
Cannibalism time budget model

Resident population dynamics:

$$\frac{d}{dt} R = r R \left(1 - \frac{R}{K}\right) - \alpha R \sum_{j=1}^k (1 - x_j) n_j$$

$$\begin{aligned} \frac{d}{dt} n_i = & (1 - x_i) n_i \left(\epsilon \alpha R - \sum_{j=1}^k \beta[x_j] x_j n_j - \delta \right) + \\ & + x_i n_i \left(\gamma \beta[x_i] \sum_{j=1}^k (1 - x_j) n_j - \delta \right) \quad \text{for } i = 1, \dots, k \end{aligned}$$

Mutant population dynamics:

$$\begin{aligned} \frac{d}{dt} m = & (1 - y) m \left(\epsilon \alpha R - \sum_{j=1}^k \beta[x_j] x_j n_j - \delta \right) + \\ & + y m \left(\gamma \beta[y] \sum_{j=1}^k (1 - x_j) n_j - \delta \right) \end{aligned}$$

Invasion fitness:

$$\begin{aligned} s_{x_1, \dots, x_k}(y) = & (1 - y) \left(\epsilon \alpha \langle R \rangle - \sum_{j=1}^k \beta[x_j] x_j \langle n_j \rangle - \delta \right) + \\ & + y \left(\gamma \beta[y] \sum_{j=1}^k (1 - x_j) \langle n_j \rangle - \delta \right) \end{aligned}$$

Three-dimensional environment:

$$E = \begin{pmatrix} \langle R \rangle \\ \sum_{j=1}^k \beta[x_j] x_j \langle n_j \rangle \\ \sum_{j=1}^k (1 - x_j) \langle n_j \rangle \end{pmatrix}$$

MONOMORPHIC RESIDENT POPULATION

```
Clear[α, β, β0, β1, γ, δ, ε, r, K, n, R]
```

■ Monomorphic resident population dynamics:

```
(* R=resource density; n=resident population density *)
```

$$dLogR = r - \frac{rR}{K} - \alpha(1-x)n;$$

$$dLogn = \epsilon\alpha(1-x)R - \delta + \gamma\beta[x]x(1-x)n - (1-x)\beta[x]xn;$$

■ Monomorphic resident population equilibrium:

```
Solve[{0 == dLogR, 0 == dLogn}, {R, n}] // Simplify
```

$$\left\{ \left\{ R \rightarrow -\frac{K(\alpha\delta - rx(-1+\gamma)\beta[x])}{K(-1+x)\alpha^2\epsilon + rx(-1+\gamma)\beta[x]}, n \rightarrow -\frac{r(\delta + K(-1+x)\alpha\epsilon)}{(-1+x)(K(-1+x)\alpha^2\epsilon + rx(-1+\gamma)\beta[x])} \right\} \right\}$$

$$R[x_] = -\frac{K(\alpha\delta - rx(-1+\gamma)\beta[x])}{K(-1+x)\alpha^2\epsilon + rx(-1+\gamma)\beta[x]};$$

$$n[x_] = -\frac{r(\delta + K(-1+x)\alpha\epsilon)}{(-1+x)(K(-1+x)\alpha^2\epsilon + rx(-1+\gamma)\beta[x])};$$

■ Invasion fitness and its derivatives:

```
s_x_[y_] = εα(1-y)R[x] - δ + γβ[y]y(1-x)n[x] - (1-y)β[x]xn[x] // Simplify;
```

```
ds[x_] = ∂y s_x[y] /. {y → x} // Simplify;
```

```
dds[x_] = ∂y ∂y s_x[y] /. {y → x} // Simplify;
```

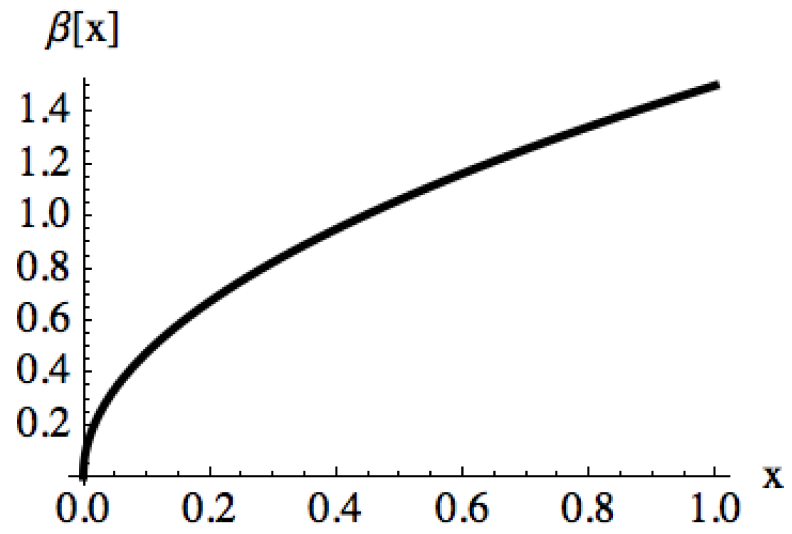
■ Default parameter values and functions (set 1):

```
α = 1; γ = 0.2; δ = 0.1; ε = 0.05; r = 1; K = 10;
```

```
β0 = 0.; β1 = 1.5; p = .5;
```

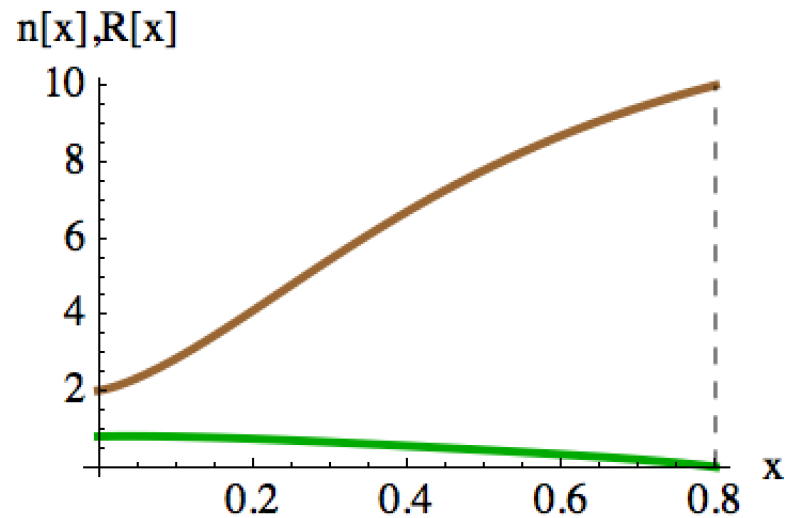
```
β[x_] := β0 + β1 xp;
```

```
Plot[ $\beta[x]$ , {x, 0, 1}, AxesLabel -> {"x", " $\beta[x]$ "}, PlotStyle -> {Black, Thick}, ImageSize -> Small]
```



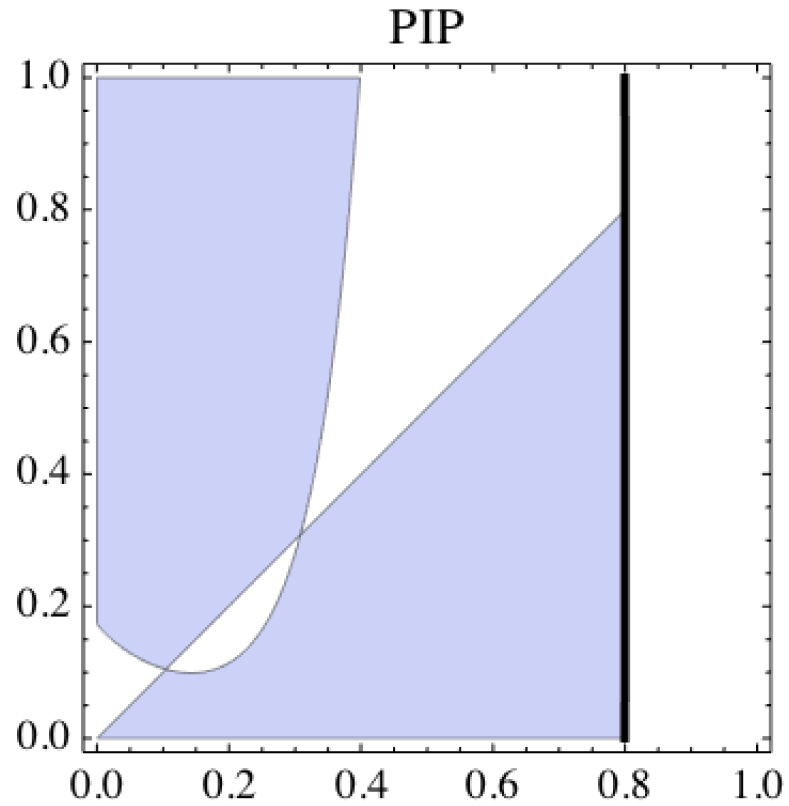
■ Plots of $R[x]$ and $n[x]$:

```
Show[  
  Plot[If[n[x] ≥ 0, R[x]], {x, 0, 1}, PlotStyle → {Brown, Thick}],  
  Plot[If[n[x] ≥ 0, n[x]], {x, 0, 1}, PlotStyle → {Darker[Green], Thick}],  
  Graphics[{Dashed, Line[{{.8, 0}, {.8, 10}]}]},  
  PlotRange → All, AxesOrigin → {0, 0}, AxesLabel → {"x", "n[x],R[x]"}, ImageSize → Small]
```



■ Pairwise invadability plot (PIP):

```
PIPint = RegionPlot[n[x] ≥ 0 && sx[y] > 0, {x, 0, 1}, {y, 0, 1}, PlotPoints → 100];  
nPos = ContourPlot[n[x], {x, 0, 1}, {y, 0, 1}, Contours → {0}, ContourStyle → {Black, Thick}, ContourShading → False, PlotPoints →  
Show[PIPint, nPos, ImageSize → Small, PlotLabel → "PIP"]
```



- **Singular strategies:**

```
xSing1 = x /. FindRoot[ds[x] == 0, {x, .1}]
```

```
xSing2 = x /. FindRoot[ds[x] == 0, {x, .3}]
```

```
0.104529
```

```
0.308179
```

- **Canonical equation:**

- **Mutation probability, mutation variance and deterministic drift:**

```
 $\mu[x_] := .001;$ 
```

```
 $\sigma^2[x_] := .01 x (1 - x);$ 
```

```
 $\text{drift}[x_] := \frac{1}{2} \mu[x] \sigma^2[x] n[x] ds[x];$ 
```

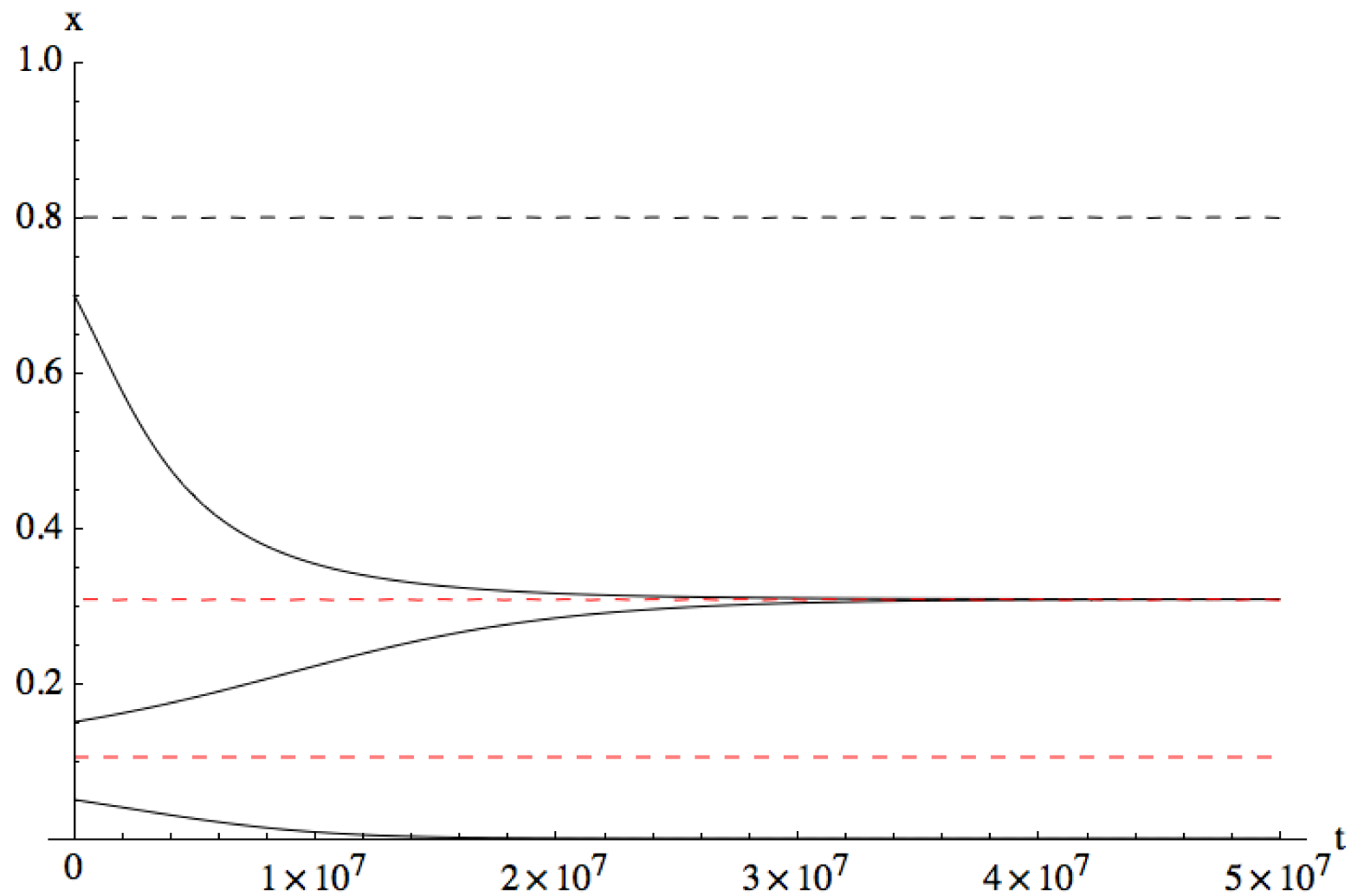
■ Deterministic orbit (Euler method):

```

x0 = {0.05, 0.15, 0.7}; (* different starting points *)
t0 = 0;
t∞ = 5 × 107;
Δt = 104;
noofStarts = Length[x0];
For[i = 1, i ≤ noofStarts, i++,
  data[i] = {};
  x = x0[[i]];
  t = t0;
  While[t ≤ t∞ && n[x] > 0,
    data[i] = Join[data[i], {{t, x}}];
    x = x + Δt drift[x];
    t = t + Δt];
];

CEorbit =
Show[
  Table[ListPlot[data[i], PlotStyle → {Black}, Joined → True], {i, 1, noofStarts}],
  ContourPlot[ds[x], {t, 0, t∞}, {x, 0, 1}, Contours → {0}, ContourShading → False, ContourStyle → {Red, Dashed}],
  ContourPlot[n[x], {t, 0, t∞}, {x, 0, 1}, Contours → {0}, ContourShading → False, ContourStyle → {Black, Dashed}],
  AxesOrigin → {0, 0}, PlotRange → {0, 1}, AxesLabel → {"t", "x"}
]

```



■ Stochastic differential equation (Ito):

■ Third absolute moment of the mutation step distribution and diffusion coefficient:

$$\theta[x_] := 2 \sigma^2[x]^{3/2} \sqrt{\frac{2}{\pi}}; (* \text{ assuming Gaussian } *)$$

$$\text{diff}[x_] := \frac{1}{2} \mu[x] \theta[x] n[x] \text{Abs}[ds[x]];$$

■ Single stochastic orbit per starting point (Euler method):

```
x0 = {0.05, 0.15, 0.7}; (* different starting points *)
```

```
t0 = 0;
```

```
t∞ = 5 × 107;
```

```
Δt = 104;
```

```
noofStarts = Length[x0];
```

```
For[i = 1, i ≤ noofStarts, i++,
```

```
  data[i] = {};
```

```
  x = x0[[i]];
```

```
  t = t0;
```

```
  While[t ≤ t∞ && n[x] > 0,
```

```
    data[i] = Join[data[i], {{t, x}}];
```

```
    z = RandomReal[NormalDistribution[0, 1]]; x = x + Δt drift[x] + z √Δt diff[x];
```

```
    t = t + Δt];
```

```
];
```

```
Colour = {Black, Blue, Green};
```

```
SDEorbit =
```

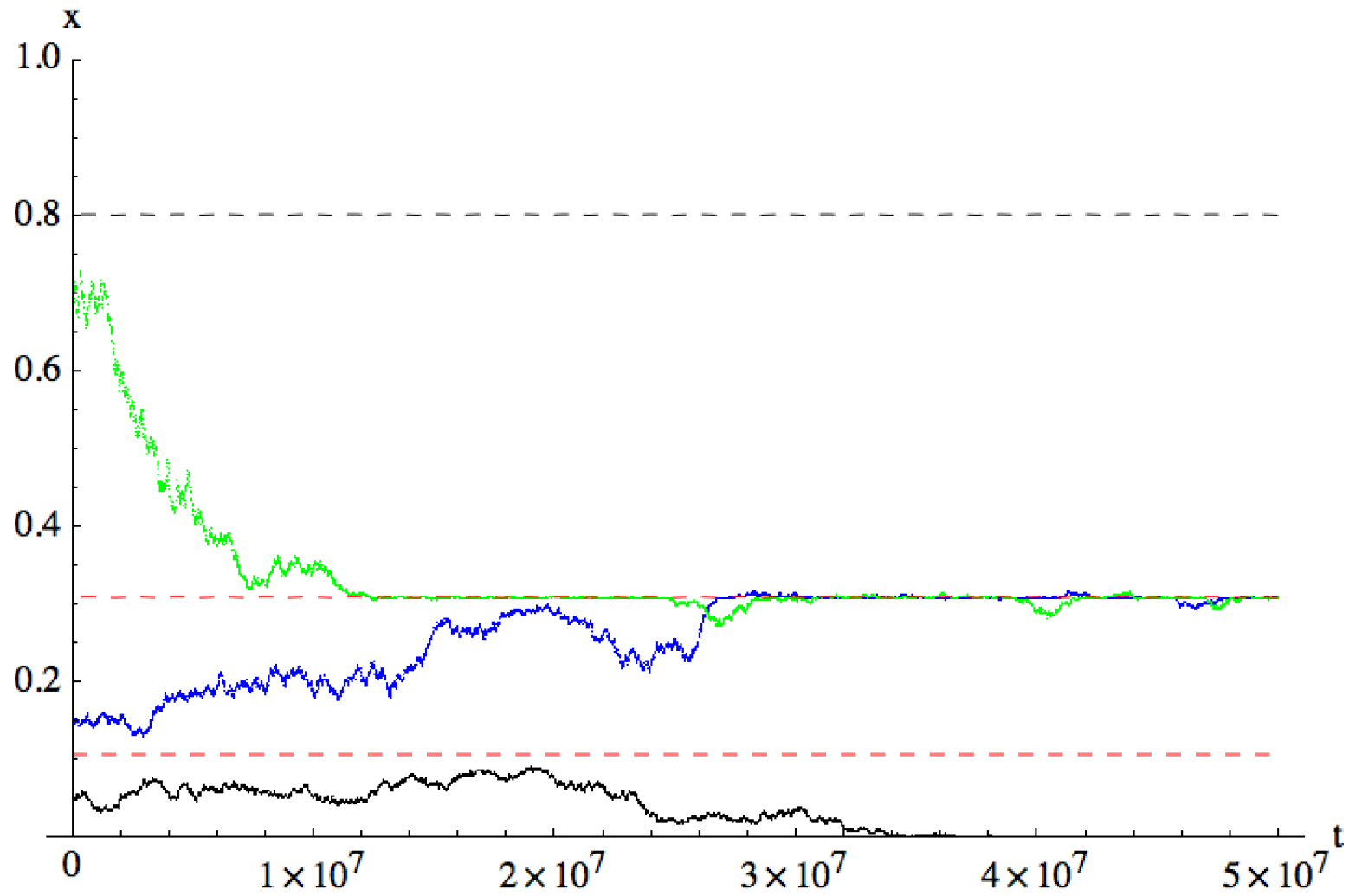
```
Show[
```

```
  Table[ListPlot[data[i], PlotStyle → {Colour[[i]], PointSize[.001]}, Joined → False], {i, 1, noofStarts}],
```

```
  ContourPlot[ds[x], {t, 0, t∞}, {x, 0, 1}, Contours → {0}, ContourShading → False, ContourStyle → {Red, Dashed}],
```

```
  ContourPlot[n[x], {t, 0, t∞}, {x, 0, 1}, Contours → {0}, ContourShading → False, ContourStyle → {Black, Dashed}],
```

```
  AxesOrigin → {0, 0}, PlotRange → {0, 1}, AxesLabel → {"t", "x"}]
```



■ Larger samples:

DIMORPHIC RESIDENT POPULATION

- Reset:

```
Clear[α, β, γ, δ, ε, r, K];
```

- Dimorphic resident population equilibrium:

$$\text{eqn} = \left\{ 0 = r - \frac{rR}{K} - \alpha \left((1-x_1)n_1 + (1-x_2)n_2 \right), 0 = \epsilon \alpha (1-x_1)R - \delta + \gamma \beta[x_1]x_1 \left((1-x_1)n_1 + (1-x_2)n_2 \right) - (1-x_1) \left(\beta[x_1]x_1n_1 + \beta[x_2]x_2n_2 \right) \right\};$$

$$0 = \epsilon \alpha (1-x_2)R - \delta + \gamma \beta[x_2]x_2 \left((1-x_1)n_1 + (1-x_2)n_2 \right) - (1-x_2) \left(\beta[x_1]x_1n_1 + \beta[x_2]x_2n_2 \right);$$

```
var = {R, n1, n2};
```

```
Solve[eqn, var] // Simplify
```

$$\left\{ \left\{ R \rightarrow \frac{K \left((x_1 - x_2) \alpha \delta + r x_1 (-1 + x_2) \gamma \beta[x_1] - r (-1 + x_1) x_2 \gamma \beta[x_2] \right)}{r \gamma (x_1 (-1 + x_2) \beta[x_1] - (-1 + x_1) x_2 \beta[x_2])}, \right. \right.$$

$$n_1 \rightarrow \left(K (x_1 - x_2) (-1 + x_2) \alpha^2 \delta \epsilon + r x_1 (-1 + x_2) \gamma (\delta + K (-1 + x_2) \alpha \epsilon) \beta[x_1] + r x_2 (\gamma (\delta - K \alpha \epsilon) + x_2 (\delta - \gamma \delta + K \alpha \gamma \epsilon)) - x_1 (\delta + K (-1 + x_2) \alpha \epsilon) \right) / \left(r \gamma (x_1 (-1 + x_2) \beta[x_1] - (-1 + x_1) x_2 \beta[x_2])^2 \right),$$

$$n_2 \rightarrow \left(r x_1 (-x_2 \delta + \gamma \delta - K \alpha \gamma \epsilon + K x_2 \alpha \gamma \epsilon + x_1 (\delta - \gamma \delta - K (-1 + x_2) \alpha \gamma \epsilon)) \beta[x_1] - (-1 + x_1) \left(K (x_1 - x_2) \alpha^2 \delta \epsilon - r x_2 \gamma (\delta + K (-1 + x_1) \alpha \epsilon) \right) \right) / \left(r \gamma (x_1 (-1 + x_2) \beta[x_1] - (-1 + x_1) x_2 \beta[x_2])^2 \right) \left. \right\}$$

(* Note: stability of equilibrium does not matter! Why? *)

$$R[x1_, x2_] := \frac{K \left((x_1 - x_2) \alpha \delta + r x_1 (-1 + x_2) \gamma \beta[x_1] - r (-1 + x_1) x_2 \gamma \beta[x_2] \right)}{r \gamma (x_1 (-1 + x_2) \beta[x_1] - (-1 + x_1) x_2 \beta[x_2])};$$

$$n1[x1_, x2_] := \left(K (x_1 - x_2) (-1 + x_2) \alpha^2 \delta \epsilon + r x_1 (-1 + x_2) \gamma (\delta + K (-1 + x_2) \alpha \epsilon) \beta[x_1] + r x_2 (\gamma (\delta - K \alpha \epsilon) + x_2 (\delta - \gamma \delta + K \alpha \gamma \epsilon)) - x_1 (\delta + K (-1 + x_2) \alpha \epsilon) \right) / \left(r \gamma (x_1 (-1 + x_2) \beta[x_1] - (-1 + x_1) x_2 \beta[x_2])^2 \right);$$

$$n2[x1_, x2_] := \left(r x_1 (-x_2 \delta + \gamma \delta - K \alpha \gamma \epsilon + K x_2 \alpha \gamma \epsilon + x_1 (\delta - \gamma \delta - K (-1 + x_2) \alpha \gamma \epsilon)) \beta[x_1] - (-1 + x_1) \left(K (x_1 - x_2) \alpha^2 \delta \epsilon - r x_2 \gamma (\delta + K (-1 + x_1) \alpha \epsilon) \right) \right) / \left(r \gamma (x_1 (-1 + x_2) \beta[x_1] - (-1 + x_1) x_2 \beta[x_2])^2 \right);$$

■ **Dimorphic invasion fitness and derivatives:**

$$s_{x1, x2}[y] := \epsilon \alpha (1 - y) R[x1, x2] - \delta + \gamma \beta[y] y ((1 - x1) n1[x1, x2] + (1 - x2) n2[x1, x2]) - (1 - y) (\beta[x1] x1 n1[x1, x2] + \beta[x2] x2 n2[x1, x2])$$

$$x1ds[x1_, x2_] := \partial_y s_{x1, x2}[y] /. \{y \rightarrow x1\};$$

$$x2ds[x1_, x2_] := \partial_y s_{x1, x2}[y] /. \{y \rightarrow x2\};$$

■ **Default parameter values and functions:**

$$\alpha = 1; \gamma = 0.2; \delta = 0.1; \epsilon = 0.05; r = 1; K = 10;$$

$$\beta_0 = 0.; \beta_1 = 1.5; p = .5;$$

$$\beta[x_] := \beta_0 + \beta_1 x^p;$$

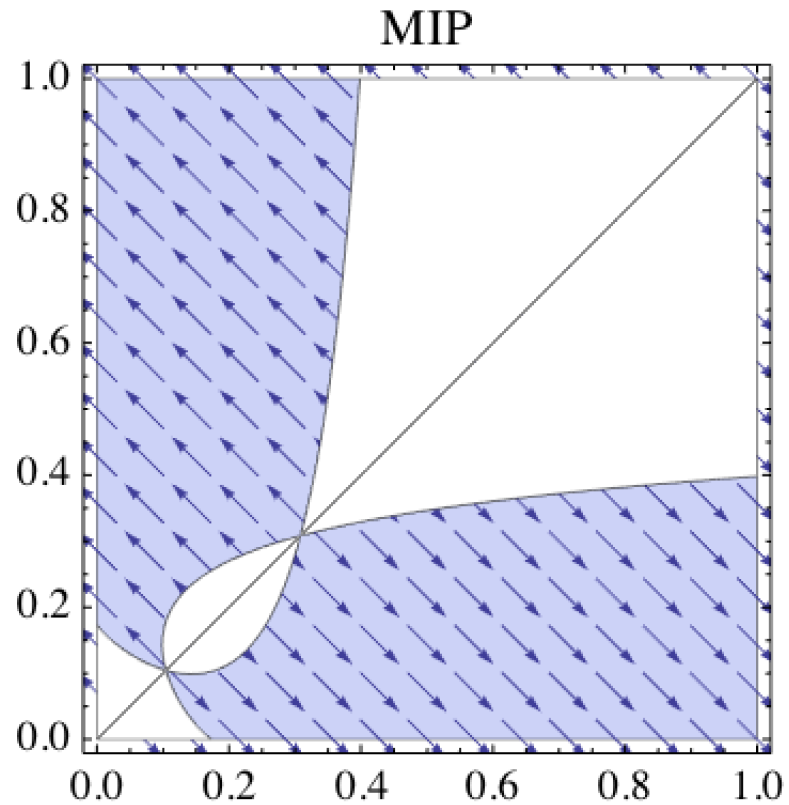
■ Coexistence plot (MIP):

```

MIP = RegionPlot[n1[x1, x2] > 0 & n2[x1, x2] > 0, {x1, 0, 1}, {x2, 0, 1}, PlotPoints -> 100] // Quiet;
antiMIP = RegionPlot[n1[x1, x2] ≤ 0 ∨ n2[x1, x2] ≤ 0, {x1, 0, 1}, {x2, 0, 1}, PlotStyle -> White, PlotPoints -> 100] // Quiet;
gradVec = VectorPlot[{Sign[x1ds[x1, x2]], Sign[x2ds[x1, x2]]}, {x1, 0, 1}, {x2, 0, 1}, VectorScale -> Small] // Quiet;

Show[MIP, gradVec, antiMIP, ImageSize -> Small, PlotLabel -> "MIP"]

```



■ Canonical equation:

■ Deterministic drift:

```
 $\mu[x\_]$  := .001;
```

```
 $\sigma^2[x\_]$  := .001 x (1 - x);
```

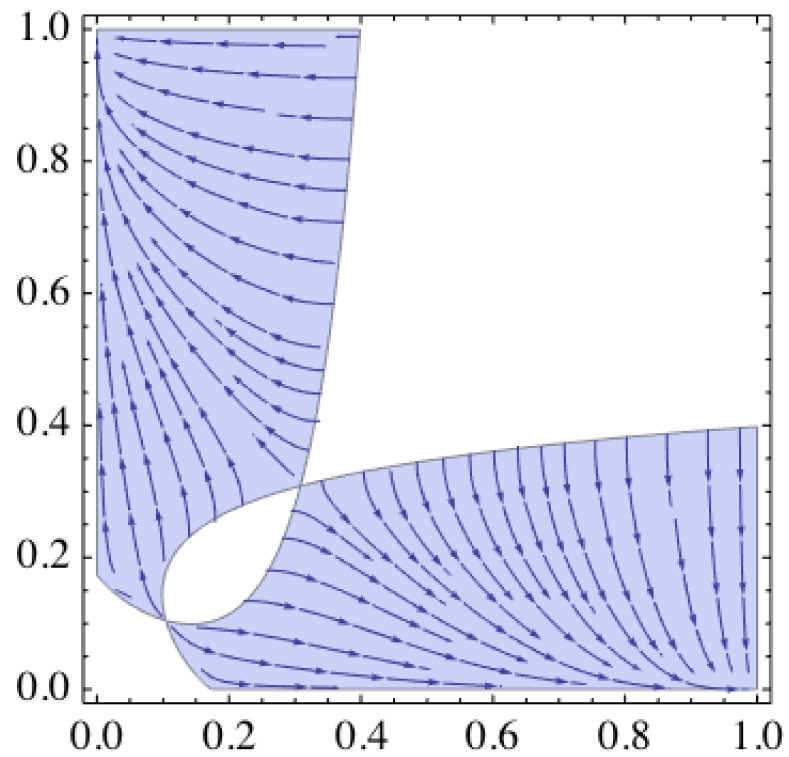
```
drift[x1_, x2_] := { $\frac{1}{2} \mu[x1] \sigma^2[x1] n1[x1, x2] x1ds[x1, x2]$ ,  $\frac{1}{2} \mu[x2] \sigma^2[x2] n2[x1, x2] x2ds[x1, x2]$ };
```

■ Stream plot:

```
CEstream = StreamPlot[If[n1[x1, x2] > 0 & n2[x1, x2] > 0, drift[x1, x2], {0, 0}], {0, 0}], {x1, 0, 1}, {x2, 0, 1}] // Quiet;
```

```
Show[MIP, CEstream, ImageSize -> Small]
```

```
(* Note: CE-orbit either horizontal or vertical at invasion boundary!  
Why? *)
```



■ **Stochastic orbits:**

■ **Diffusion coefficient:**

$$\Theta[x_] := 2 \sigma_2[x]^3/2 \sqrt{\frac{2}{\pi}}; (* \text{ assuming Gaussian } *)$$

$$\text{diff}[x1_ , x2_] := \left\{ \frac{1}{2} \mu[x1] \Theta[x1] n1[x1, x2] \text{Abs}[x1ds[x1, x2]], \frac{1}{2} \mu[x2] \Theta[x2] n2[x1, x2] \text{Abs}[x2ds[x1, x2]] \right\};$$

■ **Single stochastic orbit (Euler metod):**

```

t∞ = 1010;
Δt = 106;
x1 = xSing2 - .01;
x2 = xSing2 + .01;
data = {{x1, x2}};
t = 0;
While[t ≤ t∞ ∧ n1[x1, x2] > 0 ∧ n2[x1, x2] > 0,

  z = RandomReal[NormalDistribution[0, 1], 2]; {x1, x2} = {x1, x2} + Δt drift[x1, x2] + z √Δt diff[x1, x2];
  data = Join[data, {{x1, x2}}];
  t = t + Δt;
];

SDEorbit =
  ListPlot[data, PlotStyle → {Black, PointSize[.0075]}, Joined → False];

Show[MIP, CEstream, SDEorbit, ImageSize → Small]

```