Fertility Transitions

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Abstract

Demographic transitions in contemporary human societies have profound impacts on our social and economic lives (Dyson, 2010). Across the population sciences, there are abundant empirical observations, but few causal explanations, of fertility transition. The seeming contradiction between observed fertility patterns and fitness-maximization assumptions pose a significant challenge for evolutionary theorists. In this chapter, we explore evolutionary theories that can potentially help address this deep theoretical challenge. We argue that cultural evolutionary approaches can tackle aspects of fertility transitions that other approaches neglect. To bridge divides between evolutionary and non-evolutionary perspectives, we highlight intersections between cultural evolutionary theory and other social, economic, and political sciences.

Keywords: demographic transition, fertility decline, human reproduction, cultural evolution

1 Demographic Transition: An Overview

Demographic transition refers to long-term population trends in human societies in which birth rates and death rates fall from high to low levels alongside "modernization" and economic development (Notestein, 1945; Thompson, 1929; Kirk, 1996). Together with the Industrial Revolution, these two historical phenomena are associated with tremendous economic growth and consequent social and political transformations, shaping the contours of the modern world. The sustained economic and income growth we are used to today was not possible before around the 19th century, when humans are assumed to have been in a "Malthusian trap" or fluctuating equilibrium (Malthus, 1798) under which any extra agricultural production was consumed by the additional growth of population size, leading to "natural checks" on further population growth (though see Boserup, 1975; 1976 for an alternative explanation). New technologies and manufacturing processes brought about by the Industrial Revolution, combined with more saving and investment per capita brought about by lower fertility (Coale and Hoover, 1958; Higgins and Williamson, 1997; Oppenheim Mason, 1997; Bloom and Canning, 2001) are argued to now exempt us from this trap.

Demographic transitions have immense social and economic implications for our world (Reher, 2011). For example, most of the global population now lives in countries where fertility rates will hardly replace the population. Shrinking, ageing and long-lived populations are expected to significantly increase labor shortages and impact pension systems, decreasing income and economic growth, social mobility, health care quality, and living standards in the future.

While "demographic transition theory" (Thompson, 1929; Notestein, 1945; Kirk, 1996) highlights several stages of this phenomenon, the transition is basically determined by two major forces: mortality decline and fertility decline. In the course of economic development and modernization, mortality drops first while fertility remains high, resulting in rapid population growth. Fertility rates then begin to fall, slowing down population growth and changing the age structure, from younger to older (Chesnais, 1990).

Mortality decline has received a great deal of attention (see Wilson, 2011) and we have a relatively good grasp of its causes: improvements of farming techniques, food production, and public sanitation contributed massively to disease reduction and increased life expectancy. The reasons for fertility decline, however, remain complex despite appearing straightforward.

At the macro level, indexes of development like HDI (human development index; Lee, 2003; Bryant, 2007; Myrskylä et al., 2009) and its constituent measures, namely, per capita income (Luci and Thévenon, 2011; Myrskylä et al., 2009; Barthold et al., 2012), education level (Lutz and Kc, 2011; Axinn and Barber, 2001), and life expectancy (Lutz et al., 2006; Luy et al., 2019), are all strongly and negatively associated with fertility rates, both across countries and over time within countries. Other correlates of fertility rates include child mortality, religiosity, urbanization and population density (Lutz et al., 2006), income inequality (de la Croix and Doepke, 2003), gender equality (Myrskylä et al., 2013; Feyrer et al., 2008; McDonald, 2000), and family planning uptake (Cleland and Wilson, 1987).

At the micro level, individual low fertility is correlated with high male and female education, in turn associated with lower mortality, longer life expectancy and higher child survival rates, and these effects are stronger in high fertility countries (Lutz and Kc, 2011; Basu, 2002). Fertility is also proximately regulated by later ages at first birth and greater control over reproductive spacing and stopping. In many cases, this is facilitated by contraceptive use (Cleland, 2009) and constrained by some "intermediate" fertility variables such as induced and spontaneous abortion, fecundability (the ability to conceive), and marriage (Bongaarts, 1982). With greater autonomy granted by changes of either labor participation or contraception methods, women appear to exercise more "control" over their reproduction and their desired family size decreases as macro-level development proceeds (Goldstein et al., 2003; Pritchett, 1994).

But fertility decline is not solely driven by socioeconomic factors, it also diffuses like an epidemic (Rogers, 1995b; Rosero-Bixby and Casterline, 1993; Spolaore and Wacziarg, 2022, see Cleland, 2001 and Colleran, 2016 for review). There is overwhelming evidence to suggest that fertility decline is spread by social interactions, both between individuals and between neighboring countries and regions. Moreover, fertility decline is diffused between countries at increasingly lower levels of economic development (Bongaarts and Watkins, 1996; Montgomery and Casterline, 1996), with different cultural settings influencing the patterns of diffusion and onset of fertility decline (Knodel and van de Walle, 1979). Thus fertility levels can vary greatly between neighbouring areas with similar socioeconomic characteristics (Lesthaeghe, 1977, 1983; Alvergne and Lummaa, 2014; Colleran et al., 2014). Indeed, the patterning of contraceptive uptake cannot be understood without assuming that new ideas are diffused along established communication lines, by migration and the mass media, which can readily cross international borders (Barber and Axinn, 2004; Behrman et al., 2002; Watkins, 1991; Cleland and Wilson, 1987). Contraceptive uptake is especially linked to micro level social interactions within social networks (Montgomery and Casterline, 1996; Rogers and Kincaid, 1981; Mace and Colleran, 2009; Colleran and Mace, 2015; Alvergne et al., 2011; Colleran, 2020). The evident connections between sociocultural factors and demographic transition indicate that the process is partly driven by the diffusion of new ideas and changes in perceptions (Axinn and Yabiku, 2001; Oppenheim Mason, 1997; Cleland and Wilson, 1987; Colleran, 2016).

Despite ample evidence for the above factors, they are mostly correlational indicators, few of which can be causally separated from one another. This means that what look like law-like patterns in fertility change across and within populations are associated with everything all at once. Our poor understanding of causality is clearer if we look at their temporal relationships. Although the Princeton European Fertility Project (Coale and Watkins, 1986) identified the historical fertility decline starting in 1830s France, several other studies in economic history consistently found even earlier records of the onset to be around 1770s in French rural areas (Spolaore and Wacziarg, 2022; Blanc and Wacziarg, 2020; Cummins, 2013; Hadeishi, 2003; Weir, 1995). However, none of the abovementioned correlates seemed to be important during this earlier period. For example, child mortality is often argued to be the most important explanation for fertility transition (e.g., Notestein, 1945). But in historical France, it was net fertility (i.e., average number of births minus deaths) that was declining (Blanc and Wacziarg, 2020). And in the 19th Century U.S., there was no meaningful mortality decline before fertility decline (Haines, 1994; Guinnane, 2011): this occurred only after 1900s when improved medical science led to greater longevity (McKeown, 1976; Fogel, 2004; Deaton, 2006). Overall, our understanding of the causes of fertility decline remains limited, particularly when we examine a multitude of complications at different levels of aggregation and the temporal relationships of various factors.

2 Evolutionary Perspectives

Fertility transitions are even more puzzling from an evolutionary perspective. Why does a great ape that outcompeted and out-reproduced its competitors, whose population size exploded with the advent of agriculture (the "Neolithic demographic transition", see Bocquet-Appel, 2011), reduce its fertility exactly when the environmental conditions for reproducing are the best in its entire history? Why does the process begin in the richest, most long-lived strata of society, and why is it more dramatic there (see Clark and Cummins, 2009; Livi-Bacci, 1986)? How can voluntary reductions in fertility be in line with Darwinian fitness (Borgerhoff Mulder, 1998; Colleran, 2016)?

In a 1986 paper, Vining suggested that this conundrum is an evolutionary paradox, the now oft-cited "central theoretical problem of human sociobiology" (Vining, 1986). Though this claim may be somewhat of an overstatement (see invited comments in Vining, 1986; Borgerhoff Mulder, 1998; Alvergne and Lummaa, 2014; Stulp and Barrett, 2016), Vining's clarion-call sparked debate about the fundamental causes of demographic transitions from an evolutionary perspective (Mace, 2000; Lawson and Mace, 2011; Shenk, 2009; Borgerhoff Mulder, 1998; Colleran, 2016). Standard demography, though empirically rich, has not produced a fundamental and unifying theoretical framework for understanding why fertility declines. Evolutionary researchers should therefore be well-positioned to fill this gap. Yet convergence on a single evolutionary explanation has not occurred, mainly because of differing assumptions about the mechanisms giving rise to low fertility, the question of whether fertility decline is adaptive or not, and a tendency for researchers to focus on either socioeconomic or sociocultural factors, as well as on individual versus population-level effects (Colleran, *Forthcoming*).

There are at least three starting points for an evolutionary approach to fertility decline. First, it could be the result of a mismatch between an evolved psychology and contemporary environments. Evolutionary Psychology (EP) asserts that our psychological biases evolved in ancestral environments over the last two million years, and that evolved strategies for achieving status and sex are therefore not adapted to the radical changes in industrialized economies (Cosmides and Tooby, 1987; Tooby and Cosmides, 1990; Buss, 2019). This "adaptive lag" (Laland et al., 2016) leads to low fertility when efficient contraceptives became available (Pérusse, 1993), severing the link between sex and reproduction. From this perspective, fertility decline is simply a "maladaption": our previously-adaptive psychology has not yet caught up with environmental change, and is not expected to maximize genetic fitness. This view, however, needs to demonstrate: (1) why fertility-limiting behavior has not been selected out of the population; (2) why fertility started to decline in historical Europe even before modern contraceptives emerged (e.g., Spolaore and Wacziarg, 2022;

Blanc and Wacziarg, 2020), and (3) must reconcile the fact that the availability of contraceptives does not necessarily lead either to their uptake (Polgar and Marshall, 1976; Marshall, 1977; Levine, 1983) or to fertility decline (Alvergne et al., 2013; Mace and Colleran, 2009; Bledsoe, 2002).

A second approach views low fertility as an adaptive strategy under contemporary environments. Taken by many human behavioral ecologists (HBEs), this approach stresses analysis of the costs and benefits of reproductive behavior in any context, but also the potential maximization of genetic fitness over multiple generations. The currencies of fitness being maximized include future gene representation (i.e., the number of descendants), the "quality" of offspring, or the accumulation of wealth over generations.

A third approach views fertility behavior as fundamentally shaped by information that is socially acquired, and is therefore the outcome of cultural evolutionary (CE) processes in structured environments. Cultural processes may follow Darwinian principles, but may nonetheless be maladaptive, i.e., not fitness-maximizing. In fact, asymmetric transmission of information, biases in the ways that individuals acquire social information, structural change in social interactions, or between-group competition, can all spread norms and values that lead to fitness-limiting behavior. Since both individual-level mechanisms and group-level dynamics are jointly considered, this approach offers a multi-level perspective that can engage both individual-level studies and longer-term population dynamics.

Importantly, although much evolutionary research on demographic transition is concerned with comparing the explanatory weight of hypotheses from HBE and CE (Lawson and Mace, 2011; Shenk, 2009; Borgerhoff Mulder, 1998), many researchers agree that socioeconomic and sociocultural factors are too deeply intertwined to be isolated from one other (Oppenheim Mason, 1997; Easterlin and Crimmins, 1985; Lesthaeghe, 1983; Caldwell, 1976). In fact, different explanatory frameworks make overlapping assumptions and predictions (Shenk, 2009; Borgerhoff Mulder, 1998; Colleran, 2016; Colleran, *Forthcoming*), so are not mutually exclusive (Smith, 2000). Indeed the assumptions of HBE and CE are often highly complementary. We explore these two theoretical frameworks in more detail below.

3 Human Behavioral Ecology

Human behavioral ecology (HBE) centers the idea that humans adapt to specific ecological conditions to maximize genetic representation in future generations (Nettle et al., 2013). Individuals must allocate limited time and energy among various life events (Kirkwood et al., 1991; Roff, 1992; Stearns, 1989, 1992) such as maturation, somatic maintenance and reproduction. When reproducing, parental decisions further involve when, how often, and how many children to have (Blurton Jones, 1986), and how to allocate resources between them (Lawson and Mace, 2011).

These fundamental trade-offs are reflected empirically in the facts that (1) reproducing more tends to reduce maternal survival (Lund et al., 1990), nutritional condition (Tracer, 1991), and life span (Westendorp and Kirkwood, 1998), (2) humans almost never exhibit maximal biological fertility (Lawson et al., 2012; though see Strassmann and Gillespie, 2002 for an exception), (3) very high fertility only appears to be sustainable in agricultural societies (Bentley et al., 1993; Bocquet-Appel, 2011) where the costs of reproduction can be partially compensated via food storage and reduced mobility (Bocquet-Appel, 2011), and (4) tight birth intervals (Blurton Jones, 1986) and high fertility (Strassmann and Gillespie, 2002; Lawson et al., 2012; Penn and Smith, 2007; Meij et al., 2009; Gillespie et al., 2008) are typically negatively associated with offspring survival, even though lowering fertility to improve child survival does not translate into greater lifetime reproductive output (Lawson et al., 2012; Penn and Smith, 2007; Meij et al., 2009; Gillespie et al., 2008; see Strassmann and Gillespie, 2002 as an exception).

3.1 Reproductive Trade-offs

Many researchers, both in the evolutionary and social sciences, view low fertility as a parental trade-off between child quantity and quality, where every unit decrease in quantity is assumed to lead to an increase in "quality" (Becker, 1960; Becker and Lewis, 1973). In the evolutionary literature, "quality" usually refers to "expected reproductive success" (Grafen, 1998; Goodman et al., 2012), and some researchers measure this in terms of levels of individual capital (i.e., different forms of wealth). Borgerhoff Mulder and Beheim (2011) (see also Borgerhoff Mulder et al., 2009) categorize three types — embodied, material, and relational capital. Each could influence parental investment and fertility differently, depending on the economic context.

Lowering fertility can potentially raise children's physical well-being, increasing their embodied capital (Kaplan et al., 1995; Kaplan, 1996). Body mass, strength, and immune system could function as fitness-enhancing currencies (Kaplan et al., 1995) in foraging economies. In market-based economies with low mortality and long life expectancies, embodied capital, i.e., knowledge and skills (which economists call "human capital"; Becker, 1994) contribute to an individual's ability to thrive, find a partner, and potentially reproduce (Kaplan, 1996). These arguments resonate strongly with economic theories on parents' fertility decisions (Becker, 1960; Becker and Lewis, 1973) in industrial societies, which are considered core to fertility decline.

In contrast to both foraging and market-dependant environments, pastoral and agricultural societies often rely relatively more on "material capital" (e.g., land, livestock, consumption goods, money), which can be stored, accumulated, and transferred to children across generations. This creates positive correlations between wealth and fertility in pre-demographic transition societies (Borgerhoff Mulder, 1987; von Rueden et al., 2011). This association is weaker or even negative in industrial settings, partly because the nature and value of wealth is also changing (Nettle and Pollet, 2008; Hopcroft, 2006, 2015; Colleran et al., 2015).

Embodied and material capital are considered "rivalrous": capital transferred to one child is unavailable to another. Parental investment trade-offs could therefore reduce the benefits of having large families. Relational capital does not necessarily suffer this limitation: parents' social networks can be shared among siblings and do not necessarily diminish with the number of children.

3.2 Wealth Inheritance and Intergenerational Mobility

Depending on the context and production mode, having more or fewer children may be beneficial for parents in terms of wealth flows across generations. Wealth can flow both down and up generations, e.g., from children to parents Caldwell (1976, 1978, 1982). This is an important feature of peasant or traditional agricultural economies (Caldwell, 1978) in which high fertility can be economically beneficial.

In market economies, both embodied and material capital can play different roles in children's success — reproductively or socio-economically. Theoretical models have shown that low fertility could coevolve with (material) wealth accumulation if reproductive success is tied to heritable wealth (Hill and Kern Reeve, 2005; Mace, 1996, 1998; Rogers, 1990) — this is important where wealth transfers at marriage (dowry, brideprice) are important. Mace (1996, 1998) combined dynamic models with ethnographic data to show that the wealth requirements of both marriage and the costs of raising children can decrease optimal fertility to very low levels. Rogers (1990) similarly showed, assuming a different economic context, that long-term fitness could theoretically be increased by lowering fertility in the short-run, though he was unable to obtain the same result in a more realistic model (Rogers, 1995a). Following Lack (1968), Grafen (1998) showed that if individuals differ in their reproductive value (i.e., expected reproductive success), parents should exhibit reproductive restraint to maximize the "value" of their children instead of the absolute number. This pursuit of reproductive value generates a null or negative relationship between wealth and fertility in post-demographic transition contexts (Grafen, 1998).

Empirically, studies that have tried to find long-term fitness advantages for low fertility have not been successful, though they do typically find evidence for wealth accumulation over successive generations (Kaplan et al., 1995; Mueller, 2001; Goodman et al., 2012). Yet for low fertility to be genetically advantageous, there must be a fitness payoff to having high-quality children over multiple generations. It is unclear at present how many generations should be considered, and whether children really differ in their reproductive value.

Lowering fertility for long-term reproductive success might be driven by social stratification. Since the dilution of resources between large numbers of children increases the chances of downward intergenerational social mobility (i.e., ending up in a "lower" social class than one's parents), in stratified societies, low fertility may help avoid this outcome and/or increase the chances of upward social mobility (Lesthaeghe, 1977; Van Bavel, 2006; Van Bavel et al., 2011; Harpending and Rogers, 1990). Harpending and Rogers (1990) argue that small family sizes evolved to avoid downward social mobility when social classes have different reproductive outcomes. In their model, individuals in lower social strata could end up with lower long-term (i.e., multi-generational) fitness than individuals in higher strata, despite having more children in the first generation. Downwardly mobile individuals from the poorer stratum could end up in a "destitute" social class at the bottom of the hierarchy, with reproduction being compromised (Harpending and Rogers, 1990). Relatively poorer individuals could achieve higher long-term fitness by getting one of their offspring into a higher social class, leading natural selection to favor those who reduce fertility accordingly.

There is some evidence of fertility limitation as a response to poverty (Gurmu and Mace, 2008). Two studies of nineteenth century Belgium also find that individuals with more siblings had higher chances of downward mobility, independent of parental social status and birth order (Van Bavel, 2006; Van Bavel et al., 2011). Although low fertility might avoid downward mobility among the relatively wealthy, the same strategy has not been shown to help the poor to gain upward mobility (Van Bavel et al., 2011). Skjærvø et al. (2011) show that among historical Norwegians in the early nineteenth century, women moving down a social class had significantly lower lifetime fertility than women who moved up from an initially lower one, and women maintaining their position in the highest class had the highest lifetime fertility. Downward mobility therefore appears more costly than upward mobility is beneficial. This fits with the well-documented phenomenon that the wealthy tend to initiate fertility decline earlier and often more dramatically than the poor (Livi-Bacci, 1986).

3.3 Environmental Risks

Reproductive trade-offs are always subject to environmental changes. Winterhalder and Leslie (2002) and Leslie and Winterhalder (2002) argue that reproduction is risk- or variance sensitive. Individuals may over-produce when mortality uncertainty is high and under-produce when it is low. Using historical multi-generational data from Finland, Liu et al. (2012) similarly argue that fertility decline may be a response to the reduced risk of "breeding failure" (i.e., not raising any offspring to maturity) rather than a direct response to mortality declines. As uncertainty about survival to reproductive age goes down, the "required" threshold of fertility to avoid maternal "breeding failure" is also reduced.

Reduced fertility may trade-off with greater survivorship under periodic environmental crises. Boone and Kessler (1999) show that if population history is characterised by climatic or other stochastic events, individuals can increase the probability of lineage survival by having fewer offspring and expending more on their surviving capacity or social status (Low et al., 2002; Low et al., 2003; see Shenk et al., 2016 for similar arguments). It is easy to imagine that when resources become scarce or limited in a population bottleneck, access is likely to be inequitable, skewed towards the wealthy and high status (Low et al., 2002; Low et al., 2003; see also Boone and Kessler, 1999). Given the extreme climatic and environmental variation experienced during the Pleistocene, such bottlenecks are plausible. However, stochastic fluctuations of such magnitude were unlikely since the Neolithic period, so the enormous increases in fertility during the Neolithic transition could represent a relaxation of this trade-off.

3.4 Social Interactions and Kinship

Reproductive decisions are not only about optimal energetic investments. They include strategic considerations within a social environment, and parents might adjust their fertility decisions based on others' behavior. For example, Shenk et al. (2016) show that under high inequality and intense competition for status, higher parental investment in embodied capital and social status may lead to lower fertility. A number of theoretical models have also shown that competition between lineages for survival, rather than individual maximization of fitness, may be responsible for the evolution of low fertility (Boone and Kessler, 1999; Grafen, 1998; Low et al., 2002; Hill and Kern Reeve, 2005). The "snowballing resource competition" between individuals thus leads to ever-increased investment in the resource-earning potential of ever-decreasing numbers of children (Hill and Kern Reeve, 2005).

Competition for heritable assets among siblings can also lead to low fertility (Kaplan, 1996; Kaplan et al., 2002; Lawson and Mace, 2009, 2010a, 2011). There is evidence that mental health (Lawson and Mace, 2010b), height (Lawson and Mace, 2008), educational achievement (Desai, 1995), and parental care (Lawson and Mace, 2009) are compromised in larger families. Competition may be exacerbated by the level of wealth or development in a society (Lawson and Mace, 2010a). Early in demographic transitions, wealthier families may invest relatively more in "embodied" capital such as education, while simultaneously discriminating between children in their allocation of resources (Gibson and Sear, 2010). Sudden changes in land availability or rural development initiatives can also create novel competition between siblings for parental investment (Gibson and Gurmu, 2011). In wealthy populations where uncontested cushions against absolute poverty are available (e.g. medical care, social welfare), competition between offspring for the family's resources may increase (Lawson and Mace, 2010a; Downey, 2001).

Reproductive outcomes are often negotiations between the conflicting interests of multiple kin, and should be understood within the "kinship ecology" (Leonetti et al., 2007; Leonetti and Nath, 2009; see also Grafen, 1984). Sibling competition (Trivers, 1974) can be relaxed if extended kin step in to help (reviewed in Sear and Mace, 2008), or siblings might act as "helpers at the nest", forfeiting their own reproduction to assist that of their siblings (Kramer, 2005, 2010; Crognier et al., 2001, 2002; Turke, 1988). There may also be reproductive conflict between different generations of females: trade-offs between one's own reproduction and that of daughters or daughters-in-law. This is one hypothesis for the evolution of human menopause and post-reproductive lifespans (Lahdenperå et al., 2012; Mace and Alvergne, 2012; Cant and Johnstone, 2008; Voland and Beise, 2005; Fox et al., 2010).

Kin have been shown to have effects on infant survival (reviewed in Sear and Mace, 2008), female fertility (reviewed in Sear and Coall, 2011), and to some extent, contraceptive use (Borgerhoff Mulder, 2009; Leonetti et al., 2007, though see Mace et al., 2006; Mace and Colleran, 2009; Alvergne et al., 2011). Diverse types of allocare enabled humans to outpace the reproduction of other great apes despite a shorter reproductive window, and give rise to uniquely human life history characteristics (e.g., elongated childhood, extensive allocare and lengthy post-reproductive lifespans). Kinship appears so important to our success as a species that many now consider homo sapiens an obligate "cooperative breeder" (Alexander, 1974; Hrdy, 1999; Hrdy, 2007; Hrdy, 2009; Mace and Sear, 2005; Sear and Mace, 2008; though see Strassmann and Kurapati, 2010; Strassmann, 2011 for critique. See also Clutton-Brock, 1991).

3.5 Summary

HBE has contributed significantly to our understanding of variation in reproductive behavior. At its core, an optimality model assumes that individuals are rational reproducers who make reproductive trade-offs based on complete information and perfect cognitive capabilities (Colleran, *Forthcoming*). Despite its strengths, some predictions have only limited empirical support (see Lawson and Mulder, 2016): trade-offs between fertility and offspring survival or long-term reproductive success do not always align with predicted patterns. Additionally, measuring concepts like reproductive value remains challenging. Focusing on the historical and cultural contexts that shape human behavior will generate more comprehensive models that better capture the complexity of human reproductive decision-making.

4 Cultural Evolution

CE studies social and behavioral changes due to information acquired from conspecifics in a population. Defined as socially transmitted information, culture (Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985), on this model, spreads via the interaction of various modes of transmission at the population level and learning biases at the individual level (Colleran, *Forthcoming*).

CE highlights different transmission modes, of which oblique and horizontal transmission are especially crucial in explaining low fertility behavior. Combined with learning heuristics such as indirect and conformist biase, these can in principle accelerate the spread of behavior that is not fitness-enhancing.

Unlike models assuming optimality at the individual level in HBE or economics, CE theory does not necessarily assume specific forms of utility or payoff functions at the individual level. Instead, it looks at trait frequencies in the population and stresses more the structured (demographic or social) and constructed aspects of social environments (e.g., norms, values, and traditions) which operate at both the individual and group level.

4.1 Transmission Modes of Fertility Values

Consider that women probably inherit reproductive behavior, values and norms initially from their parents, especially their mothers, via vertical transmission. Empirically, fertility and its intermediate indicators such as age at marriage and age at last birth are positively correlated between mothers and daughters (Anderton et al., 1987; Murphy, 1999; Murphy and Wang, 2001; Reher et al., 2008; Jennings et al., 2012), and these associations are stronger in the post-demographic transition era (Murphy, 1999; Reher et al., 2008; Jennings et al., 2012). Although some argue this is a genetic process (Bocquet-Appel and Jakobi, 1993; Kohler et al., 1999; Madrigal et al., 2003; Blum et al., 2006; Pettay et al., 2005; Kosova et al., 2010), numerous studies suggest that transmissions of reproductive-related values (e.g., ideal family size, contraceptive use), childrearing practices (e.g., prolonged breastfeeding), and childrearing environments (e.g., help from mothers or other family members) are important social mechanisms increasing observed intergenerational similarities (Jennings et al., 2012; Reher et al., 2008).

On reaching maturity, women are often exposed, via their social interactions, to the reproductive norms of non-kin in their social environments (e.g., Balbo and Barban, 2014; Colleran, 2020). In contrast to genetic inheritance, this allows oblique and horizontal transmission of norms from non-parental individuals to additionally shape behaviour. Since non-kin have no genetic stake in a woman's reproductive success according to inclusive fitness theory (Hamilton, 1964), they may be less pronatal than kin (Newson et al., 2005). Using a role-play experiment, Newson et al. (2007) argues for a "kin influence hypothesis" (Newson et al., 2005) — participants primed to role-play a mother were more pronatal than those who were not.

Apart from reproductive attitudes, oblique and horizontal transmission also spread knowledge and practices about contraceptive use (Gayen and Raeside, 2010; Colleran and Mace, 2015; Denton et al., 2023), health services, childcare alternatives, or even the compatibility between parental roles and labor force participation (Montgomery and Casterline, 1996). For example, during the 1950s, U.S. women were not expected to work until their children reached school age. With industrialization and attitudinal change, it became more acceptable for women to balance family and employment, and the percentage of parents who believed "a pre-school kid is likely to suffer if his/her mother works" gradually decreased over time (Rindfuss and Brewster, 1996). Without family policies such as mandated paid leave, however, labor participation and childrearing responsibilities are somewhat incompatible, driving down fertility. It was not until institutionalized childcare became widely available, allowing women to combine work and parenthood, that the fertility rates started to climb again.

4.2 Modernization

The role of modernization in fertility transitions is crucial. There have been tremendous structural changes in social networks due to urbanization, mass communication, commercial activities, migration, education and employment. When non-kin/peers make up a higher proportion of our social interactions, their relative influence becomes more prominent. Non-kin are assumed by evolutionary anthropologists to be less pronatal, opening up the possibility for them to be the driving force of low fertility behavior in contemporary social networks (Newson et al., 2005, 2007; Newson, 2009; Newson and Richerson, 2009; Colleran, 2020). Compared to vertical transmission, oblique and horizontal transmission between non-kin/peers have an asymmetric feature whereby one individual can transmit information to many individuals (Cavalli-Sforza and Feldman, 1981), and this can spread new cultural traits even more efficiently in modern societies.

Prestige bias (Henrich and Gil-White, 2001) may play a particularly important role in explaining fertility decline in contemporary market economies, where individuals compete to achieve higher social status. Status competition create opportunities for individuals in high-prestige positions, such as teachers, to become "social models" that others imitate. This imitation is not limited to practices related to status-seeking, such as education, but also extends to fertility-reducing behaviors that these individuals engage in to achieve their high status. This "indirect bias" (Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985; Richerson and Boyd, 2005) generates associations between fertility-limiting behavior and status-seeking, and can stimulate low-fertility norms. Combined with asymmetric (one-to-many) oblique and horizontal transmission, the prominence of these role models can accelerate change even further (see also Colleran et al., 2014 on education).

4.3 Cultural Niche Construction

Humans are cultural niche constructors, altering their environments and consequently changing the selection pressures acting on them (Laland et al., 2001, 2007; Laland and Brown, 2006). Consider the situation where the distribution of one cultural trait, such as a preference for education, creates the cultural background for the percolation of a second cultural trait, e.g., a fertility-reducing preference (Ihara and W. Feldman, 2004). Denton et al. (2023) developed a model of the adoption of contraceptives in such a "constructed" environment with a background preference among individuals for education. Constructed cultural niches such as this could influence transmission probabilities even beyond local populations, which in turn could lead to various onsets and dynamics of fertility transition in different regions. A prominent feature of modern demographic transitions is that while fertility rates decrease with development (Notestein, 1953), the dynamics and pace vary substantially among different countries (Bongaarts and Watkins, 1996). Less developed countries are experiencing earlier onsets compared to historical contexts, due to the informational or ideational influences of neighboring, more-developed countries, which have higher rates of acceptance of contraceptives or small-family norms (Bongaarts and Watkins, 1996; Amin et al., 2002). Extending Ihara and W. Feldman (2004), Borenstein et al. (2006) developed a metapopulation model to illustrate such a situation. Each subpopulation, or group, has its own background context such as a particular average education level that can differentially facilitate the spread of low fertility in the group. The mean education in a group determined how sensitive the individuals were to the frequency of low fertility preferences in the metapopulation overall. In other words, the spread of low fertility in a particular group was influenced not only by the average education level in that group, but also by the overall education level and the prevalence of low fertility in the metapopulation as a whole. Because of the variation in education levels between groups, low fertility spreads not only within but also between them. This can explain why populations experience fertility declines at different economic levels, even though the decline begins in wealthy populations at first (Bongaarts and Watkins, 1996; Borenstein et al., 2006).

These models advance our understanding of how contextual factors at the group level might influence the cultural transmission of low fertility. They highlight the interactive and multilevel quality of these dynamics, i.e., the feedback between individuals and higher levels of social aggregation. They also clearly show how group-level characteristics, such as average wealth or education, influence individual propensities to pursue a strategy of low fertility. These dynamics need to be reflected in empirical work (see Colleran et al., 2014; 2015 for example). While some models above assume structured populations (see also Fogarty et al., 2019; Deffner et al., 2022), socioeconomic strata might be impacted by the average wealth in a group differently, or individuals at different periods of life may use different learning strategies. Taking socioeconomic strata or age cohorts into account might further complicate the dynamics and probably alter the model outcomes.

4.4 Cultural Group Selection

An argument that is not often made in the CE literature is that low fertility could be culturally group selected (see Henrich, 2004). That is, low fertility, while maladaptive at the individual level, may be adaptive at the group level. For this to work, groups composed of individuals with low fertility should outcompete groups composed of individuals with high fertility, and the advantage should be at the group and not necessarily the individual level.

An example of such a group level benefit comes from global economic development. One of the fundamental socioecological differences between pre- and post-industrialized societies is the extent to which populations interact with and depend on each other in international trade and supply networks (see Dang and Bauch, 2010, and references therein). Thus macro level competition and cooperation between populations or countries may have created a selective pressure for individuals within groups to invest in "embodied capital" and market-oriented skills, which are needed for the continued growth of the economy (Becker, 1994). Variation in the resource base and developmental trajectory of different countries (see Sachs, 2000) would then result in country-level variation in "reproductive equilibria", on which cultural group selection could potentially act.

Lower fertility is typical in wealthier (Bloom, 2011; Sinding, 2009; see also Mace, 2008) and more market-dependent (Reher, 2012) groups, and Moses and Brown (2003) find that there is a negative allometric relationship between national fertility rates and per capita energy consumption, coinciding with many biological laws (West et al., 1999; Peters, 1983). Increases in international trade have also been shown to have a negative effect on fertility rates within a country (Doces, 2011; Galor and Mountford, 2008). As countries become more dependent on technology and innovation for economic productivity, those that share international research and development (RD) and bilateral foreign direct investment (FDI) are more economically productive than those that do not cooperate in this way (Borensztein et al., 1998; Keller, 2000). The exchange of capital, technology, and labor thus effectively down-regulates each other's fertility rates, as shown in theoretical models of population biology (Bauch, 2008; Dang and Bauch, 2010).

Countries that offer better living conditions might be more successful in spreading their values and gaining influence through attracting more migration (Richerson and Boyd, 2008). Cultural group selection operating on such between-group differences is therefore in principle possible, though it is as yet an untested hypothesis. Empirical evidence would need to establish what groups are competing for, and whether benefits at the group level outweigh individual fitness costs. It would also be important to rule out that such phenomena are driven by individual level selection. If individuals with lower fertility simply do better on average than individuals with higher fertility, group level advantages would not be necessary to explain the phenomenon.

As Bongaarts and Watkins (1996) note, fertility decline takes place in a nested set of interactions involving individuals living in social networks, kinship ecologies, socioeconomic classes, or communities, and by interactions between communities themselves, and finally by interactions between countries in a global network. All of these levels should be investigated in future research.

5 Speaking with Social Sciences

5.1 The Divide and Its Consequences

In previous sections, we have focused on how evolutionary theories offer first-principle explanations for fertility transition. These explanations are rarely referred to in the broader social sciences of demography, sociology, and economics, which have accumulated a huge amount of literature on the same topic. The reasons for this divide range from fears of a resurgence of Social Darwinism (Degler, 1991; Leyva, 2009) and/or misunderstandings about what contemporary evolutionary research concerns are (Colleran and Mace, 2011), to resistance (van den Berghe, 1990; Pinker, 2002; Ellis,

1996) or limited exposure (Ellis, 1996; Thayer, 2004; Takács, 2018) to evolutionary concepts, and epistemological critiques (Bryant, 2004; Gould, 1981; Lewontin et al., 1984; Turner and Machalek, 2018). The time scale and resolution of research questions also differ significantly, with evolutionary theories focusing on long-term, cross-species perspectives, while non-evolutionary fields study short-term phenomena within specific institutions, countries, and time periods. Additionally, traditional social sciences are often policy-oriented, which diverts researchers' attention from purely theoretical or evolutionary understandings of their research topics to applied ones.

The consequences of this differentiation are parallel disciplines that do not engage each other. For example, (a) social learning and its macro-level outcomes is core business in cultural evolution. But in other fields like experimental economics and behavioral game theory (see Camerer, 2003; Fudenberg and Levine, 1998, for general introduction), learning mechanisms are elaborated differently. Individuals make strategic decisions and adjustments to outcomes from interactive environments according to learning rules like belief learning and fictitious play (Cournot, 1838; Brown, 1951; Robinson, 1951; Cheung and Friedman, 1997), reinforcement learning (Bush and Mosteller, 1955; Arthur, 1991, 1993; McAllister, 1991; Roth and Erev, 1995; Mookherjee and Sopher, 1997; Sarin and Vahid, 2001), and experience-weighted attraction (EWA) learning (Camerer and Hua Ho, 1999), etc. These learning rules describe human cognition and decision-making in a more fine-grained way and could potentially offer complementary insights for cultural evolutionists.

The macro-patterns, e.g., of information transmission, that cultural evolutionists are interested in are also studied in adjacent fields. One of these is the s-shaped adoption curves generated (though not uniquely) by conformist transmission or positive frequency-dependence (Boyd and Richerson, 1985; Henrich and Gil-White, 2001), whereby individuals conform disproportionately as the majority trait in a population increases. A similar pattern is common in many other social and natural processes and is not unique to cultural change. Disease transmission, the accumulation of crowd size in a social movement, the acceptance of international norms such as the nuclear taboo, responsibility to protect (R2P), and human rights, all share the same dynamic, and have been discussed extensively in political science, sociology, public health, communication studies, etc. The literature we cited in the first section from economics, namely Spolaore and Wacziarg (2022) and Montgomery and Casterline (1996), attempt to describe this spreading process without referring to any evolutionary concept. By engaging in interdisciplinary conversations, cultural evolution could become a useful analytic framework for other research areas. Conversely, empirical case studies from a wide range of disciplines can also aid the theoretical development of cultural evolution.

5.2 Scientific Implications

Social phenomena are notoriously difficult to measure, predict, and explain. When evidence is triangulated via different scientific assumptions and disciplinary traditions, we can potentially be more confident in our general insights. However, isolated intellectual endeavors also create blind spots. Inter-disciplinary conversations are essential for identifying them. For example, reproductive decisions in HBE involve intergenerational fitness maximization and resource distribution concerns. But according to the "decision sciences" (e.g., psychology, behavioral economics, and neuroeconomics), humans discount benefits in the remote future and behave myopically (Frederick et al., 2002; Doyle, 2012; Odum, 2011), and there is a great deal of behavioral evidence for this (e.g., Thaler, 1981; Wang et al., 2016). The upshot is that, even were parents able to make optimized fertility plans, the revealed behavior might not be consistent with any calculation, regardless of what level rationality is operated on. Indeed, numerous studies have found a mismatch between people's fertility intentions and their actualized fertility (e.g., Müller et al., 2022). Figuring out how to reconcile these findings might shed light on gaps as well as overlaps in different research areas on reproductive decision-making.

There are benefits to going beyond disciplinary borders. Cultural evolution focuses on cultural transmission that leads to aggregated change. Social media provides a great arena to study this kind of information spread. The blossoming studies of computational social science using digital trace data to track mis/disinformation, political opinion, and hate speech offer methodological tools for studying the spread of fertility norms or other reproductive practices (see also Acerbi, 2020). One important question is how information diffusion differs between larger and smaller-scale contexts, between different economic systems (e.g., agricultural and other subsistence structures) and between countries at different levels of international development. What are the implications for fertility behavior? We must aim to be specific about what exactly is being transmitted, given that we often can have multiple unmeasurable motivations for a single observed behavior (Colleran, 2016).

Cultural evolution has generated numerous excellent models for explaining fertility transition (e.g., Ihara and W. Feldman, 2004; Bongaarts and Watkins, 1996). Yet, these models are not designed to meet empirical data, and don't equally apply in all regions, periods, subgroups, policy contexts, or simply where people respond to incentives differently. We know very little about how cultural evolutionary processes interact with varied economic conditions, with economic growth and hardship, developmental trajectories, labor markets, and wealth inequality. How do political systems, political stability (Feng et al., 2000), and political attitudes (Fieder and Huber, 2018) affect them? How do cultural evolutionary processes relate to social trends like migration, or public policies like social welfare, parenting, and childcare policies? Finally, how do they respond to historical events like pandemics, wars, and baby booms? All of these events can be understood as culturally niche-constructed, yet they remain different social phenomena occurring over different time scales and under different contexts. To what extent can they be captured by CE models?

Finally, transdisciplinary approaches can provide non-obvious interpretations. Fertility transitions are bio-social phenomena, and severe endogeneity problems make it extremely hard to parse causality from our observations. Variations in institutions and policies (e.g., Gibson and Gurmu, 2011; Gibson and Lawson, 2011) implemented in different regions and subpopulations can also be viewed as different treatment exposures in so-called "natural experiments" (see Dunning, 2012). Causal inference tools already widely used in economics and political science (e.g., Cunningham, 2021; Huntington-Klein, 2022; Imai et al., 2011; Blackwell, 2013; Keele, 2015; Ho et al., 2007), and are increasingly popular in cultural evolution. Alongside clear study designs and conditional comparisons, we can begin to analyze our questions within the broader ecosystem of the social sciences.

6 Conclusion

Fertility transition is a complex phenomenon, constrained by biological processes and deeply intertwined with our social institutions. We have reviewed studies from anthropology, demography, and economics to outline some of the patterns of fertility transition. We then focused on attempts from human evolutionary ecology and cultural evolution to understand these patterns, stressing the importance of both socioeconomic and socio-cultural interpretations. We highlight that cultural evolution, as a multilevel framework, incorporates not only factors at individual and group levels, but also the feedback between them.

Taking inspiration from population genetics, the theoretically rich discipline of cultural evolution has laid out a unifying analytical framework, with much to offer for studying interactions between fertility behavior and trends in human history and societies. An important direction for future work though is to discern if the insights produced by those theoretical explorations are reflected in the empirical world. This involves collecting multi-level data on social learning processes, inspecting the dynamics outlined in models of cultural niche construction, and validating the concepts of cultural group selection. Guided by theoretical models, finer-grained data can in turn inform or modify our theory development to avoid equifinality (Premo, 2010), or underdetermination (Lake, 2015), and to verify our inferences. Cross-disciplinary conversation with other social sciences will help cultural evolutionists develop further our insights into human fertility behavior.

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