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Stochastic Geometry for Population-Dynamic Modeling: A Dieckmann Model with Immovable Individuals

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Abstract—A study is performed of the main approaches to investigating the stochastic process of population dynamics. Continuous time and space and immovable individuals are used to derive a denumerable system of integrodifferential equations corresponding to the dynamics of the spatial momentum of this process. A way to find an approximate solution using the momentum approach is described.

Keywords: mathematical modeling, integrodifferential equations, mathematical biology.

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1. INTRODUCTION

In recent years, computer modeling has become ever more important in different lines of research. Contemporary information technologies clarify the effect of one natural-science agent or another has on the final behavior of a considered system. This promotes a better understanding of the dependences between the objects of a system and helps to coordinate the model with real observations. In this work, we consider a model of a stationary biological society. This model was proposed in [1, 2] and studied in e.g., [3–6]. The main aim of this work is to interpret and formalize the specified model from a mathematical viewpoint and derive the main equations for the dynamics of spatial momentum.

To understand the reasons for the emergence of this model, compare the earlier descriptions of population dynamics. The simplest and best known models are the Verhulst equation and Lotka–Volterra equations for one or several continuous- quantity species. They have analytical solutions, and there are numerical ways of finding solutions for several species. These models are easily extended: these included seasonality (see [7]) and delays affecting quantities [8]), and of modeling noise using random perturbations and stochastic integration [8]. However, they cannot describe the spatial structure of a population, which can substantially affect numbers and the conditions of species coexistence. Cellular automata with determinate and stochastic rules are used to model spatial dynamics [9], but investigation of such models is hindered by the complexity of deriving the dependence of automaton behavior on variations in parameters, and by the need for a great deal of modeling to investigate the space of parameters and initial-value conditions. Reaction–diffusion equations allow us to describe the spatial structure of a population with weak intermixing caused by motion [10]), but they cannot describe immovable populations. The model proposed by Dieckmann and Law solves that problem of modeling population dynamics for plant societies with complex spatial structures.

The spatial population-dynamics model proposed by Dieckmann and Law requires a multidisciplinary approach. Many problems arise in working with this model. These include stating the problem and selecting the core biological characteristics of the modeled process; implementing the software for the stochastic process in a bound region; the relation between the spatial-dynamics process in bound and unbound regions; the statistical test of hypotheses for the bounded-region process; finding solutions

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for the process dynamics; the closure of momentum equations for stochastic point processes (allowing us to find approximate solutions for the first and second momentum); conditions of existence for solutions; and ways of seeking solutions for closed momentum equations.

In this work, we review all available results related to the mathematical formalization of this model.

2. DISCRETE POPULATION DYNAMICS: THE STOCHASTIC SPATIAL DIECKMANN–LAW MODEL

This model was first presented in [1, 2]. It allows us to describe the population dynamics of individuals who do not move during their lives (e.g., plants). The principles of this model are described locally: all possible events can be considered on the example of the interaction between two individuals. We set the following values for one individual at point x_0: mortality d (which does not depend on time and other individuals); lifetime $t_d \sim \text{Exp}(\lambda = d)$ of an isolated individual, which is a random variable distributed exponentially; and time $t_b \sim \text{Exp}(\lambda = b)$ before the birth of a new individual, which is a random variable distributed exponentially with parameter b.

If a new individual is born, it can appear close to an earlier one: the distance is given by a random value with given distribution $m(x)$, $x_b \sim m(x - x_0)$. Competitive mortality is given by function $W(\xi)$; for convenience, it is divided into parameter d' and function $w(\xi)$ normed by 1 (i.e., a function such that its integral over the entire region is 1). For two individuals, the competitive mortality of one of them is random variable distributed exponentially with parameter $d'w(x_0 - x_1)$, $t_{d'} \sim \text{Exp}(\lambda = d'w(x_0 - x_1))$.

Finally, the birth rate and mortality function are assumed to be radially symmetric, while the process itself is considered in k dimensions, $k = 1, 2, 3$. To study the global properties of the resulting models, we postulate that the distribution of individuals does not depend on coordinates and does not change with translations and rotations (i.e., it is stationary). It is impossible for two individuals to be located at one point, and an event in which two events occur at the same time cannot have nonzero probability (i.e., we have a Markov field for k spatial dimensions and one time dimension). The behavior of this process on set $\mathbb{R}^k \oplus \mathbb{R}_+$ can be studied using the theory of stochastic point processes [11].

3. DERIVING DYNAMIC EQUATIONS

Let us consider possible events in a closed bound set D with a small diameter that can exist in short time interval δt. If the initial-value condition of the stochastic point process is Φ_t, the probabilities of the birth and death in this set during this time interval are

$$f^+(x^+|\Phi_t) = \mathbb{P}(x^+ \in \Phi_{t+\delta t}/\Phi_t \cap D) = \left[b \sum_{x_0 \in \Phi_t} m(x_0 - x^+)|D| \right] \delta t + \overline{o}(\delta t)$$

and

$$f^-(x^-|\Phi_t) = \mathbb{P}(x^- \in \Phi_t/\Phi_{t+\delta t} \cap D) = N_t(D) \left[d + d' \sum_{\substack{x_0 \in \Phi_t \\ x_0 \neq x^-}} w(x_0 - x^-) \right] \delta t + \overline{o}(\delta t)$$

respectively.

Let $\Delta N_{\delta t}(D)$ be a random variable equal to the variation in quantity in region D during time interval δt. Then it is equal to the difference between f^+ and f^-:

$$\Delta N_{\delta t}(D) = \left[b \sum_{x_0 \in \Phi_t} m(x_0 - x^+)|D| - N_t(D) \left[d + d' \sum_{\substack{x_0 \in \Phi_t \\ x_0 \neq x^-}} w(x_0 - x^-) \right] \right] \delta t + \overline{o}(\delta t).$$

We take the expectations of both sides and divide them by δt and $|D|$. We then have relation

$$\frac{\mathbb{E}\Delta N_{\delta t}(D)}{\delta t|D|} = b\mathbb{E}\sum_{x_0\in\Phi_t} m(x_0-x^+) - \frac{d}{|D|}\mathbb{E}\sum_{x_0\in\Phi_t}\mathbb{1}_D(x_0) - \frac{d'}{|D|}\mathbb{E}\sum_{\substack{x_0,x^-\in\Phi_t\\ x_0\neq x^-\\ x^-\in D}} w(x_0-x^-) + \overline{o}_t(1).$$

Moving to the limit as the diameter of region D tends to zero (diam(D) $\to 0$), and considering the definitions of the first and second factorial momentum, we find that

$$\frac{\Delta g_1(x_1,t)}{\delta t} = b\int m(x_0-x_1)g_1(x_0,t)dx_0 - dg_1(x_1,t_1)$$
$$-d'\int w(x_0-x_1)g_2(x_1,x_2,t)dx_0 + \overline{o}_t(1).$$

The process is stationary, so we may assume that the second moment depends only on the relative distance, and the value of the first moment in the spatial coordinates is constant. Translation $\delta t \to 0$ yields the dynamic equation for the first moment:

$$\frac{\partial g_1(t)}{\partial t} = (b-d)g_1(t) - d'\int w(\xi)g_2(\xi,t)d\xi.$$

The same procedure can be used to find the dynamic equation for an arbitrary moment. We take n closed bound disjoint regions $D_1,\dots,D_n$ such that their shape and size are the same and the diameter is small, and we consider the probabilities of the variation in quantity in these regions. Our concern is random variable $\Delta[N_{\delta t}(D_1)\dots N_{\delta t}(D_n)]$, which is equal to the variation in quantity in domains $D_1,\dots,D_n$ during time interval δt. Since the process is stationary, it follows that

$$\Delta N_{\delta t}(D_1) = \Delta N_{\delta t}(D_k) \quad \forall k = 2,\dots,n.$$

In light of this and the Markov property, we obtain the relation

$$\Delta[N_{\delta t}(D_1)\dots N_{\delta t}(D_n)] = n\Delta N_{\delta t}(D_1)N_{\delta t}(D_2)\dots N_{\delta t}(D_n) + \overline{o}(\delta t).$$

Using the expression for $\Delta N_{\delta t}(D)$, we obtain the equation for the dynamics of variation:

$$\Delta[N_{\delta t}(D_1)\dots N_{\delta t}(D_n)] = nN_{\delta t}(D_2)\dots N_{\delta t}(D_n)$$
$$\times\left[b\sum_{\substack{x_0\in\Phi_t\\ x^+\in D_1}} m(x_0-x^+)|D_1| - N_{\delta t}(D_1)\left(d + d'\sum_{\substack{x_0\in\Phi_t\\ x_0\neq x^-\\ x^-\in D_1}} w(x_0-x^-)\right)\right]\delta t + \overline{o}(\delta t).$$

Dividing both sides by $n|D_1|\dots|D_n|\delta t$ and taking the expectation of both sides, we obtain

$$\frac{\mathbb{E}\Delta[N_{\delta t}(D_1)\dots N_{\delta t}(D_n)]}{n|D_1|\dots|D_n|\delta t} = \mathbb{E}\left[\frac{N_{\delta t}(D_2)\dots N_{\delta t}(D_n)}{|D_2|\dots|D_n|}\left(b\sum_{\substack{x_0\in\Phi_t\\ x^+\in D_1}} m(x_0-x^+)\right)\right]$$
$$-\mathbb{E}\left[\frac{N_{\delta t}(D_1)\dots N_{\delta t}(D_n)}{|D_1|\dots|D_n|}\left(d + d'\sum_{\substack{x_0\in\Phi_t\\ x_0\neq x^-\\ x^-\in D_1}} w(x_0-x^-)\right)\right] + \overline{o}_t(1).$$

We decompose the right-hand side of the relation into three parts and use the definition of indicators. Our goal is to obtain sums over reliably different points in order to move on to factorial moments afterwards. For the right-hand side, we obtain

$$\mathbb{E}\left[\frac{b}{|D_2|\dots|D_n|}\sum_{\substack{x_0\in\Phi_t\\ x^+\in D_1\\ x_2\in D_2,\dots,x_n\in D_n\\ x_0\neq x_k\forall k=2,\dots,n}} m(x_0-x^+)\right]+\mathbb{E}\left[\frac{b}{|D_2|\dots|D_n|}\sum_{\substack{k=2,\dots,n\\ x^+\in D_1\\ x_2\in D_2,\dots,x_n\in D_n}} m(x_k-x^+)\right]$$

$$-\mathbb{E}\left[\frac{d}{|D_1|\dots|D_n|}\sum_{\substack{x_0\in D_1\\ x_2\in D_2,\dots,x_n\in D_n}} w(x_0-x^-)\right]-\mathbb{E}\left[\frac{d'}{|D_1|\dots|D_n|}\sum_{\substack{x_0\in\Phi_t\\ x^-\in D_1\\ x_2\in D_2,\dots,x_n\in D_n\\ x_0\neq x_k\forall k=2,\dots,n}} w(x_0-x^-)\right]$$

$$-\mathbb{E}\left[\frac{d'}{|D_1|\dots|D_n|}\sum_{\substack{k=2,\dots,n\\ x^-\in D_1\\ x_2\in D_2,\dots,x_n\in D_n}} w(x_k-x^-)\right] \tag{1}$$

The initial two terms of Eq. (1) correspond to the birth rate; the third, to unconditional mortality; and the last two, to competitive mortality. Moving on to the limit as the size of the regions tends to zero, we obtain the relation

$$\begin{aligned}\frac{1}{n}\frac{\Delta g_n(x_1,\dots,x_n,t)}{\delta t}&=b\int m(x_0-x_1)g_n(x_0,x_2,\dots,x_n,t)dx_0\\ &+b\sum_{k=2,\dots,n} m(x_k-x_1)g_{n-1}(x_2,\dots,x_n,t)\\ -dg_n(x_1,\dots,x_n,t)&-d'\int w(x_{n+1}-x_1)g_{n+1}(x_1,\dots,x_{n+1},t)dx_{n+1}\\ &-d'\sum_{k=2,\dots,n} w(x_k-x_1)g_n(x_1,\dots,x_n,t)+\overline{o}_t(1).\end{aligned}$$

Moving to the limit as $\delta t\to 0$ and applying changes $\xi_1=x_2-x_1,\dots,\xi_{n-1}=x_n-x_1$, we obtain the dynamic equations

$$\begin{aligned}\frac{1}{n}\frac{\partial g_n(\xi_1,\dots,\xi_{n-1},t)}{\partial t}&=b\int m(\xi_0)g_n(\xi_1-\xi_0,\dots,\xi_{n-1}-\xi_0,t)d\xi_0\\ +b\sum_{k=1,\dots,n-1} m(\xi_k)&g_{n-1}(\xi_2-\xi_1,\dots,\xi_{n-1}-\xi_1,t)-dg_n(\xi_1,\dots,\xi_{n-1},t)\\ -d'\int w(\xi_0)&g_{n+1}(\xi_1,\dots,\xi_n,t)d\xi_n-d'\sum_{k=2,\dots,n} w(\xi_k)g_n(\xi_1,\dots,\xi_{n-1},t).\end{aligned}$$

For the second moment in particular, we have the equation

$$\begin{aligned}\frac{1}{2}\frac{\partial g_2(\xi_1,t)}{\partial t}&=b\int m(\xi_0)g_2(\xi_1-\xi_0,t)d\xi_0+bm(\xi_1)g_1(t)-dg_2(\xi_1,t)\\ &-d'w(\xi_1)g_2(\xi_1,t)-d'\int w(\xi_2)g_3(\xi_1,\xi_2,t)d\xi_2.\end{aligned}$$

For the third moment, we have the equation

$$\frac{1}{3}\frac{\partial g_3(\xi_1,\xi_2,t)}{\partial t} = b\int m(\xi_0)g_2(\xi_1-\xi_0,\xi_2-\xi_0,t)d\xi_0 + b\Big(m(\xi_1)+m(\xi_2)\Big)g_2(\xi_2-\xi_1,t)$$
$$- dg_3(\xi_1,\xi_2,t) - d'\Big(w(\xi_1)+w(\xi_2)\Big)g_3(\xi_1,\xi_2,t) - d'\int w(\xi_3)g_4(\xi_1,\xi_2,\xi_3,t)d\xi_3.$$

When $m(x) = w(x)$ and $d = 0$, we can obtain an analytic solution of the kind $g_n(x_1,\ldots,x_n,t) = \left(\frac{b}{d'}\right)^n$, which corresponds to the simple Poisson point process with intensity $\frac{b}{d'}$ and yields a nontrivial equilibrium state for the process of the spatial population dynamics.

4. EQUILIBRIUM AND CLOSING EQUATIONS

Our concern is the possible equilibrium states of the following system for when the derivative of each moment with respect to time is equal to zero:

$$(b-d)g_1(t) - d'\int w(\xi)g_2(\xi,t)d\xi = 0,$$
$$b\int m(\xi_2)g_2(\xi_1-\xi_2,t)d\xi_2 + bm(\xi_1)g_1(t) - dg_2(\xi_1,t)$$
$$- d'w(\xi_1)g_2(\xi_1,t) - d'\int w(\xi_2)g_3(\xi_1,\xi_2,t)d\xi_2 = 0.$$

We see that the dynamic equations for the nth spatial factorial moment include terms with the $(n+1)$th spatial moment. To resolve this incongruency, we use the closing technique broadly applied in physics. The closure of a spatial moment is treated as the expression of the kth moment via momentum of lower orders.

Closures for the third moment are the most studied closures. The first moment allows us to determine the mean quantity; the second, how the individuals are clustered and isolated. The closing of the second moment through the first is uniquely defined and reduced to the Verhulst equation for the expected density of quantity. This was studied in detail in [12]. There are many ways of closing of the third moment through the second and the first. They all satisfy the restrictions

(1) $\lim\limits_{|\xi_2|\to\infty} g_3(\xi_1,\xi_2) = g_2(\xi_1)g_1;$

(2) $\lim\limits_{|\xi_1|\to\infty} g_3(\xi_1,\xi_2) = g_2(\xi_2)g_1;$

(3) if $g_2(\xi_1) = g_1^2$, then $g_3(\xi_1,\xi_2) = g_1^3$.

Several candidates for suitable closures of spatial moments were proposed in [12]:

(1) $g_3^{(1)}(\xi_1,\xi_2) \approx g_2(\xi_1)g_2(\xi_2)/g_1;$

(2) $g_3^{(2)}(\xi_1,\xi_2) \approx g_2(\xi_1)g_1 + g_2(\xi_2)g_1 + g_2(\xi_1-\xi_2)g_1 - 2g_1^3;$

(3) $g_3^{(3)}(\xi_1,\xi_2) \approx \frac{1}{2g_1}\big(g_2(\xi_1)g_2(\xi_2) + g_2(\xi_1)g_2(\xi_2-\xi_1) + g_2(\xi_2)g_2(\xi_2-\xi_1) - g_1^4\big);$

(4) $g_3^{(4)}(\xi_1,\xi_2)) \approx \dfrac{g_2(\xi_1)g_2(\xi_2)g_2(\xi_2-\xi_1)}{g_1^3};$

(5) $g_3^{(5)}(\xi_1,\xi_2) \approx \alpha g_3^{(1)} + (1-\alpha)g_3^{(3)}.$

Integral equations obtained after closing $g_3^{(1)}$ and $g_3^{(5)}$ were investigated earlier mathematically. In [3, 13, 14], it was shown that substituting the closure of $g_3^{(1)}$ produces a linear integral equation that has no solutions unless major restrictions are imposed on parameters of the model (relation $d = 0$ is a necessary condition).

The closing of $g_3^{(5)}$ produces a nonlinear Hadamard correct integral equation. Sufficient conditions for the existence of a unique solution to the obtained equation were found in [15]. This shows that selecting a suitable closure for the third spatial moment is a fairly nontrivial problem.

It is of interest to design a software complex that performs computer simulations of the considered model and compare the results and numerical solutions to integral equations obtained by closing the latter.

Note that once the third moment is closed, we cannot distinguish between processes with equal momentum of the first and second order and different moments of orders higher than two (e.g., the simple Poisson process and the onepresented in [16]). Our concern is thus closures that providing the best approximation of the third moment in the context of equations of spatial dynamics. The search for optimum closures that work over the set of equilibrium solutions to equations of spatial dynamics is thus an active line of research.

5. DYNAMIC EQUATIONS: SYMMETRY OF SCALE

For the population-dynamic process, we can change the coordinate system and use one solution for the momentum of the process in order to obtain solutions for a family of parameters.

Time scaling. We change the variable as $\tilde{t} = \tau t$ and obtain the dynamic equations for the first moment:

$$\frac{\partial g_1\left(\frac{1}{\tau}\tilde{t}\right)}{\partial \tilde{t}} = \tau(b-d)g_1\left(\frac{1}{\tau}t\right) - \tau d' \int w(\xi) g_2\left(\xi, \frac{1}{\tau}\tilde{t}\right) d\xi.$$

We obtain the correspondence between solutions and parameters:

$$\begin{gathered}\tilde{t} = \tau t, \quad \tilde{w} = w, \\ \tilde{b} = \tau b, \quad \tilde{d}' = \tau d', \\ \tilde{d} = \tau d, \quad \tilde{m} = m, \\ \tilde{g}_n(x_1, \ldots, x_n, \tilde{t}) = g_n(x_1, \ldots, x_n, \tau t). \end{gathered} \tag{2}$$

This scaling provides no new solutions to the equilibrium equations.

Spatial scaling. We change the variable as $\tilde{x} = lx$ and obtain the dynamic equations for the first moment:

$$\frac{\partial g_1\left(\frac{1}{l}\tilde{x}_1, t\right)}{\partial t} = (b-d)g_1\left(\frac{1}{l}\tilde{x}_1, t\right) - d' \int w\left(\frac{1}{l}\tilde{\xi}\right) g_2\left(\frac{1}{l}\tilde{\xi}, t\right) d\left(\frac{1}{l}\tilde{\xi}\right).$$

We obtain the dynamic equations for the first moment (where d is the number of measurements):

$$\begin{gathered}\tilde{x} = lx, \quad \tilde{w}(\tilde{x}) = l^k w(lx), \\ \tilde{b} = b, \quad \tilde{d}' = \frac{1}{l^k} d', \\ \tilde{d} = d, \quad \tilde{m}(\tilde{x}) = l^k m(lx), \\ \tilde{g}_n(\tilde{x}_1, \ldots, \tilde{x}_n, t) = l^{kn} g_n(lx_1, \ldots, lx_n, t). \end{gathered} \tag{3}$$

With normal kernels parametrized by dispersion, this scaling allows us to obtain new solutions within the family of parameters.

6. MIXED INITIAL-VALUE CONDITIONS AND PLURALITY OF SOLUTIONS OF EQUILIBRIUM EQUATIONS

Each stationary process almost certainly contains either zero or an infinite set of points [11]. In the context of the spatial-dynamic process, the probability of transitioning from one mode to another during a finite time interval is equal to zero. Equilibrium equations treated as integrodifferential equations have at least one solution. However, we can investigate the case of mixed initial-value conditions corresponding to two equilibrium states. Such an initial-value condition remains stationary and preserves Markov's property.

We assume there exists a solution to the equilibrium equation for collection b, d, d', m, w of parameters. Let us construct a family of equilibrium states for spatial-dynamic processes. We take solution

$$g_1(x_1), g_2(x_1, x_2), \dots, g_n(x_1, \dots, x_n)$$

to the equilibrium equation.

We select probability p and use the stochastic point process as the initial-value conditions. It corresponds to the solution to an equilibrium equation with probability p and is equal to zero with probability $1 - p$. The resulting point process is in equilibrium with the population dynamics. The momentum of this process's areas is

$$\tilde{g}_1(x_1) = p g_1(x_1),$$

$$\tilde{g}_2(x_1, x_2) = p^2 g_2(x_1, x_2),$$

and

$$\tilde{g}_n(x_1, \dots, x_n) = p^n g_n(x_1, \dots, x_n).$$

The equilibrium equation thus does not provide all possible solutions for equilibrium states. To resolve this problem, one we can, e.g., add the unconditional birth-rate. This reduces the probability of being in the zero state up to zero and restores the connectedness of the spatial-dynamic process. If the added unconditional birth-rate is a simple Poisson flow with intensity ε, the initial two equilibrium equations take the form

$$(b - d)g_1(t) - d' \int w(\xi) g_2(\xi, t) d\xi = -\varepsilon$$

and

$$b \int m(\xi_2) g_2(\xi_1 - \xi_2, t) d\xi_2 + b m(\xi_1) g_1(t) - d g_2(\xi_1, t)$$
$$- d' w(\xi_1) - g_2(\xi_1, t) - d' \int w(\xi_2) g_3(\xi_1, \xi_2, t) d\xi_2 = -\varepsilon g_1(t).$$

We plan to prove in the future that the regularized equilibrium equation has only one solution that uniquely defines the limit point of the regularized process of the population dynamics for arbitrary stationary initial-value conditions that have Markov's property.

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