Spatial Models of Population Processes

Stanislav Molchanov and Joseph Whitmeyer

Abstract Recent progress has been made on spatial mathematical models of population processes. We review a few of these: the spatial Galton–Watson model, modern versions that add migration and immigration and thereby may avoid the increasing concentration of population into an ever smaller space (clusterization), models involving a random environment, and two versions of the Bolker–Pakala model, in which mortality (or birth rate) is affected by competition.

Keywords Population process · Galton–Watson model · Mean-field model
Bolker–Pacala model · Random environment

1 Introduction

Recent advances have been made in developing mathematical models for population processes over a large spatial scale, with application primarily to biological populations other than humans (e.g., [2, 3, 15]). Here, we discuss some of this work and its possible application to human populations. This work may be seen as the development of baseline models, which show the processes and patterns that emerge from basic regenerative and migration processes, prior to economic political, and social considerations. Note that in keeping with the universality of these models as

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well as their simplicity, we will use the neutral terminology of “particles” for population members. These models are in the spirit of a general approach to population dynamics as part of statistical physics (e.g., work carried out by Y. Kondratiev and his group [15, 16]).

We use these models to focus on two questions: the long-run spatial distribution and the temporal fluctuations of a population. We are particularly interested in models that describe two common features of empirical populations, stationarity in space and time and strong deviations from the classical Poissonian picture, i.e., spatial intermittency in the distribution of species (clusterization or “patches”). Let us elaborate. By stationarity, we mean roughly that the stochastic process in question depends neither on the time we begin observing it nor on the place where we observe it. Mathematically, we will take this to mean that the mean and the variance of the number of particles at a given location do not depend on either the location or the time. Empirically, this is unlikely to be completely true, for there will be ecological features that make some places more favorable to population growth than others, and events such as climatic change occur that make some stretches of time more propitious than others for population growth. Nevertheless, variation in such conditions may not be very great and stationarity is often a reasonable first approximation for many populations. Stationarity also may be a goal in some modern human societies. As for clusterization, we note that random spatial placement of population members will result in a spatial Poisson distribution, which we might describe as mild clumping of the population. Nevertheless, a variety of empirical populations, from humans to other biological populations (e.g., tropical arboreal ants [21]) to even stars, display a higher degree of clusterization than that; in the extreme, situations where there are relatively sparse locations with high population concentrations isolated by vast unpopulated regions.

Again, these are baseline, simple models. We assume an isolated population that is not involved in complex multipopulation interaction (such as a predator–prey scheme). Most of the models we discuss are branching processes or developments of branching processes and, as is typical for these processes, exclude direct interaction between particles, although in some the birth–death mechanism can create a kind of mean-field attractive potential. We discuss a model that allows inhibition or stimulation to particle reproduction due to the presence of existing particles. Both kinds of models satisfy the Markov property, namely, that evolution of the system from time t depends only on the state of the system at time t and not additionally on its state before time t.

The organization of this paper is as follows. We begin with the background to these models, the simple nonspatial Galton–Watson process. We then present nine models, roughly in order of increasing complexity. The first three lack spatial dynamics: the spatial Galton–Watson process, which produces a high level of clusterization, the same model but with immigration added, and a mean-field approximation to the Bolker–Pacala model, which is characterized by intra-population competition. The second set of six models allow migration in various ways, including one with immigration as well, two involving something of a random environment, and a multilayered Bolker–Pacala model with migration between layers.

2 Mean-Field Models

2.1 Galton–Watson Model

Recent applications of these models have been to organisms such as trees, crabgrass, and butterflies. This line of work began, however, with humans. In 1873, Francis Galton posed a problem [7] concerning the extinction of surnames, i.e., the extinction of male lines of descendants. He wanted to know, given the probability of a given number of male offspring per male, what proportion of surnames would disappear and how many people would hold a surname that survived. In 1874, Galton and the Reverend Henry William Watson published the first mathematical treatment of what has become known as the Galton–Watson process [8].

The Galton–Watson (GW) process is a simple example of a branching process [13], a term for stochastic processes arising from incorporating probability theory into population processes [12]. Both continuous- and discrete-time versions of this model exist. In the continuous-time version of the GW process, a particle in an infinitesimal period of time dt produces one offspring with probability $\beta\, dt$ and disappears (dies) with probability $\mu\, dt$. If it produced an offspring, then there are two particles, each of which can produce an offspring or die, and the process continues in the same fashion. It is well known that the entire population, encompassing all lines, becomes extinct with probability 1 for $\mu \geq \beta$. Equal birth and death rates, $\beta = \mu$, are known as the critical case. Only when $\beta > \mu$ (the supercritical case), there is a positive probability that extinction does not occur. In fact, in this case the population follows the predictions of the Reverend Malthus [19] and grows exponentially: $En(t) = N_0 e^{(\beta-\mu)t}$, where E means to take the expectation, $n(t)$ denotes the population at time t, and N_0 is the initial population [11].

A model of population processes in space may be obtained by extending the Galton–Watson process by considering independent GW processes occurring in space. Specifically, we can consider a random point field $n(t, x)$ in the d-dimensional lattice $\mathbb{Z}^d$, with a critical GW process at each occupied point and no interaction or movement in space. It is possible also to consider the branching process models in d-dimensional Euclidean space $\mathbb{R}^d$, but in this paper we treat only the lattice; results are similar for the two settings. For our applications, generally, $d = 2$. Assume that $n(0, x)$ is the initial point field on $\mathbb{Z}^d$, given by the Bernoulli law: for any independent $x \in \mathbb{Z}^d$, $P\{n(0, x) = 1\} = \rho_0$, $P\{n(0, x) = 0\} = 1 - \rho_0$, where ρ_0 is the initial density of the population members. Assume now that each initial population member (located at x for $n(0, x) = 1$) generates its own family, concentrated at the same location $x \in \mathbb{Z}^d$. Assume that the corresponding Galton–Watson processes $n(t, x)$, $t \geq 0, x \in \mathbb{Z}^d$, are critical, i.e., $\beta = \mu$. The result is a field $n(t, x)$ with independent values and constant density: $En(t, x) \equiv \rho_0$.

For large t, in this model, the majority of the cells $x \in \mathbb{Z}^d$ will be empty because $P\{n(t, x) = 0\} = \frac{\beta t}{1+\beta t} = 1 - \frac{1}{\beta t} + O(\frac{1}{t^2})$ (which gives the formula $P\{n(t, x) = 0 \mid n(0, x) = N_0\} \sim e^{-N_0/\beta t}$) [9]. The populated points, moreover, are increasingly sparse (of order $\frac{1}{\beta t}$) and contain increasingly large families (of order βt). This is the phenomenon of clusterization: the population consists of large dense groups of particles separated by large distances (the distances will be of order $t^{1/d}$, so the square root of t in two dimensions). As $t \to \infty$, the clusterization becomes stronger and stronger. Figure 1 illustrates this phenomenon by showing three progressive moments of a simulated critical spatial Galton–Watson process in discrete time on a 10×10 lattice. The initial distribution is a spatial Poisson distribution (and so at $t = 1$, the distribution is still close to spatially Poissonian). Again, being critical, the birth and death rates are equal: $\beta = \mu = \frac{1}{2}$.

2.2 Spatial Galton–Watson Process with Immigration

One simple addition to the spatial GW process is to allow immigration, that is, the appearance of a new particle at a site, uninfluenced by the presence of particles at that site or other sites. Adding immigration has two advantages. First, it increases the realism of the model. Second, it helps to alleviate the concern that the total population size is stable only in the critical case, that is, if the birth rate and death rate are precisely and, in many situations, improbably equal ($\beta = \mu$). An analysis of this model may be found in Sect. 2.1 of the preceding chapter in this volume, by Han et al. We refer the reader to that section.

2.3 Bolker–Pakala Model in Mean-Field Approximation

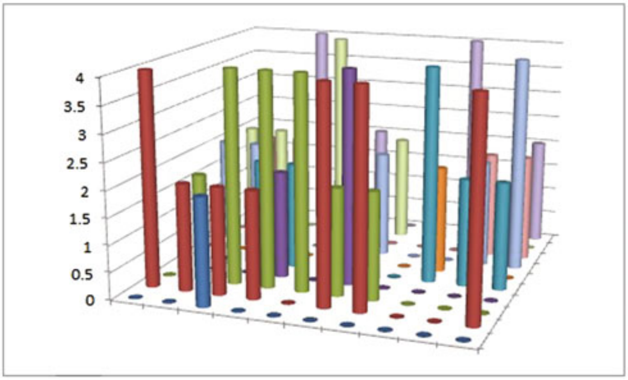
The fact that in the preceding branching process models the population is stable only in a narrow critical condition, e.g., that $b = \mu$ in the Galton–Watson model, or simply due to immigration in the model with independent immigration, may not be entirely satisfactory. In the first case, there is no obvious reason why the critical condition should hold; in the second, the results seem to rest on the extreme simplicity of the model of immigration.

One alternative model that yields a stable distribution more robustly is the Bolker–Pacala model [2, 3]. The Bolker–Pacala model, well known in the theory of population dynamics, is a stochastic spatial model that incorporates both spatial dynamics and competition. The general Bolker–Pacala model can be formulated as follows.

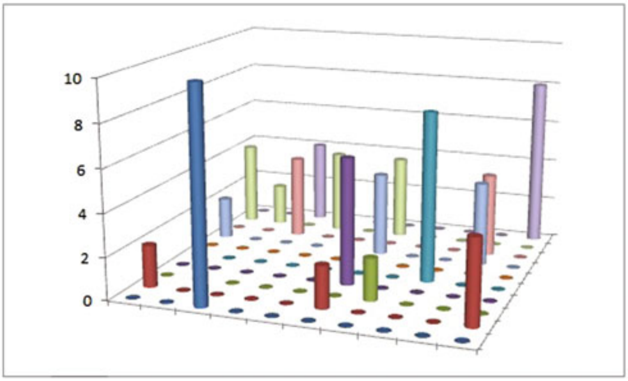
At time $t = 0$, we have an initial homogeneous population, that is, a locally finite point process

$$n_0(\Gamma) = \#(\text{individuals in } \Gamma \text{ at time } t = 0),$$

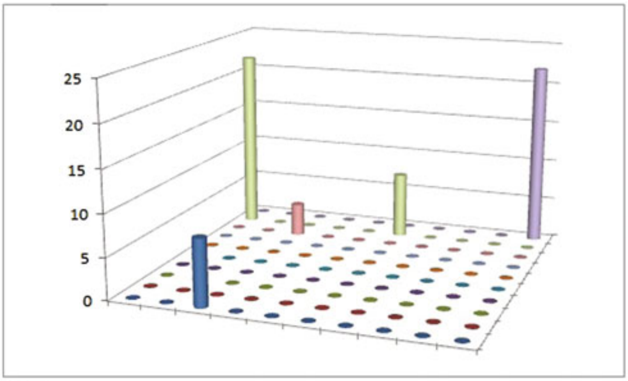
where Γ denotes a bounded and connected region in $\mathbb{R}^d$. The simplest option is for $n_0(\Gamma)$ to be a Poissonian point field with intensity $\rho > 0$, i.e.,



a) After 1 time step.



b) After 5 time steps.



c) After 20 time steps.

Fig. 1 Critical ($\beta = \mu = 1/2$) spatial Galton–Watson process at three times

$$P\{n_0(\Gamma) = k\} = \exp(-\rho|\Gamma|)\frac{(\rho|\Gamma|)^k}{k!}, \ k = 0, 1, 2, \ldots$$

where $|\Gamma|$ is the finite Lebesgue measure of Γ. The following rules dictate the evolution of the field:

(i) Each population member, independent of the others, during time interval $(t, t + dt)$ can produce a new population member(offspring) with probability $bdt = A^+dt,\ A^+ > 0$. The initial individual remains at its initial position x but the offspring jumps to $x + z + dz$ with probability

$$a^+(z)dz, \quad A^+ = \int_{\mathbb{R}^d} a^+(x)dx.$$

In the mean-field approximation, the spatial aspect is averaged and so the jump of the offspring becomes irrelevant.

(ii) Each population member at point x during the time interval $(t, t + dt)$ dies with probability $\mu\, dt$, where μ is the mortality rate.

(iii) Most important is the competition factor. If two population members are located at the points $x, y \in \mathbb{R}^d$, then each of them dies with probability $a^-(x - y)dt$ during the time interval $(t, t + dt)$ (we may assume that both do not die). This requires that $a^-(\cdot)$ be integrable; set

$$A^- = \int_{\mathbb{R}^d} a^-(z)dz.$$

The total effect of competition on a individual is the sum of the effects of competition with all population members. For modern human populations, it is probably more appropriate to include the suppressive effect of competition in the birth parameter b than to add it to mortality. The probability of production of a new population member at x, then, will become $b(x - y)$, for it will depend on the presence of individuals at points y.

In the Bolker–Pacala model, we have interacting individuals, in contrast to the usual branching process. One can expect physically that for arbitrary nontrivial competition ($a^- \in C(\mathbb{R}^d)$, $A^- > 0$), there will exist a limiting distribution of the population. At each site x, with population at time t given by $n(t, x)$, three rates are relevant, the birth rate b and mortality rate μ, each proportional to $n(t, x)$, and the death rate due to competition, proportional to $n(t, x)^2$. Heuristically, when $n(t, x)$ is small, the linear effects will dominate, which means that if $b > \mu$ the population will grow. As $n(t, x)$ becomes large, however, the quadratic effect will become increasingly dominant, which will prevent unlimited growth.

This can be seen in the mean-field approximation. We assume all particles on the lattice in fact are contained in a large but finite box of size L. The total population inside the box is described by a continuous-time random walk, the transition rates for which are

$$P\left(N_L(t+dt)=j|N_L(t)=n\right)=\begin{cases} n\kappa b\,dt+o(dt^2) & \text{if } j=n+1 \\ n\kappa\mu\,dt+\kappa\gamma n^2/L\,dt+o(dt^2) & \text{if } j=n-1 \\ o(dt^2) & \text{if } |j-n|>1 \end{cases}$$

In [1], we prove a set of limit theorems for this random walk and show that, appropriately normalized, as $L\to\infty$, the process approaches an Ornstein–Uhlenbeck process, a well-known stochastic process that may be loosely described as fluctuations around an evolving central tendency, which may be a fixed equilibrium, or may be characterized by drift.

3 Models with Spatial Dynamics

3.1 KPP Model on $\mathbb{Z}^d$ with Migration (Heavy Tails)

In order to avoid clusterization, the process must fill out empty space to compensate for the degenerating families. One simple alternative to immigration is to add to the branching process a simple random walk to nearest neighbors. Given that we are on the lattice, this move is to one of two places in dimension 1, one of four places in dimension 2, and so on. In mathematical terms, the model includes diffusion with generator Δ, where Δ is the discrete or lattice Laplacian

$$\Delta f(x)=\sum_{x':|x'-x|=1}(f(x')-f(x)).$$

In high dimensions ($d\geq 3$), this simple random walk (diffusion) with generator Δ is sufficient to eliminate clusterization. For $d\leq 2$, which is after all the appropriate setting for most demographic or ecological applications, such local diffusion is not sufficient and the clusterization still increases infinitely. If, however, we modify the simple random walk to allow for "long jumps," that is, moves an indefinitely long distance, with sufficiently heavy tails and other conditions, then we can eliminate clusterization even in two or fewer dimensions. This modified random walk may be called "migration."

We are interested in the evolution of the configuration $N(t,x)$, $x\in\mathbb{Z}^d$, meaning the total number of individuals at position x in the d-dimensional lattice at time t. The following models are similar to the Kolmogorov–Petrovskii–Piskunov (KPP) model [14], a well-known and influential model from the 1930s. Two rather technical differences that do not have much effect on the conclusions are that in the KPP model the phase (or state) space is continuous ($\mathbb{R}^d$ instead of $\mathbb{Z}^d$) and the underlying process is Brownian motion instead of a random walk, but these are rather technical points. More essential is that in the KPP model the initial population $N(0,\cdot)$ contains but a single individual. Under the condition of supercriticality, $\beta > \mu$, think of a novel, superior gene that may spread through a species or a seed that may propagate in space. We consider, in contrast, the critical case where $\beta = \mu$ with an initial population that is stationary in the phase space $\mathbb{Z}^d$ with positive finite density, and, thus, is infinite.

The central simplifying assumption of these models is the absence of interaction between individuals. As a result, we can write the total population at point y, $N(t, y)$, as the sum of subpopulations as follows. Let $n(t, y; x)$ be the particle field generated by the initial $n(0, x)$ particles at the site $x \in \mathbb{Z}^d$. Then

$$N(t, y) = \sum_{x\in\mathbb{Z}^d} n(t, y; x).$$

Each subpopulation, in turn, is the sum of the contribution (the progeny) of each individual initially at the given site x, which we can write

$$n(t, y; x) = \sum_{i=1}^{n(0,x)} n(t, y; x_i).$$

The dynamics of the process includes three components, the familiar *birth rate* β and *death rate* μ, and the *migration* of population members. Migration depends on the probability kernel $a(z)$, $z \in \mathbb{Z}^d$, $z \neq 0$, $\sum\limits_{z\neq 0} a(z) = 1$ and a rate of migration, which we can set to 1 by scaling time appropriately. An individual located at time t in some site $x \in \mathbb{Z}^d$, therefore, jumps to the point $(x + z) \in \mathbb{Z}^d$ with probability $a(z)dt$, independently of the other population members.

To implement the heavy tails assumption for migration, we assume that $a(z)$ takes the form:

$$a(z) = \frac{h_1(\theta)}{|z|^{2+\alpha}} \left(1 + O\left(\frac{1}{|z|^2}\right)\right), \; z \neq 0$$

with $0 < \alpha < 2$, $\theta = \arg \frac{z}{|z|} \in (-\pi, \pi] = T^1$, $h_1 \in C^2(T^1)$, $h_1 > 0$. The second moment of the spatial distribution $a(z)$ is infinite. The stipulation that $\sum\limits_{z\neq 0} a(z) = 1$ may be met by appropriate scaling of the bounded function h_1. The heaviness of the tails is controlled by α.

The generator for the migration process $\mathcal{L}$ is a generalization of the discrete Laplacian. The operator $\mathcal{L}$ is defined:

$$\mathcal{L}f(x) := \sum_{z\neq 0} a(z)(f(x + z) - f(x))$$

For the study of subpopulation $n(t, y; x)$, $x, y \in \mathbb{Z}^d$, let us define the generating function $u_z(t, x; y) = E_x z^{n(t,y;x)} = \sum_{j=0}^{\infty} P\{n(t, y; x) = j\} z^j$. This is a polynomial that is especially useful in generating moments. The nonlinear differential equation for $u_z(t, x; y)$ is [14]

$$\frac{\partial u_z}{\partial t} = \mathcal{L}u_z + \beta u_z^2 - (\beta + \mu)u_z + \mu \tag{3.1}$$

$$u(0, x; y) = \begin{cases} z, & x = y \\ 1, & x \neq y \end{cases}$$

Repeated differentiation over z and the substitution $z = 1$ leads to the sequence of moment equations for the factorial moments, given by

$m_1(t, x; y) = E_x n(t, y; x)$
$m_2(t, x; y) = E_x n(t, y; x)(n(t, y; x) - 1)$
$m_3(t, x; y) = E_x n(t, y; x)(n(t, y; x) - 1)(n(t, y; x) - 2)$
etc.

Then, for the critical case $\beta = \mu$

$$\frac{\partial m_1}{\partial t} = \mathcal{L}m_1, \qquad m_1(0, x; y) = \delta_y(x),$$

where $\delta_i(j) = 1$ for $i = j$ and 0 for $i \neq j$. This means $m_1(t, x; y) = p(t, x, y)$, where $p(t, x, y)$ is the transition probability from x to y in time t, i.e., $p(t, x, y) = P_x\{x(t) = y\}$ where $x(t)$ is the trajectory of the random walk (random jump!) with generator $\mathcal{L}$.

From here, we can obtain a theorem using what is known as the "method of moments" to establish the existence of a stable distribution as $t \to \infty$—in other words, no exponential decay, no exponential growth, and no clusterization. We state and explain the theorem here, but do not give the proof.

Let us note a well-known distinction concerning stochastic processes. A random walk $x(t)$ is called "recurrent" if $P\{x(t)$ returns to i infinitely often $|x(0) = i\} = 1$ and "transient" if $P\{x(t)$ returns to i infinitely often $|x(0) = i\} = 0$. An equivalent way of expressing this is $x(t)$ is transient if and only if $\int_0^\infty p(t, x, x)dt < \infty$.

Theorem 3.1 *Suppose $x(t)$ is transient, i.e., $\int_0^\infty p(t, x, x)dt < \infty$. Then,*

$$E\,N(t, x) \leq c_0^n n!$$

for some constant c_0 (Carleman conditions). For our model

$$E\,N(t, x)(N(t, x) - 1) \cdots (N(t, x) - l + 1) = m_l(t) \xrightarrow[t \to \infty]{} m_l(\infty)$$

and, therefore

$$N(t,x) \xrightarrow[t\to\infty]{\text{law}} N(\infty,x)$$

where $N(\infty,x)$ *is a steady state, that is, a random variable with a finite distribution.*

Let us elaborate two points. The Carleman conditions are time-independent bounds on the moments which, when satisfied as they are here, mean that the moments uniquely define the distribution. In other words, it is possible to construct the field $N(t,\cdot)$ and study its limiting behaviors $t\to\infty$ using the moments. The last conclusion gives us the desired result that we will have a stable population, without exponential growth or decay and without clusterization.

In the KPP case, a similar result goes back to [4, 18], who developed ideas by R.L. Dobrushin [5] using a technique involving partial differential equations. For branching random walks in $\mathbb{R}^d$, the case of so-called contact processes, [17] used what are called the "forward Kolmogorov equations" to prove the existence of the steady state $N(\infty,\infty)$. Equation 3.1, in contrast, is constructed using the related "backward" Kolmogorov equations. We proved the above theorem by using this method for individual subpopulations $n(t,y;x)$, $y\in\mathbb{Z}^d$ and then combining the results, which we were able to do because of the *independence* of these subpopulations.

The most convenient way to calculate the moments is by using the Fourier transform. In Fourier representation

$$\hat{m}_l(t,k;y)=\sum_{x\in\mathbb{Z}^d} e^{i(k,x)}m_l(t,x;y).$$

Note that, therefore

$$\sum_{x\in\mathbb{Z}^d} m_l(t,x;y)=\hat{m}_l(t,k;y)|_{k=0}.$$

It is straightforward to show that $\widehat{\mathcal{L}f(x)}=\hat{\mathcal{L}}(k)\hat{f}(k)$, where $\hat{\mathcal{L}}=\hat{a}(k)-1$; note, also, $\hat{a}(0)=1$. As a result

$$\hat{m}_1(t,k;y)=e^{\hat{\mathcal{L}}t}$$

and so

$$m_1(t,y)=\sum_{x\in\mathbb{Z}^d} m_1(t,x;y)=\hat{m}_1(t,k;y)|_{k=0}=1.$$

For the second factorial moment, Eq. 3.1 gives

$$\frac{\partial m_2(t,x;y)}{\partial t}=\mathcal{L}m_2(t,x;y)+2\beta m_1(t,x;y)^2.$$

Again, we use the Fourier transform to obtain

$$\sum_{x\in\mathbb{Z}^d} m_2(t,x;y) = \hat{m}_2(t,k;y)|_{k=0} = \beta \int\limits_{T^d} \frac{d\theta}{1-\hat{a}(\theta)} \left(1 - e^{-2t(1-\hat{a}(\theta))}\right).$$

By using cumulants and their properties, it can be shown that $m_2(t,y) = \sum_{x\in\mathbb{Z}^d} m_2 (t,x;y) + o(1) + 1$.

Intermittency or full clusterization is identified by the property

$$\frac{m_2}{m_1^2} \xrightarrow[t\to\infty]{} \infty.$$

In fact, clusterization is evident if $m_2 \gg m_1^2$. In our situation, $x(t)$ is transient if $\int\limits_{T^d} \frac{d\theta}{1-\hat{a}(\theta)} < \infty$, but the limiting distribution of particles will show some clusterization if $\int\limits_{T^d} \frac{d\theta}{1-\hat{a}(\theta)} \gg 1$.

3.2 KKP Model on $\mathbb{Z}^d$ with Multiple Offspring (Contact Process)

This introduces only one complication of the previous model. Namely, the number of offspring is no longer limited to two. When a particle splits, it may do so into j particles, $j = 2, 3, ..., \infty$, with rates b_j. We need only the assumption, setting

$$\beta := \sum_{j=2}^{\infty} b_j \quad \text{and} \quad \beta_1 := \sum_{j=2}^{\infty} j b_j,$$

that $\beta < \infty$, $\beta_1 < \infty$.

With, as before, $u_z(t,x;y) = E_x z^{n(t,y;x)}$,

$$\frac{\partial u_z}{\partial t} = \mathcal{L}u_z + \sum_{j=2}^{\infty} b_j u_z^j - (\beta+\mu)u_z + \mu$$

$$u(0,x;y) = \begin{cases} z^{\rho_0}, & x = y \\ 1, & x \neq y \end{cases}$$

where ρ_0 is the initial population density.

For the first moment

$$\begin{aligned} \frac{\partial m_1(t,x;y)}{\partial t} =& \mathcal{L}m_1(t,x;y) + \sum_{j=2}^{\infty} j b_j m_1(t,x;y) - (\beta+\mu)m_1(t,x;y), \\ m_1(0,x;y) =& \rho_0 \delta_y(x). \end{aligned}$$

As before, this is easily solved using the Fourier transform

$$\hat{m}_1(t,k;y) = \rho_0 e^{(\beta_1-\beta-\mu)t} e^{\hat{\mathcal{L}}(k)t}$$

and

$$m_1(t,y) = \hat{m}_1(t,k;y)|_{k=0} = 1 = \rho_0 e^{(\beta_1-\beta-\mu)t}.$$

This establishes $\beta_1 - \beta - \mu = 0$ as the critical setting of parameters for this process.

For the second factorial moment, we need to assume that $\beta_2 < \infty$, where $\beta_2 = \sum_{j=2}^{\infty} j(j-1)b_j$. Using the Fourier transform

$$\sum_{x\in\mathbb{Z}^d} m_2(t,x;y) = \hat{m}_2(t,k;y)|_{k=0} = \frac{\beta_2}{2}\int\limits_{T^d} \frac{d\theta}{1-\hat{a}(\theta)}\left(1-e^{-2t(1-\hat{a}(\theta))}\right).$$

Then, as above, because $m_2(t,y) = \sum_{x\in\mathbb{Z}^d} m_2(t,x;y) + o(1) + 1$, the population will be unstable due to intermittency, be stable with some clusterization, or be stable without clusterization, depending on the evaluation of $\int\limits_{T^d} \frac{d\theta}{1-\hat{a}(\theta)}$.

3.3 Stability Under a Single Point Perturbation

A natural next step is to probe the effect of perturbations on the stability created by the critical condition of the KPP-type model of the previous section. We consider, here, the same model with the critical condition that $\beta = \mu$ everywhere on the lattice $\mathbb{Z}^d$ except at a single point 0, that is,

$$\beta(x) - \mu(x) = \sigma\delta_0(x), \quad x \in \mathbb{Z}^d$$

with $\sigma > 0$. This model is due to Yarovaya (e.g., [20]).

The PDE for the first moment is then

$$\frac{\partial m_1}{\partial t} = \mathcal{L}m_1 + \sigma\delta_0(x)m_1$$
$$m_1(0,x) \equiv 1.$$

The stability of this model hinges on the value of σ. Specifically, there is a critical σ_{cr} such that if $\sigma < \sigma_{\text{cr}}$ the population attains a stable state but if $\sigma > \sigma_{\text{cr}}$ the population does not stabilize but grows indefinitely.

This follows from spectral analysis, using Fourier transforms. The spectrum of $\mathcal{L}$, $\text{Sp}(\mathcal{L}) = [\min(\hat{\mathcal{L}}), 0]$. We define the Hamiltonian $H = \mathcal{L} + \sigma\delta_0(x)$. If H has discrete eigenvalue λ_0 with eigenvector ψ_0, then, $\hat{H}\hat{\psi}_0 = \lambda_0\hat{\psi}_0$. Thus, $\hat{\mathcal{L}}(\theta)\hat{\psi}_0(\theta) + \sigma\psi_0(0) = \lambda_0\hat{\psi}_0(\theta)$. Rearranging, we obtain

$$\hat{\psi}_0(\theta) = \frac{\sigma\psi_0(0)}{\lambda_0 - \hat{\mathcal{L}}(\theta)}$$

Taking the inverse Fourier transform

$$\psi_0(x) = \frac{\sigma\psi_0(0)}{(2\pi)^d} \int\limits_{T^d} \frac{d\theta\, e^{-i(\theta,x)}}{\lambda_0 - \hat{\mathcal{L}}(\theta)}$$

$\psi_0(0) \neq 0$, otherwise $\psi_0(x) \equiv 0$, which means

$$\frac{1}{\sigma} = \frac{1}{(2\pi)^d} \int\limits_{T^d} \frac{d\theta\, e^{-i(\theta,x)}}{\lambda_0 - \hat{\mathcal{L}}(\theta)} =: I(\lambda_0)$$

$I(0) > 0$ and as λ_0 increases from 0, $I(\lambda_0)$ decreases monotonically. Consequently, if $\frac{1}{\sigma} > I(0)$, there is no $\lambda_0 > 0$. Put otherwise, we set $\sigma_{\text{cr}} = \frac{1}{I(0)}$. Then there is a simple $\lambda_0(\sigma) > 0$ iff $\sigma > \sigma_{\text{cr}}$.

The corresponding eigenfunction, up to a constant factor, is

$$\psi_0(x) = \frac{1}{(2\pi)^d} \int\limits_{T^d} \frac{d\theta\, e^{-i(\theta,x)}}{\lambda_0 - \hat{\mathcal{L}}(\theta)} = G_{\lambda_0}(0, x)$$

where $G_\lambda(0, x) = \int\limits_0^\infty e^{-\lambda t} p(t, 0, x)dt$ is the Green function of the underlying random walk, which is given by

$$\begin{aligned} &\frac{\partial p(t, x, y)}{\partial t} = \mathcal{L}p(t, x, y) \\ &p(0, x, y) = \delta_x(y). \end{aligned}$$

Because of translation invariance, we may write $p(t, y - x) = p(t, x, y)$

Set $\mu_1(t, x) = m_1(t, x) - 1$.

$$\begin{aligned} &\frac{\partial \mu_1(t, x)}{\partial t} = Hm_1(t, x) = \mathcal{L}\mu_1 + \sigma\delta_0(x)\mu_1 + \sigma\delta_0(x) \\ &\mu_1(0, x) \equiv 0. \end{aligned}$$

We now have two cases:

(1) If $\lambda_0(\sigma) > 0$, then $\mu_1 = O(1) + e^{\lambda_0 t}\sigma\psi_0(0)\psi_0(x)$, and because $\|\psi_0\| = 1$ it follows that the population size is unstable and increases exponentially; there is no steady-state population.

(2) If $\lambda_0(\sigma) < 0$, we may apply Duhamel's principle to obtain

$$\begin{aligned}\mu_1(t,x) &= \sigma\int_0^t ds \sum_z p(t-s,x-z)(\delta_0(z)\mu_1(s,z)+\delta_0(z))\\ &= \sigma\int_0^t p(t-s,x)(\mu_1(s,0)+1)ds\end{aligned}$$

$$\begin{aligned}m_1(t,x) &= 1+\sigma\int_0^t p(t-s,x)m_1(s,0)ds\\ &= 1+\sigma\int_0^t p(t-s,x)ds+\sigma^2\int_0^t\int_0^s p(t-s,x)p(s-u,0)m_1(u,0)du\,ds\\ &= 1+\sigma\int_0^t p(s,x)ds+\sigma^2\int_0^t p(t-s,x)\int_0^s p(u,0)du\,ds+\dots\end{aligned}$$

For $\sigma < \sigma_{\mathrm{cr}}$, $\sigma\int_0^\infty p(s,0)ds < 1$, and so the above series converges for all t and as $t \to \infty$.

Turning to the second moment, the PDE for the second factorial moment is

$$\begin{aligned}&\frac{\partial m_2(t,x)}{\partial t} = \mathcal{L}m_2(t,x)+\sigma\delta_0(x)(m_2(t,x)+2m_1^2(t,x))\\ &m_2(0,x)\equiv 0.\end{aligned}$$

An analysis parallel to that for the first moment shows that $m_2(\infty,x) < \infty$. Consequently, for $\sigma < \sigma_{\mathrm{cr}}$ the population stabilizes.

3.4 Spatial Galton–Watson Process with Immigration and Finite Markov Chain Spatial Dynamics

We return to the spatial Galton–Watson process with immigration, but here with the possibility of migration between sites and allowing birth, death, and immigration rates to vary across sites. The number of sites is finite, which facilitates calculations.

We present the main results, here, and sketch their rationale; for full analysis, see [10] in this volume.

Let $X = \{x, y, \ldots\}$ be a finite set. Define the following parameters. At x in X, let $\beta(x)$ be the rate of duplication, $\mu(x)$ be the rate of annihilation, and $k(x)$ be the rate of immigration. For x and y in X, let $a(x, y)$ be the rate of transition $x \to y$.

Define $\overrightarrow{n}(t) = \{n(t, x), x \in X\}$ to be the population at moment $t \geq 0$, with $n(t, x)$ the occupation number of site $x \in X$. Letting $\overrightarrow{\lambda} = \{\lambda_x \geq 0, x \in X\}$, we write the Laplace transform of the random vector $\overrightarrow{n}(t) \in \mathbb{R}^N$, $N = \mathrm{Card}(X)$ as $u(t, \overrightarrow{\lambda}) = E\, e^{-(\overrightarrow{\lambda}, \overrightarrow{n}(t))}$.

The differential equation for $u(t, \overrightarrow{\lambda})$ is

$$\begin{cases} \frac{\partial u(t, \overrightarrow{\lambda})}{\partial t} = \sum_{x \in X} (e^{-\lambda_x} - 1)(-\frac{\partial u(t, \overrightarrow{\lambda})}{\partial \lambda_x} \beta(x) + u(t, \overrightarrow{\lambda}) k(x)) + \sum_{y \in X} (e^{\lambda_y} - 1)\mu(y)(-\frac{\partial u(t, \overrightarrow{\lambda})}{\partial \lambda_y}) \\ \qquad + \sum_{x, z; x \neq z} (e^{\lambda_x - \lambda_z} - 1) a(x, z)(-\frac{\partial u(t, \overrightarrow{\lambda})}{\partial \lambda_x}) \\ u(0, \overrightarrow{\lambda}) = E\, e^{-(\overrightarrow{\lambda}, \overrightarrow{n}(0))} \end{cases} \tag{3.2}$$

By differentiating Eq. 3.2 over the variables λ_x, $x \in X$, one can get the equations for the correlation functions

$$k_{l_1 \ldots l_m}(t, x_1, \ldots, x_m) = E\, n^{l_1}(t, x_1) \cdots n^{l_m}(t, x_m),$$

where $x_1, \ldots, x_m$ are different points of X and $l_1, \ldots, l_m \geq 1$ are integers. Specifically

$$k_{l_1 \ldots l_m}(t, x_1, \ldots, x_m) = (-1)^{l_1 + \cdots + l_m} \frac{\partial^{l_1 + \cdots + l_m} n(t, \overrightarrow{x})}{\partial^{l_1} \lambda_{x_1} \ldots \partial^{l_m} \lambda_{x_m}} |_{\overrightarrow{\lambda} = 0}.$$

The corresponding equations will be linear. The central point here is that the factors $(e^{\lambda_x - \lambda_z} - 1)$, $(e^{\lambda_y} - 1)$, and $(e^{-\lambda_x} - 1)$ are equal to 0 for $\overrightarrow{\lambda} = 0$. As a result, the higher order $(n > l_1 + \ldots + l_m)$ correlation functions cannot appear in the equations for $\{k_{l_1 \ldots l_m}(\cdot), l_1 + \ldots + l_m = n\}$.

For the first moment, for example, if we assume the symmetry $a(x, z) = a(z, x)$ and define $V(v) = \beta(v) - \mu(v)$, we obtain

$$\frac{\partial m_1(t, x)}{\partial t} = A m_1 + V m_1 + k(x), \qquad m_1(0, x) = n(0, x)$$

where $A = [a(x, y)] = A^*$ is the generator of a Markov chain.

An alternative approach to the generating function method is to treat the birth and death process with immigration as a random walk with reflection on the half axis $n \geq 0$.. If we start from the simplest case, when there is one site, i.e., $X = \{x\}$, then application of known facts concerning random walks (see [6]) yields the following result.

Proposition 3.2

1. *If $\beta > \mu$, the process $n(t)$ is transient and the population $n(t)$ grows exponentially.*
2. *If $\beta = \mu$, $k > 0$, the process is not ergodic but rather it is zero-recurrent for $\frac{k}{\beta} \leq 1$ and transient for $\frac{k}{\beta} > 1$.*
3. *If $\beta < \mu$, the process $n(t)$ is ergodic. The invariant distribution for $\beta < \mu$ is given by*
$$\pi(n) = \frac{1}{\tilde{S}} \frac{k(k+\beta)\cdots(k+\beta(n-1))}{n!\mu^n}$$
where $\tilde{S} = \sum_{j=1}^{\infty} \frac{k(k+\beta)\cdots(k+\beta(j-1))}{\mu \cdot 2\mu \cdots j\mu}$.

Let us turn to the general case of the finite space X. Let $N = \text{Card}\, X$ and $\overrightarrow{n}(t)$ be the vector of the occupation numbers. The process $\overrightarrow{n}(t)$, $t \geq 0$ is a random walk on $(\mathbb{Z}_+^1)^N = \{0, 1, ...\}^N$ with continuous time. If at the moment t we have the configuration $\overrightarrow{n}(t) = \{n(t,x), x \in X\}$, then, for the interval $(t, t+dt)$, only the following events (up to terms of order$(dt)^2$) can happen:

(a) the appearance of a new particle at the site $x_0 \in X$, due to birth or immigration, with probability $n(t,x_0)\beta(x_0)dt + k(x_0)dt$.
(b) the death of one particle at the site $x_0 \in X$, with probability $\mu(x_0)n(t,x_0)dt$, for $n(t,x_0) \geq 1$.
(c) the transfer of one particle from site x_0 to $y_0 \in X$ (jump from x_0 to y_0), with probability $n(t,x_0)a(x_0,y_0)dt$, for $n(t,x_0) \geq 1$.

Theorem 3.2 in the preceding chapter in this volume, by Han et al., gives sufficient conditions for the ergodicity of the process $\overrightarrow{n}(t)$. We refer the reader to that analysis.

3.5 Branching Process with Stationary Random Environment

The last of our models without interaction between particles is a recently developed one that relaxes the artificiality of uniform birth and death rates, at β and μ, for the entire phase space. Working now in continuous space $\mathbb{R}^d$, [16] stipulates a random environment ω_m for the process with birth rate and death rates given by $b(x,\omega_m)$ and $m(x,\omega_m)$. Define the potential $V(x,\omega_m) = b(x,\omega_m) - m(x,\omega_m)$. In addition, there is migration but no immigration. Let the generator of the underlying migration $\mathcal{L}$ be the continuous version of our usual one with long jumps

$$\mathcal{L}f(x) = \int_{\mathbb{R}^d} a(z)(f(x+z) - f(x))dz.$$

The population density $\rho(t,x)$ satisfies

$$\begin{aligned} \frac{\partial \rho(t,x)}{\partial t} &= \mathcal{L}\rho(t,x) + V(x,\omega_m)\rho(t,x) \\ \rho(0,x) &\equiv \rho_0. \end{aligned}$$

Suppose that $b(x,\omega_m)$ and $m(x,\omega_m)$ are continuous, ergodic, homogeneous, and nonnegative fields. Suppose also that $\langle e^{tb(0,\omega_m)}\rangle < \infty$, where $\langle\cdot\rangle$ indicates the expectation over ω_m. Then, if $V(x,\omega_m)$ satisfies the condition that there exists a (small) $\epsilon_0 > 0$ such that for any $L > 0$

$$P\{V(z,\omega_m) \geq \epsilon_0, |z| \leq L\} > 0$$

Reference [16] show that for any open domain $D \in \mathbb{R}^d$, with the measure of the domain $|D| < \infty$, $n(t,D) \xrightarrow[t\to\infty]{} \infty$ with probability 1.

This is true, moreover, even if $\langle V\rangle < 0$, in other words, if on average the death rate exceeds the birth rate. The reason is that, despite the fact that most places the death rate prevails and the population decays to 0, there are an infinite number of places where the birth rate exceeds the death rate so that the population grows exponentially. This is sufficient for the population as a whole to grow without limit.

3.6 Multilayer Bolker–Pacala Model

Some of the most intriguing population questions involve the interplay between multiple populations. A model that can capture some of this is a generalization of the mean-field approximation to the Bolker–Pacala model. We take the idea of a mean field over a box of size L and extend that to a set of N boxes, each of size L.

As always, there are birth rates and death rates. With multiple boxes, they can vary by box, although in simpler models we may keep them uniform across boxes. Migration (the "jump of the offspring"), which was irrelevant in the one-box mean-field approximation, here, can occur between boxes and so cannot be ignored as in the simpler Bolker–Pacala model. Migration can be seen equivalently as two random events, the birth of a individual and its dispersal, as in Bolker and Pacala's presentation [2], or as a single random event, as in our model. (We stress that this differs from the classical branching process, in which the "parental" individual and its offspring commence independent motion from the same point.) We assume, of course, that all offspring evolve independently according to the same rules.

Most interesting is the competition or suppression effect, which now can occur both internally, the population in a given box suppressing its own population, and externally, the population in one box suppressing the population of other boxes. The migration and suppression parameters can vary across boxes, or, again, in the simplest models, can be kept uniform across boxes.

Different general configurations of the parameters may be more appropriate for different modeling scenarios. For example, if the multiple populations are geographical regions, migration rates and internal suppression or competition rates may be relatively high, while external suppression rates would be low. Whereas if the populations are human social classes, migration rates are likely to be low, while external suppression rates, one class's population constraining the growth of another class's population, might be relatively high. Moreover, these last rates might well be nonuniform, with not all classes affecting other social classes equally.

The N-box Bolker–Pacala model gives rise to a random walk on

$$(\mathbb{Z}_+)^N = \{(n_1, n_2, \ldots, n_N) : n_i \in \mathbb{Z}_+, 1 \le i \le N\}.$$

Consider a system of N disjoint rectangles $Q_{i,L} \subset \mathbb{R}^2$, $i = 1, 2, \ldots, N$, N fixed, with

$$|Q_{i,L} \cap \mathbb{Z}^2| = L.$$

Parameters $\beta_i, \mu_i > 0$ represent the natural (biological) birth and death rates of particles in box i, $i = 1, \ldots, N$, respectively. The migration potential a^+ and the competition potential a^- also are constant on each $Q_{i,L}$. For $\mathbf{x} \in Q_{i,L}, \mathbf{y} \in Q_{j,L}$,

$$a_L^-(\mathbf{x}, \mathbf{y}) = a_{ij}^-/L^2, \qquad i, j = 1, 2, \ldots, N, \tag{3.3}$$

and

$$a_L^+(\mathbf{x}, \mathbf{y}) = a_{ij}^+/L, \qquad i, j = 1, 2, \ldots, N. \tag{3.4}$$

Specifically, a_{ij}^- indicates the supressive effect on the population in box i due to the population in box j (such as due to competition between boxes i and j), while $a_L^+(\mathbf{x}, \mathbf{y})$ is the rate of migration from $\mathbf{x} \in Q_{i,L}$ to $\mathbf{y} \in Q_{j,L}$.

Let $\bigcup_{i=1}^N Q_{i,L} = Q_L$. Then set

$$A_i^+ := \sum_{\mathbf{y} \in Q_L} a^+(\mathbf{x}, \mathbf{y}) = \sum_{j=1}^N a_{ij}^+, \quad A_i^- := \sum_{\mathbf{y} \in Q_L} a^-(\mathbf{x}, \mathbf{y}) = \sum_{j=1}^N a_{ij}^-$$

Assume that

$$A_i^+, A_i^- \le A < \infty$$

uniformly in L.

The population in each square $Q_{i,L}$, $i = 1, \ldots, N$, at time t is represented by

$$\boldsymbol{n}(t) = \{n_1(t), n_2(t), \ldots, n_N(t)\}, \tag{3.5}$$

a continuous-time random walk on $(\mathbb{Z}_+)^N$ with transition rates, for $i, j = 1, 2, \ldots, N$

$$\boldsymbol{n}(t+dt|\boldsymbol{n}(t)) \tag{3.6}$$

$$= \boldsymbol{n}(t) + \begin{cases} e_i & \text{w. pr. } \beta_i n_i(t)dt + o(dt^2) \\ -e_i & \text{w. pr. } \mu_i n_i(t)dt + \frac{n_i(t)}{L}\sum_{j=1}^{N} a_{ij}^{-} n_j(t)dt + o(dt^2) \\ e_j - e_i & \text{w. pr. } n_i(t)a_{ij}^{+}dt + o(dt^2), \quad j \neq i \\ 0 & \text{w. pr. } 1 - \sum_{i=1}^{N}(\beta_i + \mu_i)n_i(t)dt \\ & \qquad -\frac{1}{L}\sum_{i,j} n_i(t)n_j(t)a_{ij}^{-}dt + \sum_{i,j} n_i(t)a_{ij}^{+} + o(dt^2) \\ \text{other} & \text{w. pr. } o(dt^2) \end{cases}$$

where e_i is the vector with 1 in the ith position and 0 everywhere else.

This more general model exhibits some of the same characteristics of the simple mean-field approximation but reveals some new effects as well. Once again, there is convergence, as the size of the boxes L increases, to an Ornstein–Uhlenbeck process. The N-dimensional random walk is geometrically ergodic, meaning that it shows exponential convergence to a stable distribution. New, however, is that, for at least $N = 2$ and 3 (solutions become increasingly difficult to find as N increases), the population level may have multiple nontrivial equilibria. This is true only for some rate values, however. In particular, at least some of the values of the a_{ij}^{-}, $i \neq j$, the suppression of population across boxes, must be high enough.

This creates intriguing possibilities. For example, given the perpetual probabilistic fluctuations in population size, there is a certain chance that a population fluctuating about one equilibrium could swing wildly enough to put it into the attractive basin of a different equilibrium. This phenomenon should be amenable to analysis although it has not yet been done. Research into these models is ongoing.

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