Scaling and collective phenomena in ecological systems

Simon Levin
Brazil 2014

Claudio Carere
StarFLAG EU FP6 project
We may think of ecosystems as enduring parts of nature

http://travel.nationalgeographic.com
But ecosystems and the biosphere are dynamic, with lots of species turnover, especially on local scales.
However, though species come and go, there are characteristic regularities in the macroscopic patterns in all ecosystems.
These regularities characterize biomes
Characteristic macroscopic patterns are emergent, independent of much microscopic detail.

Abundance distributions, stoichiometry, nutrient cycling.
Must scale up

Carpinteri et al., 2002, Chaos, Solitons and Fractals,
This implies a need to relate phenomena across scales, from

- cells to organisms to collectives to ecosystems and the biosphere

*and to ask*

- How robust are the properties of ecosystems?
- How does robustness of macroscopic properties relate to ecological and evolutionary dynamics on finer scales?
- Can we develop a statistical mechanics of ecological communities, and of coupled human-ecological systems?
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
A perspective from mathematics and physics can help

• “Statistical mechanics” of ecological communities
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• Conflict and collective action
Mathematical challenges: Simplification approaches

- Coarse graining
- Lagrangian to Eulerian transitions
- Moment closure schemes
- Equation-free methods
Pattern emerges even in simplest models of ecological competition
Durrett and Levin 1994
... path dependency, especially due to finite-size effects, and critical slowing down


AMAR GANDHI,* SIMON LEVIN† AND STEVEN ORSZAG

Program in Applied & Computational Mathematics, Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544-1003, U.S.A.
Forest growth models have been well-developed, and exhibit similar path dependence
(Pacala, Botkin, Shugart, others)

Conceptual Coupled Physical - Ecosystem Model

- Wind Stress
- Irradiation
- Cloud Cover
- Heat Flux
- River Inputs

Boundary Conditions

Physical Model

Pelagic Model

C, N, P, Si
Sed

Benthic Model

http://www.hpcx.ac.uk/research/environment/polcoms
For forests and oceans alike, challenge is to simplify these descriptions through aggregation and simplification, for example moment closure methods.
Another sort of scaling relates the ecological and evolutionary time scales

- Adaptive dynamics and emergent population properties
  - Features of forests, grasslands and oceans
- Public goods problems
  - N fixation
  - Stoichiometry
  - Bacterial biofilms
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.
So too are the socio-economic systems with which they are interlinked.
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?

www.aesnet.org
Critical phenomena in atmospheric precipitation

OLE PETERS1,2,3* AND J. DAVID NEELIN3

1Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, New Mexico 87501, USA
2CNLS, Los Alamos National Laboratory, MS-B258, Los Alamos, New Mexico 87545, USA
3Department 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. In systems where the tuning parameter and order parameter are coupled, the critical point can become an attractor, and self-organized criticality (SOC) results. 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 important observables conform to the simple functional forms predicted by the theory of critical phenomena. In meteorology,
2008

COMPLEX SYSTEMS

Ecology for bankers

Robert M. May, Simon A. Levin and George Sugihara

There is common ground in analysing financial systems and ecosystems, especially in the need to identify conditions that dispose a system to be knocked from seeming stability into another, less happy state.

‘Tipping points’, ‘thresholds and breakpoints’, ‘regime shifts’ — all are terms that describe the flip of a complex dynamical system from one state to another. For banking and other financial institutions, the Wall Street Crash of 1929 and the Great Depression epitomize such an event. These days, the increasingly complicated and globally interlinked financial markets are no less immune to such system-wide (systemic) threats. Who knows, for instance, how the present concern over sub-prime loans will pan out?

Well before this recent crisis emerged, the US National Academies/National Research Council and the Federal Reserve Bank of New York collaborated on an initiative to “stimulate fresh thinking on systemic risk”. The main event was a high-level conference held in May 2006, which brought together experts from various backgrounds to explore parallels between systemic risk in the financial sector and risks in the environment. In contrast to the decades that have been spent onstudying systemic risk as compared with that spent on conventional risk management in individual firms? Second, how expensive is a systemic-risk event to a national or global economy (examples being the stock market crash of 1987, or the turmoil of 1998 associated with the Russian loan default, and the subsequent collapse of the hedge fund Long-Term Capital Management)? The answer to the first question is “comparatively very little”; to the second, “hugely expensive”.

An analogous situation exists within fisheries management. For the past half-century, investments in fisheries science have focused on management on a species-by-species basis (analogous to single-firm risk analysis). Especially with collapses of some major fisheries, however, this approach is giving way to the view that such models may be fundamentally incomplete, and that the wider ecosystem and environmental context (by analogy, the full banking system) must be considered.

The global financial crisis has demonstrated that our understanding of systemic risk needs to be expanded. This may prove a useful model for fisheries and environmental management, which has lagged behind. The recent financial crisis has highlighted the importance of understanding systemic risk in complex dynamical systems, whether financial or environmental. The challenge for the future is to integrate this understanding across disciplines and scales.
ECOLOGY FOR BANKERS

Robert M. May, Simon A. Levin and George Sugihara

There is common ground in analysing financial systems and ecosystems, especially in the conditions that dispose a system to be knocked from seeming stability into another, less predictable state. ‘Tipping points’, ‘thresholds and breakpoints’, ‘regime shifts’ — all are terms that describe the flip of a complex dynamical system from one state to another. For banking and other financial institutions, the Wall Street Crash of 1929 and the Great Depression epitomize such an event. These days, the increasingly complicated and globally interlinked financial markets are no less immune to such system-wide (systemic) threats. Who knows, for instance, how the present concern over sub-prime loans will pan out?

Well before this recent crisis emerged, the US National Academies/National Research Council and the Federal Reserve Bank of New York collaborated on an initiative to “stimulate fresh thinking on systemic risk”. The main event was a high-level conference held in May 2006, which brought together experts from various backgrounds to explore parallels between systemic risk in the financial sector and in selected domains in engineering, ecology and health science. The effort was endorsed by the White House, and the National Academy of Sciences committed to supporting a follow-up workshop, which will take place in January 2008. The full results will be published in a peer-reviewed journal.

An analogous systems approach to fisheries management suggests an alternative to investments in fishery-related research geared towards management of species richness. (analogous to single-species fisheries management). However, this approach is complex, and that such models may be incomplete, and that the environmental context, as well as the complexity of financial and market systems, mean that we should not expect a simple solution. The page you have is part of a series on complex systems, with a focus on financial and ecological systems. The text emphasizes the importance of understanding tipping points and thresholds in both financial and ecological systems, and suggests that there are parallels to be drawn between these two domains. The page also mentions an initiative to stimulate fresh thinking on systemic risk, with a high-level conference held in May 2006. The results of this initiative will be published in a peer-reviewed journal.
Lecture outline

• Statistical mechanics of ecological communities

• Critical transitions
Shallow Lakes
(Scheffer, Carpenter)

http://www.lifeinfreshwater.org.uk/Web%20pages/ponds/Pollution.htm
There has been a lot of recent attention to critical transitions

Anticipating Critical Transitions

Marten Scheffer,1,2* Stephen R. Carpenter,3 Timothy M. Lenton,4 Jordi Bascompte,5 William Brock,6 Vasilis Dakos,1,5 Johan van de Koppel,7,8 Ingrid A. van de Leemput,1 Simon A. Levin,9 Egbert H. van Nes,1 Mercedes Pascual,10,11 John Vandermeer10

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 (1–3). 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 emerge. 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 (nodes being more similar) and a highly connected network may provide resistance to change until a
Many such transitions have characteristic signals

• Critical slowing down
• Increasing variance
• Increasing autocorrelation
• Flickering

More on this and the need for caution tomorrow
Alternative stable states are well-documented in ecology

review article

Thresholds and breakpoints in ecosystems with a multiplicity of stable states

Robert M. May*

Theory and observation indicate that natural multi-species assemblies of plants and animals are likely to possess several different equilibrium points. This review discusses how alternate stable states can arise in simple 1- and 2-species systems, and applies these ideas to grazing systems, to insect pests, and to some human host–parasite systems.

In all but the most trivial areas of enquiry, there arise questions about the extent to which events are shaped by predictable natural laws us against the accidents of initial conditions and perturbations. Is the human story largely a deterministic tale of civilisations marching to Tynhe’s tune, three and a half beats to disintegration, or did the hinge of historical turn on the length of Cleopatra’s nose? Such questions of the relative roles of chance and necessity are fundamental in modern cosmology, in the foundations of statistical mechanics, and in evolutionary biology and ecology, even though they may arise in less blatant and romantic fashion than the ‘what ifs’ of history and the social sciences.

Viewing the grand sweep of evolution, we can see many examples where the taxonomic details of the plant or animal that occupies a given niche at a given time and place depend on historical accident, but where the niches themselves, and the broad patterns of community organisation, are remarkably constant.

Tackling a much narrower and more local view, it is interesting to consider a particular assembly of species, with specified interactions among them, and to ask questions about the dynamics of the system. Is the dynamical behaviour described by the multi-dimensional generalisation of a single valley (a global attractor)? Or is the dynamical landscape pockmarked with many different valleys, separated by hills and watersheds? If the former, the system has a unique stable state, to which it will tend (like a marble seeking the bottom of a cup) from all initial conditions, and following any disturbance. If the latter, the state into which the system settles depends on the initial conditions, the system may
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)
KRUGER NATIONAL PARK, SAVANNA

Carla Staver
Relatively simple models can capture this behavior

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

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

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

\[G + S + T = 1\]

Staver et al. 2011 (Ecology) and Staver & Levin (Amer. Natur.)
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 transition functions can be derived from fire percolation models
(Archibald PNAS 2011; Schertzer, Staver, Levin in prep.)
At equilibrium:

\[ \omega(G) = \frac{\mu \nu}{\beta G - \nu} \]

\[ f_1(G) = \omega(G) \]

\[ f_2(G) = \frac{\mu \nu}{\beta G - \nu} \]

For stability:

\[ f_1'(G) > f_2'(G) \]
• 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
Adding Forest Trees (fire sensitive)

\[
\frac{dG}{dt} = \mu S + \nu T + \phi(G)F - \beta GT - \alpha GF
\]

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

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

\[
\frac{dF}{dt} = (\alpha(1 - F) - \phi(G))F
\]

\[G + S + T + F = 1\]

Staver and Levin, American Naturalist 2012
This model exhibits complex orbits. How real are they? Full nonlinear analysis still lacking

*Heteroclinic cycles.

Staver & Levin (American Naturalist, 2012)
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 to what appears at first sight to be an obvious corollary of reductionism: that if everything obeys the same explanation of phenomena in terms of known fundamental laws. As always, distinctions of this kind are not unambiguous, but they are clear in most cases. Solid state physics, plasma physics, and perhaps also biology are extensive. High energy physics and a good part of nuclear physics are intensive. There is always much less intensive research going on than extensive. Once new fundamental laws are discovered, a large and ever increasing activity begins in order to apply the discoveries to hitherto unexplained phenomena. Thus, there are two dimensions to basic research. The frontier of science extends all along a long line from the newest and most modern intensive research, over the extensive research recently spawned by the intensive research of yesterday, to the earliest available rudiments of knowledge.

less relevance they seem to have to the very real problems of the rest of science, much less to those of society.

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.

<table>
<thead>
<tr>
<th>X</th>
<th>Y</th>
</tr>
</thead>
<tbody>
<tr>
<td>solid state or</td>
<td>elementary particle</td>
</tr>
<tr>
<td>many-body physics</td>
<td>physics</td>
</tr>
<tr>
<td>chemistry</td>
<td>many-body physics</td>
</tr>
<tr>
<td>molecular biology</td>
<td>chemistry</td>
</tr>
<tr>
<td>cell biology</td>
<td>molecular biology</td>
</tr>
<tr>
<td>psychology</td>
<td>physiology</td>
</tr>
<tr>
<td>social sciences</td>
<td>psychology</td>
</tr>
</tbody>
</table>

But this hierarchy does not imply that science X is necessarily less fundamental than science Y. At the very least it seems to give us grounds for distinguishing between research problems that are fundamental to science as a whole and those that are more peripheral.

4 August 1972, Volume 177, Number 4047
Power laws can arise in many ways.
Vegetation patterns in semi-arid landscapes are self-organized

Pattern forms from a combination of interaction and redistribution

PATTERN GENERATION IN SPACE AND ASPECT*

SIMON A. LEVIN† AND LEE A. SEGEL‡

Abstract. A survey is presented of theories for the generation and maintenance of spatial pattern in reaction-diffusion equations and their generalizations. Applications are selected from the biological sciences and physical chemistry. Special emphasis is placed on nonlocal interaction, as manifested by the inclusion of terms involving higher derivatives or integrals. It is stressed that traditional ideas of spatial pattern generation can usefully be extended to the study of pattern in general descriptive (“aspect”) variables, particularly in understanding ecological diversity and heterogeneity.

Key words. pattern formation, reaction-diffusion, diffusion, mathematical biology, population ecology

1. Introduction. Striking spatial patterns are found in a variety of physical sys-
There is a long history concerned with the modeling of animal movements.
The null movement hypothesis: a random walk plus growth

\[ \frac{\partial n}{\partial t} = D \left( \frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2} \right) + f(n) \]
The rde approach extends easily to coupled populations

\[
\frac{\partial u}{\partial t} = F(u,v) + D_u \nabla^2 u
\]

\[
\frac{\partial v}{\partial t} = G(u,v) + D_v \nabla^2 v
\]
Developmental Biology

Alan Turing posited the existence of two interacting chemicals (morphogens) in a homogeneous space

Alan Turing (1912-1954)
Turing instabilities:

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

Uniform states can become unstable if \( \frac{D_v}{D_u} \) is above some threshold.
Dissipative structures

- Nonlinear theory (Segel and Levin)
- Multiple scale expansion
- Successive approximations
- *Stable non-uniform patterns can emerge*
Do such mechanisms underlie spatial patterns in ecology?
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.
Other approaches to movement

• Long-distance spatial contact process
• Correlated random walk

http://privatewww.essex.ac.uk/~ecodling/
Other approaches to movement

- Anomalous diffusion
  - Variance increases as a power of time

www.wikipedia.org
© EDP Sciences, Springer-Verlag 2008
DOI: 10.1140/epjst/e2008-00638-6

Superdiffusion and encounter rates in diluted, low dimensional worlds

F. Bartumeus¹,a, P. Fernández², M.G.E. da Luz³, J. Catalan⁴, R.V. Solé⁵, and S.A. Levin¹
Does Levy search optimize?

Letters to Nature

Nature 401, 911-914 (28 October 1999) | doi:10.1038/44831; Received 10 May 1999; Accepted 12 August 1999

Optimizing the success of random searches

G. M. Viswanathan¹²³, Sergey V. Buldyrev¹, Shlomo Havlin¹⁴, M. G. E. da Luz⁶, E. P. Raposo⁷ and H. Eugene Stanley¹
Levy walks are just one of a variety of more sophisticated strategies

- Random walk
- Correlated random walk
- **Levy walk**
- Gradient tracking
- Learning
- Collective behavior
Keller-Segel Model

\[
\frac{\partial n}{\partial t} = \nabla \cdot \left\{ D_n(c) \nabla n - \chi(c) n \nabla c \right\}
\]

\[
\frac{\partial c}{\partial t} = D_c \nabla^2 c - n \delta(c)
\]

Random cell movement
Directed cell movement
Chemical diffusion
Chemical degradation by cells

J. Sherratt
Lagrangian-Eulerian connections

- **Begin from microscopic (Lagrangian) rules**

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

Random  | Directed  | Grouping  | Arrayal
More generally
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 transformation

1. Start from individual-based model, in which positions or velocities change according to specific rules.
Lagrangian/Eulerian transformation

1. Start from individual-based model, in which positions or velocities change according to specific rules.

2. Write population descriptions in terms of spatial/velocity density.
Spatial/velocity density

\[ n(x, v, t + \delta t) = \int dx' \, dv' \, P_{\delta X} (x - x' - v' \, \delta t; x', v', t) \]
\[ \ast P_{\delta V} (v - v' - a\delta t; x', v', t) n(x', v', t) \]

\( P_{\delta X} = \text{probability particle at } x', \text{velocity } v', \text{time } t \)
\( \text{has random jump } \delta x = x-x'-v'\delta t, \text{etc.} \)
Lagrangian/Eulerian transformation

1. Start from individual-based model, in which positions or velocities change according to specific rules.

2. Write population descriptions in terms of spatial/velocity density.

3. To close system, assume something like Poisson distribution locally.
Closure and continuum equation

\[
\frac{\partial}{\partial t} n(x,v,t) = - \frac{\partial}{\partial x_i} \left[ v_i n(x,v,t) \right] \\
- \frac{\partial}{\partial v_i} \left[ a_i n(x,v,t) \right] \\
+ \frac{1}{2} \frac{\partial^2}{\partial v_i \partial v_j} \left[ \gamma_{ij} n(x,v,t) \right].
\]
If closures are good, these approximations work well

Flierl et al., JTB 1999

Otherwise, equation-free methods (Kevrekidis)
But real aggregations are heterogeneous assemblages of individuals
Couzin, Krause, Franks, Levin

- Utilize simulations to explore these issues
Collective decision-making

Courtey Iain Couzin
So the direction chosen by informed individuals must reconcile these tendencies.

\[ d_i(t+\Delta t) = \frac{s_i(t) + \omega g_i(t)}{|s_i(t) + \omega g_i(t)|} \]

Collective decision-making

Courtesy Iain Couzin
1 informed individuals in group of 100.

Courtey Iain Couzin
5 informed individuals in group of 100.

Courtesy Iain Couzin
Collective decision-making

10 informed individuals in group of 100.

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

From Couzin et al., 2005
Metronome Synchronization

N=5
Rate=208 +/- 2
Initial Phase: Rand
09 Oct 2005
Serial V1322
Competing preferences

Difference in preference

Collective decision-making

Courtesy Iain Couzin
Collective decision-making

Difference in preference

Courtesy Iain Couzin
Competition and consensus
Unequal numbers of leaders

Leonard, Couzin, Levin, etc.

**Kuramoto model**

\[
\begin{align*}
\dot{\theta}_j &= \sin(\bar{\theta}_1 - \theta_j) + k \sum_{l=1}^{N} \sin(\theta_l - \theta_j) & j &= 1, \ldots, N_1 \\
\dot{\theta}_j &= \sin(\bar{\theta}_2 - \theta_j) + k \sum_{l=1}^{N} \sin(\theta_l - \theta_j) & j &= N_1 + 1, \ldots, N_1 + N_2 \\
\dot{\theta}_j &= k \sum_{l=1}^{N} \sin(\theta_l - \theta_j) & j &= N_1 + N_2 + 1, \ldots, N
\end{align*}
\]

Gradient system, so all solutions go to equilibrium
The complex order parameter

\[ p_\theta = r e^{i\psi} = \sum_{j=1}^{N} e^{i\theta_j} \]

\( r \) measures the level of synchrony in the group, 
\( \psi \) gives the average direction of the group.

Courtesy, Ben Nabet
We write the dynamics for $\psi_1, \psi_2, \psi_3$ the average heading of respectively $\eta_1, \eta_2$ and $\eta_3$.

$$r_je^{i\psi_j} = \frac{1}{N_j} \sum_{l \in \eta_j} e^{i\theta_l} \quad j = 1, 2, 3$$

$$\dot{r}_je^{i\psi_j} + i\dot{\psi}_j = \frac{1}{N_j} \sum_{l \in \eta_j} i\dot{\theta}_l e^{i\theta_l} \quad j = 1, 2, 3.$$  

During the second time scale

Everyone in cluster has same heading

$$\theta_l = \psi_j$$

$$r_j = 1$$

$$\dot{r}_j = 0$$

Courtesy, Ben Nabet
We get for the second time scale

\[
\begin{align*}
\dot{\psi}_1 &= \sin(\bar{\theta}_1 - \psi_1) + kN_2 \sin(\psi_2 - \psi_1) + kN_3 \sin(\psi_3 - \psi_1) \\
\dot{\psi}_2 &= \sin(\bar{\theta}_2 - \psi_2) + kN_1 \sin(\psi_1 - \psi_2) + kN_3 \sin(\psi_3 - \psi_2) \\
\dot{\psi}_3 &= kN_1 \sin(\psi_1 - \psi_3) + kN_2 \sin(\psi_2 - \psi_3)
\end{align*}
\]
phase portrait for $K = 0$ and $\bar{\theta}_2 = 3.1416$
Preliminary conclusions

• Naïve individuals are crucial to consensus
• Non-spatial models miss key detail
• Multi-scale analyses also essential
Uninformed population can improve decision making of groups in motion

Naomi E. Leonard *, Tian Shen *, Benjamin Nabet †, Luca Scardovi ‡, Iain D. Couzin §, and Simon A. Levin §

*Department of Mechanical and Aerospace Engineering, Princeton University, Princeton, NJ, USA; †Royal Bank of Canada, New York, NY, USA; ‡Department of Electrical Engineering and Information Technology, Technical University of Munich, Munich, Germany, and §Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ, USA

Submitted to Proceedings of the National Academy of Sciences of the United States of America

It has been shown using a computational agent-based model that a group of animals moving together can make a collective decision on direction of motion, even if there is a conflict between the directional preferences of two small subgroups of “informed” individuals and the remaining “uninformed” individuals have no directional preference [1]. The model requires no explicit signaling nor identification of informed individuals; individuals merely adjust their steering in response to socially acquired information on relative motion of neighbors. We present a continuous-time version of the model, and, using stability analysis and model reduction by time-scale separation, we prove a necessary and sufficient condition for stable convergence to a collective decision in this model. The stability of the decision, which corresponds to most of the group moving in one of two alternative preferred directions, depends explicitly on the magnitude of the difference in preferred directions; for a difference above a threshold the decision is stable and below that same threshold the decision is unstable. Given qualitative agreement with the results of the simulation study of [1], we proceed to explore analytically the subtle but important role of the uninformed individuals in the continuous-time model. We derive the sensitivity of the collective decision making to the size of the uninformed population, showing that the region of attraction for the decision increases with increasing numbers of uninformed individuals.

collective decision making | dynamics | social interactions

Explaining the ability of animals that move together in a group to make collective decisions requires an understanding of the mechanisms of information transfer in spatially evolving distributions of individuals with limited sensing capability [2, 3] [references]. In groups such as fish schools and large insect swarms, it is likely that individuals can only sense the relative motion of near neighbors and may not have the capacity to coordinate their activities with individuals at a distance. As the size of a group increases, it becomes increasingly difficult for each individual to keep track of all others. In the present study, we considered a system of individuals in which the total population is divided into two subgroups, each with a distinct preferred direction of motion. We showed that, even in the absence of explicit communication or coordination, the group can make a collective decision: with two informed subgroups of equal population (one subgroup per preference alternative), a collective decision to move in one of the two preferred directions is made with high probability as long as the magnitude of the preference conflict, i.e., the difference in preferred directions, is sufficiently large. For small conflict, the group follows the average of the two preferred directions. Further, simulations in [6] show evidence that increasing the population size of uninformed individuals lowers the threshold on magnitude of conflict, making it “easier” for a collective decision to be made.

Simulations of the kind reported in [1] are highly suggestive, but because they contain so many degrees of freedom, it is difficult to identify the influences of particular mechanisms. In this paper we present an approximation to the individual-based model [1] that allows deeper analysis into the microscopic reasons for the observed macroscopic behaviors and a broader exploration of parameter space. The model we propose and study is represented by a system of ordinary differential equations. As in the formulation of [5], each agent is modelled as a particle moving in the plane at constant speed with steering rate dependent on inter-particle measurements and, for informed individuals, on a preferred direction. In [5] two time-scales, observed in the simulations of [1], are formally proved for the system of equations; in the fast time-scale, alignment is established within each subgroup of agents with the same preference (or lack of preference), while in the slow time-scale, the reduced-order model describes the average motion of each of the two informed subgroups and the uninformed subgroup.

In [5] assumptions are made that simplify the analysis.
Coupled oscillator approximation
Leonard et. al, PNAS

In subgroup 1, represent as

$$\frac{d\theta_j}{dt} = \sin(\bar{\theta}_1 - \theta_j(t)) \ . \ [1]$$

In subgroup 2 as

$$\frac{d\theta_j}{dt} = \sin(\bar{\theta}_2 - \theta_j(t)) \ . \ [2]$$
Coupled oscillator approximation

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

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

where coupling coefficients respond dynamically
Conclusions from analysis

- **Multiple scales**
- **Coupled oscillator models explain a great deal**
- **Explicit spatial models are needed**
- **Unopinionated individuals are crucial to consensus, and enhance the success of the majority viewpoint**
Fig. 1. Coupling in manifolds $M_{010}$ (Left) and $M_{001}$ (Right) among subgroups 1, 2, and 3 as indicated by arrows.
Slow time scale

\[
\frac{d\Psi_1}{dt} = \sin(\bar{\theta}_1 - \Psi_1(t)) + \frac{K_1}{N}(A_{12}N_2\sin(\Psi_2(t) - \Psi_1(t)))
+ A_{13}N_3\sin(\Psi_3(t) - \Psi_1(t)))
\]

\[
\frac{d\Psi_2}{dt} = \sin(\bar{\theta}_2 - \Psi_2(t)) + \frac{K_1}{N}(A_{12}N_1\sin(\Psi_1(t) - \Psi_2(t)))
+ A_{23}N_3\sin(\Psi_3(t) - \Psi_2(t)))
\]

\[
\frac{d\Psi_3}{dt} = \frac{K_1}{N}(A_{13}N_1\sin(\Psi_1(t) - \Psi_3(t)))
+ A_{23}N_2\sin(\Psi_2(t) - \Psi_3(t)))
\]

[6]

\[A_{ij} = 0 \text{ or } 1\]
### Table 1. Possible combinations of stable (S) and unstable (U) manifolds given $N_3 > 2N_1$

<table>
<thead>
<tr>
<th>$M_{101}$</th>
<th>$M_{110}$</th>
<th>$M_{000}$</th>
<th>$M_{010}$</th>
<th>$M_{001}$</th>
<th>$M_{100}$</th>
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<tbody>
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</tr>
</tbody>
</table>

Subscripts refer to $A_{12}$, $A_{13}$, $A_{23}$
Lecture outline

• Statistical mechanics of ecological communities
• Critical transitions
• Collective phenomena and collective motion
  – Emergence and pattern formation
• Conflict and collective action
What is the value of information?

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?
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 Guttal* 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 small insects to vertebrates, migrate in response to such gradients, using various navigational mechanisms, such as the sun compass or magnetic sensing. 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 mutual-benefit structures that represent diverse scenarios.

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 speciation 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 reciprocal 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 Guttal* and Iain D. Couzin*
Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ USA
Guttal et al.
Simple model: wide range of dynamics

Gradient detection ability

Sociality

Density=1.0

Brownian swarms

Collective Migration

Migratory Benefits per individual

Solitary Migrations

Random walking individuals

ωs

ωg

Thanks to Iain Couzin
Evolutionary branching: leaders and followers

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

Guttal and Couzin, PNAS, 2010

Thanks to Iain Couzin
Evolving specialized leadership roles

- Assume reproductive fitness is dependent on following a defined migration route
- The route is not known a priori but shown by environmental cues
- Detecting these cues is costly (e.g. lost foraging time, reduced predator vigilance, energetic costs of exploration)
- Naive following of others is a low cost alternative strategy
Evolving specialized leadership roles

- Model fluctuating environmental signal as a stochastic process
- Individual heading $\theta$ follows mean reverting process, where $\theta=0$ is the optimum migration direction

$$d\theta_t = -x_g \theta dt + \sigma dW_t$$

- Level of investment in detecting the environmental cue
- Noise term, representing fluctuations or errors in detection

- Level of investment $x_g$ is costly but following others is free
Natural selection

• Select for highest average migration speed, minus a cost function
Evolution:
In absence of social information, fitness is

\[ F = \exp\left(-\frac{\sigma^2}{4x_g}\right) \]

Mean Velocity
Quantifying the social information

- Follow Kuramoto's approach for coupled oscillators to reduce population orientations to 2 dimensional order parameter

\[
\frac{1}{N} \sum_{i=1}^{N} e^{i\theta} = \int_{-\pi}^{\pi} \rho(\theta) e^{i\theta} d\theta = re^{i\psi}
\]

- Leads to coarse grained representation of social interactions

\[
d\theta_t = -x_s(\theta - \psi)dt + \eta \sqrt{1 - r} dW_t
\]
Add these together

\[ d\theta_t = \frac{x_g \, d\theta_g + x_s \, d\theta_s}{x_g + x_s} \]
Adaptive dynamics and branching

- Evolutionary change determined by differential fitness of mutant in the resident population
  \[ s_x(y) = F(y, x) - F(x, x) \]

- Population moves toward convergence stable solution (CSS)

- But if CSS not an evolutionary stable solution (ESS) branching will occur -
  \[ \frac{\partial^2 F(y, x^*)}{\partial y^2} \bigg|_{y=x^*} > 0 \]

- Branching and specialized sub-populations of leaders and followers emerge if CSS is less than critical value (red line)
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
- Methods from mathematics and physics can inform and be inspired.