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 major reduction in fertility at a time of increased resource availability. A key stylized fact is that 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. None of these approaches, including formal cultural evolutionary models of the demographic transitions, have addressed a possible direct causal relationship between a reduction in mortality and the subsequent decline in fertility. We provide mathematical models in which *low mortality* favors the cultural selection of low fertility traits. This occurs because reduced mortality slows turnover in the model, which allows the cultural transmission advantage of low fertility traits to out-race their reproductive disadvantage. For mortality to be a crucial determinant of outcome, a cultural transmission bias is required where slow reproducers exert higher social influence. Computer simulations of our models that allow for exogenous variation in the death rate can reproduce the central features of the demographic transition process, including substantial reductions in fertility within only 1-3 generations. A model assuming continuous evolution of reproduction rates through imitation errors predicts fertility to fall below replacement levels, if death rates are sufficiently low. This can potentially explain the very low preferred family sizes in Western Europe.

1. Introduction

In the 19th century, some human populations displayed a demographic transition from relatively high fertility and high mortality towards a greatly 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 declined below replacement levels since the 1970s and 1980s [5,6], and this also applies to preferred family sizes. In German speaking countries the average reported ideal family size has fallen below replacement levels—about 1.7 children [6]. Furthermore, 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 wealth was associated with higher fertility [1,7].

A number of theories have been put forward to account for demographic transitions towards reduced fertility [1,8]. According to one line of argument, the transition to reduced fertility may be because of a mismatch between the modern environment and the ancestral one in which humans evolved. Behaviors that were advantageous in the ancestral environment could have become dysfunctional under modern socio-economic conditions, leading to a reduced reproductive output [1]. A second theory holds that 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. A third theory is based upon cultural rather than genetic evolution [9,10]. Behavior that leads to reduced fertility in certain influential individuals is copied by others, resulting in a spread of this trait.

A well-developed mathematical theory of the dynamics of cultural transmission [9,11-17] has been applied to the analysis of demographic transitions and the evolution of small family sizes [18-20]. This research has analyzed the spread of cultural traits that affect fertility, survival, or both, and the effects of these traits on the demographic structure of the population. In [19,20], the transition to reduced fertilities has been explained by cultural niche construction. According to this theory, 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. In [18] it was shown that horizontal and oblique transmission can accelerate the spread of the cultural trait, compared to vertical transmission alone. This paper provides a broad analysis and creates a model of cultural transmission of a trait that can affect fertility and/or mortality of individuals. Applications to demographic transitions are described in two contexts: (i) Neolitic demographic transition, where a fertility-increasing trait spreads through the population, is investigated with respect to different transmission modes, and (ii) 19-20 century demographic transition in Europe is modeled by using a trait that simultaneously decreases fertility and increases survival of individuals. A trait is considered where a reduction in fertility is strongly coupled to an increase of survival of individuals.

A key stylized fact about 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 [4,21,22], presumably a consequence of improved socioeconomic circumstances. This is surprising in the light of evolutionary biology [1,23], because evolution tends to maximize reproductive output, which can generally be increased when resources are more plentiful. Mathematical models of cultural evolutionary processes have so far not directly addressed the reason for the observation that fertility reduction is preceded by mortality reduction. Previously published work linked mortality reduction to other cultural traits, such as education or fertility itself. Here, we add to the existing literature by considering mathematical models of cultural transmission where the population death rate is subject to independent external influences that vary exogenously over time, due to sanitary, medical and technological advances. We investigate how such externally-driven changes in mortality affect the contagion of a fertility-reducing trait. We find that the death rate of individuals is a key parameter for determining whether the cultural spread of a fertility-reducing trait is successful. While the fertility-reducing trait fails to spread at high population death rates, it successfully spreads once the population death rate has fallen below a threshold. For this impact of the population death rate to be observed, the model further requires a cultural transmission bias towards slow reproducers, which can come about by a higher social influence of slowly reproducing individuals. The critical effect of the population death rate on outcome occurs because reduced death rates slow the rate at which early reproducers outrun delayed reproducers in the models, allowing cultural transmission of low fertility traits to outweigh the fitness advantage of fast reproduction. Computer simulations of the demographic transition process show that the empirical stylized characteristics of this process can be captured by our models on realistic time scales. The models further predict that with reduced population death rates, cultural evolutionary processes can result in the eventual decline of fertility below replacement levels. This is relevant for recent trends in Western European and other countries [5,6].

2. Concepts and modeling approaches: a roadmap

Cultural transmission dynamics can be complex, and several different mathematical modeling assumptions can be made that can potentially impact results. While simpler models are more tractable analytically, including some more realistic assumptions requires more complicated modeling approaches. Therefore, the paper is structured as follows (Figure 1).

(A) We start with the simplest modeling approach that takes into account two distinct populations: fast versus slow reproducers. Moreover, it will be assumed that all individuals mix perfectly with each other, and that logistic growth occurs that is limited by a carrying capacity. This is expressed in terms of ordinary differential equations, and basic insights will be described about the conditions required for slow reproducers to be prevalent.

(B) The same kind of dynamics (fast versus slow reproducers) will be re-considered in biologically more complex settings. These include: (i) A spatially explicit model, because the perfect mixing assumption is unrealistic and individuals are more likely to communicate with members of their local community rather than with anyone in the global population. Including spatial restriction has been shown to have significant effects not only in ecological and evolutionary models, but also in models of cultural evolution [24,25]. (ii) An age-structured model where instead of fast and slow reproduction rates, we consider early and late reproducers, because the timing of reproduction can be an important determinant of fertility. (iii) Instead of a fixed carrying capacity, we assume that more room for increased population growth is continuously generated, thus giving rise to an ever-increasing population size, which is more realistic. Using this model, we further show that a demographic transition from higher to lower fertility can occur within realistic time frames. An important conclusion from this section is that central results remain robust irrespective of the modeling approach, thus increasing the confidence in biological / sociological relevance.

(C) The longer-term evolution of fertility will be examined. This requires a different approach where the reproduction rate is allowed to continuously evolve, rather than assuming fast versus slow reproducers. The most straightforward way to model this is in terms of an agent-based model, and we will build on the spatial model considered in Bii.

3. Results

3A. Fast versus slow reproducers in well-mixed populations

We start the exploration of the evolutionary dynamics of a culturally transmitted, fertility-reducing trait by formulating a minimally parameterized model that includes (a) a fertility reducing trait and (b) cultural transmission. We assume that two traits exist in the population. The fast reproduction trait is a default state, and a slow reproductive trait can spread culturally via horizontal or vertical transmission. We will denote the population of the individuals with the fast reproductive trait as x_f and the population of the individuals with the slow reproductive trait as x_s. The dynamics can be described by a deterministic, non-spatial, asexual model expressed by ODEs:

$$\begin{aligned}\dot{x}_f &= r_f x_f W - d x_f - \beta x_f x_s / K,\\ \dot{x}_s &= r_s x_s W - d x_s + \beta x_f x_s / K.\end{aligned} \qquad (1)$$

Here, each type reproduces with its own linear reproduction rate, with $r_f > r_s$, and the competition between the two traits is expressed by term W, which for example can take the logistic form,

$$W = 1 - \frac{x_f + x_s}{K},$$

where K denotes the carrying capacity. Both types die with equal rates, d. We assume that there is a probability of switching from one type to the other, which is proportional to the abundance of the individuals of the opposite type. The total rate at which fast reproducing individuals switch to slow reproduction is given by $\beta_f x_f \frac{x_s}{K}$, and the total rate at which slow reproducers switch to fast reproduction is given by $\beta_s x_s \frac{x_f}{K}$. If we assume that $\beta_f > \beta_s$, and denote $\beta = \beta_f - \beta_s$, we have the term $\beta x_f \frac{x_s}{K}$ with the negative sign in the equation for x_f and the same term with the positive sign in the equation for x_s. These terms are equivalent in form to infection terms, see equation (1). The main postulates used here are that (a) of the two types of individuals, one grows faster than the other ($r_f > r_s$) and (b) there are more individuals switching from fast reproduction to slow reproduction than the other way around ($\beta > 0$). The latter 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 [19].

System (1) has four steady states:

0. The trivial solution, $x_f = x_s = 0$ is unstable as long as $r_s > d$ and $r_f > d$. We will assume that both populations can persist on their own, and the above inequalities hold.

1. Fast reproducers win (that is, the fast reproduction trait spreads through the whole population): $x_f = K(1 - d/r_f), \quad x_s = 0.$ This solution is stable if

$$d > d_1 \equiv \frac{r_f}{1 + (r_f - r_s)/\beta}.$$

2. Slow reproducers win: $x_f = 0, \quad x_s = K(1 - d/r_s).$ This solution is stable if

$d < d_2 \equiv \dfrac{r_s}{1+(r_f - r_s)/\beta}$. Note that $d_2<d_1$.

3. Coexistence solution, where both traits occur in the population

$$x_f = \frac{K}{\beta}(d - d_2), \quad x_s = \frac{K}{\beta}(d_1 - d).$$

This solution is positive and stable as long as

$d_2<d<d_1$.

To summarize these results, we note that the death rate of the individuals, d, controls the outcome of the competition dynamics of the two traits. For high death rates, the fast reproduction trait spreads through the population, and for low death rates, the slow reproduction trait is able to invade and take over. Modifications of the basic model (1) are considered in Section 1.1 of the Supplement, where we study different assumptions on the dynamics of switching type; it is shown that the central results are unchanged. We note that to observe these results in the current setting, the models need to include the assumption of density dependence in the population growth process. They are not observed in models assuming straightforward exponential population growth. Section 3Biii below explores models of unbounded population growth in which the results reported here remain robust.

Before we proceed, it is instructive to interpret the model from the prospective of virus dynamics, by viewing $x^{(1)}$ and $x^{(2)}$ and susceptible and infected individuals respectively. The three nontrivial equilibria are characterized by (1) susceptibles only, (2) infecteds only, and (3) coexistence of both. In order for infection to be able to spread, the basic reproductive ratio, R_0, has to be larger than 1. In the context of this system, we have $R_0 = \frac{\beta(1-d/r_f)}{d(1-r_s/r_f)}$.

Decreasing d clearly increases R_0 .

3B. Introducing more realism into the model

Because the model explored in the last section contains a number of simplifying assumptions that are known to be inconsistent with reality, it is important to determine whether the results hold robust in more realistic settings. It turns out that central results do remain robust in spatial models, models with age structure, and in models assuming that populations periodically increase their carrying capacity. This is described as follows.

(i) Spatial Dynamics:

We consider a stochastic agent-based model (ABM) that describes population dynamics on a 2D grid of size *n* x *n*. We will refer to this model as ABM1; compared to the simple ODE model, the present description includes spatial and stochastic effects. As before, the fast reproduction trait is assumed a default state of the agents, and a slow reproductive trait spreads culturally via horizontal or vertical transmission. 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 attempts to undergo either a birth-death update (including vertical cultural transmission), or a horizontal cultural transmission update. The two types of update are chosen with equal probabilities, such that on average there are M attempts of both types of update during each time step.

If the birth-death update is chosen, the individual can undergo at most one event, as follows. It attempts reproduction with a probability R_f or R_s, depending on whether this is a fast or slow reproducer (here $R_f > R_s$), or dies with a probability D (both populations are assumed to have the same death rate). For a reproductive event, 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. We assume that the reproductive strategy of the offspring is the same as that of the parent (that is, the slow reproductive trait is passed on via vertical cultural transmission). These birth-death processes on the grid are characterized by density dependence, and hence the model accounts for competition between slow and fast reproducers. The description above corresponds to infant mortality rising with increased density (crowdedness), because offspring disappear if they do not fall on an empty spot in the grid. Section Biii below explores how such processes can apply to growing human populations.

A cultural update is attempted with probability P_C, by gathering the information on the reproductive strategy of the individuals' neighbors, similar to voter models [15,26]. The probability that an agent switches its reproductive strategy is proportional to the weighed fraction of the opposing strategy among neighbors, such that slow reproducers are more influential than fast reproducers. 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, reflecting the preference of switching towards slower reproduction.

When the model is run with only the reproduction and death processes (no non-vertical cultural transmission), then the only outcome is the persistence of the fast-reproducing trait and the competitive exclusion of the slower reproducing one. This is straightforward competition dynamics behavior. If, in contrast, the model is run with only horizontal cultural transmission (no reproduction and death, so that the population is constant), 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 [15,26], the only eventual outcome is that every individual in the population has the same opinion. Which of the two opinions wins depends on the bias, Q, and on initial frequencies of the opinions in the population.

When we allow for both horizontal transmission and reproduction with vertical transmission, three outcomes are possible (Figure 2): (1) The fast reproduction trait wins and excludes the slow reproduction trait. (2) The slow reproduction trait wins and excludes the fast reproduction trait; and (3) both traits coexist in a long term equilibrium. While this is a true equilibrium in corresponding ODEs (see above), the stochastic nature of the model means that the eventual outcome is always extinction. The coexistence outcome, however, is characterized by a significantly longer time to extinction compared to the exclusion outcomes (compare Figure 2C to 2A &B).

Which outcome is observed depends on the death rate of agents, D, see Figure 3Ai. Each point on this graph depicts the time until one of the traits 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 horizontal cultural spread of the slow reproduction trait is successful, resulting in an overall reduced level of fertility.

An intuitive explanation is as follows. The death rate determines the rate at which the fast reproducers can outrun the slow reproducers. For large death rates, population density is low and the reproductive potential of individuals is highest. Therefore, fast reproducers can outcompete the slow ones at relatively fast rates, making it difficult for horizontal cultural transmission to reverse this trend. For lower death rates, densities increase, and this slows the rate at which fast reproducers can outrun slow ones. Hence, it becomes easier for horizontal cultural transmission to reverse this process.

Parameters other than the death rate further modulate the outcome of the dynamics, see Figures 3Aii and iii. 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 3Aii). The relative probability for a cultural transmission event to take place, P_C, is also an important determinant of outcome. As expected, higher values of P_C promote the cultural spread of the fertility-reducing trait. For lower values of P_C, lower population death rates are needed for cultural transmission to be successful (Figure 3Aiii).

(ii) Age structured models: early vs late reproducers

Rather than considering fast versus slow reproducers, we now modify the agent-based model to consider agents who can reproduce either early or late in their lifetimes. 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 consider four age classes. Individuals are born into age-class 1, in 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 (the “grandmother effect” has been explored in Section 2.5 of the Supplement; it only influences the main findings in a quantitative way). 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 ABM1, see Figure 3B. Some analytical insights for non-spatial, deterministic age-structured models are provided in Supplementary Materials, Section 2.

(iii) Continuously increasing population growth, and the simulation of the transition process

Our central result, that a reduction in death rate tends to select for the cultural spread of a fertility-reducing trait, relies on density-dependence in the population dynamics. It is not observed in models assuming unlimited exponential growth, where the rate of cultural transmission alone determines which population outgrows the other. With exponential growth, a reduction in death rate does not slow down the rate at which faster reproducers, by having more offspring, gain advantage over slow reproducers, as was the case with density dependence.

While human population sizes have followed long-term increasing trends, evidence for density-dependent effects and the relevance of local carrying capacities have been found in demographic data from pre-industrial European populations within individual settlements [27]. Continued population growth would then be brought about by an increase in the number of settlements or by regular increases in the carrying capacity, due to advances in society [27,28].

To capture the patterns reported in reference [27], we consider a growing population that is subdivided into neighborhoods or demes (settlements). In each deme, we impose a carrying capacity and describe the local dynamics by ODE model (1). 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, individuals in each deme have a chance to found a new, empty deme into which a fraction of the current local population moves. The probability of this occurring is proportional to how full the current deme is. This corresponds to an effective increase in population size due to new advances. 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 fraction *f* 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. While in this model, the local dynamics are described by ODEs, it is still a spatial model due to the assumed patch organization, and this approach is consistent with the documented notion of local carrying capacities [27].

In this model, we observe persistence of one trait and exclusion of the other, while the population continues to grow (Figure 4A, B). As before, the fast-reproducing trait persists for high overall death rates (Figure 4A), while the slow-reproducing trait persists for low overall death rates (Figure 4B).

We further used this model to simulate the demographic transition process (Figure 4C). The simulation was run as before, except that at a defined time point in the simulation, the death rate was continuously and gradually reduced over several time steps towards a lower, new level (Figure 4C, lower panel). 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.

In the upper panel, the fast-reproducing population is shown in purple, the slow-reproducing population in 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 (Figure 4C, lower panel) and is driven by the fast-reproducing population. The overall growth rate of the population is relatively slow at this stage because of the high death rate.

When the death rate is reduced, the fertility-reducing cultural trait can spread successfully and eventually becomes dominant. As the death rate declines, a phase of faster population growth occurs, as observed in data on demographic transitions [22]. Following a time delay after the reduction in the death rate, the average reproduction rate also declines, which is again consistent with data on demographic transitions [22] (Figure 4C, lower panel, black line).

The exact timing of events depends on model parameters. For the purpose of this simulation, we chose parameters such that it takes about 3 generations to reduce the average 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 horizontal cultural transmission (higher value of β) can lead to more rapid changes in fertility following the decline in the death rate.

To show that these dynamics are not dependent on this particular model formulation, we performed similar simulations with an age-structured model where continued population growth was allowed through regular increases in the carrying capacity parameter (rather than increasing the number of demes). Similar results were observed and are presented in the Supplementary Materials (Section 2.4).

3C. Long term cultural evolution: reproduction strategies as a continuous trait

So far, we considered two distinct populations of slow and fast (early and late) reproducers. To study longer-term evolution, rather than considering two discrete reproductive strategies, it is more realistic to assume the probability of reproduction to be a continuous variable. Because this is most easily implemented in terms of an agent-based model, we will build on the spatial agent-based model of section 3Bii. We again assume that an individual is chosen for a horizontal cultural transmission event with a probability scaled with P_C. In this model, however, instead of adopting (or rejecting) the reproductive probability of the alternative 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 horizontal cultural transmission than faster reproducers. Due to the continuous nature of the reproduction trait in the current model, this is now 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. This eventual uniformity derives from the assumption that an individual adopts the average reproduction probability of the neighborhood during a cultural transmission event.

Next, we introduce mutations of cultural traits that can occur during horizontal 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. Three types of outcomes were observed (Figure 5).

(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 5. (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 5.

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 5. This level is independent of the starting value of R (not shown).

As before, the population death probability, D, is a crucial factor (Figure 5). Evolution to maximal reproduction probabilities, R, is seen for relatively large death rates. Evolution towards low values of R and hence population extinction is observed for relatively low death rates. This could be the cultural equivalent to “evolutionary suicide” or “Darwinian extinction” [29]. Evolution towards an intermediate reproduction probability is observed for intermediate death probabilities, D. A higher probability of cultural transmission, P_C, and a lower weight of faster reproducers during the averaging process, Q, further promote evolution towards declining reproduction rates and population extinction (not shown). Section 3 of the Supplement further explains the existence of an equilibrium state and explores how the mean population reproduction rate depends on parameters.

This model demonstrates that manipulating the death rate changes the long-term cultural evolution of reproductive strategies, and that three different outcomes are possible: the two extremes (maximum reproduction and decline of reproduction rate below replacement level), as well as an evolutionary stable intermediate average reproduction probability. The latter has perhaps been most relevant for human societies, although the trajectories might be moving towards the decline below replacement levels, which is discussed further below. We note that these results were derived from a spatially explicit model. An equivalent non-spatial model is explored in the Supplementary Materials, section 3.1. In the non-spatial model, an evolutionary stable intermediate average reproduction probability is not observed, demonstrating that this outcome depends on the existence of spatially explicit interactions. Finally, the Supplementary Materials (Section 4) further demonstrate that conclusions described here remain robust in a model that assumes sexual reproduction.

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. In contrast to previous modeling approaches, we have allowed for the possibility of exogenous external influences on the population mortality rate. This exogenous parameter can be modulated as a consequence, for example, of technological development in the society. A central result was that lower population death rates select for the cultural spread of the low-fertility trait. This happens because lowering the mortality increases density, which in turn reduces the rate at which the fast reproduction trait gains in abundance relative to the slow reproduction trait. This allows horizontal transmission to tip the balance in favor of slow reproduction. The advantage of the fast reproduction trait is greater when generational turnover is rapid owing to a high death rate. When the death rate declines, there is more opportunity per generation for cultural transmission to operate in favor of the low reproduction trait. We note that the dependence of outcome on population mortality requires the assumption of a cultural transmission bias: individuals with lower reproduction rates need to carry more social weight, an assumption that has also been made in previous modeling work [19]. 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 well understood [32,33] and require further investigation.

Competition among individuals in the form of density-dependent dynamics 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 or an age-structured model with increasing carrying capacity can give rise to the same outcomes in populations that continuously grow. Hence, the results described throughout the paper hold for growing populations. We demonstrated that, depending on parameters, the model can reproduce crucial features of the “demographic transition model” [22].

Our study complements previous mathematical work that analyzed the cultural spread of small family sizes in relation to demographic transitions [18-20]. Our models consider a simpler setting involving the basic spread dynamics of the fertility-reducing trait, somewhat similar to infection models. We show that lower death rates promote the cultural spread of the low fertility trait. This result offers a simple possible explanation for the key observation that a reduction in fertility tends to be preceded by a reduction in mortality.

In addition, our model can help interpret demographic data demonstrating that fertility is density dependent [34]. Lowering the death rate in the model leads to an expansion in the slow reproduction trait, even in the context of increased resource availability and continuously growing populations. Data indicate that human fertility as well as family size preference are characterized by density dependence, even during the time frames when demographic transitions occurred. Our model results might offer an explanation for this observation [34].

Also consistent with stylized facts, our models implied that for low population death rates, the average reproduction rate of the population can decline to levels that do not sustain a stable population. In Western European countries, fertility has declined below replacement levels since the 1970s and 1980s [5,6]. Similar tendencies are observed in Japan, South Korea, Taiwan, Singapore, and Hong Kong [35]. In addition, recent surveys [6] have revealed that the mean ideal family size (MIFS) 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. In Taiwan, among women aged 18–24, the MIFS declined from 2.1 in 1993 to 1.8 in 2003, and in Hong Kong, among women aged 18–27, MIFS fell from 1.8 in 1991 to 1.5 in 2011 [36,37].

The models studied here contain a number of assumptions that we consider to be central to exploring the effect of the population death rate on the spread of a culturally transmitted, fertility-reducing trait. Further assumptions and processes could be built into the model, and a detailed exploration of this would be an interesting subject of future research. One such aspect is the grandmother effect [38,39], where individuals in later age classes (grandmothers) promote the survival of individuals in younger age classes. We present a basic exploration of this effect in the Supplement (Section 2.5) and found that this only modulates the parameter thresholds where behavioral changes of the models are observed, but does not qualitatively change outcomes. Another interesting aspect to include might be costs associated with early or late reproduction, which likely also does not lead to a qualitative change of our results. Several additional aspects could be quantified in such more complex models, but this would go beyond the focus of the current manuscript.

While some details of the model processes could be formulated in different ways (see Supplement Section 5), we have considered a range of models with different assumptions. In all models, the death rate of the population was identified as a crucial factor that determined whether the fertility-reducing trait could invade. This 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. It would be interesting for future work to integrate these cultural evolution dynamics with other potential mechanisms that might contribute to the demographic transition process, such as the offspring quality/quantity tradeoff or other economic considerations that might result in human populations having an optimal, target number of offspring.

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Figure legends:

Figure 1: Schematic representation of the structure of the papers and the types of models considered. See text for details.

Figure 2. Time series showing the different outcomes according to ABM1. Individual realizations are shown. (A) Higher death rates: the fast-reproducing trait persists and the slow-reproducing trait goes extinct on a short time scale. (B) Lower death rates: the slow-reproducing trait persists and the fast-reproducing trait goes extinct on a short time scale. (C) Intermediate death rates: both fast- and slow-reproducing traits persist for significantly longer time periods. Eventually one trait goes extinct due to the stochastic nature of the simulation. Parameters were chosen as follows. R_f=0.005; R_s=0.8R_f; P_C=0.0008; Q=0.93. For (A), D=0.001. For (B), D=0.0001. For (C), D=0.00025.

Figure 3. 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-reproducing trait went extinct, and with a purple dot if the slow-reproducing trait went extinct, as a function of the population death rate, D. For low

death rates, there are only green dots, corresponding to the slow-reproducing trait persisting and the fast-reproducing trait going extinct relatively fast. For fast death rates, there are only purple dots, corresponding to the opposite outcome. For intermediate death rates, the time until one of the traits goes extinct becomes sharply longer, and either trait 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; P_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-reproducing trait to invade, hence requiring lower population death rates. (iii) A lower rate of cultural transmission, P_C=0.0004, makes it harder for the slow-reproducing 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; P_C=0.0008; Q=0.93; A=10,000.

Figure 4. 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=0.064, d=0.05, β=0.01, K=100, α=0.001, ε=0.001. (B) The fast-reproducing trait is going extinct, and the slow-reproducing trait takes over and continues to grow. The same parameter values were used, except d=0.005. (C) Simulation of the demographic

transition process. Again, fast- and slow-reproducing traits 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 trait has an 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=100, α=0.005 ε=0.01.

Figure 5. 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. P_C=0.0003; Q=0.965. The chance to make a mistake during horizontal cultural transmission ("mutation") u=0.1. In case of a mistake, the average reproduction rate was changed by G=2%.

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Roadmap: Models and Scenarios Investigated

A. Basic Principles

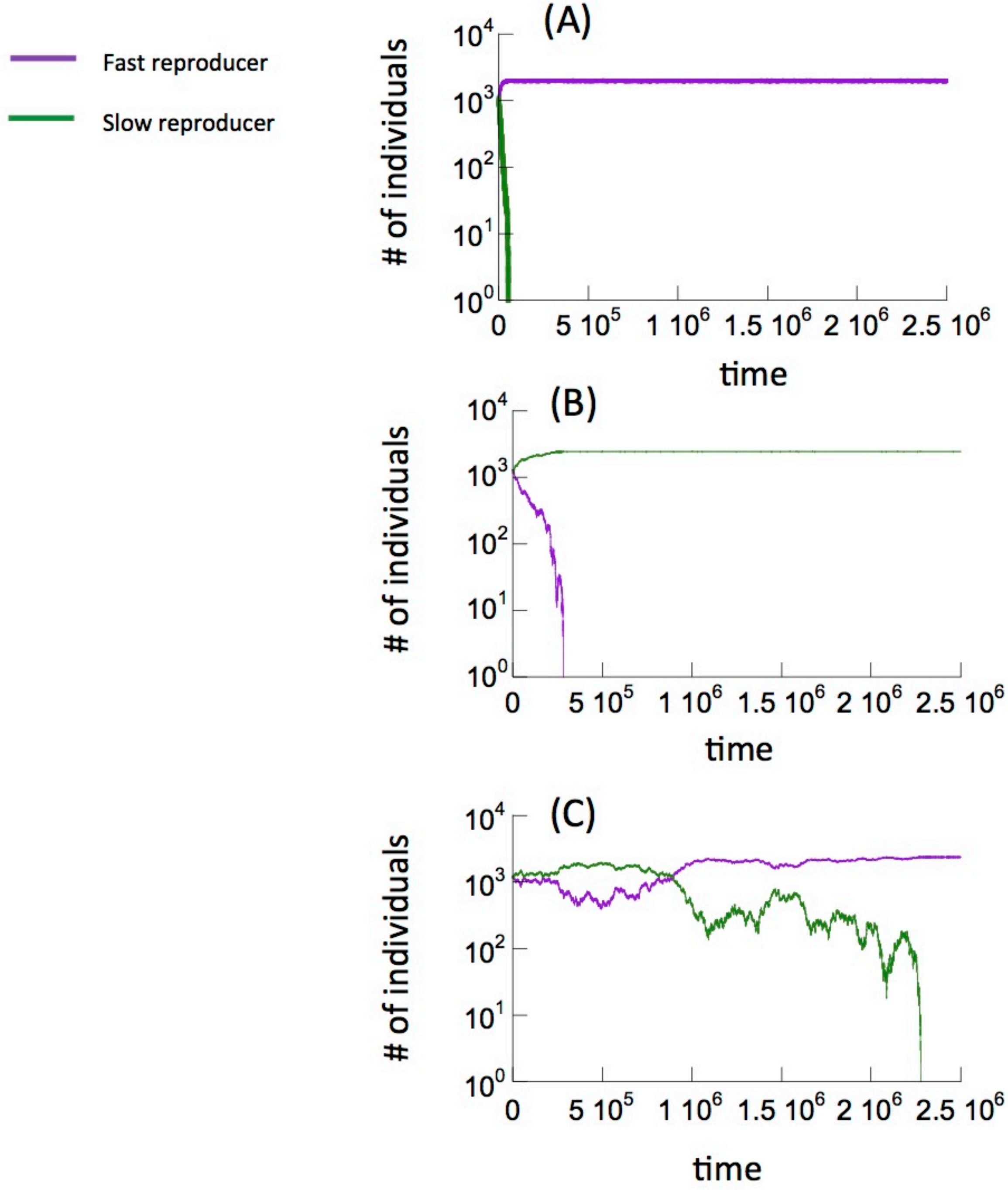
Non-spatial (ODEs), fast vs slow reproducers: Basic insights

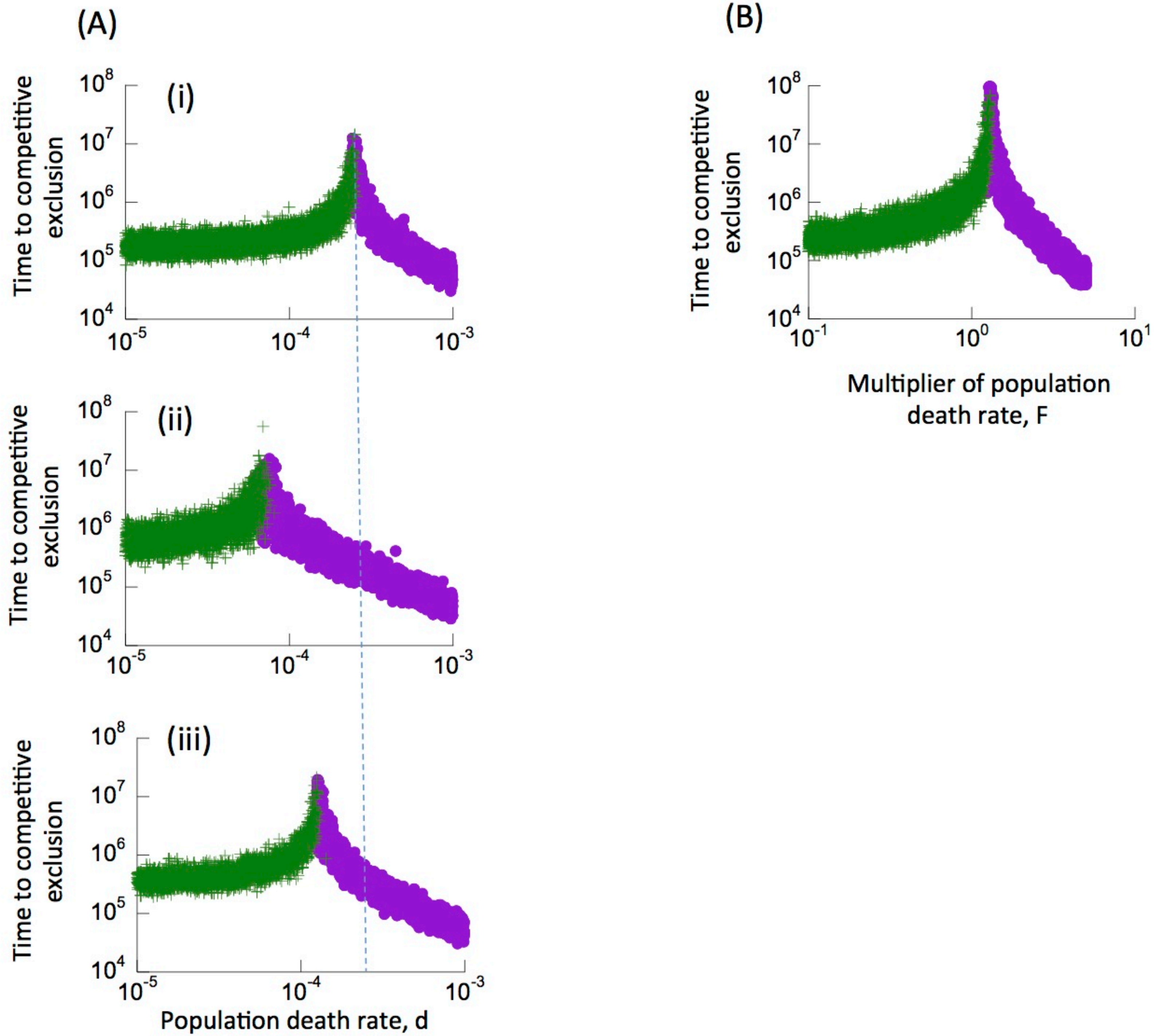
B. More realistic extensions

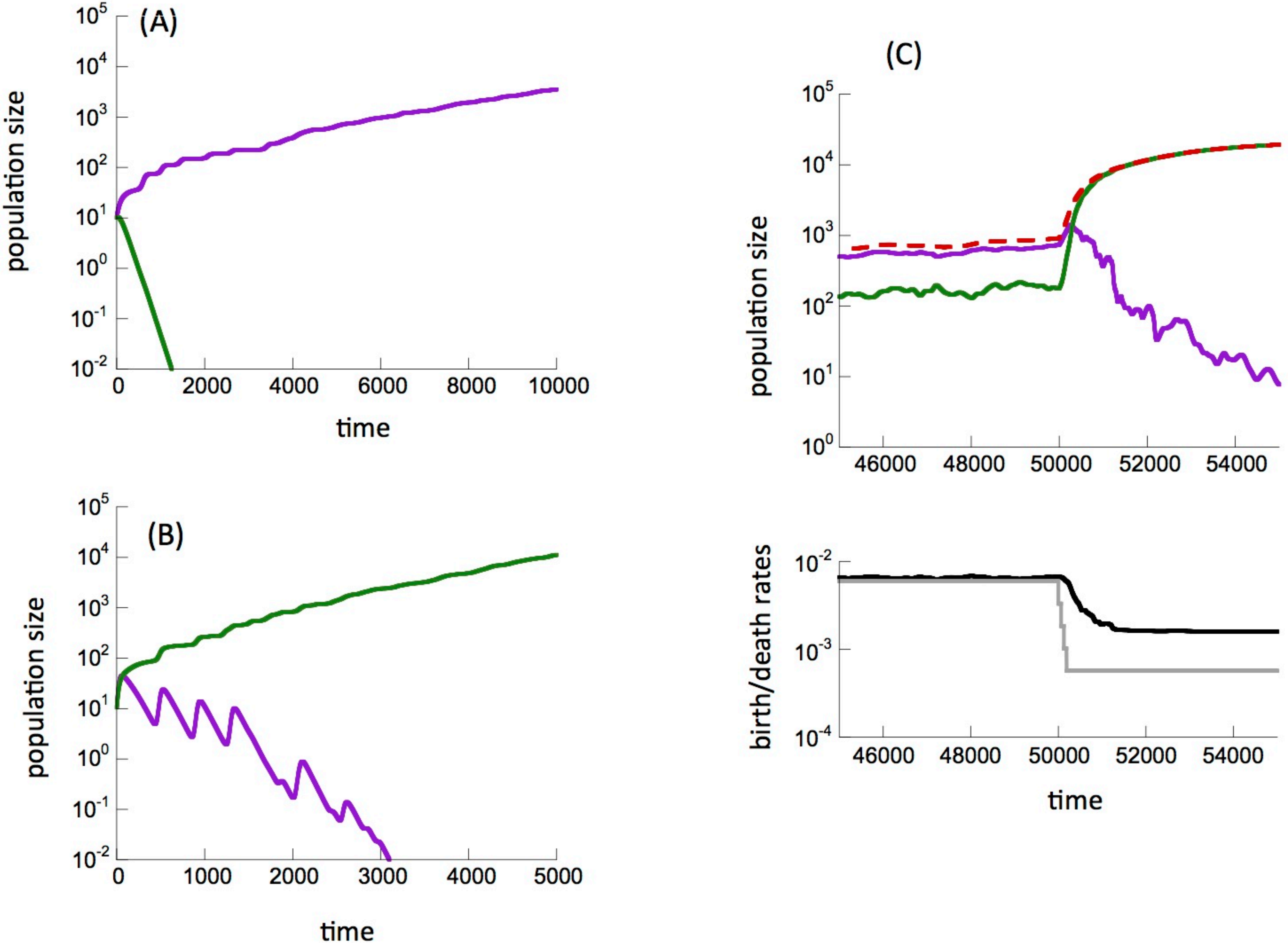
i. Spatial model: fast vs slow reproducers
ii. Age structured model: early vs. late reproducers
iii. Simulating demographic transitions

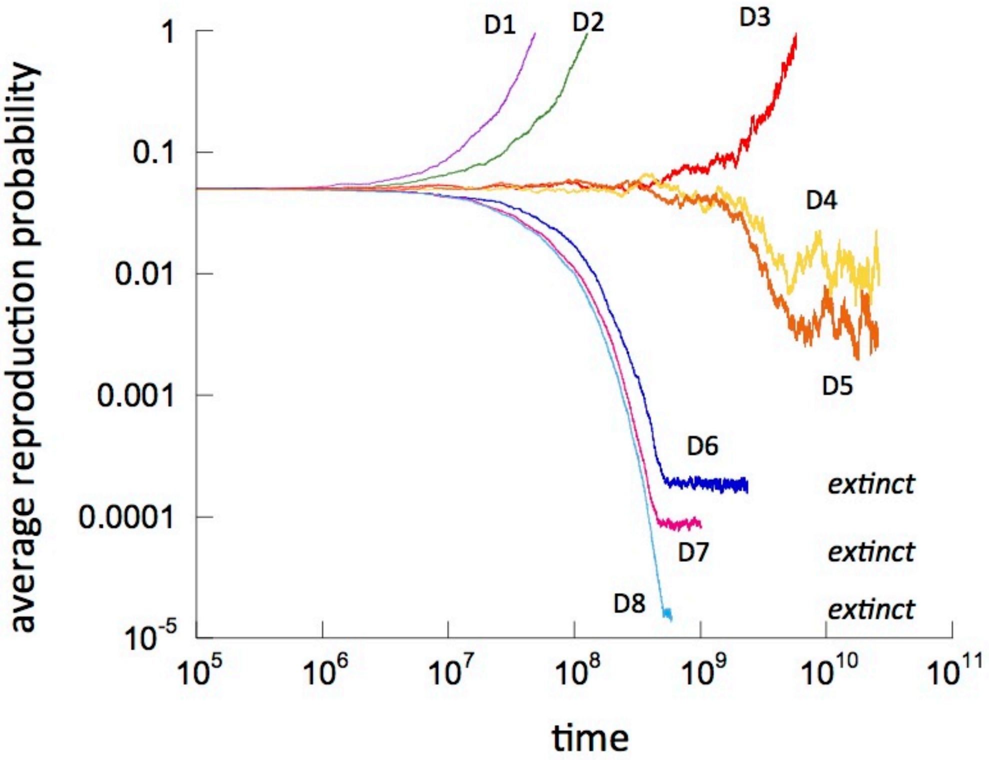
C. Longer term evolution

Continuous evolution of reproduction rate (spatial)


Fast reproducer
Slow reproducer
(A)
(B)
(C)
# of individuals
10^0
10^1
10^2
10^3
10^4
0
$5\ 10^5$
$1\ 10^6$
$1.5\ 10^6$
$2\ 10^6$
$2.5\ 10^6$
time


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


(A)
population size
time
10^5
10^4
10^3
10^2
10^1
10^0
10^{-1}
10^{-2}
0
2000
4000
6000
8000
10000
(B)
population size
time
0
1000
2000
3000
4000
5000
(C)
population size
10^0
46000
48000
50000
52000
54000
birth/death rates
10^{-2}
10^{-3}
10^{-4}
time


D1
D2
D3
D4
D5
D6
D7
D8
extinct
extinct
extinct
average reproduction probability
1
0.1
0.01
0.001
0.0001
10^{-5}
10^{5}
10^{6}
10^{7}
10^{8}
10^{9}
10^{10}
10^{11}
time

Evolutionary dynamics of culturally transmitted, fertility-reducing traits

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Supplementary information

Contents

1 In the absence of age structured dynamics

1.1 Alternative ODE models

In the model considered in Section 2.1 of the main text, the conversion process is described by the term

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

Alternatively, this term can be formulated as

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

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 is 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

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

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:

$$\begin{aligned} x_1^{(s)}(t+1) &= \sum_{j=1}^{N} a_j^{(s)} x_j^{(s)}(t) W, & (3) \\ x_i^{(s)}(t+1) &= w_{i-1}^{(s)} x_{i-1}^{(s)}(t) \left(1 - \beta_i^{(s)} \frac{\sum_{k=i}^{N} x_k^{(3-s)}(t)}{\sum_{k=i}^{N}(x_k^{(3-s)}(t) + x_k^{(s)}(t))}\right) \\ + \quad & w_{i-1}^{(3-s)} x_{i-1}^{(3-s)}(t) \beta_i^{(3-s)} \frac{\sum_{k=i}^{N} x_k^{(s)}(t)}{\sum_{k=i}^{N}(x_k^{(3-s)}(t) + x_k^{(s)}(t))}, \quad 1 < i \leq N, & (4) \end{aligned}$$

where the competition term W can be defined as

$$\begin{aligned} W &= 1 - \frac{\sum_{s=1}^{2} \sum_{k=1}^{N} x_k^{(s)}}{K} \quad \text{or} & (5) \\ W &= \left(1 + \frac{\sum_{s=1}^{2} \sum_{k=1}^{N} x_k^{(s)}}{K}\right)^{-1}. & (6) \end{aligned}$$

Equation (3) describes reproduction. Different age groups reproduce with their own rate $a_j^{(s)}$, and the offspring enters age group 1. Equation (4) describes the population moving from age group to age group. Coefficients $w_{i-1}^{(s)}$ describe the probability for an individual of type s to survive until age i. 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 i is given by

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

and is proportional to the fraction of individuals of age i and older that belong to class $3-s$. With this in mind, we can see that the first term on the right of equation (4) 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 (3-4) assumes no switching at the first stage. To include switching at the first stage, we replace equation (3) with

$$\begin{aligned} x_1^{(s)}(t+1) &= \sum_{j=1}^{N} a_j^{(s)} x_j^{(s)}(t) W \left(1-\beta_1^{(s)} \frac{\sum_{k=1}^{N} x_k^{(3-s)}(t)}{\sum_{k=1}^{N}(x_k^{(3-s)}(t)+x_k^{(s)}(t))}\right) \\ &+ \sum_{j=1}^{N} a_j^{(3-s)} x_j^{(3-s)}(t) W \beta_1^{(3-s)} \frac{\sum_{k=1}^{N} x_k^{(s)}(t)}{\sum_{k=1}^{N}(x_k^{(3-s)}(t)+x_k^{(s)}(t))}. \qquad (7) \end{aligned}$$

2.2 System behavior

System (7, 4) has two exclusion steady states (for $s=1$ and $s=2$), which for competition model (6) are given by

$$x_i^{(s)} = K \prod_{k=1}^{i-1} w_k^{(s)} \frac{r \sum_{m=1}^{N} a_m^{(s)} \prod_{k=1}^{m-1} w_k^{(s)} - 1}{\sum_{m=1}^{N} \prod_{k=1}^{m-1} w_k^{(s)}}, \quad 1 \le i \le N, \qquad (8)$$

$$x_i^{(3-s)} = 0, \quad 1 \le i \le N. \qquad (9)$$

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).

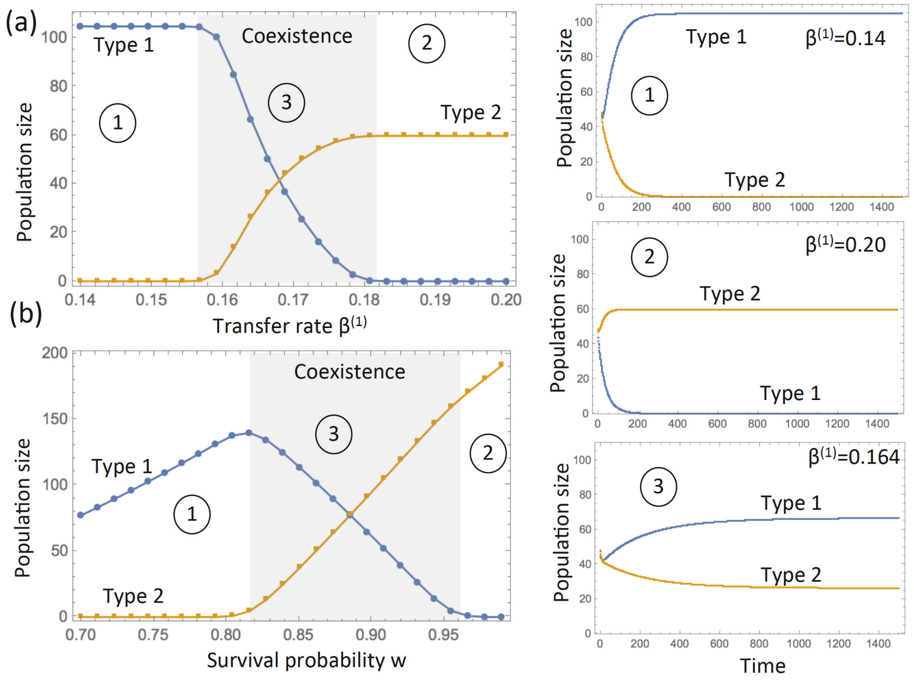

Figure 1: Age structured dynamics according to system (7, 4), numerical simulations. Total populations of individuals of type 1 and type 2 are presented. The steady state values are given on the left as functions of parameter (a) $\beta^{(1)}$ and (b) $w_i^{(s)} = w$ for all $s \in \{1,2\}, 1 \le i \le N$, 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. Sample 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 (7,4) with $N = 2$. Let us assume that $w_i^{(s)} = w$ 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, $a_i^{(s)} = a$. Further, we will assume that the coefficient of transfer is independent of the age, and is only defined by the type: $\beta_i^{(s)} = \beta^{(s)}$ for $i = 1, 2,\ s = 1, 2$. 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

$$\lambda_{1,2} = \frac{1 \pm \sqrt{1 + 4rw(1+w)^2}}{2r(1+w)^2}, \tag{10}$$

$$\lambda_{3,4} = \frac{\beta^{(1)}(2+w) \pm \sqrt{w[w(2+\beta^{(1)} - 2\beta^{(2)})^2 + 4(1+\beta^{(1)} - \beta^{(2)})(1-\beta^{(2)})]}}{2(1+w)}. \tag{11}$$

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, success of each of the types depends on 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, resulting in 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 increases success of 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.

2.4 Simulating demographic transition

In this section we present an example of an age structured model where a behavior resembling demographic transition can be observed. We use the following formulation:

$$x_1^{(s)}(t+1) = \sum_{j=1}^{N} a_j x_j^{(s)}(t), \tag{12}$$

$$\begin{aligned} x_i^{(s)}(t+1) &= W_i \left(w x_{i-1}^{(s)}(t) \left(1 - \beta^{(s)} \frac{\sum_{k=i}^{N} x_k^{(3-s)}(t)}{\sum_{k=i}^{N} (x_k^{(3-s)}(t) + x_k^{(s)}(t))} \right) \right. \\ &+ \left. w x_{i-1}^{(3-s)}(t) \beta^{(3-s)} \frac{\sum_{k=i}^{N} x_k^{(s)}(t)}{\sum_{k=i}^{N} (x_k^{(3-s)}(t) + x_k^{(s)}(t))} \right), \quad 1 < j \leq N, \end{aligned} \tag{13}$$

where we defined

$$W_i = \begin{cases} \left(1+\frac{\sum_{s=1}^{2}\sum_{k=1}^{N} x_k^{(s)}}{K}\right)^{-1}, & i=1,\\ 1, & i>1. \end{cases} \tag{14}$$

In this description, the competition term, W_i, is interpreted as infant (or early childhood) mortality, and therefore appears as a multiplier in front of the right hand side of the equation for age group 1, modifying the probability of survival until this stage.

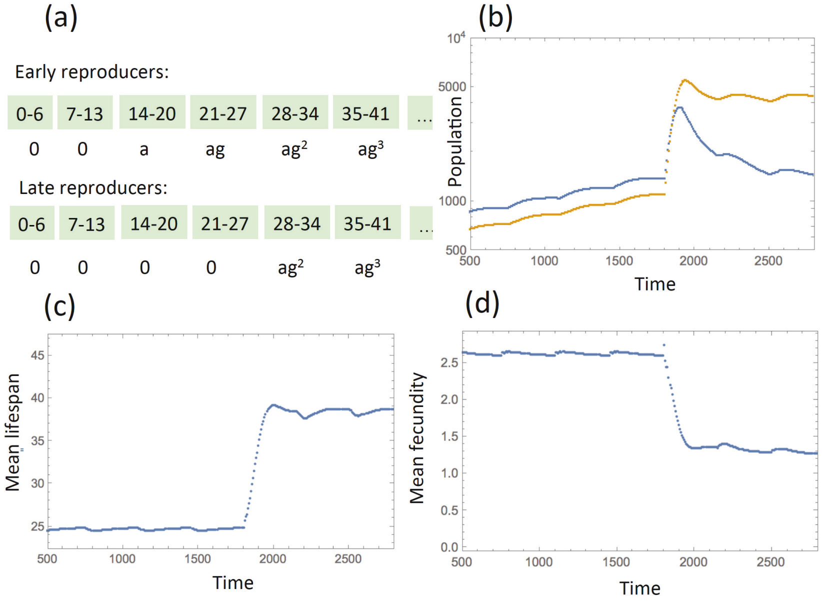

Figure 2: Simulations of an age-structured, deterministic model. (a) Age stages with early and later reproducers' age-specific fecundity are specified. (b) Simulation results for the total population sizes of early (blue) and late (yellow) reproducers, as functions of time, in a simulation with step-wise increasing carrying capacity ($K_T = 1.15\,K_{T-1}$, where T counts periods of 50 age-stages, which is 350 years). The survival probability w is increased exogenously, in a step-like manner at time 1800 from $w = 0.8$ to $w = 0.95$, marking the beginning of a change similar to demographic transition. (c) The mean lifespan of the population corresponding to the same simulation is shown as a function of time. (d) The mean number of offspring per individual is shown as a function of time. The rest of the parameters are: $N = 13$ age stages, $a = 2$, $g = 0.5$, $\beta^{(1)} = 0.4$, $\beta^{(2)} = 0.37$.

The probability to survive to the next stage is assumed stage- and type-independent, $w_i^{(s)} = w$ for $s = 1, 2$ and all i. Further, the rate of conversion is stage-independent ($\beta_i^{(s)} = \beta^{(s)}$ for all i) and parameter $a_i^{(s)}$ related to fertility is type-independent ($a_i^{(s)} = a_i$ for $s = 1, 2$).

Figure 2 presents numerical simulations of model (12-13). For these simulations, we considered 13 age-stages, which represent age groups $0-6, 7-13, 14-20$, etc. There are two types of individuals: early reproducers reproduce in stages 3-8, and later reproducers only reproduce in stages 5-8. Each stage is characterized by the mean age-specific fecundity, which decays exponentially with age and is given by parameter a at stage 3, and by ag^{k-3} at stage $3 < k \leq 8$, where $0 < g < 1$, see panel (a) of figure 2.

In the simulation, we assumed that the carrying capacity, K, that defines the maximum population size increases in a step-wise manner. This process is an idealization meant to simulate human expansion. In a space-free model it can correspond both to an increase in density and an outward expansion. In a spatial, agent-based model, a similar effect could be achieved by refining the grid, making it more and more dense. The reason to simulate expansion by increasing K instead of using a model with exponential (uninhibited, non-density dependent) growth is the notion of competition for resources and crowdedness, which are assumed to be important factors in human population dynamics. The population continues to grow through expansion, innovation, and making more resources available, but at the same time the effects of increasing density and frequent resource shortages are felt through density-dependent factors in the equations. In the current model, the density-dependent factors are presented as term W_1 entering as infant and childhood mortality factor.

In order to simulate an improvement in mortality, we assumed that the survival probability, w, increases in a step-like manner at year 1800 in the simulated system. Figure 2(b,c,d) shows numerical simulations of system (12-13). Panel (b) plots the total population sizes of early (blue) and late (yellow) reproducers as functions of time. Before the transition, the population contains a majority of early reproducers; the mean lifespan is about 25 years (panel (c)) and the mean total fecundity is above 2.5 children per individual (which in a sexually reproducing population would translate into over 5 children per woman). After the transition, the population experiences an increased growth followed by a slow-down (panel (b)). The population now consists predominantly of slow reproducers, the mean life-span increases to over 40 years, and the mean number of children drops to about 1 (equivalent to 2 children per woman). The transition happens on a relatively short time-scale equivalent to under 5 generations.

While the time-scale of the transition, mean longevity and fecundity, as well as growth rate of the population are defined by model parameters, the above simulations demonstrate that an effect similar to demographic transition can be observed in the model, and that parameters can be found such that some of the observables are not far from their realistic ranges.

2.5 Including the "grandmother hypothesis"

To include the so called "grandmother effect", we note that help of a grandparent can increase the chances of a child's survival. To incorporate this we will use system (3-4) as a basic model. For simplicity, we will keep the description asexual. As an individual ages, it passes through stages, and the probability to survive from age $i-1$ to age i is given by w_{i-1} (here we for simplicity assume no explicit dependence of mortality on type s). Note that in many contexts,

$$w_1 < w_2.$$

Here we assume that the presence of the grandmother may increase the probability of survival during the earliest stage. Let us denote the probability to have a grandmother by P_{grand}. Then we can set the probability of survival to age group 2 to be

$$w_1 + S_{grand} P_{grand}(w_2 - w_1), \tag{15}$$

where S_{grand} is a tunable parameter that sets the strength of the "grandmother effect". If this effect is nonexistent ($S_{grand}P_{grand} = 0$), then mortality of age group 1 is simply w_1. If $P_{grand}S_{grand} = 1$, then the probability to survive the first age class is as high as that for the next age class (w_2).

To calculate the probability to having a grandmother, we note that for a given newborn, this depends on the age of its parent. Having a younger parent increases the probability that the grandparent is alive. To incorporate this effect, we must use a more detailed description compared to system (3-4), and as the basic variable use

$$y_{ij}^{(s)}(t),$$

which is the number of individuals of type s of age i born to a parent of age j, at time t. These are related to the old variables $x_i^{(s)}(t)$ as

$$x_i^{(s)} = \sum_{j=i_{start}}^{i_{end}} y_{ij}^{(s)}(t),$$

where we denoted

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

The changes in each type are described by the following equations:

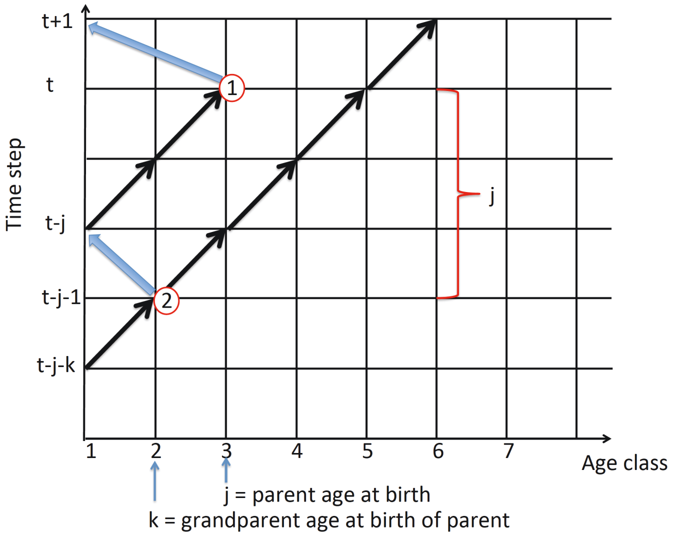

Figure 3: A schematic illustrating the grandmother effect. The two axes are the age class and time. The label "1" represents the birth of an individual, such that at time $t+1$ the newborn enters age-class 1. The age of the parent is $j = 3$ for this example. The black arrows pointing to "1" trace the growing up of the parent. The label "2" marks the birth of the parent to the grandparent of age $k = 2$. The black arrows pointing to the right and upward from "2" represent the aging of the grandparent.

$$\begin{aligned} y_{1j}^{(s)}(t+1) &= a_j^{(s)} x_j^{(s)}(t) W, && (16) \\ y_{ij}^{(s)}(t+1) &= w_{i-1,j}\, y_{i-1,j}^{(s)}(t) \left(1 - \beta^{(s)} \frac{\sum_{k=i}^{N} x_k^{(3-s)}(t)}{\sum_{k=j}^{N} (x_k^{(3-s)}(t) + x_k^{(s)}(t))}\right) \\ &+ w_{i-1,j}\, y_{i-1,j}^{(3-s)}(t)\, \beta_j^{(3-s)} \frac{\sum_{k=i}^{N} x_k^{(s)}(t)}{\sum_{k=i}^{N} (x_k^{(3-s)}(t) + x_k^{(s)}(t))}, && (17) \\ & 1 < i \le N, \quad i_{start} \le j \le i_{end}, \quad s = 1, 2. \end{aligned}$$

Let us set all the values $w_{ij} = w_2$ for all $i \geq 2$, and assume that the information about the grandmother effect is included in the mortality rate of the youngest age class, w_{1j}. We have (as in formula (15)),

$$w_{1j} = w_1 + S_{grand} P^j_{grand}(w_2 - w_1),$$

and the probability of having a grandmother depends on the age of the individual's parent, j. To calculate this we use the diagram of figure 3. If the parent's age at time t is j and the parent was born to the grandparent of age k (at time $t - j - 1$), then at time $t + 1$, the age of the grandparent is given by $k + j + 1$. The probability that the grandparent survives to time $t + 1$ is given by the product of probabilities to survive from age k to age $k + j + 1$,

$$\prod_{m=k}^{k+j} w_m,$$

where we assume that $w_m = 0$ for $m \geq N$. The probability of having a grandparent is then given by

$$P^{j,s}_{grand} = \frac{\sum_{k=1}^{N} a_k^{(s)} x_k(t - j - 1) \prod_{m=k}^{k+j} w_m}{\sum_{k=1}^{N} a_k^{(s)} x_k(t - j - 1)},$$

which is the probability that at the moment of the parent's birth the grandparent was young enough to survive to the birth of grandchild (time $t + 1$). Note that this expression makes system (16-17) non-local, that is, the equations now depends on the variable's value in the past (time $t - j - 1$).

In this version of the model, any grandparent that survives can contribute to the increased survivability of the newborn ("strong grandmother effect"). In a different version, we can assume that only grandparents that can no longer reproduce themselves participate in the care for their grandchildren ("weak grandmother effect"). In this case, we require that the age of the grandparent at time t, $k + j > i^{(s)}_{end}$:

$$P^{j,s}_{grand} = \frac{\sum_{k=i^{(s)}_{end}-j+1}^{N} a_k^{(s)} x_k(t - j - 1) \prod_{m=k}^{k+j} w_m}{\sum_{k=1}^{N} a_k^{(s)} x_k(t - j - 1)}.$$

Figure 4 shows how model behavior changes as we include strong or weak grandmother effect. In this example, there are $N = 7$ stages, and early reproducers (type 1) start reproducing in stage 2, while type 2 start at stage 3. Individuals do not reproduce in stages 6 and 7. In the absence of grandmother effect, for low values of w, type 1 individuals dominate (and exclude type 2); for high values of w the situation is reversed, and for intermediate w we have coexistence of both types. Adding the grandmother effect does not change this picture qualitatively, but gives type 1 individuals a larger advantage, such that the transition to the dominance of type 2 happens for higher values of w.

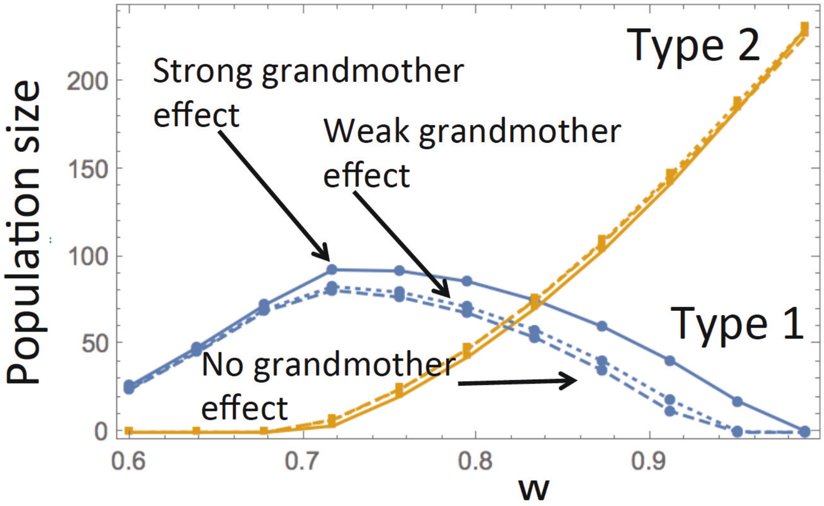

Figure 4: Age structured dynamics according to system (16-17), numerical simulations (similar to figure 1(b)), where the grandmother effect was included. Total populations of individuals of type 1 and type 2 are presented. Dashed lines correspond to no grandmother effect, dotted lines to the weak grandmother effect, and solid lines to strong grandmother effect. The parameters are: $N = 7$ age stages, $i^{(1)}_{start} = 2, i^{(2)}_{start} = 3, i^{(1)}_{end} = i^{(2)}_{end} = 5; w_1 = 0.9w, \beta^{(1)} = 0.2, \beta^{(2)} = 0.1, K = 140, S_{grand} = 1, a^{(s)}_i = 1$ during reproductive stages.

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

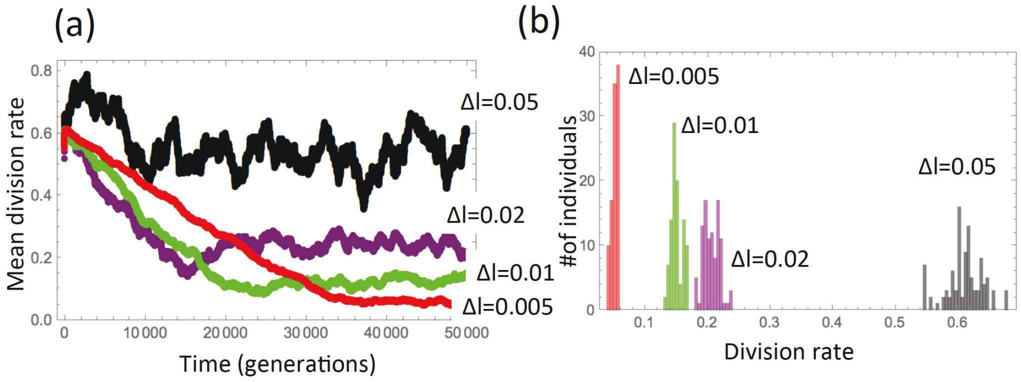

Figure 5: The dynamics of a 1D simulation with mutations. (a) The time-series of the population mean reproduction rate, for 4 different values of Δl. (b) Numerically obtained histograms of the population's reproduction rates, taken at generation 50,000, for the same 4 values of Δl. The rest of the parameter are: $N = 100$, $u = 0.04$, $\beta = 1$, $s = 0.9$.

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 5(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 5(b) shows numerically obtained histograms of reproduction rates of populations 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 6.

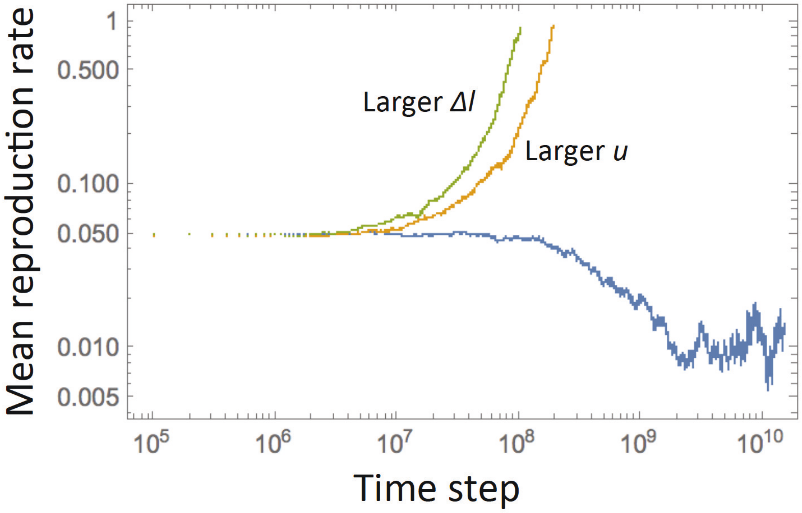

Figure 6: The dynamics of a 2D simulation with mutations. The population mean reproduction rate is plotted as a function of time, for 3 simulations. The blue line represents a base-line simulation with parameters $u = 0.1, \Delta l/l = 0.02$, the orange line a simulation with an increased mutation rate, $u = 0.3$, 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}.

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.

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:

$$\Delta L_{DB} = \sum_i \sum_j \sum_k \left(-l_i + \frac{l_j^2}{l_j + l_k} + \frac{l_k^2}{l_j + l_k} \right) f_i f_j f_k. \tag{18}$$

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

$$\Delta L_{CT} = \sum_i \sum_j \sum_k \left(-l_i + \frac{l_i + \alpha_{ij} l_j + \alpha_{ik} l_k}{1 + \alpha_{ij} + \alpha_{ik}} \right) f_i f_j f_k. \tag{19}$$

The equation

$$\Delta L_{DB} = -\beta \Delta L_{CT} \tag{20}$$

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 (19), 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 (18) 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 (18) 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 (20) is a decaying function of $\bar{l}$ which tends to zero as $\bar{l} \to \infty$, and the right hand side of equation (20) 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 (20) grows faster than the right hand side, resulting in an increase in the solution, $\bar{l}$.

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 $(\Delta l)^2\mu$:

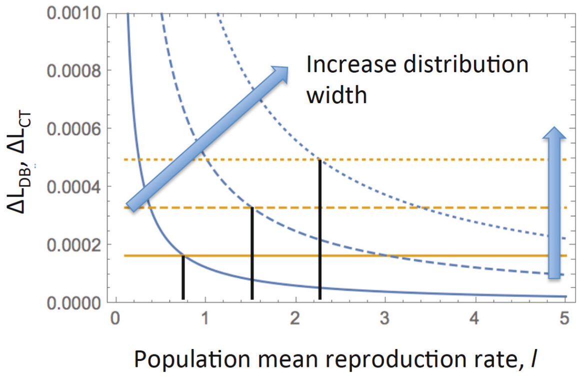

Figure 7: Finding the equilibrium reproduction rate by solving equation (20), illustrated with example (21-22). The left hand side of equation (20), ΔL_{DB}, is shown as blue lines and the right hand side, $-\beta \Delta L_{CT}$, with yellow lines, as functions of $\bar{l}$. Solid, dashed, and dotted lines correspond to three different values of Δl: $0.05, 0.10, 0.15$. The rest of the parameters are: $s = 0.9, \mu = 0.1, \beta = 1$.

$i \rightarrow$	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,

$$\Delta L_{DB} = \frac{(\Delta l)^2 \mu}{2\bar{l}} \frac{(\Delta l)^2 \mu - 4\bar{l}^2}{(\Delta l)^2 - 4\bar{l}^2}, \tag{21}$$

$$\Delta L_{CT} = \frac{\Delta l \mu (1-s)}{6(2+s)(1+2s)} \left((6-\mu)\mu s - 10s + \mu(3+\mu) - 8\right). \tag{22}$$

In figure 7, both sides of equation (20) 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.

4 Sexual reproduction

Here we provide details of model ABM4, an agent based spatial model that includes sexual reproduction.

ABM4 is based on model ABM3, in that it assumes the probability of reproduction to be a continuous trait, and also that for a cultural transmission updates, a given individual adopts the weighted average reproduction probability of the neighborhood with the possibility of “mutations” as defined in the main text for ABM3. 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.

5 Model extensions – future work

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, the details of this are not well understood. We note that results reported here depend on the assumption that individuals with lower reproduction rates carry more social weight, an assumption that has also been made in previous modeling work [1]. Another example of uncertainties in model construction is the formulation of the sexual reproduction model. We assumed monogamy, but made some obvious simplifications, as explained in the Results section. There are different assumptions that can be made in models that describe sexual reproduction, but the most important feature in the current context is that the reproduction rate of the offspring is not simply a copy of one of the parents, but represents the average of the two parents. This provides an additional mechanism of cultural change. Finally, only two types of communication networks have been considered in the agent based models here, the one where individuals interact with everyone else in the population, and the one where only interactions among nearest neighbors are allowed. A large variety of more realistic, random communication networks can be constructed, but we do not expect the results to differ from the ones obtained from the two extreme cases of networks considered here.

References

[1] Ihara Y, Feldman MW (2004) Cultural niche construction and the evolution of small family size. Theor Popul Biol 65: 105-111.