Fragile Dominion
Complexity and the Commons

S Levin
Perseus Publishing 1999

1 Biodiversity and our lives

2 Undergirding the dynamic Earth—its atmosphere, its physical and chemical fabric, and its biological essence—is a prototypical *complex adaptive system* (CAS), one that we call the *biosphere*.

9 Dissecting biodiversity: The point is that the cumulative effects of species loss may be devastating even if the loss of individual species is not.
Sea otter suppressed sea urchin population that eat kelp. Thus, land erosion is prevented by otters. They are the keystone species.
11 Because *nitrogen fixation* is essential for the maintenance of ecosystems, a keystone group comprises the species that perform this role.
To understand the structure of an ecological community is to understand what the keystone functional groups are, and how they relate to one another.

The problem of identifying functional groups, however, is not so easy. What are the crucial structural components in ecosystems, and how much functional redundancy exists within then?...

12 Complex adaptive system: Self-organizing systems have been the fascination of scientists from a diversity of disciplines because the concept of *self-organization* provides a unifying principle that allows us to provide order to an otherwise overwhelming array of diverse phenomena and structures, By self-organization I mean simply that not all the details, or "instructions" are specified in the *development* of a complex system.
In general, however, self-organization characterizes the development of complex adaptive systems, in which multiple outcomes typically are possible depending on accidents of history.

The essential feature of CAS are
(i) Diversity and individuality of components
(ii) Localized interactions among the components
(iii) An autonomous process that uses the outcomes of those local interactions to select a subset of those components for replication or enhancement.

13 What are some of the characteristic aspects of complex adaptive systems? Most fundamental is the *heterogeneity* of the components, which provides the variability on which selection can act. Typically, through *nonlinear* interactions among those components, they become organized *hierarchically* into structure arrangements that determine and are reinforced by the *flows* and interactions among the parts.

14 The other key aspects of complex adaptive systems, in Holland's lexicon, are also well illustrated in ecosystems. Nonlinearity refers to the fact that effect and cause are disproportionate, so that small changes in critical variables, such as the numbers of nitrogen fixers, can lead to disproportionate, perhaps irreversible, changes in systems properties.

Brian Arthur has emphasized the importance of similar accidents in economic systems, a phenomenon that economics refer to as *path dependency*.

15 What is fragile, however, is the maintenance of the services on which humans depend. There is no reason to expect systems to be robust in protecting those services.

2 The nature of environment

18 Adaptation and design: the essence of evolution, and more generally of complex adaptive systems, is that chance and choice, given enough time, make a powerful combination for change.
19 Jacob's tinkering.
26 The central point is that variation is typically greater at small scales than it is at large scales.
27 A global average increase of a few degrees reflects much more dramatic increases in some locations and little change in others.

33 Daisyworld is at best a caricature of how selection might operate to enhance homeostasis.[1]
35 Martin Shubik's game: higher bidder can obtain \$1. The bidder must pay the proposed price. Soon \$1 become irrelevant and this spirals away. There is no stopping.

3 Six fundamental questions

40 (1) What patterns exist in Nature?
43 (2) Are these patterns uniquely determined by local environment of has history played a role?
46 (3) How do ecosystems assemble themselves?
48 (4) How does evolution shape these ecological assemblages?
51 (5) What is the relationship between an ecosystem's structure and how it functions?
53 (6) Does evolution increase the resiliency of an ecosystem?

4 Patterns in Nature

57 The fundamental challenge in understanding the organization of any complex system is to sort out the role of history.
58 Fundamental niche (the range of conditions under which it could survive) vs realized niche (⋯ actually found).

61 There is much to be learned from correlative studies concerning the fundamental biotas of particular habitat types.

67 A solution that works can become established in the absence of intense competition, even it it is not optimal in any absolute sense. Once it is established, the competitive landscape becomes altered so that the sufficient solution can repel competitive forays by technologically superior solutions because of the dynamics of the marketplace of, in the case of evolution, the dynamics of the biological community.
68 Jacob provides numerous examples of accidents of history becoming locked in through the nonlinearities of evolution and the process of tinkering.
Adaptation builds on adaptation.
69 Nonlinearity means that one must examine evolution as a set of problems in game theory:

[1] Lenton, " Gaia and Natural Selection."

a winning type is not necessarily the best of all solutions, judged against some absolute standard; rather, it is a type that, one established in the population, cannot be displaced.

76 In the absence of new disturbance, the forest community will move inexorably toward dominance by one or two world-champion competitors.

Trophic level: at each step, typically at least 90% of the energy is lost in conversion from the biomass of one species into another.

79 Community composition and organization are the children of two parents: local environmental conditions (T, humidity) and the vagaries of history.

80 Ecosystems are self-organizing systems in which random disturbance and colonization events create a heterogeneous landscape of diverse species, which then become knitted together through nutrient fluxes and other forms of interaction.

5. Ecological Assembly

81Assembly of an ecological community following a disturbance, a process called *succession*, is quite different from putting together a new bookshelf from its parts; it is more like LEGO. Where ecosystem differ from most LEGP structures is in the constant turnover of the pieces.

85 MacArther-Wilson biogeography theory.

90 Species-area relationships $S = cA^\gamma$ (S: number of species, A area) : the exponent is 0.1 - 0.4. Such “laws” are really rules of thumb, statistical regularities that admit many exceptions and variations.

93 voter model; contact process.[2]

102 Social and economic systems are similar in that their structures and macroscopic dynamics largely emerge from the selfish behaviors of individual agents rather than from top-down control. That is why the *Tragedy of the Commons* is such a ubiquitous problem; it is also one reason we have wars.

106 David Tilman and his colleagues, in an important series of recent investigations, have shown that the productivity of ecosystems is to a large extent buffered against changes in species composition; that is, it is much less variable than are individual species abundances.[3]

112 Forest models provide beautiful examples of hoe one can use simulation techniques to understand how ecological systems self-organize.[4]
J Holland: *How adaptation builds complexity*

6 The Evolution of Biodiversity

126 The notion of optimization on landscape as a metaphor for the evolutionary process has

[2] Nowak et al., N 359 826 (1992); TPB 46 363 (1994) “The importance of being discrete and spatial.”
[3] Tolman et al N 379 718 (1996); S 277 1300 (1997).
[4] Global Change Biology 1 373 (1995).

some fundamental weakness. The main problem is that environments change, so that fitness vary and landscapes shift. Trying to climb hills on such a landscape is like trying to stay on the crest of wave.

127 Wright in 1931 presented a fundamental mechanism by which populations could escape from local peaks. He argued that a large populations will be broken up into smaller populations, distributed over a variety of habitats.

128 Frequency dependence

129 The study of evolution addresses problems in game theory.

130 Adaptation to specific microenvironments relative to others and directs attention toward the exploitation of previously neglected resources. This principle is basic to the evolution of natural communities, and it is the major force for generating and sustaining diversity.

133 IN the marketplace, diversity emerges naturally from competition and the benefits of exploitation novel ways of making living.

134 If evolution had to deal only with a fixed set of engineering challenges that could be solved by optimization, the world would be a rather boring place, with a depauperated biota.

135 The emergence of biodiversity through the working of competition can take a variety of forms. Competition for resources such as space. light, or nutrients is the most obvious example, but competition for pollinators of for safe haves from predation can work just as effectively. A fascinating example of this involves the evolution of *aspect diversity* in prey
136 species as the result of *apostatic selection* by predators.
Crypsis and apostasis interact to shape patterns of aspect diversity.

138 The phenomenon of character displacement makes it difficult to deduce the importance of competition from observation of overlap in resource use alone.

139 In the study of pattern formation, three stages are fundamental: (1) the breaking of uniformity, followed by (2) the enhancement and (3) eventually the stabilization of heterogeneity.
140 ··· They are equally relevant to understanding the generation and maintenance of ecological diversity.

For ecological diversity to arise, some rare type must enjoy a selective advantage.

142 Mutualism is common in nature, though it is likely that it most typically arises from previously exploitative relationships. *Mycorrhizae* are soil fungi that derive resources by attaching to roots of plants; they may also, however, transform mineral nutrients, especially nitrogen, into a form that would not otherwise be available to the plant host. The mycorrhizal-plant association thus has evolved into a relationship that is beneficial to both species.

143 To get people “think globally, but act locally,” one really needs to get them to think locally. The most effective ways to do this are to close feedback loops so that the consequences of individual of corporate behaviors rapidly come home to roost.

146 Repeated play changes dynamics fundamentally.

148 Dd: near neighbors are more likely to be genetically related to the anterior cells than would a randomly chosen individual.
Localization facilitated evolution.

150 Allelopathic chemical production. Such an antagonistic behavior can be studied experi-

mentally.[5] If bacteria are grown in mass culture, in which the population is well mixed, colicinogenic behavior does not evolve because there is no net advantage to compensate for the metabolic costs. In physically structured environments, however,such as on agar plates, allelopathy may really evolve.

The difference between the two situations that Chao and Levin studied is in the tightness of the feedback loop.

151 Only when the success of the group feeds back to affect the individual's fitness on relatively fast time scales can such influences represent important evolutionary forces.

152 tight vs diffuse coevolution: The myxoma-rabbit story in Australia is an example of the tight coevolution.[6]

An individual rabbit houses a group of genetically closely related virus particles, so that the benefits to a gene that conveys reduced virulence are strong. This is a trait group and the selection above the individual level becomes important.[7]
153 However, parasite-host relations are often many to many, so *Fahrenholz's rule* (natural classification of parasites corresponds with that of their hosts) is actually actively studied.[8]

155 Plant-herbivore, predator-prey interactions are usually diffuse.

Prudent predator behavior arises because pay backs are swift and localized.[9]
Where feedback loops are tight, strong selective pressures emerge, and these can lead to mechanisms to tighten of reinforce the nature of the feedback.

7. On Form and Function

158 What are the implications of elf-organization and evolutionary reinforcement on the properties of ecosystems? What structural properties emerge and how do these influence how systems operate? Where redundancy is evident, is it likely to prove useful...?

159 Tilman's Cedar Creek Reserve experiments.[10] Ecotron experiment.[11]

161 Portfolio principle: increased stability with diversity (less fluctuation of total mass though individual species may fluctuate more).[12]
As to the productivity this seems not enough.[13] However, more diverse assemblage contain

[5] L. Chao and B. R. Levin, "Structured habitats and the evolution of anticompetitor toxins in Bacteria," P 78 6324 (1981). On of the most elegant experiment demonstrating the evolution of action and inaction.

[6] cf P R Ehrlich and P H rave, "Butterflies and plants, a study in coevolution," E 18 586 (1964).

[7] D S Wilson, *The natural selection of populations and communities* (Benjamin 1980).

[8] W Eichler, Ann Magazine of Natural History 12 588 (1948); in *Fungus/insect relationships: perspective in ecology and evolution* Q Wheeler and M Blackwell ed. (Columbia U P 1983).

[9] Eric Kopfer; Kinzig + Harte; Durrett+Levin.

[10] N 367 363 (1994).

[11] N 368 734 (1994); PTRS B 347 249 (1995).

[12] Tilman + Downing; Doak et al "The statistical inevitability of stability-diversity relationships in community ecology," AN 151 264 (1998).

[13] Vegetatio 50 53 (1983); Func Ecol 9 640 (1995) [This tests various hypotheses]; S 277 1260 (1997) Short review.

more productive species that dominate the productivity.[14]

162 Not only the diversity but complexity must be taken into account. Ecological systems are not random assemblages of parts, but become organized into hierarchies, in which each species interacts strongly with a subset of other species (forming *holons*) and much more weakly with the rest.[15]
163 Hierarchical organization localizes damage and provides resilience. More generally, hierarchical structure allow for built-in redundancy, providing another mechanism for resiliency.[16]

166 Paine's keystone predator or more generally keystone species.
169 In many systems species interactions are weak and organizing species into guild (= functional groups) can deepen its understanding.

172 Environment determines primary productivity, and primary productivity influences diversity. But the relationship is complex.[17] When productivity is very high diversity begins to fall. There are many theories, but the most likely is the environmental heterogeneity is reduced.[18]

The fundamental challenge remains to determine how structure affects resilience.[19]
173 Resilience and resistance to change are two sides of the same coin.[20]

8. The ontogeny and evolution of ecosystems

179 In the development and lifetime of a biological organism, natural selection is played out many times among the cells that make up the organism.
183 The idea of edge of chaos is an untestable concept.
184 When interconnectedness is reduced, disturbances are contained—avalanches are avoided. There should be many different level of interconnectedness, so SOC cannot be universal.

187 Definition of individual is not simple. Do host and plasmid together form an individual?

189 Relatedness is fundamental, because altruistic behavior toward relatives enhances the propagation of shared genes. Benefiting a relative benefits oneself, or at least one's genes. But genetic relatedness is not the only way to gain such payback. Coalitions are perhaps most tightly held together when they involve family members, but nonrelated individuals also can form stable, long-term partnerships. These may be held together by rapid reinforcement through reciprocal altruism or through the development of societies with standards of conduct and accepted systems for penalizing those how violate the rules of behavior. Such systems of governance have coevolved with genetically based features but surely reflect a

[14] J Appl Eco 12 189 (1975);)ecologia 110, 449 (1997); Grive, "Biodiversity and ecosystem function"; Tilman et al., S 277 1300 (1997).
[15] O'Neill et al, *A hierarchical concept of ecosystems* (Monographs in Pop Bio vol 23, Princeton 1986); A Koestler and J R Smythes ed *Beyond reductionism* (Hutchinson, 1969 pp192-232); R T Paine J Anim Ecol 49 667 (1980).
[16] O'Neill et al
[17] As Tilman showed this is no one way.
[18] M Rosenzweik and Z Abramsky in Ricklefs and Scluter, *Species diversity in ecological communities.*
[19] ARES 4 1 (1973).
[20] Environmental and Developmental Economy 3 225 (1998).

form of evolution above the level of the individual.[21]
190 Such evolutionary trends have become so ingrained that they control behavior even when the direct reward and punishment loops are removed.

Given that the localization of interactions speeds evolution, it is not surprising that selection also influences the degree of localization.
191 The advantages of clustering are that individuals join together to form collectives for mutual benefit.

192 Many large, self-organizing systems naturally attain a state of self-sustaining criticality in which continual collapses and innovation reach a dynamic balance.
There is undoubtedly much truth in this view, but it is too simple. In particular, it ignores the role of selection at the diversity of levels on which it occurs.

Evolutionary pressure to reduce the consequences of uncertainty do not stop at the level of the single species. Mutualinm and other tight linkages among small numbers of species
193 evolve to provide the participants buffering against environmental vagaries. Ecosystems thus become assembled not into sandpiles but into modularly organized webs of interaction in which clusters of interacting species to some extent insulate themselves from the collapse of other clusters.

9 Where do we go from here?

198 The Eight Commandments of Environmental Management
1. Reduce uncertainty. Our ignorance makes this difficult. “Strangely, we seem willing to spend more money to search for life on other planets than to study diversity on our own.”
199 2. Expect surprise. 1 implies to transfer maximally from the knowable to the unknowable, but this commandment implies to recognize our ignorance.
201 3. Maintain heterogeneity.
203 4. Sustain modularity.
There is buffering against cascades of disaster.
5. Preserve redundancy.
204 6. Tighten feedback loops. This means getting the prices right.
205 7. Build trust.
207 8. Do unto others as you would have them do unto you.

[21] See *Cultural Transmission...*.