

Functional responses and interactions via a renewal approach

Vincent Bansaye,
with Sylvain Billiard & Jean René Chazottes,
Geoffroy Berthelot & Bertrand Cloez
Elizabeta Vergu & Maud Delattre

Ecole polytechnique

12 mars, Institut des systèmes complexes
Journée ModStatSAP



Functional responses quantify the interactions between populations and provide a mortality or natality rate in population dynamics

$$y'(t) = ay(t) + y(t)R(x(t), y(t))$$

in various contexts :

- predation

$$R(x, y) = bx; \quad bx/(1 + cx); \quad bx^2/(1 + cx^2); \quad b/(x + cy)...$$

- epidemiology

$$R(x, y) = bx; \quad b/(x + y)...$$

- mutualism, mating, horizontal genetic transfer, etc ...

They may take into account additional resources or interactions :

$$R(x, y, z) \dots$$

When counting interactions for a given population, functional responses are mostly based on phenomenological approaches (rather than individual traits)

*"[...]they must be considered **phenomenological**. That is, although they correctly reproduce the shape of natural functional responses, they are not able to explain the underlying mechanism."* (Jeschke et al. 2002)

They arise at a macroscopic level in population dynamics via

- slow fast interactions in Michaelis Menten response : $bx/(1 + cx)$, and more generally chemical reactions [Kurtz et al...], see also [Dawes and Souza] for prey predators.
- "hunger level" structured population in steady state [Jeschke et al...]

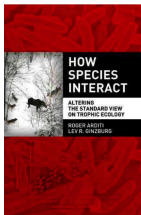
When counting interactions for a given population, functional responses are mostly based on phenomenological approaches (rather than individual traits)

*"[...]they must be considered **phenomenological**. That is, although they correctly reproduce the shape of natural functional responses, they are not able to explain the underlying mechanism."* (Jeschke et al. 2002)

They arise at a macroscopic level in population dynamics via

- slow fast interactions in Michaelis Menten response : $bx/(1 + cx)$, and more generally chemical reactions [Kurtz et al...], see also [Dawes and Souza] for prey predators.
- "hunger level" structured population in steady state [Jeschke et al...]

Is the form of R important ?

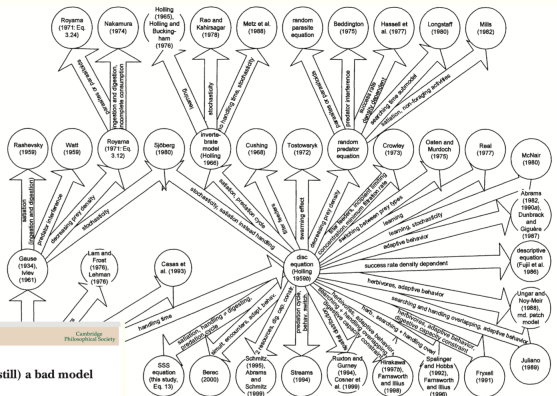


BIOLOGICAL REVIEWS
 Prof. Dr. (1974), pp. 149-166.
 doi: 10.1111/j.1365-3113.1974.tb01111.x

Why ratio dependence is (still) a bad model of predation

Peter A. Abrams*

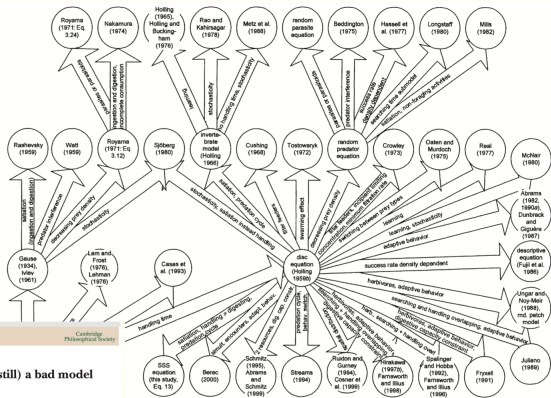
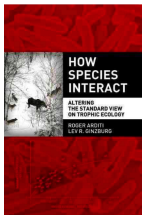
Cambridge Philosophical Society



Jeschke et al., 2002

They may give different qualitative and quantitative predictions...

Is the form of R important ?



Jeschke et al., 2002

BIOLOGICAL REVIEWS
 Prof. Dr. (Oxon.) Peter A. Abrams, Ed. D. Sc. (Yale), Ph.D.

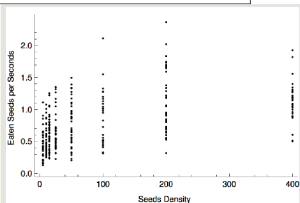
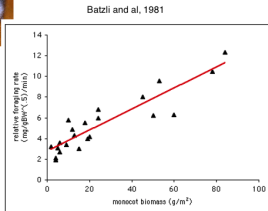
Why ratio dependence is (still) a bad model of predation

Peter A. Abrams*

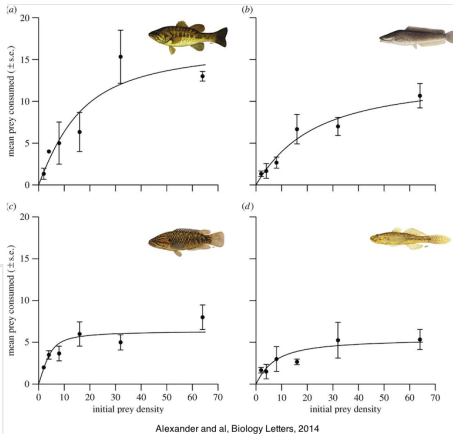
Cambridge Philosophical Society

They may give different qualitative and quantitative predictions...

How does it look like from individual(s) ?

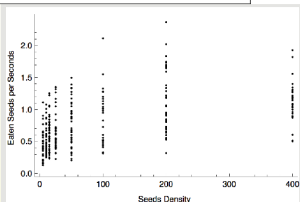
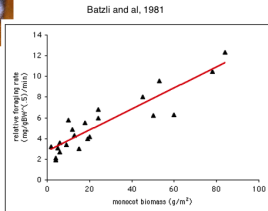


Baker et al. 2010

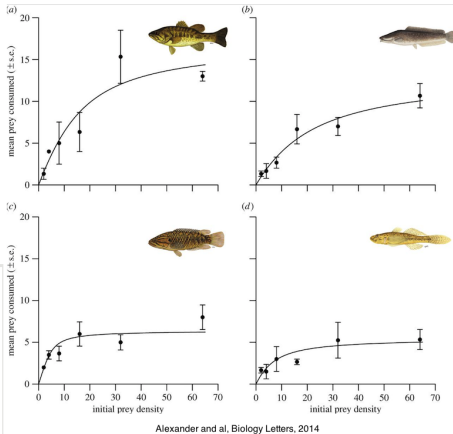


-> Large fluctuations ; affects inference and population dynamics ?

How does it look like from individual(s) ?



Baker et al. 2010



-> Large fluctuations ; affects inference and population dynamics ?

Objectives

- Provide a general approach of the functional form (from modeling individual behavior)
- Describe their fluctuations and develop inference tools
- Large population approximation for population dynamics
- Genealogies ?

Objectives

- Provide a general approach of the functional form (from modeling individual behavior)
- Describe their fluctuations and develop inference tools

- Large population approximation for population dynamics
- Genealogies ?

The successive interaction events between two species are independent (and identically) distributed as the r.v.

$$T(\mathbf{n})$$

which depends on the population sizes $\mathbf{n} = (n_1, n_2, \dots)$.
The number of interactions until time t is given by

$$N_t(\mathbf{n}) = \#\{k : S_k(\mathbf{n}) \leq t\}$$

where

$$S_k(\mathbf{n}) = T_1(\mathbf{n}) + \dots + T_k(\mathbf{n})$$

and $(T_i(\mathbf{n}) : i \geq 1)$ are i.i.d. under a **regeneration assumption** (t has to be small compared to \mathbf{n}).

Example for prey predators

Each interaction may be decomposed in successive times, with success probability, different resources or interactions.

Typically for prey predators, $\mathbf{n} = (n_1, n_2) = (\#preys, \#predators)$ and for one predator

$$T(\mathbf{n}) = T_S(n_1) + T_H$$

where

- T_S (searching time) may involve foraging strategy
- T_H (handling time) may include relapse, satiety, with a low variance and may include more density dependences.

But also (sheep, partridge,...)

$\mathbf{n} = (n_1, n_2, n_3) = (\#food\ for\ preys, \#preys, \#predators)$,

$$T(\mathbf{n}) = T_S(n_1) + T_{vigilance}(n_3) + T_H$$

Example for prey predators

Each interaction may be decomposed in successive times, with success probability, different resources or interactions.

Typically for prey predators, $\mathbf{n} = (n_1, n_2) = (\#preys, \#predators)$ and for one predator

$$T(\mathbf{n}) = T_S(n_1) + T_H$$

where

- T_S (searching time) may involve foraging strategy
- T_H (handling time) may include relapse, satiety, with a low variance and may include more density dependences.

But also (sheep, partridge,...)

$\mathbf{n} = (n_1, n_2, n_3) = (\#food\ for\ preys, \#preys, \#predators)$,

$$T(\mathbf{n}) = T_S(n_1) + T_{vigilance}(n_3) + T_H$$

Central limit theorem (renewal theory)

Under a second moment assumption,

$$N_t(\mathbf{n}) - \frac{t}{\mathbb{E}(T(\mathbf{n}))} \sim \sqrt{t} \mathcal{N}\left(0, \frac{\text{Var}(T(\mathbf{n}))}{\mathbb{E}(T(\mathbf{n}))^3}\right)$$

in law as $t \rightarrow \infty$.

A key example : Holling II, Monod functional response

For each predator, the time for interaction

$$T(x) = T_S(x) + T_H$$

with

$$\mathbb{E}(T_S(x)) = a/x$$

yields

$$N_t(x) \underset{t \rightarrow \infty}{\sim} t \frac{1}{a/x + \mathbb{E}(T_H)}$$

a.s. ie the classical function response with saturation

$$\frac{x}{a + x \cdot \mathbb{E}(T_H)}$$

An explicit simple model

Moreover with constant handling

$$\text{Var}(T_H) = 0, \quad \text{i.e. } T_H = c$$

and deterministic foraging in 1D (*random arrival point in a homogeneous prey repartition on $[0, L]$ and straightline motion*)

$$T_S(x) = \frac{\text{Uniform}[0, L/x]}{v}, \quad v = \text{speed of predator}$$

we get the second order approximation and explicit parameters

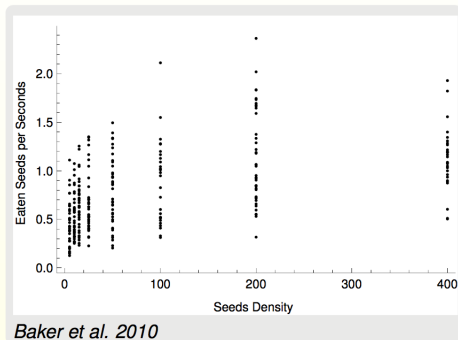
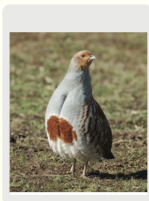
$$N_t(x) - t \frac{x}{L/4v + cx} \sim \sqrt{t} \mathcal{N} \left(0, \frac{x(L/2v)^2}{(L/2v + cx)^3} \right)$$

in law as $t \rightarrow \infty$.

Examples in 1D : searching, handling and potential interference

Functional Response ($R(\cdot)$)	Handling time (c_y)	Searching probability (p_s)	Interaction with e_z	Mean & Variance
No handling 2 species (Holling Type I)	0	1	No: $z = 0$	yl^{-1} $\frac{y}{3}l^{-1}$
With Handling 2 species (Holling Type II)	> 0	1	No: $z = 0$	$y(l + c_y y)^{-1}$ $\frac{y}{3}l^2(l + c_y y)^{-3}$
With Handling 3 species (Holling Type III)	> 0	1	Yes: $z > 0$ $c_z = 0, \beta = 0$	$y^2(l(y + \alpha z) + c_y y^2)^{-1}$ $\frac{y^2}{3}(l(y + \alpha z) + c_y y^2)^{-3}$ $\times l^2(y + \alpha z)(y + 3\alpha z)$
With Handling 2 species Predators Interference (Beddington-DeAngelis)	> 0	1	Yes : $z = x$ $c_z = c_x, \alpha = \beta$	$y(l + c_y y + c_x \alpha x)^{-1}$ $\frac{y}{3}(y + \alpha x)^{-1}(l + c_y y + c_x \alpha x)^{-3}$ $\times (3c_x^2 \alpha x(y + \alpha x)^2 + 6c_x \alpha x l(y + \alpha x) + l^2(y + 3\alpha x))$
With Handling 2 species Predators Competition (Ratio Dependence)	> 0	x^{-1}	No: $z = 0$	$\frac{y}{x}(l + c_y \frac{y}{x})^{-1}$ $\frac{y}{x} \frac{l^2}{3} x(3 - \frac{2}{x})(l + c_y \frac{y}{x})^{-3}$

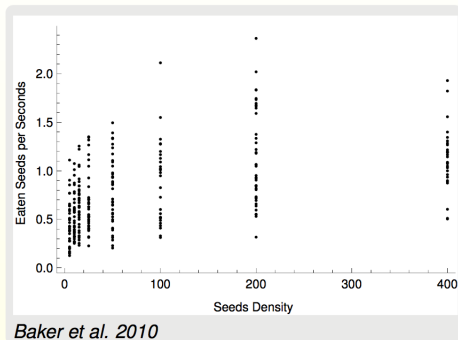
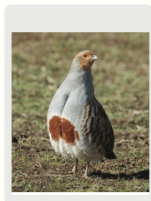
An application with data for grey partridge



Baker et al conclude that the vigilance has no effect on seeds consumption, but including fluctuations lead us to the converse result.

-> 3 sources of randomness : intrinsic +individual variability WIP,
+measurement error.

An application with data for grey partridge



Baker et al conclude that the vigilance has no effect on seeds consumption, but including fluctuations lead us to the converse result.

-> 3 sources of randomness : intrinsic +individual variability WIP,
+measurement error.

Here : two populations (n_1 preys and n_2 predators) with two size scales K_1, K_2 and

- natural births (rate proportional to the size of the population)
- prey predator interactions with searching/ foraging time and handling time :

$$T_S(x, y), \quad T_H(x, y)$$

with $x = n_1/K_1$, $y = n_2/K_2$

- deaths for predators (individual rate depends on the number of preys eaten)

Age structure of predators for interactions

$P(t)$: set of preys at time t .

$\mathcal{P}_S(t)$, resp. $\mathcal{P}_H(t)$: set of predators searching resp. handling at time t .

Let $a_i(t)$ be the **age** (for interaction) of $i \in \mathcal{P}_S(t) \cup \mathcal{P}_M(t)$, i.e. the time to find in the past the last change of state *Searching* \leftrightarrow *Handling* for i .

The population is described by a measure valued process

$$\left(n_1, \sum_{i \in \mathcal{P}_S(t)} \delta_{a_i(t)}, \sum_{i \in \mathcal{P}_H(t)} \delta_{a_i(t)} \right)$$

where $n_1 = \#preys$.

Assume that $T_S(x, y)$ and $T_H(x, y)$ have densities (resp. $f_S(\cdot, x, y)$ and $f_H(\cdot, x, y)$) and introduce the rates $\alpha_S(\cdot, x, y)$ and $\alpha_H(\cdot, x, y)$

$$\alpha_H(a, x, y) = \frac{f_S(a, x, y)}{\int_a^\infty f_S(u, x, y) du}, \quad \alpha_S(a, x, y) = \frac{f_H(a, x, y)}{\int_a^\infty f_H(u, x, y) du}$$

Age structure of predators for interactions

$P(t)$: set of preys at time t .

$\mathcal{P}_S(t)$, resp. $\mathcal{P}_H(t)$: set of predators searching resp. handling at time t .

Let $a_i(t)$ be the **age** (for interaction) of $i \in \mathcal{P}_S(t) \cup \mathcal{P}_M(t)$, i.e. the time to find in the past the last change of state *Searching* \leftrightarrow *Handling* for i .

The population is described by a measure valued process

$$\left(n_1, \sum_{i \in \mathcal{P}_S(t)} \delta_{a_i(t)}, \sum_{i \in \mathcal{P}_H(t)} \delta_{a_i(t)} \right)$$

where $n_1 = \#preys$.

Assume that $T_S(x, y)$ and $T_H(x, y)$ have densities (resp. $f_S(\cdot, x, y)$ and $f_H(\cdot, x, y)$) and introduce the rates $\alpha_S(\cdot, x, y)$ and $\alpha_H(\cdot, x, y)$

$$\alpha_H(a, x, y) = \frac{f_S(a, x, y)}{\int_a^\infty f_S(u, x, y) du}, \quad \alpha_S(a, x, y) = \frac{f_H(a, x, y)}{\int_a^\infty f_H(u, x, y) du}$$

The transitions for **interactions** are given for $a_* \in \mathcal{A}$, $a'_* \in \mathcal{A}'$ by

$$\begin{aligned} & \left(n, \sum_{a \in \mathcal{A}} \delta_a, \sum_{a' \in \mathcal{A}'} \delta_{a'} \right) \\ & \longrightarrow \left(n - 1, \sum_{a \in \mathcal{A}} \delta_a - \delta_{a_*}, \sum_{a' \in \mathcal{A}'} \delta_{a'} + \delta_0 \right) \text{ at rate } \alpha_H(a_*, n_1/K_1, n_2/K_2) \\ & \longrightarrow \left(n, \sum_{a \in \mathcal{A}} \delta_a + \delta_0, \sum_{a' \in \mathcal{A}'} \delta_{a'} - \delta_{a'_*} \right) \text{ at rate } \alpha_S(a'_*, n_1/K_1, n_2/K_2) \end{aligned}$$

plus **aging** (speed 1 for each predator),
plus individual **births and deaths**.

Trajectorial representation (SDE via Poisson Point Measure following [Tran]).

First order approximation : fast scale for interactions

Writing $K = (K_1, K_2)$ and $\lambda_K = K_1/K_2$

$$(X^K(t), Y^K(t)) = \left(\frac{\#P(\lambda_K t)}{K_1}, \frac{\#P_S(\lambda_K t) + \#P_H(\lambda_K t)}{K_2} \right)$$

and letting $K_2 \rightarrow \infty$, $\lambda_K \rightarrow \infty$, (X^K, Y^K) converges in law in $\mathbb{D}([0, \infty), (\mathbb{R}^+)^2)$ to the unique solution of

$$\begin{cases} x'(t) = ax(t) - y(t)\beta(x(t), y(t)) \\ y'(t) = by(t) - y(t)f(\beta(x(t), y(t))) \end{cases}$$

with

$$\beta(x, y) = \frac{1}{\mathbb{E}(T(x, y))} = \frac{1}{\mathbb{E}(T_S(x, y)) + \mathbb{E}(T_H(x, y))}$$

An idea of the proof

Use *stochastic averaging* [Kurtz].

Fast scale of interactions : see [Kang and Kurtz 2013] for chemical reactions (in finite dimension).

Here in **infinite dimension** (age structure).

Consider the **occupation measure**

$$\Gamma^K([s, t], dj, da) = \frac{1}{K_2} \left(\int_{[s, t]} du \delta_1(dj) \sum_{i \in \mathcal{P}_S(\lambda_K u)} \delta_{a_i(u)}(da) + \int_{[s, t]} du \delta_2(dj) \sum_{i \in \mathcal{P}_M(\lambda_K u)} \delta_{a_i(u)}(da') \right)$$

and check that its limiting point is given at time t by the stationary value of an age structured PDE (quasi equilibrium coming from the fast time scale of interactions) depending only on the quantity of preys and predators at time t .

An idea of the proof

Use *stochastic averaging* [Kurtz].

Fast scale of interactions : see [Kang and Kurtz 2013] for chemical reactions (in finite dimension).

Here in **infinite dimension** (age structure).

Consider the **occupation measure**

$$\begin{aligned} \Gamma^K([s, t], dj, da) &= \frac{1}{K_2} \left(\int_{[s, t]} du \delta_1(dj) \sum_{i \in \mathcal{P}_S(\lambda_K u)} \delta_{a_i(u)}(da) \right. \\ &\quad \left. + \int_{[s, t]} du \delta_2(dj) \sum_{i \in \mathcal{P}_M(\lambda_K u)} \delta_{a_i(u)}(da') \right) \end{aligned}$$

and check that its limiting point is given at time t by the stationary value of an age structured PDE (quasi equilibrium coming from the fast time scale of interactions) depending only on the quantity of preys and predators at time t .

Quasi equilibrium for ages of interactions

For a fixed total number of preys and predators (x, y) (which vary slower), the two age densities m_s and n_s for the populations of predators evolve as

$$\frac{\partial n_s}{\partial s} + \frac{\partial n_s}{\partial a} + \alpha_M(a, \cdot) n_s = 0; \quad n_s(0) = \int_0^\infty \alpha_S(a, \cdot) m_s(a) da$$

$$\frac{\partial m_s}{\partial s} + \frac{\partial m_s}{\partial a} + \alpha_S(a, \cdot) m_s = 0; \quad m_s(0) = \int_0^\infty \alpha_M(a, \cdot) n_s(a) da$$

and reaches the associated equilibrium $n(a, x, y)$, $m(a, x, y)$.
In particular, we can compute the flux

$$\phi(x, y) = \int_0^\infty n_s(a, x, y) a_M(a, x, y) da$$

and get

$$\phi(x, y) = \frac{1}{\mathbb{E}(T_S(x, y)) + \mathbb{E}(T_M(x, y))}$$

Quantifying fluctuations from renewal theorem

Considering the number of preys (and assuming here that the time of interaction for a predator is only prey dependent+fixed number of predators), *we expect that if*

$$K_1/K_2^2 \rightarrow +\infty$$

the process

$$U^K(t) = \sqrt{K_1}(X^K(t) - x(t))$$

converges in law in $\mathbb{D}([0, \infty), \mathbb{R})$ to the gaussian process U solution of

$$U(t) = U(0) - \int_0^t \beta'(x(s))y(0)U(s)ds + \int_0^t \sigma(x(s))\sqrt{y(0)}dB_s$$

where B is a brownian motion and

$$\beta(x) = \frac{1}{\mathbb{E}(T(x))} = \frac{1}{\mathbb{E}(T_S(x)) + \mathbb{E}(T_H(x))}$$

$$\sigma(x)^2 = \frac{\text{Var}(T(x))}{\mathbb{E}(T(x))^3} = \frac{\text{Var}(T_S(x)) + \text{Var}(T_H(x))}{(\mathbb{E}(T_S(x)) + \mathbb{E}(T_H(x)))^3}$$

An idea of the proof in the exponential case (finite dimensional Markov process), in progress

Follow [Kang Kurtz Popovic 2014] for fluctuations of multi scale process (for chemical reactions), see also [Pardoux and Veretennikov 2000s].

We have

$$U^K(t) = U^K(0) + V^K(t) + W^K(t)$$

where

$$\begin{aligned} V^K(t) &= \sqrt{K_1} \int_0^t (\beta(x(s)) - \beta(X^K(s))) ds + \\ &\quad \sqrt{K_1} \int_0^t (\beta(X^K(s)) - \alpha_H(X^K(s)) Y_S^K(s)) ds \\ W^K(t) &= -\sqrt{K_1} \int_0^t \frac{1}{K_1} 1_{u \leq \lambda_K K_2} Y_S^K(s) \alpha_H(X^K(s)) \tilde{\mathcal{N}}(duds) \end{aligned}$$

and consider the Poisson equation $Qu(x, y_S, y) = \beta(x) - \alpha_H(x) y_S$ and use a CLT for martingales.

An idea of the proof in the exponential case (finite dimensional Markov process), in progress

Follow [Kang Kurtz Popovic 2014] for fluctuations of multi scale process (for chemical reactions), see also [Pardoux and Veretennikov 2000s].

We have

$$U^K(t) = U^K(0) + V^K(t) + W^K(t)$$

where

$$\begin{aligned} V^K(t) &= \sqrt{K_1} \int_0^t (\beta(x(s)) - \beta(X^K(s))) ds + \\ &\quad \sqrt{K_1} \int_0^t (\beta(X^K(s)) - \alpha_H(X^K(s)) Y_S^K(s)) ds \\ W^K(t) &= -\sqrt{K_1} \int_0^t \frac{1}{K_1} 1_{u \leq \lambda_K K_2} Y_S^K(s) \alpha_H(X^K(s)) \tilde{\mathcal{N}}(duds) \end{aligned}$$

and consider the Poisson equation $Qu(x, y_S, y) = \beta(x) - \alpha_H(x) y_S$ and use a CLT for martingales.

An idea of the proof in the exponential case (finite dimensional Markov process), in progress

Follow [Kang Kurtz Popovic 2014] for fluctuations of multi scale process (for chemical reactions), see also [Pardoux and Veretennikov 2000s].

We have

$$U^K(t) = U^K(0) + V^K(t) + W^K(t)$$

where

$$\begin{aligned} V^K(t) &= \sqrt{K_1} \int_0^t (\beta(x(s)) - \beta(X^K(s))) ds + \\ &\quad \sqrt{K_1} \int_0^t (\beta(X^K(s)) - \alpha_H(X^K(s)) Y_S^K(s)) ds \\ W^K(t) &= -\sqrt{K_1} \int_0^t \frac{1}{K_1} 1_{u \leq \lambda_K K_2} Y_S^K(s) \alpha_H(X^K(s)) \tilde{\mathcal{N}}(duds) \end{aligned}$$

and consider the Poisson equation $Qu(x, y_S, y) = \beta(x) - \alpha_H(x) y_S$ and use a CLT for martingales.

- Complete the proofs, generalize (non-Markov and multiscale of fluctuations with births and deaths of predators) and *find an alternative approach for scaling limits* (using the duality with renewal processes ?).
Obtain also an expression of large deviation times (exit of tubes [Freindlin Wentzell]) via this duality.
- **Beyond regenerative assumption** : how does space structure then change functional responses ? (in progress with Geoffroy Berthelot, Sylvain Billiard and Elizabetha Vergu)
- **Genealogies** (ancestral linages of predators and sampling, in project : "survivors have eaten faster"),
networks of interactions ?

- Complete the proofs, generalize (non-Markov and multiscale of fluctuations with births and deaths of predators) and *find an alternative approach for scaling limits* (using the duality with renewal processes ?).
Obtain also an expression of large deviation times (exit of tubes [Freindlin Wentzell]) via this duality.
- **Beyond regenerative assumption** : how does space structure then change functional responses ? (in progress with Geoffroy Berthelot, Sylvain Billiard and Elizabetha Vergu)
- **Genealogies** (ancestral linages of predators and sampling, in project : "survivors have eaten faster"),
networks of interactions ?