Adaptive Dynamics in Finite Populations

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LAMBERT. The branching process with logistic growth. *Ann. Appl. Prob.* (2005)
CHAMPAGNAT, LAMBERT. Evolution of discrete populations and the canonical diffusion of adaptive dynamics. *Ann. Appl. Prob.* (2007)

AD : trait substitution sequence (TSS)

The trait substitution sequence (TSS, Metz et al., 1996) proceeds from the assumption of rare mutations : mutation probability multiplied by $\gamma \to 0$

- time t rescaled as t/γ
- requires only to know the fixation outcome of two-type populations
- evolution proceeds through a sequence of mutant invasions and fixations : jump process over the trait space, called TSS : trait substitution sequence.

Introduction Model TSS Canonical diffusion of AD Logistic branching
Reminder : What is adaptive dynamics ?

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AD : canonical equation of adaptive dynamics

The canonical equation of adaptive dynamics (Dieckmann and Law, 1996) proceeds from an extra assumption of small mutations applied to the TSS : mutation kernel rescaled by $\varepsilon \to 0$, and time t is rescaled as t/ε^2

- Deterministic ODE :

$$\frac{dx}{dt} = \frac{1}{2}\sigma(x)^2\mu(x)\bar{n}(x)\frac{\partial}{\partial y}f(x,x)$$

- σ^2 variance of the mutation steps
- μ probability of mutation at each birth event
- $\bar{n}$ equilibrium size of a pure x-type population
- $f(x,y)$ invasion fitness of a mutant type y in an equilibrium x-type population

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Hidden assumption

- Except in population genetics, isolated populations go extinct a.s.
- Too rare mutations $\Longrightarrow$ Extinction before first mutation
- $\Longrightarrow$ Assumption of large populations
- Consequence :
- Goal : keep population finite and stochastic to include drift in the TSS and the canonical equation.

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Model assumptions

- We consider an individual-based model of a discrete, isolated population :
  - continuous-time Markov chain
  - structured : individuals bear types (traits)
  - (possibly) varying size N_t that does not go to ∞
  - population never becomes extinct ($N_t \geq 1$)
- Interpretation : separation of timescales of mutations and extinction.
- Mathematical notion of quasistationarity : population size is conditioned to remain ≥ 1.

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General self-regulated populations

A general structured birth-and-death process with mutation

- each individual is characterized by a trait x (individual size, age at maturity,...) in a closed subset $\mathscr{X}$ of $\mathbb{R}^k$
- a population of $N(t)$ individuals holding traits $x_1, \ldots, x_{N(t)} \in \mathscr{X}$ is represented by $\nu_t = \sum_{i=1}^{N(t)} \delta_{x_i}$
- $d(x,\nu)$ is the death rate of x-type individuals in a population in state ν
- $b(x,\nu)$ is the birth rate of x-type individuals in a population in state ν
- at each birth event, mutation from $x \to x+h+dh$ with probability $\gamma\mu(x)M(x,dh)$

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Example : the logistic branching process (Etheridge 2004, Lambert 2005)

Dynamics of the multitype logistic branching process :

- as in the pure multitype branching process :
  - each individual with trait x gives birth at rate $b(x)$ to one single individual with trait x
  - each individual of type x dies at rate $d(x)$
- in addition, each individual of type $\mathbf{y}$ picks any other given individual of type $\mathbf{x}$ at rate $\mathbf{c}(\mathbf{x},\mathbf{y})$ and then kills her.
- The logistic branching process comes down from infinity. In particular, the population size cannot go to ∞.

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GL-populations

We define GL-populations as those models satisfying

- there is $\bar{b}$ such that for any ν and x, $0 < b(x,\nu) \leq \bar{b}$
- there are $\underline{c}$ and $\alpha > 0$ such that for any ν and x,

$$d(x,\nu) \geq \underline{c}\ (N-1)^{\alpha}$$

- if $\nu = \delta_x$, then $d(x,\nu) = 0$.

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In particular, extinction has zero probability.

Basic result

Theorem

*Consider a GL-population $(\nu_t; t \geq 0)$ with **no** mutation. For any initial condition, the fixation time T*

$$T := \inf\{t \geq 0 : |Supp(\nu_t)| = 1\}$$

is finite a.s.. Let x be the surviving type.
Then conditional on T and x, the post-T size process $(N(t); t \geq T)$ converges in distribution to a random integer $\xi(x)$.

Notation

- $\xi(x)$: stationary size of a clonal population with trait x
- $b(x,n)$: individual birth rate in a clonal population with trait x and size n
- $d(x,n)$: individual death rate in a clonal population with trait x and size n
- For a two-type GL-population with **no** mutation starting with n ind. of type x (resident) and m ind. of type y (mutant), the fixation probability of the mutant is denoted $u_{n,m}(x,y)$.

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Basic result

Let τ be the first mutation time.

Lemma

When $\nu_0 = n\delta_x$, $(\gamma\tau, N(\gamma\tau-))$ converges in law to (T,N) where T and N are independent, $T \sim \mathscr{E}xp(\beta(x))$ where

$$\beta(x) := \mu(x)\mathbb{E}(\xi(x)b(x,\xi(x)))$$

is the mean production rate of mutants, and

$$\mathbb{P}(N=k) = \mathbb{P}(\xi(x)=k)\frac{kb(x,k)}{\mathbb{E}(\xi(x)b(x,\xi(x)))}$$

is the $b(x,\cdot)$-size-biased stationary population size.

Convergence of the support

Let ρ_k be the k-th time when the population gets monomorphic, and V_k the then surviving type.

Theorem

Assume $\nu_0 = n\delta_x$. The process $(S_t^\gamma; t \geq 0)$ defined as $S_t^\gamma := V_k$ if $\rho_k \leq t/\gamma < \rho_{k+1}$

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Interpretation

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$$f(x,y) = \sum_{n\geq 1} \mathbb{P}(\xi(x)=n)\frac{nb(x,n)}{\mathbb{E}(\xi(x)b(x,\xi(x)))} u_{n,1}(x,y).$$

is the fixation probability of a y-type mutant in a $b(x,\cdot)$-biased stationary x-type population (invasion fitness).

Invasion fitness (Metz et al., 1992)

The invasion fitness $f(x,y)$ is the ability for an initially rare mutant of trait y to invade a monomorphic resident population of trait x at ecological equilibrium.

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- In the large population setting,

$$f(x,y) = \left(1 - \frac{D(x,y)}{B(x,y)}\right)^+,$$

where B,D are the birth/death rates of rare y-mutants in the x-resident background.

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where B,D are the birth/death rates of rare y-mutants in the x-resident background.
- This invasion fitness is in fact the survival probability for the branching process with birth/death rates B and D.

Convergence of the population size

Theorem

For any $0 < t_1 < \ldots < t_n$, $(\nu^\gamma_{t_1/\gamma}, \ldots, \nu^\gamma_{t_n/\gamma})$ converges in law to $(\zeta_{t_1}, \ldots, \zeta_{t_n})$ where $\zeta_{t_i} = N_{t_i}\delta_{Z_{t_i}}$ such that

1. *$(Z_t; t \geq 0)$ is the TSS process of the previous theorem*
2. *Conditional on $(Z_{t_1}, \ldots, Z_{t_n}) = (z_1, \ldots, z_n)$, the N_{t_i} are independent and respectively distributed as $\xi(z_i)$.*

The convergence only holds for f.d.d.

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2. *Conditional on $(Z_{t_1}, \ldots, Z_{t_n}) = (z_1, \ldots, z_n)$, the N_{t_i} are independent and respectively distributed as $\xi(z_i)$.*

The convergence only holds for f.d.d.

Assumptions

We make the following assumptions.

- $\mathscr{X} = \mathbb{R}^k$ for simplicity
- Smoothness of $b(\cdot, \nu)$ and $d(\cdot, \nu)$ ensuring that the invasion fitness

$$y \mapsto f(x,y) = \sum_{n \geq 1} \mathbb{P}(\xi(x) = n) \frac{nb(x,n)}{\mathbb{E}(\xi(x) b(x, \xi(x)))} u_{n,1}(x,y)$$

  is in $\mathscr{C}^2_b$
- the mutation kernel satisfies
  - $M(x, \cdot)$ has 0 expectation, i.e. $\int_{\mathbb{R}^k} hM(x,dh) = 0$
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Scaling of the mutation kernel

We are going to apply a limit of small jumps to the TSS, following the heuristics leading to the canonical equation of adaptive dynamics.

- Replace the mutation law $M(x,dh)$ with its image by $h \mapsto \varepsilon h$ $(\varepsilon > 0)$
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$\rightsquigarrow$ Rescaled TSS $(Z_t^\varepsilon; t \geq 0)$ with generator

$$A_\varepsilon \varphi(x) = \frac{1}{\varepsilon^2} \int_{\mathbb{R}^k} (\varphi(x + \varepsilon h) - \varphi(x)) \beta(x) f(x, x + \varepsilon h) M(x, dh)$$

Limit of the generator

Making a second-order expansion,

$$(\varphi(x+\varepsilon h)-\varphi(x))f(x,x+\varepsilon h)=\varepsilon(h'\nabla\varphi(x))f(x,x)$$
$$+\varepsilon^2(h'\nabla\varphi(x))(h'\nabla_2 f(x,x))+\frac{\varepsilon^2}{2}(h'H\varphi(x)h)f(x,x)+O(\varepsilon^3\|h\|^3)$$

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$\rightsquigarrow$ $A_\varepsilon\varphi$ converges uniformly to the function $A_0\varphi$

$$A_0\varphi(x)=\int_{\mathbb{R}^k}(h'\nabla\varphi(x))\beta(x)h'\nabla_2 f(x,x)M(x,dh)$$
$$+\frac{1}{2}\int_{\mathbb{R}^k}(h'H\varphi(x)h)\beta(x)f(x,x)M(x,dh).$$

The canonical diffusion of adaptive dynamics

Let $\sigma(x)$ be the square root of the covariance matrix of $M(x,\cdot)$.

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Theorem

As $\varepsilon\to 0$, Z^ε converges in law on $\mathbb{D}(\mathbb{R}+,\mathbb{R}^k)$ to the diffusion process solution to the SDE

$$dZ_t=\beta(Z_t)\sigma^2(Z_t)\cdot\nabla_2 f(Z_t,Z_t)dt+\sqrt{\beta(Z_t)f(Z_t,Z_t)}\sigma(Z_t)\cdot dB_t$$

where B is a standard k-dimensional Brownian motion, and ∇_2 is the gradient w.r.t. the second variable.

Discussion

- We obtain a diffusion model of evolution grounded on a microscopic realistic population dynamics
- Genetic drift proportional to $\beta(x)$, to the neutral fixation probability $f(x,x)$ and to the covariance matrix of $M(x,\cdot)$.
- Directional selection similar to the one of the canonical ODE

$$\frac{dx}{dt}=\frac{1}{2}\sigma(x)^2\mu(x)\bar{n}(x)\frac{\partial}{\partial y}f(x,x)$$

  - the covariance matrix of $M(x,\cdot)$
  - the total mutant production rate $\beta(x)$
  - the gradient of the fixation probability $f(x,y)$ of a y-type mutant in a stationary x-type resident population.
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In this case, the main force driving evolution is the mutation bias. The mutation rate $\beta(x)$ and the fixation probability $f(x,x)$ only affect the speed of evolution.

Parameters of the two-type logistic branching process

- the two-type logistic branching process is characterized by : birth vector B, competition matrix C and death vector D

$$B = \begin{pmatrix} b_1 \\ b_2 \end{pmatrix}, \qquad C = \begin{pmatrix} c_{11} & c_{12} \\ c_{21} & c_{22} \end{pmatrix}, \qquad D = \begin{pmatrix} d_1 \\ d_2 \end{pmatrix}$$

- where 1 refers to the resident type, and 2 refers to the mutant type
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Neutrality

- the case when types are exchangeable is referred to as (selective) neutrality, that is

$$B = \begin{pmatrix} b \\ b \end{pmatrix}, \qquad C = \begin{pmatrix} c & c \\ c & c \end{pmatrix}, \qquad D = \begin{pmatrix} d \\ d \end{pmatrix}$$

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Five fundamental selection coefficients (1)

We will express deviations from neutrality as

$$B = \begin{pmatrix} b \\ b \end{pmatrix} + \begin{pmatrix} 0 \\ \lambda \end{pmatrix}, \qquad D = \begin{pmatrix} d \\ d \end{pmatrix} - \begin{pmatrix} 0 \\ \sigma \end{pmatrix},$$

$$C = \begin{pmatrix} c & c \\ c & c \end{pmatrix} - \begin{pmatrix} 0 & 0 \\ \delta & \delta \end{pmatrix} + \begin{pmatrix} 0 & \alpha \\ 0 & \alpha \end{pmatrix} - \begin{pmatrix} 0 & \varepsilon \\ \varepsilon & 0 \end{pmatrix}.$$

The coefficients λ, δ, α, ε, σ are chosen to be positive when they confer an advantage to the mutant, and are called the five fundamental (additive) selection coefficients.

Five fundamental selection coefficients (2)

1. fertility λ : positive λ means increased mutant birth rate
2. defence capacity δ : positive δ means reduced competition sensitivity of mutant individuals from the rest of the population
3. aggressiveness α : positive α means raised competition pressure exerted from any mutant individual onto the rest of the population
4. isolation ε : positive ε means lighter cross-competition between different morphs
5. survival σ : positive σ means reduced mutant death rate.

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Factorization of second-order terms

Theorem

As a function of the multidimensional selection coefficient $\mathbf{s} = (\lambda, \delta, \alpha, \varepsilon, \sigma)'$, the probability u is differentiable, and in a neighborhood of $\mathbf{s} = \mathbf{0}$ (selective neutrality),

$$u = p + \mathbf{v}'.\mathbf{s} + o(\mathbf{s}),$$

*where the **selection gradient** $\mathbf{v} = (v^\lambda, v^\delta, v^\alpha, v^\varepsilon, v^\sigma)'$ can be expressed as*

$$v^\iota_{n,m} = p(1-p)\, g^\iota_{n+m} \qquad \iota \neq \varepsilon,$$

$$v^\varepsilon_{n,m} = p(1-p)(1-2p)\, g^\varepsilon_{n+m}$$

And the g's depend solely on the resident's characteristics b, c, d, and on the total initial population size $n+m$. They are called invasibility coefficients.

Invasibility coefficients

Consider a monomorphic logistic branching population $(b, c, 0)$.

- Invasibility by mutants with increased fertility :

$$g^\lambda_n = \frac{n}{2c(n+1)} \longrightarrow \frac{1}{2c}$$

- Invasibility by mutants with increased aggressiveness or survival :

$$\lim_{n\to\infty} g^\alpha_n = \lim_{n\to\infty} g^\sigma_n = \frac{1}{2c} + \frac{1}{2b}\left(1 - \frac{c}{\kappa}\right),$$

where $\kappa = b(1-2q_3/3)/q_\infty$ and

$$q_k = \mathbb{P}_k(\text{ last two survivors have distinct ancestors })$$

- Invasibility by mutants with increased isolation or defence capacity :

$$g^\varepsilon_n \sim (<) g^\delta_n \sim c^{-1}\ln(n) \qquad \text{as } n \to \infty.$$

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Example

Assume the model is logistic branching, and that

- $\mathscr{X} = \mathbb{R}$
- $c(x,y) = C(|x-y|)$ and $C(0) = 1$
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The canonical diffusion of adaptive dynamics is given by

$$dZ_t = r(Z_t)dt + \sigma(Z_t)\mu(Z_t)^{1/2}\left(\frac{b(Z_t)}{1-e^{-b(Z_t)}} - 1\right)^{1/2} dB_t$$

where

$$r(x) = \frac{\mu(x)\sigma(x)^2}{2}\left(1 + \frac{4}{b(x)} + \frac{b(x)-4}{1-e^{-b(x)}}\right) b'(x).$$

Other example : Moran model

- Two-type Moran model, constant size $N+1$
- If x is the resident trait, each pair of individuals with traits (x,y) is replaced with :

  a pair of type (y,y) at rate $c_1(x,y)$
  a pair of type (x,x) at rate $c_2(y,x)$
- The canonical diffusion of adaptive dynamics becomes :

$$dX_t = \frac{1}{2}\mu(X_t)N^2\sigma(X_t)^2\frac{\partial}{\partial y}f(X_t,X_t)dt + \sigma(X_t)\sqrt{N\mu(X_t)c(X_t,X_t)}dB_t,$$

where $c(x,x) := c_1(x,x) = c_2(x,x)$,
and the invasion fitness $f(x,y)$ is $c_1(x,y) - c_2(y,x)$.

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Further results
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...That's all, thanks for listening.