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Complexity in Ecological Systems

Ecology has been eminently a descriptive science despite some pioneering work by theoreticians such as Lotka, Volterra, Nicholson, and others. Description is a first step toward understanding a system. However, such a first step needs to be accompanied by the development of a theoretical framework in order to achieve real insight and, whenever possible, predictive power. Ecologists are increasingly facing the challenge of predicting the consequences of human-induced changes in the biosphere. For example, we need to better understand how biodiversity declines as more habitat is destroyed, or how harvested populations are driven to extinction as harvesting rates are increased. Toward that end, it is necessary to integrate field and experimental ecology with theory (Odum, 1977). This integration is much more common in the physical sciences, where theory and experimental data have always marched together (May, 2004).

This book describes a theoretical view of ecosystems based on how they self-organize to produce complex patterns. It focuses on very simple models that, despite their simplicity, encapsulate fundamental properties of how ecosystems work. They are based on the nonlinear interactions observed in nature and predict the existence of thresholds and discontinuities that can challenge the usual linear way of thinking. These models have shown the possibility of ecosystem self-organization at several scales. Simple nonlinear rules are able to generate complex patterns. This view contrasts with traditional approaches to ecological complexity based on extrinsic explanations. Thus, population cycles were said to be complex because multiple variables and external influences such as the climate are involved; spatial patterns in the distribution of a species were said to be nonhomogeneous because the spatial distribution of nutrients or perturbations is also heterogeneous; communities were said to be complex because there are hundreds of species interacting in a somewhat random way. This book presents theoretical evidence of the potential of nonlinear ecological interactions to generate nonrandom, self-organized patterns at all levels. In time, nonlinear density-dependence can generate complex dynamics such as deterministic chaos (chapter 2); in space, the combination of local nonlinear growth and short-range dispersal can generate a myriad of spatiotemporal patterns (chapter 3); at the community level, simple buildup mechanisms such as the preferential attachment of species to generalists can generate complex, invariant ecological networks (chapter 6).

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By reviewing general properties of ecological systems, we emphasize processes that are equivalent to physical systems. General predictions can be made about ecosystem dynamics and their response to human-induced perturbations. Although there are several excellent books on parts of this plethora of processes (population ecology, spatial ecology, community ecology), none integrates them into a single framework. What is to be gained from this exercise is a comprehensive view of how simple processes act to build the patterns we observe in ecology at different levels and how predictions based on linear thinking may be misleading. Another characteristic of this book is to reveal such common mechanisms by using a suite of tools from physics and mathematics. These tools are used to emphasize their connection to ecological systems. They help in relating ecological systems to other physical systems.

THE NEWTONIAN PARADIGM IN PHYSICS

The Hardy-Weinberg law in population genetics can be thought of as an equivalent evolutionary version of Newton's first law stating that gene frequencies in a population remain fixed in absence of any force applied to them (e.g., migration and selection) (May, 2004). Despite this analogy, however, most ecologists would probably agree that there is little relation between the complexity of natural ecosystems and the simplicity displayed by any example derived from Newtonian physics. The standard physical systems we are familiar with involve either a single or a small number of particles. Of course understanding such "simple" systems might not be so simple, especially when dealing with the sophisticated mathematical framework required. But beyond the difficulties of the microscopic dynamics of atoms and elementary objects, macroscopic systems composed by a few or even many units (such as the solar system) are essentially well understood in terms of fundamental laws.

Several basic examples provide a perfect illustration for these laws. A perfect pendulum, for example, is a deterministic system described by only two variables: its position and its velocity (fig. 1.1). It can be shown that two deterministic equations describe its motion, defining how the position (angle ϕ) and the velocity v change through time (Arnold, 1978; Strogatz, 1994):

$$\frac{d\phi}{dt} = v \tag{1.1}$$

$$\frac{dv}{dt} = -\mu v - \frac{g}{L} \sin \phi \tag{1.2}$$

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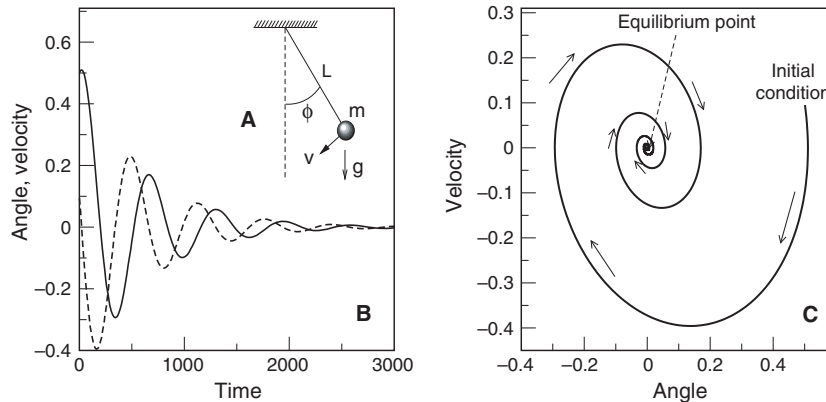


FIGURE 1.1. (A) One of the simplest examples of predictable dynamics: the pendulum. Here a ball of a given mass moves in a deterministic fashion and its state is fully characterized by only two variables: its position ϕ and its velocity v . Their evolution (for a given set of parameters) is shown in (B): Damped oscillations drive the system toward its equilibrium state. In (C) the same trajectories are represented by using the phase space (ϕ, v) .

The motion takes place under the action of the gravitatory field g acting upon a mass m and a friction force proportional to the pendulum's speed. Consistent with our experience, the system will approach a state of repose in which $\phi^* = 0$ and $v^* = 0$. This dynamical evolution is displayed in figure 1.1b. Both the position (continuous line) and the velocity (dashed line) present dampened oscillations. Such an equilibrium state will be obtained starting from any possible initial condition, and we call it the global "attractor." It can be visualized by using an appropriate *phase space* Γ , here defined by the two variables required, that is, $\Gamma = (\phi, v)$. As shown in figure 1.1c, the orbits displayed by the pendulum converge to a single point attractor $(0, 0) \in \Gamma$.

Not surprisingly, the mathematical framework required in order to describe the motion of such a regular system is simple. And since simplicity in the underlying model and simple motion seem naturally related, one might conclude that: (a) simple dynamic patterns will be describable by means of simple mathematical models, and conversely (b) simple mathematical models will display simple, predictable dynamics. Although the first is typically true, the second turned out to be false (chapter 2).

For a long time, predictability has been the hallmark of the Newtonian success: the new visit of a given comet can be predicted with the

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highest accuracy and no one is surprised by such achievement. The success of classical mechanics has been a reference point for many scientists. Is there any hope of formulating such types of general laws for ecosystems? Probably not. One obstacle for a physics-oriented theoretical ecology is the fact that physical and biological systems strongly differ in some essential ways. Biological structures involve features such as functionality that have no equivalent within physics (Hopfield, 1994). Biological entities (at least at some scales) involve reproduction and evolution, and although some physical systems can “replicate,” the implications of such event in terms of information are completely different. And of course there is a strong historical component to be added to the whole picture: species evolve, they change their interactions, and eventually the whole ecosystem changes. Ecosystems as such cannot be considered units of selection, but one may well ask if universal laws are shaping their structure at least on some scales.

The challenge posed by the previous issue is enormous, and one might ask first if physics can be an appropriate area to compare with ecological science. One possible answer is that most methods used in statistical physics are actually generic for any system composed by many parts. At its most extreme, econophysics offers a clever example (Mantegna and Stanley, 2000). Here the elementary units are so-called agents. These agents are humans, computer programs, or a mixture of both. Humans introduce an enormous level of potential complexity, and it makes no sense to write down the “microscopic” equations for them. In other words, the accurate description that would please a reductionist approach is simply forbidden. However, by assuming that these entities are not so complex *in making their decisions*, it is possible to understand, on a quantitative basis, many fundamental processes that define a market. Perhaps not surprisingly, several components of the key types of interactions that emerge in the economy are common to ecological dynamics. Actually, these similarities have been explicitly introduced within the framework of so-called computational ecologies, where networks of computers and agents display dynamic patterns not different from those recognizable as competition, cooperation, or symbiosis (Kephart et al., 1989).

Hierarchies and Levels of Description

Ecosystems can be understood and analyzed at very different, nested scales (fig. 1.2). At the most fundamental level, single species (or descriptors of some of their relevant features) define the smaller scale. Beyond this basic units, we have a level of description in which interactions with other species must be considered. At this level, new

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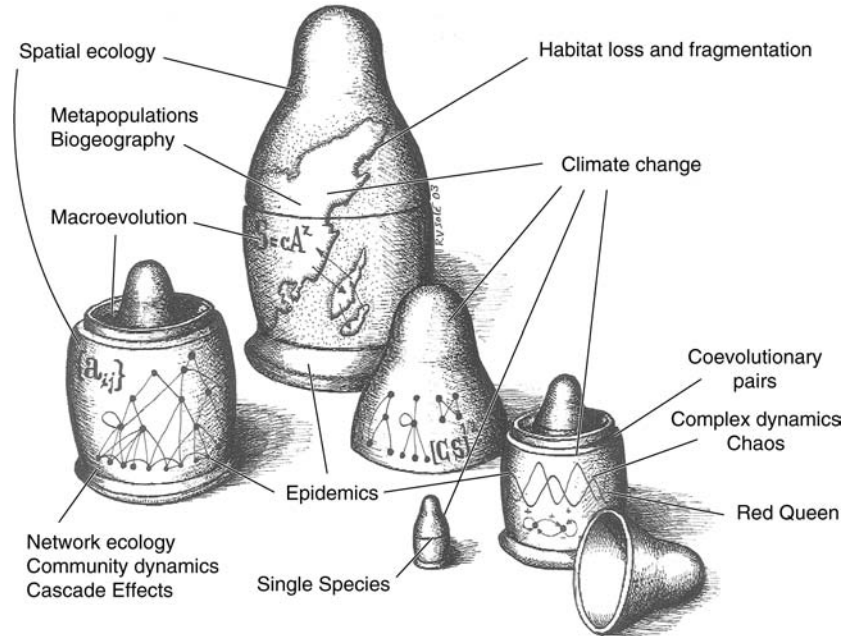


FIGURE 1.2. Levels of organization in complex ecosystems. A nested hierarchy of complexity levels can be defined, from single species to biogeographic patterns. Different properties and different problems can be identified at several scales, and some large-scale patterns cannot be reduced to the inferior levels of the hierarchy.

phenomena such as population cycles (chapter 2) can only be understood after coupling among species has been introduced. Evolutionary paths also need to consider the biotic environment, and some theories of evolutionary ecology, such as the Red Queen hypothesis (chapter 7), emerge as the natural explanatory framework. Under this scenario, new phenomena, such as the appearance of parasites and epidemics have to be taken into account. Beyond this point, the next step in the hierarchy involves the community level, in which the networks of interactions between species provide a unifying picture. At the community level, different regularities can be observed suggesting the presence of universal principles of community organization (chapter 6), but historical events implicit in the assembly process have to be taken into account. How external and internal changes propagate through the web of interactions among species and affect its stability is one key example of how ecological complexity is influenced by structural properties. At the higher level, the spatial context, the variability associated to local

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climate influences, and the global patterns of biotic organization define the top of our hierarchy. Our planet has experienced numerous large-scale changes through time, and the biosphere has been a leading actor. Through the history of life on Earth, extinction and diversification have been interacting and the first cannot be understood without the second (chapter 7).

But it would be misleading to think about the previous nested structure as a fully hierarchical one. Besides, the understanding of the upper parts of the hierarchy are somewhat, but not totally, decoupled of the lower members. The influences between each component are likely to be bidirectional. Climatic changes influence biotas, but the response of them to such change can further increase the trends (chapter 7). Habitat fragmentation (chapter 5) is a leading cause of biodiversity loss, although its effects must be understood in terms of their impact on the web of interacting species. Evolutionary responses are shaped by climate, but some overall patterns of ecosystem organization seem to largely stem from fundamental principles of community organization.

Although ecosystems are biological entities and as such include in their description concepts such as selection, adaptation, or information on a large scale, they are under the same physical laws as any other system. They also involve memory, information, and nonlinearity as essential features, and their interactions often behave in all-or-nothing ways, thus leaving little chance for the underlying details to effectively matter (chapter 4).

DYNAMICS AND THERMODYNAMICS

In a search for general, physics-inspired laws of ecological organization, the first step is thermodynamics and statistical mechanics (Ulanowicz, 1997). Since ecosystems must fulfill the three laws of thermodynamics, perhaps some of the patterns observed in complex biotas are a consequence of such laws. Energy is a quantity common to all processes. It flows, is stored, and is transformed. When dealing with energy flows, the components and the boundaries of the system must be properly specified (Odum, 1983). One standard, classical approach is to make use of energy-flow diagrams (Odum, 1983; Ulanowicz, 1997). Based on early developments in general systems theory (von Bertalanffy, 1951, 1968), energy diagrams provide holistic descriptions of the ecosystem where all parts, including the environment, are considered (fig. 1.3).

Many physical systems are made up of multiple components (in interaction or in isolation). The simplest example is provided by an ideal gas, where a huge number of atoms (or molecules) occupy a given, fixed

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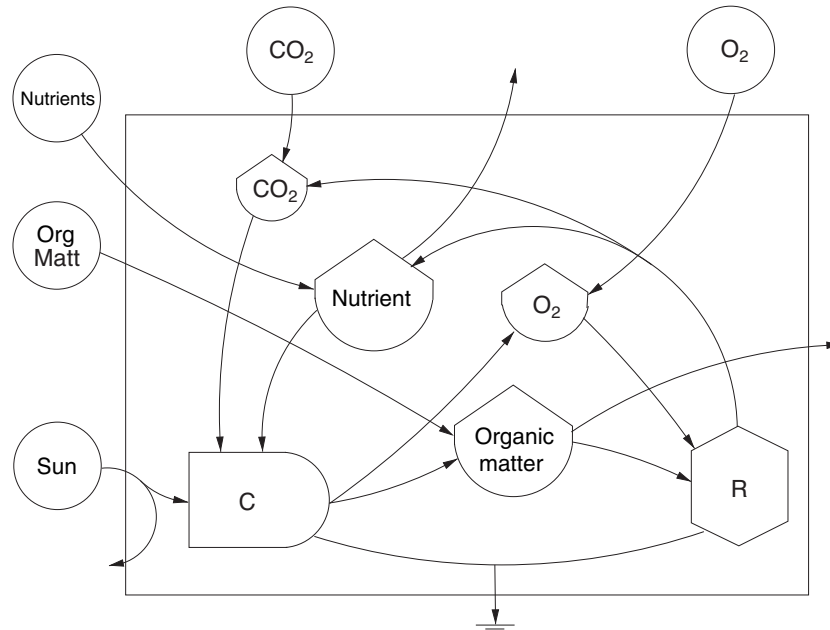


FIGURE 1.3. Energy diagram displaying the main processes involved in production, consumption, gas exchanges, and recycling in a typical aquatic ecosystem (redrawn from Odum, 1983). Here a very simple producer-consumer (C-R) model is shown. The arrows indicate energy flows. C refers to photosynthetic production and R to respiration of the consumer parts of the system.

volume of space. These molecules do not interact (or they interact very weakly) and thus can be considered independent of each other. This assumption, together with conservation in the number of particles and their energy, allows the construction of a well-defined body of theory in which we can extrapolate from single units to the whole. In other words: the average behavior of single particles provides full insight into the global behavior. For a standard physical system composed by N particles of mass m_i , an energy function can be defined as follows:

$$E(r_1, \dots, r_N; v_1, \dots, v_N) = \frac{1}{2} \left\{ \sum_{i=1}^N m_i v_i^2 + U(r_{ij}) \right\} \quad (1.3)$$

where the first part in the sum correspond to kinetic energies $T_i = m_i v_i^2 / 2$ and the second to potential energies, which in general will depend on the relative distance among particles, $r_{ij} = |r_i - r_j|$, through some functional dependence. When this term can be ignored or is too

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small compared with kinetic energy, we have a system that is basically described in terms of separated, representative items. However, once the interactions become relevant (and we talk about strongly interacting systems), collective phenomena start to modify expectations based on understanding single units. In particular, and this is an especially relevant point that will be discussed through the book, sudden changes will occur under small changes of the system's parameters. A given parameter such as temperature, precipitation rate, or infection rate can increase or decrease without having a detectable effect on a system's properties and suddenly a totally new qualitative property might appear. Within the ecological context, this corresponds to the so-called catastrophic shifts (chapter 2). Typically, these shifts end up in a new state with little resemblance to the original one, and very often there is no way back unless significant parameter changes occur. Irreversibility thus appears to be a rather common feature of ecological complexity. Such a property does not match comfortably within standard thermodynamics, where reversibility is a natural constraint. This problem will be discussed in some detail in chapter 4 in relation to the emergence of scaling laws and phase transitions in ecological systems.

Order and Disorder

Since purely thermodynamical arguments might fail to help understand the origins of ecological patterns, we should turn our attention toward a more dynamical view. Several questions emerge when dealing with ecological dynamics. What is the nature of the processes underlying the observed patterns? Is it possible to capture their main ingredients within simple mathematical equations? Are they predictable? Answering these questions forces us to look into the spectrum of expected patterns generated from deterministic and stochastic processes.

At one extreme in the spectrum of possible dynamical patterns we have randomness. Here events take place in a stochastic manner, and the appropriate description of the system must be cast in terms of probabilistic measures. Chance is here the main actor, and the coin toss the appropriate icon. Tossing a coin involves a simple mechanism but somehow it deals with a very large number of degrees of freedom. The same situation applies for a pinball machine: although it should be possible *in principle* to know how the dynamics will develop in time, it is practically impossible to do so. A coin toss, in spite of its simple definition, pervades the unpredictable character of random systems involving an infinite number of degrees of freedom.

At the other extreme in the spectrum, deterministic, simple dynamical systems offer (in principle) the other side of the coin. A deterministic

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system would provide a perfect predictability: once the initial condition is known, the future is available. This is the case of the example discussed at the beginning of this chapter.

But of course, things aren't necessarily so easy. A perfect illustration is offered by nonlinear discrete maps (to be explored in chapter 2). Consider a population of size x_n at a given year n (here $n = 1, 2, \dots$). As will be shown in chapter 2, this time-discrete approach to population dynamics is appropriate for a number of ecological systems, such as insect populations with non-overlapping generations. The population at year $n + 1$ will be obtained from the population at the previous year through some mathematical function. One of the simplest models is given by the following map:

$$x_{n+1} = \mu x_n(1 - x_n) \quad (1.4)$$

Equation (4) is called the *logistic map* and exhibits very complex dynamics in spite of its obvious simplicity. Since this complexity and its consequences will be of relevance in the next chapter, here we only highlight the random character of some specific properties of a large class of simple, deterministic dynamic systems. In particular, one class of dynamics that can be displayed by the previous model involves the generation of a sequence of values $\{x_i\}$ that never repeats itself. An example is shown in figure 1.4 for $\mu = 4$. The black dots represent the actual states, and the dotted line helps illustrate how the consecutive values are connected. By looking at the black dots, it is difficult to appreciate any regular pattern (although some correlations seem to be present).

Let us consider a given situation where we only have access to a coarse-grained description of the system's state. To be more precise, let us consider a binary space state obtained from a so-called Markov partition, where each value x_i has an associated bit S_i :

$$S_i = \begin{cases} 0 & : 0 \leq x_i < 1/2 \\ 1 & : 1/2 \leq x_i \leq 1 \end{cases} \quad (1.5)$$

This mapping creates a string of ones and zeros that only retain a very rough part of the underlying dynamics. The surprise comes when the structure of this string of bits is analyzed: although the original dynamical system is completely deterministic, the binary sequence generated from the Markov partition is not distinguishable from a coin-toss process. Randomness is obtained from determinism.

The previous result illustrates the fact that the boundaries between determinism and randomness are not so well defined as one would first suspect. This emergence of complex dynamics will interact, within

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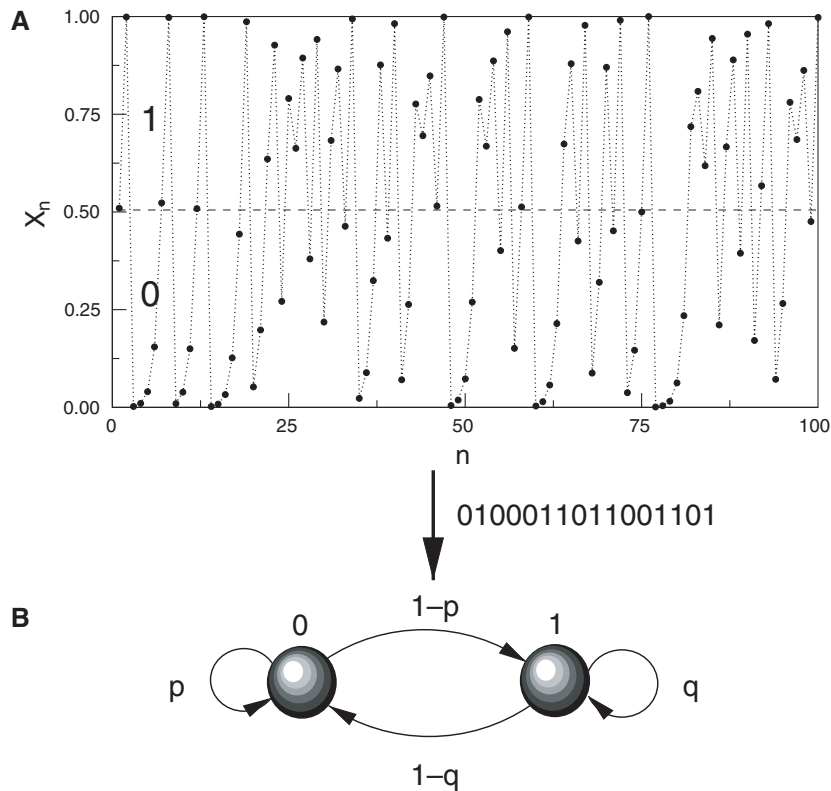


FIGURE 1.4. Order and chaos. The logistic map displays, for $\mu = 4$, very complex dynamics, here indicated as a sequence of black circles (A). If a binary partition is used in order to generate a sequence of ones and zeros, a stochastic sequence is obtained, which can be summarized in a transition diagram (B). In this picture p and q are probabilities, which for the logistic map give $p = q = 1/2$, as for a fair coin toss.

the ecological context, with other fundamental factors such as spatial degrees of freedom and evolutionary dynamics. As we will see, the results are often unexpected.

EMERGENT PROPERTIES

One key ingredient to be introduced in this book is the presence of emergent phenomena. Often, when looking at the macroscopic features of a given system, scientists have tried to find the origin of these

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properties by looking at the structure of their component parts. Such a view roughly defined the reductionist approach (Wilson, 1998). But the fact that the properties of the individual units cannot always explain the whole has been known from the earliest times of science. In this context, it is often said that the whole is more than the sum of the parts, meaning that the global behavior exhibited by a given system will display different features from those associated to its individual components. A more appropriate statement would be that “the whole is *something else* than the sum of its parts” since in most cases completely different properties arise from the interactions among components. As an example, the properties of water that make this molecule so unique for life cannot be explained in terms of the separate properties of hydrogen and oxygen, even though we can understand them in detail from quantum mechanical principles. The same limitations apply to biology: Some properties such as memory in the brain cannot be reduced to the understanding of single neurons (Solé and Goodwin, 2001). Life itself is a good example: nucleic acids, proteins, or lipids are not “alive” by themselves. It is the cooperation among different sets that actually creates a self-sustained, evolvable pattern called life. Over the last decades of the twentieth century the shortcomings of the reductionist approach had become increasingly apparent, and at some point a new type of view, known as integrative biology began to emerge.

Is reductionism the appropriate way of exploring complex systems? This is a debated issue. Within physics, extreme reductionists are not difficult to find. Advocates of reductionism, such as E. O. Wilson, have pointed out that modern science has been successful largely because of the analytic approach to reality (Wilson, 1998). But this view is being abandoned and replaced by a more global view of reality that takes into account the emergence of new properties. Let us consider one example.

Imagine a system composed by a set of n interacting species S_1, \dots, S_n whose populations are indicated as x_1, \dots, x_n . The interactions are schematically described in figure 1.5a for $n = 6$. The diagram indicates that each species requires the help of another one for its growth to occur: species S_2 needs S_1 , species S_3 needs S_2 , et cetera. This model was introduced within the context of prebiotic evolution: molecular species would cooperate to enhance their success by means of this so-called hypercycle (Eigen and Schuster, 1979). Species abundances can reach steady states, oscillate, or behave in very complex, unpredictable ways. The cooperation requires the presence of all components: the lack of a single species destroys the hypercycle.

In spite of its simplicity, the hypercycle displays an enormous set of dynamical patterns, and its relevance goes far beyond molecular repli-

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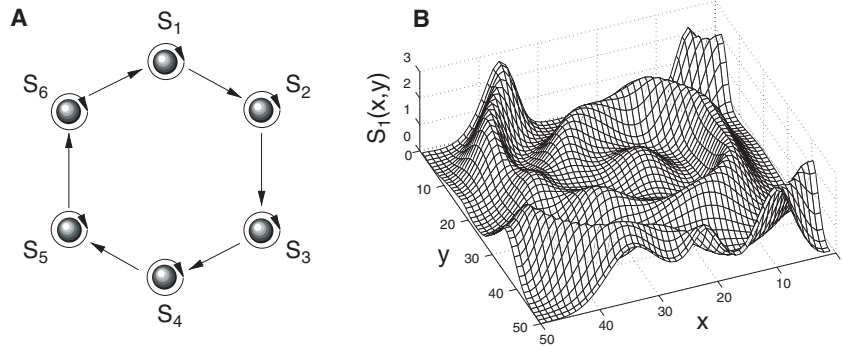


FIGURE 1.5. Emergence of long-range order in a set of cooperating species. In (A) the basic scheme of species interactions is shown. Here the reproduction of each species requires the help of another one. Such a dependence is closed, forming a catalytic cycle (the so-called hypercycle). When these populations interact within a spatially explicit, local context, complex structures, such as spiral waves (B) emerge. Here the population size of the first species $S_1(x,y)$ is shown.

cators (Maynard Smith and Szathmary, 1995; Cronhjort and Blomberg, 1997). Consider now a simple extension of the previous model. The units (molecules or organisms) move now in a two-dimensional spatial domain where initially we place random amounts of individuals of each species at each site. The domain can be a discrete square lattice of patches where each patch is linked to its four nearest ones. Movement takes place locally, and interactions (as they occur in reality) are also localized in space. Cooperation thus takes place in a well-defined spatial context where units diffuse toward the nearest locations, and interactions are limited to available molecules in a neighborhood. The surprise comes from simulating the previous model (Boerlijst and Hogeweg, 1991; Chacon and Nuno, 1995; Cronhjort, 1995) on a lattice. An example of this is shown in figure 1.5b, where the local concentration of the first species is shown for different points on a 50×50 lattice. In spite of the fact that interactions only occur inside a given patch and that molecules or individuals can only move step by step between nearest lattice sites, a large-scale structure has been formed. The size of this structure has a length that is similar to the whole spatial domain and thus its origins cannot be explained from the local nature of the interactions. The spiral wave is a common motif of patterns emerging in models of interacting populations (chapter 3) as a result of a collective synchronization phenomenon.

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Spiral waves emerge from a large number of nonlinear models with local interactions. The origin of the spatial structure can be properly explained once the transfer of information introduced by diffusion is taken into account. In other words, once local *interactions* among nearest sites are considered. These spiral waves cannot be reduced to the knowledge of the interactions among components and represent an emergent phenomenon with little relation to the species-specific features of individuals. Only interaction and diffusion rates are required in order to obtain a complete picture of the emerging structure. The impact of these structures on evolutionary responses has been explored by a number of authors (Boerlijst and Hogeweg, 1991; Boerlijst et al., 1993). Spiral waves in the invasion of parasites, and in a more general context spatially extended patterns, pervade ecological complexity and affect how ecosystems react against external stresses (chapters 3 and 5). Biodiversity patterns are also mediated by the fact that interactions are spatially localized. To a large extent, the limitations imposed by spatial interactions have a creative impact on ecological structures, allowing many different strategies to emerge (chapter 6).

ECOSYSTEMS AS COMPLEX ADAPTIVE SYSTEMS

Many macroscopic features of complex ecosystems emerge from interactions among their components. These patterns may, in turn, influence the further development of the interactions. As indicated by Simon Levin, ecosystems actually belong to a class of far-from-equilibrium systems known as complex adaptive systems (CAS). This type of system is characterized by several properties (Arthur et al., 1997; Levin, 1998), none totally independent among them. These include, together with far from equilibrium dynamics:

1. Localized interactions: Units in CAS typically interact with a limited set of neighbors. The constraints imposed by local interactions are responsible for the emergence of a large number of characteristic features, such as spatial patterns and coexistence among competing species (chapters 2 and 3).
2. Absence of well-defined top-down control: Complex patterns are obtained from local interactions and they largely influence the subsequent evolution of the system dynamics. Although top-down control appears to be present in ecosystem organization (chapter 6), it is seldom a strict one, often counterbalanced by bottom-up forces.

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3. Heterogeneity in network organization: Complex ecosystems have a network structure that pervades their behavior and response against perturbations (chapter 6). Such networks have a complex structure with a nested hierarchy of interactions. Evolution and adaptation are strongly influenced by these networks.
4. Adaptation: Ecological systems display adaptation at different levels. Species adapt to given external conditions (such as temperature fluctuations) and properly respond to them. At a larger scale, food webs may adapt to a particular regime of perturbations.
5. Evolvability, that is, the presence of mechanisms allowing new features to emerge: This is an intrinsic feature of many complex systems, from cellular to economic webs. The capacity to respond to changing conditions on an evolutionary time scale is obvious from microevolution to macroevolution (chapter 7).

Ultimately, the structure and universal properties of ecosystems are linked to evolutionary forces operating at different scales. But these forces operate within an ecological context and thus both terms cannot be separated. What are the components of evolution that shape ecological patterns?

Evolution and the Ecological Theater

Ecosystems are the result of historical processes. The building of an ecosystem involves, on short time scales, path-dependent processes defining ecological succession. On larger time scales, species themselves change and coevolutionary dynamics arise. Succession is illustrated by the progressive colonization of an abandoned field, eventually ending up in the building of a mature forest. Since succession is historical, different communities are obtained starting from a given regional species pool. Contingency thus plays a role. But what is the impact of path dependence on the overall ecosystem's structure? The analysis of mature communities reveals that, beyond the specific composition of the final community, the same macroscopic traits of community organization are universal. Examples are provided by the network structure of the food and mutualistic webs or the patterns of species abundance (chapter 6).

Such universality reminds us of a different perspective of evolutionary change emphasizing the role of fundamental constraints (Kauffman, 1993; Goodwin, 1994; Solé and Goodwin, 2001). These theories suggest that basic, universal laws of organization shape the large-scale architecture of biological systems. Some of these basic laws and principles are presented in chapters 2 and 4. They result from a limited spectrum of dynamical patterns, the presence of inherent multiplica-

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tive processes (a species with a higher population is more likely to leave more offspring, see chapter 7), and to conflicts arising from competitive forces. The latter is the case in the levels of diversity allowed in a given habitat and how species turnover proceeds: There is a conflict between forces increasing diversity (immigration and speciation) and those reducing it (due to interactions). Such a conflict (chapter 4) can explain the emergence of universal patterns of community organization (chapters 6 and 7). As it occurs in some physical systems, conflicting constraints often end up in a very small repertoire of patterns of organization, which we recognize as universals.

The previous observations actually connect with the suggestion that natural structures result from a process of tinkering (Jacob, 1977; Solé et al., 2002b). The possible and the actual would differ strongly due to constraints intrinsic to the universe of potential structures. In this context, the dynamics and evolution of complex ecosystems would be shaped not only by selection and history but also by fundamental laws and intrinsic constraints.