

A New Kind of Ecology?

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Mathematical models have a long history of use for understanding ecological systems. In a recent book, A New Kind of Science, Steve Wolfram calls into question traditional modeling approaches and calls for the increased application of cellular automata (CA) models in all areas of scientific inquiry. With reference to Wolfram's book, we review the past uses of CA models in ecology and discuss the relative utility of using traditional models versus CA models to understand ecological communities.

Keywords: spatial models, cellular automata models, frequency dependence, theoretical ecology, complexity

Unlike other basic sciences such as physics and chemistry, in which the participants are clearly defined, ecological systems consist of many interacting elements, only some of which are known and understood for any point in time and space. This makes the attempt to understand ecological systems very difficult, because not all information present in the system can be used without constructing a model as complex as the system under study. The effort to understand ecological systems has required that ecologists develop tools for simplifying these systems' complexity.

Model building in ecology has closely followed modeling applications in other areas of science. For example, some of the best-known models conceptualize species as chemical constituents that interact according to simple mathematical equations (Volterra 1926, Lotka 1932). In *A New Kind of Science*, Steve Wolfram (2002) argues that this approach to model building has been made obsolete by the power of modern computers to iterate the consequences of local interactions between entities in what are called cellular automata (CA) models. Wolfram's bold claims have drawn fire from many, including physicists and mathematicians (e.g., Weinberg 2002, Gray 2003). Of particular relevance to biologists is Wolfram's marked misunderstanding of the current conception of the evolutionary process (as noted by Weinberg [2002]). Although Wolfram does not directly address issues in ecology, given his claim to a new kind of science, it seems instructive to reflect on the science of ecology and to ask whether Wolfram's ideas can be profitably applied there.

Ecologists have embraced the use of CA models since almost the first appearance of Wolfram's landmark book *Theory and Applications of Cellular Automata* in 1986. Early

work using CA models explored the relationships between fire, landscape pattern, and seed dispersal on forest dynamics (Green 1989) and the effect of the frequency and size of disturbance on clonal growth in plants (Inghe 1989). A search of ecological journals from 1990 through 2003 turned up 64 articles that used CA models, with approximately half of these articles occurring in the journal *Ecological Modelling*. While this search probably underestimates the total number of articles, it illustrates that CA models have been widely accepted by ecologists as a useful tool for modeling ecological systems. Cellular automata models have been used to model individual plant growth (Colasanti and Grime 1993, Oborny et al. 2000), population dynamics (Molofsky 1994, Hill and Caswell 1999), community interactions (Hassell et al. 1991, Wilson and Nisbet 1997, Molofsky and Bever 2002, Kondoh 2003), and community spatial dynamics (Silvertown et al. 1992, Seabloom et al. 2001, Wootton 2001). However, despite the past use of CA models in ecology, one is left wondering whether (as Wolfram argues) fundamentally new insights can be gained from this approach. Here we review some past uses of CA models in the study of ecological systems and, with reference to Wolfram's claim of a new kind of science, suggest further ways in which CA models may illuminate major conceptual issues in the discipline of ecology.

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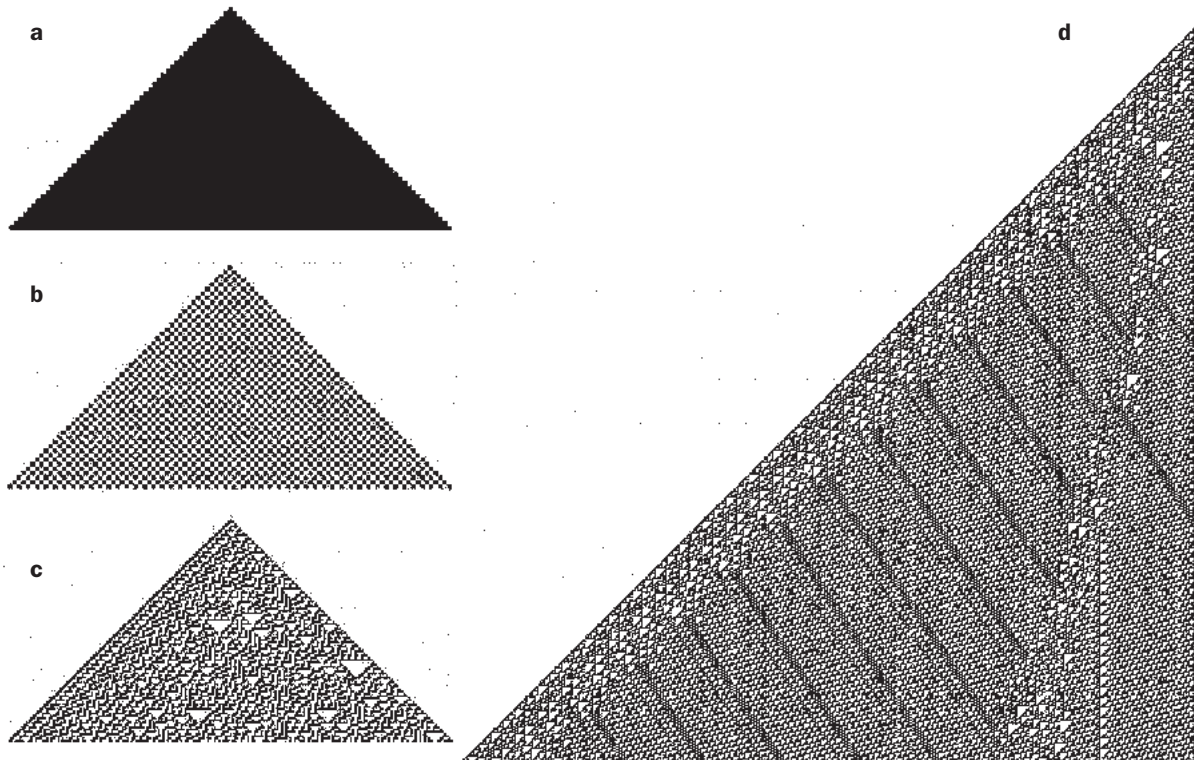


Figure 1. The dynamics that develop from simulation of one-dimensional, nearest-neighbor cellular automata (CA) models, showing Wolfram's (2002) four classes of behavior: (a) class 1 (stable dynamics; rule 254 iterated for 50 generations), (b) class 2 (cyclical dynamics; rule 178 iterated for 50 generations), (c) class 3 (chaotic dynamics; rule 30 iterated for 50 generations), and (d) class 4 (patterns composed of homogeneous regions and of regions containing complex localized structures, resulting in areas of both stable and unstable dynamics; rule 110 iterated for 500 generations). Rule numbers correspond to Wolfram's classification system of one-dimensional, nearest-neighbor CA models. In each panel, the top row represents the initial array, which begins with a single filled square (representing one individual). Each subsequent row represents a new iteration of the rule.

Wolfram's observations from cellular automata models

A cellular automata model is a model in which simple rules about how individuals interact are simulated on a one- or two-dimensional grid, and the behavior of the system develops from the iterated updating of these rules over time. The rules can be deterministic or probabilistic. Wolfram's and other researchers' interest in CA models developed from the observation that even the simplest deterministic rules could result in very complex spatial and temporal patterns (Wolfram 1986, 2002). In his books, Wolfram enumerates 256 simple two-state, one-dimensional CA rules that correspond to the complete set of possible rules for a two-state, one-dimensional, nearest-neighbor CA. From these patterns, Wolfram finds four classes of dynamic outcomes, three of which correspond to the dynamics associated with other model formulations, but one of which represents a new behavior. The four classes of outcomes are (1) development of a homogeneous fixed pattern, (2) development of a periodic pattern, (3) development of a chaotic pattern, and (4) development of patterns composed of homogeneous regions and regions containing

complex localized structures (figure 1). Classes 1, 2, and 3 correspond, respectively, to the fixed-point, limit-cycle, and chaotic behavior observed in difference and differential equation models. By contrast, class 4 dynamics do not have a direct analog with difference equation models, and it is the existence of this class of behavior that motivates much of Wolfram's perspective.

In determining which type of dynamics a set of rules is likely to produce, Wolfram emphasizes that it is not necessary to have complex rules to get very complex patterns. According to Wolfram, there appears to be a threshold above which adding further complexity to the rule structure does not add further complexity to the outcome, and this threshold, although different for each particular type of automata model studied, is less complex than would have been expected. This result, repeatedly emphasized by Wolfram in *A New Kind of Science*, is analogous to the early work in chaos theory, in which May and others showed that even very simple deterministic models could display complex and chaotic dynamics (May 1974). Thus, it is not surprising to ecologists that simple models can yield complex results. To better understand what might be a

unique contribution of Wolfram's work, we first review some applications of CA models in ecology and then consider Wolfram's main message in light of these applications.

Applications of cellular automata models to ecology

Ecological application of CA models can be classified into two broad categories: (1) abstract rule-based applications to illustrate the theoretical consequences of different rules and (2) empirical applications that have observational or experimental parameterized rule systems with direct application to natural systems. Rule-based applications can be further subdivided into deterministic and probabilistic applications, while empirical applications are typically probabilistic, since they are meant to represent the variability present in natural systems. Below we illustrate both rule-based and empirical applications.

Rule-based models: Exploring the consequences of simple processes.

Rule-based models are the most basic form of CA models and are the basis for the models that Wolfram (1986, 2002) discusses extensively. In these models, dynamics develop from the application of simple rules in concert over the entire grid. Dynamic behavior develops when a rule is applied to all cells (or individuals) within the grid. Implementing the rules is generally quite straightforward. The simplified rule-based systems have found some applications in ecology. Rule-based systems work well when the dynamics can be decomposed into a minimal categorical set of decision rules. The simplest decision rules are binary rules for which only two outcomes are possible (0 or 1). Such binary rules are the subject of intensive empirical exploration by Wolfram (1986, 2002). The benefit of using simple binary rules (as Wolfram [2002] shows) is that, for one-dimensional, nearest-neighbor rules, it is possible to explore the complete universe of possible dynamic outcomes. From this approach, one can deduce how often such dynamics occur and how small differences in the structure of a rule can affect a system's dynamics.

In general, ecological systems are not amenable to such a simplified framework, and, as a result, the one-dimensional, nearest-neighbor approach has rarely been applied in ecology. One notable exception is Molofsky (1994), who used one-dimensional binary totalistic rules to describe the dynamics of single populations that are subject to different amounts of density dependence and dispersal. In keeping with Wolfram's approach, the landscape consisted of a one-dimensional, two-state array of sites, the two states indicating, respectively, the presence (1) or absence (0) of an individual at that site. The presence or absence of an individual at a given location in the next generation was a function of the presence of individuals at the target location and its two adjacent locations. To mimic density dependence, the transition rule stated that when the target cell and both its neighboring cells were occupied (i.e., at high density), the center cell in the following generation became empty (Molofsky 1994). In addition, two types of dispersal were considered: (1) individuals dis-

persed throughout the habitat and (2) individuals dispersed only within the local neighborhood. Repeated application of these simple deterministic transition rules in concert over the entire grid created the population dynamics.

Application of these rules resulted in two different dynamic outcomes. When dispersal operated at the same scale as density dependence, chaotic dynamics resulted; however, when dispersal operated at a greater scale than density dependence, the dynamic outcome was a two-point cycle. By tabulating the outcomes of all possible rules (as advocated by Wolfram [1986]), Molofsky (1994) determined how often the different dynamic outcomes should occur in this one-dimensional totalistic system. Though the model is a simplification of any real ecological community, as is the case with simple nonspatial Lotka–Volterra models, it illustrates clearly that the inclusion of spatial information affects the resulting dynamics. The qualitative outcomes from the CA model and from the difference equation models are congruent, as both predict cyclical and chaotic dynamics resulting from strong density dependence. Their difference lies in the parameters that generate these cyclical results. The dynamics in the CA model depend on both the strength of density dependence and the scale of dispersal relative to the scale of density dependence, whereas the dynamics in nonspatial models depend on the strength of the density dependence (May 1974).

Such highly abstract, simplified systems are rarely adequate to represent any ecological situation. Slightly more complex applications involve the application of rules that have more than two states. Hassell and colleagues (1991) developed a CA model to examine how local dispersal influences host–parasitoid dynamics. The model was first constructed using difference equations applied within each location, with a fraction of hosts or parasitoids dispersing to neighboring locations at each time step. To test whether the dynamics are a function of the structure of the equations, rather than use alternative formulations of the difference equation, Hassell and colleagues constructed a nine-state CA model based on different qualitative categories of parasites and hosts, determined from the difference equation model, with local dispersal occurring between the eight neighboring cells. Simulation of the CA produced results qualitatively similar to those of the difference equation model. Thus, Hassell and colleagues concluded that their results were not a function of the specific model formulation but a true representation of the host–parasitoid system with spatially local interactions. Their results show that highly simplified CA formulations can adequately encapsulate important properties of a system.

Cellular automata models may also employ probabilistic transition rules. Molofsky and Bever (2002) constructed a probabilistic CA model of positive frequency dependence. Positive frequency dependence, in which the relative success of a species increases as its frequency of occurrence increases, can result from mutualistic ecological interactions in which different species depend on each other for their survival or reproduction. An example of an ecological interaction that may result in positive frequency dependence is the

relationship between insect pollinators and the plants they pollinate. Individuals surrounded by neighboring plants may be more likely to receive pollinators, thereby receiving more pollen and attaining higher levels of reproduction. In the absence of spatial considerations (i.e., in what is called a mean-field model), positive frequency dependence quickly leads to the loss of diversity and to the dominance of one species. To examine the dynamics within a spatial context, we imagine many species occupying positions in a two-dimensional grid. The probability that a species will occupy a site in the next generation increases as its own frequency increases in the interaction neighborhood (Molofsky and Bever 2002). The scale of dispersal into the site and the presence or absence of sites unsuitable for colonization are controlled separately (see Molofsky and Bever [2002] for details).

To illustrate the model, we start with 10 equally abundant species randomly dispersed on a grid, 40% of whose sites are unsuitable for colonization (figure 2a). From these starting conditions, the rules for local occupancy are iterated to generate patterns. When species interactions and dispersal occurred over a large scale, thereby minimizing the importance of spatial location, we found that one species quickly dominated the entire grid, as predicted by the mean-field model (figure 2b). However, when the scale of frequency dependence and dispersal were both local, monomorphic patches formed (figure 2c) and then stabilized (figure 2d). Positive frequency dependence did not result in the loss of diversity. On the contrary, diversity was maintained much longer with strong positive frequency dependence than would be expected as a result of random drift (Molofsky and Bever 2002).

These examples of CA models illustrate the utility of using systems of basic rules to identify the consequences and scale dependence of general processes. In the interest of generality, the models are deliberately kept simple and therefore are necessarily not accurate representations of any particular ecological system.

Empirical applications: Predicting dynamics in specific systems. A second type of CA model involves fitting transition state models to real systems. In these models, the transition between one time step and the next depends on the empirical relationship between the current state of the target cell and that of its neighbors. These transition probabilities are most often derived directly from field observations or direct experimentation. The goal of such studies is to provide a way to predict, from measurements taken at the small scale, the state of the system at some point in the future. These models are quite commonly used in ecology, and their nonspatial analogs are called Markov transition models (Caswell 2001). Most notably, Horn (1975) applied Markov transition models to understand the successional dynamics of eastern deciduous forests in New Jersey. Unlike the goal of rule-based models used in ecology, which is to elucidate how simple processes can create novel dynamic outcomes, the goals of these models are to predict future patterns on the basis of

empirically derived transition probabilities and to identify how patterns can be affected by modifying these probabilities.

This approach was applied by Wootton (2001) to elucidate the complex factors controlling community dynamics. Wootton used a hierarchical modeling approach to understand the dynamics of the rocky intertidal community in Tatoosh, Washington. This community is composed of sessile organisms such as mussels, filamentous algae, and diatoms that attach to bare rocks. Wootton developed a model of the mussel beds inhabiting the rocky intertidal community. By following fixed points in this community over 6 years, he estimated the transition probabilities among different states (e.g., from bare rock to occupancy by a species of mussel). Wootton initially chose 15 different transition states to represent the transitions in the rocky intertidal zone (e.g., bare space, species identity, size class of a species) and incorporated the effects of different disturbance rates, seasons, and neighbor densities on the transition probabilities. The full model did a good job of re-creating the dynamics of the mussel beds in the rocky intertidal community. Furthermore, by selectively eliminating aspects of the full model, Wootton determined that explicit consideration both of large-scale disturbance and of local interactions was necessary to generate spatial patterns that were similar to those seen in the real system.

Seabloom and colleagues (2001) used a similar approach to develop a CA landscape model of a freshwater wetland, based on detailed information about the water table; about recruitment of seeds, seedlings, and adult plants; about landscape geometry; and about the spatial patterns of existing vegetation. Like Wootton (2001), Seabloom and colleagues tested a series of models of increasing complexity to determine which factors were most important in explaining the vegetation patterns. In comparing simulation results to aerial photographs, they found that the importance of each of the factors depended on the depth of the water table. In both this and the Wootton example, the CA transition models proved to be valuable tools for analyzing the dependence of patterns on particular processes within complex data sets. Similar models have been applied to understand the processes that control vegetation banding patterns in Africa and Australia (Thiery et al. 1995, Jeltsch et al. 1996, Dunkerley 1997).

Cellular automata models designed to fit particular systems have also been used to investigate spatial pattern formation in communities. For example, Silvertown and colleagues (1992) developed a CA model that simulated interspecific competition among five grass species. Transition probabilities between species were determined from pairwise competition experiments. Spatial simulations were run either with a random arrangement of individuals in the landscape or with different arrangements of monospecific bands. Simulations performed with random initial arrangements always resulted in three of the five initial species rapidly becoming extinct, while a fourth species experienced a slower decline until only one species remained. Initiating the model with different monospecific clumps of each species, however, dramatically altered the transient dynamics, allowing all five species to

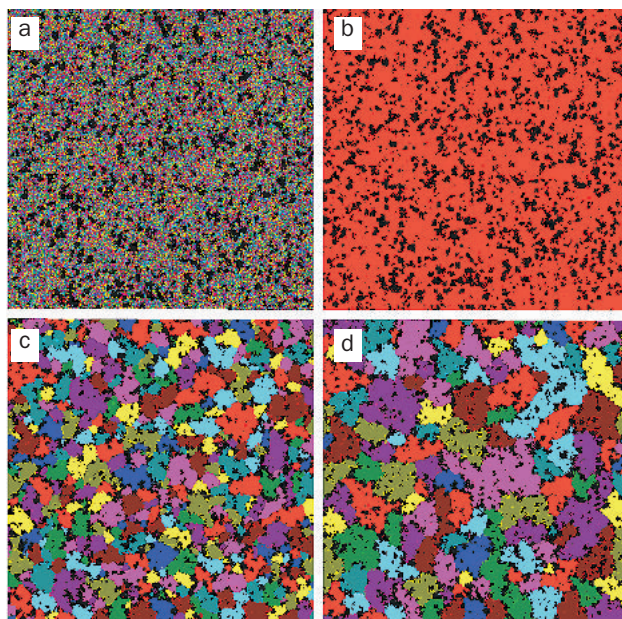


Figure 2. Spatial patterns that develop from simulation of the two-dimensional, probabilistic cellular automata (CA) model of positive frequency dependence. The CA model is initiated with 10 species (indicated by different colors) on a 400 x 400 grid. (a) Initial conditions show the 10 species randomly arrayed on the two-dimensional grid, with 40% of the space uninhabitable (black squares). (b) When positive frequency dependence is applied, with dispersal and frequency dependence occurring over a large scale to emulate spatially inexplicit models, species diversity is lost, and only one species (indicated in red) remains after 30 generations. (c, d) By contrast, when the scale of the interaction and the scale of dispersal occur locally (over the target cell and the eight surrounding neighborhood cells), species diversity is maintained by the development of monospecific clumps that can remain relatively stable (shown here after 1000 generations [c] and 1,000,000 generations [d]). The inclusion of spatially explicit local interactions (in this case, frequency dependence and dispersal) produces a unique result not seen in the nonspatial model. The unique result is a direct outgrowth of the formation of monospecific clumps, a result difficult to predict using spatially inexplicit, analytically tractable formulations. Thus, the CA model provides a unique result using a relatively easy approach for exploring spatial structure within this system.

coexist over much longer time scales. Under certain starting conditions, long-term coexistence of the two dominant species was possible, and under one starting condition, a reversal of the dominance relationships was observed over 600 generations. In this example, the use of CA models provides an easily implemented modeling approach to assess how the

specifics of a spatial pattern can affect the dynamics and patterns of species coexistence.

The spatially explicit CA models based on transition probabilities in real systems provide an alternative mechanism for modeling natural systems. Their utility depends both on how important explicit local spatial information is for understanding the community patterns and on the type and availability of data to construct the model. As seen in the studies by Wootton (2001) and Seabloom and colleagues (2001), these models can be particularly effective for determining the controlling factors of community organization, if sufficient data are available to adequately determine the model accuracy. The example of Silvertown and colleagues (1992) illustrates how short-term experiments can be combined to predict long-term system behavior and how different starting conditions can generate very different outcomes.

Reflections on the applications of cellular automata models.

The potential of spatial relationships among individuals to alter dynamics has recently attracted much attention from ecologists (Tilman and Kareiva 1997, Dieckmann et al. 2000, Bercé 2002). Although some ecological systems, such as planktonic algae, are well described without explicit consideration of their spatial relationships because they are continually well mixed (Tilman 1977), understanding the ecological dynamics of communities of sessile organisms such as plant, coral, and intertidal species often requires inclusion of their spatial arrangement.

Modeling approaches vary in the level of spatial detail that they incorporate. Early attempts to include space in ecological models, including early island biogeographic models (MacArthur and Wilson 1967) and patch occupancy or metapopulation models (Levins 1969), envisioned populations occurring in discrete patches but omitted precise spatial information. Other early approaches envisioned space and time as being continuous, with diffusion of individuals occurring among locations (Skellam 1951, Okubo 1980). Recent advances in theoretical ecology have resulted in new analytical techniques that allow researchers to include more precise spatial information about the arrangement of individuals in analytically tractable models. However, even these approaches, including pair approximations (Hiebeler 1997) and spatial moment equations (Bolker et al. 2000), may not always capture enough of the spatial complexities to adequately represent a system. Thus, these approaches require numerical approximation or individual-based simulation modeling to verify the analytical solutions (see Dieckmann et al. 2000).

By fully accounting for the spatial arrangement of individuals, CA models represent an extreme case of efforts to consider the importance of space. As such, CA models are not easily understood using the traditional analytical tools of mathematics. In Wolfram's approach, analogous analytic efforts are ignored, and the system's lack of analytical tractability is compensated for by attempting to simulate all possible rules and then hunting for generality among the results (as he does by examining the 256 two-state, one-

dimensional CA models previously discussed). Of course, even if one could develop a universal set of simple rules that would apply to different ecological situations, attempting to simulate all possible rule permutations would quickly become futile, because the number of possible combinations grows exponentially. But, more generally, we feel that there is great utility in applying multiple approaches. When multiple approaches yield qualitatively similar results, general principles about the important processes creating the dynamics are revealed, as illustrated by Hassell and colleagues (1991). Modeling the same problem with different approaches will provide direct confirmation of the importance (or lack thereof) of spatial processes. Thus, the generality of analytic results to violations of their spatial assumptions can be evaluated by complementing such studies with CA simulations (see Durrett and Levin 1994, Tilman and Kareiva 1997, Dieckmann et al. 2000, Berec 2002).

While CA models represent one extreme of a tradeoff between spatial realism and analytic tractability in model construction, the applications of CA models to ecology closely parallel the tradeoff between generality, precision, and realism that constrains all model development in ecology (Levins 1966). As we have illustrated, CA models can be useful in investigating the general consequences of ecological processes (e.g., Hassell et al. 1991, Molofsky 1994, Molofsky and Bever 2002), but these simulations do not necessarily reflect the specific biology of any particular system. Such CA models follow the tradition of difference models and differential equation models of ecological interactions, as first employed by Lotka (1932) and Volterra (1926). Alternatively, the CA approach can be fruitfully applied to the projection and investigation of dynamics within a particular system, although the results may not be relevant to other systems (e.g., Silvertown et al. 1992, Seabloom et al. 2001, Wootton 2001).

Is it “a new ecology”?

Does the CA approach constitute the basis of “a new ecology,” as Wolfram argues? We do agree with Wolfram that the CA approach is a valuable tool that can yield unique insights (Molofsky and Bever 2002). And certainly the incorporation of spatial information into model building has altered, and will continue to alter, ecologists’ understanding of ecological systems. However, from our reading of the literature, we feel that Wolfram’s claim of a scientific revolution due to the application of CA models is unwarranted. Rather, CA models represent a valuable tool in a growing and evolving toolbox that ecologists use to understand ecological systems.

There are certainly new behaviors that arise in CA models. For example, in class 4 behavior, a single rule can generate both a region that contains a static pattern and a region of apparent unpredictability (figure 1d). This is indeed a unique contribution that could potentially affect interpretations in ecology, because it means that a single process might generate a static pattern in one region and an unpredictable, chaotic pattern in an adjacent region. Nevertheless, as far as we are aware, class 4 behavior has not been demonstrated for

any of the current applications of CA models in ecology. Given that most ecological processes are best described using probabilistic rules, and that probabilistic rules cannot generate class 4 behavior, it seems unlikely that class 4 dynamics will be found for ecological systems. Furthermore, in applications of CA models that seek to explain the dynamics of real systems, it would be difficult or impossible to distinguish class 4 behavior seen in the field from random stochastic fluctuations. Thus, we feel that one of Wolfram’s most intriguing claims is unlikely to apply to the field of ecology.

Perhaps the lesson from *A New Kind of Science* is that complexity is generated very easily. Ecologists have trumpeted the idea that ecological systems are very complex and must therefore be organized by many competing processes. Yet the determination of which processes are fundamental to understanding a system’s behavior is fraught with controversy. Wolfram asserts repeatedly that one need not look for multiple or complex processes to explain observed patterns, since simple rules can generate complex behavior. Given the evidence of redundancy in the processes that control ecological dynamics, determining a priori which interactions are essential to system behavior seems unlikely. This leaves ecologists back where we started, measuring multiple processes, projecting their dynamics and interdependence, and trying to digest generality from the output. As always, the devil is in the details.

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