Collective phenomena, collective motion, and collective action in ecological systems

Claudio Carere
StarFLAG EU FP6 project

Simon Levin
SFI2013
We may think of ecosystems as enduring parts of nature.
But ecosystems and the biosphere are dynamic, with lots of species turnover, especially on local scales.
Must scale up

Carpinteri et al., 2002, Chaos, Solitons and Fractals,
A perspective from mathematics and physics can help

• “Statistical mechanics” of ecological communities
• Critical transitions
• Collective phenomena and collective motion
  – Emergence and pattern formation
  – Statistical mechanics
• Conflict and collective action
Realistic models can capture the emergence of pattern
( Pacala, Botkin, Shugart, others)

Deutschman, DH, SA Levin, C Devine and LA Buttel.
Mathematical challenges: Simplification approaches

- Coarse graining
- Lagrangian to Eulerian transitions
- Moment closure schemes
- Equation-free methods

- Similar considerations apply to ocean dynamics
At what scale is prediction possible? Ecotypes, not species, are predictable.

Darwin model: Follows, Dutkiewicz, Chisholm, ...
Ecosystems and the Biosphere are Complex Adaptive Systems

Heterogeneous collections of individual units (agents) that interact locally, and evolve based on the outcomes of those interactions.
Features of CAS

• Multiple spatial, temporal and organizational scales
• Self-organization, and consequent unpredictability
• Multiple stable states, path dependence, hysteresis
• Contagious spread and systemic risk
• Potential for destabilization and regime shifts through slow-time-scale evolution
Stock markets crash
Critical transitions occur in physiological states

Are there early warning indicators?
Critical phenomena in atmospheric precipitation

OLE PETERS\textsuperscript{1,2,3*} AND J. DAVID NEELIN\textsuperscript{3}
\textsuperscript{1}Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, New Mexico 87501, USA
\textsuperscript{2}CNLS, Los Alamos National Laboratory, MS-B258, Los Alamos, New Mexico 87545, USA
\textsuperscript{3}Department of Atmospheric Sciences and Institute of Geophysics and Planetary Physics, University of California, Los Angeles, 405 Hilgard Ave., Los Angeles, California 90095-1565, USA
*e-mail: ole.peters@physics.org

Published online: 28 May 2006; doi:10.1038/nphys314

Critical phenomena occur near continuous phase transitions. As a tuning parameter crosses its critical value, an order parameter increases as a power law. At criticality, order-parameter fluctuations diverge and their spatial correlation decays as a power law\textsuperscript{1}. In systems where the tuning parameter and order parameter are coupled, the critical point can become an attractor, and self-organized criticality (SOC) results\textsuperscript{2,3}. Here we argue, using satellite data, that a critical value of water vapour (the tuning parameter) marks a non-equilibrium continuous phase transition to a regime of strong atmospheric convection and precipitation (the order parameter)—with correlated regions on scales of tens to hundreds of kilometres. Despite the complexity of atmospheric dynamics, we find that critical phenomena occur near continuous phase transitions.

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{figure1.png}
\caption{Rescaled precipitation variance (mm h\textsuperscript{-1}).}
\end{figure}
Many such transitions have characteristic signals

- Critical slowing down
- Increasing variance
- Increasing autocorrelation
- Flickering

Anticipating Critical Transitions

Marten Scheffer, 1,2 Stephen R. Carpenter, 3 Timothy M. Lenton, 4 Jordi Bascompte, 5 William Brock, 6 Vasillis Dakos, 7,8 Johan van de Koppel, 9,10 Ingrid A. van de Leemput, 9 Simon A. Levin, 9 Egbert H. van Nes, 9,11,12 Mercedes Pascual, 11,12 John Vandermeer 12

Tipping points in complex systems may imply risks of unwanted collapse, but also opportunities for positive change. Our capacity to navigate such risks and opportunities can be boosted by combining emerging insights from two unconnected fields of research. One line of work is revealing fundamental architectural features that may cause ecological networks, financial markets, and other complex systems to have tipping points. Another field of research is uncovering generic empirical indicators of the proximity to such critical thresholds. Although sudden shifts in complex systems will inevitably continue to surprise us, work at the crossroads of these emerging fields offers new approaches for anticipating critical transitions.

About 12,000 years ago, the Earth suddenly shifted from a long, harsh glacial episode into the benign and stable Holocene climate that allowed human civilization to develop. On smaller and faster scales, ecosystems occasionally flip to contrasting states. Unlike gradual trends, such sharp shifts are largely unpredictable (1–4). Nonetheless, science is now carving into this realm of unpredictability in fundamental ways. Although the complexity of systems such as societies and ecological networks prohibits accurate mechanistic modeling, certain features turn out to be generic markers of the fragility that may typically precede a large class of abrupt changes. This is because the relatively isolated and different nodes will each shift at another level of an environmental driver (5). By contrast, homogeneity points. The basic ingredient for a tipping point is a positive feedback that, once a critical point is passed, propels change toward an alternative state (6). Although this principle is well understood for simple isolated systems, it is more challenging to fathom how heterogeneous structurally complex systems such as networks of species, habitats, or societal structures might respond to changing conditions and perturbations. A broad range of studies suggests that two major features are crucial for the overall response of such systems (7): (i) the heterogeneity of the components and (ii) their connectivity (Fig. 1). How these properties affect the stability depends on the nature of the interactions in the network.

Domino effects. One broad class of networks includes those where units (or “nodes”) can flip between alternative stable states and where the probability of being in one state is promoted by having neighbors in that state. One may think, for instance, of networks of populations (extinct or not), or ecosystems (with alternative stable states), or banks (solvent or not). In such networks, heterogeneity in the response of individual nodes and a low level of connectivity may cause the network as a whole to change gradually—rather than abruptly—in response to environmental change. This is because the relatively isolated and different nodes will each shift at another level of an environmental driver (8). By contrast, homogeneity

But there are caveats

DOI 10.1007/s12080-013-0192-6

ORIGINAL PAPER

Early warning signals: the charted and uncharted territories

Carl Boettiger · Noam Ross · Alan Hastings

Received: 19 March 2013 / Accepted: 23 May 2013 / Published online: 21 June 2013 © Springer Science+Business Media Dordrecht 2013

Abstract The realization that complex systems such as ecological communities can collapse or shift regimes suddenly and without rapid external forcing poses a serious challenge to our understanding and management of the natural world. The potential to identify early warning signals that would allow researchers and managers to predict such events before they occur has been an invaluable discovery that offers a way forward in spite of such seemingly unpredictable behavior. Research into early warning signals has demonstrated that it is possible to define and detect such early warning signals in advance of a transition in certain contexts. Here, we describe the pattern emerging as research continues to explore just how far we can generalize these results. A core of examples emerges that shares three properties: the phenomenon of rapid regime shifts, a pattern of “critical slowing down” that can be used to detect the approaching shift, and a mechanism of bifurcation driving the sudden change. As research has expanded beyond these core examples, it is becoming clear that not all systems that show regime shifts exhibit critical slowing down, statistical detection is a challenge. We review the literature that explores these edge cases and highlight the need for (a) new early warning behaviors that can be used in cases where rapid shifts do not exhibit critical slowing down; (b) the development of methods to identify which behavior might be an appropriate signal when encountering non-standard early warning signals; and (c) statistical methods that can distinguish between signatures of early warning behaviors and noise.
Shallow Lakes (Scheffer, Carpenter)

http://www.lifeinfreshwater.org.uk/Web%20pages/ponds/Pollution.htm
Climate is definitely a strong determinant of tree cover.

Savanna/Forest Distributions

Staver et al. 2011 (Ecology and Science)
Savanna-forest systems exhibit bistability in vegetation distribution

Changes in precipitation can drive system flips

Staver et al. 2011 (Ecology and Science)
Fire separates savanna from forest within the intermediate climate envelope.

Staver et al. 2011 (Ecology and Science)
Fig. 4. Broadly showing the six stages of human evolution used to determine parameters for the stochastic model runs. The parameters $\mu$ and $\rho$ were derived from published relationships between population density and fire density ($B$) and population density and land transformation ($D$), respectively; $\lambda$ was determined from field data on fire spread probability in the wet and dry seasons in a savanna national park ($C$). See Table 1 and Materials and Methods for more details on the parameterization. In $B$ and $D$ the data represent medians with 75th and 25th percentiles.
The form of the sapling transition functions can be derived from data as well as from fire percolation models (Archibald, Staver, Levin PNAS 2011; Schertzer, Staver, Levin submitted).
Relatively simple models can capture the bistability

\[
\frac{dG}{dt} = \mu S + \nu T - \beta GT
\]

\[
\frac{dS}{dt} = \beta GT - \omega(G)S - \mu S
\]

\[
\frac{dT}{dt} = \omega(G)S - \nu T
\]

\[G + S + T = 1\]

Carla Staver

Staver et al. 2011 (Ecology) and Staver & Levin 2012 (Amer.Natur.)
Intermediate precipitation

Need explicitly spatial models

Staver et al. 2011 (Ecology) and Staver & Levin 2012 (Amer Natur.)
• Responses to changes in rainfall status will be rapid, threshold transitions

• Changes will not be linear or easy to reverse

• Similar phenomena in other systems, such as lakes and pathogen systems

Modified very slightly from Scheffer et al. 2003, Nature
Current work: Fully spatial model

Staver et al. 2011 (Ecology and Science)
Lecture outline

• Statistical mechanics of ecological communities
• Critical transitions
• Collective phenomena and collective motion
  – Emergence and pattern formation
  – Statistical mechanics
More Is Different

Broken symmetry and the nature of the hierarchical structure of science.

P. W. Anderson

The reductionist hypothesis may still be a topic for controversy among philosophers, but among the great majority of active scientists I think it is accepted without question. The workings of our minds and bodies, and of all the animate or inanimate matter of which we have any detailed knowledge, are assumed to be controlled by the same set of fundamental laws, which except under certain extreme conditions we feel we know pretty well.

It seems inevitable to go on uncritically, and the last thing we need is to be reminded of the possibility that we are engaging in a blind alley. The reductionist hypothesis assumes that we can understand basic phenomena by combining the facts of elementary physics and chemistry. The results of the experiments of the 19th and early 20th centuries support this hypothesis, and the results of the investigations of the last few decades lead us to suppose that the hypothesis is valid in most cases.

The constructionist hypothesis breaks down when confronted with the twin difficulties of scale and complexity. The behavior of large and complex aggregates of elementary particles, it turns out, is not to be understood in terms of a simple extrapolation of the properties of a few particles. Instead, at each level of complexity entirely new properties appear, and the understanding of the new behaviors requires research which I think is as fundamental in its nature as any other. That is, it seems to me that one may array the sciences roughly linearly in a hierarchy, according to the idea: The elementary entities of science $X$ obey the laws of science $Y$.

$X$
- solid state
- chemistry
- molecular biology
- cell biology
- psychology

$Y$
- elementary particle physics
- many-body physics
- chemistry
- molecular biology
From physical systems to biological systems, macroscopic features **emerge** from microscopic interactions, largely independent of details.
Patterns emerge from individual interactions in bacterial communities

Ben-Jacob and Levine
Similar problems of pattern formation have been addressed for a wide range of organisms

- Slime molds
- Swarming bacteria
- Insects
- Krill
- Birds
- Fish
- Ungulates
How do we relate the macroscopic patterns to the microscopic rules?
Turing instabilities:

\[
\begin{align*}
\frac{\partial u}{\partial t} &= F(u,v) + D_u \nabla^2 u \\
\frac{\partial v}{\partial t} &= G(u,v) + D_v \nabla^2 v
\end{align*}
\]

uniform states can become unstable if \( D_v / D_u \) is above some threshold.
Vegetation patterns in semi-arid landscapes are self-organized...and Turing models seem to fit

Plankton are patchy on almost every scale
Could Turing apply to planktonic patchiness?

- **Phytoplankton** as “activators”
- **Zooplankton** as “inhibitors”

- Both Levin and Segel, and Okubo, independently proposed this
Turing mechanism didn’t work

Zooplankton are more patchily distributed

Mackas et al.
Zooplankton don’t move randomly, but aggregate
Similarly, birds actively aggregate.
For all such systems, what is the relationship between an individual agent
...and how it responds to its neighbors and local environment
...and the macroscopic properties of ensembles of such agents?
Lagrangian-Eulerian connections

- Begin from microscopic (Lagrangian) rules

\[ m\ddot{x} = F_1 + F_2 + F_3 + F_4 \]

Random    Directed    Grouping    Arrayal
But real aggregations are heterogeneous assemblages of individuals
• Utilize simulations to explore these issues
So the direction chosen by informed individuals must reconcile these tendencies.

\[ d_i(t+Dt) = \frac{s_i(t) + w g_i(t)}{|s_i(t) + w g_i(t)|} \]
1 informed individuals in group of 100.

Courtesy Iain Couzin
5 informed individuals in group of 100.

Courtesy Iain Couzin
10 informed individuals in group of 100.

Courtesy Iain Couzin
Animal groups may be led by a small number of individuals

From Couzin et al., 2005
Competing preferences

Difference in preference
Collective decision-making

Difference in preference

Courtesy Iain Couzin
Competition and consensus
Unequal numbers of leaders

Kuramoto model

\[
\dot{\theta}_j = \sin(\bar{\theta}_1 - \theta_j) + k \sum_{l=1}^{N_1} \sin(\theta_l - \theta_j)
\]

\[
\dot{\theta}_j = \sin(\bar{\theta}_2 - \theta_j) + k \sum_{l=1}^{N_1} \sin(\theta_l - \theta_j)
\]

\[
\dot{\theta}_j = k \sum_{l=1}^{N_1} \sin(\theta_l - \theta_j)
\]

Also consider variable topologies and strengths of commitment
Leonard et al., PNAS

In subgroup 1, represent as

\[
\frac{d\theta_j}{dt} = \sin(\bar{\theta}_1 - \theta_j(t)) + \frac{K_1}{N} \sum_{l=1}^{N} a_{jl}(t) \sin(\theta_l(t) - \theta_j(t)), \quad [1]
\]

in subgroup 2 as

\[
\frac{d\theta_j}{dt} = \sin(\bar{\theta}_2 - \theta_j(t)) + \frac{K_1}{N} \sum_{l=1}^{N} a_{jl}(t) \sin(\theta_l(t) - \theta_j(t)), \quad [2]
\]

and in subgroup 3 as

\[
\frac{d\theta_j}{dt} = \frac{K_1}{N} \sum_{l=1}^{N} a_{jl}(t) \sin(\theta_l(t) - \theta_j(t)). \quad [3]
\]
Coefficients change

\[
\frac{d a_{j1}}{d t} = K_2 (1 - a_{j1}(t)) a_{j1}(t) (\rho_{j1}(t) - r).
\]

\[
\rho_{j1} = \left( \frac{1}{2} + \frac{1}{2} \cos(\theta_j - \theta_l) \right)^{1/2}
\]
Results

- Slow and fast time scales
- Uninformed individuals are crucial to success
- Singular perturbation theory in $\varepsilon = \max_i (1/K_i)$
- Eight invariant manifolds

![Diagram of coupling in manifolds $M_{010}$ (Left) and $M_{001}$ (Right) among subgroups 1, 2, and 3 as indicated by arrows.]

**Fig. 1.** Coupling in manifolds $M_{010}$ (Left) and $M_{001}$ (Right) among subgroups 1, 2, and 3 as indicated by arrows.
Lecture outline

• Statistical mechanics of ecological communities
• Critical transitions
• Collective phenomena and collective motion
  – Emergence and pattern formation
• Conflict and collective action
Public goods problems are common in evolutionary theory...and economics

- Information in collective motion
- Nests
- Chelation
- Siderophores
- N fixation
- Antibiotics
- Extracellular polymers (biofilms)
Samuelson (1954): Public Goods

• ...[goods] which all enjoy in common in the sense that each individual's consumption of such a good leads to no subtractions from any other individual's consumption of that good...
William Forster Lloyd (1832)

*The Tragedy of the Commons*

Aelbert Cuyp
The Commons solution (Hardin, Ostrom)

“Mutual coercion, mutually agreed upon”

http://www.physics.ohio-state.edu/~wilkins
http://www.guardian.co.uk
The role of a fairness norm for the evolution of cooperation

with Alessandro Tavoni and Maja Schlüter

The survival of the conformist: equity-driven ostracism and renewable resource management

Pictures from http://www.lobsterfrommaine.com

JTheorBiol2011
Agents that withdraw more than socially accepted (visible by larger crop area) are ostracized and refused help -> reduction in utility

\[ U_C = \pi_C(E, R) \]

\[ U_D = \pi_D(E, R) - \omega(f_c) \left( \frac{\pi_D(E, R) - \pi_C(E, R)}{\pi_D(E, R)} \right) \]

Payoff from production | Ostracism function | Intensity of defection (inequity)
Figure 4: The $\omega(f^*c) = \pi d(e_d, R^*)$ loci guaranteeing coexistence of types given the ostracism function in Fig. 3, superimposed on the contours of the resource function at equilibrium (brighter shades indicate higher resource levels). The cooperators extract at the social optimum, while defectors above it, according to their type as given by the effort multiplier $\mu$: given the latter (e.g. $\mu = 2.5$), one can determine which equilibrium arises for a given initial $f^c$ (e.g. a Mixed equilibrium on locus $a$ with relatively high $R^*$ for $f^c = 0$). The highest level of $\mu$ on the y-axis corresponds to $\mu_{\text{nash}}$, and yields, depending on the initial $f^c$, either a Mixed or a Defector equilibrium (both with the minimal $R^*$ in their category).

Inspection of the curves in Figure 4 allows one to assess the qualitative features of the system resulting from the above condition: to the left of locus $a$, i.e. for low initial $f^c$, $\omega(f^c) < \pi d(e_d, R^*)$, so the system will evolve towards the stable defector equilibrium independently of $\mu$. If, for instance, we consider defectors who extract resource according to the Nash rule ($\mu_{\text{nash}}$: $e_{\text{d}} = e_{\text{nash}}$), the equilibrium will be characterized by $\omega(0) = 0 < \pi d(e_d, R_{\text{nash}})$ (see footnote 4). To the right of locus $a$, $\omega(f^c) > \pi d(e_d, R^*)$, so the community of appropriators following the restrictive norm will grow larger. The system will transition towards the cooperator equilibrium when the effort difference between cooperators and defectors is not too large (low $\mu$), as the above inequality will continue to hold until stable monomorphic cooperation obtains, with $\omega(1) > \pi d(e_d, R_{\text{eff}})$ (see footnote 15).
Evolution of collective behavior

Searching on Resource Landscapes

How does selection shape the trade-off between tracking resources and tracking other individuals?
Questions

- How many leaders?
- How many followers?

- Group optimality
- Game-theoretic solutions
- Lessons for cooperation in public goods situations
Distributed, communicating robots

Naomi Leonard; Photo, David Benet

Naomi Leonard
Recent work: The evolution of collective migration

Social interactions, information use, and the evolution of collective migration

Vishwesha Gutta and Iain D. Couzin

Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ, 08544

Edited by Simon A. Levin, Princeton University, Princeton, NJ, and approved July 19, 2010 (received for review May 17, 2010)

Migration of organisms (or cells) is typically an adaptive response to spatiotemporal variation in resources that requires individuals to detect and respond to long-range and noisy environmental gradients. Many organisms, from whales to bacteria, migrate on

Here, we develop an individual-based, spatially explicit evolutionary model of organismal movement and social interactions and use this to investigate migratory strategies under a wide range of densities and cost-benefit structures that represent diverse eco.

Specialization and evolutionary branching within migratory populations

Colin J. Torney, Simon A. Levin, and Iain D. Couzin

Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544

Contributed by Simon A. Levin, September 28, 2010 (sent for review April 30, 2010)

Understanding the mechanisms that drive specialization and spe-
cialization within initially homogeneous populations is a fundamental challenge for evolutionary theory. It is an issue of relevance for significant open questions in biology concerning the generation and maintenance of biodiversity, the origins of mutual cooperation, and the efficient division of labor in social or colonial organisms.

In a recent study (13) this process was examined using an individual-based model governed by localized rules of attraction, alignment etc., with differing degrees of independence and sociality. This work showed that, under certain conditions, specialized groups of leaders form. The challenge in understanding and classifying models of this type lies in identifying an appropriate

Leadership, collective motion and the evolution of migratory strategies

Vishwesha Gutta and Iain D. Couzin

Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ USA
Simple model: wide range of dynamics

Brownian swarms

Collective Migration

Random walking individuals

Sociality

Gradient detection ability

Thanks to Iain Couzin
Evolutionary branching: leaders and followers

- Small fraction of population evolve to be leaders (large $w_g$ but small $w_s$)
- the rest naively follow others (small $w_g$; large $w_s$)

Guttal and Couzin, PNAS, 2010  

Thanks to Iain Couzin
Extensions to human decision-making

• What are the dynamics of collective decisions?
• How is consensus achieved?
• Why be a leader, or a follower?
• Are there threshold numbers of collaborators for effective cooperation?
• Lessons for international agreements
Multiple models yield similar results

Uninformed Individuals Promote Democratic Consensus in Animal Groups

Iain D. Couzin,1* Christos C. Ioannou,1† Güven Demirel,2 Thilo Gross,2‡ Colin J. Torney,1 Andrew Hartnett,1 Larissa Conradt,2§ Simon A. Levin,1 Naomi E. Leonard4

Conflicting interests among group members are common when making collective decisions, yet failure to achieve consensus can be costly. Under these circumstances individuals may be susceptible to manipulation by a strongly opinionated, or extremist, minority. It has previously been argued, for humans and animals, that social groups containing individuals who are uninformed, or exhibit weak preferences, are particularly vulnerable to such manipulative agents. Here, we use theory and experiment to demonstrate that, for a wide range of conditions, a strongly opinionated minority can dictate group choice, but the presence of uninformed individuals spontaneously inhibits this process, returning control to the numerical majority. Our results emphasize the role of uninformed individuals in achieving democratic consensus amid internal group conflict and informational constraints.

Social organisms must often achieve a consensus to obtain the benefits of group living and to avoid the costs of indecision (1–12). In some societies, notably those of eusocial insects, making consensus decisions is often a unitary, conflict-free process because the close relatedness among individuals means that they typically share preferences (11). However, in other social animals, such as schooling fish, flocking birds, herding ungulates, and humans, individual behavior of the entire group (consensus). In some cases, decisions made by one group member (self-interest) can play an important role in group achievement, sometimes at the expense of the potential to control or exploit the majority, behavior of the entire group (consensus). In some cases, decisions made by one group member (self-interest) can play an important role in group achievement, sometimes at the expense of the potential to control or exploit the majority.

Consequently, for both human societies (1, 2, 6, 9, 10, 14) and group-living animals (6, 13), it has been argued that group decisions can be subject to manipulation by a self-interested and opinionated minority. In particular, previous work suggests that groups containing individuals who are uninformed, or naïve, about the decision being made are particularly vulnerable to such manipulation (2, 9, 10, 13). Under this view, uninformed individuals destabilize the capacity that uninformed individuals (defined as those who lack a preference or are uninformed about the features on which the collective decision is being made) play a central role in achieving democratic consensus.

We use a spatially explicit computational model of animal groups (15) that makes minimal assumptions regarding the capabilities of individual group members; they are assumed to avoid collisions with others and otherwise exhibit the capacity to be attracted toward, and to align direction of travel with, near neighbors (5, 16). We investigate the case of consensus decision-making regarding a choice to move to one of two discrete targets in space (thus, the options are mutually exclusive).

The direction and strength of an individual’s preference are encoded in a vector term \( \mathbf{a} \) (directed toward the individual’s preferred target). Higher scalar values of \( \| \mathbf{a} \| \) represent greater conviction in, or strength of, individual preference to move in the direction of the target and, thus, also represent greater intransigence to social influence (5). We explore the case where there are two subpopulations within the group—\( N_1 \) and \( N_2 \), respectively—that have different preferred targets. Because we are interested in determining whether a minority can exploit a majority, we set \( N_1 > N_2 \) for the simulation. The strengths of the
Conclusions

• Collective phenomena and emergence characterize systems, from microbial communities to the biosphere

• A fundamental challenge is to scale from microscopic to macroscopic

• Consensus formation is a challenge in all systems