^3 - 18 a m r2^3 - 16 b m r2^3 + 6 m^2 r2^3 + 26 a r1 r2^3 + \\
& 24 b r1 r2^3 - 20 m r1 r2^3 + 13 r1^2 r2^3 + 6 a r2^4 + 5 b r2^4 - 5 m r2^4 + 6 r1 r2^4 + r2^5) \#1^2 + \\
& (2 a^4 + 8 a^3 b + 12 a^2 b^2 + 8 a b^3 + 2 b^4 - a^3 m - 3 a^2 b m - 3 a b^2 m - b^3 m + 8 a^3 r1 + 24 a^2 b r1 + \\
& 24 a b^2 r1 + 8 b^3 r1 - 7 a^2 m r1 - 14 a b m r1 - 7 b^2 m r1 + 12 a^2 r1^2 + 24 a b r1^2 + 12 b^2 r1^2 - \\
& 11 a m r1^2 - 11 b m r1^2 + 8 a r1^3 + 8 b r1^3 - 5 m r1^3 + 2 r1^4 + 8 a^3 r2 + 24 a^2 b r2 + \\
& 24 a b^2 r2 + 8 b^3 r2 - 7 a^2 m r2 - 14 a b m r2 - 7 b^2 m r2 + 24 a^2 r1 r2 + 48 a b r1 r2 + \\
& 24 b^2 r1 r2 - 22 a m r1 r2 - 22 b m r1 r2 + 24 a r1^2 r2 + 24 b r1^2 r2 - 15 m r1^2 r2 + \\
& 8 r1^3 r2 + 12 a^2 r2^2 + 24 a b r2^2 + 12 b^2 r2^2 - 11 a m r2^2 - 11 b m r2^2 + 24 a r1 r2^2 + \\
& 24 b r1 r2^2 - 15 m r1 r2^2 + 12 r1^2 r2^2 + 8 a r2^3 + 8 b r2^3 - 5 m r2^3 + 8 r1 r2^3 + 2 r2^4) \#1^3 + \\
& (a^3 + 3 a^2 b + 3 a b^2 + b^3 + 3 a^2 r1 + 6 a b r1 + 3 b^2 r1 + 3 a r1^2 + 3 b r1^2 + r1^3 + 3 a^2 r2 + 6 a b r2 + \\
& 3 b^2 r2 + 6 a r1 r2 + 6 b r1 r2 + 3 r1^2 r2 + 3 a r2^2 + 3 b r2^2 + 3 r1 r2^2 + r2^3) \#1^4 \&, 4] \}
\end{aligned}$$

```
simplify[
Series[Det[JEqNBA2011 - x IdentityMatrix[4] /. x -> -m r1 r2 /.
{(r1 + a) (r2 + b)}], {m, 0, 1}]] O[m]^2
```

This confirms that eq. (4.29) of BA2011 is consistent with matrix J_N given in their eq. (4.28).

■ Assuming tight linkage (weak recombination)

The coordinates of the internal equilibrium under the assumption of tight linkage, i.e. $r \ll \min(a, m)$, up to and including first-order terms of r , can be obtained from eq. (4.2) in BA2011.

```
{pEqBA, qEqBA, DABEqBA} // MatrixForm
```

$$\left(\begin{array}{c} \frac{-a^2+b^2+6 a (r1+r2)-4 m (r1+r2)-(r1+r2)^2+(a-b+r1+r2) \sqrt{-8 m (r1+r2)+(a+b+r1+r2)^2}}{8 a (r1+r2)} \\ \frac{a^2-b^2+6 b (r1+r2)-4 m (r1+r2)-(r1+r2)^2+(-a+b+r1+r2) \sqrt{-8 m (r1+r2)+(a+b+r1+r2)^2}}{8 b (r1+r2)} \\ \frac{-8 m^2 (r1+r2)^2-4 m (r1+r2) \left(a^2-2 a b+b^2-2 a (r1+r2)-2 b (r1+r2)+(r1+r2)^2\right)+(a-b-r1-r2) (a+b-r1-r2) (a-b+r1+r2) \left(a+b+r1+r2-\sqrt{-8 m (r1+r2)}\right)}{32 a b (r1+r2)^2} \end{array} \right)$$

```
In[129]:= pEqWeakRec = FullSimplify[
Series[pEqBA /. {r1 -> p1 ε, r2 -> p2 ε}, {ε, 0, 1}] /. {p1 -> r1 / ε, p2 -> r2 / ε} // Normal,
Assumptions -> {0 < a < b, 0 < m, 0 < r1, 0 < r2}] // FullSimplify;
qEqWeakRec = FullSimplify[Series[qEqBA /. {r1 -> p1 ε, r2 -> p2 ε}, {ε, 0, 1}] /.
{p1 -> r1 / ε, p2 -> r2 / ε} // Normal,
Assumptions -> {0 < a < b, 0 < m, 0 < r1, 0 < r2}] // FullSimplify;
DABEqWeakRec = FullSimplify[Series[DABEqBA /. {r1 -> p1 ε, r2 -> p2 ε}, {ε, 0, 1}] /.
{p1 -> r1 / ε, p2 -> r2 / ε} // Normal,
Assumptions -> {0 < a < b, 0 < m, 0 < r1, 0 < r2}] // FullSimplify;

{pEqWeakRec, qEqWeakRec, DABEqWeakRec} // TableForm
```

$$\begin{aligned} & -\frac{-a^4+a^3 (-3 b+m)+a^2 b (-3 b+2 m)+b (b-m) m (r1+r2)+a (-b^3+b^2 m+b m (r1+r2)+m^2 (r1+r2))}{a (a+b)^3} \\ & -\frac{-a^3 b-b^4+b^3 m+b m^2 (r1+r2)+a^2 (-3 b^2+b m+m (r1+r2))+a (-3 b^3+2 b^2 m+b m (r1+r2)-m^2 (r1+r2))}{b (a+b)^3} \\ & \frac{m \left(a^4 b-b^2 (b-m) m (r1+r2)+a^3 \left(3 b^2-m (r1+r2)-b (m+r1+r2)\right)+a^2 \left(3 b^3+b m (r1+r2)+m^2 (r1+r2)-2 b^2 (m+r1+r2)\right)+a b \left(b^3+b m (r1+r2)-2 m^2 (r1+r2)\right)\right)}{a b (a+b)^4} \end{aligned}$$

Checking these against first-order terms of eq. (4.1) in BA2011:

$$\begin{aligned} & 1 - \frac{m}{a+b} - \frac{r m}{(a+b)^2} \left(\frac{b}{a} - \frac{m}{a+b} \left(\frac{b}{a} - 1 \right) \right) - pEqWeakRec /. \{r -> r1 + r2\} // FullSimplify \\ & 0 \\ & 1 - \frac{m}{a+b} - \frac{r m}{(a+b)^2} \left(\frac{a}{b} + \frac{m}{a+b} \left(1 - \frac{a}{b} \right) \right) - qEqWeakRec /. \{r -> r1 + r2\} // FullSimplify \\ & 0 \\ & \frac{m}{a+b} \left(1 - \frac{m}{a+b} \right) - \frac{r m}{(a+b)^2} \left(1 - \frac{m}{a+b} \left(1 - \frac{m}{a+b} \right) \left(2 - \frac{b}{a} - \frac{a}{b} \right) \right) - DABEqWeakRec /. \{r -> r1 + r2\} // FullSimplify \\ & 0 \end{aligned}$$

```
In[132]:= ruleApplyEqWeakRec :=
{p -> pEqWeakRec, q -> qEqWeakRec, n -> nC, DAB -> DABEqWeakRec, DAC -> 0, DCB -> 0, DACB -> 0}
```

ruleApplyEqWeakRec

$$\left\{ \begin{array}{l} p \rightarrow -\frac{1}{a(a+b)^3} (-a^4 + a^3(-3b+m) + a^2b(-3b+2m) + b(b-m)m(r1+r2) + a(-b^3 + b^2m + bm(r1+r2) + m^2(r1+r2))), \\ q \rightarrow -\frac{1}{b(a+b)^3} (-a^3b - b^4 + b^3m + bm^2(r1+r2) + a^2(-3b^2 + bm + m(r1+r2)) + a(-3b^3 + 2b^2m + bm(r1+r2) - m^2(r1+r2))), \\ n \rightarrow nC, \\ DAB \rightarrow \frac{1}{a b (a+b)^4} m (a^4 b - b^2 (b-m)m(r1+r2) + a^3 (3b^2 - m(r1+r2) - b(m+r1+r2)) + a^2 (3b^3 + bm(r1+r2) + m^2(r1+r2) - 2b^2(m+r1+r2)) + a b (b^3 + bm(r1+r2) - 2m^2(r1+r2) - b^2(m+r1+r2))), DAC \rightarrow 0, DCB \rightarrow 0, DACB \rightarrow 0 \end{array} \right.$$

JPrep // MatrixForm

$$\left(\begin{array}{cccccc} a - m - 2ap & 0 & b & 0 & 0 & 0 \\ 0 & b - m - 2bq & a & 0 & 0 & 0 \\ -2aDAB + mq & -2bDAB + mp & a + b - m - 2ap - 2bq - r1 - r2 & 0 & 0 & 0 \\ 0 & 0 & 0 & -m & a & b \\ 0 & 0 & 0 & mp & a - m - 2ap - r1 & 0 \\ 0 & 0 & 0 & mq & 0 & b - m - 2 \\ 0 & 0 & 0 & m(DAB - pq) & -2aDAB + mq & -2bDA \end{array} \right)$$

Now we see the block structure claimed in eq. (4.27) of BA2011.

```
In[133]:= JEqWeakRec = JPrep /. ruleApplyEqWeakRec // FullSimplify;
JEqWeakRec // MatrixForm
```

Out[134]//MatrixForm=

$$\left(\begin{array}{ccc} a - m + \frac{1}{4} \left(8a \left(-1 + \frac{m}{a+b} \right) + \frac{8m(b(b-m)+a(b+m))(r1+r2)}{(a+b)^3} \right) & 0 & 0 \\ 0 & b - m + \frac{1}{4} \left(8b \left(-1 + \frac{m}{a+b} \right) + \frac{8m(b(b-m)+a(b+m))(r1+r2)}{(a+b)^3} \right) & 0 \\ \frac{m \left(b \left(8 - \frac{8m}{a+b} \right) - \frac{8m(a^2+a(b-m)+bm)(r1+r2)}{(a+b)^3} - \frac{16(a b (a+b)^2 (a+b-m) - (a^2+a(b-m)+bm)(b(b-m)+a(b+m))(r1+r2))}{(a+b)^4} \right)}{8b} & \frac{m \left(a \left(8 - \frac{8m}{a+b} \right) - \frac{8m(b(b-m)+a(b+m))(r1+r2)}{(a+b)^3} - \frac{16(a b (a+b)^2 (a+b-m) - (a^2+a(b-m)+bm)(b(b-m)+a(b+m))(r1+r2))}{(a+b)^4} \right)}{8a} & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{array} \right)$$

```
In[135]:= JEqNWeakRec = JEqWeakRec[[4, 5, 6, 7], {4, 5, 6, 7}];
JEqNWeakRec // MatrixForm
```

Out[136]//MatrixForm=

$$\left(\begin{array}{c} -m \\ \frac{m \left(a \left(8 - \frac{8m}{a+b} \right) - \frac{8m(b(b-m)+a(b+m))(r1+r2)}{(a+b)^3} \right)}{8a} \\ \frac{m \left(b \left(8 - \frac{8m}{a+b} \right) - \frac{8m(a^2+a(b-m)+bm)(r1+r2)}{(a+b)^3} \right)}{8b} \\ \frac{m \left(- \left(b \left(8 - \frac{8m}{a+b} \right) - \frac{8m(a^2+a(b-m)+bm)(r1+r2)}{(a+b)^3} \right) \left(a \left(8 - \frac{8m}{a+b} \right) - \frac{8m(b(b-m)+a(b+m))(r1+r2)}{(a+b)^3} \right) + \frac{64m(a b (a+b)^2 (a+b-m) - (a^2+a(b-m)+bm)(b(b-m)+a(b+m))(r1+r2))}{(a+b)^4} \right)}{64ab} \end{array} \right) m \left(b \left(8 - \frac{8m}{a+b} \right) - \frac{8m(a^2+a(b-m)+bm)(r1+r2)}{(a+b)^3} \right)$$

■ Using the Ansatz $m_e = -\lambda_N = mz$

JEqWeakRec

$$\begin{aligned}
& \left\{ \left\{ -\frac{1}{(a+b)^3} (a^4 + a^3 (3b-m) + a^2 b (3b-m) + a (b+m) (b^2 - 2m (r1+r2)) + \right. \right. \\
& \quad b m (b^2 - 2b (r1+r2) + 2m (r1+r2)) \Big), 0, b, 0, 0, 0, 0 \Big\}, \\
& \left\{ 0, \frac{1}{(a+b)^3} (-b^4 + b^3 m - a^3 (b+m) + 2b m^2 (r1+r2) + a^2 (-3b^2 - b m + 2m (r1+r2)) + \right. \\
& \quad a (-3b^3 + b^2 m + 2b m (r1+r2) - 2m^2 (r1+r2)) \Big), a, 0, 0, 0, 0 \Big\}, \\
& \left\{ \frac{1}{b (a+b)^4} m (-a^4 b + b^2 (b^3 - b^2 m + 2b m (r1+r2) - 3m^2 (r1+r2)) + \right. \\
& \quad a b (2b^3 - 3b m (r1+r2) + 4m^2 (r1+r2) + b^2 (-m + 2(r1+r2))) + \\
& \quad a^3 (-2b^2 + m (r1+r2) + b (m + 2(r1+r2))) + \\
& \quad a^2 (-4b m (r1+r2) - m^2 (r1+r2) + b^2 (m + 4(r1+r2))) \Big), \\
& \frac{1}{a (a+b)^4} m (a^5 + a^4 (2b-m) + b^2 (b-m) m (r1+r2) + a^3 (2m (r1+r2) + b (-m + 2(r1+r2))) + \\
& \quad a b (-b^3 - 4b m (r1+r2) + 4m^2 (r1+r2) + b^2 (m + 2(r1+r2))) + \\
& \quad a^2 (-2b^3 - 3b m (r1+r2) - 3m^2 (r1+r2) + b^2 (m + 4(r1+r2))) \Big), \\
& \left. - \frac{a^2 + b^2 - 2m (r1+r2) + b (-m + r1+r2) + a (2b - m + r1+r2)}{a+b}, 0, \right. \\
& \left. 0, 0, 0 \right\}, \{0, 0, \\
& 0, -m, a, b, 0\}, \\
& \left\{ 0, 0, 0, -\frac{1}{a (a+b)^3} m (-a^4 + a^3 (-3b+m) + a^2 b (-3b+2m) + \right. \\
& \quad b (b-m) m (r1+r2) + a (-b^3 + b^2 m + b m (r1+r2) + m^2 (r1+r2)) \Big), \\
& \left. a - m - r1 + \frac{1}{(a+b)^3} 2 (-a^4 + a^3 (-3b+m) + a^2 b (-3b+2m) + b (b-m) m (r1+r2) + \right. \\
& \quad a (-b^3 + b^2 m + b m (r1+r2) + m^2 (r1+r2)) \Big), 0, b \Big\}, \\
& \left\{ 0, 0, 0, -\frac{1}{b (a+b)^3} m (-a^3 b - b^4 + b^3 m + b m^2 (r1+r2) + a^2 (-3b^2 + b m + m (r1+r2)) + \right. \\
& \quad a (-3b^3 + 2b^2 m + b m (r1+r2) - m^2 (r1+r2)) \Big), 0, \\
& \left. b - m - r2 + \frac{1}{(a+b)^3} 2 (-a^3 b - b^4 + b^3 m + b m^2 (r1+r2) + a^2 (-3b^2 + b m + m (r1+r2)) + \right. \\
& \quad a (-3b^3 + 2b^2 m + b m (r1+r2) - m^2 (r1+r2)) \Big), a \Big\}, \\
& \left\{ 0, 0, 0, \frac{1}{a b (a+b)^6} m (-(-a^3 b - b^4 + b^3 m + b m^2 (r1+r2) + a^2 (-3b^2 + b m + m (r1+r2)) + \right. \\
& \quad a (-3b^3 + 2b^2 m + b m (r1+r2) - m^2 (r1+r2)) \Big) (-a^4 + a^3 (-3b+m) + \right. \\
& \quad a^2 b (-3b+2m) + b (b-m) m (r1+r2) + a (-b^3 + b^2 m + b m (r1+r2) + m^2 (r1+r2)) \Big) + \\
& \quad (a+b)^2 m (a^4 b - b^2 (b-m) m (r1+r2) + a^3 (3b^2 - m (r1+r2) - b (m + r1+r2)) + \\
& \quad a^2 (3b^3 + b m (r1+r2) + m^2 (r1+r2) - 2b^2 (m + r1+r2)) + \\
& \quad a b (b^3 + b m (r1+r2) - 2m^2 (r1+r2) - b^2 (m + r1+r2)) \Big), \\
& \left. \frac{1}{b (a+b)^4} m (-a^4 b + b^2 (b^3 - b^2 m + 2b m (r1+r2) - 3m^2 (r1+r2)) + \right. \\
& \quad a b (2b^3 - 3b m (r1+r2) + 4m^2 (r1+r2) + b^2 (-m + 2(r1+r2))) + \\
& \quad a^3 (-2b^2 + m (r1+r2) + b (m + 2(r1+r2))) + \\
& \quad a^2 (-4b m (r1+r2) - m^2 (r1+r2) + b^2 (m + 4(r1+r2))) \Big), \\
& \left. \frac{1}{a (a+b)^4} m (a^5 + a^4 (2b-m) + b^2 (b-m) m (r1+r2) + a^3 (2m (r1+r2) + b (-m + 2(r1+r2))) + \right. \\
& \quad a b (-b^3 - 4b m (r1+r2) + 4m^2 (r1+r2) + b^2 (m + 2(r1+r2))) \Big) +
\end{aligned}$$

$$-\frac{a^2 \left(-2 b^3-3 b m (r1+r2)-3 m^2 (r1+r2)+b^2 (m+4 (r1+r2))\right)}{a+b} \Bigg\}$$

Applying the same Ansatz as above to the Jacobian obtained from the differential equations yields the following ratio between the effective and actual migration rate, $\frac{m_e}{m}$:

```

ruleApplyEqWeakRec


$$\left\{ p \rightarrow -\frac{1}{a (a+b)^3} \left( -a^4 + a^3 (-3 b + m) + a^2 b (-3 b + 2 m) + b (b - m) m (r1 + r2) + a (-b^3 + b^2 m + b m (r1 + r2) + m^2 (r1 + r2)) \right), \right.$$


$$q \rightarrow -\frac{1}{b (a+b)^3} \left( -a^3 b - b^4 + b^3 m + b m^2 (r1 + r2) + a^2 (-3 b^2 + b m + m (r1 + r2)) + a (-3 b^3 + 2 b^2 m + b m (r1 + r2) - m^2 (r1 + r2)) \right), n \rightarrow nC,$$


$$DAB \rightarrow \frac{1}{a b (a+b)^4} m \left( a^4 b - b^2 (b - m) m (r1 + r2) + a^3 (3 b^2 - m (r1 + r2) - b (m + r1 + r2)) + a^2 (3 b^3 + b m (r1 + r2) + m^2 (r1 + r2) - 2 b^2 (m + r1 + r2)) + a b (b^3 + b m (r1 + r2) - 2 m^2 (r1 + r2) - b^2 (m + r1 + r2)) \right), DAC \rightarrow 0, DCB \rightarrow 0, DACB \rightarrow 0 \Bigg\}$$


```

```

Simplify[
  Series[Det[(JEqWeakRec /. ruleApplyEqWeakRec) - x IdentityMatrix[7] /. x → -m z],
  {m, 0, 1}], Assumptions → {a ≥ 0, b ≥ 0, r1 ≥ 0, r2 ≥ 0}] // Normal
a b m (a + b + r1 + r2)^2 (a (b + r2) z + r1 (r2 (-1 + z) + b z))
Simplify[Solve[% == 0, z]]

```

$$\left\{ z \rightarrow \frac{r1 r2}{(a + r1) (b + r2)} \right\}$$

Hence, we see that the effective migration rate does not only apply for weak migration, but also for weak recombination.

■ Graphical exploration of approximation

■ Generic

We compare the approximate effective migration rate to the exact (negative) eigenvalue of J_N computed numerically.

```

In[137]:= approxEffMigRateACBFunc[a_, b_, m_, r1_, r2_] := m  $\left( \frac{r1}{a+r1} \right) \left( \frac{r2}{b+r2} \right)$ 
```



```

In[138]:= exactEffMigRateACBFunc[a_, b_, m_, r1_, r2_] := Module[{JN}, JN = {{-m, a, b, 0}, {1/8 a (r1+r2) m, -a, b, 0}};
Return[-Max[Re[Eigenvalues[JN]]]]
]
```



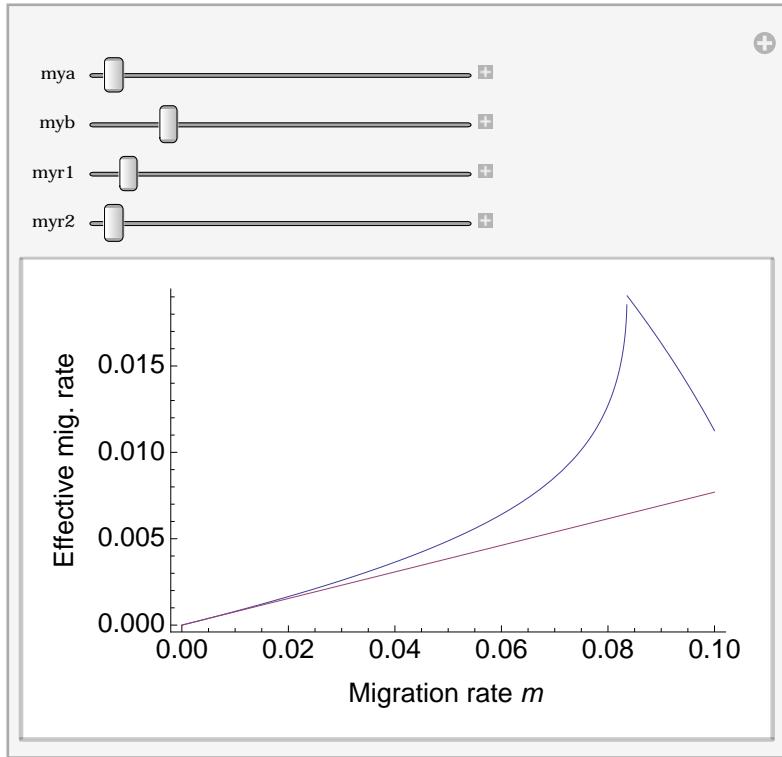
```

mya = 0.002;
myb = 0.4;
mym = 0.0024;
myr1 = 0.01 * (10);
myr2 = 0.01 * (30);
{exactEffMigRateACBFunc[mya, myb, mym, myr1, myr2],
 approxEffMigRateACBFunc[mya, myb, mym, myr1, myr2],
 approxEffMigRateACBFunc[mya, myb, mym, myr1, myr2] /
   exactEffMigRateACBFunc[mya, myb, mym, myr1, myr2] - 1}
{0.00102183, 0.0010084, -0.0131391}

```

The exact (blue) and approximate (red) effective migration rate:

```
Manipulate[Plot[{exactEffMigRateACBFunc[mya, myb, m, myr1, myr2],
  approxEffMigRateACBFunc[mya, myb, m, myr1, myr2]}, {m, 0, .1},
  Frame → True, FrameStyle → Table[{Black, Opacity[0]}, {i, 1, 2}],
  FrameLabel → {"Migration rate  $m$ ", "Effective mig. rate"}, 
  LabelStyle → {Directive[FontSize → 14], FontFamily → "Helvetica"}],
  {{mya, 0.02}, 0, 1}, {{myb, 0.4}, 0, 1}, {{myr1, 0.02}, 0, 1}, {{myr2, 0.02}, 0, 1}]
```



Order of loci: \mathcal{A} - \mathcal{B} - \mathcal{C}

We note that the definitions given in equations (1) to (37) above remain unchanged. The algorithm for the construction of difference equations under recombination also remains the same.

$$D_{ABC} = y_1 - p q n - p D_{CB} - q D_{AC} - n D_{AB} = y_1 - p q n - p [(y_1 + y_3) - q n] - q [(y_1 + y_2) - p n] - n [(y_1 + y_5) - p q] \quad (1)$$

■ Deriving the difference equations under recombination

```
In[139]:= gametes2 = {{A1, B1, C1}, {A1, B2, C1}, {A2, B1, C1},
  {A2, B2, C1}, {A1, B1, C2}, {A1, B2, C2}, {A2, B1, C2}, {A2, B2, C2}}
Out[139]= {{A1, B1, C1}, {A1, B2, C1}, {A2, B1, C1}, {A2, B2, C1},
  {A1, B1, C2}, {A1, B2, C2}, {A2, B1, C2}, {A2, B2, C2}}
```

```

matings2 = Flatten[Table[{gametes2[[i]], gametes2[[j]]},
{i, 1, Length[gametes2]}, {j, 1, Length[gametes2]}], 1]
Length[
%]

{{{A1, B1, C1}, {A1, B1, C1}}, {{A1, B1, C1}, {A1, B2, C1}},
{{A1, B1, C1}, {A2, B1, C1}}, {{A1, B1, C1}, {A2, B2, C1}},
{{A1, B1, C1}, {A1, B1, C2}}, {{A1, B1, C1}, {A1, B2, C2}}, {{A1, B1, C1}, {A2, B1, C2}},
{{A1, B1, C1}, {A2, B2, C2}}, {{A1, B2, C1}, {A1, B1, C1}}, {{A1, B2, C1}, {A1, B2, C1}},
{{A1, B2, C1}, {A2, B1, C1}}, {{A1, B2, C1}, {A2, B2, C1}}, {{A1, B2, C1}, {A1, B1, C2}},
{{A1, B2, C1}, {A1, B2, C2}}, {{A1, B2, C1}, {A2, B1, C2}}, {{A1, B2, C1}, {A2, B2, C2}},
{{A2, B1, C1}, {A1, B1, C1}}, {{A2, B1, C1}, {A1, B2, C1}}, {{A2, B1, C1}, {A2, B1, C1}},
{{A2, B1, C1}, {A2, B2, C1}}, {{A2, B1, C1}, {A1, B1, C2}}, {{A2, B1, C1}, {A1, B2, C2}},
{{A2, B1, C1}, {A2, B1, C2}}, {{A2, B1, C1}, {A2, B2, C1}}, {{A2, B1, C1}, {A1, B1, C1}},
{{A2, B2, C1}, {A1, B1, C2}}, {{A2, B2, C1}, {A2, B1, C1}}, {{A2, B2, C1}, {A2, B2, C1}},
{{A2, B2, C1}, {A1, B1, C1}}, {{A2, B2, C1}, {A1, B2, C2}}, {{A2, B2, C1}, {A2, B1, C2}},
{{A2, B2, C1}, {A2, B2, C2}}, {{A1, B1, C2}, {A1, B1, C1}}, {{A1, B1, C2}, {A1, B2, C1}},
{{A1, B1, C2}, {A2, B1, C1}}, {{A1, B1, C2}, {A2, B2, C1}}, {{A1, B1, C2}, {A1, B1, C2}},
{{A1, B1, C2}, {A1, B2, C2}}, {{A1, B1, C2}, {A2, B1, C2}}, {{A1, B1, C2}, {A1, B1, C1}},
{{A1, B1, C2}, {A2, B1, C1}}, {{A1, B1, C2}, {A2, B2, C1}}, {{A1, B1, C2}, {A2, B1, C2}},
{{A1, B2, C2}, {A1, B1, C1}}, {{A1, B2, C2}, {A1, B2, C1}}, {{A1, B2, C2}, {A2, B1, C1}},
{{A1, B2, C2}, {A2, B2, C1}}, {{A1, B2, C2}, {A1, B1, C2}}, {{A1, B2, C2}, {A1, B2, C2}},
{{A1, B2, C2}, {A2, B1, C2}}, {{A1, B2, C2}, {A2, B2, C2}}, {{A1, B2, C2}, {A1, B1, C1}},
{{A1, B2, C2}, {A1, B2, C2}}, {{A2, B1, C2}, {A2, B1, C1}}, {{A2, B1, C2}, {A2, B2, C1}}}

```

64

The gamete frequencies remain the same, as we have defined the list ‘gametes2’ appropriately:

```

{gametes2, gameteFreqs} // TableForm

A1   A1   A2   A2   A1   A1   A2   A2
B1   B2   B1   B2   B1   B2   B1   B2
C1   C1   C1   C1   C2   C2   C2   C2
y1   y2   y3   y4   y5   y6   y7   y8

```

Obviously, then, the pairs of frequencies applying to the matings remain the same, too:

```

{matings2, freqPairs} // TableForm

A1 B1 C1    A1 B1 C1
A1 B1 C1    A1 B2 C1    A2 B1 C1    A2 B2 C1    A1 B1 C2    A1 B2 C2    A1 B1 C2    A2 B1 C2
y1           y1           y1           y1           y1           y1           y1           y1
y1           y2           y3           y4           y5           y6           y6           y7

MapThread[gametesProduced[#, #1[[1]], #1[[2]], #2[[1]], #2[[2]]] &,
{matings2[[1 ;; 2]], freqPairs[[1 ;; 2]]}] // TableForm

A1 B1 C1    (1 - r1) (1 - r2) y1^2 + r1 (1 - r2) y1^2 + (1 - r1) r2 y1^2 + r1 r2 y1^2
A1 B1 C1     $\frac{1}{2}$  (1 - r1) (1 - r2) y1 y2 +  $\frac{1}{2}$  r1 (1 - r2) y1 y2 +  $\frac{1}{2}$  (1 - r1) r2 y1 y2 +  $\frac{1}{2}$  r1 r2 y1 y2
A1 B2 C1     $\frac{1}{2}$  (1 - r1) (1 - r2) y1 y2 +  $\frac{1}{2}$  r1 (1 - r2) y1 y2 +  $\frac{1}{2}$  (1 - r1) r2 y1 y2 +  $\frac{1}{2}$  r1 r2 y1 y2

```

```
In[140]:= recSep2 =
  MapThread[gametesProduced[#, 1], #1[[1]], #1[[2]], #2[[1]], #2[[2]] &, {matings2, freqPairs}];
TableForm[recSep2]

MapThread::mptd : Object matings2 at position {2, 1} in
  MapThread[gametesProduced[#, 1], #1[[1]], #1[[2]], #2[[1]], #2[[2]] &, {matings2, {y1, y1}, {y1, y2}, {y1, y3}, {y1, y4},
    {y1, y5}, {y1, y6}, {y1, y7}, {y1, y8}, {y2, y1}, {y2, y2}, {y2, y3}, {y2, y4}, {y2, y5}, {y2, y6}, {y2, y7}, {y2, y8},
    {y3, y1}, {y3, y2}, {y3, y3}, {y3, y4}, <>12>, {y5, y1}, {y5, y2}, {y5, y3}, {y5, y4}, {y5, y5}, {y5, y6}, {y5, y7},
    {y5, y8}, {y6, y1}, {y6, y2}, {y6, y3}, {y6, y4}, {y6, y5}, {y6, y6}, {y6, y7}, {y6, y8}, {y7, y1}, {y7, y2}, <>14>}}
] has only 0 of required 1 dimensions. >>

MapThread::mptd : Object matings2 at position {2, 1} in
  MapThread[gametesProduced[#, 1], #1[[1]], #1[[2]], #2[[1]], #2[[2]] &, {matings2, {y1, y1}, {y1, y2}, {y1, y3}, {y1, y4},
    {y1, y5}, {y1, y6}, {y1, y7}, {y1, y8}, {y2, y1}, {y2, y2}, {y2, y3}, {y2, y4}, {y2, y5}, {y2, y6}, {y2, y7}, {y2, y8},
    {y3, y1}, {y3, y2}, {y3, y3}, {y3, y4}, <>12>, {y5, y1}, {y5, y2}, {y5, y3}, {y5, y4}, {y5, y5}, {y5, y6}, {y5, y7},
    {y5, y8}, {y6, y1}, {y6, y2}, {y6, y3}, {y6, y4}, {y6, y5}, {y6, y6}, {y6, y7}, {y6, y8}, {y7, y1}, {y7, y2}, <>14>}}
] has only 0 of required 1 dimensions. >>

Out[141]/TableForm=
MapThread[gametesProduced[#, 1], #1[[1]], #1[[2]], #2[[1]], #2[[2]] &,
{matings2, {{y1, y1}, {y1, y2}, {y1, y3}, {y1, y4}, {y1, y5}, {y1, y6}, {y1, y7}, {y1, y8},
  {y2, y1}, {y2, y2}, {y2, y3}, {y2, y4}, {y2, y5}, {y2, y6}, {y2, y7}, {y2, y8},
  {y3, y1}, {y3, y2}, {y3, y3}, {y3, y4}, {y3, y5}, {y3, y6}, {y3, y7}, {y3, y8},
  {y4, y1}, {y4, y2}, {y4, y3}, {y4, y4}, {y4, y5}, {y4, y6}, {y4, y7}, {y4, y8},
  {y5, y1}, {y5, y2}, {y5, y3}, {y5, y4}, {y5, y5}, {y5, y6}, {y5, y7}, {y5, y8},
  {y6, y1}, {y6, y2}, {y6, y3}, {y6, y4}, {y6, y5}, {y6, y6}, {y6, y7}, {y6, y8},
  {y7, y1}, {y7, y2}, {y7, y3}, {y7, y4}, {y7, y5}, {y7, y6}, {y7, y7}, {y7, y8},
  {y8, y1}, {y8, y2}, {y8, y3}, {y8, y4}, {y8, y5}, {y8, y6}, {y8, y7}, {y8, y8}}}]
indices2 = Table[Position[recSep2[[i, 1]], gametes2[[2]]], {i, Length[recSep2]}]

{{}, {{2}}, {}, {{2}}, {}, {{3}}, {}, {{3}}, {{2}}, {{1}}, {{2}}, {{1}}, {{3}}, {{1}},
{{3}}, {{1}}, {}, {{2}}, {}, {{3}}, {}, {}, {{2}}, {{1}}, {}, {}, {{3}},
{{1}}, {}, {}, {}, {{3}}, {}, {{3}}, {}, {}, {}, {{3}}, {{1}}, {{3}}, {{1}}, {},
{}, {}, {}, {{3}}, {}, {}, {}, {}, {}, {{3}}, {{1}}, {}, {}, {}, {}, {}, {}, {}}

Flatten[Table[Part[recSep2, i, 2][[Flatten[indices2[[i]]]]], {i, Length[indices2]}]] // Total // FullSimplify

y2^2 + r1 y4 y5 - r1 r2 y4 y5 + r2 y3 y6 - r1 r2 y3 y6 + r1 y4 y6 + r2 y4 y6 - 2 r1 r2 y4 y6 +
y2 (y3 - r1 y3 + y4 + y5 - r2 y5 + y6 + y7 + r1 (-1 + r2) y7 + y8 + r1 (-1 + 2 r2) y8 - r2 (y7 + y8)) +
y1 (y2 + r2 y6 + r1 (y4 + r2 y8))
```

■ Differential equations under recombination

■ In terms of gamete frequencies

```
recTilde1 = sumPerOffspringGamete[gametes2, 1, recSep2] // FullSimplify

y1^2 + r2 (y2 + y3 + y4) y5 + r1 (-r2 y4 y5 + y3 (y5 - 2 r2 y5 + y6 - r2 y6) + y2 (y3 + r2 y7)) +
y1 (y2 + y3 + y4 - r1 y4 + y5 + y6 - r2 y6 + y7 + r1 (-1 + 2 r2) y7 + y8 + r1 (-1 + r2) y8 - r2 (y7 + y8))
```

The corresponding continuous-time differential equation:

```
yTilde1D =
  FullSimplify[Series[recTilde1 - y1 /. recScale, {ε, 0, 1}] /. recBackScale // Normal]

y1^2 + r2 (y2 + y3 + y4) y5 + r1 y3 (y2 + y5 + y6) +
y1 (-1 + y2 + y3 + y4 - r1 y4 + y5 + y6 - r2 y6 + y7 + y8 - (r1 + r2) (y7 + y8))

Collect[yTilde1D, {r1, r2}]

-y1 + y1^2 + y1 y2 + y1 y3 + y1 y4 + y1 y5 + y1 y6 + y1 y7 + y1 y8 +
r2 ((y2 + y3 + y4) y5 - y1 y6 - y1 (y7 + y8)) + r1 (-y1 y4 + y3 (y2 + y5 + y6) - y1 (y7 + y8))

FullSimplify[(-y1 + y1^2 + y1 y2 + y1 y3 + y1 y4 + y1 y5 + y1 y6 + y1 y7 + y1 y8),
Assumptions → {y8 == 1 - y1 - y2 - y3 - y4 - y5 - y6 - y7, y1 + y2 + y3 + y4 + y5 + y6 + y7 + y8 == 1}]
```

We note that 'yTilde1D' can be simplified to

```
In[142]:= yTilde1DotRec := -r1 (y1 (1 - p) - y3 p) - r2 (y1 (1 - n) - y5 n)

yTilde1DotRec - yTilde1D /. {p → y1 + y2 + y5 + y6, q → y1 + y3 + y5 + y7, n → y1 + y2 + y3 + y4} //.
{y1 → 1 - (y2 + y3 + y4 + y5 + y6 + y7 + y8)} // Simplify
0

recTilde2 = sumPerOffspringGamete[gametes2, 2, recSep2] // FullSimplify

y2^2 + r1 y4 y5 - r1 r2 y4 y5 + r2 y3 y6 - r1 r2 y3 y6 + r1 y4 y6 + r2 y4 y6 - 2 r1 r2 y4 y6 +
y2 (y3 - r1 y3 + y4 + y5 - r2 y5 + y6 + y7 + r1 (-1 + r2) y7 + y8 + r1 (-1 + 2 r2) y8 - r2 (y7 + y8)) +
y1 (y2 + r2 y6 + r1 (y4 + r2 y8))

yTilde2D =
FullSimplify[Series[recTilde2 - y2 /. recScale, {ε, 0, 1}] /. recBackScale // Normal]

y2^2 + r2 (y1 + y3 + y4) y6 + r1 y4 (y1 + y5 + y6) +
y2 (-1 + y1 + y3 - r1 y3 + y4 + y5 - r2 y5 + y6 + y7 + y8 - (r1 + r2) (y7 + y8))

Collect[yTilde2D, {r1, r2}]

-y2 + y1 y2 + y2^2 + y2 y3 + y2 y4 + y2 y5 + y2 y6 + y2 y7 + y2 y8 +
r2 (-y2 y5 + (y1 + y3 + y4) y6 - y2 (y7 + y8)) + r1 (-y2 y3 + y4 (y1 + y5 + y6) - y2 (y7 + y8))

FullSimplify[(-y2 + y1 y2 + y2^2 + y2 y3 + y2 y4 + y2 y5 + y2 y6 + y2 y7 + y2 y8),
Assumptions → {y8 == 1 - y1 - y2 - y3 - y4 - y5 - y6 - y7, y1 + y2 + y3 + y4 + y5 + y6 + y7 + y8 == 1}]
0
```

We note that 'yTilde2D' can be simplified to

```
In[143]:= yTilde2DotRec := -r1 (y2 (1 - p) - y4 p) - r2 (y2 (1 - n) - y6 n)

yTilde2DotRec - yTilde2D /. {p → y1 + y2 + y5 + y6, q → y1 + y3 + y5 + y7, n → y1 + y2 + y3 + y4} //.
{y1 → 1 - (y2 + y3 + y4 + y5 + y6 + y7 + y8)} // Simplify
0

recTilde3 = sumPerOffspringGamete[gametes2, 3, recSep2] // FullSimplify

y3^2 + y3 y4 + y3 y5 - r1 y3 y5 - r2 y3 y5 + 2 r1 r2 y3 y5 + r1 r2 y4 y5 + y3 y6 -
r1 y3 y6 - r2 y3 y6 + r1 r2 y3 y6 + y3 y7 + r2 y4 y7 - (-1 + r1) y2 (y3 + r2 y7) +
y3 y8 - r2 y3 y8 + y1 (y3 + r2 y7 + r1 (y4 + y7 - 2 r2 y7 + y8 - r2 y8))

yTilde3D =
FullSimplify[Series[recTilde3 - y3 /. recScale, {ε, 0, 1}] /. recBackScale // Normal]

y3^2 + r2 (y1 + y2 + y4) y7 + r1 y1 (y4 + y7 + y8) +
y3 (-1 + y1 + y2 - r1 y2 + y4 + y5 + y6 - (r1 + r2) (y5 + y6) + y7 + y8 - r2 y8)

Collect[yTilde3D, {r1, r2}]

-y3 + y1 y3 + y2 y3 + y3^2 + y3 y4 + y3 y5 + y3 y6 + y3 y7 + y3 y8 +
r2 (-y3 (y5 + y6) + (y1 + y2 + y4) y7 - y3 y8) + r1 (-y2 y3 - y3 (y5 + y6) + y1 (y4 + y7 + y8))

FullSimplify[(-y3 + y1 y3 + y2 y3 + y3^2 + y3 y4 + y3 y5 + y3 y6 + y3 y7 + y3 y8),
Assumptions → {y8 == 1 - y1 - y2 - y3 - y4 - y5 - y6 - y7, y1 + y2 + y3 + y4 + y5 + y6 + y7 + y8 == 1}]
0
```

We note that 'yTilde3D' can be simplified to

```
In[144]:= yTilde3DotRec := -r1 (y3 p - y1 (1 - p)) - r2 (y3 (1 - n) - y7 n)

yTilde3DotRec - yTilde3D /. {p → y1 + y2 + y5 + y6, q → y1 + y3 + y5 + y7, n → y1 + y2 + y3 + y4} //.
{y1 → 1 - (y2 + y3 + y4 + y5 + y6 + y7 + y8)} // Simplify
0
```

```

recTilde4 = sumPerOffspringGamete[gametes2, 4, recSep2] // FullSimplify
y4 (y1 + y2 + y3 + y4 - (-1 + r2) (y5 + y6 + y7)) + (r2 (y1 + y2 + y3) + y4) y8 +
r1 ((-1 + r2) y4 y5 + (r2 y3 - y4 + 2 r2 y4) y6 + y2 (y3 + y7 - r2 y7 + y8 - 2 r2 y8) - y1 (y4 + r2 y8))
yTilde4D =
FullSimplify[Series[recTilde4 - y4 /. recScale, {ε, 0, 1}] /. recBackScale // Normal]
(-1 + y1) y4 + y4 (y2 + y3 + y4 - (-1 + r2) (y5 + y6 + y7)) +
(r2 (y1 + y2 + y3) + y4) y8 + r1 (-y4 (y1 + y5 + y6) + y2 (y3 + y7 + y8))
Collect[yTilde4D, {r1, r2}]
(-1 + y1) y4 + y2 y4 + y3 y4 + y4^2 + y4 y5 + y4 y6 + y4 y7 + y4 y8 +
r2 (-y4 (y5 + y6 + y7) + (y1 + y2 + y3) y8) + r1 (-y4 (y1 + y5 + y6) + y2 (y3 + y7 + y8))
FullSimplify[((-1 + y1) y4 + y2 y4 + y3 y4 + y4^2 + y4 y5 + y4 y6 + y4 y7 + y4 y8),
Assumptions → {y8 == 1 - y1 - y2 - y3 - y4 - y5 - y6 - y7, y1 + y2 + y3 + y4 + y5 + y6 + y7 + y8 == 1}]
0

```

We note that 'yTilde4D' can be simplified to

```

In[145]:= yTilde4DotRec := -r1 (y4 p - y2 (1 - p)) - r2 (y4 (1 - n) - y8 n)

yTilde4DotRec - yTilde4D /. {p → y1 + y2 + y5 + y6, q → y1 + y3 + y5 + y7, n → y1 + y2 + y3 + y4} //.
{y1 → 1 - (y2 + y3 + y4 + y5 + y6 + y7 + y8)} // Simplify
0

recTilde5 = sumPerOffspringGamete[gametes2, 5, recSep2] // FullSimplify
y3 y5 - r1 y3 y5 - r2 y3 y5 + 2 r1 r2 y3 y5 + y4 y5 - r1 y4 y5 - r2 y4 y5 +
r1 r2 y4 y5 + y5^2 + r1 r2 y3 y6 + y5 y6 + y5 y7 + r1 y6 y7 - (-1 + r2) y2 (y5 + r1 y7) +
y5 y8 - r1 y5 y8 + y1 (y5 + r1 y7 + r2 (y6 + y7 - 2 r1 y7 + y8 - r1 y8))

yTilde5D =
FullSimplify[Series[recTilde5 - y5 /. recScale, {ε, 0, 1}] /. recBackScale // Normal]
y5^2 + r1 (y1 + y2 + y6) y7 + r2 y1 (y6 + y7 + y8) +
y5 (-1 + y1 + y2 - r2 y2 + y3 - r1 y3 + y4 - r2 (y3 + y4) + y6 + y7 + y8 - r1 (y4 + y8))
Collect[yTilde5D, {r1, r2}]
-y5 + y1 y5 + y2 y5 + y3 y5 + y4 y5 + y5^2 + y5 y6 + y5 y7 + y5 y8 +
r1 (-y3 y5 + (y1 + y2 + y6) y7 - y5 (y4 + y8)) + r2 (-y2 y5 + (-y3 - y4) y5 + y1 (y6 + y7 + y8))
FullSimplify[(-y5 + y1 y5 + y2 y5 + y3 y5 + y4 y5 + y5^2 + y5 y6 + y5 y7 + y5 y8),
Assumptions → {y8 == 1 - y1 - y2 - y3 - y4 - y5 - y6 - y7, y1 + y2 + y3 + y4 + y5 + y6 + y7 + y8 == 1}]
0

```

We note that 'yTilde5D' can be simplified to

```

In[146]:= yTilde5DotRec := -r1 (y5 (1 - p) - y7 p) - r2 (y5 n - y1 (1 - n))

yTilde5DotRec - yTilde5D /. {p → y1 + y2 + y5 + y6, q → y1 + y3 + y5 + y7, n → y1 + y2 + y3 + y4} //.
{y1 → 1 - (y2 + y3 + y4 + y5 + y6 + y7 + y8)} // Simplify
0

recTilde6 = sumPerOffspringGamete[gametes2, 6, recSep2] // FullSimplify
y6 (y1 + y2 + y3 - r1 y3 + y4 + y5 + y6 + y7 - r1 (y4 + y7)) + (r1 (y1 + y2 + y5) + y6) y8 +
r2 (- (y1 + y3 + y4) y6 + y2 (y5 + y7 - r1 y7 + y8 - 2 r1 y8)) + r1 (y4 y5 + y3 y6 + 2 y4 y6 - y1 y8))

yTilde6D =
FullSimplify[Series[recTilde6 - y6 /. recScale, {ε, 0, 1}] /. recBackScale // Normal]
y6 (-1 + y1 + y2 + y3 - r1 y3 + y4 + y5 + y6 + y7 - r1 (y4 + y7)) +
(r1 (y1 + y2 + y5) + y6) y8 + r2 (- (y1 + y3 + y4) y6 + y2 (y5 + y7 + y8))

```

```

Collect[yTilde6D, {r1, r2}]

-y6 + y1 y6 + y2 y6 + y3 y6 + y4 y6 + y5 y6 + y6^2 + y6 y7 + y6 y8 +
r1 (-y3 y6 - y6 (y4 + y7) + (y1 + y2 + y5) y8) + r2 (- (y1 + y3 + y4) y6 + y2 (y5 + y7 + y8))

FullSimplify[(-y6 + y1 y6 + y2 y6 + y3 y6 + y4 y6 + y5 y6 + y6^2 + y6 y7 + y6 y8),
Assumptions → {y8 == 1 - y1 - y2 - y3 - y4 - y5 - y6 - y7, y1 + y2 + y3 + y4 + y5 + y6 + y7 + y8 == 1}]

0

```

We note that 'yTilde6D' can be simplified to

```

In[147]:= yTilde6DotRec := -r1 (y6 (1 - p) - y8 p) - r2 (y6 n - y2 (1 - n))

yTilde6DotRec - yTilde6D /. {p → y1 + y2 + y5 + y6, q → y1 + y3 + y5 + y7, n → y1 + y2 + y3 + y4} //.
{y1 → 1 - (y2 + y3 + y4 + y5 + y6 + y7 + y8)} // Simplify

0

recTilde7 = sumPerOffspringGamete[gametes2, 7, recSep2] // FullSimplify

y7 (y1 + y2 + y3 + y4 + y5 + y6 + y7 + y8) +
r1 (y4 (y5 - r2 y5) + y3 (y5 - 2 r2 y5 - r2 y6) + ((-1 + 2 r2) y1 + (-1 + r2) y2 - y6) y7 +
(r2 y1 + y5) y8) + r2 (- (y1 + y2 + y4) y7 + y3 (y5 + y6 + y8))

yTilde7D =
FullSimplify[Series[recTilde7 - y7 /. recScale, {ε, 0, 1}] /. recBackScale // Normal]

y7 (-1 + y1 + y2 + y3 + y4 + y5 + y6 + y7 + y8) +
r1 (- (y1 + y2 + y6) y7 + y5 (y3 + y4 + y8)) + r2 (- (y1 + y2 + y4) y7 + y3 (y5 + y6 + y8))

Collect[yTilde7D, {r1, r2}]

y7 (-1 + y1 + y2 + y3 + y4 + y5 + y6 + y7 + y8) +
r1 (- (y1 + y2 + y6) y7 + y5 (y3 + y4 + y8)) + r2 (- (y1 + y2 + y4) y7 + y3 (y5 + y6 + y8))

FullSimplify[(y7 (-1 + y1 + y2 + y3 + y4 + y5 + y6 + y7 + y8)),
Assumptions → {y8 == 1 - y1 - y2 - y3 - y4 - y5 - y6 - y7, y1 + y2 + y3 + y4 + y5 + y6 + y7 + y8 == 1}]

0

```

We note that 'yTilde7D' can be simplified to

```

In[148]:= yTilde7DotRec := -r1 (y7 p - y5 (1 - p)) - r2 (y7 n - y3 (1 - n))

yTilde7DotRec - yTilde7D /. {p → y1 + y2 + y5 + y6, q → y1 + y3 + y5 + y7, n → y1 + y2 + y3 + y4} //.
{y1 → 1 - (y2 + y3 + y4 + y5 + y6 + y7 + y8)} // Simplify

0

recTilde8 = sumPerOffspringGamete[gametes2, 8, recSep2] // FullSimplify

r1 y6 (y3 + y4 + y7) - r1 (y1 + y2 + y5) y8 + y8 (y1 + y2 + y3 + y4 + y5 + y6 + y7 + y8) +
r2 (y4 (y5 - r1 y5 + y6 - 2 r1 y6 + y7) - (y1 + y2 + y3) y8 + r1 (-y3 y6 + y2 y7 + y1 y8 + 2 y2 y8))

yTilde8D =
FullSimplify[Series[recTilde8 - y8 /. recScale, {ε, 0, 1}] /. recBackScale // Normal]

r1 y6 (y3 + y4 + y7) + r2 y4 (y5 + y6 + y7) - r2 (y1 + y2 + y3) y8 -
r1 (y1 + y2 + y5) y8 + y8 (-1 + y1 + y2 + y3 + y4 + y5 + y6 + y7 + y8)

Collect[yTilde8D, {r1, r2}]

y8 (-1 + y1 + y2 + y3 + y4 + y5 + y6 + y7 + y8) +
r2 (y4 (y5 + y6 + y7) + (-y1 - y2 - y3) y8) + r1 (y6 (y3 + y4 + y7) + (-y1 - y2 - y5) y8)

FullSimplify[(y8 (-1 + y1 + y2 + y3 + y4 + y5 + y6 + y7 + y8)),
Assumptions → {y8 == 1 - y1 - y2 - y3 - y4 - y5 - y6 - y7, y1 + y2 + y3 + y4 + y5 + y6 + y7 + y8 == 1}]

0

```

We note that 'yTilde8D' can be simplified to

```
In[149]:= yTilde8DotRec := -r1 (y8 p - y6 (1 - p)) - r2 (y8 n - y4 (1 - n))

yTilde8DotRec - yTilde8D /. {p → y1 + y2 + y5 + y6, q → y1 + y3 + y5 + y7, n → y1 + y2 + y3 + y4} //.
{y1 → 1 - (y2 + y3 + y4 + y5 + y6 + y7 + y8)} // Simplify
0

■ In terms of allele frequencies and LD

allToGam

{p → y1 + y2 + y5 + y6, q → y1 + y3 + y5 + y7, n → y1 + y2 + y3 + y4}

In[150]:= pTildeDotRec := D[pDef /. {y1 → y1[t], y2 → y2[t], y5 → y5[t], y6 → y6[t]}, t] /.
{y1'[t] → yTilde1DotRec, y2'[t] → yTilde2DotRec, y5'[t] → yTilde5DotRec,
y6'[t] → yTilde6DotRec} /. gamToAllLD // FullSimplify
qTildeDotRec := D[qDef /. {y1 → y1[t], y3 → y3[t], y5 → y5[t], y7 → y7[t]}, t] /.
{y1'[t] → yTilde1DotRec, y3'[t] → yTilde3DotRec, y5'[t] → yTilde5DotRec,
y7'[t] → yTilde7DotRec} /. gamToAllLD // FullSimplify
nTildeDotRec := D[nDef /. {y1 → y1[t], y2 → y2[t], y3 → y3[t], y4 → y4[t]}, t] /.
{y1'[t] → yTilde1DotRec, y2'[t] → yTilde2DotRec, y3'[t] → yTilde3DotRec,
y4'[t] → yTilde4DotRec} /. gamToAllLD // FullSimplify
DACTildeDotRec := D[DACDef /. {y1 → y1[t], y2 → y2[t], y3 → y3[t],
y4 → y4[t], y5 → y5[t], y6 → y6[t], y7 → y7[t], y8 → y8[t]}, t] /.
{y1'[t] → yTilde1DotRec, y2'[t] → yTilde2DotRec, y3'[t] → yTilde3DotRec,
y4'[t] → yTilde4DotRec, y5'[t] → yTilde5DotRec, y6'[t] → yTilde6DotRec,
y7'[t] → yTilde7DotRec, y8'[t] → yTilde8DotRec} /.
{x_[t] → x} /. gamToAllLD // FullSimplify
DCBTildeDotRec := D[DCBDef /. {y1 → y1[t], y2 → y2[t], y3 → y3[t],
y4 → y4[t], y5 → y5[t], y6 → y6[t], y7 → y7[t], y8 → y8[t]}, t] /.
{y1'[t] → yTilde1DotRec, y2'[t] → yTilde2DotRec, y3'[t] → yTilde3DotRec,
y4'[t] → yTilde4DotRec, y5'[t] → yTilde5DotRec, y6'[t] → yTilde6DotRec,
y7'[t] → yTilde7DotRec, y8'[t] → yTilde8DotRec} /.
{x_[t] → x} /. gamToAllLD // FullSimplify
DABTildeDotRec := D[DABDef /. {y1 → y1[t], y2 → y2[t], y3 → y3[t],
y4 → y4[t], y5 → y5[t], y6 → y6[t], y7 → y7[t], y8 → y8[t]}, t] /.
{y1'[t] → yTilde1DotRec, y2'[t] → yTilde2DotRec, y3'[t] → yTilde3DotRec,
y4'[t] → yTilde4DotRec, y5'[t] → yTilde5DotRec, y6'[t] → yTilde6DotRec,
y7'[t] → yTilde7DotRec, y8'[t] → yTilde8DotRec} /.
{x_[t] → x} /. gamToAllLD // FullSimplify
DACBTildeDotRec := D[DACBDef /. {y1 → y1[t], y2 → y2[t], y3 → y3[t],
y4 → y4[t], y5 → y5[t], y6 → y6[t], y7 → y7[t], y8 → y8[t]}, t] /.
{y1'[t] → yTilde1DotRec, y2'[t] → yTilde2DotRec, y3'[t] → yTilde3DotRec,
y4'[t] → yTilde4DotRec, y5'[t] → yTilde5DotRec, y6'[t] → yTilde6DotRec,
y7'[t] → yTilde7DotRec, y8'[t] → yTilde8DotRec} /.
{x_[t] → x} /. gamToAllLD // FullSimplify

{pTildeDotRec, qTildeDotRec, nTildeDotRec, DACTildeDotRec,
DCBTildeDotRec, DABTildeDotRec, DACBTildeDotRec} // TableForm

0
0
0
-DAC (r1 + r2)
-DCB r2
-DAB r1
-DACB (r1 + r2)
```

■ A comment to the differential equations under migration and selection

The differential equations under migration and selection are independent of the ordering of the loci, as long as gametes and their frequencies are defined consistently (such as given above).

■ Differential equations under selection, migration and recombination

■ In terms of gamete frequencies

```
In[157]:= 
yTilde1Dot := y1DotSel + y1DotMig + yTilde1DotRec
yTilde2Dot := y2DotSel + y2DotMig + yTilde2DotRec
yTilde3Dot := y3DotSel + y3DotMig + yTilde3DotRec
yTilde4Dot := y4DotSel + y4DotMig + yTilde4DotRec

yTilde5Dot := y5DotSel + y5DotMig + yTilde5DotRec
yTilde6Dot := y6DotSel + y6DotMig + yTilde6DotRec
yTilde7Dot := y7DotSel + y7DotMig + yTilde7DotRec
yTilde8Dot := y8DotSel + y8DotMig + yTilde8DotRec

{yTilde1Dot, yTilde2Dot, yTilde3Dot, yTilde4Dot, yTilde5Dot,
 yTilde6Dot, yTilde7Dot, yTilde8Dot} // Simplify // TableForm

-m y1 + r1 ((-1 + p) y1 + p y3) + r2 ((-1 + n) y1 + n y5) + y1 (b (y2 + y4 + y6 + y8) + a (y3 + y4 + y7 + y8)
-m y2 + r1 ((-1 + p) y2 + p y4) + r2 ((-1 + n) y2 + n y6) + y2 (-b (y1 + y3 + y5 + y7) + a (y3 + y4 + y7 + y8)
-m y3 - r1 ((-1 + p) y1 + p y3) + r2 ((-1 + n) y3 + n y7) + y3 (-a (y1 + y2 + y5 + y6) + b (y2 + y4 + y6 + y8)
m (nC - y4) - r1 ((-1 + p) y2 + p y4) + y4 (-a (y1 + y2 + y5 + y6) - b (y1 + y3 + y5 + y7)) + r2 ((-1 + n) y4
-m y5 - r2 ((-1 + n) y1 + n y5) + r1 ((-1 + p) y5 + p y7) + y5 (b (y2 + y4 + y6 + y8) + a (y3 + y4 + y7 + y8)
-m y6 - r2 ((-1 + n) y2 + n y6) + r1 ((-1 + p) y6 + p y8) + y6 (-b (y1 + y3 + y5 + y7) + a (y3 + y4 + y7 + y8)
-m y7 - r2 ((-1 + n) y3 + n y7) - r1 ((-1 + p) y5 + p y7) + y7 (-a (y1 + y2 + y5 + y6) + b (y2 + y4 + y6 + y8)
(-a (y1 + y2 + y5 + y6) - b (y1 + y3 + y5 + y7)) y8 - m (-1 + nC + y8) - r2 ((-1 + n) y4 + n y8) - r1 ((-1 +
Map[Collect[#, {m, r1, r2}] &, {yTilde1Dot, yTilde2Dot, yTilde3Dot,
yTilde4Dot, yTilde5Dot, yTilde6Dot, yTilde7Dot, yTilde8Dot}] // TableForm

-m y1 + r1 (- (1 - p) y1 + p y3) + r2 (- (1 - n) y1 + n y5) + y1 (b (y2 + y4 + y6 + y8) + a (y3 + y4 + y7 + y8)
-m y2 + r1 (- (1 - p) y2 + p y4) + r2 (- (1 - n) y2 + n y6) + y2 (-b (y1 + y3 + y5 + y7) + a (y3 + y4 + y7 + y8)
-m y3 + r1 ((1 - p) y1 - p y3) + r2 (- (1 - n) y3 + n y7) + y3 (-a (y1 + y2 + y5 + y6) + b (y2 + y4 + y6 + y8)
m (nC - y4) + r1 ((1 - p) y2 - p y4) + y4 (-a (y1 + y2 + y5 + y6) - b (y1 + y3 + y5 + y7)) + r2 (- (1 - n) y4
-m y5 + r2 ((1 - n) y1 - n y5) + r1 (- (1 - p) y5 + p y7) + y5 (b (y2 + y4 + y6 + y8) + a (y3 + y4 + y7 + y8))
-m y6 + r2 ((1 - n) y2 - n y6) + r1 (- (1 - p) y6 + p y8) + y6 (-b (y1 + y3 + y5 + y7) + a (y3 + y4 + y7 + y8)
-m y7 + r2 ((1 - n) y3 - n y7) + r1 ((1 - p) y5 - p y7) + y7 (-a (y1 + y2 + y5 + y6) + b (y2 + y4 + y6 + y8))
m (1 - nC - y8) + (-a (y1 + y2 + y5 + y6) - b (y1 + y3 + y5 + y7)) y8 + r2 ((1 - n) y4 - n y8) + r1 ((1 - p) y4
```

■ In terms of allele frequencies and LD

nDotMig

$$m = -n + nC$$

nDotSel

$$a \text{ DAC} + b \text{ DCB}$$

```
In[165]:= 
pTildeDot := pDotSel + pDotMig + pTildeDotRec
qTildeDot := qDotSel + qDotMig + qTildeDotRec
nTildeDot := nDotSel + nDotMig + nTildeDotRec
DACTildeDot := DACDotSel + DACDotMig + DACTildeDotRec
DCBTildeDot := DCBDotSel + DCBDotMig + DCBTildeDotRec
DABTildeDot := DABDotSel + DABDotMig + DABTildeDotRec
DACBTildeDot := DACBDotSel + DACBDotMig + DACBTildeDotRec

{pTildeDot, qTildeDot, nTildeDot, DACTildeDot,
DCBTildeDot, DABTildeDot, DACBTildeDot} // FullSimplify // TableForm

b DAB - (m + a (-1 + p)) p
a DAB - (m + b (-1 + q)) q
a DAC + b DCB + m (-n + nC)
b DACB + m (n - nC) p + a (DAC - 2 DAC p) - DAC (m + r1 + r2)
a DACB + m (n - nC) q + b (DCB - 2 DCB q) - DCB (m + r2)
-DAB m + m p q + DAB (a + b - 2 a p - 2 b q) - DAB r1
a (-2 DAB DAC + DACB - 2 DACB p) + b (DACB - 2 DAB DCB - 2 DACB q) + m (-DACB + DCB p + DAC q + (n - nC)) (I
```

```

Map[Collect[#, {m, r1, r2}] &, {pTildeDot, qTildeDot, nTildeDot,
  DACTildeDot, DCBTildeDot, DABTildeDot, DACBTildeDot}] // TableForm

b DAB - m p - a (-1 + p) p
a DAB - m q - b (-1 + q) q
a DAC + b DCB + m (-n + nC)
b DACB + a (DAC - 2 DAC p) + m (-DAC - (-n + nC) p) - DAC r1 - DAC r2
a DACB + b DCB (1 - 2 q) + m (-DCB - (-n + nC) q) - DCB r2
DAB (a + b - 2 a p - 2 b q) + m (-DAB + p q) - DAB r1
a (-2 DAB DAC + DACB - 2 DACB p) + b (DACB - 2 DAB DCB - 2 DACB q) + m (-DACB + DCB p + DAC q + (n - nC)) (I)

Map[Collect[#, {DAC, DAB, DCB, DACB}] &, {pTildeDot, qTildeDot, nTildeDot,
  DACTildeDot, DCBTildeDot, DABTildeDot, DACBTildeDot}] // TableForm

b DAB - m p - a (-1 + p) p
a DAB - m q - b (-1 + q) q
a DAC + b DCB + m (-n + nC)
b DACB - m (-n + nC) p + DAC (a - m - 2 a p - r1 - r2)
a DACB - m (-n + nC) q + DCB (-m + b (1 - 2 q) - r2)
m p q + DAB (a + b - m - 2 a p - 2 b q - r1)
DAB (-2 b DCB + m (n - nC)) + DCB m p - m (n - nC) p q + DAC (-2 a DAB + m q) + DACB (a + b - m - 2 a p - 2 b q

TM1 =
Map[Collect[#, {DAC, DAB, DCB, DACB}] &, {pTildeDot, qTildeDot, nTildeDot, DACTildeDot,
  DCBTildeDot, DABTildeDot, DACBTildeDot}] /. {r1 → rAB, r2 → rCB}; TM1 // TableForm

b DAB - m p - a (-1 + p) p
a DAB - m q - b (-1 + q) q
a DAC + b DCB + m (-n + nC)
b DACB - m (-n + nC) p + DAC (a - m - 2 a p - rAB - rCB)
a DACB - m (-n + nC) q + DCB (-m + b (1 - 2 q) - rCB)
m p q + DAB (a + b - m - 2 a p - 2 b q - rAB)
DAB (-2 b DCB + m (n - nC)) + DCB m p - m (n - nC) p q + DAC (-2 a DAB + m q) + DACB (a + b - m - 2 a p - 2 b q

```

For comparison, we print the differential equations for the case of the ordering $\mathcal{A} - \mathcal{C} - \mathcal{B}$ from above:

```

Map[Collect[#, {m, r1, r2}] &,
  {pDot, qDot, nDot, DACDot, DCBDot, DABDot, DACBDot}] // TableForm

b DAB - m p - a (-1 + p) p
a DAB - m q - b (-1 + q) q
a DAC + b DCB + m (-n + nC)
b DACB + a (DAC - 2 DAC p) + m (-DAC - (-n + nC) p) - DAC r1
a DACB + b DCB (1 - 2 q) + m (-DCB - (-n + nC) q) - DCB r2
DAB (a + b - 2 a p - 2 b q) + m (-DAB + p q) - DAB r1 - DAB r2
a (-2 DAB DAC + DACB - 2 DACB p) + b (DACB - 2 DAB DCB - 2 DACB q) + m (-DACB + DCB p + DAC q + (n - nC)) (I)

Map[Collect[#, {DAC, DAB, DCB, DACB}] &,
  {pDot, qDot, nDot, DACDot, DCBDot, DABDot, DACBDot}] // TableForm

b DAB - m p - a (-1 + p) p
a DAB - m q - b (-1 + q) q
a DAC + b DCB + m (-n + nC)
b DACB - m (-n + nC) p + DAC (a - m - 2 a p - r1)
a DACB - m (-n + nC) q + DCB (-m + b (1 - 2 q) - r2)
m p q + DAB (a + b - m - 2 a p - 2 b q - r1 - r2)
DAB (-2 b DCB + m (n - nC)) + DCB m p - m (n - nC) p q + DAC (-2 a DAB + m q) + DACB (a + b - m - 2 a p - 2 b q

```

```

TM2 = Map[Collect[#, {DAC, DAB, DCB, DACB}] &,
          {pDot, qDot, nDot, DACDot, DCBDot, DABDot, DACBDot}] /. {r1 → rAC, r2 → rCB};
TM2 //
TableForm

b DAB - m p - a (-1 + p) p
a DAB - m q - b (-1 + q) q
a DAC + b DCB + m (-n + nC)
b DACB - m (-n + nC) p + DAC (a - m - 2 a p - rAC)
a DACB - m (-n + nC) q + DCB (-m + b (1 - 2 q) - rCB)
m p q + DAB (a + b - m - 2 a p - 2 b q - rAC - rCB)
DAB (-2 b DCB + m (n - nC)) + DCB m p - m (n - nC) p q + DAC (-2 a DAB + m q) + DACB (a + b - m - 2 a p - 2 b q)

```

A comparison shows that only the differentials of D_{AC} and D_{AB} change.

```

MapThread[Simplify[#1 == #2] &, {TM1, TM2}] // TableForm

True
True
True
DAC (rAB - rAC + rCB) == 0
True
DAB rAB == DAB (rAC + rCB)
DACB rAB == DACB rAC

MapThread[Simplify[#1 == #2] &,
{Map[Collect[#, {m, r1, r2}] &, {pTildeDot, qTildeDot, nTildeDot, DACTildeDot,
DCBTildeDot, DABTildeDot, DACBTildeDot}], Map[Collect[#, {m, r1, r2}] &,
{pDot, qDot, nDot, DACDot, DCBDot, DABDot, DACBDot}]}] // TableForm

True
True
True
DAC r2 == 0
True
DAB r2 == 0
True

```

Internal equilibrium

■ Coordinates

We recall the differential equations:

```

In[172]:= diffEqsTilde = Map[Collect[#, {m, r1, r2}] &, {pTildeDot, qTildeDot,
DABTildeDot, nTildeDot, DACTildeDot, DCBTildeDot, DACBTildeDot}];
diffEqsTilde // TableForm

Out[173]//TableForm=
b DAB - m p - a (-1 + p) p
a DAB - m q - b (-1 + q) q
DAB (a + b - 2 a p - 2 b q) + m (-DAB + p q) - DAB r1
a DAC + b DCB + m (-n + nC)
b DACB + a (DAC - 2 DAC p) + m (-DAC - (-n + nC) p) - DAC r1 - DAC r2
a DACB + b DCB (1 - 2 q) + m (-DCB - (-n + nC) q) - DCB r2
a (-2 DAB DAC + DACB - 2 DACB p) + b (DACB - 2 DAB DCB - 2 DACB q) + m (-DACB + DCB p + DAC q + (n - nC)) (I)

```

BA2011 (eq. 3.15) showed the coordinates of the internal stable equilibrium to be

```

In[174]:= R2 := √(a + b + r)² - 8 m r1

```

```
In[175]:= pEqTilde :=  $\frac{1}{8 a r} (b^2 - a^2 + 6 a r - r^2 - 4 m r + (a - b + r) R2) // . \{r \rightarrow r1\}$ 
qEqTilde :=  $\frac{1}{8 b r} (a^2 - b^2 + 6 b r - r^2 - 4 m r + (b - a + r) R2) // . \{r \rightarrow r1\}$ 
DABEqTilde :=  $\frac{1}{32 a b r^2} ((a - b - r) (a + b - r) (a - b + r) ((a + b + r) - R2) -$ 
 $4 m r (a^2 + b^2 + r^2 - 2 a b - 2 a r - 2 b r) - 8 m^2 r^2) // . \{r \rightarrow r1\}$ 
nEqTilde := nC
DACEqTilde := 0
DCBEqTilde := 0
DACBEqTilde := 0
```

We have used the assumption that higher-order recombination terms can be ignored, and therefore $r = r_1 + r_2$.

```
In[182]:= ruleApplyEqTilde := {p → pEqTilde, q → qEqTilde, n → nEqTilde,
DAB → DABEqTilde, DAC → DACEqTilde, DCB → DCBEqTilde, DACB → DACBEqTilde}
```

We have

```
diffEqsTilde /. ruleApplyEqTilde // FullSimplify
{0, 0, 0, 0, 0, 0, 0}
```

which confirms that this is indeed an equilibrium. We omit the proof that this equilibrium is asymptotically stable (cf. Bürger and Akerman 2011). Instead, we directly proceed to the computation of the Jacobian matrix.

■ Jacobian matrix and effective migration rate

■ Generic

```
In[183]:= JTilde := Map[Table[D[#, {i}], {i, {p, q, DAB, n, DAC, DCB, DACB}}] &, diffEqsTilde]
JTilde // MatrixForm
```

```
Out[184]/MatrixForm=

$$\begin{pmatrix} -m - a (-1 + p) - a p & 0 & b \\ 0 & -m - b (-1 + q) - b q & a \\ -2 a DAB + m q & -2 b DAB + m p & a + b - m - 2 a p - 2 b q - r1 \\ 0 & 0 & 0 \\ -2 a DAC + m (n - nC) & 0 & 0 \\ 0 & -2 b DCB + m (n - nC) & 0 \\ -2 a DACB + m (DCB - (n - nC) q) & -2 b DACB + m (DAC - (n - nC) p) & -2 a DAC - 2 b DCB + m (n - nC) m (D2 \\ D[diffEqsTilde[[7]], DACB] \\ -m + a (1 - 2 p) + b (1 - 2 q) - r1 - r2 \\ FullSimplify[Normal[Series[% /. ruleApplyEqTilde, {m, 0, 1}]], Assumptions → {0 < a < b, 0 < r1, 0 < r2}] \\ -a - b - r1 + \frac{m (a + b + 3 r1)}{a + b + r1} - r2 \\ D[diffEqs[[7]], DACB] \\ -m + a (1 - 2 p) + b (1 - 2 q) - r1 - r2 \\ FullSimplify[Normal[Series[% /. ruleApplyEq, {m, 0, 1}]], Assumptions → {0 < a < b, 0 < r1, 0 < r2}] \\ -a - b + 3 m - r1 - r2 - \frac{2 (a + b) m}{a + b + r1 + r2} \\ % - \left( -a - b - r1 - r2 + \frac{m (a + b + 3 (r1 + r2))}{a + b + r1 + r2} \right) // FullSimplify \\ 0$$

```

For comparison

J // MatrixForm

$$\begin{pmatrix} -m - a(-1 + p) - ap & 0 & b \\ 0 & -m - b(-1 + q) - bq & a \\ -2aDAB + mq & -2bDAB + mp & a + b - m - 2ap - 2bq - r1 - r2 \\ 0 & 0 & 0 \\ -2aDAC + m(n - nC) & 0 & 0 \\ 0 & -2bDCB + m(n - nC) & 0 \\ -2aDACP + m(DCB - (n - nC)q) & -2bDACP + m(DAC - (n - nC)p) & -2aDAC - 2bDCB + m(n - nC)m(D) \end{pmatrix}$$

As an intermediate step, we set n , D_{AC} , D_{CB} , and D_{ACB} to their equilibrium values n_c , 0, 0, and 0, respectively.

```
In[185]:= JTildePrep = JTilde /. {n → nc, DAC → 0, DCB → 0, DACB → 0} // FullSimplify;
JTildePrep // MatrixForm
```

Out[186]//MatrixForm=

$$\begin{pmatrix} a - m - 2ap & 0 & b & 0 & 0 & 0 \\ 0 & b - m - 2bq & a & 0 & 0 & 0 \\ -2aDAB + mq & -2bDAB + mp & a + b - m - 2ap - 2bq - r1 & 0 & 0 & 0 \\ 0 & 0 & 0 & -m & a & b \\ 0 & 0 & 0 & mp & a - m - 2ap - r1 - r2 & 0 \\ 0 & 0 & 0 & mq & 0 & b - m - 2 \\ 0 & 0 & 0 & m(DAB - pq) & -2aDAB + mq & -2bDA \end{pmatrix}$$

Now we plug in the equilibrium coordinates into the generic matrix of first-order partial derivatives:

```
In[187]:= JEqGenericTilde = JTildePrep /. ruleApplyEqTilde // FullSimplify;
JEqGenericTilde // MatrixForm
```

Out[188]//MatrixForm=

$$\begin{pmatrix} a - m - \frac{-a^2 + b^2 + 6ar1 - 4mr1 - r1^2 + (a-b+r1)\sqrt{-8mr1 + (a+b+r1)^2}}{4r1} & 0 & 0 & 0 & 0 & 0 \\ 0 & \frac{8m^2r1^2 + 4mr1(a^2 + (b-r1)^2 - 2a(b+r1)) - (a-b-r1)(a+b-r1)(a-b+r1)\left(a+b+r1 - \sqrt{-8mr1 + (a+b+r1)^2}\right) + 2mr1\left(a^2 - b^2 + 6br1 - mr1 - r1^2 + (-a-b+r1)^2\right)}{16br1^2} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \end{pmatrix}$$

This is a complicated matrix. Below, we instead plug in the weak-migration approximation to the internal equilibrium.

```
In[189]:= JEqGenericTildemSmall := Simplify[Normal[Series[JEqGenericTilde, {m, 0, 1}]]],
Assumptions → {0 < a < b, 0 < m < b, 0 < r1, 0 < r2}]
JEqGenericTildemSmall // MatrixForm
```

Out[190]//MatrixForm=

$$\begin{pmatrix} -a + \frac{m(a-b+r1)}{a+b+r1} & 0 & b & 0 & 0 & 0 \\ 0 & -b + \frac{m(-a+b+r1)}{a+b+r1} & a & 0 & 0 & 0 \\ \frac{m(-a+b+r1)}{a+b+r1} & \frac{m(a-b+r1)}{a+b+r1} & -a - b - r1 + \frac{m(a+b+3r1)}{a+b+r1} & 0 & 0 & 0 \\ 0 & 0 & 0 & -m & a & b \\ 0 & 0 & 0 & m - a - r1 + \frac{m(a-b+r1)}{a+b+r1} - r2 & 0 & 0 \\ 0 & 0 & 0 & m & 0 & -b + \frac{m(-a+b+r1)}{a+b+r1} - r2 \\ 0 & 0 & 0 & -m & \frac{m(-a+b+r1)}{a+b+r1} & \frac{m(a-b+r1)}{a+b+r1} \end{pmatrix}$$

For comparison

```
JEqmSmall // MatrixForm
```

$$\left(\begin{array}{cccccc} -a + m - \frac{2bm}{a+b+r1+r2} & 0 & b & 0 & 0 \\ 0 & -b + m - \frac{2am}{a+b+r1+r2} & a & 0 & 0 \\ \frac{m(-a+b+r1+r2)}{a+b+r1+r2} & m - \frac{2bm}{a+b+r1+r2} & -a - b - r1 - r2 + \frac{m(a+b+3(r1+r2))}{a+b+r1+r2} & 0 & 0 \\ 0 & 0 & 0 & -m & a \\ 0 & 0 & 0 & m - a + m - r1 - \frac{2bm}{a+b+r1+r2} & \\ 0 & 0 & 0 & m & 0 & -b + m \\ 0 & 0 & 0 & -m & \frac{m(-a+b+r1+r2)}{a+b+r1+r2} & m \end{array} \right)$$

```
In[191]:= JEqNGenericTilde := JEqGenericTilde[4 ; 7, 4 ; 7]
JEqNGenericTilde // MatrixForm
```

Out[192]/MatrixForm=

$$\left(\begin{array}{c} -m \\ \frac{m \left(-a^2 + b^2 + 6 a r1 - 4 m r1 - r1^2 + (a - b + r1) \sqrt{-8 m r1 + (a + b)^2} \right)}{8 a r1} \\ \frac{m \left(a^2 - b^2 + 6 b r1 - 4 m r1 - r1^2 + (-a + b + r1) \sqrt{-8 m r1 + (a + b)^2} \right)}{8 b r1} \\ \frac{m \left(- \left(-a^2 + b^2 + 6 a r1 - 4 m r1 - r1^2 + (a - b + r1) \sqrt{-8 m r1 + (a + b + r1)^2} \right) \left(a^2 - b^2 + 6 b r1 - 4 m r1 - r1^2 + (-a + b + r1) \sqrt{-8 m r1 + (a + b + r1)^2} \right) + 2 \left(-8 m^2 r1^2 - 4 m^2 r1 + 64 a b r1^2 \right)}{64 a b r1^2} \end{array} \right)$$

```
In[193]:= JEqNGenericTildemSmall := Simplify[Normal[Series[JEqNGenericTilde, {m, 0, 1}]]];
Assumptions → {0 < a < b, 0 < m < b, 0 < r1, 0 < r2}
JEqNGenericTildemSmall // MatrixForm
```

Out[194]/MatrixForm=

$$\left(\begin{array}{cccc} -m & a & b & 0 \\ m - a - r1 + \frac{m(a-b+r1)}{a+b+r1} - r2 & 0 & b & \\ m & 0 & -b + \frac{m(-a+b+r1)}{a+b+r1} - r2 & a \\ -m & \frac{m(-a+b+r1)}{a+b+r1} & \frac{m(a-b+r1)}{a+b+r1} & -a - b - r1 + \frac{m(a+b+3r1)}{a+b+r1} - r2 \end{array} \right)$$

```
TM3 = JEQNGenericTildemSmall /. {r1 → rAB, r2 → rBC};
TM3 // MatrixForm
```

$$\left(\begin{array}{cccc} -m & a & b & 0 \\ m - a - rAB + \frac{m(a-b+rAB)}{a+b+rAB} - rBC & 0 & b & \\ m & 0 & -b + \frac{m(-a+b+rAB)}{a+b+rAB} - rBC & a \\ -m & \frac{m(-a+b+rAB)}{a+b+rAB} & \frac{m(a-b+rAB)}{a+b+rAB} & -a - b - rAB + \frac{m(a+b+3rAB)}{a+b+rAB} - rBC \end{array} \right)$$

For comparison:

```
JEqNmSmall // MatrixForm
```

$$\left(\begin{array}{cccc} -m & a & b & 0 \\ m - a + m - r1 - \frac{2bm}{a+b+r1+r2} & 0 & b & \\ m & 0 & -b + m - r2 - \frac{2am}{a+b+r1+r2} & a \\ -m & \frac{m(-a+b+r1+r2)}{a+b+r1+r2} & m - \frac{2bm}{a+b+r1+r2} & -a - b - r1 - r2 + \frac{m(a+b+3(r1+r2))}{a+b+r1+r2} \end{array} \right)$$

```
TM4 = JEQNmSmall /. {r1 → rAC, r2 → rCB};
TM4 // MatrixForm
```

$$\left(\begin{array}{cccc} -m & a & b & 0 \\ m - a + m - rAC - \frac{2bm}{a+b+rAC+rCB} & 0 & b & \\ m & 0 & -b + m - rCB - \frac{2am}{a+b+rAC+rCB} & a \\ -m & \frac{m(-a+b+rAC+rCB)}{a+b+rAC+rCB} & m - \frac{2bm}{a+b+rAC+rCB} & -a - b - rAC - rCB + \frac{m(a+b+3(rAC+rCB))}{a+b+rAC+rCB} \end{array} \right)$$

```
FullSimplify[JEqNGenericTildemSmall - JEqNmSmall] // MatrixForm
```

$$\begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & r2 \left(-1 - \frac{2bm}{(a+b+r1)(a+b+r1+r2)} \right) & 0 & 0 \\ 0 & 0 & -\frac{2amr2}{(a+b+r1)(a+b+r1+r2)} & 0 \\ 0 & -\frac{2amr2}{(a+b+r1)(a+b+r1+r2)} & -\frac{2bmr2}{(a+b+r1)(a+b+r1+r2)} & -\frac{2(a+b)mr2}{(a+b+r1)(a+b+r1+r2)} \end{pmatrix}$$

■ Using the Ansatz $m_e = -\lambda_N = mz$

```
JEqGenericTilde // MatrixForm
```

$$\begin{pmatrix} a - m - \frac{-a^2 + b^2 + 6ar1 - 4mr1 - r1^2 + (a-b+r1)\sqrt{-8mr1 + (a+b+r1)^2}}{4r1} & 0 & 0 & 0 \\ 0 & \frac{8m^2r1^2 + 4mr1(a^2 + (b-r1)^2 - 2a(b+r1)) - (a-b-r1)(a+b-r1)(a-b+r1)\left(a+b+r1 - \sqrt{-8mr1 + (a+b+r1)^2}\right) + 2mr1(a^2 - b^2 + 6br1 - 4mr1 - r1^2 + (-a-b+r1)r1)}{16br1^2} & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix}$$

```
Simplify[Series[Det[JEqGenericTilde - x IdentityMatrix[7]] /. x → -mz], {m, 0, 1}], Assumptions → {a ≥ 0, b ≥ 0, r1 ≥ 0, r2 ≥ 0}] // Normal
```

$$a b m (a + b + r1) (a + r1 + r2) \\ (b^2 z + r2 (r1 (-1 + z) + r2 (-1 + z) + a z) + b ((a + r1) z + r2 (-1 + 2 z)))$$

```
Simplify[Solve[% == 0, z]]
```

$$\left\{ \left\{ z \rightarrow \frac{r2 (b + r1 + r2)}{(b + r2) (a + b + r1 + r2)} \right\} \right\}$$

which is identical to eq. (4.30) in BA2011. Or, alternatively and more directly:

```
JEqNGenericTildemSmall // MatrixForm
```

$$\begin{pmatrix} -m & a & b & 0 \\ m & -a - r1 + \frac{m(a-b+r1)}{a+b+r1} - r2 & 0 & b \\ m & 0 & -b + \frac{m(-a+b+r1)}{a+b+r1} - r2 & a \\ -m & \frac{m(-a+b+r1)}{a+b+r1} & \frac{m(a-b+r1)}{a+b+r1} & -a - b - r1 + \frac{m(a+b+3r1)}{a+b+r1} - r2 \end{pmatrix}$$

```
Simplify[Series[Det[JEqNGenericTildemSmall - x IdentityMatrix[4]] /. x → -mz], {m, 0, 1}], Assumptions → {a ≥ 0, b ≥ 0, r1 ≥ 0, r2 ≥ 0}] // Normal
```

$$-m (a + r1 + r2) (b^2 z + r2 (r1 (-1 + z) + r2 (-1 + z) + a z) + b ((a + r1) z + r2 (-1 + 2 z)))$$

```
Simplify[Solve[% == 0, z]]
```

$$\left\{ \left\{ z \rightarrow \frac{r2 (b + r1 + r2)}{(b + r2) (a + b + r1 + r2)} \right\} \right\}$$

■ Assuming weak migration

The coordinates of the internal equilibrium under the assumption of weak migration, up to and including first-order terms of m , can be obtained from eq. (4.1) in BA2011.

```
In[195]:= pEqTildeWeakMig = FullSimplify[Series[pEqTilde, {m, 0, 1}]] // Normal,
Assumptions → {0 < a < b, 0 < m, 0 < r1, 0 < r2}];
qEqTildeWeakMig = FullSimplify[Series[qEqTilde, {m, 0, 1}]] // Normal,
Assumptions → {0 < a < b, 0 < m, 0 < r1, 0 < r2}];
DABEqTildeWeakMig = FullSimplify[Series[DABEqTilde, {m, 0, 1}]] // Normal,
Assumptions → {0 < a < b, 0 < m, 0 < r1, 0 < r2}];

{pEqTildeWeakMig, qEqTildeWeakMig, DABEqTildeWeakMig} // TableForm


$$1 - \frac{m(a+r1)}{a(a+b+r1)}$$


$$\frac{ab + (b-m)(b+r1)}{b(a+b+r1)}$$


$$\frac{m}{a+b+r1}$$

```

Checking these against first-order terms of eq. (4.1) in BA2011:

$$1 - \frac{m}{a} \left(1 - \frac{b}{a+b+r} \right) - pEqTildeWeakMig /. \{r \rightarrow r1\} // FullSimplify$$

$$0$$

$$1 - \frac{m}{b} \left(1 - \frac{a}{a+b+r} \right) - qEqTildeWeakMig /. \{r \rightarrow r1\} // FullSimplify$$

$$0$$

$$\frac{m}{a+b+r} - DABEqTildeWeakMig /. \{r \rightarrow r1\} // FullSimplify$$

$$0$$

```
In[198]:= ruleApplyEqWeakMigTilde := {p → pEqTildeWeakMig, q → qEqTildeWeakMig,
n → nC, DAB → DABEqTildeWeakMig, DAC → 0, DCB → 0, DACB → 0}
```

ruleApplyEqWeakMigTilde

$$\left\{ p \rightarrow 1 - \frac{m(a+r1)}{a(a+b+r1)}, q \rightarrow \frac{ab + (b-m)(b+r1)}{b(a+b+r1)}, \right.$$

$$\left. n \rightarrow nC, DAB \rightarrow \frac{m}{a+b+r1}, DAC \rightarrow 0, DCB \rightarrow 0, DACB \rightarrow 0 \right\}$$

JTildePrep // MatrixForm

$$\begin{pmatrix} a - m - 2ap & 0 & b & 0 & 0 & 0 \\ 0 & b - m - 2bq & a & 0 & 0 & 0 \\ -2aDAB + mq & -2bDAB + mp & a + b - m - 2ap - 2bq - r1 & 0 & 0 & 0 \\ 0 & 0 & 0 & -m & a & b \\ 0 & 0 & 0 & mp & a - m - 2ap - r1 - r2 & 0 \\ 0 & 0 & 0 & mq & 0 & b - m - 2 \\ 0 & 0 & 0 & m(DAB - pq) & -2aDAB + mq & -2bDA \end{pmatrix}$$

Now we see the block structure claimed in eq. (4.27) of BA2011.

```
In[199]:= JEqTilde = JTildePrep /. ruleApplyEqWeakMigTilde // FullSimplify;
JEqTilde // MatrixForm

Out[200]//MatrixForm=

$$\begin{pmatrix} -a + m - \frac{2bm}{a+b+r1} & 0 & b & 0 \\ 0 & -b + m - \frac{2am}{a+b+r1} & a & 0 \\ \frac{m(-a(b-m)(b+r1))}{b(a+b+r1)} & \frac{m(a^2-a(b+m-r1)-mr1)}{a(a+b+r1)} & -a - b + 3m - r1 - \frac{2(a+b)m}{a+b+r1} & 0 \\ 0 & 0 & 0 & -m \\ 0 & 0 & 0 & \frac{m\left(1 - \frac{m(a+r1)}{a(a+b+r1)}\right)}{\frac{m(a(b-(b-m)(b+r1))}{b(a+b+r1)}} & -a - m - r1 + \\ 0 & 0 & 0 & \frac{m\left(\frac{(a(b-(b-m)(b+r1))\left(1 - \frac{m(a+r1)}{a(a+b+r1)}\right)}{b}\right)}{a+b+r1} \\ 0 & 0 & 0 & \frac{m(-a(b+(b-m)(b+r1))}{b(a+b+r1)} \end{pmatrix}$$


In[201]:= JEqNTilde = JEqTilde[[4, 5, 6, 7], {4, 5, 6, 7}];
JEqNTilde // MatrixForm

Out[202]//MatrixForm=

$$\begin{pmatrix} -m & a & b & 0 \\ m\left(1 - \frac{m(a+r1)}{a(a+b+r1)}\right) & -a - m - r1 + \frac{2m(a+r1)}{a+b+r1} - r2 & 0 & b \\ \frac{m(a(b-(b-m)(b+r1))}{b(a+b+r1)} & 0 & -\frac{(b+r1)(b-m+r2)+a(b+m+r2)}{a+b+r1} & a \\ m\left(m - \frac{(a(b-(b-m)(b+r1))\left(1 - \frac{m(a+r1)}{a(a+b+r1)}\right)}{b}\right) & \frac{m(-a(b-(b-m)(b+r1))}{b(a+b+r1)} & \frac{m(a^2-a(b+m-r1)-mr1)}{a(a+b+r1)} & -\frac{a^2+b^2+r1(-3m+r1+r2)+b(-m+2)}{a+b+r1} \end{pmatrix}$$


JEqTildemSmall := Simplify[Normal[Series[JEqTilde, {m, 0, 1}]]]
JEqTildemSmall // MatrixForm

Out[203]//MatrixForm=

$$\begin{pmatrix} -a + m - \frac{2bm}{a+b+r1} & 0 & b & 0 & 0 & 0 \\ 0 & -b + m - \frac{2am}{a+b+r1} & a & 0 & 0 & 0 \\ \frac{m(-a+b+r1)}{a+b+r1} & \frac{m(a-b+r1)}{a+b+r1} & -a - b - r1 + \frac{m(a+b+3r1)}{a+b+r1} & 0 & 0 & 0 \\ 0 & 0 & 0 & -m & a & b \\ 0 & 0 & 0 & m - a - r1 + \frac{m(a-b+r1)}{a+b+r1} - r2 & 0 & 0 \\ 0 & 0 & 0 & m & 0 & -b + \frac{m(-a+b+r1)}{a+b+r1} - r2 \\ 0 & 0 & 0 & -m & \frac{m(-a+b+r1)}{a+b+r1} & \frac{m(a-b+r1)}{a+b+r1} \end{pmatrix}$$


JEqNTildemSmall := JEqTildemSmall[[4 ; 7, 4 ; 7]]
JEqNTildemSmall // MatrixForm

Out[204]//MatrixForm=

$$\begin{pmatrix} -m & a & b & 0 & 0 & 0 \\ m - a - r1 + \frac{m(a-b+r1)}{a+b+r1} - r2 & 0 & b & b & 0 & 0 \\ m & 0 & -b + \frac{m(-a+b+r1)}{a+b+r1} - r2 & a & a & 0 \\ -m & \frac{m(-a+b+r1)}{a+b+r1} & \frac{m(a-b+r1)}{a+b+r1} & -a - b - r1 + \frac{m(a+b+3r1)}{a+b+r1} - r2 & -r2 & -r2 \end{pmatrix}$$


JEqNTildemSmall - JEqNGenericTildemSmall

{{0, 0, 0, 0}, {0, 0, 0, 0}, {0, 0, 0, 0}, {0, 0, 0, 0}}
```

- Using the Ansatz $m_e = -\lambda_N = m z$

JEqTilde

$$\left\{ \left\{ -a + m - \frac{2 b m}{a + b + r1}, 0, b, 0, 0, 0, 0 \right\}, \left\{ 0, -b + m - \frac{2 a m}{a + b + r1}, a, 0, 0, 0, 0 \right\}, \right.$$

$$\left. \left\{ \frac{m (-a b + (b - m) (b + r1))}{b (a + b + r1)}, \frac{m (a^2 - a (b + m - r1) - m r1)}{a (a + b + r1)}, \right. \right.$$

$$\left. \left. -a - b + 3 m - r1 - \frac{2 (a + b) m}{a + b + r1}, 0, 0, 0, 0 \right\}, \{0, 0, 0, -m, a, b, 0\}, \right.$$

$$\left\{ 0, 0, 0, m \left(1 - \frac{m (a + r1)}{a (a + b + r1)} \right), -a - m - r1 + \frac{2 m (a + r1)}{a + b + r1} - r2, 0, b \right\},$$

$$\left\{ 0, 0, 0, \frac{m (a b + (b - m) (b + r1))}{b (a + b + r1)}, 0, -\frac{(b + r1) (b - m + r2) + a (b + m + r2)}{a + b + r1}, a \right\}, \{0, 0, 0,$$

$$\left. \left. \frac{m \left(m - \frac{(a b + (b - m) (b + r1)) \left(1 - \frac{m (a + r1)}{a (a + b + r1)} \right)}{b} \right)}{a + b + r1}, \frac{m (-a b + (b - m) (b + r1))}{b (a + b + r1)}, \frac{m (a^2 - a (b + m - r1) - m r1)}{a (a + b + r1)}, \right. \right.$$

$$\left. \left. -\frac{1}{a + b + r1} (a^2 + b^2 + r1 (-3 m + r1 + r2) + b (-m + 2 r1 + r2) + a (2 b - m + 2 r1 + r2)) \right) \right\}$$

Applying the same Ansatz as above to the Jacobian obtained from the differential equations yields the following ratio between the effective and actual migration rate, $\frac{m_e}{m}$:

ruleApplyEqWeakMigTilde

$$\left\{ p \rightarrow 1 - \frac{m (a + r1)}{a (a + b + r1)}, q \rightarrow \frac{a b + (b - m) (b + r1)}{b (a + b + r1)}, \right.$$

$$\left. n \rightarrow nC, DAB \rightarrow \frac{m}{a + b + r1}, DAC \rightarrow 0, DCB \rightarrow 0, DACB \rightarrow 0 \right\}$$

Simplify[

Series[Det[(JEqTilde /. ruleApplyEqWeakMigTilde) - x IdentityMatrix[7] /. x → -m z], {m, 0, 1}], Assumptions → {a ≥ 0, b ≥ 0, r1 ≥ 0, r2 ≥ 0}] // Normal

$$a b m (a + b + r1) (a + r1 + r2)$$

$$(b^2 z + r2 (r1 (-1 + z) + r2 (-1 + z) + a z) + b ((a + r1) z + r2 (-1 + 2 z)))$$

Simplify[Solve[% == 0, z]]

$$\left\{ \left\{ z \rightarrow \frac{r2 (b + r1 + r2)}{(b + r2) (a + b + r1 + r2)} \right\} \right\}$$

Or, alternatively and more directly:

JEqNTildeSmall // MatrixForm

$$\begin{pmatrix} -m & a & b & 0 \\ m - a - r1 + \frac{m (a - b + r1)}{a + b + r1} - r2 & 0 & b \\ m & 0 & -b + \frac{m (-a + b + r1)}{a + b + r1} - r2 & a \\ -m & \frac{m (-a + b + r1)}{a + b + r1} & \frac{m (a - b + r1)}{a + b + r1} & -a - b - r1 + \frac{m (a + b + 3 r1)}{a + b + r1} - r2 \end{pmatrix}$$

- Assuming tight linkage (weak recombination)

The coordinates of the internal equilibrium under the assumption of tight linkage, i.e. $r \ll \min(a, m)$, up to and including first-order terms of r , can be obtained from eq. (4.2) in BA2011.

```

{pEqTilde, qEqTilde, DABEqTilde} // MatrixForm


$$\left( \begin{array}{c} \frac{-a^2+b^2+6 a r1-4 m r1-r1^2+(a-b+r1) \sqrt{-8 m r1+(a+b+r1)^2}}{8 a r1} \\ \frac{a^2-b^2+6 b r1-4 m r1-r1^2+(-a+b+r1) \sqrt{-8 m r1+(a+b+r1)^2}}{8 b r1} \\ \frac{-8 m^2 r1^2-4 m r1 (a^2-2 a b+b^2-2 a r1-2 b r1+r1^2)+(a-b-r1) (a+b-r1) (a-b+r1) \left(a+b+r1-\sqrt{-8 m r1+(a+b+r1)^2}\right)}{32 a b r1^2} \end{array} \right)$$


In[203]:= pEqTildeWeakRec = FullSimplify[Series[pEqTilde, {r1, 0, 1}]] // Normal,
Assumptions → {0 < a < b, 0 < m, 0 < r1, 0 < r2}] // FullSimplify;
qEqTildeWeakRec = FullSimplify[Series[qEqTilde, {r1, 0, 1}]] // Normal,
Assumptions → {0 < a < b, 0 < m, 0 < r1, 0 < r2}] // FullSimplify;
DABEqTildeWeakRec = FullSimplify[Series[DABEqTilde, {r1, 0, 1}]] // Normal,
Assumptions → {0 < a < b, 0 < m, 0 < r1, 0 < r2}] // FullSimplify;

{pEqTildeWeakRec, qEqTildeWeakRec, DABEqTildeWeakRec} // TableForm

```

$$\begin{aligned} & \frac{a (a+b)^2 (a+b-m)-m (b (b-m)+a (b+m)) r1}{a (a+b)^3} \\ & 1 - \frac{m}{a+b} - \frac{m (a^2+a (b-m)+b m) r1}{b (a+b)^3} \\ & \frac{m \left((a+b)^2 (a+b-m)-\frac{(a^2+a (b-m)+b m) (b (b-m)+a (b+m)) r1}{a b}\right)}{(a+b)^4} \end{aligned}$$

Checking these against first-order terms of eq. (4.1) in BA2011:

$$\begin{aligned} & 1 - \frac{m}{a+b} - \frac{r m}{(a+b)^2} \left(\frac{b}{a} - \frac{m}{a+b} \left(\frac{b}{a} - 1 \right) \right) - pEqTildeWeakRec /. \{r \rightarrow r1\} // FullSimplify \\ & 0 \\ & 1 - \frac{m}{a+b} - \frac{r m}{(a+b)^2} \left(\frac{a}{b} + \frac{m}{a+b} \left(1 - \frac{a}{b} \right) \right) - qEqTildeWeakRec /. \{r \rightarrow r1\} // FullSimplify \\ & 0 \\ & \frac{m}{a+b} \left(1 - \frac{m}{a+b} \right) - \frac{r m}{(a+b)^2} \left(1 - \frac{m}{a+b} \left(1 - \frac{m}{a+b} \right) \left(2 - \frac{b}{a} - \frac{a}{b} \right) \right) - DABEqTildeWeakRec /. \{r \rightarrow r1\} // FullSimplify \\ & 0 \\ \text{In[206]:= } & \text{ruleApplyEqWeakRecTilde := \{p \rightarrow pEqTildeWeakRec, q \rightarrow qEqTildeWeakRec,} \\ & \text{n \rightarrow nC, DAB \rightarrow DABEqTildeWeakRec, DAC \rightarrow 0, DCB \rightarrow 0, DACB \rightarrow 0\}} \\ & \text{ruleApplyEqWeakRecTilde} \\ & \left\{ \begin{array}{l} p \rightarrow \frac{a (a+b)^2 (a+b-m)-m (b (b-m)+a (b+m)) r1}{a (a+b)^3}, q \rightarrow 1 - \frac{m}{a+b} - \frac{m (a^2+a (b-m)+b m) r1}{b (a+b)^3}, \\ n \rightarrow nC, DAB \rightarrow \frac{m \left((a+b)^2 (a+b-m)-\frac{(a^2+a (b-m)+b m) (b (b-m)+a (b+m)) r1}{a b}\right)}{(a+b)^4}, DAC \rightarrow 0, DCB \rightarrow 0, DACB \rightarrow 0 \end{array} \right\} \end{aligned}$$

$$\begin{aligned} & JTildePrep // MatrixForm \\ & \left(\begin{array}{cccccc} a-m-2 a p & 0 & b & 0 & 0 & 0 \\ 0 & b-m-2 b q & a & 0 & 0 & 0 \\ -2 a DAB + m q & -2 b DAB + m p & a+b-m-2 a p-2 b q-r1 & 0 & 0 & 0 \\ 0 & 0 & 0 & -m & a & b \\ 0 & 0 & 0 & m p & a-m-2 a p-r1-r2 & 0 \\ 0 & 0 & 0 & m q & 0 & b-m-2 \\ 0 & 0 & 0 & m (DAB-p q) & -2 a DAB+m q & -2 b D A \end{array} \right) \end{aligned}$$

Now we see the block structure claimed in eq. (4.27) of BA2011.

```
In[207]:= JEqrWeakRecTilde = JTildePrep /. ruleApplyEqWeakRecTilde // FullSimplify;
JEqrWeakRecTilde // MatrixForm
```

Out[208]//MatrixForm=

$$\begin{pmatrix} -m + \frac{-a (a+b)^2 (a+b-2 m) + 2 m (b (b-m) + a (b+m)) r1}{(a+b)^3} & 0 \\ 0 & \frac{-(a+b)^2 (b (b-m) + a (b+m)) + 2 m (a^2 + a (b-m) + b m) r1}{(a+b)^3} \\ \frac{-(a-b) b (a+b)^2 (a+b-m) m + m (2 b (a+b) + (a-3 b) m) (a^2 + a (b-m) + b m) r1}{b (a+b)^4} & \frac{a (a-b) (a+b)^2 (a+b-m) m + m (2 a^2 + 2 a b - 3 a m + b m) (b (b-m) + a (b+m)) r1}{a (a+b)^4} \\ 0 & 0 \\ 0 & 0 \\ 0 & 0 \\ 0 & 0 \end{pmatrix}$$

```
In[209]:= JEqrNWeakRecTilde = JEqrWeakRecTilde[[{4, 5, 6, 7}, {4, 5, 6, 7}]];
JEqrNWeakRecTilde // MatrixForm
```

Out[210]//MatrixForm=

$$\begin{pmatrix} -m & -m - r1 + \frac{-i}{a+b} \\ \frac{m (a (a+b)^2 (a+b-m) - m (b (b-m) + a (b+m)) r1)}{a (a+b)^3} & \\ m \left(1 - \frac{m}{a+b} - \frac{m (a^2 + a (b-m) + b m) r1}{b (a+b)^3}\right) & \\ \frac{m (-a b (a+b)^4 (a+b-2 m) (a+b-m) + (a+b)^2 (a+b-2 m) m (a^3 + b^3 - (a-b)^2 m) r1 - m^2 (a^2 + a (b-m) + b m) (b (b-m) + a (b+m)) r1^2)}{a b (a+b)^6} & - (a-b) b (a+b)^2 (a^2 + a (b-m) + b m) r1^2 \end{pmatrix}$$

■ Using the Ansatz $m_e = -\lambda_N = m z$

JEqWeakRecTilde

$$\begin{aligned} & \left\{ \left\{ -m + \frac{-a(a+b)^2(a+b-2m) + 2m(b(b-m) + a(b+m))r1}{(a+b)^3}, 0, b, 0, 0, 0, 0 \right\}, \right. \\ & \left\{ 0, \frac{- (a+b)^2 (b (b-m) + a (b+m)) + 2 m (a^2 + a (b-m) + b m) r1}{(a+b)^3}, a, 0, 0, 0, 0 \right\}, \\ & \left\{ \frac{1}{b (a+b)^4} (- (a-b) b (a+b)^2 (a+b-m) m + m (2 b (a+b) + (a-3 b) m) (a^2 + a (b-m) + b m) r1 \right), \\ & \frac{1}{a (a+b)^4} (a (a-b) (a+b)^2 (a+b-m) m + m (2 a^2 + 2 a b - 3 a m + b m) (b (b-m) + a (b+m)) r1 \right), \\ & -a - b + m - \frac{(a+b-2m) r1}{a+b}, 0, 0, 0, 0 \}, \{ 0, 0, 0, -m, a, b, 0 \}, \\ & \left\{ 0, 0, 0, \frac{m (a (a+b)^2 (a+b-m) - m (b (b-m) + a (b+m)) r1)}{a (a+b)^3}, \right. \\ & -m - r1 + \frac{-a (a+b)^2 (a+b-2m) + 2 m (b (b-m) + a (b+m)) r1}{(a+b)^3} - r2, 0, b \}, \\ & \left\{ 0, 0, 0, m \left(1 - \frac{m}{a+b} - \frac{m (a^2 + a (b-m) + b m) r1}{b (a+b)^3} \right), 0, \right. \\ & -m + \frac{-b (a+b)^2 (a+b-2m) + 2 m (a^2 + a (b-m) + b m) r1}{(a+b)^3} - r2, a \}, \\ & \left\{ 0, 0, 0, \frac{1}{a b (a+b)^6} m (-a b (a+b)^4 (a+b-2m) (a+b-m) + (a+b)^2 (a+b-2m) m \right. \\ & (a^3 + b^3 - (a-b)^2 m) r1 - m^2 (a^2 + a (b-m) + b m) (b (b-m) + a (b+m)) r1^2, \frac{1}{b (a+b)^4} \\ & (- (a-b) b (a+b)^2 (a+b-m) m + m (2 b (a+b) + (a-3 b) m) (a^2 + a (b-m) + b m) r1 \right), \\ & \frac{1}{a (a+b)^4} (a (a-b) (a+b)^2 (a+b-m) m + m (2 a^2 + 2 a b - 3 a m + b m) (b (b-m) + a (b+m)) r1 \right), \\ & \left. - \frac{a^2 + b^2 - 2 m r1 + b (-m + r1 + r2) + a (2 b - m + r1 + r2)}{a+b} \right\} \} \end{aligned}$$

Applying the same Ansatz as above to the Jacobian obtained from the differential equations yields the following ratio between the effective and actual migration rate, $\frac{m_e}{m}$:

ruleApplyEqWeakRecTilde

$$\begin{aligned} & p \rightarrow \frac{a (a+b)^2 (a+b-m) - m (b (b-m) + a (b+m)) r1}{a (a+b)^3}, q \rightarrow 1 - \frac{m}{a+b} - \frac{m (a^2 + a (b-m) + b m) r1}{b (a+b)^3}, \\ & n \rightarrow nC, DAB \rightarrow \frac{m \left((a+b)^2 (a+b-m) - \frac{(a^2+a (b-m)+b m) (b (b-m)+a (b+m)) r1}{a b} \right)}{(a+b)^4}, DAC \rightarrow 0, DCB \rightarrow 0, DACB \rightarrow 0 \} \} \end{aligned}$$

Simplify[Series[Det[
 $(JEqWeakRecTilde /. ruleApplyEqWeakRecTilde) - x IdentityMatrix[7] /. x \rightarrow -m z],$
 $\{m, 0, 1\}], Assumptions \rightarrow \{a \geq 0, b \geq 0, r1 \geq 0, r2 \geq 0\}] // Normal$
 $a b m (a+b+r1) (a+r1+r2)$
 $(b^2 z + r2 (r1 (-1+z) + r2 (-1+z) + a z) + b ((a+r1) z + r2 (-1+2 z)))$

Simplify[Solve[% == 0, z]]

$$\left\{ \left\{ z \rightarrow \frac{r2 (b + r1 + r2)}{(b + r2) (a + b + r1 + r2)} \right\} \right\}$$

Hence, we see that the effective migration rate does not only apply for weak migration, but also for weak recombination.

- **Graphical exploration of approximation**
- Generic

We compare the approximate effective migration rate to the exact (negative) eigenvalue of J_N computed numerically.

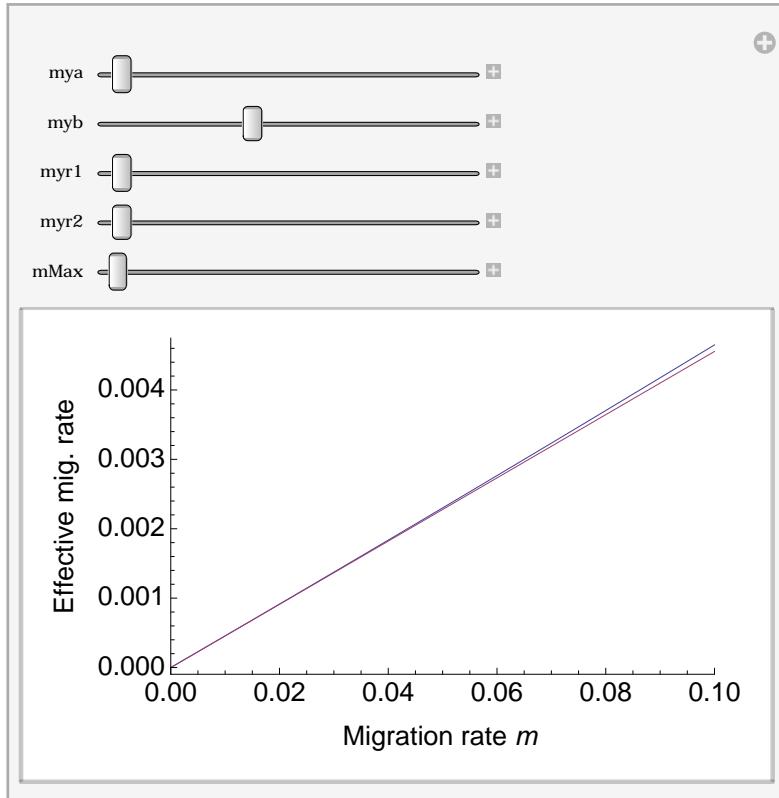
```
In[211]:= approxEffMigRateABCFunc[a_, b_, m_, r1_, r2_] := m  $\frac{r2 (b + r1 + r2)}{(b + r2) (a + b + r1 + r2)}$ 

In[212]:= exactEffMigRateABCFunc[a_, b_, m_, r1_, r2_] := Module[{JN}, JN = {{-m, a, b, 0}, { $\frac{m (-a^2 + b^2 + 6 a r1)}{-a^2 + b^2 + 6 a r1}$ }}, Return[-Max[Re[Eigenvalues[JN]]]]
]

mya = 0.002;
myb = 0.4;
mym = 0.0024;
myr1 = 0.01 * (10);
myr2 = 0.01 * (30);
{exactEffMigRateABCFunc[mya, myb, mym, myr1, myr2],
 approxEffMigRateABCFunc[mya, myb, mym, myr1, myr2],
 approxEffMigRateABCFunc[mya, myb, mym, myr1, myr2] /
 exactEffMigRateABCFunc[mya, myb, mym, myr1, myr2] - 1}
{0.00102813, 0.00102601, -0.00206156}
```

The exact (blue) and approximate (red) effective migration rate:

```
Manipulate[Plot[{exactEffMigRateABCFunc[mya, myb, m, myr1, myr2],
  approxEffMigRateABCFunc[mya, myb, m, myr1, myr2]}, {m, 0, mMax}, PlotRange -> {{0, mMax}, Automatic}, Frame -> True,
  FrameStyle -> Table[{Black, Opacity[0]}, {i, 1, 2}], FrameLabel -> {"Migration rate  $m$ ", "Effective mig. rate"}, 
  LabelStyle -> {Directive[FontSize -> 14], FontFamily -> "Helvetica"}], {{mya, 0.02}, {0, 1}, {{myb, 0.4}, {0, 1}}, {{myr1, 0.02}, {0, 1}},
  {{myr2, 0.02}, {0, 1}}, {{mMax, 0.1}, {0, 10}}]
```



■ Remark

The only difference between configurations $\mathcal{A} - C - \mathcal{B}$ and $\mathcal{A} - \mathcal{B} - C$ seems to be in the fourth element of the fourth row of the respective Jacobian matrices J_N . We double check this in the following:

```
JMTestACB := 
  {{-m, a, b, 0}, {m, -a - rAC +  $\frac{m(a - b + rAB)}{a + b + rAB}$ , 0, b}, {m, 0, -b - rCB +  $\frac{m(b - a + rAB)}{a + b + rAB}$ , a},
   {-m,  $\frac{m(b - a + rAB)}{a + b + rAB}$ ,  $\frac{m(a - b + rAB)}{a + b + rAB}$ , -a - b - rAB +  $\frac{m(a + b + 3rAB)}{a + b + rAB}$ }}
JMTestABC := {{-m, a, b, 0}, {m, -a - rAC +  $\frac{m(a - b + rAB)}{a + b + rAB}$ , 0, b},
  {m, 0, -b - rCB +  $\frac{m(b - a + rAB)}{a + b + rAB}$ , a},
  {-m,  $\frac{m(b - a + rAB)}{a + b + rAB}$ ,  $\frac{m(a - b + rAB)}{a + b + rAB}$ , -a - b - rAC +  $\frac{m(a + b + 3rAB)}{a + b + rAB}$ }}
FullSimplify[
  Normal[Series[Det[JMTestACB - x IdentityMatrix[4]] /. x -> -m  $\frac{rAC \ rCB}{(a + rAC) \ (b + rCB)}$ ,
    {m, 0, 1}]]] /. {rAB -> rAC + rCB}]
```

```

FullSimplify[
  Normal[Series[Det[JMTestABC - x IdentityMatrix[4]] /. x \[Rule] -m \frac{rCB (b + rAC)}{(b + rCB) (a + b + rAC)},
    {m, 0, 1}]]] /. {rAC \[Rule] rAB + rCB}
]

```

This confirms that the only difference is in the fourth element of the fourth row of the two matrices.

Order of loci: C - \mathcal{A} - \mathcal{B}

For reasons of symmetry, we directly obtain

$$m_e = m \frac{r_1(a + r_1 + r_2)}{(a + r_1)(a + b + r_1 + r_2)}. \quad (1)$$

- Graphical exploration of approximation
 - Generic

We compare the approximate effective migration rate to the exact (negative) eigenvalue of J_N computed numerically.

```

In[213]:= approxEffMigRateCABFunc[a_, b_, m_, r1_, r2_] := m \frac{r1 (a + r1 + r2)}{(a + r1) (a + b + r1 + r2)}

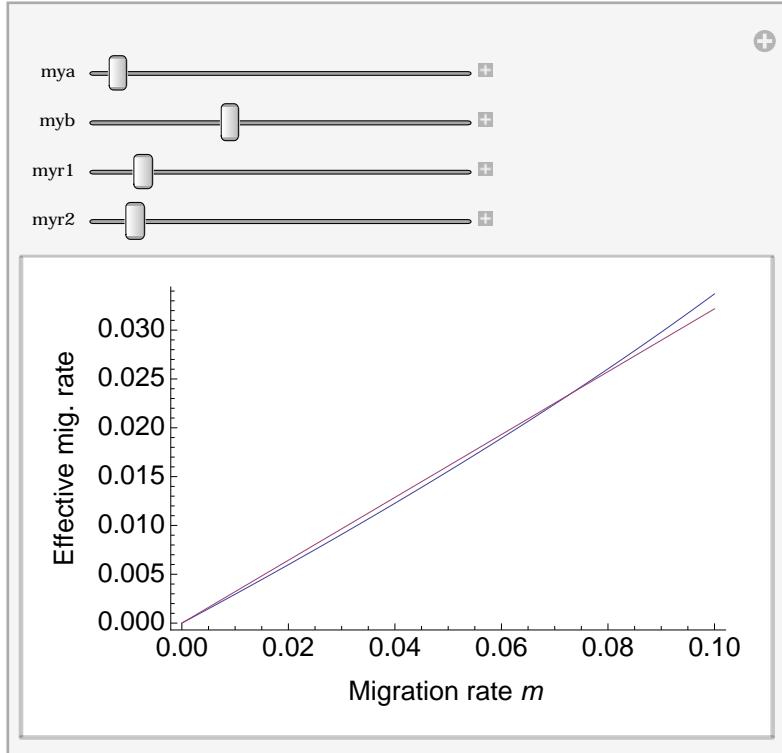
In[214]:= exactEffMigRateCABFunc[a_, b_, m_, r1_, r2_] := Module[{JN}, JN = {{-m, b, a, 0}, \frac{m \left(a^2 - b^2 + 6 b r2 - 6 a r1\right)}{r1 (a + r1 + r2)}}, Return[-Max[Re[Eigenvalues[JN]]]]]
]

mya = 0.002;
myb = 0.4;
mym = 0.0024;
myr1 = 0.01 * (10);
myr2 = 0.01 * (30);
{exactEffMigRateCABFunc[mya, myb, mym, myr1, myr2],
 approxEffMigRateCABFunc[mya, myb, mym, myr1, myr2],
 approxEffMigRateCABFunc[mya, myb, mym, myr1, myr2] /
 exactEffMigRateCABFunc[mya, myb, mym, myr1, myr2] - 1}
{0.000969913, 0.000592636, -0.38898}

```

The exact (blue) and approximate (red) effective migration rate:

```
Manipulate[Plot[{exactEffMigRateCABFunc[mya, myb, m, myr1, myr2],  
approxEffMigRateCABFunc[mya, myb, m, myr1, myr2]}, {m, 0, .1},  
Frame → True, FrameStyle → Table[{Black, Opacity[0]}, {i, 1, 2}],  
FrameLabel → {"Migration rate  $m$ ", "Effective mig. rate"},  
LabelStyle → {Directive[FontSize → 14], FontFamily → "Helvetica"}],  
{mya, 0.02}, 0, 1}, {{myb, 0.4}, 0, 1}, {{myr1, 0.02}, 0, 1}, {{myr2, 0.02}, 0, 1}]
```



$$\begin{aligned}
& \left\{ \left\{ a - m - \frac{1}{4 r1} \left(-a^2 + b^2 + 6 a r1 - 4 m r1 - r1^2 + (a - b + r1) \sqrt{-8 m r1 + (a + b + r1)^2} \right), 0, b, 0, 0, 0, \right. \right. \\
& 0 \}, \left. \left. \left\{ 0, b - m - \frac{1}{4 r1} \left(a^2 - b^2 + 6 b r1 - 4 m r1 - r1^2 + (-a + b + r1) \sqrt{-8 m r1 + (a + b + r1)^2} \right), \right. \right. \\
& a, 0, 0, 0, 0 \}, \left. \left. \left\{ \frac{1}{16 b r1^2} \left(8 m^2 r1^2 + 4 m r1 (a^2 + (b - r1)^2 - 2 a (b + r1)) - \right. \right. \right. \\
& (a - b - r1) (a + b - r1) (a - b + r1) \left(a + b + r1 - \sqrt{-8 m r1 + (a + b + r1)^2} \right) + \\
& \left. \left. \left. 2 m r1 \left(a^2 - b^2 + 6 b r1 - 4 m r1 - r1^2 + (-a + b + r1) \sqrt{-8 m r1 + (a + b + r1)^2} \right) \right) \right], \\
& \frac{1}{16 a r1^2} \left(8 m^2 r1^2 + 4 m r1 (a^2 + (b - r1)^2 - 2 a (b + r1)) - \right. \\
& (a - b - r1) (a + b - r1) (a - b + r1) \left(a + b + r1 - \sqrt{-8 m r1 + (a + b + r1)^2} \right) + \\
& \left. \left. \left. 2 m r1 \left(-a^2 + b^2 + 6 a r1 - 4 m r1 - r1^2 + (a - b + r1) \sqrt{-8 m r1 + (a + b + r1)^2} \right) \right) \right], \\
& \frac{1}{2} \left(-a - b + 2 m - r1 - \sqrt{-8 m r1 + (a + b + r1)^2} \right), 0, 0, 0, 0 \}, \{ 0, 0, 0, -m, a, b, 0 \}, \\
& \left\{ 0, 0, 0, \frac{1}{8 a r1} m \left(-a^2 + b^2 + 6 a r1 - 4 m r1 - r1^2 + (a - b + r1) \sqrt{-8 m r1 + (a + b + r1)^2} \right), \right. \\
& a - m - r1 - \frac{1}{4 r1} \left(-a^2 + b^2 + 6 a r1 - 4 m r1 - r1^2 + (a - b + r1) \sqrt{-8 m r1 + (a + b + r1)^2} \right) - r2, 0, \\
& b \}, \left\{ 0, 0, 0, \frac{1}{8 b r1} m \left(a^2 - b^2 + 6 b r1 - 4 m r1 - r1^2 + (-a + b + r1) \sqrt{-8 m r1 + (a + b + r1)^2} \right), \right. \\
& 0, b - m - \frac{1}{4 r1} \left(a^2 - b^2 + 6 b r1 - 4 m r1 - r1^2 + (-a + b + r1) \sqrt{-8 m r1 + (a + b + r1)^2} \right) - r2, a \}, \\
& \left\{ 0, 0, 0, \frac{1}{64 a b r1^2} m \left(-(-a^2 + b^2 + 6 a r1 - 4 m r1 - r1^2 + (a - b + r1) \sqrt{-8 m r1 + (a + b + r1)^2}) \right. \right. \\
& \left(a^2 - b^2 + 6 b r1 - 4 m r1 - r1^2 + (-a + b + r1) \sqrt{-8 m r1 + (a + b + r1)^2} \right) + \\
& \left. \left. 2 \left(-8 m^2 r1^2 - 4 m r1 (a^2 + (b - r1)^2 - 2 a (b + r1)) + \right. \right. \right. \\
& (a - b - r1) (a + b - r1) (a - b + r1) \left(a + b + r1 - \sqrt{-8 m r1 + (a + b + r1)^2} \right) \right) \right], \\
& \frac{1}{16 b r1^2} \left(8 m^2 r1^2 + 4 m r1 (a^2 + (b - r1)^2 - 2 a (b + r1)) - (a - b - r1) (a + b - r1) \right. \\
& (a - b + r1) \left(a + b + r1 - \sqrt{-8 m r1 + (a + b + r1)^2} \right) + \\
& \left. \left. \left. 2 m r1 \left(a^2 - b^2 + 6 b r1 - 4 m r1 - r1^2 + (-a + b + r1) \sqrt{-8 m r1 + (a + b + r1)^2} \right) \right) \right], \\
& \frac{1}{16 a r1^2} \left(8 m^2 r1^2 + 4 m r1 (a^2 + (b - r1)^2 - 2 a (b + r1)) - \right. \\
& (a - b - r1) (a + b - r1) (a - b + r1) \left(a + b + r1 - \sqrt{-8 m r1 + (a + b + r1)^2} \right) + \\
& \left. \left. \left. 2 m r1 \left(-a^2 + b^2 + 6 a r1 - 4 m r1 - r1^2 + (a - b + r1) \sqrt{-8 m r1 + (a + b + r1)^2} \right) \right) \right], \\
& \frac{1}{2} \left(-a - b + 2 m - r1 - \sqrt{-8 m r1 + (a + b + r1)^2} - 2 r2 \right) \} / . \{ r1 \rightarrow r2, r2 \rightarrow r1, a \rightarrow b, b \rightarrow a \}
\end{aligned}$$

$$\begin{aligned}
& \left\{ \left\{ b - m - \frac{1}{4 r2} \left(a^2 - b^2 + 6 b r2 - 4 m r2 - r2^2 + (-a + b + r2) \sqrt{-8 m r2 + (a + b + r2)^2} \right), 0, a, 0, 0, 0, \right. \right. \\
& \left. \left. 0 \right\}, \left\{ 0, a - m - \frac{1}{4 r2} \left(-a^2 + b^2 + 6 a r2 - 4 m r2 - r2^2 + (a - b + r2) \sqrt{-8 m r2 + (a + b + r2)^2} \right), \right. \\
& b, 0, 0, 0, 0 \}, \left\{ \frac{1}{16 a r2^2} \left(8 m^2 r2^2 + 4 m r2 (b^2 + (a - r2)^2 - 2 b (a + r2)) - \right. \right. \\
& (-a + b - r2) (a + b - r2) (-a + b + r2) \left(a + b + r2 - \sqrt{-8 m r2 + (a + b + r2)^2} \right) + \\
& \left. \left. 2 m r2 \left(-a^2 + b^2 + 6 a r2 - 4 m r2 - r2^2 + (a - b + r2) \sqrt{-8 m r2 + (a + b + r2)^2} \right) \right), \right. \\
& \frac{1}{16 b r2^2} \left(8 m^2 r2^2 + 4 m r2 (b^2 + (a - r2)^2 - 2 b (a + r2)) - \right. \right. \\
& (-a + b - r2) (a + b - r2) (-a + b + r2) \left(a + b + r2 - \sqrt{-8 m r2 + (a + b + r2)^2} \right) + \\
& \left. \left. 2 m r2 \left(a^2 - b^2 + 6 b r2 - 4 m r2 - r2^2 + (-a + b + r2) \sqrt{-8 m r2 + (a + b + r2)^2} \right) \right), \right. \\
& \frac{1}{2} \left(-a - b + 2 m - r2 - \sqrt{-8 m r2 + (a + b + r2)^2} \right), 0, 0, 0, 0 \}, \{ 0, 0, 0, -m, b, a, 0 \}, \\
& \left\{ 0, 0, 0, \frac{1}{8 b r2} m \left(a^2 - b^2 + 6 b r2 - 4 m r2 - r2^2 + (-a + b + r2) \sqrt{-8 m r2 + (a + b + r2)^2} \right), \right. \\
& b - m - r1 - r2 - \frac{1}{4 r2} \left(a^2 - b^2 + 6 b r2 - 4 m r2 - r2^2 + (-a + b + r2) \sqrt{-8 m r2 + (a + b + r2)^2} \right), 0, a \}, \\
& \left\{ 0, 0, 0, \frac{1}{8 a r2} m \left(-a^2 + b^2 + 6 a r2 - 4 m r2 - r2^2 + (a - b + r2) \sqrt{-8 m r2 + (a + b + r2)^2} \right), 0, \right. \\
& a - m - r1 - \frac{1}{4 r2} \left(-a^2 + b^2 + 6 a r2 - 4 m r2 - r2^2 + (a - b + r2) \sqrt{-8 m r2 + (a + b + r2)^2} \right), b \}, \\
& \left\{ 0, 0, 0, \frac{1}{64 a b r2^2} m \left(\left(-a^2 + b^2 + 6 a r2 - 4 m r2 - r2^2 + (a - b + r2) \sqrt{-8 m r2 + (a + b + r2)^2} \right) \right. \right. \\
& \left. \left. \left(-a^2 + b^2 - 6 b r2 + 4 m r2 + r2^2 - (-a + b + r2) \sqrt{-8 m r2 + (a + b + r2)^2} \right) + \right. \right. \\
& 2 \left(-8 m^2 r2^2 - 4 m r2 (b^2 + (a - r2)^2 - 2 b (a + r2)) + \right. \right. \\
& (-a + b - r2) (a + b - r2) (-a + b + r2) \left(a + b + r2 - \sqrt{-8 m r2 + (a + b + r2)^2} \right) \left. \right) \left. \right), \right. \\
& \frac{1}{16 a r2^2} \left(8 m^2 r2^2 + 4 m r2 (b^2 + (a - r2)^2 - 2 b (a + r2)) - (-a + b - r2) (a + b - r2) \right. \right. \\
& (-a + b + r2) \left(a + b + r2 - \sqrt{-8 m r2 + (a + b + r2)^2} \right) + \right. \right. \\
& 2 m r2 \left(-a^2 + b^2 + 6 a r2 - 4 m r2 - r2^2 + (a - b + r2) \sqrt{-8 m r2 + (a + b + r2)^2} \right) \left. \right), \right. \\
& \frac{1}{16 b r2^2} \left(8 m^2 r2^2 + 4 m r2 (b^2 + (a - r2)^2 - 2 b (a + r2)) - \right. \right. \\
& (-a + b - r2) (a + b - r2) (-a + b + r2) \left(a + b + r2 - \sqrt{-8 m r2 + (a + b + r2)^2} \right) + \right. \right. \\
& 2 m r2 \left(a^2 - b^2 + 6 b r2 - 4 m r2 - r2^2 + (-a + b + r2) \sqrt{-8 m r2 + (a + b + r2)^2} \right) \left. \right), \right. \\
& \frac{1}{2} \left(-a - b + 2 m - 2 r1 - r2 - \sqrt{-8 m r2 + (a + b + r2)^2} \right) \left. \right\}
\end{aligned}$$