Modelling adaptive dynamics for structured populations with function-valued traits

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Joint work with V.C. Tran and J.A.J. Metz.

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Evolution : Introduction

• Evolution is the change over time in the types of individuals that are found in a population

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- We want to understand mathematically how this evolutionary cycle works.

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- Population exhibits asexual reproduction.
- Work at the level of phenotypes. Only source of variation in trait values is mutation.
- Each trait value has an associated fitness value that changes with the population dynamics. Hence the adaptive landscape for evolution is no longer fixed.

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- Assumption 2 : Population size is large.
 - Allows us to work with population density.
 - Makes models more tractable.

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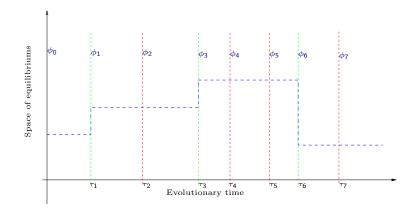
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- If invasion happens, the existing equilibrium gets disturbed and a new equilibrium gets established. Then the whole cycle starts again.
- We get a jump process over the space of equilibriums. This is called the TSS.

Adaptive dynamics : The Trait Substitution Sequence (TSS)



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- The process that gives the surviving trait value at any time is a jump process in the trait space.
- We can scale time and mutation step sizes to obtain an ordinary differential equation in the trait space.
- This differential equation describes the evolution of advantageous trait values.

 Seminal work : Hofbauer-Sigmund , Marrow-Law-Cannings, Metz-Nisbet-Geritz, Metz-Geritz-Meszéna-Jacobs-Heerwaasden and Dieckmann-Law.

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- This mathematical framework was extended to populations with trait and age structure by Tran and Méléard.
- In our case we consider infinite dimensional function-valued traits.
- We use averaging techniques to construct the TSS. This technique works equally well when the selection dynamics leads to coexistence or cyclic/chaotic attractors.

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Why are function-valued traits important ?

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- Phenotypic plasticity : Function-valued trait is the reaction norm of an organism that describes the phenotypic response to a particular set of environmental conditions (temperature, salinity etc.)
- Physiologically structured populations : The reproductive capabilities may vary continuously with size/age/weight.
- Resource utilization theory : Resources vary along a continuum. A function-valued trait may describe the harvesting rate for each resource.

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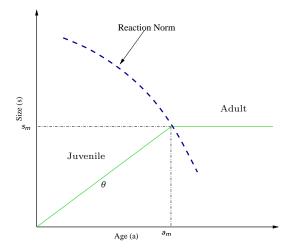
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Apart from function-valued traits, the individuals in our model are also structured by :

- Physical age.
- Noise parameter that accounts for randomness in the environment.

Ernande et. al. : Adaptive changes in harvested populations



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- The state of each individual at any time is given by a triple

 $(\phi, \mathbf{a}, \theta) \in \mathbf{E} := \mathcal{H} \times \mathbb{R}_+ \times \mathbb{R}.$

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- For an individual with state $x \in E$ in a population given by X:
 - Birth rate is

$$b(x, V * X(x)) = b\left(x, \int_E V(x, y)X(dy)\right)$$

Death rate is

$$d(x, U * X(x)) = d\left(x, \int_E U(x, y)X(dy)\right).$$

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• The functions b, U and V are bounded while

$$\sup_{x\in E} d(x,u) \leq \bar{d}(1+u).$$

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- Noise parameter : ν is chosen according to distribution $\Theta \in \mathcal{P}(\mathbb{R})$.
- No Mutation : h = 0 with probability $(1 u_k p(x))$.
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For any $x \in E$ define, $\Lambda^{K}(x) \in \mathcal{P}(\mathcal{H} \times \mathbb{R})$ as

 $\Lambda^{K}(x,dh,d\nu) = (u_{K}p(x)\Xi(x,dh) + (1-u_{K}p(x))\delta_{0})\Theta(d\nu).$

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The process X^{K} characterized by its generator L^{K} . For $F_{f}(X) = F(\langle f, X \rangle)$ we define

$$L^{K}F_{f}(X) = F'\left(\langle f, X \rangle\right) \left\langle \frac{\partial f}{\partial a}, X \right\rangle + K \int_{E} d(x, U * X(x)) \left(F_{f}\left(X - \frac{1}{K}\delta_{x}\right) - F_{f}(X) \right) X(dx)$$

$$+ K \int_{E} b(x, V * X(x)) \left[\int_{\mathcal{H} \times \mathbb{R}} \left(F_{f}\left(X + \frac{1}{K}\delta_{\bar{x}(h,\nu)}\right) - F_{f}(X) \right) \Lambda^{K}(x, dh, d\nu) \right] X(dx).$$

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Theorem (Deterministic Approximation)

Suppose that $u_K \to 0$ as $K \to \infty$. Also assume that $X^K(0) \Rightarrow \xi(0)$. Then the sequence $\{X^K : K \ge 1\}$ converges weakly in $\mathbb{D}([0,\infty), \mathcal{M}_F(E))$ to the deterministic continuous $\mathcal{M}_F(E)$ -valued process ξ which is characterized by the following equation. For all nice functions $f : E \to \mathbb{R}$

$$\langle f,\xi(t)\rangle = \langle f,\xi(0)\rangle + \int_0^t \left\langle \frac{\partial f}{\partial a},\xi(s) \right\rangle ds - \int_0^t \int_E d\left(x,\left(U * \xi(s)\right)(x)\right) f(x)\xi(s,dx)ds \\ + \int_0^t \int_E b\left(x,\left(V * \xi(s)\right)(x)\right) \left(\int_{\mathbb{R}} f(\bar{x}(0,\nu))\Theta(d\nu)\right) \xi(s,dx)ds$$

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- The mutation term does not appear in the limit.
- To prove the result we only have to worry about compact containment.
- One can show that the total weight of *mutants* produced in any time interval [0, *T*] is *O*(*u_k*).

Evolutionary time scale

• Mutations happen at rate Ku_k.

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- Mutations happen at rate Kuk.
- We assume that $Ku_K \to 0$ and compress time by the factor of $1/Ku_k$.

$$Z^{K}(t) = X^{K}\left(\frac{t}{Ku_{K}}\right).$$

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• The generator of Z^K is

$$\begin{split} \mathbb{L}^{K} F_{f}(Z) &= \left(\frac{1}{Ku_{K}}\right) L^{K} F_{f}(Z) \\ &= \int_{E} p(x) b(x, V * Z(x)) \left[\int_{\mathbb{R}} \int_{\mathcal{H}} \left(F_{f}\left(Z + \frac{1}{K} \delta_{\bar{x}(h,\nu)}\right) - F_{f}(Z) \right) \Xi(x, dh) \Theta(d\nu) \right] Z(dx) \\ &+ \frac{1}{Ku_{K}} \left[F'\left(\langle f, Z \rangle\right) \left\langle \frac{\partial f}{\partial a}, Z \right\rangle \\ &+ K \int_{E} (1 - u_{K} p(x)) b(x, V * Z(x)) \left(\int_{\mathbb{R}} \left(F_{f}\left(Z + \frac{1}{K} \delta_{\bar{x}(0,\nu)}\right) - F_{f}(Z) \right) \Theta(d\nu) \right) Z(dx) \\ &+ K \int_{E} d(x, U * Z(x)) \left(F_{f}\left(Z - \frac{1}{K} \delta_{x}\right) - F_{f}(Z) \right) Z(dx) \right] \\ &= \text{Mutation} + \left(\frac{1}{Ku_{K}}\right) \text{Population Dynamics.} \end{split}$$

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• Let $\Gamma^{\mathcal{K}}$ be the occupation measure process of $Z^{\mathcal{K}}$. For any $t \ge 0$ and $A \in \mathcal{B}(\mathcal{M}_{\mathcal{F}}(\mathcal{E}))$

$$\Gamma^{\kappa}\left([0,t]\times A\right)=\int_{0}^{t}\mathbb{1}_{A}(Z^{\kappa}(s))ds.$$

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• The sequence of random measures $\{\Gamma^K\}$ is relatively compact.

• For any continuous bounded function $G : \mathcal{M}_P(\mathcal{H}) \to \mathbb{R}$,

$$\begin{aligned} M_{G}^{\chi,\kappa}(t) &= G(\chi^{\kappa}(t)) - G(\chi^{\kappa}(0)) - \int_{0}^{t} \int_{E} b\left(x, (V * Z^{\kappa}(s))(x)\right) p(x) \\ &\int_{\mathcal{H}} \left(G(\chi^{\kappa}(s) + \delta_{\phi+h}) - G(\chi^{\kappa}(s))\right) \Xi(x, dh) Z^{\kappa}(s, dx) ds \end{aligned}$$

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- Then the following is a martingale

$$egin{aligned} &\mathcal{M}^{\chi}_{G}(t) = G(\chi(t)) - G(\chi(0)) - \int_{0}^{t} \int_{\mathcal{M}_{F}(E)} \left[\int_{E} b\left(x, V * \mu(x)
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 \bullet Define the *population dynamics* operator ${\mathbb B}$ by

$$\begin{split} \mathbb{B}F_{f}(\mu) &= F'\left(\langle f, \mu \rangle\right) \left[\left\langle \frac{\partial f}{\partial a}, \mu \right\rangle \right. \\ &+ \int_{E} \left(b(x, V * \mu(x)) \int_{\mathbb{R}} f(\bar{x}(0, \nu)) \Theta(d\nu) - d(x, U * \mu(x)) f(x) \right) \mu(dx) \right]. \end{split}$$

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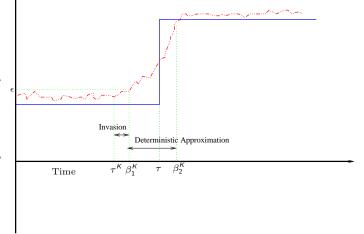
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 - The jump location is determined by the deterministic approximation.





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• For any finite set $A \subset \mathcal{H}$ define

 $\mathcal{M}_F^A(E) = \{ \mu \in \mathcal{M}_F(E) : \mu(\{h\} \times \mathbb{R}_+ \times \mathbb{R}) > 0 \text{ for all } h \in A \}$

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For φ ∈ H ∩ A^c, let π̂_A(φ) ∈ P (M_F(E)) be a small perturbation of π_A such that under π̂_A(φ) all the trait values in A ∪ {φ} coexist.

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- Let {ξ(t) : t ≥ 0} be the Markov process determined by the generator B with initial distribution π̂_A(φ).
- We assume that there exists a set $A' \subset A \cup \{\phi\}$ and a distribution $\pi_{A'} \in \mathcal{P}(\mathcal{M}_F(E))$ such that for any $C \in \mathcal{B}(\mathcal{M}_F(E))$ we have

$$\lim_{t\to\infty}\frac{1}{t}\int_0^t\mathbbm{1}_C(\xi(s))ds=\pi_{A'}(C).$$

• This assumption tells us the next stationary distribution if a mutant ϕ is able to invade the environment set by the trait values in the set A.

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$$\hat{b}(x:\Pi) = \int_{\mathcal{M}_F(E)} b(x, V * \mu(x)) \Pi(d\mu)$$

and

$$\hat{d}(x:\Pi) = \int_{\mathcal{M}_F(E)} d(x, U * \mu(x)) \Pi(d\mu).$$

• Expected number of children that a mutant with trait value ϕ will produce in its lifetime in the environment Π is

$$R_0(\phi:\Pi) = \int_{\mathbb{R}} \int_{\mathbb{R}_+} \hat{b}((\phi, a, \theta):\Pi) e^{-\int_0^a \hat{d}((\phi, \alpha, \theta):\Pi) d\alpha} da d\theta.$$

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• The invasion probability of a mutant with trait value ϕ in the environment Π can be defined as $p(\phi: \Pi) = 1 - z$ where z is the smallest solution of the equation

$$\int_{\mathbb{R}}\int_{\mathbb{R}_{+}}\hat{b}((\phi,a,\theta):\mathsf{\Pi})e^{\left((z-1)\int_{0}^{s}\hat{b}((\phi,\alpha,\theta):\mathsf{\Pi})d\alpha-\int_{0}^{s}\hat{d}((\phi,\alpha,\theta):\mathsf{\Pi})d\alpha\right)}dad\theta=1.$$

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- Let {\(\chi_t: t ≥ 0\)} be a \(\mathcal{M}_P(\mathcal{H})\)-valued process that gives the values of the surviving trait values at any time t.
- We can now characterize $\{(\chi'_t, \gamma_t) : t \ge 0\}$ as a $\mathcal{M}_P(\mathcal{H}) \times \mathcal{P}(\mathcal{M}_F(E))$ -valued Markov process.

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- This would be the TSS in our setting.
- If for all $s \ge 0$, $\gamma_s = \delta_{\hat{m}_s}$, then we recover the TSS obtained in earlier literature. In this case convergence is in the sense of finite dimensional distributions.