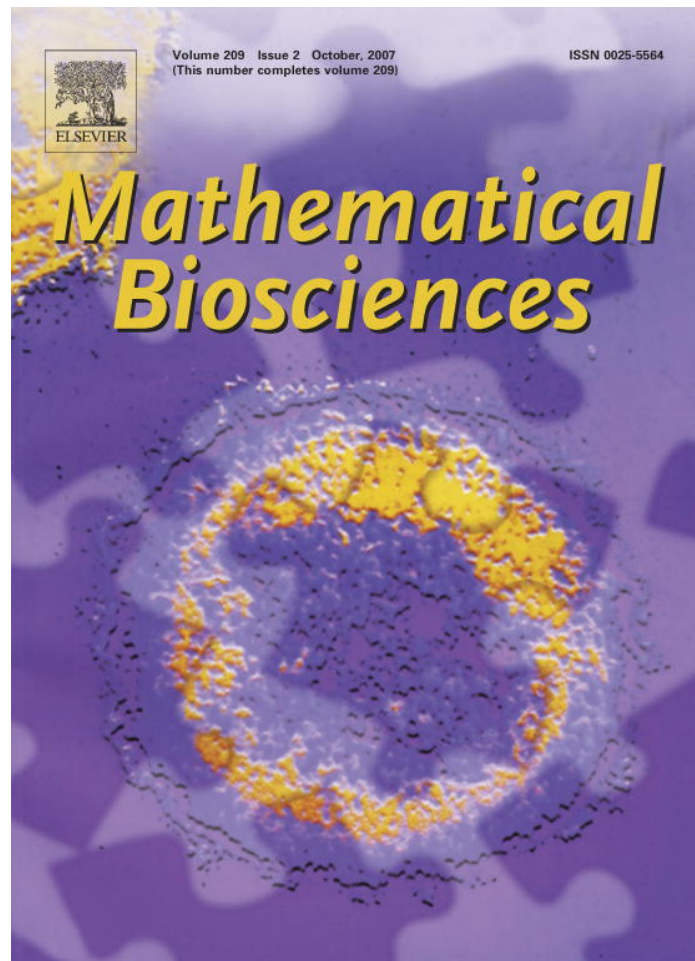


Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



This article was published in an Elsevier journal. The attached copy is furnished to the author for non-commercial research and education use, including for instruction at the author's institution, sharing with colleagues and providing to institution administration.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>

Available online at www.sciencedirect.com

Mathematical Biosciences 209 (2007) 319–335

**Mathematical
Biosciences**www.elsevier.com/locate/mbs

Blowing-up of deterministic fixed points in stochastic population dynamics

Mario A. Natiello^{a,*}, Hernán G. Solari^b^a *Center for Mathematical Sciences, Lund University, Box 118, 221 00 Lund, Sweden*^b *Departamento de Física, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Pab. I, Ciudad Universitaria, 1428 Buenos Aires, Argentina*Received 13 July 2006; received in revised form 15 January 2007; accepted 2 February 2007
Available online 22 February 2007

Abstract

We discuss the stochastic dynamics of biological (and other) populations presenting a limit behaviour for large environments (called *deterministic limit*) and its relation with the dynamics in the limit. The discussion is circumscribed to linearly stable fixed points of the deterministic dynamics, and it is shown that the cases of extinction and non-extinction equilibria present different features. Mainly, non-extinction equilibria have associated a region of stochastic instability surrounded by a region of stochastic stability. The instability region does not exist in the case of extinction fixed points, and a linear Lyapunov function can be associated with them. Stochastically sustained oscillations of two subpopulations are also discussed in the case of complex eigenvalues of the stability matrix of the deterministic system.

© 2007 Elsevier Inc. All rights reserved.

Keywords: Population dynamics; Stochastic; Deterministic limit

1. Introduction

The dynamics of biological populations, such as those considered in ecology and epidemiology, are naturally described in terms of ‘number of individuals’, this is listing how many individuals of

* Corresponding author. Tel.: +46 46 222 0919; fax: +46 46 222 4010.
E-mail address: Mario.Natiello@math.lth.se (M.A. Natiello).

the population belong to the different categories considered when modeling the process. The basic assumption behind this description is that the population under study is a collection of ‘similar’ individuals living in a common environment.¹ The population is then studied by considering the variation in time of the number of individuals in each species or subpopulation belonging to the system. These changes in time are the consequence of the occurrence of specific events such as birth, death, migration and contagion that are considered relevant for the problem. The occurrence of these events is assumed to depend on the configuration of the system at a given moment. When no better description is at hand, we assume that these events occur at random. The mathematical formulation of such dynamical description is that of a stochastic process (this describes the random occurrence of events that change the state of the system), where the states of the system are described by an array of non-negative integers (the number of individuals in each predefined subpopulation), i.e., an integer lattice. Under these assumptions, the description of population dynamics is conceived in terms of stochastic processes over integer lattices, or with greater precision, density dependent Poisson processes [1].

When population densities are considered in place of populations and the frequency of the interactions of each class for an individual depends only on the densities of the subpopulations (and perhaps directly on time), it is plausible to consider the limit case of large environments with finite subpopulation densities, describing the evolution of subpopulation densities in terms of continuous variables and associated ordinary differential equations (ODE). The mathematical situation is well described in terms of the limit theorems by Kurtz [2]. The original aim in Kurtz was to find approximations to solutions of ODE’s using Markov jump processes (i.e., the ‘inverse’ problem in some sense).

Since real systems never attain the mathematical limit, it is reasonable to assume that finite (but large) density dependent Poisson processes actually behave as the deterministic limit plus some ‘small’ random fluctuation around this limit. The larger the system, the smaller the fluctuation. The mathematical analysis of such a situation is called *perturbation theory*, frequently used in physics. The lowest order correction in these terms to the deterministic limit was also studied by Kurtz [3].

The situation in other scientific areas is similar. For example, chemical reaction kinetics deals with subpopulations consisting in different species (chemical molecules) that interact at specific rates that depend on subpopulation densities. Not surprisingly, the same kind of approximations than those described above have been considered in chemistry [4].

The use of ODEs in the description of population dynamics opens the large toolbox that has been developed for ODEs, in particular: singularity (fixed point) analysis, bifurcation theory and lately chaotic dynamics. It also opens the possibility of abuse of these tools. For example, chaos is a time-asymptotic property of the dynamics, i.e., its characterization requires infinitely long (in time) solutions, a requisite that contrasts not only with observational possibilities (we cannot access anything else than finite times) but also with the hypotheses in Kurtz’ limit theorems. More precisely, the large-system limit is achieved for fixed (and finite) time and the error bounds depend on the deviations of infinitesimally close trajectories, which in the case of chaos is diverging exponentially with time. In principle, the limits $t \rightarrow \infty$ and $V \rightarrow \infty$ (where V

¹ We will use the words *population* and *subpopulation* interchangeably, since under the stated definition there is no mathematical difference between both terms.

corresponds to a representative ‘problem-size’, see below) cannot be exchanged (for a precise discussion of chaos in epidemiological systems see [5]).

Although for short times and large systems the ‘ODE + fluctuation’ scheme may be successful, especially far away from extinction problems (so that all involved subpopulations are sufficiently large), this is nevertheless an approximation of the original problem. The original problem still has non-negative integers as descriptive units.

As an example of biological problems where the discrete-stochastic nature of the dynamics cannot be avoided we may cite biological experiments performed with the flour beetle *Tribolium* [6]. These experiments support the fact that the discrete nature of subpopulations, as well as stochasticity, play a relevant role in the dynamics. Epidemic statistics [7,8] as well as numerical computations of simple epidemic models also indicate a measurable role of the discrete-stochastic nature in the problem [9]. As a further example, populations of *Aedes aegypti* at the margins of their world-wide distribution experience recurrent extinctions of some its forms (larvae, pupae and adult) [10,11] and their modeling requires counting their numbers using non-negative integers [12].

If discreteness and stochasticity play a role in the description of population dynamics, what is the information provided by an ODE description in finite environments? How to use the insight obtained from solving the limit ODEs associated to a density dependent Markov process to understand the population dynamics problem is then one of the current goals of research in the area. This goal is manifested as a conjecture regarding the notion of deterministic skeletons somehow hidden under the stochastic dynamics of a density dependent Markov process [13–16].

Let us give more precision to the problem setup. Assume a system of interacting subpopulations, $N_\alpha \in \mathbb{Z}^+ \cup \{0\}$ developing in a large but finite environment. Let V hence be a large number representative of the size of the environment.² In terms of the resulting ODE’s under the mass-action-law, see below, V appears as a scale factor that represents the scaling of populations with environment size.

Further assume that the transition rates associated to the different events driving the Markov process, $W_j(N_\alpha, t; V)$, are represented by differentiable, non-negative functions satisfying the mass-action law

$$W_j(N_\alpha, t; V) = V w_j(N_\alpha/V, t). \tag{1}$$

The above expression of the mass-action law states that the transition rates scale with the size of the system (represented by V), i.e., that when the size of the system changes from V to V' while population densities are kept constant, the transition rates change by a factor V'/V . Notice also that $w_j(N_\alpha/V, t)$ is a non-negative real function of real arguments.

Let $\delta_{\alpha j}$ be the change produced on the $\alpha = 1, \dots, P$ subpopulation by the j th event ($j = 1, \dots, E$), and let

$$F_\alpha(N_\alpha/V, t) = \sum_{j=1, \dots, E} w_j(N_\alpha/V, t) \delta_{\alpha j} \tag{2}$$

² The precise meaning of V changes from problem to problem, in epidemiological models formulated under a constant total population hypothesis V is usually the population size [5], in the *Aedes aegypti* model [12] it is the number of breeding sites available to the mosquito in an homogeneous patch, in chemistry as well as physics, it represented the total volume of the reactor/system, in *Tribolium* experiments it can be expressed in grams of flour [17].

be the components of the vector field F , with the additional requirements that $\sum_j |\delta_{\alpha j}| w_j(N_\alpha/V, t) < \infty$ and $|F(\mathbf{x}, t) - F(\mathbf{y}, t)| \leq M|\mathbf{x} - \mathbf{y}|$.

What can, then, be inferred from the deterministic system

$$d\mathbf{x}_\alpha/dt = F_\alpha(\mathbf{x}, t) \quad (3)$$

that is relevant for the understanding of the Markov jump process $(N_\alpha, \delta_{\alpha j}, W_j, V)$? The skeleton conjecture is that there are meaningful answers to this question.

The study of stochastic systems with a deterministic limit is not new. Stochastic Differential Equations (SDE) have been often considered and some solid understanding has been constructed for them [18,19]. The relation of SDE to population dynamics, however, has remained mostly as a conjecture for several years. Actually, the diffusion approximation as is usually named, can be obtained as a formal/heuristic expansion in the form systematized by van Kampen [20] and it was precisely van Kampen who noticed that the approximation could not be carried beyond the first-order perturbative step [21]. While van Kampen's argument used formal mathematics as well as epistemological considerations, Ethier and Kurtz reached the same conclusion in terms of convergence of Markov processes [22].

The foundations for the stability analysis of SDE and related concepts were introduced by Kushner [23,24] with a larger scope than SDE. We will be building upon this foundation.

At this point it is relevant to consider if it is possible to formulate dynamical questions solely in the original discrete subpopulation description of the problem instead of first replacing the discrete problem by a continuous approximation and then recasting the continuous results again in discrete terms (it is worth noting that the SDE approach has no internal rules for addressing the final discrete-recast step). Retaining the discrete, population-wise, description we might be able to describe our original problem also in the proximities of extinctions and in other regions that lie outside of the validity range of the intermediate continuous-limit approximation. In other words, we pose and attempt to answer our questions in the original problem rather than taking a detour via the substitute problem.

Beginning with such a program we will focus our attention in the simplest equilibria, i.e., fixed points. In what follows we will show that stable fixed points of the deterministic system (3) are *blown-up* presenting in general a large stable region whose centre is *unstable*, except in the case of extinction solutions where the unstable centre is not present. This result represents the general case of the situation described in [25] and leads to sustained oscillations when the stable fixed point of the deterministic system is a *focus* (two complex eigenvalues with negative real part) in the plane.

2. Results

2.1. Assumptions

Let us review the setup of the previous section. We consider the dynamics of populations with individual-based species N_α , with $\alpha = 1, \dots, P$, each taking values in the non-negative integers. The dynamics is governed by a set of events numbered $j = 1, \dots, E$ occurring stochastically with transition probabilities $W_j(N_\alpha, t; V)$ that are density dependent and satisfy the mass-action law as in

Eq. (1). Each event alters the populations by the integer amount $\delta_{\alpha j}$ (we can collect all the alterations in an array δ_j for each event). The deterministic limit equation for the population densities is then given by Eq. (3). To lighten the notation we will use the variable $\mathbf{n} = (N_1/V, \dots, N_P/V)$.

Our fundamental assumption will be that the system given by Eq. (3) has a stable hyperbolic equilibrium point i.e., all eigenvalues in the linearization matrix around the equilibrium point $\mathbf{x} = \mathbf{n}_0$ have negative real part.

We will in the sequel consider two main situations that can to a great extent be treated together. In the general case, the fact that \mathbf{n}_0 , corresponding to some positive values $n_{\alpha,0} = N_{\alpha}^0/V$, is an equilibrium point forces that for all α , $\sum_{j=1, \dots, E} w_j(n_{\alpha,0}, t) \delta_{\alpha j} = 0$, but no additional requirements are necessary on the w 's. In the case of extinction processes, we have additionally that $w_j(x_{\alpha}, t) \rightarrow 0$ as $x_{\alpha} \rightarrow x_{\alpha,0} = 0$.

An immediate consequence of the assumptions is that the deterministic equation Eq. (3) admits a Lyapunov function $H : U \rightarrow \mathbb{R}$ defined in a suitable compact neighbourhood $U \subset \mathbb{R}^P$ of the equilibrium point (a Lyapunov function is a differentiable function taking the value zero at the equilibrium and positive otherwise, while having zero time-derivative at the equilibrium point and strictly negative derivative otherwise). The volume of U is approximated by a Riemman sum that counts the number of boxes of size $(1/V)^P$ in U (or the minimal number of them that contain U). For finite V , the number of states of the discrete population associated with U is also finite, a fact that we will use later.

As a further assumptions, we will assume that the Lyapunov function is smooth enough (i.e., at least of class C^2) so that whenever we take derivatives of H the expression is meaningful. Also, without loss of generality, we will assume the Lyapunov function has non-vanishing second derivatives at the equilibrium point. Part of our goals can be translated as understanding how this Lyapunov function behaves when considered within the stochastic process.

2.2. The embedded process

The Markov jump process can be described in the following way:

- Events occur individually and successively at exponentially distributed random time-intervals τ_n with (density dependent) rate R , where $R = \sum_{j=1}^E W_j(N_{\alpha}, t; V)$. We will write R as $R(\mathbf{n})$ when we want to explicitly indicate the point \mathbf{n} on which it is computed.
- *Which* event occurs each time, is randomly chosen according to the relative probability weight of each event. In other words, when an event occurs, the probability of it being the event having index j is $P(j) = W_j(N_{\alpha}, t; V)/R$. Because of the mass-action law this probability can be recasted in terms of the w 's as well. We rewrite it then, more explicitly, showing the dependence on the variables $\mathbf{n}_{\alpha} = N_{\alpha}/V$. We have hence, $P(\mathbf{n}, j) = w_j(\mathbf{n}, t) / \sum_k w_k(\mathbf{n}, t)$.

The Markov jump process corresponds to changes (events) occurring at random time intervals τ_l . The event occurring at $T_m = \sum_{l=1}^m \tau_l$ is the randomly chosen event j , producing a change δ_j in the populations. The state of the population is then $N_{\alpha}(t) = N_{\alpha}^m \equiv N_{\alpha}(T_m)$ for $T_m \leq t < T_{m+1}$.

The sequence of populations $\{N_{\alpha}^k\}, k = 1, \dots, m, \dots$ is called the *embedded process*. Given a sample path of a Markov jump process the embedded process is obtained as the sequence of population values after successive jumps. Conversely, given a sample path of an embedded Markov

process, sample paths of the Markov jump process can be constructed by producing the times corresponding to the occurrence of each successive event with exponentially distributed random variables.

2.3. Main results

Definition 1 (Stochastic variation). We call *stochastic variation* ΔH to the average change in the Lyapunov function H after the occurrence of one event:

$$\begin{aligned} \text{if } R(\mathbf{n}) \neq 0, \quad \Delta H(\mathbf{n}) &= \frac{\sum_{j=1}^E w_j(\mathbf{n}, t) H(\mathbf{n} + \delta_j/V)}{\sum_{j=1}^E w_j(\mathbf{n}, t)} - H(\mathbf{n}), \\ &= \sum_{j=1}^E P(\mathbf{n}, j) (H(\mathbf{n} + \delta_j/V) - H(\mathbf{n})), \end{aligned} \tag{4}$$

$$\text{if } R(\mathbf{n}) = 0, \quad \Delta H(\mathbf{n}) = 0. \tag{5}$$

We extended the definition of the stochastic variation to the extinction point $\{0\}$ with $R(0) = 0$, where no event can happen.

Let us further explore ΔH . Recalling we assumed $H(\mathbf{n})$ to be sufficiently smooth, we can expand $\Delta H(\mathbf{n})$ in terms of $1/V$. It is of course assumed that this $1/V$ -expansion is convergent in a sufficiently large V - and \mathbf{n} -region suitable for the present discussion.

Because of the mass-action law assumption, there is no explicit V -dependence on $P(\mathbf{n}, j)$. Hence,

$$\Delta H(\mathbf{n}) = \sum_{\alpha} \frac{\partial H}{\partial x_{\alpha}}(\mathbf{n}) \sum_{j=1}^E P(\mathbf{n}, j) \frac{\delta_{\alpha j}}{V} + \sum_{\alpha, \beta} \frac{\partial^2 H}{\partial x_{\alpha} \partial x_{\beta}}(\mathbf{n}) \sum_{j=1}^E P(\mathbf{n}, j) \frac{\delta_{\alpha j} \delta_{\beta j}}{V^2} + O(1/V^3). \tag{6}$$

The contribution of order $O(1/V)$ in (6) is proportional to the deterministic time-derivative of the Lyapunov function

$$\sum_{\alpha} \frac{\partial H}{\partial x_{\alpha}}(\mathbf{n}) F_{\alpha}(n_{\alpha}, t) \frac{V}{R} \tag{7}$$

(since $V F_{\alpha}(n_{\alpha}, t)/R = \sum_{j=1}^E P(\mathbf{n}, j) \delta_{\alpha j}$, they differ only in the positive factor V/R), and hence, it is negative definite except at $\mathbf{n} = \mathbf{n}_0$, where it vanishes.

Since by assumption the Hessian matrix of the Lyapunov function at \mathbf{n}_0 is positive definite (and by the assumed continuity it is positive definite in some neighbourhood of \mathbf{n}_0), the contribution of order $O(1/V^2)$ will be positive definite in some neighbourhood of \mathbf{n}_0 ; indeed this contribution $O(1/V^2)$ can be recasted as a sum (over index j) of positive terms, by inverting the order of summation in Eq. (6).

Lemma 1 (Stochastic instability region). *Under the given assumptions, for the general case of non-extinction equilibrium, the expression $U' = \{\mathbf{x} \in U, \Delta H(\mathbf{x}) \geq 0\}$ defines, for V sufficiently large, a closed and bounded region in $U \subset \mathbb{R}^P$. If, additionally, $\Delta H(\mathbf{x}) = 0$ is smooth, then the region U' is homotopic to a sphere of \mathbb{R}^P containing \mathbf{n}_0 as an interior point.*

Proof. To facilitate the analysis we may consider the expression $V\Delta H(\mathbf{x})$, since it has the same sign and zero-locus as $\Delta H(\mathbf{x})$. This expression has a negative definite term independent of V , a positive definite term proportional to $1/V$ and higher-order terms. The term independent of V can be written as:

$$\frac{\sum_{\alpha} \frac{\partial H}{\partial x_{\alpha}} F_{\alpha}(\mathbf{x}, t)}{\sum_{j=1}^E w_j(\mathbf{x}, t)}, \tag{8}$$

simply by combining Eqs. (2) and (6), as mentioned above in the discussion around Eq. (7). Moreover, the numerator in this expression can be recasted as $dH(\mathbf{x})/dt$ via Eq. (3), being hence negative definite outside the equilibrium point \mathbf{n}_0 , while the denominator is positive, since $R > 0$ for non-extinction points. Because of the assumptions, for any fixed V , we have that $\Delta H(\mathbf{n}_0) > 0$ and hence by continuity there exists a ball around \mathbf{n}_0 where $\Delta H(\mathbf{x}) > 0$. Letting V increase, the negative-definite term will eventually dominate. Hence, also by continuity, for V sufficiently large the whole set U' is contained in U and its outer border is given by the implicit expression $\Delta H(\mathbf{x}) = 0$. Provided $\nabla(\Delta H(\mathbf{x}))$ exists and is continuous, U' is homotopic to a sphere of \mathbb{R}^P . The set $\Delta H(\mathbf{x}) = 0$ corresponds to the surface of this sphere. \square

We will now proceed to define some subsets of U in terms of the states of the dynamics (the population lattice). Although the definition of these sets was inspired in the results of Lemma 1, they will serve beyond the limit of validity of the Lemma. Consider first the auxiliary set (defined on real space) $S_0 = \{\mathbf{x} \in U' : \Delta H(\mathbf{x}) = 0\}$, i.e., the border of U' in \mathbb{R}^P . Note that the solutions of $\Delta H(\mathbf{x}) = 0$ for a given value of V are real numbers that need not belong to the population lattice \mathbf{n} . Thus, it may happen that the intersection of S_0 with the population lattice is empty. However, an interesting fact about S_0 is that a continuous path going from the inside of U' towards the outside (or vice-versa) must visit S_0 .

Definition 2 (*Dynamical regions S_1, S, S_2 and L*).

$$S = \cup_{j=1, \dots, E, w_j(\mathbf{n}) > 0} (\{\mathbf{n} \in U' \text{ and } \Delta H(\mathbf{n} + \delta_j/V) \leq 0\}) \cup \{\mathbf{n} \in U', \Delta H(\mathbf{n}) = 0\}. \tag{9}$$

The points of the population lattice that belong to U' but not to S are in

$$S_1 = \cap_{j=1}^E \{\mathbf{n} \in U' : \Delta H(\mathbf{n}) > 0 \text{ and } \Delta H(\mathbf{n} + \delta_j/V) > 0\}. \tag{10}$$

While the remaining points of interest in U belong to

$$S_2 = \{\mathbf{n} \in U : \Delta H(\mathbf{n}) < 0\}. \tag{11}$$

We further define for convenience the finite set of population states (points)

$$L = (S_1 \cup S \cup S_2) \subset U.$$

Definition 3 (*Maximal Lyapunov region M*). Since $H(\mathbf{x})$ is a Lyapunov function for the deterministic system, its domain of definition is the non-empty neighbourhood U of \mathbf{n}_0 . For $h > 0$ sufficiently small, consider the region defined in the population lattice by the expression $M_h = \{\mathbf{n} : H(\mathbf{n}) \leq h\}$. Since $H(\mathbf{n}_0) = 0$, $\mathbf{n}_0 \in M_h$. Let h_{\max} be the maximal h such that $M_h \subset L$ and let the Maximal Lyapunov region M be defined as $M = M_{h_{\max}}$.

The interesting stochastic dynamics we will be able to establish occurs as long as the system remains within M .

Theorem 1 (Sub- and super-martingales). *Assume H is a Lyapunov function of the deterministic system resulting from Lyapunov's second criteria, i.e., $H = \sum_{\alpha=1}^P Q_{\alpha} (v_{\alpha} \cdot (\mathbf{x} - \mathbf{n}_0))^2 + O(|\mathbf{x} - \mathbf{n}_0|^3)$, with v_{α} the left eigenvector of the linearized vector field at \mathbf{n}_0 and $Q_{\alpha} > 0$. Under the conditions of the previous Lemma, if $R(\mathbf{n}_0) \neq 0$ and given the above definitions for S_1, S, S_2 and M , we have that:*

1. For large enough V , S_1 is not empty.
2. For large enough V , S_2 is not empty.
3. $H(\mathbf{n}(t))$ restricted to $\mathbf{n}(t) \in S_1$ is a sub-martingale relative to $\mathbf{n}(t)$.
4. $H(\mathbf{n}(t))$ restricted to $\mathbf{n}(t) \in S_2$ is a super-martingale relative to $\mathbf{n}(t)$.
5. If $\mathbf{n}(0) \in S_2$ and $\mu \geq \inf_{\mathbf{n} \in S_2} H(\mathbf{n})$ then

$$P\left(\sup_{\infty > t \geq 0} H(\mathbf{n}(t)) \geq \mu\right) \leq \frac{H(\mathbf{n}(0))}{\mu}. \tag{12}$$

6. If $\mathbf{n}(t') \in S_1$ for $t' \in [0, t]$, then t is finite with probability 1.
7. If $\mathbf{n}(t') \in S_2$ for $t' \in [0, t]$, then t is finite with probability 1.

Proof.

1. We show that $\mathbf{n}_0 \in S_1$. First, we notice that $\Delta H(\mathbf{n}_0) > 0$. We have to determine the sign of $\Delta H(\mathbf{n}_0 + \delta_j/V)$. We then notice that since the vector field is smooth and $R(\mathbf{n}_0) > 0$, the first term in (6), for $\mathbf{n}_0 + \delta_j/V \rightarrow \mathbf{n}_0$ (i.e., for large enough V) goes to zero as $|\nabla H|/V^2$, while the second term in (6) goes to zero as $1/V^2$. Hence, for any quadratic (or higher order) Lyapunov function the negative term can be made smaller than the positive term for all possible events ($W_j(\mathbf{n}_0) > 0, j = 1, \dots, E$), since $|\nabla H|$ also goes to zero. Hence, $\mathbf{n}_0 \in S_1$.
2. Consider now the point $\mathbf{n} \in U$ and $\mathbf{n} \neq \mathbf{n}_0$. Keeping \mathbf{n} fixed, and incrementing V , the first term of (6) decreases in absolute value as $1/V$ while the second term (and higher order terms) decrease as $1/V^2$, hence for V sufficiently large $\Delta H(\mathbf{n})$ is dominated by the first (negative) term. Hence, $\mathbf{n} \in S_2$ and S_2 is not empty for sufficiently large V .
3. $\Delta H(\mathbf{n}) > 0$ for $\mathbf{n} \in S_1$ is the sub-martingale condition for the embedded process. In the case of the continuous-time Markov process defined in (2.2), we have that it is a Feller process [22] and as such satisfies the relation

$$E_{\mathbf{n}}(H(\mathbf{n}_t)) = H(\mathbf{n}(0)) + E_{\mathbf{n}}\left(\int_0^t \Delta H(\mathbf{n}(s))R(\mathbf{n}(s)) ds\right) \tag{13}$$

(see [23]) where $E_{\mathbf{n}}()$ is the expectation value conditioned to the path having initial condition $\mathbf{n}(0) = \mathbf{n}$. The expression (13) can be put in terms of the embedded process since the arguments within the integral are constant between jumps. Hence

$$E_{\mathbf{n}}(H(\mathbf{n}(t))) = H(\mathbf{n}(0)) + E_{\mathbf{n}}\left(\sum_{n=0}^{n_t} \Delta H(\mathbf{n}_n)\right) \tag{14}$$

Notice that the number of steps n_t is also a stochastic variable.

4. $\Delta H(\mathbf{n}) < 0$ for $\mathbf{n} \in S_2$ is the super-martingale condition for the embedded process. The relation (14) applies as in the previous item, proving that in the region S_2 $H(\mathbf{n}(t))$ is a super-martingale.
5. The statement results from the application of Theorem 1 in [23], which in turn corresponds to observing that by (14) $E_{\mathbf{n}}(H(\mathbf{n}_t)) < H(\mathbf{n})$ and that $1/\mu \geq P(H(\mathbf{n}_t) > \mu E_{\mathbf{n}}(H(\mathbf{n}_t))) > P(H(\mathbf{n}_t) > \mu H(\mathbf{n}))$ by Markov inequality. In particular, if $\mu = h_{\max}$ we have

$$P\left(\sup_{\infty > t \geq 0} H(\mathbf{n}(t)) \geq h_{\max}\right) \leq \frac{H(\mathbf{n}(0))}{h_{\max}} \tag{15}$$

represents a bound for the probability of leaving the Lyapunov Region M .

6. No matter how large V is, the system is discrete, and hence there is a large but finite number of points in S_1 . If \mathbf{n}_0 is not an extinction point, then there is a non-zero minimum, $\Delta_m > 0$, for $\Delta H(\mathbf{n}_n)$ with $\mathbf{n}_n \in S_1$. Then, using (13) we have

$$\sup_{\mathbf{n} \in S_1} H(\mathbf{n}) > E_{\mathbf{n}}(H(\mathbf{n}_t)) > H(\mathbf{n}) + \Delta_m E_{\mathbf{n}}(t) \tag{16}$$

and since $\Delta_m > 0$, $E_{\mathbf{n}}(t)$ must be finite implying that the probability for t being infinite is zero.

7. No matter how large V is, the system is discrete, and hence there is a large but finite number of points in M . Considering that in addition there are no extinction points $\{\mathbf{n}: R(\mathbf{n}) = 0\}$ in U (extinction points would have $F_x(\mathbf{x}) = 0$ and then $\mathbf{x} \notin U$ since for $\mathbf{x} \neq \mathbf{n}_0$, $\mathbf{x} \in U$ $\sum_x \partial H(\mathbf{x}) / \partial x_x F_x < 0$) then there is a non-zero maximum, $\Delta_M < 0$, for $\Delta H(\mathbf{n}_n)$ with $\mathbf{n}_n \in S_2$. Then, using (13) again, we have

$$0 < E_{\mathbf{n}}(H(\mathbf{n}_t)) < H(\mathbf{n}) + \Delta_M E_{\mathbf{n}}(t) \tag{17}$$

and since $\Delta_M < 0$, $E_{\mathbf{n}}(t)$ must be finite implying that the probability for t being infinite is zero. \square

Corollary 1 (Recurrence). *In the conditions of the previous Theorem, a stochastic trajectory not escaping the domain $H(\mathbf{n}) < \mu$ ($\mathbf{n} \in M$) will recurrently visit the region S . Hence, \mathbf{n}_t leaves S_2 towards $S \cup S_1$ with probability larger than $1 - H(\mathbf{n}(0))/\mu$.*

Proof. By the application of item 5 in Theorem 1 there is a probability larger than $1 - H(\mathbf{n}(0))/\mu$ that a trajectory with initial condition in $\{\mathbf{n}: H(\mathbf{n}) < \mu \leq h_{\max}\}$ will always remain in this set. By items 6 and 7 in the same Theorem, the fate of such a trajectory will be to alternate finite time-intervals in S_1 with finite time-intervals in S_2 and (not necessarily finite) time-intervals in S . \square

Theorem 2 (Sustained oscillations). *In the conditions of the Lemma, for the case where $\mathbf{x} \in \mathbb{R}^2$ and the equilibrium point is of focus type (i.e., the linearization of the deterministic equation has complex conjugated eigenvalues) then the stochastic evolution of the angle variable $\phi = \arctan(y/x)$ is monotonic in the proximities of the equilibrium point.*

Proof. Consider the average increment of $\phi = \arctan(y/x)$

$$\Delta\phi = \sum_{j=1}^E \left(\arctan\left(\frac{y + \delta_{yj}/V}{x + \delta_{xj}/V}\right) - \arctan\left(\frac{y}{x}\right) \right) P(\mathbf{n}, j) \tag{18}$$

following similar ideas as in Definition 1. Expanding again in powers of $1/V$, we have

$$\Delta\phi = \sum_{j=1}^E P(\mathbf{n}, j) \left\{ \frac{1}{V} \left(\frac{\delta_{yj}x - \delta_{xj}y}{x^2 + y^2} \right) \left(1 - \frac{1}{V} \frac{\delta_{xj}x + \delta_{yj}y}{x^2 + y^2} \right) \right\} + O(1/V^3) \tag{19}$$

Hence, the first term in (19) corresponds to the time-derivative of ϕ according to the deterministic flow, re-scaled in the form: $\frac{1}{R} \frac{d\phi}{dt}$, which is non-zero by the ‘focus’ hypothesis (complex eigenvalues of the linearization). The remaining terms can be made as small as needed for V sufficiently large. \square

2.4. Extinction equilibrium

For a closed extincted population, the rate of occurrence of any event is zero. Zero population is an equilibrium point and in that point we have $R(0) = 0$. Under this circumstance, the conditions of the previous Theorems break down and a special approach is required. The study of this case has been a favourite in the literature, because of its relevance as well as its closer relation to the deterministic case, see [18] and references therein.

Since extinction is a natural limit for the population problem we want to distinguish arrays of numbers that are possible populations from those who are not.

Definition 4 (*Positive vector*). An array with non-negative entries $\mathbf{u} = (u_1, u_2, \dots, u_P)$ is called a *positive vector*.

It results natural to consider the total population as a Lyapunov function, we can then formulate the following result.

Theorem 3 (*Extinction*). Consider the extinction state, where all subpopulations are zero, $w_j(\mathbf{x}) \rightarrow 0$ as $\mathbf{x} \rightarrow 0$ (and hence $R(0) = 0$) and the associated deterministic flow has a linearly stable equilibrium at $\mathbf{x} = 0$. Then, retaining the rest of the assumptions of the previous Theorems (mass-action law and smoothness of the involved functions),

1. The linearization matrix \mathbf{A} for the deterministic equation around $\mathbf{n} = 0$ has non-negative off-diagonal elements.
2. $\exp(\mathbf{A}t)$ maps positive vectors on positive vectors.
3. The eigenvalue of \mathbf{A} with largest real part (i.e., negative and smallest in absolute value) is real and it has at least one associated eigenvector \mathbf{u} that is a positive vector. The same holds for \mathbf{A}^T .
4. There exists a left positive vector \mathbf{v} such that the function $H(\mathbf{x}) = \mathbf{v} \cdot \mathbf{x}$ is a Lyapunov function for the deterministic system, for V sufficiently large.
5. The stochastic process reaches $\mathbf{n} = 0$ with probability

$$1 - P\left(\sup_{\infty > t \geq 0} H(\mathbf{n}(t)) \geq h_{\max} \right) \geq 1 - \frac{H(\mathbf{n}(0))}{h_{\max}}. \tag{20}$$

Proof.

1. Because of the extinction assumptions and the mass-action law, for all events it holds that $w_j(\mathbf{x}) = p_{j\alpha}x_\alpha + O(x^2)$, where the $p_{j\alpha}$ are non-negative. For all $p_{j\alpha}$ that are strictly positive, we have that $\delta_{\beta j} \geq 0$ for $\beta \neq \alpha$, otherwise initial populations with $\mathbf{x}_\alpha = 1$ and $\mathbf{x}_\beta = 0$ would be dri-

ven to non-positive vectors (impossible populations) by the stochastic process. Recalling Eqs. (2) and (3), the off-diagonal elements can be computed as $A_{\beta\alpha} = \sum_j \delta_{\beta j} p_{j\alpha}$ and they are hence non-negative.

2. Suppose this is not the case, then the phase-space trajectory of an initial positive vector would cross the hypersurface $\mathbf{x}_\alpha = 0$ transversally, requiring thus that the vector field at that point has a negative component along α . But for any positive vector $\bar{\mathbf{x}}$ with $\bar{\mathbf{x}}_\alpha = 0$, the vector field defined by $\mathbf{A}\bar{\mathbf{x}}$ has a non-negative component along α , since $(\mathbf{A}\bar{\mathbf{x}})_\alpha = \sum_{\beta \neq \alpha} A_{\alpha\beta} \bar{x}_\beta$ has only non-negative factors.
3. Recall that all eigenvalues of \mathbf{A} have negative real parts because of the linear stability assumption. Both statements are immediate consequences of the previous item, since a flow with complex eigenvalues would cross transversally some hypersurface $\mathbf{x}_\alpha = 0$ in the ‘wrong’ direction and the same would hold for an initial condition having its dominant component (after sufficiently long time) on a non-positive vector. Since we only use that the off-diagonal elements of \mathbf{A} are non-negative, the same result holds for \mathbf{A}^T .
4. If the left vector \mathbf{v} has all entries strictly positive and $\mathbf{v}\mathbf{A}$ all entries strictly negative, it is immediate that $H(\mathbf{x}) = \mathbf{v} \cdot \mathbf{x}$ is zero at the origin, non-negative for any other positive vector \mathbf{x} , infinitely smooth and $dH(\mathbf{x})/dt = \mathbf{v} \cdot \mathbf{A}\mathbf{x} + O(|\mathbf{x}|^2)$ is negative definite in a ball around the origin, $|\mathbf{x}| < \epsilon$ or $|X| < \epsilon V$.

Let us show that such a \mathbf{v} always exists. Let \mathbf{v}_1 be the left eigenvector associated to λ in the previous item that is a positive vector. If all its entries are positive, then the statement is immediate. Otherwise, let us assume without loss of generality that the first p components of \mathbf{v}_1 are positive and the remaining $q = P - p$ are zero. If this is the case, the matrix A is constrained to have a special structure, namely:

$$\left(\begin{array}{c|c} A_a & A_b \\ \hline A_c & A_d \end{array} \right) \tag{21}$$

where A_b is identically zero and A_c has non-negative elements according to the second item. A_b is identically zero since the last q -components of \mathbf{v}_1 are zero, hence $0 = \sum_{i=1}^p A_{ij}(\mathbf{v}_1)_i$ for $p < j \leq P$ is a sum of non-negative numbers, and hence each term is zero. If \mathbf{v}_1^T is also a right (proper) eigenvector, A_c is also zero for an equivalent reason. A positive vector with zeros in the first p components and strictly positive elements in the remaining q components evolves by $\exp(\mathbf{A}t)$ in such a way that the last q components remain positive. We can repeat the argument in item 3 above, restricted to these components and find that there exists a positive vector $\mathbf{v}_2 = (0, \dots, 0, s_1, \dots, s_q)$ where at least some $s_k > 0$ that is a (possibly Jordan generalised) eigenvector of \mathbf{A} with real and negative eigenvalue. $\mathbf{v}_2\mathbf{A}$ may have non-zero entries in the first p elements but the important fact is that its last q components are strictly negative for the same entries that were non-zero in \mathbf{v}_2 . By choosing $r > 0$ sufficiently small, the vector $\mathbf{v} = \mathbf{v}_1 + r\mathbf{v}_2$ has $0 \leq q_1 < q$ zero entries and the remaining $P - q_1$ entries of $\mathbf{v}\mathbf{A}$ are strictly negative. Repeating this procedure if necessary one obtains the desired vector with strictly positive entries and strictly negative entries in its image by \mathbf{A} .

5. In the present case of extinction we have that S_1 is empty and the fixed point $\{0\}$ belongs to S (see (5) and (9)). For V sufficiently large, also S_2 is non-empty. Moreover, S consists of only one point, i.e., the extinction fixed point. Indeed, since H is linear, $R\Delta H = dH/dt$ and is hence negative in a suitable neighbourhood around the fixed point at $\{0\}$. The argument in item 5 of Theorem 1 still holds and hence

$$P\left(\sup_{\infty > t \geq 0} H(\mathbf{n}(t)) \geq h_{\max}\right) \leq \frac{H(\mathbf{n}(0))}{h_{\max}}.$$

The probability of not escaping the set M is then $1 - H(\mathbf{n}(0))/h_{\max}$. Moreover, in the set S_2 ΔH is strictly negative and attains a (negative) maximum value Δ_M . Hence, the reasoning in item 7 of Theorem 1 can be repeated and the trajectories not leaving M reach $\{0\}$ in finite time. \square

3. Example

We would like to illustrate the theorems and their practical use in a simple epidemiological model. The model was chosen to keep the example as simple as possible but without being trivial. Our model is a SIS-epidemic model with fluctuating population and it is described by two populations: susceptibles s , and infected, I , subject to the events of Table 1. Notice that the birth rate for very large populations has been taken as unit time, and in this mild disease the mortality of the infected individuals equals the mortality of the susceptible individuals. We note on passing that the line $\{I = 0\}$ is invariant. Since there are no events that produce infected individuals in the absence of at least one infected individual.

The resulting deterministic equations for the densities $x = s/V$, $y = I/V$ are then:

$$\begin{aligned} dx/dt &= \frac{(x + y)}{1 + b(x + y)} - mx - \beta xy + ry, \\ dy/dt &= y(\beta x - m - r). \end{aligned} \tag{22}$$

There are at most three biologically relevant equilibrium points:

$$(x, y) = (0, 0), \tag{23}$$

$$(x, y) = \left(\frac{(1 - m)}{mb}, 0\right) \quad \text{if } m < 1, \tag{24}$$

$$(x, y) = \left(\frac{(r + m)}{\beta}, \frac{(1 - m)}{mb} - \frac{(r + m)}{\beta}\right) \quad \text{if } m < 1 \text{ and } y > 0. \tag{25}$$

The solution (23) represents the extinction of the population; Eq. (24) represents the population free of disease ('sane' solution) while (25) represents the endemic solution.

Table 1
Events in the susceptible-infected-susceptible model of the example

j	Event	δ_j	Transition rate
1	Birth	(1,0)	$(s + I)/(1 + b(s + I)/V)$
2	Death s	(-1,0)	ms
3	Contagious	(-1, 1)	$\beta Is/V$
4	Recovery I	(1, -1)	rI
5	Death I	(0, -1)	mI

3.1. Stochastic stability of the extinction solution

The deterministic solution (23) is stable when $m \geq 1$, the largest eigenvalue of the stability matrix is $(1 - m)$ and its left eigenvector $(1, 1)$. Hence, by Theorem 3, we set $H = (s + I)/V = x + y$, and compute

$$R\Delta H = H \left(1 - m - \frac{H}{1 + bH} \right)$$

As already explained in Theorem 3, the region S_1 is empty. Also $S = \{0\}$ and $S_2 = \{(x, y): 0 < x + y = H(\mathbf{n}) < M\}$ for some finite $M > 1/V$. Actually, the extinction equilibrium remains stable for the stochastic process in the terms of item 5 in Theorem 3 as long as $\Delta H < 0$ in S_2 this is, as long as $(1 - m) - 1/(V + b) < 0$. The term $-1/(V + b)$ represents a finite size correction to the deterministic limit, this is, the extinction is stable for $m \geq 1$ in the deterministic system and for $m \geq 1 - 1/(V + b)$ in the stochastic system.

3.2. Stochastic stability of the 'sane' solution

The linearization of the deterministic problem around

$$\mathbf{n}_0 = \left(\frac{1 - m}{mb}, 0 \right) = (x_0, y_0)$$

produces the matrix

$$M = \begin{pmatrix} D & D - A \\ 0 & A \end{pmatrix} \tag{26}$$

with $A = \beta x_0 - r - m$ and $D = m(m - 1)$. Note that $m = 1/(1 + b(x_0 + y_0))$.

The eigenvalues are $\lambda_1 = D$, $\lambda_2 = A$ and the associated left eigenvectors are $(1, 1)$ and $(0, 1)$ respectively.

Since $y_0 = 0$ represents the extinction of the infected subpopulation we look for a Lyapunov function of the form

$$H = Q_1(x + y - x_0)^2 + Q_2 y \tag{27}$$

with $Q_1, Q_2 > 0$. Then ΔH reads

$$R\Delta H = \left(\frac{Q_1}{V^2} \right) (x + y) \left(\frac{1}{1 + b(x + y)} + m \right) - 2mb \left(\frac{Q_1}{V} \right) (x + y) \frac{(x + y - x_0)^2}{1 + b(x + y)} + \left(\frac{Q_2}{V} \right) y (\beta x - r - m). \tag{28}$$

The contributions in Q_1 and Q_2 can be analyzed independently. The Q_1 -terms determine a region,

$$\left(x + y - x_0 - \frac{1}{4V}\right)^2 \leq \frac{1}{mbV} + \frac{1}{16V^2}$$

where the contribution is positive. The term associated to Q_2 is negative provided $y > 0$ and $0 > (\beta x - r - m)$.

The region U' of Lemma 1 contains the set

$$V' = \left\{ (x, y) : y = 0, x > 0, \left|x - x_0 - \frac{1}{4V}\right| \leq \sqrt{\frac{1}{mbV} + \frac{1}{16V^2}} \right\}$$

provided that

$$\frac{r + m}{\beta} > x_0 + \frac{1}{4V} + \sqrt{\frac{1}{mbV} + \frac{1}{16V^2}}$$

so that all the $x \in V'$ satisfy the condition of stability associated to Q_2 . $V' \subset U'$ for any choice of H , i.e., for any positive values for Q_1 and Q_2 . For fixed, specified Q_1 and Q_2 U' is homotopic to a sphere and may contain other points beyond those in V' . Similarly, all points in V' are in S_1 , except the endpoints that lie in S .

It is interesting to note that our choice of Lyapunov function for the ‘sane’ fixed point lies outside the scope of all three theorems: The function is not a quadratic form in the variables (x, y) , the eigenvalues of the fixed point are not complex and the fixed point is not an extinction point. Replacing y by y^2 in the Q_2 term, Theorem 1 can be used and the recurrence Corollary as well. However, what we learn about the system with such a modification is more or less the same we learned already with the simpler Lyapunov function proposed above. Indeed, the region V' identified through H is an invariant of the dynamics both for the deterministic and for the stochastic setups. The moment the stochastic dynamics places the system in V' , it will remain there and in such case it could be described as a one-dimensional problem. The Lyapunov function H above, restricted to $y = 0$ satisfies now Theorem 1 and the recurrence Corollary holds as well: The system moves back and forth in and out of V' in finite time. The advantage as compared with using another Lyapunov function is that we have narrowed the oscillation region from a more or less thick sphere to a line segment.

3.3. Stochastic stability of the endemic solution

The endemic solution is

$$(x_1, y_1) = \left(\frac{r + m}{\beta}, x_0 - x_1\right)$$

which exists in the population space provided $y_1 = x_0 - x_1 > 0$. The matrix associated to the linearization of the vector field reads

$$M = \begin{pmatrix} D - B & D \\ B & 0 \end{pmatrix} \tag{29}$$

where $D = m(m - 1)$ and $B = \beta y_1$, with eigenvalues $\lambda_1 = D, \lambda_2 = -B$ and left eigenvectors $(1, 1)(-B, D)$ respectively.

For V sufficiently large and in a region U sufficiently small around the fixed point (x_1, y_1) the function

$$H = Q_1(x - x_1 + y - y_1)^2 + Q_2(B(x - x_1) - D(y - y_1))^2$$

is a good Lyapunov function for the system. Consequently

$$\begin{aligned} R\Delta H = & \frac{x+y}{1+b(x+y)} Q_1 \left(\frac{1}{V^2} + \frac{2}{V} ((x-x_1) + (y-y_1)) \right) \\ & + \frac{x+y}{1+b(x+y)} Q_2 \left(\frac{B^2}{V^2} + \frac{2B}{V} (B(x-x_1) - D(y-y_1)) \right) \\ & + m(x+y) Q_1 \left(\frac{1}{V^2} - \frac{2}{V} ((x-x_1) + (y-y_1)) \right) \\ & + mx Q_2 \left(\frac{B^2}{V^2} - \frac{2B}{V} (B(x-x_1) - D(y-y_1)) \right) \\ & + my Q_2 \left(\frac{D^2}{V^2} + \frac{2D}{V} (B(x-x_1) - D(y-y_1)) \right) \\ & + ry Q_2 \left(\frac{(B+D)^2}{V^2} + \frac{2(B+D)}{V} (B(x-x_1) - D(y-y_1)) \right) \\ & + \beta xy Q_2 \left(\frac{(B+D)^2}{V^2} - \frac{2(B+D)}{V} (B(x-x_1) - D(y-y_1)) \right). \end{aligned}$$

In this case Theorem 1 and its corollary can be applied straightforwardly. The system presents a recurrent behaviour (although not ‘circulating’ around the fixed point since the eigenvalues are real) and the deterministic fixed point shows up as a blurred spot. Moreover this spot is *quantitatively correct* (as opposed to an ‘ODE + fluctuation’ approach) in the sense that we can estimate the probability of finding the system in the recurrent behaviour.

4. Summary and conclusions

We have considered stochastic population processes with deterministic limit, and particularly, the meaning of linearly stable fixed points of the deterministic equations for the stochastic process. If the stability analysis of the deterministic problem is going to be meaningful for the population dynamics problem, then the size of the system must be large enough. How large, is a matter that can be studied in terms of the satisfaction of the hypothesis needed for Theorems 1 and 2 as we have shown in the example.

Two situations are worth considering as separate cases: (a) equilibrium points far from extinction and (b) extinction fixed points where all populations under consideration eventually vanish and the stochastic system reaches an *absorbing state*.

In the case (a), the deterministic fixed point blows up in the stochastic process into two regions: an unstable region and a stable one (Theorem 1 and Corollary 1).

Additionally, we have proved a conjecture of [25] with respect to sustained oscillations in systems with two sub-populations, for the case of a stable equilibrium of focus type in the deterministic problem (Theorem 2).

The case (b) is different in that the unstable region does not exist. When disperse populations remain such for a time t and the deterministic equilibrium is stable a linear Lyapunov function is enough to put lower bounds to the survival probability (Theorem 3). The mathematical situation is related to the most frequent case analysed in terms of Stochastic Differential Equations [18] although details can be added considering that the problem under consideration belongs to population dynamics.

The present work is an extension of the methods of analysis introduced by Kushner [23] adapted to the case of population dynamics, and we hope it can be further extended to the case of bifurcations of the deterministic problem.

References

- [1] R. Durrett, *Essentials of Stochastic Processes*, Springer, New York, 2001.
- [2] T.G. Kurtz, Solutions of ordinary differential equations as limits of pure jump Markov processes, *J. Appl. Prob.* 7 (1970) 49.
- [3] T.G. Kurtz, Limit theorems for sequences of jump processes approximating ordinary differential equations, *J. Appl. Prob.* 8 (1971) 344.
- [4] D.T. Gillespie, The chemical Langevin equation, *J. Chem. Phys.* 115 (1) (2000) 297.
- [5] I. Nåsell, Measles outbreaks are not chaotic, in: C. Castillo Chavez (Ed.), *Mathematical Approaches for Emerging and Reemerging Infectious Diseases: Models, Methods, and Theory*, Springer, New York, 2002, pp. 85–114.
- [6] S.M. Henson, R.F. Costantino, J.M. Cushing, Robert A. Desharnais, Brian Dennis, Aaron A. King, Lattice effects observed in chaotic dynamics of experimental populations, *Science* 294 (2001) 602.
- [7] M.S. Bartlett, Measles periodicity and community size, *J. R. Statist. Soc. A* 120 (1957) 48.
- [8] M.S. Bartlett, The critical community size for measles in the united states, *J. R. Statist. Soc. A* 123 (1960) 37.
- [9] J.P. Aparicio, H.G. Solari, Sustained oscillations in stochastic systems, *Math. Biosci.* 169 (2001) 5.
- [10] H.R. Carter, *Yellow Fever: An Epidemiological and Historical Study of Its Place of Origin*, The Williams & Wilkins Company, Baltimore, 1931.
- [11] A.E. Carbajo, S.I. Curto, N. Schweigmann, Spatial distribution pattern of oviposition in the mosquito *Aedes aegypti* in relation to urbanization in buenos aires: southern fringe bionomics of an introduced vector, *Med. Vet. Entomol.* 20 (2006) 209.
- [12] M. Otero, H. Solari, N. Schweigmann, A stochastic population dynamic model for *Aedes aegypti*: formulation and application to a city with temperate climate, *Bull. Math. Biol.* 68 (2006) 1945.
- [13] R. Durrett, S.A. Levin, The importance of being discrete (and spatial), *Theor. Popul. Biol.* 46 (1994) 363.
- [14] I. Nåsell, The quasi-stationary distribution of the closed endemic sis model, *Adv. Appl. Prob.* 28 (1996) 895.
- [15] I. Nåsell, Extinction and quasi-stationarity in the Verhulst logistic model, *J. Theor. Biol.* 211 (2001) 11.
- [16] Tim Coulson, Pejman Rohani, Mercedes Pascual, Skeletons, noise and population growth: the end of an old debate? *TRENDS Ecol. Evol.* 19 (7) (2004) 359.
- [17] R.N. Chapman, The quantitative analysis of environmental factors, *Ecology* 9 (2) (1928) 111.
- [18] L. Arnold, The unfolding of dynamics in stochastic analysis, *Comput. Appl. Math* 16 (1997) 3.

- [19] L. Arnold, *Random Dynamical Systems*, Springer, Berlin, 1998.
- [20] N.G. van Kampen, *Stochastic Processes in Physics and Chemistry*, North-Holland, Amsterdam, 1981.
- [21] N.G. van Kampen, The validity of nonlinear Langevin equations, *J. Stat. Phys.* 25 (1981) 431.
- [22] S.N. Ethier, T.G. Kurtz, *Markov Processes*, Wiley, New York, 1986.
- [23] H.J. Kushner, The concept of invariant set for stochastic dynamical systems and applications to stochastic stability, in: H.F. Karren (Ed.), *Stochastic Optimization and Control*, Wiley, 1967, pp. 47–57.
- [24] H.J. Kushner, Stochastic stability, in: A. Dold, B. Eckmann (Eds.), *Lecture Notes in Mathematics: Stability of Stochastic Dynamical Systems*, vol. 294, Springer, Berlin, 1972, pp. 97–124.
- [25] J.P. Aparicio, H.G. Solari, Population dynamics: a Poissonian approximation and its relation to the Langevin process, *Phys. Rev. Lett.* 86 (2001) 4183.