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RESEARCH ARTICLE

An ecological theory of changing human population dynamics

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Abstract

1. The dependence of humans on nature has come into focus as the human population continues to grow, resources diminish and production technology stagnates – threatening human well-being on a global scale. Numerous previous models describe human population dynamics, in relation to a multitude of different factors. However, there are no consistent driving factors of human demography through history, which makes predicting future changes more challenging.
2. Here, we review the literature on human population growth from empirical data and previous models, which allows us to highlight key trends in demography and land cover changes.
3. We then establish an ecologically driven theory of demographic change that uses resource accessibility as a proxy for socio-economic factors. The theory combines multiple concepts to represent 12 millennia of past population dynamics through simple human–nature relationships.
4. Furthermore, the model allows us to compare different scenarios related to technological progress and land cover change, for which we find that the peak human population is highly dependent on whether technological developments continue at an exponential growth rate, or if and when there is a saturation point. Likewise, agriculture is shown to be helpful for growing the population, but nature is ultimately needed to maintain the human population.

KEYWORDS
ecological theory, feedbacks, land cover change, model, population change

1 | INTRODUCTION

It is paradoxical to think that throughout much of human history people were threatened by extinction from under-population (Biraben, 2003), considering that today the question is whether we are approaching or have already reached a critical point of over-population. In the first 165,000 years of human existence, the population remained low, persisting at a few hundred thousand individuals globally. By contrast, the human population has changed markedly over the last 12,000 years, experiencing an estimated 1,860-fold increase in the population size (Roser & Ortiz-Ospina, 2017).

The years of relatively constant growth were not static; however, populations experienced boom-bust cycles (Biraben, 2003; Tallavaara & Seppä, 2012) as resource availability changed and new tools came into existence. In the last 12 millennia, technological and scientific developments have increased exponentially; however, this rapid development has been combined with a significant change in social norms, lifestyles and hunting techniques. It is thus difficult to make comparisons of demographic trends over time and establish driving factors of population change that hold true through multiple demographic transitions or time periods.

Notwithstanding, there remain fundamental components that are required to sustain the human population that are independent of any one era – for example, food, shelter, water, inter-personal interactions and waste removal. Is it realistic to make projections on where we are going or what could trigger a change in the current global society with what we know about past demographic transitions and various fundamental components? Early civilizations were highly dependent on resource availability; does this hold for contemporary societies? Is it possible for a global system to collapse, as was the case on a smaller scale with the Easter Islanders and the Mayans? Will there be advances in technology and innovation over the coming years that allow us to continue growing indefinitely?

There was a growing trend in the 1970s and 1980s of work describing population sustainability, highlighting the importance of monitoring population growth in tandem with discussing ecosystem sustainability. Earlier work discussed population size as a function of the production or consumption of material goods and foods (Schacht, 1981), but this topic became taboo following the 1994 UN Cairo conference (Kopnina & Washington, 2016). The idea that human population growth is responsible for degrading the natural system or part of complex feedbacks within the global environment has been considered unethical and 'anti-human'.

We take this opportunity to explore the dynamics between demography and resource accessibility throughout history. We introduce a new theory for modelling population dynamics in relation to the accessibility of natural land and agricultural area, which includes technological and innovative advancements. As ecologists, we focus on the importance of land cover change and ecosystem services in explaining demographic change and demonstrate how the accessibility of resources provides a reasonable proxy for socio-economic factors. This theory is then developed into a model of bidirectional feedbacks between humans and the environment to simulate past population and land cover changes, in addition to possible future scenarios. Technological advancements are a favoured solution to maintaining human well-being and food production as the population grows; however, the trajectory of technological development is uncertain, which is accounted for here by varying the rate and saturation point of technology. In addition, we investigate alternative ways of maintaining human well-being, other than technological advancement, such as reduced degradation rates. Given the complexity of demographic change and land management, we are not proposing to have a model that can accurately predict human population and land cover trends; however, we aim to provide a possible mechanism for population change and illuminate practices that are either detrimental or beneficial to the sustainability of the global human-environment system.

2 | HUMAN–NATURE INTERACTIONS: EXISTING THEORIES AND MODELS

Along with being controversial and taboo, modelling changes in human population and land cover has been widely debated in terms of driving factors (e.g. agricultural or medical advances; urban or rural lifestyles), assumptions (e.g. Malthusian or Boserupian) and feedbacks (e.g. feedbacks between fertility and mortality; feedbacks in the human-environment system) (Motesharrei, Rivas, & Kalnay, 2014; Motesharrei et al., 2016; Schacht, 1981; Warren, 2015). It is evident that the contemporary population is growing at a rate much faster than pre-modern civilizations or even societies prior to the 1700s; however, the same clarity cannot be conferred to the cause of growth. The gaps in knowledge or shifting theories are highlighted by the array of previous modelling attempts.

There is a broad diversity of theories and models describing changes in population. The discussion focuses on three main topics: carrying capacities, technological advances, and social norms and education. Modelling allows comparisons between different systems and eras, drawing commonalities and conclusions to develop theories on demographic trends and land cover change. Previous models have attempted to capture changes in demography, generally focusing on a specific transition or period of humanity. Questions arise about the validity of model assumptions and the ability to reflect past and present trends in human population and land cover change.

Initial models of population growth were very simple and often based on everyday observations. John Graunt is credited as the first demographer to describe population growth in the 17th century as a doubling rate (Graunt, 1662). This later became the basis for Malthus (1888).

2.1 | Agriculture and resources

The Malthusian model of population growth has received much criticism over the years. Malthus (1888) assumes that the population grows geometrically, with adequate resources, while food production grows arithmetically implying that the population will inevitably decline when the number of individuals surpasses the available food supply, as a result of disease, famine or war. Malthus believed the population could either choose to reduce population growth through family planning, governed by income and status, or that the amount of resources would ultimately force a reduction in population.

Over the years, many models have applied concepts of resource consumption to describe population dynamics. From the most basic models that assume the population grows linearly with land area (Schacht, 1981) to models linking carrying capacities, population size and warfare (Turchin, 2009).

Many models focus on the availability of resources, particularly agriculture. It is widely hypothesized that agricultural production is responsible for the exponential growth in the human population (Armelagos, Goodman, & Jacobs, 1991; Bocquet-Appel, 2002; May, 1978). The Neolithic revolution, the introduction of agriculture roughly 10,000 BCE and the first established demographic transition, is well-studied. It is evident that agricultural development allowed the population to grow at an unprecedented rate, more than doubling the previous peak growth rate that followed the introduction of specialized tools in the Paleolithic Era (Biraben, 2003). Much higher population densities can be attained using agriculture, when compared to an equal area of hunting and foraging land. This trend is evidenced on a global scale (Bocquet-Appel, 2002, 2011; Gignoux, Henn, & Mountain, 2011) and over the course of many millennia. Indeed, agriculture was primarily responsible for higher-birth rates and lower-mortality rates up until the 1900s (Hirschman, 2005; Overton, 1993), showing that population dynamics and land cover change were intrinsically linked during this era (Woodbridge et al., 2014).

However, too strong a dependence on one system, such as agriculture, can lead to detrimental effects when there is a sudden shock to the system (Bocquet-Appel, 2011; Downey, Haas, & Shennan, 2016). One study suggests that up to 60% of the population were lost at one point from one such bust (Shennan et al., 2013). Similar to Neolithic agricultural practices, medieval agriculture was a double-edged sword. High production allowed the population to grow, but in times of crop and pastoral failure the population suffered (Overton, 1993). Agriculture often failed as the necessary precautions were not heeded to avoid destruction of the fragile ecological equilibrium that maintains crop and livestock production. Likewise, archaeological work reveals prolonged soil nitrogen deterioration, which ultimately leads to ecological stress and agricultural failings in earlier settlements.

Reuveny (2012) provides a summary of models used to explain the collapse of historical civilizations, starting with Brander and Taylor (1998). Brander and Taylor's model, which was later elaborated on by many others (D'Alessandro, 2007; Reuveny & Maxwell, 2001; Ricardo Faria, 2000), follows one main assumption: greater resource availability leads to larger populations. This model was specifically developed to describe the Easter Island population, but fails to replicate the last two demographic transitions in the modern era. Population growth is modelled as follows,

$$L(b-d+\phi\alpha\beta S), \tag{1}$$

where b is the birth rate and d is the death rate. The population (L) is further enhanced by the availability of resources (S) multiplied by the utility of the resource (β), the efficiency of acquiring the resource (α) and a procreation coefficient (ϕ).

Anderies (2003) elaborates on Brander and Taylor's model to reflect population changes from both Malthusian and modern growth relationships. The model describes the relationship between consumption patterns and demography: (1) higher consumption of agricultural goods results in higher-birth rates, (2) higher consumption of manufactured goods decreases the birth rate, and (3) greater consumption of both agricultural and manufactured goods decreases the death rate. The modifications provide a better fit with modern populations. The change in population is given by

$$L\left(b_0\left(1-e^{-b_1 q_a}\right)e^{-b_2 q_m}-d_0 e^{-q_a d_1}e^{-q_a d_2 q_m}\right), \tag{2}$$

where the birth rate (b_0) experiences feedbacks (b_1) from agricultural goods (q_a) and feedbacks (b_2) from manufactured goods (q_m). Likewise, both goods feedbacks onto death through the coefficients d_1 and d_2.

Other models incorporate important social factors along with carrying capacities and consumption patterns. Motesharrei et al. (2014) divide the population into commoners and elites, with different levels of consumption and therefore different death rates. This division of the population incorporates important social factors that explain differences in the stage of the demographic transition for high- and low-income countries.

Before the onset of major technological advances in the 18th century, population growth dynamics could be explained by Malthus' theory. However, the human population has managed to escape the Malthusian trap numerous times (Hirschman, 2005). For example, according to Malthus the population should have collapsed in the 1900s, as growth rates exploded and agricultural expansion stagnated, presuming that agriculture would not be able to support the population. This was not the case; in reality, the United States experienced the greatest growth during this period. The yields per hectare of essential crops increased exponentially between 1930 and 1998 (Warren, 1998), as a result of the Green Revolution. The population boom in the 1900s fostered the idea that technology—for example, fertilizer, machinery and genetic modification (technology of the Green Revolution)—is responsible for human population growth.

2.2 | Technology and medical advances

An alternative to the resource-dependent population growth theory was brought forth by Boserup (1965), suggesting that technological advancements are a major driving factor in demographic changes. It is undeniable that the onset of new technology and tools has often coincided with rises in population growth. Dating back to the Paleolithic Era, advances in hunting tools increased population growth at the end of the era. Smil (1999) argued that the population explosion of the 1900s would not have been possible without the agricultural advances that increased production six-fold over the same period (Moses, 2009).

Moreover, along with technology comes advances in medicine and hygiene. There have been marked increases in population growth, since the early 19th century, as societies develop. The increases in growth have been attributed to a decline in death rates following improvements in hygiene and sanitation, enhanced nutrition, early medical care and clean water (Preston, 1980; Samir & Lutz, 2017).

Lee and Tuljapurkar (2008) model pre-industrial population dynamics using theories from both Malthus and Boserup. The population change is subdivided into different age groups and growth is calculated in terms of food consumption, winter temperatures, disease prevalence, cultural norms, technology and social factors. The model assumes that increased agricultural productivity increases population growth and well-being. The food availability depends on the labour force, in addition to cultivation techniques and environmental quality.

In two recent papers, Lafuite and Loreau (2017) and Lafuite, Mazancourt, and Loreau (2017) modelled the change in the human population (H) as a function of technological advancement (T) and biodiversity (B). The model emphasizes the dependence of people on biodiversity and ecosystem services, which ultimately impact the agricultural production that humans require. Furthermore, technology has both positive and negative influences on the human population, such that greater technological advancements in the agricultural and material goods sectors often lead to declining biodiversity, which has a negative impact on human well-being. However, technology also acts as a proxy for improved social well-being (i.e. improved health care, better education) which improves survival. The influence of socio-economic and ecological feedbacks on human population size is given in the following equation:

$$\dot{H} = \mu_{\max} H \left(1 - e^{y_{1_{\min}} - \gamma_1 B^{\Omega} T/T_m}\right) e^{-b_2 \gamma_2 T/T_m}. \tag{3}$$

The human population is assumed to depend on the consumption of agricultural (γ_1) and industrial goods (γ_2), requiring a minimum per capita consumption of agricultural goods ($y_{1_{\min}}$). $\mu_{\max}$ is the maximum human population growth rate and b_2 is the demographic transition coefficient, reflecting the sensitivity of industrial goods consumption on growth. The maximum technological efficiency (T_m) is related to biodiversity and ecosystem services (Ω).

2.3 | Social norms, wealth and education

Societal views may explain many shifts in behaviour that are related to demography and land-use. Between 1270 and present, there have been both positive and negative status–fertility relationships (Mulder, 1998). Over this period, those within a high occupation/social class switched from having more children to having slightly fewer children than those with low status. There has been a great deal of work trying to explain fertility rates. In general, researchers find that in regions or times of income insecurity and uncertain living conditions, individuals have more children as a means of supporting elderly or ailing parents, a form of 'basic social insurance' (Marchetti, Meyer, & Ausubel, 1996; Skirbekk, 2008). By contrast, wealthier families try to increase the economic success of their offspring by providing more resources to fewer individuals (Kaplan, 1996). These patterns may not exist after sudden changes or stochastic events, see for example Eberstadt (1994).

In addition to income, greater education also reduces fertility rates (Skirbekk, 2008; Smeeding, 2014). Lower-mortality rates are almost universally related to higher-education levels (Lutz & Skirbekk, 2013).

Education, wealth and technology are not independent. Factors describing social dynamics in a population are highly correlated and often difficult to tease apart, which can result in complex models with many interdependent feedbacks and processes. In an effort to find a mechanism for the demographic transition, Galor and Weil (2000) develop an agent-based model, describing population size in terms of income per capita and the availability of technology. The number of children per person is a function of education, technology, consumption behaviours and income. The use of many integrated factors allows the model to simulate a Malthusian regime, a post-Malthusian regime and modern growth.

Nitzbon, Heitzig, and Parlitz (2017) describe a socio-ecological model that explores fertility and death as a function of well-being, for which well-being represents basic nutritional needs for reproduction. Well-being (W) is a variable linking ecosystem services and the human population with carbon (terrestrial, atmospheric and geological). The premise is that the birth rate declines towards zero after the initial increase as a result of education and social security related effects. Human population (P) change is given by,

$$\dot{P} = P\left(\frac{2WW_p}{W^2 + W_p^2} p - \frac{q}{W}\right), \tag{4}$$

where p is the maximum fertility and W_p is the well-being for which fertility saturates due to biological limits. This function gives a nonlinear birth rate, where population initially increases with well-being and subsequently decreases once the saturation point has been reached. The mortality term $\left(\frac{q}{W}\right)$ decreases linearly with well-being.

3 | AN ECOLOGICALLY DRIVEN THEORY OF POPULATION GROWTH

3.1 | Birth and death dynamics

After reviewing the theories and models on demographic change, we provide a summary of possible driving factors in human birth and death rates. Starting with a simple argument: birth rates are not independent of death rates, specifically when it comes to under-five mortality. If child mortality is low, the desired number of offspring is equivalent to the number of children born, allowing for better family planning (Smeeding, 2014).

There is an abundance of data on demography and covariates from the last 60 years. From Supporting Information Table S1, it can be seen that fertility and child mortality are driven by the same factors, which allows us to describe the number of individuals entering the population and contributing to further growth as recruitment.

There is a strong interconnectedness between birth, death, food, wealth, education and technology that cannot be ignored. Therefore, any model attempting to mimic changes in population growth has to take many socio-economic and ecological factors into account. Thus, based on previous works and empirical data, we suggest that resource accessibility – defined as the availability of natural and agricultural land (Supporting Information Table S1: access to water, %GDP agriculture, % rural population), combined with technological and innovative advances (Supporting Information Table S1: access to electricity and sanitation, female literacy) – can be used as a proxy for socio-economic and ecological factors.

In a recent paper by Nitzbon et al. (2017), the authors used a nonlinear function to describe fertility with respect to well-being. We apply a similar nonlinear function to describe the dependence of population change on the accessibility of resources. Initially, population growth is a sign of prosperity and a greater need for labour. However, as the population reaches a higher quality of life, a shift occurs in family planning and the desire for offspring, such that higher birth rates signal a downturn in prosperity (Güneş, 2016; Jejeebhoy, 1995). These changes in prosperity also impact consumption rates and the impact of humans on the environment. Hirschman (2005) and many before (Ehrlich& Ehrlich, 1970, 1990; Meyer & Turner, 1992; Vörösmarty, Green, Salisbury, & Lammers, 2000) suggest that a large and growing population puts pressure on resources and ecological systems, until the population reaches a carrying capacity and ultimately implodes. This Malthusian trap has been avoided in the past through new waves of production, medicine and technology, but whether these strategies will hold in the future is a question that remains. The factors that govern population growth are widely debated and poorly understood, suggesting that reliance on any such factor in the future could lead to unwanted outcomes.

We develop a phenomenological model of the relationship between recruitment and death rates versus resource accessibility. Many previous models make assumptions that do not hold up to the current empirical data. In particular, when it comes to the birth rate, the factors that increased birth in pre-modern times (food, wealth, social status) have decreased the birth rate over the past 50 to 60 years. The theory and model developed here take into account the past 12,000 years of human population and land cover changes, combining multiple assumptions from previous works and replacing those that are not supported by past or present empirical data. This model is able to capture observed changes in human population and land cover change through bidirectional feedbacks. We use these feedbacks to make population projections under various scenarios, which is discussed in further detail below.

3.2 | Recruitment curve

As the birth rate and under-five mortality rate are highly correlated and have similar driving factors, we group the two terms, describing recruitment as an increase in the population that reaches reproductive age and has the ability to further increase the population.

Data from Supporting Information Table S1 provide support for our phenomenological representation of human population recruitment and suggest a possible mechanistic approach to explaining the recruitment rate with respect to resource accessibility. The proportion of the population that has access to electricity, sanitation and water is negatively correlated with the recruitment rate. Education, especially among women, has a strong negative correlation with the recruitment rate. Accessibility to such commodities acts as a proxy for wealth, technology, freedom and power. Contrarily, the percent of GDP from agricultural goods and the proportion of the population living in rural areas coincide with higher-recruitment rates. From Supporting Information Table S1, it can be seen that resources, that is, agricultural area and natural land area, have a positive influence on the recruitment rate, while education, technology and development have the opposite effect (Figure 1a,b). When multiplied together, the outcome is a non-monotonic function (Figure 1c).

Therefore, R is used to describe resource accessibility, defined as the combined availability of agricultural land (A) and natural land (N), in addition to technology and innovation. Part of technology and innovation takes into account the quality, efficiency of extraction and equality of distribution ($T_{A,N}$), such that $R = T_N(t)N + T_A(t)A$. The availability and access to resources are estimated from technological advancement data and pollen records (details are given in the Supporting Information). Fossil pollen records contain information about vegetation and land-use change that can serve as a proxy for land-use intensity (Lechterbeck et al., 2014). Archaeological records reveal an increasing trend in the evolution of technology, which has greatly improved the extraction and distribution of resources. Therefore, we can assume that earlier societies were less efficient (Marlowe, 2005).

In this model, technology is described independently of population size. There is most likely a feedback between population and innovation (Derex, Beugin, Godelle, & Raymond, 2013; Henrich et al., 2016; Kline & Boyd, 2010); however, there is little empirical evidence

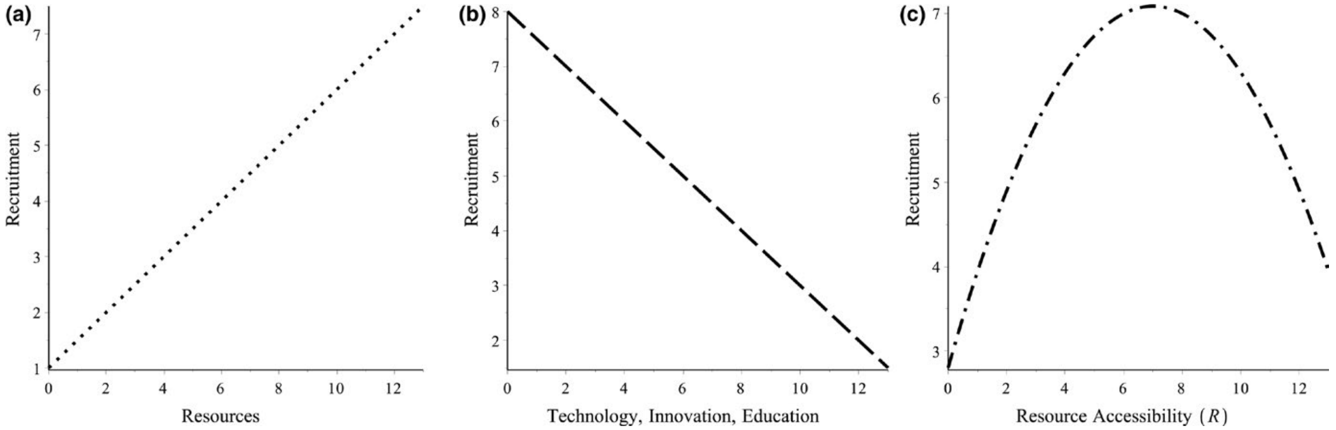

FIGURE 1 Crude representation of a possible mechanistic approach to modelling human recruitment. From the data in Table S1, it is hypothesized that recruitment increases linearly with agricultural resources and rural land area (a). By contrast, accessibility to electricity, education, water and sanitation have a negative influence on recruitment rates (b). When multiplied together, as is the case in our model, accessible resources = technology × land area. This gives a non-monotonic curve for recruitment (c) that may assist in explaining demographic transitions

to support the idea that larger populations foster greater technological development (Collard, Vaesen, Cosgrove, & Roebroeks, 2016; Vaesen, Collard, Cosgrove, & Roebroeks, 2016), rather it may be the degree of interaction between subpopulations (Powell, Shennan, & Thomas, 2009). We describe technology and innovation as an exponential function (with a similar curve to human population), which suggests a relationship between human population size and technology; however population size is not the only driving factor. Given the conflicting hypotheses, we estimate curves from empirical data to describe technology and innovation, and project various future trajectories (see Scenarios section below), to avoid making unfounded assumptions about the feedbacks between humans and technological innovation.

We use our phenomenological theory and this hypothesized accessible resource mechanism to create a recruitment curve with estimated data points from various times in history (Figure 2, details on sources for recruitment rates and calculations for accessible resources are given in the Supporting Information). Historical birth rates and child mortality rates are fit to an inverse Gaussian curve. The resulting recruitment equation is given by

$$b\left(R\right)=\beta\frac{e^{-\frac{(R-a)^2}{cR}}}{R^{1.5}}, \tag{5}$$

where α, β and *c* are coefficients describing the peak recruitment rate, when recruitment begins to increase and when recruitment begins to decline, respectively, for the Gaussian function. The parameter values are chosen to reflect empirical data for recruitment rates over the past 12,000 years (parameter description is given in Supporting Information Table S2).

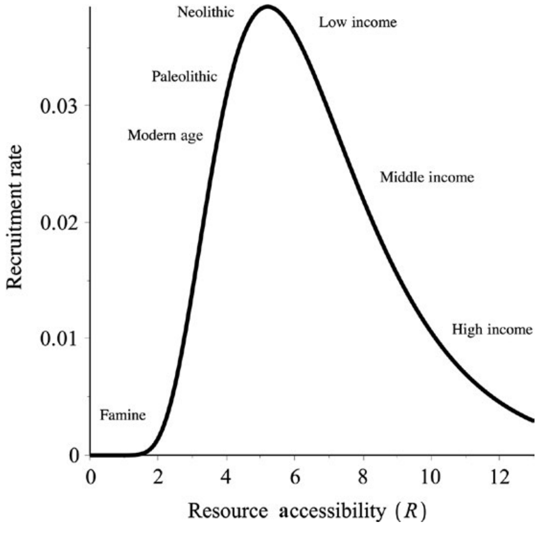

FIGURE 2 The phenomenological human recruitment curve is based on past birth rates and under-five mortality rates through humanity's history over a range of estimated resource accessibility, where accessible resources represent the available natural (*N*) and agricultural land (*A*) area multiplied by the efficiency of accessing these resources through technology and innovation ($T_{N,A}$). It is estimated that Paleolithic individuals spent more than one and a half times the energy in food acquisition compared to contemporary society Eaton and Eaton (2003). High-income countries have nearly double the access to food energy compared to low income countries (Roser & Ritchie, 2017)

Resource accessibility can be greater than the actual availability of resources ($R > N + A$), if technological advancements improve the ability to obtain resources to an extent greater than approximately double the present (≈8.5 billion hectares of natural and agricultural land). Resources can also be difficult to obtain, or of poor quality, for example in the absence of ecosystem services or nutrients, to an extent that they provide no benefits to the human population despite being abundant; in such cases, the resource accessibility would be low ($R \ll N + A$).

3.3 | Mortality curve

Using the crude death rate does not allow for comparisons between different groups of individuals. The link between crude death rate and socio-economic indicators is less convincing (average correlation coefficient magnitude for crude death rate $r \approx 0.61$, for adult death rate $r \approx 0.79$ and under-five mortality rate $r \approx 0.75$); however, by separating child mortality (included in the recruitment rate) and adult mortality, we are able to highlight potential driving factors for mortality (Supporting Information Table S1). In particular, an improved standard of living (i.e. improved education, better access to health care and nutritional food, improved hygiene, etc.) rapidly shifts the death rate from high to low. We ignore migration for now, as this is a non-spatial model. The death rate varies with resource accessibility as follows,

$$d\left(R\right)=\frac{\delta}{1+e^{(R-r_n)}}+\delta_{\min}, \tag{6}$$

where δ is the resource-based death rate, calibrated to fit empirical data (Bocquet-Appel, 2009; Food & Agriculture Organization of the United Nations, 2017; Preston, 1996), when combined with the minimum death rate, $\delta_{\min}$. The minimum death rate is based on statistics for adult mortality rates where resource accessibility is high and thereby resource-based death is negligible (The World Bank Group, 2017). The threshold for human well-being after which adult mortality decreases significantly uses the accessibility of resources as a proxy for improved standards of living. The well-being threshold is represented as r_n, using historical data on mortality and access to food and material goods to calibrate the threshold.

4 | HUMAN–ENVIRONMENT MODEL

4.1 | Human population dynamics

The resulting human population dynamics over time is the difference between recruitment and death:

$$\dot{H}=\left(b\left(R\right)-d\left(R\right)\right)H. \tag{7}$$

The relationship between growth and resource accessibility is shown in Figure 3.

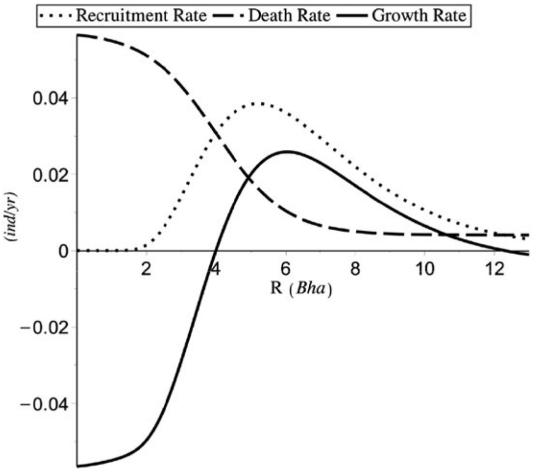

FIGURE 3 Change in population demographics over a range of accessible resources (R). $R = T_N(t)N + T_A(t)A$, where $T_{N,A}$ is the advances provided by technology and innovation and N and A are natural and agricultural land area respectively

4.2 | Land dynamics

For the purpose of our model, natural land (N) is simplified to reflect net degradation by humans for the purpose of agricultural development (c_a) and natural resource use (d_n), given by

$$\dot{N} = -c_a NH - d_n NH. \tag{8}$$

Agricultural land (A) is similarly degraded by humans at a rate of d_a. The change in agricultural land is given by

$$\dot{A} = c_a NH - d_a AH. \tag{9}$$

4.2.1 | Scenarios

Technology and innovation are modelled independently of population size and land cover, with curves for both the natural land and agricultural land sectors (see Supporting Information for details on $T_{N,A}$ curves). The $T_{N,A}$ curve grow exponentially as suggested by Kurzweil (2004) and similar to the increase in GDP seen in Motesharrei et al. (2016); however, we also include the possibility of saturating yields from technology and therefore apply logistic curves to $T_{N,A}$. We alter the steepness of the curve to reflect differences in time of onset and how rapidly the change diffuses through the population.

As the interactions between humans and the land are highly variable and difficult to predict, we simulate changes over the next 3,000 years under five different scenarios: changing natural degradation rates (d_n), changing agricultural degradation rates (d_a), $T_{N,A}$ saturating at current levels, $T_{N,A}$ saturating after a 60% increase, no saturation of $T_{N,A}$ (saturates at 500 times the current level in 18,000 years from present). A table of parameter values is given in the Supporting Information Table S2. The major components of the model are land cover change and change in innovation and technology development, therefore the scenarios involve changing the rate of agricultural and natural land degradation, saturating the degree of improvement through technology and innovation, in addition to changing the onset (γ, see Supporting Information) and diffusion patterns ($y_{\max}$) of technology and innovation ($T_{N,A}$).

5 | MODEL PROJECTIONS

5.1 | Changes in resource availability

The rate of agricultural degradation has one of the greatest impacts on peak population levels (Figure 4a). Slowing the rate of agricultural degradation results in a lower peak population, as the changes in population transition quickly through the stage of rapid population growth depicted in Figure 5 (red line, transition 3). Slower degradation results in more stable agricultural management and when combined with advances in technology and innovation results in greater harvesting efficiency and reduced need for offspring. Therefore, the human population achieves a state of greater well-being with access to abundant resources, technology and innovation, and by proxy knowledge, wealth and health care.

Increasing the degradation of agricultural land results in a much higher peak population, as the degradation of land and technological or social innovations ($T_{N,A}$) are pulling population change in opposite directions, ultimately keeping the growth rate at high levels over a longer period. The advances in $T_{N,A}$, predominantly in the agricultural sector, are masking the decline in resources, which allows the population to keep growing. However, once agriculture reaches a critically low level and technology stagnates or can no longer counterbalance the diminished supply of agricultural (A) and natural (N) resources, the human population collapses. Advances in agricultural technology are likely the cause for the peak growth rate in the 1960s; however, the Green Revolution is an ongoing process and as the population continues to grow or as demands increase there will be a need for future technological advancements (Evenson & Gollin, 2003).

Natural land degradation behaves similarly to agricultural degradation, although the impact is smaller in magnitude (Figure 4b). Slower degradation of natural resources leads to slower population growth and a reduced peak population. The population spends less time in the rapid growth stage, as the advances in technology and innovation ($T_{N,A}$) are dominant enough to force the system past the stage of rapid growth (Figure 5, red line, transition 1), given that there are adequate natural resources to supply the population demands. Rapid degradation of N leads to more rapid population growth and a sharp population decline, as resources diminish. However, the population recovers with advances in technology and innovation ($T_{N,A}$), even in spite of dwindling natural resources. The population continues to oscillate over time until $T_{N,A}$ saturates (after 18,000 years) and no longer enhances productivity, at which point the population collapses as a result of insufficient resources.

5.2 | Changes in technology and innovation

Shifting the onset of advances in technology and innovation ($T_{N,A}$) to later in time results in a lower peak population and the population peak

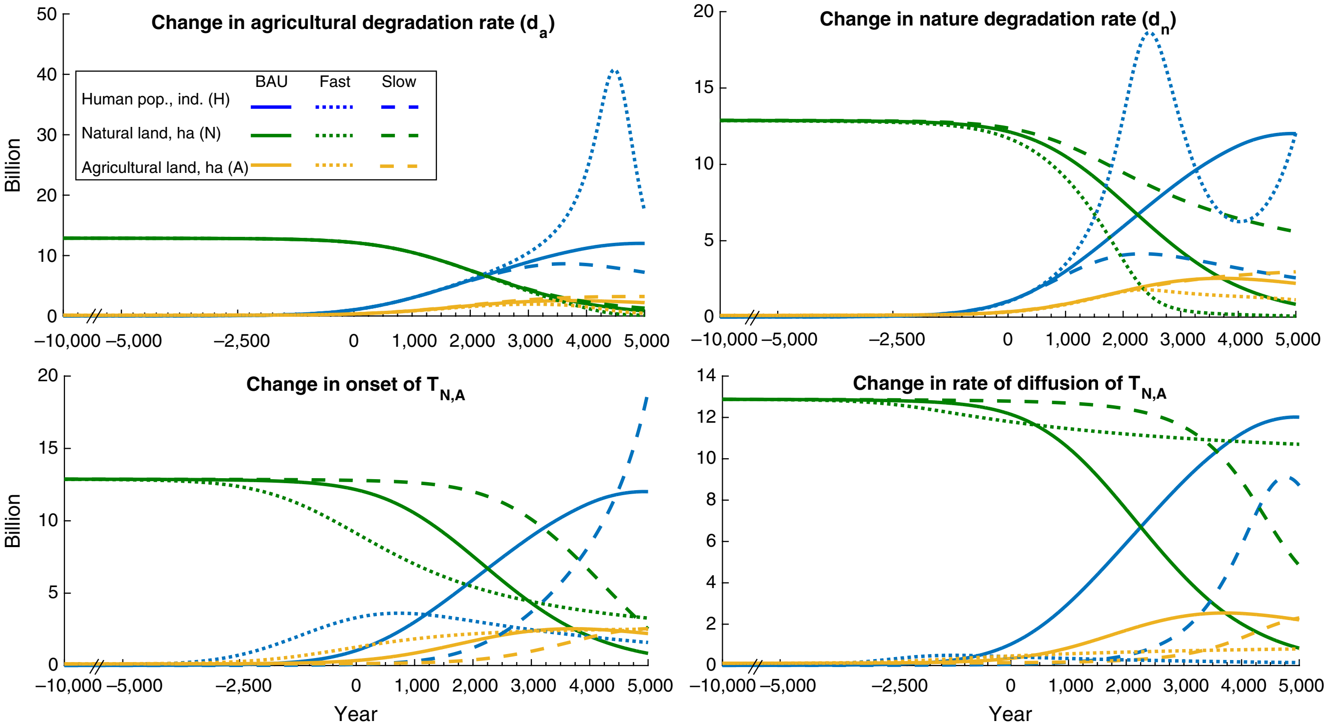

FIGURE 4 Altering land degradation rates (d_a and d_n) and $T_{N,A}$ curves. (a) Change in the rate of agricultural land (A) degradation (d_a), where rapid degradation (dotted lines) leads to an increased peak population, while reduced degradation (dashed lines) results in a lower peak population. (b) Change in the rate of natural land (N) degradation (d_n) follows similar trends, where rapid degradation (dotted lines) results in an earlier onset of a high peak population and slow degradation (dashed lines) leads to minimal population growth. (c) Shift in the onset (γ) of technological advances and innovation ($T_{N,A}$); early onset of $T_{N,A}$ (dotted lines) results in minimal population growth versus late onset of $T_{N,A}$ (dashed lines), which results in a delayed population explosion with a greater peak. (d) Change in the rate of diffusion of $T_{N,A}$ ($y_{\max}$); rapid diffusion (dotted lines) leads to negligible changes in all variables and slow diffusion of $T_{N,A}$ (dashed lines) results in a delayed and lower population peak. Solid lines represent the business as usual scenario

is reached later, as the population remains in a state of rapid growth until resources become limited (Figure 4c). Shifting the onset of $T_{N,A}$ to an earlier period results in minimal population growth. This somewhat unexpected result occurs as the human population spends very little time in the peak population growth stage, transitioning directly from high-birth, high-death rates to low-birth, low-death rates, without the middle stages of the demographic transition (Figure 5, green line).

How quickly technology or innovation ($T_{N,A}$) is dispersed and applied has an overwhelming influence on population growth. Increasing the steepness of the $T_{N,A}(t)$ curve results in negligible population growth, as there is no explosion in the population – the middle stage of the demographic transition is forestalled. Gradually introducing and applying advances in $T_{N,A}$ generates a lower and delayed peak population. Gradual change allows many individuals to adopt the change and encourages additional followers to join over a longer period; individuals get caught at peak growth rates for longer and the population continues to grow until resources diminish. A particularly slow dispersal and application of technology and innovation means that rapid growth is never reached. The population grows slowly until limited by resource availability (N and A). Once available technological or innovative solutions no longer support the higher population levels and reduced resource capacity, the population declines (Figure 5, blue lines).

In many parts of the world, it has been shown that food production efficiency is stabilizing (Food & Agriculture Organization of the United Nations, 2017), suggesting there is a limit in the ability to enhance production through technology. The results may seem counterintuitive, as unlimited advances in technology and innovation result in the lowest peak in population (12 billion individuals), considering that earlier advances in technology and innovation allowed the population to grow (i.e. Green Revolution). Rather in this case, future development leads to lower-birth/death rates and a smaller decline in population. This represents a population with higher well-being (i.e. greater resources, low-birth and low-death rates). We find that if $T_{N,A}$ saturates at current levels, the population has a higher peak population (25 billion individuals). Population growth begins to shift to the right of the growth curve (Figure 5, blue lines), as technology increases, but once it saturates the population falls back to the left of the curve (low-birth, high-death rates), as resources diminish—never reaching the high-growth rate state. A 60% increase in the current efficiency level results in the highest population (37 billion individuals). Here the population gets caught at peak growth, with adequate food to sustain the population, but not enough technology to improve well-being. This represents a low well-being society, as food and innovation are limited, resulting in high-birth and high-death rates.

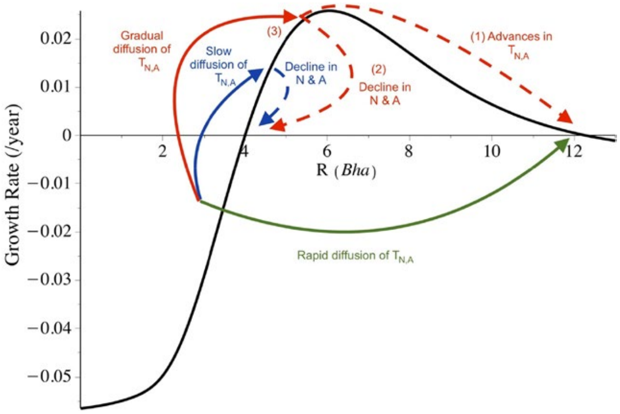

FIGURE 5 Demographic transitions. When population grows slowly and reaches the peak growth rate (red line), there are three possible transitions: (1) technology and innovation ($T_{N,A}$) force the system to a state of low-birth, low-death (i.e. greater well-being, $R = 12$); (2) natural and agricultural land cover (N & A) decline beyond compensatory effects from technology, resulting in a high-birth, high-death state (i.e. lower well-being, $R = 4$); 3) the system may spend significant time at peak growth ($R = 6$), causing the population to explode, ultimately resulting in (1) or (2). The blue line demonstrates intermediate growth that never reaches peak population growth (either from too few resources or lack of technology and innovation ($T_{N,A}$); the growth rate then declines with insufficient N & A. The green line results when there are abundant resources and rapid dispersal and application of $T_{N,A}$, going from high-birth, high-death rates to low-birth, low-death rates, avoiding the middle stages of the demographic transition

These results show how population growth is highly sensitive to a balance between technology and innovation ($T_{N,A}$) and resource availability (N and A). By contrast, the land dynamics are relatively unchanged (Figure 6), showing how advancements in technology and innovation enables the human population to detach from their connection to resources, until a critical decline in available resources results in a population collapse.

6 | DISCUSSION

This study sets out to describe human population dynamics in relation to land cover and technological advancements, applying a simple model to explore past demographic and land trends, as well as possible future scenarios. The development of theories on ecological boundaries and the Earth's carrying capacity raises concerns about the sustainability of the human-environment system. The current combination of high-resource demands, an unprecedentedly large population and waning advances in technology and innovation in resource acquisition, necessitates population stabilization or at the very least minimize resource use. Despite the seemingly trivial nature of this situation – a finite system results in a finite population – there is no consensus on what factors are crucial in securing a sustainable future for both ecological systems and humans. Some have suggested implementing a one child policy; others suggest reducing ecological footprints, while optimists cling to the notion that technological advances will sustain population growth indefinitely.

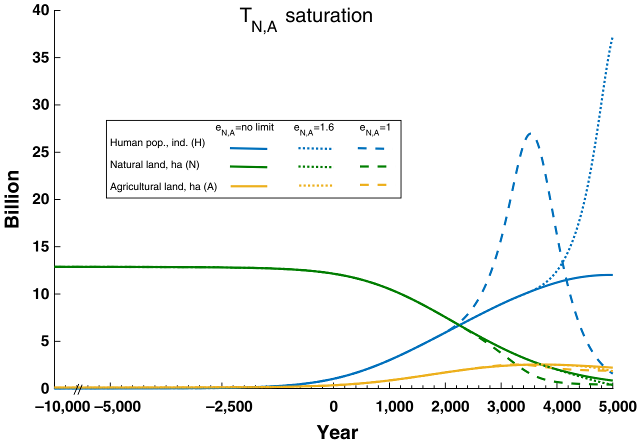

FIGURE 6 Whether technology and innovation ($T_{N,A}$) will saturate as a result of waning productivity and yield is a great unknown. Here we show potential outcomes of varying the amount of improvement provided by $T_{N,A}$. The solid line reflects no limit to the degree of improvement from $T_{N,A}$, where efficiency grows at a continuous exponential rate. The dotted line represents a 60% increase in benefits received from $T_{N,A}$ when compared to current levels ($e_{N,A} = 1.6$). The dashed line shows what happens if $T_{N,A}$ saturates at the current level ($e_{N,A} = 1$). Showing the counterintuitive and convoluted influence of technology and innovation on human population

In this work, we highlight the important role of agriculture and technology in allowing the population to expand. Likewise, we show that either natural land (i.e. ecosystem services) or continuous advances in technology are required to prevent collapse.

What is clearly shown here is that the onset and the speed of dispersal and the application of technology or innovation determine when or if the population will explode. If innovation/technology and land area combine to give humans access to many resources very quickly, the population does not experience rapid or explosive growth, as the peak growth rate is not attained. Instead, the individuals rapidly shift from a quantity to quality of offspring perspective, achieving a higher state of well-being. To our knowledge, there are no examples of this transition on a global scale in human history, although many Scandinavian countries such as Finland and Norway have experienced relatively stable growth since the 1500s—transitioning from a high-birth, high-death state, typical of the middle-ages, to a low-birth, low-death, high well-being state without a prolonged rapid growth period (Clio Infra, 2017).

In contemporary societies, a portion of the world is living in a state of post-boom, where the later generations are continuing to grow exponentially, but the birth rate is slowing with greater income. The other portion of the population had a later onset of innovation and is still at peak recruitment rates, creating a very long period of high growth (middle stage of the demographic transition) allowing the human population to expand. Growth will remain high until either an increase in technology and innovation, or a change in available resources, pulls the population to one side of the curve. There are essentially two markedly different demographic transitions underway in our current society. These contrasting demographic transitions should be further explored in a spatial model, which would allow for more cultural interactions, such as the link between evolution of technological complexity and human populations.

The model described here cannot answer what is causing the change in technology or innovation, but by applying a range of scenarios it can be seen that the peak population is highly variable depending on technological innovation time frames. Sub-Saharan Africa provides an example of misaligned time frames, which cause high-growth rates. There are basic resources to support a low level of well-being, but there is a lag in technological innovation (i.e. education, health care, family planning and nutrition) (Luiz, 2013), which would increase the quality of life and subsequently reduce fertility rates. In the absence of technological innovation, the recruitment rate remains high and the population continues to grow. The high-resource availability and high-technological innovation in wealthy countries occur over parallel time frames and therefore there are many accessible resources, lower recruitment rates, greater welfare and lower growth rates. During the Paleolithic Era, technological innovation was relatively low, as were available resources (i.e. uncertain food supply). Therefore, the advancement of both resource availability and technological innovation, or more accurately the lack thereof, occurred over the same time frame. With comparatively little technology to compensate for limited resources, the Paleolithic populations maintained low-growth rates. Therefore, technology and innovation can skew the population's perception of resource accessibility, ultimately determining growth rates. Through simulations we were able to show that advancements in technology and innovation creates a sense of detachment between humans and nature or agriculture, until such a point that the dependence cannot be ignored and the human population declines as a result of inadequate resources.

In the model, we include a scenario in which technology saturates, based on trends demonstrating stabilizing food production yield as a result of declining technological and innovative solutions (Food & Agriculture Organization of the United, 2017). However, technology has stagnated before; for example, in the early 1900s it seemed that population would be limited by available crops, until the introduction of hybridized corn and the green revolution (Johnson, 2002). The green revolution is considered to be a major contributor to the exponential population growth seen in the second half of the 20th century. Thus, it is difficult to predict when or if the population will decline, given that there could be a revolutionary change in technology and innovation that supports unfathomably high-population levels. That being said, technological advances and innovation must continue in order to maintain population levels at current standards, something that we have echoed here by showing that saturating the benefits from technology and innovation leads to higher peak populations with reduced well-being and a greater likelihood of collapse.

In addition to technology and innovation, agriculture appears to have a critical role in determining the peak population. The human population reacts impetuously to small changes in the area of agricultural land, as depicted by a peak population greater than 40 billion individuals followed by a population collapse when agriculture is rapidly degraded. Agriculture has been responsible for many past boom-busts in societies (Shennan et al., 2013), suggesting that agriculture is a convenient tool for growing the population, but is not robust; whereas natural resources are more robust, but once a critical loss occurs there are major consequences that may not be reversible.

The recruitment curve depicted here shares similar characteristics to the environmental Kuznets curve (EKC), which shows environmental degradation as a function of income per capita (Tamazian, Chousa, & Vadlamannati, 2009). The EKC has been criticized because at face value it appears to suggest that economic growth has a positive influence on the environment. Theoretically this may be true, but in practice this is not so obvious (Stern, 2004). There are few empirical examples showing a non-monotonic relationship between income and environmental degradation; the theory ignores spillover, where degradation occurs in foreign environments; and the EKC does not account for the fact that before achieving declines in environmental degradation, there is a substantial increase in environmental degradation in many cases. This suggests that there could be a threshold of no return, or the reason for decreased degradation is due to the absence of natural land to degrade. Rather than economic growth, we use resource accessibility, which neutralizes many of the contentious assumptions of the EKC. Furthermore, we have attempted to fit our recruitment curve to empirical data with reasonable results. These EKC and our curve draw an interesting comparison, as economic growth could easily be translated into resource availability, suggesting that human recruitment experiences the same response to socio-economic changes as environmental degradation. Furthermore, this reinforces the idea that environmental degradation, population change and socio-economic dynamics are intricately linked.

Population growth projections, particularly projections of peak population, are difficult, as making predictions off of past scenarios is inadvisable, especially when the mechanisms are unknown. For example, the UN population projections are constantly changing with every new publication, consistently increasing the peak population. There is most likely a limit to the global human population, but putting a tangible number on it seems elusive (Cohen, 1995). Models such as the one presented here can give ideas of qualitative trends, but should not be considered soothsayers of the future population dynamics.

That being said, the complexity of the dynamics and the inability to give precise projections should not deter modelling work on human population growth. There have been numerous models exploring particular aspects of human-nature interactions, which provide good starting points, offer insight and often raise further questions. Here we expand on these earlier models in an attempt to use resource accessibility as a proxy for many socio-economic factors. We use correlations as a syndrome, not to pin point the cause a demographic change, but to provide clues to what might signal large shifts in population dynamics.

To many in the field of ecology, the bidirectional feedbacks between humans and nature are of critical importance, yet the work on coupled systems has largely been ignored (Motesharrei et al., 2016). Much of the past human population modelling work focuses on population change in one period of time or during a specific event, failing to account for multiple stages of the demographic transition. We introduce a recruitment function that experiences an up–down shift, analogous to what has been observed in past and contemporary societies, and additionally we offer an ecologically driven mechanism for such a change. Theories that attempt to describe drivers of population change are complex, with no clear consensus; however, here we apply a simple concept, relating human population change to shifts in land area and technology/innovation. These two drivers combine to give a simple ecologically-driven theory for the complex processes of the demographic transition over time. This approach captures past and present dynamics and suggests that many of the factors that are responsible for changes in demography can be incorporated in environmental proxies. The social factors and economic factors driving changes in land change and technology/innovation advancements were certainly different over the years, but we suggest that they play into the ability of humans to access resources. We have deliberately kept the model simple, but that does not negate the importance of sociopolitical factors (e.g. war, religion and human rights), which would certainly add further dimensions to the model and incorporate stochasticity into the system.

Simple models such as this one, look at the rate of change in variables, for example land or human population, not the rate of change of the driving factors. In many cases, it is the sudden change these driving factors that causes such dramatic transitions in land cover and demography, something that cannot be captured by this model. As such, the model cannot predict the onset of a new regime (e.g. agriculture) or account for epidemics (e.g. plague). Nevertheless, this ecologically-driven theory of human population growth highlights key driving factors and provides insight into a possible mechanism for demographic change. Future work will develop on the premise of sudden dramatic changes and stochasticity.

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AUTHOR CONTRIBUTIONS

Both ML and KH conceived of the project idea and contributed to the final version of the manuscript. ML provided critical feedback and funded the project. KH developed the theory, performed the computations and wrote the first draft of the manuscript.

DATA ACCESSIBILITY

All data used to formulate and parameterize the model can be found in the main text references and the Supporting Information. The data for birth and death rates from the World Bank is accessible through https://doi.org/10.17605/OSF.IO/Q6ZRA, along with the code used to create the model.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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