Cultural Evolution Develops Its Own Rules

The Rise of Conservatism and Persuasion

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In the human sciences, cultural evolution is often viewed as an autonomous process essentially 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, it can be shown 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. Bias in cultural transmission may result purely from cultural dynamics. Freedom from genetic influence is not freedom to take any direction.

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 and Brown 2002; Rogers 1988; Richerson and Boyd 2005). Some biologists and evolutionary psychologists view culture as tightly controlled by a genetically determined human nature (Wilson 1978; Lumsden and Wilson 1985; Alexander 1979; Tooby and Cosmides 1992), while others see cultural and genetic evolution as distinct but interacting processes that jointly determine human behavior (Boyd and Richerson 1985; Feldman and Laland 1996). In the human sciences, cultural evolution is often viewed as an autonomous process essentially free of genetic influences (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 and 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 weakly influenced by others yet able to influence others. We stress that while in our models individuals have no genetic predispositions toward any trait value (a kind of tabula rasa assumption [see below]), 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 and Feldman 1981; Boyd and Richerson 1985; Nakamaru and Levin 2004). For example, the way a belief spreads depends on whether it is transmitted from parent to offspring or between peers (Cavalli-Sforza and Feldman 1981; Boyd and 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 and 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 socioeconomic 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 and Feldman 1981; Boyd and Richerson 1985; Feldman and 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 [1961]; Rogers 1988).

The Paradox of "Openness"

Our first model considers the cultural evolution of a single trait, "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 a particular value 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:

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

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 because of transitions from other P values to p and decreases because of transitions from p to other P values. This is formally expressed as

$$f_t(p) = R[N_+(p) - N_-(p)], \tag{2}$$

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 in which the observer has $P = p'$ and the model $P = p$, and (2) the observer must actually change its P value from p' to p. The latter, by definition, 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

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

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

$$N_-(p) = \int_0^1 pf(p)f(p')dp' = pf(p). \tag{4}$$

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

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

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 reducing 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 (fig. 1).

We derived equation 5 on the assumption that no one dies or is born, but the main result does not change when we introduce deaths and births. We assume that the population is stable in size—that 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
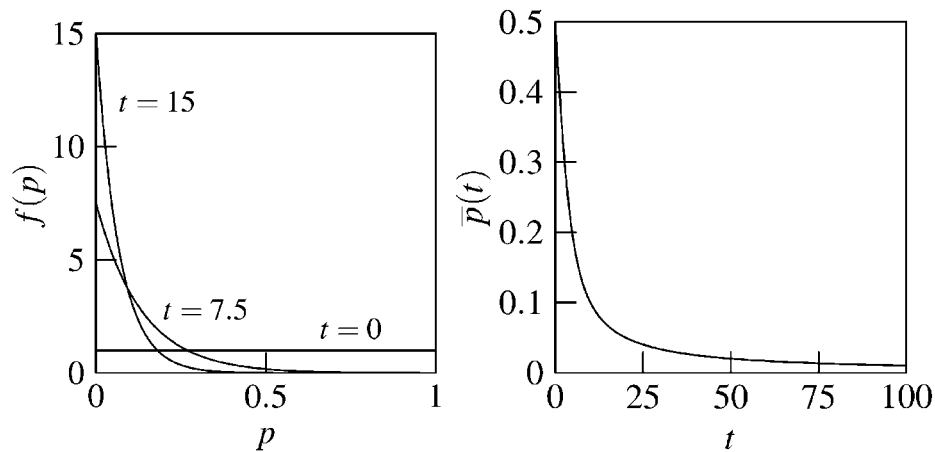
Figure 1. The decrease of openness caused by cultural transmission according to equation 1. The figures refer to a population governed by equation 5 (with $R = 1$) and starting from a uniform distribution between $p_{min} = 0$ and $p_{max} = 1$. *Left*, with the passage of time, the distribution of openness, $f(p)$, 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.

open individuals, $P = 1$, we obtain a cultural dynamics formally expressed as

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

The additional $-r$ terms in the two 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 with 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 openness 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, with the result 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 and (2) when a change in P occurs more conservative individuals change in smaller or equal steps than more open individuals. The argument can 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 ten 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.

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 toward conservatism. This is because 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 into the population lower values of openness than initially present, leading in the
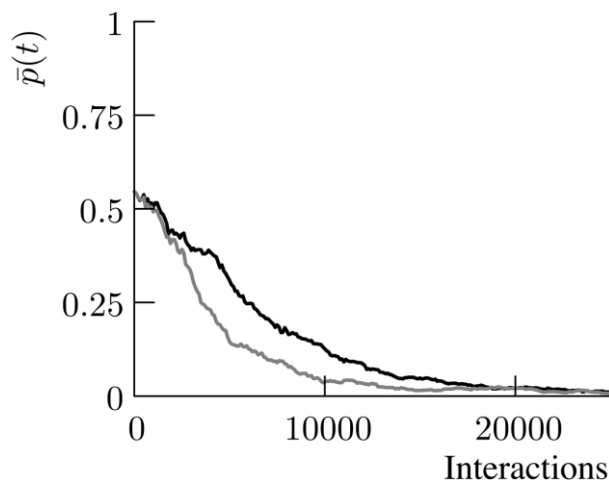
Figure 2. Simulation of cultural dynamics of openness as a compound trait. We consider 100 individuals who meet at random. Each individual has ten cultural traits, $x_1, \ldots, x_{10}$, and openness is defined as a weighted average of trait values, $p(x_1, \ldots, x_{10}) = \sum_{i=1}^{10} w_i x_i$ (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 $w_1, \ldots, w_{10}$ 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).

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 genetic evolution harbors other forces that can prevent such an outcome. We take up this issue below.

The Cultural Evolution of "Persuasion"

It is common for people to vary in their ability to persuade others to adopt their opinions, their willingness to teach or instruct others, and 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 will adopt 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

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

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

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

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 the opposite sign. Consequently, Q values below average tend to increase in frequency, while the frequency of Q values below average decreases. Thus, evolution proceeds toward 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 P and Q. The probability of this event is assumed proportional to both the observer's openness and the model's ability to persuade:

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

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

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

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 favors individuals with a low p/q ratio—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. 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, for example, religious faith (Sandomirsky and Wilson 1990; Lawton and Bures 2000; Loveland 2003) and political views (Kent Jennings and van Deth 1990; Richardson 1991), and it is common to
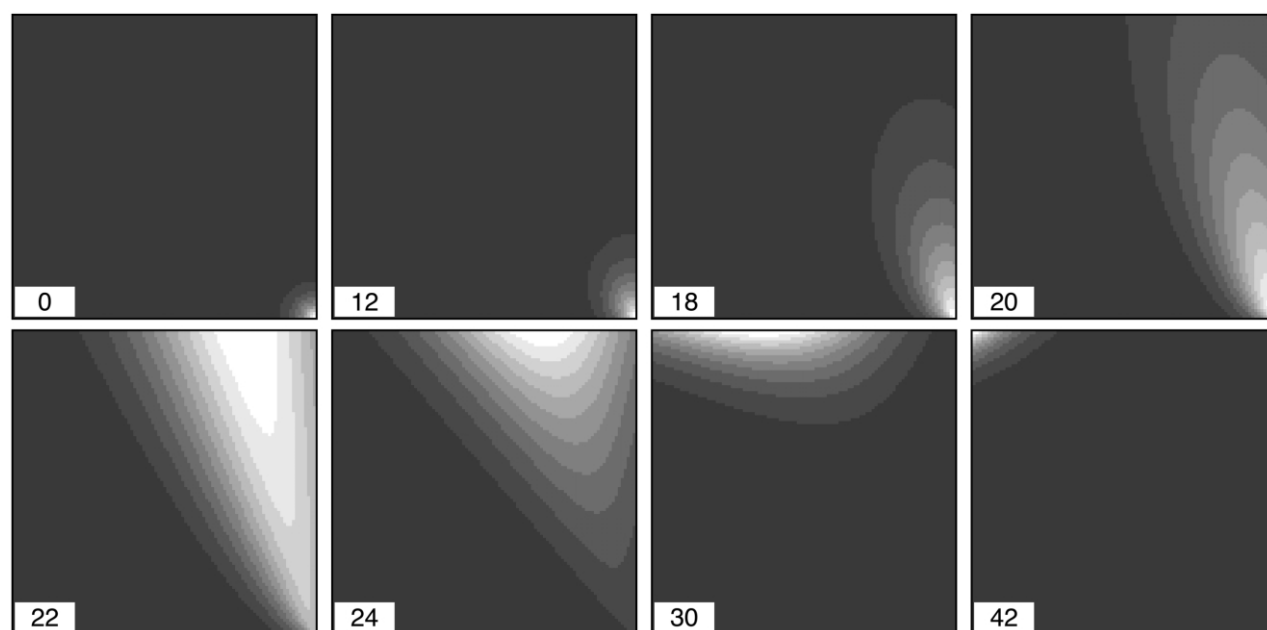
Figure 3. Cultural coevolution of openness and persuasion. In each square, a (p,q) pair is represented as the point of corresponding coordinates. Each panel represents the distribution $f(p,q)$ at an instant of time (*bottom left*). A lighter shade of gray indicates a higher value of $\hat{f}(p,q)$, 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, in which 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.

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 and Szathmáry 1995). Persuasion promotes the spreading of cultural types, which follows the general tendency of evolutionary processes to favor efficient reproduction (Dawkins 1976; Fisher 1958).

It should be possible to test whether individual personalities change in the direction predicted by our models. Personality is often studied in the so-called Big Five framework, which considers five broad dimensions along which individual personalities vary (John and 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 change (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 from the published data. These studies suggest, however, that our models could be tested by developing specific questionnaires and experiments.

Whereas in our models populations reach almost complete conservatism, this is not true of actual populations. The reasons should be sought in forces that we have ignored but that can influence the cultural evolutionary process. For instance, many personality traits are under both environmental and genetic control (Plomin et al. 2000; Laland and Brown 2002; see also "guided variation" in Boyd and Richerson 1985), and it is possible that our genetic constitution does not allow complete conservatism. In such a case a simple tabula rasa hypothesis will be inadequate to describe the dynamics of openness. Natural selection and socioeconomic processes are examples of other potent forces that can shape culture (Rich-

erson and Boyd 2005; Laland, Kumm, and Feldman 1995; Feldman and Laland 1996; Bisin and Verdier 2001). We have chosen not to examine them have because we wanted to start from a simple case in which the effects of evolvable cultural transmission were 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 the way we learn from others is under genetic control (Boyd and Richerson 1985; Henrich and Boyd 1998) and do not allow for cultural modification of transmission rules (but see Takahasi 1998). Richerson and Boyd, for instance, argue that natural selection has injected into our psychology a degree of conformism which improves our ability to choose adaptive cultural traits (Boyd and Richerson 1985; Richerson and Boyd 2005). Our arguments show that biases in cultural transmission may result purely from cultural dynamics. Thus even if genes are not structuring culture, culture structures itself. Freedom from genetic influence is not freedom to take any direction.

Acknowledgments

Appendix

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

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

where $\Pi(t) = \exp\left(R\int_0^t \bar{p}(\tau)d\tau\right)$ 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

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

Using equation A.2 in equation A.1 gives the solution

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

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

$$p_{\min} = \operatorname*{argmin}_{p} \{\hat{f}(p) > 0\}. \qquad (A.4)$$

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 $t \to \infty$ for any $p > p_{\min}$:

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

In other words, 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 thus cause the population to evolve toward reduced 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 (fig. 2). The only equilibrium that cannot be modified in this way is $\bar{p} = 0$, because it is impossible to introduce individuals with a lower value for 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:

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

The dynamics of persuasion can be treated in the same way as that of 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

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

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

Our main result, equation 7, is obtained as follows: First, 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

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

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

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

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.

With regard to interactions in which observers do not copy models exactly, we 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—that 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

$$\Delta p = p_i \Delta p_i + p_j \Delta p_j, \tag{A.10}$$

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

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

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

$$\Delta p_i = p_i' - p_i = a_i(p_j - p_i), \tag{A.12}$$

$$\Delta p_j = p_j' - p_j = a_j(p_i - p_j). \tag{A.13}$$

Using these expressions in equation A.10 we obtain

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

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—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 than or at most the same amount as more open individuals.

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