

Evolution in prey-predator systems

Manon Costa

CMAP, École Polytechnique
in collaboration with N. Loeuille, C. Hauzy and S. Méléard

02/04/2013, Aussois



Outline

Questions :

- ▶ **What are the consequences of the presence of predators for the phenotypic evolution of a prey population ?**
- ▶ **Is the evolution of preys going to drive predators to extinction ?**

Outline

Questions :

- ▶ **What are the consequences of the presence of predators for the phenotypic evolution of a prey population ?**
- ▶ **Is the evolution of preys going to drive predators to extinction ?**

Outline :

- 1 Prey-predator birth-death model
- 2 Limit in large population
- 3 Rare mutations

Evolution of preys

Each prey is characterized by a phenotypic trait x in a compact $\mathcal{X} \in \mathbb{R}$.

This trait is a defensive trait : it influences the level of predation.

The population of N_t preys of trait x_1, \dots, x_{N_t} is represented by

$$\nu_t^K = \frac{1}{K} \sum_{i=1}^{N_t} \delta_{x_i}.$$

Evolution of preys

Each prey is characterized by a phenotypic trait x in a compact $\mathcal{X} \in \mathbb{R}$.

This trait is a defensive trait : it influences the level of predation.

The population of N_t preys of trait x_1, \dots, x_{N_t} is represented by

$$\nu_t^K = \frac{1}{K} \sum_{i=1}^{N_t} \delta_{x_i}.$$

- ▶ Each prey with trait x gives birth at rate $b(x)$.

At each birth time :

- with probability $\mu(x)$ there is a mutation and the descendant has a trait $x + l$ where l follows the law $m(x, l)dl$.
- with probability $1 - \mu(x)$ the descendant is a clone and has trait x .

Evolution of preys

Each prey is characterized by a phenotypic trait x in a compact $\mathcal{X} \in \mathbb{R}$.

This trait is a defensive trait : it influences the level of predation.

The population of N_t preys of trait x_1, \dots, x_{N_t} is represented by

$$\nu_t^K = \frac{1}{K} \sum_{i=1}^{N_t} \delta_{x_i}.$$

- ▶ Each prey with trait x gives birth at rate $b(x)$.

At each birth time :

- with probability $\mu(x)$ there is a mutation and the descendant has a trait $x + l$ where l follows the law $m(x, l)dl$.
 - with probability $1 - \mu(x)$ the descendant is a clone and has trait x .
- ▶ Each prey with trait x dies at rate :

$$d(x) + \sum_{i=1}^{N_t} \frac{\alpha(x, x_i)}{K} + H_t \frac{\beta(x)}{K}.$$

Evolution of predators

The Predators

Here we will consider that predators cannot evolve phenotypically (no mutations), so we only give the number of predators $H_t^K = H_t/K$ at time t .

- ▶ Each predator give birth at rate $e \sum_{i=1}^{N_t} \frac{\beta(x_i)}{K}$, where e is the consumption rate.
- ▶ Each predator dies from natural death at rate D .

Prey-predator process

The community $(\nu_t^K, H_t^K)_{t \geq 0}$ is a markov process evolving by births, deaths and prey mutations, and taking values in $(\mathcal{M}_F(\mathcal{X}) \times \mathbb{R}_+)$.

K is a parameter which scales the size of the population.

Notations :

- ▶ $\mathcal{M}_F(\mathcal{X})$ is the set of finite measures on \mathcal{X} .
- ▶ Let f be a measurable bounded function on \mathcal{X} , and $\nu \in \mathcal{M}_F(\mathcal{X})$:
$$\langle \nu, f \rangle = \int_{\mathcal{X}} f(x) \nu(dx).$$

Generator

The generator of (ν_t^K, H_t^K) is defined for all bounded measurable functions $\Phi : \mathcal{M}_F(\mathcal{X}) \times \mathbb{R}_+ \rightarrow \mathbb{R}$ by :

$$\begin{aligned}
 L^K \Phi(\nu^K, H^K) = & \\
 & \int_{\mathcal{X}} K \nu^K(dx) \left[\left(\Phi(\nu^K + \frac{\delta_x}{K}, H^K) - \Phi(\nu^K, H^K) \right) (1 - \mu_p(x)) b(x) \right. \\
 & + \mu_p(x) b(x) \int_{\mathbb{R}} \left(\Phi(\nu^K + \frac{\delta_{x+l}}{K}, H^K) - \Phi(\nu^K, H^K) \right) m_p(x, l) dl \\
 & \left. + \left(\Phi(\nu^K - \frac{\delta_x}{K}, H^K) - \Phi(\nu^K, H^K) \right) \left(d(x) + \int_{\mathcal{X}} \nu^K(dx') \alpha(x, x') + H_s^K \beta(x) \right) \right] \\
 & + KH^K \left[\left(\Phi(\nu, H^K + \frac{1}{K}) - \Phi(\nu^K, H^K) \right) \left(e \int_{\mathcal{X}} \nu^K(dx) \beta(x) \right) \right. \\
 & \left. + \left(\Phi(\nu^K, H^K - \frac{1}{K}) - \Phi(\nu^K, H^K) \right) D \right]
 \end{aligned}$$

Limit in large population : Mean behaviour

Theorem

Fix $T > 0$. The sequence $(\nu^K, H^K)_{K \geq 0}$ taking values in $\mathbb{D}([0, T], \mathcal{M}_F(\mathcal{X}) \times \mathbb{R}_+)$ converges in law to a couple of deterministic continuous functions (ξ, h) in $\mathbb{C}([0, T], \mathcal{M}_F(\mathcal{X}) \times \mathbb{R}^+)$ unique solution of : $\forall f : \mathcal{X} \rightarrow \mathbb{R}$ measurable, bounded :

$$\left\{ \begin{array}{l} \langle \xi_t, f \rangle = \langle \xi_0, f \rangle + \int_0^t \int_{\mathcal{X}} \xi_s(dx) f(x) \left[(1 - \mu(x))b(x) - d(x) \right. \\ \left. - \int_{\mathcal{X}} \alpha(x, x') \xi_s(dx') - h(s)\beta(x) \right] ds \\ \left. + \int_0^t \int_{\mathcal{X}} \xi_s(dx) \int_{\mathbb{R}} f(x+h) m(x, h) \mu(x) b(x) dh ds \right. \\ \left. h(t) = h(0) + \int_0^t h(s) \left(\int_{\mathcal{X}} e\beta(x) \xi_s(dx) - D \right) ds \right. \end{array} \right.$$

One prey - one predator system

If the initial prey population is monomorphic with trait x and no mutation occurs ($\mu = 0$), the previous limit is solution of :

$$\begin{cases} \frac{dn_x(t)}{dt} = n_x(t) (b(x) - d(x) - \alpha(x, x)n_x(t) - \beta(x)h(t)) \\ \frac{dh(t)}{dt} = h(t) (e\beta(x)n_x(t) - D) \end{cases}$$

The possible equilibria are :

- $(0, 0)$,
- $\left(\frac{b(x) - d(x)}{\alpha(x, x)}, 0 \right)$,
- coexistence equilibrium :

$$\left(\frac{D}{e\beta(x)}, \frac{1}{\beta(x)} (b(x) - d(x) - \alpha(x, x) \frac{D}{e\beta(x)}) \right).$$

Global stability

Theorem

If we suppose that $b(x) - d(x) > 0$, then for all positive initial conditions, the solution $(n(t), h(t))$ of the previous system converges when $t \rightarrow \infty$

- ▶ *to the coexistence equilibrium if*

$$e\beta(x) \frac{b(x) - d(x)}{\alpha(x, x)} - D > 0,$$

- ▶ *else to $\left(\frac{b(x)-d(x)}{\alpha(x, x)}, 0\right)$ where only prey survives.*

We can then define $(n^*(x), h^*(x))$ **the only globally stable equilibrium.**

Two prey - one predator system

If a mutant with trait y arrives in the population :

$$\begin{cases} \frac{dn_x(t)}{dt} = n_x(t) \left(b(x) - d(x) - \alpha(x,x)n_x(t) - \alpha(x,y)n_y(t) - \beta(x)h(t) \right) \\ \frac{dn_y(t)}{dt} = n_y(t) \left(b(y) - d(y) - \alpha(y,y)n_y(t) - \alpha(y,x)n_x(t) - \beta(y)h(t) \right) \\ \frac{dh(t)}{dt} = h(t) \left(e\beta(x)n_x(t) + e\beta(y)n_y(t) - D \right) \end{cases} .$$

We are interested in the following equilibria :

- ▶ with one prey and one predator,
 $\left(\frac{D}{e\beta(x)}, 0, \frac{1}{\beta(x)} \left(b(x) - d(x) - \alpha(x,x) \frac{D}{e\beta(x)} \right) \right)$ and
 $\left(0, \frac{D}{e\beta(y)}, \frac{1}{\beta(y)} \left(b(y) - d(y) - \alpha(y,y) \frac{D}{e\beta(y)} \right) \right),$
- ▶ where the predator disappears : $\left(\frac{b(x)-d(x)}{\alpha(x,x)}, 0, 0 \right)$ $\left(0, \frac{b(y)-d(y)}{\alpha(y,y)}, 0 \right)$
 $(-, -, 0).$

Global stability

We introduce the **fitness of an invading mutant of trait y** in a population of trait x :

$$f(y; x) = b(y) - d(y) - \alpha(y, x)n^*(x) - \beta(y)h^*(x).$$

Global stability

We introduce the **fitness of an invading mutant of trait y** in a population of trait x :

$$f(y; x) = b(y) - d(y) - \alpha(y, x)n^*(x) - \beta(y)h^*(x).$$

Theorem (Takeuchi, Adachi 1983)

We suppose that $\alpha(x, x)\alpha(y, y) - \alpha(x, y)\alpha(y, x) > 0$, then

- ▶ **If the fitness $f(y; x) < 0$** then every solution of the previous system $(n_x(t), n_y(t), h(t))$ (with positive initial condition) converges as $t \rightarrow \infty$ to the equilibrium $(n^*(x), 0, h^*(x))$.
- ▶ **If the fitness $f(y; x) > 0$ and $f(x; y) < 0$** then every solution of the previous system $(n_x(t), n_y(t), h(t))$ (with positive initial condition) converges as $t \rightarrow \infty$ to the equilibrium $(0, n^*(y), h^*(y))$.

Invasion \implies Replacement

In the following , we'll suppose for all $x, y \in \mathcal{X}$:

$$b(x) - d(x) > 0,$$

$$\alpha(x, x)\alpha(y, y) - \alpha(x, y)\alpha(y, x) > 0,$$

and that either

$$f(y; x) > 0,$$

or

$$f(y; x) > 0 \text{ and } f(x; y) < 0.$$

Rare mutations hypothesis

At time 0, the population contains only preys of type x :

$$(v_0^K, H_0^K) = \left(\frac{z_1^K}{K} \delta_x, \frac{z_2^K}{K} \right).$$

We are interested in the behaviour of the community under the hypothesis of :

- ▶ **large population** : $K \longrightarrow \infty$,
- ▶ **rare mutations** : we scale the mutation frequency with a parameter u_K : at each reproduction of an individual with trait x , a mutation occurs with probability $u_K \mu(\mathbf{x})$.

Example : Evolution of a qualitative defense trait

Qualitative defense : Only depends on the type of defense, and not on the quantity of defense produced.

Parameters - $b = 4$, $d = 0$, $\alpha(x, y) = \exp(-(x - y)^2/8)$.

- The favorite trait is 0 :

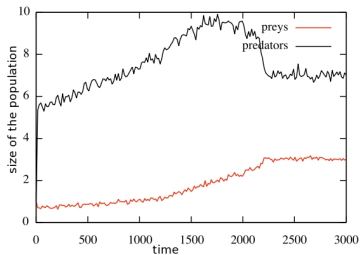
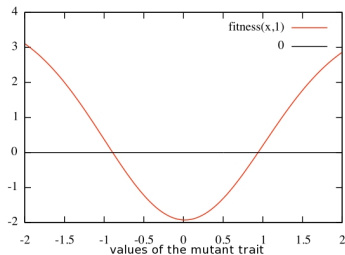
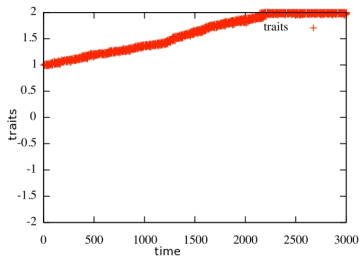
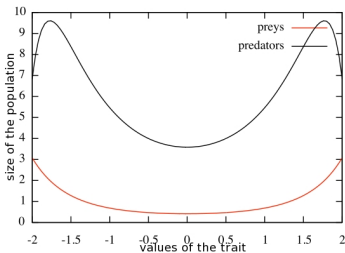
$$\beta(x) = \exp(-x^2/2).$$

- $e = 0.8$, $D = 0.333$.

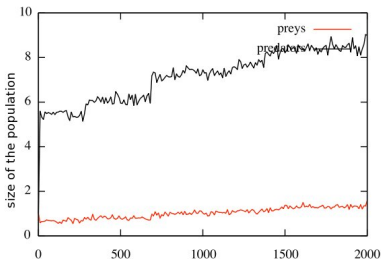
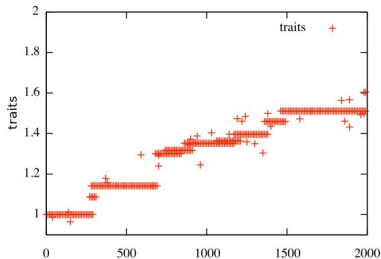
- $\mathcal{X} = [-2, 2]$.

- mutation kernel : gaussian centered on the parent trait with variance 0.01

Example : $K = 1000$, $T = 3000$, $u_K = 0.005$.



We slow down mutations



$$K = 1000,$$
$$T = 2000,$$
$$u_K = 0.00005.$$

At each time, most of the preys have the same trait.

As a mutation occurs :

- ▶ **the mutant replaces the resident population,**
- ▶ **or the mutant disappears quickly.**

Different time scales involved

We suppose that for all $V > 0$:

$$\log K \ll \frac{1}{Ku_K} \ll \exp(KV).$$

Different time scales involved

We suppose that for all $V > 0$:

$$\log K \ll \frac{1}{K u_K} \ll \exp(KV).$$

Before the first mutation : the community is given by $(N_t^K(x)\delta_x, H_t^K)$.

- ▶ The population sizes enter in finite time in an ε -neighborhood of the deterministic equilibrium $(n^*(x), h^*(x))$.
- ▶ The exit time of such a neighborhood is of the order of $\exp(KV)$ ($V > 0$). This result is obtained using a method developed by Champagnat, Jabin, Méléard (2013) based on Lyapounov functions.
- ▶ Then mutation rate is close to $K u_K \mu(\mathbf{x}) \mathbf{b}(\mathbf{x}) \mathbf{n}^*(\mathbf{x})$.

Different time scales involved

A mutant of trait y appears :

- ▶ As long as the mutant population is small, the exit time property stay true.
- ▶ The mutant population can be coupled with branching processes, to deduce that the probability for the mutant to reach a macroscopic size before 0 is close to

$$\frac{[f(y; x)]_+}{b(y)},$$

- ▶ In the case where the mutant invades, the community evolves closely to the deterministic evolution and arrives in finite time in an neighborhood of the equilibrium $(n^*(y)\delta_y, h^*(y))$.

We suppose that for all $x \in \mathcal{X}$, $h^*(x) > 0$.

Fix $x \in \mathcal{X}$. Let $(z_1^K/K, z_2^K/K)_K$ an $(\mathbb{N}/K)^2$ sequence of random variables bounded in \mathcal{L}^p converging in law to $(n^*(x), h^*(x))$.

Theorem

(Champagnat (2006))

The process $(\nu_{t/Ku_K}^K, H_{t/Ku_K}^K)_{t \geq 0}$ with initial condition $(z_1^K/K \delta_x, z_2^K/K)$ converges as $K \rightarrow \infty$ in the sense of marginal of finite dimension to :

$$(n^*(X_t) \delta_{X_t}, h^*(X_t)),$$

starting from $(n^*(x) \delta_x, h^*(x))$. Where X_t is the markov pure jump process with generator defined for all bounded measurable function Φ by :

$$A\Phi(x) = \int_{\mathbb{R}} (\Phi(x+l) - \Phi(x)) \mu(x) b(x) n^*(x) \frac{[f(x+l;x)]_+}{b(x+l)} m(x,l) dl.$$

Extinction of predators

This proof holds if the invading mutant y is such that $h^*(y) = 0$.

In this case, the limit jump process has the following behaviour : starting from $(n^*(x)\delta_x, h^*(x))$ its transitions are given by :

- from $(n^*(x)\delta_x, h^*(x))$ with $h^*(x) > 0$ to $(n^*(x+l)\delta_{x+l}, h^*(x+l))$ at infinitesimal rate

$$\mu(x)b(x)n^*(x)\frac{[f(x+l;x)]_+}{b(x+l)}m(x,l)dl.$$

- it jumps from $(\frac{b(x)-d(x)}{\alpha(x,x)}\delta_x, 0)$ to $(\bar{n}_1(x, x+l)\delta_x + \bar{n}_2(x, x+l)\delta_{x+l}, 0)$ at infinitesimal rate given by the PES defined by N. Champagnat and S. Méléard (2009)

When the predator disappears, it changes the fitness landscape.

Further questions

- ▶ In ecology, predictions on evolution are made using the canonical equation. This equation can be obtained as limit of the previous process when the size of mutations tends to 0.
 - **In such a limit, in our example, predators won't go to extinction in finite time.**
 - **As the fitness changes, we will need some regularity to have a canonical equation.**

Further questions

- ▶ In ecology, predictions on evolution are made using the canonical equation. This equation can be obtained as limit of the previous process when the size of mutations tends to 0.
 - **In such a limit, in our example, predators won't go to extinction in finite time.**
 - **As the fitness changes, we will need some regularity to have a canonical equation.**
- ▶ **What will be the structure of the community , if we allow preys and predators to evolve ?** Here we made the assumption that different types of preys cannot coexist, in this case, predators cannot coexist, but in the opposite case, it is possible.

Further questions

- ▶ In ecology, predictions on evolution are made using the canonical equation. This equation can be obtained as limit of the previous process when the size of mutations tends to 0.
 - **In such a limit, in our example, predators won't go to extinction in finite time.**
 - **As the fitness changes, we will need some regularity to have a canonical equation.**
- ▶ **What will be the structure of the community , if we allow preys and predators to evolve ?** Here we made the assumption that different types of preys cannot coexist, in this case, predators cannot coexist, but in the opposite case, it is possible.

Thank you all for your attention !