Comparison of the Jacobian of the marginal one-locus migration-selection equilibrium ($E_B$) to the mean matrix of the corresponding branching process

**Generic model**

- **General assumptions and rules**
  - \(1\) assumptionGeneric := \(0 \leq x[1] \leq 1, 0 \leq x[2] \leq 1, 0 \leq x[3] \leq 1, x[4] = 1 - x[1] - x[2] - x[3], 0 \leq m \leq 1, 0 \leq r \leq 1 / 2, 0 \leq qC \leq 1, 0 < qB < 1\)

- \(2\) assumeNoPositionEffect :=
  - \(\{w_{21} \to w_{21}, w_{31} \to w_{13}, w_{32} \to w_{14}, w_{31} \to w_{13}, w_{43} \to w_{34}, w_{42} \to w_{24}, w_{41} \to w_{14}, w_{23} \to w_{14}\}\)

- \(3\) wMat := \(\{(w_{11}, w_{12}, w_{13}, w_{14}), (w_{21}, w_{22}, w_{23}, w_{24}), (w_{31}, w_{32}, w_{33}, w_{34}), (w_{41}, w_{42}, w_{43}, w_{44})\}\)

- \(4\) simplifyNotation := \(\{x[1] \to x_1, x[2] \to x_2, x[3] \to x_3, x[4] \to x_4\}\)

- \(5\) \(w[i, j] := w\text{Mat}[i, j]\)

- **Jacobian J for the deterministic two-locus dynamics**
  - Marginal and mean fitnesses.

- \(6\) \(w[i, j] := \text{Sum}[w[i, j] \times [j], \{j, 1, 4\}]\)

  - \(wBar := \text{Sum}[w[i] \times [i], \{i, 1, 4\}]\)

  - Linkage disequilibrium.


  - Generic recursion equations for the haplotype frequencies, where \(q_c\) is the frequency of allele \(B_1\) on the continent and \(m\) is the migration rate.

- \(8\) \(x_1\text{RecGenr} := (1 - m) \times [1] \times w[1] - r \times w[1, 4] \times \text{DD} / w\text{Bar}\)

  - \(x_2\text{RecGenr} := (1 - m) \times [2] \times w[2] + r \times w[1, 4] \times \text{DD} / w\text{Bar}\)

  - \(x_3\text{RecGenr} := (1 - m) \times [3] \times w[3] + r \times w[1, 4] \times \text{DD} / w\text{Bar} + m \times qC\)

  - \(x_4\text{RecGenr} := (1 - m) \times [4] \times w[4] + r \times w[1, 4] \times \text{DD} / w\text{Bar} + m \times (1 - qC)\)

- \(9\) rec\text{Hap} := \(\{x_1\text{RecGenr}, x_2\text{RecGenr}, x_3\text{RecGenr}, x_4\text{RecGenr}\}\)

\[
\text{recHap} / . \text{simplifyNotation} // \text{MatrixForm}
\]

\[
\begin{pmatrix}
(1 - m) \times [1] \times (w_{11}x_1 + w_{12}x_2 + w_{13}x_3 + w_{14}x_4) - r \times w_{14}x_1 / x_1 \times (w_{11}x_{11} + w_{12}x_{12} + w_{13}x_{13} + w_{14}x_{14}) - w_{12}x_2 / w_{21}x_1 + w_{22}x_2 + w_{23}x_3 + w_{24}x_4 - x_3 / (w_{31}x_{11} + w_{32}x_{12} + w_{33}x_{13} + w_{34}x_{14}) - x_2 / (w_{14}x_{41} + w_{42}x_{24} + w_{43}x_{14}) + r \times w_{14}x_1 - w_{12}x_2 / (w_{21}x_1 + w_{22}x_2 + w_{23}x_3 + w_{24}x_4) + r \times w_{14} / (w_{21}x_1 + w_{22}x_2 + w_{23}x_3 + w_{24}x_4) - x_3 / (w_{31}x_{11} + w_{32}x_{12} + w_{33}x_{13} + w_{34}x_{14}) + x_1 / (w_{41}x_{41} + w_{42}x_{24} + w_{43}x_{14}) + qC + m(1 - qC)
\end{pmatrix}
\]

Generic Jacobian matrix.
The marginal one-locus migration-selection equilibrium is called $E_B$ and defined as $E_B = (p, q, D) = (0, \hat{q}_B, 0)$, where $p$ and $q$ are the frequencies of $A_1$ and $B_1$ on the island, respectively, and $D$ is the linkage disequilibrium. Moreover, $\hat{q}_B$ denotes the equilibrium frequency of $B_1$. It is defined as the non-trivial solution of the equation obtained by equating the marginal one-locus recursion equation to $q$. With generic fitnesses, this solution cannot be readily found.

Note that at $E_B$, the following holds: $\hat{x}_1 = \hat{x}_2 = 0$, $\hat{x}_3 = \hat{q}_B$ and $x_4 = 1 - \hat{q}_B$.

The Jacobian matrix evaluated at the marginal one-locus migration-selection equilibrium $E_B$.

As expected (see the case of additive fitnesses above), this is a lower triangular block matrix, $J = \begin{pmatrix} J_1 & 0 \\ J_3 & J_4 \end{pmatrix}$, where

- **Mean matrix L for the two-type branching process**
  Marginal fitnesses of types 1 and 2.

- **wBP** := w[1, 3] qB + w[1, 4] (1 - qB)
  **wBP** := w[2, 4] (1 - qB) + w[1, 4] qB

  Mean fitness of resident population.

- **wbBPBar** := qB^2 w[3, 3] + 2 qB (1 - qB) w[3, 4] + (1 - qB)^2 w[4, 4]
  The mean matrix.
\[ A := (1-m) (wBP1 - r (1 - qB) w[1, 4]) / wBPBar \]
\[ B := (1-m) r qB w[1, 4] / wBPBar \]
\[ C := (1-m) r (1-qB) w[1, 4] / wBPBar \]
\[ D := (1-m) (wBP2 - r qB w[1, 4]) / wBPBar \]

In[26]:= L := ({A, C), {B, D})

Comparison of \( L^T \) and \( J_1 \)

AssumeNoPositionEffect

\{w21 \to w21, w31 \to w13, w32 \to w14, w31 \to w13, w43 \to w34, w42 \to w24, w41 \to w14, w23 \to w14\}

Transpose[L] // FullSimplify // MatrixForm

\( J_1 \) / AssumeNoPositionEffect // FullSimplify // MatrixForm

Transpose[L] - J1 / AssumeNoPositionEffect // Simplify

\{0, 0\}, \{0, 0\}\)

We note that \( J_1 \) is equal to the transpose of the mean matrix \( L \), as long as position and parental effects on relative fitnesses can be ignored. This also holds irrespective of whether the continent is monomorphic or polymorphic.

Eigenvalues of \( J \) and \( L^T \)

FullSimplify[Eigenvalues[J1]] / AssumeNoPositionEffect,
Assumptions -> Flatten[{assumeGeneric}]]

\[ \{ (-1 + m) (w14 - r w14 + qB (w13 - w24) + w24) (2 \ qB (w34 - w44) + w44 + qB^2 (w33 - 2 w34 + w44)) + \]
\[ \sqrt{(-1 + m)^2 ((1-r) w14 + w24)^2 + qB^2 (w13 - 2 w14 + w24) - 2 qB (w14 (-1 + r) w14 + 4 r w14 + (w13 + 3 (-1 + r) w14) w24 + w24^2)}
\]
\[ 2 \ qB (w34 - w44) + w44 + qB^2 (w33 - 2 w34 + w44)}^2} \}/ \]
\[ 2 \ qB (w34 - w44) + w44 + qB^2 (w33 - 2 w34 + w44)}^2} \},
\[ (-1 + m) (w14 - r w14 + qB (w13 - w24) + w24) (2 \ qB (w34 - w44) + w44 + qB^2 (w33 - 2 w34 + w44)) + \]
\[ \sqrt{(-1 + m)^2 ((1-r) w14 + w24)^2 + qB^2 (w13 - 2 w14 + w24) - 2 qB (w14 (-1 + r) w14 + 4 r w14 + (w13 + 3 (-1 + r) w14) w24 + w24^2)}
\]
\[ 2 \ qB (w34 - w44) + w44 + qB^2 (w33 - 2 w34 + w44)}^2} \}/ \]
\[ 2 \ qB (w34 - w44) + w44 + qB^2 (w33 - 2 w34 + w44)}^2} \}

In[27]:= evalsJ1 := {-((1-m) (w14-r w14+qB (w13-w24)+w24) (2 qB (w34-w44)+w44+qB^2 (w33-2 w34+w44))}

In[28]:= evalsJ4 := FullSimplify[Eigenvalues[J4]] / AssumeNoPositionEffect,
Assumptions -> Flatten[{assumeGeneric}]]

\[ \{ 0, (-1 + m) (-qB^2 w33 w44 + (-1 + qB) (2 qB w33 + 3 qB w34 - qB w34) w44)
\]
\[ 2 \ qB (w34 - w44) + w44 + qB^2 (w33 - 2 w34 + w44)}^2} \} \)
Conclusion

We again use $e_1$ and $e_2$ for the eigenvalues of $J_1$ and $e_3$ and $e_4$ for the eigenvalues of $J_4$.

Conditional on existence of $E_B$, as a valid marginal one-locus equilibrium, we would like to know if the condition for invasion of $A_1$ can be determined exclusively based on the eigenvalues of $J_1$. If this is the case, we know that what we have shown above for the case of additive fitnesses and a monomorphic continent holds more generally: If invasion of $A_1$ via $E_B$ is possible in the two-type branching process, then it is also possible in the deterministic two-locus dynamics, and vice versa.

To illustrate the dynamics, consider the 3-simplex $\Delta^3$, which has four vertices, each of which corresponds to the fixation of one out of the four gametes $A_1B_1$, $A_1B_2$, $A_2B_1$ and $A_2B_2$. Moreover, there are six edges, each of which corresponds to the case where a particular pair of alleles segregates in the population; there are four faces, each of which corresponds to the case where all but one particular allele segregate in the population. The interior of $\Delta^3$ corresponds to all four alleles segregating. Clearly, the marginal one-locus equilibrium $E_B$ sits on the edge that connects the two vertices that correspond to fixation of $A_2B_1$ and $A_2B_2$, respectively. $E_B$ is a valid one-locus polymorphism only if it does not sit on one of these vertices, but on the edge in between.

Matrix $J_4$ is given by

$$
\begin{pmatrix}
\frac{\partial f_i}{\partial x_1} & \frac{\partial f_i}{\partial x_2} \\
\frac{\partial f_i}{\partial x_3} & \frac{\partial f_i}{\partial x_4}
\end{pmatrix},
$$

where $f_i = f_i(x_1, x_2, x_3, x_4)$ is the recursion equation of gamete frequency $i$ and for all $i \in \{1, 2, 3, 4\}$. Therefore, we see that $J_4$ characterises the dynamics along the edge of $\Delta^3$ that connects the vertices $x_4 = 1$ and $x_3 = 1$. From this, it follows that the eigenvalues of $J_4$ determine the so-called internal stability of $E_B$, that is stability along the edge of $\Delta^3$ on which $E_B$ sits. Matrix $J_1$, on the other hand, is given by

$$
\begin{pmatrix}
\frac{\partial f_i}{\partial x_1} & \frac{\partial f_i}{\partial x_2} \\
\frac{\partial f_i}{\partial x_3} & \frac{\partial f_i}{\partial x_4}
\end{pmatrix}
$$

and therefore characterises the dynamics transversal to the boundary of $\Delta^3$ that connects the vertices $x_4 = 1$ and $x_3 = 1$, i.e. the dynamics leading into or out of the interior of the simplex. From this, it follows that the eigenvalues of $J_1$ determine the so-called external stability of $E_B$. Obviously, the external stability is directly linked to the question of whether or not $E_B$ can be invaded by a mutation at locus A.

As shown above, with generic fitnesses and an arbitrary frequency $q_A$ of $B_1$ on the continent, one out of the two eigenvalues of $J_1$ is always 0. We arbitrarily assign 0 to eigenvalue $e_3$. Then, the value of $e_4$ determines i) existence of $E_B$ in the one- and two-locus dynamics, and ii) about asymptotic stability of $E_B$ in the one-locus dynamics. Both are required for the initial condition of our biological scenario, and fulfilled if and only if $e_4 < 1$. From this, it automatically follows that whenever $E_B$ becomes unstable in the two-locus dynamics (upon occurrence of $A_1$), this can only be due to either $e_1$ or $e_2$ being larger than 1. Because $e_1$ and $e_2$ are shared between $J_1$ and $L$, this argument proof what we wanted to show: If invasion of $A_1$ via $E_B$ is possible in the two-type branching process, then it is also possible in the deterministic two-locus dynamics, and vice versa.