Increasing population densities predict decreasing fertility rates over time: A 174-nation investigation

Amanda Rotella[1], Michael E. W. Varnum[2], Oliver Sng[3], & Igor Grossmann[4]

[1] Kingston University

[2] Arizona State University

[3] University of California, Irvine

[4] University of Waterloo

Corresponding Authors:

Amanda Rotella
arotella@kingston.ac,uk
Kingston University
55-59 Penrhyn Rd
Kingston-upon-Thames, UK
KT1 2EE
*Note: AR conducted most of this work wile at the University of Waterloo, 200 University Avenue West, Waterloo, Ontario, Canada N2L 3G1.

Michael Varnum
mvarnum@asu.edu
Department of Psychology
Arizona State University
PO BOX 871104
Tempe, AZ USA
85281

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Abstract

Fertility rates have been declining worldwide over the past fifty years, part of a phenomenon known as “the demographic transition.” Prior work suggests that this decline is related to population density. In the present study, we draw on life history theory to examine the relationship between population density and fertility across 174 countries over 69 years (1950 to 2019). We find a robust association between density and fertility over time, both within- and between-countries. That is, increases in population density are associated with declines in fertility rates, controlling for a variety of socioeconomic, socioecological, geographic, population-based, and female empowerment variables. We also tested predictions about environmental boundary conditions. In harsher living conditions (e.g., higher homicide or pathogen rates), the effect of increased population density on fertility rates was attenuated. The density-fertility association was also moderated by religiousness and strength of social norms, where the relationship between density and fertility was attenuated in countries with high religiosity and strong social norms. We discuss why and when changes in population density may influence fertility rates and the broader implications of this work.

Keywords: fertility, population density, demographic transition, life history theory, cross-cultural differences

Over the past fifty years, social scientists have documented a “demographic transition” – i.e., a decline in lifetime birth rates and death rates across the world (Caldwell & Mcdonald., 2006; Chesnais, 1992). These trends have caused concern in several societies where the birth replacement rate is now lower than the death rate (Lutz, O’Neill, & Scherbov, 2003; Lutz, Testa, & Penn, 2006). Such demographic shifts have important societal consequences, including implications for pension systems (Blake & Mayhew, 2006) and economic growth (Bloom, Canning, & Fink, 2010; Lee & Mason, 2010). There are also a number of cultural implications of declining fertility rates including increasing empowerment of women (Varnum & Grossmann, 2016; Shenk, 2009; Shenk et al., 2013), changes in childrearing practices and norms including later ages at first birth (Sng et al., 2017; Twenge & Park, 2019), and greater emphasis on women’s educational achievement (Anderson & Kohler, 2013).

Recent findings (e.g., Shenk et al., 2013) suggest that the demographic transition model, which proposes that the declining mortality rates lead to lower fertility, is not sufficient in understanding the decline in fertility rates across countries. So, what is driving this phenomenon? Several factors have been linked to the recent decline in fertility rates. For example, some work finds that lower risk of infant and childhood death is related to longer inter-birth intervals and reduces the need to “replace” children to attain a desired number of surviving children (Palloni & Rafalimanana, 1999). Other research suggests that people with higher education have children relatively late and have fewer children (Low, Simon, & Anderson, 2002; Shenk, 2009). Further, others have linked declines in fertility rates to changes in family values, reductions in desired family size, and increased availability of contraception and other means of family planning (Newson et al., 2007; Sanderson & Dubrow, 2000; Shenk, 2009; Shenk et al. 2013).

Additionally, there is some evidence of an association between greater prevalence of non-agricultural occupations and lower fertility rates (Shenk et al. 2013).

Another potential reason for declining fertility that has garnered increasing attention is rising population density (Lutz, Testa, & Penn, 2006; Sng et al., 2017). In fact, this link has been reported in the non-human animal literature, where density-dependent effects for survival and reproduction have been found across taxa in both domestic and wild animals. In non-human animal studies, higher population densities have been associated with reduced reproduction rates (Fowler, 1981; 1987). Further, experimental work suggests that this relationship is causal: Organisms downregulate their fertility rates in higher densities (e.g., Both, 1998; Dondt, Kempenaers, & Adrianensen, 1992; Leips et al., 2009; see Sng et al., 2018, for a recent review of this literature).

Human studies addressing the link between density and fertility have found the same relationship – as human population densities increase, fertility rates decrease (Easterlin, 1976; Firebaugh, 1982; Lutz & Quiang, 2002; Lutz, Testa, & Penn, 2006; Sng et al., 2017; Van Landigham & Hirschmann, 2000). Experimental work provides an initial causal evidence for the relationship between density and fertility in human populations: Reproductive-age participants learning about increasing population densities subsequently indicated wanting fewer children (Sng et al., 2017).

Limitations of prior work

Prior work on population density and fertility has two major limitations. First, prior cross-temporal investigations have been largely atheoretical (Firebaugh, 1982; Lutz & Qiang, 2002; Lutz, Testa, & Penn, 2006). Second, theory-based work has been largely cross-sectional (Sng et al., 2017). We aim to address these two limitations and advance our understanding of the relationship between density and fertility by using time-series methods and the most comprehensive time-series data on density and fertility to date. To this end, we assess the robustness of the relationship between population density and fertility rates over time around the globe, test plausible alternative explanations for this relationship, identify key moderators, and advance a theory-driven explanation for the effect of population density on fertility rates.

Why should population density affect fertility?

According to prior research, population density impacts a range of psychological phenomena, including juvenile delinquency and psychiatric admissions (Galle, Gove & McPherson, 1972), greater interpersonal hostility (Griffit & Veitch, 1971), and poorer task performance (Martens & Landers, 1972; but see Lawrence, 1974). More recently, dense populations have been associated with greater future time orientation (i.e., planning behaviors), later marriage age, longer life expectancies, greater sexual restrictedness (i.e., wanting more commitment from partners and fewer sexual partners), higher educational attainment, higher rates of preschool enrollment, lower fertility, and lower rates of teenage births. Importantly, most of these associations endure after accounting for wealth (i.e., gross domestic product [GDP]), urbanization, population size, and cultural tightness (Sng et al., 2017). Moreover, in experiments where participants were exposed to information about increasing population density, they reported greater future time orientations, a preference for fewer, higher investment romantic relationships, and a desire for fewer children (Sng et al., 2017). These findings suggest that perceptions of population density are associated with, and have a potential causal influence, on many behavioral outcomes.

Why would higher population densities lead to lower fertility rates? One answer to this question comes from life history theory—a framework for understanding how organisms allocate limited resources in strategic trade-offs, such as survival and reproduction (MacArthur & Wilson, 1967; Reznick, Bryant, & Bashey, 2002; Ellis, Figueredo, Brumbach, & Schlomer, 2009). This theory suggests that density can influence behaviors by altering adaptive trade-offs in resource allocations for organisms.

In this view, adaptive behavioral responses depend on ecological constraints, which can differ in high- and low-density populations. Low-density environments are often characterized by high resource availability per individual, and lower intrapopulation competition for resources. In such conditions, it is more adaptive for individuals to exploit resources at a faster pace, to reproduce earlier, and have more children. In contrast, in more dense environments, there is greater competition between individuals. For individuals to compete successfully in such an environment, one needs to build relevant skills and knowledge, which in turn delays reproductive efforts. Moreover, it’s likely that in high-density contexts, offspring also require more investment to become competitive enough to survive and reproduce. Thus, it is comparatively more advantageous to invest more heavily in fewer children in population-dense environments. This theoretical framework suggests that higher population densities should be associated with lower fertility rate, consistent with prior empirical findings.

When does population density affect fertility?

Using life history theory, we can derive predictions about the circumstances in which the association between population density and fertility should either be enhanced or attenuated. To this end, we investigated moderator variables which would impact the nature of competition, and thus influence life history strategies, including reproductive strategies.

We predicted that higher densities would lead to lower fertility. In stable, predictable environments people need to take more time to build skills to successfully compete for mates and resources, leading to greater investment of time and resources in long-term (slower) strategies. This strategy delays family planning, and in turn reduces fertility rates. Moreover, because stable and predictable population-dense environments favor slower strategies, for children to successfully compete they require more resources and time, leading to the concentration of parental investment in fewer children. In contrast, in population-dense environments that are harsh and unpredictable long-term (slower) strategies are likely have smaller fitness benefits and lower payoffs. In these harsh and unpredictable environments, competition can take more lethal forms, which higher densities may amplify (Sng et al., 2017). So instead of competing through the accumulation of skills, one might see individuals competing through the violence. Immediate threats to safety shift fitness payoffs towards shorter-term (faster) strategies, where people invest less in long-term competition. These changes in fitness payoffs have implications for fertility—people will reproduce at earlier ages and invest in having more children because the future is uncertain. Thus, in highly dense *harsh* environments, we anticipate an attenuation (or even reversal) of the expected density-fertility association. Here, we operationalize harshness using indicators such as low GDP per capita, high rates of homicide, high levels of pathogen prevalence, and high levels of income inequality (Daly, 2017; Kondo et al., 2009; Krems & Varnum, 2017). These factors are associated with higher mortality rates and faster life-history strategies.

Cultural factors may also moderate the linkage between population density and fertility. Here we focus on two cultural variables: religiousness and tightness of social norms. Although most religions promote behaviors consistent with a slow life history strategy, they also promote greater fertility. Many large religions oppose contraception (e.g., Catholicism, many Protestant sects, conservative Islamic traditions), or actively encourage adherents to have more children (e.g., Mormonism). Cultural evolution may have shaped large-scale religions such that they tend to promote greater fertility among their adherents, which likely enhanced their growth and persistence over historical time. To the extent that religious belief may guide reproductive behaviors independently of other environmental cues, we expect a weakened association between changes in density and fertility in more religious places.

Tightness-looseness is another likely moderator of the density-fertility association. Tightness-looseness refers the strength of societal norms (Gelfand, et al., 2011). Where norms are stronger, we might expect that they attenuate the impact of ecological cues on reproductive behaviors. Indeed, tight social norms are arguably a response to high levels of threat in the environment (e.g., high levels of pathogens, armed conflict, and natural disasters) that are aimed at enhancing social coordination and cohesion (Gelfand, et al., 2011; Harrington & Gelfand, 2014; Uz, 2015). Tighter norms also reign in faster life history responses, which these environments would normally favor. For example, people in tighter cultures display greater impulse control (Gelfand et al., 2011) and levels of tightness are negatively associated with teen birth rates over time (Jackson, et al., 2019). Thus, we might expect a weakened association between density and fertility in places where social norms are stronger.

The present work is the first of which we are aware to test whether these factors moderate the density-fertility association. This approach adds nuance to our understanding of the density-fertility association and sheds light on why it might be stronger in some societies than others.

Current research

In the current work we report the results of analyses from 69 years of annual data drawn from 174 countries assessing the relationship between population density and fertility over time. Although prior research has suggested links between shifts in population density and changes in fertility, the present work goes beyond these prior studies. First, the present work is more comprehensive: we assess data from a larger sample of countries, for a longer span of time, with greater temporal granularity. Second, we assess the robustness of the density-fertility relationship by using state of the art techniques to control for temporal autocorrelation, including multi-level modelling and machine learning techniques such as automated Auto-Regressive Integrated Moving Average (ARIMA), probing the robustness of the relationship across analytic approaches. We also control for a wide variety of plausible alternative explanations for shifts in fertility (GDP, resource inequality, pathogen prevalence, gender inequality, access to contraception, religiosity, and tightness/looseness of social norms). Third, we test potential moderators for the density-fertility linkage which should theoretically explain why the generally observed negative association between density and fertility would be absent or reversed in some countries. Fourth, consistent with methodological recommendations for cultural change research (Varnum & Grossmann, 2017), we provide concrete forecasts for future fertility levels for 174 countries using models that include density as a predictor.

Methods

We pre-registered the methods and analyses at https://osf.io/fbquz/?view_only=25efae20c43f46239a374f912a1f6a44 (anonymized link). Data and reproducible code for the results can be found at https://osf.io/4sgkx/?view_only=588000c042d241dd9f329a1a17f68f00.

Primary variables

Population density[1] and fertility. We obtained population density and fertility rate data from Macrotrends.net (2020). Macrotrends is a free-to-use online data source, primarily used for

[1] The correlation between log-transformed population size and population density was r = -.004 (or τ = .05), based on population size data obtained from the UN. This suggests that population size and density are independent.

economic analysis. It collects and synthesizes data from reliable sources, such as the United Nations, to provide historical data for economic variables (e.g., market indices, interest rates, GDP) and demographic variables (e.g., fertility rates, life expectancy; Macrotrends 2020a). Data for population density and fertility rates were originally sourced from United Nations.

Population density was calculated by using midyear population divided by land area in square kilometers (see United Nations Statistics Division, 2021). Fertility rate represents the number of children that would be born to a woman if she were to live to the end of her childbearing years (i.e., estimated to be 15-49 years; United Nations, 2021). Total fertility is calculated using age-specific fertility rates of the specified year (United Nations, 2021). Following prior recommendations, we log transformed population density due to a skewed distribution (Gelfand et al., 2011; Lutz, Testa, & Penn, 2006; Sng et al., 2017). We obtained yearly data from 174 countries from 1950 to 2019 for fertility rates and population density.

Control variables

Below, we briefly describe the covariates analyzed in this paper; the number of countries analyzed for each covariate analysis are provided in Supplemental Material (Table S1)., along with correlations among variables (Figure S1).

Socioeconomic variables. To determine if the relationship between population density and fertility can be accounted for by socioeconomic development, we examined several factors related to socioeconomic development.

- Gross domestic product (GDP) per capita: We used GDP per capita as an indicator of economic wealth. As per recommendations for analyzing GDP, we log-transformed the variable (Deaton, 2008). Yearly GDP data was obtained from the Macrotrends (2020), for

1960 to 2019. GDP has been previously related to density and fertility (Lutz, Testa, & Penn, 2006).

- Inequality (Gini): We examined inequality, as characterized by the Gini index which measures the inequality among household income values within a specified region. We obtained country-level data from the World Bank (2020) and included the most recent reported Gini value in our analyses.
- Homicide rates: We obtained estimates for violent homicides from the World Health Organization (2020). We used data from 2017, which was the most recent data available (genders combined).
- Human development index (HDI): HDI is a statistic composite of life expectancy, education, and per capita income indicators. Data was obtained from the Organisation for Economic Co-operation and Development (OECD) database (2020). Although data was available from 2005 to 2013, timeseries data was limited given the restricted year and missing data. Therefore, we used the country-level data available for the most recent year, 2013.
- Occupational prestige: We obtained occupational data from Santos, Varnum, and Grossmann (2017). This data was originally coded by Integrated Public Use Microdata Series-International (IPUMS-I; Minnesota Population Center, 2015) into the major occupational categories. As in Santos, Varnum, and Grossmann (2017), we weighted these categories by multiplying the percentage of people in each category by a measure of popular evaluation of occupational standing obtained from the 1996 Standard International Occupational Prestige Scale. Higher scores refer to more people working at in higher prestige jobs.
- White-collar versus agricultural jobs: We examined whether people tended to have white-collar jobs (i.e., more developed economy) or agricultural jobs. We obtained data from

Santos, Varnum, and Grossmann (2017), who used IPUMS-I data to calculate the percentage of people working as "skilled agricultural, forestry, and fishery workers" for agricultural jobs, and the percentage of people classified as "legislators, senior officials, and managers," "professionals," "technicians and associate professionals," "clerks," and "service workers and shop and market sales" as a proxy for white-collar jobs. Then, we subtracted the percentage of agricultural jobs from the percentage of white-collar jobs to create a measure where higher scores indicate a larger percentage of white-collar jobs.

Geographic variables. We investigated if the relationship between population density and fertility at the country-level is influenced by the following geographic variables:

- Pathogen prevalence: Pathogen prevalence has been previously associated with life history strategy, where greater pathogens are associated with higher fertility (Guégan, Thomas, Hochberg, de Meeûs, & Renaud, 2011). We obtained country-level data for historical and contemporary pathogen prevalence from Fincher, Thornhill, Murray, and Schaller (2008), who estimated the prevalence pathogens detrimental to human reproductive fitness and coded the estimates on a points-based scale. They used historical sources for nine pathogens and contemporary sources of 22 pathogens to create historical and contemporary estimates of pathogen prevalence (Fincher et al., 2008). The two measures were intercorrelated, $\tau s = .59$.
- Climatic stress: We obtained mean yearly temperature for each country from Statpedia (2020), which used data calculated by averaging the minimum and maximum daily temperatures in the country, averaged for the years 1961–1990. We took the absolute value of the difference between the annual mean and 22°C as a measure of the deviation from the optimal temperature for humans to characterize climatic stress (Van de Vliert, 2013).

- Precipitation: We obtained average precipitation in depth (mm/year) from the World Bank (2020). We used the most recent year for which data was available, which was 2014.

Population characteristics. We analyzed three population-based characteristics:

- Migration: Net migration rates are the differences between the number of people entering and leaving a country during the year, where higher numbers indicate greater migration. Migration rate data was obtained from the World Factbook database, through the Central Intelligence Agency (2020).
- Sex ratio: Sex ratio is the number of males for each 100 females in a population. Numbers above 100 indicate there are more males than females in the population. We obtained these estimates, which were calculated based on the age/sex distributions of United Nations Population Division's World Population Prospects 2019 revision, from the World Bank database (2020).
- Population relatedness: In non-human animals, the relatedness between members of a population has been linked to fertility rates (Lehmann & Rousset, 2010). To control for population relatedness, we obtained a measure of proportion of consanguineous marriages (i.e., those between persons genetically related as second cousins or closer) as a proxy variable from Hoben, Buunk, Fincher, Thornhill, and Schaller (2010).

Cultural variables. Previous research suggests that religiosity and tightness-looseness relate to fertility or social norms surrounding family, marriage, and children (Bott & Sillius, 2014; Kane et al., 2016; Maertens, 2013; Zhang, 2008). Thus, we investigated how these variables they affect the relationship between population density and fertility over time.

- Religiosity: Given the association between religiosity and fertility, we investigated how religiosity influences the relationship between population density and fertility. We obtained data from Joshanloo and Gebauer (2019), who computed a religiosity index for 136 countries based on Gallup World Poll data, where participants answered the question “Is religion an important part of your daily life?”.

- Tightness/Looseness: Cultural tightness (vs. looseness) refers to cultures with strong social norms and little cultural deviance (Gelfand et al., 2011). It is possible that dense ecologies may require a stronger need to enforce social norms if density is associated with more difficulties in social coordination (Sng et al., 2017). To test this hypothesis, we obtained cultural tightness data of 57 nations from Gelfand and colleagues (2020), who measured tightness using the cultural tightness scale (Gelfand et al., 2011).

Female status and empowerment. Fertility rates are affected by gender-specific factors (Lutz, Testa, & Penn, 2006). We investigated if the relationship between population density and fertility can be accounted for by female status and empowerment, using country-level data:

- Global gender-gap index (GGI): We extracted the global gender gap index from the Global Gender Gap Report 2020, created by the World Economic Forum (World Economic Forum, 2020). The GGI is an index measure from 0 to 1 which characterizes national gender gaps on economic, education, health, and political criteria (World Economic Forum, 2020). Higher numbers indicate lower gender gaps.
- Gender-based educational attainment: We used education attainment from the Global Gender Gap Report 2020. This measure captures the gap between women and men in their access to education through ratios of women to men in primary, secondary, and tertiary-level education. The values range from 0 to 1, with one indicating that there is no gender-based gap in education (World Economic Forum, 2020).

- Contraceptive use: We obtained data from the United Nations Department of Economic and Social Affairs Contraceptive Use (2019), which contains estimates of the prevalence of contraceptive use among women of reproductive age for 2019. We analyzed if women used 'any method,' which included the pill, injectables, implants, IUDs, male condoms, rhythm, withdrawal, and male or female sterilization.

Data analysis

We performed all analyses in *R* (R Core Team, 2016). Specific packages used are listed in Supplemental Material (see Table S2).

Pre-registered analyses

Density and fertility. To test growth curve effects, which allow us to test whether change in birth rates based on year are modified by density, we computed multilevel models (MLM) with *lme4* and *lmerTest* packages for R. This analysis allows us to distinguish between changes that occur at the between-country level (analogous to the inter-individual level) and changes that occur within-countries (analogous to the intraindividual level), as well to analyze clustered data. Differences between countries explained a significant proportion of variance in density and fertility, thus we nested data per year within countries. To investigate both within-country changes and between-country differences, we separated population density into between-country means and within-country change by including interactions between (i) year and the country density mean, and (ii) year and the yearly deviation from the country density mean. This method is recommended for multi-level models (Hox, Moerbeek, & van de Schoot, 2017). We tested the interaction between time and density for effects on fertility, where interaction effects indicate that the fertility trend over time is impacted by population density. As recommended for longitudinal analyses, we set the first time point to zero (Hox, Moerbeek, & van de Schoot, 2017). This allows to estimate changes over time for each country.

Next, we assessed the relationship between density and fertility for each country using auto-ARIMA with fertility as the dependent variable and population density as an exogenous predictor. Auto-ARIMA is algorithm from the *forecast* package in R that computes a large number of possible models varying in whether they include various components of an ARIMA model (autoregressive terms, differencing, and moving averages) and selects the model that best fits the data. If the final model includes the putative exogenous predictor, then this suggests that this variable is linked to the dependent variable above and beyond effects of temporal autocorrelation. We then calculated the number of countries for which density was included in the final model and for which the relationship between population density and fertility was in the predicted direction (as population density increases, fertility decreases). This analysis allows us to confirm the robustness of the associations between density and fertility.

These analyses also address temporal autocorrelation, the non-independent relationship between successive values of the same variable, which can bias parameter estimate and is therefore important to control for in time-based analyses. To our knowledge, prior work on density and fertility has not controlled for temporal autocorrelation. For a detailed discussion of how temporal autocorrelation may lead to spurious associations in cultural change research, see Varnum and Grossmann (2017).

Exploratory analyses

Residualizing out time. To investigate the country-level correlations between population density and fertility, we detrended the time series data by residualizing out the effect of year on population density and fertility. Then, we computed the Kendall’s Tau correlation for each country, which is a robust and efficient non-parametric correlational method, characterized by having a smaller gross error sensitivity and a smaller asymptotic variance compared to Spearman's Rho (Croux & Dehon, 2010). These analyses provide country-level estimates of the relationship between density and fertility while controlling for the potentially confounding effects of temporal autocorrelation.

Control variables. Next, we tested the robustness of the relationship between density and fertility using the control variables described above. To do so, we used multi-level models that included an interaction for between-country differences in density and time and an interaction for within-country changes in density (i.e., mean population density estimate, subtracted from the year-specific value) and time, as well as the respective covariate (as independent predictors) in a multi-level model predicting fertility rates (MLM; nested within country, random intercepts). This analysis allowed us to discern between-country and within-country effects of density on fertility and determine if the relationship between density and fertility continued to exist once each covariate was accounted for and after we removed the potentially confounding effects of temporal autocorrelation. We also repeated these analyses with detrended time series data on density and fertility from which year had been residualized out, yet another means of addressing the potentially confounding influence of temporal autocorrelation (see supplementary materials).

Moderator Analyses. To investigate how population density interacted with socioeconomic and socioecological covariates to predict fertility rates over time, we computed MLMs nested within country, using detrended data. To make inferences about change over time, we created deviation scores for population density by computing country-level means across time for each variable (i.e., mean from 1950-2019 for density, 1960-2019 for GDP), then creating year-specific difference scores by subtracting the country-level mean from the year-specific data. Then, we tested how population density interacted with each proposed moderator

(GDP per capita, GINI, homicide rates, pathogen prevalence, religiousness, tightness) to predict fertility. This analysis allowed us to determine how within-country change in population density contributes to change in fertility from year to year, irrespective of country-level differences, while controlling for the potentially confounding effects of temporal autocorrelation.

Results

The effect of population density on fertility

We computed Kendall's Tau correlations with detrended data between population density and fertility for 174 countries. Of these, 116 out of 174 countries (66.7%) had correlations in the predicted direction, where lower fertility rates were associated with higher population densities. Of the countries with negative relationships, 84.5% (98 out of 116) of the correlations reached statistical significance. Only 37 countries (of the full 174) showed significant reversals of this link (i.e., where fertility rates increased with density). Notably, we would have expected at least nine reversals of this relationship by chance (i.e., 5% of 174 countries). See Figure 1.

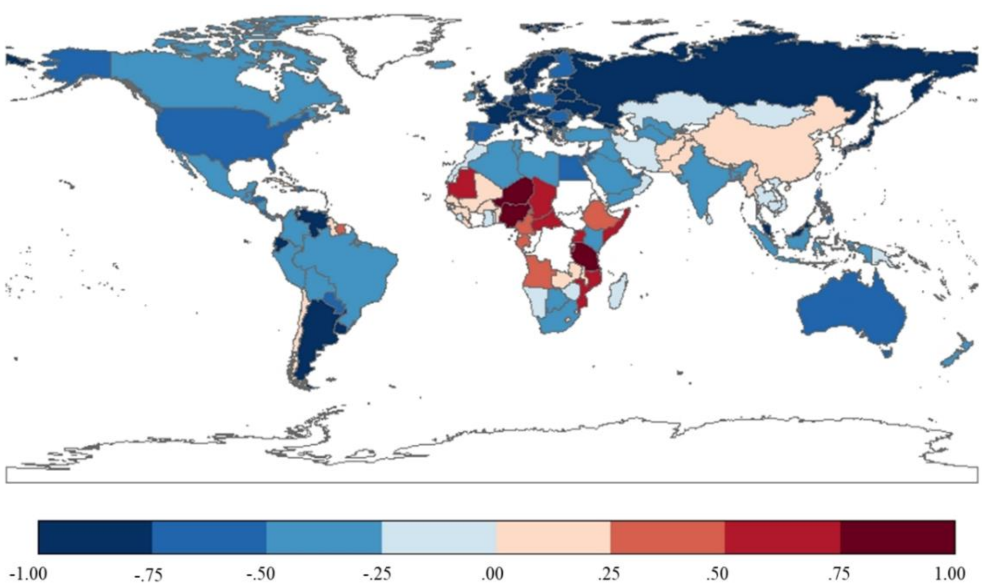

Figure 1. Kendall's Tau correlations between fertility rates and population density for the countries analyzed. Blue represents correlations in the predicted direction, while red represents

correlations in the opposite direction. Areas in white show countries with missing data. Exact correlations for each country are presented in Table S3 in the Supplemental Material.

Next, we used multi-level modelling to simultaneously assess the relationship between density and fertility at the between- and within- country levels. To do so, we tested the interaction between time and population density deviation (i.e., deviation from the country mean) for effects on fertility in a multi-level model with random slopes, where we nested year within countries. By including both between-country differences (i.e., country-level means) and within country change (i.e., population density deviations) as separate predictors in this model, we were able to test whether changes in fertility is associated with within-country changes in density over time, relative to countries mean levels of density. The interaction between density and year was significant at both the between-country level, $b = -0.01$, $SE = 0.003$, $t(177.590) = -3.40$, $p = .001$, and the within-country level, $b = -0.06$, $SE = 0.001$, $t(12397.064) = -50.52$, $p < .001$. Demonstrating that countries with higher mean density had lower in fertility, and that within-country increases in density over time were associated with greater decreases in fertility. This model accounted for 31% of variance in fertility rates ($R^2 = .31$; see supplement for full results of this model and replications within world regions).

Next, as an alternative means of assessing the relationship between population density and changes in fertility over time, we computed auto-ARIMA models to predict fertility rates over time with population density as an exogenous predictor, for each of the 174 countries. Auto-ARIMA computes several different models and returns the model with the best fit. Once the models were returned, we calculated the frequency of countries where the best-fitting model included a negative relationship between population density and fertility rates. This analysis allows us to confirm the robustness of the associations between density and fertility, using state-of-the-art methods for time series analyses. Unlike MLMs, ARIMA models estimate both linear and non-linear trends. Consistent with the results presented above, the relationship between density and fertility was in the predicted direction (i.e., as density increases, fertility decreases) for most countries. Of the best-fitting models computed for the 174 countries, 111 (64%) had negative associations between population density and fertility, replicating the MLM results using an arguably more robust method.

Taken together these results show a robust relationship between population density and decreasing fertility over time that is replicated across analytic approaches.

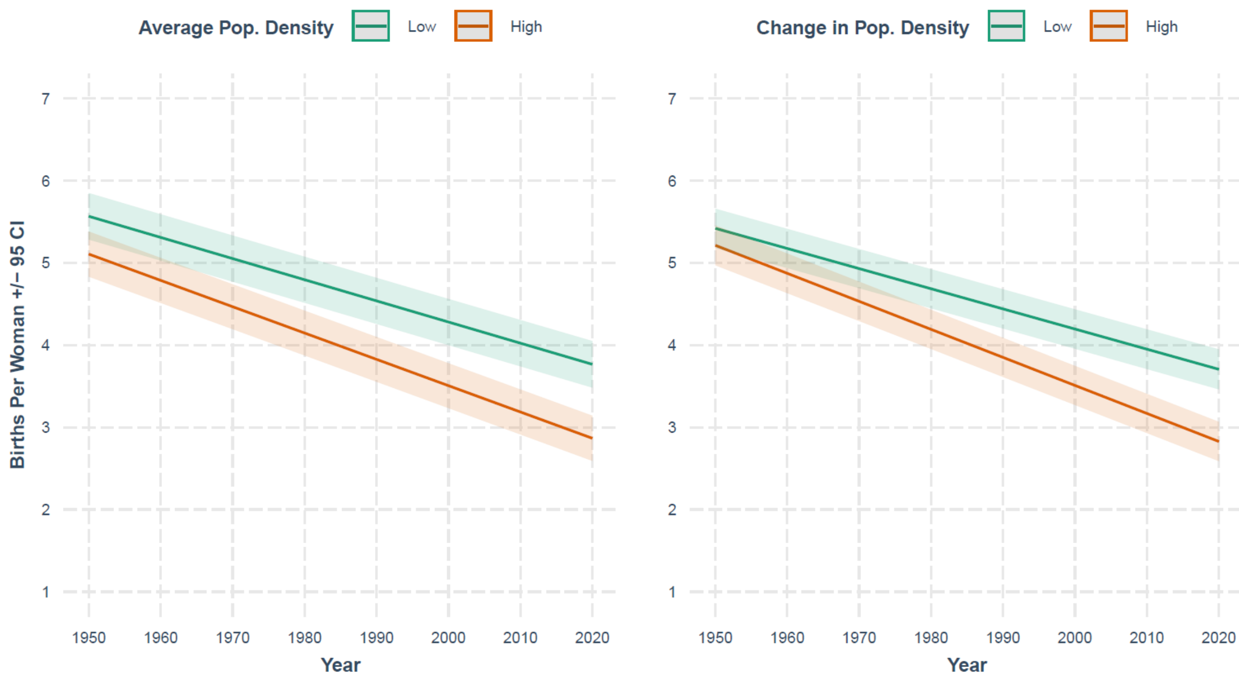

Figure 2. Fertility decreased more over time between-countries (left) and within-countries (right) in populations with higher densities. Data is separated into quantiles, where green represents countries with the highest densities (4th quantile) and orange with the lowest densities (1st quantile).

Robustness of the relationship between population density and fertility

To assess the robustness of the relationship between density and fertility, we ran a series of exploratory analyses with all covariates described above. In these analyses, we employed equivalent multi-level models to those described above, adding socioeconomic and socioecological variables as covariates. Across all analyses, there were significant interactions with time for both within-country changes in population density, *t*s < -5.64, *p*s < .001, and between-country differences in density, *t*s < -5.37, *p*s < .001, that predicted fertility rates. Thus, the within- and between-country effects of density on fertility across time hold controlling for numerous plausible alternative explanations, including gender inequality, women's access to contraception and to education, religiousness, and tightness of social norms. The relationships also held controlling for a host of economic and ecological factors, including GDP, economic inequality, human development index (HDI), prevalence of white-collar and high prestige jobs, pathogen prevalence, climatic stress, precipitation, migration, kinship, and sex ratio. All covariates were significantly associated with fertility, |*t*|s < 4.93, *p*s < .001, with the exception of average precipitation ($t = 0.96$, $p = .337$), migration rates ($t = -0.69$, $p = .488$), and sex ratio ($t = 1.50$, $p = .135$). See Table S4 in Supplemental Material for all estimates.

These analyses were robust to the statistical approach. Results were similar when we computed MLM analyses predicting fertility from population density and each covariate using detrended time series for which we residualized out the effect of year (see Table S5 in Supplemental Material). The relationship between density and fertility was also robust in auto-ARIMA analyses comparing the percentage of countries with negative relationships between density and fertility for high and low values of each covariate (see Tables S6 in Supplemental Material).

Together, these findings suggest that there is a robust effect of density on fertility at the within-country and between-country levels, and across time, when accounting for a wide range of plausible alternative explanations.

Moderator analyses

Next, we explored the effect of four moderators on the relationship between density on fertility: GDP, income inequality, homicide rates, and pathogen prevalence. Higher scores on each of these indicators are indicative of a harsher environment (except for GDP, where lower indicates harsher). In these analyses, we investigated how within-country change in population density interacted with (between-country) moderators to influence fertility rates. To this end, we used MLMs with detrended time-series data nested within country. We also conducted exploratory moderator analyses with all other control variables in this paper, which are presented in Supplemental Material (Table S6).

GDP interacted with within-country change in density, $t = -24.35$, $p < .001$. At low levels of GDP, the effect of density on fertility was eliminated: as population density increased, fertility rates remained the same. On the other hand, in countries with high GDP, population density had a greater impact on fertility rates, where fertility rates declined as population density increased (see Figure 3A). Thus, within-country changes in density have a greater impact on fertility rates in high-GDP populations.

We found an interaction between within-country change in population density and economic inequality, $t = 17.36$, $p < .001$. That is, at high levels of inequality, the effect of density on fertility was suppressed. However, at low levels of inequality, density had a greater impact on fertility rates where countries that increased in density over time had a greater decline in fertility rates (see Figure 3B). This finding suggests that within-country changes in population density has a greater influence on fertility rates at low levels of inequality.

Similarly, there was an interaction between within-country change in population density and violent homicide rates, $t = 9.80$, $p < .001$. Here, we found that there was a greater effect of within-population change in density on fertility rates in countries with low homicide rates compared to high homicide rates (see Figure 3C). This suggests that the effect of within-country changes in density is suppressed under conditions with higher rates of violence.

Additionally, we observed the same pattern of results for historical pathogen prevalence, there was an interaction between within-country change in population density and pathogen prevalence, $t = 14.33$, $p < .001$. In this analysis, we found that there was a greater effect of within-country change of population density on fertility at low levels of pathogen prevalence, compared to countries with high levels of pathogen prevalence, which appeared to suppress (but not eliminate) the relationship between density and fertility (see Figure 3D). The same pattern of results was obtained when we used contemporary pathogen prevalence as the moderator variable, $t = 7.63$, $p < .001$.

Lastly, we investigated the moderating effect of cultural variables. In separate analyses, we found an interaction between within-country change in density and religiosity, $t = 28.37$, $p < .001$, and between within-country change in density and cultural tightness, $t = 11.37$, $p < .001$. The effect of density on changes in fertility rates was suppressed in countries with greater religiosity and in countries with tighter social norms (compared to countries with looser social norms; see Figure 4).

Thus, these results suggest that the effect of density on fertility is attenuated in the following socio-ecological and cultural contexts: low GDP, high inequality, high homicide rates, high pathogen prevalence rates, in more religious cultures, and in cultures with tighter social norms. In some circumstances (i.e., low GDP per capita; high GINI; high religiosity) the effect is essentially absent, suggesting boundary conditions for the high density- low fertility link. Exact estimates for moderator analyses are presented in Table S7 in Supplemental Material.

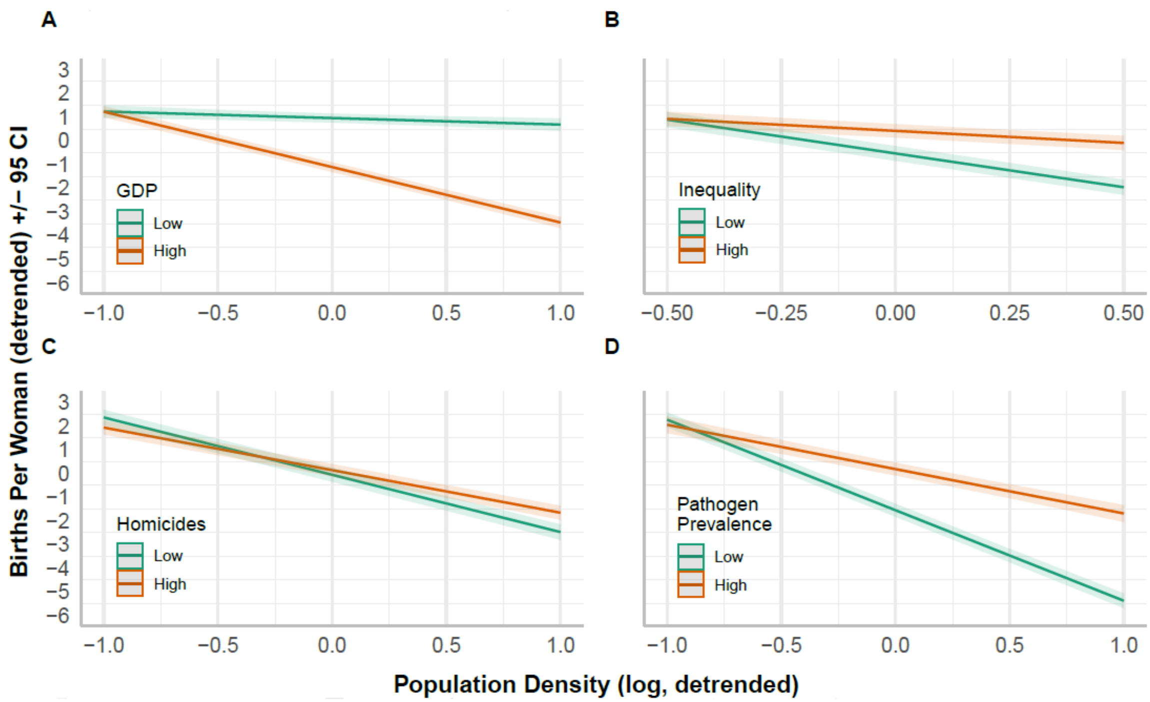

Figure 3. Interaction effects between within-country change in population density and moderator variables predicting fertility rates over time. Orange lines represent countries where population density increased (4^{th} quartile of within-country density change) while green lines represent countries where population density decreased (1^{st} quartile of within-country density change). Larger differences between the high vs low density lines indicates a greater influence of density on fertility. In all analyses above, the effect of density on fertility was suppressed in harsher environments (i.e., low GDP, high inequality, high homicide rates, high pathogen prevalence).

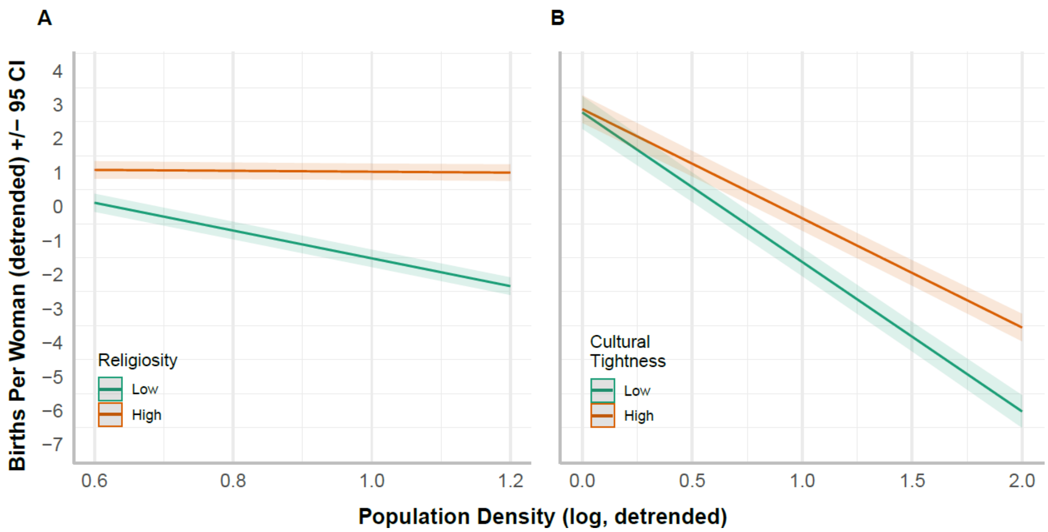

Figure 4. Interaction effects between within-country change in population density and cultural variables predicting fertility rates over time. Orange represent countries where population density increased (4th quantile of within-country density change) while green represent countries where density decreased (1st quartile of within-country density change). Larger differences between the high vs low density lines indicates a greater influence of density on fertility, where the effect of density on fertility was suppressed in countries with high religiosity and tighter social norms.

Forecasting fertility

We created forecasts for fertility over time for each of the 174 countries using auto-ARIMA models with population density included as an exogenous predictor. Forecasts for most countries predict either continued decreases in fertility rates over time or stabilization of fertility rates. For details, see Figure S2 in the Supplemental Material.

Discussion

Across 174 nations over 69 years of data, we found a robust association between population density and fertility, where between-country differences and within-country changes in densities over time predicted fertility rates, accounting for 31% of the variance in fertility. As population densities increased, fertility rates decreased. This pattern was observed in 116 out of

174 countries. These relationships were robust across a variety of analytic approaches, including different methods accounting for the potentially confounding effects of temporal autocorrelation.

Additionally, the associations between fertility rates and within-country changes and between-country differences in density, over time, were robust when controlling for a suite of socioeconomic and socioecological variables and alternative explanations for shifts in fertility: GDP, human development, inequality, homicide rates, climate stress, pathogen prevalence, population sex ratio, population relatedness, migration rates, gender inequality, access to contraception, religiosity, and tight/loose social norms. In sum, the present work provides strong evidence that declining human fertility is uniquely linked to increasing population density.

We theorized that in increasingly dense environments, longer-term reproductive strategies enhance the competitive advantage of offspring in such environments (i.e., having fewer children and investing more resources per child). However, this effect was theorized to be weaker (or eliminated) in harsh environments with high mortality risks. In these environments, density-induced competition might take on lethal forms, with density ultimately amplifying harsh conditions and shift competition to favour faster strategies (i.e., have more children, and invest fewer resources per child). Indeed, we our results support this interpretation. The effect of density on fertility was relatively weaker in cultures characterized by harsher living conditions, namely those with lower GDP, higher income inequality, higher rates of violent homicides, and higher pathogen prevalence. Additionally, the effect of density on changes in fertility was reduced in cultures with greater religiousness and tighter social norms, suggesting that cultural factors also appear to moderate this link, and in some cases suggesting boundary conditions.

At the country-level, we observed a few exceptions to the general association between density and fertility, where detrended correlations between density and fertility suggested a positive association between density and fertility (e.g., Gambia, Nigeria, Israel, Uganda, Grenada), or lower densities were associated with lower fertility rates (e.g., Chad, Niger, Tanzania, Mozambique, Samoa, Somalia). These observations are broadly consistent with the interactions we observed between density and harshness. On average, countries with high densities and high fertility rates are characterized by harsher ecological conditions such as low GDP, high inequality, high pathogen prevalence, high homicide rates. Additionally, countries with low densities and low fertility rates are known for scarcity, which may suggest that limited resources may also limit fertility rates (e.g., famine, poor nutrition, access to clean water and health care). However, these speculations regarding these countries which do not show a negative relationship between density and fertility should be taken with some caution; we generally have fewer data points for these countries compared to countries with more stable environments. Future research should investigate these cases where density is positively associated with fertility in more depth to further clarify the mechanisms involved.

A Life History Account of the Demographic Transition

We posited that higher densities would lead to lower fertility rates, which we derived from life history theory. Life history theory suggests that environmental conditions with heightened ability-based social competition (i.e., predictable and stable environments with low mortality risk), people can enhance their competitive advantage by investing more resources in long-term strategies that builds their competitive ability (e.g., education). This slower strategy also entails fewer children greater parental investment. This shift in child rearing dynamics enhances long-term competitive advantage of both adults and offspring. In harsher environments where the future is less certain (i.e., higher violence, fewer resources, greater risk of mortality) there are lower payoffs for investing in long-term strategies, which favors faster competitive strategies associated with having more children, and investing fewer resources per child.

Overall, the present results were consistent with these life history theory-based predictions, as were the observed moderation effects of environmental harshness/mortality threat. As population density increased over time within countries, fertility rates correspondingly decreased. Further, increases in density had a greater effect on declining fertility in countries with less harsh ecologies—i.e., lower homicide rates, less prevalence of infectious disease, less economic inequality, and less wealth. Additionally, we replicated the between-country effect: Higher density countries had lower fertility rates (Lutz, Testa, & Penn, 2006; Sng et al., 2017).

Although prior work has suggested a link between density and shifting fertility rates, such work has offered little explanation about why this effect occurs. We believe the present work, framed in life history theory, provides a more comprehensive account for why population density influences human fertility rates. These findings expand on prior cross-sectional work which used life history theory to predict the relationship between population density and fertility (e.g., Sng et al., 2017) to suggest that life history theory can also be used to explain *where* we would expect this relationship to be stronger or weaker.

In addition, we found that the link between density and fertility were moderated by key cultural factors. Namely, the effect of increasing density on fertility was attenuated in societies that were more religious and that had tighter social norms. This observation suggests that these cultural features may moderate links between ecological cues and relevant behavioral responses. Future work could further pursue these links and expand on the theoretical implications of cultural interactions with ecological factors.

Importantly, the present work is the first effort of which we are aware to distinguish between the effects of between-country differences and within-country change in population densities, and to disentangle their contribution to changing fertility rates over time. It is important to approach this question in a multi-level fashion to avoid the "ecological fallacy" (Piantadosi, Byar, & Green, 1988). Our results show that differences between countries densities and changes in density within countries are predictive of changes in fertility rates over time.

Before concluding, we must note some limitations of the present work. First, our analyses are correlational and therefore we cannot make strong causal inferences based on these results. It is worth noting that prior experimental work suggests that the individual-level relationship between density and fertility may indeed be causal (Sng et al., 2017). The present results provide complementary evidence suggesting that the directional relationship between density and fertility may extend beyond individual-level perceptions to societal-level shifts in ecological affordances and behaviors. Second, although life history theory provides a theoretical framework for understanding why density should affect fertility, at present little is known regarding proximal mechanisms (biological or psychological) underpinning this relationship in human beings. In other words, we believe that the present evidence speaks to *why* this relationship exists and provides insight into the *where* and *when*, but the task of uncovering the *how* still remains. Due to the aggregate nature of the present data, we cannot fully address *how* population density promotes fertility at the level of individuals.

To our knowledge, only one paper has tapped any potential psychological processes (i.e., *how* this effect operates at the individual-level). Namely, Sng and colleagues (2017) presented reproductive-age participants with information about population density, finding that information describing higher density led participants to indicate wanting fewer children (Sng et al, 2017). However, neither those prior findings, nor the present work speaks to psychological mechanisms. Additional research is needed to enhance our understanding of the social and cognitive mechanisms involved in density perceptions and fertility decisions. Further, it would be interesting to explore whether dense environments or density cues might lead to physiological changes that would affect fertility or related behavior and decisions. In other words, future efforts aimed at identifying proximal mechanisms is warranted, perhaps using large-scale experiments or agent-based models. Finally, our work suggests several factors which may moderate or serve as boundary conditions for the effects of density on changes in fertility rates. However, we note that these moderator variables came from single time points. To the extent it is possible, future work should assess these moderations using time series data on the moderator variables as well. In addition, future work might seek to assess these moderation effects at the individual level through correlational and experimental designs.

Beyond the theoretical and empirical contributions of the present work to psychological science, demography, and related disciplines, we hope that this work may serve other functions. First, this work can help make nuanced predictions regarding demographic trends that may occur when there are large shifts in a population, such as mass migrations in response to political unrest or relocations from natural disasters or climate change, based on the specific ecological factors in each situation. Moreover, in public discourse regarding declining fertility rates, population density seldom if ever features in the conversation. Popular press articles frequently point to factors like immersion in digital life, prioritization of careers, stress, and even internet pornography as causes for declining fertility rates. We hope the present work will highlight the role of density in this process. We also hope that this information might aid policy makers, institutions, and other stakeholders as they plan for changing population structures and as they contemplate steps to address the challenges and the opportunities this may pose for our societies.

Author Contributions

MEWV developed the original study concept. MEWV, IG, AR, and OS designed the study. AR gathered and analyzed the data, under IG's supervision, and drafted the manuscript. AR, MEWV, OS, and IG revised the manuscript.

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