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Evolution of Social Learning in Lattice-Structured Populations

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Individual and social learning underpin human cultural diversity and successful expansion into diverse environments. The evolution of social learning has been a subject of active debate: in particular, recent studies considering whether spatial structure favors or disfavors the evolution of social learning have produced mixed results. Here we report the results of our computational experiments in lattice-structured populations, suggesting that spatial structure disfavors the evolution of social learning in a wide parameter region. Our results also indicate that the effect of spatial structure depends on the mode of cultural transmission (from whom social learners acquire behaviors) and the updating scheme (whether individuals update their strategies synchronously or asynchronously).

Keywords
learning, spatial structure, cultural evolution

Introduction

Learning ability underpins both cultural diversity and global expansion of humans. Learning is roughly divided into two categories, individual and social learning (Boyd & Richerson, 1985). Individual learning occurs independently of any social influences, an example of which is trial-and-error. Social learning, including imitation, involves transfer of information between individuals, where a behavior exhibited by a "model" is acquired by an "observer." Social learning has the advantage of avoiding the costs of trial-and-error, while it runs the risk of acquiring maladaptive behaviors. The relative advantages of social and individual learning depend on temporal and/or spatial variability of environment (Feldman, Aoki, & Kumm, 1996). Roughly speaking, individual learning is favored by natural selection in a relatively variable environment and social learning in a stable environment.

Spatial structure is an important factor to determine the spread of information, which in turn affects the evolution of social learning. The effect of spatial structure on the evolution of social learning has been a subject of recent debate. Rendell, Fogr aty, and Laland (2010) found in their computational experiments that social learners as opposed to individual learners become more prevalent in lattice-structured than well-mixed populations. In contrast, Kobayashi and Wakano's (2012) infinite island model showed that spatial subdivision lowers the equilibrium frequency of social learners. This discrepancy has not been fully resolved. The present study investigates the evolution of social learning in a lattice-structured population to examine the effects of spatial structure and other potentially relevant factors.

A key factor that may be relevant is the pathway through which cultural traits are transmitted. Cavalli-Sforza and Feldman (1981) formalized three modes of cultural transmission: vertical, horizontal and oblique transmission, defined as transmission from a parent to offspring, from one individual to another in the succeeding generation and from one individual to anther in the same generation, respectively. The mode of cultural transmission can influence individuals' fitness in a complicated manner: for example, McElreath and Strimling (2008) showed that the relative advantages of vertical and oblique transmission depend on environmental stability and selection intensity.

Another factor concerns generational overlap. Technically speaking, outcomes of evolutionary models could be affected by the updating scheme, or whether updating is synchronous or asynchronous, which are analogous to discrete and overlapped generations, respectively. For example, Kobayashi and Aoki (2012) demonstrated that patterns of cumulative cultural evolution may differ substantially depending on the updating scheme.

In sum, our goals are to examine whether spatial structure favors the evolution of social learning and how the mode of cultural transmission and the updating scheme may affect it.

Model

We conduct individual-based simulations to investigate possible effects of spatial structure on the evolution of social learning. Consider a population of N = 2500 individuals in a fluctuating environment, where there is only one adaptive (correct) behavior and all other behaviors are equally maladaptive (wrong). The environment changes every L generations, where L measures the environmental stability. We assume that the environment never reverts when it changes (Feldman et al., 1996). We consider two types

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of population structure: a lattice-structured population and a well-mixed population. In a lattice-structured population, individuals are arranged on a two-dimensional circular lattice. Each individual interacts with the eight nearest neighbors surrounding the individual. In a well-mixed population, there is no spatial structure so that any two individuals interact with the same probability.

There are two learning strategies: each individual is either individual learner (IL) or social learner (SL). IL engages in costly try-and-error and always discovers the adaptive behavior. SL imitates others' behavior without paying the cost of individual learning, but may acquire an outdated and thus maladaptive behavior. Accordingly, SL is subdivided into SLC (social learner correct) and SLW (social learner wrong). The relative fitness of IL, SLC and SLW are given by $1-\delta c$, 1 and $1-\delta s$, respectively, where c is the cost of individual learning, s is the cost due to maladaptive behavior and δ measures the intensity of selection (Table 1). Hereafter, we limit our attention to the case $s > c > 0$ and fix the cost of individual learning to $c = 0.01$.

Table 1. The payoffs of three phenogenotypes

Phenogenotype	Fitness
IL	$1-\delta c$
SLC	1
SLW	$1-\delta s$

We consider two models of different updating schemes, namely, asynchronous and synchronous updating models. For each model, we consider two modes of cultural transmission: Mode I assumes oblique transmission and Mode II vertical and horizontal transmission. We define the modes of cultural transmission in terms of time period rather than generation (see below).

Asynchronous updating model

In each time period, one individual is replaced by another, where we regard N time periods as a generation. An individual is chosen from all individuals with probability proportional to fitness. In a lattice-structured population, the chosen individual produces an offspring that will occupy a neighboring site in the lattice chosen at random in the succeeding time period. In a well-mixed population, the offspring replaces an individual randomly chosen from the whole population. If the offspring is IL, it discovers the adaptive behavior, while if it is SL, it imitates the behavior of a "cultural model." In Mode I transmission, the cultural model is randomly chosen from the parent and the parent's neighbors when considering a lattice-structured population or from all individuals when considering a well-mixed population (oblique transmission), while in Mode II, it is always the parent (vertical transmission). In Mode II, an additional event follows, where another individual is chosen randomly from all individuals and if it is SL, it imitates an individual randomly chosen from its neighbors in a lattice-structured population or from the whole population in a well-mixed population (horizontal transmission).

Synchronous updating model

In each time period, all individuals are replaced by others, and thus each time period is regarded as a generation. In a well-mixed population, each individual reproduces offspring with probability proportional to fitness. In a lattice-structured population, reproduction into a focal site is restricted to individuals who currently occupying the site or the neighboring sites. That is, for each site, an individual is chosen from those who currently occupying that or the neighboring sites with probability proportional to fitness. The chosen individual produces an offspring that will occupy the site in the succeeding time period. The offspring either discovers the adaptive behavior if it is IL, or imitates a cultural model if it is SL. In Mode I transmission, the cultural model is chosen at random from the parent and the parent's neighbors in a lattice-structured population or from all individuals in a well-mixed population (oblique transmission). In Mode II, each SL offspring initially imitates its parent (vertical transmission), and when every offspring has acquired a behavior, it imitates a neighboring offspring chosen at random in a lattice-structured population or a random individual in a well-mixed population (horizontal transmission).

Simulations are run for 10000 generations. Each individual is initially either IL or SL with probability 0.5. Mutation on learning strategy occurs with probability $\mu = 10^{-5}$ per birth. Long-term average frequency of each strategy is obtained by averaging over the last 5000 generations. Results shown in Figures 1 and 2 are based on the averages over 100 runs.

Results

Lattice-structured versus well-mixed populations

We investigate the effect of spatial structure on the long-term average frequency of SL, which we denote p_{SL}.

Figures 1 and 2 compare p_{SL} in lattice-structured and well-mixed populations for Mode I and Mode II transmission, respectively. For both modes of transmission, p_{SL} is lower in lattice-structured than well-mixed populations for a wide parameter region, suggesting that spatial structure tends to disfavor the evolution of SL. However, p_{SL} in a lattice-structured population can exceed that in a well-mixed population under certain conditions. Specifically, this is the case for the asynchronous updating model with small cost of maladaptive behavior and large environmental stability (Figure 1a and 1c). The difference in p_{SL} between lattice-structured and well-mixed populations is smaller for

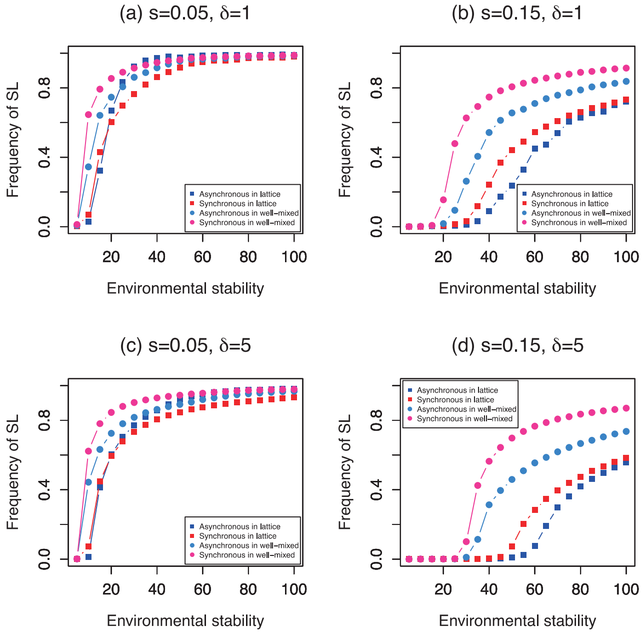

Figure 1: Long-term average frequencies of SL with Mode I transmission plotted against the environmental stability

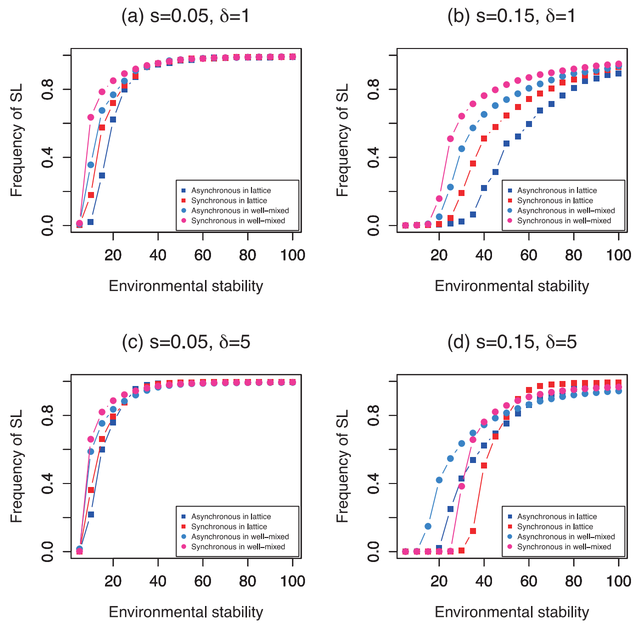

Figure 2: Long-term average frequencies of SL with Mode II transmission plotted against the environmental stability

Mode II than Mode I transmission. In well-mixed populations, p_{SL} tends to be higher for synchronous than asynchronous updating (with the exception of Figure 2d), while in lattice-structured populations, this trend is often reversed.

Edge effect

In lattice-structured populations, individuals adopting the same strategy always form clusters (Figure 3). Competition between IL and SL is restricted on and along the boundaries of these clusters. Rendell et al. (2010) suggested that this fact can cause a structured population to harbor more social learners and called this effect the "edge effect."

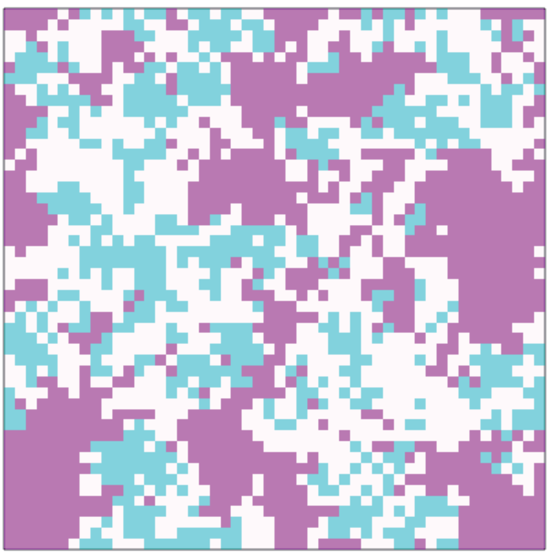

Figure 3: The blue, white and pink cells represent IL, SLC and SLW individuals, respectively, located in a lattice.

To further examine the edge effect, we perform additional simulations. We track changes in the frequency of SL for 100 generations following an environmental change, assuming no mutation and no more environmental change. The probability that each individual is initially IL is 0.01 and all others are assumed to be SLW. Figures 4 and 5 show the average trajectories of the frequency of SL over 1000 runs for Mode I and Mode II transmission, respectively. Let us provide a rough sketch of the population dynamics: firstly, SLs, who are mostly SLW because of a recent environmental change, decrease by being replaced by ILs; secondly, the proportion of SLCs, who outcompete ILs, among SLs increase through cultural transmission; and thirdly, as the proportion of SLCs becomes sufficiently high, SLs begin to increase by replacing ILs.

In Figures 4 and 5, changes in the frequency of SL is less drastic in lattice-structured than well-mixed populations (with the exception of the synchronous updating model in Figure 4d). This indicates that spatial structure mitigates competition between IL and SL at least when maladaptive behavior is not very costly or selection is not intense. The frequency of SL tends to decrease less drastically and begin to increase earlier with Mode II than Mode I transmission (note the difference in scale between Figures 4 and 5) in both lattice-structured and well-mixed populations. This may be because the spread of adaptive behaviors is faster with vertical/horizontal than oblique transmission, whether or not the population is spatially structured. In well-mixed populations, the frequency of SL decreases less drastically and

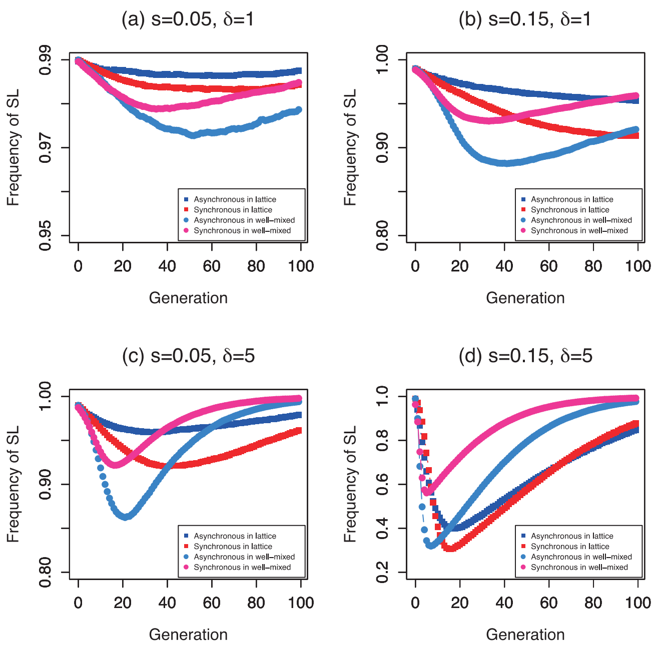

Figure 4: Average trajectories of the frequencies of SL with Mode I transmission

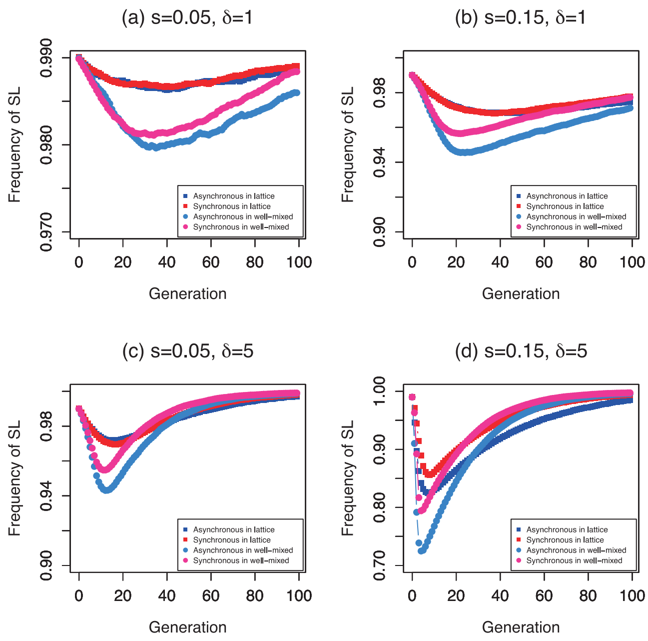

Figure 5: Average trajectories of the frequencies of SL with Mode II transmission

begins to increase earlier for synchronous than asynchronous updating, whereas this trend is often reversed in lattice-structured populations..

Discussion

We have investigated the effect of spatial structure on the evolution of social learning by comparing lattice-structured and well-mixed populations. Our results suggest that p_{SL}, the long-term average frequency of social learners (SL), is lower in lattice-structured than well-mixed populations for a wide parameter region. Intuitively, this is because spatial structure decelerates the spread of adaptive behaviors, since social learners carrying maladaptive behavior (SLW) aggregate in space. Nonetheless, spatial structure can also heighten p_{SL} under certain conditions. This is because spatial structure can mitigate competition between IL and SLW by spatially separating them (i.e., the edge effect). Overall, whether spatial structure favors the evolution of SL depends on a balance of these two opposing effects.

We find that the effect of spatial structure on p_{SL} is smaller for vertical/horizontal than oblique transmission and that the initial fall in the frequency of SL following an environmental change is less drastic and the succeeding rise begins earlier for vertical/horizontal than oblique transmission. These findings are partially congruent with the notion that vertical/horizontal transmission accelerates the spread of adaptive behaviors and thus favors the evolution of SL compared with oblique transmission. The difference in the speed of the spread of adaptive behavior between the two modes of transmission is at least partly caused by whether competition between SLC and SLW contributes the proportion of correct information among possible cultural models. In Mode I transmission, the advantage of SLC having more offspring does not result in increasing proportion of SLC in the offspring generation because offspring of SLC and SLW are equally likely to become SLC in the absence of vertical transmission. Therefore, competition between SLC and SLW has no effect on the proportion of adaptive information among cultural models. On the other hand, in Mode II transmission, replacement of SLW by SLC increases the proportion of correct models in horizontal transmission because offspring of SLC is also SLC. The difference between the two modes of cultural transmission may have larger effect on p_{SL} under stronger selection and higher cost of maladaptive behavior, which accelerate the competition between SLC and SLW.

Asynchronous updating has two features contrasting with synchronous updating: not all SLWs have learning opportunities in each generation; and the proportion of individuals behaving adaptively increases gradually within a generation. The former is expected to decelerate the spread of adaptive behaviors and the latter is to accelerate it. Overall, our results indicate, asynchronous updating tends to decelerate the spread of adaptive behaviors in well-mixed populations, resulting in lower p_{SL} unless the cost of maladaptive behavior and the intensity of selection are large. In lattice-structured populations, asynchronous updating can also mitigate competition between IL and SLW and thus favor the evolution of SL, for not all individuals on and along the boundaries of IL and SLW clusters are chosen to reproduce in each generation. Indeed, in our simulations on lattice-structured populations, p_{SL} is often higher for asynchronous than synchronous updating.

To some extent, Rendell et al.'s (2010) model is comparable with our synchronous updating model with vertical/horizontal transmission under strong selection, although the similarity is by no means perfect owing to different assumptions. In supplementary text, we show that spatial structure can strongly facilitate the evolution of social learning under extremely strong selection (Figure S1).

Spatial game theory has shown that different update rules can predict different evolutionary outcomes (e.g., Nakamaru, Nogami, & Iwasa, 1998). Thus, we investigate whether different update rules can affect the evolution of SL (Figures S2-6). Briefly, our results are not altered qualitatively by using death-birth or the Fermi rule in lieu of birth-death updating used in the present article.

Whether our results for a lattice-structured population also hold for other types of structure should be examined in future studies. Real networks of cultural transmission are often heterogeneous (Henrich & Henrich, 2011) and determined by social rather than spatial distance. Evolutionary simulations on heterogeneous networks, including scale-free networks, should be of importance.

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