V Further generalizations

So far we had a look at resident dynamics described by a system of ordinary differential equations with one equation for each resident strategy.

We now indicate how to generalize this to

- dynamics in discrete time and
- structured populations.

The adaptive dynamics of two or more coevolving species is essentially the same as for coevolving strategies in a polymorphic population of the same species, and will not be considered seperately.

Also the evolution of <u>multi-dimensional strategies</u> will not be treated, because there the theory is still very incomplete.

Invasion fitness

Invader dyn. in <u>continuous time</u>

ⓐ $\frac{dm(t)}{dt} = A(y, E(t))\, m(t) \in \mathbb{R}^d, \; d \geq 1$.

Invader dyn. in <u>discrete time</u>

ⓑ $m(t+1) = A(y, E(t))\, m(t) \in \mathbb{R}^d_+, \; d \geq 1$.

<u>Solution</u> of ⓐ or ⓑ with initial condition $(t, m) = (t_0, m_0)$:

$m(t) = m(t; t_0, m_0)$.

Since ⓐ and ⓑ are linear systems, we typically have

$\| m(t, t_0, m_0) \| \sim e^{s(t-t_0)}$ as $t \to \infty$

(i.e., exponential growth or decline).

This motivates the following definition of invasion fitness.

The invasion fitness of a strategy y in the environment E is

$$\boxed{s_E(y) := \lim_{t\to\infty} \frac{\log\|m(t;t_0,m_0)\|}{t-t_0}}$$

provided the limit exists and is independent of (t_0, m_0).

What norm is used does not matter, because in finite dimensions, all norms are equivalent.

In the context of population dynamics, the sum-norm is the most natural choice:

$m = (m_1, \ldots, m_d)$

$$\|m\| = \sum_{i=1}^{d} |m_i| = \sum_{i=1}^{d} m_i = \text{total population size.}$$

$m_i \geq 0 \; \forall i$

(pop. densities are never negative)

Case: $\boxed{\text{Unstructured population in continuous time}}$

$\dot{m} = A(y, E)\, m \quad \in \mathbb{R}^1$

$\Rightarrow \log m(t) = m_0 + \int_{t_0}^{t} A(y, E(z))\, dz$

$\Rightarrow \rho_E(y) = \lim_{t\to\infty} \frac{1}{t-t_0}\left(m_0 + \int_{t_0}^{t} A(y, E(z))\, dz\right)$

$= \langle A(y, E(t)) \rangle \quad = \left\langle \frac{d \log m(t)}{dt} \right\rangle$

which is what we've been using all along.

Case: Unstructured population in discrete time

$m(t+1) = A(y, E(t))\, m(t) \in \mathbb{R}^1_+$

$\Rightarrow \log m(t) = \log m_0 + \sum_{z=t_0}^{t-1} \log A(y, E(z))$

$\Rightarrow \rho_E(y) = \langle \log A(y, E(t)) \rangle = \left\langle \log \frac{m(t+1)}{m(t)} \right\rangle$

Example (Hamilton - May)

Annual plant species.
One plant per site.
"Lottery competition" for sites.

λ : pc seed number

x_i : fraction dispersed seeds.

ρ : survival during dispersal.

n_i : pop. dens. of strategy x_i expressed as the fraction of sites occupied.

Res. dyn

$$n_i(t+1) = \underbrace{\boxed{\frac{1-x_i}{1-x_i+\rho\sum_{j=1} x_j n_j(t)}}}_{\text{prob. of retaining an i-type site}} \cdot n_i(t)$$

$$+ \sum_{j=1}^{k} \underbrace{\frac{\rho\, x_i n_i(t)}{1-x_j+\rho\sum_{h=1}^{k} x_h n_h(t)}}_{\text{prob. of winning a j-type site.}} \cdot n_j(t)$$

(N.B. "i-type site" is a site previously owned by an x_i- plant.)

$\Rightarrow$ Invader dyn.

$$\frac{m(t+1)}{m(t)} = \frac{1-y}{1-y+\rho\sum_j x_j n_j(t)} + \sum_j \frac{\rho y n_j(t)}{1-x_j+\rho\sum_k x_k n_k(t)}$$

$$= A(y, E(t))$$

Invasion fitness

$$S_E(y) = \left\langle \operatorname{Log} \frac{m(t+1)}{m(t)} \right\rangle =$$

$$= \left\langle \log\left(\frac{1-y}{1-y+E_1(t)} + y E_2(t)\right)\right\rangle.$$

where

$$\begin{cases} E_1(t) = \rho \sum_j x_j n_j(t) \\ E_2(t) = \sum_j \dfrac{\rho n_j(t)}{1-x_j+E_1(t)} \end{cases}$$

Monomorphic res. pop.

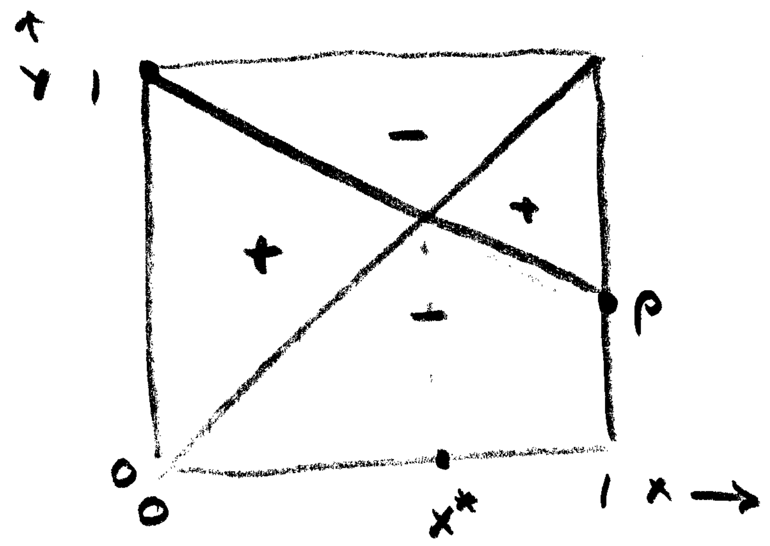
$\Rightarrow$ $n = 1$ $\forall x$.

$$\Rightarrow \quad S_x(y) = \log\left(\frac{1-y}{1-y+\rho x} + \frac{\rho y}{1-x+\rho x}\right)$$

Pairwise invadability plot:

$S_x(y) = 0 \iff$

$y = x$ or $y = 1 - x + \rho x$



Singular point:

$$x^* = \frac{1}{2-\rho}$$

- monomorphically attracting.
- uninvadable
- neighborhood invading.
- no mutual invadability.

Case:

Structured populations in continuous time

Invader dynamics.

$$\dot{m} = A(y,E)\,m \in \mathbb{R}^d \quad (d \geq 2)$$

$$\begin{cases} \|m\| := \sum m_i & \text{(pop. size)} \\ v := \dfrac{m}{\|m\|} & \text{(pop. structure)} \end{cases}$$

$$\begin{cases} \|m\|^{\cdot} = \left[\mathbb{1}^T A(y,E)\,v\right] \|m\| \\ \dot{v} = \left(A(y,E) - \left[\mathbb{1}^T A(y,E)\,v\right] I\right) v \end{cases}$$

where

$$\mathbb{1}^T := (1,\dots,1)$$

$$I := \begin{pmatrix} 1 & & 0 \\ & \ddots & \\ 0 & & 1 \end{pmatrix}$$

Notice that the dynamics of pop. structure ν are <u>independent</u> of pop. size $\|m\|$.

Moreover, notice that

$$(\log\|m\|)^{\bullet} = \mathbb{1}^T A(y,E)\,\nu$$

and so

$$s_E(y) = \left\langle \frac{d\log\|m(t)\|}{dt} \right\rangle = \left\langle \mathbb{1}^T A(y,E(t))\,\nu(t) \right\rangle.$$

Suppose the resident pop. is stable, so that $E(t) = \bar{E}$ $\forall t$, and suppose that $A(y,\bar{E})$ is <u>irreducible</u>. (→ Appendix C) with dominant eigenvalue $\lambda_{\bar{E}}(y)$ and corresponding right eigen vector $w_{\bar{E}}(y)$

Then (→ Appendix C)

$$\left.\begin{aligned} \nu(t) &\longrightarrow w_{\bar{E}}(y) \\ \mathbb{1}^T A(y,\bar{E})\,\nu(t) &\longrightarrow \lambda_{\bar{E}}(y) \end{aligned}\right|\ \text{as } t \to \infty .$$

and consequently

$$S_E(y) = \lambda_E(y) \quad \begin{pmatrix} \text{dominant eig. val.} \\ \text{of } A(y, \bar{E}) \end{pmatrix}$$

Example.

juveniles : $\dot{m}_1 = \alpha_{\bar{E}}(y)\, m_2 - \mu_{\bar{E}}(y)\, m_1 - \beta_{\bar{E}}(y)\, m_1$

adults : $\dot{m}_2 = + \mu_{\bar{E}}(y)\, m_1 - \gamma_{\bar{E}}(y)\, m_2$

$$\underbrace{\alpha_{\bar{E}}(y)\, m_2}_{\text{reproduction}} \qquad \underbrace{\mu_{\bar{E}}(y)\, m_1}_{\text{maturation}} \qquad \underbrace{\beta_{\bar{E}}(y)\, m_1,\ \gamma_{\bar{E}}(y)\, m_2}_{\text{death}}$$

In matrix notation

$$\begin{pmatrix} m_1 \\ m_2 \end{pmatrix}^{\bullet} = \underbrace{\begin{pmatrix} -\mu_{\bar{E}}(y) - \beta_{\bar{E}}(y) & \alpha_{\bar{E}}(y) \\ \mu_{\bar{E}}(y) & -\gamma_{\bar{E}}(y) \end{pmatrix}}_{A(y, \bar{E}) \text{ irreducible}} \begin{pmatrix} m_1 \\ m_2 \end{pmatrix}.$$

(→ Appendix C).

$\Rightarrow$ $S_{\bar{E}}(y) =$ dominant eigenvalue of $A(y, \bar{E})$.

Althoug the dominant eig.val. of $A(y,\bar{E})$ in the example is easy to calculate, we only need its sign.

That info we get from the trace and the determinant of $A(y,\bar{E})$. (→ Appendix A).

$S_{\bar{E}}(y) < 0 \iff m = 0$ is stable

$\iff \operatorname{tr} A(y,\bar{E}) < 0$ & $\det A(y,\bar{E}) > 0$.
(→ Appendix A).

$$\operatorname{tr} A(y,\bar{E}) = -\mu_{\bar{E}}(y) - \beta_{\bar{E}}(y) - \gamma_{\bar{E}}(y) < 0$$
ok

So, the sign of $S_{\bar{E}}(y)$ only depends on the sign of $\det A(y,\bar{E})$:

$$\det A(y,\bar{E}) = \gamma_{\bar{E}}(y)\left(\mu_{\bar{E}}(y)+\beta_{\bar{E}}(y)\right) - \alpha_{\bar{E}}(y)\,\mu_{\bar{E}}(y)$$

$$S_{\bar{E}}(y) \underset{(>)}{<} 0 \iff \det A(y,\bar{E}) \underset{(<)}{>} 0.$$

Case

Structured populations, discrete time.

Invader dynamics.

$$m(t+1) = A(y, E(t))\, m(t) \in \mathbb{R}^d_+ \quad (d \geq 2).$$

$$\begin{cases} \|m\| := \sum_i m_i & \text{(pop. size)} \\ \nu := \dfrac{m}{\|m\|} & \text{(pop. structure)}. \end{cases}$$

$$\Rightarrow \begin{cases} \|m(t+1)\| = \left[\mathbb{1}^T A(y, E(t))\nu(t)\right] \|m(t)\| \\ \nu(t+1) = \dfrac{A(y, E(t))\,\nu(t)}{\left[\mathbb{1}^T A(y, E(t))\,\nu(t)\right]} \end{cases}$$

$\Rightarrow$ • dyn. of ν indep. of dyn. of $\|m\|$.

• $$s_E(y) = \left\langle \log \frac{\|m(t+1)\|}{\|m(t)\|} \right\rangle$$

$$= \left\langle \log\left(\mathbb{1}^T A(y, E(t))\,\nu(t)\right)\right\rangle.$$

If the resident population is stable and $E(t) = \bar{E}\ \forall t$, and if $A(y, \bar{E})$ is primitive (→ Appendix C) with dominant eigenvalue $\lambda_{\bar{E}}(y)$ and corresponding right eigenvector $w_{\bar{E}}(y)$, then

$$\left.\begin{array}{l} v(t) \longrightarrow w_{\bar{E}}(y) \\ \mathbb{1}^T A(y, \bar{E})\, v(t) \longrightarrow \lambda_{\bar{E}}(y) \end{array}\right| \text{ as } t \to \infty$$

and so

$$S_{\bar{E}}(y) = \log \lambda_{\bar{E}}(y) \quad \left(\begin{array}{c}\text{log. dom.} \\ \text{eig. val.} \\ \text{of } A(y, \bar{E})\end{array}\right).$$

(→ Appendix C)

Example

$$\begin{array}{lll} \text{juveniles}: & m_1(t+1) = & \underbrace{\alpha_{\bar{E}}(y)}_{\text{reproduction}}\, m_2(t) \\ \text{adults}: & m_2(t+1) = & \underbrace{\mu_{\bar{E}}(y)}_{\text{maturation \& survival}}\, m_1(t) + \underbrace{\gamma_{\bar{E}}(y)}_{\text{survival}}\, m_2(t) \end{array}$$

In matrix notation

$$\begin{pmatrix} m_1 \\ m_2 \end{pmatrix}(t+1) = \underbrace{\begin{pmatrix} 0 & \alpha_{\bar{E}}(y) \\ \mu_{\bar{E}}(y) & \gamma_{\bar{E}}(y) \end{pmatrix}}_{A(y,\bar{E})} \begin{pmatrix} m_1 \\ m_2 \end{pmatrix}(t)$$

$A(y,\bar{E})$ is primitive
(→ Appendix C)

Eigenvalues

$$\lambda = \frac{1}{2}\left(\gamma_{\bar{E}}(y) \pm \sqrt{\gamma_{\bar{E}}(y)^2 + 4\,\alpha_{\bar{E}}(y)\,\mu_{\bar{E}}(y)}\right)$$

the '+' gives the dom eig. val.

$$\Rightarrow \quad S_{\bar{E}}(y) = \frac{1}{2}\left(\gamma_{\bar{E}}(y) + \sqrt{\gamma_{\bar{E}}(y)^2 + 4\,\alpha_{\bar{E}}(y)\,\mu_{\bar{E}}(y)}\right)$$