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Asymptotic behaviour of the stochastic Lotka–Volterra model

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Abstract

This paper examines the asymptotic behaviour of the stochastic extension of a fundamentally important population process, namely the Lotka–Volterra model. The stochastic version of this process appears to have far more intriguing properties than its deterministic counterpart. Indeed, the fact that a potential deterministic population explosion can be prevented by the presence of even a tiny amount of environmental noise shows the high level of difference which exists between these two representations.

Keywords: Lotka–Volterra model; Brownian motion; Stochastic differential equation; Moment boundedness; Asymptotic behaviour

1. Introduction

Deterministic subclasses of the Lotka–Volterra model are well-known and have been extensively investigated in the literature concerning ecological population modelling. One particularly interesting subclass describes the facultative mutualism of two species, where each one enhances the growth of the other, represented through the deterministic equations

$$\begin{aligned} \dot{x}_1(t) &= x_1(t)\big[b_1 - a_{11}x_1(t) + a_{12}x_2(t)\big], \\ \dot{x}_2(t) &= x_2(t)\big[b_2 - a_{22}x_2(t) + a_{21}x_1(t)\big] \end{aligned} \tag{1}$$

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for a_{12} and a_{21} positive constants. The associated dynamics have been developed by, for example, Boucher [1], He and Gopalsamy [2] and Wolin and Lawlor [9]. Now in order to avoid having a solution that explodes at a finite time, $a_{12}a_{21}$ is required to be smaller than $a_{11}a_{22}$. To illustrate what happens when the latter condition does not hold, suppose that $a_{11} = a_{22} = \alpha$ and $a_{12} = a_{21} = \beta$ (i.e., we have a symmetric system) and $\alpha^2 < \beta^2$. Moreover, let us assume that $b_1 = b_2 = b \geqslant 1$ and that both species have the same initial value $x_1(0) = x_2(0) = x_0 > 0$. Then the resulting symmetry reduces system (1) to the single deterministic differential equation

$$\dot{x}(t) = x(t)\big[b + (-\alpha + \beta)x(t)\big]$$

whose solution is given by

$$x(t) = \frac{b}{-(-\alpha+\beta) + \frac{b+(-\alpha+\beta)x_0}{x_0}e^{-bt}}.$$

Now the assumption that $\alpha^2 < \beta^2$ causes $x(t)$ to explode at the finite time $t = \frac{1}{b}\{\ln(b + [-\alpha+\beta]x_0) - \ln([-\alpha+\beta]x_0)\}$. Nevertheless, this can be avoided, even when the condition $a_{12}a_{21} < a_{11}a_{22}$ does not hold, by introducing (stochastic) environmental noise.

Let $(\Omega, \mathcal{F}, \{\mathcal{F}_t\}_{t\geqslant 0}, P)$ be a complete probability space with filtration $\{\mathcal{F}_t\}_{t\geqslant 0}$ satisfying the usual conditions, i.e., it is increasing and right continuous while $\mathcal{F}_0$ contains all P-null sets (see Mao [6]). Moreover, let $w(t)$ be a one-dimensional Brownian motion defined on the filtered space and $\Re^n_+ = \{x \in \Re^n\colon\ x_i > 0$ for all $1 \leqslant i \leqslant n\}$. Finally, denote the trace norm of a matrix A by $|A| = \sqrt{\mathrm{trace}(A^TA)}$ (where A^T denotes the transpose of a vector or matrix A) and its operator norm by $\|A\| = \sup\{|Ax|\colon\ |x| = 1\}$.

Now consider a Lotka–Volterra model for a system with n interacting components, which corresponds to the case of facultative mutualism, namely

$$\dot{x}_i(t) = x_i(t)\left(b_i + \sum_{j=1}^{n} a_{ij}x_j\right), \quad 1 \leqslant i \leqslant n.$$

This equation can be rewritten in the matrix form

$$\dot{x}(t) = \mathrm{diag}\big(x_1(t), \ldots, x_n(t)\big)\big[b + Ax(t)\big], \quad \forall t \geqslant 0, \tag{2}$$

where $x(t) = (x_1(t), \ldots, x_n(t))^T$, $b = (b_i)_{1\times n}$ and $A = (a_{ij})_{n\times n}$. Stochastically perturbing each parameter

$$a_{ij} \to a_{ij} + \sigma_{ij}\dot{w}(t)$$

results in the new stochastic form

$$\dot{x}(t) = \mathrm{diag}\big(x_1(t), \ldots, x_n(t)\big)\big[\big(b + Ax(t)\big)\,dt + \sigma x(t)\,dw(t)\big], \quad \forall t \geqslant 0. \tag{3}$$

Here $\sigma = (\sigma_{ij})_{n\times n}$, and we impose the condition

$$\text{(H1)} \quad \begin{cases} \sigma_{ii} > 0, & \text{if } 1 \leqslant i \leqslant n, \\ \sigma_{ij} \geqslant 0, & \text{if } i \neq j. \end{cases}$$

For a stochastic differential equation to have a unique global solution (i.e., no explosion in a finite time) for any given initial value, the coefficients of Eq. (2) are generally required to satisfy both the linear growth condition and the local Lipschitz condition (cf. [3–7]). However, the coefficients of Eq. (3) do not satisfy the linear growth condition, though they are locally Lipschitz continuous, so the solution of Eq. (3) may explode at a finite time. Under the simple hypothesis (H1), the following theorem shows that this solution is positive and global.

Theorem 1 (Mao et al. [8]). *Let us assume that hypothesis* (H1) *holds. Then, for any system parameters* $b \in \Re^n$, $A \in \Re^{n\times n}$ *and any given initial value* $x_0 \in \Re^n_+$, *there is a unique solution* $x(t)$ *to Eq.* (3) *on* $t \geqslant 0$. *Moreover, this solution remains in* $\Re^n_+$ *with probability* 1, *namely* $x(t) \in \Re^n_+$ *for all* $t \geqslant 0$ *almost surely.*

The above result reveals the important role that environmental noise plays in population dynamics. The idea that even a tiny amount of stochastic noise can suppress an imminent deterministic explosion in a number of co-habiting species brings a whole new dimension into the study of population modelling.

2. Asymptotic moment estimation

Since Eq. (3) does not have an explicit solution, the study of asymptotic moment behaviour is essential if we are to gain a deeper understanding of the underlying process. This paper is essentially a continuation of the moment results derived by Mao et al. [8].

Theorem 2. *Let the system parameters* $b \in \Re^n$ *and* $A \in \Re^{n\times n}$ *be given, and assume that hypothesis* (H1) *holds. Then, for any* $\theta \in (0,1)$, *there exists a positive constant* K_θ *such that, for any initial value* $x_0 \in \Re^n_+$, *the solution of Eq.* (3) *has the property*

$$\limsup_{t\to\infty} \frac{1}{t} E\left[\int_0^t \sum_{i=1}^n x_i^{2+\theta}(s)\,ds\right] \leqslant K_\theta. \tag{4}$$

Proof. Define a C^2-function $V:\Re^n_+ \to \Re_+$ by

$$V(x) = \sum_{i=1}^n x_i^\theta.$$

According to Itô's formula,

$$dV\big(x(t)\big) = \left[\sum_{i=1}^n \theta x_i\left(b_i + \sum_{j=1}^n a_{ij}x_j\right) + \frac{1}{2}\sum_{i=1}^n \theta(\theta-1)x_i^\theta\left(\sum_{j=1}^n x_j\sigma_{ij}\right)^2\right]dt + \sum_{i=1}^n \theta x_i^\theta \sum_{j=1}^n \sigma_{ij}x_j\,dw(t).$$

Moreover, it is easy to show that

$$\sum_{i=1}^{n}\theta x_i\left(b_i+\sum_{j=1}^{n}a_{ij}x_j\right)\leqslant\sum_{i=1}^{n}\theta x_i|b_i|+\sum_{i=1}^{n}\sum_{j=1}^{n}|a_{ij}|x_ix_j$$

and

$$\sum_{i=1}^{n}\theta(1-\theta)x_i^{\theta}\left(\sum_{j=1}^{n}x_j\sigma_{ij}\right)^2\geqslant\sum_{i=1}^{n}\theta(1-\theta)x_i^{2+\theta}\sigma_{ii}^2.$$

As a result, we obtain

$$dV\big(x(t)\big)\leqslant\left[\theta\sum_{i=1}^{n}|b_i|x_i+\sum_{i=1}^{n}\sum_{j=1}^{n}|a_{ij}|x_ix_j-\frac{\theta(1-\theta)}{2}\sum_{i=1}^{n}\sigma_{ii}^2x_i^{2+\theta}\right]dt$$
$$+\theta\sum_{i=1}^{n}x_i^{\theta}\sum_{j=1}^{n}\sigma_{ij}x_j\,dw(t). \tag{5}$$

Furthermore, by taking into consideration that fact that the polynomial

$$\theta\sum_{i=1}^{n}|b_i|x_i+\sum_{i=1}^{n}\sum_{j=1}^{n}|a_{ij}|x_ix_j-\frac{\theta(1-\theta)}{4}\sum_{i=1}^{n}\sigma_{ii}^2x_i^{2+\theta}$$

has an upper positive bound, say K_θ, inequality (5) yields

$$V\big(x(t)\big)+\frac{\theta(1-\theta)}{4}\int_0^t\sum_{i=1}^{n}\sigma_{ii}^2x_i^{2+\theta}\,ds\leqslant V\big(x(0)\big)+\int_0^t K_\theta\,ds+M(t), \tag{6}$$

where

$$M(t)=\theta\int_0^t\sum_{i=1}^{n}x_i^{\theta}\sum_{j=1}^{n}\sigma_{ij}x_j\,dw(s)$$

is a real-valued continuous local martingale vanishing at $t=0$. Taking expectations on both sides of (6) then results in

$$E\left[\int_0^t\sum_{i=1}^{n}x_i^{2+\theta}\,ds\right]\leqslant\frac{4}{\hat{\sigma}\theta(1-\theta)}\big(V\big(x(0)\big)+K_\theta t\big),$$

where

$$\hat{\sigma}=\min\big\{\sigma_{ii}^2,\ 1\leqslant i\leqslant n\big\}.$$

The required assertion (4) follows immediately. □

3. Pathwise estimation

Theorem 3. *Let us assume that hypothesis* (H1) *holds. Moreover, let the system parameters* $b \in \Re^n$, $A \in \Re^{n\times n}$ *and the initial value* $x_0 \in \Re^n_+$ *be given. Then, there exists a* $K > 0$, *which is independent of* x_0 *but not necessarily of the system parameters, such that*

$$\limsup_{t\to\infty} \frac{1}{t}\left[\ln\left(\prod_{i=1}^n x_i(t)\right) + \frac{1}{4}\lambda_{\min}(\sigma^T\sigma)\int_0^t \left|x(s)\right|^2 ds\right] \leqslant K \quad a.s., \tag{7}$$

where $\lambda_{\min}(\sigma^T\sigma)$ *is the smallest eigenvalue of the matrix* $\sigma^T\sigma$.

Proof. For each $1 \leqslant i \leqslant n$, applying Itô's formula to $\ln(x_i(t))$ results in

$$d\ln\bigl(x_i(t)\bigr) = \left[b_i + \sum_{j=1}^n a_{ij}x_j - \frac{1}{2}\left(\sum_{j=1}^n \sigma_{ij}x_j\right)^2\right]dt + \sum_{j=1}^n \sigma_{ij}x_j\,dw(t),$$

which implies that

$$\ln\bigl(x_i(t)\bigr) = \ln\bigl(x_i(0)\bigr) + \int_0^t \left[b_i + \sum_{j=1}^n a_{ij}x_j - \frac{1}{2}\left(\sum_{j=1}^n \sigma_{ij}x_j\right)^2\right]ds + M_i(t), \tag{8}$$

where

$$M_i(t) = \int_0^t \sum_{j=1}^n \sigma_{ij}x_j\,dw(s)$$

is a real-valued continuous local martingale vanishing at $t = 0$ with quadratic form

$$\bigl\langle M_i(t), M_i(t)\bigr\rangle = \int_0^t \left(\sum_{j=1}^n \sigma_{ij}x_j\right)^2 ds.$$

Fix $\varepsilon \in (0, \frac{1}{2})$ arbitrarily. For every integer $k \geqslant 1$, using the exponential martingale inequality (cf. Mao [6, Theorem 1.7.4]) we have

$$P\left\{\sup_{0\leqslant t\leqslant k}\left[M_i(t) - \frac{\varepsilon}{2}\bigl\langle M_i(t), M_i(t)\bigr\rangle\right] > \frac{2}{\varepsilon}\ln k\right\} \leqslant \frac{1}{k^2}.$$

An application of the well-known Borel–Cantelli lemma yields that, with probability one,

$$\sup_{0\leqslant t\leqslant k}\left[M_i(t) - \frac{\varepsilon}{2}\bigl\langle M_i(t), M_i(t)\bigr\rangle\right] \leqslant \frac{2}{\varepsilon}\ln k$$

holds for all but finitely many k. In other words, there exists an $\Omega_i \subset \Omega$ with $P(\Omega_i) = 1$ such that for any $\omega \in \Omega_i$ an integer $k_i = k_i(\omega)$ can be found such that

$$M_i(t) \leqslant \frac{\varepsilon}{2}\bigl\langle M_i(t), M_i(t)\bigr\rangle + \frac{2}{\varepsilon}\ln k, \quad 0 \leqslant t \leqslant k,$$

for any $k \geqslant k_i(\omega)$. Thus Eq. (8) results in

$$\ln\bigl(x_i(t)\bigr) \leqslant \ln\bigl(x_i(0)\bigr) + \int_0^t \left[b_i + \sum_{j=1}^n a_{ij}x_j - \frac{1-\varepsilon}{2}\left(\sum_{j=1}^n \sigma_{ij}x_j\right)^2 \right] ds + \frac{2}{\varepsilon}\ln k \tag{9}$$

for $0 \leqslant t \leqslant k_i(\omega)$ and $k \geqslant k_i(\omega)$ whenever $\omega \in \Omega_i$. Now let $\Omega_0 = \bigcap_{i=1}^n \Omega_i$. Clearly $P(\Omega_0) = 1$. Moreover, for any $\omega \in \Omega_0$, let $k_0(\omega) = \max\{k_i(\omega)\colon 1 \leqslant i \leqslant n\}$. Then, for any $\omega \in \Omega_0$, it follows from (9) that

$$\begin{aligned}\sum_{i=1}^n \ln\bigl(x_i(t)\bigr) \leqslant{}& \sum_{i=1}^n \ln\bigl(x_i(0)\bigr)\\ &+ \int_0^t \sum_{i=1}^n \left[b_i + \sum_{j=1}^n a_{ij}x_j - \frac{1-\varepsilon}{2}\left(\sum_{j=1}^n \sigma_{ij}x_j\right)^2 \right] ds + \frac{2n}{\varepsilon}\ln k\end{aligned}$$

for all $0 \leqslant t \leqslant k$ and $k \geqslant k_0(\omega)$. Note that $\sum_{i=1}^n(\sum_{j=1}^n \sigma_{ij}x_j)^2 = |\sigma x|^2$. Thus

$$\begin{aligned}&\ln\left(\prod_{i=1}^n x_i(t)\right) + \left(\frac{1}{4} - \frac{\varepsilon}{2}\right)\int_0^t |\sigma x|^2\,ds\\ &\quad\leqslant \ln\left(\prod_{i=1}^n x_i(0)\right) + \int_0^t \left(\sum_{i=1}^n \left[b_i + \sum_{j=1}^n a_{ij}x_j \right] - \frac{1}{4}|\sigma x|^2\right) ds + \frac{2n}{\varepsilon}\ln k.\end{aligned}$$

Since

$$\sum_{i=1}^n \left[b_i + \sum_{j=1}^n a_{ij}x_j \right] - \frac{1}{4}|\sigma x|^2 \leqslant K,$$

for some positive constant K, it follows that for $\omega \in \Omega_0$ we have

$$\ln\left(\prod_{i=1}^n x_i(t)\right) + \left(\frac{1}{4} - \frac{\varepsilon}{2}\right)\int_0^t |\sigma x|^2\,ds \leqslant \ln\left(\prod_{i=1}^n x_i(0)\right) + Kt + \frac{2n}{\varepsilon}\ln k,$$

for $0 \leqslant t \leqslant k$ and $k \geqslant k_i(\omega)$. Consequently, for any $\omega \in \Omega_0$, if $k-1 \leqslant t \leqslant k$ and $k \geqslant k(\omega)$,

$$\frac{1}{t}\left[\ln\left(\prod_{i=1}^n x_i(t)\right) + \frac{1-2\varepsilon}{4}\int_0^t |\sigma x|^2\,ds\right] \leqslant \frac{\ln(\prod_{i=1}^n x_i(0))}{k-1} + K + \frac{2n}{\varepsilon(k-1)}\ln k,$$

which implies that

$$\begin{aligned}&\limsup_{t\to\infty} \frac{1}{t}\left[\ln\left(\prod_{i=1}^n x_i(t)\right) + \frac{1-2\varepsilon}{4}\int_0^t |\sigma x|^2\,ds\right]\\ &\quad\leqslant \limsup_{k\to\infty}\left[\frac{\ln(\prod_{i=1}^n x_i(0))}{k-1} + \frac{2n}{\varepsilon(k-1)}\ln k + K\right] = K\end{aligned}$$

almost surely. On noting that $|\sigma x|^2 = x^T\sigma^T\sigma x \geqslant \lambda_{\min}(\sigma^T\sigma)|x|^2$, it then follows that

$$\limsup_{t\to\infty}\frac{1}{t}\left[\ln\left(\prod_{i=1}^n x_i(t)\right) + \lambda_{\min}(\sigma^T\sigma)\frac{1-2\varepsilon}{4}\int_0^t |x(s)|^2\,ds\right] \leqslant K \quad \text{a.s.}$$

Letting ε tend to zero yields the required assertion. □

Theorem 4. *Let us assume that hypothesis* (H1) *holds. Then, for any system parameters* $b \in \Re^n$, $A \in \Re^{n\times n}$ *and any initial value* $x_0 \in \Re^n_+$,

$$\limsup_{t\to\infty}\frac{\ln(\prod_{i=1}^n x_i(t))}{\ln(t)} \leqslant n \quad \textit{a.s.} \tag{10}$$

Proof. For each $1 \leqslant i \leqslant n$, applying Itô's formula to $e^{\gamma t}\ln(x_i(t))$ for $\gamma > 0$ results in

$$e^{\gamma t}\ln\bigl(x_i(t)\bigr) = \ln\bigl(x_i(0)\bigr) + \int_0^t e^{\gamma s}\left[b_i + \sum_{j=1}^n a_{ij}x_j - \frac{1}{2}\left(\sum_{j=1}^n \sigma_{ij}x_j\right)^2\right]ds$$
$$+ \gamma\int_0^t e^{\gamma s}\ln\bigl(x_i(s)\bigr)\,ds + M_i(t), \tag{11}$$

where

$$M_i(t) = \int_0^t e^{\gamma s}\sum_{j=1}^n \sigma_{ij}x_j\,dw(s)$$

is a real-valued continuous local martingale vanishing at $t = 0$ with quadratic form

$$\bigl\langle M_i(t), M_i(t)\bigr\rangle = \int_0^t e^{2\gamma s}\left(\sum_{j=1}^n \sigma_{ij}x_j\right)^2 ds.$$

Fix any $\varepsilon \in (0,1)$ and $\theta > 1$. For every integer $k \geqslant 1$, on using the exponential martingale inequality we have

$$P\left\{\sup_{0\leqslant t\leqslant k}\left[M_i(t) - \frac{\varepsilon}{2}e^{-\gamma k}\bigl\langle M_i(t), M_i(t)\bigr\rangle\right] > \frac{\theta e^{\gamma k}}{\varepsilon}\ln k\right\} \leqslant \frac{1}{k^\theta}.$$

By the Borel–Cantelli lemma we observe that there exists an $\Omega_i \subset \Omega$ with $P(\Omega_i) = 1$ such that for any $\omega \in \Omega_i$ an integer $k_i = k_i(\omega)$ can be found such that

$$M_i(t) \leqslant \frac{\varepsilon}{2}e^{-\gamma k}\bigl\langle M_i(t), M_i(t)\bigr\rangle + \frac{\theta e^{\gamma k}}{\varepsilon}\ln k$$

for all $0 \leqslant t \leqslant k$ and $k \geqslant k_i(\omega)$. Thus Eq. (11) leads to

$$e^{\gamma t}\ln\bigl(x_i(t)\bigr) \leqslant \ln\bigl(x_i(0)\bigr) + \gamma\int_0^t e^{\gamma s}\ln\bigl(x_i(s)\bigr)\,ds + \int_0^t e^{\gamma s}\left[b_i + \sum_{j=1}^n a_{ij}x_j - \frac{1}{2}\left(\sum_{j=1}^n \sigma_{ij}x_j\right)^2\right]ds + \frac{\varepsilon}{2}e^{-\gamma k}\int_0^t e^{2\gamma s}\left(\sum_{j=1}^n \sigma_{ij}x_j\right)^2 ds + \frac{\theta e^{\gamma k}}{\varepsilon}\ln k$$

for $0 \leqslant t \leqslant k$ and $k \geqslant k_i(\omega)$ whenever $\omega \in \Omega_i$, which can be rewritten as

$$e^{\gamma t}\ln\bigl(x_i(t)\bigr) \leqslant \ln\bigl(x_i(0)\bigr) + \gamma\int_0^t e^{\gamma s}\left[b_i + \sum_{j=1}^n a_{ij}x_j - \frac{1-\varepsilon e^{-\gamma(k-s)}}{2}\left(\sum_{j=1}^n \sigma_{ij}x_j\right)^2\right]ds + \frac{\theta e^{\gamma k}}{\varepsilon}\ln k + \int_0^t e^{\gamma s}\ln\bigl(x_i(s)\bigr)\,ds. \tag{12}$$

Now let $\Omega_0 = \bigcap_{i=1}^n \Omega_i$. Clearly $P(\Omega_0) = 1$. Moreover, for any $\omega \in \Omega_0$, let $k_0(\omega) = \max\{k_i(\omega)\colon 1 \leqslant i \leqslant n\}$. Then, for any $\omega \in \Omega_0$, it follows from (12) that

$$e^{\gamma t}\ln\left(\prod_{i=1}^n x_i(t)\right) \leqslant \sum_{i=1}^n \ln\bigl(x_i(0)\bigr) + \int_0^t e^{\gamma s}\sum_{i=1}^n\left[b_i + \sum_{j=1}^n a_{ij}x_j - \frac{1-\varepsilon e^{-\gamma(k-s)}}{2}\left(\sum_{j=1}^n \sigma_{ij}x_j\right)^2\right]ds + \frac{n\theta e^{\gamma k}}{\varepsilon}\ln k + \gamma\int_0^t e^{\gamma s}\sum_{i=1}^n \ln\bigl(x_i(s)\bigr)\,ds$$

for all $0 \leqslant t \leqslant k$ and $k \geqslant k_0(\omega)$. Since for positive constant K

$$\sum_{i=1}^n\left[b_i + \sum_{j=1}^n a_{ij}x_j - \frac{1}{2}\left(\sum_{j=1}^n \sigma_{ij}x_j\right)^2 + \gamma\ln(x_i)\right] \leqslant K, \quad \forall x \in \Re_+^n,$$

we have

$$e^{\gamma t}\ln\left(\prod_{i=1}^n x_i(t)\right) \leqslant \ln\left(\prod_{i=1}^n x_i(0)\right) + \frac{K}{\gamma}e^{\gamma t} - \frac{K}{\gamma} + \frac{n\theta e^{\gamma k}}{\varepsilon}\ln k$$

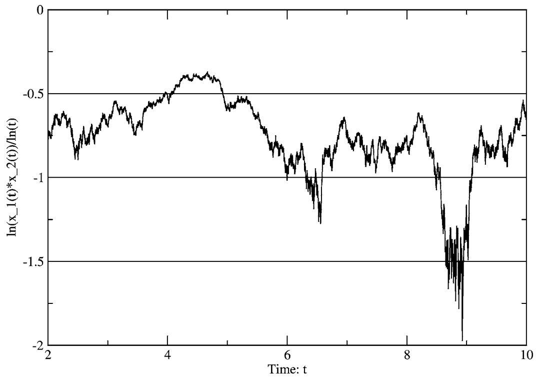

Fig. 1. A sample path of $[\ln(\prod_{i=1}^{2} x_i(t))]/\ln(t)$ produced by generating 10^6 points with time step $\Delta = 10^{-5}$ and initial condition $x_1(0) = x_2(0) = 50$.

for all $0 \leqslant t \leqslant k$ and $k \geqslant k_0(\omega)$. Consequently, for any $\omega \in \Omega_0$, if $(k-1) \leqslant t \leqslant k$ and $k \geqslant k(\omega)$, it follows that

$$\frac{\ln(\prod_{i=1}^{n} x_i(t))}{\ln(t)} \leqslant \frac{1}{\ln(k-1)} \left[e^{-\gamma(k-1)} \ln\left(\prod_{i=1}^{n} x_i(0)\right) + \frac{K}{\gamma} + \frac{n\theta e^{\gamma}}{\varepsilon} \ln k \right],$$

which implies that

$$\limsup_{t\to\infty} \frac{\ln(\prod_{i=1}^{n} x_i(t))}{\ln(t)} \leqslant \frac{n\theta e^{\gamma}}{\varepsilon} \quad \text{a.s.}$$

By letting $\varepsilon \to 1$, $\theta \to 1$ and $\gamma \to 0$, we then obtain

$$\limsup_{t\to\infty} \frac{\ln(\prod_{i=1}^{n} x_i(t))}{\ln(t)} \leqslant n \quad \text{a.s.}$$

as required. □

Figure 1 illustrates the above theoretical results by highlighting the "bounded" nature of the process (here $b_i = 1$, $a_{ij} = 1$ and $\sigma_{ij} = 10$ for every $i, j = 1, 2$). Note the controlling influence of the downward surges.

The conclusion of Theorem 4 is very powerful since it is universal in the sense that it is independent both of the system parameters $b \in \Re^n$ and $A \in \Re^{n\times n}$, and of the initial value $x_0 \in \Re_+^n$. It is also independent of the noise intensity matrix σ as long as the noise exists in the sense of hypothesis (H1). However, since estimation is based on the multiplication $\prod_{i=1}^{n} x_i(t)$, it would be better to use instead the norm $|x(t)|$. To do so we need additional conditions on the noise intensity matrix.

4. Pathwise estimation with additional conditions imposed on σ

Improved results concerning the pathwise behaviour of the solution can be achieved by introducing somewhat more restrictive assumptions. A numerical example given at the end of this section shows that applying our theoretical results to specific practical situations is a relatively simple procedure.

Consider a new hypothesis in which we assume the existence of two constants λ and ρ, with $2\rho > \lambda$, such that

$$\text{(H2)}\qquad \begin{cases} |\operatorname{diag}(x_1,\dots,x_n)\sigma x|^2 \leqslant \lambda |x|^4, & \forall x \in \Re^n_+,\\ |x^T \operatorname{diag}(x_1,\dots,x_n)\sigma x|^2 \geqslant \rho |x|^6, & \forall x \in \Re^n_+. \end{cases}$$

Then we can use this to develop a new suite of theorems.

Theorem 5. *Let us assume that hypothesis* (H1) *holds, and that there exist two positive constants λ and ρ, with $2\rho > \lambda$, such that hypothesis* (H2) *also holds. Moreover, let the system parameters $b \in \Re^n$, $A \in \Re^{n\times n}$ and the initial value $x_0 \in \Re^n_+$ be given. Then, with probability* 1,

$$\limsup_{t\to\infty} \frac{1}{t}\left[\frac{\delta}{2\rho-\lambda}\ln\left(\left|x(t)\right|^2\right) + \int_0^t \left|x(s)\right|^2 ds\right] \leqslant \frac{n\mu^2\delta^2}{(\delta-1)(2\rho-\lambda)^2} + \frac{2\mu\delta}{2\rho-\lambda}, \tag{13}$$

where $\mu = \max\{|a_{ij}|, |b_i|:\ 1 \leqslant i, j \leqslant n\}$ *and*

$$\delta = \frac{n\mu + 2 + \sqrt{n\mu(n\mu+2)}}{n\mu+2}.$$

Proof. Define a C^2-function $V : \Re^n_+ \to \Re_+$ by

$$V(x) = \ln\left(|x|^2\right).$$

Then applying Itô's formula yields

$$\begin{aligned} dV\left(x(t)\right) = {} & \frac{2}{|x|^2} x^T \operatorname{diag}(x_1,\dots,x_n)(b + Ax)\, dt \\ & + \frac{1}{|x|^2}\operatorname{trace}\left\{ \left|\operatorname{diag}(x_1,\dots,x_n)\sigma x\right|^2 \right.\\ & \qquad \left. - \frac{2}{|x|^4}\left|x^T \operatorname{diag}(x_1,\dots,x_n)\sigma x\right|^2 \right\} dt \\ & + \frac{2}{|x|^2} x^T \operatorname{diag}(x_1,\dots,x_n)\sigma x\, dw(t). \end{aligned} \tag{14}$$

Now Eq. (14) can be rewritten in the form

$$\begin{aligned} dV\left(x(t)\right) = {} & \left\{ \frac{2}{|x|^2}\left[\sum_{i=1}^n b_i x_i^2 + \sum_{i=1}^n x_i^2 \sum_{j=1}^n a_{ij} x_j\right] \right.\\ & \left. + \frac{1}{|x|^2}\left(\sum_{i=1}^n x_i^2 \sum_{j=1}^n \sigma_{ij} x_j\right)^2 - \frac{2}{|x|^4}\left(\sum_{i=1}^n x_i^2 \sum_{j=1}^n \sigma_{ij} x_j\right)^2 \right\} dt \end{aligned}$$

$$+\frac{2}{|x|^2}\sum_{i=1}^n x_i^2\sum_{j=1}^n \sigma_{ij}x_j\,dw(t).$$

Moreover, taking into account that

$$0<\left(\sum_{i=1}^n x_i\right)^2\leqslant \sum_{i=1}^n 1^2\sum_{i=1}^n x_i^2 \quad\Rightarrow\quad \sum_{i=1}^n x_i\leqslant \sqrt{n}\,|x|$$

results in

$$\frac{1}{|x|^2}x^T\,\mathrm{diag}(x_1,\dots,x_n)(b+Ax)\leqslant \mu\big(\sqrt{n}\,|x|+1\big),\quad \forall x\in\Re_+^n,$$

where $\mu=\max\{|a_{ij}|, |b_i|:\ 1\leqslant i,\ j\leqslant n\}$. Consequently, Eq. (14) becomes

$$V\big(x(t)\big)\leqslant V\big(x(0)\big)+\int_0^t\big[2\mu\big(\sqrt{n}\,|x|+1\big)+\lambda|x|^2\big]\,ds$$
$$-\int_0^t\frac{2}{|x|^4}\big|x^T\,\mathrm{diag}(x_1,\dots,x_n)\sigma x\big|^2\,ds+M_1(t), \tag{15}$$

where

$$M_1(t)=\int_0^t\frac{2}{|x|^2}\sum_{i=1}^n x_i^2\sum_{j=1}^n\sigma_{ij}x_j\,dw(s)=\int_0^t\frac{2}{|x|^2}x^T\,\mathrm{diag}(x_1,\dots,x_n)\sigma x\,dw(s)$$

is a real-valued continuous local martingale vanishing at $t=0$ with quadratic form

$$\big\langle M_1(t),M_1(t)\big\rangle=\int_0^t\frac{4}{|x|^4}\big|x^T\,\mathrm{diag}(x_1,\dots,x_n)\sigma x\big|^2\,ds.$$

Fix any $\varepsilon>0$. By the exponential martingale inequality we have that for every integer $k\geqslant 1$

$$P\left\{\sup_{0\leqslant t\leqslant k}\left[M_1(t)-\frac{\varepsilon}{4}\big\langle M_1(t),M_1(t)\big\rangle\right]>4\frac{\ln k}{\varepsilon}\right\}\leqslant k^{-2}.$$

Since $\sum_{k=1}^\infty k^{-2}$ converges, the application of the Borel–Cantelli lemma proves that for almost all $\omega\in\Omega$ there exists a random integer $k_0(\omega)$ such that for all $k\geqslant k_0(\omega)$

$$\sup_{0\leqslant t\leqslant k}\Big(M_1(t)-\frac{\varepsilon}{4}\big\langle M_1(t),M_1(t)\big\rangle\Big)\leqslant\frac{4\ln k}{\varepsilon},$$

which implies

$$M_1(t)\leqslant\frac{\varepsilon}{4}\big\langle M_1(t),M_1(t)\big\rangle+\frac{4\ln k}{\varepsilon}\quad \text{on } 0\leqslant t\leqslant k.$$

By taking into consideration inequality (15), assumption (H2), and the above results, we then obtain

$$V(x(t)) \leqslant V(x(0)) + \int_0^t \left[2\mu(\sqrt{n}\,|x| + 1) - (2\rho - \lambda - \varepsilon\rho)|x|^2\right] ds + \frac{4\ln k}{\varepsilon}.$$

Now, since $2\rho > \lambda$, we can choose ε small enough to ensure that $2\rho - \varepsilon\rho > \lambda$. Thus, for any $\delta > 1$, we have the inequality

$$2\mu(\sqrt{n}\,|x| + 1) - \frac{(\delta - 1)(2\rho - \lambda)}{\delta}|x|^2 \leqslant \frac{n\mu^2\delta}{(\delta - 1)(2\rho - \lambda)} + 2\mu.$$

As a result, we obtain

$$V(x(t)) + \left(\frac{2\rho - \lambda}{\delta} - \varepsilon\rho\right) \int_0^t |x(s)|^2\, ds$$
$$\leqslant V(x(0)) + \left[\frac{n\mu^2\delta}{(\delta - 1)(2\rho - \lambda)} + 2\mu\right] t + \frac{4\ln k}{\varepsilon} \quad \text{on } 0 \leqslant t \leqslant k.$$

In particular, for almost all $\omega \in \Omega$, if $k - 1 \leqslant t \leqslant k$ and $k \geqslant k_0(\omega)$, it follows that

$$\frac{1}{t}\left[V(x(t)) + \left(\frac{2\rho - \lambda}{\delta} - \varepsilon\rho\right) \int_0^t |x(s)|^2\, ds\right]$$
$$\leqslant \frac{1}{k - 1}\left[V(x(0)) + \frac{4\ln k}{\varepsilon}\right] + \left[\frac{n\mu^2\delta}{(\delta - 1)(2\rho - \lambda)} + 2\mu\right]\frac{k}{k - 1}.$$

Whence letting $t \to \infty$ (so $k \to \infty$), and then $\varepsilon \to 0$, results in

$$\limsup_{t\to\infty} \frac{1}{t}\left[\frac{\delta}{2\rho - \lambda}\ln(|x(t)|^2) + \int_0^t |x(s)|^2\, ds\right] \leqslant \frac{n\mu^2\delta^2}{(\delta - 1)(2\rho - \lambda)^2} + \frac{2\mu\delta}{2\rho - \lambda}.$$

Since the right-hand side of this equation is minimised when

$$\delta = \frac{n\mu + 2 + \sqrt{n\mu(n\mu + 2)}}{n\mu + 2},$$

the required assertion follows. □

Theorem 6. *Let us assume that hypothesis* (H1) *holds, and that there exist two positive constants* λ *and* ρ, *with* $2\rho > \lambda$, *such that hypothesis* (H2) *also holds. Moreover, let the system parameters* $b \in \Re^n$, $A \in \Re^{n\times n}$ *and the initial value* $x_0 \in \Re^n_+$ *be given. Then, with probability* 1,

$$\limsup_{t\to\infty} \frac{\ln(|x(t)|)}{\ln(t)} \leqslant \frac{\rho}{2\rho - \lambda}. \tag{16}$$

Proof. Let us define the following C^2-function $V : \Re_+^n \times \Re_+ \to \Re_+$ such that

$$V(x,t) = e^t \ln\bigl(|x|^2\bigr).$$

Then applying Itô's formula yields

$$\begin{aligned} dV\bigl(x(t),t\bigr) = e^t \ln\bigl(|x|^2\bigr) &+ e^t \frac{2}{|x|^2} x^T \operatorname{diag}(x_1,\dots,x_n)(b+Ax)\,dt \\ &+ e^t \frac{1}{|x|^2} \operatorname{trace}\biggl\{ \bigl|\operatorname{diag}(x_1,\dots,x_n)\sigma x\bigr|^2 \\ &\qquad - \frac{2}{|x|^4}\bigl|x^T \operatorname{diag}(x_1,\dots,x_n)\sigma x\bigr|^2 \biggr\}\,dt \\ &+ e^t \frac{2}{|x|^2} x^T \operatorname{diag}(x_1,\dots,x_n)\sigma x\,dw(t). \end{aligned} \tag{17}$$

Moreover, it is easy to show that

$$\frac{1}{|x|^2} x^T \operatorname{diag}(x_1,\dots,x_n)(b+Ax) \leqslant \mu\bigl(\sqrt{n}\,|x|+1\bigr), \quad \forall x \in \Re_+^n,$$

where $\mu = \max\{|a_{ij}|, |b_i|\colon 1 \leqslant i, j \leqslant n\}$. As a result, Eq. (17) yields

$$\begin{aligned} V\bigl(x(t),t\bigr) \leqslant V\bigl(x(0),0\bigr) &+ \int_0^t e^s \ln\bigl(\bigl|x(s)\bigr|^2\bigr)\,ds \\ &+ \int_0^t e^s \bigl[2\mu\bigl(\sqrt{n}\,\bigl|x(s)\bigr|+1\bigr) + \lambda\bigl|x(s)\bigr|^2\bigr]\,ds \\ &- \int_0^t e^s \frac{2}{|x(s)|^4}\bigl|x^T \operatorname{diag}\bigl(x_1(s),\dots,x_n(s)\bigr)\sigma x(s)\bigr|^2\,ds + M_1(t), \end{aligned} \tag{18}$$

where

$$M_1(t) = \int_0^t e^s \frac{2}{|x(s)|^2} x^T \operatorname{diag}\bigl(x_1(s),\dots,x_n(s)\bigr)\sigma x(s)\,dw(s)$$

is a real-valued continuous local martingale vanishing at $t = 0$ with quadratic form

$$\bigl\langle M_1(t), M_1(t)\bigr\rangle = \int_0^t \frac{4e^{2s}}{|x(s)|^4}\bigl|x^T(s) \operatorname{diag}\bigl(x_1(s),\dots,x_n(s)\bigr)\sigma x(s)\bigr|^2\,ds.$$

Given any $\varepsilon > 0$, $\theta > 1$ and $\alpha > 0$, on exploiting the exponential martingale inequality once again, we can show that for almost all $\omega \in \Omega$ there exists a random integer $k_0(\omega)$ such that, for all integer $k \geqslant k_0(\omega)$,

$$M_1(t) \leqslant \frac{\varepsilon e^{-k\alpha}}{4}\bigl\langle M_1(t), M_1(t)\bigr\rangle + \frac{2\theta e^{k\alpha}\ln k}{\varepsilon}, \quad \text{for all } 0 \leqslant t \leqslant k\alpha.$$

By taking into consideration inequality (18), hypothesis (H2), and the above results, we then obtain

$$V\big(x(t),t\big) \leqslant V\big(x(0),0\big) + \int_0^t e^s \ln\big(|x(s)|^2\big)\,ds + \int_0^t e^s\big[2\mu\big(\sqrt{n}\,|x(s)|+1\big) - \big(2\rho-\lambda-\varepsilon e^{-(k\alpha-s)}\rho\big)|x(s)|^2\big]\,ds + \frac{2\theta e^{k\alpha}\ln k}{\varepsilon} \tag{19}$$

for all $0 \leqslant t \leqslant k\alpha$. Now, since $2\rho > \lambda$, we can choose ε small enough to ensure that $(2-\varepsilon)\rho > \lambda$, namely, choose $\varepsilon \in (0, (2\rho-\lambda)/\rho)$. Moreover, there exists a positive constant κ such that

$$\ln\big(|x|^2\big) + 2\mu\big(\sqrt{n}\,|x|+1\big) - (2\rho-\lambda-\varepsilon\rho)|x|^2 \leqslant \kappa, \quad \forall x \in \Re_+^n.$$

Consequently, inequality (19) yields

$$e^t \ln\big(|x(t)|^2\big) \leqslant \ln\big(|x(0)|^2\big) + \kappa e^t - \kappa + \frac{2\theta e^{k\alpha}\ln k}{\varepsilon} \quad \text{on } 0 \leqslant t \leqslant k\alpha,$$

which implies that

$$\ln\big(|x(t)|^2\big) \leqslant e^{-t}\big[\ln\big(|x(0)|^2\big) - \kappa\big] + \kappa + \frac{2\theta e^{k\alpha-t}\ln k}{\varepsilon} \quad \text{on } 0 \leqslant t \leqslant k\alpha.$$

In particular, for almost all $\omega \in \Omega$, if $(k-1)\alpha \leqslant t \leqslant k\alpha$ and $k \geqslant k_0(\omega)$, it follows that

$$\frac{\ln(|x(t)|^2)}{\ln(t)} \leqslant \frac{e^{-(k-1)\alpha}}{\ln(k-1)}\big[\ln\big(|x(0)|r^2\big) - \kappa\big] + \frac{\kappa}{\ln(k-1)} + \frac{2\theta e^{\alpha}\ln k}{\varepsilon\ln(k-1)} \quad \text{on } 0 \leqslant t \leqslant k\alpha.$$

Whence letting $t \to \infty$ (so $k \to \infty$ too) yields

$$\limsup_{t\to\infty} \frac{\ln(|x(t)|^2)}{\ln(t)} \leqslant \frac{2\theta}{\varepsilon} e^{\alpha} \quad \text{a.s.}$$

Finally, by letting $\theta \to 1$, $\alpha \to 0$ and $\varepsilon \to (2\rho-\lambda)/\rho$, we obtain

$$\limsup_{t\to\infty} \frac{\ln(|x(t)|^2)}{\ln(t)} \leqslant \frac{2\rho}{2\rho-\lambda} \quad \text{a.s.}$$

which is the required assertion. □

Let us now discuss a simple numerical example which not only demonstrates that the set of functions and parameters satisfying hypothesis (H2) is not empty but also illustrates the estimation obtained by Theorem 6. Consider the case $n = 2$ with

$$\mathbf{b} = \begin{pmatrix}1\\1\end{pmatrix}, \qquad \mathbf{A} = \begin{pmatrix}1 & 1\\1 & 1\end{pmatrix} \quad \text{and} \quad \sigma = \begin{pmatrix}2 & 1\\1 & 2\end{pmatrix}.$$

It is easy to see that

$$\big|\operatorname{diag}(x_1,x_2)\sigma x\big|^2 \leqslant 5|x|^4,$$

since

$$\begin{aligned}\left|\operatorname{diag}(x_1,x_2)\sigma x\right|^2 &= \left|\begin{pmatrix} x_1 & 0 \\ 0 & x_2\end{pmatrix}\begin{pmatrix} 2 & 1 \\ 1 & 2\end{pmatrix}\begin{pmatrix} x_1 \\ x_2\end{pmatrix}\right|^2 \\ &= 4x_1^4 + 4x_1^3x_2 + 2x_1^2x_2^2 + 4x_1x_2^3 + 4x_2^4\end{aligned}$$

and

$$\begin{aligned}5|x|^4 - \left|\operatorname{diag}(x_1,x_2)\sigma x\right|^2 &= x_1^4 - 4x_1^3x_2 + 8x_1^2x_2^2 - 4x_1x_2^3 + x_2^4 \\ &= x_1^2(x_1-2x_2)^2 + x_2^2(x_2-2x_1)^2 \geqslant 0.\end{aligned}$$

Similarly, the inequality

$$\left|x^T\operatorname{diag}(x_1,x_2)\sigma x\right|^2 \geqslant 3|x|^6$$

holds, since

$$\begin{aligned}\left|x^T\operatorname{diag}(x_1,x_2)\sigma x\right|^2 &= \left|(x_1 \quad x_2)\begin{pmatrix} x_1 & 0 \\ 0 & x_2\end{pmatrix}\begin{pmatrix} 2 & 1 \\ 1 & 2\end{pmatrix}\begin{pmatrix} x_1 \\ x_2\end{pmatrix}\right|^2 \\ &= 4x_1^6 + 4x_1^5x_2 + 5x_1^4x_2^2 + 10x_1^3x_2^3 + 5x_1^2x_2^4 + 4x_1x_2^5 + 4x_2^6\end{aligned}$$

and

$$\begin{aligned}&\left|x^T\operatorname{diag}(x_1,x_2)\sigma x\right|^2 - 3|x|^6 \\ &\quad = x_1^6 + 4x_1^5x_2 - 4x_1^4x_2^2 + 10x_1^3x_2^3 - 4x_1^2x_2^4 + 4x_1x_2^5 + x_2^6 \\ &\quad = \left(x_1^3 + x_2^3\right)^2 + x_1x_2\left[x_1^2(x_1-2x_2)^2 + x_2^2(x_2-2x_1)^2 + 3\left(x_1^4 + x_2^4\right)\right] \\ &\quad \geqslant 0.\end{aligned}$$

We have therefore proved that there exists a pair of parameters, $\lambda = 5$ and $\rho = 3$, for the above specified matrix σ which satisfy hypothesis (H2). As a result, Theorem 6 yields

$$\limsup_{t\to\infty} \frac{\ln(|x(t)|)}{\ln(t)} \leqslant 3 \quad \text{a.s.} \tag{20}$$

This means that neither of two species will grow faster than a polynomial (of time t) of order 3. Figure 2 shows a sample path of $\ln(|x(t)|)/\ln(t)$ which supports this theoretical result.

5. Summary

Our aim in this paper is to discuss the asymptotic properties of the stochastic Lotka–Volterra model in populations dynamics. In our earlier paper [8] we revealed an important fact that even a tiny amount of stochastic noise can suppress an explosion in populations dynamics. Due to the page limit we have not investigated in [8] the asymptotic behaviour of the stochastic populations dynamics but the theory there guarantees the nice property that the solution of the stochastic Lotka–Volterra model will remain in the positive cone with probability one. Making use of this property we have in this paper designed various

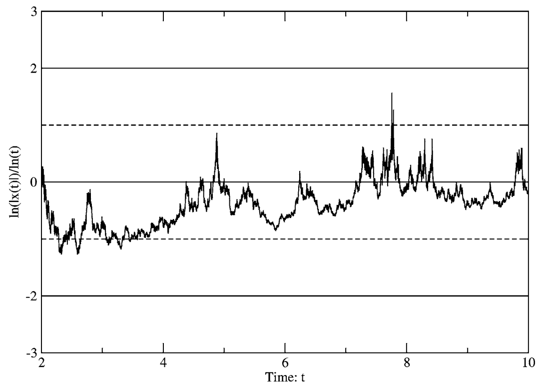

Fig. 2. A sample path of $[\ln(|x(t)|)]/\ln(t)$ produced by generating 10^6 points with time step $\Delta = 10^{-5}$ and initial condition $x_1(0) = x_2(0) = 50$.

types of Lyapunov functions to discuss the asymptotic behaviour in some detail. Several moment and pathwise asymptotic estimators are obtained. These essentially enhance each other, so that they can be used to reveal better features of the stochastic Lotka–Volterra model. Two computer simulations are presented which support the theoretical results.

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References

[1] D.H. Boucher (Ed.), The Biology of Mutualism, Groom Helm, London, 1985.
[2] X. He, K. Gopalsamy, Persistence, attractivity, and delay in facultative mutualism, J. Math. Anal. Appl. 215 (1997) 154–173.
[3] R.Z. Khasminskii, Stochastic Stability of Differential Equations, Sijthoff and Noordhoff, 1981.
[4] X. Mao, Stability of Stochastic Differential Equations with Respect to Semimartingales, Longman Scientific and Technical, 1991.
[5] X. Mao, Exponential Stability of Stochastic Differential Equations, Marcel Dekker, 1994.
[6] X. Mao, Stochastic Differential Equations and Applications, Horwood, 1997.
[7] G. Marion, X. Mao, E. Renshaw, Convergence of the Euler scheme for a class of stochastic differential equation, Internat. J. Math. 1 (2002) 9–22.
[8] X. Mao, G. Marion, E. Renshaw, Environmental Brownian noise suppresses explosions in populations dynamics, Stochastic Process. Appl. 97 (2002) 95–110.
[9] C.L. Wolin, L.R. Lawlor, Models of facultative mutualism: density effects, Amer. Natural. 124 (1984) 843–862.