

Social-ecological systems as complex adaptive systems: modeling and policy implications

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ABSTRACT. Systems linking people and nature, known as social-ecological systems, are increasingly understood as complex adaptive systems. Essential features of

these complex adaptive systems – such as nonlinear feedbacks, strategic interactions, individual and spatial heterogeneity, and varying time scales – pose substantial challenges for modeling. However, ignoring these characteristics can distort our picture of how these systems work, causing policies to be less effective or even counterproductive. In this paper we present recent developments in modeling social-ecological systems, illustrate some of these challenges with examples related to coral reefs and grasslands, and identify the implications for economic and policy analysis.

1. Introduction

In the past century, environmental issues have become increasingly global in scale. Management solutions often urge us to ‘think globally and act locally’, based on the premise that global problems reflect the collective consequences of local actions (e.g., [Geddes, 1915](#); [Rockström *et al.*, 2009](#)). Individuals repeatedly ignore the social costs of their actions ([Pigou, 1920](#)), often because the people and organizations that act locally are at least somewhat removed from those who suffer the consequences. Making matters worse, negative changes tend to accumulate gradually in the broader social-ecological environment.

These problems are particularly difficult to address when the underlying social¹ and ecological systems are complex adaptive systems ([Berkes and Folke, 1998](#)). Each system consists of individual agents able to change, to learn from experience (or to change in relative abundance over evolutionary time) and to exploit their own selfish agendas. These agents compete for limited resources, leading to behaviors of exploitation, competition, parasitism and cooperation. To support these behaviors, distinct functional groups of players with complementary roles often emerge ([Levin, 1999a, b](#)).

In social-ecological systems, macroscopic properties emerge from local actions that spread to higher scales due to agents’ collective behavior; these properties then feedback, influencing individuals’ options and behaviors, but typically only do so diffusely and over much longer time scales. The possibilities of non-marginal changes, unobserved slow structural changes, spatial variation and strategic behavior are all examples of management and policy challenges related to the complex adaptive system properties of social-ecological systems.

Modeling these processes is difficult. General and analytical results are often unobtainable. However, empirical observations suggest that simple linear and reductionist dynamics give a misleading representation of how social-ecological systems work. Moreover, important features of complex

¹ We use the term ‘social system’ in a broad sense covering all kinds of relationships between people, including market transactions. Although the behavioral changes of most interest to us are unlikely to involve a genetic component, over longer time scales, such evolutionary changes do occur, and underlie any effort to understand human behavior and cultures.

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adaptive systems must be studied and understood in an integrated way, because they all matter for the outcome of any management and policy intervention. Ignoring these characteristics might obscure crucial features that we observe in reality, like the risk of abrupt ecosystem changes, which can be difficult or even impossible to reverse. Nonlinear feedbacks along with slow processes help explain regime shifts in coral reefs, forests and lake systems (Scheffer, 2009). Hence, economic policies that do not account for complex adaptive system characteristics can lead to undesirable social-ecological outcomes. This does not mean that models must incorporate every possible detail; indeed, the art of modeling is to incorporate the essential details, and no more. Clearly, a balance must be struck. Our point is that policy analysis has tended to err on the side of leaving out key features of the underlying systems.

Putting these features in our models requires interdisciplinary approaches (Arrow *et al.*, 1995; Worm *et al.*, 2006). In this article, we focus on some of these approaches. We aim to synthesize the implications of a complex adaptive system approach for social-ecological systems in relation to economic policy. In section 2 we discuss the central properties of complex adaptive systems and the principles for their management. Section 3 discusses ways to model complex features of social-ecological systems. Section 4 analyzes the implications for economic policy and concludes by offering some final remarks.

2. Central features of complex adaptive systems and principles for management

2.1. Central features and tradeoffs in complex adaptive systems

The macroscopic properties of complex adaptive systems emerge from lower-level interactions, rather than having been optimized according to performance criteria. In ecology and the geosciences, the concept of Gaia (Lovelock, 1979) pictures the Earth system as a closely integrated, self-regulating, complex system, maintaining the conditions for life on the planet. Evolutionary biologists object to this view, saying that such properties were not selected to optimize the current conditions for life, but rather emerged from dynamic interactions between the environment and biological populations, many of which have become extinct in the process. Economies and markets are also self-organizing entities (see, e.g., Smith, 1776; von Hayek, 1929, 1931; Krugman, 1996). However, as the recent global economic crisis has reminded us, markets left to their own devices similarly carry no guarantee of progress for the benefit of the economic system, let alone for the environment or society.

All management models imply tradeoffs that relate to the central features of complex adaptive systems, like resilience, diversity, redundancy and modularity. Modularity (or compartmentalization) refers to the degree to which a system's components may be separated and recombined. Resilience and robustness are two concepts which have independently developed towards a similar meaning in the literature concerning social-ecological systems. Resilience or robustness refers to a system's ability to continue to function when intrinsic and extrinsic disturbances occur.

Resilience or robustness is achieved either when a system is resistant to change or is able to reorganize after change (Holling, 1973; Levin, 1998; Levin and Lubchenco, 2008; Folke *et al.*, 2010). Resilience and robustness are properties of a system, and are neither good nor bad – we would like to preserve the robustness or resilience of valuable ecosystem services like pollination, yet overcome patterns of human behavior that sustain extreme inequity or reduce long-run welfare. Maintaining the capacity to absorb change is costly. Features helping to maintain the status quo for a system can be good if the system performance is well suited to current conditions, but may reduce the system's capacity to adapt to changing conditions. Universal robustness or resilience against all kinds of uncertainties is impossible to achieve. For example, policies providing buffering capacity against uncertainties in fish stocks do not cope with uncertainties related to fish market price and vice versa (Anderies *et al.*, 2007). Similarly, managing river flooding by building dikes may increase short-run resilience against small yearly floods, allowing people to develop activities near the river bank, but they may not be able to contain large floods that occur less frequently, making these same people more vulnerable to climate change (Palmer *et al.*, 2008).

A tension also exists between the benefits of adapting to current environments, and the need to maintain sufficient variation to respond to new environmental challenges (Levin, 1999a; Norberg *et al.*, 2001). Such tensions exist for an animal foraging in a variable environment and for a corporation trading off present performance versus future potential. Adaptive processes like mutation and sexual reproduction have arisen through selective pressures in changing environments – for example, because of disease or limited food resources. By changing the frequencies of types and behavior, these processes drive adaptation to new conditions.

Maintaining diversity and heterogeneity sustains the system's adaptive capacity to compensate for losses of particular components, such as populations or species in ecosystems, people and organizations in social systems, or particular stocks in financial portfolios. On the other hand, functional redundancy also provides insurance against the loss of critical system components. Maintaining a habitat for wild bees secures pollination capacity in case other pollinators disappear. Similarly, having an extra pilot in the cockpit, or police officers patrolling in pairs, helps maintain capacity in case one of the pilots or officers is unable to perform for some reason. Obviously, diversity and heterogeneity on the one hand, and functional redundancy on the other, trade off against each other (Levin, 1999a, b), because making more copies of one kind of unit necessarily restricts variation. Evolution under constant conditions erodes genotypic diversity by selection, which reduces the ability to respond to a changing environment. In competitive or human-controlled situations, these selective processes also reduce diversity by increasing the frequency of the most optimal types or ideas. Market pressures have contributed to lower cultivated species diversity by promoting the most profitable crops and animals at the expense of a variety of less productive ones (e.g., varieties of apples, cattle, etc.). These species are well adapted to the present production system and taste and perform very well under current (relatively constant)

conditions. However, if conditions change, the optimal type can change as well. If disease were to strike a dominant crop or animal, the selective process might not cope if diversity were reduced because of past selection for increased productivity.

Modularity is also crucial. It prevents harmful properties from spreading through a system and provides building blocks for reorganization in the face of change. In ecological systems, modularity prevents diseases, invasive species and forest fires from spreading very far. In economic and financial systems, modularity limits the spread of crises from one country to another (May *et al.*, 2008). However, modularity comes at the expense of connectivity, which can also aid resilience – for example, by rebuilding depleted populations or spreading fruitful information. Foreign trade, specialization and knowledge spillovers often improve welfare, but financial problems spread quickly in a globalized and connected world, as when the collapse of the housing market in the United States in 2008 triggered a global economic crisis. Hence, connectivity can also contribute to systemic risk through the contagious spread of disturbance.

The net result is that optimal resilience or robustness for a particular system depends on balancing heterogeneity, redundancy and modularity (e.g., Levin, 1999a, b; Elmhirst *et al.*, 2009).

2.2. *Control of systems, policy design and complex adaptive systems*

It is fundamental to understand: (i) how individual-level behaviors create collective system-level consequences, which feedback to influence individual actions; (ii) how well social-ecological systems perform with regard to system-level properties like social welfare or productivity; and (iii) what to do about failures. The first fundamental theorem of welfare economics (Arrow, 1951; Debreu, 1959) states the conditions under which a competitive equilibrium is Pareto optimal. If these are fulfilled, letting markets emerge and self-organize would be an optimal way to produce and allocate goods and services. The outcome of this self-organizing social-ecological system could also be obtained by an optimizing central planner. However, externalities, public goods, incomplete markets, imperfect information, non-convexities and insufficiently defined property rights typically drive a wedge between the outcome that emerges from optimization by individual actors and the outcome that is first-best for the system as a whole.

The difference between the market equilibrium outcome that emerges from individual actions and the socially optimal outcome provides the basis for policy intervention. Optimal policies provide incentives to individuals who pursue their own self-interest to behave in ways that drive the system towards the socially desirable state. Hence, policy creates social frames that act as attractors and help focus markets' emergent properties towards a desired goal. In such a context, top-down optimizing models are useful for representing the parts of a social-ecological system that can sustain a Pareto optimum thanks to efficient public policy.

In reality, policy interventions are rarely efficient. They emerge out of a political process, and depend on the institutional structures in place in a particular social complex adaptive system. Rent seeking is just one example of how the political process can undermine efforts to promote efficiency.

However, optimization can still be useful as a benchmark to assess and evaluate the policy process. Modeling the political interactions underlying the policy process could also provide an indication of the expected policy impacts. This suggests bringing together economic considerations, which reflect the benchmark, and political considerations, which reflect the actual formulation of policies. For example, in a first best world, carbon taxes would be the ideal way to bring down carbon dioxide emissions, but carbon taxes have faced political opposition in many countries.

How should system problems like these be handled? One approach is to look ahead, engage in rational foresight, and explore the implications of different policies into the future. This seems a reasonable approach, but it can fail badly when key components of complex systems are poorly understood. Another approach is to be myopic, focusing on the most pressing matters and adopting 'quick fixes' as needed. The problem here is that hasty solutions often create other costly problems (Sternier *et al.*, 2006). A third approach inspired by complex adaptive systems theory is to build a policy intervention around the system's complex structure and to try to balance redundancy, heterogeneity, modularity and connectivity so as to sustain desirable system outcomes.

2.3. Social and behavioral considerations

Complex adaptive system theory provides a new lens for how to match the behavior of individual agents with social objectives. In a standard utility- or profit-maximization context, agents are often assumed to be unboundedly rational and fully optimizing. However, it is probably more sensible to assume that rationality depends on the context, varying with such things as deliberation costs, complexity, incentives, experience and market discipline (Conlisk, 1996). Adaptive expectations or imitation dynamics are ways to model bounded rationality. When agents occasionally observe and imitate the behaviors of others, they create imitation dynamics that could help explain harvesting patterns, compliance behavior and the evolution of social norms (Ehrlich and Levin, 2005).

In the global commons, the actions of individual agents affect everyone, but the level of cooperation reached often cannot secure a sustainable common future. A crucial aspect is that no individual has exclusive access to a resource. Sometimes no-one can be excluded from a resource (open access); sometimes access can be restricted to a group of persons (common property). Non-excludability can generate severe free-riding problems, often leading to a loss of resilience or robustness and, in the worst cases, to a collapse of the resource – the 'tragedy of the commons'.

Cooperation can emerge spontaneously among groups of users, particularly when the number of users is small (Ostrom *et al.*, 2002). But cooperation can break down in larger groups, where social networks are harder to maintain. Much can be learned from how animal societies achieve cooperation through natural selection, or how human societies do so through social contracts and the evolution of social norms and social learning. Norms frame the modularity versus connectivity pattern of a social system because they link some individuals to each other while excluding others. For example, religious norms link together individuals with similar

religious beliefs but exclude others who do not share these same beliefs. The processes that give rise to these norms operate on different time scales, and feedbacks may create multiple attractors, i.e., alternating paradigms (e.g., Brock and Durlauf, 1999; Olsson *et al.*, 2004). This could explain why changes in norms sometimes occur in a nonlinear way involving a substantial amount of surprise. Despite a growing literature, the development of a mechanistic understanding of the emergence and robustness of norms remains one of the most important open research challenges (Levin, 2006).

3. Advances in the optimal management of complex social-ecological systems

While economic theory has often successfully ignored most complexity in modeling economic systems, research on social-ecological systems shows that it can be very misleading to do so. Complexity entails substantial modeling challenges, but simple models can incorporate some elements of complexity to provide novel insights. Dynamical systems are starting points for modeling social-ecological systems, and agent-based models provide a natural extension that better incorporates heterogeneity among individuals. In this section we discuss some ways in which essential features of social-ecological systems as complex adaptive systems have been successfully introduced into optimal management models, and illustrate this, using examples from the management of grasslands and coral reefs.

At the core of all the recent advances are models of dynamic systems, represented by systems of differential equations. Stocks of coral reef species (e.g., coral, algae, fish) or grassland species (e.g., grass, tree saplings, adult trees), $x(t)$, evolve over time due to internal dynamics, parts of which can be controlled by the harvesting of fish or trees, $h(t)$. Note that x and h could be vectors. Functions like F in (1) describe what these dynamical changes look like depending on stock size, the control variable, and parameter values such as the growth rate of trees or coral, which are not represented here.

$$\frac{dx}{dt} = F(x, h) \quad (1)$$

In social-ecological systems, humans interact with the reef or grassland dynamics and derive some utility $U(x, h)$ either from the amount of coral, fish, trees or grass in the system (x , the stock itself) or from harvesting fish or trees or letting their cattle graze (h , controlling the stock). In such contexts, people typically are assumed to want to choose the level of harvest or cattle size to maximize the discounted (at rate δ) present value of their utility over the time horizon T they consider (which could be infinite). A common management problem is to find

$$\max \int_{t=0}^T U(x, h) e^{-\delta t} dt \quad (2)$$

subject to restriction (1).

Several branches of economic theory, ranging from natural resource management like fisheries or forestry to optimal economic growth theory,

deal with problems of this kind. In this section we will show how to specify such problems to incorporate some element of complex adaptive systems, and draw out implications of this for the management of social-ecological systems.

3.1. Nonlinear feedbacks

Coral reefs and grassland can shift between multiple basins of attraction. Algae can suddenly and rapidly invade apparently healthy coral reefs. If this invasion is persistent it can lead to massive coral death and a total reorganization of the reef's dominant species. Similarly, grasslands can rapidly change from being highly productive grass-dominated lands to ones encroached by bush. They could also transform into deserts. Non-linear and non-convex feedbacks (often sigmoidal) play an essential role in these dynamics by enabling accelerating effects, which can cause flips from one basin of attraction to another. Staver *et al.* (2011a, b) model the dynamics of tree cover in sub-Saharan Africa as an interaction between areas of grass, tree saplings and adult trees. Because grass burns, inhibiting sapling growth, but adult trees are protected against fire, the system admits multiple steady states. The dynamics reflect this by representing tree recruitment from saplings as occurring at a nonlinear (sigmoid) rate (see also Archibald *et al.*, 2011; Hirota *et al.*, 2011, for more details).

Nonlinear feedbacks can give rise to multiple steady states, hysteresis and irreversibility. The sigmoid rate of recruitment from saplings makes multiple steady states feasible and helps interpret the different vegetation covers that have been empirically documented and analyzed as representing alternative regimes when rainfall is intermediate, while high rainfall favors tree cover. Historically, human activities have altered land use and increased the role of fire in these systems; however, climate change is likely to shift the balance again (Archibald *et al.*, 2011).

Crépin (2007) illustrates the effects of nonlinear dynamics on coral reef management by modeling fish dynamics using a nonlinear Holling type III functional response to predation, which has a sigmoidal form. For low fish stocks, predation is low, slowly increasing with fish stock at an accelerating rate before it reaches a threshold, after which it starts saturating. In management problems where the dynamic constraint (1) has nonlinear components, Skiba indifference points (Skiba, 1978) may arise. These are initial states from which the regulator is indifferent between optimal trajectories into distinct domains of attraction, like coral-dominated/algae-dominated reef or grass-dominated/bush-dominated land. Hence the resulting steady state depends on history (e.g., previous management) besides intrinsic biological dynamics.

Accounting for nonlinearities increases the model complexity, and it is reasonable to ignore nonlinearities if it is clear that the system will remain within the current basin of attraction. However, if disturbances or management introduce substantial changes, the system may undergo abrupt changes known as regime shifts. To address such complexities, one must consider the full range of nonlinear dynamics. Not doing so may lead to management mistakes like choosing excessive harvest rates that could trigger an unwanted regime shift. A change from a healthy

coral reef with lots of fish to algae-dominated or bleached coral can have large negative impacts on fisheries and tourism (Moberg and Folke, 1999; Bellwood *et al.*, 2004). Similar potential system flips have been well studied for California and other coastal marine systems, in which top marine mammals, such as the sea otter, can suppress shellfish populations and indirectly foster nutrient conditions that favor finfish, with substantial economic consequences (Estes and Palmisano, 1974; Johnson, 1982; for similar approaches in other systems like spruce budworm, Ludwig *et al.*, 1978; lakes, Brock and Starrett, 2003; Mäler *et al.*, 2003; Kossioris *et al.*, 2008; grazing systems, Anderies *et al.*, 2002; Janssen *et al.*, 2004; Crépin and Lindahl, 2009).

3.2. *Different time scales and adaptive processes*

In coral reefs, algae and fish populations often evolve more rapidly than the coral. If coral dynamics change very slowly, they may appear constant, which could cause mistakes in management (Crépin, 2007). Slow coral dynamics also imply that it can take a long time before all the impacts of a particular management measure take place. Species introduced into new areas often grow exponentially on a fast time scale until carrying capacity restricts growth (Levin, 2000: 499). The interaction of fast and slow processes is an integral part of ecosystem analysis (Gunderson and Pritchard, 2002). To account for this requires that (1) must be an equation system with slow and fast terms. It is also conventional to separate time scales to analyze co-evolutionary processes and let population dynamics evolve rapidly while evolution generally takes place more slowly. Even management can impose strong evolutionary pressures on fish (to take just one example), having impacts on short time scales (Diekert *et al.*, 2010). In models of antagonistic species, co-evolution represented by the interaction of population (or biomass) dynamics and mutation (or trait) dynamics can also lead to so-called Red Queen cycles.²

For social-ecological systems being shaped over multiple time scales, management can motivate time separation. For example, concerning herbicide or antibiotic resistance, slower evolutionary processes can be instrumental for understanding the whole system and for developing sensible policies. Modeling fast–slow systems has been associated with issues like biological resource management, water management and pest control (e.g., Brock and Xepapadeas, 2004b; Grimsrud and Huffaker, 2006; Huffaker and Hotchkiss, 2006; Crépin *et al.*, 2011).

Singular perturbation analysis (e.g., Wasow, 1965; Fenichel, 1979; Berglund and Gentz, 2003) can help analyze dynamical systems evolving in a fast–slow time framework. The idea is to analyze slow and fast dynamics separately, taking, for example, coral dynamics as constant so as to analyze fast dynamics, while assuming that fish and algae reach their

² Non-point attractors in trait-space dynamics are called Red Queen races because, for example, in predator–prey systems, traits evolve against each other and move dynamically, unlike a fixed point. Red Queen cycles are observed in a slow time scale, in contrast to the population, host–parasite, dynamics, which are assumed to evolve quickly.

steady states instantaneously in the slow dynamics (Crépin, 2007). Similar techniques exist also for optimized systems (see, e.g., Naidu, 2002; Crépin, 2007). When such time-scale separation is possible, it provides substantial simplifications and can highlight interesting mechanisms that are obscured by focusing on fast dynamics only. For example, even optimal fisheries management can lead to a loss in resilience (compared to no-take reefs) when it allows a smaller shock to trigger a regime shift (Crépin, 2007).

3.3. Spatial characteristics

The effects of spatial variation and dynamics are well examined in the ecological literature (Skellam, 1973; Levin, 1974; Okubo and Levin, 2001; Murray, 2003), in meta-population models of fisheries (Sanchirico and Wilen, 1999, 2005), in forestry (Potts and Vincent, 2008), and in ecosystem management and conservation planning (Goetz and Zilberman, 2000; Elmhirst *et al.*, 2009). With few exceptions, where spatial aspects of economics are explicitly studied (e.g. Sanchirico and Wilen, 1999, 2005; Henderson and Thisse, 2004), most economic and natural resource models discard spatial heterogeneity and assume that all the economic activity occurs at one point in space. This is the case with the coral reef and savannah examples already discussed. In reality, a coral reef consists of a collection of heterogeneous patches where some species (fish, floating algae) move between patches at different speeds and in different directions while others (coral, bottom vegetation) remain within a single patch. Similarly, on land the intensity of tree cover varies often in a non-homogenous way, creating a patchiness of different landscapes where some species move around while others do not.

In a spatiotemporal version of such a system, the stocks must be place specific, e.g., defined as $x(z, t)$, with $z \in Z$ representing the set of all possible places. Among the many ways to represent the movement of individuals between patches, passive diffusion is the simplest and most commonly employed for continuous systems. However the complexities of water movements and the likelihood of advective as well as nonlinear effects complicate the story (Okubo and Levin, 2001). Thus deriving diffusion limits of individual-based (Lagrangian) models requires caution (see Durrett and Levin, 1994; Flierl *et al.*, 1999).

A common way to represent spatial dynamics is to use a diffusion term as in the Fisher equation, or for several species a reaction-diffusion system or an interacting population diffusion system. In more general models the diffusion coefficient could be dependent on the densities of the particular stock in one or several adjacent patches, or be spatially variable (Murray, 2003).

Besides traditional representation with local processes, spatial movements can also involve non-local or long-range effects (Mollison, 1977). Integro-differential equations can describe combined local and non-local/global processes (e.g. Mollison, 1977; Genieys *et al.*, 2006). Non-local effects are widely used in economics to model knowledge or productivity spillovers on production (e.g., Lucas, 2001; Lucas and Rossi-Hansberg, 2002) or to model long-range effects of knowledge accumulation (e.g., Quah, 2002). In terms of agglomeration economics, the production

externality is a force that promotes the spatial concentration of economic activity.

Spatial dimensions complicate models substantially, but can also give new system insights. Representing an alternating environment (for example, one in which forest patches alternate with grasslands), with an averaged one (sparse forest) could be misleading for management. In particular, spatial dynamics could lead to pattern formation, which can emerge endogenously (Turing, 1952; Levin, 1974). Observed spatial patterns in semi-arid grazing systems could, for example, result from spatial interactions between places with different stocks of plant biomass and underground water, where people who disregard spatiotemporal dynamics (myopic behavior) let their cattle graze to maximize private profit (Brock and Xepapadeas, 2010). Figure 1 simulates spatiotemporal evolution for plant biomass and groundwater, indicating that spatial patterns emerge and persist over time.

Under these circumstances it may even be optimal to control the system so that spatial patterns emerge (Brock and Xepapadeas, 2008, 2010). This can be compared to how economic activities tend to concentrate on particular sites, creating patterns of urban and rural areas or within city regions where industries, trading places or houses agglomerate (Krugman, 1996).

We know of no successful attempts to abandon myopic behavior and instead incorporate strategic interactions among agents in the optimal control of spatiotemporal systems. Handling such problems requires solving a nonlinear differential game evolving in at least two dimensions and with nonlinear strategies. This is undoubtedly an important area for future research.

3.4. *Strategic interactions and differential games*

The elements of complexity introduced so far only alter the dynamic constraints (1) in an optimal control problem. In contrast, strategic interactions among agents in a dynamic framework comprise an element of complexity widely studied in economics that requires another modeling approach: the use of differential games (Başar and Olsder, 1982). If people cooperate, for example when they decide how many cattle to let graze on a common grassland, they end up solving a standard optimal control problem, like (2) subject to (1). If they do not cooperate, however, the outcome depends on the information people have or acquire. People could decide their strategies for how many cattle to hold once and for all given the initial state (open-loop), they could continuously update their strategies given the current system state (closed loop or feedback strategies, which are strongly time consistent) or they could do something else. With these approaches, it is possible to study deviations between cooperative and non-cooperative behavior corresponding to open-loop and closed-loop non-cooperative Nash equilibria, and the implied regulation issues.

Dynamic strategic interactions among people are widely studied in economics, but capturing the dynamics of complex adaptive systems is tricky. If a common grassland can exist in two different regimes, farmers sharing the grassland for grazing cattle play a strategic game over a non-convex

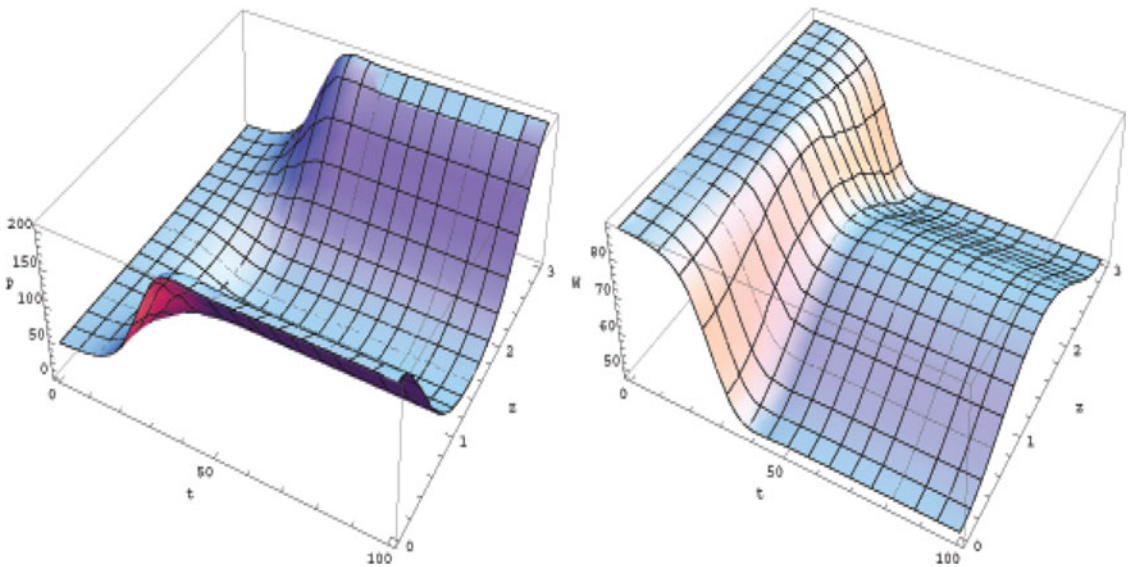


Figure 1. Pattern formation in plant biomass and groundwater

resource. Whether cattle owners cooperate or not could depend on initial conditions. Under some initial circumstances, cooperating farmers will find it optimal to keep much grass while under other circumstances a low grass state would be preferable. Non-cooperative farmers may keep less grass than optimal, which could transform a high-grass system into a low-grass system. Other initial conditions imply that non-cooperative farmers keep more grass than optimal, sometimes avoiding a flip to a low-grass state that would have been optimal (Crépin and Lindahl, 2009; see also Mäler *et al.*, 2003; Brock and Xepapadeas, 2004a; Kossioris *et al.*, 2008, 2011, for issues of strategic interactions in aquatic environments that can exist in different regimes like the design of unit taxes on phosphorous loadings to influence agents to behave as if they were cooperating).

Future research could focus on method development to determine fully nonlinear feedback Nash equilibria in stochastic environments and study strategic interactions in systems involving different time scales. Strategic interactions can be incorporated with different levels of complexity and useful insights can emerge from simple static or repeated games models that may be easier to handle than a differential games approach, if the dynamic aspects are not essential. It may also be useful to instead focus on the heterogeneity of the agents involved.

3.5. *Agent-based models*

In economic systems and ecological systems alike, heterogeneity introduces complexities of essential importance, motivating efforts to model these features. Agent-based models or individual-based models allow each individual to have unique behaviors that may change in response to others' actions, and the possibly slow evolution of macroscopic variables (Bonabeau, 2002; Couzin *et al.*, 2005; Grimm and Railsback, 2005). These models easily implement detailed assumptions about individual behavior, but suffer from a lack of analytic tractability and difficulties with extracting robust conclusions. Thus, it is important that these descriptions ultimately be embedded into an analytical framework that helps to understand the statistical mechanics of these heterogeneous ensembles (Flierl *et al.*, 1999; Couzin *et al.*, 2011).

One of the most interesting outcomes of agent-based simulations is the importance of individuals without opinions in collective decision making. This effect is neither intrinsically good nor bad. Minority viewpoints can represent either socially beneficial or socially harmful influences. However, large numbers of such individuals make it much less likely that such minority opinions can prevail (Couzin *et al.*, 2011). These effects and other aspects of collective decision making when information is limited, including the remarkable success of prediction markets, carry substantial implication for policy analysis, which have so far been barely explored. Clearly, how groups of humans make decisions is crucial to understanding how to manage the global commons, in which public attitudes are subject to sudden shifts of opinion. The earlier comments about what factors lead to robustness or resilience in complex adaptive systems apply with full force to the dynamics of opinions and social norms, at all levels (Ehrlich and Levin, 2005).

4. Policy implications of social-ecological systems as complex adaptive systems

Social-ecological systems challenge management and policy because of the high level of complexity and the multiple approaches required to understand and model them. Useful models of such systems intended for policy assessment and design must be transdisciplinary in structure³ and rely on a clear understanding of the key elements of a specific problem. In this section we review the implications of the different elements of complex adaptive systems for policy and draw conclusions about the potential for viewing social-ecological systems as complex adaptive systems.

4.1. Nonlinearity

Ignoring nonlinear dynamics in complex systems will lead to errors and mask potential surprises. Linear models cannot explain why coral reefs suddenly flip between a clear and a turbid state (Crépin, 2007), why forests may rapidly turn into grasslands (Hirota *et al.*, 2011; Staver *et al.*, 2011a, b) or why stock markets crash. The nonlinear properties of many social-ecological systems imply that steady-state analysis is not enough; dynamics far from steady states may matter as well as transition dynamics to such states. The optimal state of a social-ecological system sometimes depends on initial conditions. Thus, optimal regulation may depend on past actions (history dependence) and mistakes may be difficult to correct.

Nonlinearities could also impact on the choice between price and quantity instruments, particularly when the nonlinearities imply potential catastrophic changes (Pizer, 2003; Crépin *et al.*, 2011). If many agents share a lake, which can exist in a clear or a turbid state, and choose a strategy once and for all, it may not be possible to calculate an optimal fixed tax that will give people incentives to reach an optimal cooperative outcome (Mäler *et al.*, 2003). If instead people update their strategy continuously, reaching an optimal cooperative outcome using a tax would require combining information, coordination (because of the multiplicity of closed-loop Nash equilibria) and policy (Kossioris *et al.*, 2011).

4.2. Scale issues

Regulating nonlinear systems like fisheries with interacting species and hysteresis can be problematical if biomass dynamics are slower than economic dynamics (Brock and Xepapadeas, 2004a; Crépin, 2007). A manager who ignores this may risk system collapse. Since the fast variables converge long before the slow variables, a manager who has failed to account for slow variables might believe that the actions he/she put in place worked well and that the change in slow variables is due to something else (Sterner *et al.*, 2006). Similarly, scale issues exist in space and organizational complexity as well: regulating a part of a system without regard to feedback involving other parts of the system is like regulating with a

³ Approaches from disciplines like ecology, economics, political science, history, earth science, mathematics and statistics may need to be combined.

blindfold on. In recent years, recognition of this fact has led to a call for more ecosystem-level management of marine fisheries, but progress in this direction has been slow.

4.3. *Heterogeneity*

Scale issues are particularly evident when considering the system's spatial extent and the associated heterogeneity that spatial patterns represent. Inadequate attention to spatial patterns and dynamics can generate incorrect policy recommendations. For example, and surprisingly, closing off some areas to fishing, either when biological productivity is low or fishing costs are low, can under some circumstances generate higher fishing profits [Sanchirico et al. \(2006\)](#).

Preliminary results suggest that for some systems it may be best to use instruments like taxes or quotas that vary both among spatial zones and over different time intervals. This is a very promising area for further studies.⁴

Genetic heterogeneity can also be important, given the potential for rapid evolutionary changes in harvested populations. Whether in agriculture or in fisheries, loss of genetic diversity creates selection pressure on natural enemies, potentially accelerating the evolution of pest genotypes that can lead to collapse of the stock. When private profit-optimization incentives ignore pathogen–host co-evolution and reduce diversity, the latent potential stock collapse can lead to a welfare loss. More diverse systems, in general, are likely to be less susceptible to pest attacks ([Vandermeer, 1989](#)). Hence, maintaining biodiversity and sustaining unobserved ecosystem services can increase welfare ([Brook and Xepapadeas, 2003](#)). Harvesting renewable resources selectively can trigger the extinction of valuable genes ([Guttormsen et al., 2008](#)) and influence the choice of policy instruments like gear selectivity regulation or fish quotas ([Diekert et al., 2010](#)). Similarly, social-ecological systems depend on diversity in norms, institutions, laws, incentive structures and behavioral practices. Market competition favors productivity but leads to diversity loss which cripples the system's ability to adapt to change.

A fundamental question remains – how to manage sources of diversity like spatial connectedness, temporal variation and the strength of selective processes, which act as sinks on diversity. This is true for biological systems, but also for institutions and ideas, which can spread in human networks or exhibit temporal variations in use ([Brook and Durlauf, 1999](#); [Ostrom, 2005](#)). Analogously, the costs and benefits of trying to control social networks in order to enhance the diversity of ideas and information are hard to estimate. It is obvious, however, that addressing global change impacts requires an understanding of how to optimally manage sources of diversity in social-ecological systems.

⁴ Instruments with spatiotemporal dimension have been studied by [Goetz and Zilberman \(2000\)](#) and [Sanchirico and Wilen \(2005\)](#).

4.4. Risk and uncertainty

System complexity and important and interrelated uncertainties hinder social-ecological systems management. Sources of uncertainties include major gaps in global and national monitoring systems, and the lack of a complete inventory of species, their component populations and their actual distributions. Even more important are the lack of understanding of ecosystems' functional dynamics, a limited modeling capacity and the lack of theories to anticipate thresholds, and the emergence of surprises and unexpected consequences. These uncertainties may impede adequate scientific understanding of the underlying mechanisms and the impacts of policies. Taking these uncertainties into consideration raises issues of sensitivity, robustness and resilience (Polasky *et al.*, 2011a). The risk or uncertainty associated with the possibility of unknowingly transgressing a dangerous threshold makes economic policy particularly tricky. Such situations require developing a strategy for how to deal with the threshold (See Crépin *et al.* (2012) for an overview.) It could be wise, for example, to monitor specific variables to try to predict an impending regime shift before it occurs (Biggs *et al.*, 2009; Scheffer *et al.*, 2009). When there is substantial (Knightian) uncertainty and model misspecification cannot be detected with a limited set of data, a regulator who dislikes ambiguity and is afraid of using a wrong model can use robust controls. Such methods characterize uncertainty via perturbations of a reference model or benchmark and can help formalize a precautionary principle in resource management (Anderies *et al.*, 2007; Vardas and Xepapadeas, 2010; Athanassoglou and Xepapadeas, 2012). Another method is to use adaptive controls and parameterize uncertainty in terms of some unknown parameters or nonlinear functions and use feedback rules to learn more about these parameters or functions.

Precaution is also a way to deal with risks and uncertainty linked to complex adaptive systems. In a simple general growth model, threat of a potential future regime shift could motivate precaution. Whether precaution is optimal depends on whether the probability of a regime shift is endogenous or exogenous and whether the regime shift involves the collapse of a stock or a radical change in dynamics (Polasky *et al.* (2011b)). The exogenous probability of stock collapse motivates increased exploitation, while a change in system dynamics with endogenous probabilities supports precaution.

4.5. Concluding remarks

The insights from complex adaptive systems research challenge current policies using instruments like taxes, trading schemes and quotas. Recommendations for using such instruments are typically derived from assumptions about linear dynamics and marginal change and do not account for non-convexities, multiple scales or evolution. Furthermore, insights from the evolution of norms and cooperation in complex adaptive systems point to a stronger focus on the institutional dimension in policy recommendations. A continual learning process must be put in place and the most efficient methods available used to inform this process.

References

- Anderies, J.M., M.A. Janssen, and B.H. Walker (2002), 'Grazing management, resilience, and the dynamics of a fire-driven rangeland system', *Ecosystems* **5**(1): 23–44.
- Anderies, J.M., A.A. Rodriguez, M.A. Janssen, and O. Cifdaloz (2007), 'Panaceas, uncertainty, and the robust control framework in sustainability science', *Proceedings of the National Academy of Sciences* **104**(39): 15194–15199.
- Archibald, S., A.C. Staver, and S.A. Levin (2011), 'The evolution of human-driven fire regimes in Africa', *Proceedings of the National Academy of Sciences*; doi: 10.1073/pnas.1118648109.
- Arrow, K.J. (1951), 'An extension of the basic theorems of classical welfare economics', *Proceedings of the Second Berkeley Symposium*, Berkeley: University of California Press.
- Arrow, K., B. Bolin, R. Costanza, et al. (1995), 'Economic growth, carrying capacity, and the environment', *Science* **268**(5210): 520–521.
- Athanassoglou, S. and A. Xepapadeas (2012), 'Pollution control with uncertain stock dynamics: when and how to be precautionous', *Journal of Environmental Economics and Management* **63**(3): 304–320.
- Başar, T. and G.J. Olsder (1982), *Dynamic Non-Cooperative Game Theory*, New York: Academic Press.
- Bellwood, D., T. Hughes, C. Folke, and M. Nyström (2004), 'Confronting the coral reef crisis', *Nature* **429**: 827–833.
- Berglund, N. and B. Gentz (2003), 'Geometric singular perturbation theory for stochastic differential equations', *Journal of Differential Equations* **191**: 1–54.
- Berkes, F. and C. Folke (eds) (1998), *Linking Social and Ecological Systems: Management Practices and Social Mechanisms for Building Resilience*, Cambridge: Cambridge University Press.
- Biggs, R., S.R. Carpenter, and W.A. Brock (2009), 'Turning back from the brink: detecting an impending regime shift in time to avert it', *Proceedings of the National Academy of Sciences USA* **106**(3): 826–831.
- Bonabeau, E. (2002), 'Adaptive agents, intelligence, and emergent human organization: capturing complexity through agent-based modeling: methods and techniques for simulating human systems', *Proceedings of the National Academy of Sciences USA* **99**: 7280–7287.
- Brock, W.A. and S.N. Durlauf (1999), 'A formal model of theory choice in science', *Economic Theory* **14**: 113–130.
- Brock, W.A. and D. Starrett (2003), 'Managing systems with non-convex positive feedback', *Environmental and Resource Economics* **26**: 575–602.
- Brock, W. and A. Xepapadeas (2003), 'Valuing biodiversity from an economic perspective: a unified economic, ecological and genetic approach', *American Economic Review* **93**(5): 1597–1614.
- Brock, W. and A. Xepapadeas (2004a), 'Management of interacting species: regulation under nonlinearities and hysteresis', *Resource and Energy Economics* **26**(2): 137–156.
- Brock, W. and A. Xepapadeas (2004b), 'Ecosystem management in models of antagonistic species coevolution', DIVERSITAS Discussion Paper, [Available at] <http://ideas.repec.org/p/crt/wpaper/0503.html>.
- Brock, W. and A. Xepapadeas (2008), 'Diffusion-induced instability and pattern formation in infinite horizon recursive optimal control', *Journal of Economic Dynamics and Control* **32**: 2745–2787.
- Brock, W. and A. Xepapadeas (2010), 'Pattern formation, spatial externalities and regulation in coupled economic-ecological systems', *Journal of Environmental Economics and Management* **59**(2): 149–164.

- Conlisk, J. (1996), 'Why bounded rationality?', *Journal of Economic Literature* **34**(2): 669–700.
- Couzin, I.D., J. Krause, N.R. Franks, and S.A. Levin (2005), 'Effective leadership and decision-making in animal groups on the move', *Nature* **433**: 513–516.
- Couzin, I.D., C.C. Ioannou, G. Demirel, *et al.* (2011), 'Uninformed individuals promote democratic consensus in animal groups', *Science* **332**(6062): 1578–1580.
- Crépin, A.-S. (2007), 'Using fast and slow processes to manage resources with thresholds', *Environmental and Resource Economics* **36**: 191–213.
- Crépin, A.-S., R. Biggs, S. Polasky, M. Troell, and A. de Zeeuw (2012), 'Regime shifts and management', *Ecological Economics* **84**: 15–22.
- Crépin, A.-S. and T. Lindahl (2009), 'Grazing games: sharing common property resources with complex dynamics', *Environmental and Resource Economics* **44**: 29–46.
- Crépin, A.-S., J. Norberg, and K.-G. Mäler (2011), 'Coupled economic-ecological systems with slow and fast dynamics – modelling and analysis method', *Ecological Economics* **70**(8): 1448–1458.
- Debreu, G. (1959), *Theory of Value*, New York: John Wiley.
- Diekert, F.K., D.Ø. Hjermmann, E. Nævdal, and N.-C. Stenseth (2010), 'Non-cooperative exploitation of multi-cohort fisheries – the role of gear selectivity in the North-East Arctic cod fishery', *Resources and Energy Economics* **32**: 8–92.
- Durrett, R.T. and S.A. Levin (1994), 'The importance of being discrete (and spatial)', *Theoretical Population Biology* **46**: 363–394.
- Ehrlich, P.R. and S.A. Levin (2005), 'The evolution of norms', *PLoS Biology* **3**(6): 0943–0948, e194.
- Elmhirst, T., S.R. Connolly, and T.P. Hughes (2009), 'Connectivity, regime shifts and the resilience of coral reefs', *Coral Reefs* **28**(4): 949–957.
- Estes, J.A. and J.F. Palmisano (1974), 'Sea otters: their role in structuring nearshore communities', *Science* **185**: 1058–1060.
- Fenichel, N. (1979), 'Geometric singular perturbation theory for ordinary differential equations', *Journal of Differential Equations* **31**: 53–98.
- Flierl, G., D. Grünbaum, S.A. Levin, and D. Olson (1999), 'From individuals to aggregations: the interplay between behavior and physics', *Journal of Theoretical Biology* **196**: 397–454.
- Folke, C., S.R. Carpenter, B. Walker, M. Scheffer, T. Chapin, and J. Rockström (2010), 'Resilience thinking: integrating resilience, adaptability and transformability', *Ecology and Society* **15**(4): 20.
- Geddes, P. (1915), *Cities in Evolution*, London: Williams.
- Genieys, S., V. Volpert, and P. Auger (2006), 'Pattern and waves for a model in population dynamics with nonlocal consumption of resources', *Mathematical Modelling of Natural Phenomena* **1**(1): 65–82.
- Goetz, R. and D. Zilberman (2000), 'The dynamics of spatial pollution: the case of phosphorus runoff from agricultural land', *Journal of Economic Dynamics and Control* **24**: 143–163.
- Grimm, V. and S.F. Railsback (2005), *Individual Based Modeling and Ecology*, Princeton, NJ: Princeton University Press.
- Grimsrud, K. and R. Huffaker (2006), 'Solving multidimensional bioeconomic problems with singular-perturbation reduction methods: application to managing pest resistance to pesticidal crops', *Journal of Environmental Economics and Management* **51**: 336–353.
- Gunderson, L.H. and L. Pritchard Jr. (eds) (2002), *Resilience and the Behavior of Large-Scale Systems*, Washington, DC: Island Press.
- Guttormsen, A.G., D. Kristofersson, and E. Nævdal (2008), 'Optimal management of renewable resources with Darwinian selection induced by harvesting', *Journal of Environmental Economics and Management* **56**(2): 167–179.

- Henderson, V. and J. Thisse (eds) (2004), *Handbook of Regional and Urban Economics*, Amsterdam: Elsevier.
- Hirota, M., M. Holmgren, E.H. Van Nes and M. Scheffer (2011), 'Global resilience of tropical forest and savanna to critical transitions', *Science* **334**(6053): 232–235.
- Holling, C.S. (1973), 'Resilience and stability of ecological systems', *Annual Review of Ecology and Systematics* **4**: 1–23.
- Huffaker, R. and R. Hotchkiss (2006), 'Economic dynamics of reservoir sedimentation management: optimal control with singularly perturbed equations of motion', *Journal of Economic Dynamics and Control* **30**: 2553–2575.
- Janssen, M.A., J.M. Anderies, and B.H. Walker (2004), 'Robust strategies for managing rangelands with multiple stable attractors', *Journal of Environmental Economics and Management* **47**: 140–162.
- Johnson, A.M. (1982), 'Status of Alaska sea otter populations and developing conflicts with fisheries', US Fish & Wildlife Publications Paper No. 42, [Available at] <http://digitalcommons.unl.edu/usfwspubs/42>.
- Kossioris, G., M. Plexoyakis, A. Xepapadeas, A. de Zeeuw, and K.-G. Mäler (2008), 'Feedback Nash equilibria for non-linear differential games in pollution control', *Journal of Economic Dynamics and Control* **32**: 1312–1331.
- Kossioris, G., M. Plexoyakis, A. Xepapadeas, and A. de Zeeuw (2011), 'On the optimal taxation of common-pool resources', *Journal of Economic Dynamics and Control* **35**(11): 1868–1879.
- Krugman, P. (1996), *The Self-Organising Economy*, Oxford: Blackwell Publishing.
- Levin, S.A. (1974), 'Dispersion and population interactions', *American Naturalist* **104**: 207–228.
- Levin, S.A. (1998), 'Ecosystems and the biosphere as complex adaptive systems', *Ecosystems* **1**: 431–436.
- Levin, S.A. (1999a), *Fragile Dominion: Complexity and the Commons*, Reading, MA: Perseus Books.
- Levin, S.A. (1999b), 'Towards a science of ecological management', *Conservation Ecology* **3**(2): 6, [Available at] <http://www.consecol.org/vol3/iss2/art6>.
- Levin, S.A. (2000), 'Multiple scales and the maintenance of biodiversity', *Ecosystems* **3**: 498–506.
- Levin, S.A. (2006), 'Learning to live in a global commons: socioeconomic challenges for a sustainable environment', *Ecological Research* **21**(3): 328–333.
- Levin, S.A. and J. Lubchenco (2008), 'Resilience, robustness, and marine ecosystem-based management', *Bioscience* **58**(1): 27–32.
- Lovelock, J.E. (1979), *Gaia: A New Look at Life on Earth*, Oxford: Oxford University Press.
- Lucas, R.E. (2001), 'Externalities and cities', *Review of Economic Dynamics* **4**: 245–274.
- Lucas, R.E. and E. Rossi-Hansberg (2002), 'On the internal structure of cities', *Econometrica* **70**(4): 1445–1476.
- Ludwig, D., D. Jones, and C.S. Holling (1978), 'Qualitative analysis of insect outbreak systems: the spruce budworm and forest', *Journal of Animal Ecology* **47**: 315–332.
- Mäler, K.-G., A. Xepapadeas, and A. de Zeeuw (2003), 'The economics of shallow lakes', *Environmental and Resource Economics* **26**(4): 603–624.
- May, R.M., S.A. Levin, and G. Sugihara (2008), 'Complex systems: ecology for bankers' *Nature* **451**: 893–895.
- Moberg, F. and C. Folke (1999), 'Ecological goods and services of coral reef ecosystems', *Ecological Economics* **29**: 215–233.
- Mollison, D. (1977), 'Spatial contact models for ecological and epidemic spread', *Journal of the Royal Statistical Society* **39**(3): 283–326.

- Murray, J. (2003), *Mathematical Biology*, 3rd edn, Berlin: Springer.
- Naidu, D. (2002), 'Singular perturbations and time scales in control theory and applications: an overview', *Dynamics of Continuous, Discrete and Impulsive Systems* 9: 233–278.
- Norberg, J., D.P. Swaney, J. Dushoff, J. Lin, R. Casagrandi, and S. Levin (2001), 'Phenotypic diversity and ecosystem functioning in changing environments: a theoretical framework', *Proceedings of the National Academy of Sciences* 98(20): 11376–11381.
- Okubo, A. and S. Levin (2001), *Diffusion and Ecological Problems: Modern Perspectives*, 2nd edn, Berlin: Springer.
- Olsson, P., C. Folke, and F. Berkes (2004), 'Adaptive comanagement for building resilience in social-ecological systems', *Environmental Management* 34(1): 75–90.
- Ostrom, E. (2005), *Understanding Institutional Diversity*, Princeton, NJ: Princeton University Press.
- Ostrom, E., T. Dietz, N. Dolšák, P.C. Stern, S. Stonich, and E.U. Weber (eds) (2002), *The Drama of the Commons*, Washington, DC: Committee on the Human Dimensions of Global Change, Division of Behavioral and Social Sciences and Education, National Research Council.
- Palmer, M.A., C.A. Reidy Liermann, C. Nilsson, M. Flörke, J. Alcamo, P.S. Lake, and N. Bond (2008), 'Climate change and the world's river basins: anticipating management options', *Frontiers in Ecology and the Environment* 6(2): 81–89.
- Pigou, A.C. (1920), *The Economics of Welfare*, London: Macmillan.
- Pizer, W.A. (2003), 'Climate change catastrophes', Discussion Paper No. 03–31, Washington, DC: Resources for the Future.
- Polasky, S., S.R. Carpenter, C. Folke, and B. Keeler (2011a), 'Decision-making under great uncertainty: environmental management in an era of global change', *Trends in Ecology and Evolution* 26: 398–404.
- Polasky, S., A. de Zeeuw, and F. Wagener (2011b), 'Optimal management with potential regime shifts', *Journal of Environmental Economics and Management* 62(2): 229–240.
- Potts, M.D. and J.R. Vincent (2008), 'Harvest and extinction in multi-species communities', *Ecological Economics* 65: 336–347.
- Quah, D. (2002), 'Spatial agglomeration dynamics', *American Economic Association Papers and Proceedings* 92: 247–252.
- Rockström, J., W. Steffen, K. Noone, et al. (2009), 'A safe operating space for humanity', *Nature* 461: 472–475.
- Sanchirico, J. and J. Wilen (1999), 'Bioeconomics of spatial exploitation in a patchy environment', *Journal of Environmental Economics and Management* 37(2): 129–150.
- Sanchirico, J. and J. Wilen (2005), 'Optimal spatial management of renewable resources: matching policy scope to ecosystem scale', *Journal of Environmental Economics and Management* 50: 23–46.
- Sanchirico, J., A. Hastings, L. Malvadka, and J. Wilen (2006), 'When are no-take zones an economically optimal fishery management strategy?' *Ecological Applications* 16: 1643–1659.
- Scheffer, M. (2009), *Critical Transitions in Nature and Society*, Princeton, NJ: Princeton University Press.
- Scheffer, M., J. Bascompte, W.A. Brock, et al. (2009), 'Early-warning signals for critical transitions', *Nature* 461: 53–59.
- Skellam, J.G. (1973), 'The formulation and interpretation of mathematical models of diffusion processes in population biology', in M.S. Bartlett and R.W. Hiorns (eds), *The Mathematical Theory of the Dynamics of Biological Populations*, New York: Academic Press, pp. 63–85.

- Skiba, A.K. (1978), 'Optimal growth with a convex-concave production', *Econometrica* **46**(3): 527–539.
- Smith, A. (1776), *An Inquiry into the Nature and Causes of the Wealth of Nations*. London: Strahan and Cadell.
- Staver, A.C., S. Archibald, and S. Levin (2011a), 'Tree cover in sub-Saharan Africa: rainfall and fire constrain forest and savanna as alternative stable states', *Ecology* **92**(5): 1063–1072.
- Staver, A.C., S. Archibald, and S. Levin (2011b), 'The global extent and determinants of savanna and forest as alternative biome states', *Science* **334**: 230.
- Sterner, T., M. Troell, J. Vincent, et al. (2006), 'Quick fixes for the environment: part of the solution or part of the problem?', *Environment: Science and Policy for Sustainable Development* **48**(10): 20–27.
- Turing, A. (1952), 'The chemical basis of morphogenesis', *Philosophical Transactions of the Royal Society London* **237**: 37–72.
- Vandermeer, J.H. (1989), *The Ecology of Intercropping*, Cambridge: Cambridge University Press.
- Vardas, G. and A. Xepapadeas (2010), 'Model uncertainty, ambiguity and the precautionary principle: implications for biodiversity management', *Environmental and Resource Economics* **45**: 379–404.
- von Hayek, F. (1929), *Monetary Theory and the Trade Cycle*, London: Jonathan Cape.
- von Hayek, F. (1931), *Prices and Production*, London: Routledge.
- Wasow, W. (1965), *Asymptotic Expansions for Ordinary Differential Equations*, New York: Dover Phoenix Editions.
- Worm, B., E.B. Barbier, N. Beaumont, et al. (2006), 'Impacts of biodiversity loss on ocean ecosystem services', *Science* **314**(5800): 787–790.