

Self-organization and the Emergence of Complexity in Ecological Systems

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What explains the remarkable regularities in distribution and abundance of species, in size distributions of organisms, or in patterns of nutrient use? How does the biosphere maintain exactly the right conditions necessary for life as we know it? Gaia theory postulates that the biota regulates conditions at levels it needs for survival, but evolutionary biologists reject this explanation because it lacks a mechanistic basis. Similarly, the notion of self-organized criticality fails to recognize the importance of the heterogeneity and modularity of ecological systems. Ecosystems and the biosphere are complex adaptive systems, in which pattern emerges from, and feeds back to affect, the actions of adaptive individual agents, and in which cooperation and multicellularity can develop and provide the regulation of local environments, and indeed impose regularity at higher levels. The history of the biosphere is a history of coevolution between organisms and their environments, across multiple scales of space, time, and complexity.

Keywords: self-organization, emergence, Gaia, biosphere, complex adaptive systems

Ecological systems are at risk. We are losing biodiversity at rates unprecedented in recent times, and with it the services natural systems provide us. Hence it is natural to ask which macroscopic features of ecological systems are of most importance to humanity, how evolution has shaped them, and what stabilizes them. I will argue in this article that the emergence of the incredible complexity of nature can be fully explained in terms of physical and biological mechanisms that are well understood, given an initial soup on which these mechanisms can act, and therefore that no invocation of ecosystem-level selection or intelligent design is needed or justified. I do not address the questions of the origins of the soup, or for that matter of the laws of nature; these questions are beyond the realm of evolutionary theory.

The conclusion that the biosphere is the result of a process of self-organization, as defined within this paper (but see Keller 2005), has serious implications for the management of the biosphere, and for the preservation of the ecosystem services on which humans depend. It means that the macroscopic patterns we see, as Gould (1991) and others have argued, do not represent a unique and robust assemblage, and suggests that the larger and larger perturbations that humans are imposing on nature may in turn result in larger and larger system flips. The species losses we are now experiencing may foretoken the loss of genera and functional groups, and beyond those, of self-sustaining networks and nutrient cycles. Ecosystems as we know them will be lost, and so too will nature's services (Daily 1997). We cannot expect natural systems to heal themselves in the face of unlimited insults; they may find new asymptotic states, but not ones we will recognize.

Gaia

The stability and suitability of our environment as a habitat for humanity has fascinated scientists and theologians alike. James Lovelock (1991) attributes to James Hutton, the "father of geology," the statement that "I consider the Earth to be a superorganism and...its proper study should be by physiology" (p. 3). Hutton, in 1785 without the benefit of Darwin's insights, clearly saw the earth not only in biological but in religious terms, as an object of design for the purposes of humanity. Lovelock, inspired by Hutton and Alfred Lotka, proposed the notion of Gaia, named after the mythical goddess of nature, as a self-regulating system of organisms and their environment. Lotka, whose work led to the development of the foundations of quantitative ecology, wrote, "It is not so much the organism or the species that evolves, but the entire system, species and environment. The two are inseparable" (Lotka [1925] 1956, p. 16). Lovelock, one of the greatest geoscientists, had already elucidated the control of the biota over atmospheric gases, and demonstrated that the signature the biota left on the atmosphere could be used as an indicator of whether life might exist on other planets. Those ideas resonated with ecologists and environmentalists, who were sounding the alarm for what the loss of biodiversity would mean for the regulation of climate and of the atmosphere. But Lovelock and his colleagues took this idea several steps further, arguing that the biota controls the physicochemical

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environment at just the right conditions for its survival. In 1974, Lovelock and the brilliant microbiologist Lynn Margulis wrote that “the Gaia hypothesis views the biosphere as an active adaptive control system able to maintain the Earth in homeostasis” (Lovelock and Margulis 1974). Thus, in the extreme form of Gaia theory, the biosphere is a superorganism selected for its macroscopic properties in order to serve the biota. In what Kirchner (1991) termed “Teleological Gaia,” “the Earth’s atmosphere is more than merely anomalous; it appears to be a contrivance specifically constituted for a set of purposes” (Lovelock and Margulis 1974).

The problem with Gaia in this extreme form is that it seeks to explain macroscopic regularities in the biosphere in terms of selection acting upon the whole system, whereas, in general, evolution operates at much lower levels of organization, and not for the benefit of the system as a whole. Lovelock has recognized this contradiction explicitly in recent years (Lovelock 2002), although he still seems to hold out hope for selection operating at higher levels than would make any evolutionary biologist comfortable. Lotka’s original concept of coevolution of organism and environment creates no difficulties for modern theory (Odling-Smee et al. 2003), but it does not impose optimization arguments at the system level. Lovelock (2002) states, “We have a cool wet planet with an unstable atmosphere that stays constant and always fit for life. The odds against this are close to infinity.” James Kirchner (2002) likens this to Douglas Adams’s parable of the puddle of water. Adams (1998) wrote, “Imagine a puddle waking up one morning and thinking, ‘This is an interesting world I find myself in—an interesting *hole* I find myself in—fits me rather neatly, doesn’t it? In fact it fits me staggeringly well, must have been made to have me in it!’” The potential error in logic in Lovelock’s argument is captured in the physicists’ “anthropic principle,” which confronts the effects of observer bias. Life is here to observe the conditions in which it rests *because* those conditions permitted it to arise, not the other way around.

Self-organized criticality

A somewhat different, indeed antithetical, view was advanced by the late physicist Per Bak; it is termed “self-organized criticality” (SOC). Bak and Chan (1991) used the metaphor of a sand pile as a model for the self-organization of a wide range of physical, biological, and social systems. In this example, sand dripped continually onto a surface will eventually produce a sand pile that will wax and wane, fluctuating in aspect around a critical value, as avalanches of varying sizes are followed by reorganization phases. The cycle of collapse and reorganization is a feature of many views of system organization (Schumpeter 1942, Holling 1973), and Bak argues that the power-law distribution of avalanche sizes is also played out in the distributions of catastrophes, especially species extinctions, in a diversity of systems. This is not the place to critique Bak’s all-encompassing paradigm (but see Levin 1999); suffice it to say that, as with the Gaia concept, SOC misses the essential nature of the biosphere as a complex adaptive system in which

modularity and heterogeneity emerge and play crucial roles in mediating robustness. How do modularity and heterogeneity arise in this context, how are they maintained, and what are the implications for maintaining the robustness of ecosystems and the biosphere? To address these questions, we need to recognize the full complexity of ecological systems, and the interplay among processes at diverse scales of space, time, and complexity. Evolutionary processes at smaller scales, including the coevolution of tightly interacting species, give rise to emergent macroscopic patterns at higher levels of organization (Levin 1999), which in turn feed back to influence microscopic dynamics on longer time scales and across broader spatial scales.

Ecosystems and the biosphere as complex adaptive systems

Gaia fails as a model for understanding nature, because it treats the biosphere as if it were selected for its macroscopic properties. Lovelock (2002) recognizes the need for models that incorporate selection at lower levels of organization, but there is no reason to expect that such selection would “optimize” macroscopic properties in any meaningful sense. Lumped models that ignore the potential for evolutionary change produce radically different outcomes than do models that recognize the heterogeneity of systems (Bolker et al. 1995). Self-organized criticality, on the other hand, does not assume any macroscopic optimality; Bak simply views the SOC state as an attractor of a dynamical system. Still, the concept of SOC ignores selection among system components, and the diversity and modularity that are crucial to robustness. Some other perspective is needed, perhaps incorporating features of both views.

Ecosystems, however one defines them, self-assemble from components shaped by evolution, and self-organize as those components reproduce and express phenotypic plasticity. The evolution of the components is driven by the relative fitness of those components, not by the fitness of the system as a whole. But the truth is between the extremes. To recognize that ecosystems are not selected as wholes does not mean that one must view all selection in terms of selfish genes (Dawkins 1976). Selection can act at intermediate levels, forging mutualisms, coalitions, and even multicellular assemblages. Multicellularity, indeed, has arisen many times in evolutionary history (Bonner 2000), in all of the kingdoms of nature.

We might be tempted to view human societies as analogs of these multicellular assemblages, but at the scale of a society, it is clear that evolution need not be working for the good of the whole. Through our actions and activities, humans are endangering the future of our societies and our species. We cannot rely on the Gaian view of nature to repair the damage we cause. The problem is that, as the level of organization moves from the individual to the collective to the society to the ecosystem and biosphere, the integrity of the unit and hence the efficacy of selection decrease.

What then accounts for the robustness of the biosphere and the persistence of the patterns that characterize it? What ex-

plains the regularities in the distribution of the abundances of species, the relative size of individuals, and the nutrient cycles that sustain us and all of the biotic world? Ecosystems and the biosphere are complex adaptive systems, heterogeneous assemblages of individual agents that interact locally and that are subject to evolution based on the outcomes of those interactions. This evolution may simply involve changes in individual behaviors, such as animals that alter their bearings in group dynamics, or economic actors in the marketplace; alternatively, it may involve differential production of offspring, representing heritable change by descent. In complex adaptive systems, holistic approaches are not sufficient. Individual agents drive evolutionary change from the bottom up, so that system evolution emerges from the interplay of processes at diverse scales (Levin 2003).

In understanding how patterns arise and are maintained, therefore, the levels at which selection operates are key. Optimization or game-theoretic approaches provide insights at the levels at which selection is strongest, but other approaches are needed to understand emergent patterns. The ecosystem is not a unit of selection. Indeed, it is not even well-defined; it is to some extent in the eye of the beholder, to some extent culturally defined, to some extent an abstraction. The Clementsian view of the ecological community as a super-organism (Clements 1936) was largely destroyed by the work of Robert Whittaker (1970) and others, who showed that species were distributed individualistically along environment gradients, in accordance with the perspective of Gleason (1926). Self-organizing systems, such as ecosystems, may become more stable, and more robust, through selection at lower levels of organization. Imagine a truck with many loose parts, bouncing up a rutted country road, losing nonessential parts until none are left, growing in its robustness (as measured in the stability of its description) in the process. But it need not: That same truck may lose not just its muffler but also parts critical to its functioning, at which point it will stop running. It then may have reached a robust state, equivalent to death, but not one in which it continues to function; this too could be the fate of our ecosystems, or even our biosphere, if we rely on them to heal themselves.

The central question remains, "How are ecosystems and the biosphere organized?" Characteristic patterns emerge, to a large extent, from phenomena at levels of organization well below those at which key features are maintained (i.e., at the levels of individual agents, small spatial scales, and short time scales). They do not arise from grand design or from system-level selection. It is the domain of science to explain how such complexity can arise from local interactions, and research into complex adaptive systems is one of the most exciting and active areas of research.

Self-organization

I have spoken broadly of self-organization, but it is not entirely clear what biologists mean when we use the term. Do we mean global emergence from rules that are local in some sense? Does it matter where the rules come from? Must mul-

tiples outcomes be possible? If we impose rules such that the outcome is completely scripted, perhaps this should be regarded as directed, rather than self-organized. The process of embryogenesis is one such example, in which the outcome is to a large extent implicit in the genetic information, although the phenotypic variation that can be associated with a given genotype, and indeed the possibility that the process can break down entirely and produce grave abnormalities, might strengthen the case for calling development self-organizing. Keller (2005) provides deeper perspectives on this question.

Understanding how complexity arises in ecosystems is the central and most exciting organizing theme in biological research. Bonner (2000) and others have illuminated how multicellularity arises; the genomics revolution has led to a greater impetus to translate knowledge of the genome into an understanding of how complex organisms are assembled and function. Formal modeling of the evolution of cooperation (Axelrod 1984, Durrett and Levin 1994, Nowak et al. 1994) has led to work on animal aggregations, coalitions, social norms, and culture (Cavalli-Sforza and Feldman 1981, Boyd and Richerson 1985, Bowles and Gintis 2004, Durrett and Levin 2005, Ehrlich and Levin 2005). Autocatalytic networks of interacting species can arise through individual selection, and can be sustained against cheaters (those benefiting from the actions of others without paying a comparable price) when interactions are localized in space, though numerous challenges remain for researchers working to show how such networks translate into the flows that sustain ecosystems across broader spatial scales. The patterns that characterize ecosystems—the distribution and abundance of species, and their spatial organization, size structure distributions, and patterns of nutrient use (stoichiometry)—all can be realized as emergent from selection forces operating at much lower levels of organization, not for the benefit of the whole system but within the framework of well-established principles of evolutionary change. Indeed, the methods are so powerful that they are also providing insights into the organization of societies and economies, in terms of the actions by and rewards to individual selfish agents (see, e.g., Epstein and Axtell 1996, Watts 1999). The literature is too diverse and fast moving to allow an adequate review here; suffice it to say that the development of agent-based approaches to understanding all aspects of biospheric organization, from proteomics to nutrient cycling to civilizations, is one of the most active and exciting areas of research, crossing disciplines and yielding new insights into the workings of the world.

I have been concerned in this essay primarily with the emergence of complexity in the biosphere, and with understanding this process as one of self-organization. François Jacob (1977) compared evolution to the work of a tinkerer, rather than that of a master craftsman, emphasizing the contingent and unpredictable features of the process. Stephen Jay Gould (1991) eloquently pointed out that, were the tape of evolution to be replayed, all would come out very differently; the process of self-organization is indeterminate. I sidestep here the discussion of whether there really can be in-

determinism, deferring instead to investigators like my colleagues John Conway and Simon Kochen, who recently have proved the “free will theorem”—namely, if the physical world is deterministic, free will is impossible—which of course does not resolve the issue. As the late, great Yiddish writer Isaac Bashevis Singer said, “We must believe in free will. We have no choice.” Evolutionary theory and associated theories of the self-organization of the biosphere do not claim to explain everything. The systems of interest are not closed, and Gould’s indeterminacy will certainly be influenced, at least in part, by external physical and chemical factors that intrude upon the biota. Any evolutionary theory, by definition, also assumes certain initial conditions, the origins of which lie outside that theory. The central question evolutionary theory seeks to address is how the remarkable diversity of the biosphere could have emerged without a blueprint, and in this quest it has been spectacularly successful. Not only have the basic principles and predictions of the theory been reinforced repeatedly by empirical evidence, but also the theoretical explorations of the consequences of the basic principles have deflated any argument for grand design, intelligent or otherwise.

The emergence of global regularity from local rules has been a universal theme in the physical and biological sciences, in the social sciences, in linguistics, and elsewhere. The basic theorems of dynamical systems theory investigate the circumstances in which initial conditions and dynamical rules are sufficient to specify unique solutions, and in which bifurcations occur; in the latter case, the choice of which patterns and dynamics emerge after bifurcation may depend on conditions not included in the description of the system.

It is a common exercise in evolutionary theory to posit assumptions about interactions, and then to use the general approaches of dynamical systems theory to explore what the consequences of those assumptions would be were they valid. Although ultimately such (often mathematical) excursions run the risk of being sterile and misleading unless they are coupled with efforts at empirical verification, the exploration of the consequences of incorrect assumptions can also be important, if only to understand why those assumptions cannot be valid, or why natural selection would have eliminated the posited interactions if they had appeared by mutation or recombination. François Jacob (1982), in *The Possible and the Actual*, makes clear the need to have a universe of hypothetical possibilities in which to embed the observed, in order to understand why we see what we do, and don’t see what we don’t. The Hardy-Weinberg equilibrium, the frictionless pendulum of population biology, provides the most familiar example of a model situation that can never be completely realized, yet serves still as an invaluable touchstone for comparison. Journeys into the subjunctive can be highly illuminating. Despite their hypothetical nature, techniques that rest on theoretical idealization of nonideal situations, or on virtual separation of inseparable mechanisms, create a powerful research agenda for exploring the real world. Such theorizing based on hypothetical assumptions is orthogonal to

empirical testing of those assumptions, even if ultimately the theorizing is useless unless confronted with data.

As already stated, evolutionary theory does not attempt to explain everything; of course, it cannot. Godel’s theorem states that “within certain formal systems, there exist propositions that cannot be proved or disproved using the axioms of that system” (NAS 2005). Natural selection and theories of evolution concern themselves, similarly, entirely with how the miracle of complexity in the biosphere can result from a quite simple, though powerful, set of mechanisms acting upon an initial and simplistic soup. Darwin’s “dangerous” idea (Dennett 1996) and the logical extensions it has spurred wonderfully explain that such complexity does not require the invocation of intelligent design.

There are questions that are simply beyond the realm of science, in areas where only philosophers and theologians dare tread. These questions concern themselves with the issues scientific theories cannot address—the origins of the initial conditions, and indeed of the laws of nature and the rules of logic. On such issues, science must remain silent, because they are beyond our capacity to know. Recognition of this distinction perhaps can help to assuage the concerns of those who raise misguided objections to the triumphs of evolutionary theory in helping us to understand the world in which we live.

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