

The Lotka - Volterra cannibalism time budget model

Resident dynamics

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

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

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

Feedback environment

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

$$\frac{1}{n_i} \frac{d}{dt} n_i = \epsilon \alpha R (1 - x_i) - \delta (1 - x_i) -$$

$$(1 - x_i) \sum_{j=1}^k \beta[x_j] x_j n_j + \gamma \beta[x_i] x_i \sum_{j=1}^k (1 - x_j) n_j - \delta x_i$$

$$= \epsilon \alpha R (1 - x_i) - \delta - (1 - x_i) \sum_{j=1}^k \beta[x_j] x_j n_j + \gamma \beta[x_i] x_i \sum_{j=1}^k (1 - x_j) n_j$$

$$= A(x_i, E);$$

where

$$E = (E_1, E_2, E_3)$$

$$\frac{d}{dt} E_1 = r E_1 \left(1 - \frac{E_1}{K} \right) - \alpha E_1 E_3 \quad \text{"Resource density"}$$

$$E_2 = \sum_{j=1}^k \beta[x_j] x_j n_j \quad \text{"cannibalism pressure"}$$

$$E_3 = \sum_{j=1}^k (1 - x_j) n_j \quad \text{"'prey' density"}$$

Invader dynamics

$$\frac{1}{m} \frac{d}{dt} m = A(y, E) = \epsilon \alpha E_1 (1 - y) - \delta - (1 - y) E_2 + \gamma \beta[y] y E_3$$

Invasion fitness

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

Effective dimension of E

Principle of selective neutrality ($R = E_1$ is assumed to be log - bounded)

$$0 = r \left(1 - \frac{\langle E_1 \rangle}{K} \right) - \alpha \langle E_3 \rangle \Leftrightarrow \langle E_1 \rangle = K \left(1 - \frac{\alpha}{r} \langle E_3 \rangle \right)$$

Hence the effective dimension is 2, and

$$\begin{aligned} s_E[y] &= \epsilon \alpha (1 - y) K \left(1 - \frac{\alpha}{r} \langle E_3 \rangle \right) - \delta - (1 - y) \langle E_2 \rangle + \gamma \beta[y] y \langle E_3 \rangle \\ &= \epsilon \alpha (1 - y) K - \delta - (1 - y) \langle E_2 \rangle + \left(\gamma \beta[y] y - \epsilon \alpha K \frac{\alpha}{r} (1 - y) \right) \langle E_3 \rangle \end{aligned}$$

and at most two resident types can coexist at a time.

Monomorphic resident population

$$\begin{cases} \langle E_2 \rangle = \beta[x] x \langle n \rangle \\ \langle E_3 \rangle = (1 - x) \langle n \rangle \end{cases} \Leftrightarrow \langle E_2 \rangle = \frac{\beta[x] x}{1 - x} \langle E_3 \rangle$$

$$s_E[y] = \epsilon \alpha (1 - y) K - \delta - (1 - y) \frac{\beta[x] x}{1 - x} \langle E_3 \rangle + \left(\gamma \beta[y] y - \epsilon \alpha K \frac{\alpha}{r} (1 - y) \right) \langle E_3 \rangle;$$

$$0 = s_E(x) \Leftrightarrow 0 = \epsilon \alpha (1 - x) K - \delta - \beta[x] x \langle E_3 \rangle + \left(\gamma \beta[x] x - \epsilon \alpha K \frac{\alpha}{r} (1 - x) \right) \langle E_3 \rangle$$

$$\Rightarrow \langle E_3 \rangle = (r(\delta + K(-1 + x) \epsilon \alpha)) / (K(-1 + x) \epsilon \alpha^2 + r x (-1 + \gamma) \beta[x])$$

$$\Rightarrow s_E^{\text{mon}}[y] = s_x[y] = \epsilon \alpha (1 - y) K - \delta - (1 - y) \langle E_2 \rangle + \left(\gamma \beta[y] y - \epsilon \alpha K \frac{\alpha}{r} (1 - y) \right) \langle E_3 \rangle$$

$$\begin{aligned} &= -\delta - K(-1 + y) \epsilon \alpha - (r x (-1 + y) (\delta + K(-1 + x) \epsilon \alpha) \beta[x]) / \\ &\quad \left((-1 + x) (K(-1 + x) \epsilon \alpha^2 + r x (-1 + \gamma) \beta[x]) \right) \\ &\quad + \left((\delta + K(-1 + x) \epsilon \alpha) (K(-1 + y) \alpha \epsilon \alpha + r y \gamma \beta[y]) \right) / \\ &\quad (K(-1 + x) \epsilon \alpha^2 + r x (-1 + \gamma) \beta[x]) \end{aligned}$$

Dimorphic resident population (x_1, x_2)

$$0 = r \left(1 - \frac{\langle E_1 \rangle}{K} \right) - \alpha \langle E_3 \rangle$$

$$0 = \epsilon \alpha (1 - x_1) \langle E_1 \rangle - \delta - (1 - x_1) \langle E_2 \rangle + \gamma \beta[x_1] x_1 \langle E_3 \rangle$$

$$0 = \epsilon \alpha (1 - x_2) \langle E_1 \rangle - \delta - (1 - x_2) \langle E_2 \rangle + \gamma \beta[x_2] x_2 \langle E_3 \rangle$$

$$\begin{aligned} \Rightarrow \langle E_1 \rangle &= (K (x_2 (-\alpha \delta + r \gamma \beta[x_2])) + x_1 (\alpha \delta + r \gamma (-1 + x_2) \beta[x_1] - r \gamma x_2 \beta[x_2])) / \\ & \quad (r \gamma (x_2 \beta[x_2] + x_1 ((-1 + x_2) \beta[x_1] - x_2 \beta[x_2]))) \\ \langle E_2 \rangle &= (-x_2 (K \alpha \delta \epsilon \alpha + r \gamma (\delta - K \epsilon \alpha) \beta[x_2]) + \\ & \quad x_1 (r \gamma (\delta - K \epsilon \alpha + K \epsilon \alpha x_2) \beta[x_1] + K \epsilon \alpha (\alpha \delta - r \gamma x_2 \beta[x_2]))) / \\ & \quad (r \gamma (x_2 \beta[x_2] + x_1 ((-1 + x_2) \beta[x_1] - x_2 \beta[x_2]))) \\ \langle E_3 \rangle &= (\delta (-x_1 + x_2)) / (\gamma (x_2 \beta[x_2] + x_1 ((-1 + x_2) \beta[x_1] - x_2 \beta[x_2]))) \\ s_E^{di}[y] &= s_{x_1, x_2}(y) = \epsilon \alpha \langle E_1 \rangle (1 - y) - \delta - (1 - y) \langle E_2 \rangle + \gamma \beta[y] y \langle E_3 \rangle \end{aligned}$$

Monomorphic resident population (Simulation)

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E3[x_] := (r (\delta + K (-1 + x) \epsilon \alpha)) / (K (-1 + x) \epsilon \alpha^2 + r x (-1 + \gamma) \beta[x]); (* Note1: E3[x] =
(1-x)<n> which means the sign of E3[x] is same as the sign of <n> *)
(* Note2: if E3[x]>0(<n>>0),
then the mutant has chance to invade the resident;
otherwise there is no resident, which means no mutation happens. Hence
we need focus on the case of E3[x]>0 *)
s_x_[y_] := \epsilon \alpha (1 - y) K - \delta - (1 - y) \frac{\beta[x] x}{1 - x} E3[x] + \left( \gamma \beta[y] y - \epsilon \alpha K \frac{\alpha}{r} (1 - y) \right) E3[x];
(* Fitness *)
ds[x_] := (\partial_y s_x[y]) /. {y -> x}; (* Selection gradient *)

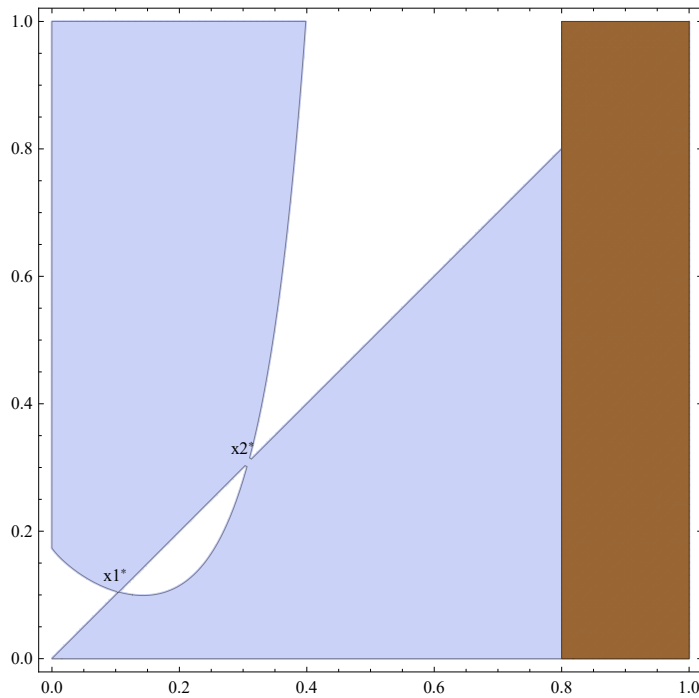
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Pairwise invadability plot (PIP)

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 $\alpha = 1; \gamma = 0.2; \delta = 0.1; \epsilon = 0.05; r = 1; K = 10; \beta_0 = 0; \beta_1 = 1.5; p = 0.5;$ 
 $\beta[x_] := \beta_0 + \beta_1 x^p;$ 
E3Neg =
  RegionPlot[E3[x] < 0, {x, 0, 1}, {y, 0, 1}, PlotPoints → 100, PlotStyle → Brown];
(* The function of E3Neg is to exclude the region
  (Brown region) that the resident does not exist. Then
  left region (the region except for Brown region)
  corresponds to the case that mutation may happen *)
PIPint = RegionPlot[sx[y] > 0, {x, 0, 1}, {y, 0, 1}, PlotPoints → 100];
(* The function of PIPint is to plot the region
  (Lightblue region) in which mutant can invade the resident *)
Show[PIPint, E3Neg, Graphics[{Text[x1*, {0.1, 0.13}]}],
  Graphics[{Text[x2*, {0.3, 0.33}]}], ImageSize → Medium]
(* Plot the functions of PIPint and E3Neg in one picture *)
Clear[ $\alpha, \gamma, \delta, \epsilon, r, K, \beta_0, \beta_1, p$ ];

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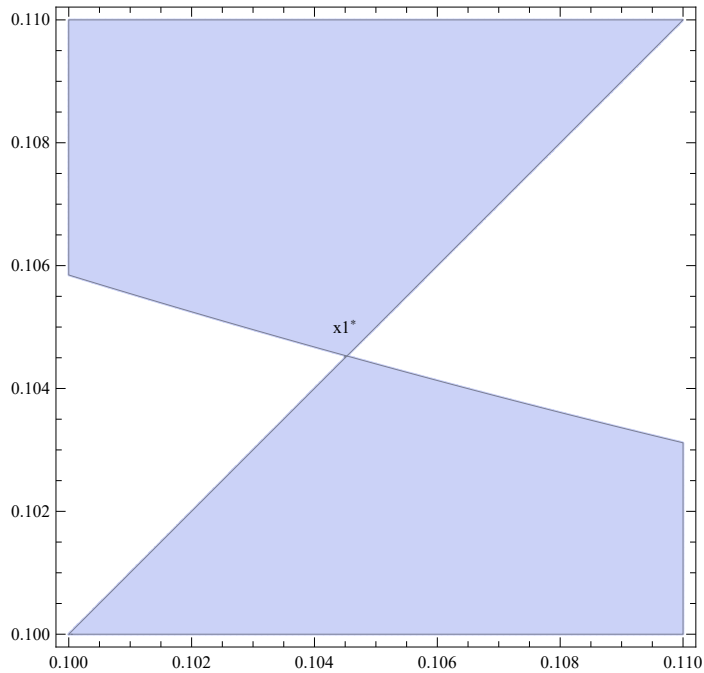
(* In above picture, the blue represents "+" and the white represents "-". x1*
and x2* are singularities. Next we enlarge the regions for every singularity
to consider which case the singularity is in terms of "8 cases" *)

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 $\alpha = 1; \gamma = 0.2; \delta = 0.1; \epsilon = 0.05; r = 1; K = 10; \beta_0 = 0; \beta_1 = 1.5; p = 0.5;$ 
 $\beta[x_] := \beta_0 + \beta_1 x^p;$ 
E3Neg = RegionPlot[E3[x] < 0, {x, 0.1, 0.11},
  {y, 0.1, 0.11}, PlotPoints → 100, PlotStyle → Brown];
PIPint = RegionPlot[sx[y] > 0, {x, 0.1, 0.11}, {y, 0.1, 0.11}, PlotPoints → 100];
Show[PIPint, E3Neg, Graphics[Text[x1*, {0.1045, 0.105}]]], ImageSize → Medium]
Clear[ $\alpha, \gamma, \delta, \epsilon, r, K, \beta_0, \beta_1, p$ ];
(* In above program, we focus on the region near singularity x1* to study it *)

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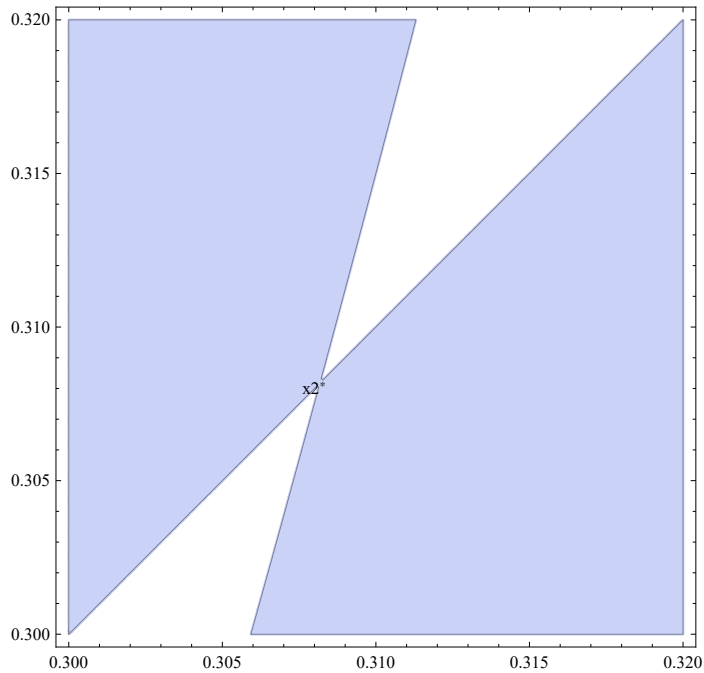
(* In above picture, singularity x1* is NOT ESS but Repellor *)

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```

α = 1; γ = 0.2; δ = 0.1; ε = 0.05; r = 1; K = 10; β0 = 0; β1 = 1.5; p = 0.5;
β[x_] := β0 + β1 x^p;
E3Neg = RegionPlot[E3[x] < 0, {x, 0.3, 0.32},
  {y, 0.3, 0.32}, PlotPoints → 100, PlotStyle → Brown];
PIPint = RegionPlot[sx[y] > 0, {x, 0.3, 0.32}, {y, 0.3, 0.32}, PlotPoints → 100];
Show[PIPint, E3Neg, Graphics[{Text[x2*, {0.308, 0.308}]}], ImageSize → Medium]
Clear[α, γ, δ, ε, r, K, β0, β1, p]; (* In above program,
we study the situation of sigularity x2* *)

```



(* In above picture,
sigularity x2* is NOT ESS but attracting. So it is Branching point *)

Dimorphic resident population (x_1, x_2) (Simulation)

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E1[x1_, x2_] := (K (x2 (-α δ + r γ β[x2]) + x1 (α δ + r γ (-1 + x2) β[x1] - r γ x2 β[x2]))) /
  (r γ (x2 β[x2] + x1 ((-1 + x2) β[x1] - x2 β[x2])));
E2[x1_, x2_] := (-x2 (K α δ ε α + r γ (δ - K ε α) β[x2]) +
  x1 (r γ (δ - K ε α + K ε α x2) β[x1] + K ε α (α δ - r γ x2 β[x2]))) /
  (r γ (x2 β[x2] + x1 ((-1 + x2) β[x1] - x2 β[x2])));
E3[x1_, x2_] := (δ (-x1 + x2)) / (γ (x2 β[x2] + x1 ((-1 + x2) β[x1] - x2 β[x2])));
Sx1,x2[y_] := ε α (1 - y) E1[x1, x2] - δ - (1 - y) E2[x1, x2] + γ β[y] y E3[x1, x2];
x1ds[x1_, x2_] := ∂y Sx1,x2[y] /. {y → x1}; (* Selection gradient for x1 *)
x2ds[x1_, x2_] := ∂y Sx1,x2[y] /. {y → x2}; (* Selection gradient for x2 *)

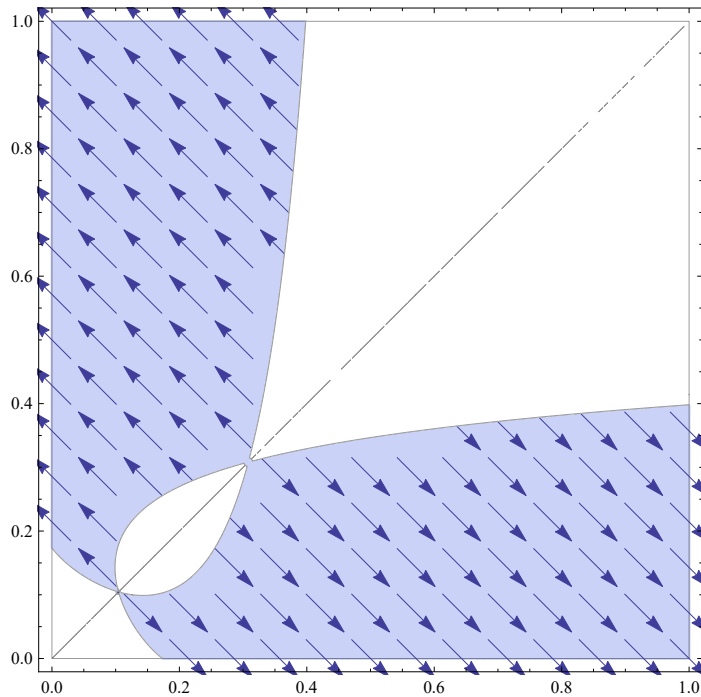
```

Mutual invadability plot (MIP)

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 $\alpha = 1; \gamma = 0.2; \delta = 0.1; \epsilon = 0.05; r = 1; K = 10; \beta_0 = 0; \beta_1 = 1.5; p = 0.5;$ 
 $\beta[x\_] := \beta_0 + \beta_1 x^p;$ 
MIP = RegionPlot[ $s_{x_2}[x_1] > 0 \ \&\& \ s_{x_1}[x_2] > 0,$ 
  {x1, 0, 1}, {x2, 0, 1}, PlotPoints  $\rightarrow$  100] // Quiet;
(* Note:  $s_x[y]$  is the fitness in monomorphic population *)
(* The function of MIP is to plot the coexistence region
  for x1 and x2 in which population with x1 can invade those
  with x2 while population with x2 can invade those with x1 *)
antiMIP = RegionPlot[ $s_{x_1}[x_2] < 0 \vee s_{x_2}[x_1] < 0,$  {x1, 0, 1},
  {x2, 0, 1}, PlotPoints  $\rightarrow$  100, PlotStyle  $\rightarrow$  White] // Quiet;
(* The function of antiMIP is to label region in which
  coexistence can not happen to be white *)
grad = VectorPlot[If[ $s_{x_1}[x_2] > 0 \ \&\& \ s_{x_2}[x_1] > 0,$ 
  {Sign[x1ds[x1, x2]], Sign[x2ds[x1, x2]]}, {0, 0}],
  {x1, 0, 1}, {x2, 0, 1}, VectorScale  $\rightarrow$  Small];
(* The function of grad is to plot the direction of
  evolution in dimorphic population *)
(* Sign[x] :=  $\begin{cases} -1, & \text{if } x < 0 \\ 0, & \text{if } x = 0. \text{ Sign[x1ds[x1,x2]] and Sign[x2ds[x1,x2]]} \\ 1 & \text{if } x > 0 \end{cases}$ 
  stand for the evolution direction of x1 and x2 respectively *)
(* Vector (0,0) means no evolution; ( $\pm 1, 0$ ) means that only
  x1 evolves to larger strategy or smaller strategy;
  (0,  $\pm 1$ ) means that only x2 evolves to larger strategy or smaller strategy;
  ( $\pm 1, \pm 1$ ) means that both x1 and x2 evolve *)
(* The arrows in the picture stand for the sum of vector *)
Show[MIP, grad, antiMIP, ImageSize  $\rightarrow$  Medium]
(* Plot MIP, grad and antiMIP in one picture *)
Clear[ $\alpha, \gamma, \delta, \epsilon, r, K, \beta_0, \beta_1, p$ ];

```



Conclusions

1) PIP shows the evolution of strategy x in the monomorphic population. There are two singularities of which one is repeller and other is branching point.

2) MIP represents the evolution of strategies x_1 and x_2 in the dimorphic population. From picture, there are two cases of evolution :

(I) : $x_1 = 1$ and $x_2 = 0$;

(II) : $x_1 = 0$ and $x_2 = 1$.

In the model, although $x_1 = 0$ (or $x_2 = 0$), the population with x_1 (or x_2) still exist. Hence final evolutionary outcome is dimorphism. And the mechanism becomes

(I) : $\boxed{R} \xrightarrow{\text{be captured}} \boxed{n2} \xrightarrow{\text{be captured}} \boxed{n1}$;

(II) : $\boxed{R} \xrightarrow{\text{be captured}} \boxed{n1} \xrightarrow{\text{be captured}} \boxed{n2}$.