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Research Article

Effects of a Fluctuating Carrying Capacity on the Generalized Malthus-Verhulst Model

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We consider a generalized Malthus-Verhulst model with a fluctuating carrying capacity and we study its effects on population growth. The carrying capacity fluctuations are described by a Poissonian process with an exponential correlation function. We will find an analytical expression for the average of a number of individuals and show that even in presence of a fluctuating carrying capacity the average tends asymptotically to a constant quantity.

1. Introduction

During the past decades, the phenomena induced by noise in nonlinear systems have received considerable attention [1–6]. In the ecological context we can mention resource management, new techniques for pollution and waste control, and a better understanding of biophysical processes in living organisms (see, e.g., [7, 8]). In this paper, we study the stochastic effects on the environment in a successful colonizing population. In absence of fluctuations of the environment, it is assumed that the population grows according to the generalized Malthus-Verhulst model

$$\dot{x} = \frac{r}{\mu} x \left[1 - \left(\frac{x}{K} \right)^{\mu} \right], \tag{1}$$

where the dot represents the time derivative. The factor μ^{-1} has been made explicit so as to include in (1) the Gompertz model [9] by taking the limit $\mu \to 0$.

In recent decades, several generalizations of the Malthus-Verhulst model have been applied, for example, to laser physics [10, 11], and have been widely used in literature (see [12, 13] for a large list of references). In the above references, the reader can find many applications to the processes of different species growth, such as animals that inhabit the rivers and seas of our planet, human populations, components of the central nervous system in living organisms, transmission of diseases by different types of viruses, growth of malignant tumors caused by abnormal and uncontrolled cell division, interaction of vortices in a turbulent fluid, coupled chemical reactions that occur in our upper atmosphere, interactions between galaxies, competition between different political parties, companies business, and talks between different countries. Furthermore, the generalized Malthus-Verhulst model, among other possible models, has the applications for other areas of knowledge, such as social science [14, 15], autocatalytic chemical reactions [3, 16], biological and biochemical processes, population of photons in a single mode laser [2], freezing of supercooled liquids [17], grain growth in polycrystalline materials [18], and cell growth in foam [19].

A fluctuating environment can affect the dynamics of (1) in different ways as follows.

(i) Changes in Net Growth Rate. Stochastic elements in the growth rate r can be introduced in the form $r \to r(t) = r_0 + \sigma\xi(t)$ where $\xi(t)$ represents noise, $r_0 = \langle r \rangle$, and σ is a parameter that controls the noise intensity. In [9, 20], the case where $\xi(t)$ is Gaussian white noise is studied. In [21], the authors studied the case where $\xi(t)$ is given by the Ornstein-Uhlenbeck process [22]. In [23], several cases of white non-Gaussian noise are examined. In [24], the problem of asymmetric Poissonian dichotomic noise is solved and an

exact expression for the probability density was found. Finally in [25], an extension to non-Poissonian dichotomic noise has been addressed.

(ii) Changes in the Upper Limit to Growth. In [9], in order to incorporate randomness in the carrying capacity K, the following modification has been considered:

$$\frac{1}{K} \longrightarrow \frac{1}{K(t)} = \frac{1}{K_0\left[1+\sigma\xi(t)\right]} \tag{2}$$

with K_0 the deterministic value of the carrying capacity, σ a constant parameter measuring the intensity of the noise, and $\xi(t)$ Gaussian white noise.

The authors obtained the probability density function at steady state. In [26], the authors considered only stochastic discrete populations growth models. The two aspects mentioned in the previous paragraph are considered and a large list of references is provided.

In this paper, we will study the effects of random fluctuations in the environment on a successful population. By this, we mean a population with a magnitude of the critical size order of the system. Thus, the number of individuals x and the changes produced by time dependent fluctuations can be treated as a continuous variable. In [9], the authors modeled environment fluctuations by white Gaussian noise which has zero correlation time. In this case, the process is Markovian and a Fokker-Planck equation for the probability density $p(x,t)$ can be obtained. However, this noise cannot always replace real noise, which has a finite correlation time, perhaps small, but not zero. In this case, the hypothesis of Gaussian white noise could be inadequate to describe the stochastic process.

Willing to take into account the color of the noise, we should choose a mathematically tractable colored noise [6]. Among many possible noises, two have drawn a lot of attention in the literature. The former is the Ornstein-Uhlenbeck process. Stochastic processes driven by this kind of noise have been studied, for example, in [5, 27] and, with respect to the white noise assumption, different features have been found. The latter noise is the two-step Markov process or dichotomous noise. This noise is not Gaussian but Markovian and its influence in the stochastic processes has been studied in [5, 28]. Experimental evidences of the dichotomic noise have been studied in literature [5, 29–31]. Interesting results, some of them quite similar to the former case, have been obtained in the stationary state. Few dynamical properties are known in this case [28, 32]. This type of noise has found a wide application in the construction of models [5]. Furthermore, by appropriate processes of limit, it can be demonstrated that the asymmetric dichotomic noise converges to Gaussian white noise, and it also converges to the white shot noise [33, 34].

This paper will focus mainly on the analytical evaluation of the average number of individuals $\langle x(t)\rangle$, exploiting the properties of the correlation function of the stochastic variable $\xi(t)$ without using the probability density $p(x,t)$. The analytical formula for $\langle x(t)\rangle$ will be supported by numerical simulations showing an excellent agreement with the analytical calculations.

2. Mean Value of $x(t)$

As in all stochastic processes, the evaluation of the average of the stochastic variable under study is important. In this section, we will evaluate the mean value of $x(t)$ without evaluating the probability density but with using the exponential properties of the correlation function of the stochastic variable ξ. Note that the equation for the probability density can be written utilizing the Shapiro-Loginov derivative [35]. Instead, to evaluate the mean value of $x(t)$, we will follow a different approach based on the properties of the correlation function of $\xi(t)$. In spite of the fact that, usually, the calculations performed using the correlation function are a hard task, sound analytical results can be found (see, e.g., [36]). In this section, we will show a technique that in principle can be applied to other stochastic equations. We may rewrite (1) as

$$\begin{aligned}\dot{x} &= \frac{r}{\mu}x\left[1-\left(\frac{x}{K_0}\right)^{\mu}(1+\sigma\xi)^{-\mu}\right]\\ &= \frac{r}{\mu}x\left[1-\left(\frac{x}{K_0}\right)^{\mu}\left(a^{\mu}+b^{\mu}\xi\right)\right],\end{aligned} \tag{3}$$

where for sake of compactness we set

$$a^{\mu} \equiv \frac{(1+\sigma)^{-\mu}+(1-\sigma)^{-\mu}}{2}, \qquad b^{\mu} \equiv \frac{(1+\sigma)^{-\mu}-(1-\sigma)^{-\mu}}{2} \tag{4}$$

and we considered the symmetric case $\langle\xi(t)\rangle = 0$. Performing the substitutions

$$x = \left[z+\left(\frac{a}{K_0}\right)^{\mu}\right]^{-1/\mu}, \qquad \tau = rt \tag{5}$$

we obtain

$$\frac{dz}{d\tau} = -z+\left(\frac{b}{K_0}\right)^{\mu}\xi. \tag{6}$$

The above equation can be solved via standard methods and we obtain for the variable $x(t)$ the following result:

$$\begin{aligned}x(\tau) &= \left[\left(\frac{a}{K_0}\right)^{\mu}+z_0\exp[-\tau]\right]^{-1/\mu}\\ &\quad\times\left[1+\frac{(b/K_0)^{\mu}\exp[-\tau]}{(a/K_0)^{\mu}+z_0\exp[-\tau]}\right.\\ &\quad\left.\times\int_0^t \exp\left[\tau'\right]\xi\left(\tau'\right)d\tau'\right]^{-1/\mu},\end{aligned} \tag{7}$$

where z_0 is related to the initial condition of the function $x(t)$ through the relation

$$x(0) = \left[\left(\frac{a}{K_0}\right)^{\mu}+z_0\right]^{-1/\mu}. \tag{8}$$

To make handier the above expression, let us define the following symbols:

$$\overline{x}(\tau) \equiv \frac{x(\tau)}{\left[(a/K_0)^{\mu} + z_0 \exp[-\tau]\right]^{-1/\mu}},$$
$$\beta(\tau) \equiv \frac{(b/K_0)^{\mu}}{(a/K_0)^{\mu} + z_0 \exp[-\tau]}, \tag{9}$$

and, taking the average with respect to the ξ realizations, we may write [37]

$$\begin{aligned}\langle \overline{x}(\tau)\rangle = & \sum_{n=0}^{\infty} \binom{-\frac{1}{\mu}}{n} \beta^{n}(\tau) \exp[-n\tau]\, n! \\ & \times \int_0^{\tau} d\tau_1 \int_0^{\tau_1} d\tau_2 \cdots \int_0^{\tau_{n-1}} d\tau_n \\ & \times \exp\left[\sum_{k=1}^{n} \tau_k\right] \langle \xi(\tau_1)\cdots\xi(\tau_n)\rangle\end{aligned} \tag{10}$$

with $\tau_1 > \tau_2 > \cdots \tau_n$. We focus our attention on a symmetric dichotomic noise with an exponential correlation function (Poissonian process); that is,

$$\left\langle \xi(t)\,\xi(t')\right\rangle = \exp\left(-\gamma\left|t - t'\right|\right). \tag{11}$$

Exploiting the factorizing of the correlation functions [37, 38], after long but straightforward algebra, we obtain

$$\begin{aligned}\langle \overline{x}(\tau)\rangle = & \sum_{n=0}^{\infty} \binom{-\frac{1}{\mu}}{2n} \beta^{2n}(\tau)(2n)! \exp[-2n\tau] \\ & \times \int_0^{\tau} d\tau_1 \cdots \int_0^{\tau_{2n-1}} d\tau_{2n} \\ & \times \exp[\gamma_-\tau_1]\exp[\gamma_+\tau_2]\cdots\exp[\gamma_+\tau_{2n}],\end{aligned} \tag{12}$$

where $\gamma_- \equiv 1 - \gamma$ and $\gamma_+ \equiv 1 + \gamma$. To obtain an analytical expression of the multiple integral, we use the Laplace transform and we obtain

$$\begin{aligned}& \mathscr{L}\left[\int_0^{\tau}\cdots\int_0^{\tau_{2n-1}} d\tau_1\cdots d\tau_{2n} \exp[\gamma_-\tau_1]\cdots\exp[\gamma_+\tau_{2n}]\right] \\ & = \prod_{k=0}^{n-1} \frac{1}{s - k(\gamma_+ + \gamma_-)} \frac{1}{s - k(\gamma_+ + \gamma_-) - \gamma_-} \frac{1}{s - n(\gamma_+ + \gamma_-)} \\ & = \prod_{k=0}^{n-1} \frac{1}{s - 2k} \frac{1}{s - 2k - \gamma_-} \frac{1}{s - 2n} \\ & = \frac{2^{-2n}\Gamma[-s/2]\,\Gamma[-s/2 + \gamma/2]}{\Gamma[n - s/2]\,\Gamma[n - s/2 + \gamma/2]} \frac{1}{s - 2n}.\end{aligned} \tag{13}$$

The quantity $\langle \overline{x}(\tau)\rangle$ is so reduced to a convolution integral

$$\begin{aligned}\langle \overline{x}(\tau)\rangle = & \sum_{n=0}^{\infty} \binom{-\frac{1}{\mu}}{2n} \beta^{2n}(\tau)(2n)! \\ & \times \int_0^{\tau} \exp[-2n(\tau - \tau_1)]\, f(\tau - \tau_1)\, d\tau_1,\end{aligned} \tag{14}$$

where

$$\begin{aligned} f(\tau) & = \mathscr{L}^{-1}\left[\tilde{f}(s)\right] \\ & = \mathscr{L}^{-1}\left[\frac{2^{-2n}\Gamma[-s/2]\,\Gamma[-s/2 + \gamma/2]}{\Gamma[n - s/2]\,\Gamma[n - s/2 + \gamma/2]}\right].\end{aligned} \tag{15}$$

For $\tau \to \infty$, we may write (14) as

$$\begin{aligned}\langle \overline{x}(\tau)\rangle & \approx \sum_{n=0}^{\infty} \binom{-\frac{1}{\mu}}{2n} \beta^{2n}(\tau)(2n)!\,\tilde{f}(2n) \\ & = F\left[\frac{1}{2\mu}, \frac{1+\mu}{2\mu}, \frac{1+\gamma}{2}, \beta^2(\tau)\right],\end{aligned} \tag{16}$$

where $\tilde{f}(2n)$ is the Laplace transform of $f(t)$ evaluated in $2n$ and $F(a, b, c, z)$ is the hypergeometric function (for more details, see, e.g., [39]). Expressing the result in terms of $\langle x(\tau)\rangle$, (9), we have

$$\begin{aligned}\langle x(\tau)\rangle = & \left[\left(\frac{a}{K_0}\right)^{\mu} + z_0 \exp[-\tau]\right]^{-1/\mu} \\ & \times F\left[\frac{1}{2\mu}, \frac{1+\mu}{2\mu}, \frac{1+\gamma}{2}, \beta^2(\tau)\right]\end{aligned} \tag{17}$$

or, going back to the time t,

$$\begin{aligned}\langle x(t)\rangle = & \left[\left(\frac{a}{K_0}\right)^{\mu} + z_0 \exp[-rt]\right]^{-1/\mu} \\ & \times F\left[\frac{1}{2\mu}, \frac{1+\mu}{2\mu}, \frac{r+\gamma}{2r}, \beta^2(rt)\right].\end{aligned} \tag{18}$$

From (8), we deduce that, for $x(0) \to 0$, $z_0 \to \infty$; that is, the more we start near to the point $x(0) = 0$, the more extended on time is the transient region (Figures 1, 2, and 3). For a deeper discussion about the dynamic near the point $x(0) = 0$, see [40]. Considering the limit for $t \to \infty$, we may write the asymptotic expression as

$$\langle x(t)\rangle_{\infty} = \frac{K_0}{a} F\left[\frac{1}{2\mu}, \frac{1+\mu}{2\mu}, \frac{r+\gamma}{2r}, \left(\frac{b}{a}\right)^{2\mu}\right]. \tag{19}$$

Some interesting conclusions can be extrapolated from the above expression taking the limits $\sigma \to 0$ and $\sigma \to 1$. The limit $\sigma \to 0$ gives the following approximated expression:

$$\langle x(t)\rangle_{\infty} \approx K_0\left[1 - \frac{\gamma(1+\mu)}{2(r+\gamma)}\sigma^2\right]. \tag{20}$$

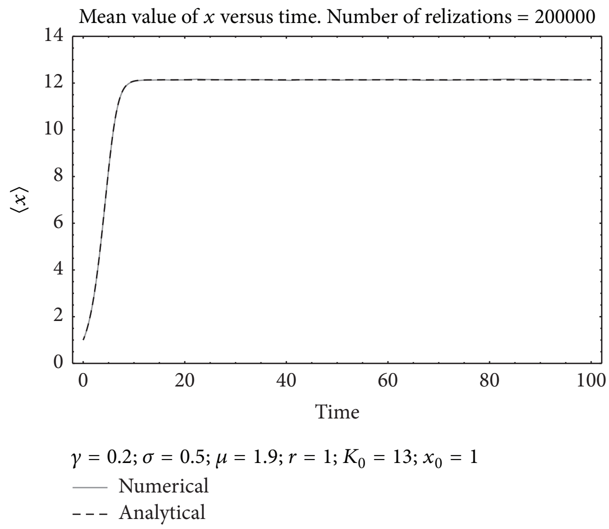

FIGURE 1: The plot of the mean value of $x(t)$ versus time in arbitrary units. The values of the parameters are $x_0 = 1$, $\gamma = 0.2$, $\sigma = 0.5$, $\mu = 1.9$, $K_0 = 13$, and $r = 1$. The analytical value of $\langle x(t) \rangle$ is given by (18). The agreement between the analytical expression (dashed line) and the numerical simulation (continuous line) is remarkable.

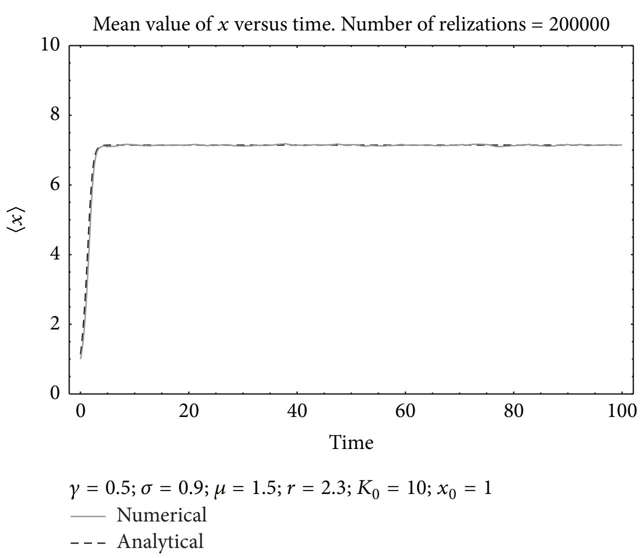

FIGURE 2: The plot of the mean value of $x(t)$ versus time in arbitrary units. The values of the parameters are $x_0 = 1$, $\gamma = 0.5$, $\sigma = 0.9$, $\mu = 1.5$, $K_0 = 10$, and $r = 2.3$. The analytical value of $\langle x(t) \rangle$ is given by (18). The agreement between the analytical expression (dashed line) and the numerical simulation (continuous line) is remarkable.

As expected for a vanishing intensity of the noise, the number of individuals takes the maximum population size allowed, namely, K_0. More, (20) shows that in general the average value of the population is always smaller than the unperturbed value of the carrying capacity K_0 even if half of the stochastic realizations exceed this value, that is, $K_0(1+\sigma)$. The deduction holds true also for an arbitrary value $0 < \sigma < 1$. Indeed, in this range of the noise intensity, the hypergeometric function

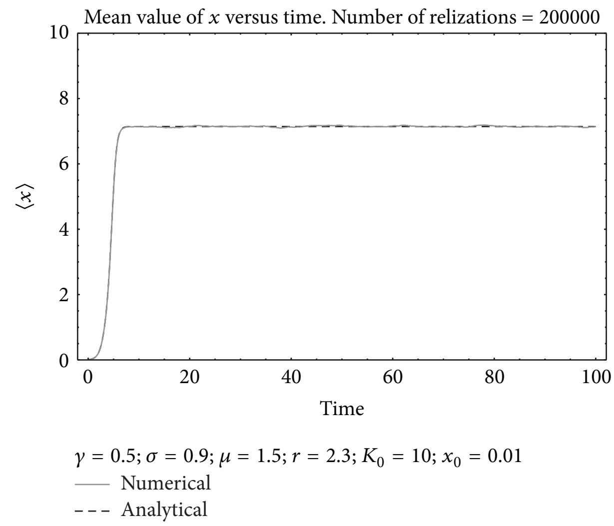

FIGURE 3: The plot of the mean value of $x(t)$ versus time in arbitrary units. The values of the parameters are $x_0 = 0.01$, $\gamma = 0.5$, $\sigma = 0.9$, $\mu = 1.5$, $K_0 = 10$, and $r = 2.3$. The analytical value of $\langle x(t) \rangle$ is given by (18). The agreement between the analytical expression (dashed line) and the numerical simulation (continuous line) is remarkable.

is decreasing and for $\sigma \to 1$ we have $\langle x(t) \rangle_\infty \to 0$. For $\sigma \to 1$, we have the following approximate expression:

$$\langle x(t) \rangle_\infty \approx K_0 \left(\left(2^{(1-\mu/2)(\gamma/r)} (1-\sigma)^{\gamma\mu/2r} \Gamma \left[\frac{r+\gamma}{2r} \right] \Gamma \left[-\frac{\gamma}{2r} + \frac{1}{\mu} \right] \right) \times \left(\sqrt{\pi} \Gamma \left[\frac{1}{\mu} \right] \right)^{-1} \right). \tag{21}$$

By a direct inspection of (21), we note that there is a relationship among the parameters (r, γ, μ), given by

$$\gamma\mu = 2r \tag{22}$$

such that the Γ function argument vanishes, producing a divergent value of the numerical coefficient in (21). Such a divergence is only apparent and it disappears considering further terms in the expansion of (19). Nevertheless, if we consider the derivative of $\langle x(t) \rangle_\infty$ with respect to σ we have that

$$\frac{\partial}{\partial \sigma} \langle x(t) \rangle_\infty \sim (1-\sigma)^{\gamma\mu/2r-1}. \tag{23}$$

This means that when the fluctuations are very large, that is, $\sigma \sim 1$, for $\gamma\mu < 2r$, the quantity $\langle x(t) \rangle_\infty$ vanishes with an infinite slope, that is to say, vanishes faster than the case $\gamma\mu > 2r$ (see Figures 4 and 5).

3. Numerical Check

In order to validate the analytical results obtained in Section 2, we solved numerically the stochastic differential

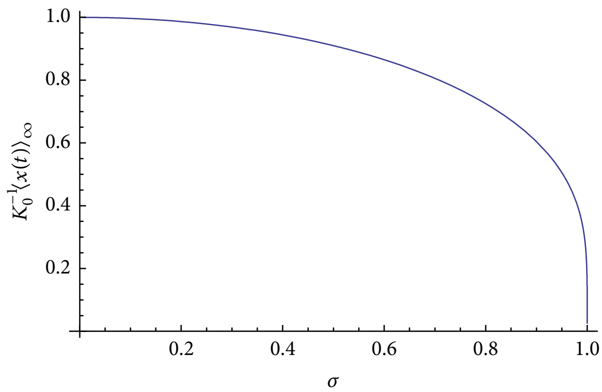

FIGURE 4: The plot of $K_0^{-1}\langle x(t)\rangle_\infty$ as function of the noise intensity σ. The values of the parameters are $\gamma = 0.8$, $\mu = 0.5$, and $r = 1$. In this case, $\gamma\mu = 0.4 < 2r$ and, for $\sigma \sim 1$, the number of individuals decreases with an infinite slope.

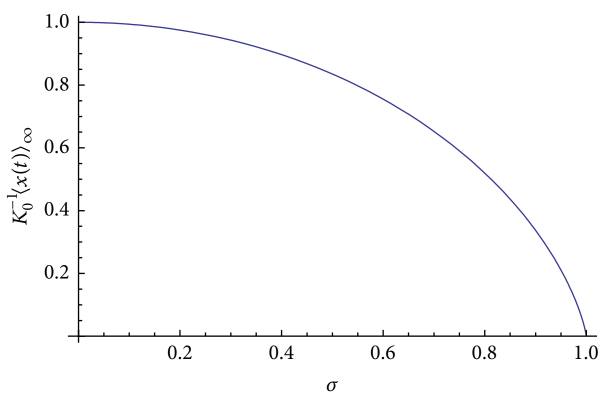

FIGURE 5: The plot of $K_0^{-1}\langle x(t)\rangle_\infty$ as function of the noise intensity σ. The values of the parameters are $\gamma = 4.8$, $\mu = 0.5$, and $r = 1$. In this case, $\gamma\mu = 2.4 > 2r$ and, for $\sigma \sim 1$, the number of individuals decreases with a finite slope.

equation (3). The numerical simulation is done by creating an ensemble of trajectories following the prescription of (3), where the random variable $\xi(t)$ fluctuates between the two values ± 1. We simulated a symmetric process so the probability to take the value 1 or -1 is the same. The initial value of $\xi(t)$, selected by tossing a fair coin, lasts for a time τ_1. At the end of this time interval, we toss again the coin and the random variable may or may not change sign according to the result of tossing the coin procedure. The random variable keeps the new sign for the whole time τ_2. This procedure is iterated at the succeeding times τ_i.

For a dichotomous process with an exponential correlation function, the waiting time distribution density is an exponential function. The time durations τ_i are drawn from a waiting time distribution $\psi(t) = \gamma \exp[-\gamma t]$. The numerical simulation is used to check the theoretical prediction of (19). As showed in Figures 1, 2, and 3, the theoretical and numerical values are in very good agreement.

4. Concluding Remarks

In this paper, we studied a generalized logistic equation (Malthus-Verhulst model) with a fluctuating carrying capacity. We found an analytical expression for the average of the number of individuals that allowed us to make few nontrivial remarks. We showed that, even in presence of a fluctuating carrying capacity, the average tends, asymptotically, to a constant quantity, (19). The asymptotic value is always smaller than the unperturbed value of the carrying capacity K_0 even if half of the stochastic realizations exceed this value. Finally, we found that, in case of very large fluctuation, in particular of the unperturbed carrying capacity size order, the number of individuals, for $\gamma\mu < 2r$, decreases with an infinite slope, while, for $\gamma\mu > 2r$, the number of individuals decreases with a finite slope. Our theoretical study has been supported by numerical simulations showing an excellent agreement with the analytical results.

Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

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