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Impacts of demographic and environmental stochasticity on population dynamics with cooperative effects

Tao Feng [a], Hongjuan Zhou [b], Zhipeng Qiu [c], Yun Kang [d,*]

[a] School of Mathematical Science, Yangzhou University, Yangzhou 225002, PR China
[b] School of Mathematical and Statistical Sciences, Arizona State University, Tempe, AZ 85287, USA
[c] Interdisciplinary Center for Fundamental and Frontier Sciences, Nanjing University of Science and Technology, Jiangyin 214443, PR China
[d] Sciences and Mathematics Faculty, College of Integrative Sciences and Arts, Arizona State University, Mesa, AZ 85212, USA

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ABSTRACT

Different types of stochasticity play essential roles in shaping complex population dynamics. This paper presents a novel approach to model demographic and environmental stochasticity in a single-species model with cooperative components that are measured by component Allee effects. Our work provides rigorous mathematical proof on stochastic persistence and extinction, ergodicity (i.e., the existence of a unique stationary distribution) and the existence of a nontrivial periodic solution to study the impacts of demographic and environmental stochasticity on population dynamics. The theoretical and numerical results suggest that stochasticity may affect the population system in a variety of ways, specifically: (i) In the weak Allee effects case (e.g., strong cooperative efforts), the demographic stochasticity from the attack rate contributes to the expansion of the population size, while the demographic stochasticity from the handling rate and the environmental stochasticity have the opposite role, and may even lead to population extinction; (ii) In the strong Allee effects case (cooperative efforts not strong enough), both demographic and environmental stochasticity play a similar role in the survival of population, and are related to the initial population level: if the initial population level is large enough, demographic stochasticity and environmental stochasticity may be detrimental to the survival of population, otherwise if the initial population level is small enough, demographic stochasticity and environmental stochasticity may bring survival opportunities for the population that deterministically would extinct indefinitely; (iii) In the extinction case, demographic and environmental stochasticity cannot change the trend of population extinction, but they can delay or promote population extinction.

1. Introduction

Stochasticity exists in all corners of the ecosystem and may affect the survival and development of creatures to varying degrees. For instance, stochasticity poses an additional extinction risk for populations that deterministically would persist indefinitely [1–3]. Failure to properly consider the effects of stochasticity may lead to severe consequences such as the extinction of endangered species and over-exploitation of resources [4]. To date, stochasticity has received attention from various aspects of ecology including population ecology [5, 6], social ecology [7–11] and biodiversity [12,13], to name just a few.

In general, stochasticity can be roughly divided into two types, namely demographic stochasticity and environmental stochasticity. Demographic stochasticity describes the within-individual variability, while environmental stochasticity refers to temporary environmental fluctuations that lead to changes in population growth rates [14,15]. Demographic stochasticity usually has a greater impact on small-scale populations, while environmental stochasticity can produce similar extinction probability in large-scale and small-scale populations [4,16]. In recent years, research on how stochasticity affects population dynamics has yielded many significant insights [17–23]. Based on the frameworks of stochastic differential equations and stochastic difference equations, valuable insights have been provided on how environmental stochasticity affects coexistence (e.g., [24–27]), extinction (e.g., [28–35]) and optimal harvesting (e.g., [36–38]) of species. Chesson [39,40] indicated that stochasticity can affect species in a variety of ways (directly or indirectly), and these effects can be positive or negative, or ineffective. Hening et al. [41] described the influence of environmental stochasticity on population systems through the classification of long-term dynamics. Most of the above literature only separately studied the impact of demographic stochasticity or environmental stochasticity on population dynamics, while there are relatively few studies on the synergistic effects of demographic stochasticity and environmental

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* Corresponding author.
E-mail addresses: taofeng@yzu.edu.cn (T. Feng), Hongjuan.Zhou@asu.edu (H. Zhou), nustqzp@njust.edu.cn (Z. Qiu), yun.kang@asu.edu (Y. Kang).

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stochasticity. Our modeling work will incorporate both demographic stochasticity and environmental stochasticity through a novel modeling approach.

In nature, many species experience cooperative feeding, mating restriction, environmental conditioning and cooperative defense [42,43] that contribute to generate Allee effects which are an important biological phenomenon in population dynamics [44]. Allee effect describes an interesting scenario: when the population density is lower than a certain value, there is a positive correlation between the individual fitness and the population density. The mechanisms that produce Allee effects usually come from the cooperation or facilitation among individuals in the species, including ecological mechanisms, human induced [45], genetic mechanisms [46] and demographic stochasticity [3]. When any measurable component (component Allee effects) or growth rate (demographic Allee effects) of individual fitness is positively correlated with population size, Allee effects may bring extinction risk to small populations [47]. The combined effects of component Allee effects and the negative density dependence such as competition can lead to weak Allee effects (demographic Allee effects with a critical population size) and strong Allee effects (demographic Allee effects without a critical population size). In recent years, examples of Allee effects have been widely reported in many research fields such as population dynamics [48,49], biological invasions [50,51], ecology [52,53] and species packing [54]. Consensus has been reached that Allee effects may have profound effect on the population dynamics of many plants and animals [1,49]. Therefore, it is of great significance to study population dynamics with cooperative components that generate Allee effects.

Mathematical modeling has been a powerful tool in studying population dynamics. In the past decades, many mathematical models have been successfully developed to study population dynamics with Allee effects (e.g., predator–prey models [55,56]; single-species models [57–59]; competition models [60,61]). For example, using difference equations and numerical simulation techniques, Scheuring [59] found that Allee effects may contribute to the dynamical stability of populations. More recently, Alves and Hilker [62] proposed a predator–prey model incorporating a cooperative term in the attack rate, who identified scenarios in which hunting cooperation contributed to the Allee effects in predators. Most of the above work are based on deterministic models to investigate the population dynamics with Allee effects. They provided important theoretical insights for the protection of population and even ecological diversity. In the meanwhile, the combinations of stochasticity and component Allee effects on population dynamics is less explored [63–67]. A notable contribution along these lines was a recent work by Yu et al. [68], which studied the potential impact of Allee effects and environmental stochasticity on small population communities based on the framework of stochastic differential equations. By constructing suitable Lyapunov functions, they obtained sufficient conditions for the stochastic persistence, extinction and ergodicity of the single-species model. They concluded that environmental stochasticity can promote population extinction. The work of Yu et al. [68] obtained some interesting insights, and leave the room for improvements. For example, their framework did not include demographic stochasticity that may affect the dynamics of small population communities, and did not further study the relationship between stochasticity and extinction time as well as initial level, which are closely related to population dynamics.

In this paper, we provide a new framework for describing and predicting how demographic and environmental stochasticity affect the population dynamics of single-species model with cooperative components that contribute to component Allee effects. This framework allows us to study: (i) the stochastic population dynamics including the stochastic persistence and extinction, the ergodicity and the existence of a unique positive solution; (ii) how stochasticity affects population dynamics in different scenarios (i.e., the weak and strong Allee effects case, and the extinction case); (iii) the relationship between stochasticity and extinction time as well as extinction probability; (iv) how initial population level affects the stochastic population dynamics. The structure of the paper is as follows. Section 2 provides the model derivation of the stochastic single-population model. Sections 3 and 4 present theoretically and numerically the stochastic dynamics of the proposed framework. Section 5 concludes the work with a summary of results, biological interpretation, and potential future work.

2. Model derivation and preliminary knowledge

We start with the single-species model with cooperative components that are measured by *component Allee effects* (see Kang and Udiani [69])

$$X' = rX\left(1-\frac{X}{K}\right) - \underbrace{\frac{aX}{haX+1}}_{\text{Component Allee Effects}}, \tag{1}$$

where $X(t)$ is the population level, r denotes the intrinsic growth rate of population $X(t)$, and K denotes the carrying capacity of population $X(t)$ in the absence of component Allee effects, i.e., the term $\frac{aX}{haX+1}$, where a and h respectively denote the attack rate and handling time of generalist predators whose sizes are assumed to be constant.

For convenience, we let $x=\frac{X}{K}, \bar{\alpha}=\frac{a}{r}, \bar{\beta}=hKr$, then Model (1) has the equivalent dynamics with the following scaled model (2)

$$x' = x\left(1-x-\frac{\bar{\alpha}}{\bar{\alpha}\bar{\beta}x+1}\right). \tag{2}$$

A simple arithmetic calculation shows that Model (2) always has an extinction equilibrium $x^0 = 0$, and can have up to two survival equilibria

$$x^K = \frac{\bar{\alpha}\bar{\beta}-1+\sqrt{(\bar{\alpha}\bar{\beta}+1)^2-4\bar{\alpha}^2\bar{\beta}}}{2\bar{\alpha}\bar{\beta}}$$

and

$$x^\theta = \frac{\bar{\alpha}\bar{\beta}-1-\sqrt{(\bar{\alpha}\bar{\beta}+1)^2-4\bar{\alpha}^2\bar{\beta}}}{2\bar{\alpha}\bar{\beta}}.$$

The equilibrium dynamics of System (2) can be summarized in Table 1.

As seen from Table 1, the dynamics of $x(t)$ is determined by the life-depending coefficients $\bar{\alpha}$ and $\bar{\beta}$. Since these coefficients can change according to the biological environment, we are interested in how the population dynamics change when these coefficients and System (2) are subjected to stochasticity. The main biological assumptions are as follows.

1. *The population $x(t)$ suffers from demographic stochasticity due to fluctuations in attack rate and handling time.* Demographic stochasticity is often described by key parameters related to survival and mortality. In this paper, we extend on the effect of demographic stochasticity on population $x(t)$ by describing the scaled attack rate $\alpha(t) : t \to \mathbb{R}_+$ and the scaled handling time $\beta(t) : t \to \mathbb{R}_+$ as stochastic processes.

(i) **The bounded case.** If $\alpha(t)$ and $\beta(t)$ are inherently bounded on $t \in [0,\infty)$, i.e., there are positive constants $\hat{\alpha}, \check{\alpha}, \hat{\beta}, \check{\beta}$ such that $\hat{\alpha} \le \alpha(t) \le \check{\alpha}$ and $\hat{\beta} \le \beta(t) \le \check{\beta}$, then we can select bounded stochastic processes (e.g., Markov process and periodic process) to describe the demographic stochasticity.

(ii) **The unbounded case.** If $\alpha(t)$ and $\beta(t)$ are inherently unbounded on $t \in [0,\infty)$, we can choose the stochastic processes as the solutions to the following stochastic differential equations (SDEs)

$$\begin{aligned} d\alpha &= f_1(\alpha)dt + g_1(\alpha)dB_\alpha(t), \\ d\beta &= f_2(\beta)dt + g_2(\beta)dB_\beta(t), \end{aligned} \tag{3}$$

where $f_1(\alpha), f_2(\beta) \in \mathscr{L}^1(\mathbb{R}_+;\mathbb{R})$, $g_1(\alpha), g_2(\beta) \in \mathscr{L}^2(\mathbb{R}_+;\mathbb{R})$, $B_\alpha(t)$ and $B_\beta(t)$ are one-dimensional independent Brownian motions defined on the complete probability space $(\Omega,\mathscr{F},\mathbb{P})$.

2. *The population $x(t)$ suffers from environmental stochasticity, and the intensity of stochasticity is positively related with the level of population*

Table 1

Existence and stability of equilibria of System (2), where GAS denotes that the equilibrium is globally asymptotically stable.

Cases	Equilibria	Existence condition	Stability condition
(A1) Weak Allee effects	x_0 and x_K	$\bar{\alpha} < 1$	x^K is GAS.
(A2) Strong Allee effects	x_0, x_K and x_θ	(1) $\frac{4}{\bar{\beta}} < 1 < \bar{\alpha}$, or (2) $\bar{\beta} < 4$ and $\max\left\{1, \frac{1}{\bar{\beta}}\right\} < \bar{\alpha} < \frac{1}{\sqrt{\bar{\beta}}}(\frac{1}{2-\sqrt{\bar{\beta}}})$	x^0 is GAS if $x(0) < x^\theta$, x^K is GAS if $x(0) > x^\theta$.
(A3) Extinction	x_0	(1) $1 < \bar{\alpha} < \frac{1}{\bar{\beta}}$ or (2) $\bar{\beta} < 4$ and $\max\{\frac{1}{\sqrt{\bar{\beta}}}(\frac{1}{2-\sqrt{\bar{\beta}}}), \frac{1}{\bar{\beta}}, 1\} < \bar{\alpha}$	x^0 is GAS.

$x(t)$. Inspired by previous work (e.g., [30,32,70]), for any initial value $x(0) = x_0$ and time step $0 \leq \Delta t \ll 1$, the solution $x(t)$ can be described by a Markov process with conditional mean

$$\mathbb{E}[x(t + \Delta t) - x(t)|x(t) = x] \approx \left[x(1 - x) - \frac{\alpha x}{\alpha \beta x + 1}\right] \Delta t$$

and conditional variance

$$\mathrm{Var}[x(t + \Delta t) - x(t)|x(t) = x] \approx \sigma_x^2 x^2 \Delta t,$$

where σ_x^2 is the intensity of environmental stochasticity. More specifically, we can formulate the dynamics of population $x(t)$ by the following stochastic system

$$dx = x\left(1 - x - \frac{\alpha}{\alpha \beta x + 1}\right) dt + \sigma_x x dB_x(t), \tag{4}$$

where $B_x(t)$ is a one-dimensional independent Brownian motion defined on the complete probability space $(\Omega, \mathscr{F}, \mathbb{P})$. As expected, if the stochasticity does not exist, i.e., $\sigma_x = 0, \alpha(t) = \bar{\alpha}, \beta(t) = \bar{\beta}$, System (4) would have equivalent dynamics with its limit system (2) (see Thieme [71]).

Since $x(t)$ represents the population level, it should be non-negative. In the bounded case, it is easy to verify that System (4) has a unique positive solution on $t \geq 0$. However, In the unbounded case, we need the following assumption to insure that System (4) is biologically well-defined.

Assumption 1. Denote by $\mathbf{C}^2$ the class of functions $V(t, x)$ twice continuously differentiable with respect to x and once continuously differentiable with respect to t, $\mathbf{L}V$ the Lyapunov operator of function V, and $I = \{t : t \geq 0\}$. Throughout this paper, when $\alpha(t)$ and $\beta(t)$ are given by the stochastic differential equations (3), we always assume that: (i) the functions $f_i(\cdot)$ and $g_i(\cdot)$ are locally Lipschitz functions for any $i = 1, 2$; (ii) there exists a nonnegative Lyapunov function $V(t, x) \in \mathbf{C}^2$ defined on the domain $I \times \mathbb{R}^3$ such that for some $c > 0$ we have $V_{\mathbf{R}} = \inf_{|x|>\mathbf{R}} V(t, x) \to \infty$ *as* $\mathbf{R} \to \infty$, and $\mathbf{L}V \leq cV$; (iii) $(\alpha(0), \beta(0)) \in \mathbb{R}_+^2$.

Assumption 1 guarantees that System (4) admits a unique positive solution $x(t)$ on $t \geq 0$ with probability one. An example that satisfies the Assumption 1 is shown below.

Example 1. Assume that

$$f_i(\eta) = \eta^{c_1}(\bar{\eta} - \eta^{c_2}), \;\; g_i(\eta) = \sigma_\eta \eta, \;\; i = 1, 2, \tag{5}$$

where $c_1, c_2 \geq 0$ are constants and satisfies $c_1 + c_2 \geq 1, c_2 > 0$. For any given initial value $x(0) \in \mathbb{R}_+$, System (4) admits a unique global positive solution on $t \geq 0$ with probability one.

The proof of Example 1 is attached in Appendix. The system (4) with feature (5) admits the following properties: (i) The long-term average of the attach rate and the handling time, that is, $\bar{\alpha}$ and $\bar{\beta}$ are finite, this is biological reasonable because the size of the generalized predators is a constant; (ii) The intensity of stochasticity $g_1(\alpha)$ (resp. $g_2(\beta)$) is positively correlated with the size of attack rate (resp. handling time).

Two typical examples of (5) can be shown as

$$d\eta = (\bar{\eta} - \eta)dt + \sigma_\eta \eta dB_\eta(t), \tag{6}$$

$$d\eta = \eta(\bar{\eta} - \eta)dt + \sigma_\eta \eta dB_\eta(t), \tag{7}$$

where $\eta(t) = \alpha(t)$ or $\eta(t) = \beta(t)$. In the following sections, we study how stochasticity affects the dynamics of population $x(t)$ both theoretically and numerically.

3. Theoretical results

In this section, we study how stochasticity affects the long-term dynamics of population $x(t)$ from the perspective of theoretical analysis. We first investigate the scenario where demographic and environmental stochasticity work together. Then we separately study scenarios where demographic stochasticity of the scaled attack rate $\alpha(t)$ and the scald handling time $\beta(t)$ play a leading role. In addition, we explore the impact of environmental stochasticity on population dynamics of $x(t)$ when demographic stochasticity does not work.

3.1. Joint effects of demographic and environmental stochasticity

In the following, we study the joint effects of demographic and environmental stochasticity on the dynamics of population $x(t)$. We first study the stochastic persistence and extinction of population $x(t)$. Then, by using the Khasminskii theorem [72], we provide sufficient conditions for the ergodicity as well as the existence of a unique positive periodic solution for System (4).

Theorem 1. *For any initial value $x(0) \in \mathbb{R}_+$, the population $x(t)$ in System (4) has the following stochastic dynamics*

*1. **The unbounded case:** Suppose the stochastic processes $\alpha(t)$ and $\beta(t)$ are given by SDEs (3). If $\alpha(t)$ and $\beta(t)$ have a unique invariant measure π_α and π_β on $\mathbb{R}$, respectively, then the expected per-capita growth rate of population $x(t)$ can be defined as*

$$\lambda_1 = 1 - \frac{1}{2}\sigma_x^2 - \int_{\mathbb{R}} \alpha(s)\pi_\alpha(ds).$$

Moreover, when $\lambda_1 > 0$, the population $x(t)$ will be stochastically persistent in probability; when $\lambda_1 < 0$, the population $x(t)$ will go extinct exponentially fast.

*2. **The bounded case:** Suppose that the stochastic process $\alpha(t)$ is bounded below by $\hat{\alpha} > 0$ and the stochastic process $\beta(t)$ is bounded above by $\check{\beta}$, then the population $x(t)$ will be strongly persistent in the mean if*

$$1 - \frac{1}{2}\sigma_x^2 - \liminf_{t \to \infty} \frac{1}{t} \int_0^t \alpha(s)ds > 0 \; almost \; surely \; (a.s.),$$

and the population $x(t)$ will become extinct exponentially fast if either

$$1 - \frac{1}{2}\sigma_x^2 - \hat{\alpha} < 0, \;\; \hat{\alpha}\sqrt{\check{\beta}} \leq 1$$

or

$$1 - \frac{1}{2}\sigma_x^2 - \frac{2\hat{\alpha}\sqrt{\check{\beta}} - 1}{\hat{\alpha}\check{\beta}} < 0, \;\; \hat{\alpha}\sqrt{\check{\beta}} > 1.$$

The proof of Theorem 1 is attached in Appendix. Theorem 1 suggests that: (i) In the unbounded case, the persistence and extinction of the population $x(t)$ is completely determined by the intensity of environmental stochasticity and the demographic stochasticity from the attack rate $\alpha(t)$. When the intensity of environmental stochasticity and the demographic stochasticity from the attack rate $\alpha(t)$ are small enough, the population $x(t)$ will be stochastically persistent in probability. Otherwise, the population $x(t)$ will become extinct. In this case, the demographic stochasticity from the handling time $\beta(t)$ does not affect the persistence of the population $x(t)$. (ii) In the bounded case, Theorem 1 provides sufficient conditions for the survival and extinction of the population $x(t)$. When the intensity of environmental stochasticity and the long-term average of the attack rate $\alpha(t)$ are small enough, the population $x(t)$ will be strongly persistent in the mean. In particular, when environmental and demographic stochasticity disappear, the condition ensures that the deterministic model (2) has a unique positive equilibrium x^K which is globally asymptotically stable, i.e., the population $x(t)$ is persistent. When the intensity of environmental stochasticity or the long-term average of the attack rate $\alpha(t)$ is large enough, the population $x(t)$ will become extinct.

Next, we study the ergodicity and the existence of positive periodic solution of System (4). As an effective stochastic analysis tool, the Khasminskii theorem [72] has been successfully applied to explore the existence of ergodic stationary distribution and positive periodic solution. In the scenario where the Khasminskii theorem works, the construction of the Lyapunov function and the application of inequalities are crucial and challenging. Since in System (4) the specific forms of $\alpha(t)$ and $\beta(t)$ are unknown, the Khasminskii theorem is difficult to use directly. Next, we start with some special cases of $\alpha(t)$ and $\beta(t)$, and provide sufficient conditions for the existence of a unique ergodic stationary distribution and positive periodic solution for System (4).

Theorem 2. *For any initial value $x(0) \in \mathbb{R}_+$, we have*

*1. **The unbounded case:** Suppose that the stochastic processes $\alpha(t)$ and $\beta(t)$ have the form of (7). If*

$$1 - \bar{\alpha} - \frac{1}{2}\sigma_x^2 > 0,$$

then System (4) admits a unique ergodic stationary distribution.

*2. **The bounded case:** Suppose that the stochastic processes $\alpha(t)$ and $\beta(t)$ are T−periodic in time t, and $\alpha(t)$ has an upper bound $\check{\alpha}$. If*

$$1 - \check{\alpha} - \frac{1}{2}\sigma_x^2 > 0,$$

then System (4) admits a nontrivial positive T−periodic solution.

The proof of Theorem 2 is attached in Appendix. Theorem 2 provides sufficient conditions for the existence of a unique ergodic stationary distribution (resp., positive periodic solution) when System (4) suffers from general (resp., periodic) demographic and environmental stochasticity. The result suggests that: (i) When the demographic and environmental stochasticity are small enough (i.e., $\bar{\alpha} + \frac{1}{2}\sigma_x^2 < 1$ or $\check{\alpha} + \frac{1}{2}\sigma_x^2 < 1$), System (4) has a unique ergodic stationary distribution (resp., positive periodic solution) which is independent of the initial level $x(0) > 0$. (ii) The demographic stochasticity from the handling time $\beta(t)$ will not affect the ergodicity (resp., the existence of a unique positive periodic solution) of System (4). (iii) The existence of a unique ergodic stationary distribution suggests that population $x(t)$ does not change its statistical properties (such as mean and variance) with time, and the population $x(t)$ has the same behavior averaged over time as averaged over the probability space. Although the expression of the unique stationary distribution is difficult to obtain, the ergodic property guarantees that we can estimate the probability distribution of the stationary distribution by simulating a single sample trajectory of the solution $x(t)$ to the stochastic system (4) (see, e.g., Mao [73], Ellner and Rees [74]).

In the absence of demographic and environmental stochasticity, i.e., $\alpha(t) = \bar{\alpha}, \beta(t) = \bar{\beta}$ and $\sigma_x = 0$, System (4) degenerates to the deterministic system (2). In this situation, the result of Theorem 2 suggests that as long as $\bar{\alpha} < 1$, the solution starting from any positive level will eventually reach a unique level, which is consistent with the global stability of the positive equilibrium x^K of the corresponding deterministic system (2).

3.2. Effects of demographic stochasticity from the scaled attack rate $\alpha(t)$

To study how demographic stochasticity from the scaled attack rate $\alpha(t)$ alone affects the population dynamics of $x(t)$. We assume that there is no environmental stochasticity in the population and the scaled handling time is a constant, i.e., $\sigma_x = 0$ and $\beta(t) = \bar{\beta}$. In this scenario, we have the following theorem about the long-term dynamics of Model (4).

Theorem 3. *For any given initial level $x(0) \in \mathbb{R}_+$, the population $x(t)$ in System (4) has the following dynamics*

*1. **The unbounded case:** Suppose the stochastic process $\alpha(t)$ is given by the stochastic differential equation (3). If*

$$1 - \liminf_{t\to\infty} \frac{1}{t}\int_0^t \alpha(s)ds > 0 \ a.s.,$$

then population $x(t)$ will be strongly persistent in the mean. If $\alpha(t)$ is ergodic with measure π and satisfies

$$1 - \int_{\mathbb{R}_+} \frac{s}{\bar{\beta}s + 1}\pi(ds) < 0,$$

then population $x(t)$ will become extinct exponentially fast.

*2. **The bounded case.** (i) If $\alpha(t)$ is bounded above by a positive constant $\check{\alpha} < 1$, then population $x(t)$ will be uniformly persistent; (ii) If $\alpha(t)$ is bounded below by $\hat{\alpha}$ and satisfies $\frac{\hat{\alpha}}{\hat{\alpha}\bar{\beta}+1} > 1$, then population $x(t)$ will become extinct exponentially fast; (iii) If $\alpha(t)$ is a periodic stochastic process with period T and satisfies*

$$1 - \frac{1}{T}\int_t^{t+T} \alpha(s)ds > 0,$$

then population $x(t)$ will be bounded below and above by positive constants $x_{\max}$ and $x_{\min}$, respectively, i.e., $x_{\max} \geq x(t) \geq x_{\min} > 0$.

The proof of Theorem 3 is attached in Appendix. Theorem 3 provides sufficient conditions for the persistence and extinction of population $x(t)$ when System (4) suffers from bounded and unbounded demographic stochasticity from attack rate $\alpha(t)$ respectively. Some of the results indicate that: (i) When the (average) relative attack rate is small enough, e.g., $\check{\alpha} < 1$ (resp. $\liminf_{t\to\infty} \frac{1}{t}\int_0^t \alpha(s)ds < 1 \ a.s.$), the population $x(t)$ will be survive. (ii) When the (average) relative attack rate is large enough, e.g., $\frac{\hat{\alpha}}{\hat{\alpha}\bar{\beta}+1} > 1$ (resp. $\int_{\mathbb{R}_+} \frac{s}{\bar{\beta}s+1}\pi(ds) > 1$), then population $x(t)$ will become extinct. The description of demographic stochasticity can be extended to a variety of scenarios related to population dynamics. For instance, when $\alpha(t)$ is a bounded stochastic process, it covers many types of life-depending coefficients in existing literature such as periodic coefficients [75,76], interval coefficients [77,78], semivarying coefficients [79], and Markov switching coefficients [80,81]. The unbounded stochastic processes can be applied to describe relevant parameters of population communities such as the unbounded growth constraints [82–85].

3.3. Effects of demographic stochasticity from the scaled handling time $\beta(t)$

In this subsection, we study how demographic stochasticity from the scaled handling time $\beta(t)$ affects the dynamics of population $x(t)$. To proceed, we set $\sigma_x = 0$ and $\alpha(t) = \bar{\alpha}$.

Theorem 4. *For any given initial level $x(0) \in \mathbb{R}_+$, we have*

1. If $\bar{\alpha} < 1$, then population $x(t)$ of System (4) will be uniformly persistent regardless of the form of $\beta(t)$, i.e., $0 < 1 - \bar{\alpha} \leq \liminf_{t\to\infty} x(t) \leq \limsup_{t\to\infty} x(t) \leq 1$.

2. If $\beta(t)$ is ergodic with measure π and satisfies $\int_{\mathbb{R}_+} \frac{\bar{\alpha}}{\bar{\alpha}s+1}\pi(ds) > 1$, then population $x(t)$ will become extinct exponentially fast. Particularly, if $\beta(t)$ is bounded above by constant $\check{\beta}$ and satisfies $\frac{\bar{\alpha}}{\bar{\alpha}\check{\beta}+1} > 1$, then population $x(t)$ will become extinct exponentially fast.

The proof of Theorem 4 is very similar to the proof of Theorem 3, so it is omitted here. Theorem 4 suggests that although the handling time suffers from demographic noise, as long as the attack rate is small enough (i.e., $\bar{\alpha} < 1$), the population $x(t)$ will be persistent. In this situation, the demographic stochasticity of the handling time will not affect the survival of the population. Moreover, when the attack rate is large enough, a sufficiently large demographic stochasticity from handling time is a sufficient condition to cause the population $x(t)$ to become extinct.

Comparison. *Both Theorems 3 and 4 show that if the attack rate is small enough, then the population will be persistent; while if the attack rate is large enough or the handling time is small enough, then the population will become extinct exponentially fast. One difference is that when the population subject to demographic stochasticity from the handling time, as long as the attack rate is small enough, the population will be persistent. At this time, demographic stochasticity from the handling time does not play a role in the persistence of the population.*

3.4. Effects of environmental stochasticity

We next explore how environmental stochasticity affects the dynamics of population $x(t)$ by studying the stochastic dynamics (e.g., stochastic ultimate boundedness, stochastic persistence and extinction, and the existence of a unique ergodic stationary distribution) of System (4). To continue, we choose $\alpha(t) = \bar{\alpha}$ and $\beta(t) = \bar{\beta}$. Now we have the following results.

Lemma 1. *For any given initial value $x(0) \in \mathbb{R}_+$, the solution of System (4) satisfies the following property*

$$\limsup_{t\to\infty} \mathbb{E}[x^p(t)] \le \left[1 + \frac{p|p-1|\sigma_x^2}{2(p+1)} - \phi\right]^{p+1}, \ \forall\ p > 0, \tag{8}$$

where $\phi = \phi(\bar{\alpha})$ is a non-negative constant, and $\phi = 0$ if and only if $\bar{\alpha} = 0$.

The proof Lemma 1 is attached in Appendix. The following theorem is straightforward by using the Chebyshev's inequality [86] to (8).

Theorem 5. *For any given initial value $x(0) \in \mathbb{R}_+$, the solution of System (4) is stochastically ultimately bounded, i.e., for any $\varepsilon \in (0,1)$, there exists a positive constant $\delta = \delta(\varepsilon)$ such that*

$$\limsup_{t\to\infty} \mathbb{P}\{x(t) > \delta\} < \varepsilon. \tag{9}$$

Stochastic ultimate boundedness is an important property of stochastic population systems, indicating that the solution will be ultimately bounded with large probability, i.e., the population system (4) is biologically well-defined. Theorem 5 shows that no matter how the environmental stochasticity changes, the stochastic ultimate boundednesss always holds for System (4), i.e., the boundedness is very robust under the environmental stochasticity.

The following theorem provides a critical threshold for the survival and extinction of population $x(t)$ in System (4).

Theorem 6. *Define the expected per-capita growth rate of population $x(t)$ as*

$$\lambda_2 = 1 - \frac{1}{2}\sigma_x^2 - \bar{\alpha} \ a.s.$$

For any given initial value $x(0) > 0$, the population $x(t)$ described by the system (4) will be stochastically persistent in probability if $\lambda_2 > 0$. Alternatively, the population $x(t)$ will become extinct exponentially fast if $\lambda_2 < 0$.

The proof of Theorem 6 is a direct application of Theorems 3.1 and 3.4 in Hening et al. [87] and is therefore omitted here. Theorem 6 provides necessary and sufficient conditions for the persistence and extinction of population $x(t)$ when environmental stochasticity plays a major role: (i) If the intensity of environmental stochasticity σ_x and the coefficient $\bar{\alpha}$ are small enough, then population $x(t)$ will be stochastically persistent in probability, i.e., the long-term level of population $x(t)$ is away from zero. (ii) If either the density of environmental stochasticity or the value of attack rate is large enough, the population $x(t)$ will die out exponential fast.

Theorem 7. *For any initial value $x(0) > 0$, System (4) admits a unique ergodic stationary distribution $\mu(\cdot)$ if $\lambda_2 > 0$.*

The proof of Theorem 7 is attached in Appendix. Theorem 7 indicates that when the environmental noise and the coefficient $\bar{\alpha}$ are small enough, System (4) has a unique ergodic stationary distribution which is independent of the initial level $x(0) > 0$. The main biological meaning of Theorem 7 is similar to that of Theorem 2, so we do not repeat it here.

4. Numerical results

We have theoretically explored how demographic and environmental stochasticity affect the long-term dynamics of population $x(t)$. However, there are some interesting biological issues about transient dynamics that remain unknown. For example: (i) *Is the effect of stochasticity on population dynamics related to the initial population level*? (ii) *When the population is definitively extinct, can stochasticity change the trend of extinction? Or can stochasticity affect the time of extinction*?

Next, we try to uncover the above interesting questions by studying how stochasticity affects the transient dynamics of population $x(t)$ in the three scenarios presented in Table 1: (A1) *the weak Allee effects case*; (A2) *the strong Allee effects case*; and (A3) *the extinction case*. In this section, all simulations are carried out using ©Matlab2019b software with Euler–Maruyama numerical method (Higham [88]) over 500 replicates. The "mean" mentioned below refers to the arithmetic mean of the solutions over 500 replicates. Moreover, $x(t)$ is considered to become extinct if the value of $x(t)$ is less than 10^{-5}.

4.1. Impact of demographic stochasticity from the scaled attack rate $\alpha(t)$

We first provide some numerical simulations on System (2) to explore how demographic stochasticity from attack rate $\alpha(t)$ affects the dynamics of population $x(t)$, i.e., the case $\sigma_x = 0, \beta(t) = \bar{\beta}$. To continue, we assume that the scaled attack rate $\alpha(t)$ has the form of (7). It is a special example of Theorem 3 for the unbounded case, which describes a type of demographic noise that has a long-term average level $\bar{\alpha}$, and the noise-intensity is proportional to the current rate of $\alpha(t)$. We first have the following estimates about the stochastic process $\alpha(t)$.

Lemma 2. *The stochastic process $\alpha(t)$ given by (7) is an ergodic process with measure π. For any given initial value $\alpha(0) \in \mathbb{R}_+$, we have*

$$\mathbb{E}[\alpha(t)] = \bar{\alpha} + (\alpha(0) - \bar{\alpha})e^{-t} \ \text{and} \ \lim_{t\to\infty} \mathbb{E}[\alpha(t)] = \bar{\alpha} \ a.s.$$

Moreover, we have

$$\limsup_{t\to\infty} \mathbb{E}[\alpha^2(t)] \le \begin{cases} \frac{\bar{\alpha}^2}{1-\sigma_\alpha^2} \ a.s., \ if \ \sigma_\alpha^2 < 1, \\ \frac{2\bar{\alpha}^2}{2-\sigma_\alpha^2} \ a.s., \ if \ \sigma_\alpha^2 \in [1,2). \end{cases}$$

The proof of Lemma 2 is attached in Appendix. Lemma 2 provides a good reference for how to choose effective density of stochasticity and other parameters.

In the following, we respectively study how demographic stochasticity from attack rate $\alpha(t)$ affects the dynamics of population $x(t)$ in the three scenarios given by Table 1. For the stochastic system (4), we specify the three scenarios according to the value of attack rate $\bar{\alpha}$ in the deterministic system. Now we have the following simulation results.

Case (A1). *In the weak Allee effects case (i.e., $\bar{\alpha} \in (0,1)$), demographic stochasticity from the attack rate σ_α may be beneficial to the population level $x(t)$.* Fig. 1 (red lines) shows that in the absence of demographic

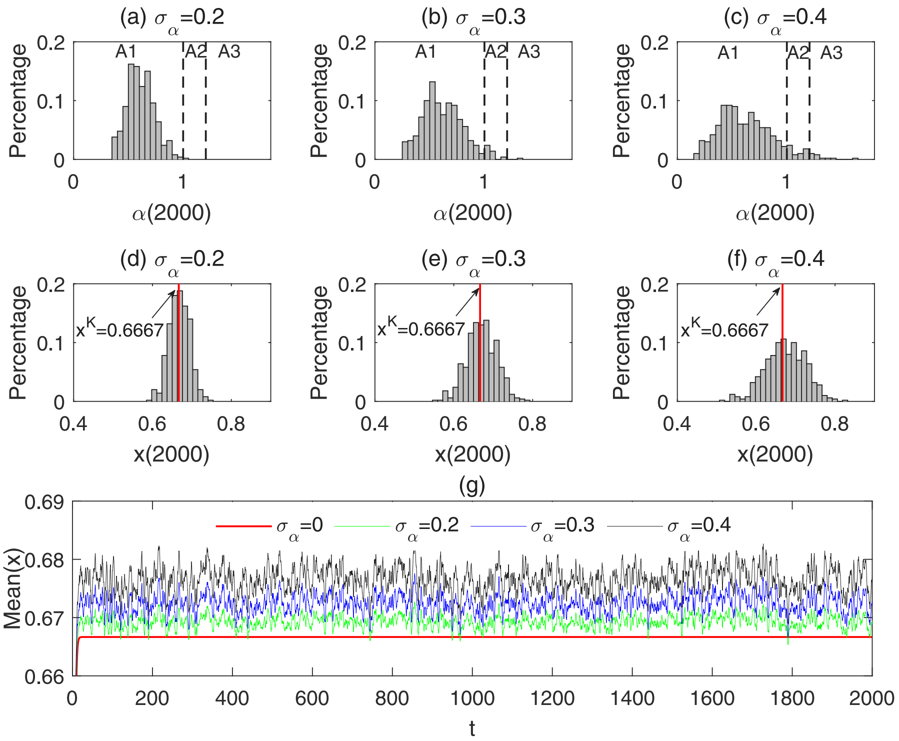

Fig. 1. Weak Allee case ($\bar{\alpha} = 0.6$). Histogram and empirical mean of the solution $x(t)$ to Model (4) with $\alpha(0) = 0.6$, $x(0) = 0.26$, $\sigma_x = 0$, $\beta(t) = \bar{\beta} = 2$ over 500 replicates. In area A1 (i.e., $\bar{\alpha} \in (0,1)$), the equilibrium x^K of Model (2) is globally asymptotically stable. In area A2 (i.e., $\bar{\alpha} \in (1,1.207)$), the equilibrium x^0 of Model (2) is globally asymptotically stable if $x(0) < x^\theta$, and the equilibrium x^K of Model (2) is globally asymptotically stable if $x(0) > x^\theta$. In area A3 (i.e., $\bar{\alpha} > 1.207$), the unique equilibrium x^0 of Model (2) is globally asymptotically stable. In Fig. 1g, the red line indicates that the survival equilibrium $x^K = 0.6667$ of Model (2) is globally asymptotically stable. The green, blue and black lines respectively are the empirical mean levels of the stochastic solution $x(t)$ over 500 replicates with $\sigma_\alpha = 0.2, 0.3$ and 0.4.

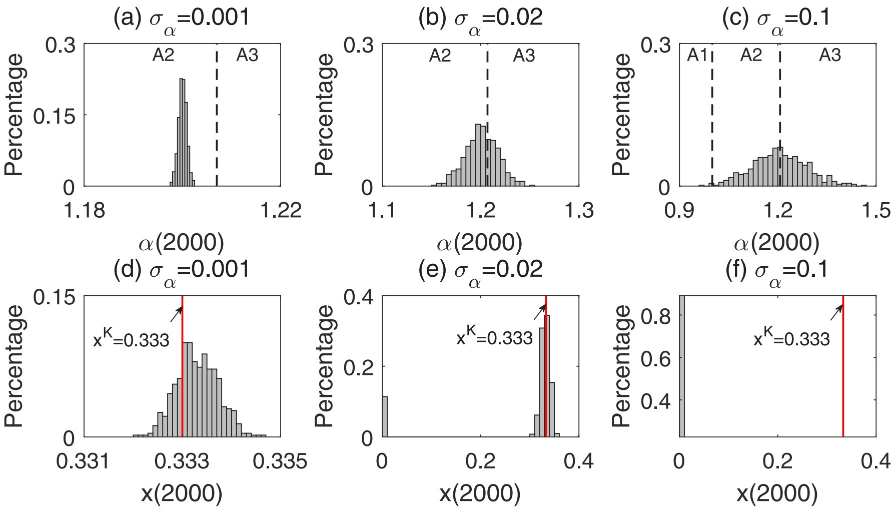

Fig. 2. Strong Allee case with $\bar{\alpha} = 1.2$. Histogram of the solution $x(t)$ to Model (4) at $t = 2000$ over 500 replicates with $\sigma_x = 0, \beta(t) = \bar{\beta} = 2, \alpha(0) = 1.2, x(0) = 0.26$. Red line indicates that the equilibrium $x^K = 0.333$ of Model (2) is globally asymptotically stable. In area A1 (i.e., $\bar{\alpha} \in (0,1)$), the equilibrium x^K of Model (2) is globally asymptotically stable. In area A2 (i.e., $\bar{\alpha} \in (1,1.207)$), the equilibrium x^0 of Model (2) is globally asymptotically stable if $x(0) < x^\theta$, and the equilibrium x^K of Model (2) is globally asymptotically stable if $x(0) > x^\theta$. In area A3 (i.e., $\bar{\alpha} > 1.207$), the unique equilibrium x^0 of the model (2) is globally asymptotically stable.

stochasticity (i.e., $\sigma_\alpha = 0$), the population $x(t)$ survives at level $x^K = 0.6667$, which is consistent with the theoretical result (see case (A1) in Table 1). To study how demographic stochasticity from attack rate $\alpha(t)$ affects the population $x(t)$, we choose $\sigma_\alpha = 0.2, 0.3$ and 0.4 respectively. The numerical simulation shows that demographic stochasticity from the attack rate can cause the mean population level $x(t)$ (over 500 replicates) to fluctuate above x^K, and the mean population level $x(t)$ is positively correlated with the intensity of demographic stochasticity σ_α (see Fig. 1g). Besides, when the time is long enough (e.g., $t = 2000$), the variance of population level $x(t)$ over 500 replicates is positively related with the intensity of demographic stochasticity σ_α (see Fig. 2d–f). From the perspective of mean level, the result suggests that demographic stochasticity from the scaled attack rate $\alpha(t)$ is beneficial to the population level $x(t)$.

Case (A2). *In the strong Allee effects case, how demographic stochasticity from the scaled attack rate $\alpha(t)$ affects population dynamics is related to the initial population level $x(0)$. If the initial population level is large enough (i.e., $x(0) > x^\theta$), demographic stochasticity from the scaled attack rate $\alpha(t)$ may be detrimental to the survival of population $x(t)$, otherwise if the initial*

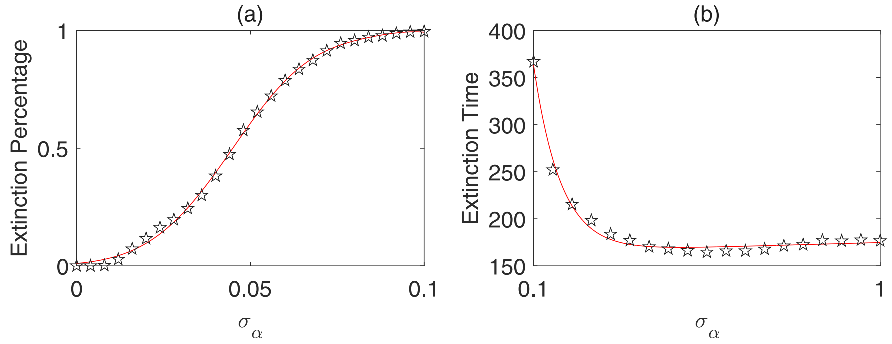

Fig. 3. Mean extinction percentage and mean extinction time of solution $x(t)$ to Model (4) over 500 replicates. The parameters are $\sigma_x = 0, \bar{\alpha} = 1.2, \beta(t) = \bar{\beta} = 2$, $\alpha(0) = 1.2$, $x(0) = 0.26$. The black pentagons and red lines denote the numerical results and fitted curves (see (10) and (11)), respectively. In this study, the mean extinction percentage is computed at time $T = 2000$, and the solution (t) is considered being extinct if $x(t) < 10^{-5}$.

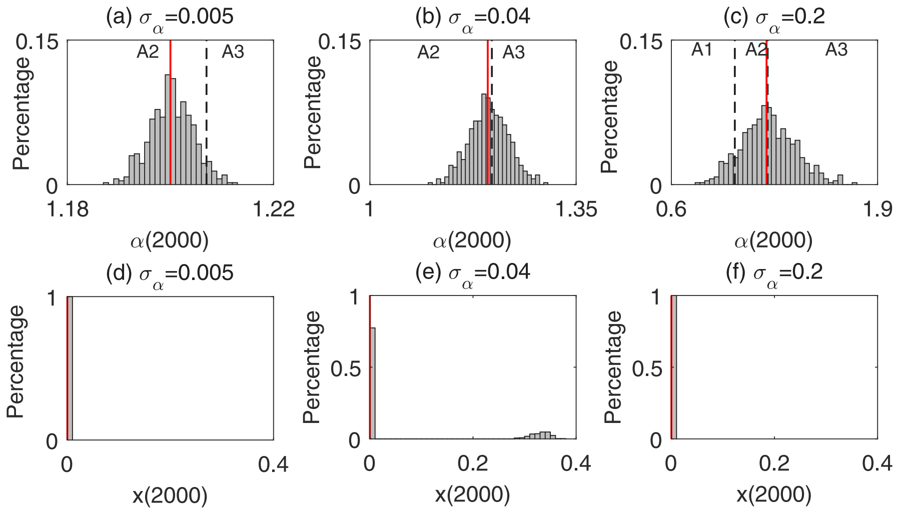

Fig. 4. Histogram of the stochastic solution $x(t)$ to Model (4) at $T = 2000$ over 500 replicates. The parameters are $\sigma_x = 0, \bar{\alpha} = 1.2, \beta(t) = \bar{\beta} = 2, \alpha(0) = 1.2, x(0) = 0.24$. Red line indicates that the equilibrium $x^0 = 0$ of Model (2) is globally asymptotically stable. In area A1 (i.e., $\bar{\alpha} \in (0, 1)$), the equilibrium x^K of Model (2) is globally asymptotically stable. In area A2 (i.e., $\bar{\alpha} \in (1, 1.207)$), the equilibrium x^0 of Model (2) is globally asymptotically stable if $x(0) < x^\theta$, and the equilibrium x^K of Model (2) is globally asymptotically stable if $x(0) > x^\theta$. In area A3 (i.e., $\bar{\alpha} > 1.207$), the unique equilibrium x^0 of Model (2) is globally asymptotically stable.

population level is small enough (i.e., $x(0) < x^\theta$), demographic stochasticity from the scaled attack rate $\alpha(t)$ may bring the possibility of survival for the deterministically extinct population $x(t)$. Choose $\bar{\alpha} = 1.2$ and $\bar{\beta} = 2$. It follows from Table 1 that the dynamics of population $x(t)$ in System (2) depends on the initial population level $x(0)$: if $x(0) < x^\theta = 0.25$, the extinction equilibrium $x^0 = 0$ is globally asymptotically stable, while if $x(0) > x^\theta$, the survival equilibrium $x^K = 0.333$ is globally asymptotically stable. In the following, we study how demographic stochasticity from $\alpha(t)$ affects the population dynamics of $x(t)$ in these two cases: $x(0) > x^\theta$ and $x(0) < x^\theta$.

We first study the case $x(0) > x^\theta$. Fig. 2 shows the histogram of the stochastic solution $x(t)$ over 500 replicates when time is large enough ($t = 2000$): (i) When low-intensity demographic stochasticity is involved, all 500 samples of the stochastic solution $x(t)$ stay within the small neighborhood of $x^K = 0.333$ (see Fig. 2a and d); (ii) As the noise intensity increases, a certain proportion of the samples still stay near $x^K = 0.333$, while the remaining part is attracted to the extinction state $x^0 = 0$ (see Fig. 2b and e). In this case, the mean extinction percentage (MEP) of the stochastic solution (over 500 replicates) attracted to $x^0 = 0$ is positively correlated with the intensity of σ_α (see Fig. 3), and the relationship can be approximated as

$$\mathrm{MEP}(\sigma_\alpha) = 0.9007e^{-\left(\frac{\sigma_\alpha - 0.1078}{0.03828}\right)^2} + 0.5996e^{-\left(\frac{\sigma_\alpha - 0.06204}{0.03064}\right)^2}, \tag{10}$$

where $\sigma_\alpha \in (0, 0.1)$. (iii) When the intensity of noise σ_α is large enough, all 500 samples of the stochastic solution $x(t)$ are attracted to the extinction state $x^0 = 0$ within a limited time (see Fig. 2c and f). In this case, the mean extinction time (MET) of the solution $x(t)$ attracted to $x^0 = 0$ is negatively related with the intensity of σ_α, and the relationship can be approximated as

$$\mathrm{MET}(\sigma_\alpha) = 1.466 \times 10^{16} e^{-\left(\frac{\sigma_\alpha + 4.446}{0.8045}\right)^2} + 216.9e^{-\left(\frac{\sigma_\alpha - 7.817}{14.67}\right)^2}, \tag{11}$$

where $\sigma_\alpha \in (0.1, 1)$.

Next, we study the case $x(0) < x^\theta$. Let $x(0) = 0.24$ and keep other parameters unchanged (compared to the case $x(0) > x^\theta$ above), it follows that $x^0 = 0$ of Model (2) is globally asymptotically stable (see reds line in Fig. 4). The simulation results in Figs. 4 and 5 indicate that: (i) When the intensity of demographic stochasticity is small or large enough, the 500 samples of the stochastic solution $x(t)$ are attracted to the extinction state (see Fig. 4d and f), and the relationship between the mean extinction time and the intensity of noise σ_α is non-monotonic: if the intensity of demographic stochasticity is small enough, the extinction time is positively correlated with the intensity of demographic stochasticity (see Fig. 5a), otherwise the extinction time is negatively correlated with the intensity of demographic stochasticity (see Fig. 5c). The relationship between the mean extinction time of stochastic solution $x(t)$ over 500 replicates and the intensity of demographic stochasticity σ_α can be expressed as

$$\mathrm{MET}(\sigma_\alpha) = \begin{cases} 70.08e^{-\left(\frac{\sigma_\alpha - 0.01654}{0.01228}\right)^2} + 89.8e^{-\left(\frac{\sigma_\alpha + 0.004321}{0.01763}\right)^2}, \\ 2.907 \times 10^{17} e^{-\left(\frac{\sigma_\alpha + 3.969}{0.6828}\right)^2} + 7307e^{-\left(\frac{\sigma_\alpha + 25.35}{12.98}\right)^2}, \end{cases} \tag{12}$$

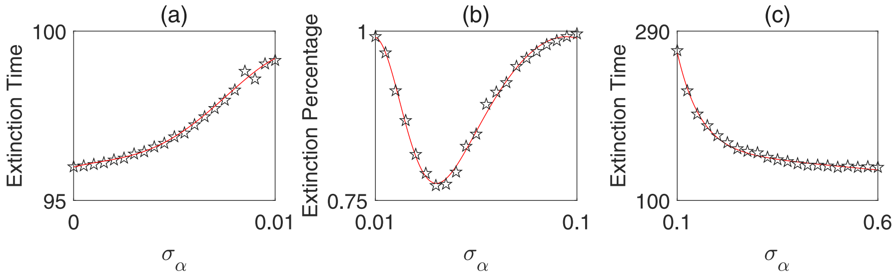

Fig. 5. Mean extinction time and mean extinction percentage of the solution $x(t)$ of Model (4) over 500 replicates. The parameters are $\sigma_x = 0, \bar{\alpha} = 1.2, \beta(t) = \bar{\beta} = 2$, $\alpha(0) = 1.2$, $x(0) = 0.24$. The black pentagons and red lines denote the numerical results and fitted curves (see (12) and (13)), respectively. In this case, the mean extinction percentage is counted at time $T = 2000$, and the solution is considered extinct if $x(t) < 10^{-5}$.

where $\sigma_\alpha \in (0, 0.01)$ and $\sigma_\alpha \in (0.1, 0.6)$, respectively. (ii) Demographic stochasticity with appropriate intensity may bring the possibility of survival for the population $x(t)$ that is determined to be extinct (see Fig. 4b, compared to Model (2) where the extinction boundary $x^0 = 0$ is globally asymptotically stable), and the relationship between the mean survival percentage of the stochastic solution $x(t)$ over 500 replicates and the intensity of demographic stochasticity σ_α can be approximated as

$$\mathrm{MEP}(\sigma_\alpha) = 0.9917 e^{-\left(\frac{\sigma_\alpha - 0.09527}{0.1024}\right)^2} + 0.513 e^{-\left(\frac{\sigma_\alpha - 0.00604}{0.02096}\right)^2}, \tag{13}$$

where $\sigma_\alpha \in (0.01, 0.1)$.

Case (A3). *In the extinction case, demographic stochasticity from the attack rate $\alpha(t)$ cannot change the extinction trend, but has delayed effects.* In this case, the unique equilibrium $x^0 = 0$ of Model (2) is globally asymptotically stable. The results show that: (i) The demographic stochasticity cannot change the population being extincted, but the variance of extinction time of the stochastic solution $x(t)$ under 500 samples increases as the intensity of demographic stochasticity σ_α increases (Fig. 6a–f); (ii) The mean extinction time of the stochastic solution $x(t)$ under 500 samples is positively correlated with the intensity of demographic stochasticity (Fig. 6g):

$$\mathrm{MET}(\sigma_\alpha) = 10.91 e^{-\left(\frac{\sigma_\alpha - 0.5399}{0.09443}\right)^2} + 95.56 e^{-\left(\frac{\sigma_\alpha - 0.4101}{0.5317}\right)^2}, \tag{14}$$

where $\sigma_\alpha \in (0, 0.5)$.

4.2. Impact of demographic stochasticity from the scaled handling time $\beta(t)$

Next, we explore how demographic stochasticity from the scaled attacking rate $\beta(t)$ affects the population dynamics of $x(t)$ by performing numerical operations on System (4) with $\sigma_x = 0, \alpha(t) = \bar{\alpha}$. Similar to Section 4.1, we assume that the handling time $\beta(t)$ is given by (7). We have the following insights.

Case (A1). *In the weak Allee effects case, an increase in the intensity of demographic stochasticity σ_β may cause a decrease in the mean level of population $x(t)$.* Fig. 7 shows that when there is no stochasticity (i.e., the deterministic case), the population level of $x(t)$ will converge to $x^K = 0.553$ (see Fig. 7g, red line). When the demographic stochasticity from the scaled handling time exists, the mean level of the population $x(t)$ under 500 replicates decreases, and the magnitude of the decrease is positively correlated with the intensity σ_β (see Fig. 7g). This result suggests that the demographic stochasticity from the scaled handling time is not conducive to the survival of the population $x(t)$. In addition, the variance (at time $t = 2000$) of the stochastic solution $x(t)$ under 500 replicates increases as the intensity of demographic stochasticity σ_β increases.

Case (A2). *In the strong Allee effects case, the influence of demographic stochasticity from the handling time $\beta(t)$ on the dynamics of population $x(t)$ is related to the initial population level. If the initial population level is large enough (i.e., $x(0) > x^\theta$), demographic stochasticity from $\beta(t)$ may be detrimental to the survival of population $x(t)$ (see Fig. 8). If the initial population level is small enough (i.e., $x(0) < x^\theta$), demographic stochasticity from $\beta(t)$ may bring the possibility of survival for the deterministically extinct population $x(t)$ (see Fig. 10).* In this scenario, the demographic stochasticity from $\beta(t)$ has a similar impact on the population $x(t)$ as that from $\alpha(t)$, so we do not elaborate here. The relationship between intensity of demographic stochasticity σ_β and mean extinction time ($\mathrm{MET}(\sigma_\beta)$) as well as mean extinction percentage ($\mathrm{MEP}(\sigma_\beta)$) is shown in Table 2.

Case (A3). *In the extinction case, demographic stochasticity from $\beta(t)$ cannot change the population being extinct, but can affect the time of population extinction.* In this case, the unique equilibrium $x^0 = 0$ of Model (2) is globally asymptotically stable. The numerical results show that (i) When the intensity of demographic stochasticity σ_β increases, the variance of extinction time of the stochastic solution $x(t)$ over 500 replicates increases (Fig. 12a–f). (ii) When the intensity of demographic stochasticity σ_β is small enough, the increase in σ_β can lead to a proportional increase in the mean extinction time (under 500 replicates). (iii) When the intensity of demographic stochasticity σ_β is large enough, the mean extinction time decreases as σ_β increases (see Fig. 12g). The relationship between the mean extinction time of population $x(t)$ over 500 replicates and the intensity of demographic stochasticity σ_β can be approximated as

$$\mathrm{MET}(\sigma_\alpha) = 183.1 e^{-\left(\frac{\sigma_\beta - 0.1198}{0.03398}\right)^2} + 126.4 e^{-\left(\frac{\sigma_\beta - 0.07592}{1.166}\right)^2}, \tag{15}$$

where $\sigma_\beta \in (0, 1)$.

4.3. Impact of environmental stochasticity

Next, we implement simulations on System (4) with $\alpha(t) = \bar{\alpha}, \beta(t) = \bar{\beta}$ to study how environmental stochasticity affects the dynamics of population $x(t)$ for the three scenarios as before. We have the following numerical results.

Case (A1). *In the weak Allee effects case, environmental stochasticity may be detrimental to the survival of the population $x(t)$: the population level $x(t)$ (on average) is negatively correlated with the intensity of stochasticity, and the population $x(t)$ may become extinct when the noise intensity is large enough.* In this scenario, the relationship between environmental stochasticity and the population level $x(t)$ is depicted in Fig. 13: (i) In the absence of environmental stochasticity, the population $x(t)$ of the deterministic model (2) will survive at level $x^K = 0.6667$ (see red lines, Fig. 13). (ii) When the environmental stochasticity with small intensity intervenes, the population level $x(t)$ will fluctuate around the level x^K (gray lines, Fig. 13a), and the mean population level $x(t)$ over 500 replicates is lower than the level in the deterministic model (2) (black line, Fig. 13a). (iii) When the intensity of environmental noise is large enough, the mean population level $x(t)$ and all the 500 samples will converge to $x^0 = 0$ within limited time (see Fig. 13b).

Case (A2). *In the strong Allee effects case, the relationship between environmental stochasticity and population level $x(t)$ depends on the initial population level. If the initial population level is large enough (i.e., $x(0) > x^\theta$), environmental stochasticity may be detrimental to the survival of*

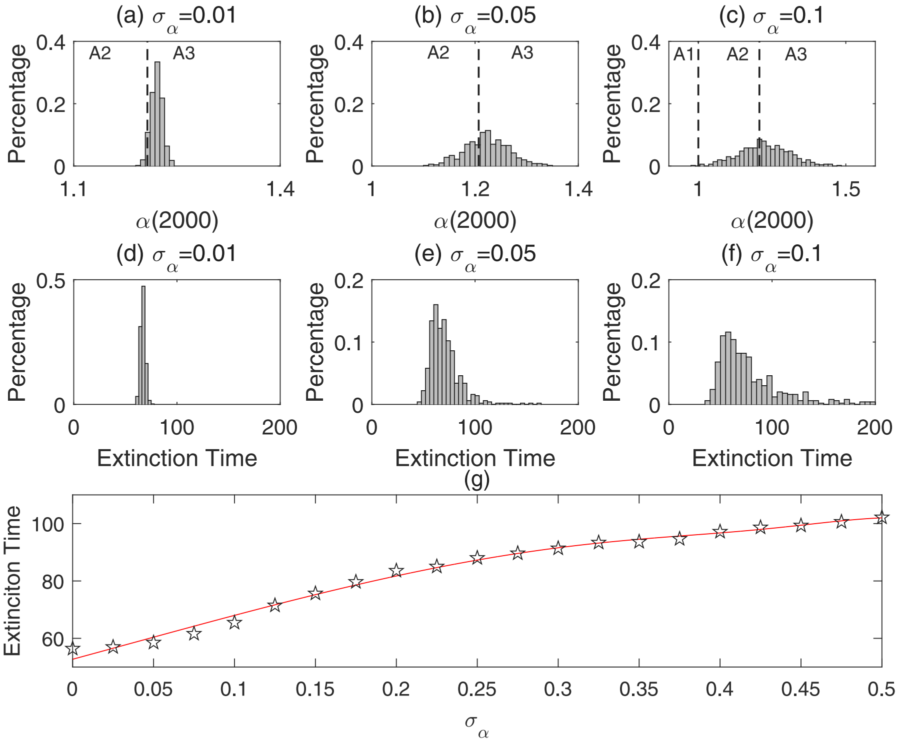

Fig. 6. Histogram of extinction time and mean extinction time of solution $x(t)$ to Model (4) over 500 replicates. The parameters are $\sigma_x = 0, \bar{\alpha} = 1.22, \beta(t) = \bar{\beta} = 2$, $\alpha(0) = 1.22$, $x(0) = 0.26$. In area A1 (i.e., $\bar{\alpha} \in (0, 1)$), the equilibrium x^K of Model (2) is globally asymptotically stable. In area A2 (i.e., $\bar{\alpha} \in (1, 1.207)$), the equilibrium x^0 of Model (2) is globally asymptotically stable if $x(0) < x^\theta$, and the equilibrium x^K of Model (2) is globally asymptotically stable if $x(0) > x^\theta$. In area A3 (i.e., $\bar{\alpha} > 1.207$), the unique equilibrium x^0 of Model (2) is globally asymptotically stable. The black pentagons and red line denote the numerical results and fitting curve (see (14)), respectively. In this case, the population is considered extinct if $x(t) < 10^{-5}$.

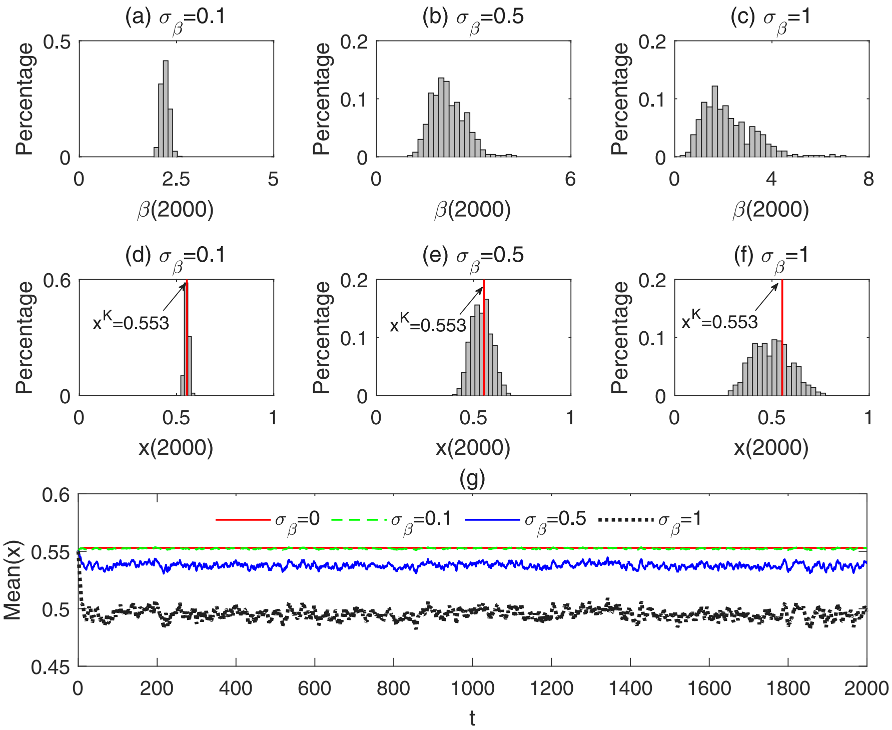

Fig. 7. Histogram and empirical mean of the solution $x(t)$ to Model (4) over 500 replicates. The parameters are $\beta(0) = 2.2$, $x(0) = 0.55$, $\sigma_x = 0$, $\alpha(t) = \bar{\alpha} = 0.98, \bar{\beta} = 2.2$. In Fig. 7g, the red line indicates that the survival equilibrium $x^K = 0.553$ of Model (2) is globally asymptotically stable. The green, blue and black lines respectively are the empirical mean levels of the stochastic solution $x(t)$ over 500 replicates with $\sigma_\alpha = 0.1, 0.5$ and 1.

population $x(t)$. If the initial population level is small enough (i.e., $x(0) < x^\theta$), environmental stochasticity may bring the possibility of survival for the deterministically extinct population $x(t)$. In this scenario, the dynamics of the deterministic system (2) depends on the initial population level:

Table 2
Relationship between the intensity of demographic stochasticity σ_β and the mean extinction percentage as well as the mean extinction time of the population $x(t)$ in System (4). The mean extinction percentage is counted at time $T = 2000$, and the population is considered extinct if $x(t) < 10^{-5}$.

Case	Mean extinction time & Mean extinction percentage	Interval	Figure
$x(0) > x^\theta$	MEP(σ_β)$= 0.403e^{-(\frac{\sigma_\beta-0.1687}{0.02345})^2} + 0.9661e^{-(\frac{\sigma_\beta-0.1239}{0.05688})^2}$	$\sigma_\beta \in (0, 0.16)$	Fig. 9a
	MET(σ_β)$= 1408e^{-14.1\sigma_\beta} + 156.4e^{-0.7124\sigma_\beta}$	$\sigma_\beta \in (0.16, 1)$	Fig. 9b
$x(0) < x^\theta$	MET(σ_β)$= 118.8e^{0.6737\sigma_\beta} + 0.1968e^{124.4\sigma_\beta}$	$\sigma_\beta \in (0, 0.022)$	Fig. 11a
	MEP(σ_β)$= \frac{1.036\sigma_\beta^2-0.1383\sigma_\beta+0.005329}{\sigma_\beta^2-0.1325\sigma_\beta+0.005242}$	$\sigma_\beta \in (0.022, 0.15)$	Fig. 11b
	MET(σ_β)$= 409.9e^{-10.4\sigma_\beta} + 129.9e^{-0.5296\sigma_\beta}$	$\sigma_\beta \in (0.15, 1)$	Fig. 11c

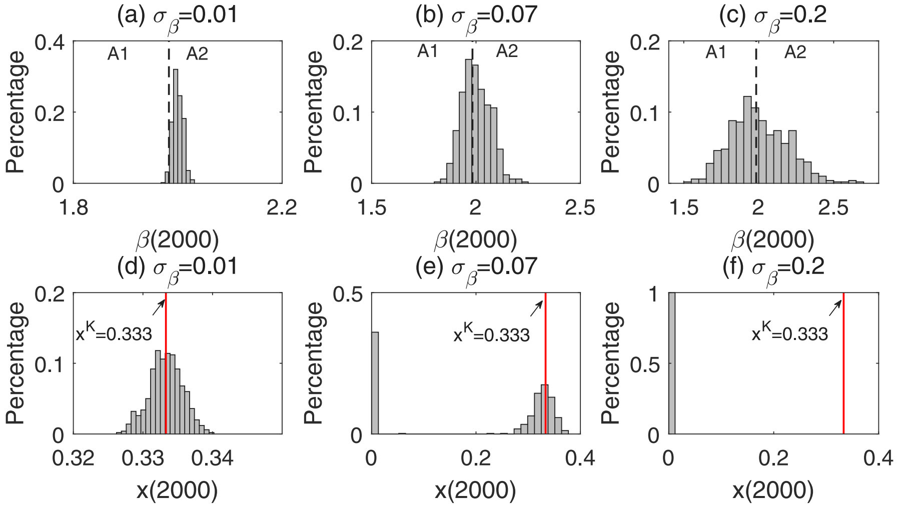

Fig. 8. Histogram of the solution $x(t)$ to Model (4) at $T = 2000$ over 500 replicates. The parameters are $\sigma_x = 0$, $\alpha(t) = \bar{\alpha} = 1.2, \bar{\beta} = 2, \beta(0) = 2, x(0) = 0.26$. In area A1 (i.e., $\bar{\beta} \in (1, 1.983)$), the equilibrium x^0 of Model (2) is globally asymptotically stable. In area A2 (i.e., $\bar{\alpha} \in (1.983, 4)$), x^K of Model (2) is globally asymptotically stable if $x(0) > x^\theta$, while if $x(0) < x^\theta$, x^0 is globally asymptotically stable. Red line indicates that the equilibrium $x^K = 0.333$ of Model (2) is globally asymptotically stable.

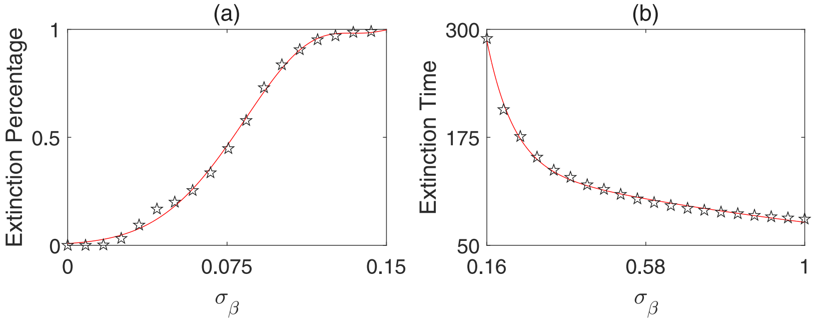

Fig. 9. Mean extinction percentage and mean extinction time of the solution $x(t)$ to Model (4) over 500 replicates. The parameters are $\sigma_x = 0$, $\alpha(t) = \bar{\alpha} = 1.2, \bar{\beta} = 2$, $\beta(0) = 2$, $x(0) = 0.26$. The black pentagons and red lines denote the numerical results and fitted curves (see Table 2), respectively. In this study, the mean extinction percentage is computed at time $T = 2000$, and the solution is considered extinct if $x(t) < 10^{-5}$.

if $x(0) > x^\theta = 0.25$, the positive equilibrium $x^K = 0.333$ is globally asymptotically stable and the population $x(t)$ will persistent (see Table 1 and red lines in Fig. 14), otherwise if $x(0) < x^\theta = 0.25$, the equilibrium $x^0 = 0$ is globally asymptotically stable and the population $x(t)$ will be extinct (see Table 1 and reds line in Fig. 16). We are interested in how environmental stochasticity affects population dynamics in these two cases.

We first study the case $x(0) > x^\theta$. Fig. 14 describes the dynamics of population $x(t)$ with different intensity of environmental noise: (i) When the noise intensity is small enough (e.g., $\sigma_x = 0.001$), all 500 samples of the stochastic solution $x(t)$ fluctuate around the level $x^K = 0.333$ (Fig. 14a); (ii) As the noise intensity increases, some samples still fluctuate around the level x^K, while the remaining part gradually moves away from the neighborhood of x^K and is eventually attracted to the extinction state $x^0 = 0$ (Fig. 14b). In this case, the result suggests that increasing the intensity of environmental noise will result in a higher percentage/probability of population extinction (Fig. 15a), and the relationship between the mean extinction percentage (MEP) and intensity of noise σ_x can be fitted as

$$\mathrm{MEP}(\sigma_x) = 0.9494e^{-\left(\frac{\sigma_x-0.04083}{0.01585}\right)^2} + 0.6537e^{-\left(\frac{\sigma_x-0.02226}{0.01102}\right)^2}, \tag{16}$$

where $\sigma_x \in (0, 0.04)$. (iii) When the noise intensity is large enough, all 500 samples of the stochastic solution $x(t)$ are attracted to $x^0 = 0$ (Fig. 14c). In this case, an increasing in the intensity of environmental noise will cause the population $x(t)$ to become extinct fast (Fig. 15b), and the relationship between the mean extinction time (MET) and the noise intensity σ_x can be approximated as

$$\mathrm{MET}(\sigma_x) = 1.586 \times 10^{17} e^{-\left(\frac{\sigma_x+2.473}{0.4265}\right)^2} + 1414e^{-\left(\frac{\sigma_x+3.03}{1.862}\right)^2}, \tag{17}$$

where $\sigma_x \in (0.04, 1)$.

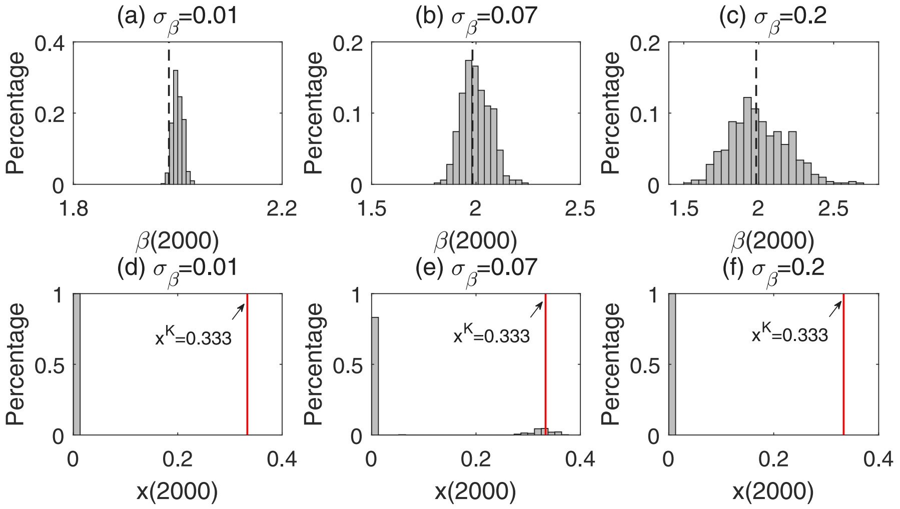

Fig. 10. Histogram of the solution $x(t)$ to Model (4) at $T = 2000$ over 500 replicates. The parameters are $\sigma_x = 0$, $\alpha(t) = \bar{\alpha} = 1.2, \bar{\beta} = 2, \beta(0) = 2, x(0) = 0.24$. In area A1 (i.e., $\bar{\beta} \in (1, 1.983)$), the equilibrium x^0 of Model (2) is globally asymptotically stable. In area A2 (i.e., $\bar{\alpha} \in (1.983, 4)$), x^K of Model (2) is globally asymptotically stable if $x(0) > x^\theta$, while if $x(0) < x^\theta$, x^0 is globally asymptotically stable. Red line indicates that the equilibrium $x^K = 0.333$ of Model (2) is globally asymptotically stable.

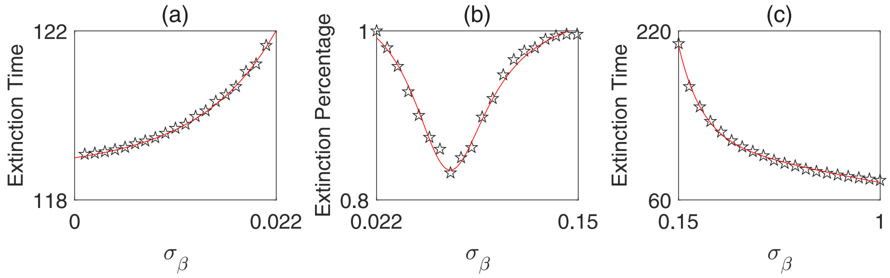

Fig. 11. Mean extinction percentage and mean extinction time of the solution $x(t)$ to Model (4) over 500 replicates. The parameters are $\sigma_x = 0$, $\alpha(t) = \bar{\alpha} = 1.2, \bar{\beta} = 2$, $\beta(0) = 2$, $x(0) = 0.24$. The black pentagons and red lines denote the numerical results and fitted curves (see Table 2), respectively. In this study, the mean extinction percentage is computed at time $T = 2000$, and the solution $x(t)$ is considered extinct if $x(t) < 10^{-5}$.

We next study the case $x(0) < x^\theta$. The numerical results show that: (i) When the intensity of environmental noise is small enough, all 500 samples of the stochastic solution $x(t)$ are attracted to the extinction equilibrium $x^0 = 0$ of the deterministic model (2) (Fig. 16a). (ii) As the intensity of noise increases, a certain percentage of the samples gradually move away from $x^0 = 0$ and are eventually attracted to the neighborhood of the survival equilibrium $x^K = 0.333$ (Fig. 16b). (iii) When the intensity of noise is large enough, some of the samples are attracted to the neighborhood of x^K within the initial period, but eventually converges to $x^0 = 0$ (Fig. 16c). Besides, in the scenarios where all samples of the stochastic solution $x(t)$ are all attracted to the extinction state $x^0 = 0$ (Fig. 16a and c), if the intensity of noise is small enough, the mean extinction time (MET) of the stochastic $x(t)$ over 500 replicates is positively correlated with the intensity of noise (Fig. 17a), otherwise if the noise intensity is large enough, the mean extinction time (MET) of the stochastic $x(t)$ over 500 replicates is negatively correlated with the intensity of noise (Fig. 17c). The relationship between the mean extinction time (MET) of the stochastic $x(t)$ over 500 replicates and the intensity of noise can be expressed as

$$\mathrm{MET}(\sigma_x) = \begin{cases} 118.9e^{0.7226\sigma_x} + 0.08592e^{737.3\sigma_x}, \\ 8.454 \times 10^{15} e^{-\left(\frac{\sigma_x + 1.058}{0.1918}\right)^2} + 229.9e^{-\left(\frac{\sigma_x + 0.2719}{0.4083}\right)^2}, \end{cases} \tag{18}$$

where $\sigma_x \in (0, 0.005)$ and $\sigma_x \in (0.03, 1)$, respectively. In the scenario where environmental stochasticty brings the possibility of survival to the deterministically extinct population $x(t)$ (Fig. 16b), the relationship between the mean extinction percentage (MEP) and the intensity of noise is non-monotonic (Fig. 17b) and can be expressed as

$$\mathrm{MEP}(\sigma_x) = 1.003e^{-\left(\frac{\sigma_x - 0.02887}{0.02906}\right)^2} + 0.5124e^{-\left(\frac{\sigma_x - 0.00273}{0.08072}\right)^2}, \tag{19}$$

where $\sigma_x \in (0.005, 0.03)$.

Case (A3). *In the extinction case, environmental stochasticity cannot change the extinction trend of population $x(t)$. However, larger environmental stochasticity may lead to smaller variance of extinction time (over 500 replicates) for the stochastic solution $x(t)$ (Fig. 18a–c) and may cause a proportionally lower mean extinction time for the stochastic solution $x(t)$ over 500 replicates (see Fig. 18d and fitted curve (20)). The relationship between the mean extinction time (MET) and the intensity of stochasticity σ_x can be fitted as*

$$\begin{aligned} \mathrm{MET}(\sigma_x) = {} & 1.314 \times 10^{11} e^{-\left(\frac{\sigma_x + 26.83}{5.85}\right)^2} + 7.603e^{-\left(\frac{\sigma_x - 0.118}{0.09938}\right)^2} \\ & - 46.49e^{-\left(\frac{\sigma_x + 0.6141}{1.402}\right)^2}, \end{aligned} \tag{20}$$

where $\sigma_x \in (0, 2.5)$.

We also studied the dynamics of population $x(t)$ when demographic and environmental stochasticity exist simultaneously through numerical simulations. However, apart from the phenomena observed in the previous Sections 4.1, 4.2 and 4.3, no new insights have been discovered. Therefore, we omit the corresponding numerical simulation here. Now we can summarize the findings of this section as follows.

Summary: The numerical results in this section address the questions that we proposed at the beginning of this section: (i) When the population undergoes strong Allee effects (i.e., bistable), how does stochasticity affect the dynamics of population $x(t)$? (ii) When the

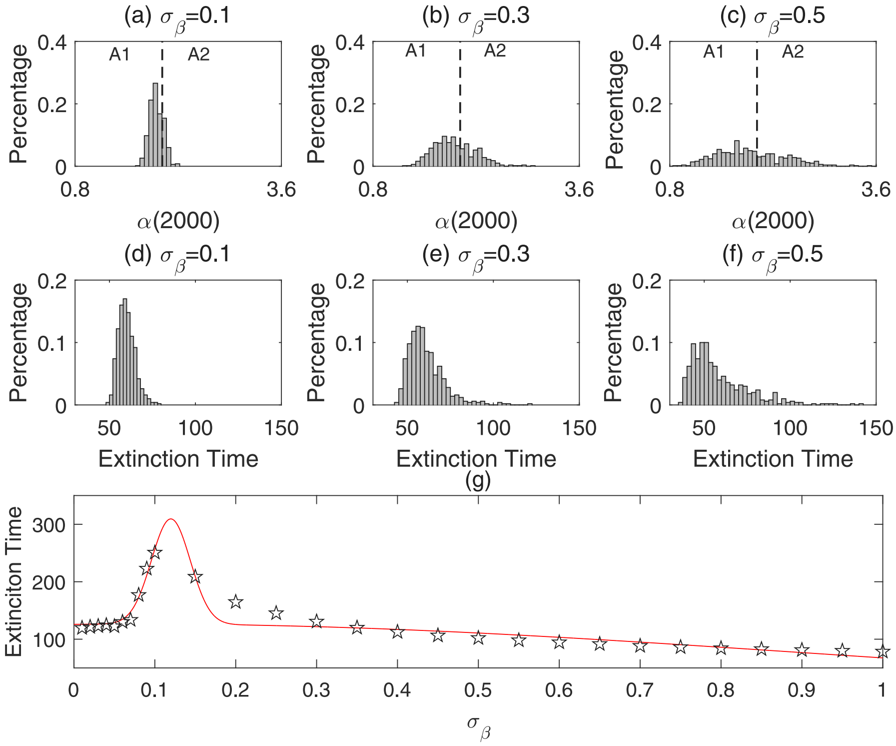

Fig. 12. Histogram of extinction time and mean extinction time of the solution $x(t)$ to Model (4) over 500 replicates. The parameters are $\sigma_x = 0$, $\alpha(t) = \bar{\alpha} = 1.2, \bar{\beta} = 1.9$, $\beta(0) = 1.9$, $x(0) = 0.26$. In area A1 (i.e., $\bar{\beta} \in (1, 1.983)$), the equilibrium x^0 of Model (2) is globally asymptotically stable. In area A2 (i.e., $\bar{\alpha} \in (1.983, 4)$), x^k of Model (2) is globally asymptotically stable if $x(0) > x^\theta$, while if $x(0) < x^\theta$, x^0 is globally asymptotically stable. In Fig. 12g, the black pentagons and red line denote the numerical results and fitted curve (see (15)), respectively. In this case, the population is considered extinct if $x(t) < 10^{-5}$.

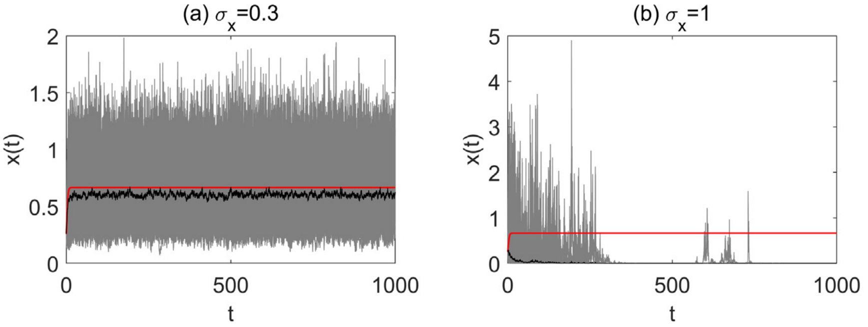

Fig. 13. Time series plot and arithmetic mean (over 500 replicates) of Model (4). The parameters are $\alpha(t) = \bar{\alpha} = 0.6, \beta(t) = \bar{\beta} = 2, x(0) = 1.2$. Gray lines denote the trajectories of the stochastic solution $x(t)$, red line indicates that the equilibrium $x^K = 0.6667$ of the deterministic model (2) is globally asymptotically stable, and black line denotes the arithmetic mean of the stochastic solution $x(t)$ over 500 replicates.

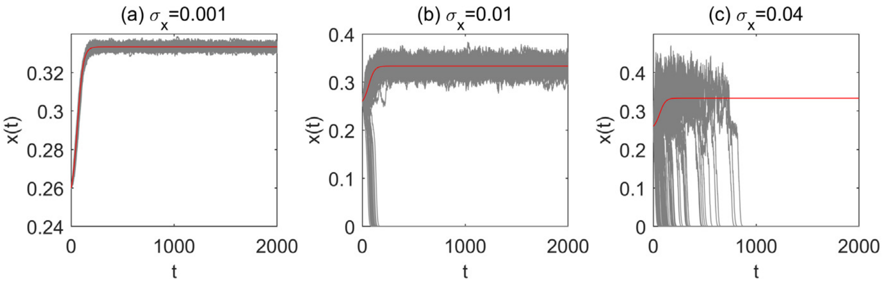

Fig. 14. Time series diagram of Model (4) over 500 replicates. The parameters are $\alpha(t) = \bar{\alpha} = 1.2, \beta(t) = \bar{\beta} = 2, x(0) = 0.26$. Red line indicates that the equilibrium $x^K = 0.333$ of the deterministic model (2) is globally asymptotically stable. Gray lines indicate the trajectories of stochastic solution $x(t)$ over 500 replicates.

population is deterministically extinct, can stochasticity change the trend of extinction? Or, can stochasticity affect the extinction time of population $x(t)$? (iii) When stochasticity leads to population extinction, what is the relationship between the intensity of stochasticity and the extinction probability or extinction time? Our findings have many profound biological significances such as

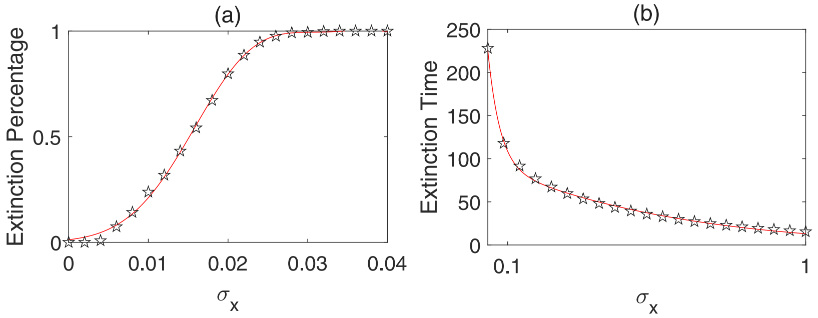

Fig. 15. Mean extinction percentage and mean extinction time of population $x(t)$ over 500 replicates. The parameters are $\alpha(t) = \bar{\alpha} = 1.2, \beta(t) = \bar{\beta} = 2, x(0) = 0.26$. The black pentagons and red lines denote the numerical results and fitted curves (see Eqs. (16) and (17)), respectively. In this case, the extinction percentage is computed at time $T = 2000$, and the solution $x(t)$ is considered extinct if $x(t) < 10^{-5}$.

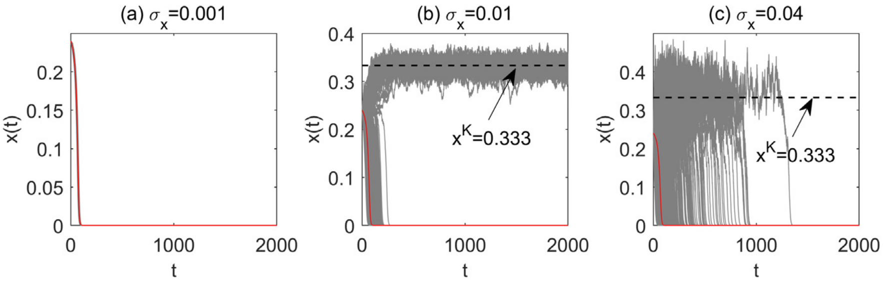

Fig. 16. Time series diagram of Model (4) over 500 replicates. The parameters are $\alpha(t) = \bar{\alpha} = 1.2, \beta(t) = \bar{\beta} = 2, x(0) = 0.24$. The red line indicates that the boundary equilibrium $x^0 = 0$ of the deterministic model (2) is globally asymptotically stable. The gray lines are the trajectories of the stochastic solution $x(t)$ over 500 replicates.

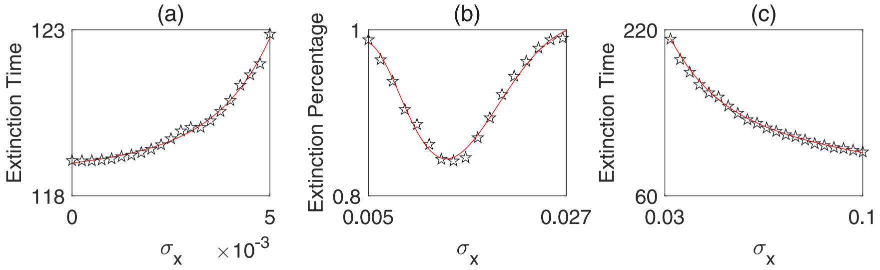

Fig. 17. Mean extinction time and mean extinction percentage of population $x(t)$ over 500 replicates. The parameters are $\alpha(t) = \bar{\alpha} = 1.2, \beta(t) = \bar{\beta} = 2,\ x(0) = 0.24$. The black pentagons and red lines denote the numerical results and fitted curves (see Eqs. (18) and (19)), respectively. In this case, the extinction percentage is computed at time $T = 2000$, and the solution is $x(t)$ considered extinct if $x(t) < 10^{-5}$.

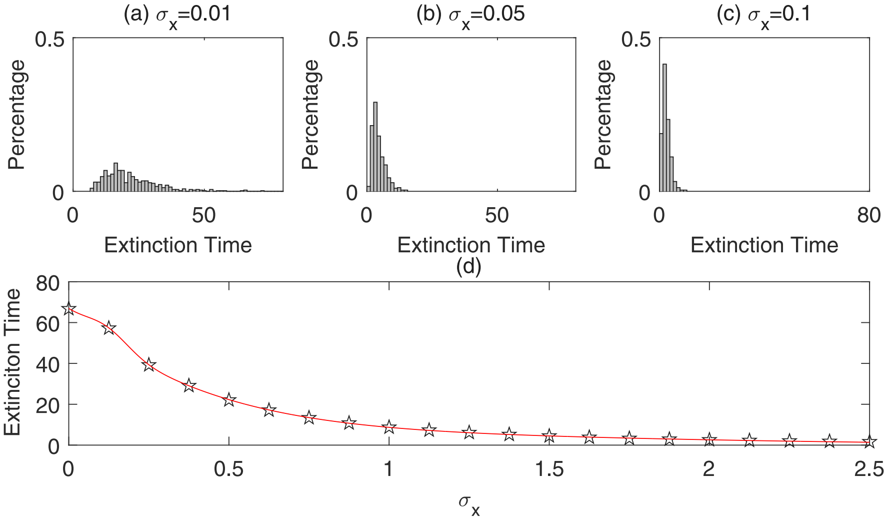

Fig. 18. Histogram of extinction time and mean extinction time of population $x(t)$ over 500 replicates. The parameters are $\alpha(t) = \bar{\alpha} = 1.22, \beta(t) = \bar{\beta} = 2,\ x(0) = 0.26$. The black pentagons and red line denote the numerical results and fitted curve (see Eq. (20)), respectively. In this case, the population is considered extinct if $x(t) < 10^{-5}$.

1. In the scenario of weak Allee effects, demographic stochasticity from attack rate $\alpha(t)$ may increase the population level $x(t)$ (in the mean sense, Fig. 1), thus contribute to the survival of the population $x(t)$. However, demographic stochasticity from handling time $\beta(t)$ and environmental stochasticity may lead to the decrease of the population level, and even the extinction of the population $x(t)$ (Figs. 7 and 13).

2. In the scenario of strong Allee effects, demographic stochasticity (from $\alpha(t)$ and $\beta(t)$) and environmental stochasticity have similar effects on the population $x(t)$, depending on the initial population level. Specifically, if the initial population level is large enough (i.e., $x(0) > x^{\theta}$), demographic and environmental stochasticity may be detrimental to the survival of population $x(t)$ (Figs. 2, 8 and 14), otherwise if the initial population level is small enough (i.e., $x(0) < x^{\theta}$), demographic and environmental stochasticity may bring the possibility of survival for the deterministically extinct population $x(t)$ (Figs. 4, 10 and 16).

3. In the scenario of extinction, both demographic stochasticity (from $\alpha(t)$ and $\beta(t)$) and environmental stochasticity cannot change the trend of population extinction, but they may affect the extinction time: (i) demographic stochasticity from $\alpha(t)$ and environmental stochasticity may have promotion effects on the extinction of population $x(t)$ (see Figs. 6 and 18); (ii) demographic stochasticity from $\beta(t)$ may delay the extinction of population $x(t)$ if the intensity σ_{β} is small enough, otherwise demographic stochasticity from $\beta(t)$ may advance the extinction of population $x(t)$ (see Fig. 12).

5. Conclusion

Literature show that stochasticity in the population dynamics of most species should be responsible for random fluctuations rather than periodic or chaotic phenomena [4]. In our work, we presented a novel modeling framework based on stochastic differential equations to study how random fluctuations including demographic and environmental stochasticity affect the dynamics of population with cooperative components that are measured by component Allee effects. This work is adopted from the single-species model proposed by Kang and Udiani [69], and is a good extension of the stochastic model presented by Yu et al. [68] that study how environmental stochasticity affects single-species dynamics with Allee effects. Our framework can be applied to other dynamic systems such as competition models [89,90], cooperation models [62,91], infectious disease models [92,93], and social insect models [94–96], to list a few.

We incorporated stochasticity into the single-population model constructed by Kang and Udiani [69] with two aspects. First, the life-depending coefficients (i.e., attack rate and handling time) of the population may suffer from random fluctuations. Without loss of generality, the coefficients can be described by stochastic processes defined on the probability space. When the coefficients suffer from bounded fluctuations (such as cyclic fluctuations driven by the seasonal factors [97]), we can use bounded stochastic processes to describe the coefficients. More generally, we can define the stochastic process as the solution to a stochastic differential equation. Second, the population may affected by environmental stochasticity. By standard arguments (see, e.g., [30,32,70]), the population level can be considered as a Markov process.

We studied the stochastic dynamics of the single-species model theoretically and numerically. These analyses addressed the question of how demographic and environmental stochasticity affect population dynamics separately and jointly. Our theoretical results provide sufficient conditions for what kind of stochastic dynamics the population may emerge, including stochastic persistent, extinction, strong persistent in the mean, stochastic ultimate bounded, the existence of a unique ergodic stationary distribution as well as periodic solution. Some of the results suggest that the population may become extinct if the demographic or environmental stochasticity is large enough (see, for example Theorem 1). On the contrary, if the demographic and environmental stochasticity are sufficiently small, the system may have a unique ergodic stationary distribution, indicting that the population will be persistent (see, for example Theorem 2). The ergodicity suggests that the population does not change its statistical properties (such as mean and variance) with time, and the population has the same behavior averaged over time as averaged over the probability space. Therefore, by the ergodicity we can estimate the probability distribution of the stationary distribution by simulating a single sample trajectory of the stochastic solution (see, e.g., Mao [73], Ellner and Rees [74]). In particular, the stochastic system may also produce positive periodic solutions when the population suffers from periodic demographic stochasticity (see, for example Theorem 2).

The influence of stochasticity on population dynamics may be diverse. For instance, in the scenario of weak Allee effects (see Table 1), larger demographic stochasticity from the attack rate may lead to larger mean population level (Fig. 1), while larger demographic stochasticity from the handling time or larger environmental stochasticity may lead to the decrease or even extinction of the population level (see Figs. 7 and 13). This result suggests that demographic stochasticity from the attack rate may have positive feedback on the survival of the population, while the demographic stochasticity from handling rate and the environmental stochasticity has the opposite effect. How stochasticity affects population dynamics may also be related to the initial population level. For instance, in the scenario of strong Allee effects, if the initial population level is large enough, larger intensity of demographic and environmental stochasticity may lead to the extinction of the population (see for example Figs. 2, 8 and 14), otherwise if the initial population level is small enough, demographic and environmental stochasticity may bring the possibility of survival for the population that deterministically would extinct indefinitely (see, for example Figs. 4, 10 and 16). Stochasticity may also affect the time of population extinction. In the extinction case, demographic stochasticity from the attack rate can delay the population being extinct (see Fig. 6), while environmental stochasticity can advance the population being extinct (see Fig. 18). The relationship between the demographic stochasticity from handling time and the extinction time of population is non-monotonic: if the intensity of demographic stochasticity is small enough, the demographic stochasticity from handling time can delay the population being extinct (see Fig. 12), otherwise the demographic stochasticity from handling time can advance the population being extinct (see Fig. 12).

To go further, empirical data should be employed to validate the theoretical results from a biological perspective. Besides, numerical simulations showed that the stochastic system may admit a unique attractor, additional theoretical analysis techniques need to be developed to study the existence of quasi-stationary distribution. How demographic and environmental stochasticity and spatial factors together affect population dynamics is also a point of future exploration.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

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Appendix

Proof of Example 1. Since the coefficients of System (4) satisfy the local Lipschitz condition (Theorem 3.4, [86]), there is a unique local positive solution $x(t)$ on $t \in [0, \tau_e)$, where τ_e is the explosion time. If $\tau_e = \infty$, then System (4) has a unique global positive solution. To continue the proof, we define n_0 as a sufficiently large positive number that $x(0) \in [n_0^{-1}, n_0]$. For any integer n greater than n_0, we define following stopping time as $\tau_n = \inf\{t \in [0, \tau_e) : \min\{x(t), \alpha(t), \beta(t)\} \leq n^{-1}$ or $\max\{x(t), \alpha(t), \beta(t)\} \geq n\}$. Set $\inf \emptyset = \infty$. It is easy to reach that $\tau_n \uparrow$ as $n \to \infty$. Since $\tau_\infty := \lim_{n\to\infty} \tau_n \leq \tau_e$, System (4) has a unique global positive solution if $\tau_\infty = \infty$. If this is not the case, i.e., $\tau_\infty < \infty$, there must be constants N and $\varepsilon \in (0,1)$ such that $\mathbb{P}\{\tau_\infty \leq N\} > \varepsilon$. As a result, there exists an integer $n_1 \geq n_0$ such that

$$\mathbb{P}\{\tau_n \leq N\} > \varepsilon, \quad \forall n \geq n_1. \tag{21}$$

To continue, we define the Lypaunov function V as

$$V = \int_1^x \frac{s-1}{s} ds + 2\int_1^\alpha \frac{s-1}{s} ds + \beta.$$

Applying Itô's formula [86] (Theorem 6.4, pp. 36) to V yields

$$\begin{aligned} dV =& \mathbf{L}V dt + (1-x)\sigma_x dB_x(t) + 2(1-\alpha)\sigma_\alpha dB_\alpha(t) \\ &+ \sigma_\beta \beta dB_\beta(t), \end{aligned} \tag{22}$$

where

$$\begin{aligned} \mathbf{L}V =& (x-1)\left(1 - x - \frac{\alpha}{\beta\alpha x + 1}\right) + \bar{\beta} - \beta + \frac{1}{2}\sigma_x^2 \\ &+ 2\left(1 - \frac{1}{\alpha}\right)\alpha^{c_1}(\bar{\alpha} - \alpha^{c_2}) + \sigma_\alpha^2 \\ \leq& -2\left(\alpha^{c_1+c_2} + \bar{\alpha}\alpha^{c_1-1} - \bar{\alpha}\alpha^{c_1} - \alpha^{c_1+c_2-1}\right) \\ &+ \alpha - (x-1)^2 + \bar{\beta} + \frac{1}{2}\sigma_x^2 + \sigma_\alpha^2 \\ :=& C < \infty. \end{aligned}$$

Integrating both sides of Eq. (22) on interval $[0, \tau_n \wedge N]$ yields that

$$\begin{aligned} &\mathbb{E}V[x(N \wedge \tau_n), \alpha(N \wedge \tau_n), \beta(N \wedge \tau_n)] \\ \leq& V(x(0), \alpha(0), \beta(0)) + CN. \end{aligned}$$

Define $\Omega_n = \{\tau_n \leq N\}$, $\forall n \geq n_1$. By Eq. (21) we know that $\mathbb{P}(\Omega_n) \geq \varepsilon$. It follows that, for any $\omega \in \Omega_n$, there exists at least one of $x(\tau_n, \omega)$, $\alpha(\tau_n, \omega)$ and $\beta(\tau_n, \omega)$ equals either n or n^{-1}. Therefore, we get

$$\begin{aligned} &V(x(\tau_n, \omega), \alpha(\tau_n, \omega), \beta(\tau_n, \omega)) \\ \geq& (n - 1 - \ln n) \wedge (n^{-1} - 1 - \ln n^{-1}). \end{aligned} \tag{23}$$

By Eqs. (22) and (23), we have

$$\begin{aligned} &V(x(0), \alpha(0), \beta(0)) + CN \\ \geq& \mathbb{E}[\mathbf{1}_{\Omega_n(\omega)} V(x(\tau_n, \omega), \alpha(\tau_n, \omega), \beta(\tau_n, \omega))] \\ \geq& \varepsilon[(n - 1 - \ln n) \wedge (n^{-1} - 1 - \ln n^{-1})], \end{aligned}$$

where $\mathbf{1}_{\Omega_n}$ is the indicator function of Ω_n. Letting $n \to \infty$, we obtain the contradiction that

$$\infty > V(x(0), \alpha(0), \beta(0)) + CN \geq \infty,$$

which indicates that $\tau_\infty = \infty$. This completes the proof of Example 1. ☐

Proof of Theorem 1. *(1) The unbounded case.* The result is straightforward by applying Theorems 3.1 and 3.4 in Hening et al. [87] and is therefore omitted here.

(2) The bounded case. Using Itô's formula for $\ln x(t)$ yields that

$$d\ln x(t) = \left(1 - x - \frac{\alpha}{\beta\alpha x + 1} - \frac{1}{2}\sigma_x^2\right) dt + \sigma_x dB_x(t). \tag{24}$$

Integrating both sides of Eq. (24), we get

$$\begin{aligned} &\frac{\ln x(t) - \ln x(0)}{t} \\ =& 1 - \frac{1}{2}\sigma_x^2 - \frac{1}{t}\int_0^t \frac{\alpha(s)}{\beta(s)\alpha(s)x(s) + 1} ds - \frac{1}{t}\int_0^t x(s)ds \\ &+ \frac{1}{t}\sigma_x B_x(t) \\ \geq& 1 - \frac{1}{2}\sigma_x^2 - \frac{1}{t}\int_0^t \alpha(s)ds - \frac{1}{t}\int_0^t x(s)ds + \frac{1}{t}\sigma_x B_x(t). \end{aligned} \tag{25}$$

Since $\limsup_{t\to\infty} \frac{\ln x(t)}{t} \leq 0$ *a.s.* (see Lemma 3, Liu et al. [98]), taking limit on both sides of Eq. (25), we get

$$\begin{aligned} \liminf_{t\to\infty} \frac{1}{t}\int_0^t x(s)ds \geq& 1 - \frac{1}{2}\sigma_x^2 - \liminf_{t\to\infty} \frac{1}{t}\int_0^t \alpha(s)ds \\ >& 0 \ a.s. \end{aligned}$$

When $\alpha(t)$ is bounded below by $\hat{\alpha} > 0$ and $\beta(t)$ is bounded above by $\check{\beta}$, we have

$$\begin{aligned} &\frac{\ln x(t) - \ln x(0)}{t} \\ \leq& 1 - \frac{1}{2}\sigma_x^2 - \frac{1}{t}\int_0^t \left(x(s) + \frac{\hat{\alpha}}{\check{\beta}\hat{\alpha}x(s) + 1}\right) ds + \frac{1}{t}\sigma_x B_x(t) \\ \leq& \begin{cases} 1 - \frac{1}{2}\sigma_x^2 - \hat{\alpha} + \frac{1}{t}\sigma_x B_x(t), \ \text{if } \hat{\alpha}\sqrt{\check{\beta}} \leq 1, \\ 1 - \frac{1}{2}\sigma_x^2 - \frac{2\hat{\alpha}\sqrt{\check{\beta}} - 1}{\hat{\alpha}\check{\beta}} + \frac{1}{t}\sigma_x B_x(t), \ \text{if } \hat{\alpha}\sqrt{\check{\beta}} > 1. \end{cases} \end{aligned}$$

Therefore,

$$\begin{aligned} \limsup_{t\to\infty} \frac{\ln x(t)}{t} \leq& \begin{cases} 1 - \frac{1}{2}\sigma_x^2 - \hat{\alpha}, \ \text{if } \hat{\alpha}\sqrt{\check{\beta}} \leq 1, \\ 1 - \frac{1}{2}\sigma_x^2 - \frac{2\hat{\alpha}\sqrt{\check{\beta}} - 1}{\hat{\alpha}\check{\beta}}, \ \text{if } \hat{\alpha}\sqrt{\check{\beta}} > 1, \end{cases} \\ <& 0 \ a.s. \end{aligned}$$

This completes the proof of Theorem 1.

Define $\mathbf{E} = \mathbb{R}^l \times I$ and $U_\mathbf{R} = \{x : |x| < \mathbf{R}\}$. To prove Theorem 2, we need the following lemmas.

Lemma 3 (*Theorem 4.2, [72]*). *Let $X(t) \in \mathbb{R}^l$ be a regular time-homogeneous Markov process given by*

$$dX(t) = b(X)dt + \sum_{r=1}^k \sigma_r(X)dB_r(t),$$

where $b, \sigma_r \in \mathbb{R}^l$, $\dot{B}_r(t)$ is a standard l-dimensional independent Brownian motion. The Markov process $X(t)$ has a unique stationary distribution if there is a bounded open domain $U \subset \mathbb{R}^l$ with regular boundary Γ satisfies the following conditions

- *B.1 In the domain U and some neighborhood thereof, the smallest eigenvalue of the diffusion matrix $A(x) = ((a_{ij}(x)))$, $a_{ij}(x) = \sum_{r=1}^k \sigma_r^i(x) \sigma_r^j(x)$ is bounded away from zero.*
- *B.2 If $x \in \mathbb{R}^l \setminus U$, the mean time τ a which a path issuing from x reaches the set U is finite, and $\sum_{x\in K} \mathbb{E}^x\tau < \infty$ for every compact subset $K \subset \mathbb{R}^l$.*

Lemma 4 (*[72]*). *For systems of the special form*

$$X(t) = X(0) + \int_{t_0}^t b(s, X(s))ds + \sum_{r=1}^k \int_{t_0}^t \sigma_r(s, X(s))dB_r(s), \tag{26}$$

where $b(s,x)$, $\sigma_1(s,x), \ldots, \sigma_k(s,x)$, $s \in [t_0, T]$, $x \in \mathbb{R}^l$ are continuous functions of (s,x), such that for some constant B the following conditions hold in every cylinder $I \times U_\mathbf{R}$

$$\begin{aligned} &|b(s,x) - b(s,y)| + \sum_{r=1}^k |\sigma_r(s,x) - \sigma_r(s,y)| \leq B|x - y|, \\ &|b(s,x)| + \sum_{r=1}^k |\sigma_r(s,x)| \leq B(1 + |x|). \end{aligned} \tag{27}$$

If the coefficients of System (26) are T-periodic in t and satisfy (27) in every cylinder $I \times U_{\mathbf{R}}$ and, moreover, that there exists a non-negative function $V \in \mathbf{C}^2$ in $I \times U_{\mathbf{R}}$ which is $T-$periodic in t with the properties

B.3 $\inf_{|x|>\mathbf{R}} V(x,t) \to \infty$ *as* $\mathbf{R} \to \infty$.

B.4 $\mathbf{L}V(x,t) \leq -1$ *outside some compact set, where the operator* $\mathbf{L}$ *is given by*

$$\mathbf{L} = \frac{\partial}{\partial t} + \sum_{i=1}^{l} b_i(x,t)\frac{\partial}{\partial x_i} + \frac{1}{2}\sum_{i,j=1}^{l} a_{ij}(x,t)\frac{\partial^2}{\partial x_i \partial x_j},$$

where $a_{ij} = \sum_{r=1}^{k} \sigma_r^i(x,t)\sigma_r^j(x,t)$.

Then there exists a solution of (26) which is a T-periodic Markov process.

Proof of Theorem 2. *Case 1*. To prove that System (4) admits a unique ergodic stationary distribution, we need to verify that System (4) satisfies the two conditions B.1 and B.2 in Lemma 3. Since the diffusion matrix of System (4) is a non-singular matrix given by

$$A(x,\alpha,\beta) = \begin{pmatrix} \sigma_x^2 x^2 & 0 & 0 \\ 0 & {\sigma_\alpha}^2\alpha^2 & 0 \\ 0 & 0 & \sigma_\beta^2\beta^2 \end{pmatrix},$$

the condition B.1 in Lemma 3 holds. In the following, we verify that the condition B.2 also holds. According to Zhu and Yin [99], to verify the condition B.2, it is sufficient to show that there is a non-negative Lyapunov function $V(x,\alpha,\beta)$ such that the differential operator $\mathbf{L}V$ is negative on $\mathbb{R}^2 \setminus U$.

Consider the Lyapunov function

$$V = \int_1^x \frac{s-1}{s}ds + m_1\int_1^\alpha \frac{s-1}{s}ds + \alpha + m_2\int_1^\beta \frac{s-1}{s}ds, \ \forall\ m_1, m_2 > 0.$$

Applying Itô's formula to V yields

$$\begin{aligned}\mathbf{L}V =&(x-1)\left(1-x-\frac{\alpha}{\beta\alpha x+1}\right)+(\bar{\alpha}-\alpha)\\ &+ m_1\left(1-\frac{1}{\alpha}\right)(\bar{\alpha}-\alpha)+m_2\left(1-\frac{1}{\beta}\right)\left(\bar{\beta}-\beta\right)\\ &+ \frac{1}{2}m_1{\sigma_\alpha}^2+\frac{1}{2}\sigma_x^2+\frac{1}{2}m_2\sigma_\beta^2\\ \leq& -(x-1)^2+\bar{\alpha}+m_1\left(\bar{\alpha}-\alpha-\frac{\bar{\alpha}}{\alpha}+1\right)+\frac{1}{2}\sigma_x^2\\ &+ m_2\left(\bar{\beta}-\beta-\frac{\bar{\beta}}{\beta}+1\right)+\frac{1}{2}m_1{\sigma_\alpha}^2+\frac{1}{2}m_2\sigma_\beta^2.\end{aligned}$$

For simplicity, we define the constant M as

$$M = \bar{\alpha}+\frac{1}{2}m_1{\sigma_\alpha}^2+\frac{1}{2}\sigma_x^2+\frac{1}{2}m_2\sigma_\beta^2.$$

It follows that

$$\mathbf{L}V \leq \begin{cases} -m_1\bar{\alpha}\times\infty+m_1(\bar{\alpha}+1)+m_2(\sqrt{\bar{\beta}}-1)^2+M \\ \to -\infty \quad as \quad \alpha \to 0^+, \\ -m_1\times\infty+m_1(\bar{\alpha}+1)+m_2(\sqrt{\bar{\beta}}-1)^2+M \\ \to -\infty \quad as \quad \alpha \to \infty, \\ -m_2\bar{\beta}\times\infty+m_2\left(\bar{\beta}+1\right)+m_1(\sqrt{\bar{\alpha}}-1)^2+M \\ \to -\infty \quad as \quad \beta \to 0^+, \\ -m_2\times\infty+m_2\left(\bar{\beta}+1\right)+m_1(\sqrt{\bar{\alpha}}-1)^2+M \\ \to -\infty \quad as \quad \beta \to \infty, \\ -1+\bar{\alpha}+m_1\left(\sqrt{\bar{\alpha}}-1\right)^2+m_2(\sqrt{\bar{\beta}}-1)^2 \\ +\frac{1}{2}m_1{\sigma_\alpha}^2+\frac{1}{2}\sigma_x^2+\frac{1}{2}m_2\sigma_\beta^2 \quad as \quad x \to 0^+, \\ -(\infty-1)^2+m_1\left(\sqrt{\bar{\alpha}}-1\right)^2+m_2\left(\sqrt{\bar{\beta}}-1\right)^2 \\ +M \to -\infty \quad as \quad x \to \infty. \end{cases} \tag{28}$$

Since $\bar{\alpha}+\frac{1}{2}\sigma_x^2 < 1$, by (28) we can choose $m_1, m_2 > 0$ small enough such that $-1+\bar{\alpha}+m_1(\bar{\alpha}-1)^2+m_2\left(\bar{\beta}-1\right)^2+\frac{1}{2}m_1{\sigma_\alpha}^2+\frac{1}{2}\sigma_x^2+\frac{1}{2}m_2\sigma_\beta^2 < 0$, which indicates that condition B.2 of Lemma 3 holds. This completes the proof of Case 1.

Case 2. Note that $\alpha(t), \beta(t)$ are bounded positive $T-$periodic functions, System (4) can be simplified to the following one-dimensional non-autonomous system

$$dx = x\left(1-x-\frac{\alpha}{\alpha\beta x+1}\right)dt+\sigma_x x dB_x(t). \tag{29}$$

Since the coefficients of System (29) satisfies the condition (27), in the following we only need to verify that System (29) meets the conditions B.3 and B.4 of Lemma 4.

Define $V_1 = x^{-p}+x-\ln x$, where $p > 0$ is a constant. By Itô's formula, we obtain that

$$\begin{aligned}\mathbf{L}V_1 =& -px^{-p}\left(1-x-\frac{\alpha}{\alpha\beta x+1}\right)+\frac{1}{2}p(p+1)\sigma_x^2x^{-p}\\ &+(x-1)\left(1-x-\frac{\alpha}{\alpha\beta x+1}\right)+\frac{1}{2}\sigma_x^2\\ \leq& px^{-p}\left(\alpha+\frac{1}{2}(p+1)\sigma_x^2-1\right)+px^{-p+1}+2x-x^2\\ &+\frac{1}{2}\sigma_x^2+\alpha-1.\end{aligned}$$

Define $V = V_1+\omega_t$, where ω_t is a $T-$periodic function satisfying

$$\omega_t' = \frac{1}{t}\int_0^T \alpha(s)ds-\alpha(t).$$

It follows that V satisfies B.3 and

$$\begin{aligned}\mathbf{L}V \leq& px^{-p}\left(\alpha+\frac{1}{2}(p+1)\sigma_x^2-1\right)+px^{-p+1}+2x-x^2\\ &+\frac{1}{2}\sigma_x^2+\frac{1}{t}\int_0^T \alpha(s)ds-1.\end{aligned}$$

Since $\breve{\alpha}+\frac{1}{2}\sigma_x^2 < 1$, we can choose a sufficiently small $p > 0$ such that $\breve{\alpha}+\frac{1}{2}(p+1)\sigma_x^2 < 1$. Therefore, we have

$\mathbf{L}V \to -\infty$ as $x \to 0^+$ or $x \to +\infty$.

That is, System (29) satisfies the condition B.4 and admits a nontrivial positive $T-$periodic solution. This completes the proof of Theorem 2. ☐

Proof of Theorem 3 (*Unbounded Case*)**.** We first study the persistence of population $x(t)$. Using Itô's formula for $\ln x(t)$, we get

$$d\ln x(t) = \left(1-x-\frac{\alpha}{\bar{\beta}\alpha x+1}\right)dt \geq (1-x-\alpha)dt. \tag{30}$$

Integrating both sides of Eq. (30) from 0 to t, we obtain

$$\frac{\ln x(t)-\ln x(0)}{t} \geq 1-\frac{1}{t}\int_0^t x(s)ds-\frac{1}{t}\int_0^t \alpha(s)ds. \tag{31}$$

Taking limit on both sides of Eq. (31) with respect to t, we get

$$\liminf_{t\to\infty}\frac{1}{t}\int_0^t x(s)ds \geq 1-\liminf_{t\to\infty}\frac{1}{t}\int_0^t \alpha(s)ds > 0 \ a.s.,$$

provided that

$$\liminf_{t\to\infty}\frac{1}{t}\int_0^t \alpha(s)ds < 1 \ a.s.$$

Next, we study the extinction of population $x(t)$. Since

$$d\ln x(t) = 1-x-\frac{\alpha}{\bar{\beta}\alpha x+1} \leq 1-\frac{\alpha}{\bar{\beta}\alpha+1},$$

it follows that

$$\frac{\ln x(t)-\ln x(0)}{t} \leq 1-\frac{1}{t}\int_0^t \frac{\alpha(s)}{\bar{\beta}\alpha(s)+1}ds.$$

Letting $t \to \infty$, by the ergodicity of $\alpha(t)$, we get

$$\limsup_{t\to\infty}\frac{\ln x(t)}{t} \leq 1-\int_{\mathbb{R}_+}\frac{s}{\bar{\beta}s+1}\pi(ds) < 0 \ a.s.,$$

provided that $\int_{\mathbb{R}_+} \frac{s}{\bar{\beta}s+1}\pi(ds) > 1$.

Bounded Case. (i) If $\alpha(t)$ is bounded above by $\check{\alpha} < 1$, then we have

$$\begin{aligned} x' =& x\left(1 - x - \frac{\alpha}{\alpha\bar{\beta}x + 1}\right) \geq x\left(1 - x - \frac{\check{\alpha}}{\check{\alpha}\bar{\beta}x + 1}\right) \\ \geq& x\left(1 - x - \check{\alpha}\right), \end{aligned}$$

which indicates that

$$0 < 1 - \check{\alpha} \leq \liminf_{t\to\infty} x(t) \leq \limsup_{t\to\infty} x(t) \leq 1.$$

(ii) If $\alpha(t)$ is bounded below by $\hat{\alpha}$, then we have

$$\begin{aligned} x' =& x\left(1 - x - \frac{\alpha}{\alpha\bar{\beta}x + 1}\right) \leq x\left(1 - x - \frac{\hat{\alpha}}{\hat{\alpha}\bar{\beta}x + 1}\right) \\ \leq& x\left(1 - x - \frac{\hat{\alpha}}{\hat{\alpha}\bar{\beta} + 1}\right). \end{aligned}$$

which indicates that $\limsup_{t\to\infty} \frac{\ln x(t)}{t} < 0$ provided that $\frac{\hat{\alpha}}{\hat{\alpha}\bar{\beta}+1} > 1$.

(iii) The assertion when $\alpha(t)$ is a periodic demographic stochasticity with periodic T is straightforward by using the Comparison theorem and Theorem 2.1 of Wesley and Allen [100], hence it is omitted here. This completes the proof of Theorem 3. □

Proof of Lemma 1. Applying Itô's formula to $e^t x^p$, we obtain that

$$\begin{aligned} d[e^t x^p(t)] =& e^t x^p \left[1 + \frac{1}{2}p(p-1)\sigma_x^2 + p\left(1 - x - \frac{\bar{\alpha}}{\bar{\alpha}\bar{\beta}x + 1}\right)\right] dt \\ &+ e^t p\sigma_x x^p dB_x(t). \end{aligned} \tag{32}$$

Choose $n_0 > 0$ such that $x(0) \in [1/n_0, n_0]$. For any integer $n \geq n_0$, we define the stopping time

$$\tau_n = \inf\{t \in \mathbb{R}_+ : \ x(t) \notin (1/n, n)\}.$$

Integrating both sides of Eq. (32) from 0 to $t \wedge \tau_n$, we get

$$\begin{aligned} &\mathbb{E}[e^{t\wedge\tau_n} x^p(t \wedge \tau_n)] - x^p(0) \\ =& \mathbb{E}\int_0^{t\wedge\tau_n} e^s x^p(s) \left[1 + \frac{p(p-1)\sigma_x^2}{2} + p\left(1 - x(s) - \frac{\bar{\alpha}}{\bar{\alpha}\bar{\beta}x(s) + 1}\right)\right] ds. \end{aligned} \tag{33}$$

Define

$$h_1(x) = x^p \left[1 + \frac{1}{2}p(p-1)\sigma_x^2 + p\left(1 - x - \frac{\bar{\alpha}}{\bar{\alpha}\bar{\beta}x + 1}\right)\right].$$

Through direct algebraic operation, we know that

$$\begin{aligned} h_1(x) \leq& x^p \left[1 + \frac{1}{2}p(p-1)\sigma_x^2 + p(1 - x)\right] \\ \leq& \left[1 + \frac{p|p-1|\sigma_x^2}{2(p+1)}\right]^{p+1}, \ \forall\ p > 0, \end{aligned}$$

and the first equal sign holds if and only if $\bar{\alpha} = 0$. It follows that for any $\bar{\alpha} > 0$, there exists a positive constant $\phi = \phi(\bar{\alpha})$ such that

$$h_1(x) \leq \left[1 + \frac{p|p-1|\sigma_x^2}{2(p+1)} - \phi\right]^{p+1}.$$

Letting $n \to \infty$, it then follows from Eq. (33) that

$$e^t \mathbb{E}[x^p(t)] \leq x^p(0) + (e^t - 1)\left[1 + \frac{p|p-1|\sigma_x^2}{2(p+1)} - \phi\right]^{p+1},$$

which indicates that

$$\limsup_{t\to\infty} \mathbb{E}[x^p(t)] \leq \left[1 + \frac{p|p-1|\sigma_x^2}{2(p+1)} - \phi\right]^{p+1}.$$

This completes the proof of Lemma 1. □

Proof of Theorem 7. To prove Theorem 7, we only need to verify that System (4) meets the conditions B.1 and B.2 of Lemma 3. Since the diffusion matrix of System (4) is a non-singular matrix, the condition B.1 holds. In the following, we verify that the condition B.2 also holds. According to Zhu and Yin [99], to verify condition B.2, it is sufficient to show that there is a non-negative Lyapunov function $V(x(t))$ such that the differential operator $\mathbf{L}V$ is negative on $\mathbb{R}_+ \setminus U$.

Consider the Lyapunov function

$$V = \int_i^x \frac{s-1}{s} ds.$$

Applying Itô's formula to V yields

$$\begin{aligned} \mathbf{L}V =& (x-1)\left(1 - x - \frac{\bar{\alpha}}{\bar{\beta}\bar{\alpha}x + 1}\right) + \frac{1}{2}\sigma_x^2 \\ =& -(x-1)^2 - (x-1)\frac{\bar{\alpha}}{\bar{\beta}\bar{\alpha}x + 1} + \frac{1}{2}\sigma_x^2. \end{aligned}$$

It follows that

$$\mathbf{L}V \leq \begin{cases} -(\infty - 1)^2 + \frac{1}{2}\sigma_x^2 \to -\infty & as \quad x \to \infty, \\ -1 + \check{\bar{\alpha}} + \frac{1}{2}\sigma_x^2 < 0 & as \quad x \to 0^+, \end{cases}$$

which indicates that condition B.2 of Lemma 3 holds. This completes the proof of Theorem 7. □

Proof of Lemma 2. The ergodicity of $\alpha(t)$ is a straightforward result by previous work (see, e.g., Mao [86], Diet et al. [101]). Through direct calculation, we obtain that $\alpha(t)$ has an explicit solution

$$\begin{aligned} \alpha(t) =& \bar{\alpha}\int_0^t e^{(1+\frac{1}{2}\sigma_\alpha^2)(s-t)+\sigma_\alpha(B_\alpha(t)-B_\alpha(s))} ds \\ &+ \alpha(0)e^{-(1+\frac{1}{2}\sigma_\alpha^2)t+\sigma_\alpha B_\alpha(t)}. \end{aligned}$$

It follows that

$$\mathbb{E}[\alpha(t)] = \bar{\alpha} + (\alpha(0) - \bar{\alpha})e^{-t}$$

and

$$\lim_{t\to\infty} \mathbb{E}[\alpha(t)] = \bar{\alpha} \ a.s.$$

Applying Itô's formula to $e^t\alpha^2(t)$, we have

$$d[e^t\alpha^2(t)] = e^t[2\bar{\alpha}\alpha + (\sigma_\alpha^2 - 1)\alpha^2]dt + 2e^t\sigma_\alpha\alpha^2 dB_\alpha(t). \tag{34}$$

Choose $n_0 > 0$ such that $\alpha(0) \in [1/n_0, n_0]$. For any integer $n \geq n_0$, we define the stopping time

$$\tau_n = \inf\{t \in \mathbb{R}_+ : \ \alpha(t) \notin (1/n, n)\}.$$

Integrating both sides of Eq. (34) from 0 to $t \wedge \tau_n$, we get

$$\begin{aligned} &\mathbb{E}[e^{t\wedge\tau_n}\alpha^2(t \wedge \tau_n)] \\ =& \alpha^2(0) + \mathbb{E}\int_0^{t\wedge\tau_n} e^s[2\bar{\alpha}\alpha(s) + (\sigma_\alpha^2 - 1)\alpha^2(s)]ds. \end{aligned} \tag{35}$$

If $\sigma_\alpha^2 < 1$, maximizing the quadratic function with respect to $\alpha(s)$ in the integrand and letting $n \to \infty$, we obtain that

$$\mathbb{E}[\alpha^2(t)] \leq (\alpha^2(0) - 1)e^{-t} + \frac{\bar{\alpha}^2}{1 - \sigma_\alpha^2}. \tag{36}$$

Taking upper limit on both sides of Eq. (36) with respect to t, we obtain

$$\limsup_{t\to\infty} \mathbb{E}[\alpha^2(t)] \leq \frac{\bar{\alpha}^2}{1 - \sigma_\alpha^2} \ a.s., \text{ if } \sigma_\alpha^2 < 1.$$

Similarly, if $\sigma_\alpha^2 \in [1, 2)$, setting $n \to \infty$ in (35), we obtain

$$\mathbb{E}[e^t\alpha^2(t)] \leq f(t) + (\sigma_\alpha^2 - 1)\int_0^t \mathbb{E}[e^s\alpha^2(s)]\ ds,$$

where

$$f(t) = \alpha^2(0) + 2\bar{\alpha}^2(e^t - 1) + 2\bar{\alpha}(\alpha(0) - \bar{\alpha})t.$$

Applying Grönwall's lemma yields

$$\mathbb{E}[\alpha^2(t)] \leq e^{-t}f(t) + e^{-t}\int_0^t f(s)(\sigma_\alpha^2 - 1)e^{(\sigma_\alpha^2-1)(t-s)}ds. \tag{37}$$

Letting $t \to \infty$ on both sides of Eq. (37), we obtain

$$\limsup_{t\to\infty} \mathbb{E}[\alpha^2(t)] \le \frac{2\bar{\alpha}^2}{2-\sigma_\alpha^2} \; a.s., \text{ if } 1 \le \sigma_\alpha^2 < 2.$$

This completes the proof of Lemma 2. □

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