Self-regulation in infinite populations with fission-death dynamics

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ABSTRACT

The evolution of an infinite population of interacting point entities placed in $\mathbb{R}^d$ is studied. The elementary evolutionary acts are death of an entity with rate that includes a competition term and independent fission into two entities. The population states are probability measures on the corresponding configuration space and the result is the construction of the evolution of states in the class of sub-Poissonian measures, that corresponds to the lack of clusters in such states. This is considered as a self-regulation in the population due to competition.

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1. Introduction

1.1. Regulating population dynamics

Simple population dynamics models are mostly based on two evolutionary acts: disappearance (death) of an entity and procreation, in the course of which new entities join the population. A commonly accepted viewpoint on the evolution of a finite population of this kind is that it either dies out or grows ad infinitum being unhampered by habitat restrictions. Clearly, such restrictions can only be ignored if the population size is small, i.e., at the early stage of its development. In developed populations, environmental restrictions force the entities to compete with each other – a crowding effect. In the mentioned models, this effect manifests itself in a state-dependent increment of the death toll. In Verhulst's phenomenological theory based on the equation $\frac{d}{dt}N = \lambda N - (\mu + \alpha N)N$, such an increment is αN. Here $N = N(t)$ is the (expected) number of entities at time t, and positive λ and μ are the intrinsic procreation and death rates, respectively. Later on, Pearl and Reed rewrote this in the form of the logistic growth equation $\frac{d}{dt}N = rN(1 - N/K)$ with $r = \lambda - \mu$ and $K = r/\alpha$. The latter parameter gives rise to the notion of *carrying capacity* as the solution $N \equiv K$ is a stationary one, to which $N(t)$ tends in the limit $t \to +\infty$. Since then, this notion is used in the the-

ory of biological populations, see Introduction in [1], and not only in the context of the competition caused crowding effect. For instance, in the Galton–Watson model with binary fission considered in [2], the probability of fission of a member of generation n consisting of Z_n entities was taken to be $K/(K + Z_n)$. Thereby, the constructed process gets super- or subcritical under or over the level K, respectively. This aspect of the theory may be viewed as a phenomenological (mean-field-like) way of regulating the population dynamics. Here *regulating* means preventing the population from infinite growth and *mean-field* corresponds to imitating interactions as state-dependent external actions (fields), cf. [6, Sect. 13].

In the theory of populations with interactions explicitly taken into account, a usual assumption is that each entity interacts mostly (or even entirely) with the subpopulation located in a compact subset of the habitat. Then the local structure of the population is determined by the network of such interactions. Since a finite population occupies a compact set, it is always local as each of its members has a compact neighborhood containing the whole remaining population. Thus, in order to understand the global behavior of populations of this kind, one should take them infinite. In the statistical mechanics of interacting physical particles developed from phenomenological thermodynamics, this conclusion had led to the concept of the infinite-volume limit, see, e.g., [6, pp. 5, 6]. In this note, and in the accompanying paper [4] where all the technical details are presented, we introduce an individual-based model of an infinite population of point entities placed in $\mathbb{R}^d$ which undergo binary fission and death caused also by crowd-

ing (local competition). Its aim is to demonstrate that the local competition – interaction explicitly taken into account – can produce a global regulating effect. Here, however, one has to make precise the very notion of regulation as the considered population is already infinite. Instead of characterizing it by the number of constituents, we will look at the spatial distribution of the population by comparing it with the distribution governed by a Poisson law.

1.2. Presenting the result

Similarly as in [3], we deal with the phase space Γ consisting of all locally finite subsets $\gamma \subset \mathbb{R}^d$, called *configurations*. Local finiteness means that $\gamma_\Lambda := \gamma \cap \Lambda$ is finite whenever $\Lambda \subset \mathbb{R}^d$ is compact. For compact Λ and $n \in \mathbb{N}_0$, we then set $\Gamma^{\Lambda,n} = \{\gamma \in \Gamma : |\gamma_\Lambda| = n\}$, where $|\cdot|$ denotes cardinality, and equip Γ with the σ-field $\mathcal{B}(\Gamma)$ generated by all such $\Gamma^{\Lambda,n}$. This allows one to consider probability measures on Γ as states of the system. In a Poisson state, the entities are independently distributed over $\mathbb{R}^d$. A homogeneous Poisson measure $\pi_\varkappa$ with intensity $\varkappa > 0$ is characterized by its values on $\Gamma^{\Lambda,n}$ given by the following expression

$$\pi_\varkappa(\Gamma^{\Lambda,n}) = \frac{(\varkappa|\Lambda|)^n}{n!} \exp(-\varkappa|\Lambda|), \tag{1}$$

where $|\Lambda|$ stands for the Lebesgue measure of Λ. Note that $\pi_\varkappa(\Gamma_0) = 0$, for all $\varkappa > 0$, where Γ_0 is the set of all finite configurations. Let $\mathcal{P}(\Gamma)$ be the set of all probability measures on Γ. We say that a given $\mu \in \mathcal{P}(\Gamma)$ is *sub-Poissonian* if, for each compact Λ, all $n \in \mathbb{N}_0$ and some $\varkappa > 0$, the following holds

$$\mu(\Gamma^{\Lambda,n}) \leq \pi_\varkappa(\Gamma^{\Lambda,n}). \tag{2}$$

It is believed that sub-Poissonian states are characterized by the lack of *clustering*, typical to procreating populations with noninteracting (noncompeting) constituents, see the corresponding discussion in [3].

In dealing with states on Γ, one employs *observables* – appropriate functions $F : \Gamma \to \mathbb{R}$. Their evolution is obtained by solving the Kolmogorov equation

$$\frac{d}{dt} F_t = L F_t, \qquad F_t|_{t=0} = F_0, \qquad t > 0,$$

in which the operator L specifies the model. The model which we introduce here is based on the following evolutionary acts: (a) an entity located at x dies with rate (probability per unit time) $m(x) + \sum_{y \in \gamma \setminus x} a(x - y)$, where $m(x) \geq 0$ corresponds to a per se mortality and $a \geq 0$ is the competition kernel; (b) an entity located at x undergoes fission, with two offsprings going to y_1 and y_2 with rate $b(x|y_1, y_2)$. According to this, the operator L takes the form

$$(LF)(\gamma) = \sum_{x \in \gamma} \left(m(x) + \sum_{y \in \gamma \setminus x} a(x - y) \right) [F(\gamma \setminus x) - F(\gamma)]$$

$$+ \sum_{x \in \gamma} \int_{(\mathbb{R}^d)^2} b(x|y_1, y_2) [F(\gamma \setminus x \cup \{y_1, y_2\}) - F(\gamma)] dy_1 dy_2. \tag{3}$$

In expressions like $\gamma \cup x$, we treat x as the singleton $\{x\}$. Note that the fission rate is state-independent. Regarding a, m and b we assume that: (a) $a : \mathbb{R}^d \to [0, +\infty)$ is a piece-wise continuous function such that $a(x) = 0$ whenever $|x| > r$ for some positive $r < \infty$; (b) $m : \mathbb{R}^d \to [0, +\infty)$ is measurable and bounded; (c) the fission kernel is translation invariant in the sense that

$b(x + z|y_1 + z, y_2 + z) = b(x|y_1, y_2)$ holding for all $z \in \mathbb{R}^d$; (d) the function $\beta : \mathbb{R}^d \to [0, +\infty)$ defined by

$$\beta(y_1 - y_2) = \int_{\mathbb{R}^d} b(x|y_1, y_2) dx \tag{4}$$

is piece-wise continuous and such that $\beta(x) = 0$ whenever $|x| > R$ for some positive $R < \infty$; (e) $\beta(x) = \beta(-x)$ for all $x \in \mathbb{R}^d$ and the following holds

$$\int_{\mathbb{R}^d} \beta(y) dy = \int_{(\mathbb{R}^d)^2} b(x|y_1, y_2) dy_1 dy_2 =: \langle b \rangle < \infty. \tag{5}$$

Note that the translation invariance and the finite-range property are imposed here only to make the presentation of the model and the results as simple as possible. The version studied in [4] is characterized by less restrictive conditions. Note also that we do not exclude the case where b is a distribution. For instance, by setting

$$b(x|y_1, y_2) = \frac{1}{2} (\delta(x - y_1) + \delta(x - y_2)) \beta(y_1 - y_2),$$

we obtain the Bolker–Pacala model [3] as a particular case of our model.

Remark 1. The function β describes the dispersal of siblings, which compete with each other. As in the Bolker–Pacala model, here the following situations may occur:

- *Short dispersal:* there exists $\omega > 0$ such that $a(x) \geq \omega \beta(x)$ for all $x \in \mathbb{R}^d$; corresponds to $R \leq r$.
- *Long dispersal:* for each $\omega > 0$, there exists $x \in \mathbb{R}^d$ such that $a(x) < \omega \beta(x)$; corresponds to $R > r$.

The direct use of L as a linear operator in an appropriate Banach space is possible only if one restricts the consideration to states on Γ_0, see [4, Sect. 3]. Otherwise, the sums in (3) – taken over infinite configurations – may not exist. In view of this, we proceed as follows. Let $C_0(\mathbb{R}^d)$ stand for the set of all continuous real-valued functions with compact support. Then the map

$$\Gamma \ni \gamma \mapsto F^\theta(\gamma) := \prod_{x \in \gamma} (1 + \theta(x)), \qquad \theta \in \Theta,$$

$$\Theta := \{\theta \in C_0(\mathbb{R}^d) : \theta(x) \in (-1, 0]\},$$

is measurable and satisfies $0 < F^\theta(\gamma) \leq 1$ for all γ. It is possible to show, see [4], that $\{F_\theta : \theta \in \Theta\}$ is a measure defining class. That is, for each two $\mu, \nu \in \mathcal{P}(\Gamma)$, it follows that $\mu = \nu$ whenever $\mu(F^\theta) := \int F^\theta d\mu = \int F^\theta d\nu =: \nu(F^\theta)$ holding for all such F^θ. Moreover, under the mentioned above assumption that both a and b in (3) have finite range, $(LF^\theta)(\gamma)$ can be calculated for each $\gamma \in \Gamma$ and $\theta \in \Theta$. We prove that, for each $\mu_0 \in \mathcal{P}_{\exp}(\Gamma)$, there exists the map $[0, +\infty) \ni t \mapsto \mu_t \in \mathcal{P}_{\exp}(\Gamma)$ such that $\mu_t|_{t=0} = \mu_0$, the map $(0, +\infty) \ni t \mapsto \mu_t(F^\theta)$ is continuously differentiable and the following holds

$$\frac{d}{dt} \mu_t(F^\theta) = \mu_t(LF^\theta). \tag{6}$$

Here $\mathcal{P}_{\exp}(\Gamma)$ is a class of measures each element of which is sub-Poissonian, see below, and such that $\mu(LF^\theta) < \infty$.