Critical function analysis

Suppose the strategy ξ is two-dimensional : $\xi = \binom{x}{z} \in \mathbb{R}^2$.

Suppose further that x, are not independent of one-another, but that they are connected via a trade-off such that

$z = \varphi(x)$ for some $\varphi : \mathbb{R} \to \mathbb{R}$.

Examples:

① In the cannibalism time-budget model, the attack rate β is a function of the proportion x of time spent attacking others.

② In the cycling predators paper, the conversion constant γ is a function of the handling time h.

We can write the invasion fitness as

$$\text{(1)} \quad \boxed{s_x(y) = f(y, \varphi(y), x, \varphi(x))}$$

If φ is known, we find the singular strategies from

$$\text{(2)} \quad \boxed{0 = \partial_1 f + \partial_2 f \, \varphi'} \quad \text{evaluated at } y = x$$

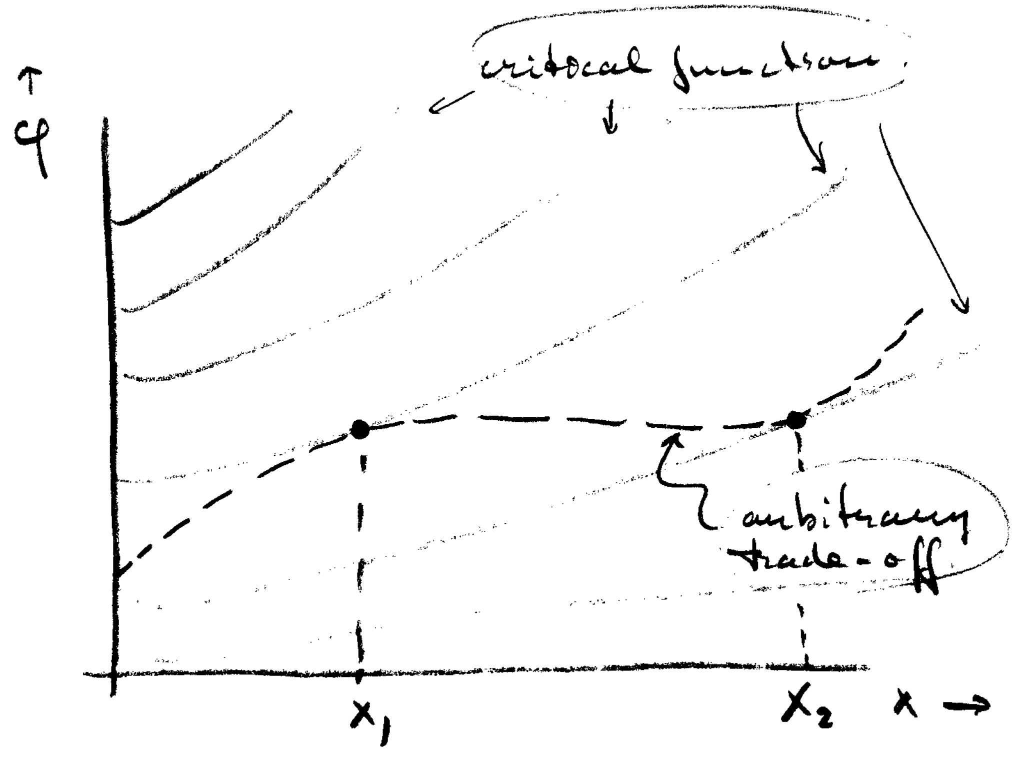
If φ is <u>not</u> known, and we want to know how the evolution depends on φ, consider (2) as an ODE for φ.

Solving for φ we get a family of solutions $\{\varphi_c\}$ which all satisfy (2) for every x.

So, if we choose $\varphi = \varphi_c$ for any choice of c, then <u>all x are singular</u>.

The functions φ_c are called <u>critical functions</u> (or trade-offs).

If we plot the critical functions in the (x, φ)-plane, we can immediately see, for <u>any arbitrary trade off</u>, which x are singular, and whether they are attracting or repelling.



ⓐ Whenever a given trade-off is tangent to a critical function, we have a singularity for that trade-off. (so, x_1 and x_2 are singular in above figure)

ⓑ If $\partial_2 f > 0$, then the singularity is attracting (repelling) if at the tangent point the trade-off is relatively concave (convex) with respect to the critical function.

(If $\partial_2 f < 0$, then it is the otherway around.)

Point ⓐ should be obvious: at the point of tangent, ② is satisfied for the given trade off.

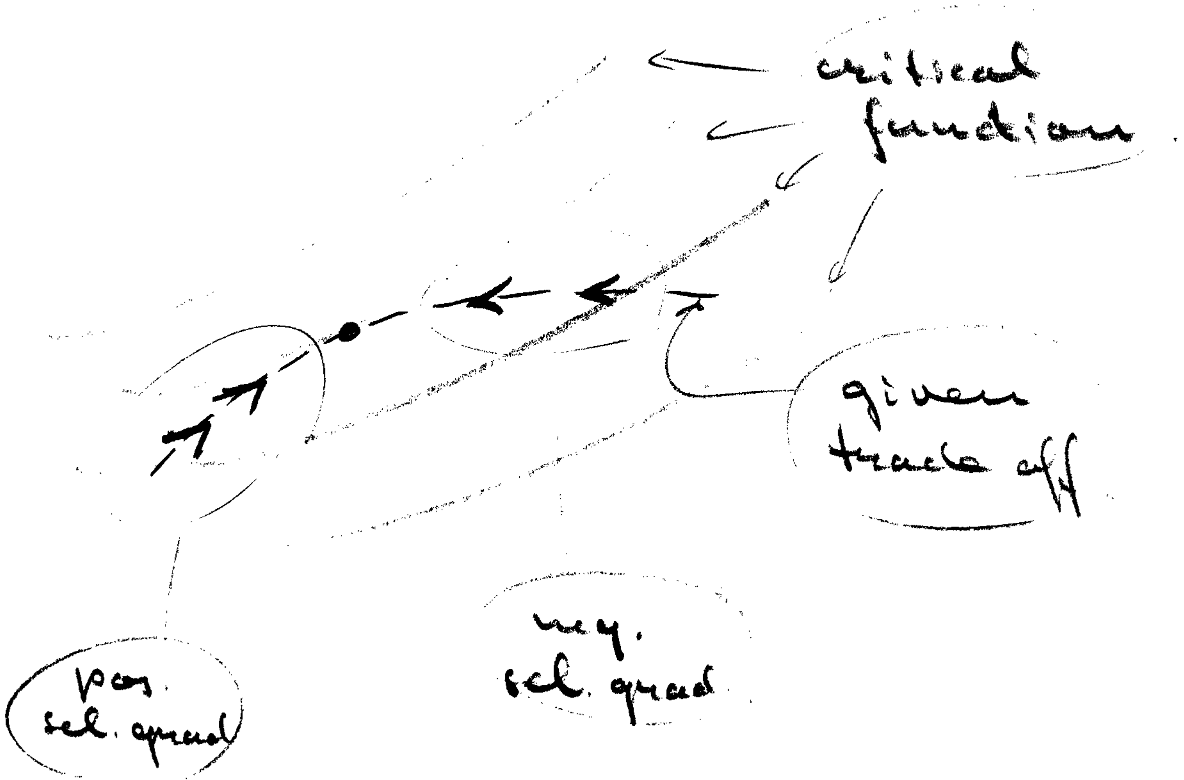
Point ⓑ becomes clear if one looks at the sign of the selection gradient

$$\partial_y s_x(y)\Big|_{y=x} = \partial_1 f + \partial_2 f \varphi' \underset{(<)}{>} 0 \iff$$

$$\boxed{\varphi' \underset{(<)}{>} -\frac{\partial_1 f}{\partial_2 f}} \leftarrow$$ which is the slope of the critical function everywhere

(for $\partial_2 f > 0$).

So, if $\partial_2 f > 0$, and the slope of the given trade-off is larger (smaller) than the slope of the critical functions, then the selection gradient is positive (negative).



$\Rightarrow$ Suppose $\partial_2 f > 0$ on page 3. Then x_1 is attracting and x_2 is repelling

(if $\partial_2 f < 0$, then it is the other way around)

Evolutionary branching

Given the critical functions, we can always construct a trade-off that gives us an attracting singularity wherever we want.

Can we make this singularity into a branching point? (i.e., is branching possible?)

A branching point is characterized by

$$\begin{cases} \partial_y S_x(y)\big|_{y=x} = 0 & \text{(singularity)} \\ C_{22} > 0 & \text{(non-ESS)} \\ C_{12} + C_{22} < 0 & \text{(attracting)} \end{cases}$$

(where

$C_{22} = \partial_{yy} S_x(y)\big|_{y=x}$, $C_{12} = \partial_{xy} S_x(y)\big|_{y=x}$)

$$(*) \quad \boxed{c_{22} = \partial_{11} f + 2\partial_{12} f\,\varphi' + \partial_{22} f\,(\varphi')^2 + \partial_2 f\,\varphi''}$$

and

$$\boxed{c_{12} = \partial_{13} f + \partial_{14} f\,\varphi' + \partial_{23} f\,\varphi' + \partial_{24} f\,(\varphi')'}$$

Note, that if we fix the position of the singularity and whether it is attracting, we fix the slope φ' at the singularity, and hence we fix c_{12}.

However, c_{22} can still be varied by varying the local curvature φ''.

Suppose that $\boxed{c_{12} < 0}$ Then, for small $c_{22} > 0$ we still have $c_{12} + c_{22} < 0$, and hence we have a branching point

Suppose $\boxed{\partial_2 f > 0}$, then we can make c_{22} slightly positive (and hence create a branching point) by making $\varphi'' > 0$ sufficiently large (convex), (but not too large, because then the singularity becomes repelling.)

If $\boxed{\partial_2 f < 0}$, we must make φ sufficiently cocave to get a branching point, but not too concave, otherwise we get that $c_{12} + c_{22} > 0$, i.e., we've got a repeller.

<u>Conclusion</u>

- If $c_{12} < 0$, we can choose a trade-off φ such that we get branching.
- If $c_{12} > 0$, then we <u>cannot</u> have branching, because $c_{12} + c_{22} > 0$ (repelling) for $c_{22} > 0$.

Plot in the (x,φ) - plane
where $c_{12} < 0$:

$$\begin{cases} c_{12} \overset{(p.7)}{=} \partial_{13}f + \partial_{14}f\,\varphi' + \partial_{23}f\,\varphi' + \partial_{24}f\,(\varphi')^2 \\ \varphi' \overset{(p.2)}{=} -\partial_1 f / \partial_2 f \end{cases}$$

$$\Longrightarrow \boxed{c_{12} = \partial_{13}f - (\partial_{14}f + \partial_{23}f)\frac{\partial_1 f}{\partial_2 f} + \partial_{24}f\left(\frac{\partial_1 f}{\partial_2 f}\right)^2}$$

which is a function of (x,φ).

Plot the zero-contour
of c_{12} in the (x,φ) plane.

Example: Cannibalism time budget.

Critical function analysis:

Reset:

In[22]:= `Clear[α, β, γ, δ, ϵ, r, k];`

Critical functions:

In[23]:= `ds_mo[x] == 0;`

`Simplify[%]`

Out[24]= $$\left(r\,(-\gamma\,\delta+k\,\alpha\,\gamma\,\epsilon+x\,(-\delta+\gamma\,\delta-k\,\alpha\,\gamma\,\epsilon))\,\beta[x]+(-1+x)\,\left(k\,\alpha^2\,\delta\,\epsilon+r\,x\,\gamma\,(\delta+k\,(-1+x)\,\alpha\,\epsilon)\,\beta'[x]\right)\right)\Big/\left((-1+x)\,\left(k\,(-1+x)\,\alpha^2\,\epsilon+r\,x\,(-1+\gamma)\,\beta[x]\right)\right)==0$$

In[25]:= `DSolve[ds_mo[x] == 0, β[x], x];`

`Simplify[%]`

Out[26]= $$\left\{\left\{\beta[x]\to\frac{1}{r\,x\,(-1+\gamma)}\,(\delta+k\,(-1+x)\,\alpha\,\epsilon)^{-1/\gamma}\left(r\,(-1+x)^{\frac{1}{\gamma}}\,(-1+\gamma)\,\delta\,C[1]-k\,(-1+x)\,\alpha\,\epsilon\left(\alpha\,(\delta+k\,(-1+x)\,\alpha\,\epsilon)^{\frac{1}{\gamma}}-r\,(-1+x)^{\frac{1}{\gamma}}\,(-1+\gamma)\,C[1]\right)\right)\right\}\right\}$$

In[27]:= `βcrit[x_] :=`

$$\frac{1}{r\,x\,(-1+\gamma)}\,(\delta+k\,(-1+x)\,\alpha\,\epsilon)^{-1/\gamma}\left(r\,(-1+x)^{\frac{1}{\gamma}}\,(-1+\gamma)\,\delta\,C[1]-k\,(-1+x)\,\alpha\,\epsilon\left(\alpha\,(\delta+k\,(-1+x)\,\alpha\,\epsilon)^{\frac{1}{\gamma}}-r\,(-1+x)^{\frac{1}{\gamma}}\,(-1+\gamma)\,C[1]\right)\right);$$

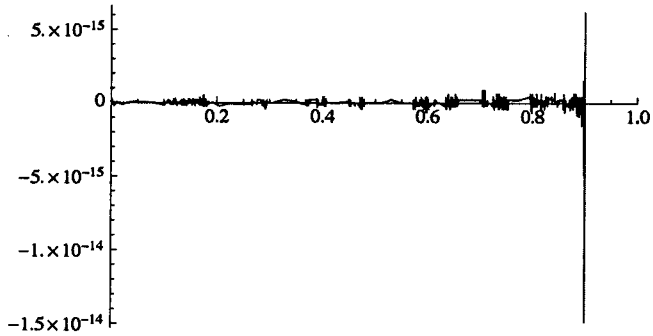
Default parameter values:

In[28]:= `α = 1; γ = 0.2; δ = 0.1; ϵ = 0.1; r = 1; k = 10;`

Test critical functions:

In[29]:=
```
β[x_] := βcrit[x];

Plot[If[(n[x] /. {C[1] → -1}) > 0, dsmo[x] /. {C[1] → -1}],
  {x, 0, 1}, PlotRange → {{0, 1}, All}]
```

Out[30]=



Plot critical functions:

In[31]:=
```
Limit[βcrit[x], x → 0]
```

Out[31]=
```
DirectedInfinity[(-1. + 0. i) - (1.21933 + 0. i) C[1]]
```

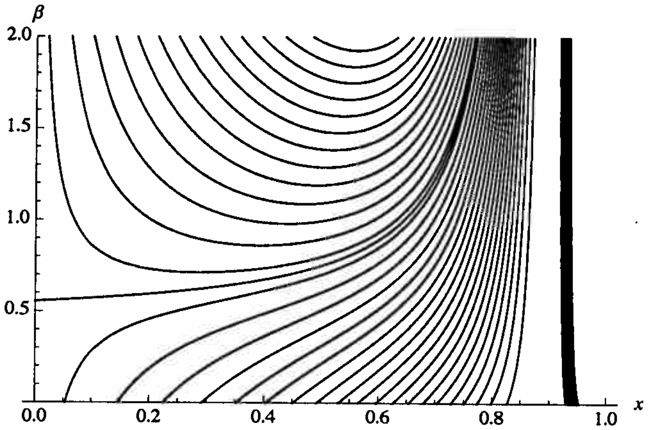
In[32]:=
```
Solve[(-1.` + 0.` i) - (1.2193263222069808` + 0.` i) C[1] ==
   0, C[1]]
```

Out[32]=
```
{{C[1] → -0.820125 + 0. i}}
```

In[33]:=
```
crit =
  Plot[
   βcrit[x] /.
    {C[1] → Join[{-0.8201249999999999`},
       Table[-i / 25, {i, 1, 50}]]}, {x, 0, 1},
   AxesOrigin → {0, 0}, PlotRange → {0, 2},
   AxesLabel → {x, β}, PlotStyle → {Black}];
```

In[34]:= Show[crit]

Out[34]=



Branching possible?

In[124]:=

$$\text{RRes} = -\frac{\text{k}\ (\alpha\,\delta - \text{r xRes}\ (-1+\gamma)\ \beta\text{Res})}{\text{k}\ (-1+\text{xRes})\ \alpha^2\,\epsilon + \text{r xRes}\ (-1+\gamma)\ \beta\text{Res}};$$

(* resource density *)

$$\text{nRes} = -\frac{\text{r}\ (\delta + \text{k}\ (-1+\text{xRes})\ \alpha\,\epsilon)}{(-1+\text{xRes})\ \left(\text{k}\ (-1+\text{xRes})\ \alpha^2\,\epsilon + \text{r xRes}\ (-1+\gamma)\ \beta\text{Res}\right)};$$

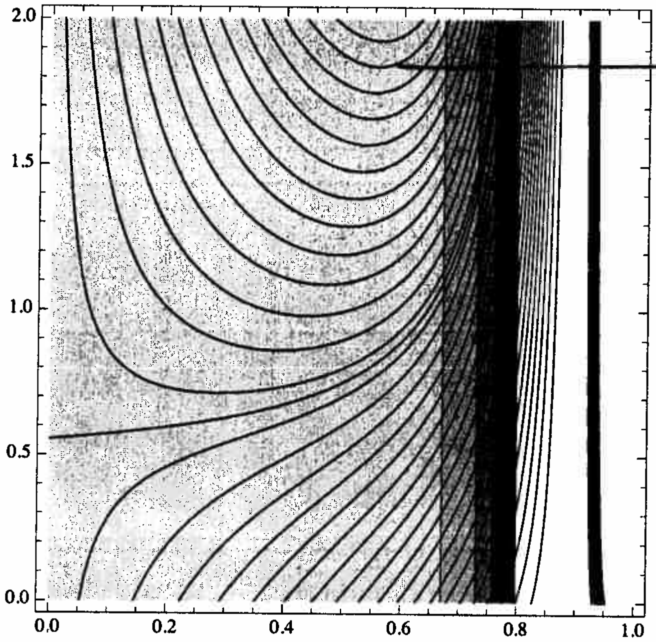
(* population density *)

```
f = ϵ α (1 - xMut) RRes - δ + γ βMut xMut (1 - xRes) nRes -
    (1 - xMut) βRes xRes nRes; (* invasion fitness *)

d1f = (D[f, xMut]) /. {xMut → xRes, βMut → βRes};
d2f = (D[f, βMut]) /. {xMut → xRes, βMut → βRes};

d13f = (D[f, xMut, xRes]) /. {xMut → xRes, βMut → βRes};
d14f = (D[f, xMut, βRes]) /. {xMut → xRes, βMut → βRes};
d23f = (D[f, βMut, xRes]) /. {xMut → xRes, βMut → βRes};
d24f = (D[f, βMut, βRes]) /. {xMut → xRes, βMut → βRes};
```

$$\text{c12} = \text{d13f} - (\text{d14f} + \text{d23f})\ \frac{\text{d1f}}{\text{d2f}} + \text{d24f}\ \left(\frac{\text{d1f}}{\text{d2f}}\right)^2;$$

```
branch = ContourPlot[If[nRes > 0, c12], {xRes, 0, 1},
    {βRes, 0, 2}, PlotPoints → 50];

Show[branch, crit]
```

Out[135]=



~~everywhere~~

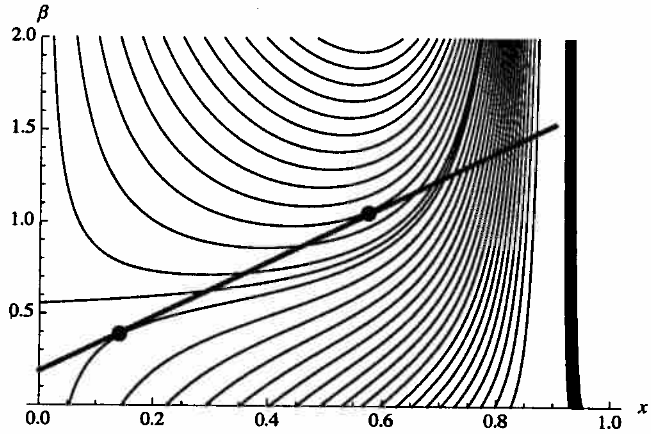
$c_{12} < 0$ everywhere.

Superimpose β on the critical functions:

Case as we had in the PIP above:

```
β[x_] := β0 + β1 x^p; β0 = 0.185; β1 = 1.5; p = 1;

βNES = Plot[If[dds_mo[x] > 0 && n[x] > 0, β[x]],
    {x, 0, 1}, PlotStyle → {Red, Thick}];

βES = Plot[If[dds_mo[x] ≤ 0 && n[x] > 0, β[x]], {x, 0, 1},
    PlotStyle → {Black, Thick}];
```

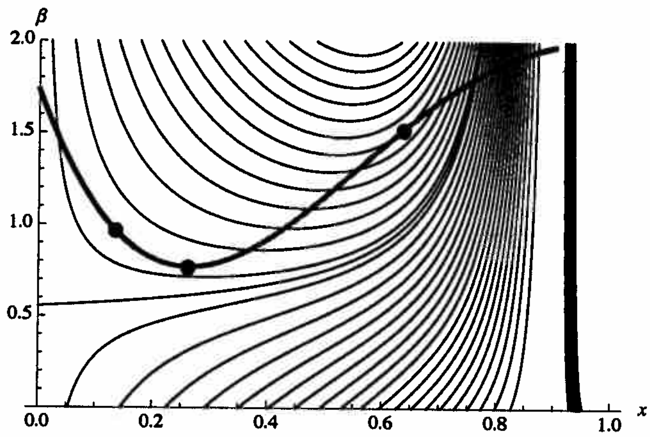
```
Show[crit, βNES, βES]
```



Case with three singular strategies:

```
β[x_] := 2 - 9 (0.03 + x)^p (1 - x)^q; p = 1; q = 2.5;

βNES = Plot[If[dds_mo[x] > 0 && n[x] > 0, β[x]],
    {x, 0, 1}, PlotStyle → {Red, Thick}];

βES = Plot[If[dds_mo[x] ≤ 0 && n[x] > 0, β[x]], {x, 0, 1},
    PlotStyle → {Black, Thick}];
```

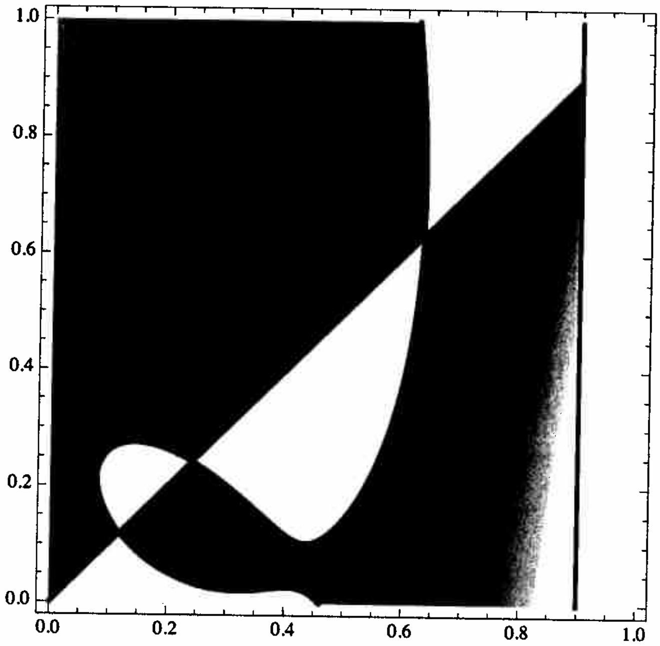
```
Show[crit, βNES, βES]
```



Pairwise invadability plot for the latter case:

```
PIPbnd = ContourPlot[If[n[x] > 0, s_mo[x, y]],
    {x, 0, 1}, {y, 0, 1}, Contours → {0},
    ContourStyle → {Black, Thick},
    ContourShading → False, PlotPoints → 100];

PIPint = DensityPlot[
    If[s_mo[x, y] > 0 && n[x] > 0, s_mo[x, y]], {x, 0, 1},
    {y, 0, 1}, PlotPoints → 50];

nPos = ContourPlot[n[x], {x, 0, 1}, {y, 0, 1},
    Contours → {0}, ContourStyle → {Black, Thick},
    ContourShading → False, PlotPoints → 10];
```

```
Show[PIPint, PIPbnd, nPos]
```



Canonical equation:

Mutation rate:

```
μ[x_] := 1;
```

Standard deviation of the mutation step distribution:

```
σ[x_] := 0.04 x (1 - x);
```

Deterministic drift:

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