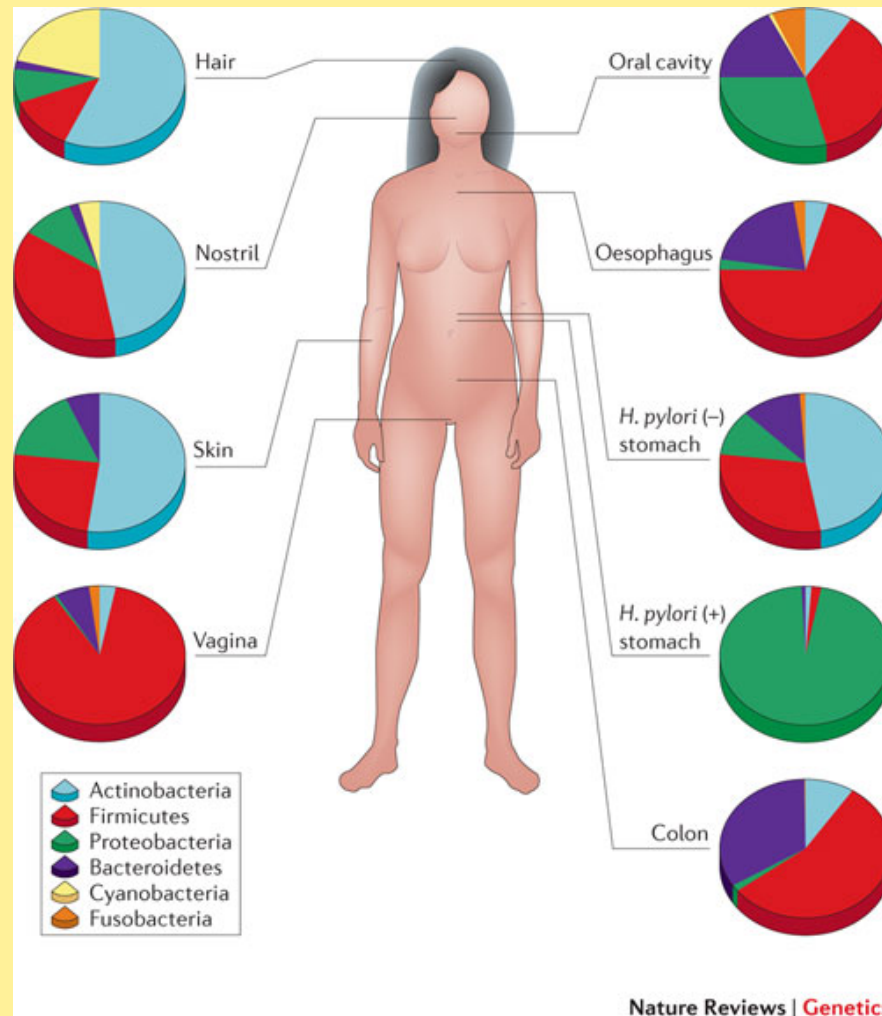


The Ecology of Microbial Communities

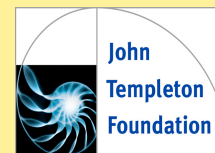


Cho and Blaser
Nature 2012

Nature Reviews | Genetics

Simon Levin Trieste 2017

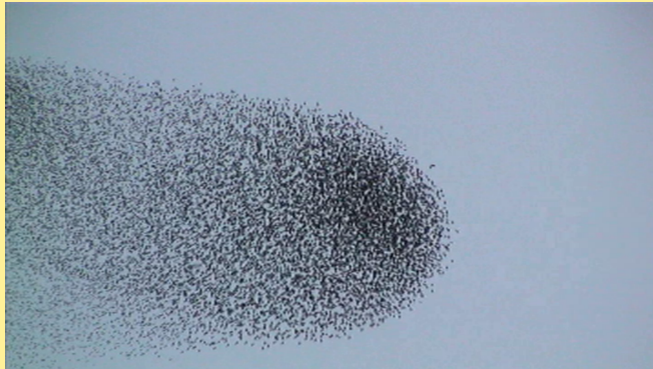
With thanks to



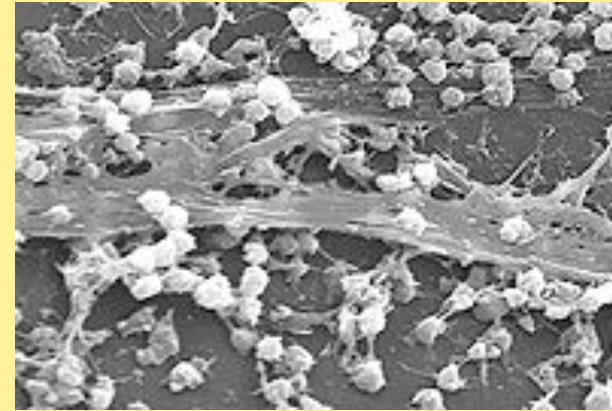
Objectives

- Raise challenges, following up on Daniel's lecture
- Explore the role of mathematics and physics
- Especially suggest the benefits of an ecological and evolutionary perspective, and in turn the benefits to ecology and evolution of studying microbial systems

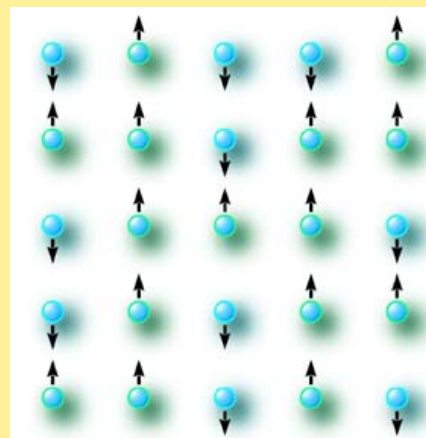
From physical systems to biological systems,
macroscopic features **emerge** from microscopic
interactions, largely independent of details



Courtesy of Claudio Carere / StarFLAG EU FP6
project



<http://en.wikipedia.org/wiki/Biofilm>

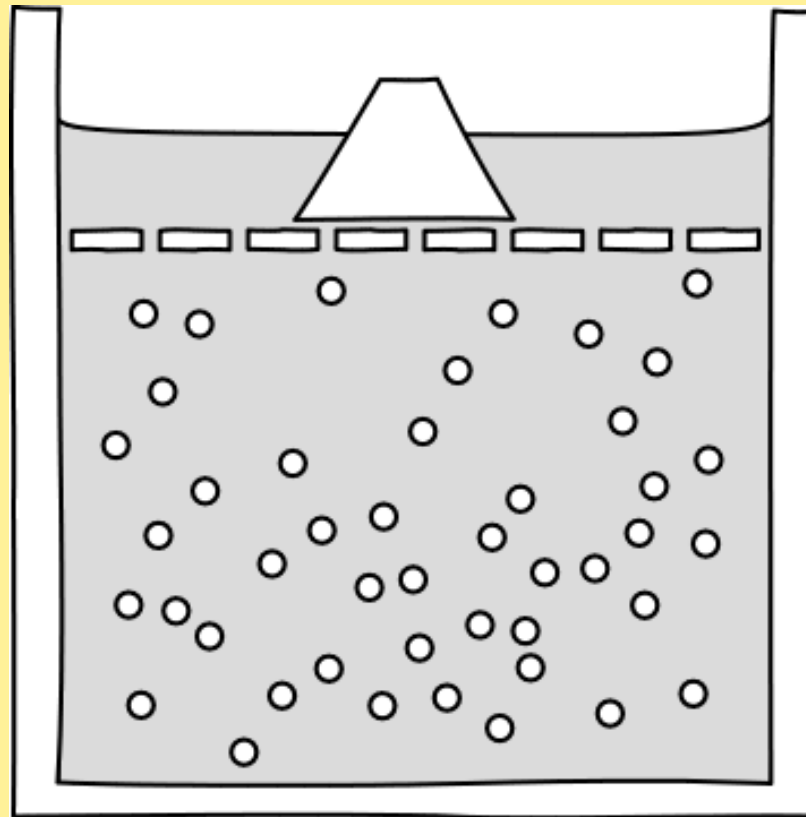


<http://www.icmp.lviv.ua/ising/galam.html>

Like these examples, microbial communities are complex adaptive systems

- Challenge to understand them as emergent from individual interactions, with complementarity of function
- And to understand the broader ecosystems of which they are part as CAS

Focus on macroscopic features must recognize that these **emerge** from microscopic interactions, but do not depend on most fine details



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 microbial systems and the ecosystems of which they are part ?

Simons Grant

- ***Deriving macroscopic equations for interaction rates, population dynamics, and nutrient fluxes from individual-based models of ecological interactions***

Levin, Hein, Hagstrom, Stocker

A New Framework for Ecological Kinetics in Natural Environments

Ocean dynamics: The MIT-DARWIN Model

$$\begin{aligned}
 \frac{\partial N_i}{\partial t} &= \underbrace{-\nabla \cdot (\mathbf{u} N_i) + \nabla \cdot (K \nabla N_i)}_{\text{u and K from ECCO2 GCM}} - \underbrace{\sum_j \mu_j P_j}_{\text{Growth}} \underbrace{R_{ij}}_{\text{Mortality}} + \underbrace{S_{N_i}}_{\text{Remineralization \& other sources}} \\
 \frac{\partial P_j}{\partial t} &= -\nabla \cdot (\mathbf{u} P_j) + \nabla \cdot (K \nabla P_j) + \underbrace{\mu_j P_j}_{\text{Growth}} - \underbrace{m_j^P P_j}_{\text{Mortality}} - \underbrace{\sum_k g_{jk} \frac{P_j Z_{k,i=1}}{P_j + k_j^P}}_{\text{Grazing}} - \underbrace{\frac{w_j^P \partial P_j}{\partial z}}_{\text{Sinking}} \\
 \frac{\partial Z_{ki}}{\partial t} &= -\nabla \cdot (\mathbf{u} Z_{ki}) + \nabla \cdot (K \nabla Z_{ki}) - m_k^Z Z_{ki} + \sum_k g_{jk} \frac{P_j R_{ij}}{P_j + k_j^P}
 \end{aligned}$$

N/P/Z= nutrients/phytoplankton/
zooplankton
Simplistic movement

Ecotypes, not species, are predictable

Follows, Dutkiewicz, Chisholm,

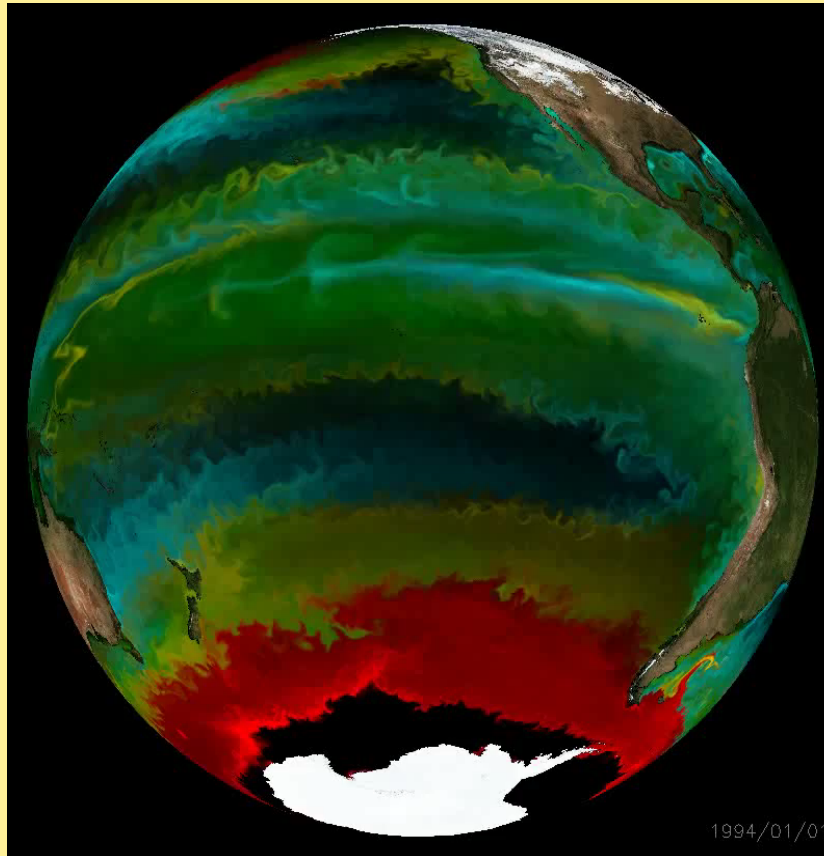
...

Prochlorococcus

Synechococcus

Diatoms

Large eukaryotes



Courtesy Follows and Dutkiewicz

Author's personal copy

Ecosystems
DOI: 10.1007/s10021-017-0114-3

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20TH ANNIVERSARY PAPER

Marine Ecosystems as Complex Adaptive Systems: Emergent Patterns, Critical Transitions, and Public Goods

George I. Hagstrom* and Simon A. Levin

Ecology and Evolutionary Biology, Princeton University, Guyot Hall, Princeton, New York 08544, USA

ABSTRACT

Complex adaptive systems provide a unified framework for explaining ecosystem phenomena. In the past 20 years, complex adaptive systems have been sharpened from an abstract concept into a series of tools that can be used to solve concrete problems. These advances have been led by the development of new techniques for coupling ecological and evolutionary dynamics, for integrating dynamics across multiple scales of organization, and for using data to infer the complex interactions among different components of ecological systems. Focusing on the development and usage of these new methods, we discuss how they have led to an improved understanding of three universal features of complex adaptive systems, emergent patterns;

tipping points and critical phenomena; and cooperative behavior. We restrict our attention primarily to marine ecosystems, which provide numerous successful examples of the application of complex adaptive systems. Many of these are currently undergoing dramatic changes due to anthropogenic perturbations, and we take the opportunity to discuss how complex adaptive systems can be used to improve the management of public goods and to better preserve critical ecosystem services.

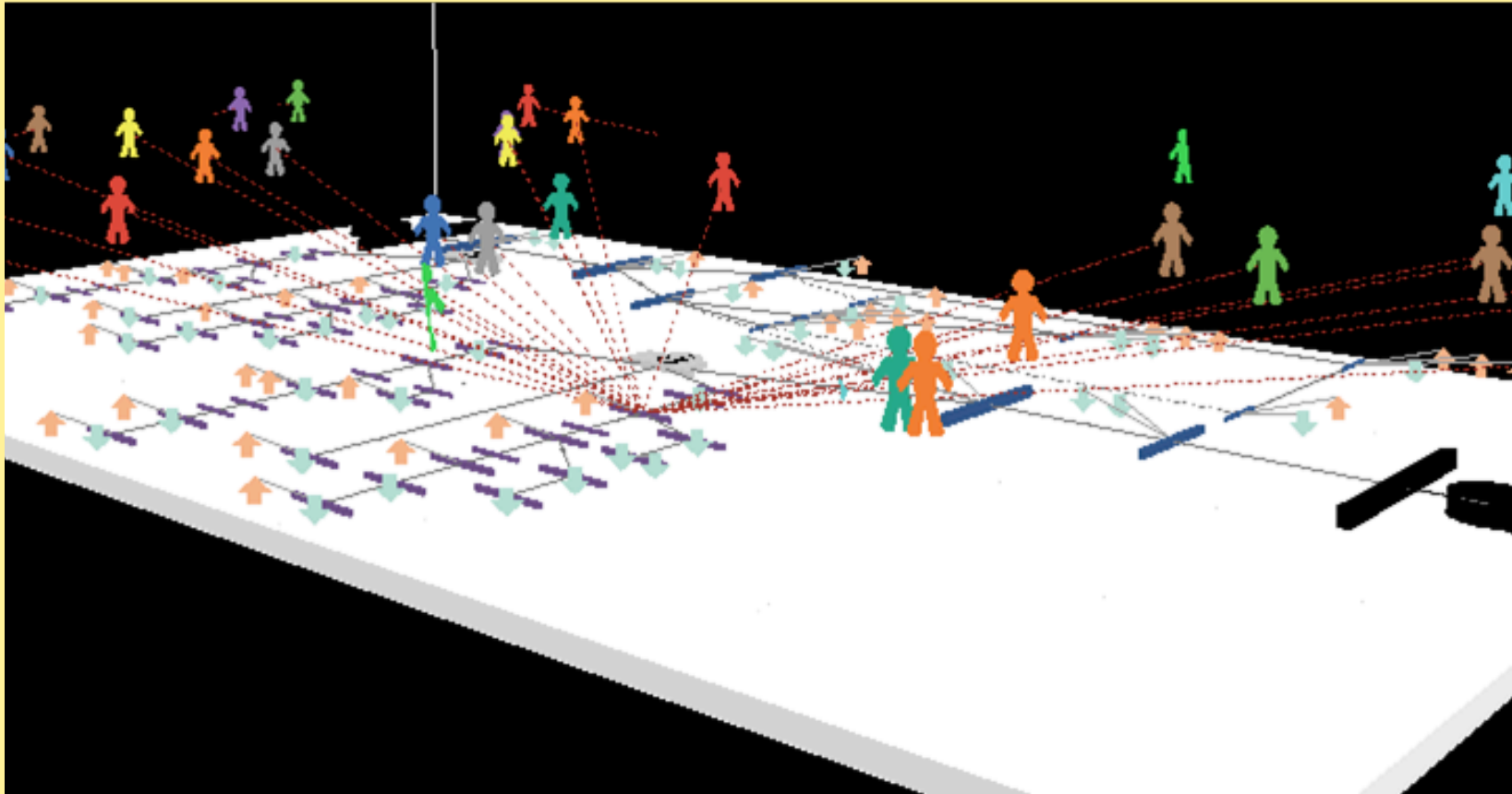
Key words: complex adaptive systems; public goods; emergent patterns; critical transitions; marine ecosystems; evolution of cooperation; theoretical ecology.

INTRODUCTION

Twenty years ago, as *Ecosystems* was setting out on its path to become one of the leading-edge outlets for

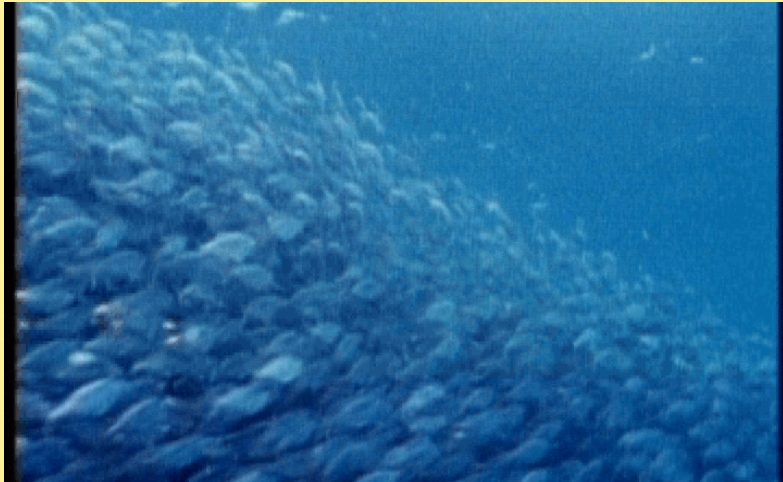
systems (Hartvigsen and others 1998; Levin 1998). Since that time, this perspective has seen impressive development, from both theoretical and applied perspectives (Scheffer and others 2012; Filotas and

Agent-based models are increasing in power

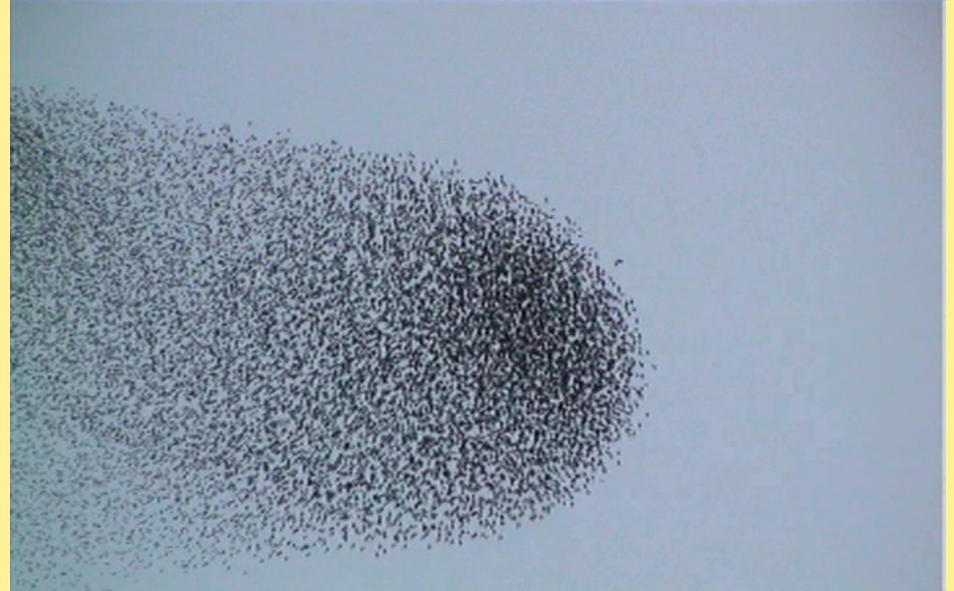


<http://ses.jrc.ec.europa.eu/agent-based-modelling-smart-grids>

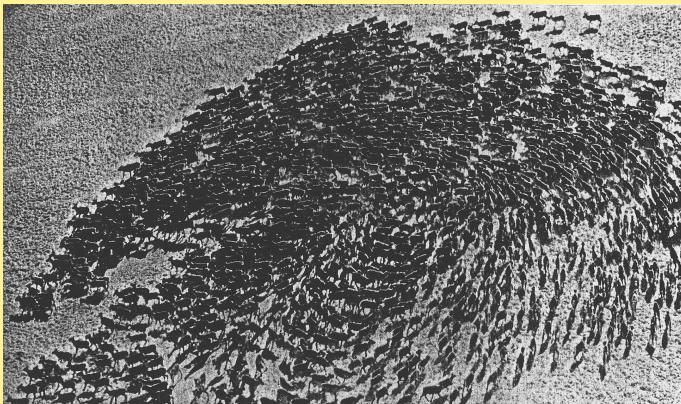
Animal flocks, herds and swarms



Couzin/BBC



Claudio Carere + StarFLAG EU FP6 project



Source Unknown

But reduced-dimensional descriptions will be essential for robustness of conclusions

- Hydrodynamic limits
- Moment closure
- Equation-free methods
- Other approaches to aggregation

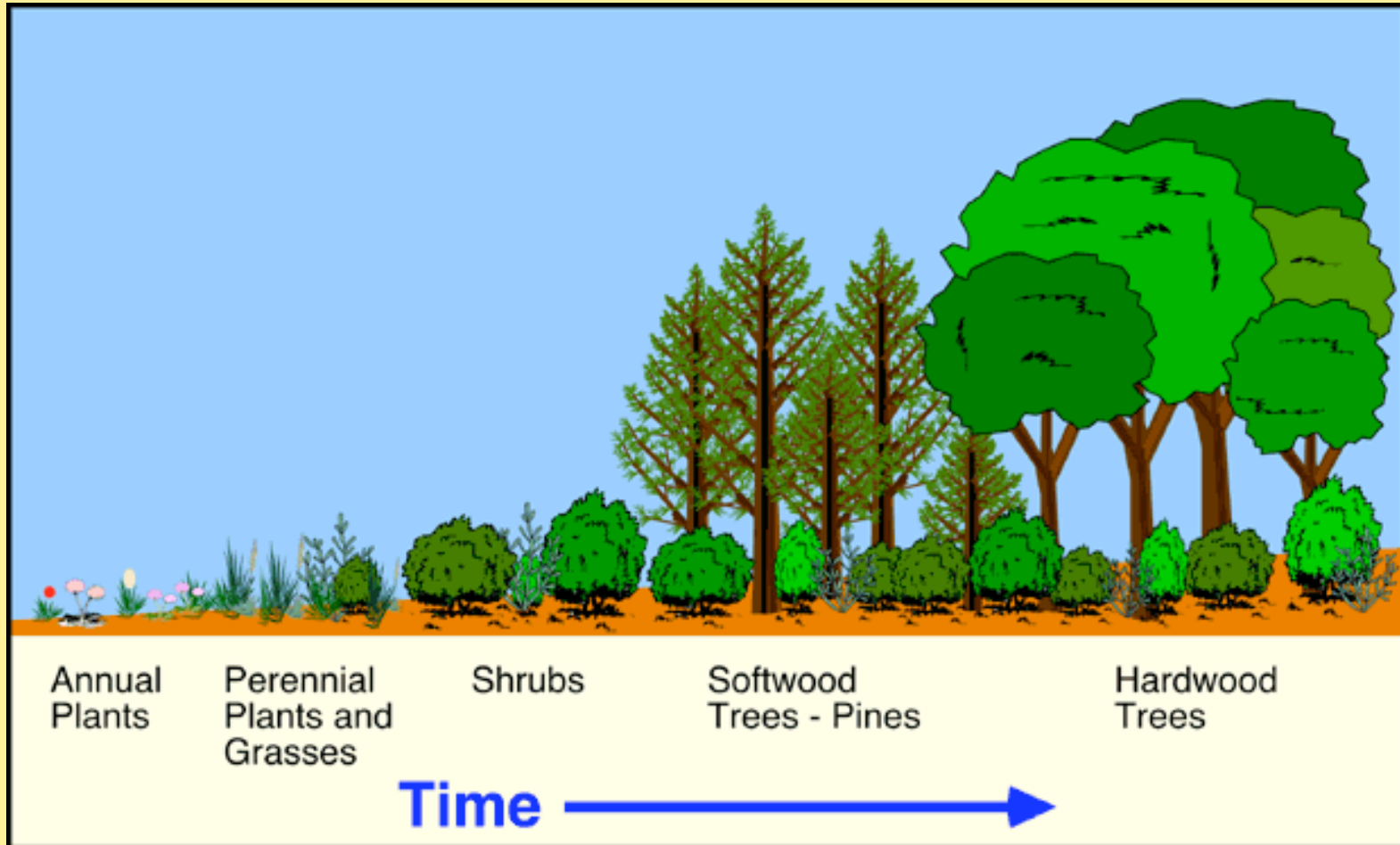
Ecosystem ecology of the microbiome: Theoretical questions

- Macroecology and geographical ecology
- Theories and measures of diversity/neutral theory
- Competitive release (*C. difficile*)
- Emergence of nutrient cycles and public goods/bads production (e.g., *H.pylori*)
- Biological invasions and probiotics/antibiotics
- Evolution and ecosystem properties

Topics of interest

- **Temporal patterning**
- Alternative stable states
- Spatial patterns
- Coupling space and time

Ecological succession



The temporal microbiome and microbial ecosystems

- What do we know about patterns of colonization and succession in the microbiome, and in microbial communities more generally?
- What about diurnal and other cycles?
- Seasonality?

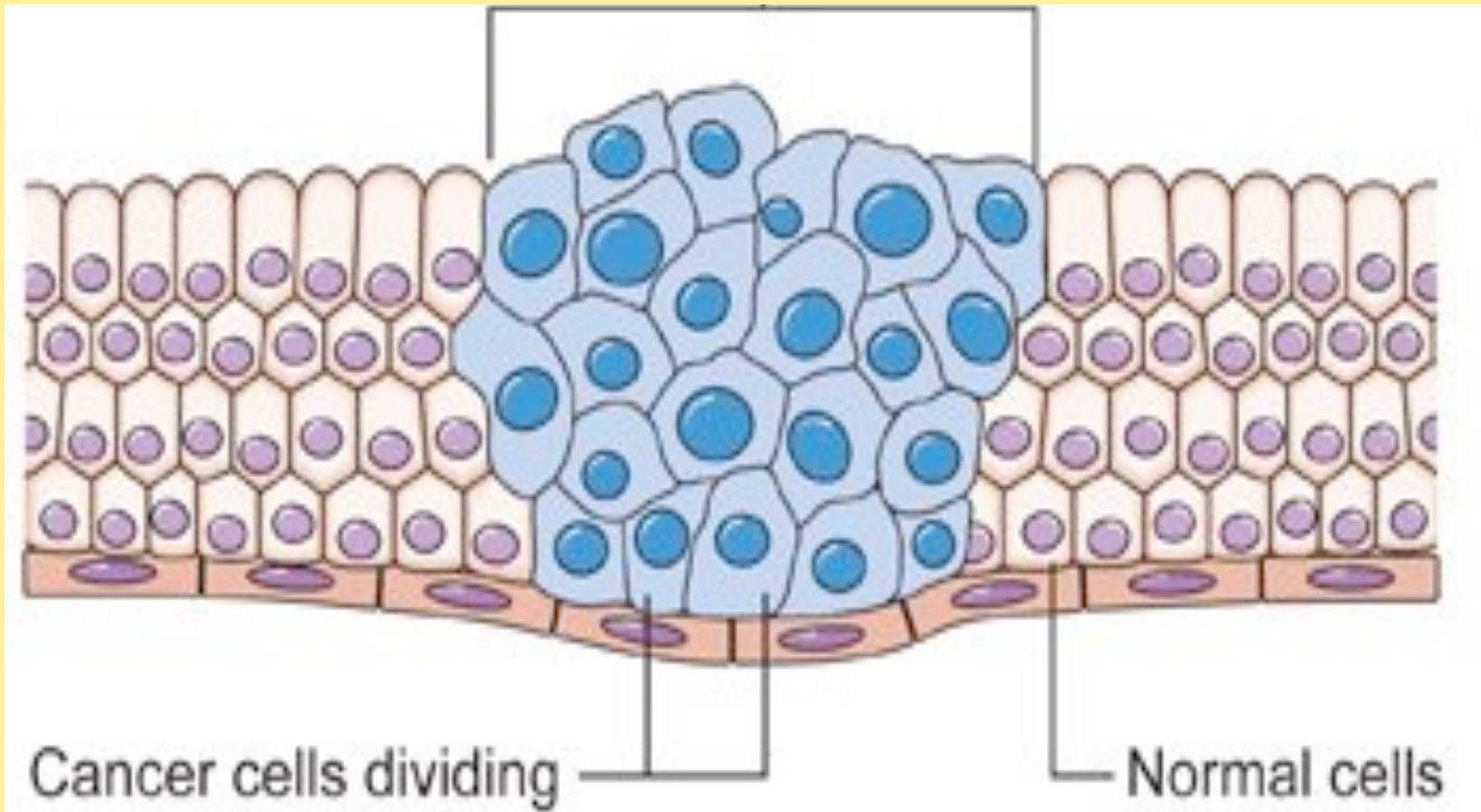
From evolution at lower levels, ecosystem structure and function emerge

- To some extent, there is coevolution, at multiple levels, to the mutual benefit of host and microbiota
- To some extent, there is self-organization, at multiple levels, sometimes to the mutual benefit of host and microbiota
- To some extent, coevolution and self-organization can be destructive to the host
- That applies as well, though less so, to our own cells (cancer is an example)

Coevolution and self-organization: H.pylori and humans

- Increased rates of stomach cancer with H.pylori
- Decreased rates of GERD and esophageal cancer
- Other costs and benefits

Tumor growth



Tumors rely on public goods as well: Selecting for cheaters to fight cancer, with



[http://www.cienciahoje.pt/
index.php?oid](http://www.cienciahoje.pt/index.php?oid)

David Dingli



[http://sweet.ua.pt/sdorogov/
photos-networkers.html](http://sweet.ua.pt/sdorogov/photos-networkers.html)

Jorge Pacheco



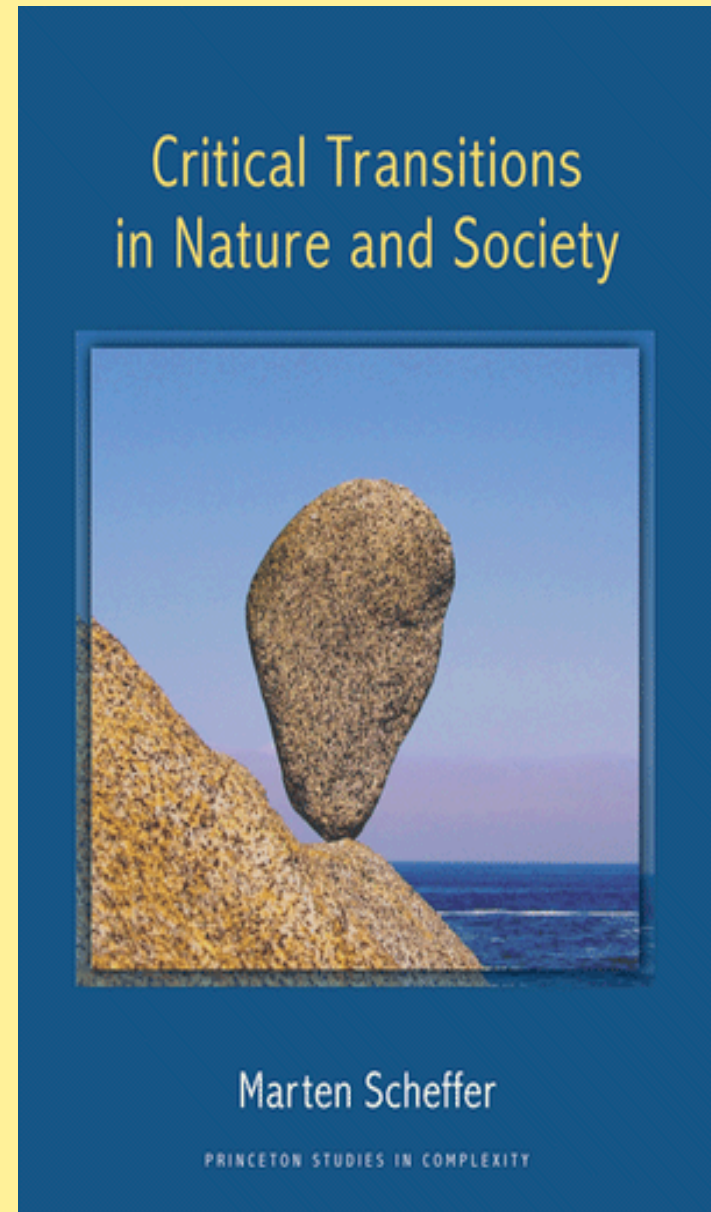
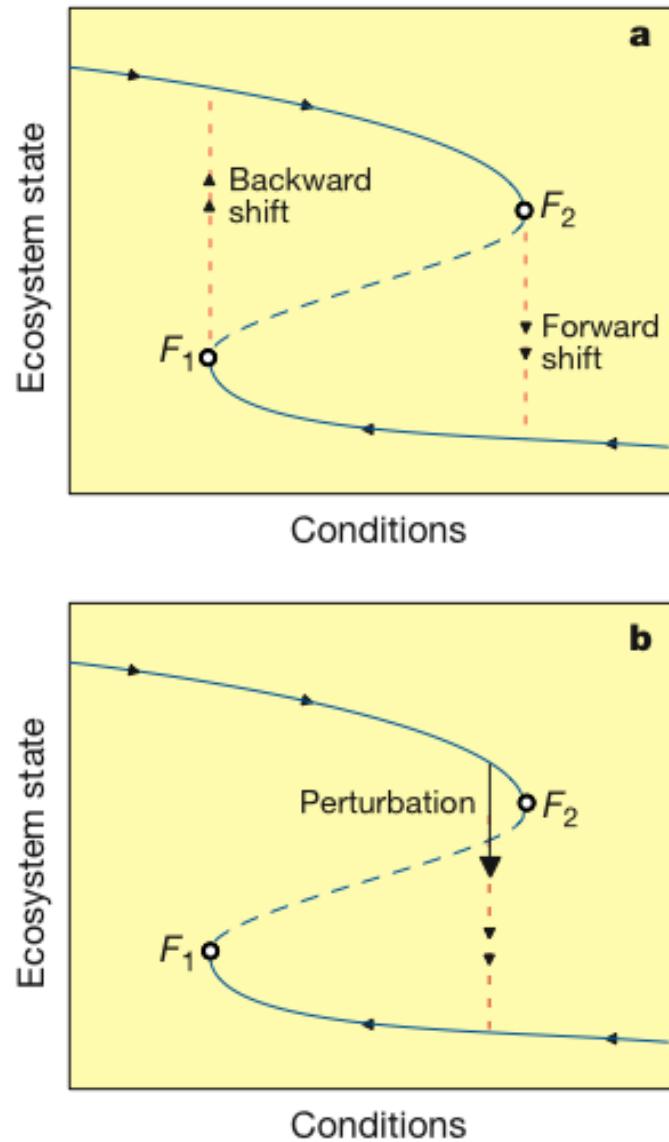
[http://www.
the-scientist.com/](http://www.the-scientist.com/)

Corina Tarnita

Topics of interest

- Temporal patterning
- **Alternative stable states**
- Spatial patterns
- Coupling space and time

Alternative states and critical transitions



REVIEWS

Early-warning signals for critical transitions

Marten Scheffer¹, Jordi Bascompte², William A. Brock³, Victor Brovkin⁵, Stephen R. Carpenter⁴, Vasilis Dakos¹, Hermann Held⁶, Egbert H. van Nes¹, Max Rietkerk⁷ & George Sugihara⁸

Complex dynamical systems, ranging from ecosystems to financial markets and the climate, can have tipping points at which a sudden shift to a contrasting dynamical regime may occur. Although predicting such critical points before they are reached is extremely difficult, work in different scientific fields is now suggesting the existence of generic early-warning signals that may indicate for a wide class of systems if a critical threshold is approaching.

It is becoming increasingly clear that many complex systems have critical thresholds—so-called tipping points—at which the system shifts abruptly from one state to another. In medicine, we have spontaneous systemic failures such as asthma attacks¹ or epileptic seizures^{2,3}; in global finance, there is concern about systemic market crashes^{4,5}; in the Earth system, abrupt shifts in ocean circulation or climate may occur⁶; and catastrophic shifts in rangelands, fish populations or wildlife populations may threaten ecosystem services^{7,8}.

It is notably hard to predict such critical transitions, because the state of the system may show little change before the tipping point is reached. Also, models of complex systems are usually not accurate enough to predict reliably where critical thresholds may occur. Interestingly, though, it now appears that certain generic symptoms

considered to capture the essence of shifts at tipping points in a wide range of natural systems ranging from cell signalling pathways¹⁴ to ecosystems^{7,15} and the climate⁶. At fold bifurcation points (F_1 and F_2 , Box 1), the dominant eigenvalue characterizing the rates of change around the equilibrium becomes zero. This implies that as the system approaches such critical points, it becomes increasingly slow in recovering from small perturbations (Fig. 1). It can be proven that this phenomenon will occur in any continuous model approaching a fold bifurcation¹². Moreover, analysis of various models shows that such slowing down typically starts far from the bifurcation point, and that recovery rates decrease smoothly to zero as the critical point is approached¹⁶. Box 2 describes a simple example illustrating this. ²⁵

The most straightforward implication of critical slowing down is

Generic Indicators for Loss of Resilience Before a Tipping Point Leading to Population Collapse

Lei Dai,^{1*} Daan Vorselen,^{2*} Kirill S. Korolev,¹ Jeff Gore^{1†}

Theory predicts that the approach of catastrophic thresholds in natural systems (e.g., ecosystems, the climate) may result in an increasingly slow recovery from small perturbations, a phenomenon called critical slowing down. We used replicate laboratory populations of the budding yeast *Saccharomyces cerevisiae* for direct observation of critical slowing down before population collapse. We mapped the bifurcation diagram experimentally and found that the populations became more vulnerable to disturbance closer to the tipping point. Fluctuations of population density increased in size and duration near the tipping point, in agreement with the theory. Our results suggest that indicators of critical slowing down can provide advance warning of catastrophic thresholds and loss of resilience in a variety of dynamical systems.

Natural populations can experience catastrophic collapse in response to small changes in environmental conditions, and recovery after such a collapse can be exceedingly difficult (1, 2). Tipping points marking population collapse and other catastrophic thresholds in natural systems may correspond to

a fold bifurcation in the dynamics of the system (3–6). Even before crossing a tipping point, a system may become increasingly vulnerable to perturbations due to loss of “ecological resilience” (i.e., size of the basin of attraction) (4, 7). There has been a growing interest in the possibility of using generic statistical indicators, primarily based on critical slowing down, as early warning signals of impending tipping points in various systems (8–16). In dynamical systems theory, critical slowing down refers to the slow recovery from small perturbations in the vicinity of bifurcations (8, 17). As the system approaches a bifurcation, the time needed to recover from

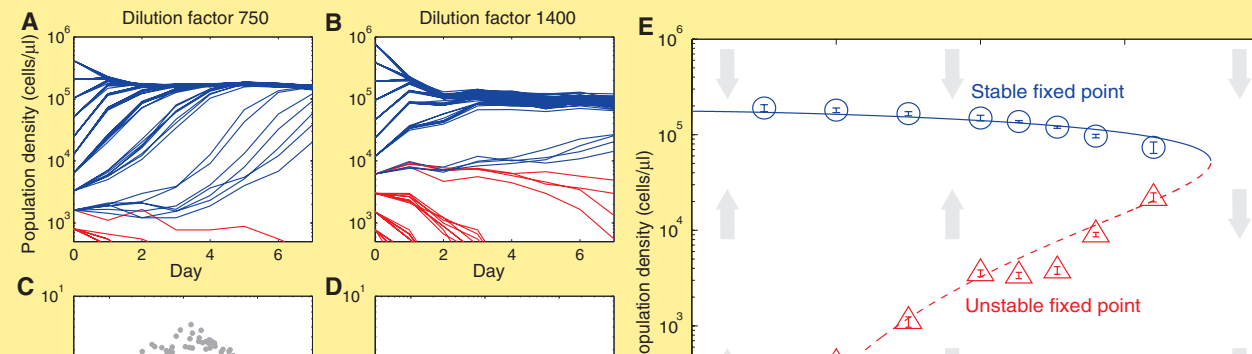
perturbations becomes longer (11, 18) and hence the system becomes more correlated with its past, leading to an increase in autocorrelation. In addition, the perturbations accumulate and result in an increase in the size of the fluctuations (10). Other statistical indicators, such as skewness, have also been proposed as warning signals because of the change in stability landscape before bifurcations (19).

An increase in variance or autocorrelation of fluctuations of the system has been observed to precede a regime shift in a lake ecosystem (13), abrupt climate change (9, 14), transitions in coordinated biological motion (20), and the cascading failure of the North America Western Interconnection power system in 1996 (21); these findings suggest the existence of bifurcation-type tipping points and associated critical dynamics in many systems. Because the complex dynamics underlying these systems makes it difficult to determine the nature of the transitions, studies in controlled systems are required. Recent studies in laboratory water fleas (12) and cyanobacterial monoculture (16) measured the warning signals under controlled conditions. However, the transition in the deteriorating-environment experiment of water fleas, probably due to a transcritical bifurcation, was noncatastrophic (fig. S1). Moreover, in both systems the tipping points were not determined directly by experiments. Thus, neither study constituted a demonstration of early warning signals before an experimentally mapped fold bifurcation in a live system. Such a study can also test directly the possibility of using critical slowing down to indicate loss of ecological

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*These authors contributed equally to this work.

†To whom correspondence should be addressed. E-mail: gore@mit.edu

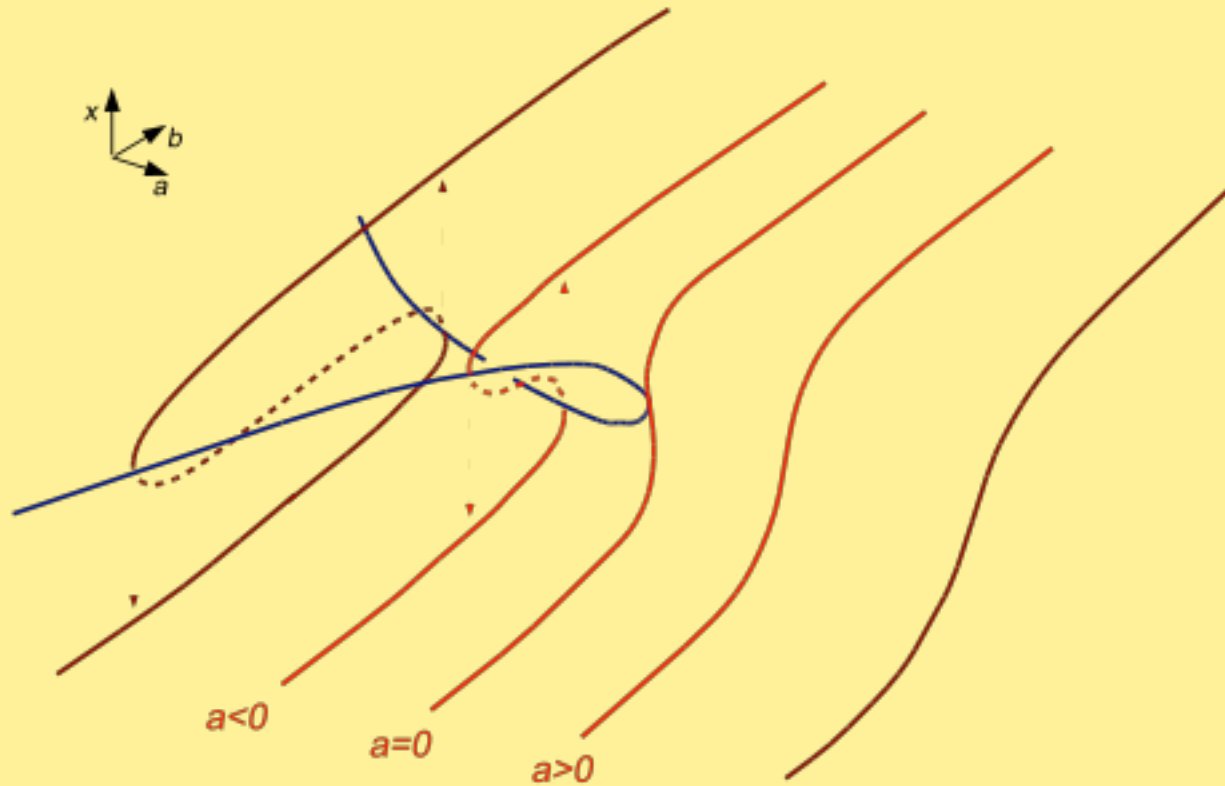


Caution is needed...mechanisms need to be identified



Thom

Structural
Stability and
Morphogenesis



http://en.wikipedia.org/wiki/Catastrophe_theory
http://en.wikipedia.org/wiki/Ren%C3%A9_Thom

Theoretical questions

- Are there alternative stable states in microbiome ecosystems?
- Can early application of antibiotics have a permanent or nearly permanent effect on community dynamics?
- Even if the effects of early application are transient with regard to community composition, can there be long-lasting ecosystem effects, e.g. on obesity?

Topics of interest

- Temporal patterning
- Alternative stable states
- Spatial patterns
- Coupling space and time

Simons Grant

- ***Account for heterogeneity in the spatial distributions of consumers and resources, and the ability of organisms to actively exploit this heterogeneity***
 - Application of foraging theory from ecology
 - Complicated by problem of detection and uncertainty

A New Framework for Ecological Kinetics in Natural Environments

////////////////////

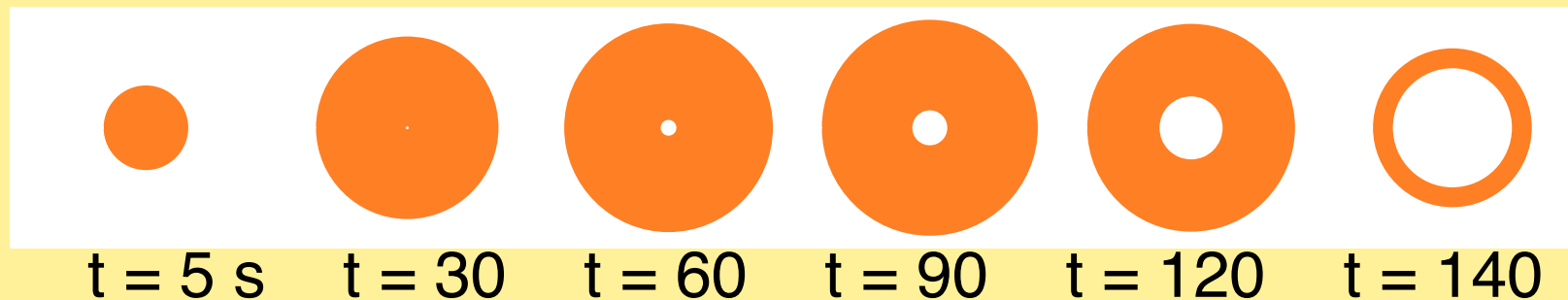
Keller-Segel Model

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

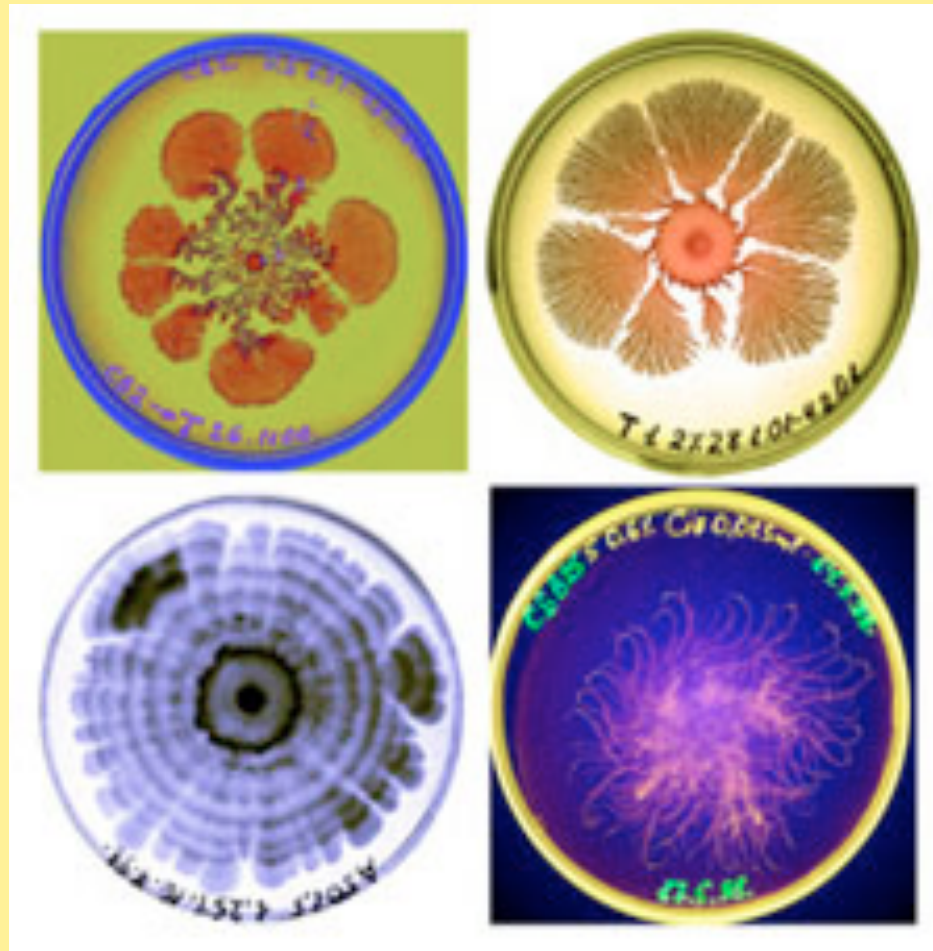
$$\frac{\partial c}{\partial t} = \underbrace{D_c \nabla^2 c}_{\text{Chemical diffusion}} - \underbrace{n \delta(c)}_{\text{Chemical degradation by cells}}$$

Simons grant: predict dynamic region where cells can do chemotaxis from first principles of sensory noise:

900 μm

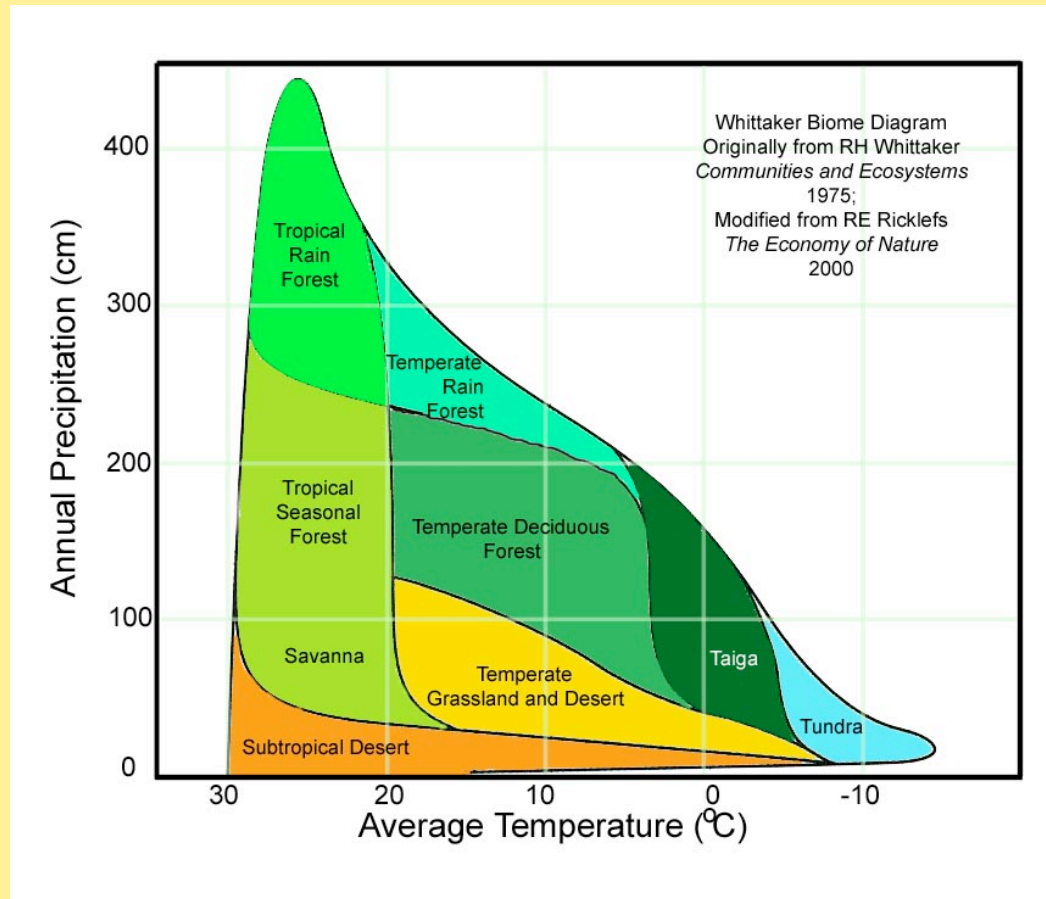


Spatial patterns emerge from individual interactions in microbial communities



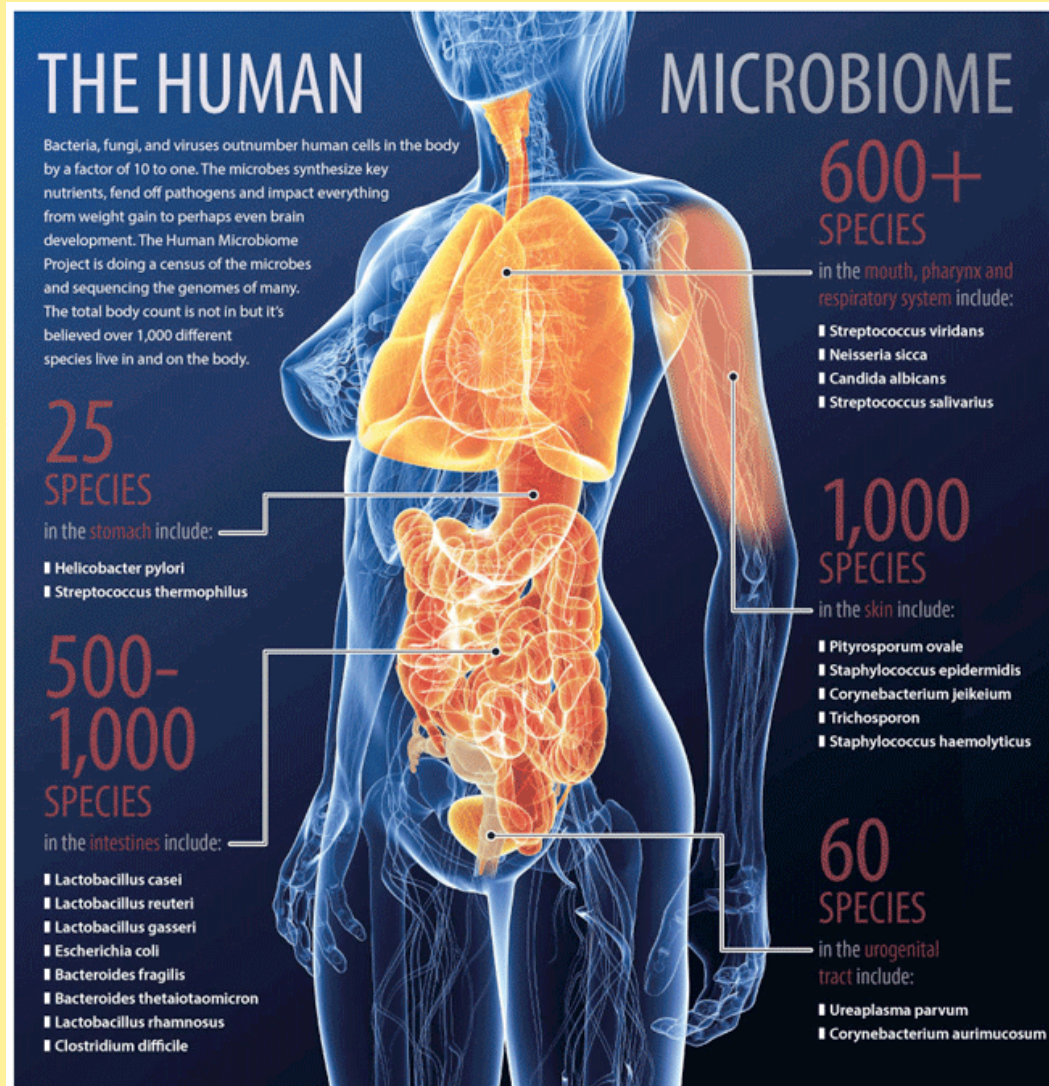
Ben-Jacob and Levine

In general, environment is a primary determinant of ecological organization



We need this for microbiome....
at several levels

Communities by environment: Temperature and moisture?



SOURCES: NATIONAL INSTITUTES OF HEALTH, SCIENTIFIC AMERICAN; HUMAN MICROBIOME PROJECT

Dean Tweed • POSTMEDIA NEWS / IMAGE: Fotolia

Geographical patterns in the human microbiome

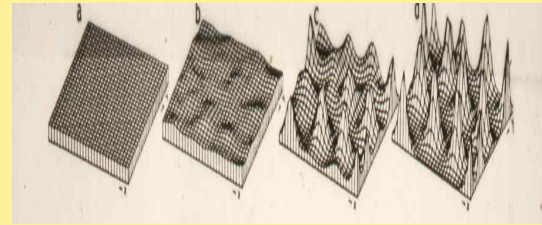
Suzuki and Worobey, *Biology Letters*, 2014

Downloaded from <http://rsbl.royalsocietypublishing.org/> on May 26, 2016



Figure 1. Distribution map of human populations used in this study. Pie chart indicates the relative abundance of two bacterial phyla: Firmicutes (dark grey) and Bacteroidetes (light grey). The numbers indicate Map ID (see table 1).

Turing instabilities:



Meinhardt



Alan
Turing
(1912-1
954)

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

uniform states can become unstable if

D_v/D_u is above some threshold.

Do such mechanisms underlie spatial patterns in ecology?

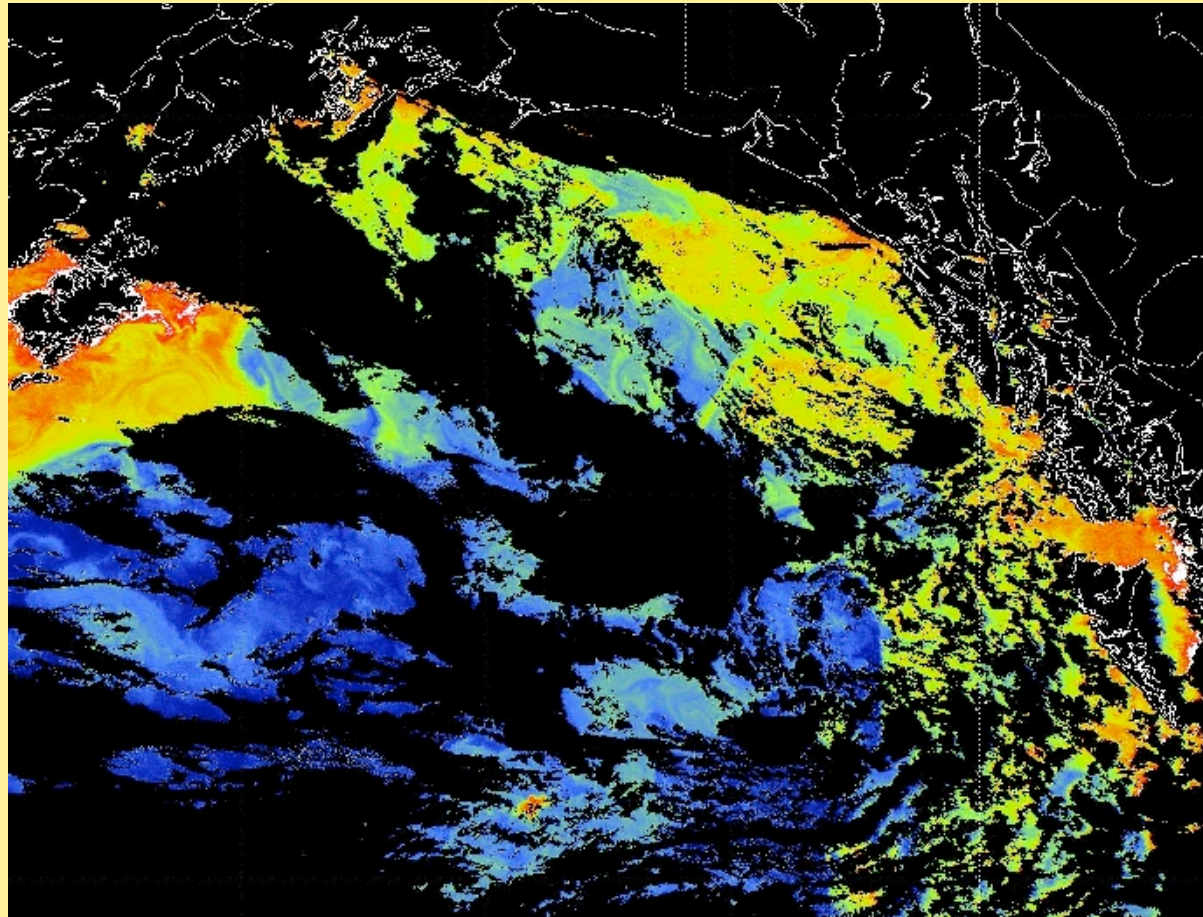


Ehud Meron

<http://geoblog.weebly.com/environmental-sciences-blog/-change>



Plankton are patchy on almost every scale

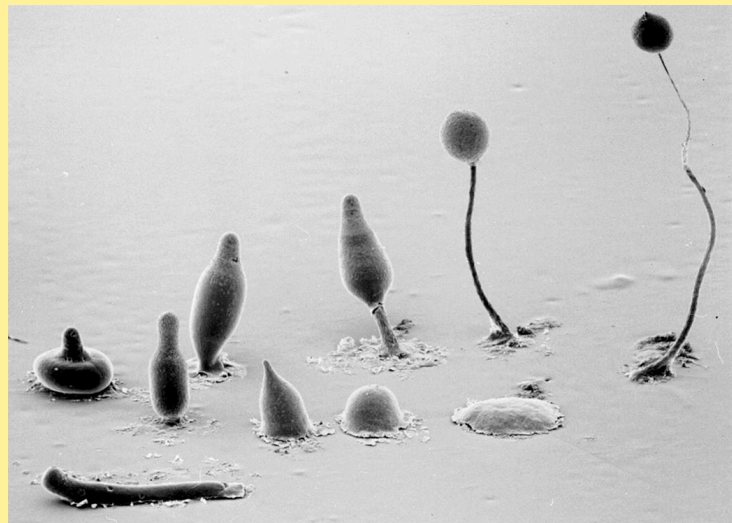


Zooplankton don't move randomly,
but aggregate



Features of interest

- Emergence and scaling
- Robustness
- Consensus and collective motion:
mathematical approaches



ncbi.nlm
.nih.gov

Lagrangian-Eulerian connections



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

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

Random Directed Grouping Arrayal



Author's personal copy

Ecosystems
DOI: 10.1007/s10021-017-0114-3

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20TH ANNIVERSARY PAPER

Marine Ecosystems as Complex Adaptive Systems: Emergent Patterns, Critical Transitions, and Public Goods

George I. Hagstrom* and Simon A. Levin

Ecology and Evolutionary Biology, Princeton University, Guyot Hall, Princeton, New York 08544, USA

ABSTRACT

Complex adaptive systems provide a unified framework for explaining ecosystem phenomena. In the past 20 years, complex adaptive systems have been sharpened from an abstract concept into a series of tools that can be used to solve concrete problems. These advances have been led by the development of new techniques for coupling ecological and evolutionary dynamics, for integrating dynamics across multiple scales of organization, and for using data to infer the complex interactions among different components of ecological systems. Focusing on the development and usage of these new methods, we discuss how they have led to an improved understanding of three universal features of complex adaptive systems, emergent patterns;

tipping points and critical phenomena; and cooperative behavior. We restrict our attention primarily to marine ecosystems, which provide numerous successful examples of the application of complex adaptive systems. Many of these are currently undergoing dramatic changes due to anthropogenic perturbations, and we take the opportunity to discuss how complex adaptive systems can be used to improve the management of public goods and to better preserve critical ecosystem services.

Key words: complex adaptive systems; public goods; emergent patterns; critical transitions; marine ecosystems; evolution of cooperation; theoretical ecology.

INTRODUCTION

Twenty years ago, as *Ecosystems* was setting out on its path to become one of the leading-edge outlets for

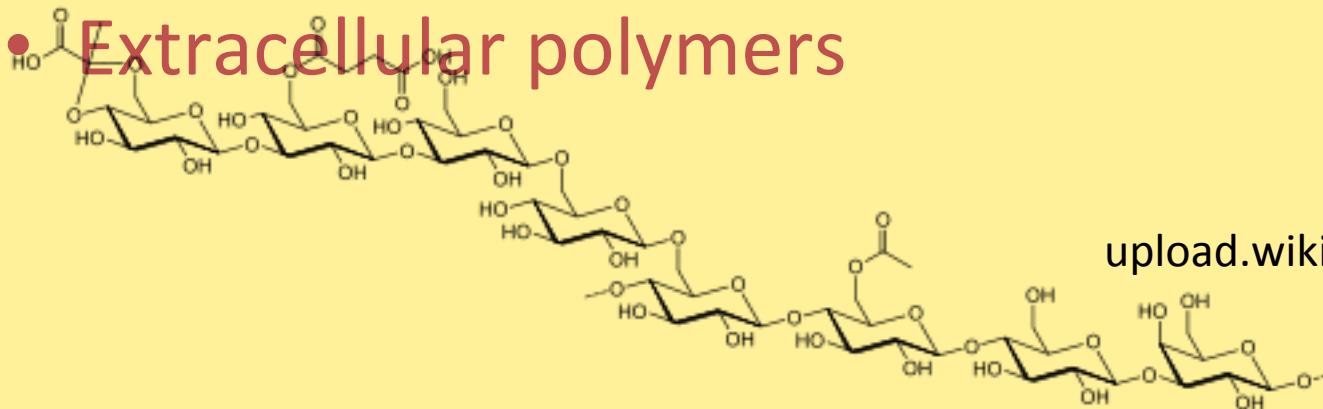
systems (Hartvigsen and others 1998; Levin 1998). Since that time, this perspective has seen impressive development, from both theoretical and applied perspectives (Scheffer and others 2012; Filotas and

Last part of Daniel's talk,
including emergence of ecosystems

Public goods and CPR in ecology

- Information (e.g. in search)
- Nutrient use in nutrient-poor regimes
- Chelation and siderophores
- N fixation
- Antibiotics

- Extracellular polymers



upload.wikimedia.org

Hagstrom-Levin

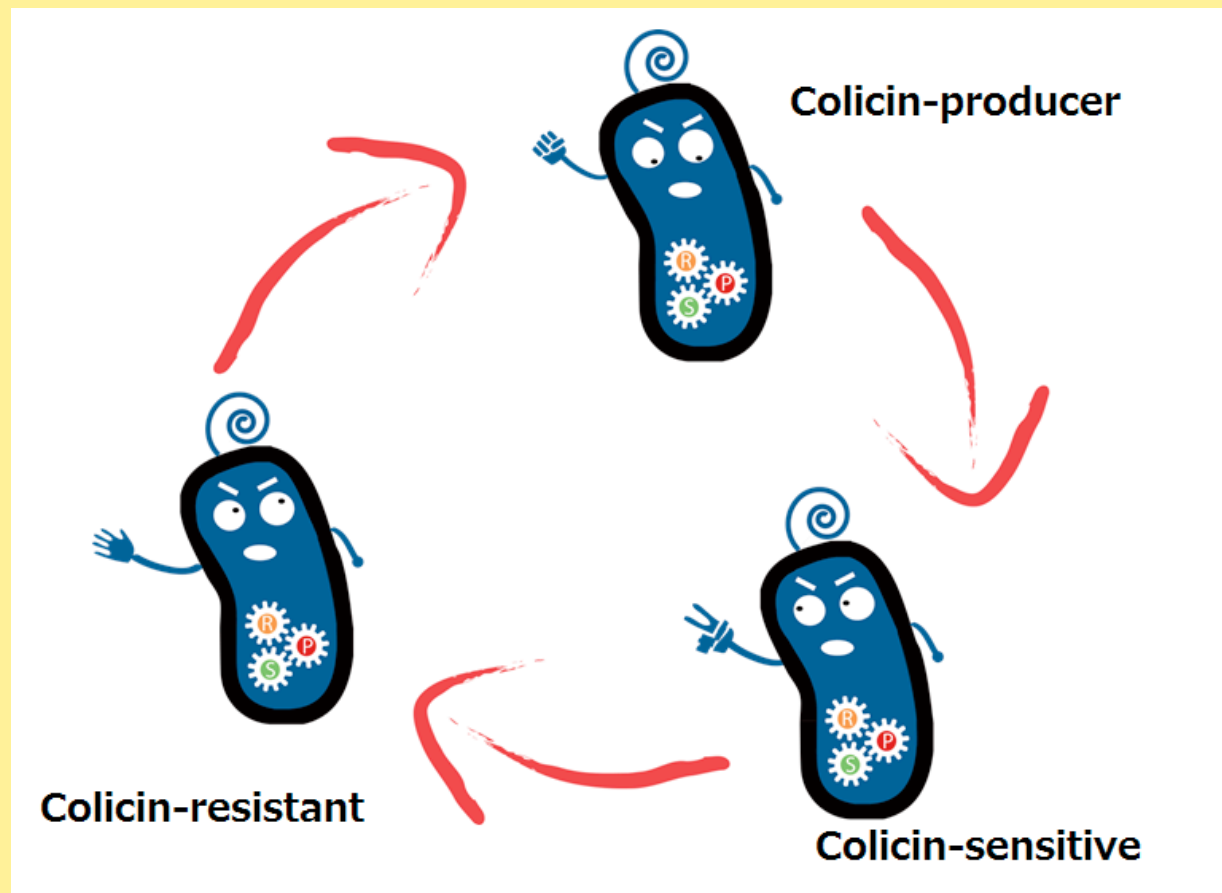
- Syntrophy: Adaptive gene loss common, in relation to the evolution of cooperation and metabolic interdependence”
- “Genes for production of different extracellular enzymes are strongly correlated with each other, suggesting that public goods are produced by a specialized subset of community members (Rakoff-Nahoum and others 2014). “

Hagstrom-Levin

- “Black-Queen hypothesis”:
- “Different lineages...either specialize in public goods production or cheating (Morris and others 2012).”
- Analogous to producers and scroungers

Bacteria also produce toxins, to which they are immune

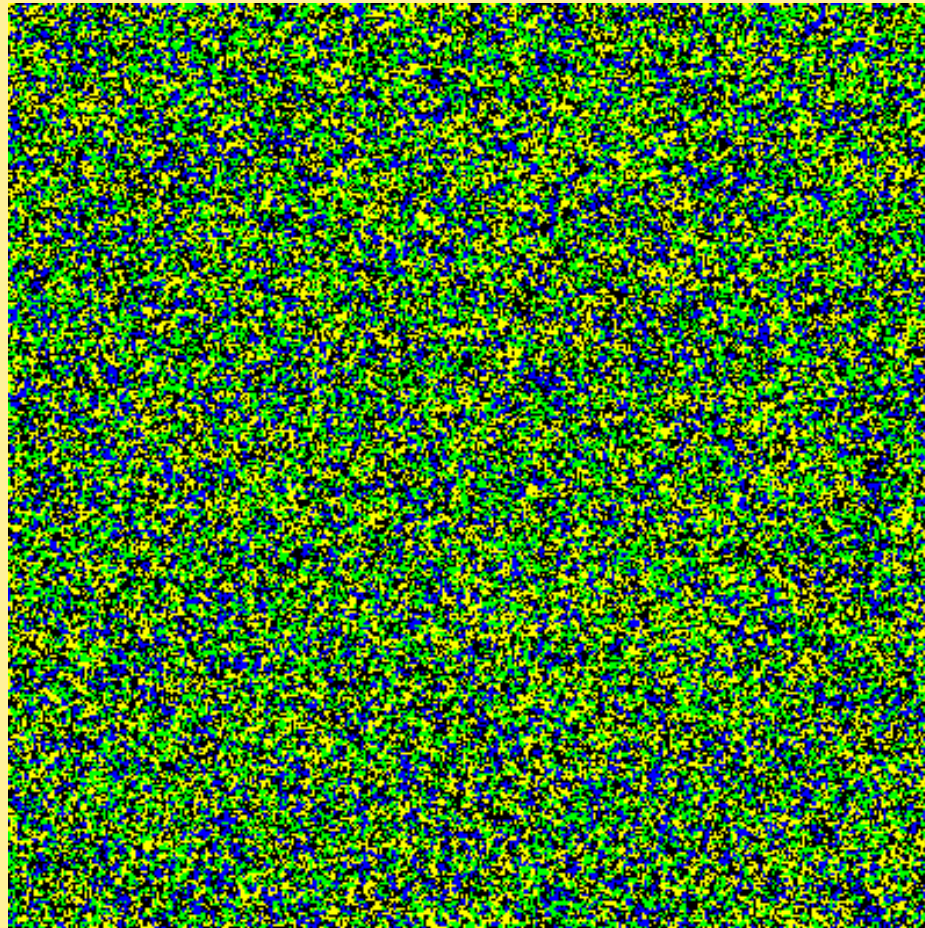
But cheaters arise, raising public goods problem (Chao and B. Levin)



Localization again makes a difference

**The evolution of allelopathy: Competition between
wild type, allelopath and cheater**

Durrett and Levin



Competing interests statement

The authors declare that they have no competing financial interests.

Correspondence and requests for materials should be addressed to M.E.P. (e-mail: matt@gps.caltech.edu).

Local dispersal promotes biodiversity in a real-life game of rock–paper–scissors

Benjamin Kerr*, Margaret A. Riley†, Marcus W. Feldman* & Brendan J. M. Bohannan*

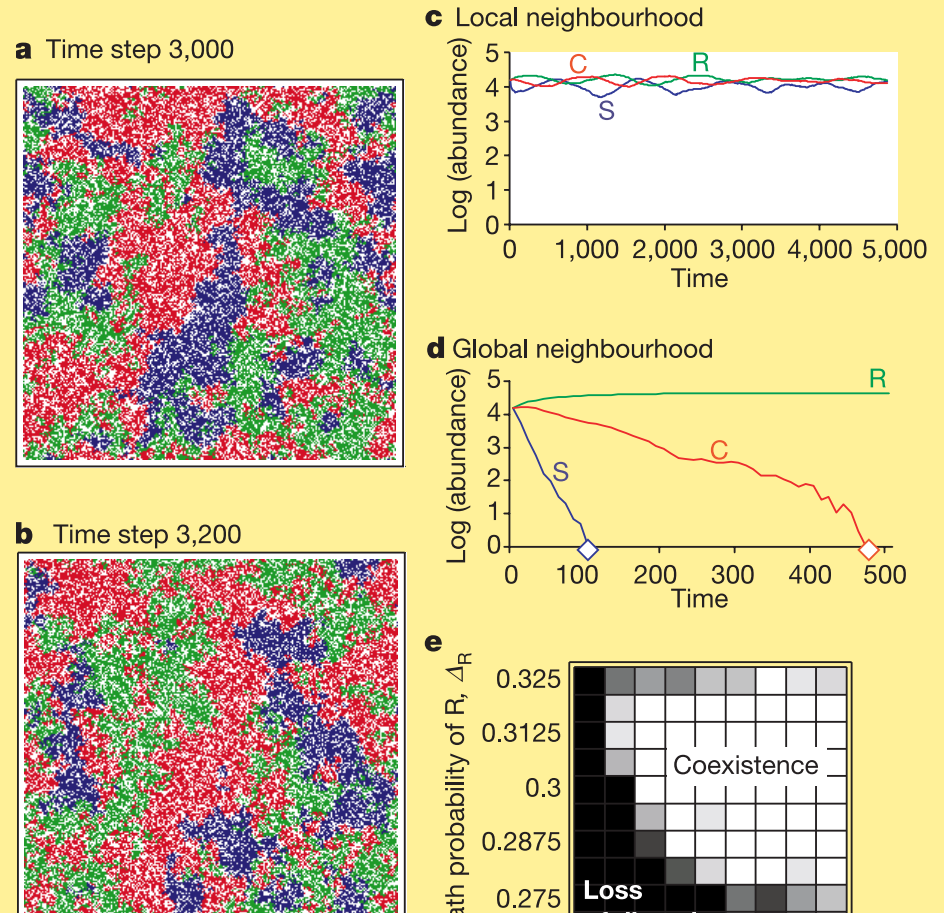
* Department of Biological Sciences, Stanford University, Stanford, California 94305, USA

† Department of Ecology and Evolutionary Biology, Yale University, New Haven, Connecticut 06511, USA

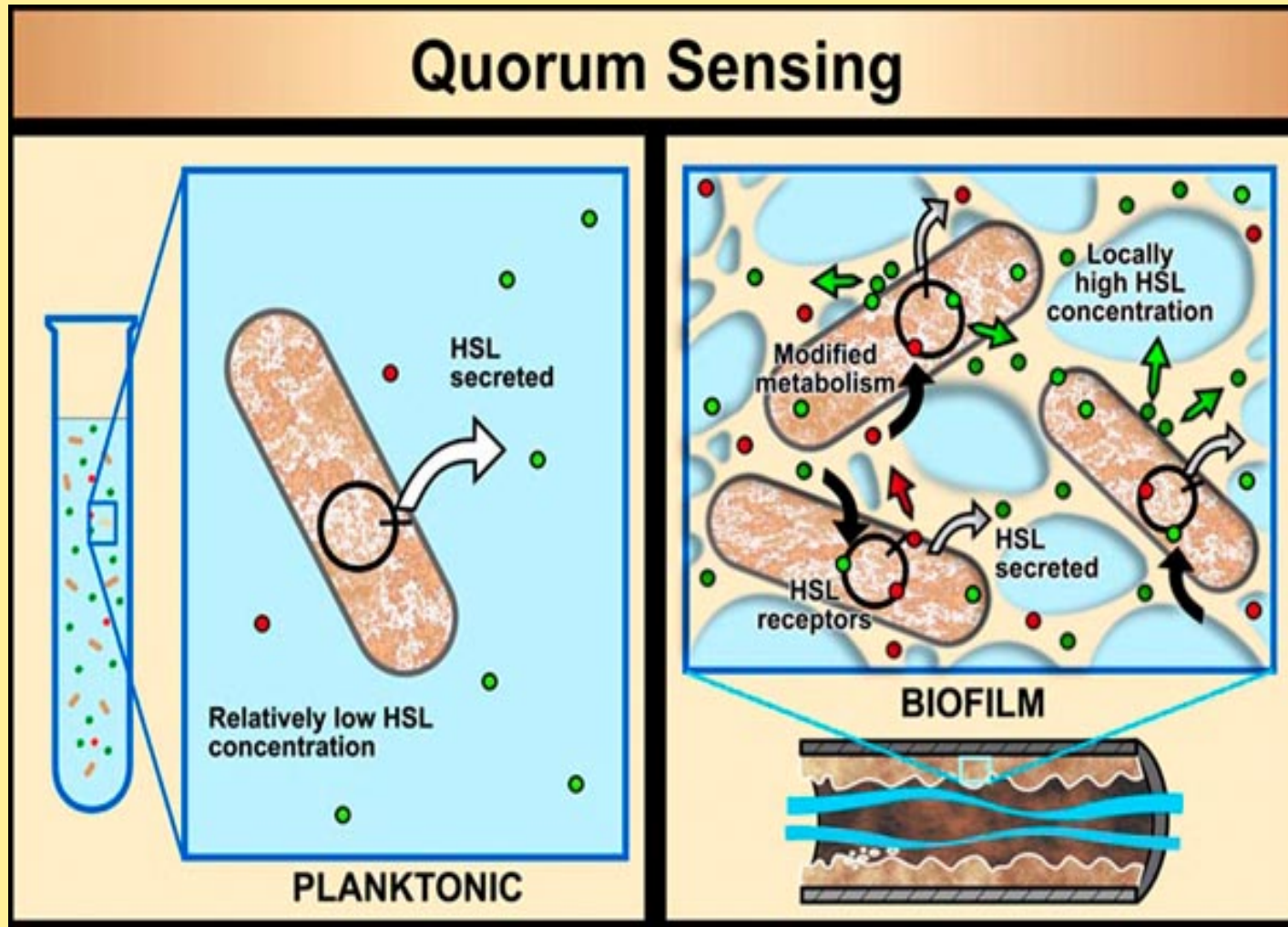
One of the central aims of ecology is to identify mechanisms that maintain biodiversity^{1,2}. Numerous theoretical models have shown that competing species can coexist if ecological processes such as dispersal, movement, and interaction occur over small spatial scales^{1–10}. In particular, this may be the case for non-transitive communities, that is, those without strict competitive hierarchies^{3,6,8,11}. The classic non-transitive system involves a community of three competing species satisfying a relationship

growth-rate advantage) and C can displace S (because C kills S). That is, the C–S–R community satisfies a rock–paper–scissors relationship.

Using a modification of the lattice-based simulation of Durrett and Levin⁶, we theoretically explored the role of the spatial scale of



Bacteria also cooperate: Classic public-goods problem



The Evolution of Quorum Sensing in Bacterial Biofilms

Carey D. Nadell^{1*}, Joao B. Xavier², Simon A. Levin¹, Kevin R. Foster^{2*}

1 Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey, United States of America, **2** Center for Systems Biology, Harvard University, Bauer Laboratory, Cambridge, Massachusetts, United States of America

Bacteria have fascinating and diverse social lives. They display coordinated group behaviors regulated by quorum-sensing systems that detect the density of other bacteria around them. A key example of such group behavior is biofilm formation, in which communities of cells attach to a surface and envelope themselves in secreted polymers. Curiously, after reaching high cell density, some bacterial species activate polymer secretion, whereas others terminate polymer secretion. Here, we investigate this striking variation in the first evolutionary model of quorum sensing in biofilms. We use detailed individual-based simulations to investigate evolutionary competitions between strains that differ in their polymer production and quorum-sensing phenotypes. The benefit of activating polymer secretion at high cell density is relatively straightforward: secretion starts upon biofilm formation, allowing strains to push their lineages into nutrient-rich areas and suffocate neighboring cells. But why use quorum sensing to terminate polymer secretion at high cell density? We find that deactivating polymer production in biofilms can yield an advantage by redirecting resources into growth, but that this advantage occurs only in a limited time window. We predict, therefore, that down-regulation of polymer secretion at high cell density will evolve when it can coincide with dispersal events, but it will be disfavored in long-lived (chronic) biofilms with sustained competition among strains. Our model suggests that the observed variation in quorum-sensing behavior can be linked to the differing requirements of bacteria in chronic versus acute biofilm infections. This is well illustrated by the case of *Vibrio cholerae*, which competes within biofilms by polymer secretion, terminates polymer secretion at high cell density, and induces an acute disease course that ends with mass dispersal from the host. More generally, this work shows that the balance of competition within and among biofilms can be pivotal in the evolution of quorum sensing.

Citation: Nadell CD, Xavier JB, Levin SA, Foster KR (2008) The evolution of quorum sensing in bacterial biofilms. PLoS Biol 6(1): e14. doi:10.1371/journal.pbio.0060014

Introduction

Once perceived as organisms that rarely interact, bacteria are now known to lead highly social lives [1–3]. Central to this sociality is an ability to detect local cell density and thereby coordinate group behaviors [4–6]. This ability, termed *quorum*

depend upon both the species under observation and the experimental conditions [28]. Four studies have emphasized how the potential for competition and conflict among strains of bacteria can shape the evolution of quorum sensing [31–34], but none have addressed biofilm formation. An open challenge for microbiology, therefore, is to disentangle the

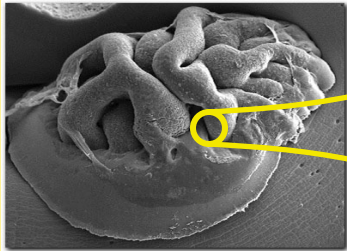
Link between group living and communication

Nadell, Xavier, Levin, Foster

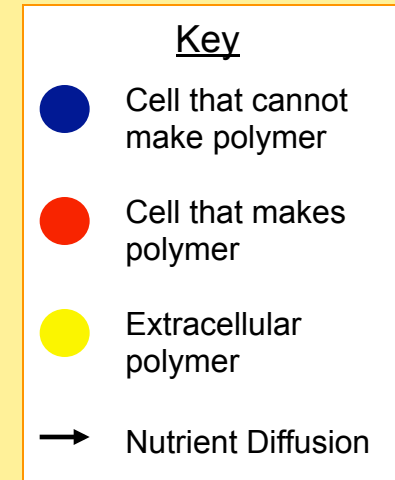
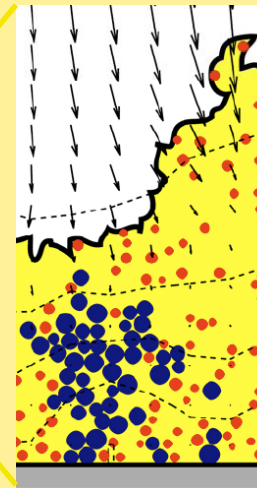
Quorum Sensing

Slime

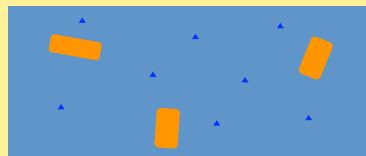
Biofilms



Extracellular Polymers (Slime)



Low cell density



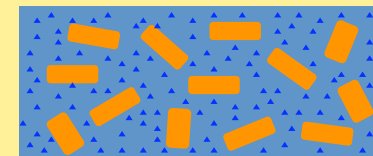
Pseudomonas aeruginosa

Slime OFF

Vibrio cholerae

Slime ON

High cell density



Slime ON

Slime OFF

Trait based models: Biofilm formation and quorum sensing



Constitutive Slime-producer



QS Strain (below quorum)

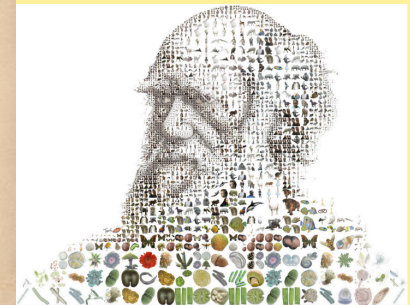
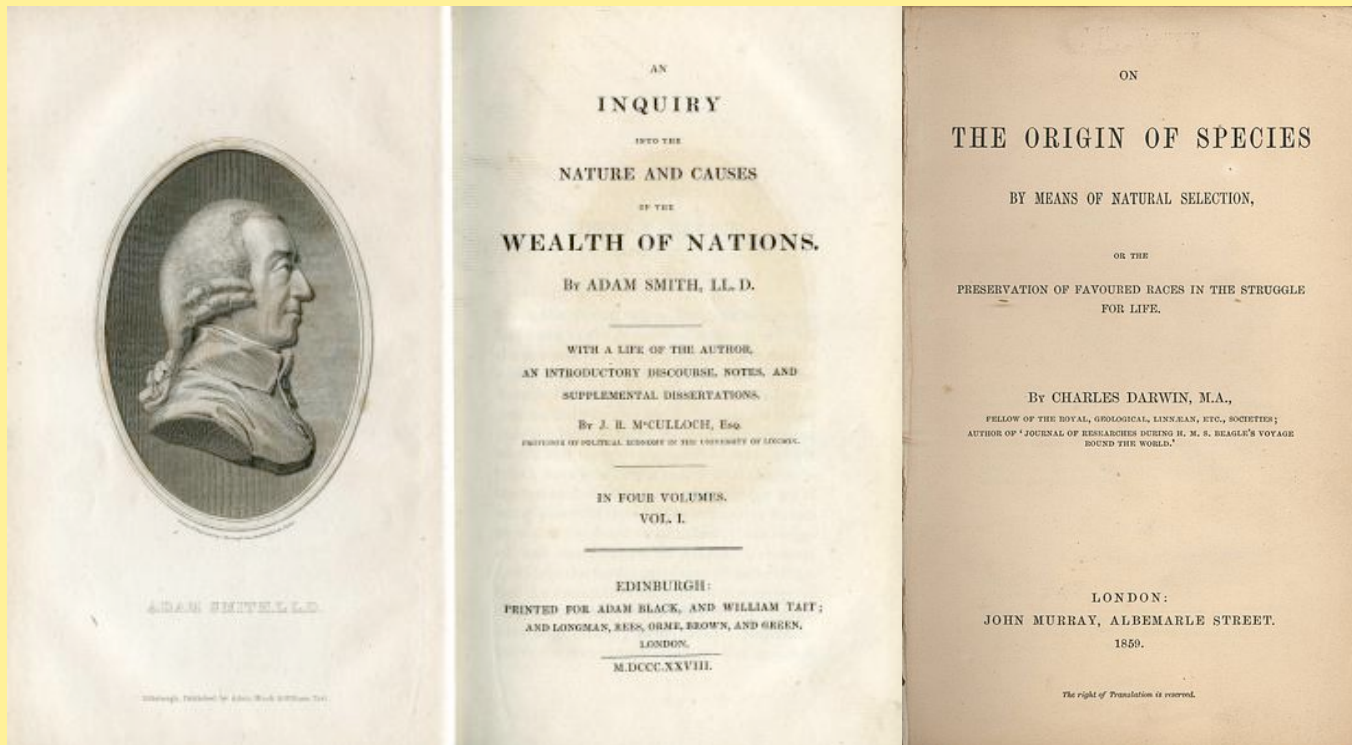


Slime



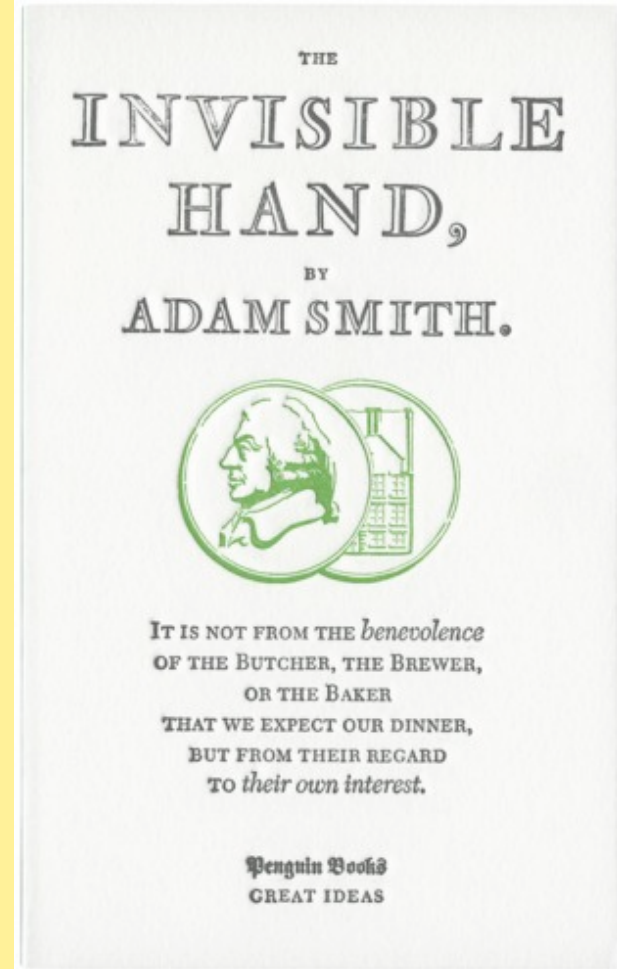
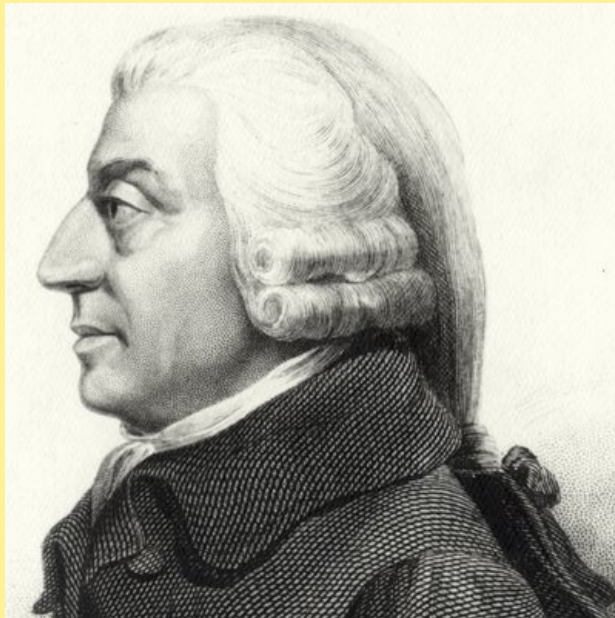
QS Strain (above quorum)

Economic perspectives can inform evolutionary questions, and vice versa



www.neoforumix.com

Adam Smith (1776)

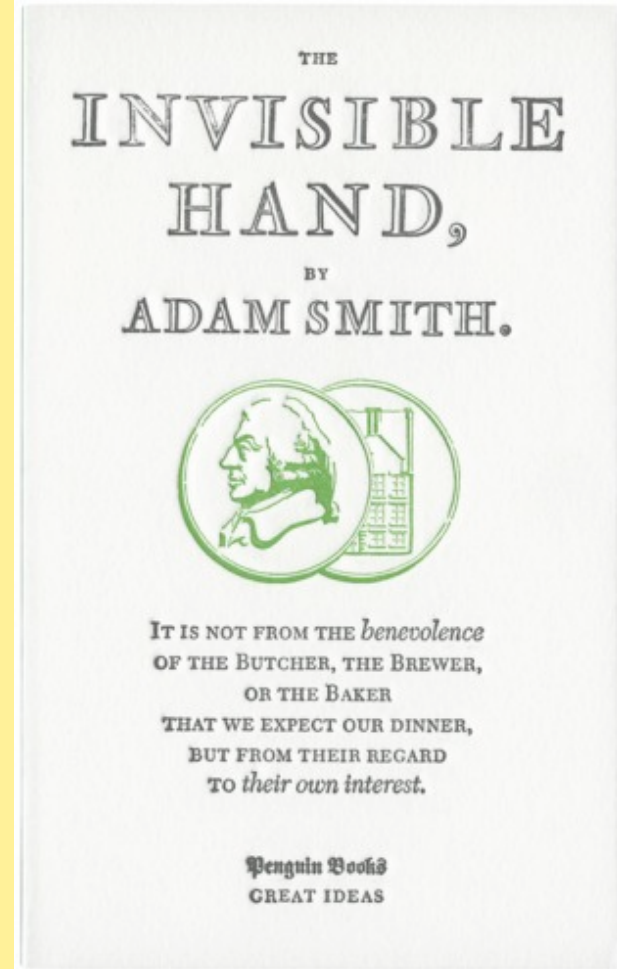
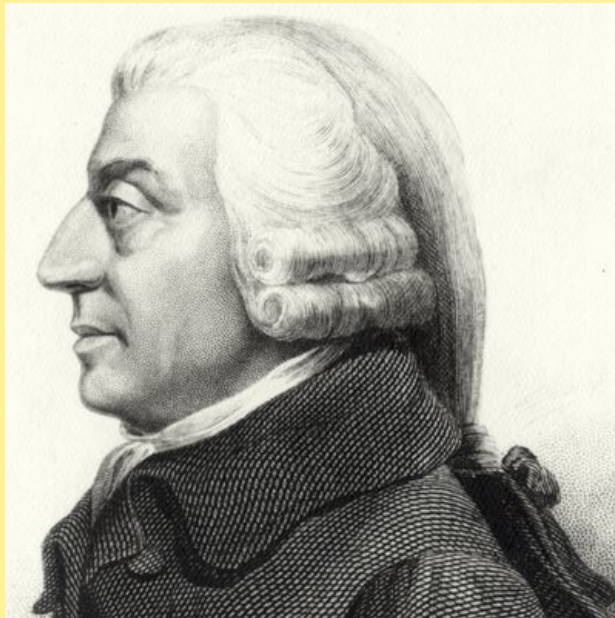


“By pursuing his own interest he frequently promotes that of the society more effectually than when he really intends to promote it.”

The invisible hand does not protect society



Adam Smith (1776)



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How do these considerations apply to microbial ecosystems?

Conclusions

- Collective phenomena and emergence characterize systems, from microbial communities to the biosphere
- Critical transitions occur
- A fundamental challenge is to scale from microscopic to macroscopic
- Consensus formation is a challenge in all systems
- So too is conflict between individuals and collectives
- Methods from mathematics, physics, ecology and evolution can inform and be inspired.