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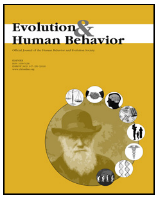

The heritability of fertility makes world population stabilization unlikely in the foreseeable future

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ABSTRACT

The forecasting of the future growth of world population is of critical importance to anticipate and address a wide range of global challenges. The United Nations produces forecasts of fertility and world population every two years. As part of these forecasts, they model fertility levels in post-demographic transition countries as tending toward a long-term mean, leading to forecasts of flat or declining population in these countries. We substitute this assumption of constant long-term fertility with a dynamic model, theoretically founded in evolutionary biology, with heritable fertility. Rather than stabilizing around a long-term level for post-demographic transition countries, fertility tends to increase as children from larger families represent a larger share of the population and partly share their parents' trait of having more offspring. Our results suggest that world population will grow larger in the future than currently anticipated.

1. Introduction

The United Nations Population Division produces regular global population estimates and projections through its World Population Prospects series (United Nations, Department of Economic and Social Affairs, Population Division, 2015; United Nations, Department of Economic and Social Affairs, Population Division, 2017). These projections are critical to understanding the sustainability and geopolitical stability challenges the world will face (Demeny, 2012; Lee, 2011). In 2014, the United Nations shifted to a Bayesian probabilistic methodology in projecting world population. Probabilistic projections were derived for the two major components of demographic change – fertility and life expectancy – and these were used to construct the population forecasts (United Nations, Department of Economic and Social Affairs, Population Division, 2014). Fertility in the post-demographic transition period is modeled as oscillating around a long-term mean estimated through a Bayesian hierarchical model. This shift in methodology showed that the stabilization of the world population was unlikely this century (only 30% probability) (Gerland et al., 2014), unlike in previous forecasts. This data-driven methodology represents a significant improvement as it provides estimates of the uncertainty around the future levels of population and fertility.

In this paper, we build on this approach and substitute the hypothesis of a long-term mean fertility with a model of fertility grounded in evolutionary demography. This choice is informed by the fact that fertility in post-transition societies is a heritable trait; that is, a proportion of the variation in the fertility in the population is due to genetic variation (Kirk et al., 2001; Murphy, 1999; Rodgers et al., 2001a; Rodgers, Kohler, Kyvik, & Christensen, 2001b). In this paper, we will use the term heritability to refer to “genetic heritability”, as we distinguish it from the possible role of cultural inheritance.

Our approach allows us to provide an alternative forecast of future fertility and population. We demonstrate that any forecast without an evolutionary underpinning may underestimate future fertility and population growth, and we provide a sense of the scale of that underestimation. However, this alternative perspective of future fertility and population is not a definitive declaration of its future path. This forecast, like that of the United Nations, could be influenced by future cultural or environmental changes, meaning that the increase in the fertility rate may ultimately occur more or less rapidly than described in this paper.

2. The genetic heritability of fertility

Heritability is defined as the proportion of the phenotypic variation attributed to genes. Quantitative genetic models make it possible to estimate the heritability of a trait and compare it to the proportion of variation which can be attributed to the shared environment (such as

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the family environment that siblings share, including culturally transmitted traits), and to the non-shared environment (the residual).

Natural selection tends to eliminate genetic variation in traits linked to reproductive success, with that elimination more rapid the stronger the link. Those traits associated with higher fertility outcompete traits associated with lower fertility, eliminating the low-fertility traits from the population and leaving the high-fertility trait at fixation. As a result, it might be expected that the heritability of fertility would be low or zero, with all of the population sharing the same fertility related traits. For pre-twentieth century populations that had not undergone a demographic transition, this appears to be the case (Murphy, 1999; Rodgers, Kohler, et al., 2001b).

However, changes in the environment can change the way in which genetically based variation in traits may affect fitness (Fisher, 1930). In the case of fertility, any of the environmental changes hypothesised to have caused the demographic transition – such as changed preference for quantity of children (Becker & Lewis, 1974; Galor & Weil, 2000; Preston, 1978) or increased effectiveness of contraceptive devices (Becker, 1960) – could have increased the heritability of fertility. People with different genetic variants respond to these environmental changes in different ways, leading to that genetic variation affecting fertility outcomes. In considering how these environmental changes affect heritability, “fertility” might be thought of as a composite of “sub-traits” that affect the number of offspring. These sub-traits might include the preference for children, personality traits such as conscientiousness, ability to accrue resources to attract mates, and physiological factors. For the purposes of this paper, we are agnostic as to the particular causal relationship with fertility but rely on the heritability of fertility itself.

In countries that have undergone the demographic transition, twin, adoption and family studies have pointed to a substantial genetic effect on fertility (Fisher, 1930; Kirk et al., 2001; Kohler, Rodgers, & Christensen, 1999; Murphy, 1999; Murphy & Knudsen, 2002; Rodgers, Hughes, et al., 2001a; Rodgers, Kohler, et al., 2001b). For example, Fisher (Fisher, 1930) found that a woman could expect 0.21 additional children for each additional child that her mother had, and 0.11 additional children for each additional child that her grandmother had. From this, Fisher suggested that the heritability of fertility at that time was 0.4 (40% of the variation in fertility is explained by genetic factors). Summarising research conducted through to 1999, Murphy (Murphy, 1999) noted that the heritability of fertility averaged around 0.2 in post-demographic transition societies, with the estimates increasing in recent periods. Kohler et al. (Kohler et al., 1999) examined data on Danish twins born in the periods 1870 to 1910 and 1953 to 1964. The first period covers the demographic transition and the second the end of the baby boom. In the first cohort, the heritability of fertility in women varied from close to zero in the pre-transition period to as high as 0.4 to 0.5 during the demographic transition. Estimates of heritability remained strong for the 1953 to 1964 cohort. From an analysis of data for Danish twins from the 1950s, Rodgers et al. (Rodgers, Kohler, et al., 2001b), attributed slightly more than one quarter of the variation in fertility to genetic factors. Rodgers and Doubty (Rodgers & Doughty, 2000) found a median heritability of 0.33 in a contemporary United States population, and heritabilities for underlying desires, ideals and expectations ranging between 0.24 and 0.76. Where measured, the variance attributable to shared environment in low-fertility populations was generally lower than the genetic effects (Kirk et al., 2001; Kohler et al., 1999; Kohler, Rodgers, Miller, Skytthe, & Christensen, 2006; Zietsch, Kuja-Halkola, Walum, & Verweij, 2014). However, the relative balance of genetic and shared environmental factors can change quickly over time (Kohler et al., 1999; Kohler et al., 2006).

That fertility is genetically heritable has also been supported by genome-wide complex trait analyses (GTCA) analysis, which uses the genetic and phenotypic similarity between unrelated individuals to examine the effect of common genetic variants on fertility (Tropf et al., 2015).

As a result of the heritability of fertility, the children of those with higher fertility will tend themselves to have higher fertility. As an illustration, Murphy and Knudsen (Murphy & Knudsen, 2002) observed in a Danish population sample that those from larger families have a disproportionate contribution on both the next generation and on numbers of more distant kin. In that case, the 8.8% of those with four or more siblings born in the 1968–69 cohort were responsible for 15.1% of births to this cohort through to the end of 1994.

This is further reflected in evidence of a link between number of children and number of grandchildren (Irons, 1998; Kaplan, 1996; Kaplan, Lancaster, Johnson, & Endler, 1995; Zietsch et al., 2014). Kaplan et al. (Kaplan et al., 1995) found a near linear relationship between the number of children and number of grandchildren and Zietsch et al. (Zietsch et al., 2014) found that the genetic influences on number of offspring and number of grand-offspring are identical. The link between offspring and grand-offspring suggests that the potential trade-off between number of offspring and the reproductive success of those offspring is minor and does not prevent high fertility being transmitted across generations.

Accordingly, over the long term, natural selection will push toward an increase in fertility rates (Fisher, 1930). This fact has recently started to be modeled by researchers (Burger & Delong, 2016; Kolk, Cownden, & Enquist, 2014). While natural selection is usually thought as taking a long time, genetic selection on fertility could result in material changes in aggregate population fertility and population size within several generations (Collins & Richards, 2013; Murphy & Wang, 2002). Natural selection has been found to be occurring in modern human populations, including on traits directly related to fertility such as age at menarche, age of first birth, age of menopause (Byars, Ewbank, Govindaraju, & Stearns, 2009; Helle, 2008; Kirk et al., 2001).

3. Model specification

Raftery et al. (Raftery, Alkema, & Gerland, 2014) developed a Bayesian method for producing probabilistic population projections. Population projections are built on Bayesian hierarchical models for the total fertility rate and life expectancy at birth. This methodology has now been adopted by the United Nations as part of its World Population Prospects series, including the 2015 and 2017 Revisions (United Nations, Department of Economic and Social Affairs, Population Division, 2015). Our model for fertility, life expectancy and population is built on this methodology described in Raftery et al. (Raftery et al., 2014) (the ‘base model’) and as implemented in the R statistical packages bayesTFR, bayesLife, bayesPop and wpp2017 (Sevcikova, 2018; Sevcikova, Alkema, Raftery, Fosdick, & Gerland, 2018; Sevcikova, Raftery, & Buettner, 2017b; Sevcikova, Raftery, & Chunn, 2017a). The base model has the total fertility rate model pass through three phases using the methodology described in Alkema et al. (Alkema et al., 2011).

Phase I is a pre-transition high-fertility phase, where fertility is stable or increasing. All countries have now completed Phase I, so this phase is not of relevance to modern fertility projections. Phase II is a transitional phase involving a decline in the fertility rate to below the replacement total fertility rate of 2.1, and is modeled using a hierarchical model estimated using Markov chain Monte Carlo. It takes a country-specific double logistic form. We also adopt this methodology for Phase II. Phase III is the post-transition period. The model for Phase III, which assumes an oscillation around a long term mean μ_c, is an autoregressive [AR(1)] model expressed as:

$$f_{c,t+1} - \mu_c = \rho_c(f_{c,t} - \mu_c) + \varepsilon_{c,t} \tag{1}$$

$$\varepsilon_{c,t} \sim \mathrm{N}(0, \sigma_\varepsilon^2)$$

where $f_{c,t}$ is the fertility rate of country c in five-year time period t, and ρ_c is the rate of regression to the long-term mean in that country.

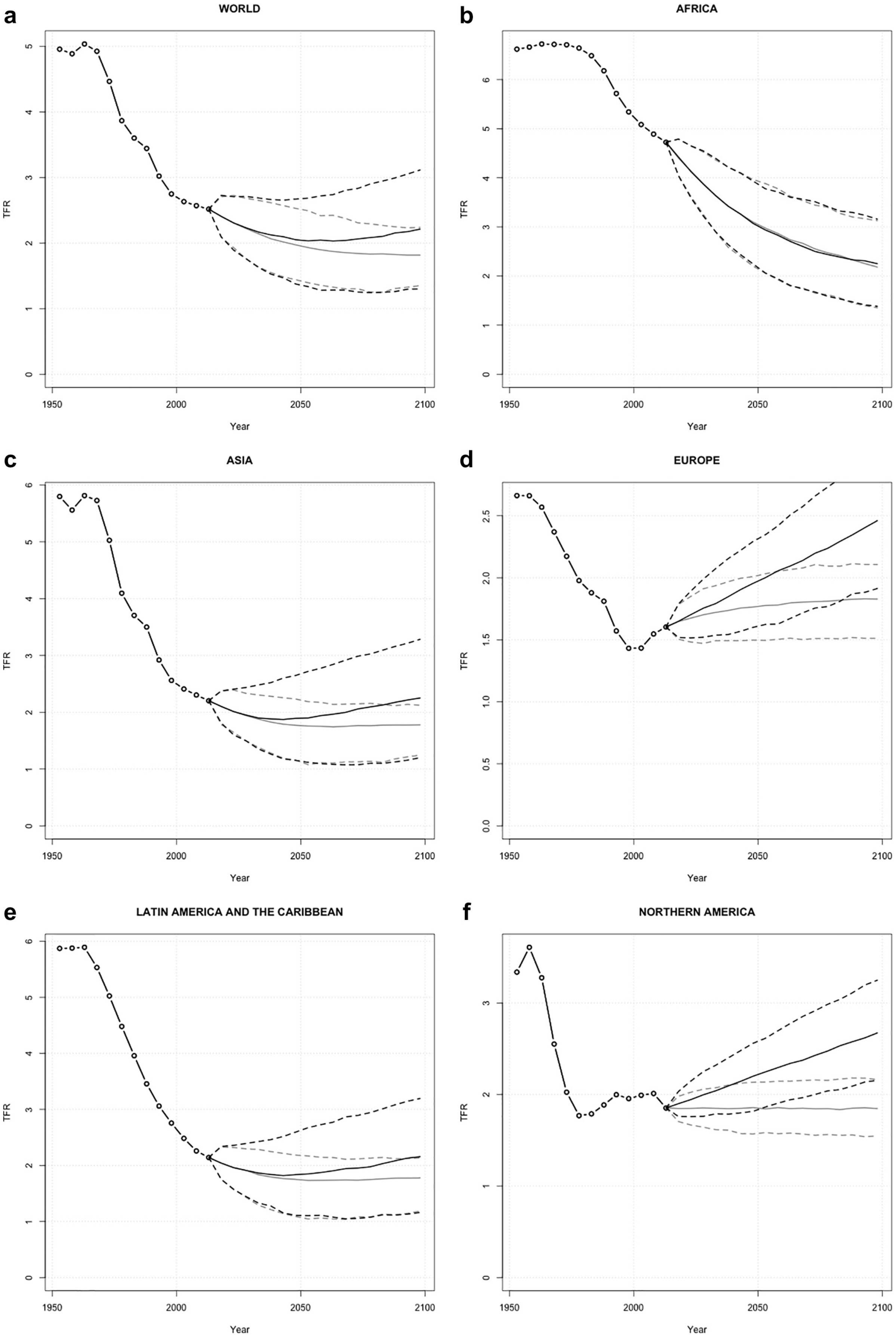

Fig. 1. Fertility forecasts globally and at the level of each continent (Gray = base case, Black = heritability model, dashed lines 90% confidence intervals). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Raftery et al. (Raftery et al., 2014) allowed μ_c and ρ_c to vary between countries using a Bayesian hierarchical model. The values of ρ_c, μ_c and σ_ε are determined by maximum likelihood estimation from the 54 observed time periods in the 21 countries that have entered Phase III.

We substitute this model with an equation commonly used to model the change in a heritable trait across generations (Hartl & Clark, 2006; Kelly, 2011; Lush, 1937) (the 'heritability model'). This equation provides an estimate of the change in a phenotypic trait under selection, which is proportional to the selection differential and the heritability of the trait. In the case of fertility between one generation and the next, $\Delta f_{c,\ t+1}$, the selection differential is the difference between the mean fertility of the total population and the mean weighted fertility of the parents (equal to the mean number of children that each child has in their family). This equation is expressed as:

$$\Delta f_{c,t+1} = \frac{h^2}{g}(\theta_{c,t} - f_{c,t}) \tag{2}$$

$$f_{c,t+1} - \theta_{c,t} = \left(1 - \frac{h^2}{g}\right)(f_{c,t} - \theta_{c,t}) + \varepsilon_{c,t}$$

where $\theta_{c,t}$ is the weighted fertility of the parents that have had children and h^2 is the heritability of fertility. As each time period in the projection model represents a five-year step rather than a generation, h^2 needs to be weighted by g, the number of five-year periods in a generation, to reflect the smaller time step. An alternative approach would be to determine the mean weighted fertility of the previous generation rather than the previous time period and use the full value of heritability. Our approach is the most tractable within the existing model.

Contrasting these equations, in Eq. (1) the total fertility rate reverts toward an equilibrium level, μ_c. In Eq. (2) the total fertility rate tends toward the average fertility rate of the parents of the children born each generation, weighted by their number of children. This average fertility of the parents is greater than the standard definition of the fertility rate over the whole population as it gives greater weight to the parents with more children.

To use Eq. (2), we require a distribution of fertility rates (or number of children) across the population. Previous studies have used distributions such as the Poisson distribution (Jennings, Lloyd-Smith, & Ironmonger, 1999) and negative binomial distribution (Waller, Rao, & Li, 1973). We use a Poisson distribution, with mean $f_{c,t}$. The proportion of families with i children at time period t, $\phi_{c,\ t}^{\ i}$, is:

$$\phi_{c,t}^i = \frac{(f_{c,t})^i e^{-f_{c,t}}}{i!} \tag{3}$$

Accordingly, the proportion of children who are in a family with i children, π_t^i, is:

$$\pi_{c,t}^i = \frac{i\phi_{c,t}^i}{f_{c,t}} \tag{4}$$

Therefore, the mean number of children each child has in its family is:

$$\theta_{c,t} = \sum_{i=0}^{n} i\pi_{c,t}^i \tag{5}$$

This approach effectively results in fertility rates retaining the structure across ages as contained in the base United Nations model. Extensions of the evolutionary approach could involve traits relating to this age structure, such as the age at which women have their first child.

A difference with the base model is that the rate of change, ρ_c in Eq. (1) is replaced by $(1 - h^2/g)$ in Eq. (2). The effective rate of change in the heritability model, h^2 captures the heritability of fertility. In modern populations it tends to be estimated in the range of 0.2 to 0.4 (Fisher, 1930; Kirk et al., 2001; Kohler et al., 1999; Murphy, 1999; Murphy & Knudsen, 2002; Rodgers, Hughes, et al., 2001a; Rodgers, Kohler, et al., 2001b). For the simulations that follow, we use a mid-point heritability of 0.3 and an assumption of six five-year steps per generation. Sensitivity analysis of different levels of heritability is contained in the supplementary material.

4. Results

Simulating the global population to 2100 under the heritability model, the median projection of the global total fertility rate declines from 2.52 in 2010–15 to 2.21 in 2095–2100 (Fig. 1). However, the total fertility rate of 2.21 is markedly above the median projected total fertility rate of 1.82 under the base model. This result is largely driven by increases in fertility in continents with populations that have completed the demographic transition. For example, the European median total fertility rate increases from 1.83 (base model) to 2.46 (heritability model), and North American fertility increases from 1.85 to 2.67.

As a result of the world total fertility rate remaining above the replacement rate, our analysis shows that not only will world population stabilization not occur this century, but population growth in post-transition countries will increase toward the end of the century. There is less than a 5% chance of world population stabilization. Our median projections indicate that world population may increase from 7.4 billion people in 2015 to 9.8 billion people in 2050 and 12.4 billion in 2100, a material increase on the 11.3 billion people in 2100 estimated from fertility projections in the base model (Fig. 2). A critical insight of this approach for forecast future population growth is that beyond this horizon, there is no particular reason to expect the world population to stabilize by itself at a sustainable level.

Fig. 2 shows that there are no substantial differences between the model forecasts for Africa, where most countries are yet to enter the low fertility state following the demographic transition. For Asia, there is a clear difference, with population remaining stable over the second half of the century rather than entering into decline. Europe sees the most dramatic turnaround with a predicted return to population growth instead of prolonged population decline. Our median estimates suggest a European population at around 800 million at the end of the century, near its current level, compared to a base model forecast of 660 million in 2100. North America's population also sees an increased rate of growth with a population estimated to be 150 million higher than in the base model in 2100, at 650 million.

The projections of future levels of fertility also impact the population support ratio (ratio of people of working age to those above 65 years). Noticeably, despite of the rise in fertility, it is still predicted to decline substantially. The support ratio decreases from 3.5 to 2.0 in the heritability model, rather than 1.7 of the base model in Europe, and from 4.0 to 2.2 rather than 1.8 in North America. Moreover, once the increase in number of children is taken into consideration, the higher number of children in the heritability model merely shifts the nature of the burden rather than ameliorating it. Including those under 15 years in the population support ratio, the ratio declines to 1.0 in Europe, down from the current 1.6 but similar to the 1.0 of the base model. Similarly, the population support ratio in North America declines from 1.5 in 2015 to 1.0 in 2100 under the heritability model, markedly lower than today but similar to the base model forecast of 1.0.

5. The gene-culture co-evolution of fertility

In addition to the vertical transmission of fertility from parent to child (whether genetic or cultural), environmental change and cultural transmission from non-parents can affect the total fertility rate (Casterline, 2001; Jennings, Sullivan, & Hacker, 2012). Both could affect the projections in this paper.

In our simulations, the presence of a cultural norm of low fertility is partially captured through the adoption of a genetic heritability less than one. This effectively weights the fertility of the next generation between that of the children's parents and that of the country in which they live. The child's fertility (relative to their parents) regresses to the

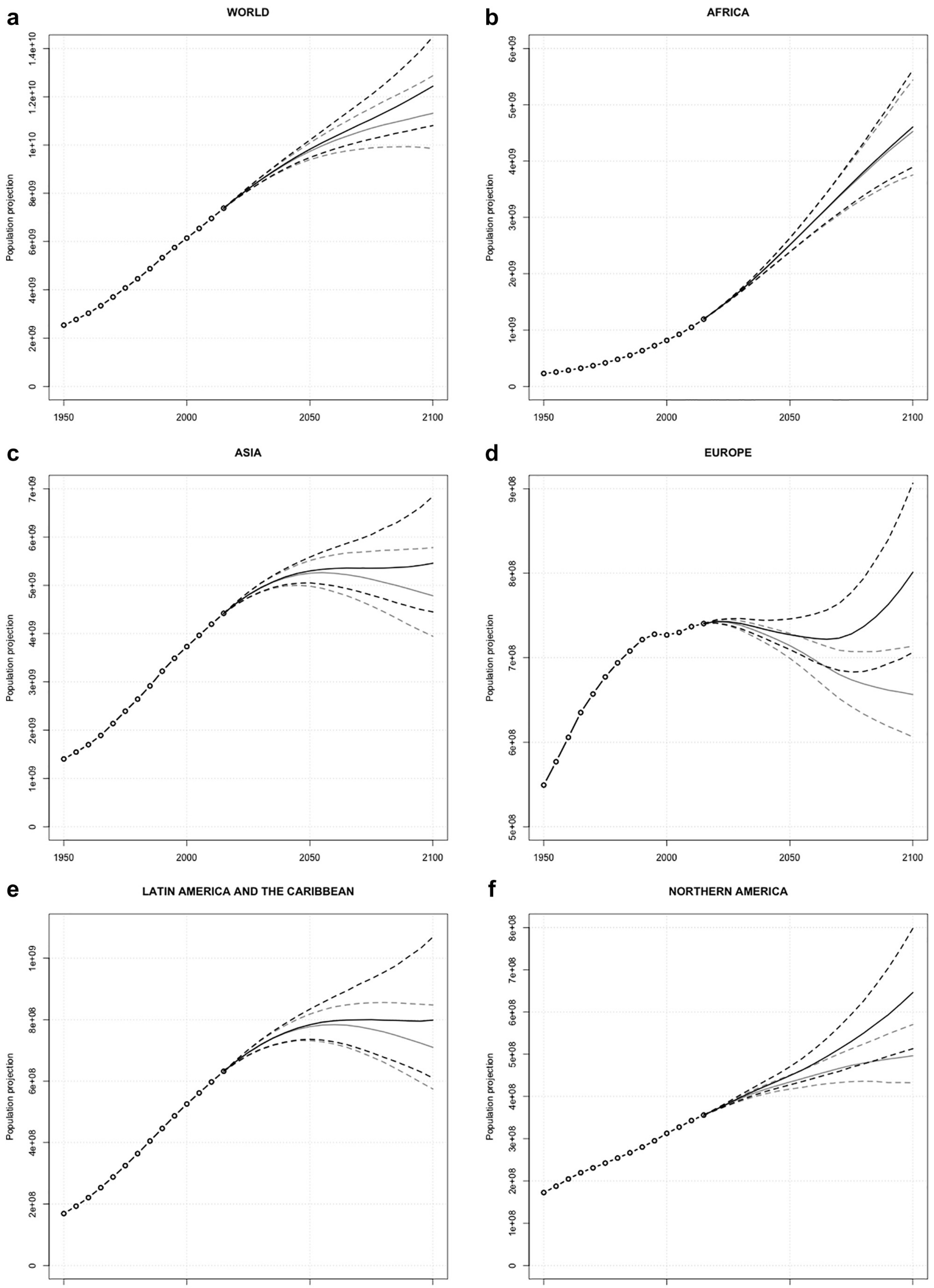

Fig. 2. Population forecast, globally and at the level of each continent (Gray = base case, Black= heritability model, dashed lines 90% confidence intervals). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

country's mean, with that mean reflecting the norms in that country.

The simulations do not, however, capture the dynamic of cultural transmission beyond that captured in historical data. Cultural transmission of fertility has been explored in a number of papers (Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981; Colleran, 2016; Fogarty, Creanza, & Feldman, 2013; Ihara & W. Feldman M., 2004; Kendal & Ihara, 2005). Of most relevance to this paper, Kolk et al. (Kolk et al., 2014) modeled a fertility decline and recovery as the interaction between fertility preferences inherited from parents and lifestyles acquired from cultural role models. They proposed that in a high-fertility population without any low-fertility role models, fertility can remain high despite an underlying preference for a low fertility lifestyle as there is no-one from which to culturally acquire that lifestyle. However, on the introduction of a low fertility lifestyle, this lifestyle can rapidly spread to reflect the population's underlying preferences, driving aggregate fertility down. Eventually, those who prefer higher fertility despite the presence of a low-fertility lifestyle grow in proportion of the population through each generation and return the aggregate fertility to higher levels.

Two important points emerge from the Kolk et al. paper. The first is that, as in the simulations in this paper, vertical transmission in fertility between generations can increase fertility rates over time. The simulations by Kolk et al. of the spread of the culturally transmitted low-fertility lifestyle captured a demographic transition, before the increase in prevalence of those preferring a high-fertility lifestyle drive a fertility recovery. The second point is that the rapid ongoing introduction of novel lifestyles can maintain low fertility. This potential for persistence of low fertility has also been demonstrated in other research on cultural transmission (Boyd & Richerson, 1985; Ghirlanda & Enquist, 2007; Ghirlanda, Enquist, & Perc, 2010).

Relative to the approach of Kolk et al., the decline in fertility simulated in this paper is already in the historical data. Our focus is on the recovery. However, we make an implicit assumption that there are no new environmental shocks or new culturally transmitted lifestyles that could reduce or constrain fertility. The occurrence of such events is not implausible. The historical pattern could be argued to be one of multiple environmental changes and the regular emergence of new lifestyles, from increased entry of women into the workforce (Becker, 1960; Mincer, 1963), to increased income (Becker & Lewis, 1974), to decreased child mortality (Preston, 1978); to improved contraception (Becker, 1960) (noting that there is considerable debate about the link between these changes and fertility). Further, it is possible to develop plausible scenarios of future changes both positively and negatively affecting fertility. This could involve further changes in income and wealth, changes in workforce participation through the development of robotics and artificial intelligence, new medical technologies affecting fertility and reproduction, or virtual reality technology so attractive that it changes the nature and level of human interaction. These could affect fertility and the selection pressures in the population, changing the path of fertility relative to our simulations or the projections of the United Nations.

A recovery in fertility does not, however, require an absence of further environmental change or new culturally-transmitted lifestyles. Fertility could recover if the response is small, which may be the case if humans are becoming better adapted to the types of environmental changes or lifestyles generated by modern living. People in developed countries now have effectively complete control over their fertility. Child mortality is close to zero. Female labour force participation is close to that of men. To decrease or continue to suppress the total fertility rate, any new environmental change or culturally transmitted lifestyle would need to be of a different form to those to which the growing part of the population have maintained their fertility in response.

For these reasons, the increase in the fertility rate may occur more or less rapidly than in the simulations in this paper, or may be delayed by further cultural or environmental changes. Many other trajectories are possible. However, to the extent we wish to make projections of fertility, ignoring the evolutionary underpinnings of fertility risks underestimating future fertility rates and population growth.

6. Discussion

Our study suggests that population may be substantially higher at the end of the century than currently anticipated. Fertility will have an intrinsic tendency to grow in post-transition countries because of the selection of individuals with higher fertility. Over time, the genetic heritability of fertility leads to the proportion of individuals with higher fertility to increase in the population. While countervailing factors (e.g. cultural, political) may constrain population growth when it reaches unsustainable levels, it may be misguided to hope that world population will stabilize in the long term at a sustainable level simply by itself.

A direction for future research is indicated through the nature of heritability. Although it is a common finding that fertility is heritable across different countries, estimates of heritability of fertility are population specific. This raises the prospect that the genes affecting heritability in each country are different, as is suggested by the findings of Tropf et al. (Tropf et al., 2016). However, it is also plausible that, while mediated by different genes, the phenotypic expression of those genes may relate to common traits.

The population specific nature of heritability estimates also points to the potential for changes in heritability over time, as occurred during the demographic transition, or changes in the nature of the heritability. For example, wealth was correlated with fertility before the demographic transition, whereas today it is correlated with lower fertility (at least in women) (Nettle & Pollet, 2008). Future changes in environment may similarly change the nature of the selection on fertility. The potential for change was demonstrated in Kohler et al. (Kohler et al., 1999). While they found that fertility was heritable in Danish populations in cohorts born at the end of the 19th and early twentieth century and those born in the mid-20th century, there were material shifts in heritability even within these small time-bands.

Future research considering the population specific nature of heritability and the potential for changes in heritability over time could involve the modelling of changes in fertility by reference to the underlying traits that affect fertility (such as preferences) or, ultimately, to underlying genes. This approach would require a methodology suitable for the modelling selection on multiple characters, such as that developed in Lande (Lande, 1979). This would then allow deeper consideration of which traits may persistently drive higher fertility, or whether further environmental change could once again change the nature of the selection. Addition of a layer of culturally-transmitted traits would also add to the richness of the analysis. That said, regardless of the traits affecting fertility, a dynamic of selection of higher fertility will place a persistent upward pressure on population fertility and ultimately, population.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.evolhumbehav.2018.09.001.

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