# Minimal Models for Spatially Resolved Population Dynamics – Applications to Coexistence in Multi – Trait Models

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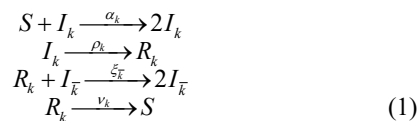rudolf.fuechslin@zhaw.ch

## Abstract

Spatial resolution is relevant for many processes in population dynamics because it may give rise to heterogeneity. Simulating the effect of space in two or three dimensions is computationally costly. Furthermore, in Euclidean space, the notion of heterogeneity is complemented by neighbourhood correlations. In this paper, we use an infinite-dimensional simplex as a minimal model of space in which heterogeneity is realized, but neighbourhood is trivial and study the coexistence of viral traits in a SIRS – model. As a function of the migration parameter, multiple regimes are observed. We further discuss the relevance of minimal models for decision support.

## Spatial Resolution in Population Dynamics

It is well known that population dynamics in spatially resolved systems show features not observed in homogeneous systems (Sun et al., 2021). Spatially structured systems enable microenvironments that give rise to local "symmetry breaking" or spatial heterogeneity. Not all microenvironments have to be in the same state, even if the fundamental laws governing the local dynamics are the same everywhere. This spatial heterogeneity may result from stochastic effects and/or reaction-diffusion processes, e.g. shown in (Turing, 1990) or the complex dynamics emerging in seemingly simple bacteria (Govindarajan et al., 2012; Shapiro et al., 2009).

A broad class of processes combine colocalization of individuals with the transfer of an attribute from an individual with this attribute to one without it. This transfer can conserve the attribute or replicate it. The former case is relevant in the study of conserved quantities in physics or economics, whereas the latter represents processes that one can understand as infections or, regarding information in societies, as knowledge transfer or teaching processes.

As application, we study a minimal model of spatial resolution to a variant of the SIRS – model with two traits:

$$
\begin{aligned}
S + I_k &\xrightarrow{\alpha_k} 2I_k \\
I_k &\xrightarrow{\rho_k} R_k \\
R_k + I_{\bar{k}} &\xrightarrow{\xi_{\bar{k}}} 2I_{\bar{k}} \\
R_k &\xrightarrow{\nu_k} S
\end{aligned}
\tag{1}
$$

As usual, the variable $S$ represents susceptibles, $I_k$ infected, and $R_k$ recovered. The index $k \in \{1,2\}$ represents the multiple traits. We set $k = 1,2 \Rightarrow \bar{k} = 2,1$. The parameter $\alpha_k$ models the infection, $\rho_k$ recovery, $\nu_k$ waning immunity and $\xi_k$ cross-infection. We emphasize that models as given in eqs. (1) are not restricted to diseases but can be transferred to, e.g., the spread of cultural innovations (Walker et al., 2021).

In eqs. (1), the infection processes are modelled by a single parameter $\alpha_k, \xi_k$ respectively. As a motivation for the presented minimal model relevant, these parameters combine (at least) three variables: The infectivity of the $I$, the susceptibility of $S, R_k$ and the contact rate of the infected and the susceptibles.

In a conventional SIRS model, there is no easy way to disentangle physiological parameters (infectivity, susceptibility) from the influence of the contact rate. One could think that doubling the contact rate can be represented by a twofold increased infection rate $\alpha_k$. This holds for low physiological infection/susceptibility parameters, but saturation effects kick in for higher values. This can easily be understood if one considers that it is not the number of contacts alone but also the time of exposure that influences the risk of infection. Transmission processes which require proximity and time of exposure (thereby limiting the number of potential sources of infection) eventually reach a saturation level for the infectivity.

## Minimal Models: Epidemiology on an Infinite Dimensional Simplex

Besides understanding a specific situation, we claim that there is an interest in studying generic phenomena resulting from spatial resolution. Whereas a study that aims to understand the details of a specific epidemiological development should map the real world as precisely as possible (complete models), a study focusing on generic properties should work with a space as simple as possible.

The notion of "space" combines a variety of mathematical structures; first, the concept of space implies that one can distinguish between here and there. Furthermore, spaces such

as the three-dimensional Euclidean space allow to quantify the "theres" (means "non-heres") by a notion of distance and thereby invoking the notion of neighbourhood and neighbourhood correlation. Studying such spaces gives detailed insight into the processes taking place in them but is computationally expensive.

Probably the simplest structure that allows some form of spatial heterogeneity but with only a trivial notion of neighbourhood is an infinite-dimensional simplex. For our purposes, a simplex is a set of discrete locations or nodes that are all mutually connected. If the number of these locations goes to infinity, one speaks of an infinite-dimensional simplex. In our investigations, a location contains two sites, see Fig. 1. Each site is occupied by a representative of the five species $S, I_k, R_k$ or empty (occupied by a $V$). As discussed in (Füchslin et al., 2019; McCaskill et al., 2001), the key point of such a simplex is that it enables to implement a mean-field formulation of a dynamics as given in eq. (1). The fundamental observation underlying this is that since all locations experience the same neighbourhood (all locations are mutually connected), the probability of being in a specific state is equal for all locations. Influx of a representative $X$ of one of the species into a location is determined by a mobility parameter $m$, the number of empty sites on the location and the average $\bar{X}$ on all other locations, see Fig. 1.

More formally, if $U$ denotes the set of all allowed states $u = (s, i_1, i_2, r_1, r_2)$ and $x(u)$ gives the number of $x$ in a state $u \in U$, we must calculate the (time-dependent) probabilities $P(s, i_1, i_2, r_1, r_2; t)$. Because we have two sites per location, it must hold $0 \leq s + i_1 + i_2 + r_1 + r_2 \leq 2$. The probabilities $P(s, i_1, i_2, r_1, r_2; t)$ are combined into a vector $\vec{P}(t)$, and one writes the dynamics of the system as:

$$\frac{d\vec{P}(t)}{dt} = A(\vec{P}(t))\vec{P}(t) \qquad (2)$$

Here $A(\vec{P}(t))$ is a matrix that depends on $\vec{P}(t)$. To illustrate the construction of $A(\vec{P}(t))$, we analyze the dynamics of the state $s = 1, i_1 = 1, i_2 = 0, r_1 = 0, r_2 = 0$. This state can be reached or left either by internal epidemiological dynamics (eqs. (1)) or by influx from some other site.
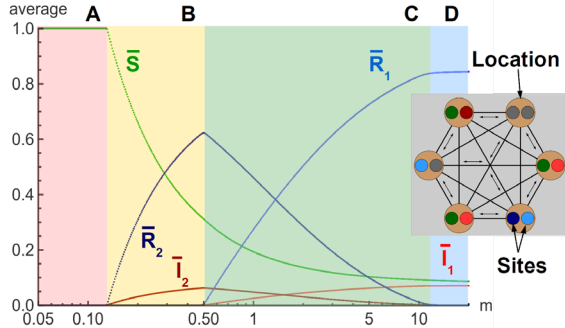


Figure 1: Longterm Averages as a function of the migration parameter $m$. The other parameters are: $\alpha_1 = 3.0, \alpha_2 = 2.0, \xi_1 = 0.03, \xi_2 = 0.04,$ $\rho_1 = 0.12, \rho_2 = 0.04, \nu_1 = \nu_2 = 0.01$. Time is given in days. The inlet shows a simplex of six locations with two sites at each location.

For the internal dynamics, we get:

$$\left.\frac{dP(1,1,0,0,0;t)}{dt}\right|_{epi} = -\alpha_1 P(1,1,0,0,0;t) + \nu_1 P(0,1,0,1,0;t) \\ + \nu_2 P(0,1,0,0,1;t) \qquad (3)$$

For state changes induced by migration, we get:

$$\left.\frac{dP(1,1,0,0,0;t)}{dt}\right|_{mig} = m\bar{S}P(0,1,0,0,0;t) + m\bar{I}_1 P(0,1,0,0,0;t) \\ - 2m\bar{V}P(1,1,0,0,0;t) \qquad (4)$$

The averages $\bar{X}$ are (with $\bar{V} = 2 - \bar{S} - \bar{I}_1 - \bar{I}_2 - \bar{R}_1 - \bar{R}_2$):

$$\bar{X} = \sum_{u \in U} x(u)P(u;t) \qquad (5)$$

As an example, we use this formalism to study an essential effect of spatial heterogeneity, namely the coexistence of different traits in a population. In recent times, questions concerning the coexistence of different traits of viruses gained attention in epidemiology (Ackleh et al., 2016; Guo & Wang, 2022; Roberts et al., 2015). As it turns out, the coexistence of traits appears in our model, see Figure 1, where the averages the system approaches after long time are shown as a function of $m$. We distinguish regions A, B, C, and D in which either no, one or both traits exist. The simple model we present illustrates an effect which is relevant with respect to public health: In case of co-existing traits, reducing $m$ may decrease one trait, but lead to an increase of the other trait. This phenomenon is no surprise but needs to be considered, if the two traits differ in the severity of the disease they cause.

## Discussion

It is clear that the presented model is not suited for predicting the course of an actual pandemic. The model is much too simple (no age dependency, et cetera), and the spatial structure does not reflect any actual geography. However, it still teaches us some important lessons: First, the coexistence of different viral traits is potentially possible but depends on the migration rate m (equivalent to the contact rate). Second, and more important for decision support, a decrease in the contact rate may suppress one trait that is dominant at higher contact rates. The decrease may, however, give room for a trait with different properties.

The SARS-CoV-2 pandemic resulted in a massive increase of interest in mathematical and model-based epidemiology. In a recent review (Gnanvi et al., 2021), the authors compare different simulation techniques for modelling the dynamics of the SARS-CoV-2 pandemics (Compartment models of the SIR- or SEIR type (46%). Only 1.3% of the studies used agent-based models). Most of these studies focused on a particular case in a specific geographic setting. This approach is sensible, particularly because the contact structure of the populations in different countries is known with a resolution concerning age and type of activity (Fumanelli et al., 2012; Prem et al., 2017). These are "complete" models in that they try to include as much of reality as possible. This comes at a price: The models contain many parameters and, in consequence, are difficult to calibrate. In contrast, minimal models may give only qualitative insight into the processes they analyze. However, this comes with the advantage that it is often easy to relate cause and effect. More concretely, concerning epidemiology, even if minimal models are not suited as tools for prediction, they justify a detailed scrutiny of variants of minor importance. This is because these variants

may become relevant after changing system parameters, e.g. via non-pharmaceutical interventions.

Giving a justification for (expensive) observations is highly relevant in decision support; it is an example of the value and importance of modelling for politics and society and helps strengthen the role of science and artificial life, in particular.

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