Ecological Modelling 383 (2018) 138–149

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

Between-group pathogen transmission: From processes to modeling

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ARTICLE INFO

Keywords:
Epidemiology
SIR model
Heterogeneous population
Transmission
Population dynamics

ABSTRACT

Pathogen transmission is a key process in epidemiology and its mathematical form plays a pivotal role when modeling pathogen spread. Much work has been devoted to the transmission function applied to a homogeneous population structure. However, between-group transmission functions, required when different groups are identified to account for a distinct epidemiological risk, are much less documented. The aim of this study is to detail the mathematical form of five between-group transmission functions and to assess its influence on predictions in epidemiological modeling. Simulations with a two-group model were carried out so as to generate prediction differences among between-group transmission functions for a large range of situations, defined by the within-group transmission pattern, the basic reproduction number, the proportion of the whole transmission due to between-group transmission and the ratio of population sizes. Pathogen spread simulations highlighted differences in prevalence among four transmission functions (frequency-dependent, density-dependent and functions representing either a temporary mixing or a proportion of visitors exposed to infectious individuals). The differences could be seen either in long-term or in transient simulated dynamics. The fifth one, representing limited interactions at a gate, was shown to be equivalent to the density-dependent function in our parametrization when keeping constant group sizes. When considering population dynamics, particularly with increasing group sizes, this function and the density-dependent one were shown to behave opposite from each other and to differ from the other functions. This work highlights the need to carefully define the between-group transmission function when modeling pathogen spread in a heterogeneous structure. Our work brings insight into the biological grounds that could guide the choice of such a function.

1. Introduction

Animal, human, as well as plant populations are structured in groups, individuals generally having more contacts within their own group than with individuals from other groups. Such a contact structure results in multi-group models and may arise because the population is structured by sex (e.g. in wildlife during the non-mating season, Beaunée et al., 2015), by age (e.g. in childhood diseases, Keeling and Grenfell, 1997), by physiological stages (e.g. in livestock, Lurette et al., 2008), spatially (e.g. in plants with short and long distance dispersal, Sapoukhina et al., 2010; or due to landscape heterogeneities, Smith et al., 2002), or because of social interactions (e.g. as related to human behavior, Funk et al., 2010).

Accounting for population heterogeneity and structure is a central issue to predict pathogen spread. It has received considerable attention in theoretical epidemiology over the last decades (to cite only a few: Post et al., 1983; Dushoff and Levin, 1995; Gudelj and White, 2004). The impact of such a population structure on pathogen spread is controversial, sometimes fastening, sometimes reducing the spread (Keeling and Rohani, 2008). It is hard to evaluate, especially (i) if individuals belonging to different groups have different levels of susceptibility and infectiousness (e.g. in paratuberculosis in cattle where young animals are the most susceptible and adults the most infectious, Marcé et al., 2011), (ii) if there is a within-group heterogeneity in individual infectiousness (as for super-shedding events, Lloyd-Smith et al., 2005), and (iii) if contacts vary over space and time (e.g. in vector-borne diseases, Charron et al., 2013).

To better understand and predict pathogen spread within a structured population of hosts, a modeling approach is appropriate and has been extensively used (Keeling and Rohani, 2008; Ezanno et al., 2012; Riley, 2007). A large number of papers concern pathogen spread on contact networks, both in human and in animal populations (Keeling and Eames, 2005; Danon et al., 2011; Dutta et al., 2014). In these networks, a node corresponds either to an individual or to a host population (in a context of metapopulation, Jesse et al., 2008), and a link corresponds to a contact between nodes. However, contacts between

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https://doi.org/10.1016/j.ecolmodel.2018.05.016
Received 20 October 2017; Received in revised form 3 May 2018; Accepted 17 May 2018

Table 1
Between-group transmission functions considered in the study. Transmission from group j to group i is represented here. β_b represents the between-group transmission rate, S_k, I_k and N_k are respectively the number of Susceptible, Infectious individuals and the size of group k.

Function	Abbreviation	References
$\beta_b^F S_i \frac{I_j}{N_j}$	**F** (Frequency-dependence)	Allen and Thrasher (1998), Ögren and Martin (2002), Klinkenberg et al. (2002), Keeling et al. (2010), Bombardt (2006), Mukandavire et al. (2009), Lunelli et al. (2009) and Evans et al. (2010)
$\beta_b^D S_i I_j$	**D** (Density-dependence)	Barlow et al. (1999), Austin et al. (1999), Noordegraaf et al. (2000), MacKenzie and Bishop (2001), Durand et al. (2004) and Riley et al. (2008)
$\beta_b^V S_i \frac{I_j}{N_i}$	**V** (Visitors)	Ögren and Martin (2002) and Wonham et al. (2006)
$\beta_b^M S_i \frac{I_i + I_j}{N_i + N_j}$	**M** (partial/temporary Mixing)	Ögren and Martin (2002) and Eblé et al. (2006)
$\beta_b^G S_i \frac{I_j}{N_i \times N_j}$	**G** (contacts at Gate or barrier)	Ögren and Martin (2002), Viet et al. (2004), D'Agata et al. (2007), Courcoul and Ezanno (2010) and Metcalf et al. (2013)

populations or groups of hosts also may occur through neighboring relationships, because of airborne transmission (Ssematimba et al., 2012), or because of host short go-and-return movements (such as commuters working in a city and living in another one, having contacts in both Keeling and Rohani, 2008; Moreno et al., 2017). Such contact patterns induce different interactions between groups in contact compared with individual movements, as a contact then can be related to indirect transmission between groups. For such an indirect transmission, the function representing the force of infection is not straightforward, leading to various definitions (Ögren and Martin, 2002). This is especially true in populations where between-group contacts cannot be easily quantified (Edmunds et al., 1997; Tompkins et al., 2011). Therefore, there is a need for a clearer definition of the biological meaning and implications of such between-group functions, as well as for the comparison of their impact on epidemiological model predictions. The biological grounds that drive the choice of the within-group transmission functions and the impact of such a choice on model predictions have largely been studied (Begon et al., 2002; McCallum et al., 2001; Hoch et al., 2008; Murray, 2009). Some authors also compared within-group transmission functions through the fitting to experimental data (Orlofske et al., 2018). However, such results can be only partly extended to the between-group transmission issue, firstly because epidemiological model outputs highly depend on the interactions between the groups, secondly because the occurrence of between-group contacts may arise from specific biological processes.

Papers aiming at representing the spread of a specific pathogen in a given structured host population while using several between-group functions and motivating their choice are very scarce. Ögren and Martin (2002) performed simulations with several between-group transmission functions in a model of an infection between airports. They considered a fixed network of airports of constant size with empirically determined transmission parameters, which prevents from a thorough comparison between functions.

Our objective was therefore to compare the predictions of epidemiological models in structured populations among scenarios of between-group transmission functions. First, functions encountered in the literature were reviewed and the biological assumptions that govern their use were described. Second, simulations were compared for the different functions over a range of epidemiological characteristics in terms of basic reproduction number (R_0), relative contribution of the between-group transmission in R_0 computation, within-group transmission pattern, and group size.

2. Methods

2.1. Identification of between-group transmission functions

To investigate the influence of the mathematical form of between group transmission functions, we chose to focus on transmission that occurs through direct contacts. Indirect transmission, for instance through a common contaminated environment, was therefore excluded from the analysis.

Several mathematical forms for between-group transmission functions are used in the literature, both in theoretical and applied works. They are summarized in Table 1. The biological meaning of each of these functions is explained and illustrated thereafter.

In most cases, especially for sake of simplicity, the classical density-dependent and frequency-dependent transmission functions are used (Keeling and Rohani, 2002; Gudelj and White, 2004). If these two functions are equivalent when subgroups have the same fixed size, it is not the case for groups of different or variable sizes. A density-dependent between-group transmission (hereafter called function **D**) assumes that the contact rate with the group acting as the infection source is proportional to the density of individuals in this group. Such a function has largely been used for modeling the between-herd spread of pathogens due to local animal or professional contacts (Durand et al., 2004; Noordegraaf et al., 2000; Barlow et al., 1999), or contacts occurring only between groups, such as between health care workers and patients in a hospital (Austin et al., 1999). A density-dependent function has also been used to represent between species transmission, with specific infectivity for each species and assuming a homogeneous mixing (Riley et al., 2008). A frequency-dependent transmission (hereafter called function **F**) assumes that the contact rate is constant and does not depend on the size of the group acting as the infection source, which is the case for instance for sexually transmissible diseases. For the same number of infectious individuals, the between-group force-of-infection will be higher for small size receiving groups than for large size ones. Such a function has been widely used to model pathogen spread in a metapopulation (Keeling et al., 2010), both in human (e.g. varicella, Allen and Thrasher, 1998; SARS, Bombardt, 2006; HIV/AIDS, Mukandavire et al., 2009; Influenza, Lunelli et al., 2009) and in animal (e.g. classical swine fever, Klinkenberg et al., 2002; porcine reproductive and respiratory syndrome, Evans et al., 2010) structured populations. Alternative functions are considered to represent other assumptions. Function **V** represents the case when a fraction of a group (denoted by $\frac{S_i}{N_i}$), for instance doctors or other health care workers, have contacts with infectious individuals (i.e. the other group consists of patients), potentially becoming infectious themselves. Here the size of the transmitting group has an effect on the risk of pathogen spread, but not the one of the receiving group. Similarities with such a function can be found in vector-borne diseases when the number of new cases in reservoir hosts does not depend on the size of this group (function called reservoir frequency-dependent by Wonham et al., 2006). Function **M** is appropriate when the individuals of the two groups are temporarily mixed within a single one, of total size $N_i + N_j$, and assuming a frequency-dependent transmission. This is the case for example when several host species (Manore et al., 2011) or different social groups (Turner et al., 2008) are interacting in a common area/