Evolutionary dynamics of culturally transmitted, fertility-reducing traits

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Abstract

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

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

evolutionary thinking, individuals evolve to maximize their reproductive potential, and to translate increased resource availability into higher reproductive success.

A number of theories have been put forward to account for demographic transitions towards reduced fertility [1,11]. According to one line of argument, the transition to reduced fertility might be maladaptive. That is, humans employ behavioral strategies that used to be advantageous in previous times, but currently result in behaviors that are not adaptive due to recent significant changes in socio-economic factors. Another line of argument suggests reduced fertility to be adaptive, because the current environment favors the production of few offspring with large parental investment rather than the generation of more offspring with lesser parental investment per child. This might be a significant consideration in parts of the world where competition among individuals for jobs and careers is fierce. A third mechanism that has been invoked to explain the observed decline in fertility is non-genetic, cultural evolution. According to this argument, behavior that leads to reduced fertility in certain influential individuals is copied by other individuals in the population, resulting in a spread of this trait throughout the population. This explanation has the advantage that cultural evolution can occur on much faster time-scales than genetic evolution, which is required to account for the relatively fast observed rate of transition to lower fertilities in human populations.

The dynamics of cultural transmission have been studied extensively with mathematical models [12-19], and these approaches have also been applied to the analysis of demographic transitions and the evolution of small family sizes, in particular by the group of Marc Feldman [20-22]. In the simplest forms, such models are given by ordinary differential equations that describe the spread of the cultural trait, similar to infection models [12]. On a more complex level, age-structured models were formulated [20,21] showing that cultural transmission dynamics can result in demographic transitions on time scales that are similar to those observed in human data. The spread of cultural traits that affect fertility, survival, or both was investigated and the effect of these traits on the demographic structure of the population was investigated. The roles of vertical, oblique, and horizontal transmission of the trait were examined, and the models indicated that horizontal and oblique learning could accelerate the spread of the cultural trait, compared to vertical transmission alone [20]. In an earlier study, it was shown that cultural niche construction could be an important component that contributed to the transition to reduced fertilities [21]. According to this mechanism, the first trait to spread is one of valuing education, which provides an environment that promotes the spread of a second, fertility-reducing trait. If the trait of valuing education is further associated with reduced mortality of individuals, the model predicts that the decline in fertility is preceded by a reduction in the population death rate, as observed in demographic data. These models were examined further in the context of spatial population structure, formulated as niche construction models in metapopulations [22].

In these studies, the increased survival / lower death rate of the population was either considered a culturally transmitted trait (similar to fertility reduction), or it was coupled to a culturally transmitted trait, e.g. by assuming that appreciation of education correlates with increased viability. Here, we consider cultural transmission models where the population death rate is an independent, exogenous variable that can be modulated (reduced) over time, e.g. as a consequence of sanitary, medical or technological advances, and investigate the effect of such changes on the ability of a fertility-reducing trait to spread. We study the spread of the fertility-reducing trait in spatially structured and non-spatial models, as well as in models with and without age structure. We first consider a model with two populations, a fast and a slow reproducing one, and subsequently consider models where the reproduction strategy is a continuous trait. Because the overall death rate of individuals negatively correlates with the economic development and the amount of resources available to the population, this analysis sheds further light onto the correlation between resource availability and the rate of population growth.

A two-dimensional agent-based model with asexual reproduction

We begin by examining the spread of a fertility-reducing cultural trait with the help of a two-dimensional, stochastic agent-based model (ABM) that describes population dynamics on a 2D grid of size nxn. We will refer to this model as ABM1. Two populations are considered which reproduce with a fast and slow rate, respectively.

During each time step (representing a generation), the grid is randomly sampled 2M times, where M is the total number of individuals currently present. When an individual is picked, it can undergo either a birth-death update, or a cultural transmission update (with equal probabilities). If the birth-death update is chosen, the individual reproduces with a probability R_f and R_s, depending on whether this is a fast or slow reproducer. A spot is chosen randomly from the eight nearest neighbors. If that target spot is empty, the offspring is placed there, otherwise, the reproduction event is aborted. With an independent probability D, the individual dies; both populations are assumed to have the same death rate.

During a cultural transmission update, the individual attempts to change its reproductive strategy with probability C. Given that the cultural transmission update is attempted, the actual change by cultural transmission occurs with the probability defined by the prevalence of individuals with the opposite strategy among the 8 nearest neighbors (including the individual under consideration), see below for more details. The ratio of the constant C to the mean division rate roughly measures prevalence of cultural transmission in the population; it roughly corresponds to the fraction of the individuals in each generation that attempt to change their reproductive strategy based on their neighbors' strategy.

A cultural update is performed by gathering the information on the reproductive strategy of the individuals' neighbors, similar to voter models [17,23]. In our model, however, we assume that slow reproducers are more effective at changing a fast reproducer's strategy than vice versa. In particular, when adding up the number of fast and slow reproducers in the neighborhood, there is a probability $Q<1$ that a fast

reproducer is taken into account, while all slow reproducers are always included. This reflects the assumption that the opinion of a slow reproducer is more influential than that of a fast reproducer. This modeling choice is motivated by the assumption that slow reproducers tend to channel the resources available to them into accumulation of wealth and/or social status, and thus they may appear as more attractive models for imitation.

Outcomes of computer simulations for model ABM1

We first discuss the effect of the two components underlying the model: the birth-death process and the cultural transmission process. If the model is run with only the reproduction and death processes (without cultural transmission), the only outcome is the persistence of the fast reproducing population and the competitive exclusion of the slower reproducing one. This is straightforward competition dynamics behavior, which underscores the notion that a slower rate of reproduction is a disadvantageous strategy. If the model is run with only cultural transmission (no reproduction and death, but a constant population), it essentially becomes a voter model, where “slow” and “fast” are different opinions held by individuals in the population. As has been described for such models [17,23], the only eventual outcome is that every individual in the population has the same opinion. Which of the two opinions wins, depends on drift dynamics and hence on initial frequencies of the opinions in the population.

When both processes are included, more complex dynamics are observed. Now three outcomes are possible (Figure 1): the fast reproducers win and exclude the slow

reproducers; the slow reproducers win and exclude the fast reproducers; both populations coexist in the longer term. Since we study stochastic models, the only eventual outcome is extinction. In what we call “coexistence”, the time until one of the populations goes extinct is significantly longer than in the parameter regimes we call “exclusion” (compare Figure 1C to 1A &B). Which outcome is observed depends on several model parameters, most notably the death rate of agents, D. This is shown in Figure 2Ai. Each point on this graph depicts the time until one of the populations goes extinct, depending on the death probability, D. The outcomes are color-coded: purple depicts fast reproducers remaining, and green slow reproducers. At higher death rates, the fast reproducers persist and extinction of the slow reproduces occurs at relatively short time scales. At low death rates, the slow reproducers persist and the fast reproducers go extinct on a relatively short time scale. At intermediate death rates, the time to extinction of one of the populations rises sharply, and either population has a chance to go extinct first. This corresponds to the coexistence regime. Therefore, lower death rates among individuals in the population create conditions in which the cultural transmission of the slow reproduction trait is successful, resulting in an overall reduced level of fertility.

Other parameters further modulate the outcome of the dynamics. Cultural transmission of the low fertility trait is promoted by lower values of Q, i.e. by a reduced influence of fast reproducers on choosing the reproduction strategy during the cultural transmission procedure. Increasing the value of Q results in a lower population death rate that is required for cultural transmission to be successful (Figure 2Aii). The relative

probability for a cultural transmission event to take place, C, is also an important determinant of outcome. As expected, higher values of C promote the cultural spread of the fertility-reducing trait. For lower values of C, lower population death rates are needed for cultural transmission to be successful (Figure 2Aiii).

Including age structure into the agent-based model

Rather than considering fast versus slow reproducers, we now modify the agent-based model to consider early versus late reproducers. This model will be referred to as ABM2. While these two concepts are related, a reduction in fertility due to a later age of first reproduction might be relevant to current times where segments of the population with higher degrees of education and more wealth tend to reproduce at later ages. In the agent-based model, we therefore consider four age classes. Individuals are born into age-class 1, at which no reproduction is possible. During each time step, all individuals age by one time unit. After A time units, an individual advances to the next age class. Reproduction can occur in age classes 2 and 3 for early reproducers, and only in age class 3 for late reproducers. In either case, reproduction occurs with a probability R. Age class 4 is a post-reproductive phase, during which the only event that can occur is death. Death can occur in all age classes, but with increasing probabilities for successive age classes, i.e. with probabilities $D_4>D_3>D_2>D_1$. This model has the same properties as the previous one, where we distinguished between slow and fast reproducers. We again observe three possible outcomes: extinction of either early or

late reproducers, or longer-term coexistence (not shown). The influence of parameters on outcome is also the same on a qualitative level. Importantly, the death rate of individuals is again a key determinant of outcome. Since in this model there are different death rates for the different age classes, we multiplied all of the death rates by a factor F, which means that all death rates change by the same amount. In Figure 2B, we plotted the outcome of the dynamics for increasing values of F, which corresponds to increasingly higher population death rates. Again, each point depicts the time until one of the two populations goes extinct. We observe the same trend as before. For higher population death rates, the fast reproducers remain. For low death rates, the slow reproducers remain. For intermediate death rates, we observe coexistence, indicated by a sharp rise in the time to extinction, where either fast or slow reproducers have a chance to persist.

Complete mixing versus spatial constraints

The spatial nature of the models explored above makes it difficult to obtain analytical insights. In this section, we formulate the same processes under the assumption that individuals mix well. Spatial constraints are most relevant to the cultural transmission aspect of the model because people are most likely to communicate with and consider the opinion of neighboring individuals. Mixing, however, can be assumed if populations are relatively small or information travels more easily through populations.

Fast and slow reproducers. First, we again consider two types of individuals that differ by their reproduction rates. In the context of well-mixed populations, this can be described by ordinary differential equations (see Section 1 of the Supplement for more details of the analysis). Denoting fast reproducers by x_f and slow reproducers by x_s, the model can be written as follows:

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

where $W = 1 - \frac{x_f + x_s}{K}$ introduces density dependence, limited by the carrying capacity *K*. Hence, both populations grow logistically and are in competition with each other, and die with a rate d (assumed to be the same for slow and fast reproducers). The rate at which individuals change opinion through cultural transmission (fast reproducers becoming slow and vice versa) is proportional to the weighted fraction of the individuals with the opposite opinion in the whole population, multiplied by the rate constant β. (For comparison, in the spatial setting, the probability to change opinion was proportional to the weighted fraction of the individuals with the opposite viewpoint among only the nearest neighbors). The coefficient $\gamma < 1$ indicates the degree to which the influence of fast reproducers is reduced compared to that of slow reproducers. The equations above simplify to the following system:

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

Another way to model the process of differential strategy switching is to assume simply that cultural transmission is more effective from slow to fast reproducers than vice versa. This can be expressed as

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

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

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

The formulation of the cultural transmission dynamics is now equivalent to an infection model with frequency-dependent infection terms [12,24]. 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 K), not its fraction in the population. Hence, we also consider the following version of the model:

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

In the Supplement we demonstrate that all three versions of the model lead to very similar conclusions. Here we show the results for the latter system, which is the simplest, and which will be subsequently referred to as the "ODE model". If the reproduction rates are larger than the death rates (r_f>d, r_s>d), the model is characterized by three equilibria:

(i) Fast reproducers win and slow reproducers go extinct, with equilibrium expressions given by $x_f = K(1-d/r_f), \quad x_s = 0.$ This equilibrium is stable if $d > d_1 \equiv \frac{r_1}{1+(r_1-r_2)/\beta}$.

(ii) Slow reproducers win and fast reproducers go extinct. The equilibrium expressions are given by $x_f = 0, x_s = K(1-d/r_s)$. The solution is stable if $d < d_2 \equiv \frac{r_s}{1+(r_f-r_s)/\beta}$.

(iii) Coexistence of fast and slow reproducers is described by the following equilibrium expressions: $x_f = \frac{K}{\beta}(d-d_2), \quad x_s = \frac{K}{\beta}(d_1-d)$. This is stable if d_2<d<d_1.

Therefore, similar to the corresponding spatial agent-based model, fast reproducers are only expected to dominate for relatively large population death rates. Lower death rates result in coexistence, and even lower death rates lead to the exclusive persistence of slow reproducers.

These results make intuitive sense in the context of the infection dynamics literature [25,26]. As the death rate of the population is decreased, the population density increases until it is large enough to allow the slow reproduction meme to spread. Essentially, a lower death rate increases the basic reproductive ratio of the slow reproduction trait above unity, allowing invasion. The less the difference between the strength of cultural trait transmission from fast→slow compared to slow→fast, the lower the death rate, d, has to be (and hence the higher the population density has to be) to allow the spread of the slow reproduction trait. Similarly, the larger the fitness difference between slow and fast reproducers (r_f - r_s), the lower the death rate d has to be to allow spread of the slow reproduction trait.

Age structure in a well-mixed model. An alternative approach is to consider a non-spatial, age structured model [27]. We will model the competition dynamics of two types that differ by their reproductive strategies (see Section 2 of the Supplement for analytical results). 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 reproduction rates in each age group, $a_i^{(s)}$. These quantities comprise the information on the reproductive strategy (how early this type is willing to start reproducing), and also the biological variation in fecundity (e.g. the assumption that fecundity may decline with age). We assume that individuals of type $s=2$ have a tendency to reproduce later than individuals of type $s=1$. We can formulate a discrete time dynamical system for these populations as follows:

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

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

Here, the first equation describes the creation of newborn individuals of type *s* by older individuals, where each age group reproduces with intensity $a_i^{(s)}$ and reproduction is 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* having the meaning of carrying capacity. The rest of the equations describe (i) the population moving from age group to age group, and (ii) the imitation dynamics. Coefficients $w_{i-1}^{(s)}$ describe the probability for an individual of type *s* in age group *j-1* to survive until age *j.* The probability of switching type (imitation) is described by terms including coefficients β. First we note that expression *3-s* simply means "the other type", as *3-s* returns 1 for *s=2* and it returns 2 for *s=1*. Further, the probability to switch from type *s* to type *3-s* while transitioning to age group *j* is given by $\beta_j^{(s)} v_j^{(3-s)}$, where

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

and is proportional to the fraction of individuals of age *j* and older that belong to "the other type". We can see that the first term on the right of equation (2) 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.

Generally, the behavior of this discrete dynamical system can be quite complex, and depending on the parameters we see exclusion equilibria (when one type is extinct and the other reaches a steady positive equilibrium), exclusion periodic solutions (again, one of the types is extinct and the other enters a steady cycle), and coexistence states (where both types are present, and may reach a steady state or a cycle). To draw the parallel between this model and those considered above, we note that parameters $w_{i-1}^{(s)}$ are responsible for survival to the next age group, and thus increasing these quantities is similar to decreasing the death rate in the previous models. We observe that exactly as before, large death rates favor the survival and dominance of the early reproducers, and small death rates lead to the exclusion of early reproducers by late reproducers.

Intuitively, this result can be explained as follows. Assume for simplicity that the transfer rate, β , does not depend on the age group, and the survival probability, w, is identical for all age groups and for both types. Fitness of each of the types is comprised of their net fecundity and their propensity to remain within their type (and not transfer to the opposite type). In the absence of imitation (transfer), clearly, the fitness 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.

Note that many other modeling choices can be made, which are described in the Supplement. The general trends described here are robust and do not depend on details on modeling choices. Analytical calculations for certain simple cases are also presented in the Supplement.

Reproductive strategy as a continuous trait

In this section, we return to the spatial model, but modify the assumptions. So far, we considered a population of slow and fast reproducers, where slow reproducers could switch to fast reproducers and vice versa. Switching occurred with a probability that was proportional to the weighed fraction of the opposing strategy among neighboring individuals. Rather than considering two discrete reproductive strategies, however, it is more realistic to assume the probability of reproduction to be a continuous variable. This model will be called ABM3. We again assume that an individual is chosen for a cultural transmission event with a probability scaled with C. In this model, however, instead of adopting (or rejecting) the reproductive probability of the opposite type, the individual adopts the weighted average of the reproduction probabilities among all neighbors (including its own reproduction probability). As in the above models, we assume that slower reproducers are more influential and contribute more to cultural transmission than faster reproducers. This is implemented during the averaging procedures across the neighborhood: we weigh the reproduction probability by a factor $Q<1$ if the

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

The outcome observed in this model is straightforward. As initial conditions, the individuals in the system are characterized by different reproduction probabilities. Over time, the reproduction probabilities converge to a spatially uniform value, the level of which depends on the initially assigned probabilities. The reason for this eventual uniformity is the assumption that an individual adopts the average reproduction probability of the neighborhood during a cultural transmission event.

Next, we introduce “mutations” that can occur during cultural transmission. Instead of simply adopting the (weighted) average strategy of the neighborhood, with probability u individuals would modify this strategy by increasing or decreasing it (with equal probabilities) by a fraction G. We examined the evolution of the average reproduction probability, R, over time, by running computer simulations, and the following outcomes were observed (Figure 3): (i) The average probability to reproduce, R, increases steadily towards the maximum possible value (R+D=1), shown by the purple, green, and red lines in Figure 3. (Simulations were stopped when R+D=1). (ii) The average probability to reproduce declines steadily, eventually resulting in population extinction, shown by the dark blue, light blue, and pink lines in Figure 3. Extinction occurs because the reproduction rate evolves to levels that are too low to maintain the population. (iii) The average probability to reproduce converges to an intermediate level, and fluctuates around this level, shown by the yellow and orange lines in Figure 3. This level is independent of the starting value of R (not shown).

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.

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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

distinguished, gender 1 and gender 2. Before reproduction can occur, two individuals of opposing gender have to form an exclusive connection, thus assuming monogamy. The following events can occur if an individual is chosen for a reproductive update. If the individual does not have a partner, a connection can be formed with a probability M if an individual of the opposite gender without a partner is present among the eight nearest neighbors. The partner is randomly chosen from the neighborhood. If the individual does have a partner, reproduction happens with a probability R_{av}, which represents the average reproduction probabilities of the two parents. For simplicity, it is assumed that once formed, a partnership cannot break, corresponding to life-long monogamy. The offspring resulting from this partnership are assigned to one of the genders with a 0.5 probability. The reproduction probability of the offspring is given by the average values of the two parents. The offspring is placed into a randomly chosen empty spot among the eight nearest neighbors of the parent that was originally picked for reproduction. If no empty spots exist within the immediate neighborhood, reproduction is not successful. Potential issues of mate preference for individuals with similar reproduction probabilities are not taken into account. Death occurs with a probability D, according to the same rules as described before.

As shown in Figure 4, the outcomes are qualitatively the same as in the corresponding model without sexual reproduction, described in the previous section. For relatively low population death rates, the reproduction probability can evolve towards reduced values until population extinction occurs. For relatively high death rates, the reproduction probability can evolve towards maximal values. For intermediate death rates, the population can fluctuate around an intermediate reproduction probability.

Simulating demographic transitions in growing populations

In the modeling approaches described so far, competition is a major driving force of outcome. In the absence of cultural transmission, faster or earlier reproducing populations outcompeted the slower or later reproducing ones. Cultural transmission could reverse the outcome of the competition if individuals were more likely to learn from slower rather than faster reproducers. Competition, however, is most prevalent if populations are close to an equilibrium or carrying capacity, which was the case in the above analysis. The patterns reported above are not observed in exponentially growing populations, because of the absence of competition (not shown). Because human populations have been growing, it is important to re-visit the above-explored processes in the context of unbounded population growth. While the population grows, individuals can still compete on a local level. Therefore, we consider a growing population that is subdivided into neighborhoods or demes. In each deme, the dynamics are modeled in the same way as in the previous sections, imposing a carrying capacity for each deme. For simplicity, we assume that in each deme, the dynamics are governed by the ODE model. As initial conditions, a single deme is populated with a majority of fast reproducers and a minority of slow reproducers. At the end of each time unit, there is a chance that a new, empty deme is founded into which a fraction of current population moves. The probability of this occurring is proportional to how full the current deme is. In addition, the probability to found a new deme is inversely proportional to the number of

existing demes. While the demes are not arranged spatially in this model, founding a new deme can be thought of as an increase in the density of the population, which gets more difficult the more demes already exist. Hence, the probability for members of an individual deme to found a new deme is given by $\frac{\alpha(x_f + x_s)}{K(\epsilon N + 1)}$, where N is the number of currently populated demes, x_f and x_s represent local population sizes of fast and slow reproducers, K is the local carrying capacity, and α and ε are constants. When a new deme is founded, a given fraction of both fast and slow reproducers moves into the new deme. As more demes become populated, the same algorithm is applied to every deme after each time unit.

In this model, we observe persistence of one type and exclusion of the other, while the population continues to grow (Figure 5A,B). As before, the fast population persist for fast overall death rates (Figure 5A), while the slow population persists for low overall death rates (Figure 5B).

We further used this model to simulate the demographic transition process (Figure 5C). The simulation was run as before, but at a defined time point in the simulation, the death rate is continuously and gradually reduced over several time steps towards a lower, new level. This exogenous reduction is shown by the grey line and is assumed to correspond to an improvement in various socio-economic factors that reduce mortality, such as an improvement in disease treatment, sanitary conditions,

technological innovations, etc. The fast reproducing population is shown in purple, the slow-reproducing population is green, and the total population size is shown by the red dashed line. Initially, the overall population death rate is relatively high, and the fast reproducing individuals enjoy a growth advantage. The average reproduction rate is shown by the black line and is driven by the fast-reproducing population. When the death rate is reduced, the fertility-reducing cultural trait can spread successfully and eventually becomes the dominant population. As the death rate declines, we observe a phase of faster population growth, as observed in data on demographic transitions [9]. Following a time delay after the reduction in the death rate, the reproduction rate also declines, which is again consistent with data on demographic transitions [9] (this is also seen in a zoomed-in graph in Figure 5D). The exact timing of events depends on model parameters. For the purpose of this simulation, we chose parameters such that it takes about 5 generations to reduce the reproduction rate two-fold. This is an order of magnitude that is similar to events observed in human populations [1] and shows that the cultural transmission dynamics underlying our model can lead to sufficiently rapid changes in fertility. A faster rate of cultural transmission (higher value of β) can lead to more rapid changes in fertility following the decline in the death rate, while the opposite holds true for slower rates of cultural transmission.

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.

Competition among individuals was a major driving force underlying the dynamics arising from the model. While in the simpler settings explored here, competition correlated with populations being close to carrying capacity, we showed how a deme model can give rise to the same outcomes in populations that continuously grow without converging to a carrying capacity. Hence, the results described throughout the paper may hold for growing populations. We demonstrated that, depending on parameters, the model can reproduce crucial features of the “demographic transition model” [9].

Our study complements previous mathematical work that analyzed the cultural spread of small family sizes in relation to demographic transitions [20-22]. Our models consider a simpler setting involving the basic spread dynamics of the fertility reducing trait, similar to infection models. The result that lower death rates promote the cultural spread of the low fertility trait is intuitive if considered in the broader context of infection dynamics models: lower death rates of individuals increase population density, and this increases the basic reproductive ratio of the infection [26]. In the context of the demographic transition towards reduced fertility, this is nevertheless an interesting result. First, it might provide a simple explanation for the typical observation that a reduction in fertility is preceded by a reduction in mortality, which our model reproduced. In addition, the dynamics exhibited by these models suggest that fertility can be characterized by density dependence, even in the context of increased resource availability and continuously growing populations. Data indicate that fertility as well as

family size preference are characterized by density dependence, the reasons for which are not fully understood [29].

An interesting result in our models was that for low population death rates, the average reproduction rate of the population can continuously decline towards levels that cannot sustain persistence anymore. In Western European countries, fertility has declined below replacement levels since the 1970s and 1980s [5,6]. In addition, recent surveys [6] have revealed that the ideal family size in German speaking countries has fallen below replacement levels, about 1.7 children, among younger people, indicating that this trend might continue in the future. These trends could be the result of the type of cultural evolutionary dynamics explored here.

Some processes in the more complex versions of the models considered here could also be formulated in slightly different ways. In ABM3 and ABM4, cultural transmission involves the calculation of the weighted average reproduction rate among individuals within the immediate neighborhood. The assumption was made that individuals with a faster reproduction rate than the agent under consideration count less in this process, irrespective of the magnitude of this difference. Alternatively, it could be assumed that the reduced weight is proportional to the difference in reproduction rates, thus taking into account the distance in social hierarchies. While it seems reasonable to assume that economically more successful individuals carry more weight in cultural 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

implications for understanding the forces that contribute to the occurrence of demographic transitions and that drive the decline of fertility below replacement levels in developed countries.

Acknowledgements: We would like to thank Simon Levin for useful discussions that helped shape this manuscript.

Figure legends:

Figure 1. Time series showing the different outcomes according to ABM1. Individual realizations are shown. (A) Higher death rates: fast reproducers persist and slow reproducers go extinct on a short time scale. (B) Lower death rates: slow reproducers persist and fast reproducers go extinct on a short time scale. (C) Intermediate death rates: both fast and slow reproducers persist for significantly longer time periods. Eventually one population goes extinct due to the stochastic nature of the simulation. Parameters were chosen as follows. R_f=0.005; R_s=0.8R_f; C=0.0008; Q=0.93. For (A), D=0.001. For (B), D=0.0001. For (C), D=0.00025.

Figure 2. Time to competitive exclusion, as a function of the death rate. (A) Model ABM1. Individual realizations of the computer simulation were run until one of the two populations (fast or slow reproducers) went extinct. This time was recorded with a green dot if the fast reproducer went extinct, and with a purple dot if the slow reproducer went extinct, as a function of the population death rate, D. For low death rates, there are only green dots, corresponding to the slow reproducer persisting and the fast reproducer going extinct relatively fast. For fast death rates, there are only purple dots, corresponding to the fast reproducers persisting and the slow reproducers going extinct in a relatively fast time scale. For intermediate death rates, the time until one of the populations goes extinct becomes sharply longer, and either population can go extinct first. This corresponds to long-term coexistence. For plot (i), parameters were chosen as follows: R_f=0.005; R_s=0.8R_f; C=0.0008; Q=0.93. Plots (ii) and (iii) explore parameter dependence of the phenomenon. (ii) A higher value of Q=0.98 makes it harder for the slow-reproduction trait to invade, hence requiring lower population death rates. (iii) A lower rate of cultural transmission, C=0.0004, makes it harder for the slow-reproduction trait to invade, hence again requiring lower population death rates. (B) Same, but according to ABM2 with age structure. Because each age class is characterized by its own death rate, we multiplied all those death rates by a variable factor F, and plotted the outcome against this parameter. The death rates for the age classes were: D_1=0.00004; D_2=0.00007; D_3=0.00009; D_4=0.0002. Other parameters are R=0.005; C=0.0008; Q=0.93; A=10,000.

Figure 3. Outcomes of ABM3 with a continuous reproduction strategy and cultural evolution. The average reproduction probability across the whole population is plotted over time. Individual simulation results are shown. Simulations were run for different death rates, decreasing from D1 to D8. For relatively high death rates, the average reproduction probability increases steadily towards maximal levels. For relatively low death rates, the average reproduction probability decreases steadily until population extinction occurs (due to the limited reproduction). For intermediate death rates, the average reproduction probability comes to oscillate around a steady value, which does not depend on initial conditions (not shown). Parameters were chosen as follows. Death rates are given by D1 = 0.002, D2 = 0.001, D3 = $4x10^{-4}$, D4 = $3.75x10^{-4}$, D5 = $3.6x10^{-4}$, D6 = 10^{-4}, D7 = $5x10^{-5}$, D8 = 10^{-5}. The reproduction probability of the individuals, R, was allowed to evolve, starting from R=0.05 for all individuals. C=0.0003; Q=0.965. The chance to make a mistake during cultural transmission ("mutation") u=0.1. In case of a mistake, the average reproduction rate was changed by G=2%.

Figure 4. Outcomes of ABM4 with continuous reproduction strategies, cultural evolution, and sexual reproduction. Simulations are in principle the same as those presented in Figure 3, but using the model with sexual reproduction. Assumed death rates decrease from D1 to D8. Results remain robust. Parameters were chosen as follows. Death rates are given by D1 = 0.002, D2 = 0.001, D3 = $7.5x10^{-4}$, D4 = $7x10^{-4}$, D5 = $6.5x10^{-4}$, D6 = $5x10^{-4}$, D7 = $2.5x10^{-4}$, D8 = $1x10^{-4}$. The reproduction probability of the individuals, R, was allowed to evolve, starting from R=0.05 among all individuals. The

population death rate, D, is indicated in the graphs. u=0.1, M=0.9; C=0.0003; Q=0.965; G=0.1; G=2%.

Figure 5. Computer simulations of the deme model, described in the text. (A) The slow-reproducing population (green) goes extinct and the fast-reproducing population (purple) continues to grow. Parameter values were chosen as follows: r_f=0.08, r_s=0.04, d=0.03, β=0.02, K=10, α=0.01, ε=0.01. (B) The fast-reproducing population is going extinct, and the slow-growing population takes over and continues to grow. The same parameter values were used, except d=0.003. (C) Simulation of the demographic transition process. Again, fast and slow reproducers are shown in purple and green, respectively. The total population size is shown by the dashed red line. The simulation is started with a death rate d=0.006. In this regime, the fast-reproducing population has the advantage and is dominant. The cultural spread of the low-fertility trait is not successful. At a defined time point, the death rate is reduced 1.8 fold every half generation until it has fallen to a value of d=0.001 (grey line). This creates conditions under which the cultural transmission of the fertility-reducing trait is successful, and the population characterized by a slow reproduction rate spreads. This leads to a decline in the average reproduction rate of the population (black line), which is delayed with respect to the reduction in the death rate. For the parameter regime considered, the average reproduction rate is halved within about 2-3 generations, which corresponds to about 50-100 years (a generation in the model is given by 1/r). The remaining 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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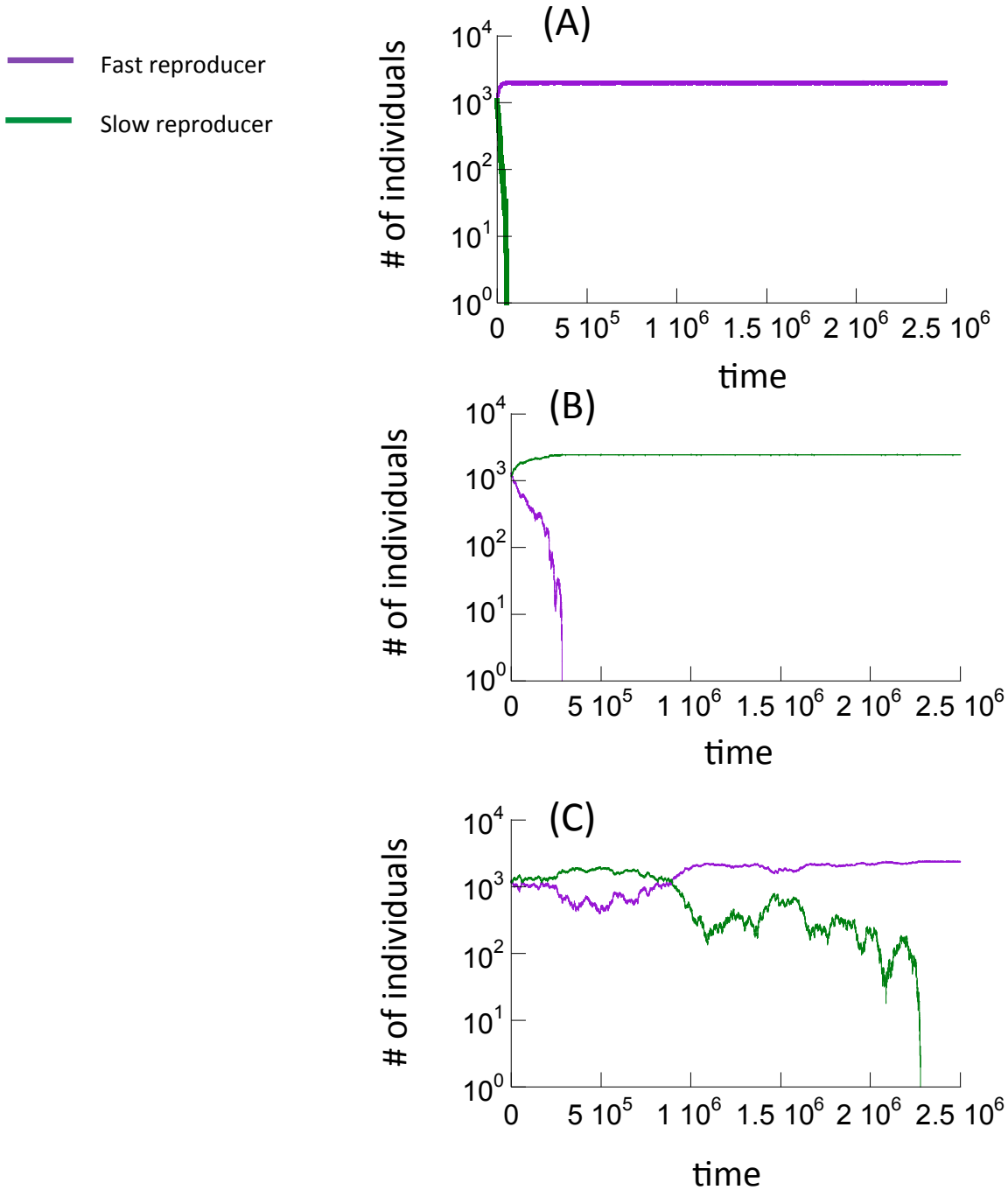
Fast reproducer
Slow reproducer
(A)
(B)
(C)
# of individuals
time
10^0
10^1
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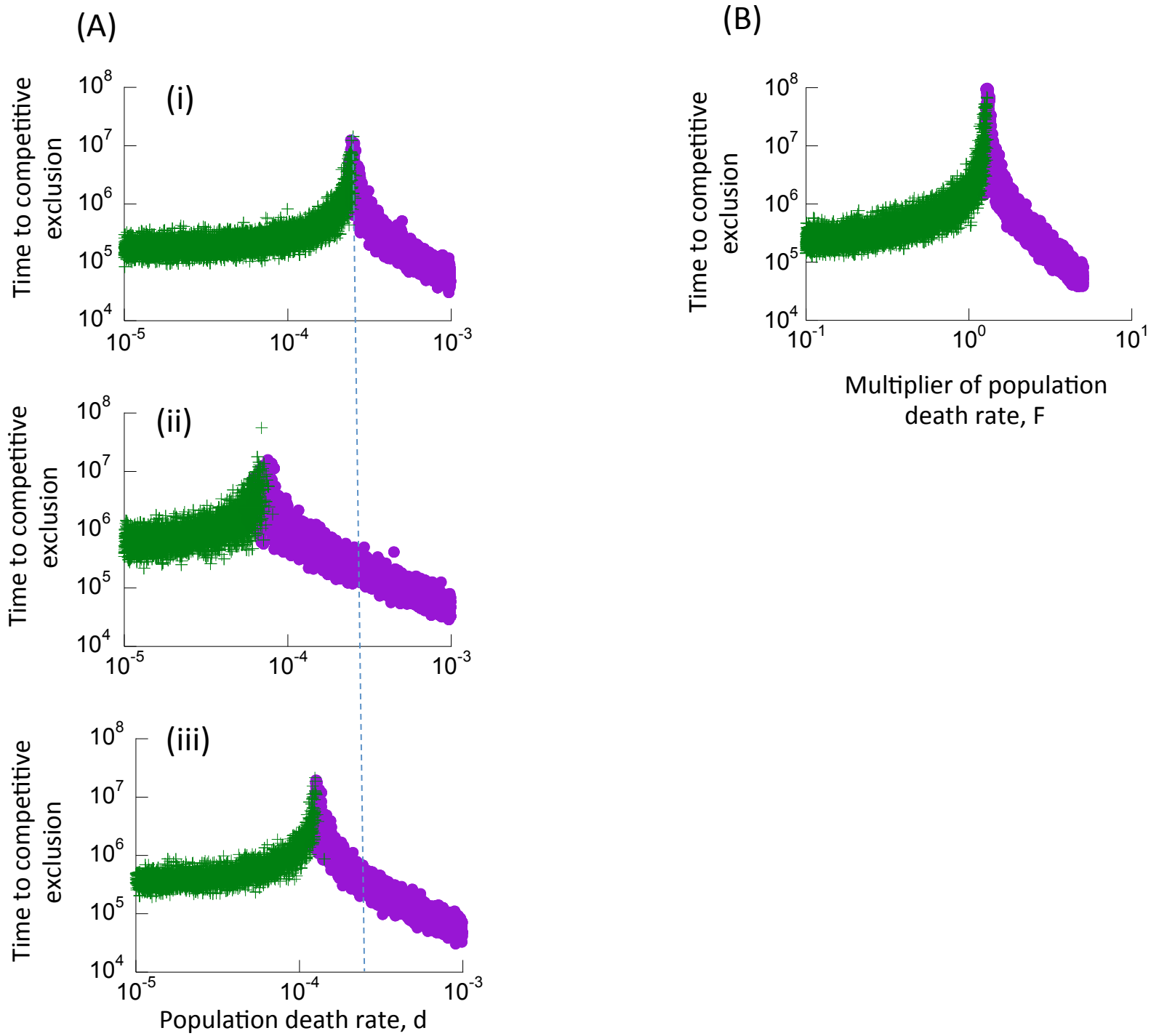
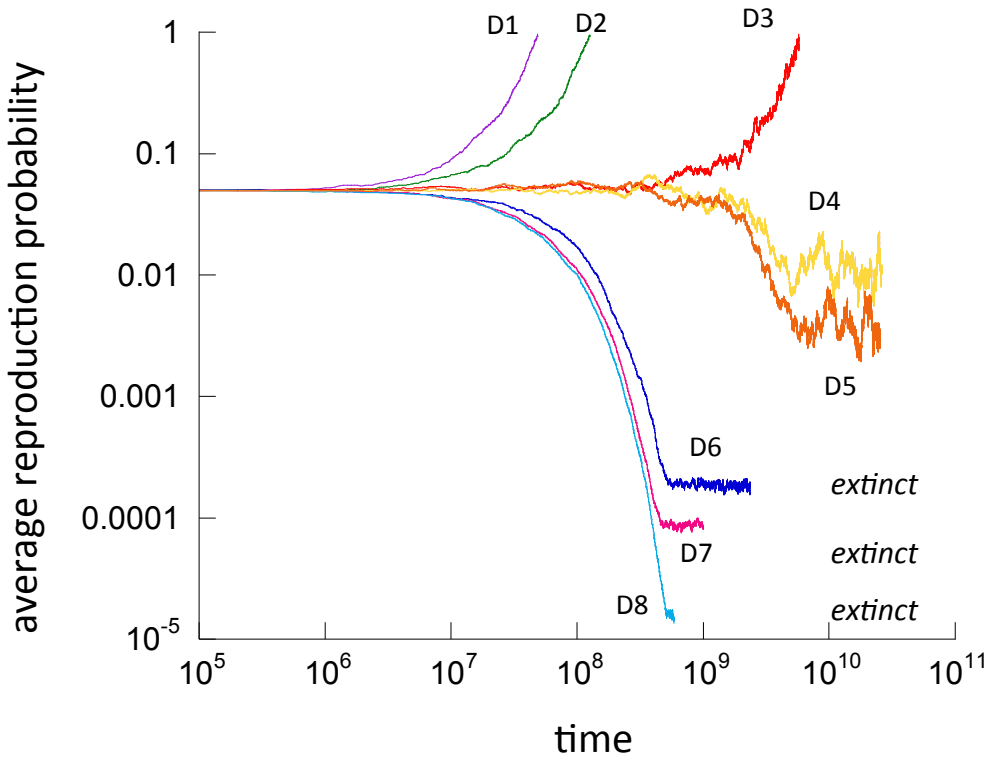
10^3
10^4
0
5 10^5
1 10^6
1.5 10^6
2 10^6
2.5 10^6


(A)
(i)
(ii)
(iii)
Time to competitive exclusion
10^8
10^7
10^6
10^5
10^4
10^{-5}
10^{-4}
10^{-3}
Population death rate, d
(B)
10^{-1}
10^0
10^1
Multiplier of population death rate, F


average reproduction probability
1
0.1
0.01
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10^{-5}
10^5
10^6
10^7
10^8
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10^{11}
time
D1
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D4
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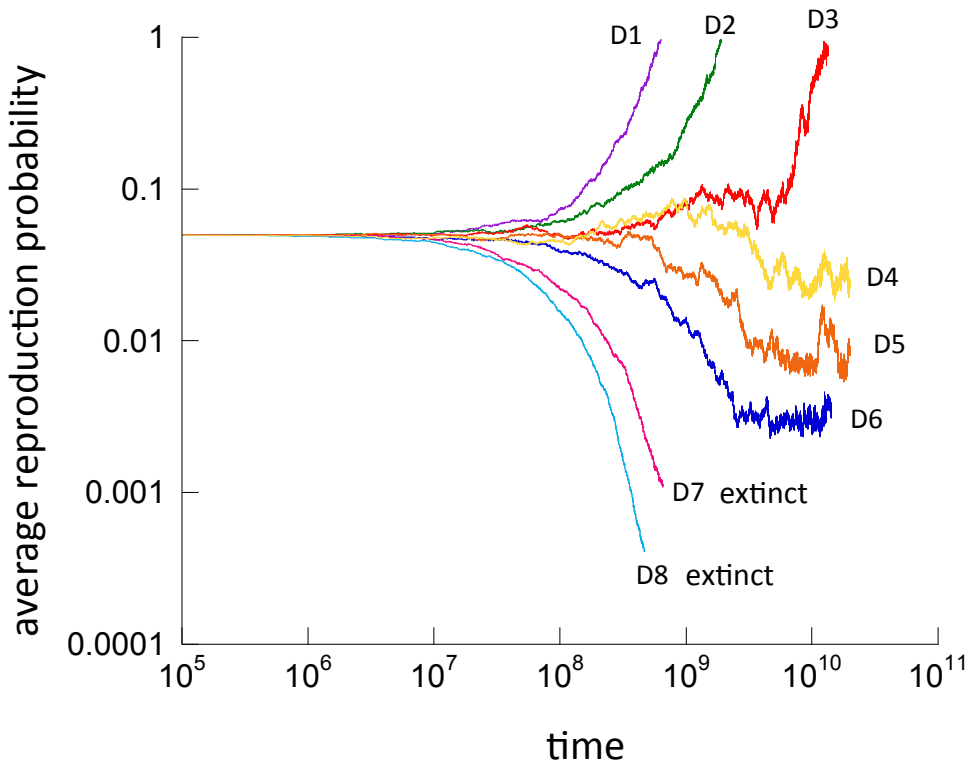
D8
extinct
extinct
extinct


average reproduction probability
1
0.1
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10^7
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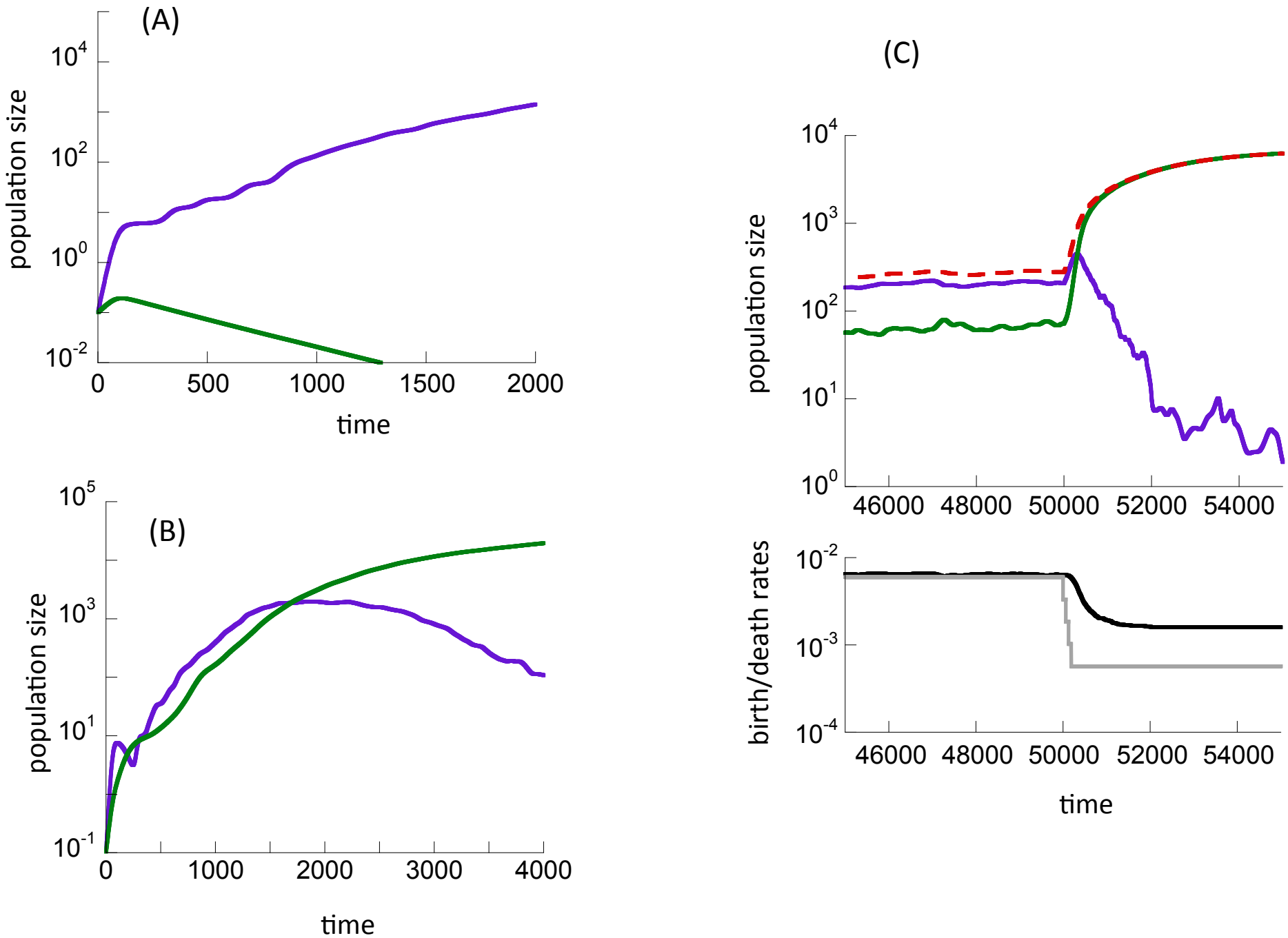
time
D1
D2
D3
D4
D5
D6
D7 extinct
D8 extinct


(A)
population size
10^4
10^2
10^0
10^{-2}
0
500
1000
1500
2000
time
(B)
population size
10^5
10^3
10^1
10^{-1}
0
1000
2000
3000
4000
time
(C)
population size
10^4
10^3
10^2
10^1
10^0
46000
48000
50000
52000
54000
birth/death rates
10^{-2}
10^{-3}
10^{-4}
46000
48000
50000
52000
54000
time

Evolutionary dynamics of culturally transmitted, fertility-reducing traits

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Supplementary information

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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

$$\dot{x}^{(1)} = r_1 x^{(1)} W - d x^{(1)} - \beta x^{(1)} x^{(2)}/K, \quad (1)$$
$$\dot{x}^{(2)} = r_2 x^{(2)} W - d x^{(2)} + \beta x^{(1)} x^{(2)}/K. \quad (2)$$

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

$$r_1 > r_2,$$

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.

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

$$\beta x^{(1)} x^{(2)}/K.$$

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,

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

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:

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

$$\begin{aligned} x_j^{(s)}(t+1) &= w_{j-1}^{(s)} x_{j-1}^{(s)}(t) \left(1 - \beta_j^{(s)} \frac{\sum_{k=j}^{N} x_k^{(3-s)}(t)}{\sum_{k=j}^{N} (x_k^{(3-s)}(t) + x_k^{(s)}(t))}\right) \\ &+ w_{j-1}^{(3-s)} x^{(3-s)}(t) \beta_j^{(3-s)} \frac{\sum_{k=j}^{N} x_k^{(s)}(t)}{\sum_{k=j}^{N} (x_k^{(3-s)}(t) + x_k^{(s)}(t))}, \quad 1 < j \leq N, \end{aligned} \tag{7}$$

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

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

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

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

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

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).

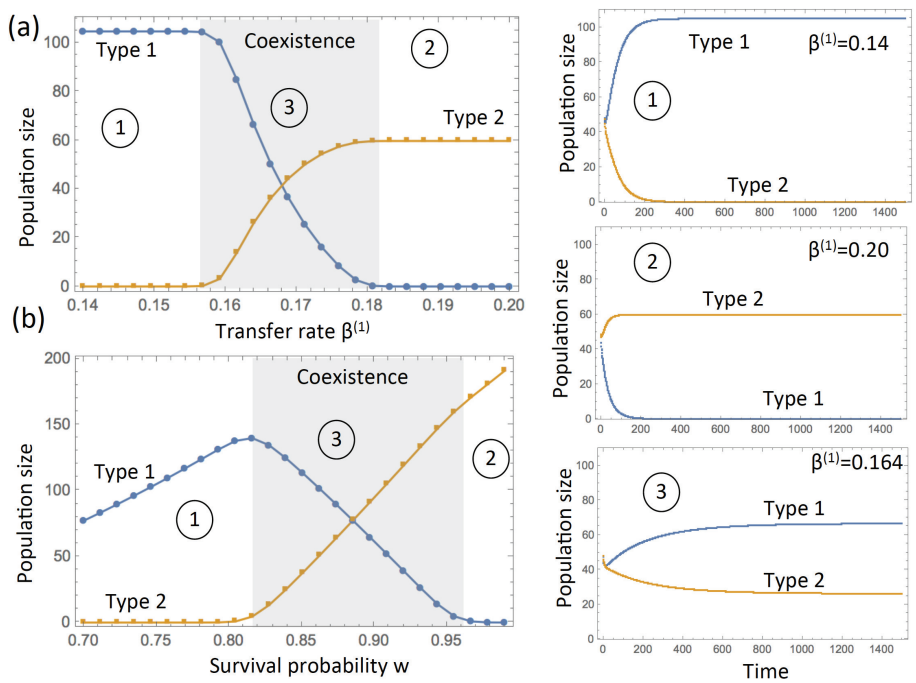

Figure 1: Age structured dynamics according to system (10, 7), numerical simulations. Total populations of individuals of type 1 and type 2 are presented. The steady state values are given on the left as functions of parameter (a) $\beta^{(1)}$ and (b) $w_i^{(s)} = w$ for all $s \in \{1, 2\}, 1 \leq i \leq N$, 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 $2 \leq i \leq 5$ for $s = 1$ and $3 \leq i \leq 5$ 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.

[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

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

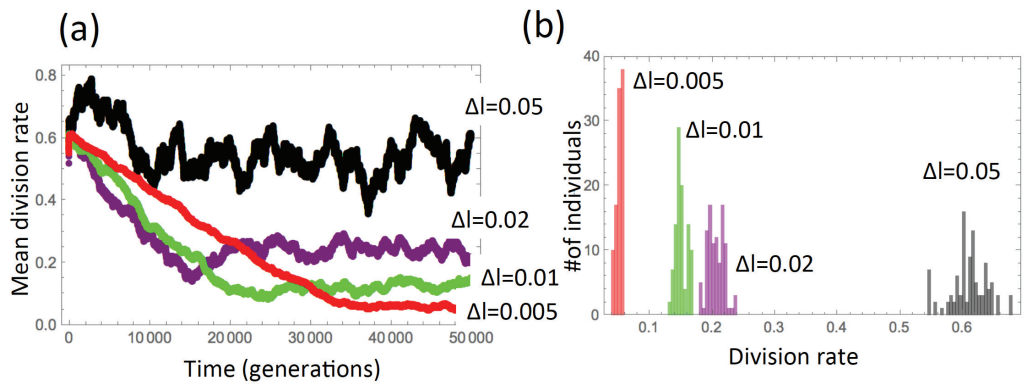

Figure 2: The dynamics of a 1D simulation with mutations. (a) The time-series of the population mean reproduction rate, for 4 different values of Δl. (b) Numerically obtained histograms of the population's reproduction rates, taken at generation 50,000, for the same 4 values of Δl. The rest of the parameter 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

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

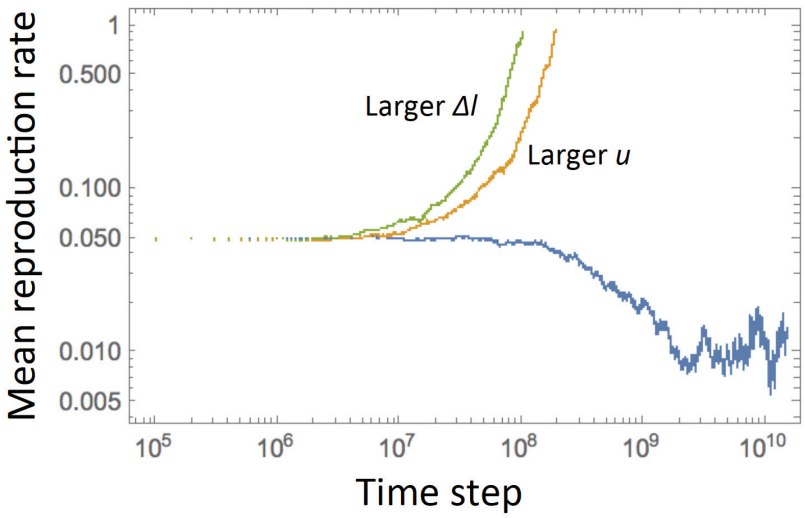

Figure 3: The dynamics of a 2D simulation with mutations. The population mean reproduction rate is plotted as a function of time, for 3 simulations. The blue line represents a base-line simulation with parameters $u = 0.1, \Delta l/l = 0.02$, the orange line a simulation with an increased mutation rate, $u = 0.3$, 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:

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

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

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

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

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

which upon averaging yields

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

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, $\bar{l}$.

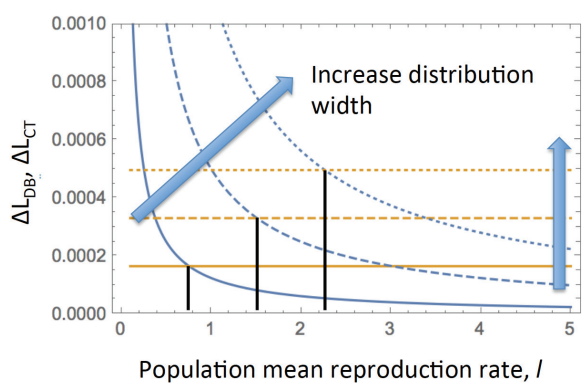

Figure 4: Finding the equilibrium reproduction rate by solving equation (17), illustrated with example (18-19). The left hand side of equation (17), ΔL_{DB}, is shown as blue lines and the right hand side, $-\beta\Delta L_{CT}$, with yellow lines, as functions of $\bar{l}$. Solid, dashed, and dotted 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.