Frequencies of genotypes

In the Notebook a complete study of two biallelic haploid loci system is performed. Equilibrium genotype frequences under mutation and selection are found, their stability is determined and the parametric portrait of the system is studied. Detailed description and biological interpretation are given in the paper: https://www.biorxiv.org/content/10.1101/477489v1.full.pdf.

Introducing the model

Frequencies after mutation; x = p(Ab), y = p(aB), z = p(ab)

In[∘]:=
```
X1[x_, y_, z_][μ_, ν_] := x + (1 - x - y - z) * ν * (1 - μ) - x * μ
Y1[x_, y_, z_][μ_, ν_] := y + (1 - x - y - z) * μ * (1 - ν) - y * ν
Z1[x_, y_, z_][μ_, ν_] := z + x * μ + y * ν + (1 - x - y - z) * μ * ν
```

Selection coefficient against **a** is s , against **b** is t; k introduces epistasis; w(AB) = 1, w(Ab) = 1-s, w(aB) = 1-t, w(ab) = (1-s)(1-t)(1-k); Mean fitness:

In[∘]:=
```
W[x_, y_, z_][s_, t_, k_] :=
 (1 - x - y - z) + x * (1 - t) + y * (1 - s) + z * (1 - s) * (1 - t) * (1 - k)
```

Frequencies after selection:

In[∘]:=
```
X2[x_, y_, z_][s_, t_, k_, μ_, ν_] := X1[x, y, z][μ, ν] *
   (1 - t) / W[X1[x, y, z][μ, ν], Y1[x, y, z][μ, ν], Z1[x, y, z][μ, ν]][s, t, k]
Y2[x_, y_, z_][s_, t_, k_, μ_, ν_] := Y1[x, y, z][μ, ν] *
   (1 - s) / W[X1[x, y, z][μ, ν], Y1[x, y, z][μ, ν], Z1[x, y, z][μ, ν]][s, t, k]
Z2[x_, y_, z_][s_, t_, k_, μ_, ν_] := Z1[x, y, z][μ, ν] * (1 - s) * (1 - t) *
   (1 - k) / W[X1[x, y, z][μ, ν], Y1[x, y, z][μ, ν], Z1[x, y, z][μ, ν]][s, t, k]
```

Equilibria

At equilibrium frequencies don’t change:

In[∘]:=
```
solution = Solve[X2[x, y, z][s, t, k, μ, ν] == x &&
   Y2[x, y, z][s, t, k, μ, ν] == y && Z2[x, y, z][s, t, k, μ, ν] == z, {x, y, z}]
```

Out[∘]=

$$\Big\{\{x \to 0, y \to 0, z \to 1\}, \Big\{x \to 0, y \to \cdots 1 \cdots, z \to \frac{\cdots 1 \cdots}{\cdots 1 \cdots}\Big\}, \cdots 1 \cdots,$$
$$\Big\{x \to -\Big(\Big((-1+t)\,(s-\mu)\,\nu\,(k+s-k\,s+t-k\,t-s\,t+k\,s\,t-\mu-\nu+\mu\,\nu)\Big)\Big/$$
$$\Big((-1+\mu)\,(-1+\nu)\,\big(k\,s\,t+s^2\,t-k\,s^2\,t+s\,t^2-k\,s\,t^2-s^2\,t^2+k\,s^2\,t^2-s\,t\,\mu-$$
$$s\,t\,\nu-k\,\mu\,\nu+k\,s\,\mu\,\nu+k\,t\,\mu\,\nu+s\,t\,\mu\,\nu-k\,s\,t\,\mu\,\nu\big)\Big)\Big), y \to \frac{\cdots 1 \cdots}{\cdots 1 \cdots},$$
$$z \to \left(\cdots 74 \cdots + \frac{\cdots 1 \cdots}{\cdots 1 \cdots} - \frac{k\,s^2\,(-1+t)\,(s-\mu)\,\mu^2\,\nu^2\,(k+s-k\,s+t-k\,t-s\,t+k\,s\,t-\mu-\nu+\mu\,\nu)}{(-1+\mu)\,(\cdots 1 \cdots)\,(k\,s\,t+s^2\,t-k\,s^2\,t+\cdots 13 \cdots+k\,t\,\mu\,\nu+s\,t\,\mu\,\nu-k\,s\,t\,\mu\,\nu)}\right)\Big/$$
$$\big(k^2\,s+2\,k\,s^2-2\,k^2\,s^2+s^3-2\,k\,s^3+k^2\,s^3+k\,s\,t-k^2\,s\,t+s^2\,t-$$
$$3\,k\,s^2\,t+\cdots 29 \cdots+2\,k^2\,s\,\mu\,\nu+s^2\,\mu\,\nu-k^2\,s^2\,\mu\,\nu-k\,t\,\mu\,\nu+$$
$$k^2\,t\,\mu\,\nu+2\,k\,s\,t\,\mu\,\nu-2\,k^2\,s\,t\,\mu\,\nu-k\,s^2\,t\,\mu\,\nu+k^2\,s^2\,t\,\mu\,\nu-s\,\mu^2\,\nu\big)\Big\}\Big\}$$

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In[•]:=
```
FullSimplify[solution[[1]]]
```

Out[•]=
$$\{x \to 0,\ y \to 0,\ z \to 1\}$$

In[•]:=
```
FullSimplify[solution[[2]]]
```

Out[•]=
$$\left\{x \to 0,\ y \to -\frac{k+t-k\,t-\nu}{(k+t-k\,t)\,(-1+\nu)},\ z \to -\frac{(-1+k)\,(-1+t)\,\nu}{(k+t-k\,t)\,(-1+\nu)}\right\}$$

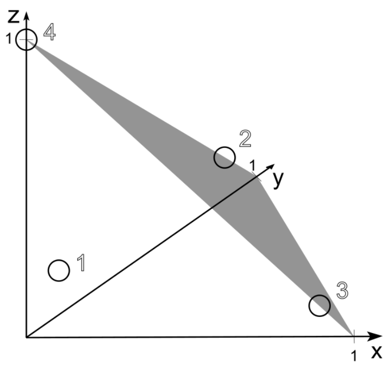
In[•]:=
```
FullSimplify[solution[[3]]]
```

Out[•]=
$$\left\{x \to -\frac{k+s-k\,s-\mu}{(k+s-k\,s)\,(-1+\mu)},\ y \to 0,\ z \to -\frac{(-1+k)\,(-1+s)\,\mu}{(k+s-k\,s)\,(-1+\mu)}\right\}$$

In[•]:=
```
FullSimplify[solution[[4]]]
```

Out[•]=
$$\{x \to ((-1+t)\,(s-\mu)\,\nu\,(s+k\,(-1+s)\,(-1+t)+t-s\,t-\mu+(-1+\mu)\,\nu))\,/$$
$$((-1+\mu)\,(-1+\nu)\,(-k\,(-1+s)\,(-1+t)\,(s\,t-\mu\,\nu)+s\,t\,(s\,(-1+t)-t+\mu+\nu-\mu\,\nu))),$$
$$y \to ((-1+s)\,\mu\,(t-\nu)\,(s+k\,(-1+s)\,(-1+t)+t-s\,t-\mu+(-1+\mu)\,\nu))\,/$$
$$((-1+\mu)\,(-1+\nu)\,(-k\,(-1+s)\,(-1+t)\,(s\,t-\mu\,\nu)+s\,t\,(s\,(-1+t)-t+\mu+\nu-\mu\,\nu))),$$
$$z \to -(((-1+k)\,(-1+s)\,(-1+t)\,\mu\,\nu\,(s\,(-1+t)-t+\mu+\nu-\mu\,\nu))\,/$$
$$((-1+\mu)\,(-1+\nu)\,(-k\,(-1+s)\,(-1+t)\,(s\,t-\mu\,\nu)+s\,t\,(s\,(-1+t)-t+\mu+\nu-\mu\,\nu))))\}$$

Equilibria can be represented in the space of genotype frequencies. Equilibrium 1 on the figure corresponds to solution 4 in the notebook and equilibrium 4 to solution 1.



Stability of the solutions in general case

None of the solutions corresponding to the fixation of one or both deleterious mutations are stable under mutation weaker than selection:
Solution 1 is not stable:

In[•]:=
```
Eigenvalues[Simplify[
  Table[D[fun, var], {fun, {X2[x, y, z][s, t, k, μ, ν], Y2[x, y, z][s, t, k, μ, ν],
      Z2[x, y, z][s, t, k, μ, ν]}}, {var, {x, y, z}}] /. solution[[1]]]]
```

Out[•]=
$$\left\{\frac{-1+t+\mu-t\,\mu}{(-1+k)\,(-1+s)\,(-1+t)},\ \frac{-1+s+\nu-s\,\nu}{(-1+k)\,(-1+s)\,(-1+t)},\ \frac{-1+\mu+\nu-\mu\,\nu}{(-1+k)\,(-1+s)\,(-1+t)}\right\}$$

In[•]:=
$$\text{eig11}[\mu\_,\ \nu\_,\ s\_,\ t\_,\ k\_]\ :=\ \frac{(1-\mu)\,(1-\nu)}{(1-k)\,(1-s)\,(1-t)}$$

In[∘]:= Assuming$\left[(\mu < s) \&\& (\nu < t) \&\& (0 < \mu < 1) \&\& (0 < \nu < 1) \&\& (0 < s < 1) \&\& (0 < t < 1),\ \text{Simplify}\left[\frac{(1-\mu)\,(1-\nu)}{(1-s)\,(1-t)} < 1\right]\right]$

Out[∘]= False

Substituting $a = \frac{(1-\mu)\,(1-\nu)}{(1-s)\,(1-t)}$

In[∘]:= Assuming$\left[a > 1 \&\& (0 < k < 1),\ \text{Simplify}\left[\frac{1}{(1-k)} * a < 1\right]\right]$

Out[∘]= False

In[∘]:= $\text{eig12}[\mu\_, \nu\_, s\_, t\_, k\_] := \frac{-1+s+\nu-s\,\nu}{(-1+k)\,(-1+s)\,(-1+t)}$

In[∘]:= $\text{eig13}[\mu\_, \nu\_, s\_, t\_, k\_] := \frac{-1+t+\mu-t\,\mu}{(-1+k)\,(-1+s)\,(-1+t)}$

In[∘]:=
```
Eigenvalues[FullSimplify[
  Table[D[fun, var], {fun, {X2[x, y, z][s, t, k, μ, ν], Y2[x, y, z][s, t, k, μ, ν],
      Z2[x, y, z][s, t, k, μ, ν]}}, {var, {x, y, z}}] /. solution⟦2⟧]]
```

Out[∘]= $\left\{-\frac{(-1+t)\,(k-k^2+t-2\,k\,t+k^2\,t)}{(-k-t+k\,t)\,(-1+\nu)},\ \frac{(-1+t)\,(-1+\mu)}{(-1+s)\,(-1+\nu)},\ \frac{-1+\mu}{-1+s}\right\}$

Solution 2 is not stable:

In[∘]:= $\text{eig21}[\mu\_, \nu\_, s\_, t\_, k\_] := \frac{-1+\mu}{-1+s}$

In[∘]:= Assuming$[(\mu < s) \&\& (0 < \mu < 1) \&\& (0 < s < 1),\ \text{Simplify}[\text{eig21}[\mu, \nu, s, t, k] < 1]]$

Out[∘]= False

In[∘]:= $\text{eig22}[\mu\_, \nu\_, s\_, t\_, k\_] := \frac{(-1+t)\,(-1+\mu)}{(-1+s)\,(-1+\nu)}$

In[∘]:= $\text{eig23}[\mu\_, \nu\_, s\_, t\_, k\_] := -\frac{(-1+t)\,(k-k^2+t-2\,k\,t+k^2\,t)}{(-k-t+k\,t)\,(-1+\nu)}$

In[∘]:=
```
Eigenvalues[Simplify[
  Table[D[fun, var], {fun, {X2[x, y, z][s, t, k, μ, ν], Y2[x, y, z][s, t, k, μ, ν],
      Z2[x, y, z][s, t, k, μ, ν]}}, {var, {x, y, z}}] /. solution⟦3⟧]]
```

Out[∘]= $\left\{-\frac{(-1+s)\,(k-k^2+s-2\,k\,s+k^2\,s)}{(-k-s+k\,s)\,(-1+\mu)},\ \frac{(-1+s)\,(-1+\nu)}{(-1+t)\,(-1+\mu)},\ \frac{-1+\nu}{-1+t}\right\}$

Solution 3 is not stable:

In[∘]:= $\text{eig31}[\mu\_, \nu\_, s\_, t\_, k\_] := \frac{-1+\nu}{-1+t}$

In[∘]:= Assuming$[(\nu < t) \&\& (0 < \nu < 1) \&\& (0 < t < 1),\ \text{Simplify}[\text{eig31}[\mu, \nu, s, t, k] < 1]]$

Out[∘]= False

In[∘]:= $\text{eig32}[\mu\_, \nu\_, s\_, t\_, k\_] := \frac{(-1+s)\,(-1+\nu)}{(-1+t)\,(-1+\mu)}$

In[∘]:= `eig33[μ_, ν_, s_, t_, k_] :=` $-\frac{(-1+s)\ (k-k^2+s-2\,k\,s+k^2\,s)}{(-k-s+k\,s)\ (-1+\mu)}$

The leading eigenvalue for 4th solution depends on difference of mutation rate and selection coefficients between two loci. But in any case it is the only stable one under m<s and n<t:

In[∘]:=
```
Eigenvalues[Simplify[
  Table[D[fun, var], {fun, {X2[x, y, z][s, t, k, μ, ν], Y2[x, y, z][s, t, k, μ, ν],
     Z2[x, y, z][s, t, k, μ, ν]}}, {var, {x, y, z}}] /. solution[[4]]]]
```

Out[∘]=
$$\Big\{\frac{-1+t}{-1+\nu},\ \frac{-1+s}{-1+\mu},\ -\Big(\Big((-1+s)\ (-1+t)\ \big(-k\,s\,t+k^2\,s\,t-s^2\,t+2\,k\,s^2\,t-k^2\,s^2\,t-s\,t^2+2\,k\,s\,t^2-k^2\,s\,t^2+s^2\,t^2-2\,k\,s^2\,t^2+k^2\,s^2\,t^2+s\,t\,\mu-k\,s\,t\,\mu+s\,t\,\nu-k\,s\,t\,\nu+k\,\mu\,\nu-k^2\,\mu\,\nu-k\,s\,\mu\,\nu+k^2\,s\,\mu\,\nu-k\,t\,\mu\,\nu+k^2\,t\,\mu\,\nu-s\,t\,\mu\,\nu+2\,k\,s\,t\,\mu\,\nu-k^2\,s\,t\,\mu\,\nu\big)\Big)\Big/\Big((-1+\mu)\ (-1+\nu)\ \big(k\,s\,t+s^2\,t-k\,s^2\,t+s\,t^2-k\,s\,t^2-s^2\,t^2+k\,s^2\,t^2-s\,t\,\mu-s\,t\,\nu-k\,\mu\,\nu+k\,s\,\mu\,\nu+k\,t\,\mu\,\nu+s\,t\,\mu\,\nu-k\,s\,t\,\mu\,\nu\big)\Big)\Big)\Big\}$$

In[∘]:= `eig41[μ_, ν_, s_, t_, k_] :=` $\frac{-1+s}{-1+\mu}$

In[∘]:=
```
Assuming[(μ < s) && (0 < μ < 1) && (0 < s < 1), Simplify[eig41[μ, ν, s, t, k] < 1]]
```

Out[∘]= True

In[∘]:= `eig42[μ_, ν_, s_, t_, k_] :=` $\frac{-1+t}{-1+\nu}$

In[∘]:=
```
Assuming[(ν < t) && (0 < ν < 1) && (0 < t < 1), Simplify[eig42[μ, ν, s, t, k] < 1]]
```

Out[∘]= True

In[∘]:=
FullSimplify[
$$-\Big(\Big((-1+s)\ (-1+t)\ \big(-k\,s\,t+k^2\,s\,t-s^2\,t+2\,k\,s^2\,t-k^2\,s^2\,t-s\,t^2+2\,k\,s\,t^2-k^2\,s\,t^2+s^2\,t^2-2\,k\,s^2\,t^2+k^2\,s^2\,t^2+s\,t\,\mu-k\,s\,t\,\mu+s\,t\,\nu-k\,s\,t\,\nu+k\,\mu\,\nu-k^2\,\mu\,\nu-k\,s\,\mu\,\nu+k^2\,s\,\mu\,\nu-k\,t\,\mu\,\nu+k^2\,t\,\mu\,\nu-s\,t\,\mu\,\nu+2\,k\,s\,t\,\mu\,\nu-k^2\,s\,t\,\mu\,\nu\big)\Big)\Big/\Big((-1+\mu)\ (-1+\nu)\ \big(k\,s\,t+s^2\,t-k\,s^2\,t+s\,t^2-k\,s\,t^2-s^2\,t^2+k\,s^2\,t^2-s\,t\,\mu-s\,t\,\nu-k\,\mu\,\nu+k\,s\,\mu\,\nu+k\,t\,\mu\,\nu+s\,t\,\mu\,\nu-k\,s\,t\,\mu\,\nu\big)\Big)\Big)$$
]

Out[∘]= $-\frac{(-1+k)\ (-1+s)\ (-1+t)}{(-1+\mu)\ (-1+\nu)}$

In[∘]:= `eig43[μ_, ν_, s_, t_, k_] :=` $-\frac{(-1+k)\ (-1+s)\ (-1+t)}{(-1+\mu)\ (-1+\nu)}$

In[∘]:=
```
Assuming[(0 < k < 1) && (a < 1), Simplify[(1 - k) * a < 1]]
```

Out[∘]= True

Symmetric case (equal selection coefficients and mutation rates at both loci)

In[ ]:=
```
solutionSymmetric = Solve[X2[x, y, z][s, s, k, μ, μ] == x &&
   Y2[x, y, z][s, s, k, μ, μ] == y && Z2[x, y, z][s, s, k, μ, μ] == z, {x, y, z}]
```

... Solve: Equations may not give solutions for all "solve" variables.

Out[ ]=
$$\left\{\left\{y\to\frac{k+s-k\,s-k\,x-s\,x+k\,s\,x-\mu+k\,x\,\mu+s\,x\,\mu-k\,s\,x\,\mu}{(-k-s+k\,s)\,(-1+\mu)},\ z\to\frac{(-1+k)\,(-1+s)\,\mu}{(-k-s+k\,s)\,(-1+\mu)}\right\},\ \{x\to 0,\ y\to 0,\ z\to 1\},\right.$$
$$\{\cdots 1\cdots\},\ \{\cdots 1\cdots\},\ \left\{x\to-\frac{(-1+s)\,\mu\,(k+2\,s-2\,k\,s-s^2+k\,s^2-2\,\mu+\mu^2)}{(-1+\mu)^2\,(k\,s+2\,s^2-2\,k\,s^2-s^3+k\,s^3+k\,\mu-2\,k\,s\,\mu-s^2\,\mu+k\,s^2\,\mu)},\right.$$
$$y\to\frac{\cdots 1\cdots}{\cdots 1\cdots^{2}\ \cdots 1\cdots},\ z\to\Bigg(k^2+3\,k\,s-4\,k^2\,s+\cdots 1048\cdots+$$
$$\frac{2\,k\,s^5\,\mu^8}{\cdots 1\cdots^{4}\ \cdots 1\cdots\ (\cdots 1\cdots)}-\frac{k^2\,s^5\,\mu^8}{(1-\mu)^4\,(\cdots 1\cdots)\,(k^2\,s+3\,k\,s^2-3\,k^2\,s^2+\cdots 18\cdots+2\,k\,s^3\,\mu-k^2\,s^3\,\mu)}\Bigg)\Big/$$
$$\left.\left.(k^2+3\,k\,s-4\,k^2\,s+2\,s^2-8\,k\,s^2+6\,k^2\,s^2-3\,s^3+7\,k\,s^3-4\,k^2\,s^3+s^4-2\,k\,s^4+\cdots 18\cdots+s^4\,\mu-2\,k\,s^4\,\mu+k^2\,s^4\,\mu+k\,\mu^2+2\,s\,\mu^2-3\,k\,s\,\mu^2-3\,s^2\,\mu^2+3\,k\,s^2\,\mu^2+s^3\,\mu^2-k\,s^3\,\mu^2)\right\}\right\}$$

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In[ ]:=
```
FullSimplify[solutionSymmetric[[1]]]
```

Out[ ]=
$$\left\{y\to\frac{s-k\,(-1+s)\,(1+x\,(-1+\mu))+s\,x\,(-1+\mu)-\mu}{(k\,(-1+s)-s)\,(-1+\mu)},\ z\to-\frac{(-1+k)\,(-1+s)\,\mu}{(k+s-k\,s)\,(-1+\mu)}\right\}$$

In[ ]:=
```
FullSimplify[solutionSymmetric[[2]]]
```

Out[ ]=
$$\{x\to 0,\ y\to 0,\ z\to 1\}$$

In[ ]:=
```
FullSimplify[solutionSymmetric[[4]]]
```

Out[ ]=
$$\left\{x\to-\frac{(-1+s)\,\mu\,\left(k\,(-1+s)^2-(s-\mu)\,(-2+s+\mu)\right)}{(-1+\mu)^2\,\left(-s^2\,(-2+s+\mu)+k\,(-1+s)^2\,(s+\mu)\right)},\right.$$
$$y\to-\frac{(-1+s)\,\mu\,\left(k\,(-1+s)^2-(s-\mu)\,(-2+s+\mu)\right)}{(-1+\mu)^2\,\left(-s^2\,(-2+s+\mu)+k\,(-1+s)^2\,(s+\mu)\right)},$$
$$\left.z\to\frac{(-1+k)\,(-1+s)^2\,\mu^2\,(-2+s+\mu)}{(-1+\mu)^2\,\left(-s^2\,(-2+s+\mu)+k\,(-1+s)^2\,(s+\mu)\right)}\right\}$$

With equal selection coefficients and mutation rates in both loci equilibria 2 and 3 merge in a single line. The condition for this merge can be found by equating leading eigenvalues of solutions 2 and 3. The resulting ratio of parameters divides the space of parameters in two regions: in one, at locus A the selection pressure is lower and/or mutation pressure is higher. In another, the same is true for locus B. The boarder of this two regions is described by the following relation:

t+m(1-t) == s+n(1-s)

At the boarder equilibrium 2 and 3 are merged in one line:

In[•]:=
```
FullSimplify[solutionSymmetric[[1]]]
```

Out[•]= $$\left\{y\to\frac{s-k\,(-1+s)\,(1+x\,(-1+\mu))+s\,x\,(-1+\mu)-\mu}{(k\,(-1+s)-s)\,(-1+\mu)},\ z\to-\frac{(-1+k)\,(-1+s)\,\mu}{(k+s-k\,s)\,(-1+\mu)}\right\}$$

This line means that all frequencies of Ab and aB that satisfy the equation, are equilibria of the system.

The line captures the result that was obtained by Charlesworths&Charlesworth in 1997. They showed that after a click of Muller’s ratchet fixation of one deleterious allele occurs. As they assumed equal selection coefficients and mutation rates, the fixation seemed to be governed by random drift. But from the above analysis it is clear that they restricted the system to the boarder of two parametric regions, at which eq.2 and 3 are merged in one equilibria.

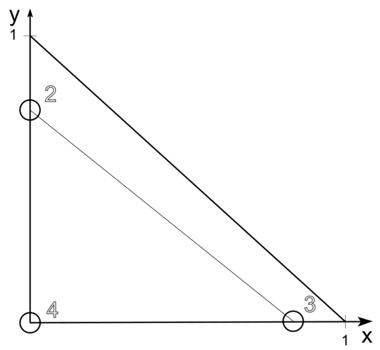
Let’s see what happens in more general case of arbitrary selection coefficients and mutation rates if we do random drift’s work manually and get rid of the best genotype AB.

Click of Muller’s ratchet

If AB is absent, then z = 1-x-y (a click of Muller’s ratchet). Equilibrium 1 (solution 4 in this notebook) disappears.

In[•]:=
```
RatchetClick = Solve[X2[x, y, z][s, t, k, μ, ν] == x &&
   Y2[x, y, z][s, t, k, μ, ν] == y && z == 1 - x - y, {x, y, z}]
```

Out[•]= $$\left\{\{x\to0,\ y\to0,\ z\to1\},\ \left\{x\to0,\ y\to\frac{k+t-k\,t-\nu}{(-k-t+k\,t)\,(-1+\nu)},\ z\to\frac{(-1+k)\,(-1+t)\,\nu}{(-k-t+k\,t)\,(-1+\nu)}\right\},\right.$$
$$\left.\left\{x\to\frac{k+s-k\,s-\mu}{(-k-s+k\,s)\,(-1+\mu)},\ y\to0,\ z\to\frac{(-1+k)\,(-1+s)\,\mu}{(-k-s+k\,s)\,(-1+\mu)}\right\}\right\}$$



As eq.4 no longer exists, either eq.2 or 3, corresponding to the fixation of deleterious allele either at locus A or B, will be stable. The stability depends on relation of the two eigenvalues: $\frac{1-m}{1-s} <> \frac{1-n}{1-t}$.

In[•]:=
```
Eigenvalues[Simplify[
  Table[D[fun, var], {fun, {X2[x, y, z][s, t, k, μ, ν], Y2[x, y, z][s, t, k, μ, ν],
     Z2[x, y, z][s, t, k, μ, ν]}}, {var, {x, y, z}}] /. RatchetClick[[2]]], -1]
```

Out[•]= $$\left\{\frac{-1+\mu}{-1+s}\right\}$$

In[•]:=
```
Eigenvalues[Simplify[
  Table[D[fun, var], {fun, {X2[x, y, z][s, t, k, μ, ν], Y2[x, y, z][s, t, k, μ, ν],
     Z2[x, y, z][s, t, k, μ, ν]}}, {var, {x, y, z}}] /. RatchetClick[[3]]], -1]
```

Out[•]= $\left\{\frac{-1+\nu}{-1+t}\right\}$

If two eigenvalues are equal, particularly if selection coefficients and mutation rates in both loci are identical, equilibria 2 and 3 are merged in one line, and in this case the fixation of deleterious allele after the click of Muller’s ratchet is governed by random drift, as was shown in Charlesworth&Charlesworth 1997.

In[•]:=
```
SymmetricRatchetClick = Solve[X2[x, y, z][s, s, k, μ, μ] == x &&
   Y2[x, y, z][s, s, k, μ, μ] == y && z == 1 - x - y, {x, y, z}]
```

Solve: Equations may not give solutions for all "solve" variables.

Out[•]= $$\left\{\left\{y\to\frac{k+s-k\,s-k\,x-s\,x+k\,s\,x-\mu+k\,x\,\mu+s\,x\,\mu-k\,s\,x\,\mu}{(-k-s+k\,s)\,(-1+\mu)},\ z\to\frac{(-1+k)\,(-1+s)\,\mu}{(-k-s+k\,s)\,(-1+\mu)}\right\},\right.$$
$$\left.\{x\to 0,\ y\to 0,\ z\to 1\},\ \left\{x\to 0,\ y\to\frac{k+s-k\,s-\mu}{(-k-s+k\,s)\,(-1+\mu)},\ z\to\frac{(-1+k)\,(-1+s)\,\mu}{(-k-s+k\,s)\,(-1+\mu)}\right\}\right\}$$

In[•]:=
```
FullSimplify[solutionSymmetric[[1]]]
```

Out[•]= $$\left\{y\to\frac{s-k\,(-1+s)\,(1+x\,(-1+\mu))+s\,x\,(-1+\mu)-\mu}{(k\,(-1+s)-s)\,(-1+\mu)},\ z\to-\frac{(-1+k)\,(-1+s)\,\mu}{(k+s-k\,s)\,(-1+\mu)}\right\}$$

In[•]:=
```
FullSimplify[solutionSymmetric[[2]]]
```

Out[•]= $\{x\to 0,\ y\to 0,\ z\to 1\}$

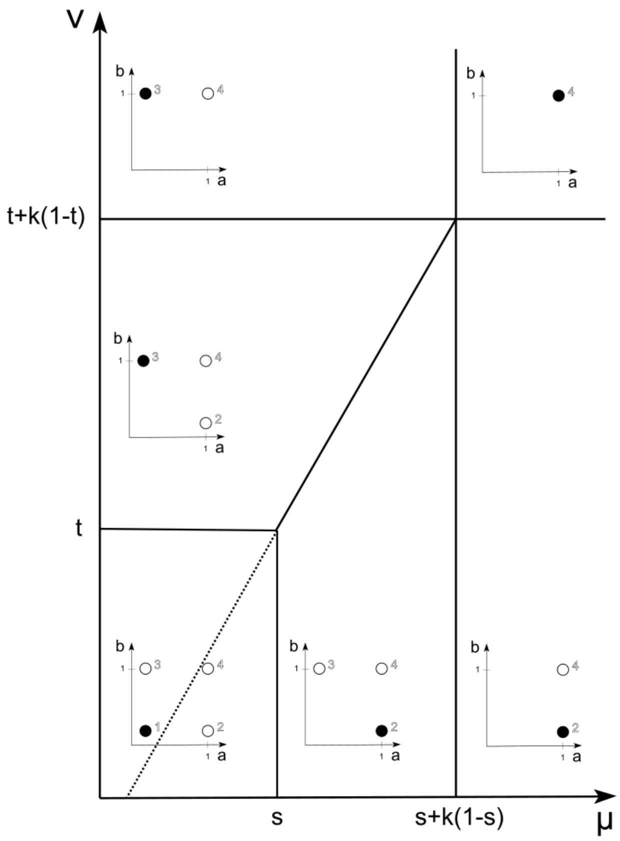
In[•]:=
```
FullSimplify[solutionSymmetric[[4]]]
```

Out[•]= $$\left\{x\to-\frac{(-1+s)\,\mu\,\left(k\,(-1+s)^2-(s-\mu)\,(-2+s+\mu)\right)}{(-1+\mu)^2\left(-s^2\,(-2+s+\mu)+k\,(-1+s)^2\,(s+\mu)\right)},\right.$$
$$y\to-\frac{(-1+s)\,\mu\,\left(k\,(-1+s)^2-(s-\mu)\,(-2+s+\mu)\right)}{(-1+\mu)^2\left(-s^2\,(-2+s+\mu)+k\,(-1+s)^2\,(s+\mu)\right)},$$
$$\left.z\to\frac{(-1+k)\,(-1+s)^2\,\mu^2\,(-2+s+\mu)}{(-1+\mu)^2\left(-s^2\,(-2+s+\mu)+k\,(-1+s)^2\,(s+\mu)\right)}\right\}$$

Parametric portrait

Here we describe the full parametric portrait of the system.

k>0



Existence of equilibria:

(with k = 0.001 and t = s = 0.1, “epistatic selection coefficients” s + k(1-s) = t + k(1-t) = 0.1009)

***v* < t:** *μ* grows, while *v* is less than t

***μ* < s**: all four equilibria exist

```
In[ ]:= AB1[0.01, 0.02, 0.1, 0.1, 0.001]
Out[ ]= 0

In[ ]:= Ab1[0.01, 0.02, 0.1, 0.1, 0.001]
Out[ ]= 0

In[ ]:= aB1[0.01, 0.02, 0.1, 0.1, 0.001]
Out[ ]= 0

In[ ]:= ab1[0.01, 0.02, 0.1, 0.1, 0.001]
Out[ ]= 1

In[ ]:= AB2[0.01, 0.02, 0.1, 0.1, 0.001]
Out[ ]= 0

In[ ]:= Ab2[0.01, 0.02, 0.1, 0.1, 0.001]
Out[ ]= 0
```

In[•]:= `aB2[0.01, 0.02, 0.1, 0.1, 0.001]`

Out[•]= `0.818147`

In[•]:= `ab2[0.01, 0.02, 0.1, 0.1, 0.001]`

Out[•]= `0.181853`

In[•]:= `AB3[0.01, 0.02, 0.1, 0.1, 0.001]`

Out[•]= `0`

In[•]:= `Ab3[0.01, 0.02, 0.1, 0.1, 0.001]`

Out[•]= `0.909992`

In[•]:= `aB3[0.01, 0.02, 0.1, 0.1, 0.001]`

Out[•]= `0`

In[•]:= `ab3[0.0100, 0.02, 0.1, 0.1, 0.001]`

Out[•]= `0.0900081`

In[•]:= `AB4[0.01, 0.02, 0.1, 0.1, 0.001]`

Out[•]= `0.74219`

In[•]:= `Ab4[0.01, 0.02, 0.1, 0.1, 0.001]`

Out[•]= `0.166993`

In[•]:= `aB4[0.01, 0.02, 0.1, 0.1, 0.001]`

Out[•]= `0.074219`

In[•]:= `ab4[0.0100, 0.02, 0.1, 0.1, 0.001]`

Out[•]= `0.0165986`

s<μ<s+k(1-s): polymorphic eq. disappears

In[•]:= `AB1[0.1008, 0.01, 0.1, 0.1, 0.001]`

Out[•]= `0`

In[•]:= `Ab1[0.1008, 0.01, 0.1, 0.1, 0.001]`

Out[•]= `0`

In[•]:= `aB1[0.1008, 0.01, 0.1, 0.1, 0.001]`

Out[•]= `0`

In[•]:= `ab1[0.1008, 0.01, 0.1, 0.1, 0.001]`

Out[•]= `1`

In[•]:= `AB2[0.1008, 0.01, 0.1, 0.1, 0.001]`

Out[•]= `0`

In[•]:= `Ab2[0.1008, 0.01, 0.1, 0.1, 0.001]`

Out[•]= `0`

In[ ]:= `aB2[0.1008, 0.01, 0.1, 0.1, 0.001]`

Out[ ]= 0.909992

In[ ]:= `ab2[0.1008, 0.01, 0.1, 0.1, 0.001]`

Out[ ]= 0.0900081

In[ ]:= `AB3[0.1008, 0.01, 0.1, 0.1, 0.001]`

Out[ ]= 0

In[ ]:= `Ab3[0.1008, 0.01, 0.1, 0.1, 0.001]`

Out[ ]= 0.00110218

In[ ]:= `aB3[0.1008, 0.01, 0.1, 0.1, 0.001]`

Out[ ]= 0

In[ ]:= `ab3[0.1008, 0.01, 0.1, 0.1, 0.001]`

Out[ ]= 0.998898

In[ ]:= `AB4[0.1008, 0.01, 0.1, 0.1, 0.001]`

Out[ ]= -0.00809616

s+k(1-s)<*μ*: additionally, eq.3 disappears:

In[ ]:= `Ab2[0.2, 0.01, 0.1, 0.1, 0.001]`

Out[ ]= 0

In[ ]:= `aB2[0.2, 0.01, 0.1, 0.1, 0.001]`

Out[ ]= 0.909992

In[ ]:= `ab2[0.2, 0.01, 0.1, 0.1, 0.001]`

Out[ ]= 0.0900081

In[ ]:= `Ab3[0.2, 0.01, 0.1, 0.1, 0.001]`

Out[ ]= -1.2277

In[ ]:= `AB4[0.2, 0.01, 0.1, 0.1, 0.001]`

Out[ ]= -1.12575

t < ν < t+k(1-t): *μ* grows, while *ν* is more than t, but less than t+k(1-t)

***μ* < s:** eq.4 disappears

In[ ]:= `AB1[0.01, 0.1008, 0.1, 0.1, 0.001]`

Out[ ]= 0

In[ ]:= `Ab1[0.01, 0.1008, 0.1, 0.1, 0.001]`

Out[ ]= 0

In[ ]:= `aB1[0.01, 0.1008, 0.1, 0.1, 0.001]`

Out[ ]= 0

```
In[ ]:= ab1[0.01, 0.1008, 0.1, 0.1, 0.001]
Out[ ]= 1

In[ ]:= AB2[0.01, 0.1008, 0.1, 0.1, 0.001]
Out[ ]= 0

In[ ]:= Ab2[0.01, 0.1008, 0.1, 0.1, 0.001]
Out[ ]= 0

In[ ]:= aB2[0.01, 0.1008, 0.1, 0.1, 0.001]
Out[ ]= 0.00110218

In[ ]:= ab2[0.01, 0.1008, 0.1, 0.1, 0.001]
Out[ ]= 0.998898

In[ ]:= AB3[0.01, 0.1008, 0.1, 0.1, 0.001]
Out[ ]= 0

In[ ]:= Ab3[0.01, 0.1008, 0.1, 0.1, 0.001]
Out[ ]= 0.909992

In[ ]:= aB3[0.01, 0.1008, 0.1, 0.1, 0.001]
Out[ ]= 0

In[ ]:= ab3[0.01, 0.1008, 0.1, 0.1, 0.001]
Out[ ]= 0.0900081

In[ ]:= AB4[0.01, 0.1008, 0.1, 0.1, 0.001]
Out[ ]= -0.00809616
```

$s < \mu < (s+v(1-s)-t)/(1-t)$: μ is more than s, but less than the line, which divides two regimes (see figure for clarification); nothing new: only 3 equilibria exist

```
In[ ]:= AB1[0.1007, 0.1008, 0.1, 0.1, 0.001]
Out[ ]= 0

In[ ]:= Ab1[0.1007, 0.1008, 0.1, 0.1, 0.001]
Out[ ]= 0

In[ ]:= aB1[0.1007, 0.1008, 0.1, 0.1, 0.001]
Out[ ]= 0

In[ ]:= ab1[0.1007, 0.1008, 0.1, 0.1, 0.001]
Out[ ]= 1

In[ ]:= AB2[0.1007, 0.1008, 0.1, 0.1, 0.001]
Out[ ]= 0
```

```
In[ ]:= Ab2[0.1007, 0.1008, 0.1, 0.1, 0.001]
Out[ ]= 0

In[ ]:= aB2[0.1007, 0.1008, 0.1, 0.1, 0.001]
Out[ ]= 0.00110218

In[ ]:= ab2[0.1007, 0.1008, 0.1, 0.1, 0.001]
Out[ ]= 0.998898

In[ ]:= AB3[0.1007, 0.1008, 0.1, 0.1, 0.001]
Out[ ]= 0

In[ ]:= Ab3[0.1007, 0.1008, 0.1, 0.1, 0.001]
Out[ ]= 0.00220411

In[ ]:= aB3[0.1007, 0.1008, 0.1, 0.1, 0.001]
Out[ ]= 0

In[ ]:= ab3[0.1007, 0.1008, 0.1, 0.1, 0.001]
Out[ ]= 0.997796

In[ ]:= Ab4[0.1007, 0.1008, 0.1, 0.1, 0.001]
Out[ ]= -0.00311116
```

μ = (s+v(1-s)-t)/(1-t): parameters in both loci equilibrate each other

```
In[ ]:= AB1[0.1008, 0.1008, 0.1, 0.1, 0.001]
Out[ ]= 0

In[ ]:= Ab1[0.1008, 0.1008, 0.1, 0.1, 0.001]
Out[ ]= 0

In[ ]:= aB1[0.1008, 0.1008, 0.1, 0.1, 0.001]
Out[ ]= 0

In[ ]:= ab1[0.1008, 0.1008, 0.1, 0.1, 0.001]
Out[ ]= 1

In[ ]:= AB2[0.1008, 0.1008, 0.1, 0.1, 0.001]
Out[ ]= 0

In[ ]:= Ab2[0.1008, 0.1008, 0.1, 0.1, 0.001]
Out[ ]= 0

In[ ]:= aB2[0.1008, 0.1008, 0.1, 0.1, 0.001]
Out[ ]= 0.00110218

In[ ]:= ab2[0.1008, 0.1008, 0.1, 0.1, 0.001]
Out[ ]= 0.998898
```

```
In[]:= AB3[0.1008, 0.1008, 0.1, 0.1, 0.001]
Out[]= 0

In[]:= Ab3[0.1008, 0.1008, 0.1, 0.1, 0.001]
Out[]= 0.00110218

In[]:= aB3[0.1008, 0.1008, 0.1, 0.1, 0.001]
Out[]= 0

In[]:= ab3[0.1008, 0.1008, 0.1, 0.1, 0.001]
Out[]= 0.998898

In[]:= Ab4[0.1008, 0.1008, 0.1, 0.1, 0.001]
Out[]= -0.00388957
```

(s+v(1-s)-t)/(1-t) < μ < s+k(1-s)

```
In[]:= AB1[0.1008, 0.1007, 0.1, 0.1, 0.001]
Out[]= 0

In[]:= Ab1[0.1008, 0.1007, 0.1, 0.1, 0.001]
Out[]= 0

In[]:= aB1[0.1008, 0.1007, 0.1, 0.1, 0.001]
Out[]= 0

In[]:= ab1[0.1008, 0.1007, 0.1, 0.1, 0.001]
Out[]= 1

In[]:= AB2[0.1008, 0.1007, 0.1, 0.1, 0.001]
Out[]= 0

In[]:= Ab2[0.1008, 0.1007, 0.1, 0.1, 0.001]
Out[]= 0

In[]:= aB2[0.1008, 0.1007, 0.1, 0.1, 0.001]
Out[]= 0.00220411

In[]:= ab2[0.1008, 0.1007, 0.1, 0.1, 0.001]
Out[]= 0.997796

In[]:= AB3[0.1008, 0.1007, 0.1, 0.1, 0.001]
Out[]= 0

In[]:= Ab3[0.1008, 0.1007, 0.1, 0.1, 0.001]
Out[]= 0.00110218

In[]:= aB3[0.1008, 0.1007, 0.1, 0.1, 0.001]
Out[]= 0
```

In[ ]:= **ab3[0.1008, 0.1007, 0.1, 0.1, 0.001]**

Out[ ]= 0.998898

In[ ]:= **Ab4[0.1008, 0.1007, 0.1, 0.1, 0.001]**

Out[ ]= -0.00355209

s+k(1-s) < *μ*: additionally, eq.3 disappears

In[ ]:= **AB1[0.2, 0.1008, 0.1, 0.1, 0.001]**

Out[ ]= 0

In[ ]:= **Ab1[0.2, 0.1008, 0.1, 0.1, 0.001]**

Out[ ]= 0

In[ ]:= **aB1[0.2, 0.1008, 0.1, 0.1, 0.001]**

Out[ ]= 0

In[ ]:= **ab1[0.2, 0.1008, 0.1, 0.1, 0.001]**

Out[ ]= 1

In[ ]:= **AB2[0.2, 0.1008, 0.1, 0.1, 0.001]**

Out[ ]= 0

In[ ]:= **Ab2[0.2, 0.1008, 0.1, 0.1, 0.001]**

Out[ ]= 0

In[ ]:= **aB2[0.2, 0.1008, 0.1, 0.1, 0.001]**

Out[ ]= 0.00110218

In[ ]:= **ab2[0.2, 0.1008, 0.1, 0.1, 0.001]**

Out[ ]= 0.998898

In[ ]:= **Ab3[0.2, 0.1008, 0.1, 0.1, 0.001]**

Out[ ]= -1.2277

In[ ]:= **Ab4[0.2, 0.1008, 0.1, 0.1, 0.001]**

Out[ ]= -1.23861

t+k(1-t) < *v*: *μ* grows, while *v* is more than t+k(1-t)

***μ* < s:** only equilibria 3 and 1 exist

In[ ]:= **AB1[0.01, 0.2, 0.1, 0.1, 0.001]**

Out[ ]= 0

In[ ]:= **Ab1[0.01, 0.2, 0.1, 0.1, 0.001]**

Out[ ]= 0

In[ ]:= **aB1[0.01, 0.2, 0.1, 0.1, 0.001]**

Out[ ]= 0

```
In[ ]:= ab1[0.01, 0.2, 0.1, 0.1, 0.001]
Out[ ]= 1

In[ ]:= aB2[0.01, 0.2, 0.1, 0.1, 0.001]
Out[ ]= -1.2277

In[ ]:= AB4[0.01, 0.2, 0.1, 0.1, 0.001]
Out[ ]= -1.12575

In[ ]:= AB3[0.01, 0.2, 0.1, 0.1, 0.001]
Out[ ]= 0

In[ ]:= Ab3[0.01, 0.2, 0.1, 0.1, 0.001]
Out[ ]= 0.909992

In[ ]:= aB3[0.01, 0.2, 0.1, 0.1, 0.001]
Out[ ]= 0

In[ ]:= ab3[0.01, 0.2, 0.1, 0.1, 0.001]
Out[ ]= 0.0900081
```

$s < \mu < s+k(1-s)$: the same

```
AB1[0.1008, 0.2, 0.1, 0.1, 0.001]
Out[ ]= 0

In[ ]:= Ab1[0.1008, 0.2, 0.1, 0.1, 0.001]
Out[ ]= 0

In[ ]:= aB1[0.1008, 0.2, 0.1, 0.1, 0.001]
Out[ ]= 0

In[ ]:= ab1[0.1008, 0.2, 0.1, 0.1, 0.001]
Out[ ]= 1

In[ ]:= aB2[0.1008, 0.2, 0.1, 0.1, 0.001]
Out[ ]= -1.2277

In[ ]:= Ab4[0.1008, 0.2, 0.1, 0.1, 0.001]
Out[ ]= -0.0196604

In[ ]:= AB3[0.1008, 0.2, 0.1, 0.1, 0.001]
Out[ ]= 0

In[ ]:= Ab3[0.1008, 0.2, 0.1, 0.1, 0.001]
Out[ ]= 0.00110218

In[ ]:= aB3[0.1008, 0.2, 0.1, 0.1, 0.001]
Out[ ]= 0
```

In[ ]:= `ab3[0.1008, 0.2, 0.1, 0.1, 0.001]`

Out[ ]= 0.998898

s+k(1-s) < μ: eq.3 disappears, only eq.1 exist

`AB1[0.2, 0.2, 0.1, 0.1, 0.001]`

Out[ ]= 0

In[ ]:= `Ab1[0.2, 0.2, 0.1, 0.1, 0.001]`

Out[ ]= 0

In[ ]:= `aB1[0.2, 0.2, 0.1, 0.1, 0.001]`

Out[ ]= 0

In[ ]:= `ab1[0.2, 0.2, 0.1, 0.1, 0.001]`

Out[ ]= 1

In[ ]:= `Ab3[0.2, 0.2, 0.1, 0.1, 0.001]`

Out[ ]= -1.2277

In[ ]:= `aB2[0.2, 0.2, 0.1, 0.1, 0.001]`

Out[ ]= -1.2277

In[ ]:= `Ab4[0.2, 0.2, 0.1, 0.1, 0.001]`

Out[ ]= -2.75965

Symmetric bifurcations occur when v grows.

Stability of equilibria:

The case of **μ < s** && **v < t** was studied in the previous sections.

s < μ < s+k(1-s) && μ > (s+v(1-s)-t)/(1-t): equilibrium 2 is stable

In[ ]:= `eig11[0.108, 0.001, 0.1, 0.1, 0.01]`

Out[ ]= 1.11125

In[ ]:= `eig12[0.108, 0.001, 0.1, 0.1, 0.01]`

Out[ ]= 1.12121

In[ ]:= `eig13[0.108, 0.001, 0.1, 0.1, 0.01]`

Out[ ]= 1.00112

In[ ]:= `eig21[0.108, 0.001, 0.1, 0.1, 0.01]`

Out[ ]= 0.991111

In[ ]:= `eig22[0.108, 0.001, 0.1, 0.1, 0.01]`

Out[ ]= 0.892893

In[ ]:= `eig23[0.108, 0.001, 0.1, 0.1, 0.01]`

Out[ ]= 0.891892

In[ ]:= `eig31[0.108, 0.001, 0.1, 0.1, 0.01]`

Out[ ]= 1.11

In[ ]:= `eig32[0.108, 0.001, 0.1, 0.1, 0.01]`

Out[ ]= 1.11996

In[ ]:= `eig33[0.108, 0.001, 0.1, 0.1, 0.01]`

Out[ ]= 0.998879

In[ ]:= `eig41[0.108, 0.001, 0.1, 0.1, 0.01]`

Out[ ]= 1.00897

In[ ]:= `eig42[0.108, 0.001, 0.1, 0.1, 0.01]`

Out[ ]= 0.900901

In[ ]:= `eig43[0.108, 0.001, 0.1, 0.1, 0.01]`

Out[ ]= 0.899891

s+k(1-s) < μ && v < t+k(1-t): equilibrium 2 is stable

In[ ]:= `eig11[0.2, 0.108, 0.1, 0.1, 0.01]`

Out[ ]= 0.889887

In[ ]:= `eig12[0.2, 0.108, 0.1, 0.1, 0.01]`

Out[ ]= 1.00112

In[ ]:= `eig13[0.2, 0.108, 0.1, 0.1, 0.01]`

Out[ ]= 0.897868

In[ ]:= `eig21[0.2, 0.108, 0.1, 0.1, 0.01]`

Out[ ]= 0.888889

In[ ]:= `eig22[0.2, 0.108, 0.1, 0.1, 0.01]`

Out[ ]= 0.896861

In[ ]:= `eig23[0.2, 0.108, 0.1, 0.1, 0.01]`

Out[ ]= 0.998879

In[ ]:= `eig31[0.2, 0.108, 0.1, 0.1, 0.01]`

Out[ ]= 0.991111

In[ ]:= `eig32[0.2, 0.108, 0.1, 0.1, 0.01]`

Out[ ]= 1.115

In[ ]:= `eig33[0.2, 0.108, 0.1, 0.1, 0.01]`

Out[ ]= 1.11375

In[ ]:=
```
eig41[0.2, 0.108, 0.1, 0.1, 0.01]
```
Out[ ]= 1.125

In[ ]:=
```
eig42[0.2, 0.108, 0.1, 0.1, 0.01]
```
Out[ ]= 1.00897

In[ ]:=
```
eig43[0.2, 0.108, 0.1, 0.1, 0.01]
```
Out[ ]= 1.12374

t < *v* < t+k(1-t) && ***μ* < (s+*v*(1-s)-t)/(1-t):** equilibrium 3 is stable

In[ ]:=
```
eig11[0.107, 0.108, 0.1, 0.1, 0.01]
```
Out[ ]= 0.993336

In[ ]:=
```
eig12[0.107, 0.108, 0.1, 0.1, 0.01]
```
Out[ ]= 1.00112

In[ ]:=
```
eig13[0.107, 0.108, 0.1, 0.1, 0.01]
```
Out[ ]= 1.00224

In[ ]:=
```
eig21[0.107, 0.108, 0.1, 0.1, 0.01]
```
Out[ ]= 0.992222

In[ ]:=
```
eig22[0.107, 0.108, 0.1, 0.1, 0.01]
```
Out[ ]= 1.00112

In[ ]:=
```
eig23[0.107, 0.108, 0.1, 0.1, 0.01]
```
Out[ ]= 0.998879

In[ ]:=
```
eig31[0.107, 0.108, 0.1, 0.1, 0.01]
```
Out[ ]= 0.991111

In[ ]:=
```
eig32[0.107, 0.108, 0.1, 0.1, 0.01]
```
Out[ ]= 0.99888

In[ ]:=
```
eig33[0.107, 0.108, 0.1, 0.1, 0.01]
```
Out[ ]= 0.99776

In[ ]:=
```
eig41[0.107, 0.108, 0.1, 0.1, 0.01]
```
Out[ ]= 1.00784

In[ ]:=
```
eig42[0.107, 0.108, 0.1, 0.1, 0.01]
```
Out[ ]= 1.00897

In[ ]:=
```
eig43[0.107, 0.108, 0.1, 0.1, 0.01]
```
Out[ ]= 1.00671

t+k(1-t) < ν && ***μ* < s+k(1-s):** equilibrium 3 is stable

In[ ]:= **eig11[0.107, 0.2, 0.1, 0.1, 0.01]**

Out[ ]= 0.890884

In[ ]:= **eig12[0.107, 0.2, 0.1, 0.1, 0.01]**

Out[ ]= 0.897868

In[ ]:= **eig13[0.107, 0.2, 0.1, 0.1, 0.01]**

Out[ ]= 1.00224

In[ ]:= **eig21[0.107, 0.2, 0.1, 0.1, 0.01]**

Out[ ]= 0.992222

In[ ]:= **eig22[0.107, 0.2, 0.1, 0.1, 0.01]**

Out[ ]= 1.11625

In[ ]:= **eig23[0.107, 0.2, 0.1, 0.1, 0.01]**

Out[ ]= 1.11375

In[ ]:= **eig31[0.107, 0.2, 0.1, 0.1, 0.01]**

Out[ ]= 0.888889

In[ ]:= **eig32[0.107, 0.2, 0.1, 0.1, 0.01]**

Out[ ]= 0.895857

In[ ]:= **eig33[0.107, 0.2, 0.1, 0.1, 0.01]**

Out[ ]= 0.99776

In[ ]:= **eig41[0.107, 0.2, 0.1, 0.1, 0.01]**

Out[ ]= 1.00784

In[ ]:= **eig42[0.107, 0.2, 0.1, 0.1, 0.01]**

Out[ ]= 1.125

In[ ]:= **eig43[0.107, 0.2, 0.1, 0.1, 0.01]**

Out[ ]= 1.12248

t+k(1-t) < ν && **s+k(1-s) < μ:** equilibrium 4 (solution 1) is stable

In[ ]:= **eig11[0.11, 0.2, 0.1, 0.1, 0.01]**

Out[ ]= 0.887891

In[ ]:= **eig12[0.11, 0.2, 0.1, 0.1, 0.01]**

Out[ ]= 0.897868

In[ ]:= **eig13[0.11, 0.2, 0.1, 0.1, 0.01]**

Out[ ]= 0.998878

In[ ]:= **eig21[0.11, 0.2, 0.1, 0.1, 0.01]**

Out[ ]= 0.988889

In[∘]:= `eig22[0.11, 0.2, 0.1, 0.1, 0.01]`

Out[∘]= 1.1125

In[∘]:= `eig23[0.11, 0.2, 0.1, 0.1, 0.01]`

Out[∘]= 1.11375

In[∘]:= `eig31[0.11, 0.2, 0.1, 0.1, 0.01]`

Out[∘]= 0.888889

In[∘]:= `eig32[0.11, 0.2, 0.1, 0.1, 0.01]`

Out[∘]= 0.898876

In[∘]:= `eig33[0.11, 0.2, 0.1, 0.1, 0.01]`

Out[∘]= 1.00112

In[∘]:= `eig41[0.11, 0.2, 0.1, 0.1, 0.01]`

Out[∘]= 1.01124

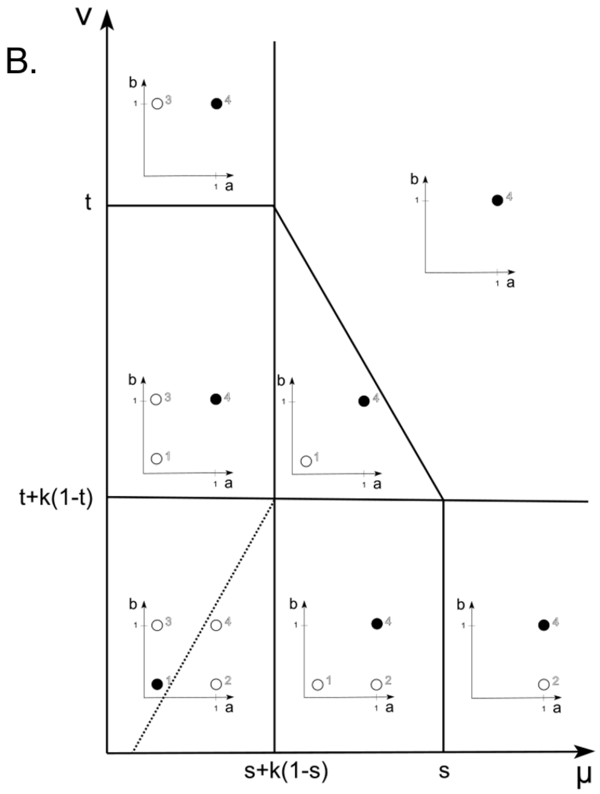
In[∘]:= `eig42[0.11, 0.2, 0.1, 0.1, 0.01]`

Out[∘]= 1.125

In[∘]:= `eig43[0.11, 0.2, 0.1, 0.1, 0.01]`

Out[∘]= 1.12626

k<0



Existence of equilibria:

(with k = -0.01 and t = s = 0.1, “epistatic selection coefficients” s + k(1-s) = t + k(1-t) = 0.091)

***ν* < t+k(1-t):** *μ* grows, while *ν* is less than t+k(1-t)

***μ* < s + k(1-s)**: all four equilibria exist

In[∘]:= **AB4[0.001, 0.001, 0.1, 0.1, -0.01]**

Out[∘]= 0.982059

In[∘]:= **Ab4[0.001, 0.001, 0.1, 0.1, -0.01]**

Out[∘]= 0.00892781

In[∘]:= **aB4[0.001, 0.001, 0.1, 0.1, -0.01]**

Out[∘]= 0.00892781

In[∘]:= **ab4[0.001, 0.001, 0.1, 0.1, -0.01]**

Out[∘]= 0.0000856643

In[∘]:= **AB3[0.001, 0.001, 0.1, 0.1, -0.01]**

Out[∘]= 0

In[∘]:= **Ab3[0.001, 0.001, 0.1, 0.1, -0.01]**

Out[∘]= 0.990001

In[∘]:= **aB3[0.001, 0.001, 0.1, 0.1, -0.01]**

Out[∘]= 0

In[∘]:= **ab3[0.001, 0.001, 0.1, 0.1, -0.01]**

Out[∘]= 0.00999901

In[∘]:= **AB2[0.001, 0.001, 0.1, 0.1, -0.01]**

Out[∘]= 0

In[∘]:= **Ab2[0.001, 0.001, 0.1, 0.1, -0.01]**

Out[∘]= 0

In[∘]:= **aB2[0.001, 0.001, 0.1, 0.1, -0.01]**

Out[∘]= 0.990001

In[∘]:= **ab2[0.001, 0.001, 0.1, 0.1, -0.01]**

Out[∘]= 0.00999901

In[∘]:= **AB1[0.001, 0.001, 0.1, 0.1, -0.01]**

Out[∘]= 0

In[∘]:= **Ab1[0.001, 0.001, 0.1, 0.1, -0.01]**

Out[∘]= 0

In[∘]:= **aB1[0.001, 0.001, 0.1, 0.1, -0.01]**

Out[∘]= 0

In[ ]:= `ab1[0.001, 0.001, 0.1, 0.1, -0.01]`

Out[ ]= 1

$s + k(1\text{-}s) < \mu < s$: eq.3 disappears

In[ ]:= `Ab3[0.095, 0.001, 0.1, 0.1, -0.01]`

Out[ ]= -0.0485702

In[ ]:= `AB4[0.095, 0.001, 0.1, 0.1, -0.01]`

Out[ ]= 0.0547019

In[ ]:= `Ab4[0.095, 0.001, 0.1, 0.1, -0.01]`

Out[ ]= 0.00049729

In[ ]:= `aB4[0.095, 0.001, 0.1, 0.1, -0.01]`

Out[ ]= 0.935403

In[ ]:= `ab4[0.095, 0.001, 0.1, 0.1, -0.01]`

Out[ ]= 0.00939768

In[ ]:= `AB2[0.095, 0.001, 0.1, 0.1, -0.01]`

Out[ ]= 0

In[ ]:= `Ab2[0.095, 0.001, 0.1, 0.1, -0.01]`

Out[ ]= 0

In[ ]:= `aB2[0.095, 0.001, 0.1, 0.1, -0.01]`

Out[ ]= 0.990001

In[ ]:= `ab2[0.095, 0.001, 0.1, 0.1, -0.01]`

Out[ ]= 0.00999901

In[ ]:= `AB1[0.095, 0.001, 0.1, 0.1, -0.01]`

Out[ ]= 0

In[ ]:= `Ab1[0.095, 0.001, 0.1, 0.1, -0.01]`

Out[ ]= 0

In[ ]:= `aB1[0.095, 0.001, 0.1, 0.1, -0.01]`

Out[ ]= 0

In[ ]:= `ab1[0.095, 0.001, 0.1, 0.1, -0.01]`

Out[ ]= 1

$s < \mu$: additionally, eq.4 (polymorphic) disappears

In[ ]:= `AB4[0.12, 0.001, 0.1, 0.1, -0.01]`

Out[ ]= -0.224867

In[ ]:= **Ab3[0.12, 0.001, 0.1, 0.1, -0.01]**

Out[ ]= -0.362138

In[ ]:= **AB2[0.12, 0.001, 0.1, 0.1, -0.01]**

Out[ ]= 0

In[ ]:= **Ab2[0.12, 0.001, 0.1, 0.1, -0.01]**

Out[ ]= 0

In[ ]:= **aB2[0.12, 0.001, 0.1, 0.1, -0.01]**

Out[ ]= 0.990001

In[ ]:= **ab2[0.12, 0.001, 0.1, 0.1, -0.01]**

Out[ ]= 0.00999901

In[ ]:= **AB1[0.12, 0.001, 0.1, 0.1, -0.01]**

Out[ ]= 0

In[ ]:= **Ab1[0.12, 0.001, 0.1, 0.1, -0.01]**

Out[ ]= 0

In[ ]:= **aB1[0.12, 0.001, 0.1, 0.1, -0.01]**

Out[ ]= 0

In[ ]:= **ab1[0.12, 0.001, 0.1, 0.1, -0.01]**

Out[ ]= 1

t+k(1-t) < *v* < t: *μ* grows, while *v* is between t+k(1-t) and t

***μ* < s + k(1-s)**: eq.2 disappears

In[ ]:= **aB2[0.09, 0.0992, 0.1, 0.1, -0.01]**

Out[ ]= -0.100033

In[ ]:= **AB4[0.09, 0.0992, 0.1, 0.1, -0.01]**

Out[ ]= 0.000179332

In[ ]:= **Ab4[0.09, 0.0992, 0.1, 0.1, -0.01]**

Out[ ]= 0.0200134

In[ ]:= **aB4[0.09, 0.0992, 0.1, 0.1, -0.01]**

Out[ ]= 0.00145259

In[ ]:= **ab4[0.09, 0.0992, 0.1, 0.1, -0.01]**

Out[ ]= 0.978355

In[ ]:= **AB3[0.09, 0.0992, 0.1, 0.1, -0.01]**

Out[ ]= 0

In[ ]:= `Ab3[0.09, 0.0992, 0.1, 0.1, -0.01]`

Out[ ]= 0.0120758

In[ ]:= `aB3[0.09, 0.0992, 0.1, 0.1, -0.01]`

Out[ ]= 0

In[ ]:= `ab3[0.09, 0.0992, 0.1, 0.1, -0.01]`

Out[ ]= 0.987924

In[ ]:= `AB1[0.09, 0.0992, 0.1, 0.1, -0.01]`

Out[ ]= 0

In[ ]:= `Ab1[0.09, 0.0992, 0.1, 0.1, -0.01]`

Out[ ]= 0

In[ ]:= `aB1[0.09, 0.0992, 0.1, 0.1, -0.01]`

Out[ ]= 0

In[ ]:= `ab1[0.09, 0.0992, 0.1, 0.1, -0.01]`

Out[ ]= 1

$\mathbf{s + k(1\text{-}s) < \mu < -\frac{v-t}{1-t}(1-s) + s + k(1-s)}$: additionally, eq.3 disappears

In[ ]:= `Ab3[0.0993, 0.0992, 0.1, 0.1, -0.001]`

Out[ ]= -0.00224066

In[ ]:= `aB2[0.0993, 0.0992, 0.1, 0.1, -0.001]`

Out[ ]= -0.00112021

In[ ]:= `AB4[0.0993, 0.0992, 0.1, 0.1, -0.001]`

Out[ ]= 0.0000278753

In[ ]:= `Ab4[0.0993, 0.0992, 0.1, 0.1, -0.001]`

Out[ ]= 0.00311088

In[ ]:= `aB4[0.0993, 0.0992, 0.1, 0.1, -0.001]`

Out[ ]= 0.00355888

In[ ]:= `ab4[0.0993, 0.0992, 0.1, 0.1, -0.001]`

Out[ ]= 0.993302

In[ ]:= `AB1[0.0993, 0.0992, 0.1, 0.1, -0.001]`

Out[ ]= 0

In[ ]:= `Ab1[0.0993, 0.0992, 0.1, 0.1, -0.001]`

Out[ ]= 0

In[ ]:= `aB1[0.0993, 0.0992, 0.1, 0.1, -0.001]`

Out[ ]= 0

In[∘]:= `ab1[0.0993, 0.0992, 0.1, 0.1, -0.001]`

Out[∘]= 1

$-\frac{v-t}{1-t}(1-s)+s+k(1-s)<\mu<s$: additionally, eq.4 disappears, only eq.1 is left

In[∘]:= `AB4[0.09999, 0.0992, 0.1, 0.1, -0.001]`

Out[∘]= -1.10624×10^{-7}

In[∘]:= `Ab3[0.09999, 0.0992, 0.1, 0.1, -0.001]`

Out[∘]= -0.00997859

In[∘]:= `aB2[0.09999, 0.0992, 0.1, 0.1, -0.001]`

Out[∘]= -0.00112021

In[∘]:= `AB1[0.09999, 0.0992, 0.1, 0.1, -0.001]`

Out[∘]= 0

In[∘]:= `Ab1[0.09999, 0.0992, 0.1, 0.1, -0.001]`

Out[∘]= 0

In[∘]:= `aB1[0.09999, 0.0992, 0.1, 0.1, -0.001]`

Out[∘]= 0

In[∘]:= `ab1[0.09999, 0.0992, 0.1, 0.1, -0.001]`

Out[∘]= 1

$s<\mu$: nothing changes

In[∘]:= `AB4[0.11, 0.0992, 0.1, 0.1, -0.001]`

Out[∘]= -0.00110524

In[∘]:= `Ab3[0.11, 0.0992, 0.1, 0.1, -0.001]`

Out[∘]= -0.123584

In[∘]:= `aB2[0.11, 0.0992, 0.1, 0.1, -0.001]`

Out[∘]= -0.00112021

In[∘]:= `AB1[0.11, 0.0992, 0.1, 0.1, -0.001]`

Out[∘]= 0

In[∘]:= `Ab1[0.11, 0.0992, 0.1, 0.1, -0.001]`

Out[∘]= 0

In[∘]:= `aB1[0.11, 0.0992, 0.1, 0.1, -0.001]`

Out[∘]= 0

In[∘]:= `ab1[0.11, 0.0992, 0.1, 0.1, -0.001]`

Out[∘]= 1

$t<v$: μ grows, while v is more than t

μ < s + k(1-s): eq.2 and eq.4 disappear

In[ ]:= **aB2[0.09, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= -0.234597

In[ ]:= **AB4[0.09, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= -0.559376

In[ ]:= **AB3[0.09, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= 0

In[ ]:= **Ab3[0.09, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= 0.0120758

In[ ]:= **aB3[0.09, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= 0

In[ ]:= **ab3[0.09, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= 0.987924

In[ ]:= **AB1[0.09, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= 0

In[ ]:= **Ab1[0.09, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= 0

In[ ]:= **aB1[0.09, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= 0

In[ ]:= **ab1[0.09, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= 1

s + k(1-s) < μ < s: additionally, eq.3 disappears, only eq.1 is left

In[ ]:= **Ab3[0.092, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= -0.0121024

In[ ]:= **aB2[0.092, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= -0.234597

In[ ]:= **AB4[0.092, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= -0.0554169

In[ ]:= **AB1[0.092, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= 0

In[ ]:= **Ab1[0.092, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= 0

In[ ]:= **aB1[0.092, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= 0

In[ ]:= **ab1[0.092, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= 1

s < *μ*: nothing changes

In[ ]:= **Ab3[0.11, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= -0.234597

In[ ]:= **aB2[0.11, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= -0.234597

In[ ]:= **Ab4[0.11, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= -0.200604

In[ ]:= **AB1[0.11, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= 0

In[ ]:= **Ab1[0.11, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= 0

In[ ]:= **aB1[0.11, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= 0

In[ ]:= **ab1[0.11, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= 1

Symmetric bifurcations occur when *v* grows.

Stability of equilibria:

***μ* < s + k(1-s)** && ***v* < t + k(1-t):** equilibrium 4 (polymorphic) is stable

In[ ]:= **eig11[0.001, 0.098, 0.1, 0.1, -0.01]**

Out[ ]= 1.10145

In[ ]:= **eig12[0.001, 0.098, 0.1, 0.1, -0.01]**

Out[ ]= 0.992299

In[ ]:= **eig13[0.001, 0.098, 0.1, 0.1, -0.01]**

Out[ ]= 1.09901

In[ ]:= **eig21[0.001, 0.098, 0.1, 0.1, -0.01]**

Out[ ]= 1.11

In[ ]:= **eig22[0.001, 0.098, 0.1, 0.1, -0.01]**

Out[ ]= 1.10754

In[ ]:= `eig23[0.001, 0.098, 0.1, 0.1, -0.01]`

Out[ ]= 1.00776

In[ ]:= `eig31[0.001, 0.098, 0.1, 0.1, -0.01]`

Out[ ]= 1.00222

In[ ]:= `eig32[0.001, 0.098, 0.1, 0.1, -0.01]`

Out[ ]= 0.902903

In[ ]:= `eig33[0.001, 0.098, 0.1, 0.1, -0.01]`

Out[ ]= 0.90991

In[ ]:= `eig41[0.001, 0.098, 0.1, 0.1, -0.01]`

Out[ ]= 0.900901

In[ ]:= `eig42[0.001, 0.098, 0.1, 0.1, -0.01]`

Out[ ]= 0.997783

In[ ]:= `eig43[0.001, 0.098, 0.1, 0.1, -0.01]`

Out[ ]= 0.907892

s + k(1-s) < μ < s && v < t + k(1-t): equilibrium 1 is stable

In[ ]:= `eig11[0.0992, 0.098, 0.1, 0.1, -0.01]`

Out[ ]= 0.993181

In[ ]:= `eig12[0.0992, 0.098, 0.1, 0.1, -0.01]`

Out[ ]= 0.992299

In[ ]:= `eig13[0.0992, 0.098, 0.1, 0.1, -0.01]`

Out[ ]= 0.990979

In[ ]:= `eig21[0.0992, 0.098, 0.1, 0.1, -0.01]`

Out[ ]= 1.00089

In[ ]:= `eig22[0.0992, 0.098, 0.1, 0.1, -0.01]`

Out[ ]= 0.99867

In[ ]:= `eig23[0.0992, 0.098, 0.1, 0.1, -0.01]`

Out[ ]= 1.00776

In[ ]:= `eig31[0.0992, 0.098, 0.1, 0.1, -0.01]`

Out[ ]= 1.00222

In[ ]:= `eig32[0.0992, 0.098, 0.1, 0.1, -0.01]`

Out[ ]= 1.00133

In[ ]:= `eig33[0.0992, 0.098, 0.1, 0.1, -0.01]`

Out[ ]= 1.0091

In[ ]:= **eig41[0.0992, 0.098, 0.1, 0.1, -0.01]**

Out[ ]= 0.999112

In[ ]:= **eig42[0.0992, 0.098, 0.1, 0.1, -0.01]**

Out[ ]= 0.997783

In[ ]:= **eig43[0.0992, 0.098, 0.1, 0.1, -0.01]**

Out[ ]= 1.00687

s < *μ* && ***v* < t + k(1-t):** equilibrium 1 is stable

In[ ]:= **eig11[0.11, 0.098, 0.1, 0.1, -0.01]**

Out[ ]= 0.981274

In[ ]:= **eig12[0.11, 0.098, 0.1, 0.1, -0.01]**

Out[ ]= 0.992299

In[ ]:= **eig13[0.11, 0.098, 0.1, 0.1, -0.01]**

Out[ ]= 0.979098

In[ ]:= **eig21[0.11, 0.098, 0.1, 0.1, -0.01]**

Out[ ]= 0.988889

In[ ]:= **eig22[0.11, 0.098, 0.1, 0.1, -0.01]**

Out[ ]= 0.986696

In[ ]:= **eig23[0.11, 0.098, 0.1, 0.1, -0.01]**

Out[ ]= 1.00776

In[ ]:= **eig31[0.11, 0.098, 0.1, 0.1, -0.01]**

Out[ ]= 1.00222

In[ ]:= **eig32[0.11, 0.098, 0.1, 0.1, -0.01]**

Out[ ]= 1.01348

In[ ]:= **eig33[0.11, 0.098, 0.1, 0.1, -0.01]**

Out[ ]= 1.02135

In[ ]:= **eig41[0.11, 0.098, 0.1, 0.1, -0.01]**

Out[ ]= 1.01124

In[ ]:= **eig42[0.11, 0.098, 0.1, 0.1, -0.01]**

Out[ ]= 0.997783

In[ ]:= **eig43[0.11, 0.098, 0.1, 0.1, -0.01]**

Out[ ]= 1.01908

***μ* < s + k(1-s)** && **t + k(1-t) < *v* < t:** equilibrium 1 is stable

In[ ]:= **eig11[0.098, 0.0992, 0.1, 0.1, -0.01]**

Out[ ]= 0.993181

In[ ]:= **eig12[0.098, 0.0992, 0.1, 0.1, -0.01]**

Out[ ]= 0.990979

In[ ]:= **eig13[0.098, 0.0992, 0.1, 0.1, -0.01]**

Out[ ]= 0.992299

In[ ]:= **eig21[0.098, 0.0992, 0.1, 0.1, -0.01]**

Out[ ]= 1.00222

In[ ]:= **eig22[0.098, 0.0992, 0.1, 0.1, -0.01]**

Out[ ]= 1.00133

In[ ]:= **eig23[0.098, 0.0992, 0.1, 0.1, -0.01]**

Out[ ]= 1.0091

In[ ]:= **eig31[0.098, 0.0992, 0.1, 0.1, -0.01]**

Out[ ]= 1.00089

In[ ]:= **eig32[0.098, 0.0992, 0.1, 0.1, -0.01]**

Out[ ]= 0.99867

In[ ]:= **eig33[0.098, 0.0992, 0.1, 0.1, -0.01]**

Out[ ]= 1.00776

In[ ]:= **eig41[0.098, 0.0992, 0.1, 0.1, -0.01]**

Out[ ]= 0.997783

In[ ]:= **eig42[0.098, 0.0992, 0.1, 0.1, -0.01]**

Out[ ]= 0.999112

In[ ]:= **eig43[0.098, 0.0992, 0.1, 0.1, -0.01]**

Out[ ]= 1.00687

$\mathbf{s + k(1\text{-}s) < \mu < -\frac{v-t}{1-t}(1-s) + s + k(1-s)}$ && $\mathbf{t + k(1\text{-}t) < v < t}$**:** equilibrium 1 is stable

In[ ]:= **eig11[0.0993, 0.0992, 0.1, 0.1, -0.01]**

Out[ ]= 0.99175

In[ ]:= **eig12[0.0993, 0.0992, 0.1, 0.1, -0.01]**

Out[ ]= 0.990979

In[ ]:= **eig13[0.0993, 0.0992, 0.1, 0.1, -0.01]**

Out[ ]= 0.990869

In[ ]:= **eig21[0.0993, 0.0992, 0.1, 0.1, -0.01]**

Out[ ]= 1.00078

In[∘]:= **eig22[0.0993, 0.0992, 0.1, 0.1, -0.01]**

Out[∘]= 0.999889

In[∘]:= **eig23[0.0993, 0.0992, 0.1, 0.1, -0.01]**

Out[∘]= 1.0091

In[∘]:= **eig31[0.0993, 0.0992, 0.1, 0.1, -0.01]**

Out[∘]= 1.00089

In[∘]:= **eig32[0.0993, 0.0992, 0.1, 0.1, -0.01]**

Out[∘]= 1.00011

In[∘]:= **eig33[0.0993, 0.0992, 0.1, 0.1, -0.01]**

Out[∘]= 1.00922

In[∘]:= **eig41[0.0993, 0.0992, 0.1, 0.1, -0.01]**

Out[∘]= 0.999223

In[∘]:= **eig42[0.0993, 0.0992, 0.1, 0.1, -0.01]**

Out[∘]= 0.999112

In[∘]:= **eig43[0.0993, 0.0992, 0.1, 0.1, -0.01]**

Out[∘]= 1.00832

$-\frac{v-t}{1-t}(1-s)+s+k(1-s)<\mu$ && $t+k(1-t)<v<t$: equilibrium 1 is stable

In[∘]:= **eig11[0.1, 0.0992, 0.1, 0.1, -0.01]**

Out[∘]= 0.990979

In[∘]:= **eig12[0.1, 0.0992, 0.1, 0.1, -0.01]**

Out[∘]= 0.990979

In[∘]:= **eig13[0.1, 0.0992, 0.1, 0.1, -0.01]**

Out[∘]= 0.990099

In[∘]:= **eig21[0.1, 0.0992, 0.1, 0.1, -0.01]**

Out[∘]= 1.

In[∘]:= **eig22[0.1, 0.0992, 0.1, 0.1, -0.01]**

Out[∘]= 0.999112

In[∘]:= **eig23[0.1, 0.0992, 0.1, 0.1, -0.01]**

Out[∘]= 1.0091

In[∘]:= **eig31[0.1, 0.0992, 0.1, 0.1, -0.01]**

Out[∘]= 1.00089

In[∘]:= **eig32[0.1, 0.0992, 0.1, 0.1, -0.01]**

Out[∘]= 1.00089

In[ ]:= `eig33[0.1, 0.0992, 0.1, 0.1, -0.01]`

Out[ ]= 1.01

In[ ]:= `eig41[0.1, 0.0992, 0.1, 0.1, -0.01]`

Out[ ]= 1.

In[ ]:= `eig42[0.1, 0.0992, 0.1, 0.1, -0.01]`

Out[ ]= 0.999112

In[ ]:= `eig43[0.1, 0.0992, 0.1, 0.1, -0.01]`

Out[ ]= 1.0091

μ < s + k(1-s) && **t < v:** equilibrium 1 is stable

In[ ]:= `eig11[0.098, 0.11, 0.1, 0.1, -0.01]`

Out[ ]= 0.981274

In[ ]:= `eig12[0.098, 0.11, 0.1, 0.1, -0.01]`

Out[ ]= 0.979098

In[ ]:= `eig13[0.098, 0.11, 0.1, 0.1, -0.01]`

Out[ ]= 0.992299

In[ ]:= `eig21[0.098, 0.11, 0.1, 0.1, -0.01]`

Out[ ]= 1.00222

In[ ]:= `eig22[0.098, 0.11, 0.1, 0.1, -0.01]`

Out[ ]= 1.01348

In[ ]:= `eig23[0.098, 0.11, 0.1, 0.1, -0.01]`

Out[ ]= 1.02135

In[ ]:= `eig31[0.098, 0.11, 0.1, 0.1, -0.01]`

Out[ ]= 0.988889

In[ ]:= `eig32[0.098, 0.11, 0.1, 0.1, -0.01]`

Out[ ]= 0.986696

In[ ]:= `eig33[0.098, 0.11, 0.1, 0.1, -0.01]`

Out[ ]= 1.00776

In[ ]:= `eig41[0.098, 0.11, 0.1, 0.1, -0.01]`

Out[ ]= 0.997783

In[ ]:= `eig42[0.098, 0.11, 0.1, 0.1, -0.01]`

Out[ ]= 1.01124

In[ ]:= `eig43[0.098, 0.11, 0.1, 0.1, -0.01]`

Out[ ]= 1.01908

s + k(1-s) < *μ* < s && **t < *ν*:** equilibrium 1 is stable

In[ ]:= **eig11[0.0992, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= 0.979968

In[ ]:= **eig12[0.0992, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= 0.979098

In[ ]:= **eig13[0.0992, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= 0.990979

In[ ]:= **eig21[0.0992, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= 1.00089

In[ ]:= **eig22[0.0992, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= 1.01213

In[ ]:= **eig23[0.0992, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= 1.02135

In[ ]:= **eig31[0.0992, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= 0.988889

In[ ]:= **eig32[0.0992, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= 0.988011

In[ ]:= **eig33[0.0992, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= 1.0091

In[ ]:= **eig41[0.0992, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= 0.999112

In[ ]:= **eig42[0.0992, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= 1.01124

In[ ]:= **eig43[0.0992, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= 1.02044

s < *μ* && **t < *ν*:** equilibrium 1 is stable

In[ ]:= **eig11[0.11, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= 0.968219

In[ ]:= **eig12[0.11, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= 0.979098

In[ ]:= **eig13[0.11, 0.11, 0.1, 0.1, -0.01]**

Out[ ]= 0.979098

```
In[ ]:= eig21[0.11, 0.11, 0.1, 0.1, -0.01]
Out[ ]= 0.988889

In[ ]:= eig22[0.11, 0.11, 0.1, 0.1, -0.01]
Out[ ]= 1.

In[ ]:= eig23[0.11, 0.11, 0.1, 0.1, -0.01]
Out[ ]= 1.02135

In[ ]:= eig31[0.11, 0.11, 0.1, 0.1, -0.01]
Out[ ]= 0.988889

In[ ]:= eig32[0.11, 0.11, 0.1, 0.1, -0.01]
Out[ ]= 1.

In[ ]:= eig33[0.11, 0.11, 0.1, 0.1, -0.01]
Out[ ]= 1.02135

In[ ]:= eig41[0.11, 0.11, 0.1, 0.1, -0.01]
Out[ ]= 1.01124

In[ ]:= eig42[0.11, 0.11, 0.1, 0.1, -0.01]
Out[ ]= 1.01124

In[ ]:= eig43[0.11, 0.11, 0.1, 0.1, -0.01]
Out[ ]= 1.03282
```

Initialization of equilibria (should be evaluated before Parametric portrait)