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Susceptible-infectious-recovered models revisited: From the individual level to the population level

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ABSTRACT

The classical susceptible-infectious-recovered (SIR) model, originated from the seminal papers of Ross [51] and Ross and Hudson [52,53] in 1916–1917 and the fundamental contributions of Kermack and McKendrick [36–38] in 1927–1932, describes the transmission of infectious diseases between susceptible and infective individuals and provides the basic framework for almost all later epidemic models, including stochastic epidemic models using Monte Carlo simulations or individual-based models (IBM). In this paper, by defining the rules of contacts between susceptible and infective individuals, the rules of transmission of diseases through these contacts, and the time of transmission during contacts, we provide detailed comparisons between the classical deterministic SIR model and the IBM stochastic simulations of the model. More specifically, for the purpose of numerical and stochastic simulations we distinguish two types of transmission processes: that initiated by susceptible individuals and that driven by infective individuals. Our analysis and simulations demonstrate that in both cases the IBM converges to the classical SIR model only in some particular situations. In general, the classical and individual-based SIR models are significantly different. Our study reveals that the timing of transmission in a contact at the individual level plays a crucial role in determining the transmission dynamics of an infectious disease at the population level.

1. Introduction

Mathematical modeling in epidemiology started with the pioneering work of Bernoulli [10] in 1760 in which he aimed at evaluating the effectiveness of inoculation against smallpox. The model of Bernoulli described the susceptible and recovered classes and already incorporated the chronological age of individuals (see [20,21]). The susceptible-infectious-recovered (SIR) model as we know today takes its origin in the fundamental works on "*a priori* pathometry" by Ross [51] and Ross and Hudson [52,53] in 1916–1917 in which a system of ordinary differential equations was used to describe the transmission of infectious diseases between susceptible and infected individuals. In 1927–1933, Kermack and McKendrick [36–38] extended Ross's ideas and model, proposed the cross quadratic term βIS linking the sizes of the susceptible (S) and infective (I) populations from a probabilistic analysis of the microscopic interactions between infective agents and/or vectors and hosts in the dynamics of contacts, and established the threshold theorem. Since then epidemic models have been extensively developed in several directions, we refer to the monographs of Bailey [7], Bartlett [9], Muench [45], Anderson and May [4], Busenberg and Cooke [13], Capasso [14], Murray [46], Daley and Gani [16], Mode and Sleeman [47], Brauer and Castillo-Chavez [11], Diekmann and Heesterbeek [19], Thieme [59], and Keeling and Rohani [35] on these topics.

In order to focus on the dynamical properties of an infectious disease itself, here we neglect the demography, namely the birth and death processes, and the immigration/emigration process. The classical SIR model takes the following form [4]:

$$\begin{cases} S' = -\beta \frac{SI}{N} \\ I' = \beta \frac{SI}{N} - \eta_R I \\ R' = \eta_R I, \end{cases} \tag{1.1}$$

where $S(t)$ is the number of susceptible individuals, $I(t)$ is the number of infective individuals (i.e. individuals who are infected and capable to transmit the disease), $R(t)$ is the number of recovered individuals at time t, respectively, and N is the total number of individuals in the population. The parameter $\beta > 0$ is called the

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infection rate (i.e. the contact rate times the probability of infection, see [59]), and $\eta_R > 0$ is the recovery rate (i.e. the rate at which infective individuals recover). The SIR model has been used successfully to describe several epidemics (see for example [15]), but as far as we understand, this rate of infection is only derived empirically, namely by comparison of the model with real data.

When one neglects the demography, an epidemic model becomes a combination of the following aspects:

(a) a rule of contacts between individuals;
(b) a rule of transmission per contact;
(c) a rule of development of the infection at the level of individuals.

Since the development of an infection is not instantaneous, rule (c) can be described by introducing a latency between the transmission of the pathogen and the moment at which an exposed individual becomes capable to transmit the infection (namely becomes infective). This latency can be described by using either an extra exposed class (when the time of latency follows an exponential law), which leads to SEIR models, or an age of infection (i.e. the time since infection), which leads to age-structured models, we refer to [61,60,33,59,41] for details on this topic. In this article, we will neglect the aspect (c) and focus only on (a) and (b).

In an epidemic of an infectious disease, the graph of contact plays a crucial role in the transmission of the disease. It is usually admitted (see [4,30]) that the SIR model (1.1) is derived by using a "*fully mixed*" population. This means that all individuals have the same probability to contact with any other individuals in the population. Here we will see that even with a fully mixed population, the SIR model may fail to reproduce the dynamics of the epidemic. Actually we will see that more sophisticated models are needed to understand the dynamical property of an epidemic.

Of course in most epidemics, the contacts between individuals will arise only locally in space. Therefore more general graphs of contact are needed, we refer to [26,48,24,25,43,8] (and references therein) for more information on this subject. Actually the space can be incorporated by using different approaches: it can be regarded as a continuous domain (see [50,54,55]) or again as a network (see [6] and references therein). In this article, we will neglect the space in order to focus on the classical SIR model.

Stochastic individual-based models (IBM) have been extensively used to investigate threshold conditions and to evaluate the efficacy of disease control measures in which each host is viewed as an individual agent whose status changes based on probabilistic events occurring over time. IBM are particularly suitable to describe the transmission of infectious diseases in a small population in which the individual behavior plays an important role in the spread of diseases [18,29,40,34]. Studies have been performed to compare different types of IBM. For instance, [57] compared two different types of individual-based models, one assumes random mixing without repetition of contacts and the other assumes that the same contacts repeat day-by-day. They tested and compared how the total size of an outbreak differs between these model types depending on the key parameters such as transmission probability, number of contacts per day, duration of the infectious period, different levels of clustering and varying proportions of repetitive contacts. If the number of contacts per day is high or if the per-contact transmission probability is high, as seen in typical childhood diseases such as measles, they showed that random mixing models provide acceptable estimates of the total outbreak size. If the number of daily contacts or the transmission probability is low, such as the infection of meticillin-resistant *Staphylococcus aureus* (MRSA), they found that particular consideration should be given to the actual structure of potentially contagious contacts when designing the model. See also the comparison of a stochastic agent-based model and a structured metapopulation stochastic model for the progression of a baseline pandemic event in Italy by Ajelli et al. [1].

We should mention that the Gillespie algorithm or Doob-Gillespie algorithm (see [22,23,27,28]) provides a method to run random Monte-Carlo simulations associated to ordinary differential equations (see [5,39]). This method was successfully used for chemical or biochemical systems of reactions. In epidemics, we will see in this article that changing the moment of pathogen's transmission from the beginning to the end of contact may influence the dynamical property of the equations.

The main issue to be addressed in this article is the comparison between the classical deterministic SIR model and its computer stochastic versions. The stochastic models will be derived by using Monte Carlo simulations or IBM. The increase in behavioral details provided by IBM, however, leads to much greater computational intensity and much greater difficulty in analyzing the significance of parameters. Some comparisons between deterministic models and IBM have been performed by Pascual and Levin [49] (in the context of predator–prey), D'Agata et al. [17] (in the context of epidemics), Hinow et al. [32] (in the context of cell population dynamics), and Sharkey [56] (in the context of epidemics in networks). But as we will see, even with rather simple rules (a) and (b), the comparison between the SIR model (1.1) and the IBM derived from these stochastic rules (at the individual level) is not clear in general. Actually we will see that more general classes of SIR models are necessary to derive a comparison with the IBM.

The paper is organized as follows. In Section 2 we make some assumptions about the rules of contacts between susceptible and infective individuals, the rules of transmission of diseases through these contacts, and the time of transmission during contacts. In Section 3 we analyze the transmission driven only by susceptible individuals and compare the numerical simulations between the classical SIR model and the IBM. In Section 4, the transmission driven only by infective individuals is modeled and analyzed. Our analysis and simulations demonstrate that in both cases, the IBM converges to the classical SIR model only in some particular situations. In general, the classical SIR model and the IBM are significantly different. A brief discussion is given in Section 5.

2. Rules of contacts and transmission

In this section we present the stochastic process describing contacts between individuals. This process will lead to the construction of a simple deterministic model. The contacts are supposed to be arbitrarily given at an initial time, and in order to describe the evolution of the contacts with time, we will use the following rules.

We would like to point out that the evolution of the contact network is indeed dynamic since it changes with time. We define the rules of contacts, the rules of transmission, and the time of transmission for the purpose of numerical and stochastic simulations of the SIR model. These rules may not affect the outcome of an epidemic from a deterministic modeling point of view. However, they are important in numerical and stochastic simulations and produce dramatically different results.

2.1. Rules of contacts

Firstly, we make some assumptions on the rules of contacts.

(a) At any time each individual has initiated exactly one contact with an individual in the population (possibly himself).
(b) The duration of a contact follows an exponential law and the average duration of a contact is $T_C > 0$.