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CONDITIONS FOR THE EVOLUTION OF CONFORMIST TRANSMISSION

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SPATIAL VARIATION AND THE NUMBER OF CULTURAL TRAITS FAVORS CONFORMIST BIASES
OVER INDIVIDUAL LEARNING, UNBIASED TRANSMISSION AND PAYOFF-BIASED TRANSMISSION

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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 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.

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 much vibrant debate. 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 et al., 2009; McElreath et al., 2008; McElreath et al., 2003; McElreath & Strimling, 2008; Rendell et al., 2007; Schlag, 1998, 1999; Wakano & Aoki, 2006; Wakano et al., 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., Henrich & McElreath, 2007; Laland, 2004; 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 et al., n.d.; Harris & Corriveau, forthcoming; 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 (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 (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 et al., forthcoming).

57 Among the proposed social learning biases in this adaptive psychological suite is frequency-

58 dependent biased transmission (Boyd & Richerson, 1985: Chapter 7). Because there is useful

59 information stored implicitly in the relative frequency of different cultural traits, learners might

60 use the frequency of a trait in the population to more effectively select locally adaptive cultural

61 traits, or at least avoid adopting maladaptive traits. Conformist transmission is a sub-category of

62 frequency-dependent biased transmission in which individuals use the frequency of the most

63 common trait, in a personal sample or the local population, as a cue in figuring out which trait to

64 adopt, potentially integrating it with other information, such as personal experience, the relative

65 success of those with different traits, and self-similarity (Henrich & Henrich, 2007: Chapter 2).

66 Conformist biases are adaptive to the degree that they can help learners integrate information

67 gleaned from other partially informed members of their community, while allowing them

68 diminish the errors that inevitably creep into the cultural transmission pathways (Henrich &

69 Boyd, 2002). The basic logic underpinning conformist transmission is enshrined in the

70 Condorcet Jury Theorem. Central to defining and identifying conformist transmission is

71 recognizing that it requires a non-linear increase in the likelihood of adopting a trait with

72 increases in the frequency of that cultural trait. This distinguishes conformist biased strategies

73 from unbiased transmission, in which learners acquire a particular trait in proportion to that

74 trait's current frequency in the population (which, for example, occurs if learners copy a random

75 person in the population).

76 Boyd and Richerson's (1985) initial efforts suggested that conformist transmission could

77 outcompete unbiased transmission in a spatially variable environment. This model, however, was

78 limited because it did not consider (a) a cost for conformist transmission, (b) any individual

79 learning, (c) more than two traits/environments, or (d) temporally varying environments. To

80 address some of these limitations, Henrich and Boyd (1998) constructed a simulation model

81 involving a large mix of strategies involving combinations of individual learning, unbiased

82 transmission, and conformist transmission in which learners have to adapt to a spatially and

83 temporally varying environment. Later, Kameda and Nakanishi (2002) augmented Henrich and

84 Boyd's code to consider conditions under which individual learning was costly, and tested these

85 predictions in a laboratory experiment. These simulations were limited in considering only two

86 cultural traits and two different environments. Overall, this early work suggested that conformist

87   transmission would outcompete unbiased transmission under a wide range of conditions, though

88   not if the environment changed too frequently or individual learning was too inaccurate.

89   More recently, several authors have developed a combination of analytical and simulation work

90   on temporally varying environments that both confirm and challenge earlier conclusions

91   (Erikksson et al., 2007; Kendal, et al., 2009; McElreath, et al., 2008; Nakahashi, 2007a; Wakano

92   & Aoki, 2007). This subsequent work suggests that in temporally varying environments, both

93   unbiased and payoff-biased transmission can dominate or eliminate conformist transmission,

94   reducing the range of conditions in which we expect conformist transmission. Interestingly,

95   during roughly the same time period, work exploring the impact of spatially variable

96   environments on the evolution of social learning did not consider conformist transmission (Aoki,

97   2010; Aoki & Nakahashi, 2008). We return to the specifics of some of these models in our

98   discussion below, as we bring these two strands of modeling together.

99   While these prior efforts make important contributions to understanding the evolutionary-

100   theoretic hypotheses that should drive empirical inquiry, we think the focus on modeling (1) only

101   two (distinguishable) cultural traits, (2) temporally varying environments, and (3) error-free

102   cultural transmission has actually obscured some of the conditions most favorable to the

103   evolution of conformist transmission. Our goal here is twofold. First, we develop an n-trait ($n \geq$

104   2) model in a spatially varying environment to illustrate how these two elements influence the

105   evolution of conformist biased learning strategies vis-à-vis unbiased transmission, pay-off biased

106   transmission, and individual learning. While we do not explicitly model transmission error here,

107   we argue below that spatial mixing creates a selective environment similar to that produced by

108   transmission errors. Second, to most effectively illustrate the contrast between the effects of

109   temporal vs. spatial variation on favored learning strategies, we draw on and in some cases

110   further develop results from two parallel models that focus only on temporal variation.

111   To outline what is to come, we first present our baseline model of the evolution of social learning

112   strategies for n different cultural traits in a spatially varying environment, and we introduce the

113   two parallel models for temporally varying environments. We then present the baseline results

114   for the simplest cases. After this comparison, we incrementally add complexity to this baseline

115   case by (1) adding a fitness cost for using conformist transmission, (2) analyzing how the

116   number of cultural traits impacts the outcomes, (3) including payoff-biased learning strategies,

117 and (4) modifying the life cycle such that individual learners can only learn before migration to a
118 novel environment. Throughout the paper, we develop the models and present the results in the
119 main text, leaving the derivations themselves in the online supplemental materials. We have
120 done this in an effort to most effectively communicate with empirically-oriented evolutionary
121 researchers who might test these hypotheses about social learning. We close by carefully
122 itemizing the empirical predictions, and by relating our findings to the effects of transmission
123 error and the evolution of social behavior in contexts of cooperation, coordination, and
124 complementarity.

2. COMPARABLE SPATIAL AND TEMPORAL MODELS OF THE EVOLUTION OF CONFORMIST TRANSMISSION

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

2.1. THE BASELINE SPATIAL MODEL

141 In our structured population individuals may occupy any of n different sites in a spatially
142 heterogeneous world. Each site has a different environment with a specific corresponding
143 cultural trait (learnable phenotype) that is adaptive at that site. Thus, we distinguish n
144 traits/phenotypes, each of which is locally adapted to one particular environment but maladaptive

145   in the n-1 other environments. Traits that are maladaptive in all n environments are not

146   incorporated into the dynamics.

147   Individuals are of three genetically distinct types: social learners (linearly frequency-dependent,

148   UT), conformist biased social learners (non-linearly frequency-dependent, CT), and individual

149   learners (IL). Later, we add payoff-biased social learners (PT). UT acquire their cultural traits by

150   copying a random member of the previous or parental generation in the site they occupy (oblique

151   transmission: Cavalli-Sforza & Feldman (1981)). CT acquire their traits by copying the most

152   common behavior in the previous generation at their sites, but suffer a mortality cost d. IL

153   always acquire the trait that is adapted to the environment of the site they currently occupy, but

154   suffer a cost c due to mistakes made before the mature behavior is realized. The parameter s is

155   the selective cost of not acquiring the locally adaptive trait. We typically assume that:

156    $0 \leq d < c < s < 1$, meaning that individual learning is the most costly (c) strategy, followed by

157   conformist transmission (d), and then unbiased social learning (which costs zero). The parameter

158   s can be thought of as the fitness consequences of not figuring out what the locally adaptive thing

159   to do is. Traits with high s have relatively larger fitness consequence.

160   To track the numbers of individuals with each of our three different strategies, we use capitalized

161   Roman letters (X_{ij}, U_{ij}, Z_{ij}), indexed by i and j to respectively mark the current site in which the

162   individuals live, and the current phenotypic trait exhibited by those individuals. Let X_{ij} (

163    $1 \leq i \leq n$, $1 \leq j \leq n$) be the number of UT at site i that are adapted to the environment of site j.

164   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

165   and $X_i - X_{ii}$ possess one of the locally non-adaptive traits. Similarly, let U_{ij} be the number of

166   CT at site i that are adapted to the environment of site j. Then, at site i there are $U_i = \sum_{j=1}^{n} U_{ij}$

167   CT, of which U_{ii} possess the locally adaptive trait, and $U_i - U_{ii}$ possess one of the locally non-

168   adaptive traits. Let Z_i ($1 \leq i \leq n$) be the number of IL at site i. IL always acquire the trait that is

169   adapted to the environment of the site they occupy, but they suffer a cost due to mistakes made

170   before the mature phenotype is realized, from the efforts and accidents of trial and error learning.

171   The total population size at site i is $N_i = X_i + U_i + Z_i$. These numbers are enumerated at the adult

172   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:

$$b(N_i) = 1 + r(1 - N_i / K) \qquad (1)$$

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, 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

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

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

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

where

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

Here, a is the strength of conformist bias, and CT always imitate the most common behavior 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 $a > 1$).

194   The third and fourth events in the life cycle are (3) migration followed by (4) individual

195   learning for IL. For migration, a fixed fraction of the individuals at each site emigrate, yielding

196   constant forward migration rate. Here we use an island model with reciprocal migration between

197   all pairs of sites at rate $m/(n-1)$ $(0 < m \leq 1/2)$. After migration, IL acquire the cultural trait

198   suitable to their new (post-migration) environment, but they suffer a fixed mortality cost, c. Note

199   that this assumption gives IL an advantage over the social learning strategies, which do not

200   update their behavior after migration. Below, we show that this assumption is crucial for the

201   survival individual learning, and works against the success of CT.

202   The final stage in the life cycle is viability selections, in which all individuals with the locally

203   adaptive trait survive while only a fraction $1-s$ of individuals with the maladaptive trait survive.

204   ### 2.1.2. RECURSIONS FOR THE BASELINE SPATIAL MODEL

205   The above assumptions entail that the recursions be written as

206

$$X'_{ii} = (1-m)X_i b(N_i)\frac{X_{ii}+U_{ii}+Z_i}{N_i} + \frac{m}{n-1}\sum_{k\neq i}^{n} X_k b(N_k)\frac{X_{ki}+U_{ki}}{N_k},$$ (4)

207

$$X'_{ij} = (1-s)\left\{ \begin{array}{l} (1-m)X_i b(N_i)\dfrac{X_{ij}+U_{ij}}{N_i} + \dfrac{m}{n-1}X_j b(N_j)\dfrac{X_{jj}+U_{jj}+Z_j}{N_j} \\[2ex] + \dfrac{m}{n-1}\sum_{k\neq i,j}^{n} X_k b(N_k)\dfrac{X_{kj}+U_{kj}}{N_k} \end{array} \right\},$$ (5)

208

209

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

210

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

211

$$Z'_i = (1-c)\left\{ (1-m)Z_i b(N_i) + \frac{m}{n-1}\sum_{k\neq i}^{n} Z_k b(N_k) \right\},$$ (8)

212   where $1 \leq i \leq n$, $1 \leq j \leq n$, and $j \neq i$ in Eqs. (6) and (8).

2.2. THE BASELINE TEMPORAL MODELS

213

214   Now we develop a parallel model for a temporally varying environment using the same pure

215   strategies, and then discuss a similar model involving mixed strategies (from Nakahashi, 2007a).

216   Both temporally varying models assume that corresponding to each environmental state, there is

217   one adaptive cultural trait or behavioral phenotype (fitness $= 1$) and other traits are equally

218   maladaptive (fitness $= 1-s$; i.e. the cost of maladaptive behavior is s). The environment changes

219   every ℓ generations ($\ell \geq 1$), so that one post-change generation experiences a different

220   environmental state from the previous generation, and $\ell - 1$ subsequent generations experience

221   the same state as that post-change generation. That is, larger values of ℓ imply more

222   environmental stability. Here we use a fixed duration between environmental shifts in place of a

223   randomly varying environment to maintain mathematical tractability. Prior work suggests that

224   for our purposes this assumption produces comparable results (Nakahashi, 2007b).

225   For our pure strategy temporal model, as in the spatial model, we assume the existence of three

226   genetically encoded and asexually reproducing learning strategies: individual learners (IL),

227   unbiased social learners (UT), and conformist social learners (CT). Later we introduce pay-off

228   biased social learners (PT). IL always achieves the adaptive behavior via individual learning, but

229   suffer a fixed cost c. Social learners (UT, CT, and later PT) copy a behavior from the previous

230   generation. When the environment changes, social learners always copy a maladaptive (wrong)

231   behavior and only IL behaves correctly. UT acquires their trait by copying a random member of

232   the parental generation. Paralleling our spatial model, CT acquires the cultural trait j with

233   probability P_j, as in equation (4), where a gives the strength of conformist transmission:

234
$$P_j = \frac{b_j^a}{b_0^a + b_1^a + b_2^a + \cdots}$$
(9)

235   This means that the probability that CT imitates trait j is expressed by (10), where $b_0, b_1, b_2 \cdots$ are

236   the frequencies of individuals in the previous generation with the traits 0, 1, 2 $\cdots$ respectively.

237   CT suffers a mortality cost d.

238   All this means that the fitness of IL is $1-c$ while the fitnesses of UT and CT are,

239   respectively, 1 and $1-d$ if they have acquired the currently adaptive trait, and $1-s$ and

240 $(1-d)(1-s)$ if they have not acquired the adaptive trait. As above, we typically assume

241 $0 \leq d < c < s < 1$.

242 To extract as much analytical insight as possible from these two models (before moving to

243 simulations) we have allowed for some differences vis-à-vis our spatial model. Both of these

244 temporally varying models assume that the number of possible environmental states is infinite,

245 so that when the environment changes it never reverts to an earlier state (infinite environmental

246 states model). This makes these models most comparable to our spatial model when n in the

247 spatial model is large (infinite), though we show n does not have to be particular large before it

248 approximates the infinite solution.

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249 ### 2.2.1. RECURSIONS FOR THE BASELINE TEMPORAL MODEL WITH PURE STRATEGIES

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250 We set the initial condition such that the environment is in state 0 in generation 0 and all

251 members have behavior 0. In the next generation (generation 1) the environment changes to state

252 1 and behavior 1 becomes optimal. We suppose that behavior i is optimal in state i. In a

253 periodically changing environment, the environment changes every ℓ generations so that the

254 environment changes from state i to state $i+1$ between generation $i\ell$ and generation $i\ell +1$.

255 Suppose that the population is now in generation k and the environment is in state n. Let the

256 frequency of UT, CT, and IL after natural selection be $x^{(k)}$, $u^{(k)}$, and $z^{(k)}$ $(x^{(k)}+u^{(k)}+z^{(k)}=1)$,

257 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,

258
$$x^{(k)} = \frac{b_n^{(k-1)} + (1-s)(1-b_n^{(k-1)})}{T_{k-1}} x^{(k-1)} \qquad (10)$$

259
$$u^{(k)} = (1-d)\frac{P_n^{(k-1)} + (1-s)(1-P_n^{(k-1)})}{T_{k-1}} u^{(k-1)} \qquad (11)$$

260
$$z^{(k)} = \frac{1-c}{T_{k-1}} z^{(k-1)} \qquad (12)$$

261
$$b_n^{(k)} = \begin{cases} \dfrac{(1-c)z^{(k-1)}}{T_{k-1}} & \text{(post - change generations)} \\[2ex] \dfrac{b_n^{(k-1)}x^{(k-1)} + (1-d)P_n^{(k-1)}u^{(k-1)} + (1-c)z^{(k-1)}}{T_{k-1}} & \text{(other generations)} \end{cases}$$
(13)

262
$$b_m^{(k)} = (1-s)\dfrac{b_m^{(k-1)}x^{(k-1)} + (1-d)P_m^{(k-1)}u^{(k-1)}}{T_{k-1}} \quad (m < n)$$
(14)

263 where

264

265
$$T_k = \begin{cases} (1-s)x^{(k)} + (1-d)(1-s)u^{(k)} + (1-c)z^{(k)} & \text{(post - change generations)} \\[1ex] \{b_n^{(k)} + (1-s)(1-b_n^{(k)})\}x^{(k)} + (1-d)\{P_n^{(k)} + (1-s)(1-P_n^{(k)})\}u^{(k)} + (1-c)z^{(k)} & \text{(other generations)} \end{cases}$$
(15)

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

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

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

280 ## 3. COMPARISON OF RESULTS FOR BASELINE MODELS

281 Let's begin with the simplest cases. For the spatial model, we initially assume n, the number of

282 cultural traits (and sites), is large and that the cost of using conformist transmission is zero ($d =$

283 0). By assuming that n is large ($n \to \infty$) we can most directly compare our spatial and temporal

284 models. We also assume a is large such that CT always copies the most common trait from the

285 previous generation. As we go along, we show that in many case when CT is stable, only $a = \infty$

286 is stable against invasion by strategies with other values of a. Appendix A presents the formal

287 details and derivations.

288 Under these conditions, for different parameter combinations, the spatial model reveals only

289 three unique and stable equilibria: (1) all IL, (2) all CT, or (3) extinction. IL is the unique stable

290 equilibrium if

291 $$c < ms \tag{16}$$

292 and

293 $$\frac{c}{1-c} < r < \frac{2+c}{1-c} \tag{17}$$

294 The first condition means that the cost of IL must be low relative to the product of migration

295 rates and the cost of not acquiring the locally adaptive trait. The second condition specifies that

296 the intrinsic rate of population growth must fall into an intermediate range that depends only on

297 c.

298 There is a second set of conditions in which CT is a unique stable equilibrium if $c > ms$ (the

299 reverse of the above condition) and

300 $$r > \frac{ms}{1-ms} \tag{18}$$

301

302 This means that if c and r are sufficiently large (relative to the product of m and s), CT is the

303 unique stable equilibrium. Moreover, as shown in Appendix A, when CT is a stable equilibrium,

304 CT strategies with larger values of a can continually invade, so CT will go to it maximum value.

305 Thus, our assuming $a = \infty$ likely does little harm.

306   If neither of these two different equilibrium conditions hold, it means this population will go

307   extinct because its intrinsic rate of reproduction is too low for the conditions posed by the

308   combination of selection, migration, and the costs of individual learning.

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

310   when

311    $$R = \frac{1}{\ell} > \frac{\ln(1-c)}{\ln(1-s)} \tag{19}$$

312   This indicates that IL is favored when environments are unstable (R is large), individual learning

313   is cheap (c is small), and getting the locally adaptive traits is important (s is large). When this

314   condition does not hold, numerical simulations indicate that the population consists of a

315   fluctuating composition of IL, CT, and UT. Below, when we introduce payoff-biased social

316   learners (PT), we solve this model analytically. Appendix B supplies these derivations.

317   Figures 1A, 1B and 1C provide a comparison of our spatial and temporal models in the (m, c)-or

318   (R, c)-parameter space. We have set s rather high at 0.5, which biases the plots in favor of IL.

319   Despite this, Figure 1A shows that in a spatially varying environment, CT is always at its

320   maximum strength and is uniquely favored, except when individual learning is cheap and

321   migration rates are high. Figure 1B shows the results of our simulations superimposed over of

322   our analytically-derived line demarcating the stable region for IL. Figure 1C shows the analytical

323   results drawn from Nakahashi (2007a) using a mixed strategy approach. Viewing Figures 1B

324   and 1C side by side highlights the similarity between the pure and mixed strategy approaches,

325   and reveals that in both approaches CT is generally only favored for intermediate values of c. If

326   the environment is sufficiently stable and the costs of individual learning are high, a mixture of

327   UT and IL emerges. The mixed strategy model (Figure 1C) indicates that CT does not evolve to

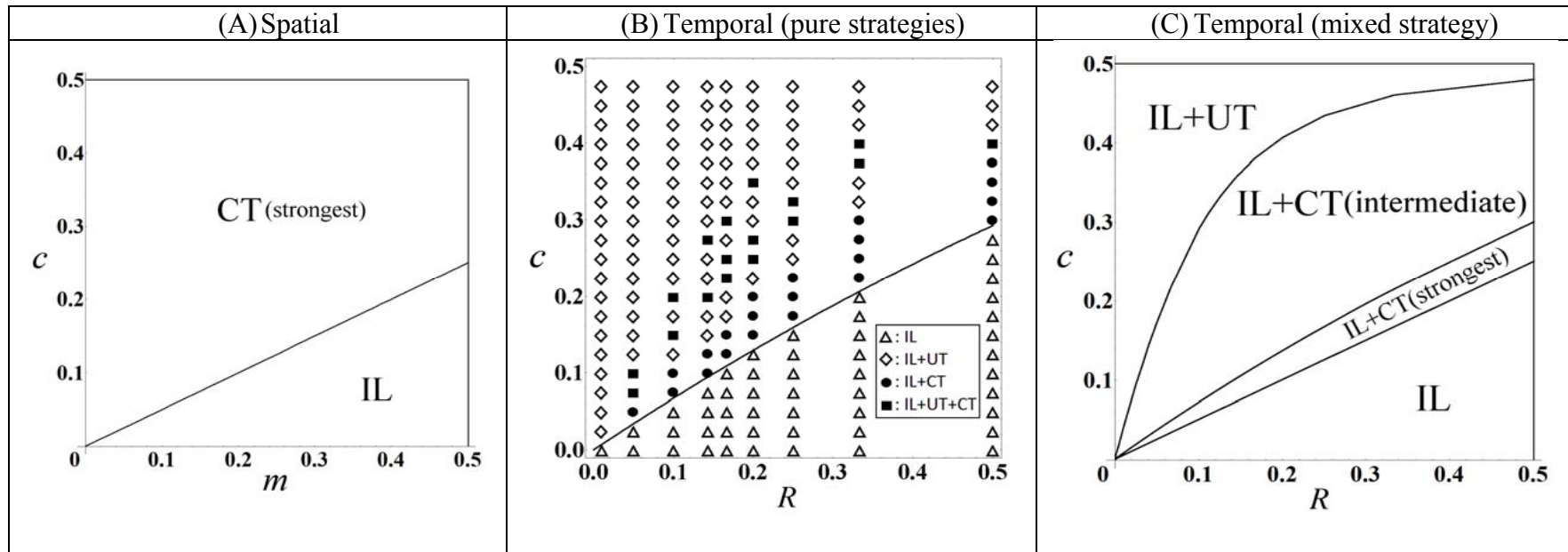328   its maximum strength, except in the narrow band shown.

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 is a unique stable equilibrium while in the "CT (strongest)" region CT is a unique stable equilibrium in which CT has the strongest conformity bias (where $a = \infty$). (B) Numerical simulation of equilibrium pure strategies in a temporally changing environment ($0 < R < \frac{1}{2}$, $0 < c < s$, $a = 10$). The "Δ" markers indicate that IL is 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 exists. 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 is 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.

329   3.1. MAKING CONFORMIST TRANSMISSION COSTLY

330   The above results assume that using conformist transmission is costless and, in particular, no

331   more costly than using unbiased social learning. Now we assume that using conformist

332   transmission imposes a mortality cost, $d > 0$, by assuming that $0 < d < c < s < 1$.

333   For the spatial model we now have five different unique stable equilibria for different parameter

334   values. For IL, nothing changes. If (17) and (18) hold, IL is the unique stable equilibrium. This

335   occurs when the costs of individual learning (c) are sufficiently small and r falls into an

336   intermediate range.

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

338        $$d < 1 - \frac{1-c}{1-ms} \tag{20}$$

339        $$d < 1 - \frac{1-m}{1-ms} - \frac{m(1-s)^2}{(1-ms)^2} \tag{21}$$

340        $$r > \frac{1-(1-d)(1-ms)}{(1-d)(1-ms)} \tag{22}$$

341   The first two conditions set thresholds for the costs of conformist transmission. The first

342   condition (21) guarantees that CT outcompete IL, which means the maximum value of d depends

343   on c and the product of m and s. The more costly individual learning is, the larger the range of

344   conditions favoring CT. The product of m and s captures the penalty suffered by migrating CTs

345   when they first arrive in a new site. The second threshold for d (22) depends only on m and s,

346   and gives the conditions for outcompeting UT. Here larger values of both m and s raise the

347   threshold for d: when d is below this CT outcompetes UT. Condition (23) merely guarantees that

348   population reproduces sufficiently rapidly to avoid extinction.

349   In the third regime, assuming (21) and (23) from above are satisfied (so, no IL and no

350   extinction), a polymorphic stable equilibrium of UT and CT exist when the cost of conformist

351   transmission falls into this range:

352        $$1 - \frac{1-m}{1-ms} - \frac{m(1-s)^2}{(1-ms)^2} < d < 1 - \frac{1-m}{1-ms} \tag{23}$$

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

354          $$ms < c < \min[m, 1 - (1 - d)(1 - ms)] \qquad (24)$$

355   as long as

356          $$r > \frac{c}{1-c} \qquad (25)$$

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

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

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

360          $$c > m \qquad (28)$$

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

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

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

368   Figure 2 compares our analytical results for the spatial model with our simulations of the
369   temporal model for the case when $d = 0.05$ (otherwise using the same parameters as in Figure
370   1). For the spatial case, adding costs to CT means that (1) when mixing rates are sufficiently low,
371   UT can be a unique stable equilibrium, (2) when mixing rates are intermediate, UT can coexist
372   with CT, and (3) a narrow region of polymorphic equilibria of UT and IL separate stable regions
373   of UT, CT, or mixes of CT and UT, from those with pure stable IL. By contrast, in the temporal
374   model, CT is only found in mixtures with IL or sometimes with both IL and UT, and this region
375   is limited to a rather narrow band. By comparing Figure 2B with Figure 1B we see that
376   occurrences of CT seem even sparser, and limited to an even narrow band of the (R, c)-parameter
377   space.

378   For the mixed strategy temporal model, the outcome depends on how the relationship of d with

379   the strength of conformist transmission (a) is modeled. If we express d as a function of a, $d(a)$,

380   and set $d(1) = 0$ to match the pure strategy model (UT is costless), then we can show that if the

381   derivative of d at $a=1$ is greater than zero, $d'(1) > 0$, then the stable regions of IL and UT in

382   Figure 1C expand. Since social learners must investigate the frequencies of cultural traits when

383    $a>1$ and this is probably costly, assuming $d'(1) > 0$ is defensible. This analysis indicates that

384   the findings from our two temporally models are at least qualitatively consistent.

385   Overall, making conformist transmission costly relative to unbiased transmission does not

386   qualitatively alter the results from our simplest models (Figure 1). In the spatial model, assuming

387   even only moderate amounts of mixing, CT always exists as long as individual learning is

388   sufficiently costly. Within this parameter range: the more mixing, the more CT is favored. By

389   contrast, in the models with temporally varying environments, CT is favored in an even narrower

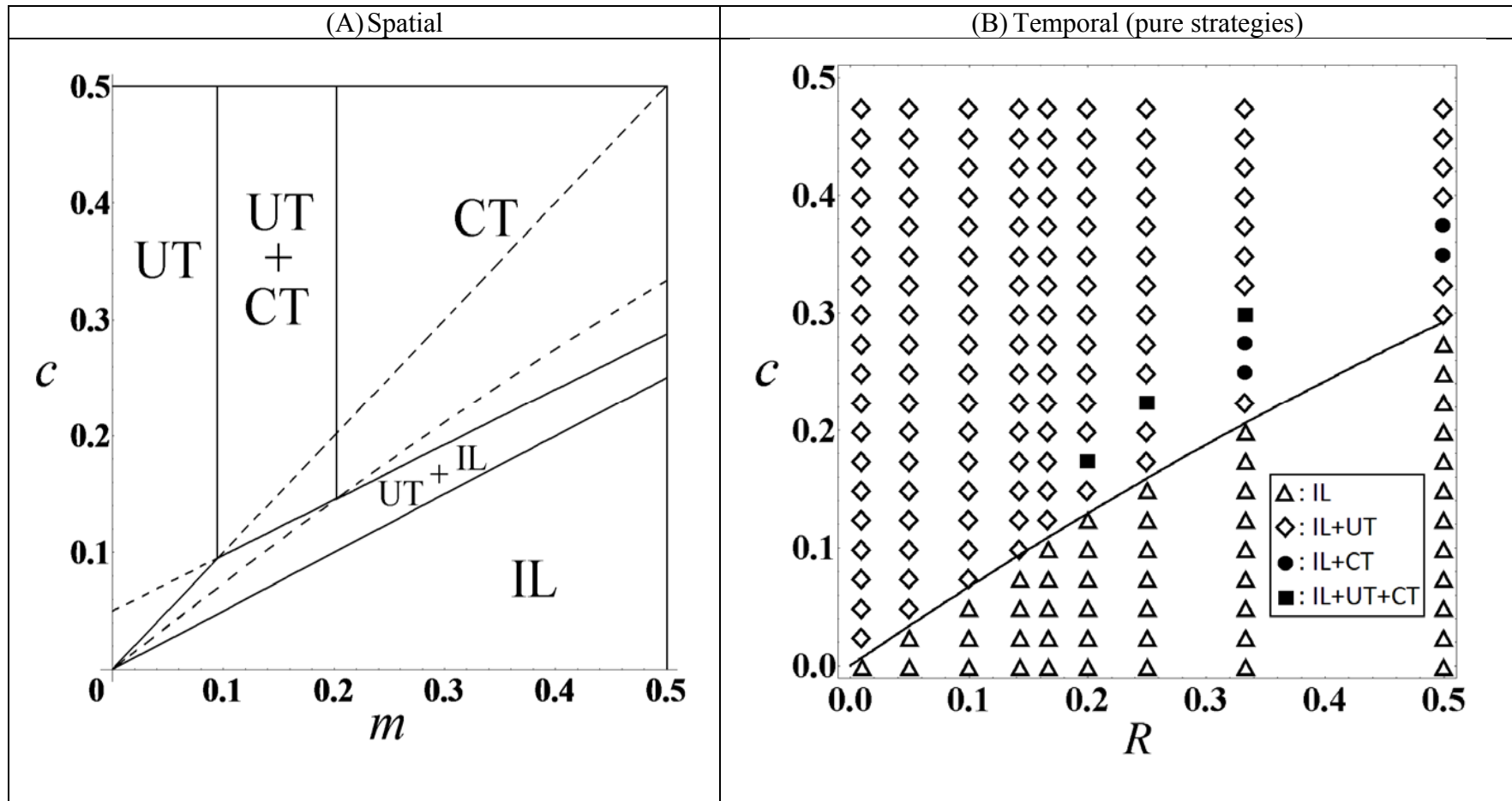390   band of parameters than in the earlier models.

391

Figure 2. Comparable plots in the (m,c)- and (R, c)-parameter space for spatially and temporally varying environments when CT 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 $0 < c < s$). The region "IL" implies that all organisms become individual learners (IL equilibrium), the region "CT" implies that all organisms become social learners with the strongest conformity bias (CT equilibrium), the region "UT+IL" implies a polymorphic equilibrium of unbiased social learners and individual learners, and the region "UT+CT" implies a polymorphic equilibrium of unbiased social learners and conformist social learners. (B) Numerical simulation of equilibrium pure strategies in a temporally changing environment ($0 < R < \frac{1}{2}$, $0 < c < s$, $a = 10$). The points "Δ" imply that all organisms become individual learners; the "◊" imply a polymorphic equilibrium of individual learners and social learner with unbiased transmission; the "●" imply a polymorphic equilibrium of individual learners and social learner with conformist transmission, and the "■" imply 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 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 ($n \rightarrow \infty$). 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. Let's begin by defining θ:

$$\theta = \left\{ m - s - \frac{(1-s)m}{n-1} + \sqrt{\left[m - s - \frac{(1-s)m}{n-1} \right]^2 + 4\frac{(1-s)m^2}{n-1}} \right\} / 2m \tag{30}$$

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

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

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 is still favored over other strategies.

If d is larger than in condition (31) 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 (32) sets the range for d at this equilibrium:

416 $$1 - \frac{1-m}{1-ms} - \frac{m(1-s)^2}{(1-ms)^2} - \frac{(1-s)sm^2}{(n-1)(1-ms)^2} < d < 1 - \frac{1-m(1-\theta)}{1-ms} \tag{32}$$

417 If both c and d are sufficiently large, UT is the third unique stable equilibrium. CT is prevented

418 from invading if d exceeds the upper threshold set in inequality (32). IL is prevented from

419 invading, and extinction is avoided if c and r exceed these thresholds:

420 $$c > m(1 - \theta) \tag{33}$$

421 $$r > \frac{m(1-\theta)}{1-m(1-\theta)} \tag{34}$$

422 A fourth equilibrium situation arises in which combinations of IL and UT create a unique stable

423 equilibrium. Under these circumstances, c must fall between these thresholds:

424 $$ms < c < \min\left[m(1 - \theta), 1 - (1 - d)(1 - ms)\right] \tag{35}$$

425 This condition guarantees that CT cannot invade while keeping IL sufficiently costly that IL

426 cannot completely take over. To avoid extinction r must be sufficiently large to satisfy (26).

427 The final situation is that the entire population goes extinct. This occurs if r is too small, and falls

428 below the smallest of the threshold conditions for r (inequalities: (33), (26), and (23)).

429 It is somewhat difficult to tell from these complicated expressions precisely how n influences the

430 conditions favoring the evolution of different learning strategies. However, as we graphically

431 show in Figure 3A and prove in Appendix A, increasing n above two substantially increases the

432 conditions favoring CT. For $n = 2, 4, 8, 16$, and ∞, Figure 3A shows the stable strategies. As n

433 increases, the values of m favoring stable CT expand, while those favoring UT and combinations

434 of UT and CT contract. The largest impact of n occurs in moving from two traits to four traits,

435 with only a small change from eight to sixteen traits. Here, when CT is favored, the strongest

436 form of conformist transmission is always favored ($a = \infty$). It is important to realize that here we

437 have set $d = 0.05$. Had we set $d = 0$, all the bars would have been entirely green (all CT at

438 maximum strength). Appendix A formally proves that increasing n decreases the size of the

439 region for fixation in UT and increases the size of the region for fixation in CT.

440 Now we compare our spatial and temporal models. To obtain comparable results for the temporal

441 case, we draw on the mixed strategy model. This provides us with the two extremes; when there

442   are only two (recognizable) traits and when the number of traits is infinite. Figure 3 compares the

443   impact of different values of n in our spatial and temporal models, using both the parameters

444   used above in prior figures and with the values of s, d and c set an order of magnitude lower.

445   Figures 3A and 3C show how increasing n increases the range of conditions dominated by

446   conformist transmission at maximum strength, with much of the effect occurring in moving from

447   two traits to four. Figures 3B and 3D show the parameter ranges that favor either mixed

448   strategies with both IL and CT or with both IL and UT. It is never the case in the temporal model

449   that CT is favored at its maximum strength, though increasing n from two to infinity

450   substantially increases the size of the regions that include some degree of CT, especially when s

451   is small (compare Figures 3B and 3D). This suggests, and results in Nakahashi (2007a) confirm,

452   that increasing n expands the conditions favoring conformist biases in social learning.

453   Note that in Figures 3B and 3D $d = 0$, while in Figures 3A and 3C $d = 0.05$ and $d = 0.005$

454   (respectively), so this figure is biased against the evolution of CT in spatially varying

455   environments. Consequently, we focus on the effects of increasing n in the different models, not

456   on the size of the regions with CT. Above, we discussed the challenges of assuming $d > 0$ in the

457   mixed strategy model, and note that if we assume $d = 0$ in the spatial model the importance of n

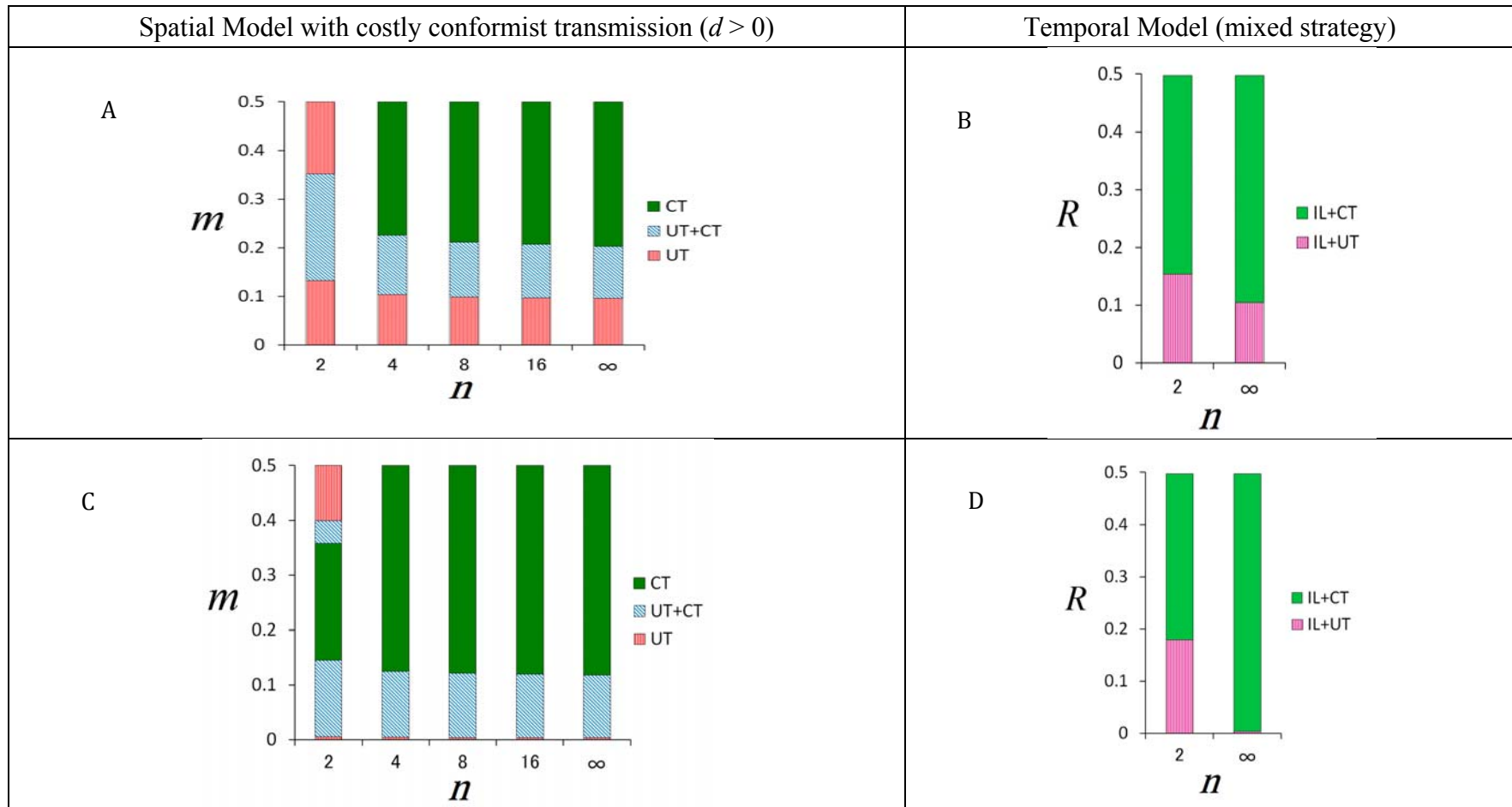458   cannot be observed since CT completely dominates for $n \geq 2$.

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 has 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).

459 ### 3.2.1. RELATIONS WITH PRIOR MODELS USING A HEURISTIC APPROACH

460 Both the spatial and temporal models indicate that increasing n above two substantially expands

461 the conditions favoring the evolution of conformist transmission, though increasing n above

462 about eight yields only small and diminishing effects (at least in the spatial model). This means

463 that considering more than two traits is important for understanding the conditions favoring the

464 evolution of conformist transmission. It also means that our above assumption of n being large

465 provides a good approximation for a wide range of conditions.

466 To intuitively understand how larger values of n (above 2) empower conformist transmission,

467 let's go back to the original formulation used by Boyd and Richerson (1985):

468 $$B(p) = p + Dp(1-p)(2p-1) \tag{36}$$

469 Here, $B(p)$ is the probability of a conformist learner acquiring a particular trait, whose frequency

470 in the population is captured by p. D gives the strength of conformist transmission, which we

471 will assume is 1 (its maximum) for this example. This was derived assuming two cultural traits

472 exist ($n = 2$) and that individuals select three models each, at random, from that population,

473 giving weight D to the most common variant in their small sample.

474 Now we compare two situations: the first with two behaviors ($n = 2$) and the second with many

475 behaviors ($n > 2$). In both situations we assume that there is only one locally adaptive behavior

476 and assign it a frequency p. Our conformist learner (CT) selects three models at random from the

477 population, and the probabilities for the trio possessing $0, 1, 2,$ or 3 of the locally adaptive traits

478 are the same in both our $n = 2$ situation and our $n > 2$ situation: (

479 $(1-p)^3, 3p(1-p)^2, 3(1-p)p^2, p^3$). In the two trait situation, CT always imitates the locally

480 adaptive (hereafter "correct") trait when the number of models with correct behavior is 2 or 3 but

481 never imitates when only 0 or 1 of models has the correct behavior. When $n = 2$, the probability

482 of imitating the correct behavior is $B = 3(1-p)p^2 + p^3 = p + p(1-p)(2p-1)$, so $B > p$ when

483 $p > 1/2$). In contrast, in the situation with $n > 2$, CT always imitates the correct trait when 2 or 3

484 models display this trait, sometimes imitates it when 1 model displays it, and never imitates it

485 when none of the three have it. That is, in this situation, even when the number of models with

486 the correct trait is 1, the other two targets sometimes have *different* non-adaptive traits so that

487 conformists can still imitate correct trait with probability 1/3. The probability that CT imitates

488 correct trait depends on the frequencies of the other non-adaptive traits. This probability, B, is

489 largest when the frequencies of non-adaptive traits are the same (i.e., $(1-p)/(n-1)$) and

490 smallest when the frequency of one non-adaptive trait is largest, almost $1-p$. When the

491 frequencies of the non-adaptive traits are the same, the probability of imitating the locally

492 adaptive behavior is

493
$$\begin{aligned} B &= p(1-p)^2\left[1-(n-1)\left(\frac{1}{n-1}\right)^2\right]+3(1-p)p^2+p^3 \\ &= p\left[1+\frac{(1-p)(np-1)}{n-1}\right] \end{aligned}$$
(37)

494 Thus, $B > p$ when $p > 1/n$. When the frequency of one of the many non-adaptive traits is almost

495 $1-p$, the probability of acquiring the correct behavior is the same as in the two trait situation. In

496 general:

497
$$p+p(1-p)(2p-1) < B \le p\left[1+\frac{(1-p)(np-1)}{n-1}\right]$$
(38)

498 By contrast, the probability that UT imitates correct behavior is the same (p) in both the $n=2$

499 and the $n>2$ situation because the frequency of correct behavior is the same. So, CT can be

500 more advantageous than UT even when $1/n < p < 1/2$.

501 Figure 4 summarizes this heuristic analysis and indicates that increasing the number of cultural

502 traits increases the strength of the selective forces favoring the evolution of conformist

503 transmission, regardless of the particular expression used to capture the idea behind conformist
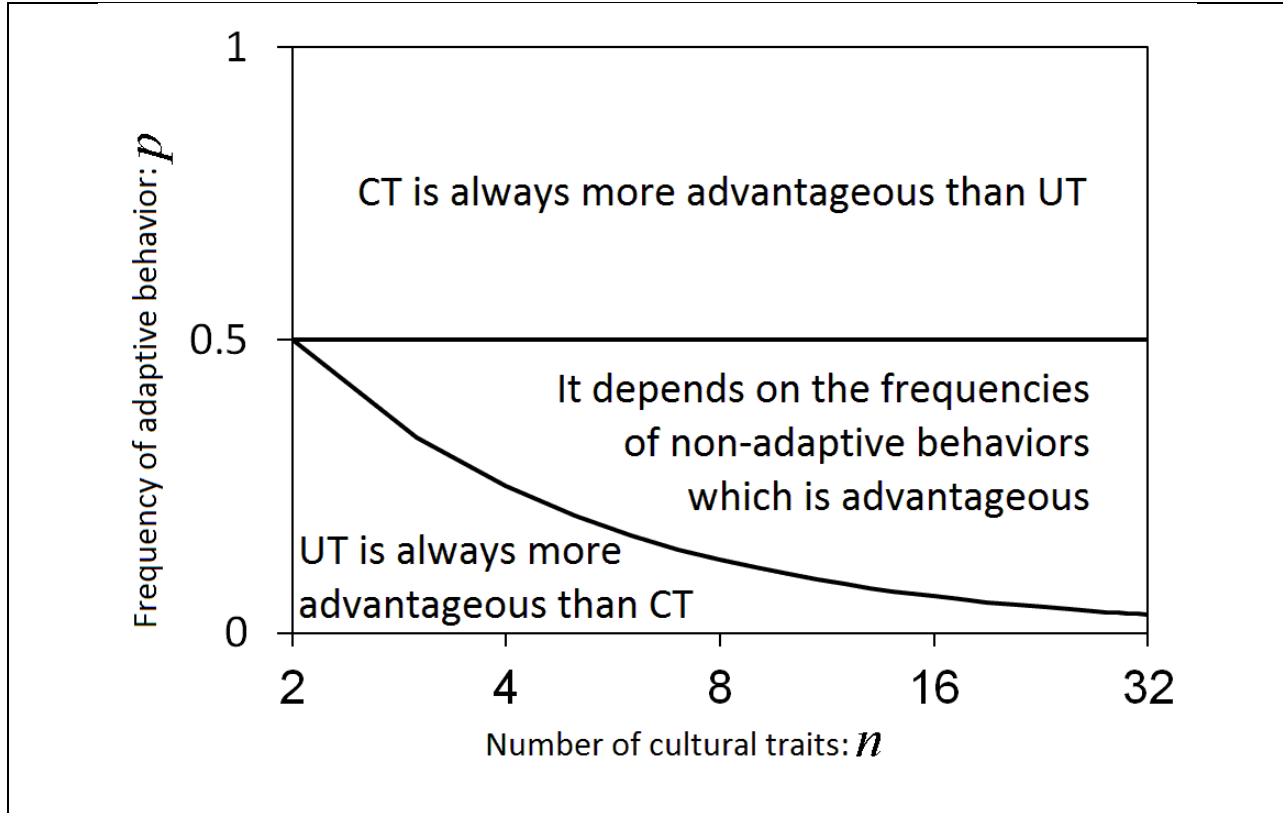
504 transmission.

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.

505

506   So far, we have made the simplifying assumption that n is both the number of sites and the

507   number of cultural traits. Appendix A explores how our results change if we separate the number

508   of sites from the number of traits. By assuming that the number of sites is large (infinite) and the

509   number of traits is n, we show that the qualitative results do not change. The threshold values for

510   the invasion of CT into a population of UT and for the stability of a pure CT equilibrium increase

511   by a factor of $\frac{n}{n-1}$. As n increases, the ratio approaches 1, so the thresholds for m approach the

512   results presented above. This indicates that as long as the number of sites is large, our

513   conclusions are not substantially affected by matching the number of sites with the number of

514   cultural traits.

515   This basic insights from this section will be important below in our discussion of how, even in

516   the absence of spatial variability, learning and transmission errors can create a steady inflow of

517   suboptimal cultural traits (increasing n) that mimics the inflow created by spatial variability and

518   mixing. This means that these insights are likely important in considering situations involving

519 both static and temporally varying environments, and especially in situations of cumulative

520 cultural evolution in which transmission errors are likely to increase as trait complexity

521 increases.

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

THE PREVIOUS RESULTS?

524 While much work has examined the evolution of conformist learning strategies in competition

525 with individual learning and unbiased or vertical transmission strategies, less work has examined

526 whether conformist transmission can evolve in the presence of strategies that use the payoff

527 differences among cultural traits in figuring out what to adopt (Kendal, et al., 2009). Now we add

528 payoff-biased cultural learning (PT) to our set of pure strategies and examine what happens in

529 both spatially and temporally varying environments.

530 To the above baseline model we add the strategy PT, which copies the cultural trait with the

531 highest payoff in the local population (the site) at a mortality cost g. We typically assume,

532 $0 \leq d < g < c < s < 1$. This assumption seems plausible, given that PT has a more complicated

533 task than CT, which involves assessing payoffs or at least relative payoff differences for the

534 cultural traits present.

535 Using the same notation as above for the baseline spatial model, we can write down the

536 recursions for the frequency of PT. V_{ii} and V_{ij} represent the number of PTs at site i who possess

537 the locally adaptive cultural trait and the number of PTs who possess the trait that is adaptive at

538 site j, respectively:

539 $$V_{ii}' = (1-g)(1-m)V_i b(N_i)$$

(39)

540 $$V_{ij}' = \frac{(1-g)(1-s)mV_j b(N_j)}{n-1}$$

(40)

541 The other recursions presented above are modified slightly to include the V's. A full derivation

542 can be found in Appendix A.

543   Given the potency of payoff-biased cultural learning in other contexts (Kendal, et al.,

544   2009; McElreath, et al., 2008), these results are surprising stark. If the cost of PT is larger than

545   that of CT (i.e., $g > d$), PT *never* evolves. That is, our findings presented above hold, unchanged

546   (Figures 1A and 2A hold even if PT enters the fray). If both CT and PT suffer no additional

547   learning cost, they are neutrally stable—both always learn the correct behavior for their home

548   site and suffer a cost when they migrate.

549   The temporal model gives quite different results. Here we focus on our pure strategy model and

550   rely on a combination of analytical and numerical simulation results. We begin by presenting key

551   findings from the available analytical results, and then combine these with simulations to

552   generate a comparison with our spatial model. The derivation can be found in Appendix B.

553   Analytically, we show that IL is the stable equilibrium when

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

(41)

555   PT can invade IL when

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

(42)

557   Assuming mutation maintains IL in the population at some low frequency, PT remains stable at

558   high frequency in the population when

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

(43)

560   We could not analytically delineate the region where CT can exist, but numerical simulation

561   suggests complex relationships with the parameters. Our simulations all indicate that CT

562   strategies are not very important in a temporally varying environment, especially when PT is in

563   the mix. Logically, if PT suffers no additional learning cost, PT is more advantageous than

564   UT/CT. But if PT suffers a cost (g), UT/CT can invade a PT+IL population because when the

565   frequency of PT and IL is sufficiently large, UT can easily imitate the locally adaptive trait, so

566   that the frequency of PT cannot exceed some value. Of course, the details should depend on g

567   and d.

568   Figure 5 combines our analytical and simulation results for this temporal pure strategy model. It

569   can be compared with Figure 2A, since our spatial model's results do not change with the

570   addition of PT (assuming $g > d > 0$). On Figure 5 the lower curve represents the analytically-

571   derived threshold of the IL equilibrium (41). The upper curve demarcates the threshold at which

572   PT can exist at equilibrium (42), and the vertical line represents the threshold of an *almost* purely

573   PT equilibrium (43). From the numerical simulation, the symbol "Δ" indicates that for that

574   parameter combination of R and c, IL evolves to fixation. The points labeled "○" indicate that PT

575   evolves to fixation. "□" indicates a polymorphic equilibrium of UT and PT. "◊" indicates a

576   polymorphic equilibrium of IL and UT. "●" indicates a polymorphic equilibrium of IL and CT.

577   "■" indicates a polymorphic equilibrium of IL, UT and CT. Filled markers indicate where CT

578   exists at equilibrium.

579   For the temporal model, this combination of numerical and analytical findings suggests that five

580   different regions exist in the temporal model. Two regions involve equilibria of pure strategies of

581   either PT or IL. A third region permits combinations of UT and PT while a fourth region has

582   combinations of IL and UT. The final region always includes IL, mixed with either UT or CT, or

583   both. A comparison of Figures 5 and 2B reveal the dramatic impact of introducing PT into the

584   mix of pure strategies, as PT dominates when both c and R are high and exists in a polymorphic

585   equilibrium with UT when c is high and R is low (stable environments).
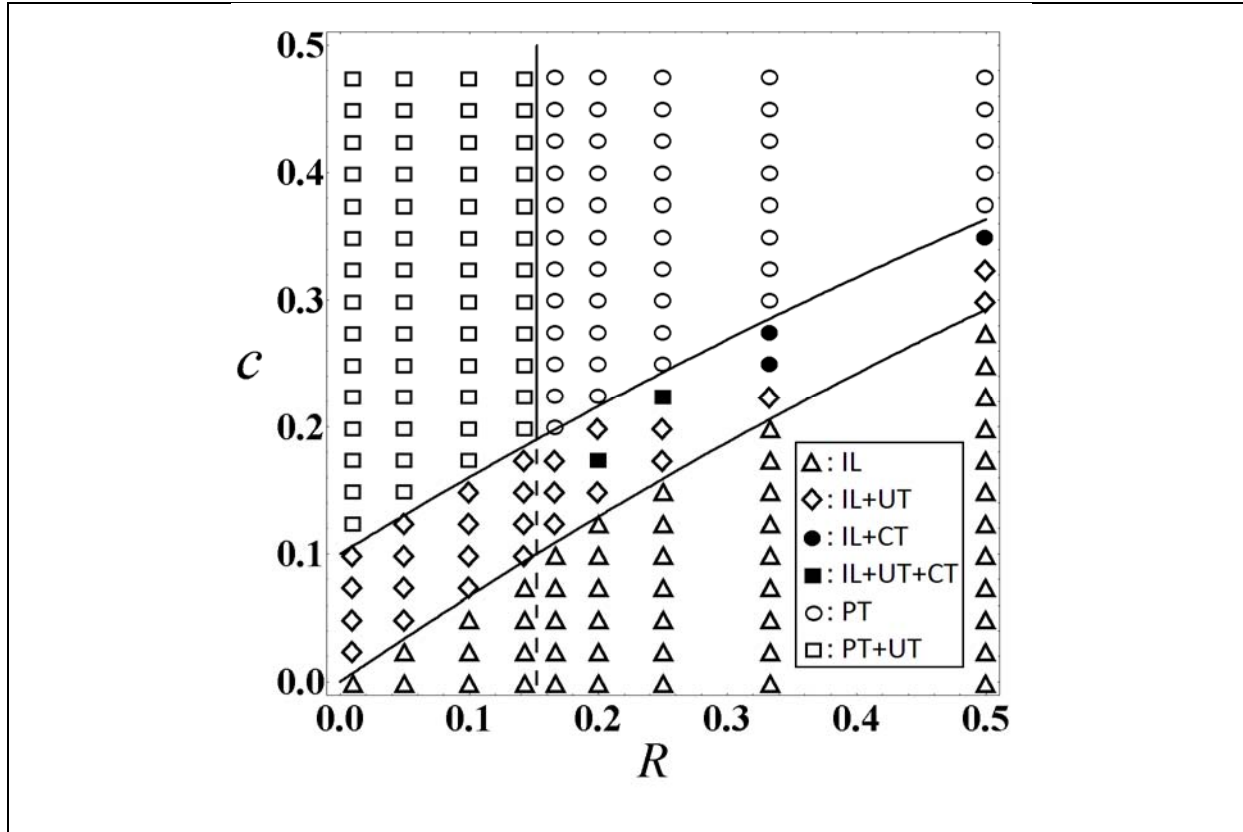
Figure 5. Equilibrium regions for our pure strategy temporal model in (R,c)-parameter space, $s = 0.5$, $a = 10$, $g = 0.1$, n $= \infty$ and $d = .05$. Numerically, we obtain the equilibrium frequencies of UT, CT, PT, and IL from several initial frequencies. The symbol "Δ" means that IL evolves to fixation. The points labeled "$\circ$" indicate that PT evolves to fixation. "$\square$" indicates a polymorphic equilibrium of UT and PT. "$\lozenge$" indicates a polymorphic equilibrium of IL and UT. "$\bullet$" indicates a polymorphic equilibrium of IL and CT. "$\blacksquare$" indicates a polymorphic equilibrium of IL, UT and CT. Filled markers indicate where CT exists at equilibrium. The lower curve represents the analytically-derived threshold of the IL equilibrium. The upper curve demarcates the threshold at which PT exists at equilibrium. The vertical line represents the threshold for a purely PT equilibrium.

586   To illustrate the dynamics of our models with PT, Figure 6 presents two simulation runs, one for

587   our spatial model (Figure 6A) and the second for our temporal model (Figure 6B). Both models

588   used these common parameters: $s = 0.5$, $c = 0.3$, $g = 0.1$, $d = 0$, $a = 10$, $K = 100$, and $r = 0.5$.

589   Note that $a = 10$ is sufficiently strong to be able to be assumed almost infinite. For the spatial

590   model we set the initial number of UT, CT, PT, and IL be $X_{ij} = U_{ij} = V_{ij} = \dfrac{K}{4n}$ for all i, j, and

591    $Z_i = K / 4$. That is, the initial frequencies of UT, CT, PT, and IL are 0.25. We also set $n = 4$, so

592   as not to give CT too much of an advantage in the spatial model and $m = 0.2$. For the temporal

593   model we set the initial frequencies of UT, CT, PT, and IL to be 0.25, and set $\ell = 5$ (R=0.2) to

594   parallel the setting m in our spatial model.

595

Figure 6. 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 $a = 10$. Note $a = 10$ is sufficiently strong to be able to be assumed almost infinite. 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, $\ell = 5$ ($R = 0.2$).
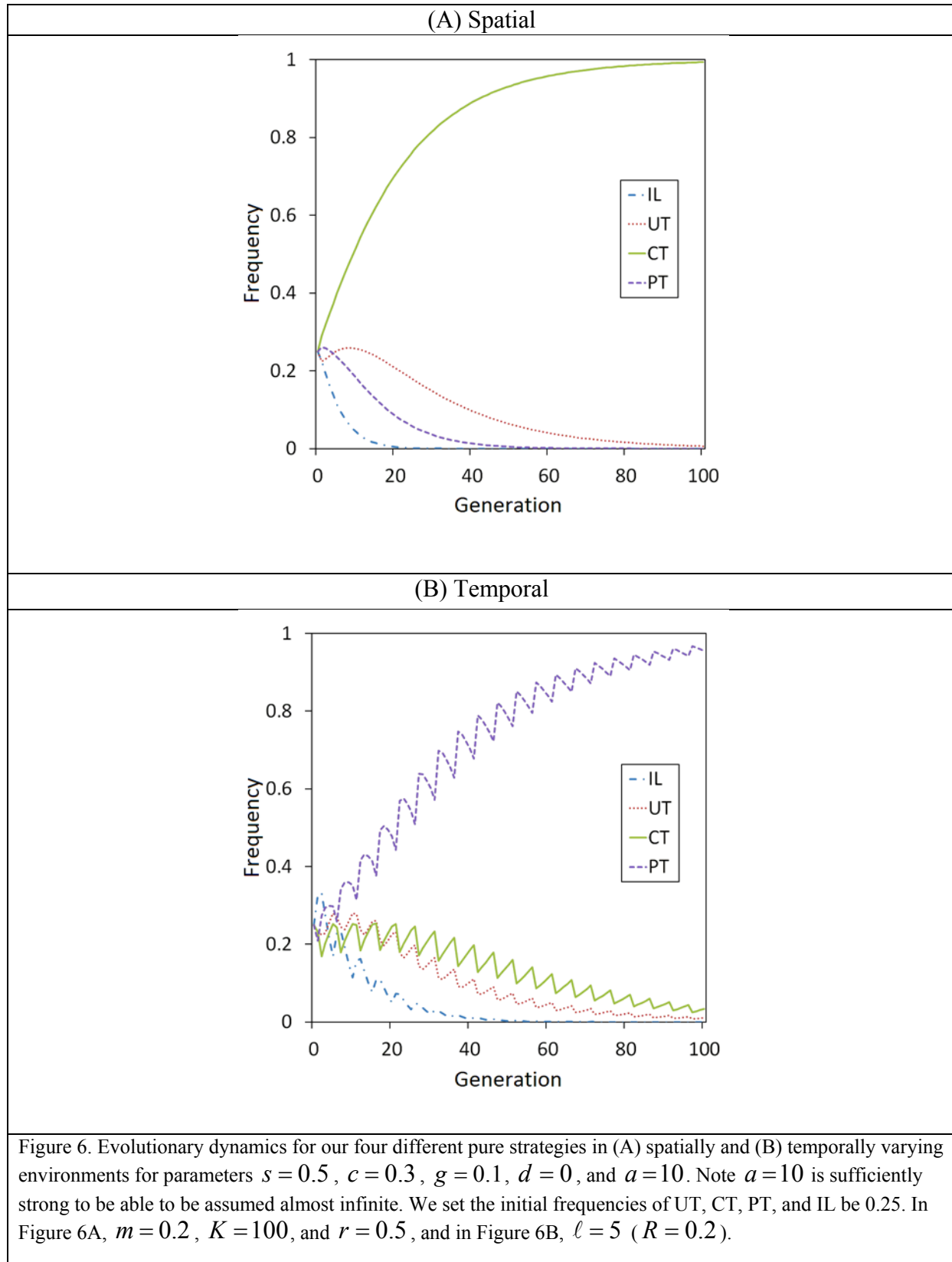
596   Both Figures 5 and 6 reveal a fairly stark contrast in how CT and PT respond to selection in

597   spatially vs. temporally varying environments. If anything, adding PT to mix of strategies

598   accentuates the difference in the selective regimes created by spatially vs. temporally varying

599   environments.

3.4. WHEN IL CANNOT LEARN AFTER MIGRATION OR ENVIRONMENTAL SHIFTS

601   Thus far our models have permitted an asymmetry among the four pure learning strategies by

602   assuming that IL can immediately acquire the locally adaptive trait after migration, or after an

603   environment shift, but UT, CT and PT cannot learn new traits later in their life cycle. Here we

604   present results from analyses in which we level the playing field so that IL cannot re-learn its

605   adult trait after migration, or after an environment shift. Like the social learners, IL is stuck with

606   whatever it learned while growing up. Our results indicate that this assumption about IL has

607   suppressed the success of CT in our spatially varying model while having no effect in our

608   temporally varying model.

609   For the spatial model, Appendix A shows how we altered our baseline recursions to

610   accommodate this change in IL's life cycle. We present only the results here. When CT suffers

611   no cost (i.e., $d = 0$), fixation of CT and extinction are the only possible stable equilibria (UT,PT,

612   and IL never evolve). If d is greater than zero but still smaller than g and c, IL and PT never

613   evolve. That is, if $0 < d < g < c < s < 1$, there are only four stable outcomes: (1) all CT, (2) all

614   UT, (3) mixtures of CT and UT, and (4) extinction. CT is the unique stable equilibrium if

615   inequalities (31) and (23) hold, which guarantees that d is sufficient small to prevent UT from

616   invading, and r is sufficiently large to prevent extinction. These are two of the three conditions

617   previously necessary for CT to remain stable in the model, when IL could learn after migration.

618   The third condition is no longer necessary, since it was the condition necessary to hold IL at

619   bay—IL's advantage obtained by being able to learn after migration. The second equilibrium

620   situation also parallels the above case, and occurs when d falls into an intermediate range set by

621   inequality (32), assuming that r is sufficiently large that (23) is not violated. In the third

622   situation, UT emerges as the sole stable equilibrium if d exceeds the upper threshold marked by

623   (32) and r is sufficiently large that (34) holds. Finally, if r fails to succeed either (23) or (34)

624   extinction is the only long-term result.

625   The results are quite different in our pure strategy temporal model, detailed in Appendix B. This

626   constraint on IL means that it cannot adapt immediately when the environment changes to obtain

627   the locally adaptive behavior. If IL cannot adapt, then neither can any of the social learning

628   strategies (UT, PT and CT). Any constraint placed on IL in this temporal model that delays

629   acquisition of the locally adaptive trait is subsequently imposed downstream on UT, PT, and CT

630   since they ultimately rely on IL to figure out the locally adaptive trait. This means that there is no

631   qualitative difference in the findings for this version of the temporal model compared to the case

632   when IL can acquire the currently adaptive trait immediately after the environmental shift.

633   Overall, leveling the playing field to constrain IL expands the range of conditions favoring CT

634   (and social learning more generally) in the spatial model, but does not change the conditions in

635   the temporal model.

636   # 4. DISCUSSION

637   In broadening, applying, and contextualizing our modeling results we focus on three areas. First,

638   we discuss how the spatial variation we analyzed above, which powerfully favors the evolution

639   of conformist transmission, is actually but one source of low-level, non-adaptive, phenotypic

640   variation. It is this non-adaptive variation, not spatial variation per se, that favors conformist

641   transmission. Other factors, like learning errors or transmission noise will also produce such a

642   persistent low volume inflow of non-adaptive variation. This means that even in the absence of

643   spatial variability, conformist transmission can provide an adaptive advantage. Second, with

644   empirical tests in mind, we develop a set of predictions from our formal results that are suitable

645   to experimental testing. Third, although our models are focused on cultural traits applied in non-

646   social contexts (e.g., which berries are edible), we consider the evolution in conformist

647   transmission for acquiring traits or strategies for interacting in social situations. We argue,

648   contrary to recent claims, that conformist transmission can still be adaptive in situations

649   involving cooperation and punishment, and even in situations involving complementarities.

650   ## 4.1. LEARNING ERROR AS SOURCE OF NON-ADAPTIVE VARIATION

651 The kind of non-adaptive phenotypic variation (in cultural traits) created in our spatial model by

652 a combination of environmental differences among sites and migration is merely one

653 manifestation of a more general adaptive challenge with which successful social learning

654 strategies must contend. Conformist transmission is frequently favored in these spatially varying

655 environments because of its ability to successfully ignore, or avoid acquiring, the non-adaptive

656 cultural traits brought in via migration from other sites. There are, however, a variety of

657 processes that can generate a similar adaptive challenge to that created by spatial environmental

658 variation, including errors or noise produced during learning and transmission.

659 Both mistakes in individual learning and a variety of errors in cultural transmission can create

660 the same kind of low-level phenotypic variation as does environmental variation and migration.

661 Even in a completely static environment, errors and mistakes by both individual and social

662 learners can inject a steady flow of non-adaptive cultural traits (increasing n and effectively m)

663 into the local population. Individual learners may sometimes "goof-up" and "invent" something

664 that is both new and non-adaptive. Social learners are likely to create a great variety of novel and

665 less adaptive cultural traits, especially when acquiring more complex cultural traits, by (a)

666 misperceiving what their models are doing, (b) making errors during the inferential steps of

667 imitation, or (c) misremembering elements of cultural traits at some later time (Henrich & Boyd,

668 2002). Successful social learners need to figure out how to avoid this constant injection of non-

669 adaptive variation. Conformist transmission provides one way to "squeeze out" this non-adaptive

670 variation at (potentially) a low cost (see analogy with robust estimators in Boyd & Richerson,

671 1985: Chapter 7).

672 Of course, there are other ways to address this challenge. Payoff-biased strategies can avoid this

673 non-adaptive variation, but these strategies are likely more costly in general, and potentially

674 *quite a bit* more costly. And, if a learner's payoff information is itself noisy, then conformist

675 transmission can still be a superior strategy (Henrich & Boyd, 2002; McElreath, et al., 2008)—

676 especially if the learner accurately perceives that he or she is likely to be less well informed

677 about payoffs than many others in the local population. Other important strategies that can

678 address this problem include blending mechanisms, which present a cousin of conformist biases,

679 and the use of ethnic markers (Boyd & Richerson, 1985: Chapter 4; Boyd & Richerson,

680 1987; McElreath, et al., 2003).

681   It is also not the case that one need choose between payoff and conformist biases. Consider a

682   social learning strategy that samples M models from the local population and estimates which N

683   of these M models have the highest payoffs, or are the most successful. Our integrated learner

684   then applies conformist learning to these N. When payoff differences are non-existent, or too

685   noisy to be successfully differentiated, this algorithm reduces to pure conformist transmission.

686   When payoff differences between traits can be recognized, but traits can be misperceived (the

687   model is doing A, but learners misread it as B), this heuristic improves the accuracy of payoff-

688   biased learning. This, and other more complex heuristics, can obtain the noise-reducing benefits

689   of conformist transmission while still achieving the rapid adaptability and flexibility of payoff-

690   biased learning (Henrich & Boyd, 2002).

691   We think this may be particularly important for understanding cumulative cultural evolution. As

692   tools, for example, evolve culturally to become more complicated, errors in cultural transmission

693   will increasingly introduce non-adaptive variation at the same time payoff differences get harder

694   to detect, or at least to trace to particular differences in the tools, or their manufacture. After

695   selectively sampling those with higher payoffs, copying the most common step or technique in

696   the manufacture of a complicated tool can still allow learners to avoid copying non-adaptive

697   variation.

698   <div align="center">

4.2. PREDICTIONS

</div>

699   One of the primary goals of evolutionary modeling is to generate clear, precise, empirical

700   predictions about the operation of psychological mechanisms, and specifically in this case about

701   the cognitive mechanisms that underpin our cultural learning abilities. Here we outline four

702   testable predictions, derived from our modeling efforts above:

703   1) Increasing the migration rates (m) among different environments (local populations)

704   should increase individuals' reliance on conformist transmission, provided the costs of

705   individual learning are not too low (Figure 2A). By contrast, increasing the rate of

706   environmental fluctuations, should not have similarly sharp effects (see Figure 2B,

707   focusing on increasing R).

708   2) Increasing n, the number of cultural traits, in the presence of low-level trait variation

709   should increase individuals' reliance on conformist transmission. This is best illustrated

710   in Figures 3A and 4. The degree of increase in reliance on conformist transmission

711   should be more pronounced in moving from two traits to four traits with declining

712   increases thereafter. See Figure 4 for heuristic relationship. Both increasing m and n raise

713   the rate of influx of local non-adaptive variation. Similar predictions should hold if

714   learning errors or transmission noise is increased, even in stable environments.

715   3) Increasing the costs of individual learning (c) in an environment with persistent low-

716   levels of phenotypic-trait variation should increase individuals' reliance on conformist

717   transmission, provided that the levels of phenotypic variation are not too low (Figure

718   2A).

719   4) Increasing the costs of non-adaptive behavior (s) should decrease individuals' reliance on

720   conformist transmission and increase reliance on individual learning provided other costs

721   (c, d, g) are constant.

4.3. SOCIAL INTERACTION, REPUTATION, PUNISHMENT AND COOPERATION

723   Like much prior work, our models analyze the evolution of different social learning strategies by

724   assuming that the traits being learned are non-social, or at least that their payoffs do not depend

725   on the frequency of other cultural traits in the local population. Skills or techniques related to

726   food choice or tool manufacture might be most appropriate. Here we consider how using various

727   learning strategies for acquiring social behavior might influence the evolution of conformist

728   transmission, or at least the range of domains or types of problems to which it might be applied.

729   We think our models are particularly useful in this regard, since as we argue below, the cultural

730   evolution of social behavior may often create a kind of spatial variability very much like what we

731   have modeled.

732   To explore this we consider three kinds of social interactions in groups, those involving (1)

733   coordination, (2) cooperation, and (3) complementarity (Erikksson, et al., 2007). In coordination

734   games, conformist transmission is clearly an adaptive strategy as learners need to figure out what

735   most people are doing among those whom they are most likely to interact with in the future. If

736   anyone expects dowries to be paid along with daughters, then our learner adopts the practices

737   associated with dowry. If bride prices or bride services are paid to the wife's family, then our

738   learner adopts this strategy. The effectiveness of conformist transmission in these situation seems

739   uncontroversial, though some have argued that payoff biases gets one the same answer. This is

740   true, but payoff biased transmission requires learners to acquire and process payoff information,

741   which is likely more costly relative to frequency information. The precise difference depends

742   heavily on the costs of various sorts of information and its relative accuracy.

743   For many different coordination problems cultural evolution can generate a wide variety of

744   solutions. The important thing in a coordination problem is to do what the majority does. This

745   applies to such problems as driving on the left or the right, relying on a lunar or solar calendar, or

746   closing the factory on a particular day of the week. If different groups wind up at different

747   solutions, a kind of spatial variation can emerge that parallels what we have modeled above. The

748   important thing for migrants is to acquire the most common behavior in whatever population

749   they end up in, while non-migrants just need to make sure they don't mistakenly copy a new

750   arrival (from a group with a different coordinated solution).

751   The second and more controversial kind of social interaction involves problems of cooperation,

752   and in particular situations of larger-scale or n-person cooperation. In this kind of social

753   interaction the group does best if everyone cooperates, but defecting individuals can free ride on

754   the cooperation of others and receive higher payoffs than those who cooperate. Eriksson et al.

755   (2007) have argued that learners ought not use conformist transmission in such a situation, and

756   especially in acquiring the punishing strategies that are so often thought to stabilize human

757   cooperation (Henrich, 2004).

758   We, however, think this view fails to recognize two different lines of theoretical work. First,

759   there is a large body of modeling showing how a variety of mechanisms related to punishment,

760   signaling, reputation, and reciprocity can effectively turn cooperative dilemma into a

761   coordination situation (Henrich & Henrich, 2007). That is, formal cultural evolutionary models

762   show how a multiplicity of stable social norms are created by a variety of mechanisms that

763   generate self-reinforcing incentives (Boyd et al., 2010; Gintis et al., 2001; Henrich & Boyd,

764   2001; Panchanathan & Boyd, 2004). The theoretical expectation from these models is that

765   different social groups will culturally evolve different norms, since a wide variety of behaviors

766   are stable once common. From the perspective of conformist transmission, the emergence of

767   self-reinforcing social norms that vary among social groups creates a situation that parallels our

768   spatial model. Different groups (sites) have different self-enforcing social norms, so migrants

769 need to figure out what locally won't get one a bad reputation or punished, and non-migrants

770 need to avoid learning from those who have made an error or are new arrivals to the group.

771 In a second line of theoretical work on cultural evolution, some approaches to larger scale

772 cooperation have shown how including punishing strategies—while not leading to stable states

773 as above—does slow the within-group decline of cooperation (when common) sufficiently that

774 between group competition can favor higher level of cooperation overall in a large structured

775 population (Boyd et al., 2003). Guzman et al. (2007), building on this work using simulations,

776 have explored the genetic evolution of payoff-biased and conformist transmission in a world in

777 which the only problem individuals confront are those involving cooperation and punishment.

778 This simulation suggests that natural selection will still, contrary to some suggestions (Hagen &

779 Hammerstein, 2006), favor the evolution of substantial conformist transmission. This simulation

780 has a complex interaction of cultural and genetic evolution in which conformist transmission

781 keeps culturally transmitted punishing and cooperating strategies common in some groups, and

782 those groups proliferate. When conformist-biased learners migrate to non-cooperative, non-

783 punishing groups, they rapidly stop paying the costs of cooperation and punishment, thus

784 reducing the selection against them. Conformist transmission, cooperation, and punishment

785 appear to be a potent culture-gene package. Using a setup similar to Guzman et al., Henrich and

786 Boyd (2001) have analytically shown that once conformist transmission evolves to even a

787 relatively weak degree, it can give rise to the same kind of stable social norms described above.

788 Either way one looks at it, the kind of spatial variability that favors conformist transmission is

789 again created.

790 The third kind of social interaction involves complementary actions. In games of

791 complementarity, individuals receive the highest payoffs when they bring skills, endowments, or

792 know-how *different* from those with which they are interacting. Copying the currently most

793 common trait here is not the road to higher payoffs for sure. However, an empirical look at

794 human societies reveals how they are organized in such a way so as to mitigate this concern. In

795 the smallest scale human societies, there is little division of labor or know-how, except by age

796 and sex (Fried, 1967). While men, for example, vary in their skills, there are not obvious

797 complementarities, and little or no occupational specialization exists (Johnson, 1995). There are,

798 at times, ritual specialists but it is not clear why the existence of these relatively rare roles would

799   inhibit the evolution of conformist transmission. As for sex and age, much prior theorizing on

800   cultural learning mechanisms have suggested that learners use cues of both sex and age to hone

801   their attention and learning efforts (Henrich & Gil-White, 2001), and that conformist

802   transmission should interface with such cues (Henrich & McElreath, 2007). Men, for example,

803   may be inclined to copy what most men do, while women should be inclined to copy what most

804   women are doing. Men and women, then, supply complementary skills to the household. Thus,

805   cultural evolution solves this problem of complementarity by partitioning individuals into sub-

806   groups within with conformist transmission can operate effectively, and making the

807   complementary interaction occur between subgroups. At the group-level, everyone merely needs

808   to *coordinate* on the same cultural beliefs about the division of labor: for example, "males hunt

809   and females gather" (which again, can be effectively acquired by conformist transmission).

810   In more complex human societies, occupational specializations of the kind associated with

811   complementary interactions emerge principally in relations *among* social groups, with whole

812   groups, castes, classes, or guilds specializing in one or another skill (Barth, 1965; Gadgil &

813   Malhotra, 1983). Farmers grow up among farmers, herders among herders, merchants among

814   merchants, nobles among nobles. Exploring this, cultural evolutionary models of complementary

815   interactions in structured populations have shown how payoff-biased transmission will

816   spontaneously give rise to specializations by local or ethnic groups in specific skills (Henrich &

817   Boyd, 2008). This means that payoff-biases—in the absence of conformist transmission—in

818   situations of complementarity will spontaneously give rise to precisely the kind of spatial

819   variation that favors the evolution of conformist transmission.

820   ## CONCLUSION

821   We have constructed, analyzed, and compared a series of formal models aimed at further

822   elucidating the evolutionary foundations of social learning, and specifically conformist

823   transmission. Our primary contribution is to clarify how spatial vs. temporal environmental

824   variation differentially influences the evolution of three different social learning strategies and

825   individual learning, as well as to examine how using more than two cultural traits affects the

826   emergence of conformist transmission. Our models also examine the effects of different fitness

827   costs for different strategies. Broadly speaking, we find that when individual learning is

828 sufficiently costly, conformist transmission is favored in spatially varying environments while

829 payoff-biased transmission is favored in temporally varying environments. With regard to the

830 number of cultural traits, our results also show that by focusing on models with two cultural

831 traits, much prior work has explored the circumstances least favorable to conformist

832 transmission. Small increases in the number of cultural traits substantially increases the range of

833 conditions favoring conformist transmission in both spatially and temporally varying

834 environments. To facilitate empirical testing, we distilled our formal results into a series of

835 predictions suited to experimentation.

836 We believe our findings have broader implications for the evolution of social learning strategies

837 beyond spatially and temporally varying environments for two reasons. First, spatial variability is

838 merely one way to generate a low-level but persistent influx of non-adaptive phenotypic

839 variation that favors conformist transmission, with learning errors being another obvious process

840 that could generate this selective force. This means that conformist transmission could be

841 similarly favored even in static or temporally varying environments with transmission noise or

842 learning errors. Second, while the learning challenge in our model is non-social, we argue that

843 social interactions involving coordination, cooperation, and complementarity can and do

844 generate a kind of variation among groups that parallels our model's spatial variation. This

845 suggests that conformist transmission to acquire phenotypes for social interactions could also be

846 favored for similar reasons.

847 Better understanding conformist transmission at both proximate and ultimate levels is important

848 for a number of reasons. To begin, it may provide a readily available explanation for some of the

849 apparent "clumpiness" observed in cultural variation (Henrich & Boyd, 1998), addressing the

850 question of why local groups, for example, might vary on numerous cultural dimensions. It may

851 also help explain the group-level heritability found in the branching signals revealed in the

852 application of phylogenetic methods to cultural datasets (Collard et al., 2006; Lipo et al., 2006),

853 something which is difficult to explain if vertical cultural transmission is assumed. Finally, by

854 reducing the variation within groups and assorting like phenotypes together, conformist

855 transmission may increase the relative importance of the between-group components of cultural

856 evolution relative to the within-group component. This suggests that cultural evolutionary

857 processes might have quite a different character with regard to the evolution of social behavior

858 when compared to vertically-transmitted genetic evolution (Boyd & Richerson, 1985; Currie &

859 Mace, 2009; Henrich & Boyd, 2001).

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