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Learning to live in a global commons: socioeconomic challenges for a sustainable environment

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Abstract Ecologists, economists and other social scientists have much incentive for interaction. First of all, ecological systems and socioeconomic systems are linked in their dynamics, and these linkages are key to coupling environmental protection and economic growth. Beyond this, however, are the obvious similarities in how ecological systems and socioeconomic systems function, and the common theoretical challenges in understanding their dynamics. This should not be surprising. Socioeconomic systems are in fact ecological systems, in which the familiar ecological phenomena of exploitation, cooperation and parasitism all can be identified as key features. Or, viewed from the opposite perspective, ecological systems are economic systems, in which competition for resources is key, and in which an evolutionary process shapes the individual agents to a distribution of specialization of function that leads to the emergence of flows and functionalities at higher levels of organization. Most fundamentally, ecological and socioeconomic systems alike are complex adaptive systems, in which patterns at the macroscopic level emerge from interactions and selection mechanisms mediated at many levels of organization, from individual agents to collectives to whole systems and even above. In such complex adaptive systems, robustness must be understood as emergent from selection processes operating at these many different levels, and the inherent nonlinearities can trigger sudden shifts in regimes that, in the case of the biosphere, can have major consequences for humanity. This lecture will explore the complex adaptive nature of ecosystems, and the implications for the robustness of ecosystem services on which we depend, and in particular examine the conditions under which

cooperative behavior emerges. It will then turn attention to the socioeconomic systems in which environmental management is based, and ask what lessons can be learned from our examination of natural systems, and how we can modify social norms to achieve global cooperation in managing our common future. Of special interest will be issues of intragenerational and intergenerational equity, and the importance of various forms of discounting.

Ecology and economics: finding common ground

Ecologists and economists have much incentive for interaction. First of all, the linkages between ecological and socioeconomic systems are key to ensuring environmental protection and economic growth. Secondly, and equally compelling, the structural similarities between ecological and socioeconomic systems raise similar theoretical challenges. Economic systems are, after all, at the core, ecological systems, in which familiar ecological processes such as exploitation, mutualism and parasitism all have obvious parallels. Or, to look at the situation from the other perspective, ecological systems are economic systems, with competition for resources, specialization of function, and most of the features that characterize socioeconomic systems. Most fundamentally, ecological and socioeconomic systems are complex adaptive systems, integrating phenomena across multiple scales of space, time and organizational complexity. In such systems, macroscopic phenomena to a large extent emerge from, and in turn influence, the individual and collective dynamics of individual agents, pursuing their own selfish agendas. In such systems as well, dynamics on faster time scales, and on smaller spatial scales, are shaped by slow dynamics on larger time scales, which in turn arise from the aggregate of dynamics on faster and smaller scales. The importance of slower, evolutionary change is well recognized as the central paradigm in ecology, and biology more

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generally. Evolutionary dynamics (without heritable genetic change) also play a core role in socioeconomic systems, although the relevant theory has been much less fully developed (Ehrlich and Levin 2005). This lecture will explore some steps toward relevant theory, and what can be learned from biological evolution that can guide management of the biosphere in a global commons.

Optimization and game theory in evolutionary change

Evolutionary theory is at the core of the study of biology. Darwin's *Voyage on the Beagle*, and his consequent syntheses of what he saw, transformed our views of nature. Darwin's penetrating insights formed the basis of a new biology, a basis that has been refined but has proved remarkably robust nearly two centuries later. Natural selection was seen as the fundamental mechanism explaining evolutionary change at the individual level, as well as the self-organization of ecological communities and the biosphere. That principle remains equally valid today and is complemented by a far deeper and strongly confirmatory understanding of the molecular and genetic mechanisms that drive that change.

Crucially, Darwin viewed natural selection as a process of gradual adaptation in a changing environment. Too easily, however, this dynamic perspective became transmogrified into an equation of evolution with optimization, in large part because the concept of continual improvement suggests a process of eventual perfection, and also in large part because the application of the principles of natural selection to plant and animal breeding is in fact a search for optima. Furthermore, Sir Ronald Fisher's elegant "Fundamental Theorem of Natural Selection" seemed to provide a mathematical underpinning for this view.

However, as has often been pointed out (Gould and Lewontin 1979), adaptation need not lead to optimization. Beyond the fact that any fitness landscape is likely to have multiple local peaks is the even more central fact that the evolutionary challenge is not a constant one. Fitnesses change, both for extrinsic reasons, and because of frequency dependence—the dependence of performance indicators on the frequencies of other types in the population, as well as in other populations (usually more generally termed coevolution). Optimization approaches may apply at the level where selection is strongest, at the individual level, as in the evolution of basic processes of development and physiology (West et al. 1997). More generally, however, other approaches are needed, moving beyond optimization theory to the theory of games in dynamic and changing environments, and the incorporation of that theory into a broader context that considers the emergence of patterns at higher levels of organization.

It was long recognized that a game-theory perspective was needed to address the challenges of evolutionary change (Lewontin 1961; Slobodkin and Rapoport 1974), but the fundamental paradigm shift came only when

John Maynard Smith (Maynard Smith 1982; Maynard Smith and Price 1973) introduced the notion of the evolutionarily stable strategy (ESS), for which he won the Kyoto Prize in 2001. In his disputation with classical game-theory challenges such as the problem of the Prisoners' Dilemma, he developed the concept of the ESS as an evolutionary strategy that, once established, could not be invaded using any other strategy. It corresponded to the game-theory notion of a Nash equilibrium, which won John Nash a Nobel Prize in Economics.

It is valuable to put the notion of the ESS in a formal mathematical context, as did Maynard Smith. Let r be the measure of the fitness of a phenotype u (in general a vector characterizing organism properties, but in this lecture usually a scalar). More specifically, $r(v, u)$ is the fitness of rare phenotype v invading a population in which the phenotype u is established. $r(v, u)$ typically is simply the linearized growth rate of the v -phenotype population near equilibrium $(0, u^*)$, corresponding to a situation in which u is absent from the population (although more general conditions, using, for example, Floquet exponents, are needed if the resident population is not at a static equilibrium). In the simplest case, an ESS is a strategy, call it w , such that when $u = w$, the fitness $r(v, u)$ is maximized as a function of v at $v = u$. From the basic principles of the calculus, this means that

$$\frac{\partial r}{\partial v} = 0, \quad \frac{\partial^2 r}{\partial v^2} \leq 0. \quad (1)$$

These are simple criteria, but the notion of the ESS turns out to be just a beginning. First of all, there may be several ESSs; the conditions in Eq. (1) are simply local conditions in strategy space. Second, the environment, and hence the fitnesses, may be fluctuating due to extrinsic factors. But most problematical, and perhaps somewhat surprising, is that an ESS may not be dynamically reachable. That is, a type that cannot be invaded cannot necessarily invade other types. This is not an odd pathological situation, but one that arises naturally in a variety of situations (see Dieckmann 1997; Dieckmann and Metz 2005). Conversely (Eshel 1983; Ludwig and Levin 1991), a type may be able to invade other types, but not be an ESS. These realizations make it clear that a full dynamic game theory is needed to cover these eventualities.

I will not present the full mathematical theory here (but see Levin and Muller-Landau 2000). However, such a theory (Dieckmann 1997; Dieckmann and Metz 2005) allows the introduction of notions like the neighborhood-invader strategy (NIS), a type that can invade nearby strategies of strategy space; the weaker notion of a convergence-stable strategy, a strategy attracting in the space of phenotypes; and finally that of the continuously stable strategy (Eshel 1983), a convergence-stable ESS. This makes not only for a rich area for mathematical investigation, but also for a powerful way to understand ecological interactions. One begins with a basic

dynamical model, allows heritable variation in the traits of interacting individuals and explores the “adaptive” dynamics of such systems. The outcome of such an approach can identify continuously stable strategies, but also a variety of other outcomes, including “evolutionary branching” at convergence-stable strategies that are not ESSs (Ludwig and Levin 1991), speciation and the consequent coexistence of types (Dieckmann 1997; Dieckmann and Metz 2005).

Adaptive dynamics of ecological and socioeconomic processes and patterns

Such approaches have received considerable attention in the ecological evolutionary literature in the past decade, but hold equal (and relatively unexplored) potential for examining behavioral interactions—the major modification needed is simply that behavioral change need not be inherited from parent to offspring, but does change within an individual. Moving from the ecological to the social or economic situation simply completes the loop—these are ideas that had their origins in economics, were adapted and modified for biology, and now find new application in their original setting.

In ecology, the evolutionary approach deriving from Maynard Smith’s penetrating insights has served to illuminate a variety of problems in biology, including the evolution of sex (Fisher 1930), the timing of migration (Iwasa and Levin 1995), as well as patterns of resource use and stoichiometry (Klausmeier et al. 2004a, b). For example, Albert Redfield observed long ago that marine ecosystems show remarkable constancy in element ratios (carbon, nitrogen, phosphorus), even though absolute levels may vary considerably. The Redfield ratios are seen in the water column, on the average among the primary producers, as well as within the consumers that feed upon those producers. Redfield asked the fundamental question, “What sets and stabilizes those ratios?” Are the biota simply responding to concentrations in the water column set by external geological conditions, or are the biota regulating the environment, or is the truth somewhere in between? Today, although it is recognized that things are not as constant as Redfield thought, the Redfield ratios continue to provide an organizing theme for research on marine ecosystems: How constant are they? How do observed ratios reflect different oceanographic regimes? How do the ratios within particular large marine ecosystems relate to the ecological and evolutionary dynamics of individual species? With several postdoctoral fellows, led by Christopher Klausmeier (Klausmeier et al. 2004a, b), I have begun to examine these questions within the adaptive dynamics framework. The basic approach is to develop models of trait-dependent dynamics on ecological time scales, and then to examine competition among types on longer, evolutionary time scales. The approach then asks, “In a game-theory sense, what strategies are most successful for

resource acquisition?” The separation of time scales is an approximation, fundamental to the basic methodology of adaptive dynamics, but which eventually must be relaxed.

Resource partitioning is, of course, one of the basic challenges both for ecological and for economic theory. The problem is not just how individuals share resources with their contemporaries, but also how they allocate their resources to current needs versus future needs, for themselves, their offspring and future generations more generally. We (Livnat et al. 2005) have applied this approach therefore to examine aspects of how individuals discount the future, and such questions are obviously central both in economic theory (e.g., the theory of intergenerational transfers, and of the shape and form of the discount curve), and in efforts to establish a sustainable future for humanity. We live in a global commons, in which what we use for our own benefit is often at the expense of what is available to others, both now and in the future. The great challenge then is to understand when and how cooperation has evolved in biological systems, and what lessons we can derive from these insights for how to achieve cooperation in dealing with our future environment. How can we restrain consumption, limit discharges into our common environment and control the profligate overuse of antibiotics? I turn to these questions in the next section.

The evolution of cooperation and social norms

The most basic ecological theories lead to a depressing conclusion. With regard to patterns of consumption, evolutionarily stable strategies (and continuously stable strategies) are often purely selfish. In fact, standard competition theory (Tilman 1994), which makes the assumption that individuals are competing through exploitation of a common resource base, has the simple result that the continuously stable strategy is the type that drives the limiting resource to the lowest possible level. Intuition is clear as to why this works: The type that can subsist at the lowest level will be the only type left standing, and can drive the resource to levels that eliminate its competitors. This is a strategy that is well understood by corporations—large airlines, for example, can survive in local markets by lowering their prices in an effort to drive out smaller competitors. This, obviously, is the antithesis of competition.

The fundamental problem, as stated several times earlier in this lecture, is that we live in a global commons, in which individual agents act largely in their own self-interest. Markets fail as mechanisms to preserve the common environment because of externalities—that is, because the social costs of individual actions are not adequately represented in market prices. This applies not only to individual people, but also to corporations, and indeed to nations as individual agents. It explains why the Kyoto protocols, which are designed to help us achieve international cooperation, have failed to gain

the crucial acceptance of my own nation. It explains why patients continue to demand antibiotics in marginal situations, when the costs—from a utilitarian perspective—far outweigh any potential benefit: those costs are borne by others, and selfish interests again prevail. It explains why we in developed nations continue to consume energy at rates far beyond our needs, despite the heavy costs: those costs again are borne by others.

How then can we achieve cooperation in addressing these problems? Is there anything to be learned from how and when cooperation has evolved in biological systems? Darwin regarded the evolution of altruism as a challenge to his original theories, which ultimately also appeared to reward selfishness. Why did individuals, especially among the haplodiploid insects, forego their own reproduction in order to benefit their close relatives? J.B.S. Haldane captured the essence of the answer succinctly in his half-serious remark that he would lay down his life for two siblings, or for eight cousins, simply reflecting the fact that he shared 1/2 of his genes with his siblings, and 1/8 with his cousins. It was W.D. Hamilton, however, who eventually put this work on a firm and formal mathematical foundation with his classic paper (Hamilton 1964), for which he won the Kyoto Prize in 1993. Close genetic relationship increases the genetic payoff to an individual who helps a sibling, and can operate to the extended benefit of the altruist. That is, a close genetic relationship tightens the feedback loop providing reward to the cooperator, the altruist. But later theory (see Levin 1999) has shown that a close genetic relationship is not necessary: Cooperation can be enhanced by repeated interactions over time (Fehr et al. 2002; Miller 1996) or through the spatial localization of interactions (Durrett and Levin 1998; Nakamaru and Iwasa 2005; Nowak et al. 1994). In any of these situations, feedback loops are tightened, so that individuals realize the costs and benefits of their actions more strongly. There is no guarantee that such tight feedback loops will lead to cooperation, of course: they mean that the consequences not only of altruistic behavior, but also of selfish behavior, will be strengthened. Thus, in biological systems, spatial localization of interactions can lead to trees shading their neighbors for competitive benefit and plants and to microbes poisoning their neighbors (Chao and Levin 1999; Durrett and Levin 1998; Iwasa et al. 1998; Kerr et al. 2002), as easily as it can lead to reduced consumption (Kinzig and Harte 1998; Klopfer 1997; Zea-Cabrera et al. 2006). Therefore, in human and other societies, social norms have arisen to enforce behavior in the communal interest (Ehrlich and Levin 2005).

Social norms and conventions are culturally influenced structures that constrain and otherwise influence individual behaviors. They include simple acts and customs such as forms of dress and greeting, as well as rules that restrict antisocial activities such as theft and murder, and that encourage communally beneficial acts such as charitable giving. They may be purely informal, though relatively robust because of common acceptance,

or may become rigidified as religious or societal laws. Fehr and Gächter (2002), in a set of elegant experiments, showed that not only can beneficial social norms, like charitable giving, evolve quickly in societies, but that their evolution can be enhanced by the coevolution of individuals' willingness to punish defectors from the social norms, even at cost to themselves. It is natural to ask then how we can evolve such norms to achieve sound environmental stewardship.

As a first step toward understanding these issues, it is valuable to understand the dynamics of collectives. Couzin et al. (2005) show that in animal societies in which individuals have a strong tendency to imitate others, groups can be led collectively to move in certain directions by a very small number of opinionated individuals. The lessons of that work carry over immediately to opinion dynamics, and imply that a few strongly motivated individuals can organize large groups to follow their lead by a transitive process of imitation.

How can we use what we have learned from natural systems? Is there hope for the future of management? We must hope and believe there is. Consumptive patterns are largely guided by social norms, sustained because of the robustness of common practice. They are, in a sense, social diseases, spread by infectious contact. Restraint in consumption can also be guided by norms, if a sense of collective responsibility can be promulgated. To do so, we must first understand the dynamics of norms, how they arise, how they are stabilized by reward structures and how we might change those incentives to attain the common good.

A nascent literature is emerging that develops models of the dynamics of norms, in relation to individual behaviors (Axelrod 1997; Bowles and Gintis 2004; Boyd and Richerson 1996; Cavalli-Sforza and Feldman 2003; Durrett and Levin 2005; Miller 1996; Nakamaru and Levin 2004). Our approach (Durrett and Levin 2005) to this issue imitates that described earlier for understanding the evolution of ecological traits: Build models of the dynamics of systems given particular behavioral rules, and then explore the adaptive dynamics by allowing mutations and introductions of rare novel behaviors. Economic studies demonstrate clearly that individuals' perceptions of what they need are to a large extent conditioned by what others have and use, through advertising, and through the spread of information. We represent this by dividing individuals into normative groups, each with their own attitudes and associated patterns of consumption. As individuals come into contact with others on a specified social network, they alter their attitudes, their actions and even their normative groups, based on the attitudes, actions and normative groups of others. The result can be a very fluid landscape, in which new ideas arise and spread, groups wax and wane in popularity, but still diversity may be maintained. Ultimately, these approaches must be extended to consider the origins of the normative groups themselves, as well as the roles of asymmetries in influence and rewards and punishment for group

membership (see Aoki et al. 2006). This is an area of research still in its infancy, but of compelling importance for addressing environmental problems.

Conclusions

The challenges of environmental protection require a quantification of the services humans derive from natural systems, an understanding of the mechanisms underlying the robustness of those services, and above all the development of linked models of ecological and socioeconomic systems. Beyond those, however, ecologists and economists have much to learn from one another in terms of the perspectives their sciences have brought to what are, ultimately, similar systems. Ecosystems and the biosphere, and the socioeconomic systems in which management is couched, are complex adaptive systems, which take shape in large part through the collective dynamics of the diverse elements that comprise them, and hence, in which genetic and non-genetic evolutionary change has shaped individual behaviors. Most of the problems of global change have arisen, and resist solution, because they involve conflicts between what individuals see as their own selfish interests, and what is in the collective good. Conflicts between today's peoples and those of future generations are perhaps the most refractory to resolution because of the asymmetries that flow from the irreversibility of time. Individuals discount even their own futures; how much easier it is to discount the futures of others!

The fundamental problems are in part problems of will, and of the development of a sense of responsibility to humanity. But their solution also requires the development of mechanisms of trust and cooperation, so that all can be made to feel they have something to gain.

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