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Imitation dynamics of vaccination behaviour on social networks

Feng Fu^{a,b,*}, Daniel I. Rosenbloom^{a,*}, Long Wang^b, Martin A. Nowak^a

^a Program for Evolutionary Dynamics, Department of Organismic and Evolutionary Biology, Department of Mathematics, Harvard University, Cambridge, Massachusetts 02138, USA

^b Center for Systems and Control, State Key Laboratory for Turbulence and Complex Systems, College of Engineering, Peking University, Beijing 100871, China

* These authors contributed equally

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Corresponding author:

Martin A. Nowak

Program for Evolutionary Dynamics, Harvard University

One Brattle Square, Suite 6

Cambridge, MA 02138 USA

Email: martin.nowak@harvard.edu

Tel: +1 (617) 496 4683

Fax: +1 (617) 496 4629

Abstract: The problem of achieving widespread immunity to infectious diseases by voluntary vaccination is often presented as a public-goods dilemma, as an individual's vaccination contributes to herd immunity, protecting those who forgo vaccination. The temptation to free-ride brings the equilibrium vaccination level below the social optimum. Here we present an evolutionary game-theoretic approach to this problem, exploring the roles of individual imitation behaviour and population structure in vaccination. To this end, we integrate an epidemiological process into a simple agent-based model of adaptive learning, where individuals use anecdotal evidence to estimate costs and benefits of vaccination. In our simulations, we focus on parameter values that are realistic for a flu-like infection. Paradoxically, as agents become more adept at imitating successful strategies, the equilibrium level of vaccination falls below the rational individual optimum. In structured populations, the picture is only somewhat more optimistic: vaccination is widespread over a range of low vaccination costs, but coverage plummets after cost exceeds a critical threshold. This result suggests parallels to historical scenarios in which vaccination coverage provided herd immunity for some time, but then rapidly dropped. Our work sheds light on how imitation of peers shapes individual vaccination choices in social networks.

Key words: vaccination dilemma, peer influence, epidemiology, evolutionary dynamics, mathematical biology

1 I. INTRODUCTION

2 Preemptive vaccination is a fundamental strategy for controlling infectious diseases (CDC
3 2009). While there is vigorous debate about the civil liberties implications of mandatory versus
4 voluntary vaccination policies (Colgrave 2006), mounting evidence shows that voluntary vaccina-
5 tion plans fail to protect populations adequately (Basu et al. 2008, Bauch et al. 2003, Bauch &
6 Earn 2004, Bauch 2005, Breban et al. 2007, Cojocaru 2008, Fine & Clarkson 1986, Galvani et
7 al. 2007, Reluga et al. 2006, van Boven et al. 2008, Vardavas et al. 2007). A recent example of
8 this failure is the sharp decline in take-up of the combined measles-mumps-rubella vaccination in
9 Britain soon after administering it to children was made voluntary (Jansen et al. 2003). Because of
10 declining familiarity with the disease and rising fears of vaccine complications, parents hoped to
11 avoid the alleged vaccination health risk to their own children while implicitly relying on enough
12 other children getting vaccinated to provide herd immunity. The “public good” created by herd
13 immunity gives rise to an enduring social dilemma of voluntary vaccination.

14 Classical game theory predicts that, when individuals act in their own interests with perfect
15 knowledge of their infection risk, their vaccination decisions converge toward a Nash equilibrium,
16 at which no individuals could be better off by unilaterally changing to a different strategy (Bauch et
17 al. 2003, Bauch & Earn 2004). Although this equilibrium is the result of each individual following
18 her self-interest, it may lead to suboptimal vaccination coverage for the community (Galvani et al.
19 2007). The collective result of vaccination decisions determines the level of population immunity
20 and thus the severity of an epidemic strain. With increasing levels of vaccination coverage in
21 the community, even the individuals who are unvaccinated are less likely to become infected;
22 therefore, they have less incentive to get the vaccine. This scenario naturally leads to the “free
23 riding” problem that is commonly observed in public goods studies (Hardin 1968).

24 Previous studies of vaccinating dynamics have typically combined a game-theoretic model
25 assuming full rationality and complete information with a model of disease transmission in ei-
26 ther homogeneously mixed populations (Bauch et al. 2003, Bauch & Earn 2004) or random net-
27 works (Perisic & Bauch 2008). In studies where the assumption of rationality is relaxed, determin-
28 istic evolutionary dynamics still recover equilibrium states equivalent to those predicted by models
29 of rational agents (Bauch 2005). It is worth noting that aggregate population models have been pa-
30 rameterized with empirical data to quantitatively predict vaccinating behavior in some cases (Basu
31 et al. 2008, Bauch 2005, Galvani et al. 2007). Here we extend this previous work by accounting

32 for decision-makers' social networks and their use of anecdotal information in making vaccina-
33 tion choices. Individuals have incomplete information and tend to rely on salient anecdotes from
34 friends and the media in order to form opinions of disease risk and prevention (Johnson et al. 1983,
35 Palekar et al. 2008, Tversky & Kahneman 1973). The rise to prominence in the British media of
36 isolated cases linking the pertussis vaccine and brain damage triggered a sharp decline in coverage
37 in the late 1970s, demonstrating the power of the anecdote (Bauch 2005, Nicoll et al. 1998). Apart
38 from these prominent cases, each person can encounter different anecdotal evidence, depending
39 on her social network (Eames 2009, Perisic & Bauch 2008). Illness of a close friend can impact
40 one's perception of infection risk and the importance of prevention in far more powerful ways than
41 media reports can (Palekar et al. 2008).

42 Motivated by the above considerations, we propose a simple agent-based model in the spirit
43 of evolutionary game dynamics (Maynard-Smith 1982, Nowak & Sigmund 2004, Nowak 2006a)
44 to study the voluntary vaccination dilemma. In order to make precise predictions, we couple the
45 vaccination dynamics with an epidemiological model, in particular the *SIR* model, which tracks
46 populations of susceptible, infected, and resistant/vaccinated individuals over time, within a single
47 season or epidemic. Such models have been used, for example, to design clinical trials of vaccines
48 or to predict whether a vaccination program will halt an epidemic before it spreads to much of the
49 population (Diekmann & Heesterbeek 2000, Levin et al. 1999).

50 Our model captures the strategic interaction between vaccinating and free-riding individuals
51 in the following way. Individuals decide whether to vaccinate during a vaccination campaign,
52 before the seasonal epidemic begins. The epidemiological model then determines whether each
53 susceptible (unvaccinated) individual becomes infected at some point during the season. Once the
54 epidemic ends, individuals can revise their vaccination decision for the next season. Such a model
55 is most appropriate for describing infections such as influenza. Flu vaccines are typically available
56 prior to a predicted outbreak and are effective for only one season due to mutation of pathogens
57 and waning immunity (Breban et al. 2007, Vardavas et al. 2007).

58 **II. MODEL & METHODS**

59 Consider a well-mixed population of individuals with a voluntary vaccination option. We model
60 the vaccination dynamics as a two-stage game (as illustrated in figure 1). The first stage is a public
61 vaccination campaign, which occurs before any infection. At this stage, each individual decides

62 whether or not to vaccinate. Vaccination incurs a cost, V , to the vaccinated individual. For simplic-
63 ity, here we assume that vaccination grants perfect immunity from the seasonal infectious disease.
64 (To account for imperfect vaccination, one may rescale the cost of vaccination by its effectiveness
65 and calculate infection risk based on the effective proportion of the population that is vaccinated.)
66 The total cost of vaccination includes the immediate monetary cost, the opportunity cost of time
67 spent to get the vaccine, and any perceived or actual adverse health effects. In the second stage,
68 the epidemic strain infects an initial number of individuals I_0 and then spreads according to SIR
69 dynamics, with per-day transmission rate r and recovery rate g (see the electronic supplemen-
70 tary material, ESM, for model details). The epidemic continues until there are no more newly
71 infected individuals (which occurred in under 200 days for all cases simulated). The final size
72 equation (Diekmann & Heesterbeek 2000) gives the infection risk for an infinite population (see
73 ESM for derivations):

$$w(x) = \frac{R(\infty)}{1-x} = 1 - e^{-R_0 R(\infty)}, \quad (1)$$

74 where $R(\infty)$ is the final size of the epidemic (fraction that have been infected at some point in the
75 season), which satisfies $R(\infty) = (1-x)(1 - e^{-R_0 R(\infty)})$; R_0 is the basic reproduction ratio; and x is
76 the fraction of vaccinated individuals.

77 The infection cost I includes health care expenses, lost productivity, and the possibility of pain
78 or mortality. After the epidemic, the individuals with the highest payoffs are those who declined
79 vaccination but avoided infection. We call these lucky individuals successful free-riders, as they
80 benefit from others' vaccination efforts. The game dynamics remain unchanged if we rescale the
81 payoffs by defining the relative cost of vaccination $c = \frac{V}{I}$ ($0 < c < 1$). The values of c appropriate
82 for modeling a particular disease can be estimated from surveys of health opinions, behaviors, and
83 outcomes, as done by, e.g., Galvani et al. (2007), but in general vaccination cost should be low
84 relative to the cost of infection. The Nash equilibrium of this game can be solved by setting the
85 expected cost of vaccination equal to that of non-vaccination, which implies the mixed strategy

$$x^* = 1 + \frac{\ln(1-c)}{cR_0}. \quad (2)$$

86 This level of vaccination uptake falls short of the social optimum $x_h = 1 - \frac{1}{R_0}$, the level which
87 achieves herd immunity (near-elimination of the risk of contacting an infectious individual) and
88 thereby minimizes the sum of all individuals' costs related to both vaccination and infection (see

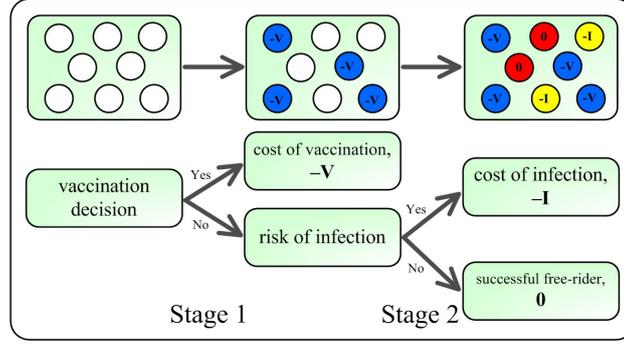


FIG. 1: Inserted here.

89 ESM). The misalignment between individual and group interests leads to a social dilemma.

90 Here, we relax the assumption of rationality and study this vaccination dilemma from an evolu-
 91 tionary perspective. Each season, an individual adopts a pure strategy, which determines whether
 92 or not she vaccinates. At the end of the season, each individual decides whether to change her
 93 strategy for the next season, depending on her current payoff. Specifically, individual i randomly
 94 chooses individual j from the population as role model. The strategy of a role model with higher
 95 payoff is more likely to be imitated. We suppose that the probability that individual i adopts indi-
 96 vidual j 's strategy is given by the Fermi function (Blume 1993, Szabó & Tóke 1998, Traulsen et
 97 al. 2007; 2010)

$$f(P_j - P_i) = \frac{1}{1 + \exp[-\beta(P_j - P_i)]}, \quad (3)$$

98 where β denotes the strength of selection ($0 < \beta < \infty$).

99 This updating dynamic diverges from a fully rational model in two ways. First, individuals ad-
 100 just their strategies retrospectively, in response only to the observed payoff outcomes and not the
 101 expected payoffs of strategies. In a population with low vaccination uptake, many non-vaccinators
 102 fall ill, but if individual i happens to choose one of the few successful free-riders as a role model,
 103 then she will be more likely to imitate the free-rider's strategy. Second, the strength of selection
 104 parameter introduces a stochastic element to the model: for small β (weak selection), individuals
 105 are less responsive to payoff differences, and an individual with a high payoff may adopt the strat-
 106 egy of a less successful role model. Large values of β (strong selection) diminish this stochastic
 107 effect, and individuals reliably switch to (or keep) the strategy with the higher observed payoff,
 108 even if the payoff difference is small. Previous work using the same update dynamic has char-
 109 acterized agents with high β as being more rational (Szabó & Tóke 1998). This characterization

110 is not appropriate in our context, as higher β only increases an agent's sensitivity to the (perhaps
111 unrepresentative) observed payoff, not the expected payoff.

112 The model presented here can be conveniently extended to structured populations by restricting
113 the neighborhood of individuals whom one can infect or imitate. In addition to the well-mixed
114 case, we simulated populations structured as square lattices, Erdős-Rényi random graphs (Erdős
115 & Rényi 1959), and Barabási-Albert scale-free networks (Barabási & Albert 1999) (see ESM).
116 The initial state consists of equal fractions vaccinators and unvaccinators, randomly distributed
117 throughout the population. Each two-stage iteration (vaccination strategy updating followed by
118 an epidemic process) updates the frequencies of each strategy. Since we are interested primarily
119 in the effect of population structure on vaccination coverage (rather than on infection risk), we
120 calibrated epidemic parameters to ensure that the infection risk in an unvaccinated population is
121 equal across all population structures (Perisic & Bauch 2008) (see ESM). Each simulation was run
122 for 3,000 iterations. The long run equilibrium results shown in figures 2–4 represent the average
123 of frequencies over the last 1,000 iterations in 100 independent simulations. We present results of
124 simulations that use population sizes between $N = 500$ and $N = 10,000$; overall results are robust
125 to varying population size for N as small as 200.

126 III. RESULTS

127 In the vaccination game, if all of one's neighbors adopt one strategy, then it is advantageous
128 to adopt the opposite strategy. We therefore always find persistent polymorphisms of vaccinated
129 and unvaccinated individuals for intermediate values of c . Figure 2 plots both the equilibrium
130 frequency of (a) vaccinated and (b) infected individuals for different values of c and β in the well-
131 mixed imitation dynamics. We find qualitative agreement between stochastic simulations and an
132 analytical prediction that uses both the equation for infection risk (1) and an infinite-population
133 approximation of the imitation dynamics (described in ESM).

134 For weak selection ($\beta = 1$ in figure 2), the imitation dynamics approximate the rational equilib-
135 rium x^* given in equation (2). One can understand this observation analytically by noting that the
136 strategy update equation (3) is roughly linear for small β . First-order approximation of the imita-
137 tion dynamics closely approximates the replicator dynamics (Hofbauer & Sigmund 1998, Schuster
138 & Sigmund 1983, Taylor & Jonker 1978), which in this game converge to the unique evolutionarily
139 stable strategy—the Nash equilibrium (see ESM). As vaccination falls with increasing c , the final

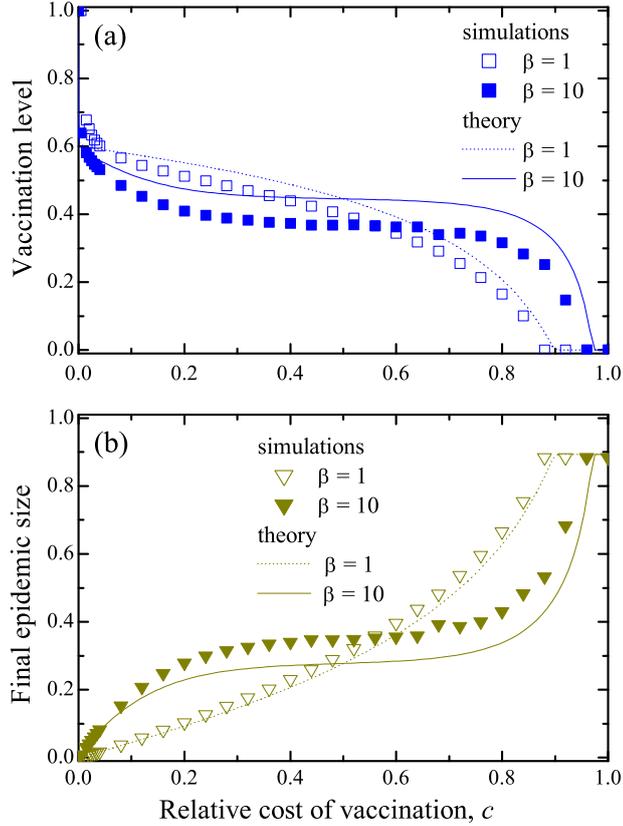


FIG. 2: Inserted Here.

140 size of the epidemic grows. Above a high cost threshold $c_H \approx 0.893$, no one chooses vaccination
 141 and the epidemic reaches its maximum size.

142 Strong selection in the imitation dynamics (represented by $\beta = 10$ in figure 2) can decrease vac-
 143 cination uptake below the level predicted by the rational equilibrium. In other words, individuals
 144 who carefully attend to peers' health outcomes and reliably copy the behavior of successful peers
 145 will end up attempting to free-ride more than they rationally "ought" to. If, for example, infection
 146 is twelve times as costly as vaccination (namely, $c = 0.08$, a reasonable assumption for influenza,
 147 see ESM), then strong selection in our model lowers vaccination coverage by 8 percentage points
 148 versus weak selection (figure 2a), which increases the epidemic size from 4% of the population to
 149 15% of the population (figure 2b). With increasing cost of vaccination, the equilibrium vaccina-
 150 tion coverage follows a rotated "S" curve, dropping rapidly (slope $\approx -\frac{\beta}{2}$) from the herd immunity
 151 threshold at low values of c , reaching a plateau near $1 - \frac{2\ln 2}{R_0}$ for intermediate values of c , and
 152 then dropping rapidly to zero as c grows large. The threshold c_H increases with selection strength
 153 (figure 2a).

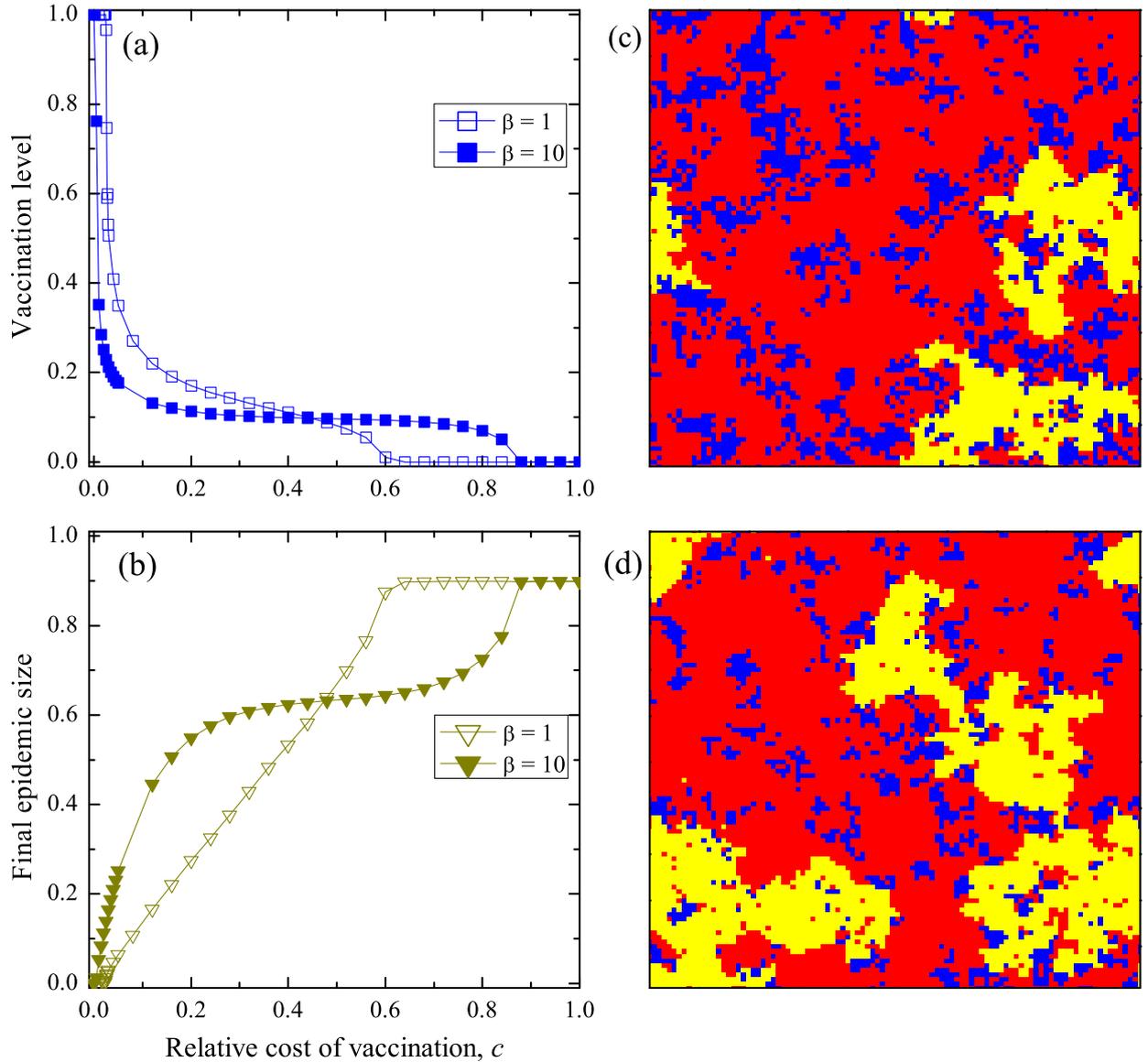


FIG. 3: Inserted Here.

154 Results are qualitatively similar for any basic reproduction ratio $R_0 > 1$ of the infection. Fig-
 155 ures S5 and S6 in the ESM compare the cases $R_0 = 2.5$ and $R_0 = 6$. The higher value increases
 156 infection risk, making the population respond with increased vaccination uptake. Increasing R_0
 157 also raises the threshold c_H .

158 Restricting interaction to local neighborhoods partly ameliorates the free-riding problem, but
 159 introduces greater sensitivity to the cost parameter c (figure 3). We consider a population of indi-
 160 viduals arranged on a square lattice where each individual has four immediately adjacent neigh-
 161 bors. While the vaccination coverage in well-mixed populations drops from herd immunity levels

162 as soon as c increases above zero, restricted spatial interaction promotes near-universal coverage
163 at a range of positive c , preventing the epidemic. To give a simple operational definition, we say
164 that vaccination “prevents the epidemic” in a structured population if the average final epidemic
165 size is less than twice the size of the initial inoculum. Define as c_L the critical vaccination cost
166 below which the epidemic is prevented. For weak selection on the lattice ($\beta = 1$ in figure 3), we get
167 $c_L \approx 0.022$. Above this threshold, the vaccination level drops precipitously, causing an epidemic
168 that is even larger than in the well-mixed case.

169 At higher selection strength, the threshold c_L is lower, and vaccination coverage is even more
170 sensitive to costs rising above c_L (figure 3a). The high cost threshold c_H rises with selection
171 strength, meaning that the transitional region between c_L and c_H , where vaccinated and unvacci-
172 nated individuals coexist, widens with larger β . Holding c constant at a value above c_L , increasing
173 the strength of selection leads to more free-riding attempts, breaking apart clusters of vaccinators,
174 thus allowing a larger epidemic to occur (figure 3c versus 3d).

175 Most actual populations are heterogeneous in the sense that different individuals may have
176 different numbers of neighbors (i.e., degree) (Barabási & Albert 1999). To account for this feature,
177 we consider vaccination dynamics on Erdős-Rényi random graphs, which have moderate degree
178 heterogeneity; on scale-free networks, which have an even more variable degree distribution, our
179 results are similar (see ESM).

180 Higher vaccination coverage is typically required to achieve herd immunity in populations with
181 greater degree heterogeneity (Pastor-Satorras & Vespignani 2002) (see also figures S2-S4 in ESM).
182 This increased vulnerability to epidemic attacks reduces the temptation to free-ride, actually mak-
183 ing it easier for a population of selfish imitators to achieve the high vaccination threshold required
184 for herd immunity. The threshold cost c_L therefore increases versus the lattice case. Vaccina-
185 tion coverage drops after cost exceeds this threshold, although the effect is not quite as extreme
186 as in lattice populations (figures 4a and 4b). Similarly to lattice populations, increased selection
187 strength increases the size of the intermediate region between c_L and c_H .

188 Degree heterogeneity triggers a broad spectrum of individual vaccinating behavior. Specifi-
189 cally, an individual’s vaccination strategy is now influenced by her role in the population, and
190 “hubs” who have many neighbors are most likely to choose to be vaccinated, as they are at great-
191 est risk of infection (figures 4c and 4d). Hubs that do manage to free-ride successfully become
192 victims of their own success, as their vaccinated neighbors of smaller degree are likely to imitate
193 them and switch strategies, potentially infecting the hubs in the following season.

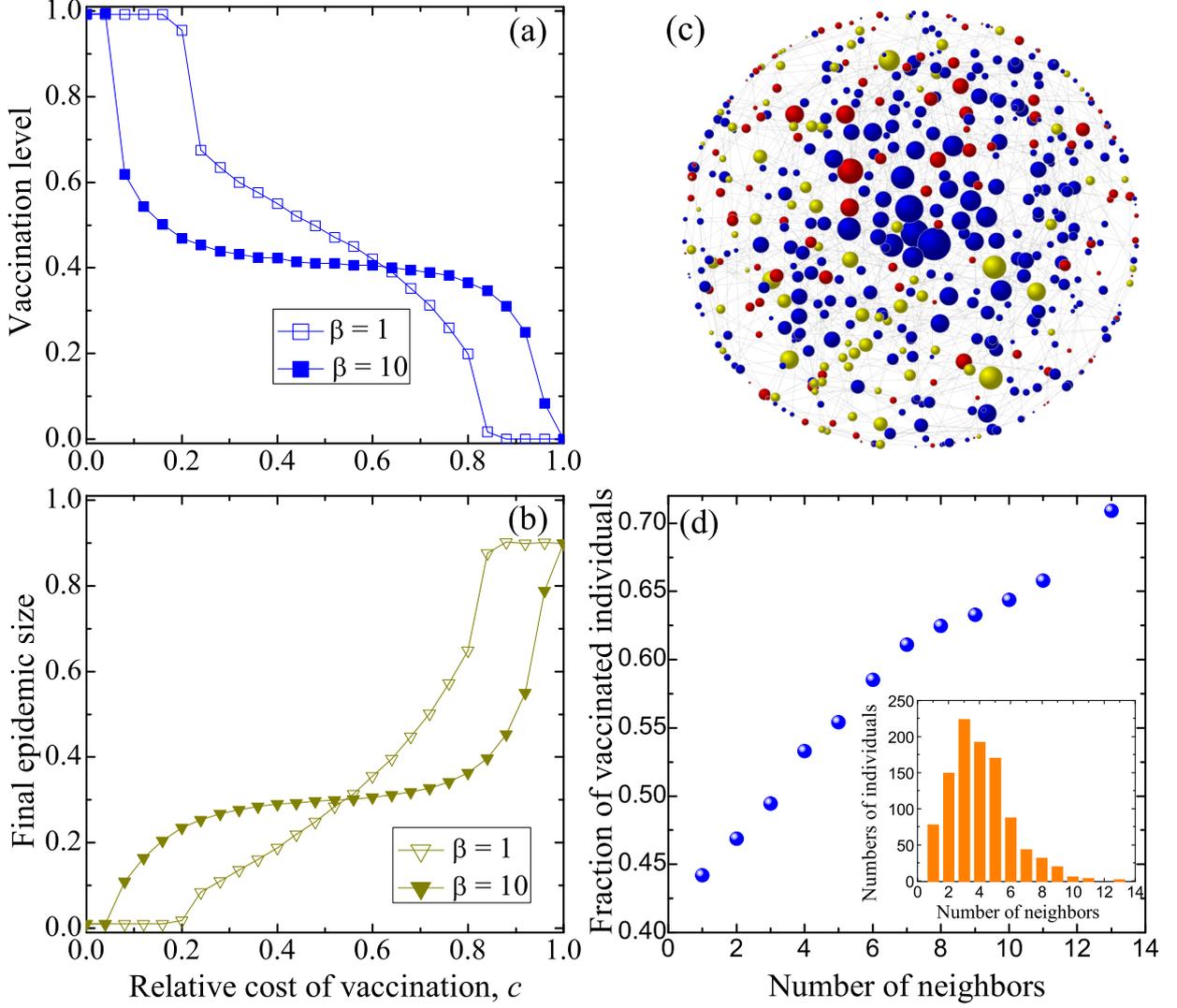


FIG. 4: Inserted Here.

194 IV. DISCUSSION & CONCLUSION

195 Our model shows how incomplete information and strong selection (high payoff-sensitivity, pa-
 196 rameterized by β) in a population of imitators causes the vaccination coverage to fall well short of
 197 the social optimum, and even below the Nash equilibrium. Weak selection in a well-mixed popu-
 198 lation recapitulates the replicator dynamics, converging to the Nash equilibrium. Strong selection,
 199 on the other hand, drives individuals to imitate successful free-riders based on a single observation,
 200 even when a rational agent with complete information would realize that attempted free-riding
 201 does poorly in expectation. This “paradox of imitation” is a very general phenomenon (Schlag
 202 1998) and may in part explain cases where public vaccination levels are low. In particular, for

203 the range of vaccination cost appropriate to influenza (i.e., $c \approx 0.002$ to 0.08 , see ESM), the imita-
204 tion dynamics with strong selection in the well-mixed case falls well short of the rational optimum,
205 leading to over-exploitation of herd immunity and an increase in preventable infections. Our model
206 describes the admittedly extreme case in which each individual observes only one randomly cho-
207 sen role model each round. Allowing imitators to learn from a somewhat larger group of peers
208 could lessen the sampling error, but would not eliminate it.

209 This kind of error is reminiscent of, but distinct from, the phenomenon of “information cas-
210 cades” that generate rationalized conformism or “groupthink” (Banerjee 1992, Bikhchandani et
211 al. 1992). Such cascades may also be obstacles to high vaccination coverage (Barton 2009). To
212 explore conformism (or, alternatively, stubbornness) in the context of our model, one might in-
213 clude an additional cost τ of switching strategy in the thermal updating rule (Szabó & Hauert
214 2002, Traulsen et al. 2010); that is, $f(\Delta P) = 1/[1 + \exp(\beta(\Delta P + \tau))]$. A large negative (positive) τ
215 would then represent the tendency to copy one’s peers (stick with the current strategy), regardless
216 of payoff comparisons. Previous studies have shown in detail how this sort of payoff-neglecting
217 imitation can lead to widespread conformism and adoption of sub-optimal strategies (Banerjee
218 1992, Bikhchandani et al. 1992).

219 It is widely known that population structure can promote the evolution of cooperative behav-
220 ior (Hauert & Doebeli 2004, Nowak & May 1992, Nowak 2006b, Nowak et al. 2010, Ohtsuki et
221 al. 2006, Tarnita et al. 2009a;b). We have shown, however, that population structure is a “double-
222 edged sword” for public health: It can promote high levels of voluntary vaccination and herd
223 immunity, but small increases in cost beyond a certain threshold c_L cause vaccination to plummet
224 – and infections to rise – more dramatically than in well-mixed populations. For example, the
225 random network population under strong selection ($\beta = 10$) can prevent the epidemic completely
226 for costs up to $c = 0.04$, but 11% of the population become infected at cost $c = 0.08$. In the
227 well-mixed population, the epidemic grows gradually, from 8% to 15%, over the same cost range.
228 This threshold effect is robust to changes in population structure and exists in lattice (figures 3a
229 and 3b) and scale-free network (figures S7a and S7b in ESM) populations as well.

230 In social networks, individuals’ degrees vary greatly, and highly-connected individuals (hubs)
231 can spread disease to a large number of peers if infected. The vaccination of hubs can play a vital
232 role in containing infections (Pastor-Satorras & Vespignani 2002), and public health programs
233 often try to promote herd immunity by allocating vaccinations preferentially to these hubs (Bansal
234 et al. 2006). Physicians who are hubs in a disease-transmission network, for instance, have high

235 rates of vaccine uptake (Capolongo et al. 2006). Our model shows that even individuals with
236 incomplete information can self-organize to achieve this pro-social outcome (figure 4). Since
237 hubs generally face greater infection risk than small-degree individuals do, they have increased
238 incentive to vaccinate; hubs' self-interest is therefore relatively well-aligned with overall welfare.

239 Recent work with a detailed model designed to mimic a smallpox outbreak on a random net-
240 work (Perisic & Bauch 2008) reaches a complementary conclusion about the fragility of high-
241 coverage equilibria: voluntary vaccination can contain a disease in low-degree networks, but as
242 the average degree increases, the system reaches a critical threshold past which it behaves like
243 a well-mixed population and the epidemic spreads. This work focused on vaccination decisions
244 made during the course of an epidemic in response to local disease prevalence, as opposed to
245 season-by-season updating of preemptive vaccination decisions. Taken together, our current work
246 and this previous result demonstrate how local disease transmission and decision-making based on
247 local context change the character of vaccination dynamics. Voluntary vaccination can be a viable
248 policy for achieving high coverage and eradicating disease, but the final outcome is sensitive to
249 small changes in (actual or perceived) vaccination cost and in the social network. This sensitivity
250 may in part explain how anecdotal evidence of vaccine-related health risks has been able to trig-
251 ger steep declines in coverage and loss of population immunity (Bauch 2005, Jansen et al. 2003,
252 Nicoll et al. 1998). Policy levers that subsidize vaccination can take advantage of these threshold
253 effects to promote disease containment and eradication.

254 Achieving socially optimal coverage through voluntary vaccination is a problem of cooperation
255 with limited information and uncertainty about outcomes. The problem is similar to public goods
256 games studied by economists (Palfrey & Rosenthal 1984), as herd immunity provides a communal
257 benefit. Individuals' use of salient anecdotes to cope with uncertainty, however, is not a typically
258 studied feature of public goods games. Two sources of uncertainty face an individual deciding
259 whether to vaccinate: uncertainty about contracting the infection if unvaccinated, and uncertainty
260 regarding adverse reactions to the vaccine itself. Our current work focuses on the former uncer-
261 tainty, treating the vaccine cost as a fixed quantity, which is a summary of all expected costs. It
262 may also be instructive to treat vaccine cost as a random variable, as a way of explicitly modeling
263 public fears concerning vaccine safety. These fears often have a tremendous impact on vaccine
264 take-up and public health (Donald & Muthu 2002, Nicoll et al. 1998).

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366 **Figure legends:**

367 **Figure 1** Schematic illustration of our model. We model the vaccination dilemma as a two-stage game. At
368 Stage 1 (vaccination choice), a proportion x of the population decides to vaccinate. Vaccination costs
369 V and provides perfect immunity from the infectious disease. At Stage 2 (health outcome), we use the
370 Susceptible-Infected-Recovered model to simulate the epidemiological process. Each unvaccinated
371 individual faces the risk of infection during the seasonal epidemic outbreak. The cost of infection is
372 I . Those unvaccinated individuals who remain healthy are free-riding off the vaccination efforts of
373 others, and they are indirectly protected by herd immunity.

374 **Figure 2** Vaccination dynamics in well-mixed populations. The fractions (a) vaccinated and (b) infected
375 are shown as functions of the relative cost of vaccination, c , for the intensity of selection $\beta = 1$
376 and 10. The lines are analytical predictions from deterministic equations (see ESM). The devia-
377 tion between simulation and theory is largely due to stochasticity in disease transmission: holding
378 vaccination constant at some level below the herd immunity threshold ($1 - \frac{1}{R_0} = 0.6$), simulated
379 infection risk is smaller than the prediction in equation (1) (see figure S1b in ESM). Individuals in
380 the simulation respond to this decreased risk by vaccinating less than in the theory, which in turn
381 leads to a larger epidemic versus the theory. Strong selection magnifies individuals' responses, pro-
382 ducing larger deviations. For vaccination coverage above the theoretical herd immunity level, the
383 deterministic approximation underestimates infection risk, leading to an opposite deviation at low
384 c . Parameters: population size $N = 5000$, $R_0 = 2.5$ (realized by setting $r = \frac{5}{6N}$ day⁻¹person⁻¹ and
385 $g = \frac{1}{3}$ day⁻¹), number of infection seeds $I_0 = 5$.

386 **Figure 3** Vaccination dynamics in lattice populations. Left panels (a), (b) show the fractions vaccinated
387 and infected, respectively, as functions of c for the intensity of selection $\beta = 1$ and 10. Right panels
388 (c), (d) show snapshots of the system at equilibrium frequencies with weak and strong selection,
389 respectively. Blue denotes vaccinated individuals, red successful free-riders, and yellow infected
390 individuals. Strong selection breaks apart clusters of vaccinators: 54% of vaccinated individuals'
391 neighbors are also vaccinated in (c), versus only 49% in (d). Parameters: population size $N =$
392 100×100 with von Neumann neighborhood, disease transmission rate $r = 0.46$ day⁻¹person⁻¹,
393 recovery rate $g = \frac{1}{3}$ day⁻¹, number of infection seeds $I_0 = 10$, (c)(d) $c = 0.08$, (c) $\beta = 1$, (d) $\beta = 10$.
394 The lines in (a) and (b) are visual guides.

395 **Figure 4** Vaccination dynamics in random network populations. Left panels (a), (b) show the fractions
396 vaccinated and infected, respectively, as functions of c for the intensity of selection $\beta = 1$ and 10.
397 Right panels: (c) Snapshot of a single simulation on a random network at equilibrium frequencies.
398 The size of a node corresponds to its degree (number of neighbors). Blue nodes are vaccinated,
399 yellow are infected, and red are successful free-riders. (d) The frequency of vaccination on a random
400 network, as a function of the number of neighbors an individual has. The inset in panel (d) shows
401 the degree distribution of the random network. Parameters: (a)-(d) average degree $\bar{k} = 4$, disease
402 transmission rate $r = 0.51 \text{ day}^{-1} \text{ person}^{-1}$, recovery rate $g = \frac{1}{3} \text{ day}^{-1}$; (a)(b)(d) $N = 1000$, $I_0 = 10$;
403 (c) $N = 500$, $I_0 = 5$; (c)(d) $c = 0.1$, $\beta = 10$. The lines in (a) and (b) are visual guides.