

Settlers and Floaters

(Case: settling as an irreversible unimolecular process and resource harvesting with Holling type I functional response)

Constant environment

RESIDENT DYNAMICS

$$\frac{dR}{dt} = \alpha (R_{in} - R) - R \sum_{j=1}^k (\beta_1 N_{1,j} + \beta_2 N_{2,j}); (* \text{ resource } *)$$

$$\frac{dN_{1,i}}{dt} = R (\gamma_1 \beta_1 N_{1,i} + \gamma_2 \beta_2 N_{2,i}) - (\delta_1 + \alpha + x_i) N_{1,i}; (* \text{ floaters } *)$$

$$\frac{dN_{2,i}}{dt} = x_i N_{1,i} \left(1 - \frac{1}{K} \sum_{j=1}^k N_{2,j} \right) - \delta_2 N_{2,i}; (* \text{ settlers } *)$$

WRITE AS

$$\frac{dR}{dt} = \alpha (R_{in} - R) - R \sum_{j=1}^k (\beta_1 N_{1,j} + \beta_2 N_{2,j}); (* \text{ resource } *)$$

$$\frac{d}{dt} \begin{pmatrix} N_{1,i} \\ N_{2,i} \end{pmatrix} = \begin{pmatrix} \gamma_1 \beta_1 \boxed{R} - \delta_1 - \alpha - x_i, & \gamma_2 \beta_2 \boxed{R} \\ x_i \left(1 - \frac{1}{K} \sum_{j=1}^k N_{2,j} \right), & -\delta_2 \end{pmatrix} \begin{pmatrix} N_{1,i} \\ N_{2,i} \end{pmatrix}$$

INVADER DYNAMICS

$$\frac{d}{dt} \begin{pmatrix} M_1 \\ M_2 \end{pmatrix} = \begin{pmatrix} \gamma_1 \beta_1 \boxed{R} - \delta_1 - \alpha - Y, & \gamma_2 \beta_2 \boxed{R} \\ Y \left(1 - \frac{1}{K} \sum_{j=1}^k N_{2,j} \right), & -\delta_2 \end{pmatrix} \begin{pmatrix} M_1 \\ M_2 \end{pmatrix}$$

Invasion in the virgin environment

ENVIRONMENT

$$N_1 = N_2 = 0$$

$$\frac{dR}{dt} = \alpha (R_{in} - R) \implies R \rightarrow R_{in}$$

INVADER DYNAMICS

$$\frac{d}{dt} \begin{pmatrix} M_1 \\ M_2 \end{pmatrix} = \begin{pmatrix} \gamma_1 \beta_1 \boxed{R_{in}} - \delta_1 - \alpha - Y, & \gamma_2 \beta_2 \boxed{R_{in}} \\ Y \boxed{1}, & -\delta_2 \end{pmatrix} \begin{pmatrix} M_1 \\ M_2 \end{pmatrix}$$

< ----- A0 [Y] ----- >

```
Clear[α, β1, β2, γ1, γ2, δ1, δ2, Rin, K];
```

```
A0[Y_] := {{γ1 β1 Rin - δ1 - α - Y, γ2 β2 Rin}, {Y, -δ2}};
```

```
Eigenvalues[A0[Y]] // Simplify
```

$$\left\{ \frac{1}{2} \left(-y - \alpha + \text{Rin} \beta_1 \gamma_1 - \delta_1 - \delta_2 - \sqrt{(y + \alpha - \text{Rin} \beta_1 \gamma_1 + \delta_1 + \delta_2)^2 - 4((y + \alpha + \delta_1) \delta_2 - \text{Rin}(y \beta_2 \gamma_2 + \beta_1 \gamma_1 \delta_2))} \right), \right. \\ \left. \frac{1}{2} \left(-y - \alpha + \text{Rin} \beta_1 \gamma_1 - \delta_1 - \delta_2 + \sqrt{(y + \alpha - \text{Rin} \beta_1 \gamma_1 + \delta_1 + \delta_2)^2 - 4((y + \alpha + \delta_1) \delta_2 - \text{Rin}(y \beta_2 \gamma_2 + \beta_1 \gamma_1 \delta_2))} \right) \right\}$$

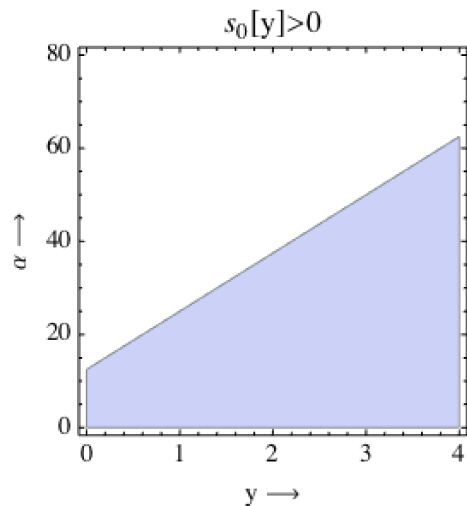
(* Invasion condition for virgine environment svir[y] *)

$$s_0[y_] := \frac{1}{2} \left(-y - \alpha + \text{Rin} \beta_1 \gamma_1 - \delta_1 - \delta_2 + \sqrt{(y + \alpha - \text{Rin} \beta_1 \gamma_1 + \delta_1 + \delta_2)^2 - 4((y + \alpha + \delta_1) \delta_2 - \text{Rin}(y \beta_2 \gamma_2 + \beta_1 \gamma_1 \delta_2))} \right);$$

$\alpha = 1.$; $\beta_1 = 1.$; $\beta_2 = 1.$; $\gamma_1 = .9$; $\gamma_2 = .9$; $\delta_1 = 1.$; $\delta_2 = 1.$; $\text{Rin} = 15.$; $\text{K} = 10.$;

RegionPlot[s0[y] > 0, {y, 0, 4}, { α , 0, 80}, PlotLabel -> "s0[y]>0", FrameLabel -> {"y ->", " α ->"}, ImageSize -> Small]

Clear[α , β_1 , β_2 , γ_1 , γ_2 , δ_1 , δ_2 , Rin, K];



(* Using -Det[A0[y]] as fitness proxy *)

Det[A0[y]]

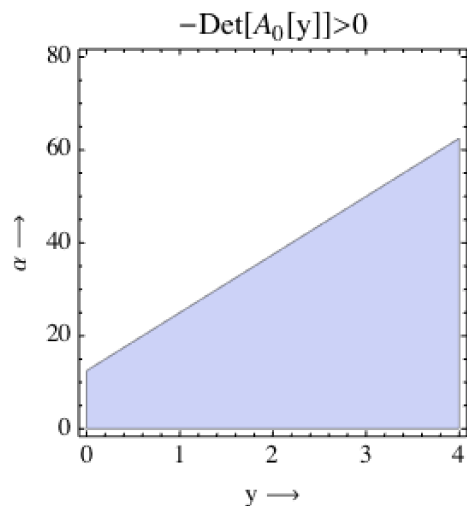
$-\text{Rin} y \beta_2 \gamma_2 + y \delta_2 + \alpha \delta_2 - \text{Rin} \beta_1 \gamma_1 \delta_2 + \delta_1 \delta_2$

Det0[y_] := $-\text{Rin} y \beta_2 \gamma_2 + y \delta_2 + \alpha \delta_2 - \text{Rin} \beta_1 \gamma_1 \delta_2 + \delta_1 \delta_2$;

$\alpha = 1.$; $\beta_1 = 1.$; $\beta_2 = 1.$; $\gamma_1 = .9$; $\gamma_2 = .9$; $\delta_1 = 1.$; $\delta_2 = 1.$; $\text{Rin} = 15.$; $\text{K} = 10.$;

RegionPlot[Det0[y] < 0, {y, 0, 4}, { α , 0, 80}, PlotLabel -> "-Det[A0[y]]>0", FrameLabel -> {"y ->", " α ->"}, ImageSize -> Small]

Clear[α , β_1 , β_2 , γ_1 , γ_2 , δ_1 , δ_2 , Rin, K];



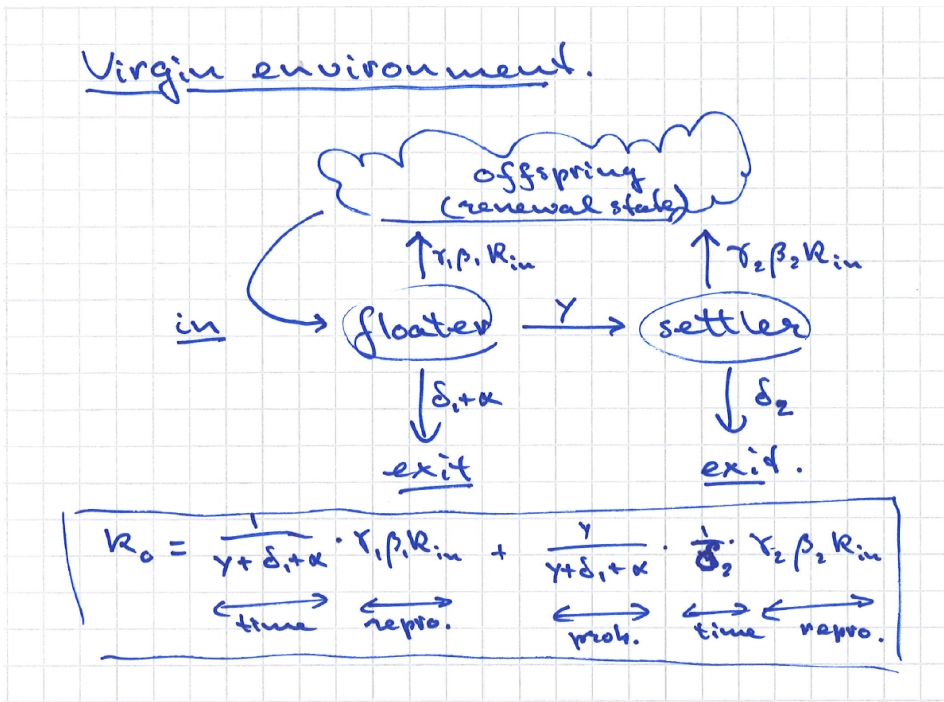
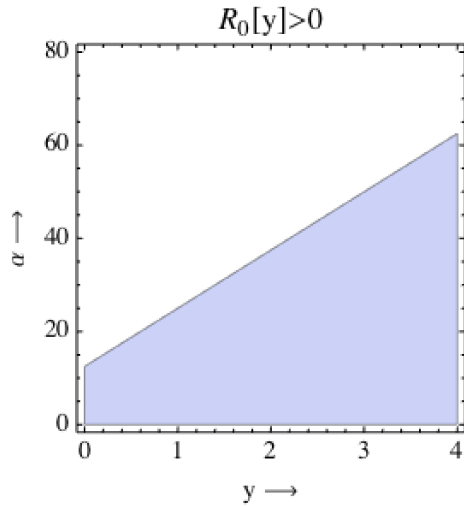
(* Using $R_0[y]-1$ as fitness proxy *)

$$R_0[y] := \frac{1}{y + \alpha + \delta_1} \gamma_1 \beta_1 R_{in} + \frac{y}{y + \alpha + \delta_1} \frac{1}{\delta_2} \gamma_2 \beta_2 R_{in};$$

$\alpha = 1.; \beta_1 = 1.; \beta_2 = 1.; \gamma_1 = .9; \gamma_2 = .9; \delta_1 = 1.; \delta_2 = 1.; R_{in} = 15.; K = 10.;$

RegionPlot[$R_0[y] > 1$, {y, 0, 4}, {α, 0, 80}, PlotLabel -> "R₀[y]>0", FrameLabel -> {"y ->", "α ->"}, ImageSize -> Small]

Clear[α, β₁, β₂, γ₁, γ₂, δ₁, δ₂, R_{in}, K];



(* Viability threshold *)

Solve[Det0[x] == 0, x]

$$\left\{ \left\{ x \rightarrow \frac{\alpha \delta_2 - R_{in} \beta_1 \gamma_1 \delta_2 + \delta_1 \delta_2}{R_{in} \beta_2 \gamma_2 - \delta_2} \right\} \right\}$$

$$xCrit := \text{Max} \left[0, \frac{\alpha \delta_2 - R_{in} \beta_1 \gamma_1 \delta_2 + \delta_1 \delta_2}{R_{in} \beta_2 \gamma_2 - \delta_2} \right];$$

Monomorphic resident population

Equilibrium

```

eqs =
{0 ==  $\alpha (Rin - R) - R (\beta_1 N_1 + \beta_2 N_2)$ ,
 0 ==  $R (\gamma_1 \beta_1 N_1 + \gamma_2 \beta_2 N_2) - (\delta_1 + \alpha + x) N_1$ ,
 0 ==  $x N_1 (1 - N_2 / K) - \delta_2 N_2$ };

vrs = {R, N1, N2};

Solve[eqs, vrs] // Simplify;
{
(* first solution: *)
{N2 -> 0, R -> Rin, N1 -> 0},

(* second solution: *) {N2 ->  $\left( \left( -x^2 \alpha - x \alpha^2 - K x^2 \beta_2 - K x \alpha \beta_2 + Rin x \alpha \beta_1 \gamma_1 - x \alpha \delta_1 - K x \beta_2 \delta_1 + K x \beta_1 \delta_2 + K \alpha \beta_1 \delta_2 + K \beta_1 \delta_1 \delta_2 + \sqrt{\left( -4 K x \alpha \beta_1 (x + \alpha + \delta_1) \left( (x + \alpha + \delta_1) \delta_2 - Rin (x \beta_2 \gamma_2 + \beta_1 \gamma_1 \delta_2) \right) + (x^2 (\alpha + K \beta_2) + K \beta_1 (\alpha + \delta_1) \delta_2 + x (\alpha^2 + \alpha (K \beta_2 - Rin \beta_1 \gamma_1 + \delta_1) + K (\beta_2 \delta_1 + \beta_1 \delta_2)) \right)^2} \right) + (x^2 \alpha + x \alpha^2 + K x^2 \beta_2 + K x \alpha \beta_2 - Rin x \alpha \beta_1 \gamma_1 + x \alpha \delta_1 + K x \beta_2 \delta_1 + K x \beta_1 \delta_2 + K \alpha \beta_1 \delta_2 + K \beta_1 \delta_1 \delta_2 + \sqrt{\left( -4 K x \alpha \beta_1 (x + \alpha + \delta_1) \left( (x + \alpha + \delta_1) \delta_2 - Rin (x \beta_2 \gamma_2 + \beta_1 \gamma_1 \delta_2) \right) + (x^2 (\alpha + K \beta_2) + K \beta_1 (\alpha + \delta_1) \delta_2 + x (\alpha^2 + \alpha (K \beta_2 - Rin \beta_1 \gamma_1 + \delta_1) + K (\beta_2 \delta_1 + \beta_1 \delta_2)) \right)^2} \right) \right) / (4 x \beta_1 \beta_2 (x + \alpha + \delta_1) (Rin x \alpha \gamma_2 + K (x + \alpha + \delta_1) \delta_2))$ ,

R ->  $\left( x^2 \alpha \gamma_2 + x \alpha^2 \gamma_2 + K x^2 \beta_2 \gamma_2 + K x \alpha \beta_2 \gamma_2 + Rin x \alpha \beta_1 \gamma_1 \gamma_2 + x \alpha \gamma_2 \delta_1 + K x \beta_2 \gamma_2 \delta_1 + 2 K x \beta_1 \gamma_1 \delta_2 + 2 K \alpha \beta_1 \gamma_1 \delta_2 - K x \beta_1 \gamma_2 \delta_2 - K \alpha \beta_1 \gamma_2 \delta_2 + 2 K \beta_1 \gamma_1 \delta_1 \delta_2 - K \beta_1 \gamma_2 \delta_1 \delta_2 + \gamma_2 \sqrt{\left( -4 K x \alpha \beta_1 (x + \alpha + \delta_1) \left( (x + \alpha + \delta_1) \delta_2 - Rin (x \beta_2 \gamma_2 + \beta_1 \gamma_1 \delta_2) \right) + (x^2 (\alpha + K \beta_2) + K \beta_1 (\alpha + \delta_1) \delta_2 + x (\alpha^2 + \alpha (K \beta_2 - Rin \beta_1 \gamma_1 + \delta_1) + K (\beta_2 \delta_1 + \beta_1 \delta_2)) \right)^2} \right) \right) / (2 \beta_1 (x (\alpha \gamma_1 + K \beta_2 (\gamma_1 - \gamma_2)) \gamma_2 + K \beta_1 \gamma_1 (\gamma_1 - \gamma_2) \delta_2)$ ,

N1 ->  $-\frac{1}{2 x \beta_1 (x + \alpha + \delta_1)} \left( x^2 \alpha + x \alpha^2 + K x^2 \beta_2 + K x \alpha \beta_2 - Rin x \alpha \beta_1 \gamma_1 + x \alpha \delta_1 + K x \beta_2 \delta_1 + K x \beta_1 \delta_2 + K \alpha \beta_1 \delta_2 + K \beta_1 \delta_1 \delta_2 + \sqrt{\left( -4 K x \alpha \beta_1 (x + \alpha + \delta_1) \left( (x + \alpha + \delta_1) \delta_2 - Rin (x \beta_2 \gamma_2 + \beta_1 \gamma_1 \delta_2) \right) + (x^2 (\alpha + K \beta_2) + K \beta_1 (\alpha + \delta_1) \delta_2 + x (\alpha^2 + \alpha (K \beta_2 - Rin \beta_1 \gamma_1 + \delta_1) + K (\beta_2 \delta_1 + \beta_1 \delta_2)) \right)^2} \right) \right)$ ,

(* third solution: THIS IS THE ONE WE NEED *)
{N2 ->  $-\left( \left( x^2 \alpha + x \alpha^2 + K x^2 \beta_2 + K x \alpha \beta_2 - Rin x \alpha \beta_1 \gamma_1 + x \alpha \delta_1 + K x \beta_2 \delta_1 + K x \beta_1 \delta_2 + K \alpha \beta_1 \delta_2 + K \beta_1 \delta_1 \delta_2 - \sqrt{\left( -4 K x \alpha \beta_1 (x + \alpha + \delta_1) \left( (x + \alpha + \delta_1) \delta_2 - Rin (x \beta_2 \gamma_2 + \beta_1 \gamma_1 \delta_2) \right) + (x^2 (\alpha + K \beta_2) + K \beta_1 (\alpha + \delta_1) \delta_2 + x (\alpha^2 + \alpha (K \beta_2 - Rin \beta_1 \gamma_1 + \delta_1) + K (\beta_2 \delta_1 + \beta_1 \delta_2)) \right)^2} \right) \right) + (x^2 \alpha + x \alpha^2 + K x^2 \beta_2 + K x \alpha \beta_2 - Rin x \alpha \beta_1 \gamma_1 + x \alpha \delta_1 + K x \beta_2 \delta_1 - K x \beta_1 \delta_2 - K \alpha \beta_1 \delta_2 - K \beta_1 \delta_1 \delta_2 + \sqrt{\left( -4 K x \alpha \beta_1 (x + \alpha + \delta_1) \left( (x + \alpha + \delta_1) \delta_2 - Rin (x \beta_2 \gamma_2 + \beta_1 \gamma_1 \delta_2) \right) + (x^2 (\alpha + K \beta_2) + K \beta_1 (\alpha + \delta_1) \delta_2 + x (\alpha^2 + \alpha (K \beta_2 - Rin \beta_1 \gamma_1 + \delta_1) + K (\beta_2 \delta_1 + \beta_1 \delta_2)) \right)^2} \right) \right) / (4 x \beta_1 \beta_2 (x + \alpha + \delta_1) (Rin x \alpha \gamma_2 + K (x + \alpha + \delta_1) \delta_2))$ ,

R ->  $\left( x^2 \alpha \gamma_2 + x \alpha^2 \gamma_2 + K x^2 \beta_2 \gamma_2 + K x \alpha \beta_2 \gamma_2 + Rin x \alpha \beta_1 \gamma_1 \gamma_2 + x \alpha \gamma_2 \delta_1 + K x \beta_2 \gamma_2 \delta_1 + 2 K x \beta_1 \gamma_1 \delta_2 + 2 K \alpha \beta_1 \gamma_1 \delta_2 - K x \beta_1 \gamma_2 \delta_2 - K \alpha \beta_1 \gamma_2 \delta_2 + 2 K \beta_1 \gamma_1 \delta_1 \delta_2 - K \beta_1 \gamma_2 \delta_1 \delta_2 - \gamma_2 \sqrt{\left( -4 K x \alpha \beta_1 (x + \alpha + \delta_1) \left( (x + \alpha + \delta_1) \delta_2 - Rin (x \beta_2 \gamma_2 + \beta_1 \gamma_1 \delta_2) \right) + (x^2 (\alpha + K \beta_2) + K \beta_1 (\alpha + \delta_1) \delta_2 + x (\alpha^2 + \alpha (K \beta_2 - Rin \beta_1 \gamma_1 + \delta_1) + K (\beta_2 \delta_1 + \beta_1 \delta_2)) \right)^2} \right) \right) / (2 \beta_1 (x (\alpha \gamma_1 + K \beta_2 (\gamma_1 - \gamma_2)) \gamma_2 + K \beta_1 \gamma_1 (\gamma_1 - \gamma_2) \delta_2)$ ,

N1 ->  $-\frac{1}{2 x \beta_1 (x + \alpha + \delta_1)} \left( x^2 \alpha + x \alpha^2 + K x^2 \beta_2 + K x \alpha \beta_2 - Rin x \alpha \beta_1 \gamma_1 + x \alpha \delta_1 + K x \beta_2 \delta_1 + K x \beta_1 \delta_2 + K \alpha \beta_1 \delta_2 + K \beta_1 \delta_1 \delta_2 - \sqrt{\left( -4 K x \alpha \beta_1 (x + \alpha + \delta_1) \left( (x + \alpha + \delta_1) \delta_2 - Rin (x \beta_2 \gamma_2 + \beta_1 \gamma_1 \delta_2) \right) + (x^2 (\alpha + K \beta_2) + K \beta_1 (\alpha + \delta_1) \delta_2 + x (\alpha^2 + \alpha (K \beta_2 - Rin \beta_1 \gamma_1 + \delta_1) + K (\beta_2 \delta_1 + \beta_1 \delta_2)) \right)^2} \right) \right)$ 
};

```

(* Positive equilibrium monomorphic resident population *)

$$\text{eqR}[x_]:= \left(x^2 \alpha \gamma_2 + x \alpha^2 \gamma_2 + K x^2 \beta_2 \gamma_2 + K x \alpha \beta_2 \gamma_2 + \text{Rin} x \alpha \beta_1 \gamma_1 \gamma_2 + x \alpha \gamma_2 \delta_1 + K x \beta_2 \gamma_2 \delta_1 + 2 K x \beta_1 \gamma_1 \delta_2 + 2 K \alpha \beta_1 \gamma_1 \delta_2 - K x \beta_1 \gamma_2 \delta_2 - K \alpha \beta_1 \gamma_2 \delta_2 + 2 K \beta_1 \gamma_1 \delta_1 \delta_2 - K \beta_1 \gamma_2 \delta_1 \delta_2 - \gamma_2 \sqrt{\left(-4 K x \alpha \beta_1 (x + \alpha + \delta_1) \left((x + \alpha + \delta_1) \delta_2 - \text{Rin} (x \beta_2 \gamma_2 + \beta_1 \gamma_1 \delta_2) \right) + \left(x^2 (\alpha + K \beta_2) + K \beta_1 (\alpha + \delta_1) \delta_2 + x (\alpha^2 + \alpha (K \beta_2 - \text{Rin} \beta_1 \gamma_1 + \delta_1) + K (\beta_2 \delta_1 + \beta_1 \delta_2) \right) \right)^2} \right) / \left(2 \beta_1 (x \alpha \gamma_1 + K \beta_2 (\gamma_1 - \gamma_2)) \gamma_2 + K \beta_1 \gamma_1 (\gamma_1 - \gamma_2) \delta_2 \right);$$

$$\text{eqN1}[x_]:= -\frac{1}{2 x \beta_1 (x + \alpha + \delta_1)} \left(x^2 \alpha + x \alpha^2 + K x^2 \beta_2 + K x \alpha \beta_2 - \text{Rin} x \alpha \beta_1 \gamma_1 + x \alpha \delta_1 + K x \beta_2 \delta_1 + K x \beta_1 \delta_2 + K \alpha \beta_1 \delta_2 + K \beta_1 \delta_1 \delta_2 - \sqrt{\left(-4 K x \alpha \beta_1 (x + \alpha + \delta_1) \left((x + \alpha + \delta_1) \delta_2 - \text{Rin} (x \beta_2 \gamma_2 + \beta_1 \gamma_1 \delta_2) \right) + \left(x^2 (\alpha + K \beta_2) + K \beta_1 (\alpha + \delta_1) \delta_2 + x (\alpha^2 + \alpha (K \beta_2 - \text{Rin} \beta_1 \gamma_1 + \delta_1) + K (\beta_2 \delta_1 + \beta_1 \delta_2) \right) \right)^2} \right);$$

$$\text{eqN2}[x_]:= -\left(\left(x^2 \alpha + x \alpha^2 + K x^2 \beta_2 + K x \alpha \beta_2 - \text{Rin} x \alpha \beta_1 \gamma_1 + x \alpha \delta_1 + K x \beta_2 \delta_1 + K x \beta_1 \delta_2 + K \alpha \beta_1 \delta_2 + K \beta_1 \delta_1 \delta_2 - \sqrt{\left(-4 K x \alpha \beta_1 (x + \alpha + \delta_1) \left((x + \alpha + \delta_1) \delta_2 - \text{Rin} (x \beta_2 \gamma_2 + \beta_1 \gamma_1 \delta_2) \right) + \left(x^2 (\alpha + K \beta_2) + K \beta_1 (\alpha + \delta_1) \delta_2 + x (\alpha^2 + \alpha (K \beta_2 - \text{Rin} \beta_1 \gamma_1 + \delta_1) + K (\beta_2 \delta_1 + \beta_1 \delta_2) \right) \right)^2} \right) \right) \left(x^2 \alpha + x \alpha^2 + K x^2 \beta_2 + K x \alpha \beta_2 - \text{Rin} x \alpha \beta_1 \gamma_1 + x \alpha \delta_1 + K x \beta_2 \delta_1 - K x \beta_1 \delta_2 - K \alpha \beta_1 \delta_2 - K \beta_1 \delta_1 \delta_2 + \sqrt{\left(-4 K x \alpha \beta_1 (x + \alpha + \delta_1) \left((x + \alpha + \delta_1) \delta_2 - \text{Rin} (x \beta_2 \gamma_2 + \beta_1 \gamma_1 \delta_2) \right) + \left(x^2 (\alpha + K \beta_2) + K \beta_1 (\alpha + \delta_1) \delta_2 + x (\alpha^2 + \alpha (K \beta_2 - \text{Rin} \beta_1 \gamma_1 + \delta_1) + K (\beta_2 \delta_1 + \beta_1 \delta_2) \right) \right)^2} \right) \right) / \left(4 x \beta_1 \beta_2 (x + \alpha + \delta_1) (\text{Rin} x \alpha \gamma_2 + K (x + \alpha + \delta_1) \delta_2) \right);$$

(* Stability of the positive equilibrium *)

```
JacMat[x_] :=
  D[{alpha (Rin - R) - R (beta1 N1 + beta2 N2), R (gamma1 beta1 N1 + gamma2 beta2 N2) - (delta1 + alpha + x) N1, x N1 (1 - N2 / K) - delta2 N2}, {R, N1, N2}] /.
  {R -> eqR[x], N1 -> eqN1[x], N2 -> eqN2[x]};
```

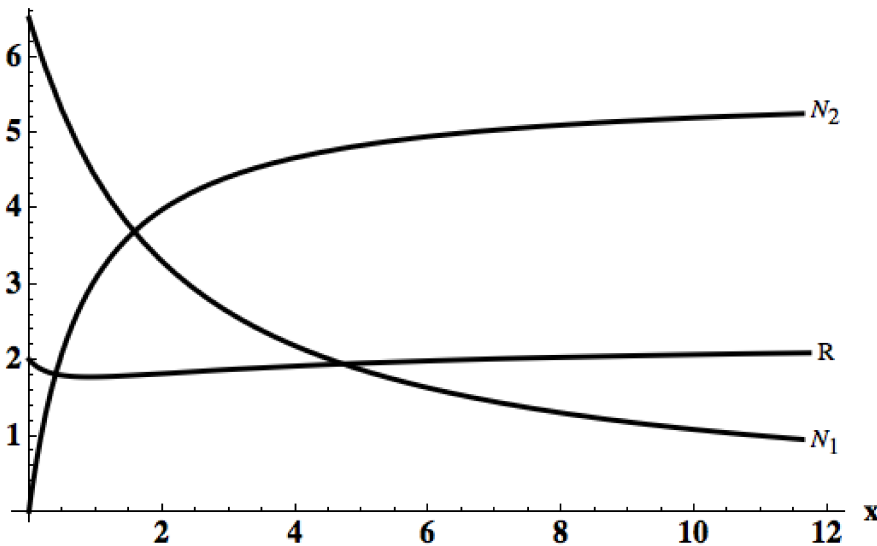
(* Parameter set 1 *)

```
alpha = 1; beta1 = 1; beta2 = 1; gamma1 = 1; gamma2 = 1; delta1 = 1; delta2 = 1; Rin = 15; K = 10;
```

```
Block[{xmin = 0, xmax = 12},
  Show[
    Plot[If[Max[Re[Eigenvalues[JacMat[x]]]] <= 0, {eqR[x], eqN1[x], eqN2[x]},
      {x, xmin, xmax}, PlotStyle -> {{Black, Thick}}],
    Plot[If[Max[Re[Eigenvalues[JacMat[x]]]] > 0, {eqR[x], eqN1[x], eqN2[x]}, {x, xmin, xmax}, PlotStyle -> {{Red, Thick}}],
    Graphics[Text[" R ", {xmax, eqR[xmax]}, Background -> White]],
    Graphics[Text[" N1 ", {xmax, eqN1[xmax]}, Background -> White]],
    Graphics[Text[" N2 ", {xmax, eqN2[xmax]}, Background -> White]],
    PlotRange -> All, AxesOrigin -> {0, 0}, AxesLabel -> {"x", "Pop. equil."}, LabelStyle -> Directive[Bold, 12]
  ]
]
```

```
Clear[alpha, beta1, beta2, gamma1, gamma2, delta1, delta2, Rin, K];
```

Pop. equil.

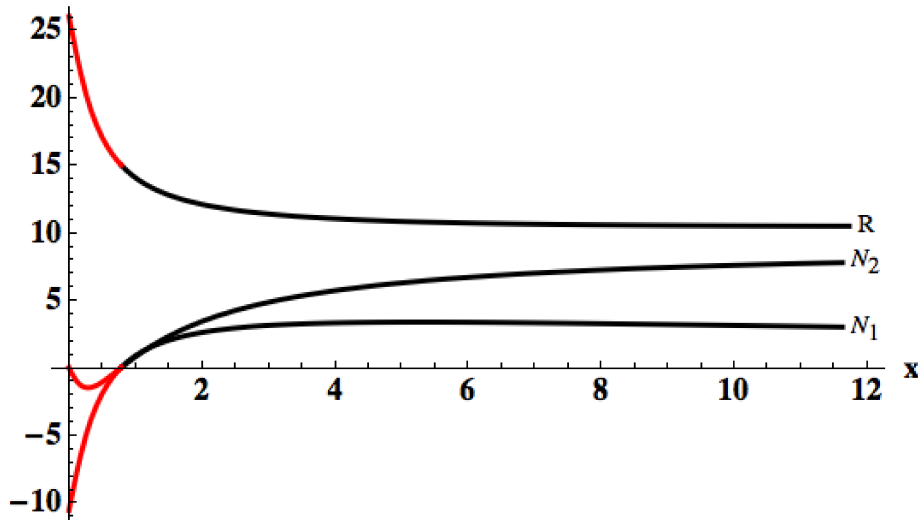


```
(* Parameter set 2 *)
 $\alpha = 25; \beta_1 = 1; \beta_2 = 1; \gamma_1 = 1; \gamma_2 = 1; \delta_1 = 1; \delta_2 = 1; R_{in} = 15; K = 10;$ 

Block[{xmin = 0, xmax = 12},
  Show[
    Plot[If[Max[Re[Eigenvalues[JacMat[x]]]  $\leq 0$ , {eqR[x], eqN1[x], eqN2[x]}],
      {x, xmin, xmax}, PlotStyle  $\rightarrow$  {{Black, Thick}}],
    Plot[If[Max[Re[Eigenvalues[JacMat[x]]]  $> 0$ , {eqR[x], eqN1[x], eqN2[x]}], {x, xmin, xmax}, PlotStyle  $\rightarrow$  {{Red, Thick}}],
    Graphics[Text[" R ", {xmax, eqR[xmax]}, Background  $\rightarrow$  White]],
    Graphics[Text[" N1 ", {xmax, eqN1[xmax]}, Background  $\rightarrow$  White]],
    Graphics[Text[" N2 ", {xmax, eqN2[xmax]}, Background  $\rightarrow$  White]],
    PlotRange  $\rightarrow$  All, AxesOrigin  $\rightarrow$  {0, 0}, AxesLabel  $\rightarrow$  {"x", "Pop. equil."}, LabelStyle  $\rightarrow$  Directive[Bold, 12]
  ]
]

Clear[ $\alpha, \beta_1, \beta_2, \gamma_1, \gamma_2, \delta_1, \delta_2, R_{in}, K$ ];
```

Pop. equil.

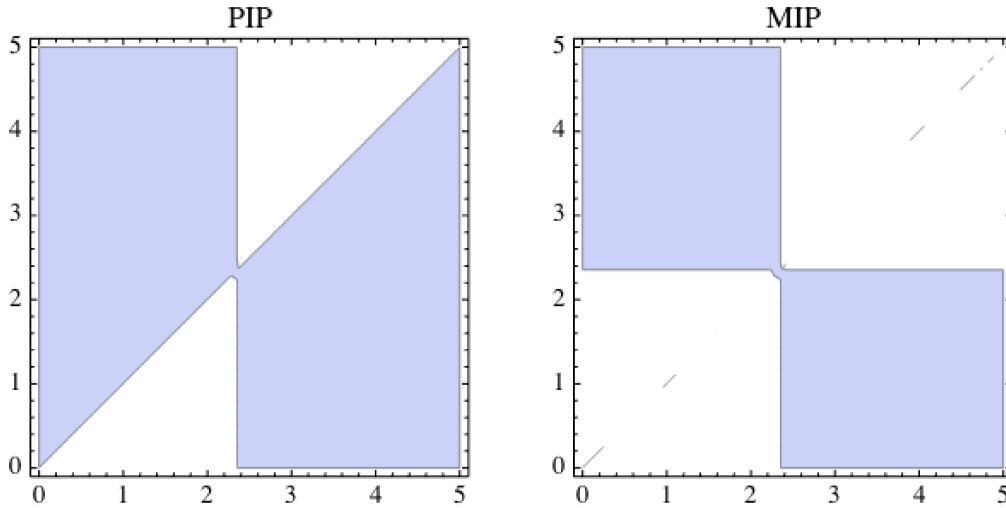


■ Invasion fitness and PIP

```
(* Generator invader dynamics *)
A1[Y_] := {{ $\gamma_1 \beta_1 R - \delta_1 - \alpha - Y, \gamma_2 \beta_2 R$ }, { $Y (1 - N_2 / K), -\delta_2$ }};
```

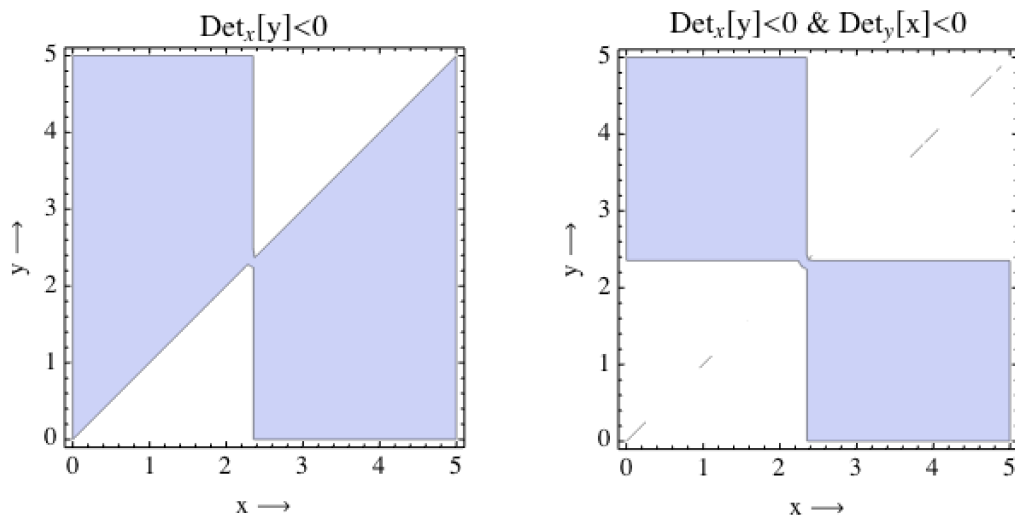
```
(* Invasion fitness *)
s_x[y_] :=
  Max[Eigenvalues[A1[y]] /. {R → eqR[x], N1 → eqN1[x], N2 → eqN2[x]}];

(* Example *)
α = 1.; β1 = 1.95; β2 = 1.; γ1 = .1; γ2 = .1; δ1 = 1.; δ2 = 1.; Rin = 15.; K = 10.;
PIP = RegionPlot[s_x[y] > 0, {x, 0, 5}, {y, 0, 5}];
MIP = RegionPlot[s_x[y] > 0 & s_y[x] > 0, {x, 0, 5}, {y, 0, 5}];
Row[{Show[PIP, PlotLabel → "PIP", ImageSize → Small], " "
  Show[MIP, PlotLabel → "MIP", ImageSize → Small]}]
Clear[α, β1, β2, γ1, γ2, δ1, δ2, Rin, K];
```



```
(* Fitness proxy: -Det[A1[y]] *)
Det_x[y_] := Det[A1[y]] /. {R → eqR[x], N1 → eqN1[x], N2 → eqN2[x]};

(* Example *)
α = 1.; β1 = 1.95; β2 = 1.; γ1 = .1; γ2 = .1; δ1 = 1.; δ2 = 1.; Rin = 15.; K = 10.;
Row[{
  RegionPlot[Det_x[y] < 0, {x, xCrit, 5}, {y, xCrit, 5},
    PlotLabel → "Det_x[y]<0", FrameLabel → {"x →", "y →"}, ImageSize → Small],
  " ",
  RegionPlot[Det_x[y] < 0 & Det_y[x] < 0, {x, xCrit, 5}, {y, xCrit, 5},
    PlotLabel → "Det_x[y]<0 & Det_y[x]<0", FrameLabel → {"x →", "y →"}, ImageSize → Small]
}]
Clear[α, β1, β2, γ1, γ2, δ1, δ2, Rin, K];
```



(* Using $R_0[y]-1$ as fitness proxy ... *)

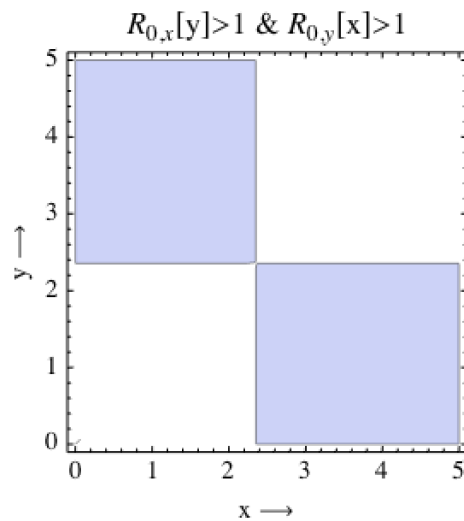
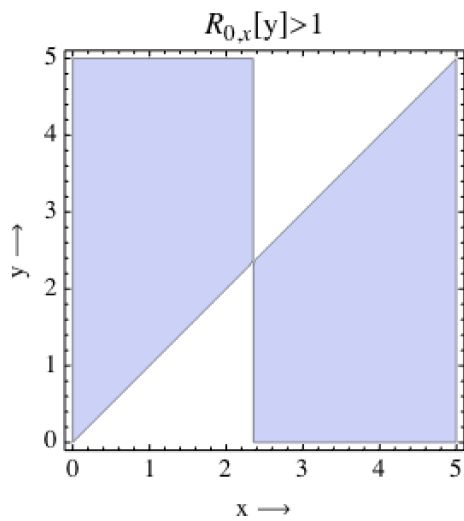
$$R_{0,x}[y] := \frac{1}{y + \alpha + \delta_1} \gamma_1 \beta_1 R + \frac{y(1 - N_2/K)}{y + \alpha + \delta_1} \frac{1}{\delta_2} \gamma_2 \beta_2 R / . \{R \rightarrow \text{eqR}[x], N_1 \rightarrow \text{eqN1}[x], N_2 \rightarrow \text{eqN2}[x]\};$$

(* Example *)

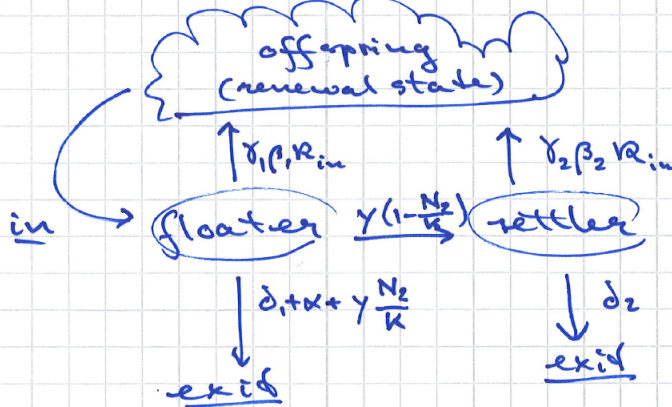
$\alpha = 1.; \beta_1 = 1.95; \beta_2 = 1.; \gamma_1 = .1; \gamma_2 = .1; \delta_1 = 1.; \delta_2 = 1.; R_{in} = 15.; K = 10.;$

```
Row[
  RegionPlot[R0x[y] > 1, {x, xCrit, 5}, {y, xCrit, 5},
    PlotLabel -> "R0,x[y]>1", FrameLabel -> {"x ->", "y ->"}, ImageSize -> Small],
  RegionPlot[R0x[y] > 1 & R0y[x] > 1, {x, xCrit, 5}, {y, xCrit, 5},
    PlotLabel -> "R0,x[y]>1 & R0,y[x]>1", FrameLabel -> {"x ->", "y ->"}, ImageSize -> Small]
]
```

Clear[$\alpha, \beta_1, \beta_2, \gamma_1, \gamma_2, \delta_1, \delta_2, R_{in}, K$];



Monomorphic resident.



$$R_0 = \frac{1}{y + \delta_1 + \alpha} \cdot \gamma_1 \beta_1 R_{in} + \frac{\gamma(1 - \frac{N_2}{K})}{y + \delta_1 + \alpha} \cdot \frac{1}{\delta_2} \cdot \gamma_2 \beta_2 R_{in}$$

\longleftarrow time \longleftarrow repro. \longleftarrow prob. \longleftarrow time \longleftarrow repro.

■ Why the vertical invasion boundary?

Det[A1[y]] // Simplify

$$(y + \alpha + \delta_1) \delta_2 + R \left(\frac{(-K + N_2) y \beta_2 \gamma_2}{K} - \beta_1 \gamma_1 \delta_2 \right)$$

Hence

$$\text{Det}_x[y] = (y + \alpha + \delta_1) \delta_2 + R[x] \left(\frac{(-K + N_2[x]) y \beta_2 \gamma_2}{K} - \beta_1 \gamma_1 \delta_2 \right)$$

which is linear in y;

Solving $\text{Det}_x[y] = 0$ for (x, y) always gives $y = x$ as a solution ;

Hence, $\text{Det}_x[y] / (y - x)$ is independent of y, and so any solution (x, y) of

$0 = \text{Det}_x[y] / (y - x)$ must be of the form $x = \text{constant}$;

Solve[0 == Det[A1[y]], y] /. {R -> eqR[x], N1 -> eqN1[x], N2 -> eqN2[x]} // Simplify

{y -> x}

(* Det_x[y]/(y-x) is independent of y *)

Det[A1[y]] / (y - x) /. {R -> eqR[x], N1 -> eqN1[x], N2 -> eqN2[x]} // Simplify

$$\left(\delta_2 \left(x^2 \alpha \gamma_1 \gamma_2 - x \alpha^2 \gamma_1 \gamma_2 + K x^2 \beta_2 \gamma_1 \gamma_2 - K x \alpha \beta_2 \gamma_1 \gamma_2 + R_{in} x \alpha \beta_1 \gamma_1^2 \gamma_2 + 2 K x \alpha \beta_2 \gamma_2^2 - x \alpha \gamma_1 \gamma_2 \delta_1 - K x \beta_2 \gamma_1 \gamma_2 \delta_1 + 2 K x \beta_2 \gamma_2^2 \delta_1 + 2 K x \beta_1 \gamma_1^2 \delta_2 - K x \beta_1 \gamma_1 \gamma_2 \delta_2 + K \alpha \beta_1 \gamma_1 \gamma_2 \delta_2 + K \beta_1 \gamma_1 \gamma_2 \delta_1 \delta_2 - \gamma_1 \gamma_2 \sqrt{\left(-4 K x \alpha \beta_1 (x + \alpha + \delta_1) \left((x + \alpha + \delta_1) \delta_2 - R_{in} (x \beta_2 \gamma_2 + \beta_1 \gamma_1 \delta_2) \right) \right)^2} \right) + \left(x^2 (\alpha + K \beta_2) + K \beta_1 (\alpha + \delta_1) \delta_2 + x (\alpha^2 + \alpha (K \beta_2 - R_{in} \beta_1 \gamma_1 + \delta_1) + K (\beta_2 \delta_1 + \beta_1 \delta_2)) \right)^2 \right) \right) / (2 x (x (\alpha \gamma_1 + K \beta_2 (\gamma_1 - \gamma_2)) \gamma_2 + K \beta_1 \gamma_1 (\gamma_1 - \gamma_2) \delta_2))$$

(* Numerator of Det[A1[y]]/(y-x) becomes zero for which x ? *)

Solve[0 == x^2 \alpha \gamma_1 \gamma_2 - x \alpha^2 \gamma_1 \gamma_2 + K x^2 \beta_2 \gamma_1 \gamma_2 - K x \alpha \beta_2 \gamma_1 \gamma_2 + R_{in} x \alpha \beta_1 \gamma_1^2 \gamma_2 +

$$2 K x \alpha \beta_2 \gamma_2^2 - x \alpha \gamma_1 \gamma_2 \delta_1 - K x \beta_2 \gamma_1 \gamma_2 \delta_1 + 2 K x \beta_2 \gamma_2^2 \delta_1 + 2 K x \beta_1 \gamma_1^2 \delta_2 - K x \beta_1 \gamma_1 \gamma_2 \delta_2 +$$

$$K \alpha \beta_1 \gamma_1 \gamma_2 \delta_2 + K \beta_1 \gamma_1 \gamma_2 \delta_1 \delta_2 - \gamma_1 \gamma_2 \sqrt{\left(-4 K x \alpha \beta_1 (x + \alpha + \delta_1) \left((x + \alpha + \delta_1) \delta_2 - R_{in} (x \beta_2 \gamma_2 + \beta_1 \gamma_1 \delta_2) \right) \right)^2} \right), x] // Simplify$$

$$\left(x^2 (\alpha + K \beta_2) + K \beta_1 (\alpha + \delta_1) \delta_2 + x (\alpha^2 + \alpha (K \beta_2 - R_{in} \beta_1 \gamma_1 + \delta_1) + K (\beta_2 \delta_1 + \beta_1 \delta_2)) \right)^2, x] // Simplify$$

$$\left\{ \{x \rightarrow 0\}, \left\{ x \rightarrow \frac{K \beta_1 \gamma_1 (-\gamma_1 + \gamma_2) \delta_2}{(\alpha \gamma_1 + K \beta_2 (\gamma_1 - \gamma_2)) \gamma_2} \right\}, \left\{ x \rightarrow -\frac{K \gamma_2 (\alpha + \delta_1) (\alpha \beta_2 \gamma_2 + \beta_2 \gamma_2 \delta_1 - \beta_1 \gamma_1 \delta_2)}{\gamma_1 (\alpha^2 \gamma_2 + \alpha \gamma_2 (K \beta_2 - R_{in} \beta_1 \gamma_1 + \delta_1) + K (\beta_2 \gamma_2 \delta_1 - \beta_1 \gamma_1 \delta_2))} \right\} \right\}$$

(* Denominator of \partial_y Det_x[y]/(y-x) becomes zero for which x *)

Solve[0 == 2 x (x (\alpha \gamma_1 + K \beta_2 (\gamma_1 - \gamma_2)) \gamma_2 + K \beta_1 \gamma_1 (\gamma_1 - \gamma_2) \delta_2), x] // Simplify

$$\left\{ \{x \rightarrow 0\}, \left\{ x \rightarrow -\frac{K \beta_1 \gamma_1 (\gamma_1 - \gamma_2) \delta_2}{(\alpha \gamma_1 + K \beta_2 (\gamma_1 - \gamma_2)) \gamma_2} \right\} \right\}$$

The numerator and denominator have a common root

$$x \rightarrow -\frac{K \beta_1 \gamma_1 (\gamma_1 - \gamma_2) \delta_2}{(\alpha \gamma_1 + K \beta_2 (\gamma_1 - \gamma_2)) \gamma_2};$$

This root is positive if and only if

$$1 < \frac{\gamma_2}{\gamma_1} < 1 + \frac{\alpha}{K \beta_2};$$

The left limit coincides with $x = 0$ and the right limit with $x = +\infty$;

The numerator becomes zero for

$$x \rightarrow -\frac{K \gamma_2 (\alpha + \delta_1) (\alpha \beta_2 \gamma_2 + \beta_2 \gamma_2 \delta_1 - \beta_1 \gamma_1 \delta_2)}{\gamma_1 (\alpha^2 \gamma_2 + \alpha \gamma_2 (K \beta_2 - R_{in} \beta_1 \gamma_1 + \delta_1) + K (\beta_2 \gamma_2 \delta_1 - \beta_1 \gamma_1 \delta_2))};$$

This root becomes zero for

$$\frac{\beta_1 \gamma_1}{\alpha + \delta_1} = \frac{\beta_2 \gamma_2}{\delta_2};$$

The root becomes \pm infinity for

$$\frac{\beta_1 \gamma_1}{\alpha + \delta_1} = \frac{\beta_2 \gamma_2}{\delta_2} \cdot \frac{1 + \frac{\alpha}{K \beta_2}}{1 + \frac{\gamma_2}{\delta_2} \frac{\alpha}{K} R_{in}};$$

(* When does x* become infinity *)

$$\text{Solve}\left[\frac{\beta_1 \gamma_1}{\alpha + \delta_1} = \frac{\beta_2 \gamma_2}{\delta_2} \frac{1 + \frac{\alpha}{K \beta_2}}{1 + \frac{\gamma_2}{\delta_2} \frac{\alpha}{K} R_{in}}, \gamma_2\right] /. \{\beta_1 \rightarrow \beta 1, \beta_2 \rightarrow \beta 2, \gamma_1 \rightarrow \gamma 1, \gamma_2 \rightarrow \gamma 2, \delta_1 \rightarrow \delta 1, \delta_2 \rightarrow \delta 2, R_{in} \rightarrow Rin\} // \text{Simplify}$$

$$\left\{\left\{\gamma 2 \rightarrow \frac{K \beta 1 \gamma 1 \delta 2}{\alpha^2 + K \beta 2 \delta 1 + \alpha (K \beta 2 - Rin \beta 1 \gamma 1 + \delta 1)}\right\}\right\}$$

■ Bifurcation plots

$\alpha = 1.; \beta 1 = 1.95; \beta 2 = 1.; \gamma 1 = .1; \gamma 2 = .1; \delta 1 = 1.; \delta 2 = 1.; Rin = 15.; K = 10.;$

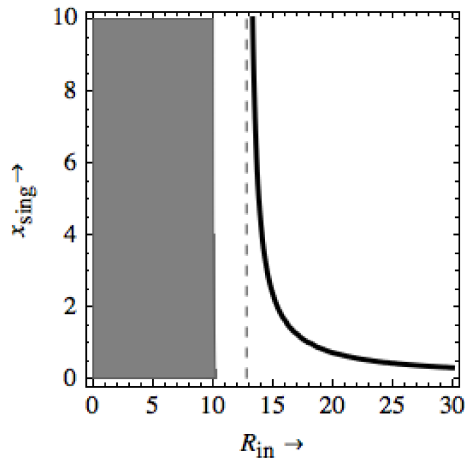
$BP = \text{ContourPlot}[\partial_y \text{Det}_x[y] /. \{y \rightarrow x\}, \{Rin, 0, 30\}, \{x, 0, 10\}, \text{Contours} \rightarrow \{0\}, \text{ContourShading} \rightarrow \text{False}, \text{ContourStyle} \rightarrow \{\text{Thick}\}];$

$XL = \text{ContourPlot}\left[\text{Rin} == \frac{(\alpha + K \beta 2) \gamma 2 (\alpha + \delta 1) - K \beta 1 \gamma 1 \delta 2}{\alpha \beta 1 \gamma 1 \gamma 2}, \{Rin, 0, 30\}, \{x, 0, 10\}, \text{ContourStyle} \rightarrow \{\text{Dashed}\}\right];$

$NV = \text{RegionPlot}[\text{Det0}[x] > 0, \{Rin, 0, 30\}, \{x, 0, 10\}, \text{PlotStyle} \rightarrow \text{Gray}];$

$\text{Show}\{\{BP, XL, NV\}, \text{FrameLabel} \rightarrow \{\text{"Rin"} \rightarrow, \text{"x_sing"} \rightarrow\}, \text{ImageSize} \rightarrow \text{Small}\}$

$\text{Clear}[\alpha, \beta 1, \beta 2, \gamma 1, \gamma 2, \delta 1, \delta 2, Rin, K];$



```
 $\alpha = 1.; \beta_1 = 1.95; \beta_2 = 1.; \gamma_1 = .1; \gamma_2 = .1; \delta_1 = 1.; \delta_2 = 1.; \text{Rin} = 15.; \text{K} = 10.;$ 
```

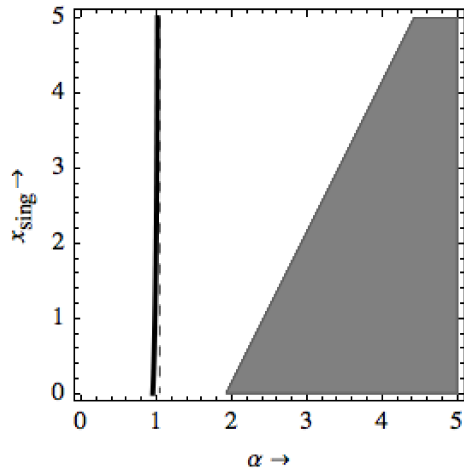
```
BP = ContourPlot[ $\partial_y \text{Det}_x[y] /. \{y \rightarrow x\}$ , { $\alpha$ , 0, 5}, { $x$ , 0, 5}, Contours -> {0}, ContourShading -> False, ContourStyle -> {Thick}];
```

```
XL = ContourPlot[ $\alpha == \frac{-\text{K} \beta_2 \gamma_2 + \text{Rin} \beta_1 \gamma_1 \gamma_2 - \gamma_2 \delta_1 + \sqrt{\gamma_2 (-4 \text{K} \beta_2 \gamma_2 \delta_1 + \gamma_2 (\text{K} \beta_2 - \text{Rin} \beta_1 \gamma_1 + \delta_1)^2 + 4 \text{K} \beta_1 \gamma_1 \delta_2)}}{2 \gamma_2}$ , { $\alpha$ , 0, 5}, { $x$ , 0, 5}, ContourStyle -> {Dashed}];
```

```
NV = RegionPlot[ $\text{Det0}[x] > 0$ , { $\alpha$ , 0, 5}, { $x$ , 0, 5}, PlotStyle -> Gray];
```

```
Show[{BP, XL, NV}, FrameLabel -> {" $\alpha$  ->", " $x_{\text{sing}}$ ->"}, ImageSize -> Small]
```

```
Clear[ $\alpha$ ,  $\beta_1$ ,  $\beta_2$ ,  $\gamma_1$ ,  $\gamma_2$ ,  $\delta_1$ ,  $\delta_2$ , Rin, K];
```



$$\alpha = \frac{\alpha \gamma_2 (\alpha - \text{Rin} \beta_1 \gamma_1 + \delta_1)}{\alpha \beta_2 \gamma_2 + \beta_2 \gamma_2 \delta_1 - \beta_1 \gamma_1 \delta_2}$$

```
 $\alpha = 1.; \beta_1 = 1.95; \beta_2 = 1.; \gamma_1 = .1; \gamma_2 = .1; \delta_1 = 1.; \delta_2 = 1.; \text{Rin} = 15.; \text{K} = 10.;$ 
```

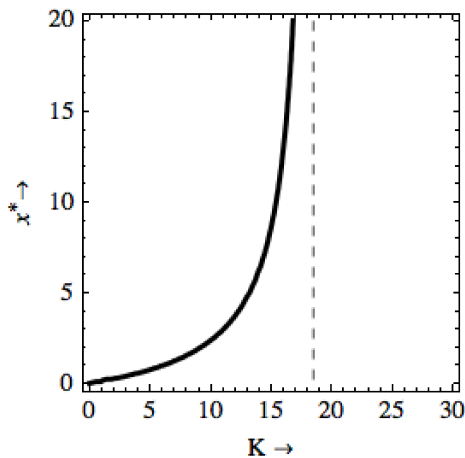
```
BP = ContourPlot[ $\partial_y \text{Det}_x[y] /. \{y \rightarrow x\}$ , {K, 0, 30}, { $x$ , 0, 20}, Contours -> {0}, ContourShading -> False, ContourStyle -> {Thick}];
```

```
XL = ContourPlot[ $\text{K} == -\frac{\alpha \gamma_2 (\alpha - \text{Rin} \beta_1 \gamma_1 + \delta_1)}{\alpha \beta_2 \gamma_2 + \beta_2 \gamma_2 \delta_1 - \beta_1 \gamma_1 \delta_2}$ , {K, 0, 30}, { $x$ , 0, 20}, ContourStyle -> {Dashed}];
```

```
NV = RegionPlot[ $\text{Det0}[x] > 0$ , {K, 0, 30}, { $x$ , 0, 20}, PlotStyle -> Gray];
```

```
Show[{BP, XL, NV}, FrameLabel -> {"K ->", " $x^*$ ->"}, ImageSize -> Small]
```

```
Clear[ $\alpha$ ,  $\beta_1$ ,  $\beta_2$ ,  $\gamma_1$ ,  $\gamma_2$ ,  $\delta_1$ ,  $\delta_2$ , Rin, K];
```



$\alpha = 1.; \beta_1 = 1.95; \beta_2 = 1.; \gamma_1 = .1; \gamma_2 = .1; \delta_1 = 1.; \delta_2 = 1.; \text{Rin} = 15.; \text{K} = 10.;$

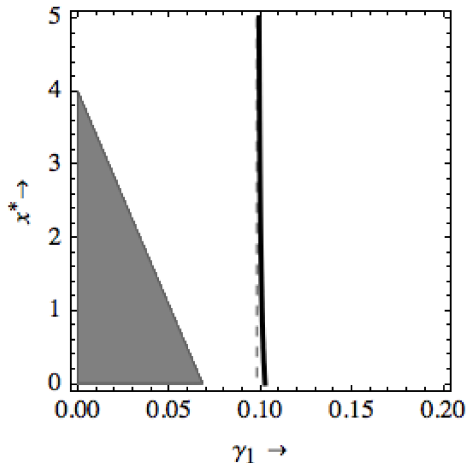
$\text{BP} = \text{ContourPlot}[\partial_y \text{Det}_x[\mathbf{y}] /. \{\mathbf{y} \rightarrow \mathbf{x}\}, \{\gamma_1, 0, .2\}, \{x, 0, 5\}, \text{Contours} \rightarrow \{0\}, \text{ContourShading} \rightarrow \text{False}, \text{ContourStyle} \rightarrow \{\text{Thick}\}];$

$\text{XL} = \text{ContourPlot}\left[\gamma_1 = \frac{(\alpha + \text{K} \beta_2) \gamma_2 (\alpha + \delta_1)}{\beta_1 (\text{Rin} \alpha \gamma_2 + \text{K} \delta_2)}\right], \{\gamma_1, 0, .2\}, \{x, 0, 5\}, \text{ContourStyle} \rightarrow \{\text{Dashed}\}];$

$\text{NV} = \text{RegionPlot}[\text{Det0}[\mathbf{x}] > 0, \{\gamma_1, 0, .2\}, \{x, 0, 5\}, \text{PlotStyle} \rightarrow \text{Gray}];$

$\text{Show}[\{\text{BP}, \text{XL}, \text{NV}\}, \text{FrameLabel} \rightarrow \{\gamma_1 \rightarrow, "x^*" \rightarrow\}, \text{ImageSize} \rightarrow \text{Small}]$

$\text{Clear}[\alpha, \beta_1, \beta_2, \gamma_1, \gamma_2, \delta_1, \delta_2, \text{Rin}, \text{K}];$



$\alpha = 1.; \beta_1 = 1.95; \beta_2 = 1.; \gamma_1 = .1; \gamma_2 = .1; \delta_1 = 1.; \delta_2 = 1.; \text{Rin} = 15.; \text{K} = 10.;$

$\text{BP} = \text{ContourPlot}[\partial_y \text{Det}_x[\mathbf{y}] /. \{\mathbf{y} \rightarrow \mathbf{x}\}, \{\gamma_2, 0, .2\}, \{x, 0, 5\}, \text{Contours} \rightarrow \{0\}, \text{ContourShading} \rightarrow \text{False}, \text{ContourStyle} \rightarrow \{\text{Thick}\}];$

$\text{XL} = \text{ContourPlot}\left[\gamma_2 = \frac{\text{K} \beta_1 \gamma_1 \delta_2}{\alpha^2 + \text{K} \beta_2 \delta_1 + \alpha (\text{K} \beta_2 - \text{Rin} \beta_1 \gamma_1 + \delta_1)}\right], \{\gamma_2, 0, .2\}, \{x, 0, 5\}, \text{ContourStyle} \rightarrow \{\text{Dashed}\}];$

$\text{NV} = \text{RegionPlot}[\text{Det0}[\mathbf{x}] > 0, \{\gamma_2, 0, .2\}, \{x, 0, 5\}, \text{PlotStyle} \rightarrow \text{Gray}];$

$\text{Show}[\{\text{BP}, \text{XL}, \text{NV}\}, \text{FrameLabel} \rightarrow \{\gamma_2 \rightarrow, "x^*" \rightarrow\}, \text{ImageSize} \rightarrow \text{Small}]$

$\text{Clear}[\alpha, \beta_1, \beta_2, \gamma_1, \gamma_2, \delta_1, \delta_2, \text{Rin}, \text{K}];$

