Deterministic and stochastic approaches for evolutionary branching in adaptive dynamics

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57th Annual AustMS Meeting, Sydney, 2nd October 2013



eterministic approach to adaptive dynamic

Stochastic approach to adaptive dynamics

Conclusion

Evolutionary branching





Adaptive dynamics Chemostat

2 Deterministic approach to adaptive dynamics

The PDE model Hamilton Jacobi equation with constraint Closed Hamilton Jacobi equation Consequences in adaptive dynamics

3 Stochastic approach to adaptive dynamics Individual-based model Limit of large population Limit of rare mutations The limit of small mutations





Darwinian evolution

Three main ingredients:

- Heredity: transmissions of individual characteristics from a generation to the next one.
- Mutation: cause of the variability in individual characteristics.
- Selection: consequence of the interactions between individuals and their environment, including the rest of the population (ecology).

First approach: population genetics (since the 30s)

- Wright-Fisher, Moran, Flemming-Viot, Kingman coalescent...models
- Put emphasis on the genetic mechanism at the molecular level
- Selection: a fixed fitness value is associated to each allele → supposes a fixed environment of the population



Conclusion

Adaptive dynamics

Adaptive dynamics (since the 90s): Hofbauer and Sigmund (1990), Metz, Geritz et al. (1992,1996), Dieckmann and Law (1996)...

- Focus on the interplay between ecology and evolution
- Ecological interactions modeled in detail
- Heredity is simplified as much as possible: asexual (clonal) reproduction

 \rightsquigarrow Density-dependent individual-based models where no fitness is given. The fitness landscape has to be constructed from the parameters of the model.

 \rightsquigarrow New phenomenon of evolutionary branching (Metz et al., 1996)

- Transition from a population concentrated around a single phenotype to a population concentrated around several distinct phenotypes, still under ecological interaction
- Mechanism of diversification
- Can lead to speciation without geographical separation (Dieckmann and Doebeli, 1999)



Biological	context
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Conclusion

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Chemostat

Chemostat (J. Monod, 1950)

A chemostat is a bioreactor in which liquid is continuously injected while volume is kept constant by an equal outflow:

- allows to control the growth rate of microorganisms in a controlled environment (temperature, pH, nutrient concentration...)
- used to grow cells or to perform a biochemical process (e.g. wastewater treatment)

The chemostat is an efficient device to make bacteria adapt to given environmental conditions, e.g. to improve nutrients consumption.





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Conclusion

Chemostat

Simple chemostat models

Our Goal: Study adaptation in a multi-resources chemostat model.

• Basic chemostat model (system of ODEs)

$$\frac{du}{dt} = u(-1 - d + \eta R)$$
$$\frac{dR}{dt} = 1 - R - R\eta u.$$

- *u* is the bacteria density
- *R* is the resource concentration
- *d* is the death rate of bacteria
- η is the efficiency of resource consumption by bacteria.
- A lot of more complicated ODE models exist (mulit-specific, multi-resources... cf. Smith and Waltman, 1995)

... so far, no adaptation.



Adaptive dynamics Chemostat

2 Deterministic approach to adaptive dynamics

The PDE model Hamilton Jacobi equation with constraint Closed Hamilton Jacobi equation Consequences in adaptive dynamics

3 Stochastic approach to adaptive dynamics Individual-based model Limit of large population Limit of rare mutations The limit of small mutations





Conclusion

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The PDE model

A PDE model of adaptation in a chemostat

We consider a population of bacteria in a chemostat

- with r resources with concentrations $R_k(t)$.
- where each bacteria is characterized by a (phenotypic) trait $x \in \mathbb{R}$ (e.g. rate of nutrient intake, body size at maturity, age at maturity...)

 \rightsquigarrow population density u(t, x).

$$\partial_t u(t,x) = \left(\sum_{k=1}^r R_k(t) \eta_k(x) - d(x)\right) u(t,x) + \int_{\mathbb{R}} K(z)(u(t,x+z) - u(t,x)) dz,$$

where

- $\eta_k(x)$ is the consumption function of resource k,
- d(x) 1 is the death rate of a bacteria with trait x,
- K(z) is the L^1 mutation kernel, satisfying $\int_{\mathbb{R}} z K(z) dz = 0$.

Stochastic approach to adaptive dynamics

Conclusion

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The PDE model

Resources dynamics

Classical chemostat models assume

$$\frac{dR_k(t)}{dt} = g_k - R_k(t) - R_k(t) \int_{\mathbb{R}} \eta_k(x) u(t, x) dx, \quad 1 \le k \le r,$$

where

- g_k is the rate of inflow of resource k in the chemostat,
- the consumption function $\eta_k(x)$ is the same as in the equation for densities (can be relaxed).

In this talk, to keep things simple, we shall assume that resources are at quasi-equilibrium for all time:

$$R_k(t) = \frac{g_i}{1 + \int_{\mathbb{R}} \eta_k(x) u(x) \, dx}, \quad 1 \le k \le r.$$

Non-local reaction-diffusion equation.

Biological context	Deterministic approach to adaptive dynamics	Stochastic approach to adaptive dynamics	
The PDE model			

An example

Two resources, trait having opposite effects on the resources consumption.

• $K(z)dz = \mathcal{N}(0, \sigma^2),$ • $d(x) = 1 + 4(x - 1/2)^2$, (minimum at 1/2), $x \in [0, 1]$, • r = 2 (2 resources), $g_1 = g_2 = 1$, • $\eta_1(x) = 2(x-1)^2$, $\eta_2(x) = 2x^2$, $x \in [0,1]$.

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Biological	

Deterministic approach to adaptive dynamics

Stochastic approach to adaptive dynamics

Conclusion

The PDE model

Simulation



Competition for two resources (Diekmann, Jabin, Mischler, Perthame, 2005)



Conclusion

Hamilton Jacobi equation with constraint

Strong selection and small mutations

Non-local interactions favor the concentration of population densities close to the "best" traits. The idea is to strengthen this concentration in order to simplify the dynamics.

Sélection forte et petites mutations :

$$\partial_t u_{\varepsilon}(t,x) = \frac{1}{\varepsilon} u_{\varepsilon}(t,x) \left(\sum_{k=1}^r R_k^{\varepsilon}(t) \eta_k(x) - d(x) \right) \\ + \frac{1}{\varepsilon} \int_{\mathbb{R}} K(z) (u_{\varepsilon}(t,x+\varepsilon z) - u_{\varepsilon}(t,x)) dz.$$





For reaction-diffusion: Fleming, Souganidis, 1986, Barles, Evans, Souganidis, 1990, Freidlin, 1990. For adaptive dynamics: Diekmann et al., 2005.

$$u_{\varepsilon}(t,x) = \exp\left(\frac{\varphi_{\varepsilon}(t,x)}{\varepsilon}\right).$$

Then $\partial_t u_{\varepsilon} = \frac{u_{\varepsilon}}{\varepsilon} \partial_t \varphi_{\varepsilon}$ and so

$$\partial_t \varphi_{\varepsilon}(t, x) = \sum_{k=1}^r R_k^{\varepsilon}(t) \eta_k(x) - d(x) + \int_{\mathbb{R}^k} K(z) \left(e^{(\varphi(t, x + \varepsilon z) - \varphi(t, x))/\varepsilon} - 1 \right) dz$$

Deterministic approach to adaptive dynamics

Stochastic approach to adaptive dynamics

Conclusion

Hamilton Jacobi equation with constraint

Hamilton-Jacobi equation with constraint

Therefore, one expects $\varphi_{\varepsilon} \to \varphi$, where

$$\partial_t \varphi = \sum_{k=1}^r R_k(t) \eta_k(x) - d(x) + H(\partial_x \varphi),$$

where $R_k^{\varepsilon}(t) \to R_k(t)$ and

$$H(p) = \int_{\mathbb{R}} K(z) \left(e^{p \, z} - 1 \right) \, dz.$$

By Jensen's inequality, $H(p) \ge 0$ and H(p) = 0 iff p = 0.

All the mass of u_ε(t, ·) is concentrated close to {x : φ(t, x) = 0}.
If 0 < <u>d</u> ≤ d(·) and 0 < <u>η</u> ≤ η_k(·) ≤ <u>η</u>,

$$\frac{d}{dt} \int_{\mathbb{R}} u_{\varepsilon}(t,x) \, dx \leq \left(\int_{\mathbb{R}} u_{\varepsilon}(t,x) \, dx \right) \frac{1}{\varepsilon} \sum_{k=1}^{r} \left(\frac{\overline{\eta}}{1 + \underline{\eta} \int_{\mathbb{R}} u_{\varepsilon}(t,x) \, dx} - \underline{d} \right)_{\overrightarrow{\varphi}}$$

$$\xrightarrow{\rightarrow} \text{ non-explosion of the total population density:}$$

$$\lim \sup_{\varepsilon \to 0} \max_{x} \varphi_{\varepsilon}(t,x) = 0.$$

Deterministic approach to adaptive dynamics

Stochastic approach to adaptive dynamics

Conclusion

nac

Hamilton Jacobi equation with constraint

Hamilton-Jacobi equation with constraints

One expects $\varphi_{\varepsilon} \to \varphi$, where

$$\partial_t \varphi = \sum_{k=1}^r R_k(t) \eta_k(x) - d(x) + H(\partial_x \varphi),$$

and $\sup_{x \in \mathbb{R}} \varphi(t, x) = 0$ for all $t \leq 0$.

How to characterize $R_k(t)$?

In order to satisfy the constraint, one should also have

• $\sum_{k=1}^{r} R_k(t) \eta_k(x) - d(x) \le 0$ for all x such that $\varphi(t, x) = 0$, • $\sum_{k=1}^{r} R_k(t) \eta_k(x) - d(x) = 0$ for at least one x such that $\varphi(t, x) = 0$.

First approach:

- R_k are Lagrange multipliers associated with these contraints. Works only in particular cases (Diekmann et al., 2005, Barles, Perthame, 2007, 2008, Mirrahimi, Perthame, Wakano, 2012...).
- Difficulty: the number of unknown r can be different from the number of constraints (number of zeroes of φ).

	Deterministic approach to adaptive dynamics	
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Closed Hamilton Jacobi	equation	

Assumptions

- Smoothness of the parameters.
- For all distinct x_1, \ldots, x_{r+1} , the vectors

$$\begin{pmatrix} \eta_1(x_1) \\ \vdots \\ \eta_1(x_{r+1}) \end{pmatrix} \cdots \begin{pmatrix} \eta_r(x_1) \\ \vdots \\ \eta_r(x_{r+1}) \end{pmatrix}, \begin{pmatrix} d(x_1) \\ \vdots \\ d(x_{r+1}) \end{pmatrix}$$

are linearly independent

• For all distinct x_1, \ldots, x_r , the vectors

$$\begin{pmatrix} \eta_1(x_1) \\ \vdots \\ \eta_r(x_1) \end{pmatrix} \dots \begin{pmatrix} \eta_1(x_r) \\ \vdots \\ \eta_r(x_r) \end{pmatrix}$$

are linearly independent.

Under these conditions, one can associate a unique environment (resources) to the set of zeroes of φ , and a unique population measure associated to this environment.

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Stochastic approach to adaptive dynamics

Conclusion

Closed Hamilton Jacobi equation

Proposition (C., Jabin, 2011)

For all closed $A \subset \mathbb{R}$, there exists a unique finite positive measure $\mu(A)$ satisfying

$$\operatorname{supp} \mu \subset A$$

if we define $\bar{R}_k(\mu) = \frac{g_k}{1 + \int \eta_k(x) \, d\mu(x)},$
$$\sum_{k=1}^r \bar{R}_k(\mu) \, \eta_k(x) - d(x) \le 0 \text{ in } A,$$

$$\sum_{k=1}^r \bar{R}_k(\mu) \, \eta_k(x) - d(x) = 0 \text{ in supp } \mu.$$

The limiting $R_k(t)$ are then obtained as

$$R_k(t) = \bar{R}_k(\mu(\{\varphi(t,.)=0\})).$$

Conclusion

Closed Hamilton Jacobi equation

A remark on the number of coexisting traits

- In view of the previous result, given distinct x_1, \ldots, x_n , one says that these traits coexist if supp $\mu(\{x_1, \ldots, x_n\}) = \{x_1, \ldots, x_n\}$.
- In order to have coexistence of x_1, \ldots, x_n , one must have

$$\sum_{k=1}^{r} \bar{R}_k(\mu) \eta_k(x_i) - d(x_i) \le 0, \quad 1 \le i \le n.$$

Because of our assumptions, this is impossible if n > r.

• This has the following biological interpretation: one cannot have coexistence of more species than resources. This is related to the concept of ecological niche.



Proof of existence

We consider the differential equation in measure space

$$\partial_t \nu = \left(\sum_{i=1}^k \bar{I}_i(\nu) \eta_i(x) - 1\right) \nu.$$

A stable steady state of this equation should satisfy the conditions of the Proposition.

Since this system has the convex, strict Lyapunov functional

$$L(\nu) = \int_{\mathbb{R}} d(x)\nu(dx) - \sum_{k=1}^{r} g_k \log(1 + \int \eta_k(x)\nu(dx)),$$

one can define the measure μ as the global minimizer of this functional. Indeed,

$$\frac{d}{dt}L(\nu_t) + -\int \left(\sum_{k=1}^r \frac{g_k\eta_k(x)}{1+\int \eta_k(y)\nu_t(dy)} - d(x)\right)^2 \nu_t(dx).$$

Deterministic approach to adaptive dynamics

Stochastic approach to adaptive dynamics

Conclusion

Closed Hamilton Jacobi equation

Theorem (C., Jabin, 2011)

Under the previous assumptions, if $u_{\varepsilon}(t=0) > 0$ is smooth enough and $\varphi_{\varepsilon}(t=0)$ converges to φ^0 in $W^{1,\infty}(\mathbb{R})$,

then, up to a subsequence extraction, φ_{ε} uniformly converges on all compact set and in $W^{1,p}_{\text{loc}}(\mathbb{R}_+ \times \mathbb{R})$ to φ , almost everywhere solution to

$$\partial_t \varphi = \sum_{k=1}^{\prime} R_k(t) \eta_k(x) - 1 + H(\partial_x \varphi),$$

where $R_k(t) = \bar{R}_k(\mu(\{\varphi(t,.) = 0\})).$

In addition, the functions R_k^{ε} converge to R_k in L^p for all $p < \infty$.

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Conclusion

Closed Hamilton Jacobi equation

Some elements of the proof of the theorem

• One cannot have existence of a solution to HJ in the strong sense. The $R_k(t)$ need not be continuous.



- We use classical a priori estimates for HJ equations, and prove that they hold for φ_{ε} uniformly in ε . In particular, we prove that $\partial_x \varphi^{\varepsilon}$ is bounded in $L^{\infty}([0, T], BV_{\text{loc}}(\mathbb{R}))$ and $\partial_{xx} \varphi_{\varepsilon} \geq -C$.
- This implies easily the strong convergence of a subsequence of φ_{ε} .
- The difficult part is the convergence of $R_k^{\varepsilon}(t)$ to the correct limit. This is done by proving uniform Lebesgue-right-continuity estimates.

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Deterministic approach to adaptive dynamics

Stochastic approach to adaptive dynamics

Conclusion

Closed Hamilton Jacobi equation

Simulation of the PDE for population densities



(Implicit finite differences)



Deterministic approach to adaptive dynamics

Stochastic approach to adaptive dynamics

Conclusion

Closed Hamilton Jacobi equation

Simulation of the HJ equation with constraints





Conclusion

Consequences in adaptive dynamics

The fitness function

The fitness function can be defined as the growth rate of a trait x in the absence of mutation and in a given environment. For example, in the environment in the HJ equation at time t (the $R_k(t)$),

$$f(x,t) = \sum_{k=1}^{r} R_k(t)\eta_k(x) - d(x).$$

More generally, given a closed subset A of \mathbb{R} , we define the fitness of a trait x in the population characterized by A as

$$f(x,A) = \sum_{k=1}^{r} \bar{R}_{k}(\mu(A))\eta_{k}(x) - d(x).$$

The sign of this fitness function characterizes the direction of evolution of the population.



Deterministic approach to adaptive dynamics

Stochastic approach to adaptive dynamics

Conclusion

Consequences in adaptive dynamics

Coevolution with the fitness landscape





Deterministic approach to adaptive dynamics

Stochastic approach to adaptive dynamics

Conclusion

Consequences in adaptive dynamics

Coevolution with the fitness landscape





Deterministic approach to adaptive dynamics

Stochastic approach to adaptive dynamics

Conclusion

Consequences in adaptive dynamics

Coevolution with the fitness landscape





Deterministic approach to adaptive dynamics

Stochastic approach to adaptive dynamics

Conclusion

Consequences in adaptive dynamics

Coevolution with the fitness landscape



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Deterministic approach to adaptive dynamics

Stochastic approach to adaptive dynamics

Conclusion

Consequences in adaptive dynamics

Coevolution with the fitness landscape



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Deterministic approach to adaptive dynamics

Stochastic approach to adaptive dynamics

Conclusion

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Consequences in adaptive dynamics

The canonical equation of adaptive dynamics: first form

- As long as there is only a single point in $\{\varphi(t, \cdot) = 0\}$, $\mu(\{\varphi(t, \cdot) = 0\}) = \bar{u}(t)\delta_{\bar{x}(t)}.$
- Since $\partial_x \varphi(t, \bar{x}(t)) = 0$, we have

$$\partial_{tx}\varphi(t,\bar{x}(t)) + \partial_{xx}\varphi(t,\bar{x}(t))\frac{d\bar{x}(t)}{dt} = 0.$$

• Since
$$\partial_t \varphi(t, x) = f(x, \{\bar{x}(t)\}) + H(\partial_x \varphi(t, x)),$$

 $\partial_{tx}\varphi(t,\bar{x}(t)) = \partial_x f(x,\{\bar{x}(t)\}) + H'(\partial_x \varphi(t,\bar{x}(t))) \partial_{xx}\varphi(t,\bar{x}(t)) = \partial_x f(x,t) + H'(\partial_x \varphi(t,\bar{x}(t))) \partial_{xx}\varphi(t,\bar{x}(t)) = \partial_x f(x,t) + H'(\partial_x \varphi(t,\bar{x}(t))) \partial_x \varphi(t,\bar{x}(t)) = \partial_x f(x,t) + H'(\partial_x \varphi(t,\bar{x}(t))) = \partial_x f(x,t) + H'(\partial_x \varphi(t,\bar{x}(t$

Therefore

$$\frac{d\bar{x}(t)}{dt} = -(\partial_{xx}\varphi(t,\bar{x}(t)))^{-1}\partial_x f(x,\{\bar{x}(t)\}).$$

This equation is called "canonical equation of adaptive dynamics".

Conclusion

Consequences in adaptive dynamics

Adaptive dynamics via the PDE approach

- Until the first time where φ has two distinct zeroes (jump or evolutionary branching), the support of the population evolves according to the canonical equation, and tries to locally increase the fitness.
- Evolutionary branching can only occur at points x^* where $\partial_x f(x, \{x^*\}) = 0$ (evolutionary singularity).
- Evolutionary branching occurs at evolutionary singularities where the fitness function is convex.



Conclusion

Consequences in adaptive dynamics

Mathematical questions

- Open problem: well-posedness of the Hamilton-Jacobi equation with contraint. Only known in special cases (a single resource or no mutation)
 - Jumps in the R_k and in $\partial_x \varphi$ are possible.
 - Vicosity solutions or variational characterizations do not extend easily to this problem.
 - This is also important in simulations.
- Smoothness of the solution is only known in special cases
 → justification of the canonical equation and of the branching criterion only in special cases.
- Open problems: time of branching, speed of branching, after evolutionary branching...



Adaptive dynamics Chemostat

2 Deterministic approach to adaptive dynamics

The PDE model Hamilton Jacobi equation with constraint Closed Hamilton Jacobi equation Consequences in adaptive dynamics

3 Stochastic approach to adaptive dynamics Individual-based model Limit of large population Limit of rare mutations The limit of small mutations





Conclusion

Individual-based model

Individual-based model

2 scaling parameters:

- K scales the size of the population (large K means large population)
- μ_K scales the probability of mutation (small μ_K means rare mutations)

Birth-death-mutation discrete process coupled with r continuous resources with concentrations $R_1^K(t), \ldots, R_r^K(t)$:

- each individual is characterized by a phenotypic trait x in \mathbb{R}
- a population of $N^{K}(t)$ individuals holding traits

 $x_1, \ldots, x_{N(t)} \in \mathcal{X}$ is represented by $\nu_t^K = \frac{1}{K} \sum_{i=1}^{N^K(t)} \delta_{x_i}$

Biological context	Deterministic approach to adaptive dynamics	5

Conclusion

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Individual-based model

Transitions

• Each individual with trait x gives birth at (inhomogeneous) rate $\sum_{k=1}^{r} \eta_k(x) R_k^K(t) \text{ to a single individual.}$

 $\eta_k(x)$ represents the consumption efficiency of resource k by bacteria with trait x. At each birth time:

- with probability $1 \mu_K$, clonal reproduction (trait x)
- with probability μ_K , mutation; the mutant trait is x + h where h has given law m(x, h) dh.
- Each individual with trait x dies or is removed from the chemostat at rate d(x).
- Resources concentrations as before in a quasi-equilibrium

$$R_{k}^{K}(t) = \frac{g_{k}}{1 + \left(\frac{1}{K}\sum_{i=1}^{N(t)}\eta_{k}(x_{i})\right)} = \frac{g_{k}}{1 + \langle\nu^{K}, \eta_{k}\rangle}.$$

 $g_k > 0$ is incoming concentration of resource k.

Deterministic approach to adaptive dynamic

Stochastic approach to adaptive dynamics

Conclusion

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Individual-based model

Simulations



Deterministic approach to adaptive dynamic:

Stochastic approach to adaptive dynamics

Conclusion

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Limit of large population

$K \to +\infty$ (without time scaling)

Theorem

If $\mu_K \to 0$ when $K \to +\infty$ and ν_0^K converges in distribution to a deterministic measure $\nu_0 = \sum_{i=1}^n u_i(0)\delta_{x_i}$, then $(\nu_t^K, t \ge 0)$ converges in distribution to the function $(\sum_{i=1}^n u_i(t)\delta_{x_i}, t \ge 0)$, where

$$\dot{u}_i = u_i \Big(-d(x_i) + \sum_{k=1}^r \eta_k(x_i) R_k \Big), \quad \forall 1 \le i \le n$$
$$R_k = \frac{g_k}{1 + \sum_{i=1}^n \eta_k(x_i) u_i}, \quad \forall 1 \le k \le r.$$

This system will be called below chemostat system.

Deterministic approach to adaptive dynamic

Stochastic approach to adaptive dynamics

Conclusion

Limit of large population

Long-time behavior of chemostat systems

Proposition (C., Jabin, Raoul, 2010)

Under the previus assumptions, for all $n \ge 1$ and all distinct $x_1, \dots, x_n \in \mathcal{X}$, there exists a unique \bar{u} in $(\mathbb{R}_+)^{n+r}$ such that any solution u(t) of the chemostat system with $u_i(0) > 0$ for any $1 \le i \le n$, converges to \bar{u} . With our previous notation, we have $\mu(\{x_1, \dots, x_n\}) = \sum_{i=1}^n \bar{u}_i \delta_{x_i}$.

We shall denote by $\overline{u}(\mathbf{x})$ this equilibrium, where $\mathbf{x} := (x_1, \ldots, x_n)$.

Deterministic approach to adaptive dynamic

Stochastic approach to adaptive dynamics

Conclusion

Limit of large population

Link with the fitness function

The case of two trait:

If n = 2, the equilibrium $(\overline{u}(x_1), 0)$ is stable iff $f(x_2, \{x_1\}) \leq 0$.

If both $(\bar{u}(x_1), 0)$ and $(0, \bar{u}(x_2))$ are unstable, i.e. if $f(x_1, \{x_2\}) > 0$ and $f(x_2, \{x_1\}) > 0$, then there exists a stable equilibrium where both traits coexist.

We will write for simplicity f(x; y) for $f(x, \{y\})$.



Limit of rare mutations

Limit of rare mutations: biological idea (Metz et al. 1996)

- The selection process has sufficient time between two mutations to eliminate disadvantaged traits (time scale separation)
- The assumption of large populations allows one to assume a deterministic population dynamics
 one can predict the outcome of competition between several traits.
- Succession of phases of mutant invasion, and phases of competition between traits



Deterministic approach to adaptive dynamic

Stochastic approach to adaptive dynamics

Conclusion

Limit of rare mutations

Simulations: rare mutations



Deterministic approach to adaptive dynamic

Stochastic approach to adaptive dynamics

Conclusion

Limit of rare mutations

Convergence to the PES (C., Jabin, Méléard, 2013)

Theorem

Assume (A). If $\nu_0^K = u_0^K \delta_x$ with $u_0^K \to \bar{u}(x)$ in probability when $K \to +\infty$. Assume also

$$\forall C > 0, \quad \log K \ll \frac{1}{K\mu_K} \ll \exp(CK),$$

then, the process $(\nu_{t/K\mu\kappa}^{K}, t \geq 0)$ converges for f.d.d. to a pure jump Markov process $(\Lambda_t, t \geq 0)$ with explicit jump rates and taking values in

$$\mathcal{M}_0 := \left\{ \sum_{i=1}^d \bar{u}_i(\mathbf{x}) \delta_{x_i}, \ d \ge 1, \ x_1, \dots, x_d \in \mathcal{X} \ coexist \right\}.$$

The process Λ_t is called Polymorphic Evolution Sequence (PES).

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Limit of rare mutations

General principle

The transition rates from a given population state of the PES are constructed in 3 steps:

- **1** wait for the first next mutation (mutation rate and mutant distribution) \rightsquigarrow mutation time scale $t/K\mu_K$
- look if the mutant individual invades the population (invasion probability)
- 3 once the mutant has invaded, the fate of the competition between the different traits in the population is given by the globally asymptotic stable equilibrium of the chemostat system.



Deterministic approach to adaptive dynamic

Stochastic approach to adaptive dynamics

Conclusion

Limit of rare mutations

After the first mutation: competition phase

- between 0 and \mathbf{t}_1 : the number of mutant individuals is close to a branching process with birth rate $\sum_k \eta_k(y) \bar{R}(x)$ and death rate d(y)
 - \rightarrow survival probability $[f(y;x)]_+/(\sum_k \eta_k(y)\bar{R}(x))$
- between t_1 and t_2 : close to the chemostat system
- after t₂: the number of resident individuals is close to a sub-critical branching process
- If $\log K \ll \frac{1}{Ku_K}$ the next mutation occurs after this phase with high probability.



Deterministic approach to adaptive dynamics

Conclusion

The limit of small mutations

The Canonical Equation of Adaptive Dynamics

- Small mutations: size of mutations scaled by ε , i.e. m(x, h)dh replaced by $\frac{1}{\varepsilon}m(x, \frac{h}{\varepsilon})dh$.
- Renormalized PES: Λ^{ε} .
- Rescaled time: t/ε^2 .

Theorem

The processes $(\Lambda_{t/\varepsilon^2}^{\varepsilon}, t \ge 0)$ converge in law as $\varepsilon \to 0$ to $(\bar{u}(x(t))\delta_{x(t)}, t \ge 0)$, where x is solution of the ODE

$$\frac{dx}{dt} = \int h^2 \bar{u}(x) \partial_1 f(x; x) m(x, h) dh$$

This is the canonical equation of adaptive dynamics (Dieckmann and Law, 1996).

 \rightsquigarrow Evolutionary branching can only occur in the neighborhood of a point where $\partial_1 f(x, x) = 0$.



Deterministic approach to adaptive dynamics

Conclusion

The limit of small mutations

A definition of evolutionary branching

Definition

For any $\eta > 0$, we say that there is η -branching at the evolutionary singularity x^* if

- There exist t > 0 such that the support of Λ^ε_t is composed of a single trait in (x^{*} − η, x^{*} + η).
- There exist s > t such that the support of Λ^ε_s is composed of two traits distant of more than η.
- Between s and t, the support of Λ^ε is always a subset of [x^{*} − η, x^{*} + η] composed of at most 2 traits.



Conclusion

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The limit of small mutations

Branching criterion

- Assume that $\partial_1 f(0;0) = 0$.
- Let $a = \partial_{11}f(0;0)$ and $c = \partial_{22}f(0;0)$. Assume that $a \neq 0$ and $a + c \neq 0$.
- The equilibrium $x^* = 0$ is stable for the canonical equation if

c > a.

Theorem

When c > a, for all sufficiently small $\eta > 0$, there exists $\varepsilon_0 > 0$ s.t. for all $\varepsilon < \varepsilon_0$,

- If a > 0, then $\mathbb{P}^{\varepsilon}(\eta$ -branching) = 1.
- If a < 0, then $\mathbb{P}^{\varepsilon}(\eta$ -branching) = 0.

Conclusion

Comparison of the two approaches (1)

- We used 3 limits in our two approaches:
 - 1 large population
 - 2 rare mutations
 - 3 small mutations
- The PDE approach corresponds to (1) then (3).
- The stochastic approach corresponds to (1)+(2) then (3).



Conclusion

Comparison of the two approaches (2)

- The two approaches give qualitatively similar results (convergence to equilibria according to a canonical equation, same branching criterion)...
- ... but quantitatively different results (the two canonical equations are different, the time scales of evolutionary branching are different).
- Both approaches are criticized by biologists: in the PDE approach, very small densities have a strong influence; in the stochastic approach, assumptions are biologically too strong (rare mutations).
- The results seem robust \rightsquigarrow intermediate approaches (e.g. small mutations only, but with simultaneously large populations)

Conclusion

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Open problems (1)

Deterministic approach

- Well-posedness theory for Hamilton-Jacobi equations with constraints, to fully characterize the limit and be sure of the biological consequences.
- Change the model so that very small densities correspond to extinction (cutoff or additional non-linear terms in the PDE, cf. Jabin, 2012, Barles, Mirrahimi, Perthame, 2013)

Stochastic approach

- Other scalings (small mutations only, or the three limits together).
- Extension of the results to higher-dimensional traits (the fitness function is not smooth in this case).
- Precise study of the time of evolutionary branching, and of what happens after the first evolutionary branching.

Conclusion

Open problems (2)

All approaches

- Evolutionary branching criteria in models with sexual reproduction.
 ~> crucial from the biological point of view.
- Some works have already be done in the subject, but they are very preliminary (Collet, Méléard, Metz, 2013).

