

Positive and negative feedbacks in human population dynamics: future equilibrium or collapse?

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The future number of people inhabiting the planet will influence the impact over natural ecosystems. In consequence, the growth of the human population represents one of the most important challenges for the near future. In this paper we used population dynamic theory to analyze human population growth. The results suggest that human population growth exhibited important fluctuations during the last 2000 years. In particular two different phases during the last 400 years can be distinguished, a positive relationship with population size implying positive feedback processes, followed by a negative relationship with population size – suggesting that negative feedback processes have been operating during the last 45 years. Our results support the view that ecological concepts derived from population ecology can be useful for understanding human dynamics. While cooperation at low densities in animal populations reminds us the Boserupian view that population growth induces economic development and higher standards of living, competition at high densities reconciles ecological theory with the original Malthusian view. We conclude that the present reduction in human per capita growth rates appears to be consequence of different limiting factors operating in combination around the globe in a similar manner, except in Africa where the factors operating appears to be very different. Humans may achieve a stable equilibrium population in the next century but the possibility of a population collapse caused by second-order oscillations should be considered.

The growth of the human population on planet Earth represents one of the most important issues and challenges for the near future (Cohen 1995, 2003). The number of people inhabiting the planet will influence the quality and quantity of resources, goods and services that people will use in the future. Scientists of very different disciplines, including sociologists, anthropologists, demographers, economists and ecologists, have tried to predict the future human population growth and to understand the complex factors determining this phenomenon (Cohen 1995, Lutz et al. 1997, 2001). However, most of the predictions of future human population size are deterministic or stochastic projections of current trends based either on exponential or faster than exponential growth models, or on models allowing changes in demographic rates driven by exogenous variables. The problem with these approaches is that they are not based on general principles of population dynamics (Berryman 1999, Turchin 2003a, 2009). As a consequence, most of the human population dynamic forecasts are based on inappropriate models because they do not take into account the effects of limiting factors and potential feedbacks (Turchin 2009). For example, the “Doomsday” prediction to be effective Friday 13 November 2026 (Von Foerster et al. 1960) is based on the accelerated population growth rate exhibited by humans during the first half of the 20th

century. Similarly, forecasts of a global world population of 9200 million people by year 2050, are based on current fertility and mortality rate trends (United Nations 2007).

Human population exhibited dramatic changes during the 20th century; the world population grew from almost 2 billion people in 1930 up to 6 billion in 2000. In 1960 almost 2 billion people lived in rural areas, while only 1 billion lived in cities (Clarke 2002); by year 2000 the fraction of people living in cities and rural areas was 50:50 suggesting that this trend will continue in the future. One of the most important phenomena in human demography occurred during 1965–1970, when the maximum per capita growth rates ever exhibited by the human population were observed (Cohen 1995). Since then, human population growth rates have declined globally, even in the least developed regions of the world (Lutz et al. 1997).

The attempts to understand human population dynamics can be traced back to Malthus (1798), who clearly perceived the potential conflicts between the growth of the human population and the availability of resources (land and energy use, food production and water provision). The negative effect of resource limitation on population growth was idealized mathematically by Verhulst (1838) through his logistic equation, the first mathematical model of a population growing in a limited environment. Almost a century later, this model

was rediscovered by Pearl and Read (1920) who used it to predict human population growth in the USA. However, because of the failure of the logistic model to accurately predict human population growth at that time, demographers abandoned logistic theory and turned to the study of population age structure and age-specific rates of births and deaths (Cohen 1995). As a consequence, while animal population ecologists developed a theory based on the notion of feedback mechanisms, logistic models, and consumer–resource interactions (Royama 1977, 1992, Berryman 1999, Turchin 2003a, Ginzburg and Colyvan 2004), human demography developed around the notion of continuous growth and the particular economics and socio-cultural determinants of variation in age-specific vital rates (Lee 1987, Keyfitz and Caswell 2005) and on the demographic transition (Coale and Treadway 1986, Coleman and Schofield 1986, Borgerhoff Mulder 1998). At first glance, human population growth seems to be determined by factors not related with its own population density or food resources, but rather to factors such as culture, technology, institutions, policies, individual reasoning, and the economy (Lee 1987). For example, some studies have attempted to explain the relationship among population growth, technological change, and the standard of living (Kremer 1993, Galor and Weil 1999, 2000). In particular, demographers and economists had been interested in developing unified models for explaining the demographic transition from a Malthusian Regime characterized by low or zero population and economic growth, to a Post-Malthusian Regime where there is a positive relationship between population and economic growth, and to the Modern Growth Regime characterized by an inverse relationship between wealth and population growth (Galor and Weil 1999). Nevertheless, the problem of population growth is not only associated with economic growth, health and well-being, but also with the capacity of natural resources to maintain human population on Earth (Dasgupta 2007).

Although some studies have attempted to reconcile conceptual elements from population dynamic theory and human demography (Lee 1987, Wood 1998, Wilson and Airey 1999, Lutz and Qiang 2002, Lutz et al. 2006), the use of ecological principles in the study of human demography has been controversial (Attenborough 2002). In this paper, our starting point is that both animal and human population dynamics must obey the same general rules of any dynamical system, such as negative and positive feedbacks, and the pressure of exogenous perturbations (Royama 1992, Berryman 1999, Turchin 2003a, Ginzburg and Colyvan 2004). These general dynamic principles are metaphors for ecological forces common to any group of living organisms, such as cooperation, competition, and consumer–resource interactions (Berryman 1999). Consequently, we used this well established theoretical framework derived from the theory of dynamical systems and animal population dynamics for analyzing and modeling human population growth (Berryman 1999, Royama 1977, 1992, Turchin 2003a).

Material and methods

Data on human population growth were taken from the historical estimates of world population from the U.S.

Census Bureau (<http://www.census.gov/ipc/www/worldhis.html>) for the period AD 1 to 1950, and from the world population prospect web site of the United Nations (<http://esa.un.org/unpp/index.asp?panel=1>) for the period AD 1950–2005.

The R -function represents the relationship between the per capita growth rate over a given period of time and the human population at the beginning of that period of growth, and can be estimated as:

$$R = \log_e N_t - \log_e N_{t-d} \quad (1)$$

R can also be expressed in terms of birth and death rates (Berryman 1999):

$$R = \log_e (1 + B - D) \quad (2)$$

Where R is the realized per capita growth rate and B and D are the per capita birth and mortality rates, respectively, and d is the time period between censuses (20 and 5 years in this study). The realized per capita growth rates can be easily estimated from population size data as $R = \log_e (N_t/N_{t-d})$. In addition, we also estimated the rate change of per capita population growth (second derivative). This measure could be important to detect accelerations in the population growth rate (Ginzburg and Colyvan 2004). The rate change of per capita population growth can be easily estimated from data as:

$$RG = R_t - R_{t-d} \quad (3)$$

First, we fitted simple linear and non-linear models using the per capita growth rate R and the rate change of per capita growth rates RG as the response variables and population size as the explanatory variable for different periods during the last 2000 years. Because the time intervals between population size estimates are different in the time series, we standardized all the estimates of R and RG in a 20 year time-step. In addition, we explored the relationship between R and population size during the last 45 years (1962–2007) for different regions of the world (below) using the generalized additive modeling (GAM) approach of Hastie and Tibshirani (1990). In these non-linear models the form of the function was determined by fitting natural cubic splines to the data, and the complexity of the curve (the number of degrees of freedom) was determined by penalized regression splines and generalized cross validation (GCV) (Wood 2001). Because these time series are short (45 years) we used a time step of 5 years between censuses. Smoothing terms were estimated using penalized regression splines, with parameters selected by minimizing the GCV. All the statistical analysis was performed in the R environment (<http://www.r-project.org/>).

For the same time period (1962–2007) we explored the relation between per capita growth rates R and some potential explanatory variables such as, per capita food production index (covers food crops that are considered edible and that contain nutrients standardized to the 1999–2001 production), arable land (ha person⁻¹), water reserves (m³ per capita), per capita gross domestic product (GDP is the gross domestic product converted to international dollars in a per

capita basis), urbanization (population in urban agglomerations of more than 1 million measured as the % of total population), per capita CO₂ emissions (metric tons per capita) and population density (people km⁻²). Data were taken from the World Bank web page (<<http://www.worldbank.org/>>) and the FAO web page (<<http://faostat.fao.org/default.aspx>>). For analyzing the relationship between *R* and the explanatory variables, we used a partial least squares (PLS) regression approach. This statistical procedure is an extension of the multiple regression analysis and it is particularly useful when the number of explanatory variables is similar or higher than the number of observations and the independent variables are highly correlated (Næs and Martens 1989, Carrascal et al. 2009). In PLS regression the original non-independent predictors are grouped in few orthogonal linear gradients (factors) of covariation maximizing the explained variation in the response variable. These fewer number of orthogonal factors can be used to deduce the relationship between predictor variables and between the latent factors and the response variables (Tobias 2003, Mevik and Wehrens 2007). We selected different regions of the world for this analysis, 1) world, 2) sub-Saharan Africa, 3) Latin-America and the Caribbean, 4) high income OECD countries, 5) Japan, 6) India, and 7) China. Similar to the GAM modeling we used a time step of 5 years in this analysis.

Results

Long-term global human population dynamics can be characterized by an almost continuous increasing trend only disrupted by the observed collapse in the fourteenth century (Fig. 1A). However, the per capita growth rates and the rate of change of growth rates (second derivative) showed a more complex picture of global human population dynamics (Fig. 1C–D). For example, human population was characterized by a period (0–800 AD) of slow or almost zero population growth (Fig. 1 C–D). The period 800–1200 AD was characterized by an increase in the per capita growth rates (Fig. 1C) and accelerated growth (Fig. 1D), this trend changed to lower (positive) per capita growth rates and a negative second derivative (rate change of growth rate) from 1250 to 1350 (Fig. 1 C–D) indicating a slower population growth. Global human population collapsed during the period 1340–1400 which is clearly observed in the per capita growth rates (negative) and the strong negative value of the rate change of growth rate (Fig. 1C–D). The population recovery observed during the period 1400–1600 (renaissance period) is clearly depicted in the rise of per capita growth rates (Fig. 1 C), but in particular in the strong acceleration of the population growth rate only comparable with the pattern observed during the late nineteenth century (Fig. 1D). At a global scale per capita growth rates decreased during the

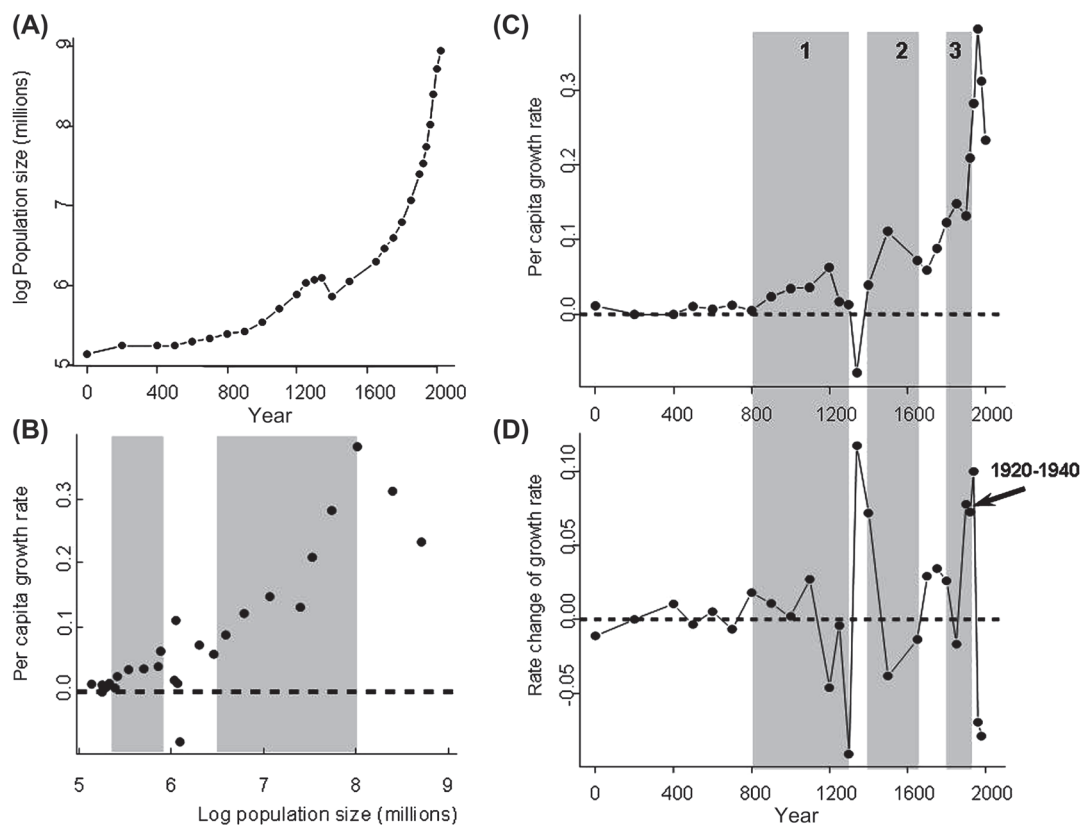


Figure 1. (A) Historical estimates of the human population size from the U. S. Census Bureau (<<http://www.census.gov/ipc/www/worldhis.html>>) for the period AD 1–1950. For the period AD 1950–2005 we used the world population prospect web site of the United Nations (<<http://esa.un.org/unpp/index.asp?panel=1>>). (B) *R*-function plot of the human population dynamics, where per capita population growth rates are plotted as a function of logarithm of population size (gray stripes represent the phases with a positive relationship with log population size). (C) Historical estimates of per capita growth rates (*R*) of the human population. (D) Historical estimates of the rate change of per capita growth rates (*RG*; second derivative) of the human population, gray stripes represent phases with changes in global climate, 1 is the medieval warm period (MWP), 2 the Little Ice Age (LIA) and 3 the cooling exhibited during the second part of the 19th century.

seventeen century, after that they showed an increasing and accelerated trend from the eighteen century until last half of the twenty century when a clear declination is observed (Fig. 1C). Despite of this positive trend in per capita growth rates, the temporal variability of the rate change of growth rates revealed two important events; 1) a strong decrease in the velocity of growth during the last half of the nineteenth century, and 2) a decrease in the acceleration of the growth increment during the period 1920–1940 (Fig. 1D). Global human population grew at an accelerated growth rate over the last 200 years (Cohen 1995), which was faster than exponential – in particular until 1965–1970 – since then, global population growth has declined (Fig. 1B–C).

A common practice in animal population dynamics is the use of the R-function for diagnosis and for modeling the feedback structure of population dynamics. The phase portrait showed in Fig. 1B strongly suggests that human R-function can be classified into different phases: a positive relationship with population size – implying positive feedback processes (cooperation) – and a negative relationship with population size – implying feedback processes (competition), interspersed among these phases there were some periods where per capita population growth rates were not related with population size (exponential growth) (Fig. 1B). Two periods appears to be characterized by

positive effects of population size on per capita growth rates, the period 400–1200 AD, and the period 1700–1960 (Fig. 2A–B, Table 1). However, the slope of the increase in per capita growth rates with population size is almost twice as much for the period 1700–1960 compared with the previous one (Table 1). The same pattern can be observed in the regression analysis between the rate changes of growth rates (RG_t ; acceleration in growth rates) and population size for the period 200–1100 and 1650–1940 (Fig. 3A, C, Table 1), suggesting the importance of population size for driving positive population growth during these two periods. Also, during the first period (200–1100 AD) there was a significant negative effect of the per capita growth rates on acceleration rate (RG_t) (Table 1). However, this variable did not show any significant effect during the second period of accelerated growth (1650–1940, Table 1). It is important to remark that between these two periods of accelerated growth there was no significant effect of population size on rate changes of growth rates (RG_t) (Fig. 3B, Table 1).

On the other hand, the last phase (1960–2010) was almost perfectly fitted by a classical logistic model (Ricker 1954;

$$R_t = R_m - e^{[aX_{t-1} + C]} \quad (4)$$

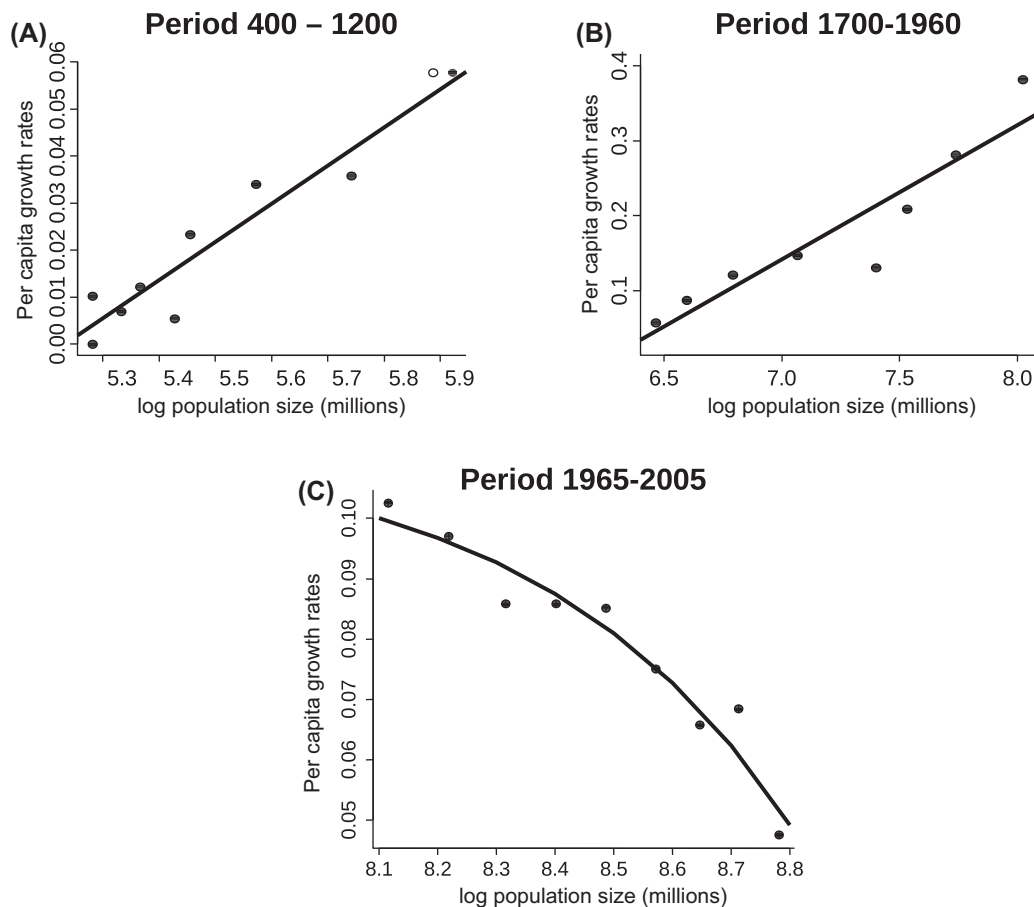


Figure 2. Fitted models of human population dynamics between per capita growth rates (R_t) and log of population size, (A) positive feedback phase of the period (AD 400–1200), (B) positive feedback phase of the period (AD 1700–1960) and (C) the negative feedback phase. See Table 1 for model details.

Table 1. Non-parametric and parametric population dynamic models fitted to the human population size data using methods discussed in the text; DF = estimated degrees of freedom of the spline term; F = F value; p = probability value, GCV = generalized cross validation score, r^2 = coefficient of determination. Variables are $X_t = \log_e$ of population size in year t , $R_t = \log_e(N_t/N_{t-1})$, and $RG_t = (R_t - R_{t-1})$.

R-function models	Parametric models		r^2
Model for the period (AD 400–1200)	$R_t = -0.42 + 0.081 \times X_{t-d}$	$F_{1,7} = 65.65; p < 0.0001$	0.90
Model for the period (AD 1700–1960)	$R_t = -0.0064 + 0.000032 \times X_{t-d}$	$F_{1,6} = 36.33; p = 0.0009$	0.86
Model for the period (AD 1965–2005)	$R_t = 0.11 - \exp(2.33 \times X_{t-d} - 23.29)$		0.94
Rate change of growth rate models (RG)			
Model for the period (AD 1–1100)	$RG_t = -0.23 + 0.044 \times X_{t-d}$	$F_{1,8} = 7.11; p = 0.029$	0.47
Model for the period (AD 1200–1650)	$RG_t = -0.49 + 0.094 \times X_{t-d} - 0.78 \times R_{t-d}$	$F_{2,7} = 10.47; p = 0.008$	0.75
	$RG_t = 0.31 - 0.052 \times X_{t-d}$	$F_{1,4} = 0.02; p = 0.90$	0.005
Model for the period (AD 1650–1940)	$RG_t = 1.67 - 0.27 \times X_{t-d} - 0.92 \times R_{t-d}$	$F_{2,3} = 1.32; p = 0.39$	0.11
	$RG_t = -0.43 + 0.067 \times X_{t-d}$	$F_{1,7} = 16.51; p = 0.005$	0.70
	$RG_t = -0.51 + 0.083 \times X_{t-d} - 0.15 \times R_{t-d}$	$F_{2,6} = 7.61; p = 0.023$	0.72
R-function models (1962–2007)	Non-parametric models	GVC	r^2
High-income countries	$R_t = f(X_{t-d}); DF = 2.33; F = 16.01; p = 0.0015$	1.38×10^{-5}	0.87
Japan	$R_t = f(X_{t-d}); DF = 3.77; F = 179.4; p < 0.0001$	1.28×10^{-5}	0.89
India	$R_t = f(X_{t-d}); DF = 3.45; F = 553.1; p < 0.0001$	3.10×10^{-6}	0.98
China	$R_t = f(X_{t-d}); DF = 1.00; F = 101.4; p < 0.0001$	0.00015	0.92
Latin-America and Caribbean	$R_t = f(X_{t-d}); DF = 3.29; F = 1528; p < 0.0001$	2.11×10^{-6}	0.99
Sub-Saharan Africa	$R_t = f(X_{t-d}); DF = 3.54; F = 39.10; p = 0.0004$	2.72×10^{-7}	0.94

which explains 94% of the variance with parameters $R_m = 0.11$, $C = -23.29$ and $a = 2.33$ (Fig. 2 C, Table 1; estimated $K = 12\,958$ million people). During the period 1200–1340 a negative relationship between per capita growth rates and population size is also observed (Fig. 1B), but there are few data points to fit a logistic model for this period.

Our results show that GAM models fit very well the negative relationship between per capita growth rates and population size for the period 1962–2007 in different regions of the world (Fig. 4A–E, Table 1). The sub-Saharan Africa is the only region of the world depicting a different pattern, there is a positive relationship for the period 1962–1987 revealing a phase with hyper-exponential growth (positive feedback) followed by a negative feedback process after the population reached 450 million people (Fig. 4F, Table 1). Nevertheless, the negative trend observed between population growth rate and population size is consistent for the other different analyzed regions (Table 1).

The PLS regression showed that global human growth rates appear to be determined by one factor of covariation among the seven variables, this factor explains 92.89% of the variance in the per capita growth rates (Table 2). The meaning of the components can be interpreted considering the weights attained by the variables. For example, variables indicating economic development, energy use, urbanization and population density showed negative effects on population growth rates (Table 2). On the other hand, variables representing “resources” such as water reserves and per capita arable land showed positive effects on per capita growth rates (Table 2). However, per capita food production showed negative effects on growth rates suggesting that this variable behave more similar to the economic and development variables than the resources variables (Table 2). The PLS regression models fitted to the India, China and Latin-America and the Caribbean areas showed the same observed pattern than at global scale (Table 2). However, the PLS regression for the high-income (OECD) countries and Japan showed

two PLS components (Table 2). The first component in the high-income countries explains 79.55% of the variation in growth rates, while the second component account for 10.56% of the variance (Table 2). In Japan, the pattern is similar, the first component explain 85.86% and the second component 6.5% of the variation in R (Table 2). In high-income countries, the loading weights indicate that variables showed the same effects as in the above PLS models for the first component, but the information content of the second component reveals that per capita income showed positive effects on growth rates, while CO_2 emissions and food production showed negative effects (Table 2). The PLS regression for Japan showed some slight differences, in the first component food production showed positive effects on per capita growth rates (Table 2), in the second component the positive effects of food production and CO_2 emissions showed the most important loading weights (Table 2). The PLS regression model fitted to sub-Saharan Africa was very different to the other regions, the first component account for 75.77% of the variance in per capita growth rates and the information content of this factor is given by only three variables, CO_2 emissions, food production and population density (Table 2). The positive effects of CO_2 emissions is the most important ($w_1 = 0.80$), while food production and population density showed negative effects (Table 2). The remaining 10.33% of the variance explained in the second component is more similar to the first component of PLS models from other regions and the total world population (Table 2). Resource variables such as water reserves, food production and arable land showed positive effects, while urbanization, population density, CO_2 emissions and income showed negative effects on per capita growth rates (Table 2).

Discussion

We showed different phases in the historical records of human population dynamics during the last twenty centuries.

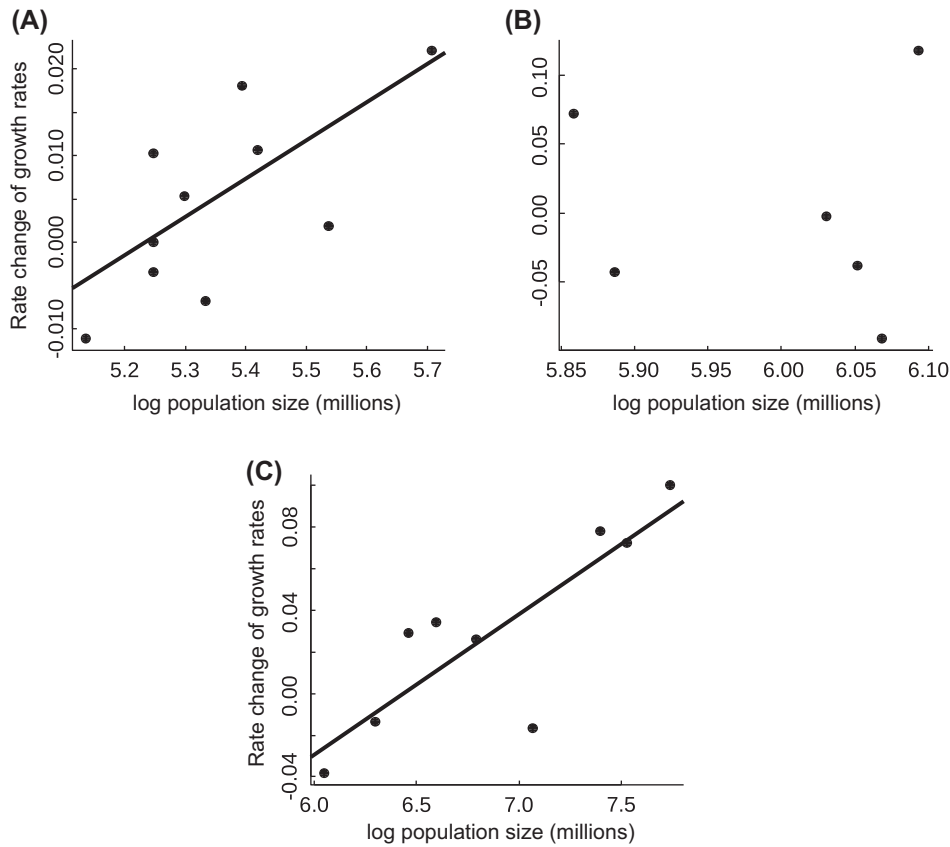


Figure 3. Fitted models of human population dynamics between the rate change of per capita growth rates (RG_t) and log of population size, (A) positive feedback phase of the period (AD 200–1100), (B) exponential growth during the period 1350–1650 showing no relationship between RG and log population size, and (C) positive feedback phase of the period (AD 1700–1940). See Table 1 for model details.

In most studies it is assumed that global population growth rate was close to zero or slightly positive previous to the industrial revolution (Diamond 1997, Galor and Weill 1999). However, some long-term fluctuations are evident, for example, the increase exhibited between the 9th and 13th centuries and the subsequent collapse observed during the 14th century (Galloway 1986, Turchin 2003b) and the recovery and collapse of Chinese and European populations during the period 1400–1700 (Zhang et al. 2007, Turchin and Nefedov 2009). The present study showed that using some analytical procedures and models from population dynamic theory, we were able to deduce some interesting patterns of historical human population fluctuations.

Two periods appear to be characterized by a positive relationship between per capita growth rates and population size, (300/400–1200 and 1700–1960), the positive feedback observed between population numbers and population growth supports the hypothesis of the fundamental role of human population size for triggering technological innovation, increased food production and economic development (Diamond 1997, Galor and Weill 1999, Johnson 2000, Hibbs and Olsson 2004). The idea that human growth population enhances the rate of technological change and food production (Boserup 1965, 1981) is in agreement with the earlier ecological concept of cooperative interactions and aggregations accentuating the growth of animal populations (Allee 1932). The Boserupian view of human dynamics explains the hyper-exponential population

growth observed during these two long periods of human dynamics and the good fit of logistic models in which carrying capacity is a dynamic variable influenced by population size (Cohen 1995, Meyer and Ausubel 1999). The signature of the industrial revolution is clearly depicted in the dramatic increase of population growth rates with population size during the period 1700–1960. During more than two and half centuries humans were able to exploit new food and energetic resources and improve health and life-expectancy as never before in history. Nevertheless, despite the dramatic increase in population growth rates during this period, the rate change of growth rate (second derivative) was able to reveal two important periods with slower than expected population growth rates. The period 1850–1900 corresponds to one of the coldest decades at the end of the Little Ice Age (LIA) (Jones and Mann 2004). On the other hand, the great depression and the beginning of the second world war could explain the lower per capita growth rates observed during the period 1920–1940. Although the industrial revolution appears to explain the cooperation phase in the global human population, the potential causes of cooperation during the period 500–1200 are less evident. One hypothesis could be related with the positive effects of the medieval warm period (MWP) on the population growth rate of humans during the period 800–1200. The simpler hypothesis is that climate warming and the improved food production achieved during this period cause an exponential growth in the human population. However, our results

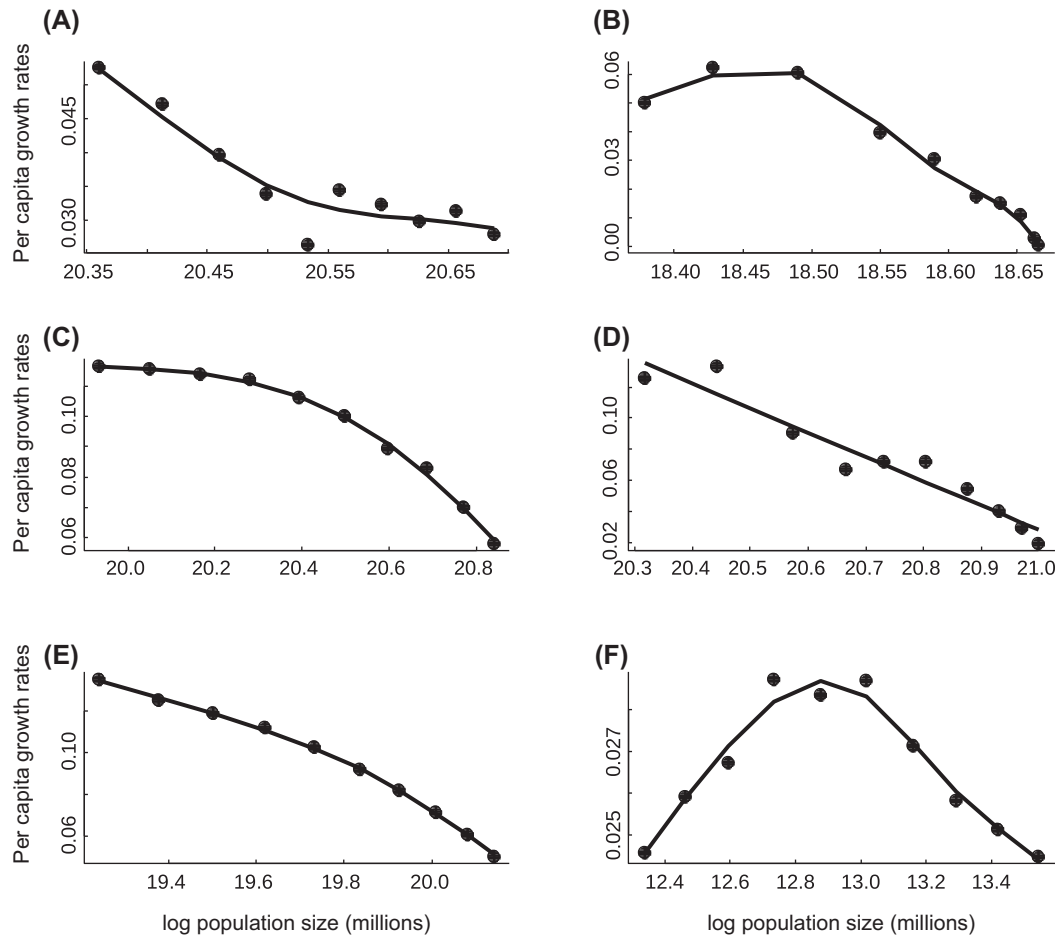


Figure 4. Nonparametric forms for the relationship between per capita growth rates (R) and population size during the period 1962–2007 obtained by using GAM models. Solid lines: fitted GAM model. See Table 1 for definition of variables and other details. (A) High-income countries, (B) Japan, (C) India, (D) China, (E) Latin America and the Caribbean, and (F) sub-Saharan Africa.

showed an important increase in per capita growth rates with population size suggesting that more people cause higher living standards (per capita growth rates) during this period. From population dynamic theory we know that this pattern is better supported by the cooperation hypothesis than simple exponential growth (Berryman 1999). Recent studies showed some indirect evidence that standard of living during the early middle ages was significantly better than during the period 1400–1700 (Steckel 2004, 2009, Koepke and Baten 2005, 2009). These studies showed a long-term U-shape of the human stature in northern Europe, with a minimum occurring near the 17th century. In fact, not until the early 20th century did northern Europeans attain their stature of the early middle ages (Steckel 2004). Our results suggest that during a long period of the early middle age, in particular during the MWP, human population size was an engine of agricultural change by improving land use and technology as predicted by the Boserupian view (Boserup 1965, 1981).

However, positive feedback loops yield unstable dynamics that cannot be persistent in time: the inflection point in the R -function observed during the period 1200–1400, and recently for the period 1965–1970, is a clear evidence that positive feedback changed to negative feedback mechanisms in human population dynamics. Our analysis showed that global human population size was almost stabilized around

420–440 million people during the period 1250–1350, when a negative feedback started to dominate human population dynamics and per capita growth rates decreased close to zero. However, human population collapsed at the beginning of the 14th century, which has been explained to be a consequence of climate cooling associated with the LIA, causing a severe decline in food production and subsequent famines, wars and spread of black pest (Zhang et al. 2007). This collapse can be interpreted as the consequence of non-additive effects of climate on population dynamics. This occurs when some exogenous factor (climate) influence the limiting resource (land productivity or area available for food production) and the population size is near the equilibrium point, any decrease in the limiting factor will cause a population collapse (Royama 1992, Berryman and Lima 2006, Lima and Berryman 2006). We can speculate that if the global temperature drop would have occurred between the 10th and 11th centuries, the dramatic collapse observed in the 14th century would never have happened. The explanation is because in this period human population was increasing and was far from the equilibrium population size. This hypothesis is closer to the view that climate change and population pressure interact to produce the past human population collapses (Lee and Zhang 2010). This phenomenon is quite well described in mammal species exhibiting severe

Table 2. Results of partial least squares regression analysis (PLS) carried out with the per capita growth rates of human population for the period 1962–2007 and seven predictor variables representing demographic, economy, energy use, development, food and natural resources. W1 and W2 are the loading weights of each variable in the first and second PLS regression components. R^2 = proportion of the variance in the response variable accounted by each component of the PLS regression. All predictor variables were standardized.

PLSR models	World		High-income OECD		Japan		India		China		Latin-America and the Caribbean		Sub-Saharan Africa	
	W1	W2	W1	W2	W1	W2	W1	W2	W1	W2	W1	W2	W1	W2
Water reserves	0.38	-0.18	0.40	-	0.40	-	0.36	-0.58	0.42	0.30	0.38	-0.18	-	0.41
Arable land	0.37	-0.37	0.36	-0.33	0.40	-0.11	0.36	-0.54	0.36	0.67	0.39	0.35	-	0.40
Food production	-0.41	-0.37	-0.41	-0.57	0.21	0.79	-0.38	-0.11	-0.38	0.26	-0.38	-0.47	-0.46	0.29
Gross domestic product	-0.40	-0.28	-0.32	0.55	-0.43	-0.30	-0.36	-0.36	-0.32	0.44	-0.37	0.11	-	-0.43
CO ₂ emissions	-0.27	0.74	-0.38	0.47	-0.33	0.47	-0.40	-0.24	-0.39	0.15	-0.36	0.66	0.81	-0.11
Urban population	-0.40	-0.21	-0.40	-	-0.39	0.19	-0.40	-0.40	-0.34	0.39	-0.38	0.37	-	-0.42
Population density	-0.40	-0.15	-0.38	0.17	-0.42	-	-0.39	-	-0.43	0.17	-0.39	-0.22	-0.34	-0.47
R ² %	92.89	3.37	79.55	10.56	85.85	6.5	96.02	2.22	91.34	3.66	98.30	1.12	75.77	10.33

collapses and irruptions (Berryman and Lima 2006, Lima and Berryman 2006, Lima et al. 2006, 2009) and it was described by Royama (1992) as “lateral perturbation effects”.

Human population dynamics during the last 45 years may be described by competition for limiting resources. At a global scale, the decrease in the per capita growth rates is caused by a dramatic reduction in fertility rates during the last 50 years (Coleman and Schofield 1986, Borgerhoff Mulder 1988), with the exception of sub-Saharan Africa, where the lower per capita population growth rates are also related with a severe decrease in the life expectancy during the last 20 years (Tabutin and Schoumaker 2004). In fact, the shape of the *R*-function phase plot of sub-Saharan Africa showed a very different pattern than the other regions of the world. A positive feedback appears to dominate the dynamics until the middle eighties, since then population growth rates have decreased with population density as in the rest of the world. This result is consistent with the hypothesis that complex and multiple factors are operating and the existence of a general explanation of this change in demography is controversial (Kirk 1996). For example, some authors have argued that fertility declines are caused by a decrease in human mortality rates (Kirk 1996), while others have postulated socio-economic forces – basically human capital becomes increasingly valuable as the society develops and there is a tradeoff between of quality over quantity of children (Galor and Weill 1999) – or cultural and educational factors among women (Bryant 2007). In addition, the decline in fertility rates can be an evolutionary response of humans to the new environment imposed by the modern postindustrial societies (Borgerhoff Mulder 1998, Mace 2008).

Nevertheless, few authors have postulated the idea that a negative feedback is now operating on human population dynamics (Wilson and Airey 1999, Lutz et al. 2006, Bauch 2008, Turchin 2009). In particular, despite humans are now living on average in much better conditions than ever before (Galor and Weill 1999, 2000, Johnson 2000), the negative relationship observed in the *R*-function strongly suggests that population size may be perceived as an underlying general force in reducing population growth (Lutz and Qiang 2002, Lutz et al. 2006). From our PLS analyses, at a global scale, predictors related to economic development such as income, CO₂ emissions, urbanization and population density correlate negatively with per capita population growth rates. This

pattern is robust for most of the different analyzed regions; this inverse relationship between economic wealth and population growth had fueled the vision that human population size can reach an equilibrium in the near future driven by socio-economic development (Galor and Weil 1999, 2000, Bauch 2008). However, the first factor in the PLS analysis also showed positive loadings of variables representing natural resources and ecosystem services (water reserves and arable land) suggesting that the depletion of natural resources is an underlying force combined with economic development (Dasgupta 2007). An interesting result is that food production showed negative loadings in most of the PLS analyses, suggesting the food is a proxy of economic development, and not a limiting factor. This result contradicts the hypothesis that human carrying capacity is mainly determined by food production (Bruinsma 2003, Hopfenberg 2003). On the other hand, the PLS analysis revealed a very different pattern in sub-Saharan Africa, the first component is composed by only three variables and the most important is the positive effect of per capita CO₂ emissions on population growth rates. This result strongly suggests that the trend in population growth rates of sub-Saharan Africa during the last 50 years is a direct response to the level of economic and social development of this continent. In this region of the world, people are less wealthy now than 40 years ago, economy productivity and energy use have declined in many areas of Africa (Dasgupta 2007) and human life expectancy have decreased in the last 20 years (Tabutin and Schoumaker 2004). The negative trend in population growth rates during the last 30 years in sub-Saharan Africa appears to be consequence of the decline in human and economic development which appears to be captured by per capita CO₂ emissions as a proxy of energy use. It is also interesting that the second component which explains a 10% of population growth rates is related to the negative effects of economic wealth, urbanization and population density and the positive loadings of natural resources, such as water reserves, arable land and food production. Behind the overwhelming effect of development, human population growth rates in Africa are still positively influenced by food and water, and negatively influenced by socio-economic factors.

The PLS analysis suggests that a combination of economic, social, cultural or psychological factors combined with natural resources is the underlying force driving the

observed negative relationship between population size and per capita growth rates (Lutz et al. 2006, Dasgupta 2007). Some authors have speculated that the observed reduction of fertility in modern societies can be interpreted as a consequence of the high demands on individuals and families required to maintain the modern production of food and other goods, and the energy consumption level in the complex economic and social system that human population experience today (Crenshaw et al. 2000). Our results support this idea, the present reduction in human per capita growth rates appears to be consequence of different limiting factors operating in combination around the globe, the sign of the effects appears to be similar for the different regions, except in Africa where the factors operating appears to be very different.

However, the fact that human population is now exhibiting logistic-like dynamics is not a strong support for the hypothesis that a stable equilibrium global population size will be achieved in the future (Cohen 1995, 2003). Dynamics characterized by a stable equilibrium point can only be produced by a first-order negative feedback loop. Ecologically speaking, what we need is an equilibrium between the per capita individual consumption and reproductive rates with the limiting resources renewal rates. This equilibrium can be difficult to attain considering the combination of different factors involved in determining population growth rates. From population dynamic theory, ecologists know that the depletion of natural resources, energy reserves and climate warming can produce delayed feedback loops and long-term cyclic oscillations (Berryman 1999, Turchin 2009). In Goldstone's demographic-structural theory and also in Turchin's models of agrarian societies, population growth is an indirect cause of social crisis for its impact on economical, political and social institutions (Goldstone 1991, Turchin 2003b, 2009). In fact, the time lag between the start of a cold climate phase and a population collapse had been increasing during the last thousand years in the agrarian societies of China, suggesting that more complex social and political structures can delay, but not prevent, population collapses (Lee and Zhang 2010). These indirect effects may cause a delayed feedback loop able to induce cyclic (second-order) population oscillations (Turchin 2009). In logistic predator-prey models, cooperation dominates the increasing phase of prey (and predator) dynamics causing the observed pattern in the *R*-function of human dynamics (Berryman 1999). Therefore, the possibility that the current human population dynamics is an underlying second-order oscillation, cannot be discarded and it should be considered as an alternative scenario for the future.

The idea of shifting limiting factors (Berryman 1999) gives us a general interpretation of some controversies in human demography and economy. It is well known in population ecology that cooperation and positive feedbacks can be observed at low population densities, while at high density competition and negative feedbacks dominate the dynamics (Berryman 1999). That is because the limiting factors operating on some animal species may shift according to population density. While cooperation at low densities in animal populations reminds us of the Boserupian view – that population growth induces economic development and higher standards of living – competition at high densities reconciles

ecology theory with the original Malthusian view (Lee 1987, Wood 1998). The idea that future human population will stabilize around 10–12 billion people in this century, is one of the two hypotheses that can be proposed for our future (Cohen 1995, 2003). However, the possibility of a future collapse caused by second-order oscillations should be taken into account as an alternative hypothesis; because history shows that population collapses and recoveries have occurred on a recurrent basis during the last 1000 years (Turchin 2009). Population dynamic theory can be an important tool for the diagnosis and understanding of human dynamics, as it provides a simple and general framework for analyzing and interpreting population growth data. Finally, it is important to remark that we are not supporting the idea of an ecological determinism in human dynamics, but that general principles from population dynamics can be useful to develop theories for dealing with demographic, social and economic changes in human societies (Turchin 2009).

Acknowledgments – ML acknowledges financial support from FONDAP-FONDECYT grant 1501-0001 (program 2). We thank Eduardo Fuentes for stimulating discussion and valuable comments on this manuscript, Lev Ginzburg gave valuable comments and suggestions to a previous version.

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