



## Evolutionary implications for interactions between multiple strains of host and parasite

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### Abstract

The interaction between multiple parasite strains within different host types may influence the evolutionary trajectories of parasites. In this article, we formulate a deterministic model with two strains of parasites and two host types in order to investigate how heterogeneities in parasite virulence and host life-history may affect the persistence and spread of diseases in natural systems. We compute the reproductive number of strain  $i$  ( $\mathcal{R}_i$ ) independently, as well as the (conditional) “invasion” reproductive number for strains  $i$  ( $\mathcal{R}_i^j, j \neq i$ ) when strain  $j$  is at a positive equilibrium. We show that the disease-free equilibrium is locally asymptotically stable if  $\mathcal{R}_i < 1$  for both strains and is unstable if  $\mathcal{R}_i > 1$  for one strain. We establish the criterion  $\mathcal{R}_i^j > 1$  for strain  $i$  to invade strain  $j$ . Subthreshold coexistence driven by coinfection is possible even when  $\mathcal{R}_i$  of one strain is below 1. We identify conditions that determine the evolution of parasite specialism or generalism based on the life-history strategies employed by hosts, and investigate how host strains may influence parasite persistence.

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### 1. Introduction

Understanding the interaction between parasite infection and host life-history responses is critical for predicting the persistence and spread of diseases in natural systems. Because of this, mathematical models have been developed to explore the evolutionary dynamics that arise when variation occurs in these parameters (May and Anderson, 1979, 1990; Anderson and May, 1981, 1982; Levin, 1982; Bremermann and Pickering, 1983; Frank, 1992).

Under natural conditions, parasites can co-occur within both host populations and host individuals. In the absence of coinfection within individual hosts, it is often assumed that parasite strains expressing higher exploitation (i.e., more virulent) will outcompete those expressing lower exploitation (i.e., a more ‘prudent parasite’) (Minchella, 1985). However, when parasites coinfect the same host,

patterns should emerge that are more complex than when parasite strains occur independently (Bremermann and Pickering, 1983; Mosquera and Adler, 1998; Nowak and May, 1994; Davies et al., 2002). For example, Tanaka and Feldman (1999) found that the process of coinfection actually facilitated the invasion and establishment of a novel parasite strain, even though the invader’s reproductive value was less than that of the resident parasite. Moreover, empirical work by Gower and Webster (2004) demonstrated that coinfection among multiple parasite strains could favor the evolution of less, rather than more-virulent parasites.

Hosts have evolved life-history strategies that mitigate infection and the subsequent damage caused by parasitism (Minchella, 1985). In some cases, some host strains may actively resist parasite attack by altering morphological, physiological or immunological factors (Sandland and Minchella, 2003a). However, these strategies can generate fitness trade-offs with other host traits such as growth, reproduction and survival (Beck et al., 1984; Bowers et al.,

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