III The ecological timescale (Continued)

What happens after an invasion event in terms of which strategy (or strategies) remain, and which are expelled from the population?

Here follow three more-or-less general results that answer this question.

Proposition 1 ("Bending theorem")

Consider a resident population of strategy $x^* \in \mathbb{R}^1$ with environment E^*, and suppose that every neighborhood of x^* contains strategies $x_1, \dots, x_k$ and every neighborhood of E^* contains an environment E such that $x_1, \dots, x_k$ can coexist in env. E.

Suppose further that $\partial_x^i S_E(x)$ $(i=1,\dots,k-1)$ exist and are continuous at (x^*, E^*).

Then necessarily $\partial_x^i S_E(x) = 0$ at (x^*, E^*) for $i = 1, \dots, k-1$.

■

In particular.

- Coexistence of similar (scalar-valued) strategies is only possible near points in the strategy space where $\boxed{\partial_y S_x(y)\big|_{y=x} = 0}$.
- Coexistence of three or more similar (scalar-valued) strategies may only happen near points where both $\boxed{\partial_y S_x(y)\big|_{y=x} = 0 \quad \text{and} \quad \partial_y^2 S_x(y)\big|_{y=x} = 0}$

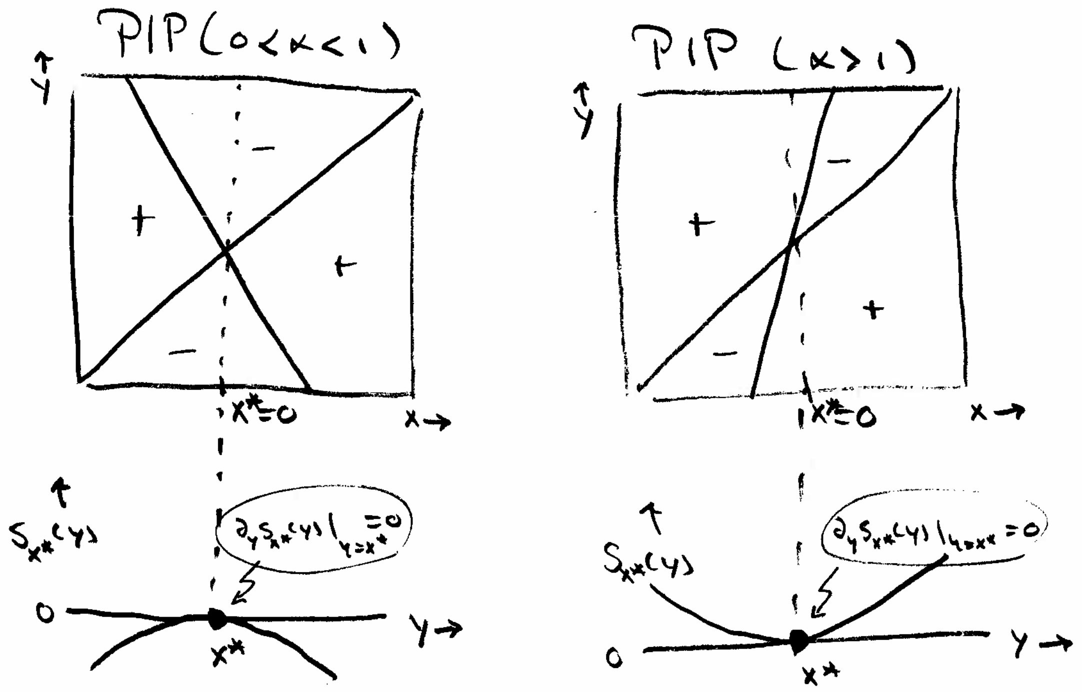
Definition

$\partial_y S_x(y)\big|_{y=x}$ is the selection gradient at x, and a strategy x where the selection gradient is zero is called a singular strategy.

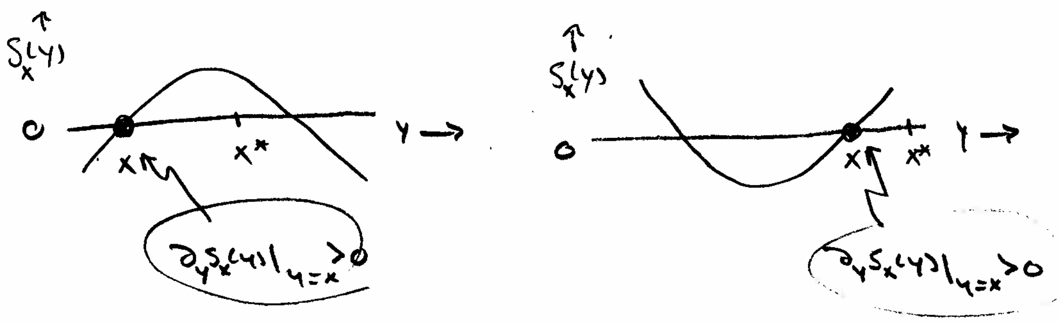
Remark.

Thus, coexistence of similar (scalar-valued) strategies is only possible near a singular strategy.

Example (LV comp. model)



⇒ In both cases $x^*=0$ is singular.



⇒ In both cases the selection gradient at $x < x^*$ is positive

Likewise we find that in both cases the selection gradient at $x > x^*$ is negative (Exercise).

So, according to Prop. ①, coexistence of similar strategies in the L.V. comp. model is only possible near $x^* = 0$

(That we already knew, because in the LV comp. model we need mutual invasion (or mutual exclusion) for coexistence, and that is possible for similar strategies only near $x^* = 0$.)

We have already calculated that in the LV comp. model

$$\partial_y^2 s_{x^*}(y)\big|_{y=x^*} = 2(\alpha - 1) \neq 0 \quad \text{for } \alpha \neq 1$$

So, according to the proposition coexistence of three or more similar strategies near $x^* = 0$ is <u>not</u> possible.

This we assumed to be the case in order to understand evolutionary branching, but now we know it has to be so, and not only in the L.V comp model but much more generally as well.

Proof of Prop. 1

Suppose every nbd of x^* contains strategies $x_1, \dots, x_k$ and every nbd of E^* contains an environment such that $x_1, \dots, x_k$ can coexist in E.

Then there can be found a sequence $\{(x_1^j, \dots, x_k^j)\}$ $(j=1,2,\dots)$ of k-tuples of strategies and a sequence $\{E^j\}$ $(j=1,2,\dots)$ of environments such that $x_i^j \to x^*$ $(i=1,\dots,k)$ and $E^j \to E^*$ as $j \to \infty$, and such that for every j the strategies $x_1^j, \dots, x_k^j$ can coexist in the environment E^j.

Then, by the principle of selective neutrality of residents among themselves, we have

$$S_{E^j}(x_1^j) = \dots = S_{E^j}(x_k^j) = 0 \quad \forall j.$$

So, for every j, the function $y \longmapsto S_{E^j}(y)$ has at least k roots in the interval spanned by the $x_1^j, \dots, x_k^j$.

But then, by the Mean Value Theorem, the function $y \longmapsto \partial_y S_{E^j}(y)$, has at least k-1 roots in the interval spanned by the $x_1^j, \dots, x_k^j$.

Repeated application of the Mean Value Theorem shows that the function

$$y \longmapsto \partial_y^i S_{E^j}(y) \qquad (i=1,\dots,k-1)$$ has

at least $k-i$ roots in the interval spanned by $x_1^j,\dots,x_k^j$.

So, we can find strategies $\xi_1^j \dots \xi_{k-1}^j$ in the interval spanned by $x_1^j,\dots,x_k^j$ such that

$$\boxed{\partial_y^i S_{E^j}(y)\Big|_{y=\xi_i^j}=0} \qquad (i=1,\dots,k-1)$$

Since $x_1^j,\dots,x_k^j \to x^*$ as $j\to\infty$, it follows that also $\xi_1^j,\dots,\xi_{k-1}^j \to x^*$ as $j\to\infty$.

Hence,

$$\partial_y^i S_{E^*}(y)\Big|_{y=x^*} = \lim_{j\to\infty} \partial_y^i S_{E^j}(y)\Big|_{y=\xi_i^j} = 0$$

for $i=1,\dots,k-1$, which is what we set out to prove.

■

Prop. ① is a pure geometric property of the invasion fitness.
It does not make any assumptions about the kind of coexistence (equilibrium, limit cycle, whatever) of the resident strategies.

The following proposition is less general, at least, we start-off more specific and generalize later

Preliminaries (resident dynamics)

Consider the res. dyn for a scalar-valued strategy x.

$$① \begin{cases} \dot{N} = N\, g(x \mid E) \\ E = h(x)\, N \end{cases}$$

notice the special structure

Let further $\hat{N}(x) > 0$ be such that

$$② \quad 0 = g(x, \hat{N}(x))$$

i.e., $\hat{N}(x)$ is an equilibrium.
We assume that $\hat{N}(x)$ is stable and attracting for all x in a given open interval I
Moreover, by scaling pop. dens. we may assume that

$$③ \quad \hat{N}(x) = 1$$

irrespective of our choice of x.

For the res. inv. dynamics we have

$$④ \begin{cases} \dot{n} = n\, g(x|E) \\ \dot{m} = m\, g(y|E) \\ E = h(x)n + h(y)m \end{cases}$$

notice the special structure of the feedback environment.

We take always $x \neq y$

Proposition ②

Let $x^* \in I$ (see prelims page 7).
Then there exists a neighborhood $\mathcal{U}$ of x^* such that

ⓐ if x^* is nonsingular, then

$$\boxed{s_x(y) > 0 \implies \text{invasion \& substitution of } x \text{ by } y}$$

ⓑ if x^* is singular, and $\partial_{xy} s_x(y)\big|_{x=y=x^*} \neq 0$, then

$$\boxed{\begin{matrix} s_x(y) > 0 \\ \& \\ s_y(x) < 0 \end{matrix} \implies \text{invasion \& substitution of } x \text{ by } y}$$

and

$$\boxed{\begin{matrix} s_x(y) > 0 \\ \& \\ s_y(x) > 0 \end{matrix} \implies \text{ivasion \& coexistence at a unique positive equilibrium}}$$

for every $x, y \in \mathcal{U}$.

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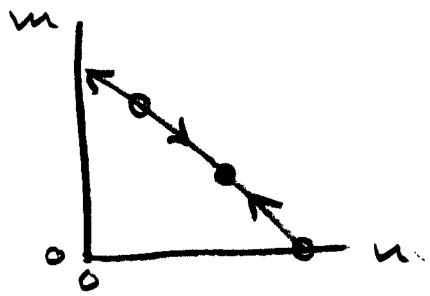
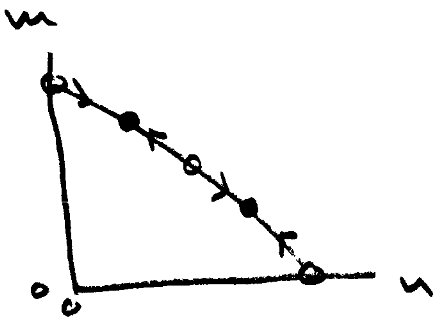
The proposition thus rules out the existence of orbits such as



"unprotected coexistence"

or



"multiple equilibria"

Proof of Prop. 2

Change of variables

$$(5)\quad \begin{cases} N := n+m \\ p := \dfrac{m}{n+m} \end{cases}$$

in the inv. res. dyn. (4) gives

$$(6)\quad \begin{cases} \dot{N} = N\big(p\,g(y|E) + (1-p)\,g(x|E)\big) \\ \dot{p} = p(1-p)\big(g(y|E) - g(x|E)\big) \\ E = N\big(p\,h(y) + (1-p)\,h(x)\big) \end{cases}$$

Write

$$x = x^* + \varepsilon\xi$$
$$y = x^* + \varepsilon\eta$$

Then:

$$(7)\quad \begin{cases} \dot{N} = N\, g(x^*|E) + O(\varepsilon) & \text{(fast dynamics)} \\ \dot{p} = O(\varepsilon) & \text{(slow dynamics).} \\ E = N\, h(x^*) + O(\varepsilon) \end{cases}$$

for small ε.

The theory of singular perturbations tells us we can study the fast and slow dynamics <u>separately on different time scales</u>.

$\boxed{\text{Fast dynamics}}$

Letting $\varepsilon \to 0$ we get

$$(8)\quad \begin{cases} \dot{N} = N\, g(x^*|E) \\ \dot{p} = 0 \\ E = N\, h(x^*) \end{cases}$$

Which is the resident dynamics on page 7 with $x = x^*$ with

$N \longrightarrow \hat{N}(x^*) = 1$ as $t \to \infty$.

Slow dynamics; non singular x^*

Slow time variable $\tau := \varepsilon t$,

and so $\frac{d}{d\tau} = \frac{1}{\varepsilon}\frac{d}{dt}$.

Rewriting the res. inv. dyn. (6) in slow time gives

$$(9)\quad \begin{cases} \varepsilon \frac{dN}{d\tau} = N\left(g(x^*|E) + O(\varepsilon)\right) \\ \frac{dp}{d\tau} = p(1-p)\left(\partial_1 g(x^*|E^*)(\eta-\xi) + O(\varepsilon)\right) \\ E = N\left(h(x^*) + O(\varepsilon)\right) \end{cases}$$

Letting $\varepsilon \to 0$ we get

scaled strategies (see bottom p. 9)

$$(10)\quad \begin{cases} 0 = N\, g(x^*|E) \\ \frac{dp}{d\tau} = p(1-p)\,\partial_1 g(x^*|E)(\eta-\xi) \\ E = N\, h(x^*) \end{cases}$$

The first and third equations give

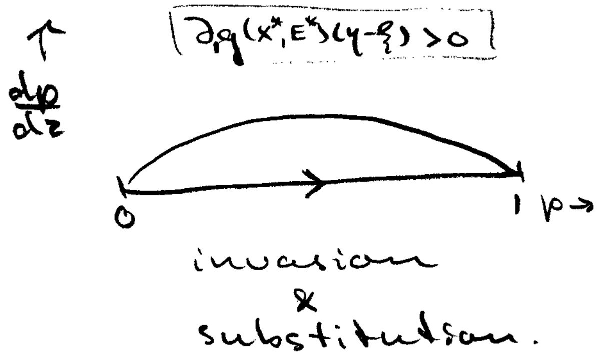
$N = \hat{N}(x^*) = 1$ and $E = h(x^*) =: E^*$

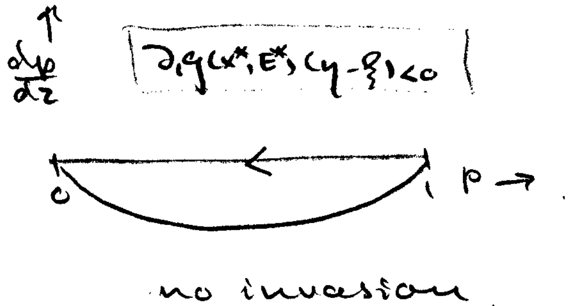
so that for $\frac{dp}{d\tau}$ we get

(11) $$\frac{dp}{d\tau} = p(1-p)\,\partial_1 g(x^*|E^*)\,(\eta-\xi)$$

non zero

Since $S_{x^*}(y) = g(y|E)$ and hence $\partial_1 g(x^*|E^*) = \partial_y S_{x^*}(y)|_{y=x^*} \neq 0$ (because x^* is assumed to be non-singular) we have only two kinds of dynamics of $p = \frac{m}{m+n}$.





Slow dynamics; singular x^*

Slow time variable $\tau = \varepsilon^2 t$, and so $\frac{d}{d\tau} = \frac{1}{\varepsilon^2}\frac{d}{dt}$.

Rewriting the res. inv. dyn. (6) gives:

$$
(12)\quad \begin{cases} \varepsilon^2 \dfrac{dN}{dz} = N\left(g(x^* | E) + O(\varepsilon)\right) \\[2mm] \dfrac{dp}{dz} = p(1-p)\left[\tfrac{1}{2}\partial_{11} g(x^*|E^*)(\eta^2-\xi^2) + \right. \\ \qquad \left. + \partial_{12} g(x^*|E^*)(\eta-\xi)\, h'(x^*)(p\eta + (1-p)\xi) + O(\varepsilon^2)\right] \\[2mm] E = N\left(h(x^*) + O(\varepsilon)\right) \end{cases}
$$

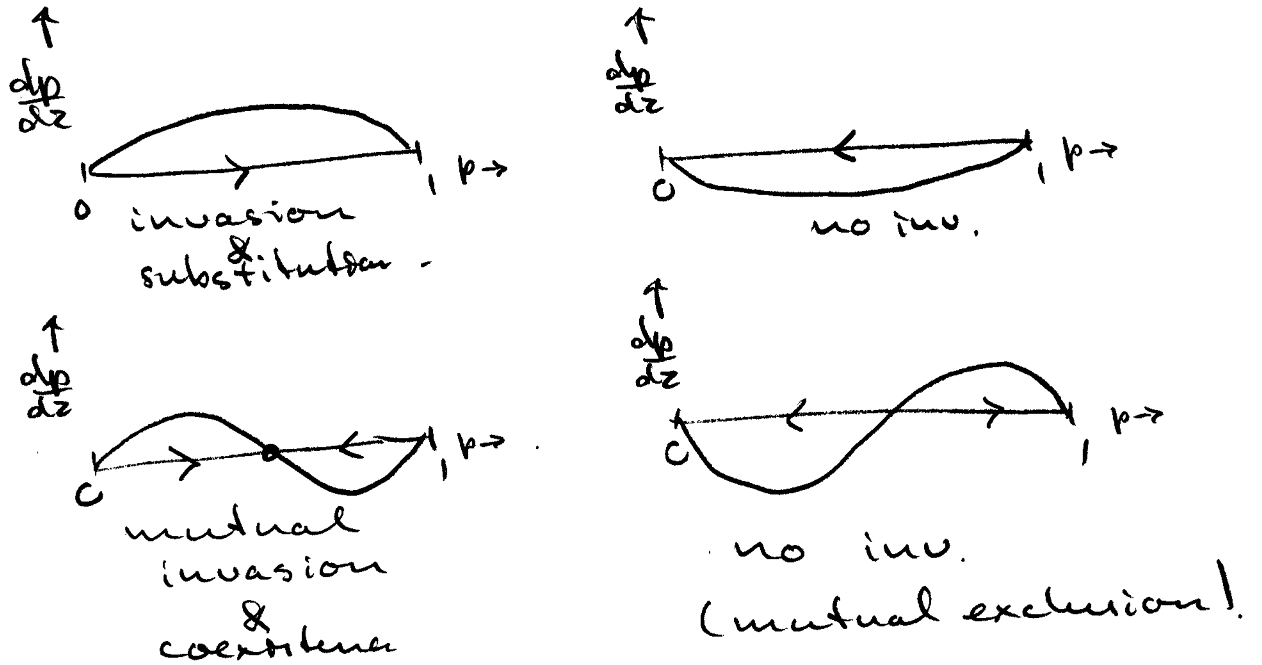
Letting $\varepsilon \to 0$ we get

$$
(13)\quad \begin{cases} 0 = N g(x^*, E) \\[2mm] \dfrac{dp}{dz} = p(1-p)(\eta-\xi)\left[\tfrac{1}{2}\partial_{11} g(x^*|E^*)(\eta+\xi) + \right. \\ \qquad \left. + \partial_{12} g(x^*|E^*)\, h'(x^*)(p\eta + (1-p)\xi)\right] \\[2mm] E = N h(x^*). \end{cases}
$$

Thus, we again find $N = \hat{N}(x^*) = 1$ and $E = \hat{N}(x^*)\, h(x^*) = h(x^*) =: E^*$. And for $\frac{dp}{dz}$ we have

$$
(14)\quad \frac{dp}{dz} = p(1-p)(\eta-\xi)\left[\tfrac{1}{2}\partial_{11} g(x^*|E^*)(\eta+\xi) + \right. \\ \left. + \partial_{12} g(x^*|E^*)\, h'(x^*)(p\eta + (1-p)\xi)\right]
$$

Assuming that $\partial_{12} g(x^*|E^*)\, h'(x^*)$ and $\frac{1}{2}\partial_{11} g(x^*|E^*)(\xi+\eta) + \partial_{12} g(x^*|E^*)\, h'(x^*)\xi$ are not both zero, there are only four kinds of dynamics.



(Notice that there are qualitatively the same outcomes as in the L.V. comp. model.)

This completes the proof of prop. 2.

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Generalizations

- We can take $h(x) = \delta_x$
  (i.e., Dirac delta function)
  (Explain further)
  In this way we are not confined to the special class of environments where $h(x)$ is an ordinary function.

- (continued ...)