Vol. 16 No. 1 (2025) 8–13
LETTERS ON EVOLUTIONARY BEHAVIORAL SCIENCE

Examining the Possibility of Maladaptive Cultural Evolution Through Oblique Transmission

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As one of the prerequisites for maladaptive cultural evolution, oblique transmission has drawn attention. However, even though maladaptive cultural evolution could occur if children choose oblique transmission frequently, can oblique transmission be selected by children in the course of genetic evolution? In addressing the question above, in this study, we conducted agent-based simulations focusing on the evolution of "oblique transmission bias," the tendency of children to choose oblique transmission when they can choose between oblique and vertical transmission. At first, we analyzed how the oblique transmission bias evolves by comparing models with two cultural traits versus five traits, manipulating the probability of environmental changes and the strength of natural selection, respectively. As a result, the oblique transmission rate evolved under limited conditions. Second, we conducted simulations under the setting of the oblique transmission rates as exogenous variables; maladaptive cultural evolution did not occur because of oblique transmission when oblique transmission bias is as strong as one evolved in the previous simulation. In addition, we show that if maladaptive culture is more likely to be imitated by children, maladaptive cultural evolution occurs.

Keywords
maladaptive cultural evolution, oblique transmission

Introduction

One of the puzzles in cultural evolution is maladaptive cultural evolution. This phenomenon occurs through the spread of maladaptive cultural traits in the population as a result of social learning (Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981). Oblique transmission has drawn attention as a prerequisite of the phenomenon, and several models have demonstrated its role in maladaptive cultural evolution (Ihara & Feldman, 2004; Richerson & Boyd, 1984). We refer to the tendency of children to choose oblique transmission when they have the option to select between oblique and vertical transmission as "oblique transmission bias."

Richerson and Boyd's (1984) model suggested that maladaptive cultural evolution would be favored by oblique transmission because adaptive traits are more likely to be transmitted by vertical transmission (Cavalli-Sforza & Feldman, 1981). Parents who have acquired adaptive traits would reproduce more children than adults with maladaptive traits; therefore, a child is more likely to learn maladaptive traits when they learn from other adults who might not have children, rather than learning from their own parents who are more likely to carry adaptive traits. However, this idea implies that oblique transmission bias is a maladaptive social learning bias. Even though maladaptive cultural evolution could occur if oblique transmission bias is strong enough, can oblique transmission bias evolve in the first place? This is the issue we explore in this paper.

Takahasi (1998) examined the conditions under which vertical transmission is favored in genetic evolution in both haploid and diploid models. Supporting our conjecture, he found that vertical transmission is generally favored. He concluded that dependence on vertical transmission may decrease if a newly arisen cultural trait is more likely to be acquired via non-vertical pathways. Ram et al. (2018) analyzed the haploid model in which children acquire one of two cultural traits through either oblique or vertical transmission. Environmental changes occur periodically, and an adaptive cultural trait in the current generation becomes maladaptive in the next generation. The rate of vertical transmission (i.e., 1 – the rate of oblique transmission) was genetically transmitted from each parent to their children. In this model, Ram et al. (2018) showed that oblique transmission bias can evolve if the period of environmental change is short. If the environment changes frequently, there is a higher probability that a non-parental adult from the previous generation has acquired an adaptive trait, compared to a child's genetic parent. Thus, under frequent environmental changes, oblique transmission becomes adaptive for children.

In the current study, we applied some modifications to Ram et al.'s (2018) model to examine the evolution of oblique transmission bias. First, while they formulated environmental change as a fixed cycle, we made environmental changes as probabilistic events (e.g., Henrich & Boyd, 1998). Second, our model explored the effects of diversity of cultural traits, while Ram et al.'s (2018) model assumed only two types of cultural traits. Because the trait that was maladaptive before the environmental change becomes adaptive afterward, oblique transmission is likely to become adaptive right after environmental change due to the default model setting. However, if the number of cultural traits increases,

doi: 10.5178/lebs.2025.124
Received 31 January 2025.
Accepted 13 April 2025.
Published online 02 May 2025.

unlike Ram et al.'s (2018) model, most maladaptive traits could remain maladaptive even after the environmental change. In cases where the impact of natural selection is strong enough to select against the maladaptive cultural traits, adaptive cultural traits may rapidly spread to the next generation through vertical transmission. Put differently, when cultural traits are more varied and transmitted under strong selection, it is possible that oblique transmission would not necessarily be favored or evolved by selection even after the environmental change. Below, we analyzed the evolution of oblique transmission bias by comparing models with two cultural traits versus five traits, manipulating the probability of environmental changes and the strength of natural selection.

Model

We conducted agent-based simulations on a population of $N = 1000$ individuals. These individuals acquired a single cultural trait from two or five traits, which number varied as a simulation parameter ($c = 2$ or 5). The fitness value was 1 for maladaptive traits and U ($U > 1$) for the adaptive trait. In each generation, agents reproduce children with a probability based on their relative fitness. The relative fitness of the agents who have acquired $Trait_i$ is calculated using the following equation: $RU_i = \frac{U_i}{\sum_{k=1}^{c} n_k U_k}$ (U represents the absolute fitness value of $Trait_i$, n_k is the number of agents who have acquired $Trait_k$, and c is the number of cultural trait types).

Each agent was assigned a rate of oblique transmission, ao ($0 \leq ao \leq 1$), as a genetic trait. We assumed a haploid model, and the values of ao were transmitted from a parent to genetic children. Children acquired a cultural trait through either oblique or vertical transmission, which was probabilistically determined by the value of ao. If a child acquired a trait through oblique transmission, they randomly selected a non-parental adult from the previous population and imitated the cultural trait of that adult. The cultural trait could be mutated into a different trait according to the probability of the mutation rate (*mu*). Gaussian noise (N [0, 0.01]) was also added to each agent's rate of oblique transmission. Finally, the environment changed with a probability in proportion to the value of e. If the environmental change occurred, the fitness of the adaptive trait and maladaptive trait was reversed: When there were five types of traits, one out of four maladaptive traits was randomly chosen as the new adaptive trait.

The above process consists of one generation, and the simulation is repeated for 5,000 generations. In Simulation 1, we examine the evolution of oblique transmission (*ao*) by manipulating the following factors: the probability of environmental changes (*e*), the number of cultural traits (*c*), the difference in fitness between maladaptive and adaptive cultural traits (*VU*), the initial frequency of maladaptive traits (*im*), and the initial rate of oblique transmission (*io*).

Results of Simulation 1

Figure 1 illustrates the mean rate of oblique transmission (*ao*) under the setting of (*im*, *io*, *mu*) = (0, 0, 0.01). Figure 1 (a) and (b) are representative evolutionary dynamics of the rate of oblique transmission. Black lines and shadow areas represent the mean and standard deviation of 50 runs. In Figure 1 (c) and (d), rows represent the differences in fitness between maladaptive and adaptive traits, and columns represent the probabilities of environmental changes. Figure 1 (c) illustrates the result when there are two traits ($c = 2$), and Figure 1 (d) illustrates the result when there are five traits ($c = 5$). The second row shows that when the difference in fitness is small ($VU = 0.1$), the higher the probability of environmental changes, the more the rate of oblique transmission increases, regardless of the number of traits. However, the oblique transmission rate did not reach 0.5 at most ($ao = 0.47$ when $c = 2$, $ao = 0.43$ when $c = 5$). In contrast, the first row shows that oblique transmission ($ao = 0.71$) evolved at a very high rate in cases where the difference in fitness is large ($VU = 1$) when there are two traits ($c = 2$) and the environment changes with a very high probability ($e = 0.5$). However, rates of oblique transmission reached only 0.24 at most in other cases. In summary, higher oblique transmission rates (> 0.5) evolved only under the limited condition where (VU, c, e) = (1, 2, 0.5).

If the environment does not change between the consecutive generations, t and $t + 1$, we can show that the rate of oblique transmission is negatively correlated with the probability for children to acquire an adaptive cultural trait at $t + 1$ (see Supplementary Information S1 for details). Suppose the environment changes and the adaptive trait at generation t becomes maladaptive at $t + 1$. In that case, the relationship is reversed—the rate of oblique transmission is positively correlated with the probability of acquiring an adaptive trait at $t + 1$. Frequent environmental change thus provides opportunities for positive selection pressure for the rate of oblique transmission. However, the strengths of each pressure vary as a function of the frequency of parents with an adaptive trait at t, the relative fitness advantage of the adaptive cultural trait, and the number of traits. The observed patterns in Figure 1 (c) and (d) are the outcomes of complex interactions between these selection pressures and mutation.

When the fitness advantage for an adaptive cultural trait is weak (i.e., $VU = 0.1$), mutation will exert a relatively stronger influence and try to bring ao values to the midpoint of the range of ao (i.e., 0.5). As the environment change rate increases, the positive selection for the environmental change gradually cancels out the negative selection pressure, and the evolved ao values approach 0.5. When the fitness advantage for an adaptive trait is relatively large (i.e., $VU = 1$), the system is more strongly influenced by the negative selection pressure for the rate of oblique transmission except for when $c = 2$ and $e = 0.5$. In this special case, the positive selection pressure is expected to be the strongest among all the conditions examined here. As is discussed in S1, the number of cultural traits weakens the positive selection pressure. With the influence of the frequent environmental changes, the positive selection pressure seemed to have exceeded the negative pressure for *ao* (see S1 for more details).

Results of Simulation 2

The previous section shows that the rate of oblique transmission evolved up to 0.7. In most conditions, evolved rates of oblique transmission were much lower and ranged

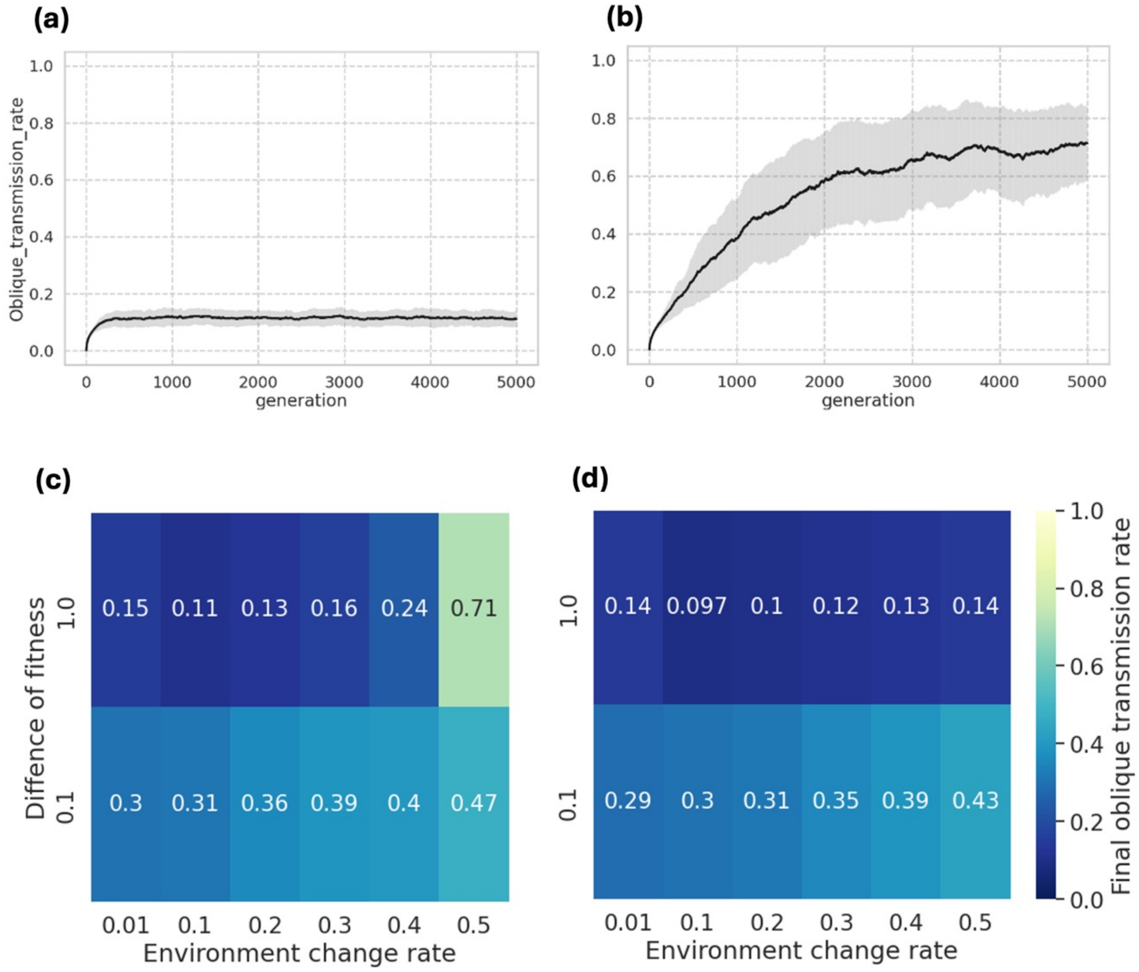

Figure 1. Results of the evolved rate of oblique transmission (*ao*) (when *im* = 0, *io* = 0, *mu* = 0.01).

Note. The top row shows the evolutionary dynamics of the rate of oblique transmission: (a) for *c* = 2, *VU* = 1, *e* = 0.1, (b) for *c* = 2, *VU* = 1, *e* = 0.5. Black lines represent the mean value, and shadow areas show the standard deviation. The bottom row shows the rate of oblique transmission at the $5{,}000^{th}$ round averaged over 50 runs: (c) for when there are two traits (*c* = 2); (d) for when there are five traits (*c* = 5). Rows in (c) and (d) illustrate the differences in fitness between maladaptive and adaptive traits (*VU* = 1, 0.1), and columns illustrate probabilities of environmental changes (*e* = 0.01, 0.1, 0.2, 0.3, 0.4, 0.5).

around 0.1 ~ 0.5. In examining Richerson and Boyd's (1984) suggestion that maladaptive culture would spread to the next generation when oblique transmission bias is strong enough, we should also ask the following question: Are rates of oblique transmission that evolved in the previous section strong enough for maladaptive cultural evolution to occur?

In addressing the question above, we conducted further simulations under the setting of the rates of oblique transmission (*ao*) as exogenous variables. In this simulation, the environment was set so as not to change. Richerson and Boyd (1984) also examined the tendency that maladaptive culture is more likely to be imitated by children than adaptive culture by a parameter *s*. When *s* = 1, there is no bias favoring maladaptive cultural traits. When *s* = 2, a maladaptive cultural trait is twice as likely to be imitated as other traits.

Figure 2 illustrates the mean frequency of maladaptive cultural traits (*m*) under the setting of (*im*, *mu*) = (0, 0.01). Rows in each figure represent the differences in fitness between maladaptive and adaptive traits, and columns represent fixed probabilities of oblique transmission. Figure 2 (a, c, e) illustrates the result when there are two traits (*c* = 2), and Figure 2 (b, d, f) illustrates the result when there are five traits (*c* = 5). Focus only on the cells surrounded by bold lines, as they show results obtained from the parameter combinations of differences in fitness (*VU*) and the evolved rate of oblique transmission (*ao*), as illustrated in Figure 1. When there is no bias favoring maladaptive traits to be imitated (*s* = 1; Figure 2[a] and 2[b]), frequencies of maladaptive cultural traits did not reach 0.2 (*m* = 0.18 when *c* = 2, *m* = 0.2 when *c* = 5). This frequency is lower than even the rate of a trait when each trait is chosen with equal probability (1/*c*). This indicates that the oblique transmission bias does not offset the impact of natural selection on maladaptive traits. Thus, maladaptive cultural evolution did not occur due to oblique transmission.

Small bias favoring maladaptive cultural traits to be imitated (*s* = 1.05; Figure 2 [c] and [d]) does not change the results so much. However, when a maladaptive trait is twice more likely to be imitated (*s* = 2; Figure 2[e] and [f]), maladaptive culture evolved at a higher frequency than even 0.8 in some cases (e.g., *m* = 0.89 when *im* = 0, *mu* = 0.01, *VU* = 0.1, *o* = 0.3, *c* = 2).

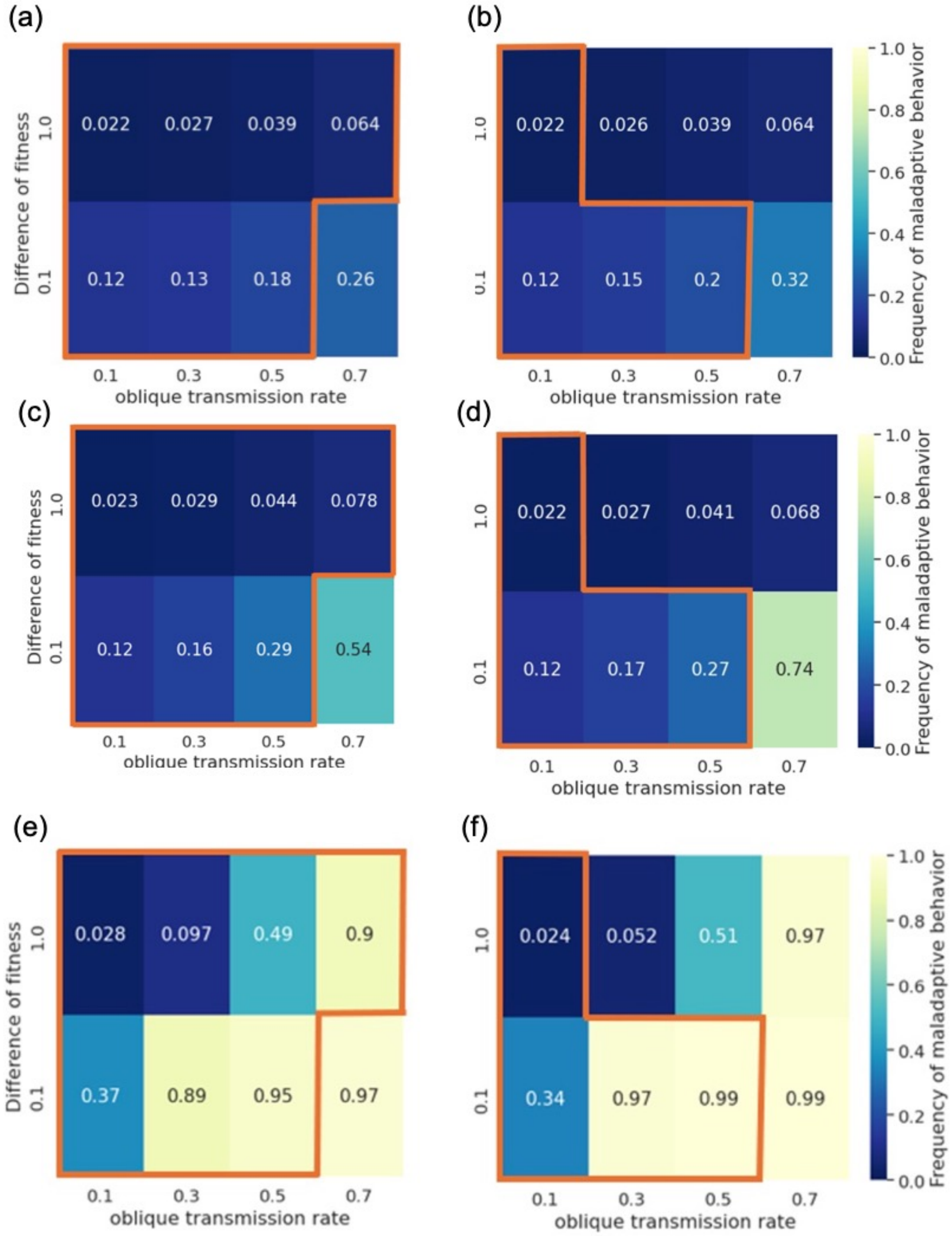

Figure 2. Results of the frequency of maladaptive cultural traits (*m*) (when *im* = 0, *mu* = 0.01).

Note. Numbers show the frequency of the maladaptive trait at 5,000th generation averaged over 50 runs: left column (a, c, e) for when there are two traits (*c* = 2); right column (b, d, f) for when there are five traits (*c* = 5). The top row (a, b) shows when there is no bias for a maladaptive trait (*s* = 1); the middle row (c, d) for when *s* = 1.05, and the bottom row (e, f) for when *s* = 2 (i.e., a maladaptive trait is twice more likely to be imitated). Rows and columns in both figures illustrate the differences in fitness between maladaptive and adaptive traits (*VU* = 1, 0.1) and the rate of oblique transmission (*ao* = 0.1, 0.3, 0.5, 0.7), respectively. Cells surrounded by bold lines used the values of oblique transmission rate evolved in Simulation 1.

Discussion

Our agent-based simulations illuminated three points. First, in Simulation 1, we showed that the evolved rate of oblique transmission bias exceeded 0.5 only under limited conditions. Second, we showed that the rates of the oblique transmission, which evolved in broad conditions, were not enough to cause the maladaptive cultural evolution in Simulation 2. Third, in Simulation 2, we showed that maladaptive cultural evolution emerged if a maladaptive culture was more likely to be imitated.

Our results of the second simulation demonstrate the robustness of some previous findings (Ram et al., 2018; Takahasi, 1998) and exhibit the effect of trait variety. Our results align with Takahasi's (1998) findings in that vertical transmission evolved in most cases, even though their model substantially differed from ours. Furthermore, our result is also consistent with the findings of Ram et al. (2018) in that oblique transmission bias would evolve only if there are two traits, and the rate of environmental change is 0.5, with a few modifications (e.g., environment changes probabilistically) being applied to their model. Unlike Ram et al.'s (2018) model, we also explored the effect of cultural trait variety, finding that if the number of traits increased, the rate of oblique transmission would not evolve even when the rate of environmental change was 0.5.

While the present research is consistent with the preceding studies mentioned above, our results did not align with McElreath and Strimling's (2008) findings. McElreath and Strimling (2008) analyzed a diploid model in which children acquired cultural traits through individual learning, oblique or vertical transmission. Provided that a new cultural trait appeared as the single adaptive trait at every environmental change occurrence, McElreath and Strimling (2008) showed that oblique transmission bias would evolve when the rate of environmental change was 0.3. This result raises two questions: How did oblique transmission evolve in McElreath and Strimling's (2008) model even with a lower environmental change rate, and which factors rendered the difference between McElreath and Strimling's (2008) findings and our results? The cultural trait variety would not render this difference, as having more cultural traits did not promote the evolution of oblique transmission bias in the present research. However, it is possible that the introduction of individual learning made oblique transmission evolve in McElreath and Strimling's (2008) model. In brief, the presence of individual learners makes oblique transmission more adaptive due to the default model setting, in which individual learners acquire adaptive cultural traits by incurring a cost. In particular, populations of the first generation soon after environmental change can acquire adaptive traits exclusively through individual learning. Oblique transmission becomes adaptive for children from subsequent generations since a child who chooses oblique transmission can imitate an individual learner of older generations without costs. Considering these conditions above, the matter of who has acquired adaptive traits appears to be an essential factor for the evolution of oblique transmission bias, and this, in turn, results in the differences between the present model and McElreath and Strimling's (2008) model. However, there are many other remaining differences in conditions between the present research and McElreath and Strimling's (2008) model besides individual learning; therefore, further examinations of potential factors that could cause the evolution of oblique transmission bias should be continued.

As a future direction, at least three investigations are essential: whether individual learning could be introduced to acquire cultural traits in addition to vertical and oblique transmission, whether oblique transmission bias evolves or not, and whether maladaptive culture evolves through oblique transmission. Although multiple simulations were conducted under various conditions in the present studies (see Figures 1 and 2, see also Supplementary Online Material), there are limitations in the result implications as our results rely on the conditions used in the simulation (see Edmonds, 2017). Follow-up research should examine the effect of introducing horizontal transmission (Cavalli-Sforza & Feldman, 1981) and the overlaps between generations (e.g., Deffner & McElreath, 2022) on models of maladaptive cultural evolution.

In conclusion, the present study indicates that maladaptive cultural evolution through oblique transmission is difficult unless another prerequisite condition is added to our model. This suggestion may serve as a stepping stone toward disentangling the puzzle of maladaptive cultural evolution.

Acknowledgments

We would like to thank Oliver Y. Hasegawa for English language editing and Shogo Homma for his comments and for helping us to code simulations. We also thank Yuta Kido for the discussion and comments.

Author contribution

C.S. and M.T. designed the computational models and computer simulations; C.S. conducted computer simulations and data analysis; and C.S. and M.T. wrote the manuscript.

Data accessibility & program code

All the simulation codes are available on The Open Science Framework (https://osf.io/tgd59/).

Supplementary material

Electronic supplementary materials are available online.

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