Human Evolutionary Demography

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7. Contextual Effects on Fertility and Mortality: Complementary Contributions from Demography and Evolutionary Life History Theory

Caroline Uggla

In this chapter, I explore the influence of the local ecology, also known as contextual or area effects, on two focal demographic outcomes: fertility and mortality. I start by outlining why ecological effects have been of interest to evolutionary scholars, provide a brief overview of life history theory as a theoretical framework, and examine the type of data that have been used to test predictions in traditional, small-scale populations. Key evolutionary concepts such as extrinsic mortality risk and phenotypic plasticity are explained. I then compare and contrast this perspective with how contextual effects have been tackled by non-evolutionary scholars within demography and related disciplines, drawing on studies mainly from high-income contexts based on broad population register data. In the final part of the chapter, I lay out some challenges for this research area, which include addressing selection biases, and attaining a greater understanding of underlying causal mechanisms. Future research is likely to be more fruitful if evolutionary and non-evolutionary lines of enquiry become increasingly integrated.

Introduction

It is widely acknowledged that reproduction and health are not determined by individual characteristics alone, but linked to the social and geographic context where people live (Diez Roux, 2001; Diez Roux and Mair, 2010; Pickett and Pearl, 2001). Health determinants associated with the local context are diverse, but evidence is clear that they are associated with marked differences in health outcomes and, ultimately, mortality. In a high-income country such as the UK, differences in life expectancy are vast; on average, a boy born in Kensington can expect to live until 83.4 years of age, whereas a boy born in Blackpool only has 74.7 years on average (ONS, 2015). The difference in these values is comparable to the life expectancies of boys born in Switzerland and Saudi Arabia, respectively (WHO, 2016). The discrepancy in the number of healthy or disability-free years in the UK is even greater — approximately two decades (ONS, 2015). These within-country differences are not unique to the UK, but exist in many regions around the globe. Moreover, fertility and age at first birth vary greatly depending on context (Balbo and others, 2013). In 2017, the total fertility rate (TFR), i.e. the number of children born per woman, ranged from 7.2 in Niger, to just above 1 in Singapore (World Bank, 2017). While both childbearing and

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length of life are clearly determined in part by genes, these patterns cannot be accounted for by genetic differences alone, but also result from changes to physiology and behaviour.

Contextual influences on behaviour and subsequent demographic outcomes can take many forms. Individuals grow up, live and die surrounded by others who impact their lives in various ways. In high-income contexts, the place where an individual lives and works may structurally define education and employment opportunities, social networks, options for health, behaviour and diet, health care access and the type and magnitude of environmental stressors he or she is exposed to in daily life, from pollution to the risk of being a victim of crime. Individuals who grow up in deprived neighbourhoods are less likely to complete secondary education, are more likely to engage in sexual risk-taking behaviour, have physical and mental health problems, have a less stable family formation and are more likely to be involved in, and arrested for, crime (for review, see Pepper and Nettle, 2017). Variation in ecological conditions and behaviours is great also in traditional populations and lower- or middle-income countries. Anthropologists studying small-scale societies have demonstrated notable differences between populations in terms of daily net caloric intake, energy expenditure, climatic stressors, disease pressures and mortality regimes. All these factors taken together, it is perhaps unsurprising that the context in which an individual lives can predict a multitude of behaviours that are linked to fertility and mortality.

Ecological, neighbourhood or area effects — what I, in this chapter, refer to as "contextual effects" — have long been integral to both demography and evolutionary sciences, even if they sometimes have been studied under different terminologies and frameworks. Until the mid-twentieth century, with few exceptions, all demographic research involved spatial areas (Voss, 2007). Data collection of national censuses based on small geographical areas were integral for early estimations of local fertility and mortality rates and for the foundation of demography as a discipline. Today, most studies concerned with contextual effects revolve around this question: are two individuals who reside in the same area more likely to be similar in terms of their reproductive behaviour and health outcomes, all else being equal, than any two individuals from that population chosen at random? If so, are these effects causal, and what is it about a given context that makes individuals act in a given way? Demographic approaches to contextual effects share similarities with other social sciences such as sociology, geography, epidemiology and public health, where neighbourhood factors have generated interest due to their purported role in shaping health inequalities. Within evolutionary life history theory, the question of how the local ecology is tied to behaviour is a central tenet that has been explored with data from small-scale populations, and, more recently, with register and survey data from high-income contexts.

Chapter Outline

In this chapter, I review how scholars working within the framework of evolutionary life history theory and demography have explored contextual effects on fertility and mortality. There is a vast number of studies on this topic, and this chapter is not intended to be a comprehensive review. Rather, my aim is to highlight the main motivations and methodologies of each discipline in relation to contextual effects. In particular, I describe the framework used in evolutionary sciences known as life history theory, and approaches used in demography to highlight areas where integration between the two has occurred or would be well-placed. The structure is as follows: part one introduces the topic and lays out the structure for the rest of the chapter; part two outlines the principles of evolutionary theory and the empirical research concerned with fertility, and, more recently, health and risk-taking behaviours associated with mortality. These two sets of outcomes might deserve separate extended reviews, but both form part of this chapter because of the theoretical foundation that unify predictions for reproduction, health behaviours and mortality. The third part describes demographic approaches, first on fertility, and then on mortality and insights thereof. I end by discussing some focal methodological and theoretical challenges for the contextual effects literature and how they can be addressed.

Evolutionary Life History Theory

Evolutionary life history theory is a framework that seeks to understand the variation within and between species in the timing of life events in terms of differential energy allocations (Roff, 1992; Stearns, 1992). It posits that all individuals have limited amounts of energy and have to allocate this energy in a manner that maximizes reproductive fitness, i.e. the proportion of genes in future generations. Decisions about how to manage trade-offs between growth, body maintenance and reproduction should depend, among other things, on the conditions imposed by the ecological environment. An individual who lives in an environment where he or she can expect a long life should delay reproduction, and spend a longer time in the growth phase in order to lessen the risk of premature death and to better manage competition with peers for mates and resources. In many animal species, mortality risk declines when a larger body size is achieved (Clutton-Brock, 1991). This means that many organisms, including humans, face a trade-off between either growing for longer and having lower mortality risk for themselves and for their offspring, or commencing reproduction early and facing a higher mortality risk (Low and others, 2008; Allal and others, 2004; Stearns, 1992). Favouring the latter is known as adopting a faster life history strategy with a higher pace of important life events, such as faster growth, earlier sexual maturation and an earlier age at first birth.

Life history theory was developed in biology to understand variation in growth and reproduction in non-human species before anthropologists and human behavioural ecologists started to apply its principles to humans in the 1980s and 1990s. By then it had been demonstrated that life history variation in growth rates, maturation and reproduction between species could be explained by the mortality rates experienced by adult individuals of that species; a higher age-specific mortality rate was associated with faster life histories (Promislow and Harvey, 1990). Life history theorists, whether concerned with humans or non-human animals, take an optimality approach and assume that observed behaviour should be close to the optimal, as predicted by the costs and benefits imposed by the local environment and an individual's state (Gadgil and Bossert, 1970; Parker and Smith, 1990). Importantly, natural selection has favoured individuals who are able to respond flexibly to their environment. The term phenotypic plasticity describes the ability to alter physiology and behaviour depending on the ecological circumstances; fitness payoffs may be maximized by favouring behaviour *a* in one context, and favouring behaviour *b* in another.

It is worth emphasizing that the evolutionary perspective does not mean that all behaviour is fitness maximizing, nor is it assumed that the strategies that maximize fitness are part of a conscious process. But, for the population health sciences, it is an important insight that individuals might be willing to engage in behaviours that are harmful to their health, if such health costs are outweighed by fitness benefits incurred from such behaviours. However, for this to hold, an important assumption is that ecological conditions are at "equilibrium", i.e. stable, so that behaviour can be adjusted to the optimum. This has implications for understanding behaviour in areas where, for example, mortality rates have risen or declined sharply with little time for the adjustment of behavioural strategies. By default, behaviour is selected for past environments, but the time lag between the environmental conditions and behaviour remains a contested topic within evolutionary anthropology (Smith, 2013).

Extrinsic Mortality Risk

Life history theory scholars working on humans have generally been concerned with testing whether the variation in the scheduling of life events, such as maturation or age at first reproduction, can be explained by the variation in extrinsic mortality risk that adult individuals are exposed to in their environment (Nettle, 2011; Low, 2005). Extrinsic risks are risks that are not linked to mating or parenting and should apply equally to all individuals within a population (Charnov, 1993). Intrinsic risks, on the other hand, are risks that an individual can mitigate through behaviour, for example by the degree of risk-taking behaviour he or she exercises. The extrinsic/intrinsic distinction is a continuum rather than a clear-cut difference, and how to best operationalize extrinsic mortality risk in a given population is a difficult question that has only recently been addressed in more detail (see further below).

Extrinsic risks exist in many domains, but it is extrinsic mortality risk that has been invoked most frequently in life history models. Mortality clearly curtails the time available for siring and raising offspring, and so individuals who are able to respond to such mortality pressures should fare better than those who are not. Mortality rates (or life expectancies) have the additional benefit that they can be calculated for all groups where basic demographic (life table) data are available, and can be compared across populations and even across species. Notably, comparisons of mortality schedules have offered insights into life history differences between our close primate relatives and us; humans have considerably lower mortality rates than chimpanzees, which might explain why humans have both an extended childhood period and slower life histories once maturity is reached (Hill and others, 2001).

Patterns between mortality risk and life history traits have been studied between different human populations to explain the immense variation we exhibit as a species in terms of reproduction and other life-course scheduling. In a study of twenty-two small-scale societies, growth and maturity covaried with life expectancy at age 15 (which ranged considerably, from 27 to 50 years) in that a faster maturation and an earlier age at birth was observed where life expectancy was lower (Walker and others, 2006). High extrinsic mortality rate has also been proposed as an explanation for differences in physiology between human populations, e.g. the short adult stature of Pygmy populations might be a consequence of a growth cessation necessary to secure reproduction in the face of high mortality (Migliano and others, 2007).

Other studies of associations between ecological conditions and fertility have come from historic data and examinations of variation between parishes, or over time with varying crop failures and famines. Historical studies of this kind tend not to estimate extrinsic mortality risk directly, but use food scarcity as a measure of the environmental quality, or examine conditions prior to or at birth as linked to subsequent reproductive success (for review, see Lummaa, 2003). Analyses based on Finnish church records have found that children born during years of low crop yield have a lower likelihood of marriage and marry later than children born during years of higher food availability (Rickard and others, 2010).

Life History Variation in High-Income Contexts and Cross-Culturally

In this section I review studies that examine both fertility and mortality outcomes and behaviours that come from high-income contexts and cross-country work. One of the first studies exploring the associations between mortality risk and reproduction in a high-income context drew on data from neighbourhoods in Chicago. This study showed that when life expectancy in the neighbourhood was lower, birth rates at younger ages were higher (Wilson and Daly, 1997). The study also reported that risk-taking in terms of homicides were higher in these neighbourhoods where life was comparatively shorter (excluding deaths from homicides). The same relationship between lower life expectancy and earlier age at first birth has been found across countries (Nettle, 2011; Low and others, 2008) and within countries over time (Quinlan, 2010).

While these earlier studies were ground-breaking and tested a central and intuitive idea, some of the early results had some methodological weaknesses, such as the use of aggregated data with relatively few data points. These can be replicated and improved upon now that demographic data at the individual level have increasingly become available. Total life expectancy (or life expectancy excluding homicide deaths as in the case of Wilson and Daly, 1997) is a rather crude measure of extrinsic mortality rate, because, in high-income populations, causes of death beyond individual control come from many sources and vary between areas and socioeconomic groups (Pampel and others, 2010; Uggla and Mace, 2015). Furthermore, when both the independent and the dependent variables are aggregated, this invokes the ecological fallacy, i.e. inferring individual-level behaviour from group-level data (Robinson 1950). In other words, an observed pattern between life expectancy and fertility rates, whether within or between countries, might be due to some unrelated factor at the neighbourhood level or country level. Cross-country comparisons are problematic both because comparability of data across contexts might be questionable, and because an independent variable measured at country level is unlikely to reflect the variation within countries to which individuals are exposed (Pollet and others, 2014). There is often variation between studies in how spatial units are defined, and within studies, both the size and population densities of administrative areas may vary greatly. This naturally has implications for how results can be interpreted, both in terms of individual studies and when trying to summarize findings from the literature overall. Towards the end of the chapter, I return to these issues and discuss some methodologies that address them.

With broad cross-country data increasingly available, it is tempting to test relationships between life expectancy and various indicators of life history variation that may be comprised in aggregate data published by international organizations such as the United Nations, or the World Health Organization. However, evolutionary scholars have to think carefully about when the assumptions of their models do not hold. For instance, when new epidemics arise (as with HIV/AIDS), individuals may not have the resources, nor the correct information needed to act in a manner that would maximize their fitness. Furthermore, the assumption that ecological conditions are at equilibrium may be violated in contexts where there has been rapid development so that life expectancy has increased or is fluctuating. Rapid change in mortality rates might be a reason why extrinsic mortality risk is a rather poor predictor of behaviour in many developing contexts (Anderson, 2010). It has been suggested that life expectancy only predicts reproduction in contexts where life expectancy is 65 or over (Low and others, 2008) though there is not yet enough work on this topic for a conclusive verdict.

The studies described above aim to explain variation in demographic events as a response to variation in the extrinsic mortality risk of the environment. As such, they generally examine the association between ecological conditions and outcomes that are relatively easily captured, such as age at first birth or fertility, on which data are commonly collected and available. However, because natural selection can only act on behavioural strategies that individuals hold, a key interest in the evolutionary life history literature is the *behaviour* of individuals, rather than the outcomes such behaviour might result in. It is also crucial that a range of demographic behaviours should be correlated with individuals with a given life history strategy; for example, individuals who reproduce early should, on average, be more likely to favour risk-taking behaviours that might increase their risk of premature mortality. Engaging in high-risk behaviours and discounting the future may be adaptive if any long-term benefits are less likely to be reaped. More recent efforts have therefore sought to examine variation in risk-taking and health behaviours of individuals. Such studies have been facilitated by other forms of data than those traditionally used by evolutionary life history scholars, namely high-resolution demographic census and register data. In the following paragraphs I outline some of this research.

Life History Theory, Extrinsic Mortality Risk and Beyond

A new strand of life history research is drawing on data sources more traditionally used within demography and non-evolutionary social sciences to map variation in individual strategies with individual level data. These studies form part of a general trend that the number of studies in evolutionary behavioural ecology using data from high-income countries has increased over the past years, and it has become more common to use register, census or survey data to test evolutionary predictions (Nettle and others, 2013). The implications for life history theory studies are several. Importantly, a broader range of life history outcomes have been explored. Health behaviours can be seen as part of a life history trade-off; although not a new idea in itself (Hill, 1993), recent work has incorporated health behaviour into the life history framework in various ways (Brown and Sear, 2017; Virgo and Sear, 2016; Uggla and Mace, 2015; Pepper and Nettle, 2014; Nettle, 2010). Moreover, the increased access to detailed national datasets has allowed testing more fine-grained predictions and acknowledging that other extrinsic risks than mortality may also matter.

Exploring Life Histories with Census Data: The Case of Northern Ireland

Detailed data on causes of death from mortality registers can be used to take seriously the question of how to operationalize extrinsic mortality risk in a given population. Ruth Mace and I set out to test whether extrinsic mortality rate at the local level was associated with age at first birth and death from risk-taking behaviours or behaviours harmful to one's health (Uggla and Mace, 2016a, 2015). We made use of census data from Northern Ireland, where the whole population is included in a longitudinal mortality study linked to the census. To construct a measure of extrinsic mortality rate, a definition from population health sciences was applied. It classified all possible causes of death into those that are preventable and those that are not, based on International Classifications of Diseases (ICD): classifications of death recorded by the medical doctor (Page and others, 2006). ICD codes are very detailed, and so distinctions can be made based on how likely it is that the individual's death was linked to their own risk-taking or health behaviour. For instance, preventable deaths comprise cancers where the role of individual behaviour is deemed to have an impact on disease aetiology (e.g. lung cancer from smoking), and traffic accidents that are due to the driver's own behaviour (e.g. involve a stationary object rather than another vehicle). A range of causes of death beyond individual control, e.g. genetically determined illnesses, are deemed unpreventable. While a perfect measure of what causes of death are within or beyond individual control is probably impossible to operationalize, this distinction captures all causes of death and whether they were deemed preventable by health care professionals. Extrinsic mortality rates on local ward level were then calculated based on deaths deemed unpreventable and showed large variation between areas.

Using this extrinsic mortality rate as an independent variable, the analysis suggested that mortality risk beyond individual control was positively associated with both reproduction and intrinsic deaths from risk-taking behaviours, but that patterns varied for different individuals. Men living in areas with higher extrinsic mortality rate, i.e. more likely to die from causes *beyond their own control*, had higher risk of death from risk-taking or poor health behaviour, than men who lived in areas with lower extrinsic mortality rate (Uggla and Mace, 2015). However, the same was not true for women. Moreover, the data suggested that the association between extrinsic mortality rate and risk-taking behaviours was greater among men with lower socioeconomic status (SES) than peers with higher SES. Heterogeneity in contextual effects has not received much attention within evolutionary sciences (probably due to a lack of data,) but evidence of this nature is common in demography and population health, albeit rarely with the intrinsic/extrinsic distinction.

Crime, Morbidity and Adult Sex Ratios

Another advantage of having access to detailed census or register data is that other potentially important factors can be explored alongside extrinsic mortality rate to compare their relative effect. Our Northern Ireland studies also explored whether other area factors such as the adult sex ratio (an indication of number of available partners) and the level of crime in the local wards were correlated to individual reproduction and risk-taking behaviour (Uggla and Mace, 2016a, 2015). Interestingly, among men, the same two area effects — extrinsic mortality rate and crime rate — predicted both early childbearing and death from risk-taking behaviours. Among women, the data suggested that earlier childbearing was, in addition to extrinsic mortality rate and crime, associated with a female-biased adult sex ratio (i.e. accelerated in areas where mates were scarce).

Local morbidity rate is another potentially important factor for life history variation. In societies where modern health care facilitates a longer life, healthy life span might matter more than absolute life span. Furthermore, it might be easier to perceive whether people in one's surroundings are healthy (and at what age health imposes constraints on lifestyle) than to perceive extrinsic mortality risks. Some recent evidence underpins the association between morbidity and reproductive behaviour; higher morbidity at the ward level has been linked to a lower abortion rate for women under the age of 25 years, but a higher abortion rate at older ages in the UK (Virgo and Sear, 2016). Virgo and Sear (2016) argue that morbidity might be a more salient cue to reproductive decision-making than mortality in their high-income population, offering a rare comparison between different area-level factors.

Summary

Contextual effects are central to evolutionary life history theory, which has sought to explain variation in important life events such as age at first birth within and between populations. In particular, extrinsic mortality risk is a population level variable that has been at the core of evolutionary life history models. Life history theory emerged from observations based on animal species, and evolutionary anthropologists were initially concerned with testing hypotheses in small-scale societies. Recently, with the increasing availability of high-quality survey, census and register data (mostly) from high-income contexts, there has been a shift towards data that allow us to test life history predictions in more detail. Simultaneously, the field has broadened its focus from reproduction (e.g. age at first birth), to include other outcomes such as abortion, breast-feeding practices and health-seeking behaviours. Two important insights from life history theory that can be of value in non-evolutionary social sciences are (i) individuals may behave in ways that are harmful to health and wellbeing in order to maximize fitness, and (ii) context should shape behavioural strategies so that an individual's outcomes fall on a trajectory (i.e. some correlation between different demographic behaviours).

Summary of the evolutionary life history framework for understanding variation in reproduction and mortality:

- Primary interest lies in understanding how natural selection has shaped human behaviour, rather than predicting trends in fertility or mortality within a specific population.
- Human behaviour has been shaped by natural selection to be highly flexible, and this so-called phenotypic plasticity is not due to genetic differences between groups.
- Early reproduction and risk-taking behaviours, while in some cases harmful to health and wellbeing, may be seen as adaptive responses to an individual's environment.
- Childbearing behaviours and risk behaviours are likely to be correlated within individuals to some extent.
- The use of demographic and health data has enabled the testing of fine-grained predictions, and the operationalizing of extrinsic mortality risk in a broad range of populations.

Contextual Effects in Demography

In this section I provide an overview of contextual studies on fertility and mortality in demography, comparing and contrasting them with the evolutionary approach to the same questions.

Overview

In contrast to evolutionary scholars concerned with generating and testing hypotheses based on evolutionary theory, demography is a discipline with relatively little or no overarching theory (Tabutin, 2007). This depends, of course, on the definition of theory, and to what extent the bringing in of theories from neighbouring disciplines (such as sociology and economics) is considered "demographic". Demography grew out of analyses of national registers and censuses, and is naturally closely entwined with social policy and advocacy. It has even been called a "wild science", due to its origins in data collection and government organizations, as opposed to academia (Petit, 2013). While there is clearly merit in descriptive demographic research, some demographers have argued that the discipline would benefit from integration of a broader range of theories (e.g. Sigle, 2016).

Given the difference in their origins, it is not surprising that demography and evolutionary sciences have differed in their foci and in the populations most often studied. In Table 1, I lay out some of the typical key interests, similarities and differences between them. Where evolutionary studies traditionally drew on small-scale populations and data collected by anthropologists, demographers interested in contextual effects often use data from both low- and high-income countries to compare different regions or residential areas. National registers and survey data, which form the basis of much demographic work, have many strengths. They often stretch over long periods of time, have multiple outcomes on the same individual, can track domestic migration, and be tied to changes in policies and society overall. This is valuable considering that one role demographers fulfil is to help nations understand and make projections about their populations and the wellbeing of their people, but is equally useful when testing predictions about human behaviour.

Table 1. Comparison of key features and interests of evolutionary life history theory and demography for contextual effects on fertility and mortality.

	Evolutionary life history theory	**Demography**
Definition	The study of human behaviour within and between societies as understood from an evolutionary framework based on natural selection	The study of populations and the cornerstones of population change: fertility, mortality and migration
Key aims	To generate and test hypotheses to develop understanding of human behaviour and evolutionary theory	To describe and forecast population patterns of fertility, mortality and migration, and improve public health and reduce inequalities
Populations of interest	Typically traditional, small-scale societies, with recent increased interest in high-income contexts	Anywhere data are available, but predominantly populations with censuses, large surveys or registers
Theory	Life history theory (and others) from evolutionary biology	Less reliant on theory, or informed by theory from the social sciences e.g. sociology
Data	Small-scale household surveys conducted by anthropologists, historical records, e.g. parish records, and more recently population registers and census data	Register, census or survey data, sometimes linked to health registers; rarely collected by those who analyze the data
Age groups of interest	Mainly (but not limited to) individuals of reproductive age, or behaviours that can be traced to that age group	Either the whole population, or specific sub-groups that can be defined for interventions, e.g. "the oldest old"
Outcomes of interest	Age at first birth, total fertility, risk-taking behaviours and intrinsic mortality. Multiple demographic behaviours are expected to fall on a continuum of a life history strategy	Measures of fertility, life expectancy, all-cause mortality or specific causes of death, often studied separately, migration
Focal area/ contextual predictors	*Extrinsic* mortality (often proxied using measures of deprivation) and more recently other indicators e.g. morbidity rate	Neighbourhood poverty, deprivation indices

Contextual Effects on Fertility

Much demographic research on tempo and quantum of fertility (when people have children and how many they have) has explored individual determinants, such as women's labour market participation and education (Hoem and others, 2006), rates of cohabitation, marriage and separation (Kohler and others, 2002) and the impact of various family policies (Neyer and Andersson, 2008). However, it is widely recognized that to predict an individual's or couple's childbearing behaviour, considering the context in which people live is important. In early demographic studies that sought to explain the first demographic transition, spatial analyses were integral as fertility decline was propelled by urban dwellers before rural family sizes followed suit (Coale and Watkins, 1986). The decisions of whether or not to have a child, when to start, how to space children and when to stop all impact fertility rates, and are complex decisions with multiple determinants governed by the norms, institutions and policies at country or regional level (for review see Balbo and others, 2013).

Many insights into, between and within country variations in fertility come from studies on the first demographic transition. One example of the latter is Belgium, a small country geographically, but diverse in terms of religion, culture, language and development: it demonstrated variation between two neighbouring provinces that could be comparable to a lag of fifty years of fertility decline (Lesthaeghe, 1977). From the late nineteenth century until 1960, fertility variation at the national level increased in Western Europe, and at the subnational level it decreased with increasing homogenization within national states (Watkins, 1990). Then in the 1960s and 1970s, Europe underwent a second demographic transition, where a gender revolution and a resurgence in female participation in the labour force that was incompatible with childcare led to the postponement of first births and an overall decrease in fertility (Lesthaeghe, 2010). Nevertheless, substantial variation in fertility has persisted between European countries and regions (Billari and Kohler, 2004).

In the debate on whether country differences in fertility will persist or whether convergence is likely to continue (Frejka and Calot, 2001; Wilson 2001), some have argued that it is surprising that there is not a greater body of work on *within*-country fertility variation (Kulu and Boyle, 2009), and the local residential context. Much of regional fertility variation has been analysed at the national or sub-national level perhaps because variables of interest, such as labour market conditions and level of economic development (Fox and others, 2018), or the impact of family policies on fertility are easily operationalized on the national or sub-national level, but make less sense at the neighbourhood level. Moreover, it is possible that the objective to avoid very low fertility *at the population level* contributes. That is to say, from a policy standpoint, very low levels of fertility are problematic at a national level, but less alarming in smaller areas of resolution, both because of how nation states are organized, and because people move between areas.

The recent surge in spatial analyses of fertility was long overdue and may be related to more refined measures and methods available from geo-coded data and multilevel models (Voss, 2007; Matthews and Parker, 2013). Echoing the early studies on urban/rural differentials, one strand of current within-country research has posed the question of whether fertility differs according to residence type. On balance, these studies tend to show that there is higher fertility in rural and suburban areas than in urban areas, which persists even when the SES composition of such areas is controlled (Kulu and Boyle, 2009). However, because some areas are seen as more suitable for bringing up a child, the "migrant selection" effect is a likely confounder (Courgeau, 1989). It is also vital that studies comparing different geographical areas (e.g. regions, census tracts, wards or some other spatial unit) separate the contextual from the compositional, the latter referring to the fact that fertility rates of a given region may be due to the composition of individuals who live there, rather some other property of the area. Evidence that fulfils these criteria is mixed; some studies suggest that context does not matter for fertility once differences at the individual level are accounted for (Hank, 2002), while others demonstrate evidence of clear regional differences that are robust even after adjustment for individual characteristics such as women's employment and civil status are made (Kertzer and others, 2009). There might also be differences with the type of outcome examined. For example, in the UK the influence of the residential area level has been found to be relevant for the transition to first birth, but second- and third-birth progressions are correlated to the characteristics of the couple, and not the area where they reside (Fiori and others, 2014).

Some contextual studies examine fertility behaviours of individuals with different language identities, or who have a different ancestry or ethnic background. Recently revisiting the subject of Belgian fertility variation, Klüsener and colleagues (2013) have demonstrated that individuals living in the German-speaking regions of Belgium, which bear the influence of German family norms but enjoy Belgian family policies, have fertility profiles that are more similar to the Belgian than the German. The authors argue that institutional context is more influential than cultural norms, although how these might be fully disentangled remains a sticky point. Another perspective on local influence comes from studies of the fertility of immigrants and their descendants, where residential segregation is used as a proxy for exposure to norms of the destination country (Kulu and González-Ferrer, 2014). For instance, child migrants to England and Wales who grow up in areas with lower levels of residential segregation have fertility levels that are more similar to those of natives, as compared with peers who grow up in more segregated areas. This points to the fact that residential context during childhood is important for future fertility behaviour (Wilson and Kuha, 2018).

Further efforts to focus on the role of context include research that goes beyond the arbitrary residential areas and investigates the influence of nearby neighbours and colleagues on fertility behaviour. Recent evidence from Norway suggests that neighbours influence couples' transition to a third birth, even after couple confounders were adjusted for (Bergsvik and others, 2016). The results held when varying the area sizes between the five hundred and the twelve nearest neighbours. In the same vein, but examining the social influence of colleagues in the workplace, data from Germany suggest that women are influenced by female colleagues; odds of progression to first birth doubled the year after a peer gives birth, after which the odds decreased and were diminished after two years (Pink and others, 2014). A recognition that meso-level factors (such as social network and family-level factors) are important, sandwiched in between micro-level (individual) and macro-level factors (institutions and norms), is growing, and provides a link between small areas and the larger contexts in which they are embedded (Balbo and others, 2013).

Teenage Childbearing and Neighbourhood Deprivation

Teenage childbearing is one aspect of fertility that has been studied extensively from a contextual perspective; these studies show that neighbourhood deprivation is associated with earlier onset of childbearing (Harding, 2003; Imamura and others, 2007). Teenage childbearing has been seen as an undesirable behaviour by policy makers, often linked to adverse birth outcomes and sexual risk-taking and, as such, subject to many policy interventions (Dickins and others, 2012; Allen and others, 2007). Nevertheless, neighbourhood deprivation studies have not generated conclusive evidence on what it is about deprivation that is associated with earlier childbearing. Some evidence suggests that the risk of teenage pregnancy is higher if a high-poverty neighbourhood is adjacent to a more prosperous neighbourhood, hinting at an effect of inequality (see also Gold and others, 2004; Wilkinson and Pickett, 2007). Contextual effects on early fatherhood have not received much attention, echoing the general trend of more emphasis on female than male fertility. Where female and male childbearing at young ages have been compared, there is some indication that different contextual effects matter for early motherhood and early fatherhood (Uggla and Mace, 2016a), however this area remains underexplored.

Covariation in Fertility and Mortality

While demographic work has established that fertility and mortality often change in concert, demographers have primarily been concerned with trying to describe shifts in fertility and mortality at the population level, rather than examining variation at the local and individual level. Even less work has attempted to ascertain the effect that population mortality rates have on individual reproductive decision-making. In contrast, the opposite relationship, i.e. the impact of an individual's childbearing on longevity, has generated interest in both demography- and evolutionary-informed work (Chereji and others, 2013; Doblhammer and Oeppen, 2003). That is not to say that the idea that mortality rates can impact fertility is a foreign one in demography. Conversely, it is well known that a decline in child mortality on the population level, together with economic development, predated the decline in fertility of the first demographic transition (Kirk, 1996). To consider children as part of an economic quality-quantity trade-off, where child quality is favoured over quantity when mortality rates decline (Becker, 1981), is an example of how economic theory has been integrated into life history models, and is central to the evolutionary study of human fertility (Hill and Kaplan, 1999; Kaplan and others, 2002).

Work on so called "mortality shocks" and their impact on fertility are analogous to evolutionary work outlined in previous sections of this chapter. For example, Nobles and colleagues used data from regions affected by the 2004 Indian Ocean tsunami, whose impact was considered to hit communities randomly, to study the impact of mortality rates on fertility (Nobles and others, 2015). They found evidence of replacement fertility (women who lost children were more likely to have another birth) and that women without children before the tsunami commenced childbearing earlier in regions affected by the tsunami (Nobles and others, 2015).

While evidence linking local mortality risk and reproductive behaviour remains rare, other factors such as economic insecurity and uncertainty have been scrutinized in detail by demographers. Economic downturns and increases in regional unemployment rates tend to be negatively associated with fertility (Sobotka and others 2011, for review). A recent study showed that, following the recent recession in 2008 in the US and Europe, both unemployment rates and overall uncertainty (measured as drop in consumer confidence and sovereign debt risk) were negatively associated with childbearing (Comolli, 2017). While the type of data and operationalizations of uncertainty differ, this type of work has much in common with evolutionary studies that have also explored the associations between uncertainty and reproductive behaviours (Nolin and Ziker, 2016; Davis and Werre, 2008). Thus, central research questions about the role of extrinsic mortality risk and uncertainty for reproduction exist in parallel, and greater cross-disciplinary integration would be beneficial.

Contextual Effects on Mortality

Recent years have seen an explosion of studies on how neighbourhood factors are associated with health and mortality. Several converging trends are likely to be responsible for this influx, including better statistical methods that allow isolating individual and area effects, developments within geo-referencing technologies, a renewed interest in health inequalities, and the idea that individual characteristics are insufficient to explain health outcomes (Diez Roux and Mair, 2010). As with fertility, the processes leading to mortality are complex. Mortality is determined by a combination of diet, physical activity, health behaviours, genetic predisposition, social support, access to health care and physical barriers such as pollutants or toxins that may vary between areas.

A key reason mortality risk is examined at the local level is because it is thought that many health interventions can be implemented at this level. However, with indications that the magnitude of the area effects are sometimes negligible, there has been debate about the usefulness of health policy implementations at the neighbourhood level (Lupton, 2003). While some studies map contextual effects on life span or all-cause mortality, others are conducted by medical experts who have an interest in a particular outcome, e.g. ischemic heart disease or suicides. When a particular disease or cause of death is of interest, it may be easier to hypothesize about the potential impact of the local context. However, rarely are different causes of mortality that could be considered under individual control categorized together. In part, this might be due to the fact that the types of death that are preventable varies over time and space (Page and others, 2006).

Most contextual studies examine the association between some form of aggregated SES measure or deprivation and mortality. These studies generally find that higher deprivation is linked to higher all-cause mortality risk after controlling for individual SES and other factors. An early example from the US reported that, after controlling for age, sex, race and health status, individuals in deprived areas had a 50% higher risk of death (Haan and others, 1987). This association is remarkably consistent across countries (in European and US datasets) (van Lenthe and others, 2005). A different set of studies examine variation or inequalities without having *a priori* predictions of why there is variation between areas. Area variances — and not just the means — are important in order to accurately understand differences between areas (Merlo and others, 2009) and provide an indication of the magnitude and change over time of health inequalities.

Heterogeneity of effects is central to understanding the plethora of results of contextual effects of mortality. There is evidence that the association between area SES and mortality is stronger for men, and for older individuals (Meijer and others, 2012). Winkleby and colleagues (2006) report that in the US, the benefits associated with residence in a more affluent area do not extend to men and women with a lower SES. Furthermore, the effect of the local area on mortality may vary depending on the individual's life stage. For instance, multiple waves of census data from Norway suggest that, for young individuals, only the most recent area of residence was linked to mortality from violence and mental health issues, whereas for older individuals, areas from previous stages of life had additional effects (Naess and others, 2008). However, because different outcomes might have different relationships with different neighbourhood characteristics, caution should be exercised when generalizing from one dependent variable (Roos and others, 2010).

Deprivation and Extrinsic Risks

Many insights gained from demographic and epidemiological studies on contextual (or neighbourhood) effects on mortality can be linked to evolutionary life history theory. Arguments related to deprivation and death are congruent with extrinsic mortality risk, because deprivation is in many cases associated with higher extrinsic mortality (Pampel and others, 2010; Uggla and Mace, 2015). Thus, the vast amount of evidence on associations between area SES and behaviours constitute a rich source that underpins arguments of extrinsic mortality risk for health and risk-behaviours. However, conclusions based directly on extrinsic mortality risk and its impact on particular health behaviours are almost non-existent. This may be because it appears circular that population mortality rate — even if it is extrinsic — at the area level would predict risk of death of individuals. One exception comes from work based on Demographic and Health Survey (DHS) data from fourteen African countries (Oster, 2012). Oster found that reductions in HIV risk-taking were higher where life expectancy (excluding HIV deaths) was higher, that is, where individuals' sexual risk-taking had greater impact on their life span. This is one plausible explanation for why behavioural response to HIV has been much slower in this context than the HIV response in some high-income contexts (Oster, 2012).

Proximate Determinants and Constraints

Demography and other data-driven disciplines are well positioned to measure proximate mortality determinants, such as healthcare access or availability of close kin, on mortality. The emphasis on proximate determinants of health and mortality outcomes is a good complement to the life history approach that has been less concerned with proximate causes. As a useful starting heuristic, evolutionary-minded scholars assume that individuals are able to make cost-benefit analyses about mortality risk because they are able to gain accurate information on the costs and benefits of their decisions (not necessarily consciously), and can respond to contextual factors largely without constraints (Borgerhoff Mulder and Schacht, 2012). This might not always be true and provides reason to think about how constraints to invest in health vary between different sub-groups. In the UK, individuals in more deprived areas report feeling less safe using green spaces for physical activity (Jones and others, 2009) and are exposed to more fast-food advertising than individuals in more affluent neighbourhoods (Adams and others, 2011). Such structural differences, coupled with physiological pathways, e.g. that women in deprived areas are more likely to have a blunted cortisol response, might make it difficult to favour day-to-day health choices that are beneficial in the long term over those that offer short-term gratification (Barrington and others, 2014).

Summary

Within demography, much emphasis is placed on describing variation in fertility patterns, though spatial differences are often examined on national or sub-national level, and few examples exist of how mortality risk influences fertility. Indirect measures such as urban versus rural residence, area deprivation and proxies for uncertainty are nevertheless insightful and often overlap with evolutionary perspectives on fertility variation. With regard to mortality, in recent years the number of studies on contextual effects on mortality has grown rapidly. Individuals in areas with high deprivation generally have higher excess mortality, even when individual characteristics have been controlled (or "accounted for"). However, there are notable differences in how determinants are operationalized, and in heterogeneity based on, for example, sex and life-course stage. An increased understanding of the feedback loops between socioeconomic factors, health and reproduction, along with broad interest in proximate pathways, is promising for the aim to decrease inequalities in mortality.

Summary of contextual effects on fertility and mortality within demography:

- Motivated by understanding determinants of fertility and improving health and wellbeing of populations.
- Takes a "bottom-up" approach and is not always strongly theoretically motivated and/or draws on theories from other social science disciplines.
- Individuals in deprived areas have higher rates of teenage childbearing and higher mortality risk, but these topics are seldom studied in unison.
- Contextual effects on mortality are part of a burgeoning literature on health inequalities which has documented differences according to type of mortality and individual characteristics.
- Demographic studies on fertility and mortality are often characterized by an emphasis on methodological quality, including selection biases, and methodologies that attempt to isolate influences.

Challenges and Future Routes of Research

In this section, I discuss some challenges to research on contextual effects, including selection biases, how to define areas, and understanding the underlying mechanisms. I offer some suggestions for future research and stress the complementary insights of evolutionary theory and demography for these questions.

Selection Biases

Both studies rooted in demography and evolutionary life history research overwhelmingly rely on observational data. While experimental study designs have been used to test life history predictions in both humans and other species, when it comes to factors influencing actual behaviour rather than preferences for childbearing, the experimental method is neither feasible, nor ethical for human subjects. Physiological experiments, including priming methods, are an exception (for review, see McAllister and others, 2016). Inherent to observational data are issues of selection biases, which are problematic when trying to make inferences about the impact of an area on the behaviour of individuals who live there. Even with longitudinal register data, factors that might be associated with a propensity to move to a certain area often cannot be adjusted for.

One way to address issues of self-selection is through randomized controlled trials. These are commonly used in medicine and for public health interventions, but are more complicated when applied to questions related to contextual effects. A rare example of experimental data on this topic is the Moving to Opportunity (MTO) project, which was implemented in five large US cities in the 1990s to test the effect of areas on individuals (Leventhal and Dupéré, 2011). In this project, randomly selected participants in high-poverty neighbourhoods were offered vouchers and support to move to less impoverished areas. There have been many studies on the MTO project, one of which reported that young girls who moved to a less deprived area had fewer mental health problems and more benefits in terms of education than non-movers (Leventhal and Dupéré, 2011). However, even if it is considered ethical, moving people to a new area is difficult, expensive and impractical and does not necessarily eliminate doubts about causation (Oakes, 2004). Thus, we are often left attempting to infer causality from observational data. Some have argued that the statistical issues such as endogeneity — the difficulty of defining appropriate geographical borders and extrapolation in multilevel analyses — mean that contextual effects are better investigated through qualitative approaches (Cummins and others, 2007). While they cannot alleviate the problem of selection biases, mixed-methods studies that draw on both qualitative and quantitative data could help to understand the experiences that produce behavioural variation between areas.

How Should Spatial Units Be Defined?

A common assumption of contextual studies is that the area where an individual lives functions as a cue to what life history strategy he or she should adopt, and is where childbearing intentions are formed. Neighbourhoods are often relatively small areas in which individuals may be familiar with the local conditions. But when areas are larger, e.g. census tracts or regions, the area might poorly capture what an individual encounters in his or her daily life. A study on area effects on all-cause mortality in Finland found an effect of residential area SES when the area was 250 x 250 meters, but this effect was attenuated, or completely absent when larger areas were used (Halonen and others, 2013). Another complication is that, in high-income countries, many individuals move between the home and the workplace and encounter multiple areas on a daily basis. Multilevel models with multiple memberships that allow simultaneous incorporation of family and work environments alongside wider contextual effects (Fielding and Goldstein, 2006), may go at least some way towards addressing this bias statistically. Where possible, areas based on a given number of nearest neighbours, applied, for example, in geography (Malmberg and Andersson, 2019), will help to fine-tune research designs so that they are congruent with the research question at hand.

Heterogeneity of Effects

From a population health perspective, heterogeneity in contextual effects is important to identify vulnerable groups, and to understand better the pathways to good health. From an evolutionary perspective, heterogeneity in contextual effects may help test detailed predictions for how costs and benefits of the local environment vary with age, sex or sociocultural context. For example, we may predict that the relationship between extrinsic mortality risk and health behaviour should be stronger among young individuals if local mortality rate has stronger fitness implications for younger than older individuals. However, the evolutionary perspective can generate predictions in different directions depending on the particular assumptions and the outcome in question. For this purpose, broad population data are required to compare different groups within populations, especially when the outcome of interest is premature mortality or other rare events. Anthropologists have often lacked data to test such effects, because, in small-scale societies, entire populations might yield sample sizes that are too small to test interactions. Thus, existing evidence from demography on contextual effect heterogeneity is useful, as it can both help to test the assumptions and to think clearly about the theoretical reasons for why effects may vary.

What Are the Underlying Mechanisms of Contextual Effects?

A major challenge for future research is to understand the pathways by which context is associated with variation in fertility and mortality. One development is the application of biomarkers that can capture how physiological characteristics differ between deprived and affluent neighbourhoods. Allostatic load, a measure of the "wear and tear" of the body has been linked to cumulative neighbourhood disadvantage (i.e. the longer the exposure to a deprived neighbourhood, the worse the condition) (Gustafsson and others, 2014). But even with such new knowledge of biomarkers, we may not be able to assert how various indicators are related to behaviours within the same areas.

Other types of data, e.g. from surveys, can help us to understand people's perceptions of local conditions, which might be as important as the observable local characteristics. James Gilbert, Ruth Mace and I tested individual perceptions in eight neighbourhoods of Belfast, Northern Ireland, and compared these to the census data of these neighbourhoods (Gilbert et al., 2016). The data suggested that while individuals had an accurate perception of neighbourhood age at death and morbidity, the discrepancies between actual and perceived levels of crime were high. Most individuals across the eight neighbourhoods reported high perceived personal safety, even though these neighbourhoods had been chosen to include both high and low ends of the crime rate distribution. One interpretation is that crime may affect only some individuals in an area and most individuals have reason to feel safe. There are clear parallels to the difficulty of perceiving local conditions accurately, which has been discussed with reference to mortality decline in low-income countries. It has been argued that perceiving mortality decline is difficult due to our tendency to acknowledge events, such as child deaths, more than non-events (child survival) (Montgomery, 2000). Future research will have to deal with the semantics, i.e. that individuals might respond in a manner that fits with the narrative of whether their area is "good" or "bad", and whether perceptions extracted verbally are meaningful.

Incorporating Life Course Factors into Contextual Effects

Both demographers and evolutionary scholars recognize the importance of the life course in shaping individual health (Ben-Shlomo and Kuh, 2002; Stulp and Sear, 2019), and it will likely continue to be integrated into new work on contextual effects. One question of interest is whether some periods during early development and childhood have more bearing on adult reproductive decision-making and health outcomes than do later periods in the life course. Whether developmental trajectories are mostly determined by the cumulative exposure to poverty, or whether certain periods, e.g. early childhood or adolescence, constitute a "critical window" is debated in both developmental biology and psychology, and within the health sciences (e.g. Braveman and Barclay, 2009; Murray and others, 2011). Another life-course question is to what extent individual reproductive, socioeconomic and health outcomes will correlate. Despite the strong theoretical motivation of life history scholars to predict multiple outcomes over the life course, they lag behind demographers who have long dealt with the issue of anticipatory analyses, i.e. that individuals may schedule life events (such as having a child) with the anticipation of other future events (such as completing higher education) (see e.g. Hoem and Kreyenfeld, 2006). This is a clear example of where theory and methodological insights from respective discipline could be successfully integrated.

Conclusion

Demographers and evolutionary life history scholars alike are interested in understanding why fertility and mortality vary between contexts. In so doing, scholars from these two fields have different aims, motivations and disciplinary origins that explain why their respective approaches to contextual effects differ — and where they overlap. While demography takes a bottom-up approach, driven by data, evolutionary sciences are top-down where data is a necessary means to answer questions that develop theory (Sear, 2015). Evolutionary anthropology has been characterized by the application of survey data from small-scale populations to understand fertility variation, rather than samples with a large number of data points that lend themselves to complex statistical techniques. The application of demographic data and methodology is now seen, for example, within anthropology, where studies have used a multi-level framework with Demographic and Health Survey data, or teamed up with local NGOs to collect rich data in different spatial areas (Lawson and others, 2015; Howard and Gibson, 2019; Uggla and Mace, 2016b). This development is relevant to area effects because it denotes a shift from the anthropological tradition of comparing populations in different contexts and with distinct cultural attributes, to comparing individuals residing in different settings while holding constant various characteristics that have been collected in a uniform manner.

Despite the differences between the disciplines, there are many shared elements and areas where integration is occurring or where continued interdisciplinary exchange seems promising. Demographers and evolutionary scholars interested in topics related to reproduction and mortality share the quest to understand the pathways that can lead to improved population health. In so doing, a better grasp of the role of life course factors, proximate physiological mechanisms and the role of structural constraints at the local level are key challenges. Identifying the determinants that link health, wellbeing and reproduction is a tall order and an endeavour that necessitates integration of different approaches and theories. The wealth of data from different populations is among the contributions of evolutionary theory to the understanding of human fertility, and it provides an extra layer of explanation that can unify existing frameworks (Sear, 2015). With the continued exchange of novel methodologies and the increased sharing of data from different contexts, further integration between these fields has great promise to enable us to better understand how the local context influences fertility and mortality.

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1 Note this chapter has been posted on the Open Science Framework website since 08/04/2020, after it was accepted for publication, so the references will reflect when the chapter was written and not the OBP publication date.

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