

Chapter 2

Applications of Single-Type Branching Processes

2.1 Introduction

Two applications of single-type branching process theory to population and epidemic processes are presented. The first application is to an epidemic model with susceptible, infectious, and recovered individuals in which there is only temporary immunity to reinfection. In the branching process approximation, the infectious stage is modeled by a birth and death process. Branching process theory provides an estimate for the probability of a major outbreak. Whittle in 1955 was the first to apply this theory in an epidemic setting [38]. The second application is to a classic competition model for two species. In this application, one species is native and the other species is nonnative and invasive. Invasive species pose a serious threat to the survival of many native species [35]. An important problem in conservation theory is how to prevent this invasive process. Branching process theory is used to investigate this problem, through analysis of a competition model between the native and the invasive species.

2.2 SIRS Epidemic

Introduction of infectious individuals into a susceptible population may result in an outbreak, causing a large increase in the number of infectious individuals. Whether an outbreak occurs depends on the rates of transmission, recovery, death, and the size of the susceptible population. In the SIR epidemic model, the population is divided into susceptible, infectious, and recovered individuals, S , I , and R , respectively. Let the parameters β and γ denote the transmission and the recovery rates, respectively. In the case of a serious disease, infection may result in disease mortality at rate α . In addition, if recovered individuals have only temporary immunity to reinfection, with a waning immunity rate δ , then recovered individuals return to

being susceptible. With waning immunity, there is a potential for a second outbreak. The model with waning immunity is referred to as an SIRS epidemic model.

For the SIRS epidemic model, the ratio $\beta/(\gamma + \alpha)$ is known as the basic reproduction number, denoted as \mathcal{R}_0 , an important parameter in epidemic theory. It is often defined as the number of secondary infections caused by introduction of one infectious individual into an entirely susceptible population. Therefore, if the magnitude of \mathcal{R}_0 is greater than one, the number of cases increases, an epidemic situation. For different infectious diseases, there have been a wide range of estimates for \mathcal{R}_0 that depend on many factors, including the infectious agent, the time, and the location [13].

Let the three random variables for the states (S, I, R) in the CTMC epidemic model be denoted as $(X_1, X_2, X_3) = \mathbf{X}$ with $N = \sum_{i=1}^3 X_i$ equal to the random variable for the total population size. The transition rates in the CTMC model are given in Table 2.1. For example, event 1 in Table 2.1 is a new infection. The transition probability for event 1 is

$$\mathbb{P}(\Delta \mathbf{X}(t) = (-1, 1, 0) | \mathbf{X}(t)) = \beta \frac{X_1(t)}{N(t)} X_2(t) \Delta t + o(\Delta t),$$

where $\Delta \mathbf{X}(t) = \mathbf{X}(t + \Delta t) - \mathbf{X}(t)$ and the MC Rate $\beta \frac{X_1(t)}{N(t)} X_2(t)$ is nonlinear.

Table 2.1 Transition rates for the CTMC SIRS epidemic model (MC Rates) and for the approximating branching process for infectious individuals, $X_2(t)$ (BP Rates). In the branching process approximation, event 1 corresponds to a birth of an infective and events 2 and 3 correspond to a death of an infective.

Event	$\Delta \mathbf{X}(t)$	MC Rates	BP Rates
1	$(-1, 1, 0)$	$\beta \frac{X_1(t)}{N(t)} X_2(t)$	$\beta X_2(t)$
2	$(0, -1, 1)$	$\gamma X_2(t)$	$\gamma X_2(t)$
3	$(0, -1, 0)$	$\alpha X_2(t)$	$\alpha X_2(t)$
4	$(1, 0, -1)$	$\delta X_3(t)$	—

The deterministic SIRS model corresponding to the CTMC model described above can be expressed as the following system of ordinary differential equations (ODEs):

$$\begin{aligned}
 \frac{dS(t)}{dt} &= -\beta \frac{S(t)}{N(t)} S(t) I(t) + \delta R(t) \\
 \frac{dI(t)}{dt} &= \beta \frac{S(t)}{N(t)} S(t) I(t) - \gamma I(t) - \alpha I(t) \\
 \frac{dR(t)}{dt} &= \gamma I(t) - \delta R(t),
 \end{aligned} \tag{2.1}$$

where $S(0) > 0, I(0) > 0, R(0) = 0$, and $S(t) + I(t) + R(t) = N(t)$. In this model, $N(t)$ is not random. Because of the nonlinearity in the state variables, the solution

$(S(t), I(t), R(t))$ corresponding to the SIRS model (2.1) is not the expectation of the random variables in the CTMC model,

$$(S(t), I(t), R(t)) \neq (\mathbb{E}(X_1(t)), \mathbb{E}(X_2(t)), \mathbb{E}(X_3(t))).$$

As will be clear from the examples, at the initiation of an outbreak and end of the outbreak, the CTMC model with discrete random variables provides a more realistic description of the disease dynamics than the ODE model. However, during an outbreak, if the population size is large, then the dynamics of the CTMC and ODE models are close. Kurtz [26–28] showed in a series of papers in the 1970s that the large population limit of a Markov chain model is a system of ODEs. In particular, the SIRS ODE model is the large population limit of the SIRS CTMC model.

Near the disease-free state, $(X_1(0), X_2(0), X_3(0)) \approx (N(0) - i_0, i_0, 0)$. If $N(0)$ is large and i_0 is small, then the transition rates are approximately linear. The CTMC infectious population can be approximated by a continuous-time branching process. Either the Markov chain hits zero, an absorbing state, or grows exponentially away from zero, a disease outbreak. The probability of hitting zero can be estimated from the branching process approximation.

The transition rates corresponding to a branching process approximation of the infectious population $X_2(t)$ are given in Table 2.1 (BP Rates). For example, event 1 in the branching process approximation is

$$\mathbb{P}(\Delta X_2(t) = 1 | X_2(t)) = \beta X_2(t) \Delta t + o(\Delta t),$$

a “birth” of an infectious individual. The branching process rate βX_2 is linear in X_2 .

The infectious population X_2 in the CTMC epidemic model has a per capita birth rate equal to $b = \beta$ and a per capita death rate equal to $d = \gamma + \alpha$ (Table 2.1). It follows from the branching process formula in Chapter 1 that the probability of extinction is equal to $q^* = d/b$ when $b > d$ (supercritical case). Expressed in terms of the basic reproduction number,

$$q^* = \begin{cases} \frac{1}{\mathcal{R}_0}, & \mathcal{R}_0 > 1 \\ 1, & \mathcal{R}_0 \leq 1. \end{cases}$$

The preceding estimate was first described by Whittle in 1955 [38] for the simpler SIR epidemic model with no disease-related mortality ($\alpha = 0$) and no waning immunity ($\delta = 0$). Given $X_2(0) = i_0$ initial infectious individuals introduced into an entirely susceptible population, the probability of no major outbreak is

$$\mathbb{P}_0(i_0) \approx (1/\mathcal{R}_0)^{i_0}.$$

The probability of a major outbreak is $1 - (1/\mathcal{R}_0)^{i_0}$. As noted above, this result depends on the fact that $X_1(0) \approx N(0)$ is sufficiently large and i_0 is small.

The graphs in Figure 2.1 illustrate the dynamics in two cases: $N(0) = 100$ and $N(0) = 500$. The branching process is supercritical, $\mathcal{R}_0 > 1$. For the ODE model, the disease becomes endemic. However, in Figure 2.1 (a) and (c), the disease in the stochastic model does not become endemic and generally ends after a single outbreak. For the larger population size of 500, in Figure 2.1 (c), the first outbreak is followed by one of smaller magnitude, where the maximum outbreak size is about 30. A single major outbreak may be followed by one or more minor ones, if there is a sufficient number of susceptible individuals after the first outbreak. It is apparent in Figure 2.1 that the stochastic sample paths are closer to the deterministic ODE solution in Figure 2.1 (c) than in Figure 2.1 (a) because of the much large population size in 2.1 (c). The MatLaB program that generated the sample paths in Figure 2.1 is given in Appendix A.2.

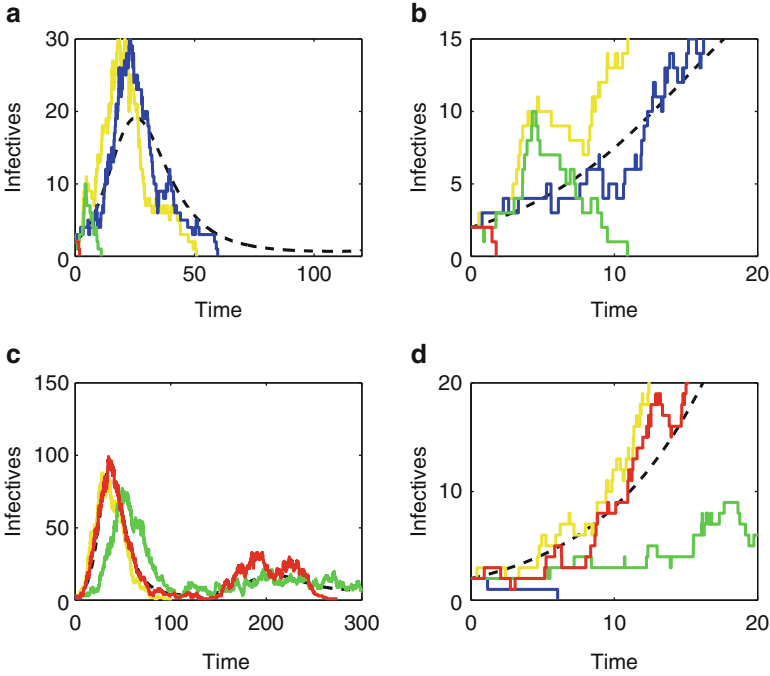


Fig. 2.1 Four sample paths of the CTMC SIRS epidemic model and the corresponding ODE solution (dashed curve). Parameter values for the SIRS epidemic model $\beta = 0.3$, $\gamma = 0.1$, $\alpha = 0.05$, $\delta = 0.01$, $I(0) = 2$, $S(0) = N(0) - 2$. In (a) and (b), $N(0) = 100$ and in (c) and (d), $N(0) = 500$. The shorter time scale in (b) and (d) illustrates the growth phase in the branching process approximation. The probability of a major outbreak is $1 - \mathbb{P}_0(2) = 1 - (1/2)^2 = 3/4$.

2.3 Species Invasion

According to the NOAA website [31], “An invasive species is an organism that causes ecological or economic harm in a new environment where it is not native.” Charles Elton’s book *The Ecology of Invasions by Animals and Plants* published in 1958 was the first to call attention to the environmental impact of invasions by nonnative species [15]. Many nonnative invasive species from amphibians and ants to water hyacinths and zebra mussels are documented in [35]. An important question in conservation theory is how to prevent and control invasive species. Models and branching processes can help address these questions and inform public policy decisions.

Four stages are generally identified in the invasion process: arrival, establishment, integration, and spread [37]. The first two stages of the invasion process may be modeled by competition between two species with one being the native species and the other, the nonnative species. The invader may arrive many times but each time it only has a small chance of success unless several propagules are introduced simultaneously.

We model competition between two species via the well-known Lotka-Volterra competition model. Let n_1 be the native species and n_2 the invader in a deterministic model for competition:

$$\begin{aligned}
 \frac{dn_1(t)}{dt} &= r_1 n_1(t) \left(1 - \frac{n_1(t)}{K_1} \right) - c_{12} n_1(t) n_2(t) \\
 &= n_1(t) \left(r_1 - r_1 \frac{n_1(t)}{K_1} - c_{12} n_2(t) \right) \\
 \frac{dn_2(t)}{dt} &= r_2 n_2(t) \left(1 - \frac{n_2(t)}{K_2} \right) - c_{21} n_2(t) n_1(t) \\
 &= n_2(t) \left(r_2 - r_2 \frac{n_2(t)}{K_2} - c_{21} n_1(t) \right).
 \end{aligned} \tag{2.2}$$

All parameters are positive. Each species in the absence of the other grows logistically to their respective carrying capacity, K_i , $i = 1, 2$. The terms c_{ij} are interspecies competition coefficients. It is well known that a stable coexistence equilibrium exists if $K_i < r_j / c_{ji}$, where $i, j = 1, 2$, $i \neq j$. However, if $K_1 < r_2 / c_{21}$ and $K_2 > r_1 / c_{12}$, then species 2 outcompetes species 1; species 1 goes extinct and species 2 approaches carrying capacity K_2 .

To formulate a CTMC model for the invasion process, we use the particular form from the Lotka-Volterra competition model (2.2) to formulate the birth and death rates. Let $\mathbf{X}(t) = (X_1(t), X_2(t))$ denote the random vector for species 1 and 2 and $\Delta \mathbf{X}(t) = \mathbf{X}(t + \Delta t) - \mathbf{X}(t)$. Assume birth and death rates for species i , respectively, are dependent on both population sizes, competition within and between species. That is, let the birth rate be

$$b_i(t) = b_{i1} X_i(t) - b_{i2} X_i^2(t), \quad X_i(t) \leq b_{i1} / b_{i2} \tag{2.3}$$

and the death rate be

$$d_i(t) = d_{i1}X_i(t) + d_{i2}X_i^2(t) + c_{ij}X_i(t)X_j(t), \quad i \neq j, \quad (2.4)$$

where $b_{i1} > 0$, $d_{i1} > 0$, $b_{i2} \geq 0$, and $d_{i2} \geq 0$. If $X_i(t) > b_{i1}/b_{i2}$, then $b_i(t) = 0$. The competition term $c_{ij}n_i(t)n_j(t)$ is assumed to contribute to the death rate. Because the dynamics of the ODE and CTMC are nonlinear in the state variables, the deterministic solution does not correspond to the mean of the stochastic model.

To compare the CTMC dynamics to those of the ODE model, assume that $r_i = b_{i1} - d_{i1} > 0$ and $b_{i2} + d_{i2} = r_i/K_i$. (See Table 2.2.) Even though the deterministic model predicts invader success, this is not the case in the stochastic model. If the invader population is not sufficiently large, then it cannot become established.

Table 2.2 Transition rates for the CTMC competition model (MC Rates) and for the continuous-time branching process approximation (BP Rates). Rates $b_i(t)$ and $d_i(t)$ are defined in (2.3) and (2.4).

Event	$\Delta \mathbf{X}(t)$	MC Rates	BP Rates
1	(1, 0)	$b_1(t)$	—
2	(0, 1)	$b_2(t)$	$b_{21}X_2(t)$
3	(-1, 0)	$d_1(t)$	—
4	(0, -1)	$d_2(t)$	$(d_{21} + c_{21}K_1)X_2(t)$

Theory from branching process can be applied when $X_1(0) = K_1$ is sufficiently large and $X_2(0) = n_{20}$ is small. To estimate the probability of species 2 invasion success, the rates for the branching process (BP Rates) for X_2 are applied from Table 2.2. The corresponding linear approximation for the ODE model for $n_2(t)$ is

$$\frac{dn_2(t)}{dt} \approx (b_{21} - d_{21} - c_{21}K_1)n_2(t).$$

The zero state for species 2 (or species 1) is an absorbing state. It follows that the branching process approximation for the invader $X_2(t)$ will have per capita birth and death rates, $b = b_{21}$ and $d = d_{21} + c_{21}K_1$, respectively. Thus, species 2 can invade species 1 iff $b > d$ iff $b_{21} > d_{21} + c_{21}K_1$ (supercritical case). This latter inequality is equivalent to the inequality $K_1 < r_2/c_{21}$. Therefore, from branching process theory, if $K_1 < r_2/c_{21}$, the probability of extinction or an unsuccessful invasion of species 2 is approximately

$$\mathbb{P}_0(n_{20}) = \left(\frac{d_{21} + c_{21}K_1}{b_{21}} \right)^{n_{20}}$$

and the probability of a successful invasion is $1 - \mathbb{P}_0(n_{20})$, where n_{20} is the initial population size of the invader.

If the interspecies competitive effect of species 1 on species 2 is relatively small, that is, $c_{21}K_1$ is small compared to b_{21} , then species 2 has a competitive advantage

and a greater chance of invasion. The stochastic model also shows that invasion success depends on the population size of the invader, n_{20} . If the invasion is successful, the outcome of the competition, either coexistence of both species or dominance by species 2, can be predicted by the ODE model. This outcome may be representative of the third stage of invasion, integration. Which of these two outcomes occurs depends on the relation of b_{11} to $d_{11} + c_{12}K_2$. If species 2 is a better competitor, $b_{11} < d_{11} + c_{12}K_2$, then species 2 will replace species 1.

An example of the CTMC species invasion model is simulated with parameter values chosen so that species 2 dominates after it successfully invades. Parameter values are $K_1 = 100$, $K_2 = 200$, and $K_1 > r_2/c_{21}$ in Figure 2.2. The four sample paths of the CTMC competition model illustrate four invasion attempts, but only one is successful.

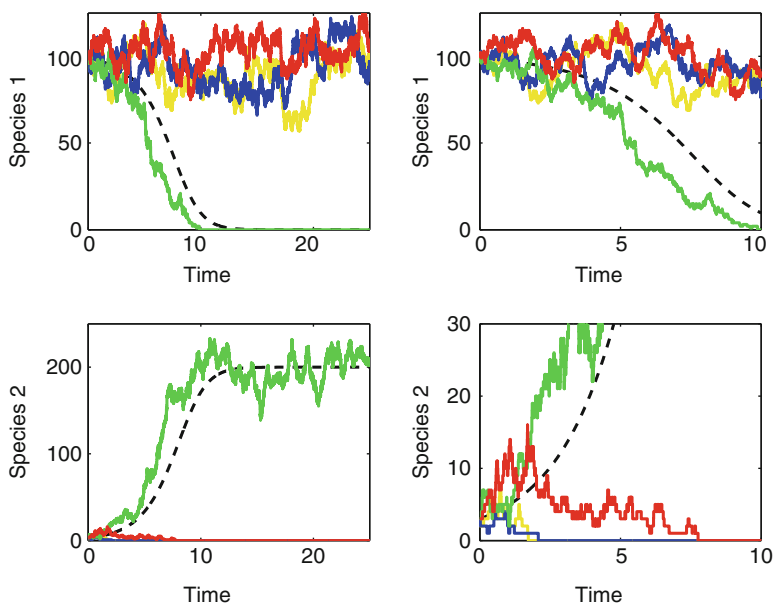


Fig. 2.2 Four sample paths of the two species CTMC competition model and the solution of the ODE model (2.2) with parameter values $r_1 = 1$, $r_2 = 2$, $b_{11} = 2$, $d_{11} = 1 = d_{21}$, $b_{21} = 3$, $d_{12} = 0$, $i = 1, 2$, $c_{12} = 0.01 = c_{21} = 0.01$, $K_1 = 100$, and $K_2 = 200$. Initial conditions are $X_1(0) = 100$ and $X_2(0) = 3$. The graphs on the left are for the time interval $[0, 25]$, whereas the graphs on the right are for the time interval $[0, 10]$. The shorter time scale illustrates the initial exponential growth of species 2 invasion. The probability that species 2 invades species 1 at equilibrium is $1 - \mathbb{P}_0(3) = 1 - (2.5/3)^3 \approx 0.421$.

2.4 Summary

Continuous-time and discrete-state branching process theory from Chapter 1 is applied to two problems. One problem is to estimate the probability of a major outbreak in an SIRS epidemic with temporary immunity and the second problem is to estimate the probability of species invasion when a native species competes with a nonnative species. Additional applications of branching process theory involving multiple species and multiple sites in the study of species invasions and epidemic outbreaks can be found in the references (e.g., [5, 6, 29, 34]).

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