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A method for the derivation of the functional and numerical responses in predator-prey models.

Joint work with Stefan Geritz, Mats Gyllenberg, Gaël Raoul.

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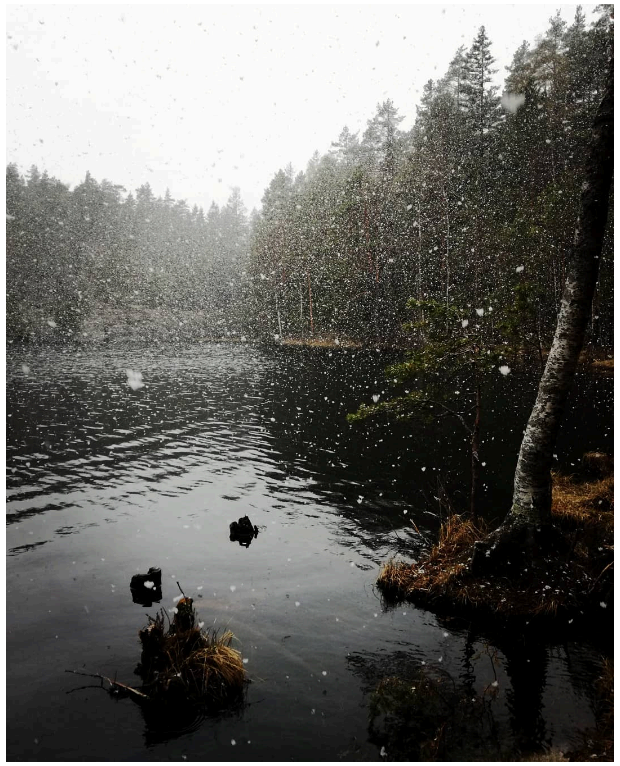

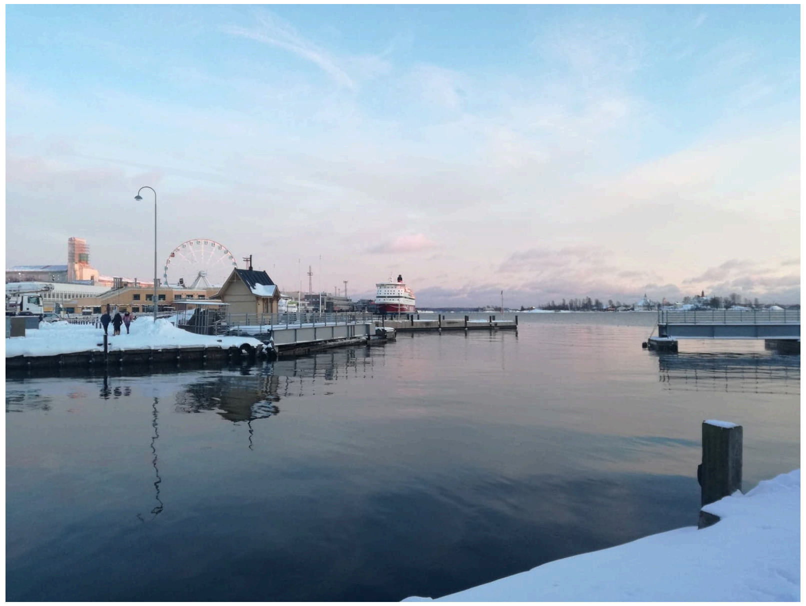

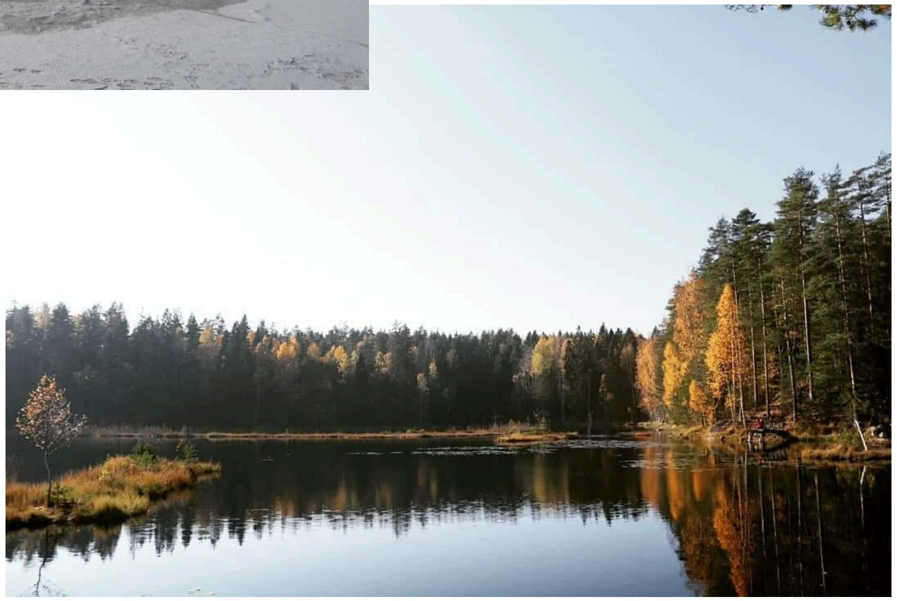

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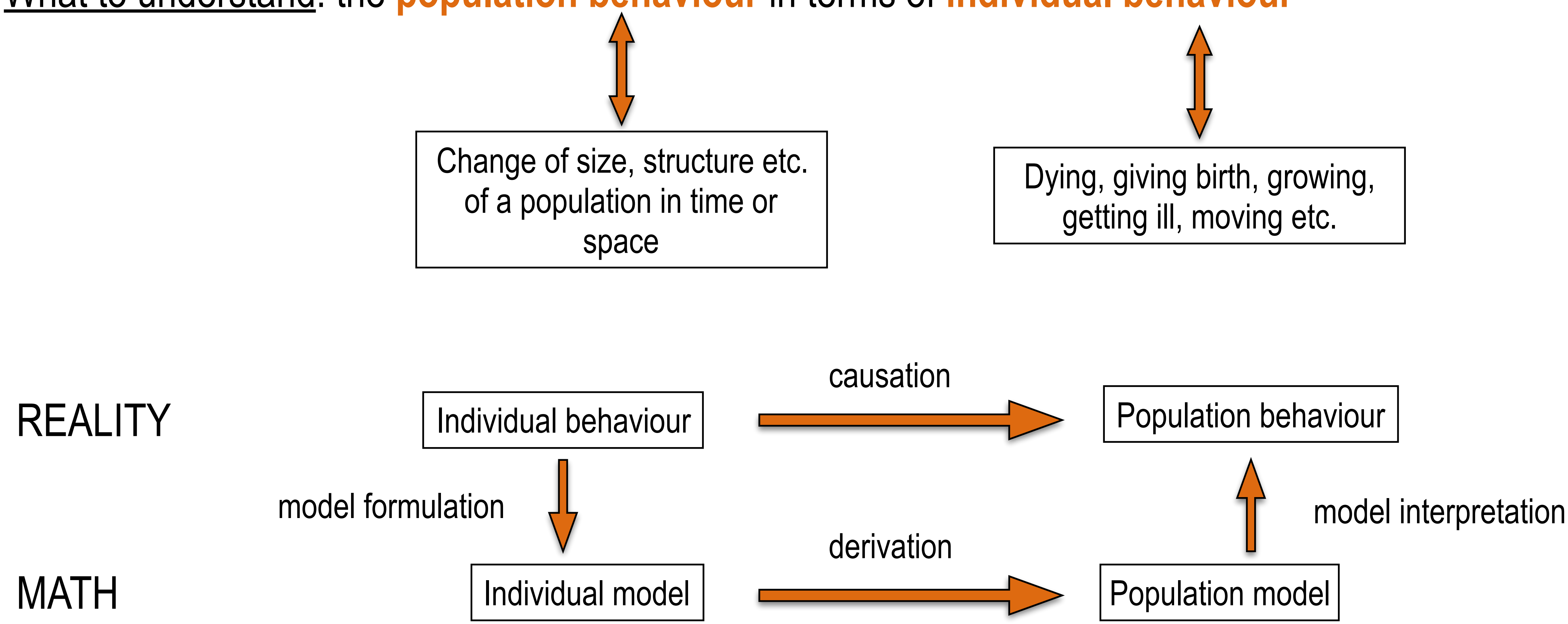
A mathematical model is a mathematical structure with an interpretation

Purpose of a model: predict & understand

What to understand: the **population behaviour** in terms of **individual behaviour**



Modelling the individual behaviour

- State of an individual (i-state) (structured population)
- Behaviour of an individual (as change of the i-state)
- interacting particles, chemical reactions

spontaneous / mono-molecular reaction $\boxed{\text{ALIVE}} \xrightarrow{\mu} \boxed{\text{DEAD}}$

bi-molecular reaction $\boxed{\text{ALIVE}} + \boxed{\text{ALIVE}} \xrightarrow{\alpha} \boxed{\text{ALIVE}} + \boxed{\text{DEAD}}$

μ : probability per unit time that the reaction occurs (1/time)

$\mu h + O(h^2)$: probability of a reaction within h units time

$T \geq 0$: waiting time till a reaction occurs

$$P(t) = \mathbb{P}(T > t)$$

$$P(t+h) = P(t) - (\mu h + O(h^2))P(t)$$

$$\frac{dP(t)}{dt} = -\mu P(t) \quad \Rightarrow P(t) = e^{-\mu t}$$

Modelling the population behaviour

Large population of A and B particles independently undergoing:

mono-molecular reaction $\boxed{\text{A}} \xrightarrow{\mu} \boxed{\text{B}}$

Strong law of large numbers: in an infinitely large population, P(t) can be interpreted as the proportion of the initial A particles that have not reacted yet.

$A(t)$: population density of A

$$P(t) = \frac{A(t)}{A(0)}$$

$$\frac{dA(t)}{dt} = A(0)\frac{dP(t)}{dt} = -A(0)\mu P(t) = -\mu A(t)$$

bi-molecular reaction $\boxed{\text{A}} + \boxed{\text{B}} \xrightarrow{\alpha}$ products

Empirical law of mass action: the probability per unit of time of one reactant undergoing a reaction is proportional to the concentration of the other reactant. $\boxed{\text{A}} \xrightarrow{\alpha B(t)}$ products

$P_A(t)$: probability that A has not undergone a reaction yet

$$\begin{cases} P_A(t+h) = P_A(t) - \alpha B(t) h P_A(t) \\ P_A(0) = 1 \end{cases} \quad \begin{cases} \frac{dP_A(t)}{dt} = -\alpha B(t) P_A(t) \\ P_A(0) = 1 \end{cases}$$

$$P_A(t) = \frac{A(t)}{A(0)}$$ (Strong law of large numbers & repeat the same passages for B)

$$\Rightarrow \begin{cases} \frac{dA(t)}{dt} = -\alpha A(t)B(t) \\ \frac{dB(t)}{dt} = -\alpha A(t)B(t) \end{cases}$$

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A typical predator-prey model consists of a description of how the predator and prey populations develop in the absence of the other species and, most importantly, of a description of the interaction between the two species.
(S.A.H.Geritz, M. Gyllenberg, 2012)

A basic predator-prey model is *(Gause, 1934)*

$$\begin{cases} \frac{dX(t)}{dt} = g(X)X - f(X)Y \\ \frac{dY(t)}{dt} = \gamma f(X)Y - \delta Y \end{cases}$$

$g(X)$: ***prey numerical response**, i.e. **per capita*** **growth rate of the prey if the predator is absent**

$f(X)$: ***functional response***, i.e. **average number of prey caught per predator per unit of time**

γ : conversion constant of prey caught into predators

δ : predator death rate

$\gamma f(X) - \delta$: ***predator numerical response***

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- Birth, death are slow processes.
- The total prey density (X) and total predator density (Y) are constant in the fast time scale and change in the slow time.

- Mechanistic derivation of **Holling type II functional response** (*Metz, Diekmann, 1986*)

<u>i-states:</u>

- $\boxed{X}$ individual prey
- $\boxed{S}$ searching predator
- $\boxed{H}$ handling predator

<u>i- (fast) processes:</u>

$$\boxed{S} \xrightarrow{cX} \boxed{H}$$

$$\boxed{H} \xrightarrow{d} \boxed{S}$$

<u>p-equations (fast dynamics):</u>

$$\begin{cases} \frac{dS}{dt} = -cXS + dH \\ \frac{dH}{dt} = +cXS - dS \end{cases}$$

<u>functional response (slow dynamics):</u>

$$f(X) = \frac{cX\hat{S}}{Y} = \frac{cX}{1 + c\frac{1}{d}X}$$

- Mechanistic derivation of **DeAngelis-Beddington functional response** *(Geritz, Gyllenberg, 2012)*

<u>i-states:</u>

- $\boxed{X_1}$ available prey
- $\boxed{X_2}$ hiding prey
- $\boxed{S}$ searching predator
- $\boxed{H}$ handling predator

<u>i- (fast) processes:</u>

$$\boxed{X_1} \underset{a}{\overset{bY}{\rightleftarrows}} \boxed{X_2}$$

$$\boxed{S} \underset{d}{\overset{cX_1}{\rightleftarrows}} \boxed{H}$$

<u>functional response (slow dynamics):</u>

$$f(X,Y) = \frac{c\hat{X}_1\hat{S}}{Y} = \frac{cX}{1 + c\frac{1}{d} + b\frac{1}{a}Y}$$

By considering a certain number of predator and prey interacting states, we are able to give a more general formulation of the functional response, including the types which have already been studied, and to derive the corresponding numerical response.

Denote with

$$x = (x_i)_{i=1}^{m} \qquad y = (y_i)_{i=1}^{n}$$

the different states of the prey and the predator, such that x_i and y_i denote the density of the prey and the predator in the i-state.

The fast time behaviour is modelled by

$$\begin{cases} \frac{dx_k}{dt}(t) = \sum_{i=1}^{n} A_{k,i} x_i(t) + \sum_{i=1}^{n} \left(\sum_{j=1}^{n} B_{i,j}^{k} y_j(t) \right) x_i(t), & k = 1, ..., m \\ \frac{dy_k}{dt}(t) = \sum_{i=1}^{n} \left(\sum_{j=1}^{n} C_{i,j}^{k} x_j(t) \right) y_i(t) + \sum_{i=1}^{n} D_{k,i} y_i(t), & k = 1, ..., n \end{cases}$$

A_{kj}: rate at which the prey move from state j to state k, $k, j = 1, ..., m$

B_{ij}^{k}: rate at which the prey move from state i to state k, by interacting with the predator state j, $i, k = 1, ..., m, j = 1, ..., n$

D_{ki}: rate at which the predators move from state i to state k, $i, k = 1, ..., n$

C_{ij}^{k}: rate at which the predators move from state i to state k, by interacting with the prey state j, $i, k = 1, ..., n, j = 1, ..., m$

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Fast time dynamics:

$$\begin{cases} \frac{dx_k}{dt}(t) = \sum_{i=1}^{n} A_{k,i} x_i(t) + \sum_{i=1}^{n} \left(\sum_{j=1}^{n} B_{i,j}^{k} y_j(t) \right) x_i(t), & k = 1, \ldots, m \\ \frac{dy_k}{dt}(t) = \sum_{i=1}^{n} \left(\sum_{j=1}^{n} C_{i,j}^{k} x_j(t) \right) y_i(t) + \sum_{i=1}^{n} D_{k,i} y_i(t), & k = 1, \ldots, n \end{cases}$$

Consistency conditions:

$$-A_{kk} = \sum_{i=1, i \neq k}^{m} A_{ik}, \text{ for all } k \in [1, m]$$

$$-D_{kk} = \sum_{i=1, i \neq k}^{n} D_{ik}, \text{ for all } k \in [1, n]$$

$$-B_{ij}^{(i)} = \sum_{k=1, i \neq k}^{m} B_{ij}^{(k)}, \text{ for all } i \in [1, n],\ j \in [1, m]$$

$$-C_{ij}^{(i)} = \sum_{k=1}^{n} C_{ij}^{(k)}, \text{ for all } i \in [1, n],\ j \in [1, m]$$

Conservation law:

$$\sum_{i=1}^{m} x_i = X \ (constant)$$

$$\sum_{i=1}^{n} y_i = Y \ (constant)$$

Matrix form:

$$\begin{cases} \dot{x} = (A + B(y))x \\ \dot{y} = (C(x) + D)y \end{cases}$$

Slow time dynamics:

$$\begin{cases} \frac{dX}{dt} = g(X,Y)X - f(X,Y)Y \\ \frac{dY}{dt} = \gamma(X,Y) f(X,Y) Y - \delta(X,Y) Y \end{cases}$$

Functional response:

$$f(X,Y) = \frac{\sum_{i=1}^{n} \sum_{j=1}^{m} b_{ij} \hat{x}_j \hat{y}_i}{Y}$$

Prey numerical response:

$$g(X,Y) = \frac{\sum_i \lambda_i \hat{x}_i}{X} - \frac{\sum_i \mu_i \hat{x}_i}{X}$$

Predator numerical response:

$$\gamma(X,Y) f(X,Y) - \delta(X,Y) = \frac{\sum_i \sum_j \gamma_{ij} b_{ij} \hat{x}_i \hat{y}_j}{Y} - \frac{\sum_i \delta_i \hat{y}_i}{Y}$$

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Individual level reactions and population equations

$\boxed{S_1} \xrightarrow{c_1 X} \boxed{H_1}$ *the satiated predator enters the handling state*

$\boxed{S_2} \xrightarrow{c_2 X} \boxed{H_2}$ *the starving predator enters the handling state*

$\boxed{H_1} \xrightarrow{d_1} \boxed{S_1}$ *from the handling to the satiated state*

$\boxed{H_2} \xrightarrow{d_1} \boxed{S_1}$ *from the handling to the satiated state*

$\boxed{S_1} \xrightarrow{d_2} \boxed{S_2}$ *from the satiated state to the starving state*

$$\begin{cases} \frac{dS_1}{dt} = -c_1 X S_1 + d_2 S_2 \\ \frac{dS_2}{dt} = -c_2 X S_2 + d_1 (H_1 + H_2) - d_2 H_2 \\ \frac{dH_1}{dt} = c_1 X S_1 - d_1 H_1 \\ \frac{dH_2}{dt} = c_2 X S_2 - d_1 H_2 \end{cases}$$

Functional response

$$f(X) = \frac{c_1 X \hat{S}_1 + c_2 X \hat{S}_2}{Y} = \frac{c_1 X (d_2 + c_2 X)}{d_2 \left(1 + c_1 \frac{1}{d_1}\right) + c_1 X \left(1 + c_2 \frac{1}{d_1} X\right)}$$

$$f(X) = \frac{aX + bX^2}{1 + cX + dX^2}, \quad a = c_1, \quad b = b = c_1 c_2 \frac{1}{d_2}, \quad c = c_1 \left(\frac{1}{d_1} + \frac{1}{d_2}\right), \quad d = \frac{c_1 c_2}{d_1 d_2}$$

Predator numerical response

$$\frac{\Gamma_1 X \hat{H}_1 + \Gamma_2 X \hat{H}_2}{Y} = \frac{c_1 \frac{1}{d_1} X^2 \left(\Gamma_1 d_2 + \Gamma_2 \left(c_2 X + d_2 - d_2 \frac{1}{d_1}\right)\right)}{d_2 \left(1 + c_1 \frac{1}{d_1}\right) + c_1 X \left(1 + c_2 \frac{1}{d_1} X\right)} = \gamma(X) f(X)$$

$$\delta(X) = \frac{\delta_1 \hat{S}_1 + \delta_2 \hat{S}_2}{Y} = \frac{\delta_1 d_2 + \delta_2 c_1 X}{d_2 \left(1 + c_1 \frac{1}{d_1}\right) + c_1 X \left(1 + c_2 \frac{1}{d_1} X\right)}$$

Different reproduction rates:

$$\Gamma_1 > \Gamma_2$$

Different death rates:

$$\delta_2 > \delta_1$$

Application: sort of anti-DeAngelis-Beddington f.r. and corresponding numerical response

Individual level reactions and population equations

$\boxed{E} \xrightarrow{a} \boxed{P}$ *the exposed prey finds a refuge*

$\boxed{P} \xrightarrow{bS} \boxed{E}$ *the protected prey leaves the refuge*

$\boxed{S} \xrightarrow{cE} \boxed{H}$ *the searching predator enters the handling state*

$\boxed{H} \xrightarrow{d} \boxed{S}$ *the handling predator quits handling*

$$\begin{cases} \frac{dE}{dt}(t) = bSP - aE \\ \frac{dP}{dt}(t) = -bSP + aE \\ \frac{dS}{dt}(t) = -cES + dH \\ \frac{dH}{dt}(t) = +cES - dH \end{cases}$$

Functional response

$$f(X,Y) = \frac{c\hat{E}\hat{S}}{Y} = \frac{cq}{2(q+X)Y}\left(pq + qY + 2XY - \sqrt{\Delta}\right), \quad p = \frac{a}{b}, \quad q = \frac{d}{c}, \quad \Delta = q\left(p^2 q + 2p(q+2X)Y + qY^2\right)$$

$$p \to 0, \quad f(X,Y) = \frac{cX}{1+\frac{c}{d}X} \qquad q \to \infty, \quad f(X,Y) = \frac{cXY}{p+Y}$$

Predator numerical response

$$\frac{\hat{H}(X,Y)}{Y} = \frac{f(X,Y)}{d}$$

Predator *per capita* birth rate

$$\delta_1 \frac{\hat{S}(X,Y)}{Y} + \delta_2 \frac{\hat{H}(X,Y)}{Y} = \delta_1\left(1 - \frac{f(X,Y)}{d}\right) + \delta_2 \frac{f(X,Y)}{d}$$

Different death rates:

$$\delta_2 > \delta_1$$

Prey numerical response

$$\frac{\hat{P}(X,Y)}{X} = 1 - \frac{df(X,Y)}{cX(d - f(X,Y))}.$$

Prey *per capita* birth rate

$$\mu_1 \frac{\hat{E}(X,Y)}{X} + \mu_2 \frac{\hat{P}(X,Y)}{X} = \mu_1 \frac{df(X,Y)}{cX(d - f(X,Y))} + \mu_2\left(1 - \frac{df(X,Y)}{cX(d - f(X,Y)}\right).$$

Different death rates:

$$\mu_1 \neq \mu_2$$

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Existence and uniqueness of the fast dynamics equilibrium

Linear case:

$$\begin{cases} \dot{x} = Ax \\ \dot{y} = Dy \end{cases}$$

The matrices A and D correspond to the transition rate matrices of a continuous time Markov chain, that is irreducible and aperiodic.

There exists a unique stationary distribution.

The convergence to the limit distribution is exponentially fast.

A similar argument is used in the *triangular case*, when the transitions of one of the two species are not affected by the other population densities.

Non-linear case:

$$\begin{cases} \dot{x} = (A + B(y))x \\ \dot{y} = (C(x) + D)y \end{cases}$$

Proposition: Under the following conditions:

- *A, B s.t. the linear system has a unique stable equilibrium*
- *B, C irreducible matrices for every y,x>0*
- *A,B,C,D transition matrices*
- *the conservation laws on total populations hold*

the system has at least one equilibrium.

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Existence and uniqueness of the fast dynamics equilibrium

$\boxed{E} \xrightarrow{bS} \boxed{P}$ *the exposed prey finds a refuge*

$\boxed{P} \xrightarrow{a} \boxed{E}$ *the protected prey leaves the refuge*

$\boxed{S} \xrightarrow{cE} \boxed{H}$ *the searching predator enter the handling state*

$\boxed{H} \xrightarrow{d} \boxed{S}$ *the handling predator quits handling*

$b \sim$ number of refuges in the environment

Two cases:

- if b is small: convergence of the fast dynamics to a unique steady state
- if b is large, no general result : no uniqueness if some conditions are relaxed (negativity of the diagonal coefficients of A, D)

Conclusions

- I have introduced a method for the derivation of the functional and numerical response, in contrast with the phenomenological approach which focuses on the population behaviour.

- The bottom-up approach, from the individual level reactions to the population equations, allows the interpretation of all the parameters involved in the population level equations.

- From the literature examples, we have derived a system of prey-predator states' interactions which gives a more general formulation for the functional response and allows also the mechanistic derivation of the numerical responses, if we suppose different birth and death rates for each state.

- An issue arises: the uniqueness of the fast dynamics steady state beyond the perturbative regime.

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Thanks for your attention!

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