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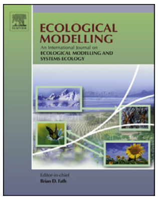

Time-delayed biodiversity feedbacks and the sustainability of social-ecological systems

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ABSTRACT

The sustainability of coupled social-ecological systems (SESs) hinges on their long-term ecological dynamics. Land conversion generates extinction and functioning debts, i.e. a time-delayed loss of species and associated ecosystem services. Sustainability theory, however, has not so far considered the long-term consequences of these ecological debts on SESs. We investigate this question using a dynamical model that couples human demography, technological change and biodiversity. Human population growth drives land conversion, which in turn reduces biodiversity-dependent ecosystem services to agricultural production (ecological feedback). Technological change brings about a demographic transition leading to a population equilibrium. When the ecological feedback is delayed in time, some SESs experience population overshoots followed by large reductions in biodiversity, human population size and well-being, which we call environmental crises. Using a sustainability criterion that captures the vulnerability of an SES to such crises, we show that some of the characteristics common to modern SESs (e.g. high production efficiency and labor intensity, concave-down ecological relationships) are detrimental to their long-term sustainability. Maintaining sustainability thus requires strong counteracting forces, such as the demographic transition and land-use management. To this end, we provide integrative sustainability thresholds for land conversion, biodiversity loss and human population size - each threshold being related to the others through the economic, technological, demographic and ecological parameters of the SES. Numerical simulations show that remaining within these sustainable boundaries prevents environmental crises from occurring. By capturing the long-term ecological and socio-economic drivers of SESs, our theoretical approach proposes a new way to define integrative conservation objectives that ensure the long-term sustainability of our planet.

1. Introduction

Current trends in human population growth (Cohen, 2003; Gerland et al., 2014) and environmental degradation (Vitousek et al., 1997) raise concerns about the long-term sustainability of modern societies, i.e. their capacity to meet their needs "without compromising the ability of future generations to meet their own needs" (Brundtland et al., 1987). Many of the ecosystem services supporting human systems are underpinned by biodiversity (Cardinale et al., 2012), and current species extinction rates threaten the Earth's capacity to keep providing these essential services in the long run (Pereira et al., 2010; Ehrlich and Ehrlich, 2013). The long-term ecological feedback of ecosystem services on human societies has been largely ignored by neo-classical economic theory, mainly due to the focus on short-term feedbacks, and the assumption that ecosystem processes can be substituted for by human capital (e.g. tools and knowledge) and labor, thereby releasing ecological checks on human population and economic growth (Boserup, 1965; Dasgupta and Heal, 1974). In particular, tremendous increases in agricultural productivity resulted in more than 100% rise in aggregate food supply over the last century (Schmidhuber and Tubiello, 2007).

However, the substitution of human capital for natural resources, also called the "technology treadmill" (Pezzey, 1992), is currently facing important limitations. One such limitation is land scarcity, as the remaining arable land reserve might be exhausted by 2050 (Lambin and Meyfroidt, 2011). Moreover, recent projections suggest a slowdown in the growth rate of agricultural Total Factor Productivity (TFP), which measures the effect of technological inputs on total output growth relative other inputs (Kumar et al., 2008). Technological improvements may not compensate for arable land scarcity (Zeigler and Steensland, 2015),

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thus questioning the potential for continued TFP growth in the future (Gordon, 2012; Shackleton, 2013). Another limitation comes from the loss of many biodiversity-dependent ecosystem services which play a direct or indirect role in agricultural production, such as soil formation (Barrios, 2007), nutrient cycling, water retention, biological control of pests (Martin et al., 2013) and crop pollination (Gallai et al., 2009; Garibaldi et al., 2011). Substituting ecological processes with energy and agrochemicals has mixed environmental impacts, with unintended consequences such as water use disturbance, soil degradation, and chemical runoff. These effects are responsible for a slowdown in agricultural yield growth since the mid-1980s (Pingali, 2012) and have adverse consequences on biodiversity, human health (Foley et al., 2005) and the stability of ecosystem processes (Loreau and de Mazancourt, 2013).

Moreover, biodiversity does not respond instantaneously to land-use changes. Habitat fragmentation (Haddad et al., 2015) increases the relaxation time of population dynamics (Ovaskainen and Hanski, 2002) - i.e. how fast a species responds to environmental degradation. As a consequence, species extinctions are delayed in time, which generates an extinction debt (Tilman et al., 1994) and a biodiversity-dependent ecosystem service debt (Isbell et al., 2015). These ecological debts may persist for more than a century, and increase as species get closer to extinction (Hanski and Ovaskainen, 2002). The accumulation of these ecological debts may have long-term effects on modern human societies.

Such time-delayed ecological feedbacks have been neglected by the most influential population projection models (Meadows et al., 1972, 2004; Turner, 2014). Yet, environmental degradation can have catastrophic consequences for human societies even without any delayed effect (Diamond, 2005; Ponting, 1991). A well-known example is Easter Island, this Polynesian island in which civilization collapsed during the 18th century due to overpopulation, extensive deforestation and overexploitation of its natural resources (Brander, 2007). In order to investigate the mechanisms behind this collapse, Brander and Taylor (1998) modeled the growth of the human population as endogenously driven by the availability of natural resources, the depletion of which was governed by economic constraints. Their model was essentially a Lotka-Volterra predator-prey model, which is familiar to ecologists, with an economic interpretation. It showed that one of Easter Island's ecological characteristics - the particularly low renewal rate of its forests - may be responsible for the famine cycles which brought forward the collapse of this civilization.

Given the unprecedented rates of current biodiversity and ecosystem service loss (Pereira et al., 2010), accounting for their long-term feedback on modern human societies appears crucial. In an attempt to delimit safe thresholds for humanity, a 10% loss in local biodiversity was defined as one of the core "planetary boundaries" which, once transgressed, might drive the Earth system into a new, less desirable state for humans (Scholes and Biggs, 2005; Steffen et al., 2015). However, in practice, the biodiversity threshold above which ecosystem processes are significantly affected varies among ecosystems (Hooper et al., 2012; Mace et al., 2014), and is correlated to other thresholds such as land-use change (Oliver, 6296). The definition of integrative thresholds thus requires that we consider the interaction between the economic and ecological components of systems.

In order to explore the long-term consequences of ecological debts for human societies, we build upon Brander and Taylor's framework, but we allow the human population to produce its own resources through land conversion. In our approach, terrestrial natural habitats provide essential ecosystem services to the agricultural lands - which are assumed to be unsuitable to biodiversity. Biodiversity and human population dynamics are coupled through the time-delayed effect of biodiversity-dependent ecosystem services on agricultural production (ecological feedback). It may be viewed as a minimal social-ecological system (SES) model that couples basic insights from market economics and spatial ecology. From market economics, we derive human *per capita* consumptions and the rate of land conversion. From spatial ecology, we use a classical species-area relationship (SAR) to capture the dependence of species diversity on the remaining area of natural habitat, and account for ecological debts through the relaxation rate of communities following habitat loss.

We investigate the behavior of the system at equilibrium analytically, and then numerically evaluate the trajectories to the equilibrium. We show that the transient dynamics of an SES depends on its ecological, economic, demographic and technological parameters. Some SESs experience large population overshoots followed by reductions in biodiversity, human population size and well-being - which we call "environmental crises". We then analytically derive an integrative sustainability criterion that captures the vulnerability of an SES to such crises. This criterion allows assessing the effects of some parameters on the long-term sustainability of the SES, and deriving integrative land conversion and biodiversity thresholds.

2. Methods

2.1. Coupling human and ecological dynamics

We model the long-term dynamics of three variables: the human population (H), technological efficiency (T) and biodiversity (B).

$$\begin{cases} \dot{\mathrm{H}} = \mu(\mathrm{B}, \mathrm{T}) \quad \mathrm{H} \\ \dot{\mathrm{T}} = \sigma \quad \mathrm{T}(1 - \mathrm{T}/T_m) \\ \dot{\mathrm{B}} = -\epsilon \quad [\mathrm{B} - S(\mathrm{H})] \end{cases} \tag{1}$$

The human population endogenously grows at a rate $\mu(\mathrm{B}, \mathrm{T})$, which is explicitly defined as a function of the *per capita* agricultural and industrial consumptions in Section 2.1.1. Technological efficiency is assumed to follow logistic growth at an exogenous rate σ, until a maximum efficiency T_m is reached (Section 2.1.2). We use an economic general equilibrium framework to derive *per capita* human consumptions at market equilibrium, i.e. when production supply equals the demand of the human population (Section 2.1.3). Using these consumptions, we derive a proportional relationship between land conversion and the size of the human population (Section 2.1.4). Land conversion affects biodiversity through a change in the long-term species richness $S(H)$. Current biodiversity B reaches its long-term level $S(H)$ at a relaxation rate ϵ (Section 2.2). Biodiversity-dependent ecosystem services then feed back on agricultural production and affect the *per capita* agricultural consumption and the human growth rate, $\mu(\mathrm{B}, \mathrm{T})$. Model structure is summarized in Fig. 1.

2.1.1. Human demography

The interaction between human population, technology and income has been mainly studied by endogenous growth theory, which distinguishes three phases of economic development (Galor and Weil, 2000; Kogel and Prskawetz, 2001): (1) a Malthusian regime with low rates of technological change and high rates of population growth preventing *per capita* income to rise; (2) a Post-Malthusian Regime, where technological progress rises and allows both population and income to grow, and (3) a Modern Growth regime characterized by reduced population growth and sustained income growth (Peretto and Valente, 2015). Transition to this third regime results from a demographic transition which reverses the positive relationship between income and population growth.

In order to consider the basic linkages between human demography and economics, the growth rate of the human population is