

III

The ecological timescale;
a more general approach

* Resident dynamics

$\underline{x} = (x_1, \dots, x_k)$ vector of different resident strategies.

$\underline{v} = (v_1, \dots, v_k)$ vector of corresponding population densities.

$\underline{\theta} = (\theta_1, \dots, \theta_l)$ vector of other ecological factors (prey, predators).

Two equivalent formulations of the resident dynamics.

$$\textcircled{1} \begin{cases} \dot{v}_i = v_i f(x_i | \underline{x}, \underline{v}, \underline{\theta}) & (i=1, \dots, k) \\ \dot{\underline{\theta}} = \underline{F}(\underline{x}, \underline{v}, \underline{\theta}) \end{cases}$$

or

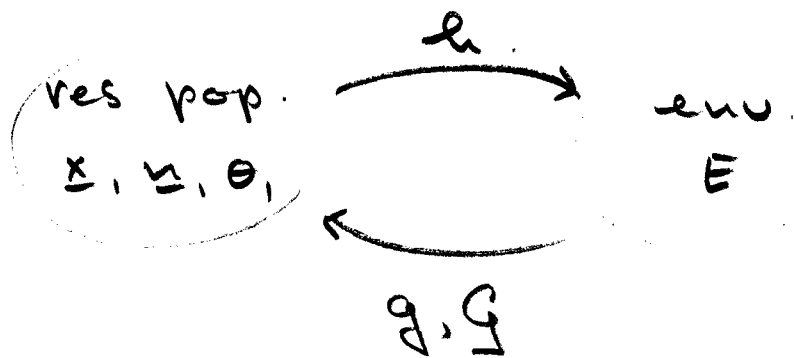
$$\textcircled{2} \begin{cases} \dot{v}_i = v_i g(x_i | E) & (i=1, \dots, k) \\ \dot{\underline{\theta}} = \underline{G}(E) \\ E = h(\underline{x}, \underline{v}, \underline{\theta}) \end{cases}$$

Formulation ② emphasizes that all non-linear aspects of the

dynamics of n_i ($i=1, \dots, k$) acts via the environment E .

(That is, given E as a function of time, the dynamics of n_i is given by a linear diff. equ.)

* Environmental feed back loop.



E as a function of time is referred to as the resident environment or the environment generated by the resident population.

* Coexistence

Given the resident environment, we say that x_1, \dots, x_k coexist if $\log n_i$ ($i=1, \dots, k$) stays bounded forward in time.

* Invaser dynamics

We now introduce a mutant with strategy γ and population density m at such low (infinitesimal) numbers that the resident environment remains unperturbed.

The pop. dyn. of the mutant is then given by:

③ $\dot{m} = m g(\gamma | E)$

* Invasion fitness

The invasion fitness $S_E(\gamma)$ of the strategy γ in the environment E is defined as

④ $S_E(\gamma) := \lim_{t \rightarrow \infty} \frac{1}{t} \int_0^t g(\gamma | E(z)) dz$

The invasion fitness is the long-term average population growth rate of the mutant.

Indeed, from ③ we get

$\log m(t) = \log m(0) + \int_0^t g(\gamma | E(z)) dz$,

and hence

$$\lim_{t \rightarrow \infty} \frac{1}{t} \log \frac{m(t)}{m(0)} = S_E(\gamma)$$

* Selective neutrality of residents.

Suppose x_1, \dots, x_k coexist given the resident environment E .

Then there exist numbers a and b such that $a < \log n_i < b$ ($i=1, \dots, k$) for all $t \gg 0$.

From the resident dynamics ② we have

$$\frac{\log n_i(t) - \log n_i(0)}{t} = \frac{1}{t} \int_0^t g(x_i | E(z)) dz$$

$\downarrow \boxed{t \rightarrow \infty}$
 0

$\downarrow \boxed{t \rightarrow \infty}$
 $S_E(x_i)$

And so, $S_E(x_i) = 0$ ($i=1, \dots, k$) whenever x_1, \dots, x_k coexist given the resident environment E .

* Time-scale separation

Because of the separate time-scales of selection (fast) and mutation (slow), we are only interested in environments generated by a resident at a population attractor (or ω -limit) such as an equilibrium or limit cycle.

To the extent that the attractor (and corresponding environment(s)) can be parameterized by the resident strategies, we can write

$$S_{\underline{x}}(y) = S_E(y).$$

(Later we may say more about ω -limits and equivalent classes of environments, but in practice it turns out not to be a big issue.)

* Example (Lotka-Volterra)

Res. dyn:

$$\dot{x}_i / x_i = r(x_i) - \sum_j a_{ij}(x_i, x_j) u_j \quad (i=1, \dots, k)$$

Juv. dyn:

$$\dot{y} / y = r(y) - \sum_j a_{ij}(y, x_j) u_j$$

Juv. fit:

$$S_x(y) = r(y) - \sum_j a_{ij}(y, x_j) \langle u_j \rangle$$

(where $\langle u_j \rangle := \lim_{t \rightarrow \infty} \frac{1}{t} \int_0^t u_j(z) dz$)

Sel. neutrality of residents.

$$0 = r(x_i) - \sum_j a_{ij}(x_i, x_j) \langle u_j \rangle \quad (i=1, \dots, k).$$

determines the values of $\langle u_j \rangle$ ($j=1, \dots, k$) without having to look in any detail at the resident dynamics.

(In particular, it does not matter whether the res. pop. has a stable equilibrium or limit cycle or what.)

Lotka-Volterra

* Example (Cannibalism time-budget model)

Res. dyn.

$$\left\{ \begin{aligned} \dot{R} &= rR \left(1 - \frac{R}{K}\right) - \alpha R \sum_j (1-x_j) n_j && \text{(resource)} \\ \dot{n}_i &= \epsilon \alpha R (1-x_i) n_i - \delta n_i + \\ &+ \gamma \beta(x_i) x_i n_i \sum_j (1-x_j) n_j + \\ &- (1-x_i) n_i \sum_j \beta(x_j) x_j n_j && (i=1, \dots, k) \end{aligned} \right.$$

Explanation:

$1-x_i$: proportion of time an individual spends on harvesting the resource R .

x_i : prop. of time an indiv. spends attacking individuals engaged in harvesting the resource.

α : harvesting rate

$\beta(x_i)$: attack rate.

$(1-x_i) n_i$: pop. dens. of individuals ^{of type x_i} engaged in harvesting.

$x_i n_i$: pop. dens. of individuals of type x_i engaged in attacking.

δ, ϵ : food conversion constants

$rR(1 - \frac{R}{K})$: logistic growth of the resource in absence of harvesting.

Inv. den.

$$\begin{aligned} \bar{m} = & \epsilon \alpha R (1-\gamma) m - \delta m + \\ & + \gamma \beta(\gamma) \gamma m \sum_j (1-x_j) n_j + \\ & - (1-\gamma) m \sum_j \beta(x_j) x_j n_j. \end{aligned}$$

Inv fitness

$$\begin{aligned} S_{\delta}(\gamma) = & \epsilon \alpha (1-\gamma) \langle R \rangle - \delta + \\ & + \gamma \beta(\gamma) \gamma \left\langle \sum_j (1-x_j) n_j \right\rangle + \\ & - (1-\gamma) \left\langle \sum_j \beta(x_j) x_j n_j \right\rangle \end{aligned}$$

So, the only thing we need to know about the resident pop. (in order to calculate the inv. fit.)

$$E_1 := \langle R \rangle \quad (\text{average resource dens.})$$

$$E_2 := \left\langle \sum_j (1-x_j) n_j \right\rangle \quad (\text{aver. dens. harvesters})$$

$$E_3 := \left\langle \sum_j \beta(x_j) x_j n_j \right\rangle \quad (\text{ " " } \text{hunters})$$

In a tri-morphic res. pop. (x_1, x_2, x_3) these numbers can be calculated using the selective neutrality of the residents:

Sel. neutrality of residents.

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$$S_x(x_i) = 0 \quad (i=1, 2, 3)$$

⇒ Explicit expressions for E_1 , E_2 and E_3 as functions of (x_1, x_2, x_3) .

- Notice that the system

$$S_x(x_i) = 0 \quad (i=1, \dots, k)$$

for $k \geq 4$ has more equations than the unknown variables E_1, E_2, E_3 and therefore (generically) has no solutions.

⇒ In this model (generically) not more than three strategies can coexist.

- For $k=1$ or 2 , we calculate $\langle R \rangle$, $\langle n_1 \rangle$ and $\langle n_2 \rangle$ from the res. dyn. using the special property of Lotka-Volterra models that the time-averages of the variables are the same as the (positive) equilibrium values.

(Exercise).

* Example (prey evolution in a predator-prey model).

Res. dyn.

$$\left\{ \begin{aligned} \dot{n}_i &= r(x_i) n_i \left(1 - \frac{\sum_j n_j}{K(x_i)} \right) - \frac{\beta(x_i) n_i \Theta}{1 + \sum_j \beta(x_j) T(x_j) n_j} \quad (\text{prey}) \\ \dot{\Theta} &= \frac{\sum_j \gamma(x_j) \beta(x_j) n_j \Theta}{1 + \sum_j \beta(x_j) T(x_j) n_j} - \delta \Theta \quad (\text{pred.}) \end{aligned} \right.$$

(Explain: functional response type II)

Juv. dyn.

$$\dot{m} = r(y) m \left(1 - \frac{\sum_j n_j}{K(y)} \right) - \frac{\beta(y) m \Theta}{1 + \sum_j \beta(x_j) T(x_j) n_j}$$

Juv. fit.

$$S_x(y) = r(y) \left(1 - \frac{E_1}{K(y)} \right) - \beta(y) E_2$$

where

$$\left\{ \begin{aligned} E_1 &= \left\langle \sum_j n_j \right\rangle \\ E_2 &= \left\langle \frac{\Theta}{1 + \sum_j \beta(x_j) T(x_j) n_j} \right\rangle \end{aligned} \right.$$

So, the only relevant information (as far as the calculation of $S_x(y)$ is concerned) about the res. pop are the time-averages E_1 and E_2 and nothing else.

Sol. units. of residents.

- If $k=2$, we can calculate E_1 and E_2 as functions of (x_1, x_2) from

$$S_i(x_i) = 0 \quad (i=1, 2).$$

- Since there are only two unknown variables (E_1 and E_2), it is clear that the present model does not allow for the coexistence of more than two resident strategies.

(Why? Hint: see previous example for a similar argument)

- An explicit expression for the inv. fitness when $k=1$ is much more troublesome to calculate, especially because the system is known to have limit cycles.

(Note: the system is not Lotka-Volterra.)

* Example (Gyllenberg & Parvinen, 2001)

res dyn.

$$\frac{\dot{n}_i}{n_i} = \frac{v(x_i) \sum_{j=1}^k n_j}{1 + \sum_{j=1}^k n_j} - 1 - \sum_{j=1}^k a(x_i, x_j) n_j$$

with $v(x) = x$ and $a(x, y) = e^{x-y}$

Ino dyn.

$$\frac{\dot{m}}{m} = \frac{y \sum_j n_j}{1 + \sum_j n_j} - 1 - e^y \sum_j e^{-x_j} n_j$$

Ino. fix.

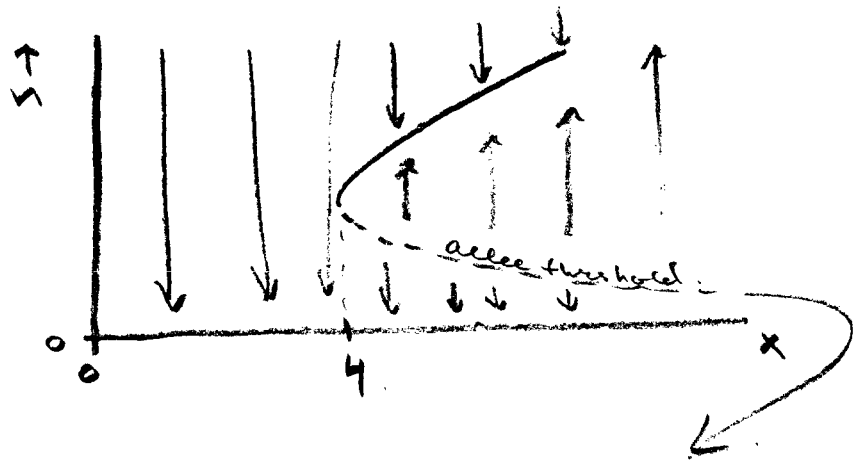
$$S_{\pm}(y) = y \underbrace{\left\langle \frac{\sum_j n_j}{1 + \sum_j n_j} \right\rangle}_{E_1} - 1 - e^y \underbrace{\left\langle \sum_j e^{-x_j} n_j \right\rangle}_{E_2}$$

So, the essential properties of the resident environment are summarized by the time averages E_1 and E_2 .

Sub. results of resident \Rightarrow

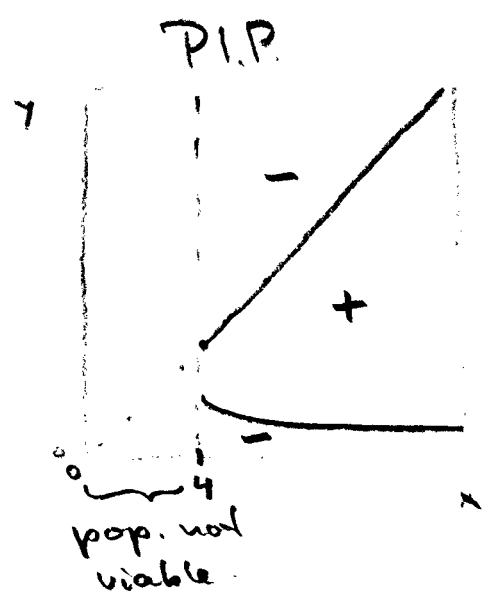
at most two resident strategies can coexist, generically.

Monomorphic res. pop.



Allee-effect (for $x \geq 4$):

Small pop. have a negative growth rate; only pop. above the Allee-threshold (see figures) can have a positive growth rate.



"evolutionary suicide"
(Discusses assumption)