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Ecological complexity and agroecosystems: seven themes from theory

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ABSTRACT

Exploring the intersection of new ideas of ecological complexity with insights from traditional agricultural systems is the fundamental subject of this article, with an emphasis on seven themes of ecological complexity, as reflecting contemporary themes in ecology. The seven themes are as follows: 1) turing processes and spatial structure, 2) chaotic dynamics, 3) stochastic processes, 4) coupled oscillators, 5) multidimensionality, 6) trait-mediated indirect interactions, and 7) critical transitions (catastrophe theory). We suggest that these themes of complexity naturally integrate to form one qualitative whole that could be considered a single subject—ecological complexity.

KEYWORDS

ecological complexity;
chaos; coupled oscillators;
stochasticity; trait-mediated
interactions

Introduction

The movement to divest from the industrial agricultural system is located not in the centers of political and economic power, but rather in the intersection of traditional knowledge, popular social movements, and the natural world. Practiced at the level of the farm, to some extent refusing modern scientific narratives, this new revolution has one central theoretical tenant that runs throughout—the fundamental rules of natural systems should be used as guidelines for planning and management of agricultural systems. Or, equivalently, the science of ecology should be foundational to agroecology. And what precisely is that science?

Ecology as science is young. Even though Darwin himself wrote extensively about it, he did not even recognize it as a scientific discipline. Ernst Haeckel (1866, II, 286) is credited with inventing the word (*Oecologie*), but certain key concepts, such as the niche and competitive exclusion, emerged only in the twentieth century. The two oldest ecological societies in the world, the British Ecological Society and the Ecological Society of America celebrated their first centenary in 2013 and 2015, respectively, which make the science of ecology little more

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than a century old. Yet, that century provided key observations, experiments and theories that today are regarded as much a scientific core for ecology as Newton's theory of gravity is for physics. In the past quarter century, the science of ecology has been enriched with ideas borrowed from complexity science, and merged into a new kind of ecology, increasingly referred to as "ecological complexity." Exploring the intersection of this new ecology with insights from traditional agricultural systems, in service of understanding the agroecosystem, is the fundamental subject of this article.

It is unlikely to be controversial to suggest that ecological systems can be very complicated. Yet the, largely correct, observation that ecological systems are complicated, is really quite different from the claim that they are complex, at least in the modern usage of those terms—complicated does not equal complex. A central feature of a complex system is that attempting to understand it by breaking it down into smaller parts and studying those parts in isolation is likely to fail. Although any scientific endeavor must simplify a system in order to study it, the complex system itself cannot be simplified—it takes on its characteristics from the whole. We cannot describe it any better than Levins and Lewontin (1985) already described it in their classic "The Dialectical Biologist:"

It is not that the whole is more than the sum of its parts. But that the parts acquire new properties. But as the parts acquire properties by being together, they impart to the whole new properties, which are reflected in changes in the parts, and so on. Parts and wholes evolve in consequence of their relationship, and the relationship itself evolves. These are the properties of things we call dialectical: that one thing cannot exist without the other that one acquires its properties from its relation to the other that the properties of both evolve as a consequence of their interpenetration.

The growth of agroecology and its connection to ecological complexity

Although remaining in the shadows of the industrial system that dominates most agricultural land in the world, it is striking, in some regions, how rapid is the growth of agroecological practices, even if not specifically called "agroecology," and despite the fact that the actual land mass they occupy remains small (Altieri and Toledo 2011; Gliessman 2013; Rosset and Martínez 2012). Small and medium scale farmers from all over the world are searching for alternatives that allow them to care for the land, conserve their resource base, improve their production capabilities, and give them more autonomy and independence from large agribusiness (Van der Ploeg 2014). Furthermore, they are organizing into social movements that

challenge the neoliberal and industrial agricultural model (Desmarais 2012; Guzmán y Martínez-Alier 2006; Rosset et al. 2011).

Agroecology has been defined as a science, a practice and a movement (Wezel et al. 2009). From a practice, it quickly became an international movement. Yet the advancement of the science associated with it has been less quick to evolve. Here, we argue that if agroecology is to adopt ecology as its scientific foundation, it must incorporate the advances of that science more explicitly than has been the case in the past. As part of that program, we propose that the concepts of “ecological complexity” that have been developed over the last few decades may represent a useful starting point. We also argue that agroecology as a movement, must incorporate the modern science of agroecology and combine it with local and traditional knowledge. Only this combination will generate a robust knowledge base that will allow farmers to develop adaptive systems that will be resilient in the phase of global change, including climate change and the vicissitudes of changes induced by political circumstances.

The science of complexity, anticipated by Rachel Carson (1951) and long advocated as the proper foundation for ecology by Levins and Lewontin (1980), should form the basis of an ecological theory for agroecology, eschewing idealistic notions such as “the balance of nature”, yet acknowledging the truth of the whole. A challenge will be to weave together this new agroecological science (based on ecological complexity) with the accumulated knowledge of generations of farmers that have cared for the land for millennia.

Agroecology as a science of ecological complexity

The literature identifies a variety of topics as part of the new ideas of ecological complexity. In this article, we identify seven themes that together we feel encapsulate the current ideas of ecological complexity, namely 1) Turing processes and spatial structure, 2) chaotic dynamics, 3) stochastic processes, 4) coupled oscillators, 5) multidimensionality, 6) trait-mediated indirect interactions, and 7) critical transitions (catastrophe theory). Few contemporary ecologists would deny the importance of any of these, yet may not go so far as to suggest, as we do, that they all combine into one qualitative whole. Others will note that we fail to include other important subjects. Both may be correct, but this is our vision, based on our experience working in agroecology, of how concepts of ecological complexity can enlighten the science and practice of agroecology as well as support the agroecological movement. We suggest that it is the interpenetration of these subjects together that constitutes what should be called ecological complexity. We briefly discuss each of these themes.

1. Turing patterns and other spatial issues

Ecologists, farmers, and pretty much anyone who has made any observations about nature are aware of the fact that biological organisms are not simply scattered across space randomly. Whether a snapshot of a population of cows in agricultural fields or a long-term study of the spatial distribution of *Rhizobium* bacteria in the soil, almost all organisms are distributed in a non-random fashion. For many of these patterns, there are underlying biological processes that can be tied to their generation, while others are clearly the direct result of underlying physico-chemical factors. Elaborating on this theme, ecologists have provided a large number of explanations that could account for such pattern formation. One elegant formulation was elaborated by the British mathematician Alan Turing (1952). It has been used as a conceptual tool to understand, qualitatively, how these sorts of spatial patterns may emerge spontaneously.

Turing's insight was motivated by the chemical reactions in developmental biology. He proposed two chemicals that reacted with one another in a concentration-dependent fashion. Chemical number one reacts with a solution of some other chemical to activate the creation of a product, which increases in intensity over time. But at some critical concentration, the reaction produces chemical number two, which suppresses the further formation of chemical number one. Thus, the two chemicals are referred to as the activator (first chemical) and the suppressor (second chemical). The key insight of Turing was to propose that the second chemical diffuses through space at a faster rate than the first one. When this happens, interesting spatial patterns emerge. It has been proposed that this activation-repressor process produces many of the patterns observed in nature, for example, the patterns in mammalian coats (Liu, Liaw, and Maini 2006).

An interesting agroecological example is the distribution of the predatory ant, *Azteca sericeasur* (formerly *A. instabilis*), in coffee farms in Mexico (Figure 1). Since this ant species is well-known as a keystone species in a complicated network of pest control, its particular spatial distribution is of some importance. Furthermore, given this importance, understanding how the spatial pattern emerges is likewise of practical interest.

The proposed mechanism for the formation of the spatial pattern of *A. sericeasur* is effectively the same as Turing's idea. The "activation" here is the simple tendency for the arboreal ant colony to bud-out (with a group of queens and worker ants) by establishing new nests in close-by trees. The "repression" emerges from a fly parasite that attacks the ant, causing mainly behavioral disruption with the result that the queen (or one of the queens) is motivated to move the nest to a different tree, or the nest eventually perishes (Vandermeer, Perfecto, and Philpott 2008). So, metaphorically, the ant, through its nest-splitting behavior, acts as an activator, while the fly parasite

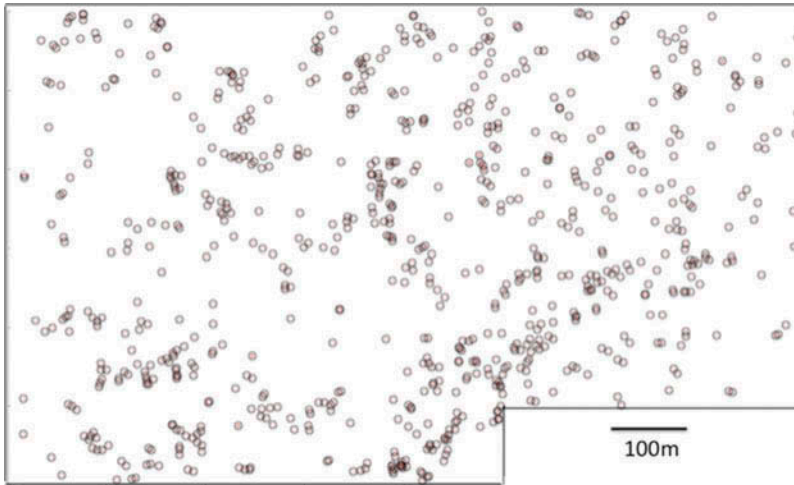


Figure 1. Spatial distribution of the ant, *Azteca sericeasur*. Each symbol indicates the location of a shade tree containing a nest.

acts as the repressor, resulting in a clustered spatial pattern. This special pattern, in turn, has important consequences for the control of several important pests of coffee, as has been discussed elsewhere (Perfecto and Vandermeer 2008; Vandermeer, Perfecto, and Philpott 2010)

2. Chaotic dynamics

Since the 1970s, there has been much written about the idea of chaos in ecology. The popular imagination is naturally stimulated significantly by a theory that seems to say that it is impossible to understand anything at all. Indeed, in the proper framework that is precisely what chaos suggests, it is profoundly upsetting. Yet perhaps it is less unsettling when we understand that its essence is familiar to all of us in our shared common experience. For example, a tornado is a typical chaotic system. Knowing the precise location of two dust particles within the tornado at one point in time will not allow you to predict the location of those two dust particles in the future. However, a tornado has a particular qualitative structure and dynamics that can easily be described, despite its underlying chaotic nature. Chaos is a mathematical property of a dynamical system. The tornado example illustrates the essential mathematical characteristic of chaos—no matter how well you measure the initial conditions of the two dust particles, you cannot predict the system in the future. This is called sensitivity to initial conditions.

With this intuitive insight into the nature of chaos, consider a more interesting example. Suppose the rate of population increase in the bacteria in the soil of an urban garden is dependent on the availability of nitrogen. But there is a complicated relationship between nitrogen and bacteria, such

that when the bacteria get too abundant, many of the bacterial cells cannot get enough nitrogen to survive and there is a massive die off of bacteria cells. So, we have a pattern of increasing bacterial sequestration of nitrogen and increasing bacterial population, eventually leading to a collapse of the bacterial population due to the overconsumption of nitrogen. Suppose we have two fields, close to one another, but separated by a hedge row or some other vegetation that keeps migration of bacteria from one field to the other at a minimum. In the spring, growth is slow and the population increases slowly, eventually reaching a threshold where it stays for a long time. Then, in the summer, because of warmer weather the bacteria reproduce much more rapidly, depleting their nitrogen supply such that their population collapses to almost zero, only to rebound when nitrogen stores are replenished. If we compare the two fields, something interesting (and somewhat disturbing) happens. If we begin with almost exactly the same number of bacterial cells and the same amount of nitrogen in both fields, for a time, the two populations behave in an almost identical fashion, but then begin to deviate, and eventually have completely distinct patterns of population dynamics. If it would be desirable to know the precise population density some time in the future, there is no way we could estimate the current population precisely enough to make that calculation, even if we have 99.99999% perfect knowledge of the population processes of birth and death. That is, almost perfect knowledge about the system will not enable its future prediction!

There are compelling reasons to believe that ecosystems are frequently chaotic or at least have chaotic elements embedded in them. Unambiguous detection of them has proven to be extremely difficult for a variety of technical reasons. Frequently the data we have to work with are insufficiently dense. For example, in [Figure 2](#), we graph a rare case of a very long time series, deduced from historical records of locust infestations in China, along with a known chaotic trajectory and a random sequence of numbers. Even here, with the longest known time series of an insect species, it is not completely clear whether we have a chaotic system or not. Yet in many *model* systems, both laboratory experiments and mathematical models, the existence of chaos is clear.

While it is difficult to say for sure whether a given data set is chaotic or not, there are some generalized qualitative structures that strongly suggest chaotic systems, especially when we add socioeconomic factors (Sakai et al. 2007). Consider a simple example of a group of farmers making decisions about their farming operations. There is an obvious time lag between making the decision about what to plant and the harvest and marketing of the produce, such that the farmers must take the cues they have today to try and predict market conditions at harvest time. If all the farmers in a region decide that tomatoes will fetch a high price at the time of harvest and all plant large quantities of tomatoes as a consequence, there will be a glut of

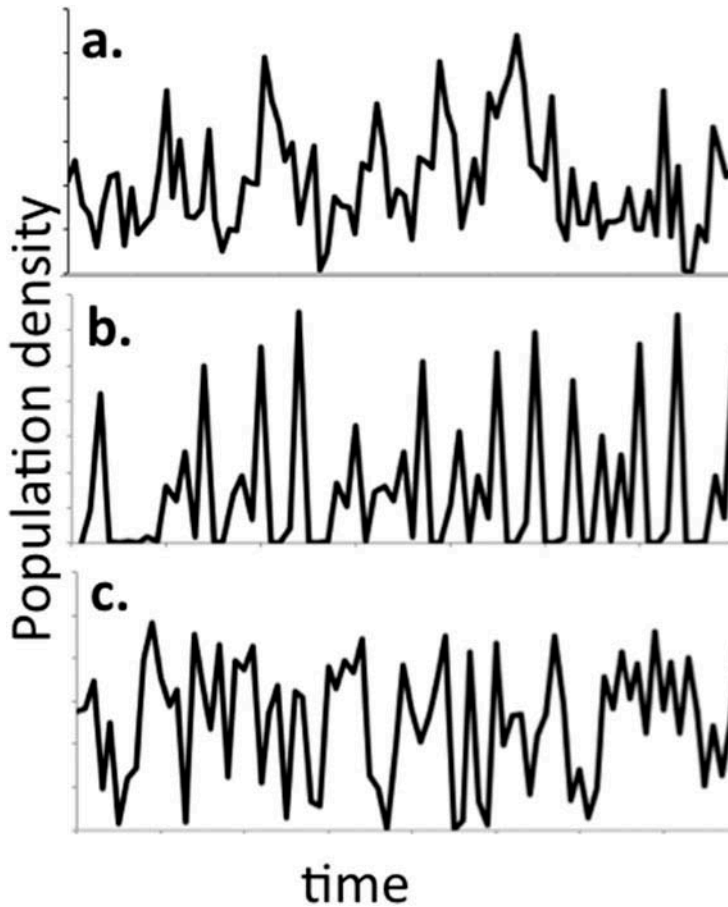


Figure 2. Three time series illustrating chaos, randomness, and an actual 300 year time series of insect populations: (a) actual time series of locust infestations in China; (b) chaotic population in theory (based on the Rickert model); (c) A sequence of random numbers.

tomatoes at harvest time over the whole region and the price will collapse. But will not farmers realize this and adjust their planting plans accordingly? Perhaps, but herein lies the germ of chaotic behavior. The basic form of the way farmers make decisions about production, coupled with the elementary notion that a glut will lead to lower prices, strongly suggests a chaotic system. Unable to know with certainty their neighbors' plans (that is the assumption here), they use market prices as a cue, but they know perfectly well that if everyone plants tomatoes the market will collapse. But if everyone pulls out of production, the one who goes full force with production will gain considerably. Much like the famous bar where "no one goes there anymore because it's too crowded," the tomato farmer must contend with the parallel problem that no one wants to produce tomatoes because too many people are producing tomatoes. This is a structure that very easily leads to chaotic price and production trajectories (Sakai et al. 2007; Vandermeer 1997).

3. Stochasticity

Stochasticity is taken as a given in most ecological framings of models or theories or experiments in ecology, and both classical and modern statistical methodologies are a standard component of the ecologist's toolkit. Formerly the operation of stochastic forces was thought of as something to be minimized, something that generated an annoying "fuzz" around the "real" value of whatever was being measured. Experiments and observations were then organized around the goal of minimizing this feature so as to get at the underlying truth. While this is a sensible position in many contexts, it is not so within the framework of ecological complexity. Indeed, stochasticity takes on a completely different meaning—it can be the main determinant of the qualitative behavior of a system, the key to understanding, rather than an annoying artifact.

The central role of stochasticity as a force capable of generating qualitative behavior can be demonstrated with elementary models. Consider, for example, a single population under density-dependent population control. Levins (1969) noted that simply adding a random element to the growth rate of such a population would lead to a change in the qualitative structure of the population. A standard mode of population behavior begins with an increase in numbers, but as the size of the population reaches higher levels, there is feedback on the growth rate and the population eventually reaches saturation, the population carrying capacity. If this population lives in an environment that imposes a strong stochastic force on its growth rate, the population will, not surprisingly, be more variable than if there is no stochastic forcing. However, depending on the relative strength of the stochasticity, the population will form qualitatively distinct patterns. Suppose that we are dealing with 50 distinct sub-populations, each of which has precisely the same average growth and death rate. If there is a small stochastic force added to the growth rate of each of the populations, we expect a distribution of population sizes after a long time of population growth, enough time that the population without stochastic forcing would reach its carrying capacity. But because of the stochasticity, some of the populations will be near the carrying capacity, but others will have experienced different growth rates over that period of time. Thus, we expect a distribution of population sizes something like illustrated in [Figure 3](#). The interesting feature is that as the stochastic forcing becomes large, the distribution of population sizes will be bimodal, with many populations effectively at zero, many others close to the carrying capacity, and fewer intermediate, as shown in [Figure 3](#). Thus, the general distribution of population sizes is qualitatively altered by a simple addition of a stochastic force.

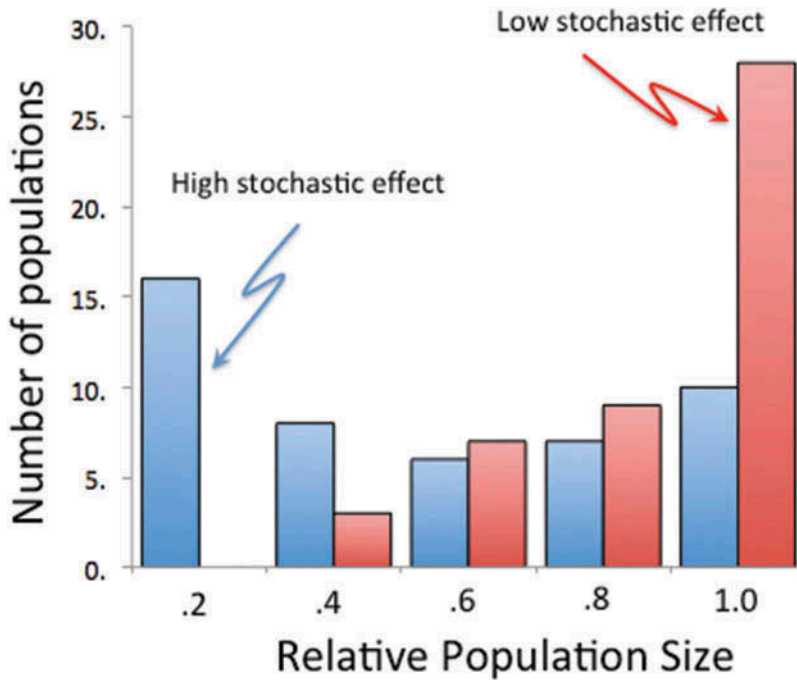


Figure 3. Expected distribution of 50 distinct populations growing with an identical average growth rate, but with two distinct levels of stochastic forcing.

4. Coupled oscillations

Lying sick in bed in 1665, the famous Dutch physicist Christian Huygens, noticed that two of his pendulum clocks, mounted on the wall, were oscillating approximately 180 degrees out of phase with one another. Curiosity drove him to change the pendula to be swinging in phase, and within a half hour, once again they had taken up an antiphase coherence with one another. Repeating this experiment, probably many times, he convinced himself that this phenomenon was a real characteristic of pendula. He wrote to a confidant that his two clocks displayed “an odd kind of sympathy . . . [when] suspended by the side of each other” (Bennett et al. 2002).

What Huygens discovered has become the foundation of a variety of applications in many sciences and a variety of engineering applications—when coupled, sometimes very subtly, two oscillators will come to “inform” one another about their oscillations and attune to each other. Many illustrations of this phenomenon can be seen in abundant video clips, and applications from signaling fireflies to electronic oscillators are well known. The behavior of coupled oscillators has important implications in ecology since one of the most evident of ecology’s rules is the consumption of one organism by another, whether bacteriophages attack bacteria in the soil or

parasitoids attack pests in maize fields. This trophic connection is, at its most foundational level, oscillatory. It is in this sense that all ecological systems are collections of coupled oscillators, and it is not surprising that this metaphor has been applied to coupled ecological systems generally, and especially to classical trophic systems (predator/prey, herbivore/plant, etc.; Blasius, Huppert, and Stone 1999; Hastings and Powell 1991; McCann, Hastings, and Huxel 1998; Vandermeer 2006).

One of the ways of coupling trophic systems is by allowing them to eat the “wrong” food—Consumer 1 preferring Resource 1 but sometimes eating Resource 2 and Consumer 2 preferring Resource 2 but sometimes eating Resource 1. This is the situation diagrammed in Figure 4a, with the two consumers sharing two resources. Here, we see that the coupling of the oscillators is through the joint utilization of the two resources, sometimes described as “the mechanism of competition is joint resource utilization,” a very common situation in both theoretical thinking about ecology and in nature. However, there is another way of coupling these oscillators that makes biological sense. It could be that the resources themselves are in competition for some other resource, but that resource is not stipulated, as shown in Figure 4b. Rather, the “phenomenon” of competition is simply stated as the impact of one resource causing a reduction in the growth rate of another resource (note that we are thinking here mainly of resources that themselves are self-replicating—not really a necessary assumption, but a convenient one). The coupling as in Figure 4a leads to the ultimate result

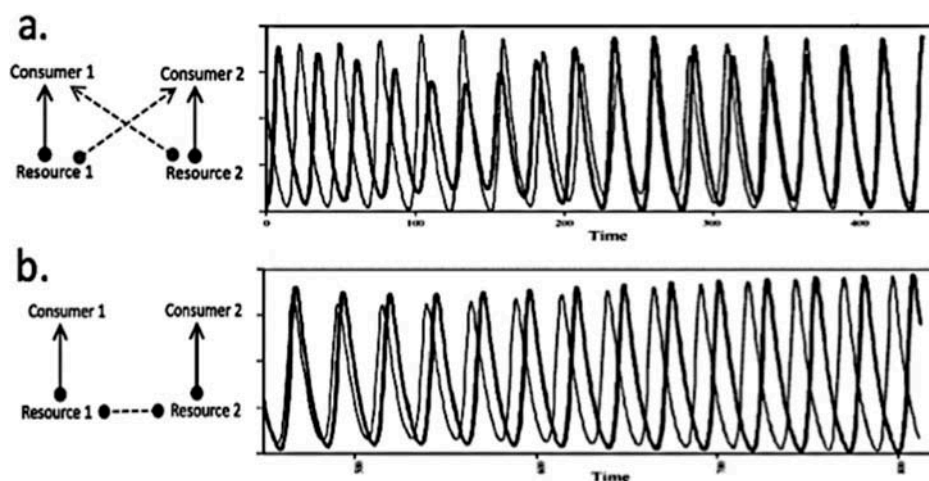


Figure 4. Simulations of weakly coupled predator/prey oscillators, showing the basic competitive connections of mechanistic competition (a) and phenomenological competition (b), along with the time course of the interacting consumer populations. In (a), populations are initiated in an “anti-phase” coordination and gradually come into phase with one another. In (b), populations are initiated in an “in-phase” coordination and gradually come into “anti-phase” coordination with one another.

that the two oscillating systems come to oscillate in the same phase. The coupling as in [Figure 4b](#) leads to the ultimate result that the two systems come to oscillate in an anti-phase cohesion. These theoretical results have been validated in real natural systems as well ([Benincà et al. 2009](#)).

Considering a slightly more complicated example, one of the most ubiquitous natural situations is a simple trophic chain (e.g., plant/herbivore/carnivore), which in principle is a system of two coupled oscillators (plant/herbivore and herbivore/carnivore). Such a simple and ubiquitous arrangement can result in some remarkable complexities, even though each component (an organism and its food) is unremarkable. Coupling these two oscillators leads, with proper parameter values, to a very specific chaotic attractor, known generally as the “teacup” attractor (due to its shape in three dimensions; [Hastings and Powell 1991](#)). In [Figure 5](#), we illustrate the time series for each of the three elements plus the three-dimensional portrait of the attractor. The behavior is well known to be chaotic, but it is important to note that there is a clear structure to the system. In three dimensions, the attractor is shaped like a “teacup”. But more importantly, here we can see the imprint of where the attractor comes from in the first place. There are basically two types of oscillations that, in a sense, share the space—long-term oscillations between top predator (lizard) and predator (beetle) and short-term oscillations between predator (beetle) and herbivore (aphid). So

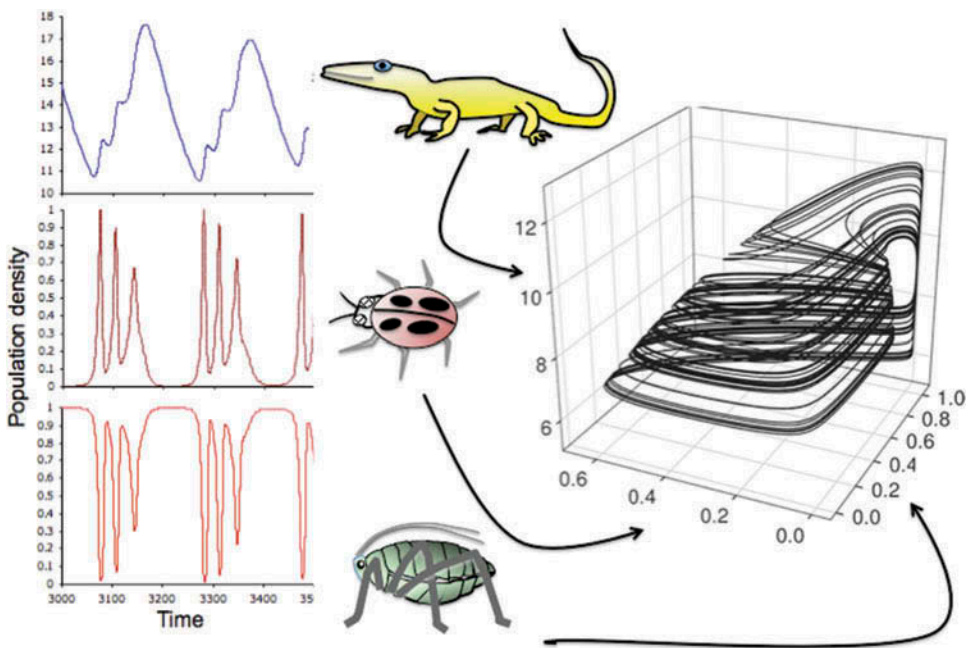


Figure 5. The tri-trophic model of [Hastings and Powell \(1991\)](#), a chaotic attractor. On the left each of the variables over time, illustrating the clear signal of two separate attractors and on the right, all three plotted in three-dimensional space, illustrating the chaotic nature of the system.

even though the overall system is chaotic, its underlying structure of two coupled oscillators is nevertheless evident, and the relative amplitude and frequency of each of the oscillators is clear within the chaos.

5. Multidimensionality

Historically, the most fundamental aspects of ecology are conceptualized in a very low dimensional space, even though it is understood that ecology in the real world involves many species, which is to say, it is multidimensional. Most ecological theory, such as population dynamics, predator/prey models and competition theory, involves only one or two dimensions. However, moving from two to three dimensions, changes some things dramatically.

Historically, we have long been accustomed to the fundamental four possible solutions to the basic Lotka-Volterra approach: 1) Species A always wins over species B, 2) species B always wins over species A, 3) the two species coexist in perpetuity, or 4) one or the other species wins, depending on where they start interacting. It may seem obvious that with three species a similar arrangement could emerge and to some extent that is true—there are actually 11 qualitatively distinct possibilities. But one arrangement has been recognized as especially important—an intransitive loop. This arrangement is analogous to the rock, paper, and scissor's game, and it occurs when species A wins over species B, which wins over species C which wins over species A. In any one pair combination, one species wins over the other, but when arranged as a triad in an intransitive loop, the outcome of the interaction may be the coexistence of all three species.

Intransitive loops can have implications for competitive interactions in agroecosystems. For example, in the practice of intercropping, when crops are generally of the same stature and generally share the same ecological requirements (similar niches), they will compete strongly and it is likely that they will not over-yield (i.e., it would be better to grow them as separate monocultures). However, if three highly competitive crops form an intransitive loop, it is possible that the three together will indeed overyield, even though none of the three pairs would do so. In the plant competition literature in general, there is a very similar assumption, frequently unstated, that plants of generally the same stature and requirements will form a strict competitive hierarchy (i.e., species A beats species B beats species C beats species D, etc.). Although it may seem intuitively obvious, the assumption is not necessarily true. An example is offered by Daniel, a Nicaraguan corn farmer of our acquaintance. As his corn is growing, a relatively dense growth of morning glory vines begins to grow beneath the corn stalks. Daniel does not “weed” them because the morning glory vines cover the purple nut sedge, a very aggressive weed, and repress its growth. After Daniel harvests his corn, he lets the morning glories grow as much as they want, completely covering

the sedge and any other weeds that might try and invade. Then, when planting time comes, he burns off the morning glories (leaving their root-stalks for the next season) and plants the corn. So, effectively there are three agents here: 1) the sedge, 2) the morning glory, and 3) the corn farmer and his corn. And they obviously form an intransitive loop since in the end the “corn-farmer-and-his-corn” agent beats the “morning glory” agent, while the “morning glory” agent beats the “sedge” agent, and the “sedge” agent, if given the chance, will beat the “corn.” Note that all three agents are, in principle, persistent in the system.

In real-world systems, we frequently must acknowledge more than just one, two or three species. The first foray in theoretical ecology beyond three dimensions was by Richard Levins in 1968. Levins basically expanded the idea of going from two species, to three, and expanded to a very large number. The community matrix (and Levins’ related loop analysis) portended a recently burgeoning literature on networks.

Network theory begins by asking the question, how much can we know about a system if all we know is which element is connected to which other element. Applied to anything from the internet to electrical distributional systems, a common biological application is to disease. Suppose, for example, a farm has banana trees scattered in the periphery of a central cropping region, in a form suggested in [Figure 6a](#). Now suppose that a banana pathogen is transmitted by local contact or very local wind currents such that only nearby trees can infect one another ([Figure 6b](#)). Note that if the plant indicated by the small arrow becomes infected, it sequentially infects all nearest neighbors (in this artificial example each plant has at most two neighbors), and, assuming that it takes about a week for one plant to infect its neighbor, infection is at 100% after 12 weeks. If we now imagine that a path had been worn in the farm such that people regularly walked through the farm along it, and that the human traffic can spread the disease propagules, there would be another connection, one that is determined by the path ([Figure 6c](#)). This arrangement is frequently referred to as a small world network based on the idea of moving rapidly to another part of the network through just a few links. The idea is related to the famous experiment done by Milgram in which he gave arbitrarily selected people in Nebraska a message that was to be delivered to a target person in Massachusetts, with no other instruction other than “give this to someone who you think might know the person or know someone who might know him or her.” The result was that a large proportion of the letters was delivered with surprising speed and an average of 5.2 intermediaries (Travers and Milgram 1969), giving rise to the popular idea of six degrees of separation. For many purposes in ecology, the small world structure generates remarkable results, especially in disease ecology, but also in many other cases where space is involved.

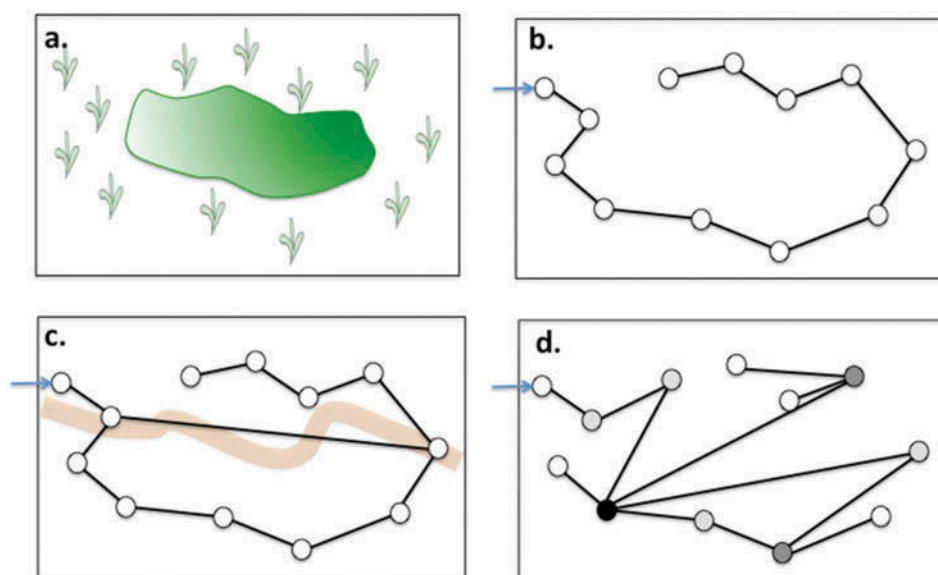


Figure 6. Idealized farm with a central region of some crop and banana plants in the periphery: (a) central cropping area and the individual banana plants; (b) representation of where the connection is based only on the nearest proximity of plants; (c) how a path through the farm can make a connection that would likely not have existed without the path, generating, in principle, a small-world network; (d) how preferential “attachment” to individual banana plants can lead to a scale-free network.

For example, in the regular graph of [Figure 6b](#), it takes 12 steps for a complete epidemic, compared to the eight steps it would take in the small world network ([Figure 6c](#)).

A completely different kind of graph may represent certain biological systems. Imagine, for example, that a bird perches regularly on some of the banana trees and, for some reasons, the birds may prefer some trees to others. Thus, in [Figure 6d](#), the nodes are shaded in proportion to the preference the birds have for them, the darker color the more the preference. This sort of graph construction is known as “preferential attachment” and results in what is known as a “scale-free” network. If you take the number of connections each node in a graph has, the distribution of those connections is formally known as the “degree distribution” and represents a measure of how preferred a node is (the network in [Figure 6d](#) has one node with five connections, two nodes with three connections, four nodes with two connections, and five nodes with one connection). Remarkably, if you plot the log of the number of attachments per node against the log of the frequency of occurrence of that number, a straight line emerges, which is to say the distribution of connections, is a power function.

6. Trait-mediated indirect interactions

The enemy of my enemy is my friend, and other such aphorisms reflect an important fact about ecological systems. In 1960, an important paper challenged ecologists to think of terrestrial ecosystems in a very general fashion (Hairston et al. 1960). Written by three ecologists from the University of Michigan, professors Hairston, Smith and Slobodkin (the paper became known as HSS), they suggested that very simple observations could lead to a major conclusion about how ecosystems were structured. Their very simple observations included one that seemed hardly contestable that the terrestrial world looks green. That is, plants, the source of that green color, basically filled up the environment. This led them to the conclusion that the things that eat plants, herbivores, were not being limited by those plants (plenty of green stuff around, they argued), and if that be the case, they must be limited by the things that eat them, the carnivores. So HSS came to the very strong conclusion that, in general, terrestrial ecosystems had the basic structure that the primary producers (plants) were limited by something other than the things that eat them (the herbivores), which themselves were limited by the things that eat them (the carnivores). If terrestrial ecosystems were basically organized along the trophic structure of plants to herbivores to carnivores, HSS hypothesized that control of the system came from above for the herbivores (“top-down control”) and from below for the plants and carnivores (“bottom-up control”). There would be a “cascade” of effect from the carnivores to the plants, through the herbivores, and that effect would be “indirect.”

As always, Darwin’s insights in several places in his masterpiece cite this curious fact that effects are not always direct, and even before, the obviousness of the whole structure was appreciated at least by ancient Chinese farmers, one of who pointed out, in approximately 300 AD,

A factor which increases the abundance of a certain bird will indirectly benefit a population of aphids because of the thinning effect which it will have on the coccinellid beetles which eat the aphids but are themselves eaten by the bird.

More modern literature refers to this basic arrangement as a “trophic cascade,” which in the end is just one example of what more generally is known as an “indirect effect.” The contrasting structure is, of course, a direct effect, in which species A directly affects species B (a predator eats a prey, a parasite attacks a host, a plant competes with another plant, etc.). When species A affects species B through its action on species C, the effect of A on B is said to be indirect, perhaps the most obvious and ubiquitous example of which is a simple trophic cascade (predator aids plant by eating herbivores, the plant’s enemies).

A less evident, but extremely common natural pattern, is what has come to be known as trait-mediated-indirect-interactions. A classic example is the well-known mutualism between ants and various hemipteran herbivores, one of the most commonly cited mutualisms in nature. The hemipterans produce a sweet substance (called honeydew) that the ants consume. As the ants are generally predators, or at least move around so much that they tend to scare away other things, their activity benefits the hemipterans by scaring away (or eating) their potential predators. So the basic energy transfers are hemipteran to ant (the honeydew) and hemipteran to predator (or parasite). Energy transfer flows 1) from the plant to the hemipteran, 2) from the hemipteran to the ant, and 3) from the hemipteran to the predator. With this simple arrangement, the per capita production of offspring by the hemipteran is a fraction of the energy it obtains from the plant minus a fraction of the energy it gives up to the ant and the parasitoid. We think it evident that the effect, the ants have on the potential predators, and parasites of the hemipteran are far more important than the interactions defined only by material transfer (plant juice to the hemipterans, hemipteran mass to the predators, honeydew to the ants). And this classical mutualism is clearly an example of a trait-mediated-indirect-interaction.

Trait-mediated indirect interactions have been shown to be as important if not more than direct density mediated interactions (Werner and Peacor 2003). The classic example involves two species of frogs in competition with one another, one of which is attacked by a dragonfly predator. Both frogs (when they are tadpoles) eat algae, but species A eats faster than species B, and is thus a potent and effective competitor, effectively eliminating species B from any small pond in which the two find themselves. That is, unless a key predator also lives in the pond. Frog B is a better competitor than frog A, but frog A has a poisonous secretion in its skin that disables the predator from attacking it. So, the predator attacks frog B, effectively helping frog A. So far, this story is identical to many three species systems in which a predator preferentially consumes one resource that is in competition with a second resource, thus indirectly benefiting that second resource.

But the system is more complicated in a very interesting way. Through a series of clever experiments, it was shown that the odor of the predator initiates a behavioral response in frog species B such that it hunkers down in the mud, dramatically reducing its rate of consumption of the algae, thus altering its competitive effect on frog species A. So the predator need not eat the tadpole to change the competitive effect. Its very presence, which the tadpole senses chemically, is enough to do so (Peacor and Werner 1997).

An example from our own work illustrates how these trait-mediated effects can become quite complicated and reinforces the notion that they may indeed be more important than the direct effects (Perfecto and Vandermeer 2015). The centerpiece of this example is the same ant species

we already introduced, *Azteca sericeasur* (Figure 1). The ant feeds on the honeydew secreted by a scale insect, *Coccus viridus* (Jha et al. 2012; Vandermeer and Perfecto 2006). In return, the ant scares away, and sometimes kills, the beetle, *Azya orbiger*, which would normally kill/eat the scale insects (Liere and Larsen 2010; Liere and Perfecto 2008). The larval stage of the beetle, however, has a waxy cuticle that the ant is unable to penetrate. The larva is thus immune to the attacks of the ant and consumes the scale insects in great quantities. And remember, beetle adults generally fly, so the adults can fly around looking for scale insects to eat, but the larvae are confined to a local area and unable to move around very much. Consequently, the larvae need to be located in a local concentration of scale insects to survive. This presents a problem for the beetles since the adults must place their eggs in the vicinity of the scale insects, indeed in a place where there is a local concentration of scale insects. But the only place where there is a local concentration of scale insects is when they are under protection from the ants, and the ants first will not allow the adults anywhere near the scale insects and second, if the adults do manage to lay an egg on the leaf, the ants will immediately eat it. These are two major problems for the beetle.

The first problem is solved ingeniously by placing the eggs underneath the scale insects, where the scale insects themselves inadvertently hide them from the attacking ants. This species of scale insect engages in a sort of parental care in that their offspring (formally known as “crawlers”) is maintained under the shell of the mother thus gaining protection from their potential natural enemies. Except, of course, for the predacious beetles that have managed to deposit their own eggs underneath the body of an unsuspecting scale insect mother. Thus is solved the first problem the beetle faces; how to get an egg, and resultant larvae, within a local concentration of scale insects. But what of the second problem, the ants will not allow adult beetles anywhere near the scale insects? And here, a remarkable complication, a new trait-mediated indirect interaction, is found.

The ant is attacked by a parasitic fly in the family Phoridae. The phorid parasitoid is able to detect the general locality of ants by being attracted to the various pheromones that the individual ants use to communicate with one another, but, because it has bad eye-sight, the phorid needs to sense movement on the part of an individual ant in order to oviposit on it. Without movement, the phorid is effectively blind. In response to this parasitoid attack, the ant has evolved a behavioral response to the phorid in which it, the ant, assumes a catatonic posture (unless it can rapidly escape into its nest), such that the phorid cannot “see” it. But the ants have also evolved a sophisticated communication system with one another with regard to this parasitoid. The first ant that is attacked by a phorid emits a special pheromone that basically says “look out, a phorid has been sighted close by,” and

all the other ants in the vicinity, in an area approximately one meters in diameter, assume that same catatonic posture (Hsieh et al. 2012).

It is precisely at that point that the beetle is able to penetrate the defense the ant offers the scale insect. Locked in a defensive position, the ants have their mutualistic function, protection of the scale insects from the predator beetle, dramatically reduced. And that is what the beetles seem to do, move in to deposit their eggs precisely at the point that the ants go catatonic. Yet, how is the beetle to know the ants are catatonic? Perhaps they can just fly around, looking for groups of catatonic ants. But they are more efficient than that. Female beetles, but not males, respond to the special pheromone that says “look out, a phorid has been sighted close by,” moving toward the origin of that particular pheromone (Hsieh et al. 2012). And only females that have already mated do this, which is to say non-gravid females either do not sense this special pheromone, or purposefully ignore it. Furthermore, the more days after copulation, the more sensitive is the gravid female to this special pheromone. This system is characterized by a trait-mediated cascade where the ant interferes with the ability of the adult beetle to eat the scales and oviposit on plants with scales, and the phorid flies cancel this effect. Thus, the presence of the phorids allows the main predator of the scale insects to reproduce and grow in patches with abundant food and provide effective biological control of scale insects in areas without ants. The system has important practical implications for the coffee agroecosystems in Mexico, where it was first discovered, since it ensures the reproduction of the beetle which is the main biological control agent of the scale insects (Perfecto and Vandermeer 2015).

7. Critical transitions

As people come to internalize the assertion that ecosystems are almost infinitely complicated, a sense of foreboding enters their expectations of the future, not sure what surprises await them, but certain the ecological world will not remain constant. Farmers have long been familiar with such worry. Their persistent claim that farming is a risky business and is traditionally thought to be mainly due to inherent instabilities and unpredictabilities not in ecology but rather in the economic system. But these claims take on new meaning when we realize that the millions of bacterial cells in the soil interact with the mycorrhizal fungi which determine the internal chemistry of the crops which affects the rate of feeding of pests which themselves may or may not be strongly attacked by parasitoids which sometimes get caught in spider webs made by spiders that sometimes get eaten by birds which need trees for nesting, and so on and so forth. Such concatenating contingencies can be overwhelming. The sensitive dependence on initial conditions the chaos revolution alerted us to looms large as we face the realities of the

complicated connections among thousands of elements in an average ecosystem. It is thus not surprising when we claim that unanticipated behavior, which is to say surprises, is likely to be inevitable in all ecosystems, including the agroecosystem. But in a rational world, such observations really ought to inspire us to study the phenomenon itself—what is the “structure of surprise” in ecosystems?

There is, fortunately, an evolving framework for understanding at least some of the structure of surprise. That framework originally stems from an obscure collection of abstract mathematical theorizing referred to as catastrophe theory. Transformations in both nature and society are frequently not simple one-to-one consequences of intentions (or driving variables, or sociopolitical conditions). The coffee rust is one example. Many others could be cited. Indeed, the phenomenon is general, and lends itself to a very abstract generalization that on the one hand “explains”, or, rather, gives us some underlying understanding about how surprises may emerge in agroecosystems. But there is a second issue, and that is perhaps more important, it is the idea of hysteresis. Consider the example of tree cover in tropical landscapes, one determinant of which is precipitation.

If the condition is amount of precipitation, as we move from low precipitation to high, the ecosystem tends to have a greater density of trees, from savannah to forest, as described many times in elementary ecology texts. However, this view in the past had been accompanied by a tacit assumption that the function translating the condition (moisture) to the response variable (density of trees) is single valued (for every point on the x axis there is only one point on the y axis—as in [Figure 7a](#) and [b](#)). More recent literature acknowledges that many ecological transformations are not at all like this, but rather follow a relationship that is not one-to-one, but rather something like illustrated in [Figure 7c](#), where there is a hysteretic zone in which alternative states are possible for particular conditions ([Scheffer 2009](#)). Indeed, many ecological examples have been proffered illustrating this pattern (e.g., turbidity in lakes [[Carpenter et al. 2011](#)]; tropical savannah/forest conversion [[Hirota et al. 2011](#); [Staver, Archibald, and Levin 2011](#)]; marine phytoplankton ([Edwards et al. 2006](#); [Wouters et al. 2015](#))). In ecology, different states generally are referred to as “regimes,” although perhaps a more useful moniker in agriculture would be “syndromes of production” ([Andow and Hidaka 1989](#); [Vandermeer and Perfecto 2012](#)). Returning to the example of tree cover, we see that if the annual rainfall begins to change, as we might expect in the near future due to climate change, if the relationship is as pictured in [Figure 7a](#), as annual rainfall declines, we expect a sort of concomitant reduction in tree cover, progressing more or less in lockstep with changes in precipitation. However, the evidence we have so far is that such a smooth transition with a particular change in rainfall leading to a

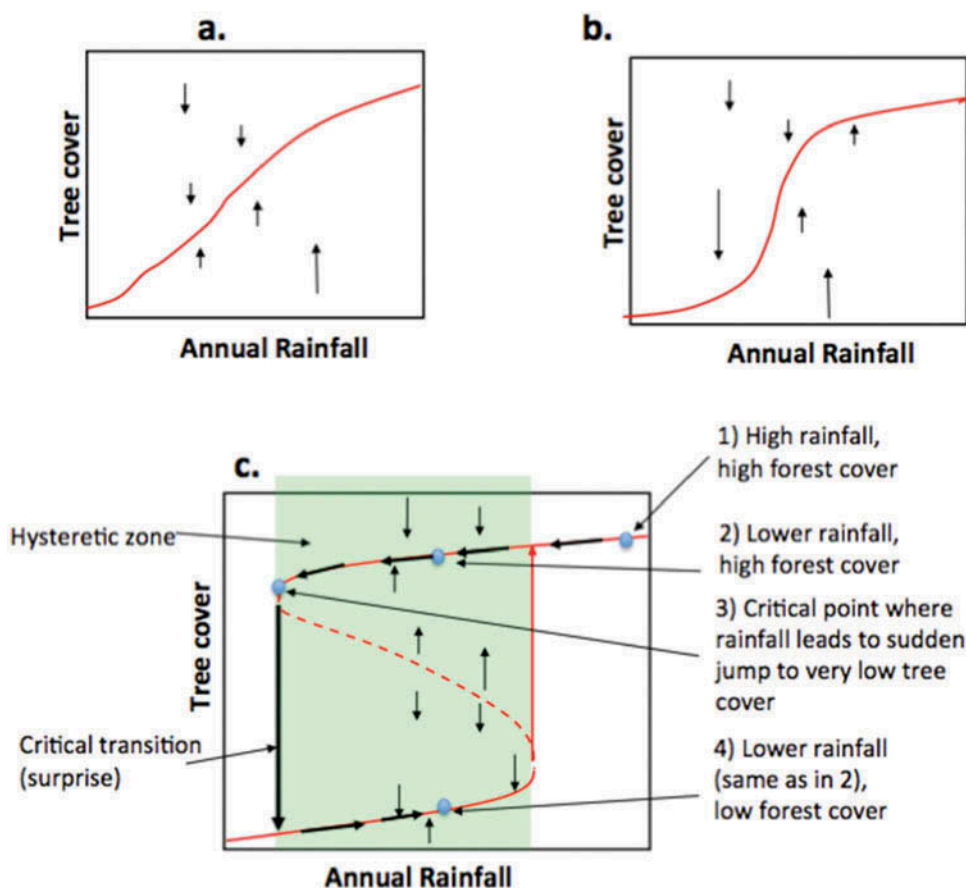


Figure 7. Examples of the qualitative relationship between ecological regime (syndrome) and ecological conditions. (a) What is sometimes assumed without much reflection, that changes in conditions (in this case, annual rainfall) produce more or less proportional changes in a response variable (in this case, tree cover). The “regimes” range continuously from high tree cover (forest) to low tree cover (savannah). (b) Adding nonlinearities to the system suggests that some changing conditions will induce more rapid changes in the response variable than other changing conditions. (c) Relaxing the assumption of a one-to-one relationship between the conditions and the response variable, producing a range of conditions for which there are two stable “regimes” (forest versus savannah).

similarly proportional change in tree cover is not likely to be the reality. More likely is a situation as pictured in Figure 7b, in which there is a zone of rapid transition, where a small change in rainfall would lead to a large change in tree cover, that is, a surprise is likely to happen at some point where previously small responses in tree cover to a particular change in rainfall suddenly give way to large changes in tree cover. This represents to some degree an underlying structure for surprise, but a more important structure emerges if we push the response function into its mode of a non one-to-one function, as in Figure 7c.

The form illustrated in Figure 7c is classically known as a critical transition graph. Imagine that you are located in a tropical area with a large annual rainfall, such that you would expect very high tree cover (see the point labeled “High rainfall, high forest cover” in Figure 7c). Due to global climate change, we now see a reduction in annual rainfall in the region such that on the graph we move according to the two arrows pointing left on the function, until we arrive at the point of “Lower rainfall, high forest cover.” Note that not much has changed on the y axis and we still are in a forested environment. Further decreases in rainfall generate the next two arrows pointing leftward eventually reaching the “critical point.” At this point, there is still a stable forest situation, but an even very slight reduction in rainfall results in a very sudden (and perhaps surprising) reduction to very low tree cover, a savannah situation. This is the structure that, in our view, is a metaphor for many sudden and surprising changes in ecosystems. And note we humans are not likely to know the precise notion of the underlying function and thus may be completely incapable of anticipating these surprises (but see below in the section on prediction of critical transitions).

But analyzing the critical transition graph further we find an even more surprising structure. Having arrived at the point of very low rainfall and savannah (after the critical transition has occurred) if we now allow the rainfall to begin increasing again, even though we may reach a point of rainfall that previously had given rise to a forested environment, we now are “stuck” with a savannah (see point number 4 in Figure 7c). There is a zone for which alternative equilibrium states are possible for any of the values on the x axis. This zone is referred to as a “hysteretic zone.”

The idea of surprise has evident practical importance. However, the related idea of hysteresis may have more practical importance. In the case of the coffee rust disease, for example, if the shade cover is one of the determining factors (many analysts feel this is the case, but it remains controversial), we see how deforestation (removing the shade trees from the system) could lead to an epidemic of the coffee rust disease. However, returning to a system of partial shade may not have the expected effect on controlling the disease because the system has been transferred to a different “regime” in which the disease is relatively endemic (i.e., we have jumped from the lower branch of equilibrium points in Figure 7c to the upper branch). Increasing the shade tree density may not have much of an effect at all since the system is likely to stay in the epidemic zone (upper branch of equilibrium points in Figure 7c), until we reach the new critical point (Vandermeer, Jackson, and Perfecto 2014; Vandermeer and Rohani 2014).

Conclusions

One basic theme in this article is that complexity in its modern sense is the backbone of today's ecological science. Coupling that theme with our assertion that ecology should be the foundational science of agroecosystems, it follows that ecological complexity needs to be acknowledged as foundational for agroecology. There has been a great deal written in both technical and popular outlets about the complex nature of ecological systems. Sometimes the vision portrayed is nothing more than a call to acknowledge that ecological processes are themselves multiple and that by envisioning just a small section of the set of these processes we run the risk of missing crucial keystone elements.

While calls to acknowledge the many connections that exist among a multitude of ecological elements are clearly sensible, they represent only a small section of what we propose is the true complexity of ecological systems. That complexity is rooted in a variety of surprising, sometimes astounding, results from mathematics, from crucial experiments in ecology, from continuing and irreplaceable natural history observations, and from direct observations and behavior of farmers. It is a framework that includes the somewhat unexpected conclusions that complex patterns emerge from very simple rules, while at the same time, simple patterns emerge from complex rules. It is rooted in fundamental principles of western science, while acknowledging roots and continuing insights from what earlier writers like Boyle and Darwin, referred to as "the trades," which in the present context would be "farmers and farmworkers." We postulate that there currently exists a convergence of traditional envisioning of ecosystems and modern western models of complexity. Attempting to give flesh to this skeleton, in this article we propose that seven key themes have come to characterize what ecosystem complexity is all about.

The transformation in understanding that we feel is emerging generally from the appreciation of complexity as a reality, is reminiscent of some earlier transformations. For example, in 1623 Galileo Galilei said:

Philosophy is written in this grand book, the universe, which stands continually open to our gaze. But the book cannot be understood unless one first learns to comprehend the language and read the letters in which it is composed. It is written in the language of mathematics, and its characters are triangles, circles, and other geometric figures without which it is humanly impossible to understand a single word of it.

What Galileo meant was far more literal than a modern reader might expect, thinking literally of solid objects like circles combining in many ways to create everything in the universe. This sort of thinking continued evolving, eventually giving way to a more systematic understanding of the particulate nature of the universe, the world of atoms (as opposed to triangles and circles —not that much of a change when we realize that Galileo's triangles could be

very tiny) and their changes in space and time. This viewpoint culminated, philosophically, in 1814 with Laplace's Demon, an entity who was described as:

An intellect which at a certain moment would know all forces that set nature in motion, and all positions of all items of which nature is composed, if this intellect were also vast enough to submit these data to analysis, it would embrace in a single formula the movements of the greatest bodies of the universe and those of the tiniest atom; for such an intellect nothing would be uncertain and the future just like the past would be present before its eyes. (from "A Philosophical Essay on Probabilities")

This point of view says that the present, as we know, is a consequence of the past, but that in the same sense, the future is a consequence of the present, which, if we know with sufficient precision and have the computational power at our disposal, will enable us to predict that future. And it is this philosophical principle that the science of complexity negates, almost as dramatically as the atomic theory of matter negated Galileo's solids theory. True, the entire enterprise of statistical mechanics already dealt it a near-fatal blow with its astounding predictive ability based on probability theory as opposed to Laplace's deterministic assumptions. But its spirit is challenged in a more practical and enlightening way by the burgeoning literature in complexity science that we see today. Applied to the science of ecology, speaking generally, complexity provides us with a new paradigm for viewing ecological systems. Their patterns in space, their chaotic characteristics, their basic trophic oscillations, their multidimensionality, their inclusion of nonlinear effects, their fundamental stochasticity, and their tendency toward critical transitions are the issues that make up that new paradigm. Or, rather, it is the intersection of these ideas that do so. When applied to agriculture, more specifically to agroecology, it is a paradigm that provides a springboard to apply ecology more deeply to the task of agriculture.

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