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WP 2020.08

Suggested citation:

L.A. Lawson (2020). A simple Ricardo-Malthusian model of population, deforestation and biodiversity loss. *FAERE Working Paper, 2020.08.*

ISSN number: **2274-5556**

www.faere.fr

A simple Ricardo-Malthusian model of population, deforestation and biodiversity loss

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ABSTRACT

This paper assesses the interactions between human societies and nature, arguing that population growth and forest resources harvest cause natural habitat conversion, which resolves into biodiversity loss. Relying on profit and utility maximization behaviours, we describe the joint evolution of population, forest and species stock by a dynamic system characterized by a locally stable steady state. Compared to existing studies, we dissociate forest cover from species stock and enlighten the possibility of total extinction of biological species (empty forests). Our analysis supports an impossible peaceful cohabitation, as in presence of human population growth, forest resources and species stock diverge from their carrying capacity. Finally, scenarios analyses associated with high fertility and preference for the resource-based good globally indicate rapid population growth followed by a sudden drop: a collapse.

KEYWORDS
Economic growth; forest clearing; habitat destruction; species loss; population

***JEL Classification*:** Q32, Q57, O44, R11

1. Introduction

The Limit to Growth (Meadows et al., 1974) is among first global level reports, discussing the ecological constraints faced by human societies and predicting population overshoot. In the same perspective, environmental degradation and unsustainable resource extraction, which translate into deforestation, habitat destruction, climate change and biodiversity loss, have provoked systematic inquiries towards understanding the cohabitation between human and nature, as well as their long-run dynamics. Thereby, several studies have been devoted to how biodiversity loss occurs and affects biogeochemical cycles and human societies.

About the causes of species loss, empirical studies largely mention economic expansion and human population growth (Fuentes, 2011; Chaudhary and Brooks, 2019), while the International Union for Conservation of Nature (IUCN) mainly blames natural habitat destruction. Theoretically, existing studies in ecological economics predominantly discussed resources depletion within economic and bioeconomics frameworks, capturing such complex environmental issues using a single parameter or indicator (Brander and Taylor, 1998; D'Alessandro, 2007). Moreover,

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it is noticeable that compared to gas emissions and energy use, biodiversity loss has received relatively few attention in the existing literature, though scientist acknowledge it impacts to rival those of many other drivers of environmental harms (Edwards and Abivardi, 1998; Millennium Ecosystem Assessment, 2005). Extending existing theoretical studies, this paper proposes a population, forest and biodiversity model, arguing that the latter occurs through forest degradation and conflicts with human population over habitat.

Two main approaches are observed in modelling population-resources dynamics: Ecologically inspired models and Economic-type models (Nagase and Uehara, 2011; Roman et al., 2018). In contrast to ecological models, the economic models provide the microeconomic foundations, (preferences or decisions), which evidently drive the dynamics of population and resources. This is the case in Brander and Taylor (1998); D'Alessandro (2007); Dalton and Coats (2000); Nagase and Uehara (2011), among others. The present paper proposes, in addition to the well-known population-forest nexus, to discuss species loss. Doing so, contrary to the common theoretical perspective, where the production technology directly uses natural resources as input, our approach considers that species richness is not a direct input in the production process, while forest resources are.

Prior Predator-Prey and human-nature dynamical models (Brander and Taylor, 1998; Motesharrei et al., 2014) provide basic foundations to the specifications used in this paper. The first component of our model is a Malthusian population dynamics, where birth and death rates drive population growth in addition to a resource-dependent fertility function. The second component describes the evolution of forest stock, specified as the difference between its regeneration and harvest. Microeconomic foundations on individual behaviours provide insights into how preferences shape the joint evolution of population and resources. The third component, the evolution of species stock, is driven by forest clearing and population growth induced species loss.

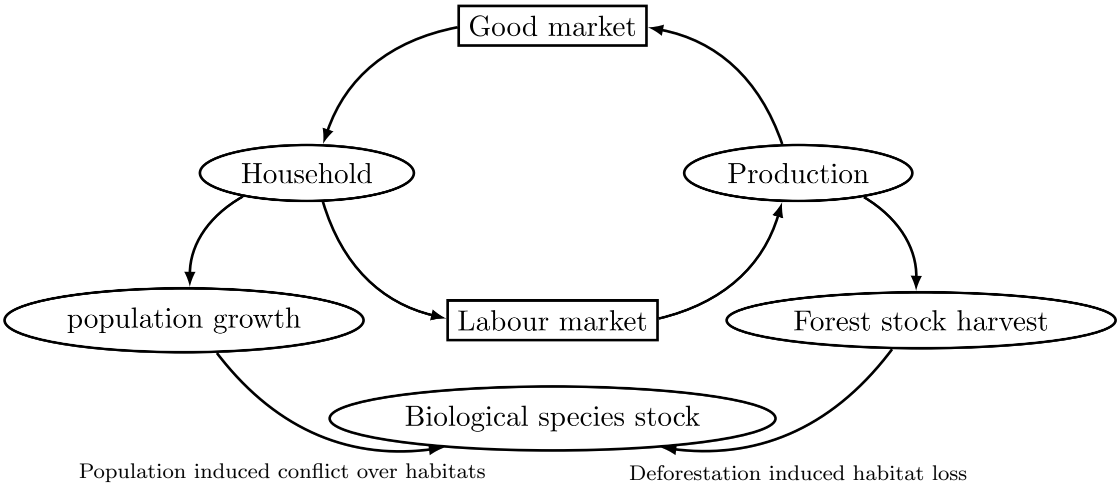

Figure 1. Synopsis of the population-forest-biodiversity model

Biodiversity, the number and variability of living organisms, reveals to be complex but can be seen as a stock.[1] Our purpose being neither estimating species population nor valuing species, we employ a single indicator of species stock. Such a perspective deliberately disregards the width and complexity of the concept of biodiversity. However, similar to physical capital, a unique indicator helps end-up with a broad and tractable model for species loss.

Section 2 presents a brief literature overview. Sections 3 and 4 respectively describe the basis structure of the model and discuss the population and resources dynamics. Section 5 analyses stability of the population-forest-biodiversity model and Section 6 assesses some scenarios. In Section 7, we discuss our results and draw some conclusions.

2. Population and resources dynamics: A brief literature review

Founding works on human-resources interactions and concerns over societal collapses are the predator-prey models and "The Limit to Growth" perspectives discussed, among others, by Levin (1974), Meadows et al. (1974) and Weitzman (1998). More recently, the literature on economic expansion, population growth and resources scarcity is animated by ecological-type models, where mostly numerical methods are exploited. On the other hand, researchers rely on microeconomic grounded models to assess how preferences affect wealth, population and resources dynamics. Both analytical frameworks and discussions about endogenous population growth and collapse of past societies seem relevant to the present paper.

Ecological-type models. This generation of studies largely derives from the Lotka-Volterra model describing the joint-evolution of two competing species (wolves and rabbits) and apply the latter to human and nature dynamics. This has been the case in Anderies (1998, 2003), Turchin (2003), Janssen and Scheffer (2004), to cite a few Thereby, Anderies (1998, 2003) exploits ritual lash-and-burn cycles to explain human-ecosystem interactions in the Tsembaga of New Guinea and the rise and fall of Easter Island. Turchin (2003), noting that population is historically characterized by oscillations, discusses and applies several population models to empirical data.

In a different perspective, computable general equilibrium models are exploited to analyse the human and nature dynamics in the works, among others, by Tschirhart (2000), Basener et al. (2008), Finnoff and Tschirhart (2008), Motesharrei et al. (2014) and Brandt and Merico (2015). Globally, these authors exploit mathematical tools to address more specific societal concerns within the Predator-Prey perspective. Thus, Finnoff and Tschirhart (2008), for instance, associate dynamic economic and ecological models to investigate how changes in price affect population, resources harvest and tourism. While Basener et al. (2008) and Brandt and Merico (2015) introduce rat infestations and epidemic in population-resources models for Easter Island, Motesharrei et al. (2014) discussed the role of social stratification (elites and commoners) in wealth accumulation and resource dynamics. Although this ecological literature provides us with tools to access population-resources dynamics, it lacks of insights into individual behaviour and preferences that shape the global dynamics.

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[1] It includes several different species, more than a million according to the most pessimistic estimates, ranging from bird and mammal species to bacteria and microscopic (Cambridge Dictionary).

Economic type models. Contrary to ecological models, economic models propose a framework inspired by neoclassical theories, using assumption with regard to utility and profit maximization. Although being restrictive due to its microeconomic foundation, this approach has received relatively large attention, at least in the economic literature. Among the most recent works on boom and bust cycles, the seminal paper by Brander and Taylor (1998) on the historical case of Easter Island has inspired a sequence of studies about environmental resources and economic systems. This is the case in Dalton and Coats (2000), Bologna and Flores (2008), Cairns and Tian (2010) and Roman et al. (2017), to cite a few.

Population-resources models associate Lotka-Volterra ecological perspectives to economic models to assess how endogenous population growth and resource degradation can lead to societal collapse. In the same vein as Brander and Taylor (1998), Dalton and Coats (2000), Erickson and Gowdy (2000) and Reuveny and Decker (2000) discuss how institutional settings, technological progress and fertility management affect the population and resource dynamics. Furthermore, while Pezzey and Anderies (2003) extend the work by Brander and Taylor (1998) to assess how subsistence level of resource consumption and institutional settings can prevent a collapse, Dalton et al. (2005) discuss the role of property-rights regimes and technological changes in slowing down (or amplifying) boom and bust cycles. In more recent literature, D'Alessandro (2007), Bologna and Flores (2008), Zhou and Liu (2010) and Roman et al. (2017) propose more general frameworks, relaxing standard assumption of the Brander and Taylor (1998)'s model, as there seems to be no-perfect specification of population-resources model (Basener et al., 2008). This has given insight into non-linearity, hopf-bifurcation in the conditions leading to collapse in population-resources models. A final aspect of these models has been investigating historical collapses such as the Mayan and Mesopotamian civilizations as well as Ancient Egypt and the Roman empire. Thereby, arguments such as cultural-historical factors, trade characteristics and war (Demarest and Rice, 2005), diseases and environmental degradations (Acuna-Soto et al., 2005; Roman et al., 2017) are noticed.

Globally, whether the focus is on biological-type or economic-type models, it is noticeable that issues related to species loss have not been specifically targeted. Indeed, Brander and Taylor (1998) and related contributions have discussed forest resource depletion. Nevertheless, these population-resources studies did not consider informative to dissociate deforestation from biological species loss. The present paper aims to fill that gap by introducing issues relative to species loss into population-forest models.

3. The basic structure of the model

As in population-resources models, this paper considers a two production sectors: A manufacture and a forest resource harvest sector. The manufactured good is produced by a representative firm using only labour, L_M, while the resource-harvest sector employs labour, L_H, and forest resources, F. Labour is freely mobile across sectors, implying wage equality between sectors ($w_H = w_M = w$). The structure of the model described hereafter closely follow resource-population discussions in Brander and Taylor (1998), Dalton and Coats (2000) and Nagase and Uehara (2011), among others.

3.1. *Firms' behaviour*

Manufactures: They are considered as numeraire using a Ricardian production function $Y_{M,t} = L_{M,t}$, where L_M stands for the quantity of labour used in sector M. Assuming the price of the good to equal one, the optimal behaviour of the representative firm is:

$$\underset{L_{M,t}}{Max}\, \Pi_{M,t} \text{ with } \; \Pi_{M,t} = Y_{M,t} - w_t L_{M,t} \equiv L_{M,t} - w_t L_{M,t} \tag{1}$$

Profit maximization yields $w_{M,t} \equiv w_t = 1$.
Harvest sector: Forest resources use is governed by the supply of good, H, using the well-known Schaefer (1957) production function, $Y_{H,t} \equiv H(F_t) = qE_tF_t$, where E_t is the harvest effort (labour) and q a positive parameter to be seen a scaling parameter or level of technological knowledge. Since there are no property rights over land, the firm i hires a quantity of labour, $L_{H,t} \equiv E_t$, to maximize the following function:

$$\underset{L_{H,t}}{Max}\, \Pi_{H,t} \text{ with } \; \Pi_{H,t} = p_H Y_{H,t} - w_{H,t} L_{H,t} \equiv p_H q L_{H,t} F_t - w_{H,t} L_{H,t} \tag{2}$$

First order condition of profit maximization yields: $p_H q F_t = w_{H,t}$ which implies:

$$p_{H,t} = \frac{w_{H,t}}{qF_t} \tag{3}$$

(3) expresses the supply price of the harvest good, $p_{H,t}$, as positively dependent on the wage rate and negatively on forest resources harvested in the production process.

3.2. *Preference and budget constraints*

At each period t, a new generation of agents is born and lives 2 periods, childhood and adulthood. Adult individuals in t (born in $t-1$) are endowed with one unit of time which they supply inelastically to labour force participation to earn w_t. By definition, children consume a fraction of their parents' time endowment and do not make any economic decision. Thus, adult individuals (N_t) choose the optimal mixture of M and H to maximize their utility function. Such formulations of individuals' behaviour are intensely described in De La Croix and Michel (2002) and Galor (2011).

The utility function of the representative agent is defined over consumption of the resources and harvest goods H_t and M_t, respectively $c_{H,t} \equiv C_{H,t}/N_t$ and $c_{M,t} \equiv C_{M,t}/N_t$. The problem of the representative individual is:

$$\underset{h_t, m_t}{Max}\, U(c_{H,t}, c_{M,t}) \text{ with } U(c_{H,t}, c_{M,t}) = (c_{H,t})^{\gamma}\, (c_{M,t})^{1-\gamma} \; \text{ where } \; \gamma \in (0,1) \tag{4}$$

$$\text{subject to } w_t = p_{H,t} c_{H,t} + c_{M,t} \; \text{ and } \; c_{H,t}, c_{M,t} > 0.$$

Solving the maximization problem for a representative agent delivers $c^*_{H,t} = w_t\gamma/p_{H,t}$ and $c^*_{M,t} = w_t(1-\gamma)$, which for N individuals correspond to:

$$C^*_{H,t} = \gamma w_t N_t / p_{H,t} \quad \text{ and } \quad C^*_{M,t} = (1-\gamma) w_t N_t \tag{5}$$

C_H^* and C_M^* are the aggregate demand for the resources and the manufactured goods.

3.3. Competitive equilibrium and market clearing

A competitive equilibrium is a sequence of allocations $\{Y_{H,t}, Y_{M,t}, F_t, L_{H,t}, L_{M,t}\}_{t=1}^{\infty}$ and prices $\{w_t, p_{H,t}\}_{t=1}^{\infty}$ given initial values F_0 and N_0 such that consumers and firms maximize their objective functions and markets clear. As there are two consumption goods in the economy, the market clearing conditions for the goods and labour markets respectively are:

- Labour market: $N_t = L_{M,t} + L_{H,t}$
  - Good markets:

$$\text{Manufactured good M:} \qquad L_{M,t} = (1-\gamma)w_t N_t \equiv C_{M,t}^* \tag{6}$$

$$\text{Resources harvest good H:} \qquad H(F_t) = \gamma w_t N_t / p_{H,t} \equiv C_{H,t}^* \tag{7}$$

Using FOC of profit maximization in resources H, $p_H q F_t = w_{H,t}$, $w_t = 1$, (7) becomes:

$$H(F_t) = \gamma q N_t F_t \tag{8}$$

Definition 1. *Considering q and γ, an equilibrium is an infinite sequence of prices $\{w_t, p_{H,t}\}_{t=1}^{\infty}$, allocation $\{C_{H,t}, C_{M,t}\}_{t=1}^{\infty}$ and $\{L_{H,t}, L_{M,t}\}_{t=1}^{\infty}$ such that:*
– Households maximize their utility function;
– Firms maximize their profit;
– Markets clear for all generations.

4. Dynamics of population, forest and species stock

4.1. Population dynamics

As biologists describe the Malthusian population growth as depending on the birth and death rates, human population growth is observed when the birth rate, (b), exceeds the death rate, (d). In addition to these two parameters, the literature in a predator-prey perspective argues that natural resources availability and harvest increase fertility and specifies population dynamics as positively depending on $\phi(F_t) \equiv H(F_t)/N_t$.

$$N_{t+1} = N_t + N_t(b - d + \alpha\phi(F_t)) \tag{9}$$

where b, d and α are positive parameters, $b - d$ is likely negative, $\alpha\phi(F_t)$ being the so-called "fertility function". Exploiting (8), the dynamical evolution of population becomes:

$$N_{t+1} = N_t + N_t(b - d + \alpha\gamma q F_t) \tag{10}$$

4.2. *Forest dynamics*

Forest resources in period t, besides being used in production H, regenerate over time. Therefore, forest clearing is essentially governed by the demand, respectively supply of the resources dependent good, thus the harvest function (8). Considering $G(F_t)$ to be the regeneration function, the evolution of forest stock is given by: $\Delta F = G(F_t) - \gamma q N_t F_t$.

Regarding regeneration of forest resources, bio-economists (Clark, 1974; Chasnov, 2009) discuss several population models for renewable resources. The most common approach is the logistic model, satisfying the conditions: $G(0) = 0$ and $G(\overline{F}) = 0$, where $\overline{F}$ is the carrying capacity. Using a logistic population model for forest resources and assuming g to be the regeneration rate, the dynamics of forest cover is given by:

$$F_{t+1} = F_t + gF_t(1 - F_t/\overline{F}) - \gamma q N_t F_t \tag{11}$$

4.3. *Dynamics of species stock*

Forest cover, providing a number of ecosystem services, is also considered to be natural habitat for biodiversity, hosting a variety of biological species, B_t. In this perspective, harvest of forest resources drives biodiversity loss, $E(B_t)$. Since extinct species cannot be recovered, we assume that, besides changes in the population of existing species, identification or discovery of new species essentially governs regeneration of biodiversity, $I(B_t)$. The dynamics of species stock can be specified as:

$$B_{t+1} = B_t + I(B_t) - E(B_t) \tag{12}$$

Biodiversity loss: Existing studies present harvest of resources as a function of labour force employed in resource sector. Regarding biodiversity however, the stock of species is not a direct input in the production function and our approach considers that species loss occurs through habitat destruction or forest resources harvest, H_t. Since habitat conversion also occurs through human settlements (McDonald et al., 2008; Mills and Waite, 2009; Freytag et al., 2012), population growth is considered as a second cause of species loss. Accounting for both forest resources harvest and human population growth as driving species loss implies: $E(B_t) \equiv E(F_t, N_t, B_t) = \delta_1 \gamma q N_t F_t B_t + \delta_2 (b - d + \alpha \gamma q F_t) N_t B_t$, where $0 < \delta_1, \delta_2 < 1$.

Species identification: Recovering extinct species being impossible, we consider new species identification as the main source of regeneration. Using a logistic growth function for biological entities (Brown, 2000; De Vries et al., 2006; Hannon and Ruth, 2014), species regeneration is given by $I(B_t) = g\left(B_t - B_t^2/\overline{B_t}\right)$, where $\overline{B_t}$ is the maximum possible species stock.

Introducing species loss and regeneration functions in (12) delivers the dynamics of biodiversity as depending on F_t and N_t. This is:

$$B_{t+1} = B_t + g\left(B_t - B_t^2/\overline{B_t}\right) - \delta_1 \gamma q N_t F_t B_t - \delta_2 (b - d + \alpha \gamma q F_t) N_t B_t \tag{13}$$

5. Steady state and linear stability analysis

5.1. Steady state

The model proposed above is characterized by the joint evolution of human population, forest resources and species stock. Combining equations (9), (11) and (13), the dynamic system is given by the following equations, assuming a positive regeneration rate:

$$\Delta N = N_t(b - d + \alpha\gamma q F_t) \tag{14}$$

$$\Delta F = gF_t(1 - F_t/\overline{F}) - \gamma q N_t F_t \tag{15}$$

$$\Delta B = g\left(B_t - B_t^2/\overline{B_t}\right) - \delta_1 \gamma q N_t F_t B_t - \delta_2(b - d + \alpha\gamma q F_t)N_t B_t \tag{16}$$

This system reaches a steady-state, if simultaneously $F_{t+1} = F_t$, $N_{t+1} = N_t$ and $B_{t+1} = B_t$. Thereby, one realises that the evolution of F_t and N_t is independent on B_t. Analysing steady-state, it is sufficient to observe the joint evolution of F_t and N_t, which actually is similar to the in-death bivariate steady-state analysis proposed in Brander and Taylor (1998); Brander and Taylor, Dalton and Coats (2000) and Bologna and Flores (2008).

Proposition 1. *The dynamic system described by equations (14), (15) and (16) exhibits four feasible steady-states. Steady states 1, 2 and 3 are corner solutions, while steady state 4 is an internal solution, respectively represented by the following threesomes.*[2]

ss1. $N^* = 0,\ F^* = 0,\ B^* = 0$
ss2. $N^* = 0,\ F^* = \overline{F},\ B^* = \overline{B}$
ss3. $N^* = \frac{g}{\gamma q}\left(1 - \frac{d-b}{\alpha\gamma q\overline{F}}\right),\ F^* = \frac{d-b}{\alpha\gamma q},\ B^* = 0.$
ss4. $N^* = \frac{g}{\gamma q}\left(1 - \frac{d-b}{\alpha\gamma q\overline{F}}\right),\ F^* = \frac{d-b}{\alpha\gamma q},\ B^* = \overline{B}\left[1 - \frac{\delta_1(d-b)}{\alpha\gamma q}\left(1 - \frac{d-b}{\alpha\gamma q\overline{F}}\right)\right]$

It is to note that $N^* = \frac{g}{\gamma q}\left(1 - \frac{d-b}{\alpha\gamma q\overline{F}}\right) \equiv \frac{g}{\gamma q}\left(1 - F^*/\overline{F}\right)$. Positivity conditions for N^*, F^* and B^* at steady-state 3 and 4 require $0 < d - b < 1$ and imply the following:

$$0 < F^* = \frac{d-b}{\alpha\gamma q} < \overline{F} \tag{17}$$

$$0 < \frac{\delta_1(d-b)}{\alpha\gamma q}\left(1 - \frac{d-b}{\alpha\gamma q\overline{F}}\right) < 1 \tag{18}$$

$$0 < B^* = \overline{B}\left[1 - \frac{\delta_1(d-b)}{\alpha\gamma q}\left(1 - \frac{d-b}{\alpha\gamma q\overline{F}}\right)\right] < \overline{B} \tag{19}$$

Our aim being the joint evolution of population, forest and species stocks, we focus on $ss.4$ and assess how changes in the model's parameters affect N^*, F^* and B^* by differentiating the latter with respect to (d), (b), (α), (γ) and (q).

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[2] Further steady states such as $N^* = 0, F^* = \overline{F}, B^* = 0$ and $N^* = 0, F^* = 0, B^* = \overline{B}$ exist but are unrealistic, since the first implies that even in the absence of population (predator), resource stocks can reach 0 and the second that in absence of forest, species stock reaches its carrying capacity.

Proposition 2. *(1) The steady-state stock of forests* F^*
– rises if the mortality rate (d) rises and birth rate (b) falls;
– rises if the fertility responsiveness to resources abundance falls (α) *and preference for the resources-based good* (γ) *rises;*
– falls with technological progress in the resources harvest sector (q).

(2) The state state adult population level N^*
– falls if mortality rate (d) rises and the birth rate (b) falls;
– rises if the fertility responsiveness rises (α) *and carrying capacity* $\overline{F}$ *rises;*
– falls if there is technological progress in the resources harvest sector (q) and $F^* < \overline{F}/2$*.*
– falls if preference for the resources-based good (γ) *rises and* $F^* < \overline{F}/2$*.*

(3) The steady-state stock of biological species B^*
– rises with increasing mortality rate (d) if $F^* > \overline{F}/2$*;*
– falls with increasing birth rate (b) if $F^* > \overline{F}/2$*;*
– falls with increasing fertility responsiveness to resources abundance (α) *if* $F^* > \overline{F}/2$*;*
– falls with increasing preference for the resources-based good (γ) *if* $F^* < 2\overline{F}/3$*;*
– falls with technological progress in the resources harvest sector (q) if $F^* < 2\overline{F}/3$*.*

Proof: See Appendix A-2 for proof elements.

5.2. Linear stability analysis

Analysing the stability of fixed points involves observing the eigenvalue of the corresponding Jacobian Matrix, evaluated at the fixed points (Galor, 2007; Anishchenko et al., 2014). Let D be a vector of deviations from the steady state, $D = (N_t - N^*, F_t - F^*, B_t - B^*)$. Small changes in D over time, using Taylor series expansion, can be expressed as the following: $dD/dt \simeq J(N^*, F^*, B^*)D + Z(N, F, B)$, where J is the Jacobian Matrix of the first-order partial derivatives with respect to N_t, F_t and B_t. $Z(N, F, B)$ stands for higher-order derivatives of the Taylor expansion, which near the steady-state can be ignored. J is:

$$J \equiv \begin{pmatrix} J_{1,1} & J_{12} & J_{1,3} \\ J_{2,1} & J_{22} & J_{2,3} \\ J_{3,1} & J_{3,2} & J_{3,3} \end{pmatrix} = \begin{pmatrix} \frac{d(\Delta N)}{dN} & \frac{d(\Delta N)}{dF} & \frac{d(\Delta N)}{dB} \\ \frac{d(\Delta F)}{dN} & \frac{d(\Delta F)}{dF} & \frac{d(\Delta F)}{dB} \\ \frac{d(\Delta B)}{dN} & \frac{d(\Delta B)}{dF} & \frac{d(\Delta B)}{dB} \end{pmatrix}$$

$$= \begin{pmatrix} b - d + \alpha\gamma q F_t & \alpha\gamma q N_t & 0 \\ -\gamma q F_t & g - 2gF_t/\overline{F} - \gamma q N_t & 0 \\ -\delta_1\gamma q F_t B_t - \delta_2(b - d + \alpha\gamma q F_t)B_t & -\delta_1\gamma q N_t B_t - \delta_2\alpha\gamma q N_t B_t & g - 2gB_t/\overline{B} - \delta_1\gamma q N_t F_t - \delta_2(b - d + \alpha\gamma q F_t)N_t \end{pmatrix}$$

where it is to recall that ΔN, ΔF and ΔB are given by (14), (15) and (16). Finally, the behaviour of the system almost entirely depends on the eigenvalues of matrix J evaluated at the corresponding steady state.

Proposition 3. *Assuming the positivity conditions (17), (18) and (19) to hold, the behaviour of the system is the following:*
– ss1., characterized by $N^* = 0$*,* $F^* = 0$ *and* $B^* = 0$*, is a saddlepoint.*

– ss2., characterized by $N^* = 0$*,* $F^* = \overline{F}$ *and* $B^* = \overline{B}$ *is a saddlepoint.*

– ss3., characterized by $N^* = \frac{g}{\gamma q}\left(1 - \frac{d-b}{\alpha\gamma q\overline{F}}\right)$*,* $F^* = \frac{d-b}{\alpha\gamma q}$ *and* $B^* = 0$ *is stable*

– ss4., characterized by $N^* = \frac{g}{\gamma q}\left(1 - \frac{d-b}{\alpha\gamma q\overline{F}}\right)$*,* $F^* = \frac{d-b}{\alpha\gamma q}$ *and* $B^* = \overline{B}\left[1 - \frac{\delta_1(d-b)}{\alpha\gamma q}\left(1 - \frac{d-b}{\alpha\gamma q\overline{F}}\right)\right]$ *is a stable node allowing for monotonic convergence, when the following condition holds:*

$$g\frac{d-b}{\alpha\gamma q\overline{F}} > 4\left[\alpha\gamma q\overline{F} - (d-b)\right] \tag{20}$$

Reciprocally, when $g\frac{d-b}{\alpha\gamma q\overline{F}} < 4\left[\alpha\gamma q\overline{F} - (d-b)\right]$*, both eigenvalues have imaginary parts associated with negative real parts, thus, ss4 is a stable focus-node converging to equilibrium with damped oscillations.*

Proof: See Appendix A-3 for proof elements.

5.3. Population, forest cover and species stock interactions

Our specification showing population growth and preferences as driving both forest harvest and species loss, an analysis of resources (F_t and B_t) dynamics conditional on population seems interesting.

Starting from (14) and (15), we first observe that in the absence of forest resources, $F^* = 0$, population also reaches a steady state $N^* = 0$ (ss1). However, in the absence of population, $N^* = 0$, forest stock reaches its carrying capacity, $\overline{F}$ (ss2). Population growth rate, $b - d + \alpha\gamma q F_t$, and forest harvest, $\gamma q N_t F_t$, positively depending on forest stock, the system reaches an interior steady state $\{N^*, F^*\} > 0$, when there is no growth in population and forest resources harvest exactly equals its extrinsic growth (Fig. 2, Panel A and B).

For any forest stock below F^* (Fig. 2), there is a decrease in population (negative population growth rate) and respectively in forest resources harvest. This process reduces resources-use pressure and favours net stock regeneration. Reciprocally, for any stock larger than F^*, increasing forest resources harvest (positive population growth rate) is observed, exceeds resources regeneration and leads to forest depletion. Hence, the higher forest stock, respectively the higher is resources harvest, the larger human population grows.

In addition to this Predator-Prey alike bivariate system, equation (16) expresses biodiversity loss as driven by both forest resources harvest and population growth. Starting from the internal steady state for the forest-population couple $\{N^*, F^*\} > 0$, Fig. 2 (Panel C) helps identify two possible steady states of species stock: $B^* = 0$ and $B^* > 0$. Technically, solving $B_t\left[g\left(1 - B_t/\overline{B_t}\right) - \delta_1\gamma q N_t F_t - \delta_2(b - d + \alpha\gamma q F_t)N_t\right] = 0$, given $\{N^*, F^*\} > 0$ delivers these solutions. The couple $\{N^* > 0, F^* > 0, B^* = 0\}$ and $\{N^* > 0, F^* > 0, B^* > 0\}$ represent further steady states of the population-forest-biodiversity model.

Compared to the referential works by Brander and Taylor (1998), Dalton and Coats (2000) and D'Alessandro (2007), and related studies, this paper points out the possibility of a long run equilibrium characterized by total extinction of biological species. This is, contrary to biological species stock which cannot reach a steady state $B^* > 0$, when there are no forest resources, $F^* = 0$, forest stock however can reach a steady state $F^* > 0$ while there is no biodiversity $B^* = 0$. Such a property of our model precisely enlightens the possibility of an empty forest equilibrium (ss.3).

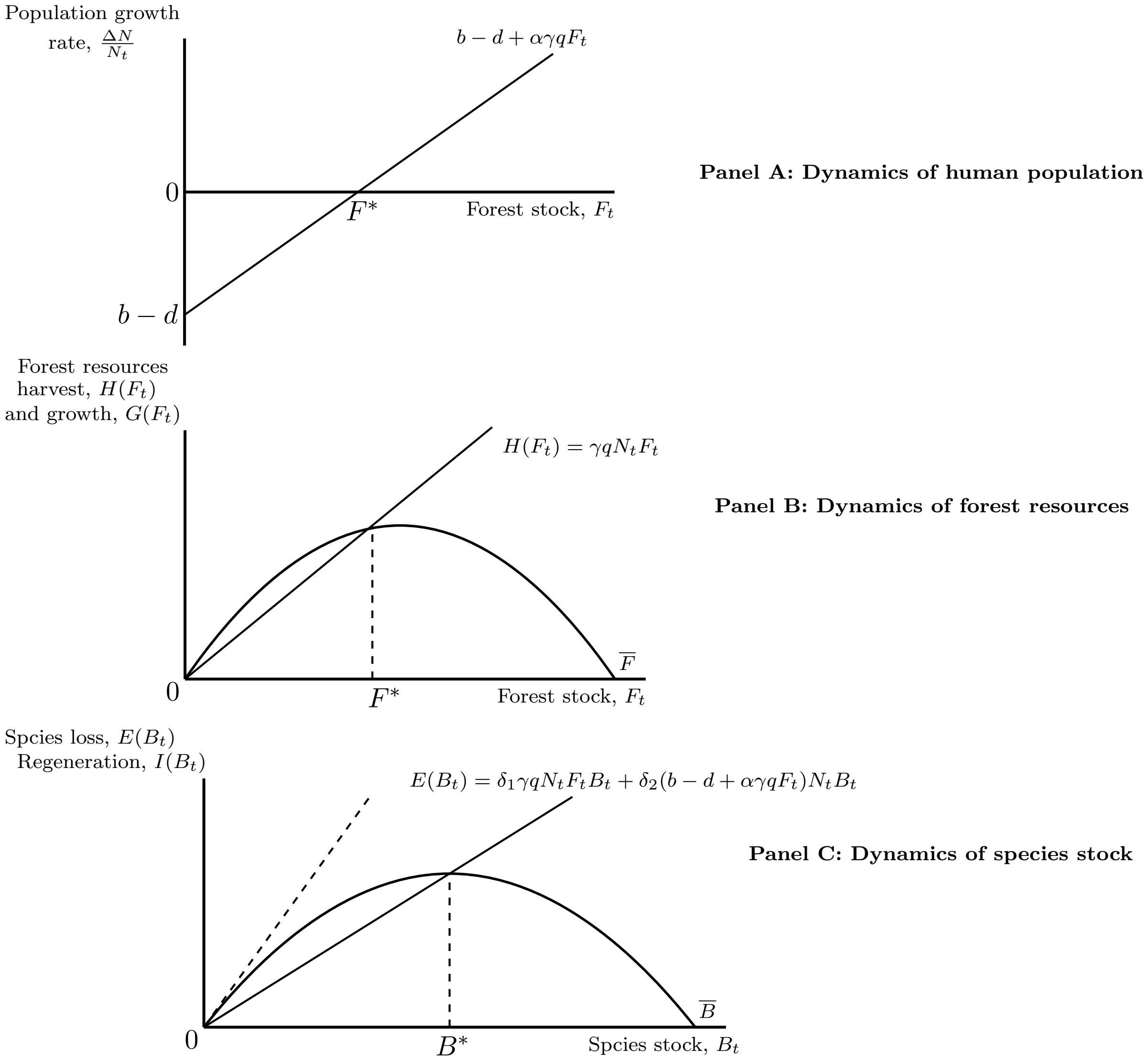

Figure 2. Illustration of the dynamics of population-forest-species stock

6. Scenarios analysis

Starting from an interior solution for population and forests, there are two locally stable steady states ($ss3$ and $ss4$), as demonstrated above. Thereby, by increasing the slope of the extinction line, $E(B_t)$ (higher ecological footprint), $ss4$ collapses to $ss3$ (Fig. 2).

6.1. Applying the population-forest-biodiversity model to Easter Island

6.1.1. Parameter choice

This paper exploring the evolution of species stock, in addition to the forest-population case proposed by Brander and Taylor (1998), and discussed by Dalton and Coats (2000) and Bologna and Flores (2008), among others, the dynamics of the system can be investigated in the similar paradigm. The Easter Island economic literature use the following values for carrying capacity of forest $\overline{F}$, intrinsic regeneration rate g, net birth rate $b-d$, labour harvesting productivity q, preference for the harvest good γ and the fertility parameter α: $\overline{F}=12000$, $g=0.04$, $b-d=-0.10$, $q=0.00001$, $\alpha=4$ and $\gamma=0.4$. The latter parameter, γ, implies that consumers prefer the manufactured good to the resource-based one.

Equation (16) includes the carrying capacity of biodiversity ($\overline{B}$) and ecological footprint parameters δ_1 and δ_2. Values for these parameters can be identified using the same intuition as the Schaefer's production function. Similar to the harvest function, where an effort L_H is used to a harvest $H=qL_HF$, lost of forests γqN_tF_t and increase of population $(b-d+\alpha\gamma qF_t)N_t$ cause biological species lost respectively given by $\delta_1(\gamma qN_tF_t)B_t$ and $\delta_2(b-d+\alpha\gamma qF_t)N_tB_t$. Therefore, values given to the parameters q, δ_1 and δ_2 are to be of comparable ranges. Moreover, δ_1 and δ_2 should take values lower than the intrinsic regeneration rate g, to allow an assessment of the role of preferences, fertility and other parameters in species loss.

Regarding $\overline{B}$, similar to $\overline{F}$ where researchers consider the starting value of forest resources as being equal to the carrying capacity, we argue that $\overline{B}=B_0$ and choose a value for biodiversity carrying capacity in the range of forest stock: $\overline{B}=10000$.[3]

6.1.2. Impact of intensive harvest, preference and fertility

Impact of population growth and intensive harvest. The evolution of the couple population-forest being largely discussed in existing study, we focus here on their interaction with species stock, given the amplitude of forest clearing and population growth. Thereby, we start from a perspective where there is no ecological footprint with regard to biodiversity, which remains equal to its carrying capacity or starting value (Fig. 3 (A)).

Firstly, with a significant ecological footprint or impact of human activities ($\{\delta_1,\delta_2\}\neq 0$), species stock diverges from its carrying capacity to converge to a new steady state below $\overline{B}$ (ss4). Secondly, since both population growth and forest clearing enhance biodiversity loss, relatively rapid decline in species stock is observed. It is also noticeable in every scenarios assessed that species stock reaches its minimum for the whole period, when human population reaches its peak. The system leading to two locally stable steady states with positive human population, Fig. 3 helps notice that for relatively high ecological footprint, ss4 becomes ss3, as species stock reaches zero.

Applying the population-forest-biodiversity model to Easter-Island reveals two

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[3] Carrying capacities are defined as equalling starting values, since forest on Easter Island has "been in place for approximately 37000 years before first colonizations" (Brander and Taylor (1998): pp.128).

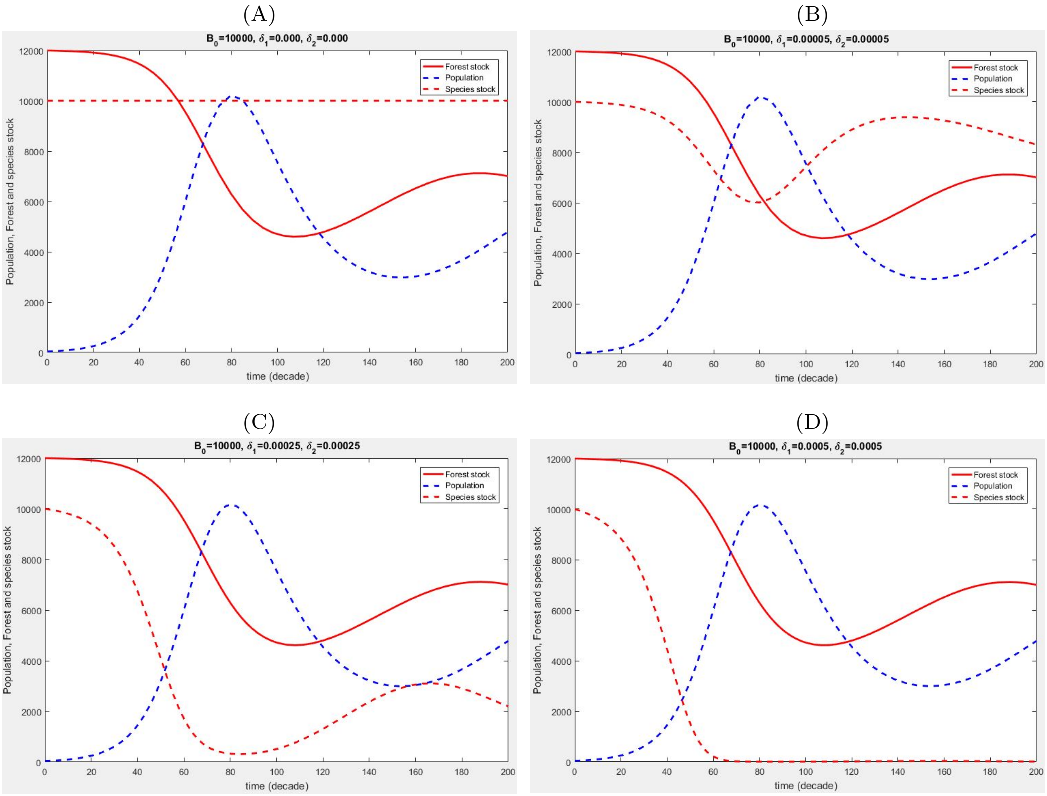

Figure 3. Scenario 1: Species loss in the Easter-Island framework

interesting teachings. Foremost, the combined impact of population growth and deforestation overwhelms natural regeneration of biological species, even when the rates of species loss due to population and deforestation $\{\delta_1, \delta_2\} \neq 0$ are quite inconsequential compared to the intrinsic regeneration rate g. Hence, as far as economic activities exploit forest or natural resources and there are conflicts over habitats between human and biological species, ecological destruction (deviations from $\overline{B}$ and $\overline{F}$) will increase until a societal collapse occurs. After a population collapse, forest and species stocks regeneration overcomes the ecological impact of human activities and stocks finally converge oscillatory to a long-run steady state. Nevertheless, when high ecological footprint lead to extinction, a significant species stock regeneration becomes impossible ($ss3$), supporting the so-called empty forest hypothesis.

Impact of changes in the preference for the resource-based good. The benchmark model and parameter choice as specified above assume that individuals prefer the manufactured goods to resource-based ones, since $\gamma = 0.4$. Starting from the case where the couple $\{\delta_1, \delta_2\}$ allows for an interior steady state with relatively low ecological impact oh human activities (Fig. 3-B), we investigate how changes in preferences affect the long-run behaviour of the system. It is then obvious that an equal preference for both goods or a higher preference for the harvest good will amplify human ecological impact, leading to rapid forest clearing and species loss. Thereby however, it is to observe that the rapid resource depletion occurs, the sooner population collapses (Fig. 4-B). Reciprocally, disfavouring resource-based goods delays (and even dampens) the occurrence of the population overshoot (Fig. 4-A).

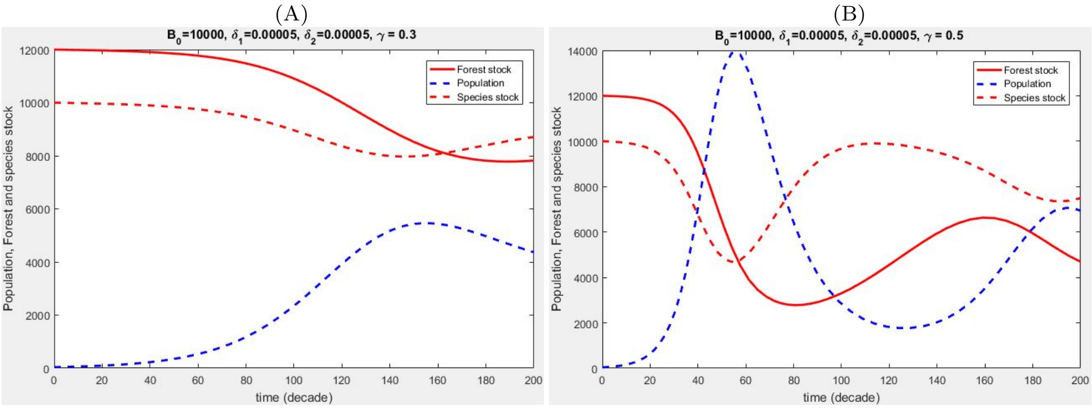
(A) (B)

Figure 4. Impact of changes in preference for the resource-based good

Impact of changes in fertility α. Besides the preference for manufactured and resource-based good, individual decisions over fertility affect demands, thus resources harvest and population dynamics. Compared to the starting model, where the fertility parameter $\alpha = 4$ (Fig. 3-B), we simulate two scenarios considering $\alpha = 3$ and $\alpha = 5$, in order to assess how changes in fertility impact the long-run equilibrium. Using the parametrization of the benchmark model (Fig. 3-B) and changing the fertility parameter produces results comparable to change in individual's preference.

Reducing the fertility parameter by 25% slows population growth (which reaches a peak of 4000 after 1400 year) and mitigate societal collapse, as a very smooth decrease in population is observed after its peak. Thereby, a very slow environmental depletion (deforestation and species loss) is noticeable. Respectively, a 25% increase in α leads to rapid population growth producing a collapse after 60 decades associated with rapid resource depletion and a relatively low steady state values for forest and species stocks.

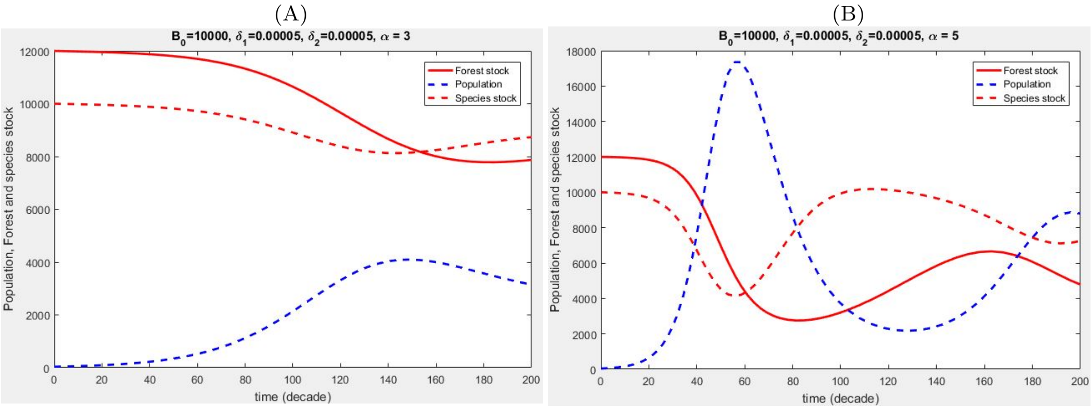
(A) (B)

Figure 5. Impact of changes in human fertility

6.2. *Population-forest-biodiversity in a developing resource-intensive economy*

Developing economies, mostly characterized by relatively high population growth, intensive resource harvest, are a group a countries the scenarios discussed above can be associated with. A feasible parametrization for resource-intensive economies should concurrently consider higher net birth rate or fertility parameter α, preference for the harvest good and human impact $\{\delta_1, \delta_2\}$. Thereby, compared to Fig. 3-A, we increase α, γ, and $\{\delta_1, \delta_2\}$, combining the different experiments conducted above.

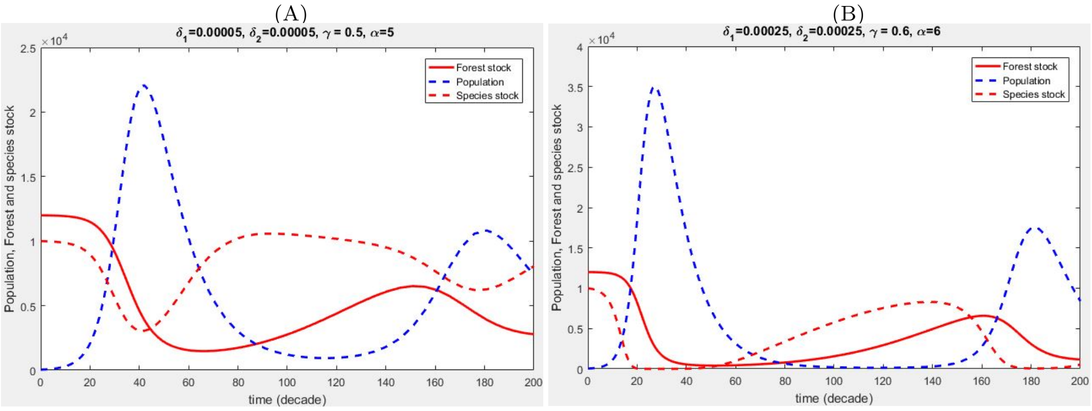
(A) (B)

Figure 6. Population, forest and biodiversity in developing resource-intensive economies

Our simulations (Fig. 6 (A)) indicate a rapid growth in population, which reaches a size higher than those observed in previous scenarios. Reciprocally, a sudden drop in forest and species stocks is noticeable following human population growth. The latter falls dramatically after 40 decades of flourishment, allowing forest and species stocks to smoothly recover. A second case increasing values of parameters displays a more rapid increase in population (of about 35000) after 25 decades, associated with rapid decline in forest and species stock, which converge to zero. As expected, the collapse of population also occurs sooner.

Globally, applying the population-forest-biodiversity model to a resource-intensive economy provides explanations to the rapid population growth and ecological destruction currently observed in developing countries (for instance Sub-Saharan Africa). It also predicts a population overshoot at some point of time: The rapid human population and ecological destruction occur, the sooner and dramatic is the societal collapse. Finally, after a societal collapse, environmental resources do not return to their initial values, suggesting that as long as there is increase in human population and production activities exploit nature, environmental resources cannot converge to their carrying capacities.

7. Discussion and concluding remarks

7.1. *Brander and Taylor, HANDY and the Population, Forest and Biodiversity model*

Throughout this paper on a Ricardo-Malthusian economic model of population, forest and biodiversity, we mentioned the seminal paper by Brander and Taylor (1998) and its extensions, among others, by D'Alessandro (2007) and Bologna and Flores (2008). These studies discuss the predator-prey system in economics mostly relying on a set of two equations which stand for population and forest resources. Environmental issues being more complex, our extension dissociates forest clearing from species loss and offers a broader perspective into environmental considerations. Indeed, in existing studies, human population growth and resources extraction cause forest resources depletion which can be seen as equalling species loss. Nevertheless, separating forest and species stocks, as we did, provides some insights into the possibility of species-empty forests. Thus, compared to the Brander and Taylor's long-run equilibrium for the so-called ecological complex and human population, our specification underlines two corresponding equilibria with regard to biodiversity: A zero species stock (species-empty forests) and a positive stock equilibria (species-poor forests).

Extension of Brander and Taylor (1998) investigated how institutional setting could have saved Easter Island, while the HANDY model discusses interconnections between social stratification, wealth and nature. Also, in these studies issues relative to ecological complex are assessed using a unique indicator, reducing more diversiform environmental issues to a homogeneous phenomenon. Therefore, in contrast to existing works on the topic, this paper can be considered as an extension of population-forest studies to biodiversity, which is not to consider as systematically flourishing when forests recover.

7.2. *Concluding remarks*

Theoretical efforts to assess environmental depletions and the role of economic activities and population has led, among others, to population-resources model exploiting economic and dynamic system analysis tools. The present paper proposes to introduce biodiversity loss within population-resources framework, exploiting predator-prey perspectives developed in the exiting literature.

Grounded on utility and profit maximization behaviours, the model described the joint evolution of human population, forest resources and biological species stocks by a system of three first-order dynamic equations. Steady states and local stability analysis show that an interior and locally stable equilibrium is feasible $\{N^* > 0, F^* > 0, B^* > 0\}$, besides a corner solution characterized by positive human population and forest stocks and where biodiversity has gone completely extinct $\{N^* > 0, F^* > 0, B^* = 0\}$. The latter solution appears to be a fallback solution, when the biodiversity impacts of population and deforestation $\{\delta_1, \delta_2\}$ are beyond a certain threshold (high ecological footprint).

Applying the population-forest-biodiversity model to economies characterized by relatively high fertility, preference for resource harvest goods, and more generally to resource-intensive economies reveals that endogenous population growth and forest clearing cause rapid extinction of biological species. Moreover, as fertility depends on forest resources stock, a societal collapse seems almost inevitable. Observing the different scenarios (Fig. 3, 4, 5, 6) suggests the following description of the population and forest stock interaction: *i*. The higher economic production exploits forest resources (reciprocally deforestation), the larger are fertility and population growth; *ii*. The higher are fertility and preference for harvest good, the sooner human population reaches its peak and collapses. Nevertheless, considering biological species, not only their stock takes positive values in the long-run, it can also reaches a zero level in presence of large ecological footprint, leading to a steady state equilibrium with total species extinction.

These numerical exercises on the case of resource-intensive economies provide some explanations to current rapid population growth and ecological destruction observed in developing countries. Our assessment, however, does not help answer the question whether (and when) a collapse will occur, as the parameters' values are essentially those used in the Easter Island case studies. Nevertheless, the population-forest-biodiversity model presented in this paper supports population-resources and HANDY perspectives on the impossibility of an infinite increase in human population and natural resource use.

Acknowledgements We are grateful to a FAERE anonymous reviewer for his/her helpful comments. We would like to thank P. Nguyen-Van, P. Combes-Motel , A. Stenger, C. O. Criado and A. Pérez-Barahona for their useful comments on a previous version of this manuscript. The usual caveat applies.

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Appendices

A-1: Proof of Proposition 1.

Proof elements involve setting $N_t(b-d+\alpha\gamma q F_t)=0$, $gF_t(1-F_t/\overline{F})-\gamma q N_t F_t=0$ and also $g\left(B_t-B_t^2/\overline{B_t}\right)-\delta_1\gamma q N_t F_t B_t-\delta_2(b-d+\alpha\gamma q F_t)N_t B_t=0$ and directly observe that steady-states 1 and 2 satisfy these conditions. Regarding steady state 3 and 4, first we solve for F^* in $(b-d+\alpha\gamma q F_t=0)$, then introduce its value into $gF_t(1-F_t/\overline{F})-\gamma q N_t F_t=0$, finding N^*. The two possible values of B^* directly derive by substituting N^* and F^* into $g\left(1-B_t/\overline{B_t}\right)-\delta_1\gamma q N_t F_t-\delta_2(b-d+\alpha\gamma q F_t)N_t=0$.

A-2: Proof of Proposition 2.

Let recall the steady-state values of forest cover, population and biological species stock:
$F^*=\frac{d-b}{\alpha\gamma q}>0$
$N^*=\frac{g}{\gamma q}\left(1-\frac{d-b}{\alpha\gamma q\overline{F}}\right)>0$
and $B^*=\overline{B}\left[1-\frac{\delta_1(d-b)}{\alpha\gamma q}\left(1-\frac{d-b}{\alpha\gamma q\overline{F}}\right)\right]\equiv\overline{B}\left[1-\frac{\delta_1\gamma q}{g}N^*F^*\right]>0.$

Proposition 2 follows by differentiating B^* with respect to the exogenous parameters.

(i) $\frac{\partial B^*}{\partial\overline{B}}=\left[1-\frac{\delta_1(d-b)}{\alpha\gamma q}\left(1-\frac{d-b}{\alpha\gamma q\overline{F}}\right)\right]>0;$

(ii) $\frac{\partial B^*}{\partial\overline{F}}=-\frac{\delta_1\gamma q\overline{B}F^*}{g}\frac{\partial N^*}{\partial\overline{F}}\equiv-\frac{\delta_1\overline{B}F^*(d-b)}{\alpha\gamma q\overline{F}^2}<0;$

(iii) $\frac{\partial B^*}{\partial d}=-\frac{\delta_1\gamma q\overline{B}}{g}\left[F^*\frac{\partial N^*}{\partial d}+N^*\frac{\partial F^*}{\partial d}\right]=-\frac{\delta_1\overline{B}}{\alpha\gamma q}\left[1-2\frac{d-b}{\alpha\gamma q\overline{F}}\right]\equiv-\frac{\delta_1\overline{B}}{\alpha\gamma q}\left[1-2\frac{F^*}{\overline{F}}\right];$

(iv) Similar to the previous case, $\frac{\partial B^*}{\partial b}=\frac{\delta_1\overline{B}}{\alpha\gamma q}\left[1-2\frac{F^*}{\overline{F}}\right];$

(v) $\frac{\partial B^*}{\partial\alpha}=-\frac{\delta_1\gamma q\overline{B}}{g}\left[F^*\frac{\partial N^*}{\partial\alpha}+N^*\frac{\partial F^*}{\partial\alpha}\right]=\frac{\delta_1(d-b)\overline{B}}{\alpha^2\gamma q}\left[1-2\frac{d-b}{\alpha\gamma q\overline{F}}\right]\equiv\frac{\delta_1(d-b)\overline{B}}{\alpha^2\gamma q}\left[1-2\frac{F^*}{\overline{F}}\right];$

(vi) $\frac{\partial B^*}{\partial\gamma}=\overline{B}\left[-\frac{\delta_1 q N^*F^*}{g}-\frac{\delta_1 q\gamma}{g}\left(F^*\frac{\partial N^*}{\partial\gamma}+N^*\frac{\partial F^*}{\partial\gamma}\right)\right]=\overline{B}\left[-\frac{\delta_1(d-b)}{\alpha\gamma^2 q}\left(1-\frac{d-b}{\alpha\gamma q\overline{F}}\right)-\frac{\delta_1(d-b)}{\alpha\gamma^2 q}\left(1-2\frac{d-b}{\alpha\gamma q\overline{F}}\right)\right]$
and is equivalent to $-\overline{B}\frac{\delta_1(d-b)}{\alpha\gamma^2 q}\left(2-3\frac{d-b}{\alpha\gamma q\overline{F}}\right)=-\overline{B}\frac{\delta_1(d-b)}{\alpha\gamma^2 q}\left(2-3\frac{F^*}{\overline{F}}\right);$

(vii) Similar to $\frac{\partial B^*}{\partial\gamma}$, one can directly deduce $\frac{\partial B^*}{\partial q}=-\overline{B}\frac{\delta_1(d-b)}{\alpha\gamma q^2}\left(2-3\frac{F^*}{\overline{F}}\right).$

A-3: Proof of Proposition 3.

– **Stability of ss1:** Evaluating the J-Matrix at ss1 delivers:

$$J_{ss1}(N^*,F^*,B^*)=\begin{pmatrix}b-d & 0 & 0\\ 0 & g & 0\\ 0 & 0 & g\end{pmatrix}\tag{21}$$

The corresponding three eigenvalues are respectively $\lambda_1=b-d<0$ and $\lambda_2=\lambda_3=g>0$. Thus, ss1 is a saddle point.

– **Stability of ss2:** Evaluating the J-Matrix at ss2 delivers:

$$J_{ss2}(N^*,F^*,B^*)=\begin{pmatrix}b-d+\alpha\gamma q\overline{F} & 0 & 0\\ -\gamma q\overline{F} & -g & 0\\ -\delta_1\gamma q\overline{FB}-\delta_2(b-d+\alpha\gamma q\overline{F})\overline{B} & 0 & -g\end{pmatrix}=\tag{22}$$

Finding the corresponding eigenvalues requires solving the equation $(b-d+\alpha\gamma q\overline{F}-\lambda)(-g-\lambda)^2=0$. The latter yields $\lambda_1=b-d+\alpha\gamma q\overline{F}$ and $\lambda_2=\lambda_3=-g$. We can see that $-1<\lambda_2=\lambda_3<0$ and further that $0<\lambda_1=b-d+\alpha\gamma q\overline{F}<\alpha\gamma q\overline{F}$. Thus, similar to ss1, ss2 is a saddlepoint.

– **Stability of ss3:** Evaluating the J-Matrix at ss3 delivers:

$$J_3^* = \begin{pmatrix} J_{11}^* & J_{12}^* & J_{13}^* \\ J_{21}^* & J_{22}^* & J_{23}^* \\ J_{31}^* & J_{32}^* & J_{33}^* \end{pmatrix} \text{ where } \begin{cases} J_{11}^* = 0 \\ J_{12}^* = \alpha g \left(1 - \frac{d-b}{\alpha\gamma q\overline{F}}\right) \equiv \alpha\gamma q N^* \\ J_{13}^* = 0 \\ J_{21}^* = -\frac{d-b}{\alpha} \equiv -\gamma q F^* \\ J_{22}^* = -g\frac{d-b}{\alpha\gamma q\overline{F}} \equiv -g\frac{F^*}{\overline{F}} \\ J_{23}^* = 0 \\ J_{31}^* = 0 \\ J_{32}^* = 0 \\ J_{33}^* = g - g\delta_1\frac{d-b}{\alpha\gamma q}\left(1 - \frac{d-b}{\alpha\gamma q\overline{F}}\right) \equiv g - \delta_1 g F^*\left(1 - F^*/\overline{F}\right) \end{cases} \tag{23}$$

A corresponding characteristic equation is: $(J_{11}^* - \lambda)\left[(J_{22}^* - \lambda)(J_{33}^* - \lambda) - J_{32}^* J_{23}^*\right] = 0$ which delivers: $\lambda_1 = J_{11}^* = 0$, $\lambda_2 = J_{22}^* = -g\frac{F^*}{\overline{F}}$ and $\lambda_3 = J_{33}^* = g\left(1 - \delta_1\frac{d-b}{\alpha\gamma q}\left(1 - \frac{d-b}{\alpha\gamma q\overline{F}}\right)\right)$. $B^* = 0$ implies the equality $1 - \frac{\delta_1(d-b)}{\alpha\gamma q}\left(1 - \frac{d-b}{\alpha\gamma q\overline{F}}\right) = 0$ holds (from (19)). Therefore, the corner steady state ss3 is stable.

– **Stability of ss4:** Evaluating the J-Matrix at ss4 delivers:

$$J_4^* = \begin{pmatrix} J_{11}^* & J_{12}^* & J_{13}^* \\ J_{21}^* & J_{22}^* & J_{23}^* \\ J_{31}^* & J_{32}^* & J_{33}^* \end{pmatrix} \text{ where } \begin{cases} J_{11}^* = 0 \\ J_{12}^* = \alpha g \left(1 - \frac{d-b}{\alpha\gamma q\overline{F}}\right) \equiv \alpha\gamma q N^* \\ J_{13}^* = 0 \\ J_{21}^* = -\frac{d-b}{\alpha} \equiv -\gamma q F^* \\ J_{22}^* = -g\frac{d-b}{\alpha\gamma q\overline{F}} \equiv -g\frac{F^*}{\overline{F}} \\ J_{23}^* = 0 \\ J_{31}^* = -\delta_1\frac{d-b}{\alpha}\overline{B}\left[1 - \frac{\delta_1(d-b)}{\alpha\gamma q}\left(1 - \frac{d-b}{\alpha\gamma q\overline{F}}\right)\right] \\ J_{32}^* = g\overline{B}(-\delta_1 - \delta_2\alpha)\left(1 - \frac{d-b}{\alpha\gamma q\overline{F}}\right)\left[1 - \frac{\delta_1(d-b)}{\alpha\gamma q}\left(1 - \frac{d-b}{\alpha\gamma q\overline{F}}\right)\right] \\ J_{33}^* = g\delta_1\frac{d-b}{\alpha\gamma q}\left(1 - \frac{d-b}{\alpha\gamma q\overline{F}}\right) - g \equiv -g + g\delta_1 F^*\left(1 - F^*/\overline{F}\right) \end{cases} \tag{24}$$

Finding the corresponding eigenvalues requires finding solution to the characteristic equation $(J_{33}^* - \lambda)\left[(J_{11}^* - \lambda)(J_{22}^* - \lambda) - J_{12}^* J_{21}^*\right] = 0$ which after some algebra corresponds to $\left(-g + g\delta_1 F^*(1 - F^*/\overline{F}) - \lambda\right)\left(\lambda^2 + \lambda g F^*/\overline{F} + g(d-b)(1 - F^*/\overline{F})\right) = 0$. The latter implies that the first eigenvalue $\lambda_1 = -g + g\delta_1 F^*(1 - F^*/\overline{F})$ and exploiting the positivity condition (19), it appears that $-1 < -g < \lambda_1 < 0$. Regarding the second part of the characteristic equation, its discriminant is $\Delta = (gF^*/\overline{F})^2 - 4g(d-b)(1 - F^*/\overline{F})$.
Case 1.: When $\Delta > 0$, thus $g\frac{d-b}{\alpha\gamma q\overline{F}} > 4\left[\alpha\gamma q\overline{F} - (d-b)\right]$, one can easily show that both eigenvalues $\lambda_2 = \frac{1}{2}(-gF^*/\overline{F} - \Delta^{\frac{1}{2}})$ and $\lambda_3 = \frac{1}{2}(-gF^*/\overline{F} + \Delta^{\frac{1}{2}})$ are negative real numbers. In this case, ss4 is stable with monotonic convergence.
Case 2.: When $\Delta < 0$, thus $g\frac{d-b}{\alpha\gamma q\overline{F}} < 4\left[\alpha\gamma q\overline{F} - (d-b)\right]$, the eigenvalues λ_2 and λ_3 are complex conjugate with negative real part and SS4 can be characterized as a stable focus.