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Authors

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Social cohesion and passive adaptation in relation to climate change and disease

Sarah T. Cherng^{1,¥}, Ivan Cangemi^{2,¥}, James A. Trostle³, Justin Remais⁴, Joseph N.S. Eisenberg^{2,*}

¹Johns Hopkins University Bloomberg School of Public Health, Department of Epidemiology (Baltimore, MD, USA)

²University of Michigan School of Public Health, Department of Epidemiology (Ann Arbor, MI, USA)

³Trinity College, Department of Anthropology (Hartford, CT, USA)

⁴University of California Berkeley School of Public Health, Department of Environmental Health Sciences (Berkeley, CA, USA)

Abstract

Climate change affects biophysical processes related to the transmission of many infectious diseases, with potentially adverse consequences for the health of communities. While our knowledge of biophysical associations between meteorological factors and disease is steadily improving, our understanding of the social processes that shape adaptation to environmental perturbations lags behind. Using computational modeling methods, we explore the ways in which social cohesion can affect adaptation of disease prevention strategies when communities are exposed to different environmental scenarios that influence transmission pathways for diseases such as diarrhea. We developed an agent-based model in which household agents can choose between two behavioral strategies that offer different levels of protection against environmentally mediated disease transmission. One behavioral strategy is initially set as more protective, leading households to adopt it widely, but its efficacy is sensitive to variable weather conditions and stressors such as floods or droughts that modify the disease transmission system. The efficacy of the second strategy is initially moderate relative to the first and is insensitive to environmental changes. We examined how social cohesion (defined as average number of household social network connections) influences health outcomes when households attempt to identify an optimal strategy by copying the behaviors of socially connected neighbors who seem to have adapted successfully in the past. Our simulation experiments suggest that high-cohesion communities are able to rapidly disseminate the initially optimal behavioral strategy compared to low-cohesion communities. This rapid and pervasive change, however, decreases behavioral diversity; i.e., once a high cohesion community settles on a strategy, most or all households adopt that behavior.

^{*}Corresponding Author. ¥Co-first authors

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Following environmental changes that reduce the efficacy of the initially optimal strategy, rendering it suboptimal relative to the alternative strategy, high-cohesion communities can fail to adapt. As a result, despite faring better early in the course of computational experiments, high-cohesion communities may ultimately experience worse outcomes. In the face of uncertainty in predicting future environmental stressors due to climate change, strategies to improve effective adaptation to optimal disease prevention strategies should balance between intervention efforts that promote protective behaviors based on current scientific understanding and the need to guard against the crystallization of inflexible norms. Developing generalizable models allows us to integrate a wide range of theories multiple datasets pertaining to the relationship between social mechanisms and adaptation, which can provide further understanding of future climate change impacts. Models such as the one we present can generate hypotheses about the mechanisms that underlie the dynamics of adaptation events and suggest specific points of measurement to assess the impact of these mechanisms. They can be incorporated as modules within predictive simulations for specific socio-ecological contexts.

INTRODUCTION

Climate change influences many components of socio-ecological systems, with important consequences for infectious disease transmission. For example, variability in rainfall and temperature, and human responses to that variability, can affect transmission systems for diseases such as malaria, cholera, and dengue (Field, 2014; Hellberg, 2016). Social networks have been shown to influence collective action, emergence of behavioral norms, and responses to interventions (Adger, 2003; Pelling, 2005; Aldrich, 2015; Tsai, 2015; Valente, 2017). To assess and respond to the impacts of climate change on disease, we need to identify how social cohesion is related to community adaptation. For instance, while highly cohesive communities often fare better during and after natural disasters (Klinenberg, 2002; Dynes, 2005), high levels of cohesion may also promote resistance to beneficial interventions (Aldrich, 2008; Villalonga-Olives, 2017). Epidemiologic studies have reached different conclusions about the impact of social cohesion on adaptations to prevent enteric disease. In a study of rural villages in Ecuador, high cohesion appeared to be associated with decreased risk of enteric disease, and this relationship was significantly mediated by use of improved water and sanitation (Zelner, 2012). In a similar study in India, cohesion was found to be negatively associated with latrine ownership, and positively associated with a general acceptance of open defecation (Shakya, 2014).

The relationship between climate change and disease outcomes is complex, and mediated both by biophysical processes, such as those governing pathogen fate and transport, as well as by social processes that determine patterns of exposure to hazards. Despite advances in mapping biophysical associations between meteorological conditions and disease (Altizer, 2013; Levy, 2016; Kraay, 2018), efforts to understand social processes that may affect the adoption of protective behaviors in the face of changing transmission systems are largely absent from the epidemiologic literature.

Continuing our reference to enteric disease epidemiology as an example, some studies have examined how changing meteorological conditions can affect a variety of weather-sensitive

transmission pathways (Levy, 2016; Kraay, 2018; Julian, 2016) and consequently, the efficacy of transmission-related behaviors associated with those pathways. For example, an investigation in Ecuador found that use of safe water was most protective against enteric disease in connection with heavy rainfall, which can flush pathogens into water sources. Alternatively, adequate sanitation only appeared to be protective under dry conditions (Bhavnani, 2014). Similarly, work on enteric disease risk during and after an eight-week flood in Dhaka, Bangladesh, found that adequate sanitation was not beneficial during the event but became protective in the following six months (Hashizume, 2008).

Establishing the potential impact of climate change on disease outcomes in any given context thus requires identifying social processes that could affect the initial adoption of protective behaviors within communities, as well as their ability to detect and adapt to changes in the efficacy of those behaviors. Mechanistic modeling—which involves specifying the causal relationships thought to connect key factors associated with an outcome of interest—is well suited for studying such processes and evaluating the potential social impact of environmental perturbations. In particular, modeling methods that focus on mechanistic abstraction and targeted extension are widely applied to study complex social phenomena within the social sciences (Hedström, 1998). These can provide the foundation for forecasting the impact of climate change on disease patterns within specific socio-ecological contexts.

This paper presents an initial model designed to explore these relationships in a manner that can easily be extended to examine a broad range of research and policy questions as circumstances require, with the goal of identifying and exploring generalizable dynamics and their mechanisms. Specifically, to explore the relationship between social cohesion and adaptation in the face of climate change, we developed an agent-based model that formalizes a straightforward process of social learning; household agents within low- and high-cohesion communities attempt to identify optimal behavioral responses to changing environmental circumstances by copying the choices of seemingly more successful network neighbors. In particular, our model is designed to explore (1) the emergence of health-enhancing norms from a background of behavioral variability; and (2) the ability of communities to adapt to environmental changes that affect the efficacy of protective behaviors.

METHODS

Model overview

The model is designed to run experiments in which household agents attempt to identify the optimal of two behavioral strategies that offer different levels of protection against exposure to pathogens from the environment. The first strategy (Strategy 1) is initially set as more protective, leading households to adopt it widely, but its efficacy is sensitive to environmental change such as increases in flooding and/or droughts. An example of this strategy might be a surface water source that in the absence of flooding or droughts contains low levels of contamination. The second strategy (Strategy 2) is initially moderately protective and is insensitive to environmental changes. An example of this strategy might be

a well water source that is further away and requires a substantial amount of time to reach. Environmental changes can influence the relative efficacy of Strategy 1.

Experiments consist of periodic environmental changes that impact the transmission system and therefore the risk of infection. We label as 'environmental cycles' the time periods between these environmental changes. The relative efficacy of different behavioral strategies, and thus the exposure potential of households, may vary from cycle to cycle.

Experiments begin with the generation of a network of households, representing either a low- or high-cohesion community. Over the course of an experiment, individuals may experience variable infection risk depending on their household's potential for exposure to pathogen contamination. A household's exposure potential represents the adoption of behaviors that activate, block, or mitigate one or more disease transmission pathways. As their occupants become infected, households can search for the optimal strategy by imitating the choices of network neighbors that seem to have adapted well in the past. The model records two types of primary outcomes: the number of households practicing each behavioral strategy at the end of environmental cycles, and the total number of infections that have occurred. These outcomes are used to compare the adaptation trajectories of low-and high-cohesion communities (described in the next section) and their effects on disease transmission.

Social network generation

Social networks within which the social learning procedure plays out are constructed based on full-population sociometric data collected from rural villages in northern coastal Ecuador as part of a long-term study on environmental change and diarrheal disease ("Ecologia, Desarrollo, Salud, y Sociedad" Project, hereafter EcoDeSS (Zelner, 2012; Bates, 2007; Trostle, 2008); for a map of the study region, see (Eisenberg, 2006). The remoteness of villages within this study area influences mobility patterns and other factors that affect social relationships and the structure of social networks. In particular, compared with easily accessible villages, remote villages tend to feature more cohesive social networks (Trostle, 2008). We used EcoDeSS data from two low-cohesion (easily accessible) and two highcohesion (remote) villages with similar numbers of households to estimate values required for the network generation procedure (S1 Appendix).

The role of social cohesion and its relation to population health has been represented in a variety of ways in the epidemiologic literature (McNeill, 2006; Diez Roux, 2007). A review of social cohesion defines the term as a concept that captures a number of social structures within communities, specifically as perceived connectedness, solidarity, and shared resources that allow people to act together. The mechanisms by which this occurs is through the ability to enforce and/or reinforce group norms for positive health behaviors (McNeill, 2006). While many social network, structure, and capital factors interweave to form the concept of social cohesion, in our implementation, social cohesion is represented in this model by the average number of network connections assigned to households (average degree). Importantly, this operationalization represents a proxy for a range of social connectivity measures, such as social capital.

All communities feature 80 household agents, each occupied by 4 individuals. Network connections are distributed randomly according to the Watts-Strogatz small-world model (Watts, 1998), which can be parameterized to capture important structural characteristics of real-world networks (Humphries, 2008). Prior EcoDeSS Project research yielded an average degree of 6 for low-cohesion communities and 12 for high-cohesion communities (S1 Appendix; Trostle et al 2008). These values produce small-world networks that approximate those empirically attested in low-cohesion and high-cohesion villages, respectively (Trostle, 2008).

Infection and recovery mechanism

Experiments begin with a fully susceptible population; changes in the health status of individuals are determined through an SIS model of enteric pathogen exposure and transmission. This framework represents the processes by which individuals in a population become infected with a given pathogen and recover, at which point they are assumed to be susceptible to other enteric pathogens. Infection events are scheduled stochastically according to a simplified version of a previously published model of environmentally mediated enteric disease transmission (Eisenberg, 2007). In particular, we assume that the pathogen dynamics are quick compared to the transmission dynamics. Our model then simplifies such that the transmission rate term becomes the rate that infected individuals shed into the environment divided by the rate that pathogens died off in the environment (Li, 2009), representing the average contamination level in the environment. The household infection hazard is therefore the average pathogen contamination caused by a household's network; i.e., the rate of shedding divided by the pathogen die-off rate times the number of infected individuals with in a household's network. Finally, the expected number of new cases is the product of three terms: 1) the infection hazard as defined above; 2) a behavioral strategy that modifies (i.e., protects against) the exposure of individuals in a household to the force of infection; and 3) the number of uninfected individuals in that household. The recovery event is scheduled as a stochastic exponential process where the mean time to recovery of infection is one over the mean event rate of the exponential process. Recovery events are determined by a recovery rate applied to all households. Parameter values governing the frequency of infection and recovery events were selected to approximate plausible infection trends based on EcoDeSS Project estimates for all-cause diarrhea (S1 Appendix).

Social learning procedure

Over the course of an experiment, household agents can shift between two behavioral strategies (Strategies 1 and 2 as describe earlier in the Model Overview) that offer different levels of protection against exposure to pathogens in the environment. At the beginning of an experiment, a small proportion of households is assigned the initially optimal strategy (Strategy 1), while the remainder is assigned the initially suboptimal strategy (Strategy 2) (S1 Appendix). This preparatory step is intended to seed the development of health-enhancing behavioral norms within the communities.

Household agents track the time intervals they experience between infections, which they use to make adaptation decisions (Fig 1); i.e., the longer the time interval the healthier the

household. Households additionally have access to the time intervals of infection for neighboring households that they share a social connection with (neighbors). These records of infection frequency represent the only source of information available to households for gauging the success of their past adaptations and comparing their performance to their neighbors. As a result, the social network determines who can influence whom within the network over the course of an experiment. Given an infection event, households proceed to adapt by randomly selecting from the strategies of network neighbors that have experienced longer mean intervals between infections than themselves. A mathematical formulation of this adaptation event is presented in Equation S1 of the Appendix. This social learning procedure is intended to model information sharing among the occupants of socially connected households and the emergence of potentially different patterns of influence within different types of networks.

Environmental change mechanism

Experiments are subdivided into multiple environmental cycles, which are conceptualized as periods of stability separated by environmental changes that impact some subset of disease transmission pathways and the efficacy of related behaviors. At the beginning of an experiment, we set the duration of these environmental cycles and the how the environmental changes that occur at the beginning of each cycle will impact the relative efficacy of the two behavioral strategies available to household agents (S1 Appendix). Environmental changes can impact the relative strategy efficacy in two ways. Minor environmental changes can change the efficacy of Strategy 1 (the environmentally sensitive strategy) but does not impact its optimality relative to Strategy 2 (the environmentally insensitive strategy). This environmental change can represent a variety of changes including changes in meteorological conditions such as rainfall and temperature. Major environmental changes will invert strategy optimality; i.e., Strategy 1 will go from suboptimal to optimal or vice-versa relative to Strategy 2.

The impacts of both major and minor environmental change on relative strategy efficacy are modeled by assigning an exposure modifier factor associated with the weather-sensitive strategy and will vary from cycle to cycle while exposure for the Strategy 2 remains constant for the duration of the experiment (Fig 2). The effects of Strategy 1 is a random number between 0.05 and 0.95 that is subtracted from 1 to obtain the initial protective value for the weather-sensitive strategy. The exposure modifier for the weather insensitive protective strategy (Strategy 2) is fixed at 1. These values are set in the model prior to the beginning of the first environmental cycle. With each subsequent environmental cycle, a new random number is drawn and either subtracted from 1 or, if a major environmental change is scheduled to occur, added to 1 to update the exposure modifier for the weather-sensitive strategy. Whether one is added or subtracted is predetermined at the beginning of the experiment, when strategy optimality is assigned (if an experiment features more than one major change, strategy optimality is inverted after each change). Accordingly, the higher the average value of the randomly generated numbers, the greater the difference in efficacy between the two strategies over the course of an experiment. This average value can be regulated through parameter settings, which we outline in the Appendix.

The occurrence of major environmental changes, which inverts the strategy that is optimal, is scheduled according to a pre-described pattern of major and minor environmental changes that occur prior to each cycle. We parameterized the timing of this environmental change to provide flexibility for future experiments that will rely on empirical data specifying environmental change intervals. We define experiments specific to a set of defined environmental change intervals as 'baseline' and 'punctuated' scenarios. The baseline scenario features no major changes, so that the weather-sensitive strategy is optimal for the full duration of the experiment (i.e., the randomly generated numbers are always subtracted from 1 to obtain the exposure modifier for the weather-sensitive strategy). Under the punctuated scenario, in contrast, the weather-sensitive strategy is implemented as optimal during the first cycle but then becomes suboptimal once a major environmental change occurs (i.e., the randomly generated numbers are subtracted from 1 before the first cycle and added to 1 thereafter). Figure 2 is an example of a punctuated scenario, where after the first cycle Strategy 1 goes from suboptimal to optimal. Thereafter, each cycle begins with a minor environmental change.

It is possible to abstractly capture any environmental change scenario of interest by controlling the parameters governing: 1) the *duration of cycles*, 2) the shape of the distribution describing the *average difference in strategy efficacy*, and 3) the regime specifying *whether and when strategy optimality is inverted*. For example, a punctuated scenario parameterized with long cycles and large average difference in strategy efficacy could represent the following real-world scenario (relevant model settings are indicated in italics):

- 1. A large proportion of a community consumes untreated water from a relatively uncontaminated nearby river as their weather sensitive strategy. Alternative behavioral strategies (Strategy 2) might theoretically offer more protection, but they incur opportunity costs that substantially increase the overall exposure potential of households that practice them. For example, the time required to collect water from a less contaminated but more distant source could limit the amount of time available to clean living spaces, monitor the activities and hygiene of children, and obtain and safely prepare nutritious food. In terms of the model, these starting conditions are achieved by the end of the first environmental cycle by: 1) running the experiment with a *large difference in strategy efficacy*, which makes it easier for households to identity the optimal strategy (consumption of water from the nearby river); and 2) having a *long cycle duration*, which ensures that a large proportion of the community will converge on this strategy.
- 2. Floods at the site of the community and upstream locations begin regularly contaminating the river water (in accordance with the *punctuated scenario*, the optimal strategy becomes suboptimal prior to the start of the second cycle).
- **3.** Households that collect water from the river begin experiencing infections more frequently (*large difference in strategy efficacy*). Their ability to adapt, however, will depend on whether alternative behavioral strategies are still sufficiently well

represented among their neighbors despite the extended period of stability prior to the onset of regular floods (*long cycle duration*)

Sensitivity analyses of all experimental parameters presented here are presented in the Appendix.

RESULTS

High cohesion can facilitate adaptation when transmission systems are relatively stable; i.e., there are no major environmental changes

In experiments comparing adaptation trajectories under the baseline environmental scenario, high-cohesion communities perform as well or better than low-cohesion communities; i.e., they converge to the optimal behavioral strategy more quickly. Under this scenario, the transmission system does not undergo substantial changes; the efficacy of the weather-sensitive behavioral strategy may vary between environmental cycles but is always greater (i.e., more protective) than that of the alternative strategy. Both low- and high-cohesion communities successfully adapt to this scenario, with a majority of households eventually converging on the weather-sensitive behavioral strategy. This process generally occurs more rapidly within high-cohesion communities (Fig 3) because households observe more network neighbors on average, and therefore are better able to resolve differences in efficacy between the optimal and suboptimal strategies. In particular, high-cohesion communities tend to adapt more successfully early in the course of experiments, when the infection-frequency records of households are still sparse. Differences are greater when environmental cycles are shorter.

The greater passive adaptation of high-cohesion communities early in the course of experiments can result in lower risk of infection (Fig 4). This is particularly evident in scenarios characterized by short environmental cycles and large average difference in strategy efficacy (Fig 4B), in which a significant gap in adaptive performance between communities tends to emerge already by the end of the first cycle (Fig 3B).

High cohesion can preclude adaptation following substantial changes to transmission systems

As discussed in connection with Fig 3, household agents within high-cohesion communities tend to adapt successfully early in the course of experiments because they have access to richer information to establish the optimality of the two behavioral strategies. While beneficial when transmission systems are relatively stable, this ability to rapidly identify and propagate the initially optimal strategy comes at the cost of reduced behavioral diversity, which can be detrimental in the long run. Under the punctuated scenario, for instance, which represents a scenario in which the weather-sensitive strategy is optimal during the first cycle but suboptimal thereafter, households should initially converge on the former strategy but then begin abandoning it during the second cycle. Low-cohesion communities adapt to the punctuated scenario in just this manner, while high-cohesion communities may fail to adapt following the first environmental cycle (Fig 5). This is because the more efficient process of adaptation within high-cohesion communities leads to the stable (initially suboptimal) strategy being represented in just a few households or even becoming extinct by the end of

the first environmental cycle. Subsequently, households within high-cohesion communities are unlikely or unable to switch to this strategy even after it becomes optimal, potentially resulting in worse health outcomes (Fig 6). In both the adaptation and infection plots, the differences between communities are most pronounced when environmental cycles are relatively long, leading to the emergence of particularly robust norms favoring the adoption of the weather-sensitive strategy within high-cohesion communities during the first cycle (Figs 5C–D, 6C–D).

DISCUSSION

Effective policy to address the impacts of climate change on disease must account for a range of dynamic variables that can yield profoundly different outcomes in different socioecological contexts. Social processes play a major role in shaping aspects of population vulnerability, or the propensity of communities to experience harm as a result of climate change (Field, 2014). Vulnerability assessments often aggregate into quantitative indices the effects of diverse factors that may be associated with outcomes of interest (Birkmann, 2006; Klein, 2009; Tonmoy, 2014). While arguably resulting in estimates that are relatively easy to communicate and interpret (Birkman, 2006; Hammond, 1995), efforts to produce composite indices become problematic when empirically documented associations are excised from the broader socio-ecological systems which shape them and which in turn they contribute to shaping over time (Tonmoy, 2014; Barnett, 2008; Hinkel, 2011). In order to remedy this problem, it is important to identify and study mechanisms that could determine associations between specific factors and outcomes of interest across different socio-ecological systems rather than focusing exclusively or primarily on isolating such associations for an evergrowing catalog of case studies. Our computational model represents an attempt to move toward this goal for associations between social cohesion and capacity to adapt to the impacts of climate change on environmentally mediated disease transmission.

Results from our model suggest that social cohesion may variously affect adaptation as environmental changes impact transmission systems over time. In our computational experiments, high levels of social cohesion can facilitate the development of behavioral norms that protect against exposure to pathogen contamination in the environment. If the disease transmission system is stable for extended periods of time, however, these norms can become so robust as to severely reduce or extinguish behavioral diversity. As a result, while high levels of social cohesion are associated with good adaptation and health outcomes under reliably stable environmental scenarios, they can preclude adaptation and lead to greater disease burdens when environmental changes substantially alter transmission systems.

Our findings concerning the context-dependent nature of associations between social cohesion and adaptation are consistent with results from recent attempts to model how the structure of social networks affects decision-making performance within groups facing complex tasks. These more general studies, which are partially inspired by longstanding debates within the social sciences (Gargiulo, 2000), are showing that decision-making performance may be highly contingent on the interaction between social network variables and task complexity (Lazer, 2007; Barkoczi, 2016). By assuming a simple mechanism of

information-sharing among the occupants of socially connected households and defining a limited set of parameters governing environmental change scenarios, we extended this line of inquiry to begin exploring how social cohesion may affect the relationship between climate change and disease transmission. The result is a flexible modeling framework that can be further extended to examine specific socio-ecological contexts, environmental change scenarios, and health outcomes as required to evaluate potential interventions and inform policy.

Along with insights from more general modeling efforts, our findings point to the importance of fostering normative plasticity for reducing vulnerability to the impacts of climate change on disease. Accordingly, policy and intervention efforts should endeavor to balance the conventional goal of promoting widespread adoption of protective behaviors based on current scientific understanding with the need to guard against the crystallization of inflexible norms. This is especially important given the high degree of uncertainty surrounding the impact of many plausible interventions to reduce the negative repercussions of climate change on health (Bouzid, 2013). Focusing on maximizing normative uptake and failing to disclose uncertainty can lead to maladaptation and mistrust as scientific knowledge and socio-ecological circumstances evolve. Efforts to identify effective ways to communicate scientific uncertainty and its implications and educate communities about the power of their social networks either to facilitate or hamper information, resource, and other types of flows should thus be prioritized to the same extent as attempts to forecast future climatic conditions and their impacts on disease transmission systems ever more accurately.

Limitations and Future Work

The central assumption of our model is that household agents adapt by imitating the choices of socially close households that seem to have performed well in the past (Fig 1). This mechanism drives the emergence of what may be considered 'descriptive norms', shaped by processes of social learning. Depending on the particular socio-ecological contexts and behaviors under consideration, however, 'injunctive norms', which are enforced more or less directly through sanctions, may also impact adaptation (Shakya, 2014; Cialdini, 1990). Extensions of the model designed to evaluate specific interventions and socio-ecological contexts directly through sancting decision-making other than social learning.

In the present implementation, information-sharing for the purposes of the social learning procedure is restricted to the network neighborhoods of individual household agents (i.e., all households to which a given household is directly connected) and remain static over time. Real-world social learning, however, may occur dynamically within different types of groups and reflect not only an amount of information transfer, but also quality and heterogeneity of information. As such, future work could explore how network analysis algorithms capable of capturing different types of social structures may result in different outcomes from the ones we presented in this manuscript. For example, groups identified through "community-detection" algorithms may reflect spheres of influence and information-sharing within communities extending beyond direct contacts (Shakya, 2014). Moreover, this work is an abstract representation of how social mechanisms (i.e., the extent

of information sharing between households) can change vulnerability of the broader community to diseases associated with climate change. Abstract models are not readily utilized for concrete intervention, and so, future work would seek to ground our findings in quantifiable measures, such as the effects of individual-household cost on chosen WaSH strategies. Such an addition would allow our model to estimate how, whether, and to what extent costs (either financial or health-specific) can also affect strategic adaptations to environmental perturbations over time. Moreover, this work highlights and demonstrates the importance of collecting social behavioral data as well. Additionally, future implementations of the model featuring more realistic transmission mechanisms should investigate the effects of asymptomatic infections, which can contribute to the hazards experienced by agents but have no effect on their adaptation decisions.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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HIGHLIGHTS

- Under stable environmental conditions, social cohesion can facilitate the development of behavioral norms that protect against exposure to pathogen contamination in the environment.
- In the face of environmental change, however, these norms can become so robust as to preclude successful adaptation to new optimal behavior strategies.
- Policy and intervention efforts should endeavor to balance the conventional goal of promoting widespread adoption of protective behaviors based on current scientific understanding with the need to guard against the crystallization of inflexible norms.
- Generalizable mechanistic models allows us to integrate a wide range of theories and multiple datasets pertaining to the relationship between social mechanisms and adaptation, which can provide further understanding of future impacts of climate change.



Fig 1. Diagram of household-level adaptation procedure following an infection.

Immediately following an infection, the affected household agent identifies network neighbors that have experienced no infections or longer average intervals between infections, suggesting that they have adapted successfully in the past. The household then randomly adopts one of the two possible behavioral strategies within the model with probability corresponding to the proportion of these neighbors that are currently practicing it. Finally, if the selected strategy differs from the one it previously practiced, the household updates the exposure potential of its occupants.

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Fig 2. Progression of sample experiment showing impact of environmental changes.

Experiments are subdivided into multiple environmental cycles, which are periods of equal duration bounded by environmental changes. These changes impact the efficacy of the weather-sensitive behavioral strategy (dashed lines), where an exposure modifier less than one reduces exposure and an exposure modifier greater than one increases exposure. The weather-insensitive strategy (dotted line) is set to an exposure modifier of 1. Prior to the beginning of the first cycle, a random number between 0.05 and 0.95 is subtracted from 1 to obtain the exposure modifier for the weather-sensitive practice. Subsequently, a random number is drawn prior to each cycle to obtain a new exposure modifier for the weather-sensitive strategy. If no major environmental changes are scheduled to occur, the random numbers continue to be subtracted from 1. A major environmental change will invert strategy optimality; e.g., if the weather-sensitive strategy was previously optimal, as in the scenario captured by the diagram, it will become suboptimal (exposure modifier > 1).

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Fig 3. Adaptation trends under the 'baseline' environmental scenario.

Proportion of households within low- and high-cohesion communities (grey and black, respectively) that engage in the weather-sensitive behavioral strategy under the baseline scenario, in which the weather-sensitive strategy is optimal during all cycles. A) environmental cycle duration: 180 days, average difference in strategy efficacy: 0.5; B) environmental cycle duration: 180 days, average difference in strategy efficacy: 0.9; C) environmental cycle duration: 730 days, average difference in strategy efficacy: 0.5; D) environmental cycle duration: 730 days, average difference in strategy efficacy: 0.9. Outcomes are averaged across 50 replicates and displayed with 95% bootstrap confidence intervals.

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Fig 4. Infection trends under the 'baseline' environmental scenario.

Cumulative incidence within low- and high-cohesion communities (grey and black, respectively) under the baseline scenario, in which the weather-sensitive strategy is optimal during all cycles. A) environmental cycle duration: 180 days, average difference in strategy efficacy: 0.5; B) environmental cycle duration: 180 days, average difference in strategy efficacy: 0.9; C) environmental cycle duration: 730 days, average difference in strategy efficacy: 0.5; D) environmental cycle duration: 730 days, average difference in strategy efficacy: 0.9; C) environmental cycle duration: 730 days, average difference in strategy efficacy: 0.9; O.9. Outcomes are averaged across 50 replicates and displayed with 95% bootstrap confidence intervals.

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Fig 5. Adaptation trends under the 'punctuated' environmental scenario.

Proportion of households within low- and high-cohesion communities (grey and black, respectively) that engage in the weather-sensitive behavioral strategy under the punctuated scenario, in which the weather-sensitive strategy is optimal during the first cycle but suboptimal thereafter. A) environmental cycle duration: 180 days, average difference in strategy efficacy: 0.5; B) environmental cycle duration: 180 days, average difference in strategy efficacy: 0.9; C) environmental cycle duration: 730 days, average difference in strategy efficacy: 0.5; D) environmental cycle duration: 730 days, average difference in strategy efficacy: 0.9. Outcomes are averaged across 50 replicates and displayed with 95% bootstrap confidence intervals.

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Fig 6. Infection trends under the 'punctuated' environmental scenario.

Cumulative incidence within low- and high-cohesion communities (grey and black, respectively) under the punctuated scenario, in which the weather-sensitive strategy is optimal during the first cycle but suboptimal thereafter. A) environmental cycle duration: 180 days, average difference in strategy efficacy: 0.5; B) environmental cycle duration: 180 days, average difference in strategy efficacy: 0.9; C) environmental cycle duration: 730 days, average difference in strategy efficacy: 0.5; D) environmental cycle duration: 730 days, average difference in strategy efficacy: 0.9. Outcomes are averaged across 50 replicates and displayed with 95% bootstrap confidence intervals.