From the distributions of times of interactions to preys and predators dynamical systems

Vincent Bansaye, Bertrand Cloez

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Abstract

We consider a stochastic individual based model where each predator searches and then manipulates its prey or rests during random times. The time distributions may be non-exponential and density dependent. An age structure allows to describe these interactions and get a Markovian setting. The process is characterized by a measure-valued stochastic differential equation. We prove averaging results in this infinite dimensional setting and get the convergence of the slow-fast macroscopic prey predator process to a two dimensional dynamical system. We recover classical functional responses. We also get new forms arising in particular when births and deaths of predators are affected by the lack of food.

Contents

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1   Introduction

Functional responses are widely used to quantify interactions between species in ecology. The way functional responses arise at the macroscopic level and describe population dynamics or evolution is a fundamental issue for species conservation or statistical inference of parameters. Indeed, their form influences the stability properties of dynamics, their long time behavior or speed of convergence. The link between individual behavior and macroscopic dynamics has attracted lots of attention for chemical reactions and population dynamics from the works of Michaelis and Menten.

Macroscopic derivations from individual based model rely in general on a large population approximation of finite dimensional Markov processes describing the number of individuals of each species, possibly structured in status (searching, handling...), space or size. In this setting, Kurtz and Popovic [KKP14] obtain the classical Michaelis Menten and Holling functional responses [Has13, AG12] in limiting dynamical systems and fluctuations of processes around these limits. In our context of preys-predators interactions, let us mention [DS13] which starts from a stochastic individual based model. They derive a finite dimensional Markov chain and convergence to ODEs involving the classical functional responses. In [CKBG14], a simple decision tree based on game-theoretical approach response is developed. Similarly, random walks and Poisson type process are used in [AKF11] to describe functional responses. The reduced model counting only the total number of preys and the total number of predators, without distinguishing their status, is also classically derived directly from the macroscopic ODEs [JKT02, BDBS96, HDB97]. Again, it uses a slow-fast scaling and the associated quasi-steady-state approximation. These Markov settings allow for justification of macroscopic equations in a context of absence of memory of interactions. Indeed, the time for associated interactions are then exponentially distributed, potentially up to the addition of the relevant successive state to describe the interaction. For other kind of justification of the macroscopic deterministic models with classical functional responses, we refer to [JC94, DMP$^+$17, BGB$^+$21]. Let us also mention [AG12, BAH$^+$22, DH20] for various stimulating applications.

Random times involved in ecological or biological interactions are in general non-exponentially distributed, see [DKPvG15, BBC18] and references therein. Indeed, handling or manipulation times may have small standard deviations compared to the mean, while exponential distribution forces the value of variance once the mean is fixed. Besides, foraging suggests that the probability of finding a prey eventually increases with searching time for a given density of preys. Finally, as far as we see, these random times seem to be distributed with one mode. The aim of this work is thus to consider general distribution for the times describing interactions. We extend approximation results relying on absence of memory and obtain a reduced model. We also obtain new features due to the fact that mortality depends on prey consumption and times are not

exponentially distributed. This paper can be seen as a continuation of [BBC18] and propose a mathematical framework for the derivation of macroscopic dynamical systems, when the interactions are modeled by renewal processes. Each predator successively searches during a random time and then manipulates during another random time, which may include rest or other interactions. We assume that these time distributions admit a density with respect to Lebesgue measure and are dependent of the prey density. Extensions of the current approach to more than two status for predators would be straightforward. We also believe that several type of preys could be considered with a similar approach.

We consider an age structure which enables us to exploit a Markov framework for the analysis. This Markov setting will be both useful for the construction of the process and the study of scaling limits, in particular thanks to the generator and martingales associated with. It consists in a classical extension of the state space of non-Markovian dynamics. In this vein, we mention in particular the epidemiological models, where age may be the biological age or infection age, or chemical reactions, where time of reaction may be non exponential. For this latter, a recent related and stimulating work [KKKR20] propose averaging results. But the interpretation of the age is different and not density dependent. Furthermore, as far as we have seen, rigorous proofs are not provided. In particular [KKKR20] does not deal with hypothesis required on time distribution to make convergence of stochastic models hold.

Let us first describe informally the model. We write $n_1 \in \mathbb{N}$ the number of preys and $n_2 \in \mathbb{N}$ the number of predators. Each predator searches (independently) preys during a random time distributed as a random variable $T_S(n_1)$. Typically the more n_1 is large, the smaller $T_S(n_1)$ should be. At the end of searching times, one prey is caught and the population of preys goes from n_1 to $n_1 - 1$. The predator which has caught a prey changes its status and now manipulates during a time distributed as $T_M(n_1 - 1)$. Several predators follow simultaneously and independently this dynamics, but they live with a common number of preys and impact each other through this common resource. Besides, each predator gives birth and dies with respective individual rates $\gamma_r(a)$ and $\beta_r(a)$, which depends on their status $r \in \{S, M\}$ and the time a from which they are in this status. Typically, the fact that the predator does not find a prey make its death rate $\beta_S(a)$ increase with a. Preys also give birth and die, with fixed rates γ and β.

We assume that the size of the populations of preys is of order of magnitude K_1 and the size of the populations of predators is of order of magnitude K_2 and that $K_1 \gg K_2$. That means that preys are much more numerous than predators. A slow-fast dynamic is considered : the time scale of prey-predator interactions is short compared to the time scale of birth and death of predators and preys. It means that each predator eats many preys during its life and, if a prey is not eaten by a predator then its life length is comparable to that of predators, up to some factor. After scaling, we show, that the couple of stochastic processes describing the quantities of preys and predators converge in law in $\mathbb{D}([0, \infty), \mathbb{R}_+^2)$ as K_1, K_2 tend to infinity, to the unique solution (x, y) of an ordinary differential equation:

$$\begin{cases} x'(t) & = & (\gamma - \beta)x(t) - y(t)\phi(x(t)) \\ y'(t) & = & y(t)\psi(x(t)), \end{cases}$$

where x is the quantity of preys and y the quantity of predators and ϕ is the death rate

of preys induced by predation and given by

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

and ψ is the growth rate of predators including the gain from prey's consumption and defined by

$$\psi(x) = \frac{\mathbb{E}\left[\int_0^{T_S(x)}(\gamma_S(a) - \beta_S(a))da + \int_0^{T_M(x)}(\gamma_M(a) - \beta_M(a))da\right]}{\mathbb{E}[T_S(x) + T_M(x)]}.$$ (2)

This limit theorem will be illustrated both by classical and new functional responses in Section 3. We observe that the response ϕ of preys due to predatory is only sensitive to mean time of interactions. It thus extends the exponential case to more general distribution. At this macroscopic scale, for the population of preys, the distribution of times involved in interactions plays a role only through its mean. In contrast, the growth rate ψ of the population of predators is in general sensitive to the other characteristics of the distribution.

The fact that the time of interactions is both density dependent and non-exponentially distributed leads us to extend the state space and consider rates of change of status which are depend on the age in the current status and the number of preys. We then exploit the generator and martingale problem and get also the age distribution of predators. The problem arising is then an averaging in infinite dimension. The strategy of proof follows the techniques developed in [KKP14] in finite dimension using the occupation measure. The averaging phenomenon in finite dimension is classical [KKP14, BKPR06, Cos16, MT12]. In infinite dimension, much less work has been done up to our knowledge. Let us mention [MT12] which considers averaging with an age structure and has also inspired this work. Two main differences appear in our context : the age structure is due to interactions and the rates involved are not bounded, since tail distribution of times may for instance decrease faster than exponentially. In this paper, at the macroscopic scale the infinite setting reduces to a finite one describing the number of preys and predators.

We consider a punctual measure whose atoms give the status and the age of predators, which is the length of time since they have been in this status. Other relevant ages could be added, in particular the time from the birth which would impact natality or mortality. However, it seems superfluous at our stage. In our slow-fast dynamics, the numbers of predators in each status are instantaneously at equilibrium. This enables to reduce the infinite-dimensional model to a two-dimensional system of equations. Following [Kur92, KKP14], the occupation measure Γ^K, given by $\Gamma^K([0,t]) = \int_0^t \delta_{Y_s^K} ds$ deals with the fast time component Y^K, here the predations. More precisely, for a set A, $\Gamma^K([0,t] \times A)$ represents the time that Y^K spends in A. In our setting, Y^K is the collection of ages and status and is thus defined as a punctual measure. Instead of considering a measure whose atoms are punctual measures, we consider the mean measure $\Gamma^K([0,t]) = \int_0^t Y_s^K ds$, which is enough for our purpose. Consequently, our measure Γ^K will not degenerate to some measure of the form $\int_0^t \delta_{f(X_s)} ds$, for some function f, but tends to some specific distribution.

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The paper is structured as follows. In Section 2, we present the model and main results in more details. In Section 3, we provide examples and simulations and illustrate the main results with different functional responses, classical or new. Section 4 is devoted to rigorous construction and description of the objects and the proofs. It relies on stochastic differential equations for punctual point processes and associated martingales. Finally, the last section is a short discussion about motivations, extensions and perspectives.

Notation. We write $a_\infty \in (0, +\infty]$ the maximal interaction age and

$$\mathcal{X} = \{S, M\} \times [0, a_\infty),$$

the state space of predators endowed with the product σ-algebra.

We denote by $\mathfrak{M}(\mathcal{S})$ the set of finite measures on any topological space $\mathcal{S}$ endowed with its Borel algebra. We endow $\mathfrak{M}(\mathcal{S})$ with the narrow (or weak) topology: that is μ_n tends to μ if and only if for every continuous and bounded function f on $\mathcal{S}$,

$$\lim_{n\to\infty} \int_{\mathcal{S}} f d\mu_n = \int_{\mathcal{S}} f d\mu.$$

For $r \in \{S, M\}$, we write $\bar{r}$ the complementary status of r, *i.e.* the unique element of $\{S, M\} \setminus \{r\}$.

We denote by $\mathcal{C}^{1,b}(\mathcal{X})$ (resp. $C^{1,b}(\mathcal{U} \times \mathcal{X})$ and $\mathcal{C}^{1,b}([0, a_\infty))$) the space of measurable and bounded functions from $\{S, M\} \times [0, a_\infty)$ (resp. $\mathcal{U} \times \{S, M\} \times [0, a_\infty)$ and $[0, a_\infty)$) to $\mathbb{R}$ such that f is continuously differentiable with respect to its second (resp. third, resp. first) variable, with bounded derivative.

Finally, $\mathbb{D}([0, T], \mathbb{R}_+)$ stands for the Skorokhod space for càdlàg functions, endowed with its usual topology; see for instance [Bil13].

2 Model and main results

In this section, we introduce the assumptions and give an informal presentation of our model. We also present our main result and detail some examples. A more rigorous construction, some mathematical complements and the proofs are postponed in Section 4.

First, for convenience and sake of realism, we assume in the whole paper that birth and deaths rate of predators are measurable and bounded (with respect to their age):

$$\bar{\gamma} := \sup_{(r,a) \in \{S,M\} \times \mathbb{R}_+} (\gamma_r(a) + \beta_r(a)) < \infty.$$

2.1 Interaction times

The random variables describing the interaction are denoted by $T_r(x)$ for a predator which has been in status $r \in \{S, M\}$ for a time $a \in \mathbb{R}_+$ when there is x preys. Working directly with sequences of random variables is not practical. Indeed, the times are dependent one from each other through the density of preys and have to be defined again once a predation occur. A classical way to deal with this matter is the use of an age structure. We thus write $\alpha_r(x, a)$ for the (hazard) rates corresponding to the speed at which event occur when a predator has been in status r during a time a. More precisely, we make the following assumption in the whole paper :

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Assumption 2.1. *There exists $a_\infty \in (0, \infty]$ such that for any $r \in \{S, M\}$,*
i) functions $\alpha_r : [0, \infty) \times [0, a_\infty) \to [0, \infty)$ are continuous.
ii) the random time for interaction $T_r(x)$ satisfies for any $x > 0$,

$$p_r(x, a) = \mathbb{P}(T_r(x) \geq a) = e^{-\int_0^a \alpha_r(x, u)du}$$

and

$$\lim_{a \to a_\infty} p_r(x, a) = 0, \qquad \forall a < a_\infty, \, p_r(x, a) > 0.$$

iii) For any $a \geq 0$, $\alpha_S(0, a) = 0$, i.e. $T_S(0) = \infty$ almost surely.

For $x > 0$, this assumption ensures that $T_r(x)$ has a support $(0, a_\infty)$ which does not depend on the density of preys nor of the status r (and no atom at the final value a_∞). In particular, these random times are positive and finite almost surely (a.s.). When there is no more prey ($x = 0$), the searching time explodes, which corresponds to *iii*). These assumptions could be relaxed at the cost of technicalities. We note that the mean interaction time is

$$\mathbb{E}(T_r(x)) = \int_{[0, a_\infty)} p_r(x, a)da \in (0, \infty].$$

Let us also highlight that under the previous assumption, $T_r(x)$ has non negative density on $[0, a_\infty)$, with respect to the Lebesgue measure, $\mathfrak{f}_r(x, \cdot)$ and

$$\alpha_r(a, x) = \frac{\mathfrak{f}_r(a, x)}{\int_{[a, a_\infty)} \mathfrak{f}_r(u, x)du}.$$

We do not assume that these interactions rates α_r are lower and upper bounded. Indeed, for instance when the time of interaction has a finite support ($a_\infty < \infty$) or a subexponential tail, it is not upper bounded, even for a fixed number of preys. Let us detail some classical distributions that will be captured in our setting:

- Exponential law: $\mathfrak{f}(a, x) = \lambda(x)e^{-\lambda(x)a}$ and $\alpha(a, x) = \lambda(x)$, for some positive bounded function λ. This is the classical exponential setting with memory less property for searching and manipulation.

- Log-normal distribution : $\mathfrak{f}(a, x) = \frac{1}{a\sigma(x)\sqrt{2\pi}} \exp\left(-\frac{(\log(a) - \mu(x))^2}{2\sigma(x)^2}\right)$, for some positive finite function σ.

- Uniform law: $\mathfrak{f}(a, x) = \mathbf{1}_{[0,1]}(a)$ and $\alpha(a, x) = (1 - a)^{-1}\mathbf{1}_{[0,1)}$.

- Pareto law : $\mathfrak{f}(a, x) = k(x)(z(x)^{k(x)}/a)^{k(x)}\mathbf{1}_{a \geq z(x)}$ and $\alpha(a, x) = k(x)/a\mathbf{1}_{a \geq z(x)}$, for some bounded functions $k : \mathbb{N} \to (0, +\infty)$ and $z : \mathbb{N} \to (1, +\infty)$.

2.2 The stochastic individual based model

In this section, we introduce informally our discrete individual based model. A definition using stochastic differential equations will be given in Section 4.

We write $X(t) \in \mathbb{N}$ the number of preys at time t and $\mathcal{P}(t)$ the set of predators at time t. Each predator is characterized by a status $r \in \{S, M\}$ and an age $a \in [0, a_\infty)$. For each predator $i \in \mathcal{P}(t)$, we write

- $r_i(t)$ as predator status at time t, with $r_i(t) = S$ meaning that predator searches and $r_i(t) = M$ that it manipulates.

- $a_i(t)$ its age at time t, i.e. the time that he has already spent in its current status $r_i(t)$.

Between two events, the age of predators grows at speed one :

$$\forall i \in \mathcal{P}(t), \quad a_i'(t) = 1.$$

Each predator that has been searching for a given time a finds a prey with rate $\alpha_S(a, x)$ when the number of preys is x. Then its status becomes M and its age 0:

$$(S, a) \longrightarrow (M, 0) \quad \text{at rate} \quad \alpha_S(a, x),$$

and for the whole population, it causes the death of a prey

$$x \longrightarrow x - 1 \quad \text{at rate} \quad \sum_{i \in \mathcal{P}, \, r_i = S} \alpha_S(a_i, x).$$

Similarly each predator that has been manipulating for a given time a switches to the searching status with rate $\alpha_M(a, x)$ when the number of preys is x:

$$(M, a) \longrightarrow (S, 0) \quad \text{at rate} \quad \alpha_M(a, x).$$

Besides, predators may give birth or die with respective measurable rates γ_r and β_r which depend on their status $r \in \{S, M\}$ and their interaction age a. We assume here that the newborn is in status M with age 0 :

$$(r, a) \longrightarrow (r, a) + (M, 0) \quad \text{at rate} \quad \gamma_r(a).$$

This choice seems natural but may sound somewhat arbitrary. It will not have an impact on the approximation result due to the fast scale. For the death transition, for each predator

$$(r, a) \longrightarrow \varnothing \quad \text{at rate} \quad \beta_r(a).$$

In the simplest case, $\gamma_r(a)$ and $\beta_r(a)$ depend neither on a nor on r. However, if a predator occupies his status for too long, in particular if it does not find food for too long, this affects his mortality or reproductive capacity. Besides hunting a prey and handling one do not require the same energy. Staying for a long time in an activity requiring energy without having any resources, regardless of its biological age, can have serious consequences on the metabolism of the individual.

Finally, preys give birth and die with constant individual rates denoted by γ and β:

$$x \longrightarrow x + 1 \quad \text{at rate} \quad \gamma; \quad x \longrightarrow x - 1, \quad \text{at rate} \quad \beta.$$

All these events, with the associated rates, are summarized in Figure 1. The population of predator is represented by a punctual measure $Y(t) = \sum_{i \in \mathcal{P}(t)} \delta_{(i, r_i(t), a_i(t))}$; see [BM15] for details on modeling through Poisson point measure. We can define the dynamics more rigorously with the help of Poisson point measure. We then prove that under Assumption 2.1, our model is well defined for any time, as soon as initially the age distribution is not chosen arbitrarily close to the bound a_∞; see forthcoming Proposition 4.1 for details.

$$(X, Y - \delta_{(i,M,a_i)} + \delta_{(i,S,0)}) \qquad (X, Y + \delta_{(\bullet,M,0)})$$

$$\forall i \in \mathcal{P}, \mathbf{1}_{r_i=M}\alpha_M(a_i, X) \Big\uparrow \begin{array}{c}\text{research}\\\text{event}\end{array} \qquad \begin{array}{c}\text{birth}\\\text{(predator)}\end{array} \Big\uparrow \forall i \in \mathcal{P}, \gamma_{r_i}(a_i)$$

$$(X-1, Y) \xleftarrow{\beta X} \begin{array}{c}\text{natural death}\\\text{(prey)}\end{array} \qquad \Large(X, Y) \qquad \begin{array}{c}\xrightarrow{\gamma X}\\\text{natural birth}\\\text{(prey)}\end{array} (X+1, Y)$$

$$\forall i \in \mathcal{P}, \mathbf{1}_{r_i=S}\alpha_S(a_i, X) \Big\downarrow \begin{array}{c}\text{capture}\\\text{event}\end{array} \qquad \begin{array}{c}\text{death}\\\text{(predator)}\end{array} \Big\downarrow \forall i \in \mathcal{P}, \beta_{r_i}(a_i)$$

$$(X-1, Y + \delta_{(i,M,0)} - \delta_{(i,S,a_i)}) \; (X, Y - \delta_{(i,r_i,a_i)})$$
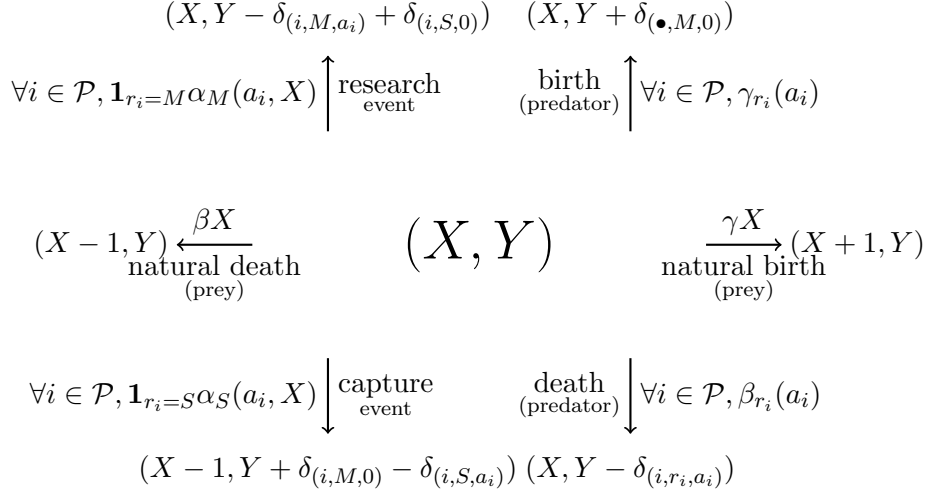
Figure 1: Summary of all possible events. The rate of events are written near the arrow of the event and the Dirac mass notation $+\delta_{(i,r,a)}$ means the addition of the individual i with status r and age a into the population and $-\delta_{(i,r,a)}$ means that it is removed.

2.3 Scaling and averaging

We introduce our scaling parameters $K = (K_1, K_2) \in (0, +\infty)^2$ respectively for the size of the populations of preys and the predators. These sizes are going to infinity. Besides, in our scaling,

$$\lambda_K = \frac{K_1}{K_2}$$

tends to infinity. The rates for interactions are now density-dependent (rather than population-size-dependent) and we set

$$\alpha_r^K(a, x) = \alpha_r(a, x/K_1) \tag{3}$$

for $r \in \{S, M\}$. Birth and death of preys and predators (but the deaths of preys due to predation) occur at a slower time scale and we set

$$\beta_r^K(a) = \lambda_K^{-1}\beta_r(a), \quad \gamma_r^K(a) = \lambda_K^{-1}\gamma_r(a), \qquad \beta^K = \lambda_K^{-1}\beta, \quad \gamma^K = \lambda_K^{-1}\gamma, \tag{4}$$

where β_r and γ_r are still non-negative and measurable and bounded functions and β, γ are non-negative numbers.

To summarize, the population of preys is of order of magntiude K_1, the population of predators is of order K_2, interactions occur at rate of order 1 but "natural" (in the sense that that there are not due to interactions) births and deaths arise at rate of order $1/\lambda_K$. To obtain existence of the process for any time $t \geq 0$, we suppose that Assumption 2.1 holds for $x \in [0, \infty)$. We note that the searching time may explode if the density of preys vanishes and it can vanish if the number of preys explode, see forthcoming section for examples. As in the previous section, the case when the number of preys is zero is a bit special.

Let us now specify the admissible initial conditions.

Assumption 2.2. *The initial number of preys and predators satisfy*

$$X^K(0) = \lfloor K_1 x_0 \rfloor, \qquad Y^K(0, \mathcal{U}, \{S, M\}, [0, a_\infty)) = \lfloor K_2 y_0 \rfloor,$$

for some constants $x_0, y_0 > 0$.
Besides there exists $a_0 \in (0, a_\infty)$ such that $\mathcal{Y}^K(0, \{S, M\}, [a_0, \infty)) = 0$ a.s. for all $K \geq 1$.

The fact that initial population sizes of preys and predators are deterministic will be convenient for proofs but could be easily relaxed. The fact that the initial age is not too close to a_∞ could also be partially relaxed using a domination of the tail distribution and additional computations.

Under Assumptions 2.1 and 2.2, for each $K = (K_1, K_2) \in (0, +\infty)^2$, forthcoming Proposition 4.1 ensures existence and strong uniqueness of the solution $Z^K = (X^K, Y^K)$ of the system of stochastic differential equations (9-10) with parameters $\alpha_r^K, \gamma_r^K, \beta_r^K, \gamma^K, \beta^K$ given above. We consider now the accelerated and scaled process defined, for all $t \geq 0$, by

$$\mathcal{Z}^K(t) = (\Xi^K(t), \mathcal{Y}^K(t, dr, da)) = \left(\frac{1}{K_1} X^K(\lambda_K t), \frac{1}{K_2} Y^K(\lambda_K t, \mathcal{U}, dr, da), \right).$$

For every $T > 0$, $(\mathcal{Z}^K(t), t \in [0, T])$ belongs to the space $\mathbb{D}([0, T], \mathbb{R}_+) \times \mathfrak{M}([0, T] \times \mathcal{X})$.

2.4 Main result

Our approximation result requires the following assumption on the interaction rates. It involves the control of time distributions when the population density of preys belongs to a compact set of $(0, \infty)$. We set for $r \in \{S, M\}$ and $\mathcal{K} > 0$,

$$\underline{\alpha}_r(a, \mathcal{K}) = \inf_{x \in (-1/\mathcal{K}, \mathcal{K})} \alpha_r(a, x), \quad \overline{\alpha}_r(a, \mathcal{K}) = \sup_{x \in (-1/\mathcal{K}, \mathcal{K})} \alpha_r(a, x).$$

Assumption 2.3. *For any $\mathcal{K} > 0$, there exists a continuous function $\mathbf{V} : [0, a_\infty) \to [1, \infty)$ such that $\lim_{a \to a_\infty} \mathbf{V}(a) = +\infty$ and for $r \in \{S, M\}$,*

$$\int_{[0, a_\infty)} \mathbf{V}(a) \left(1 + \overline{\alpha}_r(a, \mathcal{K})\right) e^{-\frac{1}{4} \int_{[0,a)} \underline{\alpha}_r(s, \mathcal{K}) \, ds} da < \infty.$$

We observe that this assumption ensures that $\mathbb{E}(T_r(x))$ is locally bounded on $(0, \infty)$. For $r \in \{S, M\}$, we recall that $p_r(x, a) = \exp(-\int_0^a \alpha_r(x, u) du)$ is the cumulative distribution of the interaction times. We define

$$\phi(x) = \frac{1}{\int_{[0, a_\infty)} (p_S(x, a) + p_M(x, a)) da} \tag{5}$$

and

$$\psi(x) = \phi(x) \int_{[0, a_\infty)} \left((\gamma_S(a) - \beta_S(a)) p_S(x, a) + (\gamma_M(a) - \beta_M(a)) p_M(x, a) \right) da. \tag{6}$$

Let us refer to Equations (1) and (2) in introduction for an expression of ϕ and ψ in terms of the random variables T_r and the demographic rates. Our last assumption concerns uniqueness of the limiting equation and the fact that the limit does not reach a boundary (in finite time). For simplicity, we also assume here existence, but the limiting procedure we prove would ensure existence up to this time when the process get close to the boundary.

Assumption 2.4. *The following system of ordinary differential equations,*

$$\begin{cases} x'(t) &=& (\gamma - \beta)x(t) - y(t)\phi(x(t)), \\ y'(t) &=& y(t)\psi(x(t)), \end{cases} \tag{7}$$

admits a unique global solution $(x, y) \in \mathcal{C}^1(\mathbb{R}_+, (\mathbb{R}_+^*)^2)$ *such that* $(x(0), y(0)) = (x_0, y_0)$.

The preceding assumption holds under classical regularity assumption and in particular, if ϕ and ψ are globally Lipschitz. Locally Lipschitz conditions are also sufficient when the system does not explode in finite time. That is enough for our purpose. Our main result can then be stated as follows.

Theorem 2.5. *Let* $(x_0, y_0) \in (\mathbb{R}_+^*)^2$. *Under Assumptions 2.1, 2.2, 2.3 and 2.4, the two following assertions hold for every* $T > 0$:

i) *the process* $(\Xi^K(t), \mathcal{Y}^K(t, \{S, M\}, [0, a_\infty)))_{t \in [0,T]}$ *converges in law to* $(x(t), y(t))_{t \in [0,T]}$ *in* $\mathbb{D}([0, T], \mathbb{R}_+^2)$,

ii) *for each* $r \in \{S, M\}$, *the measure* $\mathcal{Y}^K(t, \{r\}, da)dt$ *converges in law to the measure*

$$y_r(dt, da) = y(t)p_r(x(t), a)\phi(x(t)) \, dt \, da$$

in the space $\mathfrak{M}([0, T] \times [0, a_\infty))$ *endowed with narrow topology.*

The fact that convergence of $\mathcal{Y}^K(t, \{r\}, da)$ hold on the associated Skorokhod space is left open.

2.5   Behavior of the limiting ODEs

Writing $\lambda = \gamma - \beta$, our main result gives a microscopic interpretation of dynamical systems of the form :

$$\begin{cases} x'(t) &=& \lambda x(t) - y(t)\phi(x(t)), \\ y'(t) &=& y(t)\psi(x(t)). \end{cases}$$

Let us now consider some properties of the long-time behavior of this system, linked to our motivations. A large literature exists on the topic and we refer e.g. to [MB14, Hsu05, HS98] and references therein.

First, non-trivial equilibrium points $(x^\star, y^\star) \in \mathbb{R}_+ \times \mathbb{R}_+^*$ of this system verifies

$$\psi(x^\star) = 0, \qquad y^\star = \frac{(\gamma - \beta)x^\star}{\phi(x^\star)} = \frac{\lambda x^\star}{\phi(x^\star)}.$$

Uniqueness properties of such equilibrium may be delicate. In particular, the fact that $a \mapsto \gamma_S(a) - \beta_S(a)$, $a \mapsto \gamma_M(a) - \beta_M(a)$ and mean times of interaction $x \mapsto \mathbb{E}[T_S(x)], \mathbb{E}[T_M(x)]$ are decreasing do not guarantee uniqueness. The fact that ψ is strictly monotone provides a sufficient condition.

The Jacobian matrix at this equilibrium is equal to

$$J_{(x^\star, y^\star)} = \begin{pmatrix} (\phi(x^\star)/x^\star - \phi'(x^\star))y^\star & -\phi(x^\star) \\ \psi'(x^\star)y^\star & 0 \end{pmatrix}.$$

Consequently,

- if $\psi'(x^*) > 0$ then $J_{(x^\star, y^\star)}$ admits two real eigenvalues whose signs are opposite, consequently (x^*, y^*) is a saddle and unstable point;

- if $\psi'(x^*) < 0$ then either eigenvalues are complex conjugate or they are real with the same sign. In any case, the sign of the real part of these eigenvalues are given by the sign of $\phi(x^\star) - \phi'(x^\star)x^\star$. Consequently, this point is stable when $\phi(x^\star) - \phi'(x^\star)x^\star < 0$, and unstable if $\phi(x^\star) - \phi'(x^\star)x^\star > 0$.

In particular, for the commonly used function $\phi : x \mapsto cx$, for some $c > 0$, (see Section 3 for details), the eigenvalues have opposite signs or are pure imaginary (according to the sign of $\psi'(x^*)$). However, in this particular case, the long time behavior of this dynamical system can be described through a first integral; namely a function that is constant along the solutions of the ODE. More precisely, setting

$$L(x, y) = \lambda \log(y) - cy - \int_1^{\log(x)} \psi(e^u) du,$$

the function $t \mapsto L(x(t), y(t))$ is constant along time. In particular, when the curve $L(x, y) = L(x(0), y(0))$ is a bounded loop then (x, y) should be periodic.

3 Examples and numerical simulation

In this section, we consider some examples of dynamical systems which appear from our approximation procedure. It can be easily seen that they satisfy our assumptions by using $\mathbf{V} : a \mapsto a^\epsilon$ or $\mathbf{V} : a \mapsto (a_\infty - a)^{-(1+\epsilon)}$ in Assumption 2.3, for some $\epsilon > 0$.

Recall that $T_S(x)$ and $T_M(x)$ are the random times for searching and manipulating when the density of preys is x. The death rate of preys induced by predation is

$$\phi(x) = \frac{1}{\mathbb{E}[T_S(x)] + \mathbb{E}[T_M(x)]}.$$

Note that it may be surprising that ϕ depends both on manipulation and searching time although deaths of preys due to predation only occur after a searching time. However, since predators necessarily change their status after catching a prey, the random times between two prey captures are the sum of the time of manipulating and the time of searching. Recalling that $\gamma_r(a)$ (resp. $\beta_r(a)$) is the birth (resp. death) rate of predators which are in status r from time a and writing

$$\lambda_r(a) = \gamma_r(a) - \beta_r(a),$$

the growth rate of predators is

$$\psi(x) = \phi(x)\mathbb{E}\left[\int_0^{T_S(x)} \lambda_S(u) du + \int_0^{T_M(x)} \lambda_M(u) du\right].$$

We will present some forms of these functions from the more classical setting to the more new ones. Up to our knowledge, the setting where ϕ and ψ have a different form is already less common.

3.1 Classical setting and functional responses : memory less interactions

We assume in this section that the growth rate λ_S and λ_M of predators are constant (they do not depend on age). Besides, we suppose that the mean manipulation time is not density dependent : $t_M = \mathbb{E}[T_M(x)]$. Then

$$\phi(x) = \frac{1}{\mathbb{E}[T_S(x)] + t_M}, \quad \psi(x) = \frac{\lambda_S \mathbb{E}[T_S(x)] + \lambda_M t_M}{\mathbb{E}[T_S(x)] + t_M} = \lambda_S + (\lambda_M - \lambda_S)t_M\phi(x(t)).$$

In particular, ϕ and ψ only depend on the law of T_S, T_M through their mean. We recover classical functional responses with usual supplementary assumptions that we detail now. The limiting ODE becomes

$$\begin{cases} x'(t) & = & \lambda x(t) - y(t)\phi(x(t)) \\ y'(t) & = & \psi(x(t))y(t) = \lambda_S y(t) + (\lambda_M - \lambda_S)t_M\phi(x(t))y(t). \end{cases}$$

In this last expression, interaction terms are given by $\phi(x)y$ for preys and predators, which correspond to a mass transfert (given by usual conversion of yield rate).

Let's start by considering the working hypotheses with the least amount of memory. It corresponds to constant birth and death rates and constant rate of change of status (i.e. exponential times for each isolated events). Thus $\gamma_r = \gamma_r(a)$, $\beta_r = \beta_r(a)$ and we we can then introduce the growth rate of predators in each status $r \in \{R, M\}$ as follows:

$$\lambda_r = \gamma_r - \beta_r.$$

For searching times, it can be justified with the hypothesis of rapid mixing of the preys in the medium where predators live. In this section, we further assume that $\lambda, \lambda_M > 0$ and $\lambda_S < 0$ to study the limiting ODE system.

3.1.1 Absence of manipulation and Lotka-Volterra form

When there is no manipulation $t_M = 0$ and $\mathbb{E}(T_S(x)) = 1/(cx)$ with $c > 0$, we obtain the classical Holling type I functional response and Lotka-Volterra form:

$$\phi(x) = c\,x, \qquad \psi(x) = \lambda_S.$$

Assuming the searching time is inversely proportional to the density of preys can be justified when preys are supposed to be catch independently (minimum of exponential variables has an exponential law whose parameter is the sum of the parameters). Note however that the growth rate of predators is fixed and not linear here. Consequently, the solution of the associated ODE leads to extinction of at least one of the two populations.

3.1.2 Manipulation and Holling type II

The case
$$t_M > 0, \qquad \mathbb{E}(T_S(x)) = \frac{1}{cx},$$

where $c > 0$ leads to Holling type II functional response (see [Has13, AG12]) :

$$\phi(x) = \frac{cx}{1 + t_M cx}, \qquad \psi(x) = \lambda_S + (\lambda_M - \lambda_S)t_M\frac{cx}{1 + t_M cx}.$$

Constant $(\lambda_M - \lambda_S)t_0$ is related to the "yield constant" in microbial ecology, as in the chemostat equation for instance. The limiting ODE is also related to the Rosenzweig-MacArthur model. The difference between these two equations lies in the prey growth term which is λx in our case and $x(1-x)$ (logistic growth) in the case of Rosenzweig-MacArthur model. These difference is fundamental for the long time behavior. In particular, in our ODE system, there is a unique equilibrium point which is unstable. The long time behavior consists then to extinction/explosion of the populations.

3.1.3 Rarefaction of preys and Holling type III

If rarefaction of preys makes predators consider other species, one can let $\mathbb{E}(T_S(x))$ be larger than c/x. Taking for instance $\mathbb{E}(T_S(x)) = 1/(cx^2)$ leads to Holling type III functional response (see [Has13, AG12]). This can be found using a modeling with several species, as in [BBC18] for instance. This is not directly captured in our setting (to avoid superfluous notation) but should work without difficulty.

In contrast with the models of the two preceding section, such assumption may lead to a stable dynamical system. Indeed, when $\mathbb{E}(T_S(x)) = 1/(cx^\ell)$, with $\ell > 0$, then the ODE system reads.

$$
\begin{cases}
x' & = & \lambda x - y \dfrac{cx^\ell}{1 + t_M cx^\ell} \\
y' & = & \lambda_S y + (\lambda_M - \lambda_S) t_M \dfrac{cx^\ell}{1 + t_M cx^\ell}.
\end{cases}
$$

In particular, when $\ell > 1$ the functional response is not a not convex. For this dynamical system, there is a unique non-trivial equilibrium which is given by

$$
x^* = \left(\frac{-\lambda_S}{c\lambda_M t_M} \right)^{1/\ell}, \quad y^* = \frac{\lambda}{\lambda_M} \left(-\frac{\lambda_S}{\lambda_M t_M c} \right)^{\frac{1-\ell}{\ell}} (\lambda_M - \lambda_S).
$$

Moreover, this equilibrium is exponentially stable when

$$
\ell - 1 > -\frac{\lambda_S}{\lambda_M}.
$$

We refer to Figure 2 and Figure 3 for a numerical simulation.

3.2 A first generalization : non-exponential time of interaction

We saw in the last subsection that classical functional responses arise easily when searching times are supposed to be exponentially distributed. This can be justified though independence and rapid mixing assumptions. Relaxing these two assumptions leads different forms of functional responses. Keeping independence of prey catching but assuming heavy tailed distribution of capture events can lead for instance to the form

$$
\mathbb{E}[T_S(x)] = x^{-1/\alpha} \Gamma \left(1 + \frac{1}{\alpha} \right). \tag{8}
$$

Indeed, from extreme value theory, the minimum of independent random variables necessary belongs (asymptotically) to the Frechet, Weibull or Gumbel class of laws. Equality (8) is obtained through Frechet distribution $T_S(x)^{-1} \sim \mathcal{F}(\alpha, x^{1/\alpha}, 0)$.
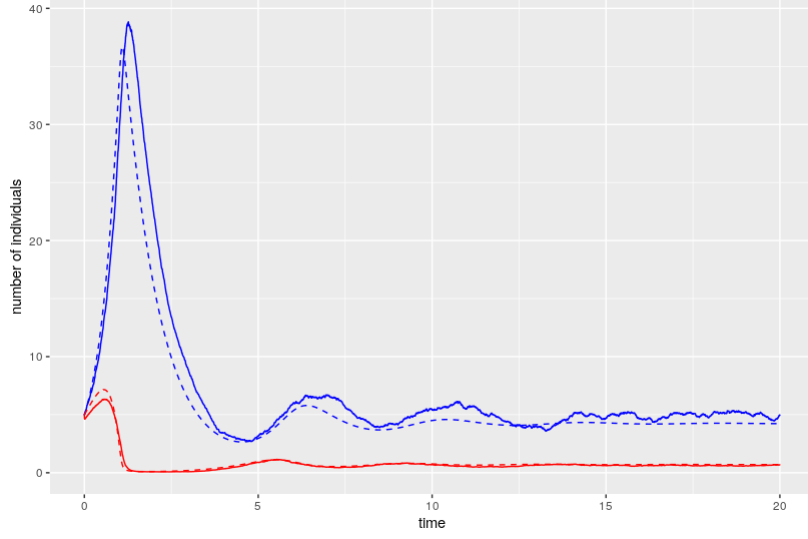
Figure 2: A sample path of the total number of preys and predator $t \mapsto (\Xi(t), \mathcal{Y}(t, \{S, M\}, [0, +\infty))$ and the limiting ODE for the model described in Subsection 3.1.3 with $K_1 = 500$, $K_2 = 50$, $\ell = 2$, $c = 1$, $t_0 = 1$, $\gamma_M = 2$, $\gamma_S = 0$, $\beta_M = 0$ $\beta_S = 1$, $\gamma = 2$, $\beta = 0$. The dashed line represents the ODE system and the solid line represents the path of only one iteration of the individual based model. The blue lines represents the predators and the red line represents the preys.
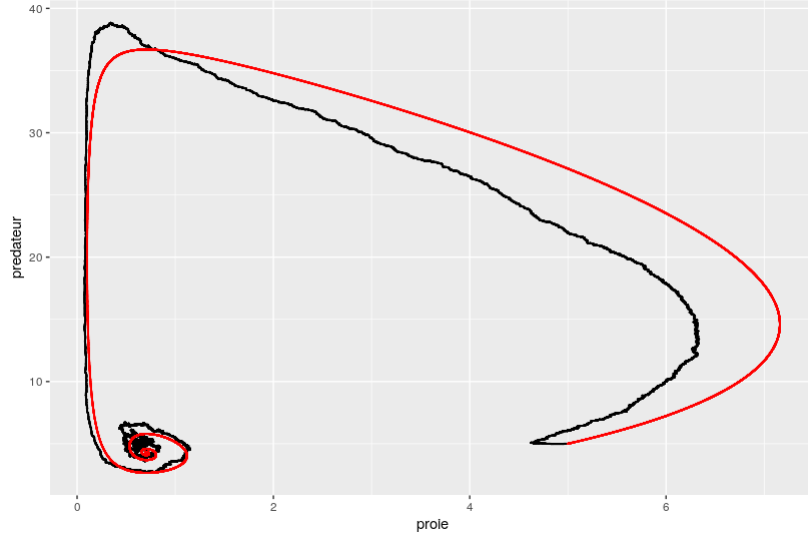

Figure 3: Phase portrait associated to the setting of Figure 2. In red we have the set $\{(x(t), y(t)\}$ and in black the set $\{(\Xi(t), \mathcal{Y}(t, \{S, M\}, [0, +\infty))\}$ for only one sample path of the individual based model.

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Other laws can be genuinely considered. For instance, in [BBC18, Page 11], preys are supposed uniformly distributed in a space of two dimension and predators are supposed to move directly, at a constant speed, towards the nearest prey. With this modeling then the expected time is

$$\mathbb{E}[T_S(x)] = \frac{1}{c\sqrt{x}}.$$

In such case and more generally for models with spatially distributed preys considered in [BBC18], the time for searching is non-exponential. Nevertheless, if we stick to this set of hypotheses, apart from demonstrating a stronger convergence result than [BBC18] (the convergence of a stochastic process), we do not provide additional keys for ecological understanding based on our dynamic modeling.

3.3 A dome-shaped example

To simplify, let us continue to assume that λ_S and λ_M are constant and $\mathbb{E}[T_S(x)] = 1/cx$. However, in contrast with the preceding model, we now do not assume that $x \mapsto \mathbb{E}[T_M(x)]$ is constant. Indeed, in some ecosystems, the number of individuals and/or preys affects the environment (creation of toxins, lack of oxygen, water resources, ...). These effects can reduce the efficiency of the predators and increase their handling time. It then may be natural to assume that $x \mapsto \mathbb{E}[T_M(x)]$ is increasing. For sake of illustration, we choose here $\mathbb{E}[T_M(x)] = dx^p$. With this choice, we have

$$\phi(x) = \frac{cx}{1 + cdx^{p+1}}, \qquad \psi(x) = \lambda_S + (\lambda_M - \lambda_S)\frac{cdx^{p+1}}{1 + cdx^{p+1}}.$$

Figure 4 and Figure 5 illustrate these two functional responses for particular parameters. In particular, we observe that ϕ is a dome-shaped function with maximum in $x = (cdp)^{-1/(p+1)}$ and that ψ has a rather radical form.
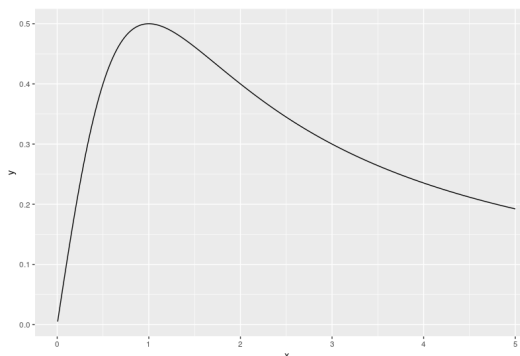

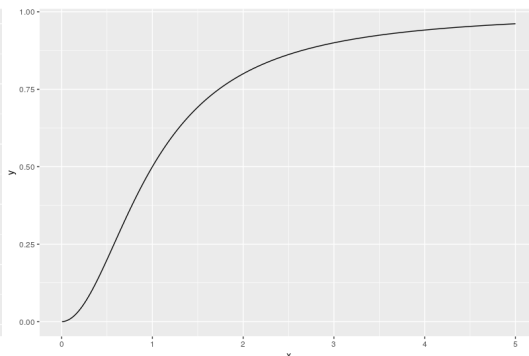Figure 4: Plot of the functional response $\phi : x \mapsto \frac{x}{1+x^2}$

Figure 5: Plot of the functional response $\psi : x \mapsto \frac{x^2}{1+x^2}$

From the results of Section 2.5, we can show for this example that the ODE system has again a trivial behavior (namely extinction and/or explosion of the one of the two populations).

3.4 Influence of the distribution of the time of interaction

Our main result states that, at the first order approximation (i.e. the deterministic limiting ODE without considering random fluctuations), the death rate of preys, induced

by predation, only depends on the interaction time distribution through its mean. Namely the form of ϕ only involves the expectation of the interaction times. In particular, assuming a Markov model, that is exponential law for these times, implies the same functional response ϕ.

Notwithstanding, the growth rate of predators depends on the whole law of the times of interactions. Indeed, the births and deaths of predators depend on the times of searching and manipulations in a non trivial way.

Let's give an explicit example. Assume that for some $A, B, C > 0$, we have for $a \geq 0$,

$$\lambda_S(a) = -A + Be^{-Ca}.$$

This models that the more a predator searches (without finding), the less it reproduces and/or the more easily it dies.

Let us assume that $T_S(x)$ is exponential distributed with mean $1/cx$, we have

$$\mathbb{E}\left[\int_0^{T_S(x)} \lambda_S(u)du\right] = -\frac{A}{cx} + \frac{B}{cx + C}.$$

and, as in the setting of Subsection 3.1, we can recover below two classical forms without directly assuming a conversion of prey into predators.

3.4.1 Case without manipulation

When there is no manipulation, we have

$$\phi(x) = cx, \qquad \psi(x) = \left(-A + B\frac{cx}{cx + C}\right)\lambda_S.$$

In particular, $\psi(x) \to_{x \to 0} -A$ and $\psi(x) \to_{x \to \infty} t_M B$. That is $\phi(x)$ behaves as exactly as in the Lotka-Volterra model in contrast to ψ which evolves as an Holling type II response. This model is relatively close to Lotka-Volterra.

In Figure 6 and Figure 7, we simulate a path of our individual based model with the associated ODE system :

$$\begin{cases} x' &= \lambda 3x - yx \\ y' &= -y(t) + \dfrac{2x^2 y}{1 + x}. \end{cases}$$

Indeed, we used the following parameters:

$$K_1 = 1000, \ K_2 = 50, \ c = 1, \ \gamma_S(a) = 2e^{-a}, \ \beta_S(a) = 1, \ \gamma = 3, \ \beta = 0.$$

Then $A = 2, B = 1$ and $C = 1$. As the Lotka-Volterra system, this new ODE system seems to have a stable orbit.

3.4.2 Case with constant manipulation (another dome-shaped response)

With constant manipulation time t_M and constant growth λ_M, we have

$$\phi(x) = \frac{cx}{1 + t_M cx}$$

and

$$\psi(x) = \frac{1}{1 + t_M cx}\left(-A + B\frac{cx}{cx + C}\right)\lambda_S + \frac{t_M \lambda_M cx}{1 + t_M cx}.$$
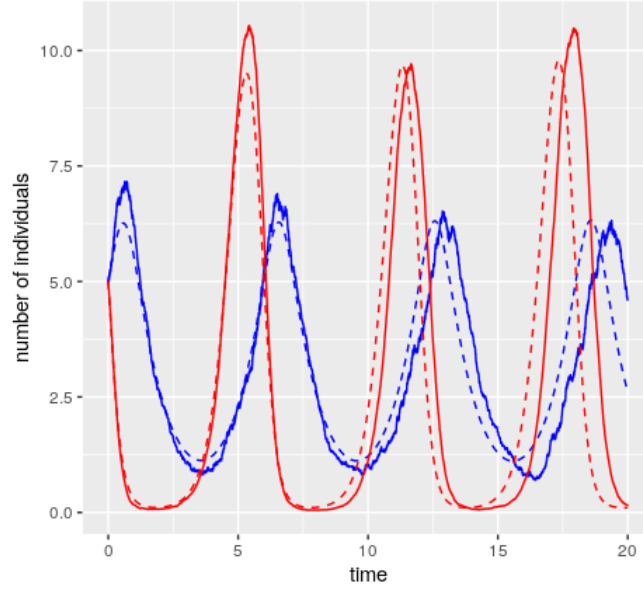
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Figure 6: A sample path of the total number of preys and predator $t \mapsto (\Xi(t), \mathcal{Y}(t, \{S, M\}, [0, +\infty))$ and the limiting ODE for the model described in Subsection 3.4.1. The dashed line represents the ODE system and the solid line represents the path of only one iteration of the individual based model. The blue lines represents the predators and the red line represents the preys.

that is $\psi(x) \to_{x \to 0} A < 0$ and $\psi(x) \to_{x \to \infty} \lambda_M > 0$ Then it behaves as classical Holling type II prey-predator model:

$$\psi(x) = -A + \mu \frac{x}{x + K}.$$

Even if this form is still asymptotically similar to the Holling type II response, it can nevertheless have very different and new forms, as shown in Figure 8. We do not see such form of functional response in the literature and then it seems to be new.

4 Proofs and additional results

4.1 Existence of the process and trajectorial representation

To formalize conveniently our modeling, we label each predator using classical Ulam-Harris-Neveu notation and describe the associated genealogical tree. The set of individuals is then

$$\mathcal{U} = \mathbb{N} \times \cup_{k \geq 0} \{1, 2\}^k.$$

For short, we write $u = u_0 u_1 \ldots u_k \in \mathcal{U}$ and u then corresponds to an individual living in generation $|u| = k$ and whose ancestor in generation i is $u_0 \ldots u_i$ for $0 \leq i \leq k$. At each reproduction event, we assume for simplicity that every predator u only gives birth to one predator and we label the mother by $u1$ and its child by $u2$. The population of predators alive at time t, denoted by $\mathcal{P}(t)$, is a random subset of $\mathcal{U}$.
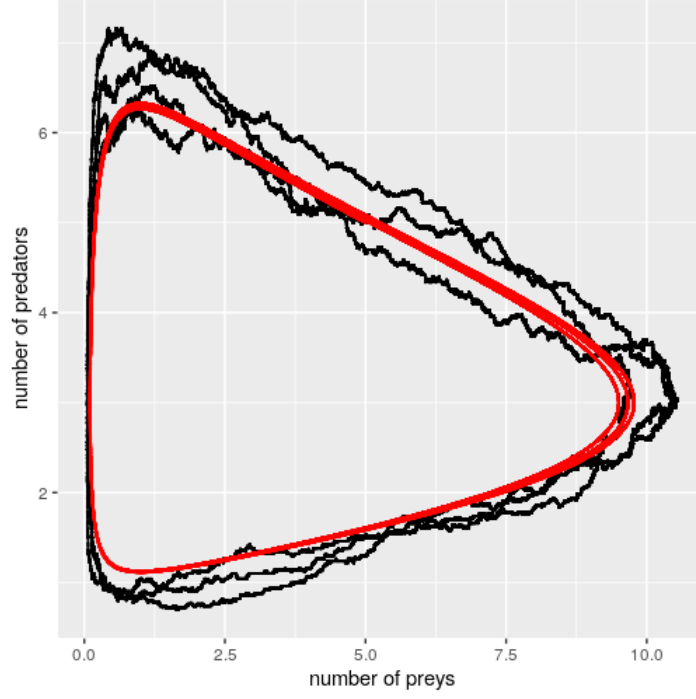
Figure 7: Phase portrait for the model described in Subsection 3.4.1. In red we have the set $\{(x(t), y(t)\}$ and in black the set $\{(\Xi(t), \mathcal{Y}(t, \{S, M\}, [0, +\infty))\}$ for only one sample path of the individual based model.
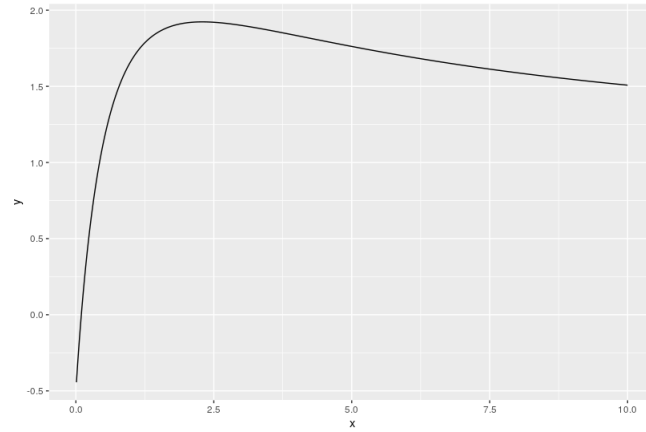

Figure 8: Plot of the functional response $\psi : x \mapsto \frac{x^2 + 10x - 1}{(x+1)(x+2)}$ of Section 3.4.2.

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The state of the population is then given by the process

$$Z = (Z(t))_{t\geq 0} = (X(t), Y(t))_{t\geq 0},$$

where the measure Y describes the predators and is given for all $t \geq 0$ by

$$Y(t) = \sum_{i \in \mathcal{P}(t)} \delta_{(i, r_i(t), a_i(t))}.$$

For any $t \geq 0$, $Y(t) \in \mathfrak{M}(\mathcal{U} \times \mathcal{X})$, where we recall that $\mathcal{X} = \{S, M\} \times [0, a_\infty)$. Besides, for any $U \subset \mathcal{U}$, the projected measure

$$Y(t, U, \{r\}, \cdot) = \sum_{i \in \mathcal{P}(t),\, r_i(t) = r} \delta_{a_i(t)}$$

gives the collection of ages of predators in status r at time t, whose labels belong to U. The total number of predators at time t is then $Y(t, \mathcal{U}, \{S, M\}, \mathbb{R}_+)$.

Following for instance [FM04, Tra06, BT10], we construct and characterize $(Z(t))_{t\geq 0}$ as the unique strong solution of a stochastic differential equation. For every $i \in \mathcal{U}$, we let $\mathcal{N}^i$ be independent Poisson punctual point measures on $\mathbb{R}_+^2$ with intensity the Lebesgue measure. These measures provide the random times when a predator changes its status between searching and manipulating. We introduce also independent Poisson point measures $\mathcal{M}^i$ and $\mathcal{Q}$ on $\mathbb{R}_+^2$ with Lebesgue measure intensity. They are independent of $(\mathcal{N}^i, i \in \mathcal{U})$ and describe births and deaths of preys and predators. We consider then the following equation for the evolution of the number of preys for $t \geq 0$,

$$X(t) = X(0) - \int_0^t \sum_{\substack{i \in \mathcal{P}(s-) \\ r_i(s-)=S}} \int_{\mathbb{R}_+} \mathbf{1}_{\{u \leq \alpha_i(s-)\}} \mathcal{N}^i(ds, du)$$

$$+ \int_0^t \int_{\mathbb{R}_+} \left(\mathbf{1}_{\{u \leq \gamma X(s-)\}} - \mathbf{1}_{\{0 < u - \gamma X(s-) \leq \beta X(s-)\}} \right) \mathcal{Q}(ds, du). \quad (9)$$

Indeed, the number of preys decreases when they are caught by a predator and also varies independently by births and deaths. For every function $f \in \mathcal{C}^{1,b}(\mathcal{U} \times \mathcal{X})$, we consider

$$\langle Y(t), f \rangle = \langle Y(0), f \rangle + \int_0^t \sum_{i \in \mathcal{P}(s-)} \partial_a f(i, r_i(s-), a_i(s-))\, ds$$

$$+ \int_0^t \sum_{i \in \mathcal{P}(s-)} \int_{\mathbb{R}_+} \mathbf{1}_{u \leq \alpha_i(s-)}\, Df(i, s-)\, \mathcal{N}^i(ds, du)$$

$$+ \int_0^t \sum_{i \in \mathcal{P}(s-)} \int_{\mathbb{R}_+} \Big(\mathbf{1}_{u \leq \gamma_i(s-)}\, \Delta f(i, r_i(s-), a_i(s-)))$$

$$- \mathbf{1}_{0 < u - \gamma_i(s-) \leq \beta_i(s-)}\, f(i, r_i(s-), a_i(s-)) \Big) \mathcal{Q}^i(ds, du), \quad (10)$$

where $\partial_a f$ stands for the partial derivative of f with respect to the third variable and

$$Df(i, s) = f(i, \overline{r_i}(s), 0) - f(i, r_i(s), a_i(s)); \quad \Delta f(i, r, a) = f(i1, r, a) + f(i2, M, 0) - f(i, r, a).$$

Recall that $\bar{r}$ is the complementary status of r, *i.e.* the unique element of $\{S, M\} \setminus \{r\}$.

Let us state the existence result and characterize the process using the previous stochastic differential equation.

Proposition 4.1. *Let $Z(0) = (X(0), Y(0))$ with $X(0) \in \mathbb{N}$ and $Y(0) \in \mathfrak{M}(\mathcal{U} \times \mathcal{X})$ a.s. such that $Y(0, \mathcal{U}, \{S, M\}, [a_0, \infty)) = 0$ a.s. for some $a_0 < a_\infty$. Under Assumption 2.1, the system of stochastic differential equations (9-10) admits a unique strong solution $Z = (X, Y)$ in $\mathbb{D}([0, \infty), \mathbb{N} \times \mathfrak{M}(\mathcal{U} \times \mathcal{X}))$ with initial condition $Z(0)$.*

Proof. The construction of the process and its uniqueness can be achieved iteratively, using the successive random times between each event, see for instance [BM15]. The proof is classical and we just give its sketch. The only point to justify is that the successive times where an event (change of status, birth or death) occur do not accumulate. For that purpose, we proceed by a localization procedure and introduce the hitting time $T_K = \inf\{t : X(t) \geq K\}$. Recalling that $T_r(x)$ is a.s. positive for any $x \in \{0, \ldots, K\}$, no accumulation of change of status occurs before T_K a.s. We also recall that birth and death rates of preys and predators are upper bounded. So a.s. the jumps of the process Z do not accumulate before T_K. We need now to justify that T_K tends a.s. to infinity as $K \to \infty$. It is achieved by dominating the process X by a pure linear birth process (Yule process) with birth rate *per capita* γ. The fact that this latter does not explode is well known and can be derived for instance from the finiteness of its first moment. Pathwise uniqueness of the system of stochastic differential equations is also obtained by induction on the successive jumps, which are provided by the common Poisson point measures. The arguments above ensure that existence and uniqueness holds for positive time. Let us finally note that the system (9-10) is closed, since $\mathcal{P}(t)$ and $(i, r_i(t), a_i(t))$ are determined (uniquely) by the measure $Y(t)$, which is itself determined by its projections $\langle Y(t), f \rangle$ for $f \in \mathcal{C}^{1,b}(\mathcal{U} \times \mathcal{X})$. $\qquad\square$

4.2 First estimates and properties

We start by a sharp and useful bound on the first moment of the punctual measures Y evaluated on tests functions which may be non bounded. For convenience, we write

$$\mathcal{Y}(t, \cdot) = Y(t, \mathcal{U}, \cdot) = \sum_{i \in \mathcal{P}(t)} \delta_{(r_i(t), a_i(t))}$$

the projection of the measure $Y(t)$ on $\mathcal{X}$. We also introduce the exit time of the number of preys of $(1/\mathcal{K}, \mathcal{K})$ for $\mathcal{K} > 0$:

$$\tau_\mathcal{K} = \inf\{t \geq 0 : X_t \notin (1/\mathcal{K}, \mathcal{K})\}.$$

We consider the associated bounds on the rate of transitions for $r \in \{S, M\}$,

$$\overline{\alpha}_r(a, \mathcal{K}) = \sup_{x \in (1/\mathcal{K}, \mathcal{K})} \alpha_r(a, x), \quad \underline{\alpha}_r(a, \mathcal{K}) = \inf_{x \in (1/\mathcal{K}, \mathcal{K})} \alpha_r(a, x),$$

which are continuous by continuity of α_r. We also recall that

$$\bar{\gamma} = \sup_{r \in \{S, M\}, \, a \in [0, a_\infty)} \gamma_r(a) < \infty.$$

Lemma 4.2. *Under assumptions of Proposition 4.1, there exists $C > 0$ such that for any continuous and non-negative function $f : [0, a_\infty) \to \mathbb{R}_+$ and $r \in \{S, M\}$ and $\mathcal{K} > 0$,*

$$\mathbb{E}\left[\int_0^{T \wedge \tau_\mathcal{K}} \int_{[0, a_\infty)} f(a) \mathcal{Y}(s, \{r\}, da) ds\right]$$

$$\leq C(1 + T) e^{\bar{\gamma} T} \int_{[0, a_\infty)} f^\star(a) e^{-\frac{\mathbf{1}_{a > t_0}}{4} \int_{[t_0, a)} \underline{\alpha}_r(u, \mathcal{K}) du} da,$$

where $t_0 = \min(1, a_\infty/2)$ and $f^\star(a) = \mathbf{1}_{[0, t_0)}(a) \sup_{[0, t_0)} f + \mathbf{1}_{[t_0, a_\infty)}(a) f(a)$.

Proof. We consider first f continuous, non negative with compact support in $[0, A)$, where $A \in [0, a_\infty)$. The conclusion for general f will follow with a monotone approximation of f by compactly supported functions. Fix $T \geq 0$ and consider an increasing sequence $(a_n)_{0 \leq n \leq n_0}$, where $a_{n+1} = a_n + t_n$ and $(t_n)_{0 \leq n \leq n_0 - 1}$ is a decreasing sequence of positive numbers and $a_{n_0} = A$. For a predator $i \in \mathcal{U}$, a status $r \in \{R, M\}$ and a level $n \in \mathbb{N}$, we set

$$u_n^{i,r} = \mathbb{E}\left[\int_0^{\tau_\mathcal{K} \wedge T} \mathbf{1}_{\{i \in \mathcal{P}(s), \, r_i(s) = r, \, a_i(s) \in [a_n, a_{n+1})\}} ds\right].$$

It is equal to the cumulative time spent by predator i, in status r and between ages a_n and a_{n+1}. Let also

$$N_n^{i,r} = \sum_{s \leq \tau_\mathcal{K} \wedge T} \mathbf{1}_{\{i \in \mathcal{P}(s), \, r_i(s) = r, \, a_i(s) = a_n\}}$$

be the number of times that predator $i \in \mathcal{U}$ reaches age a_n while it is in status r. In other words, writing $b(i)$ the birth time of individual i, for every $j \in \mathbb{N}$, we can define iteratively

$$T_{j+1,n}^{i,r} = \inf\{t > T_{j,n}^{i,r} \mid i \in \mathcal{P}(t), \, r_i(t) = r, \, a_i(t) = a_n\},$$

for $j \geq 0$, with $T_{0,n}^{i,r} = b(i)$. We get

$$N_n^{i,r} = \sum_{j \geq 1} \mathbf{1}_{\{T_{j,n}^{i,r} \leq \tau_\mathcal{K} \wedge T\}}.$$

With this notation and writing $T_j = T_{j,n+1}^{i,r}$ for convenience, we have for $n \leq n_0 - 2$,

$$u_{n+1}^{i,r} \leq \mathbb{E}\left[\sum_{j=1}^{N_{n+1}^{i,r}} \int_{T_j}^{T_j + t_{n+1}} \mathbf{1}_{\{i \in \mathcal{P}(s), \, a_i(s) \in [a_{n+1}, a_{n+2}), \, r_i(s) = r\}} \mathbf{1}_{\{\forall u \in [0,s]: X(u) \in \mathcal{K}\}} ds\right]. \quad (11)$$

Adding that $(t_n)_n$ decreases, the status cannot change twice during time t_{n+1} and reach level a_{n+1} again. So, on the event the process does not jump at all during the time period $[T_j, T_j + t_{n+1}]$ on the event considered and for $s \leq t_{n+1}$,

$$\mathbb{E}\left[\mathbf{1}_{\{i \in \mathcal{P}(T_j + s), \, a_i(T_j + s) \in [a_{n+1}, a_{n+2}), \, r_i(T_j + s) = r, \, \forall u \in [0,s]: X(T_j + u) \in \mathcal{K}\}} \mid T_j, (X(t))_{t \leq T_j + s}\right]$$

$$= \mathbb{E}\left[e^{-\int_0^s \alpha_r(a_{n+1} + u, X(T_j + u)) du} \mathbf{1}_{\{\forall u \in [0,s]: X(T_j + u) \in \mathcal{K}\}} \mid T_j, (X(T_j + u))_{u \leq s}\right]$$

$$\leq e^{-\int_0^s \underline{\alpha}_r(a_{n+1} + u, \mathcal{K}) du},$$

we get for $n \leq n_0 - 2$,

$$u_{n+1}^{i,r} \leq \mathbb{E}\left[\sum_{j=1}^{N_{n+1}^{i,r}} \int_0^{t_{n+1}} e^{-\int_0^s \underline{\alpha}_r(a_{n+1}+u, \mathcal{K})du} ds\right] \leq t_n \, p_n^r \, \mathbb{E}\left[N_{n+1}^{i,r}\right], \qquad (12)$$

where

$$p_n^r = \frac{1 - e^{-\underline{\alpha}_n^r t_{n+1}}}{\underline{\alpha}_n^r t_n}, \quad \underline{\alpha}_n^r = \inf\{\alpha_r(a, x) : a \in [a_{n+1}, a_{n+2}], x \in (1/\mathcal{K}, \mathcal{K})\}.$$

Besides, as ages increase at rate 1, either predator i is born at an age between a_{n+1} and a_{n+2} or it has exactly spent the time t_n at level between ages $[a_n, a_{n+1})$. In any case,

$$\mathbb{E}\left[N_{n+1}^{i,r}\right] \leq \mathbb{P}(A_n^i) + \frac{u_n^{i,r}}{t_n},$$

where

$$A_n^i = \{b(i) \leq T \wedge \tau_K, \, a_i(b(i)) \in [a_{n+1}, a_{n+2})\}.$$

Combining these inequalities, we obtain

$$u_{n+1}^{i,r} \leq p_n^r u_n^{i,r} + t_n p_n^r \mathbb{P}(A_n^i),$$

which then gives, by induction,

$$u_n^{i,r} \leq u_0^{i,r} \prod_{j=0}^{n-1} p_j^r + \sum_{k=0}^{n-1} t_k \mathbb{P}(A_k^i) \prod_{j=k}^{n-1} p_j^r.$$

Using now $p_j^r \leq \frac{t_{j+1}}{t_j}\left(1 - \frac{\alpha_j^r t_{j+1}}{4}\right)$, when t_{j+1} is small enough, and setting

$$S_k^n = \sum_{j=k}^{n-1} \underline{\alpha}_j^r t_{j+1}/4,$$

we get $\prod_{j=k}^{n-1} p_j^r \leq \frac{t_n}{t_k} e^{-S_k^n}$ and then

$$u_n^{i,r} \leq \frac{t_n}{t_0} u_0^{i,r} e^{-S_0^n} + t_n \sum_{k=0}^{n-1} \mathbb{P}(A_k^i) e^{-S_k^n}.$$

To conclude for f compactly supported, we set $f_n = \sup_{a \in [a_n, a_{n+1})} f(a)$ and get

$$\mathbb{E}\left[\int_0^t f(a_i(s)) \, \mathbf{1}_{i \in \mathcal{P}(s), r_i(s)=r} ds\right]$$

$$\leq \sum_{n=0}^{n_0-1} f_n u_n^{i,r}$$

$$\leq \frac{\mathbb{P}(b(i) \leq T \wedge \tau_K)}{t_0 \wedge 1} \sum_{n=0}^{n_0-1} f_n t_n e^{-S_0^n}\left(T + \sum_{k=0}^{n-1} \mathbb{P}(A_k^i \mid b(i) \leq T \wedge \tau_K) e^{S_0^k}\right),$$

since $u_0^{i,r} \leq T\,\mathbb{P}(b(i) \leq T \wedge \tau_\mathcal{K})$. Let now $t_0 = \min(1, a_\infty/2)$ and $A \in (t_0, a_\infty)$. For any $h > 0$, we consider a positive strictly decreasing sequence $(t_n^h)_{n \leq n_0^h - 1}$ such that

$$t_0^h = t_0, \qquad \limsup_{h \to 0} \sup_{n \geq 1} t_n^h = 0, \qquad a_{n_0^h}^h = \sum_{k=0}^{n_0^h - 1} t_k^h = A.$$

Using the following uniform convergence of the Darboux sum

$$\sup_{k=0,\ldots,n_0^h - 1} \left| S_0^k - \frac{1}{4} \int_{[0,a_k^h)} \underline{\alpha}_r(u) du \right| \overset{h \to 0}{\longrightarrow} 0,$$

which comes from the continuity of $\underline{\alpha}$ and uniform continuity of f on $[0, A]$, we get, by letting $h \to 0$,

$$\mathbb{E}\left[\int_0^{\tau_\mathcal{K} \wedge T} f(a_i(s)) \mathbf{1}_{\{i \in \mathcal{P}(s),\, r_i(s) = r\}} ds \right]$$

$$\leq C\,\mathbb{P}(b(i) \leq T \wedge \tau_\mathcal{K}) \int_{[0,a_\infty)} f^\star(a) e^{-\int_{[0,a)} \underline{\alpha}_r(u, \mathcal{K}) du/4} da$$

$$\times \left[T + \mathbb{E}\left(\mathbf{1}_{\{a_i(b(i)) \leq a\}} \exp\left(\int_{[0, a_i(b(i)))} \underline{\alpha}_r(u, \mathcal{K}) du/4 \right) \right) \right],$$

for some constant C, where we recall that $f^\star(a) = \mathbf{1}_{[0,t_0)}(a) \sup_{[0,t_0]} f + \mathbf{1}_{[t_0,a_\infty)}(a) f(a)$. Recall also that $a_i(b(i))$ has a compact support in $[0, a_\infty)$ under our assumptions on the initial condition (from Proposition 4.1), together with the fact that newborns have age 0. So the last term is bounded by a constant. Summing over all predators i yields the result since

$$\sum_{i \in \mathcal{U}} \mathbb{P}(b(i) \leq T \wedge \tau_\mathcal{K}) \leq \mathbb{E}\left(\#\{i \in \mathcal{U} : b(i) \leq T \wedge \tau_\mathcal{K}\} \right) \leq e^{T\bar{\gamma}}\, \mathbb{E}\left[\mathcal{Y}(0, \{S, M\}, [0, a_\infty)) \right]$$

since $\#\{i \in \mathcal{U} : b(i) \leq T \wedge \tau_\mathcal{K}\}$ is dominated by a pure birth process at time T, with individual birth rate $\bar{\gamma}$. $\qquad \square$

We define $F_{g,f} : \mathbb{R}_+ \times \mathfrak{M}(\mathcal{X}) \to \mathbb{R}$ by

$$F_{g,f}(x, \mu) = g(x) + \langle \mu, f \rangle, \tag{13}$$

where $g : \mathbb{R}_+ \to \mathbb{R}$ and $f : \mathcal{X} \to \mathbb{R}$ are measurable and bounded functions. We introduce

$$\begin{aligned}
\mathfrak{L}F_{g,f}(x, \mu) &= \gamma x(g(x+1) - g(x)) + \beta x(g(x-1) - g(x)) \\
&+ \int_\mathcal{X} \left(\frac{\partial}{\partial a} f(r, a) + \gamma_r(a) f(M, 0) - \beta_r(a) f(r, a) \right) \mu(dr, da) \\
&+ \int_\mathcal{X} \alpha_r(a, x)(\mathbf{1}_{r=S}\,(g(x-1) - g(x)) + f(\bar{r}, 0) - f(r, a)) \mu(dr, da).
\end{aligned}$$

The operator $\mathfrak{L}$ is the generator of the Markov process $(X(t), \mathcal{Y}(t))_{t \geq 0}$. More precisely, our SDE representation (9-10) yields the following family of martingales. Let $g : \mathbb{R}_+ \to \mathbb{R}$ be measurable and bounded and $f \in \mathcal{C}^{1,b}(\mathcal{X})$. We define $M(t) = M_{g,f}(t)$ for $t \geq 0$ by

$$M(t) = F_{g,f}(X(t), \mathcal{Y}(t)) - F_{g,f}(X(0), \mathcal{Y}(0)) - \int_0^t \mathfrak{L}F_{g,f}(X(s), \mathcal{Y}(s)) ds$$

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Lemma 4.3. *Under assumptions of Proposition 4.1 and assuming further that for any $\mathcal{K} > 0$ and $r \in \{S, M\}$,*

$$\int_{[0,a_\infty)} \overline{\alpha}_r(a, \mathcal{K}) e^{-\frac{1}{4} \int_{[0,a)} \underline{\alpha}_r(u, \mathcal{K}) du} da < \infty, \tag{14}$$

then $(M(t))_{t \geq 0}$ is a local martingale. Besides $(M(t \wedge \tau_\mathcal{K}))_{t \geq 0}$ is a square-integrable martingale and its bracket is given, for all $t \geq 0$, by

$$
\begin{aligned}
&\langle M \rangle (t \wedge \tau_\mathcal{K}) \\
&= \int_0^{t \wedge \tau_\mathcal{K}} \left(\gamma X(s)(g(X(s) + 1) - g(X(s)))^2 + \beta X(s)(g(X(s) - 1) - g(X(s)))^2 \right) ds \\
&\quad + \int_0^{t \wedge \tau_\mathcal{K}} \sum_{i \in \mathcal{P}(s)} \alpha_i(s) \left(\mathbf{1}_{r_i(s)=S}(g(X(s) - 1) - g(X(s))) + (f(\overline{r_i}(s), 0) - f(r_i(s), a_i(s)))\right)^2 ds \\
&\quad + \int_0^{t \wedge \tau_\mathcal{K}} \sum_{i \in \mathcal{P}(s)} \left(\gamma_i(s) f(M, 0)^2 + \beta_i(s) f(r_i(s), a_i(s))^2 \right) ds.
\end{aligned}
$$

Proof. The fact that M is a local martingale and the computation of its square variation is derived from our SDE representation (9-10) . Indeed one can write the semi-martingale decomposition of $F_{g,f}(X, \mathcal{Y})$ using the compensation of the Poisson point measures, see for instance [FM04, BM15]. We only give details for the first component X:

$$
\begin{aligned}
g(X(t)) &= g(X(0)) + \int_0^t \sum_{\substack{i \in \mathcal{P}(s-) \\ r_i(s-)=S}} \alpha_i(s-)(g(X(s-) - 1) - g(X(s-)) \, ds \\
&\quad + \int_0^t \sum_{\substack{i \in \mathcal{P}(s-) \\ r_i(s-)=S}} \int_{\mathbb{R}_+} \mathbf{1}_{\{u \leq \alpha_i(s-)\}}(g(X(s-) - 1) - g(X(s-)) \widetilde{\mathcal{N}}^i(ds, du) \\
&\quad + \int_0^t \left(\gamma X(s-)((g(X(s-) + 1) - g(X(s-)) + \beta X(s-)(g(X(s-) - 1) - g(X(s-))) \right) ds \\
&\quad + \int_0^t \int_{\mathbb{R}_+} \Big(\mathbf{1}_{\{u \leq \gamma X(s-)\}}((g(X(s-) + 1) - g(X(s-)) \\
&\qquad\qquad + \mathbf{1}_{\{0 < u - \gamma X(s-) \leq \beta X(s-)\}}(g(X(s-) - 1) - g(X(s-)) \Big) \widetilde{\mathcal{Q}}(ds, du),
\end{aligned}
$$

where $\widetilde{\mathcal{N}}^i$ and $\widetilde{\mathcal{Q}}$ are the compensated measures of $\mathcal{N}^i$ and $\mathcal{Q}$.

Finally, square integrability of $(M(t \wedge \tau_\mathcal{K}))_{t \geq 0}$ is a consequence of Lemma 4.2 applied to $f = \overline{\alpha}_r$ and Doob's inequality and our integrability assumption (14). $\qquad\square$

4.3   Construction and tightness of the sequence of scaled processes

hyp:timeint The proof is based on standard tightness and uniqueness arguments involving the occupation measures and averaging [Kur92, KKP14] and localization. The main new difficulties lie in the infinite dimension in the averaging procedure due to the age structure combined with unboundedness of the interactions rates α_r inherent in our framework. In this section, we always assume that Assumptions 2.1 and 2.2 hold and do not recall it in the statements.

First, under these assumptions, for each $K = (K_1, K_2) \in (0, +\infty)^2$, Proposition 4.1 ensures existence and strong uniqueness of the solution $Z^K = (X^K, Y^K)$ of the system of stochastic differential equations (9-10) with parameters $\alpha_r^K, \gamma_r^K, \beta_r^K, \gamma^K, \beta^K$ given in (3-4). Recall that we consider the accelerated and scaled process defined, for all $t \geq 0$, by

$$\mathcal{Z}^K(t) = (\Xi^K(t), \mathcal{Y}^K(t, dr, da)) = \left(\frac{1}{K_1} X^K(\lambda_K t), \frac{1}{K_2} Y^K(\lambda_K t, \mathcal{U}, dr, da), \right).$$

Furthermore, Lemma 4.2 above directly implies the following counterpart for the scaled process. It allows us to localize the age distribution. We set

$$\tau_{\mathcal{K}}^K = \inf\{t \geq 0 : \Xi_t^K \notin (1/\mathcal{K}, \mathcal{K})\}.$$

Lemma 4.4. *There exists $C > 0$ such that for any continuous non-negative function f on $[0, a_\infty)$ and $r \in \{S, M\}$ and $\mathcal{K} > 0$,*

$$\mathbb{E}\left[\int_0^{T \wedge \tau_{\mathcal{K}}^K} \int_{[0, a_\infty)} f(a) \mathcal{Y}^K(s, \{r\}, da) ds \right]$$

$$\leq C(1+T) e^{\bar{\gamma} T} \int_{[0, a_\infty)} f^\star(a) e^{-\frac{\mathbf{1}_{a > t_0}}{4} \int_{[t_0, a)} \underline{\alpha}_r(u, \mathcal{K}) du} da,$$

where $t_0 = \min(1, a_\infty/2)$ and $f^\star(a) = \mathbf{1}_{[0, t_0)}(a) \sup_{[0, t_0]} f + \mathbf{1}_{[t_0, a_\infty)}(a) f(a)$.

Proof. We have

$$\mathbb{E}\left[\int_0^{T \wedge \tau_{\mathcal{K}}^K} \int_{[0, a_\infty)} f(a) \mathcal{Y}^K(s, \{r\}, da) ds \right]$$

$$= \frac{1}{\lambda_K K_2} \mathbb{E}\left[\int_0^{\lambda_K(T \wedge \tau_{\mathcal{K}}^K)} \int_{[0, a_\infty)} f(a) Y^K(s, \{r\}, da) ds \right].$$

Adding that $\lambda_K \tau_{\mathcal{K}}^K$ is the exit time of $(K_1/\mathcal{K}, K_1 \mathcal{K})$ for X^K and $Y^K(0, \mathcal{U}, \{S, M\}, [0, a_\infty)) = \lfloor K_2 y_0 \rfloor$ and $\gamma_r^K(a) = \lambda_K^{-1} \gamma_r(a)$, the conclusion comes from Lemma 4.2. $\qquad\square$

We now give the counterpart of the martingales of Lemma 4.3 for the scaled process. Recalling that $F_{g,f}(x, \mu) = g(x) + \langle \mu, f \rangle$ where $g : \mathbb{R}_+ \to \mathbb{R}$ is a bounded measurable function and $f \in \mathcal{C}^{1,b}(\mathcal{X})$, we set

$$\mathcal{L}^K F_{f,g}(x, \mu) = K_1 x \big(\gamma(g(x + 1/K_1) - g(x)) + \beta(g(x - 1/K_1) - g(x)) \big)$$

$$+ \int_{\mathcal{X}} (\gamma_r(a) f(M, 0) - \beta_r(a) f(r, a)) \, \mu(dr, da)$$

$$+ \lambda_K \int_{\mathcal{X}} \left(\frac{\partial}{\partial a} f(r, a) + \alpha_r(a, x) \left(\mathbf{1}_{r=S} (g(x - 1/K_1) - g(x)) + f(\bar{r}, 0) - f(r, a) \right) \right) \mu(dr, da).$$

Lemma 4.5. *Suppose that Assumption 2.3 also holds. Let $g : \mathbb{R}_+ \to \mathbb{R}$ be a bounded measurable function and $f \in \mathcal{C}^{1,b}(\mathcal{X})$. Then the process M^K defined for $t \geq 0$ by*

$$M^K(t) = F_{f,g}(\mathcal{Z}^K(t)) - F_{f,g}(\mathcal{Z}^K(0)) - \int_0^t \mathcal{L}^K F_{f,g}(\mathcal{Z}^K(s)) ds,$$

is a local martingale. Besides $(M^K(t \wedge \tau_{\mathcal{K}}^K))_{t \geq 0}$ is a square integrable martingale and

$$
\begin{aligned}
\langle M^K \rangle & (t \wedge \tau_{\mathcal{K}}^K) \\
&= \int_0^{t \wedge \tau_{\mathcal{K}}^K} \Xi^K(s) \left(\gamma(g(\Xi^K(s) + 1/K_1) - g(x))^2 + \beta(g(\Xi^K(s) - 1/K_1) - g(x))^2 \right) ds \\
& \quad + \lambda_K \int_0^{t \wedge \tau_{\mathcal{K}}^K} \sum_{i \in \mathcal{P}(s)} \alpha_{r_i(s)}(a_i(s), \Xi^K(s)) \\
& \quad \times \left(\mathbf{1}_{r_i(s)=S}(g(\Xi^K(s) - 1/K_1) - g(\Xi^K(s))) + \frac{1}{K_2}(f(\overline{r_i}(s), 0) - f(r_i(s), a_i(s))) \right)^2 ds \\
& \quad + \int_0^{t \wedge \tau_{\mathcal{K}}^K} \sum_{i \in \mathcal{P}(s)} \left(\gamma_{r_i(s)}(a_i(s)) \frac{f(M,0)^2}{K_2^2} + \beta_{r_i(s)}(a_i(s)) \frac{f(r_i(s), a_i(s))^2}{K_2^2} \right) ds.
\end{aligned}
$$

We introduce now the measures $\Gamma_{\mathcal{K}}^K$ on $\mathbb{R}_+ \times \{S, M\} \times [0, a_\infty)$ defined a.s. for every bounded measurable functions H by

$$
\Gamma_{\mathcal{K}}^K(H) = \int_{\mathbb{R}_+} \int_{\mathcal{X}} H(s, r, a) \Gamma_{\mathcal{K}}^K(ds, dr, da) = \int_0^{\tau_{\mathcal{K}}^K} \int_{\mathcal{X}} H(s, r, a) \mathcal{Y}^K(s, dr, da) ds
$$

We also set

$$
\Xi_{\mathcal{K}}^K(t) = \Xi^K(t \wedge \tau_{\mathcal{K}}^K), \qquad \mathcal{Y}_{\mathcal{K}}^K(t) = \mathcal{Y}^K(t \wedge \tau_{\mathcal{K}}^K, \{S, M\}, [0, a_\infty))
$$

for the localized version of the processes counting preys and predators. Considering such space-time measures for proving averaging results is inspired from [Kur92, KKP14]. However, we do not consider here the occupation measure of the fast variables $\mathcal{Y}^K(t, dr, da)$.

Lemma 4.6. *Suppose that Assumption 2.3 also holds, for every $\mathcal{K} > 0$ and $T > 0$, the sequence $(\Xi_{\mathcal{K}}^K, \mathcal{Y}_{\mathcal{K}}^K, \Gamma_{\mathcal{K}}^K)_K$ is tight in $\mathbb{D}([0,T], \mathbb{R}_+)^2 \times \mathfrak{M}([0,T] \times \mathcal{X})$.*

Proof. On the first hand, using a domination of the process $\mathcal{Y}^K(\cdot, \{S, M\}, [0, a_\infty))$ by a linear birth process, we have

$$
\sup_{K \geq 1} \mathbb{E} \left(\sup_{t \leq T} \mathcal{Y}^K(s, \{S, M\}, [0, a_\infty)) \right) < \infty. \tag{15}
$$

Then the first moment of the sequence of random variables $(\Gamma_{\mathcal{K}}^K([0,T] \times \{S, M\} \times [0, a_\infty)))_K$ is bounded and it is a tight sequence in $\mathbb{R}$.

On the second hand, we can combine Assumption 2.3 with Lemma 4.4 to obtain

$$
\sup_{K \geq 1} \mathbb{E} \left[\int_0^{\tau_{\mathcal{K}}^K \wedge T} \int_{[0, a_\infty)} \mathbf{V}(a) \mathcal{Y}^K(s, \{r\}, da) \, ds \right] < +\infty \tag{16}
$$

for $r \in \{S, M\}$. Then we get

$$
\sup_{K \geq 1} \mathbb{P}(\Gamma_{\mathcal{K}}^K([0,T] \times \{S, M\} \times [a, a_\infty)) \geq \varepsilon) \leq \varepsilon
$$

for a close enough to a_∞. Moreover, as $H \geq 1$, this also implies tightness of $(\Gamma_{\mathcal{K}}^K([0,T] \times \mathcal{X}))_{K \geq 1}$. Lemma 1.1 of [Kur92] then entails the relative compactness of the sequence $(\Gamma_{\mathcal{K}}^K)_{K \geq 1}$ in the space of finite measures embedded with the weak (narrow) topology.

Now, we show that $(\Xi_\mathcal{K}^K)_{K \geq 1}$ is tight by using the Aldous-Rebolledo criterion. Lemma 4.5 gives the semi-martingale decomposition

$$\Xi_\mathcal{K}^K = \Xi_\mathcal{K}^K(0) + A^K + M^K,$$

where

$$A^K(t) = \int_0^{t \wedge \tau_\mathcal{K}^K} (\gamma - \beta)\Xi_\mathcal{K}^K(s)ds - \int_0^{t \wedge \tau_\mathcal{K}^K} \int_{[0,a_\infty)} \alpha_S(a, \Xi_\mathcal{K}^K(s))\mathcal{Y}^K(s, \{S\}, da)ds,$$

$$\langle M^K \rangle(t) = \frac{1}{K_1} \int_0^{t \wedge \tau_\mathcal{K}^K} (\gamma + \beta)\Xi_\mathcal{K}^K(s)ds + \frac{1}{K_1} \int_0^{t \wedge \tau_\mathcal{K}^K} \int_{[0,a_\infty)} \alpha_S(a, \Xi_\mathcal{K}^K(v))\mathcal{Y}^K(v, \{S\}, da)ds.$$

Hence, writing $\mathcal{T}^K$ the set of stopping times associated to $\Xi_\mathcal{K}^K$, for any $\sigma \in \mathcal{T}^K$ and $h > 0$,

$$\mathbb{E}\left[|A^K(\sigma) - A^K(\sigma + h)|\right]$$
$$\leq h\,\mathcal{K}\,|\gamma - \beta| + \mathbb{E}\left[\int_{\sigma \wedge \tau_\mathcal{K}^K}^{(\sigma+h) \wedge \tau_\mathcal{K}^K} \int_{[0,a_\infty)} \alpha_S(a, \Xi^K(v))\mathcal{Y}^K(v, S, da)dv\right].$$

Using again Assumption 2.3 and Lemma 4.4 with now $f(a) = \overline{\alpha}_S(a, \mathcal{K})$, we get

$$\lim_{b \to a_\infty} \sup_{K \geq 1} \mathbb{E}\left[\int_0^{\tau_\mathcal{K}^K \wedge T} \int_{[b,a_\infty)} \alpha_S(a, \Xi^K(v))\,\mathcal{Y}^K(s, \{S\}, da)ds\right] = 0.$$

Using (15) and that α_S is bounded on compacts sets of $[0, a_\infty) \times (0, \infty)$ by continuity, we obtain for any $b \in [0, a_\infty)$,

$$\lim_{h \to 0} \sup_{\substack{K \geq 1, \\ \sigma \in \mathcal{T}^K, h \leq \delta}} \mathbb{E}\left[\int_{\sigma \wedge \tau_\mathcal{K}^K}^{(\sigma+h) \wedge \tau_\mathcal{K}^K} \int_{[0,b]} \alpha_S(a, \Xi^K(v))\mathcal{Y}^K(v, S, da)dv\right] = 0.$$

Combining these estimates yields

$$\lim_{\delta \to 0} \sup_{\substack{K \geq 1, \\ \sigma \in \mathcal{T}^K, h \leq \delta}} \mathbb{E}\left[|A^K(\sigma) - A^K(\sigma + h)|\right] = 0. \tag{17}$$

Besides, for each $t \geq 0$, the family of random variables $(A^K(t))_K$ is tight since the same integrability argument ensures that $(\mathbb{E}(|A^K(t)|))_K$ is bounded. Proceeding analogously for the quadratic variation of M^K and using [JM86, Theorem 2.3.2] ends the proof of tightness of $(\Xi_\mathcal{K}^K)_{K \geq 1}$. The proof of tightness of $(\mathcal{Y}_\mathcal{K}^K)_{K \geq 1}$ is similar since birth and death rates are bounded. $\quad\square$

4.4 Identification of limiting values and proof of convergence

We proceed now with identification of limiting points. In this section, we assume that Assumptions 2.1 and 2.2 and 2.3 hold. Recall that the survival function of interaction times is denoted by $p_r = \mathbb{P}(T_r(x) \geq a) = \exp(-\int_0^a \alpha_r(x, u)du)$ and response for prey is ϕ, see (5).

Lemma 4.7. *Let $T > 0$, $\mathcal{K}_0 > 0$ and consider a limiting point $(\Xi_{\mathcal{K}_0}, \Gamma_{\mathcal{K}_0})$ of $(\Xi_{\mathcal{K}_0}^K, \Gamma_{\mathcal{K}_0}^K)$ in $\mathbb{D}([0,T], \mathbb{R}_+) \times \mathfrak{M}([0,T] \times \mathcal{X})$. For all but countably many $\mathcal{K} < \mathcal{K}_0$, it satisfies for any $r \in \{S, M\}$, and f continuous bounded on $\mathbb{R}_+ \times [0, a_\infty)$,*

$$
\int_0^{\tau_\mathcal{K}} \int_{[0,a_\infty)} f(s,a) \Gamma_{\mathcal{K}_0}(ds, \{r\}, da)
$$
$$
= \int_0^{\tau_\mathcal{K}} \int_{[0,a_\infty)} f(s,a) p_r(\Xi_{\mathcal{K}_0}(s), a) \phi(\Xi_{\mathcal{K}_0}(s)) \, \Gamma_{\mathcal{K}_0}(ds, \{S, M\}, [0, a_\infty)) da \qquad a.s.,
$$

where

$$
\tau_\mathcal{K} = \inf \{t \geq 0 \mid \Xi_{\mathcal{K}_0}(t) \notin (1/\mathcal{K}, \mathcal{K})\}.
$$

Proof. To avoid the use of a sub-sequence, we assume that the sequence $(\Xi_{\mathcal{K}_0}^K, \Gamma_{\mathcal{K}_0}^K)_K$ converges in law to $(\Xi_{\mathcal{K}_0}, \Gamma_{\mathcal{K}_0})$ as $K \to \infty$. Using Skorokhod representation, we also assume that this convergence holds a.s. Following the proof of [EK09, Theorem 4.1 p.354], for all but countably many $\mathcal{K} < \mathcal{K}_0$, $(\tau_\mathcal{K}^K)_K$ converges a.s. to $\tau_\mathcal{K}$. Indeed, from [JS13, Proposition 2.11, Chapter VI], the hitting time $\tau_\mathcal{K}^K$ is a continuous function of the process $\Xi_{\mathcal{K}_0}^K$, except for discontinuity points of $\Xi_{\mathcal{K}_0}^K$. This set of points is at most countable, see [JS13, Lemma 2.10 b), Chapter VI].

Let us use Lemma 4.5 with $g = 0$ and $f \in \mathcal{C}^{1,b}(\mathcal{X})$ such that $f(M, \cdot) = 0$. Writing $f(S, \cdot) = f \in \mathcal{C}^{1,b}([0, a_\infty))$,

$$
M^K(t) = \frac{1}{\lambda_K} \left\{ \int_{[0,a_\infty)} f(a) \mathcal{Y}_{\mathcal{K}_0}^K(t \wedge \tau_\mathcal{K}^K, \{S\}, da) - \int_{[0,a_\infty)} f(a) \mathcal{Y}_{\mathcal{K}_0}^K(0, \{S\}, da) \right\}
$$
$$
- \int_0^{t \wedge \tau_\mathcal{K}^K} \int_{\mathcal{X}} H(\Xi_{\mathcal{K}_0}^K(s), r, a) \Gamma_{\mathcal{K}_0}^K(ds, dr, da)
$$
$$
+ \frac{1}{\lambda_K} \int_0^{t \wedge \tau_\mathcal{K}^K} \int_{[0,a_\infty)} (\gamma_S(a) - \beta_S(a)) f(a) \mathcal{Y}_{\mathcal{K}_0}^K(s, \{S\}, da) ds,
$$

is a square integrable martingale, where

$$
H(x, S, a) = \partial_a f(a) - \alpha_S(x, a) f(a), \quad H(x, M, a) = \alpha_M(x, a) f(0). \tag{18}
$$

Step 1. Let us prove that

$$
\lim_{K \to \infty} \int_0^{t \wedge \tau_\mathcal{K}^K} \int_{\mathcal{X}} H(\Xi_{\mathcal{K}_0}^K(s), r, a) \Gamma_{\mathcal{K}_0}^K(ds, dr, da)
$$
$$
= \int_0^{t \wedge \tau_\mathcal{K}} \int_{\mathcal{X}} H(\Xi_{\mathcal{K}_0}(s), r, a) \Gamma_{\mathcal{K}_0}(ds, dr, da) \quad \text{in probability}
$$

Assumption 2.3 and Lemma 4.4 guarantee that

$$
\mathbf{C} = \sup_{K \geq 1} \mathbb{E} \left[\int_0^{t \wedge \tau_\mathcal{K}^K} \int_{\mathcal{X}} \mathbf{V}(a)(1 + \overline{\alpha}_r(a, \mathcal{K})) \Gamma_{\mathcal{K}_0}^K(ds, dr, da) \right] < +\infty.
$$

Furthermore, Fatou Lemma ensures that

$$
\mathbb{E} \left[\int_0^{t \wedge \tau_\mathcal{K}^K} \int_{\mathcal{X}} \mathbf{V}(a)(1 + \overline{\alpha}_r(a, \mathcal{K})) \Gamma_{\mathcal{K}_0}(ds, dr, da) \right] \leq \mathbf{C}.
$$

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The fact that $\mathbf{V}(a) \to \infty$ as $a \to a_\infty$ and

$$\sup_{x \in \mathcal{K}, a \in [0, a_\infty)} \frac{|H(x, r, a)|}{1 + \overline{\alpha}_r(a, \mathcal{K})} < \infty$$

ensure by Markov inequality that for any $\varepsilon > 0$,

$$\lim_{b \to a_\infty} \sup_K \mathbb{P}\left(\int_0^{t \wedge \tau_\mathcal{K}^K} \int_{\{S,M\} \times (b, a_\infty)} H(\Xi_{\mathcal{K}_0}^K(s), r, a) \Gamma_{\mathcal{K}_0}^K(ds, dr, da) \geq \varepsilon \right) = 0$$

$$\lim_{b \to a_\infty} \mathbb{P}\left(\int_0^{t \wedge \tau_\mathcal{K}} \int_{\{S,M\} \times (b, a_\infty)} H(\Xi_{\mathcal{K}_0}(s), r, a) \Gamma_{\mathcal{K}_0}(ds, dr, da) \geq \varepsilon \right) = 0.$$

To conclude the first step, we need to prove that for any $b \in (0, a_\infty)$,

$$\lim_{K \to \infty} \int_0^{t \wedge \tau_\mathcal{K}^K} \int_{\{S,M\} \times [0,b]} H(\Xi_{\mathcal{K}_0}^K(s), r, a) \Gamma_{\mathcal{K}_0}^K(ds, dr, da)$$

$$= \int_0^{t \wedge \tau_\mathcal{K}} \int_{\{S,M\} \times [0,b]} H(\Xi_{\mathcal{K}_0}(s), r, a) \Gamma_{\mathcal{K}_0}(ds, dr, da) \quad \text{a.s.}$$

Indeed, we observe that $|\Delta \Xi_{\mathcal{K}_0}^K(s, r, a)| \leq \frac{1}{K}$, and the limiting process $\Xi_{\mathcal{K}_0}$ is continuous and the convergence of $(\Xi_{\mathcal{K}_0}^K)_K$ is uniform on $[0, T]$. We add that the convergence of $(\Gamma_{\mathcal{K}_0}^K)$ to $\Gamma_{\mathcal{K}_0}$ as K goes to infinity ensures that

$$\sup_{K \geq 1} \Gamma_{\mathcal{K}_0}^K([0, T \wedge \tau_\mathcal{K}^K] \times \{S, M\} \times [0, b]) < +\infty.$$

We obtain

$$\lim_{K \to \infty} \int_0^{t \wedge \tau_\mathcal{K}^K} \int_{\{S,M\} \times [0,b]} H(\Xi_{\mathcal{K}_0}^K(s), r, a) \Gamma_{\mathcal{K}_0}^K(ds, dr, da)$$

$$- \int_0^{t \wedge \tau_\mathcal{K}} \int_{\{S,M\} \times [0,b]} H(\Xi_{\mathcal{K}_0}(s), r, a) \Gamma_{\mathcal{K}_0}^K(ds, dr, da) = 0 \quad \text{a.s.}$$

Finally the fact that H is continuous and bounded on $\mathcal{K} \times \{S, M\} \times [0, b]$ ensures that

$$\lim_{K \to \infty} \int_0^{t \wedge \tau_\mathcal{K}^K} \int_{\{S,M\} \times [0,b]} H(\Xi_{\mathcal{K}_0}(s), r, a) \Gamma_{\mathcal{K}_0}^K(ds, dr, da)$$

$$- \int_0^{t \wedge \tau_\mathcal{K}} \int_{\{S,M\} \times [0,b]} H(\Xi_{\mathcal{K}_0}(s), r, a) \Gamma_{\mathcal{K}_0}(ds, dr, da) = 0 \quad \text{a.s,}$$

which ends the proof.

Step 2. We can now prove that that for any $t \geq 0$ and $f \in \mathcal{C}^{1,b}([0, a_\infty))$, we have

$$\int_0^{t \wedge \tau_\mathcal{K}} \int_0^\infty H(\Xi_{\mathcal{K}_0}(s), r, a) \Gamma_{\mathcal{K}_0}(ds, dr, da) = 0 \text{ a.s.} \tag{19}$$

where we recall that H is defined in (18). Indeed, (15) ensures that

$$\lambda_K^{-1} \left| \int_{[0, a_\infty)} f(a) \mathcal{Y}_{\mathcal{K}_0}^K(t, \{S\}, da) - \int_{[0, a_\infty)} f(a) \mathcal{Y}_{\mathcal{K}_0}^K(0, \{S\}, da) \right| \tag{20}$$

$$\leq \frac{C\|f\|_\infty}{\lambda_K} \sup_{t \leq T} \mathcal{Y}_{\mathcal{K}_0}^K(t, \{S\}, [0, a_\infty)),$$

which tends to 0, in probability, as $K \to \infty$. Similarly, in probability,

$$\lim_{K \to \infty} \frac{1}{\lambda_K} \int_0^{t \wedge \tau_{\mathcal{K}}^K} \int_{[0,a_\infty)} (\gamma_S(a) - \beta_S(a)) f(a) \mathcal{Y}_{\mathcal{K}_0}^K(s, \{S\}, da) ds = 0.$$

Combining this three last convergence results, we obtain that M^K converges in law to M, given, for all $t \geq 0$, by

$$M(t) = - \int_0^{t \wedge \tau_{\mathcal{K}}} \int_{\mathcal{X}} H(\Xi_{\mathcal{K}_0}(s), r, a) \Gamma_{\mathcal{K}_0}(ds, dr, da).$$

Process M remains a martingale. It is also a.s. Lipschitz because function H is bounded. Consequently, it is null. It proves (19) and ends step 2.

Step 3. Using the previous step, let us prove that for $r \in \{S, M\}$

$$\Gamma_{\mathcal{K}_0}(ds, \{r\}, da) = \gamma_{\mathcal{K}_0}(s, \{r\}, [0, a_\infty)) \frac{p_r(\Xi_{\mathcal{K}_0}(s), a)}{\int_{[0,a_\infty)} p_r(\Xi_{\mathcal{K}_0}(s), w) dw} da \Lambda_r(ds) \quad a.s., \qquad (21)$$

where $\gamma_{\mathcal{K}_0}(s, \{r\}, \cdot)$ is a measure on $[0, a_\infty)$ for any $s \geq 0$ and Λ_S a measure on $\mathbb{R}_+$. Thanks to [Kur92, Lemma 1.4], there exist $s \mapsto \gamma_{\mathcal{K}_0}(s, \{r\}, \cdot)$ is a measurable application from $[0, T]$ to the space of probabilities on $[0, a_\infty)$, and Λ_S is a measure on $\mathbb{R}_+$ such that

$$\Gamma_{\mathcal{K}_0}(ds, \{S\}, da) = \gamma_{\mathcal{K}_0}(s, \{S\}, da) \Lambda_S(ds).$$

As (19) holds for every $t \geq 0$, focusing on functions f such that $f(0) = 0$, we obtain a.s. and for Λ_S-almost all $s \leq t \wedge \tau_{\mathcal{K}}$,

$$\int_0^\infty H(\Xi_{\mathcal{K}_0}(s), S, a) \gamma_{\mathcal{K}_0}(s, \{S\}, da) = 0.$$

In conclusion, for every $f \in \mathcal{C}^{1,b}([0, a_\infty))$ such that $f(0) = 0$ and for Λ_S-almost all $s \leq t \wedge \tau_{\mathcal{K}}$, we almost surely have

$$\int_{[0,a_\infty)} (\partial_a f_S(a) - \alpha_S(\Xi_{\mathcal{K}_0}(s), a) f(a)) \gamma_{\mathcal{K}_0}(s, \{S\}, da) = 0. \qquad (22)$$

Let us show now that this functional equation imposes the form of $\gamma_{\mathcal{K}_0}$ through the solutions of the associated Poisson Equation. We proceed with a fix realization of the process and the results hold a.s. Consider $s \leq t \wedge \tau_{\mathcal{K}}$. For any test function $g \in C_c^1([0, a_\infty))$ such that

$$\int_0^\infty g(v) p_S(\Xi_{\mathcal{K}_0}(s), v) dv = 0,$$

the function f defined by

$$f : a \mapsto p_S(\Xi_{\mathcal{K}_0}(s), a)^{-1} \int_0^a g(v) p_S(\Xi_{\mathcal{K}_0}(s), v) dv$$

is well-defined for each fixed s and belongs to $\mathcal{C}^{1,b}(\mathcal{X})$. This function verifies $f(0) = 0$ and is solution of the Poisson equation:

$$\forall a \in [0, a_\infty), \qquad \partial_a f(a) - \alpha_S(\Xi_{\mathcal{K}_0}(s), a) f(a) = g(a) \text{ a.s.}$$

By (22), it yields

$$\int_{[0,a_\infty)} g(a)\,\gamma_{\mathcal{K}_0}(s,\{S\},da) = 0.$$

We extend this identity to $g \in C^1([0,a_\infty))$ such that $\int_0^\infty g(v)p_S(\Xi_{\mathcal{K}_0}(s),v)dv = 0$ by an approximation argument. We can then apply this identity to $g : a \mapsto h(a) - \int_{[0,a_\infty)} h(v)p_S(\Xi_{\mathcal{K}_0}(s),v)dv$ for any $h \in C^1([0,a_\infty))$. Using that $\gamma_{\mathcal{K}_0}(s,\{S\},da)$ is a probability measure, we obtain that $p_S(\Xi_{\mathcal{K}_0}(s),\cdot)$ is the density of the measure $\gamma_{\mathcal{K}_0}(s,\{S\},\cdot)$ with respect to Lebesgue measure. It proves (21) for $r = S$ and the case $r = M$ is obtained similarly.

Step 4. We can now conclude. Using (19) with $f \equiv 1$ yields for every $t \geq 0$,

$$\int_0^{t\wedge\tau_{\mathcal{K}}} \int_{[0,a_\infty)} \alpha_S(a,\Xi_{\mathcal{K}_0}(s))\Gamma_{\mathcal{K}_0}(ds,\{S\},da) = \int_0^{t\wedge\tau_{\mathcal{K}}} \int_{[0,a_\infty)} \alpha_M(a,\Xi_{\mathcal{K}_0}(s))\Gamma_{\mathcal{K}_0}(ds,\{M\},da).$$

This implies the following equality of measures

$$\int_{[0,a_\infty)} \alpha_S(a,\Xi_{\mathcal{K}_0}(s))\Gamma_{\mathcal{K}_0}(ds,\{S\},da) = \int_{[0,a_\infty)} \alpha_M(a,\Xi_{\mathcal{K}_0}(s))\Gamma_{\mathcal{K}_0}(ds,\{M\},da).$$

Integrating (21) over $[0,a_\infty)$ and using the previous equality, we obtain

$$\frac{\gamma(s,\{S\},[0,a_\infty))}{\int_0^\infty p_S(\Xi_{\mathcal{K}_0}(s),w)dw}\Lambda_S(ds) = \frac{\gamma(s,\{M\},[0,a_\infty))}{\int_0^\infty p_M(\Xi_{\mathcal{K}_0}(s),w)dw}\Lambda_M(ds).$$

Finally, we have

$$\gamma(s,\{r\},[0,a_\infty))\Lambda_r(ds) = \frac{\int_{[0,a_\infty)} p_r(s,w)dw}{\overline{p}(\Xi_{\mathcal{K}_0}(s))}\Gamma_{\mathcal{K}_0}(ds,\{S,M\},[0,a_\infty)),$$

and

$$\Gamma(ds,\{r\},da) = \frac{p_r(\Xi_{\mathcal{K}_0}(s),a)}{\overline{p}(\Xi_{\mathcal{K}_0}(s))}\Gamma_{\mathcal{K}_0}(ds,\{S,M\},[0,a_\infty))\,da.$$

It ends the proof. $\qquad\square$

Let us now focus on the number of preys and the whole number of predators. We prove that limiting points of the corresponding processes satisfy the ODE (7).

Lemma 4.8. *Let $T > 0$ and $\mathcal{K}_0 > 0$ and $(\Xi_{\mathcal{K}_0}, \Gamma_{\mathcal{K}_0})$ be a limiting point of $(\Xi_{\mathcal{K}_0}^K, \Gamma_{\mathcal{K}_0}^K)_K$ in $\mathbb{D}([0,T],\mathbb{R}_+) \times \mathfrak{M}([0,T] \times \mathcal{X})$. For all but countably many $\mathcal{K} < \mathcal{K}_0$, the measure $\mathbf{1}_{s\leq\tau_{\mathcal{K}}}\Gamma_{\mathcal{K}_0}(ds,\{S,M\},[0,a_\infty))$ admits a density $\mathcal{Y}_{\mathcal{K}_0}$ with respect to the Lebesgue measure and the couple $(\Xi_{\mathcal{K}_0}, \mathcal{Y}_{\mathcal{K}_0})$ satisfies for all $t \geq 0$,*

$$\Xi_{\mathcal{K}_0}(t \wedge \tau_{\mathcal{K}}) = \Xi_{\mathcal{K}_0}(0) + \int_0^{t\wedge\tau_{\mathcal{K}}} ((\gamma - \beta)\,\Xi_{\mathcal{K}_0}(s) - \mathcal{Y}_{\mathcal{K}_0}(s)\phi(\Xi_{\mathcal{K}_0}(s)))\,ds$$

$$\mathcal{Y}_{\mathcal{K}_0}(t \wedge \tau_{\mathcal{K}}) = \mathcal{Y}_{\mathcal{K}_0}(0) + \int_0^{t\wedge\tau_{\mathcal{K}}} \mathcal{Y}_{\mathcal{K}_0}(s)\psi(\Xi_{\mathcal{K}_0}(s))ds.$$

Proof. As in Lemma 4.7, to avoid the use of sub-sequences, we assume that $(\Xi_{\mathcal{K}_0}^K, \Gamma_{\mathcal{K}_0}^K)$ converges to $(\Xi_{\mathcal{K}_0}, \Gamma_{\mathcal{K}_0})$ in law. We use again Lemma 4.5, with now $f \equiv 0$ and $g \equiv \mathrm{Id}$. It ensures that M^K, defined for every $t \geq 0$ by

$$M^K(t) = \Xi_{K_0}^K(t \wedge \tau_{\mathcal{K}}^K) - \Xi_{\mathcal{K}_0}^K(0) + \int_0^{t \wedge \tau_{\mathcal{K}}^K} (\beta - \gamma)\, \Xi_{\mathcal{K}_0}^K(s) ds$$
$$- \int_0^{t \wedge \tau_{\mathcal{K}}^K} \int_0^\infty \alpha_S(a, \Xi_{\mathcal{K}_0}^K(s)) \Gamma_{\mathcal{K}_0}^K(ds, \{S\}, da),$$

is a square integrable martingale. Then, using similar arguments to the first step of the proof of Lemma 4.7, $M^K(t)$ converges in law to $M(t)$ as $K \to \infty$ for every $t \geq 0$, where M is defined by

$$M(t) = \Xi_{\mathcal{K}_0}(t \wedge \tau_{\mathcal{K}}) \quad - \quad \Xi_{\mathcal{K}_0}(0) + \int_0^{t \wedge \tau_{\mathcal{K}}} (\beta - \gamma)\, \Xi_{\mathcal{K}_0}(s) ds$$
$$- \int_0^{t \wedge \tau_{\mathcal{K}}} \phi(\Xi_{\mathcal{K}_0}(s)) \Gamma_{\mathcal{K}_0}(ds, \{S, M\}, [0, a_\infty)).$$

Besides M is a local martingale. Similarly and as computed in the proof of Lemma 4.6, the bracket of $\left(M_{t \wedge \tau_{\mathcal{K}}^K}^K\right)_{t \geq 0}$ converges to 0 in probability and then $M_{t \wedge \tau_{\mathcal{K}}} = 0$ a.s. It proves the first part of the result.

We need now to describe $\Gamma^{\mathcal{K}_0}(ds, \{S, M\}, [0, a_\infty))$. Again, we apply Lemma 4.5 but now with $f \equiv 1$ and $g \equiv 0$, to obtain that M^K defined for all $t \geq 0$ by

$$M^K(t) = \mathcal{Y}^K(t \wedge \tau_{\mathcal{K}}^K, [0, a_\infty)) - \mathcal{Y}^K(0, [0, a_\infty)) + \int_0^{t \wedge \tau_{\mathcal{K}}^K} \int_{\mathcal{X}} (\beta_r(a)) - \gamma_r(a)) \, \Gamma_{\mathcal{K}_0}^K(ds, dr, da)$$

is a square integrable martingale and

$$\langle M^K \rangle(t) = \frac{1}{K_2^2} \int_0^{t \wedge \tau_{\mathcal{K}}^K} \sum_{i \in \mathcal{P}(s)} \left(\gamma_{r_i}(s)(a_i(s)) + \beta_{r_i(s)}(a_i(s)) \right) ds.$$

Using (15) ensures that $\mathbb{E}(\langle M^K \rangle(T \wedge \tau_{\mathcal{K}}^K))$ converges in law to 0 as $K \to \infty$, for any $T \geq 0$. By Doob and Cauchy Schwarz inequality, it implies that the random variable $\int_0^{T \wedge \tau_{\mathcal{K}}} M^K(t) dt$ tends in law to 0 as $K \to \infty$. Letting each term of the expression of M^K converge, we get by identifying the limits

$$0 = \Gamma_{\mathcal{K}_0}([0, T \wedge \tau_{\mathcal{K}}], \{S, M\}, [0, a_\infty)) - \mathcal{Y}(0, [0, a_\infty))(T \wedge \tau_{\mathcal{K}})$$
$$+ \int_0^{T \wedge \tau_{\mathcal{K}}} dt \int_{[0,t] \times \mathcal{X}} (\beta_r(a) - \gamma_r(a)) \Gamma_{\mathcal{K}_0}(ds, dr, da).$$

Using Lemma 4.7 with $f(s, a) = \mathbf{1}_{s \leq t}(\beta_r(a)) - \gamma_r(a))$ and the definition of ψ yields

$$\Gamma_{\mathcal{K}_0}([0, T \wedge \tau_{\mathcal{K}}], \{S, M\}, [0, a_\infty))$$
$$= \mathcal{Y}(0, \{S, M\}, [0, a_\infty))(T \wedge \tau_{\mathcal{K}}) + \int_0^{T \wedge \tau_{\mathcal{K}}} dt \int_0^t \psi\left(\Xi_{\mathcal{K}_0}(s)\right) \Gamma_{\mathcal{K}_0}(ds, \{S, M\}, [0, a_\infty)).$$

This means that the measure $\mathbf{1}_{s \leq \tau_{\mathcal{K}}} \Gamma_{\mathcal{K}_0}(ds, \{S, M\}, [0, a_\infty))$ has a density $\mathcal{Y}$ with respect to the Lebesgue measure, where $\mathcal{Y}$ is defined for all $t \geq 0$ by

$$\mathcal{Y}(t) = \mathcal{Y}(0, \{S, M\}, [0, a_\infty)) + \int_0^t \psi\left(\Xi_{\mathcal{K}_0}(s)\right) \mathcal{Y}(s) ds.$$

It is the desired result. $\qquad\qquad\square$

Adding that uniqueness of the limiting ODE holds under Assumption 2.4, we can conclude the proof of the approximation result.

Proof of Theorem 2.5. Let $(x_0, y_0) \in (\mathbb{R}_+^*)^2$ be the initial condition of (x, y). Assumption 2.4 guarantees that for any time horizon $T > 0$, there exists $\mathcal{K}_0 > 0$ such that for all $t \leq T$, $x(t) \in (1/\mathcal{K}_0, \mathcal{K}_0)$. Let $(\Xi_{\mathcal{K}_0}, \mathcal{Y}_{\mathcal{K}_0}, \Gamma_{\mathcal{K}_0})$ be any limiting values of $(\Xi_{\mathcal{K}_0}^K, \mathcal{Y}_{\mathcal{K}_0}^K, \Gamma_{\mathcal{K}_0}^K)_K$ in $\mathbb{D}([0, T], \mathbb{R}_+)^2 \times \mathfrak{M}([0, T] \times \mathcal{X})$. By continuity of x, we can choose some $\mathcal{K} < \mathcal{K}_0$ such that conclusion of Lemma 4.7 and Lemma 4.8 hold and $x(t) \in (1/\mathcal{K}, \mathcal{K})$ for any $t \leq T$. Consequently, $(\Xi_{\mathcal{K}_0}, \mathcal{Y}_{\mathcal{K}_0})$ and (x, y) satisfy the same evolution equation (7) on time interval $[0, T \wedge \tau_{\mathcal{K}}]$. Uniqueness guaranteed by Assumption 2.4 ensures that they coincide up to time $T \wedge \tau_{\mathcal{K}}$. It follows that $\tau_{\mathcal{K}} \geq T$ because $x(t)$ belongs to $(1/\mathcal{K}, \mathcal{K})$ for any $t \leq T$. For any continuous and bounded function g, we have

$$\int_0^{T \wedge \tau_{\mathcal{K}}} g(t) \mathcal{Y}_{\mathcal{K}_0}^K(t) dt \overset{K \to \infty}{\longrightarrow} \int_0^{T \wedge \tau_{\mathcal{K}}} g(t) \mathcal{Y}_{\mathcal{K}_0}(t) dt.$$

By Lemma 4.7 and Lemma 4.8, we also observe that

$$\Gamma_{\mathcal{K}_0}(dt, \{r\}, da) = y(t) p_r(x(t), a) \phi(x(t)) \, dt \, da.$$

and using $\sum_{r \in \{S, M\}} \int_0^{a_\infty} p_r(x(t), a) \phi(x(t)) \, da = 1$, we get

$$\int_0^{T \wedge \tau_{\mathcal{K}}} g(t) \mathcal{Y}_{\mathcal{K}_0}^K(t) dt \overset{K \to \infty}{\longrightarrow} \int_0^{T \wedge \tau_{\mathcal{K}}} g(t) y(t) dt.$$

Identification of the two previous limits ensures that

$$\mathcal{Y}_{\mathcal{K}_0}(t) = y(t) \qquad \text{for almost every } t \geq 0.$$

As trajectories are *càdlàg*, this identity holds for every $t \geq 0$. Using now Lemma 4.6, it ensures the convergence of $(\Xi^K, \mathcal{Y}^K(\cdot, \{S, M\}, [0, a_\infty)), \Gamma^K)$ over $[0, T]$ to $(x, y, y(t) p_r(x(t), a) \phi(x(t)) \, dt \, da)$ in $\mathbb{D}([0, T], \mathbb{R}_+)^2 \times \mathfrak{M}([0, T] \times \mathcal{X})$. $\qquad\square$

5 Discussion

This work is a continuation of [BBC18] which aims at connecting in a general way the successive time (and their distribution) spent at the individual level for interactions and the macroscopic evolution of population sizes. The work [BBC18] was dedicated to count the number of interactions, when the variations of density of preys and predators were neglected. It was thus a way to relate the individual behavior (and potentially measurable quantities) to the functional response which quantifies the speed at which interactions occur on a short time window. In the current paper, we also take into account births and

deaths in the population and the way these events are affected by interactions (in particular fertility and survival of predators depend on the searching time). This additional step allows to connect the individual behavior to the macroscopic population dynamics. Compared to the literature, the major mathematical difficulty is to take into account memory effects (due to non exponential time distribution). It leads us to add an age structure to describe the interactions and develop averaging techniques for slow fast systems in infinite dimension. Another difficulty to achieve such averaging is the role of the scales, which allow to know in which case the deterministic ODE is a valid approximation.

In this work, we were interested in cases where the number of preys is much larger than the number of predators and the time for interactions is much shorter that the time to give birth or the time to die for preys and predator. Besides the time for searching may impact the survival of offsprings (via natality rate) or the death probability.
This seems reasonable for many interactions. For instance, fox-rabbit, wolf-deer/caribou, white bear-seal, bear-fish, bird-worm, where the time for searching is of order of days or a week, while reproduction is of order of a year for both (and several years for death). A relevant extension of the model considered here would consist in letting the mortality or natality of predators depend not only on the time from the last change of status. Lack of food could be taken into account more generally through the quantity of food eaten in a largest period.

For most of the species mentioned above, extension of the model to several preys for one predator and interference between several predators should be considered. Also adding the biological age or non-exponential clock for birth and death (season effect, maturity, menopause ...) are interesting points to address. We have focused in this work on relaxing the memory less properties of interactions. But extensions mentioned above seem accessible via the framework and techniques developed here even if technicalities may fast increase.

Determining stochastic fluctuations around the limiting deterministic system is a challenging and interesting problem. It is relevant in particular when population sizes are not very large. The variance of interaction times should appear to describe fluctuations and may be much larger than in the exponential case. The averaging approach of [KKP14] provides a path for this issue via Poisson equation. Adapting these techniques seems an interesting perspective and complement to this work. Owing to our infinite dimensional, it is probably a challenging question.

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