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Rapid evolution of social learning

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Abstract

Culture is widely thought to be beneficial when social learning is less costly than individual learning and thus may explain the enormous ecological success of humans. Rogers (1988. Does biology constrain culture. *Am. Anthropol.* **90**: 819–831) contradicted this common view by showing that the evolution of social learning does not necessarily increase the net benefits of learned behaviours in a variable environment. Using simulation experiments, we re-analysed extensions of Rogers' model after relaxing the assumption that genetic evolution is much slower than cultural evolution. Our results show that this assumption is crucial for Rogers' finding. For many parameter settings, genetic and cultural evolution occur on the same time scale, and feedback effects between genetic and cultural dynamics increase the net benefits. Thus, by avoiding the costs of individual learning, social learning can increase ecological success. Furthermore, we found that rapid evolution can limit the evolution of complex social learning strategies, which have been proposed to be widespread in animals.

Introduction

Social learning is a mechanism that allows animals to acquire behaviours by copying other individuals without engaging in trial and error learning (Heyes, 1994). Thus, social learning is widely assumed to be a beneficial trait that increases ecological success. In particular, it is widely believed that social learning allowed rapid population growth and expansion of humans into a wide variety of different habitats (Henrich & McElreath, 2003). The main mechanism by which social learning increases ecological success is often assumed to be the avoidance of costs of individual learning, such as time or energy expenditure (Lumsden & Wilson, 1981; Boyd & Richerson, 1985). Using a simple mathematical model Rogers (1988) contradicted this assumption, which implied that other mechanisms must be involved in explaining how social learning can increase ecological success.

Rogers' model described interactions between genetic evolution, i.e. the change in gene frequency for social

learning, and cultural evolution, i.e. the change in the frequency of an adaptive behaviour that can be acquired through individual or social learning, in a variable environment. The model assumed that individual learning is achieved through trial and error learning. Individual learning is costly but provides a way to acquire an adaptive behaviour, which in this context refers to the behaviour that yields the highest fitness benefits in a particular environment. In contrast, a social learner gains the adaptive behaviour more cheaply by copying others. However, there is no guarantee that social learners will acquire the most adaptive behaviour. For example, they might copy individuals that lack the trait. The model therefore has two ways to obtain the adaptive behaviour: to pay the costs of individual learning and reap the fitness benefits, or to learn socially at lower cost but potentially pay the fitness costs of not having the adaptive behaviour. Using this model, Rogers showed that the frequency of social learners in a population increases if the costs of individual learning increase and if the variability of the environment decreases. The model further showed that while social learning is likely to evolve under many conditions, in the long term this does not increase the mean fitness of the population (Fig. 1).

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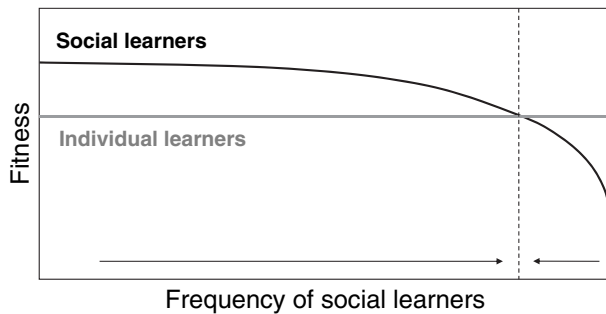e-mail: mathias.franz@eva.mpg.de

Fig. 1 Illustration of Rogers' finding that the evolution of social learning does not increase the mean fitness of the population. At low frequencies social learners have a higher fitness than individual learners because they cheaply acquire the adaptive behaviour. However, with increasing frequency, social learners are more likely to copy outdated behaviours from other social learners. This leads to a decrease in fitness of social learners with increasing frequency of individuals with this strategy. In contrast, the fitness of individual learners is independent of the frequency of social learners. In an evolutionary process, the frequency of social learners will converge to a point at which social and individual learners have the same fitness (indicated by the dashed line). At this point, the fitness of the population is the same as in a population with only individual learners.

Rogers (1988) assumed that the mean fitness of the population is a measure of adaptation. His finding that the evolution of social learning does not increase population mean fitness seems to contradict the assumption that social learning is beneficial. Thus, Rogers' finding has sometimes been termed 'Rogers' paradox'. Rogers (1988) acknowledged that the use of the term 'adaptation' in this context is problematic. In particular, evolutionary biologists typically use adaptation to refer to fitness differences between individuals rather than differences between groups, and in keeping with this focus on individual differences, Rogers showed that social learners could invade a population of individual learners. However, Rogers measured 'adaptation' by comparing the mean fitness of groups, which he took to mean 'net benefits' or 'ecological success', as used above. The expectation that social learning increases ecological success in this case is not based on group selection thinking, but is rather motivated by trying to find explanations for the mechanisms that drove the massive geographic expansion and population growth of humans. Rogers' (1988) important finding in this context was that avoiding costs of individual learning by social learners is insufficient to explain the enormous ecological success of humans.

Since Rogers' (1988) paper was published, researchers have invested much effort to identify mechanisms by which social learning increases ecological success. The main mechanisms that have been proposed involved more complex behavioural strategies used by individuals to decide when to stick with a behaviour that was acquired by one mechanism or to use alternative learning mechanisms (e.g. Boyd & Richerson, 1995; Galef, 1995; Kameda & Nakanishi, 2002, 2003; Laland, 2004; Enquist et al., 2007). For instance, Enquist et al. (2007) proposed critical social learning as a strategy by which individuals assess the success of social learning (i.e. if they acquired the most adaptive behaviour) and, if unsuccessful, then perform individual learning.

Rogers made the assumption that genetic evolution is much slower than cultural evolution. The assumption that genetic and ecological (or cultural) dynamics occur on very different time scales is common, and it was used by Rogers to obtain an analytical solution for long-term genetic dynamics. However, this assumption might not be well justified in light of accumulating findings of rapid evolution in biological systems. Evolution can be considered rapid 'when it occurs at the same time as, and results in, alterations to ecological dynamics' (Hairston et al., 2005). Note that according to this definition the term 'rapid evolution' does not necessarily imply that evolutionary changes occur within few decades or centuries. Instead, rapidity is assessed in comparison to an ecological time scale (e.g. to environmental changes, which might occur within a few years or a few millennia). In addition, rapid evolution does not necessarily involve a high mutation rate that introduces new alleles into the gene pool of the population. Rapid evolution can also occur if the number of different genotypes does not change over time, provided that changes in frequencies of these genotypes occur on the same time scale as ecological dynamics.

A famous example of rapid evolution involves measurable changes in beak size and shape in Darwin's finches over a 30-year period. These changes were mainly triggered by changes in precipitation that altered food supply (Grant & Grant, 2002). Other examples include predator–prey dynamics (Hairston & Dillon, 1990; Yoshida et al., 2003), host–parasite interactions (Duffy & Sivars-Becker, 2007), biological invasions (Lambrinos, 2004) and sexual signals (Zuk & Tinghitella, 2008). Furthermore, theoretical research has shown that overlap between ecological and evolutionary time scales can alter predator–prey dynamics (Van Der Laan & Hogeweg, 1995; Abrams & Matsuda, 1997) and establishment of parasites in host populations (Antia et al., 2003).

We investigated the effects of rapid evolution in the context of cultural dynamics. For this purpose we used simulation experiments to re-analyse a more general version of Rogers' model. By simulating model dynamics we did not make any assumptions about the speed of genetic evolution relative to cultural evolution. Thus, we were able to investigate under which parameter settings rapid evolution occurs and what effects it has on model dynamics. In an additional analysis, we also included 'critical social learning' – a complex behavioural learning strategy that Enquist et al. (2007) showed can increase

the mean fitness of a population. In keeping with Rogers' model, we also focused on mean population fitness as a proxy for ecological success. Our results show that rapid evolution of social learning can strongly increase the mean fitness of a population. Furthermore, we show that rapid evolution can constrain the evolution of complex social learning strategies.

Methods

Model description

We used a model that is based on Enquist et al. (2007), which is a more general version of the model described by Rogers (1988). This model assumes that individuals live in a variable environment that changes its state with a certain probability from one generation to the next. To perform optimally in a specific environment, individuals can obtain an adaptive behaviour (which yields the highest fitness pay-off) either through individual learning (i.e. by trial and error learning) or by social learning (i.e. by copying the behaviour of others). The individuals are assumed to reproduce asexually. Thus, the learning behaviour of an individual is assumed to match that of its parent (subject to a low rate of mutation, described below).

The lives of the animals consist of two main phases: firstly learning and secondly reproduction. Learning the currently adaptive behaviour increases the individual's fitness by a certain amount b. Individual learners will always obtain the adaptive behaviour, but they have to pay a cost c_i (relative to b). The fitness of individual learners w_i is therefore always:

$$w_i = 1 + b \times (1 - c_i) \tag{1}$$

where '1' is the baseline fitness of individuals, which is not affected by learning. The index i refers to 'individual learning'.

Social learners are assumed to copy the behaviour of an individual from the previous generation. This strategy is cost-free, but it is more risky than individual learning because there is no guarantee that a social learner will acquire the behaviour that is adaptive in the current generation. Because social learners are assumed to copy from a randomly selected individual, the probability of obtaining the currently adaptive behaviour equals the frequency of this behaviour in the previous generation. The fitness of social learners w_s in a specific generation t is therefore given by:

$$w_{s,t} = 1 + a_{t-1} \times b \tag{2}$$

where a_{t-1} is the frequency of individuals in the previous generation that acquired the currently adaptive behaviour.

Environmental dynamics are determined by the parameter u, which is a measure of environmental uncertainty. The value of u gives for each generation the probability of an environmental change. The Enquist

et al. (2007) model used here extends Rogers' (1988) model by assuming that an infinite number of possible environmental states and behaviours exists. Thus, once a state and its associated behaviour are used, the model does not revert back to that state (as compared with a situation in which the environment switches between two states). Therefore, it is assumed that after an environmental change all behaviours that were performed in the previous generation are no longer adaptive and will not be in the future. Because in this case the frequency of the currently adaptive behaviour in the previous generation is zero, no social learner is able to acquire the adaptive behaviour after an environmental change.

Enquist et al. (2007) and Rogers (1988) did not provide explicit functions for how fitness affects reproduction (and thus genetic dynamics). An analytical solution for long-term genetic dynamics can be calculated without an explicit description of genetic dynamics if one assumes that genetic evolution is much slower than cultural evolution. In this case one can assume that short-term cultural dynamics generated through environmental changes have a negligible impact on genetic dynamics, such that only the accumulated (i.e. average) effects of cultural dynamics over a longer time period cause a measurable change in gene frequencies. Therefore, it is possible to calculate for a fixed frequency of social learners and a fixed value of environmental uncertainty the average frequency of adaptive behaviour over a longer time period. The average frequency of adaptive behaviour can then be used to calculate the average fitness of social learners (e.g. Rogers, 1988; Enquist et al., 2007). This information is then sufficient to calculate the long-term outcome of genetic dynamics, as illustrated in Fig. 1.

To investigate the effects of rapid evolution we included an explicit description of how gene frequencies change from one generation to the next. The frequency q of learning strategy x in generation t was calculated as follows:

$$q_{x,t} = q_{x,t-1} \times w_{x,t-1} / w_{m,t-1} \tag{3}$$

where $w_{m,t-1}$ is the mean fitness of the population in generation $t-1$. Additionally, we assumed a constant mutation rate of 10^{-6} in each time step, which gives the probability that a social learner has an individual learner as offspring and vice versa. We included the mutation rate to avoid numerical problems when the frequency of one strategy approaches zero (since the model implicitly assumes an infinitely large population no strategy should ever reach a frequency of zero).

We also investigated evolutionary dynamics when a third strategy of 'critical social learning' was present (Enquist et al., 2007). Individuals with this strategy always start life by learning socially. Afterwards they 'critically' evaluate whether they were successful in acquiring the currently adaptive behaviour. If they were not successful, critical social learners will additionally learn individually, for which they pay the associated

costs. We further assumed that critical social learning entails some fitness costs c_{cs} (relative to b) associated with evaluating whether social learning was successful. Because we assumed that the critical evaluation is error free, critical social learners will always acquire the currently adaptive behaviour. However, their fitness also depends on the frequency of adaptive behaviours in the previous generation because this determines how many of them will learn individually and pay the associated costs. The fitness of critical social learners w_{cs} in generation t is, therefore, given by:

$$w_{cs,t} = 1 + b + c_i \times b \times (1 - a_{t-1}) - c_{cs} \times b \qquad (4)$$

where the other symbols match those given in eqns 1 and 2.

In this extended model, the frequency of each of the three learning strategies was calculated according to eqn 3. We again assumed a mutation rate of 10^{-6}, which gives the probability that an offspring has a different learning strategy from its parent. As there were three

possible learning strategies, we assumed that if a mutation occurred then one of the two other learning strategies emerges with 50% probability.

Enquist *et al.* (2007) included additional extensions of the basic model. For example, they included costs for social learning and errors in individual and social learning. We omit these extensions here for reasons of simplicity.

Model analysis

The most of our analyses focused on the long-term outcome of genetic and cultural dynamics in which only individual and social learners were considered. For this purpose we simulated model dynamics for different parameter values of benefits from acquiring the currently adaptive behaviour b (0.1, 1 and 10), relative costs of individual learning c_i (the range of 0.02–0.98 was covered in increments of 0.02) and environmental uncertainty u (0.01–0.98, where the range between 0.02 and 0.98 was covered in incre-
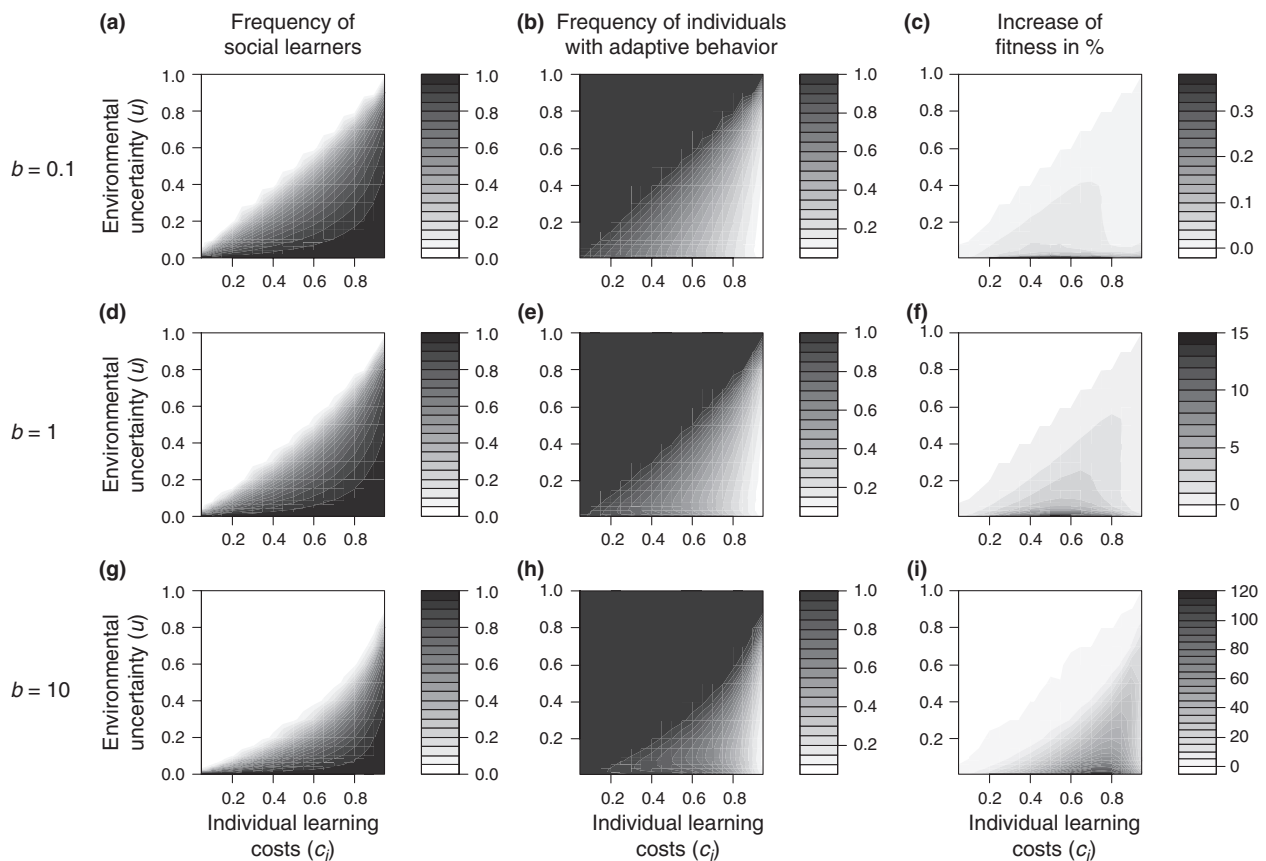

Fig. 2 Long-term outcome of genetic and cultural dynamics in the model in which only individual and social learners are considered. Model dynamics were investigated for different parameter values of b, c_i and u. For each parameter combination model dynamics were simulated for 200 000 generations. During the last 100 000 generations we recorded the average frequency of social learners (a, d, g), the average frequency of adaptive behaviour (b, e, h) and the average fitness of the population, from which we calculated the percent fitness increase compared with the fitness of individual learners (c, f, i). In all simulations, the initial frequency of social learners was set to 10^{-6} and the initial frequency of adaptive behaviour was set to 0.5.
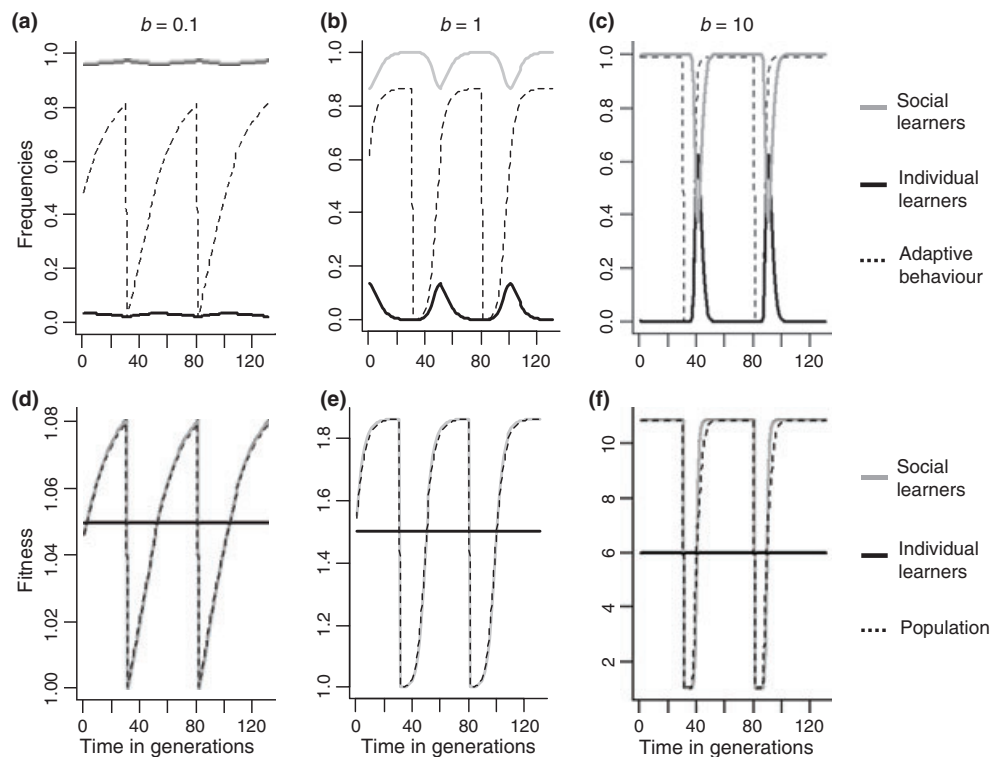
Fig. 3 Example of effects of changing the value of benefits of acquiring the adaptive trait b on temporal dynamics in the model with individual and social learners. Panels (a, b, c) show temporal dynamics of the frequency of social and individual learners and of the frequency of adaptive behaviour and (d, e, f) show temporal dynamics of the fitness of social and individual learners and of the mean fitness of the population. Environmental changes occurred in a regular interval of 50 generations (which corresponds to $u = 0.02$). The simulation was performed for $c_i = 0.5$ and $b = 1$. Depicted dynamics were recorded after simulating 10 000 generations. The initial frequency of social learners was set to 10^{-6} and the initial frequency of adaptive behaviour was set to 0.5.

ments of 0.02). For each parameter combination we simulated model dynamics for 200 000 generations and calculated during the last 100 000 generations (1) the average frequency of social learners, (2) the average frequency of adaptive behaviour and (3) the increase in mean population fitness compared with the fitness of a population of individual learners. Visual inspections of model dynamics revealed that stationary distributions were typically reached before 10 000 generations had passed, making the cut-off of 100 000 generations a conservative assumption. In all simulations, the initial frequency of social learners was set to 10^{-6} and the initial frequency of adaptive behaviour was set to 0.5.

To visualize temporal dynamics for different parameter sets, we performed additional simulations in which environmental changes occurred at regular intervals (rather than randomly). To do this we simulated 10 000 generations and then plotted temporal dynamics using the same initial conditions as described above.

To investigate the long-term outcome of genetic dynamics in populations that included critical social learners, simulations were performed in the same way as described above but restricted to cases in which the value of b equaled 1. The initial frequency of critical social learners was also set to 10^{-6} and the relative costs for critical social learning c_{cs} were set to 0.1. In addition to recording the frequency of social learners, we calculated the mean frequency of critical social learners during the last 100 000 generations.

Results

Our results confirmed Rogers' findings that higher costs of individual learning and lower environmental uncertainty favour the evolution of social learning (Fig. 2). Additionally, we found that the benefit of acquiring the adaptive behaviour is a factor that influences genetic and cultural evolution. Importantly, for many parameter combinations we detected an increase in the mean fitness of the population in the long term, in some cases up to 120% of the fitness of a population of pure individual learners (see the right-hand panels of Fig. 2).

The amount of fitness increase relative to the fitness of individual learners depended on all three investigated
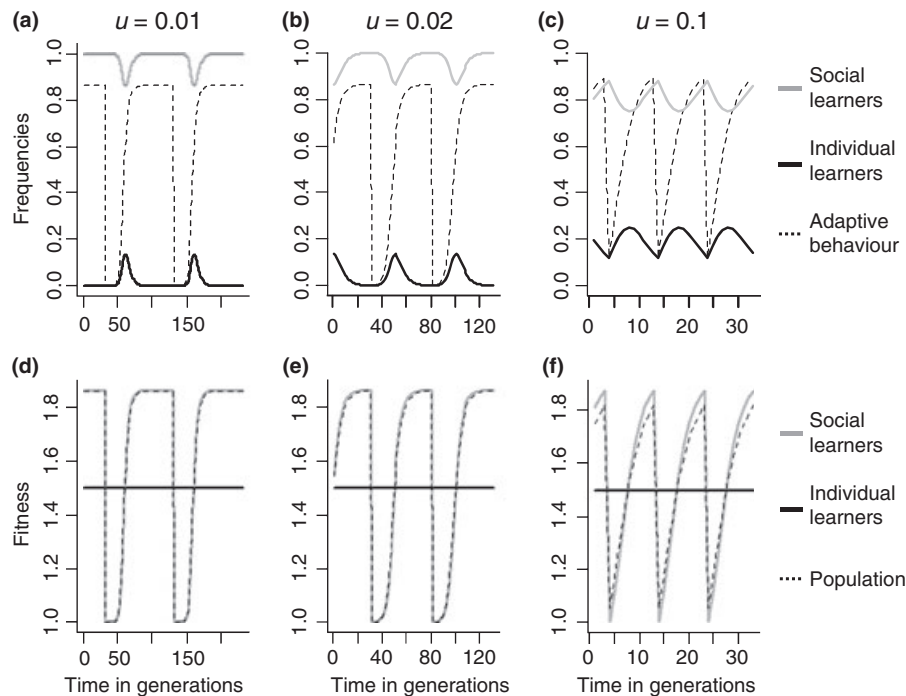
Fig. 4 Example of effects of changing the value of environmental uncertainty u on temporal dynamics in the model with individual and social learners. Panels (a, b, c) show temporal dynamics of the frequency of social and individual learners and of the frequency of adaptive behaviour and (d, e, f) show temporal dynamics of the fitness of social and individual learners and of the mean fitness of the population. Environmental changes occurred in regular intervals (100, 50 and 10 generations, corresponding to $u = 0.01$, 0.02 and 0.1 respectively). Depicted dynamics were recorded after simulating 10 000 generations. The simulation was performed for $c_i = 0.5$ and $b = 1$. The initial frequency of social learners was set to 10^{-6} and the initial frequency of adaptive behaviour was set to 0.5.

parameters (Fig. 2). The population mean fitness generally increased with increasing benefits from acquiring the adaptive behaviour (Fig. 3) and decreasing environmental uncertainty (Fig. 4). Furthermore, the fitness increase was favoured by intermediate costs for individual learning (Fig. 5).

Based on our finding that simple social learning can increase the mean fitness of the population, we suspected that effects of rapid evolution might reduce the relative advantages of using more complicated social learning strategies. We found support for this hypothesis in an additional analysis in which critical social learning was included as a third learning strategy in the model. Our results revealed that if critical social learning is costly then it only evolves to high frequencies for intermediate values of environmental uncertainty and intermediate costs of individual learning (Fig. 6).

Discussion

Our re-analysis of Rogers' (1988) model contradicts Rogers' conclusion that by avoiding costs of individual learning, social learning can not increase the mean fitness of a population. The differences between Rogers' and our model were restricted to assumptions about the

possible number of environmental states and the explicit description of genetic dynamics. Enquist *et al.* (2007) showed that generalizing the model to include an infinite number of environmental states produces results that are congruent with Rogers' original findings. The assumptions related to genetic dynamics that we made are in line with Rogers' assumption that the strategy with higher fitness will over time increase in frequency. The reason for the increase in population mean fitness that we found must therefore relate to the explicit description of genetic dynamics, which in our model allowed for genetic and cultural dynamics to take place on the same time scale. Simulations in which the environment changed on a regular basis revealed that in many cases environmental changes generated strong responses not only in cultural but also in genetic dynamics (Figs 3–5). Thus, by allowing rapid evolution, social learning can increase the ecological success of a population by reducing the costs of individual learning.

An increase in the mean fitness of a population emerged when genetic dynamics could respond to the cultural context, i.e. the proportion of individuals with the adaptive behaviour (e.g. Fig. 3b). Thus, genetic evolution could lead to an increase in individual learners when the frequency of adaptive behaviours was low,
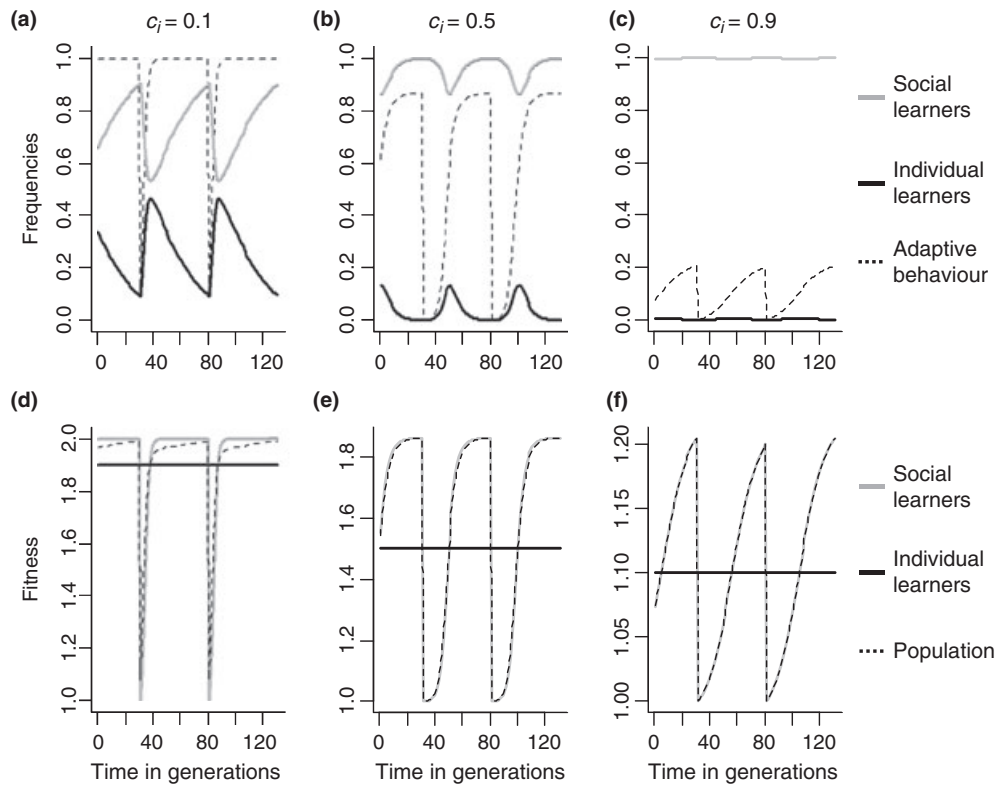
Fig. 5 Example of effects of changing the value of costs for individual learning c_i on temporal dynamics in the model with individual and social learners. Panels (a, b, c) show temporal dynamics of the frequency of social and individual learners and of the frequency of adaptive behaviour and (d, e, f) show temporal dynamics of the fitness of social and individual learners and of the mean fitness of the population. In the performed simulation, environmental changes occurred in a regular interval of 50 generations (corresponding to $u = 0.02$). Depicted dynamics were recorded after simulating 10 000 generations. The simulation was performed with $b = 1$. The initial frequency of social learners was set to 10^{-6} and the initial frequency of adaptive behaviour was set to 0.5.
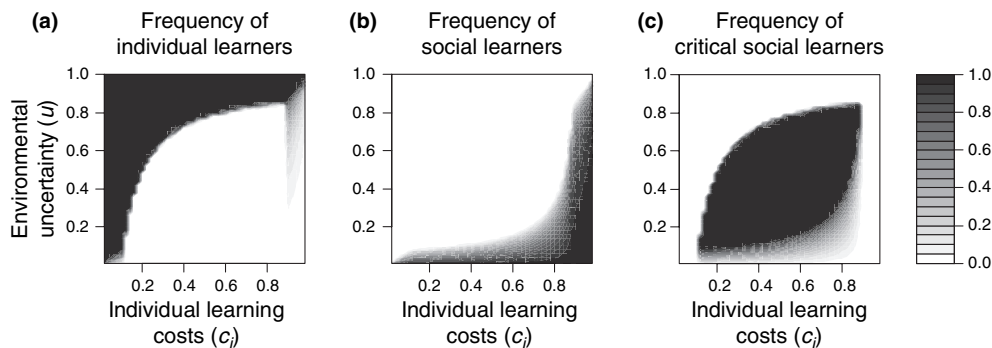

Fig. 6 Long-term outcome of genetic evolution with critical social learners in the population. Model dynamics were investigated for different parameter values of c_i and u. For each parameter combination model dynamics were simulated for 200 000 generations. During the last 100 000 generations we recorded the average frequency of individual learners (a), the average frequency of social learners (b) and the average frequency of critical social learners (c). In all simulations, the initial frequency of social learners and critical social learners was set to 10^{-6} and the initial frequency of adaptive behaviour was set to 0.5. All simulations were performed for $b = 1$ and $c_{cs} = 0.1$.

which happened typically after an environmental change. As the proportion of individuals exhibiting the adaptive trait accumulated in the population following the increase in individual learners, selection favoured social learning and the number of social learners increased. Because costly individual learning increased when it was needed

after the environment changed and decreased when social learning was sufficient to acquire the adaptive behaviour, the mean fitness of the population exceeded the fitness of a population of individual learners.

Increasing the benefits from acquiring the adaptive behaviour led to an increase in the average fitness of individuals in the population over time. This effect emerged because of enhanced fitness differences between individual and social learners, especially during stable phases of the environment and directly after an environmental change. The associated increased intensity of changes in gene frequencies enabled faster cultural recovery from environmental changes, which enhanced the increase in the mean fitness of the population (Fig. 3).

The increase in population mean fitness also increased with decreasing environmental uncertainty. This observation is mainly related to the fact that increased environmental variability led to shorter intervals in which social learners evolved to high frequencies (Fig. 4). This effect reduced the frequency at which large parts of the population could acquire the adaptive behaviour by cheap social learning, which explains the reduced increase in population mean fitness.

Fitness increase was favoured by intermediate costs of individual learning because both low and high costs reduced the potential for fitness increases. With decreasing costs, social learners evolved to lower frequencies because of decreasing fitness differences between individual and social learners (Fig. 5), which reduced the potential that social learners could impact the mean fitness of the population. In contrast, high costs for individual learning favoured the evolution of social learners to high frequencies. However, in this case, the fitness disadvantages of individual learners were so severe that they did not evolve to higher frequencies after an environmental change, which also prevented high frequencies of adaptive behaviour from accumulating in the population. This strongly impacted the fitness of social learners and thus their potential to increase the fitness of the population. At intermediate costs both effects were balanced and thus allowed a higher fitness increase.

Rogers' finding that population fitness does not increase is only a good approximation of the model dynamics if environmental uncertainty is high, benefits from acquiring the adaptive behaviour are low compared with the baseline fitness (which is unaffected by learning), or if costs of individual learning are low or high (Fig. 2). Assessing which parameter values are most appropriate for modelling the evolution of social learning in humans and other animals is difficult. For most animals, including Pleistocene hominins, relatively stable environments seems to be a reasonable assumption, e.g. values of $u < 0.1$ (a value of 0.1 implies that the environmental changes occur on average every 10 generations). For instance, climatic changes during the last glacial occurred on millennial timescales (Fronval et al., 1995); in the respective parameter space we

observe the strongest increases in mean fitness of the population. It is also difficult to assess assumptions concerning costs of individual learning and benefits of acquiring the adaptive behaviour in comparison with the baseline fitness. For many animals and especially for humans, however, it is often thought that benefits arising from social learning contribute substantially to individual fitness (which would correspond to high benefits).

Although our results demonstrate that Rogers' finding of non-increased population fitness might not be as relevant for gene-culture co-evolution in humans and other animals, it remains valuable because it illustrates basic features that influence the evolution of social learning. As argued by Kameda & Nakanishi (2002), Rogers' finding can be appreciated in a more general framework of a producer–scrounger dilemma similar to that found in social foragers (Barnard & Sibly, 1981; Vickery et al., 1991). If we view an adaptive behaviour as information that individuals acquire to adapt to their environment, we can imagine individual learners as information producers because they find new solutions to environmental challenges. Social learners, in contrast, rely on the efforts of others. They simply copy the behaviours of other individuals and, thus, save the costs of producing information themselves. Therefore, social learners can also be viewed as information scroungers. While scrounging is beneficial when many information producers exist, scrounging is not beneficial in a population of scroungers because there is nothing useful to scrounge following environmental change.

Rapid evolution of different social learning strategies

Complex social learning strategies that lead to an increased population fitness have been assumed to be widespread in animals (Laland, 2004), yet our results indicate that this might not be the case. In our model critical social learning evolved only under conditions of intermediate environmental variability and intermediate costs for individual learning (Fig. 6). At high environmental uncertainty individual learners dominated the population because social learning was rarely useful and thus costs for critical evaluation resulted in fitness disadvantages to critical social learners. This effect was stronger for low costs of individual learning, which explains why the frequency of individual learners increased with decreasing costs. At low environmental uncertainty simple social learners evolved to high frequencies because they could save costs involving critical evaluation, which was rarely needed. Furthermore, increasing cost of individual learning decreased the fitness of critical social learners compared with the fitness of simple social learners. Therefore, simple social learners also dominated the population if costs for individual learning were high. In the extreme case, the combined costs of individual learning and critical social learning exceeded the benefits from acquiring the adaptive trait.

Under these conditions, individual learners had a higher fitness than critical social learners, which explains why their frequencies increased at high costs of individual learning and intermediate environmental uncertainty.

Based on this finding, we expect that among species that shows social learning, behavioural strategies such as critical social learning are more likely to evolve in less stable environments. Thus, collecting empirical data on learning strategies in animals and performing a comparative analysis would allow tests for the occurrence of rapid evolution. Modern humans should not be included in such an analysis because our cultures are characterized by cumulative cultural evolution, which might favour the evolution of complex learning strategies independently of prevailing environmental dynamics (Laland, 2004; Enquist & Ghirlanda, 2007).

Acknowledgments

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