Functional responses and interactions via a renewal approach

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27 june, CIRM

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

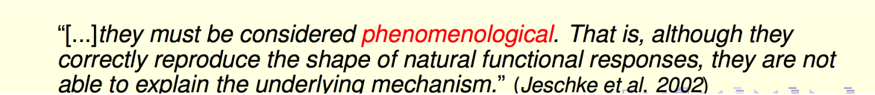
$$y'(t) = ay(t) + y(t)R(x(t), y(t))$$

in various contexts :

- predation
  $R(x, y) = \ bx;\ \ bx/(1 + cx);\ \ bx^2/(1 + cx^2);\ \ b/(x + cy)$...
- epidemiology
  $R(x, y) = \ bx;\ b/(x + y)$...
- mutualism, mating, horizontal genetic transfer, etc ...

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

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...]

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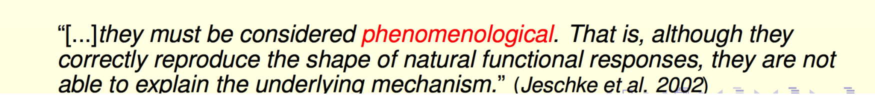

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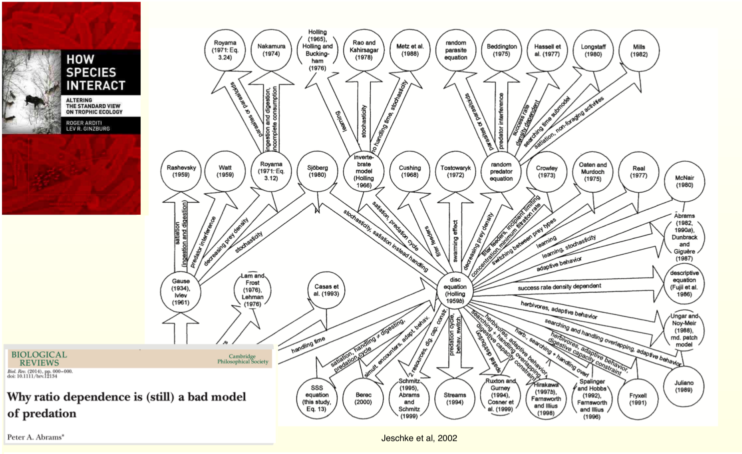

HOW SPECIES INTERACT

ALTERING THE STANDARD VIEW ON TROPHIC ECOLOGY

ROGER ARDITI
LEV R. GINZBURG

BIOLOGICAL REVIEWS

Cambridge Philosophical Society

Biol. Rev. (2014), pp. 000–000.
doi: 10.1111/brv.12134

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Peter A. Abrams*

Jeschke et al, 2002

They may give different qualitative and quantitative predictions...

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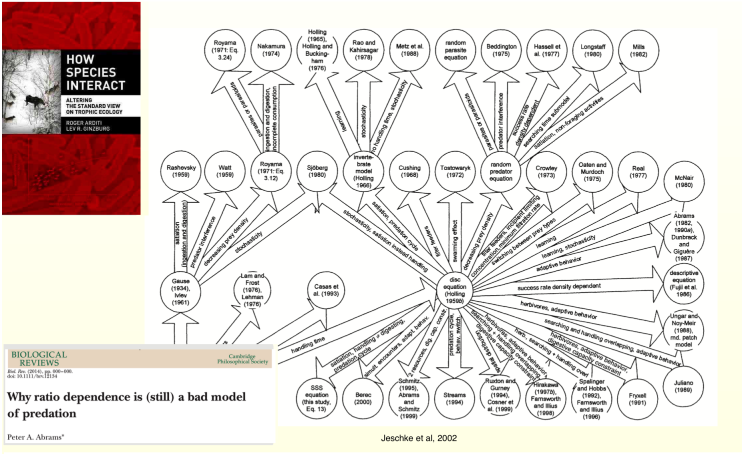

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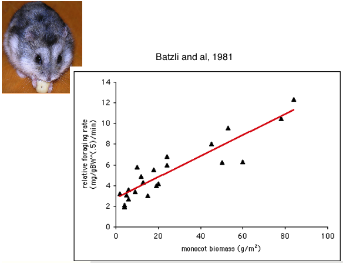
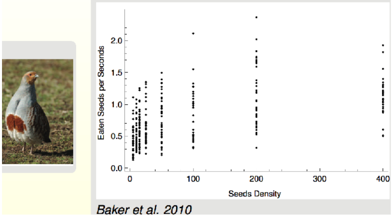
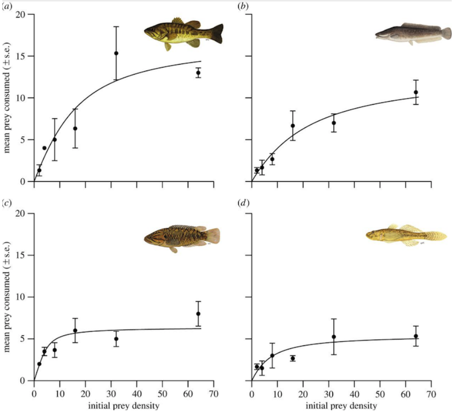




Baker et al. 2010



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-> Large fluctuations ; affects inference and population dynamics ?

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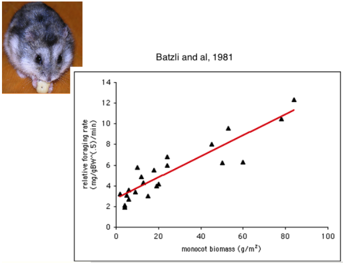
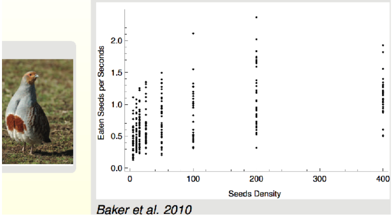


Batzli and al, 1981



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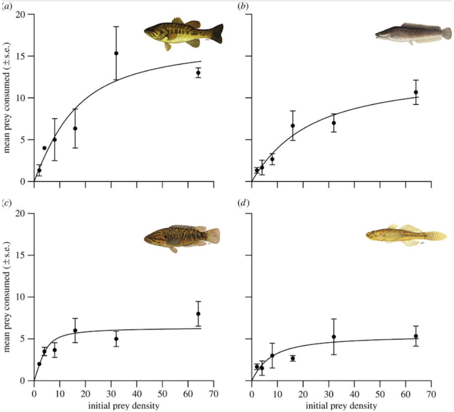

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Objectives

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

- Large population approximation for population dynamics
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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 $\mathbf{n} = (n_1, n_2, ...)$.
The number of interactions until time t is given by

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

where

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

and $(T_i(\mathbf{n}) : i \geq 1)$ are i.i.d. under 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 ressources 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,...)
$\mathbf{n} = (n_1, n_2, n_3) = (\#food\ for\ preys, \#preys, \#predators)$,

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Central limit theorem (renewal theory)

Under 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 $t \to \infty$.

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

$$N_t(x) \sim_{t\to\infty} t\frac{1}{a/x + \mathbb{E}(T_{handling})}$$

a.s. ie the classical function response with saturation

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

An explicit simple model

Moreover with constant handling

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

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

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

we get the second order approximation and explicit parameters

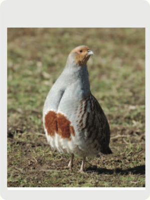
$$N_t(x) - t\frac{x}{L/4v + cx} \sim \sqrt{t}\mathcal{N}\left(0, \frac{x(L/2v)^2}{(L/2v + cx)^3}\right)$$

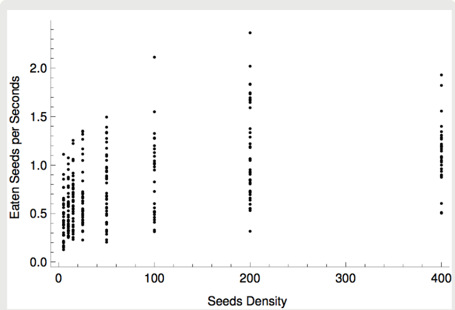
in law as $t \to \infty$.

Examples in 1D : searching, handling and potential interference

Functional Response ($R(.)$)	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 : $z = x$ $c_z = c_x,\ \alpha = \beta$	$y(l + c_y y + c_x \alpha x)^{-1}$ $\frac{y}{3}(y + \alpha x)^{-1}(l + c_y y + c_x \alpha x)^{-3}$ $\times \big(3c_x^2 \alpha x(y + \alpha x)^2 + 6c_x \alpha x l(y + \alpha x)$ $+ l^2(y + 3\alpha x)\big)$
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. 2010

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

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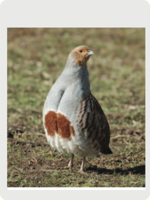

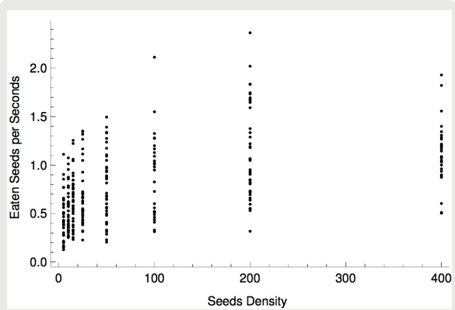

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Here : two populations (n_1 *preys* and n_2 *predators*) with two size scales K_1, K_2 and

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

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

  with $x = n_1/K_1$, $y = n_2/K_2$
- death (individual rate for predator 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* $<->$ *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. $f_S(., x, y)$ and $f_H(., x, y)$) and introduce the rates $\alpha_S(., x, y)$ and $\alpha_H(., x, y)$

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

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

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

plus aging (speed 1 for each predator),

plus individual births and deaths.

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

First order approximation

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

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

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

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

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].
See [Kang and Kurtz 2013] for chemical reactions in finite dimension), for the fast scale of interactions, here in infinite dimension (age structure).

Consider the occupation measure

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

and check that its limiting point is given at time t by a 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.

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Quantifying fluctuations from renewal theorem

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

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

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

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

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

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

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

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

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  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)
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