The Lotka - Volterra cannibalism time budget model

Strategies:

x: proportion of time spent attacking conspecifics;
1-x: proportion of time harvesting the resouce;

$x \in [0,1]$ set of possible strategies;

Resident dynamics :

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

$$\frac{d}{dt} n_i = \epsilon \alpha R (1 - x_i)\, n_i - (1 - x_i)\, n_i \sum_{j=1}^{k} \beta(x_j)\, x_j\, n_j$$

$$+ \gamma \beta(x_i)\, x_i\, n_i \sum_{j=1}^{k} (1 - x_j)\, n_j - \delta\, n_i \qquad \text{for } i = 1, \ldots, k$$

Feedback environment :

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

$$\frac{1}{n_i} \frac{dn_i}{dt} = \epsilon \alpha R (1 - x_i) - (1 - x_i) \sum_{j=1}^{k} \beta(x_j)\, x_j\, n_j$$

$$+ \gamma \beta(x_i)\, x_i \sum_{j=1}^{k} (1 - x_j)\, n_j - \delta \qquad \text{for } i = 1, \ldots, k$$

Rewrite :

$$\frac{1}{n_i} \frac{dn_i}{dt} = \epsilon \alpha E_1 (1 - x_i) - (1 - x_i) E_2 + \gamma \beta (x_i)\, x_i\, E_3 - \delta$$

with

$$\frac{d\mathbf{E_1}}{dt} = r\,\mathbf{E_1}\left(1 - \frac{\mathbf{E_1}}{K}\right) - \alpha\,\mathbf{E_1}\cdot\mathbf{E_3}$$ (resource densit

$$\mathbf{E_2} = \sum_{j=1}^{k} \beta(x_j)\, x_j\, n_j$$ ("cannibalism pressure

$$\mathbf{E_3} = \sum_{j=1}^{k} (1 - x_j)\, n_j$$ ("prey" densi

Invader dynamics :

$$\frac{1}{m}\frac{dm}{dt} = \epsilon\,\alpha\,(1-y)\,E_1 - (1-y)\,E_2 + \gamma\,\beta(y)\,y\,E_3 - \delta$$

Invasion fitness :

$$s_E(y) = \epsilon\,\alpha\,(1-y)\,\langle E_1\rangle - (1-y)\,\langle E_2\rangle + \gamma\,\beta(y)\,y\,\langle E_3\rangle - \delta$$

Effective dimension of *E* :

$$s_E(y) = (1-y)\left(\boxed{\epsilon\,\alpha\,\langle E_1\rangle - \langle E_2\rangle}\right) + \beta[y]\,y\,\boxed{\gamma\,\langle E_3\rangle} - \delta$$

Hence, the effective dimension is 2 with
$\boxed{\epsilon\,\alpha\,\langle E_1\rangle - \langle E_2\rangle}$ and $\boxed{\langle E_3\rangle}$
and at most two resident types can coexist at a time;

Virgin environment :

$\langle E_1\rangle = K$; $\langle E_2\rangle = 0$; $\langle E_3\rangle = 0$;

$$s_{vir}(y) = \epsilon\,\alpha\,(1-y)\,K - \delta$$

$$s_{vir}(y) > 0 \Longleftrightarrow y < 1 - \frac{\delta}{K\,\alpha\,\epsilon}$$

Monomorphic resident population :

$$\frac{1}{R}\frac{dR}{dt} = r\left(1 - \frac{R}{K}\right) - \alpha\ (1 - x)\ n$$

$$\frac{1}{n}\frac{dn}{dt} = \epsilon\,\alpha\,R\ (1 - x) - \beta[x]\ (1 - x)\ x\,n + \gamma\,\beta[x]\ (1 - x)\ x\,n - \delta$$

Assume Log – bounded population densities

$$\langle R\rangle = \frac{-K\,\alpha\,\delta + K\,r\,x\ (-1 + \gamma)\ \beta[x]}{K\ (-1 + x)\ \alpha^2\,\epsilon + r\,x\ (-1 + \gamma)\ \beta[x]}$$

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

Dimorphic resident population :

$$s_E(x_1) = s_E(x_2) = 0$$

$$0 = (1 - x_1)\ \left(\boxed{\alpha\,\epsilon\,\langle E_1\rangle - \langle E_2\rangle}\right) + x_1\,\beta[x_1]\ \boxed{\gamma\,\langle E_3\rangle} - \delta$$

$$0 = (1 - x_2)\ \left(\boxed{\alpha\,\epsilon\,\langle E_1\rangle - \langle E_2\rangle}\right) + x_2\,\beta[x_2]\ \boxed{\gamma\,\langle E_3\rangle} - \delta$$

and so

$$\alpha\,\epsilon\,\langle E_1\rangle - \langle E_2\rangle = \frac{-\delta\,x_1\,\beta[x_1] + \delta\,x_2\,\beta[x_2]}{x_2\,\beta[x_2] + x_1\ ((-1 + x_2)\ \beta[x_1] - x_2\,\beta[x_2])}$$

$$\gamma\,\langle E_3\rangle = \frac{\delta\ (-x_1 + x_2)}{x_2\,\beta[x_2] + x_1\ ((-1 + x_2)\ \beta[x_1] - x_2\,\beta[x_2])}$$

Lotka - Volterra cannibalism time budget m

- **Virgin environment:**

In[1]:= $x_{crit} := 1 - \frac{\delta}{K\,\alpha\,\epsilon}$; (* maximum viable strategy *)

- **Monomorphic resident population dynamics:**

In[2]:= $R[x\_] := \frac{-K\,\alpha\,\delta + K\,r\,x\,(-1+\gamma)\,\beta[x]}{K\,(-1+x)\,\alpha^2\,\epsilon + r\,x\,(-1+\gamma)\,\beta[x]}$

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

- **Invasion fitness and gradient**

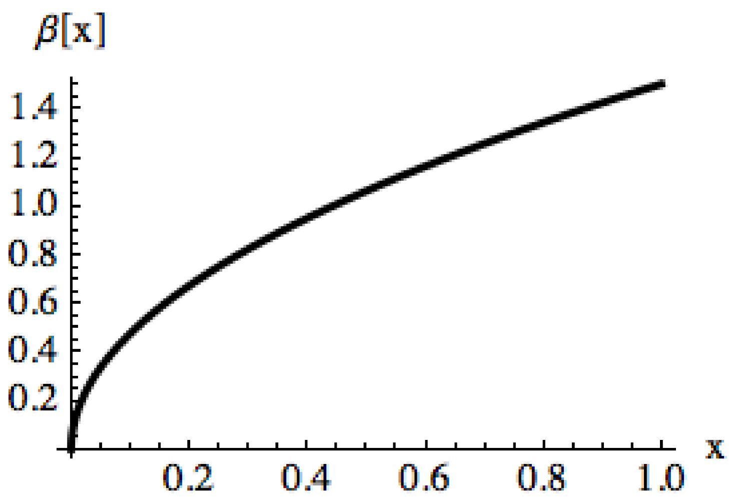
In[4]:= $s_{x\_}[y\_] := \epsilon\,\alpha\,R[x]\,(1-y) - (1-y)\,\beta[x]\,x\,n[x] + \gamma\,\beta[y]\,y\,(1-x)\,n$

$ds[x\_] := \partial_y s_x[y]$ /. {y → x};

- **Numerics:**

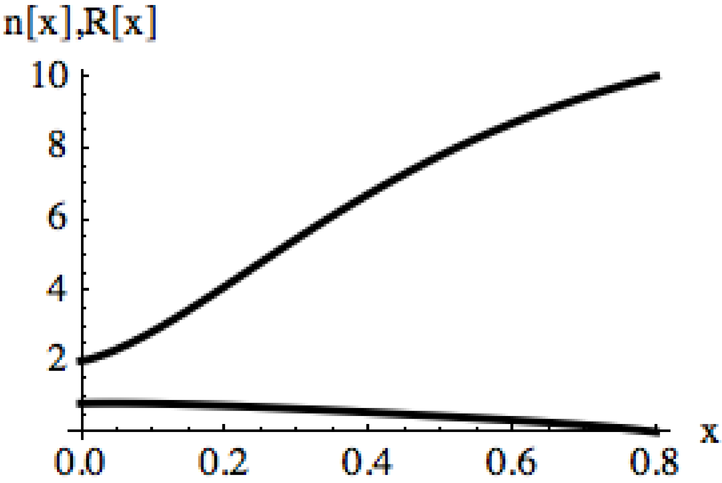
In[6]:= α = 1; γ = 0.2; δ = 0.1; ϵ = 0.05; r = 1; K = 10;
β0 = 0.; β1 = 1.5; p = .5;
$\beta[x\_] := \beta 1\, x^p + \beta 0$;

In[9]:= Plot[β[x], {x, 0, 1}, PlotStyle → {Black, Thick}, AxesLabel → {

Out[9]=


In[10]:=
```
Plot[{R[x], n[x]}, {x, 0, x_crit}, PlotStyle → {{Black, Thick}},
```

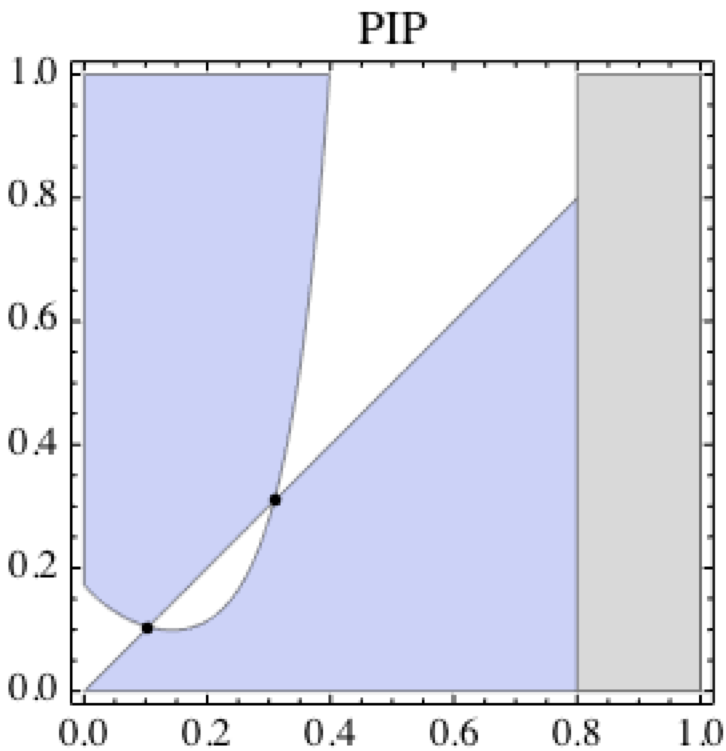
Out[10]=



In[11]:=
```
(* Singularities *)
x1 = x /. Last[Minimize[{Abs[ds[x]], .0 < x < .2}, x]]; x2 = x /.
```

In[12]:=
```
Show[
 RegionPlot[s_x[y] > 0, {x, 0, 1}, {y, 0, 1}, PlotPoints → 50],
 RegionPlot[n[x] ≤ 0, {x, 0, 1}, {y, 0, 1}, PlotStyle → LightGr
 Graphics[Point[{{x1, x1}, {x2, x2}}]],
 PlotLabel → "PIP", ImageSize → Small]
```

Out[12]=



Critical functions analysis

■ Reset:

In[13]:=
```
Clear[α, β, γ, δ, ϵ, r, K];
```

■ Critical functions:

In[14]:=
```
(* Equation for singular strategy or
   differential equation for critical function β=β_crit *)0 =
```

Out[14]=

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

In[15]:=
```
DSolve[0 == ds[x], β[x], x] // FullSimplify
```

Out[15]=

$$\left\{\left\{\beta[x] \to \frac{-\frac{K\ (-1+x)\ \alpha^2\ \epsilon}{r\ (-1+\gamma)} + (-1+x)^{\frac{1}{\gamma}}\ (\delta + K\ (-1+x)\ \alpha\ \epsilon)^{\frac{-1+\gamma}{\gamma}}\ C[1]}{x}\right\}\right\}$$

In[16]:=

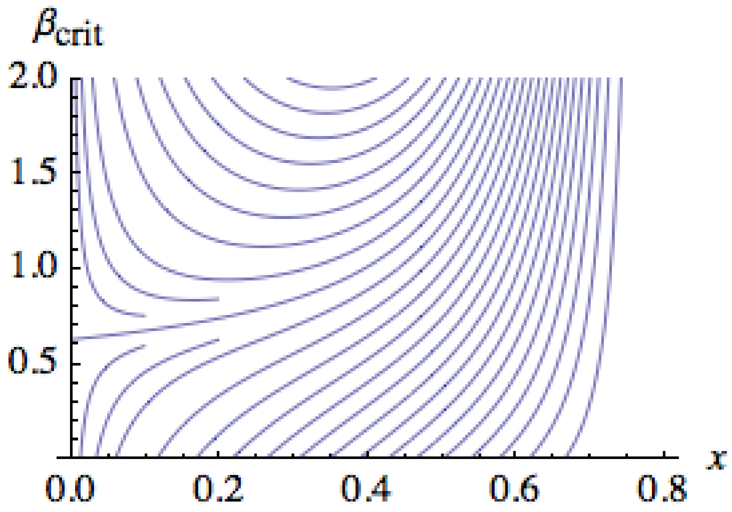
$$\beta_{crit}[x\_,\ c\_] := \frac{1}{x}\left(-\frac{K\ (-1+x)\ \alpha^2\ \epsilon}{r\ (-1+\gamma)} + (-1+x)^{\frac{1}{\gamma}}\ (\delta + K\ (-1+x)\ \alpha\ \epsilon)\right.$$

■ Numerics:

In[17]:=
```
α = 1; γ = 0.2; δ = 0.1; ϵ = 0.05; r = 1; K = 10;
```

In[18]:=
```
critFunc =
 Show[
  Plot[Table[βcrit[x, c], {c, -.024, -.001, .001}], {x, 0, xcri
  Plot[Table[βcrit[x, c], {c, {-.0165, -.01545}}], {x, 0, .2},
  Plot[Table[βcrit[x, c], {c, {-.0162, -.0158}}], {x, 0, .1}, I
  AxesLabel → {x, βcrit}, ImageSize → Small]
```

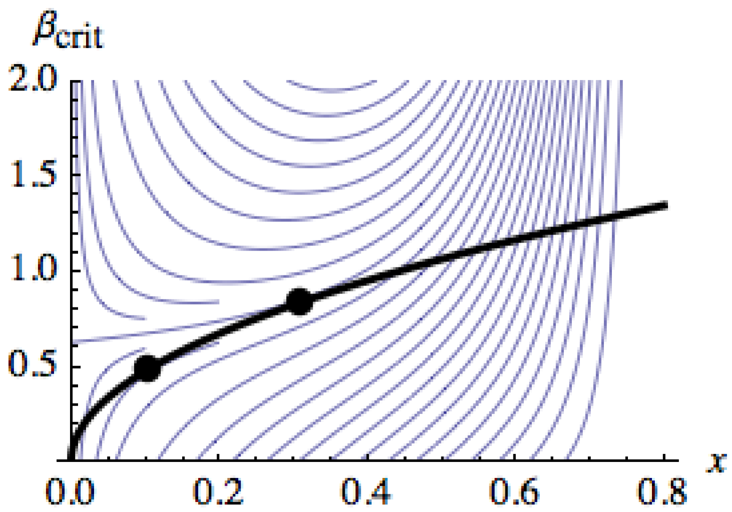
Out[18]=



■ **Example 1**

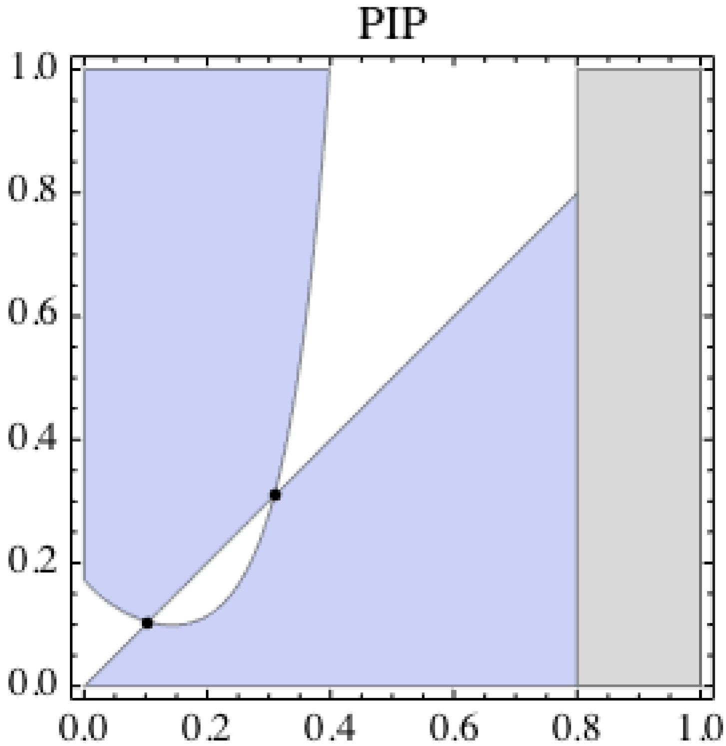
In[19]:=
```
β[x_] := β1 x^p + β0; β0 = 0.; β1 = 1.5; p = .5;

Show[
 critFunc,
 Plot[β[x], {x, 0, xcrit}, PlotStyle → {Black, Thick}],
 Graphics[{PointSize[Large], Point[{{x1, β[x1]}, {x2, β[x2]}}
 AxesLabel → {x, βcrit}, ImageSize → Small]
```

Out[20]=



In[21]:=
```
Show[
 RegionPlot[sx[y] > 0, {x, 0, 1}, {y, 0, 1}, PlotPoints → 50],
 RegionPlot[n[x] ≤ 0, {x, 0, 1}, {y, 0, 1}, PlotStyle → LightGr
 Graphics[Point[{{x1, x1}, {x2, x2}}]],
 PlotLabel → "PIP", ImageSize → Small]
```

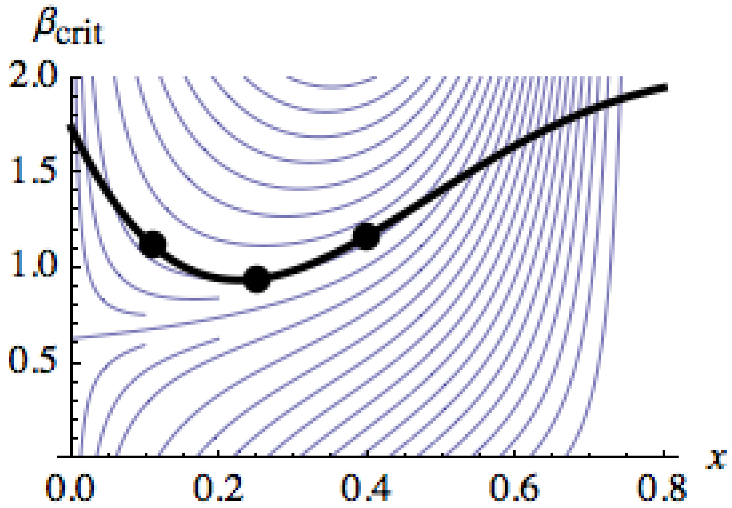
Out[21]=



■ Example 2

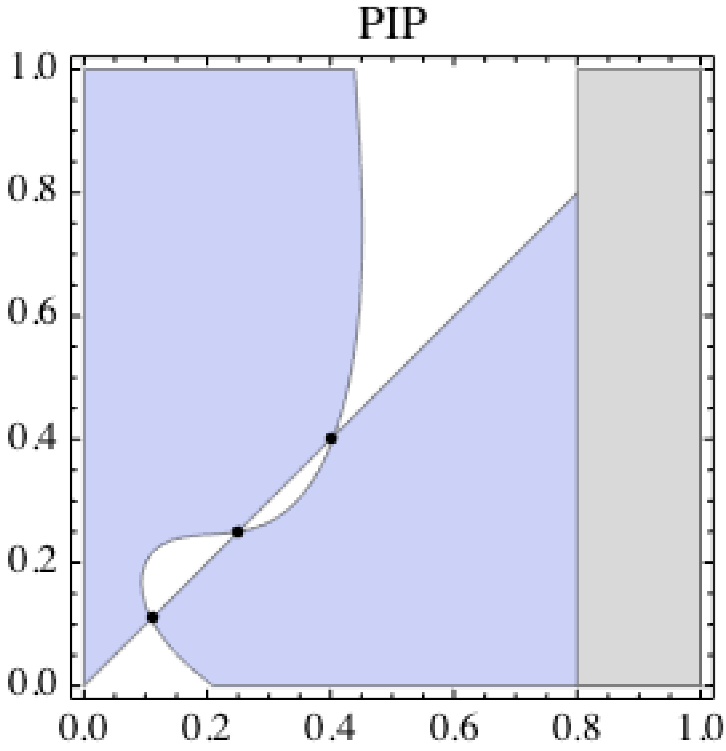
In[22]:=
```
β[x_] := 2 - 9 (0.03 + x)^p (1 - x)^q; p = 1; q = 3;

(* Singularities *)
x1 = x /. Last[Minimize[{Abs[ds[x]], .0 < x < .2}, x]]; x2 = x /.
x3 = x /. Last[Minimize[{Abs[ds[x]], .3 < x < .4}, x]];

Show[
 critFunc,
 Plot[β[x], {x, 0, x_crit}, PlotStyle → {Black, Thick}],
 Graphics[{PointSize[Large], Point[{{x1, β[x1]}, {x2, β[x2]}
 AxesLabel → {x, β_crit}, ImageSize → Small]
```

Out[25]=



In[26]:=
```
Show[
 RegionPlot[sx[y] > 0, {x, 0, 1}, {y, 0, 1}, PlotPoints → 100],
 RegionPlot[n[x] ≤ 0, {x, 0, 1}, {y, 0, 1}, PlotStyle → LightGr
 Graphics[Point[{{x1, x1}, {x2, x2}, {x3, x3}}]],
 PlotLabel → "PIP", ImageSize → Small]
```

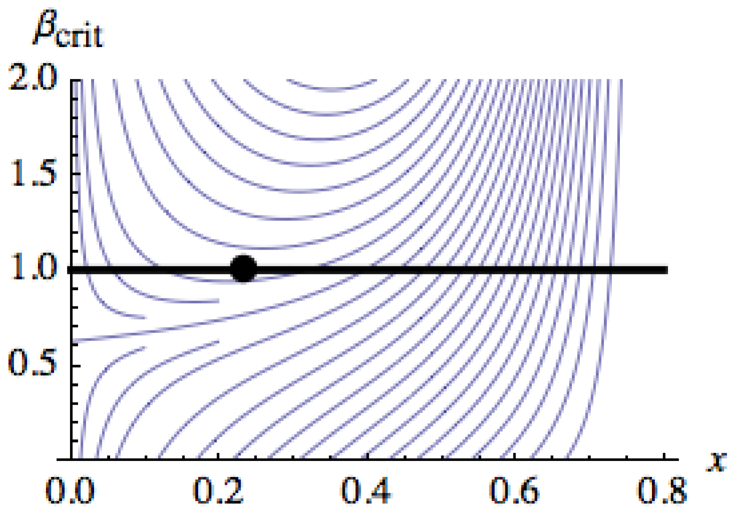
Out[26]=



- **Example 3**

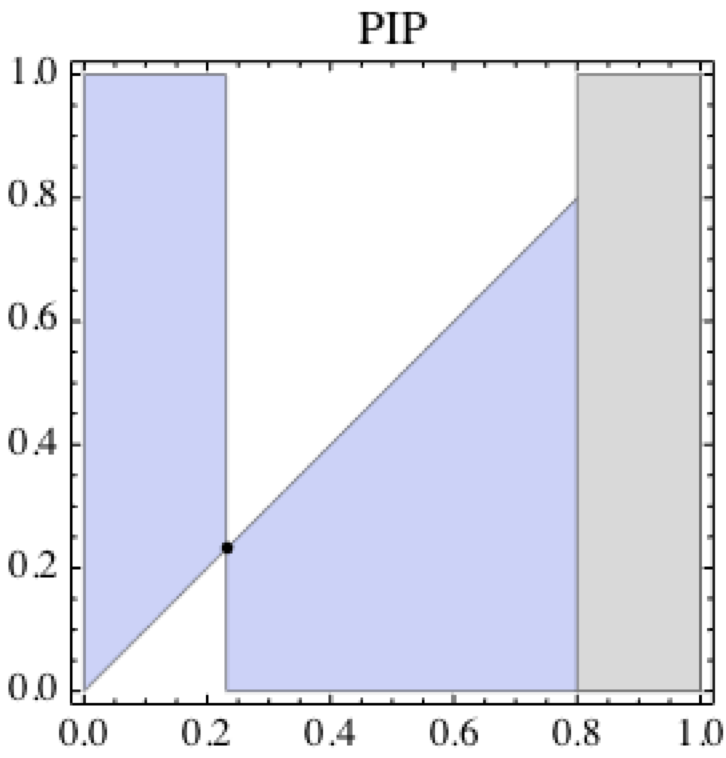
In[27]:=
```
β[x_] := 1;

(* Singularities *)
x1 = x /. Last[Minimize[{Abs[ds[x]], .1 < x < .3}, x]];

Show[
 critFunc,
 Plot[β[x], {x, 0, xcrit}, PlotStyle → {Black, Thick}],
 Graphics[{PointSize[Large], Point[{{x1, β[x1]}}]}],
 AxesLabel → {x, βcrit}, ImageSize → Small]
```

Out[29]=



In[30]:=
```
Show[
 RegionPlot[s_x[y] > 0, {x, 0, 1}, {y, 0, 1}, PlotPoints → 100],
 RegionPlot[n[x] ≤ 0, {x, 0, 1}, {y, 0, 1}, PlotStyle → LightGr
 Graphics[Point[{{x1, x1}}]],
 PlotLabel → "PIP", ImageSize → Small]
```

Out[30]=



- **Reset:**

In[31]:=
```
Clear[α, β, γ, δ, ϵ, r, K];
```

- **Can we have evolutionary branching?**

In[32]:=
```
(* evolutionary branching is possible iff
   the cross derivative of s_x[y] is negative *)

C_12[x_] := ∂_{x,y} s_x[y] /. {y → x}; (* C12*)
```

In[33]:=
```
(* Want to know the value of βcrit[x,c] and
   ∂xβcrit[x,c] at the point (x,β); the first
   is equal to β; the second is found from
   the singularity equation 0==ds[x] *)

Solve[0 == ds[x], β'[x]] /. {β[x] → β} // FullSimplify
```

Out[33]= $\left\{\left\{\beta'[x] \to \frac{r\,\beta\,(x+\gamma-x\,\gamma)\,\delta + K\,(-1+x)\,\alpha\,(r\,\beta\,\gamma-\alpha\,\delta)\,\epsilon}{r\,(-1+x)\,x\,\gamma\,(\delta+K\,(-1+x)\,\alpha\,\epsilon)}\right\}\right\}$

In[34]:= $C_{12}[x]$ /. $\left\{\beta[x] \to \beta,\ \beta'[x] \to \frac{r\,\beta\,(x+\gamma-x\,\gamma)\,\delta + K\,(-1+x)\,\alpha\,(r\,\beta\,\gamma -}{r\,(-1+x)\,x\,\gamma\,(\delta+K\,(-1+x)\,\alpha\,\epsilon)}\right.$

Out[34]= $\frac{\delta^2}{(-1+x)^2\,\gamma\,(\delta+K\,(-1+x)\,\alpha\,\epsilon)}$

In[35]:=
```
(* cross derivative C12 at (x,β) *)
```

$C_{12}[x\_, \beta\_] := \frac{\delta^2}{(1-x)^2\,\gamma\,(\delta-K\,(1-x)\,\alpha\,\epsilon)}$;

Notice that

$$C_{12}[x, \beta] = \frac{-\delta^2}{K\,\alpha\,\epsilon\,(1-x)^2\,\gamma\,(x_{crit}-x)}$$

where

$$0 \le x < x_{crit} := 1 - \frac{\delta}{K\,\alpha\,\epsilon} \quad (*\ \text{viability condition}\ *)$$

Hence

$$C_{12}[x, \beta] < 0$$

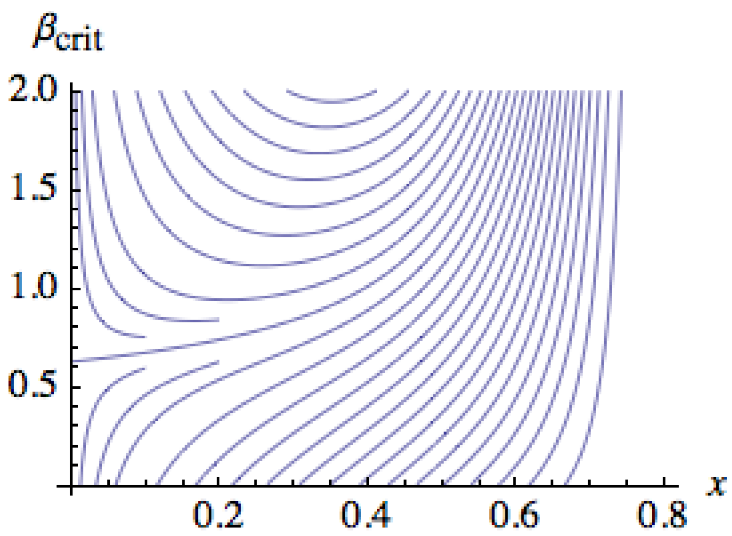
for every viable x. So, branching is possible everywhere.

Numerics

Example 1

In[36]:=
```
α = 1; γ = 0.2; δ = 0.1; ϵ = 0.05; r = 1; K = 10;

Show[
 RegionPlot[CD[x, β] < 0, {x, 0, x_crit}, {β, 0, 2}, PlotStyle → I
 critFunc,
 Frame → False, Axes → True, AspectRatio → 1.5^-1, AxesLabel → {
```

Out[37]=



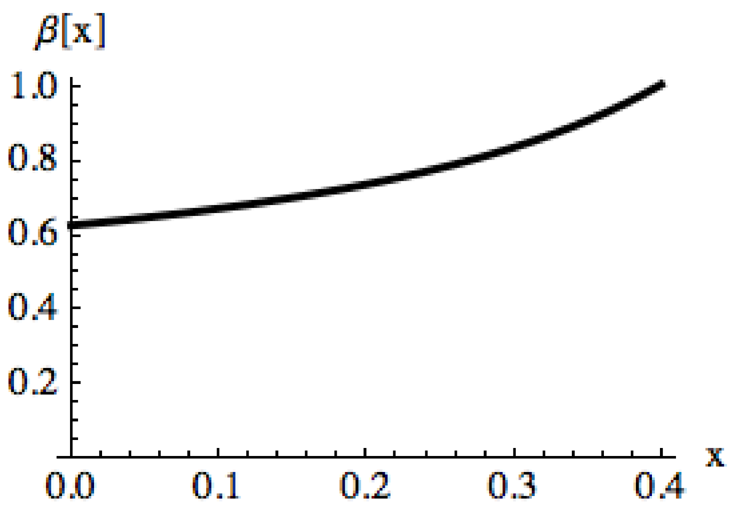
In[38]:=
```
(* Conclusion: branching is possible everywhere *)
```

Set β equal to critical function

In[39]:=
```
β[x_] := Max[0, β_crit[x, -.016]];
```

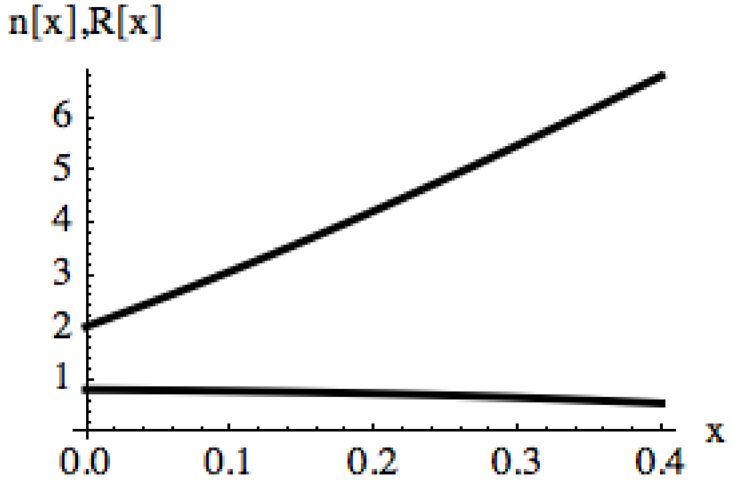
In[40]:=
```
Plot[β[x], {x, 0, .4}, PlotRange → {0, Automatic}, PlotStyle →
```

Out[40]=



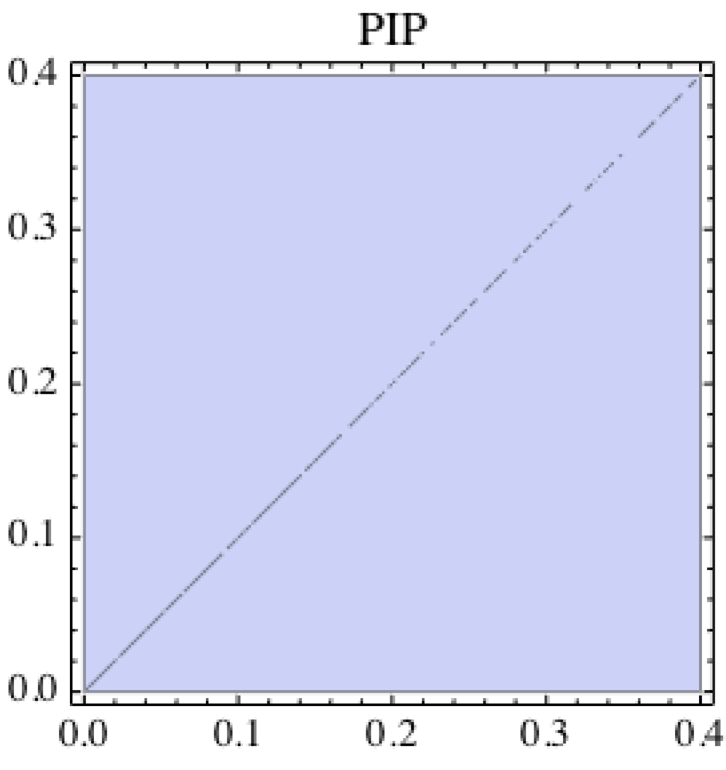
In[41]:=
```
Plot[{R[x], n[x]}, {x, 0, .4}, PlotStyle → {{Black, Thick}}, A:
```

Out[41]=



In[42]:=
```
Show[
 RegionPlot[sx[y] > 0, {x, 0, .4}, {y, 0, .4}, PlotPoints → 100]
 RegionPlot[n[x] ≤ 0, {x, 0, .4}, {y, 0, .4}, PlotStyle → Light
 PlotLabel → "PIP", ImageSize → Small]
```

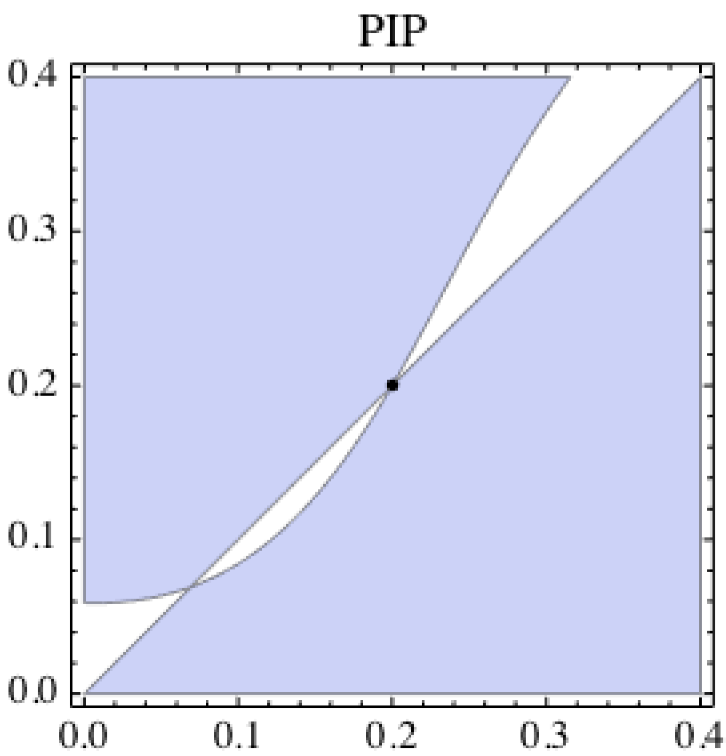
Out[42]=



- **First perturbation of β**

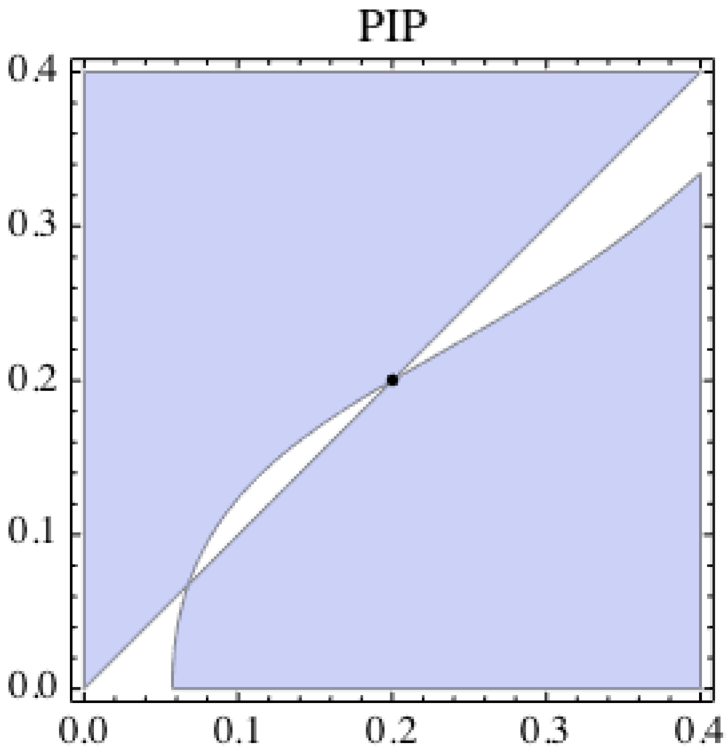
In[43]:=
```
β[x_] := Max[0, e^(-2 (x-.2)^2) β_crit[x, -.016]];

x1 = x /. Last[Minimize[{Abs[ds[x]], .2 < x < .4}, x]];

Show[
 RegionPlot[s_x[y] > 0, {x, 0, .4}, {y, 0, .4}, PlotPoints → 100]
 RegionPlot[n[x] ≤ 0, {x, 0, .4}, {y, 0, .4}, PlotStyle → Light
 Graphics[Point[{{x1, x1}}]],
 PlotLabel → "PIP", ImageSize → Small]
```

Out[45]=



- **Second perturbation of β**

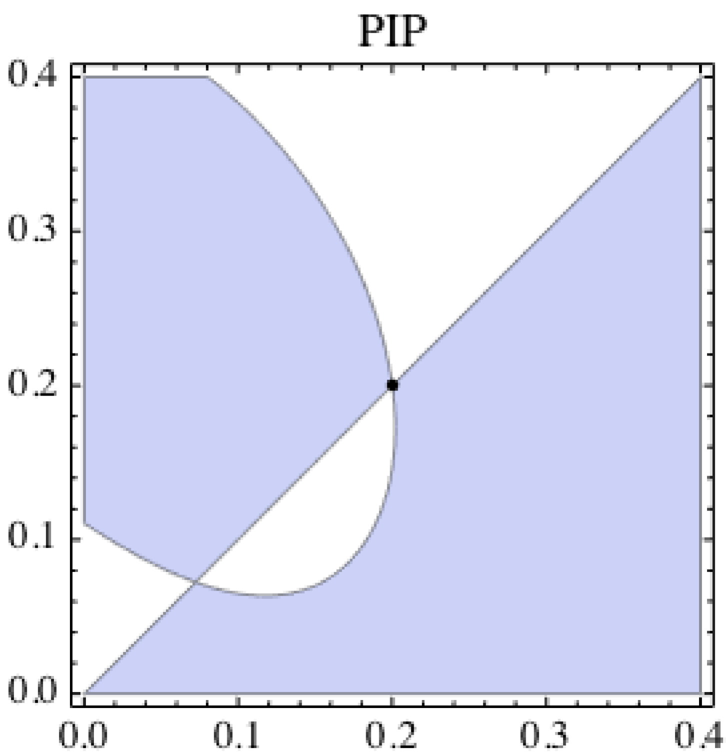
In[46]:=
```
β[x_] := Max[0, e^(+2 (x-.2)^2) β_crit[x, -.016]];

x1 = x /. Last[Minimize[{Abs[ds[x]], .2 < x < .4}, x]];

Show[
 RegionPlot[s_x[y] > 0, {x, 0, .4}, {y, 0, .4}, PlotPoints → 100]
 RegionPlot[n[x] ≤ 0, {x, 0, .4}, {y, 0, .4}, PlotStyle → Light
 Graphics[Point[{{x1, x1}}]],
 PlotLabel → "PIP", ImageSize → Small]
```

Out[48]=


■ Third perturbation of β

In[49]:=
```
β[x_] := Max[0, e^(-10 (x-.2)^2) β_crit[x, -.016]];

x1 = x /. Last[Minimize[{Abs[ds[x]], .2 < x < .4}, x]];

Show[
 RegionPlot[s_x[y] > 0, {x, 0, .4}, {y, 0, .4}, PlotPoints → 100]
 RegionPlot[n[x] ≤ 0, {x, 0, .4}, {y, 0, .4}, PlotStyle → Light
 Graphics[Point[{{x1, x1}}]],
 PlotLabel → "PIP", ImageSize → Small]
```

Out[51]=



- **Foutrh perturbation of β**

```
In[52]:= β[x_] := Max[0, e^(+10 (x-.2)^2) β_crit[x, -.016]];

x1 = x /. Last[Minimize[{Abs[ds[x]], .2 < x < .4}, x]];

Show[
 RegionPlot[s_x[y] > 0, {x, 0, .4}, {y, 0, .4}, PlotPoints → 100
 RegionPlot[n[x] ≤ 0, {x, 0, .4}, {y, 0, .4}, PlotStyle → Light
 Graphics[Point[{{x1, x1}}]],
 PlotLabel → "PIP", ImageSize → Small]
```

Out[54]=