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THE LOTTERY MODEL FOR ECOLOGICAL COMPETITION IN NONSTATIONARY ENVIRONMENTS*

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Abstract. A two-species lottery competition model with nonstationary reproduction and mortality rates of both species is studied. First, a diffusion approximation for the fraction of sites occupied by each adult species is derived as the continuum limit of a classical discrete-time lottery model. Then a nonautonomous SDE on sites occupied by the species as well as a Fokker–Planck equation on its transitional probability are developed. Existence, uniqueness, and dynamics of solutions for the resulting SDE are investigated, from which sufficient conditions for the existence of a time-dependent limiting process and coexistence of species in the sense of stochastic persistence are established. A unique classical solution to the Fokker–Planck equation is also proved to exist and shown to be a probability density. Numerical simulations are presented to illustrate the theoretical results.

Key words. lottery competition model, nonstationary diffusion process, nonautonomous SDE, Fokker–Planck equation, coexistence, stochastic persistence

AMS subject classifications. 34F05, 35Q84, 60H10, 60J60, 60K37, 92D40

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1. Introduction.

A long-standing question in ecology is the role of stochastic temporal environmental fluctuations in the dynamics and structure of ecological communities [1, 11, 17, 18, 29, 36]. Among contentious debates over the importance of such fluctuations (see, e.g., [36, 29]), one particular view is that stochastic fluctuations may change the very structure of a biological community rather than just causing population to fluctuate about an equilibrium or other deterministic attractor (see, e.g., [29, 12]). Although some models with regular environmental fluctuations supported this view, it was not until Chesson and Warner developed the lottery model [12] that stochastic temporal environmental fluctuations were shown to promote coexistence. From a mathematical perspective, the key requirements are nonlinearities in the model structure that cause temporal averages of population growth rates to deviate from the growth rates under average environments. By including in a model commonly understood biological responses to environmental variation, the original lottery model has proved to have generic properties characteristic of a family of models in which environmental fluctuations promote species coexistence [8].

While the original analysis of the lottery model demonstrated that many species could persist in the stochastic sense by having a stationary distribution of population fluctuations on the positive real numbers, it did not provide much information on the nature of the distribution itself [14]. Thus, general predictions about the magnitudes of the population fluctuations of the coexisting species were not clear except in some key limiting cases. Two kinds of approximations subsequently led to more general understanding. The first of these was an approximation for long-lived organisms

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that showed that although environmental fluctuations are necessary for coexistence, in long-lived species the resulting population fluctuations can be quite small, leading to very stable species coexistence [15]. The second kind of approximation was a diffusion approximation achieved by rescaling time and the magnitude of population change to achieve convergence on a continuous time diffusion process [26, 27]. As a consequence, a more general understanding of the stability of the coexisting species was possible. All of this previous work on population fluctuations, however, assumes stationary environmental fluctuations, generally in fact independent and identically distributed. Although stationary fluctuations and indeed identically distributed fluctuations were a good starting point and provided a great deal of information, it is now generally understood temporal that environmental variation in nature may depart importantly from the stationary case [37]. This fact is now increasingly on the minds of researchers as natural systems become strongly affected by anthropogenically driven climate change. For this reason, a new program of research on nonstationary community ecology is being developed [9, 10].

Notice that although species coexistence results are available for the nonstationary lottery model [10], a general understanding of population fluctuations and the stability of species coexistence is lacking for the nonstationary case. The purpose of this paper is to fill this gap with nonstationary diffusion approximations to the nonstationary lottery model. More precisely, the reproduction rates and adult mortality rates are assumed to be nonstationary stochastic processes with time-dependent moments. To that end, we first derive a nonautonomous SDE from the nonhomogeneous diffusion processes approximating the classical discrete-time lottery model. Then by analyzing the solution of the resulting SDE, we prove that if the expectations, variances, and the covariances of the environment parameters are all bounded, the population trajectories remain positive with probability one. Moreover, by investigating long-term dynamics of the SDE, we show that two competing species can coexist in the sense of stochastic persistence under intense environmental fluctuation. The results in this work are obtained by using different analytical tools but are qualitatively consistent with those in [14, 27]. Indeed, our results include more general cases with more precise mathematical descriptions and recover the conditions established in [27] in the special stationary scenario. Furthermore, to gain more statistical insight, a Fokker–Planck equation on the transition probability density governed by the diffusion processes is formulated and studied.

The paper is organized as follows. In section 2 we introduce the classical discrete-time lottery model and derive its associated nonstationary diffusion processes. In section 3 we first formulate a nonautonomous SDE governed by the diffusion processes obtained in section 2 and then study the existence, uniqueness, and dynamics of solutions. In section 4 we develop the Fokker–Plank PDE on the transitional probability density and prove the existence of nonnegative probability density solutions. Numerical simulations are presented in section 5 to illustrate the theoretical results established in sections 3 and 4, and in the end some closing remarks are provided in section 6.

2. The model. For simplicity of exposition, in this work we restrict our attention to the lottery model with two ecological species in a single habitat competing for a limited number of sites. Given any fixed $h > 0$, let the discrete time t take values in $\{jh : j \in \mathbb{N}\}$, and let $X_i(t)$ be the fraction of the sites occupied by adults of the ith species at time t. Denote by $\nu_i^h(t)$ the death rate of adults of the ith species during the time period $(t, t+h]$. Then the term $(1-\nu_i^h(t))X_i(t)$ represents the fraction of sites

occupied by surviving adults of the ith species during $(t, t+h]$, and the proportion of new sites available for settling by juveniles is $\sum_{i=1}^{n} \nu_i^h(t) X_i(t)$. Let $\beta_i^h(t) \in [0,1]$ be the per capita net reproduction by adults of the ith species during time $(t, t+h]$; i.e., for each adult of species i at time t, $\beta_i^h(t)$ larvae reach the settling stage during $(t, t+h]$. Following an intuitive ecological interpretation that the next generation is given by the sum of surviving adults and new recruitments [14, 16], the original discrete-time lottery model for two competing species can be formulated as

(2.1)
$$X_i(t+h) = X_i(t)(1-\nu_i^h(t)) + \frac{(X_1(t)\nu_1^h(t) + X_2(t)\nu_2^h(t))X_i(t)\beta_i^h(t)}{X_1(t)\beta_1^h(t) + X_2(t)\beta_2^h(t)}, \quad i = 1, 2,\ h > 0.$$

Let the initial time of the system (2.1) be t_0, and assume that initial fractions of species satisfy

$$X_i(t_0) := x_{i,0} > 0, \quad i = 1, 2, \quad \text{with} \quad x_{1,0} + x_{2,0} = 1. \tag{2.2}$$

Then it is straightforward to check that any solution of (2.1) under the assumption (2.2), if it exists, satisfies $X_1(t) + X_2(t) = 1$ for all $t \geq t_0$. Therefore, the system (2.1) can be reduced to a one-dimensional difference equation, and it suffices to focus on $X_1(t)$ only. Throughout the rest of this manuscript, we write $X_1(t)$ as $X(t)$ and $X_2(t) = 1 - X(t)$ when the context is clear.

When the environment fluctuates randomly with respect to time, it is natural to assume that the time-dependent parameters $\nu_i^h(t)$ and $\beta_i^h(t)$, as well as $X(t)$, are stochastic processes. Notice that most of existing works on the system (2.1)–(2.2) in the literature considered stationary environment; i.e., $\nu_i^h(t)$ and $\beta_i^h(t)$ are jointly a stationary stochastic processes with constant moments. This assumption, however, is at best an approximation to temporal environmental variation in nature (see, e.g., [9, 13, 34]). The aim of this work is to investigate detailed stochastic dynamics and probabilistic properties of the system (2.1)–(2.2), when the environment is nonstationary, i.e., when $\nu_i^h(t)$ and $\beta_i^h(t)$ are nonstationary stochastic processes.

Let $(E, \mathscr{F}, P)$ be a probability space. For each $t \in \{jh : j \in \mathbb{N}\}$, let $\nu^h(t)$ and $\beta^h(t)$ be nonnegative real-value random variables on $(E, \mathscr{F}, P)$. More specifically, it is assumed that at any different discrete time instants t and s, $\nu^h(t)$ and $\nu^h(s)$ are independent, and $\beta^h(t)$ and $\beta^h(s)$ are also independent. Due to such independence structure of $\nu^h(t)$ and $\beta^h(t)$, the process $\{X(t)\}_{t\in\{jh:j\in\mathbb{N}\}}$ forms a discrete-time Markov chain, as $X(t+h)$ can be predicted inductively given information of $X(t)$, $\beta^h(t)$ and $\nu^h(t)$. To construct a continuous counterpart of the discrete process $\{X(t)\}_{t\in\{jh:j\in\mathbb{N}\}}$, define the space $\Omega = \mathcal{C}([0,\infty), \mathbb{R})$ to be the collection of all continuous paths from $[0,\infty)$ into $\mathbb{R}$. For any real number $s \geq 0$ and $\omega \in \Omega$, set $x(s,\omega) = \omega(s)$, and define the metric on Ω by

$$\varrho(\omega, \omega') = \sum_{n=1}^{\infty} \frac{1}{2^n} \frac{\sup_{0\leq s\leq n} |x(s,\omega) - x(s,\omega')|}{1 + \sup_{0\leq s\leq n} |x(s,\omega) - x(s,\omega')|} \quad \forall\ \omega,\ \omega' \in \Omega.$$

Then (Ω, ϱ) is a complete separable metric space [40]. Next, let $\mathscr{M}$ be the Borel σ-field on (Ω_s, D), i.e., $\mathscr{M} = \sigma[x(s) : s \geq 0]$ [40]. For any $s_1,\ s_2 > 0$, define

$$\mathscr{M}_{s_1,s_2} = \sigma[x(s) : s_1 \leq s \leq s_2] \text{ and } \mathscr{M}_{s_1} = \sigma[x(s) : s \geq s_1].$$

Let $x_{t_0,x}$ be the linear interpolation of $X(t)$ with $X(t_0) = x$; i.e., for any $q \in E$ let

$$x_{t_0,x}(s,q) = \begin{cases} X(t_0,q) & \text{for } s = t_0, \\ \frac{(j+1)h-s}{h} X(t_0+jh,q) & \\ \quad + \frac{s-jh}{h} X(t_0+(j+1)h,q) & \text{for } jh \le s < (j+1)h,\ j \in \mathbb{N}. \end{cases}$$

Then $x_{t_0,x}(s,q)$ is a continuous time process on $(E,\mathcal{F},P)$ that defines a measurable mapping from $(E,\mathcal{F})$ into $(\Omega,\mathscr{M}_{t_0})$ given by $q \mapsto x_{t_0,x}(\cdot,q)$. Therefore, it induces a probability measure $P^h_{t_0,x}$ on $(\Omega,\mathscr{M}_{t_0})$ that satisfies

$$\begin{cases} P^h_{t_0,x}[x_{t_0,x}(t_0) = x] = 1, \\ P^h_{t_0,x}\left[x_{t_0,x}(s) = \frac{(j+1)h-s}{h} X(t_0+jh) + \frac{s-jh}{h} X(t_0+(j+1)h),\ jh \le s < (j+1)h\right] \\ \qquad = 1, \quad j \in \mathbb{N}, \\ P^h_{t_0,x}\left[x_{t_0,x}(t_0+(j+1)h) \in \Gamma \mid \mathscr{M}_{t_0+jh}\right] = \Pi_h(t_0,x,t_0+jh,\Gamma), \quad j \in \mathbb{N} \text{ and } \Gamma \in \mathscr{B}_{\mathbb{R}}, \end{cases}$$

where $\mathscr{B}_{\mathbb{R}}$ is the Borel σ-algebra in $\mathbb{R}$ and $\Pi_h(t_0,x,t_0+t,\cdot)$ is the probability transition function of $X(t)$ on $\mathbb{R}$ for any $t \in \{jh : j \in \mathbb{N}\}$. According to Theorem 11.2.3 in [40], $P^h_{t_0,x}$ converges to a probability $P_{t_0,x}$ weakly as $h \to 0$.

Remark 2.1. Theorem 11.2.3 in [40] states the weak convergence of $P^h_{t_0,x}$ to $P_{t_0,x}$ in the time-homogeneous case. But the proof can be extended to the time-inhomogeneous case as in this work without loss of generality.

The first step of this work is to derive the diffusion approximation of the system (2.1) governed by $P_{t_0,x}$ defined above. Recall that the diffusion approximation of the process $\{X(t)\}_{t\in\{jh:j\in\mathbb{N}\}}$ is characterized by its infinitesimal mean and variance, defined, respectively, as

$$f(t,x) = \lim_{h\to 0} \frac{1}{h} \mathbb{E}[X(t+h) - X(t) | X(t) = x], \tag{2.3}$$

$$g^2(t,x) = \lim_{h\to 0} \frac{1}{h} \mathbb{E}[(X(t+h) - X(t))^2 | X(t) = x]. \tag{2.4}$$

Throughout the rest of this section, we derive the infinitesimal mean and variance of solutions to the difference equation (2.1), which are presented in (2.10)–(2.11) below.

Notice it follows directly from (2.1) that

$$X(t+h) - X(t) = -\nu^h_1(t)X(t) + \frac{(\nu^h_1(t)X(t) + \nu^h_2(t)(1-X(t)))\beta^h_1(t)X(t)}{\beta^h_1(t)X(t) + \beta^h_2(t)(1-X(t))},$$

which can be rewritten as

$$X(t+h) - X(t) = \frac{X(t)(1-X(t))\left(\frac{\nu^h_2(t)\beta^h_1(t)}{\nu^h_1(t)\beta^h_2(t)} - 1\right)}{\frac{\beta^h_1(t)\nu^h_2(t)}{\nu^h_1(t)\beta^h_2(t)}\frac{1}{\nu^h_2(t)}X(t) + \frac{1}{\nu^h_1(t)}(1-X(t))}. \tag{2.5}$$

Similar to [27], define the stochastic processes $\xi^h(t)$ and $\gamma^h_i(t)$ by

$$\xi^h(t) = \ln \frac{\beta^h_1(t)\nu^h_2(t)}{\beta^h_2(t)\nu^h_1(t)}, \quad \gamma^h_i(t) = \ln \nu^h_i(t) - \ln d^h_i(t), \quad i = 1,2, \tag{2.6}$$

where $d_i^h(t)$ is the geometric mean of $\nu_i^h(t)$. Then $\mathbb{E}[\gamma_i^h(t)] = 0$ for all $t \geq 0$ and $h > 0$. Notice that $\xi^h(t)$ compares the log of birth-death rate ratios $\beta_i^h(t)/\nu_i^h(t)$ for the two species. It reflects interactions between species caused by the environmental fluctuations on a log scale [16] and plays a crucial role for analysis in the following.

Next, inserting (2.6) into (2.5) results in

(2.7)
$$X(t+h) - X(t) = \frac{d_1^h(t)d_2^h(t)X(t)(1-X(t))\left(e^{\xi^h(t)}-1\right)}{d_1^h(t)X(t)e^{\xi^h(t)-\gamma_2^h(t)} + d_2^h(t)(1-X(t))e^{-\gamma_1^h(t)}}, \qquad t \in \mathbb{R},\ h > 0.$$

It then follows immediately from (2.3)–(2.4) that

$$f(t,x) = \lim_{h\to 0}\frac{1}{h}\mathbb{E}\left[\frac{R_h(t)}{S_h(t)}\right], \qquad g^2(t,x) = \lim_{h\to 0}\frac{1}{h}\mathbb{E}\left[\frac{R_h^2(t)}{S_h^2(t)}\right],$$

where

$$R_h(t) = d_1^h(t)d_2^h(t)x(1-x)\left(e^{\xi^h(t)}-1\right),$$
$$S_h(t) = d_1^h(t)xe^{\xi^h(t)-\gamma_2^h(t)} + d_2^h(t)(1-x)e^{-\gamma_1^h(t)}.$$

Different from [27] and other related works in the literature, here we assume that $\xi^h(t)$ and $\gamma_i^h(t)$ are nonstationary stochastic processes. More precisely, suppose

(2.8)
$$\mathbb{E}[\xi^h(t)] = h\mu(t), \quad \mathrm{Var}[\xi^h(t)] = h\sigma^2(t), \quad \mathrm{Var}[\gamma_i^h(t)] = h\sigma_i^2(t), \quad t \in \mathbb{R},\ h > 0.$$

Moreover, assume that

$$\mathrm{Cov}\left[\gamma_1^h(t), \xi^h(t)\right] = h\theta_1(t), \qquad \mathrm{Cov}\left[\gamma_2^h(t), -\xi^h(t)\right] = h\theta_2(t). \tag{2.9}$$

Furthermore, let $\nu_i(t)$ be the instantaneous death rate at time t, i.e., $\nu_i(t) = \lim_{h\to 0}\nu_i^h(t)$, and let $d_i(t)$ be geometric mean of the instantaneous death rate $\nu_i(t)$. Notice that for any $t \geq 0$, $\nu_i^h(t)$ is nondecreasing with respect to h. Thus, by the dominated convergence theorem, $d_i(t) = \lim_{h\to 0} d_i^h(t)$ for all $t \geq 0$.

Now by using the assumptions (2.8)–(2.9), Taylor expansion of exponential functions, and the approximation [20, 41]

$$\mathbb{E}\left[\frac{R(t)}{S(t)}\right] \approx \frac{\mathbb{E}[R(t)]}{\mathbb{E}[S(t)]} - \frac{\mathrm{Cov}[R(t),S(t)]}{\mathbb{E}[S^2(t)]} + \frac{\mathrm{Var}[S(t)]\mathbb{E}[R(t)]}{\mathbb{E}[S^3(t)]}$$

and following technical calculations similar to those presented in the appendix of [27], we obtain that

$$\begin{aligned} f(t,x) &\approx \lim_{h\to 0}\frac{1}{h}\left(\frac{\mathbb{E}[R_h(t)]}{\mathbb{E}[S_h(t)]} - \frac{\mathrm{Cov}[R_h(t),S_h(t)]}{\mathbb{E}[S_h^2(t)]} + \frac{\mathrm{Var}[S_h(t)]\mathbb{E}[R_h(t)]}{\mathbb{E}[S_h^3(t)]}\right) \\ &= \frac{d_1(t)d_2(t)x(1-x)}{(d_1(t)x + d_2(t)(1-x))^2}\big(d_1(t)xC_1(t) + d_2(t)(1-x)C_2(t)\big), \end{aligned} \tag{2.10}$$

$$\begin{aligned} g^2(t,x) &\approx \lim_{h\to 0}\frac{1}{h}\left(\frac{\mathbb{E}[R_h^2(t)]}{\mathbb{E}[S_h^2(t)]} - \frac{\mathrm{Cov}[R_h^2(t),S_h^2(t)]}{\mathbb{E}[S_h^4(t)]} + \frac{\mathrm{Var}[S_h^2(t)]\mathbb{E}[R_h^2(t)]}{\mathbb{E}[S_h^6(t)]}\right) \\ &= \left(\frac{d_1(t)d_2(t)x(1-x)}{d_1(t)x + d_2(t)(1-x)}\right)^2\sigma^2(t), \end{aligned} \tag{2.11}$$

where

$$C_1(t) := \mu(t) - \theta_2(t) - \frac{\sigma^2(t)}{2}, \qquad C_2(t) := \mu(t) + \theta_1(t) + \frac{\sigma^2(t)}{2}. \tag{2.12}$$

Remark 2.2. Both the drift and the diffusion coefficients do not depend on $\sigma_i(t)$. This, however, does not imply that the variances of death rates do not play a role in the diffusion process. In fact, the death rate parameters $\nu_i^h(t)$ $(i = 1, 2)$ do affect the parameter $\xi^h(t)$, whose variance $\sigma^2(t)$ appears in both coefficients of the diffusion process.

Remark 2.3. The drift and diffusion terms f and g^2 are the same as those obtained in [27], except that the moment functions μ, σ^2, d_i, θ_i $(i = 1, 2)$ here are all time dependent.

3. The lottery SDE. Due to Theorem 11.2.3 in [39], the solution to the discrete lottery model (2.1) converges weakly to the diffusion process with infinitesimal mean and variance given by (2.10) and (2.11), respectively. Denote by $Y(t)$ the limiting diffusion process for $X(t)$, the fraction of the sites occupied by adults of the first species at time t. Then $Y(t)$ satisfies the following SDE:

$$\text{(3.1)}\quad \mathrm{d}Y(t) = f(t, Y(t))\mathrm{d}t + g(t, Y(t))\mathrm{d}W(t), \quad t \geq t_0, \quad Y(t_0) = y_0 := x_{1,0} \in (0, 1),$$

where $W(t)$ is a one-dimensional Brownian motion and $f(t, \cdot)$ and $g(t, \cdot) > 0$ are defined by (2.10) and (2.11), respectively. In this section we first prove the existence of a unique nonnegative solution to the SDE (3.1) and then investigate its long-term dynamics. Throughout this section it is assumed that all the time-dependent moments of environmental parameters are smooth and bounded; i.e.,

(A1) the functions $\mu(t)$, $\sigma(t)$, $\theta_i(t)$, $d_i(t)$ $(i = 1, 2)$ are continuously differentiable and bounded for all $t \geq t_0$ with

$$\begin{aligned} &\mu^m \leq \mu(t) \leq \mu^M, \qquad 0 < \sigma_m^2 \leq \sigma^2(t) \leq \sigma_M^2, \\ &\theta_i^m \leq \theta_i(t) \leq \theta_i^M, \qquad 0 < d_i^m \leq d_i(t) \leq d_i^M, \quad i = 1, 2. \end{aligned}$$

Remark 3.1. The boundedness of the moment functions $\mu(t)$, $\sigma(t)$, $d_i(t)$, and $\theta_i(t)$ $(i = 1, 2)$ does not require the nonstationary environmental parameters $\xi^h(t)$, $\gamma_i^h(t)$ to be bounded themselves.

The following theorem concerns the existence, uniqueness, and positiveness of solutions to the SDE (3.1). The proof uses the same approach as in, e.g., [25, 33, 42], with different technical calculations. For the reader's convenience, we still provide the proof.

THEOREM 3.2. *Let Assumption* (A1) *hold. Then for any* $\omega \in \Omega$, *the SDE* (3.1) *has a pathwise unique solution* $Y(t) = Y(t; t_0, y_0, \omega)$ *on* (t_0, ∞). *Moreover, the solution* $Y(t) \in (0, 1)$ *a.s. for all* $t \geq t_0$.

Proof. First note that the drift and diffusion coefficients $f(t, Y)$ and $g(t, Y)$ are continuously differentiable in t and locally Lipschitz in Y. Then by classical theory for SDEs (see, e.g., [35, 38]), the initial value problem (3.1) possesses a unique local solution $Y(t)$ on $[0, \tau_e)$ with $Y(t) \in (0, 1)$ a.s., where τ_e is the explosion time. The existence of a global solution will be proved by showing $\tau_e = \infty$ a.s. below.

Let $k_0 > 0$ be a positive integer such that $y_0 \in (1/k_0, 1 - 1/k_0)$. For any $k \geq k_0$, define the sequence of "stopping times," $\{\tau_k\}$, by

$$\tau_k = \inf\left\{t \in [0, \tau_e) : Y(t) \notin \left(\frac{1}{k}, 1 - \frac{1}{k}\right)\right\}.$$

Clearly $\{\tau_k\}$ is an increasing sequence. Denote by $\tau_\infty = \lim_{k\to\infty}\tau_k$; then $\tau_\infty \le \tau_e$ a.s. We next show that $\tau_\infty = \infty$ a.s. by contradiction. To this end, define

$$V(Y) = \frac{1}{Y} + \frac{1}{1-Y}.$$

Then $V(Y) > 0$ for all $Y \in (0,1)$, and it follows from (3.1) and Itô's lemma that

(3.2)

$$\begin{aligned}&\mathrm{d}V(Y(t))\\ &\quad= \Big(f(t,Y(t))V'(Y(t)) + \frac{1}{2}g^2(t,Y(t))V''(Y(t))\Big)\mathrm{d}t + g(t,Y(t))V'(Y(t))\mathrm{d}W(t).\end{aligned}$$

Note it follows directly from Assumption (A1) that the functions C_1 and C_2 defined in (2.12) satisfy

$$C_1^m := \mu^m - \theta_2^M - \frac{\sigma_M^2}{2} \le C_1(t) \le \mu^M - \theta_2^m - \frac{\sigma_m^2}{2} := C_1^M, \tag{3.3}$$

$$C_2^m := \mu^m + \theta_1^m + \frac{\sigma_m^2}{2} \le C_2(t) \le \mu^M + \theta_1^M + \frac{\sigma_M^2}{2} := C_2^M. \tag{3.4}$$

Then by Assumption (A1) we have that for all $Y(t) \in (0,1)$, the drift terms on the right-hand side of (3.2) satisfy, respectively,

$$\begin{aligned}&f(t,Y(t))V'(Y(t))\\ &\quad= \frac{d_1(t)d_2(t)(d_1(t)Y(t)C_1(t) + d_2(t)(1-Y(t))C_2(t))}{(d_1(t)Y(t) + d_2(t)(1-Y(t)))^2}(2Y(t)-1)V(Y(t))\\ &\quad\le \frac{d_1^M d_2^M\left(d_1^M + d_2^M\right)\max_{i=1,2}\{|C_i^m|, |C_i^M|\}}{\left(\min\{d_1^m, d_2^m\}\right)^2}V(Y(t)) := K_1V(Y(t)),\end{aligned} \tag{3.5}$$

$$\begin{aligned}&g^2(t,Y(t))V''(Y(t))\\ &\quad= \frac{d_1^2(t)d_2^2(t)\sigma^2(t)}{(d_1Y(t) + d_2(1-Y(t)))^2}\cdot\left(\frac{(1-Y(t))^2}{Y(t)} + \frac{Y^2(t)}{1-Y(t)}\right)\\ &\quad\le \frac{(d_1^M d_2^M)^2\sigma_M^2}{\left(\min\{d_1^m, d_2^m\}\right)^2}V(Y(t)) := K_2V(Y(t)).\end{aligned} \tag{3.6}$$

Inserting (3.6) and (3.6) into (3.2) results in

$$\mathrm{d}V(Y(t)) = KV(Y(t))\mathrm{d}t + g(t,Y(t))V'(Y(t))\mathrm{d}W(t), \quad K = \max\{K_1, K_2\}. \tag{3.7}$$

Now in order to show $\tau_\infty = \infty$ a.s., suppose (for contradiction) that there exist $T > 0$ and $\varepsilon > 0$ such that $\mathbb{P}(\tau_\infty \le T) > \varepsilon$. Consequently, due to Egorov's theorem, there exists $N \ge k_0$ such that

$$\mathbb{P}(\tau_k \le T) > \frac{\varepsilon}{2} \quad \text{for all } k \ge N. \tag{3.8}$$

Then it follows from (3.7) that

$$V(Y(\tau_k \wedge T)) \le V(Y(t_0)) + \int_{t_0}^{\tau_k\wedge T} KV(Y(t))\mathrm{d}t + \int_{t_0}^{\tau_k\wedge T} g(t,Y(t))V'(Y(t)\mathrm{d}W(t).$$

Taking expectations of the inequality above gives

$$\begin{aligned}\mathbb{E}[V(Y(\tau_k \wedge T))] &\le V(Y(t_0)) + \mathbb{E}\Big[\int_{t_0}^{\tau_k \wedge T} KV(Y(t))\mathrm{d}t\Big] \\ &\le V(Y(t_0)) + \int_{\Omega}\int_{t_0}^{T} \chi_{[t_0,\tau_k(\omega)\wedge T]}(t) KV(Y(t))\mathrm{d}t\mathrm{d}\mathbb{P}, \end{aligned} \tag{3.9}$$

where χ is the indicator function, Ω the sample space, and $\mathbb{P}$ the probability measure. Set

$$\begin{aligned}\Omega_1(t) &= \{\omega \in \Omega : \tau_k(\omega) < t\}, \\ \Omega_2(t) &= \{\omega \in \Omega : t \le \tau_k(\omega) \le T\}, \\ \Omega_3 &= \{\omega \in \Omega : \tau_k(\omega) > T\},\end{aligned}$$

and rearrange integrals in (3.9) to obtain

$$\begin{aligned}&\mathbb{E}[V(Y(\tau_k \wedge T))] \\ &\quad\le V(Y(t_0)) + \int_{t_0}^{T}\int_{\Omega_1(t)\cup\Omega_2(t)\cup\Omega_3} \chi_{[t_0,\tau_k(\omega)\wedge T]}(t) KV(Y(t))\mathrm{d}\mathbb{P}\mathrm{d}t \\ &\quad\le V(Y(t_0)) + \int_{t_0}^{T}\int_{\Omega_1(t)} KV(Y(\tau_k \wedge t))\mathrm{d}\mathbb{P}\mathrm{d}t + \int_{t_0}^{T}\int_{\Omega_3} \chi_{[t_0,T]}(t) KV(Y(t))\mathrm{d}\mathbb{P}\mathrm{d}t \\ &\qquad+ \int_{t_0}^{T}\int_{\Omega_2(t)} \chi_{[t_0,\tau_k(\omega)]}(t) KV(Y(t))\mathrm{d}\mathbb{P}\mathrm{d}t \\ &\quad= V(Y(t_0)) + \int_{t_0}^{T}\int_{\Omega_1(t)\cup\Omega_2(t)\cup\Omega_3} KV(Y(\tau_k \wedge t))\mathrm{d}\mathbb{P}\mathrm{d}t \\ &\quad= V(Y(t_0)) + K\int_{t_0}^{T} \mathbb{E}[V(Y(\tau_k \wedge t))]\mathrm{d}t.\end{aligned}$$

Applying Gronwall's lemma to the above inequality results in

$$\mathbb{E}[V(Y(\tau_k \wedge T))] \le V(t_0)\cdot e^{K(T-t_0)}. \tag{3.10}$$

On the other hand, due to (3.8) we have

$$\begin{aligned}\mathbb{E}[V(Y(\tau_k \wedge T))] &\ge \int_{\Omega_1(t)\cup\Omega_2(t)} V(Y(\tau_k \wedge T))\mathrm{d}\mathbb{P} \\ &= \int_{\Omega_1(t)\cup\Omega_2(t)} V(Y(\tau_k(\omega)))\mathrm{d}\mathbb{P} \ge \big(k + \frac{1}{1-\frac{1}{k}}\big)\frac{\varepsilon}{2}.\end{aligned}$$

Combining (3.10) and (1) gives

$$V(t_0)\cdot e^{K(T-t_0)} \ge \left(k + \frac{1}{1-\frac{1}{k}}\right)\frac{\varepsilon}{2}, \quad k \ge N.$$

Notice that K is independent of k; hence, the above inequality fails as $k \to \infty$. Therefore, $\tau_\infty = \infty$ a.s., and as a result $\tau_e = \infty$. The proof is complete. ∎

The above theorem ensures that given any $\omega \in \Omega$ and an initial value $y_0 \in (0,1)$, a unique solution of the SDE (3.1) exists globally in time and stays within (0, 1) a.s.

Since the SDE (3.1) is nonautonomous, solutions from differential initial values may not approach a stationary process as time goes on (see, e.g., [7, 31]). Nevertheless, they may still all converge to each other, and this implies the existence of a nonstationary limiting process that attracts all solutions as $t \to \infty$. Within the framework of nonautonomous dynamical systems, this "attracting" process is a singleton trajectory that lies in the forward set of attraction (see, e.g., [30, 31, 32]). In the ecological context, such a process can be precisely described by the new concept of AEDT, i.e., asymptotically environmentally determined trajectory, developed in [9]. In particular, for the lottery model in the nonstationary context, AEDT was first proposed in [9], and later the forward convergence on the AEDT was established and bounded by a nonstationary Beverton–Holt process in [10]. In Theorem 3.3 below, we construct sufficient conditions under which all solutions of (3.1) converge in mean; i.e., given any $t_0 \geq 0$, $\omega \in \Omega$, and $y_1, y_2 \in (0,1)$, the solutions of (3.1) with initial conditions $Y(t_0) = y_1$ and $Y(t_0) = y_2$ satisfy

$$\lim_{t\to\infty} \int_\Omega |Y(t; t_0, y_1, \omega) - Y(t; t_0, y_2, \omega)| \, \mathrm{d}\omega = 0. \tag{3.11}$$

In addition to Assumption (A1) above, one or more of the following assumptions will be needed:

(A2) $d_1^M \sigma_M^2 - \sigma_m^2 < 2\mu^m + 2\theta_1^m$.
(A3) $\sigma_M^2 - d_2^m \sigma_m^2 \leq 2\mu^m - 2\theta_2^M$.
(A4) $\left(\frac{d_2^M}{2d_1^m} + d_1^M\right)\sigma_M^2 - \frac{3}{2}\sigma_m^2 < -\left(\frac{d_2^M}{d_1^m} + 1\right)\mu^M + 2\mu^m - \frac{d_2^M}{d_1^m}\theta_1^M + 2\theta_1^m + \theta_2^m$.
(A5) $d_2^M \sigma_M^2 - d_1^m \sigma_m^2 \leq -2(d_1^m + d_2^M)\mu^M + 2d_1^m\theta_2^m - 2d_2^M\theta_1^M$.
(A6) $d_1^M \leq 2d_2^m$.

THEOREM 3.3. *Assume* (A1)–(A2) *hold. Then all solutions of equation* (3.1) *with different initial values converge in mean as* $t \to \infty$ *if either* (A3)–(A4) *or* (A5)–(A6) *hold.*

Proof. Due to technical difficulties encountered while analyzing dynamics of $Y(t)$ directly, we utilize the transformation [9]

$$Z(t) = Z(t; t_0, z_0) = \ln \frac{Y(t; t_0, y_0)}{1 - Y(t; t_0, y_0)}, \quad z_0 = \ln \frac{y_0}{1 - y_0}.$$

Note that this is a monotone transformation that changes the domain of state from $Y \in (0,1)$ to $Z \in (-\infty, \infty)$. Then by Itô's formula and (3.1), it can be derived that $Z(t)$ satisfies the nonautonomous SDE

$$\mathrm{d}Z(t) = \frac{F(t)Y(t) - G(t)}{\big(d_1(t)Y(t) + d_2(t)(1 - Y(t))\big)^2}\mathrm{d}t + \frac{d_1(t)d_2(t)\sigma(t)}{d_1(t)Y(t) + d_2(t)(1 - Y(t))}\mathrm{d}W(t), \tag{3.12}$$

where $C_1(t)$ and $C_2(t)$ are as defined in (2.12), $Y(t) = \frac{e^{Z(t)}}{1+e^{Z(t)}}$, and

$$F(t) = d_1^2(t)d_2(t)C_1(t) + d_1^2(t)d_2^2(t)\sigma^2(t) - d_1(t)d_2^2(t)C_2(t), \tag{3.13}$$

$$G(t) = -d_1(t)d_2^2(t)C_2(t) + \frac{1}{2}d_1^2(t)d_2^2(t)\sigma^2(t). \tag{3.14}$$

Given $z_0^1, z_0^2 \in \mathbb{R}$ with $z_0^1 > z_0^2$ and $\omega \in \Omega$, let $Z_1(t) = Z(t; t_0, z_0^1, \omega)$ and $Z_2(t) = Z(t; t_0, z_0^2, \omega)$ be two solutions of the SDE (3.12) with initial values $Z(t_0) = z_0^1$ and

$Z(t_0) = z_0^2$, respectively. Denote by $\Delta_Z(t) = Z_1(t) - Z_2(t)$; then Δ_Z satisfies the SDE

$$\mathrm{d}\Delta_Z(t) = \frac{F(t)H_1(t) + G(t)H_2(t)}{H_3^2(t)}\Delta_Y(t)\mathrm{d}t + H_4(t)\Delta_Y(t)\mathrm{d}W(t), \tag{3.15}$$

where $Y_i = Y_i(t) = \frac{e^{Z_i(t)}}{1+e^{Z_i(t)}}$ for $i = 1, 2$, $\Delta_Y(t) = Y_1(t) - Y_2(t)$, and

$$\begin{aligned}
H_1(t) &= -\big(d_1(t) - d_2(t)\big)^2 Y_1 Y_2 + d_2^2(t),\\
H_2(t) &= \big(d_1(t) - d_2(t)\big)^2 (Y_1 + Y_2) + 2(d_1(t) - d_2(t))d_2(t),\\
H_3(t) &= \big(d_1(t)Y_1 + d_2(t)(1 - Y_1)\big)\big(d_1(t)Y_2 + d_2(t)(1 - Y_2)\big),\\
H_4(t) &= \frac{d_1(t)d_2(t)\sigma(t)(d_2(t) - d_1(t))}{H_3(t)}.
\end{aligned}$$

Next, integrating the SDE (3.15) gives

$$\Delta_Z(t) = z_0^1 - z_0^2 + \int_{t_0}^t \frac{F(s)H_1(s) + G(s)H_2(s)}{H_3^2(s)}\Delta_Y(s)\mathrm{d}s + \int_{t_0}^t H_4(s)\Delta_Y(s)\mathrm{d}W(s). \tag{3.16}$$

Terms within the numerator on the integrand of the first integral in (3.16) can be simplified to be

$$\begin{aligned}
F(s)H_1(s) &= d_1(s)d_2(s)\big(d_1(s)C_1(s) + d_1(s)d_2(s)\sigma^2(s) - d_2(s)C_2(s)\big)\\
&\quad \cdot \Big(d_2^2(s) - \big(d_1(s) - d_2(s)\big)^2 Y_1 Y_2\Big),\\
G(s)H_2(s) &= \frac{1}{2}d_1(s)d_2^2(s)\left(-2C_2(s) + d_1(s)\sigma^2(s)\right)\\
&\quad \cdot \left((d_1(s) - d_2(s))^2(Y_1 + Y_2) + 2(d_1(s) - d_2(s))d_2(s)\right),
\end{aligned}$$

which, after being rearranged, give

$$\begin{aligned}
&F(s)H_1(s) + G(s)H_2(s)\\
&= d_1(s)d_2^2(s)\left(-2C_2(s) + d_1(s)\sigma^2(s)\right)(d_1(s) - d_2(s))^2\left(\frac{Y_1 + Y_2}{2} - Y_1 Y_2\right)\\
&\quad + d_1(s)d_2^3(s)\left(d_1C_1 + d_2C_2\right) + d_1^2(s)d_2^3(s)\left(-2C_2(s) + d_1(s)\sigma^2(s)\right)\\
&\quad - d_1(s)d_2(s)\left(d_1C_1 + d_2C_2\right)\big(d_1(s) - d_2(s)\big)^2 Y_1 Y_2.
\end{aligned} \tag{3.17}$$

Inserting (3.17) into and (3.16) then taking expectation of the resulting equation results in

$$\mathbb{E}[\Delta_Z(t)] = z_0^1 - z_0^2 + \mathbb{E}\left[\int_{t_0}^t \frac{C_3(s) + C_4(s)}{H_3^2(s)}\Delta_Y(s)\mathrm{d}s\right], \tag{3.18}$$

where

$$\begin{aligned}
C_3(s) &= d_1(s)d_2^2(s)\left(-2C_2(s) + d_1(s)\sigma^2(s)\right)(d_1(s) - d_2(s))^2\left(\frac{Y_1 + Y_2}{2} - Y_1 Y_2\right),\\
C_4(s) &= d_1(s)d_2^3(s)\left(d_1(s)C_1(s) + d_2(s)C_2(s)\right) + d_1^2(s)d_2^3(s)\left(-2C_2(s) + d_1(s)\sigma^2(s)\right)\\
&\quad - d_1(s)d_2(s)(d_1(s) - d_2(s))^2(d_1(s)C_1(s) + d_2(s)C_2(s))Y_1 Y_2.
\end{aligned}$$

Notice that under Assumptions (A1) and (A2),

$$-2C_2(s)+d_1(s)\sigma^2(s)\le -2\mu^m-2\theta_1^m-\sigma_m^2+d_1^M\sigma_M^2:=K_3<0. \tag{3.19}$$

Also, since $d_i(t)>0$ for $i=1,2$ and $Y_1,Y_2\le 1$, then $\frac{Y_1+Y_2}{2}-Y_1Y_2\ge 0$, and thus

$$C_3(s)\le 0. \tag{3.20}$$

We next estimate $C_4(s)$ under two scenarios, where $d_1(s)C_1(s)+d_2(s)C_2(s)$ is positive or negative, respectively. In fact, $d_1(s)C_1(s)+d_2(s)C_2(s)>0$ under Assumption (A3), and $d_1(s)C_1(s)+d_2(s)C_2(s)<0$ under Assumption (A5).

(i) Note the inequality (3.19) implies that $C_2(s)>\frac{d_1(s)\sigma^2(s)}{2}$. Thus, by Assumptions (A1) and (A3) and (3.3)–(3.4),

$$\begin{aligned} d_1(s)C_1(s)+d_2(s)C_2(s)&>d_1(s)\left(C_1(s)+d_2(s)\frac{\sigma^2(s)}{2}\right)\\ &\ge \frac{d_1(s)}{2}\left(2\mu^m-2\theta_2^M-\sigma_M^2+d_2^m\sigma_m^2\right)\ge 0, \end{aligned}$$

and consequently, due to $Y_1,Y_2\ge 0$, (3.3)–(3.4), and Assumptions (A1) and (A4), we have

$$\begin{aligned} C_4(s)&\le d_1^2(s)d_2^3(s)\left(C_1(s)+\frac{d_2(s)}{d_1(s)}C_2(s)-2C_2(s)+d_1(s)\sigma^2(s)\right)\\ &\le (d_1^m)^2(d_2^m)^3\left(C_1^M+\frac{d_2^M}{d_1^m}C_2^M-2C_2^m+d_1^M\sigma_M^2\right):=K_4<0. \end{aligned} \tag{3.21}$$

(ii) Since $C_2(s)\ge 0$, then by Assumption (A5) and (3.3)–(3.4), we have

$$\begin{aligned} &d_1(s)C_1(s)+d_2(s)C_2(s)\\ &\quad\le d_1(s)\left(C_1^M+\frac{d_2^M}{d_1^m}C_2^M\right) \end{aligned} \tag{3.22}$$

$$= d_1(s)\left(\mu^M-\theta_2^m-\frac{1}{2}\sigma_m^2+\frac{d_2^M}{d_1^m}\left(\mu^M+\theta_1^M+\frac{1}{2}\sigma_M^2\right)\right)\le 0, \tag{3.23}$$

and consequently, from $Y_1,Y_2\le 1$, it follows that

$$\begin{aligned} C_4(s)\le\ & d_1^2(s)d_2(s)\left(d_1(s)C_1(s)+d_2(s)C_2(s)\right)\left(-d_1(s)+2d_2(s)\right)\\ &+d_1^2(s)d_2^3(s)\left(-2C_2(s)+d_1(s)\sigma^2(s)\right). \end{aligned} \tag{3.24}$$

Assumptions (A1) and (A6) ensure that

$$-d_1(s)+2d_2(s)\ge -d_1^M+2d_2^m\ge 0,$$

and therefore (3.24) along with (3.19) imply that

$$C_4(s)\le d_1^2(s)d_2^3(s)\left(-2C_2(s)+d_1(s)\sigma^2(s)\right)\le (d_1^m)^2(d_2^m)^3K_3<0.$$

Without loss of generality, assume that $z_0^1-z_0^2>0$. Then by the uniqueness of solutions, $\Delta_Z(t)=\Delta_Z(t;t_0,z_0^1-z_0^2,\omega)\ge 0$ for all $t\ge t_0$ and any $\omega\in\Omega$, and

hence $\Delta_Y = \Delta_Y(t; t_0, y_0^1 - y_0^2, \omega) \geq 0$ for all $t \geq t_0$ and any $\omega \in \Omega$. Noting that $H_3(t) \leq (d_1^M + d_2^M)^2$ and inserting (3.20) and (3.21) into (3.18) results in

$$\mathbb{E}[\Delta_Z(t)] \leq z_0^1 - z_0^2 + \frac{K_4}{(d_1^M + d_2^M)^4} \mathbb{E}\left[\int_{t_0}^t \Delta_Y(s) \mathrm{d}s\right]. \tag{3.25}$$

Similarly, inserting (3.20) and (3.24) into (3.18) results in

$$\mathbb{E}[\Delta_Z(t)] \leq z_0^1 - z_0^2 + \frac{(d_1^m)^2 (d_2^m)^3 K_3}{(d_1^M + d_2^M)^4} \mathbb{E}\left[\int_{t_0}^t \Delta_Y(s) \mathrm{d}s\right]. \tag{3.26}$$

On the other hand, due to the mean value theorem, there exists some $y \in (0, 1)$ such that

$$\mathbb{E}[\Delta_Z(t)] = \mathbb{E}\left[\left(\frac{1}{y} + \frac{1}{1-y}\right) \Delta_Y(t)\right] \geq 4\mathbb{E}[\Delta_Y(t)].$$

The above inequality along with (3.25)–(3.26) and the Fubini theorem give

$$\mathbb{E}[\Delta_Y(t)] \leq \frac{z_0^1 - z_0^2}{4} + \frac{\alpha}{4} \int_{t_0}^t \mathbb{E}[\Delta_Y(s)] \mathrm{d}s \text{ with } \alpha := \frac{\max\left\{K_4, (d_1^m)^2 (d_2^m)^3 K_3\right\}}{(d_1^M + d_2^M)^4} < 0.$$

Finally, it follows immediately from Gronwall's lemma that

$$\mathbb{E}[\Delta_Y(t)] \leq \frac{z_0^1 - z_0^2}{4} e^{\frac{\alpha}{4}(t - t_0)} \to 0, \text{ as } t \to \infty,$$

which implies that all solutions with different initial values converge in $\mathcal{L}^1(\Omega)$ sense. The proof is complete. ∎

The conditions constructed in the theorem above are sufficient but not necessary. They consist of only the upper and lower bounds of the moments of the nonstationary parameters. The corollary below provides a set of time-dependent assumptions, which are weaker and guaranteed by the assumptions in Theorem 3.3. In addition to Assumption (A1) above, one or more of the following assumptions will be needed:

- (B2) There exists $\epsilon > 0$ such that $\big(1 - d_1(t)\big)\sigma^2(t) + 2\mu(t) + 2\theta_1(t) \geq \epsilon$ for $t \in [t_0, T]$.
- (B3) $\big(1 - d_2(t)\big)\sigma^2(t) \leq 2\mu(t) - 2\theta_2(t)$ for $t \in [t_0, T]$.
- (B4) There exists $\epsilon > 0$ such that for $t \in [t_0, T]$, $(d_1(t) - d_2(t))\mu(t) + (2d_1(t) - d_2(t))\theta_1(t) + d_1(t)\theta_2(t) + (\frac{3}{2}d_1(t) - d_1^2(t) - \frac{1}{2}d_2(t))\sigma^2(t) \geq \epsilon$.
- (B5) $(d_2(t) - d_1(t))\sigma^2(t) \leq -2(d_1(t) + d_2(t))\mu(t) + 2(d_1(t)\theta_2(t) - d_2(t)\theta_1(t))$ for $t \in [t_0, T]$.
- (B6) $d_1(t) \leq 2d_2(t)$ for $t \in [t_0, T]$.

Corollary 3.4. *Assume* (A1) *and* (B2) *hold. Then all solutions of equation* (3.1) *with different initial values converge in mean as* $t \to \infty$ *if either* (B3)–(B4) *or* (B5)–(B6) *hold.*

Proof. Note that Assumption (B3) implies $d_1(t)C_1(t) + d_2(t)C_2(t) \geq 0$, and Assumptions (B2) and (B5) together imply that $d_1(t)C_1(t) + d_2(t)C_2(t) \leq 0$. Also, Assumptions (B2) and (B4) ensure, respectively,

$$\begin{aligned} -2C_2(t) + d_1(t)\sigma^2(t) &\leq -\epsilon < 0, \\ d_1(t)C_1(t) + d_2(t)C_2(t) - 2d_1(t)C_2(t) + d_1^2(t)\sigma^2(t) &\leq -\epsilon < 0. \end{aligned}$$

The assertions then follow from arguments similar to the proof of Theorem 3.3. ∎

Remark 3.5. For the special case when the environment is stationary, i.e., $\sigma, d_i, \mu, \theta_i$ are all constant, Assumptions (A2) and (B2) both reduce to $(1-d_1)\sigma^2 > -2(\mu+\theta_1)$, and Assumptions (A3) and (B3) both reduce to $(1-d_2)\sigma^2 \le -2\mu+2\theta_2$. These recover the conditions for the existence of stationary distributions obtained in [26, 27]. The extra conditions (A4) and (A6), (B4) and (B6) are because of the nonstationary character of the problem, as well as to compensate the discussions based on $d_i \ge 1$ or $d_i \le 1$ in [26, 27] that are not required here.

Theorem 3.3 and Corollary 3.4 imply the existence of a time-dependent limiting process for the nonautonomous SDE (3.1) as $t \to \infty$, which can be regarded as a counterpart of the stationary distribution for autonomous SDEs. For the autonomous lottery diffusion model, the existence of such a stationary distribution means that two species coexist in the sense of stochastic boundedness, i.e., $\Pr(\lim_{t\to\infty} Y(t) = 1) = \Pr(\lim_{t\to\infty} Y(t) = 0) = 0$ [27]. However, for the nonautonomous diffusion model (3.1), while the results in Theorem 3.3 and Corollary 3.4 ensure that all solutions converge together as $t \to \infty$, they do not preclude them from approaching the boundaries $Y = 0$ and $Y = 1$ as $t \to \infty$ and hence do not sufficiently justify the coexistence of the two species. In the theorem below, we further establish conditions for coexistence in the sense of stochastic persistence of $Y(t)$.

THEOREM 3.6. *Let Assumptions* (A1), (A2), *and* (A5) *hold. In addition, assume that*

(A7) $d_2(t) \le d_1(t) \le 2d_2(t)$ for all $t \ge t_0$.

Then there exists a deterministic function $Y^*(t) \in [Y_m^*, Y_M^*]$ *for all* $t \ge t_0$ *with* $Y_m^* > 0$ *and* $Y_M^* < 1$ *such that*

$$\limsup_{t\to\infty} \big(Y(t) - Y^*(t)\big) \ge 0, \quad \liminf_{t\to\infty} \big(Y(t) - Y^*(t)\big) \le 0, \quad a.s.$$

Proof. Let $Z(Y(t)) = \ln \frac{Y(t)}{1-Y(t)}$. Then from the proof of Theorem (3.3), $Z(t)$ satisfies the SDE

$$\mathrm{d}Z(t) = U(Y(t),t)\mathrm{d}t + \frac{d_1(t)d_2(t)\sigma(t)}{d_1(t)Y(t) + d_2(t)(1-Y(t))}\mathrm{d}W(t), \quad \text{with} \tag{3.27}$$

$$U(Y(t),t) := \frac{F(t)Y(t) - G(t)}{\big(d_1(t)Y(t) + d_2(t)(1-Y(t))\big)^2}, \tag{3.28}$$

where $F(t)$ and $G(t)$ are defined by (3.13)–(3.14).

First notice that by Assumptions (A1) and (A2), the inequality (3.19) still holds, and thus

$$G(t) \le \frac{1}{2} d_1^m (d_2^m)^2 \left(-2\mu^m - 2\theta_1^m - \sigma_m^2 + d_1^M \sigma_M^2\right) := G^M < 0 \quad \forall\, t \ge t_0. \tag{3.29}$$

On the other side, by Assumption (A1) and (3.29), we have

$$0 > G(t) \ge \frac{1}{2} d_1^M (d_2^M)^2 \left(-2\mu^M - 2\theta_1^M - \sigma_M^2 + d_1^m \sigma_m^2\right) := G^m \quad \forall\, t \ge t_0. \tag{3.30}$$

The inequalities (3.29) and (3.19) together with Assumption (A5) imply that

$$C_3(t) := d_1(t)C_1(t) + \frac{1}{2} d_1(t)d_2(t)\sigma^2(t) < d_1(t)C_1(t) + d_2(t)C_2(t) \le 0 \quad \forall\, t \ge t_0.$$

Therefore, by (3.30) and reusing (3.23), we obtain

$$d_1^M d_2^M C_3^m + G^m < d_1(t)d_2(t)C_3(t) + G(t) = F(t) < 0 \quad \forall t \geq t_0, \tag{3.31}$$

where $C_3^m = d_1^M \left(\mu^m - \theta_2^M - \frac{\sigma_M^2}{2}\right) + \frac{1}{2} d_1^m d_2^m \sigma_m^2$.

It follows immediately from (3.29) and (3.31) that $U(Y(t), t) = 0$ always has a positive root $Y^*(t) = G(t)/F(t)$. Moreover, due to (3.29) and (3.31),

$$Y^*(t) \geq \frac{G^M}{d_1^M d_2^M C_3^m + G_m} := Y_m^* > 0 \quad \forall\, t \geq t_0. \tag{3.32}$$

In addition, using that $C_3(t) \leq d_1^m(\mu^M - \theta_2^m - \frac{\sigma_m^2}{2}) + \frac{1}{2} d_1^M d_2^M \sigma_M^2 := C_3^M < 0$ and noticing that $Y^*(t)$ is a decreasing function with respect to G, we get

$$Y^*(t) \leq \frac{G^m}{d_1^m d_2^m C_3^M + G^m} := Y_M^* < 1 \quad \forall\, t \geq t_0. \tag{3.33}$$

We next show that $\limsup_{t\to\infty} \big(Y(t) - Y^*(t)\big) \geq 0$ a.s. To that end, assume for contradiction that it does not hold. Then there exists $\varepsilon \in (0,1)$ sufficiently small such that

$$\mathbb{P}[\Omega_4(t)] > \frac{1}{2}\varepsilon \quad \text{for} \quad \Omega_4(t) = \left\{\omega : \limsup_{t\to\infty} \big(Y(t,\omega) - Y^*(t)\big) \leq -\varepsilon\right\}.$$

Thus, for every $\omega \in \Omega_4(t)$, there exists $T_1(\omega, \varepsilon)$ such that

$$Y(t,\omega) - Y^*(t) \leq -\frac{1}{2}\varepsilon, \quad \forall\ t \geq T_1(\omega, \varepsilon). \tag{3.34}$$

Notice that due to (3.29) and (3.31), the function U defined in (3.28) satisfies $U(Y = 0, t) > 0$ and $U(Y = 1, t) < 0$ for all $t \geq t_0$. Moreover, under Assumption (A7),

$$\begin{aligned}\frac{\partial U}{\partial Y} &= \frac{-F(t)d_1(t)Y(t) + F(t)d_2(t)Y(t) + 2G(t)d_1(t) + F(t)d_2(t) - 2G(t)d_2(t)}{\big(d_1(t)Y(t) + d_2(t)(1 - Y(t))\big)^3} \\ &= \frac{F(t)Y(t)(2d_2(t) - d_1(t)) + F(t)d_2(t)(1 - Y(t)) + 2G(t)(d_1(t) - d_2(t))}{\big(d_1(t)Y(t) + d_2(t)(1 - Y(t))\big)^3} < 0,\end{aligned}$$

which implies that $U(Y, t)$ is decreasing with respect to Y for any $Y \in (0,1)$ and $t \geq t_0$. This together with (3.34) give

$$U(Y(t,\omega), t) \geq U\left(Y^*(t) - \frac{1}{2}\varepsilon, t\right) > U(Y^*(t)) = 0 \quad \forall\ t \geq T_1(\omega, \varepsilon). \tag{3.35}$$

Inserting (3.35) into (3.27), we have

$$\begin{aligned}Z(Y(t,\omega)) \geq Z(y_0) &+ \int_{t_0}^{T_1(\omega,\varepsilon)} U(Y(s), s)\mathrm{d}s + U\left(Y^*(t) - \frac{1}{2}\varepsilon, t\right)(t - T_1(\omega, \varepsilon)) \\ &+ \int_{t_0}^{t} \frac{d_1(s)d_2(s)\sigma(s)}{d_1(s)Y(s) + d_2(s)(1 - Y(s))}\mathrm{d}W(s,\omega) \quad \forall\ t \geq T_1(\omega, \varepsilon).\end{aligned}$$

Then by the large number theorem of martingales, there exists $\Omega_5 \in \Omega$ with $\mathbb{P}[\Omega_5] = 1$ such that

$$\liminf_{t\to\infty} \frac{1}{t} Z(Y(t,\omega)) \geq U\left(Y^*(t) - \frac{1}{2}\varepsilon, t\right) > 0, \quad \omega \in \Omega_4(t) \cap \Omega_5,\ t \geq T_1(\omega, \varepsilon).$$

This yields $\lim_{t\to\infty} Z(Y(t,\omega)) = \infty$, i.e., $\lim_{t\to\infty} Y(t,\omega) = 1$, which contracts (3.33) and (3.34). Therefore, $\limsup_{t\to\infty} \big(Y(t) - Y^*(t)\big) \geq 0$ a.s.

To prove that $\liminf_{t\to\infty} \big(Y(t) - Y^*(t)\big) \leq 0$ a.s., we again assume for contradiction that it does not hold. Then there exists $\varepsilon \in (0,1)$ sufficiently small such that

$$\mathbb{P}[\Omega_6(t)] > \frac{1}{2}\varepsilon \quad \text{for} \quad \Omega_6(t) = \Big\{\omega : \liminf_{t\to\infty} \big(Y(t,\omega) - Y^*(t)\big) \geq \varepsilon\Big\}.$$

Thus, for every $\omega \in \Omega_6(t)$, there exists $T_2(\omega,\varepsilon)$ such that

$$Y(t,\omega) - Y^*(t) \geq \frac{1}{2}\varepsilon \quad \forall\, t \geq T_2(\omega,\varepsilon). \tag{3.36}$$

Following similar analysis as above, we obtain that $\lim_{t\to\infty} Z(Y(t,\omega)) = -\infty$, i.e., $\lim_{t\to\infty} Y(t,\omega) = 0$, which contracts (3.32) and (3.36). Therefore, $\liminf_{t\to\infty} \big(Y(t) - Y^*(t)\big) \leq 0$ a.s. The proof is complete. ∎

Conclusions of the above theorem imply that given any $y_0 \in (0,1)$, the solution of the nonautonomous SDE (3.1) will rise to or above the level $Y^*(t)$ infinitely often with probability 1. When $Y^*(t)$ is a constant, this means stochastic persistence (see, e.g., [2, 3, 4, 6, 25, 28]), and the species coexist in the sense of stochastic persistence. This concept of coexistence can be naturally generalized to the case with $Y^*(t)$ time-dependent here because $0 < Y_m^* \leq Y^*(t) \leq Y_M^* < 1$. More precisely, $Y(t)$ will oscillate infinitely often about the time-dependent trajectory $Y^*(t)$, which is away from both boundaries, and hence the two species also coexist in the sense of stochastic persistence.

Notice that Assumption (A7) of Theorem 3.6 ensures Assumption (A6) of Theorem 3.3. Thus, under the assumptions of Theorem 3.6, there also exists a limiting process that attracts all solutions as $t \to \infty$. The additional requirement of $d_1(t) \geq d_2(t)$ in Theorem 3.6 essentially puts a balance between the death rates of two species and thus promotes their coexistence. It is worth mentioning that for the special nonstationary case when the SDE (3.1) is periodic, i.e., $\sigma(t)$, $d_i(t)$, $\mu(t)$, and $\theta_i(t)$ are periodic functions with the same period, conditions weaker than those in Theorem 3.6 for the coexistence may be obtained by utilizing the method of Lyapunov exponents [2].

4. Fokker–Planck equation for the lottery model. In the previous section the existence of a unique global solution to the SDE governed by the lottery model is established, and long-term dynamics of the solution is analyzed. More precisely, pathwise dynamics of the state, i.e., fraction of sites occupied by each species, is investigated. This section is devoted to the probabilistic behavior of the state. In particular, we first present the Fokker–Planck equation on the transition probability density of the diffusion processes derived in section 2 and then prove the existence and uniqueness of solutions.

Consider the diffusion process $Y(t)$ determined by the drift and diffusion coefficients f and g defined in (2.10) and (2.11). For any $(s,x) \in \mathbb{R} \times (0,1)$ and $(t,y) \in (s,\infty) \times (0,1)$, let $P(t,y|s,x) = \mathbb{P}[Y(t) \leq y | Y(s) = x]$ be the transition probability, and let $p(t,y|s,x)$ be the corresponding transition probability density. Then it follows from standard arguments (see, e.g., [23, 24]) that $p(t,y|s,x)$ satisfies the Fokker–Planck equation

$$\frac{\partial}{\partial t} p(t,y|s,x) = -\frac{\partial}{\partial y}(f(t,y)p(t,y|s,x)) + \frac{1}{2}\frac{\partial^2}{\partial^2 y}\left(g^2(t,y)p(t,y|s,x)\right), \tag{4.1}$$

with the initial condition $p(s,y|s,x) = \delta(y-x)$, where δ is the Dirac function.

Remark 4.1. Recall that $Y(t)$ is the diffusion approximation for fraction of space occupied by the first species and that 0 and 1 are invariant for Y; i.e., if $Y(\tau) = 0$ or $Y(\tau) = 1$ for some $\tau > t_0$, then it is impossible for $Y(t)$ to achieve any other value in $(0, 1)$ for $t > \tau$. This implies that we have an absorbing barrier problem [22].

From (4.1) we can formulate the Fokker–Planck equation corresponding to the SDE (3.1) as

(4.2)
$$\frac{\partial}{\partial t}p(t, y|t_0, y_0) = -\frac{\partial}{\partial y}\big(f(t, y)p(t, y|t_0, y_0)\big)+\frac{1}{2}\frac{\partial^2}{\partial^2 y}\big(g^2(t, y)p(t, y|t_0, y_0)\big) \text{ in } (0, \infty)\times(0, 1)$$

with boundary and initial conditions

(4.3)
$$p(t, 0|t_0, y_0) = p(t, 1|t_0, y_0) = 0 \text{ for } t > t_0, \qquad p(t_0, y|t_0, y_0) = \delta(y - y_0) \text{ for } y \in (0, 1).$$

The goal of this section is to prove the existence and uniqueness of solutions for the above PDE system (4.2)–(4.3).

Notice that (4.2) is a degenerate parabolic equation because $g(t, 0) = g(t, 1) = 0$, and classical existence theorems on nondegenerate parabolic problems do not apply here. To overcome the technical difficulties resulting from the degeneracy of (4.2), similar to section 3, we consider the following transformation:

$$Z(t) = \ln \frac{Y(t)}{1 - Y(t)}, \quad t \geq t_0.$$

Let $Q(t, z|s, x) = \mathbb{P}[Z(t) \leq z|Z(s) = x]$ be the transition probability of the process $Z(t)$, and let $q(t, z|s, x)$ be the corresponding transition probability density of $Z(t)$. Since Z is strictly increasing with respect to Y and given any $y_0 \in (0, 1)$,

$$\begin{aligned} P(t, y|t_0, y_0) &= \mathbb{P}[Y(t) \leq y|Y(t_0) = y_0] \\ &= \mathbb{P}\left[Z(t) \leq \ln \frac{y}{1 - y}\Big|Z(t_0) = z_0\right] = Q\left(t, \ln \frac{y}{1 - y}\Big|t_0, \ln \frac{y_0}{1 - y_0}\right). \end{aligned}$$

Differentiating both sides of the above equations gives the following relation between the transition probability densities of $Z(t)$ and $Y(t)$:

$$p(t, y|t_0, y_0) = q\left(t, \ln \frac{y}{1 - y}\Big|t_0, \ln \frac{y_0}{1 - y_0}\right) \frac{1}{y(1 - y)}. \tag{4.4}$$

Indeed, if $q(t, z|t_0, z_0)$ is a transition probability density, then

$$\begin{aligned} \int_0^1 p(t, y|t_0, u_0)\mathrm{d}y &= \int_0^1 q\Big(t, \ln \frac{y}{1 - y}\big|t_0, \ln \frac{y_0}{1 - y_0}\Big) \frac{1}{y(1 - y)}\mathrm{d}y \\ &= \int_0^1 q\Big(t, \ln \frac{y}{1 - y}\big|t_0, \ln \frac{y_0}{1 - y_0}\Big)\ \mathrm{d}\big(\ln \frac{y}{1 - y}\big) \\ &= \int_0^1 q\Big(t, z|t_0, \ln \frac{y_0}{1 - y_0}\Big)\mathrm{d}z = 1. \end{aligned}$$

Therefore, it suffices to prove the existence of solutions for the equation satisfied by $q(t, z|t_0, z_0)$ on $\mathbb{R}^2$. Recall that $Z(t)$ satisfies the SDE (3.12), which is equivalent to

$$\mathrm{d}Z(t) = \tilde{f}(t, Z)\mathrm{d}t + \tilde{g}(t, Z)\mathrm{d}W(t)$$

with

$$\tilde{f}(t,z)=\frac{d_1(t)d_2(t)\,(1+e^z)}{(d_1(t)e^z+d_2(t))^2}\Big(e^z d_1(t)C_1(t)+d_2(t)C_2(t)+\frac{1}{2}d_1(t)d_2(t)\sigma^2(t)\,(e^z-1)\Big),$$
$$\tilde{g}(t,z)=\frac{d_1(t)d_2(t)(1+e^z)\sigma(t)}{d_1(t)e^z+d_2(t)}.$$

It follows from (4.1) that the transition probability density $q(t,z|t_0,z_0)$ for the diffusion process $Z(t)$ follows the Fokker–Planck equation

(4.5)
$$\frac{\partial}{\partial t}q(t,z|t_0,z_0)=-\frac{\partial}{\partial z}(\tilde{f}(t,z)q(t,z|t_0,z_0))+\frac{1}{2}\frac{\partial^2}{\partial^2 z}(\tilde{g}^2(t,z)q(t,z|t_0,z_0)) \text{ in } (0,\infty)\times\mathbb{R},$$

with the initial condition

$$q(t_0,z|t_0,z_0)=\delta(z-z_0)\quad \text{for } z\in\mathbb{R}. \tag{4.6}$$

Note that the boundary condition in (4.3) no longer exists because the domain for the new PDE (4.5) is now the whole real line $\mathbb{R}$.

Without loss of generality, assume that $\sigma(t)>0$ for all $t\in\mathbb{R}$. Then the problem (4.5)–(4.6) is uniformly parabolic on $[0,\infty)\times\mathbb{R}$. The existence of classical solutions for (4.5)–(4.6) is ensured by the results in [21] (Theorem 11, Chapter 1) and [19] (Theorem 3), and the uniqueness of a classical solution is ensured by [5] (Theorem 9.4.3, Chapter 9). Moreover, following the proof in [5] (Theorem 6.6.2, Chapter 6), it can be shown that the unique classical solution of (4.5)–(4.6) is a probability density. These assertions along with the relation (4.4) imply the following theorem.

THEOREM 4.2. *Let Assumption* (A1) *hold. Then the problem* (4.2)–(4.3) *has a unique classical solution* $p(t,y|t_0,y_0)$. *Moreover,* $p(t,y|t_0,y_0)$ *is a probability density.*

It is worth mentioning that solutions to (4.5)–(4.6) may exist uniquely in a more general sense (see, e.g., [5], Theorem 6.6.2, Chapter 6, and [5], Theorem 9.4.3, Chapter 9). Theorem 4.2 can then be generalized to the following version.

THEOREM 4.3. *Let* $\mu(t),\sigma(t),\theta_i(t),d_i(t)$ $(i=1,2)$ *be bounded Lebesgue measurable functions on* $[t_0,\infty)$, *and assume that* $\inf_{t\ge t_0}\{\sigma(t)\}>0$. *Then the problem* (4.2)–(4.3) *has a unique solution* $p(t,y|t_0,y_0)$. *Moreover,* $p(t,y|t_0,y_0)$ *is a subprobability density with* $\int_0^1 p(t,y|t_0,y_0)\mathrm{d}y\le 1$.

Remark 4.4. In Theorem 4.3, the solution of the problem (4.2)–(4.3) exists in the sense that for every function $\varphi\in\mathcal{C}_c^\infty(0,1)$, there exists a set of full measure subset J_φ of $(0,\infty)$ such that for all $t\in J_\varphi$ we have

$$\int_0^1\varphi\cdot p(t,y|t_0,y_0)\mathrm{d}y-\int_0^1\varphi\cdot\delta(y-y_0)\mathrm{d}y=\lim_{\tau\to 0+}\int_\tau^t\int_0^1 L_{f,g}(\varphi)\cdot p(r,y|t_0,y_0)\mathrm{d}y\mathrm{d}r,$$

where $L_{f,g}(\varphi)=\frac{1}{2}g^2(t,y)\frac{\partial^2\varphi}{\partial y^2}+f(t,y)\frac{\partial\varphi}{\partial y}$ (see, e.g., [5]).

Notice that the solution in Theorem 4.3 is a subprobability density. This is due to weaker assumptions on the environment parameters. More specifically, different from Theorems 3.2 and 4.2, the environment parameters in Theorem 4.3 do not need to be continuous. Thus, in an extreme scenario with fierce environmental fluctuations, one of the species may become extinct.

5. Numerical simulations. In this section, we present numerical simulations to illustrate the theoretical results obtained in previous sections. In all simulations below, the initial time is picked to be $t_0 = 0$. In addition, we choose a set of time-dependent moment functions for the nonstationary environmental processes that satisfy the assumptions (A1), (B2), (B5), (B6), and (A7):

$$\text{(5.1)}\quad \begin{cases} \mu(t) = \frac{1+2t}{1+t} + \frac{0.5\cos e^t}{2+\cos(\sqrt{2}e^t)}, & \sigma(t) = \frac{15+20t}{1+t} + \frac{\cos e^t}{2+\cos(\sqrt{2}e^t)}, \\ d_1(t) = \frac{1+3t}{5+10t} + \frac{0.1\cos e^t}{2+\cos(\sqrt{2}e^t)}, & d_2(t) = \frac{1+t}{7+5t} + \frac{0.05\cos e^t}{2+\cos(\sqrt{2}e^t)}, \\ \theta_1(t) = \frac{0.5\cos e^t}{2+\cos(\sqrt{2}e^t)}, & \theta_2(t) = -\frac{0.25\cos e^t}{2+\cos(\sqrt{2}e^t)}. \end{cases}$$

In Figure 1 below, we present simulated solutions of the SDE (3.1) with 10 different initial values $\{y_j\}_{j=1,\dots,10}$, using one sample, $\omega \in \Omega$. It is clearly observed that all solutions converge forwardly onto a nonstationary limiting process. This nonstationary process is referred to as AEDT in [9], which describes asymptotic dynamics of $Y(t)$ solely determined by the environment but not the initial states in the context of lottery models.

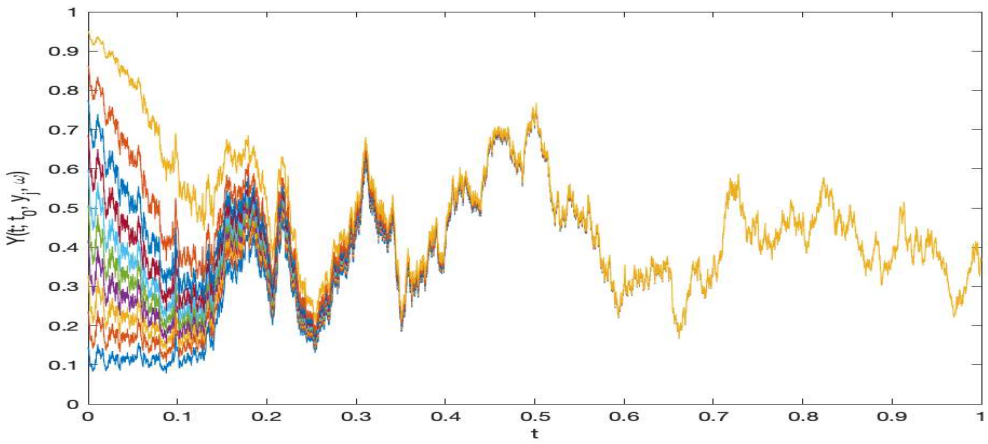


FIG. 1. *Solutions to* (3.1) *with* 10 *different initial values using the same sample* $\omega \in \Omega$.

In Figure 2 below, we plot the empirical average and variance of 100 solutions with 100 different initial values, using one sample, $\omega \in \Omega$. More precisely, given $\omega \in \Omega$ and $y_j \in (0,1)$ for $j = 1, \dots, 100$, the average of solution $\bar{Y}(t) = \frac{1}{100}\sum_{j=1}^{100} Y(t; t_0, y_j, \omega)$ is plotted on the left, and the variance $V(Y(t)) = \frac{1}{100}\sum_{j=1}^{100}\left(Y(t; t_0, y_j, \omega) - \bar{Y}(t)\right)^2$ is plotted on the right. It can be further confirmed that while the average of solutions fluctuates randomly, the variance approaches 0, which implies that all solutions converge pathwise.

Notice that the convergence shown in Figure 1 is in fact almost sure convergence, which is stronger than the convergence in mean shown in Theorem 3.3. To directly demonstrate convergence in mean, we simulate the solutions of (3.1) with two arbitrarily picked initial conditions y_1, $y_2 \in (0,1)$ and compute the mean of their difference $|Y(t; t_0, y_1, \omega_i) - Y(t; t_0, y_2, \omega_i)|$ by using 1000 difference samples $\omega_i \in \Omega$, $i = 1, \dots, 1000$. In Figure 3 below, the difference $|Y(t; t_0, y_1, \omega_i) - Y(t; t_0, y_2, \omega_i)|$ for

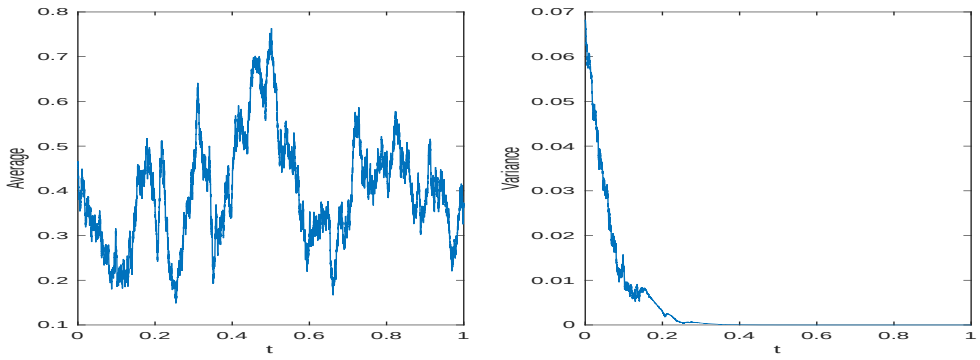


FIG. 2. *Average and variance of solutions to* (3.1) *with* 100 *different initial values using the same sample* $\omega \in \Omega$.

each $\omega_i \in \Omega$ is presented on the left, and the average of the difference

$$\frac{1}{1000}\sum_{i=1}^{1000} |Y(t;t_0,y_1,\omega_i) - Y(t;t_0,y_2,\omega_i)|$$

as an approximation of the mean difference $\mathbb{E}[|Y(t;t_0,y_1) - Y(t;t_0,y_2)|]$ is presented on the right.

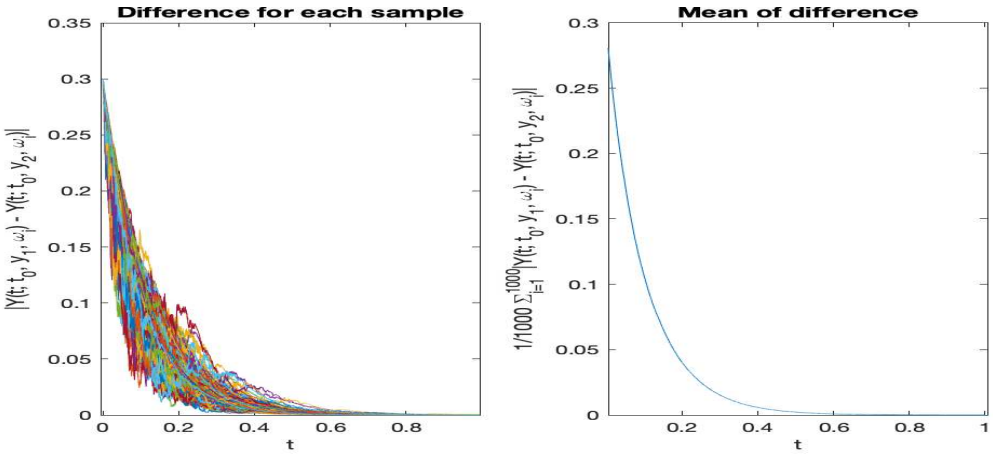


FIG. 3. *Convergence in mean of solutions of* (3.1).

To further examine the impact of environmental fluctuations on coexistence of species, we also simulate the deterministic counterpart of the SDE (3.1) for comparison purpose. To that end, let $\nu_i^h(t)$, $\xi^h(t)$ be deterministic functions instead of stochastic. Then

$$\xi^h = \mathbb{E}[\xi^h(t)] = h\mu(t) \quad \text{and} \quad \nu_i^h(t) = e^{\mathbb{E}[\ln \nu_i^h(t)]} = d_i^h(t),$$
$$\gamma_i(t) = \mathbb{E}[\gamma_i(t)] = 0, \quad i = 1, 2.$$

Applying the above relations to the difference equation (2.7), we obtain its deterministic counterpart

$$X(t+h)-X(t)=\frac{d_1^h(t)d_2^h(t)X(t)(1-X(t)\left(e^{h\mu(t)}-1\right)}{d_1^h(t)X(t)e^{h\mu(t)}+d_2^h(t)(1-X(t))}.$$

Then dividing both sides of the above equation by h and letting $h\to 0$ and using $\lim_{h\to 0} d_i^h(t)=d_i(t)$ for $i=1,2$ and $\lim_{h\to 0}\frac{e^{h\mu(t)}-1}{h}=\mu(t)$ results in the continuum deterministic lottery model

$$\frac{\mathrm{d}X(t)}{\mathrm{d}t}=\frac{d_1(t)d_2(t)X(t)(1-X(t)\mu(t)}{d_1(t)X(t)+d_2(t)(1-X(t))}. \tag{5.2}$$

Using the same set of functions $\mu(t)$, $d_1(t)$, and $d_2(t)$ as in (5.1), we simulate solutions of the ODE (5.2) with three different initial values and compare them with solutions to solutions of the SDE (3.1) with the same initial values, respectively. The trajectories are plotted in Figure 4. It is clearly observed that starting from each of the initial values, $X(t)$ eventually approaches 1 in the deterministic case; i.e., the second species eventually becomes extinct, whereas both species persist in the stochastic case. This phenomena, in fact, is consistent Chesson's coexistence theory that environmental stochasticity promotes coexistence of species (see, e.g., [14]).

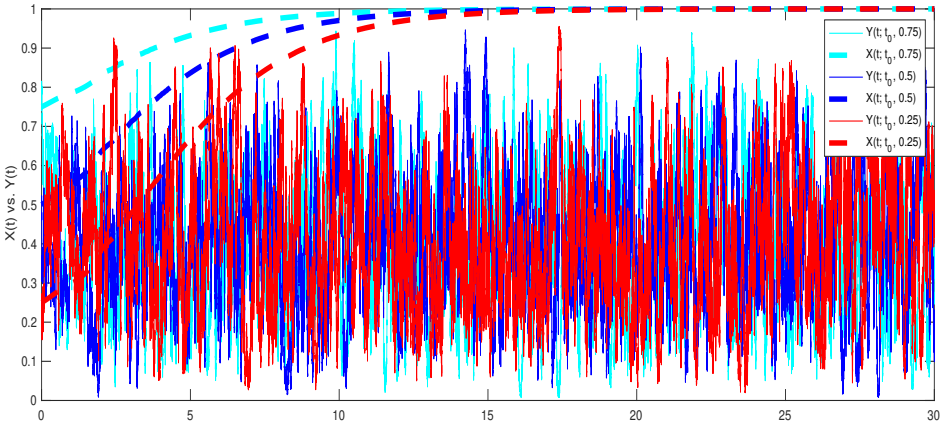
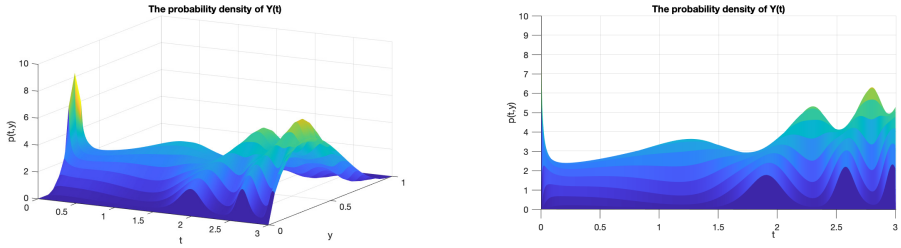


FIG. 4. *Solutions to the ODE* (5.2) *with initial values* 0.25, 0.5, 0.75 *(plotted by dashed lines) compared with solutions to the SDE* (3.1) *with the same initial values (plotted by solid lines).*

In the end, we simulate the Fokker–Planck equation (4.2) with coefficients determined by functions in (5.1). In the simulation, the initial condition $p_0(y)=\delta(y-0.3)$ is approximated by the following piecewise continuous function that peaks at $y=0.3$ and satisfies $\int_0^1 p_0(y)\mathrm{d}y=1$:

$$p_0(y)=\begin{cases}0, & 0\le y\le 0.2,\\ 22.523e^{\frac{1}{100(y-0.3)^2-1}}, & 0.2<y<0.4,\\ 0, & 0.4\le x\le 1.\end{cases}$$



(a) A three-dimensional view. (b) A two-dimensional view on p-t plane.

FIG. 5. *Numerical solutions of PDE system* (4.2)–(4.3) *with initial condition* $p_0(y)$.

The numerical solution of PDE system (4.2)–(4.3) with the initial condition $p_0(y) = \delta(y - 0.3)$ is shown in Figure 5a. A two-dimensional view from the time axis of the three-dimensional graph in Figure 5a on the p-t plane is shown in Figure 5b to better illustrate the nonstationarity of the asymptotic probability density function.

6. Closing remarks. The aim of this work is to study the time evolution of the sites occupied by ecological species governed by nonstationary lottery models from both dynamical and probabilistic perspectives. The key assumption that makes this work different from those in the literature is that environmental parameters are nonstationary stochastic processes with time-dependent moment functions. As a result, the SDE derived from diffusion approximation is nonautonomous and does not have a steady state as in autonomous systems. The solution of the resulting SDE is shown to be unique, remains in $(0, 1)$ a.s., and converges onto a time-dependent trajectory in mean under specific environmental assumptions. This trajectory can be regarded as an analog of the steady state in the nonautonomous context that characterizes long-term behavior of systems under fluctuating environments. Another technical difficulty of this work lies in the degeneracy and bounded domain of the Fokker–Planck equation governing the transition probability density for the diffusion process. This was overcome by a transformation of the state variable that changes the domain from $(0, 1)$ to $(-\infty, \infty)$ and removes the degeneracy property. This work provides rigorous evidence that nonstationary environmental fluctuations may promote coexistence of species as well as a general understanding of population fluctuations and species coexistence for the lottery model under nonstationary environments. It thus contributes to a new research field, nonstationary community theory, which seeks to extend classical results in theoretical community ecology to nonstationary environments. This field was developed in recognition that environmental fluctuations in nature do depart importantly from the stationary case and to develop the theoretical tools for understanding community dynamics under the current environmental regime of strong anthropogenically driven change.

Nonstationary environmental fluctuations provide serious scientific challenges due to the fact that repeatability relied on in science need not be maintained. Although the specific examples here concern periodic environments, it is important that the general theorems simply require bounds on moments that are otherwise unspecified smooth functions of time. Notably, asymptotically with time, the behavior of the trajectories

does not depend on the initial conditions. Thus, in the parlance of Chesson [9, 10], the system has a forward AEDT, meaning that the environmental trajectories, along with the rules for the dynamics, not arbitrary initial conditions, govern long-term behavior. Thus, conditions on the moments specifying environmental fluctuations can be expected to characterize long-term behavior. The existence of a forward AEDT in a nonstationary environment has also been established for the original discrete-time version of the lottery model [10], along with some limits on the nature of the long-term population fluctuations that arise. In the continuous-time model developed here, numerical solutions of the Fokker–Planck equations pave the way for detailed understanding of those long-term fluctuations.

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