ADAPTIVE SOCIAL LEARNING STRATEGIES IN TEMPORALLY AND SPATIALLY VARYING ENVIRONMENTS

HOW TEMPORAL VS. SPATIAL VARIATION, THE NUMBER OF CULTURAL TRAITS, AND THE COSTS OF LEARNING INFLUENCE THE EVOLUTION OF CONFORMIST-BIASED TRANSMISSION, PAYOFF-BIASED TRANSMISSION AND INDIVIDUAL LEARNING

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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 $0 \leq d < g < c < 1$.

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} $(1 \leq i \leq n$, $1 \leq j \leq n)$ 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 $(1 \leq i \leq n)$ 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

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

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

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

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

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

where

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

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

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

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 $m/(n-1)$ ($0 < m \leq 1/2$).

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:

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

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

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

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

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

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

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

where $1 \le i \le n$, $1 \le j \le n$, and $j \neq i$ 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,

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

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

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:

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

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

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

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

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

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

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

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

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

Since

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

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

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

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 $\dfrac{1-c}{(1-d)(1-ms)}$. 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

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

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

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

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

and

$$\frac{1-c}{1-ms}<1. \qquad (\text{A}.15c)$$

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*.

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

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

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.

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

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

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

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

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

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

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

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 $X_i = \sum\nolimits_{j=1}^{n} X_{ij}$ $(1 \le i \le n)$ satisfy

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

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

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

yielding

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

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,

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

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

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

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

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.31*a*) and (A.31*b*), $b(\hat{N}) = \dfrac{1}{(1-d)(1-ms)}$, 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

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

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

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

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

where

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

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

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

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

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

where $1 \leq i \leq n$, $1 \leq j \leq n$, 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,

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

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

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,

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

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 $\dfrac{(1-c)(1-ms)}{1-m(1-\theta)}$. 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

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

and

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

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

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

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

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

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

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

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

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,

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

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

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

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

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

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

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.

ABSTRACT

Long before the origins of agriculture human ancestors had expanded across the globe into an immense variety of environments, from Australian deserts to Siberian tundra. Survival in these environments did not principally depend on genetic adaptations, but instead on evolved learning strategies that permitted the assembly of locally adaptive behavioral repertoires. To develop hypotheses about these learning strategies, we have modeled the evolution of learning strategies to assess what conditions and constraints favor which kinds of strategies. To build on prior work, we focus on clarifying how spatial variability, temporal variability, and the number of cultural traits influence the evolution of four types of strategies: (1) individual learning, (2) unbiased social learning, (3) payoff-biased social learning, and (4) conformist transmission. Using a combination of analytic and simulation methods, we show that spatial—but not temporal—variation strongly favors the emergence of conformist transmission. This effect intensifies when migration rates are relatively high and individual learning is costly. We also show that increasing the number of cultural traits above two favors the evolution of conformist transmission, which suggests that the assumption of only two traits in many models has been conservative. We close by discussing how (1) spatial variability represents only one way of introducing the low-level, non-adaptive phenotypic trait variation that so favors conformist transmission, the other obvious way being learning errors, and (2) our findings apply to the evolution of conformist transmission in social interactions. Throughout we emphasize how our models generate empirical predictions suitable for laboratory testing.

Keywords: Learning strategies; Individual learning; Social learning; Conformist transmission; Payoff-biased transmission

1. INTRODUCTION

The application of evolutionary principles to understanding the origin and operation of social learning in humans has generated a wide range of insights, as well as vibrant debates. Rooted in the seminal modeling work of Boyd and Richerson (1985), much theoretical work has explored the conditions and contexts favoring the evolution of social learning, often generating hypotheses about adaptive learning mechanisms using cues related to success, payoffs, trait content (direct bias), credibility, ethnic markers, adoption rates, and conformity (Kendal, Giraldeau, & Laland, 2009; R. McElreath et al., 2008; R. McElreath, Boyd, & Richerson, 2003; Richard McElreath & Strimling, 2008; Rendell, Hoppitt, & Kendall, 2007; Schlag, 1998, 1999; Wakano & Aoki, 2006; Wakano, Aoki, & Feldman, 2004). Such theoretical work indicates that social learning mechanisms interact competitively and synergistically with each other, and with individual learning, at the population level. In addition to informing our understanding of how cultural abilities evolve in humans, and more recently in other species, such models provide disciplined theoretical foundations for generating specific evolutionary predictions about the contexts in which various learning strategies should be deployed, and the kind of cues likely to activate them.

While still in its gestational stage, the empirical testing of psychological and behavioral hypotheses generated by these evolutionary models has been surprisingly successful, in both humans and other species, with evidence coming from Economics, Psychology, Biology and Anthropology (e.g., J. Henrich & McElreath, 2007; Laland, 2004; R. McElreath, et al., 2008). Recently, confirming earlier predictions, a blossoming of experimental studies in young children and infants is revealing solid evidence for imitative biases related to prestige, success, competence (reliability), dialect, and age (Chudek, Heller, Birch, & Henrich, 2012; Harris & Corriveau, 2011; Stenberg, 2009), most of which have previously been demonstrated in Western adults (Mesoudi, 2009). Field evidence is also beginning to show converging lines of evidence for these adaptive biases in small-scale societies, and in economically important domains (J. Henrich & Broesch, forthcoming). Some work has even connected these learning biases to the generation and maintenance of stable, adaptive cultural patterns in small-scale societies (J. Henrich & Henrich, 2010). Finally, in non-human social learners, some of the best experimental tests of these models comes from work with rats (Galef & Whiskin, 2008) and fish (Laland, Atton, & Webster, 2011).

Among the proposed social learning biases in this adaptive psychological suite is frequency-dependent biased transmission (Boyd & Richerson, 1985: Chapter 7). Because there is useful information stored implicitly in the relative frequency of different cultural traits, learners might use the frequency of a trait in the population to more effectively select locally adaptive cultural traits, or at least avoid adopting maladaptive traits. Conformist transmission is a sub-category of frequency-dependent biased transmission in which individuals use the frequency of the most common trait, in a personal sample or the local population, as a cue in figuring out which trait to adopt, potentially integrating it with other information, such as personal experience, the relative success of those with different traits, and self-similarity (N. Henrich & Henrich, 2007: Chapter 2; Rendell et al., 2011). Conformist biases are adaptive to the degree that they can help learners integrate information gleaned from other members of their community, while allowing them to filter the errors that inevitably creep into the pathways of cultural transmission (J. Henrich & Boyd, 2002). The basic logic underpinning conformist transmission is enshrined in the Condorcet Jury Theorem. Central to defining and identifying conformist transmission is recognizing that it requires a non-linear increase in the likelihood of adopting a trait with increases in the frequency of that cultural trait. This distinguishes conformist biased strategies from unbiased transmission, in which learners acquire a particular trait in proportion to that trait's current frequency in the population (which, for example, occurs if learners copy a random person in the population).

Boyd and Richerson's (1985) initial efforts suggested that conformist transmission could outcompete unbiased transmission in a spatially variable environment. This model, however, was limited because it did not consider (a) a cost for conformist transmission, (b) any individual learning, (c) more than two traits or environments, or (d) temporally varying environments. To address some of these limitations, Henrich and Boyd (1998) constructed a simulation model involving a large mix of strategies involving combinations of individual learning, unbiased transmission, and conformist transmission in which learners had to adapt to a spatially and temporally varying environment. Later, Kameda and Nakanishi (2002) augmented Henrich and Boyd's code to consider conditions under which individual learning was costly, and tested these predictions in a laboratory experiment. These simulations were limited in considering only two cultural traits and two different environments. Overall, this early work suggested that conformist transmission would outcompete unbiased transmission under a wide range of conditions, though not if the environment changed too frequently or individual learning was too inaccurate.

More recently, several authors have developed a combination of analytical and simulation work on temporally varying environments that both confirm and challenge earlier conclusions (Erikksson, Enquist, & Ghirlanda, 2007; Kandler & Laland, 2009; Kendal, et al., 2009; R. McElreath, et al., 2008; Nakahashi, 2007a; Wakano & Aoki, 2007; Whitehead, 2007). Some of this work suggests that in temporally varying environments both unbiased and payoff-biased transmission can dominate or even eliminate conformist transmission, reducing the range of conditions in which we expect conformist transmission. During roughly the same time period, work exploring the impact of spatially variable environments on the evolution of social learning considered only unbiased transmission (Aoki, 2010; Aoki & Nakahashi, 2008). Here we bring these two strands of modeling together.

While these prior efforts make important contributions to understanding the evolutionary-theoretic hypotheses that should drive empirical inquiry, we think the focus on modeling (1) only two (distinguishable) cultural traits, (2) temporally varying environments, and (3) error-free cultural transmission has actually obscured some of the conditions most favorable to the evolution of conformist transmission. Our goal here is twofold. First, we develop an n-trait ($n \geq 2$) model in a spatially varying environment to illustrate how these two elements influence the evolution of conformist biased learning strategies vis-à-vis unbiased transmission, pay-off biased transmission, and individual learning. While we do not explicitly model transmission error here, we argue below that spatial mixing creates a selective environment similar to that produced by transmission errors. Second, to most effectively illustrate the contrast between the effects of temporal vs. spatial variation on favored learning strategies, we draw on and in some cases further develop results from two parallel models that focus only on temporal variation.

We first present our baseline model of the evolution of social learning strategies for n different cultural traits in a spatially varying environment, and we introduce the two parallel models for temporally varying environments. We then present the baseline results for the simplest cases. We then incrementally add complexity to this baseline case by (a) adding a fitness cost for using conformist transmission, (b) analyzing how the number of cultural traits impacts the outcomes, (c) including payoff-biased learning strategies, and (d) modifying the life cycle such that individual learners can only learn before migration to a new site. Throughout the paper, we develop the models and present the results in the main text, leaving the derivations themselves in the online supplemental materials. We have done this in an effort to most effectively communicate with empirically-oriented evolutionary researchers who might test these hypotheses about learning strategies. We close by itemizing the empirical predictions, and by relating our findings to the effects of transmission error and the evolution of social behavior in contexts of cooperation, coordination, and complementarity.

2. COMPARABLE SPATIAL AND TEMPORAL MODELS OF THE EVOLUTION

Here we develop parallel models of the evolution of different social learning strategies in both spatially and temporally varying environments. The spatially varying model is developed in full in this paper by extending Aoki and Nakahashi (2008), and is solved analytically. To compare the effects of spatial vs. temporal variability, we draw on findings from two similar models of temporal variability: one developed here that most closely parallels our spatial model in using pure strategies, and a second previously published model (Nakahashi, 2007a) that uses mixed strategies similar to those explored by Henrich and Boyd (1998). We use both models because neither one can be fully solved analytically, so we draw on analytical results where possible and otherwise rely on simulations for comparisons. Nakahashi (2007b) has previously shown that these two models of temporal variability generate similar results under most conditions. Comparing results across these similar models allows us to illuminate the differential impacts of spatial vs. temporal variation on the evolution of social learning in general, and on conformist transmission specifically.

2.1. THE BASELINE SPATIAL MODEL

In our structured population, individuals may occupy any of n different sites in a spatially heterogeneous world. Each site has a different environment with a specific corresponding cultural trait (learnable phenotype) that is adaptive at that site. Thus, we distinguish n

traits/phenotypes, each of which is locally adapted to one particular environment but maladaptive in the *n*-1 other environments. Traits that are maladaptive in all *n* environments are not incorporated into the dynamics.

Individuals are of three genetically distinct types: unbiased social learners (UT: unbiased transmission is linearly frequency-dependent), conformist-biased social learners (CT: conformist transmission is non-linearly frequency-dependent), and individual learners (IL). Later, we add payoff-biased social learners (PT: payoff-biased transmission copies according to payoff differences). UT acquire their cultural traits by copying a random member of the previous or parental generation in the site they occupy (oblique transmission: Cavalli-Sforza & Feldman (1981)). CT acquire their traits by copying the most common trait in the previous generation at their sites, but suffer a mortality cost *d* due to abilities or activities associated with figuring out the most common trait. IL always acquire the trait that is adapted to the environment of the site they currently occupy, but suffer a cost *c* due to mistakes made before the mature behavior is realized. The parameter *s* is the selective cost of not acquiring the locally adaptive trait. We typically assume that: $0 \le d < c < s < 1$, meaning that individual learning is the most costly (*c*) strategy, followed by conformist transmission (*d*), and then unbiased social learning (which costs zero). The parameter *s* can be thought of as the fitness consequences of not figuring out what the locally adaptive thing to do is. Traits with high *s* have relatively larger fitness consequences.

To track the numbers of individuals with each of our three different strategies, we use capitalized letters (X_{ij}, U_{ij}, Z_{ij}), indexed by *i* and *j* to respectively mark the current site in which the individuals live, and the current phenotypic trait exhibited by those individuals. 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} possess the locally adaptive trait and $X_i - X_{ii}$ possess one of the locally non-adaptive traits. Similarly, let U_{ij} be the number of CT 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, of which U_{ii} possess the locally adaptive trait, and $U_i - U_{ii}$ possess one of the locally non-adaptive traits. Let Z_i ($1 \le i \le n$) be the number of IL at site *i*. IL always acquire the trait that is adapted to the environment of the site they occupy, but they suffer a cost from the efforts and accidents of trial and error learning. The total population size at site *i* is $N_i = X_i + U_i + Z_i$. These numbers are enumerated at the adult stage just prior to reproduction.

2.1.1. THE LIFE CYCLE

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

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

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

At the second step of the life cycle social learning occurs, either unbiased or conformist-biased, as UT and CT acquire their traits by copying 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

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

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

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

where

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

Here, *a* is the strength of conformist bias, and CT always imitate the most common trait when $a = \infty$. Developed in Nakahashi (2007a), this formulation of conformist transmission guarantees that the probability of acquiring the most common trait in a local population is greater than the frequency of that trait in the population (assuming $a > 1$).

The third and fourth events in the life cycle are migration followed by individual learning for IL. For migration, a fixed fraction of the individuals at each site emigrate, yielding a constant forward migration rate. Here we use an island model with reciprocal migration between all pairs of sites at rate $m/(n-1)$ $(0 < m \le 1/2)$. After migration, IL acquire the cultural trait suitable to their new (post-migration) environment, but they suffer a fixed mortality cost, c. Note that this assumption gives IL an advantage over the social learning strategies, which do not update their trait after migration. Below, we show that this assumption is crucial for the survival of individual learning, and works against the success of CT in the spatial model.

The final stage in the life cycle is viability selection, in which all individuals with the locally adaptive trait survive while only a fraction $1-s$ of individuals with the maladaptive trait survive.

2.1.2. RECURSIONS FOR THE BASELINE SPATIAL MODEL

The above assumptions entail that the recursions be written as

$$X'_{ii} = (1-m)X_i b(N_i)\frac{X_{ii}+U_{ii}+Z_i}{N_i} + \frac{m}{n-1}\sum_{k\neq i}^{n} X_k b(N_k)\frac{X_{ki}+U_{ki}}{N_k}, \tag{5}$$

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

$$U'_{ii} = (1-d)\left\{(1-m)U_i b(N_i)\rho_{ii} + \frac{m}{n-1}\sum_{k\neq i}^{n} U_k b(N_k)\rho_{ki}\right\}, \tag{7}$$

$$U'_{ij} = (1-d)(1-s)\left\{(1-m)U_i b(N_i)\rho_{ij} + \frac{m}{n-1}\sum_{k\neq i}^{n} U_k b(N_k)\rho_{kj}\right\} \tag{8}$$

$$Z_i' = (1-c)\left\{(1-m)Z_i b(N_i) + \frac{m}{n-1}\sum_{k\neq i}^{n} Z_k b(N_k)\right\}, \tag{9}$$

where $1 \le i \le n$, $1 \le j \le n$, and $j \ne i$ in Eqs. (6) and (8).

2.2. THE BASELINE TEMPORAL MODELS

Now we develop a parallel model for a temporally varying environment using the same pure strategies, and then discuss a similar model involving mixed strategies (from Nakahashi, 2007a). Both temporally varying models assume that corresponding to each environmental state, there is one adaptive cultural trait or behavioral phenotype (fitness = 1) and other traits that 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 from 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. Here we use a fixed duration between environmental shifts in place of a randomly varying environment to maintain mathematical tractability. Prior work suggests that, for our purposes, this assumption does not produce essentially different results (Nakahashi, 2007b).

For our pure strategy temporal model, as in the spatial model, we assume the existence of three genetically encoded and asexually reproducing learning strategies: individual learners (IL), unbiased social learners (UT), and conformist social learners (CT). Later we introduce pay-off biased social learners (PT). IL always achieve the adaptive trait via individual learning, but suffer a fixed cost c. Social learners (UT, CT, and later PT) copy a trait from the previous generation. When the environment changes, social learners always copy a maladaptive (wrong) trait and only IL behave correctly. UT acquire their trait by copying a random member of the parental generation. Paralleling our spatial model, CT acquire the cultural trait j with probability P_j, as in equation (4), where a gives the strength of conformist transmission:

$$P_j = \frac{b_j^a}{b_0^a + b_1^a + b_2^a + \cdots} \tag{10}$$

This means that the probability that CT imitate trait j is expressed by (10), where $b_0, b_1, b_2 \cdots$ are the frequencies of individuals in the previous generation with the traits 0, 1, 2 $\cdots$ respectively. CT suffer a mortality cost d.

All this means that the fitness of IL is $1-c$ while the fitnesses of UT and CT are, respectively, 1 and $1-d$ if they have acquired the currently adaptive trait, and $1-s$ and $(1-d)(1-s)$ if they have not acquired the adaptive trait. As above, we typically assume $0 \le d < c < s < 1$.

To extract as much analytical insight as possible from these two models (before moving to simulations), we have allowed for some differences vis-à-vis our spatial model. Both of these temporally varying models 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). This makes these models most comparable to our spatial model when *n* in the spatial model is large (infinite), though we show *n* does not have to be particularly large before it approximates the infinite solution.

2.2.1. RECURSIONS FOR THE BASELINE TEMPORAL MODEL WITH PURE STRATEGIES

We set the initial condition such that the environment is in state 0 in generation 0 and all members have trait 0. In the next generation (generation 1) the environment changes to state 1 and trait 1 becomes optimal. We suppose that trait *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 in state *n*. Let the frequency of UT, CT, and IL after natural selection be $x^{(k)}$, $u^{(k)}$, and $z^{(k)}$ $(x^{(k)}+u^{(k)}+z^{(k)}=1)$, respectively, that of trait *i* be $b_i^{(k)}$ and $P_i^{(k)}=(b_i^{(k)})^a / \sum_{j=0}^{n}(b_j^{(k)})^a$. Then,

$$x^{(k)}=\frac{b_n^{(k-1)}+(1-s)(1-b_n^{(k-1)})}{T_{k-1}}x^{(k-1)} \tag{11}$$

$$u^{(k)}=(1-d)\frac{P_n^{(k-1)}+(1-s)(1-P_n^{(k-1)})}{T_{k-1}}u^{(k-1)} \tag{12}$$

$$z^{(k)} = \frac{1-c}{T_{k-1}} z^{(k-1)} \tag{13}$$

$$b_n^{(k)} = \begin{cases} \dfrac{(1-c)z^{(k-1)}}{T_{k-1}} & \text{(post-change generations)} \\ \dfrac{b_n^{(k-1)}x^{(k-1)} + (1-d)P_n^{(k-1)}u^{(k-1)} + (1-c)z^{(k-1)}}{T_{k-1}} & \text{(other generations)} \end{cases} \tag{14}$$

$$b_m^{(k)} = (1-s)\frac{b_m^{(k-1)}x^{(k-1)} + (1-d)P_m^{(k-1)}u^{(k-1)}}{T_{k-1}} \quad (m < n) \tag{15}$$

where

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

$$\tag{16}$$

From this model we will sometimes extract analytical insights, and supplement with simulations when necessary.

To complement our use of the pure strategy model in temporally varying environments, we also draw on results from a mixed strategy model that is otherwise very similar to the above model (Nakahashi, 2007a). In this model, individuals have two parameters. The first sets the degree of reliance on either individual or social learning. The second specifies the strength of conformist transmission, *a*. That is, the probability that an individual who relies on social learning imitates trait *j* with the frequency b_j in the previous generation is expressed as (10). Below we will also sometimes present analytical findings from this model to provide a point of comparison.

To compare spatial variability to temporal variability, we focus on comparing the impact of the parameter *m*, which gives the migration rate among sites in the spatial model (and thus the degree of mixing), with the parameter $R=1/\ell$. Since ℓ is the number of periods between environmental shifts, ranging from 2 to infinity, *R* gives a measure of temporal variability between 0 and 0.5 that parallels that provided by *m*.

3. COMPARISON OF RESULTS FOR BASELINE MODELS

Let's begin with the simplest cases. For the spatial model, we initially assume *n*, the number of cultural traits (and sites), is large and that the cost of using conformist transmission is zero ($d = 0$). By assuming that *n* is large ($n \to \infty$) we can most directly compare our spatial and temporal models. We also assume *a* is large such that CT always copy the most common trait from the previous generation. As we go along, we show that in many cases when CT are stable, only $a = \infty$ is stable against invasion by strategies with other values of *a*. Appendix A presents the formal details and derivations.

Under these conditions, for different parameter combinations, the spatial model reveals only three unique and stable equilibria: (a) all IL, (b) all CT, or (c) extinction. IL are the unique stable equilibrium if

$$c < ms \tag{17}$$

and

$$\frac{c}{1-c} < r < \frac{2+c}{1-c} \tag{18}$$

The first condition means that the cost of individual learning must be low relative to the product of the migration rate and the cost of not acquiring the locally adaptive trait. The second condition specifies that the intrinsic rate of population growth must fall into an intermediate range that depends only on *c*.

There is a second set of conditions in which CT are a unique stable equilibrium if $c > ms$ (the reverse of the above condition) and

$$r > \frac{ms}{1-ms} \tag{19}$$

This means that if *c* and *r* are sufficiently large (relative to the product of *m* and *s*), CT is the unique stable equilibrium. Moreover, as shown in Appendix A, when CT are a stable equilibrium, CT with larger values of *a* can continually invade, so *a* will go to it maximum value. Thus, our assuming $a = \infty$ likely does little harm.

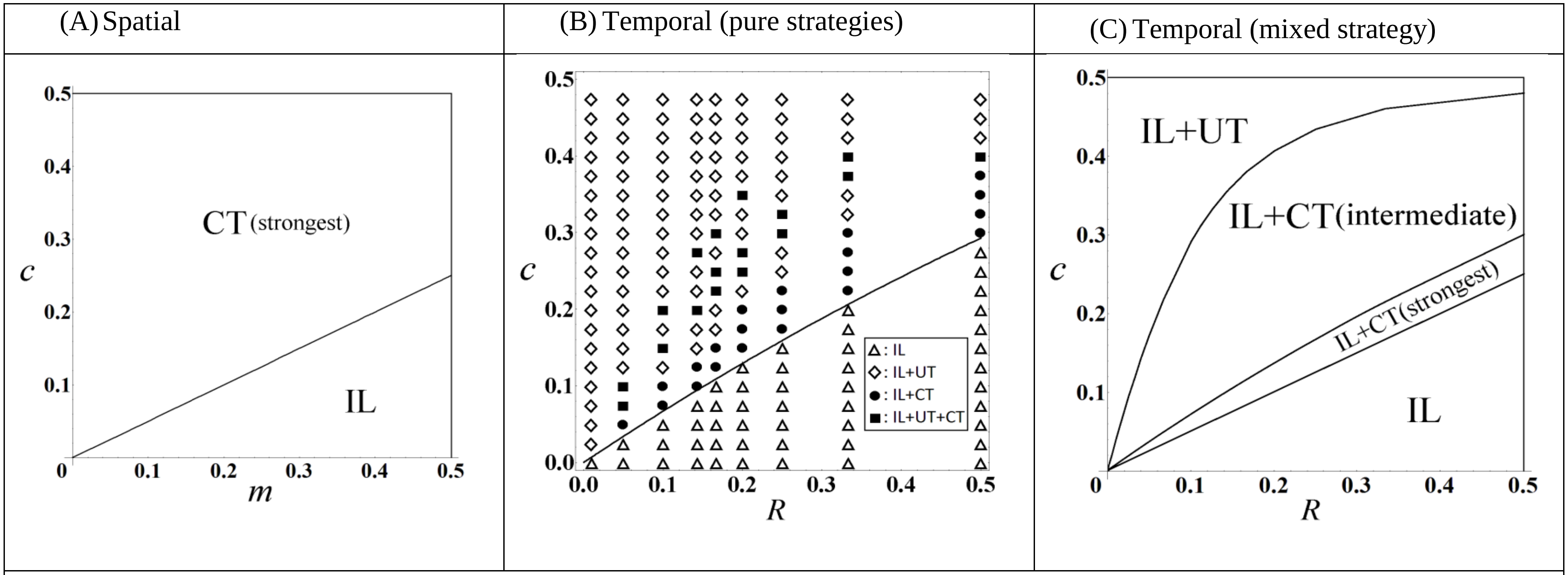
If neither of these two different equilibrium conditions hold, it means this population will go extinct because its intrinsic rate of reproduction is too low for the conditions posed by the combination of selection, migration, and the costs of individual learning.

In the temporal model with pure strategies, we show that IL are a unique and stable equilibrium when

$$R = \frac{1}{\ell} > \frac{\ln(1-c)}{\ln(1-s)} \tag{20}$$

This indicates that IL are favored when environments are unstable (*R* is large), individual learning is cheap (*c* is small), and getting the locally adaptive traits is important (*s* is large). When this condition does not hold, numerical simulations indicate that the population consists of a fluctuating composition of IL, CT, and UT. Below, when we introduce payoff-biased social learners (PT), we solve this model analytically. Appendix B supplies these derivations.

Figures 1A, 1B and 1C provide a comparison of our spatial and temporal models in the (*m*, *c*)- or (*R*, *c*)-parameter space. We have set *s* rather high at 0.5, which biases the plots in favor of IL. Despite this, Figure 1A shows that in a spatially varying environment, conformist bias is always at its maximum strength and is uniquely favored, except when individual learning is cheap and migration rates are high. Figure 1B shows the results of our simulations superimposed over of our analytically-derived line demarcating the stable region for IL. Figure 1C shows the analytical results drawn from Nakahashi (2007a) using a mixed strategy approach. Viewing Figures 1B and 1C side by side highlights the similarity between the pure and mixed strategy approaches, and reveals that in both approaches CT are generally only favored for intermediate values of *c*. If the environment is sufficiently stable and the costs of individual learning are high, a mixture of UT and IL emerge. The mixed strategy model (Figure 1C) indicates that conformist bias does not evolve to its maximum strength, except in the narrow band shown.



(A) Spatial

(B) Temporal (pure strategies)

(C) Temporal (mixed strategy)

Figure 1. Comparable plots in the (m, c)- and (R, c)-parameter space for spatially and temporally varying environments when $d = 0$ and n is infinite ($s = 0.5$, $K = 100$, and $r = 0.5$). (A) The stable equilibrium strategies in a spatially heterogeneous environment assuming ($0 < m < 1/2$ and $0 < c < s$). In the "IL" region IL are a unique stable equilibrium while in the "CT (strongest)" region CT are a unique stable equilibrium in which CT have the strongest conformity bias (where $a = \infty$). (B) Numerical simulation of equilibrium pure strategies in a temporally changing environment ($0 < R < ½$, $0 < c < s$, $a = 10$). The "Δ" markers indicate that IL are the stable equilibrium, the "◊" markers indicate a polymorphic stable state for IL and UT, the "●" markers indicate a polymorphic equilibrium of IL and CT, and the "■" markers indicate a polymorphic equilibrium of IL, UT and CT. Filled markers mean the points where CT exist. The line in Figure 1B represents the threshold for the purely IL equilibrium, captured by equation (20). The precise region where CT can exist is impossible to obtain analytically, and the numerical simulations suggest a complex relationship among the parameters. (C) The ESS (mixed strategy) in temporally changing environment is shown in the (R, c)-parameter space ($0 < R < 1/2$, $0 < c < s$). The region "IL" indicates that IL are the unique stable equilibrium; the region "IL+CT(strongest)" indicates that mixed strategies with a mixture of individual learning and conformist transmission are an ESS, and that conformist transmission (when used) is at its maximum strength; the "IL+CT(intermediate)" region indicates stable mixed strategies involving individual learning and conformist transmission (but at which conformist transmission is not maximum strength); and the "IL+UT" region indicates a stable mixed strategy involving both individual learning and unbiased transmission.

3.1. MAKING CONFORMIST TRANSMISSION COSTLY

The above results assume that using conformist transmission is costless and, in particular, no more costly than using unbiased social learning. Now we assume that using conformist transmission imposes a mortality cost, $d > 0$, by assuming that $0 < d < c < s < 1$.

For the spatial model we now have five different unique stable equilibria for different parameter values. For IL, nothing changes. If (17) and (18) hold, IL are the unique stable equilibrium. This occurs when the costs of individual learning (c) are sufficiently small and r falls into an intermediate range.

In the second situation, CT are a unique stable equilibrium if these three conditions are satisfied:

$$d < 1 - \frac{1-c}{1-ms} \tag{21}$$

$$d < 1 - \frac{1-m}{1-ms} - \frac{m(1-s)^2}{(1-ms)^2} \tag{22}$$

$$r > \frac{1-(1-d)(1-ms)}{(1-d)(1-ms)} \tag{23}$$

The first two conditions set thresholds for the costs of conformist transmission. The first condition (21) guarantees that CT outcompete IL, which means the maximum value of d depends on c and the product of m and s. The more costly individual learning is, the larger the range of conditions favoring CT. The product of m and s captures the penalty suffered by migrating CTs when they first arrive in a new site. The second threshold for d (22) depends only on m and s, and gives the conditions for outcompeting UT. Here larger values of both m and s raise the threshold for d: when d is below this CT outcompete UT. Condition (23) merely guarantees that the population reproduces sufficiently rapidly to avoid extinction.

In the third regime, assuming (21) and (23) from above are satisfied (so, no IL and no extinction), a polymorphic stable equilibrium of UT and CT exist when the cost of conformist transmission falls into this range:

$$1-\frac{1-m}{1-ms}-\frac{m(1-s)^2}{(1-ms)^2}<d<1-\frac{1-m}{1-ms} \quad (24)$$

In the fourth regime, a mixture of IL and UT are a unique stable equilibrium if

$$ms<c<\min[m,1-(1-d)(1-ms)] \quad (25)$$

as long as

$$r>\frac{c}{1-c} \quad (26)$$

Note that if $d = 0$, condition (25) is never satisfied, and this is generally a rather narrow region.

In the fifth regime, UT are a unique stable equilibrium if these three conditions are satisfied:

$$d>1-\frac{1-m}{1-ms} \quad (27)$$

$$c>m \quad (28)$$

$$r>\frac{m}{1-m} \quad (29)$$

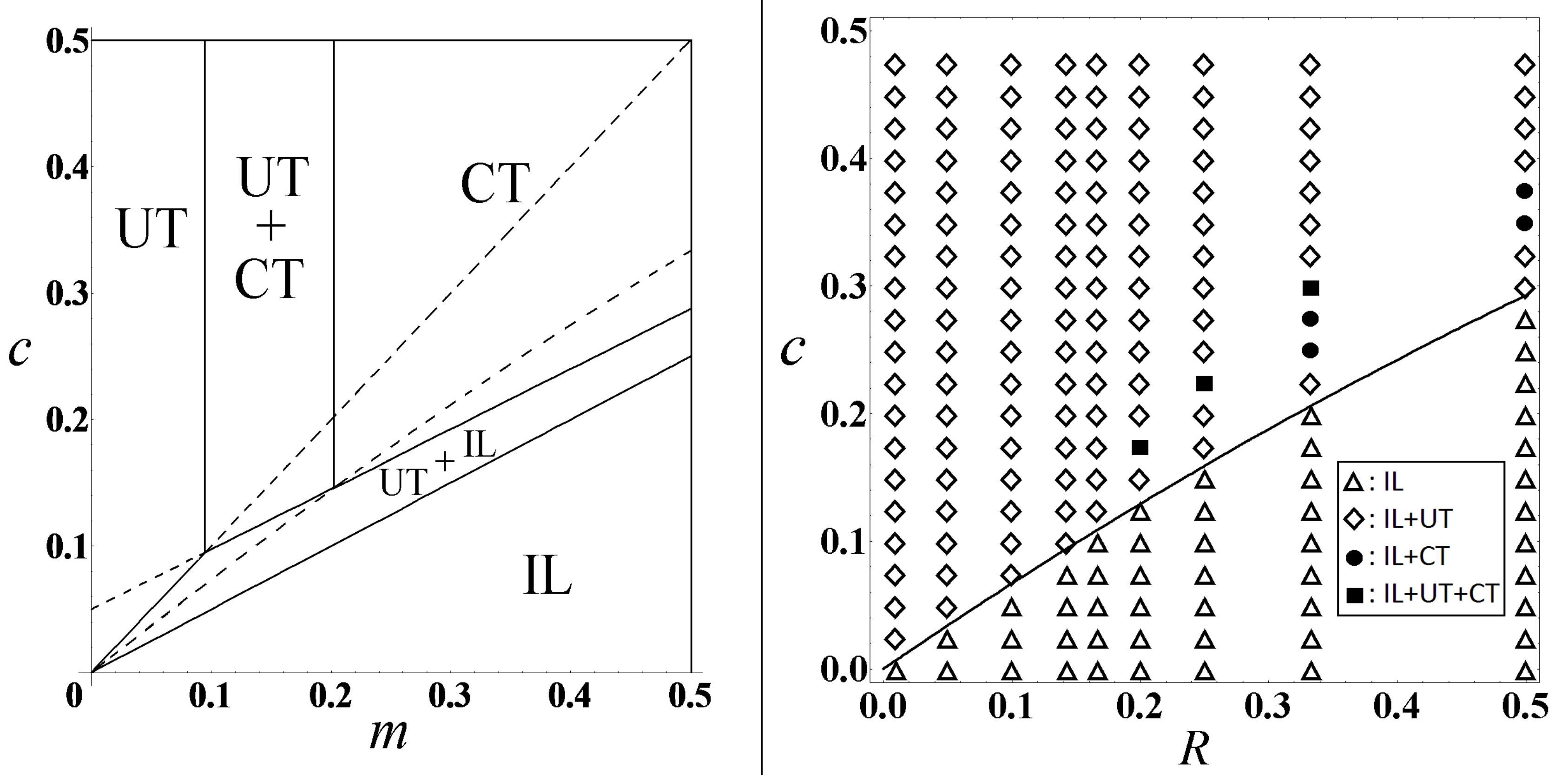
Finally, if the intrinsic rate of growth of the population is too slow, the population will go extinct.

For the pure strategy temporal model with $d>0$ we can analytically derive the region in which IL are the unique stable strategy, and it turns out to be the same as in (20). However, beyond this, we must rely on simulations of our pure strategy model. Below we also discuss the mixed strategy temporal model.

Figure 2 compares our analytical results for the spatial model with our simulations of the temporal model for the case when $d=0.05$ (otherwise using the same parameters as in Figure 1). For the spatial case, adding costs for conformist transmission means that (a) when mixing rates are sufficiently low, UT can be a unique stable equilibrium, (b) when mixing rates are intermediate, UT can coexist with CT, and (c) a narrow polymorphic region of equilibria involving UT and IL separate stable regions of UT, CT, or mixes of CT and UT, from those with pure stable IL. By contrast, in the temporal model, CT are only found in mixtures with IL or sometimes with both IL and UT, and this region is limited to a rather narrow band. By comparing Figure 2B with Figure 1B we see that occurrences of CT seem even sparser, and limited to an even narrower band of the (R, c)-parameter space.

For the mixed strategy temporal model, the outcome depends on how the relationship of d with the strength of conformist transmission (a) is modeled. If we express d as a function of a, $d(a)$, and set $d(1) = 0$ to match the pure strategy model (UT is costless), then we can show that if the derivative of d at a=1 is greater than zero, $d'(1) > 0$, then the stable regions of IL and UT in Figure 1C expand. Since social learners must investigate the frequencies of cultural traits when a>1 and this is probably costly, assuming $d'(1) > 0$ is defensible. This analysis indicates that the findings from our two temporally models are at least qualitatively consistent.

Overall, making conformist transmission costly relative to unbiased transmission does not qualitatively alter the results from our simplest models (Figure 1). In the spatial model, assuming even moderate amounts of mixing, CT always exist as long as individual learning is sufficiently costly. Within this parameter range: the more mixing, the more CT are favored. By contrast, in the models with temporally varying environments, CT are favored in an even narrower band of parameters than in the earlier temporal model.



(A) Spatial

(B) Temporal (pure strategies)

Figure 2. Comparable plots in the (m,c)- and (R, c)-parameter space for spatially and temporally varying environments when conformist transmission is costly ($d = 0.05$) and n is infinite ($s = 0.5$, $K = 100$, and $r = 0.5$). (A) The equilibrium in a spatially heterogeneous environment assuming ($0 < m < 1/2$ and $0 < c < s$). In the "IL" region all organisms are individual learners (IL equilibrium), while in the "CT" region all organisms are social learners with the strongest conformity bias (CT equilibrium); in the "UT+IL" region the polymorphic equilibrium consists of unbiased social learners and individual learners, while the "UT+CT" region is a polymorphic equilibrium of unbiased social learners and conformist social learners. (B) shows the outcomes of numerical simulations of equilibrium pure strategies in a temporally changing environment ($0 < R < ½$, $0 < \mathrm{c} < \mathrm{s}$, $a = 10$). The points "Δ" mean that all organisms become individual learners; the "◊" marks a polymorphic equilibrium of individual learners and social learners with unbiased transmission; the "●" marks a polymorphic equilibrium of individual learners and social learners with conformist transmission, and the "■" marks a polymorphic equilibrium of individual learners, unbiased social learners, and conformist social learners. Filled points indicate situations in which some conformist social learners exist. The line represents the analytical threshold for the pure individual learning equilibrium (equation (20) above).

3.2. HOW DOES THE NUMBER OF CULTURAL TRAITS INFLUENCE THE EVOLUTION OF CONFORMIST TRANSMISSION?

Thus far we have assumed that the number of cultural traits (*n*), as well as the number of sites in the spatial model, is large ($n \to \infty$). This has allowed us to simplify the mathematical expressions above and provide a more direct comparison with the infinite trait models of temporally varying environments. Now we consider how increasing *n* above two traits influences the evolution of conformist transmission. This is especially important since most prior models have assumed only two cultural traits. Exploring this also allows us to consider how broadly applicable our prior assumption of large *n* is.

The effect of trait number, *n*, in the spatial model is to increase the range of conditions favoring CT over polymorphic equilibria of CT and UT, and to increase the range of conditions favoring polymorphic equilibria of CT and UT *over* UT alone. Since the conditions favoring the fixation of IL are the same as those above, this leaves us with five additional equilibrium situations.

In the first of our five equilibrium situations, CT are a unique stable equilibrium if (21), (23) and

$$d < 1 - \frac{1-m}{1-ms} - \frac{m(1-s)^2}{(1-ms)^2} - \frac{(1-s)sm^2}{(n-1)(1-ms)^2} \tag{30}$$

are satisfied. This inequality reveals the relationship between *n* and *d*. As *n* increases the fourth term on the right-hand side of this inequality shrinks by a fraction $1/(n-1)$. Thus, as *n* gets large, this term goes to zero (reducing the condition back to (22)), which increases the maximum value of *d* under which CT are still favored over other strategies.

If *d* is larger than in condition (30) while (21) and (23) are still satisfied, then UT and CT will exist in a stable polymorphic equilibrium provided *d* is not too large. Inequality (31) sets the range for *d* at this equilibrium:

$$1 - \frac{1-m}{1-ms} - \frac{m(1-s)^2}{(1-ms)^2} - \frac{(1-s)sm^2}{(n-1)(1-ms)^2} < d < 1 - \frac{1-m(1-\theta)}{1-ms} \tag{31}$$

where

$$\theta = \left\{ m - s - \frac{(1-s)m}{n-1} + \sqrt{\left[m - s - \frac{(1-s)m}{n-1} \right]^2 + 4\frac{(1-s)m^2}{n-1}} \right\} / 2m \quad (32)$$

If both *c* and *d* are sufficiently large, UT are the third unique stable equilibrium. CT are prevented from invading if *d* exceeds the upper threshold set in inequality (31). IL are prevented from invading, and extinction is avoided if *c* and *r* exceed these thresholds:

$$c > m(1-\theta) \quad (33)$$

$$r > \frac{m(1-\theta)}{1-m(1-\theta)} \quad (34)$$

A fourth equilibrium situation arises in which combinations of IL and UT create a unique stable equilibrium. Under these circumstances, *c* must fall between these thresholds:

$$ms < c < \min[m(1-\theta), 1-(1-d)(1-ms)] \quad (35)$$

This condition guarantees that CT cannot invade while keeping individual learning sufficiently costly that IL cannot completely take over. To avoid extinction, *r* must be sufficiently large to satisfy (26).

The final situation is that the entire population goes extinct. This occurs if *r* is too small, and falls below the smallest of the threshold conditions for *r* (inequalities: (34), (26), and (23)). In these models, the intrinsic growth rate *r* only affects whether the entire population goes extinct and does not affect the evolution of conformity or the other strategies.

It is somewhat difficult to tell from these complicated expressions precisely how *n* influences the conditions favoring the evolution of different learning strategies. However, as we graphically show in Figure 3A and prove in Appendix A, increasing *n* above two substantially increases the conditions favoring CT. Figure 3A shows the stable strategies for *n* = 2, 4, 8, 16, and ∞. As *n* increases, the values of *m* favoring stable CT expand, while those favoring UT and combinations of UT and CT contract. The largest impact of *n* occurs in moving from two traits to four traits, with only a small change from eight to sixteen traits. Here, when CT are favored, the strongest form of conformist transmission is always favored ($a = \infty$). It is important to realize that here we have set $d = 0.05$. Had we set $d = 0$, all the bars would have been entirely green (all CT at maximum strength). Appendix A formally proves that increasing n decreases the size of the region for fixation in UT and increases the size of the region for fixation in CT.

Now we compare our spatial and temporal models. To obtain comparable results for the temporal case, we draw on the mixed strategy model. This provides us with the two extremes; when there are only two (recognizable) traits and when the number of traits is infinite. Figure 3 compares the impact of different values of n in our spatial and temporal models, using both the parameters used above in prior figures and the values of s, d and c that set an order of magnitude lower. Figures 3A and 3C show how increasing n increases the range of conditions dominated by conformist transmission at maximum strength. Figures 3B and 3D show the parameter ranges that favor either mixed strategies with both IL and CT or with both IL and UT. It is never the case in the temporal model that CT are favored at its maximum strength, though increasing n from two to infinity substantially increases the size of the regions that include some CT, especially when s is small (compare Figures 3B and 3D). This suggests, and results in Nakahashi (2007a) confirm, that increasing n in our temporal model expands the conditions favoring conformist biases in social learning.

Note that in Figures 3B and 3D $d = 0$, while in Figures 3A and 3C $d = 0.05$ and $d = 0.005$ (respectively), so this figure is biased against the evolution of CT in spatially varying environments. Consequently, we focus on the effects of increasing n in the different models, not on the size of the regions with CT. Above, we discussed the challenges of assuming $d > 0$ in the mixed strategy model, and note that if we assume $d = 0$ in the spatial model the importance of n cannot be observed since CT completely dominate for $n \geq 2$.

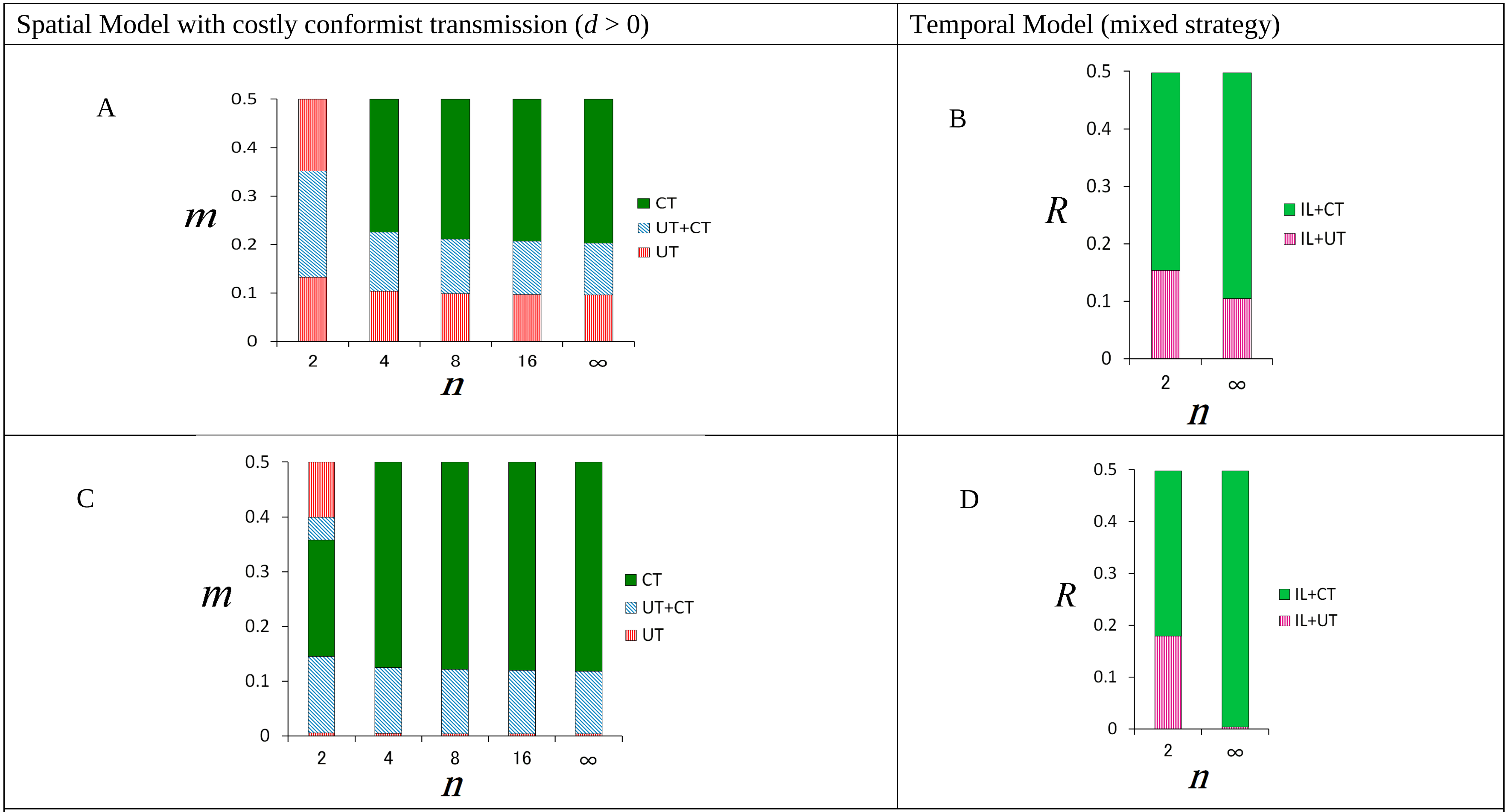


Figure 3. These plots illustrate the relative impact of different numbers of cultural traits on the learning strategies favored in spatially and temporally varying environments. For Figures 3A and 3B, the parameters are the same as those used above: $s = 0.5$, $c = 0.3$, $K = 100$, and $r = 0.5$, while for Figures 3C and 3D the parameters are $s = 0.05$, $c = 0.03$, $K = 100$, and $r = 0.5$. The lower panels allow us to observe the effect of n on conformist transmission when s is an order of magnitude smaller than used above. Figures 3A and 3C show the effect of the number of traits (sites) in the spatial model by comparing $n = 2, 4, 8,$ 16, and ∞, where $d = 0.05$ and $d = 0.005$, respectively. The regions are marked as in previous figures. For Figures 3A and 3C, CT have the strongest conformity bias. Realize that if we assume $d = 0$, as in Figures 3B and 3D, all the bars in Figures 3A and 3C would be green (all CT). Figures 3B and 3D, drawing on Models 2 and 3 of Nakahashi (2007a), shows the effect of the number of traits in a temporally changing environment for $n = 2$ and ∞. The "IL+CT" region marks the conditions where the favored mixed strategy deploys both individual learning and conformist transmission (with an intermediate strength).

In Figure 1A ($n = 2$), the dominance of UT at both low and high migration rates, with a mixture of UT and CT in the middle range, highlights an interesting feature of these evolutionary processes. When m is low (few migrants), UT get the adaptive trait almost as often as CT. Since CT pay a mortality cost for its conformist abilities, UT can dominate at low m. As m increases, CT non-migrants get the adaptive trait relatively more frequently than UT non-migrants, resulting in a polymorphic equilibrium. When m is high, many CT and UT are migrants to new sites. At new sites, CT never has the locally adaptive trait, and thus suffers both mortality costs s and d. Compared to CT, UT migrants are more likely to possess the locally adaptive trait for their new site (which is non-adaptive back in their home site). This effect is strongest when $n = 2$ because UT migrants who have adopted the locally non-adaptive trait in their home population always end up moving into a site in which their trait is now adaptive. CT migrants never end up in such a site. However, as n increases, UT's chances of ending up in a site where their behavior is locally adaptive plummets as $\frac{1}{n-1}$.

3.2.1. RELATIONS WITH PRIOR MODELS USING A HEURISTIC APPROACH

Both the spatial and temporal models indicate that increasing n above two substantially expands the conditions favoring the evolution of conformist transmission, though increasing n above about eight yields only small and diminishing effects (at least in the spatial model). This means that considering more than two traits is important for understanding the conditions favoring the evolution of conformist transmission. It also means that our above assumption of n being large provides a good approximation for a wide range of conditions.

To intuitively understand how larger values of n (above 2) empower conformist transmission, let's go back to the original formulation used by Boyd and Richerson (1985):

$$B(p) = p + Dp(1-p)(2p-1) \tag{36}$$

Here, $B(p)$ is the probability of a conformist learner acquiring a particular trait, whose frequency in the population is captured by p. D gives the strength of conformist transmission, which we will assume is 1 (its maximum) for this example. This was derived assuming two cultural traits exist (n = 2) and that individuals select three models each, at random, from that population, giving weight D to the most common variant in their small sample.

Now we compare two situations: the first with two traits ($n = 2$) and the second with many traits ($n > 2$). In both situations we assume that there is only one locally adaptive trait and assign it a frequency p. Our conformist learner (CT) selects three models at random from the population, and the probabilities for the trio possessing 0,1,2, or 3 of the locally adaptive traits are the same in both our n = 2 situation and our n > 2 situation: $(1-p)^3$, $3p(1-p)^2$, $3(1-p)p^2$, p^3. In the two trait situation, CT always imitate the locally adaptive trait when the number of models with adaptive trait is 2 or 3 but never imitates when only 0 or 1 of models has the adaptive trait. When n = 2, the probability of imitating the adaptive trait is $B = 3(1-p)p^2 + p^3 = p + p(1-p)(2p-1)$, so $B > p$ when $p > 1/2$. By contrast, in the situation with n > 2, CT always imitate the adaptive trait when 2 or 3 models display this trait, sometimes imitates it when 1 model displays it, and never imitates it when none of the three have it. That is, in this situation, even when the number of models with the adaptive trait is 1, the other two targets sometimes have *different* non-adaptive traits so that conformists still imitate the adaptive trait with probability 1/3. The probability that CT imitate the adaptive trait depends on the frequencies of the other non-adaptive traits. This probability, B, is largest when the frequencies of non-adaptive traits are the same (i.e., $(1-p)/(n-1)$) and smallest when the frequency of one non-adaptive trait is largest, almost $1-p$. When the frequencies of the non-adaptive traits are the same, the probability of imitating the locally adaptive trait is

$$\begin{aligned} B &= p(1-p)^2\left[1-(n-1)\left(\frac{1}{n-1}\right)^2\right] + 3(1-p)p^2 + p^3 \\ &= p\left[1+\frac{(1-p)(np-1)}{n-1}\right] \end{aligned} \tag{37}$$

Thus, $B > p$ when $p > 1/n$. When the frequency of one of the many non-adaptive traits is almost $1-p$, the probability of acquiring the adaptive trait is the same as in the two trait situation. In general:

$$p + p(1-p)(2p-1) < B \le p\left[1+\frac{(1-p)(np-1)}{n-1}\right] \qquad (38)$$

For UT, the probability of acquiring the adaptive trait is the same (p) in both the $n = 2$ and the $n > 2$ situations because the frequency of the adaptive trait is the same in both cases. So, CT can be favored over UT even when $1/n < p < 1/2$.

Figure 4 summarizes this heuristic analysis and indicates that increasing the number of cultural traits increases the strength of the selective forces favoring the evolution of conformist transmission, regardless of the particular expression used to capture the idea behind conformist transmission. Importantly, note that there are no explicit fitness costs or environmental variation in this heuristic approach.

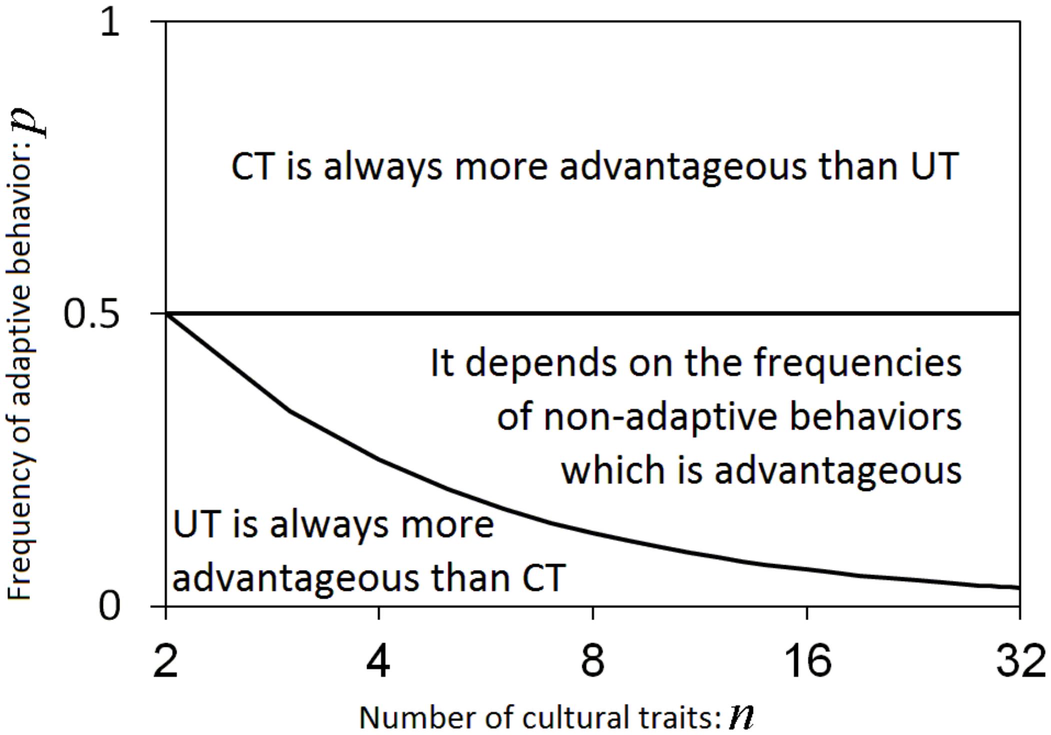


Figure 4. Illustration of our heuristic analysis of the effects of increasing the number of cultural traits on the relative advantage of CT vs. UT.

So far, we have made the simplifying assumption that n is both the number of sites and the number of cultural traits. Appendix A explores how our results change if we separate the number of sites from the number of traits. By assuming that the number of sites is large (infinite) and the number of traits is *n*, we show that the qualitative results do not change. The threshold values for the invasion of CT into a population of UT and for the stability of an pure CT equilibrium increase by a factor of $\frac{n}{n-1}$. As *n* increases, the ratio approaches 1, so the thresholds for *m* approach the results presented above. This indicates that as long as the number of sites is large, our conclusions are not substantially affected by matching the number of sites with the number of cultural traits.

The basic insights from this section will be important below in our discussion of how, even in the absence of spatial variability, learning and transmission errors can create a steady inflow of suboptimal cultural traits (increasing *n*) that mimics the inflow created by spatial variability and mixing. This means that these insights are likely important in considering situations involving both static and temporally varying environments, and especially in situations of cumulative cultural evolution in which transmission errors are likely to increase as trait complexity and diversity increases.

3.3. HOW DOES THE INCLUSION OF PAYOFF-BIAS SOCIAL LEARNING CHANGE THE PREVIOUS RESULTS?

While much work has examined the evolution of conformist learning strategies in competition with individual learning and unbiased or vertical transmission strategies, less work has examined whether conformist transmission can evolve in the presence of strategies that use the payoff differences among cultural traits in figuring out what to adopt (Kendal, et al., 2009). Now, we add payoff-biased cultural learning (PT) to our set of pure strategies and examine what happens in both spatially and temporally varying environments.

To the above baseline model we add the strategy PT, which copies the cultural trait with the highest payoff in the local population (the site) at a mortality cost *g*. We typically assume, $0 \le d < g < c < s < 1$. This assumption seems plausible, given that PT have more complicated task than CT, which involves assessing payoffs or at least relative payoff differences for the cultural traits present. There may be particular situations in which $d > g$; this will expand the range of conditions favoring PT.

Using the same notation as above for the baseline spatial model, we can write down the recursions for the frequency of PT. V_{ii} and V_{ij} represent the number of PTs at site *i* who possess the locally adaptive cultural trait and the number of PT who possess the trait that is adaptive at site *j*, respectively:

$$V_{ii}' = (1-g)(1-m)V_i b(N_i) \tag{39}$$

$$V_{ij}' = \frac{(1-g)(1-s)mV_j b(N_j)}{n-1} \tag{40}$$

The other recursions presented above are modified slightly to include the *V*'s. A full derivation can be found in Appendix A.

Given the potency of payoff-biased cultural learning in other contexts (Kendal, et al., 2009; R. McElreath, et al., 2008), our results are surprisingly stark. If the cost to PT is larger than that to CT (i.e., $g > d$), PT *never* evolve. That is, our findings presented above hold, unchanged (Figures 1A and 2A hold even if PT enters the fray). If both CT and PT suffer the same mortality costs ($d = g$), they are neutrally stable—both always learn the adaptive trait for their home site and suffer a cost when they migrate.

The temporal model gives quite different results. Here we focus on our pure strategy model and rely on a combination of analytical and numerical simulation results. We begin by presenting key findings from the available analytical results, and then combine these with simulations to generate a comparison with our spatial model. The derivation can be found in Appendix B.

Analytically, we show that IL are the stable equilibrium when

$$R = \frac{1}{\ell} > \frac{\ln(1-c)}{\ln(1-s)} \tag{41}$$

PT can invade IL when

$$R = \frac{1}{\ell} < \frac{\ln(1-c) - \ln(1-g)}{\ln(1-s)} \tag{42}$$

Assuming mutation maintains IL in the population at some low frequency, PT remain stable at high frequency in the population when

$$R = \frac{1}{\ell} > \frac{\ln(1-g)}{\ln(1-s)} \tag{43}$$

We could not analytically delineate the region where CT can exist, but numerical simulation suggests complex relationships with the parameters. Our simulations all indicate that CT are not very important in a temporally varying environment, especially when PT are in the mix. Logically, if PT suffer no additional learning cost, PT are favored over UT/CT. But if PT suffer a cost (g), UT/CT can invade a PT+IL because when the frequency of PT and IL are sufficiently large, UT can easily imitate the locally adaptive trait, so that the frequency of PT cannot exceed some value. Of course, the details should depend on g and d.

Figure 5 combines our analytical and simulation results for this temporal pure strategy model. It can be compared with Figure 2A, since our spatial model's results do not change with the addition of PT (assuming $g > d > 0$). On Figure 5, the lower curve represents the analytically-derived threshold of the IL equilibrium (41). The upper curve demarcates the threshold at which PT can exist at equilibrium (42), and the vertical line represents the threshold of an *almost* purely PT equilibrium (43).

For the temporal model, this combination of numerical and analytical findings suggests that five different regions exist in the temporal model. Two regions involve equilibria of pure strategies of either PT or IL. A third region permits combinations of UT and PT while a fourth region has combinations of IL and UT. The final region always includes IL, mixed with either UT or CT, or both. A comparison of Figures 5 and 2B reveal the dramatic impact of introducing PT into the mix of pure strategies, as PT dominate when both c and R are high and exists in a polymorphic equilibrium with UT when c is high and R is low (stable environments).

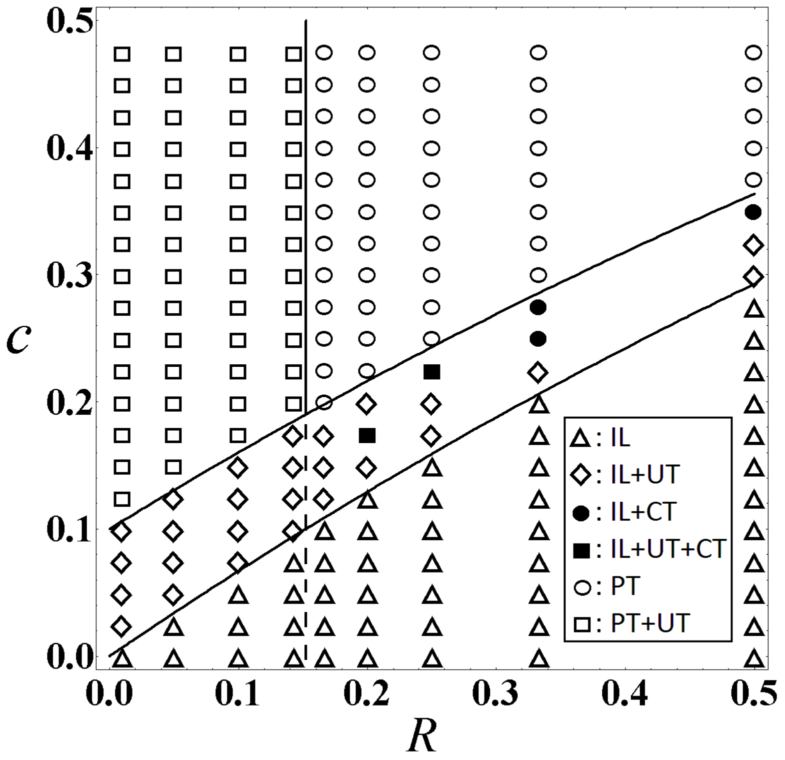
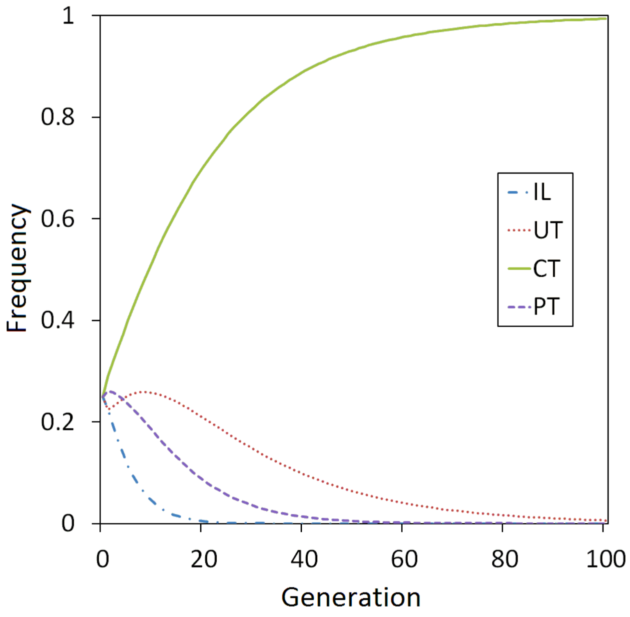


Figure 5. Equilibrium regions for our pure strategy temporal model in (*R*,*c*)-parameter space ($s = 0.5$, $a = 10$, $g = 0.1$, $n = \infty$ and $d = .05$). Numerically, we obtain the equilibrium frequencies of UT, CT, PT, and IL from several initial frequencies. The symbol "Δ" means that IL evolve to fixation. The points labeled "○" indicate that PT evolve to fixation. "□" indicates a polymorphic equilibrium of UT and PT. "◊" indicates a polymorphic equilibrium of IL and UT. "●" indicates a polymorphic equilibrium of IL and CT. "■" indicates a polymorphic equilibrium of IL, UT and CT. Filled markers indicate where CT exist at equilibrium. The lower curve represents the analytically-derived threshold of the IL equilibrium. The upper curve demarcates the threshold at which PT exist at equilibrium. The vertical line represents the threshold for a purely PT equilibrium.

To illustrate the dynamics of our models with PT, Figure 6 presents two simulation runs, one for our spatial model (Figure 6A) and the second for our temporal model (Figure 6B). Both models used these common parameters: $s = 0.5$, $c = 0.3$, $g = 0.1$, $d = 0$, $a = 10$, $K = 100$, and $r = 0.5$. Note that $a = 10$ is sufficiently strong to closely approximate $a = \infty$. For the spatial model we set the initial number of UT, CT, PT, and IL to be $X_{ij} = U_{ij} = V_{ij} = \frac{K}{4n}$ for all *i*, *j*, and $Z_i = K/4$. That is, the initial frequencies of UT, CT, PT, and IL are 0.25. We also set $n = 4$, so as not to give CT too much of an advantage in the spatial model and $m = 0.2$. For the temporal model we set the initial frequencies of UT, CT, PT, and IL to be 0.25, and set $\ell = 5$ (*R*=0.2) to parallel the setting *m* in our spatial model.

(A) Spatial



(B) Temporal

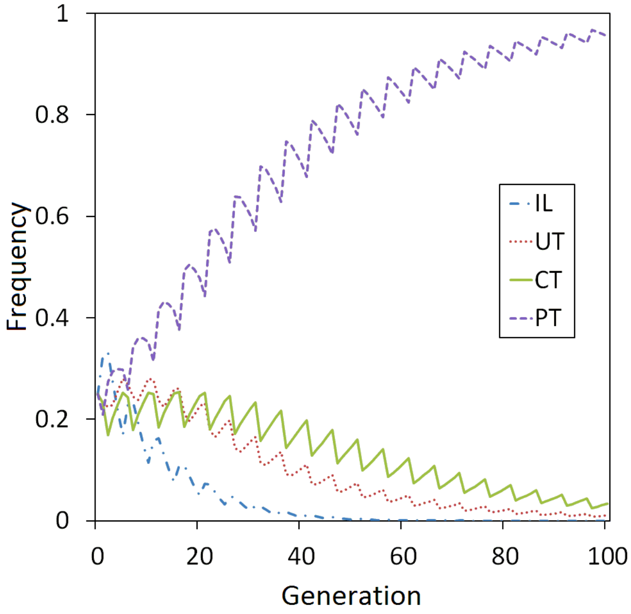


Figure 6. Illustrative evolutionary dynamics for our four different pure strategies in (A) spatially and (B) temporally varying environments for parameters $s = 0.5$, $c = 0.3$, $g = 0.1$, $d = 0$, and $a = 10$. We set the initial frequencies of UT, CT, PT, and IL be 0.25. In Figure 6A, $m = 0.2$, $K = 100$, and $r = 0.5$, and in Figure 6B, $\ell = 5$ ($R = 0.2$).

Both Figures 5 and 6 reveal a fairly stark contrast in how CT and PT respond to selection in spatially vs. temporally varying environments. If anything, adding PT to a mix of strategies accentuates the difference in the selective regimes created by spatially vs. temporally varying environments.

3.4. WHEN IL CANNOT LEARN AFTER MIGRATION OR ENVIRONMENTAL SHIFTS

Thus far our models have permitted an asymmetry among the four pure learning strategies by assuming that IL can immediately acquire the locally adaptive trait after migration, or after an environmental shift, but UT, CT and PT cannot learn new traits later in their life cycle. Here we present results from analyses in which we level the playing field so that IL cannot re-learn its adult trait after migration, or after an environmental shift. Like the social learners, IL are stuck with whatever it learned while growing up. Our results indicate that this assumption about IL has suppressed the success of CT in our spatially varying model while having no effect in our temporally varying model.

For the spatial model, Appendix A shows how we altered our baseline recursions to accommodate this change in IL's life cycle. We present only the results here. 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). If d is greater than zero but still smaller than g and c, IL and PT never evolve. That is, if $0 < d < g < c < s < 1$, there are only four stable outcomes: (1) all CT, (2) all UT, (3) mixtures of CT and UT, and (4) extinction. CT are the unique stable equilibrium if inequalities (31) and (23) hold, which guarantees that d is sufficiently small to prevent UT from invading, and r is sufficiently large to prevent extinction. These are two of the three conditions previously necessary for CT to remain stable in the model, when IL could learn after migration. The third condition is no longer necessary, since it was the required condition to hold IL at bay—IL's advantage obtained by being able to learn after migration. The second equilibrium situation also parallels the above case, and occurs when d falls into an intermediate range set by inequality (32), assuming that r is sufficiently large that (23) is not violated. In the third situation, UT emerge as the sole stable equilibrium if d exceeds the upper threshold marked by (32) and r is sufficiently large that (34) holds. Finally, if r fails to exceed either (23) or (34) extinction is the only long-term result.

The results are quite different in our pure strategy temporal model, detailed in Appendix B. This constraint on IL means that it cannot adapt immediately when the environment changes to obtain the locally adaptive trait. If IL cannot adapt, then neither can any of the social learning strategies (UT, PT and CT). Any constraint placed on IL in this temporal model that delays acquisition of the locally adaptive trait is subsequently imposed downstream on UT, PT, and CT since they ultimately rely on IL to figure out the locally adaptive trait. This means that there is no qualitative difference in the findings for this version of the temporal model compared to the case when IL can acquire the currently adaptive trait immediately after the environmental shift.

Overall, leveling the playing field to constrain IL expands the range of conditions favoring CT (and social learning more generally) in the spatial model, but does not change the conditions in the temporal model. Future work should examine what happens with all of our strategies can learn after migration but before selection.

4. DISCUSSION

In broadening, applying, and contextualizing our modeling results we focus on three areas. First, we discuss how the spatial variation we analyzed above, which powerfully favors the evolution of conformist transmission, represents but one source of low-level, non-adaptive, phenotypic trait variation. By non-adaptive trait variation we mean the presence of additional cultural variants (phenotypes) that are distinct to the learner, but not distinguishable from many other variants in terms of payoffs in the current environment. It is this non-adaptive variation, not spatial variation per se, that favors conformist transmission. Other factors, like learning errors or transmission noise will also produce a similarly persistent low volume inflow of non-adaptive variation. This means that even in the absence of spatial variability, conformist transmission can provide an adaptive advantage. Second, with empirical tests in mind, we develop a set of predictions from our formal results that are suitable to experimental testing. Third, although our models are focused on cultural traits applied in non-social contexts (e.g., which berries are edible), we consider the evolution in conformist transmission for acquiring traits or strategies for interacting in social situations. We argue, contrary to recent claims, that conformist transmission can still be adaptive in situations involving cooperation and punishment, and even in situations involving complementarities.

4.1. LEARNING ERROR AS SOURCE OF NON-ADAPTIVE VARIATION

The kind of non-adaptive phenotypic trait variation (cultural traits) created in our spatial model by a combination of environmental differences among sites and migration is merely one manifestation of a more general adaptive challenge with which successful social learning strategies must contend. Conformist transmission is frequently favored in these spatially varying environments because of its ability to successfully ignore, or avoid acquiring, the non-adaptive cultural traits brought in via migration from other sites. There are, however, a variety of processes that can generate a similar adaptive challenge to that created by spatial environmental variation, including errors or noise produced during learning and transmission (which we did not explicitly model).

Both mistakes in individual learning and a variety of errors in cultural transmission can create the same kind of low-level trait variation as does environmental variation and migration. Even in a completely static environment, errors and mistakes by both individual and social learners can inject a steady flow of non-adaptive cultural traits (increasing n and effectively m) into the local population. Individual learners may sometimes “goof-up” and “invent” something that is both new and non-adaptive. Social learners are likely to create a great variety of novel and less adaptive cultural traits, especially when acquiring more complex cultural traits, by (a) misperceiving what their models are doing, (b) making errors during the inferential steps of imitation, or (c) misremembering elements of cultural traits at some later time (J. Henrich & Boyd, 2002). Successful social learners need to figure out how to avoid this constant injection of non-adaptive variation. Conformist transmission provides one way to “squeeze out” this non-adaptive variation at (potentially) a low cost (see analogy with robust estimators in Boyd & Richerson, 1985: Chapter 7).

Of course, there are other ways to address this challenge. Payoff-biased strategies can avoid this non-adaptive variation, but these strategies are likely more costly in general, and potentially *quite a bit* more costly. And, if a learner’s payoff information is itself noisy, then conformist transmission can still be a superior strategy (J. Henrich & Boyd, 2002; R. McElreath, et al., 2008)—especially if the learner accurately perceives that he or she is likely to be less well informed about payoffs than many others in the local population. Other important strategies that can address this problem include blending mechanisms, which present a cousin of conformist biases, and the use of ethnic markers (Boyd & Richerson, 1985: Chapter 4; Boyd & Richerson, 1987; R. McElreath, et al., 2003).

It is also not the case that one need choose between payoff and conformist biases. Consider a social learning strategy that samples M models from the local population and estimates which N of these M models have the highest payoffs, or are the most successful. Our integrated learner then applies conformist learning to these N. When payoff differences are non-existent, or too noisy to be successfully differentiated, this algorithm reduces to pure conformist transmission. When payoff differences between traits can be recognized, but traits can be misperceived (the model is doing A, but learners misread it as B), this heuristic improves the accuracy of payoff-biased learning. This, and other more complex heuristics, can obtain the noise-reducing benefits of conformist transmission while still achieving the rapid adaptability and flexibility of payoff-biased learning (J. Henrich & Boyd, 2002).

We think this may be particularly important for understanding cumulative cultural evolution. As tools, for example, evolve culturally to become more complicated, errors in cultural transmission will increasingly introduce non-adaptive variation at the same time as payoff differences get harder to detect, or at least, to trace to particular differences in the tools, or their manufacture. After selectively sampling those with higher payoffs, copying the most common step or technique in the manufacture of a complicated tool can still allow learners to avoid copying non-adaptive variation.

4.2. PREDICTIONS

One of the primary goals of evolutionary modeling is to generate clear, precise, empirical predictions about the operation of psychological mechanisms, and specifically in this case about the cognitive mechanisms that underpin our cultural learning abilities. Here we outline four testable predictions, derived from our modeling efforts above:

1) Increasing the migration rates (m) among different environments (local populations) should increase individuals' reliance on conformist transmission, provided the costs of individual learning are not too low (Figure 2A). By contrast, increasing the rate of environmental fluctuations, should not have similarly sharp effects (see Figure 2B, focusing on increasing R).
2) Increasing n, the number of cultural traits, in the presence of low-level trait variation should increase individuals' reliance on conformist transmission. This is best illustrated in Figures 3A and 4. The degree of increase of reliance on conformist transmission should be more pronounced in moving from two traits to four traits with declining increases thereafter. See Figure 4 for a heuristic relationship. Both increasing m and n raises the rate of influx of local non-adaptive traits variation. Similar predictions should hold if learning errors or transmission noise is increased, even in stable environments.
3) Increasing the costs of individual learning (c) in an environment with persistent low-levels of trait variation should increase individuals' reliance on conformist transmission, provided that the levels of trait variation are not too low (Figure 2A).
4) Increasing the costs of non-adaptive behavior (s) should decrease individuals' reliance on conformist transmission and increase reliance on individual learning provided other costs (c, d, g) are constant.

These predictions can drive new field and experimental research on learning strategies, while informing existing work showing substantial heterogeneity in individual strategies (Efferson, Lalive, & Fehr, 2008; Efferson, Lalive, Richerson, McElreath, & Lubell, 2008; R. McElreath, et al., 2008).

4.3. SOCIAL INTERACTION, REPUTATION, PUNISHMENT AND COOPERATION

Like much prior work, our models analyze the evolution of different social learning strategies by assuming that the traits being learned are non-social, or at least that their payoffs do not depend on the frequency of other cultural traits in the local population. Skills or techniques related to food choice or tool manufacture might be most appropriate. Here we consider how using various learning strategies for acquiring social behavior might influence the evolution of conformist transmission, or at least the range of domains or types of problems to which it might be applied. We think our models are particularly useful in this regard, since as we argue below, the cultural evolution of social behavior may often create a kind of spatial variability much like what we have modeled.

To explore this we consider three kinds of social interactions in groups, those involving (1) coordination, (2) cooperation, and (3) complementarity (Erikksson, et al., 2007). In coordination games, conformist transmission is clearly an adaptive strategy as learners need to figure out what most people are doing among those whom they are most likely to interact with in the future. If everyone expects dowries to be paid along with daughters, then our learner adopts the practices associated with dowry. If bride prices or bride services are paid to the wife's family, then our learner adopts this strategy. The effectiveness of conformist transmission in these situation seems uncontroversial, though some have argued that payoff biases gets one the same answer. This is true, but payoff biased transmission requires learners to acquire and process payoff information, which is likely more costly relative to frequency information. The precise difference depends heavily on the costs of various sorts of information and its relative accuracy.

For many different coordination problems cultural evolution can generate a wide variety of solutions. The important thing in a coordination problem is to do what the majority does. This applies to such problems as driving on the left or the right, relying on a lunar or solar calendar, or closing the factory on a particular day of the week. If different groups wind up at different solutions, a kind of spatial variation can emerge that parallels what we have modeled above. The important thing for migrants is to acquire the most common behavior in whatever population they end up in, while non-migrants just need to make sure they don't mistakenly copy a new arrival (from a group with a different coordinated solution).

The second and more controversial kind of social interaction involves problems of cooperation, and in particular situations of larger-scale or *n*-person cooperation. In this kind of social interaction the group does best if everyone cooperates, but defecting individuals can free ride on the cooperation of others and receive higher payoffs than those who cooperate. Eriksson et al. (2007) have argued that learners ought not use conformist transmission in such a situation, and especially in acquiring the punishing strategies that are so often thought to stabilize human cooperation (J. Henrich, 2004).

We, however, think this view fails to recognize two different lines of theoretical work. First, there is a large body of modeling showing how a variety of mechanisms related to punishment, signaling, reputation, and reciprocity can effectively turn cooperative dilemmas into coordination situations (N. Henrich & Henrich, 2007). That is, formal cultural evolutionary models show how a multiplicity of stable social norms are created by a variety of mechanisms that generate self-reinforcing incentives (Boyd, Gintis, & Bowles, 2010; Gintis, Smith, & Bowles, 2001; J. Henrich & Boyd, 2001; Panchanathan & Boyd, 2004). The theoretical expectation from these models is that different social groups will culturally evolve different norms, since a wide variety of behaviors are stable once common. From the perspective of conformist transmission, the emergence of self-reinforcing social norms that vary among social groups creates a situation that parallels our spatial model. Different groups (sites) have different self-enforcing social norms, so migrants need to figure out what locally won't get one a bad reputation or punished, and non-migrants need to avoid learning from those who have made an error or are new arrivals to the group.

In a second line of theoretical work on cultural evolution, some approaches to larger scale cooperation have shown how including punishing strategies—while not leading to stable states as above—does slow the within-group decline of cooperation (when common) sufficiently that between group competition can favor higher levels of cooperation overall in a large structured population (Boyd, Gintis, Bowles, & Richerson, 2003; Boyd, Richerson, & Henrich, 2011). Guzman et al. (2007), building on this work using simulations, have explored the genetic evolution of payoff-biased and conformist transmission in a world in which the only problem individuals confront are those involving cooperation and punishment. This simulation suggests that natural selection will still, contrary to some suggestions (Hagen & Hammerstein, 2006), favor the evolution of substantial conformist transmission. This simulation has a complex interaction of cultural and genetic evolution in which conformist transmission keeps culturally transmitted punishing and cooperating strategies common in some groups, and those groups proliferate. When conformist-biased learners migrate to non-cooperative, non-punishing groups, they rapidly stop paying the costs of cooperation and punishment, thus reducing the selection against them. Conformist transmission, cooperation, and punishment appear to be a potent culture-gene coevolutionary package. Using a setup similar to Guzman et al., Henrich and Boyd (2001) have analytically shown that once conformist transmission evolves to even a relatively weak degree, it can give rise to the same kind of stable social norms described above. Either way one looks at it, the kind of spatial variability that favors conformist transmission is again created.

The third kind of social interaction involves complementary actions. In games of complementarity, individuals receive the highest payoffs when they bring skills, endowments, or know-how *different* from those with which they are interacting. Copying the currently most common trait here is not the road to higher payoffs for sure. However, an empirical look at human societies reveals how they are organized in such a way so as to mitigate this concern. In the smallest scale human societies, there is little division of labor or know-how, except by age and sex (Fried, 1967). While men, for example, vary in their skills, there are not obvious complementarities, and only mild amounts of occupational specialization exists (Johnson, 1995). There are, at times, ritual specialists but it is not clear why the existence of these relatively rare roles would inhibit the evolution of conformist transmission. As for sex and age, much prior theorizing on cultural learning mechanisms have suggested that learners use cues of both sex and age to hone their attention and learning efforts (J. Henrich & Gil-White, 2001), and that conformist transmission should interface with such cues (J. Henrich & McElreath, 2007). Men, for example, may be inclined to copy what most men do, while women should be inclined to copy what most women do. Men and women, then, supply complementary skills to the household. Thus, cultural evolution solves this problem of complementarity by partitioning individuals into sub-groups within which conformist transmission can operate effectively, and making the complementary interaction occur between subgroups. At the group-level, everyone merely needs to *coordinate* on the same cultural beliefs about the division of labor: for example, “males hunt and females gather” (which again, can be effectively acquired by conformist transmission).

In more complex human societies, occupational specializations of the kind associated with complementary interactions emerge principally in relations *among* social groups, with whole groups, castes, classes, or guilds specializing in one or another skill (Barth, 1965; Gadgil & Malhotra, 1983). Farmers grow up among farmers, herders among herders, merchants among merchants, and nobles among nobles. Exploring this, cultural evolutionary models of complementary interactions in structured populations have shown how payoff-biased transmission will spontaneously give rise to specializations by local or ethnic groups in specific skills (J. Henrich & Boyd, 2008). This means that payoff-biases—in the absence of conformist transmission—in situations of complementarity will spontaneously give rise to precisely the kind of spatial variation that favors the evolution of conformist transmission.

CONCLUSION

We have constructed, analyzed, and compared a series of formal models aimed at further elucidating the evolutionary foundations of different learning strategies. Our primary contribution is to clarify how spatial vs. temporal environmental variation differentially influences the evolution of three different social learning strategies and individual learning, as well as to examine how using more than two cultural traits affects the emergence of conformist transmission. Our models also examine the effects of different fitness costs for different strategies. Broadly speaking, we find that when individual learning is sufficiently costly, conformist transmission is favored in spatially varying environments while payoff-biased transmission is favored in temporally varying environments. With regard to the number of cultural traits, our results also show that by focusing on models with two cultural traits, much prior work has explored the circumstances least favorable to conformist transmission. A small increase in the number of cultural traits substantially expands the range of conditions favoring conformist transmission in both spatially and temporally varying environments. To facilitate empirical testing, we distilled our formal results into a series of predictions suited to experimentation.

We believe our findings have broader implications for the evolution of social learning strategies beyond spatially and temporally varying environments for two reasons. First, spatial variability is merely one way to generate a low-level but persistent influx of non-adaptive trait variation that favors conformist transmission, with learning errors being another obvious process that could generate this selective force. This means that conformist transmission could be similarly favored even in static or temporally varying environments with transmission noise or learning errors. Second, while the learning challenge in our model is non-social, we argue that social interactions involving coordination, cooperation, and complementarity can and do generate a kind of variation among groups that parallels our model’s spatial variation. This suggests that conformist transmission to acquire phenotypes for social interactions could also be favored for similar reasons.

Better understanding conformist transmission at both proximate and ultimate levels is important for a number of reasons. To begin, it may provide a readily available explanation for some of the apparent “clumpiness” observed in cultural variation (J. Henrich & Boyd, 1998), addressing the question of why local groups, for example, might vary on numerous cultural dimensions (Bell, Richerson, & McElreath, 2009). It may also help explain the group-level heritability found in the branching signals revealed in the application of phylogenetic methods to cultural datasets (Collard, Shennan, & Tehrani, 2006; Lipo, O'Brien, Collard, & Shennan, 2006), something which is difficult to explain if vertical cultural transmission is assumed. Third, because conformist transmission enhances the stability of local norms, it may help explain the impressive persistence of maladaptive behaviors, and potentially societal collapses (Whitehead & Richerson, 2009), in societies throughout the ethnographic and historical record (Durham, 1991; Edgerton, 1992). And finally, by reducing the variation within groups and assorting like phenotypes together, conformist transmission may increase the relative importance of the between-group components of cultural evolution relative to the within-group component. This suggests that cultural evolutionary processes might have quite a different character with regard to the evolution of social behavior when compared to vertically-transmitted genetic evolution (Bell, et al., 2009; Boyd & Richerson, 1985; Currie & Mace, 2009; J. Henrich & Boyd, 2001).

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TABLE OF CONTENT FOR THE APPENDICES

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:

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

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

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

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

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

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

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

where $1 \le i \le n$, $1 \le j \le n$, and $j \neq i$ 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,

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

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

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:

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

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

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

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

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

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

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

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

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

Since

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

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

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

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

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

Similarly, since

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

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

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

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 $\dfrac{1-c}{(1-d)(1-ms)}$. 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

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

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

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*.

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

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

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.

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

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

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

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

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

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

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

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 $X_i = \sum\nolimits_{j=1}^{n} X_{ij}$ $(1 \le i \le n)$ satisfy

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

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

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

yielding

$$c<ms \text{ and } \frac{c}{1-c}<r<\frac{2+c}{1-c}. \tag{A.22b}$$

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.6a) and (A.6b) and dividing the latter by the former, we find that θ is the larger and positive root of the quadratic equation

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

Solving Eq. (A.23) explicitly yields

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

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,

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

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

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.31*a*) and (A.31*b*), $b(\hat{N}) = \dfrac{1}{(1-d)(1-ms)}$, 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

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

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

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

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

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

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

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

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

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

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 $\dfrac{(1-d)(1-ms)}{1-m(1-\theta)}$, $\dfrac{(1-g)(1-ms)}{1-m(1-\theta)}$, and $\dfrac{(1-c)(1-ms)}{1-m(1-\theta)}$, respectively. Since $d<g<c$, the conditions for UT equilibrium to be stable are

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

and

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

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

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

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

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

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

From (A.41*a*) and (A.41*b*), $b(\hat{N})=\dfrac{1}{(1-d)(1-ms)}$, and from (A.41*c*) and (A.41*d*), $b(\hat{N})=\dfrac{1}{(1-c)(1-ms)}$. 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

$$P_j = \frac{b_j^a}{b_0^a + b_1^a + b_2^a + \cdots} \tag{B.1}$$

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,

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

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

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

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

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

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

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.