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APPENDIX A: THE MODEL OF SPATIAL VARIABILITY

THE BASELINE MODEL

There are four genetically distinct types of organisms: (1) social learners (linearly frequency-dependent, UT), (2) conforming social learners (disproportionately frequency-dependent, CT), (3) payoff-biased social learners (PT), and (4) individual learners (IL).

- UT acquire their phenotypes by copying a random member of the parental generation in the site they occupy (oblique transmission).
- CT acquire their phenotypes by copying the most common behavior of the parental generation in the site they occupy, but suffer a mortality cost *d*.
- PT acquire their phenotypes by copying the behavior of the parental generation with the highest payoff in the site they occupy, but suffer a mortality cost *g*.
- IL always acquire the phenotype that is adapted to the environment of the site they occupy, but suffer a cost *c* due to mistakes made before the mature behavior is realized.

We assume $0 \le d < g < c < 1$.

Organisms may occupy any of *n* sites in a spatially heterogeneous world. Each site has a different environment. We distinguish *n* phenotypes, each of which is locally adapted to one particular environment, but maladaptive in the $n-1$ other environments. Phenotypes that are maladaptive in all *n* environments are not incorporated into the dynamics. Let X_{ij} ($1 \le i \le n$, $1 \le j \le n$) be the number of UT at site *i* that are adapted to the environment of site *j*. Then, at site *i* there are $X_i = \sum_{j=1}^{n} X_{ij}$ UT in all, of which X_{ii} are behaving adaptively (UTC, for short) and $X_i - X_{ii}$ are behaving maladaptively (UTW, for short). Similarly, let U_{ij} and V_{ij} be the number of CT and PT at site *i* that are adapted to the environment of site *j*. Then, at site *i* there are $U_i = \sum_{j=1}^{n} U_{ij}$ CT and $V_i = \sum_{j=1}^{n} V_{ij}$ PT in all, of which U_{ii} and V_{ii} are behaving adaptively (CTC and PTC, for short), and $U_i - U_{ii}$ and $V_i - V_{ii}$ are behaving maladaptively (CTW and PTW, for short). Moreover, let Z_i ($1 \le i \le n$) be the number of IL at site *i*. By assumption, IL always acquire the phenotype that is adapted to the environment of the site they occupy, but suffer a cost due to mistakes made before the mature behavior is realized. Therefore $N_i = X_i + U_i + V_i + Z_i$ is the total population at site *i*. These numbers are enumerated at the adult stage just prior to reproduction.

The life cycle begins with reproduction, where each organism gives birth asexually to $b(N_i)$ offspring according to the discrete logistic equation

$$b(N_i) = 1 + r(1 - N_i / K)\,. \tag{A.1}$$

Here, $r > 0$ and $K > 0$ are assumed to be the same for all sites. Since the offspring are genetically identical to their parents, the numbers of UT, CT, PT, and IL among the newborns at site *i* are $X_i b(N_i)$, $U_i b(N_i)$, $V_i b(N_i)$, and $Z_i b(N_i)$, respectively.

At the second step of the life cycle, UL, CT, and PT acquire their phenotypes by copying a behavior of the parental generation. All members of the parental generation die immediately afterward. As a result, the number of UT at site *i* that are adapted to the environment of site *j* becomes

$$X_i b(N_i)(X_{ij} + U_{ij} + V_{ij} + Z_i \delta_{ij}) / N_i\,, \tag{A.2}$$

where δ_{ij} is Kronecker's delta ($\delta_{ij} = 1$ when $i = j$ and 0 otherwise). The number of CT at site *i* that are adapted to the environment of site *j* becomes

$$(1 - d) U_i b(N_i) \rho_{ij} \tag{A.3}$$

where

$$\rho_{ij} = \frac{[(X_{ij} + U_{ij} + V_{ij} + Z_i \delta_{ij}) / N_i]^a}{\sum_{k=1}^{n} [(X_{ik} + U_{ik} + V_{ik} + Z_i \delta_{ik}) / N_i]^a} \tag{A.4}$$

Here, *a* is the strength of conformist bias, and CT always imitate the most common behavior when $a = \infty$. The number of PT at site *i* that are adapted to the environment of site *j* becomes

$$(1 - g) V_i b(N_i) \delta_{ij} \tag{A.5}$$

because we assume there are organisms behaving adaptively in the parental generation. The number of individual learners remains the same.

The third step of the lifecycle is migration, where a fixed fraction of the organisms at each site emigrate (constant forward migration rate). For the island model, we assume reciprocal migration between all pairs of sites at rate $m/(n-1)$ ($0 < m \le 1/2$).

In the fourth step of the life cycle, IL acquire the phenotype suitable to their new environment but suffer a fixed mortality cost *c*. Finally, viability selection occurs, and all organisms behaving adaptively (UTC, CTC, PTC, IL), and a fraction $1-s$ of organisms behaving maladaptively (UTW, CTW, PTW) survive. We assume $0 < d < g < c < s < 1$.

RECURSIONS

Based on the above assumptions, we generate the following recursions:

$$X'_{ii} = (1-m)X_i b(N_i)\frac{X_{ii}+U_{ii}+V_{ii}+Z_i}{N_i} + \frac{m}{n-1}\sum_{k\neq i}^{n} X_k b(N_k)\frac{X_{ki}+U_{ki}+V_{ki}}{N_k}, \tag{A.6a}$$

$$X'_{ij} = (1-s)\left\{\begin{array}{l}(1-m)X_i b(N_i)\dfrac{X_{ij}+U_{ij}+V_{ij}}{N_i} + \dfrac{m}{n-1}X_j b(N_j)\dfrac{X_{jj}+U_{jj}+V_{jj}+Z_j}{N_j} \\ + \dfrac{m}{n-1}\sum_{k\neq i,j}^{n} X_k b(N_k)\dfrac{X_{kj}+U_{kj}+V_{kj}}{N_k}\end{array}\right\}, \tag{A.6b}$$

$$U'_{ii} = (1-d)\left\{(1-m)U_i b(N_i)\rho_{ii} + \frac{m}{n-1}\sum_{k\neq i}^{n} U_k b(N_k)\rho_{ki}\right\}, \tag{A.6c}$$

$$U'_{ij} = (1-d)(1-s)\left\{(1-m)U_i b(N_i)\rho_{ij} + \frac{m}{n-1}\sum_{k\neq i}^{n} U_k b(N_k)\rho_{kj}\right\} \tag{A.6d}$$

$$V'_{ii} = (1-g)(1-m)V_i b(N_i), \tag{A.6e}$$

$$V'_{ij} = \frac{(1-g)(1-s)mV_j b(N_j)}{n-1} \quad \text{(A.6}f\text{)}$$

$$Z'_i = (1-c)\left\{(1-m)Z_i b(N_i) + \frac{m}{n-1}\sum_{k\neq i}^{n} Z_k b(N_k)\right\}, \quad \text{(A.6}g\text{)}$$

where $1 \le i \le n$, $1 \le j \le n$, and $j \ne i$ in Eqs. (A.6*b*), (A.6*d*), and (A.6*f*).

STABILITY OF CT EQUILIBRIUM

When $r > [1-(1-d)(1-ms)]/(1-d)(1-ms)$, a CT equilibrium exists where other social learners (UT, PT) and IL are absent, and CT occur in equal numbers at each site; formally,

$$\hat{X}_{ij} = \hat{V}_{ij} = \hat{Z}_i = 0,$$

$$\hat{U}_{ii} = \frac{K(1-m)}{1-ms}[1-\frac{1-(1-d)(1-ms)}{r(1-d)(1-ms)}], \hat{U}_{ij} = \frac{Km(1-s)}{(1-ms)(n-1)}[1-\frac{1-(1-d)(1-ms)}{r(1-d)(1-ms)}] \quad (i \ne j) \quad \text{(A.7)}$$

for $1 \le i \le n$, $1 \le j \le n$.

When the recursion (A.6) is linearized at this equilibrium in the variables X_{ij}, $U_{ij} - \hat{U}_{ij}$, V_{ij} and Z_i, the coefficient matrix becomes a $(3n^2+n)\times(3n^2+n)$ matrix as follows:

$$X'_{ii} = \frac{1}{(1-d)(1-ms)^2}\left\{(1-m)^2 X_i + \frac{(1-s)m^2}{(n-1)^2}\sum_{k\neq i}^{n} X_k\right\}, \quad \text{(A.8}a\text{)}$$

$$X'_{ij} = \frac{(1-s)m}{(1-d)(n-1)(1-ms)^2}\left\{(1-m)(1-s)X_i + (1-m)X_j + \frac{(1-s)m}{n-1}\sum_{k\neq i,j}^{n} X_k\right\}, \quad \text{(A.8}b\text{)}$$

$$U'_{ii} - \hat{U}_{ii} = \frac{1-m}{1-ms}[2-(1+r)(1-d)(1-ms)](U_i - \hat{U}_i), \quad \text{(A.8}c\text{)}$$

$$U'_{ij} - \hat{U}_{ij} = \frac{(1-s)m}{(1-ms)(n-1)}[2-(1+r)(1-d)(1-ms)](U_j - \hat{U}_j)\,, \tag{A.8d}$$

$$V'_{ii} = \frac{(1-g)(1-m)}{(1-d)(1-ms)}V_i\,, \tag{A.8e}$$

$$V'_{ij} = \frac{(1-g)(1-s)m}{(1-d)(1-ms)(n-1)}V_j\,, \tag{A.8f}$$

$$Z'_i = \frac{1-c}{(1-d)(1-ms)}\left\{(1-m)Z_i + \frac{m}{n-1}\sum\nolimits_{k\neq i}^{n} Z_k\right\}. \tag{A.8g}$$

The matrix is reducible into four submatrices. The coefficient matrix of Eq. (A.8*a*) and (A.8*b*) has *n* sets of identical columns each of multiplicity *n*, which entails that (at least) $n(n-1)$ eigenvalues are equal to 0. Moreover, the transformed variables $X_i = \sum\nolimits_{j=1}^{n} X_{ij}$ $(1 \le i \le n)$ satisfy

$$X'_i = \frac{1}{(1-d)(1-ms)^2}\left\{(1-m)[(1-s)^2 m + 1 - m]X_i + \frac{(1-s)m}{n-1}\left[1 - ms + \frac{ms}{n-1}\right]\sum\nolimits_{k\neq i}^{n} X_k\right\} \tag{A.9a}$$

i.e.,

$$\begin{pmatrix} X'_1 \\ X'_2 \\ X'_3 \\ \vdots \\ \vdots \\ X'_n \end{pmatrix} = \begin{pmatrix} \alpha & \beta & \beta & \cdots & \cdots & \beta \\ \beta & \alpha & \beta & \cdots & \cdots & \beta \\ \beta & \beta & \alpha & \ddots & & \beta \\ \vdots & \vdots & \ddots & \ddots & \ddots & \vdots \\ \vdots & \vdots & & \ddots & \alpha & \beta \\ \beta & \beta & \beta & \cdots & \beta & \alpha \end{pmatrix} \begin{pmatrix} X_1 \\ X_2 \\ X_3 \\ \vdots \\ \vdots \\ X_n \end{pmatrix}, \tag{A.9b}$$

where

$$\alpha = \frac{(1-m)[(1-s)^2 m + 1 - m]}{(1-d)(1-ms)^2}, \beta = \frac{(1-s)m}{(n-1)(1-d)(1-ms)^2}\left[1 - ms + \frac{ms}{n-1}\right]. \quad \text{(A.9}c\text{)}$$

Since

$$\begin{vmatrix} \alpha & \beta & \beta & \cdots & \cdots & \beta \\ \beta & \alpha & \beta & \cdots & \cdots & \beta \\ \beta & \beta & \alpha & \ddots & & \beta \\ \vdots & \vdots & \ddots & \ddots & \ddots & \vdots \\ \vdots & \vdots & & \ddots & \alpha & \beta \\ \beta & \beta & \beta & \cdots & \beta & \alpha \end{vmatrix} = \begin{vmatrix} \alpha+(n-1)\beta & \beta & \beta & \cdots & \cdots & \beta \\ \alpha+(n-1)\beta & \alpha & \beta & \cdots & \cdots & \beta \\ \alpha+(n-1)\beta & \beta & \alpha & \cdots & \cdots & \beta \\ \vdots & \vdots & \ddots & \ddots & \ddots & \vdots \\ \vdots & \vdots & \ddots & & \alpha & \beta \\ \alpha+(n-1)\beta & \beta & \beta & \cdots & \beta & \alpha \end{vmatrix}$$

$$= \begin{vmatrix} \alpha+(n-1)\beta & 0 & 0 & \cdots & \cdots & 0 \\ \alpha+(n-1)\beta & \alpha-\beta & 0 & \cdots & \cdots & 0 \\ \alpha+(n-1)\beta & 0 & \alpha-\beta & \ddots & & 0 \\ \vdots & \vdots & \ddots & \ddots & \ddots & \vdots \\ \vdots & \vdots & & \ddots & \alpha-\beta & 0 \\ \alpha+(n-1)\beta & 0 & 0 & \cdots & 0 & \alpha-\beta \end{vmatrix}$$

$$= \begin{vmatrix} \alpha+(n-1)\beta & 0 & 0 & \cdots & \cdots & 0 \\ 0 & \alpha-\beta & 0 & \cdots & \cdots & 0 \\ 0 & 0 & \alpha-\beta & \ddots & & 0 \\ \vdots & \vdots & \ddots & \ddots & \ddots & \vdots \\ \vdots & \vdots & & \ddots & \alpha-\beta & 0 \\ 0 & 0 & 0 & \cdots & 0 & \alpha-\beta \end{vmatrix}, \quad \text{(A.10)}$$

the coefficient submatrix of the linearized recursions in the variables X_{ij} yields the maximal eigenvalue

$$\begin{aligned}\alpha+(n-1)\beta &= \frac{(1-m)[(1-s)^2 m+1-m]}{(1-d)(1-ms)^2}+\frac{(1-s)m}{(1-d)(1-ms)^2}\left[1-ms+\frac{ms}{n-1}\right] \\ &= \frac{1}{(1-d)(1-ms)^2}\left\{(1-m)(1-ms)+m(1-s)^2+\frac{(1-s)sm^2}{n-1}\right\}\end{aligned}. \qquad \text{(A.11)}$$

Similarly, since

$$U_i' - \hat{U}_i = \frac{1}{1-ms}[2-(1+r)(1-d)(1-ms)]\left\{(1-m)(U_i-\hat{U}_i)+\frac{(1-s)m}{n-1}\sum_{k\neq i}^{n}(U_k-\hat{U}_k)\right\}, \qquad \text{(A.12)}$$

the coefficient submatrix of the linearized recursions in the variables $U_{ij}-\hat{U}_{ij}$ yields the maximal eigenvalue $2-(1+r)(1-d)(1-ms)$, and since

$$V_{ii}' = \frac{(1-g)}{(1-d)(1-ms)}\left\{(1-m)V_i+\frac{(1-s)m}{n-1}\sum_{k\neq i}^{n}V_k\right\}, \qquad \text{(A.13)}$$

the coefficient submatrix of the linearized recursions in the variables V_{ij} yields the maximal eigenvalue $(1-g)/(1-d)$. Moreover, from (A.8*g*), the coefficient submatrix of the linearized recursions in the variables Z_i yields the maximal eigenvalue $\frac{1-c}{(1-d)(1-ms)}$. If all of these maximal eigenvalues have their absolute values smaller than unity, then the CT equilibrium is stable. Since $(1-g)/(1-d)<1$, the condition is

$$\frac{1}{(1-d)(1-ms)^2}\left\{(1-m)(1-ms)+m(1-s)^2+\frac{(1-s)sm^2}{n-1}\right\}<1, \qquad \text{(A.14}a\text{)}$$

$$2-(1+r)(1-d)(1-ms)<1, \qquad \text{(A.14}b\text{)}$$

and

$$\frac{1-c}{(1-d)(1-ms)} < 1. \tag{A.14c}$$

When CT suffer no additional learning cost (i.e., $d = 0$), the condition becomes

$$\frac{1}{(1-ms)^2}\left\{(1-m)(1-ms) + m(1-s)^2 + \frac{(1-s)sm^2}{n-1}\right\} < 1, \tag{A.15a}$$

$$1 < (1+r)(1-ms), \tag{A.15b}$$

and

$$\frac{1-c}{1-ms} < 1. \tag{A.15c}$$

Since $n \geq 2$ and $0 < m \leq 1/2$, (A.15*a*) is always satisfied. Therefore, the CT equilibrium is stable against invasion with any combinations of NT, CT, PT and IL when $ms < c$ and $ms < r/(1+r)$.

Here we consider CT with strongest conformity bias ($a = \infty$). As shown below, even when we consider CT with intermediate strength of conformity bias (CTI) ($1 < a < \infty$), the CT (strongest) equilibrium is stable. Let T_{ij} ($1 \leq i \leq n$, $1 \leq j \leq n$) be the number of CTI at site *i* that are adapted to the environment of site *j*.

$$T'_{ii} = \frac{1}{1-ms}\left\{(1-m)\gamma T_i + \frac{m}{n-1}\sum\nolimits_{k \neq i}^{n} \kappa T_k\right\}, \tag{A.16a}$$

$$T'_{ij} = \frac{1-s}{1-ms}\left\{(1-m)\kappa T_i + \frac{m}{n-1}\gamma T_j + \frac{m}{n-1}\sum\nolimits_{k \neq i,j}^{n} \kappa T_k\right\}, \tag{A.16b}$$

where $\gamma = \rho_{ii} = \dfrac{(1-m)^a}{(1-m)^a + \dfrac{m^a(1-s)^a}{(n-1)^{a-1}}}$ and $\kappa = \rho_{ij} = \dfrac{\dfrac{m^a(1-s)^a}{(n-1)^a}}{(1-m)^a + \dfrac{m^a(1-s)^a}{(n-1)^{a-1}}}$ $(i \neq j)$. Similar to above, the transformed variables $T_i = \sum_{j=1}^{n} T_{ij}$ $(1 \le i \le n)$ satisfy

$$T_i' = \frac{1}{1-ms}\left\{(1-m)[\gamma + (1-s)(n-1)\kappa]T_i + \frac{m[(1-s)\gamma + (1-s)(n-1)\kappa + s\kappa]}{n-1}\sum_{k \neq i}^{n} T_k\right\} \qquad \text{(A.17)}$$

so that the coefficient submatrix of the linearized recursions in the variables T_{ij} yields the maximal eigenvalue

$$\frac{1}{1-ms}\{(1-ms)\gamma + [(1-s)(n-1) + ms]\kappa\}. \qquad \text{(A.18}a\text{)}$$

Since $\gamma + (n-1)\kappa = 1$, (A.18*a*) can be rewritten as

$$\begin{aligned} &\frac{1}{1-ms}\{(1-ms)[1-(n-1)\kappa] + [(1-s)(n-1) + ms]\kappa\} \\ &= 1 - \frac{s\kappa[(n-1)(1-m) - m]}{1-ms} < 1 \end{aligned} \qquad \text{(A.18}b\text{)}$$

so that the CT (strongest) equilibrium is stable even when we consider the invasion of CT with intermediate strength of conformity bias (CTI).

STABILITY OF IL EQUILIBRIUM

When $r > c/(1-c)$, an IL equilibrium exists where social learners (UT, CT, PT) are absent and IL occur in equal numbers at each site, formally,

$$\hat{X}_{ij} = \hat{U}_{ij} = \hat{V}_{ij} = 0, \hat{Z}_i = \hat{Z} = K[1 - c/r(1-c)] \text{ for } 1 \le i \le n,\ 1 \le j \le n. \qquad \text{(A.19)}$$

As expected, $\hat{Z}$ monotonically decreases in *c*. When the recursion (A.6) is linearized at this equilibrium in the variables X_{ij}, U_{ij}, V_{ij} and $Z_i - \hat{Z}$, the coefficient matrix becomes a $(3n^2+n)\times(3n^2+n)$ matrix as follows.

$$X'_{ii} = \frac{1-m}{1-c} X_i \,, \tag{A.20a}$$

$$X'_{ij} = \frac{(1-s)m}{(1-c)(n-1)} X_j \,, \tag{A.20b}$$

$$U'_{ii} = \frac{(1-d)(1-m)}{1-c} U_i \,, \tag{A.20c}$$

$$U'_{ij} = \frac{(1-d)(1-s)m}{(1-c)(n-1)} U_j \,, \tag{A.20d}$$

$$V'_{ii} = \frac{(1-g)(1-m)}{1-c} V_i \,, \tag{A.20e}$$

$$V'_{ij} = \frac{(1-g)(1-s)m}{(1-c)(n-1)} V_j \,, \tag{A.20f}$$

$$Z'_i - \hat{Z} = [1+c-r(1-c)]\left\{(1-m)(Z_i-\hat{Z}) + \frac{m}{n-1}\sum_{k\neq i}^{n}(Z_k-\hat{Z})\right\}, \tag{A.20g}$$

The matrix is reducible into four submatrices. The coefficient matrix of Eq. (A.20*a*) and (A.20*b*) has *n* sets of identical columns each of multiplicity *n*, which entails that (at least) $n(n-1)$ eigenvalues are equal to 0. Moreover, the transformed variables $X_i = \sum_{j=1}^{n} X_{ij}$ $(1 \le i \le n)$ satisfy

$$X'_i = \frac{1-m}{1-c} X_i + \sum_{j\neq i}^{n} \frac{(1-s)m}{(1-c)(n-1)} X_j \,. \tag{A.21}$$

Solving these linear equations, the coefficient submatrix of the linearized recursions in the variables X_{ij} yields the maximal eigenvalue $(1-ms)/(1-c)$. Similarly, the variables U_{ij} and V_{ij}

yield the maximal eigenvalues $(1-d)(1-ms)/(1-c)$ and $(1-g)(1-ms)/(1-c)$, respectively. On the other hand, the coefficient submatrix of the linearized recursions in the variables $Z_i - \hat{Z}$ yields the maximal eigenvalue $1+c-r(1-c)$. If all of these maximal eigenvalues have their absolute values smaller than unity, then the IL equilibrium is stable. The condition is

$$-1 < \frac{1-ms}{1-c} < 1 \quad \text{and} \quad -1 < 1+c-r(1-c) < 1 \qquad \text{(A.22}a\text{)}$$

yielding

$$c < ms \quad \text{and} \quad \frac{c}{1-c} < r < \frac{2+c}{1-c}. \qquad \text{(A.22}b\text{)}$$

STABILITY OF UT EQUILIBRIUM

$\hat{X}_{ii} = \hat{X} > 0,\ \hat{X}_{ij} = \hat{Y} > 0\ (i \neq j),\ \hat{Z}_i = U_{ij} = V_{ij} = 0$ for $1 \le i \le n$, $1 \le j \le n$. A mixture of UTC and UTW occur at each site. Each site is occupied by $\hat{X}$ UTC (which are adapted to that site) and $(n-1)\hat{Y}$ UTW (which are adapted to the environments of the $n-1$ other sites). There are no CT, PT, and IL. Clearly, the population of each site is $\hat{N}_i = \hat{N} = \hat{X} + (n-1)\hat{Y}$, and hence an equilibrium of this kind is completely symmetric (the structure of the equilibrium is identical at all sites). Let $\theta = \hat{Y}/\hat{X}$. Substituting $\hat{X}_{ii} = \hat{X} > 0,\ \hat{X}_{ij} = \hat{Y} > 0\ (i \neq j),\ \hat{Z}_i = U_{ij} = V_{ij} = 0$ in Eqs. (A.6*a*) and (A.6*b*) and dividing the latter by the former, we find that θ is the larger and positive root of the quadratic equation

$$m\theta\left[\theta - \left(1 - \frac{s}{m}\right)\right] + \frac{(1-s)m}{n-1}(\theta - 1) = 0. \qquad \text{(A.23)}$$

Solving Eq. (A.23) explicitly yields

$$\theta = \left\{m - s - \frac{(1-s)m}{n-1} + \sqrt{\left[m - s - \frac{(1-s)m}{n-1}\right]^2 + 4\frac{(1-s)m^2}{n-1}}\right\} / 2m. \qquad \text{(A.24)}$$

Note: $1-s/m<\theta<1$ and $1-\theta\geq s$. When $n\to\infty$, $\theta\to 1-s/m$ if $s<m$ and $\theta\to 0$ if $s>m$.

Equation (1) entails that $\hat{N}>0$ if and only if $\hat{b}(\hat{N})=\hat{b}<1+r$. Since Eq. (A.1) reduces to

$$\hat{b}=\frac{1}{1-m(1-\theta)}, \tag{A.25}$$

this equilibrium exists if and only if

$$r>m(1-\theta)/[1-m(1-\theta)]. \tag{A.26}$$

Solving as above, since

$$U'_{ii}=\frac{(1-d)(1-m)}{1-m(1-\theta)}U_i, \tag{A.27a}$$

$$U'_{ij}=\frac{(1-d)(1-s)m}{[1-m(1-\theta)](n-1)}U_j, \tag{A.27b}$$

$$V'_{ii}=\frac{(1-g)(1-m)}{1-m(1-\theta)}V_i, \tag{A.27c}$$

$$V'_{ij}=\frac{(1-g)(1-s)m}{[1-m(1-\theta)](n-1)}V_j, \tag{A.27d}$$

$$Z'_i=\frac{1-c}{1-m(1-\theta)}\left\{(1-m)Z_i+\frac{m}{n-1}\sum\nolimits_{k\neq i}^{n}Z_k\right\}, \tag{A.27e}$$

the coefficient submatrix of the linearized recursions in the variables U_{ij}, V_{ij}, and Z_i yields the maximal eigenvalues $\frac{(1-d)(1-ms)}{1-m(1-\theta)}$, $\frac{(1-g)(1-ms)}{1-m(1-\theta)}$, and $\frac{1-c}{1-m(1-\theta)}$, respectively. If all of these maximal eigenvalues have their absolute values smaller than unity, then the UT equilibrium is stable. Since $d<g$, the condition is

$$(1-d)(1-ms) < 1-m(1-\theta)\,, \tag{A.28a}$$

$$c > m(1-\theta)\,, \tag{A.28b}$$

and (A.26).

STABILITY OF PT EQUILIBRIUM

Next, let us consider the stability of PT equilibrium, formally,

$$\hat{X}_{ij} = \hat{U}_{ij} = \hat{Z}_i = 0\,,$$

$$\hat{V}_{ii} = \frac{K(1-m)}{1-ms}[1-\frac{1-(1-g)(1-ms)}{r(1-g)(1-ms)}], \hat{V}_{ij} = \frac{Km(1-s)}{(1-ms)(n-1)}[1-\frac{1-(1-g)(1-ms)}{r(1-g)(1-ms)}] \quad (i \neq j) \tag{A.29}$$

for $1 \le i \le n$, $1 \le j \le n$.

When the recursion (A.6) is linearized at PT equilibrium,

$$U'_{ii} = \frac{(1-d)(1-m)}{(1-g)(1-ms)} U_i\,, \tag{A.30a}$$

$$U'_{ij} = \frac{(1-d)(1-s)m}{(1-g)(1-ms)(n-1)} U_j\,, \tag{A.30b}$$

so that

$$U'_i = \frac{1-d}{(1-g)(1-ms)} \left\{ (1-m)U_i + \frac{(1-s)m}{n-1} \sum_{k \neq i}^{n} U_k \right\}. \tag{A.30c}$$

Therefore, the coefficient submatrix of the linearized recursions in the variables U_{ij} yields the maximal eigenvalue $(1-d)/(1-g)$. Since $g > d$, this eigenvalue is always larger than unity, so that PT equilibrium is always unstable.

POLYMORPHIC EQUILIBRIUM OF IL AND CT

Assume that polymorphic equilibrium of IL and CT (and others) exist. Then IL and CT occur in equal numbers at each site, formally, $\hat{U}_{ii} = \hat{U}$, $\hat{U}_{ij} = \hat{\hat{U}} \quad (i \neq j)$, $\hat{Z}_i = \hat{Z}$, and $\hat{N}_i = \hat{N}$. From the recursion (A.6), they satisfy

$$\hat{U} = (1-d)(1-m)[\hat{U} + (n-1)\hat{\hat{U}}]b(\hat{N}), \tag{A.31a}$$

$$\hat{\hat{U}} = (1-d)(1-s)\frac{m}{n-1}[\hat{U} + (n-1)\hat{\hat{U}}]b(\hat{N}), \tag{A.31b}$$

$$\hat{Z} = (1-c)\left\{(1-m)\hat{Z} + \frac{m}{n-1}(n-1)\hat{Z}\right\}b(\hat{N}). \tag{A.31c}$$

From (A.31a) and (A.31b), $b(\hat{N}) = \dfrac{1}{(1-d)(1-ms)}$, and from (A.31$c$), $b(\hat{N}) = \dfrac{1}{1-c}$. Therefore, this type of equilibrium can exist only if $1-c = (1-d)(1-ms)$, i.e., polymorphic equilibrium of IL and CT (and others) never exist when $1-c < (1-d)(1-ms)$ or $1-c > (1-d)(1-ms)$.

Similarly, polymorphic equilibrium of PT and CT (and others), and that of PT and IL (and others) never exist.

RESULTS SUMMARY

The conditions for the existence and stability of equilibria can be mapped onto six regions of the (m, c)-parameter space. First, if $c < ms$ and $c/(1-c) < r < (2+c)/(1-c)$, fixation of IL is the unique stable equilibrium (region I). Second, if $ms < c < \min[m(1-\theta), 1-(1-d)(1-ms)]$ where

$$\theta = \left\{ m - s - \frac{(1-s)m}{n-1} + \sqrt{\left[m - s - \frac{(1-s)m}{n-1}\right]^2 + 4\frac{(1-s)m^2}{n-1}} \right\} / 2m, \tag{A.24}$$

polymorphism of IL and UT is the unique stable equilibrium provided $r > c/(1-c)$ (region II). Third, if $c > m(1-\theta)$ and $m(1-\theta) < 1-(1-d)(1-ms)$, fixation of UT is the unique stable equilibrium provided $r > m(1-\theta)/[1-m(1-\theta)]$ (region III). Fourth, if $c > 1-(1-d)(1-ms)$ and $(1-m)(1-ms) + m(1-s)^2 + \frac{(1-s)sm^2}{n-1} < (1-d)(1-ms)^2$, fixation of CT is the unique stable equilibrium provided $r > [1-(1-d)(1-ms)]/(1-d)(1-ms)$ (region IV). Fifth, if $c > 1-(1-d)(1-ms)$ and $1-m(1-\theta) < (1-d)(1-ms) < 1-m+\frac{m(1-s)^2}{1-ms}+\frac{(1-s)sm^2}{(n-1)(1-ms)}$, polymorphism of UT and CT is the unique stable equilibrium provided $r > [1-(1-d)(1-ms)]/(1-d)(1-ms)$ (region V). Sixth, if $r < \min\{m(1-\theta)/[1-m(1-\theta)], [1-(1-d)(1-ms)]/(1-d)(1-ms)\}$ and $r < c/(1-c)$, extinction is the unique stable equilibrium (region VI). Provided the cost of PT is larger than that of CT (i.e., $g > d$), PT never evolve. When CT suffer no cost (i.e., $d = 0$), fixation of IL, fixation of CT, and extinction are the possible stable equilibria (UT and PT never evolve).

INCREASING TRAIT NUMBER AND THE REGION OF CT

We show that the region for fixation of UT decreases and that for fixation of CT increases as *n* increases. Since the (necessary) condition for fixation of UT is

$$m(1-\theta) < 1-(1-d)(1-ms), \tag{A.32}$$

i.e., $\theta > \frac{(1-d)(1-ms)-(1-m)}{m} = 1-s(1-d)-\frac{d}{m}$, and θ decreases as *n* increases, the region for fixation of UT decreases as *n* increases. When $d > 0$, (A.32) is always satisfied at $m \to 0$, and (A.32) can be violated when *m* exceeds a threshold value, which we write $m_{UT \to UT+CT}$. Since $m_{UT \to UT+CT} = \frac{d}{1-s(1-d)-\theta}$, and θ decreases as *n* increases, $m_{UT \to UT+CT}$ decreases as *n* increases.

Moreover, since the (necessary) condition for fixation of CT is

$$(1-m)(1-ms)+m(1-s)^2+\frac{(1-s)sm^2}{n-1}<(1-d)(1-ms)^2, \tag{A.33}$$

i.e., $\frac{1}{n-1}<\frac{(1-d)(1-ms)^2-(1-m)(1-ms)-m(1-s)^2}{(1-s)sm^2}$, the region for fixation of CT increases as *n* increases. When $d>0$, (A.33) is always unsatisfied at $m\to 0$, and (A.33) can be satisfied when *m* exceeds a threshold value, which we write $m_{UT+CT\to CT}$. $m_{UT+CT\to CT}$ is, if it exists, the smaller root of the quadratic equation

$$(1-m)(1-ms)+m(1-s)^2+\frac{(1-s)sm^2}{n-1}-(1-d)(1-ms)^2=0, \tag{A.34}$$

and the necessary condition for the existence of $m_{UT+CT\to CT}$ is $s(1-s)-4d(1-s-\frac{1}{n-1})>0$. Since the coefficient of quadratic term decreases as *n* increases, $m_{UT+CT\to CT}$ decreases as *n* increases.

INCREASING THE COSTS OF NON-ADAPTIVE BEHAVIOR AND THE REGION OF CT

When the costs of non-adaptive behavior (*s*) increases, from (A.14*b*) and (A.14*c*), CT equilibrium decreases because of the extinction and the invasion of IL. When *n* is large ($n\to\infty$) or *d* is small ($d<<1$), from (A.28a), UT equilibrium is less likely to be invaded by CT. Overall, the region where CT can evolve (regions UT+CT and CT) decreases when *s* increases.

WHEN IL LEARN BEFORE MIGRATION

RECURSIONS

When IL learn before migration, IL do not always have correct behavior. Let Z_{ij} ($1\le i\le n$, $1\le j\le n$) be the number of IL at site *i* that are adapted to the environment of site *j*, and $Z_i=\sum_{j=1}^{n}Z_{ij}$. Then, the recursions is written as

$$X'_{ii} = (1-m)X_i b(N_i)\frac{X_{ii}+U_{ii}+V_{ii}+Z_{ii}}{N_i} + \frac{m}{n-1}\sum_{k\neq i}^{n} X_k b(N_k)\frac{X_{ki}+U_{ki}+V_{ki}+Z_{ki}}{N_k}, \tag{A.35a}$$

$$X'_{ij} = (1-s)\left\{\begin{array}{l}(1-m)X_i b(N_i)\dfrac{X_{ij}+U_{ij}+V_{ij}+Z_{ij}}{N_i} + \dfrac{m}{n-1}X_j b(N_j)\dfrac{X_{jj}+U_{jj}+V_{jj}+Z_{jj}}{N_j} \\ \quad + \dfrac{m}{n-1}\sum_{k\neq i,j}^{n} X_k b(N_k)\dfrac{X_{kj}+U_{kj}+V_{kj}+Z_{kj}}{N_k}\end{array}\right\}, \tag{A.35b}$$

$$U'_{ii} = (1-d)\left\{(1-m)U_i b(N_i)\rho_{ii} + \frac{m}{n-1}\sum_{k\neq i}^{n} U_k b(N_k)\rho_{ki}\right\}, \tag{A.35c}$$

$$U'_{ij} = (1-d)(1-s)\left\{(1-m)U_i b(N_i)\rho_{ij} + \frac{m}{n-1}\sum_{k\neq i}^{n} U_k b(N_k)\rho_{kj}\right\}, \tag{A.35d}$$

where

$$\rho_{ij} = \frac{[(X_{ij}+U_{ij}+V_{ij}+Z_{ij})/N_i]^a}{\sum_{k=1}^{n}[(X_{ik}+U_{ik}+V_{ik}+Z_{ik})/N_i]^a} \tag{A.4)'$$

$$V'_{ii} = (1-g)(1-m)V_i b(N_i), \tag{A.35e}$$

$$V'_{ij} = \frac{(1-g)(1-s)mV_j b(N_j)}{n-1}, \tag{A.35f}$$

$$Z'_{ii} = (1-c)(1-m)Z_i b(N_i), \tag{A.35g}$$

$$Z'_{ij} = \frac{(1-c)(1-s)mZ_j b(N_j)}{n-1}, \tag{A.35h}$$

where $1 \le i \le n$, $1 \le j \le n$, and $j \neq i$ in Eqs. (A.35*b*), (A.35*d*), (A.35*f*), and (A.35*h*).

When IL learn before migration, the stability of CT equilibrium becomes as follows.

Let Z_{ij} ($1 \le i \le n$, $1 \le j \le n$) be the number of IL at site *i* that are adapted to the environment of site *j*. When the recursion (A.35) is linearized at CT equilibrium,

$$Z'_{ii} = \frac{(1-c)(1-m)}{(1-d)(1-ms)} Z_i , \tag{A.36a}$$

$$Z'_{ij} = \frac{(1-c)(1-s)m}{(1-d)(1-ms)(n-1)} Z_j , \tag{A.36b}$$

so that

$$Z'_i = \frac{1-c}{(1-d)(1-ms)} \left\{ (1-m)Z_i + \frac{(1-s)m}{n-1} \sum_{k \ne i}^{n} Z_k \right\} . \tag{A.36c}$$

Therefore, the coefficient submatrix of the linearized recursions in the variables Z_{ij} yields the maximal eigenvalue $(1-c)/(1-d)$. Since $c > d$, this eigenvalue is always smaller than unity, so that IL cannot invade CT equilibrium. Therefore, the condition for CT equilibrium to be stable is

$$\frac{1}{(1-d)(1-ms)^2} \left\{ (1-m)(1-ms) + m(1-s)^2 + \frac{(1-s)sm^2}{n-1} \right\} < 1, \tag{A.14a}$$

$$(1+r)(1-d)(1-ms) > 1 , \tag{A.14b)'}$$

Next, let us consider the stability of IL equilibrium, formally,

$$\hat{X}_{ij} = \hat{U}_{ij} = \hat{V}_{ij} = 0 ,$$

$$\hat{Z}_{ii} = \frac{K(1-m)}{1-ms}[1 - \frac{1-(1-c)(1-ms)}{r(1-c)(1-ms)}], \hat{Z}_{ij} = \frac{Km(1-s)}{(1-ms)(n-1)}[1 - \frac{1-(1-c)(1-ms)}{r(1-c)(1-ms)}] \quad (i \ne j) \tag{A.37}$$

for $1 \le i \le n$, $1 \le j \le n$.

When the recursion (A.35) is linearized at IL equilibrium,

$$U'_{ii} = \frac{(1-d)(1-m)}{(1-c)(1-ms)} U_i , \tag{A.38a}$$

$$U'_{ij} = \frac{(1-d)(1-s)m}{(1-c)(1-ms)(n-1)} U_j , \tag{A.38b}$$

so that

$$U'_i = \frac{1-d}{(1-c)(1-ms)} \left\{ (1-m)U_i + \frac{(1-s)m}{n-1} \sum\nolimits_{k\neq i}^{n} U_k \right\}. \tag{A.38c}$$

Therefore, the coefficient submatrix of the linearized recursions in the variables U_{ij} yields the maximal eigenvalue $(1-d)/(1-c)$. Since $c > d$, this eigenvalue is always larger than unity, so that IL equilibrium is always unstable.

Next, let us consider the stability of UT equilibrium, formally,

$$\hat{X}_{ii} = \hat{X} > 0,\ \hat{X}_{ij} = \hat{Y} > 0\ (i \neq j),\ \hat{Z}_i = U_{ij} = V_{ij} = 0 \text{ for } 1 \le i \le n,\ 1 \le j \le n . \tag{A.39}$$

When the recursion (A.35) is linearized at UT equilibrium,

$$Z'_{ii} = \frac{(1-c)(1-m)}{1-m(1-\theta)} Z_i , \tag{A.40a}$$

$$Z'_{ij} = \frac{(1-c)(1-s)m}{[1-m(1-\theta)](n-1)} Z_j , \tag{A.40b}$$

so that

$$Z'_i = \frac{1-c}{1-m(1-\theta)} \left\{ (1-m)Z_i + \frac{(1-s)m}{n-1} \sum\nolimits_{k\neq i}^{n} Z_k \right\}. \tag{A.40c}$$

Therefore, the coefficient submatrix of the linearized recursions in the variables Z_{ij} yields the maximal eigenvalue $\frac{(1-c)(1-ms)}{1-m(1-\theta)}$. Since recursions of CT and PT are the same as (A.27), the coefficient submatrix of the linearized recursions in the variables U_{ij}, V_{ij}, and Z_{ij} yields the maximal eigenvalues $\frac{(1-d)(1-ms)}{1-m(1-\theta)}$, $\frac{(1-g)(1-ms)}{1-m(1-\theta)}$, and $\frac{(1-c)(1-ms)}{1-m(1-\theta)}$, respectively. Since $d < g < c$, the conditions for UT equilibrium to be stable are

$$(1-d)(1-ms) < 1-m(1-\theta) \quad (A.28a)$$

and

$$r > m(1-\theta)/[1-m(1-\theta)]. \quad (A.26)$$

Just as in the condition where IL learn after migration, PT equilibrium is always unstable when IL learn before migration.

Moreover, if polymorphic equilibrium of IL and CT (and others) exist, equilibrium values $\hat{U}_{ii} = \hat{U}$, $\hat{U}_{ij} = \hat{\hat{U}} \quad (i \neq j)$, $\hat{Z}_{ii} = \hat{Z}$, $\hat{Z}_{ij} = \hat{\hat{Z}} \quad (i \neq j)$, and $\hat{N}_i = \hat{N}$ satisfy

$$\hat{U} = (1-d)(1-m)[\hat{U} + (n-1)\hat{\hat{U}}]b(\hat{N}), \quad (A.41a)$$

$$\hat{\hat{U}} = (1-d)(1-s)\frac{m}{n-1}[\hat{U} + (n-1)\hat{\hat{U}}]b(\hat{N}), \quad (A.41b)$$

$$\hat{Z} = (1-c)(1-m)[\hat{Z} + (n-1)\hat{\hat{Z}}]b(\hat{N}), \quad (A.41c)$$

$$\hat{\hat{Z}} = (1-c)(1-s)\frac{m}{n-1}[\hat{Z} + (n-1)\hat{\hat{Z}}]b(\hat{N}), \quad (A.41d)$$

From (A.41*a*) and (A.41*b*), $b(\hat{N}) = \frac{1}{(1-d)(1-ms)}$, and from (A.41*c*) and (A.41*d*), $b(\hat{N}) = \frac{1}{(1-c)(1-ms)}$. Since $c > d$, these conditions are never satisfied simultaneously so that polymorphic equilibrium of IL and CT (and others) never exist.

Similarly, polymorphic equilibrium of PT and CT (and others), and that of PT and IL (and others) never exist.

RESULTS SUMMARY

The conditions for the existence and stability of equilibria can be mapped on to four regions of the (m,c)-parameter space. First, if $m(1-\theta)<1-(1-d)(1-ms)$, fixation of UT is the unique stable equilibrium provided $r>m(1-\theta)/[1-m(1-\theta)]$ (region I). Second, if $(1-m)(1-ms)+m(1-s)^2+\frac{(1-s)sm^2}{n-1}<(1-d)(1-ms)^2$, fixation of CT is the unique stable equilibrium provided $r>[1-(1-d)(1-ms)]/(1-d)(1-ms)$ (region II). Third, if $1-m(1-\theta)<(1-d)(1-ms)<1-m+\frac{m(1-s)^2}{1-ms}+\frac{(1-s)sm^2}{(n-1)(1-ms)}$, polymorphism of UT and CT is the unique stable equilibrium provided $r>[1-(1-d)(1-ms)]/(1-d)(1-ms)$ (region III). Fourth, if $r<\min\{m(1-\theta)/[1-m(1-\theta)],[1-(1-d)(1-ms)]/(1-d)(1-ms)\}$, extinction is the unique stable equilibrium (region IV). Provided the cost of IL and PT are larger than that of CT (i.e., $c>g>d$), IL and PT never evolve. When CT suffer no cost (i.e., $d=0$), fixation of CT and extinction are the only possible stable equilibria (UT,PT, and IL never evolve) .

WHAT HAPPENS IF THE NUMBER OF TRAITS AND SITES DIFFER?

Here we consider an infinite number of islands and *n* behavior model, where each behavior is adapted to the same number of sites. In this situation, we can regard the sites where the same behavior is adaptive as one site, so this situation is almost the same as normal island model with *n* site but migration rate is different. That is, we can ignore the migration between sites where the same behavior is adaptive, so effective migration rate in this model is

$$m^*=\frac{(n-1)m}{n}. \qquad \text{(A.42)}$$

Therefore, the conditions for fixation of UT, those for CT, etc. are basically the same as in the above model, but $m\to m^*$. The threshold values of *m* for $UT\to UT+CT$ and $UT+CT\to CT$

are $\frac{n}{n-1}$ times as large as those in the normal n island model. Since both the threshold values in the normal model and $\frac{n}{n-1}$ decrease as n increases, the threshold values in this model also decrease as n increases.

APPENDIX B: A MODEL OF TEMPORAL VARIABILITY WITH PURE LEARNING STRATEGIES

The method of numerical simulation for the evolution of learning in temporally changing environment is as follows. We assume that the number of possible environmental states is infinite so that when the environment changes it never reverts to an earlier state (infinite environmental states model). Corresponding to each environmental state, there is one optimal (correct) behavior (fitness: 1). All other behaviors are equally maladaptive (fitness: $1-s$; i.e. the cost of maladaptive behavior is *s*). The environment changes every ℓ generations ($\ell \geq 1$), so that one post-change generation experiences a different environmental state to the previous generation, and $\ell - 1$ subsequent generations experience the same state as that post-change generation. That is, larger values of ℓ imply more environmental stability.

We assume a population of haploid asexual organisms. A tetra-allelic locus determines whether an organism is an individual learner, a social learner with unbiased transmission, a social learner with conformist transmission, and a social learner with payoff-biased transmission (abbreviated IL, UT, CT, and PT, respectively). IL always achieves the optimal (correct) behavior by individual learning, but suffers a fixed cost *c*. Social learners (UT, CT, PT) copy a behavior of the previous generation. So, when the environment changes, social learners always copy a maladaptive (wrong) behavior and only IL behaves correctly. UT acquire their phenotypes by copying a random member of the parental generation in the site they occupy (oblique transmission). CT suffer a mortality cost *d* to acquire their phenotypes. Here we assume CT with a conformity bias *a*. Therefore, the probability that CT imitates a behavior *j* with the frequency b_j in the previous generation can be expressed as

$$P_j = \frac{b_j^a}{b_0^a + b_1^a + b_2^a + \cdots} \quad \text{(B.1)}$$

where $b_0, b_1, b_2 \cdots$ are the frequencies of organisms with the behavior 0, 1, 2 $\cdots$ respectively. PT acquire their phenotypes by copying the behavior of the parental generation with the highest payoff, but suffer a mortality cost *g*. Provided IL exist in the population, PT can copy optimal (correct) behavior in every generation except post-change generations. In post-change generations, PT copy a behavior that is optimal in the previous generation.

The fitness of IL is $1-c$, that of social learners (UT, CT, PT) behaving correctly (UTC, CTC, PTC) is 1, $1-d$, and $1-g$, respectively, and that of social learners behaving incorrectly (UTW, CTW, PTW) is $1-s$, $(1-d)(1-s)$, and $(1-g)(1-s)$, respectively ($0<d<g<c<s<1$).

We set the initial condition such that the environment is in state 0 in generation 0 and all members have behavior 0. In the next generation (generation 1) the environment changes to state 1 and behavior 1 becomes optimal. We suppose that behavior *i* is optimal in state *i*. In a periodically changing environment, the environment changes every ℓ generations so that the environment changes from state *i* to state *i*+1 between generation $i\ell$ and generation $i\ell+1$.

Suppose that the population is now in generation *k* and the environment is state *n*. Let the frequency of UT, CT, PT, and IL after natural selection be $x^{(k)}$, $u^{(k)}$, $v^{(k)}$, and $z^{(k)}$ ($x^{(k)}+u^{(k)}+v^{(k)}+z^{(k)}=1$), respectively, that of behavior *i* be $b_i^{(k)}$ and $P_i^{(k)} = (b_i^{(k)})^a / \sum_{j=0}^{n} (b_j^{(k)})^a$.

Then,

$$x^{(k)} = \frac{b_n^{(k-1)} + (1-s)(1-b_n^{(k-1)})}{T_{k-1}} x^{(k-1)} \quad \text{(B.2}a\text{)}$$

$$u^{(k)} = (1-d)\frac{P_n^{(k-1)} + (1-s)(1-P_n^{(k-1)})}{T_{k-1}} u^{(k-1)} \quad \text{(B.2}b\text{)}$$

$$v^{(k)} = \begin{cases} \dfrac{(1-g)(1-s)}{T_{k-1}} v^{(k-1)} & \text{(post-change generations)} \\ \dfrac{1-g}{T_{k-1}} v^{(k-1)} & \text{(other generations)} \end{cases} \tag{B.2c}$$

$$z^{(k)} = \frac{1-c}{T_{k-1}} z^{(k-1)} \tag{B.2d}$$

$$b_n^{(k)} = \begin{cases} \dfrac{(1-c)z^{(k-1)}}{T_{k-1}} & \text{(post-change generations)} \\ \dfrac{b_n^{(k-1)}x^{(k-1)} + (1-d)P_n^{(k-1)}u^{(k-1)} + (1-g)v^{(k-1)} + (1-c)z^{(k-1)}}{T_{k-1}} & \text{(other generations)} \end{cases} \tag{B.3a}$$

$$b_m^{(k)} = \begin{cases} (1-s)\dfrac{b_m^{(k-1)}x^{(k-1)} + (1-d)P_m^{(k-1)}u^{(k-1)} + (1-g)v^{(k-1)}}{T_{k-1}} & \text{(post-change generations; } m = n-1) \\ (1-s)\dfrac{b_m^{(k-1)}x^{(k-1)} + (1-d)P_m^{(k-1)}u^{(k-1)}}{T_{k-1}} & \text{(post-change generations; } m < n-1) \\ (1-s)\dfrac{b_m^{(k-1)}x^{(k-1)} + (1-d)P_m^{(k-1)}u^{(k-1)}}{T_{k-1}} & \text{(other generations; } m < n) \end{cases} \tag{B.3b}$$

where

$$T_k = \begin{cases} (1-s)x^{(k)} + (1-d)(1-s)u^{(k)} + (1-g)(1-s)v^{(k)} + (1-c)z^{(k)} & \text{(post-change generations)} \\ \{b_n^{(k)} + (1-s)(1-b_n^{(k)})\}x^{(k)} + (1-d)\{P_n^{(k)} + (1-s)(1-P_n^{(k)})\}u^{(k)} + (1-g)v^{(k)} + (1-c)z^{(k)} & \text{(other generations)} \end{cases} \tag{B.4}$$

Since the fitness of social learners over one cycle (ℓ generations) is always smaller than $(1-s)^1 1^{\ell-1} = 1-s$ and that of IL over one cycle is $(1-c)^\ell$, IL equilibrium is stable when

$$\frac{1}{\ell} > \frac{\ln(1-c)}{\ln(1-s)}. \tag{B.5}$$

It can also be shown that IL and PT never coexist at stable equilibrium, except when

$$\frac{1}{\ell} = \frac{\ln(1-c) - \ln(1-g)}{\ln(1-s)}. \tag{B.6}$$

When IL exist, the fitness of IL over one cycle is $(1-c)^{\ell}$, and that of other coexisting strategies must be the same fitness. However, when IL do not exist, the fitness of PT over one cycle is $(1-s)(1-g)^{\ell}$. Therefore, IL and PT coexist at stable equilibrium only when $\frac{1}{\ell}=\frac{\ln(1-c)-\ln(1-g)}{\ln(1-s)}$. When $\frac{1}{\ell}>\frac{\ln(1-c)-\ln(1-g)}{\ln(1-s)}$, PT cannot invade the equilibrium population of IL (and others). When $\frac{1}{\ell}<\frac{\ln(1-c)-\ln(1-g)}{\ln(1-s)}$, the frequency of IL decreases, but if IL go extinct, the fitness of PT over one cycle becomes $(1-s)^{\ell}(1-g)^{\ell}$. Since $c<s$, IL can invade this equilibrium population of PT (and others), but when IL invades, the fitness of PT over one cycle becomes $(1-s)(1-g)^{\ell}$ again, so the frequency of IL decreases again. Assuming that the frequency of IL never becomes 0 because of low frequency mutation, the frequency of IL is almost 0 at equilibrium when $\frac{1}{\ell}<\frac{\ln(1-c)-\ln(1-g)}{\ln(1-s)}$. When $\frac{1}{\ell}<\frac{\ln(1-c)-\ln(1-g)}{\ln(1-s)}$, PT equilibrium (with low frequency IL) is stable if and only if

$$\frac{1}{\ell}>\frac{\ln(1-g)}{\ln(1-s)} \tag{B.7}$$

because when the frequency of PT is almost 1, the fitness of UT over one cycle is $(1-s)^2$ and that of CT over one cycle is $(1-s)^2(1-d)^{\ell}<(1-s)^2$ because they learn the wrong behavior in post-change generation and the next generation, but learn correct one in other generations. When $\frac{1}{\ell}>\frac{\ln(1-c)-\ln(1-g)}{\ln(1-s)}$ and $\frac{1}{\ell}<\frac{\ln(1-g)}{\ln(1-s)}$, polymorphism of PT and other social learning strategy (UT and/or CT) will be achieved. These analytical results are confirmed by the numerical simulation.

For Figure 6B, we set the initial frequencies of UT, CT, PT, and IL be 0.25. Parameters are $s=0.5$, $c=0.3$, $g=0.1$, $d=0$, $\ell=5$, and $a=10$. For Figure 5, we obtain the equilibrium frequencies of UT, CT, PT, and IL from several initial frequencies of them. Parameters are $s=0.5$, $g=0.1$, $d=0.05$, and $a=10$. Note $a=10$ is sufficiently strong such that it can be assumed to be almost infinite.

IL LEARN BEFORE THE ENVIRONMENTAL CHANGE

If IL learn before environmental change, IL also have a wrong behavior in post-change generations. Then, all members have a wrong behavior in post-change generations, so social learners (UT, CT, PT) always copy a wrong behavior in the next generation of the post-change generation. Therefore, the fitness of social learners over one cycle (ℓ generations) is always smaller than $(1-s)^2 1^{\ell-2} = (1-s)^2$, that of IL over one cycle is $(1-s)(1-c)^{\ell}$, and that of PT over one cycle is $(1-s)^2(1-g)^{\ell}$. Thus, IL equilibrium is stable when $\frac{1}{\ell} > \frac{\ln(1-c)}{\ln(1-s)}$, IL and PT never coexist except when $\frac{1}{\ell} = \frac{\ln(1-c)-\ln(1-g)}{\ln(1-s)}$, and PT equilibrium (with low frequency IL) is stable if and only if $\frac{1}{\ell} < \frac{\ln(1-c)-\ln(1-g)}{\ln(1-s)}$ and $\frac{1}{\ell} > \frac{\ln(1-g)}{\ln(1-s)}$ are satisfied. That is, the results are basically the same as in the case that IL learn after environmental change.