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Do we have to choose between feeding the human population and conserving nature? Modelling the global dependence of people on ecosystem services

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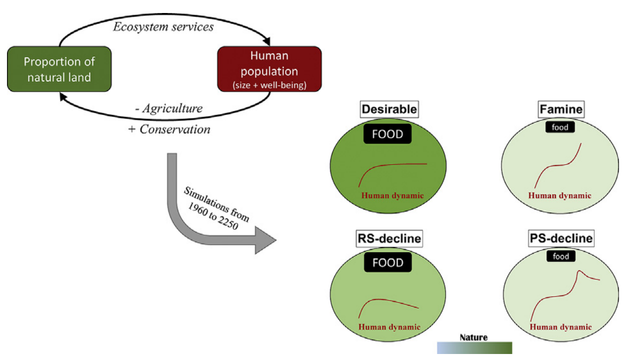
HIGHLIGHTS

- Human population faces a trade-off between food supply and ecosystem services.
- We modelled the common dynamics of human population and global proportion of nature.
- Famine and lack of regulating services are serious threats for the future population.
- Between the two, a desirable future exists with both food and ecosystem services.
- Nature conservation is crucial but needs to take food supply into account.

GRAPHICAL ABSTRACT



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ABSTRACT

The ability of the human population to continue growing depends strongly on the ecosystem services provided by nature. Nature, however, is becoming more and more degraded as the number of individuals increases, which could potentially threaten the future well-being of the human population. We use a dynamic model to conceptualise links between the global proportion of natural habitats and human demography, through four categories of ecosystem services (provisioning, regulating, cultural recreational and informational) to investigate the common future of nature and humanity in terms of size and well-being. Our model shows that there is generally a trade-off between the quality of life and human population size and identifies four short-term scenarios, corresponding to three long-term steady states of the model. First, human population could experience declines if nature becomes too degraded and regulating services diminish; second the majority of the population could be in a famine state, where the population continues to grow with minimal food provision. Between these scenarios, a desirable future scenario emerges from the model. It occurs if humans convert enough land to feed all the population, while maintaining biodiversity and ecosystem services. Finally, we find a fourth scenario, which combines famine and a decline in the population because of an overexploitation of land leading to a decrease in food production. Human demography is embedded in natural dynamics; the two factors should be considered together if we are to identify a desirable future for both nature and humans.

1. Introduction

Two thousand years ago, approximately 300 million people lived on Earth. After a millennium with no significant variations, the human

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population started to increase and reached one billion at the beginning of the 19th century. Between 1800 and 2000, it increased by more than 700% (UN, 1999). If population growth were to continue along the same trajectory, there would be 256 billion people in 2150 (UN, 2001). As of 1960, however, the global growth rate has been declining (UN, 1999), suggesting that the human population is not limitless.

The growing human population puts an expansive demand on land and resources. To supply people with habitation and infrastructure, urban land expanded from 1.1 to 2.8% of total land area between 1960 and 2007 (Hooke et al., 2012). To meet the food needs of the growing population, with a dramatic increase in consumption per person (Tilman et al., 2011), the agricultural area (crops, arable land and permanent pastures) has expanded from 35.0 to 38.6% between 1960 and 2007 (Hooke et al., 2012; Alexandratos and Bruinsma, 2012). In the same time, agricultural production per unit area nearly quadrupled (FAOSTAT, 2017; Green, 2005) thanks to the intensification of agriculture practices including mechanisation, use of fertilisers and pesticides. This intensification process from extensive to intensive farming has had a negative environmental impact (Green, 2005).

Degrading nature comes with several costs to the human population, as natural land provides ecosystem services, defined as "the direct and indirect contributions of ecosystems to human well-being" (Braat and de Groot, 2012). The Millenium Ecosystem Assessment classified ecosystem services into four categories (MA, 2003): provisioning services (e.g., food, fuelwood, fiber, genetic resources), regulating services (e.g., regulation of climate, disease spread, water and air quality, pollination), cultural services (e.g., recreation, education, spiritual, aesthetic or religious values of ecosystems), and supporting services (services that support others, such as biodiversity, soil formation, nutrient cycling).

Ecosystem services are associated with human well-being, an umbrella term that includes basic materials for a good life, freedom of choice, health, good social relations and security (MA, 2003). Provisioning services bring palpable benefits to human survival, such as food, drinking water or heating. Regulating services, such as air and water purification or disease control, increase well-being by improving health and safety (MA, 2003), especially in urban areas (Dearborn and Kark, 2010). Cultural services are also important for the health and well-being of individuals (Butler and Oluoch-Kosura, 2006; Daniel et al., 2012) as exposure to natural environments can improve cardiovascular, immune and endocrine health conditions (Bowler et al., 2010), provide a better psychological well-being (Fuller et al., 2007), and generally lead to a happier society (Diener and Chan, 2011).

The loss of ecosystem services is thought to have led to the collapse of several human civilisations in the past. The most famous case is Easter Island, where, according to Diamond (1994), the local human population increased to a maximum, estimated at above 10,000, around 1500 A.D., at which point the forest cover shrank to almost zero according to pollen records (de la Croix and Dottori, 2008). Subsequently, the soil eroded and it became impossible to farm. Moreover, animal populations (mostly birds) vanished because of intensive hunting and the disappearance of natural habitats. Finally, the population had nothing left to eat and collapsed as a result of an insufficient amount of ecosystem services that enable sustainable food production (Diamond, 1994). However, there exists an alternative explanation for the Easter Island collapse - the spread of disease brought by European colonisation (Hunt and Lipo, 2009).

Similar declines happened in non-isolated societies. For example, the Anasazi civilisation, living in the current USA South-West, vanished from its original living area 700 years ago because of deforestation and soil exhaustion, combined with a prolonged drought. Ancient civilisations disappeared about 10,000 years ago from the Fertile Crescent in Mesopotamia as a result of the increased salt content of the soil due to irrigation. Both civilisations damaged the soil irreversibly, and these two areas have remained deserts since (Diamond, 1994).

Modelling the link between nature and human demography has been used in several studies to better understand population collapses, especially in Easter Island. The earliest model, developed by Brander and Taylor (1998) was similar to a predator-prey Lotka-Volterra model with humans consuming a natural renewable resource. Later models added complexity by including social and economic processes such as technology improvement, individual responses to lack of food, and the price of goods and wood needed for construction (Türkgülü, 2008; Taylor, 2009; Reuveny, 2012). All these models highlighted the importance of nature, especially forest cover and soil fertility, in supplying food and other vital products to the human population. All were able to reproduce, to some degree, the collapse of the Easter Island society.

In his book, Diamond (2005) compared the Easter Island society to the current global human population and argued that it is possible to drive the global Earth system to a similar collapse by over-exploitation of land. This idea has been propagated by the recent breadth of publications describing "planetary boundaries", which conceptualises the overexploitation of the Earth's resources by humans in terms of the risk of destabilization. In particular, it has been suggested that biodiversity loss and land use change might lead to catastrophic consequences at the global scale (Rockström et al., 2009), although evidence for this hypothesis is still lacking (Montoya et al., 2018). Page (2005) criticised Diamond's theory and argued that the two societies are not comparable because of their vastly different scales and because of the diversity of current societies. Different societies might respond differently to an impending global collapse, and some efficient responses to stop the collapse might be found. However, Page acknowledged that some factors might prevent humans from responding to a risk of collapse, because, for instance, of the difficulty in anticipating the collapse, the complexity of the problem, the failure to recognise the problem in time and the failure to respond collectively.

One difference among current societies, compared with societies that collapsed in the past, is that some efforts are being made to conserve nature and ecosystem services. According to Alkemade et al. (2009), the protection of 20% of all large ecosystems would allow a reduction in the rate of biodiversity loss that might be enough to maintain a high level of ecosystem services. Restoration of natural habitats from degraded ecosystems also enhances biodiversity and regulating and supporting ecosystem services (Benayas et al., 2009). Thus, conservation is an important process to include in models aiming to study the future relation between nature and the human population.

As there exists a clear interdependence between people and nature through ecosystem services, it is important to study the coupled dynamics of these entities by considering humans as an important driver of the natural system dynamics. Although theoretical studies investigating the relationship between humankind and nature are beginning to emerge (Motesharrei et al., 2016), they are still scarce. Nitzbon et al. (2017) recently developed a model linking ecological (carbon sequestration, temperature), economic (fuel and biomass use, economic production and capital) and demographic (population size and well-being) variables. Lafuite and Loreau (2017) and Lafuite et al. (2017) built an ecological-economic dynamical model to study the effects of a time delay in the response of biodiversity and ecosystem services to human impacts on the sustainability of the coupled social-ecological system. In both of these studies, however, only a single ecosystem service was considered (carbon sequestration or food production). Here, we present a dynamical model of human-nature interactions in which humans depend on nature through a range of different types of ecosystem services. Our aim is to broaden our understanding of the connections between humankind and nature, and explore potential strategies for the management of natural systems.

2. Model and methods

2.1. Variables and ecosystem services

The model is a two-dimensional dynamical model involving the human population (H, in billion people) and the proportion of natural land in the Earth's total land surface, excluding ice (N). As in Hooke et al. (2012), natural land is defined as an unused (or light use) area with high biodiversity. Non-natural land, called exploited land, is defined as an area used by humans with low biodiversity, i.e., intensive agriculture, permanent pastures and urban areas. It also includes areas that are degraded naturally by events such as forest fires, floods or drought.

The model includes four types of ecosystem services following Braat and ten Brink (2008): provisioning services (hereafter PS), regulating services (RS), and cultural services, divided into recreational services (CR) and informational services (CI). Recreational services are defined as physical enjoyment provided by the ecosystem structure or components such as landscape, animal or plant species, and streams. Informational services include all the other cultural services such as knowledge and spiritual or artistic outcomes of nature. Braat and ten Brink (2008) suggested that these services are a function of the intensity of land use, from natural to degraded through light-use, extensive and intensive farming. In the function they suggested, RS and CI increase with nature and biodiversity. CR also increase with nature but if the land is too natural (i.e., pristine), CR are less accessible and drop. PS increase with the exploitation of land and thus decrease with the proportion of nature. But, when natural area is diminished, some supporting services such as biodiversity or soil fertility, and RS such as pollination or pest control, also dwindle and production efficiency ultimately decreases (Braat and ten Brink, 2008).

$$PS(N) = 50.5(0.0556 + 0.75N)^{0.337}.e^{-1.8-0.9N} - 3.155$$
$$RS(N) = e^{3.1(N-1)}$$
$$CR(N) = 0.295(22 - 20N)^2.e^{8N-8.8}$$
$$CI(N) = e^{3(N-1)}$$

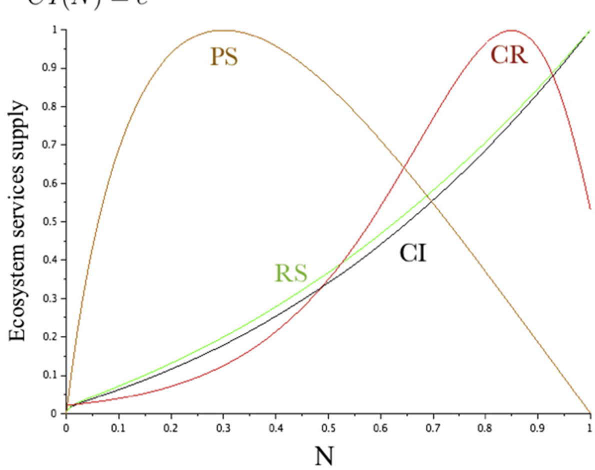


Fig. 1. Supply of four ecosystem services as a function of exploitation of land, with PS (provisioning services), RS (regulating services), CR (cultural recreational services) and CI (cultural informational services). We adapted the curves from Braat and ten Brink (2008). Benefits from ecosystem services (y-axis) are maximised at 1 for the purpose of our model. We calibrated the proportion of nature for which PS are maximal ($PS = 1$) to 0.3 based on the quantitative work of Morandin and Winston (2006). Equations of the curves used in the model are given above the graphic.

In our model, we used these curves, maximised at 1, to represent the supply of each ecosystem service as a function of the proportion of natural land on Earth (Fig. 1). We calibrated the value of natural land providing maximum PS to 0.3 based on a modelling quantitative work suggesting that the maximal production in an agricultural landscape is provided with 10 to 30% of natural land depending on the type of crops (Morandin and Winston, 2006).

2.2. Model

The model comprises two equations that describe the dynamics of the proportion of natural land and the human population respectively:

$$\frac{dN}{dt} = -P(N,H,t) - F(N) - A(N,H) + R(N) + C(N) \quad (1)$$

$$\frac{dH}{dt} = B(N,H,t) - D(N,H,t) \quad (2)$$

The various terms in these equations, respectively provisioning conversion ($P(N,H,t)$), natural degradation($F(N)$), anthropogenic degradation ($A(N,H)$), natural regeneration ($R(N)$) and conservation ($C(N)$) in Eq.(1) and birth ($B(N,H,t)$) and death ($D(N,H,t)$) rates in Eq.(2), are specified in the following sections.

2.2.1. Natural land

The conversion of land for food production, called provisioning conversion ($P(N,H,t)$), is a critical component of land use changes, given by

$$P(N,H,t) = \alpha \cdot N \cdot \left(1 - e^{-\beta \frac{H}{PS(N) \cdot Eff(t)}}\right) \quad (3)$$

α is the maximum conversion rate. Conversion is assumed to decrease exponentially with the available amount of food per person, $Q(N,H,t)$. This exponential term includes the parameter β, a coefficient describing the demand for converted land, based on the amount of food required per person. Between 1961 and 2014, the agricultural area increased by 10% while food production increased by 290%. A boom in land-use efficiency is responsible for the discrepancy between increases in land area and food production (World-Bank, 2008). The model takes into account changes in production efficiency, with a time explicit function ($Eff(t)$) corresponding to the amount of food produced per area unit a given year. The available amount of food per person is then $Q(N,H,t) = \frac{PS(N) \cdot Eff(t)}{H}$.

The increase in agricultural efficiency, however, has slowed down in high-income countries for several crops. For instance, Alston et al. (2009) showed a reduction in rates of yield growth for maize, rice, soy and wheat since 1990 and Ewert et al. (2005) suggested it could reach a maximum in the coming decades. This plateauing of production efficiency is already observable, all crops considered, in several high-income countries such as France, Japan, UK, Ireland, Sweden and Finland (FAOSTAT, 2017). As the future trend for agricultural efficiency is hard to predict, we included three possible trends, fitted to FAO efficiency data between 1960 and 2014, all assuming that production efficiency will not increase endlessly. The most optimistic scenario in our model is that production efficiency will double between 2014 and 2100, following a logistic growth curve. A second scenario also assumes logistic growth but stabilises at 1.4 times higher than in 2014. A third plausible scenario considered is a decrease in efficiency, which could be induced by the overexploitation of soil, the disappearance of non-renewable resources (fuel or phosphorus for instance) or the effect of climate change through frequent droughts, stress on plant physiology, pest spreads, or change in species composition (Wheeler and von Braun, 2013; Pimentel and Pimentel, 2008; Cordell et al., 2009; Easterling et al., 2007).

We modelled this scenario with a maximum efficiency of 1.5 in 2050 followed by a decrease eventually stabilising at the present value. The equations and curves for the three scenarios are included at the top of Fig. 6.

Natural land can be degraded through two other processes. The first one is natural degradation ($F(N)$), which occurs without human intervention through floods, forest fires, prolonged droughts or pest invasion (Braat and ten Brink, 2008). RS can prevent and decrease the frequency of these events (Braat and de Groot, 2012). The frequency of natural degradation events is represented by δ_n, where RS contribute to the ability of a system to resist or recover from natural degradation events. As RS tends to zero, natural degradation increases and as RS tends to one (maximum value), $F(N)$ is low ($0.1\delta_n$).

$$F(N) = \delta_n \cdot (1.1 - RS(N)) \cdot N \tag{4}$$

The second process is anthropogenic degradation ($A(N,H)$), which accounts for land degradation caused by humans through processes other than land conversion for food production, such as urban areas, roads and other transport infrastructure, bare soils or land used for energy production. Anthropogenic degradation is assumed to occur linearly at a rate δ_h:

$$A(N,H) = \delta_h \cdot H \cdot N \tag{5}$$

Exploited land can be converted into natural land through two processes, one natural (natural regeneration) and one controlled by humans (conservation). Natural regeneration ($R(N)$) depends on the degradation level of the ecosystem, particularly RS. Several civilisations collapsed because they degraded soils beyond sustainable levels, which prevented the ecosystem from regenerating (Diamond, 1994). As a result, we assume exploited land $(1 - N)$ to regenerate linearly with RS and to reach a rate of r when RS = 1.

$$R(N) = r \cdot RS(N) \cdot (1 - N) \tag{6}$$

Conservation of natural land ($C(N)$) can independently preserve one or several of the non-food related ecosystem services (RS, CR, CI). Therefore, this term is split into three parts:

$$C(N) = (c_{RS} \cdot (1 - RS(N)) + c_{CR} \cdot (2 \cdot CR(N)^2 - 2 \cdot CR(N) + 1) + c_{CI} \cdot CI(N)) \cdot (1 - N) \tag{7}$$

Regulating services (RS) are directly related to human survival (MA, 2003), thus we expect humans to protect nature when they lack RS even if they can also, to some extent, build artificial substitutes. Such is the case in urban environments where greater and greater efforts are made to protect green areas and biodiversity (Kowarik, 2011) in order, among other things, to preserve RS such as air purification (Dearborn and Kark, 2010). Thus, we assume RS-based conservation equals a rate c_{RS} when $RS = 0$ and decreases linearly with RS supply.

Teisl and O'Brien (2003) showed that people enjoying cultural recreational services (CR) are more likely to adopt pro-environmental behaviours. Thus, we expect conservation to increase with CR. On the other hand, we know that CR are an important part of human well-being (Bowler et al., 2010; Daniel et al., 2012). When these services are scarce, as in urban environments, big conservation efforts can be made to increase green areas and biodiversity (Dearborn and Kark, 2010). To consider these two opposite observations, we suggest that conservation will be high if CR are either very high (because people enjoying nature will preserve it) or very low (to increase human well-being). We used a parabolic function with a maximum of c_{CR} for $N = 0$ and $N = 1$ and a minimum of $c_{CR}/2$ for $N = 0.5$.

The recognition of nature and environmental issues is a prerequisite to conservation (Chawla and Cushing, 2007). Thus, we expect people to conserve more if cultural informational services (CI) are high. We assume CI-based conservation to be zero when $CI = 0$ and to increase linearly until reaching a rate c_{CI} when $CI = 1$.

2.2.2. Human demography

The human demography equation is split into two parts: birth rate ($B(N,H,t)$) and death rate ($D(N,H,t)$). The birth rate per country between 1960 and 2014 is negatively correlated with food supply (Pearson correlation test, $r = -0.76$, $N = 7388$, $p - value < 2.2 \cdot 10^{-16}$, Fig. S1), defined by the FAO as the amount of Kcal per capita per day. This correlation between food and birth rate is well known and has been documented earlier (Ali, 1985). The FAO database offers data for the world's net production of food per capita every year since 1961, which we scaled to fit the PS supply of our model in 2014 (see Box.S1 for data and details of this calibration). These data confirm the decrease in birth rate as the amount of food per person increases (Fig. 2, blue dots). However, the literature also suggests that when populations are severely lacking food, as in famines, the reproduction rate is reduced (Dyson, 1993; Kidane, 1989). Thus, we used a function with a steep increase of the birth rate at low amounts of food per person and decreasing after this peak (Fig. 2, blue line), qualitatively following Nitzbon et al. (2017). As these data are temporal trends, they include other social processes such as health care improvement and changes in religion and traditional values, which can modulate the decrease in the birth rate. Therefore, we did not fit the function to the data and used a function less steep than the trend showed by data. The birth rate used in our model is given by:

$$B(N,H,t) = (2.62(Q + 0.12)^{-6.4} + (Q + 0.12)^{-2.5}) \cdot 1.07 \cdot 10^{-6} \cdot Q^{0.6} + 0.0074 \cdot (1 - e^{-13Q}) \tag{8}$$

We considered the death rate to be a function of both PS and RS. Because death is unavoidable, the death rate must be positive even if RS and food provision are maximal, hence we included a constant minimum death rate, d_0. To parameterise this mortality function, we used a non-linear regression to reflect three mortality components (d_0, PS-dependent, RS-dependent), fitted to data on mortality and food per person (Fig. 2, red dots). Worldwide death rate decreased while the amount of food per person increased between 1961 and 2014. Therefore, we assumed the PS-dependent component of the death rate to be a logistic function, which decreases when the amount of food per person increases. This function includes two parameters, a, the steepness of the curve, and b, the amount of food per person at the inflection point. Death is also driven by RS as it increases when air and water pollution are high and epidemics are widespread (WHO, 2017; MA, 2003). We modelled RS-dependent mortality as a decreasing exponential function of RS, where c relates to the curve steepness. Maximal mortality, reached when the amount of food per person and RS are minimal, is $d_0 + d_M$, with d_M a parameter that we fixed at 0.1. The death rate (D) is given by

$$D = d_0 + f \cdot \frac{d_M}{1 + e^{-a \cdot (b - PS(N) \cdot Eff(t)/H)}} + (1 - f) \cdot d_M \cdot \left(1 - e^{c \cdot \left(1 - \frac{1}{RS(N)}\right)}\right) \tag{9}$$

where the constant f represents the relative strength of PS-dependent death over RS-dependent death. We investigated its

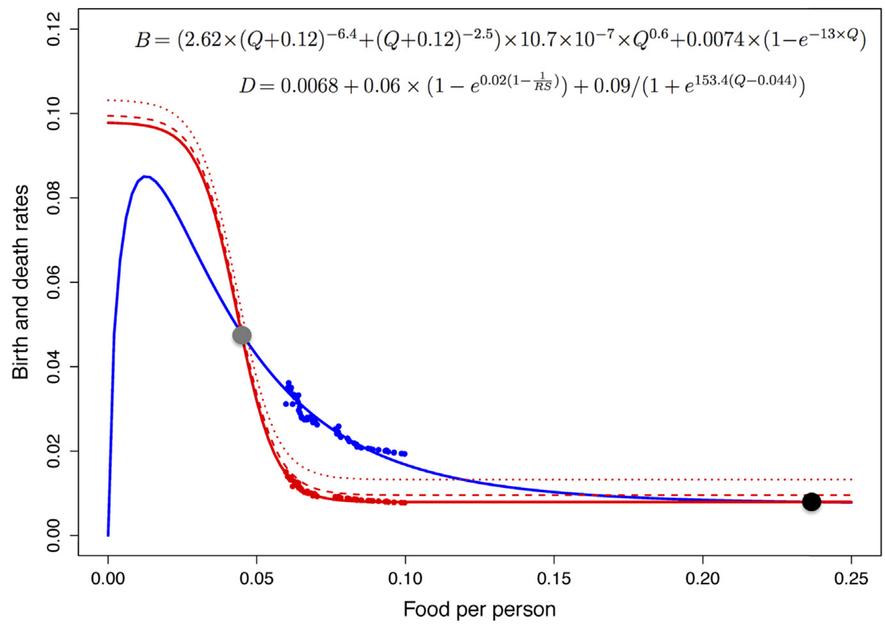


Fig. 2. Birth (blue) and death (red) rates as functions of net worldwide production of food per person. Blue and red dots represent global data (one dot per year between 1961 and 2014, data from FAOSTAT (2017) for food supply and World-Bank (2017) for birth and death) and lines represent functions used in the model. The death rate equation was fit with parameter $f = 0.6$ and also varies with RS. For comparison, we hold RS constant at 0.52 (solid line), 0.3 (dashed) and 0.15 (dotted). Grey and black dots show human population equilibria, for low and high food per person, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

effect through sensitivity analysis, presented in the appendix. The resulting equation for $f = 0.6$ is presented in Fig. 2.

When the amount of food per person is high, we assumed that the birth and death rates are equal, as is currently the case in Europe (Fig. S2).

2.3. Model analysis

The model was implemented under Scilab (Scilab Enterprises, 2012) and outcomes of simulations were analysed under R 3.3.1 (R Core Team, 2016).

Phase portraits and isoclines were drawn and analysed graphically, but it was not possible to go further analytically due to the complexity of the model. Hence, most of the results are based on simulations.

A range of reasonable values were arbitrarily fixed, based on exploratory simulations (Table 1), to explore potential future scenarios. Parameter sets were then categorised into realistic and unrealistic simulation scenarios, based on natural land cover and human population trends between 1960 and 2014. Simulations were deemed realistic if, by 2014, the human population was between 6 and 8 billion (the 2014 population was estimated at 7.261) and the proportion of nature was between 0.55 and 0.63 (the calculated natural land area is 0.614). We stopped the simulations in 2250 and analysed their outcomes even if a steady state was not reached.

A baseline value, arbitrarily chosen around the middle of the parameter range, was attributed to each parameter (Table 1). The quantitative importance of all parameters was analysed using a linear regression model. Four different scenarios in the simulations were identified and analysed, for which we were able to classify parameter sets depending on the model trajectory. To do so, we distinguished parameters we were most interested in, referred to as highlighted parameters, which are involved in the tension between nature conservation and food supply (conservation and provisioning conversion parameters) from other parameters (natural regeneration, degradation parameters, importance of PS in death). The effects of highlighted parameters were analysed using a parameter plot and plots representing the parameter value against human population

Table 1
Definitions, reasonable ranges and baseline values of model parameters.

Parameter	Definition	Range	Baseline value	Unit
α[a]	Maximum provisioning conversion rate, reached when food per person tends to 0	0.005–0.23	0.02	1/t
β[a]	Provisioning conversion exponential coefficient	0.005–0.035	0.015	
δ_n	Natural degradation rate	0.0001–0.001	0.0006	1/t
δ_h	Anthropogenic degradation rate	0.0001–0.001	0.0005	1/t
r	Natural regeneration rate	0.001–0.01	0.007	1/t
c_{RS}[a]	Conservation rate for regulating services (RS)	0–0.017	0.008	1/t
c_{CR}[a]	Conservation rate for recreational services (CR)	0–0.017	0.008	1/t
c_{CI}[a]	Conservation rate for informational services (CI)	0–0.017	0.003	1/t
f	Relative importance of PS over RS in death rate	0.5–0.8	0.6	

[a] Indicate highlighted parameters, which are involved in the tension between nature conservation and food supply.

and food per person. We conducted a sensitivity analysis to check for the influence of other parameters (i.e., not highlighted parameters) on our results and conclusions.

3. Results

3.1. Steady states and stability

To study the behaviour of the model over the long term, phase portrait analyses were generated, keeping food production efficiency held constant at two (the saturation value) to remove the time explicit term, which only impacts the first 150 years.

The human population equilibria can be categorised into two different types. The first equilibrium category occurs with a low amount of food per person, when the population is starving, which leads to an increased death rate (Fig. 2, grey dot). The second equilibrium category occurs when the population has enough food per person to decrease its birth rate to the same level as the death rate (Fig. 2, black dot). These two equilibria lead to two different human isoclines in the (H, N) phase space (Fig. 3 b and d). The higher human isocline (solid line) represents human equilibria with a low amount of food per person, the maximum human population at equilibrium is reached when $N = 0.3$ because PS are maximal at this point. The lower human isocline (dashed line) represents human equilibria with a large amount of food per person.

To reach a steady state, the model has to reach one of these human equilibria, together with an equilibrium for the natural system. The natural equilibrium results from a trade-off between N and H, as a high human population exploits land heavily, leading to a low N equilibrium. In contrast, if H is low, N is high at equilibrium.

The H isocline can vary with the f parameter (the weight given to the impact of PS/RS on death), but all other parameters do not directly influence the H isocline, as they are not included in the H differential equation. On the other hand, the N isocline shifts with many parameters, including the highlighted parameters, which are involved in the tension between nature conservation and food supply (Table 1) ; therefore, the highlighted parameters indirectly influence

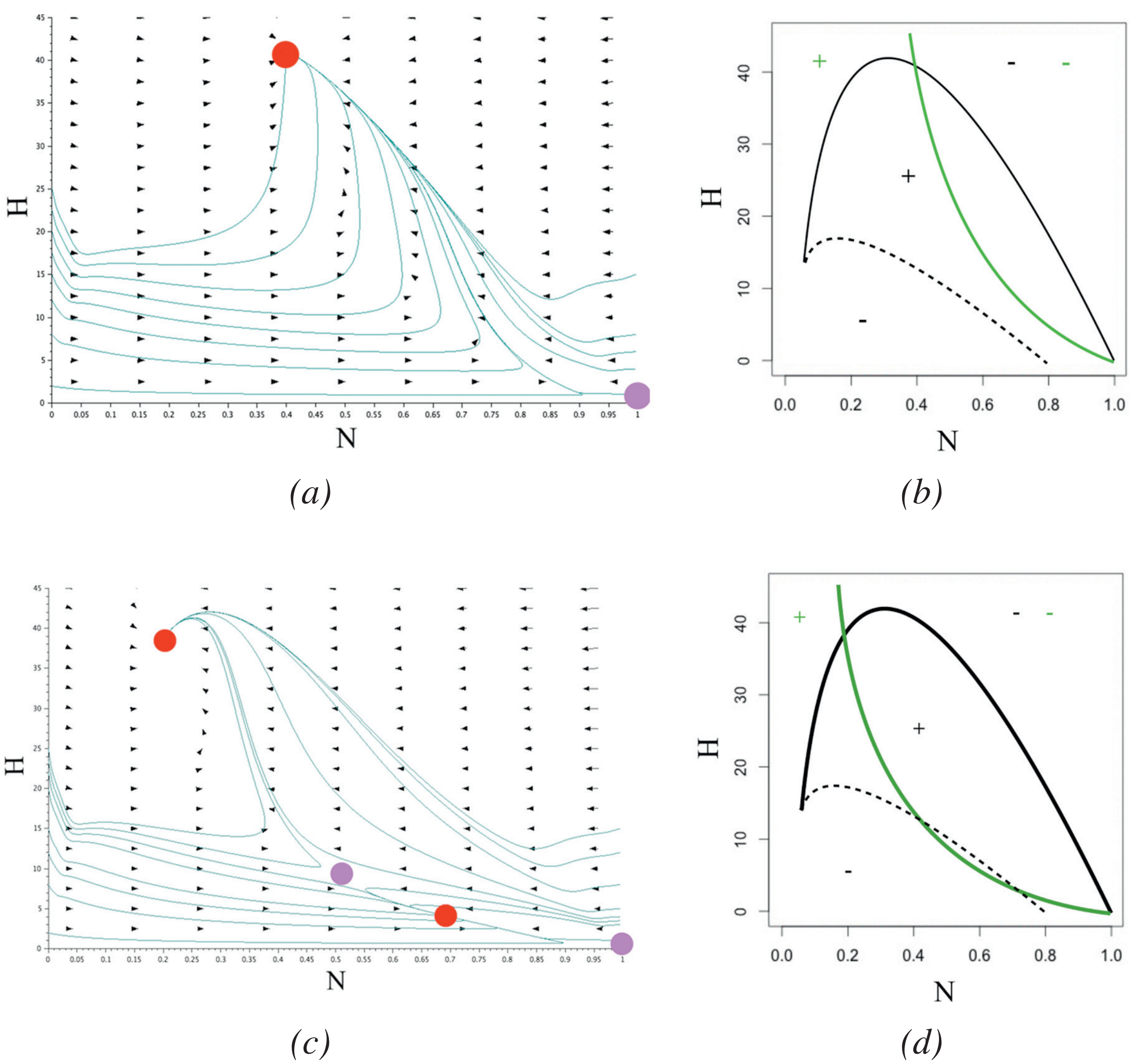


Fig. 3. Phase plot (a, c) and isoclines (b, d) for the model with two steady states (a, b) or four steady states (c, d). In the phase plots, blue lines show trajectories for different initial conditions after 200,000 years and red dots indicate the stable steady states, whereas purple dots show saddle points. For isoclines, black lines represent the H isocline (solid for low food isocline, dashed for high food isolcine) and green lines show the N isocline. + and − refer to an increasing or decreasing H (black) or N (green). Efficiency was fixed at 2 to remove the time explicit term. When N and H are both low, food per person is high while RS are low; therefore mortality is higher when RS are lacking, contrary to birth rate, which is low. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the H steady states through the N isocline. Depending on the parameter set chosen, the N and H isoclines will intersect to create two or four steady states (Fig. 3).

The trivial steady state ($N = 1, H = 0$) is always a saddle point and can only be reached when the initial human population is zero.

When only two steady states are possible, the N isocline does not cross the high food H isocline (dotted line). The non-trivial steady state is then stable and reached with a high human population, a low amount of food per person and a low proportion of natural land. The high food steady state does not exist in this case, as not enough food is produced to reach the point where the birth rate decreases to the level of the death rate. When four steady states are possible (Fig. 3, bottom), the N isocline crosses the high food H isocline at two points, adding two steady states. The steady state with the lowest human population is stable and reached with a large amount of food per person along with a high proportion of natural land. Between the two stable steady states, there is an unstable steady state, with an intermediate human population (about 10 billion people), an intermediate proportion of natural land (around 0.5) and a large amount of food per person. Although this steady state is unstable, both model variables can plateau around this point for several millennia before shifting to one of the alternative stable steady states. Across the entire parameter space, this steady state, with relatively high levels of food per person and natural land, was always reached with a human population under 15 billion people.

Although the stability of the steady states gives important insights into the long-term behaviour of the model, they provide no information about the transient states humanity might experience in the next decades or centuries. We then focused on the short-term transient dynamics of the global system, between 1960 and 2250, to gain insights into human population trends in the near future.

3.2. A trade-off between human population size and quality of life

After running the model through the entire parameter space, and selecting only realistic simulations, a clear trade-off between population size in 2250 and the amount of food per person, appears (Fig. 4a). Many simulations reach a high population, around 30 billion people with a maximum of 42 billion. In these simulations, the population suffers from famine as the low food human equilibrium is reached.

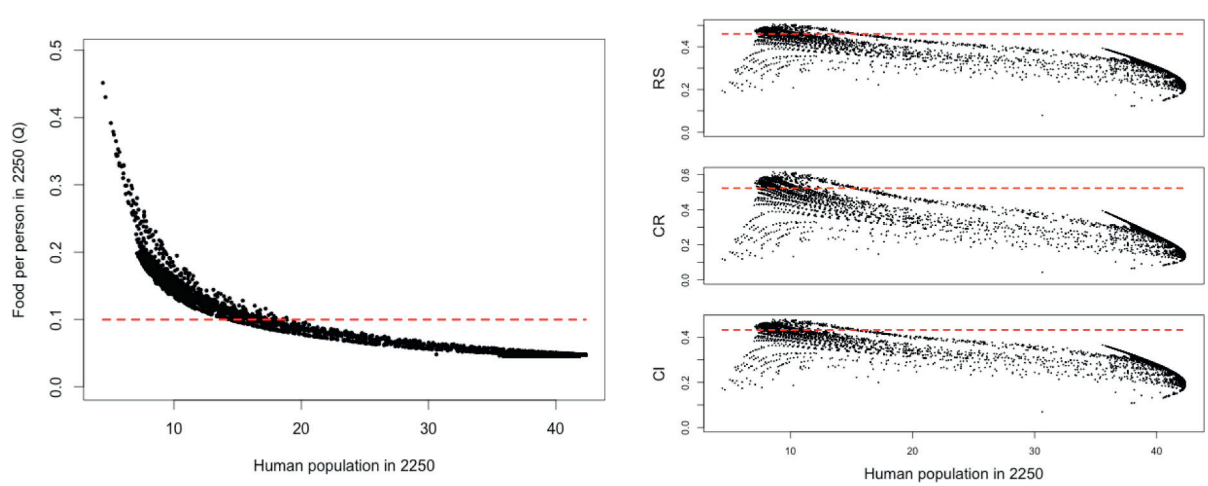
A higher population size by the end of the simulation also has a negative impact on the supply of regulating services (RS), cultural recreational services (CR) and cultural informational services (CI) (Fig. 4b) as a result of a high human-induced degradation of natural land. Some simulations, however reach a low human population and low levels of ecosystem services, as a result of excessive degradation of natural land, to such an extent that the human death rate increases from a lack of RS, which in turn generates a decline in the human population.

3.3. Different human-nature dynamics

Based on this trade-off between population size and quality of life, we identified four different human population trajectories between 1960 and 2250: desirable future (no famine, no decline in the human population), RS-decline (no famine, population decline induced by the lack of RS), famine (famine, no decline in the human population) and PS-decline (famine and population decline induced by a decrease in PS), represented in Fig. 5. The desirable future and RS-decline scenarios never lead to a large population because the large amount of food per person allows the birth rate to decrease to the death rate. The desirable future scenario corresponds to the trajectory approaching the alternative saddle point with a large amount of food per person by 2250, before shifting to one of the two stable steady states in the long run. The RS-decline scenario corresponds to the trajectory approaching the stable steady state with a decline in the population induced by the lack of RS, such as air and water quality regulation or pest and disease control (Fig. 3).

In the famine and PS-decline scenarios, which correspond to trajectories approaching the low food stable steady state, by 2250, the human equilibrium is reached when a notable decrease in the amount of food per person leads to an increase in the death rate. The PS-decline scenario only occurs when food production decreases, either because of a decline in PS or in food production efficiency ($Eff(t)$), which leads to a population decline.

To categorise simulations within these four scenarios, we define a decline in human population as a decrease greater than 200 million people between the maximum population attained over the simulation and the population size in 2250. We define famine as a state



(a) (b)

Fig. 4. Trade-off between global population size in 2250 and food available per person (a) and non-food related ecosystem services (b). Each dot represents the outcome of a different simulation along the parameter space under the assumption of doubling efficiency. The red lines show the 2014 levels of food per person (a) and ecosystem services (b) respectively.

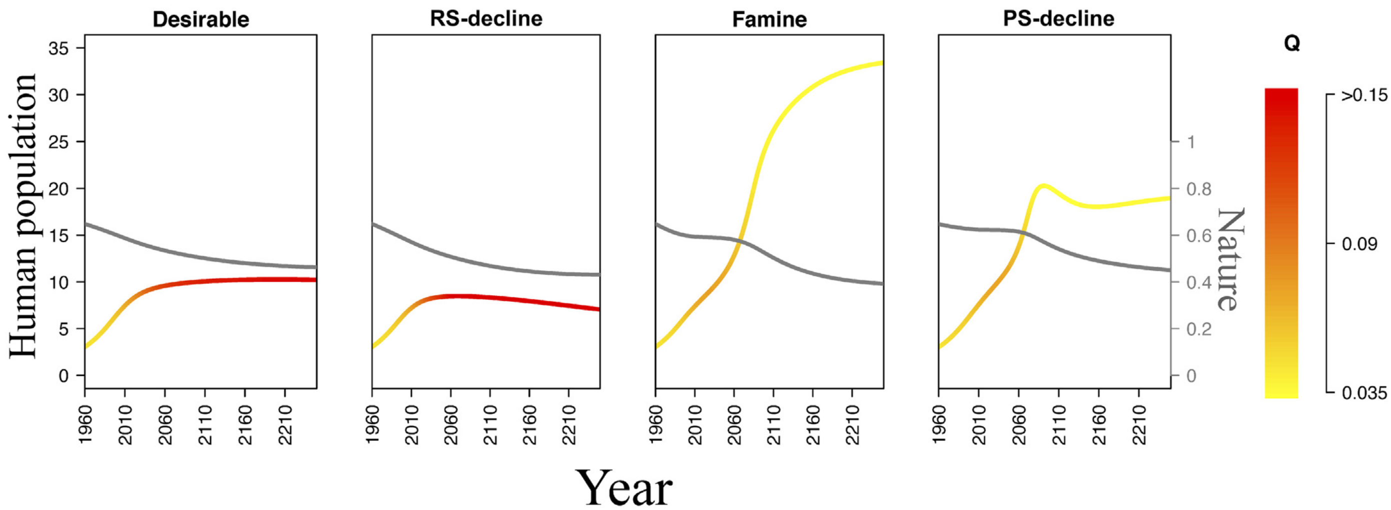


Fig. 5. Typical dynamics for the four scenarios after 290 years of model simulations. The grey line represents the proportion of natural area, the coloured line represents human population size (in billion individuals). The shading shows the food available per person as $Q(N,H,t) = PS(N).Eff(t)/H$, red reflects high food per person and yellow reflects low food per person. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

in which food per person falls below what was available in 1960 (0.0584, FAOSTAT, 2017).

3.4. Effects of parameter values on system behaviour

To understand the effects of the various parameters on the behaviour of the system, we set all the parameters to their baseline value (specified in Table 1), except for two parameters that are varied along a continuum in the parameter plane. Fig. 6 shows parameter planes for highlighted parameters, α,β (provisioning conversion parameters), c_{RS}, c_{CR} and c_{CI} (conservation parameters). Provisioning conversion parameters, α and β can either drive the system to one of the steady states with high food per person if the values are high, or to famine if they are low. RS-decline is reached with higher values of α and β than desirable future. With a very high land conversion rate, ecosystem services would be extensively degraded causing increased mortality from a lack of RS, ultimately leading to a population decline. Both α and β heavily influence conversion of land and as such play a critical role in determining the future size and well-being of the human population.

The three conservation parameters (c_{RS}, c_{CR} and c_{CI}) have similar impacts on the behaviour of the system (Fig. 6). With high conservation, the RS-decline scenario is less likely than with low conservation. Thus, conservation prevents nature from excessive degradation, which in turn increases the supply of non-food related ecosystem services (RS, CR and CI). However, more conservation can also drive the system to famine as it can slow provisioning conversion to such an extent that nutritional requirements are no longer met. In this case, the high food equilibrium cannot be reached. For the three conservation parameters, the slope between RS-decline and desirable future is less steep than between famine and desirable future (Fig. 6). Thus, conservation has a greater influence on the RS-decline/desirable interface, whereas α (maximum provisioning conversion rate) more strongly impacts the famine/desirable interface.

The doubling efficiency assumption (first column of Fig. 6) allows the human population to easily reach the equilibrium where birth and death rates balance each other, suggesting that increased food production efficiency reduces the risk of famine. Under the 40% increase efficiency and the declining efficiency assumptions (columns 2 and 3 of Fig. 6), the famine scenario occurs with a greater frequency because it is harder to reach an equilibrium with a large amount of food per person, given the limited food production. Thus, the higher future food production efficiency will be, the greater the threat of RS-decline over the threat of famine will be.

The PS-decline scenario occurs only under the assumption of declining efficiency. In this case, the starving population sees the amount of food per person decrease, leading to an increased death rate and a decline in the human population size.

To check the sensitivity of these results to various parameter values, especially non highlighted parameters (Table 1), we have run the model across all the parameters' space under the doubling efficiency assumption and analysed the output. All parameters had a significant influence on N and H by the end of the simulation (Table S1). However, varying the parameters did not have a qualitative impact on the outcome (i.e., the same trends emerge under different parameter selection) or the effect of conservation and provisioning conversion parameters (Fig. S4). If we shift the natural land cover providing maximal PS from $N = 0.3$ to $N = 0.4$ on Fig. 1, conservation can have a positive effect on food per person as it prevents land from being over-exploited and food production from decreasing (see Box. S2).

4. Discussion

The model shows two potential future paths for the global human population, with markedly different well-being standards, corresponding to the two stable steady states reached by the model. In the first case, the human population stabilises when the amount of food per person is low, increasing the death rate to such a point that it balances the birth rate. Alternatively, a smaller population can be maintained with a large amount of food per person if the birth rate decreases to such a point that it equals the death rate, a trend that is presently observed in many high-income countries, especially in Europe.

Famine occurs if the high food equilibrium is not reached quickly, as the birth rate is high when the amount of food per person is low. This paradoxical demographic response to a lack of food is well-documented in contemporary societies (Ali, 1985; UN, 2015). Alexandratos and Bruinsma (2012) suggested that it may be a problem in the future for countries with low food resources. For instance, the population of Niger is projected to increase from 14 million in 2006 to 58 million in 2050 although people have been suffering from undernourishment and low food security for decades. Based on this demographic response, our famine scenario leading to

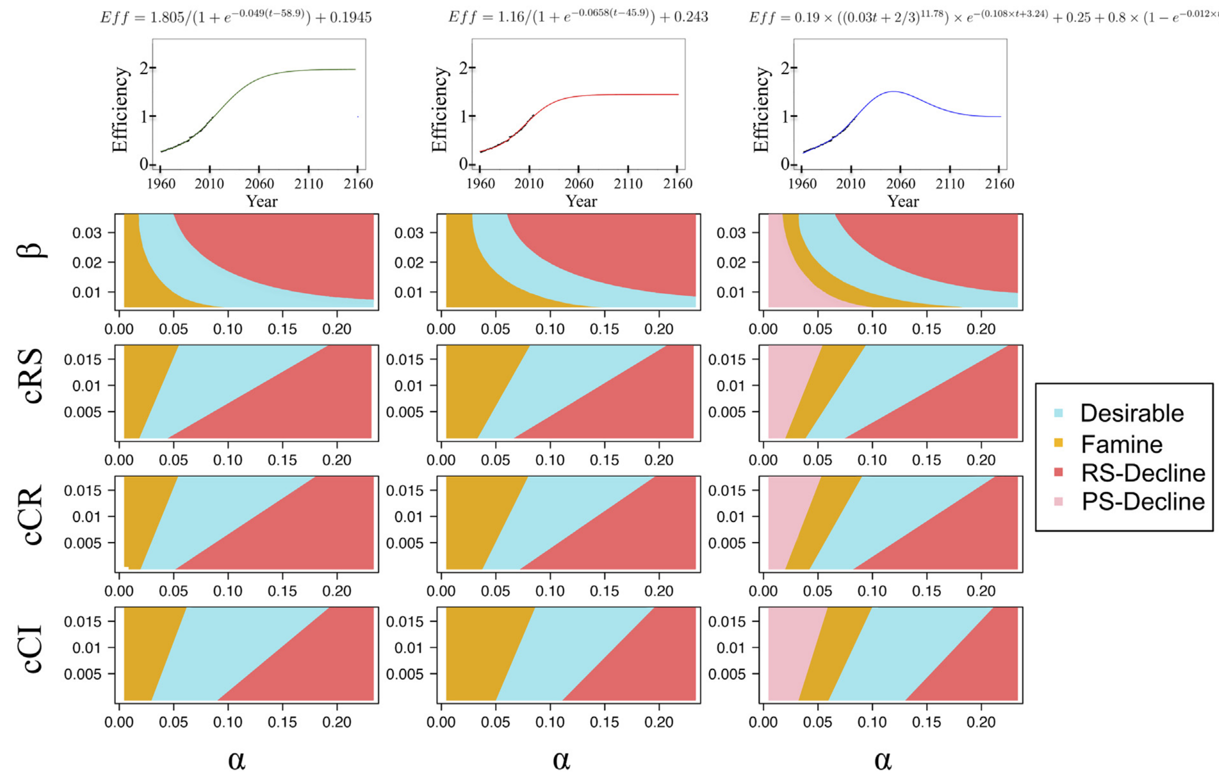


Fig. 6. Parameter plots showing the impact of α, β (provisioning conversion parameters), c_{RS}, c_{CR} and c_{CI} (conservation parameters) on human population. For each value of the varied parameters, the colour of the plot shows the scenario reached by the end of the simulation. Three trends of food production efficiency have been tested: doubling efficiency, low increase, decline in efficiency, they are represented on the top of each column with formulas above and black dots showing past data from FAOSTAT (2017). All other parameters are fixed to their baseline value, given in Table 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

a large population because of a vicious circle between the amount of food per person and the growth rate, does not seem unreasonable, although it has not yet been described in the scientific literature to our knowledge.

In addition to the lower quality of life induced by the lack of food, famine also has a negative effect on nature. Indeed, a malnourished population has a high birth rate and while the population increases, people convert more natural land into agricultural land to increase food supply. Because of this trade-off between human population size and both food availability per person and nature, helping low-income countries to reach the high food equilibrium is a way of bringing both humans and nature to a brighter future. This trade-off is consistent with Cohen's (1995) view that there is not a single value for the human carrying capacity, but that it depends on the quality of life, in terms of food and natural environments. In our model, famine is mainly induced by a low conversion of natural land into agricultural land as it prevents the population from satisfying its food needs. On the other hand, famine also happens when conservation, as defined in our model, is high. This is explained by the same process: if conservation is too high, the population cannot get enough agricultural land and lacks food. The assumptions leading to such an effect of conservation will be discussed further, but we note that situations of extreme food scarcity might lead to poaching or political pressure for the degazettement of protected areas. This could alter conservation efforts, leading to a more rapid decline in conditions (poaching), or generate amendments to allow greater food provision (political pressure) (Adams, 2004).

Our model shows that famine is not the only threat to humans. If nature is over-exploited, humans might experience a population decline because of a lack of regulating services (RS) such as air and water quality regulation, disease regulation and biological control (MA, 2003). In this scenario, which we called RS-decline, the human population tends to reach the high food equilibrium, but as nature becomes too degraded, its death rate increases from a lack of regulating services and the human population eventually declines. Tonn (2009) suggested that nature degradation, biodiversity loss or climate change could lead, or contribute, to a collapse or a significant decline in the human population. Even a simple decline of the human population might be the end of human life as we know it, as it is likely to significantly alter social structure. This scenario is driven by an intense agricultural conversion and a low level of nature conservation. It is an illustration of a world where natural land is inadequately taken into account and food is the main focus of the population. In our model, conservation can prevent the human population from reaching this RS-decline scenario.

Striking the right balance between food production and regulating services is essential for creating a desirable future. This scenario is only possible with a relatively small human population, around 10 billion people. This population size matches UN predictions ranging between 9 and 13 billion people in 2050 before plateauing (UN, 2015). It occurs when provisioning conversion is efficient enough to avoid famine but when nature is sufficiently preserved to provide regulating services and avoid a decline in the population. Reaching this equilibrium between ecosystem services and food, has been identified as an important target in order to reach sustainable development at the international level. Indeed, UN Sustainable Development Goals include both natural targets (e.g., life on land, life below water, climate action) and well-being targets (e.g., zero hunger, good health and well-being, reduced inequalities) (UN, 2016). This desirable scenario, however, is unstable in the long term, suggesting that avoiding both famine and lack of RS needs constant attention to stay close to the desirable future steady state.

Technology has played an important role in food production and population growth throughout history and never has it been as crucial as in the last 60 years. Our growing population depends on high agricultural yields. If agricultural production efficiency were to decline below current levels, the over-consumptive and large population would decline as a result of famine. For example, our model shows that if technological advances were unable to counteract the degradation of natural land, such that provisioning services decrease as a result of declining regulating services (soil fertility, pollination, pest control) (Braat and ten Brink, 2008), the population would decline. We called this scenario PS-decline. We found that in such cases, conservation of regulating services has a positive influence. In an alternative hypothetical scenario, agricultural efficiency could decrease in the future as a result of processes such as climate change and the disappearance of resources needed for mechanised agriculture. In this scenario, the human population suffers from famine and declines.

Our model does not predict a complete collapse of the human population under a realistic set of parameter values based on ‘sloppy sensitivities’ (Gutenkunst et al., 2007). However big declines in the population could happen under the RS-decline scenario if nature were highly degraded. This is mainly because natural land requires many years to regenerate, if it can return to the original state at all, and further requires a decrease in anthropogenic pressure. Population declines can also happen under the PS-decline scenario, if the efficacy of harvesting, distributing, and extracting goods falls drastically; as was the case on Easter Island when production efficiency dropped (Türkgülü, 2008), it could nearly collapse the entire global human population.

Future changes in agriculture's efficiency are very uncertain. Production efficiency per hectare is slowing down for several major crops such as maize, rice, soy and wheat (Alston et al., 2009). Moreover, data from the FAO suggest a plateau in total production efficiency in high-income countries such as France, Japan, UK, Ireland, Sweden and Finland (FAOSTAT, 2017). Therefore, it seems unreasonable to think that agricultural efficiency will keep its exponential increase. We made two saturating assumptions, one with double the current efficiency level and one with a lower efficiency (plateauing at 1.4 times its current level). Our model suggests that famine is a greater threat to the human population under the low efficiency assumption because when efficiency saturates, it becomes more difficult to increase the amount of food per person. If the population is not yet stabilised when efficiency plateaus, the risk of going to a global famine is high. A third possibility considered is a decrease in production efficiency. This would amplify the risk of famine and could lead to a PS-decline scenario. Even though it may seem impossible, with our current technology, to have a decline in agricultural efficiency, several problems could lead to this chaotic eventuality. Several studies suggest that climate change can have a negative effect on agricultural production because crops will not be adapted to the new climatic conditions in terms of temperature or precipitation (Wheeler and von Braun, 2013; Ainsworth and Ort, 2010). Another issue that agriculture could face is the disappearance of a non-renewable resource, such as fuel, which is necessary for mechanised agriculture (Pimentel and Pimentel, 2008), or phosphorus, a key fertiliser that is becoming scarcer and might be depleted in 50 or 100 years (Cordell et al., 2009).

Our model is based on the relationships between ecosystem services and the natural land that Braat and ten Brink (2008) drew from the literature. We assumed these functions to be correct on a proportion of natural land gradient and we did not study the effect of small changes in the functions. The decreases in regulating and cultural services with nature degradation and biodiversity loss are well-documented (Ehrlich and Ehrlich, 1981; Balmford and Bond, 2005; Díaz et al., 2006). The biggest uncertainty relates to provisioning services, which we assumed to increase almost linearly until a given percentage of natural land remains, and then decline because of the lack of regulating services such as pollination, pest control and soil fertility. Predicting the response of provisioning services to land conversion is difficult without including an explicit spatial component (Nelson et al., 2009), which is not included in the model.

Our model makes a number of simplifying assumptions, such as the description of land-use in two categories (natural or exploited), a homogeneous human population, and the omission of several social factors. Thus, our model was not designed to have a strong predictive power; improving the predictive power of such models will be a key point for further research in order to be able to guide policy decision. Our goal here, was to conceptualise and model the links between human demography and nature through ecosystem services, and to highlight the interdependence between these two variables.

The first simplifying assumption was to omit ocean surfaces from the model even though these can provide both food and ecosystem services and therefore be involved in the trade-off between feeding populations and conserving nature.

Second, in choosing a non-spatial model, we made a homogeneity assumption about land quality. Here we described land as made up of two categories, natural and exploited land. However, in reality there is a mix of land varying from pristine to fully degraded land, including diverse intensification levels in agriculture. Our simplifying description led us to define conservation as a transformation from exploited to natural land, which tends to reduce food supply. Our model cannot distinguish between qualitative properties of land, for example the difference between urban centres and degraded agricultural land, or organic farming and extensive farming, which may either over- or under-estimate food production and conservation needs. Moreover, this assumption ignores that land production capacity is not homogeneous across space and that protected areas are often located in low-production areas (Joppa and Pfaff, 2009). These simplifying assumptions were implemented in order to build upon Braat and ten Brink's work.

Our third simplifying assumption is the homogeneity of the human population. In the model, all humans have the same amount of food, the same level of ecosystem services and the same demographic rates. This disregards spatial heterogeneity and inequalities in food supply between humans despite the significant real world disparities (Alexandratos and Bruinsma, 2012). Currently some areas, such as Europe and North America, have a high food availability combined with low birth and death rates while other countries in Africa or Asia suffer from famine and bad health care. Reducing inequalities by helping economically developing countries to meet their food, health and educational needs could reduce their growth rate and help the global population to plateau at a lower size (UN, 2001).

Finally, the model does not take into account a number of social factors, that are likely to affect human demographic rates, such as religion, health care, education and war (Ali, 1985; Tonn, 2009). This was a deliberate choice as our goal was specifically to explore the dependence of human demography on nature and ecosystem services. This means that the only social factors considered are included implicitly in food production efficiency or in birth and death rates. The functions we used, however, were designed based on current observations. Although they might be inexact quantitatively, we believe they are qualitatively consistent.

Perhaps the most uncertain factor in our model is how the birth rate might change when regulating services become so scarce that the death rate increases (as it happens under RS-decline scenario). In this case, the birth rate might increase temporarily to avoid a decline in population size. The death rate, however, would still be higher than usual. This might affect the population trend in the RS-decline scenario but it should not affect the low quality of life in this scenario.

5. Conclusion

Our model suggests that humanity is facing two threats related to its dependence on nature. The first one occurs when nature is so degraded, due to an emphasis on food production, that regulating services, such as air and water quality or disease spread regulation, are substantially altered, which induces an increase in the death rate. The other threat, famine, occurs if humans are not able to convert enough land to feed themselves and to reach a steady point with a large amount of food per person. In the latter case, the birth rate remains higher than the death rate and the population increases until reaching a famine steady state. Both scenarios are driven by antagonistic processes as one occurs more with low conversion for food and high conservation while the other one occurs more with high conversion parameters and low conservation. However both are indisputably negative for human well-being and are negative also for nature purposes. Indeed, the highest level of non food-related ecosystem services is reached in the desirable future scenario, thanks to a trade-off between nature conservation and land conversion for agriculture.

Based on these results, we suggest that converting too much natural land into exploited land has negative consequences for regulating services; conserving nature can help avoid undesirable declines in regulating services. But our model also suggests that conserving nature, to such an extent that humans are prevented from using the area for food purposes, could locally increase the birth rate and ultimately results in a greater natural degradation. This conclusion is not antithetic to nature conservation, it rather cautions that conservation could have unexpected and undesirable feedbacks in fragile and politically unstable countries if it interferes with basic human needs. It is not enough to consider only natural land area or biodiversity when developing conservation efforts; population growth is crucial for both human well-being and nature conservation itself. Human demography should be an essential part of any land management strategy in the long run, at regional, national, and ultimately global scales.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2018.03.360.

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