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

Vincent Bansaye\* and Bertrand Cloez†

March 29, 2021

## Abstract

We consider a stochastic individual based model where each predator searches during a random time and then manipulates its prey or rests. The time distributions may be non-exponential. 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.

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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 Michael and Menten.

Macroscopic derivation 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 in limiting dynamical systems and fluctuations of processes around these limits. In our context of prey-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.

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, as far as we see, these times seem to be distributed with one mode. Finally, foraging suggests that the probability of finding a prey eventually increases with searching time for a given density of preys. The aim of the paper is 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 life length is not exponentially distributed. Following in particular [BBC18] and references therein, we model the interaction by a renewal process for each predator, with two status. Each predator successively searches during a random time and then manipulates during an other random time, which may include rest or other interactions. We assume that these time distributions admit a density with respect to Lebesgue measure and density dependence. Extension of the current approach to more than two status for predators would be straightforward.

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. Predators then search 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 this time, one prey is caught and the population of preys becomes  $n_1 - 1$ . The predator 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  $\gamma_r(u)$  and  $\beta_r(u)$ , which depends on their status  $r \in \{S, M\}$  and the time  $u$  from which they are in this status. Typically, the fact that the predator does not find a prey make its death rate  $\beta_S(u)$  increase with  $u$ . Preys also give birth and die, with fixed rates  $\gamma$  and  $\beta$ .

We assume that preys are at scale  $K_1$  and predators at scale  $K_2$  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 the ones of predators. After scaling, we show, that the couple of stochastic processes describing the quantities of preys of 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

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

and

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

This limit theorem will be illustrated both by classical and new functional responses in Section 4. We observe that the response  $\phi$  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  $\psi$  of the population of predators is in general sensitive to the other characteristics of the distribution. We add that the distribution of time of interactions should also impact the dynamics of the population of preys at a second order, *i.e.* for fluctuations. This is relevant in particular when population are not too large and left for a future work.

The fact that the time of interactions is both density dependent and non-exponentially distributed leads us to extend the state space. This procedure to get the Markov setting is classical and consists here in an additional age structure. We then exploit the generator and martingale problem and get also the age distribution of preys. 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. 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.

We consider a punctual measure whose atoms give the status and the age of predators, which is here the length of time since they have been in this status. Other relevant ages could be added, in particular the time from the birth. However, it seems superfluous at our stage. In our slow-fast dynamics, there is an averaging phenomenon and 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. The averaging phenomenon in finite dimension is classical [KKP14, BKPR06, Cos16, MT12]. The reduction of the infinite setting to a finite one describing the number of preys and predators may be less. Following [Kur92, KKP14], the occupation measure  $\Gamma^K$ , 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. In our setting,  $Y^K$  is the distribution 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  $\Gamma^K$  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.

The paper is structured as follows. In Section 2, we define the integer valued model without any time or population size scaling. We characterize the process as the unique strong solution of a stochastic differential equation and give first properties about its semimartingale decomposition. In particular, the key technical point is the control of the age distribution in our setting, by exploiting the local time associated to the renewal procedure. In Section 3, we introduce the scaled process and state our main result, Theorem 3.4. The result is proved by tightness and identification of the limit using the occupation measure. Finally, we end our work through several examples in Section 4.

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

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

the state space of predators endowed with the product  $\sigma$ -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  $\mu_n$  tends to  $\mu$  if and only if for every continuous and bounded function  $f$  on  $\mathcal{S}$ ,

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

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 finally denote by  $\mathcal{C}^{1,b}(\mathcal{X})$  (resp.  $\mathcal{C}^{1,b}(\mathcal{U} \times \mathcal{X})$  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.

## 2 The stochastic individual based model

In this section, we define the discrete individual based model using stochastic differential equations with jumps. The accelerated normalized process and its approximation will be studied in the next section using properties and estimates obtained here. Each predator is characterized by a status  $r \in \{S, M\}$  and an age  $a \in [0, a_\infty)$ . To formalize conveniently this modeling, we label each predator using classical Ulam-Harris-Neveu notation and describe the associated genealogical tree. The set of individuals is

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

For short, we write  $u = u_0 u_1 \dots u_k \in \mathcal{U}$  and  $u$  then corresponds to an individual living in generation  $|u| = k$  and whose ancestor in generation  $i$  is  $u_0 \dots u_i$  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  $t$  is denoted by  $\mathcal{P}(t)$  and is a subset of  $\mathcal{U}$ . For each predator  $i \in \mathcal{P}(t)$ , we write  $r_i(t) \in \{S, M\}$  its status at time  $t$ , which indicate respectively that it searches or manipulates. We write  $a_i(t)$  its age, namely the time from which it searches or manipulates. Finally, we write  $X(t) \in \mathbb{N}$  the number of preys at time  $t$ . 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  $Y(t, \mathcal{U}, \{S, M\}, \mathbb{R}_+)$ .

Let us now describe the population dynamic. For status  $r \in \{S, M\}$  and in the presence of  $x \in \mathbb{N}$  preys, we assume that the time for interaction  $T_r(x)$  is a random variable with support  $[0, a_\infty)$ . We also assume that it admits a density, with respect to the Lebesgue measure,  $f_r(x, \cdot)$ . The associated jump rate  $\alpha$  is defined for  $(a, x) \in \mathcal{X}$  by

$$\alpha_r(a, x) = \frac{f_r(a, x)}{\int_{[a, a_\infty)} f_r(u, x) du},$$

It gives the rate at which a predator changes its status when its age in its current status is equal to  $a$  and the number of preys is  $x$ . If the predator was searching, it provokes a death of a prey. We do not assume that these interactions rates  $\alpha_r$  are lower and upper bounded. Indeed, for instance in the case when the time of interaction has a finite support ( $a_\infty < \infty$ ) or a subexponential tail, it is not upperbounded, even for a given number of preys. Let us consider some classical distribution that will be captured in our setting:

- Exponential law:  $f(a, x) = \lambda(x)e^{-\lambda(x)a}$  and  $\alpha(a, x) = \lambda(x)$ , for some bounded function  $\lambda$ .
- Log-normal distribution :  $f(a, x) = \frac{1}{a\sigma(x)\sqrt{2\pi}} \exp\left(-\frac{(\log(a)-\mu(x))^2}{2\sigma(x)^2}\right)$  and  $\alpha$  has no explicit form.
- Uniform law:  $f(a, x) = \mathbf{1}_{[0,1]}(a)$  and  $\alpha(a, x) = (1-a)^{-1}\mathbf{1}_{[0,1]}$ .
- Pareto law :  $f(a, x) = k(x)(z(x)^{k(x)}/a)^{k(x)}\mathbf{1}_{a \geq z(x)}$  and  $\alpha(a, x) = k(x)/a\mathbf{1}_{a \geq z(x)}$ , for some bounded functions  $k : \mathbb{N} \rightarrow (0, +\infty)$  and  $z : \mathbb{N} \rightarrow (1, +\infty)$ .

Finally, predators may give birth or die with respective measurable rates  $a \mapsto \gamma_r(a)$  and  $a \mapsto \beta_r(a)$  which depend on their status  $r \in \{S, M\}$  and their interaction age  $a$ . In particular, lack of nutrition affects survival and reproduction and  $\gamma_S$  may be decreasing and  $\beta_S$  may be increasing. For sake of simplicity and realism, we assume these rates are bounded. For the preys, birth and death rates are non-negative numbers denoted by  $\gamma$  and  $\beta$ .

## 2.1 Existence and trajectorial representation

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 punctual point measures  $\mathcal{M}^i$  and  $\mathcal{Q}$  on  $\mathbb{R}_+^2$  with intensity the Lebesgue measure. They are independent of  $(\mathcal{N}^i, i \in \mathcal{U})$  and describe births and deaths of preys and predators. For convenience, we write

$$\alpha_i(s) = \alpha_{r_i(s)}(a_i(s), X(s)), \quad \gamma_i(s) = \gamma_{r_i(s)}(a_i(s)), \quad \beta_i(s) = \beta_{r_i(s)}(a_i(s)).$$

We consider the following equation for the evolution of the number of preys for  $t \geq 0$ ,

$$\begin{aligned} X(t) = X(0) &- \int_0^t \sum_{\substack{i \in \mathcal{P}(s-) \\ r_i(s-) = S}} \int_{\mathbb{R}_+} \mathbf{1}_{\{u \leq \alpha_i(s-)\}} \mathcal{N}^i(ds, du) \\ &+ \int_0^t \int_{\mathbb{R}_+} \left( \mathbf{1}_{\{u \leq \gamma X(s-)\}} - \mathbf{1}_{\{0 < u - \gamma X(s-) \leq \beta X(s-)\}} \right) \mathcal{Q}(ds, du). \end{aligned} \quad (3)$$

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

$$\begin{aligned} \langle Y(t), f \rangle &= \langle Y(0), f \rangle + \int_0^t \sum_{i \in \mathcal{P}(s-)} \partial_a f(i, r_i(s-), a_i(s-)) ds \\ &+ \int_0^t \sum_{i \in \mathcal{P}(s-)} \int_{\mathbb{R}_+} \mathbf{1}_{u \leq \alpha_i(s-)} Df(i, s-) \mathcal{N}^i(ds, du) \\ &+ \int_0^t \sum_{i \in \mathcal{P}(s-)} \int_{\mathbb{R}_+} \left( \mathbf{1}_{u \leq \gamma_i(s-)} \Delta f(i, r_i(s-), a_i(s-)) \right. \\ &\quad \left. - \mathbf{1}_{0 < u - \gamma_i(s-) \leq \beta_i(s-)} f(i, r_i(s-), a_i(s-)) \right) \mathcal{Q}^i(ds, du), \end{aligned} \quad (4)$$

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

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

Recall that  $\bar{r}$  is the complementary status of  $r$ , *i.e.* the unique element of  $\{S, M\} \setminus \{r\}$ . In this equation, status of new born are supposed to be in the manipulation state  $M$ . This choice seems natural but may sound somewhat arbitrary. However, more complex choices would require additional notations and should have no macroscopic impact.

Let us state the existence result and characterize the process using the previous stochastic differential equation. For convenience, we make the following boundedness and regularity assumptions, which are relevant for our purpose.

**Assumption 2.1.** *There exists  $a_0 \in (0, a_\infty)$  such that  $Y(0, \{S, M\}, [a_0, a_\infty)) = 0$  a.s. Besides, for any  $r \in \{S, M\}$  and  $\mathcal{K} > 0$ ,*

$$\inf_{x \in [0, \mathcal{K}]} \mathbb{E}(T_r(x)) > 0, \quad \sup_{a \in [0, a_\infty)} (\gamma_r(a) + \beta_r(a)) < \infty$$

and  $a \rightarrow \alpha_r(a, x)$  is continuous on  $[0, a_\infty)$  for any  $x \in \mathbb{N}$ .

**Proposition 2.2.** *Let  $Z(0) = (X(0), Y(0))$  with  $X(0) \in \mathbb{N}$  and  $Y(0)$  being a punctual measure in  $\mathfrak{M}(U \times \mathcal{X})$  a.s. Under Assumption 2.1, the system of stochastic differential equations (3-4) admits a unique strong solution  $Z = (X, Y)$  in  $\mathbb{D}([0, \infty), \mathbb{N} \times \mathfrak{M}(U \times \mathcal{X}))$  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 classical localization procedure and introduce the hitting time  $T_K = \inf\{t : X(t) \geq K\}$ . Before time  $T_K$ , by Assumption 2.1, mean time of change of status are lower bounded and birth and death rates of preys and predators are upper bounded. So a.s. no accumulation of jumps occurs. We need now to justify that  $T_K$  tends a.s. to infinity as  $K \rightarrow \infty$ . It is achieved by dominating the process  $X$  by a pure linear birth process (Yule process) with birth rate *per capita*  $\gamma$ . 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 argument above ensure that uniqueness holds for any positive time. Let us finally note that the system (3-4) 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  $f \in \mathcal{C}^{1,b}(U \times \mathcal{X})$ .  $\square$

## 2.2 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  $r \in \{S, M\}$ ,

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

which are continuous by continuity of  $\alpha_r$  and

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

**Lemma 2.3.** *Under Assumption 2.1, there exists  $C > 0$  such that for any continuous function  $f : [0, a_\infty) \rightarrow \mathbb{R}_+$  and  $r \in \{S, M\}$  and  $\mathcal{K} > 0$ ,*

$$\mathbb{E} \left[ \int_0^{T \wedge \tau_{\mathcal{K}}} \int_{[0, a_\infty)} f(a) \mathcal{Y}(s, \{r\}, da) ds \right] \leq C(1 + T) e^{\bar{\gamma} T} \int_{[0, a_\infty)} f(a) e^{-\int_0^a \underline{\alpha}_r(u, \mathcal{K}) du / 2} da.$$

*Proof.* Fix  $T \geq 0$  and consider an increasing sequence  $a_n$ , where  $a_{n+1} = a_n + t_n$  and  $(t_n)_n$  is a decreasing sequence of positive numbers fixed hereafter. 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

$$u_{n+1}^{i,r} \leq \mathbb{E} \left[ \sum_{j=1}^{N_{n+1}^{i,r}} \int_{T_j}^{T_j + t_{n+1}} \mathbf{1}_{\{i \in \mathcal{P}(s), a_i(s) \in [a_{n+1}, a_{n+2}), r_i(s) = r\}} \mathbf{1}_{\{\forall u \in [0, s]: X(u) \in \mathcal{K}\}} ds \right]. \quad (5)$$

Adding that  $(t_n)_n$  decreases, the status cannot change twice during time  $t_{n+1}$  and come back at level  $a_{n+1}$ . So the process does not change at all during this time and for  $s \leq t_{n+1}$ ,

$$\begin{aligned} & \mathbb{E} \left[ \mathbf{1}_{\{i \in \mathcal{P}(T_j + s), a_i(T_j + s) \in [a_{n+1}, a_{n+2}), r_i(T_j + s) = r, \forall u \in [0, s]: X(T_j + u) \in \mathcal{K}\}} \mid T_j, (X(t))_{t \leq T_j + s} \right] \\ &= \mathbb{E} \left[ e^{-\int_0^s \alpha_r(a_{n+1} + u, X(T_j + u)) du} \mathbf{1}_{\{\forall u \in [0, s]: X(T_j + u) \in \mathcal{K}\}} \mid T_j, (X(T_j + u))_{u \leq s} \right] \\ &\leq e^{-\int_0^s \underline{\alpha}_r(a_{n+1} + u, \mathcal{K}) du}, \end{aligned}$$

we get

$$u_{n+1}^{i,r} \leq \mathbb{E} \left[ \sum_{j=1}^{N_{n+1}^{i,r}} \int_0^{t_{n+1}} e^{-\int_0^s \underline{\alpha}_r(a_{n+1+u}, \mathcal{K}) du} ds \right] \leq t_n p_n^r \mathbb{E} \left[ N_{n+1}^{i,r} \right], \quad (6)$$

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

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

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  $p_j^r \leq \frac{t_{j+1}}{t_j} \left( 1 - \frac{\underline{\alpha}_j^r t_{j+1}}{2} \right)$  and setting

$$S_k^n = \sum_{j=k}^{n-1} \underline{\alpha}_j^r t_{j+1} / 2,$$

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 any continuous function  $f$ , we set  $f_n = \sup_{a \in [a_n, a_{n+1}]} f(a)$  to have

$$\begin{aligned} & \mathbb{E} \left[ \int_0^t f(a_i(s)) \mathbf{1}_{i \in \mathcal{P}(s), r_i(s)=r} ds \right] \\ & \leq \sum_{n \geq 0} f_n u_n^{i,r} \\ & \leq \frac{\mathbb{P}(b(i) \leq T \wedge \tau_{\mathcal{K}})}{t_0 \wedge 1} \sum_{n \geq 0} f_n t_n e^{-S_0^n} \left( T + \sum_{k=0}^{n-1} \mathbb{P}(A_k^i \mid b(i) \leq T \wedge \tau_{\mathcal{K}}) e^{S_k^n} \right), \end{aligned}$$

since  $u_0^{i,r} \leq T \mathbb{P}(b(i) \leq T \wedge \tau_{\mathcal{K}})$ . Choose now  $t_0 < a_\infty$  be a fixed constant and for  $n \geq 1$ ,  $t_n = t_n^h$  any positive sequence, depending on a parameter  $h$ , in such a way

$$\limsup_{h \rightarrow 0} \lim_{n \geq 1} t_n^h = 0, \quad \lim_{n \rightarrow \infty} a_n^h = \lim_{n \rightarrow \infty} \sum_{k=0}^n t_k^h = a_\infty.$$

For instance, we can choose  $t_n^h = h$  when  $a_\infty = +\infty$ . Using the convergence of the Darboux sum  $S_0^k$  to  $\int_{[0,a)} \underline{\alpha}_r(u) du/2$  when  $a_k^h \rightarrow a$ , which comes from the continuity of  $\underline{\alpha}$  and  $f$ , we get, by letting  $h \rightarrow 0$ ,

$$\begin{aligned} & \mathbb{E} \left[ \int_0^{\tau_{\mathcal{K}} \wedge T} f(a_i(s)) \mathbf{1}_{\{i \in \mathcal{P}(s), r_i(s)=r\}} ds \right] \\ & \leq C \mathbb{P}(b(i) \leq T \wedge \tau_{\mathcal{K}}) \int_{[0, a_\infty)} f(a) e^{-\int_{[0,a)} \underline{\alpha}_r(u, \mathcal{K}) du/2} da \\ & \quad \times \left[ T + \mathbb{E} \left( \mathbf{1}_{\{a_i(b(i)) \leq a\}} \exp \left( \int_0^{a_i(b(i))} \underline{\alpha}_r(u, \mathcal{K}) du/2 \right) \right) \right]. \end{aligned}$$

More precisely, the previous inequality is obtained using uniform continuity when  $f$  is compactly supported over  $[0, a_\infty)$  and extended for every function by a truncation argument and Fatou Lemma.

Recall that  $a_i(b(i))$  has a compact support in  $[0, a_\infty)$  by Assumption 2.1 and 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

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

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  $\bar{\gamma}$ .  $\square$

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

$$F_{g,f}(x, \mu) = g(x) + \langle \mu, f \rangle, \quad (7)$$

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

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

The operator  $\mathfrak{L}$  is the generator of the Markov process  $(X(t), \mathcal{Y}(t))_{t \geq 0}$ . More precisely, our SDE representation (3-4) ensures the following classical martingale problem.

**Lemma 2.4.** *Assume that Assumption 2.1 holds and that for any  $\mathcal{K} > 0$  and  $r \in \{S, M\}$ ,*

$$\int_{[0, a_\infty)} \bar{\alpha}_r(a, \mathcal{K}) e^{-\int_0^a \underline{\alpha}_r(u, \mathcal{K}) du/2} da < \infty. \quad (8)$$

Let  $g : \mathbb{R}_+ \rightarrow \mathbb{R}$  be measurable and bounded and  $f \in \mathcal{C}^{1,b}(\mathcal{X})$ . Then  $(M(t))_{t \geq 0}$  defined for  $t \geq 0$  by

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

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

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

*Proof.* The fact that  $M$  is a local martingale and the computation of its square variation is derived from our SDE representation (3-4). Indeed one can write the semi-martingale decomposition of  $F_{g,f}(X, \mathcal{Y})$  using the Poisson point measure and its compensation, see [IW14]. We only give details for the first component  $X$ :

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

where  $\tilde{\mathcal{N}}^i$  and  $\tilde{\mathcal{Q}}$  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 2.3 applied to  $f = \bar{\alpha}_r$  and Doob's inequality and our integrability assumption (8).  $\square$

### 3 Scaling and averaging

#### 3.1 Approximation of the scaled process by a dynamical system

Let us now 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 initial number of preys and predators satisfy

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

for some constants  $x_0, y_0 > 0$ . The rates for interactions are now density-dependent (rather than population-size-dependent) and we set

$$\alpha_r^K(a, x) = \alpha_r(a, x/K_1)$$

for  $r \in \{S, M\}$ , where  $\alpha_r$  is measurable on  $[0, a_\infty) \times \mathbb{R}_+$ . Interactions occur at a fast time scale which arises here through an acceleration of time. Birth and death of preys and predators (but the deaths of preys due to predation) occur at a slower time scale and we set

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

where  $\beta_r^K$  and  $\gamma_r^K$  are non-negative, measurable and bounded functions and  $\beta, \gamma$  are non-negative numbers. See Section 4.5 for a discussion on our scaling.

**Assumption 3.1.** *There exists  $a_0 \in (0, a_\infty)$  such that  $\mathcal{Y}^K(0, \{S, M\}, [a_0, \infty)) = 0$  a.s. for all  $K \geq 1$ . Besides, for any  $r \in \{S, M\}$  and  $\mathcal{K} > 0$ ,*

$$\inf_{x \in [0, \mathcal{K}]} \mathbb{E}(T_r(x)) > 0, \quad \sup_{a \in [0, a_\infty)} \gamma_r(a) + \beta_r(a) < \infty$$

and  $a \rightarrow \alpha_r(a, x)$  is continuous on  $[0, a_\infty)$  for any  $x \in \mathbb{R}_+$ .

Under this assumption, for each  $K = (K_1, K_2) \in (0, +\infty)^2$ , Proposition 2.2 ensures existence and strong uniqueness of the solution  $Z^K = (X^K, Y^K)$  of the system of stochastic differential equations (3-4) with parameters  $\alpha_r^K, \gamma_r^K, \beta_r^K, \gamma^K, \beta^K$  given above. We consider the accelerated and scaled process defined, for all  $t \geq 0$ , by

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

For every  $T > 0$ , Process  $(\mathcal{Z}^K(t), t \in [0, T])$  belongs to the space  $\mathbb{D}([0, T], \mathbb{R}_+) \times \mathfrak{M}([0, T] \times \mathcal{X})$ . Space  $\mathbb{D}([0, T], \mathbb{R}_+)$  is the classical Skorokhod space with its usual topology; see for instance [Bil13]. Space  $\mathfrak{M}([0, T] \times \mathcal{X})$  is the space of finite positive measures on  $[0, T] \times \{S, M\} \times [0, a_\infty)$  embedded with narrow convergence.

Our result relies on the following assumption on the interaction rates. It is slightly stronger than (8) and is involved in tightness proof to localize age in compact sets of  $[0, a_\infty)$ .

Analogously to the un-scaled setting, we set for  $r \in \{S, M\}$  and  $\mathcal{K} > 0$ ,

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

and

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

**Assumption 3.2.** For any  $\mathcal{K} > 0$ , there exists a continuous function  $\mathbf{V} : [0, a_\infty) \rightarrow [1, \infty)$  such that  $\lim_{a \rightarrow a_\infty} \mathbf{V}(a) = +\infty$  and for  $r \in \{S, M\}$ ,

$$\int_{[0, a_\infty)} \mathbf{V}(a) (1 + \bar{\alpha}_r(a, \mathcal{K})) e^{-\int_{[0, a)} \underline{\alpha}_r(s, \mathcal{K}) ds/2} da < \infty.$$

For  $r \in \{S, M\}$ , we write for convenience

$$p_r(x, a) = e^{-\int_0^a \alpha_r(x, u) du} \quad (9)$$

the cumulative distribution of the interaction times. We define

$$\phi(x) = \frac{1}{\int_{[0, a_\infty)} (p_S(x, a) + p_M(x, a)) da} \quad (10)$$

and

$$\psi(x) = \phi(x) \int_{[0, a_\infty)} (\beta_S(a) p_S(x, a) + \beta_M(a) p_M(x, a)) da. \quad (11)$$

Let us refer to Equation (1) and (2) in introduction for an expression of  $\phi$  and  $\psi$  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. 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 3.3.** The following system of ordinary differential equations,

$$\begin{cases} x'(t) &= (\gamma - \beta)x(t) - y(t)\phi(x(t)), \\ y'(t) &= y(t)\psi(x(t)), \end{cases} \quad (12)$$

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  $\phi$  and  $\psi$  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 be stated as follows.

**Theorem 3.4.** Under Assumptions 3.1, 3.2 and 3.3, for every  $T > 0$ , the two following assertions hold :

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  $\mathfrak{M}([0, T] \times [0, a_\infty))$ .

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

### 3.2 Proofs

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  $\alpha_r$  inherent in our framework.

First, Lemma 2.3 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 3.5.** *Under Assumption 3.1, there exists  $C > 0$  such that for any continuous function  $f$  on  $[0, a_\infty)$  and  $r \in \{S, M\}$  and  $\mathcal{K} > 0$ ,*

$$\mathbb{E} \left[ \int_0^{T \wedge \tau_{\mathcal{K}}^K} \int_{[0, a_\infty)} f(a) \mathcal{Y}^K(s, \{r\}, da) ds \right] \leq C(1+T)e^{\bar{\gamma}_r T} \int_{[0, a_\infty)} f(a) e^{-\int_{[0, a)} \underline{\alpha}_r(u, \mathcal{K}) du / 2} da.$$

*Proof.* We have

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

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 2.3.  $\square$

We now give the counterpart of the martingales of Lemma 2.4 for the scaled process. Recalling that  $F_{g,f}(x, \mu) = g(x) + \langle \mu, f \rangle$  where  $g : \mathbb{R}_+ \rightarrow \mathbb{R}$  is a bounded measurable function and  $f \in \mathcal{C}^{1,b}(\mathcal{X})$ , we set

$$\begin{aligned} \mathcal{L}^K F_{f,g}(x, \mu) &= K_1 x (\gamma(g(x + 1/K_1) - g(x)) + \beta(g(x - 1/K_1) - g(x))) \\ &+ \int_{\mathcal{X}} (\gamma_r(a) f(M, 0) - \beta_r(a) f(r, a)) \mu(dr, da) \\ &+ \lambda_K \int_{\mathcal{X}} \left( \frac{\partial}{\partial a} f(r, a) + \alpha_r(a, x) (1_{r=S} (g(x - 1/K_1) - g(x)) + f(\bar{r}, 0) - f(r, a)) \right) \mu(dr, da). \end{aligned}$$

**Lemma 3.6.** *Suppose that Assumptions 3.1 and 3.2 hold. Let  $g : \mathbb{R}_+ \rightarrow \mathbb{R}$  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

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

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

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

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 3.7.** *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

$$\sup_K \mathbb{E} \left( \sup_{t \leq T} \mathcal{Y}^K(s, \{S, M\}, [0, a_\infty)) \right) < \infty. \quad (13)$$

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

On the second hand, we can combine Assumption 3.2 with Lemma 3.5 to obtain

$$\sup_{K \geq 1} \mathbb{E} \left[ \int_0^{\tau_{\mathcal{K}}^K \wedge T} \int_{[0, a_\infty)} \mathbf{V}(a) \mathcal{Y}^K(s, \{r\}, da) ds \right] < +\infty. \quad (14)$$

for  $r \in \{S, M\}$ . Then  $\sup_K \Gamma_{\mathcal{K}}^K(H) < \infty$ , with  $H(r, a, s) = \mathbf{V}(a) \mathbf{1}_{s \leq T}$  tending to infinity as  $a \rightarrow a_\infty$ , uniformly for  $s \leq T$ . 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 3.6 gives the semi-martingale decomposition

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

where

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

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

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

Using again Assumption 3.2 and Lemma 3.5 with now  $f(a) = \bar{\alpha}_S(a, \mathcal{K})$ , we get

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

Using (13) and that  $\alpha_S$  is bounded on compact sets of  $[0, a_\infty) \times (0, \infty)$  by continuity, we obtain for any  $b \in [0, a_\infty)$ ,

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

Combining these estimates yields

$$\lim_{\delta \rightarrow 0} \sup_{\substack{K \geq 1, \\ \sigma \in \mathcal{T}^K, h \leq \delta}} \mathbb{E} [|A^K(\sigma) - A^K(\sigma + h)|] = 0. \quad (15)$$

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.  $\square$

We proceed now with identification of limiting points. Recall that the survival function of interaction times is denoted by  $p_r$  in (9) and response for prey is  $\phi$ , see (10).

**Lemma 3.8.** *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  $\mathbb{R}_+ \times [0, a_\infty)$ ,*

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

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  $K \rightarrow \infty$ . 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 in law 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]. Consequently, for all but countably many  $\mathcal{K} < \mathcal{K}_0$  and  $r \in \{S, M\}$ , we have for any continuous and bounded function  $f$  on  $[0, a_\infty)$ ,

$$\lim_{K \rightarrow \infty} \int_0^{\tau_{\mathcal{K}}^K} \int_{[0, a_\infty)} f(a) \mathcal{Y}^K(s, \{r\}, da) ds = \int_0^{\tau_{\mathcal{K}}} \int_{[0, a_\infty)} f(a) \Gamma_{\mathcal{K}_0}(ds, \{r\}, da). \quad (16)$$

Using arguments of [KKP14, Lemma 2.9], which can be applied thanks to integrability condition of Assumption 3.2 and Lemma 3.5, this convergence already holds for continuous space-time function  $f : [0, T] \times [0, a_\infty) \mapsto \mathbb{R}$  which are dominated by  $(1 + \alpha_r)$ . Let us use Lemma 3.6 with  $g = 0$  and  $f \in \mathcal{C}^{1,b}(\mathcal{X})$  such that  $f(M, \cdot) = 0$ . Writing  $f(S, \cdot) = f \in \mathcal{C}^{1,b}([0, a_\infty))$ ,

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

is a square integrable martingale, where

$$H(x, S, a) = \partial_a f(a) - \alpha_S(x, a) f(a), \quad H(x, M, a) = \alpha_M(x, a) f(0). \quad (17)$$

Using (16) guarantees that we have the following convergence in law

$$\begin{aligned} \lim_{K \rightarrow \infty} \int_0^{t \wedge \tau_{\mathcal{K}}^K} \int_{\mathcal{X}} H(\Xi_{\mathcal{K}_0}^K(s), r, a) \Gamma_{\mathcal{K}_0}^K(ds, dr, da) \\ = \int_0^{t \wedge \tau_{\mathcal{K}}} \int_{\mathcal{X}} H(\Xi_{\mathcal{K}_0}(s), r, a) \Gamma_{\mathcal{K}_0}(ds, dr, da). \end{aligned}$$

Besides (13) ensures that

$$\begin{aligned} \lambda_K^{-1} \left| \int_{[0, a_\infty)} f(a) \mathcal{Y}_{\mathcal{K}_0}^K(t, \{S\}, da) - \int_{[0, a_\infty)} f(a) \mathcal{Y}_{\mathcal{K}_0}^K(0, \{S\}, da) \right| \\ \leq \frac{C \|f\|_\infty}{\lambda_K} \sup_{t \leq T} \mathcal{Y}_{\mathcal{K}_0}^K(t, \{S\}, [0, a_\infty)), \end{aligned} \quad (18)$$

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

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

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. We have then proved that for every  $t \geq 0$  and  $f \in \mathcal{C}^{1,b}([0, a_\infty))$ , we have

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

for  $H$  defined in (17). Now, thanks to [Kur92, Lemma 1.4], we can decompose  $\Gamma_{\mathcal{K}_0}(ds, \{S\}, da)$  as  $\Gamma_{\mathcal{K}_0}(ds, \{S\}, da) = \gamma_{\mathcal{K}_0}(s, \{S\}, da) \Lambda_S(ds)$ . As (19) holds for every  $t \geq 0$ , focusing on functions  $f$  such that  $f(0) = 0$ , we obtain a.s. and for  $\Lambda_S$ -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  $\Lambda_S$ -almost all  $s \leq t \wedge \tau_{\mathcal{K}}$ , we almost surely have

$$\int_{[0, a_\infty)} (\partial_a f_S(a) - \alpha_S(\Xi_{\mathcal{K}_0}(s), a) f(a)) \gamma_{\mathcal{K}_0}(s, \{S\}, da) = 0. \quad (20)$$

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:

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

By (20), 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  $h \in C^1([0, a_\infty))$ . 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. Hence,

$$\Gamma_{\mathcal{K}_0}(ds, \{S\}, da) = \gamma_{\mathcal{K}_0}(s, \{S\}, [0, a_\infty)) \frac{p_S(\Xi_{\mathcal{K}_0}(s), a)}{\int_0^\infty p_S(\Xi_{\mathcal{K}_0}(s), w) dw} \Lambda_S(ds) da. \quad (21)$$

Similarly, we can prove

$$\Gamma_{\mathcal{K}_0}(ds, \{M\}, da) = \gamma_{\mathcal{K}_0}(s, \{M\}, [0, a_\infty)) \frac{p_M(\Xi_{\mathcal{K}_0}(s), a)}{\int_{[0, a_\infty)} p_M(\Xi_{\mathcal{K}_0}(s), w) dw} \Lambda_M(ds) da. \quad (22)$$

Now, 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) and (22) 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

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

and

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

It ends the proof.  $\square$

Let us now focus on the number of preys and the whole number of predators. We prove that limiting points satisfy the ODE (12).

**Lemma 3.9.** *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, which verifies, for all  $t \geq 0$ ,*

$$\begin{aligned} \Xi_{\mathcal{K}_0}(t \wedge \tau_{\mathcal{K}}) &= \Xi_{\mathcal{K}_0}(0) + \int_0^{t \wedge \tau_{\mathcal{K}}} ((\gamma - \beta) \Xi_{\mathcal{K}_0}(s) - \mathcal{Y}_{\mathcal{K}_0}(s) \phi(\Xi_{\mathcal{K}_0}(s))) ds \\ \mathcal{Y}_{\mathcal{K}_0}(t \wedge \tau_{\mathcal{K}}) &= \mathcal{Y}_{\mathcal{K}_0}(0) + \int_0^{t \wedge \tau_{\mathcal{K}}} \mathcal{Y}_{\mathcal{K}_0}(s) \psi(\Xi_{\mathcal{K}_0}(s)) ds. \end{aligned}$$

*Proof.* As in Lemma 3.8, 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 3.6, with now  $f \equiv 0$  and  $g \equiv \text{Id}$ . It ensures that  $M^K$ , defined for every  $t \geq 0$  by

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

is a square integrable martingale. It then converges in law to  $M$ , defined for every  $t \geq 0$  by

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

Besides  $M$  is a local martingale. Similarly and as computed in the proof of Lemma 3.7, the bracket of  $(M_{t \wedge \tau_{\mathcal{K}}}^K)_{t \geq 0}$  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 3.6 but now with  $f \equiv 1$  and  $g \equiv 0$ , to obtain that  $M^K$  defined for all  $t \geq 0$  by

$$\begin{aligned} M^K(t) &= \mathcal{Y}^K(t \wedge \tau_{\mathcal{K}}^K, [0, a_\infty)) - \mathcal{Y}^K(0, [0, a_\infty)) \\ &+ \int_0^{t \wedge \tau_{\mathcal{K}}^K} \int_{[0, a_\infty)} \beta_S(a) \Gamma_{\mathcal{K}_0}^K(ds, \{S\}, da) + \int_0^{t \wedge \tau_{\mathcal{K}}^K} \int_{[0, a_\infty)} \beta_M(a) \Gamma_{\mathcal{K}_0}^K(ds, \{M\}, da) \end{aligned}$$

is a square integrable martingale and

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

Using (13), it ensures that  $\mathbb{E}(\langle M^K \rangle(t \wedge \tau_{\mathcal{K}}^K))$  converges to 0. Consequently, the process  $(\int_0^{t \wedge \tau_{\mathcal{K}}} M^K(t) dt)_{t \in [0, T]}$  tends in law to 0 in  $\mathbb{D}([0, T], \mathbb{R}_+)$  as  $K \rightarrow \infty$ . It also tends to

$$\begin{aligned} 0 &= \Gamma_{\mathcal{K}_0}([0, T \wedge \tau_{\mathcal{K}}], \{S, M\}, [0, a_\infty)) - \mathcal{Y}(0, [0, a_\infty))(T \wedge \tau_{\mathcal{K}}) \\ &+ \int_0^{T \wedge \tau_{\mathcal{K}}} \int_{\mathcal{X}} \beta_S(a) \Gamma_{\mathcal{K}_0}(ds, dr, da) dt. \end{aligned}$$

Using Lemma 3.8 and the definition of  $\psi$ , it yields

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

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 defined for all  $t \geq 0$  by

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

It is the desired result.  $\square$

*Proof of Theorem 3.4.* Let  $(x_0, y_0) \in (\mathbb{R}_+^*)^2$  be the initial condition of  $(x, y)$ . Assumption 3.3 guarantees that for any time horizon time  $T > 0$ , 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  $(\Xi_{\mathcal{K}_0}^K, \mathcal{Y}_{\mathcal{K}_0}^K, \Gamma_{\mathcal{K}_0}^K)$  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 3.8 and Lemma 3.9 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 (12) on time interval  $[0, T \wedge \tau_{\mathcal{K}}]$ . Uniqueness guaranteed by Assumption 3.3 ensure 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  $t \leq T$ .

By Lemma 3.8 and Lemma 3.9, we also have that

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

Besides, for any continuous and bounded function  $g$ , we have both

$$\int_0^{T \wedge \tau_{\mathcal{K}}} g(t)\mathcal{Y}_{\mathcal{K}_0}^{\mathcal{K}}(t)dt \xrightarrow{K \rightarrow \infty} \int_0^{T \wedge \tau_{\mathcal{K}}} g(t)\mathcal{Y}_{\mathcal{K}_0}(t)dt$$

and

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

since  $\sum_{r \in \{S, M\}} \int_0^{a_\infty} p_r(x(t), a)\phi(x(t)) da = 1$ . It ensures that

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

As trajectories are *càdlàg*, this identity holds for every  $t \geq 0$ . Using now Lemma 3.7, it ensures the convergence of  $(\Xi^K, \mathcal{Y}^K(\cdot, \{S, M\}, [0, a_\infty)), \Gamma^K)$  over  $[0, T]$  to  $(x, y(t)p_r(x(t), a)\phi(x(t)) dt da)$  in  $\mathbb{D}([0, T], \mathbb{R}_+)^2 \times \mathfrak{M}([0, T] \times \mathcal{X})$ .  $\square$

## 4 Examples and comments

In this section, we illustrate and apply our convergence results to examples motivated from ecology. We both recover classical limiting dynamical systems and functional responses and consider some new cases. We do not discuss of technical points here. Time distributions of interactions considered in this section satisfy Assumption 3.2. It can be checked by using  $\mathbf{V} : a \mapsto a^\epsilon$  or  $\mathbf{V} : a \mapsto (a_\infty - a)^{-(1+\epsilon)}$  for some  $\epsilon > 0$ .

Let us first recall that  $T_S(x)$  and  $T_M(x)$  are the random time for searching and manipulating when the density of preys is  $x$  preys. As expected and seen above, the macroscopic death rate of preys induced by predation is

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

Besides, writing

$$\lambda_S(a) = \gamma_S(a) - \beta_S(a), \quad \lambda_M = \gamma_M - \beta_M$$

the growth rate of the population size of predators is

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

#### 4.1 Classical setting and functional responses : memory less interactions

Let's start by the classical case where memory less property is assumed for each component of the dynamic (interaction, birth, death). Times involved are then exponential. This assumption is probably not realistic for manipulating time in general. For searching time it can be justified with the hypothesis of rapid mixing of the preys in the medium where predators live. In this case, the growth rate  $\psi$  of predators simplifies as

$$\psi(x) = \frac{\lambda_S \mathbb{E}[T_S(x)] + \lambda_M \mathbb{E}[T_M(x)]}{\mathbb{E}[T_S(x)] + \mathbb{E}[T_M(x)]}.$$

We recover some classical functional responses with usual supplementary assumptions :

*i) No manipulation and search time inversely proportional to the density:*

$$T_M(x) = 0 \quad \mathbb{E}[T_S(x)] = \frac{1}{cx},$$

for some  $c > 0$ . This assumption is justified for instance where rapid mixing allows to say that each prey meets independently the predator with a small probability after an exponential time, since the minimum of independent exponential variables is exponential distributed and its parameter is the sum of each parameter.

It leads to the classical Holling type I functional response and Lotka-Volterra form for the consumption of preys (while its counterpart for predators is linear instead of bilinear):

$$\phi(x) = cx, \quad \psi(x) = (\gamma_S - \beta_S). \quad (23)$$

Let us mention that in our framework we have assumed that  $\mathbb{E}(T_M(x))$  is lower bounded on compact set, which excludes the degenerated case  $T_M = 0$ . But our proofs extend directly to this situation (with a single status instead of two) or can be obtained, at the limit, by letting  $\mathbb{E}(T_M^\varepsilon(x))$  decrease to 0 as  $\varepsilon \rightarrow 0$ .

*ii) Fixed mean manipulation time and search time inversely proportional to the density:*

$$\mathbb{E}[T_M(x)] = t_0 > 0, \quad \mathbb{E}[T_S(x)] = \frac{1}{cx}$$

for some  $c > 0$ . It leads to the classical Holling type II functional response and Rosenzweig MacArthur / Monod model :

$$\phi(x) = \frac{cx}{1 + t_0cx}, \quad \psi(x) = \lambda_S + (\lambda_M - \lambda_S)t_0 \frac{cx}{1 + t_0cx}.$$

Constant  $(\lambda_M - \lambda_S)t_0$  is related to the "yield constant" in microbial ecology, as in the chemostat equation for instance.

*iii) Fixed mean manipulation time and generalist predator.* Another usual response make the searching time of the prey increase faster with low density since the predator may dedicate more time to other species. This can leads to assuming the following assumption:

$$\mathbb{E}[T_M(x)] = t_0 > 0, \quad \mathbb{E}[T_S(x)] = \frac{1}{cx^2}.$$

This ensures the Holling type III functional response. To describe this generalist behavior of the predator more precisely, this would require to consider additional species in our model, see also [BBC18] for instance.

## 4.2 A first generalization : non-exponential time of interaction

In the models considered in the previous section, without fast mixing, we do not expect that searching time is exponentially distributed. We refer e.g. [BBC18] for some simple models where the law of the searching time is described or to [DKPvG15] for some data.

For instance, if preys are spatially uniformly distributed with fixed positions, a toy model [BBC18, Page 11] with motion towards the nearest prey leads to

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

Besides, the manipulating is not expected to be exponentially distributed either.

A first consequence of our results is that we can extend the convergence results to this non-exponentially distributed times. From the point of view of prey consumption and at the first order of the macroscopic scale, the form of the distribution has no effect (beyond its mean). Let us turn to new effects due to non-exponential laws.

## 4.3 Influence of distribution of time interaction

The consumption of prey at a first order macroscopic approximation is only sensitive to mean time of interactions through the function  $\phi$ . The impact of predation on the evolution of predators may be more subtle.

Let's give an explicit example. Assume that the individual growth rate is linked to the consumption of preys via the following age dependance

$$\forall a \leq 0, \lambda_S(a) = -A + Be^{-Ca}.$$

for some  $A, B, C > 0$ . Assuming  $A + B > 0$ , it models the fact that the more a predator is waiting for a prey, the less it (successively) reproduces and/or the fastest it dies. For sake of simplicity and following Section 4.1, let us consider the case when  $T_S(x)$  has exponential distribution with mean  $1/cx$ , we have

$$\mathbb{E} \left[ \int_0^{T_S(x)} \lambda_S(u) du \right] = -\frac{A}{cx} + \frac{Bcx}{Ccx + 1}.$$

and, again in the setting of Subsection 4.1, this gives

i) Without manipulation, i.e.  $T_M(x) = 0$ , we get

$$\phi(x) = cx, \quad \psi(x) = -A + B \frac{(cx)^2}{Ccx + 1}. \quad (24)$$

In particular,  $\psi(x) \rightarrow -A$  as  $x \rightarrow 0$  and  $\psi(x) \sim_{x \rightarrow \infty} \frac{Bc}{C}x$ . That is  $\psi(x)$  behaves as  $-A + B'x$ , with  $A < 0$  as in the Lotka-Volterra model.

ii) With fixed positive manipulation, i.e.  $t_0 = \mathbb{E}(T_M(x))$  and  $\lambda_M(x) = \lambda_M$ :

$$\phi(x) = \frac{cx}{1 + t_0cx}, \quad \psi(x) = \frac{cx}{1 + t_0cx} \left( -\frac{A}{cx} + \frac{Bcx}{Ccx + 1} + \lambda_M t_0 \right)$$

Thus is  $\psi(x) \rightarrow A < 0$  as  $x \rightarrow 0$  and  $\psi(x) \rightarrow \frac{B}{Ct_0} + c\lambda_M > 0$  as  $x \rightarrow \infty$ . Then it behaves as classical Holling type II prey-predator model:

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



We then recover here the two classic forms without directly assuming a conversion of prey into predators.

#### 4.4 About the behavior of the limiting ODEs

In this work, we show the relevance of dynamical system of the form :

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

Let us just give some hints on its long-time behavior, even if a large literature exists, for the study of Lotka-Volterra type systems, in which these remarks are detailed in more details.

On the first hand, when  $\phi : x \mapsto cx$ , for some  $c > 0$ , then it can be easily shown that, whatever the function  $\psi$ , the function

$$t \mapsto L(x(t), y(t))$$

is constant with the law conservation

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

In particular, when the curve  $L(x, y) = L(x(0), y(0))$  is bounded then  $(x, y)$  is periodic, this is for instance the case when (24) holds. In contrast, even if there is a conservation law, the choice (23) leads the predator number going to infinity and prey number to 0.

On the second hand, in more generality, an equilibrium point  $(x^*, y^*)$  of this system verifies

$$\psi(x^*) = 0, \quad y^* = \frac{\lambda x^*}{\phi(x^*)}.$$

Natural assumptions are decreasing rates  $a \mapsto \lambda_S(a)$ ,  $a \mapsto \lambda_M(a)$  and mean times of interaction  $x \mapsto \mathbb{E}[T_S(x)]$  and  $x \mapsto \mathbb{E}[T_M(x)]$ . Unfortunately, under these assumptions, we cannot state uniqueness of an equilibrium points.

Moreover the Jacobian at this equilibrium is equal to

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

When  $(x^* \phi(x^*) - \phi'(x^*))y^* \neq 0$  (this naturally exclude  $\phi : x \mapsto cx$ ) and  $\psi(x^*) \neq 0$  then the associated equilibrium is unstable. In others cases, it is not exponentially stable.

#### 4.5 Discussion, scaling and extensions

In this work, we are 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).

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 focused here on relaxing the memory less of properties of interactions. Such extensions seems to be 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 natural path for this issue via Poisson equation. Adapting the techniques to our infinite dimensional setting seems challenging.

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