

Fragile Dominion: Complexity and the Commons

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Simon Levin

Perseus Books, 1999

ISBN 0-738-20111-1

256 pages, \$27.00

In his book *The End of Certainty*, Prigogine notes that “If the world were formed by stable dynamical systems, it would be radically different from the one we observe around us. It would be a static, predictable world, but we would not be here to make the predictions.” In *Fragile Dominion*, Simon Levin describes the evolution and dynamics of the world’s ecosystems and the loss of biological diversity attendant upon human activities. These losses, we learn, are largely the result of our inability to cope with complex, nonlinear systems. Thus, while life is in essence derived from non-linearity, we risk the loss of life and biodiversity through the fine sensitivities of these essential processes. It is appropriate therefore to endeavor to understand how populations, communities, and ecosystems are constructed, both in the long term through mutation and selection and in the shorter term through colonization and competition. In this way we might arrive at decisions and policies with fewer adverse consequences for our planet.

Historically, these differences in time scales have translated into evolutionary versus ecological

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approaches to biological diversity; Hutchinson contrasted the ecological theatre with the evolutionary play. Thus Darwin sought to understand the origins of diversity among individuals and species, while ecologists such as Elton and Hutchinson have tended to concentrate on the maintenance of diversity at the species level and above. As

Levin repeatedly informs us, this division of processes is largely expedient and need not reflect what is going on in nature. The ecology of the future will be one that explains selection acting at many scales of organization and therefore is made a partner of evolutionary theory. This will include describing ecological patterns using measures of fitness derived at lower levels of organization. The advantages are obvious: in place of descriptive theories of patterning, one obtains an optimality criterion upon which to base the observed order.

The interweaving of individual evolutionary processes and ecology forms the warp and woof of this book. Good examples of this approach are “individual-based” models of populations and ecosystems, an area of research in which Levin has made considerable contributions. In these models, large scale structure is derived from the

bottom up—as the statistical outcome of the behavior of countless, selfish, Darwinian replicators. Consider Levin’s work on the dynamics of herds. Many species spontaneously form social groups in which some spatial structure emerges from the coordination of individual members. Reflecting a “Lagrangian” approach, these models consider the locations $r_i = (x_i(t), y_i(t))$ of each individual i at time t , moving at some velocity towards a target with a velocity component derived from the interaction with other individuals. Hence $\dot{r}_i = \sum_{j=1}^2 w_{ij}$, $i = 1, \dots, n$, where w_{i1} is the intrinsic velocity vector and w_{i2} the complement. These interaction components are attractive towards distant neighbors and repulsive towards close neighbors. The tendency of groups to fragment at some threshold density can be characterized by the magnitude of these opposing forces. Furthermore, by allowing the velocities to vary across the population, diverse patterns of motion can be produced: slow speeds tend to produce bands, whereas fast speeds produce columns.

The first two chapters offer an overview of ideas and themes. In the first chapter we are introduced to the scientific study of biodiversity, which examines, for example, how certain “keystone” species play a vital role in preserving species’ heterogeneity and the implications this might have on myopic stewardship of the environment. In the second we are introduced to the notion of the self-organizing system. Such systems are typified by patterns that emerge from nonlinear interactions among simple constituents rather than through imposition from above. A common example one finds in biology is Turing’s reaction-diffusion formulation for steady-state heterogeneous spatial patterns. Thus, if one has a vector describing the abundance of two species c which interact nonlinearly according to $f(c)$ and where each species has a constant rate of diffusion (represented by positive diagonal entries in the 2-square matrix D), then one can write an equation of the form $\partial c / \partial t = f(c) + D \nabla^2 c$. If the diagonal entries in D are not equal, Turing showed how this system could give rise to diffusion-driven instability. The earth or biosphere can be viewed as a very elaborate self-organizing system in which the majority of global patterns we observe are derived from local interactions among countless biotic and abiotic components. Complex adaptive systems, by contrast, are modified by selection acting most forcibly at the level of the individual components. In these cases we can refer to the structures as “evolved” for some purpose. Nonadaptive and adaptive systems share some characteristics, such as a diversity of components, localized nonlinear interactions, some form of hierarchical organization, and flows or energy connecting the hierarchies. But only the adaptive system has undergone systematic modification under pressure of selection. Levin

goes to some length to clarify these ideas, as so often in biology it is wrongly assumed that patterning implies some form of selection. It is refreshing to read that “What is good for the ecosystem is neither well defined nor relevant evolutionarily.” For those of us struggling with strong versions of the Gaia hypothesis (the earth as a complex adaptive system), this is a great source of comfort.

In the third chapter we are presented with six fundamental questions, each of which is covered in one chapter and around which the remainder of the book is structured. The questions are: (1) What patterns exist in nature? We are introduced to the “facts” of ecology relating to species diversity at numerous different scales. (2) Are these patterns determined by the current environment or by historical processes? In other words, can we understand ecological patterns through an appreciation of the environment, or have a large number of unpredictable events throughout history culminated in the patterns that we observe today? (3) How do ecosystems assemble themselves? Can we understand the competitive processes leading to biodiversity, and how do these relate to the evolution of individual characteristics? (4) How does evolution shape these ecological assemblages? We accept that evolution can act on individuals making up the species and thereby influence multispecies patterns, but is there a sense in which these higher-level patterns feed back on selection at the individual level? (5) What is the relationship between ecosystem structure and function? How do the parts contribute to the stability of the whole, and are there components which make a disproportionate contribution to the total assemblage? (6) Does evolution increase the resilience of an ecosystem? Do higher levels of selection lead to communities typified by robustness, or are ecosystems at some critical threshold and prone to dramatic losses of diversity?

The tendency of the human mind to uncover patterns is somewhat bewildering: we have seen weasels in clouds and prurient posturing in spilt ink. The extent to which nature manifests interesting order rather than reflects cognitive biases represents a serious challenge to biological science. This becomes very clear when one considers that just about everything in nature above the species level is an arbitrary classification. Herein lies a problem for ecology, as ecologists seek to understand the details of species numbers and distributions and their aggregate properties as populations, communities, guilds, and ecosystems. Is it possible to have a science for these higher levels of organization when we remain uncertain whether they exist as natural types?

Great progress in describing the abundance of species derived from the work of Wilson, MacArthur, and Simberloff analyzing the diversity

of islands in the 1960s. The “equilibrium theory” of island biogeography states that the number of species on islands is determined by a balance of immigration and extinction. A previously unoccupied island, or one that has been cleared of most species, such as Java after the eruption of Krakatoa, is rapidly colonized by a large number of different species. As the numbers of resident species increase, the rate of immigration diminishes, reaching zero once the island’s biodiversity matches that of the source population (on the mainland). However, on the island, species will be going extinct both through maladaptedness to the new environment and through competitive exclusion. The result is that extinction is proportional to species richness. The equilibrium solution of this dynamical system gives a measure of the biodiversity on an island. One can think about this using an ordinary differential equation in which the number of species x changes in time according to $\dot{x} = c(1 - x) - ex$, where c is a colonization parameter and e an extinction parameter. The equilibrium solution is given by $x^* = c/(c + e)$. If one assumes that extinction decreases as island diameter (S) increases such that $e = e_0 \exp(-aS)$, and if colonization decreases as the distance to the mainland (D) increases such that $c = c_0 \exp(-bD)$, then one can derive an approximate expression for the number of species at equilibrium: $x^* = c_0 \exp(-bD)/(c_0 \exp(-bD) + e_0 \exp(-aS))$. This assumes of course that all species are equally adept at migrating and equally strong competitors. Simberloff’s experiments on mangrove swamps in the Florida Keys, in which he removed species by fumigation and then chartered recolonization, bore out the predictions of the model.

An important question in ecology has been whether there is a true “island effect” or whether the reduced biodiversity on islands is a simple consequence of small areas. Thus the colonization terms in the “equilibrium” model could be replaced with a speciation function or a general dispersal kernel and still produce good approximations simply because competitive processes remain the dominant determinants of species richness. To evaluate this possibility, a general model of species-area relationships is required. The most general finding in ecology has been that the logarithm of the species richness R is proportional to the logarithm of the area A plus some constant. Thus the species area relationship is described by a power law of the form $R \approx A^p$. One feature of these relationships is that the exponent p lies in the range 0.15 to 0.4 in different regions around the world. Levin, in collaboration with Durrett, has used simple spatial models to derive the power law relationship from interactions among individuals and has attempted to explain the variation in the parameter p based on individual mechanisms. These models are stochastic cellular automata. Space is

divided into square cells positioned on a two-dimensional integer lattice. At any given time the state of the system is determined by the ensemble of species at each site. The dynamics of the system are determined by speciation/immigration, dispersal, and competition. The model is a multiple contact process with mutation. Speciation/immigration is modeled by occupying a vacant site with a new species at a rate α . Dispersal to another site occurs with a probability proportional to the distance between sites at a rate β , and competition is approximated by including a constant death rate d at which sites become vacant. The timing of events is independent and described by the exponential distribution $\exp(-\lambda t)$. It can be shown that this system has a unique nontrivial equilibrium when $\beta/d > \lambda_c$, where λ_c is a critical value of λ . Such a model produces a power law relationship for which the parameter α has the greatest impact on the value of the exponent. Thus these models suggest there is an “island effect”, as the source of new biodiversity has the greatest impact on species richness. As speciation is orders of magnitude slower than immigration, the “distance effect” (the rate at which new species reach the island) provides a strong explanation for diversity.

The attraction of these simple models is that we obtain a good insight into qualitative properties of ecosystems. The pioneering work of May on complexity in simple model ecosystems taught us that we need not assume that the mechanisms underlying biodiversity are as elaborate as the product. The canonical example is the discrete logistic map in which the state of a variable x_t at time t is mapped onto a new value at $t + 1$ according to $x_{t+1} = rx_t(1 - x_t)$. This is a noninvertible map whose behavior depends critically on the parameter r . Gradually increasing the parameter r leads to a series of bifurcations, attracting limit cycles, and eventually chaos. In ecology the value of r can be loosely interpreted as fertility. The disadvantage of simple models is that we cannot incorporate detailed knowledge gleaned from the field in order to generate new quantitative predictions. This has led to two approaches to modeling ecosystems: those based on simple analytical reasoning and those based on simulations parameterized by much of the available data. The disadvantage of many of these simulations was articulated by Janzen, who stated that they got “all the nouns, but none of the verbs.” Levin is very much in the “verb” school of modeling and well aware of the risks of not seeing the forest for the trees. Nonetheless, in Chapter 5 we are provided with a fascinating introduction to Botkin and Pacala’s individual-based forest simulations, which have to a large extent bridged the gap between these two cultures. Pacala’s recent work has been to derive expressions for the moments (mean densities and spatial covariances) of ensembles of

organisms as approximations of stochastic spatial models. The first and second moments are written as an ordinary differential equation for the average density of individuals and an integro-partial differential equation describing the average spatial covariance across all possible interactions.

Chapter 6 grapples with the relationship between ecological diversity (at many scales) and the evolutionary process. If we assume we start with a homogeneous system, how do we arrive at diversity? This is the problem of pattern formation in which symmetry must be broken and subsequent heterogeneity enhanced and maintained. It was Darwin and his successors' great insight that mutation and selection could achieve this result. While Darwin tended to think about the match between the individual and the environment (optimization), we now realize that fitness tends to be frequency dependent. This means that individual fitness is a function of the strategies employed by other individuals in the population. Hence "perpetual adaptation does not necessarily translate into optimization." The theoretical framework for investigating frequency-dependent fitness is evolutionary game theory. Game theory involves determining the existence, accessibility, and stability properties of a large family of equilibria. The most well known of these is the Nash equilibrium. If one considers two individuals A and B who can play strategies p or q , the pair of strategies (p_A, p_B) are Nash equilibria if p_A is the best reply against p_B and vice versa. If p_A is the unique best reply to p_B and p_B the unique best reply to p_A , then this is a strict Nash equilibrium.

The evolution of altruism provides a test case for such a notion of fitness, as individual success is determined largely by interaction with conspecifics. Altruism presented a serious challenge to Darwin, as nature, "red in tooth and claw," should rarely favor a strategy that enhances the reproductive output of others at the expense of one's own fitness. In other words, how can cooperation reach a Nash equilibrium when selfish behavior increases an individual's fitness? Haldane presaged the answer in his remark that he would lay down his life for two of his siblings or eight of his cousins. This intuition was provided with a full theoretical explanation in William Hamilton's revolutionary work on kin selection in the 1960s. The essential idea is that fitness is the net contribution of a shared set of genes to the population gene pool. Thus closely related individuals have an overlapping fitness referred to as "inclusive fitness" with respect to their shared genes, expressed as a correlation coefficient of relatedness. The correlation is between individual and group fitness. The greater the correlation, the more frequently altruism evolves. This insight is summarized by Hamilton's rule, which states that altruism can evolve provided that $rB - C > 0$, where r is the re-

latedness, B the reproductive increment to the recipient(s) of an action, and C the cost to the actor of providing the benefit.

Levin demonstrates how limiting dispersal, thereby promoting spatially structured populations, can produce such correlations. One way to think about this is to realize that fitness in a mean-field model (nonspatial or fully mixed) is defined simply as the per capita growth rate of mutants when rare. A mutant is simply an individual adopting a unique strategy in the population, while the growth rate is given by the invasion exponent or dominant eigenvalue of a "jacobian" matrix evaluated at the wildtype population's steady-state value. In spatially viscous populations, multiple differential equations are required to capture the invasion dynamics. If one represents this system in matrix form, Van Baalen and Rand have shown how the dominant eigenvalue provides information about invasion and the corresponding eigenvector, the structure of clusters of the rare mutants. It turns out that these clusters correspond to the coefficient of relatedness defined locally. Thus spatial structure favors the emergence of altruistic strategies, because as Levin states, "the success of the group feeds back to affect the individual's fitness on relatively fast time scales."

The importance of short feedback loops for stability is a recurrent theme in Levin's discussions and in May's earlier work on stability and complexity. These interactions are responsible for the robustness of populations, ecosystems, and communities. In recent years it has become common to see treatments of complex adaptive systems couched in terms of critical phenomena. Two of the most prominent are Kauffman's metaphor of "life at the edge of chaos" and Bak's "self-organizing criticality". While these are very different theories, they share a perspective that life is positioned close to a critical state, which upon perturbation undergoes a phase transition to disorder. Bak and colleagues have interpreted periodicities in the fossil record as evidence of self-organized criticality. This result is reached by observing that fluctuations in species abundance through time can be described by a $1/f$ power spectrum $P(f)$ which measures the contribution of each frequency f to the time series. Self-similarity is observed in these data as $P(f) \approx f^{-\beta}$ with $0 < \beta < 2$. Such a relationship can be generated by modeling individuals using contact processes as discussed above, and then the system evolves to a critical point with $1/f$ fluctuations. However, recent work suggests that the results on the fossil record could be an artifact of interpolation which can produce spurious correlations in data. Levin's position is quite different and closer to the biology. He argues that selection has led to a situation in which individuals obtain a high fitness in a complicated network of interactions. Those species without robust properties

are rarely observed. By extension, those ecosystems that are volatile have been prone to extinction, and those that we observe are among those that were able to remain stable. We can ask what are features of the ecosystems that we observe, adopting an assumption akin to the “anthropic principle”, which avers that the mere existence of complex interactions argues for some stability mechanisms. The properties we see are hierarchical organization into modular-like components. The importance of modularity is that it partitions variance in such a way that ablation of one module has a minimal impact on the remaining structure. Thus few species are members of keystone functional groups, those groups whose activity has an impact on many other species. Similarly, food webs have characteristic numbers of levels, limiting the range of influence. These properties arise quite naturally out of a consideration of individual-based selection.

The book closes with some thoughts on how we as humans might deal with these insights. The notion of tight feedback is as useful an insight into human perception and behavior as into the behavior of dynamical systems in general. Thus by becoming responsible for our actions locally (tight feedback) we are far more likely to behave with ecological probity. Levin’s final thoughts are presented as “eight commandments of environmental management”: (1) reduce uncertainty, (2) expect surprise, (3) maintain heterogeneity, (4) sustain modularity, (5) preserve redundancy, (6) tighten feedback loops, (7) build trust, and (8) Do unto others as you would have them do unto you. All of these are necessary as we now find ourselves the guardians of this fragile dominion. It is reassuring to have Levin as a guide.