Title: **A paradox of cumulative culture**

Running Title: Cumulative culture

Authors: Yutaka Kobayashi[a,b], Joe Yuichiro Wakano[c], Hisashi Ohtsuki[d]

Affiliations: [a]Research Center for Social Design Engineering, Kochi University of Technology, Kochi 782-8502, Japan, [b]Department of Management, Kochi University of Technology, Kochi 782-8502, Japan, [c]Meiji Institute for Advanced Study of Mathematical Sciences, Nakano, Tokyo 164-8525, Japan, [d]The Graduate University for Advanced Studies, Shonan Village, Hayama, Kanagawa 240-0193, Japan

Corresponding author: Yutaka Kobayashi, Department of Management, Kochi University of Technology, Kochi 782-8502, Japan, Tel +81-887-57-2344, Email kobayashi.yutaka@kochi-tech.ac.jp

Keywords: social learning, cultural evolution, gene culture coevolution, dual inheritance theory, cultural social dilemma

Abstract

Culture can grow cumulatively if socially learned behaviors are improved by individual learning before being passed on to the next generation. Previous authors showed that this kind of learning strategy is unlikely to be evolutionarily stable in the presence of a trade-off between learning and reproduction. This is because culture is a public good that is freely exploited by any members of the population in their model (cultural social dilemma). In this paper, we investigate the effect of vertical transmission (transmission from parents to offspring), which decreases the publicness of culture, on the evolution of cumulative culture in both infinite and finite population models. In the infinite population model, we confirm that culture accumulates largely as long as transmission is purely vertical. It turns out, however, that introduction of even slight oblique transmission drastically reduces the equilibrium level of culture. Even more surprisingly, if the population size is finite, culture hardly accumulates even under purely vertical transmission. This occurs because stochastic extinction due to random genetic drift prevents a learning strategy from accumulating enough culture. Overall, our theoretical results suggest that introducing vertical transmission alone does not really help solve the cultural social dilemma problem.

1. Introduction

Rogers (1988) argued that the presence of culture *per se* does not imply improvement of population-level adaptability. This result, which contradicted the apparent advantages of culturally transmitted technologies in humans, was received with some astonishment by researchers of the day (Boyd and Richerson, 1995a). Nowadays, it is acknowledged that this “paradox” is a consequence of the specific structure of Rogers’ model and can be “resolved” by taking realistic properties of human culture into account (Enquist et al. 2007; Aoki and Feldman, 2014). One of them, which may be the most relevant, is the cumulativeness of culture (Aoki et al. 2012). That is, human culture does not, as in Rogers’ model, have just two states (adaptive vs. maladaptive), but evolves gradually by accumulating modifications over many generations to finally yield complex artifacts that cannot be invented by a single individual (Richerson and Boyd, 2005). It is well known that chimpanzees socially learn how to crack nuts using stones and also to fish termites using sticks (Whiten et al., 1999), but such behavior is not cumulative culture, as it fall well within the inventive capacity of a single individual. It is not comparable with spacecraft, mobile phones, and quantum mechanics, which are clearly beyond the inventive capacity of a single individual. Even basic hunter-gatherer tools like a spear are products of cumulative cultural evolution, being composed of multiple parts that cannot be made without some other tools like scrapers or wrenches, which may already be complex enough (Richerson and Boyd, 2005). On the other hand, ethnobotanical knowledge for food-gathering and processing can be cumulative in a more quantitative sense, built upon numerous trials and errors, which can never be exerted within the lifetime of a single individual. In this view, Rogers' model is not a model of cumulative cultural evolution.

While many animal species engage in social learning and hence have culture to varying degrees (Slater, 1986; Box and Gibson, 1999; Whiten et al., 1999; Krützen et al., 2005), it is only humans that are known to have cumulative culture (Laland and Hoppitt, 2003; Tennie et al. 2009; Mesoudi, 2011a; see also Mithen, 1999). Many researchers consider that cumulative cultural evolution is a major source of adaptation in modern humans (Tomasello, 1999; Richerson and Boyd, 2004).

More than two decades after Rogers' study, another paradox, which is more relevant to human evolution, has emerged. Obviously, culture can accumulate over generations only if socially learned traits undergo improvements before or while being passed on to the next generation. Such improvements can be made through deliberate individual learning (Aoki et al., 2012) or inaccurate social learning combined with success-biased transmission (Henrich, 2004). In the latter case, positive cultural growth is ensured in a sufficiently large, well connected population (Henrich, 2004; Powell et al., 2009; Mesoudi, 2011b; Kobayashi and Aoki, 2012). As to the former mechanism, recent models show that a learning schedule in which social learning occurs in an earlier life stage than individual learning is indeed favored by natural selection (Aoki et al. 2012). The optimal learning schedule allows culture to accumulate largely as long as improvement of traits is the sole concern of each individual. Interestingly, however, such a learning schedule loses evolutionary stability as soon as a trade-off in terms of time between learning and reproductive effort is introduced (Wakano and Miura, 2014). It has been presumed that this occurs because of the publicness of culture; that is, a strategy that spends a lot of time to improve socially learned traits (and hence contributes to culture) allows invasion by selfish mutants that just scrounge the culture and spend the rest of time reproducing. Therefore, culture decays until finally the benefit of social learning is also lost. This results in a final state where individuals engage mainly in biological replication and little in learning (Lehmann et al. 2013; Wakano and Miura, 2014). This result contradicts the observation that modern humans possess highly cumulative, sophisticated technologies, which must have largely contributed to their current demographic success on the global scale.

Wakano and Miura (2014) recognized this theoretical problem as a social dilemma, where temptation to cheat prevents the population from reaching an adaptive, cooperative state. They speculated that the dilemma would be overcome if cultural transmission occurs mainly between close relatives, preventing cheaters from accessing adaptive cultural products. For clarity, let us imagine an extreme hypothetical situation where reproduction is asexual and transmission of culture is purely "vertical" (i.e. from parents to their offspring (Cavalli-sforza and Feldman, 1981)). In this case, each genetic lineage can be seen as an isolated population, and hence a strategy that promotes accumulation of culture and is optimal from the population viewpoint should also be favored by natural selection. In fact, Lehmann et al.'s (2010) model, which treats only within-generation accumulation of culture, shows that culture can accumulate beyond the capacity of a single individual if culture is horizontally transmitted between close relatives in the same generation. However, no study tested the effect of kin transmission on the evolution of between-generation cumulative culture.

Below, we investigate the effect of vertical transmission on the evolution of between-generation cumulative culture using infinite and finite population models. Our primary purpose is to test whether the privatization of culture through vertical transmission can function as a theoretical mechanism to solve the above-mentioned social dilemma problem. In the infinite population model, we first confirm that pure vertical transmission indeed solves the above-mentioned cultural social dilemma and allows a large accumulation of culture. It turns out, however, that introduction of even slight “oblique” transmission (i.e. transmission from a non-parental adult in the parental generation (Cavalli-sforza and Feldman, 1981)) drastically reduces the equilibrium level of culture. Even more surprisingly, if the population size is finite, culture hardly accumulates even under pure vertical transmission. This occurs because stochastic extinction of learning strategies prevents culture from accumulating enough to exert its effect. In the Discussion, we will argue implications of our theoretical results for empirical research.

2. Methods

2.1. Model description

We work on a simplified model to extract the essence of the problem while keeping analytical tractability. In particular, we ignore the effects of environmental fluctuation, which have been extensively studied by previous authors (e.g. Boyd and Richerson, 1985; Feldman et al., 1996; Wakano et al., 2004; Wakano and Aoki, 2006). Notation used in this model is summarized in Table 1. We assume an asexually reproducing population in which generations are overlapping insofar as cultural transmission occurs.

The population size is constant but may be either infinite or finite. In the finite case we denote the population size by N.

Within each generation, time passes continuously; we let τ and t represent the generation and the within-generation time, respectively. We assume that each individual in the population is distinguished from others by a unique label i. We may say "individual (i,τ)" instead of saying "individual i in generation τ" whenever it is convenient. Individuals engage in three activities in a sequential manner: they first learn socially, second learn individually, and finally exploit environments to reproduce. We may call the first two stages collectively the learning stage. We assume this order of the three activities and the discontinuous switching between activities (i.e. "bang-bang" control) because they were well established in previous studies by means of dynamic optimization theory (Aoki et al. 2012; Lehmann et al. 2013; Wakano and Miura, 2014). It must here be noted that by the term "individual learning" we refer to an effort to add to or improve knowledge or skills that an individual already possess, while "social learning" refers to copying others' knowledge or skills. In this respect, we follow a series of previous theoretical models (Aoki et al., 2012; Lehmann et al., 2013; Wakano and Miura, 2014). We focus on the evolution of the length of time allocated to each activity, which determines the extent to which culture accumulates. Each individual (i,τ)

allocates fractions $v_{i,\tau}(1-x_{i,\tau})$, $v_{i,\tau}x_{i,\tau}$, and $1-v_{i,\tau}$ of the total lifetime T to social learning, individual learning, and exploitation, respectively. Without loss of generality, we set $T=1$ throughout the paper; this means that we measure time in units of the lifetime of an individual. Evolving parameters are v and x, i.e. the fraction of time used for learning and the ratio of the time used for individual learning to the whole learning time. We assume that the strategy (x, v) is coded for by a single haploid locus. In the ESS analysis we assume that there are only two alleles, a wild-type allele and a mutant allele, on this locus. In computer simulations, on the other hand, we allow existence of multiple alleles on this locus.

Following previous authors, we assume that the cultural state of each individual (i,τ) at within-generation time t is represented by a positive real number $z_{i,\tau}(t)$ (e.g. Henrich, 2004; Powell et al., 2009; Aoki et al. 2012; Kobayashi and Aoki, 2012; Lehmann et al. 2013; Wakano and Miura, 2014). The z-value $z_{i,\tau}(t)$ of an individual (i,τ) may represent its degree of skillfulness (e.g., in making tools), the level of sophistication of knowledge (e.g. how to manufacture wild plants to extract nutrient or detract toxins as efficiently as possible), or the amount of knowledge in a certain category (e.g. a list of edible plants). For simplicity, we assume that $z_{i,\tau}(0)=0$ for newborns. The z-value of an individual grows during its lifetime through social and individual learning. In the stage of social learning, each individual (i, τ) chooses an individual in the parental generation τ-1 as a role model and absorbs its knowledge. We let $(\rho_\tau(i), \tau\text{-}1)$ denote the role model of an individual (i, τ). Zarger (2002) shows that, in a Mayan farming village, the amount of ethnobotanical knowledge of a child grows roughly in a decelerating, saturating manner during the age period from 4-14 through social learning. In light of this, we assume that the z-value of individual (i, τ) grows in the social learning stage as follows:

$$\frac{d}{dt} z_{i,\tau}(t) = \beta(z_{\rho_\tau(i),\tau-1}(T) - z_{i,\tau}(t)), \quad (0 \le t \le v_{i,\tau}(1 - x_{i,\tau})), \qquad (1)$$

where β is the efficiency of knowledge absorption. This equation allows $z_{i,\tau}(t)$ to grow in a decelerating manner, conforming with the empirical data (Zarger, 2002). Note that $z_{\rho_\tau(i),\tau-1}(T)$ gives the z-value of individual $(\rho_\tau(i), \tau\text{-}1)$ at the end of its lifetime, which we call the *mature* z-value of individual $(\rho_\tau(i), \tau\text{-}1)$. The role model $(\rho_\tau(i), \tau\text{-}1)$ is (i, τ)'s parent and a random adult chosen from generation τ-1 including the parent with probabilities q and 1-q, respectively. In other words, q and 1-q give the (backward) probabilities of vertical and random oblique transmission, respectively. We ignore the horizontal transmission in the present model to focus on between-generation accumulation of culture. This simplification is acceptable as a first step toward more realistic modeling given that horizontal transmission is rare compared to vertical and oblique transmission in traditional societies (Hewlett and Cavalli-Sforza, 1986; Ohmagari and Berkes, 1997; Shennan and Steele, 1999; Reyes-Garcia et al., 2009).

In the stage of individual learning, the $z_{i,\tau}(t)$ grows as follows:

$$\frac{d}{dt} z_{i,\tau}(t) = \alpha \,, \qquad (v_{i,\tau}(1 - x_{i,\tau}) \le t \le v_{i,\tau}) \qquad (2)$$

where α is the efficiency of individual learning. Throughout this paper, we set α=1. This implies that the unit of the z-value is the mature z-value that a life-long individual learner could achieve.

Note that $z_{i,\tau}(t)$ grows in a decelerating manner in the social-learning stage while it grows at a constant rate in the individual-learning stage. This is a common feature of existing learning-schedule models and is essential for the evolution of a combined use of social and individual learning in a constant environment. By virtue of this feature, it is beneficial to engage in social learning first, and then switch to individual learning when the knowledge absorption rate in social learning drops to the same level as the efficiency of individual learning, i.e. when

$\beta(z_{\rho_\tau(i),\tau-1}(T)-z_{i,\tau}(t))=\alpha=1$. In the stage of exploitation, the *z*-value stays at the mature value attained by the end of the learning stage, i.e.

$$\frac{d}{dt}z_{i,\tau}(t)=0\,. \qquad\qquad (v_{i,\tau}\le t\le 1=T) \quad (3)$$

Note that the mature *z*-value $z_{i,\tau}(T)$ may be used as the target of social learning in the next generation by the offspring of the focal individual or some other members of the population. We assume that the efficiency of exploitation is proportional to this mature *z*-value. In addition, we assume that the fitness of an adult is proportional to the total resource income. This is a reasonable assumption, given that in humans energetic income by an adult is expended not only for its own survival and reproduction but also for children's survival and growth (Kaplan et al. 2000). Thus, the fitness of individual (i,τ) is given by

$$w_{i,\tau}=z_{i,\tau}(T)\cdot(1-v_{i,\tau})\,. \qquad\qquad (4)$$

Fig. 1 sketches what happens in the *finite*-population model on the between-generation time scale. We assume a so-called "Wright-Fisher"-type update for the genetic state of the population; i.e. each adult in generation τ is chosen as a parent of a newborn in generation $\tau+1$ with a probability proportional to its fitness. Offspring inherit their parent's strategy (x,v). Thus, the genetic state of the population changes from generation to generation due to natural selection and sampling drift (random genetic drift). In the infinite-population model we consider the limit of the finite-population model as the population size tends to infinity in such a way that sampling drift disappears.

Although the z-value for newborns is $z_{i,\tau}(0)=0$ by assumption, the mature z-value, i.e. $z_{i,\tau}(T)$ may vary even in a genetically monomorphic population. This is because the mature z-value of an individual (i, τ) depends on the mature z-value of its role model $(\rho_\tau(i), \tau\text{-}1)$, which in turn depends on the mature z-value of the role model's role model $(\rho_{\tau\text{-}1}(\rho_\tau(i)), \tau\text{-}2)$, and so on. However, given that the population is genetically fixed for a strategy, say (x, v), $z_{i,\tau}(T)$ reaches an equilibrium value, which is denoted by $\tilde{z}(T)$. Therefore, the fitness also reaches an equilibrium value, which is denoted by $\tilde{w}$ (see Online Appendix A).

2.2. Aim of analysis

The aim of our analysis is to compare three solutions based on different optimality criteria: (i) the coordinated optimal strategy (COS), (ii) the evolutionarily stable strategy (ESS) based on invasion growth rate in an infinite population model, and (iii) the ESS based on fixation probability in a finite population model. Key parameters are the vertical transmission rate and the population size, which have crucial effects on the behavior of the model, as revealed in the result section.

The COS is defined as the strategy that maximizes the equilibrium value of fitness under the constraint that the population is genetically monomorphic (i.e. no mutants are allowed). It does not depend on whether the population size is infinite or finite. We use symbols x°, v°, and $\tilde{z}^{\circ}(T)$ to denote the COS values of x, v, and $\tilde{z}(T)$, respectively. The COS was previously referred to as the “Pareto-optimal” strategy (Wakano and Miura, 2014) but this is inappropriate given that these two concepts are not always equivalent. While the COS is an ideal strategy from the viewpoint of ultimate species success, there is no guarantee that it is favored by natural selection. We hence derive the evolutionarily stable strategy (ESS) both for an infinite population and for a finite population of size N and compare it with that under the COS. We use symbols x^{*}, v^{*}, and $\tilde{z}^{*}(T)$ to denote the ESS values of x, v, and $\tilde{z}(T)$, respectively.

The COS analysis requires only that we work on the cultural dynamics in a genetically monomorphic population. The ESS analysis, on the other hand, requires that we track both the genetic and cultural states of each individual simultaneously. Specifically, we consider the fate of a mutant allele introduced into a resident population which is at equilibrium with respect to the z-value (Fig. 1). In the case of an infinite population, sampling drift is absent and the frequency of a mutant allele hence changes deterministically; therefore, as in traditional analysis, we may define an ESS as a strategy that does not allow any slightly deviant strategy to have a positive growth rate (Maynard Smith, 1982). In the finite case, however, the frequency of a mutant allele undergoes stochastic fluctuation due to sampling drift. We therefore use a definition of an ESS based on a fixation probability (e.g. Nowak et al., 2004). Let N be the population size. We say that a strategy (x^*, v^*) is evolutionarily stable if and only if the fixation probability of any slightly deviated strategy in the population of the resident strategy (x^*, v^*) is lower than $1/N$, i.e. the fixation probability under neutrality.

Unfortunately, we could not confirm analytically the second-order stability of the ESS's we obtained. To confirm the evolutionary stability of the analytically derived formulae and the validity of the approximations, we conducted some individual-based simulations. See Online Appendices for all mathematical details.

3. Results

3.1. Coordinated optimal strategy

As shown in Online Appendix A, the equilibrium fitness in a genetically monomorphic population with strategy (*x*, *v*) is given by

$$\tilde{w} = v(1-v)xe^{\beta v(1-x)}. \qquad (5)$$

The COS is the strategy (*x*, *v*) that maximizes eq. (5). It is easily shown that, if $\beta<2$, the COS is given by

$$x^{\circ} = 1, \quad (6a)$$

$$v^{\circ} = \tilde{z}^{\circ}(T) = \frac{1}{2}. \qquad (6b)$$

Thus, the COS involves no social learning when $\beta<2$. On the other hand, if $\beta>2$, the COS involves social learning and is given by

$$x^{\circ} = \frac{1}{\beta - 1}, \qquad (6c)$$

$$v^{\circ} = 1 - \frac{1}{\beta}, \qquad (6d)$$

$$\tilde{z}^{\circ}(T) = \frac{1}{\beta} e^{\beta - 2}. \quad (6e)$$

One might wonder why β=2 gives the threshold for the emergence of social learning. The absence of social learning requires β<2 for the following reason. Note that from eq. (2) the absence of social learning (x=0) entails $z_{i,\tau}(T)$ =v. Thus, the equilibrium mature z-value is also given by $\tilde{z}(T)$ = v. Therefore, the equilibrium fitness is given by $\tilde{w} = \tilde{z}(T) \cdot (1-v) = v(1-v)$, which is maximized at v=1/2. Thus, the COS without social learning, if possible, must satisfy that $v^{\circ} = \tilde{z}^{\circ}(T)$ =1/2 in addition to x° =1. However, since the COS by definition maximizes the fitness, the fitness must not increase by introducing social learning. This entails that the rate of social learning is lower than that of individual learning already at birth, i.e. $\beta(\tilde{z}^{\circ}(T) - 0) < \alpha = 1$. Given that $\tilde{z}^{\circ}(T)$ =1/2, this condition reduces to β<2. These arguments reveal that β<2 is a necessary condition for the COS to satisfy x° =1.

Eq. (6) shows that the COS is solely determined by the efficiency of social learning β. It also shows that reliance on individual learning (x°) decreases with social learning efficiency (β) while the learning time (v°) and the equilibrium mature z-value ($\tilde{z}^{\circ}(T)$) both increase. In particular, individuals should exert maximal effort for transmission of culture and minimal effort for individual learning and exploitation ($v^{\circ} \to 1,\ \ x^{\circ} \to 0$) when social learning is highly efficient ($\beta \to \infty$). The equilibrium mature z-value ($\tilde{z}^{\circ}(T)$) can take a huge value when social learning efficiency (β) is high (Fig. 2). This implies that a massive accumulation of culture is possible if the members of a society try to maximize future fitness in a coordinated manner.

3.2. ESS in an infinite population

In Online Appendix B, we derive an Euler-Lotka characteristic equation that gives the invasion growth rate of a rare mutant strategy in an infinite population. Using this equation, we can derive the ESS analytically under the assumption of small mutation size (i.e. the mutant strategy is sufficiently close to the resident one). If $\beta>2$, an ESS with a positive investment in social learning ($x^*<1$) exists and satisfies

$$x^* = \frac{1}{\beta v^*}, \qquad \text{(7a)}$$

$$\beta(1-v^*) - q = (1-q)e^{\beta v^* - 1}, \qquad \text{(7b)}$$

$$\tilde{z}^*(T) = \frac{1}{\beta} e^{\beta v^* - 1}. \qquad (7c)$$

If β<2, the COS is also the ESS (eqs. (6a-b)). Eq. (7) shows that the ESS is unique and given as an implicit function of parameters β and q. When the cultural transmission is purely vertical (q=1), the ESS becomes equivalent to the COS ($x^* = x^\circ$, $v^* = v^\circ$), as expected (see also Fig. 2). Close inspection of eq. (7) reveals that both learning time (v^*) and the equilibrium mature z-value ($\tilde{z}^*(T)$) are monotonically increasing and reliance on individual learning (x^*) is monotonically decreasing with respect to vertical transmission probability (q). Thus, the equilibrium mature z-value attained by the ESS is always lower than that attained by the COS.

The equilibrium mature z-value ($\tilde{z}^*(T)$) and reliance on individual learning (x^*) are monotonically increasing and decreasing, respectively, with respect to social learning efficiency (β). The learning time (v^*) is, however, not monotonic unless transmission is purely vertical (q=1) (Fig. 2). The ESS for very high social learning efficiency ($\beta \to \infty$) differs qualitatively between when transmission is purely vertical (q=1) and when it is not (q<1). If transmission is purely vertical, the ESS is identical with the COS; hence individuals tend to exert maximal effort for transmission of culture and the equilibrium mature z-value diverges ($v^* \to 1$, $x^* \to 0$ and $\tilde{z}^*(T) \to \infty$ hold as $\beta \to \infty$) (Fig. 2). If transmission is partially oblique (q<1), on the other hand, we obtained the following approximate formula for large β

$$v^* \approx \frac{1}{\beta} \log \frac{\beta e}{1-q}, \quad \text{(8a)}$$

$$\tilde{z}^*(T) \approx \frac{1}{1-q}. \quad \text{(8b)}$$

This suggests that, when social learning efficiency (β) is large, introduction of rather weak oblique transmission can result in a drastic fall in the equilibrium mature z-value. For example, when β=10, the COS attains $\tilde{z}^{\circ}(T) \approx 298$, while the ESS under q=0.99 (q=0.9) attains only $\tilde{z}^*(T) \approx 24.9$ ($\tilde{z}^*(T) \approx 4.33$). This drastic reduction in the equilibrium mature z-value ($\tilde{z}^*(T)$) in response to slight oblique transmission reflects a steep reduction in the learning time (v^*). For example, when β =10 and q=0.99 (q=0.9), it holds that $v^* \approx 0.652$ ($v^* \approx 0.477$), which is much lower than v° =0.9 (see also Fig. 2). Although the ESS invests more in reproduction than the COS, this is not enough to compensate for the reduction in the mature z-value; that is, the ESS generally attains a lower fitness at equilibrium than the COS. This is obvious because by definition no strategy can attain a higher fitness at equilibrium than the COS in a monomorphic population. In fact, when β=10 and q=0.99, the ESS attains the equilibrium fitness of about 8.67 ($\approx \tilde{z}^*(T)\times(1-v^*) = 24.9\times(1-0.652)$), which is much lower than that of the COS, 29.8 ($= \tilde{z}^\circ(T)\times(1-v^\circ) = 298\times(1-0.9)$). Thus, notable here is not the sign but the magnitude of the effect of the vertical transmission rate.

The drastic reduction of the equilibrium mature z-value in response to slight oblique transmission may be explained as follows. Let us consider the fate of a mutant strategy that increases investment in learning compared to the resident. Although the mutant can potentially reach a higher cultural level than the resident, culture needs to accumulate for several generations to compensate for the fitness loss caused by reduced investment in reproduction. For example, if 100 generations of accumulation is necessary to compensate for the fitness loss, the compensation occurs only with probability q^{100}. Importantly, a single failure of vertical transmission (i.e., oblique transmission) would reset the cultural level, bringing all the increased learning efforts by ancestors to naught. This explains why the ESS and the mature z-value are so sensitive to the introduction of slight oblique transmission. We will give a more general (but technical) explanation in the Discussion section.

3.3. ESS in a finite population

In Online Appendix C, we derive an approximate formula for the fixation probability of a mutant strategy in a finite population of size N for the special case of purely vertical transmission (q=1) using the method introduced by Rousset (2004). Using this formula, we can derive the ESS for q=1 analytically under the assumption of small mutation size. If β>2, the ESS and the equilibrium mature z-value ($\tilde{z}^*(T)$) under purely vertical transmission satisfy eqs. (6a) and (6c) plus

$$\beta(1-v^*)-1+\frac{1}{N}=\frac{1}{N}e^{\beta v^*-1}. \qquad (9)$$

If β<2, the COS is again the ESS. For partially oblique transmission (q<1), we resort to individual-based simulations (see the next subsection).

Comparison of eqs. (7) and (9) reveals that the ESS for a finite population of size N under purely vertical transmission (q=1) is exactly equal to the ESS for an infinite population in which the vertical transmission rate is q=1-1/N. Therefore, decreasing the population size has essentially the same effect as decreasing (increasing) the vertical (oblique) transmission rate (see Fig. 2). In particular, when social learning efficiency (β) is large, the reciprocal of population size (1/N) has a huge impact, as expected from the effect of vertical transmission rate (q) revealed in the infinite-population model. For very high social learning efficiency ($\beta \to \infty$), we obtain eq. (7a) plus the following:

$$v^* \approx \frac{1}{\beta} \log eN\beta, \quad (10a)$$

$$\tilde{z}^*(T) \approx N. \qquad (10b)$$

Thus, the equilibrium mature z-value is asymptotically equal to the population size.

Eq. (10b) implies that a population of 100 people can accumulate valuable traits that account for about 100 generations. Although one might think this result convincing, the load potentially imposed by population-size finiteness should not be underestimated. For example, when β=10, the COS reaches $\tilde{z}^\circ(T) \approx 298$ as already argued. On the other hand, the ESS under N=100 reaches only $\tilde{z}^*(T) \approx 24.9$. Moreover, in reality there would be some oblique transmission, which should further drastically reduce the equilibrium mature z-value. In the next subsection, this effect is explored by means of computer simulations.

The finiteness of population size causes the drastic reduction in the ESS cultural level because it creates room for stochastic extinction of rare alleles. As mentioned in the previous subsection, a mutant strategy that invests more in learning than the resident must endure for several generations before culture accumulates enough to compensate for the fitness loss caused by decreased investment in reproduction. In other words, such mutant strategy is far-sighted compared to the resident, investing in the future cultural quality at the expense of present reproduction. If the population size is infinite and transmission is purely vertical, this may be a good strategy; although the mutant population would initially decrease, it may eventually start increasing after culture enough accumulates. In a finite population, however, the mutant strategy is highly likely to go extinct in the initial stage where the mutant still has lower fitness than the resident. For this reason, near-sighted strategies (i.e. large investment in reproduction) tend to be favored over far-sighted ones (i.e. large investment in learning) in a small population. We will provide a more detailed explanation in the Discussion.

3.4. Individual-based simulations

In the simulations we explicitly tracked the changes in both genetic and cultural states of each of N individuals. We assumed that each of traits $x_{i,\tau}$ and $v_{i,\tau}$ of each individual can independently mutate in every generation with the same probability μ=0.001. If mutation occurred to a trait, the new trait value was sampled from a Gaussian distribution centered around the original trait value with variance σ^2=0.001. If the sampled value turns out to be outside a boundary (0 or 1), the new trait value was set to the boundary value. As a result of recurrent mutation, many different strategies coexist at each snapshot, whereas in the analytical theory we assumed there were at most only two strategies (the mutant and the resident). All the other assumptions were unchanged from the description in section 2.

We first checked if the ESS for purely vertical transmission (q=1) predicted by eqs. (7a), (7c), and (9) is attained in individual-based simulations. Fig. 3 shows a typical time-series behavior of the population-averages of $x_{i,\tau}$, $v_{i,\tau}$, and $z_{i,\tau}(T)$, which are denoted by $\bar{x}$, $\bar{v}$, and $\bar{z}(T)$, respectively. Clearly, these values all converge to the analytical ESS values (broken bold lines). In the simulation of Fig. 3, the initial trait values are set to the COS; i.e. β=10, $v_{i,\tau}=v^\circ$=0.9, $x_{i,\tau}=x^\circ$=0.1 (see eqs. (6c) and (6d)). The role model's z-value in the first generation was set to zero for all individuals. Thus, if there were no genetic evolution, the average mature z-value $\bar{z}(T)$ should increase to $\tilde{z}^\circ(T) \approx 298$ according to eq. (6e). In fact, as Fig. 3b shows, $\bar{z}(T)$ initially increases up to about $\tilde{z}^\circ(T)$ but subsequently decreases to $\tilde{z}^*(T)$ following the evolutionary changes in $\bar{x}$ and $\bar{v}$.

Fig. 4 shows the effect of q on the equilibrium values of $\bar{x}$, $\bar{v}$, and $\bar{z}(T)$. The figure again shows that in general the analytical theory accurately predicts simulation results under purely vertical transmission except the equilibrium values of $\bar{z}(T)$ for some large β (Fig. 4c). This deviation occurred because the value of $\bar{z}(T)$ fluctuates a lot when β is large. As expected from the result of the infinite-population model (Fig. 2), $\bar{x}$ is not sensitive to change in q (Fig. 4a). On the other hand, $\bar{v}$ significantly decreases with decreasing q (Fig. 4b) and, as a result, $\bar{z}(T)$ sharply decreases (Fig. 4c).

4. Discussion

4.1. Summary of results

Wakano and Miura (2014) argued that the public nature of culture prevents the evolution of between-generation cumulative culture. They proposed kin selection as a mechanism to avoid this cultural social dilemma problem. We have confirmed that in our simple infinite-population model cumulative culture can evolve if social transmission is purely vertical and hence the relatedness between the donor and the recipient of information is unity (R=1). However, as soon as a small probability of oblique transmission is introduced, the equilibrium level of culture drastically reduces.

Moreover, by analyzing a model of finite population, we have shown that the equilibrium mature z-value is largely limited by the population size even under pure vertical transmission.

4.2. Effect of oblique transmission

These surprising results illuminate another (i.e. other than being public) pitfall of between-generation cumulative culture, which was previously not perceived. Namely, it takes a number of generations before culture accumulates enough to compensate for the fitness loss caused by an increased investment in learning. Therefore, a mutant strategy that increases investment in learning compared to the resident must accumulate culture vertically for a number of generations without interruption by oblique transmission before it can enjoy increased fitness. Thus, the crucial determinant for the success of the mutant is the expected number of generations until a sequence of vertical transmission is terminated by oblique transmission, which is given by the reciprocal of the oblique transmission rate, i.e. $1/(1-q)$. This quantity is obviously very sensitive to q when q is close to unity and reduces to a very small value as soon as q gets away from unity. Interestingly, the equilibrium mature z-value under the ESS is also given by the reciprocal of the oblique transmission $1/(1-q)$ when β is very large (eq. (8b)). These arguments reveal why the ESS and its equilibrium mature z-value are both very sensitive to the introduction of oblique transmission. Note that many authors investigated the effects of transmission modes on cultural evolution (e.g., Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985; Enquist et al., 2010; Aoki, et al., 2011; Kobayashi and Aoki, 2012), but we have first investigated the effects of transmission modes on the coevolutionary dynamics of learning and between-generation accumulation of culture from the viewpoint of kin selection and the cultural social dilemma.

4.3. Effect of population size

On the other hand, it may be more difficult to understand the large effect of population size on the evolution of cumulative culture, which is evident even under pure vertical transmission. To understand this effect, let us consider why a mutant with the COS cannot be successful in the population of the ESS. Suppose that the transmission is purely vertical and the COS is initially expressed by a single mutant individual. Since the COS invests less in reproduction than the ESS, the fitness of mutants is lower than residents in early generations. However, it gradually increases because of the cumulative effect of culture, eventually exceeding the resident fitness (Fig. 5).

Therefore, if the population size were *infinite*, mutants should first decrease but eventually start increasing, finally reaching fixation. In a finite population, however, mutants are highly likely to go extinct in the initial phase of reduced fitness before they can enjoy increased fitness (see Fig. 5). This is why the COS cannot invade the ESS in a finite population. Likewise, it is easy to show that the COS cannot resist against invasion by the ESS in a finite population.

These arguments are consistent with the result of Lehmann et al. (2010), who showed that culture can accumulate beyond the capacity of a single individual *within* a generation if horizontal transmission of culture occurs mainly between genetically related individuals, so that culture is essentially private. In their model, fitness reduction of an elaborate learner due to decreased time for reproduction is immediately compensated by beneficial information horizontally transmitted from its relatives. Thus, the delay effect revealed in our model is absent in their model of within-generation cumulative culture. Further arguments about this subject are given in section 4.5.

4.4. Order of learning and reproduction

In the current model, we assumed that each individual engages in social learning, individual learning, and exploitation of the environment in this order. Although this assumption is based on the results of previous theoretical models, it would obviously be desirable to have some empirical evidence to support it. As to the assumption that learning occurs in an earlier stage than exploitation of the environment, it is known that in hunter-gatherer societies the energetic income by an individual during the childhood is typically negligible or very small but shows a steep increase from the adolescence to the early adulthood (Kaplan et al., 2000). On the other hand, most subsistence knowledge and skills are mastered by the early adulthood (e.g. Ohmagari and Berkes, 1997; Zarger, 2002). Thus, our assumption that the learning stage precedes the exploitation stage may be acceptable (though learning often requires children to accompany adults on subsistence work for observation and hands-on practices, see e.g. Ohmagari and Berkes, 1997).

Unfortunately, there is little empirical support for the assumption that individual learning occurs in a later stage of life than social learning. It is relatively well understood how social learning proceeds in the lifespan of an individual; for example, Zarger (2002) reports that children’s ethnobotanical knowledge (names and use of plants) grows rapidly during the age period of 4-7 years and then at a lower rate until finally it reaches the adult level during the age period of 10-14 years. On the other hand, it is largely unknown how and when individual learning takes place.

Importantly, however, the assumption that social learning precedes individual learning in the learning stage is not crucial to our analysis. In fact, even if each individual engages in individual learning with probability x and in social learning with probability 1-x at any moment in the learning stage, we can reach the same conclusion. To see this, let us interpret the skill level $z_{i,\tau}(t)$ specifically as the amount of (e.g. ethnobotanical) knowledge individual (i, τ) has obtained through individual and social learning by time t. In addition, assume that the knowledge produced by individual learning does not overlap with that obtained by social learning. Then, as revealed in Online Appendix D, the final amount of knowledge (or the skill level) obtained by the end of the learning stage is given by exactly the same equation as in the original model. Thus, our results do not necessarily depend on the sequential occurrence of social and individual learning.

4.5. Stacking versus gathering

Perhaps it would be useful to conceptualize two kinds of cultural accumulation, which are on the two extremes of a continuum. The first is accumulation in a horizontal sense. In this type of accumulation, each individual reaches a high skill level by gathering various pieces of knowledge from peers in the same generation. Each generation inherits little culture from earlier generations. The second is accumulation in a vertical sense. In this type, each individual reaches a high skill level by stacking the wisdom of ancestors. There is little communication between different lines of stacks except for sharing common cultural ancestors at certain points in the past. Lehmann et al. (2010) suggest that the former type of accumulation is favored by natural selection, while our study suggests that the latter is not. It is largely unknown to what extent intermediate types of accumulation are favored by natural selection. Further theoretical research is demanded.

It is worth noting that horizontal transmission *per se* does not generate information inflow into a generation from outside. It just allows individuals of the same generation to exchange skills and knowledge, decreasing the variation between them (Cavalli-Sforza and Feldman, 1981). On the other hand, between-generation transmission allows information inflow into a generation from past generations. Our naïve intuition tells us that modern technologies are built upon a stack of knowledge accumulated over centuries or even millennia. However, the cultural social dilemma in this type of cumulative cultural evolution (i.e., the vertical sort of accumulation) turned out to be very difficult to avoid, at least by means of privatization of culture, compared to the same problem in the horizontal sort of knowledge accumulation.

4.6. Interpretation of empirical data in light of the theoretical results

Empirical data from traditional societies apparently show that knowledge and skills are mostly transmitted vertically or obliquely, and rarely horizontally between peers of similar ages (Hewlett and Cavalli-Sforza, 1986; Ohmagari and Berkes, 1997; Shennan and Steele, 1999; Reyes-Garcia et al., 2009). For example, according to Hewlett and Cavalli-Sforza (1986), the vertical transmission rates of various skills in Aka pygmies, depending on skill categories, range from q=0.519 (for singing skills) to q=0.893 (for food acquisition skills) and is on average q=0.807. Reyes-Garcia et al. (2009), analyzing the relative contributions of vertical, oblique, and horizontal transmission for ethnobotanical knowledge in Tsimane', an Amerindian gatherer-horticulturalist society, concluded that contribution of oblique transmission dominates over that of vertical transmission, suggesting that q<0.5. Eq. (8b) shows that the ESS mature z-value under q=0.5 never exceeds 2. The exact value of the ESS mature z-value depends on the efficiency of social learning β. If 10% of the lifetime is required to learn a half of the role model's knowledge, ($\beta \approx 6.93$), the ESS mature skill level is $\tilde{z}^*(T) \approx 1$, which equals the level that an individual would attain if he/she spends 100% of his/her lifetime in individual learning. On the other hand, the corresponding value for the COS under the same value of β is $\tilde{z}^{\circ}(T) \approx 20$. Thus, in light of empirical data on vertical transmission rates, our model suggests that the privatization of culture by vertical transmission cannot provide a satisfactory explanation for the avoidance of the cultural social dilemma problem in human societies.

Given that vertical transmission is not a promising mechanism to avoid the cultural social dilemma, we may hypothesize that culture is actually accumulating mainly in a horizontal fashion (see section 4.5). This hypothesis, however, again seems contradict data; i.e., horizontal transmission rates between peers in empirical data usually appear to be too low to explain cumulative culture (Hewlett and Cavalli-Sforza, 1986; Ohmagari and Berkes, 1997; Reyes-Garcia et al., 2009). For example, Reyes-Garcia et al. “did not find any evidence of horizontal transmission of ethnobotanical knowledge” in the Tsimane’ (Reyes-Garcia et al., 2009). Shennan and Steele (1999), summarizing a range of ethnographic information concerning cultural transmission of craft skills, found that vertical transmission is the dominant mode in most cases and horizontal transmission is in contrast very rare with few exceptions. If culture is mostly transmitted between, not within, generations as suggested by data, how can the cultural social dilemma problem be solved?

One possibility is that horizontal transmission rate is “effectively” much higher than it appears to be (Zarger, 2002). Claidière and Andrè (2012) point out, reviewing a considerable number of studies, that the mode of cultural transmission typically depends (not only on the *categories* but also) on the *contents* of information transmitted. In particular, data suggest that novel skills are much more likely to be transmitted horizontally than well-established skills (Claidière and Andrè, 2012). Indeed, the skill for making a crossbow, which is relatively new, spread exceptionally through horizontal transmission in Aka pygmies (Hewlett and Cavalli-Sforza, 1986). This transmission mode is not exactly the same as the success-biased transmission mode typically assumed in mathematical models. In models, it is usually assumed that a social learner simply chooses the best among several potential role models (Boyd and Richerson, 1985; Henrich, 2004). However, in the transmission mode under consideration, a social learner chooses a “default” role model (often the same-sex parent) unless he/she finds a remarkably successful role model. More empirical studies are demanded to confirm the ubiquity of such content-dependent switching between a default and temporary transmission mode.

4.7. Lucky mistakes versus deliberate inventions

It is worth noting again that in our terminology the term “individual learning” refers to deliberate effort to add to or improve knowledge that one already bears, as opposed to absorbing knowledge that others bear. So far, all of our arguments stand upon the premise that such individual learning is a prerequisite for cumulative cultural evolution. We remark that this is not a widely accepted view. As briefly mentioned in the introduction, theory predicts that success-biased transmission can drive cumulative cultural evolution by filtering errors made in the process of social learning and selecting only adaptive ones (Enquist and Ghirlanda, 2007; Henrich, 2004). This mechanism is free from the cultural social dilemma problem, and therefore can be an alternative mechanism to explain observed cumulative culture in human societies. We remark that the essential difference between deliberate individual learning and copy error is whether it is a genetically heritable strategy or not. Heritable propensities toward increased errors, if any, would respond to natural selection, and therefore would suffer from a similar problem to that found in our model.

A relevant question would be then what are the relative contributions of deliberate individual learning versus copy errors in cumulative cultural evolution. Unfortunately, we do not know of any empirical data to answer this question. Although complex artifacts or knowledge such as spacecraft or quantum mechanics is probably not a mere collection of successful copy errors accumulated by scientists for decades, we have to be careful in claiming this because Darwinian evolutionary processes, which are driven by copy errors filtered by natural selection, can shape much more complicated and well-functioning machineries than ever been made by humans (Dawkins, 1976). Empirical studies are strongly demanded to elucidate the relative contributions of individual learning and copy errors to human cumulative culture.

4.8. Other hypotheses and remarks

To be fair, we remark that the above-mentioned inconsistency between theory and data might possibly be an artifact. In particular, as previous authors already pointed out, learning and exploitation may not always be mutually exclusive (Wakano and Miura, 2014). In reality, experiences gained through exploitation of environments may promote learning, for example, by increasing the probability of success in trial and error. It is also possible that our models correctly describe real human evolution and the paradox does not exist in this sense. This view entails that our culture is the result of the competition among selfish individuals (i.e., ESS), and our modern technologies can, contrary to our intuition, be accounted for by a few generations of individual learning. This in turn implies that, if we had tried our best in a more coordinated manner (i.e., COS), we might have achieved much higher technology; e.g., we might have already colonized another solar system.

Finally, yet another interesting interpretation of our counterintuitive result is that it is the very reason why cumulative culture is so rare in the biological world while culture itself is not (Boyd and Richerson, 1995b). That is, cumulative culture is in general disfavored, but only modern humans may have solved this problem. Then, how did they solve the problem? One possible answer is the cooperative nature of humans. There is evidence from paleoanthropology that evolution of human cooperativeness preceded emergence of behavioral modernity, suggesting that the former was a prerequisite for the latter (Dubreuil, 2010). For example, if role models are paid back from novices in some way, motivation to learn might overwhelm temptation to take a free ride on culture, promoting the evolution of cumulative culture. However, recent experiments suggest that information access costs may inhibit the evolution of cumulative culture by reducing the benefit of social learning (Mesoudi, 2008). On the other hand, another experiment shows the price of information depends on whether sellers and buyers share a common interest (Derex et al., 2014). Clearly, in future work we need to combine economic and evolutionary modeling to see how information trading within cooperatively breeding groups affects the evolution of cumulative culture.

Whatever interpretation we take, population size should have played a crucial role in the evolution of cumulative culture in modern humans (see eq. (8b)). Some researchers hypothesize that population size was a crucial determinant of the Upper Paleolithic revolution and the subsequent demographic expansion of modern humans (Powell et al., 2009). This hypothesis is based on the theoretical prediction that a larger population has a higher chance of yielding successful transmission errors, which can subsequently spread over the population through success-biased social learning (Henrich, 2004). The significance of population size on cumulative cultural evolution has also been confirmed by experiments (Derex et al. 2013; Kempe and Mesoudi, 2014). Our result supports the importance of demography, although the underlying mechanism is quite different from those proposed in previous studies.

Acknowledgments. We thank MW Feldman, the editor, and three anonymous reviewers for valuable comments. This work is supported by Monbukagakusho grant 22101004 to JYW and YK and Monbukagakusho grant 25101704 and 25118006 to HO.

Literature Cited

Aoki, K., Feldman, M. W. 2014. Evolution of learning strategies in temporally and spatially variable environments: A review of theory. Theor. Popul. Biol. 91, 3-19.

Aoki, K., Lehmann, L., Feldman, M. W., 2011. Rates of cultural change and patterns of cultural accumulation in stochastic models of social transmission. Theor. Popul. Biol. 79, 192-202.

Aoki, K., Wakano, J. Y., Lehmann, L. 2012. Evolutionarily stable learning schedules and cumulative culture in discrete generation models. Theor. Popul. Biol. 81, 300-309.
Box, H. O., Gibson, K. R., 1999. Mammalian Social Learning. Cambridge University Press, Cambridge.

Boyd, R., Richerson, P. J. 1985. Culture and the evolutionary process. The University of Chicago Press, Chicago.

Boyd, R., Richerson, P. J. 1995a. Why does culture increase human adaptability? Ethol.

Sciobiol. 16, 125-143.

Boyd, R., Richerson, P. J. 1995b. Why culture is common, but cultural evolution is rare. Proc. Brit. Acad. 88, 73-93.

Cavalli-sforza, L. L., Feldman, M. W. 1981. Cultural transmission and evolution: A quantitative approach. Princeton University Press, Princeton.

Claidière, N., Andrè, J.-B., 2012. The transmission of genes and culture: a questionable analogy. Evol. Biol. 39, 12-24.

Dawkins, R. 1976. The selfish gene. Oxford University Press, Oxford.

Derex, M., Beugin, M.-P. Godelle, B., Raymond, M. 2013. Experimental evidence for the influence of group size on cultural complexity. Nature 503, 389-391.

Derex, M., Godelle, B., Raymond, M. 2014. How does competition affect the transmission of information? Evol. Hum. Behav. 35, 89-95.

Dubreuil, B. 2010. Paleolithic public goods games: why human culture and cooperation did not evolve in one step. Biol. Philos. 25, 53-73.

Enquist, M., Eriksson, K., Chirlanda, S. 2007. Critical social learning: A solution to Rogers' paradox of nonadaptive culture. Am. Anthropol. 109, 727-734.

Enquist, M., Strimling, P., Eriksson, K., Laland, K., Sjostrand, J., 2010. One cultural parent makes no culture. Anim. Behav. 79, 1353-1362.

Feldman, M. W., Aoki, K., Kumm, J. 1996. Individual versus social learning: Evolutionary analysis in a fluctuating environment. Anthropol. Sci. 104: 209-232.

Enquist, M., Ghirlanda, S., 2007. Evolution of social learning does not explain the origin of human cumulative culture. J. Theor. Biol. 246, 129-135.

Henrich, J. 2004. Demography and cultural evolution: how adaptive cultural processes can produce maladaptive losses – the Tasmanian case. Am. Antiquity 64, 197-214.

Hewlett, B. S., Cavalli-Sforza, L. L., 1986. Cultural transmission among Aka pygmies. Am. Anthropol. 88, 922-934.

Kaplan H., Hill, K., Lancaster, J. Hurtado, A. M., 2000. A theory of human life history evolution: diet, intelligence, and longevity. Evol. Anthropol. 9, 156-185.

Kobayashi, Y., Aoki, K., 2012. Innovativeness, population size, and cumulative cultural evolution. Theor. Popul. Biol. 82, 38-47.

Krützen, M., Mann, J., Heithaus, M. R., Connor, R. C., Bejder, L., Sherwin, W. B., 2005. Cultural transmission of tool use in bottlenose dolphins. Proc. Natl. Acad. Sci. USA 102, 8939-8943.

Laland, K. N., Hoppitt, W. 2003. Do animals have culture? Evol. Anthropol. 12, 150-159.

Lehmann, L., Feldman, M. W., and Kaeuffer, R. 2010. Cumulative cultural dynamics and the coevolution of cultural innovation and transmission: an ESS model for panmictic and structured populations. J. Evol. Biol. 23, 2356-69.

Lehmann, L., Wakano, J. Y., and Aoki, K. 2013. On optimal learning schedules and the marginal value of cumulative cultural evolution. Evolution, 67, 1435-1445.

Maynard Smith, J. 1982. Evolution and the Theory of Games. Cambridge University Press.

Mesoudi, A. 2008. An experimental simulation of the “copy-successful-individuals” cultural learning strategy: adaptive landscapes, producer-scrounger dynamics, and informational access costs. Evol. Hum. Behav. 29, 350-363.

Mesoudi, A., 2011a. Cultural evolution. The University of Chicago Press, Chicago.

Mesoudi, A., 2011b. Variable cultural acquisition costs constrain cumulative cultural evolution. PLoS ONE, 6(3), e18239. doi:10.1371/journal.pone.0018239

Nowak, M. A., Sasaki, A., Taylor, C. Fundenberg, D. 2004. Emergence of cooperation and evolutionary stability in finite populations. Nature 428: 646-650.

Ohmagari, K., Berkes, F., 1997. Transmission of indigenous knowledge and bush skills among the western James Bay Cree women of subarctic Canada. Hum. Ecol. 25, 197-222.

Powell, A., Shennan, S., Thomas, M. G. 2009. Late Pleistocene demography and the appearance of modern human behavior. Science 324: 1298-1301.

Reyes-Garcia, V., Broesch, J., Calvet-Mir, L., Fuentes-Peláez, N., McDade, T. W., Parsa, S., Tanner, S., Huanca, T., Leonard, W. R., Martínez-Rodríguez, M. R., 2009. Cultural transmission of ethnobotanical knowledge and skills: an empirical analysis from an Amerindian society. Evol. Hum. Behav. 30, 274-285.

Richerson, P. J., Boyd, R. 2004. Not by genes alone. The University of Chicago Press, Chicago.

Rogers, A. R. 1988. Does biology constrain culture? Am. Anthropol. 90, 819-831.

Shennan, S. J., Steele, J., 1999. Cultural learning in hominids: a behavioural ecological approach, in: Box, H. O., Gibson, K. R. (Eds.), Mammalian Social Learning. Cambridge University Press, Cambridge, pp. 367-399.

Slater, P. J. B., 1986. The cultural transmission of bird song. Trends Ecol. Evol. 1, 94-97.

Tennie, C., Call, J., Tomasello, M. 2009. Ratcheting up the ratchet: on the evolution of cumulative culture. Philos. Trans. R. Soc. B. 2009, 364, 2405-2415.

Tomasello, M. The cultural origins of human cognition, Harvard University Press.

Wakano, J. Y., Aoki., K. 2006. A mixed strategy model for the emergence and intensification of social learning in a periodically changing natural environment. Theor. Popul. Biol. 70:486-497.

Wakano, J. Y., Aoki, K., Feldman, M. W. 2004. Evolution of social learning: a mathematical analysis. Theor. Popul. Biol. 66:249-258.

Wakano, J. Y., Miura, C. 2014. Trade-off between learning and exploitation: The Pareto-optimal versus evolutionarily stable learning schedule in cumulative cultural evolution. Theor. Popul. Biol. 91, 37-43.

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R W., Boesch. C. 1999. Cultures in chimpanzees. Nature 399, 682-685.

Zarger, R. K., 2002. Acquisition and transmission of subsistence knowledge by Q'eqchi' Maya in Belize, in: Stepp, J. R., Wyndham, F. S., Zarger, R. K. (Eds.), Ethnobiology and Biocultural Diversity. University of Georgia Press, Athens, pp. 593-603.

Figure captions

Fig. 1: A schematic diagram to illustrate the between-generation processes in the finite-population model. Circles and squares in each row represent resident and mutant individuals, respectively, in a specific generation, where the generation number increases downward. Solid and dotted arrows represent genetic and cultural transmission, respectively. Simultaneous occurrence of genetic and vertical cultural transmission is represented by a two-headed solid arrow. Each individual (i, τ) is given two numbers, the lower one of which represents the mature *z*-value $z_{i,\tau}(T)$ of the individual and the upper one the mature *z*-value of the role model $z_{\rho_\tau(i),\tau-1}(T)$ (for simplicity we omitted the subscript of ρ). The values of $z_{i,\tau}(T)$ and $z_{\rho_\tau(i),\tau-1}(T)$ in the diagram are not precise values obtained from theory but are artificial values for illustration. In generation 1, a single mutant is introduced in a resident population of size 5 which is at cultural equilibrium (the star represents the point where mutation occurred). The equilibrium *z*-value of the resident strategy is set as 5. It is assumed that the mutant strategy invests more time in individual and/or social learning than the resident, so that mutants tend to increase the mature *z*-value. The diagram shows a case where mutants go extinct in generation 4. Such extinction can be caused either by i) the

decrease in mutant's fitness due to increased learning time or ii) by random genetic drift even if mutant strategy has selective advantage.

Fig. 2: Effect of β on (a) x*, (b) v*, and (c) $\tilde{z}^*(T)$ for different values of q in the infinite population model. The thick solid lines represent the COS (i.e., x°, v°, and $\tilde{z}^{\circ}(T)$). The same graphs also represent the results for different population sizes in the finite population model with pure vertical transmission (corresponding population sizes are shown in parentheses). Note that the infinite population model and the finite population model with pure vertical transmission yield equivalent results when q=1-1/N.

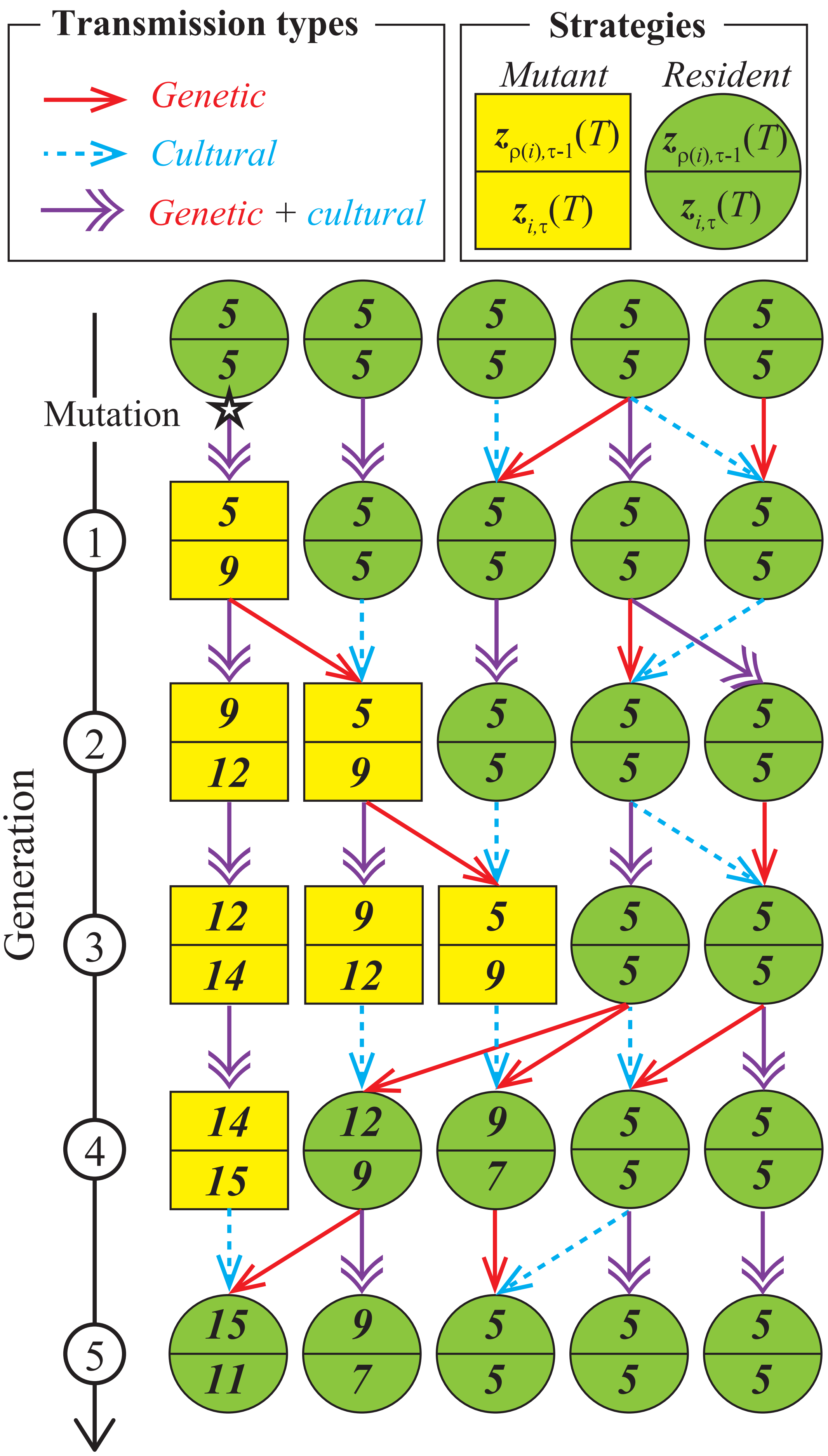
Fig. 3: A typical time-series behavior of (a) $\bar{x}$, $\bar{v}$, and (b) $\bar{z}(T)$ (all averaged over the population) obtained in the individual-based simulations. Parameter values are β=10, q=1.0, and N=100. The thick dotted lines represent equilibrium values predicted by the analytical theory. The initial condition is x=0.1 and v=0.9 for all individuals.

Fig. 4: The effect of β on the equilibrium values of (a) $\bar{x}$, (b) $\bar{v}$, and (c) $\bar{z}(T)$ (all averaged over the population) for three values of q (1.0, 0.99, and 0.9). Population size is N=100. The equilibrium values are computed by running a simulation for 10^7

generations and then averaging the values over the last 5×10^6 generations.

Fig. 5: The dynamics of the mutant (thin solid line) and resident (thick solid line) fitnesses in the finite-population model when the mutant strategy is the COS and the resident strategy is the ESS. The dotted line represents the probability that mutants do not go extinct before a given generation under selective neutrality. Parameter values are β=10, N=100, and q=1.0.

Figure 1



Transmission types
Genetic
Cultural
Genetic + cultural
Strategies
Mutant
Resident
$z_{\rho(i),\tau-1}(T)$
$z_{i,\tau}(T)$
$z_{\rho(i),\tau-1}(T)$
$z_{i,\tau}(T)$
Mutation
Generation
1
2
3
4
5
5 5
5 5
5 5
5 5
5 5
5 9
5 5
5 5
5 5
5 5
9 12
5 9
5 5
5 5
5 5
12 14
9 12
5 9
5 5
5 5
14 15
12 9
9 7
5 5
5 5
15 11
9 7
5 5
5 5
5 5

Figure 2

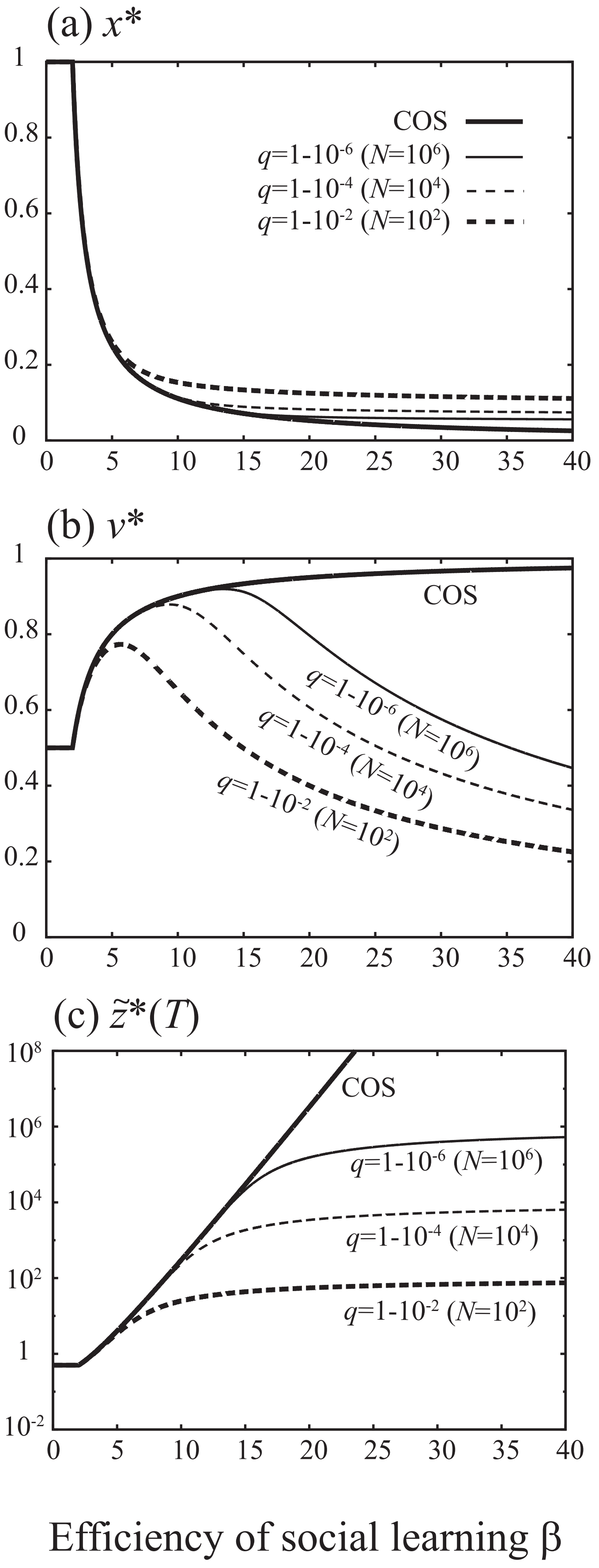

(a) x*
1
0.8
0.6
0.4
0.2
0
0
5
10
15
20
25
30
35
40
COS
q=1-10-6 (N=106)
q=1-10-4 (N=104)
q=1-10-2 (N=102)
(b) v*
1
0.8
0.6
0.4
0.2
0
0
5
10
15
20
25
30
35
40
COS
q=1-10-6 (N=106)
q=1-10-4 (N=104)
q=1-10-2 (N=102)
(c) z̃*(T)
108
106
104
102
1
10-2
0
5
10
15
20
25
30
35
40
COS
q=1-10-6 (N=106)
q=1-10-4 (N=104)
q=1-10-2 (N=102)
Efficiency of social learning β

Figure 3

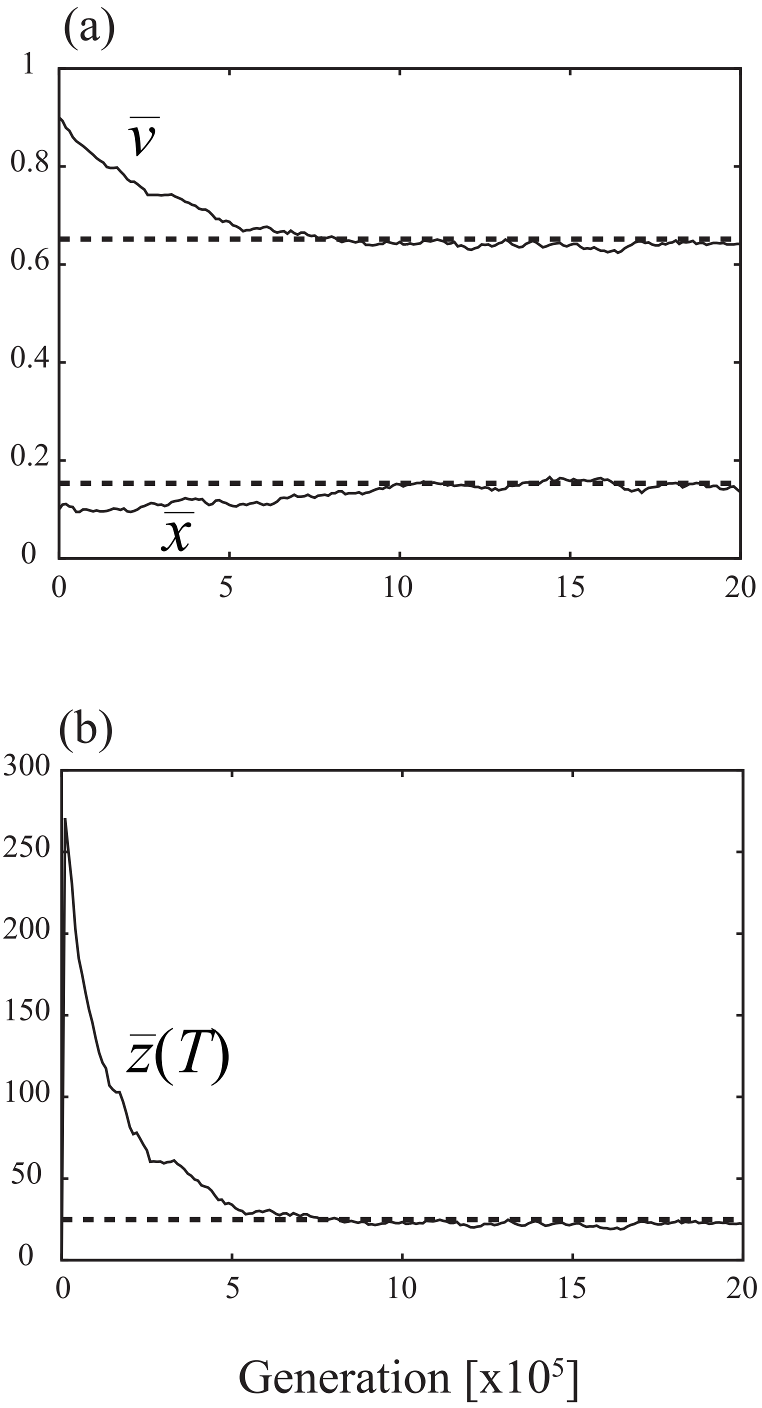

(a)
1
0.8
0.6
0.4
0.2
0
$\overline{v}$
$\overline{x}$
0
5
10
15
20
(b)
300
250
200
150
100
50
0
$\bar{z}(T)$
0
5
10
15
20
Generation [x10^5]

Figure 4

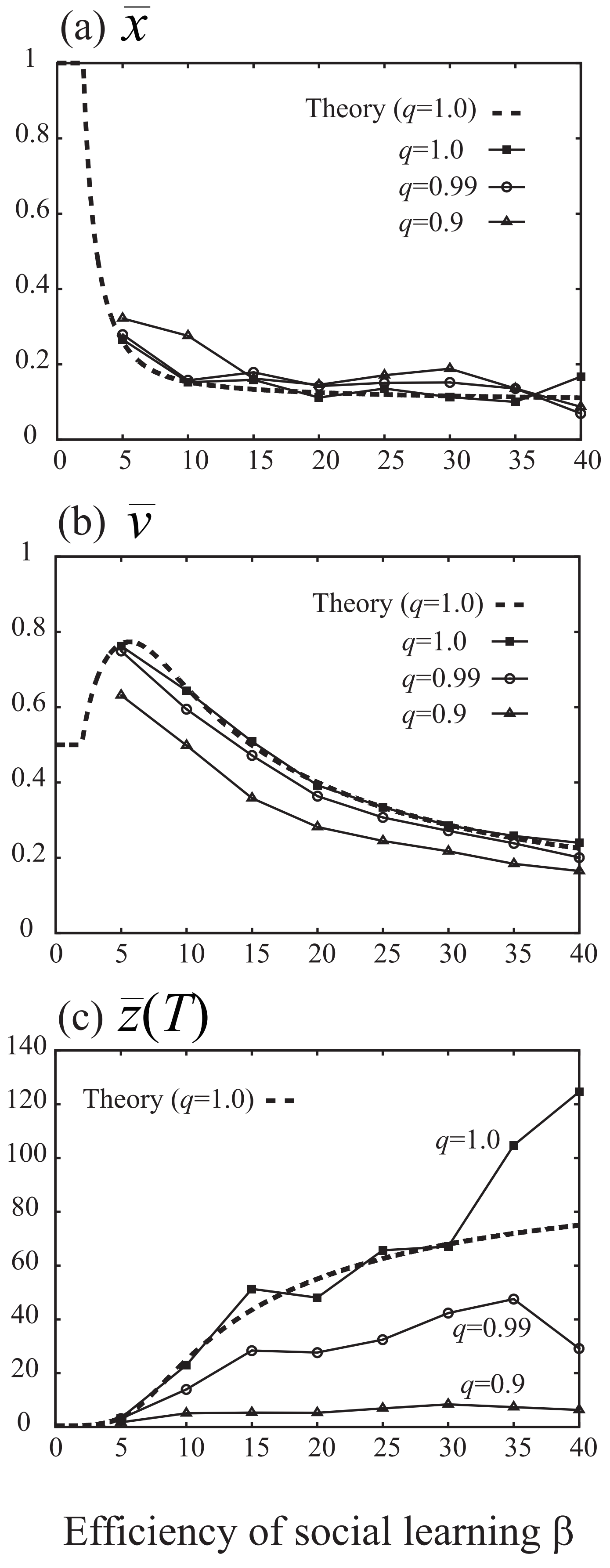
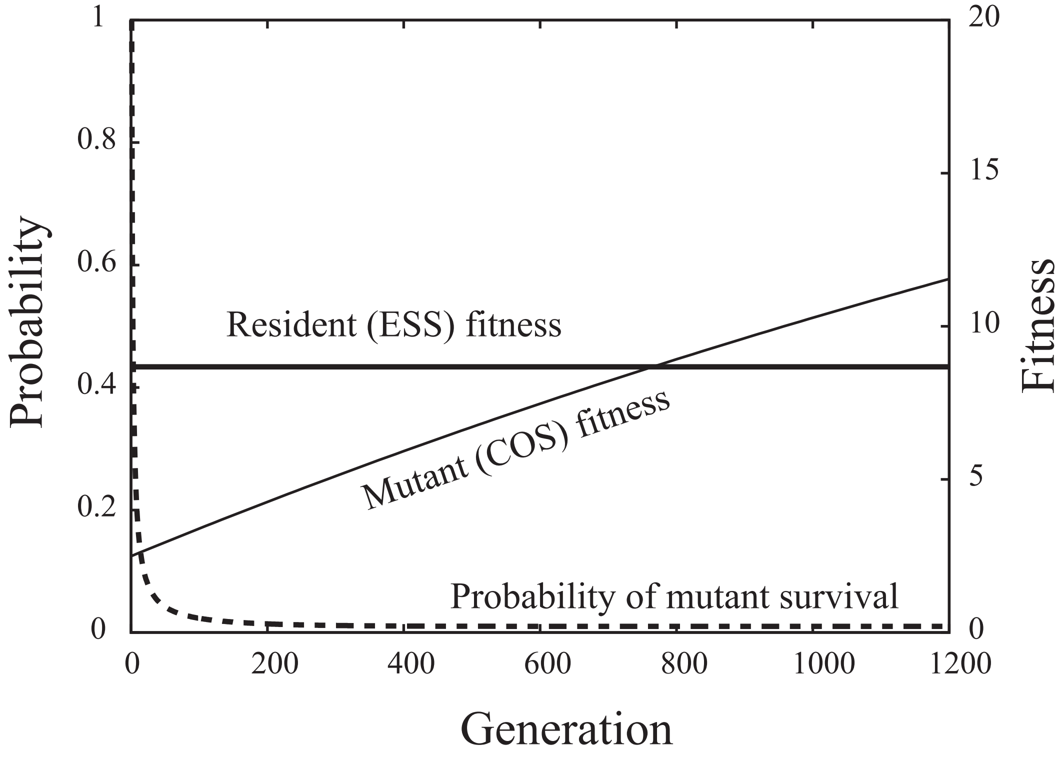

(a) $\bar{x}$
1
0.8
0.6
0.4
0.2
0
0 5 10 15 20 25 30 35 40
Theory (q=1.0)
q=1.0
q=0.99
q=0.9
(b) $\bar{v}$
1
0.8
0.6
0.4
0.2
0
0 5 10 15 20 25 30 35 40
Theory (q=1.0)
q=1.0
q=0.99
q=0.9
(c) $\bar{z}(T)$
140
120
100
80
60
40
20
0
0 5 10 15 20 25 30 35 40
Theory (q=1.0)
q=1.0
q=0.99
q=0.9
Efficiency of social learning β

Figure 5



Probability
Fitness
Generation
1
0.8
0.6
0.4
0.2
0
20
15
10
5
0
0
200
400
600
800
1000
1200
Resident (ESS) fitness
Mutant (COS) fitness
Probability of mutant survival

Tables

N	Population size
q	Vertical transmission rate
T	Lifetime
β	Efficiency of social learning
α	Efficiency of individual learning
$v_{i,\tau}$	The fraction of the lifetime invested in learning by individual (i,τ)
$x_{i,\tau}$	The fraction of the learning time invested in individual learning by individual (i,τ)
$z_{i,\tau}(t)$	The *z*-value of individual (i,τ) at within-generation time *t*.
$\tilde{z}(T)$	The equilibrium mature *z*-value in a genetically monomorphic population
$w_{i,\tau}$	The fitness of individual (i,τ)
$\tilde{w}$	The equilibrium fitness in a genetically monomorphic population
v°, x°, $\tilde{z}^\circ(T)$	The COS values of $v_{i,\tau}$, $x_{i,\tau}$, and $\tilde{z}(T)$, respectively.
v^*, x^*, $\tilde{z}^*(T)$	The ESS values of $v_{i,\tau}$, $x_{i,\tau}$, and $\tilde{z}(T)$, respectively.
$\bar{v}$, $\bar{x}$, $\bar{z}(T)$	The population averages of $v_{i,\tau}$, $x_{i,\tau}$, and $\tilde{z}(T)$, respectively.

Table 1: Notation

Supporting information

A Paradox of Cumulative Culture

Yutaka Kobayashi[a,b], Joe Y. Wakano[c], Hisashi Ohtsuki[d]

March 12, 2015

[a]Research Center for Social Design Engineering, Kochi University of Technology, Kochi 782-8502, Japan, [b]Department of Management, Kochi University of Technology, Kochi 782-8502, Japan, [c]Meiji Institute for Advanced Study of Mathematical Sciences, Nakano, Tokyo 164-8525, Japan, [d]The Graduate University for Advanced Studies, Shonan Village, Hayama, Kanagawa 240-0193, Japan

Appendix A: Derivation of the COS

To derive the COS, let us assume that the population is monomorphic for a learning strategy (x, v). Solving eq. (1) in the main text with respect to

$z_{i,\tau}(t)$ under the assumption that $z_{i,\tau}(0) = 0$ and $(x_{i,\tau}, v_{i,\tau}) = (x, v)$, we have

$$z_{i,\tau}(t) = z_{\rho_\tau(i),\tau-1}(T)(1 - e^{-\beta t}). \tag{11}$$

It follows that the z-value at the end of the social learning stage ($t = v(1-x)$) is given by

$$z_{i,\tau}(v(1-x)) = z_{\rho_\tau(i),\tau-1}(T)(1 - e^{-\beta v(1-x)}). \tag{12}$$

Further, from eq. (2) in the main text, the value of $z_{i,\tau}(t)$ at the end of the individual-learning stage ($t = v$) is given by

$$\begin{aligned} z_{i,\tau}(v) &= z_{i,\tau}(v(1-x)) + vx \\ &= z_{\rho_\tau(i),\tau-1}(T)(1 - e^{-\beta v(1-x)}) + vx. \end{aligned} \tag{13}$$

Noting that $z_{i,\tau}(v) = z_{i,\tau}(T)$, we have

$$z_{i,\tau}(T) = z_{\rho_\tau(i),\tau-1}(T)(1 - e^{-\beta v(1-x)}) + vx. \tag{14}$$

This equation gives the between-generation dynamics of $z_{i,\tau}(T)$. From eq. (14), the equilibrium value of $z_{i,\tau}(T)$, denoted by $\tilde{z}(T)$, is given by

$$\tilde{z}(T) = \lim_{\tau\to\infty} z_{i,\tau}(T) = vxe^{\beta v(1-x)}. \tag{15}$$

The equilibrium fitness function, denoted by $\tilde{w}$, is therefore given by

$$\begin{aligned} \tilde{w} = \lim_{\tau \to \infty} w_{i,\tau} &= \lim_{\tau \to \infty} z_{i,\tau}(T) \cdot (1 - v) \\ &= v(1 - v)xe^{\beta v(1-x)}. \end{aligned} \tag{16}$$

The COS is the strategy (x, v) which maximizes eq. (16). It is easily shown that the strategy (x°, v°) given by eq. (6) in the main text maximizes eq. (16) and hence gives the COS.

Appendix B: Derivation of the ESS in an infinite population

We define an evolutionarily stable learning strategy in an infinite population as a learning strategy that is resistant against invasion by rare mutants with any slightly deviated strategy. We will derive eq. (7) in the main text, which an ESS must satisfy.

Let (x, v) and (x', v') denote the resident and mutant strategies, respectively. We assume that the resident population is at cultural equilibrium, so that all residents have the z-value given by eq. (15) at the end of the learning stage. In order to derive the ESS, we classify individuals as follows. Residents are class 0. The mutants who socially learned from residents are class 1. The mutants who socially learned from class-1 individuals are class 2. Class-j individuals are defined recursively. Note that offspring of class-j mutants fall back to class 1 when their cultural role models are residents (oblique social learning). In this case, cultural accumulation over j generations by mutants is reset.

From eq. (14), the mature z-value of an individual (i,τ) in class $j\geq 1$ satisfies

$$z_{i,\tau}(T)=z_{\rho_\tau(i),\tau-1}(T)(1-e^{-\beta v'(1-x')})+v'x'. \tag{17}$$

Note that the above equation recursively applies, so that $z_{\rho_\tau(i),\tau-1}(T)$ is given as a function of $z_{\rho_{\tau-1}(\rho_\tau(i)),\tau-2}(T)$, which is in turn given as a function of $z_{\rho_{\tau-2}(\rho_{\tau-1}(\rho_\tau(i))),\tau-3}(T)$, and so on. Given that individual (i,τ) belongs to class j, individual $(\rho_{\tau-(j-1)}(\rho_{\tau-(j-2)}(\dots(\rho_{\tau-1}(\rho_\tau(i)))\dots)),\tau-j)$ belongs to class 0 and is hence a resident. Noting this and eq.(15), eq. (17) can be solved to yield

$$z_{i,\tau}(T)=v'x'e^{\beta v'(1-x')}+r^{C_\tau(i)}(vxe^{\beta v(1-x)}-v'x'e^{\beta v'(1-x')}), \tag{18}$$

where $C_\tau(i)$ denotes the class of individual (i,τ) and

$$r=1-e^{-\beta v'(1-x')}. \tag{19}$$

Note that eq. (18) does not depend on i and τ but only on the class $C_\tau(i)$ of individual (i,τ). This implies that the fitness of an individual also depends only on its class. Therefore, we let w'_j denote the fitness of class-j *mutants*:

$$w'_{C_\tau(i)} := z_{i,\tau}(T)(1-v'), \qquad (C_\tau(i) \geq 1) \tag{20}$$

It is easily confirmed that mutants have the same fitness as residents irrespective of classes (i.e. $w'_j = \tilde{w} = v(1-v)xe^{\beta x(1-v)}$ for arbitrary $j \geq 1$) if they adopt the same strategy as residents $((x', v') = (x, v))$.

Let $p_{j,\tau}$ denote the frequency of class-j mutants $(j \geq 1)$ in the population in generation τ. Since mutants are rare, we may assume that a mutant's role model is a mutant only when vertical transmission occurs. The offspring of a class-j mutant hence belong to class-$(j+1)$ and class-1 with probabilities q and $1-q$, respectively. Further, because of rarity of mutants, the average fitness of the population is approximated by the residents' fitness $\tilde{w}$ given by eq. (16). From these arguments, it holds that

$$p_{1,\tau+1} = \sum_{j=1}^{\infty}(1-q)\frac{w'_j}{\tilde{w}}p_{j,\tau}, \tag{21}$$

$$p_{j+1,\tau+1} = q\frac{w'_j}{\tilde{w}}p_{j,\tau}, \tag{22}$$

where $j \geq 1$.

Note that the above equation is formally equivalent to the standard model of age structure. Substituting $p_{j,\tau+1} = \lambda p_{j,\tau}$ into eqs. (21) and (22) and rearranging the resulting equations, it is easily shown that the leading eigenvalue λ, i.e. the asymptotic growth rate of mutants, should satisfy the following

(Euler-Lotka) characteristic equation:

$$1 = \sum_{i=0}^{\infty}(1-q)q^i\lambda^{-i-1}\prod_{j=1}^{i+1}\frac{w'_j}{\tilde{w}}. \tag{23}$$

Note that, when mutants have the same fitness as residents (i.e. $w_j = \tilde{w}$ for all j's), $\lambda = 1$ is the only solution of eq. (23). This implies that the frequency of mutants remains constant when they adopt the same strategy as residents.

Differentiating eq. (23) with respect to a mutant strategic variable y' ($y' \in \{x', v'\}$) yields

$$\begin{aligned} 0 &= \sum_{i=0}^{\infty}(1-q)q^i(-i-1)\lambda^{-i-2}\frac{\partial\lambda}{\partial y'}\prod_{j=1}^{i+1}\frac{w'_j}{\tilde{w}} + \\ &\quad \sum_{i=0}^{\infty}(1-q)q^i\lambda^{-i-1}\sum_{k=1}^{i+1}w_k'^{-1}\frac{\partial w'_k}{\partial y'}\prod_{j=1}^{i+1}\frac{w'_j}{\tilde{w}}. \end{aligned} \tag{24}$$

Substituting $x' = x$, $v' = v$, $w'_j = \tilde{w}$, and $\lambda = 1$ into eq. (24) and rearranging the resulting equation yield

$$\tilde{w}\left.\frac{\partial\lambda}{\partial y'}\right|_{x'=x,v'=v} = \left.\frac{\partial w'}{\partial y'}\right|_{x'=x,v'=v}, \tag{25}$$

where

$$w' = \sum_{i=1}^{\infty}(1-q)q^{i-1}w'_i. \tag{26}$$

If the stationary growth rate of mutants is larger than one, mutants can invade. Therefore, for the resident strategy (x, v) to be evolutionarily stable,

λ must be maximized at $(x', v') = (x, v)$ as a function of the mutant strategy (x', v'). However, this and eq. (25) together imply that w' is maximized at $(x', v') = (x, v)$. Thus, for our ESS analysis we may treat w' like the mutant invasion fitness.

In fact, w' can be interpreted as the asymptotic average of the mutant invasion fitness, as follows. Note that the leading eigenvector of the system (21-22) is given by $(1, q, q^2, \ldots, q^{i-1}, \ldots)$. This means that the fraction of class i among mutants asymptotically approaches $(1-q)q^{i-1}$ when selection is absent ($(x', v') = (x, v)$). Thus, when selection is sufficiently weak, the average fitness of mutants is asymptotically given by $\sum_{i=1}^{\infty}(1-q)q^{i-1}w'_i = w'$.

Using eq. (18), (26) and (20), we find that

$$\begin{aligned} w' &= (1-v')v'x'e^{\beta v'(1-x')} \\ &\quad +(1-v')\frac{r(1-q)}{1-rq}(vxe^{\beta v(1-x)} - v'x'e^{\beta v'(1-x')}). \end{aligned} \tag{27}$$

For (x, v) to be the ESS, w' as a function of (x', v') must be maximized at $(x', v') = (x, v)$. Thus, the ESS (x^*, v^*) satisfies

$$\left.\frac{\partial w'}{\partial x'}\right|_{x'=x=x^*, v'=v=v^*} = 0, \tag{28}$$

$$\left.\frac{\partial w'}{\partial v'}\right|_{x'=x=x^*, v'=v=v^*} = 0. \tag{29}$$

It is easily shown that these equations reduce to eqs. (7a) and (7b) in the main text. Finally, substituting eq. (7a) in the main text into eq. (15) yields eq. (7c).

Appendix C: Derivation of the ESS in a finite population

Here we derive the ESS in a finite population assuming pure vertical transmission ($q = 1$) (eq. (9) in the main text). More specifically, we show that the ESS for a finite population of size N under $q = 1$ is identical with the ESS for an inifinite population under $q = 1 - 1/N$. Thus, in terms of the ESS, decreasing the population size from ∞ to N under $q = 1$ has exactly the same effect as decreasing q by $1/N$ in an infinite population.

To compute the ESS under $q = 1$, we need the fixation probability of a mutant strategy that is initially expressed by a single individual. For this purpose, we apply the method introduced by Rousset (2004) below.

Imagine that a mutant strategy (x', v') is expressed by a single individual in the population of the resident strategy (x, v). For convenience sake, let us reuse the classification of individuals introduced in Appendix B. Then, the initial single mutant is obviously of class 1 because there is no mutant in the previous generation. Since $q = 1$ (pure vertical transmission), any mutant in any generation τ inherits culture from its own parent, which is a mutant in generation $\tau - 1$. This implies that all mutants in generation τ belong to class τ ($C_\tau(i) = \tau$ for any mutant (i, τ)), given that the mutant was introduced in generation 1. Therefore, all mutants in generation τ have equal fitnesses given by w'_τ in eq. (20). It is important that the mutant fitness is not a stochastic variable but is determined by the number of generations passed since introduction of the initial mutant. By virtue of this property, we can treat this process as a Wright-Fisher process in which the selection coefficient depends deterministically on time (see below).

Let P_τ denote the frequency of mutants in generation τ. Since all mutants in generation τ belong to class τ, it holds that $P_\tau = \sum_j p_{j,\tau} = p_{\tau,\tau}$ in Appendix B's notation. Note that we assume a Wright-Fisher-type update for the genetic state of the population and also culture is transmitted between adjacent generations; thus, P_τ obeys a time-inhomogeneous Markov process with the initial state $P_1 = 1/N$. Obviously, this stochastic process has only two absorbing states: $P_\tau = 1$ (fixation) and $P_\tau = 0$ (extinction). Let π denote the fixation probability of the mutant strategy. Then, the expected frequency of mutants in the infinitely distant future should be given by

$$\lim_{\tau\to\infty} E[P_\tau] = 1 \cdot \pi + 0 \cdot (1-\pi) = \pi, \tag{30}$$

where $E[\cdot]$ denotes expectation. Below we use this relationship to compute π.

Note that we can write

$$P_\tau = P_1 + \Delta P_1 + \Delta P_2 + \ldots + \Delta P_{\tau-1}, \tag{31}$$

where $\Delta P_\tau = P_{\tau+1} - P_\tau$ denotes the frequency change between generations

τ and $\tau + 1$ and is a stochastic variable itself. Substituting eq. (31) into eq. (30) yields

$$\begin{aligned} \pi &= E[P_1 + \sum_{\tau=1}^{\infty} \Delta P_\tau] \\ &= \frac{1}{N} + \sum_{\tau=1}^{\infty} E[\Delta P_\tau], \end{aligned} \tag{32}$$

where we used $E[P_1] = P_1 = 1/N$. From the standard theory of population genetics, the frequency change ΔP_τ is given by

$$\Delta P_\tau = \frac{w'_\tau - \tilde{w}}{\tilde{w} + P_\tau (w'_\tau - \tilde{w})} P_\tau (1 - P_\tau), \tag{33}$$

where $\tilde{w}$ is the equilibrium fitness of residents given by eq. (16). Let us define the selection coefficient s_τ as

$$s_\tau = \frac{w'_\tau - \tilde{w}}{\tilde{w}}. \tag{34}$$

Substituting (34) into eq. (33) yields

$$\Delta P_\tau = \frac{s_\tau}{1 + P_\tau s_\tau} P_\tau (1 - P_\tau) \approx s_\tau P_\tau (1 - P_\tau), \tag{35}$$

where the approximation holds for small s_τ.

Substituting eq. (35) into eq. (32) yields

$$\pi \approx \frac{1}{N} + \sum_{t=1}^{\infty} s_\tau E[P_\tau (1 - p_\tau)]. \tag{36}$$

Note that the expectation $E[P_\tau(1-P_\tau)]$ in the above equation is itself affected by selection coefficients of up to generation $\tau - 1$ (i.e., $s_1, s_2, s_3, \ldots, s_{\tau-1}$). However, Rousset (2004) has shown that the expectation $E[\cdot]$ can be approximately replaced by the expectation under neutrality (i.e. $s_0 = s_1 = \ldots = s_t = \ldots = 0$) provided selection is sufficiently weak. We denote the expectation under neutrality by $E^\circ[\cdot]$ following Rousset (2004). Thus, it holds that

$$\pi \approx \frac{1}{N} + \sum_{t=1}^{\infty} s_\tau E^\circ[P_\tau(1-P_\tau)]. \tag{37}$$

Note that $E^\circ[2P_\tau(1-P_\tau)]$ can be interpreted as the probability that two individuals drawn at random with replacement from generation τ have different genotypes under selective neutrality. Such two individuals can have different genotypes only if their ancestral lineages trace back to generation 1 without coalescing and, in addition, only one of them hits the initial mutant. From the standard coalescent theory this probability is given by

$$\begin{aligned} E^\circ[2P_\tau(1-P_\tau)] &= \left(1-\frac{1}{N}\right)^{\tau-1} \cdot 2P_1(1-P_1) \\ &= 2\frac{1}{N}\left(1-\frac{1}{N}\right)^{\tau}, \end{aligned} \tag{38}$$

where we used $P_1 = 1/N$.

Substituting eqs. (34) and (38) into eq. (37) yields

$$\pi \approx \frac{1}{N} + \frac{1}{N}\sum_{\tau=1}^{\infty}\left(\frac{w'_\tau}{\tilde{w}} - 1\right)\left(1-\frac{1}{N}\right)^{\tau}$$

$$= \frac{1}{N} + \left(1 - \frac{1}{N}\right)\left(\frac{w'}{\tilde{w}} - 1\right), \tag{39}$$

where

$$w' = \sum_{\tau=1}^{\infty} w'_{\tau} \frac{1}{N}\left(1 - \frac{1}{N}\right)^{\tau-1}. \tag{40}$$

Remember that for a finite population we define an ESS as the strategy that never allows a mutant strategy expressed by a single individual to have a fixation probability higher than $1/N$ (i.e. the fixation probability of the ESS itself). This implies that for our ESS analysis we can treat w' like the mutant invasion fitness in the standard ESS analysis in an infinite-population model. Note that eq. (40) is formally identical with eq. (26) except that q is replaced by $1 - 1/N$. This implies that the ESS for a finite population under pure vertical transmission ($q = 1$) is equivalent with the ESS for an infinite population with $q = 1 - 1/N$.

Appendix D: Probabilistic engagement in social and individual learning

In the main text, we assumed that social and individual learning occur in separate stages of life. In this Appendix, we instead assume that each individual engages in individual and social learning with probabilities x and $1 - x$, respectively, at any moment in the learning stage and derive eq. (14) under some additional assumptions. Thus, the results of the present paper all apply to this modified model.

Suppose that $z_{i,\tau}(t)$ represents the amount of knowledge that the individual (i,τ) acquires by time t through individual and social learning. Let $z_{i,\tau,IL}(t)$ and $z_{i,\tau,SL}(t)$ denote the amounts of knowledge acquired through individual and social learning, respectively, by time t. In addition, assume that the knowledge acquired through individual learning never overlaps with that acquired through social learning. This implies that any piece of knowledge produced by an individual through individual learning is always new to the role model of the focal individual as well as the focal individual itself. Then, the total amount of knowledge individual (i,τ) bears is given by $z_{i,\tau}(t) = z_{i,\tau,SL}(t) + z_{i,\tau,IL}(t)$.

Note that each individual engages in social learning with probability $1-x$ at any moment in the learning stage. This implies that $z_{i,\tau,SL}(t)$ grows in the learning stage as follows:

$$\frac{d}{dt} z_{i,\tau,SL}(t) = \beta(1-x)(z_{\rho_\tau(i),\tau-1}(T) - z_{i,\tau,SL}(t)). \qquad (0 \le t \le v) \tag{41}$$

Likewise, $z_{i,\tau,IL}(t)$ follows

$$\frac{d}{dt} z_{i,\tau,IL}(t) = \alpha x = x. \qquad (0 \le t \le v) \tag{42}$$

Integrating both equations yield

$$z_{i,\tau,SL}(v) = z_{\rho_\tau(i),\tau-1}(T)(1 - e^{-\beta v(1-x)}). \tag{43}$$

$$z_{i,\tau,IL}(v) = xv. \tag{44}$$

Summing up eqs. (43) and (44) yields

$$\begin{aligned} z_{i,\tau}(v) &= z_{i,\tau,SL}(v) + z_{i,\tau,IL}(v) \\ &= z_{\rho_\tau(i),\tau-1}(T)(1 - e^{-\beta v(1-x)}) + xv. \end{aligned} \tag{45}$$

Since knowledge does not grow in the exploitation stage, we have $z_{i,\tau}(T) = z_{i,\tau}(v)$. Substituting this into eq. (45) yields eq. (14).

Note that the above derivation requires to specify the interpretation of the z-value and the structure of knowledge. On the other hand, the separate-step framework of the original model incorporates a wider class of knowledge structure and allows more general interpretations of the results in this respect.

Literature Cited

- Rousset, F. 2004. *Genetic structure and selection in subdivided populations.* Princeton University Press.