

## RESEARCH ARTICLE

## Social imitation dynamics of vaccination driven by vaccine effectiveness and beliefs

Feng Fu <sup>1,2\*</sup>, Ran Zhuo<sup>1</sup>, Xingru Chen<sup>3\*</sup>

**1** Department of Mathematics, Dartmouth College, Hanover, New Hampshire, United States of America, **2** Department of Biomedical Data Science, Geisel School of Medicine at Dartmouth, Lebanon, New Hampshire, United States of America, **3** School of Artificial Intelligence, Beihang University, Beijing, China

\* [fufeng@gmail.com](mailto:fufeng@gmail.com) (FF), [xingrucz@gmail.com](mailto:xingrucz@gmail.com) (XC).



## Abstract

Declines in vaccination coverage for vaccine-preventable diseases, such as measles and chickenpox, have enabled their surprising comebacks and pose significant public health challenges in the wake of growing vaccine hesitancy. Vaccine opt-outs and refusals are often fueled by beliefs concerning perceptions of vaccine effectiveness and exaggerated risks. Here, we quantify the impact of competing beliefs – vaccine-averse versus vaccine-neutral – on social imitation dynamics of vaccination, alongside the epidemiological dynamics of disease transmission. These beliefs may be pre-existing and fixed, or coevolving attitudes. This interplay among beliefs, behaviors, and disease dynamics demonstrates that individuals are not perfectly rational; rather, they base their vaccine uptake decisions on beliefs, personal experiences, and social influences. We find that the presence of a small proportion of fixed vaccine-averse beliefs can significantly exacerbate the vaccination dilemma, making the tipping point in the hysteresis loop more sensitive to changes in individuals' perceived costs of vaccination and vaccine effectiveness. However, in scenarios where competing beliefs spread concurrently with vaccination behavior, their double-edged impact can lead to self-correction and alignment between vaccine beliefs and behaviors. The results show that coevolution of vaccine beliefs and behaviors makes populations more sensitive to abrupt changes in perceptions of vaccine cost and effectiveness compared to scenarios without beliefs. Our work provides valuable insights into harnessing the social contagion of even vaccine-neutral attitudes to overcome vaccine hesitancy.

 OPEN ACCESS

**Citation:** Fu F, Zhuo R, Chen X (2025) Social imitation dynamics of vaccination driven by vaccine effectiveness and beliefs. *PLoS Computat Biol* 21(10): e1013586. <https://doi.org/10.1371/journal.pcbi.1013586>

**Editor:** Christian Hilbe, Interdisciplinary Transformation University IT:U, AUSTRIA

**Received:** March 6, 2025

**Accepted:** October 2, 2025

**Published:** October 13, 2025

**Copyright:** © 2025 Fu et al. This is an open access article distributed under the terms of the [Creative Commons Attribution License](https://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

**Data availability statement:** All data have been included in the manuscript. The code to reproduce the results is available at: <https://github.com/fufeng/vaccinebeliefs>.

**Funding:** This work was supported in part by a research grant from Investigator-Initiated Studies Program of Merck Sharp & Dohme Corp to F.F. (MISP #100861). The opinions expressed in this paper are those of the authors and do not necessarily represent those of Merck Sharp & Dohme Corp. X.C. is supported

## Author summary

Vaccination is one of the most cost-effective interventions for preventing and controlling infectious diseases, yet the world is experiencing declines in vaccination rates due to growing vaccine hesitancy. This hesitancy is often fueled by beliefs about vaccine effectiveness and perceived risks. Here, we study how these preexisting or coevolving beliefs,

by the Beijing Natural Science Foundation, China (grant no. 1244045). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

**Competing interests:** The authors have declared that no competing interests exist.

combined with social influences and personal experiences, shape vaccination behavior and affect disease spread. We find that even a small fraction of individuals with fixed vaccine-averse beliefs can create significant hurdles, making populations more sensitive to changes in perceived vaccine costs or effectiveness. Interestingly, this tipping-point fragility becomes less pronounced when vaccine beliefs coevolve and spread inter-personally. Our work underscores the importance of addressing both individual and social factors in promoting vaccination confidence and demand in the face of vaccine hesitancy.

## Introduction

Mass vaccination is one of the most cost-effective pharmaceutical interventions for the prevention and control of infectious diseases [1,2]. Long before the advent of modern vaccine technology, people in China, around 1000 AD, used pus from cows infected with cowpox to inoculate humans against smallpox [3]. Fast forward to today, the worldwide deployment of modern vaccines has drastically reduced morbidity and mortality, particularly for childhood diseases. Despite the fact that vaccines have saved millions of lives over decades—most notably with the record-breaking innovation of mRNA vaccines during the recent COVID-19 pandemic [4–6]—achieving widespread population immunity through voluntary vaccination remains a persistent public health challenge [7].

In recent years, for example, the world has seen a resurgence of vaccine-preventable diseases, such as measles [8], polio [9] and pertussis (whooping cough) [10]. Notably, measles has recently reached the very verge of an endemic disease in France [8]. Polio, once on the brink of global eradication, remains endemic in Afghanistan and Pakistan [9]. Whooping cough is on the rapid rise in North America and Europe [11].

Such resurgent outbreaks of measles and other diseases suggest substandard vaccination compliance [12], despite tremendous efforts to address vaccine hesitancy [13,14], especially given how cost-effective these vaccines actually are. For instance, prior study estimates that, as compared to the cost of one measles vaccine \$20, the cost to treat each measles infection is \$10,376, while the total cost to contain each outbreak is \$124,517 [15]. Even though resurgent measles outbreaks impose huge risks for those unvaccinated and even in some European regions it has become an endemic disease [8,13], the coverage of measles vaccination still remains insufficient [12], for more than a decade following the infamous MMR vaccination and autism controversy [16].

Notably in the aftermath of a sharp decline in vaccination coverage triggered by concerns regarding vaccine safety and efficacy, the recovery of vaccination rate from nadir to levels needed to attain herd immunity has been remarkably slow. For example, it takes almost two decades for the recovery in the uptake of whole-cell pertussis vaccine from rock bottom 30% in 1978 to 91% in 1992 in England and Wales [17–19]. This suggests that the recovery of vaccination rate depends not just on the extent of mitigating perceived cost of vaccination and improving vaccine efficacy, but also on the past vaccination trajectory, hence possibly hindering a rapid increase. To shed light on this puzzling phenomenon, recent theoretical study finds that social imitation dynamics of vaccination can exhibit *hysteresis* [20], namely, the dependence of population vaccination rate on its past trajectory. Such a hysteresis effect makes the population sensitive to changes in factors that drives vaccination behavior, such as cost and effectiveness. The presence of hysteresis also can hinder the recovery of vaccine uptake, in spite of decreases in the perceived cost of vaccination or improvement of vaccine efficacy, as the vaccination trajectory can get stuck in the hysteresis loop.

Among others, over the past decade, researchers have proposed *behavioral epidemiology* as a means of integrating the study of epidemiology with the influence of human behavior including but limited to health decisions made by individual actors responding to infection risks [21,22]. As such, a feedback loop exists between health behaviors and the spread of an epidemic: individuals may take preventative measures, such as vaccination or reduced contact with others, in response to perceived risks. These responses in turn modify the spread of infection. The interplay between changing opinions of vaccination and epidemic spreading on social networks constitutes a “dueling contagion” process [23–25]. It is of fundamental significance to achieve a comprehensive understanding of the rich dynamics generated by this sort of dueling contagion [26,27].

In particular, the use of behavior-disease interaction models has become an important approach to study how vaccine compliance can be influenced by a wide range of factors [20, 28–45], ranging from vaccine scares [46] to disease awareness [47]. Prior work shows that a misalignment between individual interest and the population interest can cause suboptimal vaccination coverage [48–52], thereby leading to a tragedy of the commons in vaccination uptake [53,54].

An individual’s vaccination contributes to herd immunity, meaning those who forgo vaccination can be indirectly protected by the presence of herd immunity. The problem of vaccine compliance is thus often represented as a public-goods dilemma. A misalignment between individual self-interest and population interest can yield the “free rider” problem in vaccine uptake [48,49,55–58], thereby causing suboptimal vaccination coverage [59]. Moreover, the long-standing dilemma of voluntary vaccination is exacerbated by spreading concerns about vaccine safety and efficacy [20,31,60–64]. Recently, considerable attention has been paid to improving our understanding of the role of social factors in epidemiology [23,24,26,27,40,65–72].

Understanding the impact of social networks on public health behavior and especially vaccination choices is of particular interest [26]. A vaccine’s success can become its own demise. Once the incidence of vaccine-preventable common childhood diseases becomes rare, parents who are unfamiliar with the diseases pay more attention to concerns regarding the risks of vaccination rather than the disease itself [7]. This leads to social contagion of vaccine scares or skepticisms, which can hinder vaccination efforts [65,73]. Vaccine-averse attitudes amplify the costs of vaccination due to heightened concerns about vaccine safety and risks [62]. The issue is further complicated by anecdotes or personal experience regarding vaccine effectiveness, as vaccines may be imperfect and confer only partial protection against diseases [20,74]. The impact of heterogeneous beliefs on vaccination dynamics remains poorly understood, particularly when a small fraction of individuals hold pre-existing, fixed belief as opposed to vaccine-neutral attitudes.

Motivated by these considerations, here we investigate the social imitation dynamics of vaccination in well-mixed and spatial populations driven by vaccine effectiveness and beliefs. We quantify and compare the sensitivity and fragility of vaccination coverage in the presence of pre-existing or coevolving vaccine beliefs. Our work shows that even a small fraction of individuals with fixed vaccine-averse beliefs can exacerbate the hysteresis effect, causing vaccination coverage to be more sensitive to changes in the perceived cost of vaccination and vaccine effectiveness, compared to cases without any beliefs. Furthermore, the coevolution of vaccine beliefs and behavior choices has a lesser impact than rigid, fixed beliefs but still reduces the population’s resilience to perturbations in perceived vaccination cost and effec-

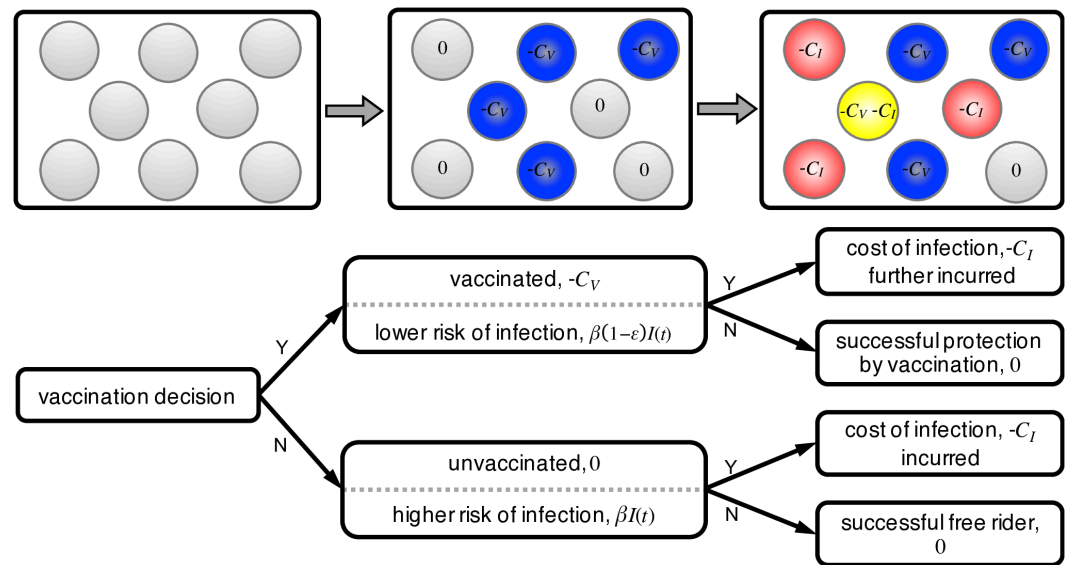
tiveness. By revealing the interference between epidemic spreading and the social contagion process of vaccine beliefs that shape public perceptions of vaccine safety and risk, our work provides deep insights into the social factors that drive vaccination decisions and as well as barriers to boosting vaccine uptake.

### Results

To begin, we first study how social imitation dynamics of vaccination, where individuals are not perfectly rational, can be impacted by the presence of an imperfect vaccine. In addition to weighing the perceived cost of vaccination with the risk of infection, the effectiveness of vaccination is also an important factor driving vaccination decisions. Specifically, we model the vaccination dynamics under imperfect vaccines as a two-stage game as shown in Fig 1. At stage 1 (vaccination choice), a proportion  $V_0$  of the population decides to vaccinate. Vaccination costs  $C_v$  and provides *imperfect* protection against the infectious disease. At stage 2 (health outcome), we use the Susceptible-Infected-Recovered (SIR) model with preemptive vaccination in stage 1 to simulate the epidemiological process:

$$\frac{dS}{dt} = -\beta SI,$$

$$\frac{dI}{dt} = \beta SI + (1 - \varepsilon)\beta VI - \gamma I,$$



**Fig 1. Model schematic.** We model the vaccination dynamics under imperfect vaccine as a two-stage game. At stage 1 (vaccination choice), a proportion  $V_0$  of the population decides to vaccinate. Vaccination costs  $C_v$  and provides *imperfect* protection against the infectious disease. At stage 2 (health outcome), we use the Susceptible-Infected-Recovered (SIR) model with preemptive vaccination to simulate the epidemiological process. Every individual faces the risk of infection, which depends on their vaccination status and the number of infectious neighbors,  $I(t)$ , they have. The transmission rate of the disease (per day per infectious neighbor) to unvaccinated individuals is  $\beta$ , as compared to  $\beta(1 - \varepsilon)$  for vaccinated. Here, the parameter  $\varepsilon \in [0, 1]$  denotes the level of vaccine effectiveness. The cost of infection is  $C_I$ . Without loss of generality, we use the relative cost of vaccination,  $c = C_v/C_I \in [0, 1]$  in the remainder of this paper. Those unvaccinated individuals who remain healthy are free-riders off the vaccination efforts of others, as they are indirectly protected to some extent by herd immunity.

<https://doi.org/10.1371/journal.pcbi.1013586.g001>

$$\begin{aligned}\frac{dV}{dt} &= -(1 - \varepsilon)\beta VI, \\ \frac{dR}{dt} &= \gamma I.\end{aligned}\tag{1}$$

Here, the transmission rate of the disease to an unvaccinated individual is  $\beta$ , as compared to  $(1 - \varepsilon)\beta$  for a vaccinated individual. Denote by  $\gamma$  the disease recovery rate. We assume recovered individuals remain immune to the disease throughout the current epidemic season.

After stage 1, every individual faces the risk of infection, which depends on their vaccination status and the number of infectious neighbors,  $I(t)$ , they have. Thus the parameter  $\varepsilon$  quantifies the effectiveness of vaccination in protecting against the disease during the epidemic season modeled by the SIR-V model above. For perfect vaccines,  $\varepsilon = 1$ , vaccinated individuals have zero risk of infection, as already analyzed in previous studies [32]. For imperfect vaccines,  $0 < \varepsilon < 1$ , vaccinated individuals still face the risk of getting infected but with a reduced likelihood compared to unvaccinated individuals [20]. The cost of infection is  $C_I$ . Those unvaccinated individuals who remain healthy are free-riders off the vaccination efforts of others, as they are indirectly protected to some extent by herd immunity [32].

Without loss of generality, we assume the relative cost of vaccination to infection is  $c = C_v/C_I \in (0, 1)$ . As shown in Fig 1, there are four possible health outcomes, and thus, we have four different payoffs at the end of the current season. Up to a positive constant factor, the payoff for a vaccinated individual who remained healthy during the epidemic (denoted by the fraction  $x_0$ ) is  $-c$ , the payoff for a vaccinated individual who still contracted the disease (denoted by the fraction  $x_1$ ) is  $-1 - c$ ; the payoff for an unvaccinated individual who became infected (denoted by the fraction  $y_1$ ) is  $-1$  while the payoff for an unvaccinated individual who remained healthy (denoted by the fraction  $y_0$ ) is 0. The proportions of these four types of outcomes are determined by the SIR-V dynamics as given in Eq. (1) and the vaccination level  $x$  (see Materials and Methods). At the end of stage 2 (the current epidemic season), individuals revisit their vaccination choices through social imitation, a social learning process based on pairwise comparison [75]. Therefore, stage 1 (vaccination decision) starts off again, followed by stage 2 (health outcomes determined by the unfolding epidemic season), and so on until the population reaches an equilibrium vaccination coverage.

Regarding vaccination strategy updating, an individual  $i$  with strategy  $S_i$  and payoff  $\pi_i$  randomly chooses one of their neighbors  $j$  with strategy  $S_j$  and payoff  $\pi_j$  and switches to  $j$ 's vaccination choice with the probability  $\phi_{S_j \rightarrow S_i}$  given by the Fermi function [76–78]:

$$\phi_{S_j \rightarrow S_i} = \frac{1}{1 + \exp[-K(\pi_j - \pi_i)]},\tag{2}$$

where the parameter  $K > 0$  can be seen as the inverse of the temperature in the original Fermi function [77,78]. In the context of individual decision-making or social imitation,  $K$  represents the intensity of selection and quantifies the level of rationality. For  $K \rightarrow 0$ , the switching probability  $\phi_{S_j \rightarrow S_i}$  approaches 1/2, corresponding to random choices. At the other extreme,  $K \rightarrow \infty$  indicates perfect rationality: individuals only switch to vaccination strategies with strictly higher payoffs. For  $0 < K < \infty$ , individuals exhibit bounded rationality: they adopt vaccination strategies with higher payoffs with probability greater than 1/2 but less than one, but also can adopt strategies with lower payoffs with nonzero probability, albeit less than 1/2.

In a well-mixed population, the replicator-like equation for the evolution of vaccination choice is given by:

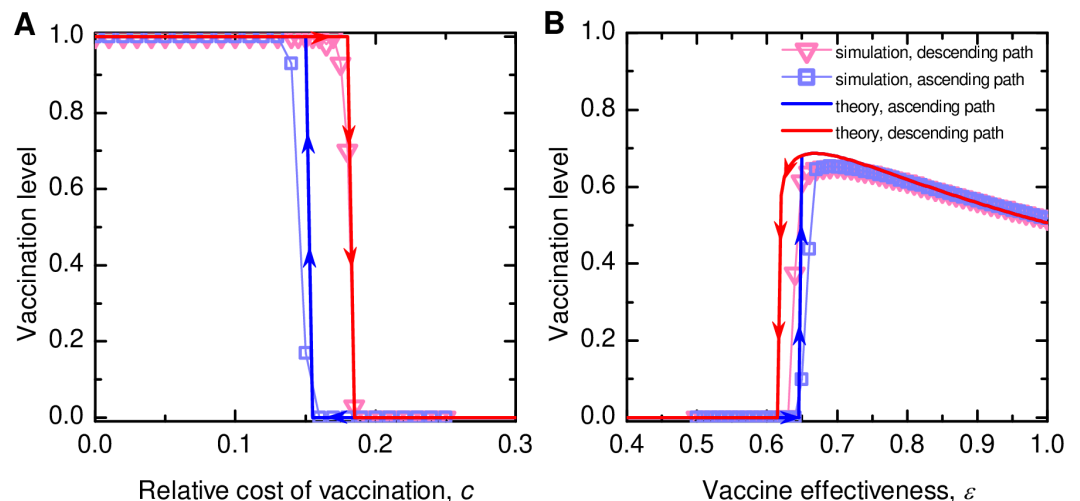
$$\dot{x} = x_0 y_0 \tanh\left[\frac{K}{2}(-c - 0)\right] + x_0 y_1 \tanh\left[\frac{K}{2}(-c + 1)\right] \quad (3)$$

$$+ x_1 y_0 \tanh\left[\frac{K}{2}(-c - 1 - 0)\right] + x_1 y_1 \tanh\left[\frac{K}{2}(-c - 1 + 1)\right], \quad (4)$$

where  $x_0 + x_1 = x$  and  $y_0 + y_1 = 1 - x$ .

We now proceed with bifurcation analysis and identify parameter regions that enable bistability and thus allow the hysteresis loop to occur. We present stochastic agent-based simulation results in Fig 2 along with the numerical theoretical analysis based on the system of differential equations. As predicted by the theoretical analysis, the population exhibits bistability with respect to varying the relative cost of vaccination  $c$  and vaccination effectiveness  $\varepsilon$  and the population abruptly transitions from high vaccination level to complete opt-outs when  $c$  increases beyond a threshold and  $\varepsilon$  drops below a threshold (the descending path). However, to recover the vaccination level to previously high coverage, the ascending path takes a different route instead of reversing the descending path, requiring an even lower threshold in cost and higher vaccine effectiveness. Here, we confirm the occurrence of this hysteresis effect for social learning that allows irrationality (with  $K = 1$  in Fig 2), where individuals imitate with higher probability those with higher payoffs but still can imitate those with lower payoffs.

Overall, our simulations agree well with the theoretical predictions (Fig 2); the discrepancies are partly due to finite size effects arising in agent-based simulations. The discrepancy is



**Fig 2. Bistability of equilibrium vaccination levels and the emergence of hysteresis loops in well-mixed populations.**

We simulate the social imitation of vaccination dynamics in a finite, well-mixed population and obtain hysteresis loops, composed of the ascending and descending paths, in response to variations to model parameters: (A) the relative cost of vaccination,  $c$ , and (B) vaccine effectiveness,  $\varepsilon$ . The population can exhibit bistability within certain ranges of the model parameters  $c$  and  $\varepsilon$ . Stochastic agent-based simulation results align with theoretical analysis, with noticeable discrepancies attributable to finite population effects. Parameters: population size  $N = 1000$ , infection seeds  $I_0 = 10$ . For the first simulation, the initial number of vaccinated individuals is  $V_0 = 500$ . For subsequent simulations, the results of the preceding simulations are used as the initial conditions, while the model parameters are varied in a prescribed sequence of increasing and then decreasing values. Disease transmission rate  $\beta N = 0.25$ , recovery rate  $\gamma = 0.1$ , intensity of selection  $K = 1$ . (A) effectiveness  $\varepsilon = 0.4$ , (B)  $c = 0.35$ . Simulation results are averaged over 100 independent runs.

<https://doi.org/10.1371/journal.pcbi.1013586.g002>

more pronounced along the descending path of the hysteresis loop with respect to varying  $\varepsilon$  (Fig 2B). This is partly because low vaccine effectiveness amplifies the impact of the initial infection seeds ( $I_0 = 10$  used in simulations) on disease outcomes, thus making the population more sensitive to reductions in  $\varepsilon$  compared to the infinitely large well-mixed populations. Together, this leads to a smaller value of  $\varepsilon$  below which universal vaccine opt-out occurs, compared to the threshold predicted by theory.

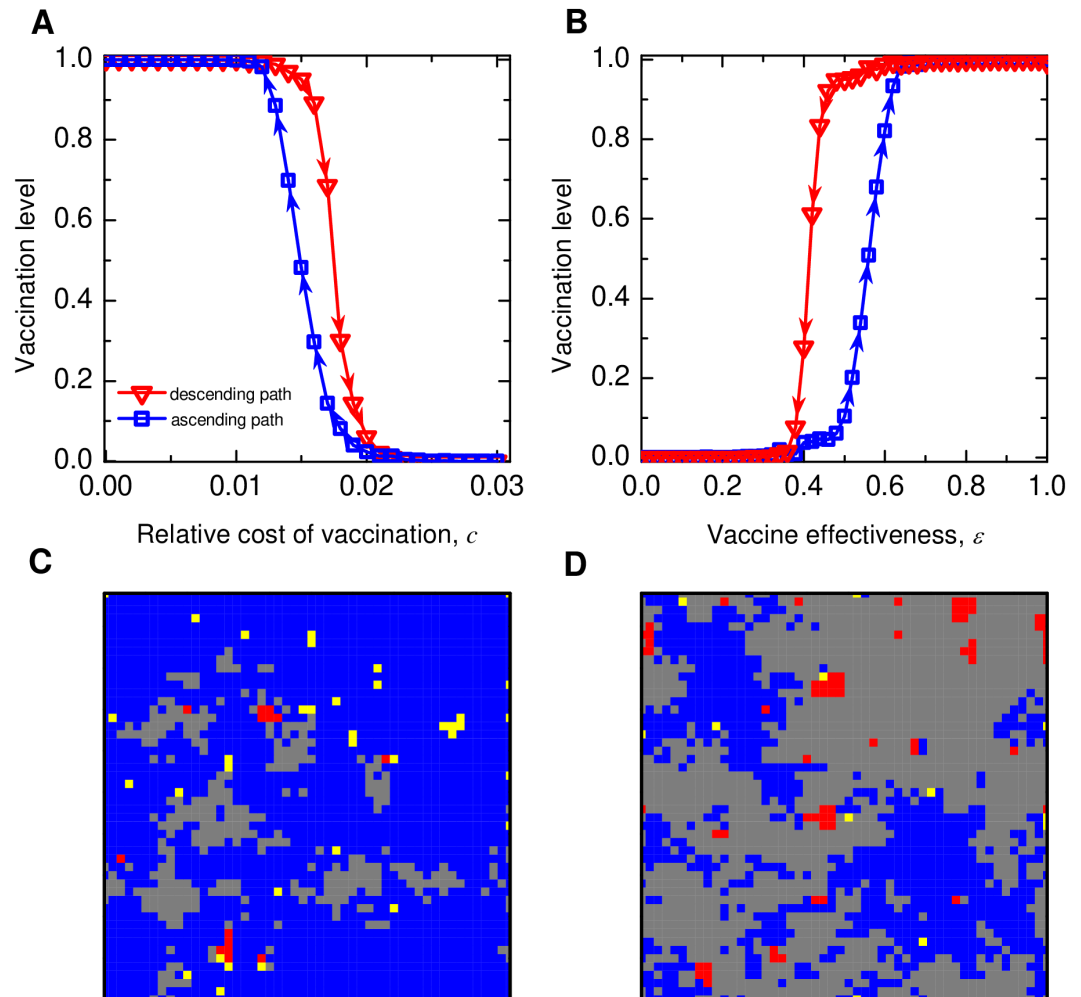
Aside from well-mixed populations, we also study vaccination dynamics in spatial populations, where, for example, individuals are situated on a square lattice with the von Neumann neighborhood [77]. Such population structure restricts whom individuals can imitate, or be infected by, to just their immediate neighbors. Individuals' vaccination decisions and health outcomes determine their payoffs. They can revisit their vaccination choices by imitating more successful strategies among their immediate neighbors. It is straightforward to study vaccination dynamics in a variety of networks, including random networks and scale-free networks [32]. In general, we confirm the existence of a threshold for vaccine effectiveness  $\varepsilon$ , below which multiple stable vaccination equilibria emerge. We use simulations to determine whether population structure, as compared to the well-mixed case, can strengthen the *hysteresis effect*, thereby further hindering the recovery of vaccine uptake. In what follows, we detail these results to better understand the role of population structure in vaccine uptake behavior, especially in the presence of imperfect vaccines as well as fixed or coevolving vaccine beliefs.

We observe a high sensitivity of vaccination coverage in structured populations. For comparable disease impact without vaccination, the spatial population manifests drastic fragility to changes in the perceived cost of vaccination, even for more effective vaccination (Fig 3A) and requires much more improvement in vaccination effectiveness in order to boost high vaccination levels, even for a smaller cost of vaccination (Fig 3B). One reason is that population structure promotes assortment, and clusters of unvaccinated and vaccinated individuals together (see Fig 3C and 3D) strengthen the vaccination coverage's sensitivity to changes, indicating a double-edged sword effect of population structure [32].

We emphasize that social contagions may also promote the spread of misinformation and bad health behaviors, as well [73]. The spread of vaccine scares among parents (via social contagion) has caused the vaccination rates of newborns to plunge from high levels [62], which, in turn, has increased the incidence of several childhood diseases (via biological contagion). These fears are fueled not only by face-to-face interaction, but also by changing opinions of vaccination that are expressed in online social media [73]. It is critical for us to better understand these spreading processes so public health efforts can take advantage of the positive effects of social contagion, while ameliorating its potential negative impacts.

We first study the scenario when a fixed population of individuals believes vaccines impose elevated risks. To inform our choice of the proportion of negative vaccine views, we use the recent Pew Research data, which shows that 7% of respondents believe the preventive health benefits of MMR vaccines are low [79]. To incorporate this consideration, we introduce an additional perceived vaccination cost,  $\theta$ , for this subpopulation in our model. To illustrate how a small proportion of individuals with vaccine-averse beliefs can disproportionately impact vaccine uptake, we set their proportion as low as 2% in our simulations. Despite such a small fraction of individuals with fixed beliefs about the amplified cost of vaccination (with  $\theta = 0.1$ ), the population exhibits much higher sensitivity and fragility of high vaccination levels to perturbations. Fig 4 demonstrates that the occurrence of the hysteresis loop at a much smaller cost of vaccination (Fig 4A) and at a much higher vaccination effectiveness (Fig 4B), reducing the critical thresholds of relevant vaccine parameters by more than half (cf. Fig 3).

The corresponding spatial snapshots in Fig 4C and 4D reveal that the opt-out behavior of vaccine-skeptical individuals can spread to their neighbors, leading to noncompliance even

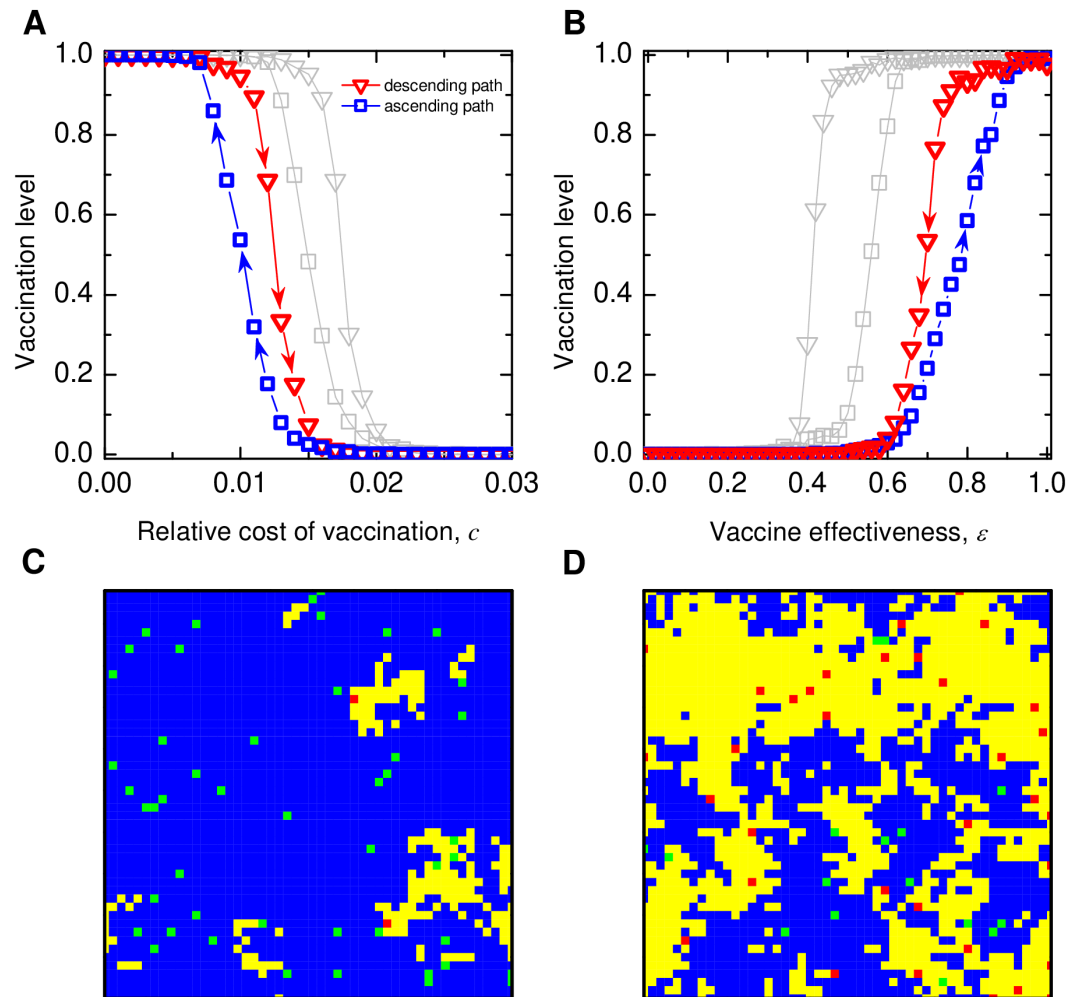


**Fig 3. Hysteresis and sensitivity of vaccination dynamics in lattice populations.** (A) and (B) depict the hysteresis loops, represented by the descending and ascending paths of the population's equilibrium vaccination level, in response to variations in the relative cost of vaccination,  $c$ , and vaccine effectiveness,  $\varepsilon$ , respectively. Overall, the critical parameter region where the hysteresis occurs depends on specific model parameter choices. The spatial population is highly sensitive to changes in  $c$  and  $\varepsilon$  and abruptly transitions between complete opt-out and universal coverage of vaccination. (C) and (D) show spatial snapshots of population states along the descending and ascending paths of Fig 3A for a fixed  $c = 0.015$ , respectively. The color codes of individuals are the same as in Fig 1: Blue represents individuals who were vaccinated and remained healthy during the season, yellow represents individuals who were vaccinated but still became infected, grey represents individuals who were unvaccinated yet remained healthy, and red represents individuals who were unvaccinated and became infected. Parameters: Square lattice  $N = 50 \times 50$  with the von Neumann neighborhood, infection seeds  $I_0 = 30$ , initial number of vaccinated  $V_0 = 1250$ , disease transmission rate  $\beta = 0.04$ , recovery rate  $\gamma = 0.1$ , intensity of selection  $K = 1$ . (A) effectiveness  $\varepsilon = 0.8$  (B)  $c = 0.01$ . (C) (D):  $c = 0.015$ ,  $\varepsilon = 0.8$ . Simulation results are averaged over 150 independent runs.

<https://doi.org/10.1371/journal.pcbi.1013586.g003>

among vaccine-neutral individuals. Conversely, vaccination by those with neutral attitudes can convert those individuals holding vaccine-averse views. Taken together, the presence of rigid fixed beliefs, even in a tiny proportion of the population, can render the population significantly more sensitive to changes compared to cases without such beliefs.

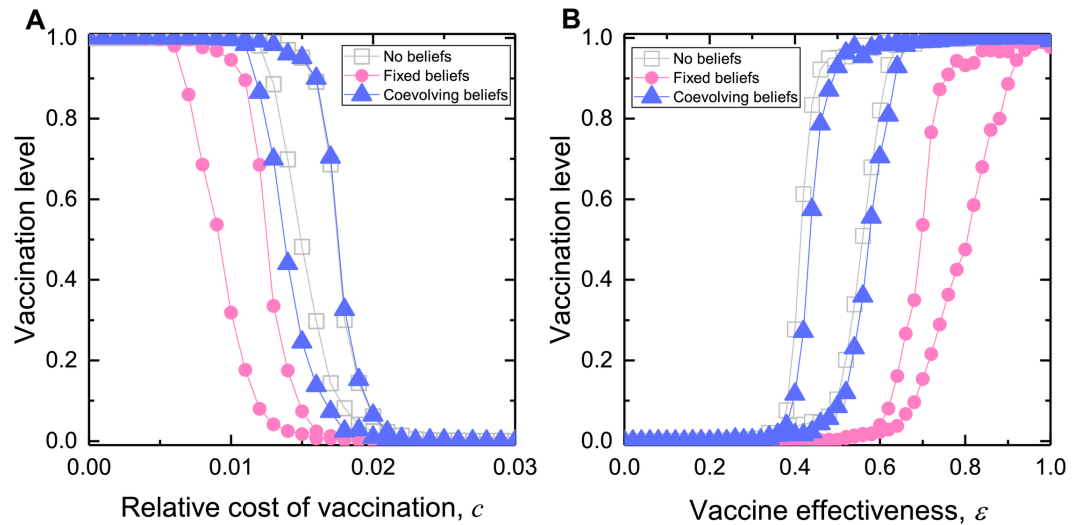
Finally we study the scenario where competing beliefs spread interpersonally and coevolve with vaccination behavior in a manner similar to disease transmission (Fig 5). Individuals can revisit and change both their vaccine beliefs and behavior choices via social contagion.



**Fig 4. Impact of pre-existing, fixed vaccine beliefs on vaccination dynamics.** The presence of vaccine-averse (skeptical) beliefs, even at low frequencies, can render the population more sensitive to the cost of vaccination and vaccine effectiveness. Shown are the hysteresis loops of vaccination levels with respect to changes in (A) the cost of vaccination and (B) the vaccine effectiveness. For comparison sake, the grey lines are the results in Fig 2 without any vaccine beliefs. (C) and (D) show spatial snapshots of population states in the descending and ascending paths respectively. The color of individuals indicates their specific combinations of vaccine beliefs and uptake behaviors: blue: vaccinated individuals with vaccine-neutral attitude; yellow: unvaccinated individuals with vaccine-neutral attitude; green: vaccinated individuals with vaccine-averse attitude; red: unvaccinated individuals with vaccine-averse attitude. Parameters: square lattice  $50 \times 50$  with von Neumann neighborhood, initial number of infection seeds  $I_0 = 30$ , initial number of vaccinated  $V_0 = 1250$ , fixed number of vaccine skeptical individuals 50, disease transmission rate  $\beta = 0.04$ , recovery rate  $\gamma = 0.1$ ,  $\theta = 0.1$ ,  $K = 1$ . (A) effectiveness  $\epsilon = 0.8$  (B)  $c = 0.01$ , (C) (D):  $c = 0.01$ ,  $\epsilon = 0.8$ . Simulation results are averaged over 150 independent runs.

<https://doi.org/10.1371/journal.pcbi.1013586.g004>

The combination of beliefs and behavior results in coevolutionary dynamics of four types, coupled with disease spreading. Just as before, a particular combination of vaccine belief and behavior is more likely to spread whenever it yields higher payoffs. Unlike fixed beliefs, this extended scenario allows individuals to adjust their vaccine beliefs in addition to their vaccination decisions, based on their own experiences and peer influence. The coevolution of belief and behavior may lead to belief-behavior consistency through self-correcting social imitation. That said, while the concurrent spreading of beliefs and behavior choices results in slightly less



**Fig 5. Coevolution of vaccine beliefs and uptake behavior.** Plotted are the hysteresis loops of equilibrium vaccination levels as a function of (A) the relative cost of vaccination,  $c$ , and (B) vaccine effectiveness,  $\epsilon$ . For comparison, we include the simulation results in the absence of any vaccine beliefs (Fig 3) as well as those with fixed vaccine beliefs (Fig 4). Compared to the case without vaccine beliefs, the concurrent spreading of beliefs—where a vaccine-neutral attitude competes with a vaccine-averse attitude alongside the social contagion (imitation) process of vaccine behavior choices—lead to slightly less favorable condition for vaccination. However, this impact is much less severe than in the scenario where a small proportion of individuals hold a vaccine-averse attitude and remain unchanged. Parameters: (A, B) square lattice  $50 \times 50$  with von Neumann neighborhood, initial number of infection seeds  $I_0 = 30$ , initial number of vaccinated  $V_0 = 1250$  (50%), initial number of vaccine skeptical individuals 1250 (50%), disease transmission rate  $\beta = 0.04$ , recovery rate  $\gamma = 0.1$ ,  $\theta = 0.1$ ,  $K = 1$ . (A) for fixed effectiveness  $\epsilon = 0.8$ , and (B) for fixed  $c = 0.01$ . Simulation results are averaged over 150 independent runs.

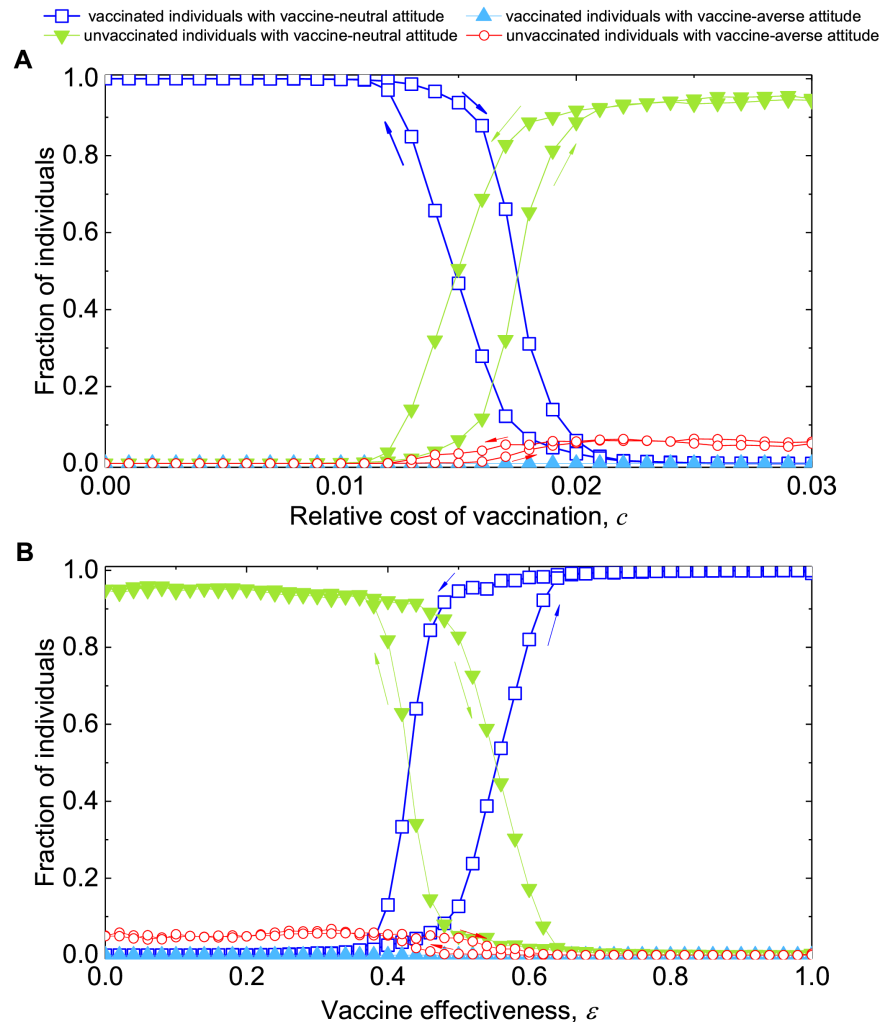
<https://doi.org/10.1371/journal.pcbi.1013586.g005>

favorable conditions for the stability of vaccination coverage, it still fares much better than the case with fixed beliefs (see Fig 5).

Fig 6 provides a detailed view of the four types of individuals via their hysteresis loops, rather than their overall vaccination levels in Fig 5. It is notable that unvaccinated individuals with vaccine-averse attitudes arise in the population, whereas individuals with vaccine-neutral attitudes seldom opt for vaccination. The spread of vaccine-averse beliefs can reach a maximum at 6% under extremely unfavorable conditions for vaccination, characterized by high perceived costs  $c$  and low vaccine effectiveness  $\epsilon$ . Vaccine-averse individuals are almost exclusively noncompliant with vaccination. Fig 6 also suggests that the emergence of vaccine-averse attitudes arises and persists in the population, driven by the perceived cost of vaccination and compromised vaccine effectiveness. The descending path to mitigate these opinions requires much higher levels of improvement in vaccine confidence and trust. These results highlight that it is crucial for public health to harness the power of social contagion – which, while exhibiting a dual impact – to ameliorate the impact of vaccine-averse beliefs and boost vaccination confidence and demand.

## Discussion and conclusion

Compared to non-pharmaceutical interventions requiring repeated adherence, vaccination is typically one-off action that can provide sufficient protection during an ongoing epidemic [21]. Under noncompulsory, voluntary vaccination, populations can achieve high vaccination coverage for small costs of vaccination, provided the vaccine is effective. Complications arise when exaggerated perceived risk or cost of vaccination—due to adverse



**Fig 6. Microscopic view of the hysteresis loops arising from the coevolution of vaccine beliefs and uptake behavior.** Shown are hysteresis loops, indicated by the corresponding descending and ascending paths of the equilibrium fractions of individuals grouped into four types based on the combinations of their vaccine beliefs and behavior choices, as a function of (A) the relative vaccination cost  $c$  and (B) the vaccine effectiveness  $\varepsilon$ . The equilibrium fraction of individuals with a vaccine-averse attitude who also opt for vaccination is almost zero across the parameter space studied. The proportion of vaccine-averse individuals almost exclusively opt out of vaccination, and their fraction can reach a maximum of around 6% in the population. Parameters: square lattice  $50 \times 50$  with von Neumann neighborhood, initial number of infection seeds  $I_0 = 30$ , initial number of vaccinated  $V_0 = 1250$  (50%), initial number of vaccine skeptical individuals 1250 (50%), disease transmission rate  $\beta = 0.04$ , recovery rate  $\gamma = 0.1$ ,  $\theta = 0.1$ ,  $K = 1$ . (A) for fixed effectiveness  $\varepsilon = 0.8$  (B) for fixed  $c = 0.01$ . Simulation results are averaged over 150 independent runs.

<https://doi.org/10.1371/journal.pcbi.1013586.g006>

side effect though uncommon—and concerns about vaccine safety undermine public confidence [7]. Such beliefs erode individuals' intention to vaccinate [14,63]. In this work, we study how the presence of small fraction of vaccine-averse beliefs can disproportionately impact vaccination coverage's sensitivity and fragility to small changes in perceived vaccination cost and vaccine effectiveness.

It is not surprising that the spread of such beliefs occurs alongside individual vaccination behavior [65,73]. Vaccine-averse beliefs can gain a foothold in the population, especially when the perceived cost of vaccination increases or vaccine effectiveness is comprised [62].

Beyond the hysteresis loop of vaccination levels, our work demonstrates the existence of a similar hysteresis effect for vaccine beliefs, presenting an additional roadblock to efforts to increase vaccination rates. Individuals are not perfectly rational, and skeptical beliefs about vaccines can replace fear of disease. Ironically, because vaccines reduce the incidence and severity of diseases, people become overly focused on anecdotes and occasional vaccination failures [61]. Therefore, effectively communicating the efficacy and cost-effectiveness of vaccination become pivotal—not to intentionally create pro-vaccine beliefs but at least to foster vaccine-neutral attitudes, as our results suggest.

However, there are two types of vaccine failures: primary and secondary [20,80]. Our current work accounts for primary failure, in which the vaccine provides only partial protection throughout the season (stage 2), with effectiveness quantified by the parameter  $\epsilon$ . Secondary failure refers to the waning of immunity acquired through vaccination. In this latter case, the vaccine provides sufficient protection only for a period of time, but this protection weakens, eventually leading to failure. This is the rationale for vaccine boosters [81], namely repeated vaccinations aimed at maintaining the desired level of protection. Since our work focuses on seasonal vaccination through repeated two-stage games (Fig 1), we explicitly account for primary failure in our results while implicitly assuming secondary failure. In other words, even though individuals were vaccinated in previous seasons, they are assumed to have zero protection if not vaccinated again. Furthermore, if secondary failure were also allowed to occur at a certain point in stage 2 due to waning immunity, this extended scenario would likely make the population even less inclined to vaccinate compared to our current model.

In the current model, we also assume that recovered individuals, regardless of their vaccination status, cannot be reinfected during the current epidemic season in stage 2. Just as immunity acquired from vaccination weakens over time, immunity acquired from infection can also wane. Therefore, it is not plausible that individuals can be infected more than once due to rapid waning immunity [82]. This consideration would make effective vaccination more attractive, since vaccines typically impose a much smaller cost than infections.

In this study, we examine the interplay between individual beliefs, vaccination decisions, and social and biological contagion processes. Our model incorporates boundedly rational decision-making driven by social imitation with incomplete information, capturing the nuances of human behavior influenced by vaccine-related beliefs. We analyze how the presence, as well as concurrent spread, of vaccine skepticism in spatial populations can amplify small increases in perceived vaccination costs, leading to significant declines in vaccine uptake. By coupling belief-behavior coevolution with epidemiological dynamics, our model highlights the indirect pathways through which beliefs (misinformation) about vaccines propagates and undermines public health efforts.

Our findings highlight the importance of addressing vaccine hesitancy as both a behavioral and social phenomenon [26]. Through simulations, we demonstrate that even a modest fraction of vaccine-averse individuals can create cascading effects that significantly impact the fragility of herd immunity thresholds. Moreover, we identify potential targeted network interventions—such as effective communication campaigns that reduce the fear of vaccination or incentives that subsidize the cost of vaccination—can mitigate the spread of vaccine skepticism. These insights provide a pathway for designing more resilient public health strategies that address both the direct epidemiological challenges of vaccine-preventable diseases and the social dimensions of belief formation [25]. That said, real-world data, such as vaccine sentiment expressed online [83] and vaccination rates observed offline, can be combined with our modeling to shed light on the rise and fall of anti-vaccine beliefs and their impact on vaccine uptake [8].

Perceived vaccination effectiveness can also change in the context of growing concerns about the disease [59] or increasing concerns about vaccine risks [60]. In the present study, we assume these perceptions are fixed and uniform for vaccine-averse individuals. It would be meaningful to incorporate environmental feedback into individuals' perceived costs. This extension introduces additional uncertainties into the behavior–disease interaction with co-evolving risk perceptions. In particular, fluctuations in perceived risks are likely to give rise to waves of vaccination confidence and demand, thereby leading to oscillatory ‘tragedy of the commons’ [27]. It is promising for future studies to study this coevolving perceived risks along with vaccination decisions [84].

The resurgence of vaccine-preventable disease outbreaks underscores the tradeoff between individual choices and collective responsibility [48]. Fundamentally, the vaccination dilemma is one example of real-world human cooperation problems, among many others [84]. We are interconnected, and so is our health [85]. Leveraging the power of social contagion to overcome vaccine hesitancy is key to avoiding the tragedy of the commons in biological contagions. Our work provides model-based insights into the presence and spread of vaccine related beliefs in social networks and their impact on health interventions aimed at improving vaccine compliance.

## Materials and methods

In view of the recurrent outbreaks of infections such as influenza and vaccination effectiveness, we use an evolutionary game-theoretical approach to study the seasonal vaccination game. A feedback loop exists between the vaccination decisions of individuals and their health outcomes. Disease incidence is influenced by vaccination behavior: a high level of vaccine coverage can reduce disease incidence to very low levels, which in turn lowers the perceived risk of infection and reduces the demand for vaccination [21]. As vaccination coverage drops, the number of susceptible individuals increases. When the proportion of susceptible, unvaccinated individuals exceeds a threshold (the complement of the herd immunity threshold), an outbreak of infectious disease can occur [1]. A surge in disease incidence can, in turn, convince individuals to start vaccinating again [29].

The vaccination dilemma game consists of two stages: a vaccination decision-making process at the beginning of the season, followed by the disease epidemic [20,32]. The proposed model is illustrated in Fig 1. During the first stage, individuals make a preemptive vaccination decision, choosing whether or not to get vaccinated based on social imitation of peers' choices, taking into account the costs of vaccination and infection. A vaccinated individual pays a cost  $C_v > 0$  while an unvaccinated individual incurs no direct upfront cost. This vaccination cost includes the time spent in receiving the vaccine, the perceived risks of vaccination, long-term health impacts, and other intangible factors. Denote by  $x$  the vaccination level at the end of stage 1.

During the epidemic season (stage 2), the epidemic is initiated by a number  $I_0$  of infected individuals and then spreads in the population (both well-mixed and lattice populations) according to the susceptible-infected-recovered-vaccinated (SIR-V) dynamics, with a per day per infected neighbor transmission rate  $\beta$  and a per day recovery rate  $\gamma$ . The basic reproduction number  $R_0$  is defined as  $R_0 = \beta/\gamma$ . Let vaccination effectiveness be  $\epsilon$ ; then the vaccinated population has a reduced transmission rate of  $\beta(1 - \epsilon)$ . The epidemic continues until there are no more newly infected individuals (which typically occurs in under 200 days for all cases simulated). The SIR-V epidemiological process is simulated by the Gillespie algorithm [32]. Once the epidemic ends, individuals can revisit their vaccination decisions for the next season.

The final epidemic size  $R(\infty)$  satisfies the transcendental equation:

$$x (\exp(-R_0 R(\infty)) - \exp(-(1 - \varepsilon)R_0 R(\infty))) - R(\infty) + 1 - \exp(-R_0 R(\infty)) = 0. \quad (5)$$

At the end of the season, the relative fraction of individuals infected ( $x_1$ ) among vaccinated individuals ( $x$ ) is

$$\frac{x_1}{x} = 1 - \exp(-(1 - \varepsilon)R_0 R(\infty)), \quad (6)$$

while the relative fraction of individuals infected ( $y_1$ ) among unvaccinated individuals ( $y$ ) is

$$\frac{y_1}{y} = 1 - \exp(-R_0 R(\infty)). \quad (7)$$

Infection incurs a cost  $C_I > 0$ , which includes expenses and time for health care as well as an elevated chance of mortality. Without loss of generality, we use the relative cost of vaccination  $c = C_v/C_I$ , while setting  $C_I = 1$ . Thus,  $0 \leq c = C_v \leq 1$ .

Individuals adjust their vaccination strategies by imitation, where successful individual's strategy is more likely to be followed [28,32,34,46]. An individual's imitation behavior is based on the current payoff difference between herself and a randomly selected neighbor. If the strategy of the selected neighbor has a higher payoff than her own strategy in the past epidemic season, then the individual imitates her neighbor's strategy with a higher probability. In this work, we use the Fermi function to determine the probability of imitation, accounting for bounded rationality in the decision process [76–78]. Specifically, Individual  $i$  randomly selects one neighbor  $j$  from her immediate neighborhood. The probability that individual  $i$  adopts individual  $j$ 's strategy is given by [76–78]:

$$W(S_j \rightarrow S_i) = \frac{1}{1 + \exp(-K(\pi_j - \pi_i))}, \quad (8)$$

where  $S_i$  means the vaccination choice for individual  $i$ : vaccination or non-vaccination.  $\pi_i$  denotes the current payoff of individual  $i$  at the end of current season. For  $i$ 's payoff, we have four possible outcomes:

- $\pi_i = -c$  if  $i$  is vaccinated and is not infected;
- $\pi_i = -c - 1$  if  $i$  is vaccinated and is infected;
- $\pi_i = -1$  if  $i$  is not vaccinated and is infected;
- $\pi_i = 0$  if  $i$  is not vaccinated and is not infected.

The parameter  $K$  is the intensity of selection, indicating how strongly individuals are responsive to payoff difference. This updating rule diverges from a perfect rationality model. Here we adopt  $K = 1$  for our simulations [32]. It is worth noting that individuals adjust their strategies based on the realized payoffs, not expected payoffs. In a population with low vaccination uptake, many non-vaccinators fall ill, but if individual  $i$  happens to choose one of the few successful free riders as a role model, then she will be more likely to imitate the free rider's strategy [32].

To obtain hysteresis loops with respect to varying relevant model parameters for our base model, we run a sequence of simulations with the model parameter varied in both increasing and decreasing order. For the first simulation in each sequence (corresponding to ascending or descending path of the identified hysteresis loop), we use the same initial state, which

consists of a fraction  $V_0$  of vaccinated individuals, randomly distributed throughout the population. Each two-stage iteration (vaccination strategy updating followed by an epidemic process) updates the proportion of vaccination strategies. For the stochastic epidemiological process, where the number of initial infection seeds is denoted as  $I_0$ , we use the Gillespie algorithm with a maximum duration of  $10^4$  to ensure the complete exhaustion of every infected individual. The equilibrium results are obtained by averaging over the last 1000 iterations from a total of 4000 iterations, and each data point reported in this paper is the result of an average of at least 100 independent realizations. For our extended models with vaccine beliefs, we use similar simulation procedures with the model parameters and initial conditions specified in the respective figure captions.

In our base model, we assume that individuals have homogenous perceptions of the cost of vaccination:  $c$  is the same for all individuals. In our extended model, we consider two groups of individuals holding vaccine-neutral versus vaccine-averse attitudes. For the latter, an additional vaccination cost  $\theta > 0$  is incurred. The perceived payoffs differ for these two groups as follows. For vaccine-neutral individuals, the payoffs are the same as those described above. For vaccine-averse individuals, we have:

- $\pi_i = -c - \theta$  if  $i$  is vaccinated and is not infected;
- $\pi_i = -c - \theta - 1$  if  $i$  is vaccinated and is infected;
- $\pi_i = -1$  if  $i$  is not vaccinated and is infected;
- $\pi_i = 0$  if  $i$  is not vaccinated and is not infected.

We investigate two scenarios for our extended model: one in which beliefs about vaccination, comprising vaccine-neutral and vaccine-averse attitudes, are fixed, and the other in which beliefs are contagious and concurrently spread in the same way as the imitation dynamics in vaccination decisions based on payoff differences. In this way, we explore systems in which both social contagion and epidemiological contagion are coupled, offering insight into the resulting disease-behavior system that exhibits dynamics not possible when the two subsystems are isolated from one another [23].

## Author contributions

**Conceptualization:** Feng Fu, Ran Zhuo, Xingru Chen.

**Data curation:** Feng Fu.

**Formal analysis:** Feng Fu, Ran Zhuo, Xingru Chen.

**Funding acquisition:** Feng Fu, Xingru Chen.

**Investigation:** Feng Fu, Ran Zhuo, Xingru Chen.

**Methodology:** Feng Fu, Ran Zhuo, Xingru Chen.

**Project administration:** Feng Fu, Xingru Chen.

**Resources:** Feng Fu.

**Software:** Feng Fu, Ran Zhuo.

**Supervision:** Feng Fu, Xingru Chen.

**Validation:** Feng Fu, Ran Zhuo, Xingru Chen.

**Visualization:** Feng Fu, Ran Zhuo, Xingru Chen.

**Writing – original draft:** Feng Fu, Ran Zhuo, Xingru Chen.

**Writing – review & editing:** Feng Fu, Xingru Chen.

## References

1. Anderson R. Infectious diseases of humans: Dynamics and control. Oxford University Press; 1991.
2. Pastor-Satorras R, Vespignani A. Immunization of complex networks. *Phys Rev E Stat Nonlin Soft Matter Phys.* 2002;65(3 Pt 2A):036104. <https://doi.org/10.1103/PhysRevE.65.036104> PMID: 11909162
3. Needham J. China and the origins of immunology. Centre of Asian Studies, University of Hong Kong; 1980.
4. Kabir KMA, Tanimoto J. Evolutionary game theory modelling to represent the behavioural dynamics of economic shutdowns and shield immunity in the COVID-19 pandemic. *R Soc Open Sci.* 2020;7(9):201095. <https://doi.org/10.1098/rsos.201095> PMID: 33047059
5. Siegler AJ, Luisi N, Hall EW, Bradley H, Sanchez T, Lopman BA, et al. Trajectory of COVID-19 vaccine hesitancy over time and association of initial vaccine hesitancy with subsequent vaccination. *JAMA Netw Open.* 2021;4(9):e2126882. <https://doi.org/10.1001/jamanetworkopen.2021.26882> PMID: 34559232
6. Oană I, Hâncean MG, Perc M, Lerner J, Mihăilă BE, Geantă M. Online media use and COVID-19 vaccination in real-world personal networks: Quantitative study. *J Med Internet Res.* 2024;26(e58257).
7. Wadman M, You J. The vaccine wars. 2017.
8. Jansen VAA, Stollenwerk N, Jensen HJ, Ramsay ME, Edmunds WJ, Rhodes CJ. Measles outbreaks in a population with declining vaccine uptake. *Science.* 2003;301(5634):804. <https://doi.org/10.1126/science.1086726> PMID: 12907792
9. Tediosi F, Villa S, Levison D, Ekeman E, Politi C. Leveraging global investments for polio eradication to strengthen health systems' resilience through transition. *Health Policy Plan.* 2024;39(Supplement\_1):i93–i106.
10. Asch DA, Baron J, Hershey JC, Kunreuther H, Meszaros J, Ritov I, et al. Omission bias and pertussis vaccination. *Med Decis Making.* 1994;14(2):118–23. <https://doi.org/10.1177/0272989X9401400204> PMID: 8028464
11. Smout E, Mellon D, Rae M. Whooping cough rises sharply in UK and Europe. 2024.
12. Majumder MS, Cohn EL, Mekar SR, Huston JE, Brownstein JS. Substandard vaccination compliance and the 2015 measles outbreak. *JAMA Pediatr.* 2015;169(5):494–5. <https://doi.org/10.1001/jamapediatrics.2015.0384> PMID: 25774618
13. Antona D, Lévy-Bruhl D, Baudon C, Freymuth F, Lamy M, Maine C. Measles elimination efforts and 2008–2011 outbreak, France. *Emerg Infectious Diseases.* 2013;19(3):357.
14. Gowda C, Dempsey AF. The rise (and fall?) of parental vaccine hesitancy. *Hum Vaccin Immunother.* 2013;9(8):1755–62. <https://doi.org/10.4161/hv.25085> PMID: 23744504
15. Sugerman DE, Barskey AE, Delea MG, Ortega-Sanchez IR, Bi D, Ralston KJ, et al. Measles outbreak in a highly vaccinated population, San Diego, 2008: Role of the intentionally undervaccinated. *Pediatrics.* 2010;125(4):747–55.
16. Burgess DC, Burgess MA, Leask J. The MMR vaccination and autism controversy in United Kingdom 1998–2005: Inevitable community outrage or a failure of risk communication? *Vaccine.* 2006;24(18):3921–8.
17. Miller E, Vurdien JE, White JM. The epidemiology of pertussis in England and Wales. *Commun Dis Rep CDR Rev.* 1992;2(13):R152–4. PMID: 1285134
18. Baker JP. The pertussis vaccine controversy in Great Britain, 1974–1986. *Vaccine.* 2003;21(25–26):4003–10.
19. Rohani P, Earn DJ, Grenfell BT. Pertussis transmission in England and Wales. *Lancet.* 2000;355(9214):1553–4. [https://doi.org/10.1016/s0140-6736\(05\)74604-3](https://doi.org/10.1016/s0140-6736(05)74604-3)
20. Chen X, Fu F. Imperfect vaccine and hysteresis. *Proc Biol Sci.* 2019;286(1894):20182406. <https://doi.org/10.1098/rspb.2018.2406> PMID: 30963866
21. Bauch C, d'Onofrio A, Manfredi P. Behavioral epidemiology of infectious diseases: An overview. Modeling the interplay between human behavior and the spread of infectious diseases; 2013. p. 1–19.
22. Galvani AP, Bauch CT, Anand M, Singer BH, Levin SA. Human-environment interactions in population and ecosystem health. *Proc Natl Acad Sci U S A.* 2016;113(51):14502–6. <https://doi.org/10.1073/pnas.1618138113> PMID: 27956616

23. Fu F, Christakis NA, Fowler JH. Dueling biological and social contagions. *Sci Rep*. 2017;7:43634. <https://doi.org/10.1038/srep43634> PMID: 28252663
24. Chen X, Fu F. Highly coordinated nationwide massive travel restrictions are central to effective mitigation and control of COVID-19 outbreaks in China. *Proc Math Phys Eng Sci*. 2022;478(2260):20220040. <https://doi.org/10.1098/rspa.2022.0040> PMID: 35450022
25. Fügenschuh M, Fu F. Overcoming vaccine hesitancy by multiplex social network targeting: An analysis of targeting algorithms and implications. *Appl Netw Sci*. 2023;8(1):67. <https://doi.org/10.1007/s41109-023-00595-y> PMID: 37745797
26. Bauch CT, Galvani AP. Epidemiology. Social factors in epidemiology. *Science*. 2013;342(6154):47–9. <https://doi.org/10.1126/science.1244492> PMID: 24092718
27. Glaubitz A, Fu F. Social dilemma of nonpharmaceutical interventions: Determinants of dynamic compliance and behavioral shifts. *Proc Natl Acad Sci U S A*. 2024;121(50):e2407308121. <https://doi.org/10.1073/pnas.2407308121> PMID: 39630869
28. Bauch CT. Imitation dynamics predict vaccinating behaviour. *Proc Biol Sci*. 2005;272(1573):1669–75. <https://doi.org/10.1098/rspb.2005.3153> PMID: 16087421
29. Reluga TC, Bauch CT, Galvani AP. Evolving public perceptions and stability in vaccine uptake. *Math Biosci*. 2006;204(2):185–98. <https://doi.org/10.1016/j.mbs.2006.08.015> PMID: 17056073
30. Vardavas R, Breban R, Blower S. Can influenza epidemics be prevented by voluntary vaccination? *PLoS Comput Biol*. 2007;3(5):e85. <https://doi.org/10.1371/journal.pcbi.0030085> PMID: 17480117
31. Wu B, Fu F, Wang L. Imperfect vaccine aggravates the long-standing dilemma of voluntary vaccination. *PLoS One*. 2011;6(6):e20577. <https://doi.org/10.1371/journal.pone.0020577> PMID: 21687680
32. Fu F, Rosenbloom DI, Wang L, Nowak MA. Imitation dynamics of vaccination behaviour on social networks. *Proc Biol Sci*. 2011;278(1702):42–9. <https://doi.org/10.1098/rspb.2010.1107> PMID: 20667876
33. Zhang H, Fu F, Zhang W, Wang B. Rational behavior is a 'double-edged sword' when considering voluntary vaccination. *Phys A: Stat Mech Its Applic*. 2012;391(20):4807–15. <https://doi.org/10.1016/j.physa.2012.05.009>
34. Ndeffo Mbah ML, Liu J, Bauch CT, Tekel YI, Medlock J, Meyers LA, et al. The impact of imitation on vaccination behavior in social contact networks. *PLoS Comput Biol*. 2012;8(4):e1002469. <https://doi.org/10.1371/journal.pcbi.1002469> PMID: 22511859
35. Shim E, Chapman GB, Townsend JP, Galvani AP. The influence of altruism on influenza vaccination decisions. *J R Soc Interface*. 2012;9(74):2234–43. <https://doi.org/10.1098/rsif.2012.0115> PMID: 22496100
36. Cardillo A, Reyes-Suárez C, Naranjo F, Gómez-Gardeñes J. Evolutionary vaccination dilemma in complex networks. *Phys Rev E Stat Nonlin Soft Matter Phys*. 2013;88(3):032803. <https://doi.org/10.1103/PhysRevE.88.032803> PMID: 24125308
37. Wu Z-X, Zhang H-F. Peer pressure is a double-edged sword in vaccination dynamics. *EPL*. 2013;104(1):10002. <https://doi.org/10.1209/0295-5075/104/10002>
38. Oraby T, Thampi V, Bauch CT. The influence of social norms on the dynamics of vaccinating behaviour for paediatric infectious diseases. *Proc Biol Sci*. 2014;281(1780):20133172. <https://doi.org/10.1098/rspb.2013.3172> PMID: 24523276
39. Zhang H-F, Wu Z-X, Tang M, Lai Y-C. Effects of behavioral response and vaccination policy on epidemic spreading—An approach based on evolutionary-game dynamics. *Sci Rep*. 2014;4:5666. <https://doi.org/10.1038/srep05666> PMID: 25011424
40. Wang Z, Bauch CT, Bhattacharyya S, d'Onofrio A, Manfredi P, Perc M. Statistical physics of vaccination. *Physics Reports*. 2016;664:1–113.
41. Khan MM-U-R, Arefin MR, Tanimoto J. Time delay of the appearance of a new strain can affect vaccination behavior and disease dynamics: An evolutionary explanation. *Infect Dis Model*. 2023;8(3):656–71. <https://doi.org/10.1016/j.idm.2023.06.001> PMID: 37346475
42. de Miguel-Arribas A, Aleta A, Moreno Y. Interplay of epidemic spreading and vaccine rates under complex social contagion; 2024. <https://doi.org/arXiv:241211766>
43. Lu Y, Wang Y, Liu Y, Chen J, Shi L, Park J. Reinforcement learning relieves the vaccination dilemma. *Chaos*. 2023;33(7):073110. <https://doi.org/10.1063/5.0153951> PMID: 37408157
44. Glaubitz A, Fu F. Population heterogeneity in vaccine coverage impacts epidemic thresholds and bifurcation dynamics. *Heliyon*. 2023;9(9):e19094. <https://doi.org/10.1016/j.heliyon.2023.e19094> PMID: 37810104
45. He Z, Bauch CT. Effect of homophily on coupled behavior-disease dynamics near a tipping point. *Math Biosci*. 2024;376:109264. <https://doi.org/10.1016/j.mbs.2024.109264> PMID: 39097225

46. Bauch CT, Bhattacharyya S. Evolutionary game theory and social learning can determine how vaccine scares unfold. *PLoS Comput Biol*. 2012;8(4):e1002452. <https://doi.org/10.1371/journal.pcbi.1002452> PMID: 22496631
47. Wang W, Liu Q-H, Cai S-M, Tang M, Braunstein LA, Stanley HE. Suppressing disease spreading by using information diffusion on multiplex networks. *Sci Rep*. 2016;6:29259. <https://doi.org/10.1038/srep29259> PMID: 27380881
48. Fine PE, Clarkson JA. Individual versus public priorities in the determination of optimal vaccination policies. *Am J Epidemiol*. 1986;124(6):1012–20. <https://doi.org/10.1093/oxfordjournals.aje.a114471> PMID: 3096132
49. Bauch CT, Galvani AP, Earn DJD. Group interest versus self-interest in smallpox vaccination policy. *Proc Natl Acad Sci U S A*. 2003;100(18):10564–7. <https://doi.org/10.1073/pnas.1731324100> PMID: 12920181
50. Bauch CT, Earn DJD. Vaccination and the theory of games. *Proc Natl Acad Sci U S A*. 2004;101(36):13391–4. <https://doi.org/10.1073/pnas.0403823101> PMID: 15329411
51. Galvani AP, Reluga TC, Chapman GB. Long-standing influenza vaccination policy is in accord with individual self-interest but not with the utilitarian optimum. *Proc Natl Acad Sci U S A*. 2007;104(13):5692–7. <https://doi.org/10.1073/pnas.0606774104> PMID: 17369367
52. Cornforth DM, Reluga TC, Shim E, Bauch CT, Galvani AP, Meyers LA. Erratic flu vaccination emerges from short-sighted behavior in contact networks. *PLoS Comput Biol*. 2011;7(1):e1001062. <https://doi.org/10.1371/journal.pcbi.1001062> PMID: 21298083
53. Hardin G. The tragedy of the commons. *Science*. 1968;162(3859):1243–8.
54. Shen C, Guo H, Hu S, Shi L, Wang Z, Tanimoto J. How committed individuals shape social dynamics: A survey on coordination games and social dilemma games. *EPL*. 2023;144(1):11002. <https://doi.org/10.1209/0295-5075/acfb34>
55. Perisic A, Bauch CT. Social contact networks and disease eradicability under voluntary vaccination. *PLoS Comput Biol*. 2009;5(2):e1000280. <https://doi.org/10.1371/journal.pcbi.1000280> PMID: 19197342
56. Breban R, Vardavas R, Blower S. Mean-field analysis of an inductive reasoning game: Application to influenza vaccination. *Phys Rev E Stat Nonlin Soft Matter Phys*. 2007;76(3 Pt 1):031127. <https://doi.org/10.1103/PhysRevE.76.031127> PMID: 17930219
57. Basu S, Chapman GB, Galvani AP. Integrating epidemiology, psychology, and economics to achieve HPV vaccination targets. *Proc Natl Acad Sci U S A*. 2008;105(48):19018–23. <https://doi.org/10.1073/pnas.0808114105> PMID: 19015536
58. Larson HJ, Jarrett C, Eckersberger E, Smith DM, Paterson P. Understanding vaccine hesitancy around vaccines and vaccination from a global perspective: A systematic review of published literature, 2007–2012. *Vaccine*. 2014;32(19):2150–9.
59. Omer SB, Salmon DA, Orenstein WA, deHart MP, Halsey N. Vaccine refusal, mandatory immunization, and the risks of vaccine-preventable diseases. *N Engl J Med*. 2009;360(19):1981–8. <https://doi.org/10.1056/NEJMsa0806477> PMID: 19420367
60. Chen RT. Vaccine risks: Real, perceived and unknown. *Vaccine*. 1999;17 Suppl 3:S41–6. [https://doi.org/10.1016/s0264-410x\(99\)00292-3](https://doi.org/10.1016/s0264-410x(99)00292-3) PMID: 10559533
61. Amanna I, Slifka MK. Public fear of vaccination: Separating fact from fiction. *Viral Immunol*. 2005;18(2):307–15. <https://doi.org/10.1089/vim.2005.18.307> PMID: 16035942
62. Hughes V. News feature: A shot of fear. *Nat Med*. 2006;12(11):1228–9. <https://doi.org/10.1038/nm1106-1228> PMID: 17088878
63. Coelho FC, Codeço CT. Dynamic modeling of vaccinating behavior as a function of individual beliefs. *PLoS Comput Biol*. 2009;5(7):e1000425. <https://doi.org/10.1371/journal.pcbi.1000425> PMID: 19593365
64. Hu S, Liu Y, Wu B. Evolutionary dynamics of voluntary vaccination for imperfect multi-efficacy vaccines. In: *Proceedings A*. vol. 480. The Royal Society; 2024. p. 20230743.
65. Salathé M, Bonhoeffer S. The effect of opinion clustering on disease outbreaks. *J R Soc Interface*. 2008;5(29):1505–8. <https://doi.org/10.1098/rsif.2008.0271> PMID: 18713723
66. Funk S, Salathé M, Jansen VAA. Modelling the influence of human behaviour on the spread of infectious diseases: A review. *J R Soc Interface*. 2010;7(50):1247–56. <https://doi.org/10.1098/rsif.2010.0142> PMID: 20504800
67. Funk S, Gilad E, Watkins C, Jansen VAA. The spread of awareness and its impact on epidemic outbreaks. *Proc Natl Acad Sci U S A*. 2009;106(16):6872–7. <https://doi.org/10.1073/pnas.0810762106> PMID: 19332788
68. Eames KTD. Networks of influence and infection: Parental choices and childhood disease. *J R Soc Interface*. 2009;6(38):811–4. <https://doi.org/10.1098/rsif.2009.0085> PMID: 19447820

69. Saad-Roy CM, Traulsen A. Dynamics in a behavioral-epidemiological model for individual adherence to a nonpharmaceutical intervention. *Proc Natl Acad Sci U S A*. 2023;120(44):e2311584120. <https://doi.org/10.1073/pnas.2311584120> PMID: 37889930
70. Shi S, Wang Z, Chen X, Fu F. Determinants of successful disease control through voluntary quarantine dynamics on social networks. *Math Biosci*. 2024;377:109288. <https://doi.org/10.1016/j.mbs.2024.109288> PMID: 39222905
71. Espinoza B, Saad-Roy CM, Grenfell BT, Levin SA, Marathe M. Adaptive human behaviour modulates the impact of immune life history and vaccination on long-term epidemic dynamics. *Proc Biol Sci*. 2024;291(2033):20241772. <https://doi.org/10.1098/rspb.2024.1772> PMID: 39471851
72. Saad-Roy CM, Morris SE, Boots M, Baker RE, Lewis BL, Farrar J, et al. Impact of waning immunity against SARS-CoV-2 severity exacerbated by vaccine hesitancy. *PLoS Comput Biol*. 2024;20(8):e1012211. <https://doi.org/10.1371/journal.pcbi.1012211> PMID: 39102402
73. Salathé M, Khandelwal S. Assessing vaccination sentiments with online social media: Implications for infectious disease dynamics and control. *PLoS Comput Biol*. 2011;7(10):e1002199. <https://doi.org/10.1371/journal.pcbi.1002199> PMID: 22022249
74. Gandon S, Mackinnon MJ, Nee S, Read AF. Imperfect vaccines and the evolution of pathogen virulence. *Nature*. 2001;414(6865):751–6. <https://doi.org/10.1038/414751a> PMID: 11742400
75. Traulsen A, Pacheco JM, Nowak MA. Pairwise comparison and selection temperature in evolutionary game dynamics. *J Theor Biol*. 2007;246(3):522–9. <https://doi.org/10.1016/j.jtbi.2007.01.002> PMID: 17292423
76. Blume LE. The statistical mechanics of strategic interaction. *Games Econ Behav*. 1993;5(3):387–424. <https://doi.org/10.1006/game.1993.1023>
77. Szabó G, Tóke C. Evolutionary prisoner's dilemma game on a square lattice. *Phys Rev E*. 1998;58(1):69–73. <https://doi.org/10.1103/physreve.58.69>
78. Traulsen A, Semmann D, Sommerfeld RD, Krambeck H-J, Milinski M. Human strategy updating in evolutionary games. *Proc Natl Acad Sci U S A*. 2010;107(7):2962–6. <https://doi.org/10.1073/pnas.0912515107> PMID: 20142470
79. Americans' Largely Positive Views of Childhood Vaccines Hold Steady. <https://www.pewresearch.org/science/2023/05/16/americans-largely-positive-views-of-childhood-vaccines-hold-steady/>.
80. Anders JF, Jacobson RM, Poland GA, Jacobsen SJ, Wollan PC. Secondary failure rates of measles vaccines: A metaanalysis of published studies. *Pediatr Infect Dis J*. 1996;15(1):62–6. <https://doi.org/10.1097/00006454-199601000-00014> PMID: 8684879
81. Wagner CE, Saad-Roy CM, Grenfell BT. Modelling vaccination strategies for COVID-19. *Nat Rev Immunol*. 2022;22(3):139–41. <https://doi.org/10.1038/s41577-022-00687-3> PMID: 35145245
82. Saad-Roy CM, White A, Boots M. The evolution of post-infection mortality. *Proc Biol Sci*. 2024;291(2035):20241854. <https://doi.org/10.1098/rspb.2024.1854> PMID: 39561798
83. Chang HCH, Fu F. The niche connectivity paradox: Multichrome contagions overcome vaccine hesitancy more effectively than monochromacy; 2025. <https://doi.org/arXiv:250509605>
84. Wang X, Fu F. Eco-evolutionary dynamics with environmental feedback: Cooperation in a changing world. *EPL*. 2020;132(1):10001. <https://doi.org/10.1209/0295-5075/132/10001>
85. Smith KP, Christakis NA. Social networks and health. *Annu Rev Sociol*. 2008;34(1):405–29.