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Impact of the topology of metapopulations on the resurgence of epidemics rendered by a new multiscale hybrid modeling approach

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ABSTRACT

Simulating epidemics in metapopulations is a challenging issue due to the large demographic and geographic scales to incorporate. Traditional epidemiologic models choose to simplify reality by ignoring both the spatial distribution of populations and possible intrapopulation heterogeneities, whereas more recent solutions based on Individual-Based Modeling (IBM) can achieve high precision but are costly to compute and analyze. We introduce here an original alternative to these two approaches, which relies on a novel hybrid modeling framework and incarnates a multiscale view of epidemics. The model relies on a technical fusion of two modeling paradigms: System Dynamics (SD) and Individual-Based Modeling. It features an aggregated representation of local outbreaks rendered in SD, and at the same time a spatially-explicit simulation of the spread between populations simulated in IBM. We first present the design of this deterministic model, show that it can reproduce the dynamics of real resurgent epidemics, and infer from the sensitivity of several spatial factors absent in compartmental models the importance of having large-scale epidemiological processes represented inside of an explicitly disaggregated metapopulation. After discussing the implications of results obtained from simulation runs and the applicability of this model, we conclude that SD–IB hybrid modeling can be an interesting choice to represent epidemics in a spatially-explicit way without necessarily taking into account individual heterogeneities, and therefore it can be considered as a valuable alternative to simple compartmental models suffering from detrimental effects of the well-mixed assumption.

1. Introduction

The vast majority of epidemic models described so far are *compartmental*, meaning that individuals are classified and grouped depending on their health status (Anderson and May, 1991; Bailey, 1975; Kermack and McKendrick, 1927). A famous example in ecology is the model of fox rabies in Europe (Anderson and May, 1979). This class of models presents the advantage of manipulating proportions of a same population and not having to deal with individualities. This line of reasoning has proven to be very efficient, especially from a mathematical and computational point of view, as models taking account of individual heterogeneities pose tractability problems for large populations and can be hard to analyze. Nevertheless, an insidious corollary of the compartmental approach has been the assumption that the population under consideration is well-mixed. Even if this sounds reasonable to describe small local populations, the broadening of this property to the metapopulation scale seems hazardous. In populations of wild animals as well as in human societies, individuals are generally grouped in high-density *sites* (i.e. cities, farms, and forest patches) separated spatially by large zones from which they are absent or present in negligible density only. Between these sites, elements of the landscape strongly affect the intensity at which individuals from different sites can interact (Real and Biek, 2007). The number of contacts each individual has is usually considerably smaller than the metapopulation size (Keeling and Eames, 2005). Therefore, the idea of a metapopulation-wide random-mixing of individuals does not seem to stand. While the variations of compartmental models have been overly studied (Hethcote, 1995), little attention has been paid to the correctness of the postulates on which this class of models relies.

In this paper, we detail a generic model that can be used to represent dynamic processes like epizootics in a spatially-explicit way, thereby lifting the need for the well-mixed assumption at the metapopulation scale, and without relinquishing the simplicity offered by the compartmental approach. Our solution relies on an approach offering great flexibility to model complex multiscale systems by uniting *System Dynamics* (SD) (Ford, 1999; Forrester, 1971) and *Individual-Based Modeling* (IBM) (Grimm and Railsback, 2005). The philosophy and framework supporting this technique is referred to as System Dynamics–Individual-Based (SD–IB) hybrid modeling (Vincenot et al., 2011) and represents a novel modeling paradigm unused so far in ecology to our knowledge. Compartmental models are probably the most efficient way to simulate the dynamics of an epidemic as long as the well-mixed assumption is met (Fig. 2, top). System Dynamics is a very advantageous technique to build such models, because it is based on an ordinary

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differential equation (ODE) solver and features stock-and-flow display, which is capable of great analytical power through its related tools (e.g. causal loop diagrams). Furthermore, it makes the model's structure easier and more straightforward to understand than raw differential equations. On the other hand, Individual-Based Modeling (IBM), technically originating from Agent-Based Modeling (ABM), is inherently capable of representing network structures in a spatially-explicit way making it possible to take into account distances between sites. In addition, it can handle large numbers of sites in a more efficient way than SD (Fig. 2, bottom). Thus, it is a perfect candidate to simulate the global spread of a disease in a network-like structure. These considerations motivated the use of an SD–IB hybrid model to reproduce the contagion mechanisms in an accurate, understandable, and tractable manner.

We start by describing the design of our hybrid model of epizootics in population networks. Then we show through simulations how it can render characteristic behaviors of large-scale epidemics, which are generally absent from compartmental models. Afterwards, we discuss the significance and implications of these results as well as the pertinence of the solution proposed here.

2. Method

2.1. Description of the hybrid model

We follow hereafter the updated 7-points Overview-Design concepts-Details (ODD) standard protocol formulated by Grimm et al. (2006, 2010) for describing individual-based models.

2.1.1. Purpose

The purpose of this model is to simulate the dynamics of disease contagion in very large fragmented populations at both the local and global scales. Here, we use this model to study the impact of network topology on the global evolution of epidemics.

2.1.2. Entities, state variables, and scales

This model is based on a geographic breakdown of metapopulations, and features a single entity called *site*. Each site actually equals to one population and is basically defined by three state variables (represented as stocks in the System Dynamics submodel) dividing the local population into classes of susceptible (S), infected (I), and recovered (R) individuals. On top of these, two more state variables keep track of ongoing emigration and immigration of infectious individuals. Each site is also characterized by its unique two-dimensional spatial coordinates set at initialization time and invariant thereafter. Fundamentally, the model integrates disease dynamics at two spatial scales, namely inside of sites (local outbreaks) and between sites (global epidemics). For this purpose, connections between neighboring sites are also taken into account. A neighboring site is defined as any site closer than a threshold distance given by the *neighborhood range* parameter. The simulations, running in steps of one week, are meant to reproduce disease propagation inside of a 500×500 km study area in a time frame of several months to years after its introduction.

2.1.3. Process overview and scheduling

Two processes take place in the following order inside of the model: the rendering of local outbreak dynamics in each site, and the migrations of infectious individuals between sites. Variables are updated synchronously inside of each process. The global model runs in hybrid time with local outbreaks calculated in continuous time, and the migrations happening as discrete events. Note that an integration step (Δt) of 0.01 week was used to compute the results reported in this study.

2.1.4. Design concepts

2.1.4.1. Basic principles. First, the model is built on the assumption that network structures, extensively studied in social sciences and graph theory, play an important role in the understanding of epidemiological processes (Keeling and Eames, 2005, and references therein). Indeed, large-scale epidemical outbreaks occur between several sites on which individuals are present in high density. At the metapopulation scale, a disease spreads when it is transferred by infected individuals (or third-party vectors) from site to site. As a result, each site can be regarded as the *node* of a large *network*.

Second, an underlying idea supporting this model is that epidemics take place concurrently at two different scales: local (inside of each site/node) and global (between sites/nodes inside of the network). The bond between these two dimensions is manifest in spatially-explicit observational datasets (Fig. 1). That is why the goal of the hybrid model presented here was to offer the possibility to simulate accurately disease transmission at both levels.

2.1.4.2. Emergence. The dynamics of the global epidemics emerge from the interactions of concurrent local outbreaks. As such, the dynamics of local outbreaks are primarily dependent on epidemiological parameters especially during the first epidemic wave, whereas the global epidemic arises entirely from the interaction of concurrent outbreaks.

2.1.4.3. Interaction. Migration of individuals, described in detail in Section 2.1.6, is the only form of direct interaction between sites.

2.1.4.4. Stochasticity. The model is entirely deterministic and does not integrate any stochastic process.

2.1.4.5. Observation. The prevalence of the disease, more precisely the value of $\frac{I}{S+I+R}$, is the main data sampled for observation. In one experiment (Fig. 6), the immigration and infection processes (i.e. in SD terminology, the inflows to stock I) are observed jointly with the evolution of the number of infected individuals (I).

2.1.5. Initialization

At initialization, sites are set to be organized in random spatial layouts, except in the experiment related in Fig. 4 in which sites are filling the available space by being placed at a regular interval from their neighbors (i.e. the so-called “arranged” or “regular” layout). The spatial arrangement changes neither at runtime nor between runs of the same experiment. Links between sites are automatically established by the framework for sites lying within their neighborhood range (i.e. 150 km, except in the experiment related in Fig. 4). Also, at the beginning of the simulation, inside of each site, the entire population is concentrated in the susceptible (S) state variable and no infectious individual exists. The first infection is triggered manually at runtime. Parameter values used in the hybrid model and their sources are given in Table 1.

2.1.6. Submodels

The hybrid model can reproduce the two-scale dynamics of an epidemic outbreak inside of a metapopulation structured in a network of sites by merging an IBM submodel and an SD submodel (Fig. 3). Their description is given hereafter.

2.1.6.1. Local outbreaks computation (SD). We assert that each site contains a closed and homogeneously mixed population. Hence, a classic SIRS epidemic model with delayed recovery is used to model the dynamics of outbreaks inside of sites. The content of this type of compartmental model has been described extensively in the literature (Anderson and May, 1979; Hethcote et al., 1981) and has been used to study diseases involving potential recovery which confers temporary immunity (e.g. Orthomyxoviridae causing the seasonal flu). It features three compartments representing generic infection stages of individuals in a population: susceptible (S), infected (I), and recovered