Ecological Economics 154 (2018) 272–281

Contents lists available at ScienceDirect

Ecological Economics

journal homepage: www.elsevier.com/locate/ecolecon

Analysis

Sustainable Land-use Management Under Biodiversity Lag Effects

A.-S. Lafuite*, G. Denise, M. Loreau

Centre for Biodiversity Theory and Modelling, Theoretical and Experimental Ecology Station, CNRS and Paul Sabatier University, Moulis, France

ARTICLE INFO

Keywords:
Biodiversity
Ecosystem services
Extinction debt
Social-ecological system
Sustainability
Land tax

ABSTRACT

The destruction of natural habitats for agricultural production results in local biodiversity loss. Biodiversity loss in turn affects agricultural production indirectly through a range of biodiversity-dependent ecosystem services. Land conversion thus results in a negative externality, mediated by changes in biodiversity. When the consequences of this externality are delayed in time, lack of internalization results in overshoot-and-collapse dynamics, which are undesirable from a sustainability perspective. Here, we emphasize the importance of forward-looking policies for the long-term sustainability of human–nature interactions. We show that the internalization of this externality through a land tax can result in several win-win effects in the long run. First, more biodiversity is preserved at equilibrium, which increases the carrying capacity and total well-being of the human population. Second, a taxation path that maximizes the discounted sum of human utilities prevents or greatly alleviates overshoot-and-collapse crises, thus increasing the sustainability of the system. In particular, this result holds in the case of imperfect information regarding the precise temporal dynamics of biodiversity loss, suggesting that the design of efficient land-use management policies is possible despite incomplete ecological data. This study highlights the need to internalize biodiversity-dependent externalities through economic incentives, especially under uncertainty regarding long-term ecological dynamics.

1. Introduction

Human use of land has transformed ecosystems across most of the terrestrial biosphere for millennia (Ellis et al., 2013). The conversion of natural lands to croplands, pastures and urban areas represents the most visible form of human impact on the environment (Meyer and Turner, 1992), with 40% of Earth's land surface being currently under agriculture (Sanderson et al., 2002), and 75% experiencing measurable human pressures (Venter et al., 2016). These pressures are rapidly intensifying in biodiversity-rich places, since most land conversion occurs in the tropics through forest conversion to agriculture (McGranahan et al., 2005; Hansen et al., 2013). As a consequence, land use and land cover changes are among major drivers of biodiversity loss, at both local (Newbold et al., 2015) and global scales (Foley et al., 2005).

In turn, biodiversity loss affects the provisioning of essential ecosystem services, such as pollination, pest control, nutrient cycling and erosion control (Cardinale et al., 2012), with consequences on many human activities, and especially for agricultural production (Foley et al., 2005). Biodiversity loss is thus a major and underestimated feedback that may affect human population growth in the long run (Motesharrei et al., 2016), and concerns about the potential of land-use changes to push terrestrial biodiversity beyond major planetary boundaries are rising (Newbold et al., 2016).

These impacts of land-use changes on biodiversity are poorly reflected in market prices, and hence have been mostly ignored by decision-makers, despite their large cost for human economies. The estimated value for global ecosystem services was \$145 trillion in 2011, which represents up to \$20 trillion loss per year between 1997 and 2011 (Costanza et al., 2014b). Loss of biodiversity-dependent ecosystem services thus constitutes a negative externality, which threatens intergenerational equity (Brundtland et al., 1987) along with the sustainability of coupled human–nature systems (Lafuite and Loreau, 2017). As a result, taking this loss into account is crucially needed to implement prudent and forward-looking policies that address biodiversity and natural habitat loss.

At the global scale, natural habitat loss is primarily driven by the growth of the human population (Dietz et al., 2007), and arable lands are rapidly shrinking (Lambin and Meyfroidt, 2011). Recent evidence suggests that land use efficiency has been rising at the global scale (Venter et al., 2016). However, such efficiency gains may not help save natural habitats and biodiversity in the long run, due to economic rebound effects, i.e., if lower prices stimulate demand and if higher yields raise profits, thus encouraging agricultural expansion (Lambin and Meyfroidt, 2011). By increasing the opportunity cost of conservation,

* Corresponding author.
E-mail address: lafuite.as@gmail.com (A.-S. Lafuite).

https://doi.org/10.1016/j.ecolecon.2018.08.003
Received 18 April 2018; Received in revised form 3 August 2018; Accepted 8 August 2018
0921-8009/

these effects undermine the efficiency of regulatory environmental policies, such as government protected forests and natural habitats, in protecting biodiversity (Phalan et al., 2016).

Land-sparing mechanisms that could help overcome these rebound effects include land zoning, incentive-based economic instruments (e.g., land taxes, subsidies and payments), spatially strategic intensification and voluntary standards (Phalan et al., 2016). Especially, incentive-based mechanisms such as land taxes may allow internalizing the externality of land conversion on biodiversity-dependent ecosystems services and agricultural production (Cropper and Oates, 1992). Such mechanisms are based on economic efficiency concepts, so as to achieve the maximum amount of resource protection for a given production level.

During the past decade, the European Union has widely used incentive-based mechanisms to reduce gas emissions from motor fuels and vehicles, but also plastic bags, landfill waste, batteries, pesticides, and fertilizers. Mounting evidence shows that taxes have helped reducing pollution and the consumption of natural resources in many cases, with a higher efficiency and at lower costs than conventional regulatory approaches (Costanza et al., 2014a). However, use of such negative price signals for environmentally damaging activities has been less spread in the US, where tax credits and deductions are favored. More generally, interest group pressures, extensive data requirements (e.g., regarding the external costs of human activities) and scientific uncertainty tend to reduce the level of acceptance of taxes.

Indeed, the efficiency of conventional taxes is limited by available scientific knowledge. This is especially true for the relationship between biodiversity-dependent ecosystem service loss and land use changes, for which there is still a high uncertainty regarding the long-term temporal dynamics of ecosystems in the context of accumulating extinction and functioning debts (Tilman et al., 1994; Isbell et al., 2015; Haddad et al., 2015; Lafuite and Loreau, 2017; Lafuite et al., 2017), i.e., the time-delayed loss of species and services following a change in land use. Moreover, conventional taxes do not necessarily guarantee intergenerational equity and sustainability, i.e., they do not prevent the over-use of natural capital and reductions in human well-being over time (Brundtland et al., 1987; Pezzey, 1992).

As a result, some authors have proposed to define a broad natural capital depletion tax to ensure that resource inputs from the environment to the economy remain sustainable (Costanza, 1991; Costanza and Daly, 1992; Perrings, 1991). Implementation of such a tax would raise prices of natural resources, thus encouraging technological advances while slowing down the rate of environmental depletion (Costanza et al., 2014a). Other authors have proposed a corrected version of the net national product in order to account for the effect of agricultural land development on biodiversity, while ensuring a constant social welfare (Hartwick, 1995; Endres and Radke, 1999).

However, these developments have poorly accounted for the temporal dynamics of biodiversity-dependent ecosystem service loss, and have ignored its consequences for human demography. Biodiversity-dependent agricultural consumption affects human demography, resulting in a dynamic feedback loop between biodiversity loss and human population growth, mediated by land conversion (Lafuite and Loreau, 2017; Lafuite et al., 2017). Time delays between land conversion and biodiversity loss, i.e., extinction debts (Tilman et al., 1994), result in a lagged feedback on agricultural production (Pingali, 2012; Haddad et al., 2015; Isbell et al., 2015). Such lag effects can result in overshoot-and-collapse population cycles that transiently reduce human well-being, and undermine the sustainability of the system (Lafuite and Loreau, 2017; Lafuite et al., 2017).

In this paper, we propose to assess the efficiency of a natural land depletion tax in securing sustainability and preserving biodiversity, despite uncertainty about the temporal dynamics of biodiversity loss. The paper is organized as follows. In Section 1, we present a dynamical system model that couples human demography and technological change to biodiversity loss, through the effect of land conversion on the flow of biodiversity-dependent ecosystem services to agricultural production (Lafuite and Loreau, 2017; Lafuite et al., 2017). In Section 2, the externality of land conversion on biodiversity is internalized through a natural land depletion tax τ per unit of converted land. We show how this tax affects the consumption levels, the ratio of the production inputs, and the rate of land conversion. In Section 3, we analyze the effects of this tax on the long-term equilibrium and sustainability of the system, as captured by a criterion ensuring a non-decreasing human well-being over time. We show that a land tax can increase both biodiversity and total agricultural production at equilibrium, when the substitution of labor and ecosystem services for land has a net positive effect on total agricultural production. The land tax also reduces the vulnerability of the system to time delays, but its ability to prevent crises depends on its level at equilibrium, and thus on the land conversion policy. Section 4 derives the optimal land conversion policy designed by a foresighted planner, who aims to internalize the externality of land conversion on biodiversity under the assumption that the temporal dynamics of biodiversity is unknown. We illustrate the efficiency of such a policy in preserving biodiversity, increasing total production, and preventing the unsustainable consequences of time-delayed ecological feedbacks. Our paper thus emphasizes the importance of forward-looking policies for the long-term sustainability of human–nature interactions, especially under lagged biodiversity feedbacks.

2. A Simple Land-Biodiversity-Demography Model

2.1. Substitution of Production Inputs for Natural Capital

We build upon the model of Lafuite and Loreau (2017), which considers a population of consumers whose demand for agricultural ($i = 1$) and industrial ($i = 2$) goods requires the conversion of their common natural habitat. The two goods in the model are each produced using labor L_i and land A_i. We assume full-employment, i.e., total labor is equal to the size of the human population. Only converted land is capable of producing these goods, while land not converted for production remains as natural habitat capable of supporting a diversity of species, which provides a range of biodiversity-dependent ecosystem services to agricultural production (Cardinale et al., 2012).

By using Cobb-Douglas production functions (Eq. (1)), we allow for the partial substitution between production inputs (labor and land), natural capital (biodiversity-dependent services) and technology.

$$Y_1 = \underbrace{\mathrm{TB}^{\Omega}}_{TFP} L_1^{\alpha_1} A_1^{1-\alpha_1} \qquad Y_2 = \underbrace{\mathrm{T}}_{TFP} L_2^{\alpha_2} A_2^{1-\alpha_2} \tag{1}$$

Total factor productivity (TFP) increases with technological efficiency in both sectors, as well as with biodiversity-dependent ecosystem services in the agricultural sector. The ecosystem services provided by this community of species are assumed to increase with biodiversity and saturate at high levels of species richness, through a power-law relationship B^{Ω}, where $\Omega \in [0,1]$ (O'Connor et al., 2017). Technological efficiency is also assumed to follow a logistic growth towards a maximum efficiency, T_m, in order to reproduce past agricultural productivity rise and current stagnation (Zeigler and Steensland, 2016) (Fig. 1).

2.2. Dynamical System

The long-term behavior of the population is captured by a feedback loop between three dynamical variables: the human population H (Eq. (2)), biodiversity B (Eq. (3)), and technological efficiency T (Eq. (4)).

$$\dot{\mathrm{H}} = \mu \mathrm{H}(1 - \exp(y_1^{min} - y_1(\mathrm{B, T})))\exp(-b_2 y_2(\mathrm{T})) \tag{2}$$

$$\dot{\mathrm{B}} = -\epsilon(\mathrm{B} - S(\mathrm{H})) \tag{3}$$

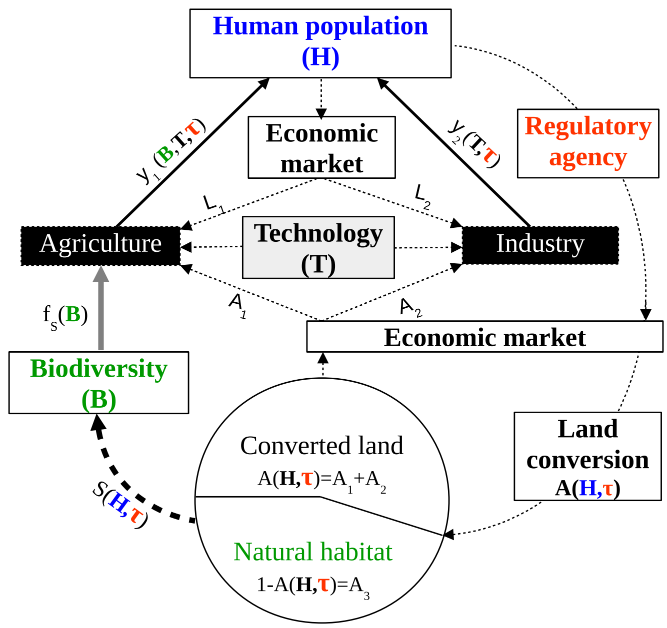

Fig. 1. A simple land use, biodiversity and human demography model. τ: natural land depletion tax; y_1: *per capita* agricultural consumption; y_2: *per capita* industrial consumption; L: labor; A: land; S: species-area relationship; f_S: biodiversity-dependent ecosystem services.
Source: Modified from Lafuite and Loreau (2017).

$$\dot{\mathrm{T}} = \sigma\mathrm{T}(1 - \mathrm{T}/T_m) \tag{4}$$

Human demography can be related to the agricultural and industrial consumptions (Galor and Weil, 2000; Kogel and Prskawetz, 2001; Anderies, 2003; Peretto and Valente, 2015), y_1(B,T) and y_2(T) respectively. These consumptions are derived at market equilibrium (Appendix):

$$y_1 = \gamma_1 \mathrm{B}^{\Omega}\mathrm{T}/T_m \qquad y_2 = \gamma_2\mathrm{T}/T_m \tag{5}$$

where γ_1 and γ_2 are functions of the parameters of the system (Table 2). A higher agricultural production allows the population to grow at a maximum rate μ while the average *per capita* consumption is higher than a minimum consumption, y_1^{min}. Human population growth is slowed down by a demographic transition factor, the strength of which increases with industrial production, technological efficiency, and a scaling parameter b_2. The number of remaining species S is determined by a species–area curve relationship, $S(\mathrm{H}) = (1 - \mathrm{H}/\phi)^z$, where z is a constant parameter (Connor and McCoy, 1979; McGuiness, 1984; Storch et al., 2012; Rybicki and Hanski, 2013), and ϕ is the density of the human population on converted land at market equilibrium (Table 2).

Human population growth results in land conversion that reduces the number of species S(H) supported by natural habitat, thus leading to species extinction. As a result of extinction debts, these extinctions are delayed in time (Tilman et al., 1994; Hanski and Ovaskainen, 2002), hence the long-term species richness may be reached only after decades (Wearn et al., 2012). In order to account for this temporal dynamics, we build upon theoretical and experimental evidence regarding the relaxation rate of natural communities following habitat loss (Diamond, 1972; Wearn et al., 2012). We thus assume that this rate is proportional to the difference between current biodiversity B and its long-term equilibrium value under current conditions, S(H), scaled by a relaxation parameter ϵ.

2.3. Sustainability Conditions

In order to meet the basic requirements for sustainability (Brundtland et al., 1987), sustainability conditions must ensure a non-declining human well-being over time (Hartwick, 1995; Endres and Radke, 1999). As a proxy for human well-being, we use consumption utility $U = y_1^{\eta} y_2^{1-\eta}$, which is a function of the agricultural and industrial consumptions, y_1 and y_2, and the preference for agricultural goods η. Model analysis allows deriving two necessary conditions for its stability and sustainability (Lafuite and Loreau, 2017), which involve (1) a sufficiently high level of substitution of technology for natural capital on the one hand (Eq. (6)), and (2) the resistance to transient overshoot-and-collapse population crises on the other (Eq. (7)).

Condition (6) implies that rising technological efficiency only compensates for the negative feedback of biodiversity-dependent ecosystem services on agriculture if it is higher than the loss of services in terms of human well-being, i.e.,

$$T_m/\mathrm{T}(0) > (\mathrm{B}(0)/\mathrm{B}^*)^{\Omega\eta} \tag{6}$$

However, this condition is not sufficient to ensure sustainability, since time delays in the feedback of biodiversity loss on human demography can result in unsustainable overshoot-and-collapse population cycles. In order to secure sustainability in the long run, the difference between the rates of biodiversity loss and human population growth must not be too large, so that condition (7) can be met.

$$\epsilon > \sigma\mu \tag{7}$$

where σ is a function of the parameters of the system (Table 2). Let us define $\Delta = \epsilon - \sigma\mu$, so that condition (7) can be rewritten as $\Delta > 0$.

In the following, we aim at assessing the efficiency of a land tax in preserving the sustainability of this system under a time-delayed biodiversity feedback on human population growth. First, we show how the tax affects the consumption levels, conversion rate and long-term equilibria of the system.

3. A Natural Land Depletion Tax

3.1. Production

A tax τ per unit of converted area is added to the maintenance cost of κ units of labor per unit of land. At each period, the production profit in sector $i = \{1,2\}$ is

$$\Pi_i = p_i \mathrm{T} \quad \mathrm{B}^{\Omega} \quad \mathrm{L}_i^{\alpha_i} \quad \mathrm{A}_i^{1-\alpha_i} - wL_i - (\kappa w + \tau)A_i$$

with L_i the human labor, A_i the exploited area in sector i, p_i the price of the output, w the consumer wage, and α_i the elasticity of labor. Profit maximization gives the production supply for each sector (Appendix), and the relationship between input factors in each sector (Eq. (8)) shows that a tax τ increases the optimal ratio of labor to land, thus generating an incentive to substitute land for labor.

$$\mathrm{L_i}/\mathrm{A_i} = (\kappa + \tau)\alpha_i/(1 - \alpha_i) \tag{8}$$

3.2. Consumption

The total revenue of the tax τA, where $\mathrm{A} = A_1 + A_2$ is total converted land, is then redistributed among the consumers, who are assumed to maximize their consumption utility U under their revenue constraint $p_1y_1 + p_2y_2 \le w + \tau\mathrm{A}/\mathrm{H}$. As a result of this redistribution, the total demand for agricultural and industrial goods (Eq. (9)) increases with the land tax.

$$p_1 Y_1^D = \eta(w + \tau\mathrm{A}/\mathrm{H})\mathrm{H} \qquad p_2 Y_2^D = (1 - \eta)(w + \tau\mathrm{A}/\mathrm{H})\mathrm{H} \tag{9}$$

At the equilibrium between supply and demand, the optimal allocations of labor and land (Appendix) provide the equilibrium consumptions in the agricultural and industrial sectors:

$$y_{1\tau} = (\phi/\phi_\tau)(1 + \tau/\kappa)^{\alpha_1} y_1 \qquad y_{2\tau} = (\phi/\phi_\tau)(1 + \tau/\kappa)^{\alpha_2} y_2 \tag{10}$$

where y_1 and y_2 are the business-as-usual consumptions (Eq. (5)), and ϕ

and ϕ_τ (Eq. (11)) are the densities of the human population on converted land, in the business-as-usual and the regulated cases, respectively.

3.3. Land Conversion

The density of the human population on converted land, $\phi_\tau = \mathrm{H}/\mathrm{A}$, also derives from the labor market equilibrium $L_1 + L_2 + \kappa\mathrm{A} = \mathrm{H}$, where $\kappa\mathrm{A}$ is the labor required for land conversion and maintenance.

$$\phi_\tau = \phi + \tau(\phi/\kappa - 1) \tag{11}$$

where ϕ is the population density in the absence of regulation (Table 2). Note that $\phi > \kappa$ since $\alpha_i \in [0,1]$ and $\eta \in [0,1]$, so that $\phi_\tau > \phi$. A tax τ per unit of converted land thus increases the human population density on converted land, which affects the converted surface $\mathrm{A} = \mathrm{H}/\phi_\tau$, and the long-term number of species that the remaining natural habitat can support, $S(\mathrm{H}) = (1 - \mathrm{H}/\phi_\tau)^z$.

Since ϕ_τ increases with τ, the effect of the tax on consumptions (Eq. (10)) is not straightforward, and depends on the economic parameters of the system. Moreover, a land taxation policy will only help preserve more natural habitats and biodiversity compared with a business-as-usual case, if the human population density on converted land ϕ_τ increases faster than the size of the human population, H. The next section explores the conditions under which this objective can be met, by studying the effects of the tax on the equilibrium features of the model.

4. Dynamical System Analysis

Here, we analyze the effect of a land tax τ on the equilibria of the regulated system:

$$\begin{cases} \dot{\mathrm{H}} = \mu \quad \mathrm{H} \quad (1 - \exp(y_1^{min} - y_{1\tau}(\mathrm{B}, \mathrm{T})))\exp(-b_2 y_{2\tau}(\mathrm{T})) \\ \dot{\mathrm{T}} = \sigma\mathrm{T}(1 - \mathrm{T}/T_m) \\ \dot{\mathrm{B}} = -\epsilon \quad [\mathrm{B} - (1 - \mathrm{H}/\phi_\tau)^z] \end{cases} \tag{12}$$

Parameters and functions are summarized in Tables 1 and 2.

4.1. Steady States and Sustainability Conditions

The equilibrium of the system is reached when technological efficiency is at its maximum level T_m ($\dot{\mathrm{T}} = 0$), human consumption is at its equilibrium level y_1^{min} so that human population cannot grow anymore ($\dot{\mathrm{H}} = 0$), and the extinction debt of biodiversity has been entirely paid, so that $\mathrm{B} = S(\mathrm{H})$ ($\dot{\mathrm{B}} = 0$).

There are two possible equilibria: (1) a desirable equilibrium, $(H_\tau^*, T_m, B_\tau^*)$, and (2) an undesirable equilibrium, $(0, T_m, 1)$.

$$B_\tau^* = (y_1^{min}/\gamma_{1\tau})^{1/\Omega} \qquad H_\tau^* = \phi_\tau(1 - B_\tau^{*1/z})$$

where $\gamma_{1\tau}$ and ϕ_τ are explicitly defined in Table 2.

The sustainability conditions (6) and (7) of the system now depend on the tax τ (Table 2):

$$T_m/\mathrm{T}(0) > (\mathrm{B}(0)/B_\tau^*)^{\Omega\eta} \qquad \Delta_\tau > 0 \tag{13}$$

4.2. Effects of the Tax on Equilibrium Properties

The effect of the tax τ on the equilibrium properties of the model is mediated by the relationships $\gamma_{1\tau}(\tau)$, i.e., the level of substitution of land and labor for natural capital in the agricultural production, and $\gamma_{2\tau}(\tau)$, i.e., the *per capita* level of industrial consumption at equilibrium. Indeed, biodiversity at equilibrium B_τ^* directly depends on $\gamma_{1\tau}$, which in turn determines the level of human population H_τ^*, while $\gamma_{2\tau}$ determines the level of industrial consumption, and thus human well-being at equilibrium, $u^* = (y_1^{min})^\eta \gamma_{2\tau}^{1-\eta}$.

The shapes of $\gamma_{1\tau}(\tau)$ and $\gamma_{2\tau}(\tau)$ depend on the economic parameters of the system, and especially on the labor elasticities in the agricultural and industrial sectors, α_1 and α_2. Labor elasticity captures the increase in output resulting from a 1% increase in labor. Since the main effect of the tax is to increase the ratio of labor to land, varying labor elasticities between sectors result in differing effects of the taxation policy on the equilibrium features of the system.

Table 1
Definition and default values of the parameters and dynamical variables. H: units of labor; t: units of time.

	Parameters	Default values
Economic parameters		
η	Agents' preference for agricultural goods	0.5
α_1	Agricultural labor elasticity	*Varies*
α_2	Industrial labor elasticity	*Varies*
δ	Discount rate	0.04
Technological parameters		
T_m	Maximum technological efficiency	1
σ	Rate of technological change	3
κ	Land operating cost	0.2
Demographic parameters		
μ	Maximum growth rate	1
y_1^{min}	Minimum *per capita* agricultural consumption	0.3
b_2	Sensitivity to industrial goods' consumption	0.1
Ecological parameters		
Ω	Concavity of the BES relationship	0.4
z	Concavity of the SAR	0.3
ϵ	Ecological relaxation rate	1
	Variables	**Initial values**
H	Human population size	0.1
B	Biodiversity	1
T	Technology	0.5

Table 2
Functions and aggregate parameters expression and definition. The expressions in the unregulated case are obtained by taking $\tau = 0$, so that $\gamma_1 = \gamma_{1(\tau=0)}$, $\gamma_2 = \gamma_{2(\tau=0)}$, $\Delta = \Delta_{(\tau=0)}$.

	Functions and aggregate parameters	Definition
ϕ	$\frac{\kappa}{1-\alpha_1\eta-\alpha_2(1-\eta)}$	Population density without regulation
ϕ_τ	$\phi + \tau\left(\frac{\phi-\kappa}{\kappa}\right)$	Population density with regulation
$\gamma_{2\tau}$	$T_m(1-\eta)\alpha_2^{\alpha_2}\left(\frac{1-\alpha_2}{\kappa}\right)^{1-\alpha_2}\frac{\phi}{\phi_\tau}\left(\frac{\kappa+\tau}{\kappa}\right)^{\alpha_2}$	Max. *per capita* industrial consumption
$\gamma_{1\tau}$	$T_m\eta\alpha_1^{\alpha_1}\left(\frac{1-\alpha_1}{\kappa}\right)^{1-\alpha_1}\frac{\phi}{\phi_\tau}\left(\frac{\kappa+\tau}{\kappa}\right)^{\alpha_1}$	Max. *per capita* agricultural consumption
Δ_τ	$\epsilon - 4\Omega z y_1^{min}\left(\left(\frac{\gamma_{1\tau}}{y_1^{min}}\right)^{\frac{1}{\Omega z}} - 1\right)e^{-b_2\gamma_{2\tau}\mu}$	Sustainability criterion

4.2.1. Effect on Biodiversity, Sustainability and Population Size

It can be shown that

$$\partial(B_\tau^* - B^*)/\partial\tau > 0 \quad \mathit{for} \quad \alpha_1 \le \alpha_2 \tag{14}$$

so that the tax τ always has a positive effect on the long-term level of biodiversity, when the labor elasticity of the industrial sector is higher than or equal to that of the agricultural sector ($\alpha_2 \ge \alpha_1$), which corresponds to the most common situation in real-world systems.

Under the assumption that $\alpha_1 \le \alpha_2$, we distinguish two situations:

(1) labor elasticity is higher in the industrial than in the agricultural sector ($\alpha_2 > \alpha_1$), so that $\gamma_{1\tau}$ decreases with τ while $\gamma_{2\tau}$ increases (Fig. 2A/C/E/G) and (2) labor elasticity in the industrial and agricultural sectors are similar ($\alpha_2 \approx \alpha_1$), so that both $\gamma_{1\tau}$ and $\gamma_{2\tau}$ decrease with τ (Fig. 2B/D/F/H).

In both cases, a tax τ thus increases biodiversity at equilibrium, since $\gamma_{1\tau}$ decreases with τ (Fig. 2C and D). By increasing the ratio of labor to land, the tax reduces land conversion and allows preserving more biodiversity. This higher biodiversity level at equilibrium ensures a higher sustainability of the system, which becomes less vulnerable to transient overshoot-and-collapse crises, as captured by our sustainability criterion $\Delta_\tau > 0$ (Fig. 2G and H).

This reduction of land conversion is not only compensated by a higher natural capital, but also by a larger labor force, which increases the size of the human population (Fig. 2A and B). However, the effect of the tax on the size of the human population at equilibrium is non-linear, since high tax levels reduce the incentive for land conversion to the point where it becomes economically unviable to convert more land, thus reducing the size of the human population at high tax levels (Fig. 2A and B).

4.2.2. Effect on Industrial Consumption and Human Well-being

The difference between cases (1) and (2) lies in the effect of τ on the consumption of industrial goods at equilibrium, $\gamma_{2\tau}$, and thus on human well-being. When labor elasticity is higher in the industrial than in the agricultural sector ($\alpha_2 > \alpha_1$), land taxation increases industrial consumption at equilibrium compared with the business-as-usual case (Fig. 2E). However, if the industrial labor elasticity is lower ($\alpha_2 \approx \alpha_1$), land taxation reduces industrial consumption (Fig. 2F).

The tax level required to achieve a positive sustainability criterion (Fig. 2G and H) or to maximize human well-being (Fig. 2A and B) is much higher in case (2) than in case (1), so as to compensate for the lower labor-to-land ratio of the industrial sector. Thus, the total labor force is also higher than in case (1) (Fig. 2A and B). This increase in population size reduces both *per capita* industrial consumption and human-well-being (Fig. 2E and F). Despite its positive effects on biodiversity and sustainability, a land tax may thus reduce *per capita* well-being if the initial labor elasticities are too low, through a large increase in labor, i.e., population size.

Finally, in both cases, the higher the extinction debt, the higher the tax on land conversion should be in order to avoid unsustainable trajectories (Fig. 2G and H). As a result, a given tax level may not necessarily guarantee sustainability. For example, a tax τ_{opt} that maximizes human population size and total well-being at equilibrium (Fig. 2A), only guarantees sustainability for low extinction debts, e.g., $\epsilon = 1$, since $\Delta_{\tau=\tau_{opt}} > 0$ in this case, but not for larger debts, e.g., $\epsilon = 0.01$ (Fig. 2G). In the next section, the optimal land conversion policy is derived in the case of a foresighted regulator, and its efficiency in preventing crises is explored.

5. Optimal Land Conversion Policy

Here, we allow the tax to vary with the dynamical variables of the system, so as to internalize the negative effects of biodiversity loss on agricultural production at each time.

5.1. Analytical Derivations

At each time, and for a population size H, a technological efficiency T, and a biodiversity level $\mathrm{B} = (1 - \mathrm{H}/\phi_\tau)$, we assume that a benevolent social planner aims at maximizing the total discounted utility of consumers,

$$U_\tau(\mathrm{B, T, H}) = \mathrm{H}\cdot y_{1\tau}(\mathrm{B, T})^\eta y_{2\tau}(\mathrm{T})^{1-\eta}$$

using a land tax τ per unit of converted land as control. This land tax limits the conversion of natural habitat so as to internalize the negative externalities on biodiversity and agricultural production, and varies with the dynamical variables of the system.

The objective of the social planner is to maximize the present value of a continuous sum of discounted utilities, at an annual rate δ, subject to the dynamics of the human population, $\dot{\mathrm{H}}$ (Eq. (2)), technological change $\dot{\mathrm{T}}$ (Eq. (4)), the consumptions levels $y_{1\tau}$ and $y_{2\tau}$, as well as to the loss of biodiversity, $\mathrm{B} = (1 - \mathrm{H}/\phi_\tau)$. Thus, we assume here that the social planner does not know the temporal dynamics of biodiversity loss, $\dot{\mathrm{B}}$ (Eq. (3)). However, he accounts for the long term effects of land conversion on biodiversity, through the use of a species-area relationship, which is one of the best-known patterns in ecology (Rosenzweig, 1995).

$$\max \int_{t_0}^{\infty} \exp(-\delta t)\cdot U_\tau(\mathrm{B, T, H})\,\mathrm{d}t$$

subject to

$$\begin{cases} \dot{\mathrm{H}} = \mu\mathrm{H}(1 - \exp(y_1^{min} - y_{1\tau}(\mathrm{B, T}))\exp(-b_2 y_{2\tau}(\mathrm{T})) \\ \dot{\mathrm{T}} = \sigma\mathrm{T}(1 - \mathrm{T}/T_m) \\ \mathrm{B} = (1 - \mathrm{H}/\phi_\tau)^z \\ y_{1\tau} = \gamma_{1\tau}\mathrm{B}^\Omega\mathrm{T}/T_m \\ y_{2\tau} = \gamma_{2\tau}\mathrm{T}/T_m \end{cases} \tag{15}$$

The Hamiltonian function for this problem is

$$\mathscr{H} = U_\tau(\mathrm{B, T, H}) + \lambda_H\dot{\mathrm{H}} + \lambda_T\dot{\mathrm{T}} \tag{16}$$

where λ_H and λ_T are adjoint variables. First order conditions are

$$\partial\mathscr{H}/\partial\tau = 0,\ \partial\mathscr{H}/\partial\mathrm{H} = \delta\lambda_H - \dot{\lambda}_H,\ \partial\mathscr{H}/\partial\mathrm{T} = \delta\lambda_T - \dot{\lambda}_T \tag{17}$$

and transversality conditions are

$$\lim_{t\to+\infty} \mathrm{H}(t)\cdot\lambda_H(t) = 0 \qquad \lim_{t\to+\infty} \mathrm{T}(t)\cdot\lambda_T(t) = 0$$

Solving for the first order condition $\partial\mathscr{H}/\partial\tau = 0$ gives the optimal tax τ as a solution of the following equation:

$$\begin{aligned}&(\partial y_{1\tau}/\partial\tau)(\eta(y_{2\tau}/y_{1\tau})^{1-\eta} + \lambda_H\mu\exp((y_1^{min} - y_{1\tau} - b_2 y_{2\tau})))\\ &\quad = (\partial y_{2\tau}/\partial\tau)(b_2\lambda_H\mu exp(-b_2 y_{2\tau})(1 - exp(y_1^{min} - y_{1\tau}))\\ &\qquad - (1-\eta)(y_{1\tau}/y_{2\tau})^\eta)\end{aligned} \tag{18}$$

Solving for the first order condition $\partial\mathscr{H}/\partial\mathrm{H} = \delta\lambda_H - \dot{\lambda}_H$ gives the dynamics of the adjoint variable λ_H as a function of the other dynamical variables of the system (B,H,T) and the control τ:

$$\begin{aligned}\dot{\lambda}_H = &\ \lambda_H(\delta - \mu\exp(-b_2 y_{2\tau})[(1 - \exp(y_1^{\min} - y_{1\tau}))\\ &+ \mathrm{H}\exp(y_1^{\min} - y_{1\tau})(\partial y_{1\tau}/\partial\mathrm{H})]) - U_\tau - \mathrm{H}(\partial U_\tau/\partial\mathrm{H})\end{aligned}$$

We do not need the last condition, which gives the temporal dynamics $\dot{\lambda}_T$, since technological efficiency varies exogenously, and thus does not depend on the other variables of the system, nor on the control τ.

We then simulate system (12) along with the dynamics of the adjoint variable $\dot{\lambda}_H$, by solving at each time step for τ using Eq. (18)[1]. Thus, though the social planner does not account for time-delayed biodiversity loss, the numerical simulations do include the effect of extinction debts on agricultural production, human consumption and human demography, through the dynamics of biodiversity $\dot{\mathrm{B}}$ (system (12)). Simulations allow exploring the effects of the tax on the transient dynamics of the regulated system.

5.2. Numerical Simulations

Parameters are chosen so as to meet the sustainability condition (6) in the business-as-usual case. This guarantees that the substitution of

[1] MATLAB code and figures are available at https://figshare.com/s/6e8e25a44071f3c544ff.

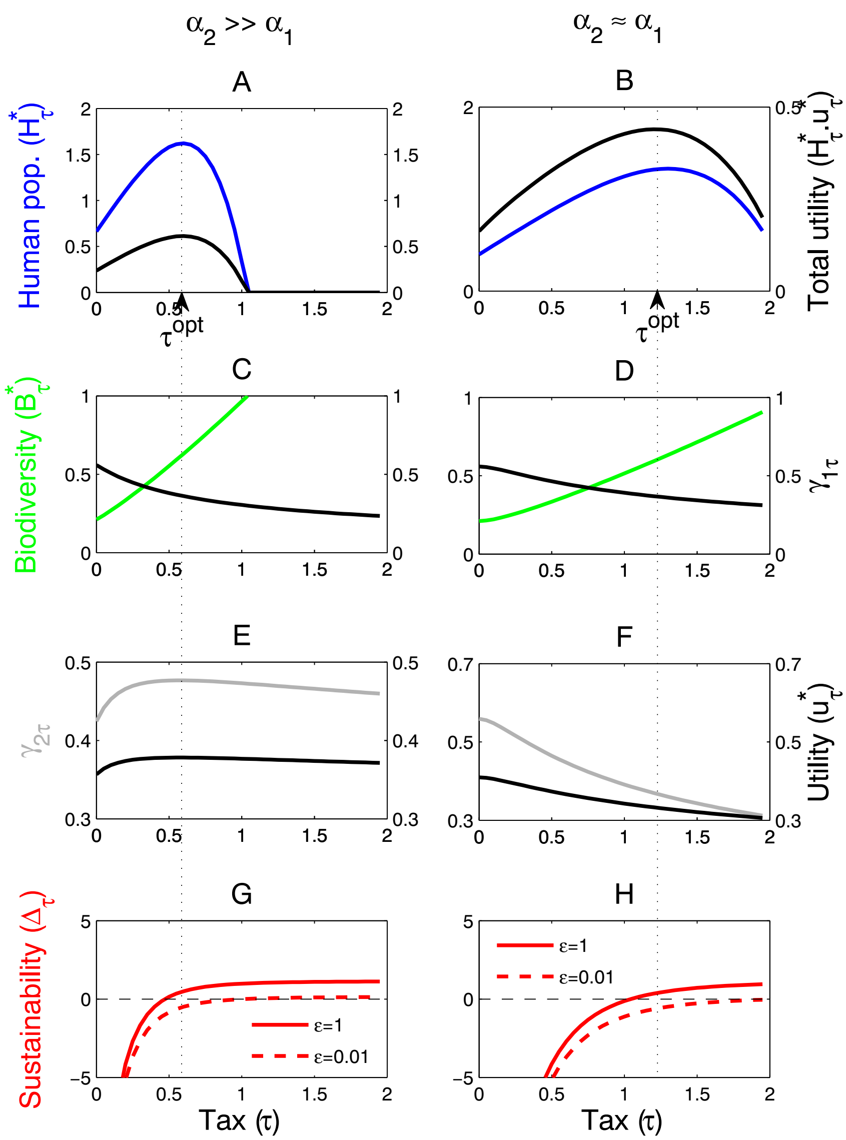

Fig. 2. Effect of a land tax τ on the equilibrium features of the model, for various labor elasticities α_1 and α_2.

technology for natural capital is high enough to ensure a non-declining human well-being over time. Since the tax policy necessarily preserves more biodiversity at equilibrium, the condition remains true in the regulated case. Thus, we can focus on the consequences of ecological time delays for sustainability, by comparing their effects on the regulated and business-as-usual scenarios.

In the case of a negligible extinction debt (e.g., $\epsilon = 1$), both the regulated and business-as-usual trajectories are sustainable, i.e., do not experience transient overshoot-and-collapse population crises. Fig. 3 confirms the effect of land taxation presented in the previous section, since the tax increases biodiversity (Fig. 3C) and human population size (Fig. 3A) at equilibrium, compared with the business-as-usual case.

The optimal tax increases with the size of the human population, before reaching its equilibrium level, previously denoted as τ^{opt} (Fig. 3E). This regulatory policy increases the carrying capacity of the human population, i.e., the maximum population size that the environment can support (Fig. 3A). Moreover, the distance between the population equilibrium and the carrying capacity is larger in the regulated than in the business-as-usual case, a feature that increases the resistance of the system to time delays, i.e., its sustainability (Lafuite and Loreau, 2017).

For a higher extinction debt (e.g., $\epsilon = 0.005$), the regulated system appears much more resistant to transient population crises than is the business-as-usual scenario (Fig. 3B). The transient dynamics of the optimal taxation path also changes at high extinction debts, since the tax reaches higher levels during the initial growth phase of the human population (Fig. 3F) to counteract the faster population growth and prevent it from overshooting its carrying capacity. The efficiency of the optimal taxation policy thus holds for higher extinction debts, and makes the system very resistant to time-delayed feedbacks, despite incomplete knowledge regarding the precise temporal dynamics of biodiversity loss.

Fig. 4 shows the effect of this taxation policy when the system is initially overshooting its carrying capacity ϕ, for various ecological relaxation rates ϵ. Implementation of the optimal tax stops the unsustainable population growth, through a high tax value that fosters land restoration (Fig. 4C). The resultant reduction in the size of the human population (Fig. 4A) leads the tax value to decrease until the sustainable equilibrium is reached, while biodiversity is slowly recovering (Fig. 4B). A larger time delay in biodiversity recovery results in a longer degrowth phase of the human population, the size of which falls below its equilibrium value before increasing again.

In the unregulated scenario, the initial overshoot results in more population growth (Fig. 4A) and biodiversity loss (Fig. 4B), especially at

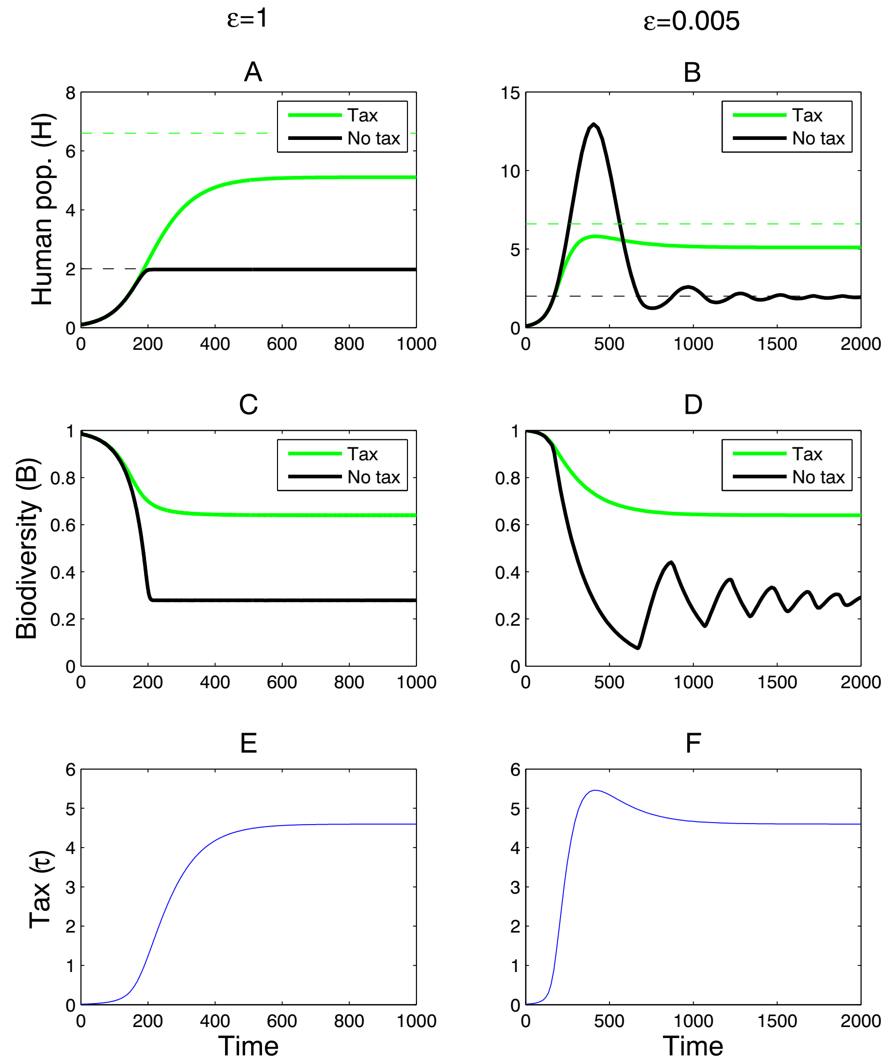

Fig. 3. Land-use management scenarios for varying ecological relaxation rates (ϵ). Dashed lines represent the carrying capacities ϕ of the human population in each case. Initial values: $B(0) = 1$; $H(0) = 0.1$; $T(0) = 0.5$; $\lambda_H(0) = -12$. Parameter values: $\alpha_1 = 0.5$; $\kappa = 1$; $\mu = 0.1$; $y_1^{\min} = 0.3$; $\Omega = 0.4$; $z = 0.3$; $T_m = 1$; $\delta = 0.04$; $\sigma = 0.3$; $\eta = 1$.

high extinction debts. The business-as-usual scenario leads to a larger long-term population reduction than in the regulated case. Policy regulation thus greatly alleviates long-term population crises in a system in overshoot, even when biodiversity recovery is very slow.

6. Conclusions and Discussion

6.1. Summary of the Results

In this paper, we linked a simple general equilibrium market model with a dynamical system coupling human demography, technological change and time-delayed biodiversity loss. We used this toy-model to emphasize the crucial importance of forward-looking policies to preserve both biodiversity and human well-being in the long run, since the implementation of a natural land depletion tax had positive effects on the long-term biodiversity, human carrying capacity, human well-being, and sustainability of the system. The mechanism behind this positive effect of the land tax is the substitution of labor and biodiversity-dependent ecosystem services for land in the agricultural sector. In other words, for the same level of technology, land taxation fosters labor-intensive agricultural practices that preserve natural habitats and biodiversity, such as small-scale agro-ecological farms, as opposed to land-intensive practices that convert more natural habitat and require less human labor. Furthermore, such land-intensive systems are often more technology-intensive, so as to compensate for the lower inputs in human labor and ecological services, a feature which reduces their sustainability even more due to rebound effects, i.e., further land conversion (Lafuite and Loreau, 2017), as well as other deleterious consequences on ecological systems, e.g., pollution.

Internalization of biodiversity-dependent externalities on agricultural production thus fosters ecologically-intensive agricultural systems, that preserve more biodiversity and can support a larger human population. To the extent that biodiversity is aligned with the sustainability of the system, i.e., its resistance to overshoot-and-collapse population crises resulting from a time-delayed loss of biodiversity-dependent ecosystem services (Lafuite and Loreau, 2017), such a land taxation policy means more stability and sustainability. However, a land tax can have adverse consequences for the *per capita* human well-being through its effect on industrial consumption, especially in systems with a low industrial labor intensity, in which substitution of labor for land is not compensated by an increase in natural capital. This result may change when considering a symmetrical effect of biodiversity on both the agricultural and industrial sectors, since many industrial activities rely on natural services. As an example, deforestation and biodiversity loss can affect regional and global climate with feedbacks on hydrology (Shukla et al., 1990) and other important provisioning

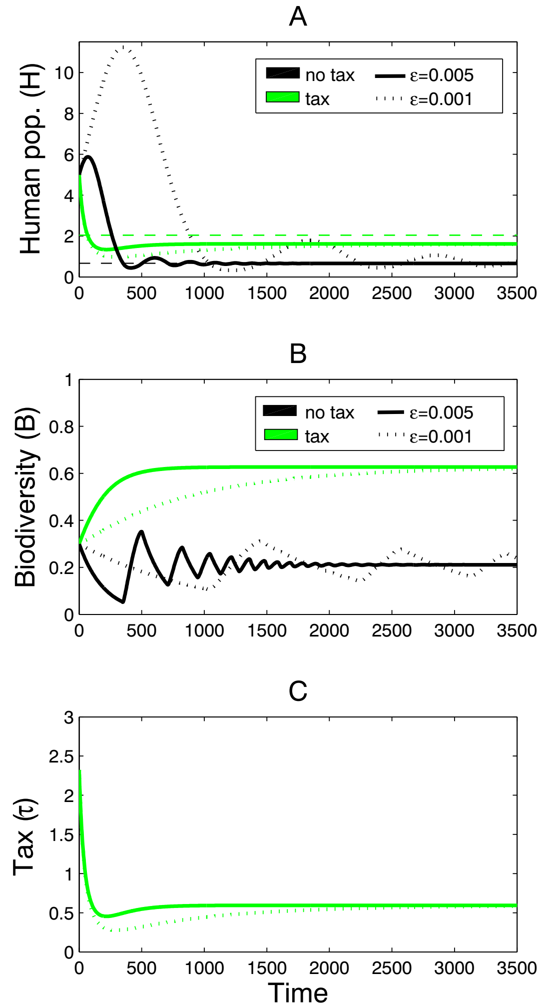

Fig. 4. Land-use management scenarios from an overshoot situation, and for varying ecological relaxation rates (ϵ). The dashed lines represent the carrying capacities ϕ and ϕ_τ of the human population. Initial values: $B(0) = 0.2$; $H(0) = 5$; $T(0) = 0.5$; $\lambda_H(0) = -12$. Parameter values are given in Table 1, except for $\mu = 0.11$. Green curves: regulated system; black curves: business-as-usual; dotted curves: $\epsilon = 0.001$; continuous curves: $\epsilon = 0.005$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

services to the industrial sector, such as wood production and clean water (Lima et al., 2014).

6.2. Steps Forward

The model we developed in this paper was kept relatively simple in order to make clear the basic logic of how economic incentives can affect land conversion, biodiversity conservation and sustainability. For example, the proportional relationship between human population growth and land conversion, which results from the assumption of a constant maintenance cost of κ units of labor per unit of converted land, is unrealistic. Drivers of land use and land cover change are abundant, complex and scale-dependent (Carr and Bilsborrow, 2001). At the global scale, recent evidence that human population and the world economy are growing faster than the human footprint suggests a globally more efficient use of land (Venter et al., 2016), so that endogenizing efficiency gains and technological change along with economic growth appears essential in order to gain realism in the relationship between human population growth and land conversion. There are a number of other ways in which the model could be enriched, both on the economic side and on the ecology side. We assumed that the provisioning of services to productive lands depends on the total area of natural habitat only. In reality, service provisioning is spatially- and distance-dependent, since intermediate habitat heterogeneity and fragmentation is required to provide access to localized services such as pest control and pollination (Mitchell et al., 2015). In turn, habitat fragmentation affects the viability of communities and generates extinction debts (Hanski and Ovaskainen, 2002; Haddad et al., 2015). Expanding the model in this way requires the spatialization and differentiation of economic incentives, and the distinction between local and regional species richness and services. Second, the assumption that species can only utilize natural habitat is also too restrictive, since certain species can persist in human-dominated landscapes (agricultural fields and managed forests). Third, an alternative way to model the demographic sector of the model would be to distinguish between the fertility and death rates, instead of considering the aggregate growth rate of the human population. This would provide a potential mechanism for the fertility decline, since an increasing death rate due to resource scarcity seems to be a more general mechanism than the demographic transition to explain human population growth over large timescales (Motesharrei et al., 2014). Finally, we have modeled utility as a function of the indirect effect of global species richness on private consumption. It is equally plausible that alternative measures of biodiversity enter the utility function, such as its cultural, spiritual, and aesthetic values. Including these would require a different objective function, but would not qualitatively alter the results of this paper.

Enriching both the economic and ecological sides of the model could add insights and greater realism to the analysis of the links between land-use management, sustainability, and biodiversity conservation. Directing policy on the basis of this work, however, will require going beyond the conceptual model presented here. A way to do this would be to include biodiversity as a dynamical feedback on the human demography in existing Integrated Assessment Models (IAMs). For instance, the Integrated Valuation of Ecosystem Services and Tradeoffs (InVEST) model (Nelson et al., 2009) considers multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales, but poorly accounts for the relationships between biodiversity and services, and ignores human demography. Other global Integrated Assessment Modeling frameworks have been developed to specifically address climate change (Carmichael et al., 2004) or water availability (Hejazi et al., 2014) issues. For example, the Dynamic Integrated Climate-Economy (DICE) model has been extensively used to inform optimal tax policies aimed at reducing greenhouse-gas emissions (Nordhaus, 1993); the Global Change Assessment Model (GCAM) couples the economy, energy sector, land use and water with a climate model, but ignores biodiversity feedbacks (Edmonds and Reilly, 1985); the Integrated Global System Modeling (IGSM) framework simulates the evolution of economic, demographic, trade and technological processes, and the resulting greenhouse gas emissions, conventional air and water pollutants, and land-use/land-cover change (Sokolov et al., 2005; Prinn, 2012); the Model for Energy Supply Strategy Alternatives and their General Environmental Impact (MESSAGE) focuses on the global economy and its main sectors (energy, agriculture, forestry), thus neglecting biodiversity feedbacks (Messner and Strubegger, 1995); the Integrated Model to Assess the Global Environment (IMAGE) represents interactions between society, the biosphere and the climate system, but considers population, economy, policy and technology as external drivers (Stehfest et al., 2014); Modelling International Relationships in Applied General Equilibrium (MIRAGE) is a multi-sectoral and multi-regional computable general equilibrium model dedicated to trade policy analysis, in which biodiversity feedbacks could also be included (Decreux and Valin, 2007). Future research should build upon the strengths of each of these IAMs in order to fully account for the complexity of coupled social-ecological systems, including bidirectional feedbacks between biodiversity and human population variables (Motesharrei et al., 2016). Such IAMs are greatly needed to strengthen the emergence of prudent biodiversity policies. These complex models, however, would still contain the basic insights into how time delays and land taxes affect sustainability and biodiversity conservation in the long run, which are highlighted in this paper.

6.3. Towards Forward-looking Biodiversity Policies

Our model considered the use of converted land taxation as a way to preserve natural habitats. Property taxes have been used in several other contexts (Bird and Slack, 2004), as a source of revenue (Skinner, 1991b), a way of promoting urbanization (Oates and Schwab, 1997) or conversely, in order to reduce the use of land for house building (Needham, 2000) and foster land-use efficiency (Bird and Slack, 2004). However, despite the established efficiency of taxes as a way of internalizing the externalities of human activities (Pirard, 2012), such as those of modern agriculture (Pretty et al., 2001), land taxes are rarely used for conservation purposes, especially in rural areas (Skinner, 1991a). Reasons include a higher riskiness of net farmer income, difficulty to administer progressive tax rates based on land holdings, political acceptability of negative price signals (Skinner, 1991b), and costly administration and informational requirements (Lockie, 2013). Indeed, despite mounting evidence of synergies between biodiversity and multiple ecosystem services (Balvanera et al., 2001; Macfadyen et al., 2012; Austin et al., 2016), scientific understanding of ecosystem production functions remains a limiting factor in incorporating natural capital into economic decisions (Daily, 2008). For these reasons, taxes remain marginal in both research and policy to internalize ecosystem services (Pirard, 2012) in comparison with national governmental payment programs (Schomers and Matzdorf, 2013), such as the green payments and subsidies implemented by the European Common Agricultural Policy, whose efficiency in preserving biodiversity appears limited (Kleijn et al., 2001; Kleijn and Sutherland, 2003).

Interestingly, our results suggest that the stabilizing effect of the tax does not require a precise knowledge of the ecological dynamics of the system, and especially of the temporal dynamics of biodiversity loss. Thus, lack of data and uncertainty about complex ecological dynamics should not prevent land-use decision-makers to adopt a precautionary approach to environmental uncertainty (Costanza and Perrings, 1990). Sustainable land-use management policies should build upon well-known ecological patterns, such as species-area relationships (Rosenzweig, 1995), as well as recent advances in ecological research that allow making large-scale predictions up to continental or global scales, ranging from the future distribution of biological diversity to changes in ecosystem functioning and services (Petchey et al., 2015; Isbell et al., 2017). Strong political will is crucially needed to shift the current paradigm and improve the efficiency of agricultural policies, through a better identification and management of the conflicts between agriculture and biodiversity conservation (Henle et al., 2008), and the development of more integrated approaches to policy, land-use, human demography, and biodiversity (Mattison and Norris, 2005).

Acknowledgments

We thank Matthieu Barbier, David Shanafelt, and François Salanié for valuable discussions, and anonymous reviewers for useful comments on the manuscript.

Funding

This work was supported by the TULIP Laboratory of Excellence (ANR-10-LABX-41) and the Midi-Pyrénées Region. This research was conducted within the framework of the BIOSTASES project, funded by the European Research Council (ERC) under the European Union's Horizon 2020 - Research and Innovation Framework Programme (grant agreement No. 666971).

Competing Interests

The authors have no competing interests.

Appendix

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolecon.2018.08.003.

References

Anderies, J.M., 2003. Economic development, demographics, and renewable resources: a dynamical systems approach. Environ. Dev. Econ. 8 (02), 219–246.

Austin, Z., McVittie, A., McCracken, D., Moxey, A., Moran, D., White, P.C.L., 2016. The co-benefits of biodiversity conservation programmes on wider ecosystem services. Ecosyst. Serv. 20, 37–43.

Balvanera, P., Daily, G.C., Ehrlich, P.R., Ricketts, T.H., Baileys, S.-A., Kark, S., Kremen, C., Pereira, H., 2001. Conserving biodiversity and ecosystem services. Science 291 (5511), 2047.

Bird, R.M., Slack, N.E. (Eds.), 2004. International Handbook of Land and Property Taxation. Edward Elgar.

Brundtland, G., Khalid, M., Agnelli, S., Al-Athel, S., Chidzero, B., Fadika, L., Hauff, V., Lang, I., Shijun, M., Morino de Botero, M., Singh, M., Okita, S., et al., 1987. Our Common Future (The Brundtland Report). Oxford University Press.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on humanity. Nature 486 (7401), 59–67.

Carmichael, J., Tansey, J., Robinson, J., 2004. An integrated assessment modeling tool. Glob. Environ. Chang. 14 (2), 171–183.

Carr, D., Bilsborrow, R., 2001. Population and land use/cover change: a regional comparison between Central America and South America. J. Geogr. Educ. 43, 7–16.

Connor, E., McCoy, E., 1979. The statistics and biology of the species-area relationship. Am. Nat. 113, 119–130.

Costanza, R., 1991. Ecological Economics: The Science and Management of Sustainability. Columbia University Press, New York.

Costanza, R., Cumberland, J.H., Daly, H., Goodland, R., Norgaard, R.B., Kubiszewski, I., Franco, C., 2014a. An Introduction to Ecological Economics, 2nd ed. CRC Press.

Costanza, R., Daly, H., 1992. Natural capital and sustainable development. Conserv. Biol. 6 (1), 37–46.

Costanza, R., de Groot, R., Sutton, P., van der Ploeg, S., Anderson, S.J., Kubiszewski, I., Farber, S., Turner, R.K., 2014b. Changes in the global value of ecosystem services. Glob. Environ. Chang. 26 (1), 152–158.

Costanza, R., Perrings, C., 1990. A flexible assurance bonding system for improved environmental management. Ecol. Econ. 2 (1), 57–75.

Cropper, M., Oates, W., 1992. Environmental economics: a survey. J. Econ. Lit. 30 (2), 675–740.

Daily, G., 2008. Ecosystem services: from theory to implementation. Proc. Natl. Acad. Sci. 105 (28), 9455–9456.

Decreux, Y., Valin, H., 2007. Mirage, updated version of the model for trade policy analysis with a focus on agriculture and dynamics. In: CEPII Working Paper (2007-15).

Diamond, J., 1972. Biogeographic kinetics: estimation of relaxation times for avifaunas of Southwest Pacific Islands. Proc. Natl. Acad. Sci. U. S. A. 69 (11), 3199–3203.

Dietz, T., Rosa, E., York, R., 2007. Driving the human ecological footprint. Front. Ecol. Environ. 5 (1), 13–18.

Edmonds, J., Reilly, J., 1985. Global Energy: Assessing the Future. Oxford University Press, New York.

Ellis, E., Kaplan, J., Fullet, D., Vavrus, S., Goldewijk, K., Verburg, P., 2013. Used planet: a global history. Proc. Natl. Acad. Sci. 110 (20), 7978–7985.

Endres, A., Radke, V., 1999. Land use, biodiversity, and sustainability. J. Econ. 70 (1), 1–16.

Foley, J.A., Defries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., Snyder, P.K., 2005. Global consequences of land use. Science (New York, N.Y.) 309 (5734), 570–574.

Galor, O., Weil, D., 2000. Population, technology, and growth: from Malthusian stagnation to the demographic transition and beyond. Am. Econ. Rev. 90 (4), 806–828.

Haddad, N.M., Brudvig, L. a., Clobert, J., Davies, K.F., Gonzalez, a., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, a. J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B. a., Nicholls, a. O., Orrock, J.L., Song, D.-X., Townshend, J.R., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci. Adv. 1 (2) (e1500052-e1500052).

Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O., Townshend, J.R.G., 2013. High-resolution global maps of 21st-century forest cover change. Science 342 (6160), 850–853.

Hanski, I., Ovaskainen, O., 2002. Extinction debt at extinction threshold. Conserv. Biol.

16 (3), 666–673.
Hartwick, J.M., 1995. The Economics and Ecology of Biodiversity Decline. Cambridge University Press Ch. Decline in biodiversity and risk-adjusted net national product.
Hejazi, M., Edmonds, J., Clarke, L., Kyle, P., Davies, E., Chaturvedi, V., Wise, M., Patel, P., Eom, J., Calvin, K., Moss, R., Kim, S., 2014. Long-term global water projections using six socioeconomic scenarios in an integrated assessment modeling framework. Technol. Forecast. Soc. Chang. 81, 205–226.
Henle, K., Alard, D., Clitherow, J., Cobb, P., Firbank, L., Kull, T., McCracken, D., Moritz, R., Niemela, J., Rebane, M., Wascher, D., 2008. Identifying and managing the conflicts between agriculture and biodiversity conservation in Europe-a review. Agric. Ecosyst. Environ. 124 (1–2), 60–71.
Isbell, F., Gonzalez, A., Loreau, M., Cowles, J., Díaz, S., Hector, A., Mace, G.M., Wardle, D.A., O'Connor, M.I., Duffy, J.E., Turnbull, L.A., Thompson, P.L., Larigauderie, A., 2017. Linking the influence and dependence of people on biodiversity across scales. Nature 546, 65–72.
Isbell, F., Tilman, D., Polasky, S., Loreau, M., 2015. The biodiversity-dependent ecosystem service debt. Ecol. Lett. 18 (2), 119–134.
Kleijn, D., Berendse, F., Smit, R., Gilissen, N., 2001. Agri-environment schemes do not effectively protect biodiversity in dutch agricultural landscapes. Nature 413, 723–725.
Kleijn, D., Sutherland, W., 2003. How effective are European agri-environment schemes in conserving and promoting biodiversity? J. Appl. Ecol. 40 (6), 947–969.
Kogel, T., Prskawetz, A., 2001. Agricultural productivity growth and escape from the Malthusian trap. J. Econ. Growth 6, 337–357.
Lafuite, A.-S., De Mazancourt, C., Loreau, M., 2017. Delayed behavioural shifts undermine the sustainability of social-ecological systems. Proc. R. Soc. B Biol. Sci. 284 (1868).
Lafuite, A.-S., Loreau, M., 2017. Time-delayed biodiversity feedbacks and the sustainability of social-ecological systems. Ecol. Model. 351, 96–108.
Lambin, E.F., Meyfroidt, P., 2011. Global land use change, economic globalization, and the looming land scarcity. Proc. Natl. Acad. Sci. U. S. A. 108 (9), 3465–3472.
Lima, L., Coe, M., Soares Filho, B., Cuadra, S., Dias, L.C., Costa, M.H., Lia, L.S., Rodrigues, H.O., 2014. Feedbacks between deforestation, climate, and hydrology in the Southwestern Amazon: implications for the provision of ecosystem services. Landsc. Ecol. 29 (2), 261–274.
Lockie, S., 2013. Market instruments, ecosystem services, and property rights: assumptions and conditions for sustained social and ecological benefits. Land Use Policy 13, 90–98.
Macfadyen, S., Cunningham, S.A., Costamagna, A.C., Schellhorn, N.A., 2012. Managing ecosystem services and biodiversity conservation in agricultural landscapes: are the solutions the same? J. Appl. Ecol. 49 (3), 690–694.
Mattison, E., Norris, K., 2005. Bridging the gaps between agricultural policy, land-use and biodiversity. Trends Ecol. Evol. 20 (11), 610–616.
McGranahan, G., Marcotullio, P., Bai, X., Balk, D., Braga, T., et al., 2005. Ecosystems and Human Well-being: Current Status and Trends. Washington, DC: Island, Ch. Urban systems.
McGuiness, K., 1984. Equations and explanations in the study of species-area curves. Biol. Rev. 59, 423–440.
Messner, S., Strubegger, M., 1995. User's Guide for Message III. International Institute for Applied Systems Analysis WP-95-69.
Meyer, W.B., Turner, B.L., 1992. Human population growth and global land-use/cover change. Annu. Rev. Ecol. Syst. 23 (1), 39–61.
Mitchell, M., Bennett, E., Gonzalez, A., 2015. Strong and non-linear effects of fragmentation on ecosystem service provision at multiple scales. Environ. Res. Lett. 10 (9).
Motesharrei, S., Rivas, J., Kalnay, E., 2014. Human and nature dynamics (HANDY): modeling inequality and use of resources in the collapse or sustainability of societies. Ecol. Econ. 101, 90–102.
Motesharrei, S., Rivas, J., Kalnay, E., Asrar, G., Busalacchi, A., Cahalan, R., Cane, M., Colwell, R., Feng, K., Franklin, R., Hubacek, K., Miralles-Wilhelm, F., Miyoshi, T., Ruth, M., Sagdeev, R., Shirmohammadi, A., Shukla, J., Srebric, J., Yakovenko, V., Zeng, N., 2016. Modeling sustainability: population, inequality, consumption, and bidirectional coupling of the earth and human systems. Nat. Sci. Rev. 3 (4), 470–494.
Needham, B., 2000. Land taxation, development charges, and the effects on land-use. J. Prop. Res. 17 (3), 241–257.
Nelson, E., Mendoza, G., Regetz, J., Polasky, S., Tallis, H., Cameron, D., Chan, K.M., Daily, G.C., Goldstein, J., Kareiva, P.M., Lonsdorf, E., Naidoo, R., Ricketts, T.H., Shaw, M., 2009. Modeling multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales. Front. Ecol. Environ. 7 (1), 4–11.
Newbold, T., Hudson, L., Hill, S., Contu, S., Lysenko, I., Senior, R., Börger, L., Bennett, D., Choimes, A., Collen, B., Day, J., De Palma, A., Dr'iaz, S., Echeverria-Londono, S., Edgar, M., Feldman, A., Garon, M., Harrison, M., Alhusseini, T., Ingram, D., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Correia, D., Martin, C., Meiri, S., Novosolov, M., Pan, Y., Phillips, H., Purves, D., 2015. Global effects of land use on local terrestrial biodiversity. Nature 520, 45–50.
Newbold, T., Hudson, L.N., Arnell, A.P., Contu, S., De Palma, A., Ferrier, S., Hill, S.L.L., Hoskins, A.J., Lysenko, I., Phillips, H.R.P., Burton, V.J., Chng, C.W.T., Emerson, S., Gao, D., Pask-Hale, G., Hutton, J., Jung, M., Sanchez-Ortiz, K., Simmons, B.I., Whitmee, S., Zhang, H., Scharlemann, J.P.W., Purvis, A., 2016. Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment. Science 353, 288–291.
Nordhaus, W., 1993. Optimal greenhouse-gas reductions and tax policy in the "DICE" model. Am. Econ. Rev. 83 (2), 313–317.
Oates, W.E., Schwab, R.M., 1997. The impact of urban land taxation: the Pittsburgh experience. Natl. Tax J. 50 (1), 1–21.
O'Connor, M.I., Gonzalez, A., Byrnes, J., Cardinale, B., Duffy, J., Gamfeldt, L., Griffin, J., Hooper, D., Hungate, B., Paquette, A., Thompson, P., Dee, L., Dolan, K., 2017. A general biodiversity-function relationship is mediated by trophic level. Oikos 126 (1), 18–31.
Peretto, P., Valente, S., 2015. Growth on a finite planet: resources, technology and population in the long run. J. Econ. Growth 20 (3), 305–331.
Perrings, C., 1991. Ecological sustainability and environmental control. Struct. Chang. Econ. Dyn. 2 (2), 272–295.
Petchey, O.L., Pontarp, M., Massie, T.M., Kéfi, S., Ozgul, A., Weilenmann, M., Palamara, G.M., Altermatt, F., Matthews, B., Levine, J.M., Childs, D.Z., McGill, B.J., Schaepman, M.E., Schmid, B., Spaak, P., Beckerman, A.P., Pennekamp, F., Pearse, I.S., 2015. The ecological forecast horizon, and examples of its uses and determinants. Ecol. Lett. 18 (7), 597–611.
Pezzey, J., 1992. Sustainability: an interdisciplinary guide. Environ. Values 1, 321–362.
Phalan, B., Green, R.E., Dicks, L.V., Dotta, G., Feniuk, C., Lamb, A., Strassburg, B., Williams, D., zu Ermgassen, E.K., Balmford, A., 2016. How can higher-yield farming help to spare nature? Science 351 (6272), 450–451.
Pingali, P.L., 2012. Green Revolution: impacts, limits, and the path ahead. Proc. Natl. Acad. Sci. 109 (31), 12302–12308.
Pirard, R., 2012. Market-based instruments for biodiversity and ecosystem services: a Lexicon. Environ. Sci. Policy 19–20, 59–68.
Pretty, J., Brett, C., Gee, D., Hine, R., Mason, C., Morison, J., Rayment, M., Van Der Bijl, G., Dobbs, T., 2001. Policy challenges and priorities for internalizing the externalities of modern agriculture. J. Environ. Plan. Manag. 44 (2), 263–283.
Prinn, R., 2012. Development and application of earth system models. Proc. Nat. Ac. Sc. 110 (suppl. 1), 3673–3680.
Rosenzweig, M., 1995. Species Diversity in Space and Time. Cambridge University Press.
Rybicki, J., Hanski, I., 2013. Species-area relationships and extinctions caused by habitat loss and fragmentation. Ecol. Lett. 16 (SUPPL.1), 27–38.
Sanderson, E., Jaiteh, M., Levy, M., Redford, K., Wannebo, A., Woolmer, G., 2002. The human footprint and the last of the wild. BioScience 52 (10), 891–904.
Schomers, S., Matzdorf, B., 2013. Payments for ecosystem services: a review and comparison of developing and industrialized countries. Ecosyst. Serv. 6, 16–30.
Shukla, J., Nobre, C., Sellers, P., 1990. Amazon deforestation and climate change. Science 247, 1322–1325.
Skinner, J., 1991a. If agricultural land taxation is so efficient, why is it so rarely used? World Bank Econ. Rev. 5 (1), 113–133.
Skinner, J., 1991b. Prospects for agricultural land taxation in developing countries. World Bank Econ. Rev. 5 (3), 493–511.
Sokolov, A., Schlosser, C., Dutkiewicz, S., Paltsev, S., Kicklighter, D., Jacoby, H., Prinn, R., Forest, C., Reilly, J., Wang, C., Felzer, B., Sarofim, M., Scott, J., Stone, P., Melillo, J., Cohen, J., 2005. The MIT integrated global system model (IGSM) version 2: model description and baseline evaluation. In: Joint Program Report Series 124.
Stehfest, E., van Vuuren, D., Bouwman, L., Kram, T., Alkemade, R., Bakkenes, M., Biemans, H., Bouwman, A., den Elzen, M., Janse, J., Lucas, P., van Minnen, J., Müller, C., Gerdien Prins, A., 2014. Integrated Assessment of Global Environmental Change With IMAGE 3.0: Model Description and Policy Applications. PBL Netherlands Environmental Assessment Agency.
Storch, D., Keil, P., Jetz, W., 2012. Universal species-area and endemics-area relationships at continental scales. Nature 488 (7409), 78–81.
Tilman, D., May, R.M., Lehman, C.L., Nowak, M.A., 1994. Habitat destruction and the extinction debt. Nature 371 (6492), 65–66.
Venter, O., Sanderson, E., Magrach, A., Allan, J., Beher, J., Jones, K., Possingham, H., Laurance, W., Wood, P., Fekete, B., Levy, M., Watson, J., 2016. Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. Nat. Commun. 7 (12558).
Wearn, O.R., Reuman, D.C., Ewers, R.M., 2012. Extinction debt and windows of conservation opportunity in the Brazilian Amazon. Science 337 (6091), 228–232.
Zeigler, M., Steensland, A., 2016. Global Agricultural Productivity Report (GAP Report). Global Harvest Initiative.