

8

Spatial Heterogeneity in Infectious Disease Epidemics

DAVID L. SMITH

Abstract

Infectious disease epidemics in populations are inherently spatial—infectious agents are spread by contact from an infectious host to a susceptible host nearby. Among-host differences can determine which hosts suffer disease and the population dynamics of infectious disease epidemics. From the perspective of the infectious agent, a host is a habitat patch; among-host differences that are epidemiologically important are related to the concepts of compositional and configurational heterogeneity in landscape ecology. Heterogeneous mixing in epidemiology encompasses factors that determine who comes into contact with whom; it is analogous to configurational heterogeneity in landscape ecology. Other sorts of heterogeneity are analogous to compositional heterogeneity, including among-host differences in the duration of an infection, susceptibility to infection, or the amount of an infectious agent that is dispersed from an infected host. In real epidemics, compositional heterogeneity and configurational heterogeneity can introduce an overwhelming amount of complexity. Mathematical modeling provides a method for understanding epidemic processes and for taming the complexity. The idea of epidemic distance is introduced as a way of comparing and contrasting two different epidemic processes, and it is used to compare and contrast some of the mathematical models used to understand the role of space and spatial heterogeneity in epidemiology. In understanding real epidemics, the notion of parsimony is a guiding principle—heterogeneity should be weighed and ignored whenever possible. Several case studies are presented in which compositional and configurational heterogeneity are shown to be important.

Introduction

Infectious disease epidemics in populations are inherently spatial. Infectious agents persist by spreading from an infectious host to a susceptible

host nearby. Each host has a location, although “nearby” and “location” have a different meaning for each infectious agent. Infectious agents spread along a network of hosts characterized by the biology of the host population, the transmission mode of the infectious agent, and the course of an infection. Location in an epidemic network may be determined by geographical position, position in a social or sexual network, proximity to vector breeding sites, the movement of hosts or infectious agents through commerce, air travel, wind, or something else. For example, the influenza A virus is spread by airborne particles; airborne transmission requires that two people must be within a few meters of the same place within a few minutes. In contrast, an *Anopheles* mosquito becomes infectious 10 days or more after becoming infected with malaria; the next host infected may be several kilometers away. Thus, location may have a different meaning for each infectious agent in each host population.

Infectious disease epidemics are complex processes involving heterogeneous host populations and genetically diverse parasite populations. Heterogeneous host factors may include genetics, behavior, immune status, or any epidemiologically important trait that is spatially distributed among hosts. From the perspective of a parasite, a host is a habitat patch. Epidemiologically important differences among hosts fall into two categories. The first category includes any factor that affects the position of a host in a contact network or the configuration (topology) of the network. Collectively, these differences are called heterogeneous mixing. Heterogeneous mixing is analogous to configurational heterogeneity in landscape ecology. In contrast, compositional heterogeneity refers to other differences among hosts. Important kinds of compositional heterogeneity include differences in the duration of the infectious period, susceptibility to infection following exposure, or the amount of an infectious agent that is shed or dispersed into the environment from an infected host.

Infectious disease epidemics are complex, nonlinear processes. Understanding epidemics involves statistical analysis combined with mathematical modeling. Homogeneous population models—those that assume all individuals are alike—are a useful starting point in a hierarchical approach to model building and play a role similar to statistical null models. Heterogeneous population models modify the simple assumptions of homogeneous models to incorporate heterogeneity in the distribution of some epidemiologically significant trait, whether it is configurational or compositional. Heterogeneity is often manifested in unique ways in each system. Put another way, homogeneous populations are all alike, but each heterogeneous population is heterogeneous its own way, like unhappiness in the Karenina family in Tolstoy’s *Anna Karenina*. Heterogeneity is not something that can or should be studied for its own sake; heterogeneity must be understood in context. Thus, understanding heterogeneity is often limited to case studies, although some important generalizations can be made.

Some general observations about the effects of heterogeneity may be best understood by considering *simple* departures from homogeneity, such as the