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A paradox of cumulative culture

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HIGHLIGHTS

- Infinite and finite population models of gene-culture coevolution are considered.
- A social dilemma caused by the publicness of culture disfavors cumulative culture.
- Privatization of culture by vertical transmission is considered.
- Slight oblique transmission is enough to prevent cumulative cultural evolution.
- Genetic drift in a finite population prevents cumulative cultural evolution.

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ABSTRACT

Culture can grow cumulatively if socially learnt 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 member 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 versus 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, 2004). 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 a behavior is not cumulative culture, as it falls 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, 2004). On the other hand, ethnobotanical knowledge for food-gathering and processing

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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 who 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 learnt 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 learnt 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 Section 4, 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

Table 1
Notation.

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
$v^{\circ}, x^{\circ}, \tilde{z}^{\circ}(T)$	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
$\overline{v}, \overline{x}, \overline{z}(T)$	the population averages of $v_{i,\tau}$, $x_{i,\tau}$, and $z_{i,\tau}(T)$, respectively