

# Cultural niche construction in a metapopulation

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## Abstract

Cultural niche construction is the process by which certain evolving cultural traits form a cultural niche that affects the evolution of other genetic and cultural traits [Laland, K., et al., 2001. Cultural niche construction and human evolution. *J. Evol. Biol.* 14, 22–33; Ihara, Y., Feldman, M., 2004. Cultural niche construction and the evolution of small family size. *Theor. Popul. Biol.* 65, 105–111]. In this study we focus on cultural niche construction in a metapopulation (a population of populations), where the frequency of one cultural trait (e.g. the level of education) determines the transmission rate of a second trait (e.g. the adoption of fertility reduction preferences) within and between populations. We formulate the Metapopulation Cultural Niche Construction (MPCNC) model by defining the cultural niche induced by the first trait as the construction of a social interaction network on which the second trait may percolate. Analysis of the model reveals dynamics that are markedly different from those observed in a single population, allowing, for example, different (or even opposing) dynamics in each population. In particular, this model can account for the puzzling phenomenon reported in previous studies [Bongaarts, J., Watkins, S., 1996. Social interactions and contemporary fertility transitions. *Popul. Dev. Rev.* 22 (4), 639–682] that the onset of the demographic transition in different countries occurred at ever lower levels of development.

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## 1. Introduction

Bongaarts and Watkins (1996) examined the correlation between the level of development<sup>1</sup> and the onset of the demographic transition<sup>2</sup> across various countries and noted a puzzling phenomenon: although the earliest countries to undergo the demographic transition were

those that were most highly developed, with the passage of time, the onset of the transition in different countries occurred at ever lower levels of development. They attributed this phenomenon to the influence of social interactions at varying levels (e.g. via local, national and international channels) on the diffusion dynamics of information and ideas. They presented a comprehensive interpretation of such multilevel social interactions and their effect on the adoption of fertility control, calling for further research and modeling of this phenomenon. Furthermore, evolution-minded human scientists have struggled to produce a satisfactory evolutionary explanation for the demographic transition (Borgerhoff Mulder, 1998), and to many researchers this remains a puzzle. In this respect, the analysis by Ihara and Feldman (2004) provides a potential, if partial, solution. In this paper we build on this work and construct such a model in terms of a metapopulation that incorporates the concept of cultural niche construction (Odling-Smee et al., 2003; Ihara and Feldman, 2004).

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<sup>1</sup>Using the human development index proposed by UNDP, 1990.

<sup>2</sup>The demographic transition is characterized, typically, by an increase in socioeconomic development, a reduction in mortality, and a subsequent (often many years later) reduction in fertility (Coale, 1974). Such a ‘fertility transition’ is thought to result not only from rising costs and declining economic value of children (e.g. Notestein, 1953; Mace, 1996, 2000), but also from the social transmission of information concerning fertility control, and social influences, such as conformity, affecting the preference for fertility control (Cleland and Wilson, 1987; Borgerhoff Mulder, 1998).

Traditionally, biologists regarded organismic evolution as a complex dynamic process, taking place in an autonomously changing environment. However, organisms can modify their environment and thus significantly alter the selection pressures governing the evolution of their own or other species (Lewontin, 1983). This phenomenon, termed *niche construction* (Odling-Smee et al., 2003; Laland et al., 1996, 2001), may have a profound effect on the evolutionary process, markedly changing evolutionary trajectories. Laland et al. (1996) used two-locus genetic models to investigate the evolutionary consequences of niche construction. In their models, it was assumed that a first locus governs niche-constructing behavior of individuals by affecting the amount of some resource in the environment. Viability selection, acting at a second locus, was assumed to depend on the amount of this resource. They showed that niche construction may generate selection pressures that lead to fixation of otherwise deleterious alleles, maintain genetic polymorphism where none is expected, eliminate what would otherwise be stable polymorphism, and produce time lags in the response to selection, as well as other unusual evolutionary dynamics.

For humans (and perhaps some other species), cultural traits can be analyzed in an analogous manner. In recent studies (Ihara and Feldman, 2004; Kendal et al., 2005), an analog of the two-locus model was applied to demonstrate the effect of cultural niche construction. Two culturally transmitted traits were considered where the frequency of the first vertically transmitted trait (e.g. level of education) acts as a cultural niche or background that affects the rate of oblique or horizontal transmission of a second cultural trait (e.g. adoption of fertility-reducing preferences). They showed that cultural niche construction may facilitate the ‘*demographic transition*’ as an increase in the mean level of education facilitates, following a time lag, an increase in the preference for fertility control.

These studies assumed an unstructured population, and focused on the effects that the cultural niche may have on the cultural transmission process within that population. However, as pointed out by Bongaarts and Watkins (1996), human populations are structured, with levels of organization, hierarchy and subgroups that may markedly affect the dynamics of cultural transmission. Thus, in this study we extend the single population cultural niche construction model to incorporate population structure. We examine the process of cultural niche construction in a metapopulation (a population of populations) where the local frequency of one cultural trait in each population influences the transmission rate of a second trait both within and between the different populations. Cultural niche construction is introduced using a weighted social network that represents the level of communication within and between populations and we examine the propagation dynamics of a second cultural trait on this network. We demonstrate how variation in the onset of cultural transitions between populations, for example the fertility transition, can be accounted for by the structure of a cultural background

that facilitates social interactions between different populations.

The remainder of this paper is organized as follows. In Section 2, we present the Metapopulation Cultural Niche Construction (MPCNC) model. We examine the resulting dynamics in Section 3, demonstrating the emergence of analogous phenomena to that described by Bongaarts and Watkins (1996), and present a local stability analysis of the equilibrium states as well as a sensitivity analysis. The paper concludes with a discussion of future work and a brief summary.

## 2. The MPCNC model

The MPCNC model considers a metapopulation of  $n$  populations and two cultural traits. The first cultural trait,  $E$ , provides a cultural background or niche that may affect the evolution of the second cultural trait,  $A$ . The frequencies of individuals in population  $i$ , and at generation  $t$ , that exhibit the combination of traits  $EA$ ,  $Ea$ ,  $eA$  and  $ea$  are given by  $x_{22,i}^t$ ,  $x_{21,i}^t$ ,  $x_{12,i}^t$  and  $x_{11,i}^t$ , respectively, where  $x_{22,i}^t + x_{21,i}^t + x_{12,i}^t + x_{11,i}^t = 1$ . The frequencies of traits  $E$  and  $A$  within population  $i$  at generation  $t$  are given by  $p_i^t = x_{21,i}^t + x_{22,i}^t$  and  $q_i^t = x_{12,i}^t + x_{22,i}^t$ , respectively. In the context of fertility transitions, the frequency of trait  $E$  might represent some index, or correlate, of human development such as the mean level of education in a population, while trait  $A$  represents the preference to adopt fertility control.

During each generation two phases of cultural transmission take place. In the first phase, traits  $E$  and  $A$  are vertically transmitted<sup>3</sup> (from parents to offspring) within each population  $i$ , with probabilities  $b_{3,i}$ ,  $b_{2,i}$ ,  $b_{1,i}$  and  $b_{0,i}$  for mother-father mating pairs of type  $E-E$ ,  $E-e$ ,  $e-E$  and  $e-e$ , respectively, and with probabilities  $c_{3,i}$ ,  $c_{2,i}$ ,  $c_{1,i}$  and  $c_{0,i}$  for mating pairs of type  $A-A$ ,  $A-a$ ,  $a-A$  and  $a-a$ , respectively<sup>4</sup> (in accordance with Cavalli-Sforza and Feldman, 1981). Note that traits  $e$  and  $a$  simply represent the default states of those that have not adopted  $E$  or  $A$ , respectively. The fertility selection coefficient,  $f$ , represents a fitness cost to parents that have adopted trait  $A$ , such that the relative number of offspring for mating pairs with traits  $A-A$ ,  $A-a$  (or  $a-A$ ) and  $a-a$  is  $1-f$ ,  $1-\frac{f}{2}$  and  $1$ , respectively. Assuming a simple random mating scheme, the frequencies of the four types,  $EA$ ,  $Ea$ ,  $eA$  and  $ea$  in the offspring generation after vertical transmission (superscript,  $v$ ), are shown in Appendix A.1. Furthermore, assuming that for population  $i$  at generation  $t = 0$ , there is no statistical association between traits  $E$  and  $A$ , that is,

<sup>3</sup>See, for example, Cavalli-Sforza et al. (1982), providing evidence for parent-offspring correlation in attitudes to education.

<sup>4</sup>In the case of fertility transitions, we assume that the costs and benefits associated with the adoption of a high level of education (that may affect the rate of diffusion of trait  $E$ ) are subsumed within the vertical transmission coefficient,  $b$  (see Eqs. (1) and (2)) for each population. The validity of the assumptions underlying the dynamics of trait  $E$  is addressed in the general discussion.

$D_i = x_{22,i} - p_i q_i = 0$  (this assumption will be validated below), the analysis can be simplified from the recursion in the four combinations of traits (shown in Appendix A.1, Eqs. (A.1)–(A.4)) to recursion in the two traits. Under this assumption, the frequencies of the two traits in the offspring generation after vertical transmission (indicated by superscript,  $t, v$ ) are given by

$$p_i^{t,v} = b_{3,i}(p_i^{t-1})^2 + (b_{2,i} + b_{1,i})p_i^{t-1}(1 - p_i^{t-1}) + b_{0,i}(1 - p_i^{t-1})^2, \quad (1)$$

$$W_i^{t-1} q_i^{t,v} = (1 - f)c_{3,i}(q_i^{t-1})^2 + \left(1 - \frac{f}{2}\right)(c_{2,i} + c_{1,i})q_i^{t-1} \times (1 - q_i^{t-1}) + c_{0,i}(1 - q_i^{t-1})^2. \quad (2)$$

The frequency of trait  $A$  in population  $i$  after fertility selection is normalized by dividing by the mean fitness in the population,  $W_i^{t-1} = 1 - q_i^{t-1}f$ . Throughout, we consider the simple case where  $b_{3,i} = c_{3,i} = 1$ ,  $b_{0,i} = c_{0,i} = 0$  for all populations. Also, we assume for simplicity that for each population  $i$ , there is no parental transmission bias of  $E$ ,  $b_{2,i} = b_{1,i} = b_i$ , and that  $c_{2,i} = c_{1,i} = c = 0.5$  (i.e. vertical transmission of trait  $A$  is completely unbiased in all populations). Eqs. (1) and (2) then simplify to

$$p_i^{t,v} = (p_i^{t-1})^2 + 2b_i p_i^{t-1}(1 - p_i^{t-1}), \quad (3)$$

$$q_i^{t,v} = \left[ (1 - f)(q_i^{t-1})^2 + \left(1 - \frac{f}{2}\right)2c q_i^{t-1}(1 - q_i^{t-1}) \right] / (1 - q_i^{t-1}f). \quad (4)$$

It should be noted that in these settings, if no other transmission phase would take place, the fitness cost of parents that have adopted trait  $A$  (i.e.  $f > 0$ ) will prevent trait  $A$  from spreading in the population.

In the second phase, trait  $A$  is transmitted horizontally, (within the offspring generation), percolating across a social network connecting the various populations. The social network includes  $n$  vertices, each representing a population. The weight of the edge  $(i, j)$ ,  $e_{ij}$ , connecting vertex  $i$  to vertex  $j$ , represents the level of communication (and thus affects the transmission rate) between populations  $i$  and  $j$ . We assume that the level of communication between each pair of populations is determined by the cultural background (i.e. the frequency of trait  $E$ ) in each of these populations. In our model, the weight of each edge  $(i, j)$  at generation  $t$  is given by

$$e_{ij}^t = \mu_0 K^2 + \mu_1 \bar{p}^{t,v} + \mu_2 p_i^{t,v} p_j^{t,v}, \quad (5)$$

where  $K$  is some constant and  $\bar{p}^{t,v}$  denotes the average frequency of trait  $E$  across all populations at generation  $t$ . The first term in this expression,  $\mu_0 K^2$ , represents a baseline communication level that is not affected by the cultural background. Hence, when  $\mu_0 > 0$  but  $\mu_1 = \mu_2 = 0$ , the selection on  $A$  is independent of  $E$  and no niche construction occurs. The second term,  $\mu_1 \bar{p}^{t,v}$ , represents the effect of global niche construction that results from the mean cultural background in the metapopulation, while

not distinguishing between the various populations. Applying these two terms alone reduces the model to the simpler scenario of cultural niche construction in one population (the union of all populations in the metapopulation) similar to Kendal et al. (2005). Finally, the third term,  $\mu_2 p_i^{t,v} p_j^{t,v}$ , represents a local niche construction effect, specific to population  $i$  and its relationship with population  $j$  in the metapopulation.

By adjusting the values of  $\mu_0$ ,  $\mu_1$  and  $\mu_2$ , we can examine the influence of each of these metapopulation niche construction ‘modes’.<sup>5</sup> As will be demonstrated in the next section, in order to reveal the unique characteristics of niche construction in a metapopulation (as opposed to one, uniform population), the third term of this expression, representing the local niche construction mode, is necessary.

Overall, trait  $A$  is transmitted horizontally from population  $j$  to population  $i$  with a probability that is dependent on the edge weighting,  $e_{ij}^t$ , the frequency of trait  $A$  in population  $j$  and the horizontal transmission coefficient  $h$ . We also assume that individuals in population  $i$  conform to the preference of the majority in their population, i.e. preferring trait  $A$  or the default,  $a$ , according to a conformity coefficient  $\psi$ . For  $\psi > 0$ , the conformity term,  $1 + \psi(2q_i^{t,v} - 1)$ , ranges from  $1 - \psi$  (reduced transmission) for  $q_i^{t,v} = 0$  to  $1 + \psi$  (enhanced transmission) for  $q_i^{t,v} = 1$  and does not affect transmission in a balanced population,  $q_i^{t,v} = 0.5$ . The frequency of trait  $A$  in population  $i$  after this horizontal transmission phase is calculated by averaging the effect of the transmission of trait  $A$  from all the populations in the metapopulation to population  $i$  and is thus given by (see also Appendix A.2)

$$q_i^t = q_i^{t,v} + \frac{1}{n} \sum_{j=1}^n (e_{ij}^t q_j^{t,v}) h (1 - q_i^{t,v}) [1 + \psi(2q_i^{t,v} - 1)]. \quad (6)$$

Note that the total probability of horizontal transmission is the sum across all edges in the social network. The frequency of trait  $E$  in population  $i$  does not change in this phase, that is,  $p_i^t = p_i^{t,v}$ .

Considering these transmission phases, Appendix A.3 corroborates the validity of our assumption concerning the lack of statistical association between traits  $E$  and  $A$  (i.e.  $D_i = x_{22,i} - p_i q_i = 0$ ).

### 3. Analysis

#### 3.1. Dynamics

We first examine the influence of trait  $E$ , the cultural niche, on the horizontal transmission of trait  $A$  at a certain generation (the index  $t$  is thus omitted). Considering the ‘effective’ frequency of trait  $A$ , that is, the mean frequency

<sup>5</sup>The case  $\mu_0 = \mu_1 = \mu_2 = 0$  induces  $e_{ij} = 0$  (no communication between the different populations), and hence, no horizontal transmission. This scenario will not be examined in this analysis as under the settings described above it always results in the extinction of trait  $A$ .

of individuals across the metapopulation from whom trait  $A$  might be acquired when weighted by local social network connections, we get

$$\begin{aligned} \frac{1}{n} \sum_{j=1}^n [e_{ij} q_j^v] &= \mu_0 K^2 \bar{q}^v + \mu_1 \bar{p}^v \bar{q}^v + \frac{\mu_2}{n} \sum_{j=1}^n (p_j^v q_j^v) p_i^v \\ &= \alpha + \beta p_i^v, \end{aligned} \tag{7}$$

where both  $\alpha = (\mu_0 K^2 + \mu_1 \bar{p}^v) \bar{q}^v$  and  $\beta = \frac{\mu_2}{n} \sum_{j=1}^n (p_j^v q_j^v)$  are identical for all populations at generation  $t$ . The form (7) is then incorporated into (6). Hence, the effect of the cultural niche construction on the spread of trait  $A$  in population  $i$  is positively correlated with the frequency of trait  $E$  (e.g. the *education level*) in this population. This phenomenon can be conceived as an analogue of the *rich-get-richer* phenomenon (though concerning the frequencies of trait  $E$  and  $A$  rather than actual wealth), whereby populations with a high frequency of the cultural background trait  $E$  are more affected by the level of trait  $A$  across the metapopulation, and subsequently adopt this trait faster than populations with a low frequency of trait  $E$  (a similar phenomenon was found by Bongaarts and Watkins (1996)). However, as both traits also vary over time via vertical transmission, this simple analysis is not sufficient to characterize the overall complex behavior of this model. We therefore use a detailed simulation analysis to explore the joint dynamics of the system (1)–(6).

We examine the correlation between the frequency of trait  $E$ , and the diffusion of trait  $A$  across populations. In the following simulation runs  $n = 50$ ,  $c = 0.5$ ,  $f = 0.1$ ,  $h = 0.3$ ,  $\psi = 0.1$  and  $K = 1$ , unless otherwise stated. However, the qualitative results are robust across a wide range of parameter values. All populations start with relatively low frequencies of  $E$  and  $A$  ( $p_i^0 = q_i^0 = 0.05$ ). The rate of vertical transmission of trait  $E$ , (i.e.  $b_i$ ) in each population is randomly selected at the beginning of the simulation from a uniform distribution on the interval  $[0.5, 0.6]$ , allowing for the level of cultural background (i.e. frequency of  $E$ ) in the various populations to diverge over time. Clearly, populations for which  $b_i$  is higher adopt the cultural background trait,  $E$ , faster (see, for example, Fig. 1a top panel, where the curves depicting the frequency of trait  $E$  in the different populations are basically ordered according to the value of  $b_i$  in each population). Examining the spread of trait  $A$  using different values of  $\mu_0$ ,  $\mu_1$  and  $\mu_2$ , the effect of the different modes of the metapopulation niche construction is demonstrated clearly (Fig. 1). While both global and local niche construction result in trait  $A$  spreading across the various populations, applying the local niche construction term also induces variation in trajectories for the spread of  $A$  (Fig. 1b).<sup>6</sup> Bongaarts and Watkins (1996) have arbitrarily measured the demographic

<sup>6</sup>Using no niche construction (i.e.  $\mu_0 = 1$ ,  $\mu_1 = \mu_2 = 0$ ) results in a qualitatively similar behavior to that demonstrated for global niche construction where all the populations go through the transition at the same time.

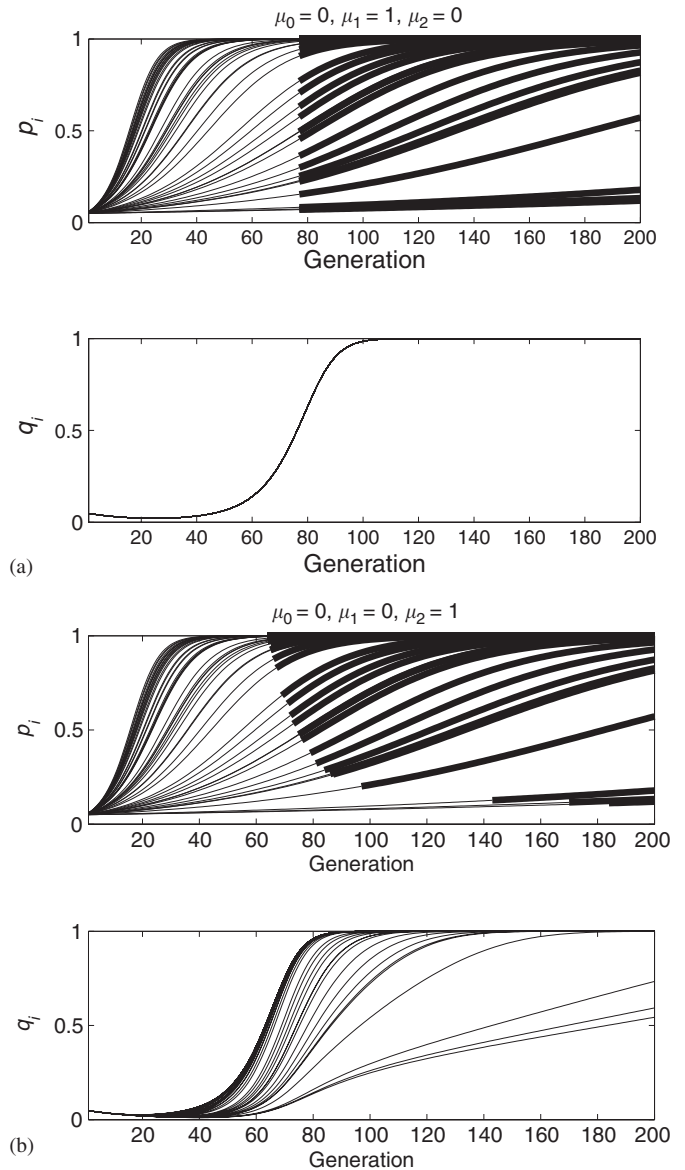


Fig. 1. An illustration of a simulation run of the model. The different curves depict the frequency of traits  $E$  (top panels) and  $A$  (bottom panels) for each of the  $n = 50$  populations in the metapopulation over 200 generations. Parameter values are set to  $c = 0.5$ ,  $f = 0.1$ ,  $h = 0.3$ ,  $\psi = 0.1$ ,  $K = 1$  and  $p_i^0 = q_i^0 = 0.05$ .  $b_i$  in each population is randomly selected from a uniform distribution on the interval  $[0.5, 0.6]$  (populations for which  $b_i$  is higher adopt trait  $E$  faster). In the top panel of each figure, the curves change from thin lines to thick lines when the frequency of  $A$  exceeds 0.5, indicating the onset of trait  $A$  transition (e.g. the demographic transition). (a) Applying global niche construction yields a uniform transition of trait  $A$ . (b) Local niche construction results in the various populations going through the transition at different times though at ever lower frequencies of trait  $E$ .

transition onset by a fall of 10 percent in fertility from its pretransitional maximum. Here, we define trait  $A$  transition as the point in time where  $q_i > 0.5$ ; however, similar results are obtained for other values. Examining the transition onset in the various populations, Fig. 1b demonstrates that populations with higher frequencies of trait  $E$  (induced by higher transmission coefficient values,  $b_i$ ), undergo trait  $A$  transition before populations

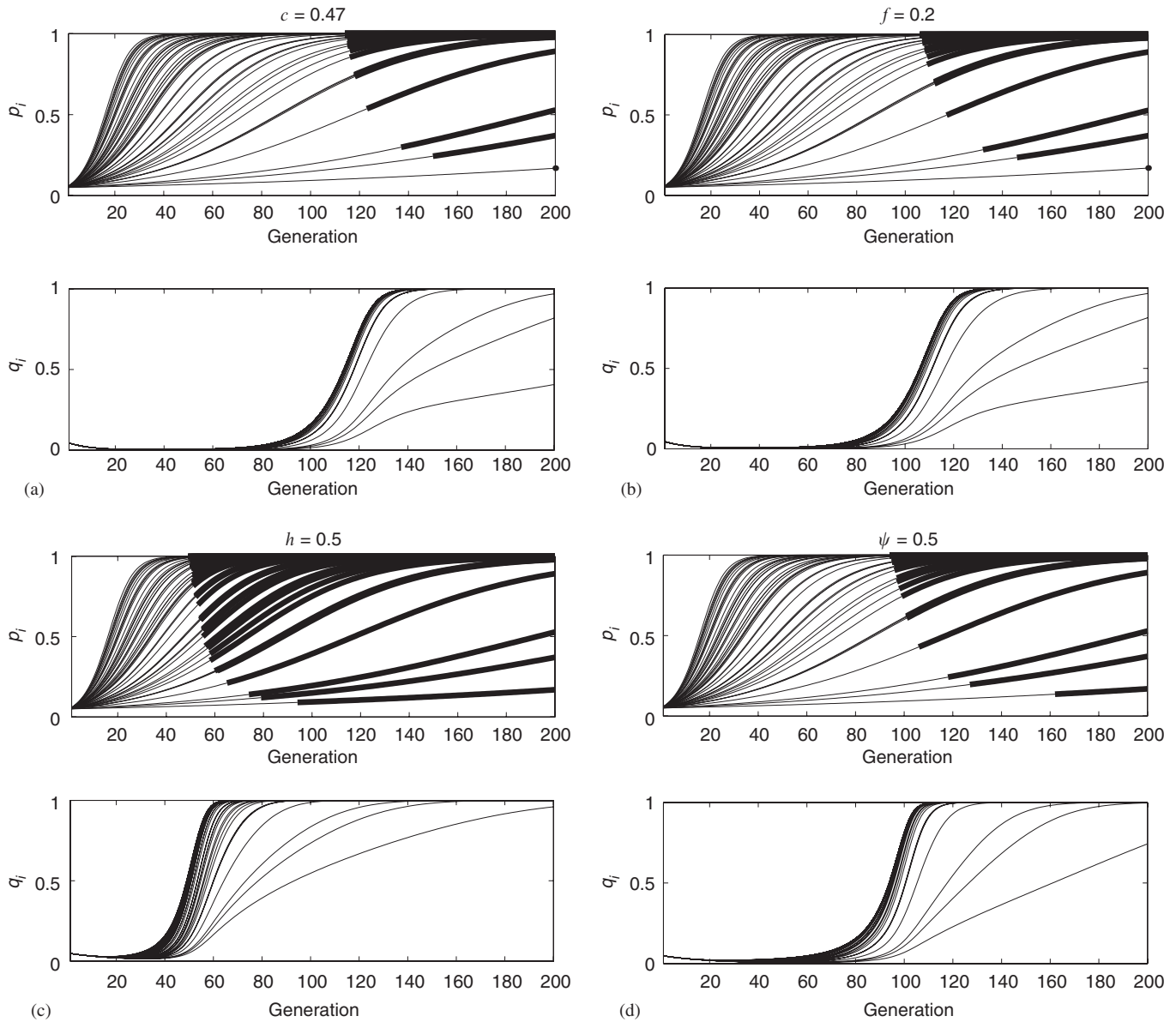


Fig. 2. An illustration of a simulation run of the model using various parameter values. Aside from the modified values listed in the title of each panel, the parameters values are the same as the ones used in Fig. 1b. Evidently, while affecting the overall spreading dynamics of trait *A*, all the examined parameter values still result in a qualitatively similar phenomena where the onset of a transition in trait *A* in each population occurs at lower levels of trait *E* over time.

with lower trait *E* frequencies. However, the onset of a transition in trait *A* in each population occurs at lower levels of trait *E* over time. Assuming that the frequency of trait *E* is a measure of the development level in each population and trait *A* represents the adoption of fertility-reduction preferences, this phenomenon is similar to the one described in Bongaarts and Watkins (1996). The robustness of this phenomena is further demonstrated in Fig. 2, illustrating the resulting dynamics under various modified parameter values.

The markedly different frequencies of trait *E*, at which the onset of trait *A* transitions occur, suggests that this effect cannot be solely attributed to varying horizontal transmission rates *within* each population. Clearly, if this

were the case, different populations would have experienced the onset of transition at approximately the same level of local cultural background (i.e.  $p_i \approx p_j$ ).<sup>7</sup> To confirm the contribution of niche construction *between* populations we have conducted an additional set of simulations in which the percolation of trait *A* either *within* populations or *between* populations is examined in isolation. In these simulations, local niche construction is still assumed (i.e.  $\mu_0 = \mu_1 = 0, \mu_2 = 1$ ), but slightly modified versions of horizontal transmission are used. These modified horizontal

<sup>7</sup>Though not identical, as the rate of diffusion of trait *E* may differ across populations, resulting, over time, in variation in the influence of within-population niche construction on transition onset.

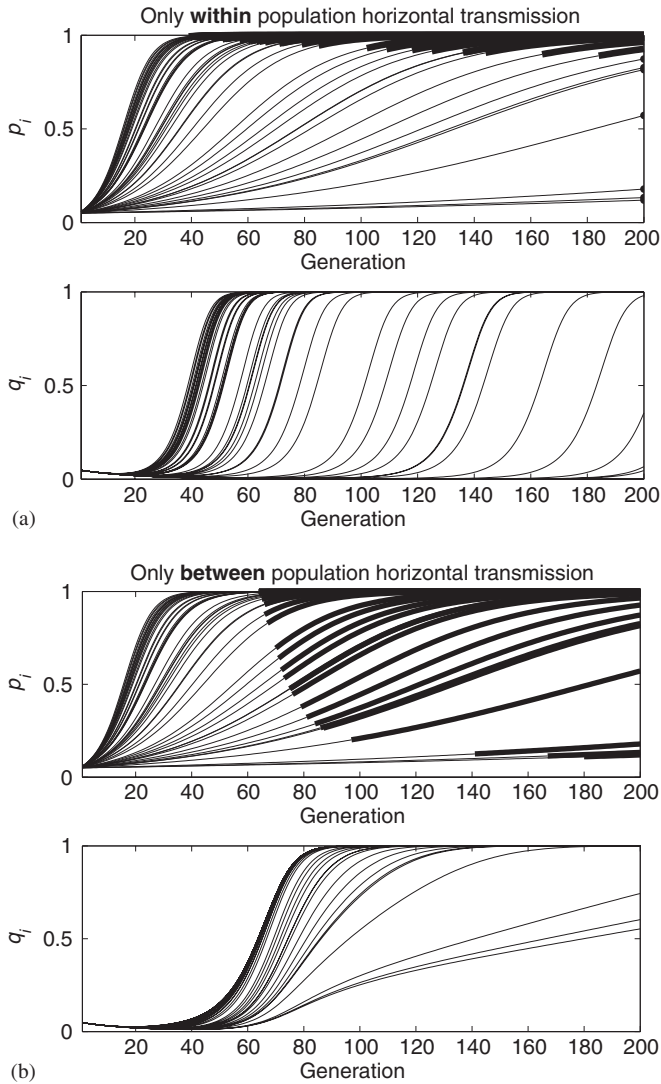


Fig. 3. An illustration of the effect of within population (a) and between population (b) niche construction (i.e. using Eqs. (8) and (9) instead of Eq. (6)). Aside from the modified version of horizontal transmission described above, the parameters values are the same as the ones used in Fig. 1b.

transmission models are given by

$$q_{i\text{-within}}^t = q_i^{t,v} + (e_{ii}^t q_i^{t,v})h(1 - q_i^{t,v})[1 + \psi(2q_i^{t,v} - 1)], \quad (8)$$

$$q_{i\text{-between}}^t = q_i^{t,v} + \frac{1}{n-1} \sum_{j=1}^n [(e_{ij}^t q_j^{t,v})(1 - \delta_{ij})] \times h(1 - q_i^{t,v})[1 + \psi(2q_i^{t,v} - 1)], \quad (9)$$

where  $e_{ij}^t$  is still calculated according to (5) and  $\delta_{ij}$  denotes the Kronecker delta function.<sup>8</sup> Expressions (8) and (9) thus partition the total effect of horizontal transmission in the metapopulation (6) into two components, one accounting only for the horizontal transmission within each population and the other accounting only for horizontal transmission

<sup>8</sup>The Kronecker delta is defined as having the value one when  $i = j$ , and zero when  $i \neq j$ .

between different populations (leaving out transmission within the populations). As demonstrated in Fig. 3, within-population niche construction indeed results in all the populations experiencing the onset of trait A transition at approximately the same frequency of trait E. Thus, the behavior demonstrated in Fig. 1b can be attributed, almost in its entirety, to the process of local cultural niche construction between populations. In the rest of the paper we thus revert to the original model (i.e. using Eqs. (3)–(6)).

The relationship between the variance in the time to reach trait A transition and the level of local niche construction effect is illustrated further in Fig. 4. The variance is calculated for a set of simulation runs with varying degrees of local niche construction coefficient,  $\mu_2$ . To maintain a similar overall communication level,  $\mu_1$  is set to  $1 - \mu_2$  ( $\mu_0 = 0$  in all simulations). Evidently, with higher levels of local niche construction, the variance in the onset of transitions increases. This measure could be used to estimate the relative contribution of global and local niche construction modes in human societies that exhibit this pattern of transition delay.

### 3.2. The invasion and spread of trait A

The conditions for invasion and local stability of the four ‘corner’ equilibrium states, denoted by  $Q_i(0,0,0)$ ,  $Q_i(1,0,0)$ ,  $Q_i(0,1,0)$  and  $Q_i(1,1,0)$  (where  $Q_i(\hat{p}_i, \hat{q}_i, D_i)$  denotes the equilibrium state), are derived from the non-collapsed version of the model (recursions (A.1)–(A.8)) and presented in Appendix B. In concordance with the findings of Kendal et al. (2005), it is shown that the range of parameter values under which trait A invades population  $i$  is positively related to both the coefficient of global and

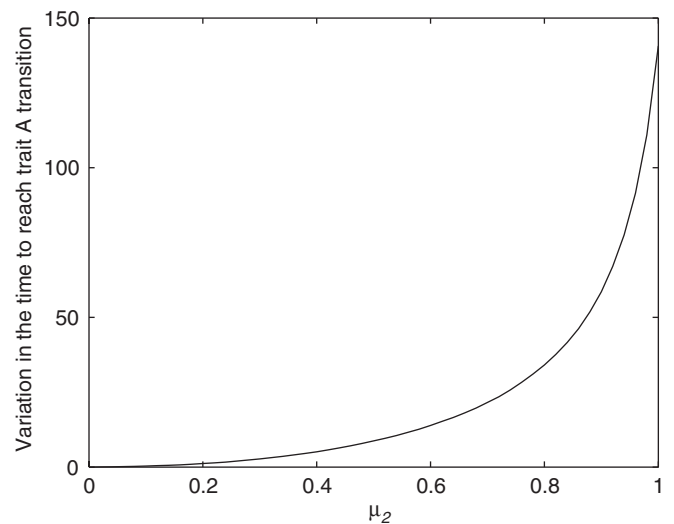


Fig. 4. The statistical variance of the time to reach trait A transition in the metapopulation as a function of  $\mu_2$ . The curve represents the average of 100 simulation runs. For each value of  $\mu_2$ , we set  $\mu_1 = 1 - \mu_2$ . As demonstrated, a higher level of local niche construction yields on average higher variance.

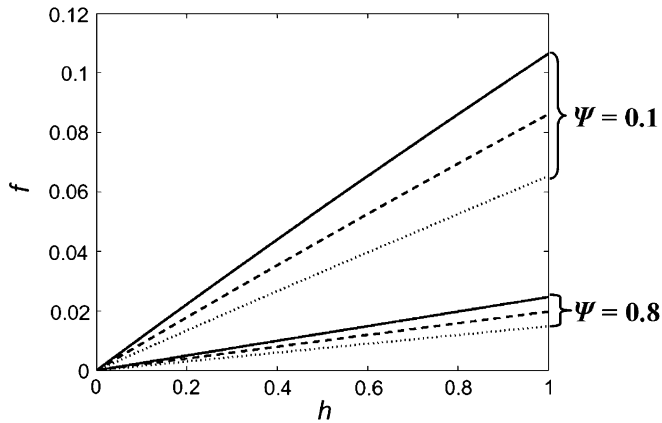


Fig. 5. Trait  $A$  invades under each line, given by (B.5), in a single population. This figure shows the effect of the coefficient of conformity,  $\psi$ , and the effect of global niche construction,  $\mu_1$ , on the region of invasion of trait  $A$  when perturbed from  $Q_i(0,0,0)$ , where  $\mu_1 = 1$  (continuous line),  $\mu_1 = 0.8$  (dashed line), and  $\mu_1 = 0.6$  (dotted line), where, in all cases, an arbitrary value of  $\bar{p} = \frac{1}{n} \sum_{i=1}^n p_i = 0.25$  was used. In particular, note that for a high level of global niche construction, trait  $A$  is predicted to invade under a lower coefficient of horizontal transmission,  $h$ , for a given level of fertility selection,  $f$ , than for a low level of global niche construction. Furthermore, global niche construction has less effect on the range of parameters for which trait  $A$  invades at high levels of conformity than at low levels of conformity. Finally, the invasion of trait  $A$  is not possible if the conformity coefficient,  $\psi = 1$ . Although not shown, similar trends are evident when the range of parameter values under which trait  $A$  invades population  $i$  from  $Q_i(1,0,0)$  is affected by local niche construction.

local niche construction. Fig. 5 provides an example, showing the effect of global niche construction,  $\mu_1$ .

We also examine the spread of trait  $A$  across the metapopulation as a function of the fertility selection,  $f$ , and the horizontal transmission coefficient,  $h$ , with varying modes of niche construction. Using a simulation run of the MPCNC model, we tested how many populations went through the trait  $A$  transition for varying levels of  $f$  and  $h$ , both from 0 to 1. The total number of generations was set to 200 to allow comparison with the dynamics described in Section 3.1 (other simulation parameters are set as before). As demonstrated in Fig. 6, higher values of fertility selection require also a high level of horizontal transmission  $h$  for trait  $A$  to spread. Thus, the effects of  $f$  and  $h$  on the trait  $A$  transition are similar to their effects on the invasion of  $A$  (see, for example, Fig. 5). A comparison between Fig. 6a and Figs. 6b–d shows that, typically, the conditions supporting trait  $A$  transition are less restrictive when no niche construction is applied (i.e.  $\mu_1 = \mu_2 = 0$ ) than under either global or local niche construction. This finding, however, may be the result of the different baseline communication level,  $\mu_0$ . Note also, that in the case of  $\mu_0 = \mu_1 = \mu_2 = 0$ , no horizontal transmission takes place and trait  $A$  will never spread due to its fitness cost. Furthermore, as can be seen in Figs. 6b–d, the conditions under which trait  $A$  spreads do not change significantly when the balance between global and local niche construction is varied. However, a comparison of the width of

region II in Figs. 6b–d (representing parameter values in which some populations are still in the pre-transitional state) indicates that the time to reach the transition under certain  $h$  and  $f$  parameter values increases with the coefficient of local niche construction (see also the discussion in Section 4).

### 3.3. Sensitivity analysis

Here, we examine the relative sensitivity of the change in frequency of trait  $A$  in population  $i$  over horizontal transmission,  $\partial \Delta q_i$ , to a small change in the frequency of trait  $E$  in population  $j$ ,  $\partial p_j$ , compared with a small change in the frequency of trait  $E$  within population  $i$ , given by  $\partial p_i$ . This is a measure of the relative effect of niche construction between populations  $i$  and  $j$  compared to within population  $i$ , on trait  $A$  adoption in population  $i$ . We find from (5) and (6) that

$$\frac{\partial \Delta q_i}{\partial p_j} = \frac{2\mu_1 \bar{p} \bar{q} + \mu_2 p_i q_j}{2\mu_1 \bar{p} \bar{q} + \mu_2 (\sum_{k=1}^n p_k q_k + p_i q_i)}, \quad (10)$$

where  $\bar{p} = \frac{1}{n} \sum_{j=1}^n p_j$ ,  $\bar{q} = \frac{1}{n} \sum_{j=1}^n q_j$  and  $\Delta q_i = \frac{1}{n} \sum_{j=1}^n (e_{ij} q_j) h (1 - q_j) [1 + \psi (2q_i - 1)]$ .

It is clear from (10) that if there is only global niche construction (i.e.  $\mu_1 > 0$  and  $\mu_2 = 0$ ), there is no difference in the sensitivity of  $\Delta q_i$  to a small change in the frequency of trait  $E$  within population  $i$  compared to that in population  $j$ , as all populations experience the same average network weightings (i.e.  $\mu_1 \bar{p}$ ) and thus are exposed to the same frequency of trait  $A$  (i.e.  $\bar{q}$ ). However, if there is only local niche construction (i.e.  $\mu_1 = 0$  and  $\mu_2 > 0$ ), (10) is positively related to  $\mu_2 p_i q_j$  (i.e. the frequency of trait  $A$  in population  $j$  that affects population  $i$  as a result of local niche construction), and is negatively related to  $\mu_2 \sum_{k=1}^n p_k q_k$  and  $\mu_2 p_i q_i$  (i.e. both the total frequency of trait  $A$  across the metapopulation and the frequency of trait  $A$  within population  $i$  that affects population  $i$  as a result of local niche construction).

If we consider the special case where the frequency of trait  $A$  is the same in all populations (i.e. for any two populations,  $i$  and  $j$ ,  $q_i = q_j = \bar{q}$ ), Eq. (10) simplifies to

$$\frac{\partial \Delta q_i}{\partial p_j} = \frac{2\mu_1 \bar{p} + \mu_2 p_i}{2\mu_1 \bar{p} + \mu_2 (n\bar{p} + p_i)}. \quad (11)$$

Fig. 7 shows that under these conditions, sensitivity of the change in the frequency of trait  $A$  appears to be most affected by local niche construction (e.g.  $\mu_1 = 0$ ,  $\mu_2 = 1$ ) between populations  $j$  and  $i$  compared to within population  $i$  when the level of the cultural background in population  $i$  (or  $p_i$ ) is high. This appears to be consistent with the rich-get-richer rule. Fig. 7 further demonstrates that the same holds when the mean level of the cultural background

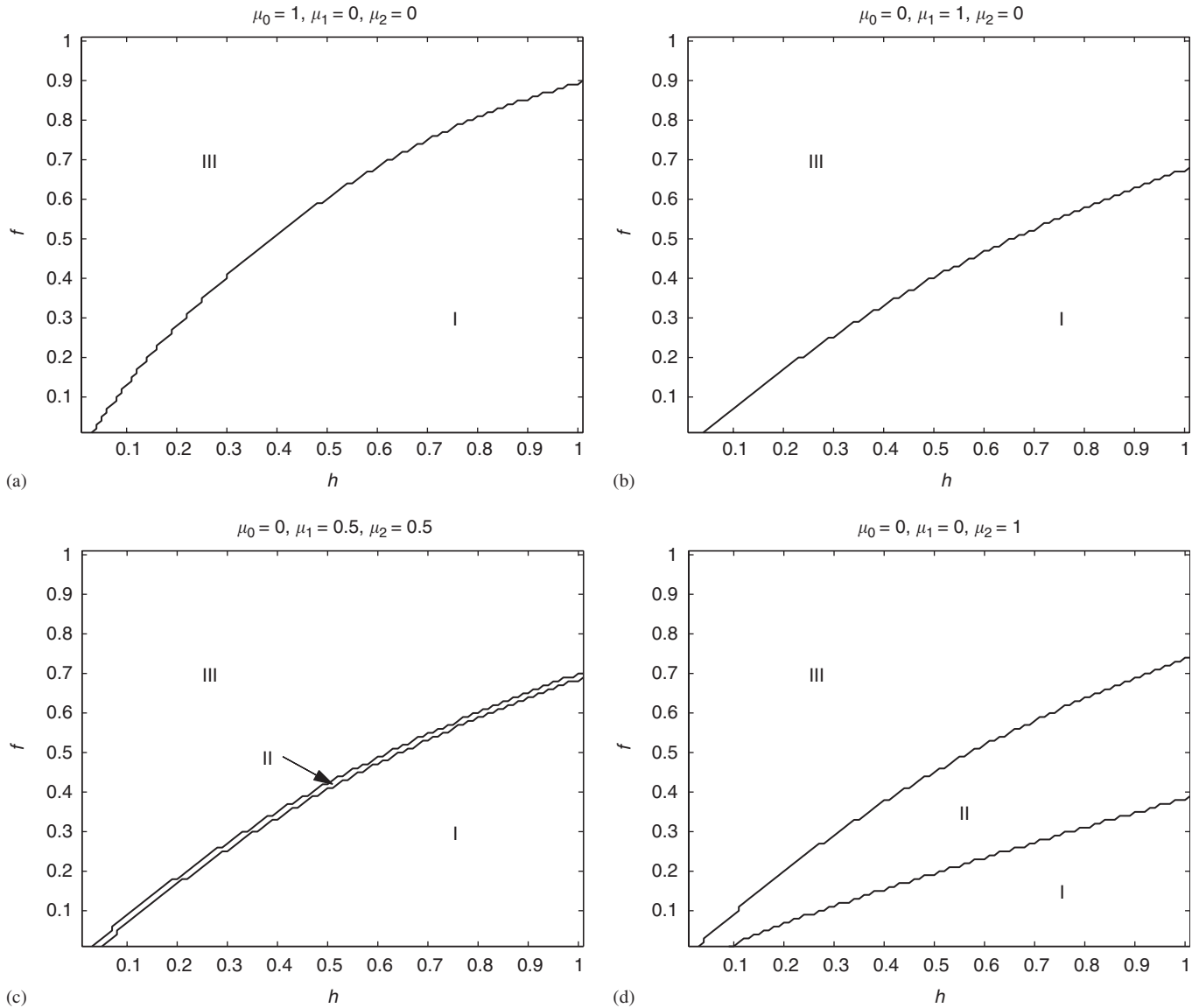


Fig. 6. The spread of trait  $A$  as a function of the fertility selection,  $f$ , and the horizontal transmission coefficient,  $h$ , within the first 200 generations. Region I represents  $f$  and  $h$  values for which all 50 populations reached trait  $A$  transition (set arbitrarily as the point in time where  $q_i > 0.5$ ), while region III indicates that the transition did not occur in *any* population. Region II represents an intermediate case where some populations are post-transitional while others are still in the pre-transitional state. Additional simulations, applying a larger number of generations, indicate that populations in region II eventually go through the transition. Comparing (a) with (b)–(d), it is shown that using a different baseline communication level,  $\mu_0$ , modifies the conditions under which trait  $A$  spreads within 200 generations. (b)–(d) further demonstrate that varying balance between the global and local niche construction terms has relatively little effect on the spreading conditions (i.e. the regions of the  $h$  and  $f$  parameter space in which populations go to transition), although, region II in (d) indicates that the variance in the spread of  $A$  under local niche construction may not allow all the populations to experience the transition within the first 200 generations.

across the metapopulation (or  $\bar{p}$ ) is particularly low and there are few populations ( $n$ ) in the metapopulation.

An additional illustration of the effect that different niche construction modes may have on the spreading dynamics of trait  $A$  is shown in Fig. 8. In this simplified version of the model we consider only two populations ( $n = 2$ ), and examine the change in the frequency of trait  $A$  over a single generation as a function of the frequencies of trait  $E$  in both populations using different niche construction modes. The starting point of each arrow represents the frequencies of trait  $E$  ( $p_1$  and  $p_2$ ) in the two populations.

Both populations have the same arbitrary initial  $A$  frequencies,  $q_1 = q_2 = 0.5$ . The horizontal and vertical components of each arrow (i.e. its projections on the horizontal and vertical axes) represent the change in the frequency of trait  $A$  in both populations,  $\Delta q_1$  and  $\Delta q_2$ , respectively, after one generation.

Clearly, in the absence of niche construction, the frequencies of trait  $E$  have no effect on the spread of trait  $A$ ;  $\Delta q_1 = \Delta q_2$  and they are equal for every  $p_1$  and  $p_2$  (Fig. 8a). When global niche construction is applied (Fig. 8b), the spread of trait  $A$  is influenced by the cultural



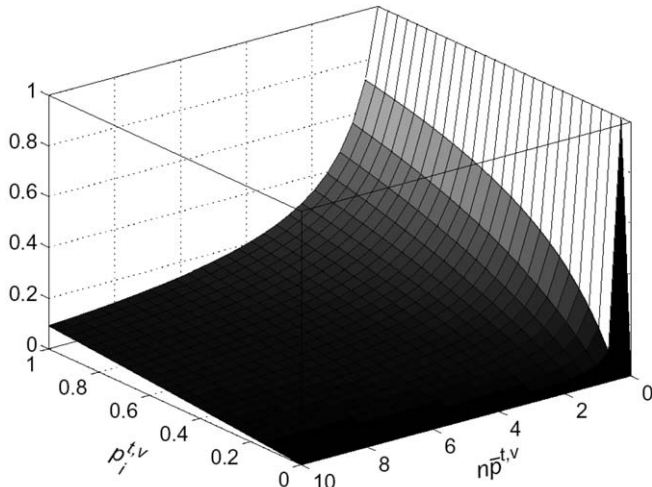


Fig. 7. The effect of local niche construction on the sensitivity of the change in frequency of trait  $A$  in population  $i$  to the change in frequency of trait  $E$  in population  $j$ , relative to the change in frequency of trait  $E$  within population  $i$ . The vertical axis shows values for Eq. (11) while the other two axes show the frequency of trait  $E$  in population  $i$ ,  $p_i$ , and the product of the number of populations and the mean frequency of trait  $E$  across the metapopulation,  $n\bar{p}$ .

background and thus  $\Delta q_1$  and  $\Delta q_2$  vary for different values of  $p_1$  and  $p_2$ . For example, when  $p_1$  and  $p_2$  are low, the horizontal transmission rate is not sufficient to overcome the cost of fertility selection and the frequencies of trait  $A$  in both populations actually go down. Note also that the length of the arrow is the same, where  $p_1 + p_2$  is constant, as all populations experience the same average network weightings and are exposed to the same frequency of trait  $A$ . Furthermore, since in global niche construction both populations are affected similarly by the average level of the cultural background,  $\Delta q_1 = \Delta q_2$ , regardless of  $p_1$  and  $p_2$ .

Only when the local niche construction mode is applied (Fig. 8c), may the change in frequency of trait  $A$  differ between populations. Apparently, as also implied by (7), the spread of trait  $A$  is faster in the population with the higher level of cultural background. In fact, in some cases, we may get opposing dynamics of trait  $A$  in the two populations such that trait  $A$  spreads in one population and declines in the other (see for example the arrow for  $p_1 = 0.8$ ,  $p_2 = 0.1$ ). These findings again demonstrate the *rich-get-richer* phenomenon we have found in our initial analysis, whereby a higher level of trait  $E$  in one population (e.g. population 1 in the case where  $p_1 > p_2$ ), entails a faster spread of trait  $A$  or even determines whether trait  $A$  will spread or not in that population.

#### 4. Discussion

The MPCNC model examines the process of cultural niche construction in a metapopulation, extending previous models of niche construction in an unstructured popula-

tion. Using a novel approach for cultural niche construction, we represent the cultural background as a dynamic social network on which other traits may percolate. This approach fuses two fundamental concepts of cultural evolution (namely, social networks and niche construction) and facilitates the analysis of markedly more realistic social interactions: Social networks, the vehicle of cultural evolution, are not static, but rather change over time, often owing to the evolutionary dynamics of other co-evolving cultural traits. As was demonstrated by our results, this manifestation of cultural niche construction, should not be ignored.

Notably, analysis of our model reveals markedly different dynamics from those observed in an unstructured population facing only a global niche construction process. The spread of trait  $A$  in each population is affected not only by the level of trait  $E$  in that population but also by the level of both traits in the rest of the metapopulation. In particular, we find that introducing local niche construction results in the onset of trait  $A$  transition in each population occurring later at lower levels of trait  $E$ . The contribution of *between* (vs. *within*) population niche construction to this phenomenon has also been validated. Applying this model to the case of development (or education) and fertility control, we find that *it can account for the interesting dynamics previously reported by Bongaarts and Watkins (1996), namely, the onset of the demographic transition in different countries occurring at ever lower levels of development.*

The relative frequency of global and local niche construction, does not appear to have a significant impact on the regions of the  $h$  and  $f$  parameter space in which populations go through the transition in the long term (see Fig. 6). However, for certain  $h$  and  $f$  values, local niche construction yields a slower spread of trait  $A$  in comparison to global niche construction (see, for example, region II in Fig. 6d), preventing some populations from going through the transition in a limited time (e.g. 200 generations). This finding coincides with our intuition that second order processes control fine-tuned details of the system whereas the overall dynamics are not affected.

Finally, our study reveals a number of interesting characteristics associated with local niche construction. For instance, local niche construction can yield different (or even opposing) dynamics in each population, and typically appears to facilitate the rich-get-richer rule. Furthermore, the effect of local niche construction between populations, relative to within a population, is sensitive to the number of populations in the metapopulation,  $n$ .

Interestingly, a second characteristic of the demographic transition is the observation that rich families reduce their fertility earlier and to a greater degree than poor families. To some extent, the analysis presented in this paper can be interpreted as describing semi-isolated subsections of a single population, rather than multiple interacting populations. The resulting dynamics can thus also provide an explanation for this second characteristic.

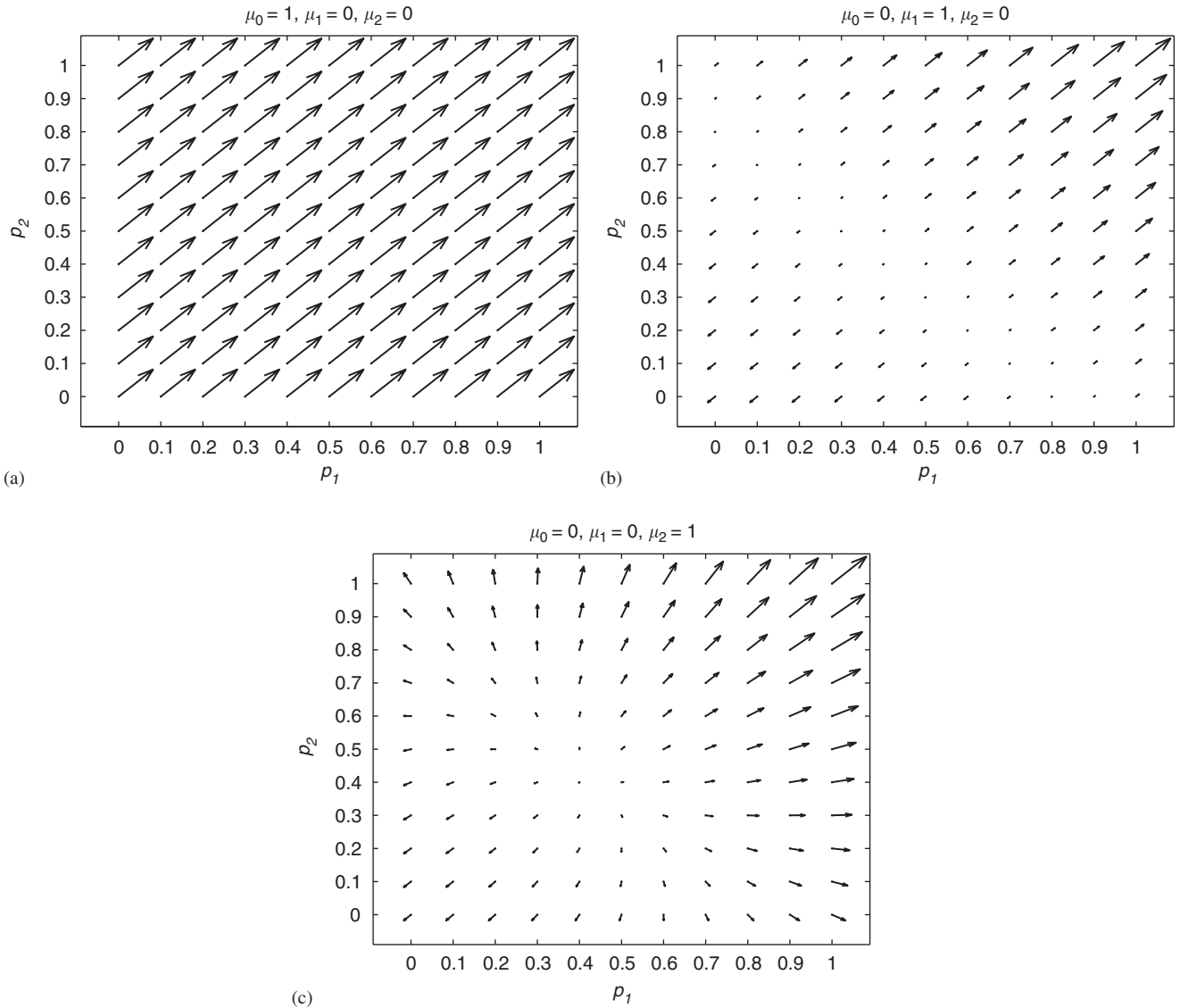


Fig. 8. The change in the frequency of trait  $A$  in two populations over a single generation as a function of the frequency of trait  $E$  in these populations using different modes of cultural niche construction. The origin of each arrow represents the starting frequencies of trait  $E$  in the two populations ( $p_1$  and  $p_2$ ). In both populations,  $b$  (the vertical transmission coefficient of trait  $E$ ) is set to 0.5. The horizontal and vertical components of each arrow (i.e. its projections on the horizontal and vertical axes) represent, respectively, the change in  $q_1$  and  $q_2$  in a single generation. Both populations have the same initial  $A$  frequencies,  $q_1 = q_2 = 0.5$ . The lengths of the arrows in each panel are scaled to fit the image grid.

The MPCNC model can be extended further to embody better the complex social interactions that exist in modern human societies. Bongaarts and Watkins (1996) describe several type of social interactions (the transmission of information and ideas, joint evaluation and social influence), but also several levels of social interaction channels (e.g. local, national and global). A more complex social network that may comprise of several hierarchies can encapsulate some of these concepts and may shed light on the importance of multi-level transmission. Similarly, there may exist more than two interacting traits, and a more elaborate interaction scheme. Furthermore, our model, as most traditional models of niche construction, assumes that the background trait evolves independently and is not affected by the niche it generates. Specifically, we assume

that trait  $E$  is transferred only vertically, and does not percolate across the same social network that it itself creates. Although reasonable, it may be interesting to relax this assumption and allow a significantly more complex model where the evolution of trait  $E$  not only shapes the social network but is also affected by it (as may be the case, for example, in education over the Internet).

The model presented in this paper further assumes that people do not migrate from one population to the other. Clearly, migration can have a strong impact on the resulting dynamics. For example, an unbiased migration (i.e. a process where people migrate randomly from one population to another) may serve as an equalizing force, reducing the variance in the frequency of the cultural traits between populations. To some extent, such dynamics may

be analogous to increasing the coefficient of global niche construction (which depends only on the overall frequency of the cultural background in the metapopulation) while reducing the local niche construction coefficient. Other models may assume biased migration where people are more likely to migrate from large populations (e.g. due to increased fertility) to smaller ones, or from less developed populations to highly developed ones. The effect of such migration schemes could be further examined through an extension of the MPCNC model that embodies this plausible process. The current model also assumes that adopting trait  $E$  does not entail any fitness cost. However, considering the case of development and fertility control, and the expenses associated with acquiring education, applying a fitness cost to the adoption of trait  $E$  may be an additional reasonable extension. In principle, however, a simple cost function should not qualitatively change the resulting dynamics induced by this model but it may slow down the spread of trait  $E$  and consequently may also hinder trait  $A$  transition.

Clearly, as extensive as the model may be, it can still encapsulate only a fraction of the real-world social interaction dynamics. However, we believe that our approach, incorporating both the cultural evolution processes and the evolution of the social network underlying these processes, can contribute to the understanding of central issues concerning the spread of cultural traits in human societies.

## Acknowledgments

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## Appendix A. The model recursions

### A.1. Vertical transmission

After independent vertical transmission of each of  $E/e$  and  $A/a$ , the frequency of the four cultural types in the offspring generation are given by

$$\begin{aligned}
 W_i x_{22,i}^{t,v} = & (1-f)c_{3,i} \left[ b_{3,i} x_{22,i}^{t-1,2} \right. \\
 & + (b_{1,i} + b_{2,i}) x_{22,i}^{t-1} x_{12,i}^{t-1} + b_{0,i} x_{12,i}^{t-1,2} \\
 & + (1-f/2)c_{2,i} \left[ b_{3,i} x_{22,i}^{t-1} x_{21,i}^{t-1} + b_{2,i} x_{22,i}^{t-1} x_{11,i}^{t-1} \right. \\
 & + b_{1,i} x_{21,i}^{t-1} x_{12,i}^{t-1} + b_{0,i} x_{12,i}^{t-1} x_{11,i}^{t-1} \\
 & + (1-f/2)c_{1,i} \left[ b_{3,i} x_{22,i}^{t-1} x_{21,i}^{t-1} + b_{2,i} x_{21,i}^{t-1} x_{12,i}^{t-1} \right. \\
 & + b_{1,i} x_{22,i}^{t-1} x_{11,i}^{t-1} + b_{0,i} x_{12,i}^{t-1} x_{11,i}^{t-1} \\
 & + c_{0,i} \left[ b_{3,i} x_{21,i}^{t-1,2} + (b_{2,i} + b_{1,i}) x_{21,i}^{t-1} x_{11,i}^{t-1} \right. \\
 & \left. \left. + b_{0,i} x_{11,i}^{t-1,2} \right] \right], \quad (\text{A.1})
 \end{aligned}$$

$$\begin{aligned}
 W_i x_{21,i}^{t,v} = & (1-f)(1-c_{3,i}) \left[ b_{3,i} x_{22,i}^{t-1,2} \right. \\
 & + (b_{1,i} + b_{2,i}) x_{22,i}^{t-1} x_{12,i}^{t-1} + b_{0,i} x_{12,i}^{t-1,2} \\
 & + (1-f/2)(1-c_{2,i}) \left[ b_{3,i} x_{22,i}^{t-1} x_{21,i}^{t-1} + b_{2,i} x_{22,i}^{t-1} x_{11,i}^{t-1} \right. \\
 & + b_{1,i} x_{21,i}^{t-1} x_{12,i}^{t-1} + b_{0,i} x_{12,i}^{t-1} x_{11,i}^{t-1} \\
 & + (1-f/2)(1-c_{1,i}) \left[ b_{3,i} x_{22,i}^{t-1} x_{21,i}^{t-1} + b_{2,i} x_{21,i}^{t-1} x_{12,i}^{t-1} \right. \\
 & + b_{1,i} x_{22,i}^{t-1} x_{11,i}^{t-1} + b_{0,i} x_{12,i}^{t-1} x_{11,i}^{t-1} \\
 & + (1-c_{0,i}) \left[ b_{3,i} x_{21,i}^{t-1,2} + (b_{2,i} + b_{1,i}) x_{21,i}^{t-1} x_{11,i}^{t-1} \right. \\
 & \left. \left. + b_{0,i} x_{11,i}^{t-1,2} \right] \right], \quad (\text{A.2})
 \end{aligned}$$

$$\begin{aligned}
 W_i x_{12,i}^{t,v} = & (1-f)c_{3,i} \left[ (1-b_{3,i}) x_{22,i}^{t-1,2} \right. \\
 & + (2-b_{1,i} - b_{2,i}) x_{22,i}^{t-1} x_{12,i}^{t-1} + (1-b_{0,i}) x_{12,i}^{t-1,2} \\
 & + (1-f/2)c_{2,i} \left[ (1-b_{3,i}) x_{22,i}^{t-1} x_{21,i}^{t-1} \right. \\
 & + (1-b_{2,i}) x_{22,i}^{t-1} x_{11,i}^{t-1} \\
 & + (1-b_{1,i}) x_{21,i}^{t-1} x_{12,i}^{t-1} + (1-b_{0,i}) x_{12,i}^{t-1} x_{11,i}^{t-1} \\
 & + (1-f/2)c_{1,i} \left[ (1-b_{3,i}) x_{22,i}^{t-1} x_{21,i}^{t-1} \right. \\
 & + (1-b_{2,i}) x_{21,i}^{t-1} x_{12,i}^{t-1} \\
 & + (1-b_{1,i}) x_{22,i}^{t-1} x_{11,i}^{t-1} + (1-b_{0,i}) x_{12,i}^{t-1} x_{11,i}^{t-1} \\
 & + c_{0,i} \left[ (1-b_{3,i}) x_{21,i}^{t-1,2} + (2-b_{2,i} - b_{1,i}) x_{21,i}^{t-1} x_{11,i}^{t-1} \right. \\
 & \left. \left. + (1-b_{0,i}) x_{11,i}^{t-1,2} \right] \right], \quad (\text{A.3})
 \end{aligned}$$

$$\begin{aligned}
 W_i x_{11,i}^{t,v} = & (1-f)(1-c_{3,i}) \left[ (1-b_{3,i}) x_{22,i}^{t-1,2} \right. \\
 & + (2-b_{1,i} - b_{2,i}) x_{22,i}^{t-1} x_{12,i}^{t-1} + (1-b_{0,i}) x_{12,i}^{t-1,2} \\
 & + (1-f/2)(1-c_{2,i}) \left[ (1-b_{3,i}) x_{22,i}^{t-1} x_{21,i}^{t-1} \right. \\
 & + (1-b_{2,i}) x_{22,i}^{t-1} x_{11,i}^{t-1} \\
 & + (1-b_{1,i}) x_{21,i}^{t-1} x_{12,i}^{t-1} + (1-b_{0,i}) x_{12,i}^{t-1} x_{11,i}^{t-1} \\
 & + (1-f/2)(1-c_{1,i}) \left[ (1-b_{3,i}) x_{22,i}^{t-1} x_{21,i}^{t-1} \right. \\
 & + (1-b_{2,i}) x_{21,i}^{t-1} x_{12,i}^{t-1} \\
 & + (1-b_{1,i}) x_{22,i}^{t-1} x_{11,i}^{t-1} + (1-b_{0,i}) x_{12,i}^{t-1} x_{11,i}^{t-1} \\
 & + (1-c_{0,i}) \left[ (1-b_{3,i}) x_{21,i}^{t-1,2} \right. \\
 & + (2-b_{2,i} - b_{1,i}) x_{21,i}^{t-1} x_{11,i}^{t-1} + (1-b_{0,i}) x_{11,i}^{t-1,2} \left. \right] \right], \quad (\text{A.4})
 \end{aligned}$$

where  $W_i = 1 - f(x_{22,i}^{t-1} + x_{12,i}^{t-1}) = 1 - f q_i^{t-1}$ . Throughout, we consider the simple case where  $b_{3,i} = c_{3,i} = 1$  and  $b_{0,i} = c_{0,i} = 0$  for all populations. Also, we assume that, for population  $i$ ,  $b_{1,i} = b_{2,i} = b_i$  and thus any bias in vertical transmission of trait  $E$  is specific to each population,  $i$ ,

while assuming that  $c_{1,i} = c_{2,i} = c = 0.5$ , so vertical transmission of trait  $A$  is unbiased in all populations.

A.2. Horizontal transmission

After horizontal transmission of trait  $A$ , the frequencies of the four cultural types in population  $i$  at generation  $t + 1$  are given by

$$x_{22,i}^t = x_{22,i}^{t,v} + \frac{1}{n} \sum_{j=1}^n e_{ij}^t h(x_{12,j}^{t,v} + x_{22,j}^{t,v}) x_{21,i}^{t,v} \times [1 + \psi(2(x_{22,i}^{t,v} + x_{12,i}^{t,v}) - 1)], \tag{A.5}$$

$$x_{21,i}^t = x_{21,i}^{t,v} - \frac{1}{n} \sum_{j=1}^n e_{ij}^t h(x_{12,j}^{t,v} + x_{22,j}^{t,v}) x_{21,i}^{t,v} \times [1 + \psi(2(x_{22,i}^{t,v} + x_{12,i}^{t,v}) - 1)], \tag{A.6}$$

$$x_{12,i}^t = x_{12,i}^{t,v} + \frac{1}{n} \sum_{j=1}^n e_{ij}^t h(x_{12,j}^{t,v} + x_{22,j}^{t,v}) x_{11,i}^{t,v} \times [1 + \psi(2(x_{22,i}^{t,v} + x_{12,i}^{t,v}) - 1)], \tag{A.7}$$

$$x_{11,i}^t = x_{11,i}^{t,v} - \frac{1}{n} \sum_{j=1}^n e_{ij}^t h(x_{12,j}^{t,v} + x_{22,j}^{t,v}) x_{11,i}^{t,v} \times [1 + \psi(2(x_{22,i}^{t,v} + x_{12,i}^{t,v}) - 1)], \tag{A.8}$$

where

$$e_{ij}^t = \mu_0 K^2 + \mu_1 \left[ \frac{1}{n} \sum_{j=1}^n (x_{22,j}^{t,v} + x_{21,j}^{t,v}) \right]^2 + \mu_2 (x_{22,i}^{t,v} + x_{21,i}^{t,v})(x_{22,j}^{t,v} + x_{21,j}^{t,v}) = \mu_0 K^2 + \mu_1 (\bar{p}^{t,v})^2 + \mu_2 p_i^{t,v} p_j^{t,v}. \tag{A.9}$$

A.3. Statistical association between the traits

The changes in the frequencies of traits  $E$  and  $A$  between generations  $t - 1$  and  $t$  in population  $i$  are given by (dropping the superscript  $t - 1$  on the right-hand side)

$$\Delta p_i = p_i(1 - p_i)(2b_i - 1) - \frac{D_i}{W_i} f[b_i - p_i(2b_i - 1)] \tag{A.10}$$

and

$$\Delta q_i = (1 - \Gamma) \frac{q_i(1 - q_i)}{W_i} [2c(1 - f/2) - 1] + \Gamma(1 - q_i), \tag{A.11}$$

respectively, where  $\Gamma = \frac{1}{n} \sum_{j=1}^n (e_{ij}^t q_j^{t,v}) h[1 + \psi(2q_i^{t,v} - 1)]$  and  $D_i = x_{22,i} - p_i q_i$  denotes the statistical association between the two traits in population  $i$ .

The change in the mean frequency of traits  $E$  and  $A$  in a population, between generations  $t$  and  $t + 1$ ,

is given by

$$\Delta \bar{p} = \frac{1}{n} \sum_{i=1}^n \Delta p_i, \tag{A.12}$$

and

$$\Delta \bar{q} = \frac{1}{n} \sum_{i=1}^n \Delta q_i, \tag{A.13}$$

respectively.

If, at generation  $t = 0$ , there is no statistical association between traits  $E$  and  $A$  in population  $i$  (i.e.  $D_i^{t=0} = 0$ ), then there is no change in the statistical association over time ( $\Delta D_i = 0$ ) and  $D_i^t$  remains 0. This can be shown by noting that when  $D_i^t = 0$ , the frequencies of the four cultural types are given by

$$\begin{aligned} x_{22,i}^t &= p_i^t q_i^t, \\ x_{21,i}^t &= p_i^t(1 - q_i^t), \\ x_{12,i}^t &= q_i^t(1 - p_i^t), \\ x_{11,i}^t &= (1 - p_i^t)(1 - q_i^t). \end{aligned} \tag{A.14}$$

Substituting the right-hand sides of (A.14) into recursions (A.1)–(A.8) reveals that  $D_i^{t+1} = 0$  and thus  $\Delta D_i = 0$ . This makes intuitive sense as the model assumes that vertical transmission of each trait is independent of the other, while the horizontal transmission of trait  $A$  may be affected by the frequency of trait  $E$  in the population, but is not affected by whether individuals demonstrating trait  $A$  exhibit trait  $E$  or not. Also note that while  $D_i = 0$ , a statistical association between traits  $E$  and  $A$  over the metapopulation may result from the Wahlund effect (Wahlund, 1928). This statistical association, or covariance, is defined as  $D_{metapopulation} = (\sum_i^n p_i - \bar{p})(\sum_i^n q_i - \bar{q})$  and is accounted for in the model (see Eqs. (1)–(6)) by keeping track of  $p_i$  and  $q_i$  for each population,  $i$ .

For simulations of the model, we make the simplifying assumption that at generation  $t = 0$ ,  $D_i^{t=0} = 0$ . Thus, there is never a statistical association between the two traits and so, given (A.14), recursions (A.1)–(A.8) can be collapsed to recursions for the frequency of traits  $E$  and  $A$ , over time, given by Eqs. (1)–(6). Numerical analysis confirmed that recursions in (A.1)–(A.8) and recursions in (1)–(6) generate the same results when  $D_i^{t=0} = 0$ .

Appendix B. Local stability of equilibria

Here, we consider, for population  $i$ , the four ‘corner’ equilibrium states, denoted by  $Q_i(0, 0, 0)$ ,  $Q_i(1, 0, 0)$ ,  $Q_i(0, 1, 0)$  and  $Q_i(1, 1, 0)$  (where  $Q_i(\hat{p}_i, \hat{q}_i, D_i)$  denotes the equilibrium state). From (A.10) and (A.11), the equilibrium state  $Q_i(0, 0, 0)$  may exist if the mean frequency of trait  $A$  in the metapopulation,  $\bar{q} = \frac{1}{n} \sum_{j=1}^n q_j = 0$ . If  $\bar{q} > 0$  and  $\bar{p} = 0$ , the equilibrium state  $Q_i(0, 0, 0)$  requires that  $K^2 \mu_0 = 0$ . Furthermore, if  $\bar{q} > 0$  and, in addition, the mean frequency

of trait  $E$  in the metapopulation  $\bar{p} > 0$ , the equilibrium state  $Q_i(0, 0, 0)$  requires that  $\mu_1 = K^2\mu_0 = 0$ .

From (A.10) and (A.11), the equilibrium state  $Q_i(1, 0, 0)$  may exist if  $\bar{q} = 0$ . If  $\bar{q} > 0$ , the equilibrium state  $Q_i(1, 0, 0)$  requires that  $K^2\mu_0 = \mu_1 = 0$ . Furthermore, if  $\bar{q} > 0$  and, in addition, there is a population  $j$ , for which  $p_j > 0$  and  $q_j > 0$ , the equilibrium state  $Q_i(1, 0, 0)$  requires that  $\mu_2 = K^2\mu_0 = \mu_1 = 0$ . Finally, from (A.10) and (A.11), there are two corner equilibrium states given by  $Q_i(0, 1, 0)$  and  $Q_i(1, 1, 0)$ . When analyzing the local stability of each of the four corner equilibria in population  $i$ , we assume that the conditions required for each equilibrium to exist are satisfied and that all other populations,  $j \neq i$ , are at an equilibrium state.

$Q_i(0, 0, 0)$  and  $Q_i(1, 0, 0)$  are unstable and invaded by trait  $E$  and by trait  $e$  if

$$b_i > 1/2 \tag{B.1}$$

and

$$b_i < 1/2, \tag{B.2}$$

respectively.

If inequalities (B.1) or (B.2) are violated, the respective equilibrium states,  $Q_i(0, 0, 0)$  and  $Q_i(1, 0, 0)$ , are unstable and invaded by trait  $A$  when

$$2c(1 - f/2) > 1/[1 + (K^2\mu_0 + \hat{p}^2\mu_1 + \hat{p}_i^2\mu_2)h(1 - \psi)]. \tag{B.3}$$

Meanwhile, the equilibrium states  $Q_i(0, 1, 0)$  and  $Q_i(1, 1, 0)$  are unstable and invaded by trait  $E$  and by trait  $e$ , respectively, if the respective inequalities, (B.1) and (B.2), are satisfied. If inequalities (B.1) and (B.2) are violated, the respective equilibrium states,  $Q_i(0, 1, 0)$  and  $Q_i(1, 1, 0)$ , are unstable and invaded by trait  $a$  when

$$2(1 - c) \frac{(1 - f/2)}{1 - f} > 1 / \left[ 1 - \frac{1}{n} \sum_{j=1}^n (K^2\mu_0 + \hat{p}_j^2\mu_1 + \hat{p}_i\hat{p}_j\mu_2)q_j h(1 + \psi) \right] \tag{B.4}$$

Inequality (B.3) can be rearranged to derive the line

$$f = \frac{2h[\mu_1\hat{p}^2 + \mu_2\hat{p}_i^2](1 - \psi)}{1 + h[\mu_1\hat{p}^2 + \mu_2\hat{p}_i^2](1 - \psi)}, \tag{B.5}$$

under which trait  $A$  may invade from either equilibrium states  $Q_i(0, 0, 0)$  or  $Q_i(1, 0, 0)$ , where  $\mu_0 = 0$  and  $c = 1/2$ .

### References

Bongaarts, J., Watkins, S., 1996. Social interactions and contemporary fertility transitions. *Popul. Dev. Rev.* 22 (4), 639–682.

Borgerhoff Mulder, 1998. The demographic transition: are we any closer to an evolutionary explanation? *Trends Ecol. Evol.* 13, 266–270.

Cavalli-Sforza, L., Feldman, M., 1981. *Cultural Transmission and Evolution: A Quantitative Approach*. Princeton University Press, Princeton, NJ.

Cavalli-Sforza, L., Feldman, M., Chen, K., Dornbusch, S., 1982. Theory and observation in cultural transmission. *Science* 4567 (218), 19–27.

Cleland, J., Wilson, C., 1987. Demand theories of the fertility transition: an iconoclastic view. *Popul. Stud.* 41, 5–30.

Coale, A., 1974. The history of the human population. *Sci. Am.* 231, 40–51.

Ihara, Y., Feldman, M., 2004. Cultural niche construction and the evolution of small family size. *Theor. Popul. Biol.* 65, 105–111.

Kendal, J., Ihara, Y., Feldman, M., 2005. *Cultural Niche Construction with Application to Fertility Control: A Model for Education and Social Transmission of Contraceptive Use*. Morrison Institute for Population and Resource Studies, Working Paper 102.

Laland, K., Odling-Smee, F., Feldman, M., 1996. The evolutionary consequences of niche construction: a theoretical investigation using two-locus theory. *J. Evol. Biol.* 9, 293–316.

Laland, K., Odling-Smee, F., Feldman, M., 2001. Cultural niche construction and human evolution. *J. Evol. Biol.* 14, 22–33.

Lewontin, R., 1983. Gene, organism, and environment. In: Bendall, D. (Ed.), *Evolution from Molecules to Men*. Cambridge University Press, Cambridge.

Mace, R., 1996. When to have another baby: a dynamic model of reproductive decision-making and evidence from gabbra pastoralists. *Ethol. Sociobiol.* 17, 263–273.

Mace, R., 2000. An adaptive model of human reproductive rate where wealth is inherited: why people have small families. In: Cronk, L., Chagnon, N., Irons, W. (Eds.), *Adaptation and Human Behaviour*. Aldine de Gruyter, NY, pp. 261–282.

Notestein, F., 1953. Economic problems of population change, In: *Proceedings of the Eighth International Conference of Agricultural Economists*. Oxford University Press, London, pp. 13–31.

Odling-Smee, F., Laland, K., Feldman, M., 2003. *Niche Construction: The Neglected Process in Evolution*. Princeton University Press, Princeton.

Wahlund, S., 1928. Zusammensetzung von populationen und korrelationserscheinungen vom standpunkt der vererbungslehre aus betrachtet. *Hereditas* 11, 65–106.