

CHAPTER 8

EMERGENCE IN ECOLOGICAL SYSTEMS

JAMES A. DRAKE*

*Complex Systems Group, Department of Ecology and Evolutionary Biology,
University of Tennessee, Knoxville, TN 37996*

**Corresponding Author: Phone: 1-865-974-2371, Fax: 1-865-974-3067, E-mail: jdrake@utk.edu*

MICHAEL M. FULLER³

*Complex Systems Group, Department of Ecology and Evolutionary Biology,
University of Tennessee, Knoxville, TN 37996, USA*

CRAIG R. ZIMMERMANN

Department of Biological Sciences², Texas Tech University, Lubbock, TX 79409, USA

AQ1

JAVIER G.P. GAMARRA

Department of Renewable Resources³, University of Alberta, Edmonton, AB, Canada T6G 2H1

8.1	Abstract	158
8.2	Introduction	159
8.3	A Brief Account of Emergence	160
8.4	A View of Ecological Systems	163
8.5	Attractor Processes: Inadvertent Authors of Emergence	167
8.5.1	A scenario	169
8.5.2	Uncharted territory	173
8.5.2.1	Transience, dynamical capture and collapse	173
8.5.2.2	Interactions in the attractor space	175
8.6	Conclusions: When you can't get there from here!	178
8.7	Acknowledgments	179
8.8	Literature Cited	179

8.1 ABSTRACT

The quest to understand animate nature, its origins, current state and future course, its dynamical underpinnings and interface with the physical world, is surely the tacit aspiration of contemporary ecology. As a field of inquiry, academic ecology emerged in earnest from the descriptive realm of natural history in the late nineteenth century when observers of nature, pondering similarity and difference, sought cause. Adopting the classic approach to science, ecologists further described, but also dissected, modeled, conceptualized, and manipulated the parts of ecological systems. What emerged is the modern framework of ecology, built upon the struts of population dynamics and tempered by interactions between species, all within an environmental context.

Yet with the Earth as a laboratory containing millions of extant and evolving species, the number and variety of plausible ecological studies is functionally inexhaustible. A quick glance through any ecological journal reveals surprising novelty and nuance at every turn. Hence, one is compelled to ask whether progress in ecology is best served by strict adherence to a reductionistic program and unending description, or whether this approach should be blended with more general and epiphenomenological complements. This question is apropos to all of science. Attempts at such a synthesis are well underway sparked by the realities of a complex and decidedly nonlinear nature. In this complex nature *one + one* need not always equal *two*, and the simple logical operator *if-then* requires *else*. In ecology, *if* and *then* produces a highly contingent mapping of their own accord. Add *else*, and we have the fundamental reason for the diversity of nature and the nuance of its expression. What then are mechanisms, the holy grail of reductionist ecology, but manifestations of an emergent nature? Nature can be described by the action of mechanisms explicit in our logical operator. Yet understanding nature requires a deeper knowledge of how the action of the mechanism emerged.

Here we present a solution to the recalcitrant problem of true or hard emergence, the existence of which has been debated, demonized, and exalted for centuries. We suggest that emergence is hidden within the attractor space of dissipative dynamical systems, or more precisely the interaction between multiple attractors. Our arguments while tentative, suggest that two independent systems can interact in the attractor space and produce a persistent attractor that are essentially offspring of the parents. Emergence in this case is absolute because no trajectories exist linking the child to either parent. You cannot get there from here. Our arguments are based on a long series of experimental studies that have explored the assembly or construction of ecological communities. We offer this notion of emergence as a general solution to all things emergent independent of any particular system.

Regarded from the broadest possible viewpoint, the vegetation of the earth presents itself as a flowing stream, undergoing constant change. It is not a simple stream but a "braided" one, of enormous complexity, with its origin in the far distant past. . . . Vegetation as we see it today is thus a mere cross section of this complex stream. (Cooper 1926)

8.2 INTRODUCTION

The singular ambition of science rests in the orchestration of two distinct yet entangled constructs, the realization of pattern, structure and process, and its antecedent implicate cause. Yet, as with any human concern, perception and description are intrinsically subjective. Despite attempts to address nature from within structured intellectual formalisms such as the scientific method, reality is simultaneously elusive and readily apparent, the observers' perspective making it so. In many cases, increasingly precise measurement and finer-scale description serves the observer well, by revealing the internal workings of some larger system. However, it is often the case that some macroscale behavior fails to yield to dissection, it is irreducible and the pieces belie the whole. It is here where traditional approaches to science falter. When further reduction proves inadequate, intellectual patches are developed within the existing framework of understanding, or the problem is cast aside as unsolvable or deemed beyond the domain of science. The epicycles of Ptolemy serve as a fundamental lesson. Ptolemy gave elegant structure to patterns observed in the night sky, referential to a central and stationary Earth. Increasingly anomalous observations, however, forced Ptolemy into increasingly convoluted machinations in order to preserve his geocentric cosmology. The cataclysmic revelation of Copernicus, that the Earth was but an inconsequential spot in the cosmos shuddered the foundations of science and society.

In science, progress is typically slow and methodical peppered with bursts of insight and rapid evolution—punctuated thought as it were (Kuhn 1962). Modern science seems to be in the midst of such a revolution, driven by the profound realization that nature in all its forms exhibits fundamental similarities despite profound differences in the system at hand. Time and space are one, nature is fractal and self-organizing, networks emerge with common architecture, and structure can be simultaneously complicated, complex, and simple. Are there fundamental organizing rules at play, and if so what are they and how can they be revealed? Surprisingly, ecological systems provide the ideal platform from which to address this question. Not because they are simple and readily manipulated but because they have proven so difficult to understand. There is no contradiction here because the analytical difficulties posed by these systems are a direct reflection of their complex nature.

Ecological systems are temporally and spatially contingent, a reflection of history tempered by contemporary mechanism and process. The building blocks that comprise these systems are not fixed entities; they reproduce, move, evolve, and interact in myriad fashion. As such, the rules that govern system structure and function, and define the realized attractor space, are continually rewritten. This fluidity is constrained in a fashion similar to Jacob's (1977) evolutionary tinkerer, and as such new rules do not necessarily imply complete novelty in structure and behavior (Solé et al. 2003). Moreover, ecological systems are embedded within a complex and fluctuating physical environment that exacts

a substantial controlling function. Consequently, systems observed today have derived much of their structure from history to such a degree that experimentation in real time is largely incapable of distinguishing between the cause and maintenance of structure (Drake et al. 1996). This epistemological dilemma is further amplified in the arena of evolutionary time, exemplified by questions about the origin and maintenance of recombination and the construction of phylogenies. The *ghost of systems past* has proven to be a serious impediment to understanding nature, and remains a fundamental challenge as we evaluate proximate explanation and hypothesis in the face of a complex ecology (Ulanowicz 1997, 2000, Wagner 1999, cf. Leibniz 1697).

Our present goal is to offer an exemplar for understanding the sources of irreducible complexity in ecological systems. Our concept of emergence is founded on the nature and behavior of attractors, and interactions between attractors that occur in dynamical systems with many degrees of freedom. Recent theoretical and empirical studies in nonlinear dynamics have revealed startling intricacies and unfathomable behaviors during the temporal evolution of even the simplest of dynamical systems. Attractors collide and annihilate one another; fragments of trajectories wander through an infinite space, and attractor basins contain holes sharing solutions with other basins. We suggest that hidden deeply within the exotic behavior of such systems rest the keys to understanding the genesis of emergent properties *and* structure. As a foundation to our arguments, we provide perspectives on two essential issues: first, a brief account of emergence highlighting our perception of this crucial phenomenon; and second, a discussion of the general nature and operation of ecological systems.

8.3 A BRIEF ACCOUNT OF EMERGENCE

In a colloquial venue, the terms *complex* and *complicated* are often synonymic. Within the realm of dynamical systems, however, these terms assume unique meanings. Complicated systems may actually be quite simple, while simple systems may be complex. Systems that are complicated are typically deemed so because they contain a dizzying array of constituent parts. Yet a mapping of these parts, linking piece to piece much like an auto mechanics repair guide or architect's blueprints, completely describes such systems. Such systems are simple. Complex systems, on the other hand, cannot be so readily decomposed, even if they contain but a few pieces. They comprise a class of systems that self-organize, exhibit nonlinearities, nonequilibrium behavior, and feedbacks across scales that, in concert, are expressed in some macroscopic fashion. Most importantly perhaps, they are historically contingent systems. For example, the butterfly attractor of Lorenz with its fractal structure, food web topologies that confer invasion resistance, the existence of alternative community states, and indeed life itself are all macroscopic reflections of

mathematically permissible dynamical themes. It is important to note that historical contingency, determinism, and in fact moderate doses of randomness are not at all mutually exclusive.

How do even simple levels of organization, structure, and pattern arise to acquire a dynamical character in the first place? One means is through self-organization, which has been posited as a process capable of producing such structure from simpler entities (e.g., Ashby 1947, Nichols and Prigogine 1989, Solé and Bascompte 2006). It is a generative device of nature, and all definitions of self-organization contain the following premise—structure and organization develop in the absence of external impositions or forcing functions providing directionality. Implicit is the requirement that thermodynamic realities, particularly the envelope of constraint created by entropy, and the existence of an inviolate mathematics are internal to the system. Whatever the pieces of the system, and the manner in which they encounter one another, entropic realities and mathematic plausibility are capable of selectively identifying and distinguishing between alternatives. The only directionality provided is one of information gain against the gradient provided by entropy, and the constraints imposed by historical contingency. Viewed in this fashion, self-organization is a systems response to its own existence rather than a process per se. When bits and pieces of nature interact, a manifold or space is created which outlines plausible configurations and behavior. Self-organization is some vector of movement on that manifold.

Self-organization produces a structure, collective or ensemble that exhibits properties in addition to those of the constituent pieces. Organisms, for example, have properties lacking in their constituent parts—genes, cells, and molecular pathways. It is here that we encounter the concept of emergence and two irreconcilable schools of thought. All definitions of emergence have at their core the some form of irreducibility, whereby properties manifest at a given level of organization are not present at lower levels of organization. The reductionist school readily accepts the existence of such properties but with two important caveats. First, these properties are either a consequence of hierarchically organized structures or are a function of large-number systems and are statistical in nature. Second, they are irreducible only in the sense that they are manifest at specific levels of organization. While these macroscopic properties vanish at lower levels of organization, the parts of the system contain all the information needed to understand the property. This form of emergence has been variously termed and conceived as *soft*, *weak*, *incomplete*, *aggregative*, *contingent*, or *contextual* emergence (e.g., Simon 1962, 1996, Wimsatt 1997, Davies 2004, Emmeche et al. 1997). The complex-holist school, however, suggest that a more formidable form of emergence exists in nature where irreducibility is inviolate. Termed hard or strong emergence, the essential feature of such systems is a complete mechanistic decoupling between the property and the elements of the system,

a phenomenon captured by the common phrase “the whole is more than the sum of the parts.”

At first glance hard emergence seems nonsensical, invoking wizardry and in violation of foundational mathematics. How is it possible that the very pieces that comprise a system cannot be used to explain the properties and even perhaps the structure of that system? Confronted with such a system and property, the reductionist school argues that it is a contingent class of properties awaiting explanation, and a consequence of observer naiveté, or that it simply is an intractable problem for the moment (Crutchfield 1994). For example, before the airfoil was understood, bird flight was thought to be the result of so much of wing flapping. Of course this view ultimately implies that given any set of pieces, all possible macroscopic behaviors can be predicted (cf. Davies 2004). If so it should be possible to fully map the neural network of an individual and thereby understand sentience, or given a handful of atoms, distinguish between that which will produce a frog, a bird or some inanimate object (cf. Borges 1941). Whether such a feat is logistically possible is immaterial to the argument, systems exist that cannot be approached through the myopia of reductionism.

Distinguishing between something that might be softly emergent, but not yet understood, and the antithetical postulate of hard emergence creates a kind of Gödelian conundrum. One that cannot be resolved until the system either yields to decomposition, or it is proven that decomposition fails and the genesis of the property is otherwise understood. It is insufficient in our view to simply state, or even demonstrate that a property is emergent having dissected the system to the very asymptotic levels of existence. Nature is simultaneously pieces and wholes with primacy belonging to neither. Uncovering the means by which pieces and wholes generate properties and structure of the hard kind is central to comprehending the nature of nature (Laughlin et al. 2000).

Approaches to understanding the evolution of emergence have had a long and discursive history in virtually every academic field. The result being a vast and intriguing literature, one that is frequently insightful and elegant but often burdened by obfuscation, assertion, philosophical meandering, and even mysticism. Among the more promising efforts, emergence has been cast in terms of a grammar, a set theoretic, an entropic consequence, a quantum phenomenon, a formal logical device, a dynamical consequential, an information theoretic, and a system of variously interacting agents to name but a few. It is not possible for us to provide a conceptual review of such approaches here; hence we invite the motivated reader to explore the works of Mill 1843, Pepper 1926, Ablowitz 1939, Blitz 1992, Rosen 1985, 1991, Klee 1984, Baas 1994, Collier and Muller 1998, Solé et al. 2003, Emmeche et al. 2000, Bonabeau et al. 1995, Schneider and Kay 1994, Holland 1998, Salthe 1985 and Bar-Yam 2004. And from there, step through the door, or perhaps the looking glass, into discourses on one of most captivating and beguiling concepts of human thought.

8.4 A VIEW OF ECOLOGICAL SYSTEMS

Ecology is a singular and synthetic discipline, a blend of biology, mathematics, the physical sciences, and philosophy. Consequently, the fundamental nature of ecological systems remains open to definition, a fact reflected by vastly different conceptualizations. Many believe that ecological systems, communities for example, are compositionally limited by the challenges of the physical environment and dispersal. Surely the environment and species source pool play a powerful role, but such a view fails to explain the vast differences in community organization observed in apparently similar environments. Those who see the world in stochastic and neutral terms have invoked a chance to explain such differences, and indeed chance does play a powerful role in nature. Yet alternative states are recurrent themes and $N!$ states are not observed. In a similar fashion, some see a largely idiosyncratic nature that is hopelessly complicated by historical contingency. Contingently driven, yes, idiosyncratic, perhaps on occasion, but in general this idiosyncrasy stems from a lack of historical information. Most see a finer structure to nature, one driven by mechanisms such as competition and predation, variously tuning food web patterns and directing successional change. Often, however, the focus of this approach is necessarily limited to the presently observed state.

Stephan Forbes, Frederic Clements, Umberto D'Ancona, Lorenzo Camerano, Eugene Odum, and Ramon Margalef among others anticipated many of the more refined notions of ecological reality long ago. While the ideas have been there, the quantitative information and analytical machinery needed to exploit that information, is only now becoming available. At present we have much more sophisticated models and the computational power needed to explore their behavior. We have numerous journals full of experimental results and an explicit understanding of many mechanisms and processes. Yet we have little generality. Ecology is replete with examples and counterexamples such that any premise is laden with qualification. Predation, competition, and disturbance, behave in one fashion here but not there, and relative abundance and diversity correlate with variables X here and Y there. As a result some have suggested that nature is highly idiosyncratic, dooming ecology to a science of case studies. This challenge, in a very real sense, provided the impetus behind macroscale approaches (Brown 1995, Brown and Maurer 1989, Gaston and Blackburn 2003). Still, the cogs and gears of ecology's own epicycle burden attempts at synthesis because the systems are being approached as if they were simply complicated and in reductionistic fashion.

What we see in the real world—species, individuals, populations, guilds, communities, mechanisms, and processes—are all transient and at radically different scales. A community described a century ago is no longer as described, and the community described today is in route elsewhere. While concepts like species evolution and community succession have played a role in ecological thought for over a century, the paradigms of ecology remain largely structured

around short-term, readily observable phenomena. Any given system can be described in considerable detail over some period of years, perhaps decades; but such analyses constitute a simple snapshot in time. As a result, examinations of the role of competition, predation, and invasion reveal a contingent explanation of those dynamics. We have argued elsewhere that the most significant question is not precisely *how* a mechanism operates here and there, but rather the ontological production of that mechanism (Drake et al. 1996). This does not diminish the primacy of ecological experimentation in academic ecology, but rather it places it into an essential and broader developmental context (Ulanowicz 1997).

We view ecological systems as dissipative, self-organizing, historically derived, nonlinear systems that are typically far from equilibrium. Living systems not only exist within the context of entropic reality (Schneider and Kay 1994), they exploit it. Structure and organization are hierarchical spanning many levels of organization linked by direct and indirect interactions and accompanied by positive and negative feedbacks. These feedbacks provide integrative information across scales tuning observed structure and adjusting hierarchical organization. Within and between these levels, self-organization and the dynamical constraints and opportunities imposed by nonlinearity couple with natural selection, and constrain system development to a finite range of structures and behaviors or attractor basins. The manners in which the mechanisms of ecology operate are so defined, with observed structure and pattern as a consequence.

So described, these systems exhibit sensitive dependence to events occurring in system development creating a multiplicity of possibilities (Cushing et al. 2003). Even apparently inconsequential differences in the initial abundance of a population can lead to radically different behaviors, the signature of chaotic population growth (Costantino et al. 1997, Hastings et al. 1993, May 1974, 1976). While there is no single solution or even a fixed attractor for real ecological systems, there are recurrent themes. For example, we see regularities in food web patterns, species relative abundance, and evolutionary convergence to similar solutions. But even these recurrent themes give way to new solutions as the context of the system changes. The environment, the appearance of evolutionary novelties, and species invasion, are all eminently capable of changing the rules and overriding the control exacted by an attractor.

Ecological attractor basins typically contain multiple local attractors, producing the alternative states commonly observed. The realization of one state with deference to another occurs for many reasons ranging from even the most trivial of variations in initial conditions, to chance events with subsequent dynamical consequences, and the relative roles of determinism and indeterminism during development. For example, many studies have shown that simple modifications in the timing of species arrival in a community enable new portions of the attractor space that were previously unavailable (Drake 1991,

Drake et al. 1993, 1996, Drake et al. in press, Fukami 2004a). The consequence of this adjustment in the attractor is profound, influencing species diversity, productivity, invasibility, the action of mechanisms, and patterns of species coexistence (Gamarra et al. 2005, Fukami and Morin 2003, Cardinale et al. 2002, McGrady-Steed et al. 1997).

As species evolve, invade, or disappear from a system, the rules may change to such an extent that the original attractor is destroyed all together and is replaced with a new one. For example, during assembly studies Drake (1991) found that alternative attractors arose due to small variation in the number of eggs carried by colonizing *Daphnia*. Despite identical population sizes upon invasion, this difference in fecundity led to sustained oscillations in one treatment while no such oscillations occurred in other treatments. A consequence of this difference was variation in community vulnerability to invasion. Even in the absence of these structural changes, *crises* can arise in nonlinear dynamical systems having profound consequences for system development and subsequent structure (Vandermeer and Yodzis 1999, Gamarra et al. 2001). If all of these sources of complexity were not enough, the collective and emergent properties inherent in an ensemble of species further refines and controls structure. Hence, we have an immensely complex nature manifest in millions of species.

This leads us to suggest that attractor mechanics, the dynamics of dynamics, is the key to a deeper ecological understanding. The answers are partially found in mathematics and its rich catalog of dynamical behavior. The relevance of these formal axiomatic systems has been established by a number of recent studies that have compared model expectation with real world behavior. For example, clear evidence exists documenting the existence of chaotic dynamics (Costantino et al. 1995, 1997), and behavior similar to a Hopf bifurcation (Fussmann et al. 2000) in real populations. Self-similarity has been observed in both structure and time series in plant biophysical geometry (Enquist and Niklas 2002, West et al. 1999a, b), and landscape structure reflects fractal pattern (Milne 1992, Solé and Manrubia 1995). The pieces of ecological systems and the systems themselves *can* behave as offered by contemporary mathematics. Yet an essential element is missing, a developmental complement to natural selection and self-organization. We offer that this element is deeply hidden in the fundamental nature of attractors and is manifest as emergence.

We are cognizant of the pitfalls that accompany assertions that some property or structure is emergent. However, we have additional insight from direct experimentation that we believe points the way to an explanation of emergence (Drake 1991, Drake et al. 1993, Drake et al. in press, Cadotte and Fukami 2005, Cadotte in press, Fukami 2004a, b, Fukami and Morin 2003; see also Drake 1990, Warren et al. 2003). These experiments focused on the construction or assembly of ecological communities in the highly controlled confines of the laboratory (Figure 8.1). For example, vastly different ecological communities

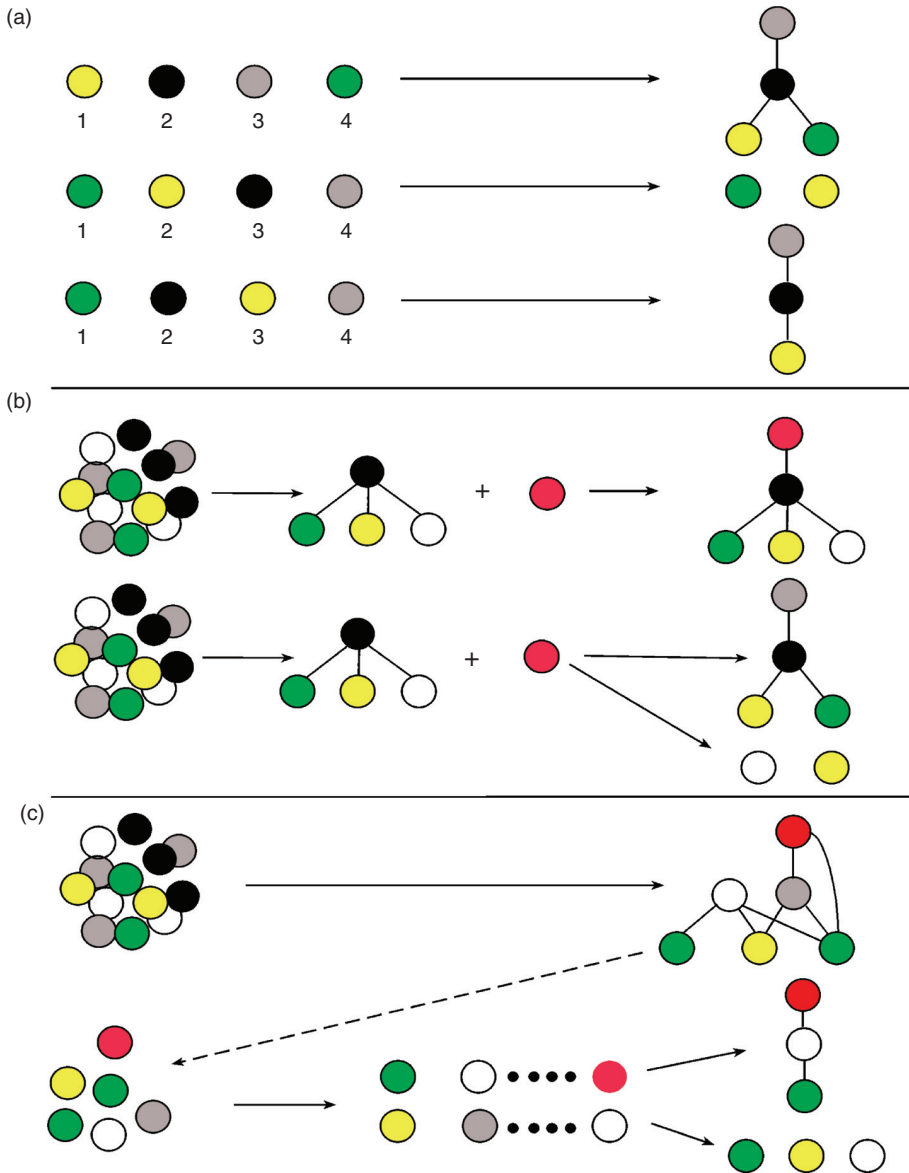


Figure 8.1. Experimental results depicting the rich dynamical behavior exhibited during the construction or assembly of ecological communities. A fixed species pool, depicted as the cluster of species in panel *b*, was established from which populations of each species were introduced to an initially sterile environment. Using different invasion sequences (e.g., species *one* colonizes at time *t*, species *two* colonizes at time *t*+1, and so on) as treatments, the mechanics of community assembly were explored. Panel *a* documents the effect of altering colonization history. Alternative community states are readily generated, representing the activation of specific attractors within the basin of

can be generated from a finite species pool, as a function of colonization sequence and sensitive dependence to initial conditions (Figure 8.1). In fact sensitive dependence need not be constrained to some starting point, rather it exists in compound fashion in time series and is readily switched *on* and *off* by events as mundane as the order and timing of species colonization and hidden differences in fecundity. This switch is capable of inducing purely deterministic and indeterministic behavior from the same set of species and without exogenous forcing.

Are these behaviors the result of emergent properties and the emergence of structure? We believe so because the structures ultimately produced by assembly, and the dynamical differences that developed, could not be recreated using only those species present in the final community state. These structures represent pure irreducible novelty, because the final community state is fully decoupled from the attractor series that created it. The system effectively does not contain a solution to itself; hence the pieces cannot describe the whole. In what follows we provide a solution to genesis of emergence.

8.5 ATTRACTOR PROCESSES: INADVERTENT AUTHORS OF EMERGENCE

An attractor is not as simple to define as reason might suggest. As ecologists, we have a fundamental feel for the term acquired through our cognitive, semiotic and derivative philosophical perspectives (Beisner et al. 2003, Cuddington 2001, Egerton 1973). We perceive change in nature—population growth and decline, succession, convergence, divergence, evolution, species turnover, and extinction—trends in one direction or another. As mathematicians our formal axiomatic constructs offer explicit, though varied, definitions of this dynamical consequence (Ruelle 1981, Milnor 1985, Strogatz 1994). In general, dynamical systems possess one or more attractors, solutions to the dynamics towards which the system evolves over time. For example, the familiar carrying capacity (K) of a population growing logistically in continuous time is an attractor of the dynamics. Much like the course of a marble released into a bowl at various starting points within that bowl, a population's initial size creates an alternative trajectory or route to the attractor.

attraction. Further, some assembly sequences were perfectly replicable resulting in identical communities. However, other assembly sequences were never replicable because the dynamical space created by the sequence effect was either indeterministic or *apparently* indeterministic. Panel *b* illustrates the occurrence of assembly trajectories derived from alternate invasion sequences that crossed in time. That is, at a common point in their development these communities converged to the same structure. In both cases the communities were probed by introducing that same species, illustrated using the red dot. In one trajectory the invader was always successful, while in the other it always failed. Panel *c* presents the Humpty Dumpty effect. Here, an assembly trajectory was employed that produced perfectly replicable end-point communities. Subsequently, a species pool was recreated from these species alone (follow the dashed line), after which an attempt was made to reconstruct the end-point community. Reconstruction proved impossible.

The set of all possible initial conditions defines a basin of attraction, a virtual asymptotic roadmap of the dynamics. This roadmap may lead exclusively to a fixed point like a carrying capacity, or to a repeating sequence of states as in the case of a limit cycle (Ruelle and Takens 1971). The attractor can also be *strange*, having a noninteger dimension or exhibit chaotic dynamics. In nonlinear systems, an attractor basin boundary is often a place of extraordinary events, ranging from trajectory leaps into alternative domains of attraction to collisions with the boundary itself inducing bifurcation and subsequent chaos. In the case of our bowl analogy this boundary is clearly defined in the three-dimensional space of human experience. Should another bowl be present, our marble is at the basin boundary if it has a limit of points within each of the basins. But where the marble goes from there becomes a complicated and even complex mathematical situation (Greborgi et al. 1983a, b, c, Alexander et al. 1992).

Of course there are considerable differences between the marble and its animate analogue. Species interact with other species and in so doing create a high dimensional system. This situation is akin to our marble variously interacting with other marbles. Even more of an aberrant, species evolve; hence the marble changes mass or shape, and as a consequence the attractor and its basin change (Wright 1932, Van Valen 1973, Gavrillets 2004). In many systems reducing dimensionality for the sake of tractability is a simple task. While common practice in both theoretical and experimental ecology, such dimensional reduction is simultaneously an essential and dangerous practice. Our *ecology* is based on tractable mathematics and logistically feasible experimentation. In light of these additional complexities, we find it essential to offer a hybrid view of the attractor and series of conjectures, which we outline below. This view is attentive to the mathematics, but not fully constrained by the limits of our experimental, mathematical, and computational circumstance.

Because attractors are invariant to the dynamics, asymptotic solutions have until recently been the natural focus. However, complex systems demand both a finer and broader scale of observation. Classically, the dynamical middle ground has been viewed as the means to an end, rather than the source of mechanism, structure, and process. Hastings (2004) provides an excellent review of this issue, pointing out that transient dynamics are entirely relevant to understanding systems at commonly viewed time scales (Hastings 2001, Hastings and Higgins 1994). We take Hastings view a step further and suggest that asymptotic behavior is seldom realized in the real world because *nature* happens. Invasion, disturbance, evolution, species movement, and fluctuating resources to name a few, variously eliminate, reshape, and replace attractors altogether. One might ask then, what value is there in understanding an attractor's short-term behavior or long-term solution given this fickle nature? The answer to this query is a simple duality with profound implications. An attractor is defined by the components of some system under plausible dynamics given that set yet attractors interact and evolve in space and time.

8.5.1 A scenario

Consider the behavior of Verhulst's logistic model of population growth brought to fruition by May 1976 (see also Verhulst 1845, 1847, Feigenbaum 1978, 1979). Many excellent expositions of the properties of this and allied systems are available and we refer the interested reader to May 1976, Strogatz 1994, and Ott et al. 1994. This simple equation cast as a quadratic recurrence equation, has the form:

$$X_{n+1} = \lambda X_n(1 - X_n) \quad (8.1)$$

which is typically referred to as the logistic map. The behavior of the logistic map can be visualized by iteration assuming some starting value of x_n across some range of values of λ , the growth rate. For example, the first three iterates are:

$$x_1 = \lambda x_0(1 - x_0)$$

$$x_2 = \lambda^2(1 - x_0)x_0(1 - \lambda x_0 + \lambda x_0^2)$$

$$x_3 = \lambda^3(1 - x_0)x_0(1 - \lambda x_0 + \lambda x_0^2)(1 - \lambda^2 x_0 + \lambda^2 x_0^2 + \lambda^3 x_0^2 - 2\lambda^3 x_0^3 + \lambda^3 x_0^4)$$

For a range of values of λ over x (where $x \approx 3.569$), no simple attractor exists as can be seen in the well-known period doubling route to chaos (Figure 8.2). Among the more interesting properties observed in nonlinear models such as the logistic map is the occurrence of extraordinary dynamical changes over time, periods of chaotic and regular behavior, and the sudden appearance of persistent cycles over some ranges of λ . While indeed complex there is also generality.

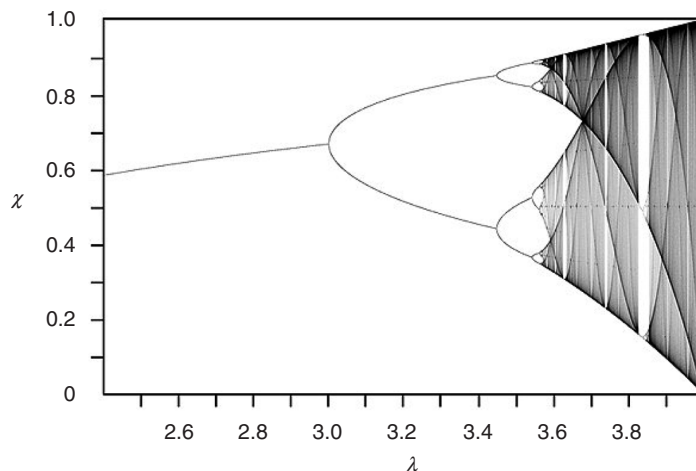


Figure 8.2. The classic logistic bifurcation map revisited. This common numerical simulation illustrates a period-doubling route to chaos that results as a single parameter is tuned.

For example, any system that can be described by a logistic map follows a period doubling route to chaos in identical fashion yielding a similar fractal structure (Feigenbaum 1978, 1979, Grossmann and Thomae 1977, Coulet and Tresser 1978). Scaling relationships such as this are suggestive of common developmental themes and underlying general rules.

At this point we explore a simple scenario. Consider two independent systems X and Y each residing somewhere on some attractor. Each system has the form of Eq. (8.1) with unique parameter values. If an interaction develops between these systems the dynamics become coupled and the individual attractors vanish. We now have a system of two equations:

$$X_{n+1} = \lambda_x X_n(1 - x_n)(1 - q) + q\lambda_y Y_n(1 - y_n) \quad (8.2)$$

$$Y_{n+1} = \lambda_y Y_n(1 - y_n)(1 - q) + q\lambda_x X_n(1 - x_n) \quad (8.3)$$

where q is some coupling value. Clearly when $q = 0$ there is no coupling and populations are independent. When $q = 1$ the equations are coupled and become a reciprocal input-output pair. Coupled forms of nonlinear models have received considerable attention revealing intricate and surprising dynamics (Kaneko 1989, Heagy et al. 1994, Strogatz and Stewart 1993). However, defining appropriate coupling functions remains guesswork despite the fact that this term is at least as important as the base equations. It is possible that the dynamics observed in nature are those that “play well” with the universe of plausible coupling functions. Regardless, the properties of such mathematical representations can be reconstructed because time is fully reversible. This fact limits the emergence of properties of such systems to the soft form, regardless of the dimensionality of the system and its spatial extent. Whether or not such feats are computationally feasible is irrelevant.

Now imagine two sets X and Y , where $X = \{x_a, y_a\}$ and $Y = \{x_b, y_b\}$, each containing a pair of identical uncoupled systems with unspecified but deterministic dynamics. Assume X and Y are replicates, with the members of each set serving as precursors to the establishment of metaset dynamics. In the uncoupled state the paired systems are autonomous but upon interaction this autonomy is lost, and as above we have coupled equations. Assuming identical initial conditions the trajectories of each system are mirror images, moving in lockstep on the attractor. If the initial conditions of x_a and x_b vary, the models exhibit sensitive dependence but the attractors and their basins remain identical, only the route to the solution has changed. This symmetry occurs whether x_a or x_b become coupled with their counterparts at $t = 0$ or some $t > 0$, such points remain initial conditions in X and Y .

However, relaxing the temporal congruity among $\{x_a, x_b\}$ and $\{y_a, y_b\}$ such that coupling occurs at different points during the evolution of each system, redefines the plausible trajectories to the attractors. Destroying the lockstep symmetry observed above. If, for example, x_a of pair $\{x_a, y_a\}$, had begun to exhibit period four oscillations, while x_b of pair $\{x_b, y_b\}$ was in a regular or

chaotic realm, upon initiation of their respective metastructures the newly coupled systems exhibit *phenotypic* differences.

Consider what happens when two previously independent systems such as *A* and *B* interact. For example, suppose two previously independent communities are connected, such that individuals can migrate from one community to the other. If the dynamics of the two systems differ (as above), the influence of one community on the dynamics of the other may be asymmetrical. For example, different population dynamics (e.g., limit cycles versus chaos) generate different rates of reproduction. If the rate at which colonists arrives from system *X* to system *Y* is determined by the reproduction rate, then the system with the higher rate will exert a greater influence on the dynamics of the coupled metasystem. For a given species, such asymmetry may mean the difference between invasion success and failure. Criminale et al. (2004) have provided support for this notion (Matthews et al. 1991, Pastor et al. 1993). They examined the “competitive interaction” between the dynamics of a set of coupled systems, where one system exhibited a strange attractor and the other a limit cycle. In the absence of external forcing (such as an imposed signal), they found a striking asymmetry in effect contingent upon which attractor type forced the other.

Laboratory experimentation conducted by members of the Complex Systems Group has demonstrated that attractor forcing similar to that above occurs in ecological communities (Cadotte 2005, Cadotte in press, Drake et al. 1993, Fukami and Morin 2003, Cadotte and Fukami 2005). For example, Drake et al. 1993 constructed sets of interconnected community patches that were derived from a common species pool (Figure 8.3). Movement of species occurred as discrete unidirectional events from the source pool to increasingly distant patches, similar to the scenario posed above. This was accomplished by transferring a small subsample from a source community to an adjacent “downstream” community. The rate at which different species arrived at a given downstream patch was not manipulated and tended to be proportional to the species population density in the source pools. Population and community dynamics occurring in source communities served as forcing functions to the dynamics occurring in downstream or target systems, and so on throughout the landscape of patches. Differences among replicate source communities sometimes developed suddenly, most likely because sensitive dependence was induced by small variation in subsamples. As one might expect, differences readily appeared among previously identical target systems. AQ2

Still time is reversible in our model, but we now have a means of generating a visible distortion between pairs of dynamical systems. Are there circumstances under which time can become functionally irreversible, or where some forward and reverse operation on a system produces solutions that differ in their stability? The phenomenon of hysteresis provides a well-known example of such an asymmetry (Krasnosel'skii and Pokrovskii 1989). Here, a system subject to a symmetric change in some controlling parameter fails to return to its original state. Rather like increasing the volume of a radio by say 10 dB, but

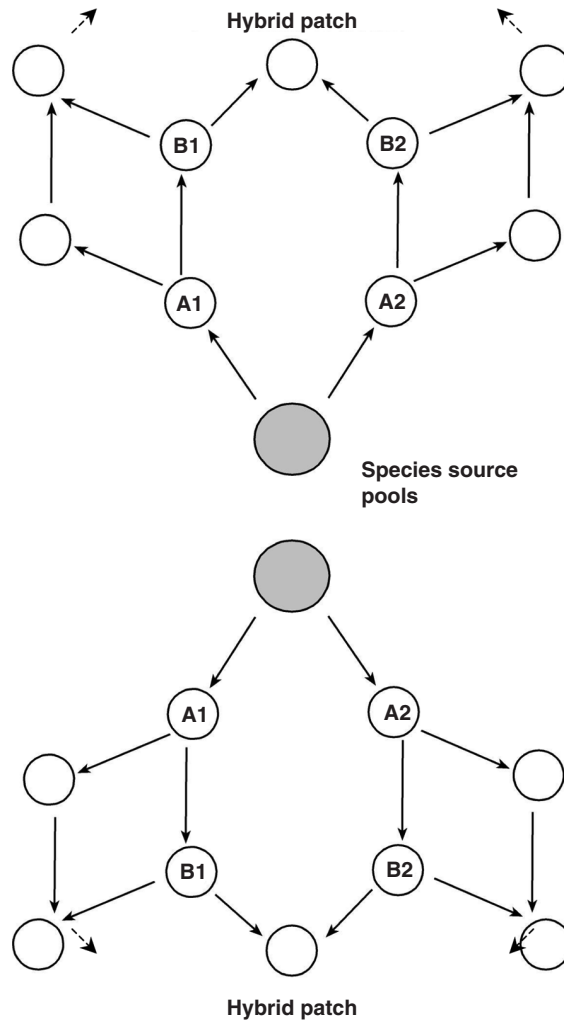


Figure 8.3. A small portion of the landscape topology from a set of experimental studies that explored a spatially extended, laboratory based ecological landscape. Species source pools (grey circles) were assembled by sequentially adding species from a defined species pool of common pond organisms. Arrows indicate colonization pathways. Community patches (A1, A2) were the source of entry into various landscape segments. Assembly processes eventually produced differences in the dynamics of A1 and A2 community patches, patches that interacted via colonization events with developing B level patches. Similarly, B level communities developed alternative dynamics resulting in differences in species composition and relative abundance. Blending B level communities into hybrid patches did not result in convergent structure among hybrid patches.

upon reducing the volume 10 dB the result is something other than the volume that existed before the operation was performed. Of course hysteresis generally refers to the behavior of a particular dynamical system. In our scenario, irreversibility arises because the dynamical system itself has changed, such changes may also occur in coupled hysteretic systems.

8.5.2 Uncharted territory

8.5.2.1 Transience, dynamical capture and collapse

Systems develop organization, structure, and pattern by gaining and losing elements through a series of coupling and decoupling events. This is effectively an assembly process and it is driven by an exceedingly complex mechanics (Drake et al. 1996). Of particular interest is the dynamical nature of transients that accompany each assembly step—a coupling or decoupling. Transients may be long-lived expressing different dynamics along their course. Hence, the properties of a system far from an attractor can differ markedly from that observed upon closer approach to its attractor (Manrubia and Mikhailov 2000, Hastings 2001). For example, the oscillations characteristic of some predator and prey interactions are preceded by entirely different dynamics. Our experimental work has shown that the transient behaviors that accompany assembly steps in some developmental trajectories can be a rich source of variation. In other such trajectories no variation of consequence is permissible. Based on these results we suppose that the transient dynamics initiated by coupling or decoupling within a metasytem contain several temporally distinct regions of behavior.

Immediately upon coupling, the metasytem enters into a relatively short-lived stage, reflecting a temporary loss of coordination among and within system components as previous dynamical controls collapse. As coordination is asserted under the new dynamics, the residual information contained in the precoupled systems is dissipated. Once dissipated, the dynamics of the coupled system are fully engaged under the new dynamics. We suspect that a system in this early stage will respond differently to exogenous effects than it would once dynamical control has been asserted. By the same token, a system entering into this stage may exhibit sensitive dependence such that residual dynamics are dissipated differently and potentially with alternative solutions. In such a case the systems that comprise the coupled unit, define a family of possible approaches to the attractor, and in fact multiple attractors.

While the earliest events in the life of transients remain unexplored, many studies have documented their long-term behavior (Koelle and Vandermeer 2005, Hastings and Higgins 1994, Ermentrout and Kopell 1994, Pikovsky and Maistrenko 2003, Chazottes and Fernandez 2005). Here, it is not uncommon to observe sequential or cyclic transitions through various limit cycles, quasiperiodic, regular, and chaotic behaviors—all occurring in route to a stable or quasistable attractor that was born by a coupling event. In nature there are no rules demanding that subsequent coupling events must wait until a system

reaches its attractor. Hence, the outcome of coupling depends upon the dynamical nature of both systems at the time. The possible variation is striking and exploitable by self-organizing systems of nature.

The route to hard emergence requires the occurrence of events or processes that lead to irreversible steps in time. Emergence derived otherwise is necessarily soft. Any given deterministic system is of course reversible by definition, however this condition is one that is localized in the dynamics. That is, given some arbitrary dynamics the route from the any plausible initial conditions to the attractor(s) and back again can be retraced. Altering system dynamics modifies this localization, with the processes or events responsible for that alteration becoming a feature of the new dynamics. While the system has changed, it remains reversible with reference to the alteration. Coupling systems masks localizations, the coupled system behaving vastly different than its components, but does not remove it. Here we draw a fine, yet critical line. Self-organized, assembled, or evolutionary systems can potentially lose this localization when historically contingent events like coupling initiate a dimensional collapse during development. At the community level, for example, a dimensional collapse will result if an invading species induces extinctions. Subsequent development will most likely restore or surpass the systems previous dimensionality, though species composition may vary.

Whether or not an interaction develops between systems is contingent on many factors. In nature the opportunity to couple might depend upon chance events placing systems in close spatial proximity, or on the presence or absence of other systems. Dynamical considerations exist as well. The relative location of systems in their respective phase space, a kind of dynamical synchrony, strongly regulates the likelihood of coupling when the opportunity is presented. For example, a predator that encounters a potential prey species whose population happens to be in a dynamical trough, may very well leave the system. Yet that same predator may engage the system if the potential prey has some other abundance. In this case the cause of specific prey population dynamics becomes an indirect mechanism involved in coupling. Our predator may colonize the system because a competitor of its prey has vanished or diminished in numbers. Should the development of an interaction be contingent on itinerant dynamics or events, further system development may result in a system whose representation is irreducible (Kamp and Reyle 1990, Fulton and Harris 1991). Essential components of development cannot be recovered.

A contingent event that permits or prohibits colonization by some species acts as a dynamical switch. When the result of coupling is a new system whose dimensionality is less than or equal to that of the precoupled systems, a dynamical collapse has occurred. For example, a change in system dynamics can easily lead to extinctions. Should that extinction involve the switch, the reduction in dimensionality yields a system whose remaining parts may contain insufficient information to recreate *self*. This is effectively a distortion in the correlation between microscopic (within system) properties and macroscopic (whole system

and its time series) properties. Alteration of the macroscopic state, as in the sequence of events described above, leaves microscopic properties only partially correlated to subsequent macroscopic states. Historical contingency can become embedded within such systems (Kaneko 1998), but it may not be recoverable. To an external observer with complete historical insight, these fleeting events permit a causal understanding. While the system can be recreated from this vantage point, reconstruction cannot be accomplished with the pieces that comprise that system alone. As such the system and its properties are fully emergent in the hard sense.

Such historical contingency is a key feature in higher dimensional nonlinear systems. These systems appear to be dominated by Milnor attractors, which have the curious property of being asymptotically unstable (Milnor 1985, Kaneko 1997). Milnor attractors can dominate significant regions of a multi-attractor basin, yet they are unable to hold all orbits in their local neighborhood. In the absence of disturbance, the system behaves as if it were a classic multistable system, but given arbitrarily small disturbance the trajectories can escape. Under such conditions periodic disturbance has a clear and significant effect. For example, Tsuda and Umemura (2003) show that the existence of Milnor attractors, and their riddled basins, leads to phase shifts or chaotic cycling and itinerancy. Trajectories visit attractor after attractor, exhibiting equilibrium behavior but without the presence of equilibria. Milnor attractors create a situation of extended transience with abrupt discontinuities in the trajectory as it wanders among attractors.

Should the location of previously visited attractors drift, for whatever reason, it becomes impossible to reproduce a system governed by Milnor attractors. Given that systems in early transient stages are at the most malleable stage of their evolution, systems dominated by Milnor attractors should be capable of producing extraordinary novelty. Coupling in such systems should have the same effect as described above, a system whose organization and properties are owed to past transient phases. Further, it is plausible that the trajectory of the system may visit regions of phase space that lay *outside* of the original attractor basin of one or more of the precoupled systems. That is, the coupled system contains space (realizable configuration of structure) that does not exist in the uncoupled state for one of the subsystems. A coupling induced dimensional collapse is a reduction in the degrees of freedom in such a region, and could leave a former system element beyond the confines of its dynamically specified basin. While we are uncertain of the consequences of such a condition, the orphaned system element remains susceptible to coupling to, or *dynamical capture* by, other systems. If this should prove possible, such dynamical capture immediately generates hard emergence.

8.5.2.2 *Interactions in the attractor space*

Our search for just such a route to emergence began after noticing a curious experimental and theoretical result (Drake 1990, 1991, Drake et al. 1993).

Ecological communities can sometimes be assembled that cannot be reconstructed from their constituent parts. This *Humpty Dumpty* effect is a direct result of historical contingency driven by system development in the face of coupling and decoupling. The presence of one or more transient species, or their dynamics, is required to generate the final community state. The mechanics are simple. The presence of transient species at specific times during development actualizes new regions of state space while eliminating others. The result is a modification of the attractor and its equilibria. Among the many consequences associated with such a reconfiguration are changes in species composition, relative abundance, species-specific community invasibility, and the mode of action of specific mechanisms.

After the system has entered a newly created region of phase space, and the species that defined that region is uncoupled from the system, the attractor again changes. Does it return precisely to its previous configuration? Not necessarily so. For example, the timely presence of some species may mitigate the effects of preexisting dynamics such as competition long enough for an alternative outcome to occur. A competitor headed for extinction, but rescued by a transient species, owes its existence to the altered attractor space produced by that species. It would seem that the residence time of transient species is somehow correlated with the probability of such novelty occurring. When the transient species are absent from the final state, the *Humpty Dumpty* effect emerges. Within the dynamical realm, the final community state has no solution to its own structure.

Such dynamics are consistent with the presence of Milnor attractors that route trajectories first here and then there much like the action of the cushion of a billiard table. Imagine the game of billiards where portions of the table cushion occasionally shift from a reflective to an absorbing boundary—so determined by the relative position of balls on the table at each step. Assuming the ball reappears on the table, the dynamics have clearly changed for further play. In direct analogy, our experiments have shown that the same fixed species pool that created the *Humpty Dumpty* effect also contains routes to fully reconstructible community solutions. These systems are not emergent in any sense, and their nature can be fully exposed by reductionistic methodologies. On theoretical grounds it follows two communities comprised of the same species can exist, where one exhibits emergence while the other does not. This duality suggests that emergence can be something more than a system-level property as defined by the elements that compose the system. Dynamics are involved and the existence of alternative dynamical realms, not simply different dynamics as a function of time, may underlie much of the variation in community assembly patterns observed in nature. We are suggesting that emergence is function of the manner in which systems are created, and ultimately the outcome of interactions between attractors.

This leads us to the question of how interactions occur between dynamical systems, while each system's generative dynamics remain autonomous and uncoupled. At first glance contemplating such an interaction seems contrary

to experience and untenable. If an interaction exists, that interaction must explicitly exist in the underlying equations. After all two species cannot compete unless they are competing for something, and in that case terms are readily specified. Indeed this is the case, and many interactions are appropriately modeled with coupling terms. However, it is also plausible that interactions can occur vicariously in the attractor spaces of dynamical systems where direct interaction terms are inappropriate. Here, the generative dynamics of one system modifies the attractor space of another system precluding previously viable trajectory routes and creating others. In ecological systems, where spatial extents are explicit, such processes surely exist when two or more communities serve as source pools for the creation of a new community.

As an example, consider two or more rule-based cellular automata (CA) operating independently but on the same grid or lattice. In such a system, an occupied or open cell, produced by the evolution of one system potentially modifies the developmental trajectory of others (Figure 8.4). There can be no doubt that each system will evolve in a fashion that differs from the situation when operated on independent grids. Certain trajectories are preempted while

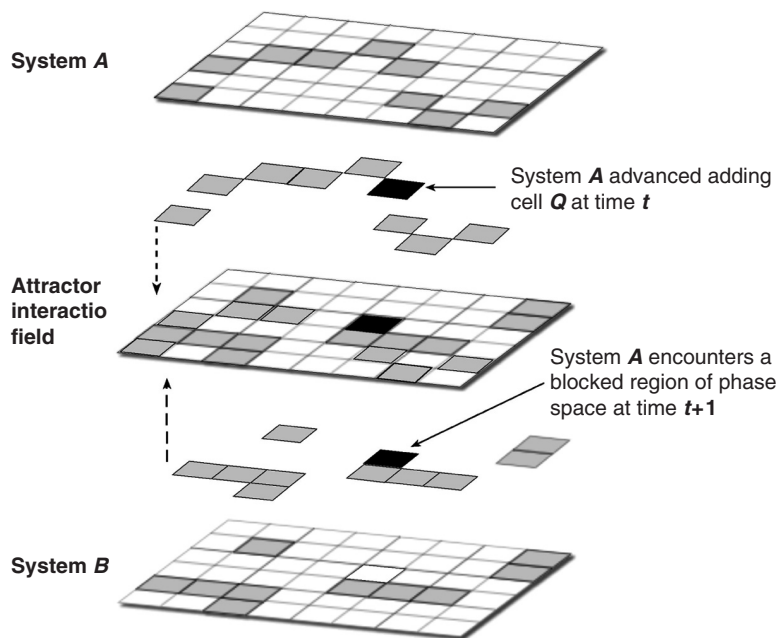


Figure 8.4. The interaction between two systems without explicit dynamical coupling is most easily visualized by considering two two-dimensional cellular automata. Systems, A and B , are shown developing independently in the top and bottom lattices. However, the *attractor interaction field* represents a situation where both systems coexist on the same lattice. System A and B come into conflict over cell Q which system A occupied immediately before the trajectory of system B reached that location. This situation effectively represents a change in the boundary conditions of system B .

others are created to such an extent that the familiar “creatures” (e.g., gliders, blinkers) produced by a single rule base may no longer evolve in the coupled system. Our thought experiment suggests that coexisting yet autonomous systems, can distort the available attractor space by functionally eliminating solutions to some trajectories while enhancing others. This distortion is a source of novelty capable of creating dynamical opportunities that could not otherwise exist.

It is important to recognize that an attractor’s character is defined at multiple levels of scale that are discordantly viewed by constituents of the system. In the absence of hard emergence, the system expresses collective dynamics, and its constituents, express dynamics decomposable from the system. Thus the constituents define a basin of attractor and the subsequent movement of that system in space and time. But what of systems where collective dynamics are irreducible, creating caveats in the fundamental mathematical operators of ($=$, $+$, $-$), and simply eliminating associative and commutative algebras?

8.6 CONCLUSIONS: WHEN YOU CAN’T GET THERE FROM HERE!

Inquiry in science generally proceeds by noting some macroscale pattern, structure, or phenomena, followed by dissection of the system in question. The observer, armed with information about interrelationships among pieces that comprise the system, variously manipulates those pieces with the explicit aim of implicating the mechanisms and processes responsible for observation. This approach works exceedingly well in a broad class of simple hierarchically structured systems, and provides some degree of operational adequacy. However, this approach stumbles when confronted with complex systems, retreating to statistics, and the contingent level of understanding available by focusing of the maintenance of structure. Maintenance and cause represent two very different levels of understanding, one proximate and one fundamental. There is a limit, an asymptote if you will, to the knowledge attainable given our predisposition to reduction. While the decomposition of a complex system can lead to a level of mechanical operability, it does so at the expense of understanding.

Pattern and structure arise via many processes and mechanisms inextricably woven together with emergence. Self-organization and chance create opportunity that subsequently derives directionality from assembly mechanics while being tested by natural selection. The operation of process and mechanism is ultimately shaped by system-level constraints operating at various scales of organization. As such, the mode of action permitted under the dynamics, and plausible under the constraints, is but the phenotype of causal processes that are historically derived.

We began this paper based upon conjectures we have developed to explain the intriguing behavior of the assembly experiments discussed above. These experiments have shown that (1) the attractor space is richly varied and complex, (2) a portion of this space is deterministic, while a portion is indeterministic,

(3) attractors can dynamically break, after which may be no link, trajectory or solution from the original attractor or parent to the new or child attractor. The Humpty Dumpty effect is real. The only explanatory recourse remaining is to conclude that hard emergence exists, and that its source is in the creation, evolution, destruction, and interaction of dynamical attractors. Hence, emergent properties and structures are not magical or mystical manifestations, they are not simply systems that push the bounds of human logistical and computational limits, nor are they philosophical or linguistic constructs of the mind. Routes to emergence necessarily exist because emergent systems exist, and as such emergence can be understood. Nevertheless, the parts of such systems in extant reality cannot explain the whole.

In this discourse we have offered the essential key and some of the foundational elements necessary to understanding emergent property and structure. Without doubt our framework is incomplete and additional elements remain hidden waiting to be uncovered. Considerable work also remains in developing a robust mathematical approach to attractor interactions, beginning first with interactions among low-dimensional systems and then approaching more realistic high-dimensional systems. Academic ecology, one of the driving forces behind the movement known as complexity, is at a critical intellectual juncture along with a handful of other scientific disciplines. While more case studies and documentation are indeed valuable, we are now in a position to step past pure dissection and description, and realize the promise of a causal understanding; arguably, for the very first time in human history. Emergence is at the center of this foray and within an understanding of this dynamical realm is the solution to nature.

8.7 ACKNOWLEDGMENTS

We are most grateful to the editors of this volume for allowing us the freedom to explore, invent, speculate, and offer ideas often without solutions. We wish to thank Stan Salthe, Aaron King, Tom Hallam, Sergey Gavrillets, Jurek Kolasa, and Neil Young for offering advice and criticism. The senior author (JAD) wishes to include the following. This paper is dedicated to Peter Yodzis, a delightful friend and colleague who will be missed. Peter's unique style and grace have left an indelible impression—a gentle approach to all things. As a young graduate student Peter offered me encouragement and support that had a considerable effect on my academic pursuits. So to Peter, everything in the paper is your fault—he would smile at that.

8.8 LITERATURE CITED

- Ablowitz R (1939) The theory of emergence. *Philosophy of Science* 6:1–16
 Alexander JC, Yorke JA, You Z, Kan I (1992) Riddled basins. *International Journal of Bifurcation and Chaos* 2:795–813

- Ashby WR (1947) Principles of the self-organizing dynamic system. *Journal of General Psychology* 37:125–128
- Baas NA (1994) Emergence, hierarchies, and hyperstructures. In: Langton CG (ed) *Artificial life III: Santa Fe Studies in the Sciences of Complexity Proceedings*, vol 17. Addison-Wesley, Redwood City, CA, pp 515–537
- Bar-Yam Y (2004) A mathematical theory of strong emergence using multiscale variety. *Complexity* 9:5–24
- Besiner B, Haydon DT, Cuddington K (2003) Alternative conceptions of alternative stable states in ecology. *Frontiers in Ecology and the Environment* 1:376–382
- Blitz D (1992) Emergent evolution: Qualitative novelty and the levels of reality. Kluwer, New York
- Bonabeau E, Desselles JL, Grumbach A (1995) Characterizing emergent phenomena 1. A conceptual framework. *Revue Internationale de Systemique* 9:327–346
- Borges JL (1941) *The library of Babel* (JE Irby English Translation 1962) In: Yates DA, Irby JE (eds) *Labyrinths, selected stories and other writings*. New Directions, Norfolk, CT
- Brown JH (1995) *Macroecology*. University of Chicago Press, Chicago
- Brown JH, Maurer BA (1989) Macroecology: the division of food ad space amongspecies on continents. *Science* 243:1145–1150
- Cadotte MW Multiplicative effects of dispersal on community richness: ametacommunity experiment using a microbial microcosms. *Ecology* (in press)
- Cadotte MW, Fukami T (2005) Dispersal, spatial scale and species diversity in ahierarchically structured experimental landscape. *Ecology Letters* 8:548–557
- Cardinale BJ, Palmer MA, Collins SL (2002) Species diversity increases ecosystem functioning through interspecific facilitation. *Nature* 415:426–429
- Chazottes J-R, Frenandez B (eds) (2005) Dynamics of coupled map lattices and of related spatially extended systems. *Lecture Notes in Physics*, vol 671. Springer, New York
- Collier JD, Muller SJ (1998) The dynamical basis of emergence in dynamical hierarchies. In: Farre G, Oksala T (eds) *Emergence, complexity, hierarchy and organization*. Acta Polytechnica Scandinavica MA91. Finish Academy of Technology, Espoo
- Cooper WS (1926) The fundamentals of vegetational change. *Ecology* 7:391–413
- Costantino RF, Cushing JM, Dennis B, Desharnais RA (1995) Experimentally induced transitions in the dynamic behavior of insect populations. *Nature* 375:227–230
- Costantino RF, Desharnais RA, Cushing JM, Dennis B (1997) Chaotic dynamics in an insect population. *Science* 275:389–391
- Couillet P, Tresser C (1978) Iterations d'endomorphismes et groupes de renormalisation. *CR Acad Sci Paris* 287:577–580
- Criminale WO, Jackson TL, Nelson PW (2004) Limit cycle-strange attractor competition. *Studies in Applied Mathematics* 112:133–160
- Crutchfield JP (1994) Is anything ever new? Considering emergence. In: Cowen G, Pines D, Melzner D (eds) *Sante Fe Institute Studies in the Sciences of Complexity*, vol XIX. Addison-Wesley, Redwood City, CA
- Cuddington K (2001) The 'Balance of Nature' metaphor and equilibrium in population ecology. *Biology and Philosophy* 16:463–479
- Cushing JM, Costantino RF, Dennis B, Desharnais R, Henson S (2003) *Chaos in ecology*. Elsevier, Amsterdam
- Davies PCW (2004) Emergent biological principles and the computational properties of the universe. *Complexity* 10:11–15
- Drake JA (1990) The mechanics of community assembly and succession. *Journal of Theoretical Biology* 147:213–233
- Drake JA (1991) Community assembly mechanics and the structure of an experimental species ensemble. *The American Naturalist* 137:1–26
- Drake JA et al. (1993) The construction and assembly of an ecological landscape. *Journal of Animal Ecology* 62:117–130

AQ3

- Drake JA, Hewitt CL, Huxel GR, Kolasa J (1996) Diversity and higher levels of organization. In: Gaston K (ed) *Biodiversity: a biology of numbers and differences*. Blackwell, Oxford, pp 149–166
- Drake JA, McMahon S, Zimmermann C, Flum T Constructing nature: Complexity and design in ecological systems. *Ecological Complexity* (in press)
- Egerton FN (1973) Changing concepts of balance of nature. *Quarterly Review of Biology* 48:322–350
- Emmeche C, Køppe S, Stjernfelt F (1997) Explaining emergence-towards an ontology of levels. *Journal for General Philosophy of Science* 28:83–119
- Emmeche C, Køppe S, Stjernfelt F (2000) Levels, Emergence, and three versions of downward causation. In: Emmeche C, Finnemann N, Christiansen P (eds). *Downward causation, minds, bodies and matter*. Aarhus University Press, Denmark, pp 13–34
- Enquist BJ, Niklas KJ (2002) Global allocation rules for biomass partitioning in seed plants. *Science* 295:1517–1520
- Ermentrout GB, Kopell N (1994) Inhibition-produced patterning in chains of coupled nonlinear oscillators. *SIAM Journal on Applied Mathematics* 54:478–507
- Feigenbaum M (1978) Quantitative universality for a class of nonlinear transformations. *Journal of Statistical Physics* 19:25–52
- Feigenbaum MJ (1979) The universal metric properties of nonlinear transformations. *Journal of Statistical Physics* 21:669–706
- Fukami T (2004a) Assembly history interacts with ecosystem size to influence species diversity. *Ecology* 85:3234–3242
- Fukami T (2004b) Community assembly along a species pool gradient: implications for multiple-scale patterns of species diversity. *Population Ecology* 46:137–147
- Fukami T, Morin PJ (2003) Productivity–biodiversity relationships depend on the history of community assembly. *Nature* 424:423–426
- Fulton W, Harris J (1991) *Representation theory: a first course*. Springer, New York
- Fussman GF, Elner SP, Shertzer KW, Hairston NG (2000) Crossing the Hopf Bifurcation in a live predator-prey System. *Science* 290:1358–1360
- Gamarra JGP, Solé RV, Alonso D (2001) Control, synchrony, and the persistence of chaotic populations. *Chaos Solitons and Fractals* 12:235–249
- Gamarra JGP, Montoya JM, Alonso D, Solé R (2005) Competition and introduction regime shape exotic bird communities in Hawaii. *Biological Invasions* 7:297–307
- Gaston KJ, Blackburn TM (2003) Why is macroecology important? In: Blackburn TM, Gaston KJ, Web NR (eds) *Macroecology: concepts and consequences*. Blackwell, Oxford
- Gavrilets S (2004) *Fitness landscapes and the origin of species*. Princeton University Press, Princeton
- Greborgi CE, Ott E, Yorke JA (1983a) Fractal basin boundaries, long-lived chaotic transients, and unstable-unsatble pair bifurcation. *Physical Review Letters* 50:935–938
- Greborgi CE, Ott E, Yorke JA (1983b) Crises, sudden changes in chaotic attractors and transient chaos. *Physica D Nonlinear Phenomena* 7:181–200
- Greborgi C, McDonald SW, Ott E, Yorke JA (1983c) Final state sensitivity: an obstruction of predictability. *Physics Letters* 99A:415–418
- Grossmann S, Thomae S (1977) Invariant distributions and stationary correlations of the one-dimensional logistic process. *Zeitschrift für Naturforsch* 32A:1353–1357
- Hastings A (2001) Transient dynamics and persistence of ecological systems. *Ecology Letters* 4:215–220
- Hastings A (2004) Transients: the key to long-term ecological understanding? *Trends in Ecology and Evolution* 19:39–44
- Hastings A, Higgins K (1994) Persistence of transients in spatially structured ecological models. *Science* 263:1133–1136
- Hastings A, Hom C, Ellner S, Turchin P, Godfray HCJ (1993) Chaso in ecology: is mother nature a strange attractor? *Annual Reviews of Ecology and Systematics* 24:1–33

AQ4

- Heagy JF, Carroll TL, Pecora LM (1994) Synchronous chaos in coupled oscillator systems. *Physical Review E* 50:1874–1885
- Holland JH (1998) *Emergence*. Addison-Wesley, Reading, MA
- Jacob F (1977) Evolution as tinkering. *Science* 196:1161–1166
- Kamp H, Reyle U (1990) *From discourse to logic: introduction to model theoretic semantics of natural language, Formal logic and discourse representation theory*. Kluwer, New York
- Kaneko K (1989) Spatiotemporal chaos in one- and two-dimensional coupled map lattices. *Physica D Nonlinear Phenomena* 37:60–82
- Kaneko K (1997) Dominance of Milnor attractors and noise-induced selection in a multi-attractor system. *Physical Review Letters* 78:2736–273
- Kaneko K (1998) On the strength of attractors in a high-dimensional system: Milnor attractor network, robust global attraction, and noise-induced selection. *Physica D Nonlinear Phenomena* 124:322–344
- Klee RL (1984) Micro-determinism and concepts of emergence. *Philosophy of Science* 51:44–63
- Koelle K, Vandermeer J (2005) Dispersal-induced desynchronization: from metapopulations to metacommunities. *Ecology Letters* 8:165–175
- Krasnosel'skii M, Pokrovskii A (1989) *Systems with Hysteresis*. Springer, New York
- Kuhn TS (1962) The Structure of scientific revolutions. In: Neurath O, Carnap R (eds) 1955. *International encyclopedia of unified science*, vol 2, No 2. University of Chicago Press, Chicago
- Laughlin RB, Pines D, Schmalian J, Stojkovic BP, Wolynes P (2000) The middleway. *Proceedings of the National Academy of Sciences of the United States of America* 97:32–37
- Leibniz GW (1697) De rerum originatione radicali (On the radical origination of things). In: Loemker LE (ed) 1969 *G. W. Leibniz philosophical papers and letters*. Dordrecht
- Manrubia SC, Mikhailov AS (2000) Very long transients in globally coupled maps. *Europhysics Letters* 50:580–586
- Matthews PC, Mirollo RE, Strogatz SH (1991) Dynamics of a large system of coupled nonlinear oscillators. *Physica D Nonlinear Phenomena* 52:293–331
- May RM (1974) Biological populations with nonoverlapping generations: stable points, stable cycles and chaos. *Science* 186: 645–647
- May RM (1976) Simple mathematical models with very complicated dynamics. *Nature*. 261: 459–467
- McGrady-Steed J, Harris PM, Morin PJ (1997) Biodiversity regulates ecosystem predictability. *Nature* 390:162–165
- Mill JS (1843) *System of Logic, Ratiocinative and inductive being a connected view of the principles of evidence and the methods of scientific investigation*. Longmans, London, UK
- Milne BT (1992) Spatial aggregation and neutral models in fractal landscapes. *The American Naturalist* 139:32–57
- Milnor J (1985) On the concept of attractor. *Communications in Mathematical Physics* 99:177–195
- Nichols, G. and I. Prigogine (1989) *Exploring complexity: an introduction*. Freeman, New York
- Ott E, Sauer T, Yorke JA (1994) *Coping with chaos: analysis of chaotic data and the exploitation of chaotic systems*. Wiley, New York
- Pastor VM et al. (1993) Ordered and chaotic behavior of 2 coupled oscillators. *Physical Review E* 48:171–182
- Pepper S (1926) *Emergence*. *Journal of Philosophy* 23:241–245
- Pikovsky A, Maistrenko Y (eds) (2003) *Synchronization: theory and application*. Kluwer, Dordrecht
- Rosen R (1985) *Anticipatory systems*. Pergamon Press, New York
- Rosen R (1991) *Life Itself: a comprehensive inquiry into the nature, origin, and fabrication of life*. Columbia University Press, New York
- Ruelle D (1981) Small random perturbations of dynamical systems and the definition of attractors. *Communications in Mathematical Physics* 82: 137–151

- Ruelle D, Takens F (1971) On the nature of turbulence. *Communications in Mathematical Physics* 20:67–192
- Salthe S (1985) *Evolving hierarchical systems*. Columbia University Press, New York
- Schneider ED, Kay JJ (1994) Life as a manifestation of the second law of thermodynamics. *Mathematical Computer Modelling* 19:25–48
- Simon HA (1962) The architecture of complexity. *Proceedings of the American Philosophical Society* 106:467–482
- Simon HA (1996) *The sciences of the artificial*, 3rd ed. MIT Press, Boston
- Solé RV, Manrubia SC (1995) Are rainforests self-organized in a critical state? *Journal of Theoretical Biology* 173:31–40
- Solé RV, Bascompte J (2006) *Self-organization in complex ecosystems*. Monographs in population biology. Princeton University Press, Princeton
- Solé RV, Ferrer-Cancho R, Montoya JM, Valverde S (2003) Selection, tinkering and emergence in complex networks. *Complexity* 8:20–33
- Strogatz SH (1994) *Nonlinear dynamics and chaos: With applications to physics biology, chemistry, and engineering*. Addison-Wesley, Reading, MA
- Strogatz SH, Stewart I (1993) Coupled oscillators and biological synchronization. *Scientific American* 269(6):102–109
- Tsuda I, Umemura T (2003) Chaotic itinerancy generated by coupling of Milnor attractors. *Chaos: An Interdisciplinary Journal of Nonlinear Science* 13:937–946
- Ulanowicz RE (1997) *Ecology: The ascendent perspective*. Columbia University Press, New York
- Ulanowicz RE (2000) *Growth and development: ecosystems phenomenology*. iUniverse, Lincoln, NE
- Vandermeer J, Yodzis P (1999) Basin boundary collisions as a model of discontinuous change in ecosystems. *Ecology* 80:1817–1827
- Van Valen L (1973) A new evolutionary law. *Evolutionary Theory* 1:1–30
- Verhulst PF (1845) *Recherches mathématiques sur la loi d'accroissement de la population*. *Nouveaux Mémoires de l'Académie Royale des Sciences et Belles-Lettres de Bruxelles* 18:1–41
- Verhulst PF (1847) *Deuxième mémoire sur la loi d'accroissement de la population*. *Mémoires de l'Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique* 20:1–32
- Wagner A (1999) Causality in complex systems. *Biology and Philosophy* 14:83–101
- Warren PH, Law R, Weatherby AJ (2003) Mapping the assembly of protist communities in microcosms. *Ecology* 84:1001–1011
- West GB, Brown JH, Enquist BJ (1999a) The fourth dimension of life: fractal geometry and allometric scaling of organisms. *Science* 284:1677–1679
- West GB, Brown JH, Enquist BJ (1999b) A general model for the structure, and allometry of plant vascular systems. *Nature* 400:664–667
- Wimsatt WC (1997) Aggregativity: reductive heuristics for finding emergence. *Philosophy of Science Supplement* 96:372–384
- Wright S (1932) The roles of mutation, inbreeding, crossbreeding and selection in evolution. *Proceedings of the 6th International Congress of Genetics* 1:356–366

Author Queries

- AQ1: The "2" is not mentioned in Author names. Please check
- AQ2: List in the references or delete
- AQ3: Please update
- AQ4: Please update

