Scaling and collective phenomena in ecological systems

Claudo Carere
StarFLAG EU FP6 project

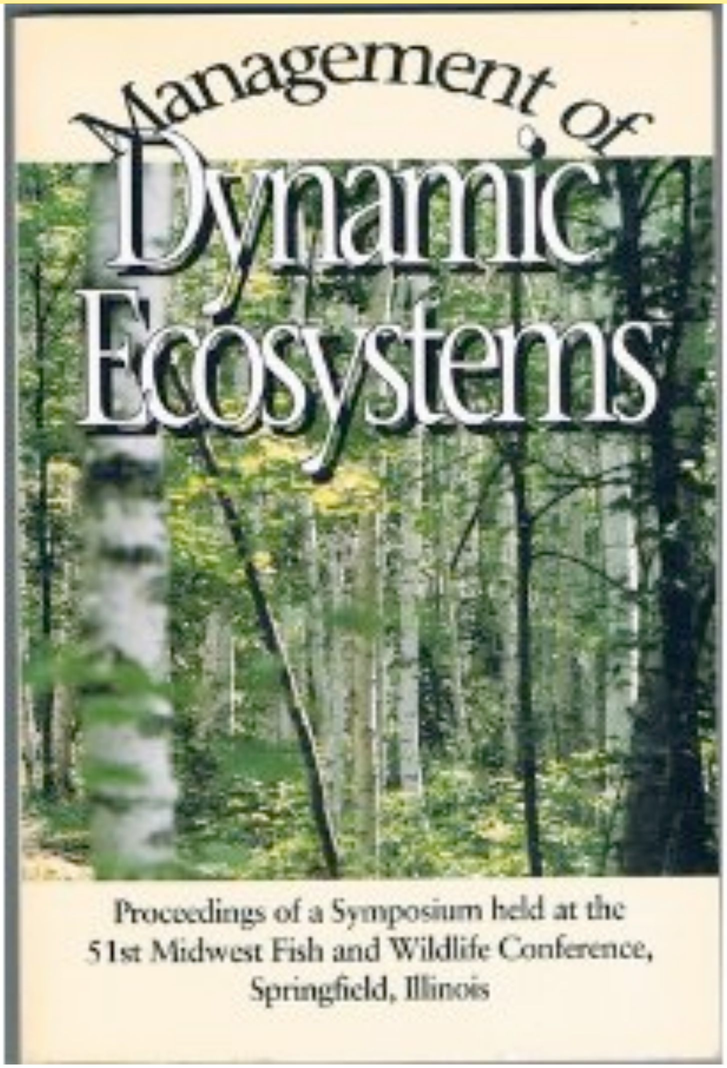
Simon Levin

Brazil2014

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



Sweeney . Ed..

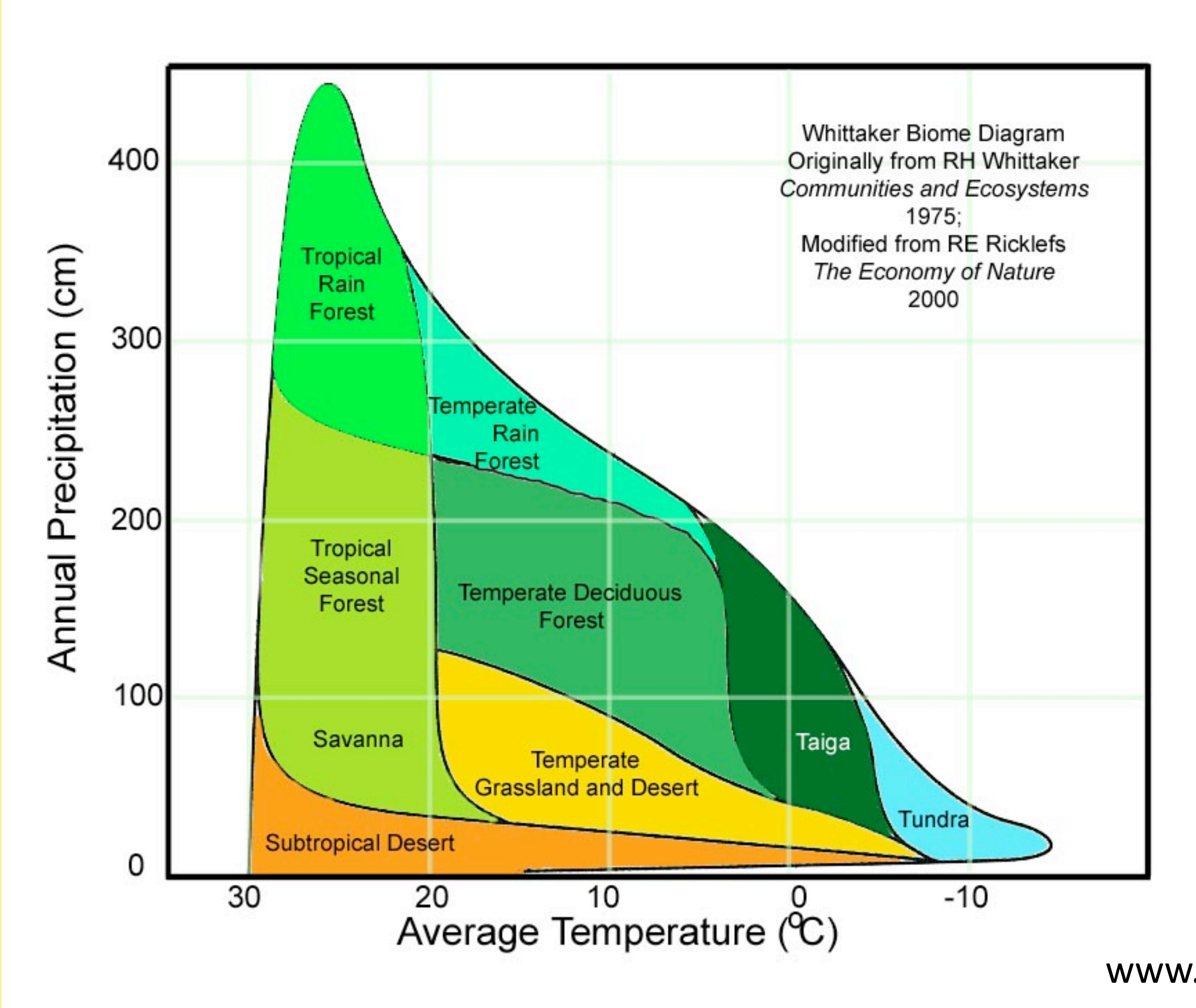
However, though species come and go, there are characteristic regularities in the macroscopic patterns in all ecosystems

www.bio.unc.edu

www.yale.edu/yibs

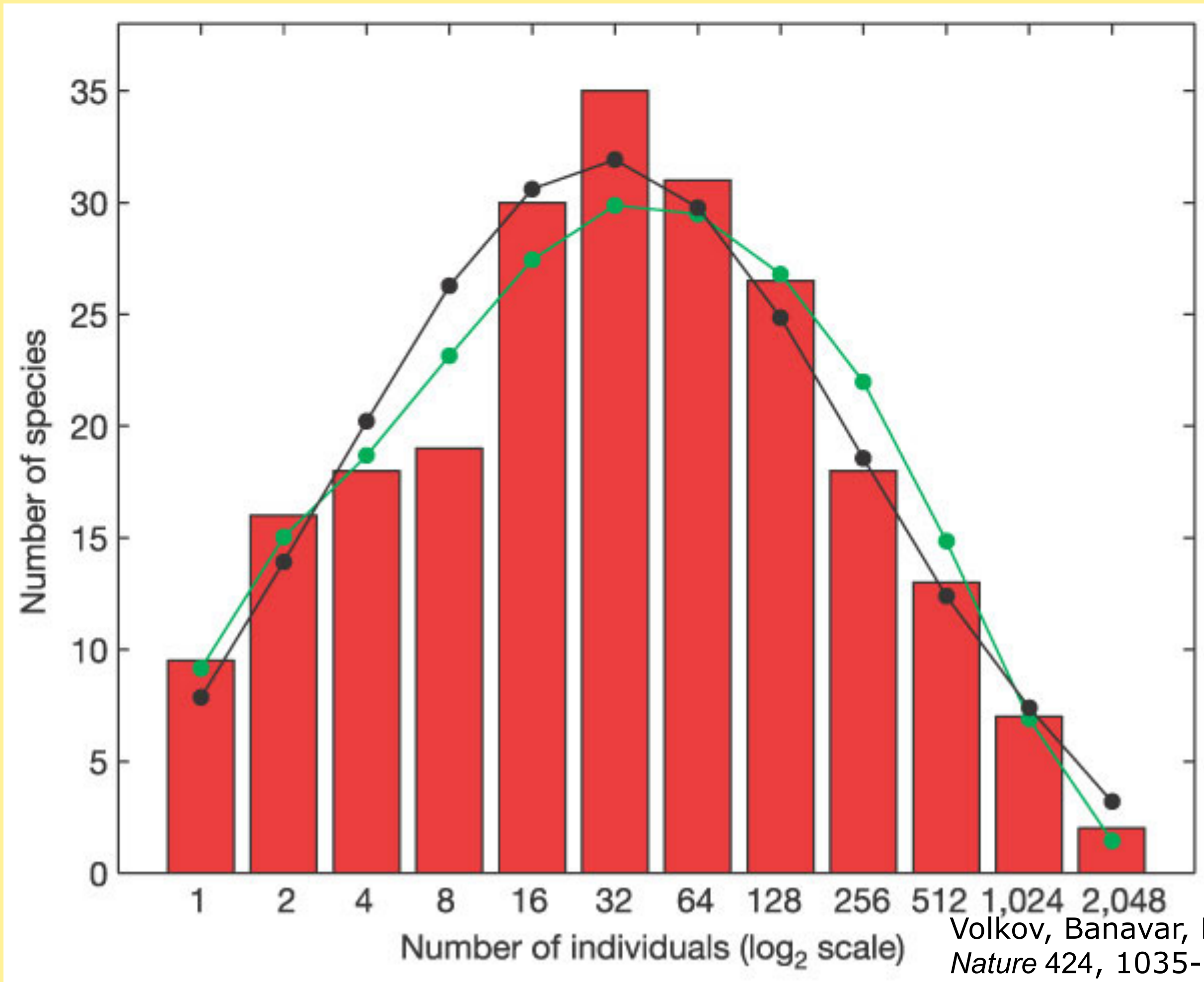
www.csiro.au

These regularities characterize biomes



www.marietta.edu

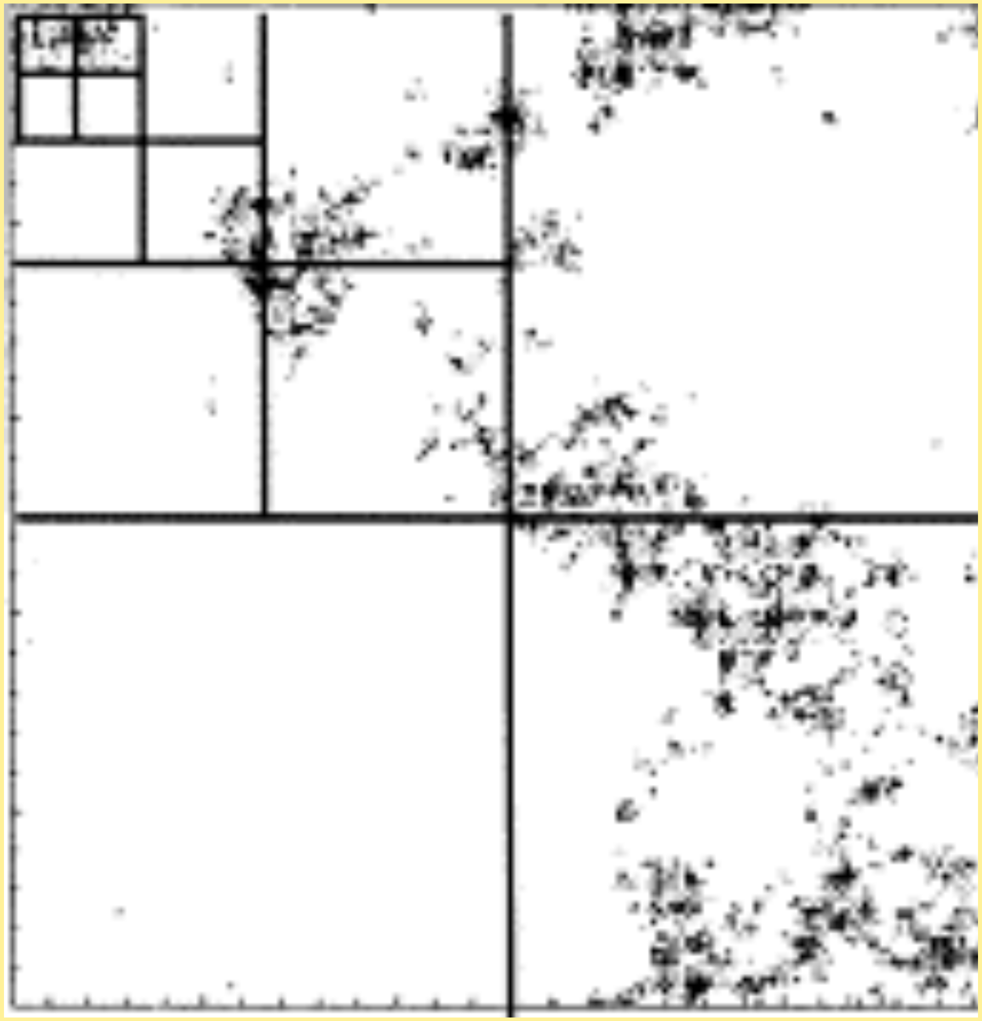
Characteristic macroscopic patterns are emergent, independent of much microscopic detail



Volkov, Banavar, Hubbell and Maritan
Nature 424, 1035-1037

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

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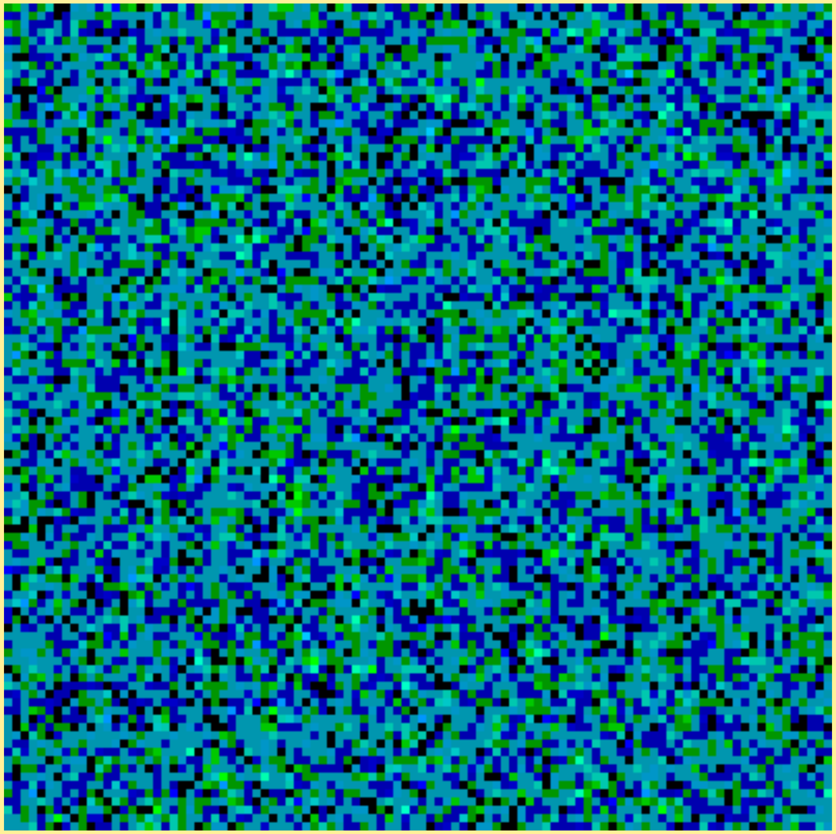
Mathematical challenges: Simplification approaches

- 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

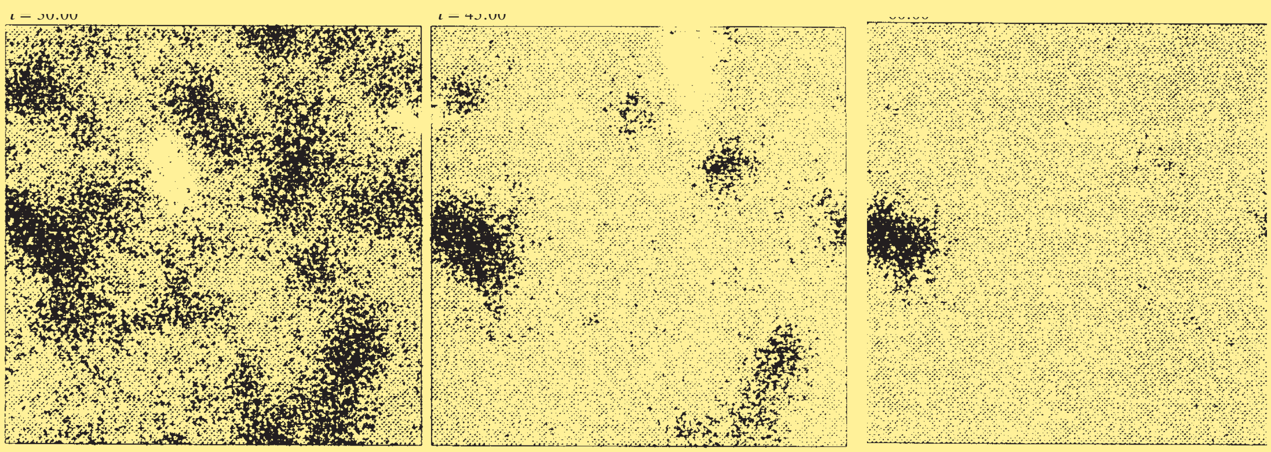


… path dependency, especially due to finite-size effects, and critical slowing down

"Critical Slowing Down" in Time-to-extinction: an Example of Critical Phenomena in Ecology

AMAR GANDHI,* SIMON LEVIN† AND STEVEN ORSZAG

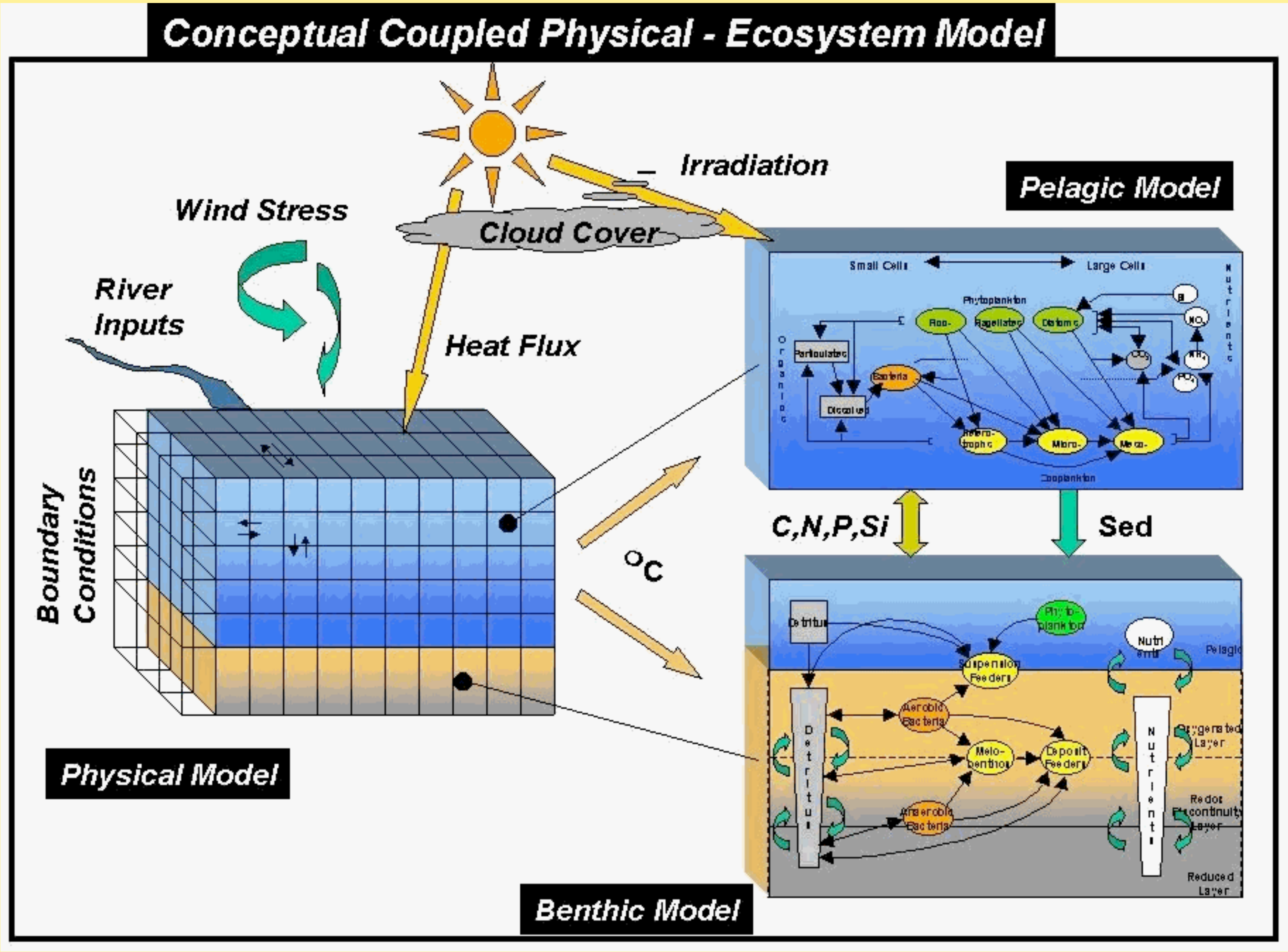
Program in Applied & Computational Mathematics, Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544-1003, *U.S.A.*



Forest growth models have been well-developed, and exhibit similar path dependence

(Pacala, Botkin, Shugart, others)

Deutschman, DH, SA Levin, C Devine and LA Buttel. 1997. Science **277**:1688.



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.

NOAA

So too are the socio-economic systems with which they are interlinked

www.suite101.com

Features of CAS

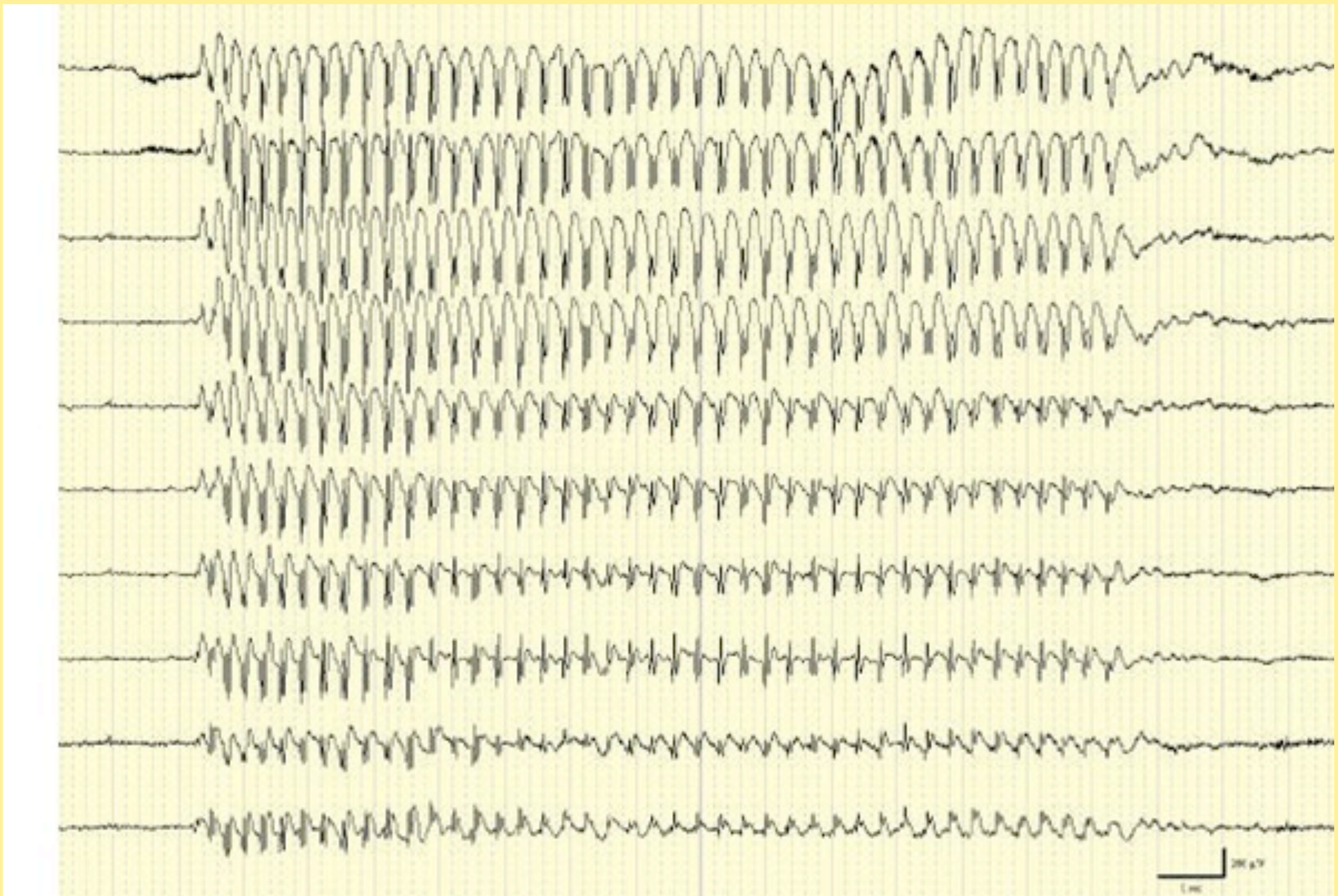
- Multiple spatial, temporal and organizational scales
- Self-organization, and consequent unpredictability
- Multiple stable states, path dependence, hysteresis
- Contagious spread and systemic risk
- Potential for destabilization and regime shifts through slow-time-scale evolution

Stock markets crash

Critical transitions occur in physiological states

http://www.edmontonneurotherapy.com/treatment_of_migraine.html

Are there early warning indicators?



www.aesnet.org

nature physics VOL 2 JUNE 2006 www.nature.com/naturephysics

Critical phenomena in atmospheric precipitation

OLE PETERS[1,2,3]* AND J. DAVID NEELIN[3]

[1]Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, New Mexico 87501, USA

[2]CNLS, Los Alamos National Laboratory, MS-B258, Los Alamos, New Mexico 87545, USA

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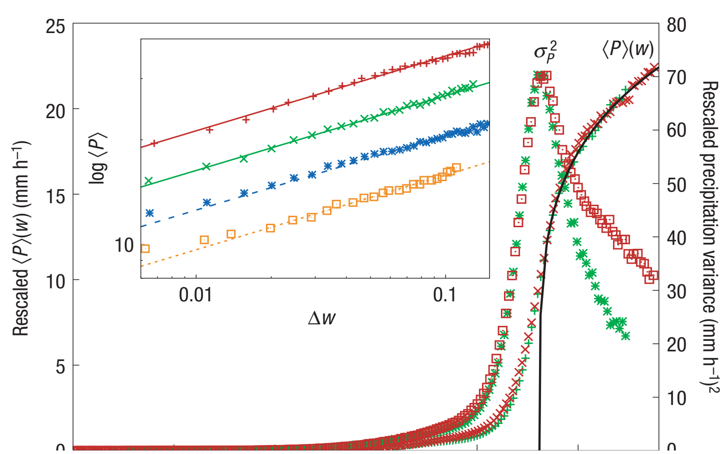
*e-mail: ole.peters@physics.org

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[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[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 important observables conform to the simple functional forms predicted by the theory of critical phenomena. In meteorology



NEWS & VIEWS

2008

COMPLEX SYSTEMS

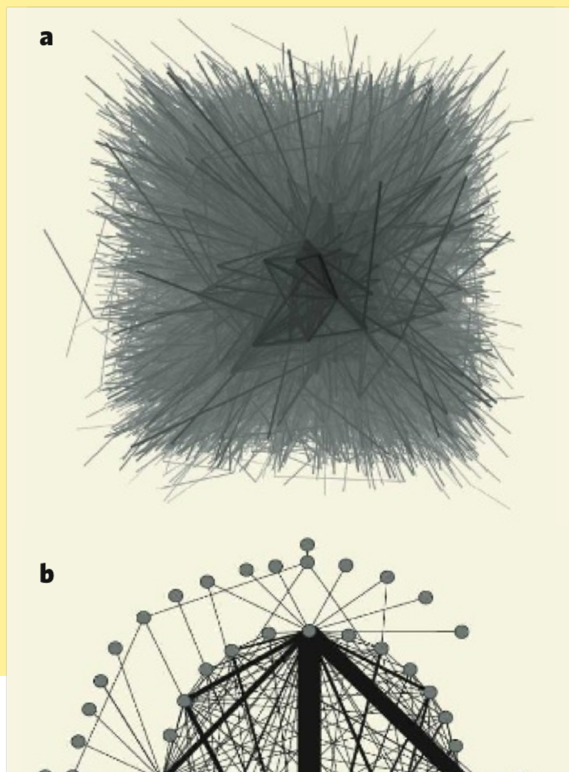
Ecology for bankers

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[1] 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



spent on studying 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

NEWS &

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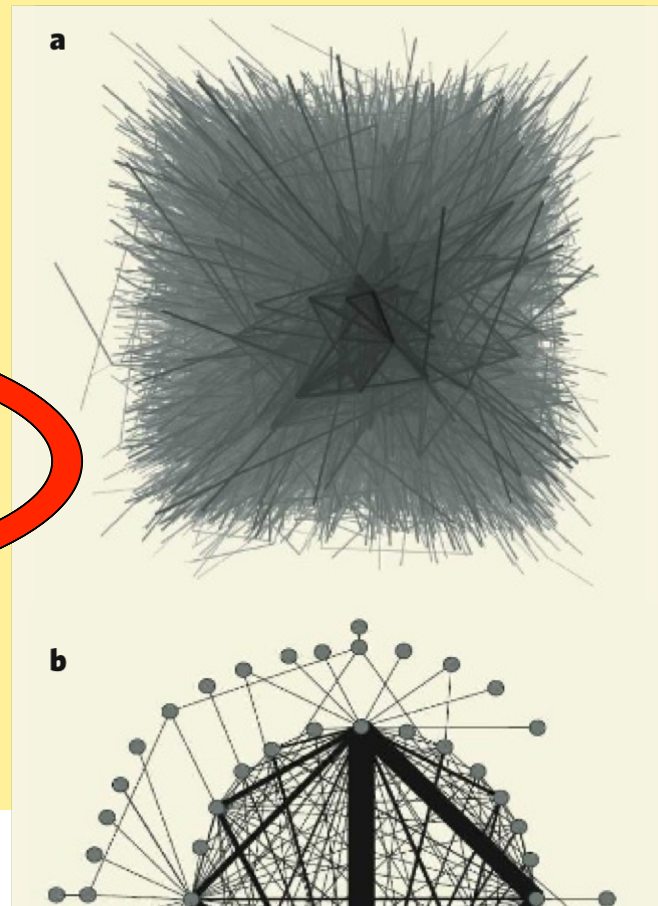

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Lecture outline

- 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

REVIEW

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 Vandermeer[10]

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 emerging research areas and discuss how exciting opportunities arise from the combination of these so far disconnected fields of work.

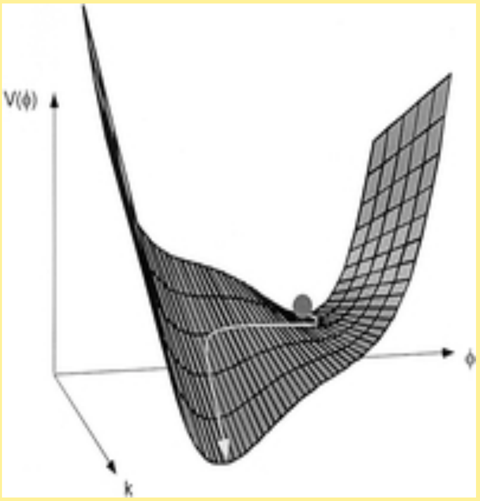
The Architecture of Fragility

Sharp regime shifts that punctuate the usual fluctuations around trends in ecosystems or societies may often be simply the result of an unpredictable external shock. However, another possibility is that such a shift represents a so-called critical transition (*3, 4*). The likelihood of such transitions may gradually increase as a system approaches a "tipping point" [i.e., a catastrophic 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 (nodes being more similar) and a highly connected network may provide resistance to change until a

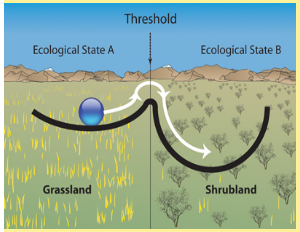
Many such transitions have characteristic signals

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



Bardy, B.; Oullier, O.; Bootsma, R. J.; Stoffregen, T. A.;J. Exp. Psych. Vol 28(3): 499-514.

More on this and the need for caution tomorrow



www.greateryellowstonescience.org

Alternative stable states are well-documented in ecology

Nature Vol. 269 6 October 1977 **471**

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 as against the accidents of initial conditions and perturbations. Is the human story largely a deterministic tale of civilisations marching to Toynbee's tune, three and a half beats to disintegration, or did the hinge of history turn on the length of Cleopatra's nose? Such questions of the relative roles of chance and necessity[1] are fundamental in modern cosmology[2,3], in the foundations of statistical mechanics[4,5], and in evolutionary biology[1] 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[6–9].

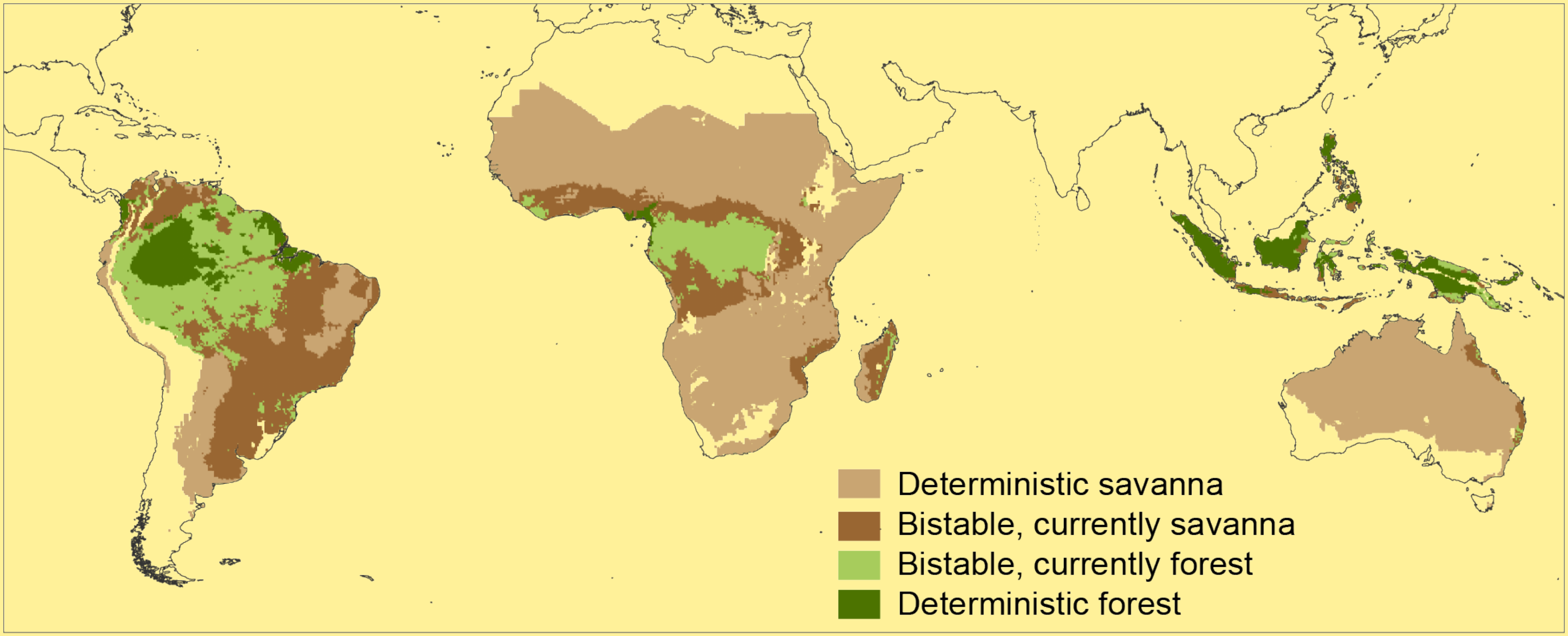
Taking a much narrower and more local view, it is interesting to consider a particular assembly of species, with specified interactions among them, and to ask questions about the dynamics of the system. Is the dynamical behaviour described by the multi-dimensional generalisation of a single valley (a 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

able reality." A similar conclusion emerges from Connell's and Slatyer's[12] survey of mechanisms of succession in natural communities.

The view that complicated ecosystems possess many alternative stable states is also supported by theoretical studies of mathematical models that caricature such systems. From the growing number of possible examples, I mention only two, chosen from opposite ends of the spectrum. Austin and Cook[13] have made computer studies of a system in which 94 species (embracing plants, herbivores and carnivores) are linked together by interactions that aim to be relatively realistic; the system has many equilibrium points, and is easily transferred from one to another. Case and Gilpin[14] have explored a relatively abstract system, in which the coefficients in the interaction matrix for a n-species Lotka–Volterra model are assigned random values; if n is at all large, the system typically collapses to one or other of a variety of simpler systems with fewer species, and this final steady state depends on the initial population values. The notion of 'resilience' has been introduced by Holling[15] in an attempt to characterise the degree to which a system can endure perturbations without collapsing or being carried into some new and qualitatively different state. Theoretical ideas about resilience, along with interpretive reviews of diverse other meanings that can be attached to 'stability' in an ecological context, are the subject of many recent papers[16–22].

It is thus clear that real ecosystems possess multiple stable states, as do plausible mathematical models. Unfortunately, the complications inherent in multi-species systems almost invariably

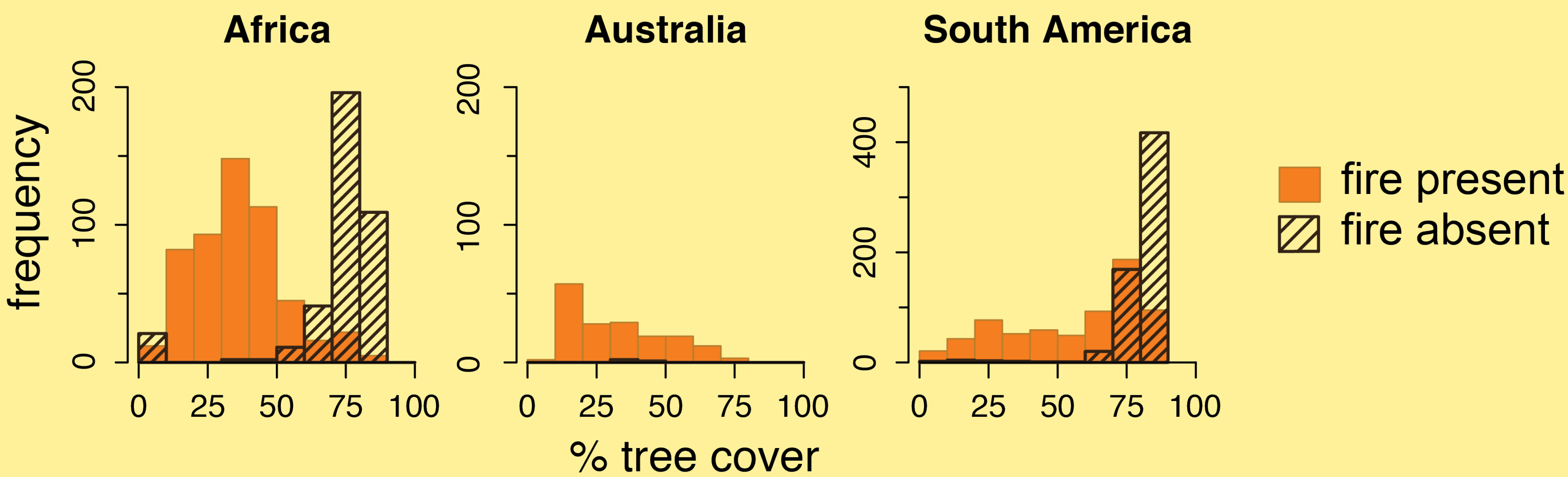
Savanna-forest systems exhibit bistability in vegetation distribution



Changes in precipitation can drive system flips

Staver *et al.* 2011 (*Ecology* and *Science)*

Fire separates savanna from forest within the intermediate climate envelope.

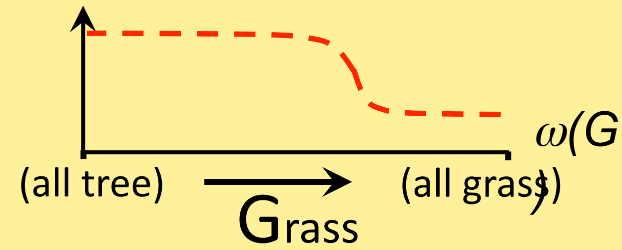


Staver *et al.* 2011 (*Ecology* and *Science)*

KRUGER NATIONAL PARK, SAVANNA

Carla Staver

Relatively simple models can capture this behavior



Grass
$$\frac{dG}{dt} = \mu S + \nu T - \beta G T$$

Saplings
$$\frac{dS}{dt} = \beta G T - \omega(G) S - \mu S$$

Trees
$$\frac{dT}{dt} = \omega(G) S - \nu T$$

$$G + S + T = 1$$

Staver *et al.* 2011 (*Ecology*) and Staver & Levin (Amer.Natur.)

Archibald, Staver, Levin PNAS2011
Recreating historical regimes

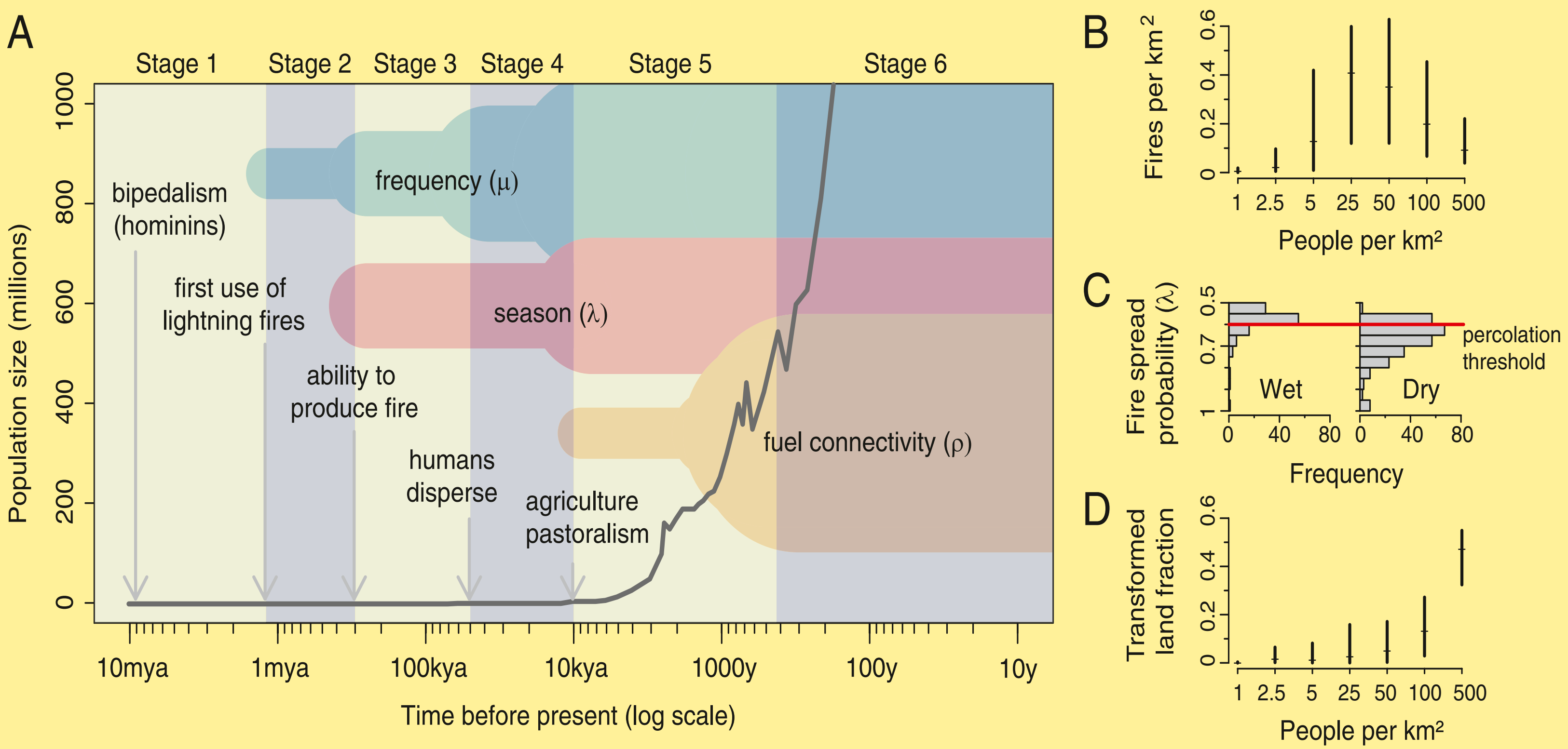
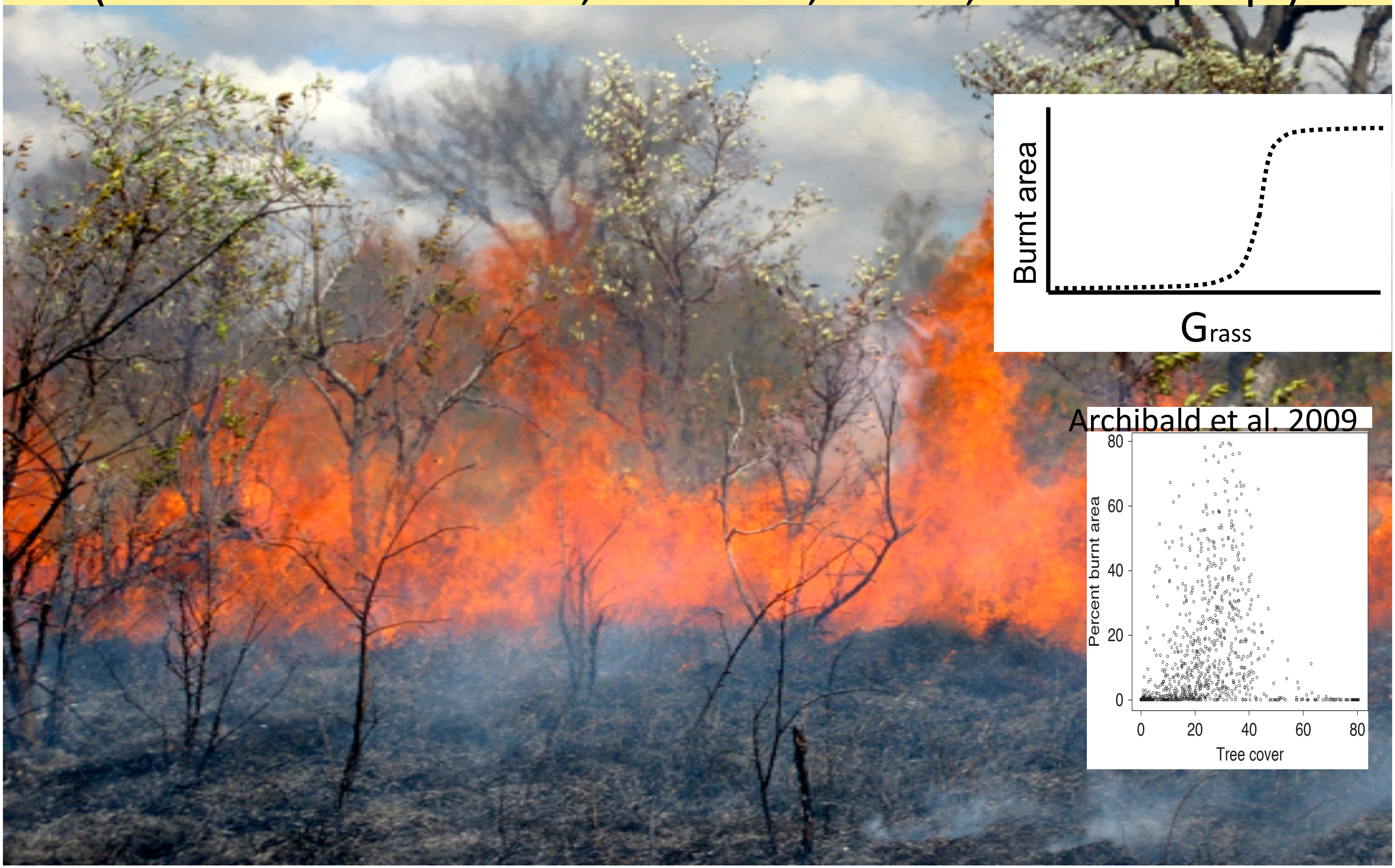


Fig. 4. Broadly showing the six stages of human evolution used to determine parameters for the stochastic model runs. The parameters μ and ρ were derived from published relationships between population density and fire density (*B*) and population density and land transformation (*D*), respectively; λ 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:

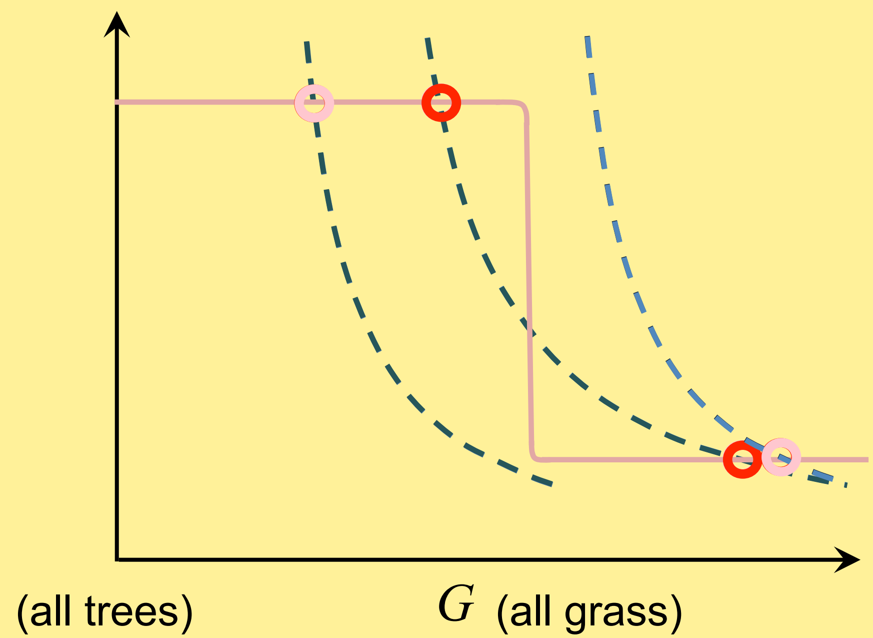
$$\omega(\overline{G}) = \frac{\mu\nu}{\beta\overline{G} - \nu}$$

$$f_1(G) = \omega(G)$$

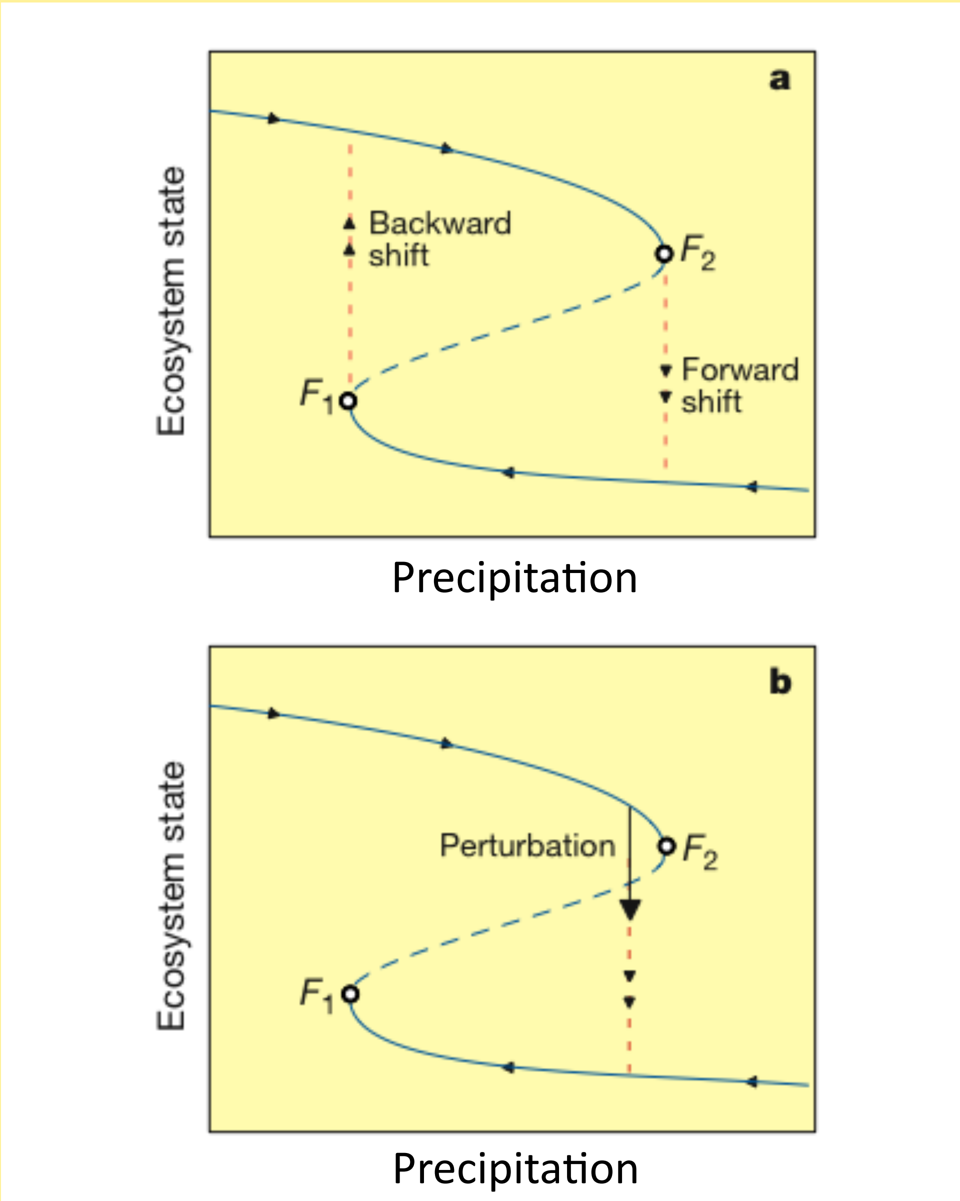
$$f_2(G) = \frac{\mu\nu}{\beta G - \nu}$$

For stability:

$$f_1'(G) > f_2'(G)$$



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



Modified very slightly from Scheffer *et al.* 2003, Nature

- 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

Adding Forest Trees (fire sensitive)

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

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

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

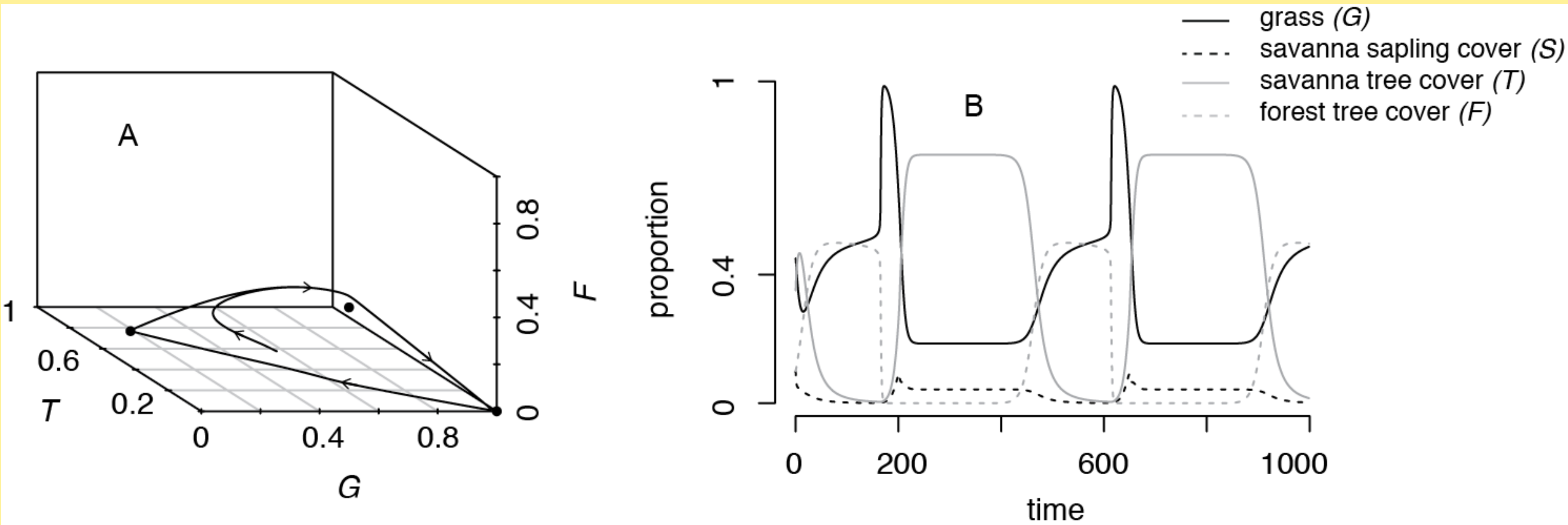
$$\frac{dF}{dt} = (\alpha\left(1 - F\right) - \phi(G))F$$

$$G + S + T + F = 1$$

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

4 August 1972, Volume 177, Number 4047

SCIENCE

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

planation 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

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.

X	Y
solid state or many-body physics	elementary particle physics
chemistry	many-body physics
molecular biology	chemistry
cell biology	molecular biology
•	•
•	•
•	•
psychology	physiology
social sciences	psychology

But this hierarchy does not imply

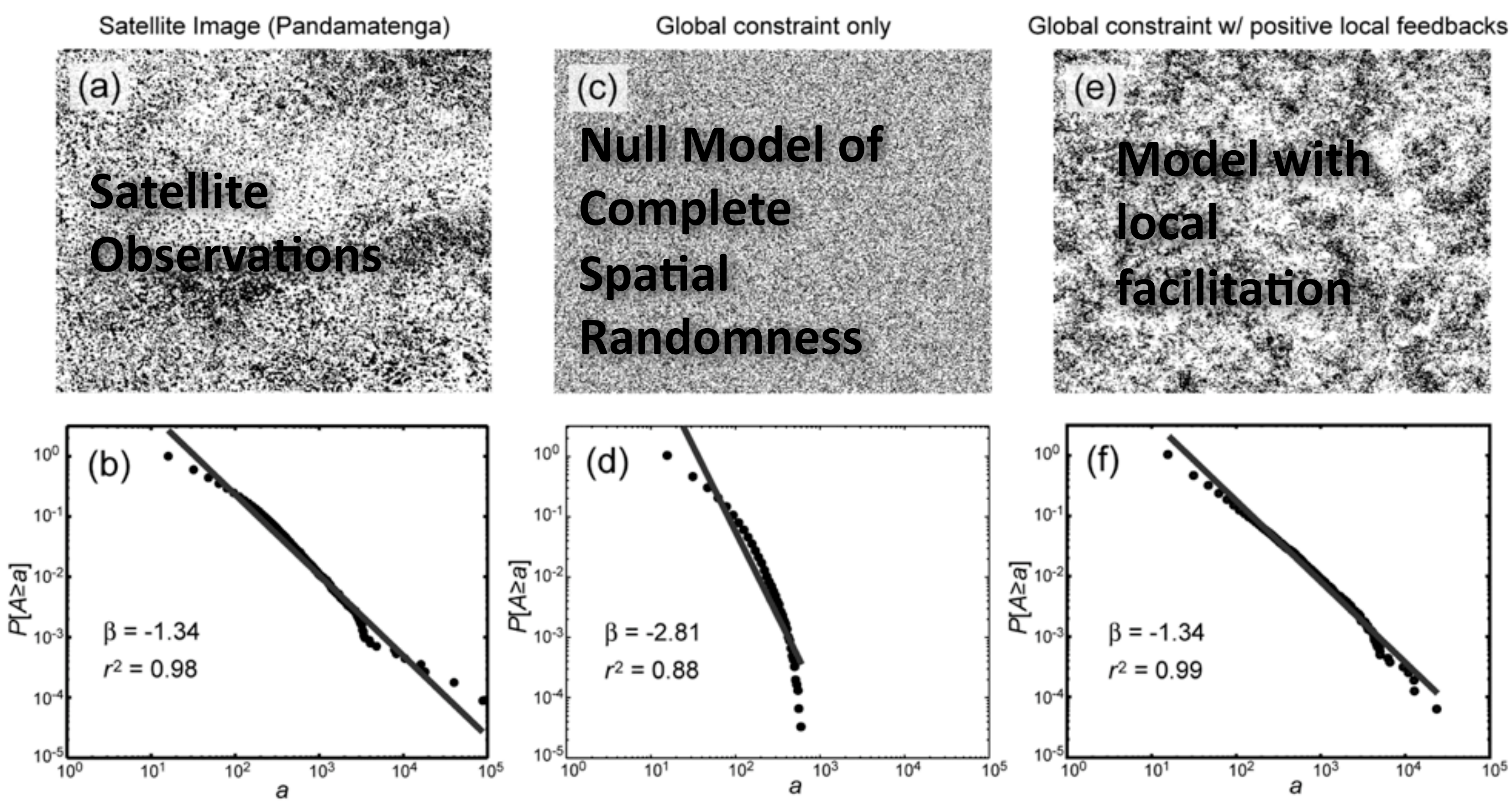
Vol 449|13 September 2007|doi:10.1038/nature06060

LETTERS

Positive feedbacks promote power-law clustering of Kalahari vegetation

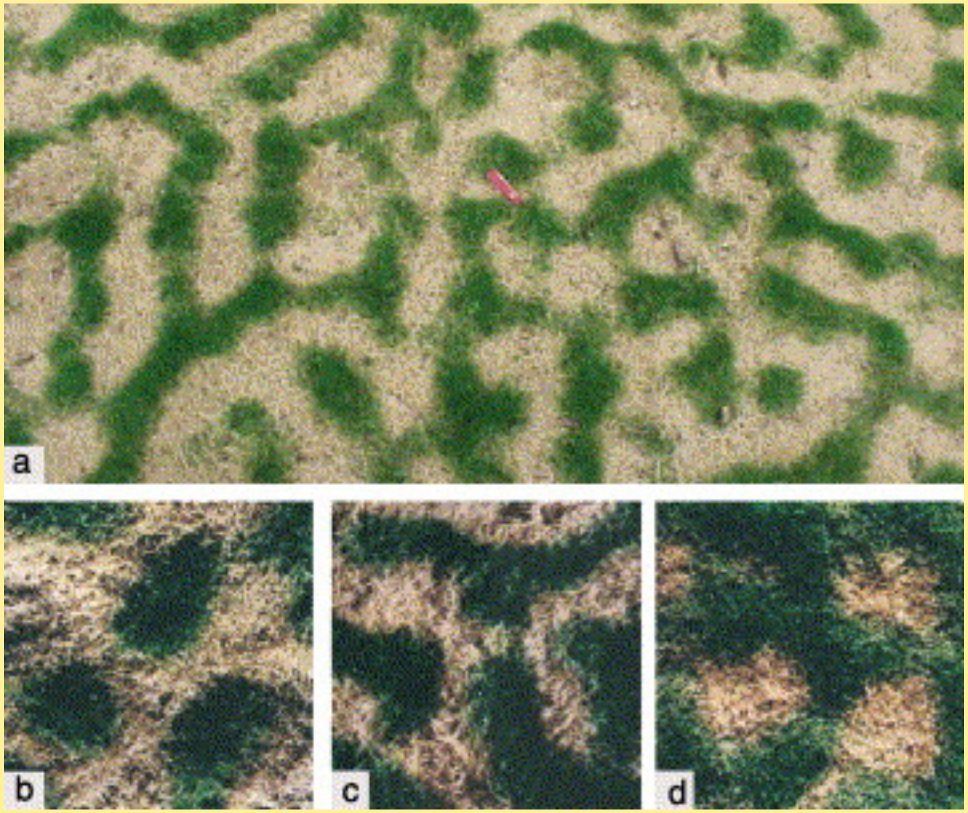
Todd M. Scanlon[1], Kelly K. Caylor[2], Simon A. Levin[3] & Ignacio Rodriguez-Iturbe[4]

Power laws can arise in many ways



Courtesy Kelly Caylor

Vegetation patterns in semi-arid landscapes are self-organized



Meron et al. 2004. [Chaos, Solitons & Fractals
Volume 19, Issue 2, January 2004, Pages 367–376]

Pattern forms from a combination of interaction and redistribution

SIAM REVIEW
Vol. 27, No. 1, March 1985

002

PATTERN GENERATION IN SPACE AND ASPECT*

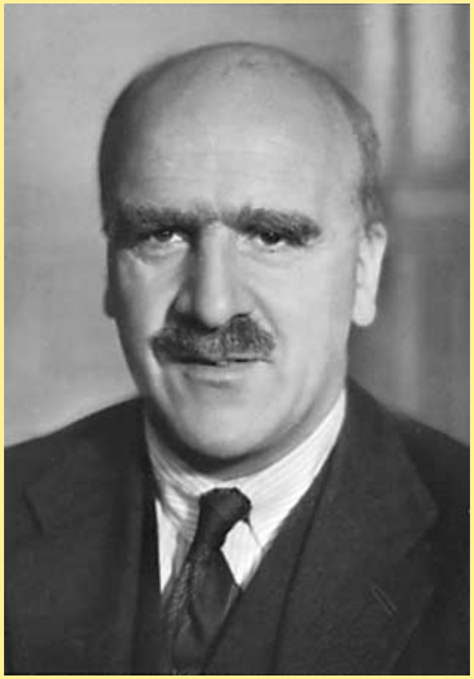
SIMON A. LEVIN† AND LEE A. SEGEL‡

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

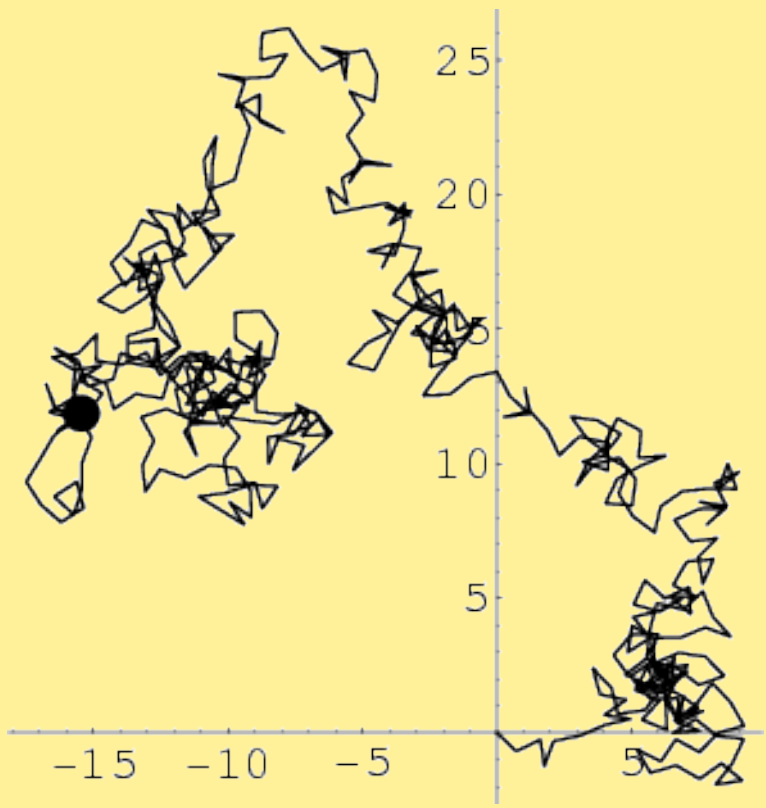


Haldane

Fisher

Wright

The null movement hypothesis: a random walk plus growth



$$\partial n / \partial t = D(\partial^2 n / \partial x^2 + \partial^2 n / \partial y^2) + f(n)$$

mathworld.wolfram.com

The rde approach extends easily to coupled populations

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

$$\frac{\partial v}{\partial t} = G(u,v) + D_v \nabla^2 v$$

Alan Turing (1912-1954)

Developmental Biology

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

Turing instabilities:

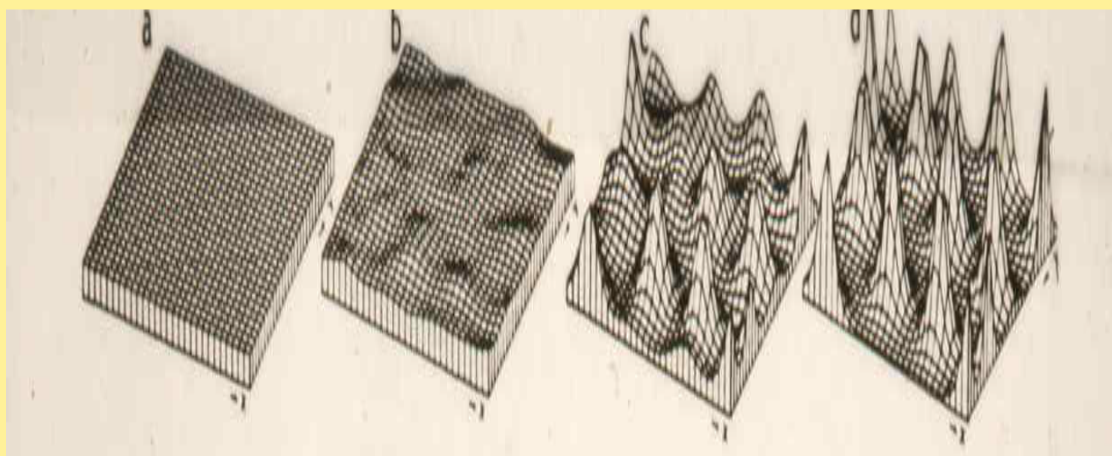
$$\frac{\partial u}{\partial t} = F(u,v) + D_u \nabla^2 u$$

$$\frac{\partial v}{\partial t} = G(u,v) + D_v \nabla^2 v$$

uniform states can become unstable if 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*

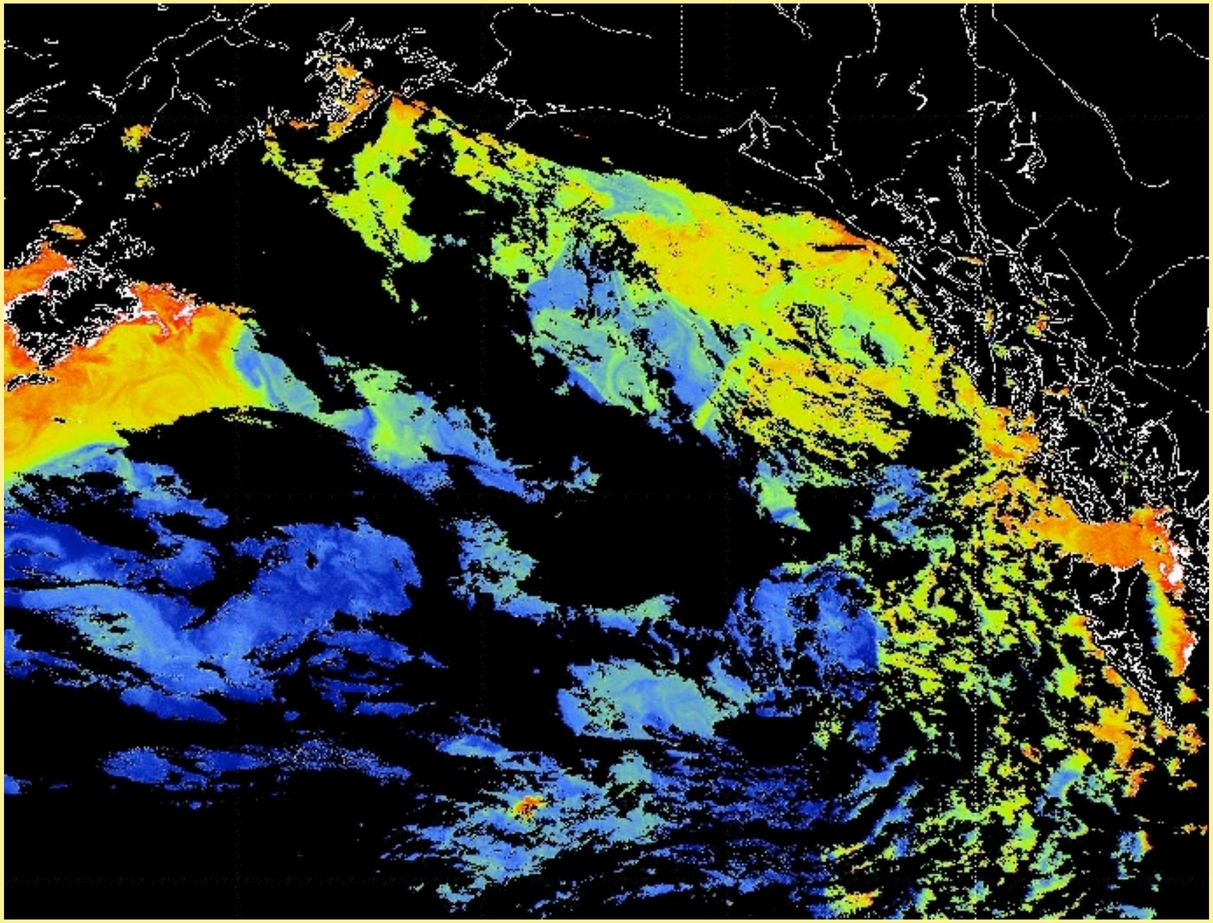


Meinhardt

Do such mechanisms underlie spatial patterns in ecology?

arts.monash.edu.au/ges/staff/ddunkerley

Plankton are patchy on almost every scale



disc.sci.gsfc.nasa.gov

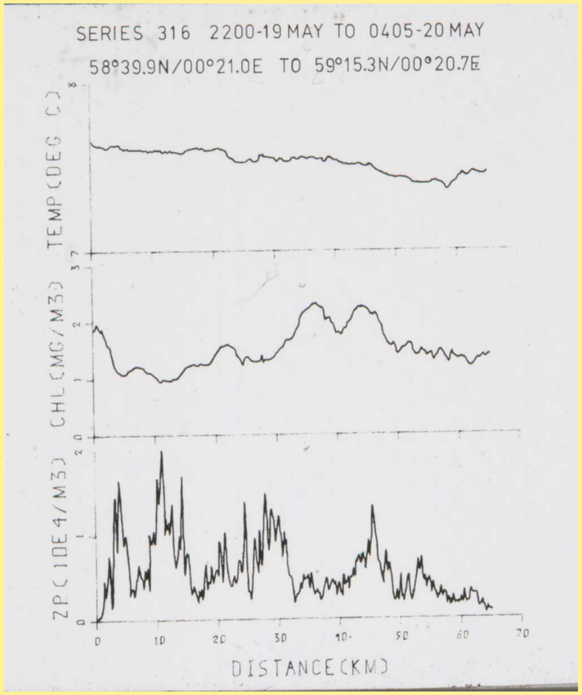
Could Turing apply to planktonic patchiness?

- Phytoplankton as "activators"
- Zooplankton as "inhibitors"

- Both Levin and Segel, and Okubo, independently proposed this

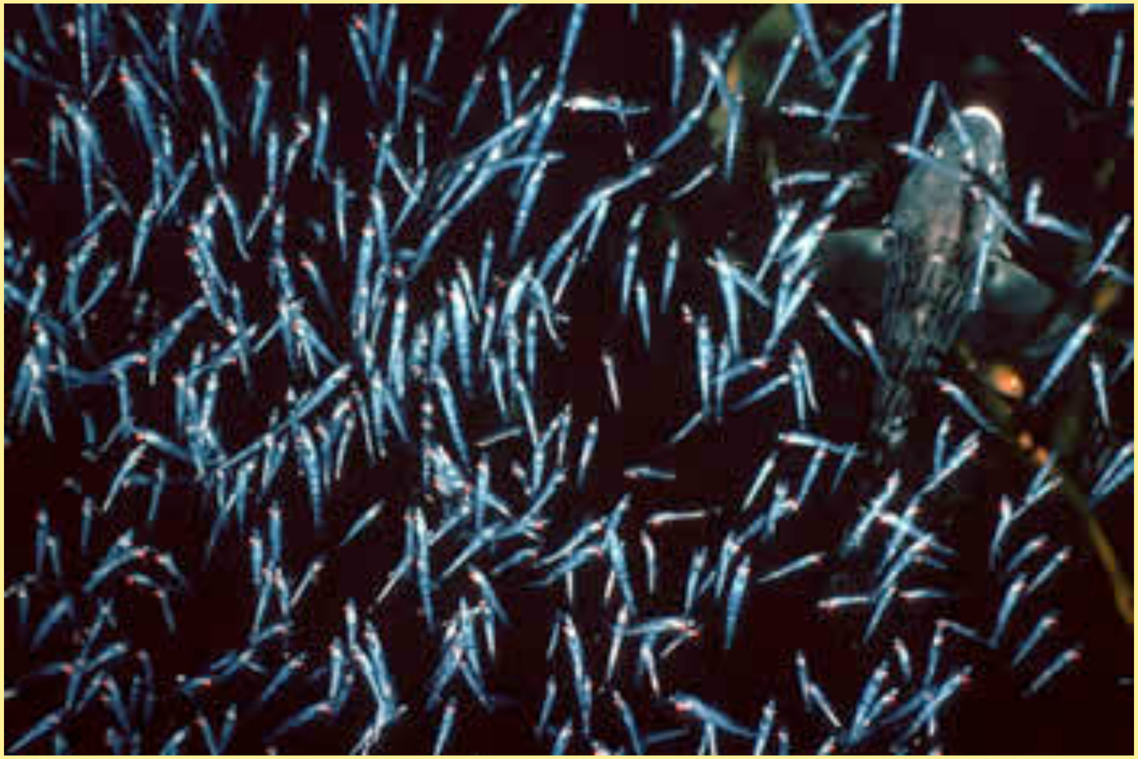
Turing mechanism didn't work

Zooplankton are more patchily distributed



Mackas et al

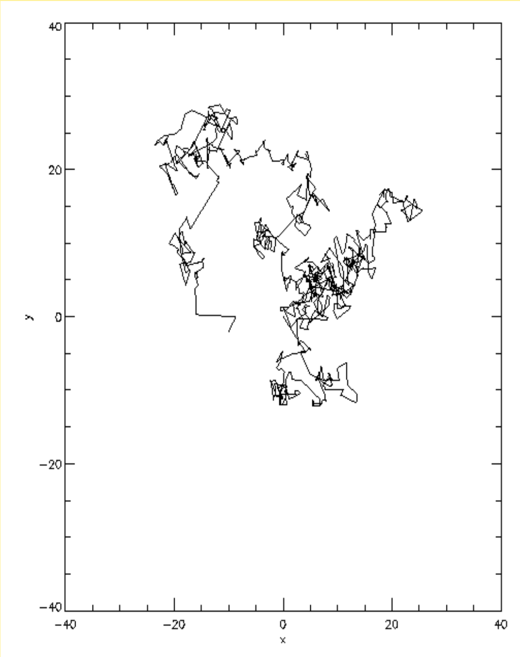
Zooplankton don't move randomly, but aggregate

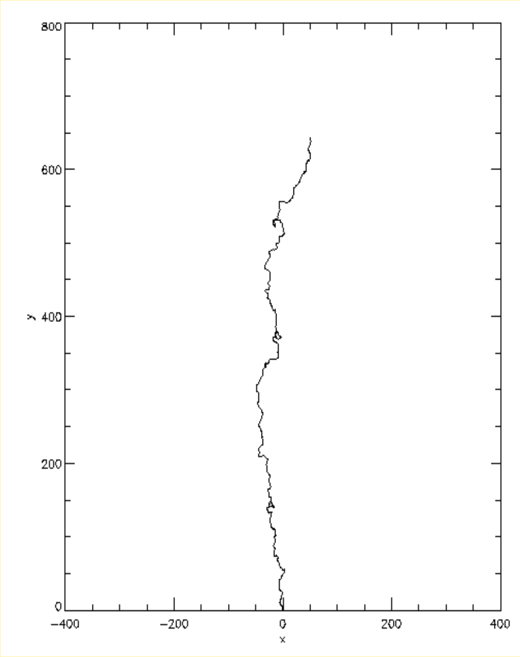


www2.le.ac.uk

Other approaches to movement

- Long-distance spatial contact process
- Correlated random walk

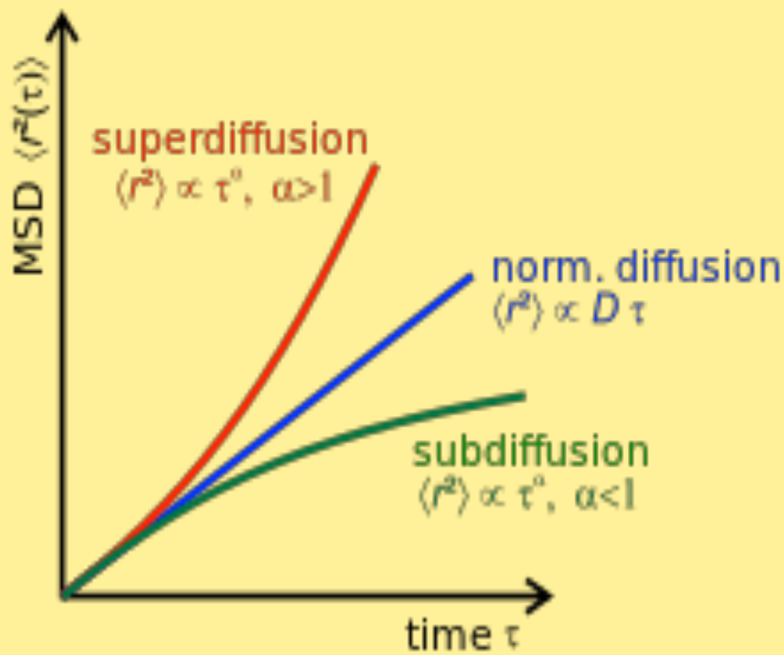




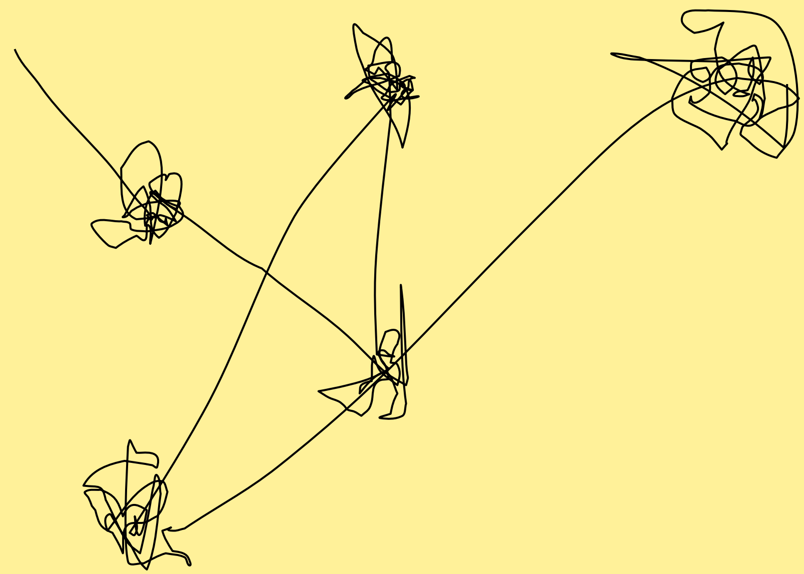
http://privatewww.essex.ac.uk/~ecodling/

Other approaches to movement

- Anomalous diffusion
  - Variance increases as a power of time



www.wikipedia.org



Eur. Phys. J. Special Topics **157**, 157–166 (2008)

DOI: 10.1140/epjst/e2008-00638-6

THE EUROPEAN PHYSICAL JOURNAL
SPECIAL TOPICS

Superdiffusion and encounter rates in diluted, low dimensional worlds

F. Bartumeus[1,a], P. Fernández[2], M.G.E. da Luz[3], J. Catalan[4], R.V. Solé[5], and S.A. Levin[1]

Does Levy search optimize?

Letters to Nature

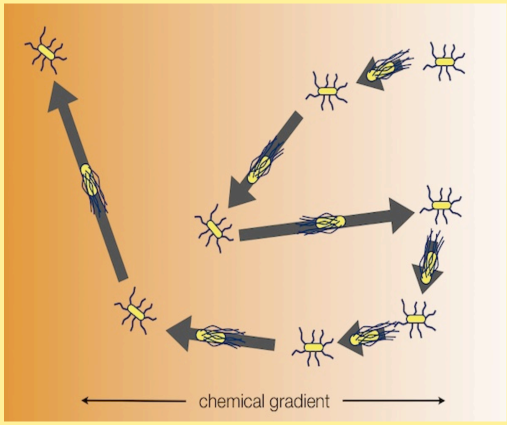
Nature **401**, 911-914 (28 October 1999) | doi:10.1038/44831; Received 10 May 1999; Accepted 12 August 1999

Optimizing the success of random searches

G. M. Viswanathan[1,2,3], Sergey V. Buldyrev[1], Shlomo Havlin[1,4], M. G. E. da Luz[6], E. P. Raposo[7] and H. Eugene Stanley[1]

Levy walks are just one of a variety of more sophisticated strategies

- Random walk
- Correlated random walk
- Levy walk
- Gradient tracking
- Learning
- Collective behavior



Christina Agapakis Scientific American | October 17, 2011

Keller-Segel Model

$$\frac{\partial n}{\partial t} = \nabla \cdot \{\overbrace{D_n(c)\nabla n}^{\text{Random cell movement}} - \overbrace{\chi(c) n \nabla c}^{\text{Directed cell movement}}\}$$

$$\frac{\partial c}{\partial t} = \underbrace{D_c \nabla^2 c}_{\text{Chemical diffusion}} - \underbrace{n\,\delta(c)}_{\text{Chemical degradation by cells}}$$

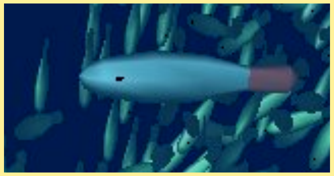
J. Sherratt

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?

Flierl, Grunbaum, Levin, Olson 1999

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

$$n\left(x, v, t+\delta t\right) =$$

$$\int dx'\, dv'\, \mathcal{P}_{\delta X}\,(x - x' - v'\,\delta t\,; x', v', t)$$

$$*\, \mathcal{P}_{\delta V}\,(v - v' - a\delta t\,; x', v', t)\, n\,(x', v', t)$$

$\mathcal{P}_{\delta x}$ = probability particle at x´, velocity v´, time t has random jump δx = x-x´-v´δt, 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

$$\frac{\partial}{\partial t} n(\mathrm{x},\mathrm{v},t) = -\frac{\partial}{\partial x_i}\left[v_i n(\mathrm{x},\mathrm{v},t)\right.$$

$$-\frac{\partial}{\partial v_i}\left[a_i n(\mathrm{x},\mathrm{v},t)\right]$$

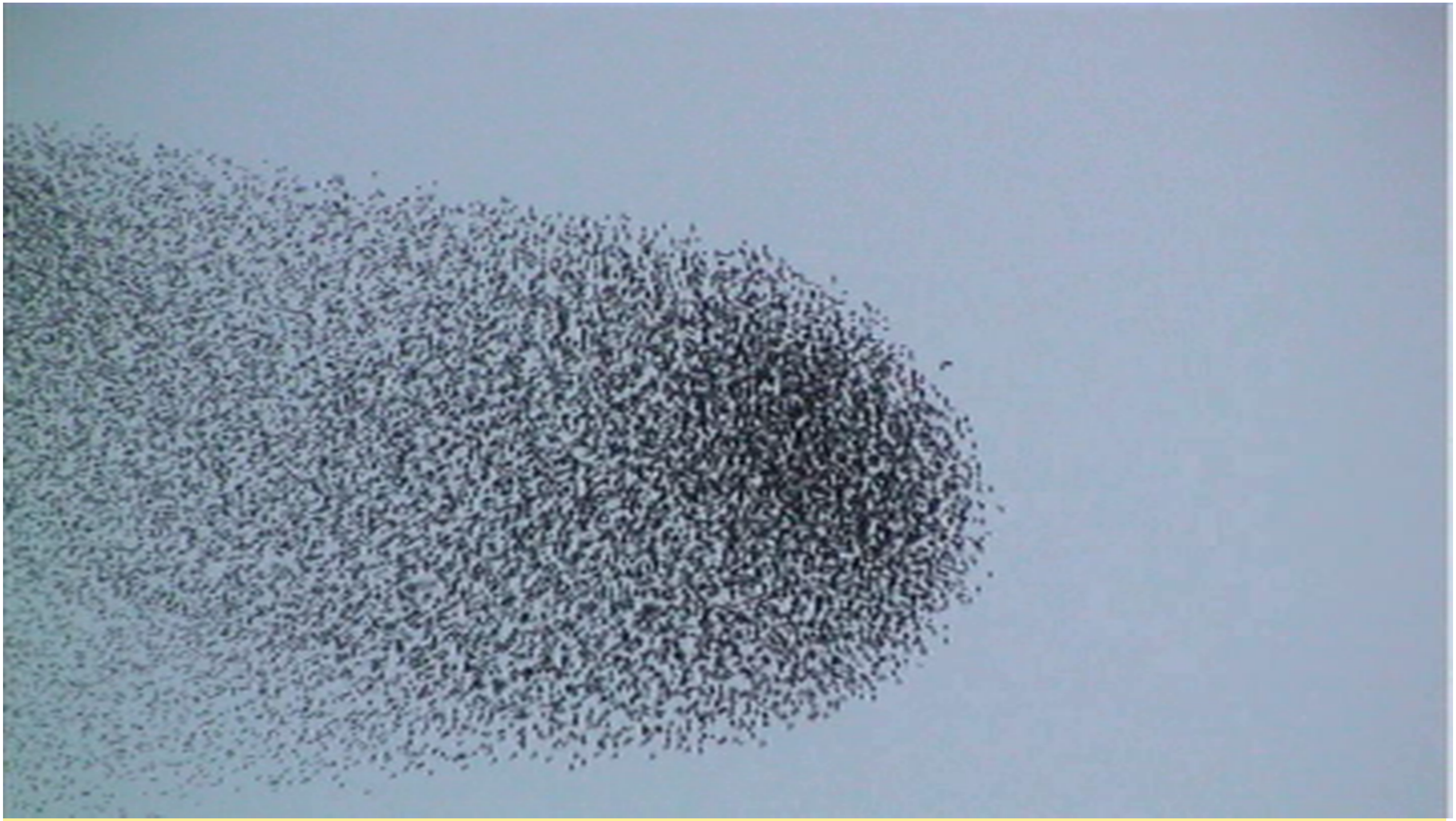
$$+\frac{1}{2}\frac{\partial^2}{\partial v_i \partial v_j}\left[\gamma_{ij} n(\mathrm{x},\mathrm{v},t)\right.$$

If closures are good, these approximations work well

Flierl et al., JTB 1999

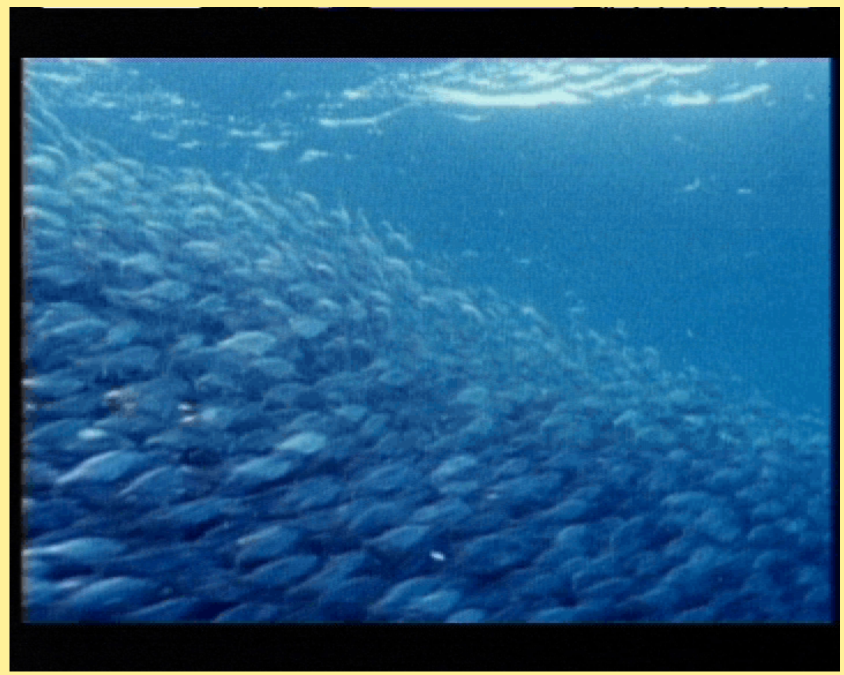
Otherwise, equation-free methods (Kevrekidis)

But real aggregations are heterogeneous assemblages of individuals



Claudo Carere
StarFLAG EU FP6 project

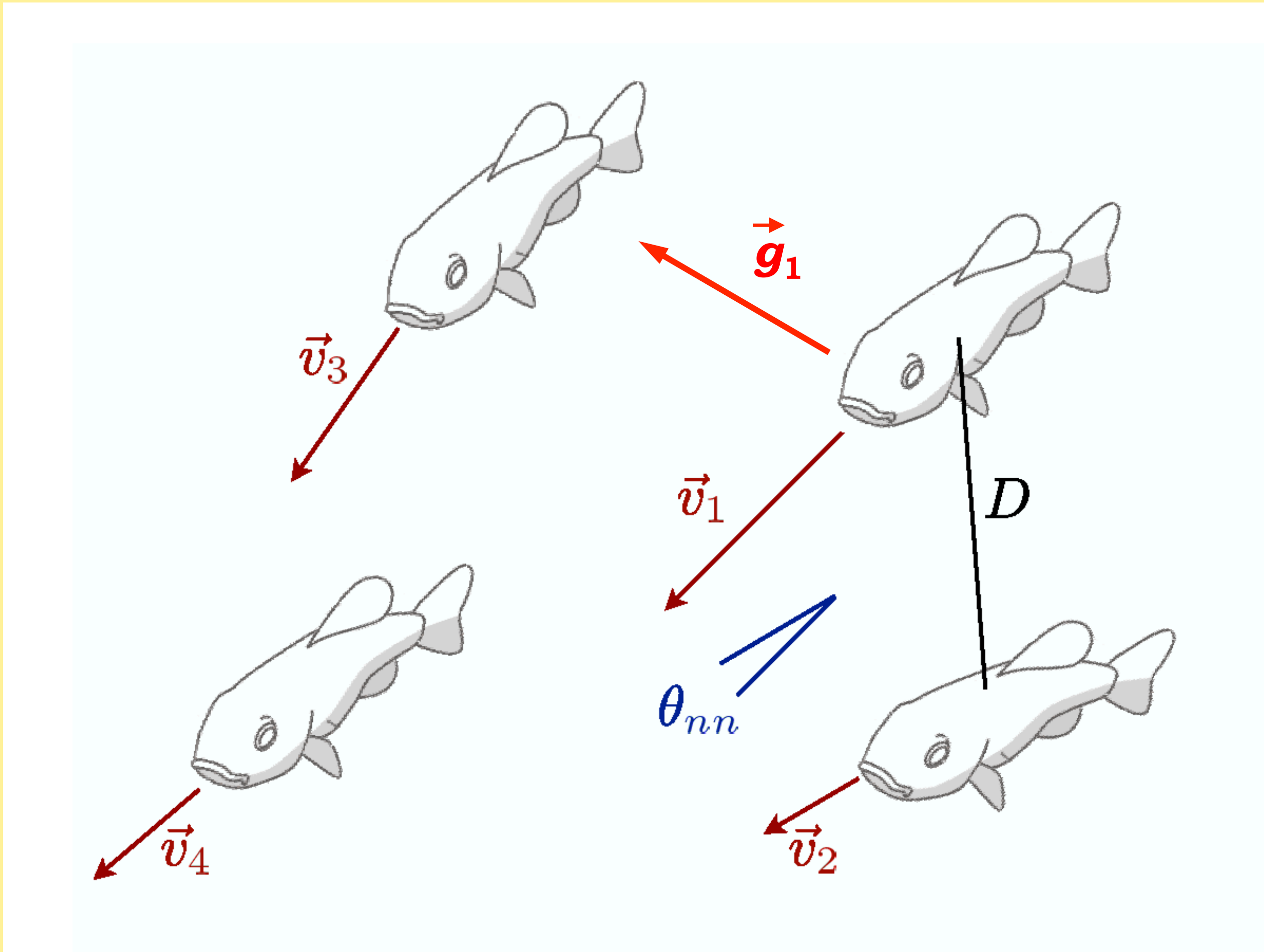
Couzin, Krause, Franks, Levin



Iain Couzin/BBC

- Utilize simulations to explore these issues

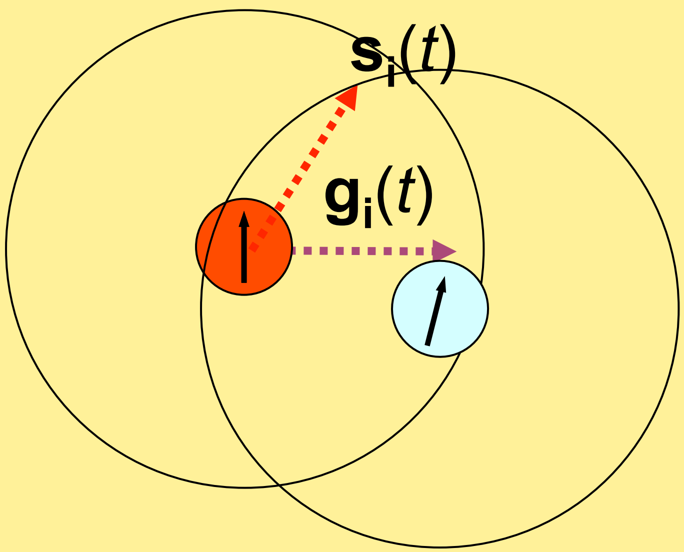
Collective decision-making



Courtey Iain Couzin

Collective decision-making

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



$$\mathbf{d_i}(t+\Delta t) = \frac{\mathbf{s_i}(t) + \omega\, g_i(t)}{|\,\mathbf{s_i}(t) + \omega\, g_i(t)\,|}$$

Courtey Iain Couzin

Collective decision-making

1 informed individuals in group of 100.

Courtey Iain Couzin

Collective decision-making

5 informed individuals in group of 100.

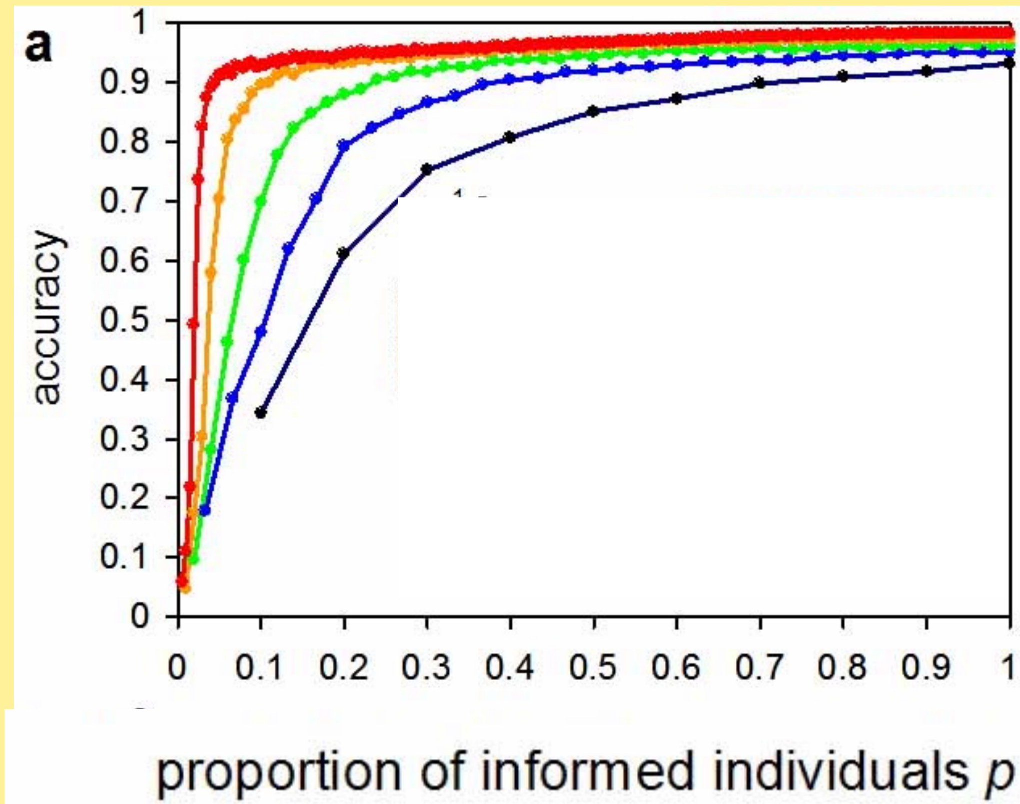
Courtey Iain Couzin

Collective decision-making

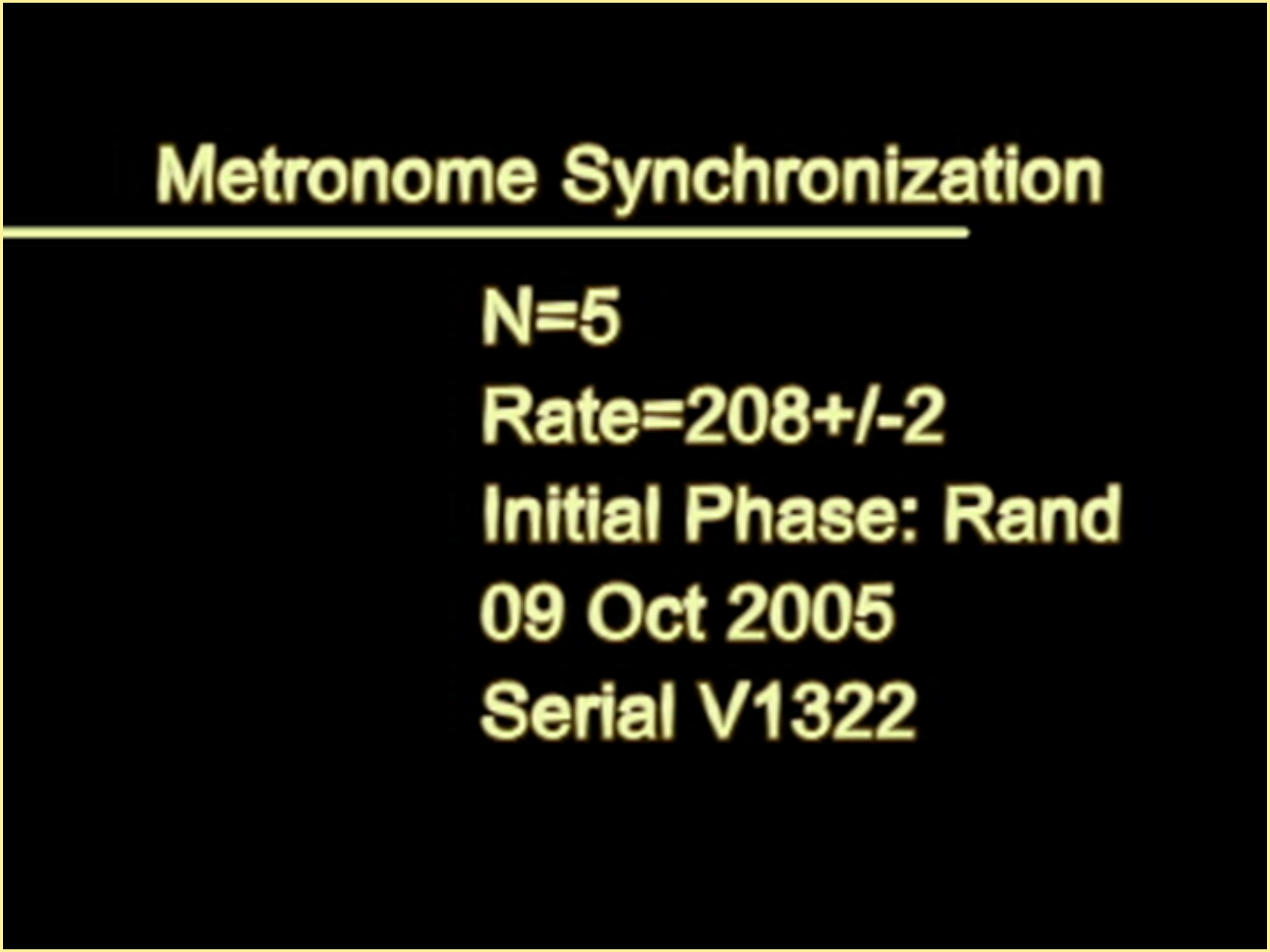
10 informed individuals in group of 100.

Courtey Iain Couzin

Animal groups may be led by a small number of individuals



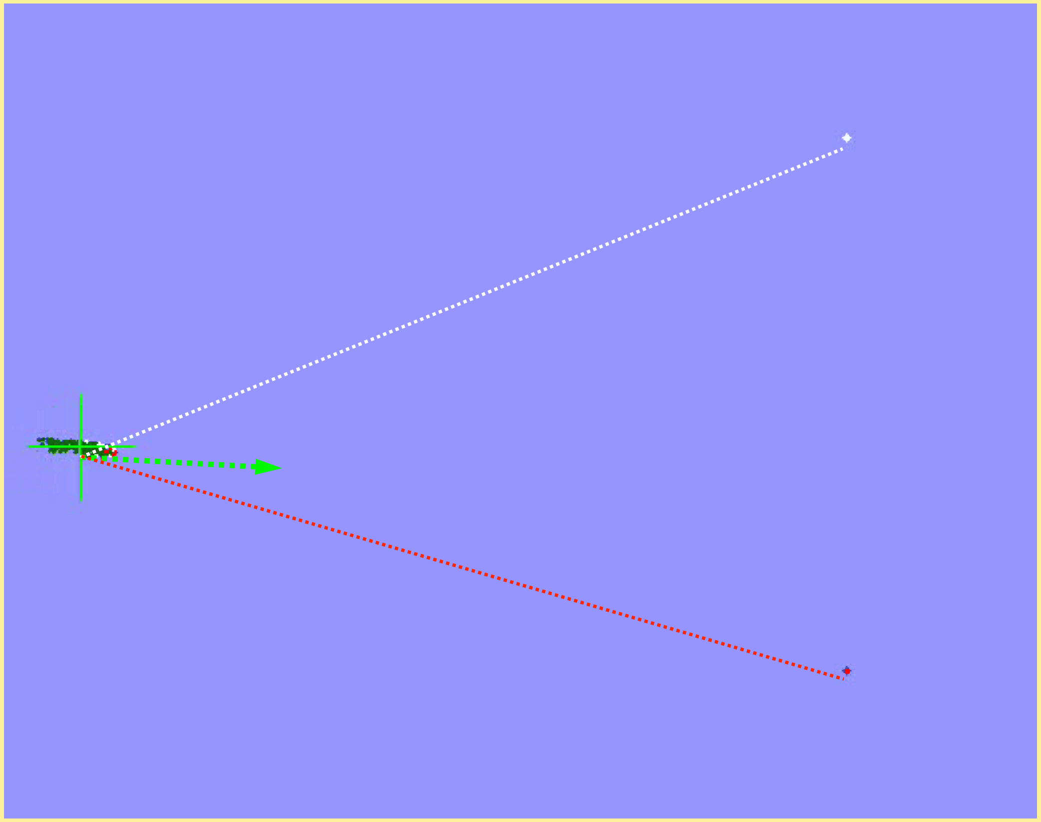
From Couzin et al., 2005


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

Collective decision-making

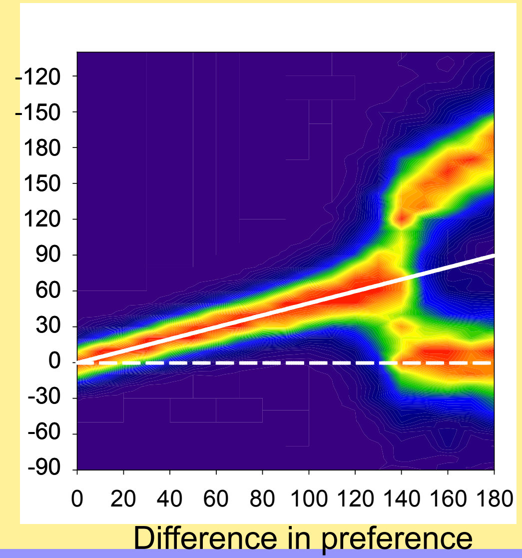
Competing preferences

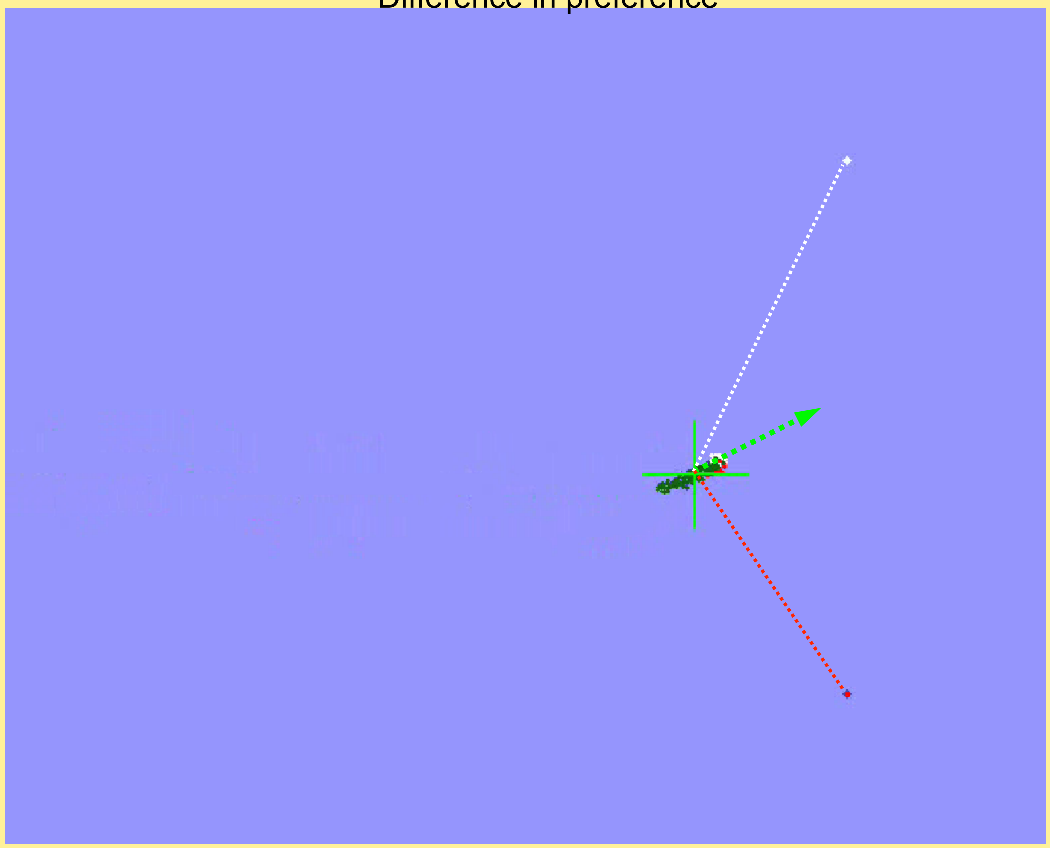
Difference in preference



Courtey Iain Couzin

Collective decision-making

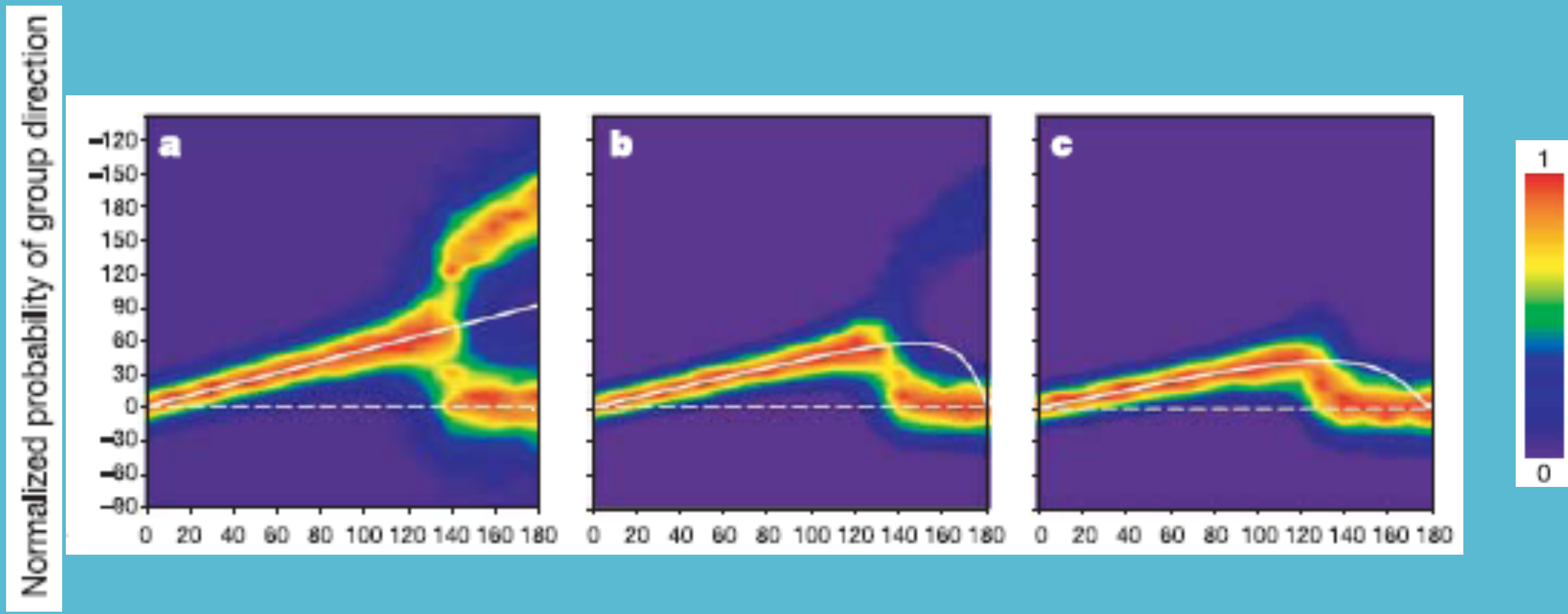




Courtey Iain Couzin

Competition and consensus

Unequal numbers of leaders



Couzin, I.D., Krause, J., Franks, N.R. and Levin, S.A. (2005) *Effective leadership and decision-making in animal groups on the move.* Nature 434, 513-516

Leonard, Couzin, Levin, etc.

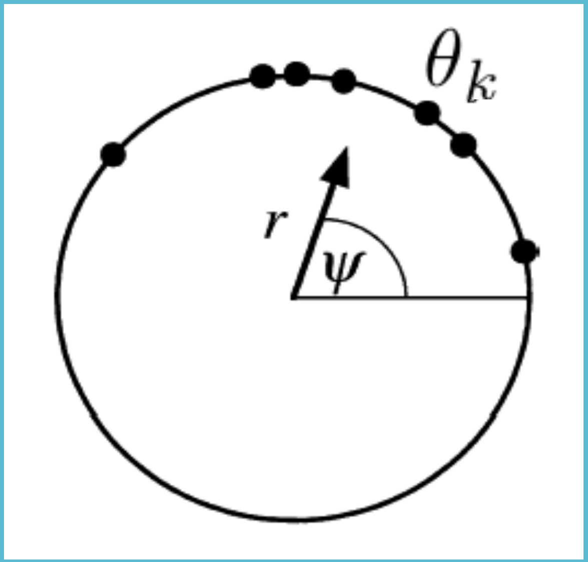
Kuramoto model

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

Gradient system, so all solutions go to equilibrium

The complex order parameter

$$p_\theta = re^{i\psi} = \sum_{j=1}^{N} e^{i\theta_j}$$



r measures the level of synchrony in the group,
ψ gives the average direction of the group.

Courtesy, Ben Nabet

We write the dynamics for ψ_1, ψ_2, ψ_3 the average heading of respectively η_1, η_2 and η_3.

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

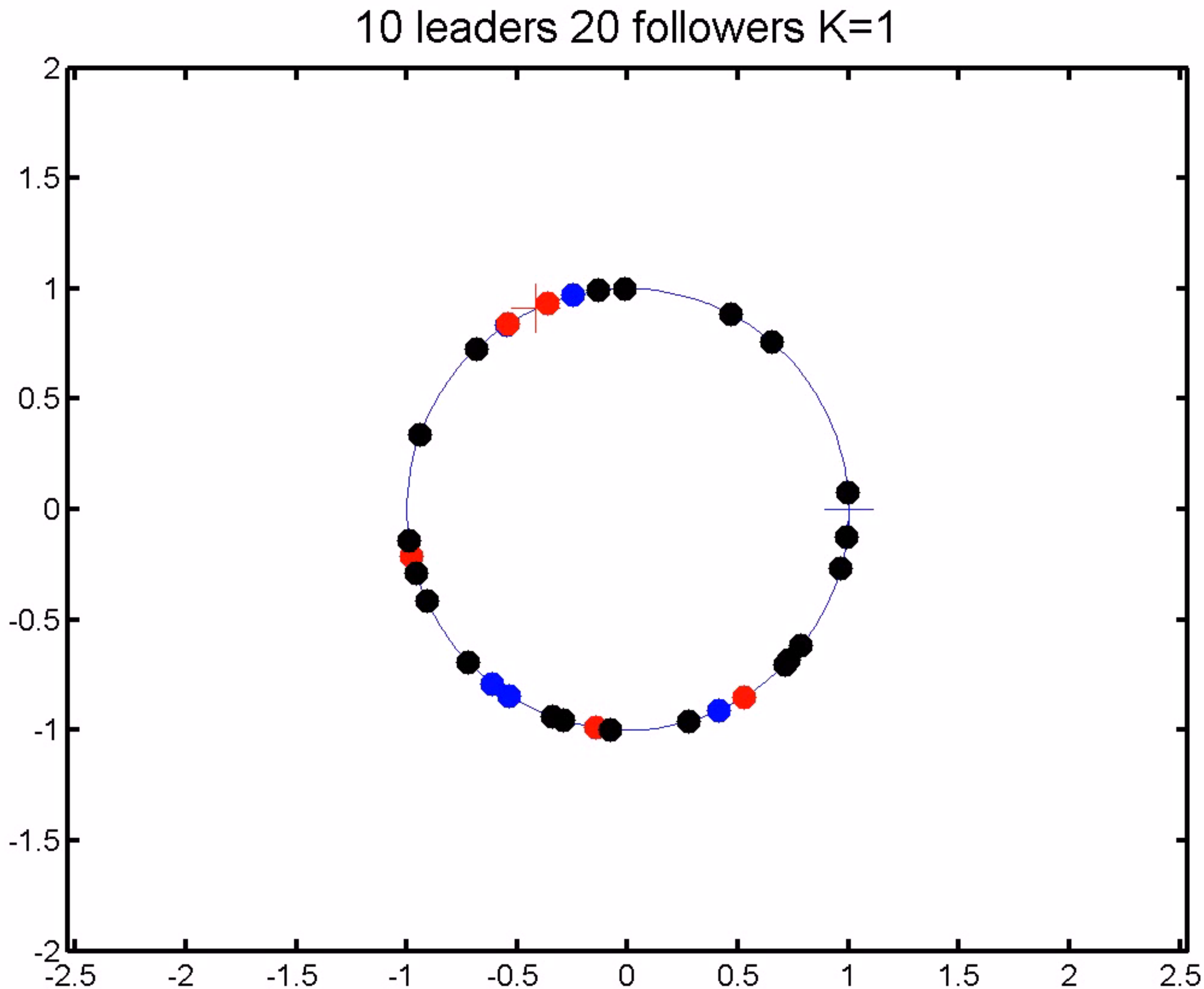
$$\dot{r}_j e^{i\psi_j} + i\dot{\psi}_j = \frac{1}{N_j} \sum_{l \in \eta_j} i\dot{\theta}_l e^{i\theta_l} \quad j = 1, 2, 3.$$

During the second time scale

Everyone in cluster has same heading

$$\begin{aligned} \theta_l &= \psi_j \\ r_j &= 1 \\ \dot{r}_j &= 0 \end{aligned}$$

Courtesy, Ben Nabet

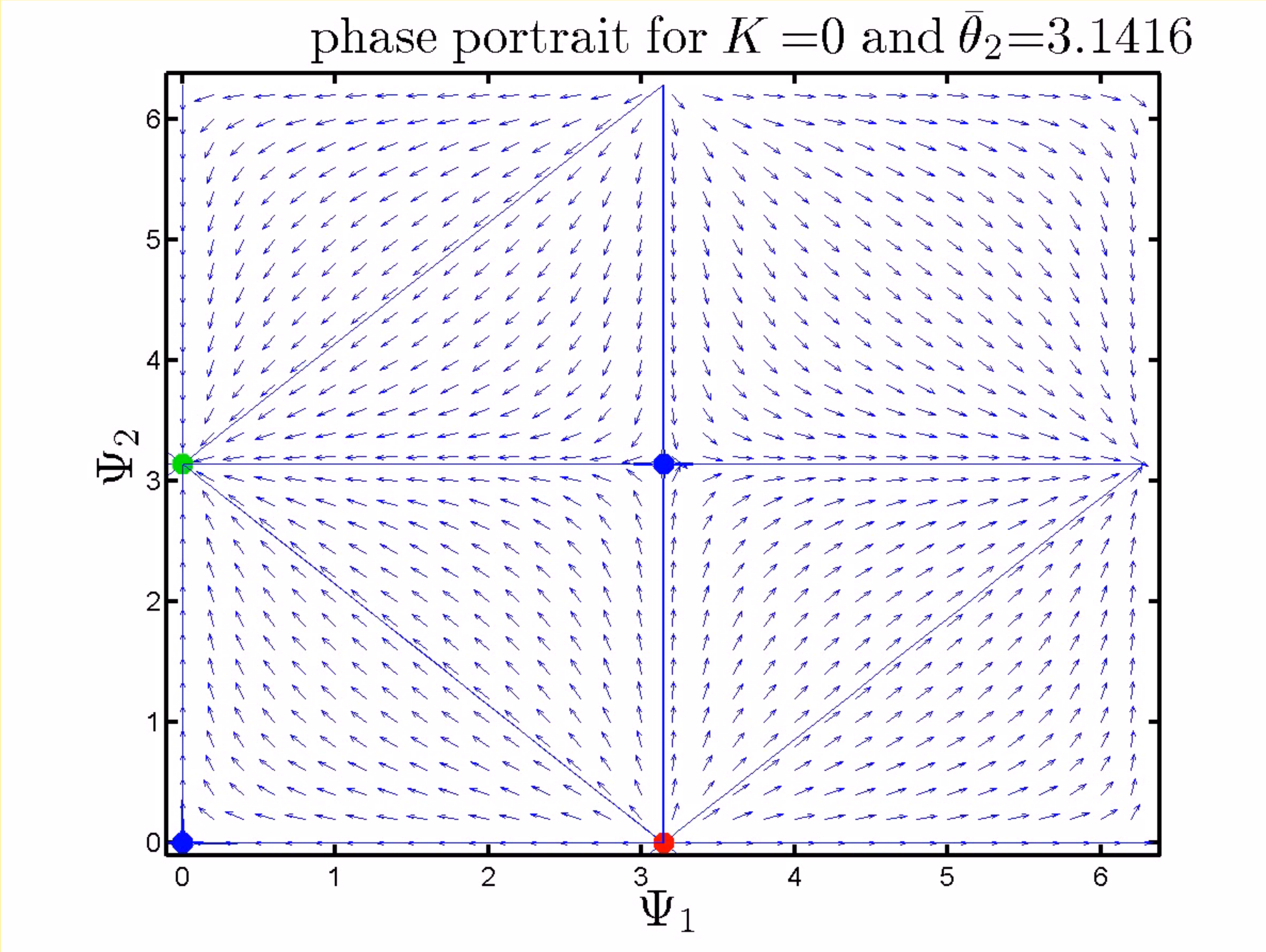


Nabet, Leonard, et al.

We get for the second time scale

$$
\begin{aligned}
\dot{\psi}_1 &= \sin(\bar{\theta}_1 - \psi_1) + kN_2 \sin(\psi_2 - \psi_1) + kN_3 \sin(\psi_3 - \psi_1) \\
\dot{\psi}_2 &= \sin(\bar{\theta}_2 - \psi_2) + kN_1 \sin(\psi_1 - \psi_2) + kN_3 \sin(\psi_3 - \psi_2) \\
\dot{\psi}_3 &= kN_1 \sin(\psi_1 - \psi_3) + kN_2 \sin(\psi_2 - \psi_3)
\end{aligned}
$$

Courtesy, Ben Nabet



Courtesy Ben Nabet

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 ca- 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

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

in subgroup 2 as

$$\frac{d\theta_j}{dt} = \sin(\bar{\theta}_2 - \theta_j(t)) \cdot \qquad [\mathbf{2}]$$

Coupled oscillator approximation

Leonard et. al, PNAS

In subgroup 1, represent as

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

in subgroup 2 as

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

and in subgroup 3 as

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

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*

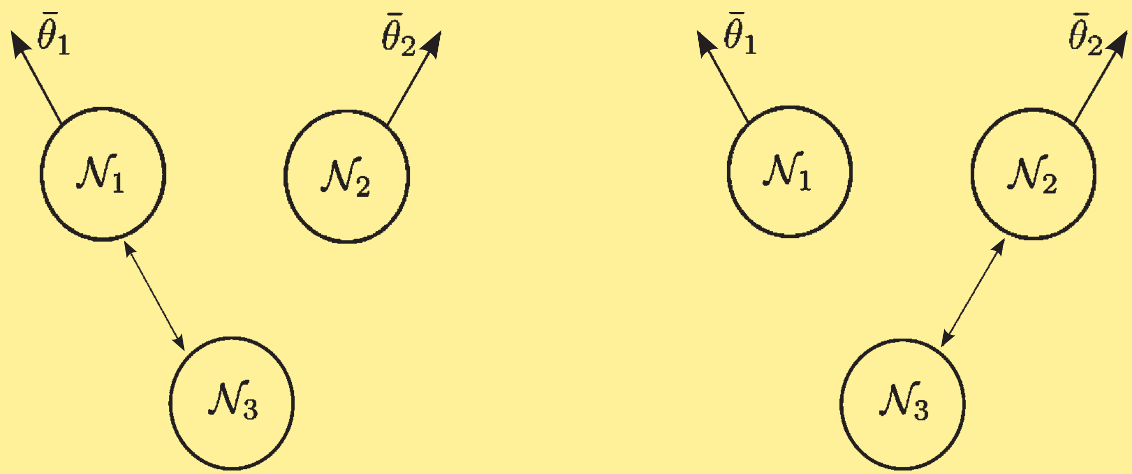


Fig. 1. Coupling in manifolds $\mathcal{M}_{010}$ (*Left*) and $\mathcal{M}_{001}$ (*Right*) among subgroups 1, 2, and 3 as indicated by arrows.

Slow time scale

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

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

$$\frac{d\Psi_3}{dt} = \frac{K_1}{N}(A_{13}N_1\sin(\Psi_1(t) - \Psi_3(t)) + A_{23}N_2\sin(\Psi_2(t) - \Psi_3(t))). \quad \textbf{[6]}$$

A_{ij}=0 or 1

Table 1. Possible combinations of stable (*S*) and unstable (*U*) manifolds given $N_3 > 2N_1$

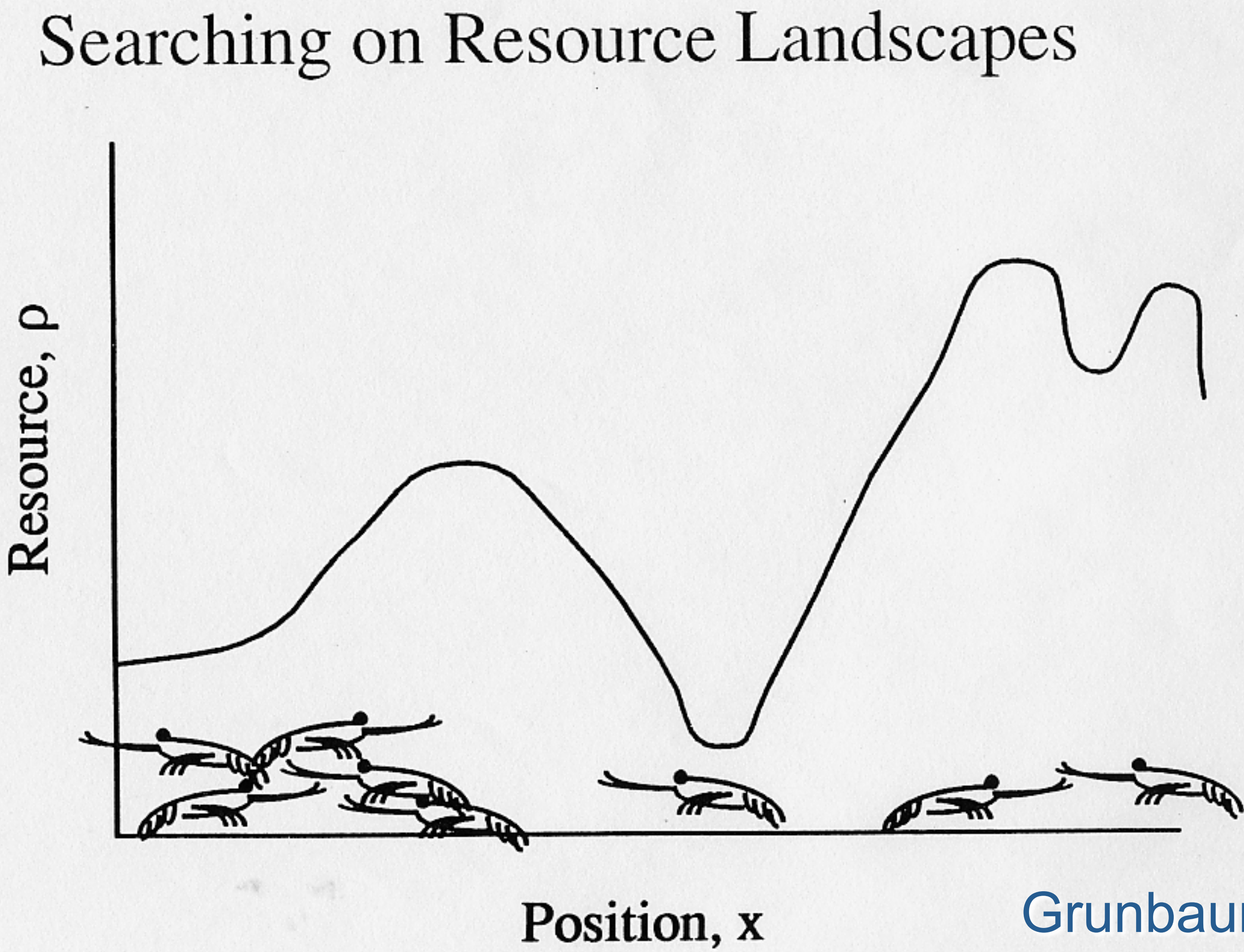
$\mathcal{M}_{101}$	$\mathcal{M}_{110}$	$\mathcal{M}_{000}$	$\mathcal{M}_{010}$	$\mathcal{M}_{001}$	$\mathcal{M}_{100}$	$\mathcal{M}_{011}$	$\mathcal{M}_{111}$
U	*U*	*S*	*S*	*S*	*U*	*U*	*U*
U	*U*	*S*	*S*	*S*	*U*	*S*	*U*
U	*U*	*S*	*S*	*S*	*S*	*U*	*U*
U	*U*	*S*	*S*	*S*	*S*	*S*	*U*
U	*U*	*U*	*U*	*U*	*S*	*U*	*S*

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?



Grunbaum

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

Questions

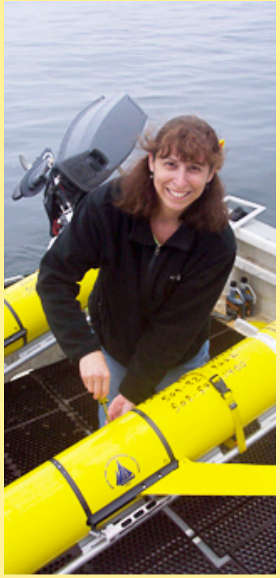
- How many leaders?
- How many followers?

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

PNAS

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

Vishwesha Guttal[1] and Iain D. Couzin[1]

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 wildebeest to bacteria, migrate en

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-

PNAS

Specialization and evolutionary branching within migratory populations

Colin J. Torney[1], 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

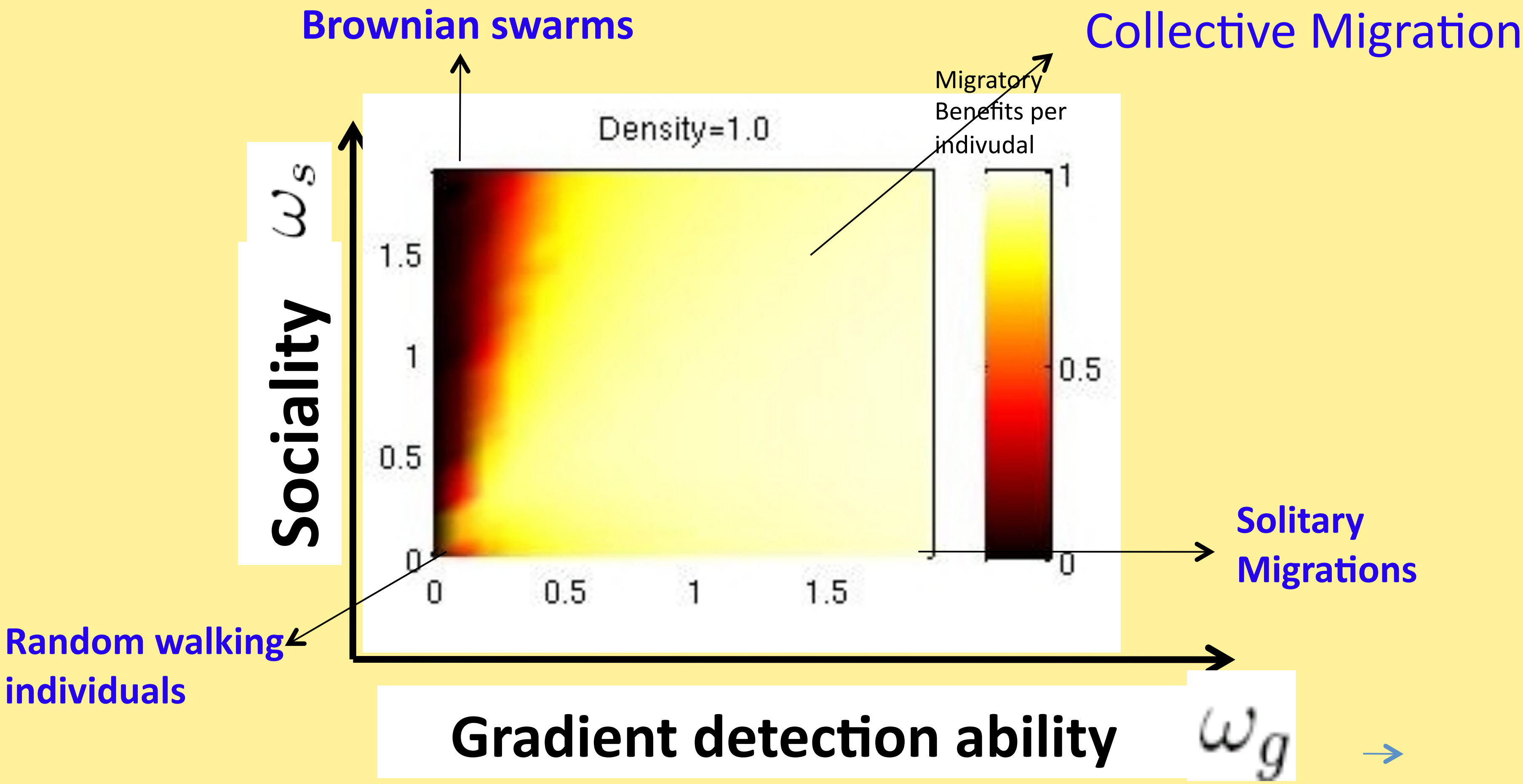
Leadership, collective motion and the evolution of migratory strategies

Vishwesha Guttal* and Iain D. Couzin*

Department of Ecology and Evolutionary Biology; Princeton University; Princeton, NJ USA

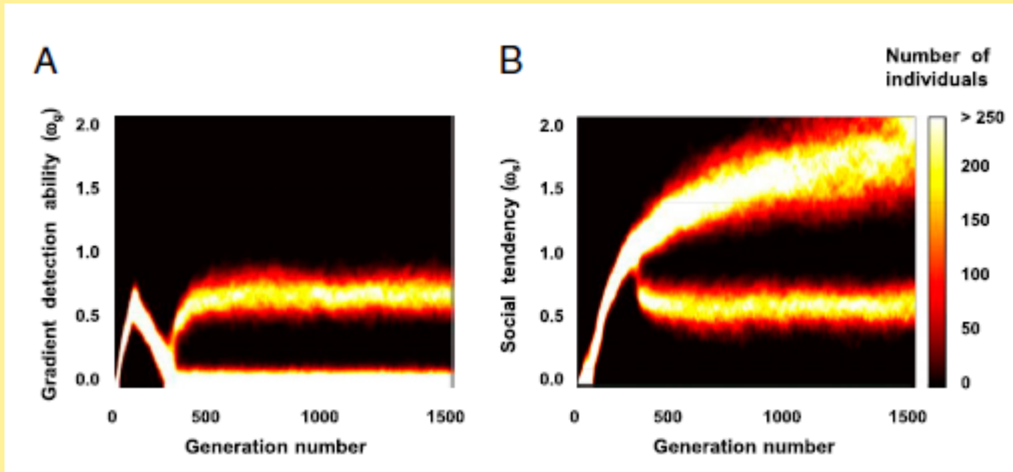
Guttal et al.

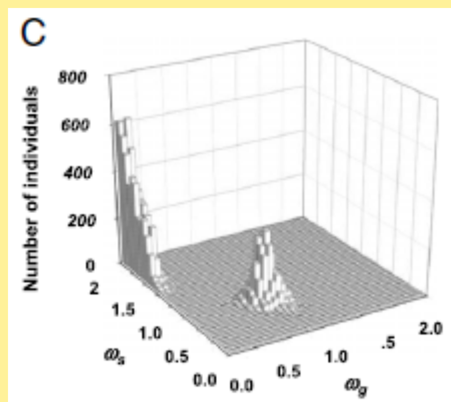
Simple model: wide range of dynamics



Thanks to Iain Couzin

Evolutionary branching: leaders and followers





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

Guttal and Couzin, PNAS, 2010

Thanks to Iain Couzin

Torney, Levin and 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

Specialization and evolutionary branching within migratory populations
Colin Torney, Simon A. Levin & Iain D. Couzin (PNAS, to appear

Evolving specialized leadership roles

- Model fluctuating environmental signal as a stochastic process
- Individual heading θ follows mean reverting process, where θ=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

$$F = \exp(-\sigma^2 / 4 x_g)$$

Mean Velocity

Quantifying the social information

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

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

Average heading

Degree of ordering, *r = 0* complete disorder, *r* = 1 completely aligned

- Leads to coarse grained representation of social interactions

$$d\theta_t = -x_s(\theta - \psi)dt + \eta\sqrt{(1-r)}dW_t$$

Level of sociality

Turns toward mean population heading

Noise is decreasing function of degree of ordering

Add these together

$$d\theta_t = (x_g d\theta_g + x_s d\theta_s)/(x_g + x_s)$$

Adaptive dynamics and branching

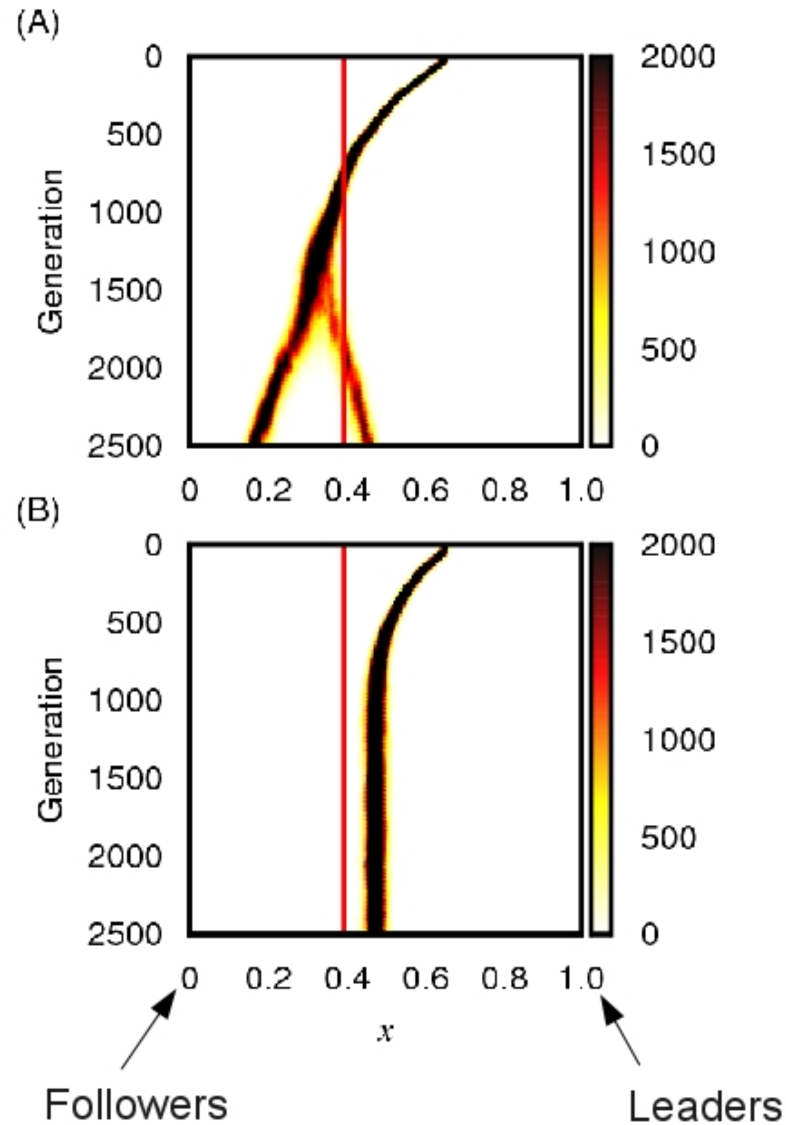
- Evolutionary change determined by differential fitness of mutant in the resident population

$$s_x(y) = F(y,x) - F(x,x)$$

- Population moves toward convergence stable solution (CSS)
- But if CSS not an evolutionary stable solution (ESS) branching will occur -

$$\left.\frac{\partial^2 F(y,x^*)}{\partial y^2}\right|_{y=x^*} > 0$$

- 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.