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Evolutionary dynamics of culturally transmitted, fertility-reducing traits

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Abstract

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19   Human populations in many countries have undergone a phase of demographic
20   transition, characterized by a significant reduction in fertility at a time of increased
21   resource availability. Typically, the reduction in fertility is preceded by a reduction in
22   mortality and a consequent increase in population density. Various theories have been
23   proposed to account for the demographic transition process, including maladaptation,
24   increased parental investment in fewer offspring, and cultural evolution. Aspects of
25   cultural evolutionary processes in relation to demographic transitions have been studied
26   with mathematical models. The reason for the observation that fertility reduction tends
27   to be preceded by a decline in mortality, however, remains poorly understood. Using a
28   variety of mathematical modeling approaches, we show that the cultural selection of low
29   fertility traits crucially depends on the population death rate: if mortality is relatively high,
30   the trait fails to spread. If mortality is reduced, the trait can spread successfully, thus
31   offering an explanation for the observed trends. Computer simulations can reproduce
32   the central characteristics of the demographic transition process, including significant
33   changes in reproductive behavior within only 1-3 generations. A model tracking the
34   continuous evolution of reproduction rates through "errors" in the cultural transmission
35   process predicts fertility to fall below replacement levels if death rates are sufficiently
36   low. This can potentially explain the very low ideal family sizes in Western Europe.

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Introduction

In the 19th century, some human populations displayed a demographic transition from relatively high fertility and high mortality towards a significantly reduced fertility and lower mortality [1-4]. This first occurred in more developed parts of the world, such as Europe, the United States, Japan, Australia, and New Zealand, and coincided with an overall increase in resource availability (judged by economic considerations). In Western European countries, fertility has declined below replacement levels since the 1970s and 1980s [5,6], and this also applies to the perceived ideal family size. In German speaking countries the ideal family size has fallen below replacement levels, about 1.7 children [6].

Similarly, it has been observed that fertility reduction tends to be more pronounced in population segments that are economically advantaged than in poorer segments [1]. This is in contrast to trends observed before these demographic transitions, when increased wealth was associated with higher fertility [1,7].

An interesting characteristic of demographic transitions is that the reduction in fertility tends to be preceded by a reduction in the death rate of individuals, and by a consequent temporary population growth phase [4,8,9]. Transitions towards a reduced rate of reproduction following a rise in wealth and resources can be considered paradoxical, especially in the context of evolutionary biology [1,10]. According to

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60 evolutionary thinking, individuals evolve to maximize their reproductive potential, and to

61 translate increased resource availability into higher reproductive success.

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63   A number of theories have been put forward to account for demographic

64 transitions towards reduced fertility [1,11]. According to one line of argument, the

65 transition to reduced fertility might be maladaptive. That is, humans employ behavioral

66 strategies that used to be advantageous in previous times, but currently result in

67 behaviors that are not adaptive due to recent significant changes in socio-economic

68 factors. Another line of argument suggests reduced fertility to be adaptive, because the

69 current environment favors the production of few offspring with large parental

70 investment rather than the generation of more offspring with lesser parental investment

71 per child. This might be a significant consideration in parts of the world where

72 competition among individuals for jobs and careers is fierce. A third mechanism that

73 has been invoked to explain the observed decline in fertility is non-genetic, cultural

74 evolution. According to this argument, behavior that leads to reduced fertility in certain

75 influential individuals is copied by other individuals in the population, resulting in a

76 spread of this trait throughout the population. This explanation has the advantage that

77 cultural evolution can occur on much faster time-scales than genetic evolution, which is

78 required to account for the relatively fast observed rate of transition to lower fertilities in

79 human populations.

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81   The dynamics of cultural transmission have been studied extensively with

82   mathematical models [12-19], and these approaches have also been applied to the

83   analysis of demographic transitions and the evolution of small family sizes, in particular

84   by the group of Marc Feldman [20-22]. In the simplest forms, such models are given by

85   ordinary differential equations that describe the spread of the cultural trait, similar to

86   infection models [12]. On a more complex level, age-structured models were formulated

87   [20,21] showing that cultural transmission dynamics can result in demographic

88   transitions on time scales that are similar to those observed in human data. The spread

89   of cultural traits that affect fertility, survival, or both was investigated and the effect of

90   these traits on the demographic structure of the population was investigated. The roles

91   of vertical, oblique, and horizontal transmission of the trait were examined, and the

92   models indicated that horizontal and oblique learning could accelerate the spread of the

93   cultural trait, compared to vertical transmission alone [20]. In an earlier study, it was

94   shown that cultural niche construction could be an important component that contributed

95   to the transition to reduced fertilities [21]. According to this mechanism, the first trait to

96   spread is one of valuing education, which provides an environment that promotes the

97   spread of a second, fertility-reducing trait. If the trait of valuing education is further

98   associated with reduced mortality of individuals, the model predicts that the decline in

99   fertility is preceded by a reduction in the population death rate, as observed in

100   demographic data. These models were examined further in the context of spatial

101   population structure, formulated as niche construction models in metapopulations [22].

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103   In these studies, the increased survival / lower death rate of the population was

104   either considered a culturally transmitted trait (similar to fertility reduction), or it was

105   coupled to a culturally transmitted trait, e.g. by assuming that appreciation of education

106   correlates with increased viability. Here, we consider cultural transmission models

107   where the population death rate is an independent, exogenous variable that can be

108   modulated (reduced) over time, e.g. as a consequence of sanitary, medical or

109   technological advances, and investigate the effect of such changes on the ability of a

110   fertility-reducing trait to spread. We study the spread of the fertility-reducing trait in

111   spatially structured and non-spatial models, as well as in models with and without age

112   structure. We first consider a model with two populations, a fast and a slow reproducing

113   one, and subsequently consider models where the reproduction strategy is a continuous

114   trait. Because the overall death rate of individuals negatively correlates with the

115   economic development and the amount of resources available to the population, this

116   analysis sheds further light onto the correlation between resource availability and the

117   rate of population growth.

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A two-dimensional agent-based model with asexual reproduction

121   We begin by examining the spread of a fertility-reducing cultural trait with the help of a

122   two-dimensional, stochastic agent-based model (ABM) that describes population

123   dynamics on a 2D grid of size nxn. We will refer to this model as ABM1. Two

124   populations are considered which reproduce with a fast and slow rate, respectively.

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125   During each time step (representing a generation), the grid is randomly sampled 2M

126   times, where M is the total number of individuals currently present. When an individual

127   is picked, it can undergo either a birth-death update, or a cultural transmission update

128   (with equal probabilities). If the birth-death update is chosen, the individual reproduces

129   with a probability R_f and R_s, depending on whether this is a fast or slow reproducer. A

130   spot is chosen randomly from the eight nearest neighbors. If that target spot is empty,

131   the offspring is placed there, otherwise, the reproduction event is aborted. With an

132   independent probability D, the individual dies; both populations are assumed to have

133   the same death rate.

134   During a cultural transmission update, the individual attempts to change its

135   reproductive strategy with probability C. Given that the cultural transmission update is

136   attempted, the actual change by cultural transmission occurs with the probability defined

137   by the prevalence of individuals with the opposite strategy among the 8 nearest

138   neighbors (including the individual under consideration), see below for more details. The

139   ratio of the constant C to the mean division rate roughly measures prevalence of cultural

140   transmission in the population; it roughly corresponds to the fraction of the individuals in

141   each generation that attempt to change their reproductive strategy based on their

142   neighbors' strategy.

143   A cultural update is performed by gathering the information on the reproductive

144   strategy of the individuals' neighbors, similar to voter models [17,23]. In our model,

145   however, we assume that slow reproducers are more effective at changing a fast

146   reproducer's strategy than vice versa. In particular, when adding up the number of fast

147   and slow reproducers in the neighborhood, there is a probability Q<1 that a fast

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148   reproducer is taken into account, while all slow reproducers are always included. This

149   reflects the assumption that the opinion of a slow reproducer is more influential than that

150   of a fast reproducer. This modeling choice is motivated by the assumption that slow

151   reproducers tend to channel the resources available to them into accumulation of wealth

152   and/or social status, and thus they may appear as more attractive models for imitation.

153

Outcomes of computer simulations for model ABM1

155   We first discuss the effect of the two components underlying the model: the birth-death

156   process and the cultural transmission process. If the model is run with only the

157   reproduction and death processes (without cultural transmission), the only outcome is

158   the persistence of the fast reproducing population and the competitive exclusion of the

159   slower reproducing one. This is straightforward competition dynamics behavior, which

160   underscores the notion that a slower rate of reproduction is a disadvantageous strategy.

161   If the model is run with only cultural transmission (no reproduction and death, but a

162   constant population), it essentially becomes a voter model, where "slow" and "fast" are

163   different opinions held by individuals in the population. As has been described for such

164   models [17,23], the only eventual outcome is that every individual in the population has

165   the same opinion. Which of the two opinions wins, depends on drift dynamics and

166   hence on initial frequencies of the opinions in the population.

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168   When both processes are included, more complex dynamics are observed. Now three

169   outcomes are possible (Figure 1): the fast reproducers win and exclude the slow

170 reproducers; the slow reproducers win and exclude the fast reproducers; both

171 populations coexist in the longer term. Since we study stochastic models, the only

172 eventual outcome is extinction. In what we call "coexistence", the time until one of the

173 populations goes extinct is significantly longer than in the parameter regimes we call

174 "exclusion" (compare Figure 1C to 1A &B). Which outcome is observed depends on

175 several model parameters, most notably the death rate of agents, D. This is shown in

176 Figure 2Ai. Each point on this graph depicts the time until one of the populations goes

177 extinct, depending on the death probability, D. The outcomes are color-coded: purple

178 depicts fast reproducers remaining, and green slow reproducers. At higher death rates,

179 the fast reproducers persist and extinction of the slow reproduces occurs at relatively

180 short time scales. At low death rates, the slow reproducers persist and the fast

181 reproducers go extinct on a relatively short time scale. At intermediate death rates, the

182 time to extinction of one of the populations rises sharply, and either population has a

183 chance to go extinct first. This corresponds to the coexistence regime. Therefore, lower

184 death rates among individuals in the population create conditions in which the cultural

185 transmission of the slow reproduction trait is successful, resulting in an overall reduced

186 level of fertility.

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188 Other parameters further modulate the outcome of the dynamics. Cultural

189 transmission of the low fertility trait is promoted by lower values of Q, i.e. by a reduced

190 influence of fast reproducers on choosing the reproduction strategy during the cultural

191 transmission procedure. Increasing the value of Q results in a lower population death

192 rate that is required for cultural transmission to be successful (Figure 2Aii). The relative

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193   probability for a cultural transmission event to take place, C, is also an important

194   determinant of outcome. As expected, higher values of C promote the cultural spread of

195   the fertility-reducing trait. For lower values of C, lower population death rates are

196   needed for cultural transmission to be successful (Figure 2Aiii).

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199   Including age structure into the agent-based model

200   Rather than considering fast versus slow reproducers, we now modify the agent-based

201   model to consider early versus late reproducers. This model will be referred to as

202   ABM2. While these two concepts are related, a reduction in fertility due to a later age of

203   first reproduction might be relevant to current times where segments of the population

204   with higher degrees of education and more wealth tend to reproduce at later ages. In

205   the agent-based model, we therefore consider four age classes. Individuals are born

206   into age-class 1, at which no reproduction is possible. During each time step, all

207   individuals age by one time unit. After A time units, an individual advances to the next

208   age class. Reproduction can occur in age classes 2 and 3 for early reproducers, and

209   only in age class 3 for late reproducers. In either case, reproduction occurs with a

210   probability R. Age class 4 is a post-reproductive phase, during which the only event that

211   can occur is death. Death can occur in all age classes, but with increasing probabilities

212   for successive age classes, i.e. with probabilities $D_4 > D_3 > D_2 > D_1$. This model has the

213   same properties as the previous one, where we distinguished between slow and fast

214   reproducers. We again observe three possible outcomes: extinction of either early or

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215 late reproducers, or longer-term coexistence (not shown). The influence of parameters

216 on outcome is also the same on a qualitative level. Importantly, the death rate of

217 individuals is again a key determinant of outcome. Since in this model there are different

218 death rates for the different age classes, we multiplied all of the death rates by a factor

219 F, which means that all death rates change by the same amount. In Figure 2B, we

220 plotted the outcome of the dynamics for increasing values of F, which corresponds to

221 increasingly higher population death rates. Again, each point depicts the time until one

222 of the two populations goes extinct. We observe the same trend as before. For higher

223 population death rates, the fast reproducers remain. For low death rates, the slow

224 reproducers remain. For intermediate death rates, we observe coexistence, indicated by

225 a sharp rise in the time to extinction, where either fast or slow reproducers have a

226 chance to persist.

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Complete mixing versus spatial constraints
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230 The spatial nature of the models explored above makes it difficult to obtain analytical

231 insights. In this section, we formulate the same processes under the assumption that

232 individuals mix well. Spatial constraints are most relevant to the cultural transmission

233 aspect of the model because people are most likely to communicate with and consider

234 the opinion of neighboring individuals. Mixing, however, can be assumed if populations

235 are relatively small or information travels more easily through populations.

236

237   **Fast and slow reproducers.** First, we again consider two types of individuals that differ

238   by their reproduction rates. In the context of well-mixed populations, this can be

239   described by ordinary differential equations (see Section 1 of the Supplement for more

240   details of the analysis). Denoting fast reproducers by x_f and slow reproducers by x_s, the

241   model can be written as follows:

242
$$\dot{x}_f = r_f x_f W - dx_f - \beta x_f \frac{x_s}{x_s + \gamma x_f} + \beta x_s \frac{\gamma x_f}{x_s + \gamma x_f}$$

$$\dot{x}_s = r_s x_s W - dx_s + \beta x_f \frac{x_s}{x_s + \gamma x_f} - \beta x_s \frac{\gamma x_f}{x_s + \gamma x_f},$$

243   where $W = 1 - \dfrac{x_f + x_s}{K}$ introduces density dependence, limited by the carrying capacity

244   *K*. Hence, both populations grow logistically and are in competition with each other, and

245   die with a rate d (assumed to be the same for slow and fast reproducers). The rate at

246   which individuals change opinion through cultural transmission (fast reproducers

247   becoming slow and vice versa) is proportional to the weighted fraction of the individuals

248   with the opposite opinion in the whole population, multiplied by the rate constant β. (For

249   comparison, in the spatial setting, the probability to change opinion was proportional to

250   the weighted fraction of the individuals with the opposite viewpoint among only the

251   nearest neighbors). The coefficient $\gamma < 1$ indicates the degree to which the influence of

252   fast reproducers is reduced compared to that of slow reproducers. The equations above

253   simplify to the following system:

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$$\dot{x}_f = r_f x_f W - dx_f - \beta(1-\gamma)\frac{x_f x_s}{x_s + \gamma x_f},$$

254

$$\dot{x}_s = r_s x_s W - dx_s + \beta(1-\gamma)\frac{x_f x_s}{x_s + \gamma x_f}.$$

255 Another way to model the process of differential strategy switching is to assume simply

256 that cultural transmission is more effective from slow to fast reproducers than vice

257 versa. This can be expressed as

$$\dot{x}_f = r_f x_f W - dx_f - \beta_s x_f \frac{x_s}{x_s + x_f} + \beta_f x_s \frac{x_f}{x_s + x_f}$$

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$$\dot{x}_s = r_s x_s W - dx_s + \beta_s x_f \frac{x_s}{x_s + x_f} - \beta_f x_s \frac{x_f}{x_s + x_f},$$

259 where, importantly, $\beta_s > \beta_f$. If we denote $\beta = \beta_s - \beta_f$, then the model can be re-written as

$$\dot{x}_f = r_f x_f W - dx_f - \beta x_f \frac{x_s}{x_s + x_f}$$

260

$$\dot{x}_s = r_s x_s W - dx_s + \beta x_f \frac{x_s}{x_s + x_f}.$$

261 The formulation of the cultural transmission dynamics is now equivalent to an infection

262 model with frequency-dependent infection terms [12,24]. It turns out that for our

263 analysis, the frequency dependence is not essential, and we can assume that switching

264 occurs at a rate proportional to the abundance of the opposite type (scaled by the

265 carrying capacity K), not its fraction in the population. Hence, we also consider the

266 following version of the model:

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267
$$\dot{x}_f = r_f x_f W - dx_f - \frac{\beta x_f x_s}{K}$$
$$\dot{x}_s = r_s x_s W - dx_s + \frac{\beta x_f x_s}{K}.$$

268   In the Supplement we demonstrate that all three versions of the model lead to very

269   similar conclusions. Here we show the results for the latter system, which is the

270   simplest, and which will be subsequently referred to as the "ODE model". If the

271   reproduction rates are larger than the death rates ($r_f > d$, $r_s > d$), the model is characterized

272   by three equilibria:

273   *(i)* Fast reproducers win and slow reproducers go extinct, with equilibrium expressions

274   given by $x_f = K(1 - d/r_f)$, $x_s = 0$. This equilibrium is stable if $d > d_1 \equiv \dfrac{r_1}{1 + (r_1 - r_2)/\beta}$.

275   *(ii)* Slow reproducers win and fast reproducers go extinct. The equilibrium expressions

276   are given by $x_f = 0, x_s = K(1 - d/r_s)$. The solution is stable if $d < d_2 \equiv \dfrac{r_s}{1 + (r_f - r_s)/\beta}$.

277   *(iii)* Coexistence of fast and slow reproducers is described by the following equilibrium

278   expressions: $x_f = \dfrac{K}{\beta}(d - d_2)$, $x_s = \dfrac{K}{\beta}(d_1 - d)$. This is stable if $d_2 < d < d_1$.

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280   Therefore, similar to the corresponding spatial agent-based model, fast reproducers are

281   only expected to dominate for relatively large population death rates. Lower death rates

282   result in coexistence, and even lower death rates lead to the exclusive persistence of

283   slow reproducers.

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285   These results make intuitive sense in the context of the infection dynamics

286   literature [25,26]. As the death rate of the population is decreased, the population

287   density increases until it is large enough to allow the slow reproduction meme to spread.

288   Essentially, a lower death rate increases the basic reproductive ratio of the slow

289   reproduction trait above unity, allowing invasion. The less the difference between the

290   strength of cultural trait transmission from fast→slow compared to slow→fast, the lower

291   the death rate, d, has to be (and hence the higher the population density has to be) to

292   allow the spread of the slow reproduction trait. Similarly, the larger the fitness difference

293   between slow and fast reproducers (r_f - r_s), the lower the death rate d has to be to allow

294   spread of the slow reproduction trait.

295

296   **Age structure in a well-mixed model.** An alternative approach is to consider a non-

297   spatial, age structured model [27]. We will model the competition dynamics of two types

298   that differ by their reproductive strategies (see Section 2 of the Supplement for

299   analytical results). Assume the existence of N discrete age groups for the two types,

300   and denote the abundance of type s in age group i as $x_i^{(s)}$. Reproduction behavior of

301   type s is described by reproduction rates in each age group, $a_i^{(s)}$. These quantities

302   comprise the information on the reproductive strategy (how early this type is willing to

303   start reproducing), and also the biological variation in fecundity (e.g. the assumption that

304   fecundity may decline with age). We assume that individuals of type $s=2$ have a

305   tendency to reproduce later than individuals of type $s=1$. We can formulate a discrete

306   time dynamical system for these populations as follows:

$$x_1^{(s)}(t+1) = \sum_{i=1}^{N} a_i^{(s)} x_i^{(s)}(t) W, \qquad (1)$$

307

$$x_j^{(s)}(t+1) = w_{j-1}^{(s)} x_{j-1}^{(s)}(t)(1 - \beta_j^{(s)} v_j^{(3-s)}(t)) + w_{j-1}^{(3-s)} x_{j-1}^{(3-s)}(t) \beta_j^{(3-s)} v_j^{(s)}, \quad 1 < j \leq N \qquad (2)$$

308   Here, the first equation describes the creation of newborn individuals of type s by older

309   individuals, where each age group reproduces with intensity $a_i^{(s)}$ and reproduction is

310   density-dependent, described by term W, e.g. $W = \left(1 + \sum_{s=1}^{2} \sum_{k=1}^{N} x_k^{(s)} / K \right)^{-1}$, with parameter K

311   having the meaning of carrying capacity. The rest of the equations describe (i) the

312   population moving from age group to age group, and (ii) the imitation dynamics.

313   Coefficients $w_{i-1}^{(s)}$ describe the probability for an individual of type s in age group j-1 to

314   survive until age j. The probability of switching type (imitation) is described by terms

315   including coefficients β. First we note that expression 3-s simply means "the other

316   type", as 3-s returns 1 for s=2 and it returns 2 for s=1. Further, the probability to switch

317   from type s to type 3-s while transitioning to age group j is given by $\beta_j^{(s)} v_j^{(3-s)}$, where

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$$v_j^{(3-s)} = \frac{\sum_{k=j}^{N} x_k^{(3-s)}(t)}{\sum_{k=j}^{N} (x_k^{(3-s)}(t) + x_k^{(s)}(t))},$$

319   and is proportional to the fraction of individuals of age j and older that belong to "the

320   other type". We can see that the first term on the right of equation (2) multiplies the

321   probability that an individual does not switch to the other type, and the second term

322   multiplies the probability that switching from 3-s to s occurs.

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323   Generally, the behavior of this discrete dynamical system can be quite complex,

324   and depending on the parameters we see exclusion equilibria (when one type is extinct

325   and the other reaches a steady positive equilibrium), exclusion periodic solutions (again,

326   one of the types is extinct and the other enters a steady cycle), and coexistence states

327   (where both types are present, and may reach a steady state or a cycle). To draw the

328   parallel between this model and those considered above, we note that parameters $w_{i-1}^{(s)}$

329   are responsible for survival to the next age group, and thus increasing these quantities

330   is similar to decreasing the death rate in the previous models. We observe that exactly

331   as before, large death rates favor the survival and dominance of the early reproducers,

332   and small death rates lead to the exclusion of early reproducers by late reproducers.

333   Intuitively, this result can be explained as follows. Assume for simplicity that the

334   transfer rate, β , does not depend on the age group, and the survival probability, w, is

335   identical for all age groups and for both types. Fitness of each of the types is comprised

336   of their net fecundity and their propensity to remain within their type (and not transfer to

337   the opposite type). In the absence of imitation (transfer), clearly, the fitness of type 1 is

338   larger than that of type 2. But this can be offset by a larger probability of transfer (if we

339   assume that $\beta^{(1)}$ is larger than $\beta^{(2)}$ by a sufficient margin). Small death rates (and

340   therefore large values of w) work against type 1 individuals and benefit type 2

341   individuals. If w is large, more individuals survive to later stages, and thus type 2 has a

342   better chance to reproduce. Further, for larger values of w, there will be a larger influx of

343   individuals transferring from type 1 to type 2: they simply have a longer time to stay

344   alive and decide to switch. Thus, living longer adds fitness to type 2, such that after a

345   threshold of w, type 2 becomes stronger and drives type 1 extinct.

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346   Note that many other modeling choices can be made, which are described in the

347   Supplement. The general trends described here are robust and do not depend on

348   details on modeling choices. Analytical calculations for certain simple cases are also

349   presented in the Supplement.

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351

Reproductive strategy as a continuous trait

353   In this section, we return to the spatial model, but modify the assumptions. So far, we

354   considered a population of slow and fast reproducers, where slow reproducers could

355   switch to fast reproducers and vice versa. Switching occurred with a probability that was

356   proportional to the weighed fraction of the opposing strategy among neighboring

357   individuals. Rather than considering two discrete reproductive strategies, however, it is

358   more realistic to assume the probability of reproduction to be a continuous variable. This

359   model will be called ABM3. We again assume that an individual is chosen for a cultural

360   transmission event with a probability scaled with C. In this model, however, instead of

361   adopting (or rejecting) the reproductive probability of the opposite type, the individual

362   adopts the weighted average of the reproduction probabilities among all neighbors

363   (including its own reproduction probability). As in the above models, we assume that

364   slower reproducers are more influential and contribute more to cultural transmission

365   than faster reproducers. This is implemented during the averaging procedures across

366   the neighborhood: we weigh the reproduction probability by a factor $Q<1$ if the

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367   reproduction probability of a neighbor is faster than that of the individual under

368   consideration.

369   The outcome observed in this model is straightforward. As initial conditions, the

370   individuals in the system are characterized by different reproduction probabilities. Over

371   time, the reproduction probabilities converge to a spatially uniform value, the level of

372   which depends on the initially assigned probabilities. The reason for this eventual

373   uniformity is the assumption that an individual adopts the average reproduction

374   probability of the neighborhood during a cultural transmission event.

375

376   Next, we introduce "mutations" that can occur during cultural transmission.

377   Instead of simply adopting the (weighted) average strategy of the neighborhood, with

378   probability u individuals would modify this strategy by increasing or decreasing it (with

379   equal probabilities) by a fraction G. We examined the evolution of the average

380   reproduction probability, R, over time, by running computer simulations, and the

381   following outcomes were observed (Figure 3): (i) The average probability to reproduce,

382   R, increases steadily towards the maximum possible value (R+D=1), shown by the

383   purple, green, and red lines in Figure 3. (Simulations were stopped when R+D=1). (ii)

384   The average probability to reproduce declines steadily, eventually resulting in

385   population extinction, shown by the dark blue, light blue, and pink lines in Figure 3.

386   Extinction occurs because the reproduction rate evolves to levels that are too low to

387   maintain the population. (iii) The average probability to reproduce converges to an

388   intermediate level, and fluctuates around this level, shown by the yellow and orange

389   lines in Figure 3. This level is independent of the starting value of R (not shown).

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390   Parameter values determine which outcome is observed. As before, the population

391   death probability, D, is a crucial factor (Figure 3). Evolution to maximal reproduction

392   probabilities, R, is seen for relatively large death rates. Evolution towards low values of

393   R and hence population extinction is observed for relatively low death rates. This could

394   be the cultural equivalent to "evolutionary suicide" or "Darwinian extinction" [28].

395   Evolution towards an intermediate reproduction probability is observed for intermediate

396   death probabilities, D. A higher probability of cultural transmission, C, and a lower

397   weight of faster reproducers during the averaging process, Q, further promote evolution

398   towards declining reproduction rates and population extinction (not shown). Section 3 of

399   the Supplement further explains the existence of an equilibrium state and explores how

400   the mean population reproduction rate depends on parameters.

401

402

403   Model with sexual reproduction

404   So far, all models considered assumed asexual reproduction, which is an obvious

405   oversimplification when considering human populations. Here, we repeat the analysis of

406   the last section by introducing sexual reproduction into this modeling framework,

407   referred to as ABM4. The same model as in the last section will be used, assuming the

408   probability of reproduction to be a continuous trait, and also assuming that for a cultural

409   transmission updates, a given individual adopts the weighted average reproduction

410   probability of the neighborhood with the possibility of "mutations" as defined above.

411   Sexual reproduction is incorporated in the following way. Two genders are

412 distinguished, gender 1 and gender 2. Before reproduction can occur, two individuals of

413 opposing gender have to form an exclusive connection, thus assuming monogamy. The

414 following events can occur if an individual is chosen for a reproductive update. If the

415 individual does not have a partner, a connection can be formed with a probability M if an

416 individual of the opposite gender without a partner is present among the eight nearest

417 neighbors. The partner is randomly chosen from the neighborhood. If the individual

418 does have a partner, reproduction happens with a probability R_{av}, which represents the

419 average reproduction probabilities of the two parents. For simplicity, it is assumed that

420 once formed, a partnership cannot break, corresponding to life-long monogamy. The

421 offspring resulting from this partnership are assigned to one of the genders with a 0.5

422 probability. The reproduction probability of the offspring is given by the average values

423 of the two parents. The offspring is placed into a randomly chosen empty spot among

424 the eight nearest neighbors of the parent that was originally picked for reproduction. If

425 no empty spots exist within the immediate neighborhood, reproduction is not successful.

426 Potential issues of mate preference for individuals with similar reproduction probabilities

427 are not taken into account. Death occurs with a probability D, according to the same

428 rules as described before.

429   As shown in Figure 4, the outcomes are qualitatively the same as in the

430 corresponding model without sexual reproduction, described in the previous section. For

431 relatively low population death rates, the reproduction probability can evolve towards

432 reduced values until population extinction occurs. For relatively high death rates, the

433 reproduction probability can evolve towards maximal values. For intermediate death

434 rates, the population can fluctuate around an intermediate reproduction probability.

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435

436

Simulating demographic transitions in growing populations

438   In the modeling approaches described so far, competition is a major driving force of

439   outcome. In the absence of cultural transmission, faster or earlier reproducing

440   populations outcompeted the slower or later reproducing ones. Cultural transmission

441   could reverse the outcome of the competition if individuals were more likely to learn

442   from slower rather than faster reproducers. Competition, however, is most prevalent if

443   populations are close to an equilibrium or carrying capacity, which was the case in the

444   above analysis. The patterns reported above are not observed in exponentially growing

445   populations, because of the absence of competition (not shown). Because human

446   populations have been growing, it is important to re-visit the above-explored processes

447   in the context of unbounded population growth. While the population grows, individuals

448   can still compete on a local level. Therefore, we consider a growing population that is

449   subdivided into neighborhoods or demes. In each deme, the dynamics are modeled in

450   the same way as in the previous sections, imposing a carrying capacity for each deme.

451   For simplicity, we assume that in each deme, the dynamics are governed by the ODE

452   model. As initial conditions, a single deme is populated with a majority of fast

453   reproducers and a minority of slow reproducers. At the end of each time unit, there is a

454   chance that a new, empty deme is founded into which a fraction of current population

455   moves. The probability of this occurring is proportional to how full the current deme is. In

456   addition, the probability to found a new deme is inversely proportional to the number of

22

457   existing demes. While the demes are not arranged spatially in this model, founding a

458   new deme can be thought of as an increase in the density of the population, which gets

459   more difficult the more demes already exist. Hence, the probability for members of an

460   individual deme to found a new deme is given by $\dfrac{\alpha(x_f + x_s)}{K(\epsilon N + 1)}$, where N is the number of

461   currently populated demes, x_f and x_s represent local population sizes of fast and slow

462   reproducers, K is the local carrying capacity, and α and ε are constants. When a new

463   deme is founded, a given fraction of both fast and slow reproducers moves into the new

464   deme. As more demes become populated, the same algorithm is applied to every deme

465   after each time unit.

466

467   In this model, we observe persistence of one type and exclusion of the other,

468   while the population continues to grow (Figure 5A,B). As before, the fast population

469   persist for fast overall death rates (Figure 5A), while the slow population persists for low

470   overall death rates (Figure 5B).

471

472   We further used this model to simulate the demographic transition process

473   (Figure 5C). The simulation was run as before, but at a defined time point in the

474   simulation, the death rate is continuously and gradually reduced over several time steps

475   towards a lower, new level. This exogenous reduction is shown by the grey line and is

476   assumed to correspond to an improvement in various socio-economic factors that

477   reduce mortality, such as an improvement in disease treatment, sanitary conditions,

23

478 technological innovations, etc. The fast reproducing population is shown in purple, the

479 slow-reproducing population is green, and the total population size is shown by the red

480 dashed line. Initially, the overall population death rate is relatively high, and the fast

481 reproducing individuals enjoy a growth advantage. The average reproduction rate is

482 shown by the black line and is driven by the fast-reproducing population. When the

483 death rate is reduced, the fertility-reducing cultural trait can spread successfully and

484 eventually becomes the dominant population. As the death rate declines, we observe a

485 phase of faster population growth, as observed in data on demographic transitions [9].

486 Following a time delay after the reduction in the death rate, the reproduction rate also

487 declines, which is again consistent with data on demographic transitions [9] (this is also

488 seen in a zoomed-in graph in Figure 5D). The exact timing of events depends on model

489 parameters. For the purpose of this simulation, we chose parameters such that it takes

490 about 5 generations to reduce the reproduction rate two-fold. This is an order of

491 magnitude that is similar to events observed in human populations [1] and shows that

492 the cultural transmission dynamics underlying our model can lead to sufficiently rapid

493 changes in fertility. A faster rate of cultural transmission (higher value of β) can lead to

494 more rapid changes in fertility following the decline in the death rate, while the opposite

495 holds true for slower rates of cultural transmission.

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Discussion and Conclusion

We have used a variety of modeling approaches to investigate the basic dynamics by

which a fertility-reducing trait can spread via cultural transmission. A central result was

that lower population death rates select for the cultural spread of the low-fertility trait.

In a first set of models, the dynamics of two populations were followed, which were

fast/slow or early/late reproducers in age structured models. This was done both in the

context of nearest neighbor interactions and assuming perfect mixing. Both

assumptions have value, depending on the population size and the connectivity of

communication networks among individuals; in application to the modern population

dynamics, a complete mixing assumption may correspond to the role of media in

opinion spread. In a second set of models, the reproduction rate was modeled as a

continuous trait, and cultural transmission corresponded to an individual adopting the

(weighted) average reproduction rate found within the neighborhood. Assumptions

about inaccuracies during cultural transmission allowed us to study the evolution of the

average reproduction rate over time. In accordance with the simpler models, faster

death rates resulted in evolution towards maximal reproduction rates, while lower death

rates resulted in evolution towards ever decreasing reproduction rates, which likely

induced in population extinction. Intermediate death rates were found to result in the

evolution towards intermediate reproduction rates. These results were true both for

asexual and sexual reproduction in the models.

521   Competition among individuals was a major driving force underlying the

522   dynamics arising from the model. While in the simpler settings explored here,

523   competition correlated with populations being close to carrying capacity, we showed

524   how a deme model can give rise to the same outcomes in populations that continuously

525   grow without converging to a carrying capacity. Hence, the results described throughout

526   the paper may hold for growing populations. We demonstrated that, depending on

527   parameters, the model can reproduce crucial features of the "demographic transition

528   model" [9].

529

530   Our study complements previous mathematical work that analyzed the cultural

531   spread of small family sizes in relation to demographic transitions [20-22]. Our models

532   consider a simpler setting involving the basic spread dynamics of the fertility reducing

533   trait, similar to infection models. The result that lower death rates promote the cultural

534   spread of the low fertility trait is intuitive if considered in the broader context of infection

535   dynamics models: lower death rates of individuals increase population density, and this

536   increases the basic reproductive ratio of the infection [26]. In the context of the

537   demographic transition towards reduced fertility, this is nevertheless an interesting

538   result. First, it might provide a simple explanation for the typical observation that a

539   reduction in fertility is preceded by a reduction in mortality, which our model reproduced.

540   In addition, the dynamics exhibited by these models suggest that fertility can be

541   characterized by density dependence, even in the context of increased resource

542   availability and continuously growing populations. Data indicate that fertility as well as

543 family size preference are characterized by density dependence, the reasons for which

544 are not fully understood [29].

545

546 An interesting result in our models was that for low population death rates, the

547 average reproduction rate of the population can continuously decline towards levels that

548 cannot sustain persistence anymore. In Western European countries, fertility has

549 declined below replacement levels since the 1970s and 1980s [5,6]. In addition, recent

550 surveys [6] have revealed that the ideal family size in German speaking countries has

551 fallen below replacement levels, about 1.7 children, among younger people, indicating

552 that this trend might continue in the future. These trends could be the result of the type

553 of cultural evolutionary dynamics explored here.

554

555 Some processes in the more complex versions of the models considered here

556 could also be formulated in slightly different ways. In ABM3 and ABM4, cultural

557 transmission involves the calculation of the weighted average reproduction rate among

558 individuals within the immediate neighborhood. The assumption was made that

559 individuals with a faster reproduction rate than the agent under consideration count less

560 in this process, irrespective of the magnitude of this difference. Alternatively, it could be

561 assumed that the reduced weight is proportional to the difference in reproduction rates,

562 thus taking into account the distance in social hierarchies. While it seems reasonable to

563 assume that economically more successful individuals carry more weight in cultural

564 transmission than individuals who are less successful [30,31], the details of this are not

565   well understood [32,33]. We note that results reported here depend on the assumption

566   that individuals with lower reproduction rates carry more social weight, an assumption

567   that has also been made in previous modeling work [21]. Another example of

568   uncertainties in model construction is the formulation of the sexual reproduction model.

569   We assumed monogamy, but made some obvious simplifications, as explained in the

570   results section. There are different assumptions that can be made in models that

571   describe sexual reproduction, but the most important feature in the current context is

572   that the reproduction rate of the offspring is not simply a copy of one of the parents, but

573   represents the average of the two parents. This provides an additional mechanism of

574   cultural change. Finally, only two types of communication networks have been

575   considered in the agent based models here, the one where individuals interact with

576   everyone else in the population, and the one where only interactions among nearest

577   neighbors are allowed. A large variety of more realistic, random communication

578   networks can be constructed, but we do not expect the results to differ from the ones

579   obtained from the two extreme cases of networks considered here.

580

581   While some details of the model processes could be formulated in different ways,

582   we have considered a range of models with different assumptions: with and without

583   spatial restrictions, in the presence or absence of age structure, with sexual versus

584   asexual reproduction, with different ways in which cultural transmission changes the

585   reproduction rate, and in models with different population structure. In all models, the

586   death rate of the population was identified as a crucial factor that determined whether

587   cultural transmission of a fertility-reducing trait was successful or not, which could have

588   implications for understanding the forces that contribute to the occurrence of

589   demographic transitions and that drive the decline of fertility below replacement levels in

590   developed countries.

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597

598   **Figure legends:**

599   **Figure 1.** Time series showing the different outcomes according to ABM1. Individual

600   realizations are shown. (A) Higher death rates: fast reproducers persist and slow

601   reproducers go extinct on a short time scale. (B) Lower death rates: slow reproducers

602   persist and fast reproducers go extinct on a short time scale. (C) Intermediate death

603   rates: both fast and slow reproducers persist for significantly longer time periods.

604   Eventually one population goes extinct due to the stochastic nature of the simulation.

605   Parameters were chosen as follows. R_f=0.005; R_s=0.8R_f; C=0.0008; Q=0.93. For (A),

606   D=0.001. For (B), D=0.0001. For (C), D=0.00025.

607

608   **Figure 2.** Time to competitive exclusion, as a function of the death rate. (A) Model

609   ABM1. Individual realizations of the computer simulation were run until one of the two

610   populations (fast or slow reproducers) went extinct. This time was recorded with a green

611   dot if the fast reproducer went extinct, and with a purple dot if the slow reproducer went

612   extinct, as a function of the population death rate, D. For low death rates, there are only

613   green dots, corresponding to the slow reproducer persisting and the fast reproducer

614   going extinct relatively fast. For fast death rates, there are only purple dots,

615   corresponding to the fast reproducers persisting and the slow reproducers going extinct

616   in a relatively fast time scale. For intermediate death rates, the time until one of the

617   populations goes extinct becomes sharply longer, and either population can go extinct

618   first. This corresponds to long-term coexistence. For plot (i), parameters were chosen

619   as follows: R_f=0.005; R_s=0.8R_f; C=0.0008; Q=0.93. Plots (ii) and (iii) explore parameter

620   dependence of the phenomenon. (ii) A higher value of Q=0.98 makes it harder for the

621   slow-reproduction trait to invade, hence requiring lower population death rates. (iii) A

622   lower rate of cultural transmission, C=0.0004, makes it harder for the slow-reproduction

623   trait to invade, hence again requiring lower population death rates. (B) Same, but

624   according to ABM2 with age structure. Because each age class is characterized by its

625   own death rate, we multiplied all those death rates by a variable factor F, and plotted

626   the outcome against this parameter. The death rates for the age classes were:

627   D_1=0.00004; D_2=0.00007; D_3=0.00009; D_4=0.0002. Other parameters are R=0.005;

628   C=0.0008; Q=0.93; A=10,000.

629

630 **Figure 3.** Outcomes of ABM3 with a continuous reproduction strategy and cultural

631 evolution. The average reproduction probability across the whole population is plotted

632 over time. Individual simulation results are shown. Simulations were run for different

633 death rates, decreasing from D1 to D8. For relatively high death rates, the average

634 reproduction probability increases steadily towards maximal levels. For relatively low

635 death rates, the average reproduction probability decreases steadily until population

636 extinction occurs (due to the limited reproduction). For intermediate death rates, the

637 average reproduction probability comes to oscillate around a steady value, which does

638 not depend on initial conditions (not shown). Parameters were chosen as follows. Death

639 rates are given by D1 = 0.002, D2 = 0.001, D3 = 4×10^{-4}, D4 = 3.75×10^{-4}, D5 = 3.6×10^{-4},

640 D6 = 10^{-4}, D7 = 5×10^{-5}, D8 = 10^{-5}. The reproduction probability of the individuals, R, was

641 allowed to evolve, starting from R=0.05 for all individuals. C=0.0003; Q=0.965. The

642 chance to make a mistake during cultural transmission ("mutation") u=0.1. In case of a

643 mistake, the average reproduction rate was changed by G=2%.

644

645 **Figure 4.** Outcomes of ABM4 with continuous reproduction strategies, cultural

646 evolution, and sexual reproduction. Simulations are in principle the same as those

647 presented in Figure 3, but using the model with sexual reproduction. Assumed death

648 rates decrease from D1 to D8. Results remain robust. Parameters were chosen as

649 follows. Death rates are given by D1 = 0.002, D2 = 0.001, D3 = 7.5×10^{-4}, D4 = 7×10^{-4}, D5

650 = 6.5×10^{-4}, D6 = 5×10^{-4}, D7 = 2.5×10^{-4}, D8 = 1×10^{-4}. The reproduction probability of the

651 individuals, R, was allowed to evolve, starting from R=0.05 among all individuals. The

31

652   population death rate, D, is indicated in the graphs. u=0.1, M=0.9; C=0.0003; Q=0.965;

653   G=0.1; G=2%.

654

655   **Figure 5.** Computer simulations of the deme model, described in the text. (A) The slow-

656   reproducing population (green) goes extinct and the fast-reproducing population

657   (purple) continues to grow. Parameter values were chosen as follows: r_f=0.08, r_s=0.04,

658   d=0.03, β=0.02, K=10, α=0.01, ε=0.01. (B) The fast-reproducing population is going

659   extinct, and the slow-growing population takes over and continues to grow. The same

660   parameter values were used, except d=0.003. (C) Simulation of the demographic

661   transition process. Again, fast and slow reproducers are shown in purple and green,

662   respectively. The total population size is shown by the dashed red line. The simulation

663   is started with a death rate d=0.006. In this regime, the fast-reproducing population has

664   the advantage and is dominant. The cultural spread of the low-fertility trait is not

665   successful. At a defined time point, the death rate is reduced 1.8 fold every half

666   generation until it has fallen to a value of d=0.001 (grey line). This creates conditions

667   under which the cultural transmission of the fertility-reducing trait is successful, and the

668   population characterized by a slow reproduction rate spreads. This leads to a decline in

669   the average reproduction rate of the population (black line), which is delayed with

670   respect to the reduction in the death rate. For the parameter regime considered, the

671   average reproduction rate is halved within about 2-3 generations, which corresponds to

672   about 50-100 years (a generation in the model is given by 1/r). The remaining

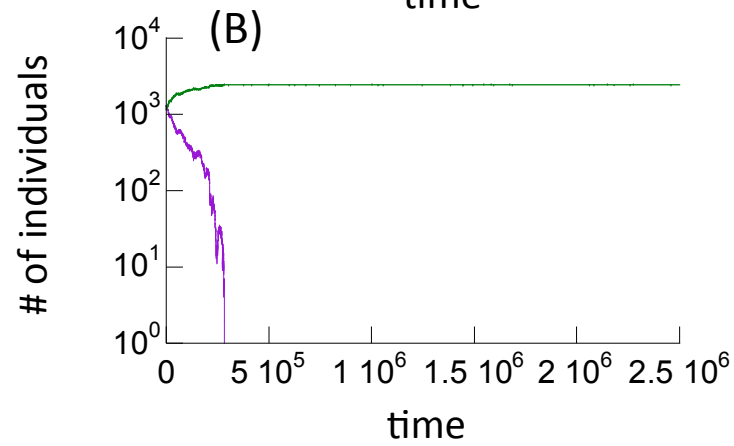673   parameters are given as follows. r_f=0.008, r_s=0.0016, β=0.2, K=10, α=0.01, ε=0.01.
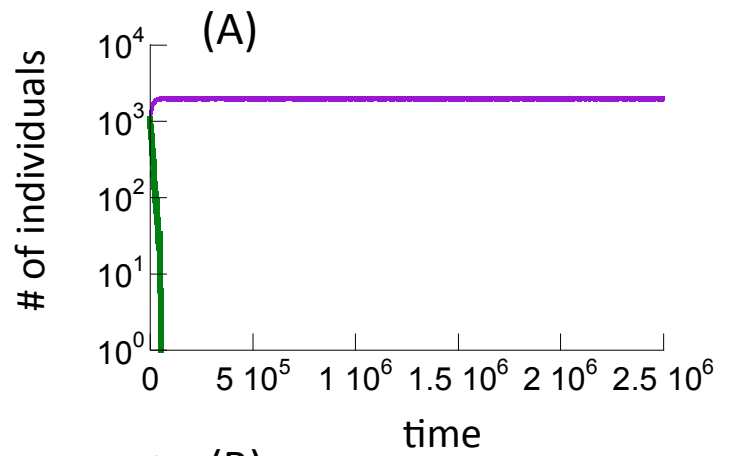
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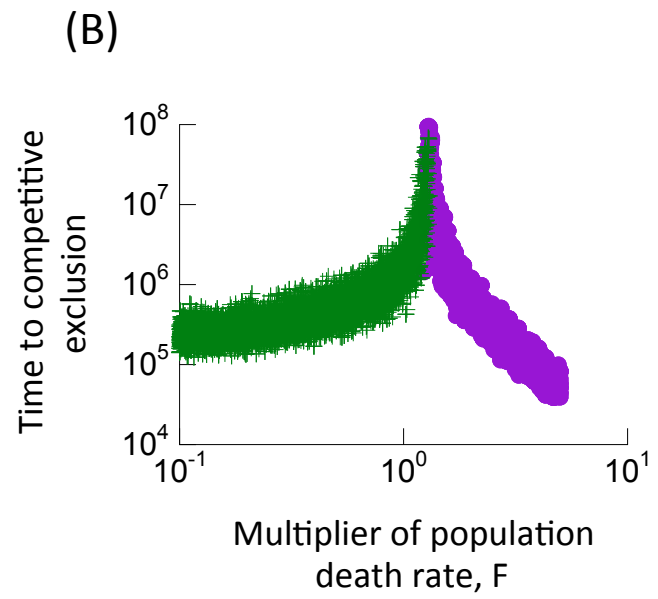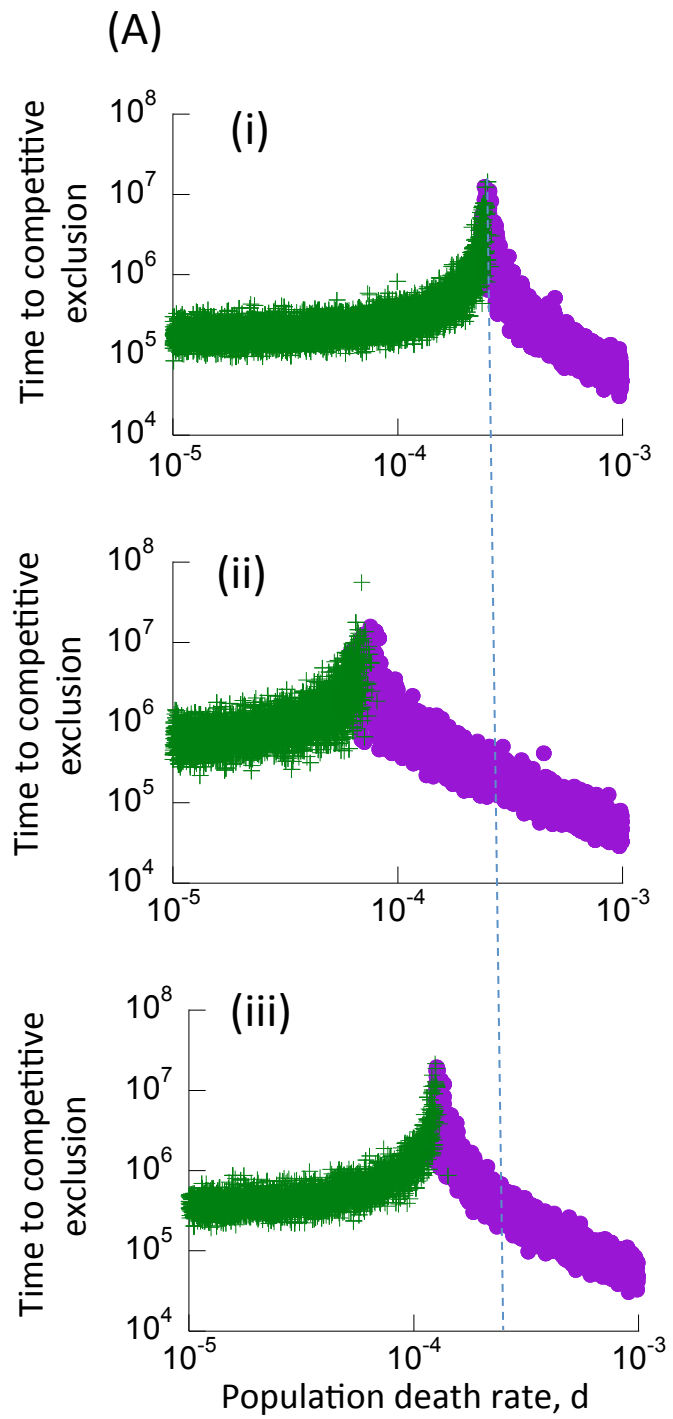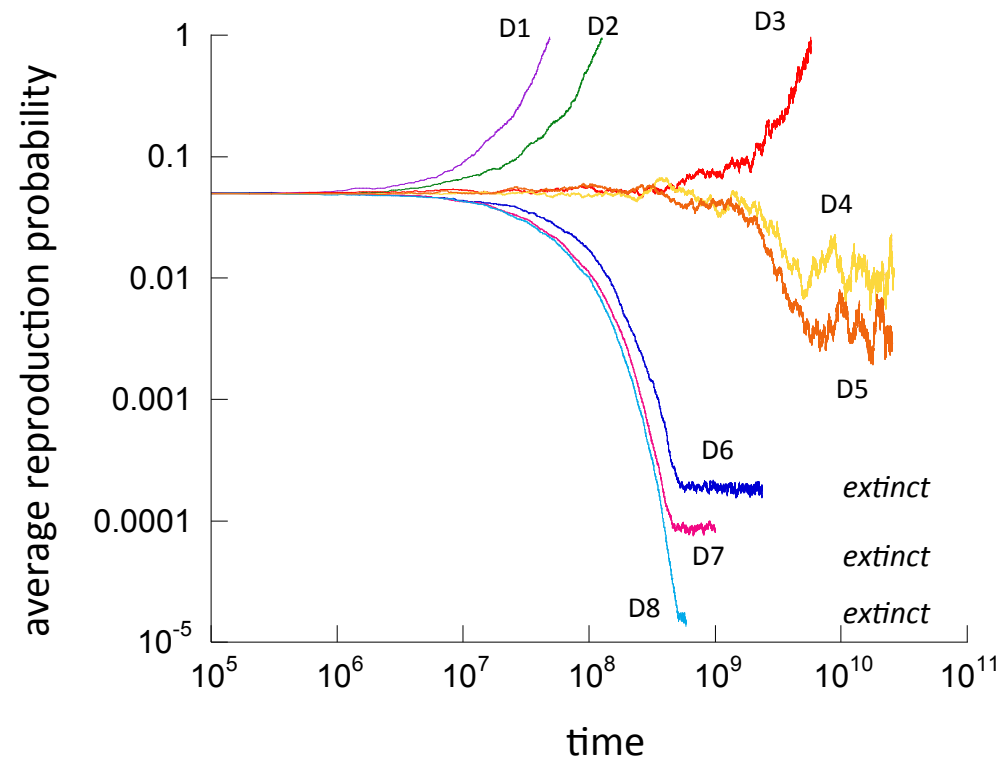
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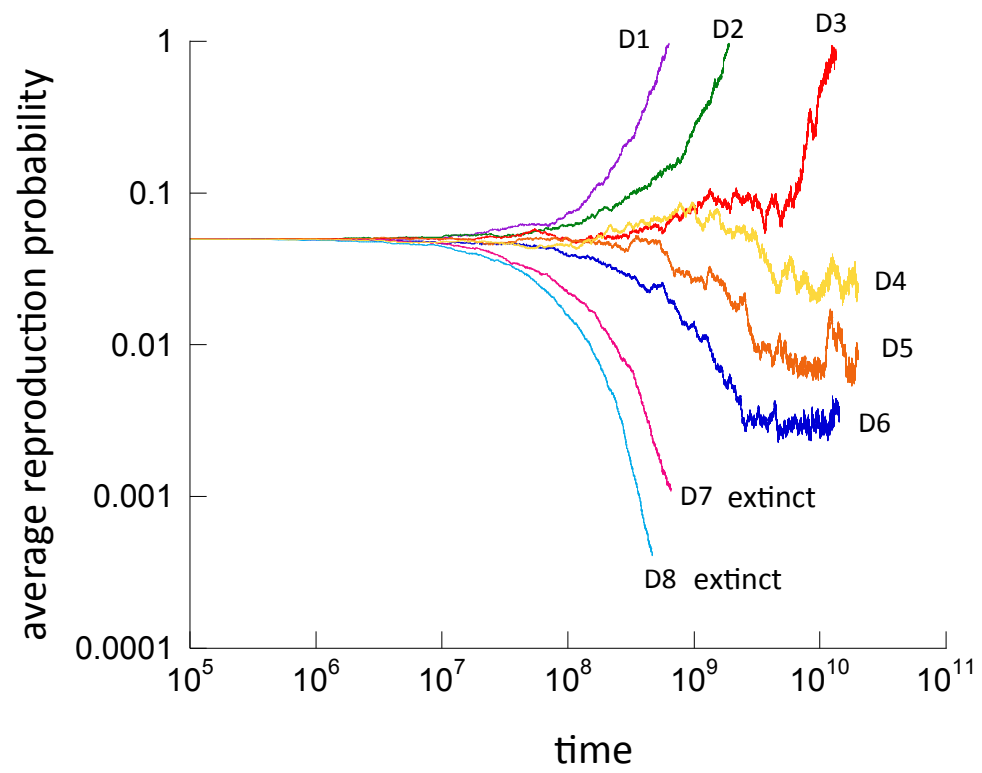
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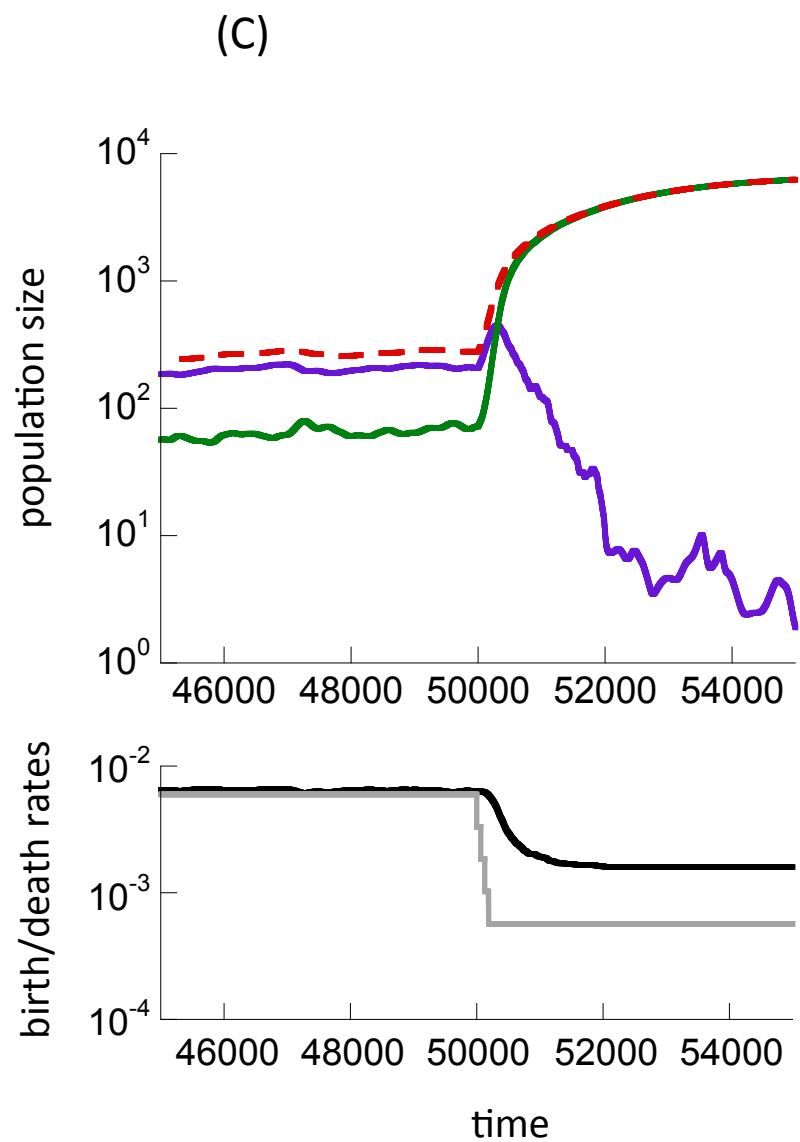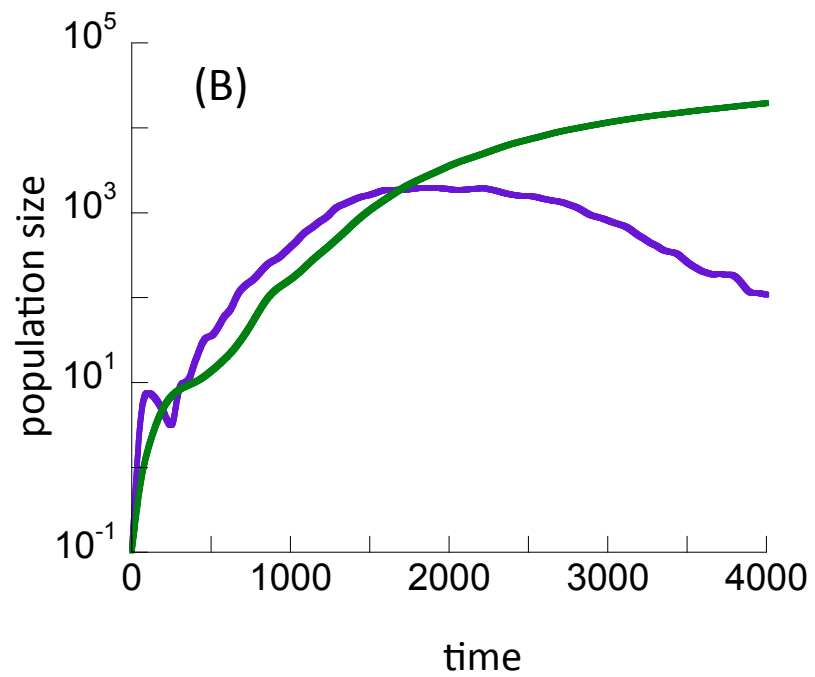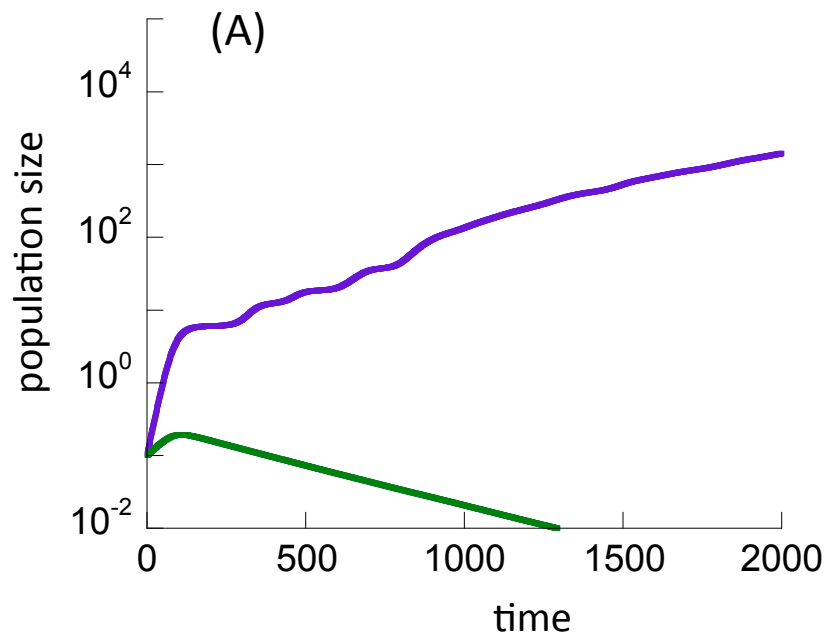738   leaders in human groups. Journal of The Royal Society Interface 16: 20180938.

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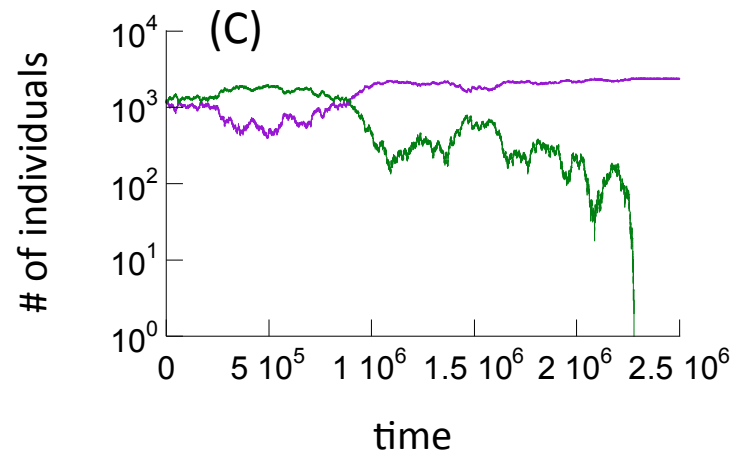
(A)

(i)

(ii)

(iii)

Time to competitive exclusion

Population death rate, d

(B)

Time to competitive exclusion

Multiplier of population death rate, F

2

Evolutionary dynamics of culturally transmitted, fertility-reducing traits

Dominik Wodarz, Shaun Stipp, Natalia L. Komarova

Supplementary information

Contents

1   In the absence of age structured dynamics

1.1   The basic ODE model

Let us describe the dynamics of two competing types of individuals, fast reproducers and slow reproducers. We will denote the population of the former type as $x^{(1)}$ and the population of the latter type as $x^{(2)}$. We have

$$\dot{x}^{(1)} = r_1 x^{(1)} W - d x^{(1)} - \beta x^{(1)} x^{(2)}/K, \tag{1}$$

$$\dot{x}^{(2)} = r_2 x^{(2)} W - d x^{(2)} + \beta x^{(1)} x^{(2)}/K. \tag{2}$$

Here, each type reproduces with its own linear reproduction rate, with

$$r_1 > r_2,$$

1

and the competition is expressed by term W, which for example can take the logistic form,

$$W = 1 - \frac{x^{(1)} + x^{(2)}}{K},$$

where K denotes carrying capacity. Both types die with equal rates, d. There is also a probability of switching from one type to the other, which is proportional to the abundance of the individual of the opposite type. So, the total rate at which type 1 switches to type 2 is given by

$$\beta_1 x^{(1)} \frac{x^{(2)}}{x^{(1)} + x^{(2)}},$$

and the total rate at which type 2 switches to type 1 is given by

$$\beta_2 x^{(2)} \frac{x^{(1)}}{x^{(1)} + x^{(2)}}.$$

If we assume that $\beta_1 > \beta_1$ and denote $\beta = \beta_1 - \beta_2$, we have term

$$\beta x^{(1)} \frac{x^{(2)}}{x^{(1)} + x^{(2)}}$$

with the minus sign in the equation for $x^{(1)}$, and the same term with the plus sign in the equation for $x^{(2)}$. These terms are equivalent in form to frequency dependent infection. It turns out that for our analysis, the frequency dependence is not essential, and we can assume that switching occurs at a rate proportional to the abundance of the opposite type (scaled by the carrying capacity), not its percentage in the population. Therefore we will use equations of the form (1-2). The main assumptions are that

- Type 1 grows faster than type 2, $r_1 > r_2$, and

- There are more individuals switching from type 1 to type 2 than the other way around, that is, $\beta > 0$.

System (1-2) has four steady states.

0. The trivial solution, $x^{(1)} = x^{(2)} = 0$ is unstable as long as $r_1 > d$ and $r_2 > d$. We will assume that both types are viable and the above inequalities hold.

2

1. Type 1 (fast reproducers) wins:
$$x^{(1)} = K(1 - d/r_1), \quad x^{(2)} = 0.$$

   This solution is stable if
   $$d > d_1 \equiv \frac{r_1}{1 + (r_1 - r_2)/\beta}.$$

2. Type 2 (slow reproducers) wins:
$$x^{(1)} = K(1 - d/r_1), \quad x^{(2)} = 0.$$

   This solution is stable if
   $$d < d_2 \equiv \frac{r_2}{1 + (r_1 - r_2)/\beta}.$$

   Note that $d_2 < d_1$.

3. Coexistence solution,
$$x^{(1)} = \frac{K}{\beta}(d - d_2), \quad x^{(2)} = \frac{K}{\beta}(d_1 - d).$$

   This solution is positive as long as
$$d_2 < d < d_1. \tag{3}$$

   The characteristic polynomial is given by
$$\lambda^2 + \frac{d(r_1 - r_2)}{\beta}\lambda + \frac{\beta + r_1 - r_2}{\beta}(d_1 - d)(d - d_2),$$

   and the eigenvalues have negative real part as long as the free term is positive, which is only satisfied by condition (3), which means that inequality (3) is the stability condition for the coexistence solution.

1.2 Other ODE models

In the model just considered the conversion process is described by the term
$$\beta x^{(1)} x^{(2)}/K.$$

3

Alternatively, this term can be formulated as

$$\beta \frac{x^{(1)}x^{(2)}}{x^{(1)} + x^{(2)}},\tag{4}$$

where the conversion happens proportionally to the current fraction of the individuals of the opposite type. In this case, we have a very similar solution structure. The competitive exclusion solutions are the same as in the previous model, the threshold d values are given by

$$d_1 = \frac{\beta}{1 - r_2/r_1}, \quad d_2 = \frac{\beta}{r_1/r_2 - 1},$$

and the coexistence solution is given by

$$x^{(1)} = \frac{K}{\beta}\left(1 - \frac{\beta}{r_1 - r_2}\right)(d - d_2), \quad x^{(2)} = \frac{K}{\beta}\left(1 - \frac{\beta}{r_1 - r_2}\right)(d_1 - d).$$

In a different modeling approach we assume that conversion happens at the same rate for both strategies, but it isn proportional to the weighted fraction of the two strategies in the population. Assuming that strategy 1 is weighed with coefficient $\gamma < 1$, we obtain that the change in numbers for strategy 1 is given by

$$\beta(1 - \gamma)\frac{x^{(1)}x^{(2)}}{\gamma x^{(1)} + x^{(2)}}.\tag{5}$$

In this case, the competitive exclusion solutions are the same as in the previous model, the threshold d values are given by

$$d_1 = \frac{\beta(1 - \gamma)}{\gamma(1 - r_2/r_1)}, \quad d_2 = \frac{\beta(1 - \gamma)}{r_1/r_2 - 1},$$

and the coexistence solution is given by a somewhat different expression,

$$\begin{aligned}
x^{(1)} &= \frac{K}{\beta + d}\left(\frac{\beta}{r_1 - r_2} + \frac{\beta + d}{\gamma r_2 - r_1}\right)\left(\beta + d + \frac{r_1 - \gamma r_2}{\gamma - 1}\right), \\
x^{(2)} &= \frac{K}{\beta + d}\left(\frac{d\gamma}{\gamma - 1} + \frac{\beta(\beta + d - r_1)}{r_2 - r_1} - \frac{(\beta + d)^2\gamma}{\gamma r_2 - r_1}\right).
\end{aligned}$$

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2 Age structured dynamics

2.1 Model formulation

We will model the competition dynamics of two types that differ by their reproductive strategies. Assume the existence of N discrete age groups for the two types, and denote the abundance of type s in age group i as $x_i^{(s)}$. Reproduction behavior of type s is described by the vector $a_i^{(s)}$, with entries in $[0, 1]$ denoting relative rate of reproduction of this type in age i. Individuals of the first type, $s = 1$, correspond to "fast reproducers", and the second type, $s = 2$, to the "slow reproducers" in the previous section. The latter type generally has a tendency to reproduce later than individuals of type 1. In the approach implemented here, type s is characterized by two integers, $i_{start}^{(s)}$ and $i_{end}^{(s)}$, denoting the first and last age groups where reproduction is possible. We have

$$a_i^{(s)} > 0 \ \text{ if } \ i_{start}^{(s)} \leq i \leq i_{end}^{(s)}, \quad a_i^{(s)} = 0 \text{ otherwise,}$$

where

$$i_{start}^{(1)} < i_{start}^{(2)}.$$

We can formulate a discrete time dynamical system for these populations as follows:

$$x_1^{(s)}(t+1) \ = \sum_{i=1}^{N} a_i^{(s)} x_i^{(s)}(t) W, \tag{6}$$

$$x_j^{(s)}(t+1) \ = w_{j-1}^{(s)} x_{j-1}^{(s)}(t) \left(1 - \beta_j^{(s)} \frac{\sum_{k=j}^{N} x_k^{(3-s)}(t)}{\sum_{k=j}^{N}(x_k^{(3-s)}(t) + x_k^{(s)}(t))} \right)$$

$$+ \quad w_{j-1}^{(3-s)} x^{(3-s)}(t) \beta_j^{(3-s)} \frac{\sum_{k=j}^{N} x_k^{(s)}(t)}{\sum_{k=j}^{N}(x_k^{(3-s)}(t) + x_k^{(s)}(t))}, \quad 1 < j \leq N, \tag{7}$$

where the competition term W can be defined as

$$W \ = \ 1 - \frac{\sum_{s=1}^{2} \sum_{k=1}^{N} x_k^{(s)}}{K} \quad \text{or} \tag{8}$$

$$W \ = \ \left(1 + \frac{\sum_{s=1}^{2} \sum_{k=1}^{N} x_k^{(s)}}{K} \right)^{-1}. \tag{9}$$

Equation (6) describes reproduction. Different age groups reproduce with their own rate $s_i^{(s)}$, and the offspring enters age group 1. Equation (7) describes the population moving from age group to age group. Coefficients $w_{j-1}^{(s)}$ describe the probability for an individual of type s to survive until age j. The probability of switching type is described by terms including coefficient β. First we note that expression $3 - s$ for $s \in \{1, 2\}$ simply returns the type different from type s, because $3 - s$ gives 2 if $s = 1$ and it gives 1 if $s = 2$. The probability to switch from type s to type $3 - s$ while transitioning to age group j is given by

$$\beta_j^{(s)} \frac{\sum_{k=j}^{N} x_k^{(3-s)}(t)}{\sum_{k=j}^{N} (x_k^{(3-s)}(t) + x_k^{(s)}(t))},$$

and is proportional to the fraction of individuals of age j and older that belong to class $3 - s$. With this in mind, we can see that the first term on the right of equation (7) multiplies the probability that an individual does not switch to the other type, and the second term multiplies the probability that switching from $3 - s$ to s occurs. System (6-7) assumes no switching at the first stage. To include switching at the first stage, we replace equation (6) with

$$
\begin{aligned}
x_1^{(s)}(t+1) \ &= \ \sum_{i=1}^{N} a_i^{(s)} x_i^{(s)}(t) W \left(1 - \beta_1^{(s)} \frac{\sum_{k=1}^{N} x_k^{(3-s)}(t)}{\sum_{k=1}^{N} (x_k^{(3-s)}(t) + x_k^{(s)}(t))} \right) \\
&+ \ \sum_{i=1}^{N} a_i^{(3-s)} x_i^{(3-s)}(t) W \beta_1^{(3-s)} \frac{\sum_{k=1}^{N} x_k^{(s)}(t)}{\sum_{k=1}^{N} (x_k^{(3-s)}(t) + x_k^{(s)}(t))}. \quad (10)
\end{aligned}
$$

2.2 System behavior

System (10, 7) has two exclusion steady states (for $s = 1$ and $s = 2$), which for competition model (9) are given by

$$x_j^{(s)} \ = \ K \prod_{k=1}^{j-1} w_k^{(s)} \frac{r \sum_{m=1}^{N} a_m^{(s)} \prod_{k=1}^{m-1} w_k^{(s)} - 1}{\sum_{m=1}^{N} \prod_{k=1}^{m-1} w_k^{(s)}}, \quad 1 \le j \le N, \quad (11)$$

$$x_j^{(3-s)} \ = \ 0, \quad 1 \le j \le N. \quad (12)$$

In figure 1 the behavior of a system with $N = 5$ stages is shown. We assumed that for fast reproducers, $i_{start}^{(1)} = 2$, and for slow reproducers, $i^{(2)} = 3$,

while $i_{end}^{(s)} = 5$ for both types. For simplicity we assumed that within the reproductive stages, the values $a_i^{(s)}$ were equal to a constant (independent on type and stage). Further, we assumed that the rates $w_i^{(s)}$ were s- and i-independent, and transfer coefficients $\beta_i^{(s)}$ were i-independent (but dependent on s).
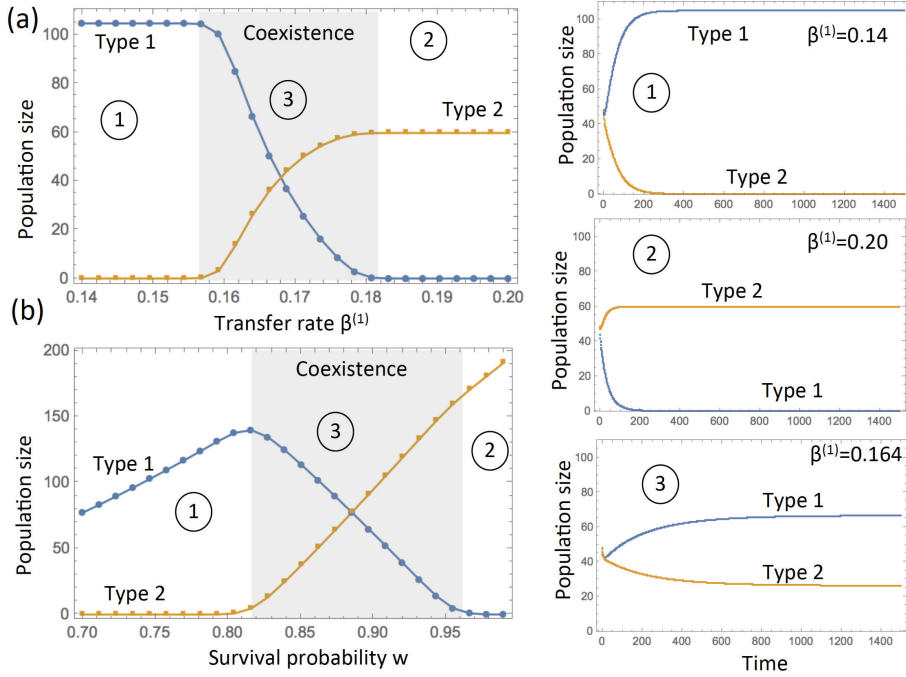

Figure 1: Age structured dynamics according to system (10, 7), numerical simulations. Total populations of individuals of type 1 and type 2 are presented. The steady state values are given on the left as functions of parameter (a) $\beta^{(1)}$ and (b) $w_i^{(s)} = w$ for all $s \in \{1, 2\}, 1 \le i \le N$, the survival probability. Solution types are denoted by a circled number. The parameters are $w = 0.9$ in (a), $\beta^{(1)} = 0.17$ in (b), and $K = 50, \beta_i^{(2)} = 0.1$. The reproductive rate $a_i^{(s)} = 1$ when $2 \le i \le 5$ for $s = 1$ and $3 \le i \le 5$ for $s = 2$. Initially, all populations $x_i^{(s)} = 10$.

In figure 1(a), by fixing all the parameters except for $\beta^{(1)}$, we observed that three different solution types were stable. Solution 1 corresponds to the fast reproducers excluding the slow reproducers and is stable for smaller values transfer away from type 1, $\beta^{(1)}$. Solution 2 corresponds to the slow reproducers excluding the fast reproducers, and corresponds to larger $\beta^{(1)}$. For intermediate values of $\beta^{(1)}$ we observe stable coexistence of both types. Sam-

ple time series of the three solution types (corresponding to three different values of $\beta^{(1)}$) are presented on the right on the figure.

Alternatively, if we fix $\beta^{(1)} > \beta^{(2)}$ and vary the survival probability, w, the same three solution types are observed, 1(b). In particular, we note that low survival rates (that is, high death rates) lead to the dominance of fast reproducers, and high survival rate (low death rates) to the dominance of slow reproducers.

2.3 A two-age system

The simplest nontrivial system that captures the phenomenon of interest is system (10,7) with $N = 2$. Let us assume that $w_j^{(s)} = w$ for both types (that is, mortality is the same for both types). Further, let

$$i_{start}^{(1)} = 1, \quad i_{end}^{(1)} = 2, \quad i_{start}^{(2)} = 2, \quad i_{end}^{(1)} = 2,$$

in other words, type 1 reproduces both in ages 1 and 2, and type 2 only reproduces in age 2. The trivial solution[1] is unstable if $wa_2^{(2)} > 1$ or $wa_2^{(1)} > 1 - a_1^{(1)}$. The following are some of the non-trivial long-term solutions (compare to the equilibria of section 1):

1. Type 1 (fast reproducers) wins – a competitive exclusion steady state:

$$x_1^{(1)} = \frac{K[r(a_1^{(1)} + wa_2^{(1)}) - 1]}{1 + w}, \quad x_2^{(1)} = \frac{Kw[r(a_1^{(1)} + wa_2^{(1)}) - 1]}{1 + w}, \quad x_1^{(2)} = x_2^{(2)} = 0.$$

2. Type 2 (slow reproducers) wins – a competitive exclusion steady state:

$$x_1^{(1)} = x_2^{(1)} = 0, \quad x_1^{(2)} = \frac{K[ra_2^{(2)}w - 1]}{1 + w}, \quad x_2^{(2)} = \frac{Kw[ra_2^{(2)}w - 1]}{1 + w}.$$

3. A coexistence state.

4. Periodic solutions.

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[1]For the analysis of the trivial solution one has to modify the original system by adding a small constant in the denominators of all the equations, otherwise we have a singularity which is meaningless, because the transfer terms multiplying β must be zero if the population is zero.

Stability of the two exclusion states can be investigated. For simplicity, let us set all nonzero values of fecundity to a constant, $a_j^{(s)} = a$. Further, we will assume that the coefficient of transfer is independent of the age, and is only defined by the type: $\beta_j^{(s)} = \beta^{(s)}$ for $j = 1, 2$, $s = 1, 2$. Let us analyze stability of solution 1 above (fast reproducers win). Stability of the discrete system requires all the eigenvalues of the Jacobian to satisfy $|\lambda| < 1$. The eigenvalues are given by

$$\lambda_{1,2} = \frac{1 \pm \sqrt{1 + 4rw(1+w)^2}}{2r(1+w)^2}, \tag{13}$$

$$\lambda_{3,4} = \frac{\beta^{(1)}(2+w) \pm \sqrt{w[w(2+\beta^{(1)}-2\beta^{(2)})^2 + 4(1+\beta^{(1)}-\beta^{(2)})(1-\beta^{(2)})]}}{2(1+w)}. \tag{14}$$

The first two eigenvalues do not depend on the transfer rates and correspond to the stability of the type 1 population in the absence of the other population. We can show that $|\lambda_{1,2}| \leq 1$ for all $0 \leq w \leq 1$ and $r \geq 1$. In particular, $\lambda_1 \geq 0$, we have $\lambda_1 = 1$ when $r = 1, w = 0$, it decays with r and w for $r \leq 2$, and for a given $r > 2$, it has a maximum value $(1-w)/2$ when

$$r = \frac{2}{(w-1)^2(w+1)}.$$

Further, $\lambda_2 \in (-1, 0]$ for all values $w \in [0, 1]$ and $r \geq 1$, since $\partial \lambda_2 / \partial r > 0$, and for $r = 1$, $\lambda_2 = 1 - \sqrt{1 + 4w(1+w)^2}/(2(1+w)^2) \in [1/8(1 - \sqrt{17}), 0]$.

The eigenvalues $\lambda_{3,4}$ describe stability against an invasion of type 2 individuals. The solution can become unstable if $\lambda_3 > 1$. This happens when

$$w > w_1 \equiv \frac{(1 - \beta^{(1)})^2}{(\beta^{(2)} - \beta^{(1)})(2 - \beta^{(2)})}.$$

Clearly, if $\beta^{(1)}$ is large (close to 1), the type 1 solution is unstable (because of frequent transfers to type 2). In fact, as long as

$$\beta^{(1)} < \frac{4 - \beta^{(2)} - \sqrt{5(\beta^{(2)})^2 - 16\beta^{(2)} + 12}}{2},$$

the type 1 solution is stable for any values of $w < 1$, because $w_1 > 1$. If however the inequality above is revered (that is, the transfer rate is larger

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than a threshold for type 1), the solution becomes unstable for sufficiently large values of w.

Intuitively, fitness of each of the types is comprised of their net fecundity and their propensity to stay (and not transfer to the opposite type). Clearly, the fecundity of type 1 is larger than that of type 2. But this can be offset by a larger probability of transfer (if we assume that $\beta^{(1)}$ is larger than $\beta^{(2)}$ by a sufficient margin). Small death rates (and therefore large values of w) work against type 1 individuals and benefit type 2 individuals. If w is large, more individuals survive to later stages (and thus type 2 has a better chance to reproduce). Further, for larger values of w, there will be a larger influx of individuals transferring from type 1 to type 2: they simply have a longer time to stay alive and decide to switch. Thus, living longer adds fitness to type 2, such that after a threshold of w, type 2 becomes stronger and drives type 1 extinct.

Investigating the stability of type 2 equilibrium, we discover that it is unstable (in this simple 2-age model) for all values of w except for $w = 1$, where it is neutral. Note that for systems with more age stages, this is not the case, and we have a stable type 2 equilibrium (see the previous section). For the 2-age system, for values $w < 1$, but close to 1, instead of equilibrium 1, we observe a stable cycle which contains only type 2 individuals.

3 Birth-death, imitation, and mutation dynamics

3.1 Model formulation and numerical results

Envisage the following process. In a 1D spatial system of a constant size, N, each individual, i, is characterize by a reproduction rate, l_i. During each time unit, N updates are performed, each consisting of two parts, a death-birth (DB) update and a cultural transmission (CT) update. Each update proceeds as follows:

- A DB update: An individual is chosen, randomly and fairly, to be removed (say, this is the individual at location i_1). Then it is replaced by the progeny of one of its two neighbors: the individual at location

i_1+1 reproduces with probability $l_{i_1+1}/(l_{i_1+1}+l_{i_1-1})$, and the individual at location $i_1 - 1$ reproduces with probability $l_{i_1-1}/(l_{i_1+1} + l_{i_1-1})$. The offspring inherits the reproduction rate of the parent.

- A CT update: this event happens with probability β, which sets the relative time scale of the two types of updates. Pick an individual, randomly and fairly, to perform an imitation update (say this is the individual at location i_2). This individual will change its reproduction rate from l_2 to

$$\tilde{l} = \frac{\sum_{j=i_2-1}^{i_2+1} \alpha_{i_2,j} l_j}{\sum_{j=i_2-1}^{i_2+1} \alpha_{i_2,j}},$$

where

$$\alpha_{i,j} = \begin{cases} 1, & l_j \leq l_i, \\ s, & l_j > l_i, \end{cases}$$

and $0 < s < 1$ is a constant that indicates by how much the strategy of fast reproducers is discounted. In other words, a weighted average of all the strategies around the focal individual at i_2 is formed, such that the strategy of those who reproduce faster than the focal individual is discounted with coefficient s. The focal individual adopts the resulting strategy with probability $1 - u$. With probability u, strategy $\tilde{l}$ is increased or decreased (with equal likelihood) by an amount Δl (unless $l < \Delta l$, in which case it can no longer decrease). This process is equivalent to mutations, whereby the phenotype is modified with a certain probability to give rise to variation.

We would like to characterize the equilibrium of this system. First we note that in the absence of mutations ($u = 0$), the state with $l_i = l$ for all i is a equilibrium for any value of l. As a result, the system will converge to one of these neutral equilibria, depending, for example, on the initial condition.

The dynamics change drastically in the presence of mutations, $u > 0$. Now, uniform states are no longer equilibrium states, and the equilibrium reproduction rates will be distributed around some mean value, $\bar{l}$, with the variance that increases with u and Δl. In figure 2(a) we present the time series of the population mean reproduction rates, for 4 different values of Δl, the increment of the reproduction rate. We can see that the population settles to a stochastic equilibrium, where the mean population mean reproduction rate increases with Δl, and convergence time decreases with Δl. Figure 2(b) shows numerically obtained histograms of reproduction rates of populations
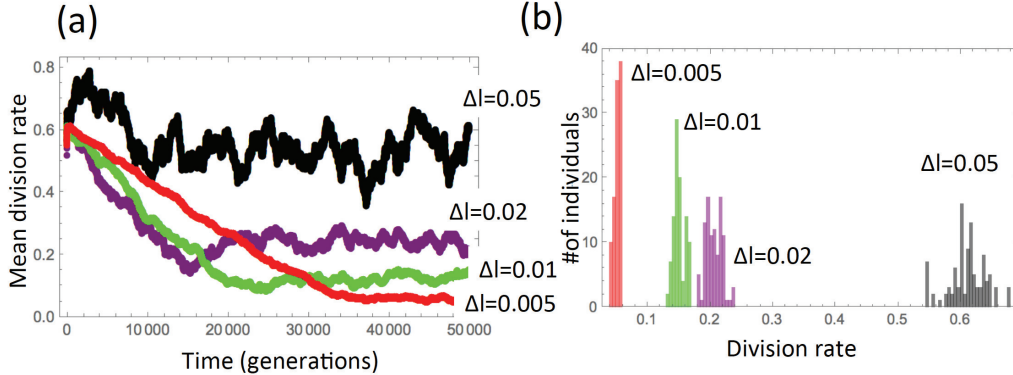
Figure 2: The dynamics of a 1D simulation with mutations. (a) The time-series of the population mean reproduction rate, for 4 different values of Δl. (b) Numerically obtained histograms of the population's reproduction rates, taken at generation 50,000, for the same 4 values of Δl. The rest of the parameter are: $N = 100$, $u = 0.04$, $\beta = 1$, $s = 0.9$.

at equilibrium, for the same four values of Δl. We can see that the standard deviation increases with Δl. Similar trends are observed when we vary the mutation rate, u (not shown). 2D simulations that show the same trends are shown in figure 3.

3.2 Analytical considerations

To find the mean equilibrium value of the reproduction rates, we use the following argument. Suppose that the equilibrium distribution[2] of the reproduction rates is given by $\{f_k\}$, such that the probability for an individual to have reproduction rate L_k is given by f_k, with

$$\sum_k f_k L_k = \bar{l}.$$

Under a BD event, suppose an individual at position i_1 with reproduction rate L_1 is picked for replacement, and suppose further than its two neighbors have reproduction rates L_2 and L_3. Then the expected increment in the

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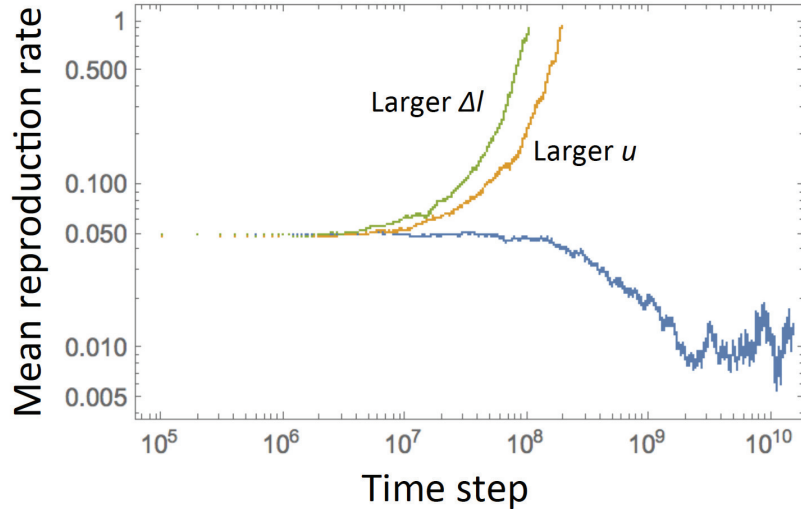[2]A similar argument for continuous distributions can be developed.

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Figure 3: The dynamics of a 2D simulation with mutations. The population mean reproduction rate is plotted as a function of time, for 3 simulations. The blue line represents a base-line simulation with parameters $u = 0.1, \Delta l/l = 0.02$, the orange line a simulation with an increased mutation rate, $u = 0.3$, and the green line a simulation with an increased $\Delta l/l = 0.04$. The rest of the parameters are as in Fig.3 of the main text, with the death rate 3.75×10^{-4}.

reproduction rate of the focal individual is given by

$$-L_1 + L_2 \frac{L_2}{L_2 + L_3} + L_3 \frac{L_3}{L_2 + L_3}.$$

Averaging over all the possible reproduction rates, we obtain the expected increment in reproduction rate from a DB update:

$$\Delta L_{DB} = \sum_i \sum_j \sum_k \left(-l_i + \frac{l_j^2}{l_j + l_k} + \frac{l_k^2}{l_j + l_k} \right) f_i f_j f_k. \qquad (15)$$

Similarly, we can calculate the expected increment in the reproduction rate resulting from a cultural transmission event:

$$\Delta L_{CT} = \sum_i \sum_j \sum_k \left(-l_i + \frac{l_i + \alpha_{ij}l_j + \alpha_{ik}l_k}{1 + \alpha_{ij} + \alpha_{ik}} \right) f_i f_j f_k. \qquad (16)$$

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The equation

$$\Delta L_{DB} = -\beta \Delta L_{CT} \tag{17}$$

characterizes the equilibrium. Note that the right hand side of this equation is positive, because the mean increment resulting from CT updates is negative, due to a diminished weight of high reproduction rates in the weighted averages. The left hand side is also positive, because DB updates tend to increase the reproduction rates due to competition among individuals.

Let us assume that the width of the distribution of the equilibrium reproduction rates is defined by the mutation rate (and the increment Δl), and keep it fixed, while varying the mean $\bar{l}$. Note that in equation (16), the expression in the parentheses can be rewritten as

$$\frac{\alpha_{ij}(l_j - l_i) + \alpha_{ik}(l_k - l_j)}{1 + \alpha_{ij} + \alpha_{ik}}.$$

For each location i, let us present $L_i = \bar{l} + \epsilon m_i$, where all m_i are IID with a zero mean and a variance that we denote by $(\sigma/\epsilon)^2$. We can see that $\bar{l}$ cancels from the above expression, and its statistics will only depend on the distribution width. In other words, the mean decrement received by the population reproduction rate as a result of a CT update is defined by the difference between the focal reproduction rate and a weighted average of its neighboring reproduction rates, and does not depend of the absolute value of the rates.

On the contrary, the DB increment defined by equation (15) depends on the magnitude of $\bar{l}$. Intuitively, neighbors compete for filling the empty spot, and the amount of advantage experienced by a neighbor with a higher reproduction rate is proportional to the relative, and not absolute, difference in the rates. Therefore, the increment scales with the relative amount of spread in reproduction rates, and is thus inversely proportional to $\bar{l}$. Again, for each location i, we present $l_i = \bar{l} + \epsilon m_i$, where all m_i are IID with a zero mean and variance $(\sigma/\epsilon)^2$. Then, expanding the expression in parentheses in (15) in terms of ϵ we obtain

$$\left(\frac{m_j + m_k}{2} - m_i\right)\epsilon - \frac{\epsilon}{2}\frac{(m_j - m_k)^2}{m_j + m_k}\sum_{n=1}^{\infty}\left(-\frac{(m_j + m_k)\epsilon}{2\bar{l}}\right)^n.$$

The first term averages to zero, and the second term is given by

$$\frac{\epsilon^2}{4\bar{l}}(m_j - m_k)^2,$$

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which upon averaging yields

$$\frac{\sigma^2}{2\bar{\bar{l}}},$$

a quantity inversely proportional to the mean reproduction rate of the population. We further see that it depends on the square of σ in the lowest order.

From the above analysis it follows that the left hand side of equation (17) is a decaying function of $\bar{l}$ which tends to zero as $\bar{l} \to \infty$, and the right hand side of equation (17) is $\bar{l}$-independent. There will be a unique intersection of the two curves as long as β is chosen to be sufficiently low. This intersection defines the equilibrium value of the population mean reproductive rate.

We further note that the quantities Δ_{DB} and $-\Delta_{CT}$ both grow with the distribution width of the reproduction rates, but while $-\Delta_{CT}$ is linear in σ, Δ_{DB} is quadratic in this quantity, and thus grows faster as we increase the width of the distribution of l. Therefore, as u increases and the distribution width increases, the left hand side of equation (17) grows faster than the right hand side, resulting in an increase in the solution, $\bar{l}$.
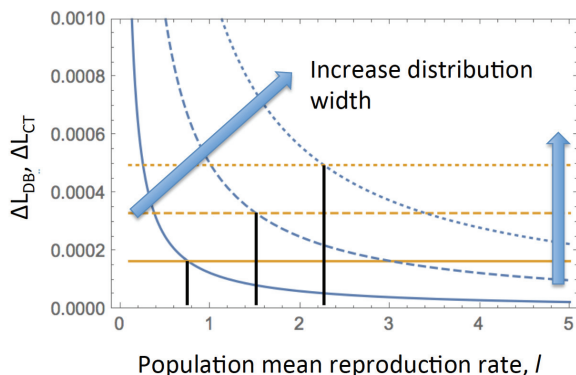

Figure 4: Finding the equilibrium reproduction rate by solving equation (17), illustrated with example (18-19). The left hand side of equation (17), ΔL_{DB}, is shown as blue lines and the right hand side, $-\beta \Delta L_{CT}$, with yellow lines, as functions of $\bar{l}$. Solid, dashed, and dotted lines correspond to three different values of Δl: $0.05, 0.10, 0.15$. The rest of the parameters are: $s = 0.9, \mu = 0.1, \beta = 1$.

This is illustrated in an example where we assumed that the division

rates are distributed according to the following three-valued distribution with mean $\bar{l}$ and variance $(\Delta l)^2\mu$:

$i \rightarrow$	1	2	3
L_i	$\bar{l} - \Delta l$	$\bar{l}$	$\bar{l} + \Delta l$
f_i	$\mu/2$	$1 - \mu$	$\mu/2$

The expressions for ΔL_{DB} and ΔL_{CD} can be obtained explicitly,

$$\Delta L_{DB} = \frac{(\Delta l)^2\mu}{2\bar{l}} \frac{(\Delta l)^2\mu - 4\bar{l}^2}{(\Delta l)^2 - 4\bar{l}^2}, \tag{18}$$

$$\Delta L_{CT} = \frac{\Delta l \mu (1-s)}{6(2+s)(1+2s)} \left((6-\mu)\mu s - 10s + \mu(3+\mu) - 8 \right). \tag{19}$$

In figure 4, both sides of equation (17) are plotted as functions of $\bar{l}$, and their intersections are marked with vertical lines, for three values of Δl, which represent an increase in the distribution width. We can see that the corresponding solutions $\bar{l}$ become larger for larger distribution widths.