Since January 2020 Elsevier has created a COVID-19 resource centre with free information in English and Mandarin on the novel coronavirus COVID-19. The COVID-19 resource centre is hosted on Elsevier Connect, the company's public news and information website.

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Editorial

Mathematical epidemiology for a later age

With the central role that mathematical epidemiology has played in understanding the spread of COVID-19 in its various phases, projecting the path of the pandemic, and assisting real-time public health planning, the last two years have seen major societal contributions of which the community of theoretical population biologists can be proud. The pandemic has illuminated the unity of mathematical epidemiology with other areas of theoretical population biology, in demography, ecology, evolution, and genetics, as both mathematical epidemiologists and theoretical scientists in these adjacent areas have successfully applied their theoretical population biology training to contribute to the response effort. The pandemic has also revealed a phenomenon in which contributions to mathematical modeling developed over many decades without having immediate public health needs in mind—research that can be described as "for a later age" (Rosenberg, 2021)—have now been adapted and deployed for urgent epidemiological assessment and response.

As described in a commentary by Andreasen and Gog (2020), a pioneering *TPB* study by Pease (1987) provides an illustration. The study is concerned with modeling styles in mathematical epidemiology at a level distant from practical concerns. Andreasen and Gog (2020) describe how earlier compartmental models had difficulty explaining patterns of reinfection and partial immunity that occur in influenza. Pease (1987) overcame these limitations by creatively introducing a modeling framework that permits sequential evolutionary changes in pathogenic strains, showing how the modeling of genetic changes in the pathogen could explain long-term dynamics of the disease. Andreasen and Gog (2020) discuss the importance of the innovative Pease (1987) paper as an early link between epidemiology and evolution, a preview of the phylodynamic thinking now fundamental to the field, and a foundation for a vast body of work on influenza dynamics and control.

Which ideas in mathematical epidemiology from recent *TPB* studies will become similarly significant? In the last ten years, *TPB* disease modeling studies with creativity and depth have examined such topics as network effects (Duncan et al., 2014; Vickers and Osgood, 2014; Shams and Khansari, 2015; Maltz and Fabricius, 2016; Johnstone-Robertson et al., 2020), estimation of the basic reproduction number in complex settings (Rebuli et al., 2018; Johnstone-Robertson et al., 2020; McLure and Glass, 2020; Shaw and Kennedy, 2021), and animal diseases and animal reservoirs (Boni et al., 2013; Glass and Barnes, 2013; Sykes and Rychtář, 2015; Babylon et al., 2018; Barnes et al., 2019; McLure and Glass, 2020). They have linked to classic topics of ecology and evolution, considering abstract ecological settings with multiple interacting species (Manica et al., 2013; Bulai and Hilker, 2019), scenarios of long-term host evolution and host–pathogen coevolution (MacPherson and Otto, 2018; Boëte et al., 2019; MacPherson et al., 2021), and dynamics of competing pathogens (Hu et al., 2015; Nicoli et al., 2015; Ndii et al., 2016; Ferreri et al., 2017; Turelli and Barton, 2017; Maliyoni et al., 2019; Li and Liu, 2020),

An interest in models of human behavior during epidemics is a common theme in these studies. Walters and Kendal (2013) consider the effect of conformity bias—the concept from cultural evolution in which, by social learning, individuals adopt a behavior with a propensity disproportionate to its frequency in the population—on the dynamics of a harmful health behavior that itself is transmitted like a pathogen. The magnitude of the conformity bias is an important driver of the spread of the behavior, potentially leading it to an endemic equilibrium. This study, for which the authors use the example of conformity bias in the adoption of binge drinking, represents a growing area concerned with epidemic dynamics in the spread of cultural traits, and with the integration of epidemiological models with studies of cultural evolution.

Several studies consider human behavior particularly in the context of control measures for infectious disease. In a model of avian influenza, Boni et al. (2013) examine the economic interactions of epidemics, poultry prices, culling practices, and farmer investment in flock size and infection control. Glass and Barnes (2013) investigate the experience by livestock of occasional high-density gatherings—such as horse race events—with significant disease transmission risk. They assess the merits of different approaches to vaccination in relation to human behaviors that affect the animal gatherings and their associated disease risks. Feng et al. (2020) also study vaccination prioritization strategies, but in a human setting of measles and rubella. They seek to minimize disease transmission as a function of the vaccination strategy, taking into account that age-varying human behavior produces age-specific risk of disease transmission. The study combines an epidemiological model with control practices that account for age-structured demography.

A second theme among recent mathematical epidemiology papers in *TPB* is a focus on host immunological protection and evolution of pathogen strains. Examining the sexually transmitted bacterial pathogen *Chlamydia trachomatis*, Vickers and Osgood (2014) investigate the effect of antibiotic treatment on population-level immunity and subsequent epidemic dynamics. The dynamics depend on a distribution of stages of individual infections and on associated stages of individual immunity; because treatment can slow the development of immunity within

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a host, high treatment coverage can extend the epidemic as recovered individuals are re-exposed with a low immunity level. The effect of treatment on the epidemic depends on the stage distribution of infections and on the contact network structure in the host population. MacPherson and Otto (2018) consider long-term epidemiological dynamics, modeling "red queen" cycles of reciprocal natural selection in a host and pathogen. Integrating epidemiological models with classic evolutionary ideas, they use a two-locus population-genetic model defining strains of host and pathogen to consider the effect of epidemiological dynamics on evolutionary dynamics and vice versa. The study examines the cyclical patterns that occur in both sets of dynamics and the conditions that lead to their dissipation.

Strands of epidemic modeling that integrate behavioral and immunological dynamics converge in a recent study. Deka and Bhattacharyya (2022) examine the effect of social learning of vaccination behavior in a setting with strain competition, considering the different levels of immunity conferred by a vaccine to resident and mutant strains. Individual choice to vaccinate is treated as dependent on perceived risk for the resident and mutant strains, and perceived severity of current epidemic conditions induces vaccination through social learning. The study finds that due to reduced cross-immunity conferred by the vaccine to the mutant compared to the resident strain, vaccination reduces the prevalence of the resident strain to a greater degree than it does the mutant strain. A perception of severity of the mutant can thus hasten the speed at which the mutant invades and outcompetes the resident strain. We write this editorial in a stage of the COVID-19 pandemic in which the emergence of the latest novel mutant, the Omicron variant, and the associated perception of increased infection risk have potential to convert non-vaccinees to vaccinees—with the vaccines having been designed for protection not against Omicron, but against earlier variants present at the time of vaccine development. The simultaneous consideration of social learning, vaccine uptake, and immunity-mediated strain competition, lightly motivated by consideration of influenza in the work of Deka and Bhattacharyya (2022), clearly has a broader relevance in epidemiology and a specific application to the Omicron phase of COVID-19.

TPB contributions on mathematical epidemiology are often linked by an interest in understanding specific organisms, diseases, or behaviors while focusing on general principles that have applications beyond the motivating scenarios. They combine epidemiology with various other subfields of population biology, including cultural evolution and human behavioral modeling, demography, and population genetics, and they can have a far-reaching influence, as the depth and generality of their ideas can inform public health research far into the future. In light of the potential for theoretical work in mathematical epidemiology to provide a foundation for adaptable, deployable models, and given the increased attention the field is now receiving due to COVID-19, it can be hoped that theoretical innovations in mathematical epidemiology that emerge from ongoing events will assist in planning for and controlling outbreaks and pandemics in the next "later age."

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