

Pair Approximations for Ecological Models with Additional Neighborhood Effects

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Abstract—The spatial interaction plays an important role in many ecological situations. A lattice model is a popular tool for creating such a grid structure of discrete individuals together with their possible connection. The procedure, however, is very computation time consuming depending on the model complexity. Therefore, master equations, correlation equations, and pair approximations are proposed as analytical methods. In this paper, a new approach to pair approximation method is introduced. The main assumption beyond this approach is that the space average and the probabilistic average are identical when the total population size is large enough. This technique is suitable for a model composed of individuals whose event rates such as birth rate, death rate, transmission rate, and recovery rate are additionally affected by their nearby neighbor. We, finally, apply this technique to a simple SIS epidemic model.

Keywords—Pair approximation, Probability distribution, SIS epidemic model, Spatial model.

I. INTRODUCTION

PAIR approximation was first used to describe population dynamics by Matsuda et al. [1] in 1992. His method, so-called the ordinary pair approximation (OPA) and the doublet decoupling approximation, was developed to construct a simple model as an ordinary differential equation where the global and the local densities are the state variables. Two years later, Sato et al. [2] improved the OPA by considering that the reproduction of host and pathogen take place only at its nearest neighbor site. Since then, the Japanese researchers have continuously contributed theoretical results and also applied to many biological phenomena [3]-[8]. Rand [9], however, used the pair approximation as a moment closure approximation where the number of sites and the number of pairs are the state variables. Moreover, he discussed how to calculate master equations and correlation equations. Pair approximation has an enormous potential for applications because the effect of spatial structure is usually considered. It has provided an attractive framework for studying epidemiology [10]-[14], ecology [15]-[17], and evolution [18], [19].

In order to contribute theoretical results understandably and precisely, we introduce some notations and conventions in section II. In section III, we provide the formulation of pair

approximation by using new approach (NPA). Then we apply the NPA to a simple SIS model in section IV. In section V, the numerical results are shown. Finally, we discuss the results and draw conclusion. In addition, the complicated mathematical expressions are collected in Appendix.

II. NOTATIONS AND DEFINITIONS

Under a given configuration $\underline{\sigma} = (\sigma_k)$ where $k \in \{x, e\}$, the following notations are defined.

- σ_x means the state of the site or the individual x ,
- σ_e means the state of the pair or the edge e ,
- $\sigma_x = i$ means that the state of the individual x is i ,
- $\sigma_e = ij$ means that one end of the edge e is in state i , e_i , while the other is in state j , e_j ,
- $[i],[ij],[ijk]$ are the number of sites, edges, and triples in state i , ij , and ijk , respectively,
- $Q_x(i)$ is the number of neighbors of the sites x which are in state i ,
- Q_x is the number of neighbors of the sites x ,
- $Q_{e_j}(i)$ is the number of neighbors of the sites e_j which are in state i ,
- $\langle Z_x \rangle_{\sigma_x=i}$ is the average of quantity Z_x over all individuals x which are in state i ,
- $\langle Z_{e_i} \rangle_{\sigma_e=ij}$ is the average of quantity Z_{e_i} over all edges e which are in state ij ,
- $\langle Q_x(i) \rangle_{\sigma_x=j}$ is the average value of the number of i -state neighbors of a j -state site,
- $\langle Q_{e_j}(i) \rangle_{\sigma_e=jk}$ is the average value of the number of i -state neighbors of a j -state site in a jk -state edge,
- Q is the average number of neighbors,
- N is the total population size,
- q_i equals $[i]/N$, and
- q_{ij} equals $[ij]/Q[j]$.

An example is shown in Fig. 1.

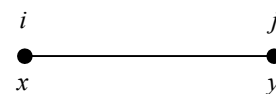


Fig. 1 $\sigma_x = i, \sigma_y = j, \sigma_e = ij$

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III. FORMULATION OF PAIR APPROXIMATION

We, firstly, construct a population network over a regular d -dimensional lattice model whose site can be occupied by an individual carrying only one of many different states. An unoccupied or empty site, sometimes, is considered. We, then, assume that our system is composed of n individuals carrying k different types of population with $k \geq 2$. For $i = 1, \dots, k$, each type of the population, the number of each type, and the proportion of each type in the population are denoted by M_1, \dots, M_k , m_1, \dots, m_k , and p_i , respectively. If $M = (M_1, \dots, M_k)$ has a multinomial distribution together with parameters n and $p = (p_1, \dots, p_k)$, then the following probability can be calculated by using this formula

$$\Pr(M_1 = m_1, \dots, M_k = m_k) = \binom{n}{m_1, \dots, m_k} p_1^{m_1} \dots p_k^{m_k}$$

where $\binom{n}{m_1, \dots, m_k} = \frac{n!}{m_1! \dots m_k!}$. Moreover, $E(M_i) = np_i$ and $Var(M_i) = np_i(1 - p_i)$ for $i = 1, \dots, k$.

In this paper, we have mainly focused on a latticed model with a constant number of neighbors, Q , as mentioned in the following assumption.

Assumption 1. Assume $Q_x \equiv Q$ is independent of x and $Q_x(i)$ with $\sigma_x = j$ is multinomially distributed with parameters Q and p_i where $p_i = q_{ij}$.

The next two assumptions imply that $Q_{e_i}(k)$ and $Q_{e_j}(k)$ are independent when $\sigma_e = ij$.

Assumption 2. For all k , $Q_x(k)$ and $Q_y(k)$ are independent when $x \neq y$ because there is no triangle and no multiple connections.

Assumption 3. $\Pr(Q_{e_i}(k) = q) = \Pr(Q_x(k) = q | Q_x(j) \geq 1)$.

The final assumption implies that the space average and the probabilistic average are identical.

Assumption 4. (Large N hypothesis)

Where the total system size N is large ($N \rightarrow \infty$), we can identify the configuration averages $\langle Z_x \rangle_{\sigma_x=i}$ and $\langle Z_e \rangle_{\sigma_e=ij}$, respectively with the P -expectations $E_p(Z_x)$ and $E_{P_i}(Z_{e_i})$.

Consequently, we can present a new way to approximate some special higher order terms that the OPA cannot do in the following theorems.

Theorem 1. $\langle Q_x(i) \rangle_{\sigma_x=j} = \frac{[ij]}{[j]}$.

Proof. By definition.

Theorem 2. $\langle Q_x(i_1)Q_x(i_2) \rangle_{\sigma_x=j} = \begin{cases} Qq_{i_1|j} + \frac{Q!}{(Q-2)!}q_{i_1|j}^2 & ; i_1 = i_2 \\ \frac{Q!}{(Q-2)!}q_{i_1|j}q_{i_2|j} & ; i_1 \neq i_2 \end{cases}$.

Proof.

Case 1. $i_1 = i_2$

$$\begin{aligned} \langle Q_x(i_1)Q_x(i_1) \rangle_{\sigma_x=j} &= \sum_{m=0}^Q m^2 \Pr(Q_x(i_1) = m | \sigma_x = j) \\ &= \sum_{m=0}^Q m^2 \binom{Q}{m} q_{i_1|j}^m (1 - q_{i_1|j})^{Q-m} \end{aligned}$$

Finally, we obtain

$$\langle Q_x(i_1)Q_x(i_1) \rangle_{\sigma_x=j} = Qq_{i_1|j} + \frac{Q!}{(Q-2)!}q_{i_1|j}^2$$

because

$$\sum_{k=0}^n \frac{k^2 n!}{k!(n-k)!} A^k (1-A)^{n-k} = nA + \frac{n!}{(n-2)!} A^2.$$

Case 2. $i_1 \neq i_2$

$$\begin{aligned} \langle Q_x(i_1)Q_x(i_2) \rangle_{\sigma_x=j} &= \sum_{m=0}^Q \sum_{n=0}^{Q-m} mn \Pr(Q_x(i_1) = m, Q_x(i_2) = n | \sigma_x = j) \\ &= \sum_{m=0}^Q \sum_{n=0}^{Q-m} \frac{mnQ!}{m!n!(Q-m-n)!} q_{i_1|j}^m q_{i_2|j}^n (1 - q_{i_1|j} - q_{i_2|j})^{Q-m-n}. \end{aligned}$$

Finally, we obtain

$$\langle Q_x(i_1)Q_x(i_2) \rangle_{\sigma_x=j} = \frac{Q!}{(Q-2)!} q_{i_1|j} q_{i_2|j}$$

because

$$\sum_{k_1=0}^n \sum_{k_2=0}^{n-k_1} \frac{k_1 k_2 n!}{k_1! k_2! (n - k_1 - k_2)!} A^{k_1} B^{k_2} (1 - A - B)^{n - k_1 - k_2} = \frac{n!}{(n-2)!} AB.$$

The next two theorems have already been proved in [19].

Theorem 3. $\langle Q_{e_j}(l) \rangle_{\sigma_e=ij} = \begin{cases} (Q-1)q_{lj} & ; l \neq i \\ (Q-1)q_{lj} + 1 & ; l = i \end{cases}$.

Theorem 4.

$$\langle Q_{e_j}(l_1)Q_{e_j}(l_2) \rangle_{\sigma_e=ij} = \begin{cases} (Q-1)q_{l_1|j} + \frac{(Q-1)!}{(Q-3)!}q_{l_1|j}^2 & ; l_1 = l_2 \\ \frac{(Q-1)!}{(Q-3)!}q_{l_1|j}q_{l_2|j} & ; l_1 \neq l_2 \end{cases}$$

In order to see how the average calculation works, we apply NPA to the simplest epidemic model.

IV. THE SIS SPATIAL MODEL

The simple SIS epidemic model is a good example to see the usefulness of the new approach of pair approximation. As usual, the simple SIS model can be separated into two possible states, that is, S (a susceptible individual) and I (an infective individual). The state of each site and edge can evolve over time according to two major types of events such as infection and recover. Clearly, infection changes the state $\sigma_e = SI$ of the edge e into the state $\sigma_e = II$ at rate β . Moreover, recovery changes the state $\sigma_x = I$ of a site x into the state $\sigma_x = S$ at rate δ .

Consequently, we can derive the master equations for the simple SIS model (as shown in Appendix A) by summing over all events in the population which affect f . In addition, the total change produced by those events is

$$\frac{df}{dt} = \sum_{\varepsilon \in \text{events}} r(\varepsilon) \Delta f_{\varepsilon}$$

where $r(\varepsilon)$ is the rate of event ε and Δf_{ε} is the change produced in f by event ε . According to the concept of space average,

$$\sum_{\sigma x=j} Q_x(i) = [j] \langle Q_x(i) \rangle_{\sigma x=j} \quad \text{and} \quad \sum_{\sigma e=jk} Q_e(i) = [jk] \langle Q_e(i) \rangle_{\sigma e=jk}$$

the master equations, then, can be rewritten in average forms instead of summation terms as shown in Appendix B. Finally, we can use the NPA to obtain pair approximation of the SIS model. Particularly, if the infection rate and the recovery rate are constant, then the OPA and NPA are obviously identical.

However, the human-to-human transmission of Swine Flu occurs by inhalation of infectious droplets and droplet nuclei, and by direct contact, which is facilitated by air and land travel and social gatherings [20]. Therefore, the transmission rate and the recovery rate could vary depending on the surrounding infectious people. Consequently, we able to assume that the infection rate and the recovery rate are $\beta = b_0 + b_1 Q_{\varepsilon}(I)$ and $\delta = d_0 - d_1 Q_x(I)$, respectively where b_0, b_1, d_0, d_1 are constant. Then we can see the limitation of OPA. In Appendix C, we derive the correlation equations by using the NPA.

Firstly, we neglect spatial structure altogether by ignoring the correlation between neighboring sites on the lattice [6]. Hence the superscript M , the superscript P , and the subscript e symbolize for mean-field approximation, pair approximation, and equilibrium, respectively.

A. Mean-field Approximation

In this case, it implies that the local density (q_{ij}) equals the global density (q_i). Consequently, we obtain fewer equations. The following equation is the change of infectious people

$$\frac{d[I]}{dt} = -b_1 Q(Q-1)[I]^3 + [b_1 Q^2 - b_0 Q - 2b_1 Q + d_1 Q][I]^2 + [b_0 Q + b_1 Q - d_0][I] \quad (1)$$

Case 1. $b_1 = 0$, the equilibrium points are

$$[I]_{e_{1,2}}^M = 0, \frac{N(b_0 Q - d_0)}{Q(b_0 - d_1)}$$

Case 2. $b_1 \neq 0$, the equilibrium points are

$$[I]_{e_{1,2}}^M = 0, \frac{NL \pm N\sqrt{L^2 + 4b_1 Q(Q-1)(b_0 Q + b_1 Q - d_0)}}{2b_1 Q(Q-1)}$$

where $L = -b_0 Q + b_1 Q(Q-2) + d_1 Q$.

B. Pair Approximation

Instead of neglecting the difference between the local and the global densities. We can also search for the equilibrium in the same manner.

Case 1. $b_1 = 0$, the equilibrium equations are

$$[S]_{\varepsilon}^P = \frac{d_0 N(Q-1)}{b_0 Q(Q-1) - d_0} - \frac{(b_0 Q - d_0)(Q-1)N}{(b_0 Q(Q-1) - d_0)b_0} d_1 + O(d_1^2) \quad (2.1)$$

$$[I]_{\varepsilon}^P = \frac{NQ(b_0(Q-1) - d_0)}{b_0 Q(Q-1) - d_0} + \frac{(b_0 Q - d_0)(Q-1)N}{(b_0 Q(Q-1) - d_0)b_0} d_1 + O(d_1^2) \quad (2.2)$$

$$[SI]_{\varepsilon}^P = \frac{d_0 N Q (b_0(Q-1) - d_0)}{(b_0 Q(Q-1) - d_0)b_0} - \frac{(b_0 Q(Q-1) - d_0)(2Q-1)(b_0 Q - d_0)N}{(b_0 Q(Q-1) - d_0)b_0^2} d_1 + O(d_1^2) \quad (2.3)$$

$$[SS]_{\varepsilon}^P = \frac{d_0^2 N Q}{(b_0 Q(Q-1) - d_0)b_0} - \frac{(2Q-1)(b_0 Q - d_0)d_0 N}{(b_0 Q(Q-1) - d_0)b_0^2} d_1 + O(d_1^2) \quad (2.4)$$

$$[II]_{\varepsilon}^P = \frac{NQ(b_0 Q - d_0)(b_0(Q-1) - d_0)}{(b_0 Q(Q-1) - d_0)b_0} + \frac{(2b_0 Q(Q-1) - d_0(2Q-1))(b_0 Q - d_0)N}{(b_0 Q(Q-1) - d_0)b_0^2} d_1 + O(d_1^2) \quad (2.5)$$

Unluckily, we cannot obtain the explicit form of the equilibrium point when $b_1 \neq 0$.

V. NUMERICAL RESULTS

In this section we mainly investigate the density of infected individuals, defined by $q_i = [I]/N$, along the time series. Consequently, we have to modify (1) by dividing N both sides. The upcoming figures indicate the asymptotic behavior of solutions of the modified equation. In case that the infection rate and the recovery rate are not affected by the surrounding infectious individuals ($b_1 = 0, d_1 = 0$), the solution curves are visualized in Fig. 2 with the fixed parameters $b_0 = 0.3, d_0 = 0.2$ and the varying parameter $Q = 1, 2, 4, 8$. Obviously, the highest solution curve occurs when $Q = 8$ which means that the more neighbors, the higher density of infected individuals at the equilibrium point.

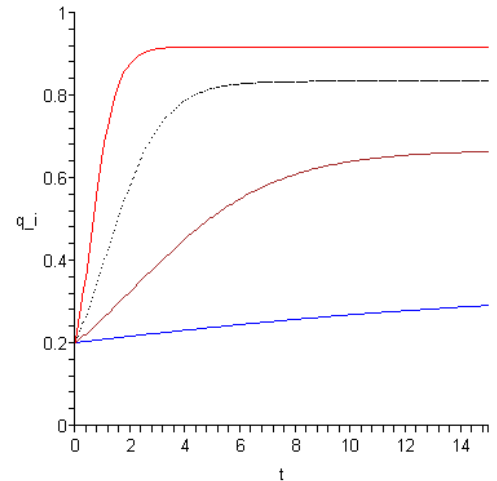


Fig. 2 Time evolution of the density of infected individuals q_i . Parameters: $b_0 = 0.3, b_1 = 0, d_0 = 0.2, d_1 = 0$ and $Q = 8, 4, 2, 1$ (from top to bottom, respectively).

In case that only the infection rate is affected by the surrounding infectious individuals ($b_1 \neq 0, d_1 = 0$), Fig. 3 shows

the solution curve when $b_0 = 0.3, d_0 = 0.2, Q = 4$ are fixed and b_1 is assigned with the following values $0.9, 0.3, 0.05, 0.01$. The highest solution curve occurs when $b_1 = 0.9$ implying that the stronger effect of the surrounding infectious individuals on the infection rate, the higher density of infected individuals at the equilibrium point.

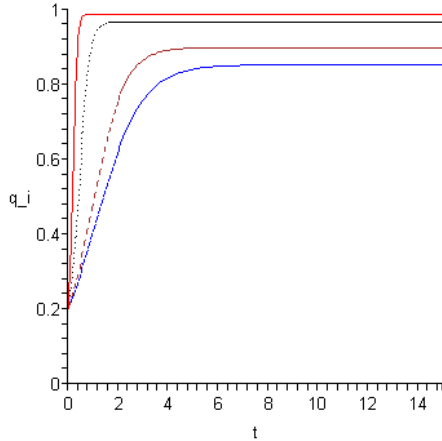


Fig. 3 Time evolution of the density of infected individuals q_i . Parameters: $b_0 = 0.3, d_0 = 0.2, d_1 = 0, Q = 4$ and $b_1 = 0.9, 0.3, 0.05, 0.01$ (from top to bottom respectively).

In case that only the recovery rate is affected by the surrounding infectious individuals ($b_1 = 0, d_1 \neq 0$), the solution curves are then illustrated in Fig. 4 with the fixed parameters $b_0 = 0.3, b_1 = 0, d_0 = 0.2, Q = 4$ and the varying parameter $d_1 = 0.05, 0.04, 0.02, 0$. The highest solution curve occurs when $d_1 = 0.05$ referring that the stronger effect of the surrounding infectious individuals on the recovery rate, the higher density of infected individuals at the equilibrium point.

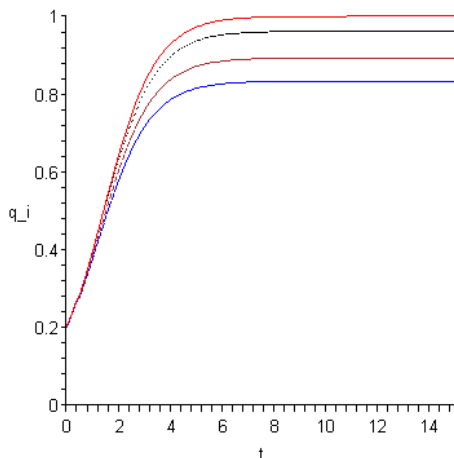


Fig.4 Time evolution of the density of infected individuals q_i . Parameters: $b_0 = 0.3, b_1 = 0, d_0 = 0.2, Q = 4$ and $d_1 = 0.05, 0.04, 0.02, 0$ (from top to bottom respectively).

Next Fig. 5 shows the solution curves obtained by setting $b_0 = 0.3, b_1 = 0.1, d_0 = 0.2, d_1 = 0.01$ and $Q = 8, 4, 2, 1$.

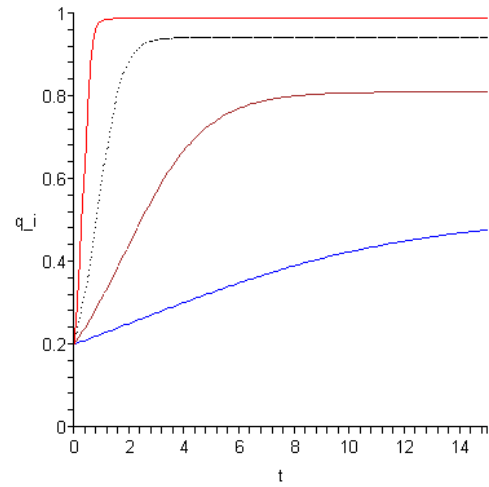


Fig. 5 Time evolution of the density of infected individuals q_i . Parameters: $b_0 = 0.3, b_1 = 0.1, d_0 = 0.2, d_1 = 0.01$ and $Q = 8, 4, 2, 1$ (from top to bottom respectively).

Not only do we focus on (1), but we also observe the behavior of (2) by comparing the numbers of infected individuals and links between two infected individuals at the equilibrium point. For example, we could enter the following parameter values $b_0 = 0.3, d_0 = 0.2, b_1 = 0, d_1 = 0.01, Q = 4, N = 100$ into (2.2) and (2.5). After some calculations, we obtain $[I]_e^p \approx 85$ and $[II]_e^p \approx 294$. Obviously, $[I]_e^p < [II]_e^p$ implying that the infected individuals prefer staying close together or tend to be clumped spatially.

VI. CONCLUSION

Intuitively, people infect flu virus easily from their nearby neighbors. The health organization usually suggests infectious people to have some rest and be away from public places. It implies that if we surrounding with more infectious people, then we have higher chance to infected and/or lower chance to recover as shown in the numerical results.

Not only useful for a simple SIS epidemic model, does this given technique (NPA) is also suitable for a model evolving according to the transition rates affecting additionally by neighbors.

APPENDIX

A. The master equations: version 1

$$\frac{d[S]}{dt} = \sum_{\sigma x=I} \delta - \sum_{\sigma e=SI} \beta$$

$$\frac{d[I]}{dt} = -\sum_{\sigma x=I} \delta + \sum_{\sigma e=SI} \beta$$

$$\begin{aligned} \frac{d[SI]}{dt} &= -\sum_{\sigma x=I} \delta Q_x(S) + \sum_{\sigma e=SI} \beta(Q_{e_s}(S) - Q_{e_s}(I)) \\ &\quad + \sum_{\sigma x=I} \delta Q_x(I) \\ \frac{d[SS]}{dt} &= 2\sum_{\sigma x=I} \delta Q_x(S) - 2\sum_{\sigma e=SI} \beta Q_{e_s}(S) \\ \frac{d[II]}{dt} &= 2\sum_{\sigma e=SI} \beta Q_{e_s}(I) - 2\sum_{\sigma x=I} \delta Q_x(I) \end{aligned}$$

B. The master equations: version 2

$$\begin{aligned} \frac{d[S]}{dt} &= d_0[I] - d_1[I]\langle Q_x(I) \rangle_{\sigma x=I} - b_0[SI] - b_1[SI]\langle Q_{e_s}(I) \rangle_{\sigma e=SI} \\ \frac{d[I]}{dt} &= -\frac{d[S]}{dt} \\ \frac{d[SI]}{dt} &= -d_0[I]\langle Q_x(S) \rangle_{\sigma x=I} + d_1[I]\langle Q_x(I)Q_x(S) \rangle_{\sigma x=I} \\ &\quad + b_0[SI]\langle Q_{e_s}(S) \rangle_{\sigma e=SI} + b_1[SI]\langle Q_{e_s}(I)Q_{e_s}(S) \rangle_{\sigma e=SI} \\ &\quad - b_0[SI]\langle Q_{e_s}(I) \rangle_{\sigma e=SI} - b_1[SI]\langle Q_{e_s}(I)Q_{e_s}(I) \rangle_{\sigma e=SI} \\ &\quad + d_0[I]\langle Q_x(I) \rangle_{\sigma x=I} - d_1[I]\langle Q_x(I)Q_x(I) \rangle_{\sigma x=I} \\ \frac{d[SS]}{dt} &= 2d_0[I]\langle Q_x(S) \rangle_{\sigma x=I} - 2d_1[I]\langle Q_x(I)Q_x(S) \rangle_{\sigma x=I} \\ &\quad - 2b_0[SI]\langle Q_{e_s}(S) \rangle_{\sigma e=SI} - 2b_1[SI]\langle Q_{e_s}(I)Q_{e_s}(S) \rangle_{\sigma e=SI} \\ \frac{d[II]}{dt} &= 2b_0[SI]\langle Q_{e_s}(I) \rangle_{\sigma e=SI} + 2b_1[SI]\langle Q_{e_s}(I)Q_{e_s}(I) \rangle_{\sigma e=SI} \\ &\quad - 2d_0[I]\langle Q_x(I) \rangle_{\sigma x=I} + 2d_1[I]\langle Q_x(I)Q_x(I) \rangle_{\sigma x=I} \end{aligned}$$

C. The spatial SIS model

$$\begin{aligned} \frac{d[S]}{dt} &= d_0[I] - d_1[II] - b_0[SI] - b_1[SI][(Q-1)q_{IIS} + 1] \\ \frac{d[I]}{dt} &= -\frac{d[S]}{dt} \\ \frac{d[SI]}{dt} &= -d_0[SI] + d_1[I]\frac{Q!}{(Q-2)!}q_{II}q_{SII} \\ &\quad + b_0[SI](Q-1)q_{SIS} + b_1[SI]\frac{(Q-1)!}{(Q-3)!}q_{IIS}q_{SIS} \\ &\quad - b_0[SI][(Q-1)q_{IIS} + 1] \\ &\quad - b_1[SI]\left[(Q-1)q_{IIS} + \frac{(Q-1)!}{(Q-3)!}q_{IIS}^2\right] \\ &\quad + d_0[II] - d_1[I]\left(Qq_{II} + \frac{Q!}{(Q-2)!}q_{II}^2\right) \\ \frac{d[SS]}{dt} &= 2d_0[SI] - 2d_1[I]\frac{Q!}{(Q-2)!}q_{II}q_{SII} \\ &\quad - 2b_0[SI](Q-1)q_{SIS} - 2b_1[SI]\frac{(Q-1)!}{(Q-3)!}q_{IIS}q_{SIS} \\ \frac{d[II]}{dt} &= 2b_0[SI][(Q-1)q_{IIS} + 1] \\ &\quad + 2b_1[SI]\left[(Q-1)q_{IIS} + \frac{(Q-1)!}{(Q-3)!}q_{IIS}^2\right] \\ &\quad - 2d_0[II] + 2d_1[I]\left(Qq_{II} + \frac{Q!}{(Q-2)!}q_{II}^2\right) \end{aligned}$$

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