# Define payoffs and fitness

In[79]:=
```
(*s1 and s2 are individuals, each represented by a vector (x,y) *)
Payoff[{s1_, s2_}] := Module[{bx, by, cx, cy},
  bx = (s1[[1]] + s2[[1]]) - b (s1[[1]] + s2[[1]])^2;
  by = (s1[[2]] + s2[[2]]) - b (s1[[2]] + s2[[2]])^2;
  cx = c (s1[[1]] - d (s1[[1]])^2);
  cy = c (s1[[2]] - d (s1[[2]])^2);
  (1 - α) (bx - cx) + α (by - cy)]
```

In[80]:=
```
P[s_] := ArrayReshape[Payoff /@ Tuples[s, 2], {Length[s], Length[s]}]
```

In[81]:=
```
Frequencies[s_] := Module[{f}, f = Inverse[P[s]] . ConstantArray[1, Length[s]];
  f / Total[f]]
```

In[82]:=
```
InvasionFitness[{invader_, population_}, frequencies_] :=
 Module[{f, mutantPayoffs, g, residentPayoffs, mutantFitness, residentFitness},
  (*Calculate payoffs of mutant*)
  f[r_] := Payoff[{invader, population[[r]]}];
  mutantPayoffs = f /@ Range[Length[population]];

  (*Calculate payoffs of resident*)
  g[r_] := Payoff[{population[[1]], population[[r]]}];
  residentPayoffs = g /@ Range[Length[population]];

  mutantFitness = Total[mutantPayoffs * frequencies];
  residentFitness = Total[residentPayoffs * frequencies];

  (mutantFitness - residentFitness) (*Mutant invasion fitness at n-hat*)
 ]
```

# Numerical simulation

In[83]:=
```
b = 1.05;
c = 0.9;
d = 1.65;
ess = -(c - 1) / (2 (2 b - c d));
max = 1 / (4 b); α = 0.5;
```

In[84]:=
```
(*Rows: strain number; Columns: trait x, y*)
s = {{s1x[τ], s1y[τ]}, {s2x[τ], s2y[τ]}}; s // MatrixForm
```

Out[84]//MatrixForm=

$$\begin{pmatrix} s1x[\tau] & s1y[\tau] \\ s2x[\tau] & s2y[\tau] \end{pmatrix}$$

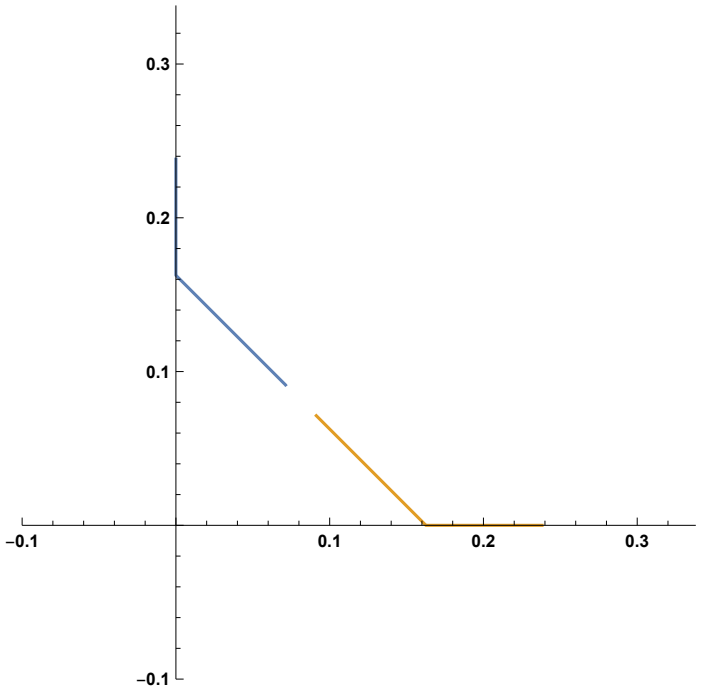
Numerical simulations show that the strains diverge toward (0, max) and (max, 0) or toward (0, 0) and (max, max), depending on starting condition:

In[85]:=
```
IF = InvasionFitness[{{mx, my}, s}, Frequencies[s]];
SG1x = D[IF, mx] /. {mx → s1x[τ], my → s1y[τ]};
SG2x = D[IF, mx] /. {mx → s2x[τ], my → s2y[τ]};
SG1y = D[IF, my] /. {mx → s1x[τ], my → s1y[τ]};
SG2y = D[IF, my] /. {mx → s2x[τ], my → s2y[τ]};
```

In[98]:=
```
sol = NDSolve[{
    D[s[[1, 1]], τ] == {Frequencies[s][[1]] * SG1x   0 < s[[1, 1]] < max
                       {0                            True                 ,

    D[s[[1, 2]], τ] == {Frequencies[s][[1]] * SG1y   0 < s[[1, 2]] < max
                       {0                            True                 ,
    D[s[[2, 1]], τ] == {Frequencies[s][[2]] * SG2x   0 < s[[2, 1]] < max
                       {0                            True                 ,
    D[s[[2, 2]], τ] == {Frequencies[s][[2]] * SG2y   0 < s[[2, 2]] < max
                       {0                            True                 ,
    (s[[1, 1]] /. τ → 0) == (ess - 0.01),
    (s[[1, 2]] /. τ → 0) == (ess + 0.01),
    (s[[2, 1]] /. τ → 0) == (ess + 0.01),
    (s[[2, 2]] /. τ → 0) == (ess - 0.01)
   },
   {s[[1, 1]], s[[1, 2]], s[[2, 1]], s[[2, 2]]},
   {τ, 0, 50}
  ];
ParametricPlot[
 {Evaluate[{s1x[τ], s1y[τ]} /. sol], Evaluate[{s2x[τ], s2y[τ]} /. sol]},
 {τ, 0, 50}, PlotRange → {{-0.1, max + 0.1}, {-0.1, max + 0.1}}]
```

Out[99]=



# Invasion of a third strain, starting from (0,0) and (max, max)

In[103]:=
```
Clear[max, α]
```

In[102]:=
```
(*Rows: strain number; Columns: trait x, y*)
s = {{0, 0}, {max, max}}; s // MatrixForm
```

Out[102]//MatrixForm=

$$\begin{pmatrix} 0 & 0 \\ \max & \max \end{pmatrix}$$

In[107]:=
```
Payoff[{s1_, s2_}] :=
 (1 - α) (Be[s1[[1]] + s2[[1]]] - Co[s1[[1]]]) + α (Be[s1[[2]] + s2[[2]]] - Co[s1[[2]]])
P[s] // FullSimplify;
% /. {Be[0] → 0, Co[0] → 0} /. α → 0.5 // FullSimplify // MatrixForm
```

Out[109]//MatrixForm=

$$\begin{pmatrix} 0 & \text{Be}[\max] \\ \text{Be}[\max] - \text{Co}[\max] & \text{Be}[2\max] - \text{Co}[\max] \end{pmatrix}$$

In[112]:=
```
freqs = Frequencies[s] /. {Be[0] → 0, Co[0] → 0} // FullSimplify
```

Out[112]=

$$\left\{\frac{\text{Be}[\max] - \text{Be}[2\max] + \text{Co}[\max]}{2\,\text{Be}[\max] - \text{Be}[2\max]}, \frac{\text{Be}[\max] - \text{Co}[\max]}{2\,\text{Be}[\max] - \text{Be}[2\max]}\right\}$$

In[188]:=
```
(*Calculate payoffs of mutant*)
f[r_] := Payoff[{{mx, my}, s[[r]]}]
f /@ Range[Length[s]]
mutpay =
 Total[% * freqs] /. {mx → 0, my → max} /. {α → 0.5, Be[0] → 0, Co[0] → 0} // FullSimplify
```

Out[189]=

$$\left\{(1-\alpha)\left(\text{Be}[\text{mx}] - \text{Co}[\text{mx}]\right) + \alpha\left(\text{Be}[\text{my}] - \text{Co}[\text{my}]\right),\right.$$
$$\left.(1-\alpha)\left(\text{Be}[\max + \text{mx}] - \text{Co}[\text{mx}]\right) + \alpha\left(\text{Be}[\max + \text{my}] - \text{Co}[\text{my}]\right)\right\}$$

Out[190]=

$$0. + \frac{1.\,\text{Be}[\max]^2}{2\,\text{Be}[\max] - \text{Be}[2\max]} - \frac{1.\,\text{Be}[\max]\,\text{Co}[\max]}{2\,\text{Be}[\max] - \text{Be}[2\max]}$$

In[195]:=
```
(*Calculate payoffs of resident*)
f[r_] := Payoff[{{0, 0}, s[[r]]}]
f /@ Range[Length[s]]
respay = Total[% * freqs] /. {α → 0.5, Be[0] → 0, Co[0] → 0} // FullSimplify
```

Out[196]=

$$\left\{(1-\alpha)\left(\text{Be}[0] - \text{Co}[0]\right) + \alpha\left(\text{Be}[0] - \text{Co}[0]\right), (1-\alpha)\left(\text{Be}[\max] - \text{Co}[0]\right) + \alpha\left(\text{Be}[\max] - \text{Co}[0]\right)\right\}$$

Out[197]=

$$0. + \frac{1.\,\text{Be}[\max]\left(\text{Be}[\max] - \text{Co}[\max]\right)}{2\,\text{Be}[\max] - \text{Be}[2\max]}$$

In[187]:=
```
mutpay - respay // FullSimplify
```

Out[187]=
```
0.
```

# Invasion of a third strain, starting from (0, max) and (max, 0)

In[244]:=
```
Clear[max, α]
```

In[245]:=
```
(*Rows: strain number; Columns: trait x, y*)
s = {{max, 0}, {0, max}}; s // MatrixForm
```

Out[245]//MatrixForm=

$$\begin{pmatrix} \max & 0 \\ 0 & \max \end{pmatrix}$$

In[246]:=
```
Payoff[{s1_, s2_}] :=
 (1 - α) (Be[s1[[1]] + s2[[1]]] - Co[s1[[1]]]) + α (Be[s1[[2]] + s2[[2]]] - Co[s1[[2]]])
P[s] // FullSimplify;
% /. {Be[0] → 0, Co[0] → 0} // FullSimplify // MatrixForm
```

Out[248]//MatrixForm=

$$\begin{pmatrix} -(-1+\alpha)\left(\text{Be}[2\max] - \text{Co}[\max]\right) & \text{Be}[\max] + (-1+\alpha)\,\text{Co}[\max] \\ \text{Be}[\max] - \alpha\,\text{Co}[\max] & \alpha\left(\text{Be}[2\max] - \text{Co}[\max]\right) \end{pmatrix}$$

In[249]:=
```
freqs = Frequencies[s] /. {Be[0] → 0, Co[0] → 0} /. {α → 0.5} // FullSimplify
```

Out[249]=
```
{0.5, 0.5}
```

In[250]:=
```
(*Calculate payoffs of mutant*)
f[r_] := Payoff[{{mx, my}, s[[r]]}]
tmp = f /@ Range[Length[s]]
mutdef =
 Total[tmp * freqs] /. {mx → 0, my → 0} /. {α → 0.5, Be[0] → 0, Co[0] → 0} // FullSimplify
mutcoop = Total[tmp * freqs] /. {mx → max, my → max} /.
    {α → 0.5, Be[0] → 0, Co[0] → 0} // FullSimplify
```

Out[251]=
```
{(1 - α) (Be[max + mx] - Co[mx]) + α (Be[my] - Co[my]),
 (1 - α) (Be[mx] - Co[mx]) + α (Be[max + my] - Co[my])}
```

Out[252]=
```
0. + 0.5 Be[max]
```

Out[253]=
```
0.5 Be[max] + 0.5 Be[2 max] - 1. Co[max]
```

In[254]:=
```
(*Calculate payoffs of resident*)
f[r_] := Payoff[{{0, max}, s[[r]]}]
f /@ Range[Length[s]]
respay = Total[% * freqs] /. {α → 0.5, Be[0] → 0, Co[0] → 0} // FullSimplify
```

Out[255]=
```
{(1 - α) (Be[max] - Co[0]) + α (Be[max] - Co[max]),
 (1 - α) (Be[0] - Co[0]) + α (Be[2 max] - Co[max])}
```

Out[256]=
```
0. + 0.5 Be[max] + 0.25 Be[2 max] - 0.5 Co[max]
```

# Invasion of a fourth strain, starting from specialists + defector

In[258]:=
```
Clear[max, α]
```

In[259]:=
```
(*Rows: strain number; Columns: trait x, y*)
s = {{max, 0}, {0, max}, {0, 0}}; s // MatrixForm
```

Out[259]//MatrixForm=

$$\begin{pmatrix} \text{max} & 0 \\ 0 & \text{max} \\ 0 & 0 \end{pmatrix}$$

In[260]:=
```
Payoff[{s1_, s2_}] :=
 (1 - α) (Be[s1[[1]] + s2[[1]]] - Co[s1[[1]]]) + α (Be[s1[[2]] + s2[[2]]] - Co[s1[[2]]])
P[s] // FullSimplify;
% /. {Be[0] → 0, Co[0] → 0} // FullSimplify // MatrixForm
```

Out[262]//MatrixForm=

$$\begin{pmatrix} -(-1+\alpha)\left(\text{Be}[2\,\text{max}] - \text{Co}[\text{max}]\right) & \text{Be}[\text{max}] + (-1+\alpha)\,\text{Co}[\text{max}] & -(-1+\alpha)\left(\text{Be}[\text{max}] - \text{Co}[\text{max}]\right) \\ \text{Be}[\text{max}] - \alpha\,\text{Co}[\text{max}] & \alpha\left(\text{Be}[2\,\text{max}] - \text{Co}[\text{max}]\right) & \alpha\left(\text{Be}[\text{max}] - \text{Co}[\text{max}]\right) \\ -(-1+\alpha)\,\text{Be}[\text{max}] & \alpha\,\text{Be}[\text{max}] & 0 \end{pmatrix}$$

In[272]:=
```
freqs = Frequencies[s] /. {Be[0] → 0, Co[0] → 0} /. {α → 0.5} // FullSimplify;
```

In[304]:=
```
(*Calculate payoffs of mutant*)
f[r_] := Payoff[{{max, max}, s[[r]]}]
tmp = f /@ Range[Length[s]];
cooppay = Total[tmp * freqs] /. {mx → max, my → max} /.
    {α → 0.5, Be[0] → 0, Co[0] → 0} // FullSimplify;
```

In[307]:=
```
(*Calculate payoffs of resident*)
f[r_] := Payoff[{{max, max}, s[[r]]}]
f /@ Range[Length[s]];
respay = Total[% * freqs] /. {α → 0.5, Be[0] → 0, Co[0] → 0} // FullSimplify;
```

In[311]:=
```
cooppay - respay /. {α → 0.5, Be[0] → 0, Co[0] → 0} // FullSimplify
```

Out[311]=
```
0.
```

# Invasion of a fourth strain, starting from specialists + cooperator

In[312]:=
```
Clear[max, α]
```

In[313]:=
```
(*Rows: strain number; Columns: trait x, y*)
s = {{max, 0}, {0, max}, {max, max}}; s // MatrixForm
```

Out[313]//MatrixForm=

$$\begin{pmatrix} \max & 0 \\ 0 & \max \\ \max & \max \end{pmatrix}$$

In[314]:=
```
Payoff[{s1_, s2_}] :=
 (1 - α) (Be[s1[[1]] + s2[[1]]] - Co[s1[[1]]]) + α (Be[s1[[2]] + s2[[2]]] - Co[s1[[2]]])
P[s] // FullSimplify;
% /. {Be[0] → 0, Co[0] → 0} // FullSimplify // MatrixForm
```

Out[316]//MatrixForm=

$$\begin{pmatrix} -(-1+\alpha)\left(\text{Be}[2\max] - \text{Co}[\max]\right) & \text{Be}[\max] + (-1+\alpha)\,\text{Co}[\max] & \alpha\,\text{Be}[\max] \\ \text{Be}[\max] - \alpha\,\text{Co}[\max] & \alpha\left(\text{Be}[2\max] - \text{Co}[\max]\right) & \text{Be}[\max] \\ \alpha\,\text{Be}[\max] - (-1+\alpha)\,\text{Be}[2\max] - \text{Co}[\max] & \text{Be}[\max] - \alpha\,\text{Be}[\max] + \alpha\,\text{Be}[2\max] - \text{Co}[\max] & \end{pmatrix}$$

In[317]:=
```
freqs = Frequencies[s] /. {Be[0] → 0, Co[0] → 0} /. {α → 0.5} // FullSimplify;
```

In[318]:=
```
(*Calculate payoffs of mutant*)
f[r_] := Payoff[{{0, 0}, s[[r]]}]
tmp = f /@ Range[Length[s]];
cooppay = Total[tmp * freqs] /. {α → 0.5, Be[0] → 0, Co[0] → 0} // FullSimplify;
```

In[321]:=
```
(*Calculate payoffs of resident*)
f[r_] := Payoff[{{0, 0}, s[[r]]}]
f /@ Range[Length[s]];
respay = Total[% * freqs] /. {α → 0.5, Be[0] → 0, Co[0] → 0} // FullSimplify;
```

In[324]:=
```
cooppay - respay /. {α → 0.5, Be[0] → 0, Co[0] → 0} // FullSimplify
```

Out[324]=
```
0.
```