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Epidemics in two competing species

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Abstract

An SIS epidemic model in two competing species with the mass action incidence is formulated and analysed. Thresholds for the existence of boundary equilibria are identified and conditions for their local asymptotic stability or instability are found. By persistence theory, conditions for the persistence of either hosts or pathogens are proved. Using Hopf bifurcation theory and numerical simulations, some aspects of the complicated dynamic behaviours of the model are shown: the system may have zero up to three internal equilibria, may have a stable limit cycle, may have three stable attractors. Through the results on persistence and stability of the boundary equilibria, some important interactions between infection and competition are revealed: (1) a species that would become extinct without the infection, may persist in presence of the infection; (2) a species that would coexist with its competitor without the infection, is driven to extinction by the infection; (3) an infection that would die out in either species without the interinfection of disease, may persist in both species in presence of this factor.

Keywords: Epidemic model; Multihost infection; Species extinction; Uniform persistence; Hopf bifurcation; Periodic solutions

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1. Introduction

Models for ecological interactions, and models for host-pathogen interactions were initially developed separately. However, it has been recognized that a strong interaction may arise between these factors: a pathogen may tilt the balance between competing species, or may provoke a negative influence between the densities of two species that are not otherwise interacting (“apparent competition”), even causing the extinction of one of them; a pathogen may be able to persist in a community of two (or more) competing species, but not in any of them in isolation.

The problem, however, is that the models become quickly very difficult to analyse. Even the simplest possible model with an SI epidemics spreading in two not interacting species [1] gives rise to a 4-dimensional ODE model that may have multiple stable attractors often in the form of limit cycles [2].

It must be however remarked that the behaviour of the model becomes much simpler [3] if one assumes that infection incidence is proportional to the infected fractions in each species (‘standard’ incidence) and not to the densities of infectives. Which is the most appropriate form for the infection rate has been debated in several papers, and the

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conclusion should clearly depend on the actual transmission routes on the pathogen. Considering a generic infection that is indirectly (through airborne propagules or through the soil) transmitted among competing species, we believe that the standard bilinear form (mass action incidence) used in [1] is quite reasonable, and we will use it in our model.

Some empirical investigations on epidemics in competing species have been performed, with the help of epidemic models, by Begon et al. [4] on the cowpox virus in coexisting populations of bank voles and wood mice, and by Tompkins et al. [5] on a pathogen in competing squirrel species. Begon et al. [6] suggest that the lack of a clear threshold density in the data is incompatible with the mass action incidence, but their data mainly testify to the relevance of stochastic persistence at low numbers of the host population, without really excluding either hypothesis as for the transmission law. Moreover, while the social structure of a species may be such that the number of inter-species contacts are almost independent of population density, in agreement with the standard incidence law, we see no reason why this should be true for interspecific contacts, nor are we aware of relevant data. Thus, we find it definitely worth studying the interaction of competition and infection, using the mass-action law for incidence.

Models for two species which share a disease without competition have been discussed in some papers. In their works, Holt and Pickering [7], Begon and Bowers [1,8] conjectured that the models have the classic endemic model behaviour: the infected coexistence equilibrium is relevant and stable if and only if no other stable equilibrium exists in the nonnegative orthant. But this conjecture was soon denied by some counterexamples given by Greenman and Hudson [2]. On the other hand, Hethcote et al. [9] later found that the models have the behaviour of a classic endemic model if the frequency-dependent incidence is used.

Epidemic models in competing species have also been studied previously. Anderson and May [10] considered a host-competitor-pathogen model which involves two direct competitors, one subject to a pathogen. They examined the effect of a pathogen on conventional competition. Bowers and Turner [11] introduced a prototypical model of two hosts sharing a pathogen and competing directly. They studied the interplay between infection and competition. In their model, the death rates are density-independent. Venturino [12] analysed the dynamics of two competing species when one of them is subject to a disease. In his model with mass action incidence, he obtained limit cycles. Han et al. [13] studied an SIRS epidemic model of two competitive species without disease-related deaths. They analysed the effect of inter-infection of disease on the dynamic behaviours of the model. Van den Driessche and Zeeman [14] investigated the interaction of disease and competition dynamics in a system of two competing species in which only one species is susceptible to disease. In their model, vertical disease transmission and horizontal transmission are introduced. They found that if in the absence of disease there is competitive exclusion between the two species, then the presence of disease can lead to stable or oscillatory coexistence of both species. Saenz and Hethcote [3] considered some models of SIS, SIR and SIRS type with frequency-dependent incidence. They found that the models have the classic endemic model behaviour. In their paper, a key result is that the disease must either die out in both species or remain endemic in both species.

Our model is different from the previous models, because it uses the mass action incidence, both density-dependent and disease-related death rates, and both species can be infected. Because of the complicated behaviours of the system, shown by [2], we do not aim at a complete analysis. Rather, instead of considering the global stabilities of the equilibria, we focus on the concept of persistence, and present conditions that guarantee the persistence (or the nonpersistence) of either hosts or pathogens, following ideas by Thieme [15]. Together with the discussion on the local stabilities of the equilibria, by the analysis of persistence, we investigate the interactions between infection and competition. Moreover, by Hopf bifurcation theory and numerical simulations, some complex behaviours of the model are shown.

The organization of this paper is as follows. in the next section, we introduce the model and some preliminary results. In Section 3, the existences and stabilities of the equilibria are discussed. In Section 4, we analyse the persistence of either hosts or pathogens. In Section 5, we study the bifurcation phenomena and analyse the periodic orbits and the number of the internal equilibria. Finally, in Section 6, the detailed discussion and conclusions are given.

2. Formulation of the model

We consider two competing species, whose densities are denoted by N_1 and N_2, whose dynamics follow a standard Lotka–Volterra system. K_i are the carrying capacity of each species in isolation, $r_i = b_i - d_i$ the intrinsic growth rates, α_{12} and α_{21} the competition coefficients. When considering the spread of an infectious disease in a species that grows logistically, it becomes necessary to specify explicitly the birth and the death rate; we follow Gao and Hethcote