

DEPARTMENT OF INTERNATIONAL AND EUROPEAN ECONOMIC STUDIES

ATHENS UNIVERSITY OF ECONOMICS AND BUSINESS

ON THE CO-EVOLUTION OF ECONOMIC AND ECOLOGICAL SYSTEMS

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Working Paper Series

20-34

October 2020

On the Co-evolution of Economic and Ecological Systems

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Abstract

This survey provides: a description of common and distinct characteristics of economic and ecological systems; examples of the ways in which these characteristics can be incorporated into models adequately describing the co-evolution of the two component systems to produce a unified economic-ecological system in time, space and appropriate scale; and a discussion of policy design when the policy maker takes into account this co-evolution, along with potential biases when the co-evolution is ignored. We propose the development of integrated assessment models of the co-evolving systems which will embody the variety of common and distinct characteristics identified in this survey. We expect that such an approach will provide useful insights regarding the efficient management of co-evolving ecological-economic systems.

Keywords: economic-ecological systems, co-evolution, space, scale, heterogeneity, uncertainty

JEL codes: Q5, Q57, Q58

1. INTRODUCTION

Economic and ecological systems are interlinked complex adaptive systems (Arrow et al. 2014b, Levin et al. 2013), and hence building blocks in a higher-level complex adaptive system. Because of these interlinkages, they co-evolve with one another, as changes in ecological systems affect those in economic systems, and vice versa. This inseparability presents unique challenges for management of either.

Complex adaptive systems (CAS) are understood to be systems made up of individual agents, which interact with each other at small scales, giving rise to emergent patterns that feed back to affect individual behaviors and interactions. They are characterized by three basic properties, as having "sustained diversity and individuality of components ... localized interactions among those components," and an adaptive process, namely "an autonomous process that uses the outcomes of those interactions to select a subset of those components for replication or enhancement" (Levin 1998, p. 432). Hence the adaptive component is at the local level, meaning that the emergent properties are not necessarily of benefit to the agents or the system as a whole.

Indeed, CAS are dynamic nonlinear systems, evolving (in the broad sense) in time and space, which self-organize from local interactions and are characterized by historical dependencies, complex dynamics, thresholds, and multiple basins of attraction (Carpenter et al. 1999, Levin 1999). As already mentioned, the actions of individuals at the "microscopic" level affect the aggregate or macroscopic characteristics of the system, and the emergent macroscopic characteristics feed back to influence the actions of individuals. Thus the challenges faced in addressing such systems include rules for scaling from small scales to large, characterizing emergence and the potential for critical transitions, and resolving conflicts between the myopic interests of individuals and the longer-term interests of the collectives, including future generations.

It is clear that economic and ecological systems are interlinked in multiple ways; in particular, the agents of the economic system – individuals, firms, governments – compete for resources to optimize their objectives – utility, profits, social welfare – by using services provided by the natural capital of the ecosystems. The ecosystems' agents, from the genetic level through to populations and beyond, compete for resources, exploit other agents, and cooperate to eventually accumulate natural capital, which in turn provides useful services to the economic system. The response of ecosystems to the actions of the economic systems, which result in excess consumption of natural capital, is manifested by the reduction of the quality and quantity of services provided. When this is deemed not desirable by the economic agents, since it involves damages (e.g., from local pollution or climate change damages), governments or regulatory agencies undertake policies to promote the efficient use of these services and thus reduce damages. These policies are designed and formulated in terms of the objectives of the economic system, and usually involve damage minimization or social welfare maximization, perhaps subject to constraints that lead to second-best solutions.

To summarize, the two systems involve agents – economic, social or biological – that seek, directly or indirectly, to optimize their objectives¹ by competing for resources that could be common.² The agents may include individuals, collectives and institutions, setting up conflicts where public goods and common-pool resources are involved. The optimizing behavior of the agents results in macroscopic structures, that is macro-economy and ecosystems, whose characteristics feed back and affect the behavior of the agents. The two systems are interlinked, since the economic systems use the services of the ecosystems and

¹ In this paper we follow the mainstream, at least for economics, approach of optimizing behavior. It would be interesting to reframe the discussion and the concepts put forward in this paper in terms of Herbert Simon's (1947) concept of satisficing, as a decision-making rule which is not based on the global rationality assumption.

 $^{^2}$ Despite the profound similarities between the economic and the ecological systems, there are differences. For example, in the economic systems agents are forward-looking, which means that they form expectations about the future when they optimize their objectives. This may be the case for non-human agents as well, but likely to a lesser degree.

consume natural capital accumulated by them. Excess consumption and depletion of natural capital generate damages to the economic system, which induce policy responses mainly for economic institutions.

The two systems evolve in time, through accumulation processes, and in space, through transportation processes. Thus, spatiotemporal evolution³ creates another level of interlinkages between the two systems.

In the context described above, the purpose of this review is to provide a description of the specific, common in many cases, characteristics of the economic and ecological systems; to provide examples of the ways in which these characteristics can be incorporated in models adequately describing the co-evolution of the two component systems to produce a unified economic-ecological system in time and space; and finally to discuss policy design when the policy maker takes into account this co-evolution, and potential biases when the co-evolution is ignored.

2. SPATIOTEMPORAL DYNAMICS OF UNIFIED ECOLOGICAL-ECONOMIC SYSTEMS

Ecological theory is fundamentally influenced by the incorporation of a spatial dimension, which allows for much greater biological diversity through exploitation of underlying environmental variation, or indeed biologically-generated spatiotemporal variation (Levin 1974, 1976), than would be the case in a well-mixed system. In such spatially-heterogeneous environments, it is crucial to take into account the movement of both abiotic and biotic components, from nutrients and pollutants to pollen, seeds, organisms and information (Levin 1974, Okubo & Levin 2001).

³ We use evolution in the more general mathematical sense, and not necessarily implying a genetic basis.

The objective of models of these processes is to capture the spread of these elements and agents across space, to couple movement with demographic processes, and ultimately perhaps to investigate the role of human activities such as harvesting and land use. Species interactions have been extensively studied in spatial domains, with the movement of the species across space modeled by appropriate transport mechanisms (Okubo & Levin 2001). The abiotic components of the system, from nutrients to pollutants, also spread spatially, as do labor and capital in the economic parts of the system. The generation of products and pollutants is associated with economic activities – production or consumption – while their reduction is also associated with economic activities related to abatement.

In ecological systems, the spatiotemporal evolution of interacting biological agents is associated with the generation and maintenance of spatial and spatiotemporal patterns (Levin & Segel 1985). Endogenous pattern formation can arise from a variety of mechanisms, including the existence of multiple stable states, of localized disturbances, and of differential dispersal rates as suggested 70 years ago by Alan Turing (1952). (See also Levin 1974; Rietkerk & van de Koppel 2008; Meron 2015, chapter 3; Pringle & Tarnita 2017.) Multiple modes of spatial redistribution may be important, from local diffusive spread to long-range transport (Skellam 1951).

The simplest models of spread rest on limits of random walks or on a Fickian assumption of movement from locations of high to low concentration; however, even at local scales, more complicated mechanisms involving chemotaxis, aggregation, anomalous diffusion or other processes may be important (Okubo & Levin 2001). Multiple scales of redistribution may also be important, even for a single dispersing agent: plants, for example, may drop some seeds locally, while relying on winds or animals to spread others over longer distances. Pest species, including the agents of infectious disease, spread both through local contacts and by catching rides via biological agents like birds, airplanes, boats, or other floating objects.

In economics, the spatial dimension has been extensively studied in the context of economic geography, and especially the *new economic geography*. The main focus of that work is the emergence of agglomerations and clusters at different spatial scales, as a result of interactions between scale economies and spatial spillovers (e.g., Krugman 1996, 1998). In this context, endogenous agglomerations and clustering could emerge when the rate of change of manufacturing in a location depends on the concentration of manufacturing at all other locations on a spatial domain described by a circle (Krugman 1996). The emergence of endogenous agglomerations, that is, pattern formation in the realm of economics, may also be based on processes analogous to the Turing mechanism (Levin & Xepapadeas 2017). In ecological systems, clustering is also a central issue, and multiple mechanisms have been shown to underlie such patterns (Bonachela et al. 2015). Indeed, many animal populations are known to aggregate actively through collective behavior (Flierl et al. 1999, Couzin et al. 2005), to improve foraging or mating success, or reduce predation risk.

Most models of spatiotemporal dynamics and pattern formation in ecology and biology as well as in the early applications of the new economic geography, examine spatial patterns as emerging from the individual responses of organisms, including humans, to environmental cues; forward-looking behavior is not usually a factor, though certainly evolutionary forces have shaped the behaviors of even bacteria and slime molds in their responses to local cues in ways shaped by relative fitnesses. Though individual fish in schools and birds in flocks likely are not making calculations about the distant future in their movement responses, their behaviors have indeed been shaped by evolution to improve relative foraging abilities, to confound predators or to improve the chances of finding mates. Thus the resultant behaviors are in a sense indirectly forward-looking.

In resource management, one natural way in which ecology and economics are linked is through a harvesting process. If economic agents harvest a natural resource that moves across space, and the purpose of harvesting is the optimization of some objective, e.g., profit maximization or cost minimization, then the spatiotemporal dynamics of the resource under harvesting act as constraints to the economic optimization problem. In terms of pollution control, the objective is to minimize the pollution cost for the entire spatial domain when the pollutant disperses across locations. Management strategies hence must be forward-looking, even in the face of uncertain information.

To this end, Wilen and co-authors coupled conventional fishery management models with metapopulation models to develop optimal harvesting models when fish populations move across discrete patches.^{4,5} The main policy implications of these models stress the need to take into account the interconnection of spatial gradients of economic and biological dispersal in the design of policy instruments. Thus, it is not just the economic and biological variables that affect policy but also the way in which these variables disperse in space. In related work, Baskett and collaborators (Baskett et al. 2007) study the effects of marine reserves on harvesting strategies, and the consequent natural selection on dispersal tendency of individuals. In part, such work is inspired by the observation that strong selective pressures of the sort imposed by marine reserves can lead to rapid evolutionary responses, as in the loss of the ability to fly by insects on islands. Optimal foraging theory (Pyke et al. 1977) is another parallel; in both economic systems and ecological systems, efficiently navigating space or a more general set of options is a fundamental operations research problem, and recent work on the multi-armed bandit problem resonates with research challenges in both disciplines.

Mäler (1989) was the first to use dispersion to study the so-called "acid rain game" in which acid deposits damage locations because of acid rain generated by sulphur emissions in

⁴ For further analysis of bioeconomic models in patchy environments and issues related to marine reserves, see for example Smith & Wilen (2003), Costello & Polasky (2008), Sanchirico & Wilen (2005), and Smith et al. (2009).

⁵ For the analysis of metapopulation models, see Levin (1974, 1976), Hastings (1982), and Hastings & Harrison (1994).

different locations, and derive policy recommendations (see also Mäler & de Zeeuw 1998). Metapopulation models have been also used to study the optimal control of biological invasion across heterogeneous regions (e.g., Epanchin-Nieli & Wilen 2012). Brock & Xepapadeas (2002) analyze a species competition for a limited resource in a patchy environment and derive optimal patch dependent policy rules. Levin & Xepapadeas (2017) study a two-region model in which capital moves towards the region with the higher rate of return and pollution moves from the region of higher concentration to the region of lower concentration. Using the Turing mechanism in the two-region world, they derived conditions that induce spatial heterogeneity in capital and pollution, a form of pattern formation in a two-region model. Figure 1 shows the emergence and the disappearance of patterns after an initial spatial disturbance at an initial time (Brock, Xepapadeas & Yannacopoulos 2014b). The patterns emerge in the context of the Turing mechanism.





Figure 1: (a) Patterns emergence and (b) patterns disappearance.

Dispersion of heat from the equator to the North Pole has been used as a mechanism for explaining Polar amplification in the context of "box models" of climate science in which heat moves from a box around the Equator to boxes further North or South. Give the expected economic damages associated with Polar amplification (mainly Arctic amplification) the incorporation of heat transport into integrated assessment models of climate change is another research area in which ecological processes are coupled with economics. Brock, Engström & Xepapadeas (2014) and Brock & Xepapadeas (2017) studied Polar amplification in the context of climate change economics and derived rules that suggest regionally-differentiated climate policy.

Groundwater management in which spatial dynamics induced by hydrological factors such as seepage or aquifer transmissivity introduce a spatial pumping externality and induce policies with spatial structures; semi-arid systems with reaction-diffusion characteristics in which plant biomass and soil water interact and diffuse in space; pollution control and the use of the Gaussian plume to describe pollution dispersion are other areas in which economic optimization was linked to the spatial dynamics of the ecological systems.⁶ The main outputs of these approaches were spatially-structured policies of price or quantity instruments and identification of conditions under which the coupled ecological-economic system generates spatial patterns.

Wilen (2007) pointed out the lack of attention by resource economists in comparison to the extended use of spatial dynamic systems in physics or biology. Over recent decades this situation has changed, since spatial dynamics are becoming a part of coupled ecologicaleconomic models. The result of this co-evolution is the emergence of policies with explicit spatial structure, which could increase the efficiency of regulation for controlling environmental externalities. As climate change leads to shifts in the distribution of fish populations as well as fisheries (Pinsky et al. 2013), such approaches are going to become increasingly important.

⁶ For examples of spatial dynamics in resource management, see, e.g., Goetz & Zilberman (2000), Xabadia et al. (2006), Brock & Xepapadeas (2010), Brozovic et al. (2010), Pfeiffer & Lin (2010), Kuwayama & Brozovic (2013), and Camacho & Pérez-Barahona (2015).

3. NONLINEARITIES AND FEEDBACKS

Krugman (1996) provides a very clear explanation of a nonlinear business cycle by replacing the standard linear expenditure function of Keynesian economics with a nonlinear one, which generates multiple equilibria which could be stable or unstable. In a more general context, Brock (1988) defines nonlinear science as the study of complex dynamics in stochastic and deterministic dynamical systems. Complex dynamics in this context means that most trajectories of a dynamical system do not converge to rest points or limit cycles. For the case of coupled ecological-economic systems, conditions associated with the emergence of complex dynamics include: high discount rate for the future; abandonment of concavity for preferences, technology, or transition dynamics; increasing returns combined with externalities; and population dynamics coupled with nonlinear feedbacks. The last condition provides a direct link between economic and ecological models. Added to this list of largely economic mechanisms, however, must be the role of ecological dynamics. Even simple ecological models can give rise to such complicated outcomes, including heteroclinic cycles, chaos and worse (May 1976, Touboul et al. 2018).

In dynamic ecological systems, even without consideration of human interference, the presence of nonlinearities and positive feedbacks – which amplify the impact of a forcing factor – can generate multiple steady states with various stability characteristics, limit cycles, hysteresis, flips from one basin of attraction to another with different qualitative characteristics, heteroclinic cycles, chaos and irreversibilities. Multiple basins of attraction can be found in systems such as coral reefs, grasslands, or lakes. In coral reefs, fast intrusion of algae could lead to coral death and reorganization of the coral reefs' dominant species (Crépin 2007, Mumby et al. 2007, McManus et al. 2019). In grasslands, grass-dominated land can be encroached by trees, or vice versa, leading to regime shifts; climate change and shifting

precipitation can facilitate such transitions (Staver & Levin 2012, Touboul et al. 2018). In lakes, heavy phosphorous loadings from agricultural run-off combined with a feedback of phosphorous release from the sediments could flip the lake from an oligotrophic state with high ecological services to a eutrophic lake with low services (Carpenter et al. 1999, Scheffer & Carpenter 2003, Scheffer 2009).

In climate change, an important feedback relates to the already-mentioned Arctic amplification (AA). AA is associated with the surface albedo effect and heat transport from the Equator to the North Pole. This results in a faster change of the surface temperature in the North Pole relative to southern latitudes (IPCC 2013). AA results in extensive melting of seaice which intensifies the albedo effect and induces another feedback that is related to permafrost thawing, which could release large amounts of greenhouse gasses stored in the permafrost (IPCC 2013). AA generates an important spatial externality since the increase in temperature in the North can generate damages in lower latitudes due to extreme weather events (Francis & Skific 2015, Francis 2017). Internalization of this spatial externality requires regional-specific policy differentiation regarding carbon taxes (Hassler & Krusell 2012, Desmet & Rossi-Hansberg 2015, Brock & Xepapadeas 2020). In the cases mentioned above, the ecological system might reach a tipping point and a regime shift could take place as the system moves to another basin of attraction. The change could be irreversible or could be characterized by hysteresis. Such possibilities exist for a wide range of ecological systems, as well as the underlying hydrodynamics (Lenton et al. 2008).

The economic dimension may enter the picture by embedding the nonlinear dynamic system into an optimal control problem. In this problem, human forcing is the control variable with a time path chosen such that present value of the objective – utility, profit, costs – is optimized subject to nonlinear transition dynamics over a finite or infinite time horizon (Clark 1976). Thus, the problem becomes a nonlinear, non-convex optimal management problem. In

coral reef management the control is fish harvesting (Crépin 2007); in grasslands the control may be livestock management; in the lake problem the control is fertilizer used in agriculture; while in climate change the control is greenhouse gas emissions.

The existence of multiple basins of attraction introduces an interesting question. Given an initial state for the ecological system and the possibility of reaching alternative steady states through the optimal control process, what is the most desirable or globally-optimal steady state in terms of the optimizing objective? The answer to this question relates to the existence of Skiba indifference points in the optimal control of systems with positive feedbacks represented by sigmoid curves. A Skiba point is an initial state, such that a regulator or planner is indifferent between controlling the system to distinct basins of attraction. In the case of the lake management problem, this means that depending on history which specifies the initial state, it may be optimal to control the system to an oligotrophic or eutrophic steady state. This depends on the location of the initial state of the system relative to the Skiba point (see, for example, Mäler et al. 2003, Dasgupta & Mäler 2004). Even given the existence of a more favorable alternative, the costs of transformation may mitigate against making the change, locking the system into an inferior basin of attraction (Levin et al. 1998).

Figure 2 indicates the emergence of multiple steady states and a Skiba point in the optimal control of a climate with nonlinear feedbacks due to Arctic amplification.

{Insert Figure 2 about here}



Figure 2: Multiple steady states and a Skiba point in the optimal control of a climate model. *T* is global average temperature and λ is its shadow cost.

This management option introduces a distinction between a purely ecological system and a coupled economic-ecological system. Given the objective to optimize and the history, it may be optimal to control the system to a steady state with low ecological services (e.g., eutrophic lake, algae-dominated coral reef). In these cases, the economic-ecological system could be trapped in a low ecological services basin and more instruments that could override history by changing initial conditions – such as reducing phosphorous concentration in the lake at the outset of the management process – are necessary.

Nonlinear feedbacks can be combined with the spatiotemporal dynamics prescribed in the previous section. Brock & Xepapadeas (2008) extended the lake model by including, along with the nonlinear feedback, diffusion of phosphorus along a circular lake. They found that the emergence of multiple steady states is crucial for the generation of spatial patterns in the shadow price–phosphorous quantity system through a modified Turing mechanism and efficient regulation introduction of efficient spatial instruments. In a similar context, Brock & Xepapadeas (2010) studied the optimal management of a semi-arid vegetation system in a spatiotemporal context. The coupling of multiple steady states with generalized Turing mechanisms (in which non-infinitesimal perturbations of the uniform steady state are needed to generate patterns) have also been observed by Bonachela et al. (2015) for savanna models.

4. STRATEGIC INTERACTIONS

In an environment with many agents, strategic interactions occur when agents in the pursuit of own objectives take into account the action of others as they seek to satisfy their corresponding objective. In ecology, such forces are implicit or explicit in models of collective behavior (Couzin et al. 2005). In ecological-economic models, strategic interactions have been mainly studied from the point of view of forward-looking optimizing economic agents. The main approach for modeling strategic interactions among economic agents is to consider the situation in which the objective of the agent (e.g., utility, profit, cost) depends on a variable that characterizes the state of the system – a state variable – whose evolution over time and space depends on the actions of all agents.

This approach is common in ecological-economic models, in which an ecological state variable such as the biomass of a renewable resource (e.g., a fishery), the stock of a depletable resource (e.g., fossil fuels or groundwater aquifers), the stock of greenhouse gasses in the atmosphere, the stock of a pollutant (e.g., phosphorous in a lake) or the amount of land covered by forest, is not managed by a sole owner or a regulator, but rather by economic agents who can independently affect the state variable through harvesting, extraction, emissions or deforestation. In harvesting, extraction, or deforestation cases, individual profits depend on resource stocks through externalities, and the evolution of the resource stock depends on actions by all agents. In global pollution problems (e.g., climate change), an individual country's utility depends on the stock of global pollutant (greenhouse gasses) through a damage function, and the evolution of the global pollutant depends on emissions by all agents. The analytical tools for studying these problems are differential games, which are situations of conflict where players choose strategies over time.

Crucial to the structure of the differential game is the specification of the information about the state of the game gained and recalled by each player at each point in time. There are a number of possible information structures for a differential game (Başar & Olsder 1982); the two which are most often considered are: (i) the open loop, in which agents are committed to the entire paths of actions (e.g., harvesting, pollution) at the outset of the game; and (ii) closed loop or feedback in which the players adjust their actions by observing the current state of the state variable. There is extensive literature on the use of differential games in resource management problems such as fishery or groundwater management, as well as in pollution management, acid rain and climate change (see for example the surveys by Jorgenson et al. 2010 or de Zeeuw 2014a).

Differential games could more easily be applicable to CAS if spatial interactions, nonlinear feedbacks or different time scales representing fast and slow variables are incorporated into the transition dynamics of the state variables. A commonly-used method of modeling these nonlinear feedbacks is the Holling type-III functional response, which was used by Ludwig et al. (1978) to understand the dynamics of the spruce budworm. The same type of response was used in the lake problem discussed in the previous section. The introduction of nonlinear feedbacks in the management of ecological-economic systems increases the complexity of the problem and requires the use of numerical methods. Mäler et al. (2003) and Kossioris et al. (2008, 2011) studied open loop and closed loop solutions to the lake problem and derived policy rules. Grass et al. (2017) studied an extended lake problem with phosphorous accumulation in fast and slow time, and identified multiple steady states and the possibility of pollution traps under open loop strategic interactions. The closed loop characterization in nonlinear systems with fast and slow variables is an open research issue.

The common characteristics of these solutions is that, due to the multiplicity of steady states and hysteretic effects induced by nonlinearities, the policy instruments are time dependent and quite complex. This makes it difficult, and sometimes not feasible, to characterize even numerically policy instruments, which in a decentralized regulated framework would be able to reproduce the socially-optimal paths. In these cases, what is feasible are policy instruments that would attain the socially-optimal steady state in the long run but the optimal path from the initial time (see Xepapadeas 1992, Kossioris et al. 2011). This remains an issue for further research in the context of optimal regulation.

Another open research issue is the incorporation of spatial interactions along with the strategic interactions and the other ingredients of the CAS into the optimal management of dynamic ecological-economic models. Spatial interactions introduce another level of complexity because they induce an additional spatial externality. De Frutos & Martín-Herran (2019) studied such a problem, but more research is needed.

5. RISK AND DEEP UNCERTAINTY

Economic and ecological models are permeated by uncertainties associated with the economic or/and the ecological system and their interactions. Risk and uncertainty are, in this respect, fundamental concepts for understanding the structure and the evolution of coupled ecologicaleconomic systems. In ecology, how evolution has shaped responses to uncertain conditions is perhaps the central issue, and the manifold solutions to the problem explain to large extent the maintenance of biological diversity. In resource economics, the impact of risk and uncertainty on the evolution of resource stocks or stocks of pollutants, market conditions or technological conditions can in general be identified.⁷

From a management perspective, uncertainties associated with ecosystems include major gaps in global and national monitoring systems, the emergence of surprises and unexpected consequences, the lack of a complete inventory of species and their actual distributions or the limited modeling capacity and lack of theories to anticipate thresholds, as well as how humans will respond to changing conditions.

Climate change is a major source of uncertainty for both economic and ecological systems. Uncertainties regarding climate change are mainly associated with the accumulation of greenhouses gasses and the mechanisms of global warming, and the socioeconomic impacts

⁷ There is extensive literature related to risk and uncertainty in environmental and resource economics which we do not cite due to space considerations. A very useful survey of the field and relevant references can be found in Mäler & Fisher (2005).

of climate change. An important source of scientific uncertainty relates to parameters such as equilibrium climate sensitivity (Meinshausen et al. 2009), or the transient response to emissions (Matthews et al. 2009, MacDougall et al. 2017), or other parameters of the climate system. Another source is related to socioeconomic factors, mainly the expected damages in terms of lost GDP from climate change, and the values of welfare parameters such as the discount rate (Weitzman 2009, 2011; Pindyck 2013; Heal & Milner 2014).

The traditional approach in dealing with risk and uncertainty in economics is the expected utility framework based on the von Neumann & Morgenstern (1947) expected utility theory in which risk is summarized by objective numerical probabilities associated with possible outcomes, and decisions are based on the maximization of expected utility. This framework was extended to subjective probability by de Finetti (1931) and Savage (1954) in which even if states of the world cannot be associated with objective probabilities, the individual decision maker – given the structure of preferences implied by the relevant axioms – acts as if she/he is an expected utility maximizer.

Expected utility maximization using objective or subjective probabilities analyses has been the standard approach in the study of unified economic-ecological models. As in ecology, however, using expectations addresses only part of the story, and relies upon an ability to average. Lewontin & Cohen (1969) demonstrate how, in a simple process analogous to gambler's ruin, the expectation can increase exponentially while the probability of extinction tends to 1, because of the multiplicative nature of payoffs in such situations. The whole basis of insurance arrangements exploits the trade-offs between these two tendencies.

During recent decades, another way of approaching risk and uncertainty has emerged. This approach goes back to ideas developed by Keynes (1921), Knight (1921) and Ramsey (1926). These ideas make a sharp distinction between risk – a situation in which probabilities, objective or subjective, can be assigned to states of the world – and uncertainty. As Frank Knight suggested, there is a need to distinguish between risk and uncertainty for situations where there is ignorance or not enough information to assign probabilities, objective or subjective, to events. Knightian uncertainty, or ambiguity, can be regarded as a more appropriate framework for studying ecological-economic systems in stochastic environments in which – given the complexities and the multiple sources of uncertainty affecting both systems – it might be difficult or even impossible to associate probabilities with uncertain prospects affecting the ecosystem evolution.⁸ More specifically, in ecological-economic systems we observe high structural uncertainty over the physical processes of environmental phenomena, and the high sensitivity of model outputs to modeling assumptions. As a result, adequate scientific understanding of the underlying ecosystem mechanisms and the impacts of policies applied to ecosystems may be seriously impeded, while models that are "close" to each other may arrive at dramatically different policy recommendations.

Recent papers (see, e.g., Barnett et al. 2020) distinguish three forms of uncertainty.

(i) Risk: The probabilities (objective or subjective) of uncertain outcomes are known, and the decision maker is confident about the model used. Uncertainty exists within the model.

(ii) Ambiguity: There are a large number of potential models which could be used by the decision maker. There is a question regarding the decision maker's level of confidence in each model.

(iii) Misspecification: The question here is how the decision maker uses models that are not perfect and may have unknown laws.

⁸ Knightian uncertainty should be contrasted with risk (measurable or probabilistic uncertainty) where probabilities can be assigned to events and are summarized by a subjective probability measure or a single Bayesian prior.

Ambiguity and misspecification, sometimes called "deep uncertainty," require new approaches to decision making that incorporate uncertainty or ambiguity aversion.⁹ Inspired by the work of Knight and subsequently Ellsberg (1961) and Gilboa et al. (2008), Gilboa & Schmeidler (1989) developed the axiomatic foundations of maxmin expected utility, an alternative to classical expected utility for environments characterized by deep uncertainty. Gilboa & Schmeidler's insights were extended to dynamic optimization problems (see e.g., Hansen & Sargent 2008), thus introducing the concept of robust control in decision making. Robust control can be characterized as a decision-making process which provides a framework through which decision makers can investigate the fragility of decision rules by considering worst-case scenarios. This approach can be used to study management under ambiguity or deep uncertainty. Robust control methods have been applied in climate change (Athanassoglou & Xepapadeas 2012, Barnett et al. 2020), in water management (Roseta-Palma & Xepapadeas 2013).

Klibanoff et al. (2005) developed an axiomatic framework: the "smooth ambiguity" model in which different degrees of aversion for uncertainty are explicitly parametrized in the decision maker's preferences. A survey of applications to climate change can be found in, for example, Heal & Milner (2014). As has been shown by Maccheroni et al. (2006), robust control and smooth ambiguity are special cases of more general preferences called variational preferences which incorporate ambiguity aversion.

The concepts of deep uncertainty and aversion to ambiguity are important in understanding the management of ecological-economic systems, while the CAS aspects of these systems discussed above can be incorporated in the deep uncertainty framework. The dynamic aspects have already been incorporated in robust control and smooth ambiguity

⁹ Uncertainty aversion, or ambiguity aversion, means that the decision makers tend to prefer situations with known probabilities to unknown ones, to the extent that these can be compared.

models. The spatial aspect was first introduced by Brock, Xepapadeas & Yannacopoulos (2014a), who identified spatial hot spots, in which aversion to ambiguity is so high that the regulation breaks down and new regulatory schemes or new information to reduce uncertainties is required. The emergence of regulatory hot spots is important in the analysis of climate change because of the existence of tipping points (Lenton et al. 2008), which are locations surrounded by large uncertainties and associated with the triggering of big damages if the tipping points are crossed.¹⁰

The introduction of variational preferences that incorporate deep uncertainty and ambiguity aversion could be an important aspect in the efficient management of ecologicaleconomic systems since the very nature of these systems is characterized by deep uncertainties.

6. HETEROGENEITY

In ecology, the earliest models of population interaction dealt with simplified models, in which all individuals within a species were treated as identical, interacting according to mean-field assumptions within a homogeneous environment (Volterra 1926). Not surprisingly, the conclusions that arose, such as the powerful competitive exclusion principle were basically null models. For example, we know that many species can coexist on limited numbers of resources (Hutchinson 1961); the simple models then become points of departure to ask, for example, how so many species do coexist in Nature.

In general, heterogeneity is the explanation: underlying environmental heterogeneity in space or time can allow differential specialization on aspects of a resource, and, in concert, the structure of populations as regards genetics, age, behavior or spatial location becomes crucial. Of course, the genetic structuring of populations is the foundation for evolutionary theory while

¹⁰ Brock & Xepapadeas (2020) applied robust control methods to regional climate change models.

demographic models that account for age-dependent or size-dependent variation in life-history parameters like survival and fecundity are the basis of mathematical demography.

The incorporation of spatial heterogeneity and movement into dynamic models had its origins in population genetics nearly a century ago, and in ecology in the 1950s (Skellam 1951). Most of that work was on individual populations; but the implications for species coexistence and community and ecosystem theory transformed theory a half-century ago (Levin 1974). Clearly, such heterogeneity must make its way into ecological-economic models; but the problem is to determine the appropriate level of detail for the purposes at hand (Ludwig & Walters 1985, Levin 1992).

7. TIPPING POINTS AND EARLY WARNING INDICATORS

The existence of multiple stable states in ecological models was recognized even by Alfred J. Lotka and Vito Volterra in their early studies (and the notion of "contingent competition" and founder effects is covered even in the least mathematical ecological textbooks). As described earlier in this paper, in recent years, however, there has been increasing attention paid to the potential for systems to flip, either due to exogenous changes or slow evolution of endogenous variables, from one state (normally a healthy one, like an oligotrophic lake) to another (less healthy one, like a eutrophic lake).

Tipping points have long been of interest in ecology (May 1972), and Holling (1973) emphasized the relation to the search for resilience in ecological and managed systems. The fundamental methods for studying such a "critical transition" derive from a variety of mathematical and physical approaches, including especially bifurcation theory (Crawford 1991), catastrophe theory (Thom 1969, Golubitsky 1978, Arnol'd 1986), and the theory of phase transitions and renormalization groups (Goldenfeld 1992).

The spruce-budworm model of Ludwig et al. (1978) is a masterpiece of exposition, and created considerable ecological interest in such phenomena; in recent years the work of Carpenter, Scheffer and others has become central (see, e.g., Scheffer & Carpenter 2003). Many such transitions exhibit characteristic early-warning indicators – critical slowing down, increased variance, increased autocorrelation, and flickering – and numerous empirically-based studies have sought to find those indicators in data (Scheffer & Carpenter 2003). Where they do exist, they can be useful, but the science is complicated. Such early-warning indicators are associated with only a subset of phase transitions in physics, so are not universal; and on the other hand may not presage any transition at all. This is an exciting area of research, but caution must be employed, and much more research is necessary (Hagstrom & Levin 2017).

The study of regime shifts in the management of coupled ecological-economic models basically started with the lake model and the analysis of the conditions for the system to shift from an oligotrophic to a eutrophic state. In optimal management under the possibility of regime shifts, there are important trade-offs between the loss of ecosystem services when the system crosses a tipping point and a regime shift occurs, and the potential benefit of economic activities which induce the shift. Regime shifts are uncertain and the optimal reaction to uncertain future tipping points is an issue which emerges naturally in climate change (e.g., van der Ploeg & de Zeeuw 2018) or resource management (e.g., Polasky et al. 2011, de Zeeuw 2014b). The introduction of the concept of an early-warning indicator into models of optimal management under regime shifts is an area for further research.

8. SCALE AND SCALING, EMERGENCE AND CONFLICTS BETWEEN LEVELS

The fundamental challenge of dealing with CAS is that phenomena play out across multiple scales of space, time and organizational complexity (Levin 1992, Chave & Levin 2003). As has been described in the earlier parts of this paper, this leads to challenges as to how to relate

the processes on larger scales to those on smaller scales, essentially by developing appropriate nonlinear statistical mechanics.

However, from either an evolutionary or a management perspective, the conflicts between levels create special challenges, especially as regards the management of public goods and common-pool resources. These are familiar problems in economics (Samuelson & Nordhaus 1989, Ostrom 1990) as well as in the management of socio-ecological systems (Hardin 1968). Perhaps less familiar to the readers of this volume is the importance of such conflicts across scales of biological organization, from selfish DNA to tumor cells (which undermine the public good) to slime molds to bird flocks (Levin 2014). Indeed, consideration of such issues across scales is one of the great challenges in dealing with coupled economic and social systems (Levin 2020).

Scale separation with important policy implications emerges with respect to time. Separate time scales are used to analyze co-evolutionary processes with population dynamics evolving rapidly while evolution generally takes place more slowly. Management can impose strong evolutionary pressures on resources such as fish, with impacts on short time scales (Diekert et al. 2010). The so-called Red Queen cycles which are observed in slow time emerge through the interaction of population dynamics and mutation (or trait) dynamics operating in different time scales. Modeling fast–slow systems and Red Queen dynamics has been associated with issues like biological resource management, water management and pest control (e.g., Brock & Xepapadeas 2003; Grimsrud & Huffaker 2006; Crepin et al. 2011).

9. DISCOUNTING

Discounting refers to the process of assigning a lower weight (i.e., importance) to a unit of consumption benefit or cost in the future than in the present time. Following Dasgupta (2008, p. 144), the social rate of discount (SDR) between today's and tomorrow's consumption is the

additional consumption demanded tomorrow in order to give up one unit of consumption today. Thus, if ρ is the SDR, society would demand $(1 + \rho)$ units of additional consumption tomorrow as a price for giving up one unit of consumption today, meaning that society regards an additional unit of consumption tomorrow as being worth $1/(1 + \rho)$ units of additional consumption today.

Thus, an additional unit of consumption *n* years from now will be worth $1/(1 + \rho)^n$ of additional consumption units today, which is the weight or the discount factor associated with this future consumption. The SDR, ρ , is the appropriate discount rate to use in environmental or climate change cost-benefit analysis.

When long-term projects are evaluated – note that the vast majority of environmental, and especially climate-change-related, projects are long term – the weights refer to the benefits and costs associated with future generations. This creates a moral dilemma.

Discounted costs and benefits accruing in the distant future have a very small present value if the discount rate, ρ , is high. These values illustrate what David Pearce referred to as the 'tyranny of discounting' (Pearce et al. 2006, p. 23). Therefore, if ρ is relatively high, benefits from preventing damages to ecological systems or climate change damages which occur in the distant future and affect future generations, will have a very small present value now. Since the cost of preventing ecosystem collapse or climate change will be incurred now, this makes it difficult, using cost-benefit rules, to get acceptance for projects which are designed to prevent detrimental impacts in the distant future.

Under certain assumptions which are common in economics, the annual SDR is calculated by the "Ramsey formula" (e.g., Arrow et al. 2014a), defined as

$$r_t = \rho + \eta \cdot g_t,$$

where ρ is the utility discount rate, η is the (minus) elasticity of marginal utility with respect to consumption, and g_t is the annualized growth rate of consumption between time 0 and t. If g_t is constant, then the SDR is constant.¹¹

The basic Ramsey formula is adjusted when uncertainty is introduced. Uncertain consumption growth (Dasgupta 2008) leads to reduction of the SDR through a *precautionary effect*. More complex types of uncertainty – such as positively-correlated consumption shocks over time, subjective uncertainty about the mean and the volatility of the consumption process, or uncertainty about the discount rate itself (which is case of "gamma discounting"; Weitzman 2001) – lead to declining discount rates over time (Gollier 2012; Weitzman 2009).¹² Considerable literature exists on how gamma discounting or hyperbolic discounting arises, and its implications (Dasgupta & Maskin 2005).

The increasing attention given recently to the financial costs of climate change in relation to the uncertain arrival of environmental disasters which are positively related with the increase in global average temperature has led to another adjustment of the SDR. Bansal et al. (2016) show that the discount rate should be reduced by a temperature effect and a disaster effect which increase with global average temperature. This approach provides a clear link between climate change and the SDR.

10. CONCLUSIONS: POLICY ISSUES AND ECOSYSTEM MANAGEMENT

Ecological systems provide services – ecosystem services – which are the conditions and processes through which natural ecosystems and the species that comprise them sustain human life and support the human economy (Daily 1997). The Millennium Ecosystem Assessment (2005) links ecosystem services – supporting, provisioning, regulating, and cultural – with the

¹¹ For indicative numerical estimates of the SDR, see for example Dasgupta (2008) or Arrow et al. (2014a).

¹² Declining social discount rates are used by the French and the UK governments.

constituents of human well-being, which include security, basic material and good life, health, good social relations, freedom, and choice of action.

Human economies use these services either directly, mainly in the cases of provisioning¹³ and cultural services, or indirectly, mainly in the cases of supporting or regulating services. Ecosystem services provided in a market economy have two important characteristics: either markets for these services do not exist; or, due to property rights not being well-defined, common pool or open access conditions emerge in the appropriation of services by humans. Arrow (1969) points out that when markets fail to exist, externalities emerge, with the externalities being the indirect (positive or negative) effect of the consumption or production of a good by an agent on the production set or the consumption set of another agent. As is well known in the non-cooperative competitive context, externalities lead to inefficiencies. Inefficiencies are higher the stronger the extrality is (e.g., climate change). On the other hand, common pool or open access situations lead to inefficient overexploitation of a resource and the tragedy of the commons (Hardin 1968).

Correction of negative externalities through decentralized schemes can in general be obtained either through the creation of markets in the spirit of Arrow (1969) or through taxation of negative externalities or subsidization of positive externalities.¹⁴

The correction of negative environmental externalities emerging from the use of ecosystem services has generated a regulatory framework which includes three basic categories of policy instruments:

¹³ Provisioning services should be understood not just as harvesting resources, such as timber or fish, but in a more general concept of provision of "space" for the accumulation of pollutants generated by human activities. For example, the atmosphere, the land ecosystems and the ocean provide sinks for greenhouse gasses emitted by the use of fossil fuels. Accumulation of greenhouse gasses leads to climate change.

¹⁴ Pigou (1920) attributed the externality-related inefficiencies to the divergence between private and social costs or benefits and suggested taxes (Pigouvian taxes) or subsidies as correcting measures. Coase (1960) suggested negotiation between a polluter and a pollutee. For further analyses of decentralization with externalities, see for example Starrett (1972) or Laffont (1976).

- (i) Command-and-control policy, which refers to environmental policy that relies on regulation such as permissions, prohibition, standard setting and enforcement (OECD 2017b).
- (ii) Market-based regulatory instruments, which aim at changing the behavior of consumers or producers by providing appropriate economic incentives which, in the majority of cases, change relative prices. The OECD (2017a) includes in this category, environmentally-related taxes, fees and charges, tradable emission permits, and tradable property rights for natural resources (e.g., tradable fishing rights), deposit-refund systems, subsidies, and payments for ecosystem services and biodiversity.¹⁵
- (iii) Voluntary approaches, which are not economic instruments but commitments by firms or industries to improve their environmental performance beyond legal obligation (Segerson & Miceli 1998, Dawson & Segerson 2008; Ahmed & Segerson 2011).

Typically regulatory instruments in environmental economics are characterized both in qualitative and quantitative terms by a damage function¹⁶ which reflects damages from the externality, as well as the deviation between a socially-optimal outcome for the use of ecosystem services and a privately-optimal outcome which ignores externalities. This damage function in many cases is supposed to present a summary description of the linkages between the economic system and the ecological system. The deviations between the socially-optimal outcome, which internalizes ecosystem damages, and the privately-optimal outcome, which

¹⁵ For further discussion on market-based instruments, see for example Stavins (2002). For a discussion about carbon taxes, which are a classic market-based instrument addressing climate change, see for example the High-Level Commission on Carbon Prices (2017). For a discussion of policy instruments based on information provision, see for example Petrakis et al. (2005). For policies based on changing social norms, see Nyborg et al. (2016).

¹⁶ Typically, a fully internalizing Pigouvian tax in a perfectly-competitive context is equal to marginal environmental damages evaluated at the socially-optimal pollution level.

does not internalize these effects, can be used as a basis for designing a regulatory scheme (e.g., controls, taxes, tradable permits, agreements). Regulation aims at bringing the regulated private outcome closer to the socially-optimal outcome. Such a regulatory scheme supports ecosystem management which promotes the socially-efficient use of ecosystem services by humans.

In this paper we described in broad terms the most important characteristics underlying the co-evolution of ecological and economic systems which ultimately tend to result in a unified economic-ecological system evolving in time and space. This discussion points to the need to study the implications of these factors when ecosystem management is designed. While it is true of course that the characteristics described above have been introduced in ecosystem management problems, as the discussion and the references in the relevant sections reveal, this has been done mainly by allowing for one "extension" of the traditional approach. That is, by allowing for non-convexities and positive feedback or spatial diffusion or deep uncertainty or tipping points. An interesting basic research issue, but also a policy question, could be to explore what the management implications of a general integrated assessment model of a unified ecological-economic system would be. Economic theory teaches us that, in the presence of more than one externality, more than one policy instrument is required for their correction.

In the context of a unified ecological-economic system, correcting the potential multiple externalities emerging from the factors discussed here generate new challenges which go beyond the postulation of a simple damage function. The issue is not just to add more levels of complexity to a setup which is already complex. The important issue is to explore whether the omission of some of the unifying factors – and the possible underlying externalities – which characterize the co-evolution of the unified system, create biases and inefficiencies in management. To put it differently, how should command-and-control, market-based and voluntary policy instruments be modified when they are derived in the context of a unified co-

evolving ecological-economic system? Are the policies derived from the relatively simplified "economy only" or "ecology only" approaches sufficient?

Allowing for the temporal but not the spatial dimension of the problem might obscure the need for spatially-differentiated paths for policy instruments, or additional policy instruments. Ignoring the interactions between fast and slow process will not provide policies appropriate for the regulation of slow variables which, if left unregulated, might cross thresholds or tipping points. Allowing for heterogeneity could be important in the design of biodiversity policies. Recognizing the importance of tipping points generates the need to introduce policies which will provide early-warning indicators. Not allowing for deep uncertainty will distort the precautionary principle. Ignoring positive feedbacks and nonconvexities (e.g., oligotrophic vs eutrophic steady states, permafrost thawing) might hide the existence of multiple steady states which could be "bad" or "good" in terms of the regulator's objective, and thus produce management which steers the unified system to an undesirable steady state.

The issues raised above suggest that the incorporation of factors which govern the coevolution of unified ecological-economic systems into the design of policies for the management of these systems brings new challenges in the design of policy instruments. Our aim in this paper was to identify some of the important factors shaping this co-evolution, review the ways in which these factors have been studied in the literature, and provide some insights regarding the management of co-evolving ecological-economic systems.

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