

# The limits to prediction in ecological systems

BRIAN BECKAGE,<sup>1,†</sup> LOUIS J. GROSS,<sup>2</sup> AND STUART KAUFFMAN<sup>3</sup>

<sup>1</sup>*Department of Plant Biology, University of Vermont, Burlington, Vermont 05405 USA*

<sup>2</sup>*National Institute for Mathematical and Biological Synthesis, University of Tennessee, Knoxville, Tennessee 37996-1527 USA*

<sup>3</sup>*Department of Mathematics, Department of Biochemistry, and Complexity Group, University of Vermont, Burlington, Vermont 05405 USA*

**Citation:** Beckage, B., L. J. Gross, and S. Kauffman. 2011. The limits to prediction in ecological systems. *Ecosphere* 2(11):125. doi:10.1890/ES11-00211.1

**Abstract.** Predicting the future trajectories of ecological systems is increasingly important as the magnitude of anthropogenic perturbation of the earth systems grows. We distinguish between two types of predictability: the intrinsic or theoretical predictability of a system and the realized predictability that is achieved using available models and parameterizations. We contend that there are strong limits on the intrinsic predictability of ecological systems that arise from inherent characteristics of biological systems. While the realized predictability of ecological systems can be limited by process and parameter misspecification or uncertainty, we argue that the intrinsic predictability of ecological systems is widely and strongly limited by computational irreducibility. When realized predictability is low relative to intrinsic predictability, prediction can be improved through improved model structure or specification of parameters. Computational irreducibility, however, asserts that future states of the system cannot be derived except through computation of all of the intervening states, imposing a strong limit on the intrinsic or theoretical predictability. We argue that ecological systems are likely to be computationally irreducible because of the difficulty of pre-stating the relevant features of ecological niches, the complexity of ecological systems and because the biosphere can enable its own novel system states or adjacent possible. We argue that computational irreducibility is likely to be pervasive and to impose strong limits on the potential for prediction in ecology.

**Key words:** chaos; climate change; computational irreducibility; computational incompressibility; ecological communities; invasive species; niche; prediction.

**Received** 25 July 2011; revised 7 October 2011; accepted 12 October 2011; **published** 21 November 2011. Corresponding Editor: D. P. C. Peters.

**Copyright:** © 2011 Beckage et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits restricted use, distribution, and reproduction in any medium, provided the original author and sources are credited.

† **E-mail:** Brian.Beckage@uvm.edu

## INTRODUCTION

Ecological systems are strongly impacted by anthropogenically induced perturbations such as global climate change and the spread of non-native species (Beckage et al. 2008, Stevens and Beckage 2009). Predicting the effects of these perturbations on natural systems is increasingly important as the magnitude and severity of

anthropogenic perturbations intensify (e.g., Clark et al. 2001, Tang and Beckage 2010). But are ecological systems fundamentally predictable? What are the limits to prediction in ecological systems? The assumption underlying efforts to predict ecological responses to anthropogenic perturbations is that their responses are, in fact, predictable. We examine this assumption and provide a framework for understanding the

potential for and limits to prediction in biological systems generally and in ecological systems in particular. We begin by defining predictability, and then outline two processes, chaos and computational irreducibility, that can limit predictability in biological systems but in very different ways.

*Prediction.*—We use ‘prediction’ to refer to the use of a computational or mathematical model to forecast the future state of a system to some specified level of accuracy (e.g., mismatch between predicted and actual state) before the system reaches its future state. We distinguish between two kinds of predictability following Lorenz (2006): intrinsic and realized predictability. The intrinsic predictability of an ecological system refers to the predictability of the system when the optimum model and parameters are used. This is the greatest predictive capacity that can theoretically be achieved for a given metric across all possible models of the system. In contrast, the realized predictability is the predictability that is actually achieved using available models and parameterizations. The difference between the realized and intrinsic predictability represents the potential for model improvement.

Failures to accurately predict the behavior of any given system, such as identifying a priori non-native species that will be invasive, is often assumed to reflect a low realized predictability rather than low intrinsic predictability. The lack of success is perceived to result from model misspecification rather than to be a fundamental characteristic of the ecological system. In the former case, the clear course of action is to improve the model formulation and parameterization, including potentially obtaining new observations on the system, to increase the realized predictability of the system. There is a long history, for example, of adding more realistic components to ecological models to account for temporal and spatial heterogeneity (Levin 1976). But what if low predictability results not from misspecification of the model but instead reflects the inherently low intrinsic predictability of the system?

*Determinism and predictability.*—Achieving an understanding of process or underlying mechanism has become a central objective of ecological research (Schoener 1986). An understanding of

process can allow for prediction outside of the range of conditions for which the process has been directly observed, which is generally not feasible when utilizing purely statistical models. Vegetation models that are physiologically based, for instance, are more likely to be useful in understanding ecological responses to climate change than purely statistical models that map vegetation to current climates because future climates are likely to be novel (Kaplan et al. 2003, Sitch et al. 2003, Williams et al. 2007, Tang and Beckage 2010). We typically cannot model all of the relevant processes in ecological systems, however, so our consideration is limited to a select subset of processes. The processes not included in the model are then often treated stochastically as unstructured noise. Seed dispersal, for example, is often modeled probabilistically (Clark et al. 1998) as it is difficult to completely account for the physical basis of wind dispersal (e.g., Nathan et al. 2002) or the details of animal-mediated dispersal without incorporating a model for the dispersal agents. The implication is that increased understanding and broader inclusion of relevant processes will reduce stochasticity and increase the quality of predictions of ecological dynamics, i.e., that the problem of poor prediction is one of low realized rather than low intrinsic predictability.

Determinism, however, should not be equated with high intrinsic predictability. Attributes of physical and biotic systems can impose strong limits on the intrinsic predictability of ecological systems even in the absence of real stochasticity, i.e., stochasticity that does not just stand in for unidentified process. These system attributes include chaotic dynamics and computational irreducibility. These processes are not stochastic, but nevertheless can severely limit the intrinsic predictability of ecological systems. While chaotic dynamics are well known to ecologists, computational irreducibility may be less familiar. We discuss these processes below.

## CHAOS

The predictability of a system defined by a known deterministic process is related to how errors in the specification of initial conditions grow or dampen over time (Lorenz 2006). Chaos refers to the apparent unpredictability of com-

pletely deterministic systems, where the unpredictability is driven by exponential growth of errors in the specification of the initial state. Ecologists have long been aware that nonlinearities and feedbacks from time delays can lead to chaos in population models (May 1974, Levin and May 1976). Systems that exhibit chaotic behavior can be very simple, and, in fact, chaos was first widely recognized in ecology in notably uncomplicated population models (May 1974). Chaos demonstrates that even when the exact representation of the underlying deterministic process is known, which is usually not the case in ecology, accurate predictions of the future state of the system still may not be possible. Precise specification of the initial conditions is also necessary to predict the future state of the system, and arbitrarily small errors can result in large departures from the actual future system state. Chaos was first widely recognized in meteorology (Lorenz 1963), where explosive growth of errors in the specification of initial conditions limits prediction of many aspects of weather to no more than about two weeks into the future.

*Chaos in ecological systems.*—Chaos may be commonplace in ecological systems (Hastings et al. 1993). Chaotic dynamics have been identified in some experimental manipulations of populations (Constantino et al. 1997), but most evidence of chaos has come from models of ecological processes (e.g., Maquet et al. 2007, Upadhyay 2009, Gassmann et al. 2005). The presence of chaos in models of ecological systems, however, does not necessarily mean that the ecological systems themselves are, in reality, chaotic (Rai 2009), and chaos is likely to be difficult to definitely detect in ecological data (e.g., Dennis et al. 2003, Ellner and Turchin 2005, Scheuring and Domokos 2007, Upadhyay 2009). But if chaos is common in ecological systems, then ecologists have two problems in prediction: First, identifying the precise form of the dynamical process governing the evolution of a given ecological system and, second, establishing with arbitrary precision the system state at some initial time. These are difficult challenges that are likely to impose strong limits on the realized predictability of ecological systems that are chaotic—greater challenges than faced by, for example, meteorologists who at least have well-

understood physical equations that govern the evolution of the climate system. Thus, while the intrinsic predictability of chaotic systems might be high, the realized predictability is expected to be low and difficult to substantially improve.

If chaos does not widely occur in ecological systems, then errors arising from misspecification of the initial system state may only be linearly related to errors in model projection. In this case, neither initial states nor the formulation of the governing process need to be known exactly, but only approximately: the predictive error should scale with the precision of this approximation. We suggest that even in these cases, however, there is another barrier to prediction: computational irreducibility.

### COMPUTATIONAL IRREDUCIBILITY

An ecological system changes through time, updating its state continuously, and the process of system evolution can be thought of as computation (Wolfram 2002). Our use of the term ‘system evolution’ is much broader in meaning than biological evolution, and also includes changes in abundance, location and interactions between individuals irrespective of species, and the interface between the biotic and abiotic components of the system, e.g., flux of nutrients, water, etc. Predictive models, then, are able to forecast the future state of the system before the system performs the intermediate computations to reach its updated state. An astronomical model, for example, might predict the earth’s position and orientation relative to the sun millions of years into the future, without the need for the solar system to perform the intervening computations. The intervening computations that the system performs can be circumvented to predict its future state. The astronomical model might, for example, be used to predict the latitudinal and seasonal distribution of insolation on earth, which describes the past orbital forcing of the climate system, for comparison with paleoclimatic data (e.g., EPICA community members 2004).

Computational irreducibility refers to systems where the intervening computations cannot be bypassed using a simplified model. The dynamics of a system that is computationally irreducible cannot be predicted without allowing for the

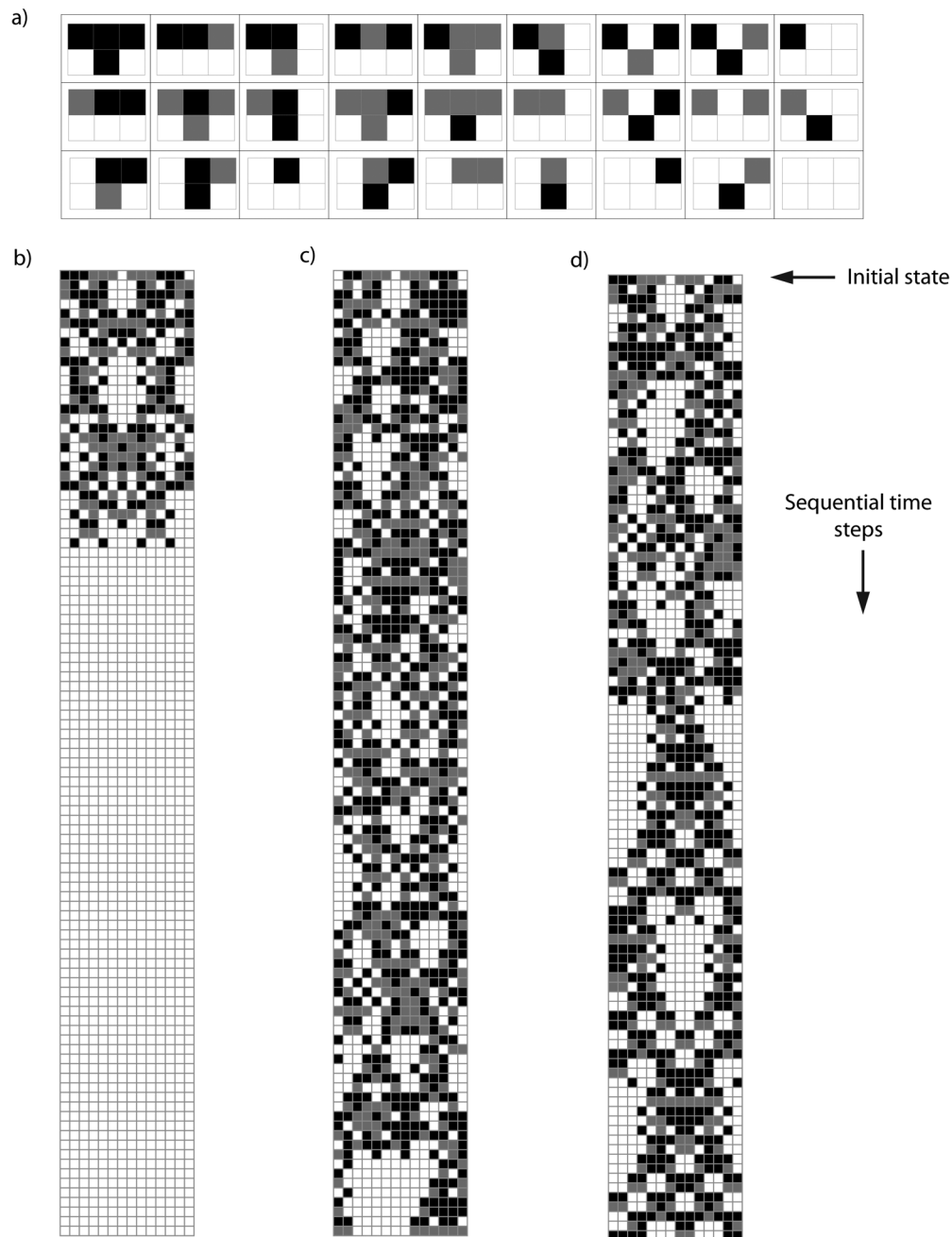


Fig. 1. Computational irreducibility can occur in even simple cellular automata (CA). Predicting the state of the system can be challenging without actually allowing the system to evolve by performing its intrinsic calculations. (a) The set of rules governing the evolution of the system state. Three states are possible: A cell may be white, black, or gray. The state of the focal cell in the next time step depends on its current state and its bordering neighbors (a 3-tuple). The top row of each 3-tuple of cells represents the initial state of the neighborhood, while the middle cell beneath the 3-tuple represents the state of the focal cell at the next time step. There are 27 possible configurations (i.e., rules governing the dynamics) in this case. In general, there are  $n^n$  configurations for an  $n$ -tuple, which could correspond, for example, to spatial effects extending beyond nearest neighbors. We show the evolution of this cellular automaton for 100 time steps starting from three different initial conditions in panels (b), (c), and (d).

actual evolution of the system (Fig. 1). A simplified model that can predict the future state of the system does not exist. Thus, the only way to ascertain the future state of the system is to allow the system to evolve on its own characteristic time scale. Computational irreducibility does not imply that the underlying processes are stochastic or chaotic, but that they are complex. The complexity can be manifested through high levels of contingency, interactions among system components, and nonlinearity. In fact, systems that evolve according to simple deterministic processes with exactly-known initial conditions can give rise to a complex state evolution that cannot be exactly predicted except by allowing the system to evolve in real time (Wolfram 2002) (Fig. 2). Computational irreducibility, furthermore, may be a fundamental characteristic of some systems and does not merely reflect a shortcoming of proposed models or modeling techniques. This implies that the intrinsic predictability of these systems is inherently low.

*Computational irreducibility in ecological systems.*—We argue that the dynamics of many ecological systems are computationally irreducible. We base this assertion on three attributes: (1) the difficulty of pre-stating the relevant features of the niche, (2) the complexity of ecological communities, and (3) their potential to enable novel system states (e.g., niche creation) through the adjacent possible.

*Relevant niche features.*—The relationship between species and their environment can be characterized by a high-dimensional niche space (Clark et al. 2007). Ecological models are challenged to account for the myriad effects of diverse environmental variables on species. The difficulty stems from the challenge of pre-stating the relevant features of the niche in any given environment. Modeling the responses of species to environmental change, for instance, requires selecting the dimensional subset of the niche space most relevant to mapping a species to its

environment. If environmental forcing moves the system into a novel area of environmental space (Williams et al. 2007), then species responses to this forcing, by definition, have not been previously observed and there is little basis for a priori selecting the relevant niche features. Furthermore, the most relevant features of the niche space are likely to be contextually sensitive to and vary with both the abiotic and biotic (e.g., presence of competitors, predators, etc.) environment.

*Complexity.*—Ecological assemblages are networks of locally interacting individuals of diverse species both within and across trophic levels. The complexity of ecological communities increases rapidly with the addition of species as the number of potential interconnections between system components grows nonlinearly: The potential for diverse system responses explodes with the number of species interactions. The strength and sign of the interactions between components of this ecological network can change as species enter (or are lost from) the community and as environmental conditions change. Differential species responses to climate change can result, for example, from phenological mismatches between interacting species and can lead to novel community assemblages without analog (Møller et al. 2008, Williams and Jackson 2007). If the environmental change is large enough to allow new species to enter into the community as others leave, resulting in novel species assemblages, then the system connectedness is altered in a manner such that no observations or experience exists to parameterize a model or to guide prediction. The system behavior is unknown. Furthermore, species are likely to respond nonlinearly to forcings (environmental variation) with responses expected to vary within and across species. The interconnectedness of the system components means that responses or perturbations of individual components cascade through the system, propagating across the network of interactions within and

---

Fig. 1 (continued). The initial condition is shown at the top of each panel with subsequent time steps in the evolution of the system shown in sequence below the initial state. The dramatic differences in the evolution of the system in (b), (c), and (d) result from a change in the initial state of only one cell, emphasizing the difficulty of predicting the state of the system without allowing the system to actually compute this state. This cellular automaton rule corresponds to code 1599 in Wolfram (2002).



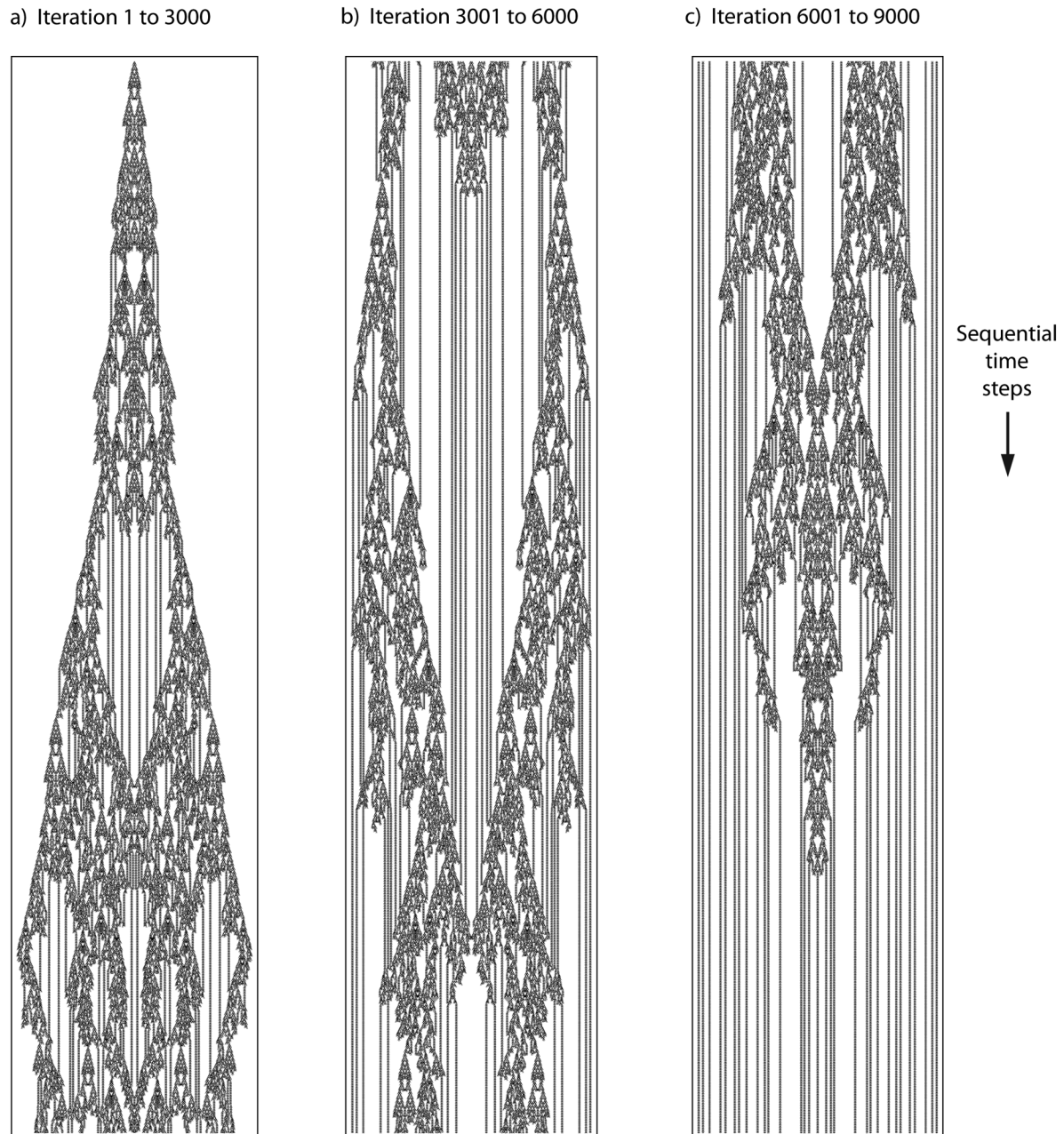


Fig. 2. The evolution of the cellular automaton in Fig. 1 for 9,000 time steps beginning from a single gray cell with neighboring white cells (top of panel a). Each panel contains the initial condition + 3000 iterations of the cellular automaton; the initial condition for panels (b) and (c) are the final state of the cellular automaton in the previous panel. The system appears to arrive at a stable state near the bottom of panel c but it is not clear that this state could be predicted without allowing the actual system to evolve. This figure follows Wolfram (2002: page 70).

across tropic levels. We suggest that the net effect of these complex cascades on the system state are unknowable a priori: The effect of these interac-

tions on the system cannot be known until these computations are actually performed by the system (e.g., Huisman and Weissing 2001). The

system dynamics can only be understood as the system evolves and thus is computationally irreducible.

*Niche creation and the adjacent possible.*—Biological systems are uniquely able to construct and structure their own environments and to enable their own opportunities for growth and evolution through the creation and modification of niche space. The ‘adjacent possible’ represents the potential for creation of or extension of that niche space that is immediately adjacent to current niche space. The evolution of plants, for instance, allowed for the evolution of herbivores. The emergence of trees created a diverse new set of niches that formerly did not exist—everything from spring ephemerals to epiphytes to arboreal vertebrates. Biological change begets more biological change. The process of creation of new biological opportunities allows for the emergence of new organisms to fill these opportunities, and new ecological networks and interactions emerge. This process is intrinsically driven by positive feedbacks that can potentially result in an explosion of biological and ecological diversity. The biosphere continuously creates and moves into the adjacent possible. We assert that this process is enormously creative and unpredictable *a priori*.

*Relationship to other conceptual frameworks.*—Holling and colleagues have developed a conceptual framework (‘panarchy’) to describe the dynamics of complex systems, including ecological systems (Gunderson and Holling 2002). Their framework views the complexity of ecological systems as not stemming from the interactions of a large number of components but from a small number of controlling processes. System dynamics are then characterized as continuing adaptive cycles of growth, accumulation, release, and reorganization that are hierarchically linked across spatial and temporal scales. The release and reorganization phases of the adaptive cycle are inherently innovative and creative, so that even minimally complex systems can be unpredictable (Holling 2001). We suggest that the source of the creativity and the process driving the subsequent unpredictability are the adjacent possible and computational irreducibility.

The adjacent possible is also related but not limited to two other concepts in ecology: ecological engineering and niche construction. Niche

construction and ecological engineering describe two ways that the biosphere creates and expands into the adjacent possible. Ecological engineers modulate the availability of resources while creating or modifying habitats (Jones et al. 1994). Beavers, for example, create wetlands that are then utilized by other organisms. Ecological engineering does not imply any benefit to the engineer and, in fact, other species can realize most of the benefit. In niche construction, in contrast, the organism modifies its environment to increase its own fitness. Most of the benefit must be realized by the organism constructing the niche for niche construction to be evolutionarily stable (Krakauer et al. 2009). The expansion of the biosphere into the adjacent possible includes both niche construction and ecological engineering, but can also include other processes. The process of evolution, for example, creates organisms and life forms that intrinsically create new opportunities for expansion of the biosphere. The biosphere itself modifies the earth system, e.g., high levels of oxygen in the atmosphere, in a manner that is broader than creation of a specific habitat. An analogy to predicting the future state of a biological system might be predicting the nature of the economy a century in advance. The economy creates and moves into its own adjacent possible as products and services create the opportunities for other products and services. A century ago, it would have been difficult to predict the economic value of a company providing an internet search engine as neither the worldwide web nor electronic computers existed. We argue that predicting the future state of the biosphere is similarly difficult.

## ECOLOGICAL EXAMPLES

*Climate change.*—We contend that the responses of ecological systems to anthropogenic climate change are likely to be computational irreducible. Current climate change represents a rapid and complex multivariate shift in the environmental conditions experienced by individual organisms. Global temperatures are rapidly rising and approaching a region of climate space not likely experienced for the past 1 million years (Hansen et al. 2006), implying that extant species have not experienced the climatic conditions expected

with anthropogenic forcing. Species are likely to alter their ranges at differential rates with idiosyncratic responses and unique shifts in geographic range (e.g., Davis and Shaw 2001, Moritz et al. 2008). Species that do not currently co-occur may interact under future climatic conditions, while other species that now co-occur may become geographically separated; these responses may collectively result in novel species assemblages without current analogs (Williams and Jackson 2007). We argue that the magnitude and even the sign of these novel interactions are unknown, cannot be predicted *a priori*, and cannot be ascertained experimentally. There is evidence that responses to climate change will also vary across trophic levels (Voigt et al. 2003, Winder and Schindler 2004), disrupting the interactions of even currently co-occurring species that could then cascade through the system. Individualistic responses to climate change can result in complex changes in highly linked ecological systems. The dynamics of ecological systems in response to climate change are thus likely to be computationally irreducible: We will only know future states once climate has changed, and species and ecological communities have responded.

*Invasive species.*—Predicting which introduced non-native species will displace native species and which ecological communities are vulnerable to invasion are two principle goals of invasion ecology that have not been achieved (Kolar and Lodge 2001). Instead, invasion biology has largely been an *ad hoc*, retrospective analysis of why certain species have become invasive when introduced into new habitats (e.g., Rosecchi et al. 2001, Roura-Pascual et al. 2009). We suggest that the prediction of species invasions and community invasibility has proven to be such an intractable problem because it is computationally irreducible for reasons similar to those outlined above for climate change. The response of an introduced species to the concurrent effects of introduction into a novel high-dimensional environmental space while also merging into an existing network of interacting species is a problem for which, by definition, we have little empirical basis for prediction. Experience does indicate, however, that the introduction of an invasive species can cascade through a community with complex and apparently random effects

on community structure (Sanders et al. 2003). Thus, the only way to understand the potential for an introduced species to be invasive in a particular ecological community may be to observe empirically whether it is invasive in that ecological community. We assert that the prediction of species invasion into ecological system is computationally irreducible, and invasion ecology is thus predominately comprised of retroactive case studies of species invasion.

## IMPLICATIONS FOR PREDICTION

Complex systems with extremely large numbers of components can sometimes become predictable from a macro-level perspective due to the averaging of a very large number of separate interactions. In statistical physics, for example, an approximate description of the mean state of a gas is possible without an exact description of the velocities and locations of each molecule; the temperature and pressure of a gas can be described using the ideal gas law. An ecological analogy to the ideal gas law might be the species composition of a forest. Forest composition is ultimately an emergent property that results from the local interactions of many individuals and processes, i.e., seed production and dispersal, competition, growth rates, trade-offs, etc. While it may not be possible to determine the outcome of all of these complex interactions to predict the species identity of the tree species that captures a given canopy gap, the overall composition of the forest can be predictable to some approximation (e.g., Clark and McLachlan 2003). While this statistical averaging of interactions is the standard assumption in many deterministic ecological models, it may be more accurate to view most ecological systems as small-to-middle-number systems because local interactions are quite relevant in affecting system behavior. In this case, there would be a general lack of the homogeneous mixing necessary for a purely statistical mechanics view to be applicable.

We conjecture that skill in predicting the future states of ecological systems will decrease as system complexity increases up to some threshold level. Further increases in system complexity beyond this threshold, for example, through expanding interconnected components of the



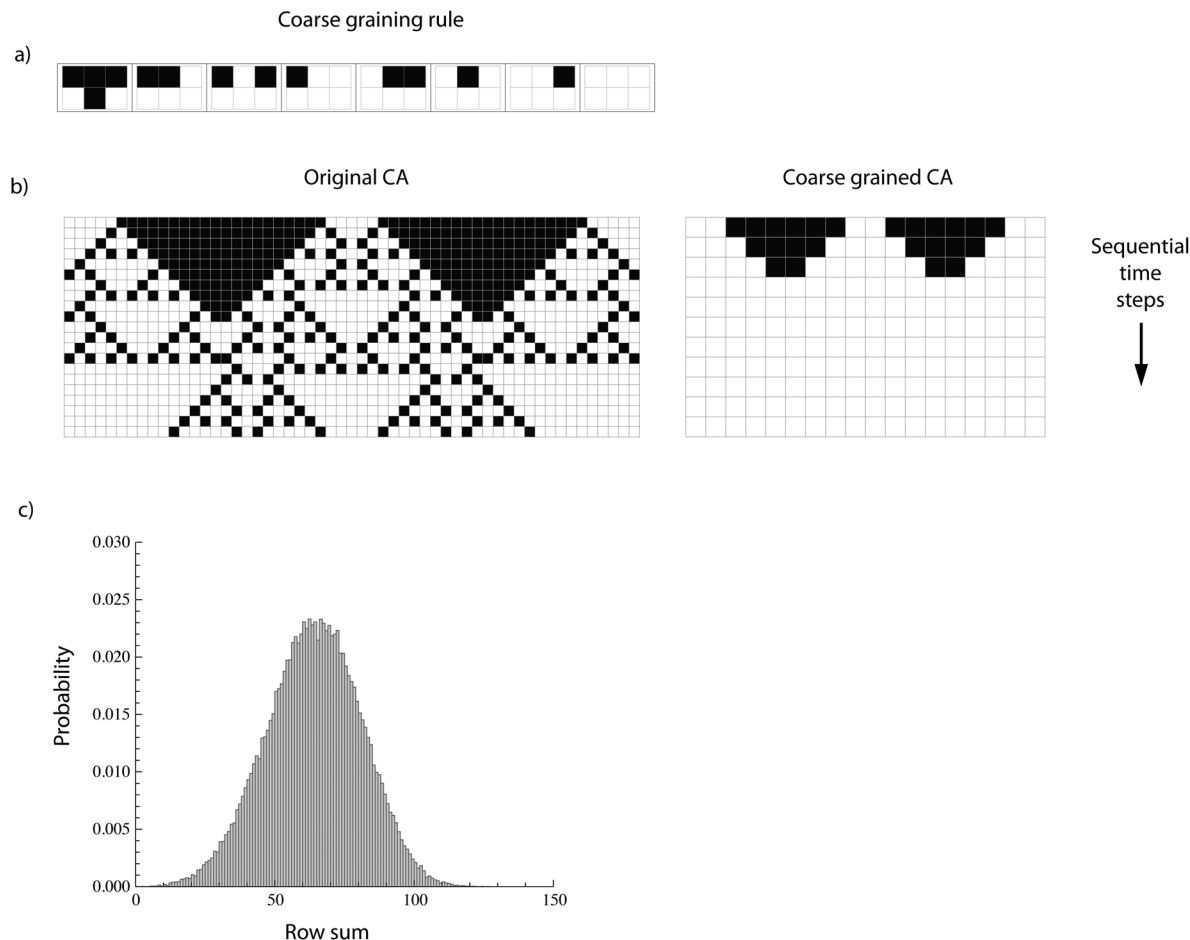


Fig. 3. Some aspects of complex systems can be predictable. (a) A rule for coarse-graining cellular automaton rule 146 using rule 128 (Israeli and Goldenfeld 2006). (b) Evolution of the original and coarse-grained cellular automaton. Some aspects of the system can be predicted more quickly than the actual system evolves, but with accompanying information loss. (c) Probabilistic statements can be made regarding the distribution of CA metrics such as row sums. We show the distribution of row sums of rule 1599 (i.e., Fig. 1) at 100 time steps from 100,000 realizations with random initial conditions. White cells were assigned values of 0, gray cells 1, and black cells 2.

system or increasing potential for nonlinear interactions, will not result in further losses in predictability (Wolfram 2002). Furthermore, this threshold may occur at relatively low system complexity. We note, however, that the behavior of complex ecological systems can often be readily deconstructed and explained in hindsight as the cascade of interactions and nonlinearities is examined and understood. We emphasize that this may not aid predictions of future system states due to computational irreducibility.

*Prediction in computationally irreducible systems.*—The predictability achieved by this statis-

tical averaging approach is similar to coarse-graining of computationally irreducible cellular automata (Fig. 3) (Israeli and Goldenfeld 2004, 2006). In coarse-graining, some predictability of computationally irreducible systems can be gained through spatial aggregation of cells into larger units with a new set of updating rules. This allows some patterns of the system to be predictable prior to the system actually computing its future state. The predictability results from a spatial averaging, but comes at the cost of information loss. In the context of landscape metrics, however, Wu (2004) notes that some

metrics scale predictably with spatial aggregation but others do not. This indicates the capacity for enhanced prediction of some metrics at broader spatial extent, but not for others. It is unclear whether it is possible to develop a general theory for determining under what circumstances and for what metrics coarse-graining of ecological systems leads to enhanced predictive capacity. In addition, it remains uncertain how much predictability can be achieved in biological systems through a coarse-graining approach, because the future probability space itself changes through niche creation and the emergence of the adjacent possible.

## SUMMARY

We believe that it is important to create a framework for understanding the potential for and limits to prediction in ecological systems. Poor model predictions can result from either low realized predictability or low intrinsic predictability, but very different responses are merited in each case. Low realized predictability can be improved through better estimation of model parameters, improved model structure, and more precise specification of initial conditions. Accumulating data and additional experiments would be expected to gradually and incrementally improve model predictions (Ellison 2004, Lavine 2006). Systems with low intrinsic predictability, however, have strong inherent limitations on the potential for model improvement. In these systems, prediction may often not be possible and, when it is possible, proceeds with information loss that results from spatial or temporal coarse-graining. The challenges then are distinguishing between low intrinsic and realized predictability, establishing computational irreducibility, and determining the potential predictability of ecological systems including those that are computationally irreducible. We do not suggest that attempts at model development and prediction are useless, even in the presence of computational irreducibility, but only that the processes limiting these efforts should be understood as a potentially fundamental characteristic of complex systems. Predictive capacity might be gained by coarsening the temporal or spatial scale of the predic-

tions, e.g., the limitations of forecasting short-term weather compared to successful prediction of long-range climate (National Research Council 1999), although with information loss. The widespread presence of computational irreducibility, however, would suggest that living systems with their near infinitely rich behaviors, interactions, and dynamics are not amenable to long range prediction.

## ACKNOWLEDGMENTS

Brian Beckage gratefully acknowledges the support of the National Institute for Climate Changes Research and the National Science Foundation (Award 0950347), and is grateful for sabbatical support from the University of Vermont and the National Institute for Mathematical and Biological Synthesis, University of Tennessee, Knoxville, Tennessee. This work was supported by the National Institute for Mathematical and Biological Synthesis, an Institute sponsored by the National Science Foundation, the U.S. Department of Homeland Security, and the U.S. Department of Agriculture through NSF Award #EF-0832858, with additional support from The University of Tennessee, Knoxville. This paper is dedicated to Simon Levin on the occasion of his 70<sup>th</sup> birthday in honor of his many contributions to ecological theory.

## LITERATURE CITED

- Beckage, B., B. Osborne, D. G. Gavin, C. Pucko, T. G. Siccama, and T. Perkins. 2008. A rapid upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont. *Proceedings of the National Academy of Sciences* 105:4197–4202.
- Clark, J. S., S. R. Carpenter, M. Barber, S. Collins, A. Dobson, J. A. Foley, D. M. Lodge, M. Pascual, R. Pielke, Jr., W. Pizer, C. Pringle, W. V. Reid, K. A. Rose, O. Sala, W. H. Schlesinger, D. H. Wall, and D. Wear. 2001. Ecological forecasts: an emerging imperative. *Science* 293:657–660.
- Clark, J. S., M. Dietze, S. Chakraborty, P. K. Agarwal, I. Ibanez, S. LaDeau, and M. Wolosin. 2007. Resolving the biodiversity paradox. *Ecology Letters* 10:647–659.
- Clark, J. S., E. Macklin, and L. Wood. 1998. Stages and spatial scales of recruitment limitation in southern Appalachian forests. *Ecological Monographs* 68:213–235.
- Clark, J. S. and J. S. McLachlan. 2003. Stability of forest biodiversity. *Nature* 423:635–638.
- Constantino, R. F., et al. 1997. Chaotic dynamics in an insect population. *Science* 275:389–391.
- Davis, M. B., and R. G. Shaw. 2001. Range shifts and

- adaptive responses to Quaternary climate change. *Science* 292:673–679.
- Dennis, B., R. A. Desharnais, J. M. Cushing, S. M. Henson, and R. F. Costantino. 2003. Can noise induce chaos? *Oikos* 102:329–339.
- Ellison, A. M. 2004. Bayesian inference in ecology. *Ecology Letters* 7:509–520.
- Ellner, S. and P. Turchin. 2005. When can noise induce chaos and why does it matter: a critique. *Oikos* 111:620–631.
- EPICA community members. 2004. Eight glacial cycles from an Antarctic ice core. *Nature* 429:623–628.
- Gassmann, F., F. Klotzli, and G. R. Walther. 2005. Vegetation change shows generic features of non-linear dynamics. *Journal of Vegetation Science* 16:703–712.
- Gunderson, L. H., and C. S. Holling, editors. 2002. *Panarchy: understanding transformations in human and natural systems*. Island Press, Washington, D.C., USA.
- Hansen, J., M. Sato, R. Ruedy, K. Lo, D. W. Lea, and M. Medina-Elizade. 2006. Global temperature change. *Proceedings of the National Academy of Sciences* 103:14288–14293.
- Hastings, A., C. L. Hom, S. Ellner, P. Turchin, and H. C. J. Godfray. 1993. Chaos in ecology: Is mother nature a strange attractor? *Annual Review of Ecology and Systematics* 24:1–33.
- Holling, C. S. 2001. Understanding the complexity of economic, ecological, and social systems. *Ecosystems* 4:390–405.
- Huisman, J., and F. J. Weissing. 2001. Fundamental unpredictability in multispecies competition. *The American Naturalist* 157:488–494.
- Israeli, N. and N. Goldenfeld. 2004. Computational irreducibility and the predictability of complex physical systems. *Physical Review Letters* 92:074105.
- Israeli, N. and N. Goldenfeld. 2006. Coarse-graining of cellular automata, emergence, and the predictability of complex systems. *Physical Review E* 73:026203.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos* 69:373–386.
- Kaplan, J. O., et al. 2003. Climate change and Arctic ecosystems II: modeling, paleodata-model comparisons, and future projections. *Journal of Geophysical Research* 108:8171. [doi: 10.1029/2002JD002559]
- Kolar, C. S., and D. M. Lodge. 2001. Progress in invasion biology: predicting invaders. *Trends in Ecology & Evolution* 16:199–204.
- Krakauer, D. C., K. M. Page, and D. H. Erwin. 2009. Diversity, dilemmas, and monopolies of niche construction. *The American Naturalist* 173:26–40.
- Lavine, M. 2006. Introduction to statistical thought. <http://www.math.umass.edu/~lavine/Book/book.pdf>
- Levin, S. A. 1976. Population dynamic models in heterogeneous environments. *Annual Review of Ecology and Systematics* 7:1287–1311.
- Levin, S. A. and R. M. May. 1976. A note on difference-delay equations. *Theoretical Population Biology* 9:178–187.
- Lorenz, E. N. 1963. Deterministic nonperiodic flow. *Journal of the Atmospheric Sciences* 20:130–141.
- Lorenz, E. N. 2006. Predictability—a problem partly solved. In T. Palmer and R. Hagedorn, editors. *Predictability of weather and climate*. Cambridge University Press, Cambridge, UK.
- Maquet, J., C. Letellier, and L. A. Aguirre. 2007. Global models from the Canadian lynx cycles as a direct evidence for chaos in real ecosystems. *Journal of Mathematical Biology* 55:21–39.
- May, R. M. 1974. Biological populations with nonoverlapping generations: stable points, stable cycles, and chaos. *Science* 186:645–647.
- Møller, A. P., D. Rubolini, and E. Lehikoinen. 2008. Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proceedings of the National Academy of Sciences* 105:16195–16200.
- Moritz, C., J. L. Patton, C. J. Conroy, J. L. Parra, G. C. White, and S. R. Beissinger. 2008. Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science* 322:261–264.
- National Research Council. 1999. *Making climate forecasts matter*. National Academy Press, Washington, D.C., USA.
- Nathan, R., G. G. Katul, H. S. Horn, S. M. Thomas, R. Oren, R. Avissar, S. W. Pacala, and S. A. Levin. 2002. Mechanisms of long-distance dispersal of seeds by wind. *Nature* 418:409–413.
- Rai, V. 2009. Ecological vs. mathematical chaos. *Ecological Complexity* 6:147–149.
- Rosecchi, E., F. Thomas, and A. J. Crivelli. 2001. Can life-history traits predict the fate of introduced species? A case study on two cyprinid fish in southern France. *Freshwater Biology* 46:845–853.
- Roura-Pascual, N., L. Brotons, A. T. Peterson, and W. Thuiller. 2009. Consensual predictions of potential distributional areas for invasive species: a case study of Argentine ants in the Iberian Peninsula. *Biological Invasions* 11:1017–1031.
- Sanders, N. J., N. J. Gotelli, N. E. Heller, and D. M. Gordon. 2003. Community disassembly by an invasive species. *Proceedings of the National Academy of Sciences* 100:2474–2477.
- Scheuring, I. and G. Domokos. 2007. Only noise can induce chaos in discrete populations. *Oikos* 116:361–366.
- Schoener, T. W. 1986. Mechanistic approaches to community ecology: a new reductionism? *American Zoologist* 26:81–106.

- Sitch, S., B. Smith, I. C. Prentice, A. Arneth, A. Bondeau, W. Cramer, J. O. Kaplan, S. Levis, W. Lucht, M. T. Sykes, K. Thonicke, and S. Venevsky. 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology* 9:161–185.
- Stevens, J., and B. Beckage. 2009. Fire feedbacks facilitate invasion of pine savannas by Brazilian pepper (*Schinus terebinthifolius*). *New Phytologist* 184:365–375.
- Tang, G. and B. Beckage. 2010. Projecting the distribution of forests in New England in response to climate change. *Diversity and Distributions* 16:144–158.
- Upadhyay, R. K. 2009. Observability of chaos and cycles in ecological systems: lessons from predator-prey models. *International Journal of Bifurcation and Chaos* 19:3169–3234.
- Voigt, W., J. Perner, A. J. Davis, T. Eggers, J. Schumacher, R. Bahrmann, B. Fabian, et al. 2003. Trophic levels are differentially sensitive to climate. *Ecology* 84:2444–2452.
- Williams, J. W., and S. T. Jackson. 2007. Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment* 5:475–482.
- Williams, J. W., S. T. Jackson, and J. E. Kutzbach. 2007. Projected distributions of novel and disappearing climate by 2100 AD. *Proceedings of the National Academy of Sciences* 104:5738–5742.
- Winder, M., and D. E. Schindler. 2004. Climate change uncouples trophic interactions in an aquatic ecosystem. *Ecology* 85:2100–2106.
- Wolfram, S. 2002. *A new kind of science*. Mathematica, Urbana, Illinois, USA.
- Wu, J. 2004. Effects of changing scale on landscape pattern analysis: scaling relations. *Landscape Ecology* 19:125–138.