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Citation	Nunn, Charles Lindsay, Peter H. Thrall, Kevin Bartz, Tirthankar Dasgupta, and Christophe Boesch. 2009. Do transmission mechanisms or social systems drive cultural dynamics in socially structured populations? <i>Animal Behaviour</i> 77(6): 1515-1524.
Published Version	doi:10.1016/j.anbehav.2009.02.023
Accessed	February 18, 2015 6:29:10 PM EST
Citable Link	http://nrs.harvard.edu/urn-3:HUL.InstRepos:4317716
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Do transmission mechanisms or social systems drive cultural dynamics in socially structured populations?

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Word count: 9085 (including all references and figure legends)

23 **Abstract:** Cultural traits spread via multiple mechanisms among individuals within social groups,
24 including transmission biases which occur when subordinates copy from dominants (prestige
25 transmission) or common cultural trait variants are favored over rare ones (consensus transmission). Most
26 animal populations are subdivided into social groups where cultural learning occurs, yet theoretical
27 studies of cultural trait transmission have tended to focus on within-group transmission dynamics. Thus,
28 we lack an understanding of the factors that influence the spread of cultural traits in socially structured
29 populations. We developed an agent-based model of cultural transmission in which a trait arises in one
30 individual and either persists until a stable population equilibrium is reached or goes extinct. With this
31 model, we systematically varied group size, rates of dispersal among groups, mortality rates, transmission
32 characteristics, the benefit of the cultural trait (including possibly negative benefits, i.e. costly traits), and
33 whether individuals disperse locally or randomly to any group. We used generalized linear models to
34 examine how changes in these parameters influence the probability of trait extinction, equilibrium
35 prevalence, and the time to equilibrium. Four traits increased the probability of extinction: smaller group
36 size, higher background mortality, lower transmission rate, and more costly traits. Local dispersal and
37 biased transmission mechanisms (prestige and consensus) had no significant impacts on extinction
38 probability, and similar patterns were found for equilibrium prevalence. By comparison, we found that a
39 lower dispersal rate and local dispersal slowed the time required for a trait to reach equilibrium, as did
40 smaller groups, lower transmission rates, and lower costs. Although increasing costs increased extinction
41 rates, even costly traits sometimes persisted in the simulated populations. Collectively, these analyses
42 provide new insights into the dynamics of cultural traits in socially structured populations, including that
43 prestige and consensus transmission can have weaker effects than other factors associated with
44 demographic and social conditions. In addition, local dispersal and a lower dispersal probability reduced
45 the rate of trait spread but not its prevalence in the population.

46

47 *Keywords:* social systems, culture, transmission, individual-based model, social learning.

48

48 A striking feature of human evolution is the incredible diversity of cultures that exist around the world.
49 For example, linguists have counted over 6,000 languages (Gordon 2005), and humans are thought to
50 practice more than 4,300 religions (faith groups). Many human cultural traits are likely to be adaptive,
51 such as those related to resource allocation and health practices, and are thus subject to natural selection
52 (Mesoudi et al. 2004). Other cultural traits, such as decorations on pottery, are probably driven less by
53 natural selection, but they may provide social or sexual benefits that indirectly translate to higher
54 reproduction. Some persistent cultural traits in humans are even associated with costs. For example, a
55 celibate priesthood dramatically reduces the reproductive success of individuals that become priests,
56 while scarification, excision and circumcision increase the risks of lethal infections, especially in societies
57 living without access to safe medical practices. Potential cultural traditions also have been documented in
58 many nonhuman systems, including nut cracking in chimpanzees (Boesch et al. 1994; Boesch and
59 Boesch-Achermann 2000), potato washing in Japanese macaques (Kawai 1965), and New Caledonian
60 crows that use tools to obtain invertebrates from the vegetation (Hunt 2003). Understanding the spread of
61 cultural traits in non-human systems could provide insights to human evolution and the factors leading to
62 the explosive growth of cultural traits in the human lineage.

63 A critical question in studies of cultural evolution involves features that impact the dynamics of
64 cultural traits, both in terms of the proportion of individuals that express the trait and the rate at which the
65 behavior spreads through a population. In addition to the cost or benefit of the trait in question, two
66 factors are thought to be important to the spread of cultural traits: the mechanism by which behaviors are
67 learned and the social context in which transmission takes place. First, concerning mechanisms, cultural
68 transmission usually occurs through social learning, in which an individual learns a new behavior by
69 watching other individuals perform the behavior. In nonhuman primates, for example, social learning has
70 been proposed in the case of potato washing in Japanese macaques and nut-cracking in chimpanzees
71 (Kawai 1965; Boesch and Boesch-Achermann 2000). Importantly, different models of cultural
72 transmission may operate, depending on the social system in which the individual is embedded and the
73 mechanisms by which traits are acquired. For example, individuals may be more likely to copy the

74 behaviors of more dominant individuals, which would be adaptive if dominants possess behavioral traits
75 that made them more successful (Boesch and Tomasello 1998; Boyd and Richerson 1985; Henrich and
76 McElreath 2003). Similarly, individuals may be more likely to adopt traits when more individuals in the
77 group express the trait through a “conformity” or “majority rule” mechanism (Boesch and Tomasello
78 1998; Henrich and McElreath 2003, hereafter called consensus transmission). While these transmission
79 biases are not mutually exclusive, neither are they completely congruent.

80 Second, social context is likely to be important for the spread of cultural traits. At the population
81 level, most primates and humans live in socially structured populations, and the limited evidence
82 available suggests that cultural traits tend to spread more commonly among members of the same social
83 group than between groups (Kawamura 1959; Boesch 2003; Leca et al. 2007). Within social groups, the
84 rate of cultural transmission is expected to be higher when group sizes are larger, with larger numbers of
85 more tolerant individuals providing more opportunities for invention and social learning (van Schaik et al.
86 1999). Opportunities for learning can be modified by other factors, such as proximity of individuals and
87 their capacity for social learning (van Schaik and Pradhan 2003). Mortality rates and movement between
88 social groups can also be important in a socially structured population. If dispersal occurs only between
89 neighboring groups and at a low rate, for example, then the trait in question may take longer to establish
90 in the larger population, and will thus be more prone to cultural extinction if the group is lost due to other
91 factors. Similarly, if individuals who possess a costly cultural trait die at a higher rate, fewer other
92 individuals will have an opportunity to learn the skills that are needed to express the behavior.

93 In this manuscript, we use an agent-based model (Grimm and Railsback 2005) to investigate how
94 cultural traits spread through animal social systems, focusing in particular on features involving group
95 size, dispersal, and background mortality (i.e., a death rate that is independent of expressing the cultural
96 trait). We also examine how different mechanisms of social learning – specifically involving prestige and
97 consensus models – influence the spread of cultural traits, and how different probabilities of acquiring the
98 trait and the selective benefits (or costs) of the trait affect transmission dynamics. The model is spatially

99 explicit and incorporates three social transmission mechanisms, and individuals can disperse either locally
100 (a spatial model) or randomly to any of the groups (a non-spatial model). In addition, the model allows
101 for variation in group size, dispersal rates, mortality, and the selective benefit (or cost) of the cultural trait
102 (expressed by adjusting the baseline mortality rate among individuals with the trait). The model can
103 therefore be applied to study cultural traits in a wide range of systems in which individuals live in socially
104 structured populations, including humans, non-human primates, and other animals. Our work adds to a
105 growing number of agent-based models of cultural trait transmission, including in the context of foraging
106 (van der Post and Hogeweg 2006, 2008) and the spread of traits through social networks (Franz and Nunn
107 2009).

108 Social learning is a key component of the model. We call the two roles in this exchange the
109 *observer*, who learns the behavior, and the *performer*, who exhibits the behavior and therefore serves as
110 the role model for social learning to take place. We investigated three different transmission mechanisms
111 (Boesch and Tomasello 1998; Henrich and McElreath 2003). The first transmission mechanism, referred
112 to as the *random transmission model*, is the simplest. In this scenario the probability of cultural
113 transmission between two individuals is independent of sex, social affiliation, the proportion of group-
114 mates with the trait, and dominance rank. The other mechanisms represent modifications of the random
115 model. In the *prestige transmission* model, transmission probabilities are positively correlated with the
116 dominance rank of the individual expressing the trait (Boyd and Richerson 1985; Henrich and Gil-White
117 2001). *Consensus transmission* addresses the importance of social conformity, with increasing probability
118 that an individual adopts a trait as the proportion of group-mates expressing the trait increases (Boyd and
119 Richerson 1985; Henrich and Boyd 1998). We designed the simulation model so that the mean rate of
120 transmission would be approximately equal across the three transmission mechanisms.

121 We investigated four main questions regarding the relative impacts of social system and
122 transmission characteristics on the spread of cultural traits. In particular we were interested in how these

123 features interact to determine the probability of extinction, the equilibrium proportion of individuals with
124 the trait, and the time to equilibrium:

125 1. *Does local dispersal in a spatially explicit model (i.e., local dispersal) produce different outcomes*
126 *than a non-spatial model, in which dispersing individuals can move to any social group?* Random
127 movement from one group to any other group increases the probability that a dispersing individual
128 with the trait will land in a group that has yet to experience the trait. Once within a group, it is
129 expected to spread rapidly. Thus, random movement should increase the rate of trait spread and favor
130 the establishment of traits in the population. In contrast, local dispersal should slow the rate of
131 cultural dispersion at the population level. Less is known about how local dispersal impacts the
132 prevalence of a trait or its probability of extinction, but we expect that spatially localized traits are
133 more likely to go extinct through stochastic processes.

134 2. *Do cultural traits spread more rapidly – and reach higher prevalence – in populations composed of*
135 *larger social groups, or in populations characterized by higher rates of individual movement among*
136 *groups?* These two social parameters could interact, with larger groups potentially producing more
137 migrants that carry the trait to other groups. Here, we focus on actual movement of individuals
138 between groups (migration), thus assuming that casual observation of individuals in neighboring
139 groups is insufficient for social learning to occur (cf. Boyd and Richerson 2002).

140 3. *How does mortality impact the prevalence of a cultural trait in a population?* In epidemiological
141 models, higher rates of mortality remove individuals carrying a disease from the population, making
142 it more difficult for the pathogen to become established and reducing overall prevalence (Anderson
143 and May 1979; Thrall et al. 2000). Similar principles should apply to cultural traits. Thus, increased
144 background mortality – i.e., mortality that is independent of the expression of the cultural trait –
145 should negatively impact the equilibrium prevalence of the trait. *The selective advantage of cultural*
146 *traits should modify these patterns.* Higher benefits (holding costs constant) should lead to lower
147 mortality among individuals with the trait and result in more opportunities for the trait to spread.

148 Traits with a net cost should lead to the opposite pattern, resulting in lower prevalence and increased
149 probability that the trait will go extinct.

150 4. *How do social learning mechanisms influence the spread of cultural traits?* One aspect of social
151 learning involves the probability that a trait will spread from one individual to another. A higher rate
152 of transmission (β) could increase prevalence, or reduce the time until equilibrium prevalence is
153 reached. Another aspect of social learning involves the transmission mechanisms discussed above,
154 which effectively modify β based on individual characteristics (*prestige transmission*) or prevalence
155 of the trait in a group (*consensus transmission*). Compared to a random model, do cultural traits
156 spread more rapidly or reach higher equilibrium prevalence under a prestige or consensus model?

157

158 METHODS

159

160 Simulation Model Structure

161 We developed a simulation model using the computer package MATLAB (version 7, Natwick,
162 Massachusetts) to simulate the spread of an introduced cultural trait in a socially structured population.
163 The basic design of the model was developed as part of a previous investigation of the impact of host
164 social group structure on the spread of an emerging infectious disease (Nunn et al. 2008). In that study, an
165 initial infection was introduced into a population of susceptible hosts. Individuals that died from disease
166 were not replaced (as is typical of wildlife epidemics), and group composition was allowed to depart from
167 initial conditions as animals died or dispersed from groups. Here, we extend the model to study the spread
168 of culturally inherited traits by including three different transmission mechanisms and adaptive value to
169 the trait (i.e., positive or negative net benefits, representing a beneficial or costly trait, respectively).

170 We were particularly interested in examining the spread of cultural traits in a spatial context,
171 given that previous studies on infectious disease have shown that spatial structure can significantly impact
172 disease dynamics and longer-term evolutionary processes (Thrall and Antonovics 1995; Gandon et al.

173 1996; Boots and Sasaki 1999; Roy and Kirchner 2000; Carlsson-Graner and Thrall 2002; O'Keefe and
174 Antonovics 2002). For each simulation run, groups of individuals were formed based on user-specified
175 values for group size. Groups were distributed on a 12 x 12 matrix (i.e., 144 groups on a square lattice)
176 and formed as random draws from a Poisson distribution assuming an equal number of males and
177 females. Deaths, births and dispersal of individuals will tend to cause the initial social conditions to drift
178 over a simulation run, especially when simulations are run for many time steps. To deal with this issue,
179 we retained a matrix of the initial numbers of males and females in each group. This “initiating matrix”
180 was used to stochastically adjust probabilities associated with demographic parameters (birth and
181 dispersal) to help maintain initial conditions for each group throughout a simulation run.

182 The cultural trait was initiated in a single individual, and the trait was allowed to spread through
183 the population in discrete time steps. In each time step, an individual remained in its original group or
184 dispersed to other groups in the population, as determined by the probability of dispersal per time step.
185 We assumed that dispersing individuals lacked contact with conspecifics. We further assumed that
186 dominance rank of a migrant equaled the rank of that individual in the previous group and that this rank
187 did not impact the probability of emigrating or immigrating. Individuals that dispersed were not allowed
188 to enter groups from which they had most recently departed. The simulation was allowed to run until the
189 cultural trait either went extinct in the population or the prevalence of the cultural trait stabilized at a non-
190 zero value.

191

192 **Mechanisms of Cultural Transmission**

193 Cultural traits spread by social learning within groups, and the probability of transmission (β) represents
194 the per-contact probability of an observer acquiring a cultural trait from an individual that expresses the
195 behavior. Mechanistically, β encapsulates the combined probability that one individual exhibits the trait
196 while another naïve individual can view and potentially learn from the performer, including the time
197 needed for the observer to learn techniques associated with performing the trait. Thus, lower values of β

198 could represent behaviors that are more complex (and thus more difficult to learn) or behaviors that are
199 performed more rarely. Individuals that acquire the trait serve as performers in the next time step, and
200 agents retain the trait throughout their lives in a simulation run. In our model, the selective benefits (or
201 costs) of cultural traits are expressed by altering the background probability of death (see below).

202 In the random model, contact rates and per-contact probabilities of transmission were equal
203 among all individuals in a social group regardless of dominance rank and the proportion of individuals
204 exhibiting the trait. Thus, contact rate increased with group size, analogous to predictions from standard
205 mass-action epidemiological models (May and Anderson 1979; Anderson and May 1981). Thus, contacts
206 within groups are assumed to have no spatial restrictions, in comparison to contacts between groups
207 (where contact can only occur through dispersal). Analytically, the probability of a susceptible individual
208 *not* acquiring the trait as a result of contacts with members of its group is equal to $(1 - \beta)^I$, where I
209 represents the number of individuals in a social group expressing the cultural trait. Thus, the overall
210 probability that an individual learns the trait from one or more performers in a time step is given by $1 - (1$
211 $- \beta)^I$.

212 The prestige model calculates the individual probability that a trait spreads between individuals
213 based on the rank of the performer, under the assumption that observers prefer to copy more dominant
214 individuals within the population, including the possibility that animals possess simple heuristics in which
215 subordinates emulate dominants as a way to learn successful foraging, competitive and hunting behaviors
216 (Boyd and Richerson 1985; Boesch and Tomasello 1998; Henrich and McElreath 2003). At the time of
217 group formation, individuals were assigned dominance ranks (d_i) using values from a uniform
218 distribution. Use of a uniform distribution was preferred to the normal or other distributions because it
219 captures the essence of dominance as a linear ranking, while also allowing some fine differences among
220 individuals in rank. In the process of simulating the spread of cultural traits in the prestige model, user-
221 defined values of β were adjusted as follows for spread of a trait from performer i to observer j :

222

223
$$\beta' = \beta (0.01 + 1.98 r_i')$$

224

225 where r_i' is the standardized rank of the performer, with standardization of ranks within each group
226 ranging from 0 to 1 [$r_i' = (r_i - r_{min}) / (r_{max} - r_{min})$]. This procedure gives a range of values for β' of 0.01 to
227 1.99 times the user-specified β , with the midpoint centered on the user-specified value β . In this way, the
228 individual with the lowest possible dominance rank (=0) had an adjusted β greater than zero ($\beta' = 0.01$),
229 thus preventing deterministic extinction of the trait if the first performer of the trait happened to be the
230 lowest ranking individual in a group. When $\beta > 0.5$, the probability of transmission could exceed 1 for
231 higher-ranking individuals. As our values of β were always less than 0.04 (Table 1), this should have no
232 effect on model outcomes. Although a stronger version of the prestige model might not allow
233 transmission from the lowest ranking performer to occur, it is worth noting that in our model, the
234 probability of transmission for the lowest ranking individual is two orders of magnitude smaller than a
235 middle-ranking individual; thus, rank has substantial effects on the probability of transmission. In one run
236 of the simulation using the prestige model, we found that the normalized dominance rank of the performer
237 was higher than the observer (t=37.7, n=427 transmission events, P<0.0001), with the average rank of the
238 source 0.667 and the average of the recipient 0.495. For the other transmission models, both performer
239 and observer had similar ranks (average of 0.50).

240 In the consensus model, transmission rates were adjusted based on the percentage of individuals
241 in the group that expressed the trait, p . The adjusted β was calculated using a linear transformation:

242

243
$$\beta' = \beta + (p - 0.5) \beta$$

244

245 Thus, when less than 1/2 of the group members expressed the trait, β was adjusted downwards, and when
246 the majority of individuals expressed the trait, β was adjusted upwards. It is important to stress that only
247 the per-contact probability of transmission parameter (β) was adjusted, and this reflects the probability of

248 transmission between two individuals in the same group; the mass action effect of increasing numbers of
249 ‘culturally infected’ individuals represents an independent effect that tends to increase the spread of traits
250 as more individuals in a group acquire the behavior.

251 The consensus and prestige models were designed to be as simple as possible in their
252 implementation and to have equal average probabilities of transmission, thus allowing comparison among
253 the different transmission models. We acknowledge, however, that different mechanisms of maintaining a
254 constant “average” transmission rate are possible and could produce dynamics that differ from those
255 reported here. We consider this in more depth in the Discussion, along with alternative forms of biased
256 transmission that could be investigated in the future.

257

258 **Maintaining Starting Conditions: Deaths, Births and Dispersal**

259 The causes of death were identified during a simulation run as being due to background mortality (m),
260 such as predation and old age, or the presence of a costly cultural trait (as this increased mortality rates
261 through a linear transformation of background mortality). An individual that died from natural causes was
262 replaced by an individual of the same sex. Newly generated healthy individuals were placed in one of the
263 existing groups with a probability that was adjusted according to how current group composition
264 compared to the initiating matrix. If the number of individuals of the sex of the individual being replaced
265 was less than the initiating values for that group, then the probability of assignment was increased. The
266 new group was then determined based on a random draw from a list of all groups, with each group listed
267 once and groups that were deficient given an additional entry. Thus, individuals could be added to any of
268 the groups, but the addition was more likely if the group exhibited a deficit in the number of individuals
269 of that sex, relative to the initiating matrix. As in our previous model (Nunn et al. 2008), we assumed that
270 mortality rates are independent of age and that deaths attributed to a costly trait were not replaced by new
271 individuals (as might be expected if populations are unable to respond demographically to these losses in
272 the time horizons simulated here).

273 To investigate the effect of selective benefits (and costs) of a cultural trait, we assumed that
274 selection on cultural traits acts by increasing or decreasing mortality. The mortality rate of individuals
275 with the cultural trait was multiplied by a selection multiplier, s_m , which was user-defined and ranged
276 from 0.001 to 2 (Table 1). Thus, selective benefits produced a death rate that was as low as 1/1000 of the
277 baseline mortality ($s_m = 0.001$), and selective costs could increase baseline mortality by as much as 2
278 times ($s_m = 2$). In exploratory simulations, values of $s_m > 2$ tended to result in rapid and consistent
279 extinction of the trait.

280 We also varied the rate of dispersal, which was measured as the per-day probability that an
281 individual disperses from a group (Table 1). We assumed that dispersal was more likely for groups in
282 which the number of individuals of a particular sex was above the initiating values for the number of
283 individuals for that sex, thus using a procedure similar to that described above for mortality to maintain
284 the initial population structure. Once dispersal was initiated, individuals were capable of entering a new
285 group as soon as the next day. The dispersing individual moved in a random walk on the two-dimensional
286 lattice of cells representing the different social groups. The lattice was bounded spatially and was not
287 reflective; thus, a dispersing individual that hit a boundary did not move in that time step. When floaters
288 entered a new group, they were capable of transmitting cultural traits as early as the next daily time step
289 of the simulation.

290 In summary, group composition was adjusted to maintain initial, user-specified values by
291 preferentially adding individuals to groups with a deficiency in males or females through births and
292 removing individuals from groups with an excess number of males or females through dispersal events.

293

294 **Sampling Parameter Space and Simulation Procedures**

295 To explore how different parameters influence cultural dynamics, we undertook multivariate analysis
296 using *random sampling*. Random sampling was conducted using Latin hypercube sampling (Blower and
297 Dowlatabadi 1994; Seaholm et al. 1988; Rushton et al. 2000), which is a type of stratified Monte Carlo
298 sampling that has been used in epidemiological modeling and is more efficient in this context than

299 random sampling regimes or those that include all possible parameter values (Blower and Dowlatabadi
300 1994; Seaholm et al. 1988). Seven parameters were varied in the Latin hypercube sample: transmission
301 model, group size, transmission probability, background mortality, net benefit of the cultural trait, rate of
302 dispersal, and a spatial versus non-spatial dispersal model. Table 1 gives ranges of parameter values. The
303 discretely coded parameters (transmission model, spatial model) were represented as continuously
304 varying traits in the Latin hypercube sample, which were then binned into equal numbers of the discrete
305 traits. We assessed the sample size needed for the Latin hypercube sample by computing the theoretical
306 variance and relative bias of parameter estimates for a range of possible sample sizes. To obtain rough
307 approximations of the aforesaid variance and bias, we fit preliminary models from a few pilot simulation
308 runs. From these computations, we determined that a sample size of 1500 would be sufficient to
309 investigate the effects of parameter variation shown in Table 1.

310 As noted above, each simulation run continued until the prevalence of the cultural trait reached
311 equilibrium or prevalence fell to 0 (i.e., the cultural trait went extinct). For cases in which the trait
312 persisted, equilibrium prevalence was determined empirically. Specifically, the simulation was stopped
313 when six inter-related conditions were met. The cultural trait had (1) spread to all groups (even if
314 subsequently going extinct in one or more groups). The correlation between time and prevalence was (2)
315 non-significant at $P > 0.05$ and (3) explained less than 1% of the variation over the previous window of
316 200 time steps. Similarly, we examined the standard error of overall prevalence and required that it
317 became (4) non-significant at $P > 0.05$ and (5) explained less than 1% of the variation over the previous
318 200 time steps. Finally, we required that (6) the median standard error of overall prevalence was less than
319 the median for 200 time steps. We also examined variation in the time to equilibrium, defined as the first
320 time step in which the estimated equilibrium value was reached, and we investigated factors that led to
321 extinction of the trait. Figure 1 provides an example from one simulation run. The trait spread rapidly and
322 reached an equilibrium prevalence of about 0.80 among individuals in the population after approximately
323 500 time steps. From this, the equilibrium prevalence was calculated as 0.798 and the time to equilibrium
324 following infection of all groups occurred on day 504. To satisfy the criteria for identifying equilibrium,

325 the actual simulation ran for an order of magnitude time longer than the time to equilibrium, with these
326 criteria finally satisfied on day 5537.

327

328 **Analyses of Simulation Output**

329 We analyzed the output from the simulation using both generalized linear models (GLMs) and regression
330 and classification trees (De'ath and Fabricius 2000; Roff and Roff 2003). We constructed three linear
331 models to explain the simulation outcomes in terms of their parameters. First, all variables were scaled to
332 the unit interval so that the magnitudes of their fitted effects could be compared on an absolute scale. To
333 test for possible interaction effects among the simulation settings, we fit each model using two sets of
334 explanatory variables: a *reduced set* incorporating only main effects and a *full set* including all possible
335 interactions. The reduced set was comprised of the seven variables in Table 1 and the particular
336 interaction of background mortality (*m*) and the cost multiplier of the trait (*c*), both of which were
337 hypothesized to drive the response. The second set included these factors along with all 27 possible
338 pairwise interactions. For each of the three outcomes, the full and reduced models were compared using
339 the likelihood ratio test and Wald test (McCullagh and Nelder 1989) to assess the significance of the full
340 set of pairwise interactions. All linear models were estimated using standard packages from the R
341 statistical software.

342 Regression and classification trees were calculated for the analysis of extinction probability and
343 time to equilibrium using the Statistics Toolbox in MATLAB v. 7.0. We split impure nodes when the
344 number of observations for that node was 100 for regression trees (time to equilibrium analysis) and 10
345 for classification trees (extinction analysis). After creating an initial tree using the simulation output, we
346 used 10-fold cross-validation to identify the pruning level with the minimal cost (De'ath and Fabricius
347 2000), identified as the tree with the minimum error rate. Using this pruned tree, we calculated the
348 percentage of variance explained by comparing predicted and observed values for the regression trees.
349

RESULTS

General Patterns

The simulation model produced a diversity of outcomes, with some traits quickly going extinct and others reaching an equilibrium in which the majority of individuals in the population expressed the trait. These variable outcomes reflected both stochastic effects and the effects of the parameters on the simulation dynamics. Among the 1500 simulations, the cultural trait persisted in 52.5% of the runs, as defined by the equilibrium conditions described in the Methods; in the remaining simulation runs, the cultural trait went extinct. Of the simulations resulting in trait persistence, the model ran for an average of 1513 time steps (range: 453 to 11,198 time steps). In cases of extinction, the model ran for an average of 842 time steps (range: 1 to 7,477 time steps). In cases of trait persistence, the average proportion of individuals expressing the trait was 0.931 (range: 0.19 to 1.0) and the time to reach this equilibrium “prevalence” was 447 days (range: 18 to 8,893 days). In cases of extinction, the trait spread to an average of 81.2 groups prior to going extinct (range: 1 to 144). Thus, even traits that eventually went extinct often spread widely in the population.

The net benefit of the trait varied in the Latin hypercube sample (along with other parameters in Table 1). In general, traits with higher costs tended to more commonly go extinct, while higher benefits favored the establishment of a cultural trait (Figure 2). Remarkably, in 57.7% of simulations of costly traits, the trait managed to spread to all 144 groups in the population (although not all groups necessarily had the trait simultaneously). In 68% of these cases of pervasive spread, however, the costly trait subsequently went extinct. Thus, costly social traits spread widely in the simulation, but these traits typically fail to reach a stable equilibrium and eventually go extinct. The analyses below provide more insights into how costs impact trait establishment and spread.

Probability of extinction

We first investigated the factors that influence the probability of extinction. We fit a logistic regression

376 model for the full and reduced variable sets, treating extinction as the binary outcome for all 1,500
377 simulations. Using the Wald test for the significance of the pairwise interaction effects in the full model,
378 we found them to be non-significant ($\chi^2_{27} = 8.31; p = 0.99$). Consequently, we settled on the reduced
379 model (Table 2). The main drivers in this model are trait cost, background mortality, transmission
380 probability and group size. We found that group size has a strongly negative effect on the probability of
381 extinction, illustrated in the first panel of Figure 3. The effect of trait cost and background mortality on
382 extinction was stronger (based on the parameter estimates) and is shown in the first panel of Figure 4. The
383 probability of extinction increases with cost, and is further driven by an interaction effect with
384 background mortality. Transmission probability (β) had a negative coefficient, indicating that increases in
385 β reduced the risk of trait extinction. We also found that higher rates of dispersal reduced the probability
386 of extinction, although this effect only approached significance ($p=0.07$). In contrast to these factors, the
387 coefficients associated with the transmission model and spatial models were negligibly small and not
388 significant, indicating that the results were similar across all transmission models and were minimally
389 impacted by either local dispersal or transmission biases.

390 To visualize the effects of the parameters on the probability of extinction, we also ran a
391 classification tree analysis. The resulting tree (Figure 5) revealed that traits were more likely to go extinct
392 at higher costs and higher mortality. The tree also predicts that for beneficial traits, a higher transmission
393 probability (β) reduces the probability of extinction. The classification tree analysis confirmed the
394 interaction between costliness of the trait and mortality in the generalized linear model (Table 2), but
395 failed to detect an effect of group size. The tree also provided no evidence for effects of local dispersal or
396 transmission model.

397

398 **Equilibrium Prevalence**

399 The second set of analyses involved the factors that influenced the proportion of individuals that exhibited
400 the cultural trait at equilibrium (i.e., equilibrium prevalence). For the 787 simulations in which the trait

401 did not go extinct, we fit a binomial GLM for prevalence, modeling the mean proportion of individuals
402 who have the trait at the end of the simulation. We again tested for interaction effects additional to
403 mortality x cost using the likelihood ratio test and found none to be significant ($\chi^2_{27} = 26.07$; $p = 0.49$),
404 leading us to accept the reduced model. The resulting regression estimates are shown in Table 3.

405 As expected, most of the coefficients for the extinction model were reversed in sign for the model
406 describing equilibrium prevalence (i.e., factors that increase prevalence should decrease the probability of
407 extinction). The relative magnitudes of the parameters varied. In the binomial GLM for prevalence, the
408 transmission probability (β) had a major impact on prevalence of the cultural trait, with greater values of
409 β increasing equilibrium prevalence. Group size (Figure 3), background mortality and trait cost all
410 negatively impacted prevalence, with a strong interaction between mortality and cost (Figure 4). The
411 results were again similar across most transmission and spatial models, although we found a nearly
412 significant effect indicating that consensus transmission results in higher prevalence (as compared to the
413 random model).

414

415 **Time to Equilibrium**

416 We analyzed the factors that influence the speed with which the trait spreads in the population by again
417 focusing on the 787 simulations in which the traits reached an equilibrium. Since the equilibrium times
418 were highly right-skewed, we fit a log-linear model of time to equilibrium. In this case, the full model,
419 with main effects and all pairwise interactions, yielded a significantly better fit than the reduced model,
420 leading the likelihood ratio test to reject the reduced model ($\chi^2_{27} = 49.31$; $p = 0.005$). Table 4 shows the
421 most significant effects and interactions from the full model, which explained 75% of the variation in log-
422 transformed time to equilibrium.

423 The major drivers of time to equilibrium were group size, dispersal rate, cost of the trait and
424 transmission probability. Time to equilibrium decreased with larger group sizes (Figure 3) and greater
425 dispersal rates (Figure 6). A strong negative coefficient indicated that greater transmission probabilities

426 (β) also increase the rate at which a cultural trait penetrates a population (Figure 6). Among this set of
427 simulations that resulted in equilibrium, higher costs were associated with more rapid establishment of
428 equilibrium prevalence. The analysis also revealed several significant interaction effects. The
429 combination of greater transmission probability and greater cost and background mortality increased time
430 to equilibrium substantially. While the results were similar across transmission models, time to
431 equilibrium was generally much greater in the spatial model than the non-spatial model, as reflected in
432 both panels of Figure 6.

433 We also ran a regression tree analysis to illustrate the effects of the parameters in Table 1 on the
434 time to equilibrium, which was log-transformed for this analysis (Figure 7). The resulting tree explained
435 64% of the variation in the time required for a cultural trait to reach equilibrium. Dispersal rate was found
436 at the highest node, as well as in lower parts of the regression tree; in all cases, higher rates of dispersal
437 reduced the time required for a trait to reach equilibrium. Subsequent effects were different at low and
438 high rates of dispersal. When the probability of dispersal was less than 0.0047, group size played a major
439 role in influencing the time required for a trait to reach equilibrium; with group sizes less than 20.3, the
440 time to equilibrium was predicted to be nearly one order of magnitude higher (based on the log-
441 transformed durations given on the tips of the tree). By contrast, at higher rates of dispersal, a non-spatial
442 model resulted in a marked increase in the rate of trait spread at the population level (predicted values of
443 2.50 for local dispersal, versus 2.13 for random dispersal to any group). As expected, a higher
444 transmission probability increased the rate of trait spread. However, prestige and consensus transmission
445 again had no effects on cultural trait dynamics at the population level.

446

447

DISCUSSION

448

449 In animal societies, most social learning occurs among individuals within groups, and the same was likely
450 to be true of prehistoric human populations. In socially structured populations, establishment of a cultural

451 trait at the population level requires that the trait spread beyond a single social group, yet with few
452 exceptions (e.g., Henrich and Boyd 1998; Boyd and Richerson 2002), most work on cultural transmission
453 has focused on within-group dynamics. We investigated a set of transmission mechanisms, including
454 biases due to prestige or consensus transmission, and social system parameters to determine which factors
455 influence cultural dynamics in socially structured populations. Among the transmission parameters, the
456 transmission probability (β) affected trait persistence and equilibrium levels of trait prevalence, with
457 higher transmission probability resulting in higher prevalence (and also more rapid spread of the trait).
458 Among the social system parameters, increased group size favored the establishment of the trait and
459 enhanced its spread, while increased mortality and trait costs increased the probability of trait extinction
460 and reduced equilibrium prevalence. Remarkably, we found that transmission biases involving prestige or
461 consensus effects had no significant effects on trait dynamics at the population level (although consensus
462 transmission showed evidence for some weak effects on equilibrium prevalence). Another interesting
463 result was that local dispersal slowed the rate of trait spread in the population, but had no significant
464 effects on the probability of extinction or prevalence.

465 One conclusion from these analyses is that the effects of biased transmission involving consensus
466 and prestige effects were minor relative to other factors. Biased transmission may have minor effects
467 because cultural traits can spread rapidly within groups, and the mass-action effect of increasing the
468 number of animals acting as performers may outweigh any minor adjustments in transmission probability
469 caused by prestige or consensus mechanisms. We designed the simulation so that the mean rate of
470 transmission would be approximately equal across the three transmission models that we used. We
471 suggest that effects of biased transmission, if they exist, are weaker than other effects, such as the
472 costliness of the cultural trait.

473 We acknowledge, however, that different implementation of the consensus and prestige models
474 could alter this conclusion. Instead of our simple model of “linear majority rules” for the consensus
475 model, for example, the probability of transmission could have a different shape, including possibly a

476 more rapid rise at lower prevalence, which could alter the dynamics to speed up trait spread and reduce
477 extinction risk. Similarly, we assumed that the effect of dominance was linear, and that only the rank of
478 the performer was relevant (rather than the difference in the ranks of observer and performer). If we
479 assumed instead that dominants were also more likely to acquire beneficial traits – i.e., that a link exists
480 between dominance rank and the acquisition of beneficial traits – this could impact cultural trait dynamics
481 (e.g., Boyd and Richerson 1985; Boesch and Tomasello 1998; Henrich and Gil-White 2001; Henrich and
482 McElreath 2003). Similarly, we might expect that migration is more likely by lower-ranking individuals.
483 In such a case, the rate of trait spread could slow, as lower-ranking individuals moving into a new group
484 would be less likely to be copied. Thus, our model provides a foundation for exploring the conditions
485 under which prestige and consensus mechanisms have an impact on par with the effect of social system
486 parameters.

487 An almost limitless set of cultural transmission mechanisms is possible (e.g., Laland 2004), and
488 thus we were forced to select a small subset of key factors that might bias transmission (Boesch and
489 Tomasello 1998; Henrich and McElreath 2003). We further aimed to implement these transmission
490 models as simply as possible, for example by using linear transformations of the probability of
491 transmission based on dominance rank of culturally-skilled individuals (prestige model) or the percentage
492 of animals in the group that expressed the trait (consensus model). Future research could consider variants
493 on these models, and also constraints. For example, there could be greater opportunities for transmitting
494 traits within the sexes than between them (e.g., clothing fashions). Similarly, social groups themselves are
495 often composed of networks of interactions involving kin, alliances and sexual partners, and some traits
496 might be transmitted vertically from mother to offspring. Age effects might also be important, with
497 transmission to an observer more likely during age-specific periods when learning is more likely, or the
498 behaviors themselves only expressed at a particular life stage; such effects would be expected to slow the
499 spread of the cultural trait. It would also be interesting to investigate competition among traits that have
500 different transmission mechanisms or benefits to individuals with the traits. Finally, it is worth keeping in

501 mind that the prestige and consensus models are not mutually exclusive. Although we treated them
502 separately here, it might be interesting to investigate their combined effects on cultural trait dynamics.

503 The social factors that we investigated have clear analogies to the spread of infectious disease in
504 socially structured populations, particularly for costly cultural traits that can negatively impact fitness.
505 Returning to the case of individuals copying dominants, for example, similar patterns can be found with
506 sexually transmitted diseases (STDs). In epidemiological models of STDs in animals, more dominant
507 individuals are more likely to be infected, and thus more likely to spread the disease (Thrall et al. 2000;
508 Kokko et al. 2002). Similarly, disease spread can be impacted by group size, patterns of dispersal, and
509 mortality rates (Anderson and May 1991; Wilson et al. 2003; Nunn and Altizer 2006).

510 However, important differences exist between the spread of cultural traits and infectious disease,
511 particularly with regard to the selective benefits of many cultural traits (in comparison to costs usually
512 associated with disease). As compared to disease transmission, for example, cultural evolution in socially
513 structured populations is likely to set up a group selection scenario, in which advantageous cultural traits
514 could lead to larger groups and higher rates of dispersal (Wilson 1983; Soltis et al. 1995). In addition,
515 cultural traits in animals and early humans tend to spread directly between individuals in close proximity,
516 while infectious diseases can be transmitted indirectly (e.g., through vectors or contaminated soil). Lastly,
517 innovation is possible in cultural systems, even if it is often “primed” by previous innovations or cultural
518 structures, whereas infectious diseases do not typically arise *de novo* in a population (although they could
519 appear to do so when spillover from a reservoir host occurs, or when hybridization among pathogens
520 opens up new hosts to exploit). In other words, you do not actually have to have direct contact with an
521 “infected” individual to get a good idea; individual learning can also play a role, and is ultimately
522 responsible for the origin of cultural behaviors.

523 A beneficial cultural trait is expected to spread rapidly and reach high prevalence, and our
524 simulations confirmed this expectation under a wide range of conditions. Advantageous behaviors are
525 also likely to reduce the likelihood of group extinction, which could create opportunities for group
526 selection in natural situations. On the other hand, one can easily think of cultural traits that are clearly not

527 advantageous for survival, yet spread throughout populations. These are superficially similar to
528 establishment of infectious diseases, which entail a cost to the host but still can reach a stable equilibrium.
529 Our simulations suggest that costly cultural traits can spread widely, but as costs increase the probability
530 of extinction also increases.

531 The results of our analysis suggest that the explosion of cultural behaviors and variants in human
532 evolution should have resulted when group size, contact between groups and the benefits of cultural traits
533 increased. Many cultural traits in humans are technological. Hence, these traits would be likely to carry a
534 very strong benefit, favoring their establishment in both species. Second, the higher technological skills
535 seen in human evolution, with the inclusion of many stone tools, could reasonably have led to a reduction
536 in mortality rates. This would have favored the further development of larger social groups, which as we
537 saw in our analysis, favor the establishment of cultural traits. Lastly, in comparison to other apes, humans
538 live in more dispersed social groups, in much larger home ranges, and with regular contact including
539 more than only direct neighbors; these social groups likely had more contact with other groups as trade
540 took place. Our results suggest that these contacts would have increased the rate at which cultural traits
541 spread, and might have reduced the probability that they went extinct.

542 To conclude, it is useful to return to the four questions that we posed in the Introduction. The
543 simulations revealed that local dispersal increases the time required for a trait to reach equilibrium
544 (Question 1), and that cultural traits are buffered from extinction in larger groups (Question 2). We also
545 found that higher rates of dispersal increase the rate of trait spread in the population, with weaker effects
546 (approaching significance) on the probability of extinction. In terms of mortality, we found that mortality
547 rates have an impact on cultural dynamics, including through effects of the cultural trait on mortality itself
548 (Question 3). Thus, higher costs of the trait and higher background mortality increase extinction
549 probability and reduce the prevalence of the trait. Lastly, we found that the rate of transmission impacts
550 all of the outcome variables that we examined, but that transmission mechanisms involving prestige or
551 consensus had no statistically discernible effects on trait dynamics (Question 4). As noted above, this
552 conclusion could be sensitive to how prestige and consensus transmission were implemented, and

553 therefore should be explored further in future research. Along similar lines, it would be interesting to
554 explore other transmission mechanisms that might influence the spread of traits among contact networks
555 within groups, including vertical transmission, sex- and age-specific transmission, and patterns of kinship.
556

556

Acknowledgements

557

558 We thank Richard McElreath, Mathias Franz, Derek Roff, Monique Borgerhoff Mulder and members of
559 the “culture group” at UC Davis and the “primate group” at Harvard for helpful suggestions and
560 discussion. Markus Bayer provided help compiling the MATLAB code and using the computer cluster.

561 This research was supported by the Max Planck Society.

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- 661

Figure Legends

661

662

663 **Figure 1. Detecting equilibrium.** Plot shows output from one simulation run using default parameters.

664 The text provides details on equilibrium prevalence and time step at which this was first reached, as

665 calculated by the simulation program.

666

667 **Figure 2. Trait persistence in relation to net benefits of the cultural trait.** Bars indicate number of
668 cases in which the trait reached an equilibrium, as compared to the alternative of going extinct. Increasing

669 benefits are shown to the left of the central line, while increasing costs are shown to the right. Results are

670 based on the output from 1500 simulations. As the Latin hypercube sample provided a flat distribution for

671 the values, including costs of the trait shown along the x-axis, this plot reveals that higher costs are

672 associated with higher extinction, but that some costly traits nonetheless reach an equilibrium.

673

674 **Figure 3. Modeled extinction, prevalence and time to equilibrium by size.** The three panels show the

675 modeled extinction rate, prevalence and time to equilibrium by scaled group size. The rates correspond to

676 default values of the other settings.

677

678 **Figure 4. Modeled extinction and prevalence by background mortality and trait cost.** The two panels

679 show the modeled extinction and prevalence rates across a range of cost levels at two different

680 background mortality rates (scaled on the interval 0 to 1). The other settings are at default values.

681

682 **Figure 5. Classification tree for extinction.** Extinction is indicated as a dichotomous trait on the tips of

683 the tree, where “survive” indicates that the trait is predicted to reach an equilibrium rather than go extinct.

684

685 **Figure 6. Modeled time to equilibrium by dispersal rate.** The plots show the effects of dispersal rate,

686 transmission probability and spatial model on time to equilibrium. The other settings are at default values.

687

688 **Figure 7. Regression tree for time to equilibrium.** Time to equilibrium is log-transformed, with

689 predicted values shown at the tips of the tree.

690

690 **Table 1. Parameter values investigated in the simulation.**

Symbol	Definition	Range of Values
g	average number of females in groups, g_m	4 to 40
d	baseline probability of dispersal per day	0.0001 to 0.02
β	per-contact transmission probability	0.0001 to 0.04
m	baseline mortality rate per day	0.0001 to 0.04
c	benefit or cost of cultural trait (multiplier for m)	0.001 to 2
S	spatial vs. non-spatial model (categorical)	0,1
T	transmission model (categorical, corresponding to random, consensus and prestige transmission)	0,1,2

691

692

692 **Table 2. Parameter estimates in the logistic regression model for extinction probability.**

Parameter	Estimate	Std. Error	p-value
Intercept	-3.35	0.68	<0.001
<i>g</i>	-1.42	0.38	<0.001
<i>d</i>	-0.67	0.37	0.070
β	-1.81	0.39	<0.001
<i>m</i>	0.04	1.03	0.971
<i>c</i>	6.01	0.92	<0.001
<i>T</i> (<i>consensus vs. random</i>)	0.37	0.26	0.153
<i>T</i> (<i>prestige vs. random</i>)	0.36	0.27	0.178
<i>S</i> (<i>spatial vs. non-spatial</i>)	0.16	0.21	0.453
<i>m * c</i>	7.93	1.92	<0.001

693

694

694 **Table 3. Parameter estimates in the binomial GLM model for trait prevalence.**

Parameter	Estimate	Std. Error	p-value
Intercept	2.43	0.18	<0.001
<i>g</i>	1.84	0.12	<0.001
<i>d</i>	0.12	0.11	0.293
β	2.91	0.13	<0.001
<i>m</i>	-0.79	0.24	0.001
<i>c</i>	-1.95	0.31	<0.001
<i>T (consensus vs. random)</i>	0.14	0.08	0.065
<i>T (prestige vs. random)</i>	-0.09	0.08	0.214
<i>S (spatial vs. non-spatial)</i>	0.04	0.06	0.455
<i>m * c</i>	-4.89	0.58	<0.001

695

696

696 **Table 4. Significant parameter estimates in the log-linear model for time to equilibrium.**

Parameter	Estimate	Std. Error	p-value
Intercept	7.52	0.22	<0.001
g	-1.68	0.26	<0.001
d	-1.21	0.25	<0.001
β	-1.56	0.27	<0.001
c	-1.23	0.33	<0.001
S (<i>spatial vs. non-spatial</i>)	0.82	0.15	<0.001
$d * \beta$	-0.47	0.23	0.042
$\beta * m$	0.69	0.23	0.003
$\beta * c$	1.38	0.33	<0.001
(27 others)			

697

Fig. 1

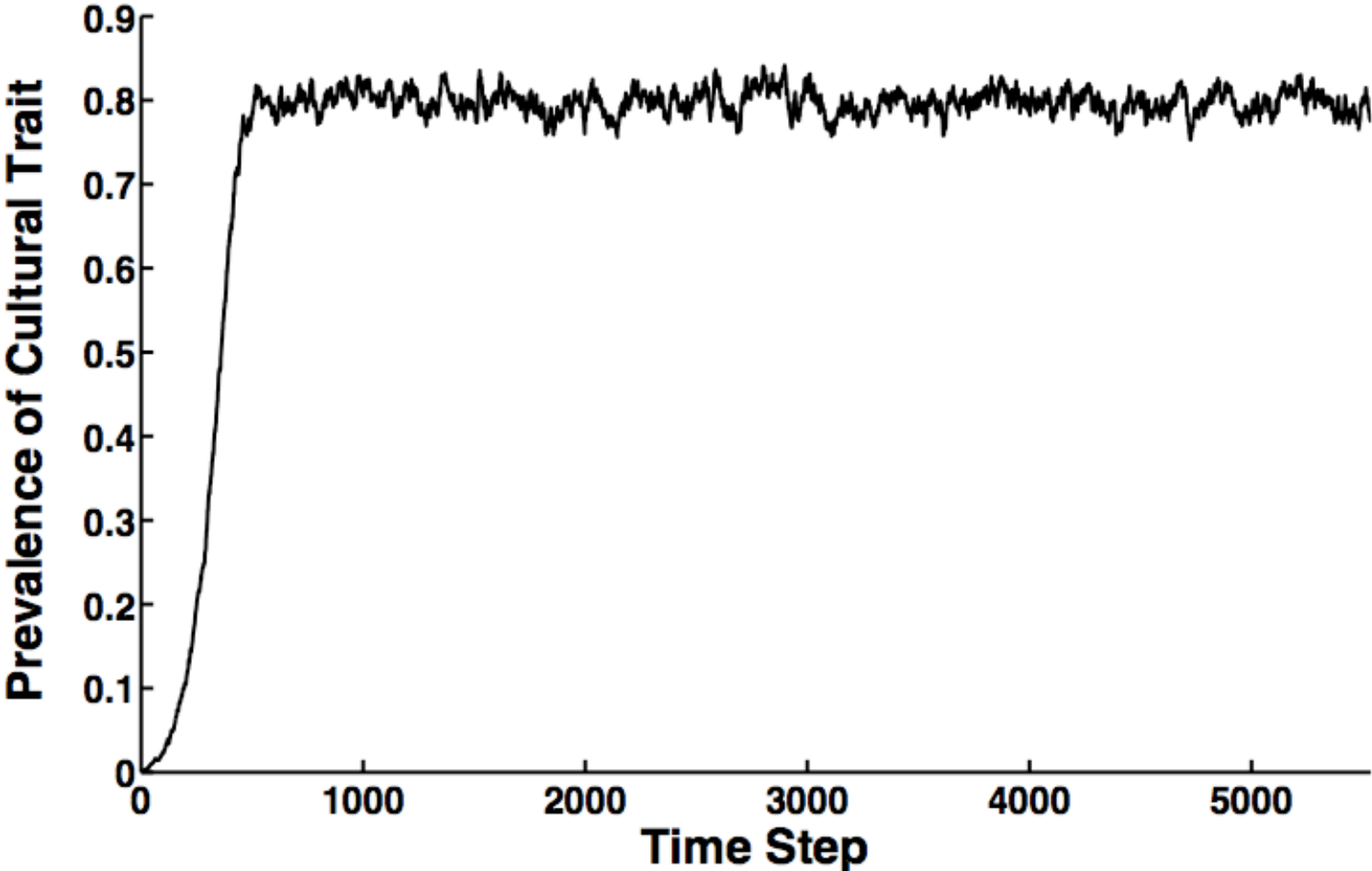


Fig. 2

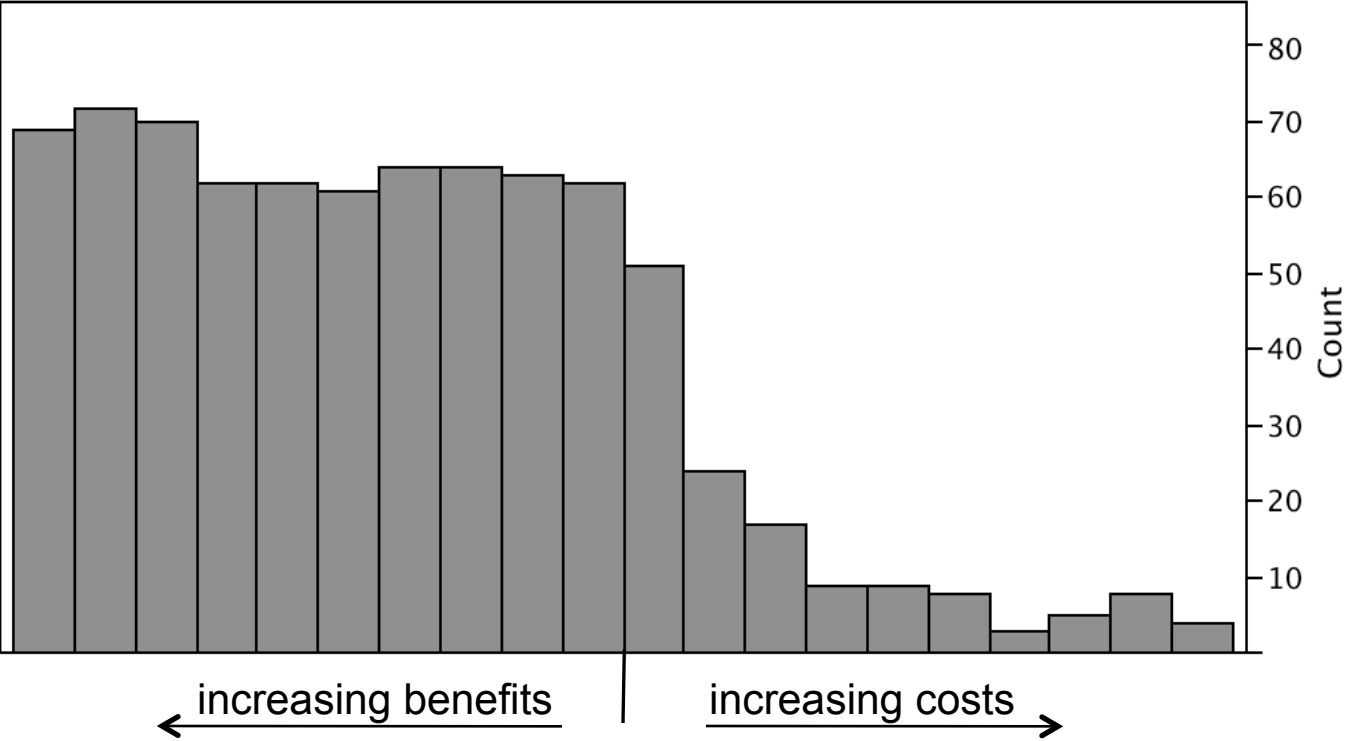


Fig. 3

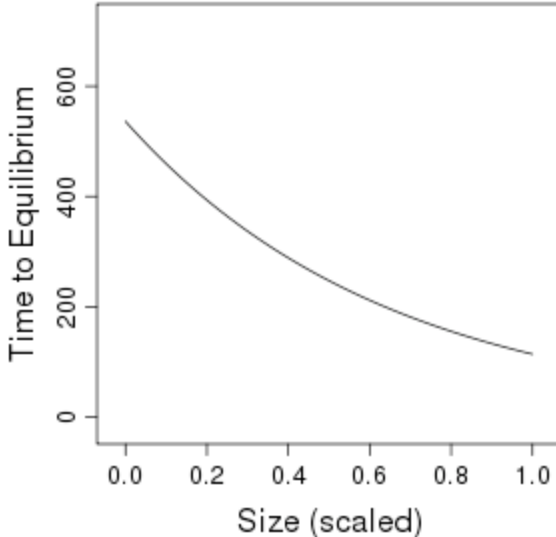
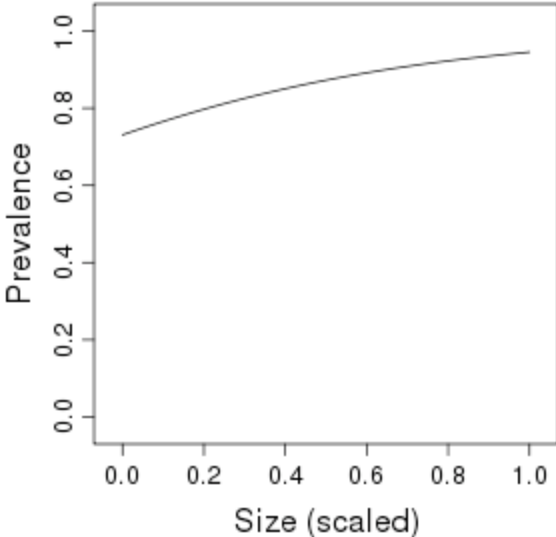
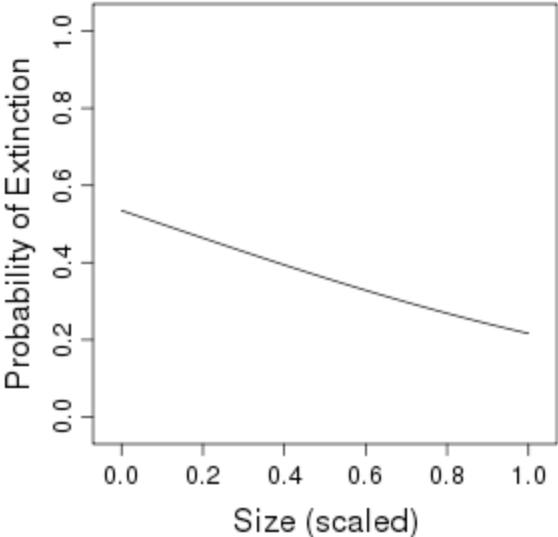


Fig. 4

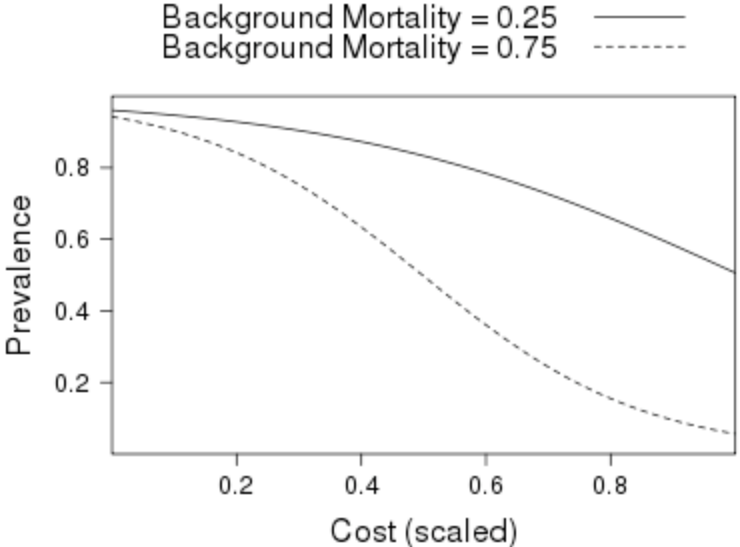
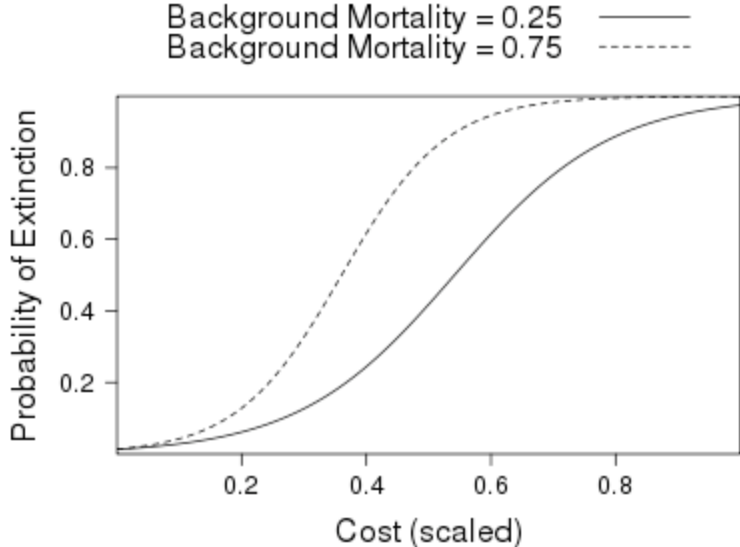


Fig. 5

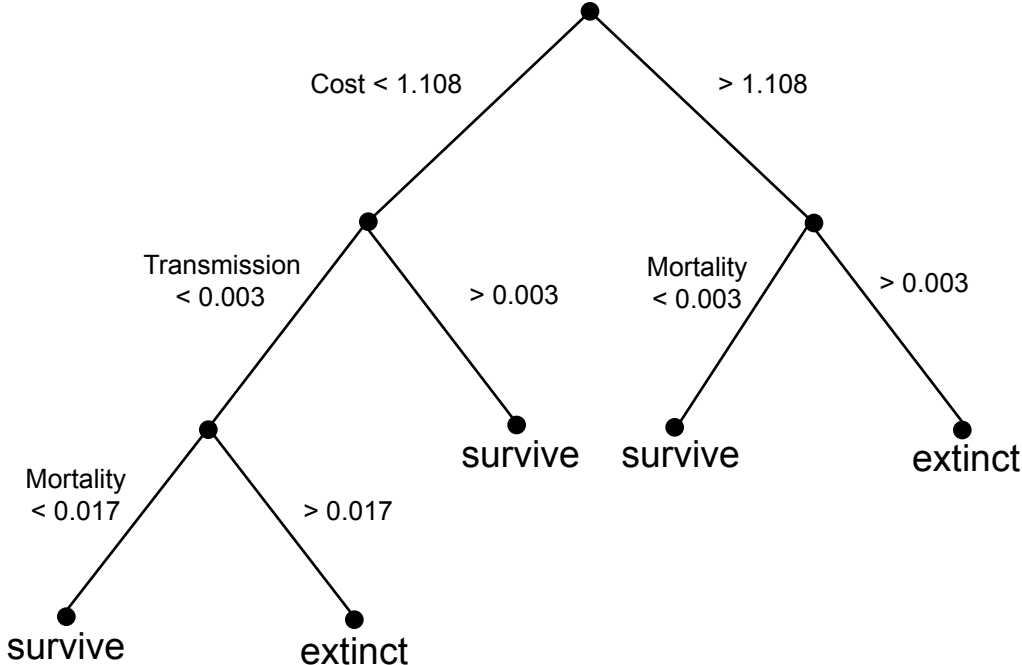


Fig. 6

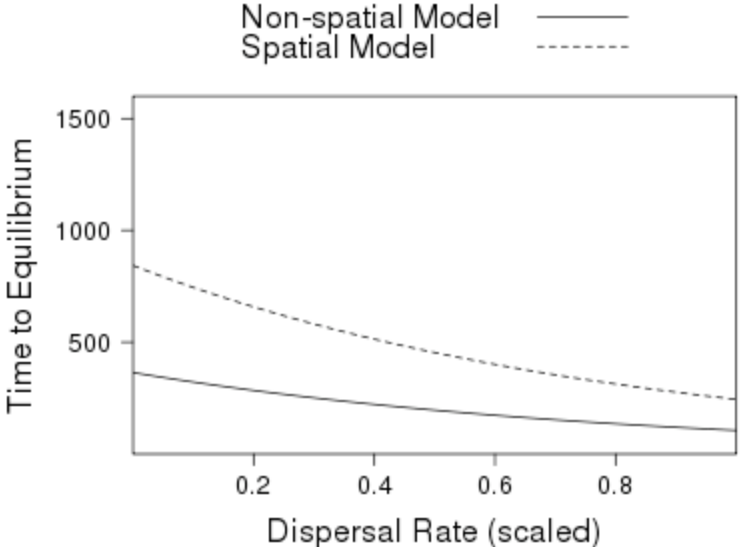
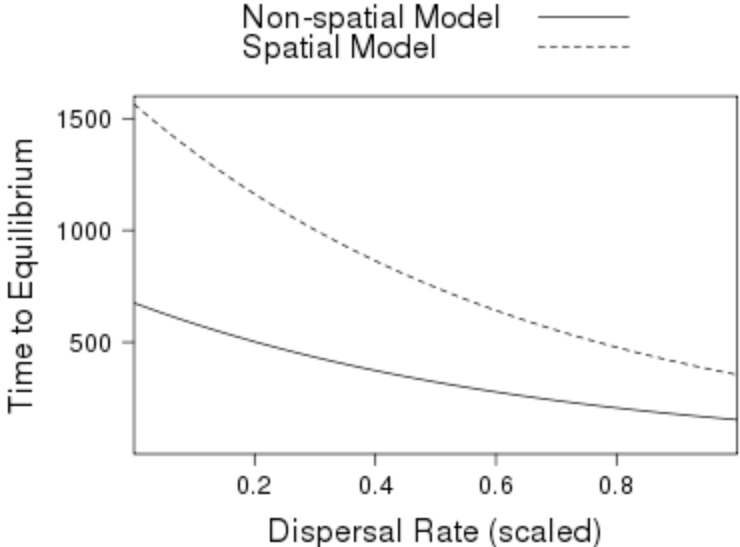


Fig. 7

