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► **To cite this version:**

Alexandre Suire, Minus van Baalen. Rumour propagation and the eco-evolutionary dynamics of social information use. *Proceedings of the Royal Society B: Biological Sciences*, 2018, 285, 10.6084/m9 . hal-02342278

HAL Id: hal-02342278

<https://hal.science/hal-02342278v1>

Submitted on 31 Oct 2019

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Cite this article: Suire A, van Baalen M. 2018 Rumour propagation and the eco-evolutionary dynamics of social information use. *Proc. R. Soc. B* **285**: 20180088. <http://dx.doi.org/10.1098/rspb.2018.0088>

Received: 17 January 2018

Accepted: 26 February 2018

Subject Category:

Evolution

Subject Areas:

evolution, theoretical biology, ecology

Keywords:

social information, rumours, epidemiology, host–parasite interactions, eco-evolutionary dynamics

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Electronic supplementary material is available online at <https://dx.doi.org/10.6084/m9.figshare.c.4024501>.

Rumour propagation and the eco-evolutionary dynamics of social information use

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Information is a crucial currency for living organisms as it allows them to adjust their behaviour to environmental fluctuations. Thus, natural selection should have favoured the capacity of collecting information from different sources, including social interactions whereby individuals could quickly gain reliable information. However, such conditions may also favour the gathering of potentially detrimental information, such as false or misinterpreted accounts of environmental and social phenomena such as rumours, which may spread via informational cascades. We applied ecological and evolutionary principles to investigate how the propagation of social information at a populational level affects the propensity to assimilate it, here defined as the gullibility. Our results show that the evolution of an individual's susceptibility to assimilate information strongly depends on eco-evolutionary feedbacks, in particular when both useful and detrimental information circulate. We discuss our results regarding the different information transmission mechanisms involved with particular attention to specific cases of social learning.

1. Introduction

Information is a crucial resource for all living organisms. Unicellular or multicellular, animal or plant, an organism often relies on the gathering, assessment and assimilation of relevant information about current and future environments. By reducing uncertainty, information crucially helps individuals to adapt their behaviour in response to fluctuating ecological and social environments [1]. Ecosystems generate fluxes of visual, auditory and chemical information in the form of cues (abiotic parameters, such as changes in temperature or luminosity) and signals (information produced with a certain intention and destined to one or several receivers [2]). Acquiring and processing information are part of a dynamical process: individuals must assess the cues they perceive with respect to prior knowledge (taking into account that some cues may provide contradictory information [3]), and if necessary update their knowledge, while taking into account the information possessed by others [1,4]. Ultimately, we would expect individuals to carefully weigh all options available to them and their potential consequences in terms of fitness pay-off [5,6].

There are typically two ways to acquire information: from personal experience (for instance by trial-and-error tactics) or from other individuals (by using available social information). The latter results from social interactions that encompass a vast array of transmission mechanisms, including, among others, true communication, imitation, developmental imprinting and teaching [7]. Whether it is communicated intentionally or inadvertently, social information is of a particular importance in decision-making because it facilitates individuals to solve a given life-history problem by observing the behaviour of fellow beings faced with a similar situation [8,9]. Not only does it generally reduce the costs of

obtaining information by itself, but also it is usually perceived as a more reliable and faster way of gaining information [8]. A large body of work has shown that social transmission of information is a widespread phenomenon in the animal kingdom, used in a variety of situations. Among the most obvious examples is, of course, the human species in which social information plays a crucial role in the everyday life context, be it decision-making, problem-solving, assessing competitors and mate choosiness [10]. Many examples are also well-documented in other species, for instance in foraging contexts (e.g. individuals monitoring others probing success of resource quality and breeding patches [11]), sexual selection (e.g. mate choice, influenced from the exposure of watching mating interactions of others [12]) and the learning of new behavioural skills (e.g. social learning in offspring [13]).

Like any type of biological information, social information should always allow individuals to increase their fitness, provided that it is well interpreted and used optimally [14]. However, in social species, socially acquired information comes from the behavioural decisions of other individuals rather than the cues on which these decisions are based. Moreover, individuals may also be subject to social manipulation [15,16]. Thus, the quantity of social information may be poor and can lead to sub-optimal decisions and even wrong (and hence maladaptive) decision-making behaviour. In turn, this can induce informational cascades whereby potentially maladaptive social information propagates inside a population [17]. Owing to the scarcity of information and situational uncertainty, information is passed on between individuals who often lack the means to check it. In this context, particular types of social information such as rumours offer an interesting example. They can be defined as unconfirmed, neither completely true or false, consisting of social information that is more or less public, and that it usually propagates rapidly over a short temporal window [18].

Susceptible–infected–recovered (SIR) models of epidemiology have been adapted to describe rumour propagation since [19,20]. In analogy with epidemiology of infectious diseases, the population is subdivided into three groups: those who are unaware of the rumour (ignorants), those who spread the rumour (spreaders) and those who are aware of the rumour but do not spread it (stiflers). Although subsequent studies retained this approach, these models were too simplistic and only considered homogeneously mixed population with no social structure. As then, numerous theoretical models incorporated spatial structure using network theory [21,22], considered new subclasses (such as ‘hibernators’ [22]) or various individual’s properties (such as denial and skepticism [23]; remembering mechanisms [24]; forgetting mechanisms [25]). Such studies have proven useful in understanding overall patterns of propagation and diffusion behaviour within a structured population and specific networks. However, although considerable research has been dedicated to the topic of rumours, to our knowledge, it has received scant attention from an evolutionary perspective, especially when one is interested in the evolution of collecting social information.

In this context, host–parasite models could constitute a similar starting point, as these may provide guidelines and inspiration on how to model the dynamical process of the spread of different information of uncertain value at the population level. Epidemiology allows insightful views on how a given state (here, being informed) spreads, behaves

and potentially competes with other states within a host population. From these different informational states, the adaptive dynamics framework allows us to assess fitness consequences and evolutionarily stable strategies (ESSs) of collecting rumours [26], with and without social structure in the form of a contact network [27]. By applying the methods of eco-evolutionary dynamics to study the evolution of social information use, we formalized and explored a simple model to study the following questions: (i) what are the conditions for the coexistence of different rumours, given their specific characteristics (concerning dissemination, loss and interaction with other rumours) within a population? (ii) how does the capacity to collect rumours evolve over time, i.e. how can we link the dynamics of the informational state of individuals (which may change over time through communication and loss) to their fitness? and (iii) how does the outcome depend on eco-evolutionary feedbacks?

To address these questions, we will develop and analyse a series of simple models that track the population dynamics and its evolutionary consequences through what we define as the ‘informational state’ of individuals. Rumour propagation is an obvious example where such states evolve (as aforementioned for SIR models in humans), but social ‘scrounging’ (inferring the informational state of conspecifics by observing their behaviour) is another and perhaps more general one in nature [8,17].

2. Theory, methods and results

(a) Introducing the epidemiological model

Consider a fixed population of N individuals in which two distinct rumours (hereafter also termed information) circulate. We denote individuals that have received rumour 1 or 2, respectively, I_1 and I_2 , and $I_{1,2}$ if they have received both. Naive individuals are denoted S and we will assume that all individuals are born naive.

Individuals communicate the information they possess to conspecifics with given probabilities α_1 and α_2 , respectively, for I_1 and I_2 and we assume that these probabilities are fixed. We also assume that the information is not modified when passed on between individuals (i.e. it is perfectly replicated). Note that individuals pass on information only if they are in close contact either through observation (i.e. imitation) or by true communication (i.e. with the intention to provide information to conspecifics). There is no broadcasting of information. The probability per unit time of acquiring information i is proportional to the density of i -spreading individuals:

$$\lambda_i = \alpha_i(I_i + I_{1,2}).$$

In epidemiological contexts (where parasites are spreading instead of rumours), this is called the ‘force’ of infection. For lack of a more appropriate term, we will call λ_i here the ‘pressure’ of i -information. For simplicity, we assume that individuals carrying both types of information transmit them as quickly as individuals carrying one type of information only.

Individuals can also forget the information they possess with given probabilities per unit of time β_1 and β_2 , respectively, for I_1 and I_2 . Individuals may assess the information not reliable or irrelevant in regards to social interactions, survival or reproduction, all of these latter processes contributing to the forgetting of information. We assume that individuals do not acquire or forget both units of information

simultaneously (i.e. go directly from state S to state $I_{1,2}$, and conversely). Thus, $I_{1,2}$ individuals will communicate both rumours but independently (that is, not both at the same time to the same individual).

We further assume that individuals have a characteristic probability to assimilate received information, regardless of the information it already possesses, given the parameter δ . This probability directly refers to the susceptibility of assimilating social information. For instance, if $\delta = 0$, individuals are completely naive and do not assimilate information; if $\delta = 1$ they will retain all information they receive. Thus, δ corresponds to the notion of ‘gullibility’ as defined by Krakauer & Pagel [28]. To many people, ‘naive’ and ‘gullible’ are synonyms, but as we define these terms, ‘naive’ corresponds with a state while ‘gullibility’ is associated with transitions (see the electronic supplementary material, appendix S1 for a representation of the states’ transitions). ‘Gullibility’ may be referred to a general tendency to use social information as social systems evolve in complexity (increased number of interactions between conspecifics).

In the first part of our analysis, we keep the total population density N constant so that

$$S = N - I_1 - I_2 - I_{1,2}.$$

The dynamics of the system over time is thus fully described by the following differential equations:

$$\frac{dI_1}{dt} = \delta S \lambda_1 + \beta_2 I_{1,2} - \beta_1 I_1 - \delta I_1 \lambda_2,$$

$$\frac{dI_2}{dt} = \delta S \lambda_2 + \beta_1 I_{1,2} - \beta_2 I_2 - \delta I_2 \lambda_1,$$

and
$$\frac{dI_{1,2}}{dt} = \delta I_1 \lambda_2 + \delta I_2 \lambda_1 - (\beta_1 + \beta_2) I_{1,2}$$

after substitution of the conservation law defined above.

(b) The conditions for the coexistence of rumours

We will start by considering the conditions for invasion of the two types of rumour and the conditions for coexistence. To study the dynamics of a rumour it is useful to consider the dynamics of the total density of individuals that carries it, $\hat{I}_i = I_i + I_{1,2}$. The dynamics of \hat{I}_2 turns out to be given by

$$\frac{d\hat{I}_2}{dt} = \delta(S + I_1)\lambda_2 - \beta_2(I_2 + I_{1,2}),$$

as $\lambda_2 = \alpha_2 \hat{I}_2$, and $S + I_1 = N - \bar{I}_2$ can be written as

$$\frac{d\hat{I}_2}{dt} = (\alpha_2 \delta(N + \hat{I}_2) - \beta_2) \hat{I}_2$$

(and an equivalent equation can be derived for rumour 1). The fact that the dynamics of rumour 2 does not depend on the presence of rumour 1 implies that the two rumours circulate fully independently in the population. The condition for invasion of rumour 2 is, therefore, simply

$$\frac{\alpha_2 \delta N}{\beta_2} > 1,$$

and the equivalent condition holds for the invasion of rumour 1. Note that the simple condition for coexistence would not result if we would allow different rumours to interact within individuals. For instance, the rate of dissemination could depend on whether the ‘host’ has acquired other rumours. A rumour could make its ‘host’ forget other rumours

and it could make its ‘hosts’ more or less gullible. These are very interesting cases to study, but fall outside of the scope of this study.

Inspection of the invasion condition for a rumour shows that it may be selected to try to increase its rate of dissemination α , for instance by attracting attention. But of course, it could also try to become more persistent in a given individual by reducing its rate of loss β . Finally, and significantly, a rumour may try to reduce the probability that its individual acquire new ones by manipulating δ . As in the evolution of parasite virulence, the eventual outcome will depend on the constraints that delimit the α , β and δ parameters.

The coexistence of different types of information may be applicable to general situations of social learning, whereby new information spreads independently of other information. For instance, the discovery of a new type of edible food is unlikely to interfere with information about the presence of predators, how to deal with a particular habitat or the presence of a new cultural item. The resulting informational cascades can be propagated through observation or true communication [29]. However, what happens if two rumours have different fitness outcomes has not been considered yet. To study the evolutionary consequences, we will always ensure that both rumours can persist in the population.

3. Information and individual fitness

(a) Informational states

In this section, we ask ourselves how, given the potential diversity of rumours circulating in the population, an individual should increase or decrease its readiness to assimilate them. Of course, the answer is clear if all information has a beneficial effect or all information has a detrimental effect, but what an individual should do in the presence of rumours of potentially contrasting effects (e.g. some of them are true and useful, others are not) is less obvious.

The diversity of rumours causes individuals to be in different informational states, potentially affecting differently their fitness. We suppose that an individual is characterized by its ‘gullibility’ δ , the probability that it assimilates a rumour when presented with it. The question then becomes what is the evolutionarily stable value δ^* . To study this question, we extended the system such that we have a resident population from which mutants can arise and in turn assimilate the information that circulates, according to the methodology of adaptive dynamics [26].

We will, therefore, assume that the resident population is at a stable equilibrium such that the information pressures are at equilibria, indicated by the asterisk and given by

$$\lambda_i^* = \alpha_i(\bar{I}_i + \bar{I}_{1,2}),$$

with the resident densities at equilibria indicated by the overbars.

Now mutants may arise with their own properties of assimilating information (indicated by the label ‘mut’). We will denote probabilities of the mutants being in particular states as π_S (the probability of being naive), π_1 (having received rumour 1), π_2 (having received rumour 2) and $\pi_{1,2}$ (having received both rumours). The changes of these probabilities

through time driven by the forces of acquiring and losing information are given by

$$\frac{d\pi_s}{dt} = -(\delta^{\text{mut}}\lambda_1^* + \delta^{\text{mut}}\lambda_2^*)\pi_s + \beta_1\pi_1 + \beta_2\pi_2,$$

$$\frac{d\pi_1}{dt} = \delta^{\text{mut}}\lambda_1^*\pi_s + \beta_2\pi_{1,2} - \beta_1\pi_1 - \delta^{\text{mut}}\lambda_2^*\pi_1,$$

$$\frac{d\pi_2}{dt} = \delta^{\text{mut}}\lambda_2^*\pi_s + \beta_1\pi_{1,2} - \beta_2\pi_2 - \delta^{\text{mut}}\lambda_1^*\pi_2,$$

$$\text{and } \frac{d\pi_{1,2}}{dt} = \delta^{\text{mut}}\lambda_2^*\pi_1 + \delta^{\text{mut}}\lambda_1^*\pi_2 - (\beta_1 + \beta_2)\pi_{1,2}.$$

This system describes all transition processes and corresponds to a standard continuous Markov chain. The equilibrium probability distribution of the mutants' states can be easily solved (see the electronic supplementary material, appendix S2 for the solution) and is given by

$$\begin{pmatrix} \bar{\pi}_s \\ \bar{\pi}_1 \\ \bar{\pi}_2 \\ \bar{\pi}_{1,2} \end{pmatrix} = \frac{1}{D} \begin{pmatrix} \beta_1\beta_2 \\ \beta_2\delta^{\text{mut}}\lambda_1^* \\ \beta_1\delta^{\text{mut}}\lambda_2^* \\ (\delta^{\text{mut}})^2\lambda_1^*\lambda_2^* \end{pmatrix},$$

where $D = (\beta_1 + \delta^{\text{mut}}\lambda_1^*)(\beta_2 + \delta^{\text{mut}}\lambda_2^*)$.

If being in state i corresponds with rate of reproduction w_i , the expected fitness of a mutant will be given by

$$w^{\text{mut}} = w_s\bar{\pi}_s + w_1\bar{\pi}_1 + w_2\bar{\pi}_2 + w_{1,2}\bar{\pi}_{1,2},$$

which is just the expectation of w_i given fixed probabilities $\bar{\pi}_i$. A more complicated expression would result if information affected survival instead of reproduction, but for the sake of simplicity we do not consider this case here.

We assume that an individual cannot assess the fitness value of a rumour it acquires (i.e. it cannot have a discriminative, or filtering, strategy such that $\delta_1^{\text{mut}} \neq \delta_2^{\text{mut}}$). The question then is which is the best strategy, avoiding rumours altogether ($\delta^{\text{mut}} = 0$), acquire all rumours as quickly as possible ($\delta^{\text{mut}} = 1$), or adopt some optimal intermediate value? We can easily calculate the mutant's state probabilities at equilibrium and obtain the following expression for the mutant's fitness:

$$w^{\text{mut}} = \frac{\beta_1\beta_2w_s + \beta_2\delta^{\text{mut}}\lambda_1^*w_1 + \beta_1\delta^{\text{mut}}\lambda_2^*w_2 + \delta^{\text{mut}^2}\lambda_1^*\lambda_2^*w_{1,2}}{(\beta_1 + \delta^{\text{mut}}\lambda_1^*)(\beta_2 + \delta^{\text{mut}}\lambda_2^*)}.$$

From this equation, we can infer (see the electronic supplementary material, appendix S3) that it pays to have at least some attention to rumours if

$$\frac{\lambda_1\Delta w_1}{\beta_1} + \frac{\lambda_2\Delta w_2}{\beta_2} > 0,$$

where $\Delta w_i = w_i - w_s$, so that rumour i is useful if Δw_i is positive, and costly if it is negative (relative to being naive). Intermediate optima given by the solution of a quadratic equation (see third equation in the electronic supplementary material, appendix S3) are possible if at least one of Δw_1 , Δw_2 and $\Delta w_{1,2}$ is negative.

Given these results, three scenarios are possible. If all information that circulates (concerning edible food, the presence of new a predator or a new cultural item) is fitness-enhancing, then individuals are selected to being fully gullible. If all information is fitness-decreasing, individuals will obviously evolve to be fully skeptical. The third, more interesting scenario is when some information is fitness-enhancing whereas others are fitness-decreasing. Then, the intermediate gullibility may be selected which, as

we will show, will result in a sensitive eco-evolutionary feedback. Cases with mixed-effect information are likely to be quite general. A well-known example is that of Batesian mimicry, where a conspicuous pattern may either convey useful information (allowing avoidance of a bad experience) or misleading information (leading to a missed meal) [30]. Another example is when individuals are confronted with both deceptive and honest individuals in complex social systems (although one individual can switch between these two forms of behaviour) and is well documented in primates [31]. Cases involving individuals attracted to feeding conspecifics where patches deplete rapidly fail to learn habitat quality, leading to aggregation in poor patches (in addition to travel costs), leading to severe populational consequences [32]. In particular, for the more general scenario where it is not immediately obvious to a user whether the information is useful or detrimental, we have to incorporate the feedbacks that result when information circulates through a population.

(b) The evolution of assimilating information

In this section, we will carry out an adaptive dynamics analysis of the gullibility of individuals (their propensity to assimilate the rumours they are confronted with) and its effects on the population level, represented by δ in our model. We consider two strategies (a resident strategy, indicated by the label 'res', which dominates the population and a rare mutant strategy indicated by the label 'mut') which differ in the likelihood to assimilate information ($\delta^{\text{mut}} \neq \delta^{\text{res}}$). The value of the mutant trait determines its invasion fitness, which tells us if it can invade or will go extinct. The goal in adaptive dynamics is to determine what happens if the resident population(s) generates new mutants that may also have an effect on the state of the system. In most studies, the simplifying assumption is made that mutations are so rare that if one does invade, it will replace the ancient resident before the next mutant comes around. The goal is then to work out what happens when this so-called 'trait-substitution process' is iterated [26]. When a resident population resists invasion by all possible mutants, we have an ESS. Not all ESSs are evolutionary attractors, however; some ESSs can be evolutionary repellers. So-called pair-wise invasibility plots (or PIPs, which shows the sign of the mutant's invasion fitness in the $\delta^{\text{mut}} \times \delta^{\text{res}}$ plane) can show that under certain conditions a population that is not exactly at the ESS, the process of repeated invasions will lead the population away from the ESS instead of being pulled towards it.

Here, we will start with our system dominated by a resident population that is at equilibrium. As the system described in the first section comprises three nonlinear equations, numerical solutions are needed to estimate the equilibria of the resident (i.e. $\bar{I}_1, \bar{I}_2, \bar{I}_{1,2}$). Different equilibria are possible but we are typically looking at the one where both rumours are present (i.e. $\bar{I}_1, \bar{I}_2, \bar{I}_{1,2} > 0$), which will be used to calculate the information pressures λ_1^* and λ_2^* at equilibria. What is important to remember here is that those equilibria are entirely determined by the current value of δ^{res} .

Now, we can determine the fitness of the mutants using the equation in the previous section, which yields

$$w^{\text{mut}}(\delta^{\text{mut}}, \delta^{\text{res}}) = \frac{\beta_1\beta_2w_s + \beta_2\delta^{\text{mut}}\lambda_1^*w_1 + \beta_1\delta^{\text{mut}}\lambda_2^*w_2 + \delta^{\text{mut}^2}\lambda_1^*\lambda_2^*w_{1,2}}{(\beta_1 + \delta^{\text{mut}}\lambda_1^*)(\beta_2 + \delta^{\text{mut}}\lambda_2^*)},$$

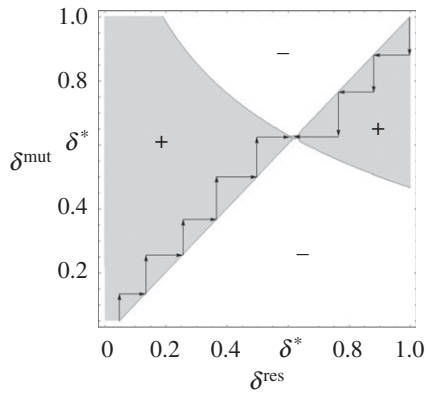


Figure 1. A pairwise invasibility plot of information assimilation strategies. Each of the drawn lines (grey lines) is a fitness contour and circumscribe the areas where the fitness of the mutant is positive (grey-shaded area) and negative (white area). The arrows represent the iteration of invasion of successive mutants as represented in the fitness landscapes. For instance, a new mutant appears with a susceptibility value that confers positive fitness (vertical arrow), consequently invading the system in which all individuals will have the same trait value (horizontal arrow). This process continues until the system reaches the ESS, denoted δ^* (here $\delta^* \approx 0.6$).

in which λ_i^* , β_i and the fitness of the informational states are determined by the resident δ^{res} where the fitness of the resident is given by $w^{\text{res}}(\delta^{\text{res}}) = w^{\text{mut}}(\delta^{\text{res}}, \delta^{\text{res}})$.

According to the PIP shown in figure 1 there is a single ESS which is evolutionary convergent (i.e. the singularity is an evolutionary attractor), meaning that the susceptibility of individuals to assimilate information slowly but inevitably evolves towards the value δ^* . When the parameters change the value of δ^* changes, but the structure of the PIP remains the same, we have not found examples of other evolutionary outcomes.

The most important conclusion to draw here is that the simultaneous coexistence of beneficial and detrimental information may favour an intermediate information use strategy (other than full ignorance or maximum gullibility) which depends on the relative information pressures and thus on the ecology of the population. In the next section, we will see if structured populations affect the evolution of gullibility.

4. Rumour dynamics in structured populations

By fixing population density and by assuming that rumours are passed on between random individuals, we make quite strong assumptions about the effect of information on population dynamics. In this section, we will relax these assumptions to explore the interaction between rumours and population structure and dynamics.

We assume that individuals live on a lattice of sites and interact only with their nearest neighbours. That is, both reproduction (into an empty neighbouring site) and communication (transmission to a neighbour) are local processes. This set-up leads to an (asynchronous) probabilistic cellular automaton, for which a suite of numerical and analytical methods are available. Here, we will just outline how we construct and analyse a cellular automaton version of the model that we considered so far; for more information about the technical details we refer to [33,34].

Cellular automata are defined in terms of a lattice of sites (typically laid out in a two-dimensional grid) and a set of events that change the state of the lattice. In our case, the events represent reproduction (into neighbouring sites), mortality and the transfer of information between neighbours (which changes the state of an individual as discussed before). We could incorporate movement or dispersal too but will refrain from doing so to avoid adding more parameters to consider (see the electronic supplementary material, appendix S5 for more information on how to construct and analyse this type of model).

Quite arbitrarily, we will assume here that information has no effect on reproduction (so $r(x_5) = r(x_1) = r(x_2) = r(x_{12}) = r_0$) but may affect survival such that having the first rumour helps individuals to survive ($d(x_1) < d_0$ where $d(x_5) = d_0$), whereas the second rumour has no other effect than neutralizing the beneficial effect in mixed-informed individuals (similar results occur if the second rumour has a slightly deleterious effect). The helpful information has a lower transmission rate than the detrimental information ($\alpha_1 < \alpha_2$); we will further assume that both rumours are forgotten with the same rate ($\beta_1 = \beta_2$).

The rumours circulating in the population may have strong effects on its dynamics: when helpful information is abundant, the population grows, until detrimental information becomes prevalent and the population decreases again (in the simulation, the detrimental information spreads faster but has no beneficial effect, figure 2a). Because reproduction is local, individuals will produce clustered distributions, and the dynamics of the rumour is even stronger clustered as information only spreads within these clusters (figure 2b). Through the beneficial effects, clusters dominated by useful rumours will expand until they are invaded by detrimental rumours. Because detrimental rumours convey no benefit, they tend to overexploit the clusters they reside in, which stop growing and may even die out.

Probabilistic cellular automata and related individual-based models can be easily used to study the ecological dynamics of such systems, but they are less appropriate to study evolutionary dynamics. The most important difficulty is that for every resident system the fitness of an entire set of mutants needs to be calculated, which essentially squares the computing time. To carry out an evolutionary analysis, we used a correlation dynamics approach [33,34]: this approximation models the dynamics of the set of spatial correlations that allows assessment of the effects of spatial structure to a first approximation and can be used to apply the basic methodology of adaptive dynamics, that is, first determine the dynamics of a resident strategy and then assess the invasion fitness of the set of mutants. Figure 3 shows a pairwise invasibility plot for a non-spatial (a) and a spatial (b) version of the model, of susceptibility to information (δ) when there is useful and detrimental rumours.

For this set of parameters, spatial structure favours a higher level of susceptibility to information ($\delta \approx 0.7$) than the ESS for non-spatial models ($\delta \approx 0.5$). Increased susceptibility is favoured under those conditions because cluster structure segregates the information types, allowing individuals to benefit from useful rumours while protecting them from detrimental ones. In other words, the spatial segregation allows clusters of related individuals [33] to benefit from the useful information. Thus, social information may interact with kin selection.

These intermediate levels of susceptibility result from global but also local population-dynamical feedbacks and are thus very sensitive to the spatial ecology of the

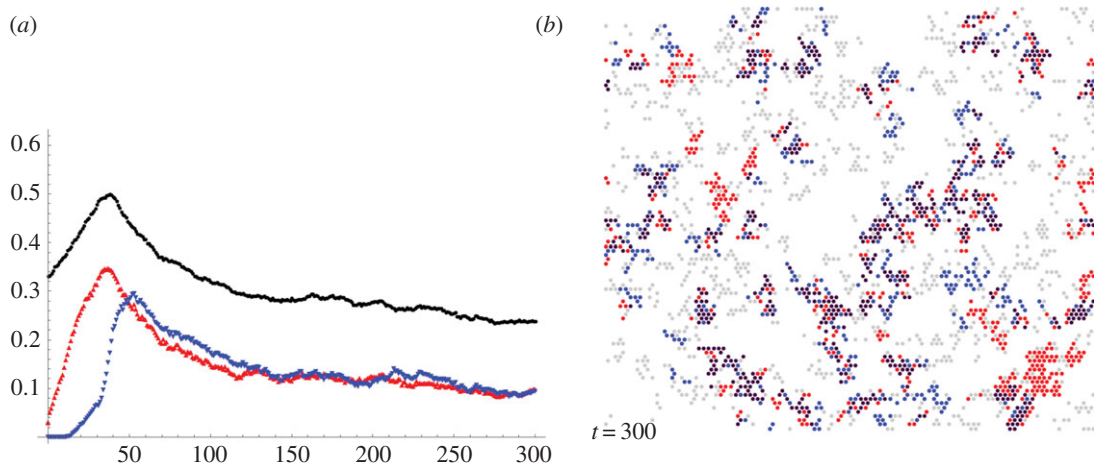


Figure 2. Probabilistic cellular automaton simulation of the resident system. (a) Global density (black) and the density of the useful rumours (red triangles) and detrimental rumours (blue inverted triangles). (b) A spatial snapshot at $t = 300$; purple dots indicate individuals of both information units. Parameter values: $\alpha_1 = 10$, $\alpha_2 = 12$, $\beta_1 = \beta_2 = 1$, $\delta = 1$, $r_0 = 0.15$, $d_0 = d_2 = d_{12} = 0.1$, $d_1 = d_0/10$ (individuals of exclusively useful information live 10 times as long); the (toroidal) lattice has 10 000 sites in a triangular pattern so that every site has six neighbours. Initially, the lattice is seeded with a proportion of $1 - d_0/r_0$ individuals in a random distribution, of which a proportion of 0.001 carries rumour 1. The detrimental information arises through misunderstanding events, which occur once every 10^4 transmissions.

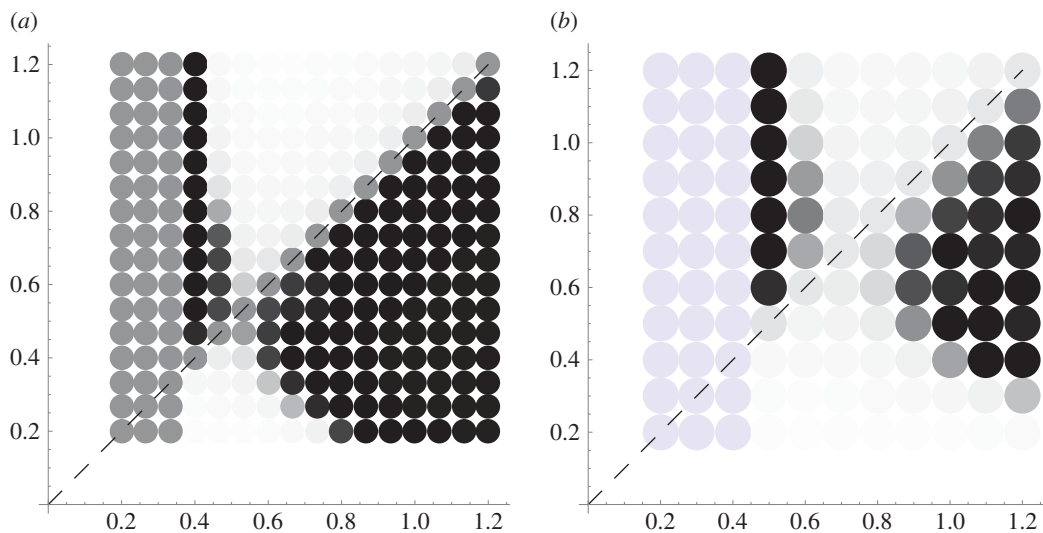


Figure 3. Pairwise invasibility plot of (a) a dynamical but non-spatial (mean-field) version and (b) a correlation dynamics version of the model. Parameters as in figure 2. Blue circles indicate δ values for which both rumours go extinct and hence δ is neutral; the grey circles indicate the value of invasion fitness: black to grey implies positive fitness, grey to white implies negative fitness. Every circle shows the average rate of increase of a mutant over $t \in [285, 300]$ (a time interval chosen such that the resident has sufficiently converged to its equilibrium) for those parameter combinations where information gets transmitted by the resident population (when not, the circles are coloured in blue).

population. The ESS susceptibility also depends strongly on the effects of the different rumours circulating in the population: if detrimental information is more harmful, lower values of δ are favoured. Any modification of the model is likely to have an effect on the end result, which implies that we may not fully understand the evolution of information use without taking into consideration its entire ecological setting.

5. Discussion

The fitness of individuals will often depend on their informational state, or, more explicitly, on what knowledge they have about the actual state of their environment. Much of this information is, of course, obtained either genetically or

individually (through experience) but often some of it is obtained socially, either just by observing others or actively through communication. While some of the social information may indeed convey useful knowledge, some of it is of no use (or even detrimental) to individuals but spread nevertheless. When individuals have no way of verifying rumours, they can only adopt an overall strategy of assimilating rumours, that is, have a certain level of 'gullibility'. Here, we show that even in the absence of eco-evolutionary feedbacks, natural selection may select an intermediate level of gullibility when both useful and costly rumours circulate. However, when information actually does have an effect on individual fitness, feedbacks may arise that cause the population to evolve towards an entirely different level of information use. Would the population as a whole be very skeptical, information (including detrimental information) will not spread easily. Under those

conditions, it pays to increase the assimilation rate to benefit from advantageous information. This benefit will cause the population to increase in density, and with it, potential for rumours to circulate, which favours the invasion of detrimental information. Thus, the use of social information is favoured to a certain extent. However, if the assimilation rate increases beyond the ESS value, detrimental information will spread too and more skeptical assimilation strategies will be favoured. This feedback is likely to depend on every detail of the population's structure and dynamics, as well as the particular mechanisms of information transfer.

Our model is based on three critical assumptions which limit its applicability: (i) transmission is done through pairwise contact, (ii) information is not checked, and (iii) information does not change in long transmission chains. Regarding the first assumption, our model does not include broadcasting of information, which is nevertheless quite common. For instance, alarm calls signalling the presence of a predator is generally public information transferred simultaneously to many individuals. Also, observational or imitation mechanisms typically involve several observers, such as when individuals scrounge for food or learn specific behaviours [35]. However, even in our model, information spreads swiftly in connected groups so this limitation is not so serious. The second assumption (i.e. that individuals have no way of checking the value of a rumour) calls for careful attention in the results presented in §§3 and 4. Sometimes an individual that imitates a conspecific can immediately check the information value. For instance, an individual observing a conspecific feeding or performing a particular behaviour can immediately check the value of the information by testing it. However, a few informational cascades have been reported. For instance, in laboratory conditions, guppies continued to use social maladaptive information (i.e. when seeking feeding patches) spread by founding members, even when other beneficial information was still present (i.e. less costly information to another feeding route) [36]. In nature, this can occur when individuals are attracted to feeding conspecifics and it can have important consequences in spatial distribution and population dynamics, especially when considering various quality patches that can deplete rapidly [32]. The sudden departure of a few individuals from a flock without the absence of a predator in avian collective movements might be another example [37], although such cases involve ephemeral information (e.g. spreading over short temporal window) and must probably be treated separately. Finally, this assumption also implies that individuals have no previous experience or pre-existing knowledge to deal with the new information they are confronted with, which needs to be accounted for in real ecological and social settings. Finally, our third assumption also needs particular attention. Long transmission chains are possible in the aforementioned examples. In culture, while there are some cases of animal traditions that seem to be rather stable over long transmission chains [38,39], the vast majority of studies of social learning are concerned with single transmissions only. Of course, this does not mean that it is always like this in nature. Transmission chain studies are rather scarce and often limited in other ways owing to the difficulty of studying such aspects in nature [40]. However, animal traditions in the wild where stable transmission over many generations have been well recorded (including humans) [41], and in this sense our results may be applied to cultural transmission.

Our model is very simple and thus does not apply to many cases *sensu stricto*, which calls for careful examination to results presented here when confronted to cases of social transmission of information in nature. However, modelling the spread of rumours using an epidemiological structure allows a more general view on the propagation of information of uncertain fitness value. This leaves a few points to be discussed regarding the modelling of information spreading as parasites within informational cascades.

For instance, as we have shown, structure is likely to impact the evolution of assimilating information. As in the epidemiology of infectious diseases, rumour spreading patterns are strongly influenced by the structure of social networks [42]. For instance, when an individual tries to pass on a rumour to a close contact it may be that this individual already received it through another route (for instance, via a common contact). This obviously applies to humans but it is also observed in animal species with pronounced social organizations [43]. Indeed, individuals typically do not interact randomly with each other, but according to some social structure involving relatives or neighbours. Not only does this affect the transmission patterns (i.e. to whom information is transferred), but also the speed at which it propagates through the population. The model we considered assumes interactions among neighbours that occupy sites on a regular lattice, but other network topologies are possible, and likely to have effects [21,22]. Moreover, just as in epidemiology the modes of transmission or the levels of contact may differ between diseases [44], rumour diffusion may depend on their specific informational content. For instance, rumours pertaining to local political events in human societies seem to spread more swiftly and widely than information concerning how to deal with climate change even if in the long run the latter is probably more important.

Some differences between information and parasites also need to be considered. Perhaps the most important one is that a given rumour may not induce the same, characteristic informational state in every host and thus induce different effects and spreading modes. Whereas parasites are clear aetiological agents, precisely what is transmitted during the transfer of a rumour is less clear. Moreover, it is widely assumed that parasite evolution is limited by physiological constraints linking transmission rate and virulence [45]; the constraints, if any, that delimit the spreading capacity of rumours are essentially unknown. The kind of susceptible–infected–susceptible (SIS) (and SIR) models of rumour propagation that we considered may therefore not give the full picture. Somehow or other, models should incorporate the fact that information is a product of cognitive processes rather than simple and blind replication when transmitted by contact. To study their propagation, one needs to consider all events potentially occurring along a cognitive chain of transmission [46], especially when studying information cascades. The representation of the transmitted information probably differs widely among individuals and its content may be altered, potentially changing at every transmission step. To take into account such aspects, one can implement a ‘mutation rate’ (resulting from either accidentally passing on wrong information or misinterpreting received information) in the model. This aspect could be particularly important in rumours because they are subject to ‘chinese whispers’ style modification along the way. As this may give rise to the transmission of a whole cloud of different versions of the rumour, Claidière and Sperber [40] argue that we need to know the properties of such clouds and how they are affected

by what they term ‘transmission chains’. Finally, individual properties may also need to be considered, as previously done in SIR and SIS models of rumours, such as denial and skepticism, remembering, forgetting, refutation and the presence of external forces acting upon diffusion behaviours, and may shed light on how information propagates and how individuals can act upon information diffusion [23–25].

Data accessibility. This article has no additional data.

Author’s contributions. Both authors agree to submission of this manuscript and both authors carry an equal degree of responsibility for the accuracy, integrity and ethics of this entire manuscript and works described therein. Alexandre Suire and Minus van Baalen contributed equally and substantially to every aspect of this work, from the development of the theoretical model to the writing of the manuscript.

Competing interests. We declare we have no competing interests.

Funding. We received no funding for this study.

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