Some stochastic functional responses in ecology

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What are functional responses ?

Functional responses quantify the interactions between populations in various contexts :

- **predation**

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

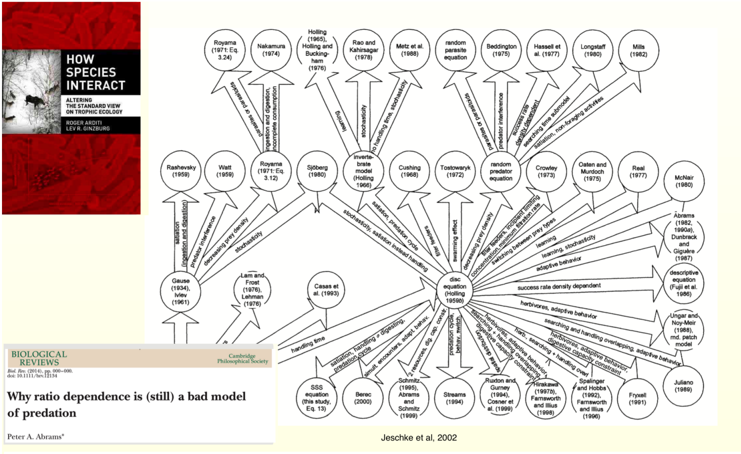
  the speed of consumption at the level of one consumer/predator. The macroscopic population population dynamics

$$\begin{cases} x'(t) = ax(t) - y(t)\mathbf{R}(x(t),y(t)), \\ y'(t) = -by(t) + y(t)\phi(\mathbf{R}(x(t),y(t))). \end{cases}$$

- epidemiology
  $R(x,y) = \ bx; \ b/(x+y)...$
- mutualism, mating, horizontal genetic transfer, etc ...

They may take into account additional ressources or interactions : $R(x,y,z)$...

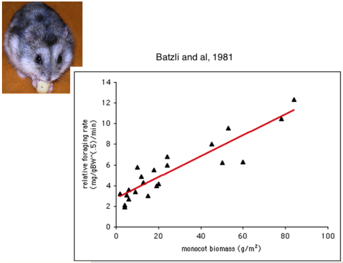
Is the form of R important ?

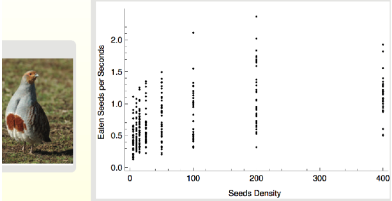


They may give different qualitative and quantitative predictions...

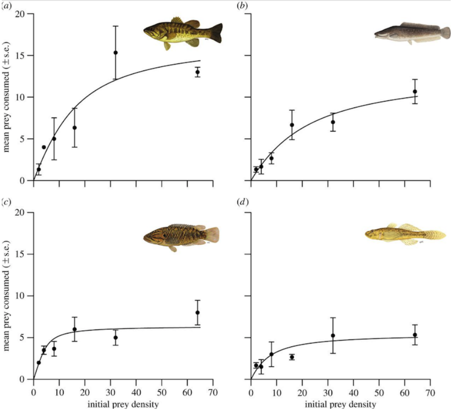
How does it look like from individual(s) ?

Batzli and al, 1981





Baker et al. 2010



Alexander and al, Biology Letters, 2014

Large fluctuations observed : which source ? (dynamic, individual variability, environment, measures...) ? does it affect inference and population

Main objectives and literature

- Mechanistic modeling of functional response (from individual behavior)
- Describe their fluctuations and develop inference tools
- Derive large population approximation for population dynamics

In the literature, convergence from individual based model

- models without space and without memory (for instance chemostat, with well mixed population) through slow/fast dynamics and averaging techniques by Kurtz, Popovic et al.
- some spatial models without motion (contact and votant and pertubations) by Durrett, Neuheuser, Cox, Perkins et al.

Here $\longrightarrow$ Motion of predators, memory and/or space in interactions.
See also [Popovic, Véber].

Renewal framework

The time between two interactions is given by the random variable

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

which depends on the population sizes $\mathbf{n} = (n_1, n_2, ...)$.
When t is small compared to $\mathbf{n}$, the successive times of interactions are

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

where $(T_i(\mathbf{n}) : i \geq 1)$ are i.i.d. distributed as $T(\mathbf{n})$.

The number of interactions until time t is given by

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

By duality, under a second moment assumption,

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

in law as $t \to \infty$.

Prey predators

Each interaction $T(\mathbf{n})$ may be decomposed in successive times and

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

and for each predator

- T_S (searching time) may involve foraging strategy and usually prey density dependences
- T_H (handling time) may include relapse, satiety. It usually has a lower variance.

leading to (without predators interference)

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

When $\mathbb{E}(T_S(n_1)) = a/n_1, \mathbb{E}(T_H) = \tau_H$, we get stochastic Holling II/Monod functional response :

$$N_t(\mathbf{n}) \sim_{t\to\infty} t\,\frac{n_1}{a+\tau_H n_1} + \sqrt{t}\,\mathcal{N}\left(0, \frac{Var(T_S(n_1)) + Var(T_H(n_1))}{[a/n_1+\tau_H]^3}\right)$$

Question : how does it impact the large population approximation ?

The model

Two populations : n_1 *preys* and n_2 *predators*

- two size scales $K_1 \gg K_2$: much more preys, predators eats "lots of preys" during their life
- interactions : searching time and handling time of predators :

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

  with $x = n_1/K_1$.
- birth of preys and deaths due in particular to predation.
- birth and deaths of predators, at a slower time scale (factor K_2/K_1), influenced by the time of last prey eaten.

Age structure for modeling interactions of predators

Assume that $T_S(x)$ and $T_H(x)$ have densities resp. $f_S(.,x)$ and $f_H(.,x)$. Intercations can be described by a Markov process (memory less property but in higher dimension) where

$$\alpha_S(a,x) = \text{rate at which a predator who has searched during time } a \text{ finds a prey} = \frac{f_S(a,x)}{\int_a^\infty f_S(u,x)du}$$

$$\alpha_H(a,x) = \text{rate at which a predator who has handled during time } a \text{ starts searching} = \frac{f_H(a,x)}{\int_a^\infty f_H(u,x)du}$$

and $\lambda_\star(a), \mu_\star(a)$ the individual birth and death rate of predators when they are in state $\star \in \{S, M\}$ from time a.

$\mathcal{P}_S(t)$, resp. $\mathcal{P}_H(t)$: set of predators *Searching*, resp. *Handling* at time t.
Let $a_i(t)$ be the age (for interaction) of $i \in \mathcal{P}_S(t) \cup \mathcal{P}_M(t)$.
The population is described by a measure valued process

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

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

$$\left(n, \sum_{a \in \mathcal{A}} \delta_a, \sum_{a \in \mathcal{A}'} \delta_{a'} \right)$$

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

$$\longrightarrow \left(n, \sum_{a \in \mathcal{A}} \delta_a + \delta_0, \sum_{a' \in \mathcal{A}'} \delta_{a'} - \delta_{a'_*} \right) \quad \text{ at rate } \alpha_S(a'_*, n_1/K_1)$$

anf aging (speed 1 for each predator) and births and deaths (at slowler time scale for predators).
SDE representation via Poisson Point Measure following [Tran].

First order approximation : fast scale for interactions

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

$$(X^K(t), Y^K(t)) = \left(\frac{\#\text{Preys}(\lambda_K t)}{K_1}, \frac{\#\text{Predators}(\lambda_K t)}{K_2} \right)$$

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

$$\begin{cases} x'(t) = ax(t) - y(t)\phi(x(t)) \\ \\ y'(t) = by(t) - y(t)\psi(x(t)) \end{cases}$$

with

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

$$\psi(x) = \frac{\mathbb{E}\left[\int_0^{T_S(x)} (\lambda_S(a) - \mu_S(a))da\right] + \mathbb{E}\left[\int_0^{T_M(x)} (\lambda_M(a) - \mu_M(a))da\right]}{\mathbb{E}[T_S(x)] + \mathbb{E}[T_M(x)]}$$

An idea of the proof

Use *stochastic averaging* [Kurtz, Popovic] in infinite dimension [Méléard, Tran], with an age structure due to intercations, with potentially unbounded rates (due to the tail of times distribution).

Consider the occupation measure

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

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

What about spatial models ? Range of random walks

First order approximation of the number of distinct sites visited after n steps [Dvoretzky, Erdös] in dimension 2,

$$\mathcal{N}_n = \#\{X_i : i \leq n\} \sim_{n\to\infty} \pi \frac{n}{\log n} \qquad \text{a.s.}$$

The following convergence in law [Le Gall] holds for the second order

$$\frac{(\log n)^2}{n}(\mathcal{N}_n - \mathbb{E}(\mathcal{N}_n)) \stackrel{n\to\infty}{\Longrightarrow} -2\pi^2\Gamma$$

where Γ is the "compensated self intersection local time" for planar Brownian motion [Varadhan].

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Handling time on a spatial model

Preys are located on $\mathbb{Z}^2$, with Δ the time needed to go from one site to another and τ_H the handling time.

$$\frac{\left(\log\left(\frac{t}{\Delta}\right)\right)^2}{\frac{t}{\Delta}}\left(R_t - \frac{\pi\,\frac{t}{\Delta}}{\log\left(\frac{t}{\Delta}\right)}\right) \Rightarrow -\pi\left(2\pi\Gamma + \frac{\pi\,\tau_H}{\Delta} + \gamma\right),$$

in law as $t \to +\infty$.

Elements of proof.
Duality relations to rely on $\mathcal{N}_n \longrightarrow \Gamma, \tau_H$.
Second order approximation of $\mathbb{E}(\mathcal{N}_n)$ using fine estimates on return time of random walks [Uchiyama, 2012] $\longrightarrow \gamma$.
Uniform integrability via exponential moments to get the asymptotic coefficient of variations $\longrightarrow$ decreases as $\log t$.

Extensions, robustness

- Non homogeneity : percolation of preys and extension of the convergence in law of fluctuations by Fourier transform.
- Random time of motion and handling.
- Perturbation (larger jumps, memory of the random walk...)

===> Robustness (but for a drift !)

Dimension has a great impact ($d = 1, 2, 3$) and the coefficient of variation

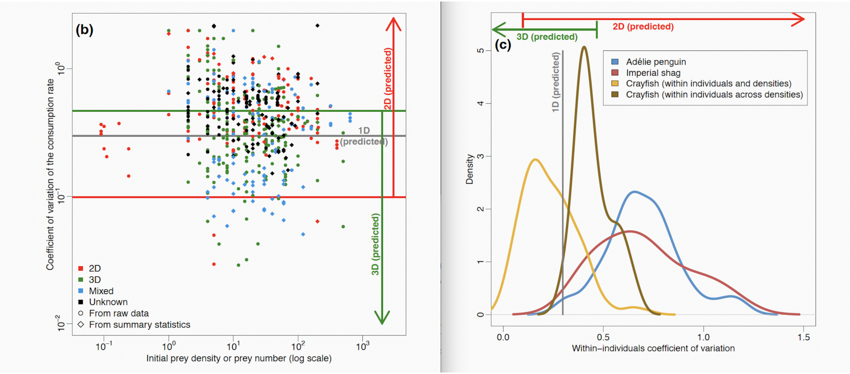
$$C_v^d(t) := \frac{\sqrt{\mathrm{Var}(R_t)}}{\mathbb{E}(N_t)}$$

is a signature of space

$$C_v^1 = \mathcal{O}(1) \gg C_v^2 = \mathcal{O}(1/\log t) \gg C_v^3 \approx \mathcal{O}(1/\sqrt{t})$$

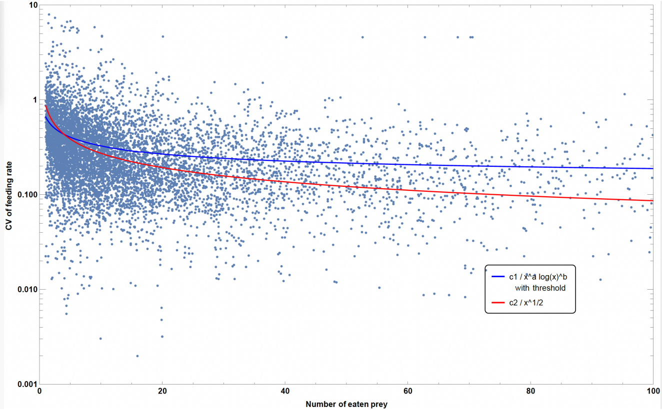
What about data ?

Look at the coefficient of variation $C_v^d(t) = \sqrt{\mathrm{Var}(R_t)}/\mathbb{E}(N_t)$.



Left : medium quality data, right high quality

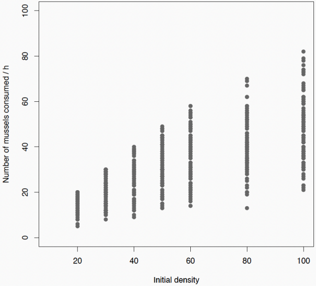
What about data ?



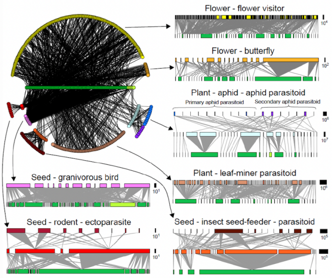
Renewal framework versus spatial random walk

Open questions

- Fluctuation of process in regenerative framework : a duality ?
- Population dynamics in spatial (phD in progress)
- Inference and mixed effects models
- From function responses to trophic web ecological network and evolution



Linzmaier *et al.* 2019



(Pocock et al. 2012)