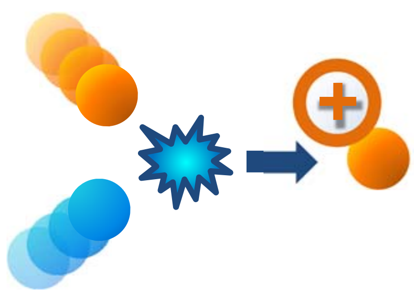
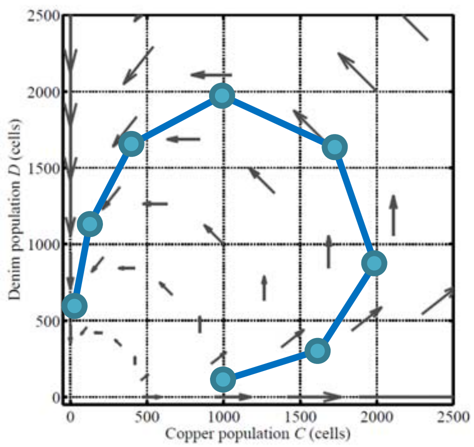
Evolutionary game theory for biologists

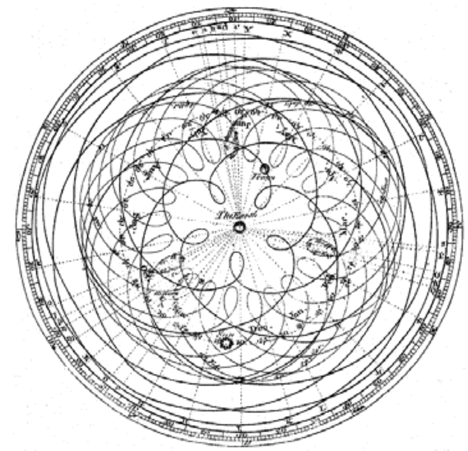
Population dynamics



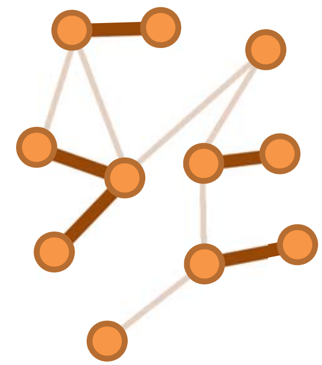
Manual data analysis



Epicycles



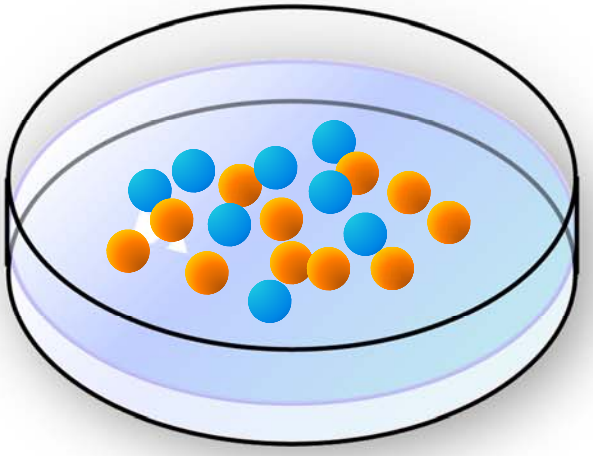
Modularity



David Liao
Analyst, Tlsty Lab, UCSF

2013 August 12
Princeton/Johns Hopkins Game Theory Workshop, Baltimore, MD

Basic model with pairwise interactions



Population dynamics

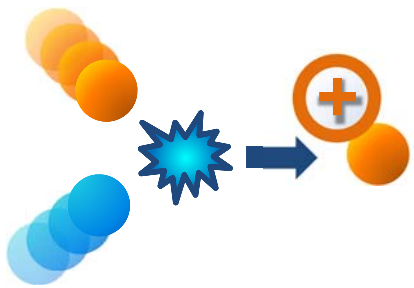
$$\frac{dC}{dt} = (Rp_C + Sp_D)C \qquad p_C = \frac{C}{(C+D)}$$

$$\frac{dD}{dt} = (Tp_C + Pp_D)D \qquad p_D = \frac{D}{(C+D)}$$

Note: Using labels *C*, *D*, *T*, *R*, *P*, and *S* does not, itself, logically imply that this model be a "prisoner's dilemma"

Evolutionary game theory for biologists

Population dynamics



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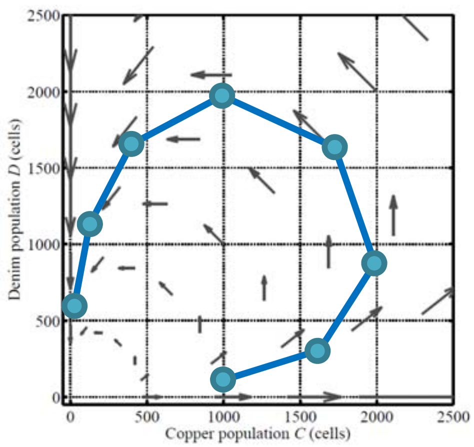

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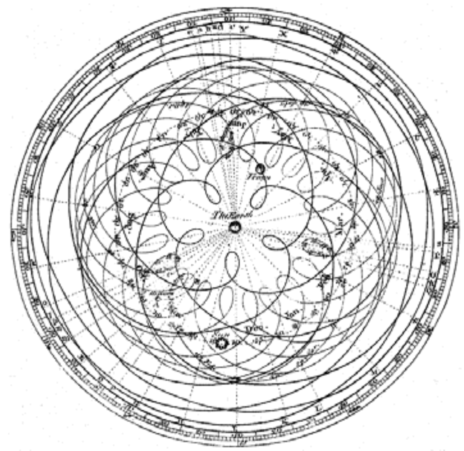

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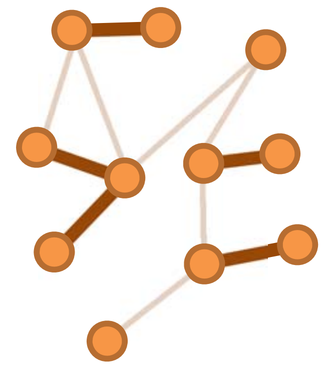

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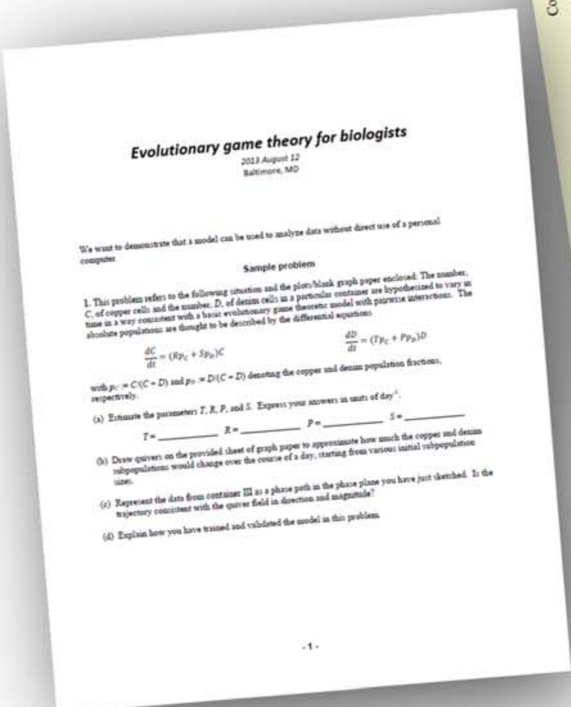
Back-of-the-envelope data analysis



Evolutionary game theory for biologists

2013 August 12

Baltimore, MD

We want to demonstrate that a model can be used to analyze data without direct use of a personal computer.

Sample problem

1. This problem refers to the following situation and the plots/blank graph paper enclosed: The number, C, of copper cells and the number, D, of denim cells in a particular container are hypothesized to vary in time in a way consistent with a basic evolutionary game theoretic model with pairwise interactions. The absolute populations are thought to be described by the differential equations

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with $p_C := C/(C+D)$ and $p_D := D/(C+D)$ denoting the copper and denim population fractions, respectively.

(a) Estimate the parameters T, R, P, and S. Express your answers in units of day^{-1}.

T = ________ R = ________ P = ________ S = ________

(b) Draw quivers on the provided sheet of graph paper to approximate how much the copper and denim subpopulations would change over the course of a day, starting from various initial subpopulation sizes.

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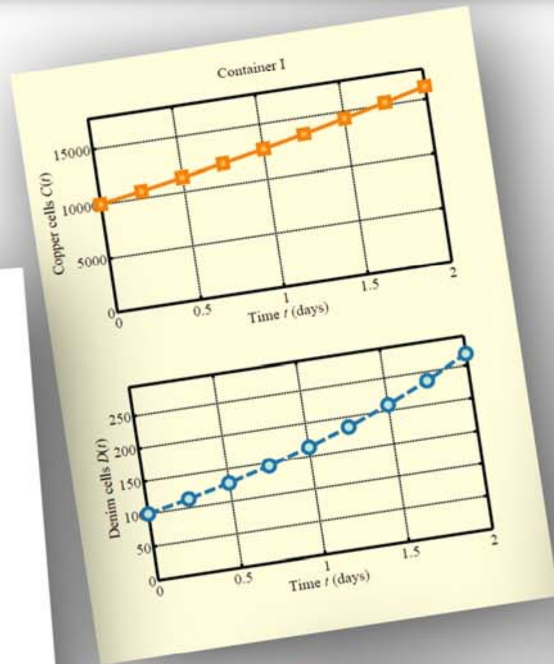
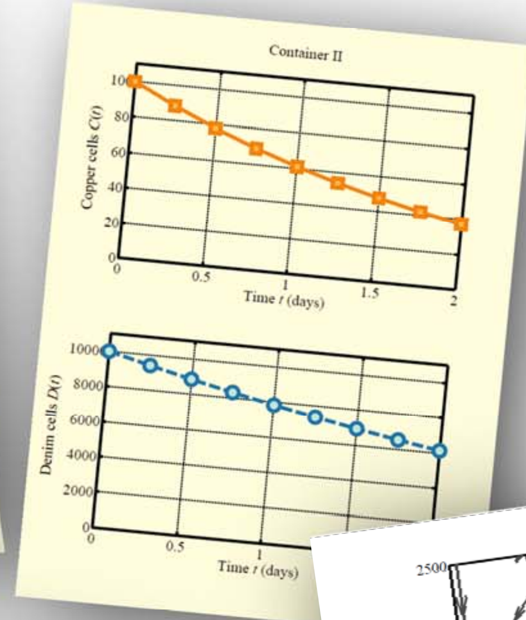
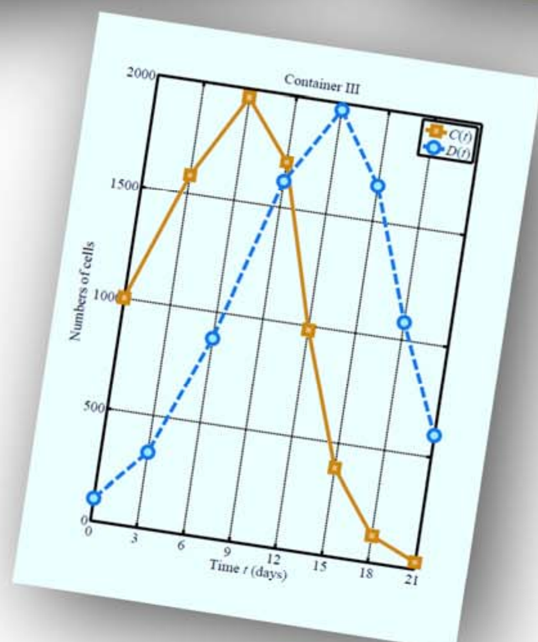
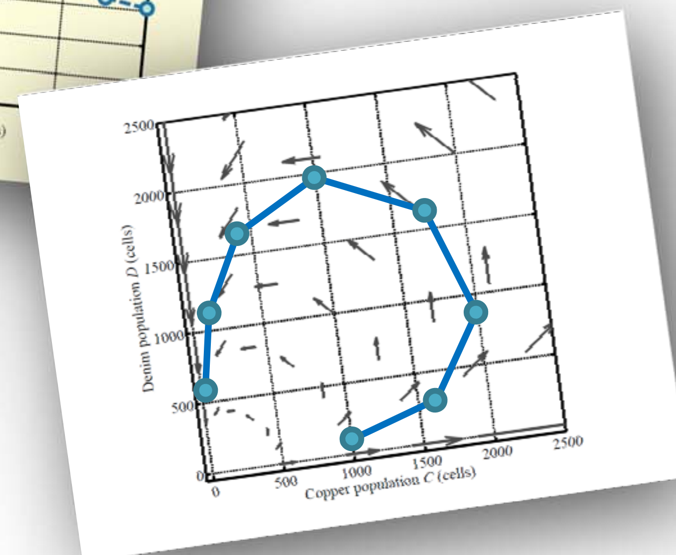








Estimating rate coefficient from initial slope

(a) Estimate the parameters *T*, *R*, *P*, and *S*. Express your answers in units of day^{-1}.

T =   *R* =   *P* =   *S* =

$$\frac{dC}{dt} = (Rp_C + Sp_D)C$$

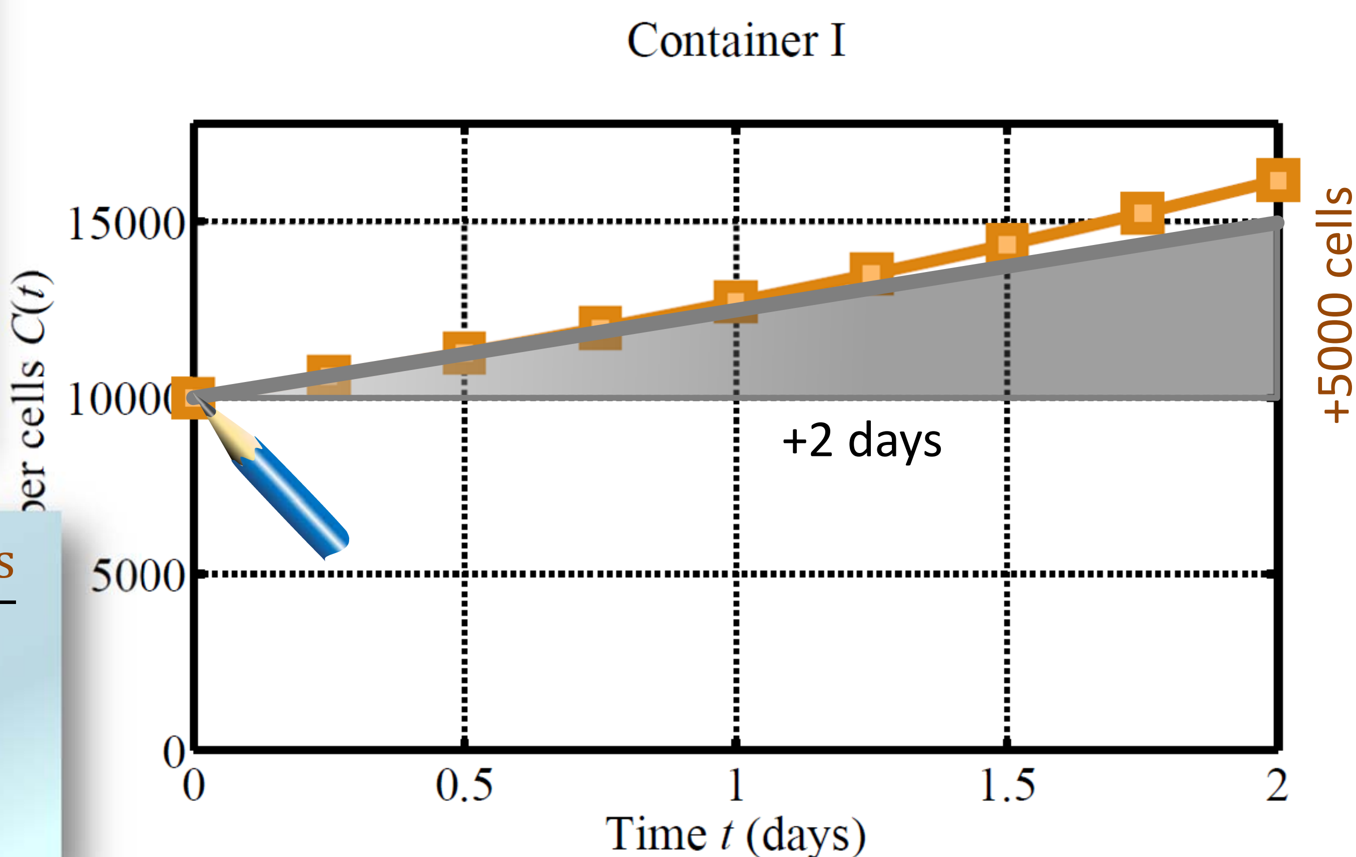
$$\frac{dC}{dt} \approx RC \quad \text{(if } p_C \sim 1\text{)}$$

$$\frac{1}{C}\frac{\Delta C}{\Delta t} \approx R$$

$$R \approx \frac{1}{10{,}000 \text{ cells}} \frac{+5000 \text{ cells}}{+2 \text{ days}}$$

$$= \frac{1}{4} \text{day}^{-1}$$

Seeded 10,000 copper cells and only 100 denim cells



Using a model to fill in a phase plane

(b) Draw quivers on the provided sheet of graph paper to approximate how much the copper and denim subpopulations would change over the course of a day, starting from various initial subpopulation sizes.

Start from $C = D = 2000$, find population change over a day?

$$\Delta C \approx \frac{dC}{dt}\Delta t \qquad \frac{dC}{dt} = (Rp_C + Sp_D)C$$

$$\Delta C \approx [(0.25\ \text{day}^{-1})(0.5) + (-0.5\ \text{day}^{-1})(0.5)](2000\ \text{cells})(1\ \text{day})$$

$$\Delta C \approx -250\ \text{cells}$$

$$\Delta D \approx \frac{dD}{dt}\Delta t \qquad \frac{dD}{dt} = (Tp_C + Pp_D)D$$

$$\Delta D \approx [(0.5\ \text{day}^{-1})(0.5) + (-0.25\ \text{day}^{-1})(0.5)](2000\ \text{cells})(1\ \text{day})$$

$$\Delta D \approx +250\ \text{cells}$$

$T = 0.5\ \text{day}^{-1}$; $R = 0.25\ \text{day}^{-1}$;
$P = -0.25\ \text{day}^{-1}$; $S = -0.5\ \text{day}^{-1}$

Using a model to fill in a phase plane

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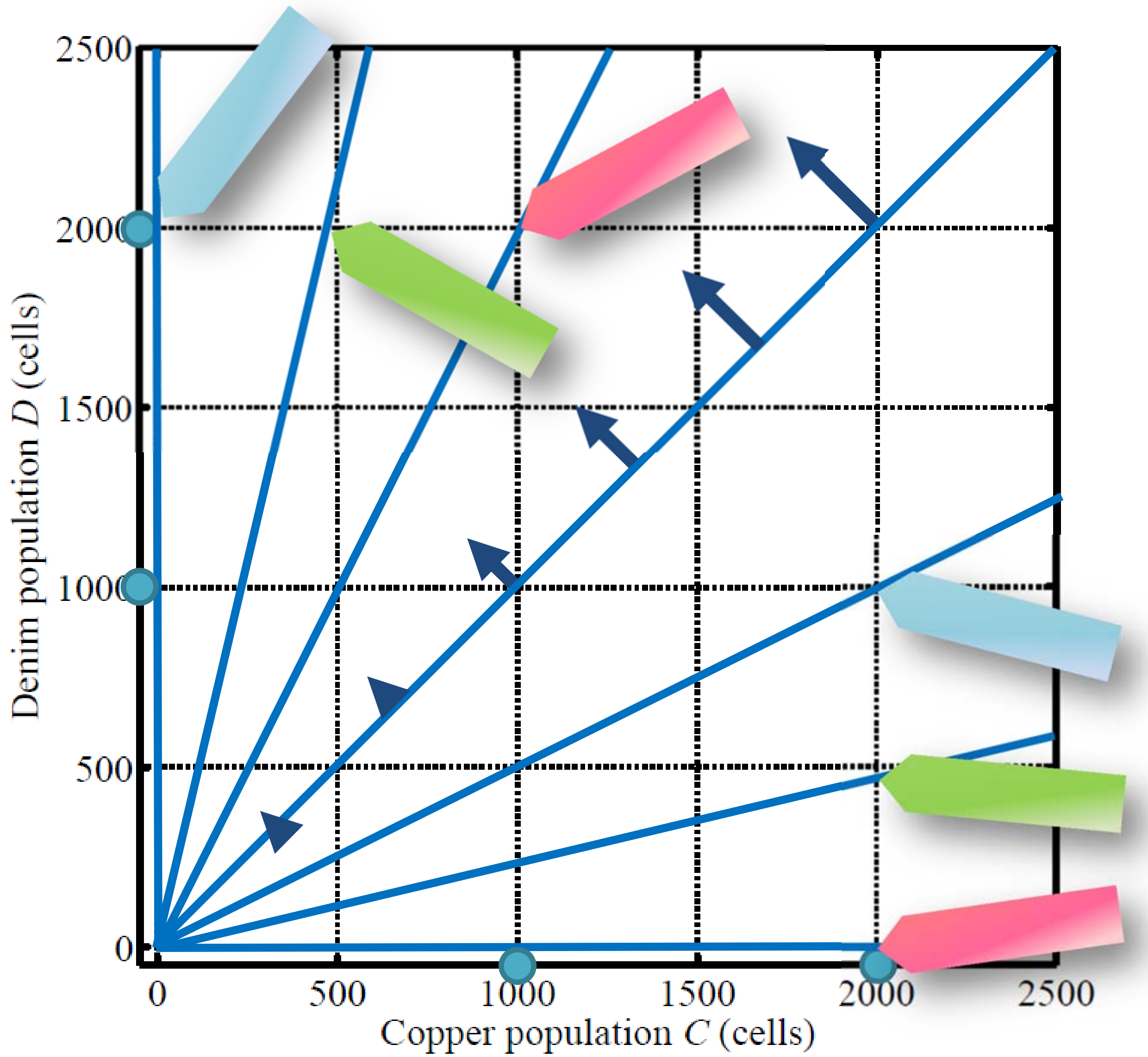

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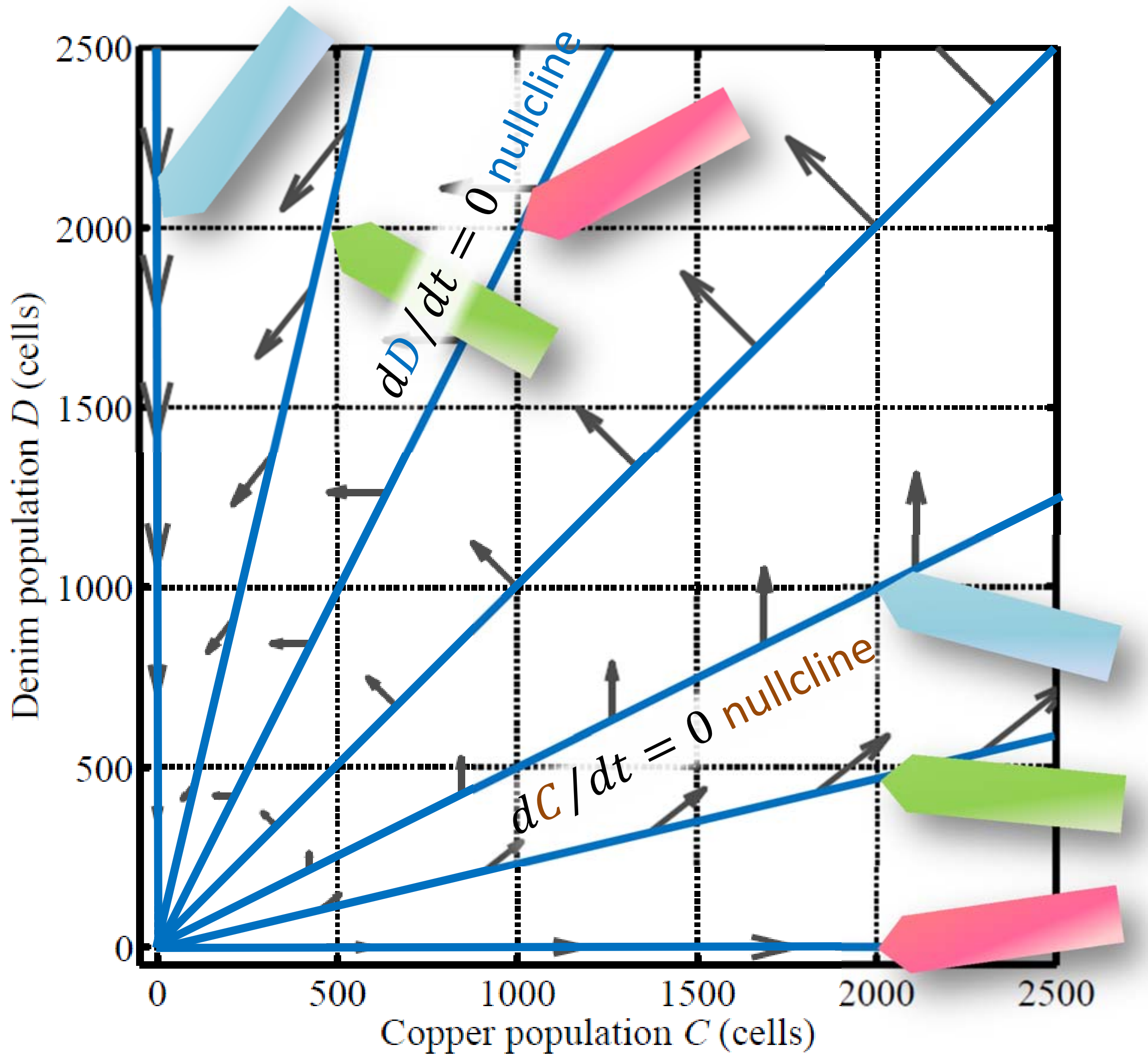
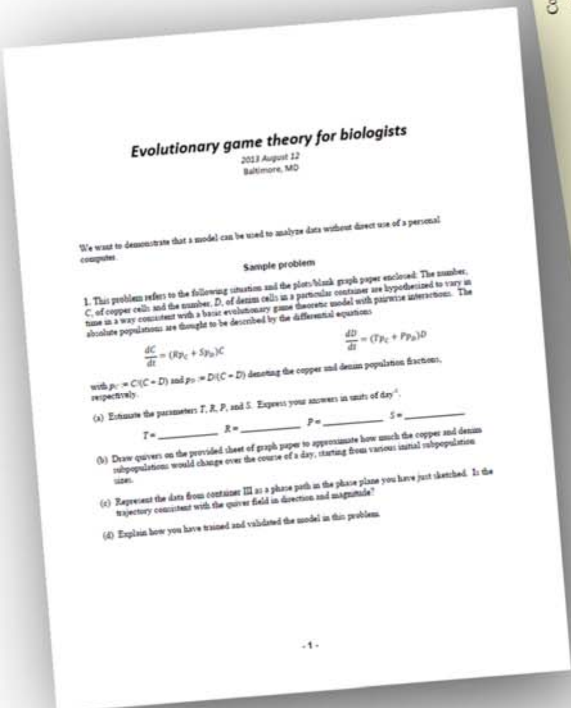


Back-of-the-envelope data analysis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2013 August 12

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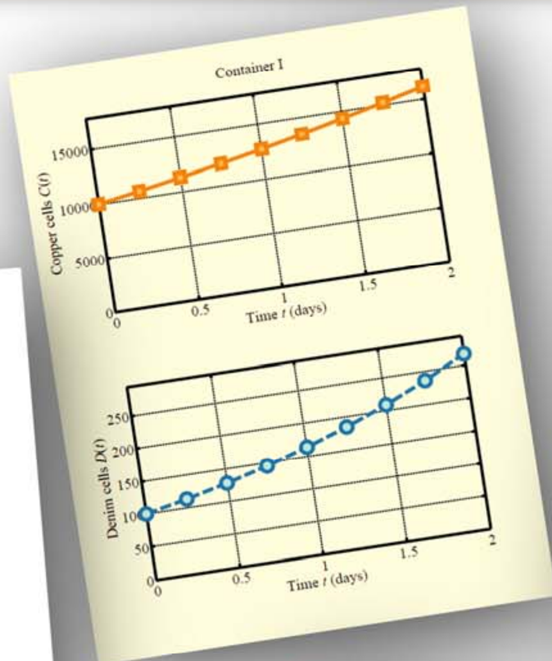
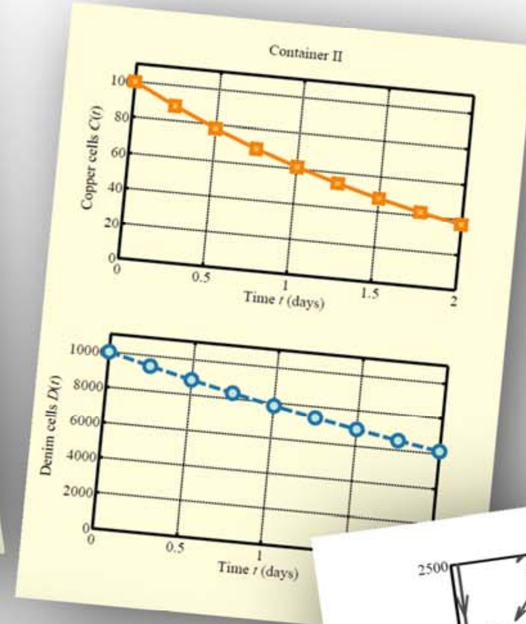
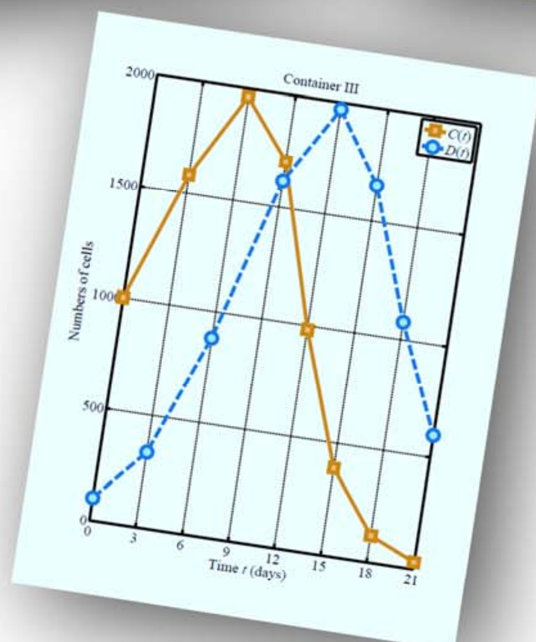
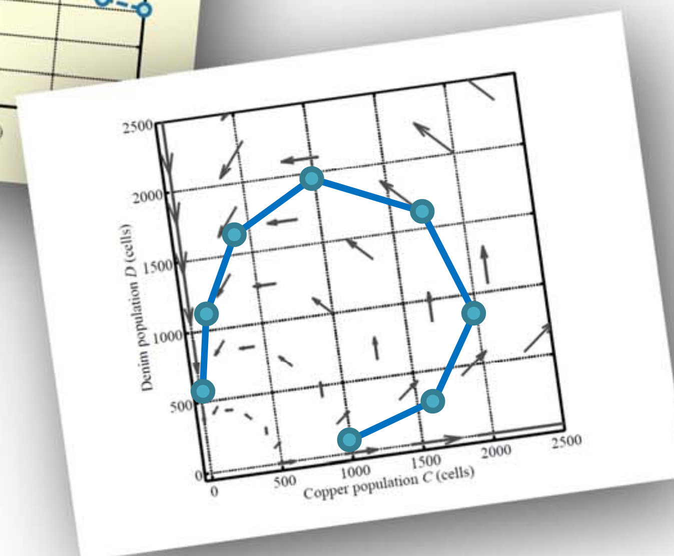


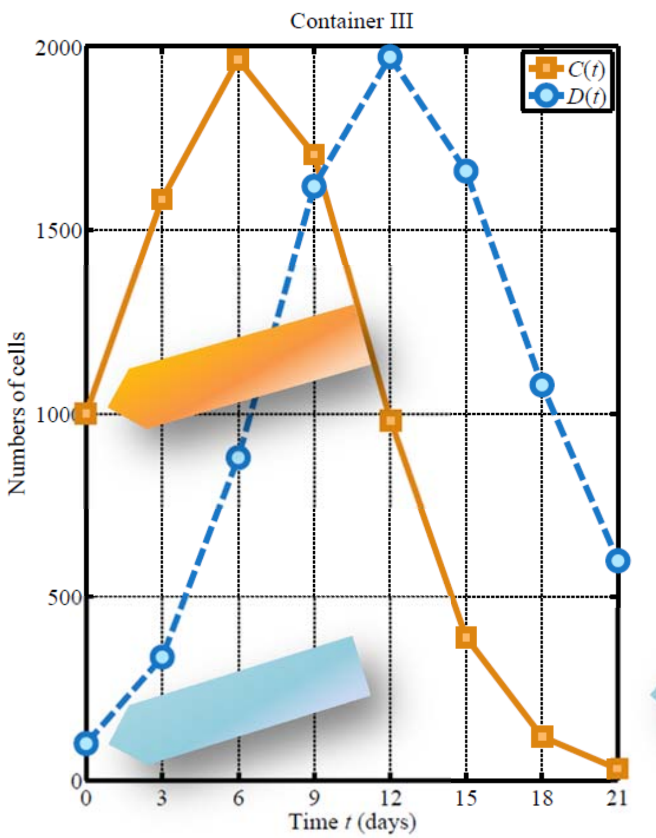


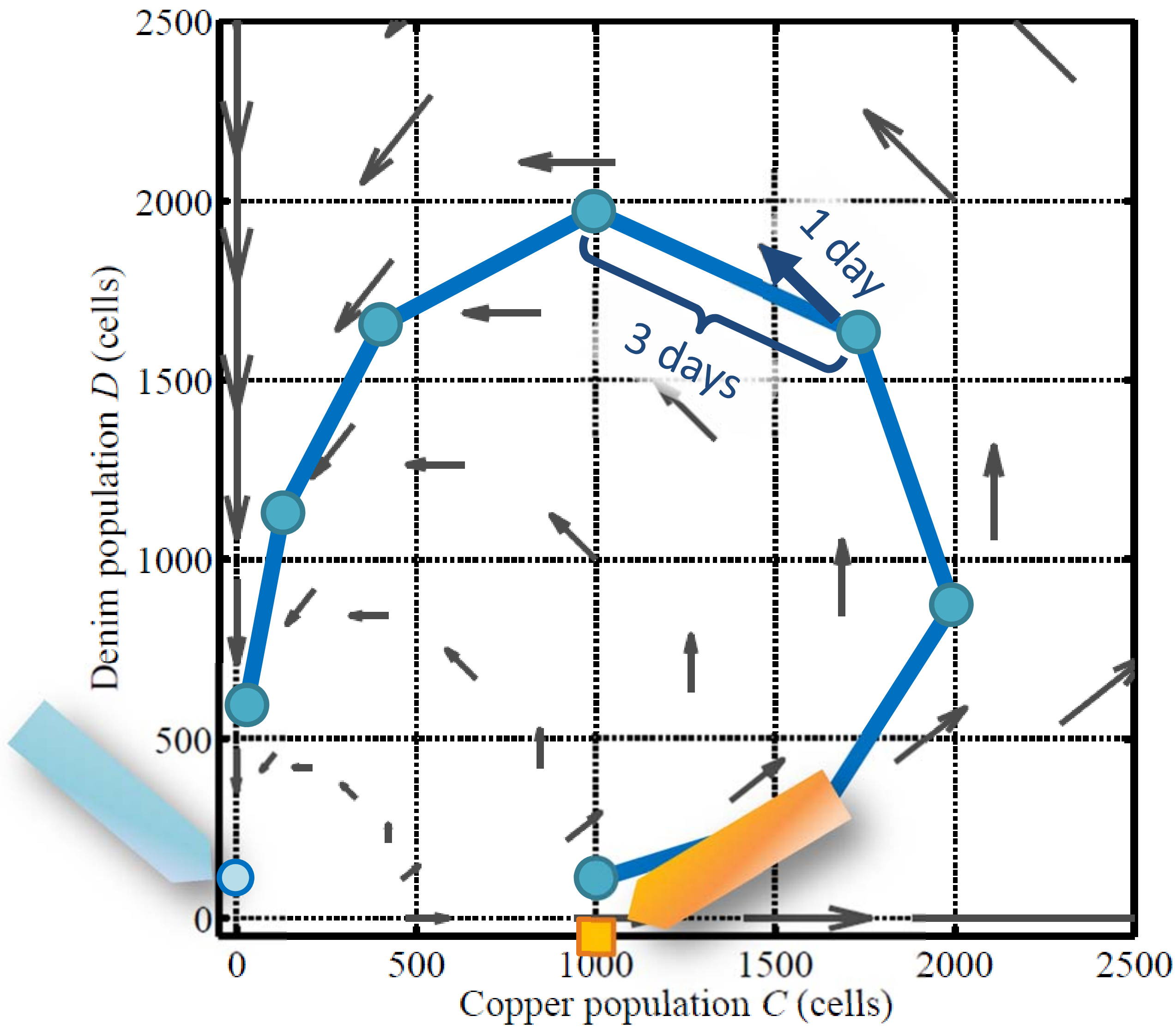




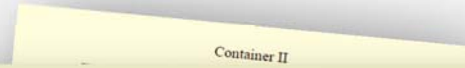
Validating model using phase path

(c) Represent the data from container III as a **phase path** in the phase plane you have just sketched. Is the trajectory consistent with the quiver field in **direction** and **magnitude**?



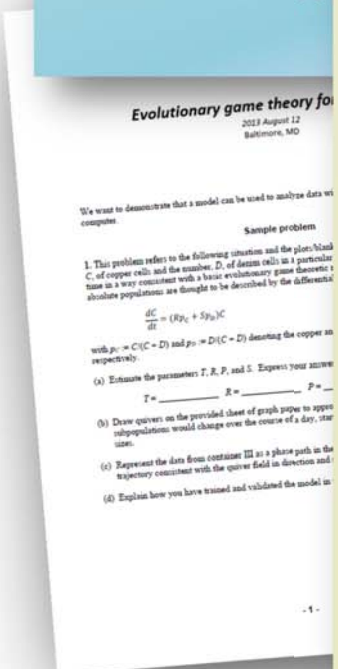


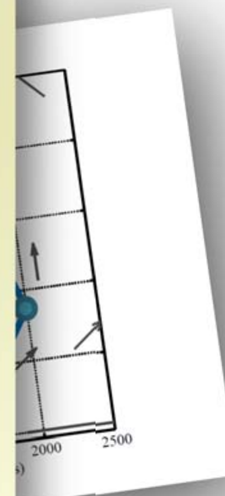
Back-of-the-envelope data analysis



Momentum

with
position





Recently, ideas about **complexity, self-organization, and emergence**--when the whole is greater than the sum of its parts--have come into fashion as alternatives for metaphors of control. But such explanations offer only **smoke and mirrors**, functioning merely to provide **names for what we can't explain**; they elicit for me the same dissatisfaction I feel when a physicist says that a particle's **behavior is caused by** the equivalence of two terms in **an equation**. . . .

The hope that general principles will explain the regulation of all the diverse complex dynamical systems that we find in nature can lead to **ignoring anything that doesn't fit a pre-existing model**. When we learn more about the specifics of such systems, we will **see where analogies between them are useful and where they break down**.

--Deborah Gordon (2007)
Control without hierarchy. *Nature* **446:** 143

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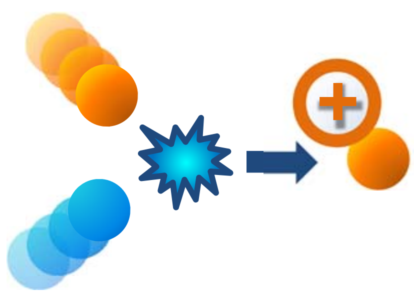
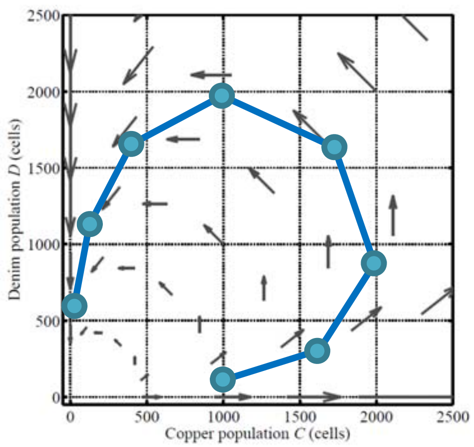
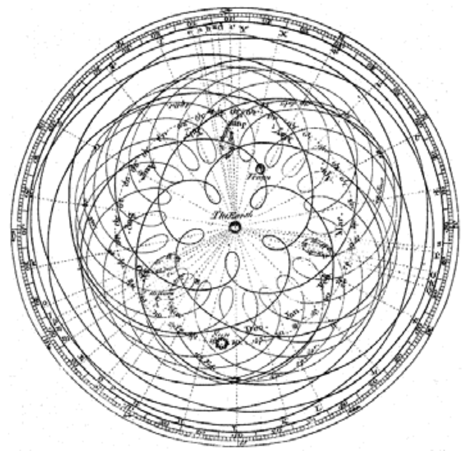
Population dynamics



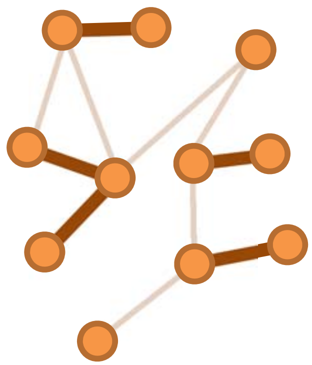
Manual data analysis



Epicycles



Modularity



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Mass action, Taylor series, and epicycles

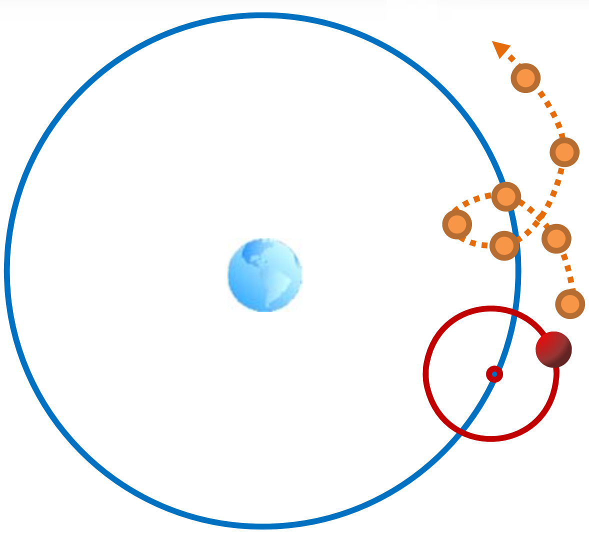
Population dynamics

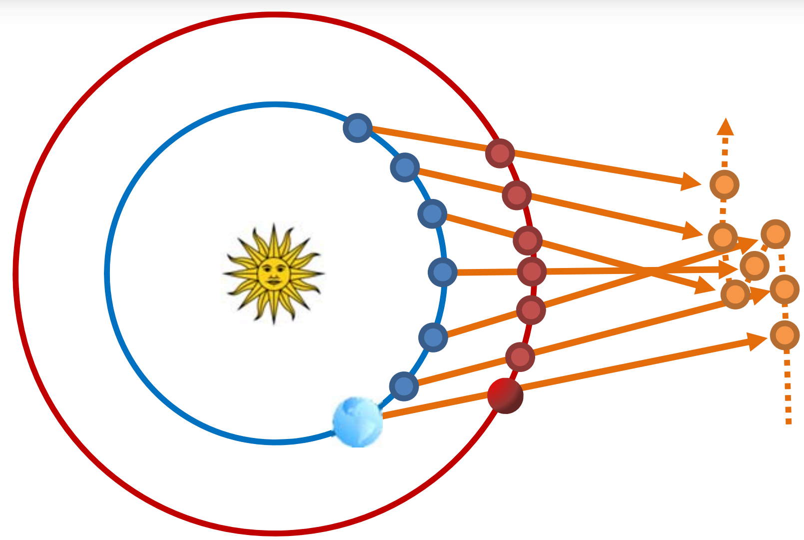
$$\frac{dC}{dt} = (Rp_C + Sp_D)C$$

Pairwise collisions **3-way collisions** **≥ 4-way**

$$\frac{dC}{dt} = (\underbrace{\overbrace{Rp_C + Sp_D}^{\text{Pairwise collisions}} + \overbrace{A_{CC}p_C^2 + A_{CD}p_Cp_D + A_{DD}p_D^2}^{\text{3-way collisions}} + \overbrace{\cdots}^{\geq\text{4-way}}}_{\text{Power-series for generic analytic function}})C$$

Power-series for generic analytic function





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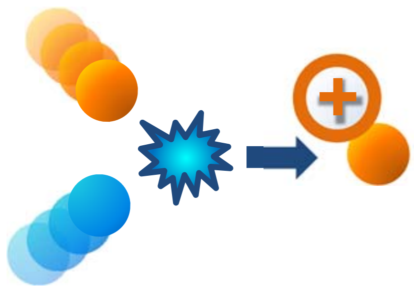
Population dynamics



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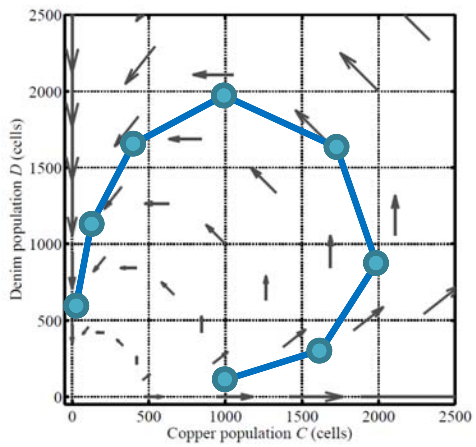

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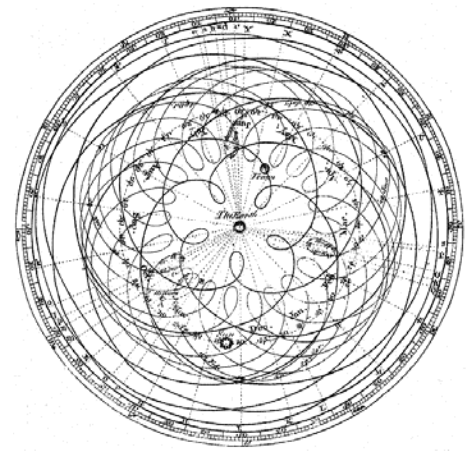

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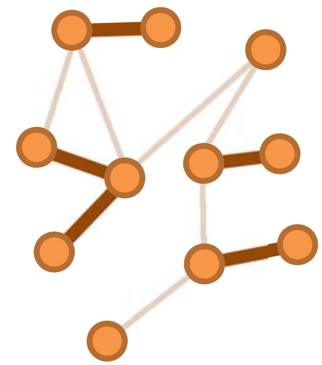

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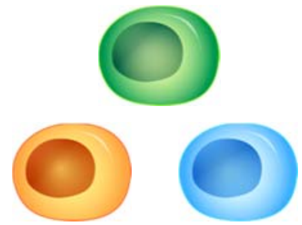
How complicated must our model be?

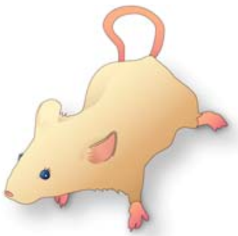
Intracellular

2 cell subpopulations

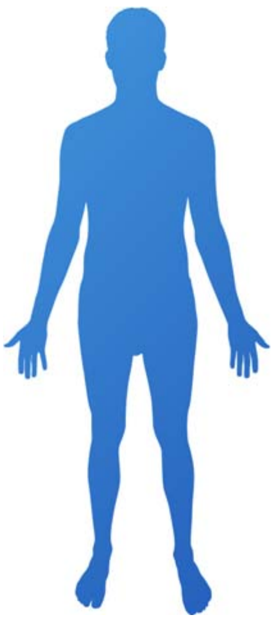
3 cell subpopulations



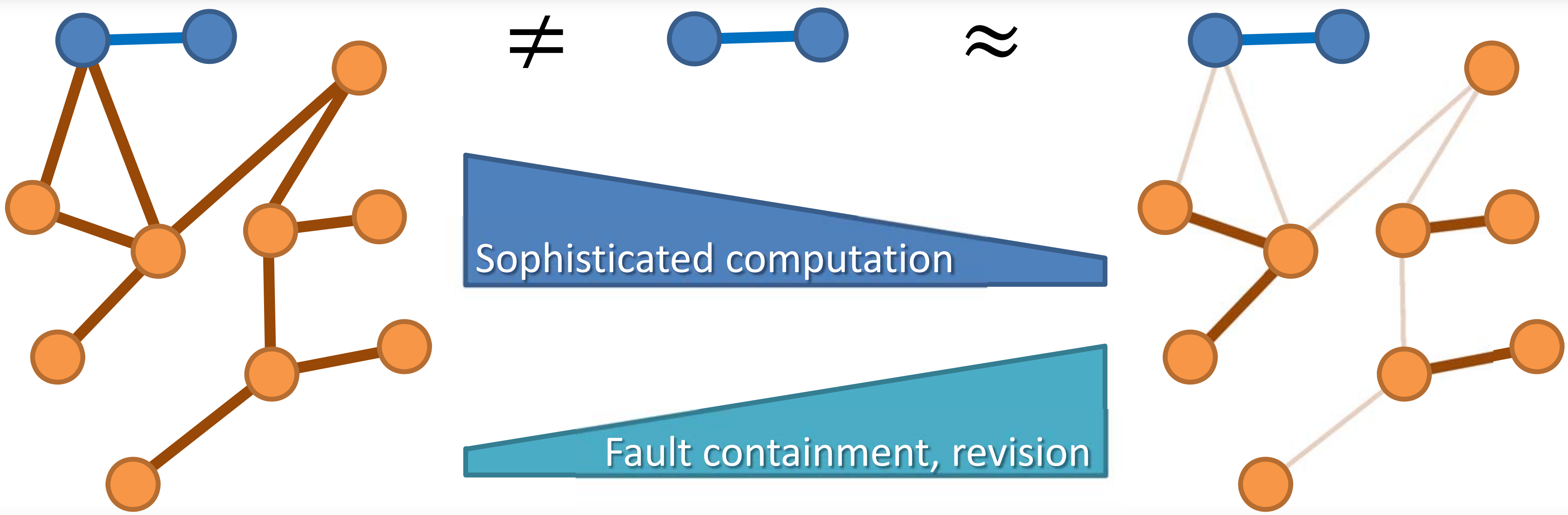
. . .



Patient

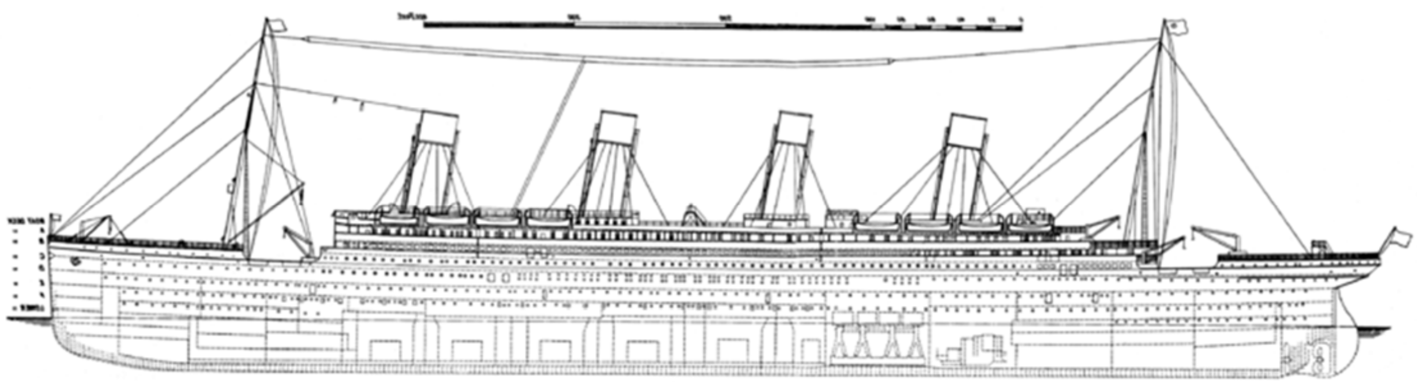


Modularity



How does time-varying environment in which life evolves determine scale(s) at which and mechanisms by which a system is integrated and/or segregated?

Given risks and economics, should compartments be tightly connected or well isolated?



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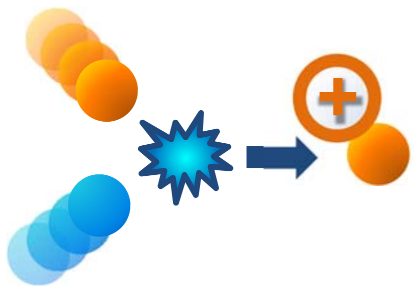

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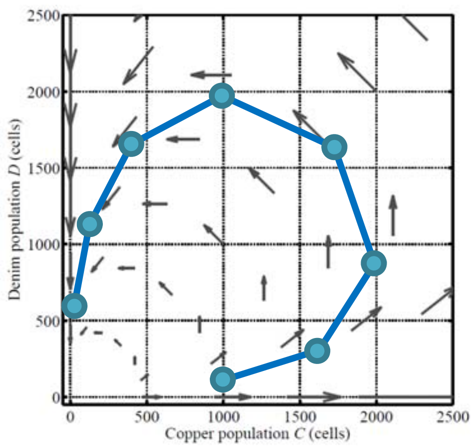

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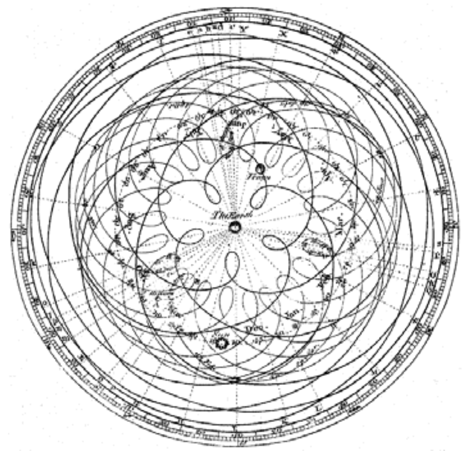

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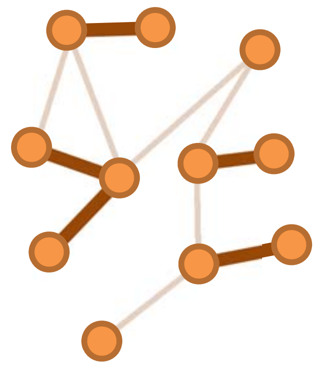

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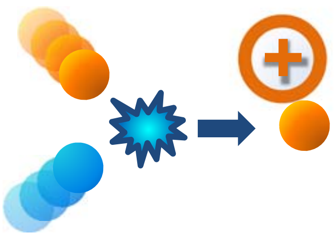
Questions

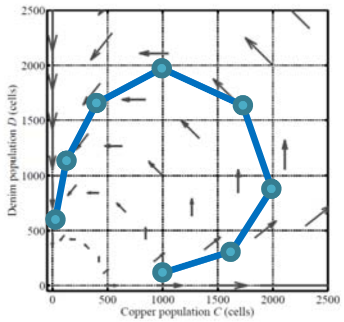


$$\frac{dx_i}{dt} = f(x_i) + \eta_i(t)$$

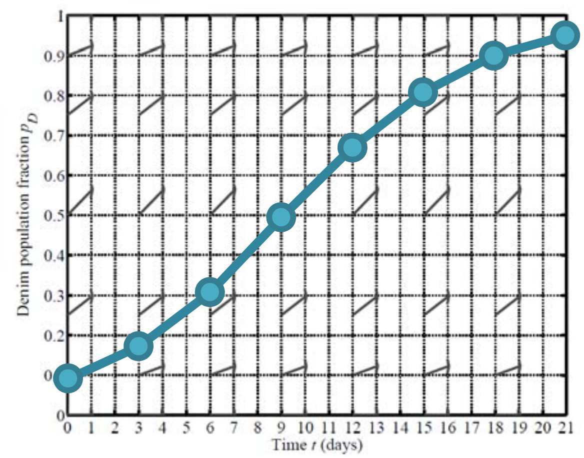
$$\frac{dC}{dt} = (Rp_C + Sp_D)C$$

$$\frac{dD}{dt} = (Tp_C + Pp_D)D$$

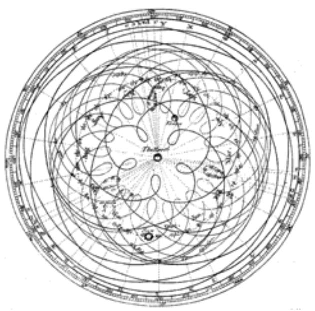
Why doesn't origin look like a saddle?



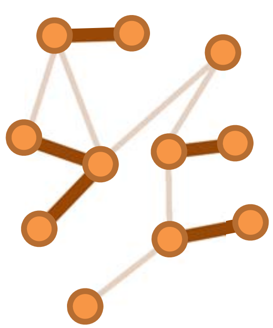
Mechanisms
Direct contact
Indirect contact: Short-lived soluble factor



This validation of a **mutation-free** model also validates model with **mutation**



Compare results from 2-, 3-, 4-subpopulation experiments to infer modularity?



Motifs vs. modules
Kashtan & Alon 2005
Huang & Kauffman 2013

Acknowledgments
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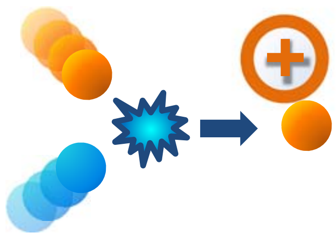
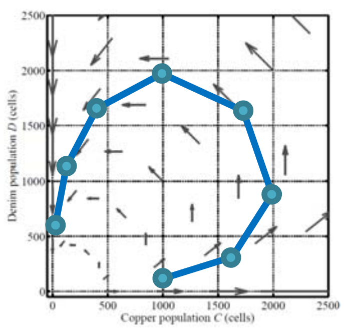
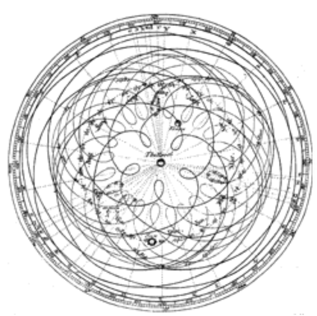
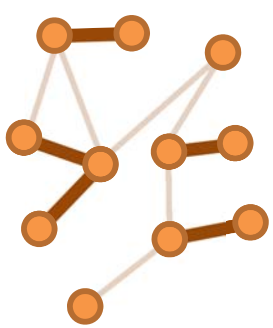
Validation of mutation-free model consistent with social mutation









$$\frac{dC}{dt} = (Rp_C + Sp_D)C \qquad \frac{dD}{dt} = (Tp_C + Pp_D)D$$

In this example, $S = -T$

$$\frac{dC}{dt} = Rp_C C - Tp_D C \qquad \frac{dD}{dt} = Pp_D D + \overbrace{T\frac{C}{C+D}D}^{+Tp_D C}$$

Let $T = k_1 - k_2$

$$\frac{dC}{dt} = Rp_C C - k_1 p_D C + k_2 p_D C$$

$$\frac{dC}{dt} = Rp_C C - k_1 p_D C + \underbrace{k_2 \frac{D}{C+D} C}_{+k_2 p_C D}$$

Socially modulated mutation

$$\frac{dC}{dt} = Rp_C C - k_1 p_D C + k_2 p_C D$$

$$\frac{dD}{dt} = Pp_D D + k_1 p_D C - k_2 p_C D$$