Ecosystems and the Biosphere as Complex Adaptive Systems

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ABSTRACT

Ecosystems are prototypical examples of complex adaptive systems, in which patterns at higher levels emerge from localized interactions and selection processes acting at lower levels. An essential aspect of such systems is nonlinearity, leading to historical dependency and multiple possible outcomes of dynamics. Given this, it is essential to determine the degree to which system features are determined by environmental conditions, and the degree to which they are the result of self-organization. Further-more, given the multiple levels at which dynamics become apparent and at which selection can act, central issues relate to how evolution shapes ecosystems properties, and whether ecosystems become buffered to changes (more resilient) over their ecological and evolutionary development or proceed to critical states and the edge of chaos.

Key words: Gaia; self-organization; complex adaptive system; homeostasis; nonlinearity; keystone species; functional group.

INTRODUCTION

Perhaps the fundamental theoretical and applied issues confronting ecologists today concern the stunning loss of biodiversity, and the implications for the loss of services on which humans depend (Daily 1997). The biota not only provides direct benefits to humans, for example, as a source of food, fiber, and fuel; it also helps process nutrients essential to life, sequesters potentially harmful chemicals, and mediates regional and global climatic and atmospheric processes.

The notion of measuring biodiversity loss, however, is a complex one. Simple species counts are a place to start, but do not alone capture the features that are most important for sustaining ecosystem functioning. Not all species are equally important to the maintenance of key processes; furthermore, the essential dimensions of diversity extend above and below the level of species. A problem of basic importance, therefore, is the determination of ways to quantify those aspects of biodiversity that are most central to the functioning of ecosystems.

The relationship between structure and functioning is a fundamental one in ecosystems science. Ecosystems, and indeed the global biosphere, are prototypical examples of *complex adaptive systems*, in which macroscopic system properties such as trophic structure, diversity–productivity relationships, and patterns of nutrient flux emerge from interactions among components, and may feed back to influence the subsequent development of those interactions. Elucidating these interactions across scales is fundamental to resolving the issue of biodiversity and ecosystem functioning, and requires a blending of insights both from population biology and from ecosystems science.

An evolutionary perspective—that is, one that recognizes and explores the properties of the biosphere as a complex adaptive system whose components are subject to selection—is essential for examining these issues. Unquestionably, ecosystems show regularities in structure and functioning across regions. To what extent can the patterns of distribution of ecosystem properties be explained by underlying variation in physical variables, such as regional climate and soil conditions, and to what extent are they the result of self-organization? How important

is history in the assembly and evolution of ecosystems?

At the global level, the homeostatic nature of processes crucial to the maintenance of life, especially atmospheric processes, has inspired the development of concepts such as Gaia (Lovelock 1972; Margulis and Lovelock 1974), which treats the biosphere as a superorganism, the result of the coevolution of earth's biotic and abiotic parts. But such a view does not rest comfortably with population biologists, because it seems to be based on group selective principles operating at levels far above those of the primary units of selection (Ehrlich 1991). The recognition of the biosphere and of its constituent ecosystems as complex adaptive systems is an essential step to explaining ecosystem-level regularities and homeostasis in terms of established mechanisms, rather than by appeal to hypothetical processes operating at the level of whole systems.

COMPLEX ADAPTIVE SYSTEMS

The study of complex adaptive systems has fascinated natural and social scientists from across a tremendous range of disciplines. It is easy to find books that discuss, with varying degrees of specificity, ecosystems, the biosphere, economies, organisms, or brains as complex adaptive systems. It is much harder to find a formal definition, as if investigators fear that by defining a complex adaptive system (CAS), they will somehow limit a concept that is meant to apply to everything.

A particularly useful discussion of complex adaptive systems may be found in the work by Arthur and colleagues (1997), who identify six properties that characterize any economy: dispersed interaction, the absence of a global controller, cross-cutting hierarchical organization, continual adaptation, perpetual novelty, and far-from-equilibrium dynamics. Arthur and colleagues point out that these features apply as well to any complex adaptive system. However, although these properties may indeed typify complex adaptive systems, I suggest that the actual definition of a CAS must take a simpler form, restricted to the basic mechanisms. Indeed, it is the blurring of lines between the simple and the complex that has made the notion of adaptive systems so seductive (Slobodkin 1992; Gell-Mann 1994). The study of complex adaptive systems is a study of how complicated structures and patterns of interaction can arise from disorder through simple but powerful rules that guide change. The essential elements, in my view, are simply

- Sustained diversity and individuality of components (Gell-Mann 1994)

- Localized interactions among those components
- An autonomous process that selects from among those components, based on the results of local interactions, a subset for replication or enhancement

The properties identified by Arthur and coworkers (1997) all flow from this simpler set, but intersperse the basic mechanisms with properties that are emergent. In particular, the dispersed and local nature of an autonomous selection process assures continual adaptation, the absence of a global controller, and the emergence of hierarchical organization. The maintenance of diversity and individuality of components implies the generation of perpetual novelty, and far-from-equilibrium dynamics. Thus, the preceding listed set of three properties seems the most parsimonious one possible and the essential definition of features of a CAS.

Examples of complex adaptive systems abound in biology. A developing organism, an individual learning to cope, a maturing ecosystem, and the evolving biosphere all provide cases in point. Natural selection is the prototypical example of the autonomous process referred to in the third property. Artificial selection is not; it is not autonomous because it relies on a global controller.

John Holland, who coined the term *adaptive nonlinear networks* to describe systems that satisfy Arthur and his colleagues' six characteristics, identifies four basic properties of any CAS: aggregation, nonlinearity, diversity, and flows (Holland 1995).

Aggregation

This refers simply to the ways we group individuals into populations, populations into species, and species into functional groups. Any complex system develops inhomogeneities in terms of how its basic elements are organized. Those inhomogeneities enable us to recognize groups of individuals that are, in some sense, more similar to one another than they are to the background. A species is one such aggregation, but there are many other ways to organize individuals—some taxonomic and others not. The fundamental point is that the development of patterns of aggregation and hierarchical organization is both a natural consequence of the self-organization of any complex system [for example, see O'Neill and others (1988) and Holling (1992)] and an essential element in the later development of the system.

Aggregation and hierarchical assembly are not imposed on complex adaptive systems, but emerge from local interactions through endogenous pattern formation (Levin and Segel 1985; Murray 1989). Once they arise, however, such patterns of aggregation constrain interactions between individuals and thereby profoundly influence the system's further

development [for example, see Kauffman (1993) and Pacala and Levin (1997)].

Nonlinearity

Because complex adaptive systems change primarily through the reinforcement of chance events, such as mutation and environmental variation, operating at local levels, the potential for alternative developmental pathways is enormous. François Jacob (1977) emphasizes the analogy of evolution as a tinkerer, which operates by modifying previous designs slightly and is thereby constrained by history in exploring a landscape of otherwise uncountable possibilities (Kauffman and Levin 1987). The same restrictions apply to any complex adaptive systems, which typically show path dependency in their development (Arthur 1994), and frozen accidents of history that resist modification (Kauffman 1993). Such resistance to change can be interpreted as resilience (Holling 1973) or *rigor mortis,* depending on the situation and one's perspective (Levin and others 1998).

Path dependency is a consequence of *nonlinearity,* which refers simply to the fact that the local rules of interaction change as the system evolves and develops. The colonization history of an island, or of a patch in a forest, will exhibit such path dependency, as early recruitment changes the landscape for future potential colonists. A corollary of path dependency is the existence of alternative stable states in ecosystem development, and the potential for threshold behavior and qualitative shifts in system dynamics under changing environmental influences.

Diversity

The usual place to begin in measuring biodiversity is simply a count of the number of species present, but such a measure clearly misses the fundamental importance of diversity below as well as above the species level. From the viewpoint of the maintenance of ecosystem services, it will matter little that an essential species continues to exist if it has been reduced to a few small and genetically fairly homogeneous populations (Hughes and others 1997; Levin and Ehrlich 1998).

Even at the level of species, bald counts of the number of types are misleading. It is clear that not all species are of equal importance to the maintenance of system functioning, and study of the ecosystem as an integrated system must somehow account for these differences. Perhaps the most important advance in this regard was Robert Paine's identification of *keystones* in the intertidal (Paine 1966), species that played roles disproportionate to their numbers in the dynamics of their communities. As Paine demonstrated, the removal of a keystone species can trigger nonlinear responses that lead to cascades of local extinction and a fundamental change in the nature of the ecosystem. Paine's original insight has stimulated the identification of keystone species in other systems, with the most cited example being that of the California sea otter [for example, see Estes and Palmisano (1974)].

More generally, critical ecosystem processes will not be under the control of individual species, but may be mediated nonetheless by a small set of species that thereby form a *keystone functional group.* For example, the groups of microbial species that fix nitrogen, or that nitrify or denitrify, control processes more fundamental to the persistence of ecosystems than those affected by keystone species. Clearly, diversity within a functional group provides some degree of buffering and homeostasis for critical ecosystem processes, in the same way that diversity within a species provides resiliency and a hedge against extinction. The question remains, however, of the degree to which such buffering actually exists, and in particular of how evolutionary forces operating at the level of the individual components should be expected to affect such system-level properties. The generation and maintenance of diversity is fundamental to adaptive evolution, whether this means evolution via natural selection or the analogous processes that operate in any complex adaptive system. The essential challenge is to understand what sustains that diversity at the level of ecosystems and the biosphere.

Flows: Obviously, any ecosystem is characterized by flows: flows of nutrients and energy, flows of materials, and flows of information. It is such flows that provide the interconnections between parts, and transform the community from a random collection of species into an integrated whole, an ecosystem in which biotic and abiotic parts are interrelated.

The ontogeny of an ecosystem represents a particular form of evolution, which Lewontin (1977) terms *transformational evolution* to distinguish it from the *selective evolution* that applies to its parts. In that transformational process, clusters form (the aggregations discussed earlier), flows become modified, and the system assumes shape through a process of self-organization. Autotrophs capture energy, providing a base for the appearance of exploiters, which establish pathways of energy flow that give the system its character. The similarities that exist across systems in the structure of trophic networks (Pimm 1982; Cohen 1989; Polis 1991) represent commonalities that emerge because all ecosystems are complex adaptive systems, governed by similar thermodynamic principles and local selection. The differences that may be discriminated represent the

role of chance, spatial variation and history, magnified through nonlinearity to guide systems down unique developmental pathways (Levin 1998).

FROM POPULATIONS TO ECOSYSTEMS TO GAIA

Life can exist only under a very limited range of conditions, conveniently well matched by the conditions found on earth. Earth's atmosphere, in particular, has homeostatic mechanisms that maintain it with minimal variation and allow life to persist. This matching of life and the conditions for life has inspired views of the earth as a superorganism (Hutton 1788), with a biota and an atmosphere that have coevolved (Lovelock 1972; Margulis and Lovelock 1974). How valid is such a perspective?

To some extent, the pleasant coincidence of the conditions for life where life exists is nothing more than what physicists term the *anthropic principle* [see, for example, Davies (1978)], which simply recognizes a sample and observer bias. There are many different worlds, only a few of which will have the requisite atmosphere and other essentials for life to evolve. If life does evolve, it will not surprisingly be found in exactly those places where it can be found, and nowhere else. That we find ourselves reporting we exist under just the conditions that enable us to exist is, therefore, to some degree tautological.

But there remain things to be explained. The fact that in some world the conditions exist for life to evolve does not guarantee that it will evolve. Few would argue with the claim that properties of the physical environment affect the evolution of species, or that the evolution of the biota feeds back to affect those physical properties, on all scales from the local to the biosphere. The latter point, indeed, is the source of current concern about the effects of the loss of biodiversity on ecosystem processes. What is at issue, however, is the degree to which system-level properties simply emerge from local evolutionary forces, and the degree to which those local processes are influenced and shaped by their effect on the persistence and continued functioning of ecosystems or the biosphere. Such questions represent classic and fundamental issues within the study of complex adaptive systems in general; to what extent, for example, do the characteristics of a developing economy simply represent properties that emerge from the selfish behaviors of individual agents, and to what extent are they imposed at higher levels of organization?

Understanding how the population communicates with the ecosystem, much less the biosphere, represents a fundamental challenge for ecologists; these levels have traditionally been separated by a chasm that has also often, and regrettably, separated population and ecosystem scientists. Ecosystems are complex adaptive systems, which are assembled from parts that have evolved over longer time scales and broader spatial scales. In turn, the collective experiences of species across a range of ecosystems over evolutionary time shapes the collection of parts from which community assembly can occur. The biosphere is thus itself a complex adaptive system whose composition changes evolutionarily in response to the dynamics of its component complex adaptive systems, ecosystems, and feeds back to affect their further dynamics by changing the attributes of the players.

Unquestionably, the primary units of selection are at the level of individuals and their genomes, but any population biologist would acknowledge the role of selection operating at the level of kin groups, or of parasite–host or plant–pollinator associations. These all represent examples in which tight linkages between members of interacting species provide reliable and rapid feedbacks for individual behaviors, the essentials for tight coevolution [for example, see Ehrlich and Raven (1964), Futuyma and Slatkin (1983), and Levin (1983)]. More generally, however, as any ecosystem, or as the biosphere, develops patterns of aggregation during its ontogeny, it perforce develops networks of components that have varying strengths of mutual connectedness. Parasite–host pairs provide one example of a particularly tight linkage, but a continuum of degrees of interaction can arise for other associations. In general, the stronger the interaction, the stronger is the mutual evolutionary influence. System-level properties represent the consequences of diffuse interactions, so that evolutionary influences will be weak; but intermediate levels of structure may exert more substantial forces.

CONCLUDING REMARKS: THE CHALLENGE

The study of ecosystems and the biosphere as complex adaptive systems addresses some of the central questions for ecology, in particular the relationship between the organization of biodiversity and the functioning of those systems. In a forthcoming book, representing a series of lectures (the Ulam Lectures) presented at the Santa Fe Institute, I extract from these considerations six fundamental questions that must be addressed to understand

ecosystems as complex adaptive systems (Levin 1998). In particular,

- What patterns exist in the distribution and organization of biodiversity?

- Are these patterns uniquely determined by local conditions or are they historically and spatially contingent?

- How do ecosystems become assembled over ecological time?

- How does evolution shape ecosystem properties?

- What are the relationships between ecosystem structure and functioning?

- Does evolution increase resiliency or lead to criticality? Does it lead to the edge of chaos?

The last question, in particular, interfaces some of the most stimulating but speculative issues in the theory of complex adaptive systems (Hartvigsen and Levin 1997). Per Bak and his colleagues (Bak and Chan 1995; Sneppen and others 1995) argue that any complex adaptive system, in particular an ecosystem, will evolve to a critical state, that is, to the edge of a transition zone between qualitatively different configurations. Such critical states are characterized by power law distributions of catastrophes, such as the Phanerozoic extinctions. The consequences of being in a perpetual state of criticality is that ecosystems, according to Bak (1996) and to Kauffman (1993), sit in a critical state, in which continual extinctions and replacements provide the variation on which adaptation can operate. These are indeed stimulating ideas, but are still without substantial empirical support.

There are, indeed, strong management implications in the answers to these questions. Developing sustainable approaches to system use implies understanding what maintains resilience and how human intervention might affect it. The key to resilience in any complex adaptive system is in the maintenance of heterogeneity, the essential variation that enables adaptation (Levin and others 1998). Heavily managed systems, such as in agriculture or forestry, are not purely complex adaptive systems, in that their simplified structures are imposed exogenously rather than arising endogenously. As such, they are fragile, vulnerable to single stresses such as pest outbreaks that cause system crashes in the absence of adaptive responses. Thus, if resilience is a goal, managers must understand the properties that enable an ecosystem, as a complex adaptive system, to maintain its integrity in the face of changing environmental conditions and human impacts. That the resilience properties of ecosystems emerge from selection

at lower levels, rather than being the targets of evolution, makes them no less important as management objectives.

This set of six questions represents, for me, the fundamental challenge for ecologists in identifying what the properties of their objects of study are, and what the connections are between the ecological and evolutionary levels. Explicitly or implicitly, they are likely to define a research agenda for the indefinite future.

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