

# Cultural evolution developing its own rules: The rise of conservatism and persuasion\*

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## Abstract

In the human sciences, cultural evolution is often viewed as an autonomous process free of genetic influence. A question that follows is, If culture is not influenced by genes, can it take any path? Employing a simple mathematical model of cultural transmission in which individuals may copy each other's traits, we show that cultural evolution favors individuals who are weakly influenced by others and able to influence others. The model suggests that the cultural evolution of rules of cultural transmission tends to create populations that evolve rapidly toward conservatism, and that bias in cultural transmission may result purely from cultural dynamics. Freedom from genetic influence is not freedom to take any direction.

## 1 Introduction

The extent to which culture is influenced by our genes has been a major topic in the human and biological sciences and remains strongly debated (Segerstråle, 2000; Laland & Brown, 2002; Rogers, 1988; Richerson & Boyd, 2005). Some biologists and evolutionary psychologists view culture as tightly controlled by a genetically determined human nature (Wilson, 1978; Lumsden & Wilson, 1985; Alexander, 1979; Tooby & Cosmides, 1992), while others see cultural and genetic evolution as distinct but interacting processes that jointly determine human behavior (Boyd

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& Richerson, 1985; Feldman & Laland, 1996). In the human sciences, cultural evolution is often viewed as an autonomous process essentially free of genetic influence (see e.g. Kroeber, 1917; Geertz, 1965; *Science for the People*, 1976; Harris, 1979). This view is also common in meme-based approaches to culture (Dennett, 1995; Blackmore, 1999; Laland & Brown, 2002). According to it, genes provide us with the abilities that make culture possible (e.g., learning and language skills) but do not bias culture in any particular direction.

Within this debate, this report addresses one general and one specific question. The general question is: If culture is not influenced by genes, can it take any path? We believe that the answer is no because culture itself harbors forces that favor some outcomes relative to others. We make this point by considering some specific forces that arise from the process of cultural transmission. We employ a simple mathematical model of cultural transmission in which individuals may copy each other's cultural traits, including traits that can affect the copying process itself. In particular, we consider as cultural traits the extent to which individuals are prepared to imitate others ("openness") and the extent to which they are able to persuade others to adopt their own cultural traits ("persuasion"). In the model, these traits affect their own transmission as well as the transmission of other traits. We show that cultural evolution favors individuals who are at once weakly influenced by others and yet able to influence others. We stress that whole in our models individuals have no genetic predispositions toward any trait value (a kind of *tabula rasa* assumption [see below]), yet definite trends emerge from the very dynamics of culture.

We are interested in traits that influence cultural transmission because theoretical studies show that modes of transmission can deeply affect cultural evolution (Campbell, 1975; Cavalli-Sforza & Feldman, 1981; Boyd & Richerson, 1985; Nakamaru & Levin, 2004). For example, the way a belief spreads depends on whether it is transmitted from parent to offspring or between peers (Cavalli-Sforza & Feldman, 1981; Boyd & Richerson, 1985). Empirical data also demonstrate many subtleties of cultural transmission, among them imitation of some individuals or behaviors but not others (Bandura, 1986). At the same time, what determines the rules of cultural transmission remains poorly understood. One possibility is that they are genetically programmed (Wilson, 1978; Lumsden & Wilson, 1981). Our models investigate another possibility: that they emerge from cultural evolution.

We do not endorse any extreme *tabula rasa* view of humans (Kroeber, 1917; Watson, 1924; Geertz, 1965). Rather, we strip models of cultural evolution of genetic influences to understand culture's potential to structure itself. Moreover, understanding what *tabula rasa* assumptions imply is important for evaluating those assumptions in the face of reality. In a similar spirit of theoretical exploration, we consider an extremely simplified cultural dynamics in which cultural transmission

is the only force that modifies the frequency of cultural traits. Our aim is not to minimize the role of other forces (e.g., natural selection or socio-economic processes), but to understand the potential effects of a single force before attempting to understand how it interacts with others.

## **The modeling framework**

We consider culture a dynamic system whose evolution depends on many forces (Cavalli-Sforza & Feldman, 1981; Boyd & Richerson, 1985; Feldman & Laland, 1996). “Evolution” means here simply “change,” and progress may or may not result. For simplicity, we consider a large, unstructured population in which individuals interact at a given rate. Each interaction involves two randomly chosen individuals, *model* and *observer*. The observer may adopt part or all of the cultural type of the model, in which case we say that cultural transmission has occurred. Our aim is to study how transmission changes the distribution of cultural traits in the population and to identify any long-term tendencies. With respect to birth and death, we study two cases. We first assume that individuals live forever. This case is studied mainly for its simplicity, but it may apply to cultural phenomena so rapid that births and deaths are negligible, such as fashions or shifts in political opinion. We then consider deaths and births explicitly. We assume that newborns are maximally open to acquiring culture but otherwise devoid of cultural traits. This recognizes that genes provide newborns with basic functionality such as memory and learning ability, and is consistent with most tabula rasa views (Kroeber, 1917; Geertz, 1965; Quigley, 1979; Rogers, 1988).

## **The paradox of “openness”**

Our first model considers the cultural evolution of a single trait, called “openness.” It corresponds to the everyday experience that people differ in the ease with which they change habits and beliefs. Intuition suggests that openness may be an important factor in cultural transmission and evolution. In reality, openness is of course not an atomic aspect of human personality: it arises from the combination of many individual traits, such as one’s attitudes toward traditional lifestyles or the habits of older generations, aspects of personality such as self-confidence and extroversion, and opinions about others in general (e.g., whether they should be trusted). To illustrate our argument, however, we start by modeling openness as a single trait that can be directly transmitted between individuals. Later we consider the more realistic case in which openness changes indirectly as a result of the cultural transmission of other traits.

Formally, we define an observer’s openness as the probability that the observer

will adopt the cultural type of the model. We use uppercase  $P$  for openness as a variable and lowercase  $p$  for particular values of  $P$ . As hinted above, openness can affect its own evolution as well as that of other traits. That is, whether an observer adopts the openness of the model,  $p_m$ , depends on the observer's own openness,  $p_o$ . More precisely, our definition of openness implies that the observer changes from  $p_o$  to  $p_m$  with probability  $p_o$ :

$$\text{Prob}(p_o \rightarrow p_m) = p_o \quad (1)$$

What will such an interaction lead to? We write  $f(p)$ , the distribution of openness in the population at time  $t$  (leaving dependence on  $t$  understood), and we seek to determine how  $f(p)$  changes with time. Let  $R$  be the number of interactions that occur, per unit time, between individuals, and let  $N_+(p)$  be the number of transitions that occur from values  $p' \neq p$  to the value  $p$ ; similarly  $N_-(p)$  is defined as the number of transitions from  $p$  to other values  $p' \neq p$ . The distribution  $f(p)$  at a particular point  $P = p$  increases due to transitions from other  $P$  values to  $p$ , and decreases due to transitions from  $p$  to other  $P$  values. This is formally expressed as:

$$f_t(p) = R[N_+(p) - N_-(p)] \quad (2)$$

where  $f_t$  is the time derivative (rate of change) of  $f$ . We now calculate  $N_+(p)$ . For a transition from  $p'$  to  $p$  to happen, two events must occur:

1. a couple must form where the observer has  $P = p'$  and the model  $P = p$ ;
2. the observer must actually change its  $P$  value from  $p'$  to  $p$ .

The latter, by definition of openness, occurs with probability  $p'$  (equation (1)). The probability that the couple is formed is, if models and observers are selected at random,  $f(p)f(p')$ . The average number of transitions from  $p'$  to  $p$  is obtained by averaging over all possible values of  $p'$  the product of these two factors,  $p'f(p')f(p)$ , which yields:

$$N_+(p) = \int_0^1 p' f(p') f(p) dp' = \bar{p} f(p) \quad (3)$$

where  $\bar{p}$  is the population average of  $P$  at time  $t$ . A similar argument gives

$$N_-(p) = \int_0^1 p f(p) f(p') dp' = p f(p) \quad (4)$$

Substituting equation (3) and equation (4) in equation (2) gives the following expression for the cultural dynamics of openness:

$$f_t(p) = R(\bar{p} - p)f(p) \quad (5)$$

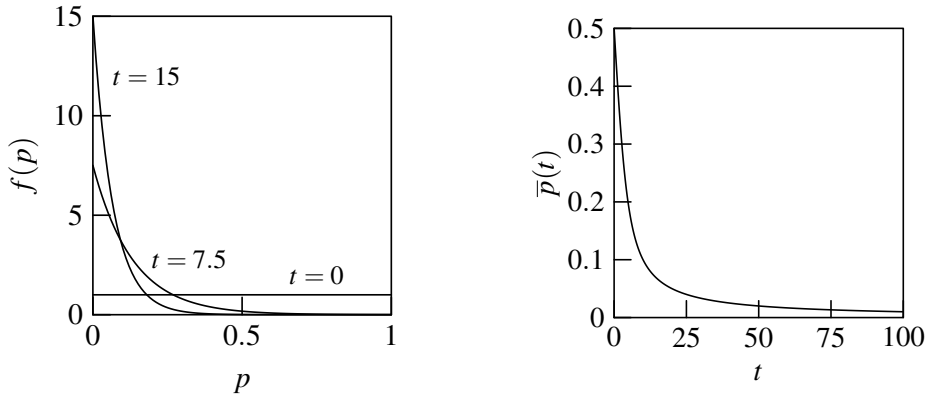


Figure 1: The decrease of openness caused by cultural transmission according to equation (1). The figures refer to a population governed by equation (5) (with  $R = 1$ ) and starting from a uniform distribution between  $p_{\min} = 0$  and  $p_{\max} = 1$ . Left: with the passage of time, the distribution of openness,  $f(p)$ , is increasingly concentrated at low values of  $P$ ; Right: consequently, the average openness  $\bar{p}$  decreases with time. Analytical expressions for the plotted functions are given in the appendix.

The meaning of equation (5) is that  $P$  values above average decrease in frequency, while the frequency of  $P$  values below average increases. In fact, the change in  $f(p)$  is negative if  $p > \bar{p}$  and positive if  $p < \bar{p}$ . These changes go in the direction of lowering openness in the population. Indeed, we show in the Appendix that in the long term all individuals will have the same  $P$  value,  $p_{\min}$ , equal to the minimum initially present in the population (see figure 1).

We derived equation (5) under the assumption that no individuals die nor are born, but the main result does not change when we introduce deaths and births. We assume that the population is stable in size, i.e. births and deaths occur at the same rate,  $r$ . If newborns have a random  $P$  value, and if death strikes at random, openness continues to follow equation (5), and nothing changes. If we assume that births introduce maximally open individuals,  $P = 1$  (see above), we obtain a cultural dynamics formally expressed as

$$\begin{cases} f_t(p) = [R(\bar{p} - p) - r]f(p) & 0 \leq p < 1 \\ f_t(1) = [R(\bar{p} - 1) - r]f(1) + r & p = 1 \end{cases} \quad (6)$$

The additional  $-r$  terms in both equations represent the unselective removal of individuals with rate  $r$ , due to deaths, while the  $+r$  term in the second equation represents the injection of individuals with  $P = 1$ . We show in the Appendix that only two  $P$  values remain in the long term:  $P = 1$  (continuously created by births) and the minimum present in the initial population,  $p_{\min}$ . The average  $P$  value can

be calculated as

$$\bar{p} = p_{\min} + \frac{r}{R} \quad (7)$$

If death and birth are rare events, compared to interacting with others, then  $r$  is much smaller than  $R$  and  $\bar{p}$  is very close to  $p_{\min}$ .

In summary, our models suggest that the cultural evolution of rules of cultural transmission tends to create populations with average openness equal or close to the minimum present in the initial population. This result emerges from few assumptions and appears potentially general. An important generalization, as discussed at the beginning of this section, considers that openness is the result of many individual traits (attitudes, ideas, behaviors, etc.) rather than something that can be transmitted directly between individuals. It is plausible that in this case only some individual traits are modified in an interaction between model and observer, so that openness will change smoothly rather than abruptly as in equation (1). Our results, however, hold whenever interactions are more likely to decrease  $P$  than to increase it. More precisely, we show in the Appendix that our results hold provided that: 1) observers become, on average, more similar to models as a result of the interaction; 2) when a change in  $P$  occurs, more conservative individuals change in smaller or equal steps than more open individuals. The argument can also be illustrated directly by means of a computer simulation of cultural dynamics. Figure 2 (black line) shows the time course of openness in a simulation in which an individual's openness is a weighted sum of 10 cultural traits. Cultural transmission occurs as before with probability  $p_o$ , but the observer copies just one of the model's traits (selected at random) rather than copying the model's  $P$  value directly. The outcome is that the openness of the whole population decreases to a very low value, as in our formal model (see the legend to figure 2 for simulation details).

The gray line in figure 2 is from a similar simulation in which cultural transmission is not perfect (when transmission occurs, the observer's trait value is set to the model's value plus a small random number). Transmission errors do not seem to modify our conclusions, and indeed the population evolves more rapidly towards conservatism. The reason is that the assumed cultural dynamics implies that a transmission error that decreases openness is more likely to be preserved in the population than an error that increases openness. Indeed, errors in transmission will introduce in the population lower values of openness than initially present, leading in the long run to a more conservative population (see also the Appendix).

In summary, extending the model so that openness is the result of many individual traits, each of which may be subject to transmission errors, does not seem to alter our main result that evolvable cultural transmission should cause populations to become very conservative. An important issue is whether cultural or

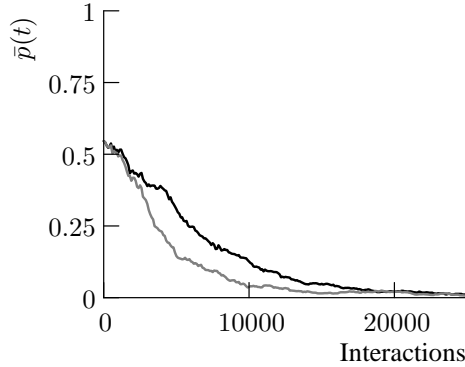


Figure 2: Simulation of cultural dynamics of openness as a compound trait. We consider 100 individuals that meet at random. Each individual has 10 cultural traits,  $x_1, \dots, x_{10}$ , and openness is defined as a weighted average of trait values,  $p(x_1, \dots, x_{10}) = \sum_{i=1}^{10} w_i x_i$  (if  $p < 0$  arises from this computation, then  $p$  is set to 0.001; if  $p > 1$  arises, then  $p$  is set to 1). The weights  $w_1, \dots, w_{10}$  are drawn from a normal distribution at the start of the simulation and are the same for all individuals. The initial trait values are drawn from a uniform distribution, with the constraint that the minimum  $p$  value in the population is below 0.01 and the population average is above 0.5. Black line: error-free cultural transmission (model traits are exactly copied by observers); gray line: cultural transmission with errors (observers acquire models' traits plus a number drawn from a normal distribution with standard deviation of 0.1).

genetic evolution harbor other forces that can prevent such an outcome. We take up this issue in the Discussion.

## Cultural evolution of “persuasion”

We turn now to another trait capable of influencing cultural transmission. It is common to see that people vary in their ability to persuade others to adopt their opinions, in their willingness to teach or instruct others, in the degree to which they advertise their traits. Let a variable  $Q$  summarize all such properties, for simplicity referred to as “persuasion”. Formally, we define  $Q$  as a characteristic of the model giving the probability that the observer adopts the model's cultural type. As above, we note that  $Q$  is a trait that influences its own evolution. The analogue of equation (1) is:

$$\text{Prob}(q_o \rightarrow q_m) = q_m \quad (8)$$

Via the same route leading to equation (5) we derive the following equation for the population distribution  $g(q)$  of  $Q$ :

$$g_t(q) = R(q - \bar{q})g(q) \quad (9)$$

where  $\bar{q}$  is the average of  $Q$  at time  $t$ . This equation is very similar to equation (5), but the right-hand side has opposite sign. Consequently,  $Q$  values below average tend to increase in frequency, while the frequency of  $Q$  values above average decreases. Thus, evolution proceeds towards the highest existing  $Q$  value. Other modifications of the model (births and deaths, persuasion as a compound trait, transmission errors) can be treated as above and yield the same conclusion: in the long term all individuals will have a  $Q$  value equal or close to the maximum present in the initial population.

## Coevolution of “openness” and “persuasion”

Our last model considers openness and persuasion together. We assume for simplicity that, when transmission occurs, observers copy both the models’  $P$  and  $Q$ . The probability of this event is assumed proportional to both the observer’s openness and the model’s ability to persuade:

$$\text{Prob}(p_o q_o \rightarrow p_m q_m) = p_o q_m \quad (10)$$

With reasoning similar to that leading to equations (5) and (9), it can be shown that the joint distribution of openness and persuasion,  $f(p, q)$ , evolves according to:

$$f_t(p, q) = R(q\bar{p} - p\bar{q})f(q, p) \quad (11)$$

In this equation, the proportion of individuals with the cultural type  $(p, q)$  increases if  $p/q < \bar{p}/\bar{q}$ , and decreases if  $p/q > \bar{p}/\bar{q}$ . Thus, cultural evolution favours individuals with a low  $p/q$  ratio, i.e. conservative and persuasive individuals. An equilibrium distribution  $f(p, q)$  is such that  $p/q = \bar{p}/\bar{q}$  for all pairs  $(p, q)$  for which  $f(p, q) > 0$ . At a stable equilibrium, all individuals have  $P = p_{\min}$ , the minimum present in the initial population (see above). If  $p_{\min} > 0$ , all individuals will also have  $Q = q_{\max}$ , while if  $p_{\min} = 0$  some individuals may retain a  $Q$  value lower than  $q_{\max}$  (because individuals with  $P = 0$  cannot change). These conclusions are minimally modified by introducing births and deaths or gradual change in  $P$  and  $Q$ . Figure 3 shows an example of coevolution between  $P$  and  $Q$ .

## Discussion

Our models suggest that cultural evolution should produce individuals who are reluctant to copy others and yet promote being copied by others. Empirical data provide some support: people tend to stick to their ideas, including e.g. religious faith (Sandomirsky & Wilson, 1990; Lawton & Bures, 2000; Loveland, 2003) and political views (Kent Jennings & van Deth, 1990; Richardson, 1991), and it is common



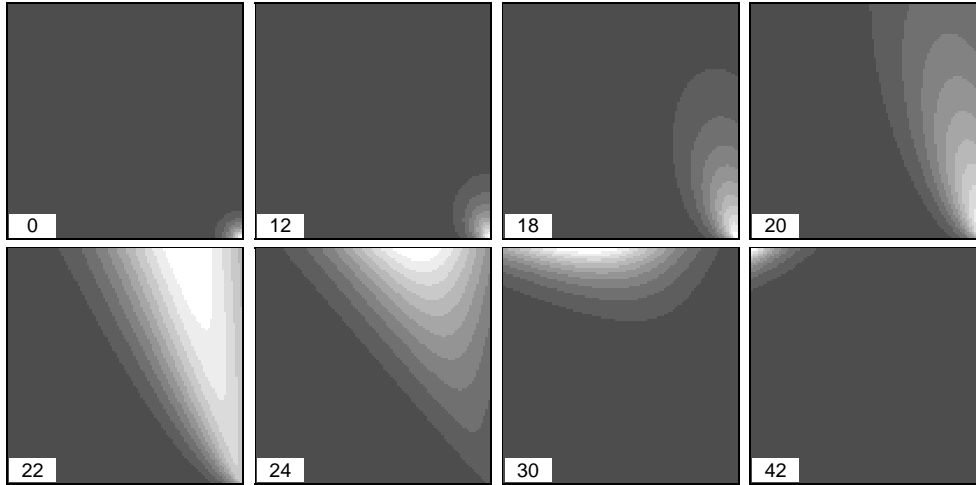


Figure 3: Cultural coevolution of openness and persuasion. In each square, a  $(p, q)$  pair is represented as the point of corresponding coordinates. Each panel represents the distribution  $f(p, q)$  at an instant of time (as given at bottom left). A lighter shade of grey indicates a higher value of  $f(p, q)$ , with white corresponding to the current maximum. The sequence shows how a population, initially concentrated in a region of high  $P$  and low  $Q$ , is progressively changed by cultural evolution into the opposite situation, where low  $P$  and high  $Q$  are most common. The time steps are not evenly spaced; rather they have been selected to illustrate the change in shape of  $f(p, q)$  over the whole process. The initial distribution was  $\hat{f}(p, q) = e^{-20d(p, q)}$ , where  $d(p, q)$  is the distance from the point  $(p, q) = (1, 0)$  (bottom-right corner of the square). The figure is based on numerical integration of equation (11).

to advertise or argue for one’s views. These traits have interesting parallels in genetic evolution. “Conservatism” promotes the integrity of cultural types, and may be compared to mechanisms of genomic integrity (Maynard Smith, 1995). “Persuasion” promotes the spreading of cultural types, which follows the general tendency of evolutionary processes to favour efficient reproduction (Dawkins, 1976; Fisher, 1958).

It should be possible to test whether individual personalities change during life in the direction predicted by our models. Personality is often studied within the so-called “Big Five” framework, which considers five broad dimensions along which individual personalities vary (John & Srivastava, 1999). Recent studies observe some significant correlations between personality measures and age, but it is difficult to relate these results to our models. For instance, while one of the Big Five dimensions is referred to as “openness”, it is not defined exactly as in our models (e.g., it includes intelligence as well as curiosity). It is nevertheless interesting to note that a decrease in openness (*sensu* Big Five) with age is one

of the most robust findings in studies of long-term personality changes (McCrae et al., 1999; Labouvie-Vief et al., 2000; Srivastava et al., 2003). Traits that are potentially involved in persuading others appear in most, if not all, Big Five dimensions, and no clear conclusion seems possible based on published data. These studies suggest, however, that our models could be tested by developing specific questionnaires and experiments.

In our models population reach almost complete conservatism, but this is not true of actual populations. The reasons should be sought in forces that we ignored yet can influence the cultural evolutionary process. For instance, many personality traits are under both environmental and genetic control (Plomin et al. 2000; Laland & Brown 2002; see also “guided variation” in Boyd & Richerson 1985) and it is possible that our genetic constitution does not allow complete conservatism. In such a case a pure *tabula rasa* hypothesis would not be adequate to study the dynamics of openness. Natural selection and socio-economic processes are examples of other, potent forces that can shape culture (Richerson & Boyd, 2005; Laland et al., 1995; Feldman & Laland, 1996; Bisin & Verdier, 2001). We have chosen not to study them in this paper because we wanted to start from a simple case in which the effects of evolvable cultural transmission is not confounded with other forces. Such effects are poorly known and it seemed to us premature to study a complex model before having understood simpler ones. Most mathematical models of cultural evolution assume that how we learn from others is under genetic control (Boyd & Richerson, 1985; Henrich & Boyd, 1998) and do not allow for cultural modification of transmission rules (but see Takahasi, 1998). Richerson & Boyd, for instance, argue that natural selection has injected in our psychology a degree of conformism which improves our ability to choose adaptive cultural traits (Boyd & Richerson, 1985; Richerson & Boyd, 2005). Our arguments show that biases in cultural transmission may result purely from cultural dynamics. Thus even if the genes are not structuring culture, culture structures itself. Freedom from genetic influences is not freedom to take any direction.

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## Appendix

### Analysis of equations (5) and (9)

The solution of equation (5) can be derived as follows. First, the equation can be solved formally by separation of variables, yielding

$$f(p) = \Pi(t) e^{-Rtp} \hat{f}(p) \quad (\text{A.1})$$

where  $\Pi(t) = \exp(R \int_0^t \bar{p}(\tau) d\tau)$  is an unknown function, because  $\bar{p}(t)$  is as yet unknown. It can be determined by enforcing the normalization  $\int_0^1 f(y) dy = 1$  in equation (A.1), leading to

$$\Pi(t) = \frac{1}{\int_0^1 \hat{f}(y) e^{-Rty} dy} \quad (\text{A.2})$$

Using equation (A.2) in equation (A.1) gives the solution:

$$f(p) = \frac{\hat{f}(p) e^{-Rtp}}{\int_0^1 \hat{f}(y) e^{-Rty} dy} \quad (\text{A.3})$$

Let us now define  $p_{\min}$  as the lowest value for which the initial distribution  $\hat{f}(p)$  is non zero:

$$p_{\min} = \underset{p}{\operatorname{argmin}} \{ \hat{f}(p) > 0 \} \quad (\text{A.4})$$

We can now see that the whole population concentrates in the long run at  $p_{\min}$ . It is sufficient to note that, according to equation (A.3), the ratio  $f(p)/f(p_{\min})$  goes to zero for  $t \rightarrow \infty$  for any  $p > p_{\min}$ :

$$\lim_{t \rightarrow \infty} \frac{f(p)}{f(p_{\min})} = \frac{\hat{f}(p)}{\hat{f}(p_{\min})} \lim_{t \rightarrow \infty} e^{-R(p-p_{\min})t} = 0 \quad (\text{A.5})$$

That is, the share of the population with any  $P$  value larger than  $p_{\min}$  becomes negligible in the long run. Equation (A.3) also implies that the solution with  $\bar{p} = 0$  is the only stable solution. In fact, if  $\bar{p} > 0$  it is possible to introduce individuals in the population that lower  $p_{\min}$  and hence cause the population to evolve toward lower openness. This can happen, for instance, in the presence of transmission errors whereby an observer sometime ends up with a lower  $P$  value than the model (figure 2). The only equilibrium that cannot be modified in this way is  $\bar{p} = 0$ , because it is not possible to introduce individuals with a lower value of openness.

If  $\hat{f}(p)$  is a uniform distribution between 0 and 1 ( $\hat{f}(p) = 1$ ), we can write from equation (A.3) the following explicit expressions for  $f(p)$  and  $\bar{p}$ , which have been used to draw figure 1:

$$f(p) = \frac{Rte^{-Rtp}}{1 - e^{-Rt}} \quad \bar{p} = \frac{1}{Rt} - \frac{e^{-Rt}}{1 - e^{-Rt}} \quad (\text{A.6})$$

The dynamics of persuasion can be treated in the same way as openness, with obvious changes such as that  $\bar{q} = 1$  rather than  $\bar{p} = 0$  is the global attractor. The solution of equation (9) is

$$g(q) = \frac{\hat{g}(q)e^{Rtq}}{\int_0^1 \hat{g}(y)e^{Rty} dy} \quad (\text{A.7})$$

where  $\hat{g}$  is the initial distribution of persuasion.

### Analysis of equation (6)

Our main result, equation (7), is obtained as follows. First, note that the equilibrium condition  $f_t = 0$  in equation (6), top, implies that there can be only one  $P$  value (other than  $P = 1$ ) for which  $f(p) \neq 0$ . From the same equation we derive that such a value, written  $p^*$ , satisfies

$$\bar{p} = p^* + \frac{r}{R} \quad (\text{A.8})$$

It is then easy to establish that  $p^* = p_{\min}$  following the same method used above. Formal integration of equation (6), top, yields:

$$f(p) = \hat{f}(p)\Pi(t)e^{-(Rp+r)t} \quad (\text{A.9})$$

where  $\Pi(t)$  is defined as in equation (A.1) (but has a different explicit expression). Equation (A.5) is now valid for every  $p$  such that  $p_{\min} < p < 1$  (it is not valid for  $P = 1$  because individuals with  $P = 1$  are continuously created). Since  $p_{\min}$  is the only  $P$  value that survives in the long run, other than  $P = 1$ , we have  $p^* = p_{\min}$  as claimed.

### More general interactions

We turn now to interactions in which observers do not copy models exactly. Consider the possible interactions between two individuals with  $P$  values  $p_i$  and  $p_j$ . If individual  $i$  is the observer, we have a change  $p_i \rightarrow p'_i$  with probability  $p_i$ , where

$p'_i$  is the  $P$  value of individual  $i$  after the interaction. We assume that  $p'_i$  is, on average, closer to  $p_j$  than  $p_i$ , i.e. interactions tend to make individuals more similar. Likewise, if individual  $j$  is the observer, we have a change  $p_j \rightarrow p'_j$  with probability  $p_j$ . Given such possible transitions, the expected change in the mean  $P$  value of these individuals,  $p = (p_i + p_j)/2$ , can be calculated as

$$\Delta p = p_i \Delta p_i + p_j \Delta p_j \quad (\text{A.10})$$

where  $\Delta p_i = p'_i - p_i$  is the change in individual  $i$ 's  $P$  value if a transition occurs (which, in turn, happens with probability  $p_i$ ). If  $p'_i$  is more similar to  $p_j$  than  $p_i$ , we can write

$$p'_i = a_i p_j + (1 - a_i) p_i \quad 0 < a_i < 1 \quad (\text{A.11})$$

where, in general,  $a_i$  may be a function of  $p_i$  and  $p_j$  (see below). We can now write

$$\Delta p_i = p'_i - p_i = a_i (p_j - p_i) \quad (\text{A.12})$$

$$\Delta p_j = p'_j - p_j = a_j (p_i - p_j) \quad (\text{A.13})$$

Using these expressions in equation (A.10) we obtain

$$\Delta p = -(a_i p_i - a_j p_j) (p_i - p_j) \quad (\text{A.14})$$

The sign of this expression determines whether the interaction has, on average, increased or decreased the average openness of the interacting individuals (hence, of the whole population). The sign is negative, i.e. average openness decreases, if  $a_i = a_j$ , or if  $p_i > p_j$  implies  $a_i \geq a_j$ . These are very reasonable conditions, because they mean that, when a change in  $P$  occurs, more conservative individuals change less, or at most the same amount, than more open individuals.

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