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A simple spatial model of population dynamics

ABSTRACT. A mathematical model is presented that describes the dynamics of a spatially distributed population, incorporating the effects of external migration. The evolution of the population density is governed by a simple integro-differential equation. In the spatially homogeneous case, the model is reduced to the classical logistic equation with an additional constant term and its behavior is fully characterized. In the inhomogeneous case, the dynamics is examined through numerical simulations and typical long-term behavior is illustrated.

1. Introduction. The dynamics of population growth has been a subject of scientific research for centuries. Modeling efforts perhaps began with the famous Fibonacci model, which represents a simplified case of unbounded population growth. These efforts were continued much later with the well-known works of the late 18th and 19th centuries by Thomas Malthus [5], Benjamin Gompertz [1] and Pierre Verhulst [7], as well as such 20th century researchers as Vito Volterra [8]. This research continues to this day, with increasingly advanced models being developed, often incorporating sophisticated mathematical methods.

This work aims to present a model of population dynamics that is relatively simple, yet quite general. It can potentially be used to study a variety of phenomena, such as the impact of migration on population growth or the expansion of population into a new environment.

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2. The model. A fundamental characteristic of the model described in this work is the existence of two conceptual layers influencing the population dynamics. The main layer, which is explicitly included in the model, represents the segment of the population under study. Its state is described by a density function $\varrho : \mathbb{R}^d \rightarrow \mathbb{R}$, which is generally assumed to be bounded. The argument of the density function is referred to as location, one possible interpretation of which is spatial position. The outer layer, in contrast, corresponds to the portion of the population that lies outside the scope of the study and is not modeled directly.

For example, consider studying the dynamics of a population within a given city. The city's population constitutes the main layer – it is the subject of the research, and its dynamics is explicitly modeled. The outer layer, in this case, could be the population of the surrounding region, the country, or even the entire world. Its influence is crucial, but its state is not tracked or modeled.

Interactions within the main layer are modeled separately from interactions between the main and outer layers. The influence of internal interactions is represented by a^+ for positive effects (for example fertility) and a^- for negative effects (like competition). The influence of the outer layer on the main layer is captured by b^+ (positive) and b^- (negative), see Figure 1 for a schematic representation. Any interactions within the outer layer are ignored, as this layer is not directly included in the model.

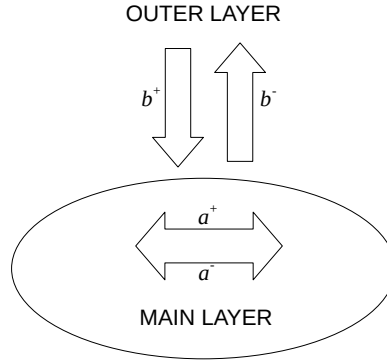


FIGURE 1. Scheme of interactions included in the model: a^+ and a^- model the influence of interactions within the main layer, while b^+ and b^- the influence of interactions between main and outer layers.

The dynamics of the system is described by a map $t \rightarrow \varrho_t$, where $t \geq 0$ denotes the time variable and ϱ_t represents population density at time t .

As is customary, this mapping corresponds to the solution of a differential equation, which, in the case of the model under consideration, takes the following form:

$$(2.1) \quad \frac{\partial}{\partial t} \varrho_t(x) = b^+(x) + \int a^+(x-y) \varrho_t(y) dy - \left[b^-(x) + \int a^-(x-y) \varrho_t(y) dy \right] \varrho_t(x),$$

where a^+ , a^- , b^+ and b^- are suitable functions that serve as parameters of the model. Mathematical assumptions imposed on these functions, as well as on the densities ϱ_t , depend on the object of study. In general, all of them are assumed to be non-negative. Additionally, a^+ and a^- are assumed to be integrable, while b^+ and b^- to be bounded.

The parameter function b^+ describes the influx of new members into the studied population. It is assumed to be independent of the state of the population. In the simplest case, it can also be independent of the coordinate x in the inner layer, although the model allows for location dependence. The function b^- describes the outflux of population members, which may include emigration and/or mortality. In the case of mortality, members of population are not transferred to the outer layer but are simply removed from the main layer. Since the state of the outer layer is not tracked, mortality can be incorporated into the outflux described by b^- . This approach might resemble the classical SIR epidemiological model [3] in which the “recovered” (R) compartment can also include deceased members of the population. In the model under consideration, the outflux of population members is assumed to be proportional to the population density.

The influence of the parameter functions a^+ and a^- depends significantly on the state of the model. The function a^+ can be interpreted as a fertility kernel. The larger its total mass $\langle a^+ \rangle = \int a^+(x) dx$, the greater the potential increase in population density it induces. However, this effect also strongly depends on the shape of a^+ and the profile of the population density ϱ . Typically, a^+ is a symmetric function concentrated around zero. Then the increase at coordinate x is stimulated by the state of the population near x .

The function a^- can be interpreted as a competition kernel. Its influence on the population at a given location x is negative and proportional to the population density at x , similarly to b^- . However, unlike b^- , it also depends on the global state of the system in a manner analogous to a^+ . In general, the greater the total mass $\langle a^- \rangle = \int a^-(x) dx$, the stronger this influence. Still, the effect is highly sensitive to the specific shape of a^- and the profile of the population density. As with a^+ , kernel a^- is typically a symmetric function concentrated around zero, meaning that population growth is influenced – both positively and negatively – by the surrounding

population. By choosing specific forms of the functions a^+ and a^- , one can investigate a wide range of interaction scenarios.

A key assumption of the model, stemming from the form of equation (2.1), is that the influence of a^+ and a^- depends on location only indirectly – through the state of the system, that is the population density. On the other hand, the model allows for location-dependent influence on population growth through the functions b^+ and b^- . To keep the model simple, all the interactions described above are not directly time-dependent. However, with the exception of b^+ , they exhibit time dependence indirectly through the evolving state of the system.

As mentioned earlier, the states of the system are described by functions $\varrho : \mathbb{R}^d \rightarrow \mathbb{R}$. One possible interpretation of such densities is probabilistic in nature. Specifically, the expected number of individuals in a cube $A \subset \mathbb{R}^d$, is given by $\int_A \varrho(x) dx$. For a more detailed discussion, see [4], where a connection with the corresponding microscopic model is established.

3. Homogeneous case. The differential equation (2.1) introduced in the previous section, appears too complex to admit a general analytical solution. Even establishing its well-posedness is a nontrivial task. Therefore, to analyze the behavior of the system, it is necessary to restrict the parameter functions to specific forms and possibly employ numerical methods to obtain approximate solutions.

In the simplest case, one would assume that the initial density ϱ_0 , as well as functions b^+ and b^- , are constant, that is $\varrho_0(x) = r_0$, $b^+(x) = \beta^+$ and $b^-(x) = \beta^-$ for each $x \in \mathbb{R}^d$ and some nonnegative real r_0, β^+ and β^- . Then, the density of population ϱ_t remains homogeneous, that is $\varrho_t(x) = r_t$ for each $x \in \mathbb{R}^d$ and some nonnegative real r_t . In such a homogeneous case, in order to predict the behavior of the system, it is enough to solve the following simple Riccati type ODE with constant coefficients:

$$(3.1) \quad \begin{cases} \frac{d}{dt} r_t = \beta^+ + (\langle a^+ \rangle - \beta^-) r_t - \langle a^- \rangle r_t^2, \\ r_{t=0} = r_0, \end{cases}$$

where $\langle a^\pm \rangle = \int a^\pm(x) dx$ denotes the total mass of respectively a^+ and a^- .

Assuming that $\langle a^- \rangle > 0$, by substituting $r = \frac{x'}{\langle a^- \rangle x}$, equation (3.1) can be reduced to a second-order linear homogeneous ODE of the form

$$(3.2) \quad x'' + (\beta^- - \langle a^+ \rangle) x' - \beta^+ \langle a^- \rangle x = 0.$$

With additional assumption $\langle a^+ \rangle \neq \beta^-$ or $\beta^+ > 0$, characteristic polynomial of (3.2) has two distinct roots

$$(3.3) \quad p^\pm = \frac{1}{2}(\langle a^+ \rangle - \beta^- \pm \delta) \text{ with } \delta = \sqrt{(\langle a^+ \rangle - \beta^-)^2 + 4\beta^+ \langle a^- \rangle},$$

so (3.2) has the general solution

$$x(t) = C_1 e^{p^+ t} + C_2 e^{p^- t}.$$

Substituting this result back into (3.1), we obtain

$$r_t = \frac{p^+ e^{tp^+} + C p^- e^{tp^-}}{\langle a^- \rangle (e^{tp^+} + C e^{tp^-})}$$

with $C = \frac{C_2}{C_1}$. Taking into account the initial condition of (3.1), we get

$$(3.4) \quad r_t = \frac{r^+ (r_0 - r^-) + (r^+ - r_0) r^- e^{-\delta t}}{r_0 - r^- + (r^+ - r_0) e^{-\delta t}}$$

for $r^\pm = \frac{p^\pm}{\langle a^- \rangle}$ and p^\pm, δ as in (3.3).

From (3.4), it is clear that in the analyzed case, the system stabilizes over time, with r_t tending to r^+ as $t \rightarrow \infty$. Exemplary solutions are presented in Figure 2. In the left panel, the parameters of the system satisfy $\langle a^- \rangle = 2$, $\beta^+ = 4$, and $\langle a^+ \rangle - \beta^- = 2$. Trajectory $r_t^{(1)}$ corresponds to the initial condition $r_0^{(1)} = 1$, while $r_t^{(2)}$ corresponds to the initial condition $r_0^{(2)} = 2.5$. Both trajectories approach the value $r^+ = 2$. In the right panel, the parameters satisfy $\langle a^- \rangle = 2$, $\beta^+ = 6$ and $\langle a^+ \rangle - \beta^- = -1$, with initial conditions $r_0^{(3)} = 0$ and $r_0^{(4)} = 2.5$, respectively. In this scenario, both trajectories converge to $r^+ = 1.5$.

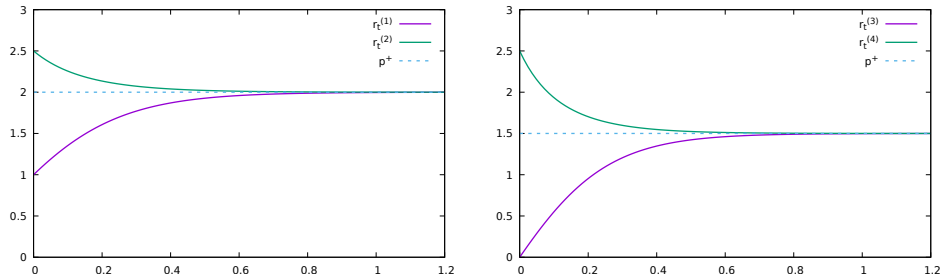


FIGURE 2. Solutions (3.4) of (3.1): r_t versus t for selected parameters and initial conditions

Another example of the solution given by (3.4) is shown in Figure 3. In this case, the parameter $\beta^+ = 0.01$ is relatively small compared to the other parameters, which are $\langle a^- \rangle = 1$ and $\langle a^+ \rangle - \beta^- = 5$. The initial conditions are set to $r_0^{(5)} = 0$ and $r_0^{(6)} = 6$. The trajectory $r_t^{(5)}$ resembles an S -shaped curve, characteristic of logistic growth.

This similarity is not coincidental – first line of equation (3.1) can be rewritten as

$$(3.5) \quad \frac{d}{dt} r_t = k r_t \left(1 - \frac{r_t}{K} \right) + \beta^+$$

with $k = (\langle a^+ \rangle - \beta^-)$ and $K = \frac{\langle a^+ \rangle - \beta^-}{\langle a^- \rangle}$.

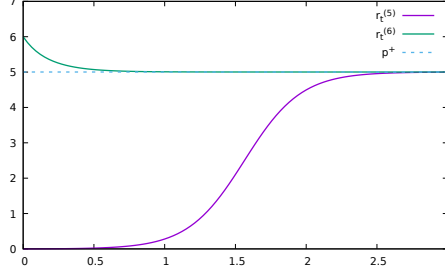


FIGURE 3. Solutions (3.4) of (3.1): r_t versus t for small parameter β^+

Therefore, the equation (3.1) can be considered as a modified logistic (or Verhulst) model, compare with e.g. Chapter 1.5 of [2], with an additional term β^+ representing external influx into the population. When this influx is relatively small, it has little impact on the overall population dynamics – except in the case of a very low initial population. This effect is clearly illustrated in Figure 3 by trajectory $r_t^{(5)}$, where the population begins to grow despite being initially absent. Such behavior would be impossible in the classical logistic model.

Recall that in the logistic model, the asymptotic population size – equal to the environment’s carrying capacity – is precisely the parameter K as in (3.5). In the studied model

$$K = \frac{\langle a^+ \rangle - \beta^-}{\langle a^- \rangle}$$

and it still can be interpreted as the environment’s carrying capacity. However, the asymptotic population size is modified due to the appearance of the term β^+ and is given by

$$\lim_{t \rightarrow \infty} r_t = r^+ = \frac{1}{2\langle a^- \rangle} \left(\langle a^+ \rangle - \beta^- + \sqrt{(\langle a^+ \rangle - \beta^-)^2 + 4\beta^+ \langle a^- \rangle} \right).$$

Since both β^+ and $\langle a^- \rangle$ are nonnegative, it is clear that $r^+ \geq K$ and $r^+ \approx K$ for sufficiently small values of β^+ . The above inequality can be interpreted as follows: due to the constant external influx into the population, its asymptotic size exceeds the environment’s carrying capacity.

At this point, it is important to recall that the actual object of study is not the model given by ODE (3.1) but rather the one described by (2.1). Therefore, visualizing the evolution of states requires more than showing the time dynamics of a single real variable as in Figures 2 and 3. The states of the system are functions $\varrho_t : \mathbb{R}^d \rightarrow \mathbb{R}$. Even in the case $d = 1$, a

more appropriate approach is to plot $\varrho_t(x)$ versus x at selected time points. An example of such presentation is shown in Figure 4 which illustrates the evolution of states ϱ_t corresponding to values $r_t^{(5)}$ previously depicted in Figure 3. One can observe from the plot in Figure 4 that the initial density was close to zero and then it slowly increase. The rate of this increase accelerated between $t = 1$ and $t = 2$ and then slowed down as the density approached its asymptotic value. While this form of presentation is clearly less informative in the homogeneous case, it may be the only viable option in the more general setting, where either the initial population density or the parameter functions b^+ and b^- are not constant.

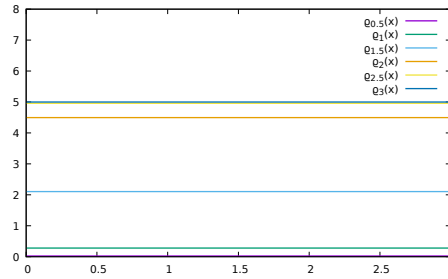


FIGURE 4. Evolution of population density in the homogeneous one-dimensional system: $\varrho_t(x)$ versus x for selected values of t

4. Numerical simulations. As mentioned in previous sections, equation (2.1) is generally too complex to be solved analytically. Therefore, to investigate the system's behavior, numerical methods may be employed to approximate the evolution of its states. In this section, the selected results obtained through this approach are presented. For the sake of clarity in the presentation, as well as to make numerical calculations faster, within this section the spatial dimension is restricted to $d = 1$. Even with such a restriction, it must be acknowledged that an accurate simulation of the evolution of states may be infeasible if the initial density ϱ_0 or parameter functions a^\pm and b^\pm are too complex. Nonetheless, there exist several scenarios in which such simulations can be reliably carried out.

The principal challenges that hinder numerical simulation and must be addressed are the continuity and unboundedness of both time and space. A standard approach to mitigating continuity issues, involves time and space discretization. For a more detailed discussion in a similar setting, see [6]. Rather than analyzing the evolution of original system, one considers a discrete analogue, in which the spatial domain \mathbb{R}^d is replaced by a suitably dense lattice Λ and continuous time is approximated by a sequence of discrete time steps. Consequently, system states, originally represented as

functions $\varrho_t : \mathbb{R}^d \rightarrow \mathbb{R}$, are replaced by sequences of values defined on Λ . Provided the discretization is sufficiently fine, the discrete system typically exhibits behavior that approximates that of the original system, at least in cases involving regular initial densities and parameter functions.

The unboundedness of time and space presents a more significant challenge. In particular, numerical methods are generally not very well suited for analyzing the long-time behavior of systems, as errors tend to accumulate progressively over time. These errors arise both from the discretization process itself and from numerical inaccuracies inherent in the computations performed. Nevertheless, in many cases, the general behavior of the system is preserved even over extended simulation times, particularly when the system tends toward a stationary state. A similar approach can be applied to address spatial unboundedness. If, over the time interval under consideration, the system's evolution is effectively confined to a bounded region of space, the remainder of the infinite domain may be disregarded. In such cases, it is sufficient to restrict the simulation to this bounded subdomain – referred to as the numerical domain – while still capturing the essential dynamics of the system. If necessary, the numerical domain may be dynamically extended during the course of the simulation. This approach is valid only when the initial condition and the parameter functions are integrable. In the case of infinite systems – where the density functions are bounded but not integrable – it is generally not applicable and a suitable numerical treatment remains unclear. However, certain special cases permit reliable simulation. One such case is a periodic system. Specifically, if the initial condition ϱ_0 , along with the parameter functions b^+ and b^- , are periodic with a common period p , then the population density ϱ_t remains periodic with the same period p for all $t \geq 0$. It allows the numerical domain to be restricted to a single spatial window of size corresponding to the period p , while preserving the full dynamics of the system. Spatially periodic systems are more easily simulated than finite systems, as the numerical domain remains invariant over time.

The system can exhibit a wide range of behaviors due to the multitude of possible initial density profiles and parameter functions. As it is not possible to explore all such possibilities, we focus here on several simple scenarios for spatially periodic systems that serve as illustrative examples of typical system dynamics. These scenarios demonstrate relatively rapid convergence to stationary states, resembling the behavior of the homogeneous system described in the previous section.

To maintain a concise description, we first introduce some notions that will be used in both scenarios. Let $\text{Gauss}(c, r)$, or briefly, $G(c, r)$ denote a Gaussian function defined by

$$G(x; c, r) = \frac{c}{r\sqrt{2\pi}} \exp\left(-\frac{x^2}{2r^2}\right).$$

For a given period p define $\text{Gauss}(c, r, s)$, or briefly $G_p(c, r, s)$, as a p -periodic infinite sum of shifted Gaussians

$$G_p(x; c, r, s) = \sum_{n \in \mathbb{Z}} G(x - s + np; c, r).$$

First, we consider a periodic system with period $p = 20$. The parameter functions of the model are defined as follows: $a^\pm = G(1, 1)$, $b^+ = G_p(10, 5, 5)$ and $b^- = G_p(10, 5, -5)$. This selection implies that interactions related to fertility and competition are mostly short-ranged. Moreover, population influx is greater in regions around $x = 5 + 20n$, while population outflux (or mortality) is higher in regions around $x = -5 + 20n$.

Consider the initial density to be specified by the function $G_p(20, 5, 5)$, which exhibits a shape resembling a sinusoidal wave with local maxima located at $x = 5 + 20n$ and local minima at $x = -5 + 20n$ for every $n \in \mathbb{Z}$. The approximated evolution of this system inside the numerical domain is presented in Figure 5 (left panel), where the population density is plotted at selected time points. The initial density and the density at the final simulation time $t = 20$ are indicated by thicker lines.

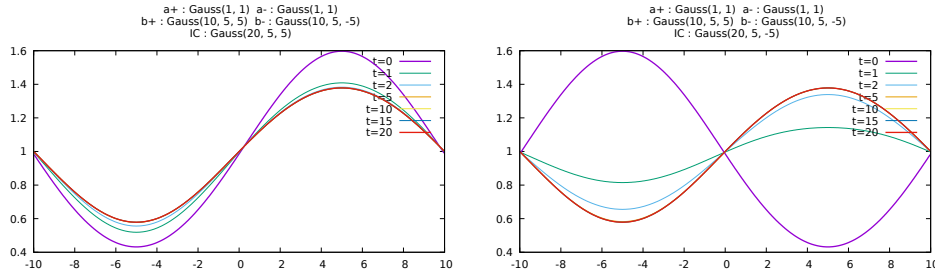


FIGURE 5. Approximated solutions of (2.1) in the first two scenarios: $q_t(x)$ versus x for selected values of t

The initial population density is specified by the function $G_p(20, 5, -5)$, which has a shape resembling a sinusoidal wave. It has local maxima at $x = -5 + 20n$ and local minima at $x = 5 + 20n$ for every $n \in \mathbb{Z}$. Over time, the initial spatial heterogeneity of the population is preserved, though to a lesser extent. Initially, the population density decreases at the maxima and increases at minima, but this trend gradually slows down, suggesting that system is approaching a stable state – the density profiles at $t = 5, 10, 15, 20$ already visually overlap.

In the case of dynamics shown in the right panel of Figure 5, we consider a different initial density, defined by $G_p(20, 5, 5)$. This is the same function as in the previous case, but shifted so that the positions of its minima and maxima are interchanged. Despite the significant difference in the initial

density, the system appears to approach the same stable state at a similar rate as before.

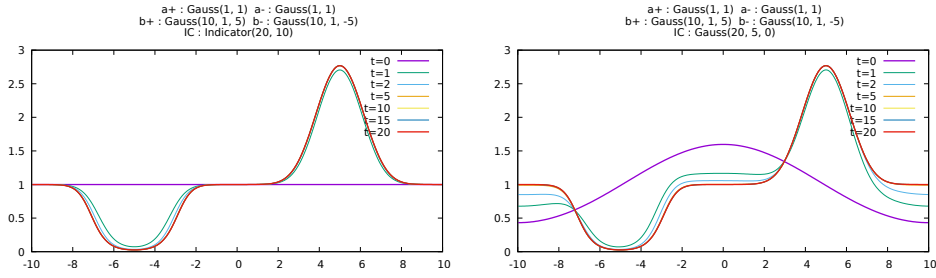


FIGURE 6. Approximated solutions of (2.1) in the case of sharper parameters b^\pm for two distinct initial conditions: $\varrho_t(x)$ versus x for selected values of t

In the next scenario, we again consider a periodic system with period $p = 20$ and unchanged parameters a^\pm , but now with $b^+ = G_p(10, 1, 5)$ and $b^- = G_p(10, 1, -5)$, which are much more sharply concentrated around their maxima compared to those used previously. Figure 6 presents the dynamics of this system for two distinct initial conditions: in the left panel, a constant initial density $\varrho_0 = 1$ (which can also be represented as an infinite sum of shifted indicator functions of an interval) and in the right panel, $\varrho_0 = G_p(20, 5, 0)$. In both cases, the system approaches a stationary state characterized by a spatial division into regions of low and high population density separated by regions of density close to 1. The low-density regions emerge near the maxima of b^+ , the high-density regions near the maxima of b^- and the intermediate regions maintain a density close to 1 – the asymptotic density of homogeneous system with the same a^\pm and $b^\pm = 0$.

The scenarios presented above illustrate typical behavior of the described spatial population model, in which the population density approaches a stationary state that resembles a distorted version of the stationary state of a homogeneous system. However, these examples are far from sufficient to capture the full spectrum of possible dynamics exhibited by the model, even for periodic systems and when the class of parameter functions is restricted to Gaussians, as in the presented cases.

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