PERSPECTIVE

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**Perspective**

# Perspective on the spatio-temporal spread of epidemics in metapopulation networks

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**Abstract** – We review the recent progress of epidemic dynamics in metapopulation networks. Firstly, we give an introduction of the concepts about epidemic models and metapopulation network. Then, the theoretical characterization of epidemics spread in metapopulation networks is summed up. The measures of how to curb the spread of epidemics are summarized. The applications of inferring epidemic pathways based on epidemic data and reconstruction of epidemic transmission by phylogeographic are introduced. Finally, we present the outlooks about further research of epidemic dynamics on metapopulation networks.



Over the past few years, many serious infectious diseases have broken out worldwide [1–8], which have taken a huge toll on global economies and people's health. Especially at the end of 2019, New Coronavirus disease (SARS-CoV-2) broke out and then it quickly spread to more than 200 countries [9–11]. As of 13 February 2023, there have been 755703002 confirmed cases of COVID-19, including 6836825 deaths, reported to WHO [12]. Therefore, it is very necessary to explore the spatio-temporal expansion factors affecting the pandemic's transmission dynamics and control measures.

In order to investigate the transmission dynamics of epidemics, the whole population is usually classified as the susceptible, infected and recovered parts to construct compartment models. These models can be based on agents (individuals), single population, metapopulation and other infrastructure. For the individual network model, nodes represent the individuals (agents), and edges (path or link) represent the relationship between the two nodes and the epidemic is spread through the link. This model takes the heterogeneity of the interaction into account. Single population model also called compartment model is the most basic model and widely used in the simulation and prediction of epidemics in local areas. At the large-scale and spatial level, considering the heterogeneity of different regions and the mobility of people among regions, metapopulation network [13] with different compartment models is also proposed. The metapopulation network divides the whole population into connected spatial subpopulations according to areas. Usually, the model assumes that individuals in a subpopulation are a homogeneous mixing. Individuals in a subpopulation move to one of its neighboring subpopulations governed by diffusion rate.

The spatio-temporal expansion of infectious diseases in the metapopulation networks can be regarded as a reaction-diffusion [14,15] or reaction-commuting process [16,17]. The reaction-diffusion (reaction-commuting) process indicates that individuals undergo epidemic infection reactions within subpopulations, while diffusion (commuting) between subpopulations occurs. This first

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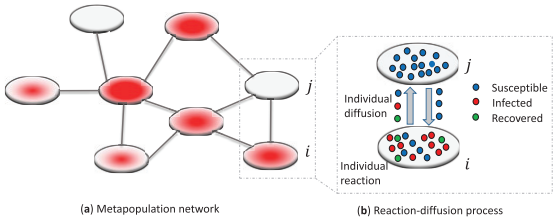


Fig. 1: A metapopulation network with Susceptible-Infected-Recovered (SIR) reaction-diffusion process.

Fig. 2: Illustration of the air transportation network in the U.S. From Brockmann *et al.* [18].

process is suitable for describing the epidemic transmission behavior of individuals on large-scale, long-distance networks such as air transportation networks. The latter are suitable for describing the daily commuting behavior of individuals in adjacent cities or within cities. Figure 1 shows a metapopulation network with SIR reaction-diffusion process.

In this letter, we mainly discuss the research advances on the structure of metapopulation networks, the theoretical characterization and control measures of epidemic spatial diffusion, and how to use observation data to infer or reconstruct its spatial diffusion and other scientific issues. Specifically, the first section discusses the structure characteristics of transportation networks. The second presents the theoretical characterization affecting the spread of epidemics, and the third is on what effective control measures we can take and their impact on the face of epidemic outbreaks. The fourth is on reconstruction of epidemic transmission by epidemic arrival data or surveillance of infection data. The fifth shows how to use geoinformatics related fields to reconstruct the spread of epidemics, so as to better study the development and control of the epidemics. The sixth section gives the outlooks.

**Topological properties of metapopulation networks.** – In real life, air transportation network is the most representative metapopulation network. To model the spatio-temporal spreading of infectious diseases, air transportation networks are usually adopted as carriers, whose structure characteristics are essential to the epidemic spreading [19]. Thus, it is necessary to explore structure characteristics of transportation networks. Amaral *et al.* found that the worldwide air transportation network is a class of small-world network [20]. Barrat *et al.* found that the correlation behavior of the average weight as a function of the end-point degrees can be well approximated by a power-law dependence for the worldwide air transportation network [21]. Guimera *et al.* found anomalous centrality, community structure, and cities' global roles of the worldwide air transportation network [22]. The national air transportation networks are also with some small-world properties. For example, air transport network of China shows a cumulative degree distribution captured by an exponential function, and exhibits some small-world network properties with a low average path length and a high clustering coefficient [23], the airport network of India [24] is a small-world network characterized by a truncated power-law degree distribution and has a signature of hierarchy. Besides, the U.S. air transportation network (see fig. 2) and Italian air transportation network are also scale-free small-world networks [25,26].

**Theoretical characterization of epidemics spread in metapopulation networks.** –

*Epidemic arrival time (EAT).* Here we introduce the concept *epidemic arrival time*, which is the first arrival time that infected individuals in an infected subpopulation move to its susceptible neighbor subpopulations. Gautreau *et al.* attempted to build a theory for calculating the expected EAT for epidemic spreading from the epidemic origin to a directly connected subpopulation using the approximation of Gumbel process [27]. They also tried to calculate the expected EAT between any two subpopulations in the metapopulation network using an approximation of the underlying shortest paths tree. Brockmann *et al.* [28] attempted to approximate the expected EAT using a simple network metric called *effective distance*. Wang *et al.* [29] developed a mathematical framework allowing us to calculate the distribution of EAT from the epidemic origin population to any other population in the worldwide air transportation network. Importantly, the framework proposed by Wang *et al.* [29] can be used to infer the key epidemic parameters of an emerging epidemic (*e.g.*, basic reproduction number, under-reporting proportion) using the observed epidemic arrival data.

*Invasion threshold.* The global invasion threshold of epidemic spreading in heterogenous metapopulation network is expressed as $p_c = \frac{\langle k\rangle^2}{\langle k^2\rangle - \langle k\rangle}\frac{\mu R_0^2}{2(R_0-1)^2}/\bar{N}$ [30], where $p_c$ is the critical mobility value, $\bar{N}$ is the average population size, $\mu$ is the recover rate, $R_0$ is the basic reproductive number and $\langle k\rangle$ is the average degree. Then, the global invasion thresholds in homogeneous metapopulation networks is deduced [31], and also for the cases of metapopulation networks with traffic and population-dependent mobility rates. The effects of identical diffusion rates on epidemic threshold in metapopulation networks

are studied [32]. By modeling human mobility responses to the large-scale spreading of epidemics, it was found that prevalence-based travel limitations did not alter the epidemic invasion threshold in metapopulation network [33]. Through microscopic Markovian method, Gómez-Gardeñes *et al.* [17] investigated the epidemic threshold in metapopulation networks with reactiondiffusion processes. Wang *et al.* [34] studied the coupled interaction of epidemic spreading and information propagation over a two-layer metapopulation network and explored how individuals migrate, where aware and unaware individuals separately take different migration routes. Gao *et al.* [35] proposed a novel metapopulation-based network model and investigated the epidemic spreading coupled with awareness propagation.

*Epidemic predictability.* One of the main tasks of epidemic modeling is to predict or forecast the number of infected individuals and peak values of the entire metapopulation network or subpopulations. Currently, some studies discuss how to make predictions and the factors that affect predictability. Rvachev and Longini proposed a mathematical model to forecast the global spread of new strain of influenza A based on the international air transportation network [36]. Hufnagel *et al.* proposed a probabilistic epidemic model to describe infectious diseases spread on the global aviation network with 500 largest airports [37]. They found the high degree of predictability is caused by the strong heterogeneity of the aviation network. Colizza *et al.* presented a stochastic computational metapopulation model for the world air transportation network with 3880 nodes (airports) [38]. They defined a set of metrics to quantitatively describe the level of heterogeneity of network and predictability of the epidemic pattern. The model was also used to construct a multiscale mobility network and predict the spatial spreading of infectious diseases [39]. After that, the GLEAMviz simulator was developed to simulate the global spreading of epidemics [40], which covered more than 3800 commercial airports in about 230 countries, and more than 78000 administrative regions in more than 40 countries.

**Effective control measures.** – In order to curb the spread of the epidemic, there are several intervention strategies including controlling flight routes, closing airports, isolating internal personnel and home isolation policies. Therefore, how to specify corresponding strategies for different regions also needs to be considered.

*The impact of non-pharmaceutical interventions (NPIs).* In terms of travel restrictions, Aleta *et al.* [41] found that travel restrictions may be an effective measure in the short term, but they are ineffective when it comes to the complete elimination of this epidemic because it is impossible to eliminate the risk of spreading the epidemic to other areas. Arenas *et al.* [42] analyzed the spread of the epidemic in different populations and geographic environments and found that reducing the contact rate between susceptible people and infected people by implementing strict social distancing is one of the most effective measures to control SARS-CoV-2. Clifford *et al.* [43] evaluated interventions for air travelers and found that the combination of syndrome screening and traveler sensitization may slightly delay the outbreak of SARS-CoV-2 in unaffected countries. Shi *et al.* [44] also verified the effectiveness of intervention in air travel, but the effect of such measures is limited, and it is necessary to emphasize the importance of strengthening local disease surveillance and control capabilities. Chang *et al.* [45] considered policies including restrictions on international air travel, case isolation, family isolation, different levels of compliance with social distancing, school closures, and found a balance between epidemic prevention measures and social consumption. Wang *et al.* [46] explored a network structure-based intervention strategy based on the assumption that interventions deployed in a patch depend on its population size or economic level, aiming at understanding the interplay between intervention strategy and other factors including mobility patterns, initial population, as well as the network structure. Matsuki *et al.* [47] considered a SIR metapopulation model that the mobility of individuals is assumed to be uniformly spread and the local plaques change from high-risk plaques to low-risk plaques through intervention and found that interventions for high-grade plaques are more effective in controlling the epidemic than random interventions. Hou *et al.* [48] assessed the impact of spatial heterogeneity with business traffic, age, and race on the spread of the epidemic. Zhang *et al.* [49] used a nationwide mobile phone data set to develop a networked meta-population model, and demonstrated that both the time of initiating an intervention and its effectiveness have a very large impact on controlling the epidemic, and the current Chinese intense social distancing intervention has reduced the impact substantially but would have been even more effective had it started earlier.

*The impact of vaccination.* With the normalization of epidemics, vaccination has played a significant role in decreasing the spread of the epidemic. Gong *et al.* [50] proposed epidemic spreading model based on metapopulation networks to study the impact of heterogeneous vaccination on epidemic dynamics, and revealed the non-trivial dependence of vaccination heterogeneity. Kabir *et al.* [51] introduced a two-layer SIR/V-UA epidemic spread model into the metapopulation migration model of random walkers, and studied the influence of cognition (rumor) on the evolutionary vaccination game method. The information in the meta-population model can be disseminated with migration to improve the effectiveness of the epidemic threshold and help overcome the control problem of disease spread. Saldaña *et al.* [52] investigated how vaccination coverage, effectiveness, and delivery time affect the control of the transmission dynamics of COVID-10 compared with mobility restrictions. As of July 2022, 66.6% of the world population has received at least one dose of a COVID-19 vaccine. In the epidemic

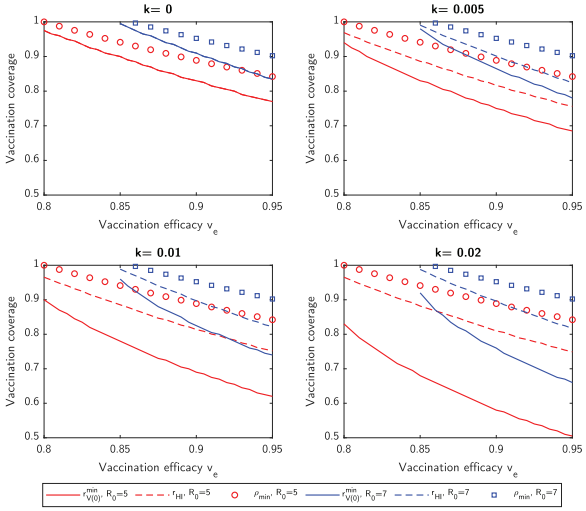


Fig. 3: Minimum vaccination threshold required such that the cumulative number of hospitalizations and isolations is less than $0.1N$, for different vaccine efficacies $v_e$ and vaccination rates $k$, and no NPIs. The theoretical herd immunity threshold $\rho_{\min}$ is also shown. From Wang *et al.* [53].

transmission model under the action of the COVID-19 vaccine, there should be more complete discussions and research. In the work [53], Wang *et al.* found a new phenomenon. For the theoretical herd immunity threshold $\rho_{\min} = 0.1N$ case, the dynamic vaccination threshold can be much lower than the theoretical herd immunity threshold, with post-infection natural immunity becoming a major factor towards achieving herd immunity. See fig. 3.

**Inferring epidemic spatio-temporal pathways by epidemic arrival data or surveillance of infection data.** – As we know, the signal of new outbreak of a region often attract more attention. New outbreaks of regions are caused by invasions of infected and moved individuals. Thus, to study how the infected individuals in a subpopulation invade another subpopulation is a very important topic related to public health and control of epidemic spreading. Many inspiring works have been presented to investigate the spatial transmission by using epidemic arrival data or surveillance of infection data. Here we introduce the concept *subpopulation been invaded:* Only the infected individual enters the susceptible subpopulation at the first arrival time (*i.e.*, for the first time) to be called subpopulation been invaded. If the subpopulation is invaded, it must be in an infected state.

In this section, we discuss the problem of inferring epidemic pathways and epidemic networks. Herein *epidemic pathways* mean the (directed) edges that infected individuals moves from an infected subpopulation to another susceptible neighbor subpopulation. We divide the relevant works into two categories, *i.e.*, epidemic pathways based on EAT and epidemic pathways based on infection data.

*Epidemic pathways based on EAT.* The average arrival time [27] between two subpopulations was calculated

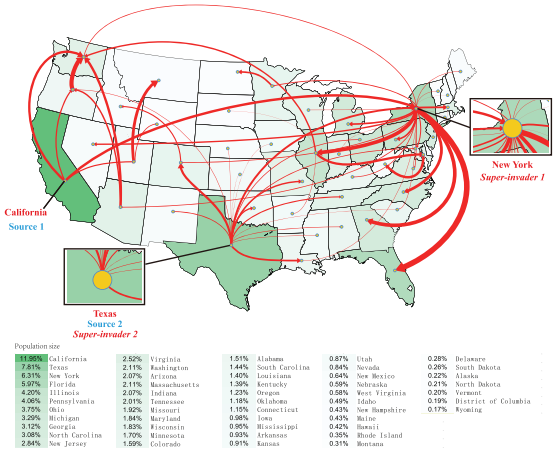


Fig. 4: Inferred invasion pathways of 2009 A(H1N1) on the aggregated air transportation network of USA. From Wang *et al.* [54].

and then the shortest paths tree of the network can also be figured out. Balcan *et al.* [39] used a large number of simulations to extract the minimum spanning tree of disease transmission by Monte Carlo method, which was also called invasion tree. In this way, the directed distance between any two subpopulations that spread from the initial source subpopulation on the metapopulation network can be calculated. Then, the Chu-Liu-Edmunds algorithm can be used to calculate the minimum spanning tree of the epidemic pathways. In addition, the measurement "effective distance" [28] was used to extract the most likely path tree of the propagation process.

Furthermore, the IPI-SI [55] and IPI-SIR algorithms [54] were proposed to infer invasion pathways for the SI and SIR model on metapopulation networks. Figure 4 shows the inferred invasion pathways between the states of the 2009 A (H1N1) epidemic in the United States inferred by the IPI-SIR algorithm, and reproduces the non-trivial spatial invasion pattern of this flu. In fact, each invasion pathway contains a label of a specific arrival time. We observed that two states (New York and Texas) are so-called "super-invaders". These two super-invaders respectively invaded 50% and 33.3% of all states (see ref. [54]).

*Epidemic pathways based on surveillance of infection data.* Maeno [56] used the maximum likelihood estimation method to calculate the disease network among 11 countries and regions based on SARS infection data and artificial metapopulation model. The calculated disease network is undirected, that is to say, no causal relationship is given on whom infected whom. Eggo *et al.* [57] used mortality data from the 1918 influenza pandemic to infer 246 population centers in England and Wales, and infection trees in 47 US cities. Based on population size, infectivity, distance and density, a gravity model of population movement between cities is constructed. With the help of Markov Chain Monte Carlo method, the parameters of the model are estimated. Then they separately estimated the most likely disease transmission trees

in these countries. Wan *et al.* [58] collected the infection data of 2009 A(H1N1) in Hong Kong and divided Hong Kong into 18 administrative regions which were regarded as 18 nodes. Then 6 linear models were used as individual transfer models and genetic algorithm is used to optimize the objective function, and figure out the disease transfer network. Shi *et al.* [59] analyzed the transfer network of diurnal infectious protozoa with humans and Anopheles as hosts, and collected the time series, temperature and mutation amount of malaria infected individuals in 62 towns in 4 counties in Yunnan Province, China in 2005. Yang *et al.* [60] used an improved network model combined with Kalman filtering and Bayesian indication to develop a set of alternative spatio-temporal methods, and then discovered the 2014–2015 Ebola transfer network in Sierra Leone based on infection data. Wang *et al.* [61] proposed a network inference model to infer metapopulation spread network incorporating the power-law distribution prior and data prior for intra-city infectious disease control and prevention.

**Reconstruction of epidemic transmission by phylogeographic.** – SARS-CoV-2 is an RNA virus with a very high mutation rate, and can evolve in the host through quasi-specific processes. The regular emergence and release of new variants replace the previous variants, such as the Delta variant [62]. With the further spread and prevalence of mutants, genomic data can be used to investigate the diversity of viral pathogens and viral transmission routes, so as to quickly find the origin and transmission of epidemics and determine the late source of local epidemics [63]. Scientific modeling and bias system geographic reasoning can further help us: 1) Understanding the global law of international movement under the intervention of SARS-CoV-2. 2) Measuring the spread of intercontinental new coronary pneumonia. 3) Identifying the prevalence, which is the main source of the spread of the virus in the world. 4) Revealing the sources of the main strains prevalent in different countries and regions [64].

*Real time gene detection.* The SARS-CoV-2 data set makes it possible to study the spatial propagation dynamics with abnormally high resolution. Through the construction of gene sequence transmission pedigree, it is further clarified that SARS-CoV-2 also has the phenomenon of recessive transmission [65]. At the same time, the epidemic at the urban level is usually composed of many mutual transmission chains, which are introduced independently, such as in the coastal areas of Kenya [66], which makes the scope of its spread very wide in local areas at the initial stage of the epidemic outbreak. Similarly, Lu *et al.* [67] also proved that this phenomenon also exists in Guangzhou. They used the combination of large genome sequencing and amplicons to generate gene sequences to solve the problems of molecular epidemiology and genetic diversity of SARS-CoV-2. The pedigree combines epidemiology and phylogeny, and defines the time, scale and duration of the local transmission chain, and can well inhibit the transmission of new crown after the restrictions of national travel restrictions and large-scale intensive monitoring and intervention measures in the province. However, due to the increase in the number of imported cases from other regions, in order to prevent the increase of the secret transmission process, we need immediate COVID-19 monitoring.

*Reconstruct the infection path.* Researchers have proved that when the data of human mobility and virus evolution are integrated together [68], the prediction of spatial transmission of influenza is the most accurate. Cao *et al.* [69] also adopted Bayesian maximum entropy (BME) method to simulate its temporal and spatial propagation dynamics and the results reveal that there is an autocorrelation in a certain space-time distance. In all molecular epidemiological studies using real-world data, it is found that relatively small and unevenly distributed samples can infer the spatio-temporal pattern of virus transmission in the region [70]. Therefore, Yang *et al.* used the asymmetric discrete trait analysis in BEAST v1.10.4 for systematic geographic inference. The universal time reversible (GTR) nucleotide substitution model and the model combining discrete gamma distribution and four rate categories and invariant sites are used to explain the rate heterogeneity between sites. In addition to the heterogeneity of intercontinental travel, the heterogeneity promotes the intercontinental transmission of SARS-CoV-2 and forms the temporal and spatial characteristics SARS-CoV-2 [64]. Layan *et al.* [71] sampled the degree and pattern of genetic diversity of the genome of SARS-CoV-2 to estimate the arrival date of the common source and the exponential growth rate of the virus population in their region, and obtained the common source of this branch and defined its transmission path.

However, the temporal and spatial bias of genome sampling will seriously confuse the systematic geographic inference of discrete traits. Dellicour *et al.* [72] integrated personal travel history data into Bayesian system. Geographic inference proved that including travel history data can produce: 1) More realistic virus transmission assumptions than including only sampling sites; 2) the higher accuracy of *a posteriori* prediction. This, together with the consideration of unsampled diversity, can alleviate the spatio-temporal sampling bias in the early propagation and reconstruction of SARS-CoV-2. Mir *et al.* [73] also used Bayesian phylogeography and molecular dynamics to infer the frequency of virus transmission between Brazil and Uruguay, and accurately infer the geographical source and time of virus introduction in Uruguay, which is helpful to further control the epidemic situation.

**Outlooks.** – In this letter, we reviewed the spread of epidemics in metapopulation networks. For the future research, we have the following outlooks:

1) In fact, there is no further research on the predictability of epidemics on metapopulation networks,

especially the lack of some theoretical results. That is, how much is the predictability of a metapopulation network with a specific structure and a specific initial condition? Further clarification is needed.

2) In the previous text, we mainly discussed the case of reaction-diffusion process on metapopulation networks. Actually, it is also worth paying attention to the case of reaction-commuting, especially for the spreading dynamics of the metapopulation network combining the long-distance reaction-diffusion and the short-term reaction-commuting. In addition, there is still a lack of work on time-varying and multilayer metapopulation networks, which needs further exploration.

3) With regard to non-pharmaceutical intervention measures combined with vaccines, and then using the metapopulation network, it is worth using our time to predict the impact of COVID-19 variants on humanbeings over a long period of time (such as several years).

4) In the reconstruction of the epidemic through phylogeographic, the analysis that combines the communication chain with sequence position and human movement data will further reveal the spatial scale and driving factors of communication. For example, including the network community structure in system dynamics reasoning can have a better effect on controlling the spread of epidemics. At the same time, the unique geographic database including environmental, socioeconomic, topographic and demographic variables is essential for future efforts to explain the spatial variability of disease incidence, and there should be further work.

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*Data availability statement*: The data that support the findings of this study are available upon reasonable request from the authors.

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