A PIECEWISE DETERMINISTIC MODEL FOR A PREY-PREDATOR COMMUNITY

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We are interested in prey–predator communities where the predator population evolves much faster than the prey's (e.g., insect-tree communities). We introduce a piecewise deterministic model for these prey–predator communities that arises as a limit of a microscopic model when the number of predators goes to infinity. We prove that the process has a unique invariant probability measure and that it is exponentially ergodic. Further on, we rescale the predator dynamics in order to model predators of smaller size. This slow–fast system converges to a community process in which the prey dynamics is averaged on the predator equilibria. This averaged process admits an invariant probability measure which can be computed explicitly. We use numerical simulations to study the convergence of the invariant probability measures of the rescaled processes.

1. Introduction. Prey–predator communities represent elementary blocks of complex ecological communities and their dynamics has been widely studied. The coupled dynamics of the prey and predator populations are often described as a coupled system of differential equations. The most famous of them was introduced by Lotka [34] and Volterra [45] in the 1920s. There exist also stochastic models for these prey–predator communities as coupled birth and death processes (see Costa et al. [17]) or as stochastic perturbations of deterministic systems (e.g., Rudnicki and Pichór [43]).

In this paper, we are interested in prey–predator communities in which the predator dynamics is much faster than the prey one. Such communities are common in the wild, especially if we consider the interaction between trees and insects (see Robinson et al. [42] for the study of Aspen canopy and its arthropod community or Ludwig et al. [35] for the interaction between spruce budworm and the forest). In these communities, the number of predators is much larger than the prey number and the predator mass is smaller than the prey one. As a consequence, the reproduction and death events will be more frequent in the predator population than in the prey population. Such slow–fast scales have been studied

in some Lotka–Volterra systems, mainly in the case of periodic solutions (e.g., [41]). In the following, we study two successive scaling (large predator population and small predator mass) of a microscopic model of the prey–predator community and introduce new stochastic processes for slow–fast prey–predator systems which corresponds to these scalings limits. In particular, one interest of our work is that these processes never assume that the prey population size is infinite, as it is the case for models based on ordinary differential equations.

We introduce a hybrid model for the demographic dynamics of the community where the prey population evolves according to a birth and death process while the dynamics of predators is driven by a differential equation. The community has a deterministic dynamics between the jumps of the prey population. This piecewise deterministic process arises as limit of a prey–predator birth and death process, when the number of predators tends to infinity while the prey number remains finite. Such piecewise deterministic Markov processes (PDMP in short) were introduced by Davis in 1984 [22, 23]. They are used to model different biological phenomena. As an example, the dynamics of chemostats has been described as a piecewise deterministic model [11, 15, 20, 29]. Chemostats, in which bacteria evolve in an environment with controlled resources, correspond to the opposite setting where the prey population (the resources) evolves faster than their predators (the bacteria). Other examples can be found in neuroscience, to model the dynamics of electric potentials in neurons (see Austin [5]) or in molecular biology, where piecewise deterministic processes appear as various limits of individual based models of gene regulatory networks when the different interactions happen on different time scales (see Crudu et al. [19]).

In this paper, we study the long time behavior of the prey–predator community process. A vast literature concerns the long time behavior of continuous time Markov processes. In the setting of piecewise deterministic processes, general results have been obtained by Dufour and Costa on the relationships between the stationary behavior of the process and a sampled chain (see [18, 25]). We focus on the theory of Harris-recurrent processes (see Meyn and Tweedie [39, 40] and references therein) that relies on Foster–Lyapunov inequalities. These inequalities satisfied by the infinitesimal generator of the process, ensure that the populations do not explode in some sense. Combined with irreducibility properties, they ensure the existence of a unique invariant probability measure and that the semi-group of the process converges at exponential rate to this measure. The irreducibility of the process is nontrivial because the randomness only derives from the jumps of the slow component. Our proof relies on a fine analysis of the trajectories of the process.

Further on, we rescale the predator dynamics by dividing the coefficients of the predator differential equation by a small parameter ε. This scaling derives from the metabolic theory and illustrates the fact that the predator mass goes to 0 while the prey mass remains constant. The metabolic theory links the mass of individuals with their metabolic rates. Numerous experimental studies display relationships between the individual mass and the birth and death rates or the community car-

rying capacity (see Brown et al. [10], Damuth [21]). Here, we simplify these relationships by assuming that the predator metabolic rates increase as the invert of their mass. This slow–fast system converges as ε goes to 0 to an averaged process. In the averaged community, the predator population will always be at an equilibrium that depends on the prey number. Therefore, the prey population evolves as a birth and death process where the predator impact is constant between jumps. In this case, computations concerning the stationary behavior of the averaged process are easier because the community is fully described by the discrete dynamics of the prey population.

This paper is organized as follows. In Section 2, we present the piecewise deterministic process and the main results of this article. We give the first properties of the piecewise deterministic prey–predator community process and explain how it derives from an individual based prey–predator community process. In Section 3, we study the ergodic properties of the prey–predator community process. These properties derive from a Foster–Lyapunov inequality and the irreducibility of the continuous time process and of discrete time samples. In Section 4, we rescale the dynamics of predators and prove the convergence of the slow–fast prey–predator community to the averaged process. We prove that this averaged community admits an invariant distribution and study the convergence of the sequence of invariant measures of the slow–fast process as $\varepsilon \to 0$ with numerical simulations. Finally, we discuss in Section 5 our results in view of biological and ecological applications.

2. Model and main results.

2.1. *The piecewise deterministic model.* We consider a community of prey individuals and predators in which the predator dynamics is faster than the prey dynamics. The community is described at any time by a vector $Z_t = (N_t, H_t)$ where $N_t \in \mathbb{N}$ is the number of living prey individuals at time t and $H_t \in \mathbb{R}_+$ is the density of predators.

We assume that the prey population evolves according to a birth and death process. The individual birth rate is denoted by $b > 0$, the individual death rate by $d \geq 0$. The logistic competition among the prey population is represented by a parameter $c > 0$. The predation intensity exerted at time t on each prey individual is $B H_t$.

The predators density follows a deterministic differential equation whose parameters depend on the prey population. The individual birth rate at time t is $r B N_t$. It is proportional to the amount of prey consumed by the predator. The parameter $r \in (0, 1)$ represents the conversion efficiency of prey biomass into predator biomass. The predator individual death rate $D + C H_t$ includes logistic competition among predators ($D \geq 0$, $C > 0$).

The community dynamics is given by the differential equation

$$(2.1) \qquad \frac{d}{dt} H_t = H_t(r B N_t - D - C H_t),$$

coupled with the jump mechanism

$$
\mathbb{P}(N_{t+s} = j | N_t = n, H_t)
$$

$$
= bns + o(s) \qquad \text{if } j = n + 1, n \geq 1,
$$

$$
= n(d + cn + BH_t)s + o(s) \qquad \text{if } j = n - 1, n \geq 2,
$$

(2.2)

$$
= 1 - (b + d + cn + BH_t)ns + o(s) \qquad \text{if } n = j, n \geq 2,
$$

$$
= 1 - bs + o(s) \qquad \text{if } n = j = 1,
$$

$$
= 0 \qquad \text{otherwise.}
$$

Between the jumps of the prey population process N, the dynamics of the predator density H is deterministic. If the process Z_t is at a point $(n, h) \in \mathbb{N}^* \times \mathbb{R}_+$ after a jump, then the predator dynamics is governed by the flow ϕ_n associated with equation (2.1). More precisely, ϕ_n satisfies

$$
(2.3) \qquad \frac{d}{dt}\phi_n(h, t) = \phi_n(h, t)\big(rBn - D - C\phi_n(h, t)\big), \qquad \phi_n(h, 0) = h.
$$

Then for all $t \geq 0$,

$$
(2.4) \qquad \phi_n(h, t) = \frac{he^{t(rBn-D)}}{1 + \frac{hC}{rBn-D}(e^{t(rBn-D)} - 1)}.
$$

For $h > 0$, the solution $\phi_n(h, t)$ remains positive for all $t \geq 0$ and converges as $t \to \infty$ toward an equilibrium h_n^* given by

$$
(2.5) \qquad h_n^* = \frac{rBn - D}{C} \vee 0,
$$

where $a \vee b$ stands for the maximum of a and b. For sake of simplicity, we introduce the global flow on $\mathbb{N}^* \times \mathbb{R}_+$ $\phi((n, h), t) = (n, \phi_n(h, t))$ for $(n, h) \in \mathbb{N}^* \times \mathbb{R}_+$ and $t \geq 0$.

In the following, the state space of the prey–predator process is denoted by $E = \mathbb{N}^* \times \mathbb{R}_+$; we also define the subset $E' = \mathbb{N}^* \times (h_1^*, +\infty)$. A generic point $z \in E$ is a vector (n, h) with $n \in \mathbb{N}^*$ and $h \in \mathbb{R}_+$. The process $Z_t = (N_t, H_t)_{t \geq 0}$ belongs to the class of *Piecewise Deterministic Markov Processes* introduced by Davis (see [23]). It is a E-valued Markov process whose infinitesimal generator

$$
\mathcal{A}f(n, h) = h(rBn - D - Ch)\partial_2 f(n, h) + \big(f(n + 1, h) - f(n, h)\big)bn
$$

(2.6)

$$
+ \big(f(n - 1, h) - f(n, h)\big)n(d + cn + Bh)\mathbf{1}_{n \geq 2}
$$

is well defined for functions $f : \mathbb{N}^* \times \mathbb{R}_+ \to \mathbb{R}$ bounded measurable, continuously differentiable with respect to their second variable with bounded derivative. The domain of the extended generator (2.6) has been characterized by Davis (Theorem 26.14 in [23]).

We denote by P_t the transition semi-group and by $\mathbb{P}_{(n,h)}$ (or $\mathbb{P}_z$) the law of the process with initial condition $z = (n, h) \in E$.

REMARK 2.1. In this model, we assume that the prey population cannot become extinct since the death rate is 0 when there is only one prey individual left. When this assumption is not satisfied, the prey population process can be dominated by a population process without predator which evolves as a logistic birth and death process. It is thus absorbed in 0 in finite time. The nonextinction assumption for the prey population is biologically relevant for trees-insects communities, for example, where the tree population rarely disappears thanks to a migration of trees (e.g., seeds driven by the wind). Here, we chose to replace the migration probability of new prey individuals by the nonextinction of the prey population. This choice allows to describe the prey-predator dynamics only with individual metabolic parameters such as birth and death rates. However, it is possible to include explicitly a migration at rate $m > 0$ in the prey population. We therefore define an alternative process $(N^{(m)}, H^{(m)})$ whose infinitesimal generator is given by

$$
\begin{aligned}
\mathcal{A}^{(m)} f(n, h) = {} & h(rBn - D - Ch)\partial_2 f(n, h) \\
& + \big(f(n+1, h) - f(n, h)\big)(bn + m) \\
& + \big(f(n-1, h) - f(n, h)\big)n(d + cn + Bh).
\end{aligned}
$$
(2.7)

The process $(N^{(m)}, H^{(m)})$ is a piecewise deterministic Markov process taking its value in $E^{(m)} = E \cup \{0\} \times \mathbb{R}_+$. In the sequel, we will mention when our results hold for this alternative model including migration and explain the modification induced by the migration.

2.2. *Main results.* Our main questions on the prey–predator process are twofold. First, we are interested in the long time behavior of the process Z.

THEOREM 2.2. *The community process $(Z_t)_{t \geq 0}$ is exponentially ergodic. It converges toward its unique invariant probability measure π at an exponential rate. There exist $0 < \rho < 1$ and $0 < R < \infty$ such that, for all $z = (n, h) \in E'$,*

$$
\| P_t(z, \cdot) - \pi \|_{\mathrm{TV}} \leq R\rho^t\big(n + hr^{-1}\big).
$$

Section 3 is devoted to the proof of the exponential ergodicity of Z. Our theorem relies on the theory of Harris recurrent processes, whose main results are recalled in Section 3.1. In the setting of piecewise deterministic processes, these results have been used to derive ergodic properties of different processes (e.g., an additive increase multiplicative decrease process [30], a stress release process [33] or a wealth-employment process [7]). There exists also general results proven by [8] in the specific case where the deterministic dynamics admits a compact positive invariant set. The case of the prey–predator process $Z = (N, H)$ is more complex since the process is in dimension 2 and neither the jump rates nor the deterministic trajectories are bounded.

Our second main result concerns a scaling limit of the process Z corresponding to the biological assumption that the predator mass is small. We introduce a sequence of processes Z^ε for the rescaled parameters $r^\varepsilon = r/\varepsilon$, $D^\varepsilon = D/\varepsilon$ and $C^\varepsilon = C/\varepsilon$. As ε tends to 0, the dynamics of the fast component H^ε is accelerated between the jumps of the slow component N^ε. Therefore, we expect that in the slow–fast limit, the prey population only depends on the equilibrium h_n^* of the predator density. The following theorem is a simplified version of our convergence result stated in Theorem 4.2.

THEOREM 2.3.   *Fix $T > 0$ and assume $rB - D > 0$. We suppose that the sequence of initial conditions $(Z_0^\varepsilon)_{0<\varepsilon\leq 1}$ converges to $\overline{Z}_0$ in law, and moreover, that*

$$\sup_{0<\varepsilon\leq 1} \mathbb{E}\big((N_0^\varepsilon)^4\big) < \infty, \qquad \sup_{0<\varepsilon\leq 1} \mathbb{E}\big((H_0^\varepsilon)^4\big) < \infty.$$

Then the sequence N^ε converges in law toward $\overline{N}$ in $\mathbb{D}([0, T], \mathbb{N})$ as $\varepsilon \to 0$.

The process $\overline{N}$ is a pure jump process on $\mathbb{N}^*$ whose infinitesimal generator is well defined for every measurable and bounded function $f : \mathbb{N}^* \to \mathbb{R}$ by

$$(2.8) \quad \mathcal{L}f(n) = \big(f(n+1) - f(n)\big)bn + \big(f(n-1) - f(n)\big)n\big(d + cn + Bh_n^*\big)\mathbf{1}_{n\geq 2}.$$

The proof of the convergence, stated in Section 4 relies on a compactness-identification technique. The result proven in Section 4, Theorem 4.2, also states the convergence in law of the sequence of occupation measures associated with the fast component H^ε (see [31]). The main interest of this result is that in the limit, the study of the prey-predator community is simplified, since it is entirely described by the one-dimensional birth and death process $\overline{N}$.

2.3. *Pathwise construction and first properties.* Following Fournier and Méléard [28], we construct a trajectory of the prey–predator process Z as a solution of a stochastic differential equation driven by Poisson point processes. Let $Q_1(ds, du)$ and $Q_2(ds, du)$ be two independent Poisson point measures on $\mathbb{R}_+ \times \mathbb{R}_+$ with intensity $ds\, du$ the product of Lebesgue measures. We define for any initial condition $(n, h) \in E$ the coupled dynamics

$$N_t = n + \int_0^t \int_{\mathbb{R}_+} \mathbf{1}_{u\leq bN_{s-}} Q_1(ds, du)$$

$$(2.9) \qquad - \int_0^t \int_{\mathbb{R}_+} \mathbf{1}_{u\leq N_{s-}(d+cN_{s-}+BH_{s-})}\mathbf{1}_{N_{s-}\geq 2} Q_2(ds, du),$$

$$\frac{d}{dt}H_t = H_t(rBN_t - D - CH_t), \qquad H_0 = h.$$

A unique solution of these equations exists as long as the number of individuals remains finite.

THEOREM 2.4. *Under the assumption that there exists $p \geq 1$ such that*

$$\mathbb{E}\big((N_0)^p\big) < \infty \quad and \quad \mathbb{E}\big((H_0)^p\big) < \infty,$$

(i) *For all $T > 0$*

$$\mathbb{E}\Big(\sup_{t \in [0,T]} (N_t)^p \Big) < \infty \quad and \quad \mathbb{E}\Big(\sup_{t \in [0,T]} (H_t)^p \Big) < \infty,$$

(ii) *If $p \geq 1$, there exists a unique solution $(Z_t)_{t \geq 0} \in \mathbb{D}(\mathbb{R}_+, E)$ of (2.9). Its infinitesimal generator is given by (2.6) for any bounded measurable functions f with $f(n, \cdot) \in \mathcal{C}_b^1(\mathbb{R}_+)$ for all $n \in \mathbb{N}^*$.*

Moreover, the process Z_t is a Feller process in the sense that for any $g : E \to \mathbb{R}$ continuous and bounded, the function $z \mapsto \mathbb{E}_z(g(Z_t))$ is continuous and bounded on E, $\forall t \geq 0$.

(iii) *If $p \geq 2$, for all bounded measurable functions f with $f(n, \cdot) \in \mathcal{C}_b^1(\mathbb{R}_+)$ for all $n \in \mathbb{N}^*$ and for all $z \in \mathbb{N}^* \times \mathbb{R}_+$,*

$$M_t^f = f(Z_t) - f(z) - \int_0^t \mathcal{A}f(Z_s)\, ds,$$

is a L^2-martingale starting at 0 with quadratic variation

$$\langle M^f \rangle_t = \int_0^t \big(f(N_s + 1, H_s) - f(N_s, H_s) \big)^2 b N_s$$
$$+ \big(f(N_s - 1, H_s) - f(N_s, H_s) \big)^2 N_s(d + cN_s + BH_s)\, ds.$$

PROOF. (i) Let us remark that the process $(N_t, t \geq 0)$ is stochastically dominated by a pure birth process $(\widetilde{N}_t, t \geq 0)$ that jumps from n to $n + 1$ at rate bn. From Theorem 3.1 in [28], we know that for all $T > 0$ $\mathbb{E}(\sup_{t \in [0,T]}(\widetilde{N}_t)^p) < \infty$, and thus $\mathbb{E}(\sup_{t \in [0,T]}(N_t)^p) < \infty$.

Concerning the predator density, we notice that for all $(n, h) \in \mathbb{N}^* \times \mathbb{R}_+$ the solution $\phi_n(h, t)$ of (2.3) satisfies

(2.10) $$\forall t \geq 0 \qquad 0 < \phi_n(h, t) \leq h \vee h_n^*.$$

Since $h_n^* \leq rBn/C$, we obtain that for all $t \geq 0$

$$H_t \leq H_0 \vee \frac{rB}{C} \sup_{s \in [0,t]} N_s.$$

Then

$$\mathbb{E}\Big(\sup_{t \in [0,T]} (H_t)^p \Big) \leq \mathbb{E}\big((H_0)^p\big) + \frac{rB}{C}\mathbb{E}\Big(\sup_{t \in [0,T]} (N_t)^p \Big) < \infty.$$

The fact that the infinitesimal generator is given by (2.6) and the proof of (iii) can be easily adapted from [28].

It remains to prove that Z_t is a Feller process. We adapt the method introduced by Davis [23]. The prey–predator community process differs from Davis' setting since the jump rates of the prey population are not bounded. However, we overcome this difficulty using the moment properties given in (i). We denote by $(T_1, T_2, \ldots)$ the sequence of jump times of the prey population. It is always well defined since the jump rate admits a positive lower bound b. Let $g \in \mathcal{C}_b(E)$ and $\psi \in \mathcal{C}_b(E \times \mathbb{R}_+)$. We define the application G_ψ on $E \times \mathbb{R}_+$ by

$$G_\psi(z, t) = \mathbb{E}_z\big(g(Z_t)\mathbf{1}_{t \le T_1} + \psi(Z_{T_1}, t - T_1)\mathbf{1}_{t > T_1}\big).$$

Let $e_1 = (1, 0)$ be the first vector of the canonical basis on E and let us define a function Θ on $E \times \mathbb{R}_+$ by $\Theta(z, t) = \int_0^t \theta(\phi(z, s)) \, ds$ with

$$(2.11) \qquad \theta(z) = \theta(n, h) = n(b + d + cn + Bh).$$

The function $t \mapsto 1 - e^{-\Theta(z, t)}$ is the cumulative distribution function of the first jump time T_1 conditionally on $\{Z_0 = z\}$. Then

$$G_\psi(z, t) = e^{-\Theta(z, t)} g\big(\phi(z, t)\big) + \int_0^t \int_E e^{-\Theta(z, t)}\big[\psi\big(\phi(z, s) + e_1, t - s\big)bn$$
$$+ \psi\big(\phi(z, s) - e_1, t - s\big)n\big(d + cn + B\phi_n(h, s)\big)\big] ds.$$

Let us remark that $z \mapsto G_\psi(z, t)$ is continuous since $z \mapsto \phi(z, t)$ is continuous by Cauchy–Lipschitz theorem for all $t \ge 0$, and the integrand is locally bounded.

We now iterate the kernel G_ψ. From Lemma (27.3) in [23], we get that $\forall k \in \mathbb{N}$,

$$G_\psi^{k+1}(z, t) = G_{G_\psi}^k(z, t) = \mathbb{E}_z\big(g(Z_t)\mathbf{1}_{t \le T_{k+1}} + \psi(Z_{T_{k+1}}, t - T_{k+1})\mathbf{1}_{t > T_{k+1}}\big).$$

Then

$$\big|G_\psi^k(z, t) - \mathbb{E}_z\big(g(Z_t)\big)\big| \le \mathbb{E}_z\big(\big(|g(Z_t)| + |\psi(Z_{T_k}, t - T_k)|\big)\mathbf{1}_{t > T_k}\big)$$
$$\le \big(\|g\|_\infty + \|\psi\|_\infty\big)\mathbb{P}_z(T_k < t).$$

We deduce from (i) with $p = 1$, that the sequence of jump times $(T_k)_{k \in \mathbb{N}}$ converges almost surely to ∞, hence $\mathbb{P}_z(T_k < t) \longrightarrow_{k \to \infty} 0$. To obtain the continuity of $z \mapsto P_t g(z)$, it is sufficient to prove that the probability $\mathbb{P}_z(T_k < t)$ converges to 0 uniformly on compact sets of E.

Let K be a compact set of E, and set $N_+ = \sup\{n; (n, h) \in K\}$ and $H_+ = \sup\{h; (n, h) \in K\}$. We construct a sequence of jump times $(S_k)_{k \in \mathbb{N}}$ that stochastically dominates the sequence of jump times $(T_k)_{k \in \mathbb{N}}$ for any initial condition in K. We start by bounding from above the prey and the predator populations. Similarly as above, we define a prey pure jump process $(X_t)_{t \ge 0}$ starting from N_+ and a deterministic predator population process Y_t starting from H_+:

$$X_t = N_+ + \int_0^t \int_{\mathbb{R}_+} \mathbf{1}_{u \le b X_{s-}} Q_1(ds, du),$$

$$\frac{d}{dt} Y_t = Y_t(r B X_t - D - C Y_t), \qquad Y_0 = H_+.$$

The difference with point (i) lies in the fact that this coupling bounds from above every trajectory with initial condition in K: more precisely for any initial condition $z \in K$, $N_t \leq X_t$ and $H_t \leq Y_t$ for all $t \geq 0$, almost surely.

We introduce a Poisson point process with intensity $\theta(X_t, Y_t)\, dt$ and denote by $(S_i)_{i \in \mathbb{N}}$ its sequence of jump times. Since the rate function θ increases, we deduce that for all $z \in E$ and $t > 0$,

$$\mathbb{P}_z(T_k < t) \leq \mathbb{P}(S_k < t).$$

The probability $\mathbb{P}(S_k < t)$ converges toward 0 as $k \to \infty$, since for all $T > 0$, $\mathbb{E}(\sup_{s \in [0,T]} X_s) < \infty$ and $\mathbb{E}(\sup_{s \in [0,T]} Y_s) < \infty$. $\quad\square$

2.4. *Derivation from an individual-based model.* In this part, we justify that the model (2.1)–(2.2) derives from a microscopic model for the prey–predator community. We introduce a scaling parameter K tending to ∞ and consider that the number of predator is of order K while the prey number remains of order 1. At each time $t \geq 0$, the microscopic community is represented by a vector (N_t^K, H_t^K) where $N_t^K \in \mathbb{N}$ is the prey number and $H_t^K \in \mathbb{N}$ is the number of predators. This process is a two-type continuous time Markov process whose transition rates are given for all $(n, h) \in \mathbb{N}^2$ by

$$(n, h) \to (n+1, h) \qquad \text{at rate } nb,$$
$$(n-1, h) \qquad \text{at rate } n(d + cn + B^K h)\mathbf{1}_{n \geq 2},$$
$$(n, h+1) \qquad \text{at rate } hr^K B^K n,$$
$$(n, h-1) \qquad \text{at rate } h(D^K + C^K h).$$

The parameters B^K, r^K, D^K and C^K are chosen as follows:

$$B^K = \frac{B}{K}, \qquad r^K = Kr, \qquad D^K = D, \qquad C^K = \frac{C}{K}.$$

The predation and the competition among predators are normalized following [12, 28]. The parameter of conversion efficiency r^K is scaled in order to maintain constant the benefit from predation.

We consider the limit as $K \to \infty$ of the rescaled process $(N^K, \frac{H^K}{K})$.

THEOREM 2.5. *Assuming that the sequence of initial conditions* $(N_0^K, \frac{H_0^K}{K})_{K \geq 0}$ *satisfies*

$$(2.12) \qquad \sup_K \mathbb{E}\left(\left(N_0^K + \frac{H_0^K}{K}\right)^3\right) < \infty$$

and converges in law toward $(n_0, h_0) \in E$, *then for all* $T > 0$ *the process* $(N^K, \frac{H^K}{K})_{K \geq 0}$ *converges in law in* $\mathbb{D}([0, T], E)$ *toward the piecewise deterministic process* (N_t, H_t) *defined by* (2.1)–(2.2) *with initial condition* (n_0, h_0).

The proof of this theorem is based on a compactness-uniqueness argument which derives from Theorem 3.1 in [19] and will not be developed here. The moment assumptions (2.12) ensure that the processes Z^K and Z are well defined and that the assumptions of Theorem 3.1 in [19] are satisfied. In the latter, the authors prove a similar result for a gene regulatory network in which the chemical reactions occur at slow or fast speed.

3. Ergodic properties. In this section, we study the ergodic properties of the prey–predator community process Z. We will prove the irreducibility of the process and of specific sampled chains. From these properties and a Foster–Lyapunov criterion, we will show that there exists a unique invariant probability measure and that the process is exponentially ergodic.

3.1. *Some definitions and known results.* Let us first recall some definitions. Let $(X_t)_{t \geq 0}$ be a Feller process taking values in E a locally compact and separable metric space. We denote by $\mathcal{L}$ its infinitesimal generator and by P_t its semi-group. For every $A \in \mathcal{B}(E)$, we set $\tau_A = \inf\{t \geq 0, X_t \in A\}$.

The process X_t is *irreducible* if there exists a σ-finite measure ν on E, called irreducibility measure, such that for all $A \in \mathcal{B}(E)$

$$\nu(A) > 0 \quad \Longrightarrow \quad \forall x \in E, \qquad \mathbb{E}_x\left(\int_0^\infty \mathbf{1}_A(X_t)\,dt\right) > 0.$$

The process X_t is *Harris recurrent* if there exists a σ-finite measure μ on E such that $\forall A \in \mathcal{B}(E)$

$$\mu(A) > 0 \quad \Longrightarrow \quad \forall x \in E, \qquad \mathbb{P}_x(\tau_A < \infty) = 1.$$

A Harris recurrent Markov process is always irreducible (see [39]).

Moreover, a Harris recurrent process X_t has an invariant measure π (see [6]). In the case where this measure is finite, we say that X_t is *positive Harris recurrent*.

For continuous time processes, the positive Harris recurrence can be derived from a Foster–Lyapunov inequality satisfied by the infinitesimal generator on some *petite* set. Recall that a set $C \subset E$ is *petite* if there exist a probability measure α on $\mathbb{R}_+$, and a nondegenerate measure ν_α on E such that for any $z \in C$

$$\int_0^\infty P_t(z, \cdot)\alpha(dt) \geq \nu_\alpha(\cdot).$$

For an irreducible Feller process whose irreducibility measure has a support with a nonempty interior, all compact sets of E are *petite* sets (from Theorem 5.1 and 7.1 in [44]).

We recall sufficient conditions for the positive Harris recurrence of a Feller process.

THEOREM A (Theorem 4.2 in [40]). *Let $(X_t)_{t \geq 0}$ be a Feller process taking values in E. If the following conditions are satisfied*:

(i) *X is irreducible with respect to some measure whose support has a non-empty interior.*

(ii) *Foster–Lyapunov inequality: there exist a function $V : E \to [1, \infty[$ such that $\lim_{|z| \to \infty} V(z) = \infty$, a compact set $K \subset E$ and two constants $\delta, \gamma > 0$ such that*

$$\mathcal{L}V(z) \leq -\gamma V(z) + \delta \mathbf{1}_K(z) \qquad \forall z \in E.$$

Then X is positive Harris recurrent and there exists a unique invariant probability measure π. Moreover $\pi(V) < \infty$.

The process X_t is *ergodic* if it has a unique invariant probability measure π and if

$$\lim_{t \to \infty} \| P_t(x, \cdot) - \pi \|_{\mathrm{TV}} = 0 \qquad \forall x \in E.$$

Moreover, X_t is *exponentially ergodic* if there exist a function $R : E \to (0, \infty)$ and $0 < \rho < 1$ such that

$$\| P_t(x, \cdot) - \pi \|_{\mathrm{TV}} \leq R(x) \rho^t \qquad \forall x \in E.$$

In the case of continuous time Markov processes on continuous state spaces, the ergodicity is related to the behavior of skeletons of the process. A skeleton corresponds to a sampling of the continuous time process at some fixed time. For all $\Delta > 0$, the Δ-skeleton of X is the Markov chain $(X_{k\Delta})_{k \in \mathbb{N}}$ with transition kernel P_Δ. We recall sufficient conditions for exponential ergodicity of a Feller process.

THEOREM B (Theorem 6.1 in [39] and Theorem 6.1 in [40]). *Let $(X_t)_{t \geq 0}$ be a Feller process taking values in E which satisfies both conditions* (i) *and* (ii) *in Theorem* A. *If furthermore there exists an irreducible skeleton $(X_{k\Delta})_{k \in \mathbb{N}}$ ($\Delta > 0$), then X is exponentially ergodic and there exist $0 < \rho < 1$ and $0 < R < \infty$ such that, for all $z \in E$,*

$$\| P_t(z, \cdot) - \pi \|_{\mathrm{TV}} \leq R \rho^t V(z).$$

Let us briefly explain the origin of the condition on the skeleton of the process. Since X_t is positive Harris recurrent, the irreducible skeleton $(X_{k\Delta})_{k \in \mathbb{N}}$ has an invariant probability measure. Hence, the skeleton chain is positive recurrent and aperiodic (see Theorem 5.1 in [39]). The irreducibility is crucial to obtain the aperiodicity.

Moreover, from the Foster–Lyapunov inequality (ii) in Theorem A, we deduce that the skeleton chain also satisfies a Foster–Lyapunov inequality with the same function V: there exist $\gamma' < 1$ and $\delta' > 0$ such that for every initial condition $z \in E$

$$\mathbb{E}_z\big(V(X_\Delta)\big) \leq \gamma' V(z) + \delta'.$$

From Theorem 6.3 in [38], we deduce that the skeleton $(X_{k\Delta})_{k\in\mathbb{N}}$ is geometrically ergodic. There exist $0 < \rho < 1$ and $0 < R < \infty$ such that for all $z \in E$

$$\|P_{k\Delta}(z, \cdot) - \pi\|_{\mathrm{TV}} \leq R\rho^k V(z).$$

The exponential ergodicity of the continuous time process then derives from the semi-group property.

3.2. *Irreducibly.*   In this section, we study the irreducibility of $(Z_t)_{t\geq 0}$ in $E = \mathbb{N}^* \times \mathbb{R}_+$. Let us highlight that a Borel set $A \in \mathcal{B}(E)$ can always be written as

$$A = \bigcup_{k\geq 1}\{k\} \times A_k,$$

where $A_k \in \mathcal{B}(\mathbb{R}_+)$. We introduce the measure σ on E as the product of the counting measure on $\mathbb{N}^*$ and the Lebesgue measure λ on $\mathbb{R}_+$:

$$(3.1) \qquad\qquad \forall A \in \mathcal{B}(E) \qquad \sigma(A) = \sum_{k\geq 1}\lambda(A_k).$$

In particular, if $\sigma(A) > 0$, then there exist $k \in \mathbb{N}^*$ such that $\lambda(A_k) > 0$.

THEOREM 3.1.   (i) *If $rB - D \leq 0$, then the process $(Z_t, t \geq 0)$ is irreducible for the measure σ on E given by* (3.1).

(ii) *Otherwise, the process $(Z_t, t \geq 0)$ is irreducible for the measure σ' which is the restriction of σ to the space $E' = \mathbb{N}^* \times (h_1^*, +\infty)$, for h_1^* defined in* (2.5).

The dichotomy in this result derives from the fact that when $h_1^* > 0$, the set $\mathbb{N}^* \times (0, h_1^*)$ is transient for the dynamics. Indeed, the flows $t \mapsto \phi_n(h, t)$ are increasing functions for $(n, h) \in \mathbb{N}^* \times (0, h_1^*)$ and, therefore, the trajectories cannot enter this area.

In the sequel, we prove a stronger result on the probability for the process Z_t to reach open Borel sets, from which Theorem 3.1 follows.

THEOREM 3.2.   (i) *In the case where $rB - D \leq 0$, we consider an interval $I = \{k\} \times (h_-, h_+)$ with $0 \leq h_- < h_+$ and $k \in \mathbb{N}^*$. Then for every initial condition $(n, h) \in E$, there exists $t_0 > 0$ such that $\forall t \geq t_0$,*

$$\mathbb{P}_{(n,h)}(Z_t \in I) > 0.$$

(ii) *We have a similar result in the case where $rB - D > 0$ for any interval $I \subset E'$ such that $\sigma'(I) > 0$ and any initial condition $(n, h) \in E'$.*

The proof derives from the construction of ideal trajectories and from comparisons between the different predator flows.

PROOF OF THEOREM 3.2.   (i) We assume that $rB - D \leq 0$ which is equivalent to $h_1^* = 0$.

We consider different cases depending on the position of the interval $I = \{k\} \times (h_-, h_+)$ with respect to the line $n \mapsto h_n^*$ of the predator equilibria and on the initial condition $(n, h) \in E$. These cases are illustrated in Figures 1 to 7. In these figures, the state space E is represented as the positive quadrant of $\mathbb{R}^2$ separated by the line $n \mapsto h_n^*$. The process $(Z_t, t \geq 0)$ can only cross this line by a jump of the prey number. When the process is above this line, the predator density decreases, while it increases when the process is under this line. The intervals which cross this line [i.e., such that $h_k^* \in (h_-, h_+)$] will play a specific role in the proof since they are stable by the predator flow ϕ_k.

We introduce additional notations: for all $m \in \mathbb{N}^*$, and $x, y \in \mathbb{R}_+$ we set $r^m(x, y)$ the time needed for the flow ϕ_m to go from x to y. This time is well defined for $x \geq y > h_m^*$ or $x \leq y < h_m^*$. In these cases, it satisfies

$$\phi_m(x, r^m(x, y)) = y.$$

First case: *The interval I is stable for the flow ϕ_k (i.e., $h_k^* \in (h_-, h_+)$ if $h_k^* > 0$ or $h_- = h_k^* = 0$ otherwise).* Our aim is to prove that for any $t > t_0$, $\mathbb{P}_{(n,h)}(Z_t \in I) > 0$ for some $t_0 \geq 0$. The idea is to construct simple trajectories which enter the interval I and arise with positive probability.

We split the reasoning into different sub-cases depending on the initial condition. We focus on initial conditions such that $h > h_n^*$. The other cases can be treated similarly by symmetry.

(A) *If $n \leq k$ and $h_- \vee h_n^* < h$.*

We first consider the specific sub-case where $n \leq k$ and $h_- < h_n^* \leq h \leq h_+$ (see Figure 1).

In this setting, we are interested in trajectories with exactly $k - n$ prey births. These trajectories reach the line $\{k\} \times \mathbb{R}_+$. Furthermore, the number of predators
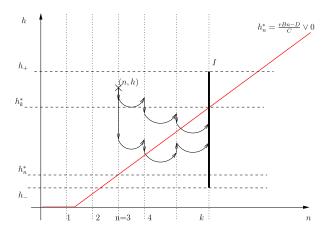

FIG. 1. *Case* 1(A). *Different ideal trajectories for the specific sub-case where the initial condition (n, h) satisfies $n \leq k$ and $h_- < h_n^* \leq h \leq h_+$. The red line is the map $m \mapsto h_m^*$.*

remains in the interval $[h_n^*, h \vee h_k^*] \subset (h_-, h_+)$. This property derives from the fact that the predator density decreases as long as $H_t \geq h_{N_t}^*$ and remains therefore smaller than h but greater than $h_{N_t}^* \geq h_n^*$ since $N_t \geq n$. If the process jumps below the line $n \mapsto h_n^*$, then the predator density increases and remains bounded by h_k^*. Thus, after $k - n$ births events, the process reaches the interval I.

Let us now prove that such trajectories occur with positive probability. We first compute the probability that the first jump is a birth:

$$\mathbb{P}_{(n,h)}(\text{first jump is a birth}) = \mathbb{E}_{(n,h)}\big(\mathbb{E}(\mathbf{1}_{\text{first jump is a birth}}|T_1)\big)$$

$$= \mathbb{E}_{(n,h)}\left(\frac{bn}{\theta(n, \phi_n(h, T_1))}\right)$$

$$\geq \frac{bn}{\theta(n, \phi_n(h, h \vee h_n^*))},$$

where the total jump rate $\theta(n, h)$ defined in (2.11) increases in n and h.

Then by induction, the probability that the $k - n$ first jumps are births, is greater than

$$\frac{bn}{\theta(n, h \vee h_n^*)} \times \frac{b(n+1)}{\theta(n+1, h \vee h_n^*)} \times \cdots \times \frac{b(k-1)}{\theta(k-1, h \vee h_n^*)} > 0.$$

Recall that the sequence of jump times of the prey population is denoted by $(T_m)_{m \in \mathbb{N}}$. Let us fix $t > 0$. Using the lower bound h_n^* of the predator population size, we bound from below the probability that the $k - n$ births happen before t by

$$\mathbb{P}_{(n,h)}(T_{k-n} < t | k - n \text{ births}) \geq \mathbb{P}\big(\mathcal{P}\text{oiss}\big(t\theta(n, h_n^*)\big) \geq k - n\big) > 0,$$

where $\mathcal{P}\text{oiss}(t\theta(n, h_n^*))$ is a random variable with Poisson distribution of parameter $t\theta(n, h_n^*)$. Finally, we request that no other jump occurs before t, then

$$\mathbb{P}(n, h)(T_{k-n+1} > t | T_{k-n} < t \text{ and } k - n \text{ births}) \geq \exp\big(-t\theta(k, h_+)\big) > 0.$$

Then the event $\{T_{k-n+1} > t \text{ and } T_{k-n} < t \text{ and } k - n \text{ births}\}$ has positive probability, and on this event $Z_t \in I$.

Let us come back to the general case where $n \leq k$ and $h_- \vee h_n^* < h$ (see Figure 2).

We will consider the trajectories which remain on $\{n\} \times \mathbb{R}_+$ until H_t reaches h_+. Then we will request that $k - n$ births occur before the predator population size reaches h_-.

Therefore, we define $r_1 = r^n(h, h_+)$ when it exists and set $r_1 = 0$ otherwise. The first step is to require that $T_1 > r_1$. Since in this case $h_+ > h_k^* \geq h_n^*$ and $h > h_n^*$, the flow $\phi_n(h, \cdot)$ decreases, and thus

$$\mathbb{P}_{(n,h)}(T_1 > r_1) = \exp\left(-\int_0^{r_1} \theta\big(n, \phi_n(h, s)\big) ds\right) \geq \exp\big(-r_1\theta(n, h)\big) > 0.$$

Then we define $r_2 = r^n(h_+, h_-)$ when it exists [i.e., if $h_n^* \in (h_-, h_+)$] and set $r_2 = +\infty$ otherwise. It is important to remark that $r_1 + r_2 = r^n(h, h_-)$. The specific case considered above corresponds to $r_1 = 0$ and $r_2 = +\infty$.
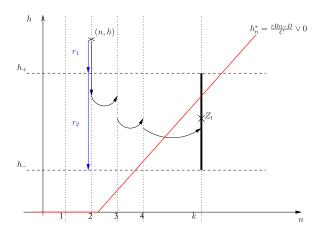
FIG. 2. *Case* 1(A). *An ideal trajectory. The vertical blue arrows represent the time needed by the flow to get from the tail to the head of the arrow.*

We request that $T_{k-n} < r_1 + r_2$ and that these $k - n$ jumps are births. An easy adaptation of the previous result shows that this event has positive probability.

Moreover, at time T_{k-n}, $H_{T_{k-n}} \in (h_-, h_+)$. The upper bound $H_{T_{k-n}} < h_+$ derives from the same reasoning as above. The lower bound of the predator density comes from comparisons of the different flows. We denote by F_l the vector field associated with ϕ_l: $F_l(y) = y(rBl - D - Cy)$, for $l \in \mathbb{N}^*$.

The first birth occurs at time $r_1 < T_1 < r_1 + r_2$ and $H_{T_1} = \phi_n(h, T_1) > h_-$. The second jump happens at $T_2 < r_1 + r_2$ and $H_{T_2} = \phi_{n+1}(H_{T_1}, T_2 - T_1) > h_-$. Since $F_{n+1}(y) > F_n(y)$ for all $y \in \mathbb{R}_+$, then $\phi_{n+1}(H_{T_1}, T_2 - T_1) \geq \phi_n(H_{T_1}, T_2 - T_1)$, and thus $H_{T_2} \geq \phi_n(h, T_2)$. Then by iteration, we deduce that $H_{T_{k-n}} \geq \phi_n(h, T_{k-n}) > \phi_n(h, r_1 + r_2) \geq h_-$.

We define the time $t_0 = r_1 + r_2 \mathbf{1}_{r_2 < +\infty}$. Let us now consider $t > t_0$ and finally request that $T_{k-n+1} > t$. As in the previous case, we deduce that these trajectories occur with positive probability and satisfy $Z_t \in I$.

(B) *If $n \leq k$ and $h_n^* \leq h \leq h_-$. (See Figure 3.)*

The challenge is to increase the predator density up to h_-. Let us fix a time $s > 0$. We consider trajectories which have exactly $k - n$ jumps before s, which are births. Then using a similar reasoning to case (A), we deduce that $H_s \geq \phi_n(h, s)$. We define the time $r_1 = r^k(\phi_n(h, s), h_-)$. Therefore, for every $t > t_0 = s + r_1$, if no jump occurs on the time interval $[s, t]$, then

$$H_t = \phi_k(H_s, t - s) > \phi_k(H_s, r_1),$$

since $t - s > r_1$. Moreover, $\phi_k(H_s, r_1) \geq \phi_k(\phi_n(h, s), r_1) = h_-$ as $H_s \geq \phi_n(h, s)$. Thus, $Z_t \in I$.

(C) *If $n > k$ and $h > h_n^*$. (See Figure 3.)*

The reasoning is similar to the previous case, except that we aim at decreasing the predator density. We consider trajectories which have exactly $n - k$ deaths
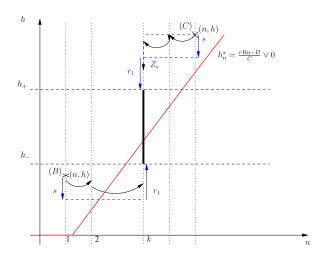
FIG. 3. *Cases* 1(B) *and* 1(C). *Examples of ideal trajectories.*

before $s > 0$. Then $H_s \leq \phi_n(h, s)$. We define the time $r_1 = r^k(\phi_n(h, s), h_+)$ when $\phi_n(h, s) \geq h_+$ and set $r_1 = 0$ otherwise. For every $t > t_0 = s + r_1$, if no jump occurs on the time interval $[s, t]$, then $Z_t \in I$.

Second case: *The interval* I *is below the line* $n \mapsto h_n^*$ (*i.e.*, $h_k^* > h_+$). We will construct an auxiliary interval which is stable for the predator flow. Then we will prove that starting from this interval, the process enters I in some finite time.

We introduce the integer $m = \max\{l \in \mathbb{N}^*, h_l^* < h_+\}$. Once again, we split the reasoning in three cases depending on the position of h_m^* with respect to (h_-, h_+) and the positivity of h_m^*.

(A) *If* $h_- < h_m^* < h_+$.

We define the interval $J = \{m\} \times (\frac{h_+ + h_m^*}{2}, h_-)$ which is stable for the flow ϕ_m (see Figure 4). Then, from the first case, there exists t_0, such that $\forall t \geq t_0$, $\mathbb{P}(Z_t \in J) > 0$.

We set $r_1 = r^k(\frac{h_+ + h_m^*}{2}, h_+)$. Let us remark that the trajectories starting from $(n_0, h_0) \in J$ such that exactly $k - m$ births occur during r_1 satisfy that $Z_{r_1} \in I$. This derives once again from comparisons of the flows ϕ_l for $m \leq l \leq k$. Moreover, such trajectories arise with positive probability.

Therefore, for any $t \geq t_0 + r_1$, we deduce from the Markov property at time $t - r_1$ that

$$\mathbb{P}_{(n,h)}(Z_t \in I) \geq \mathbb{E}_{(n,h)}\big(\mathbb{P}_{Z_{t-r_1}}(Z_{r_1} \in I)\mathbf{1}_{Z_{t-r_1} \in J}\big)\mathbb{P}_{(n,h)}(Z_{t-r_1} \in J) > 0.$$

(B) *If* $0 < h_m^* \leq h_- < h_+$.

For this configuration, we use the invertibility of the flow ϕ_k. We will construct an interval $I' = \{k\} \times (u, v)$ such that $\phi_k(u, s_0) = h_-$ and $\phi_k(v, s_0) = h_+$ for some $s_0 > 0$ and that furthermore satisfies that $u < h_m^* < v$ (see Figure 5).

To this aim, we fix $\varepsilon \in (0, h_m^*)$ and remark that for any $k \geq 1$ and $0 < \varepsilon < y \leq h < h_k^*$, the equation $\phi_k(y, s) = h$ is equivalent to $y = \psi_{k,h}(s)$, where $\psi_{k,h}(s)$ is
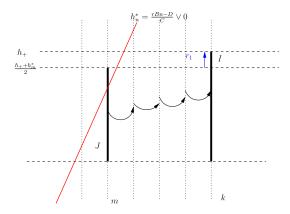
FIG. 4. *Case* 2(A). *Construction of the auxiliary interval and of an ideal trajectory.*

the inverse image by the flow $\phi_k(\cdot, s)$ of the point h. We deduce from (2.4) that the application $\psi_{k,h}$ is defined from $[0, r^k(\varepsilon, h)]$ to $[\varepsilon, h]$ by

$$\psi_{k,h}(s) = \frac{h}{e^{s(rBk-D)} - \frac{hC}{rBk-D}(e^{s(rBk-D)} - 1)}.$$

It is continuous and strictly decreasing on $[0, r^k(\varepsilon, h)]$.

Furthermore, from the uniqueness of the flow we deduce that for any $r^k(\varepsilon, h) \geq s \geq 0$:

$$\psi_{k,h_+}(s) > \psi_{k,h_-}(s).$$

Therefore, there exists a time $s_0 > 0$ such that the points $v = \psi_{k,h_+}(s_0)$ and $u = \psi_{k,h_-}(s_0)$ satisfy $u < h_m^* < v$ and we set $I' = \{k\} \times (u, v)$.
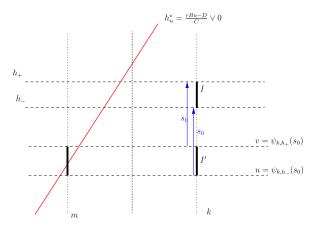

FIG. 5. *Case* 2(B). *Construction of the auxiliary interval I'.*
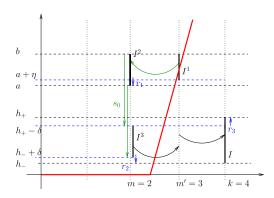
FIG. 6.   *Case* 2(C). *Construction of the auxiliary intervals* I_1, I_2 *and* I_3.

From the case 2(A), we deduce that there exists t_1 such that $\forall t \geq t_1$,

$$\mathbb{P}_{(n,h)}(Z_t \in I') > 0.$$

For any trajectory which is in I' at time t, we request that no jump occurs during s_0, which happens with positive probability. Therefore, using the Markov property at time t, we deduce that

$$\mathbb{P}_{(n,h)}(Z_{t+s_0} \in I) > 0.$$

(C) *If* $h_m^* = 0$.

In this case, the above construction 2(B) does not work because the only stable interval on $\{m\} \times \mathbb{R}_+$ are of the form $\{m\} \times (0, a)$ with $a > 0$, which would impose $s_0 = +\infty$.

Let us fix a small $\delta > 0$ and define the interval $I^3 = \{m\} \times (h_- + \delta, h_+ - \delta)$. We remark that we can adapt the previous reasoning to prove that for every $(n, h) \in E$ there exists $t_0 > 0$, such that $\forall t \geq t_0$,

$$\mathbb{P}_{(n,h)}(Z_t \in I^3) > 0.$$

Let us explain this construction (see Figure 6). We first define $m' = \min\{q \in \mathbb{N}^*, h_q^* > h_- + \delta\}$. As in the step 2(B), we construct an auxiliary interval $I^2 = \{m\} \times (a, b)$ with $s_0 > 0$

$$h_+ - \delta = \phi_m(b, s_0),$$

$$h_- + \delta = \phi_m(a, s_0) \quad \text{and}$$

$$a < h_{m'}^* < b.$$

We fix $\eta > 0$ such that $h_{m'}^* > a + \eta$ and set $I^1 = \{m'\} \times (a + \eta, b)$. From the first step, there exists t_1 such that $\forall t \geq t_1$, $\mathbb{P}_{(n,h)}(Z_t \in I^1) > 0$. Starting from I^1, we request furthermore that exactly $m' - m$ successive deaths occur on the time
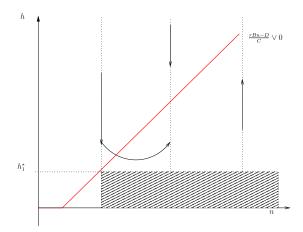
FIG. 7. *The hatched area corresponds to the points that cannot be reached starting from an initial condition which is not in this zone.*

interval $[t, t + r_1]$ with $r_1 = r^m(a + \eta, a)$. This ensures that $Z_{t+r_1} \in I^2$. Furthermore, we request that no jump occurs on $[t + r_1, t + r_1 + s_0]$, and thus, $\forall t \geq t_1$
$$\mathbb{P}_{(n,h)}(Z_{t+r_1+s_0} \in I^3) > 0.$$

We now define the times $r_2 = r^m(h_-, h_- + \delta)$ and $r_3 = r^k(h_+ - \delta, h_+)$ and set $t_2 = \min(r_2, r_3)$. For any trajectory which is at time $t + r_1 + s_0$ in I^3, we request furthermore that exactly $k - m$ successive births occur before the time $t + r_1 + s_0 + t_2$. Therefore, we deduce from the Markov property that $\forall t \geq t_0$

$$\mathbb{P}_{(n,h)}(Z_{t+r_1+s_0+t_2} \in I) > 0.$$

Third case: $h_k^* < h_-$. The proof is very similar to the second case. We introduce the smallest integer m such that $h_m^* > h_-$ and adapt the previous reasoning by inverting birth and death events.

(ii) Let us now consider the situation where $h_1^* > 0$. Starting from a point $(n_0, h_0) \in E$ such that $h \geq h_1^*$, the process cannot reach the set $\{z \in E, h \leq h_1^*\}$ which corresponds to the hatched zone on Figure 7. Therefore, we restrict ourselves to the measure σ' and initial conditions in E'. The proof is the similar to above. $\square$

PROOF OF THEOREM 3.1. We give the proof in the case where $h_1^* = 0$, the other case being an easy adaptation.

For any $A \in \mathcal{B}(E)$ such that $\sigma(A) > 0$, there exist an integer $k \in \mathbb{N}^*$ and a Borel set $A_k \in \mathcal{B}(\mathbb{R})$ such that $\{k\} \times A_k \subset A$ and $\lambda(A_k) > 0$. Once again, we split the proof in two sub-cases.

First case: Let us first assume that there exists an open interval $(h_-, h_+) \subset A_k$ with $h_- < h_+$ and define $I = \{k\} \times (h_-, h_+)$.

We choose ε small enough such that the interval $I_\varepsilon = \{k\} \times (h_- + \varepsilon, h_+ - \varepsilon)$ still satisfies $\sigma(I_\varepsilon) > 0$ and fix a small $\delta > 0$ such that $\forall (k, h') \in I_\varepsilon, \phi_k(h', \delta) \in I$.

From Theorem 3.2, we can construct trajectories that belong to the interval I_ε at time $t \geq t_0$ with positive probability for some $t_0 > 0$. We ask furthermore that no jump occurs during a time δ. Then for any $t \geq t_0$

$$\mathbb{P}_{(n,h)}(Z_s \in I, \forall s \in [t, t+\delta])$$
$$\geq \mathbb{P}_{(n,h)}(Z_t \in I_\varepsilon \text{ and no jump occurs on } [t, t+\delta])$$
$$\geq e^{-\delta\theta(k,h_+-\varepsilon)}\mathbb{P}_{(n,h)}(Z_t \in I_\varepsilon) > 0.$$

Therefore,

$$\mathbb{E}_{(n,h)}\left(\int_0^\infty \mathbf{1}_A(Z_s)\, ds\right) \geq \delta\mathbb{P}_{(n,h)}(Z_s \in I, \forall s \in [t, t+\delta]) > 0.$$

Second case: We now consider the case where A_k does not contain any interval (as an example $\mathbb{R} \setminus \mathbb{Q}$, or a fat Cantor set). We consider an open bounded interval (h_-, h_+) such that $\lambda(A \cap (h_-, h_+)) > 0$. Such an interval always exists since

$$\lambda(A_k) = \sum_{M=0}^\infty \lambda(A_k \cap (M, M+1)) > 0.$$

Moreover, it is possible to choose (h_-, h_+) such that $h_k^* \notin [h_-, h_+]$, that is, this interval is not stable for the flow ϕ_k. Indeed, the opposite case would imply by successive divisions of the interval, that for any $\varepsilon > 0$, $\lambda(A_k \setminus (h_k^* - \varepsilon, h_k^* + \varepsilon)) = 0$. Thus, we would have that $0 < \lambda(A_k) = \lambda(A_k \cap (h_k^* - \varepsilon, h_k^* + \varepsilon)) \leq 2\varepsilon$ for any $\varepsilon > 0$, which is not possible.

We now restrict ourselves to the set $B_k = A_k \cap (h_-, h_+)$ with $\lambda(B_k) > 0$ and assume that the flow ϕ_k increases on (h_-, h_+) (the other case being an easy adaptation).

Let us fix $\varepsilon > 0$. In the sequel, we consider the trajectories that reach the interval $(h_- - \varepsilon, h_-)$ and then, we ask that no jump occurs until these trajectories attain h_+. Then the time spent by those trajectories in B_k will be positive since the flows are continuous. More precisely, from Theorem 3.2 we deduce that there exists t_0 such that $\forall t \geq t_0$, $\mathbb{P}_{(n,h)}(Z_t \in \{k\} \times (h_- - \varepsilon, h_-)) > 0$. We define the positive time $r_1 = r^k(h_- - \varepsilon, h_+)$ needed for the flow ϕ_k to go from $h_- - \varepsilon$ to h_+. For all $t \geq t_0$, we consider the event

$$\mathcal{E}_t = \{Z_t \in \{k\} \times (h_- - \varepsilon, h_-) \text{ and no jump occurs on } [t, t+r_1]\}.$$

Then $\mathbb{P}_{(n,h)}(\mathcal{E}_t) > 0$ and

$$\mathbb{E}_{(n,h)}\left(\int_t^{t+r_1} \mathbf{1}_{\{k\}\times B_k}(Z_s)\, ds | \mathcal{E}_t\right)$$
$$= \mathbb{E}_{(n,h)}\left(\int_0^{r_1} \mathbf{1}_{B_k}(\phi_k(Z_t, s))\, ds | \mathcal{E}_t\right).$$

Since the flow ϕ_k is invertible, we make the change of variable $u = \phi_k(Z_t, s)$ and obtain

$$\mathbb{E}_{(n,h)}\left(\int_t^{t+r_1} \mathbf{1}_{\{k\} \times B_k}(Z_s)\, ds \Big| \mathcal{E}_t\right)$$

$$= \mathbb{E}_{(n,h)}\left(\int_{Z_t}^{\phi_k(Z_t, r_1)} \frac{\mathbf{1}_{B_k}(u)}{u(rBk - D - Cu)}\, du \Big| \mathcal{E}_t\right).$$

Since, $Z_t \in (h_- - \varepsilon, h_-)$ and $\phi_k(Z_t, r_1) \in (h_+, h_k^*)$, we deduce that for some constant $v > 0$,

$$\mathbb{E}_{(n,h)}\left(\int_t^{t+r_1} \mathbf{1}_{\{k\} \times B_k}(Z_s)\, ds \Big| \mathcal{E}_t\right) > v\lambda(B_k) > 0.$$

Thus, $\mathbb{E}_{(n,h)}(\int_0^\infty \mathbf{1}_{B_k}(Z_s)\, ds) > 0$ which completes the proof of the irreducibility. $\square$

3.3. *Positive Harris recurrence.*

We recall the expression of the infinitesimal generator of the prey–predator process given in (2.6). We prove in the following that it satisfies a Foster–Lyapunov criterion.

PROPOSITION 3.3. *Let $V : E \mapsto [1, +\infty[$ be the function $V(n, h) = n + h/r$. Then there exist $\delta, \gamma > 0$ and a compact set K such that*

$$(3.2) \qquad \mathcal{A}V(z) \leq -\gamma V(z) + \delta \mathbf{1}_K(z) \qquad \forall z \in E.$$

We combine Theorem 3.1 and Proposition 3.3, to deduce from Theorem A in Section 3.1 that:

THEOREM 3.4. *The process Z_t is positive Harris recurrent, and thus there exists a unique invariant probability measure π on E' which furthermore satisfies $\pi(V) < \infty$.*

PROOF OF PROPOSITION 3.3. For all $(n, h) \in E$,

$$\mathcal{A}V(n, h) = \frac{h}{r}(rBn - D - Ch) + bn - n(d + cn + Bh)\mathbf{1}_{n \geq 2}$$

$$= \begin{cases} -h\left(h\dfrac{C}{r} - \dfrac{D}{r}\right) - n(nc - (b - d)), & \text{if } n \geq 2, \\ -h\left(h\dfrac{C}{r} - \dfrac{D}{r} - B\right) + b, & \text{if } n = 1. \end{cases}$$

For any $\gamma > 0$, we obtain easily that there exists $n_0 \in \mathbb{N}^*$ and $h_0 > 0$ such that

$$-n(nc - (b - d)) \leq -\gamma n \qquad \forall n \geq n_0 \quad \text{and}$$

$$-h\left(h\frac{C}{r} - \frac{D}{r}\right) \leq -\gamma \frac{h}{r} \qquad \forall h \geq h_0.$$

Then for all (n, h) with $n \geq n_0$ and $h \geq h_0$, $\mathcal{A}V(n, h) \leq -\gamma V(n, h)$. Moreover, since n_0 is finite, there exists $h_1(n_0)$ such that $\forall (n, h)$ with $n < n_0$ and $h \geq h_1$, $\mathcal{A}V(n, h) \leq -\gamma V(n, h)$. Similarly, there exists $n_1(h_0)$ such that $\forall (n, h)$ with $h < h_0$ and $n \geq n_1$, $\mathcal{A}V(n, h) \leq -\gamma V(n, h)$.

Therefore, setting $K = \{1, \ldots, \max(n_0, n_1)\} \times [0, \max(h_0, h_1)]$ and $\delta = \max\{V(n, h), (n, h) \in K\}$, the function V introduced above clearly satisfies the Foster–Lyapunov criterion (3.2). $\quad \square$

REMARK 3.5. The function V introduced in Proposition 3.3 is not the only Lyapunov function of the system. An easy computation leads to the fact that $W(n, h) = n^2 + h$ also satisfies (3.2). With Theorem 3.4, we conclude that $\pi(W) < \infty$ which improves our knowledge of the invariant probability measure π.

3.4. *Exponential ergodicity.* In this section, we investigate the convergence in total variation norm of the transition kernel toward the invariant measure. Let us first recall Theorem 2.2.

THEOREM (Theorem 2.2). *The community process $(Z_t)_{t \geq 0}$ is exponentially ergodic. It converges toward its invariant probability measure π at an exponential rate. There exist $0 < \rho < 1$ and $0 < R < \infty$ such that, for all $z \in E'$,*

$$(3.3) \qquad \qquad \left\| P_t(z, \cdot) - \pi \right\|_{\mathrm{TV}} \leq R\rho^t V(z).$$

PROOF. From Theorem B in Section 3.1, it remains to prove that a skeleton chain of the prey–predator process is irreducible. This condition is actually equivalent to the ergodicity for positive Harris recurrent processes (Theorem 6.1 [39]).

It derives immediately from Theorem 3.2, that any skeleton chain $(Z_{k\Delta})_{k \in \mathbb{N}}$ (with $\Delta > 0$) reaches any open Borel set with positive probability. Indeed, let O be an open set of $\mathcal{B}(E')$ with $\lambda(\mathcal{O}) > 0$ then there exists an interval $I \subset \mathcal{O}$ with $\lambda(I) > 0$, and thus, for any $z \in E'$ and for q large enough, $\mathbb{P}_z(Z_{q\Delta} \in \mathcal{O}) \geq \mathbb{P}_z(Z_{q\Delta} \in I) > 0$.

To generalize from open Borel sets to Borel sets, we need some regularity of the function $z \mapsto \mathbb{P}_z(Z_\Delta \in A)$ for $A \in \mathcal{B}(E')$. We compute this probability by distinguishing the trajectories with the number of jumps $J(\Delta)$ occurring on $[0, \Delta]$, then for all $z \in E'$ and $A \in \mathcal{B}(E')$,

$$(3.4) \qquad \qquad \mathbb{P}_z(Z_\Delta \in A) = \sum_{k=0}^{\infty} \mathbb{P}_z\left(Z_\Delta \in A \text{ and } J(\Delta) = k\right).$$

We recall that the sequence of jump times of the prey population is denoted by $(T_k)_{k \in \mathbb{N}}$ and that $\mathbb{P}_z(T_1 \geq t) = e^{-\Theta(z,t)}$ where $\Theta(z, t) = \int_0^t \theta(\phi(z, s)) \, ds$ and the total jump rate $\theta(z)$ is given by (2.11).

The first term of (3.4) handles trajectories where no jump occurs. It is given by

$$\mathbb{P}_z\left(Z_\Delta \in A \text{ and } J(\Delta) = 0\right) = e^{-\Theta(z, \Delta) \, ds} \mathbf{1}_A\left(\phi(z, \Delta)\right).$$

This function is not continuous in z since the indicator function $\mathbf{1}_A$ is not continuous and the total flow $\phi(z, \Delta)$ is continuous.

The idea is then to bound from below $\mathbb{P}_z(Z_\Delta \in A)$ by a continuous function (see Chapter 6 of [37] and [7]). In the sequel, we consider

$$\mathbb{P}_z(Z_\Delta \in A) \geq \mathbb{P}_z(Z_\Delta \in A \text{ and } J(\Delta) = 1),$$

and prove that for any $A \in \mathcal{B}(E')$, the function $z \mapsto T(z, A) = \mathbb{P}_z(Z_\Delta \in A \text{ and } J(\Delta) = 1)$ is continuous on E'. The continuity will derive from the fact that the law of first jump time has a density with respect to the Lebesgue measure.

Indeed, for any $z = (n, h) \in E'$

$$\mathbb{P}_z(Z_\Delta \in A \text{ and } J(\Delta) = 1)$$
$$= \mathbb{P}_z(Z_\Delta \in A \text{ and } T_1 \leq \Delta < T_2)$$
$$= \int_0^\Delta \mathbf{1}_A(n + 1, \phi_{n+1}(\phi_n(h, s), \Delta - s)) bn e^{-\Theta(n,h,s)} e^{\Theta(n+1, \phi_n(h,s), \Delta - s)} \, ds$$
$$+ \int_0^\Delta \mathbf{1}_A(n - 1, \phi_{n-1}(\phi_n(h, s), \Delta - s)) n(d + cn + B\phi_n(h, s)) \mathbf{1}_{n \geq 2}$$
$$\times e^{-\Theta(n,h,s)} e^{\Theta(n-1, \phi_n(h,s), \Delta - s)} \, ds.$$

The first integral corresponds to the event where a birth occurs at T_1 while the second interval to the event where a death happens at T_1. In the sequel, we consider the first integral. The study on the second integral is very similar and will not be detailed. The predator density at time Δ conditioned on the fact that only one jump happens on $[0, \Delta]$ and is a birth occurring at time $s \in [0, \Delta]$ is given by

$$g_{(n,h,\Delta)}(s) = \phi_{n+1}(\phi_n(h, s), \Delta - s).$$

We note that for any s and Δ, the application $(n, h) \mapsto g_{(n,h,\Delta)}(s)$ is continuously differentiable. To perform the change of variable $y = g_{(n,h,\Delta)}(s)$ in the previous integral, we have to verify that $\frac{d}{ds} g_{(n,h,\Delta)}(s)$ does not vanish.

$$\frac{d}{ds} g_{(n,h,\Delta)}(s) = \partial_2 \phi_n(h, s) \cdot \partial_1 \phi_{n+1}(\phi_n(h, s), \Delta - s) - \partial_2 \phi_{n+1}(\phi_n(h, s), \Delta - s).$$

We recall that ϕ_n is the flow associated with (2.3), then

$$\partial_2 \phi_n(h, s) = \phi_n(h, s)(rBn - D - C\phi_n(h, s)).$$

From the exact expression (2.4), we obtain that

$$\partial_1 \phi_n(h, s) = \frac{\phi_n(h, s)}{h(1 + \frac{hC}{rBn-D}(e^{(rBn-D)s} - 1))}.$$

Then an easy calculation using (2.4) leads to

$$\frac{d}{ds} g_{(n,h,\Delta)}(s) = -rB \frac{g_{(n,h,\Delta)}(s)}{1 + \frac{\phi_n(h,s)C}{rB(n+1)-D}(e^{(rB(n+1)-D)(\Delta-s)} - 1)} < 0.$$

Let us finally remark that

$$g_{(n,h,\Delta)}(0) = \phi_{n+1}(h, \Delta) \quad \text{and} \quad g_{(n,h,\Delta)}(\Delta) = \phi_n(h, \Delta),$$

hence

$$
\begin{aligned}
(3.5) \quad &\int_0^\Delta \mathbf{1}_A(n+1, \phi_{n+1}(\phi_n(h, s), \Delta - s)) bn e^{-\Theta(n,h,s)} e^{\Theta(n+1, \phi_n(h,s), \Delta - s)} \, ds \\
&= \int_{\phi_n(h,\Delta)}^{\phi_{n+1}(h,\Delta)} \mathbf{1}_A(n+1, y) f(n, h, \Delta, y) \, dy,
\end{aligned}
$$

where

$$
f(n, h, \Delta, y) = bn \frac{e^{-\Theta(n,h,g_{(n,h,\Delta)}^{-1}(y))} e^{\Theta(n+1, \phi_n(h, g_{(n,h,\Delta)}^{-1}(y)), \Delta - g_{(n,h,\Delta)}^{-1}(y))}}{|\frac{d}{ds} g_{(n,h,\Delta)}(s)|_{s = g_{(n,h,\Delta)}^{-1}(y)}|}.
$$

The function of (n, h) given defined by (3.5) is continuous since the upper and the lower bounds of the integral are continuous functions of (n, h) on E' and the integrand is continuous in (n, h) on E' and locally bounded.

To conclude with the irreducibility of $(Z_{k\Delta})_{k \in \mathbb{N}}$, we fix a point $z_0 \in E'$ and remark that the measure $T(z_0, \cdot) = \mathbb{P}_z(Z_\Delta \in \cdot \text{ and } J(\Delta) = 1)$ is nondegenerate since $T(z_0, E') > 0$.

For any $A \in \mathcal{B}(E')$ such that $T(z_0, A) > 0$, there exists, by continuity of T, an open neighborhood $\mathcal{O}$ of z_0 such that $\forall z \in \mathcal{O}, T(z, A) > T(z_0, A)/2$. Moreover, we deduce from Theorem 3.2 that for any initial condition (n, h) there exists $q \in \mathbb{N}$ such that $\mathbb{P}_{(n,h)}(Z_{q\Delta} \in \mathcal{O}) > 0$. Then it derives from the Markov property at time $q\Delta$ and from the properties of the kernel T that

$$
\begin{aligned}
\mathbb{P}_{(n,h)}(Z_{(q+1)\Delta} \in A) &\geq \mathbb{E}_{(n,h)}\big(\mathbf{1}_{Z_{(q+1)\Delta} \in A} \mathbb{E}_{Z_{q\Delta}}(\mathbf{1}_{Z_\Delta \in \mathcal{O}})\big) \\
&\geq \mathbb{P}_{(n,h)}(Z_{q\Delta} \in \mathcal{O}) \frac{T(z_0, A)}{2} > 0.
\end{aligned}
$$

Hence, $(Z_{k\Delta})_{k \in \mathbb{N}}$ is irreducible with respect to the measure $T(z_0, \cdot)$. $\quad \square$

REMARK 3.6. Here, we chose to study the behavior of skeletons of the process in order to derive the exponential ergodicity of the process. This standard method has already been used in the context of PDMP (see, e.g., [7, 33]). Costa and Dufour [18, 25] developed a different approach based on an embedded Markov chain whose long time behavior is equivalent to those of the PDMP. For the prey–predator process Z, it seems to us more natural to study the continuous time trajectories since comparisons where possible. Moreover, in future work, we aim at deriving from these trajectory constructions more quantitative convergence speeds using recently developed coupling methods for PDMP (e.g., [9, 27]).

REMARK 3.7.   The results of this section can be extended to the model including migration introduced in Remark 2.1. Indeed, using the very same trajectory construction, one can prove that the process $(N^{(m)}, H^{(m)})$ is irreducible on $E^{(m)}$ for the Lebesgue measure σ. Moreover, the infinitesimal generator (2.7) satisfies a Foster–Lyapunov inequality with the same Lyapunov function. Therefore, $(N^{(m)}, H^{(m)})$ admits a unique probability invariant measure. Finally, by adapting the proof of Theorem 2.2 we get that it is exponentially ergodic.

4. Rescaling the predator dynamics.

We introduce a new parameter ε which rescales the predator dynamics and illustrates the biological assumption that the predator mass is almost negligible comparing to the prey mass. There exists an important literature about the metabolic theory which describes the relationships between mass and metabolic characteristics of living individuals (see among others [10, 21]). Following this theory, the demographic parameters of individuals increase when their mass decreases. Here, we simplify these relationships by assuming that the predator parameters vary as $1/\varepsilon$.

For any $\varepsilon \in (0, 1]$, we consider the community process $Z^\varepsilon = (N^\varepsilon, H^\varepsilon)$ where for all $t \geq 0$,

$$(4.1) \qquad \frac{d}{dt} H_t^\varepsilon = \frac{H_t^\varepsilon}{\varepsilon} \left(r B N_t^\varepsilon - D - C H_t^\varepsilon \right)$$

and the dynamics of N^ε is given by the jump mechanism (2.2) associated with the predator population H^ε. The process studied in the previous sections corresponds to $\varepsilon = 1$ or to the parameters $r^\varepsilon = r/\varepsilon$, $D^\varepsilon = D/\varepsilon$ and $C^\varepsilon = C/\varepsilon$.

This scaling changes the time scale of the predator flow. If ϕ_n^ε is the flow associated with (4.1), then

$$(4.2) \qquad \phi_n^\varepsilon(h, t) = \phi_n^1 \left(h, \frac{t}{\varepsilon} \right) \qquad \forall t \geq 0, \forall (n, h) \in E.$$

4.1. *Convergence toward an averaged process.*   In the sequel, we study the limit as ε tends to 0 of the sequence Z^ε in $\mathbb{D}([0, T], E)$. The prey–predator process is a slow–fast system. As ε diminishes, the predator process converges faster to its equilibrium between the jumps of the prey population. The slow dynamics of the prey population is then averaged on the predator equilibria.

We first give the expression of the infinitesimal generator of the process Z^ε defined above: $\forall f \in \mathcal{E}$ and $(n, h) \in E$

$$\mathcal{A}^\varepsilon f(n, h) = \partial_2 f(n, h) \frac{h(r B n - D - C h)}{\varepsilon} + bn \big(f(n + 1, h) - f(n, h) \big)$$
$$+ n(d + cn + Bh) \big(f(n - 1, h) - f(n, h) \big) \mathbf{1}_{n \geq 2}.$$

To carry out the limit as $\varepsilon \to 0$, we use the fact that the convergence speed of the flow ϕ_n^ε to its equilibrium h_n^* is uniform in ε. This is only true if the number of

predators remains bounded from below by some strictly positive constant. To this aim, we make the following assumptions:

(4.3)

(i) $rB - D > 0$. This implies that the predator population cannot become extinct;

(ii) We restrict ourselves to initial conditions in the set

$$E' = \{1, \ldots\} \times [h_1^*, \infty).$$

The state space E' is stable for the prey–predator dynamics and is the support of the irreducibility measure σ' introduced in Theorem 3.1(ii).

PROPOSITION 4.1. *Under Assumption* (4.3), *there exists* $\delta > 0$ *such that for all* $(n, h) \in E'$,

(4.4)
$$\left|\phi_n^\varepsilon(h, t) - h_n^*\right| \leq |h - h_n^*| e^{-\delta \frac{t}{\varepsilon}}.$$

PROOF. Let us remark that thanks to (4.2), it is sufficient to prove the result for $\varepsilon = 1$.

Using (2.4), an easy computation leads to

$$\left|\phi_n(h, t) - h_n^*\right| = \left| \frac{h - h_n^*}{1 + \frac{h}{h_n^*}(e^{-t(rBn-D)} - 1)} \right| \qquad \forall (n, h) \in E' \text{ and } t \geq 0.$$

Therefore, it is enough to find $\delta > 0$ satisfying $\forall (n, h) \in E'$ and $t \geq 0$:

$$e^{\delta t} \leq 1 + \frac{h}{h_n^*}(e^{-t(rBn-D)} - 1).$$

The function $t \mapsto 1 + \frac{h}{h_n^*}(e^{-t(rBn-D)} - 1) - e^{\delta t}$ equals 0 for $t = 0$, and increases as soon as $hC \geq \delta$ and $rBn - D \geq \delta$. Since $h \geq h_1^* > 0$, we choose $\delta < Ch_1^*$ to obtain (4.4). □

Following Kurtz [31], we introduce the predator occupation measure:

(4.5)
$$\Gamma^\varepsilon([0, t], A) = \int_0^t \mathbf{1}_A(H_s^\varepsilon) \, ds \qquad \forall t \geq 0 \text{ and } A \in \mathcal{B}(\mathbb{R}^+).$$

This random measure belongs to the set $\mathcal{M}_m(\mathbb{R}_+)$ of measures μ on $\mathbb{R}_+ \times \mathbb{R}_+$ such that $\mu([0, t] \times \mathbb{R}_+) = t$, $\forall t \geq 0$. For any $t \geq 0$, we denote by $\mathcal{M}_m^t(\mathbb{R}_+)$ the set of the measures $\mu \in \mathcal{M}_m(\mathbb{R}_+)$ restricted to $[0, t] \times \mathbb{R}_+$.

In the sequel, we prove using the averaging method developed in [31] that the sequence $(N^\varepsilon, \Gamma^\varepsilon)$ converges in law. This method allows us to avoid the difficulties related to the fast convergence of the predator flow to its equilibrium.

THEOREM 4.2.   *Fix $T > 0$ and assume* (4.3). *We suppose that the sequence of initial conditions $(Z_0^\varepsilon)_{0<\varepsilon\leq 1}$ converges to $\overline{Z}_0$ in law, and moreover, that*

$$(4.6) \qquad \sup_{0<\varepsilon\leq 1} \mathbb{E}\big((N_0^\varepsilon)^4\big) < \infty, \qquad \sup_{0<\varepsilon\leq 1} \mathbb{E}\big((H_0^\varepsilon)^4\big) < \infty.$$

Then the sequence $(N^\varepsilon, \Gamma^\varepsilon)$ converges in law toward $(\overline{N}, \Gamma)$ in $\mathbb{D}([0,T], \mathbb{N}) \times \mathcal{M}_m^T(\mathbb{R}_+)$ as $\varepsilon \to 0$.

The process $\overline{N}$ is a pure jump process on $\mathbb{N}^*$ whose infinitesimal generator is well defined for every measurable and bounded function $f : \mathbb{N}^* \to \mathbb{R}$ by

$$(4.7) \quad \mathcal{L}f(n) = \big(f(n+1) - f(n)\big)bn + \big(f(n-1) - f(n)\big)n\big(d + cn + Bh_n^*\big)\mathbf{1}_{n\geq 2}.$$

Moreover, the limiting measure is defined by $\Gamma(ds \times dy) = \delta_{h^*_{\overline{N}_s}}(dy)\,ds$.

We say that $\overline{N}$ is an averaged process since it behaves as if the predator density is constant at its equilibrium. Let us consider the specific case where $D = 0$. In this case, the averaged prey population $\overline{N}$ evolves almost as a logistic birth and death process with individual birth rate b and individual death rate $d + \tilde{c}n$ where $\tilde{c} = c + rB^2/C$. The logistic parameter $\tilde{c}$ corresponds to the apparent competition pressure (see [3]): it takes into account both the prey competition c and the effect of predation.

PROOF OF THEOREM 4.2.   We divide the proof in several steps. The first three steps are devoted to the convergence of the prey population process. We use a standard compactness-identification method inspired from Genadot [29]. In the fourth step, we use the averaging method developed by Kurtz [31] to prove the convergence of the predator occupation measures.

STEP 1: We prove that there exists an unique (in law) solution to the martingale problem associated to (4.7): for every measurable and bounded function $f : \mathbb{N}^* \to \mathbb{R}$,

$$f(\overline{N}_t) - f(\overline{N}_0) - \int_0^t \mathcal{L}f(\overline{N}_s)\,ds$$

is a martingale.

It derives from the representation Theorem 3.2 in [32] and a localization argument (see Theorem 4.6.3 in [26]) that the uniqueness of the solution of this martingale problem is equivalent to the uniqueness in law of the solution $\overline{N}$ of the following stochastic differential equation provided that $\sup_{s\leq t} \overline{N}_s < \infty$ a.s. for any $t \geq 0$:

$$(4.8) \qquad \overline{N}_t = \overline{N}_0 + \int_0^t \int_{R_+} \mathbf{1}_{u\leq b\overline{N}_{s-}} - \mathbf{1}_{b\overline{N}_{s-}<u\leq \overline{N}_{s-}(b+d+c\overline{N}_{s-}+Bh^*_{\overline{N}_{s-}})}\,Q(ds, du),$$

where Q is a Poisson point measure on $(\mathbb{R}_+)^2$ with intensity the product of Lebesgue measure $ds\,du$. The uniqueness of the weak solution of (4.8) can be

adapted from [28]. Moreover, if $\mathbb{E}(\overline{N}_0) < +\infty$, then this solution is well defined on $\mathbb{R}_+$ and $\sup_{s \leq t} \overline{N}_s < \infty$ a.s. for any $t \geq 0$.

STEP 2: Tightness of $(N_t^\varepsilon, 0 \leq t \leq T)$. Similar to the proof of Theorem 2.4, we construct a pure birth process X independent from H_0^ε, and thus from ε, which dominates the prey population. Then we deduce from (4.6) that $\forall z \in E'$

$$(4.9) \qquad \sup_{0 < \varepsilon \leq 1} \mathbb{E}_z \Big(\sup_{s \in [0,T]} (N_s^\varepsilon)^4 \Big) \leq \mathbb{E}_z \Big(\sup_{s \in [0,T]} (X_s)^4 \Big) < +\infty.$$

Let us now fix $\eta, \delta > 0$ and consider stopping times σ, τ such that $\sigma \leq \tau \leq (\sigma + \delta) \wedge \tau$. Using the trajectory's construction (2.9), we write

$$N_t^\varepsilon = N_0^\varepsilon + \int_0^t N_s^\varepsilon (b - (d + cN_s^\varepsilon + BH_s^\varepsilon)\mathbf{1}_{N_s^\varepsilon \geq 2}) \, ds + M_t^\varepsilon,$$

where M_t^ε is a pure jump martingale with quadratic variation

$$\langle M^\varepsilon \rangle_t = \int_0^t N_s^\varepsilon (b + (d + cN_s^\varepsilon + BH_s^\varepsilon)\mathbf{1}_{N_s^\varepsilon \geq 2}) \, ds.$$

Hence,

$$\mathbb{E}((N_\tau^\varepsilon - N_\sigma^\varepsilon)^2)$$
$$= \mathbb{E}\Big(\Big(\int_\sigma^\tau N_s^\varepsilon (b - (d + cN_s^\varepsilon + BH_s^\varepsilon)\mathbf{1}_{N_s^\varepsilon \geq 2}) \, ds + M_\tau^\varepsilon - M_\sigma^\varepsilon \Big)^2 \Big)$$
$$\leq 2 \Big[\mathbb{E}\Big(\Big(\int_\sigma^\tau N_s^\varepsilon (b + d + cN_s^\varepsilon + BH_s^\varepsilon) \, ds \Big)^2 \Big) + \mathbb{E}((M_\tau^\varepsilon - M_\sigma^\varepsilon)^2) \Big].$$

We deduce from (2.10) that the first term is bounded above by

$$\mathbb{E}\Big(\Big(\int_\sigma^\tau N_s^\varepsilon \Big(b + d + cN_s^\varepsilon + B \Big(H_0^\varepsilon + \frac{rB}{C} \sup_{u \in [0,s]} N_u^\varepsilon \Big) \Big) \, ds \Big)^2 \Big).$$

Therefore, using (4.6) and (4.9), there exists a constant $C_T > 0$ such that

$$\mathbb{E}\Big(\Big(\int_\sigma^\tau N_s^\varepsilon (b + d + cN_s^\varepsilon + BH_s^\varepsilon) \, ds \Big)^2 \Big) \leq C_T \delta^2.$$

For the second term,

$$\mathbb{E}((M_\tau^\varepsilon - M_\sigma^\varepsilon)^2) = \mathbb{E}\Big(\int_\sigma^\tau N_s^\varepsilon (b + (d + cN_s^\varepsilon + BH_s^\varepsilon)\mathbf{1}_{N_s^\varepsilon \geq 2}) \, ds \Big)$$
$$\leq \mathbb{E}\Big(\int_\sigma^\tau N_s^\varepsilon \Big(b + d + cN_s^\varepsilon + B \Big(H_0^\varepsilon + \frac{rB}{C} \sup_{u \in [0,s]} N_u^\varepsilon \Big) \Big) \, ds \Big),$$

where the last inequality derives from (2.10). Combining this two inequalities (4.6) and (4.9), we deduce that

$$\mathbb{E}((N_\tau^\varepsilon - N_\sigma^\varepsilon)^2) \leq \delta C_T,$$

for some constant $C_T > 0$ independent of ε which leads to the tightness of the laws of $(N_t^\varepsilon, t \in [0, T])$ in $\mathbb{D}([0, T], \mathbb{N})$ using Aldous tightness criterion [1].

STEP 3: Identification of the limit. Let us consider a sub-sequence of $(N_t^\varepsilon, 0 \leq t \leq T)$ (still denoted N^ε) which converges in law when $\varepsilon \to 0$ toward a process $(\overline{N}_t, 0 \leq t \leq T)$. In the sequel, we prove that $\overline{N}$ is the unique solution of the martingale problem associated to (4.7).

We consider bounded functions $f, g_1, \ldots, g_k$ on $\mathbb{N}^*$ and times $0 \leq t_1 < \cdots < t_k < t < t + s \leq T$. We deduce from Theorem 2.4 that

$$
\mathbb{E}\left[\left(f(N_{t+s}^\varepsilon) - f(N_t^\varepsilon) - \int_t^{t+s} \mathcal{L}f(N_u^\varepsilon)\, du\right) \prod_{i=1}^k g_i(N_{t_i}^\varepsilon)\right]
$$

$$
+ \mathbb{E}\left[\left(\int_t^{t+s} (f(N_u^\varepsilon - 1)\right.\right.
$$

(4.10)

$$
\left.\left. - f(N_u^\varepsilon))N_u^\varepsilon B(H_u^\varepsilon - h_{N_u^\varepsilon}^*)\mathbf{1}_{N_u^\varepsilon \geq 2}\, du\right) \prod_{i=1}^k g_i(N_{t_i}^\varepsilon)\right]
$$

$$
= 0.
$$

From the convergence in law of N^ε to $\overline{N}$ and (4.9), the first term converges as $\varepsilon \to 0$ to

$$
\mathbb{E}\left[\left(f(\overline{N}_{t+s}) - f(\overline{N}_t) - \int_t^{t+s} \mathcal{L}f(\overline{N}_u)\, du\right) \prod_{i=1}^k g_i(\overline{N}_{t_i})\right].
$$

Let us prove that

$$
\lim_{\varepsilon \to 0} \mathbb{E}\left[\left(\int_t^{t+s} (f(N_u^\varepsilon - 1) - f(N_u^\varepsilon))\right.\right.
$$

(4.11)

$$
\left.\left. \times N_u^\varepsilon B(H_u^\varepsilon - h_{N_u^\varepsilon}^*)\mathbf{1}_{N_u^\varepsilon \geq 2}\, du\right) \prod_{i=1}^k g_i(N_{t_i}^\varepsilon)\right] = 0.
$$

We first remark that

$$
\mathbb{E}\left[\left(\int_t^{t+s} (f(N_u^\varepsilon - 1) - f(N_u^\varepsilon))N_u^\varepsilon B(H_u^\varepsilon - h_{N_u^\varepsilon}^*)\mathbf{1}_{N_u^\varepsilon \geq 2}\, du\right) \prod_{i=1}^k g_i(N_{t_i}^\varepsilon)\right]
$$

$$
\leq \prod_{i=1}^k \|g_i\|_\infty \mathbb{E}\left[\int_t^{t+s} |f(N_u^\varepsilon - 1) - f(N_u^\varepsilon)|\right.
$$

$$
\left. \times N_u^\varepsilon B|H_u^\varepsilon - h_{N_u^\varepsilon}^* - |\mathbf{1}_{N_u^\varepsilon \geq 2}\, du\right].
$$

We split the integral according to the sequence of jump times $(T_k^\varepsilon, k \in \mathbb{N})$ of the prey population:

$$\left| \mathbb{E}\left(\int_t^{t+s} |f(N_u^\varepsilon - 1) - f(N_u^\varepsilon)| N_u^\varepsilon B |H_u^\varepsilon - h_{N_u^\varepsilon}^*| \mathbf{1}_{N_u^\varepsilon \geq 2} \, du \right) \right|$$

$$\leq 2\|f\|_\infty B \sum_{k=0}^\infty \sum_{n=1}^\infty \mathbb{E}\left(\mathbf{1}_n(N_{T_k^\varepsilon}^\varepsilon) n \int_{T_k^\varepsilon}^{T_{k+1}^\varepsilon \wedge (t+s)} |h_{N_u^\varepsilon}^* - H_u^\varepsilon| \, du \right).$$

Since on the event $\{N_{T_k^\varepsilon}^\varepsilon = n\}$, for any $u \in [T_k^\varepsilon, T_{k+1}^\varepsilon \wedge (t+s)]$, the predator density is given by $H_u^\varepsilon = \phi_n^\varepsilon(H_{T_k^\varepsilon}^\varepsilon, u - T_k^\varepsilon)$, we derive from Proposition 4.1 that

$$|h_{N_u^\varepsilon}^* - H_u^\varepsilon| \leq |h_{N_u^\varepsilon}^* - H_{T_u^\varepsilon}^\varepsilon| e^{-\frac{\delta(u - T_k^\varepsilon)}{\varepsilon}}.$$

Hence,

$$\left| \mathbb{E}\left(\int_t^{t+s} (f(N_u^\varepsilon - 1) - f(N_u^\varepsilon)) N_u^\varepsilon B (H_u^\varepsilon - h_{N_u^\varepsilon}^*) \mathbf{1}_{N_u^\varepsilon \geq 2} \, du \right) \right|$$

$$\leq 2\|f\|_\infty B \sum_{k=0}^\infty \sum_{n=1}^\infty \mathbb{E}\left(\mathbf{1}_n(N_{T_k^\varepsilon}^\varepsilon) n \int_{T_k^\varepsilon}^{T_{k+1}^\varepsilon \wedge (t+s)} |h_n^* - H_{T_k^\varepsilon}^\varepsilon| e^{-\frac{\delta(u - T_k^\varepsilon)}{\varepsilon}} \, du \right).$$

From (2.10), we obtain that for every $T > 0$

$$(4.12) \qquad \sup_{u \in [0,T]} H_u^\varepsilon \leq H_+ + \frac{rB}{C} \sup_{u \in [0,T]} N_u^\varepsilon < +\infty.$$

Since $h_n^* \leq rBn/C$, we deduce that for all $u \in [T_k^\varepsilon, T_{k+1}^\varepsilon \wedge (t+s)]$

$$|h_{N_{T_k^\varepsilon}^\varepsilon}^* - H_{T_k^\varepsilon}^\varepsilon| \leq H_+ + 2\frac{rB}{C} \sup_{u \in [0,T]} N_u^\varepsilon.$$

With a change of variable $u \to u - T_k^\varepsilon$, we obtain that

$$\int_{T_k^\varepsilon}^{T_{k+1}^\varepsilon \wedge (t+s)} e^{-\frac{\delta(u - T_k^\varepsilon)}{\varepsilon}} \, du = \int_0^{T_{k+1}^\varepsilon \wedge (t+s) - T_k^\varepsilon} \exp\left(-\frac{\delta u}{\varepsilon} \right) \, du$$

$$\leq \int_0^{t+s} \exp\left(-\frac{\delta u}{\varepsilon} \right) \, du \, \mathbf{1}_{T_k^\varepsilon \leq t+s}$$

$$\leq \frac{\varepsilon}{\delta} \mathbf{1}_{T_k^\varepsilon \leq t+s}.$$

Combining these two inequalities, we have that

$$\left| \mathbb{E}\left(\int_t^{t+s} (f(N_u^\varepsilon - 1) - f(N_u^\varepsilon)) N_u^\varepsilon B (H_u^\varepsilon - h_{N_u^\varepsilon}^*) \mathbf{1}_{N_u^\varepsilon \geq 2} \, du \right) \right|$$

$$\leq 2\|f\|_\infty B \mathbb{E}\left(\left(H_+ + 2\frac{rB}{C} \sup_{u \in [0,T]} N_u^\varepsilon \right) \sup_{u \in [0,T]} N_u^\varepsilon \sum_{k=1}^\infty \mathbf{1}_{T_k^\varepsilon \leq t+s} \right) \frac{\varepsilon}{\delta}.$$

It remains to bound the expectation independently of ε. To this aim, we denote by J_t^ε the number of jumps before time t. By neglecting the non-positive terms, we deduce from the trajectorial construction (2.9) that

$$\sup_{t\in[0,T]} N_t^\varepsilon J_T^\varepsilon \leq \int_0^T \int_{\mathbb{R}_+} (N_{s-}^\varepsilon + J_{s-}^\varepsilon + 1)\mathbf{1}_{u\leq bN_{s-}^\varepsilon} Q_1(ds, du)$$

$$+ \int_0^T \int_{\mathbb{R}_+} (N_{s-}^\varepsilon)\mathbf{1}_{u\leq N_{s-}^\varepsilon(d+cN_{s-}^\varepsilon+BH_{s-}^\varepsilon)} Q_2(ds, du).$$

Then we choose $S \geq T$ and taking expectations we deduce from (4.6) and (4.9) that there exists a positive constant C_S such that

$$\mathbb{E}\Big(\sup_{t\in[0,T]} N_t^\varepsilon J_T^\varepsilon \Big) \leq C_S + \mathbb{E}\Big(\int_0^T bJ_t^\varepsilon \sup_{s\in[0,t]} N_s^\varepsilon \, dt \Big).$$

We conclude using Gronwall lemma that $\mathbb{E}(\sup_{t\in[0,T]} N_t^\varepsilon J_T^\varepsilon) < \infty$. A very similar computation leads to

$$\mathbb{E}\Big(\sup_{t\in[0,T]} (N_t^\varepsilon)^2 J_T^\varepsilon \Big) \leq \mathbb{E}\Big(\int_0^T 2b(N_s^\varepsilon)^2 J_s^\varepsilon + bN_s^\varepsilon J_s^\varepsilon + bN_s^\varepsilon(1 + N_s^\varepsilon)$$

$$+ (N_s^\varepsilon - 1)^2 N_s^\varepsilon(d + cN_s^\varepsilon + BH_s^\varepsilon) \, ds \Big).$$

We conclude with (4.6), (4.9) and Gronwall lemma that

$$\mathbb{E}\Big(\sup_{t\in[0,T]} (N_t^\varepsilon)^2 J_T^\varepsilon \Big) < \infty.$$

Therefore, we deduce that there exists a constant $C_{S,T} > 0$ such that

$$\Big| \mathbb{E}\Big(\int_t^{t+s} (f(N_u^\varepsilon - 1) - f(N_u^\varepsilon)) N_u^\varepsilon B(H_u^\varepsilon - h_{N_u^\varepsilon}^*)\mathbf{1}_{N_u^\varepsilon \geq 2} \, du \Big) \Big| \leq C_{S,T} \frac{\varepsilon}{\delta}.$$

Thus, (4.11) is verified.

Therefore,

$$\mathbb{E}\Big[\Big(f(\overline{N}_{t+s}) - f(\overline{N}_t) - \int_t^{t+s} \mathcal{L}f(\overline{N}_u) \, du \Big) \prod_{i=1}^k g_i(\overline{N}_{t_i}) \Big] = 0,$$

and thus $\overline{N}$ is a solution of the martingale problem associated with $\mathcal{L}$. From (4.6), we deduce that $\mathbb{E}(\overline{N}_0) < \infty$ and then from the first step, N^ε converge in law to the unique solution of the martingale problem associated with $\mathcal{L}$ which is a birth and death process, which jumps from $n \to n+1$ at rate bn and from $n \to n-1$ at rate $n(d + cn + Bh_n^*)\mathbf{1}_{n\geq 2}$.

STEP 4: Limit behavior of the predator population size. We prove the weak convergence of the sequence of occupation measures Γ^ε introduced in (4.5). From,

Lemma 1.3 in [31], the sequence of the laws of Γ^ε is tight in the set $\mathcal{M}_m^T(\mathbb{R}_+)$ if for any $\delta > 0$ and $t \in [0, T]$ there exists a compact $K \subset \mathbb{R}_+$ such that

$$\inf_\varepsilon \mathbb{E}\big(\Gamma^\varepsilon([0, t] \times K)\big) \geq (1 - \delta)t.$$

From (4.12), we deduce that the family $\{H_s^\varepsilon, \varepsilon \in (0, 1], s \in [0, T]\}$ is relatively compact, and thus the sequence of the laws of $(\Gamma^\varepsilon)_{\varepsilon \in (0,1]}$ is tight.

Hence, the pair $(N^\varepsilon, \Gamma^\varepsilon)$ is tight and we consider a sub-sequence, still denoted $(N^\varepsilon, \Gamma^\varepsilon)$, that converges toward $(\overline{N}, \Gamma)$.

Since $\Gamma^\varepsilon([0, t], \mathbb{R}^+) = t$, for all $\varepsilon \in (0, 1)$ and $t \in [0, T]$, we deduce (see Lemma 1.4 in [31]) that there exists a process γ_s taking values in the set of probability measures on $\mathbb{R}^+$, measurable with respect to (ω, s), such that for every measurable and bounded function h on $[0, T] \times \mathbb{R}_+$

$$\int_0^T \int_{\mathbb{R}_+} h(s, y)\Gamma(ds \times dy) = \int_0^T \int_{\mathbb{R}_+} h(s, y)\gamma_s(dy)\, ds.$$

Using (4.9), we deduce from Theorem 2.1 in [31] that for every function f on $\mathbb{N}^*$ continuous and bounded and $t \leq T$

(4.13)
$$f(\overline{N}_t) - f(\overline{N}_0) - \int_0^t \int_{R_+} \big[(f(\overline{N}_s + 1) - f(\overline{N}_s))b\overline{N}_s$$
$$+ \big(f(\overline{N}_s - 1) - f(\overline{N}_s)\big)\overline{N}_s(d + c\overline{N}_s + By)\mathbf{1}_{\overline{N}_s \geq 2}\big]\gamma_s(dy)\, ds$$

is a martingale.

Concerning the predator dynamics, for every function $g \in \mathcal{C}_b^1(R_+)$, the process

$$\varepsilon M_g^\varepsilon(t) = \varepsilon g\big(H_t^\varepsilon\big) - \varepsilon g\big(H_0^\varepsilon\big) - \int_0^t g'\big(H_s^\varepsilon\big)H_s^\varepsilon\big(rBN_s^\varepsilon - D - CH_s^\varepsilon\big)\, ds;$$

is a martingale. Using (4.9), we prove easily that $(\varepsilon M_g^\varepsilon(t))_{0 < \varepsilon \leq 1, t \in [0,T]}$ is uniformly integrable and that

$$\lim_{\varepsilon \to 0} \mathbb{E}\big(\big|\varepsilon M_g^\varepsilon(t) - \widetilde{M}_g(t)\big|\big) = 0,$$

where $\widetilde{M}_g(t) = \int_0^t \int_{\mathbb{R}_+} g'(y)y(rB\overline{N}_s - D - Cy)\gamma_s(dy)\, ds$. Therefore, we deduce from the uniform integrability of $\varepsilon M_g^\varepsilon$ that $\widetilde{M}_g(t)$ is a martingale. Since it is also a continuous and finite variation process, it must be null. Thus,

(4.14)
$$\int_{\mathbb{R}^+} g'(y)y(rB\overline{N}_t - D - Cy)\gamma_t(dy) = 0$$

for dt-almost every $t \in [0, T]$.

We recall that the infinitesimal generator of $\overline{N}$ is given by (4.7), then by identification in (4.13) we deduce that for all $t \in [0, T]$,

(4.15)
$$\int_{\mathbb{R}^+} y\gamma_t(dy) = h_{\overline{N}_t}^*.$$

Then we apply (4.14) to the function $g(y) = \int_y^\infty f(u)\,du$, where f is continuous on a compact of $\mathbb{R}_+$,

$$\int_{\mathbb{R}^+} f(y)y(rB\overline{N}_t - D - Cy)\gamma_t(dy) = 0, \qquad \text{for } dt\text{-almost every } t \in [0, T].$$

From the Riesz theorem, the measure $\mu(\cdot) = \int y(rB\overline{N}_t - D - Cy)\gamma_t(dy)$ on $\mathbb{R}_+$ is null for almost every $t \in [0, T]$. Then, for almost every $t \in [0, T]$, γ_t only charges 0 and $h^*_{\overline{N}_t}$. Finally, using (4.15) we conclude that $\gamma_t(dy) = \delta_{h^*_{\overline{N}_t}}(dy)$ for dt-almost every $t \in [0, T]$. $\quad\square$

REMARK 4.3.   The proof of Theorem 4.2 relies on the uniform convergence of the flows $\phi_n(h, t)$ to their equilibrium h^*_n as $t \to \infty$, $\forall(n, h) \in E'$. It is not possible to extend this reasoning to the process $(N^{(m)}, H^{(m)})$ including migration introduced in Remark 2.1, since its state space is $\mathbb{N} \times \mathbb{R}_+$. However, we can still prove using the same method that the accelerated sequence $(N^{(m),\varepsilon}, \Gamma^{(m),\varepsilon})$ is tight (with obvious notation). The difficulty to extend Theorem 4.2 to the migration case lies in the identification of the limiting values.

4.2. *Long time behavior of the averaged process.*   We are interested in the long time behavior of the averaged prey population $\overline{N}$.

PROPOSITION 4.4.   *The process $\overline{N}$ is positive recurrent on $\mathbb{N}^*$ and converges toward its unique invariant probability measure $\overline{\mu} = \sum_{n=1}^\infty \mu_n \delta_n$, which satisfies the system*:

$$(4.16) \qquad \forall n \geq 2 \qquad \mu_n = \frac{b^{n-1}}{n \prod_{i=2}^n (d + ci + Bh^*_i)} \mu_1.$$

The proof is very classical and left to the reader (see, e.g., [2], page 216). Moreover, we are interested in the process $\overline{Z} = (\overline{N}, h^*_{\overline{N}})$ which represents the averaged prey and predator populations. We obtain immediately the form of its invariant distribution since $h^*_{\overline{N}}$ is a function of $\overline{N}$.

COROLLARY 4.5.   *The process $\overline{Z} = (\overline{N}, h^*_{\overline{N}})$ admits a unique invariant probability measure $\overline{\pi}$ given by*

$$(4.17) \qquad \overline{\pi} = \sum_{n \geq 1} \mu_n \delta_{(n, h^*_n)},$$

where the sequence μ_n satisfies (4.16).

The expression of $\overline{\pi}$ is not explicit, however thanks to (4.16) we can derive information on the shape of the distribution. In the sequel, we denote by $\lceil x \rceil = \min\{m \in \mathbb{Z}; m \geq x\}$ for $x \in \mathbb{R}$.

PROPOSITION 4.6. *The invariant probability measure $\overline{\pi}$ admits a unique maximum at 1 if $\mu_1 \geq \mu_2$ and at $n_1 > 1$ otherwise. The value of n_1 can be explicitly computed in function of the model parameters.*

PROOF. The study of the existence of maxima of the distribution $\overline{\pi}$ and thus $\overline{\mu}$ is equivalent to we study of $\frac{\mu_{n+1}}{\mu_n} - 1 = \xi(n)$ for ξ the function defined by

$$\xi(x) = \frac{b}{(x+1)(d + c(x+1) + B(rB(x+1) - D)/C)} - 1 \qquad \forall x \in [1, +\infty).$$

The sign of $\xi(x)$ is given by the sign of the polynomial

(4.18) $$\alpha x^2 + \beta x + \gamma = 0$$

with

$$\alpha = c + \frac{rB^2}{C},$$

$$\beta = d + 2c + 2\frac{rB^2}{C} - \frac{BD}{C},$$

$$\gamma = -b + d + c + \frac{rB^2}{C} - \frac{BD}{C}.$$

Its discriminant equals

$$\beta^2 - 4\alpha\gamma = \left(d - \frac{BD}{C}\right)^2 + 4\left(c + \frac{rB^2}{C}\right)b,$$

which is always positive. Therefore, the polynomial (4.18) admits 2 real roots:

$$x_0 = \frac{-\beta - \sqrt{(\beta^2 - 4\alpha\gamma)}}{2\alpha} \quad \text{and} \quad x_1 = \frac{-\beta + \sqrt{(\beta^2 - 4\alpha\gamma)}}{2\alpha}.$$

The smallest root x_0 is always negative. If $x_1 > 1$, then the invariant distribution $\overline{\mu}$ admits exactly one mode at $n_1 = \lceil x_1 \rceil$. Otherwise, the sequence $(\overline{\mu}_n)_{n \geq 1}$ is decreasing. To complete the proof, it remains to remark that the condition $x_1 > 1$ is equivalent to $\xi(1) > 0$ which is the condition given in the proposition. $\square$

4.2.1. *Numerics.* For each $\varepsilon \in (0, 1]$, we proved in Section 3 that there exists a unique invariant probability measure π^ε for the process Z^ε. In this section, we study with numerical simulations the behavior of the sequence of invariant probability measures $(\pi^\varepsilon)_\varepsilon$ as $\varepsilon \to 0$. An approximation of the invariant measure π^ε is obtained by simulating 3000 times the prey–predator process Z^ε on a long time interval. One interest of the process Z^ε is that the flow for the fast predator population admits an explicit formula (2.4). Therefore, we are able to compute exact simulations of the process Z^ε for every $\varepsilon \in (0, 1]$. The code for these simulations is available in [16] (Chapter 3, Appendix A).
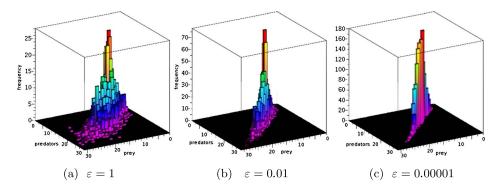
(a) $\varepsilon = 1$ (b) $\varepsilon = 0.01$ (c) $\varepsilon = 0.00001$

FIG. 8. *Approximation of the invariant measure π^ε for different values of ε. These histograms are built from* 3000 *iterations of the community process Z^ε until time* 1000. *The parameters are $b = 0.4$, $d = 0$, $c = 0.005$, $B = 0.02$, $r = 2$, $D = 0$ and $C = 0.04$.*

In the simulations, the demographic parameters are given by

$$b = 0.4, \qquad d = 0, \qquad c = 0.005, \qquad B = 0.02, \qquad r = 2,$$

$$D = 0 \quad \text{and} \quad C = 0.04.$$

In Figure 8, we draw three-dimensional histograms of the distributions of the invariant measure π^ε for different values of ε [in (a) $\varepsilon = 1$, in (b) $\varepsilon = 0.1$ and in (c) $\varepsilon = 0.00001$]. We observe that the support of these measures concentrates as $\varepsilon \to 0$ on the set $\{(n, h_n^*), n \in \mathbb{N}^*\}$. This set corresponds to the support of the stationary distribution $\overline{\pi}$.

We now compare these measures π^ε with the measure $\overline{\pi}$. With the parameters of the simulations, the averaged invariant measure $\overline{\pi} = \sum_{n=1}^\infty \mu_n \delta_{(n, h_n^*)}$ satisfies

$$\mu_n = \frac{b^{n-1}}{(\widetilde{c})^{n-1} n (n!)} \mu_1 \qquad \forall n \geq 2,$$

$$\sum_{n=1}^\infty \mu_n = 1,$$

where $\widetilde{c} = c + r B^2 / C$ is the apparent competition.

In the simulation, we approximate μ_1 by

$$\mu_1 \simeq \frac{1}{\sum_{k=1}^{50} (b/\widetilde{c})^{k-1} k(k)!} \simeq 2,69 \cdot 10^{-5}.$$

In Figure 9, we consider the marginal distribution of prey and predators given by the previous simulations ($\varepsilon = 1$ in the left column, $\varepsilon = 0.1$ the middle column and $\varepsilon = 0.00001$ in the right column). These distributions are projections of the histograms in Figure 8. We compare them with the projections of the averaged distribution $\overline{\pi}$ represented with a black line joining the points (n, μ_n). For these
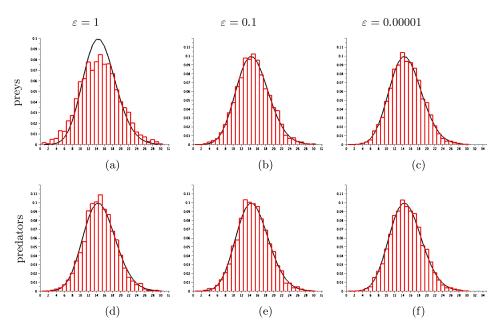
$\varepsilon = 1$ $\varepsilon = 0.1$ $\varepsilon = 0.00001$

(a)   (b)   (c)

(d)   (e)   (f)

FIG. 9. *Marginal invariant distributions of the prey population in* (a)–(b)–(c) *and of the predator population* (d)–(e)–(f) *for different values of* ε ($\varepsilon = 1$ *in* (a)–(d), $\varepsilon = 0.1$ *in* (b)–(e) *and* $\varepsilon = 0.00001$ *in* (c)–(f). *These histograms are built from* 3000 *iterations of the community process* Z^{ε} *until time* 1000. *The parameters are* $b = 0.4$, $d = 0$, $c = 0.005$, $B = 0.02$, $r = 2$, $D = 0$ *and* $C = 0.04$.

histograms, we chose subdivisions centered in the integers for the prey population and in the $(h_n^*)_{\geq 1}$ for the predator populations.

We observe a rapid convergence of the marginal distributions of prey and of predators, toward the marginal averaged distributions.

In these simulations, the sequence $(\pi^{\varepsilon})_{\varepsilon}$ seems to converge in law to π^{ε} but we have yet no mathematical proof of this result.

5. Discussion. We introduced new models for prey–predator communities in which the predator dynamics is faster than the prey one. These stochastic models derive from a microscopic model of the community under the successive scalings of large predator population size and small predator mass. In both cases, we assume that the prey population size remains finite. This assumption corresponds to a biological reality as in the case of forest or experimental settings, for example, in [42] the authors study trees-insects communities in which the number of trees is of the order of a hundred. These models can be easily simulated and their dynamics are simple, therefore, they represent an alternative to slow–fast Lotka–Volterra dynamical systems [41].

From an ecological point of view, we proved that our prey–predator process admits a long time distribution. Since the convergence to the invariant measure is exponentially fast, this invariant measure can be rapidly simulated using trajectories

of the process. This distribution gives insight on the composition of prey–predator systems and can be used to compute the composition of trees-insects communities when the counting of insects may be difficult to do experimentally. Moreover, in the situation where the mass ratio between prey individuals and predators is small, the limiting distribution admits an explicit expression, which is valuable for applications.

In this article, our approach was to consider first a large predator population size and then the small size of predators. The interest of these successive scalings was to introduce two different models corresponding to two different biological configurations. It would also be possible, and biologically relevant, to consider both scalings simultaneously by considering accelerated birth and death events as in [13] (Section 4.2). In this case, other processes would arise as the coupling of a birth death process and a diffusion. The study of such processes will be considered in future works.

Knowing the long time behavior the prey–predator community is crucial to consider the evolutionary dynamics of the community. Indeed, if we are interested in the phenotypic evolution of phenotype traits of prey and/or predators (as the development of specific tree defenses or of specialist insects strategies [42]), one might be interested to consider the arrival of rare mutations as in adaptive dynamics settings (e.g., [24, 36]). In this setting, the stationary distribution represents the state of the resident community as a mutant arises. Therefore, its knowledge is important to study the possible invasion of the mutant phenotype and to characterize the favorable strategies for prey or predators [14].

Finally, even if our motivation was to describe the dynamics of ecological communities such as trees-insects communities, these models or methods could also be applied to very different questions such as epidemiology. For example, the study of the propagation of insect transmitted diseases such as malaria impose to consider the interaction between insect and human populations [4]. In this case the dynamics of insects is much faster than the human dynamics. Therefore, piecewise deterministic processes could be introduce to model the dynamics of the disease and to study its outbreaks.

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