Stationary solutions of selection mutation equations

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Introduction

Selection-Mutation equations

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- Population Genetics (**Crow, Kimura (64, 65), Bürger (89, 91, 96, 00)**).
- Phenotypic evolution (**Perelló, Calsina, Saldaña (89, 94, 95, 03) Magal, Webb (00)**).

Introduction

$u(x,t)$ density of individuals with respect to some **evolutionary trait** x.

Individuals are characterized by their type x, where $x \in \Omega$ (space of all admissible types) $\Omega = \mathbb{R}$ or $\Omega = [0,1]$ or $\Omega = \mathbb{R}^n$ (for instance).

$u(x,t) \geq 0$, $u(x,t)$ integrable with respect to x for any fixed t ($\int_\Omega u(x,t)\mathrm{d}x =$ Total population).

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- Selection $\longrightarrow$ Process by which organisms with traits well adapted to an environment survive and reproduce at a greater rate.
  Nonlinear terms that model the competitive interaction between individuals.

- Mutation $\longrightarrow$ Changes in the genetic material which can be passed from parents to offspring.
  Incorporated as a linear operator which must model the diffusive effect on the trait space of inaccurate replication.

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- Laplacian Operator $\mu\Delta u$ (where μ denotes the mutation rate).
- Integral operator with a kernel $\beta(x, y)$ representing the density of probability that an individual with trait y has offspring with trait x.

Example

One parameter family competing for a limited amount of resources (Calsina, Perelló)

$$\begin{cases} u_t = \left(x - \int_0^1 u\right)u + au_{xx} \quad x \in (0,1), \\ u(x,0) = u_0(x), \\ u(0,t) = u(1,t) = 0. \end{cases}$$

$u(x,t)$: density of population at time t of individuals with $x \in [0,1]$,
x : population's rate of growth without restriction (total growth rate decreased by total population because they share limited resources),

au_{xx} : diffusion that represents the mutation.

Example : A model for the maturation age I (Calsina, C.)

$$\begin{cases} u_t(x,t) &= \int_0^\infty b(y)\beta_\varepsilon(x,y)v(y,t)\mathrm{d}y \\ & \quad -m_1\Big(\int_0^\infty u(y,t)\mathrm{d}y\Big)u(x,t) - xu(x,t), \\ v_t(x,t) &= xu(x,t) - m_2\Big(\int_0^\infty v(y,t)\mathrm{d}y\Big)v(x,t). \end{cases}$$

$x = \frac{1}{T}$, $b(x)$ trait specific fertility, m_i mortality rates,
$\beta_\varepsilon(x,y)$ is the density of probability that the trait of the offspring of an individual with trait y is x,
($\int_0^\infty \beta_\varepsilon(x,y)\mathrm{d}x = 1$),
supp$\beta_\varepsilon(\cdot,y)$ contains the interval $(\max(0, y-\delta), y+\delta)$,
ε (maximum) size of the mutation.

Example: A model for the maturation age II (Calsina, C.)

$$\begin{cases} u_t(x,t) &= (1-\varepsilon)b(x)v(x,t) \\ & \quad +\varepsilon \int_0^\infty b(y)\gamma(x,y)v(y,t)\mathrm{d}y \\ & \quad -m_1\big(\int_0^\infty u(y,t)\mathrm{d}y\big)u(x,t) - xu(x,t), \\ v_t(x,t) &= xu(x,t) - m_2\big(\int_0^\infty v(y,t)\mathrm{d}y\big)v(x,t). \end{cases}$$

ε stands for the probability of mutation,

$\gamma(x,y)$ is the density of probability that the trait of the mutant offspring of an individual with trait y is x.

Example: Predator prey model (Calsina, C.)

$$\begin{cases} f'(t) = \left(a - \mu f(t) - \int_0^\infty \frac{\beta(x)u(x,t)}{1+\beta(x)hf(t)}\mathrm{d}x\right) f(t), \\ \frac{\partial u(x,t)}{\partial t} = -d(x)u(x,t) + (1-\varepsilon)\frac{\alpha\beta(x)f(t)u(x,t)}{1+\beta(x)hf(t)} \\ \qquad + \ \varepsilon \int_0^\infty \gamma(x,y)\frac{\alpha\beta(y)f(t)u(y,t)}{1+\beta(y)hf(t)}\mathrm{d}y, \end{cases}$$

a and μ intrinsic growth rate and competition coefficient of the prey population, $\beta(x)$ searching efficiency, x index of activity of the predator population, $d(x)$ mortality rate of the predator population.

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- Study of the equilibria of these equations for the density of individuals with respect to a phenotypic evolutionary trait and their relation with the **evolutionarily stable values (ESS)** of the underlying ecological models .

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- Stability of these equilibria.

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Evolutionarily Stable Strategies (ESS) (**Maynard Smith and Price, 73**) $\longrightarrow$ Stationary values of the evolutionary process.

Definition. *A strategy (phenotypic characteristic) x is an ESS if a clonal population of individuals with strategy x (resident population) cannot be invaded by another small clonal population of individuals with a different strategy y (mutant population).*

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An ESS is stable against the invasion of mutants but not necessarily an evolutionary attractor (not necessarily a limiting value of a sequence of strategies driven by natural selection).

Evolutionary dynamics

Mathematical formulation of the ESS concept for systems of the form

$$\vec{u}_t = A(\vec{u}, x)\vec{u}$$

where $\vec{u}$ denotes the resident population, x is a parameter denoting the strategy of the population and $A(\vec{u}, x)$ is a linear operator. We assume that the system has a unique attractor which is a hyperbolic non trivial equilibrium point $\vec{u}_x$.

Evolutionary dynamics

Small mutant population, $\vec{u}^i$, with strategy y.
System for the couple of populations

$$\begin{cases} \vec{u}_t = A(\vec{u}, \vec{u}^i, x)\vec{u}, \\ \vec{u}^i_t = A(\vec{u}, \vec{u}^i, y)\vec{u}^i, \end{cases} \qquad (0)$$

where $\forall \vec{u}, x \quad A(\vec{u}, 0, x) = A(\vec{u}, x)$.
The value x of the strategy is an ESS if the equilibrium point $(\vec{u}_x, \vec{0})$ is hyperbolic and asymptotically stable for this system for any $y \neq x$.

Equilibria

Selection mutation equations can be written in a (rather) general way

$$\vec{u}_t = A_\varepsilon(F(\vec{u}))\vec{u}$$

where $F : L^1(I, \mathbb{R}^n) \longrightarrow \mathbb{R}^m$ (linear and continuous). For fixed E, $A_\varepsilon(E)$ infinitesimal generator of a positive semigroup.

Let us assume that $A_\varepsilon(E)$ has a dominant eigenvalue $\lambda_\varepsilon(E)(= s(A_\varepsilon(E)))$ with a normalized (positive) eigenvector $\vec{u}_{\varepsilon,E}(x)$. Moreover, we assume that $\vec{u}_{\varepsilon,E}(x)$ is the only positive eigenvector of $A_\varepsilon(E)$.

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$$\vec{u}_t = A_\varepsilon(F(\vec{u}))\vec{u}$$

for $\varepsilon > 0$ if an only if there exist $c > 0$ and $E \in \mathbb{R}^m$ such that $\vec{u} = c\vec{u}_{\varepsilon,E}$ and c and E satisfy

$$\begin{cases} \lambda_\varepsilon(E) = s\big(A_\varepsilon(E)\big) = 0, \\ F\big(c\vec{u}_{\varepsilon,E}\big) - E = 0. \end{cases} \tag{1}$$

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1+dim(F). equations (1+dim(F) unknowns (c, E)).

Eigenvalue problem + Fixed point problem.

Equilibria

Let us assume that, for every (sufficiently small) $\varepsilon > 0$ there exists an equilibrium solution $\vec{u}_\varepsilon := c_\varepsilon \vec{u}_{\varepsilon, E_\varepsilon}$ of the nonlinear equation $\vec{u}_t = A_\varepsilon(F(\vec{u}))\vec{u}$.

How does this steady state behave when $\varepsilon \longrightarrow 0$?

Equilibria

Let us consider, for fixed x, the n-dimensional ordinary differential equations system

$$\vec{v}_t = A_0(x, G(x, \vec{v}))\vec{v} \tag{1}$$

where $G(x, \cdot)$ is a linear function from $\mathbb{R}^n$ to $\mathbb{R}^m$, $\big(G(x, \vec{v}) = F(\vec{v}\delta_x)\big)$, $x \in I$ is a real parameter and $A_0(x, E)$ is a $n \times n$ matrix. Let $\hat{x}$ denote the value of ESS of this system.

Equilibria

Then the family of equilibria $\vec{u}_\varepsilon$ satisfies

$$\vec{u}_\varepsilon \xrightarrow{\varepsilon\to 0} \vec{v}_{\hat{x}}\delta_{\hat{x}}$$

in the weak star topology (of $L^1(I,\mathbb{R}^n)$) where $\vec{v}_{\hat{x}}$ is the positive equilibrium of the system

$$\vec{v}_t = A_0(x, G(x,\vec{v}))\vec{v}$$

for $x = \hat{x}$ (ESS value).

Moreover $\int_0^\infty u_\varepsilon^i(x)\mathrm{d}x \xrightarrow{\varepsilon\to 0} v_{\hat{x}}^i$, $i = 1\ldots n$.

Equilibria

Under reasonable hypotheses,

$$\vec{u}_t = A_\varepsilon(F(\vec{u}))\vec{u}$$

has a family of equilibria $\vec{u}_\varepsilon$ that tend to concentrate at the ESS of the finite dimensional "limit" system

$$\vec{v}_t = A_0(x, G(x, \vec{v}))\vec{v}$$

when ε tends to 0.
Moreover, the integral of $\vec{u}_\varepsilon$ (the total population at equilibrium) tends to the equilibrium of the finite dimensional "limit" system for the value $\hat{x}$ of the parameter.

Stability

$$\vec{u}_t = A_\varepsilon(F(\vec{u}))\vec{u} \tag{2}$$

where $F : L^1(I, \mathbb{R}^n) \longrightarrow \mathbb{R}^m$ (linear and continuous).

Stability

$$\vec{u}_t = A_\varepsilon(F(\vec{u}))\vec{u} \qquad (2)$$

where $F : L^1(I, \mathbb{R}^n) \longrightarrow \mathbb{R}^m$ (linear and continuous).
Assumptions:

- For fixed E, $A_\varepsilon(E)$ generates an analytic positive semigroup.
- $A_\varepsilon(E)$ can be written as the sum of a constant (independent of E) operator and a bounded linear operator depending smoothly on E.
- There exists a positive equilibrium solution $\vec{u}_\varepsilon$ of (2).

Stability

Stability by the linear approximation $\longrightarrow$ If the spectrum of the linearization of $\vec{u}_t = A_\varepsilon(F(\vec{u}))\vec{u}$ at the equilibrium point $\vec{u}_\varepsilon$ lies in $\{\mathrm{Re}\lambda < \beta\}$ for some $\beta < 0$ then $\vec{u}_\varepsilon$ is uniformly asymptotically stable.

Stability

Linearizing, we obtain

$$\vec{v}_t = A_\varepsilon(E_\varepsilon)\vec{v} + DA_\varepsilon(E_\varepsilon)F(\vec{v})\vec{u}_\varepsilon$$

$$=: \tilde{A}_\varepsilon\vec{v} + S_\varepsilon\vec{v}.$$

$E_\varepsilon := F(\vec{u}_\varepsilon)$,
S_ε is a linear operator with finite dimensional range ($\leq m$)
(generated by $\{DA_\varepsilon(E_\varepsilon)e_i\vec{u}_\varepsilon\}_{i=1}^m$ where $\{e_i\}_{i=1}^m$ is a basis of $\mathbb{R}^m$).

Stability

Computing the spectrum of the operator $\tilde{A}_\varepsilon + S_\varepsilon$ we obtain

$$\sigma(\tilde{A}_\varepsilon + S_\varepsilon) \subset \sigma(\tilde{A}_\varepsilon) \cup \{\lambda : \det\Big(Id + S_\varepsilon \big(\tilde{A}_\varepsilon - \lambda Id\big)^{-1}\Big) = 0\}.$$

where $\det\Big(Id + S_\varepsilon \big(\tilde{A}_\varepsilon - \lambda Id\big)^{-1}\Big) =: \omega_\varepsilon(\lambda)$

Weinstein Aronszajn determinant defined as

$$\det\Big(Id + S_\varepsilon (\tilde{A}_\varepsilon - \lambda Id)^{-1}\Big) = \det\Big(\big(Id + S_\varepsilon (\tilde{A}_\varepsilon - \lambda Id)^{-1}\big)_{|_{R(S_\varepsilon)}}\Big).$$

where $R(S_\varepsilon)$ denotes the range of the operator S_ε

Stability

$$\vec{v}_t = A_0(x, G(x, \vec{v}))\vec{v},$$

$\hat{x}$ ESS and $\vec{v}_{\hat{x}}$ equilibrium (asymptotically stable).
Linearizing $\vec{v}_t = A_0(\hat{x}, G(\hat{x}, \vec{v}))\vec{v}$

$$\begin{aligned} \vec{w}' &= A_0(\hat{x}, E_0)\vec{w} + \Big(\frac{\partial A_0}{\partial G}(\hat{x}, E_0)G(\hat{x}, \vec{w})\Big)\vec{v}_{\hat{x}} \\ &=: \tilde{A}_0\vec{w} + S_0\vec{w}. \end{aligned}$$

where $E_0 := G(\hat{x}, \vec{v}_{\hat{x}})$.

$$\omega_0(\lambda) := \det\Big(Id + S_0(\tilde{A}_0 - \lambda Id)^{-1}\Big).$$

Stability

$\omega_0(\lambda)$ is holomorphic for $\lambda \notin \sigma(\tilde{A}_0)$.

If 0 is a dominant eigenvalue of $\tilde{A}_0$ then $\omega_0(\lambda)$ is holomorphic for λ such that $\mathrm{Re}\,\lambda \geq 0$, $\lambda \neq 0$.

As we assume that the equilibrium point $\vec{v}_{\hat{x}}$ is hyperbolic and asymptotically stable, $\omega_0(\lambda)$ does not vanish for λ such that $\mathrm{Re}\,\lambda \geq 0$, $\lambda \neq 0$.

For ε small enough, does $\omega_\varepsilon(\lambda)$ have the same property?

Stability

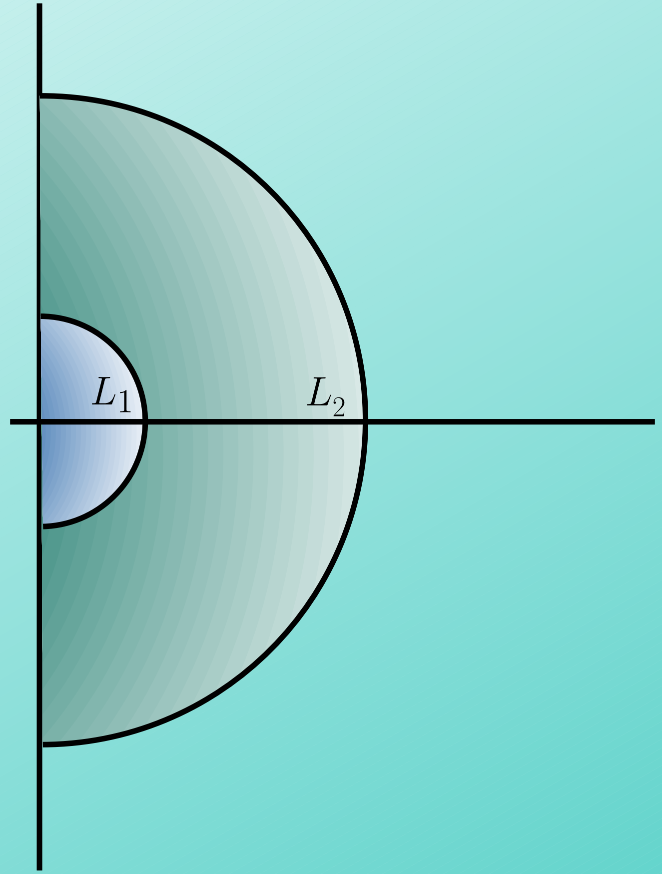
By **Rouche**'s theorem, if $\omega_\varepsilon(\lambda) \xrightarrow{\varepsilon \to 0} \omega_0(\lambda)$ uniformly on λ in compact sets then $\forall L_1 > 0\ \exists \varepsilon$ small enough such that

$$\omega_\varepsilon(\lambda) \neq 0$$

for $\lambda \in \{\lambda \in \mathbb{C} \quad \text{s.t.} \quad \text{Re}\lambda \geq 0, 0 < L_1 \leq |\lambda| \leq L_2\}$.

($\vec{v}_{\hat{x}}$ asymptotically stable $\longrightarrow \omega_0(\lambda) \neq 0$ for $\lambda \in \{\lambda \in \mathbb{C} \quad \text{s.t.} \quad \text{Re}\lambda \geq 0, \lambda \neq 0\}$).

Stability



Stability

If there exists $L_1 > 0$ such that for ε small

$\{\lambda \in \mathbb{C} \quad \text{s.t.} \quad \text{Re}\lambda \geq 0, |\lambda| < L_1\} \cap \sigma(\tilde{A}_\varepsilon + S_\varepsilon) = \emptyset$

then for ε small enough, the equilibrium solution $\vec{u}_\varepsilon$ of the nonlinear equation $\vec{u}_t = A_\varepsilon(F(\vec{u}))\vec{u}$

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Case F one dimensional ($F : L^1(I, \mathbb{R}^n) \longrightarrow \mathbb{R}$)
(Weinstein-Aronszajn formula).