

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



Simon Levin

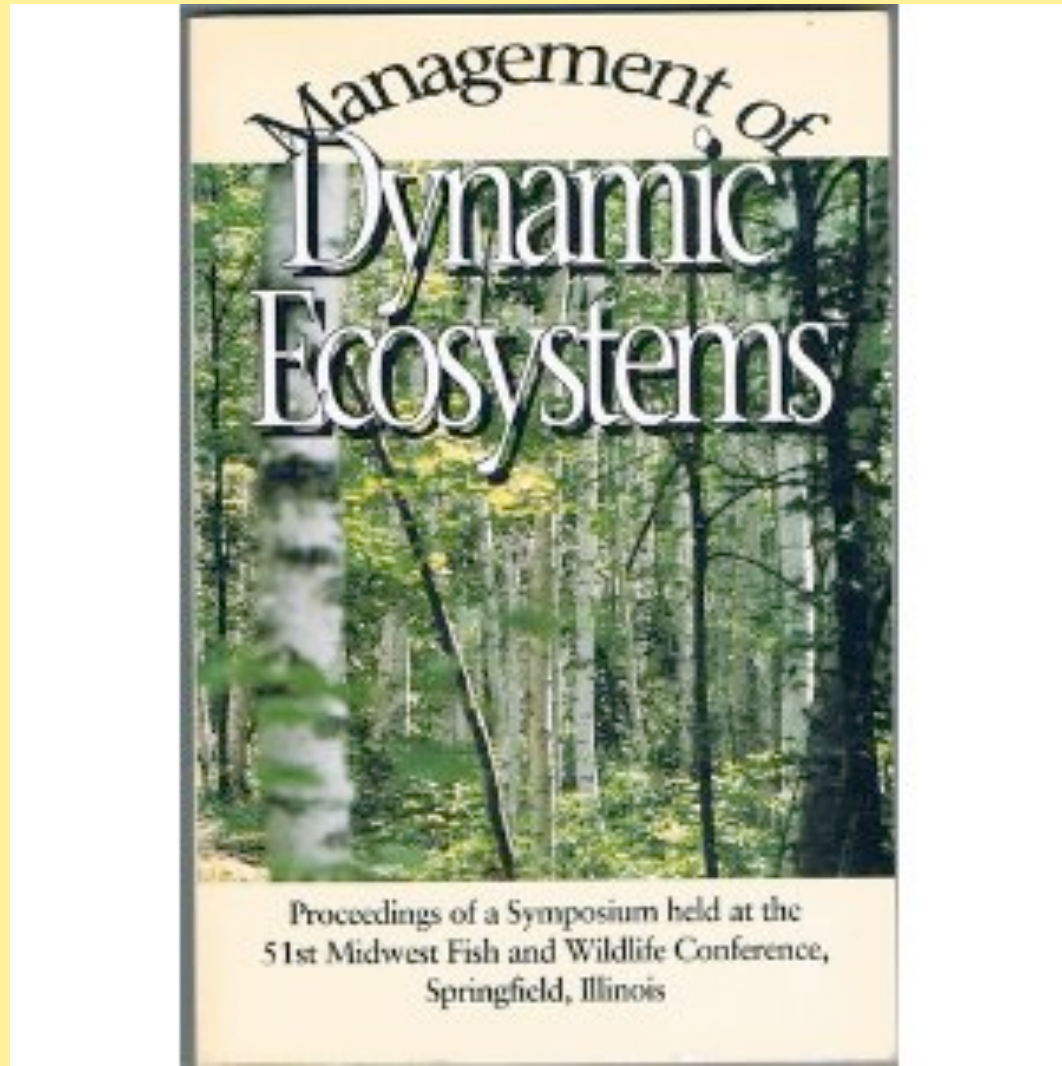
SFI2013

Claudio Carere
StarFLAG EU FP6 project

We may think of ecosystems as
enduring parts of nature

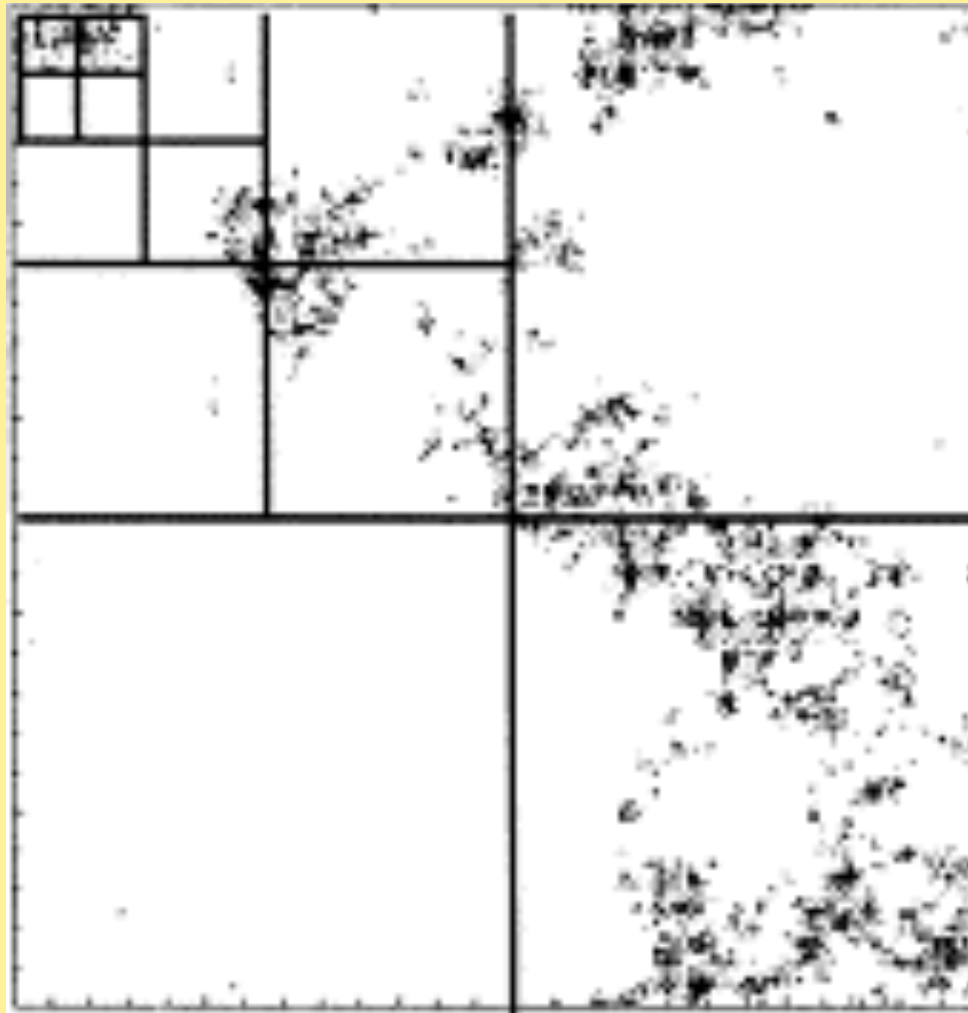


But ecosystems and the biosphere are dynamic, with lots of species turnover, especially on local scales



Sweeney . Ed..

Must scale up



Carpinteri et al., 2002, Chaos, Solitons and Fractals,

A perspective from mathematics and physics can help

- “Statistical mechanics” of ecological communities
- Critical transitions
- Collective phenomena and collective motion
 - Emergence and pattern formation
 - Statistical mechanics
- Conflict and collective action

Realistic models can capture the emergence of pattern

(Pacala, Botkin, Shugart, others)



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

Mathematical challenges: Simplification approaches

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

- Similar considerations apply to ocean dynamics

At what scale is prediction possible?

Ecotypes, not species, are predictable

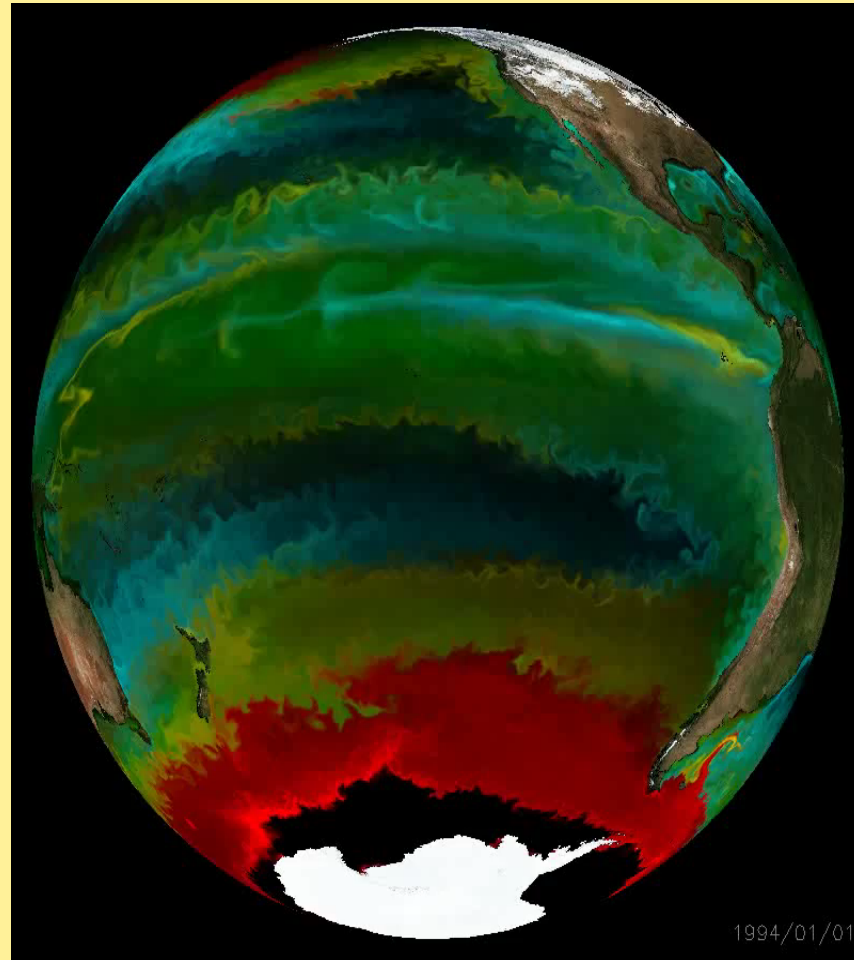
Darwin model: Follows, Dutkiewicz, Chisholm, ...

Prochlorococcus

Synechococcus

Diatoms

Large eukaryotes



Ecosystems and the Biosphere are Complex Adaptive Systems

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



Features of CAS

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

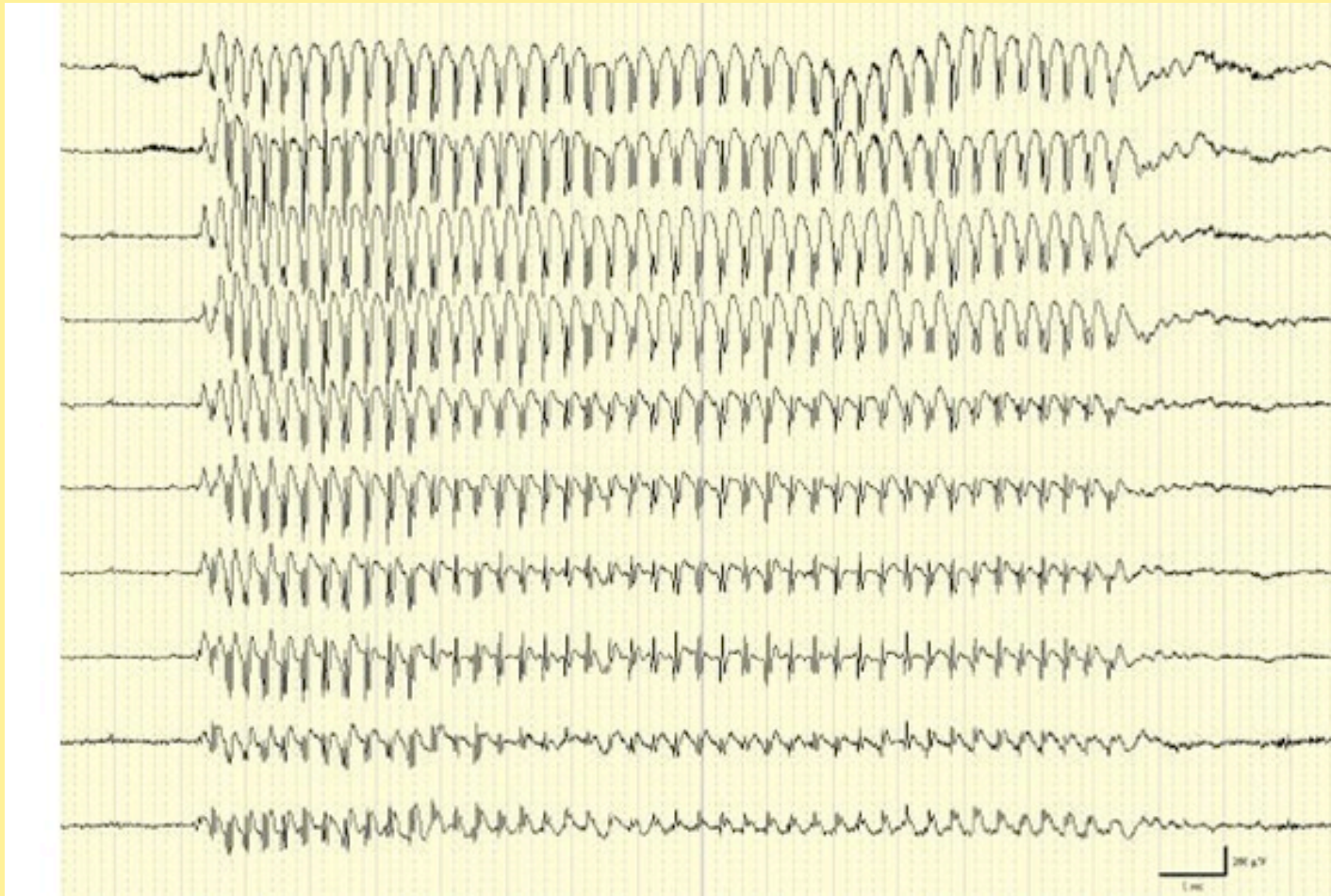
Stock markets crash



Critical transitions occur in physiological states



Are there early warning indicators?



Critical phenomena in atmospheric precipitation

OLE PETERS^{1,2,3*} AND J. DAVID NEELIN³

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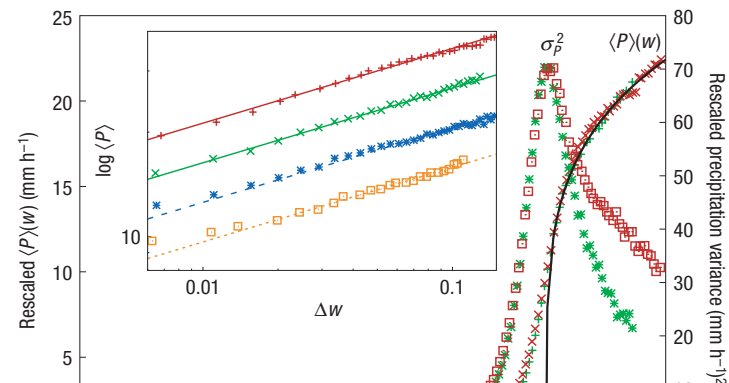
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³Department of Atmospheric Sciences and Institute of Geophysics and Planetary Physics, University of California, Los Angeles, 405 Hilgard Ave., Los Angeles, California 90095-1565, USA

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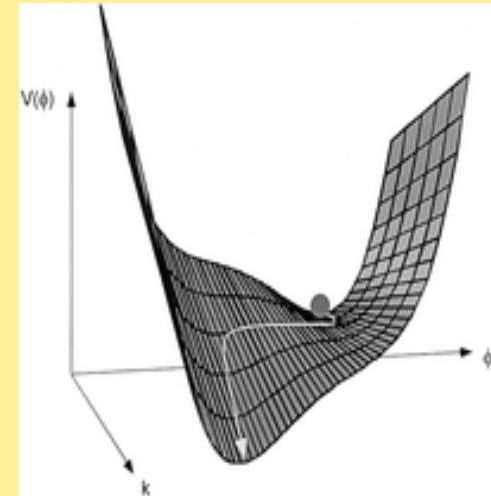
Published online: 28 May 2006; doi:10.1038/nphys314

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 law¹. 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



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.

REVIEW

Anticipating Critical Transitions

Marten Scheffer,^{1,2*} Stephen R. Carpenter,³ Timothy M. Lenton,⁴ Jordi Bascompte,⁵ William Brock,⁶ Vasilis Dakos,^{7,8} Johan van de Koppel,^{9,8} Ingrid A. van de Leemput,⁴ Simon A. Levin,⁹ Egbert H. van Nes,³ 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 ac-

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 tran-

sitions. The basic ingredient for a tipping point is a positive feedback that, once a critical point is passed, propels change toward an alternative state (6). Although this principle is well understood for simple isolated systems, it is more challenging to fathom how heterogeneous structurally complex systems such as networks of species, habitats, or societal structures might respond to changing conditions and perturbations. A broad range of studies suggests that two major features are crucial for the overall response of such systems (7): (i) the heterogeneity of the components and (ii) their connectivity (Fig. 1). How these properties affect the stability depends on the nature of the interactions in the network.

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

But there are caveats

Theor Ecol (2013) 6:255–264
DOI 10.1007/s12080-013-0192-6

ORIGINAL PAPER

Early warning signals: the charted and uncharted territories

Carl Boettiger · Noam Ross · Alan Hastings

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Abstract The realization that complex systems such as ecological communities can collapse or shift regimes suddenly and without rapid external forcing poses a serious challenge to our understanding and management of the natural world. The potential to identify early warning signals that would allow researchers and managers to predict such

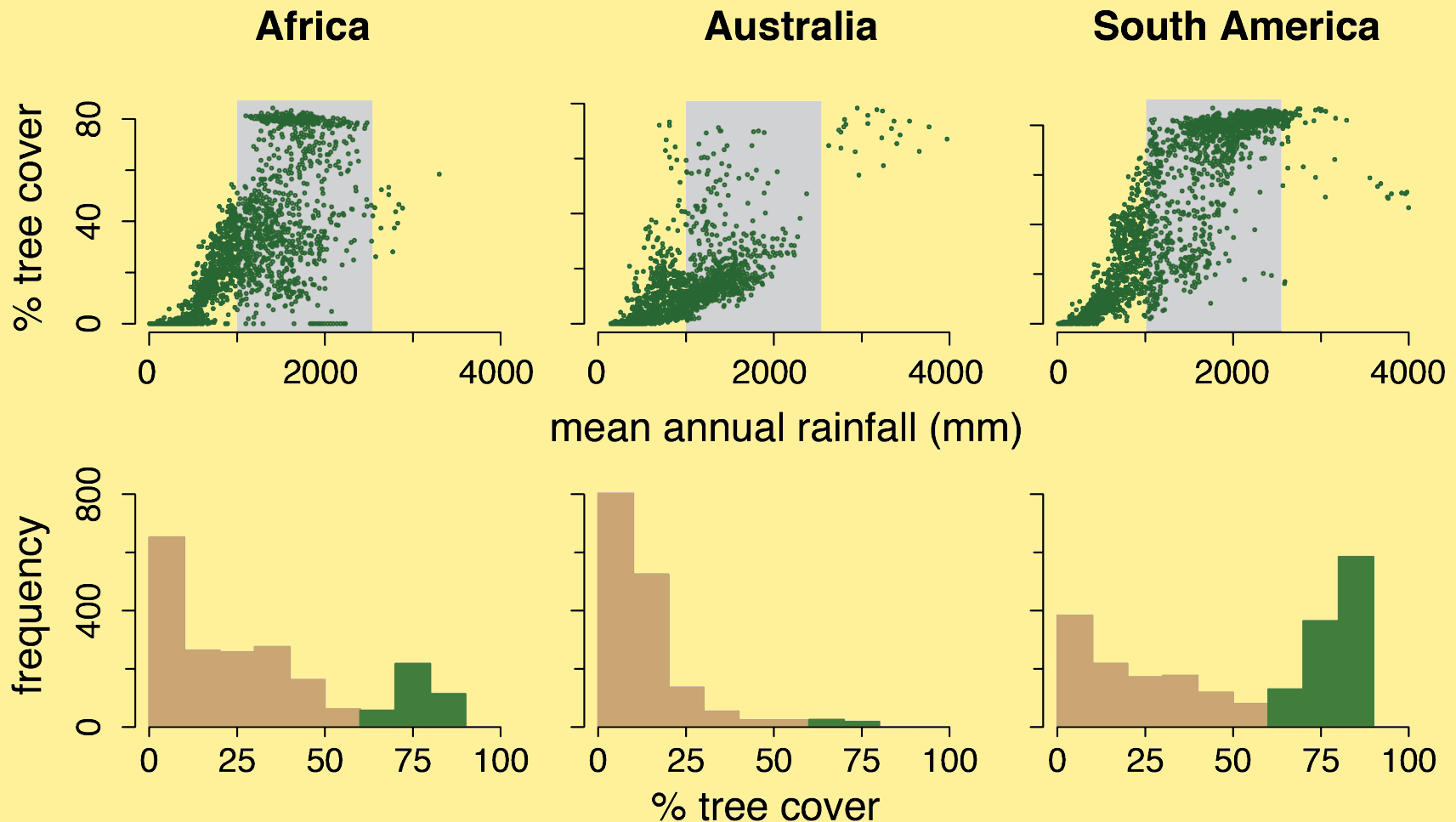
down, statistical detection is a challenge. We review the literature that explores these edge cases and highlight the need for (a) new early warning behaviors that can be used in cases where rapid shifts do not exhibit critical slowing down; (b) the development of methods to identify which behavior might be an appropriate signal when encountering

Shallow Lakes (Scheffer, Carpenter)

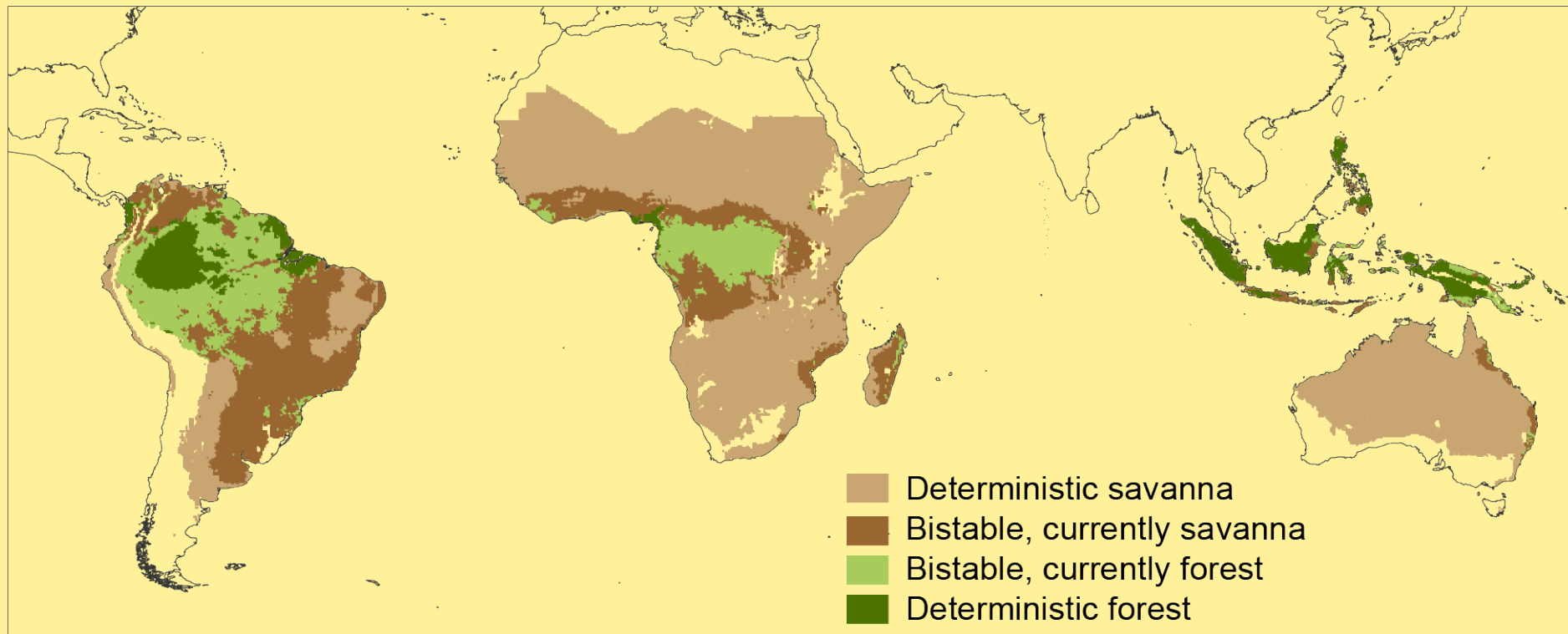


<http://www.lifeinfreshwater.org.uk/Web%20pages/ponds/Pollution.htm>

Climate is definitely a strong determinant of tree cover.



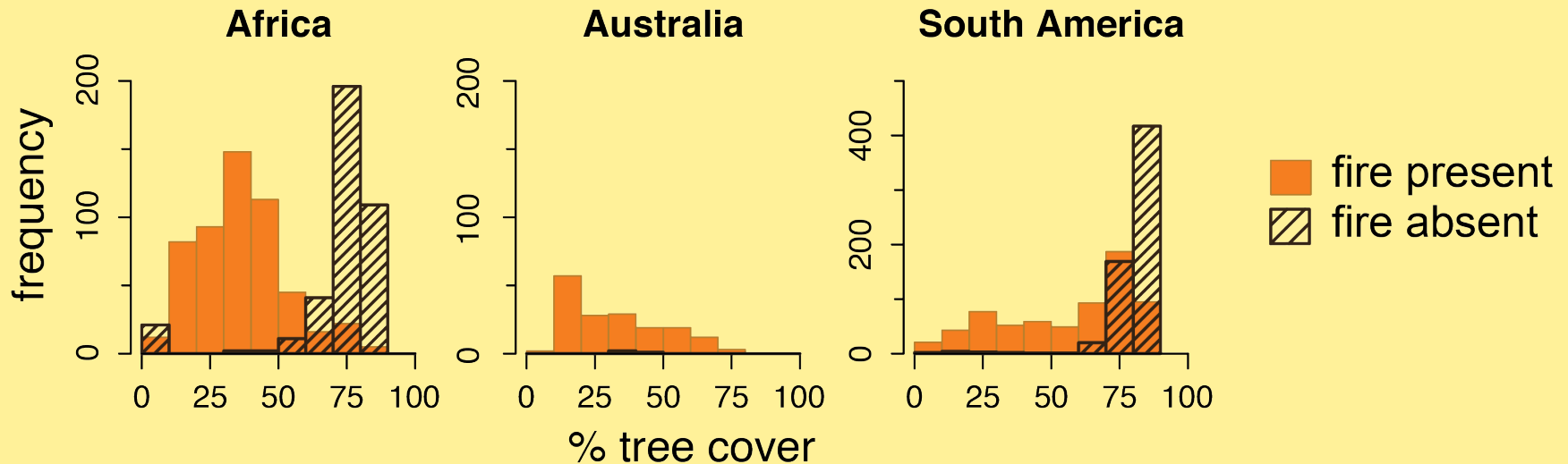
Savanna-forest systems exhibit bistability in vegetation distribution



Changes in precipitation can drive system flips

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

Fire separates savanna from forest within the intermediate climate envelope.



Archibald, Staver, Levin PNAS2011

Recreating historical regimes

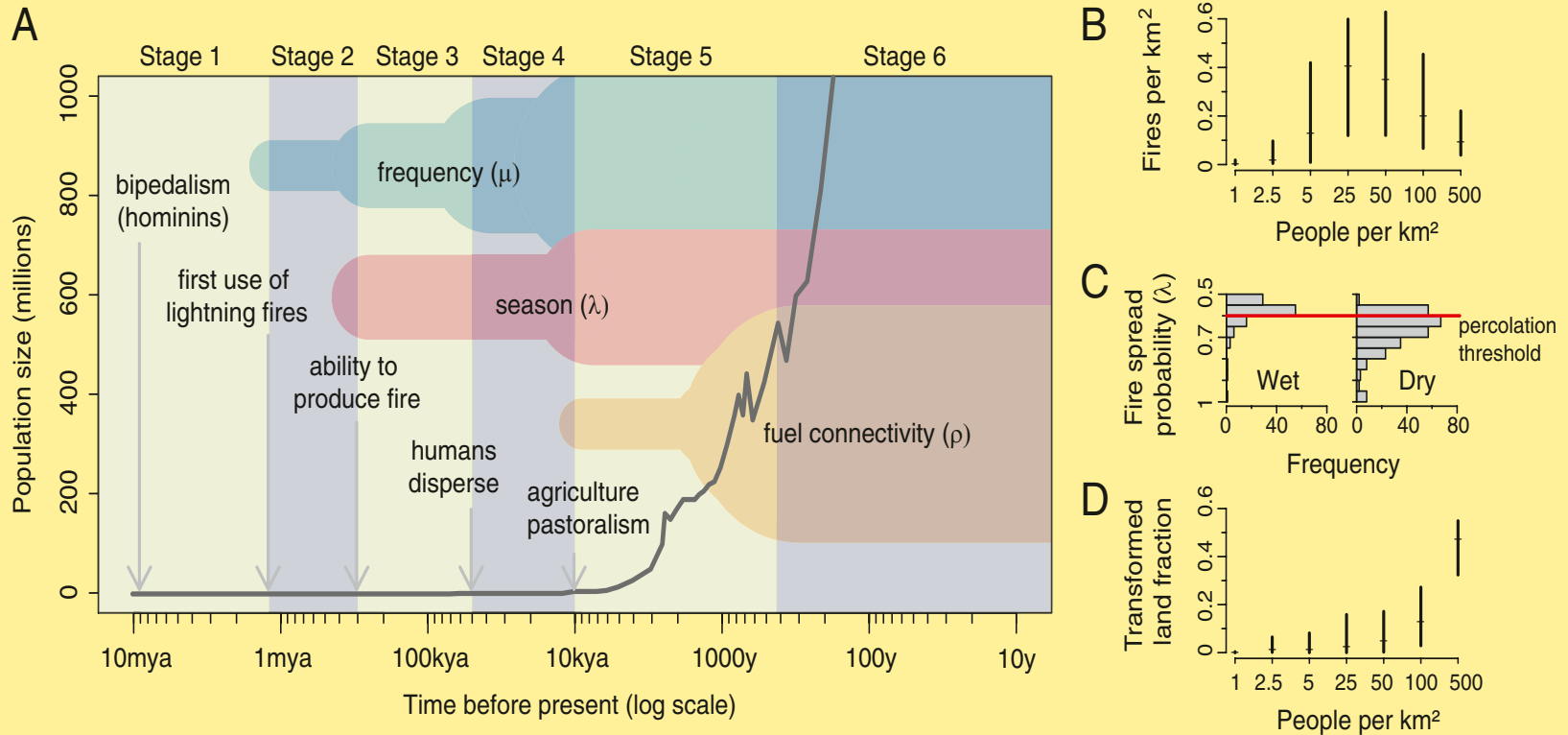
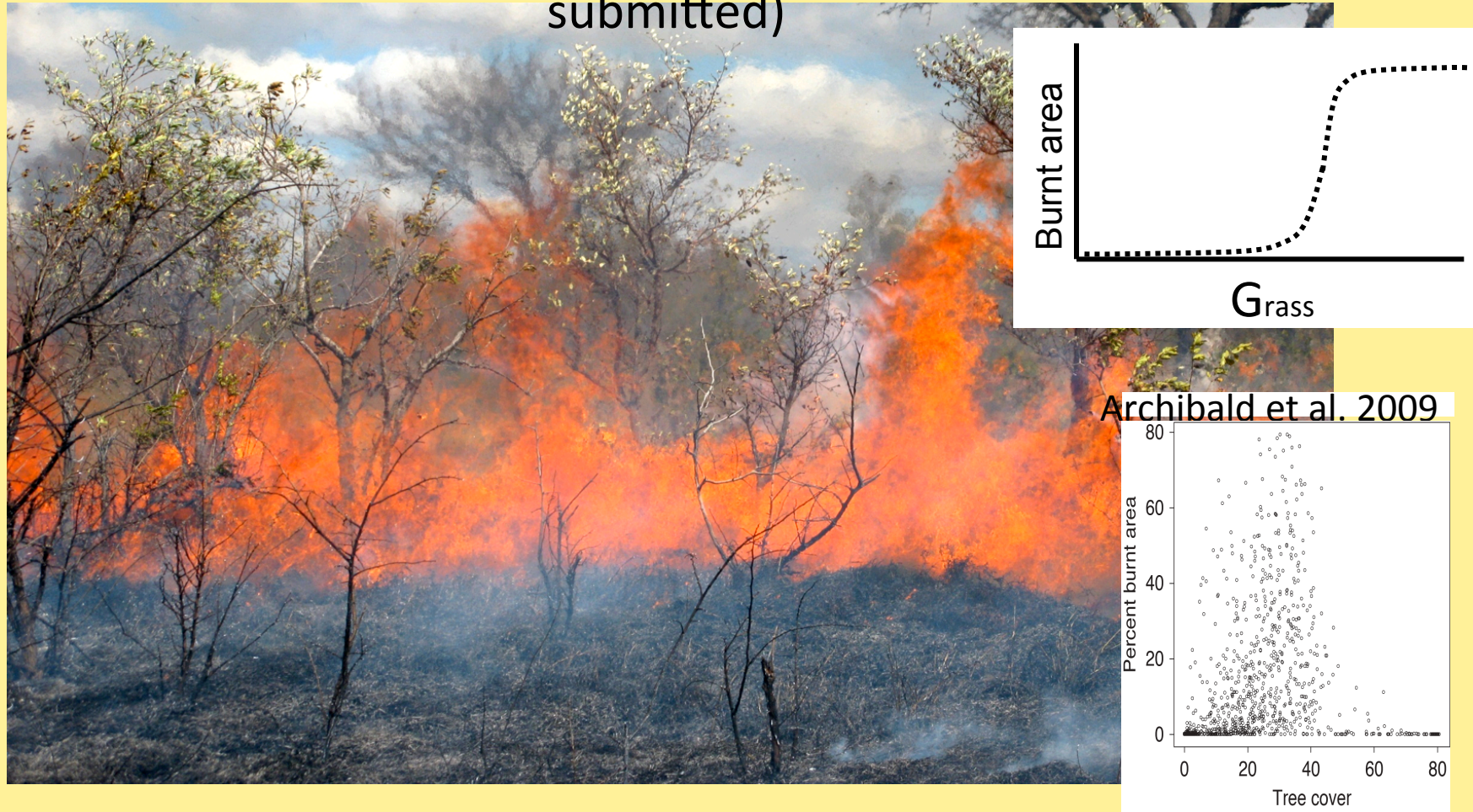


Fig. 4. Broadly showing the six stages of human evolution used to determine parameters for the stochastic model runs. The parameters μ and ρ were derived from published relationships between population density and fire density (B) and population density and land transformation (D), respectively; λ was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

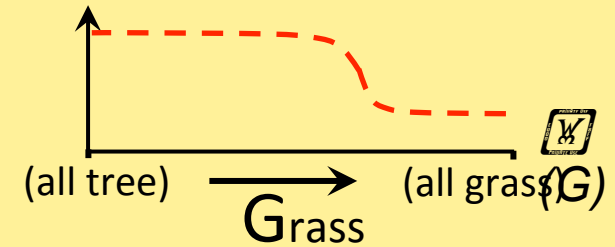
The form of the sapling transition functions can be derived from data as well as from fire percolation models

(Archibald, Staver, Levin PNAS 2011; Schertzer, Staver, Levin submitted)



Archibald et al. 2009

Relatively simple models can capture the bistability



Grass

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

Saplings

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

Trees

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

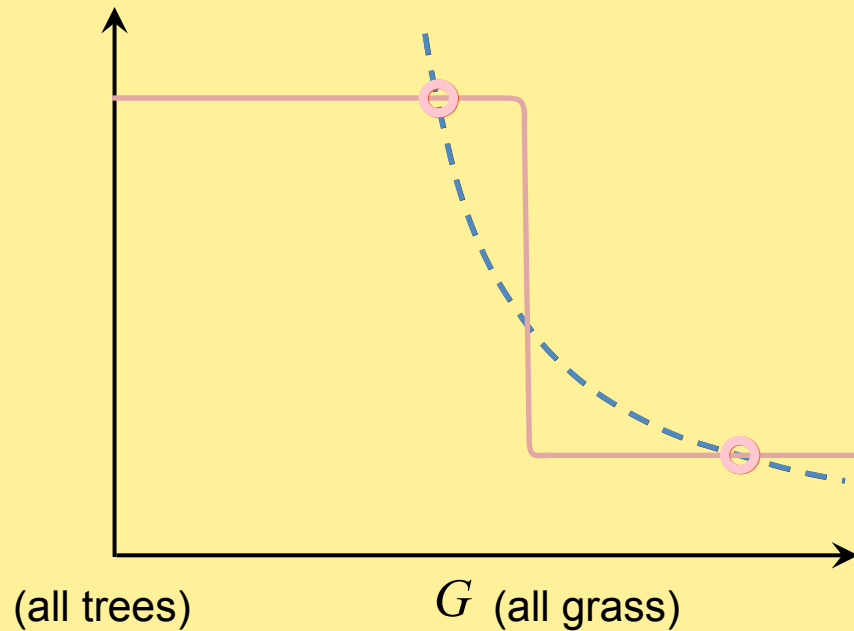
$$G + S + T = 1$$



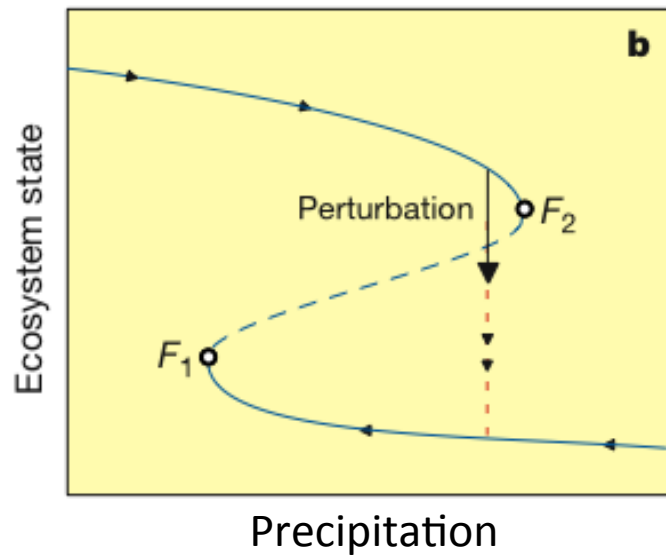
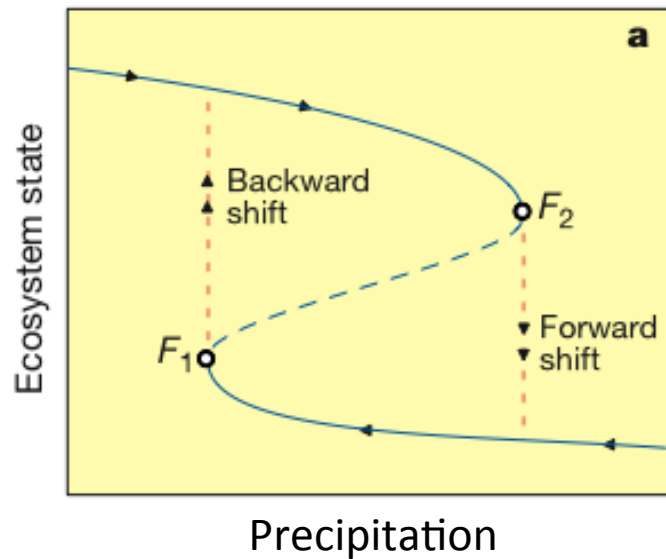
Carla Staver

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

Intermediate precipitation

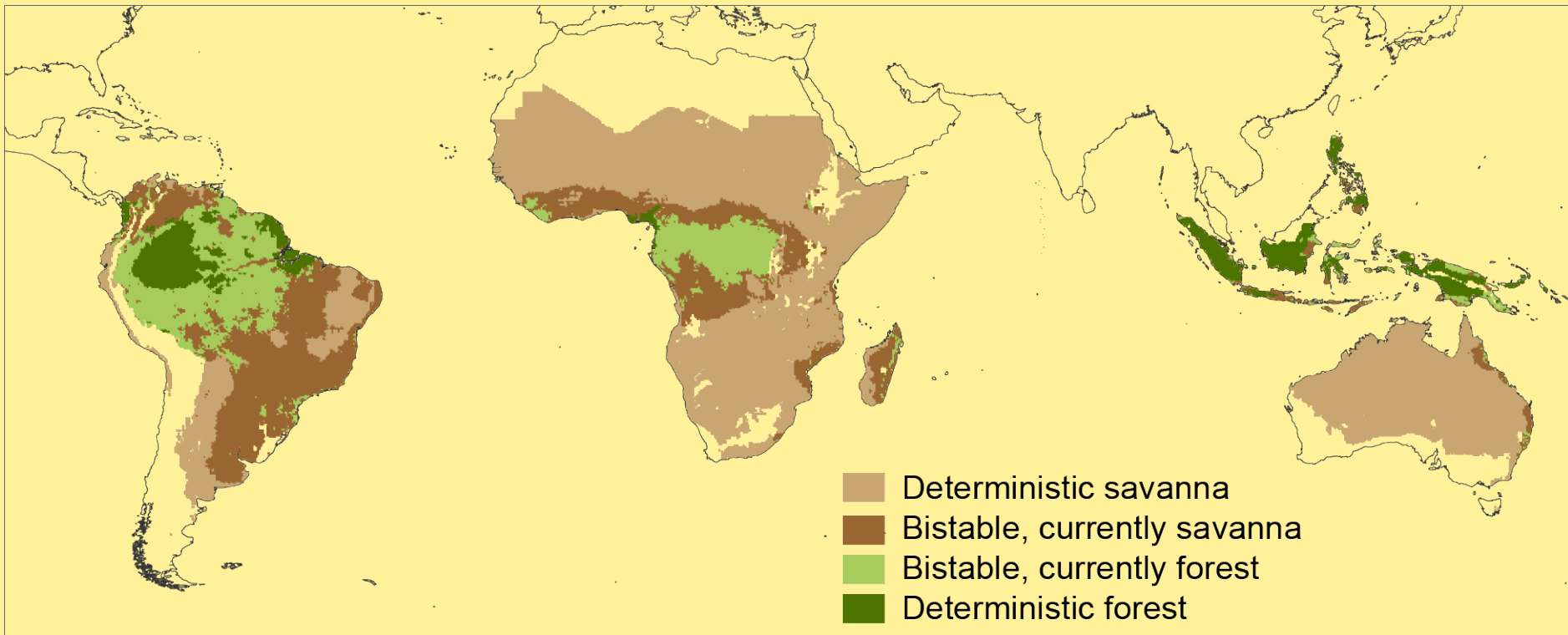


Need explicitly spatial models



- 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

Current work: Fully spatial model



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 uncrit-

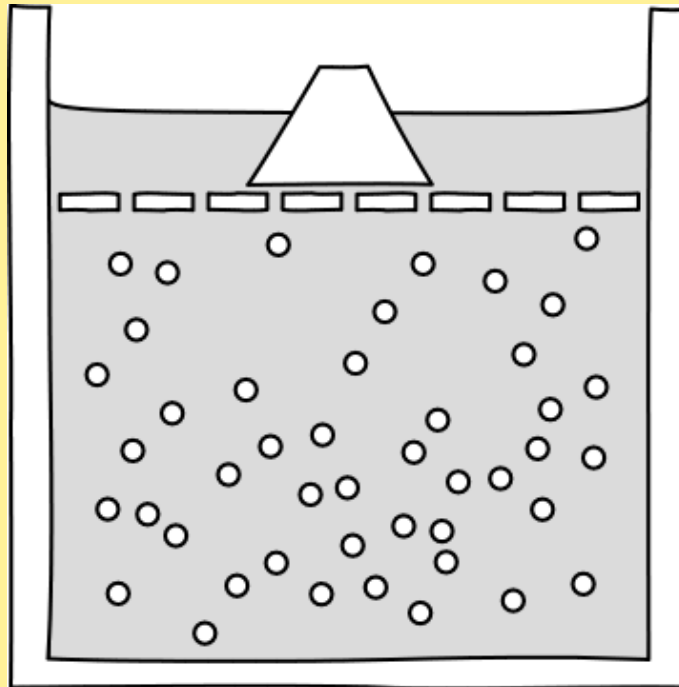
planation of phenomena in terms of known fundamental laws. As always, distinctions of this kind are not unambiguous, but they are clear in most cases. Solid state physics, plasma physics, and perhaps also biology are extensive. High energy physics and a good part of nuclear physics are intensive. There 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 narrow and most

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

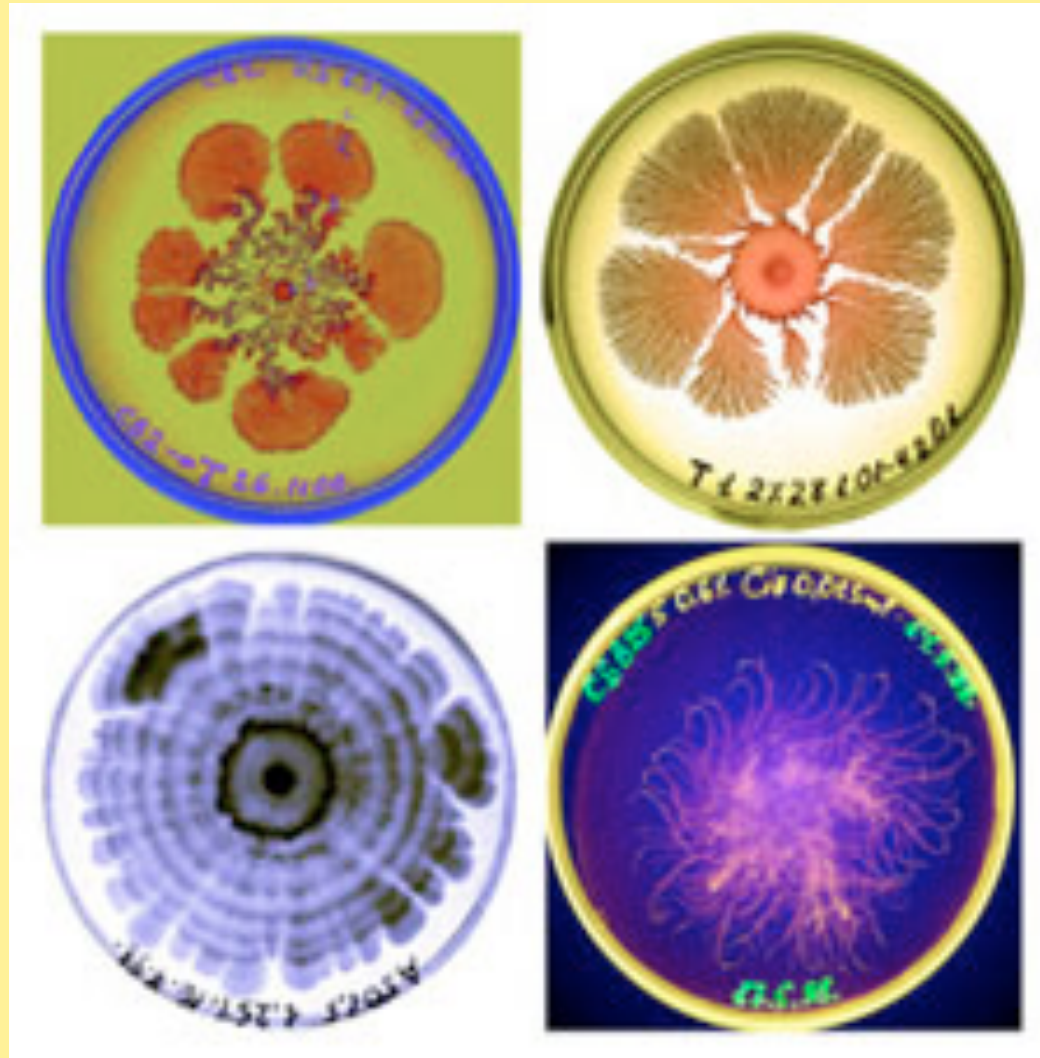
The constructionist hypothesis breaks down when confronted with the twin difficulties of scale and complexity. The behavior of large and complex aggregates of elementary particles, it turns out, is not to be understood in terms of a simple extrapolation of the properties of a few particles. Instead, 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

From physical systems to biological systems,
macroscopic features **emerge** from microscopic
interactions, largely independent of details



Patterns emerge from individual interactions in bacterial communities



Similar problems of pattern formation have been addressed for a wide range of organisms

- Slime molds
- Swarming bacteria
- Insects
- Krill
- Birds
- Fish
- Ungulates





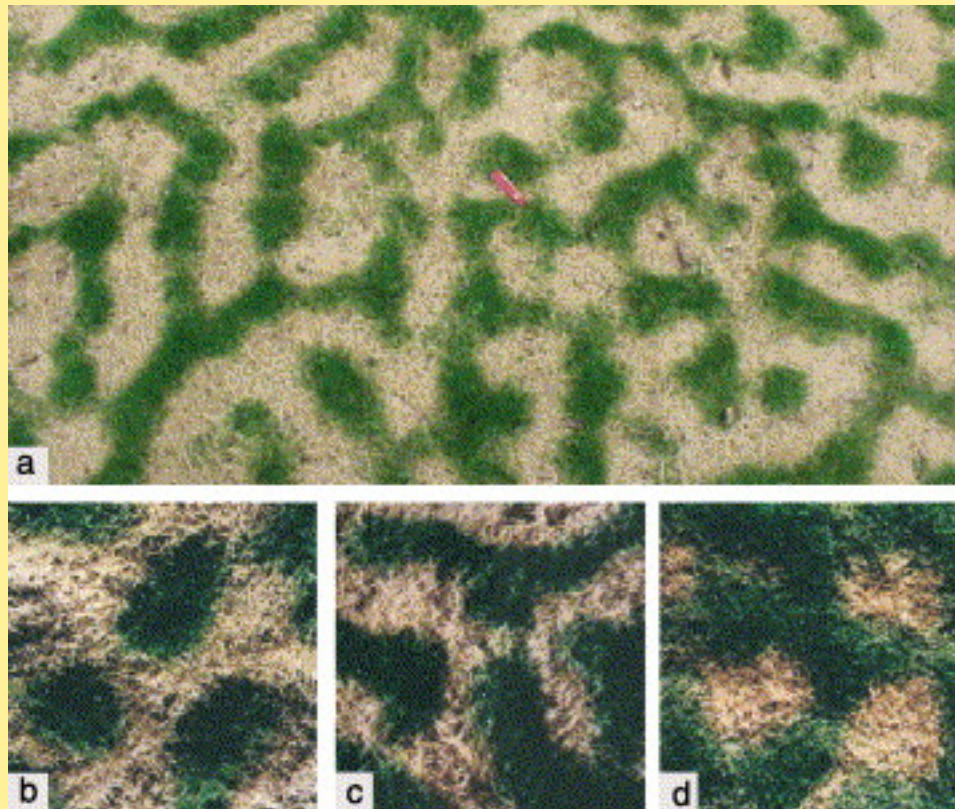
How do we relate the macroscopic patterns to the microscopic rules?

Turing instabilities:

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

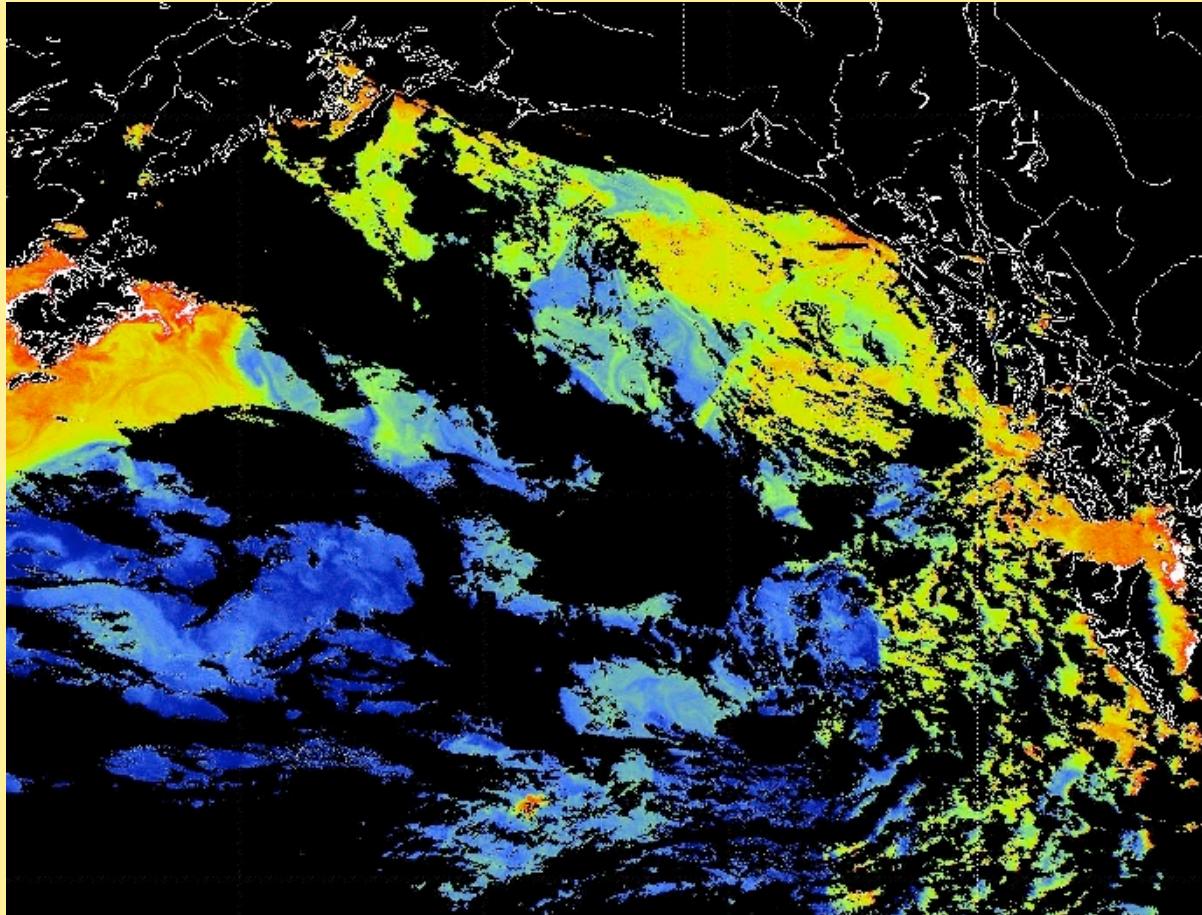
uniform states **can** become unstable if
 D_v/D_u is above some threshold.

Vegetation patterns in semi-arid
landscapes are self-organized..and
Turing models seem to fit



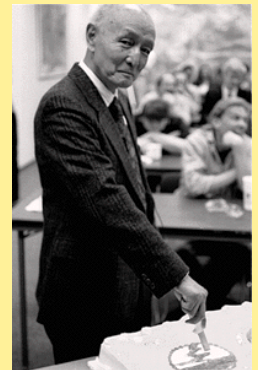
Meron et al. 2004. [Chaos, Solitons & Fractals](#)
[Volume 19, Issue 2, January 2004, Pages 367–376](#)

Plankton are patchy on almost every scale



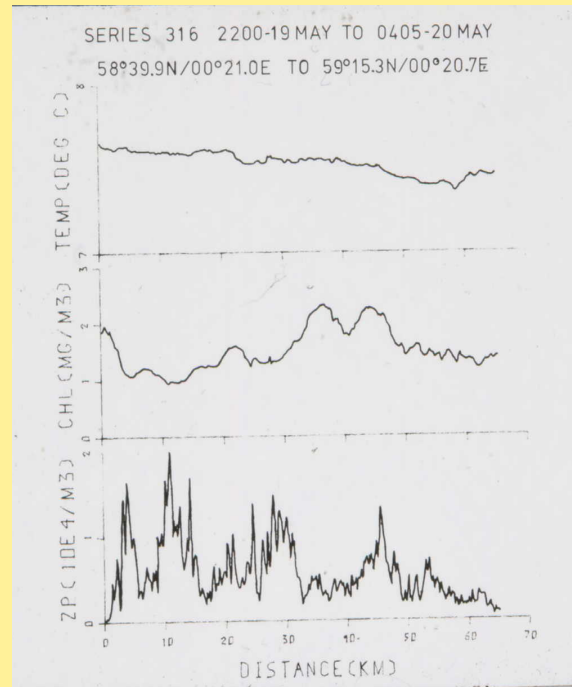
Could Turing apply to planktonic patchiness?

- Phytoplankton as “activators”
- Zooplankton as “inhibitors”
- Both Levin and Segel, and Okubo, independently proposed this



Turing mechanism didn't work

Zooplankton are more patchily distributed

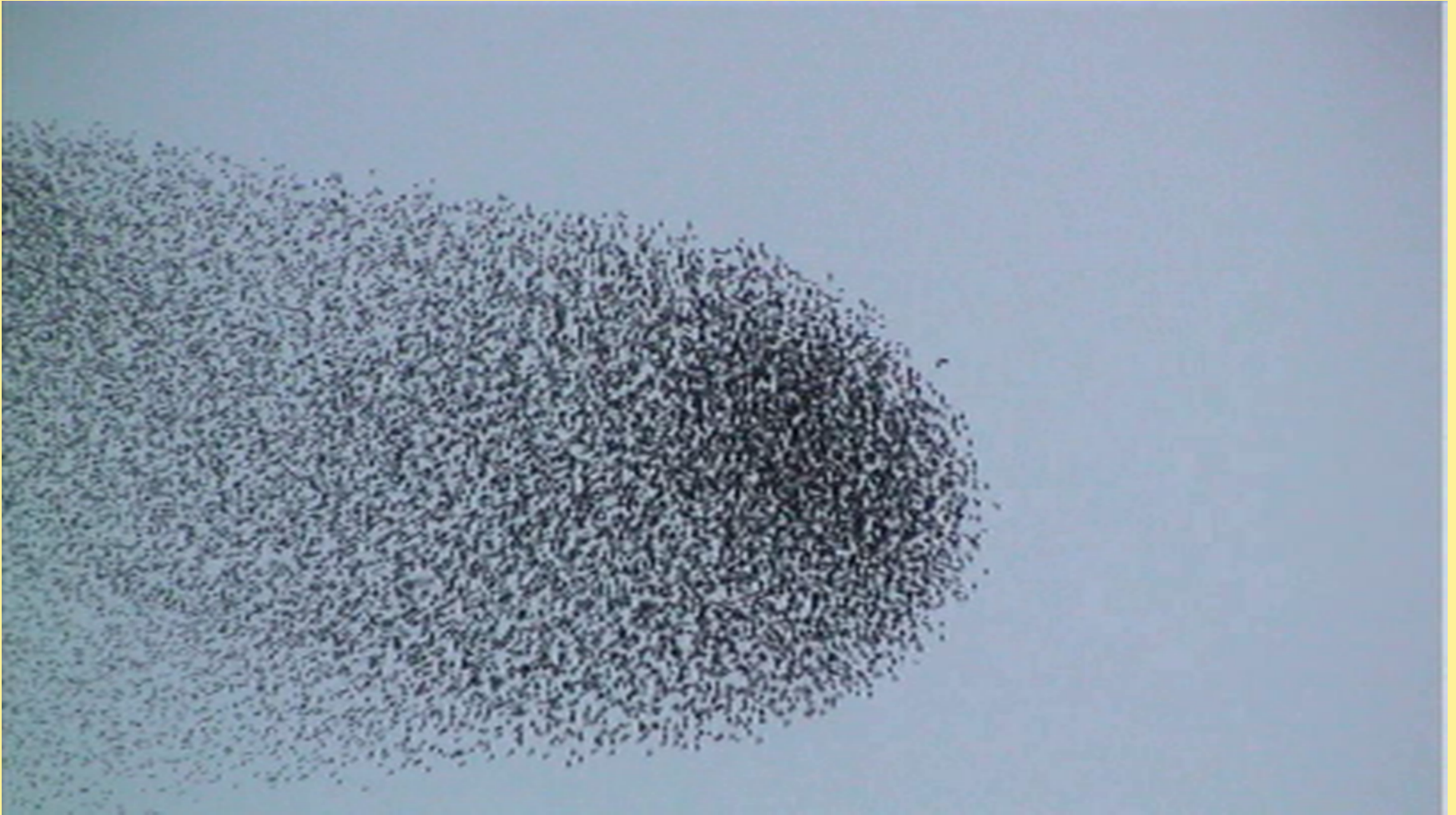


Mackas et al

Zooplankton don't move randomly,
but aggregate



Similarly birds actively aggregate



Claudo Carere

StarFLAG EU FP6 project

For all such systems, what is the
relationship between an individual
agent



...and how it responds to its
neighbors and local environment



...and the macroscopic properties of ensembles of such agents?



Lagrangian-Eulerian connections



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

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

Random Directed Grouping Arrayal



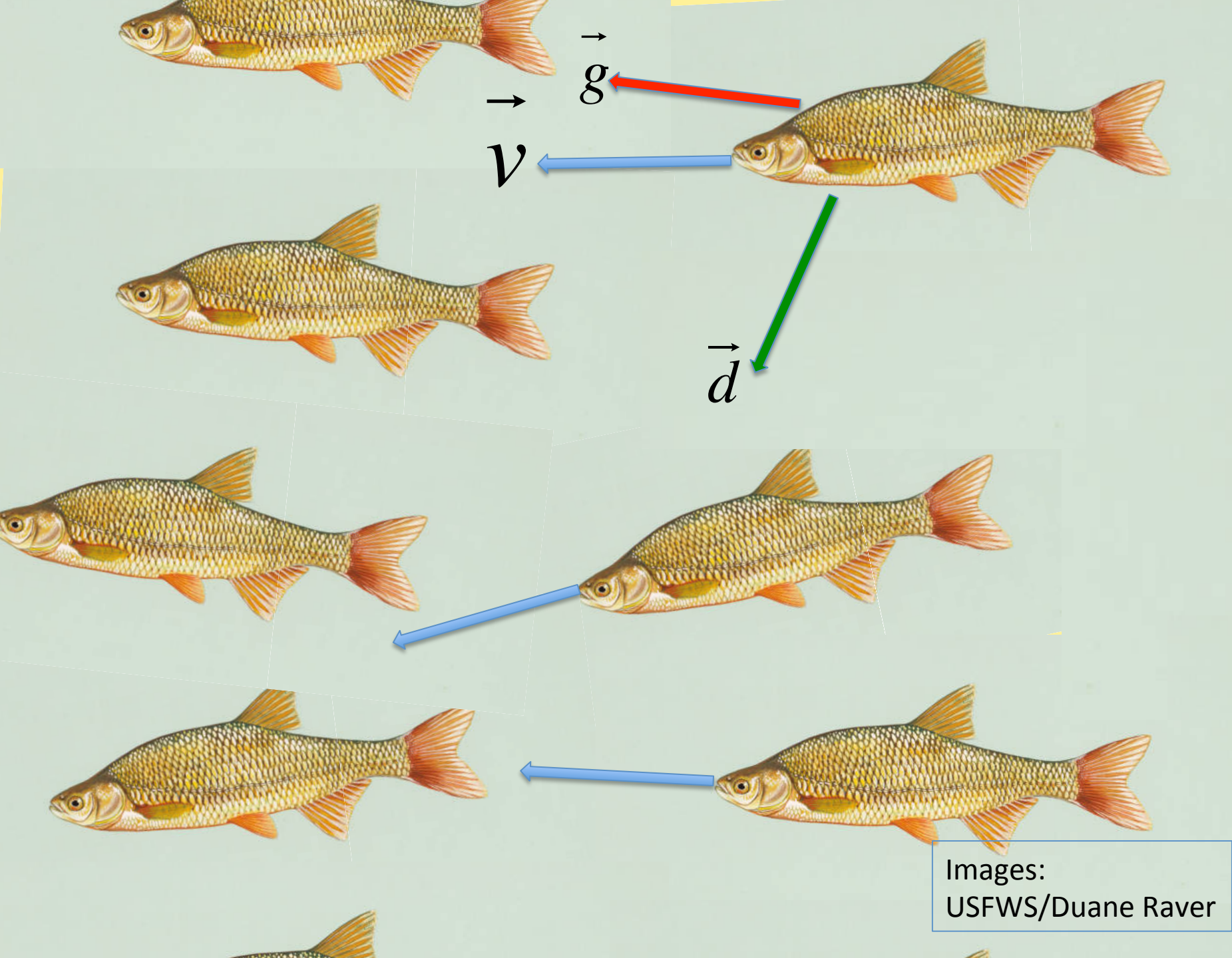
But real aggregations are
heterogeneous assemblages of
individuals

Couzin, Krause, Franks, Levin



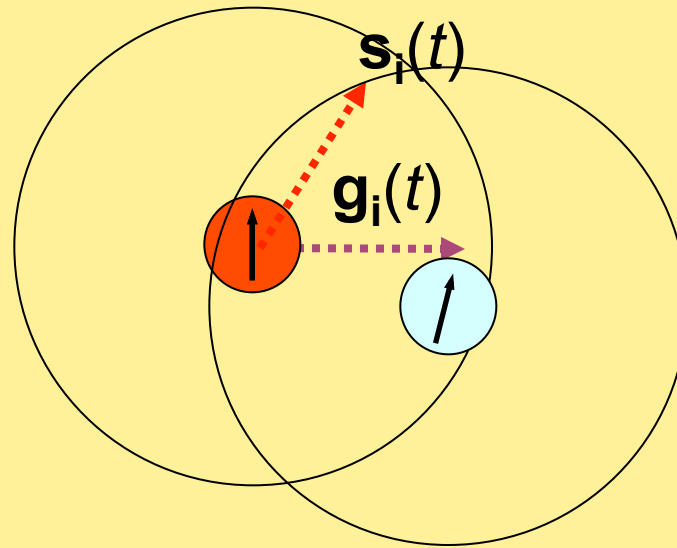
Iain Couzin/BBC

- Utilize simulations to explore these issues



Images:
USFWS/Duane Raver

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



$$\mathbf{d}_i(t+Dt) = \frac{\mathbf{s}_i(t) + \mathbf{w}\mathbf{g}_i(t)}{|\mathbf{s}_i(t) + \mathbf{w}\mathbf{g}_i(t)|}$$

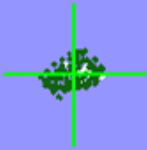
Unregistered Screen Recorder Gold

1 informed individuals in group of 100.

Courtesy Iain Couzin

5 informed individuals in group of 100.

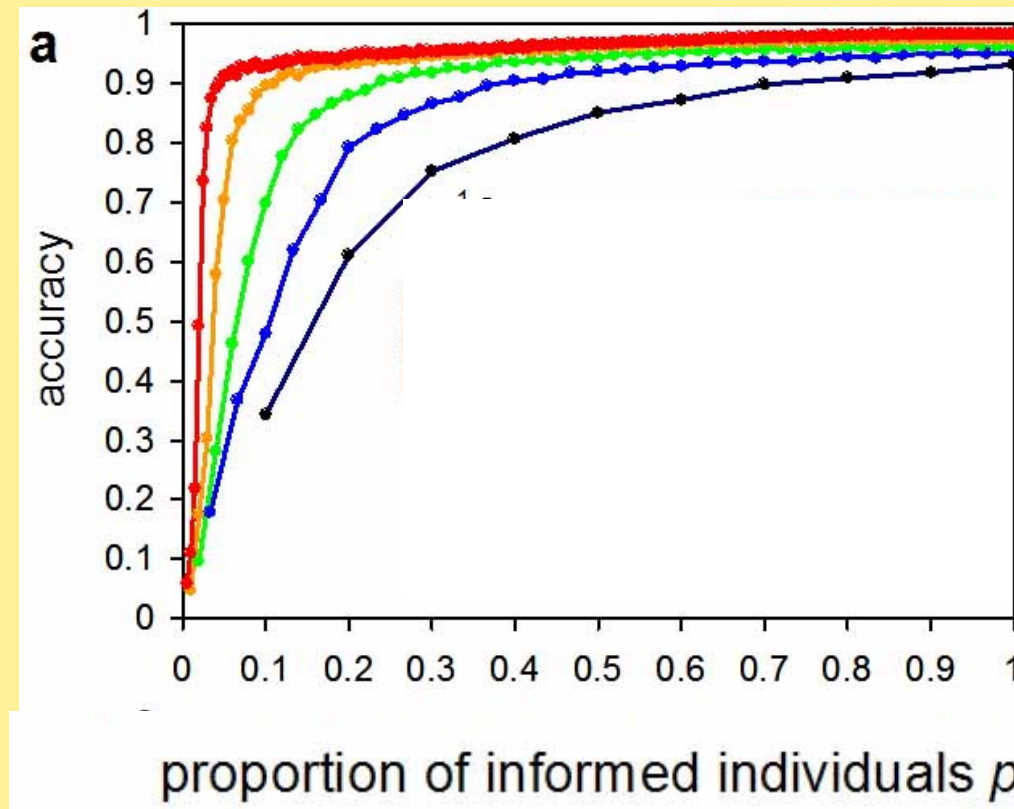
Unregistered Screen Recorder Gold



10 informed individuals in group of 100.

Courtesy Iain Couzin

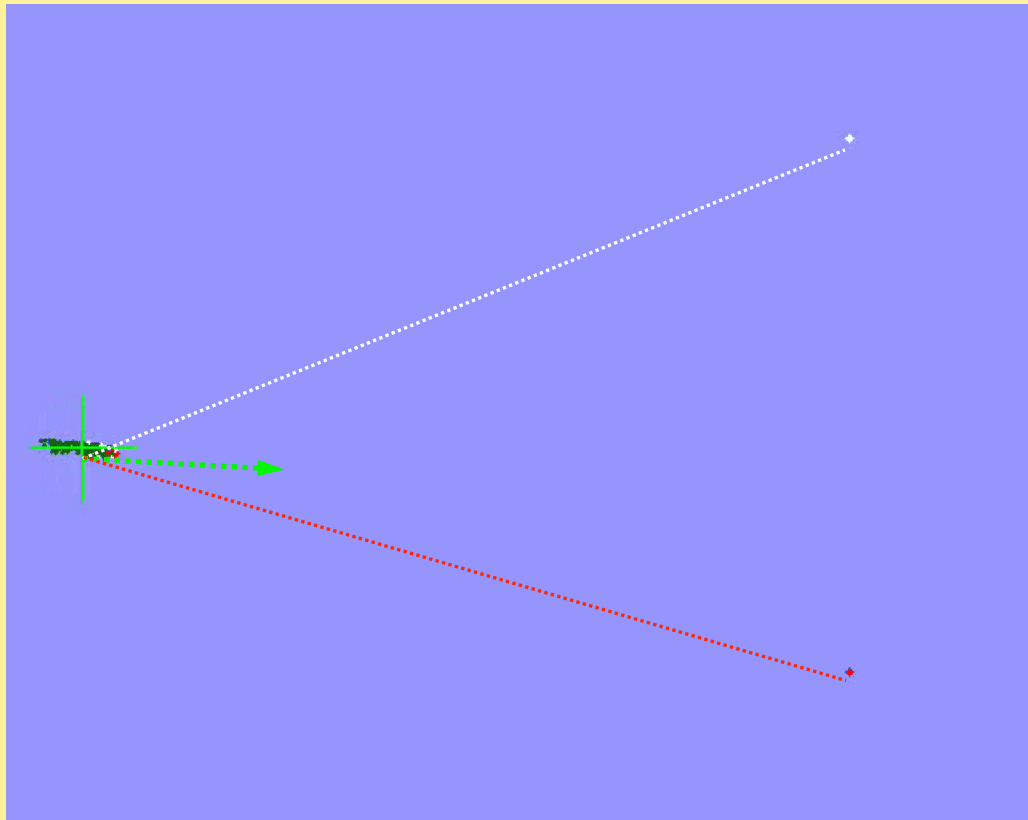
Animal groups may be led by a small number of individuals



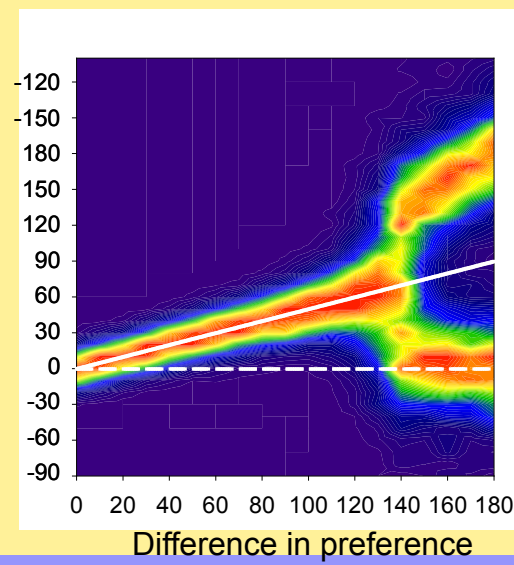
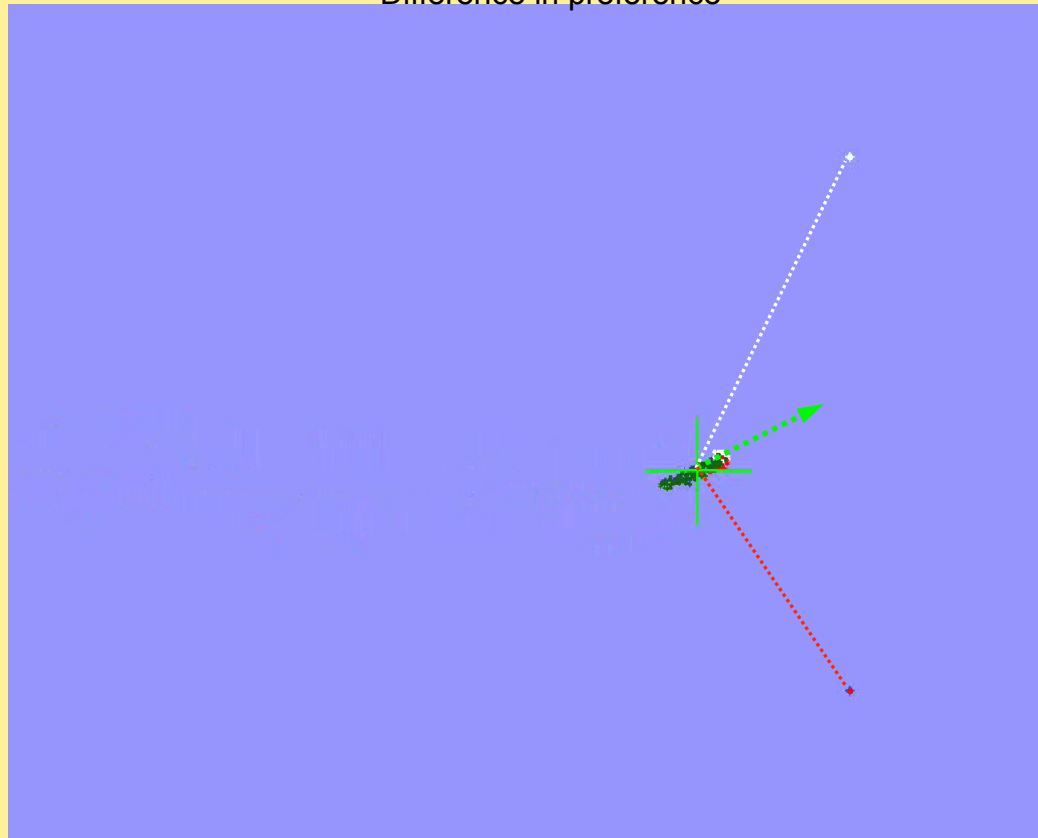
From Couzin et al., 2005

Competing preferences

Difference in preference



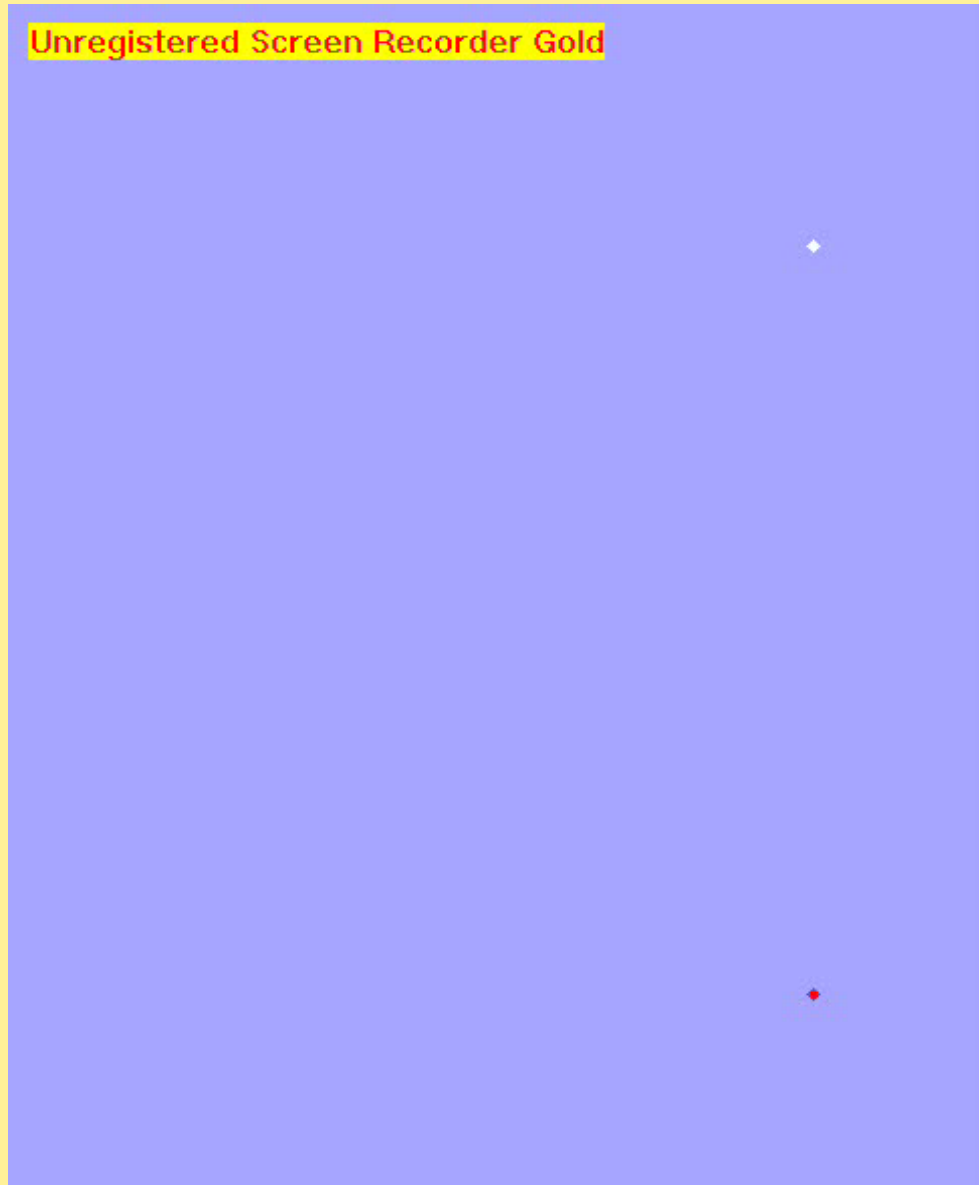
Collective decision-making



Courtesy Iain Couzin

Competition and consensus

Unregistered Screen Recorder Gold

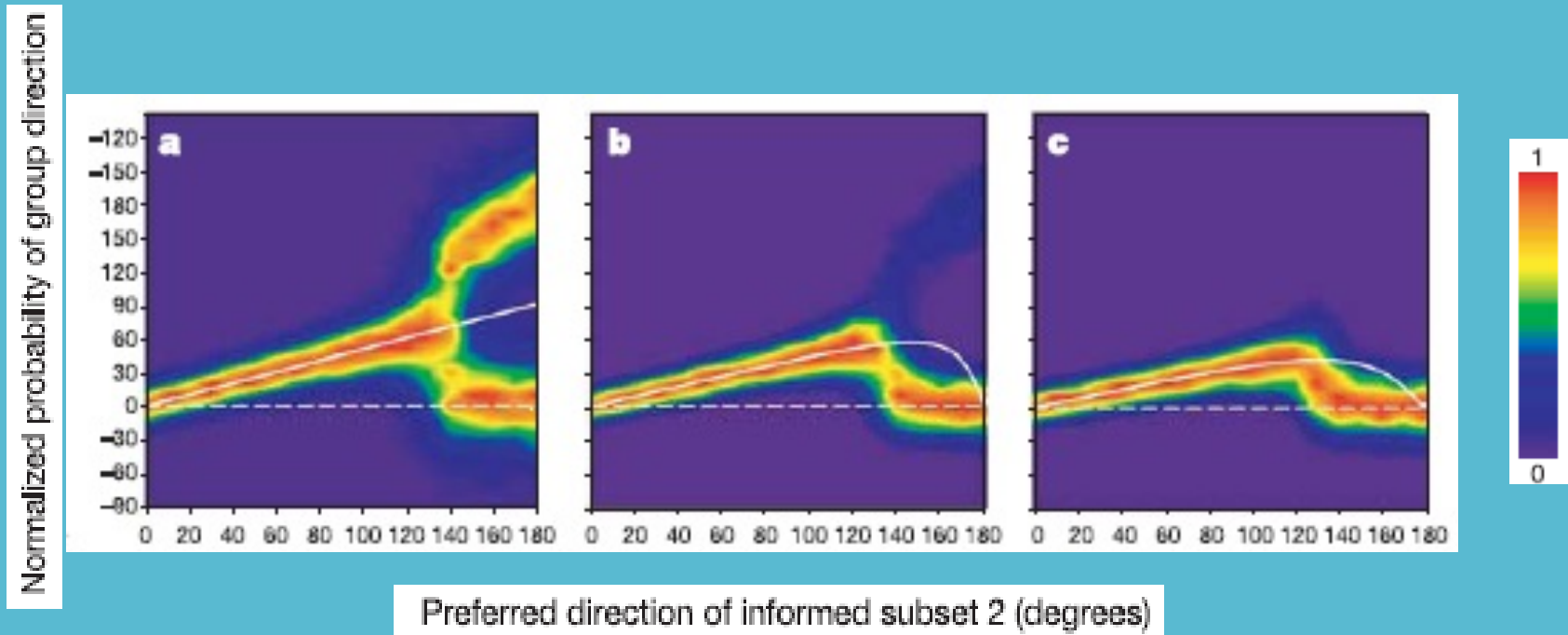


Courtesy Iain Couzin

Unregistered Screen Recorder Gold



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

Kuramoto model



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

$$j = 1, \dots, N_1$$

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

$$j = N_1 + 1, \dots, N_1 + N_2$$

$$\dot{\theta}_j = k \sum_{l=1}^N \sin(\theta_l - \theta_j)$$

$$j = N_1 + N_2 + 1, \dots, N$$

Also consider variable topologies and
strengths of commitment

Leonard et. al, PNAS

In subgroup 1, represent as

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

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

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

Coefficients change

$$\frac{da_{jl}}{dt} = K_2(1 - a_{jl}(t))a_{jl}(t)(\rho_{jl}(t) - r).$$

$$\rho_{jl} = \left(\frac{1}{2} + \frac{1}{2} \cos(\theta_j - \theta_l)\right)^{1/2}$$

Results

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

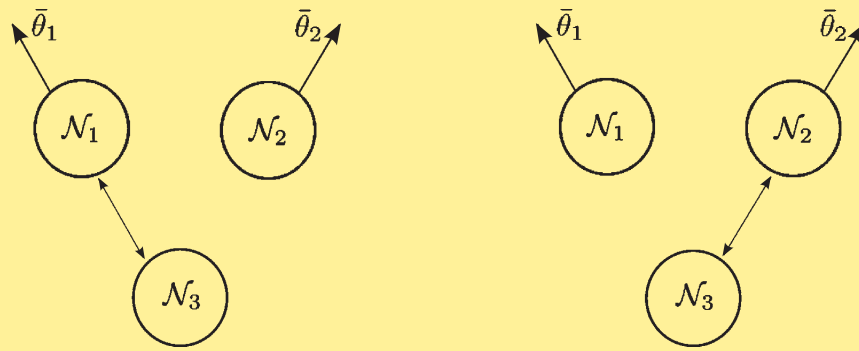


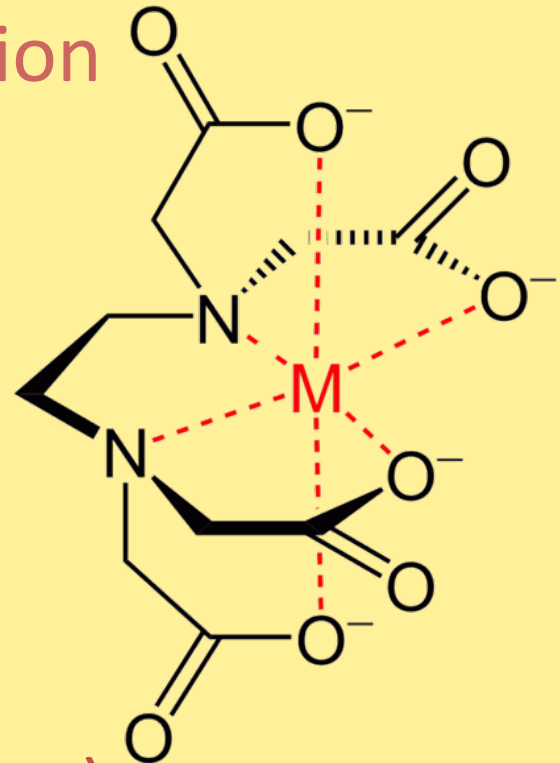
Fig. 1. Coupling in manifolds \mathcal{M}_{010} (Left) and \mathcal{M}_{001} (Right) among subgroups 1, 2, and 3 as indicated by arrows.

Lecture outline

- Statistical mechanics of ecological communities
- Critical transitions
- Collective phenomena and collective motion
 - Emergence and pattern formation
- Conflict and collective action

Public goods problems are common in evolutionary theory...and economics

- Information in collective motion
- Nests
- Chelation
- Siderophores
- N fixation
- Antibiotics
- Extracellular polymers (biofilms)



upload.wikimedia.org

Samuelson (1954): Public Goods

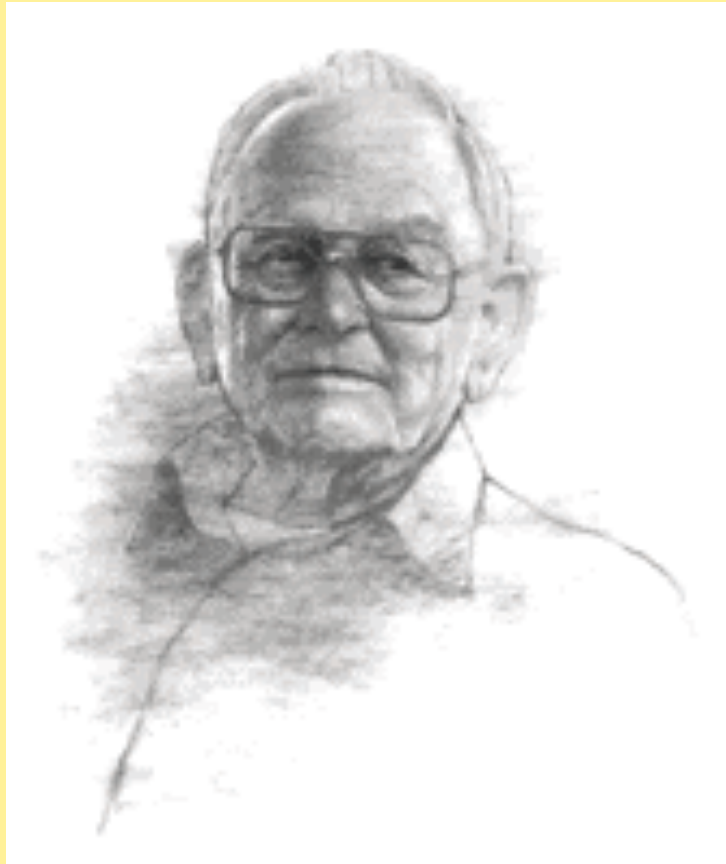
- *...[goods] which all enjoy in common in the sense that each individual's consumption of such a good leads to no subtractions from any other individual's consumption of that good...*



William Forster Lloyd (1832)
The Tragedy of the Commons



The Commons solution (Hardin, Ostrom)



“Mutual coercion, mutually agreed upon”

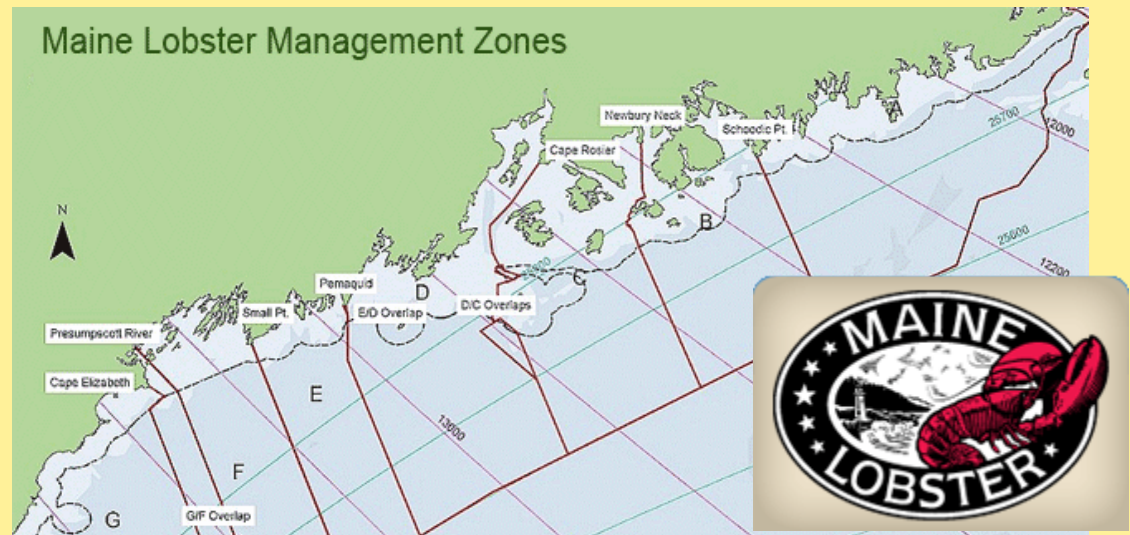
<http://www.physics.ohio-state.edu/~wilkins>

<http://www.guardian.co.uk>

The role of a fairness norm for the evolution of cooperation

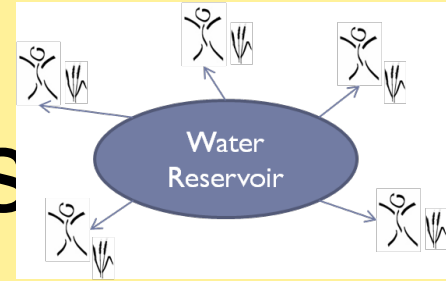
with Alessandro Tavoni and Maja Schlüter

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



Pictures from <http://www.lobsterfrommaine.com>

Equity-driven ostracis



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

$$U_C = \pi_C(E, R)$$

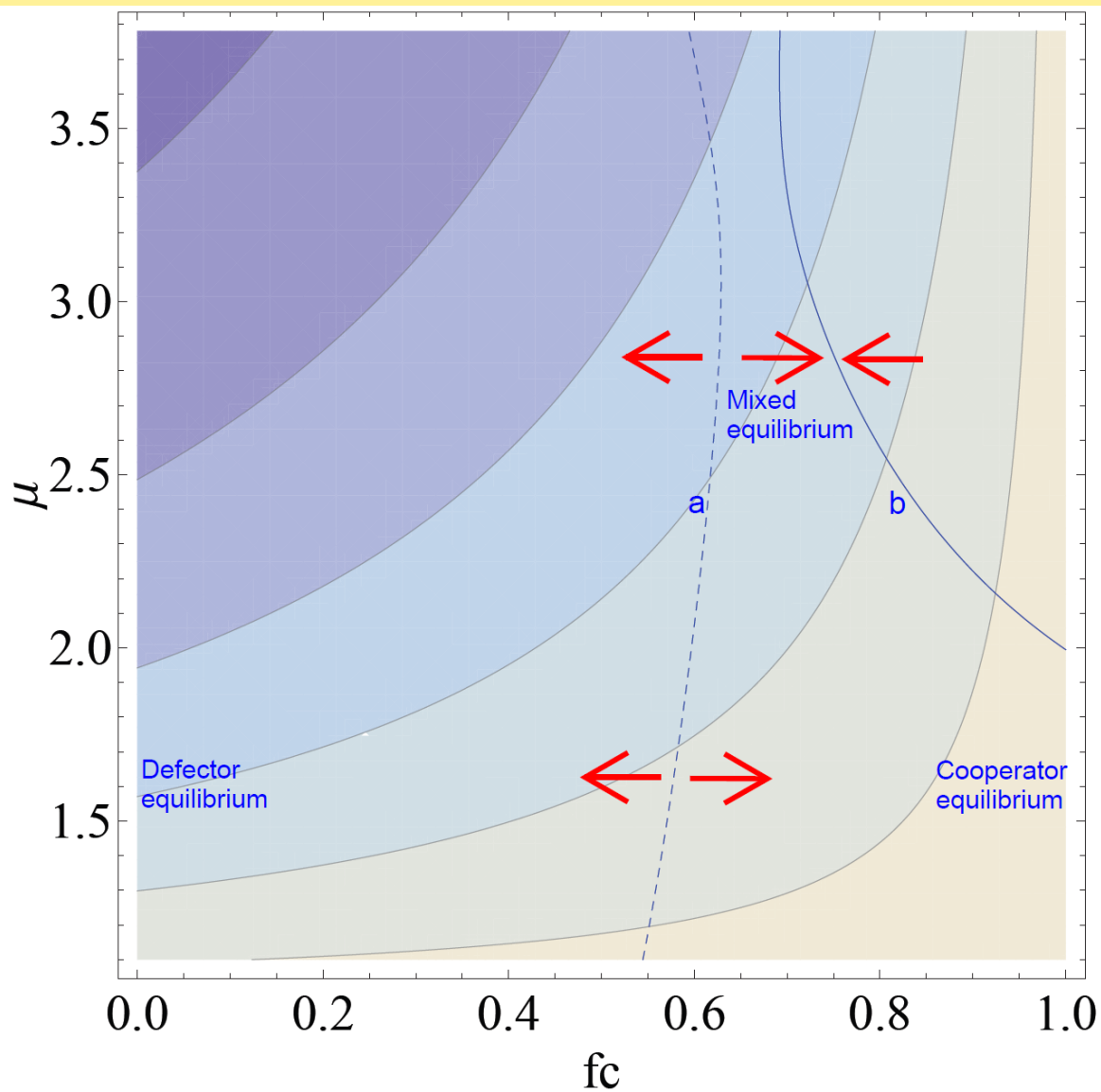
$$U_D = \pi_D(E, R) - \omega(f_c) \frac{\pi_D(E, R) - \pi_C(E, R)}{\pi_D(E, R)}$$

Payoff from
production

Ostracism
function

Intensity of defection
(inequity)

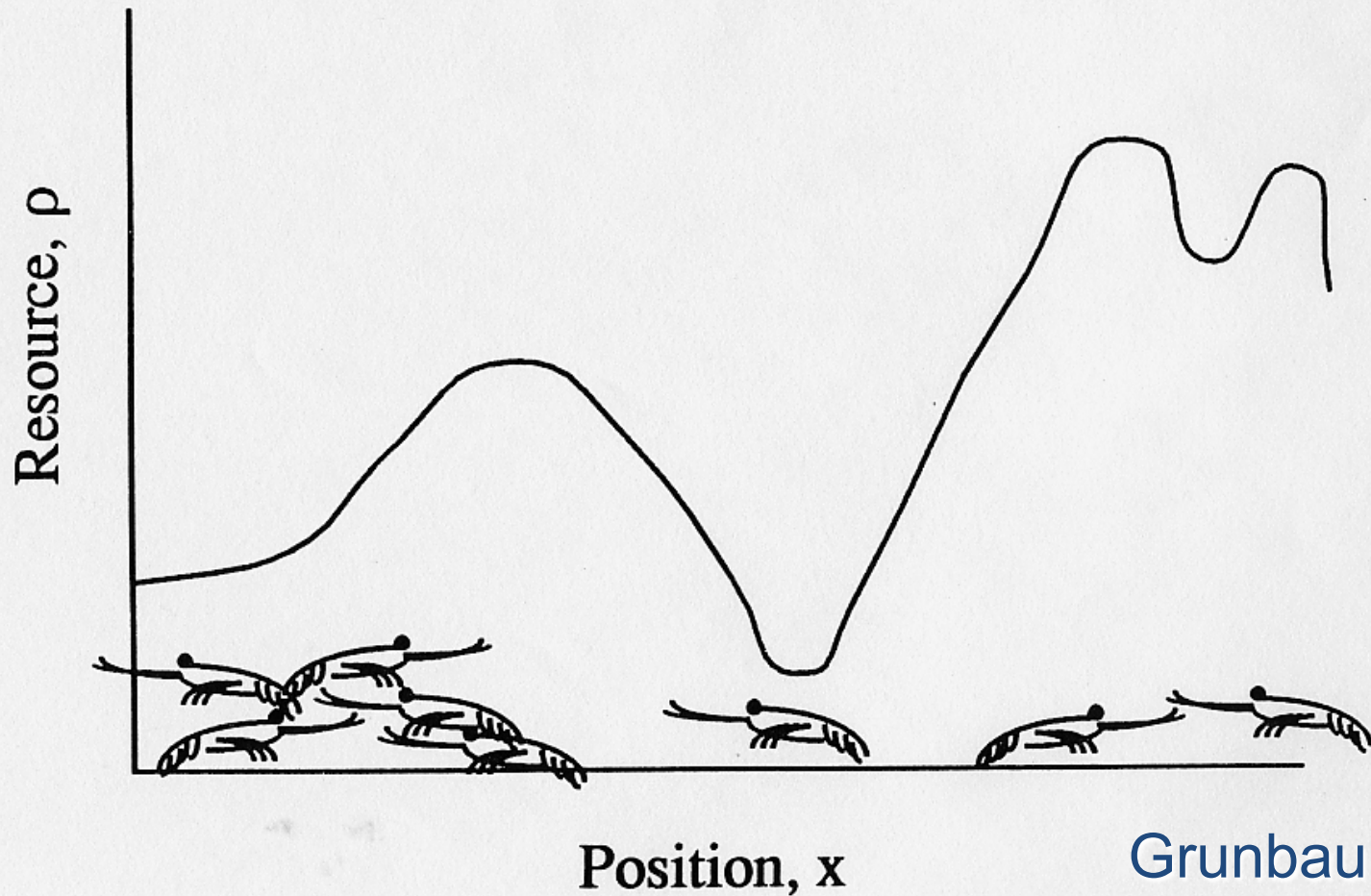
Selfishness



Frequency of cooperators

Evolution of collective behavior

Searching on Resource Landscapes

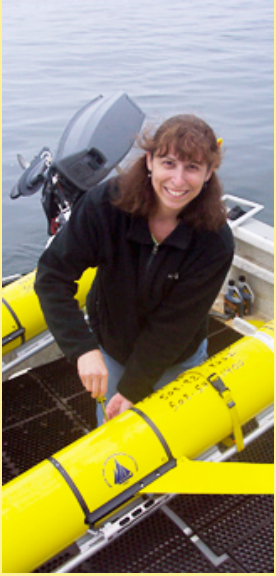


How does selection shape the trade-off between tracking resources and tracking other individuals?

Questions

- How many leaders?
- How many followers?
- Group optimality
- Game-theoretic solutions
- Lessons for cooperation in public goods situations

Distributed, communicating robots



**Naomi
Leonard;
Photo, David Benet**



Naomi Leonard

Recent work : The evolution of collective migration

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

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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-

Specialization and evolutionary branching within migratory populations

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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 sociability. 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



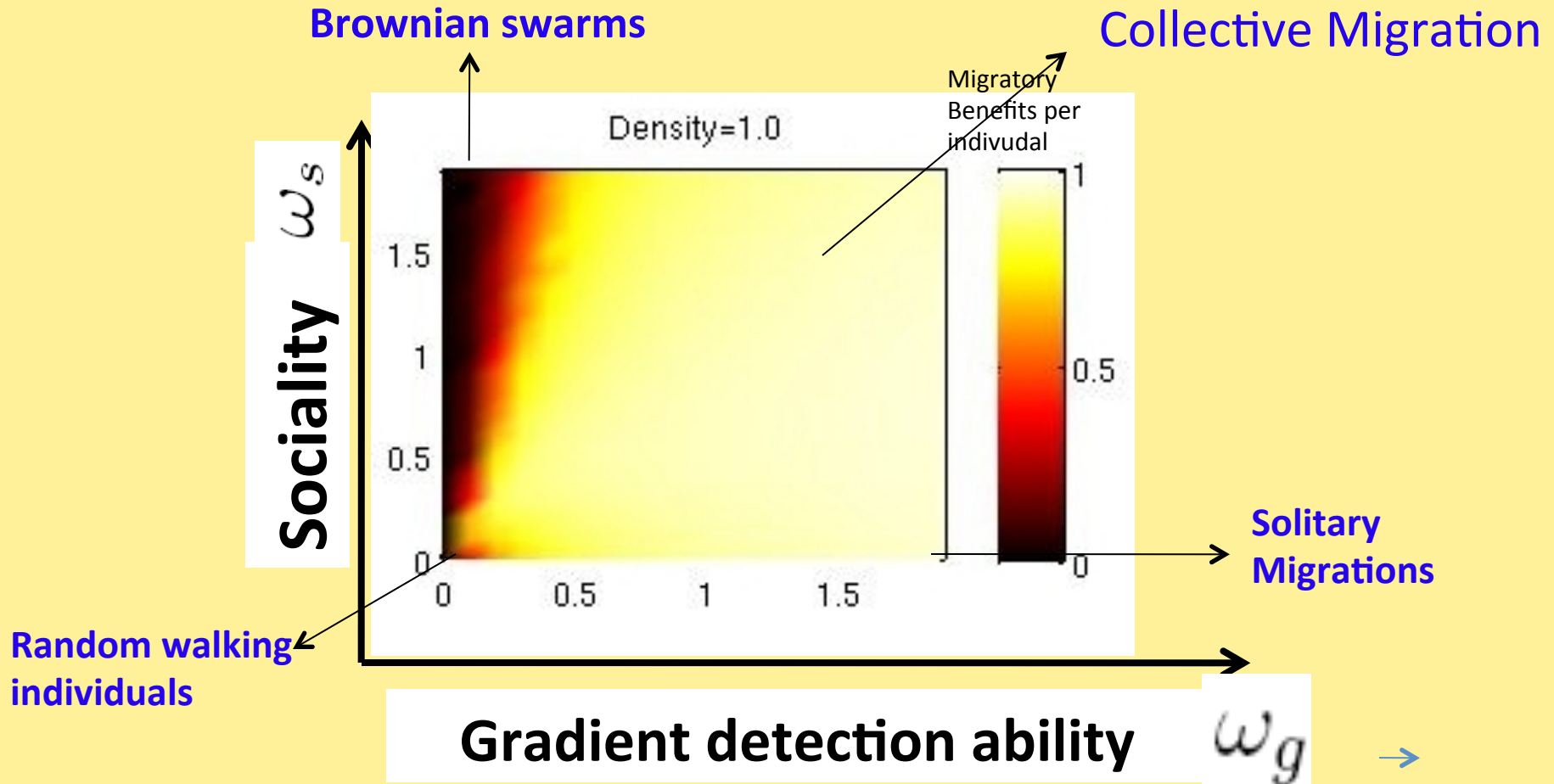
Leadership, collective motion and the evolution of migratory strategies

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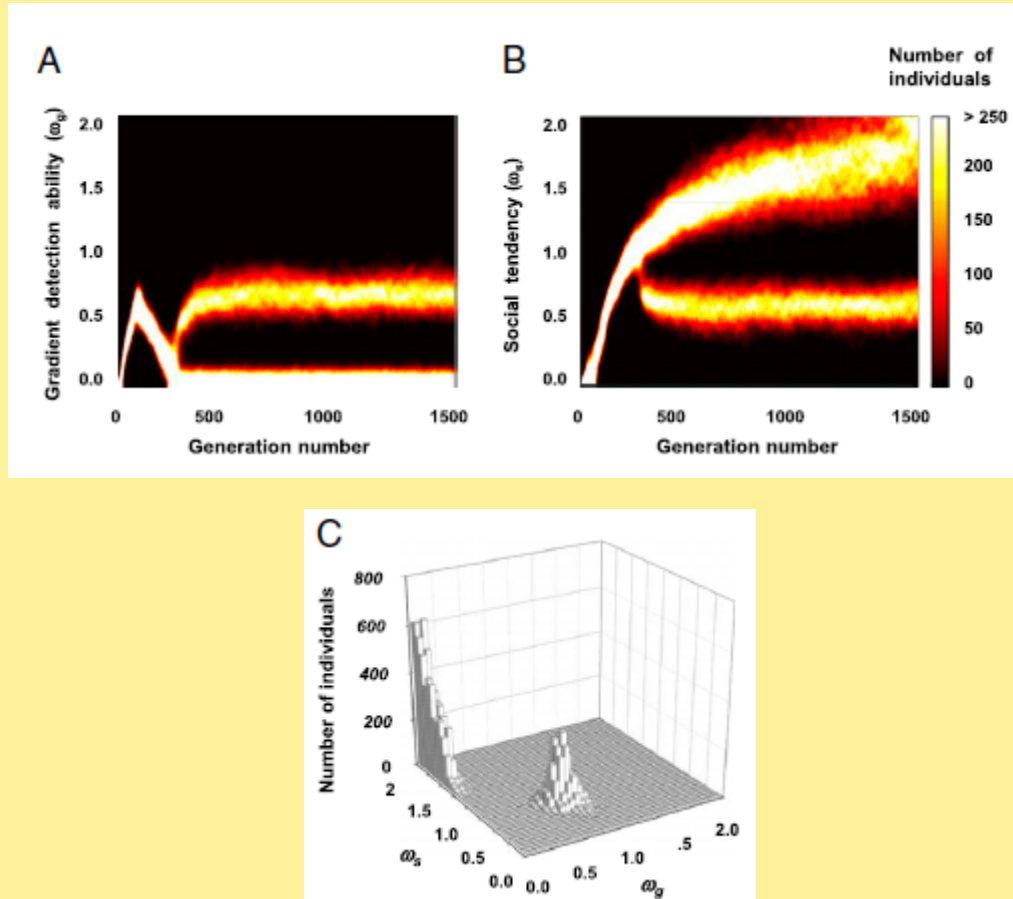
Guttal et al.

Simple model: wide range of dynamics



Thanks to Iain Couzin

Evolutionary branching: leaders and followers



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

Extensions to human decision-making

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

Multiple models yield similar results

REPORTS

Uninformed Individuals Promote Democratic Consensus in Animal Groups

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

Social organisms must often achieve a consensus to obtain the benefits of group living and to avoid the costs of indecision (1–12). In some societies, notably those of eusocial insects, making consensus decisions is often a unitary, conflict-free process because the close relatedness among individuals means that they typically share preferences (11). However, in other social animals, such as schooling fish, flocking birds, herding ungulates, and humans, individual

Consequently, for both human societies (1, 2, 6, 9, 10, 14) and group-living animals (6, 13), it has been argued that group decisions can be subject to manipulation by a self-interested and opinionated minority. In particular, previous work suggests that groups containing individuals who are uninformed, or naïve, about the decision being made are particularly vulnerable to such manipulation (2, 9, 10, 13). Under this view, uninformed individuals destabilize the capacity

that uninformed individuals (defined as those who lack a preference or are uninformed about the features on which the collective decision is being made) play a central role in achieving democratic consensus.

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

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

Conclusions

- Collective phenomena and emergence characterize systems, from microbial communities to the biosphere
- A fundamental challenge is to scale from microscopic to macroscopic
- Consensus formation is a challenge in all systems