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# Inclusive fitness analysis of cumulative cultural evolution in an island-structured population

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ABSTRACT

The success of humans on the globe is largely supported by our cultural excellence. Our culture is cumulative, meaning that it is improved from generation to generation. Previous works have revealed that two modes of learning, individual learning and social learning, play pivotal roles in the accumulation of culture. However, under the trade-off between learning and reproduction, one's investment into learning is easily exploited by those who copy the knowledge of skillful individuals and selfishly invest more efforts in reproduction. It has been shown that in order to prevent such a breakdown, the rate of vertical transmission (*i.e.* transmission from parents to their offspring) of culture must be unrealistically close to one. Here we investigate what if the population is spatially structured. In particular, we hypothesize that spatial structure should favor highly cumulative culture through endogenously arising high kinship. We employ Wright's island model and assume that cultural transmission occurs within a local island. Our inclusive fitness analysis reveals combined effects of direct fitness of the actor, indirect fitness through relatives in the current generation, and indirect fitness through relatives in future generations. The magnitude of those indirect benefits is measured by intergenerational coefficients of genetic relatedness. Our result suggests that the introduction of spatial structure raises the stationary level of culture in the population, but that the extent of its improvement compared with a well-mixed population is marginal unless spatial localization is extreme. Overall, our model implies that we need an alternative mechanism to explain highly cumulative culture of modern humans.



## 1. Introduction

Perhaps one of the most prominent characteristics of modern humans is their advanced culture. Although debates exist about its definition, culture is often defined as the information that is acquired from others through social learning (Boyd and Silk, 2009) or the resulting group-typical behavioral pattern (Laland and Hoppitt, 2003). Several studies have suggested that not only humans have culture. For example, chimpanzees in different areas show diversified patterns of behavior, but their difference cannot fully be explained by their local ecological conditions only (Whiten et al., 1999). New Caledonian crows are excellent tool manufacturers, but the shapes of their tools show regional differences (Hunt, 1996). Those examples suggest that some non-human animals can also be engaged in social learning. Human culture is, however, characterized by the accumulation of cultural improvements from generation to generation to a higher level (Boesch and Tomasello, 1998; Laland and Hoppitt, 2003; Tennie et al., 2009; Mesoudi, 2011; Dean et al., 2015; but see Pradhan et al., 2012 for the possibility of cumulative culture in great-apes). It is possibly this cumulative feature of human culture that made us so distinct from other animals. It also made us so successful on the globe (Boyd and Richerson, 1985; Tomasello, 1994, 1999; Richerson and Boyd, 2004; Boyd et al., 2011); our modern society fully depends on the accumulated knowledge about nature such as physics, chemistry, biology, geology, as well as that in engineering, agriculture, medicine, and so on; none of which can be realized by the effort of a single individual.

Many theoretical works on the evolution of culture have focused on various learning strategies and/or their capability in

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coping with varying environments (Boyd and Richerson, 1985, 1988; Rogers, 1988; Feldman et al., 1996; Wakano et al., 2004; Aoki et al., 2005; Aoki and Nakahashi, 2008; Rendell et al., 2010; Kobayashi and Wakano, 2012; Aoki and Feldman, 2014; Kobayashi and Ohtsuki, 2014). In particular, two different learning modes have been intensively studied. One is individual learning (hereafter shortened as IL), which refers to a mode of learning that does not rely on others, such as trial-and-error, insight, or deduction. The other is social learning (shortened as SL), the process by which one's learning is enhanced by the presence of others (Laland, 2008), for example, via local enhancement, emulation, imitation, or teaching (Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985; Rogers, 1988). Theoretical results suggest that IL is favored more when environmental variation, either temporal or spatial, is large, and that SL is the better strategy when the variation is small.

However, to explain cumulative culture, the combination of these two learning modes is important (Enquist et al., 2007; Borenstein et al., 2008; Aoki, 2010; Lehmann et al., 2010). Knowledge or skill is improved from generation to generation, in terms of its amount or quality, when one inherits culture from previous generations by SL and modifies it through IL. Such intergenerational transmission of information is a key factor supporting the accumulation of cultural traits (Tomasello, 1999). It is argued that human children are very good at copying (and even at overcopying) others' actions, which provides a basis of a "copy-all, refine/correct-later" strategy (Flynn and Whiten, 2008; Whiten et al., 2009). Striano et al. (2001) report that the fraction of novel actions that human infants perform relative to imitative ones increases with age. Those studies suggest the importance of understanding learning in the framework of one's lifetime schedule strategy. In fact, recent theoretical studies have considered an optimal learning schedule, namely which should come first in one's lifetime, IL or SL. The answer depends on details of the model, but under reasonable assumptions "SL first and IL second" is often proved to be an adaptive strategy (Aoki et al., 2012; Lehmann et al., 2013). In addition, Aoki et al. (2012) found that the evolutionarily stable (ES) learning schedule was also the one that achieves the highest cultural level.

However, learning is costly in the sense that it requires time and energy (Kaplan et al., 2000). Once an evolutionary cost of learning is explicitly incorporated as a trade-off between learning and reproduction, the group optimum and the individual optimum deviate from each other. In particular, a theory predicts that much less time will be invested into learning by the ES schedule (Wakano and Miura, 2014). This is because of the public nature of culture; producing new knowledge through individual learning is costly, but this new knowledge becomes available to anyone in future generations via social learning. In other words, individual learning means the costly production of a public good, hence it creates a social dilemma about who produces the knowledge. This is known as a producer–scrounger game (Barnard and Sibly, 1981; Vickery et al., 1991; Lehmann and Feldman, 2009) of information. In such a situation, it is predicted that the benefit of cumulative culture is exploited by selfish individuals who do not invest into individual learning, ultimately leading to the collapse of cumulative culture (Wakano and Miura, 2014). In other words, a more realistic model with an evolutionary trade-off between learning and reproduction fails to explain how and why we were able to attain our modern, highly cumulative culture.

Kobayashi et al. (2015) intensively studied vertical transmission of cultural information in their trade-off model. Imagine that one passes its acquired knowledge preferentially to its offspring only. Such vertical transmission changes the public good to the "private good" which cannot be exploited by others through social learning, and hence it could yield an inclusive fitness benefit to the individual learner who bears its cost. Surprisingly, however, Kobayashi et al. (2015) have shown that highly cumulative culture is established as an evolutionary outcome of individual fitness maximization only if the vertical transmission rate is considerably close to one. In other words, a rare chance of social learning from a non-parent is enough to lead to a dramatic decline in the investment into individual learning, and to the collapse of cumulative culture. Hence vertical transmission alone cannot solve the paradox of cumulative culture, because it is unrealistic to assume that 99% of knowledge, for example, is exclusively transmitted to one's offspring only. In fact, Reyes-Garcia et al. (2009) reported that the cultural transmission of ethnobotonical knowledge in Tsimane', hunter-horticulturalists in Bolivia, is mostly oblique (*i.e.* learning from adults in the parental generation, not from direct parents).

It is possible that the failure to explain cumulative culture in Kobayashi et al. (2015) is partly due to their restrictive assumption that individuals are surrounded by strangers and that one's effort into individual learning can easily be exploited by them. We hypothesize that if the population is subdivided into small groups and if one is surrounded by genetically related individuals, such cultural exploitation will be hindered, and one could enjoy the inclusive fitness benefit through individual learning even if the rate of vertical transmission is not close to one. As a result, we expect that people should invest more into learning, and culture should accumulate significantly at an evolutionary equilibrium.

Another factor that hinders the accumulation of culture is the finiteness of population size. Under the trade-off between learning and reproduction, more investment in learning has a negative effect on one's own reproduction but can be beneficial to its descendants. In a finite population, however, there is always a risk of stochastic extinction of one's lineage before the beneficial knowledge is fully enjoyed. For that reason, evolution tends to disfavor investment into learning in a small population (Kobayashi et al., 2015).

In this paper we study the evolution of time allocation among the two modes of learning (IL and SL) and the effort into reproduction in a spatially structured population. More specifically, we assume a finite population which is subdivided into many small islands connected by migration. Then we will derive an evolutionarily stable life-history strategy to see if this ES schedule allows the highly cumulative culture as we see in our modern society.

## 2. Model and methods

### 2.1. Model description

We consider Wright's island model (Wright, 1931), with $n(>1)$ many islands labeled as $k = 1, \ldots, n$, each being colonized by exactly $N$ many adult individuals labeled as $i = 1, \ldots, N$. We employ a dynamical learning model to study the evolution of life-history learning schedule (Lehmann et al., 2010, 2013; Aoki et al., 2012; Wakano and Miura, 2014; Kobayashi et al., 2015). Each individual has its genetically-encoded learning strategy $(x, v)$ that prescribes the usage of its juvenile time ($0 \leq x, v \leq 1$). More specifically, an individual with strategy $(x, v)$ spends (i) $(1 - x)v$ of its juvenile time for *social learning* (SL), (ii) $xv$ of its time for *individual learning* (IL), (iii) and the remaining fraction $1 - v$ of its time for *exploitation*, in this order, because this order, especially SL preceding IL, has been established as an adaptive one in previous studies (Aoki et al., 2012; Lehmann et al., 2013) and it has empirical supports, too (Beck et al., 2011; Cutting et al., 2011). In other words, $v$ represents the proportion of time one spends for either mode of learning (SL + IL), and $x$ represents the proportion of time one spends for IL out of its total learning time.