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Cultural niche construction with application to fertility control: A model for education and social transmission of contraceptive use

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In memory of our colleague and friend Freddy Christiansen

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ABSTRACT

The evolution of a cultural trait may be affected by niche construction, or changes in the selective environment of that trait due to the inheritance of other cultural traits that make up a cultural background. This study investigates the evolution of a cultural trait, such as the acceptance of the idea of contraception, that is both vertically and horizontally transmitted within a homogeneous social network. Individuals may conform to the norm, and adopters of the trait have fewer progeny than others. In addition, adoption of this trait is affected by a vertically transmitted aspect of the cultural background, such as the preference for high or low levels of education. Our model shows that such cultural niche construction can facilitate the spread of traits with low Darwinian fitness while providing an environment that counteracts conformity to norms. In addition, niche construction can facilitate the 'demographic transition' by making reduced fertility socially accepted.

1. Introduction

Niche construction is the "modification of selective environments by organisms" (Laland et al., 2016, p. 191 see also Lewontin, 1983, 2000; Odling-Smee, 1988; Odling-Smee et al., 1996; Laland et al., 2000, 2001 and Odling-Smee et al., 2003). This process occurs in a wide variety of taxa; for example, cyanobacteria release oxygen into their environments, earthworms alter the chemical composition of their soil, termites can build mounds, and chimpanzees can build tools to pull termites out of their mounds (Suzuki et al., 1995). In the context of a constructed niche, the evolution of biological traits and/or cultural traits may be very different from their evolution in the absence of the niche (Feldman, 2003; Ihara and Feldman, 2004; Feldman, 2008; Brown and Feldman, 2009; Kendal, 2011; Laland and O'Brien, 2011; Fogarty and Creanza, 2017).

Humans have engaged in niche construction to an enormous extent. Not only do we construct much of our physical niche space, including shelters, modes of transportation, institutions, and more, but we also display a great deal of cultural niche construction, defined as "the process by which certain evolving cultural traits form a cultural niche that affects the evolution of other genetic and cultural traits" (Borenstein et al., 2006, p. 92). For example, the invention of fire and the practice of cooking food served as a cultural niche that gave rise to profound changes in the human digestive tract (Wrangham, 2009). The socially learned practice of dairy farming led to the spread of genes implicated in lactase persistence (Beja-Pereira et al., 2003). Tanaka et al. (2002) show how the cultural transmission of 'careful' or 'risky' behavior can act as a cultural background influencing the rate of disease transmission.

In another example, the preference, or not, for sons over daughters may provide a cultural background, influencing the preference for sex-selective abortion and also the sex ratio at birth (SRB) in China (Laland et al., 1995; Li et al., 1999a,b, 2000a; Lipatov et al., 2011; Fogarty and Feldman, 2012; Liu and Feldman, 2021). Components of the cultural background for a particular trait may themselves be subject to evolution that is influenced by other cultural traits. For example, the preference for sons over daughters is typically associated with high fertility and the prevalence of virilocal over uxorilocal marriage (Li et al., 2000a,b, 2003; Lipatov et al., 2008; Brown and Feldman, 2009). Furthermore, the greater prevalence of virilocal than uxorilocal marriage systems is thought to be associated with cultural factors such as a patriarchal family system and economic factors including high bride-cost and dowry, high labour demand, the reliability of old-age support and earning potential of a son versus that of a son-in-law (Li et al., 2000a; Bhattacharjya et al., 2008; Lipatov et al., 2008; Brown and Feldman, 2009; Lipatov et al., 2011).

Demographic transitions may also be influenced by the social spread of cultural norms. A norm of low fertility may spread from

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individuals in high socio-economic strata to those in lower socio-economic strata. The coevolution of age-structure and socio-economic structure will be strongly influenced by the form and strength of cultural transmission of attitudes regarding family size as well as the societal milieu in which the attitudes are formed (Fogarty and Feldman, 2012; Fogarty et al., 2013, 2019).

Optimality models have often been used to analyze the evolution of fertility-reducing behaviors (Rogers, 1990, 1995; Kaplan et al., 1995; Mace, 1996, 2000; Bhattacharjya et al., 2008). However, recent models and reviews of fertility control have acknowledged that rather than individuals making entirely rational, optimal decisions, limited only by budget constraints, fertility control can be affected by socially learned information and also by social influence (Cleland and Wilson, 1987; Pollak and Watkins, 1993; Bongaarts and Watkins, 1996; Montgomery and Casterline, 1996; Borgerhoff Mulder, 1998; Montgomery et al., 2001; Behrman et al., 2002). The term social influence is commonly used to define social processes such as conformity that can affect an individual's behavioral preferences and is often considered separately from the probability of social learning (Montgomery and Casterline, 1996; Henrich and Boyd, 1998; Wakano and Aoki, 2007; Morgan et al., 2012; Kandler and Laland, 2013; Muthukrishna et al., 2016).

Gene-culture coevolutionary theory and cultural evolutionary theory (Cavalli-Sforza and Feldman, 1973, 1976, 1981; Boyd and Richerson, 1985; Feldman et al., 2013), derived from classical population genetics theory, provides a suitable framework to study fertility control. It considers evolutionary dynamics as processes of frequency change, necessary to capture the effects of social learning and social influence, while defining transmission mechanisms and selection coefficients to incorporate any economic constraints. Unlike most optimality models, this approach has the advantage that it focuses on the detailed causes of frequency change rather than a maximization of functions chosen a priori by the investigator (Feldman, 2001; Spencer and Feldman, 2005).

In a recent analysis of worldwide total fertility rates (TFR), level of education (mean school years for females) showed a stronger negative correlation with TFR than per capita GDP, contraceptive prevalence rate, and strength of family planning programs (Götmark and Andersson, 2020). Although it is difficult to establish a causal chain between these societal markers, theoretical models that assume specific relationships among them can be helpful. In particular, in the cultural niche construction framework, the presence or level of one aspect of a culture – in this case, level of education – can influence the transmission and spread of another cultural trait, such as fertility control.

Ihara and Feldman (2004) developed cultural evolutionary models to consider the effect of cultural niche construction on the mode of transmission of a second cultural trait. In particular, they focused on how preferences for a high or low level of education (i.e., 'background predisposition') could affect the evolution of small family size (i.e., 'fertility-reducing preference'). In their models, niche construction affects the selective environment of the latter trait by influencing its mode of transmission. Specifically, the mean level of education in the population is assumed to affect the probability that traits are transmitted obliquely–e.g., from teachers to students – instead of vertically, from parents to offspring. Of the individuals who transmit traits obliquely, individuals with fewer offspring are overrepresented relative to those with more offspring, because, for example, the former can allocate more time and resources to achieving high status social roles (Richerson and Boyd, 1989; Nakajima and Aoki, 2002). The results of this model showed that "even a slight overrepresentation of those with fewer offspring can drive the evolution of small family size, provided that the rate of oblique transmission depends strongly on the cultural background" (Ihara and Feldman, 2004, p. 105).

Here, we consider the effect of cultural niche construction on the rate of horizontal and oblique transmission of a cultural trait, such as the acceptance of the idea of using some form of fertility control or contraceptive. In addition to vertical transmission (parent to offspring) and oblique transmission (parental generation to offspring generation), these traits may be transmitted through horizontal transmission (among individuals in the same generation), for example, through peer groups or social networks (Montgomery and Casterline, 1996; Montgomery et al., 2001; Behrman et al., 2002; Colleran and Mace, 2015). We also investigate the effects of conformity to the norm on the evolution of a cultural trait. Conformity constrains the adoption of a rare trait but facilitates the adoption of popular traits (Boyd and Richerson, 1985; Moscovici, 1985; Montgomery and Casterline, 1996; Denton et al., 2020, 2021). We also consider the evolution of traits that may have relatively low 'Darwinian fitness' (as defined by Cavalli-Sforza and Feldman (1981)). For example, parents who accept the idea of contraception may typically have fewer offspring than those who do not. Cultural evolutionary theory provides a natural framework to investigate this evolutionary conundrum (Mace, 2014).

We consider a cultural background that consists of a vertically transmitted cultural trait, using the example of the preference for a high or low level of school education.[1] While there may be many inter-related factors influencing the adoption of a high (or low) level of education, we focus on the effects of a cultural niche that is constructed through vertical transmission.[2] Many hypotheses have been proposed to explain the well established negative relationship between level of education and fertility and also the positive relationship between the level of education and contraceptive use Chaudhury, 1984; Heaton and Forste, 1998; Koc, 2000; Waiz, 2000; Capo-chichi and Juarez, 2001; Basu, 2002; Murthi, 2002; McNay et al., 2003; Baksu et al., 2005; Brice, 2018. Here, we focus on the effect of education on the rate of horizontal or oblique transmission.

Features of the cultural background, such as the average level of education in the population, are likely to influence the rate of horizontal transmission of traits in a number of ways. First, members of a social network may be more likely to be exposed to new ideas taught at school, including methods of contraception, if the average level of education is high rather than low (Cleland and Wilson, 1987; Colleran et al., 2014). Second, education may enhance the fidelity of information transmission; for example, literacy may allow information to spread by written word with a lower mutation rate than by word of mouth. Third, the level of education is often positively related to wealth (Rogers, 1995; Mace, 1998, 2000). Wealthy, educated populations may be likely to enhance the rate of non-vertical transmission of traits by using communication infrastructures such as a telephone network that cannot be afforded in poorer populations. Furthermore, the spread of traits such as the use of contraception may be facilitated in wealthy populations that have access to healthcare (Murthi, 2002), which can provide individuals with the option to use contraceptives. Healthcare may also reduce child mortality and thus increase the preference for the use of fertility control.

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[1] 'High' and 'low' levels of education simply refer to the amount of formal school education received by the child.

[2] Note that some costs or economic constraints associated with the adoption of a high (or low) level of education may be assumed to be subsumed within the coefficient of vertical transmission.

Table 1
Cultural Transmission of E, e, A, a.

Type of mating pair	Offspring	
Mother ×Father	E	e
$E \times E$	b_3	$1 - b_3$
$E \times e$	b_2	$1 - b_2$
$e \times E$	b_1	$1 - b_1$
$e \times e$	b_0	$1 - b_0$
	A	a
$A \times A$	c_3	$1 - c_3$
$A \times a$	c_2	$1 - c_2$
$a \times A$	c_1	$1 - c_1$
$a \times a$	c_0	$1 - c_0$

2. The model

2.1. Model without viability selection

The model considers two cultural traits. The first cultural trait, $\boldsymbol{E}$, provides a cultural background or niche that may affect the evolution of the second cultural trait, $\boldsymbol{A}$. There are two forms of each trait, E and e and A and a. The frequencies of individuals of the four cultural types EA, Ea, eA, and ea are given by x_1, x_2, x_3, and x_4, respectively. The frequencies of types E and A are given by $p = x_1 + x_2$ and $q = x_1 + x_3$, respectively.

The cultural niche, $\boldsymbol{E}$, may represent the level of education in a human population with E representing a high level of education and e representing a low level of education. Offspring inherit E or e from their parents with probabilities b_i and $1 - b_i$, respectively, as shown in the upper half of Table 1 (where $0 \leq b_1 \leq 1$ and $i = 0, 1, 2, 3$ distinguish the mating pair types (mother-father) ee, eE, Ee, and EE, respectively). In our analysis, we assume that $b_3 = 1$ and $b_0 = 0$. Then, if $b_1 + b_2 > 1$, vertical transmission bias favors E over e, whereas if $b_1 + b_2 < 1$, it favors e over E.

The second cultural trait, $\boldsymbol{A}$, also has two variants, A and a, representing the acceptance or non-acceptance, respectively, of the idea of contraception. As in Ihara and Feldman (2004), we assume that the fertility of a mating pair decreases as the number of individuals with variant A increases from 0 to 1 to 2, so that the relative numbers of offspring for the mother-father pairs AA, Aa, aA, and aa are, respectively, $1 - f$, $1 - f/2$, $1 - f/2$, and 1 (where $0 \leq f \leq 1$). A is transmitted horizontally within the offspring generation. However for this process to occur, A must be present in the offspring generation. Thus, prior to horizontal transmission, it is assumed that states A and a are vertically transmitted from parents to offspring with probabilities c_i and $1 - c_i$, respectively (where $0 \leq c_i \leq 1$), as shown in the lower half of Table 1. The frequencies x_i^v ($i = 1, 2, 3, 4$) after vertical transmission are shown in Appendix A. Similar to the top half of Table 1 with $b_0, \ldots, b_3$, we assume throughout our analysis that $c_3 = 1$ and $c_0 = 0$; if $c_1 + c_2 > 1$, vertical transmission bias favors A over a; and if $c_1 + c_2 < 1$, vertical transmission bias favors a over A.

After vertical transmission of trait $\boldsymbol{A}$, type A is transmitted horizontally within the offspring generation. The rate at which individuals acquire A through non-vertical transmission, α, is dependent, in part, on a coefficient of horizontal transmission of A, denoted by h, and the frequency of A in the offspring generation $q^v = x_1^v + x_3^v$. α is also affected by the frequency of type E in the offspring generation, p^v, with a magnitude determined by the niche construction parameter, γ.[3] Further, it is assumed that α is affected by conformity to the norm, represented by the function $1 + \psi(2q^v - 1)$. Thus, for positive values of the conformity coefficient, ψ, horizontal transmission of A is reduced when $q^v < 1/2$ and enhanced when $q^v > 1/2$. Then after horizontal transmission, the vector of frequencies in the offspring generation, $\boldsymbol{x}' = (x_1', x_2', x_3', x_4')$, is given by

$$\boldsymbol{x}' = \boldsymbol{H}\boldsymbol{x}^v, \tag{1}$$

where the matrix $\boldsymbol{H}$ is

$$\boldsymbol{H} = \begin{pmatrix} 1 & \alpha & 0 & 0 \\ 0 & 1-\alpha & 0 & 0 \\ 0 & 0 & 1 & \alpha \\ 0 & 0 & 0 & 1-\alpha \end{pmatrix}, \tag{2a}$$

with

$$\alpha = hq^v(1 + \gamma p^v)[1 + \psi(2q^v - 1)]. \tag{2b}$$

We assume that $0 \leq h \leq 1$ and $0 \leq \psi \leq 1$. In addition, to ensure that $\alpha \leq 1$ even when q^v and p^v are at their maxima ($q^v = p^v = 1$), we assume that $h(1+\gamma)(1+\psi) \leq 1$. The recursion (1) computes the frequencies of the four 2-trait phenotypes at the point of offspring reproduction in terms of the frequencies at the parental point of reproduction.

In α, the term hq^v can be conceptualized as the probability that an individual accepts the idea of contraception after encountering an individual who has accepted this idea, i.e., who has type A after vertical transmission (which occurs with probability q^v). A value of h less than 1 indicates imperfect horizontal transmission of A. Here, we do not consider horizontal transmission of type a, because our focus is on how acceptance of the idea of contraception may evolve. In α, the term $(1 + \gamma p^v)$ pertains to the enhanced tendency – above the standard, 1 – to adopt type A if there is a non-zero frequency of type E ($p^v > 0$) as well as niche construction ($\gamma > 0$). Finally, $1 + \psi(2q^v - 1)$ is the conformity function in the absence of other factors. These three terms are multiplied, rather than added, together because we assume these processes occur independently of one another.

For simplicity, recall that we focus on the case where $b_3 = 1$, $b_0 = 0$, $c_3 = 1$, and $c_0 = 0$. The change in the frequencies of E and A between generations are given by

$$\Delta p = p(1-p)(b_1+b_2-1) - \frac{D}{W} f \left[\frac{b_1 + b_2}{2} - (b_1 + b_2 - 1)p \right] \tag{3a}$$

and

$$\Delta q = (1-\alpha)\frac{q(1-q)}{W} \left[(c_1 + c_2)\left(1 - \frac{f}{2}\right) - 1 \right] + \alpha(1-q), \tag{3b}$$

respectively, where the cultural disequilibrium between the two traits, $D = x_1x_4 - x_2x_3$, is a measure of their statistical association. The mean fitness of the population is $W = 1 - fq$. The difference equations (3a) and (3b) are obtained by using the expressions for x_i^v (after vertical transmission) in Appendix A. We compute $p^v = x_1^v + x_2^v$ and $q^v = x_1^v + x_3^v$ and insert them into the expression for α in Eq. (2b). Then, for example, $\Delta q = x_1' + x_3' - x_1 - x_3 = q^v + \alpha(1 - q^v) - q$ (from Eq. (1)), and completing the algebra gives (3b). Eq. (3a) is obtained similarly, noting that $x_1' + x_2' = p'$ and $x_1^v + x_2^v = p^v$ (again from Eq. (1)). Note that the parameters b_1 and b_2 enter into Eqs. (3a) and (3b) only through their sum, $b_1 + b_2$. The same is true for the parameters c_1 and c_2. From (3b), for an equilibrium with $q \neq 0, 1$ (i.e., a polymorphism A, a) to exist (with $\alpha > 0$), it is necessary that $(c_1 + c_2)(1 - f/2) < 1$.

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[3] Note that we focus on the niche constructive effects of the mean level of education in the population rather than effects of the level of education adopted by each individual.

From Eqs. (1) and (2),

$$D' = x_1'x_4' - x_2'x_3' = (1-\alpha)D^v, \tag{3c}$$

where $D^v = x_1^v x_4^v - x_2^v x_3^v$. Referring to the expressions in Appendix A for x_i^v, and carrying out the algebra, we see that if $D = x_1x_4 - x_2x_3 = 0$ then also $D^v = 0$. Thus $D = 0$ is an equilibrium of the complete dynamical system, although we cannot show that it is the only equilibrium. Note that if $D = 0$ at equilibrium, then from (3a) that equilibrium must lie on a boundary where $\hat{p} = 0$ or $\hat{p} = 1$, i.e., where allele e is fixed or allele E is fixed, respectively. Numerical analysis of recursions (3a, b, c) suggests that D remains very small throughout most of the evolutionary trajectory.

2.2. Model with viability selection

The average level of education is in general positively correlated with other measures of development, including income and life expectancy (U.N.D.P., 1990; Bongaarts and Watkins, 1996). Here, we assume that, in addition to the parameter α, the frequency p of type E affects the viability of individuals. Following Ihara and Feldman (2004), we assume that the proportion of juveniles that die before they reach reproductive age is $1-v_0(1+v_1p)$ (where $0 < v_1 < 1$ and $0 < v_0 < 1/(1+v_1)$). If all individuals are type e and $p = 0$, then this proportion is $1 - v_0$. The relative mortality of the population, m, is given by

$$m = \frac{1 - v_0(1+v_1p)}{1 - v_0}, \tag{4}$$

where $0 < m < 1$ and m is a decreasing function of p.

3. Results

3.1. Results without viability selection

The first term of (3b) represents the change in the frequency of A that results from vertical transmission and fertility selection. Recall that in the absence of other processes, vertical transmission from parents to offspring is unbiased if $c_1+c_2 = 1$, biased to favor the transmission of A over a if $c_1 + c_2 > 1$, and biased to favor the transmission of a over A if $c_1 + c_2 < 1$. The second term of (3b) represents the change in the frequency of A that results from horizontal transmission. There is no change in the frequency of A if $q = 0$ or $q = 1$, since

$$q^v = q\left\{\frac{1-q}{W}\left[(c_1+c_2)\left(1-\frac{f}{2}\right) - 1\right] + 1\right\} \tag{5}$$

and α has a factor of q^v.

Below, we explore the local stability of the four 'corner' equilibrium states for $(\hat{p}, \hat{q})$, corresponding to $\hat{x}_1 = 1$, $\hat{x}_2 = 1$, $\hat{x}_3 = 1$, and $\hat{x}_4 = 1$, i.e., fixation on EA, Ea, eA, and ea, respectively. In Section 3.1.1, we investigate the case where $\gamma = 0$ (no niche construction) and in Section 3.1.2 we investigate the case where $\gamma > 0$.

3.1.1. Local stability without niche construction ($\gamma = 0$)

If $\gamma = 0$ then there is no niche construction, meaning that the spread of variants A and a is not affected by the levels of education E and e. Thus, the change in the frequency of A over one generation, Δq in Eq. (3b), does not depend on p, the frequency of type E.

In this case, we would expect that invasion by A of the equilibrium $\hat{x}_4 = 1$ (all ea), occurs under the same conditions as invasion by A of the equilibrium $\hat{x}_2$ (all Ea). Suppose that we start near the equilibrium $\hat{x}_4 = 1$ (all ea), and assume that $b_1 + b_2 < 1$ so that vertical transmission bias favors e over E and therefore E will not invade. Then this equilibrium is unstable, meaning that A invades, if

$$(c_1+c_2)\left(1-\frac{f}{2}\right) > \frac{1}{1+h(1-\psi)}. \tag{6}$$

Similarly, suppose we start near the equilibrium $\hat{x}_2 = 1$ (all Ea) and assume that $b_1 + b_2 > 1$ so that vertical transmission favors E over e and therefore e will not invade. This equilibrium is unstable (owing to invasion by A) if inequality (6) holds.

Assuming that the vertical transmission of A is unbiased ($c_1 + c_2 = 1$), (6) can be rearranged to show that the line

$$f = 2\left(1 - \frac{1}{1+h(1-\psi)}\right) \tag{7}$$

specifies values of f below which A invades (see Fig. 1a). It becomes easier for A to invade when fertility selection, f, is low, as having A increases individuals' tendencies to adopt contraception. However, even with high fertility selection (f large), A can invade if the coefficient of horizontal transmission of A, h, is also high and conformity, ψ, is low or absent. When A is rare (q small), conformity to a constrains the invasion by A. Invasion by A becomes impossible when the conformity coefficient, ψ, is 1.

Following a similar argument, we would expect that in the absence of niche construction, the conditions under which a invades the equilibrium $\hat{x}_3 = 1$ (all eA) match the conditions under which a invades the equilibrium $\hat{x}_1 = 1$ (all EA). If the population starts near the equilibrium $\hat{x}_3 = 1$ (all eA) and $b_1 + b_2 < 1$ so that vertical transmission favors e over E and the latter will not invade, then the equilibrium is unstable, with invasion by a, if

$$(c_1+c_2)\left(1-\frac{f}{2}\right) < 1 - \frac{(1-f)h(1+\psi)}{1-h(1+\psi)}. \tag{8}$$

If $b_1 + b_2 > 1$, the equilibrium $\hat{x}_1 = 1$ (all EA) is unstable due to the invasion by a if inequality (8) holds.

If vertical transmission of A is unbiased ($c_1 + c_2 = 1$), then (8) can be rearranged to show that the line

$$f = 2\left(1 - \frac{1}{1+h(1+\psi)}\right) \tag{9}$$

specifies values of f *above* which a invades (Fig. 1b). In Fig. 1b, unlike in Fig. 1a, the factors that facilitate invasion by a include high fertility selection, f, and low horizontal transmission of type A, h. Similar to Fig. 1a, higher conformity, ψ, in Fig. 1b makes it more difficult for the rare type (in this case, a) to invade because conformity hinders the spread of rare types.

In the next section, we explore how these dynamics may or may not change when niche construction is included in the model ($\gamma > 0$).

3.1.2. Local stability with niche construction ($\gamma > 0$)

Suppose the population begins near an equilibrium in which all individuals have type e, and $b_1 + b_2 < 1$ so that vertical transmission favors e over E. Such an equilibrium may be $\hat{x}_4 = 1$ (all ea) or $\hat{x}_3 = 1$ (all eA). In these cases, $p = x_1 + x_2 = 0$ and therefore $p^v = 0$, so the term γp^v in Eq. (2b) is also zero and γ does not affect the dynamics. In other words, when all individuals have a low level of education e, niche construction

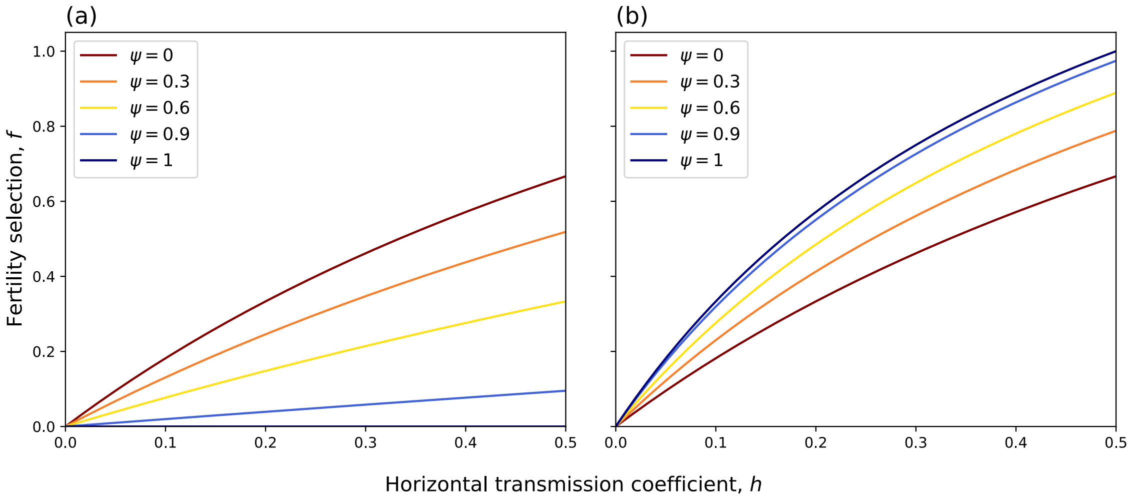

Fig. 1. In the absence of niche construction ($\gamma = 0$) and given that $c_1 + c_2 = 1$, (a) type *A* invades an equilibrium fixed on *a* in the regions under the lines given by Eq. (7), plotted for various values of f, h, and ψ. (b) Type *a* invades an equilibrium fixed on *A* in the regions above the lines given by Eq. (9), plotted for various values of f, h, and ψ.

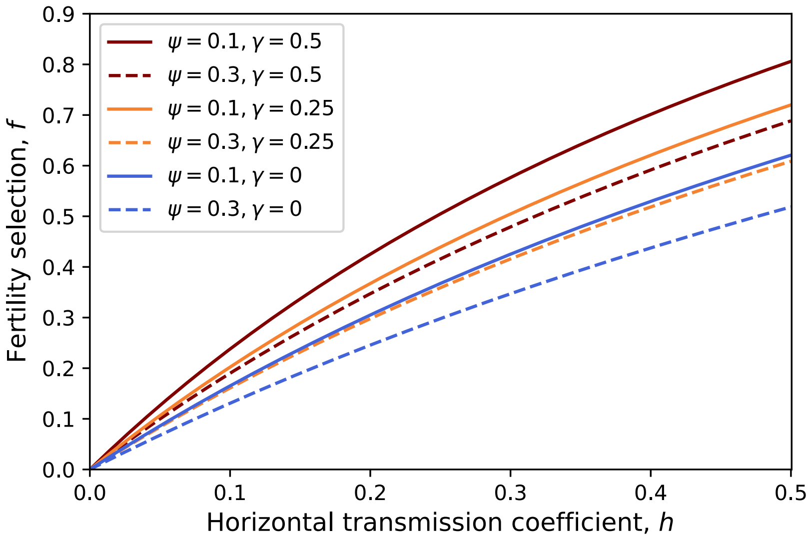

Fig. 2. $\hat{x}_2 = 1$ where *Ea* is fixed, is unstable in the regions under the lines given by Eq. (12) for the shown values of the conformity coefficient, ψ, and niche construction strength, γ, across the given values of fertility selection, f, and horizontal transmission coefficients, h, where $c_1 + c_2 = 1$ and $b_1 + b_2 > 1$.

does not affect transmission of contraception in this model. Thus, with $b_1 + b_2 < 1$, the equilibrium $\hat{x}_4 = 1$ (all *ea*) is unstable if inequality (6) from the previous section holds, while $\hat{x}_3 = 1$ (all *eA*) is unstable if inequality (8) from the previous section holds. If $b_1 + b_2 > 1$, both $\hat{x}_4 = 1$ and $\hat{x}_3 = 1$ are unstable.

The equilibria $\hat{x}_2 = 1$ (all *Ea*) and $\hat{x}_1 = 1$ (all *EA*) are both unstable if $b_1 + b_2 < 1$, where vertical transmission favors *e* over *E*. If $b_1 + b_2 > 1$ and *E* is favored over *e* by vertical transmission, then $\hat{x}_2 = 1$ is unstable and invaded by *A* if

$$(c_1 + c_2)\left(1 - \frac{f}{2}\right) > \frac{1}{1 + h(1-\psi)(1+\gamma)}, \tag{10}$$

while $\hat{x}_1 = 1$ is unstable and invaded by *a* if

$$(c_1 + c_2)\left(1 - \frac{f}{2}\right) < 1 - \frac{(1-f)h(1+\psi)(1+\gamma)}{1 - h(1+\psi)(1+\gamma)}. \tag{11}$$

These equilibria are locally stable if (10) and (11) are reversed, respectively. These conditions differ from the stability conditions in the previous section where γ was zero, as when allele *E* is fixed in the population ($\hat{p} = 1$), niche construction γ affects the population dynamics.

Assuming that the vertical transmission of *A* is unbiased ($c_1 + c_2 = 1$), from (10) the line

$$f = 2\left(1 - \frac{1}{1 + h(1-\psi)(1+\gamma)}\right) \tag{12}$$

specifies values of f below which *A* invades the equilibrium $\hat{x}_2 = 1$ (all *Ea*).

In Fig. 2, the condition (12) with $\gamma > 0$ (maroon and orange lines) is compared to the corresponding condition (7) with $\gamma = 0$ (blue lines). At $\hat{x}_2 = 1$, $\hat{p} = 1$, and thus positive values of the niche construction coefficient ($\gamma > 0$) increase the region of parameter space (f, h, and ψ) in which A is predicted to invade the population. In particular, Fig. 2 shows that for a given level of fertility selection in the presence of niche construction, fertility control (A) is predicted to invade under a lower coefficient of horizontal transmission than in the absence of niche construction. Fig. 2 also shows the interaction between niche construction (γ) and conformity (ψ) in determining regions of stability. As in the absence of niche construction, the invasion by type A is constrained by the level of conformity (i.e., ψ) to type a.

3.1.3. Rates of change of preferences for contraception

Partial differentials were taken to clarify the impact of each of the parameters (f, h, γ, ψ, and $c_{\text{tot}} = c_1+c_2$) on the rate of change in the frequency of A (see Appendix B). Increasing the strength of fertility selection, f, decreases the rate of change Δq of the frequency of A, which is intuitive because A is the acceptance of the idea of fertility control (and reduces fertility). The rate of change Δq is positively related to the fidelity of vertical transmission of A, $c_{\text{tot}} = c_1 + c_2$, the coefficient of horizontal transmission of A, h, and the niche construction coefficient, γ.

The model assumes that individuals only conform to A if it is more frequent than a in the population. Thus, through the horizontal transmission rate α, the conformity coefficient, ψ, is positively related to the rate of change in the frequency of A when $q^v > 1/2$ and negatively related when $q^v < 1/2$. Fig. 3 shows examples where for different fixed values of the niche construction strength, γ, and rate of horizontal transmission of A, h, increasing conformity to a when A is rare delays the initial increase in the frequency of A (solid lines). The spread of fertility control (A) would be more difficult in a population with strong fertility selection (f large) and conformity to a norm of unrestricted fertility ($q^v < 1/2$) so that $1 + \psi(2q^v - 1) < 1$.

3.1.4. Global stability analysis

Numerical analysis shows that if there is vertical transmission bias favoring e over E (i.e., $b_1 + b_2 < 1$), E always goes extinct ($\hat{p} = 0$), while if vertical transmission bias favors E over e (i.e., $b_1 + b_2 > 1$), E always spreads to fixation ($\hat{p} = 1$).

The evolution of A in the absence of conformity, $\psi = 0$

In this case, (3b) can be rearranged to give

$$\Delta q = \frac{q(1-q)}{W^2} F(p, q), \tag{13}$$

where $F(p, q)$ is given by the following function of q and p:

$$F(p,q) = q^2\phi_2^2 h(1+\gamma p^v) + q[\phi_1(\phi_1+\phi_2) + \phi_2 h(2+\phi_1)(1+\gamma p^v)] + \phi_1 + (1+\phi_1)h(1+\gamma p^v),$$

where $\phi_1 = (c_1 + c_2)(1 - f/2) - 1$ and $\phi_2 = (2 - c_1 - c_2)(1 - f/2) - 1$.

In addition to the four fixation equilibria ($\hat{x}_1 = 1, \hat{x}_2 = 1, \hat{x}_3 = 1, \hat{x}_4 = 1$), the system may have an equilibrium on the edge where $\hat{x}_3 + \hat{x}_4 = 1$ and $\hat{x}_3 = \hat{q}_0$, with $0 < \hat{q}_0 < 1$, and an equilibrium on the edge where $\hat{x}_1 + \hat{x}_2 = 1$ and $\hat{x}_1 = \hat{q}_1$, where $0 < \hat{q}_1 < 1$. The roots of $F(p, q)$ may give equilibria of type $\hat{q}_0$ if $b_1 + b_2 < 1$ and of type $\hat{q}_1$ if $b_1 + b_2 > 1$. These equilibria exist if the corners (fixations) are unstable. Next, we outline the conditions under which the equilibria are locally stable. Here, we assume $b_1 + b_2 > 1$, in which case E becomes fixed in the population ($\hat{p} = 1$ and thus $p^v = 1$). Note that at equilibrium, there is no effect of niche construction on A if $b_1 + b_2 < 1$. Thus, the equivalent conditions for stability can be found by setting $\gamma = 0$, in which case F can be regarded as a function of q, written $F(0, q)$.

If $0 < q < 1$, the sign of Δq is the same as that of $F(0, q)$. Now

$$F(1,0) = (c_1 + c_2)\left(1 - \frac{f}{2}\right)[1 + h(1+\gamma)] - 1, \tag{14}$$

and thus, from (10), $\hat{x}_2 = 1$ is locally stable if $F(1, 0) < 0$ and unstable when $F(1, 0) > 0$. In addition,

$$F(1,1) = (1-f)\left\{1 - f - (2 - c_1 - c_2)\left(1 - \frac{f}{2}\right)[1 - h(1+\gamma)]\right\}, \tag{15}$$

and thus, from (11), $\hat{x}_1 = 1$ is locally stable if $F(1, 1) > 0$ and unstable if $F(1, 1) < 0$.

Fig. 4a is a case where $\hat{x}_2 = 1$ is locally stable ($F(1, 0) < 0$) and $\hat{x}_1 = 1$ is unstable ($F(1, 1) < 0$), and the frequency of A decreases to the equilibrium $\hat{x}_2 = 1$. There is no edge equilibrium as both the roots of the quadratic function, $F(1, q) = 0$, lie outside the range $0 \le q \le 1$. Thus, the equilibrium $\hat{x}_2 = 1$ is globally stable.

If $\hat{x}_1 = 1$ is stable ($F(1, 1) > 0$), since we can express $F(1, 0)$ as

$$F(1,0) = \frac{F(1,1)}{1-f} + (2-f)(c_1 + c_2 - 1)h(1+\gamma p), \tag{16}$$

for $F(1, 0) < 0$, it is necessary that $c_1 + c_2 < 1$. When $F(1, 0) < 0$ and $F(1, 1) > 0$, $\hat{x}_2 = 1$ is also stable, and there is one unstable edge equilibrium $\tilde{q}_1$, where $\tilde{q}_1$ is the larger of the two roots of the quadratic, $F(1, q) = 0$. Fig. 4b shows a case where A approaches one of the fixation points, $\hat{x}_1 = 1$ or $\hat{x}_2 = 1$, depending on the initial state; from some starting conditions the niche construction parameter γ is large enough to overcome the weaker vertical transmission.

If $\hat{x}_2 = 1$ (fixation on Ea) is unstable ($F(1, 0) > 0$), since we can express $F(1, 1)$ as

$$F(p,1) = (1-f)[F(1,0) - (2-f)(c_1 + c_2 - 1)h(1+\gamma p^v)], \tag{17}$$

for $F(1, 1) < 0$, it is necessary that $c_1 + c_2 > 1$. When $F(1, 0) > 0$ and $F(1, 1) < 0$, both $\hat{x}_2 = 1$ and $\hat{x}_1 = 1$ are unstable and the frequency of A moves to a globally stable equilibrium, $\hat{q}_1$, where $\hat{q}_1$ is the smaller root of the quadratic $F(1, q) = 0$ (Fig. 4c). If $\hat{x}_2 = 1$ is unstable ($F(1, 0) > 0$) and $\hat{x}_1$ is stable ($F(1, 1) > 1$), numerical analysis reveals that there may either be zero or two edge equilibria within the range $0 < q_1 < 1$, depending on the parameter values. The example in Fig. 4d shows that if there are two such edge equilibria and γ is large enough, the smaller frequency edge equilibrium is stable in the $\hat{p} = 1$ edge while the higher frequency edge equilibrium is unstable. The frequency of A moves to either $\hat{q}_1$ or $\hat{x}_1 = 1$, depending on the initial state. In Fig. 4e, $\hat{x}_1 = 1$ is globally stable if there is no edge equilibrium. In Fig. 4 we see that spread of fertility control, i.e., increase of A, is enhanced by increased niche construction, i.e., larger values of γ, for the same amount of vertical transmission ($c_1 + c_2$).

In summary, the trajectories in Fig. 4 illustrate some of the possible outcomes of evolution under this model of horizontal transmission. In particular, when α (and h) represent the effects of horizontal transmission, and the corners on the $x_1 + x_2 = 1$ edge are unstable, there is at least one polymorphic equilibrium on this edge. This equilibrium is a root of a fourth degree polynomial, and the numerical analysis indicates if $b_1 + b_2 > 1$, for example, the equilibrium on the $x_1 + x_2 = 1$ edge, is stable. We have not determined how many other stable or unstable equilibria are possible, although cases with one stable and two unstable equilibria have been seen on $x_1 + x_2 = 1$.

The evolution of A with conformity, $\psi > 0$

We were unable to solve $\Delta p = 0$, $\Delta q = 0$ in (3) and derive all equilibrium states explicitly. However, numerical analysis reveals

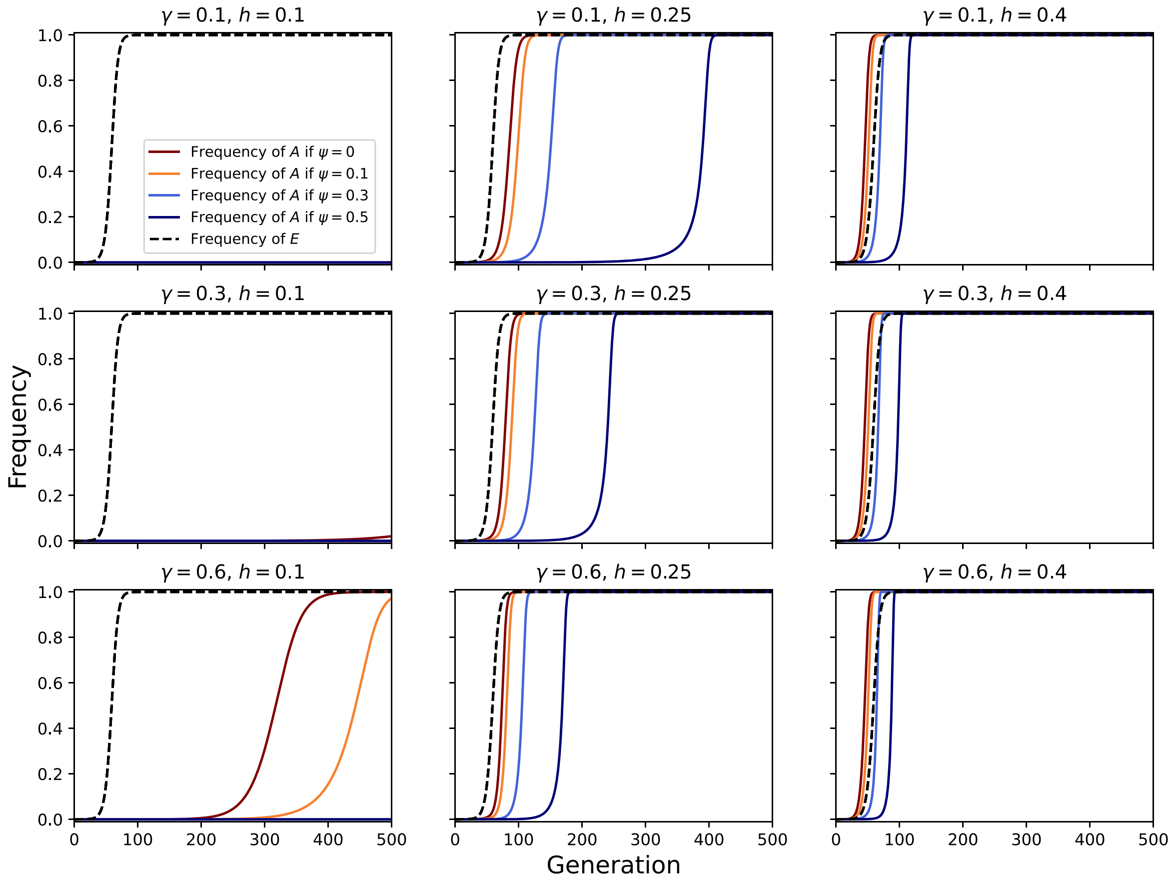

Fig. 3. Frequency p of E (dashed lines) and q of A (solid lines) over 500 generations. Here, $b_1 = b_2 = 0.6$, $c_1 = c_2 = 0.5$, values of γ and h are shown in sub-plot titles, and $f = 0.2$. Initially, $x_1 = 1 \times 10^{-5}$, $x_2 = 1.1 \times 10^{-5}$, and $x_3 = 1.2 \times 10^{-5}$, so the populations begin close to $\hat{x}_4 = 1$ (ea). We see that when q is small, larger values of ψ increase conformity to type a which delays the increase in q. For each of the values of ψ, the trajectories of E were very similar (shown overlapping in the plots).

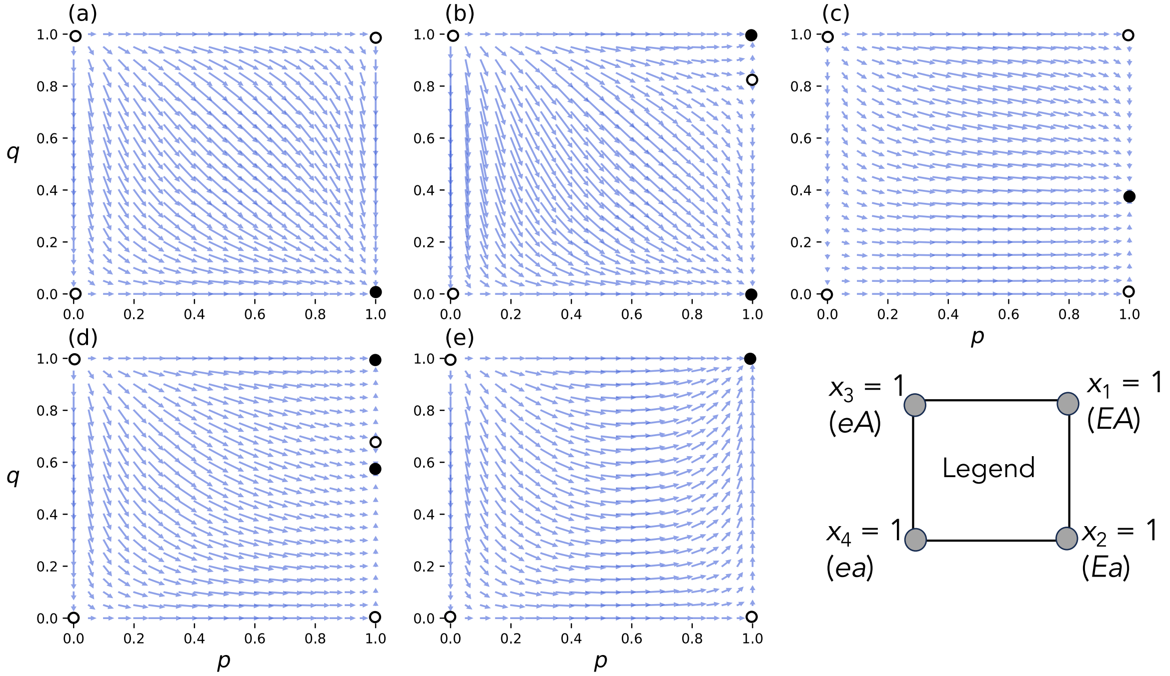

Fig. 4. Changes in frequencies of traits ***A*** and ***E*** and equilibria when $\psi = 0$ and there is horizontal transmission of trait ***A***. Different initial values of p and q are shown at the base of each arrow (and the initial value for D is always zero), and the tip of each arrow shows the corresponding values of p' and q' after one generation. The filled circles represent locally stable equilibria while the empty circles are unstable equilibria. (a) $c_2 = c_1 = 0.5$, $\gamma = 0.2$; (b) $c_2 = c_1 = 0.4$, $\gamma = 2$; (c) $c_2 = c_1 = 0.59$, $\gamma = 0.2$; (d) $c_2 = c_1 = 0.5$, $\gamma = 1.25$; and (e) $c_2 = c_1 = 0.5$, $\gamma = 2$. Other parameter values are $b_2 = b_1 = 0.6$, $f = 0.6$, and $h = 0.2$.

that the conditions under which $\hat{x}_3 = 1$ (or $\hat{x}_1 = 1$) is locally stable do not always preclude stability of $\hat{x}_4 = 1$ (or $\hat{x}_2 = 1$). In other words, the local stability of either $\hat{x}_3 = 1$ or $\hat{x}_1 = 1$ does not guarantee their global stability. Hence, the initial increase of A when it is rare may not always entail that it goes to fixation.

Numerical analysis also reveals that if $b_1 + b_2 < 1$, the population will converge to one of $\hat{x}_4 = 1$, $\hat{x}_3 = 1$, or a locally stable edge equilibrium, $\hat{q}_0$ where ea and eA are both present. In addition, there can be up to two unstable edge equilibria. We denote an unstable edge equilibrium by $\tilde{q}_0$. If neither $\hat{x}_4 = 1$ nor $\hat{x}_3 = 1$ is locally stable, the population always converges to $\hat{q}_0$. We are able to determine (see Appendix C) that for this to occur it is necessary that $c_1 + c_2 > 1 + \psi$. In this case, an edge equilibrium may be attained if there is a bias in vertical transmission favoring A and the bias exceeds the strength of conformity, thus preventing A from being lost when it is rare even if conformity favors type a. If one of $\hat{x}_4 = 1$ or $\hat{x}_3 = 1$ is locally stable, then an unstable edge equilibrium, $\tilde{q}_0$, and a locally stable edge equilibrium, $\hat{q}_0$, exist under certain parameter conditions. If $\hat{x}_4 = 1$ and $\hat{x}_3 = 1$ are both locally stable, there exists either one unstable edge equilibrium, $\tilde{q}_0$, or under a highly restricted set of parameter conditions, a locally stable edge equilibrium of intermediate frequency between two unstable edge equilibria.

Similarly, if $b_1 + b_2 > 1$, numerical analysis shows that the population will converge to one of $\hat{x}_2 = 1$, $\hat{x}_1 = 1$, or $\hat{q}_1$, and there can be up to two unstable equilibria on this edge where E is fixed. If neither $\hat{x}_2 = 1$ nor $\hat{x}_1 = 1$ is locally stable, the population always converges to $\hat{q}_1$ also requiring $c_1 + c_2 > 1 + \psi$ to be satisfied. However, if one of $\hat{x}_2 = 1$ or $\hat{x}_1 = 1$ is locally stable, then an unstable edge equilibrium, $\tilde{q}_1$, and a locally stable edge equilibrium, $\hat{q}_1$, exist under certain parameter conditions. If $\hat{x}_2 = 1$ and $\hat{x}_1 = 1$ are both locally stable, there exists either one unstable edge equilibrium, $\tilde{q}_1$, or under a highly restricted set of parameter conditions, a locally stable edge equilibrium of intermediate frequency between two unstable edge equilibria. Our numerical analysis suggests that equilibria that are locally stable are in fact globally stable in the simplex $0 \leq x_1, x_2, x_3, x_4$; $\sum_{i=1}^{4} x_i = 1$.

To illustrate some of the dynamics when $\psi \geq 0$, we explore the interesting case in which the population begins near the fixation state $\hat{x}_4 = 1$ (all ea) and the level of education increases over time ($b_1 + b_2 > 1$). Fig. 5 shows which equilibrium the population eventually reaches. With sufficiently low conformity, ψ, and fertility selection, f, as well as sufficiently high niche construction, γ, and horizontal transmission of A, h, the population can reach EA at equilibrium. Otherwise, either Ea or, in a small subset of cases, a polymorphism with a and A (and fixation of E) is reached at equilibrium.

Fig. 3 showed the trajectories of type E and A over time for $f = 0.2$, various values of ψ, and each of the γ and h values from Fig. 5. In all of the cases, E underwent a similar trajectory. The trajectories of A, however, could vary substantially in the different sub-plots of Fig. 3. If h and γ are sufficiently small, A does not increase in the 500 generations shown. As h and γ become larger but not too large, A increases to fixation at a slower rate than E (provided ψ is sufficiently low to allow A to increase at all). With large enough h and γ, it is possible that A reaches fixation prior to the fixation of E (but again, only if ψ is sufficiently low).

Up to this point, our analysis has assumed that non-vertical transmission occurs at rate α with h representing the rate of horizontal transmission. In this case, α is a function of q^v and p^v, the frequencies of A and E in offspring after vertical cultural transmission. In the next section, we explore the case in which h is the rate of oblique transmission, and α depends on q and p.

Oblique cultural transmission

If cultural transmission is oblique, then Eqs. (1) and (2) are modified by replacing p^v and q^v in Eq. (2b) by p and q so that

$$\alpha = hq(1 + \gamma p)[1 + \psi(2q - 1)]. \tag{18}$$

In most cases, the dynamics under horizontal and oblique cultural transmission are qualitatively similar (Cavalli-Sforza and Feldman, 1981). The model here, however, produces the following interesting difference. Inequality (6) giving the condition for corner equilibria $\hat{x}_4 = 1$, where ea is fixed, to be invaded by A is replaced by

$$\left(1 - \frac{f}{2}\right)(c_1 + c_2) > 1 - h(1 - \psi). \tag{19}$$

The condition for invasion of $\hat{x}_3 = 1$ by type a under oblique transmission remains the same as inequality (8). Interestingly, these two inequalities (19) and (8) may both be satisfied and, as a result, a polymorphic equilibrium with eA and ea may exist and be stable in the edge $x_3 + x_4 = 1$ that connects these two corners. No such polymorphism was seen with horizontal transmission. However, this polymorphism does not appear to be stable with respect to the interior of the simplex, and invasion by E leads to a polymorphism in the $x_1 + x_2 = 1$ edge where E is fixed. An example is shown in Fig. 6c.

The compound parameter α is much simpler in the oblique case than in the case of horizontal transmission. Consequently, on the edges $x_1 + x_2 = 1$ and $x_3 + x_4 = 1$, where E and e, respectively, are fixed, the equilibrium situation is simpler than in the horizontal case. In fact, with oblique transmission, if $\hat{x}_1 = 1$ and $\hat{x}_2 = 1$ are both unstable and $b_1 + b_2 > 1$, a single A, a polymorphism exists and is stable. Similarly, the analogous polymorphism on the $x_3 + x_4 = 1$ edge is unique and stable in the $x_3 - x_4$ edge, but if $b_1 + b_2 > 1$, it is unstable in the full simplex (Fig. 6c).

3.2. The effect of the cultural background on the viability of individuals

In Fig. 7, trajectories of p, q, m, and W are shown over 330 generations. As in Ihara and Feldman (2004), we find that under conditions where both E and A increase from low values to fixation, the increase in E is accompanied by a decrease in mortality, and the increase in A is accompanied by a decline in fertility. Parts (a) and (b) of Fig. 7 compare the dynamics under conditions where niche construction is required for the fixation of A. In the absence of niche construction ($\gamma = 0$, Fig. 7a) the decline in mortality is not followed by a decline in fertility. Fig. 7c shows an example where A becomes fixed in the absence of niche construction because the coefficient of horizontal transmission of A, h, is particularly high. However, in such cases the fixation of A is always slower than in the presence of niche construction (Fig. 7d).

It is worth noting that there can be large variation in the time lag between the change in frequency of E accompanied by m, and A accompanied by W, depending on the parameter values. Indeed, A can even spread to fixation faster than E if the rate of horizontal transmission is sufficiently high and fertility selection is sufficiently low. Finally, in all cases where A increases in frequency in the absence of niche construction, both mortality and fertility decline simultaneously (i.e., starting at generation zero) (e.g., Figs. 7c–d). However, if niche construction is required for A to spread, there is a time-lag between the decline in mortality and fertility, lasting until the average level of education is sufficient to drive an increase in the frequency of fertility control (e.g., Fig. 7b).

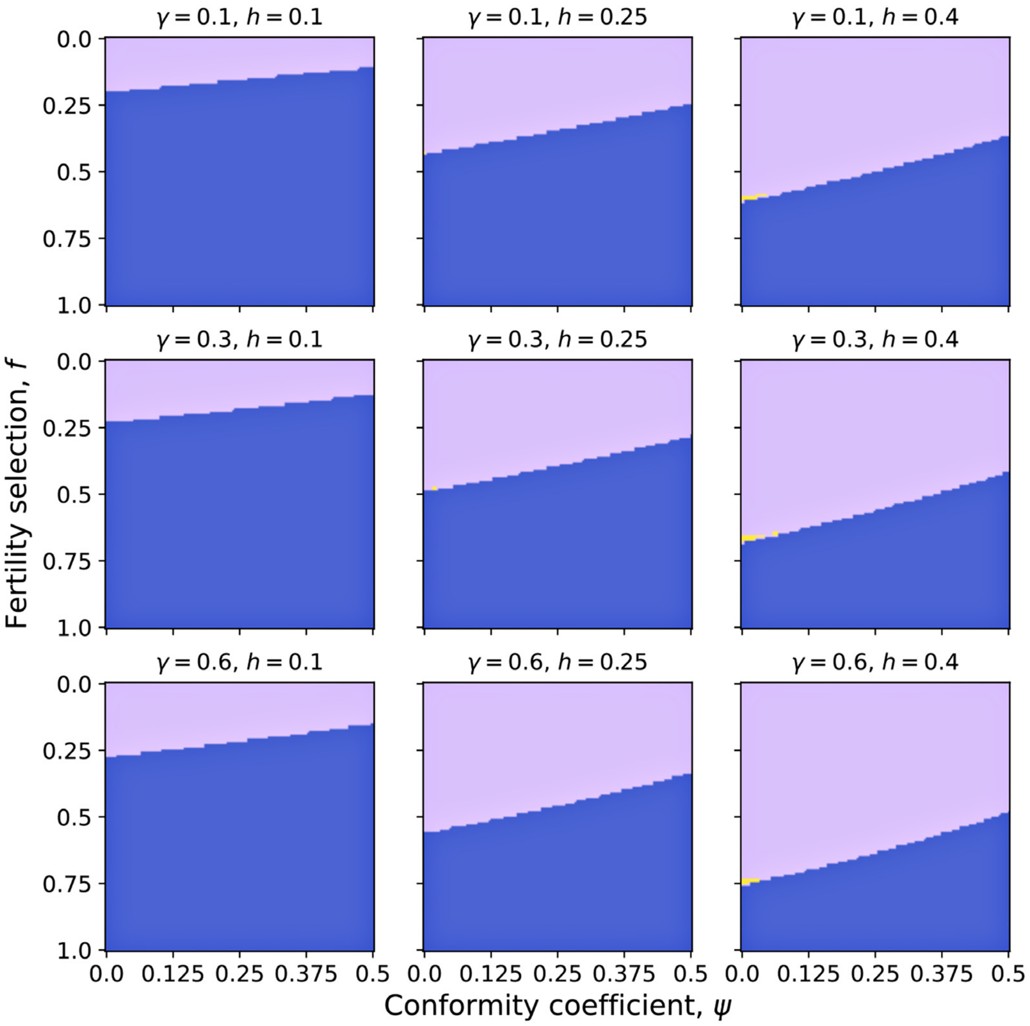

Fig. 5. Regions of the parameter space in which the population stabilized at an equilibrium of $\hat{x}_1 = 1$ (all *EA*) (purple), $\hat{x}_2 = 1$ (all *Ea*) (blue), or a polymorphism in *A* and *a* with fixation of *E* (yellow; barely seen). ψ values are on the *x*-axes, f values are on the *y*-axes, γ and h values are in the titles of the sub-plots, $c_1 = c_2 = 0.5$, and $b_1 = b_2 = 0.6$. Initially, $x_1 = 1 \times 10^{-5}$, $x_2 = 1.1 \times 10^{-5}$, and $x_3 = 1.2 \times 10^{-5}$, so the population began close to $\hat{x}_4 = 1$ (*ea*).

4. Discussion

A bias in the vertical transmission of a cultural background favoring a high level of education over a low level of education may facilitate the horizontal transmission of a trait such as a preference for contraception. This type of social or cultural niche construction can be a critical factor in allowing the preference for contraceptive use (or controlled fertility, more generally) to spread either to a polymorphic equilibrium or to fixation, despite fertility selection favoring *a* over *A* and conformity to *a* when *A* is rare. Thus cultural niche construction can facilitate the spread of traits with low Darwinian fitness and can provide an environment that counteracts conformity to norms.

The model predicts that for acceptance of the idea of contraception (A) to spread through a population, the rate of horizontal transmission of A (h) must be sufficiently high to counteract any reduction in the trait frequency that results from fertility selection (f). If these processes balance one another, it is possible for the trait to reach a polymorphic equilibrium. Under such circumstances, promotion of fertility control by the media or by institutional changes may be necessary for the rate of horizontal transmission to be sufficiently enhanced that fertility control spreads to fixation.

Montgomery and Casterline (1996, p.168) suggested that social effects may help to explain “the curious lags in the response of fertility to changes in underlying determinants and, conversely, sudden bursts of change in fertility”. Our model shows how conformity can suppress the response of a preference for fertility control to changes in the average level of education. Conversely, the model shows that once the majority of the population have adopted fertility control, the rate of change in its adoption is positively related to the coefficient of conformity (ψ).

The spread of the use of contraception may contribute to the ‘demographic transition’, characterized by a reduction in fertility often found in societies undergoing industrialization (Vining, 1986). A demographic transition is typically associated with an increase in the level of education and a decrease in mortality, followed by a reduction in fertility. As summarized in Ihara and Feldman (2004, p. 110):

> “[T]here are at least three evolutionary hypotheses for the demographic transition (reviewed in Borgerhoff Mulder, 1998). First, small family size may be evolutionarily advantageous

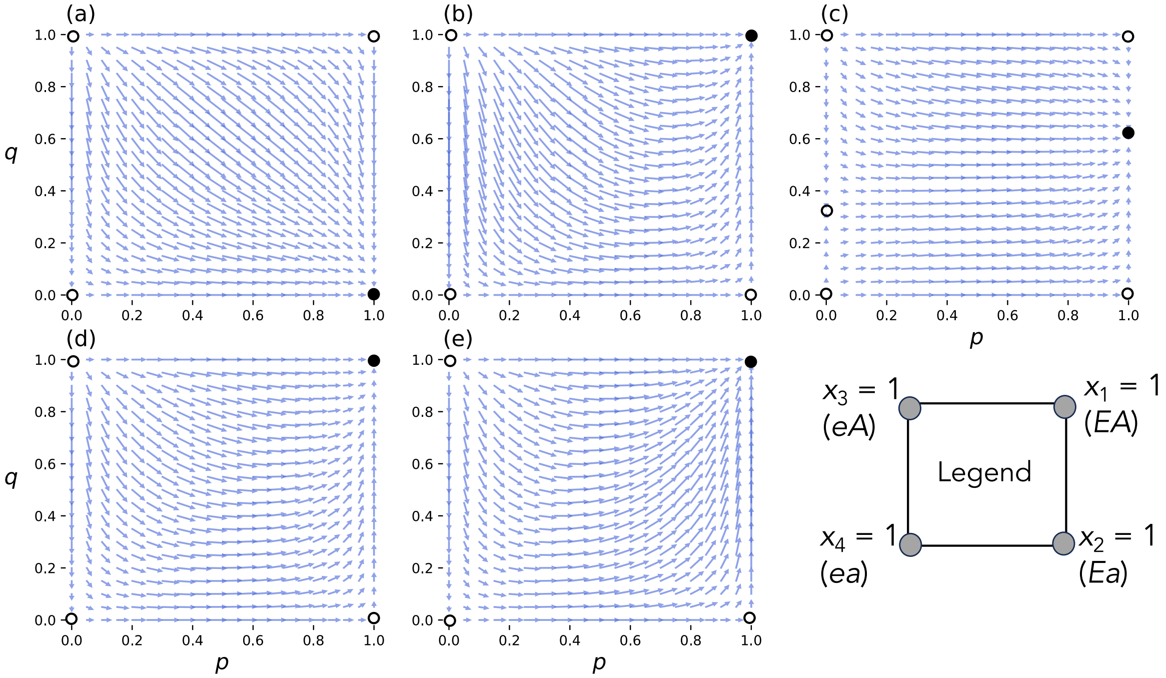

Fig. 6. Changes in frequencies of traits $\boldsymbol{A}$ and $\boldsymbol{E}$ and equilibria when $\psi = 0$ and there is oblique transmission of trait $\boldsymbol{A}$. Different initial values of p and q are shown at the base of each arrow (and the initial value for D is always zero), and the tip of each arrow shows the corresponding values of p' and q' after one generation. The filled circles represent locally stable equilibria while the empty circles are unstable equilibria. As in Fig. 4, (a) $c_2 = c_1 = 0.5$, $\gamma = 0.2$; (b) $c_2 = c_1 = 0.4$, $\gamma = 2$; (c) $c_2 = c_1 = 0.59$, $\gamma = 0.2$; (d) $c_2 = c_1 = 0.5$, $\gamma = 1.25$; and (e) $c_2 = c_1 = 0.5$, $\gamma = 2$. Other parameter values are $b_2 = b_1 = 0.6$, $f = 0.6$, and $h = 0.2$.

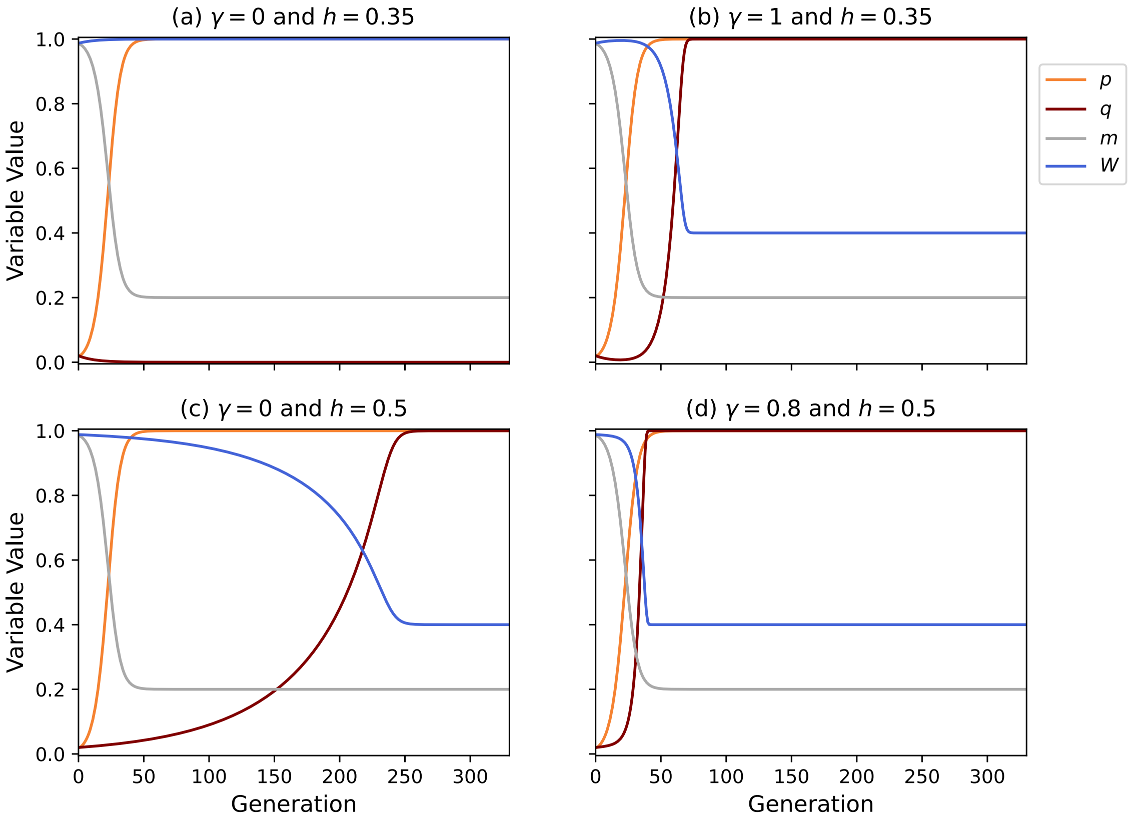

Fig. 7. Changes in the frequency of E, p, the frequency of A, q, the average relative mortality, m, and the average relative fertility, W, over 330 generations, where $v_0 = 0.5$, $v_1 = 0.8$, $b_1 = b_2 = 0.6$, $c_1 = c_2 = 0.5$, $f = 0.6$, and $\psi = 0.1$. Niche construction, determined by γ, occurs in parts (b) and (d) but not parts (a) and (c). The coefficient of horizontal transmission, h, is higher in parts (c) and (d) than in parts (a) and (b). Note $\alpha < 1$ throughout the dynamics (see Ihara and Feldman, 2004).

> in conditions where parental investment is critical for offspring reproduction. Second, the decrease in fertility may be a maladaptive response to the modern environment, which has changed drastically from that in which human psychological and physiological mechanisms evolved. Third, the decrease in fertility may be a result of Darwinian cultural evolution, which may not necessarily maximize genetic fitness".

As in Ihara and Feldman (2004), the present study coincides with the third hypothesis (Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985). The model shows that an increase in the level of education may provide a cultural background that facilitates a subsequent reduction in fertility by increasing the rate of horizontal transmission of traits such as a preference for contraception.

We have assumed an unstructured population. However the cultural niche may also affect the rate of horizontal transmission between populations, within a metapopulation. For example, Bongaarts and Watkins (1996) note that the demographic transition first occurred in countries that were highly developed, measured as a linear combination of literacy, life expectancy and real GDP per capita. However, at later points in time, this transition occurred at lower levels of development. Moreover, they found that "the pace of fertility decline is related to the level of development at the onset of a transition rather than to the pace of subsequent development" (Bongaarts and Watkins, 1996, p.668). They suggest that the decline in fertility is affected by a nested set of social interactions: within social networks, between social networks within a country, and between countries within the global community. Thus, niche construction may have affected patterns of fertility control between social networks and also between countries.

Education may influence the evolution of a fertility-reducing trait by enhancing the rate of horizontal transmission. Ihara and Feldman (2004) showed that education may also influence the evolution of a fertility-reducing trait as a function of the mode of transmission by assuming that high education facilitates the rate of oblique transmission relative to vertical transmission. As in the current model, their model generates dynamics that are consistent with a demographic transition. In both Ihara and Feldman (2004) and the current study, the common influence of the average level of education on the evolution of a low-fertility trait is for the former to enhance the rate with which the latter is transmitted. An interesting difference between the outcome of the models is that Ihara and Feldman's oblique transmission model always generates a single globally stable equilibrium, while for our horizontal transmission model, in the absence of conformity, two equilibria can be locally stable under a single set of parameter values (see Figs. 4b and 4d). The various assumptions and predictions of our model can be tested by estimating the rate of vertical and horizontal transmission of traits (Hewlett and Cavalli-Sforza, 1986; Guglielmino et al., 1995; Li et al., 2000a; Hewlett et al., 2002).

Using the simple 'two locus' modeling paradigm, both Ihara and Feldman (2004) and the current study show that an increase in the level of education may contribute to a demographic transition by affecting the rate at which fertility-reducing traits are adopted. However, many other factors must be considered to explain a demographic transition completely (Watkins, 1990; Kaplan et al., 1995; Borgerhoff Mulder, 1998; Basu, 2002; Murthi, 2002). For example, influences on fertility control may include the cost of education, changes in child-mortality, women's education in particular, the mass media and institutional changes, parental investment and the inheritance of wealth (Borgerhoff Mulder, 1998; Mace, 2000; Basu, 2002; Murthi, 2002).

Götmark and Andersson (2020) found that a third factor, level of religiosity, showed a positive correlation with TFR (except in western Europe and some parts of Asia). An extension of the "two trait" analysis of education and fertility described here to include a third trait, religiosity, whose spread would produce a "cultural conflict" with the effects of education on TFR, could produce interesting results (see, e.g., Fogarty et al., 2013; Creanza and Feldman, 2014; Fogarty et al., 2019).

Evolution of the mode of horizontal transmission, even if this transmission is restricted to a segment of the population, can enhance the strength of cultural niche construction. For example, increased access to social media can enhance the niche in which negative (or, for that matter, positive) norms may spread. Horizontal transmission and level of conformity may then vary among segments of a population and work to increase behavioral diversity or polarization.

There may be a wide range of cases for which similar models could be developed to predict the influence of a vertically transmitted trait on the evolution of a horizontally transmitted trait. For example, a vertically transmitted preference for sons over daughters may influence the horizontal transmission of information about availability of ultrasound B for foetal sex detection or the behavioral act of carrying out sex-selective abortion (Li et al., 1999a,b, 2000a; Feldman, 2003). Traits that are vertically transmitted in many societies, for example, religious beliefs and preferences for particular social stratification may influence the horizontal transmission of traits concerning political change, sexual equality, etc. The mechanism of the interaction between the two traits, however, may differ between each of these cases. Indeed, horizontally transmitted traits may sometimes provide a cultural niche that affects the persistence of vertically transmitted traits. For instance, the horizontal transmission of technological innovations in tools or tool use may influence vertically transmitted division of labour between sexes for skills such as food gathering, farming and manual labour.

Data availability

No data was used for the research described in the article.

Acknowledgments

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Appendix A. The frequencies $x_1 - x_4$ after vertical transmission

$$\begin{aligned} Wx_1^v &= (1-f)c_3[b_3x_1^2 + (b_2+b_1)x_1x_3 + b_0x_3^2] \\ &\quad + (1-f/2)c_2(b_3x_1x_2 + b_2x_1x_4 + b_1x_2x_3 + b_0x_3x_4) \\ &\quad + (1-f/2)c_1(b_3x_1x_2 + b_2x_2x_3 + b_1x_1x_4 + b_0x_3x_4) \\ &\quad + c_0[b_3x_2^2 + (b_2+b_1)x_2x_4 + b_0x_4^2] \end{aligned} \tag{A.1}$$

$$\begin{aligned} Wx_2^v &= (1-f)(1-c_3)[b_3x_1^2 + (b_2+b_1)x_1x_3 + b_0x_3^2] \\ &\quad + (1-f/2)(1-c_2)(b_3x_1x_2 + b_2x_1x_4 + b_1x_2x_3 + b_0x_3x_4) \\ &\quad + (1-f/2)(1-c_1)(b_3x_1x_2 + b_2x_2x_3 + b_1x_1x_4 + b_0x_3x_4) \\ &\quad + (1-c_0)[b_3x_2^2 + (b_2+b_1)x_2x_4 + b_0x_4^2] \end{aligned} \tag{A.2}$$

$$\begin{aligned}Wx_3^v = {} & (1-f)c_3[(1-b_3)x_1^2 + (2-b_2-b_1)x_1x_3 + (1-b_0)x_3^2] \\ & + (1-f/2)c_2[(1-b_3)x_1x_2 + (1-b_2)x_1x_4 \\ & + (1-b_1)x_2x_3 + (1-b_0)x_3x_4] \\ & + (1-f/2)c_1[(1-b_3)x_1x_2 + (1-b_2)x_2x_3 \\ & + (1-b_1)x_1x_4 + (1-b_0)x_3x_4] \\ & + c_0[(1-b_3)x_2^2 + (2-b_2-b_1)x_2x_4 + (1-b_0)x_4^2]\end{aligned} \tag{A.3}$$

$$\begin{aligned}Wx_4^v = {} & (1-f)(1-c_3)[(1-b_3)x_1^2 + (2-b_2-b_1)x_1x_3 \\ & + (1-b_0)x_3^2] \\ & + (1-f/2)(1-c_2)[(1-b_3)x_1x_2 \\ & + (1-b_2)x_1x_4 + (1-b_1)x_2x_3 + (1-b_0)x_3x_4] \\ & + (1-f/2)(1-c_1)[(1-b_3)x_1x_2 + (1-b_2)x_2x_3 \\ & + (1-b_1)x_1x_4 + (1-b_0)x_3x_4] \\ & + (1-c_0)[(1-b_3)x_2^2 + (2-b_2-b_1)x_2x_4 + (1-b_0)x_4^2]\end{aligned} \tag{A.4}$$

where $W = 1 - f(x_1 + x_3) = 1 - fq$.

Appendix B. Partial derivatives for q, the frequency of A

$$\frac{\partial \Delta q}{\partial f} = -\frac{1-\alpha}{2W^2} q(1-q)[c_{\text{tot}}(1-q) + (2-c_{\text{tot}})q] \tag{B.1}$$

$$\begin{aligned}\frac{\partial \Delta q}{\partial h} = {} & \frac{1-\alpha}{W}\left[1-q+q\left(1-\frac{f}{2}\right)(2-c_{\text{tot}})\right] q^v(1+\gamma p^v) \\ & \times [1+\psi(2q^v-1)]\end{aligned} \tag{B.2}$$

$$\begin{aligned}\frac{\partial \Delta q}{\partial \gamma} = {} & \frac{1-q}{W}\left[1-q+q\left(1-\frac{f}{2}\right)(2-c_{\text{tot}})\right] hp^v q^v \\ & \times [1+\psi(2q^v-1)]\end{aligned} \tag{B.3}$$

$$\frac{\partial \Delta q}{\partial c_{\text{tot}}} = \frac{1-q}{W} q(1-\alpha)\left(1-\frac{f}{2}\right) \tag{B.4}$$

$$\begin{aligned}\frac{\partial \Delta q}{\partial \psi} = {} & \frac{1-q}{W}\left[1-q+q\left(1-\frac{f}{2}\right)(2-c_{\text{tot}})\right] hq^v \\ & \times (1+\gamma p^v)(2q^v-1)\end{aligned} \tag{B.5}$$

where $c_{\text{tot}} = c_1 + c_2$. The right-hand side of (B.1) is negative, the right-hand sides of (B.2)–(B.4) are positive, and the right-hand side of (B.5) depends on q^v (see main text).

Appendix C. Necessary conditions for the stability of edge equilibria where $0 < \hat{q} < 1$

First we consider $b_1 + b_2 > 1$, in which case the population will converge to one of $\hat{x}_2 = 1$, $\hat{x}_1 = 1$, or $\hat{q}_1$. From (10) and (11), for both $\hat{x}_2 = 1$ and $\hat{x}_1 = 1$ to be unstable, it is necessary that

$$\frac{1}{1+h(1-\psi)(1+\gamma)} < 1 - \frac{(1-f)h(1+\psi)(1+\gamma)}{1-h(1+\psi)(1+\gamma)}, \tag{C.1}$$

or that

$$\frac{2h(1+\gamma)\{(1-f/2)(1+\psi)[1+h(1+\gamma)(1-\psi)]-1\}}{[1+h(1+\gamma)(1-\psi)][1-h(1+\gamma)(1+\psi)]} < 0. \tag{C.2}$$

From the numerator of the left-hand side of (C.2), it is clear that (C.1) is true if

$$1 - \frac{f}{2} < \frac{1}{(1+\psi)[1+h(1-\psi)(1+\gamma)]}. \tag{C.3}$$

If both $\hat{x}_2 = 1$ and $\hat{x}_1 = 1$ are unstable, inequalities (10), (11) and (C.3) are satisfied simultaneously. Inequalities (10) and (C.3) are satisfied if

$$c_1 + c_2 > 1 + \psi. \tag{C.4}$$

The same procedure reveals the same result (C.4) where $b_1+b_2 < 1$ and the population converges to one of $\hat{x}_4 = 1$, $\hat{x}_3 = 1$, or $\hat{q}_0$.

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