On ecological models with sublinear growth

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Abstract

Deterministic sublinear growth models have been used recently to enlighten the diversity-stability debate [9]. Some values of the parameter θ, quantifying the super- or sub-linearity of births or deaths in the model, lead to unbounded individual birth rates for small densities, which suggests that the path to extinction in these models might make them biologically unrealistic and hence unsuitable to model ecological dynamics. In this work, we examine stochastic birth-death and diffusion versions of these models, for which we fully characterize the extinction properties. Our analysis leads us to conclude that sublinear models show some mathematical appeal but should be taken with caution when modeling biological phenomena, since they give rise to stochastic dynamics that either never go extinct, even for small initial populations, or go extinct almost surely, but on unrealistically long time scales.

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1 Introduction

Recent works on food web and community patterns [9, 13] have brought into focus a family of population growth models named sublinear models, which have been known for more than 50 years [6, 17, 15]. In particular, in a recent paper published in *Science*, the sublinear model has been used by Hatton et al. [9] to resolve the diversity-stability debate (see also [12]) and to explain macroecological patterns.

The sublinear model, however, presents some complexities, particularly regarding the possibility of extinction or the path to extinction, which was considered unsuitable for representing ecological dynamics [1, 2]. However, it is not clear if this is the case in the context of their stochastic counterparts. The purpose of this letter is to discuss the prospects and limitations of stochastic sublinear models as models of ecological phenomena.

In Section 2, we recall the deterministic sublinear growth model and its basic properties. In Section 3 we present stochastic versions of this model, in the form of birth and death or diffusion models. We discuss their global properties, particularly regarding extinction, and whether they are well-suited for ecological modeling or not. We finally present a discussion of our results in Section 4. The proofs of the mathematical results discussed in this note are given in Supporting Information.

2 Sublinear models

The general form of sublinear growth models (after appropriate nondimensionalization and time scalings) is the following ordinary differential equation (ODE):

$$\dot{x} = \frac{x}{\theta}\left(1 - x^{\theta}\right), \tag{1}$$

where $x(t) \geq 0$ is the (scaled) population density at time $t \geq 0$ and $\theta \in \mathbb{R} \setminus \{0\}$ is a parameter.

The case $\theta = 1$ corresponds to the classical logistic equation, where the relation between per capita growth rate and density is linear, and cases where $-1 < \theta < 0$ are called sublinear (SG). The cases $\theta > 0$ are related to a linear growth rate and a superlinear death rate associated with crowding effects [7]. The ODE corresponding to the parameter $\theta = 0$ can be easily derived letting $\theta \to 0$ and takes the form of the classical Gompertz equation, which is quite popular and efficient for tumor growth modeling [16]:

$$\dot{x} = x \log(1/x). \tag{2}$$

As pointed out by [1] the per capita birth rate of the SG system tends to infinity as x goes to zero. Notice that the intrinsic dynamics in [1] and [9] are the same as above, and correspond to the θ-model by taking $\theta + 1 = k$. Thus, the SG model in our case corresponds with this notation to $0 < k < 1$.

Although most often only values of θ between -1 and 1 are discussed in the literature, the range of values of θ estimated from population time series in [9] is broader than the interval $[-2, 2]$.

For all values of θ (including 0), this ODE is well-posed (existence for all positive times and uniqueness of a solution for any initial condition in $\mathbb{R}_+$), has two equilibria at $x = 0$ and $x = 1$, the former being unstable and the latter stable (in the general sense, cf. e.g. [8], because local linearization may be degenerate depending on the value of θ). In addition, the equilibrium 1 is globally asymptotically stable, which means that, for any initial condition $x(0) > 0$, the solution $x(t)$ converges to 1 when $t \to +\infty$. Therefore, the qualitative asymptotic behavior of the deterministic ODE system is the same for any value of θ. However, when one tries to build corresponding stochastic processes, the picture is different.

3 Stochastic models with sublinear growth and their extinction properties

In the sequel we deal with two classes of stochastic models that are, in some sense, close relatives of (1). The first class corresponds to an individual-based formulation which, after suitable limiting procedures (which amount essentially to re-scaling the size of the populations) yields the SG model as the macroscopic description. So, this class of models can be regarded as a microscopic explanation which is compatible with the SG equation. The second class of models is based on extensions of the SG model by considering possible stochastic perturbations of the dynamics.

The first class of models is realized as a family of birth-and-death processes; the second class is realized as solutions of some stochastic differential equations. For both families of models we study the almost sure extinction in finite time, and we show that this property depends strongly on the value of the parameter θ and the type of stochastic models under consideration.

3.1 Birth and death process with sublinear growth

Observe that, for $\theta > 0$, the system (1) can be written as

$$\dot{x} = \frac{x}{\theta} - \frac{x^{1+\theta}}{\theta},$$

for $\theta = 0$ as

$$\dot{x} = x|\log(x)|\mathbb{1}_{x<1} - x|\log(x)|\mathbb{1}_{x>1}$$

and for $\theta < 0$ as

$$\dot{x} = \frac{x^{1+\theta}}{|\theta|} - \frac{x}{|\theta|}.$$

On the right-hand side of the three previous equations, the positive term can be interpreted as a birth rate and the negative term as a death rate.

The mathematical analysis of the discrete birth and death process version of the ODEs (1) and (2) (see Supporting Information Propositions 1.3 and 1.4) shows that extinction eventually occurs for all values of θ, but that strong contrasts for survival of small populations appear depending on θ. In the classical logistic case (i.e. $\theta = 1$), if the population starts from a very small density, even though the equilibrium 0 is unstable, the logistic birth and death process has a positive probability to go extinct fast. Biologically, this property is very relevant because the risk of extinction is ubiquitous for small populationn [14]. This property remains true for positive values of θ. However, extinction is impossible for sublinear birth and death processes with $\theta \leq 0$, except on extremely large, unrealistic time scales (exponential in K, see Supporting Information Proposition 1.4 and associated proof). This means that sublinear birth and death models with $\theta \leq 0$, thus including SG, are not suitable to model ecological phenomena.

3.2 Diffusion models with sublinear growth

We consider two different stochastic processes related to the sublinear growth model (1). The first one is obtained by introducing a Brownian noise similar to the one of Feller's classical diffusion model of branching populations [11, 3] or to classical diffusion models of population genetics [10, 5]. The second one is the diffusion approximation of the birth and death model of Section 3.1.

The first model takes the form of the stochastic differential equation (SDE)

$$dX_t = X_t \frac{1 - X_t^{\theta}}{\theta} dt + \sqrt{\gamma X_t} dB_t \tag{3}$$

for some parameter $\gamma > 0$ and where $(B_t)_{t\geq 0}$ is a standard Brownian motion. The rationale for the diffusion term is that independent randomness of birth and death events is attached to each individual in the population, so that the variance of noise scales linearly with the population size. In this sense, this term models demographic stochasticity, rather than environmental stochasticity which is usually modeled with a diffusion term of the form $X_t dB_t$ and does not allow in general for extinction of the population in finite time.

Let us recall some well-known properties of the logistic Feller diffusion, given by (3) with $\theta = 1$ (cf. e.g. [11]): 0 is an absorbing point which is an exit boundary and $+\infty$ is an entrance boundary. In particular, this implies that, for all $x > 0$,

$$\mathbb{P}(\exists t \geq 0,\ X_t = 0 \mid X_0 = x) = 1. \tag{4}$$

This means that extinction in finite time occurs almost surely, regardless of the initial condition, making (3) relevant for ecological modeling.

Instead, for general θ the behavior can be quite different: we prove in Proposition 2.1 in Supporting Information that, as in the logistic case, extinction occurs almost surely in finite time for $\theta \geq -1$, but it almost surely never occurs for $\theta < -1$. This means that the model is well-behaved in the SG case ($-1 < \theta < 0$) but it is not for smaller values of θ. Such values of θ are considered in several references dealing with sublinear growth models, in particular a large proportion of time-series fitted in [9] correspond to values of θ in $[-2, -1]$.

Finally, another diffusion model with sublinear growth can be obtained as the diffusion approximation [10, 4] of the birth and death process of Section 3.1 (see Supporting Information for its derivation): for any $\theta \neq 0$, this diffusion approximation $(Z_t)_{t\geq 0}$ is solution to the SDE

$$dZ_t = Z_t \frac{1 - Z_t^\theta}{\theta} + \sqrt{\frac{Z_t}{K|\theta|}(1 + Z_t^\theta)} dB_t, \tag{5}$$

where $(B_t)_{t\geq 0}$ is a standard Brownian motion and K is the carrying capacity of the birth and death model.

For this SDE, we prove (see Supporting Information Proposition 2.2) that for all $x > 0$ and any value of θ,

$$\mathbb{P}(\exists t \geq 0,\ Z_t = 0 \mid Z_0 = x) = 1,$$

i.e. that extinction in finite time almost surely occurs regardless of the values of the parameter θ. Therefore, the sublinear growth diffusion approximation model always have an ecologically realistic behavior regarding extinction.

4 Conclusion

Deterministic sublinear growth models have been used recently to enlighten the diversity-stability debate [9]. Some values of the parameter θ, quantifying the super- or sub-linearity of births or deaths in the model, lead to unbounded individual birth rates for small densities, which suggests that the path to extinction in these models might make them biologically unrealistic and hence unsuitable to model ecological dynamics.

In this work, we examined stochastic versions of these models, for which extinction properties can be fully characterized. We first studied birth and death processes and showed that, although ultimate extinction always occur almost surely in finite time, this time can be of very different order of magnitudes in realistic models such as the logistic birth and death model: for positive initial density, the time to extinction scales exponentially with respect to the carrying capacity of the system, whereas for small initial populations, there is a positive probability that the populations goes extinct fast, modeling convincingly the ubiquitous risk of extinction of small populations. This property, however is no longer true for negative values of θ, making the use of the birth and death model with sublinear growth biologically questionable for ecological modeling.

We also studied a Feller diffusion models with sublinear growth and obtained here an even more drastic behavior: for values of θ smaller than -1 extinction becomes impossible on any time scale, making this model biologically unrealistic. Only the diffusion approximation model is well-behaved in terms of extinction: it occurs almost surely in finite time for every value of the parameter θ.

These results show that the behavior of stochastic versions of a given deterministic system may drastically change depending on the type of stochasticity (discrete or continuous) added to the system and also on the details of this stochasticity (e.g. the variance of the noise in diffusion processes). In addition, stochastic population models are very different from their deterministic versions, so the overuse of deterministic approaches is problematic since it can lead to ignoring important characteristics of the system such as the extinction time scale.

Our analysis leads us to conclude that sublinear models show some mathematical appeal but should be taken with caution when modeling biological phenomena, since they give rise to stochastic dynamics that either never go extinct or go extinct almost surely, but on unrealistically long time scales. The diffusion approximation, however, could offer a good alternative to model ecological phenomena.

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Supporting Information: On ecological models with sublinear growth

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1 Discrete stochastic models of sublinear growth

Observe that, for $\theta > 0$, Eq. (1) and (2) in the main text can be written as

$$\dot{x} = \frac{x}{\theta} - \frac{x^{1+\theta}}{\theta}, \tag{1.1}$$

for $\theta = 0$ as

$$\dot{x} = x|\log(x)|\mathbb{1}_{x<1} - x|\log(x)|\mathbb{1}_{x>1}, \tag{1.2}$$

and for $\theta < 0$ as

$$\dot{x} = \frac{x^{1+\theta}}{|\theta|} - \frac{x}{|\theta|}. \tag{1.3}$$

In the right-hand side of all the three previous equations, the positive term can be interpreted as a birth rate and the negative term as a death rate.

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Therefore, introducing a parameter $K \geq 1$ corresponding to the carrying capacity of the system, this suggests to introduce the following birth and death process version of the ODEs Eq. (1) and (2) in the main text: let $(Z_t^K)_{t\in\mathbb{R}_+}$ be a Markov process taking values in $\{0, 1/K, 2/K, \dots\}$ and which jumps from n/K to $(n+1)/K$ at rate $Kb(n/K)$ and jumps from n/K to $(n-1)/K$ at rate $Kd(n/K)$, where

$$b(x) = \begin{cases} \frac{x}{\theta} & \text{if } \theta > 0, \\ x|\log(x)|\mathbb{1}_{x<1} & \text{if } \theta = 0, \\ \frac{x^{1+\theta}}{|\theta|} & \text{if } \theta < 0 \end{cases}$$

and

$$d(x) = \begin{cases} \frac{x^{1+\theta}}{\theta} & \text{if } \theta > 0, \\ x|\log(x)|\mathbb{1}_{x>1} & \text{if } \theta = 0, \\ \frac{x}{|\theta|} & \text{if } \theta < 0. \end{cases}$$

The rationale for the normalization of the population size by K and the multiplication of the rates b and d by K in the definition is explained in the next proposition.

Proposition 1.1. *For any $\theta \in \mathbb{R}$, assume that Z_0^K converges in law to a deterministic $x_0 > 0$. Then, for all $T > 0$, the stochastic process $(Z_t^K)_{t\in[0,T]}$ converges in probability for the $L^\infty([0,T])$ norm to the unique solution of* (1.1)*,* (1.2) *or* (1.3) *(depending on the value of θ) with initial condition $x(0) = x_0$.*

Proof. This result can be deduced from [3, Chap. 11, Thm. 2.1], which gives a similar result but for bounded and globally Lipschitz functions b and d. Here these function are not bounded near 0 or near $+\infty$ and are only locally Lipschitz in $(0, +\infty)$. However, since the limit dynamics (1.1), (1.2) or (1.3) started from $x_0 > 0$ converges to the unique globally asymptotically stable equilibrium 1 for large times, the solution $\phi(s)$ to (1.1), (1.2) or (1.3) with initial value $x_0 > 0$ remains for all positive time in a compact subset of $(0, +\infty)$ of the form $[\varepsilon, 1/\varepsilon]$ for some $\varepsilon \in (0, 1)$. Then, we consider bounded and globally Lipschitz functions $\tilde{b}$ and $\tilde{d}$ on $\mathbb{R}_+$ such that, for all $x \in [\varepsilon/2, 2/\varepsilon]$,

$$\tilde{b}(x) = b(x) \quad \text{and} \quad \tilde{d}(x) = d(x)$$

and we define the birth and death process $(\tilde{Z}_t^K)_{t\geq 0}$ taking values in $\{0, 1/K, 2/K, \dots\}$ exactly as $(Z_t^K)_{t\geq 0}$ but replacing b and d by $\tilde{b}$ and $\tilde{d}$. We also assume that $\tilde{Z}_0^K = Z_0^K$.

Theorem 2.1 of [3, Chap. 11] applies to the process $(\tilde{Z}_t^K)_{t\geq 0}$, so that this process converges in probability in $L^\infty([0,T])$ for all $T>0$ to $\tilde{\phi}(s)$, unique solution to

$$\frac{d\tilde{\phi}}{ds}(s)=\tilde{b}(\tilde{\phi}(s))-\tilde{d}(\tilde{\phi}(s))$$

such that $\tilde{\phi}(0)=x_0$. Since $\phi(s)$ is a solution to (1.1), (1.2) or (1.3) that never exits $[\varepsilon,1/\varepsilon]$ and since the vector field of these equations, given by $b-d$, is equal to $\tilde{b}-\tilde{d}$ on this interval, we deduce that $\tilde{\phi}(s)=\phi(s)$ for all $s\geq 0$.

Now, fix $T>0$. It follows from the above convergence result that

$$\lim_{K\to+\infty}\mathbb{P}\left(\sup_{t\in[0,T]}|\tilde{Z}_t^K-\phi(t)|\geq\frac{\varepsilon}{2}\right)=0,$$

so in particular

$$\lim_{K\to+\infty}\mathbb{P}\left(\tilde{Z}_t^K\in\left[\frac{\varepsilon}{2},\frac{2}{\varepsilon}\right],\ \forall t\in[0,T]\right)=1.$$

Now, by definition of $\tilde{b}$ and $\tilde{d}$, the processes $(\tilde{Z}_t^K)_{t\geq 0}$ and $(Z_t^K)_{t\geq 0}$ can be constructed on the same probability space so that $\tilde{Z}_t^K=Z_t^K$ for all $t\leq T_{K,\varepsilon}$, where $T_{K,\varepsilon}$ is the first exit time of $(\tilde{Z}_t^K)_{t\geq 0}$ from $[\varepsilon/2,2/\varepsilon]$. Therefore, the last equation implies that

$$\lim_{K\to+\infty}\mathbb{P}\left(Z_t^K=\tilde{Z}_t^K,\ \forall t\in[0,T]\right)=1.$$

Since $(\tilde{Z}_t^K)_{t\geq 0}$ converges in probability in $L^\infty([0,T])$ to ϕ, we deduce that $(Z_t^K)_{t\geq 0}$ satisfies the same property. Hence Proposition 1.1 is proved. □

Note that the same result holds true if we replace b and d by any $\tilde{b}$ and $\tilde{d}$ such that $\tilde{b}(x)-\tilde{d}(x)=b(x)-d(x)$ for all $x\geq 0$. In particular, given any parameter $\alpha\geq 0$, Proposition 1.1 also holds true for the birth and death process $(Z_t^{K,\alpha})_{t\geq 0}$ defined as $(Z_t^K)_{t\geq 0}$ but replacing b and d by

$$b_\alpha(x)=b(x)+\alpha x\quad\text{and}\quad d_\alpha(x)=d(x)+\alpha x.$$

This means that the constant α is added to both, per individual birth and death rates. Hence, the parameter α does not change the overall ecological interactions in the population, but it adds birth and death events at the same rate that does not depend on the population density. For future reference, let us introduce the infinitesimal generator $L^{K,\alpha}$ of the birth and death process $(Z_t^{K,\alpha})_{t\geq 0}$: for any bounded function f on $\{0,1/K,2/K,\ldots\}$ and all $x\in\{0,1/K,2/K,\ldots\}$,

$$L^{K,\alpha}f(x)=Kb_\alpha(x)\left(f\left(x+\frac{1}{K}\right)-f(x)\right)+Kd_\alpha(x)\left(f\left(x-\frac{1}{K}\right)-f(x)\right). \tag{1.4}$$

Let us recall some well-known results on the logistic case ($\theta=1$).

Proposition 1.2 (Thm. 3 and Thm. 4 of [2]). *Assume $\theta=1$ and $\alpha\geq 0$. Then, for all $k\in\mathbb{N}$ and all $K\geq 1$,*

$$\mathbb{P}(\exists t\geq 0,\ Z_t^{K,\alpha}=0\mid Z_0^{K,\alpha}=k/K)=1$$

and there exists $V>0$ such that, for all $x_0>0$, if $Z_0^{K,\alpha}$ converges in law to x_0, then

$$\lim_{K\to+\infty}\mathbb{P}(Z^{K,\alpha}_{\exp(VK)}>0)=1.$$

In addition,

$$\begin{aligned}&\lim_{K\to+\infty}\mathbb{P}(\exists t\leq\log K,\ Z_t^{K,\alpha}=0\mid Z_0^{K,\alpha}=1/K)\\ &=\lim_{K\to+\infty}\mathbb{P}(\exists t\leq e^{VK},\ Z_t^{K,\alpha}=0\mid Z_0^{K,\alpha}=1/K)=\frac{\alpha}{1+\alpha}.\end{aligned}$$

This result means that extinction always occurs in finite time in the logistic birth and death process, in an exponentially large time for positive initial density. In addition, if the population starts from a very small density, even though the equilibrium 0 is unstable, the logistic birth and death process has a positive probability to go extinct fast. Biologically, this property is very relevant because the risk of extinction is ubiquitous for small populations [7]. Note also that, since $b(0)=d(0)=0$, 0 is an absorbing point for the birth and death process, $Z_t^{K,\alpha}=0$ for all $t\geq 0$ if $Z_0^{K,\alpha}=0$. The first hitting time of 0 by the process $Z^{K,\alpha}$ is called extinction time. For all values of θ, we can prove that extinction occurs almost surely in finite time.

Proposition 1.3. *For all $\theta\neq 0$ and all $\alpha\geq 0$ and for $\theta=0$ and $\alpha>0$,*

$$\mathbb{P}(\exists t\geq 0,\ Z_t^{K,\alpha}=0)=1.$$

Proof. We use the classical criterion of extinction of continuous-time birth and death processes that can be found for example in [1]: a birth and death process on $\mathbb{N}$ with birth (resp. death) rate $\lambda_i>0$ (resp. $\mu_i>0$) in state

$i \in \mathbb{N}^*$ satisfies $T_0 < +\infty$ almost surely, where T_0 is the first hitting time of 0 by the process, if and only if

$$\sum_{k=1}^{+\infty} \frac{\mu_1 \dots \mu_k}{\lambda_1 \dots \lambda_k} = +\infty.$$

We fix $K \geq 1$, $\alpha \geq 0$ and $\theta > 0$, and we check that, for the birth and death process $(KZ_t^{K,\alpha})_{t\geq 0}$, with the above notations,

$$\frac{\mu_1 \dots \mu_k}{\lambda_1 \dots \lambda_k} = \prod_{i=1}^{k} \frac{\left(\frac{i}{K}\right)^{\theta} + \alpha\theta}{1 + \alpha\theta} \xrightarrow[k\to+\infty]{} +\infty.$$

Similarly, given $K \geq 1$, $\alpha \geq 0$ and $\theta < 0$, we have

$$\frac{\mu_1 \dots \mu_k}{\lambda_1 \dots \lambda_k} = \prod_{i=1}^{k} \frac{1 + \alpha|\theta|}{\left(\frac{i}{K}\right)^{-|\theta|} + \alpha|\theta|} \xrightarrow[k\to+\infty]{} +\infty,$$

and for $K \geq 1$, $\alpha > 0$ and $\theta = 0$,

$$\frac{\mu_1 \dots \mu_k}{\lambda_1 \dots \lambda_k} = \prod_{i=1}^{k} \frac{|\log(i/K)|\mathbb{1}_{i>K} + \alpha}{|\log(i/K)|\mathbb{1}_{i<K} + \alpha} \xrightarrow[k\to+\infty]{} +\infty,$$

Therefore, in all cases, $T_0 < \infty$ almost surely for the process $(Z_t^{K,\alpha})_{t\geq 0}$. $\square$

The following result studies the case of a small initial population. It shows in particular that the extinction properties for negative values of θ are very different from those of Proposition 1.2 in the logistic case.

Proposition 1.4. *Let $\alpha \geq 0$. For all $\theta > 0$, there exists $V > 0$ such that*

$$\lim_{K\to+\infty} \mathbb{P}(\exists t \leq e^{VK},\ Z_t^{K,\alpha} = 0 \mid Z_0^{K,\alpha} = 1/K) = \frac{\alpha\theta}{1+\alpha\theta}. \tag{1.5}$$

For all $\theta \leq 0$, for all $\eta > 0$,

$$\lim_{K\to+\infty} \mathbb{P}(\exists t \geq 0,\ Z_t^{K,\alpha} \geq 1-\eta \mid Z_0^{K,\alpha} = 1/K) = 1, \tag{1.6}$$

and there exists a constant $V > 0$ such that

$$\lim_{K\to+\infty} \mathbb{P}(\exists t \leq e^{VK},\ Z_t^{K,\alpha} = 0 \mid Z_0^{K,\alpha} = 1/K) = 0. \tag{1.7}$$

In other words, extinction is impossible when $\theta \leq 0$, except on extremely large time scales (exponential in K), even for small initial populations. Note that the exponential bound in (1.7) may not be optimal: we actually conjecture a superexponential extinction time if $\theta \leq 0$. This means that sublinear birth and death models with $\theta \leq 0$ are completely irrelevant from the ecological point of view.

Proof. We consider the embedded Markov chain of the birth and death process $Z^{K,\alpha}$, i.e. the Markov chain $(\tilde{Z}^{K,\alpha}_n)_{n\in\mathbb{N}}$ defined by $\tilde{Z}^{K,\alpha}_n = Z^{K,\alpha}_{J_n}$ where J_n is the n-th jump time of $Z^{K,\alpha}$. This Markov chain has transition probability from n/K to $(n+1)/K$ of $\frac{b_\alpha(n/K)}{b_\alpha(n/K)+d_\alpha(n/K)}$ and from n/K to $(n-1)/K$ of $\frac{d_\alpha(n/K)}{b_\alpha(n/K)+d_\alpha(n/K)}$. For all $x > 0$, we also denote by T_x (resp. $\tilde{T}_x$) the first hitting time by $Z^{K,\alpha}$ (resp. $\tilde{Z}^{K,\alpha}$) of $[x, +\infty)$ and by T_0 (resp. $\tilde{T}_0$) the first hitting time by $Z^{K,\alpha}$ (resp. $\tilde{Z}^{K,\alpha}$) of 0. To simplify notations, we also denote $\mathbb{P}_n = \mathbb{P}(\cdot \mid Z^{K,\alpha}_0 = \tilde{Z}^{K,\alpha}_0 = n/K)$ for all $n \in \mathbb{N}$.

Fix $\varepsilon > 0$. We shall first prove that, for all $\theta \neq 0$ and all $K \geq 1$, there exist positive constants $\underline{p}_{\alpha,\theta,K}(\varepsilon) < \bar{p}_{\alpha,\theta,K}(\varepsilon)$ such that:

$$\underline{p}_{\alpha,\theta,K}(\varepsilon) \leq \mathbb{P}_1(\tilde{T}_\varepsilon < \tilde{T}_0) = \mathbb{P}_1(T_\varepsilon < T_0) \leq \bar{p}_{\alpha,\theta,K}(\varepsilon)$$

satisfying:

$$\lim_{\varepsilon\to 0}\lim_{K\to+\infty} \underline{p}_{\alpha,\theta,K}(\varepsilon) = \lim_{\varepsilon\to 0}\lim_{K\to+\infty} \bar{p}_{\alpha,\theta,K}(\varepsilon) = \begin{cases} \frac{1}{1+\alpha\theta} & \text{if } \theta > 0, \\ 1 & \text{if } \theta \leq 0. \end{cases} \tag{1.8}$$

For all $x \in (0, \varepsilon]$, if $\theta > 0$,

$$\frac{b_\alpha(x)}{b_\alpha(x)+d_\alpha(x)} = \frac{1+\alpha\theta}{1+2\alpha\theta+x^\theta} \in \left[\frac{1+\alpha\theta}{1+2\alpha\theta+\varepsilon^\theta}, \frac{1+\alpha\theta}{1+2\alpha\theta}\right],$$

if $\theta = 0$ and $\alpha > 0$,

$$\frac{b_\alpha(x)}{b_\alpha(x)+d_\alpha(x)} = \frac{\alpha+|\log(x)|}{2\alpha+|\log(x)|} \in \left[1 - \frac{\alpha}{2\alpha+|\log(\varepsilon)|}, 1\right],$$

and if $\theta < 0$,

$$\frac{b_\alpha(x)}{b_\alpha(x)+d_\alpha(x)} = \frac{1+\alpha|\theta|x^{|\theta|}}{1+(1+2\alpha|\theta|)x^{|\theta|}} \in \left[\frac{1+\alpha|\theta|\varepsilon^{|\theta|}}{1+(1+2\alpha|\theta|)\varepsilon^{|\theta|}}, 1\right].$$

Therefore, usual coupling techniques show that, for all $n \leq \tilde{T}_0 \wedge \tilde{T}_\varepsilon$, under $\mathbb{P}_1$, almost surely,

$$\frac{A_n}{K} \leq \tilde{Z}^{K,\alpha}_n \leq \frac{B_n}{K},$$

where $(A_n)_{n\geq 0}$ and $(B_n)_{n\geq 0}$ are random walks on $\mathbb{Z}$ with jumps ± 1, such that $A_0 = B_0 = 1$ and with probability of making a $+1$ jump at any time step given by:

$$\begin{cases} \frac{1+\alpha\theta}{1+2\alpha\theta+\varepsilon^\theta} & \text{for } (A_n)_{n\geq 0} \text{ if } \theta > 0; \\ 1 - \frac{\alpha}{2\alpha+|\log(\varepsilon)|} & \text{for } (A_n)_{n\geq 0} \text{ if } \theta = 0; \\ \frac{1+\alpha|\theta|\varepsilon^{|\theta|}}{1+(1+2\alpha|\theta|)\varepsilon^{|\theta|}} & \text{for } (A_n)_{n\geq 0} \text{ if } \theta < 0; \\ \frac{1+\alpha\theta}{1+2\alpha\theta} & \text{for } (B_n)_{n\geq 0} \text{ if } \theta > 0; \\ 1 & \text{for } (B_n)_{n\geq 0} \text{ if } \theta \leq 0. \end{cases}$$

Therefore,

$$\begin{aligned} \underline{p}_{\alpha,\theta,K}(\varepsilon) &:= \mathbb{P}(A_n \text{ hits } \lceil \varepsilon K \rceil \text{ before } 0) \\ &\leq \mathbb{P}_1(\tilde{T}_\varepsilon < \tilde{T}_0) \leq \mathbb{P}(B_n \text{ hits } \lceil \varepsilon K \rceil \text{ before } 0) =: \bar{p}_{\alpha,\theta,K}(\varepsilon) \end{aligned}$$

and standard results on hitting times of random walks entail that

$$\underline{p}_{\alpha,\theta,K}(\varepsilon) = \begin{cases} \frac{\frac{\varepsilon^\theta+\alpha\theta}{1+\alpha\theta}-1}{\left(\frac{\varepsilon^\theta+\alpha\theta}{1+\alpha\theta}\right)^{\lceil \varepsilon K \rceil}-1} & \text{if } \theta > 0, \\ \frac{\frac{\alpha}{\alpha+|\log(\varepsilon)|}-1}{\left(\frac{\alpha}{\alpha+|\log(\varepsilon)|}\right)^{\lceil \varepsilon K \rceil}-1} & \text{if } \theta = 0, \\ \frac{\frac{(1+\alpha|\theta|)\varepsilon^{|\theta|}}{1+\alpha|\theta|\varepsilon^{|\theta|}}-1}{\left(\frac{(1+\alpha|\theta|)\varepsilon^{|\theta|}}{1+\alpha|\theta|\varepsilon^{|\theta|}}\right)^{\lceil \varepsilon K \rceil}-1} & \text{if } \theta < 0, \end{cases}$$

and

$$\bar{p}_{\alpha,\theta,K}(\varepsilon) = \begin{cases} \frac{\frac{\alpha\theta}{1+\alpha\theta}-1}{\left(\frac{\alpha\theta}{1+\alpha\theta}\right)^{\lceil \varepsilon K \rceil}-1} & \text{if } \theta > 0, \\ 1 & \text{if } \theta \leq 0. \end{cases}$$

It is straightforward to check (1.8) from these formula.

Fix $\eta_0 \in (0, 1/2)$ and $\delta > 0$. There exists $\varepsilon > 0$ such that, if $\theta > 0$,

$$\frac{1}{1+\alpha\theta} - \delta \leq \underline{p}_{\alpha,\theta,K}(\varepsilon) \leq \bar{p}_{\alpha,\theta,K}(\varepsilon) \leq \frac{1}{1+\alpha\theta} + \delta$$

and if $\theta \leq 0$,

$$1 - \delta \leq \underline{p}_{\alpha,\theta,K}(\varepsilon) \leq \bar{p}_{\alpha,\theta,K}(\varepsilon) \leq 1.$$

Let $\phi_\varepsilon(t)$ be the solution to Eq. (1.1), (1.2) or (1.3) (depending on the value of θ) with initial condition $\phi_\varepsilon(0) = \varepsilon$. Since $\phi_\varepsilon(t) \to 1$ when $t \to +\infty$, there exists a deterministic time t_ε such that $\phi_\varepsilon(t_\varepsilon) > 1 - \eta_0/2$. Applying Proposition 1.1, we deduce that, for K large enough,

$$\mathbb{P}\left(T_{1-\eta_0} < T_0 \;\middle|\; Z_0^{K,\alpha} = \frac{\lceil K\varepsilon \rceil}{K}\right) \geq \mathbb{P}\left(Z_{t_\varepsilon}^{K,\alpha} \geq 1 - \eta_0 \;\middle|\; Z_0^{K,\alpha} = \frac{\lceil K\varepsilon \rceil}{K}\right) \\ \geq 1 - \delta.$$

Finally, we can deduce from large deviation estimates exactly as in Theorem 3(c) of [2] that there exists a constant $V = V(\eta_0) > 0$ such that

$$\mathbb{P}\left(\forall t \leq e^{KV},\ Z_t^{K,\alpha} \in [1 - 2\eta_0, 1 + 2\eta_0] \;\middle|\; Z_0^{K,\alpha} = \frac{\lceil K(1-\eta_0) \rceil}{K}\right) \xrightarrow[K\to+\infty]{} 1.$$

Therefore, assuming $\theta > 0$ and applying the strong Markov property at time T_ε on the event $\{T_\varepsilon < T_0\}$ and at time $T_{1-\eta}$ on the event $\{T_{1-\eta_0} < T_0\}$, we have for K large enough

$$\begin{aligned}\mathbb{P}_1(\exists t \leq e^{VK},\ Z_t^{K,\alpha} = 0) &\geq \mathbb{E}_1\Big[\mathbb{1}_{T_\varepsilon < T_0}\mathbb{E}\Big(\mathbb{1}_{T_{1-\eta_0} < T_0}\mathbb{P}\big(\forall t \leq e^{KV}, \\ &\qquad Z_t^{K,\alpha} \in [1 - 2\eta_0, 1 + 2\eta_0] \mid Z_0^{K,\alpha} = \lceil K(1-\eta_0) \rceil/K\big) \mid Z_0^{K,\alpha} = \lceil K\varepsilon \rceil/K\Big)\Big] \\ &\geq \mathbb{P}_1(T_\varepsilon < T_0) - 2\delta \\ &\geq \frac{1}{1+\alpha\theta} - 3\delta.\end{aligned}$$

Similarly,

$$\mathbb{P}_1(\exists t \leq e^{VK},\ Z_t^{K,\alpha} = 0) \leq \mathbb{P}_1(T_\varepsilon < T_0) + \delta \leq \frac{1}{1+\alpha\theta} + 2\delta.$$

Since $\delta > 0$ was arbitrary, we have proved (1.5).

When $\theta \leq 0$, the same computation gives, for arbitrary values of $\eta > 0$ and $\delta > 0$, for K large enough,

$$\begin{aligned}\mathbb{P}_1(T_{1-\eta} < T_0) &= \mathbb{E}_1\Big[\mathbb{1}_{T_\varepsilon < T_0}\mathbb{P}\big(T_{1-\eta} < T_0 \mid Z_0^{K,\alpha} = \lceil K(1-\eta) \rceil/K\big)\Big] \\ &\geq \mathbb{P}_1(T_\varepsilon < T_0) - \delta \geq 1 - 2\delta,\end{aligned}$$

so (1.6) is proved. Similarly, (1.7) follows when $\theta \leq 0$ using the same calculation as the one used to prove (1.5) above with $V = V(\eta_0)$ for the same fixed value of η_0 chosen above. □

2 Diffusion models of sublinear growth

Similarly, we consider diffusion models associated to the ODE model of sublinear growth. Three methods are usual to construct such models: either consider a stochastic differential equation (SDE) with noise proportional to the population density, or with noise proportional to the square root of the population density, or consider diffusion approximation of the birth and death process of Section 1. The first one takes the form

$$dX_t = X_t \frac{1 - X_t^\theta}{\theta} dt + \sigma X_t dB_t \tag{2.1}$$

for some $\sigma > 0$, where $(B_t)_{t \geq 0}$ is a standard Brownian motion, the second one takes the form

$$dX_t = X_t \frac{1 - X_t^\theta}{\theta} dt + \sqrt{\gamma X_t} dB_t \tag{2.2}$$

for some $\gamma > 0$, and the third one will be discussed in Subsection 2.2.

The stochastic term in the SDE (2.1) can be interpreted as modeling an environmental noise: indeed, the term σdB_t can be considered as being added to the growth rate per individual of every individual in the population, i.e. each individual is influenced by a common, environmental noise. The stochastic term in the SDE (2.2) is similar to the one of Feller's classical branching diffusion (which is an example of continuous state branching process). The rationale for this term is that independent randomness of birth and death events is attached to each individual in the population, so that the variance of noise scales linearly with the population size. In this sense, this term models demographic stochasticity, rather than environmental stochasticity.

It is standard to check that no solution to (2.1) can hit 0 in finite time, so this model is not relevant for our discussion here. Therefore, we will focus in the sequel on Feller's diffusion with sublinear growth (2.2) in Subsection 2.1, and on diffusion approximation in Subsection 2.2.

2.1 Feller's branching diffusion with sublinear growth

Let us recall some well-known properties of the logistic Feller diffusion, given by (2.2) with $\theta = 1$ (cf. e.g. [6]): there is strong existence and pathwise uniqueness for this SDE, 0 is an absorbing point which is an exit boundary and $+\infty$ is an entrance boundary. In particular, this implies that, for all $x > 0$,

$$\mathbb{P}(\exists t \geq 0,\ X_t = 0 \mid X_0 = x) = 1. \tag{2.3}$$

This means that extinction in finite time occurs almost surely, regardless of the initial condition. This is biologically relevant.

For general θ, since the coefficients are locally Lipschitz, there is strong existence and pathwise uniqueness of a solution to (2.2) up to the first hitting time of 0 or a possibly finite explosion time. Let us call S this random time. The next result shows that the property (2.3) is not true for all values of θ. In particular, Feller's diffusion with sublinear growth is not relevant for ecological modeling.

Proposition 2.1. *For all $x > 0$, if $\theta \geq -1$,*

$$\mathbb{P}(\exists t \geq 0,\ X_t = 0 \mid X_0 = x) = 1 \tag{2.4}$$

and if $\theta < -1$,

$$\begin{aligned}\mathbb{P}(S = \infty \mid X_0 = x) &= \mathbb{P}(\inf_{t\in\mathbb{R}_+} X_t = 0 \mid X_0 = x) \\ &= \mathbb{P}(\sup_{t\in\mathbb{R}_+} X_t = +\infty \mid X_0 = x) = 1. \end{aligned} \tag{2.5}$$

Proof. A scale function of the SDE (2.2) is given, for all $x > 0$, by

$$\begin{aligned} p(x) &= \int_1^x \exp\left(-\frac{2}{\gamma\theta}\int_1^y (1 - z^\theta)dz\right) dy \\ &\propto \int_1^x \exp\left(\frac{2}{\gamma\theta}\left(\frac{y^{1+\theta}}{1+\theta} - y\right)\right) dy. \end{aligned}$$

One can then check that $p(+\infty) = +\infty$ for all $\theta \in \mathbb{R}^*$ and that $p(0+) > -\infty$ if $\theta \geq -1$ and $p(0+) = -\infty$ if $\theta < -1$. Therefore, if $\theta < -1$, (2.5) follows from [4, Prop. 5.22], and if $\theta \geq 1$, we deduce from the same result that

$$\mathbb{P}\left(\lim_{t\to S} X_t = 0 \,\middle|\, X_0 = x\right) = \mathbb{P}\left(\sup_{0\leq t<S} X_t < +\infty \,\middle|\, X_0 = x\right) = 1.$$

The almost sure finiteness of the time S follows from Feller's test for explosion [4, Thm. 5.29], so (2.4) will follow if we can prove that

$$\int_0^1 p'(x)\int_x^1 \frac{2dy}{\gamma y p'(y)} dx < +\infty, \tag{2.6}$$

i.e.

$$\int_0^1 \exp\left(\frac{2}{\gamma\theta}\left(\frac{x^{1+\theta}}{1+\theta} - x\right)\right)\int_x^1 \exp\left(-\frac{2}{\gamma\theta}\left(\frac{y^{1+\theta}}{1+\theta} - y\right)\right)\frac{dy}{y}\, dx < +\infty.$$

If $\theta \geq -1$, $\exp(\frac{2}{\gamma\theta}(\frac{x^{1+\theta}}{1+\theta} - x))$ is bounded and bounded away from 0 for $x \in [0,1]$ and converges to 1 when $x \to 0$, so, when $x \to 0$,

$$\int_x^1 \exp\left(-\frac{2}{\gamma\theta}\left(\frac{y^{1+\theta}}{1+\theta} - y\right)\right)\frac{dy}{y} \sim \int_x^1 \frac{dy}{y} = \log(1/x),$$

hence (2.6) follows and the proof is completed. $\square$

2.2 Diffusion approximation of birth and death processes with sublinear growth

The diffusion approximation of a birth and death process with carrying capacity K is obtained heuristically by expanding the infinitesimal generator of the birth and death process in a Taylor series as $K \to +\infty$ and dropping terms beyond the second order [5, 3]. The operator thus obtained is the generator of the diffusion approximation. Here, a second-order expansion of (1.4) gives for all $f \in C^2(\mathbb{R}_+)$

$$A^\alpha f(x) = (b_\alpha(x) - d_\alpha(x))f'(x) + \frac{b_\alpha(x) + d_\alpha(x)}{2K}f''(x).$$

Hence, for any $\theta \neq 0$, the diffusion approximation $(Z_t)_{t\geq 0}$ is solution to the SDE

$$dZ_t = Z_t\frac{1 - Z_t^\theta}{\theta}dt + \sqrt{\frac{Z_t}{K|\theta|}(1 + 2\alpha|\theta| + Z_t^\theta)}dB_t$$

and for $\theta = 0$

$$dZ_t = Z_t \log(1/Z_t)dt + \sqrt{\frac{Z_t}{K}(|\log(Z_t)| + 2\alpha)}dB_t,$$

where $(B_t)_{t\geq 0}$ is a standard Brownian motion.

We can carry out a similar analysis as in Subsection 2.1 to obtain the following result, which entails that the diffusion approximation of the sublinear birth and death model is biologically relevant for all values of θ.

Proposition 2.2. *For all $\theta \neq 0$ and $\alpha \geq 0$ of for $\theta = 0$ and all $\alpha > 0$, for all $x > 0$,*

$$\mathbb{P}(\exists t \geq 0,\ Z_t = 0 \mid Z_0 = x) = 1.$$

Proof. The arguments go along the same lines as in the proof of Proposition 2.1. We start with the case $\theta \neq 0$. In this case, a speed function for the diffusion is given by:

$$p(x) = \int_1^x \exp\left\{-2K\mathbf{sign}(\theta)\int_1^y \frac{1 - z^\theta}{1 + 2\alpha|\theta| + z^\theta}dz\right\}dy.$$

Observe that for $\theta > 0$:

1. the integrand is bounded in a neighborhood of 0, and in particular $p(0+) > -\infty$.
2. For large z, the fraction in the integral of the exponential is close to -1, and in particular $p(+\infty) = +\infty$.

If instead $\theta < 0$:

1. the innermost integrand is close to $1/(1 + 2\alpha|\theta|)$ for large values of z, so the outemost integrand grows exponentially fast as $y \to +\infty$; in particular $p(+\infty) = +\infty$.
2. For z close to 0, the fraction in the integral of the exponential is close to -1, and in particular $p(0+) > -\infty$.

We deduce $p(+\infty) = +\infty$, $p(0+) > -\infty$ in all cases.

Next, consider:

$$v(0+) := \int_{0+}^{1} \left\{ p'(x) \int_{x}^{1} \frac{2K|\theta|}{p'(y)(1 + 2\alpha|\theta| + y^{\theta})} dy \right\} dx. \tag{2.7}$$

Observe that:

$$p'(x) = \exp\left\{ 2K\mathbf{sign}(\theta) \int_{x}^{1} \frac{1 - z^{\theta}}{1 + 2\alpha|\theta| + z^{\theta}} dz \right\}; \tag{2.8}$$

consequently, for $\theta > 0$, p' is positive, continuous and bounded in a neighborhood of 0, and we easily verify from equation (2.7) that $v(0+)$ is finite in this case. In the case $\theta < 0$, the integrand in (2.8) is close to -1 in a neighborhood of 0; so, the innermost integrand in (2.7) is $O(y^{-\theta})$ in a neighborhood of 0; once again, we deduce $v(0+) < \infty$ in this case.

If $\theta = 0$, we obtain

$$p(x) = \int_{1}^{x} \exp\left\{ -2K \int_{1}^{y} \frac{\log(1/z)}{2\alpha + |\log(z)|} dz \right\} dy$$

and

$$v(0+) := \int_{0+}^{1} \left\{ p'(x) \int_{x}^{1} \frac{2K}{y(2\alpha + |\log(y)|)} dy \right\} dx.$$

The innermost integral in the definition of $p(x)$ converges to 1 when $z \to 0$ and to -1 when $z \to +\infty$, thus $p(0+) > -\infty$ and $p(+\infty) = +\infty$. In the definition of $v(0+)$, $p'(x)$ converges to a positive constant when $x \to 0$ and the innermost integral is $O(\log(\log(1/z)))$ when $z \to 0$, so $v(0+) < \infty$ and we conclude as above. $\square$

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