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Author for correspondence:
Oskar Burger
e-mail: ofb@kent.ac.uk

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What if fertility decline is not permanent? The need for an evolutionarily informed approach to understanding low fertility

Oskar Burger[1,2] and John P. DeLong[3]

[1]School of Anthropology and Conservation, University of Kent, Canterbury CT27NR, UK
[2]Max Planck Institute for Demographic Research, Konrad-Zuse-Strasse 1, Rostock 18057, Germany
[3]School of Biological Sciences, University of Nebraska, Lincoln, Lincoln, NE, USA

'Demographic transition theory' assumes that fertility decline is irreversible. This commonly held assumption is based on observations of recent and historical reductions in fertility that accompany modernization and declining mortality. The irreversibility assumption, however, is highly suspect from an evolutionary point of view, because demographic traits are at least partially influenced by genetics and are responsive to social and ecological conditions. Nonetheless, an inevitable shift from high mortality and fertility to low mortality and fertility is used as a guiding framework for projecting human population sizes into the future. This paper reviews some theoretical and empirical evidence suggesting that the assumption of irreversibility is ill-founded, at least without considerable development in theory that incorporates evolutionary and ecological processes. We offer general propositions for how fertility could increase in the future, including natural selection on high fertility variants, the difficulty of maintaining universal norms and preferences in a large, diverse and economically differentiated population, and the escalating resource demands of modernization.

1. Introduction

Explaining fertility change in humans is as crucial as it is difficult. Crucial, because it is the primary source of error for population forecasts [1,2] as well as a major determinant of future population structure, size, and growth rate [3]. Difficult, because it is seemingly influenced by many social and environmental factors acting at multiple scales. Fertility responds to biology, economics, and technology, but it is commonly held that ideational factors of individual preferences and social norms are the primary determinants of the timing and amount of childbearing, especially at fairly low levels of fertility [4]. Using evolutionary theory to explain the causes of very low fertility is likely to be controversial, particularly if accompanied by any hint of critique of other approaches. However, the study of fertility is also an area where evolutionary theory may be especially useful as, indeed, there currently is not a strong body of theory for explaining fertility decreases in humans, which in turn limits the ability to predict the future of fertility [4–6]. Indeed, experts in the field of population projection have called for inputs from multiple viewpoints and disciplines, including evolutionary anthropology, in order to help develop stronger theory and predictive ability [6].

One central assumption is especially relevant to both the explanation of the fertility transition of the past 100 years or so and the endeavour to predict what fertility might do in the future. The assumption is that the fertility reduction is irreversible; once fertility begins to decline it becomes subject to its own momentum and will fall, although at an uncertain rate, inevitably to a destination in the ballpark of two births per woman. While there is significant variation in timing and rate, the broad process of fertility decline has been fairly consistent across the globe [7,8]. Because of the similarity of fertility declines across countries, it is widely assumed that the passage of time alone is sufficient to drive the entire human population to replacement-level fertility (once some unspecified degree of fertility reduction has begun, triggered by some unknown level of modernization [8]). With this assumption, forecasting future population sizes involves predicting the timing and rate of future fertility declines from historical trends [1].

Declining fertility in historical and recent populations is an empirical generality. The assumption of irreversibility, however, takes this descriptive observation about the past and raises it to a certainty about the future. For example, Coleman [9] said that the demographic transition 'described the reduction of birth and death rates from traditionally high levels to the low levels now nearly universal in industrial societies. Whatever the arguments about its causation, few now question its irreversibility…'. Likewise, Basten *et al.* [5] state that: 'Fertility forecasting has been dominated by the paradigm of the demographic transition. Fertility was thought to fall from a high comparatively stable level to a low comparatively stable level. This transition was considered to be irreversible, so once a low enough level of fertility was achieved it would never increase.' Furthermore, Lutz [6] states that: 'In fact, the social sciences as a whole have yet to come up with a useful theory to predict the future fertility level of post-demographic transition societies. Forecasters can only try to define a likely range of uncertainty. As the fertility transition is irreversible, we are quite sure that the fertility rate will not go back to pre-transitional high levels…'.

One demographic criticism of the dogma surrounding the fertility transition is that fertility levels often do not stabilize at a new equilibrium near replacement level [4,5,7,10,11]. Rather, in many countries, the trend of fertility reduction has continued to levels well below replacement, failing to stop at the hypothesized replacement-level equilibrium. This observation is part of the rationale for there being a 'second' demographic transition [12]. The degree to which fertility continuing to fall to levels below replacement poses a problem depends on how one conceives of the demographic transition. For some, the emphasis is on a broad historical process and less so on the hypothesized endpoint, but for others the levelling off of birth and death rates is considered as a defining attribute of the demographic transition, and the fact that fertility continued to drop requires special explanation (along with other changes in the behaviour of very low-fertility societies). For present purposes we need only note that the endpoint of the transition is a challenge for theoretical prediction and there is disagreement on how to interpret very low levels of fertility. As such, the possibility of fertility increase in the future tends to be discussed as a recovery from sub-replacement back to replacement levels. Such increases may potentially come from tempo effects [13] or upticks at high levels of development that are at least partly driven by increased gender equality [14,15]. However, these discussions do not tend to consider the possibility of an increase in fertility that would beget significant increases in population growth. For instance, recent work has questioned the validity of a two-child norm because many countries seem headed toward one child per woman and hence the two-child assumption may be too high. Likewise, a survey of a panel of 170 experts found that opinions were divided on whether global fertility levels would converge to a level of 1.75 or 2.0 births per woman, with most of the experts favouring 1.75 [5]. Alternatively, some have questioned the assumption that fertility will rise as high as replacement level, focusing instead on the concern that fertility levels will drop to very low levels for long into the future [4]. Thus, current views allow for small increases in fertility but do not generally deviate from the broad assumption that the demographic transition is irreversible and that fertility will not return to above-replacement levels.

Our goal is to question the assumption that the transition to very low fertility is irreversible. There are several good reasons to question the assumption. First, neither the endpoint of the demographic transition nor fertility behaviour of the future is predictable with current theory [6]. Without a solid predictive framework, we cannot know how fertility will respond to changing social and environmental cues in the future. Second, life-history theory predicts variability in demographic traits across conditions, such that we should not expect fertility to lose the majority of its variation and go to one value (replacement fertility) over the course of an uncertain and complex future. Third, many classic approaches to the demographic transition would in fact predict increases in fertility levels if socio-economic conditions changed. For example, Becker's well-known human capital argument would imply a fertility reversal if the cost of children decreased dramatically or if the returns for investments in human capital were to disappear or diminish more rapidly [16,17]. The implicit assumption in much of economics and demography is that economic development and improvements in standard of living will continue to increase into the distant future. For the human capital model, and for many other approaches to the problem, sustained growth (perhaps by assumption) is what prevents consideration of a major fertility reversal, rather than any theoretically grounded demographic principle.

While the importance of forecasts for informing policy and discussions of critical societal issues such as pension systems is widely recognized, we wish to amplify the argument of how important forecasts are for discussions of sustainability and environmental quality. As populations increase in size, the total amount of both energy consumed and pollutants emitted increase, often at super-linear rates [18]. Thus, expectations for future resource consumption and harmful waste production are closely tied to population forecasts. It is commonly thought that increases in modernization help drive fertility downward, but the rising costs, in terms of energy used and waste produced, of increased modernization are not widely appreciated as relevant for our demographic future. Figure 1 shows long-term trends for several European countries in terms of energy consumption and carbon emissions spanning the past 100–215 years. In both cases, the typical slope of the log–log relationship is greater than unity [18,20]. So the concern is not just that larger populations use more energy and emit more waste, but as populations grow both of these may increase faster than population size. As such, there is a lot riding on the irreversibility assumption. A reversal all the way to pre-transition levels of fertility is not necessary for fertility reversal in general to be a concern. If projections assume fertility levels that are below or near replacement, then even small increases to still relatively low levels of fertility (above 2.5 or so) are sufficient to greatly increase population growth rate, which may in turn bring the escalating costs implied by figure 1 [21]. Although the irreversibility assumption has been a handy (and at times necessary) simplifying assumption, it is time to face the challenge of this added complexity and how it influences our understanding of global human population dynamics.

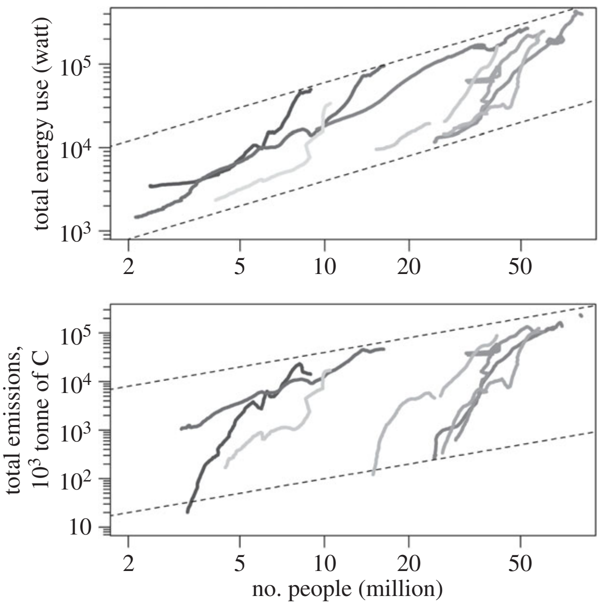

Figure 1. Total energy use and total emissions as functions of total population size in Europe. Each grey line is a unique country's trajectory. The dotted lines are 1 : 1; when the trajectories rise more steeply than the dotted lines there are escalating costs and consequences of population size. Using a 20-year running window, ordinary least-squares regressions were run on these log–log relationships for the countries depicted. For energy use, the exponent was greater than unity for 75% of the time. For emissions, the exponent was greater than unity for 78% of the time. For total energy use, the data depicted are from 1800 to 2008 for each of the following countries: Sweden, The Netherlands, England, Germany, France, Italy, Spain and Portugal; data from [19]. For total emissions, the data depicted are: Sweden 1834–2008; The Netherlands 1846–2008; France 1802–2008; Germany 1800–1946 and 1991–2010; Italy 1860–2008; Spain 1830–2008; Portugal 1870–2008; data from Tom Boden and Bob Andres (Oak Ridge National Laboratory) and Gregg Marland (Appalachian State University).

2. Rationale for applying evolutionary theory to low-fertility populations

Our primary goal is to encourage skepticism toward the widely held assumption that the fertility transition is irreversible. Doing this, however, highlights the fact that a new set of assumptions—or better, an actual predictive theory about the evolution of fertility in human populations—are not readily available to supplant the current set of assumptions [6]. On balance, evolutionary and ecological approaches to population change are under-represented in population projection specifically (but see [22,23]), and in the study of fertility change in low-fertility contexts generally [24]. Interdisciplinary collaboration and appreciation of multiple approaches—including evolutionary theory—will be needed to develop alternative population projections in the future [6].

In a prominent review article about population projections, Lee [1] noted the lack of guiding theory by saying: 'Lacking practical guidance from grand dynamic theories, forecasters rely on a *largely descriptive framework* known as the demographic transition...' (emphasis added). Within demography, the demographic transition has been referred to as a theory, a model, a paradigm, and a description [3,5,8,9,17]. We agree with Lee that the appropriate term is descriptive framework. The lack of guiding theory contributes to the fact that different projections can be wildly divergent. Until recently, the United Nations medium forecasts often predicted zero growth by the end of the century, but the recent revisions have population still increasing through the year 2100. Another prominent forecast predicts peak population as early as 2070, with three decades of decline already occurring before 2100 [25]. These two forecasts differ by 2 billion people (11 billion and 9 billion total people, respectively) and more than 30 years difference in the timing of a population peak. The former forecast has the global population declining at the end of the century while the latter has growth still positive. These differences in forecast population size derive from inclusion of a relationship between education and fertility in [25]. This innovation is critical in that it begins to bring some type of contingency to the forecasts. This is a positive direction, although evidence is already mounting that the relationship between fertility and education may not be as universal, or as causal, as commonly thought [26–28].

Including education as a causal covariate is innovative because including economic and ecological constraints on population growth are rare in population forecasts [1]. The standard procedure is to forecast uncertainty in future vital rate change using error in the estimates of historical trends. Granted, access to education may not seem like an ecological variable to many, but for present purposes it can be thought of as an ecological change in that education alters the information content of key social interactions, changes opportunity costs for productive activities, influences the density of mates and resources, and probably brings with it exposure to a wider range of norms that directly or indirectly influence the tempo and quantum of fertility. Interestingly, adopting an optimistic outlook for how education will affect fertility in the future, and ignoring economic and ecological constraints on growth, brings increased rates of fertility decline and lower population size at the century's end [25]. Yet, as discussed below, including only an energetic/ecological constraint brings increases in total fertility due to an inability to pay for the costs of modernization [21]. Clearly, accounting for additional causal factors can substantially alter predictions of future population growth.

In evolutionary demography, vital rates are phenotypes that change through time depending on an array of evolutionary, ecological, and developmental processes. Thus, an evolutionarily informed approach to understanding low fertility would provide information about the link between fertility and environmental signals, and then a feedback between future environments and fertility could be built into population projections. In contrast with the evolutionary demographic view, the argument that fertility decline is irreversible rests on two factors: (i) the wide generality of the trend of fertility reduction across industrialized/modernized societies (i.e. there seem to be no exceptions) and (ii) the notion that reproductive behaviour is completely driven by social norms and individual preferences that have essentially nothing to do with evolution. For instance, Lutz [4] states that 'through the introduction of modern contraception, the evolutionary link between the sex drive and procreation has been broken and now reproduction is merely a function of individual preferences and culturally determined norms'.

While we are somewhat skeptical of this view, because it excludes other possible influences on fertility aside from culturally determined norms, we suggest that even if fertility is determined only by norms and preferences, an evolutionary approach is still warranted. There is an entire field of study devoted to cultural evolution, and fertility decline is a commonly addressed topic [29,30]. We especially disagree with the notion that contraception breaks the link between human fertility and the processes of evolution. Although norms and preferences are clearly an essential part of fertility decision-making in humans (we consider that view non-controversial), both age at first birth and total number of births are genetically heritable [27,31,32], which by definition means they are partly under genetic control. Twin studies show heritability (often over 0.2) for number of children ever born for males and females and for age at first birth in females. Even in low-fertility settings a significant portion of the variation in fertility traits is due to non-shared environmental factors [27,33]. Moreover, genome-wide association studies have shown that there are in fact detectable genetic variants (single nucleotide polymorphisms) that underlie fertility-relevant traits including age at menarche and menopause [27].

Regardless of the degree of genetic influence, even decisions that are strongly influenced by socially transmitted norms are useful to study from an evolutionary point of view [29,34]. The mind, culture and consciousness are also products of evolution. If preference for low fertility becomes common, it is still important to know how those preferences evolved and how changing social and economic circumstances caused preferences to shift to maximizing currencies other than fitness, such as wealth, status, or education. However, it should also be noted that most of the potential currencies that substitute for fitness are still linked to traits that are fitness-relevant because they bring reductions in mortality or increases in access to status or resources. It is not surprising, nor is it contradictory, that humans have motivations for lower mortality and higher social status environments.

An evolutionary approach is also useful for understanding how social interactions amplify demands for products and disrupt or increase rates of transmission of social norms, and such an approach also may help understand how the mind tracks certain cues that alter behaviour [35]. An evolutionary perspective might emphasize how traits respond to selection along socio-ecological gradients, while also considering developmental plasticity and how evolved tendencies might be pushed down maladaptive pathways in unusual environments that are biologically unprecedented for being low in mortality hazard [36], high in energy availability [37], and with enormous returns on investment for capital [38]. In short, an evolutionary perspective might allow us to predict from a more robust set of principles, compared with pure statistical extrapolation, how fertility might change in the future. If fertility is responsive to environmental and cultural signals, then rather than being stuck on an irreversible and inevitable path to replacement (or post-transition) levels, it might increase or decrease. There is a dearth of hypotheses about what these signals might be, but three broad types include those from genes, culture (norms, preferences, and institutions) and energy availability.

3. What does this mean for irreversibility?

The assumption of irreversibility does not rest on a firm body of theory and the consequences are severe if it is incorrect. But what reasons are there to suspect that fertility might increase? We offer five propositions and one counter-argument.

Proposition 1. All else being equal, selection will act to increase higher fertility variants.

We suspect little agreement on how much of a role genetics will play in the future of fertility. We briefly summarized a few findings above, showing that fertility is both correlated with fitness and that fitness-related traits are linked to specific alleles that should go up in frequency as those individuals have more children. Several additional studies have shown that natural selection is acting on humans in ways that favour increased fertility [31,39]. These studies are based on a range of approaches, from twin studies, to genome surveys, to studies of the relationship between fertility and fitness. Fertility-related phenotypes can respond to natural selection in human populations according to the expectations of quantitative genetics [40]. Further, as mortality and fertility decline during the demographic transition, there is an increase in the opportunity for selection to act on fertility because fertility becomes a greater contributor to variation in relative fitness [41]. Thus, all else being equal, and in spite of the generality of fertility decline that accompanies modernization during the industrial age, it is likely that there is a constant process of natural selection favouring higher fertility genotypes. Note also that recent work on eco-evolutionary dynamics shows that rates of change in life history need not take many generations [42]; thus genetically influenced adjustments to vital rates could plausibly occur within the time horizons of population projections.

In contemporary evolutionary theory, it is widely recognized that several mechanisms of inheritance affect observed phenotypes, and some of these are non-genetic, including cultural inheritance [43,44]. If fertility is heritable, the mechanism of inheritance does not affect the prediction that high fertility variants will increase in frequency [45]. That is, even if fertility is completely socially determined, with no genetic influence, we should expect fertility to rise if it is heritable, which it clearly is. Typical population projections inadvertently assume that the heritability of fertility is near zero, an assumption that is not supported by empirical observations [31,33,45,46].

Proposition 2. Cultural norms change and may not keep fertility low in the long-term.

In contrast with Proposition 1, culture may indeed be masking background selection for higher fertility with stronger incentives for low fertility and the technology to keep it there. We suspect that this possibility is in line with mainstream thought on the subject. One could surmise that alleles related to the tempo and quantum of fertility can change substantially in a population and not have much of an effect in populations that have abundant and easy access to contraception, have strong social incentives to limit family size, and are encouraged to pursue non-fertility-related goals by parents and peers. If these factors do indeed 'swamp' the effects of natural selection acting on fertility-relevant genetic variants, there are still reasons to doubt that the spreading of norms will have a uniform and predictable influence on fertility behaviour in the long-term across a large heterogeneous and growing global population. For instance, studies of culturally transmitted traits show that they can exhibit volatile or unreliable undulations and even that population dynamics governed by 'culture' are not likely to be sustainable [47,48].

Indeed, one of the most interesting (and under-appreciated) elements of the demographic transition is that reproductive traits are phenotypes seemingly driven in the opposite direction of what a simple quantitative genetics model would predict. For instance, age at first birth is negatively correlated with fitness and is heritable [31,39], which means that all else being equal, age at first birth should decline from one generation to the next. The fact that it is increasing while selection is favouring younger first births could indicate that cultural concerns are driving the phenotype in a maladaptive direction, or at least that there are contributors to the sources of variance in the trait that push it away from a fitness maximizing value. This is a complicated issue, but assuming that norms and preferences solely dictate reproductive timing means that this exception to selection acting on earlier births will persist indefinitely, and it is currently unclear how long a trait can change in a direction that opposes the gradient of selection acting on it. If cultural pressures relax or opportunity costs of children decrease, however, these underlying genetic proclivities may be more likely to express themselves, which would lead to fertility increase.

Furthermore, Kolk *et al*. [45] suggest, based on the results of an analytical model, that maintaining fertility at low levels requires a constant supply of new low-fertility norms to be continually adopted by those who inherit high fertility preferences or proclivities. This raises the question of where the constant supply of low-fertility norms will come from. This need for novel low-fertility preferences to continually emerge in order for fertility to remain at very low levels is certainly not built into many population forecasts [45].

Proposition 3. Failure to meet the resource cost of modernization will lead to fertility increase.

The global reduction of fertility to a two-child norm (or similar) assumes universal adoption of the same preference, the ability to spread modernization widely enough to allow populations to achieve that preference, and that the heritability of fertility declines to zero. It also assumes that resource supply rates can remain sufficiently high to pay the cost of modernization required to achieve a two-child norm (or lower) globally. As noted by Lee [1], economic and/or resource constraints are rarely included in forecasts in spite of the inescapable fact that they must limit population growth in fundamental ways. Factors of positive and negative feedback have clearly been prevalent in the long history of population growth since the industrial revolution (as a balance of Malthusian and Boserupian processes) [49,50], but the process of growth must be ultimately 'limited by natural resource constraints' [1].

One exception to the lack of attention to the ecological side of this problem is work on the relationship between *per capita* energy use and vital rates. Population growth rate, fertility rate, lifespan, infant mortality, and other vital rates are all significantly correlated with *per capita* energy use [37]. Importantly, the development that fosters the demographic transition is supported by substantial increases in energy use that help to reduce mortality. Thus, going through the demographic transition requires increasing *per capita* energy use. The assumption of irreversible fertility decline, and the forecast that all countries will go through the demographic transition, therefore, requires the additional assumption of sufficient energy supplies. This assumption does not hold up to scrutiny. The relationship between population growth rate and *per capita* energy from the past few decades can be used to calculate the amount of energy required to meet, for example, the UN medium projection [21]. Comparing the energy requirement forecast to even optimistic energy availability forecasts suggests that the energy cost of bringing the entire globe through the demographic transition is far greater than the fossil fuel energy that will be available. Despite this problem, population forecasts generally assume that all the modernization required for distributing resources and infrastructure sufficient to drive the entire world to two children per women can come without energy expenditures. This, in our minds, is a rather strong assumption that is in need of further evaluation.

From a dynamic systems perspective, current low fertility is a fragile, unstable state that requires continued energy input to maintain [51] (see also [48]). The UN medium projection shows a levelling of the human population that has the look of a population growing towards its carrying capacity (the traditional Malthusian or logistic equilibrium). However, carrying capacities are stable attractors generated by a reduction in *per capita* resource supplies that drive mortality up and birth rates down until they are equal. In the demographic transition and the projection of a stabilized global population that results, *increasing* energy use drives *both* mortality and fertility rates down until they are equal. It is logical then, that major reductions in energy use could allow both mortality and fertility to go back up. This means that the UN medium projection is not stable because reductions in energy use could cause the population to start growing again, in turn further reducing *per capita* energy availability.

Proposition 4. Increasing wealth inequality may make it difficult to keep fertility low.

Wealth inequality has received increased attention lately due to the widely publicized work of Thomas Piketty [52]. Wealth inequality is predicted to continue to increase in the future. This can affect resource distribution (Proposition 3) and patterns of social transmission (Proposition 2). Education is commonly invoked as causally related to fertility decline, but of course resources are required to build schools and supply them with knowledge to transmit. Students probably need to perceive a benefit to education, but if socio-ecological conditions plummet too far they may be less likely to follow the route to low fertility through increased education. Quality of education also matters [26], which is at least partially connected to infrastructure and resource availability. The difficult fact of wealth inequality is that pressure from energy shortages will not be experienced equally across society, which could lead to major reductions in *per capita* access to resources for large segments of the population. This is probably true both within and among countries. Wealth inequality, then, implies a route that could accelerate resource limitation in certain contexts.

Wealth inequality may also interact with cultural transmission and social displays. From evolutionary studies of cultural transmission, we know that people signal to perceived audiences and may preferentially imitate individuals at particular (high) levels of status [30,53]. Drastic increases in wealth inequality may change whom people perceive as being in their 'audience' and/or which individuals constitute cultural models worthy of emulation. Likewise, status competition can take many forms, and increasing wealth inequality may shift the currency of status from material possessions back to family size, which could lead to a rather significant increase in fertility. Because the rules of cultural transmission are still poorly understood, but are clearly volatile and able to change rapidly, increasing wealth inequality could alter the ability of low-fertility norms to spread and persist, even independently of the ability to adequately circulate resources and information. The prediction that increasing economic differentiation within a society can impede cultural transmission is actually very old in sociology. Lesthaeghe & Surkyn [54] attribute the idea to Tarde [55] and Sorokin [56], in pointing out that if economic boundaries between classes become more rigid, the transmission of traits among classes can be greatly impeded. If wealth inequality increases beyond some threshold, the ability for lower fertility norms to filter from upper to lower economic strata could change such that high fertility becomes more common in economically impoverished settings.

Proposition 5. Institutional adjustments alter the opportunity costs of childbearing, which can lead to significant fertility increase among the wealthy and educated.

The general trend of decreasing fertility with rising development has reversed at very high levels of development [15,57,58]. The uptick in fertility is fairly modest, but it exceeds what can be accounted for by tempo effects in childbearing [59]. Myrskylä *et al.* [60] have shown that most of the fertility increase in highly developed countries is due to improvements in gender equality. From a structural perspective these adjustments reflect the evolution of preferences at the individual level, which eventually manifest in changes to institutions. They might also reflect that some of the fertility declines were due to people failing to meet their desired number of children in the past. Most importantly, this work shows that a certain type of reversal may already be underway, and that the potential for fertility reversal is not constrained to resource limited contexts. Fertility has the capacity to increase even if economic development and resource distribution can keep pace with demand.

Counter-argument 1. The above propositions are all woefully incorrect.

If the propositions above are ill-founded and cultural and genetic evolution can quite easily keep fertility at very low levels, there remains a need to understand why this may be. Ideally, this understanding would be aided by a well-grounded, mechanistic theory that can foster predictions of fertility in the future. The theory should also account for the stunning reduction in variability for this typically highly variable trait. Perhaps the costs of having children are simply too great, and just about any human mind will realize that once they have access to a low mortality niche and the technology needed to match fertility outcomes with fertility preferences, they will choose fewer children. While we see plenty of reason to be suspicious of the idea that fertility declines are irreversible, a plausible evolutionary and/or ecological theory predicting long-term stability of very low fertility may exist and we have just not thought of it. If this is the case, the core of our critique remains. The assumption of irreversibility is currently not founded on theory and the potential consequences for getting it wrong are substantial. Humans evolved through evolutionary processes linked to complex ecological settings [61]. A theory of fertility that brings our evolutionary past to bear on the present and near future is still needed, even if to test hypothesized pathways that would keep fertility low into the distant future.

4. Synopsis and conclusion

To be fair, the notion of *evolutionary demography* as a field comes with a need to be cautious. In many cases, the level of explanation required for demographic questions is proximate, and many issues need to be framed in sociological terms in order to be communicable to the target audience (e.g. [62]). Likewise, in many cases, the evolutionary and the mainstream approaches are quite similar. For example, the quantity–quality offspring trade-off is quite similar in certain areas of demography and evolutionary anthropology [16,63–65]. The role of cultural norms, and how they spread, is an emerging area of study in both social demography and evolutionary demography [34,45,66], which makes it an area of potential collaboration between fields. Thus, as part of our argument, it is important to add the caveat that there are wide areas of demography where the potential utility of an evolutionary approach, while always present, may be less immediate than in others. However, the topic of low fertility in humans is an area where evolutionary theory has particularly strong potential and should be more widely applied. It is an area with perhaps the greatest need for infusion of evolutionary (and ecological) theory and increased cross-disciplinary dialogue [6].

Regardless of the mechanism driving fertility down, inputs are needed for fertility to stay low. Some of these inputs may be ideational but many of them are the resource requirements of meeting demand to produce and transport goods and services. Even the ideational requirement is such that increased low-fertility incentives need to be generated [45]. If culture fails to deliver fertility-limiting norms to any major portion of society, fertility may rise. That being said, perhaps there are enough factors to keep fertility low. Such factors could exist because many creature comforts are more attainable with fewer children. However, at very high levels of development in several wealthy countries, fertility levels are currently increasing [15,57]. These increases seem to be due to institutional adjustments that effectively increase gender equality, or reduce the relative costs of childbearing. This suggests that it is not just a distaste of larger families that is keeping fertility low even in highly modernized contexts [57]. It also suggests that a fertility uptick may already be underway.

Resource inputs are also required to keep fertility low. Goods, services and information must all be manufactured, transported, packaged and delivered. Studies of the demographic transition widely acknowledge the role of modernization as a driver of fertility decline, but do not acknowledge that there is a sizeable energetic cost to modernization [67]. This cost may be difficult to precisely estimate in terms of fuel demands, but the fact that the cost exists and is part of our demographic future is an inescapable fact. Culture and resource availability may interact in complicated ways, especially as wealth inequality increases and/or if there are significant declines in *per capita* access to resources.

Future changes in fertility levels are difficult to predict. We wish to amplify certain calls, often made by experts in the field of population forecasts and projections, that the topic is sufficiently complicated to require inputs from multiple fields [6], and especially that resource and economic constraints are not usually included [1]. A combination of demographically oriented approaches, that include but are not limited to those from evolutionary and ecological theory, can increase appreciation for certain facts of population ecology and genetics that can provide valuable insights, synergy and nuance for this compelling and highly important topic.

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