Cooperation, cheating, and collapse in microbial populations

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Two questions:

Can we tell whether a population is going to collapse?

How can evolution lead to cooperation?

Collapse of cod population in Newfoundland

Individuals often do best in the presence of others

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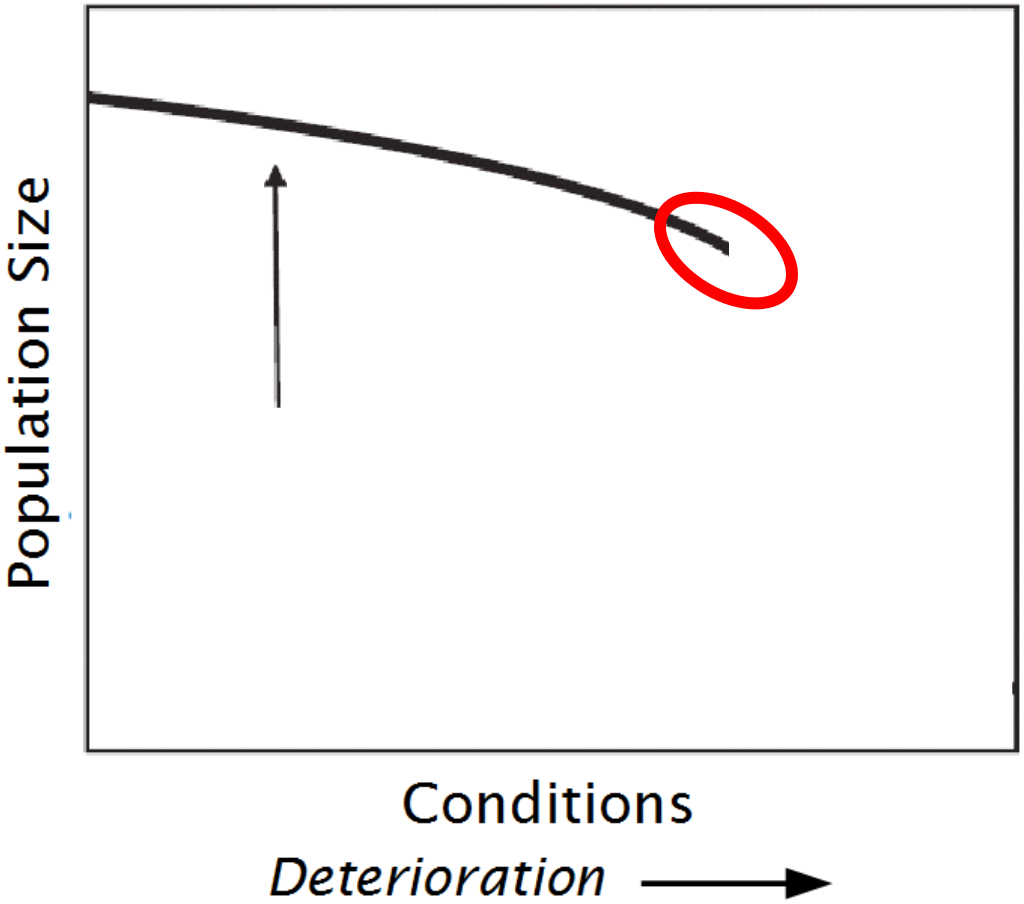
Bistability can result in sudden collapse



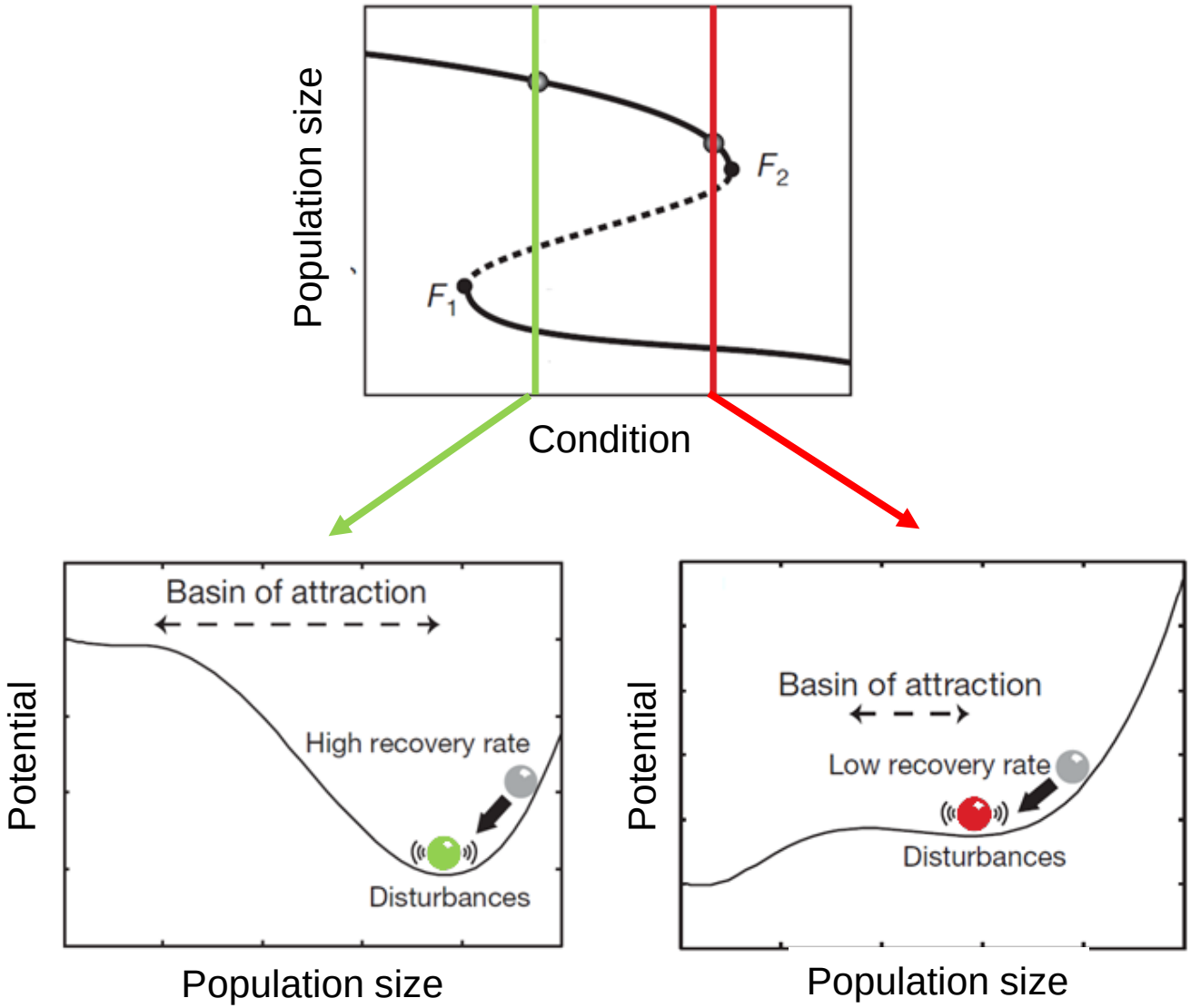
Underlies other sudden transitions:

- Ecosystems
- Climate
- Finance

Are there any early warning indicators of impending collapse?

Scheffer *et al.*, *Nature* (2009)

Fluctuations may provide early warning of collapse



Schetter *et al.*, *Nature* (2009)

Possible early warning signals:

1) Fluctuations get larger

2) Fluctuations get slower

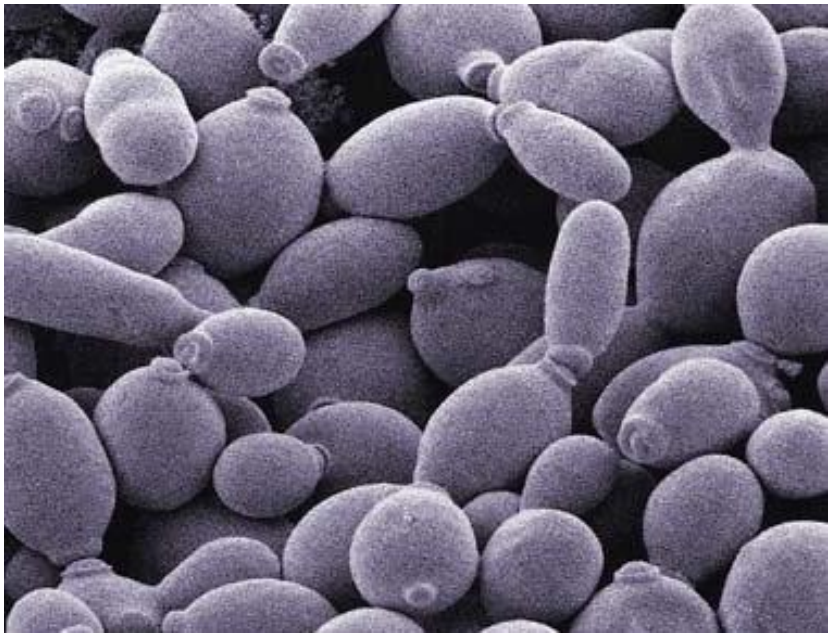
“Can these early warning indicators be measured experimentally?”

Lei Dai

Daan Vorselen

Dai, Vorselen, Korolev, Gore, *Science* (2012)

Why use microbial populations?



Experimentally tractable:

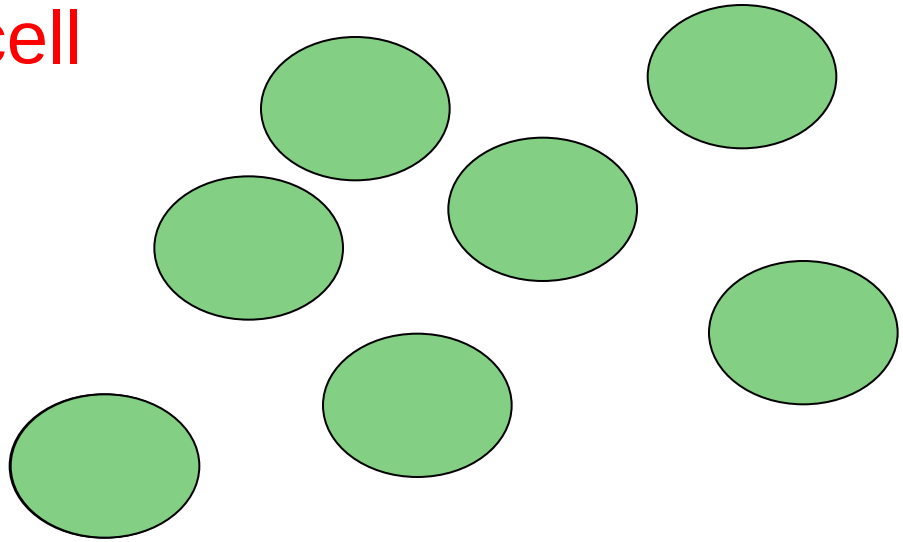
- Small and simple
- Short generation time
- Quantitative measurements
- Environmental control
- Genetic manipulations

  → Control strategies

Dai, Vorselen, Korolev, Gore, *Science* (2012)

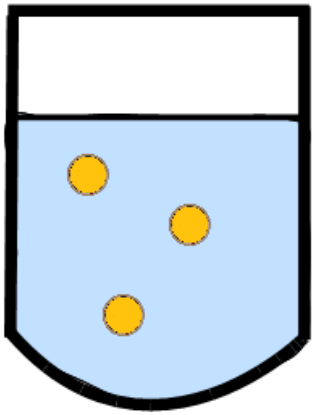
Yeast benefit from other yeast in the population

Sucrose is broken down outside of the cell



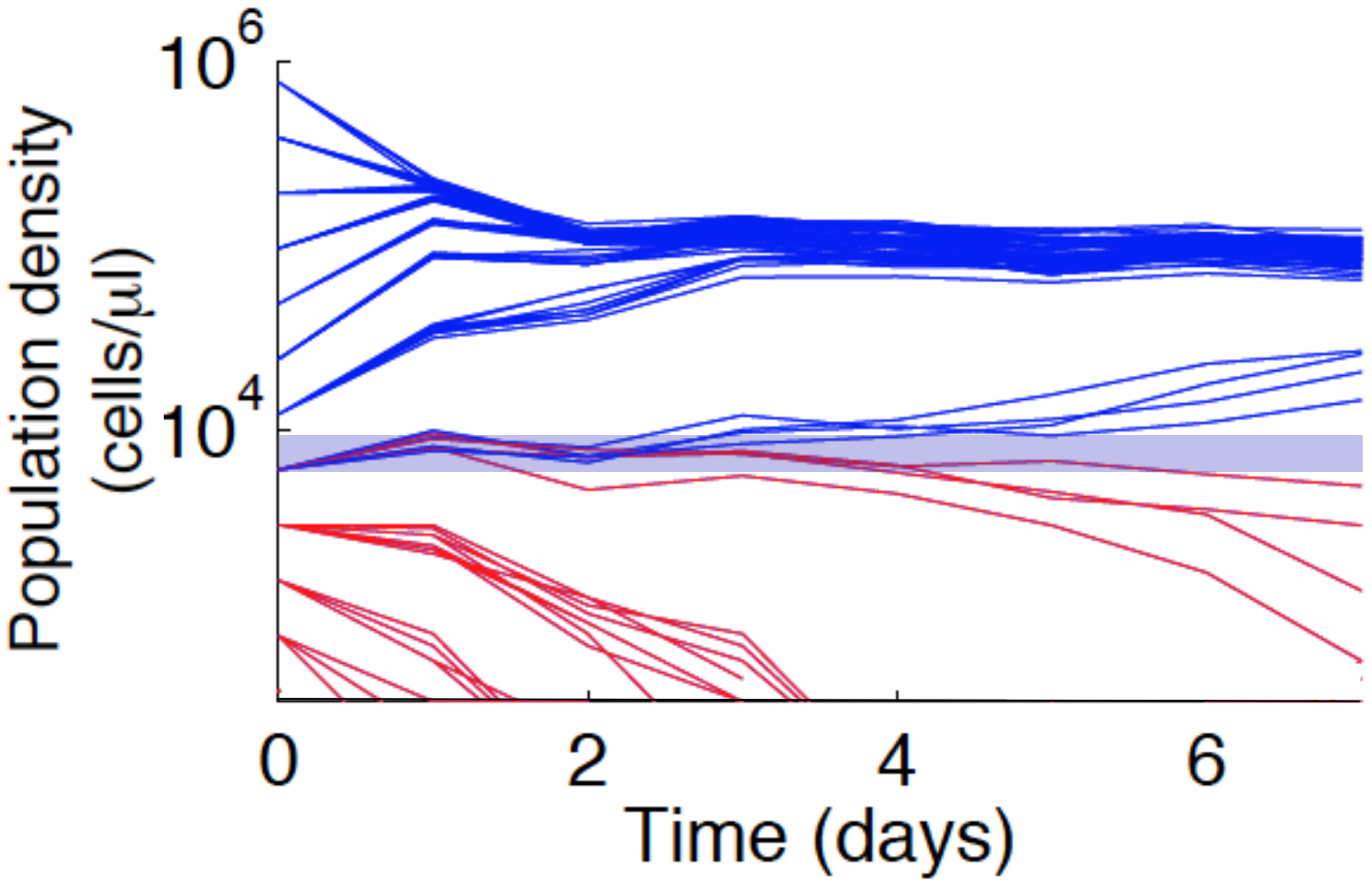
Yeast divide more rapidly at higher cell density → Possibility of sudden collapse!

Experimental procedure: Serial batch culture



Initial cell density

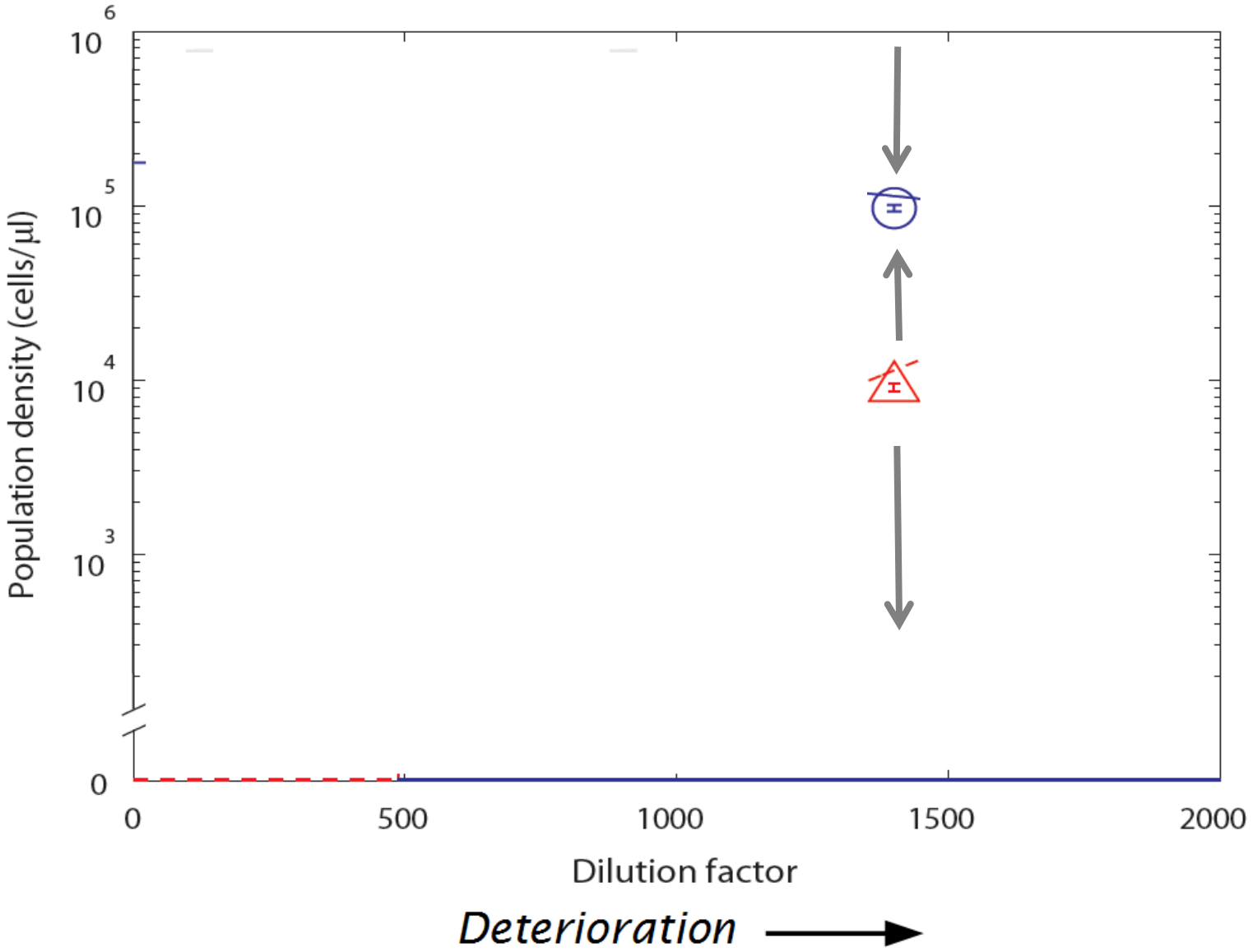
Yeast population size is bistable



Dilution Factor = 1400

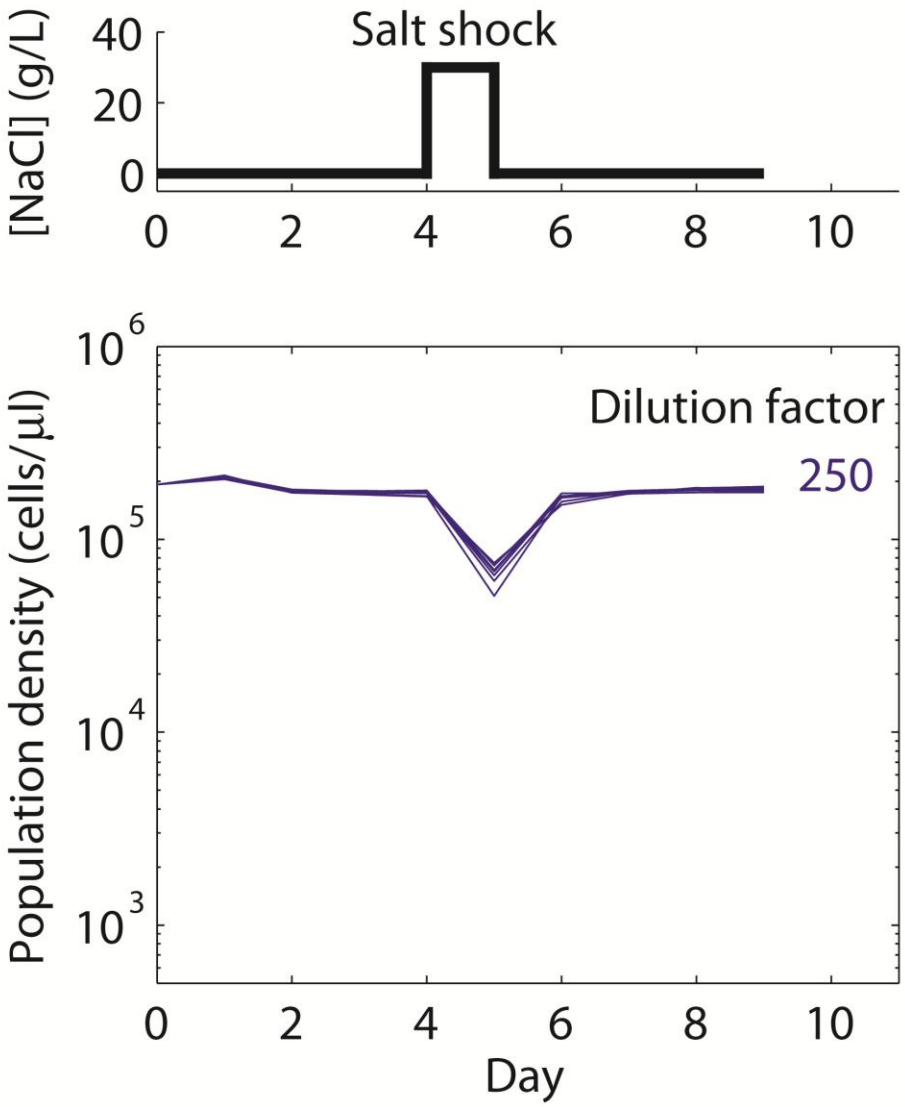
Dai, Vorselen, Korolev, Gore, *Science* (2012)

An experimental bifurcation diagram



Dai, Vorselen, Korolev, Gore, *Science* (2012)

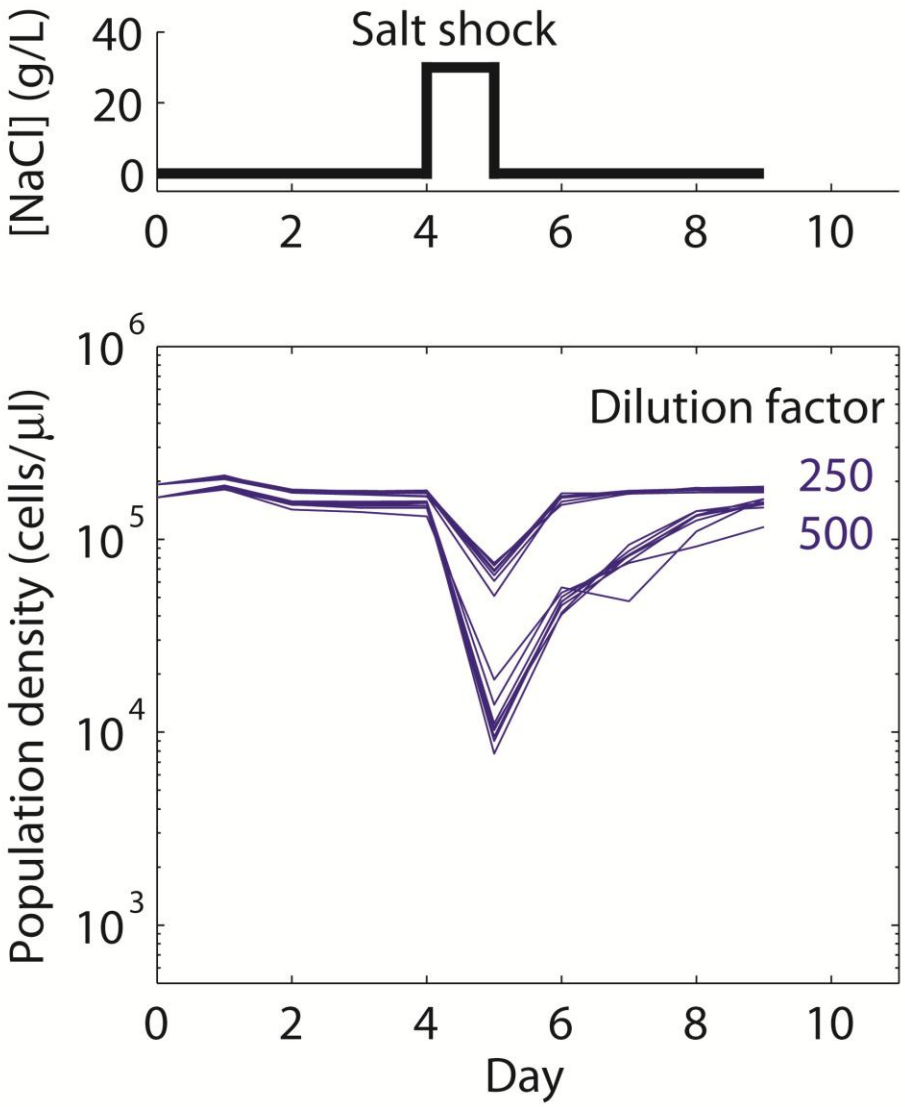
Population less resilient near tipping point



Benign conditions
→ recovery

Dai, Vorselen, Korolev, Gore, *Science* (2012)

Population less resilient near tipping point



Benign conditions
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Dai, Vorselen, Korolev, Gore, *Science* (2012)

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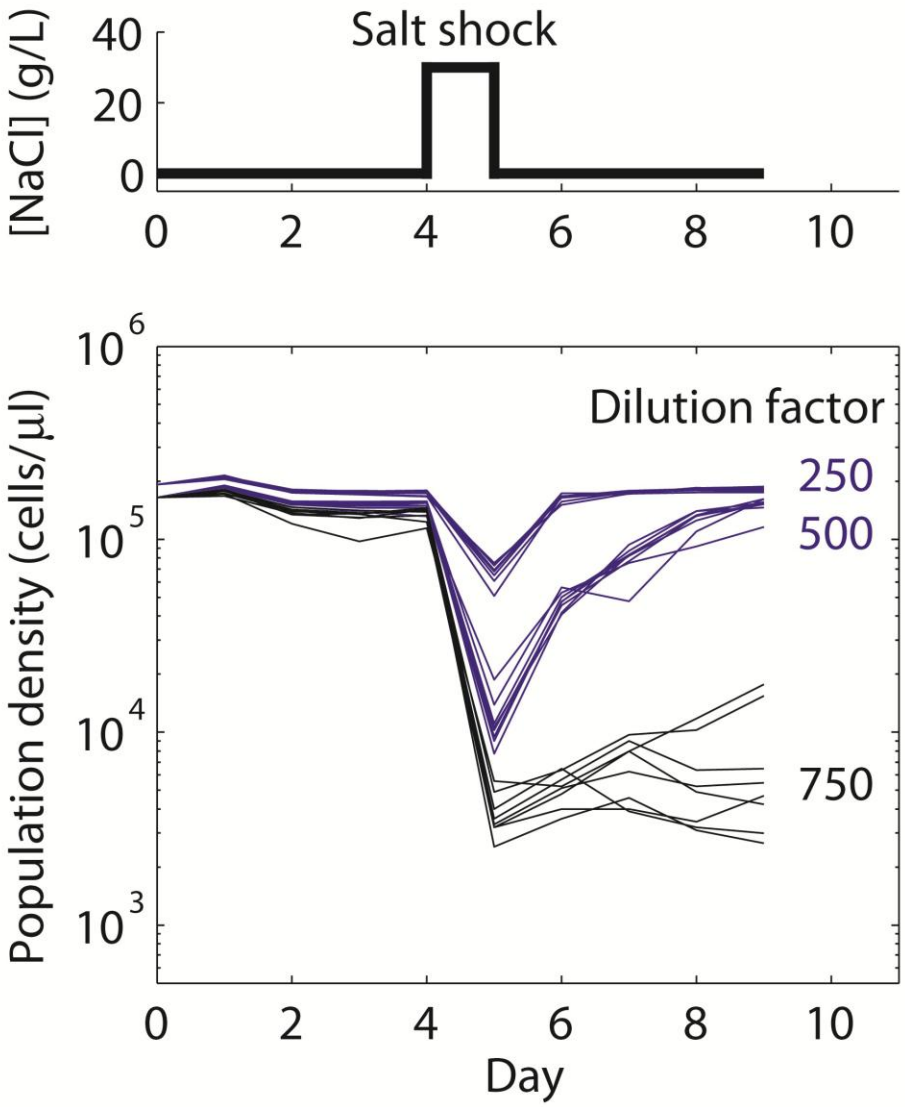

Benign conditions
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Dai, Vorselen, Korolev, Gore, *Science* (2012)

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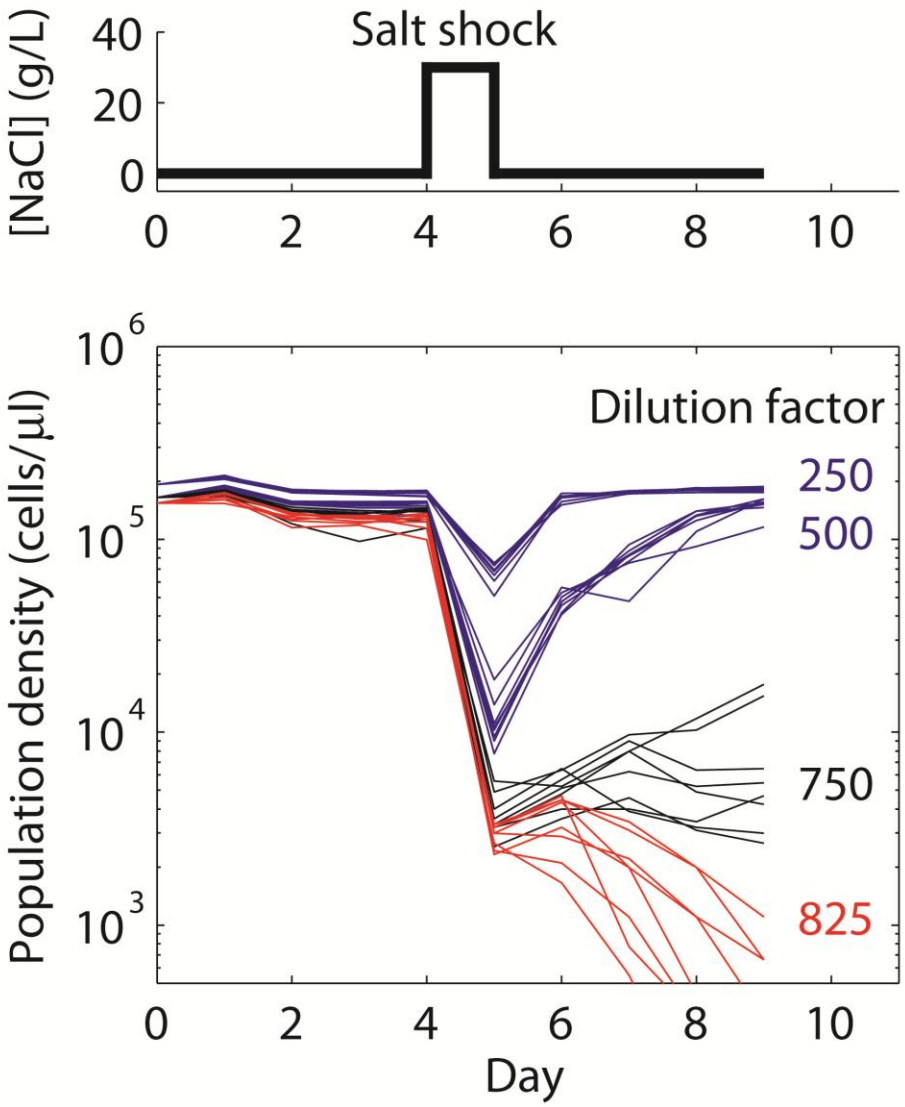
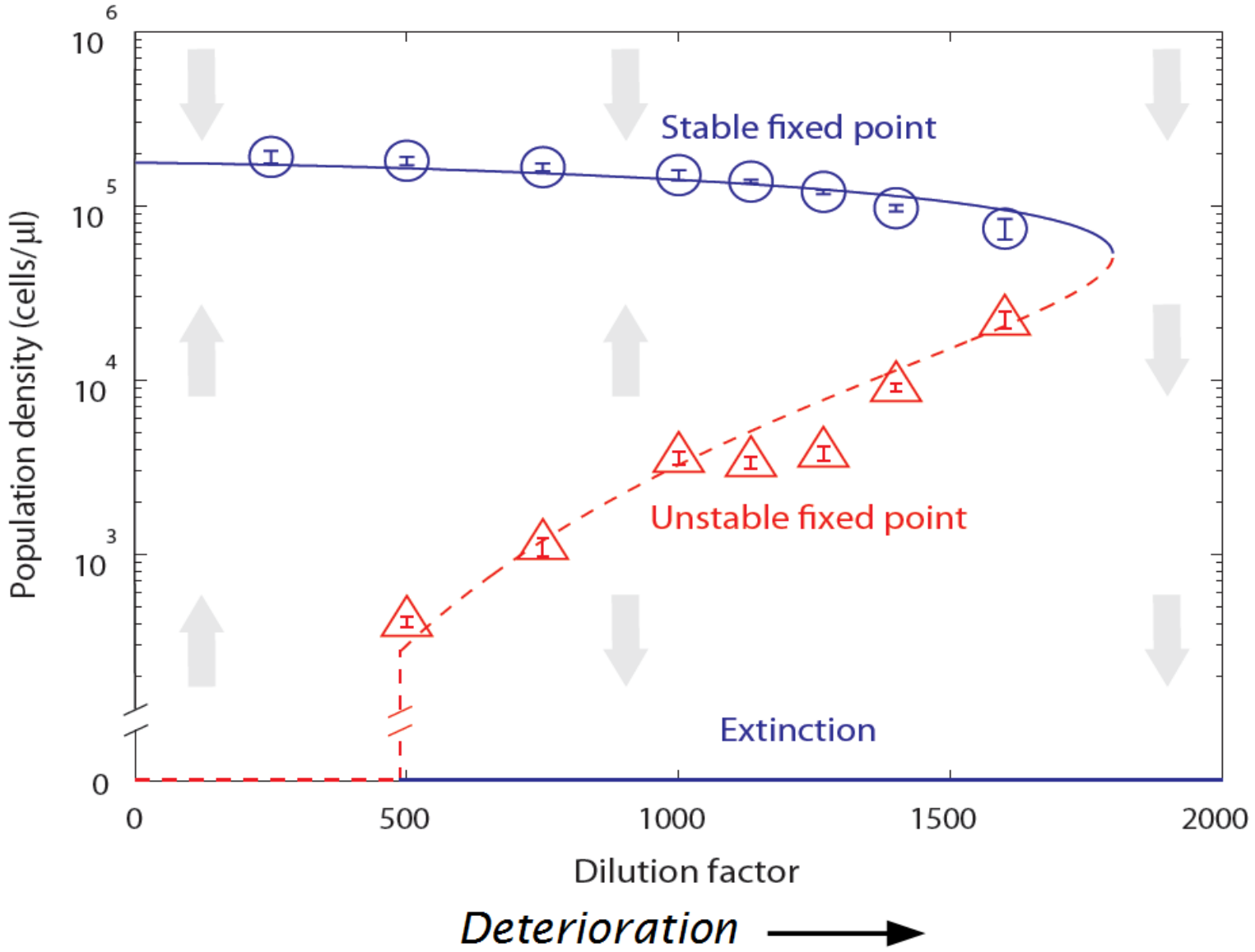


Benign conditions
→ recovery

Poor conditions
→ collapse

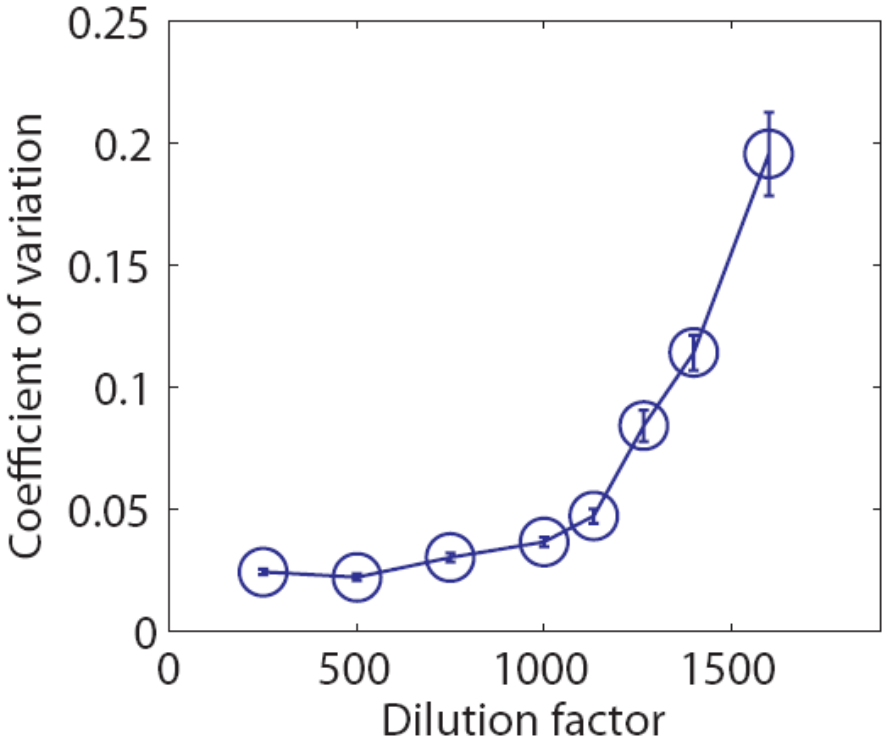
Dai, Vorselen, Korolev, Gore, *Science* (2012)

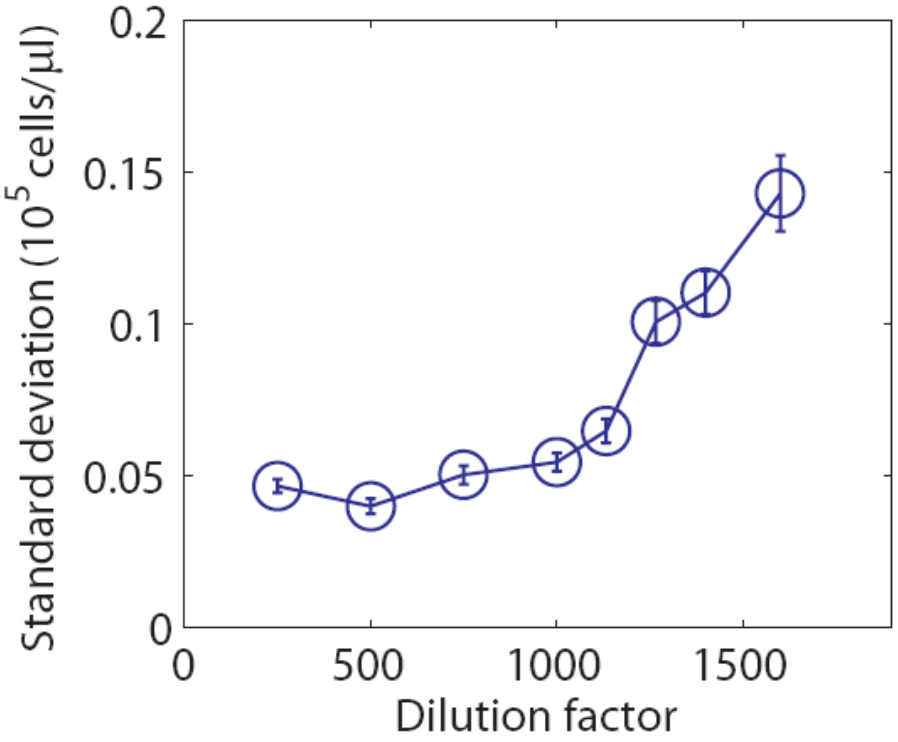
Can indicators be observed before tipping point?



Dai, Vorselen, Korolev, Gore, *Science* (2012)

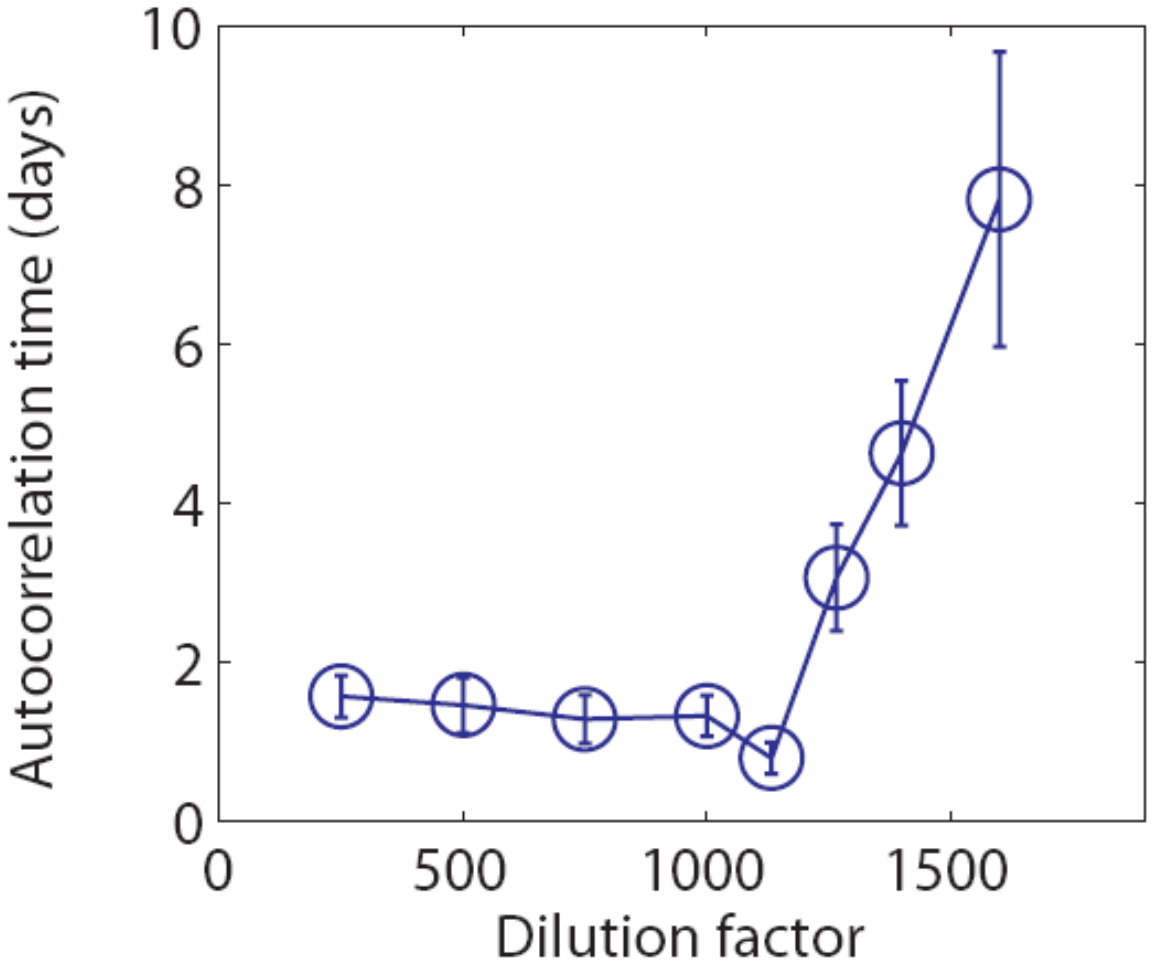
Population fluctuations increase near the tipping point





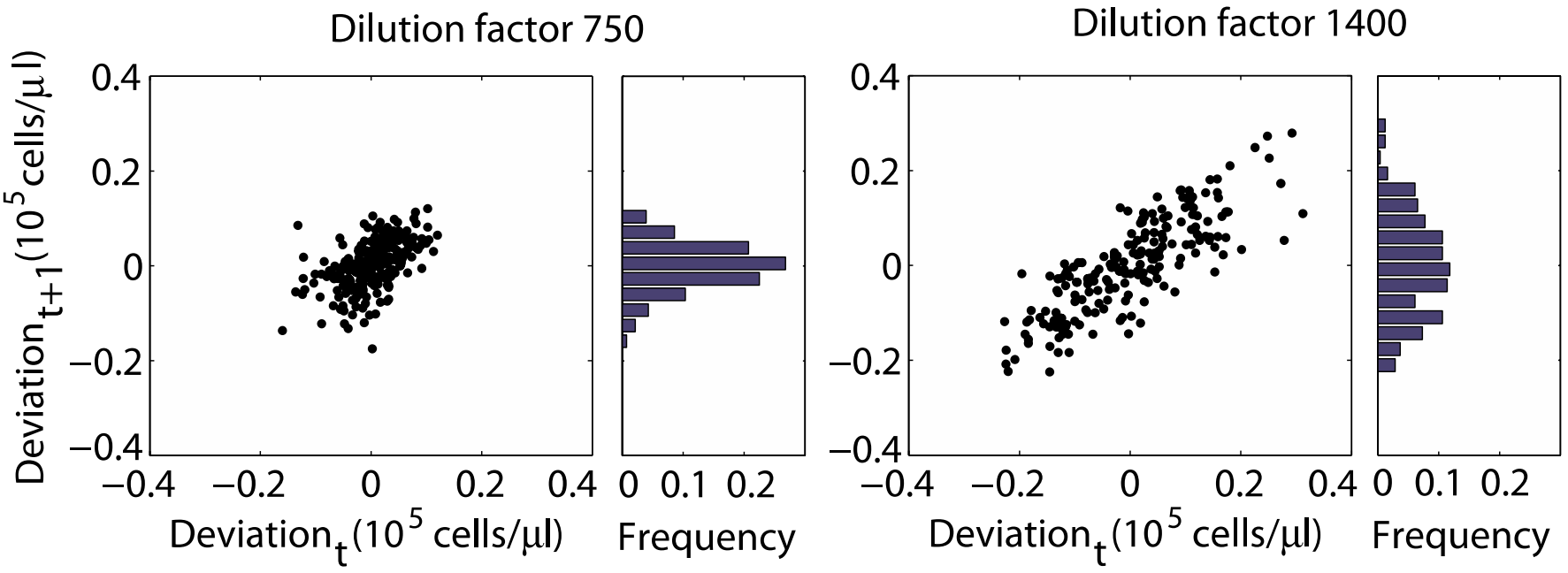
Dai, Vorselen, Korolev, Gore, *Science* (2012)

Population fluctuations also slow down near the tipping point



Dai, Vorselen, Korolev, Gore, *Science* (2012)

Change in fluctuations can be visualized directly



Dai, Vorselen, Korolev, Gore, *Science* (2012)

What about…

Can these indicators be observed in a continuously deteriorating environment? ✓

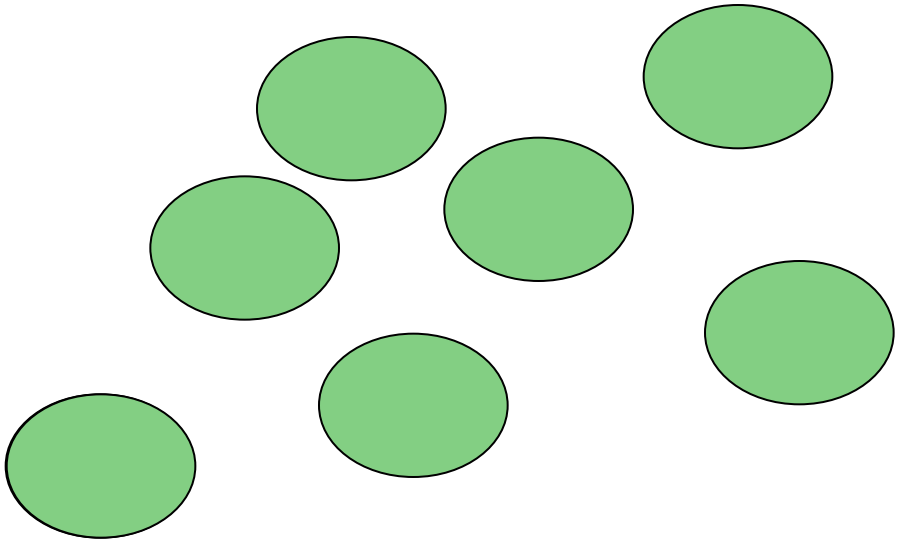
What about other ways of deteriorating the environment? ✓

What about the skewness of fluctuations? Can you see this early warning indicator? ✗

What about spatial patterns before collapse? ✓

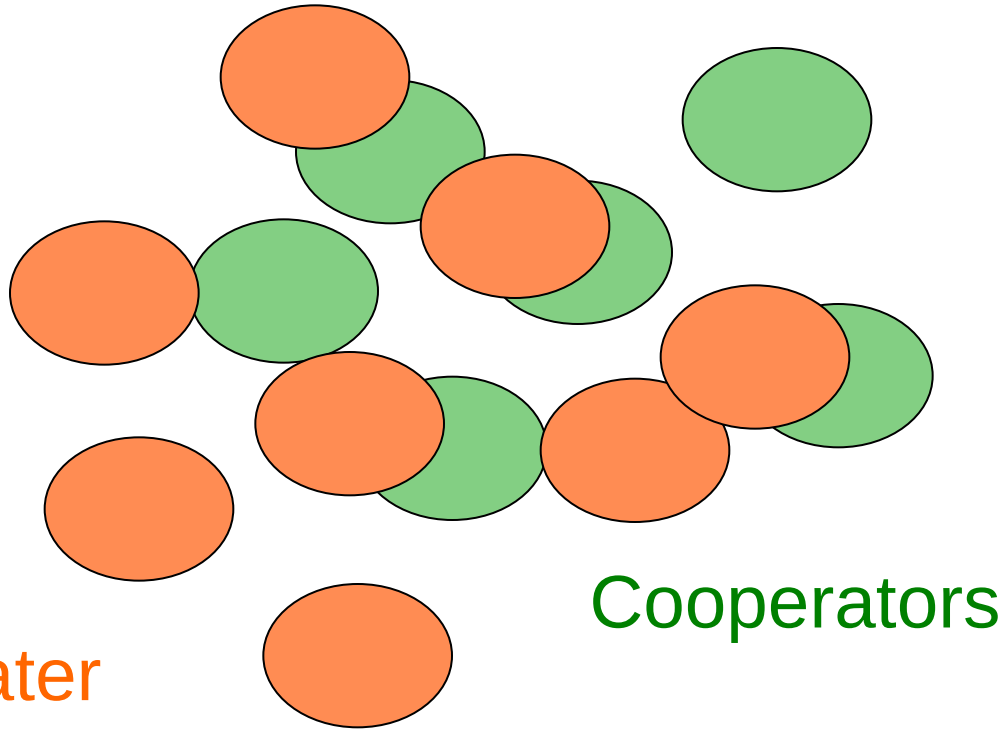
Our yeast are collectively breaking down the sucrose. What happens if one of them stops contributing?

Cooperation not always stable



Population of yeast happily growing on sucrose

Cheaters can often take advantage of cooperators



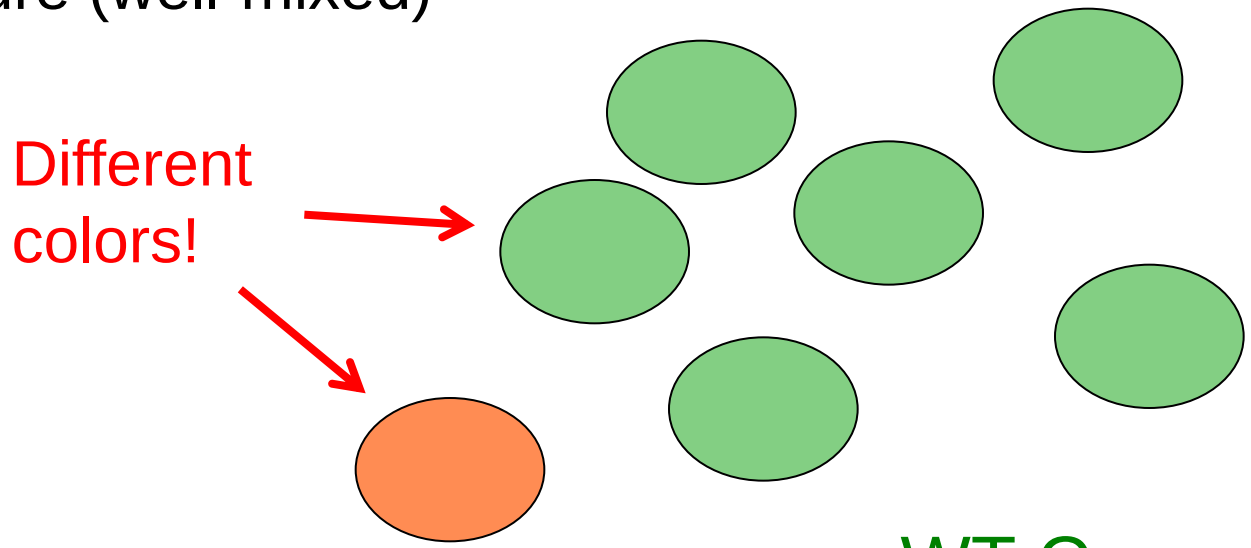
Always better to be a cheater

→ extinction of cooperation!

Prisoner's Dilemma

Experimental design

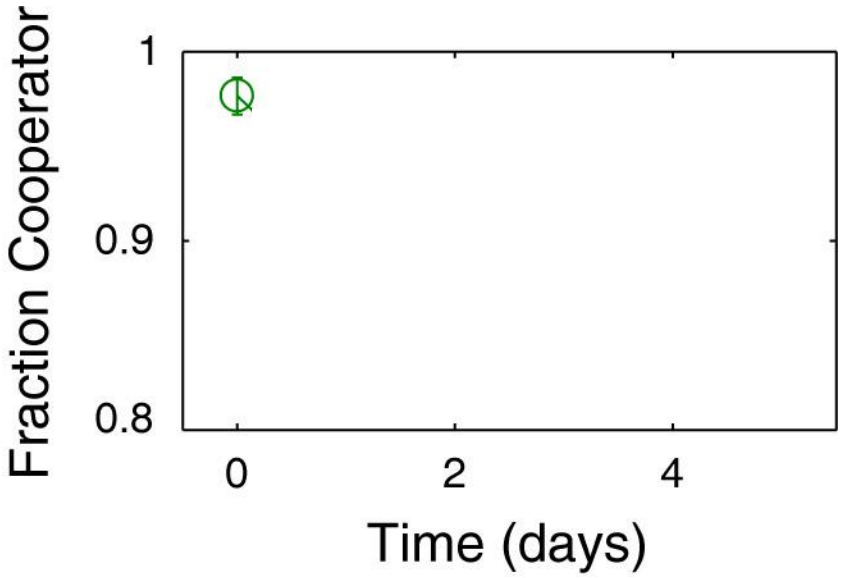
Compete in liquid batch culture (well-mixed)



WT Cooperators

Cheater:
Invertase knockout

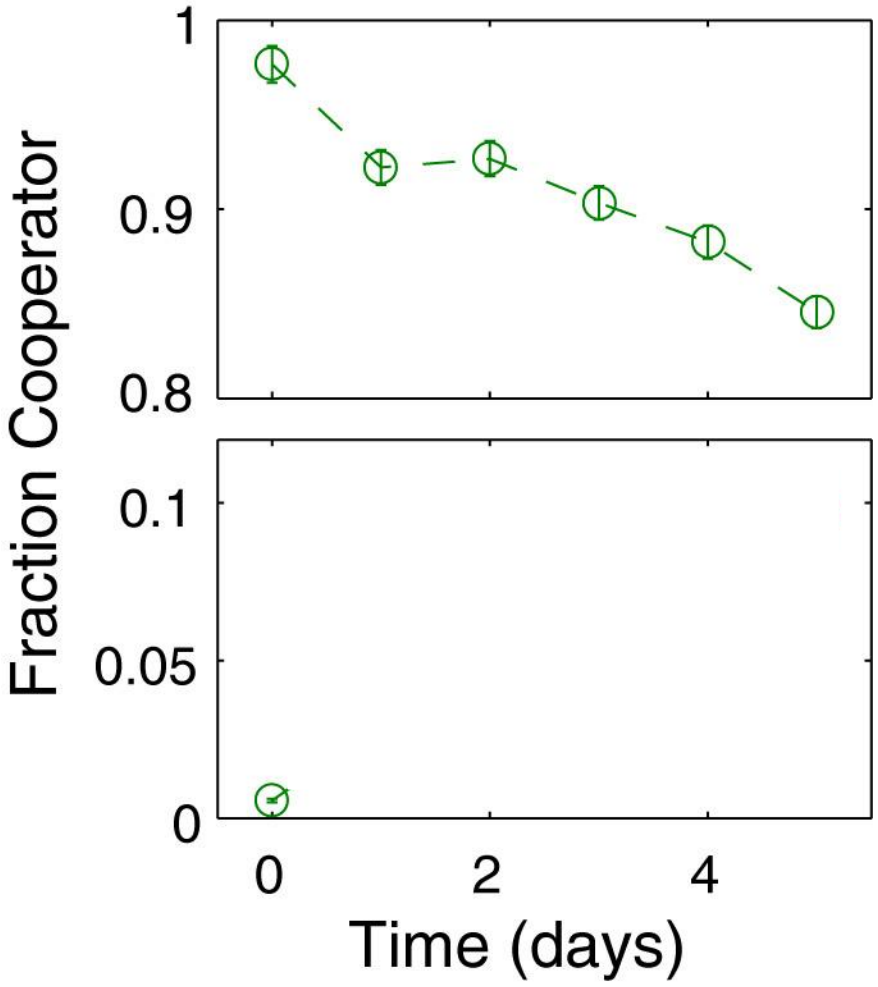
Cheater can invade a population of cooperators



Growth rate decreasing!

Gore et al, *Nature* (2009)

Cheater can invade a population of cooperators, Cooperator can invade a population of cheaters



Coexistence
→Snowdrift game

Gore et al, *Nature* (2009)

Snowdrift game: Cheat if your opponent cooperates

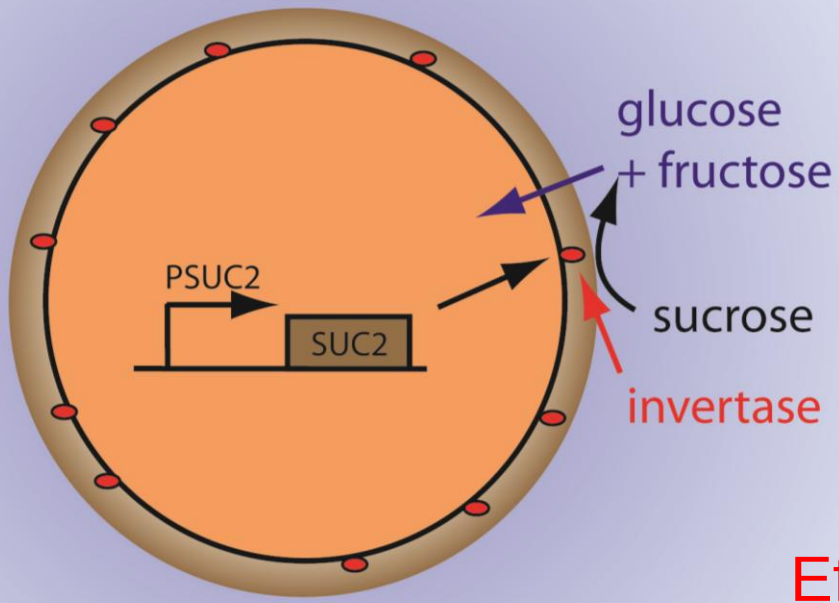
igem.org

Gore et al, *Nature* (2009)

How can cooperators survive?

Why is the “game” not a prisoner’s dilemma?

A bit of glucose captured before being shared



Preferential access also leads to coexistence between antibiotic resistant and sensitive bacteria!

Efficiency of glucose capture:

$$\varepsilon = \frac{\text{Glucose captured}}{\text{Glucose created}}$$

$$\varepsilon \approx 0.01$$

Gore et al, *Nature* (2009)

Ecological factors that favor cooperation

Hasan Celiker

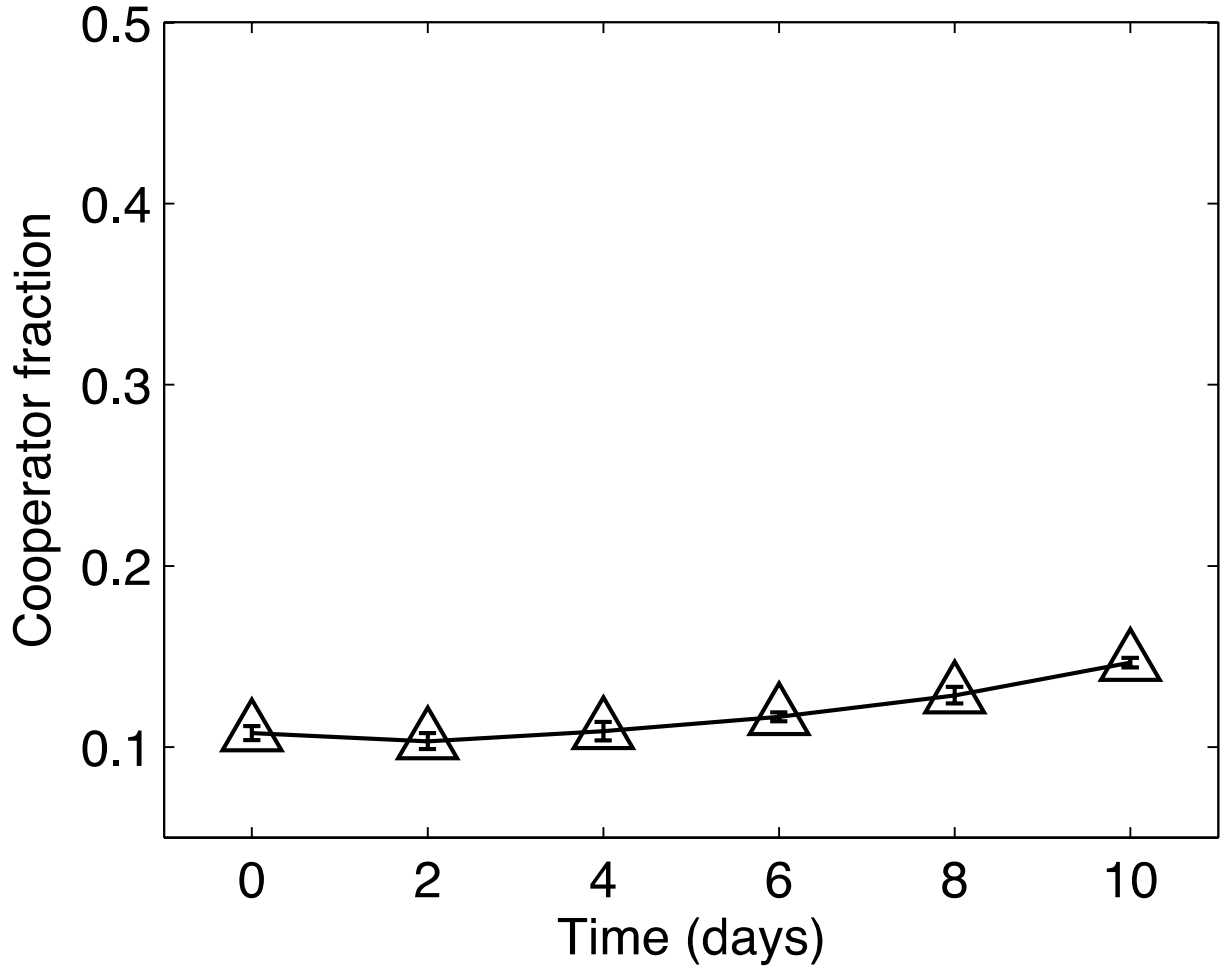
Competition between species can stabilize cooperation within a species, *Molecular Systems Biology* (2012)

Manoshi Datta

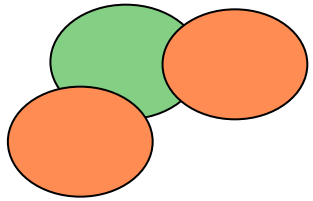
Kirill Korolev

Range expansion stabilizes cooperation in an experimental microbial metapopulation, *in revision at PNAS*

Bacterial competition drives yeast cooperation

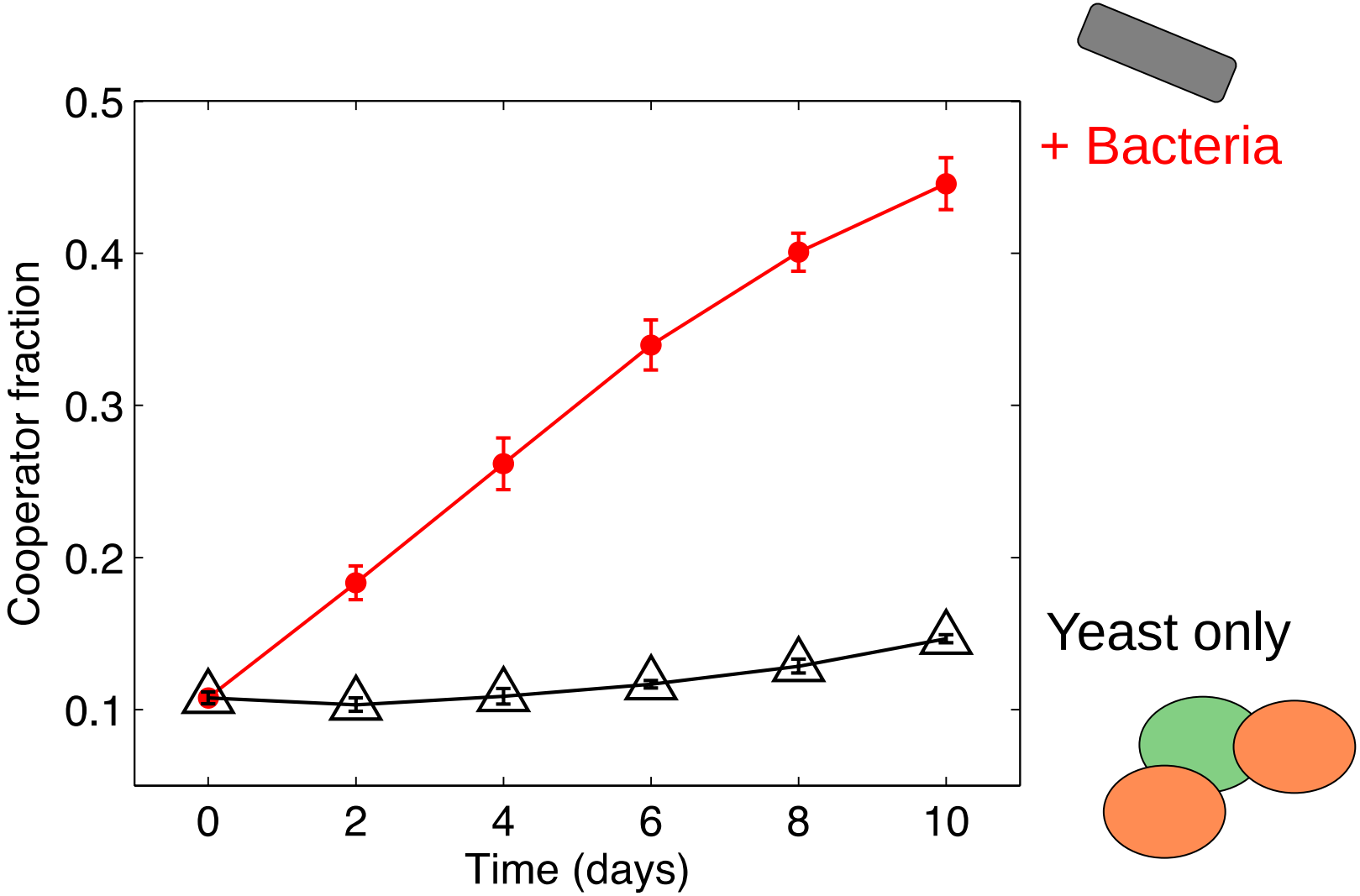


Yeast only



Celiker and Gore, *Molecular Systems Biology, (2012)*

Bacterial competition drives yeast cooperation

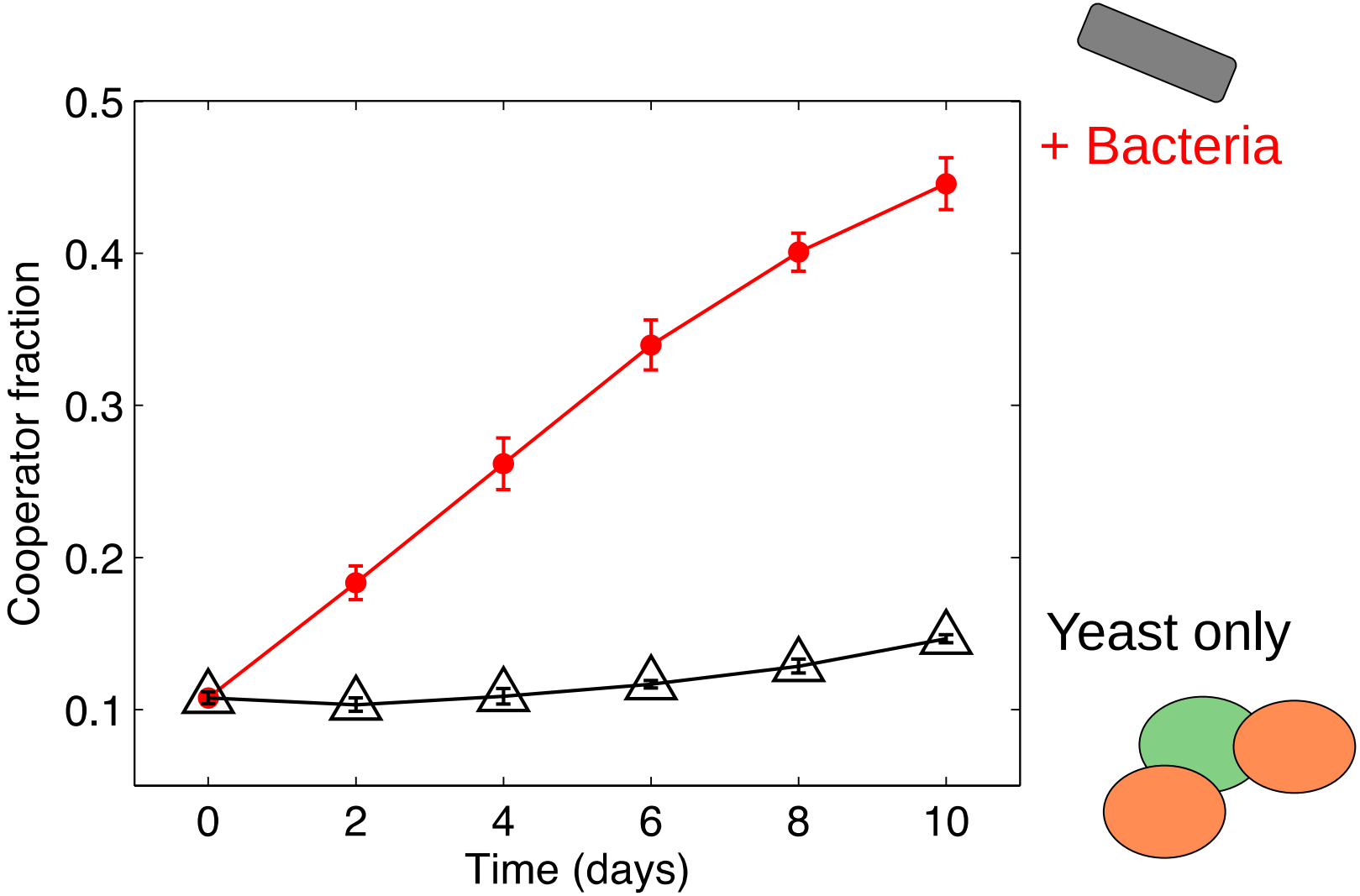


Celiker and Gore, *Molecular Systems Biology, (2012)*

Why does adding bacteria increase cooperation?

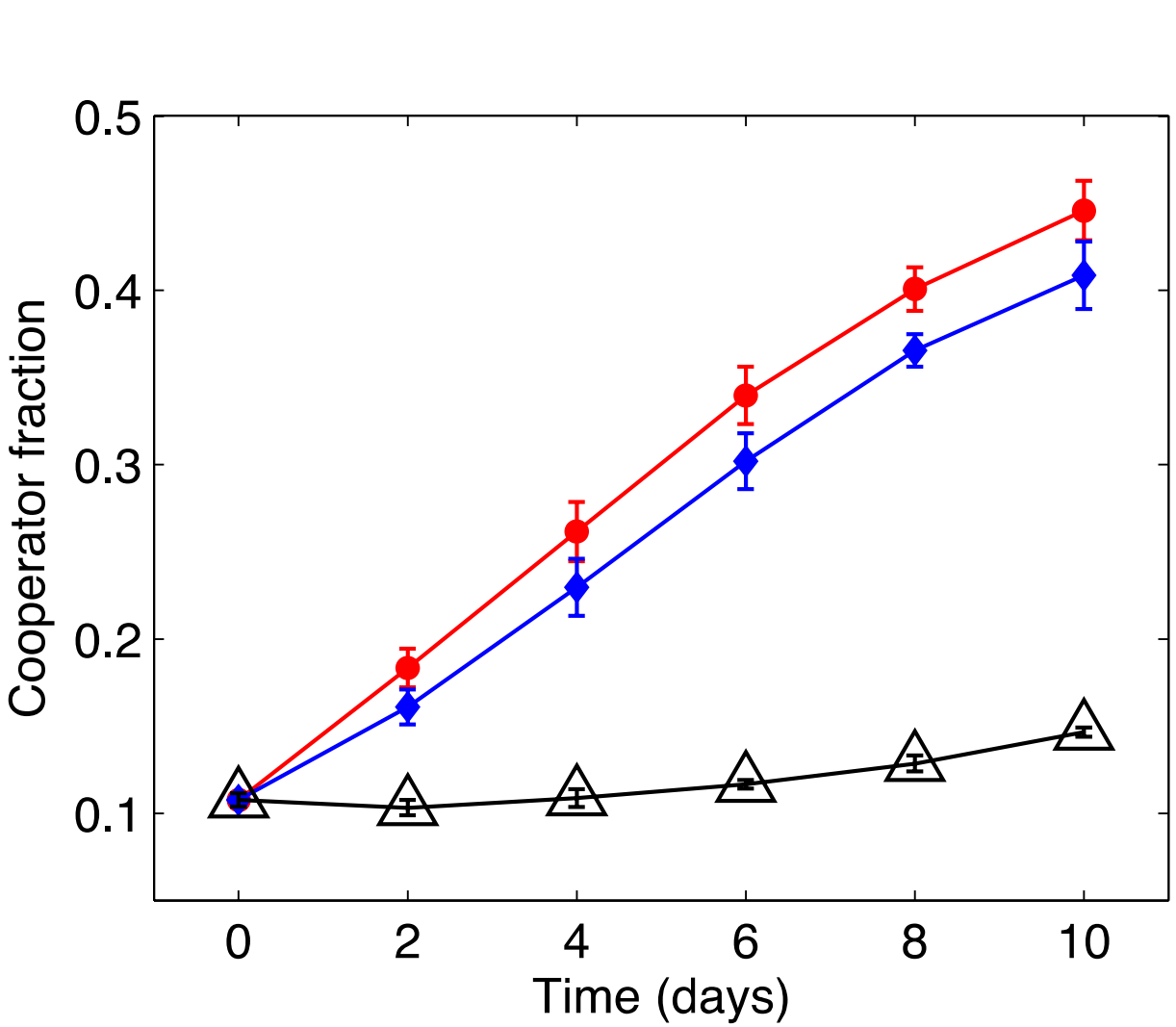
Celiker and Gore, *Molecular Systems Biology, (2012)*

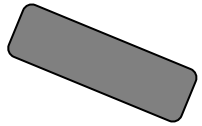
Bacterial competition drives yeast cooperation



Celiker and Gore, *Molecular Systems Biology, (2012)*

Bacteria not just superior cheater

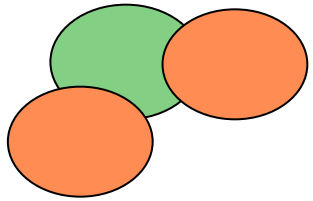




+ Bacteria

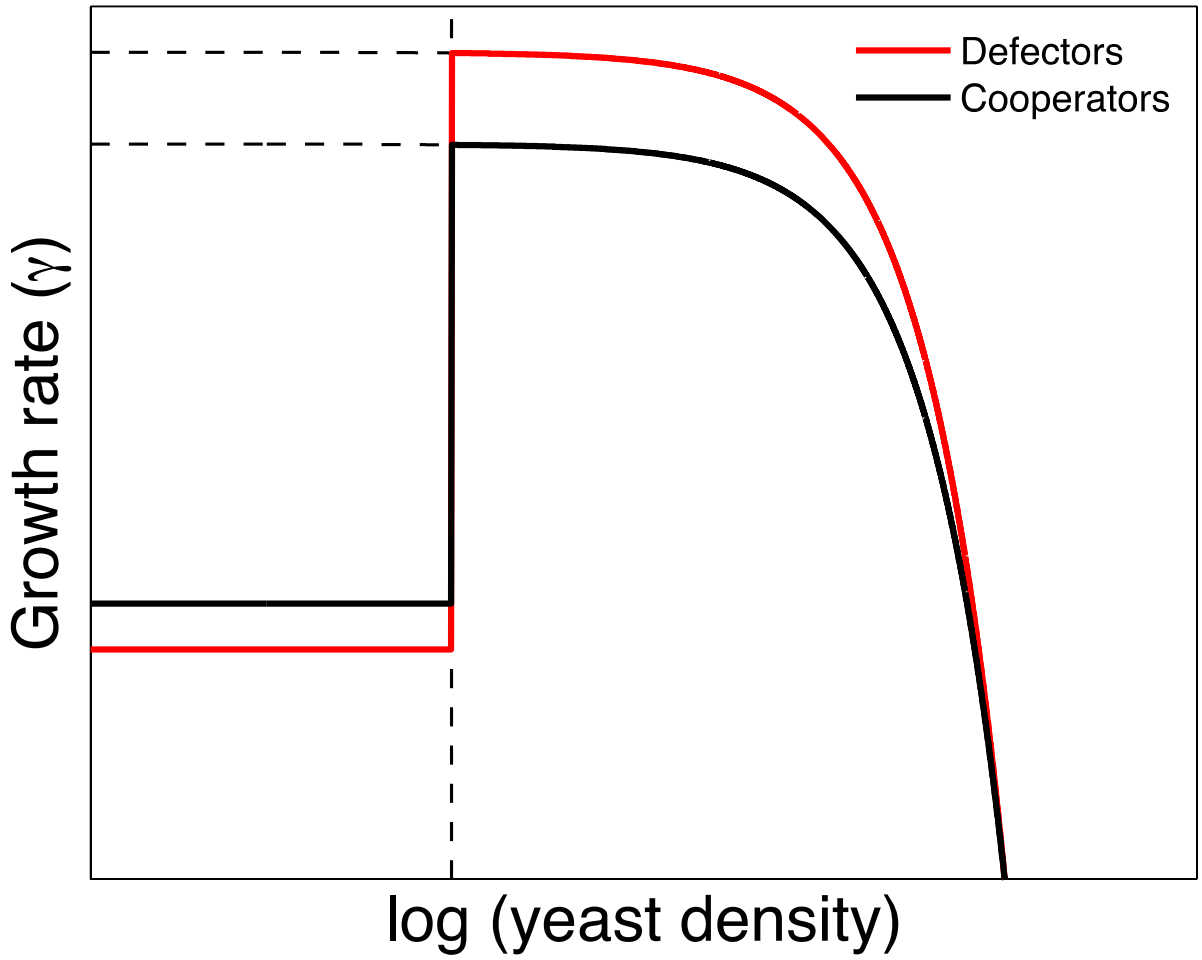
+ Bacteria (limited glucose uptake)

Yeast only



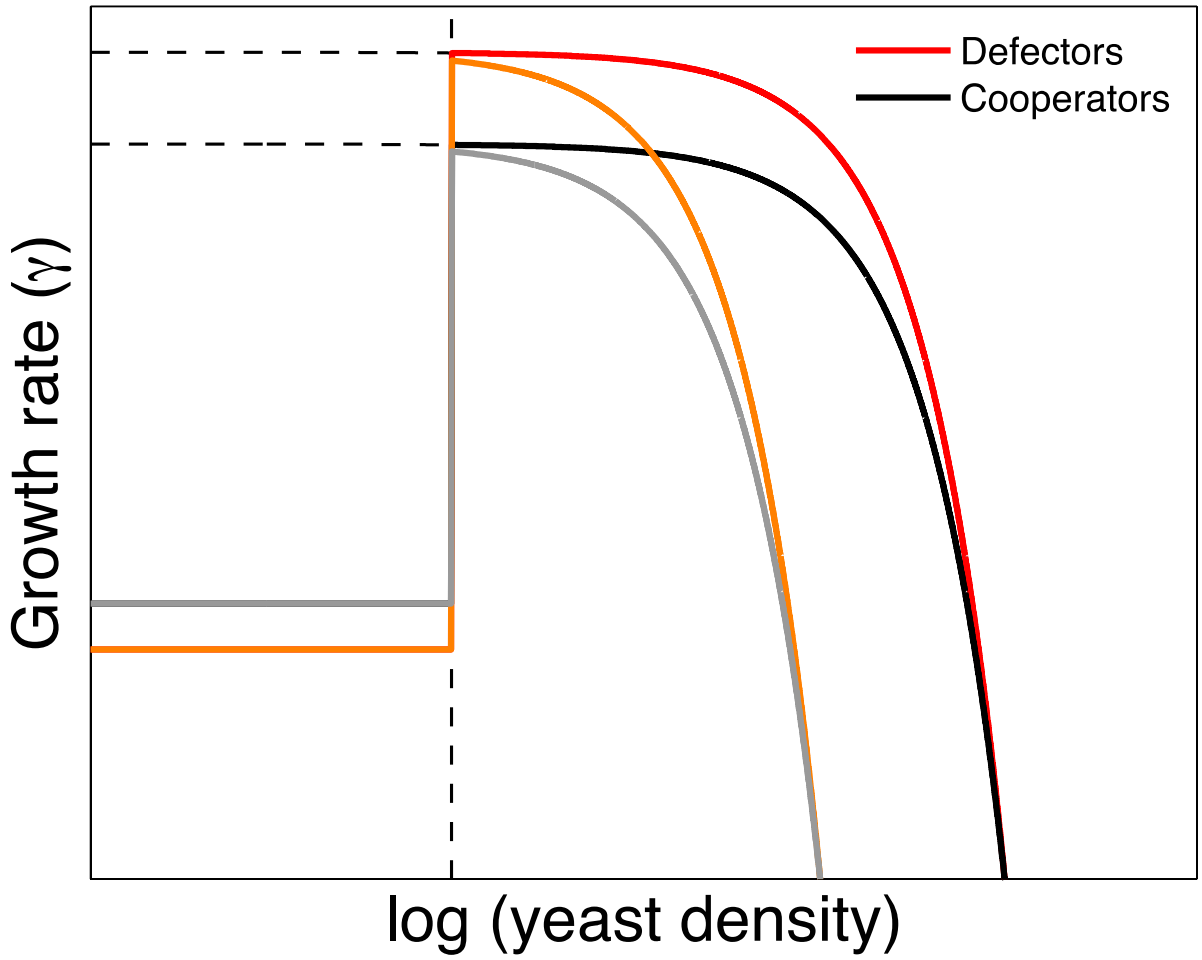
Celiker and Gore, *Molecular Systems Biology, (2012)*

Defectors have growth advantage at high density



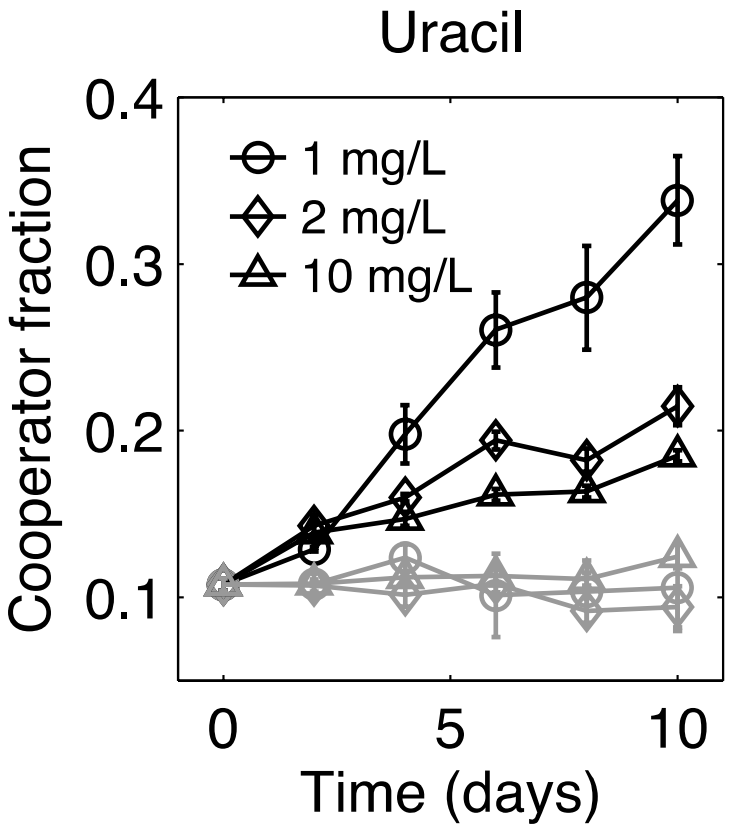
Celiker and Gore, *Molecular Systems Biology, (2012)*

Bacteria limit the carrying capacity of yeast



Celiker and Gore, *Molecular Systems Biology, (2012)*

Manually limiting yeast population → cooperation



Resource limitation

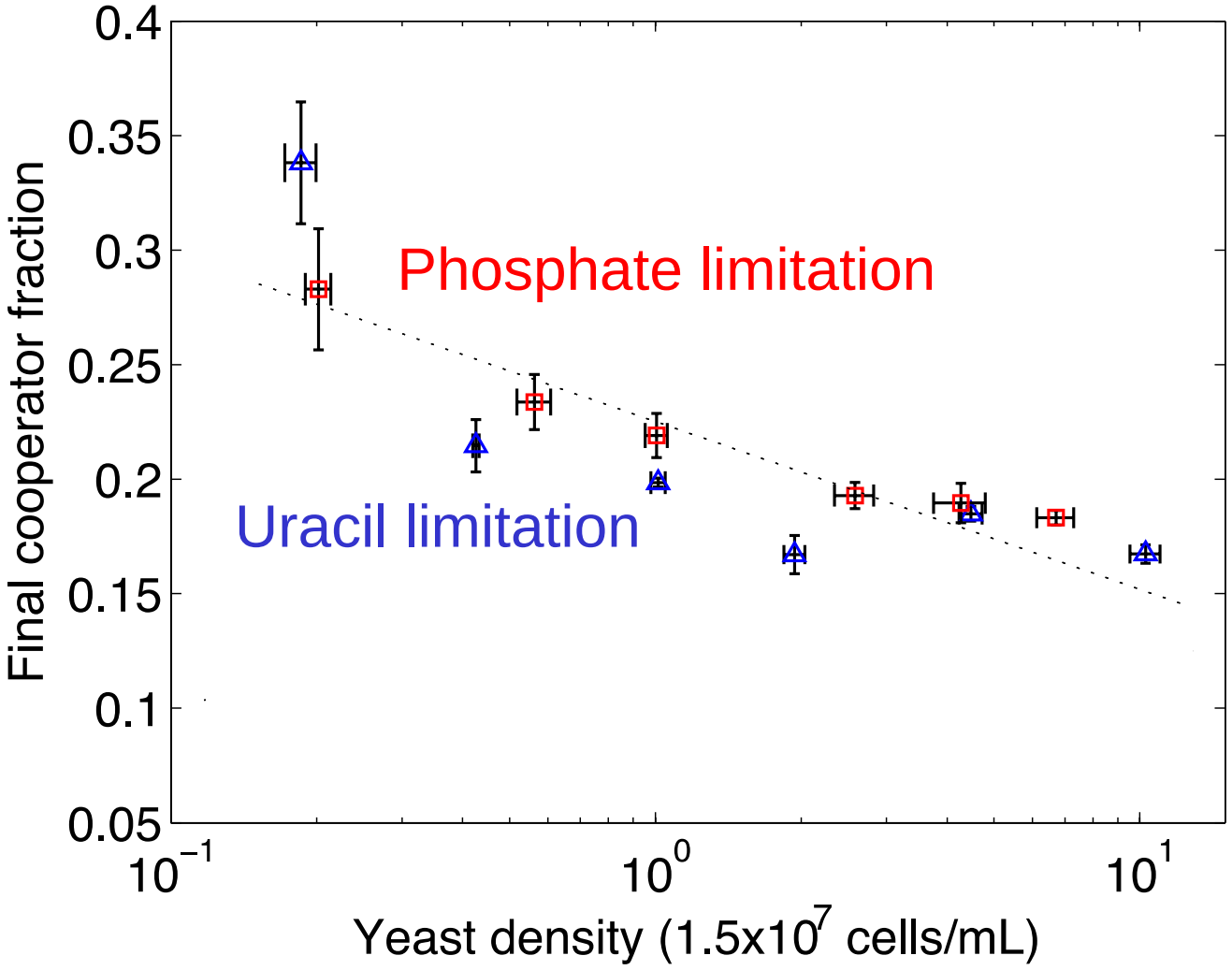
+glucose

Resource limitation

+glucose

Celiker and Gore, *Molecular Systems Biology, (2012)*

Lower yeast density → Higher cooperator frequency

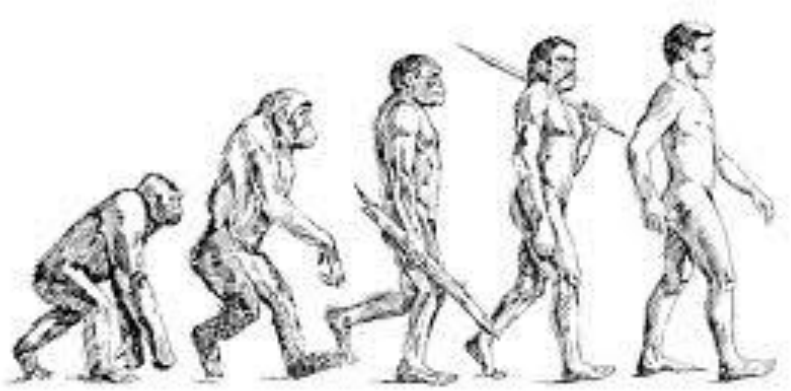


Alvaro Sanchez

“Are population dynamics and evolutionary dynamics coupled?”

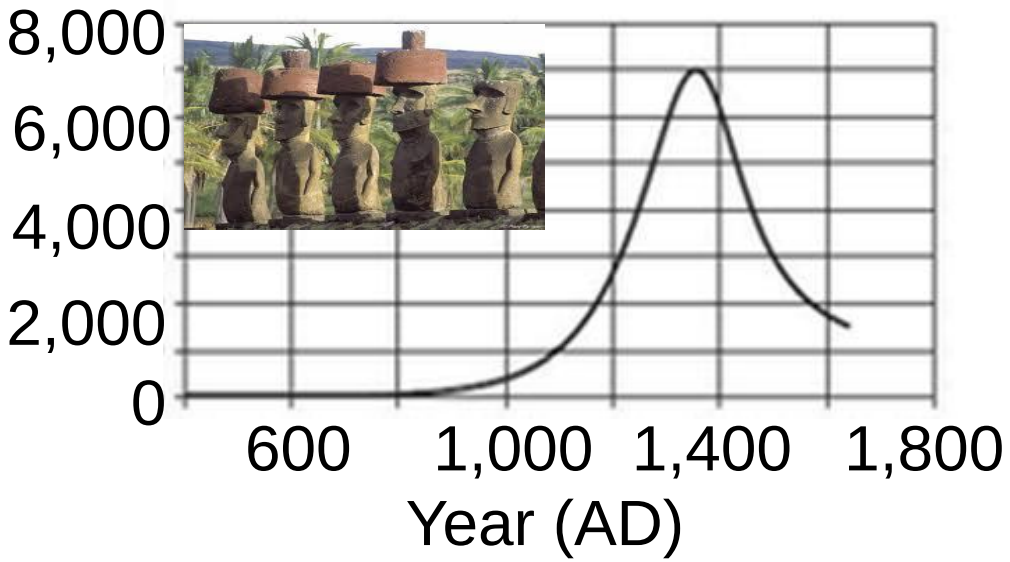
Evolution and population dynamics: Different timescales?

Evolution



~ 1 Million Years

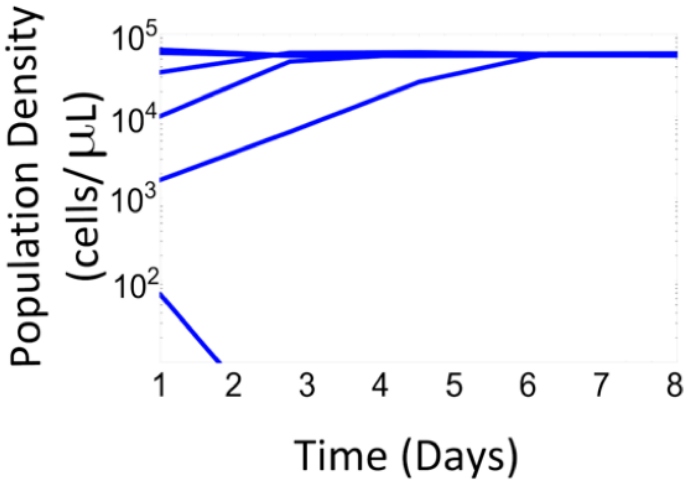
Population Dynamics



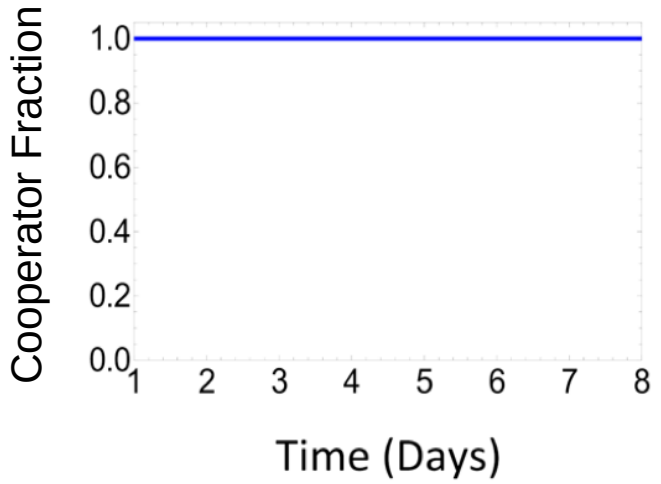
Bologna & Flores, EPL (2008)

Seemingly erratic behavior of individual populations

Population Dynamics

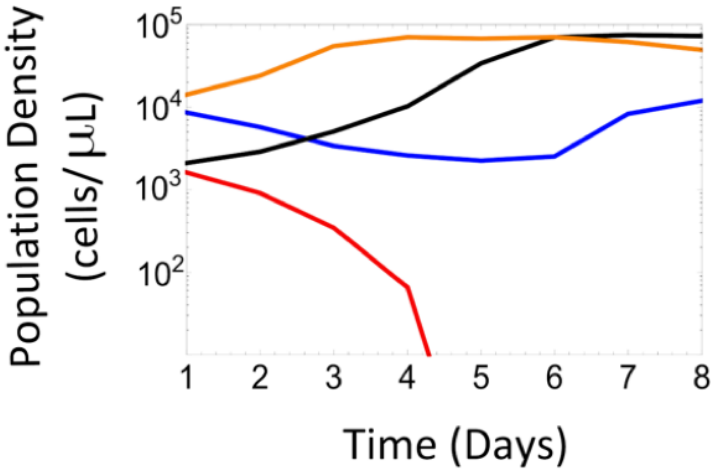


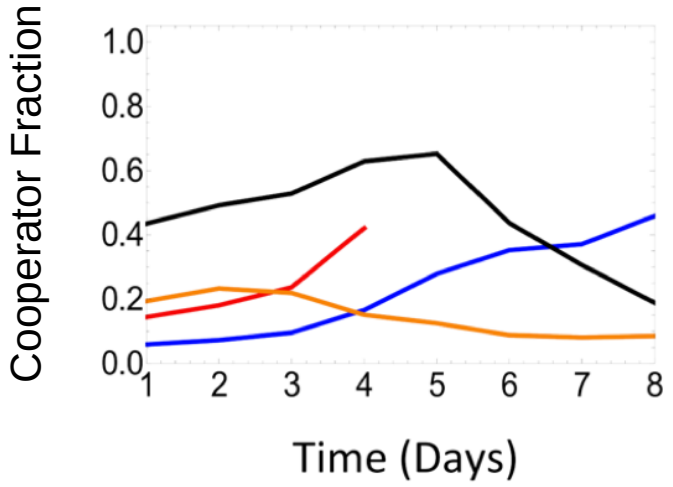
Evolutionary Dynamics



Sanchez and Gore, *submitted*

Patterns revealed by the eco-evolutionary trajectory



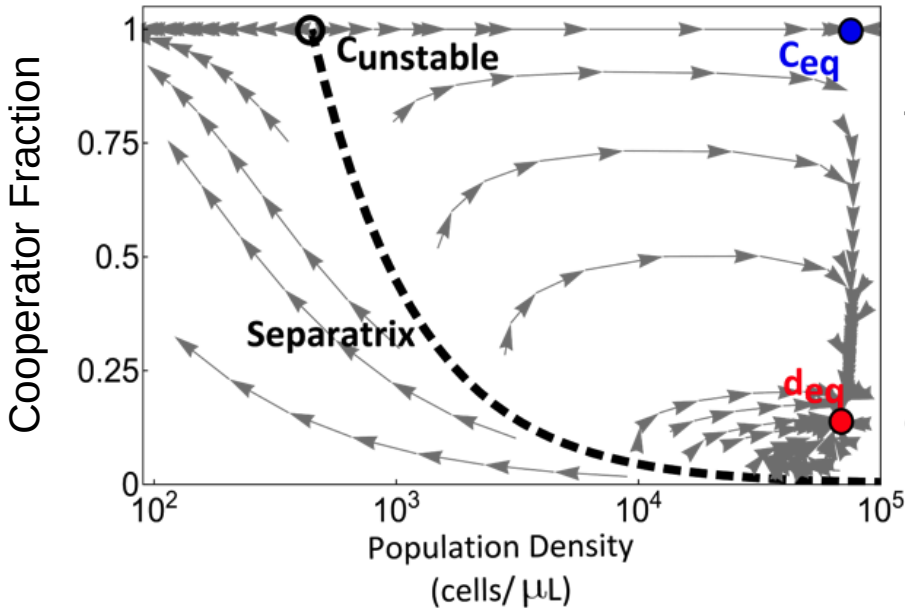


"Spirals" are eco-evolutionary feedback!

Sanchez and Gore, *submitted*

Tracking of trajectory in eco-evolutionary space

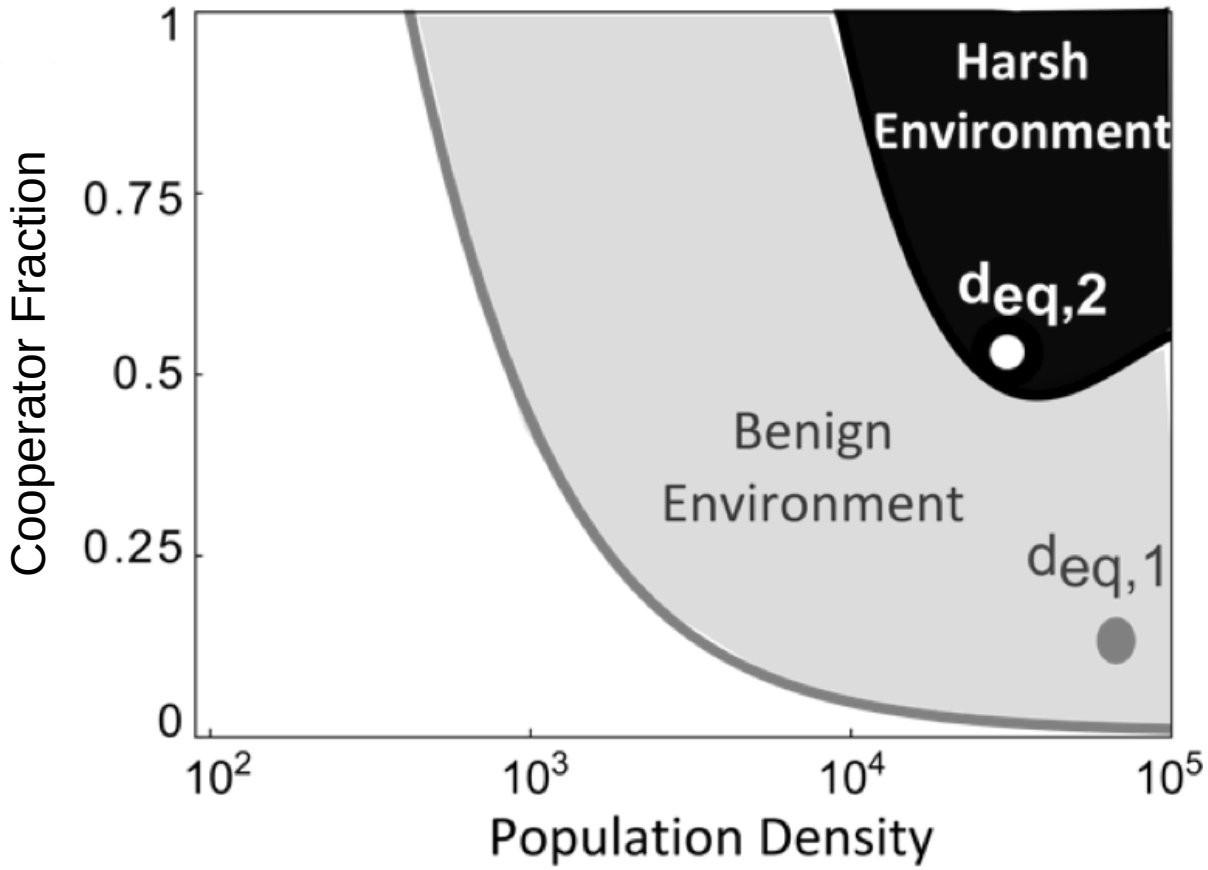
Model



Cheaters don't significantly reduce population size!

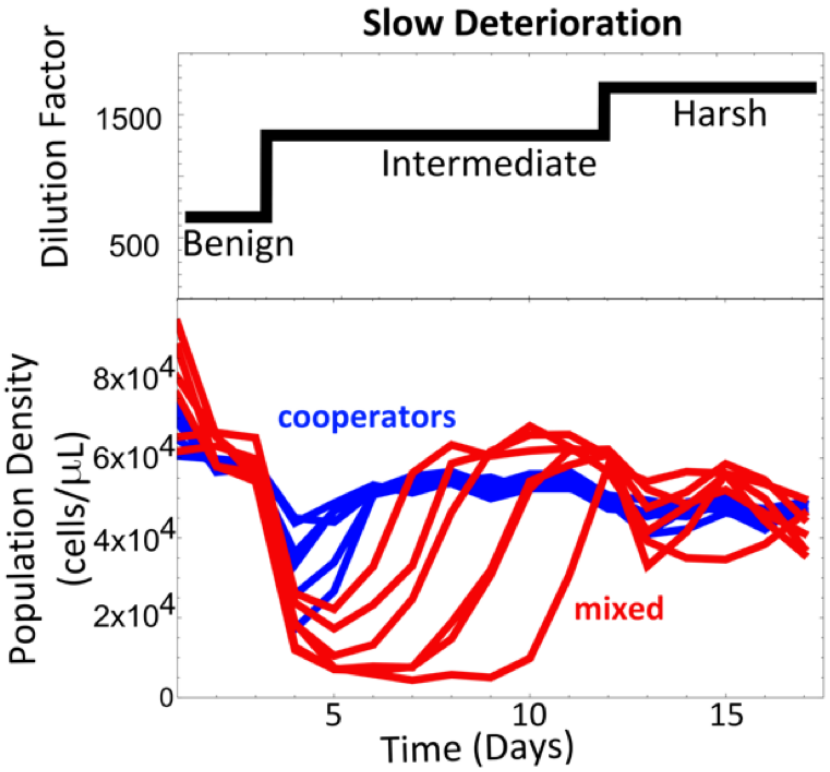
Sanchez and Gore, *submitted*

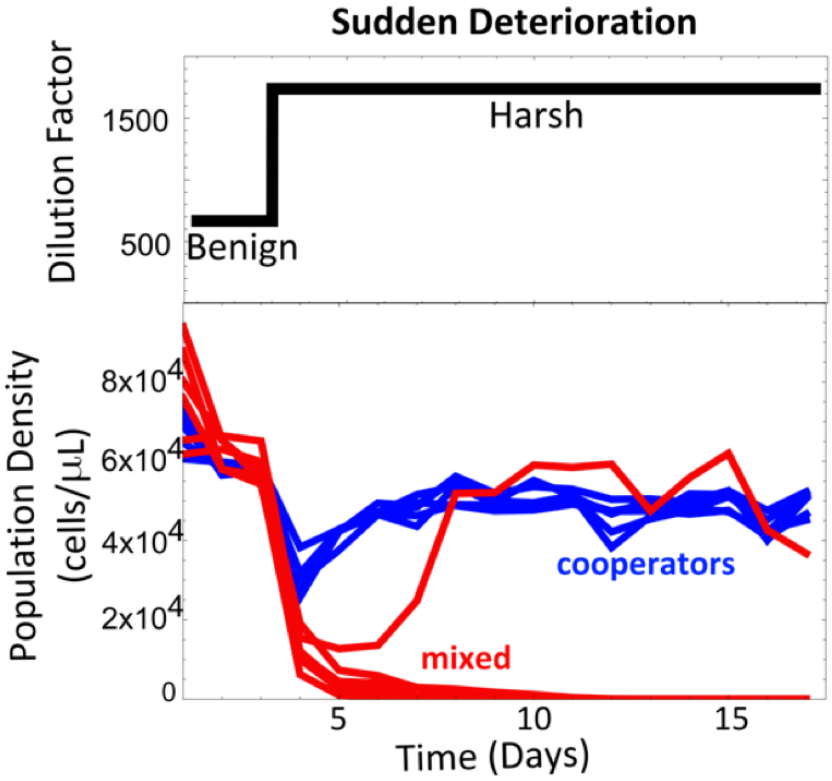
Model predicts collapse in rapidly deteriorating environment



Sanchez and Gore, *submitted*

Collapse in rapidly deteriorating environment





Sanchez and Gore, *submitted*

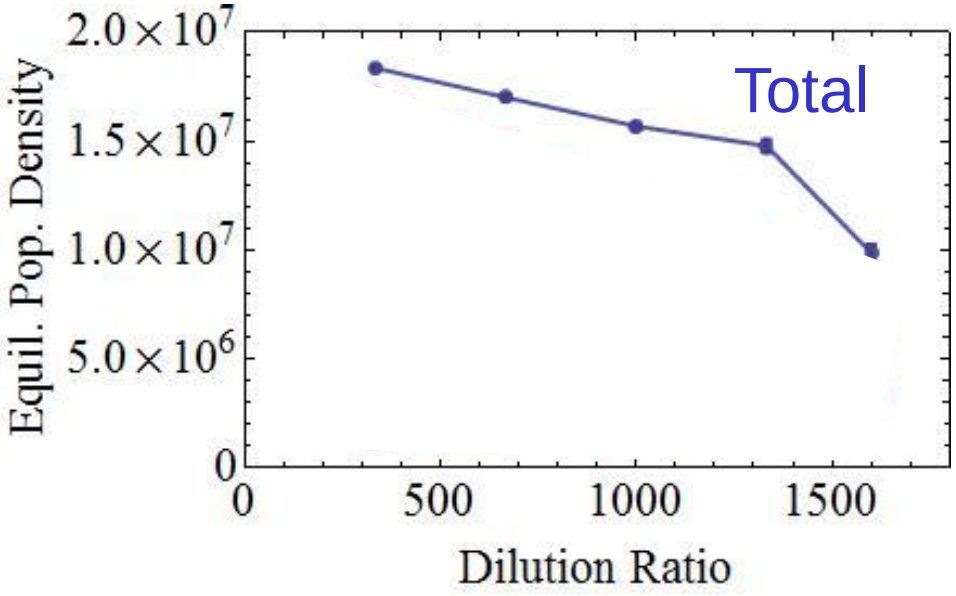
“What will the early warning indicators look like in this more complicated ecosystem?”

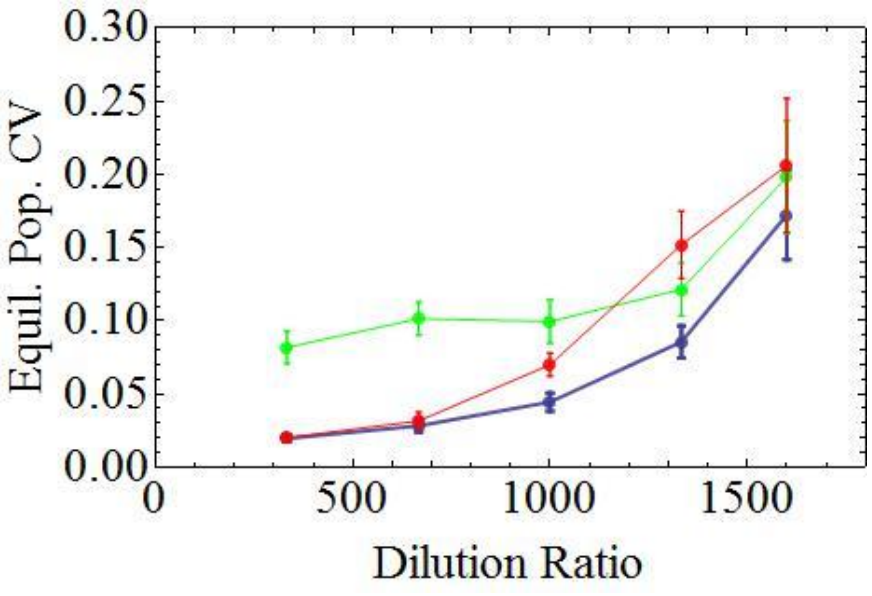
Alvaro Sanchez

Andrew Chen

Cooperator density increases in poor environment…

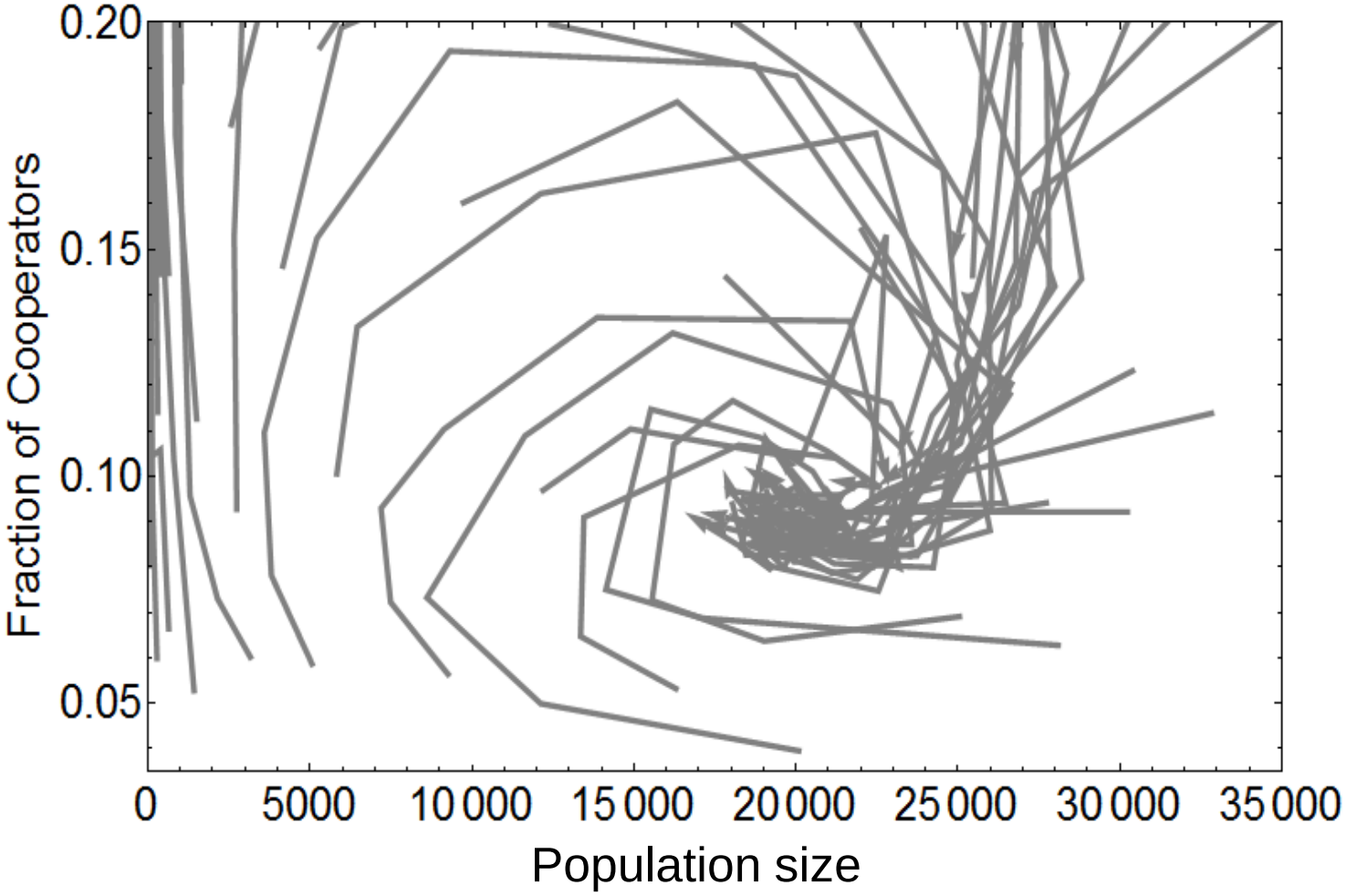
…but fluctuations increase in both sub-populations





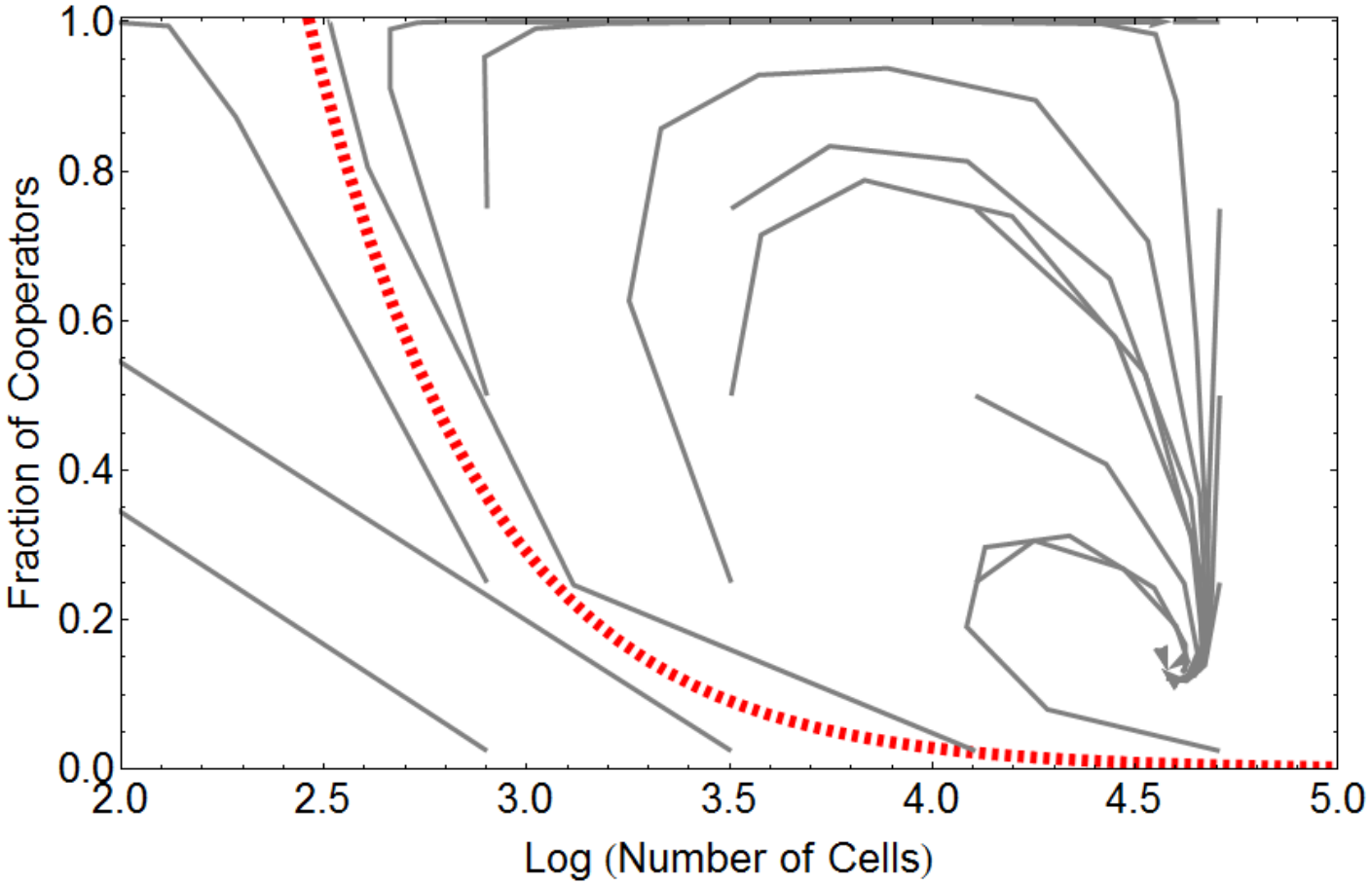
Chen, Sanchez, and Gore, *in preparation*

How do spirals change near collapse?



Chen, Sanchez, and Gore, *in preparation*

A simple model of yeast growth yields spirals



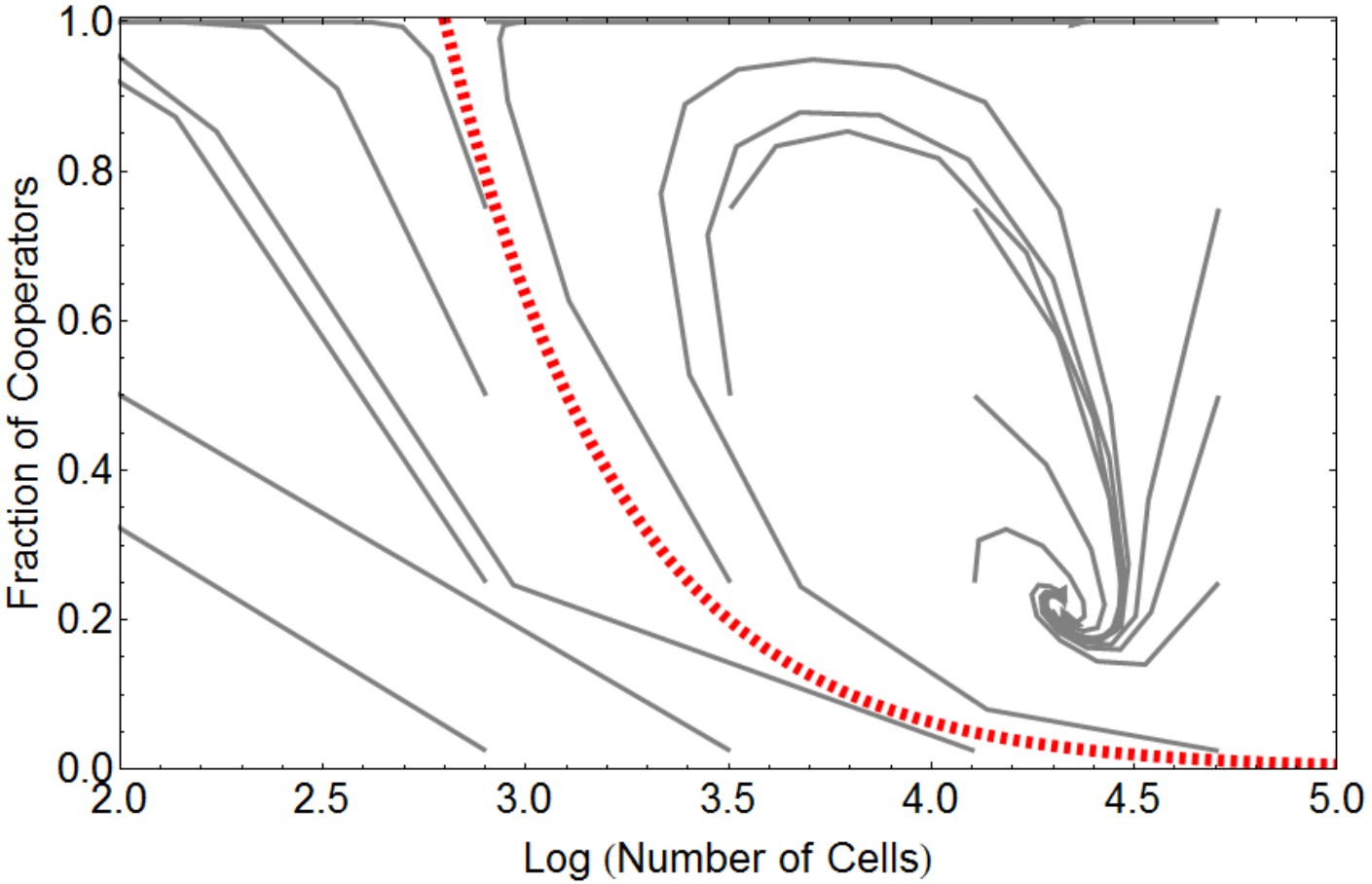
2200

800

Death Rate
(Dilution Factor)

Chen, Sanchez, and Gore, *in preparation*

Spiral changes as environment deteriorates



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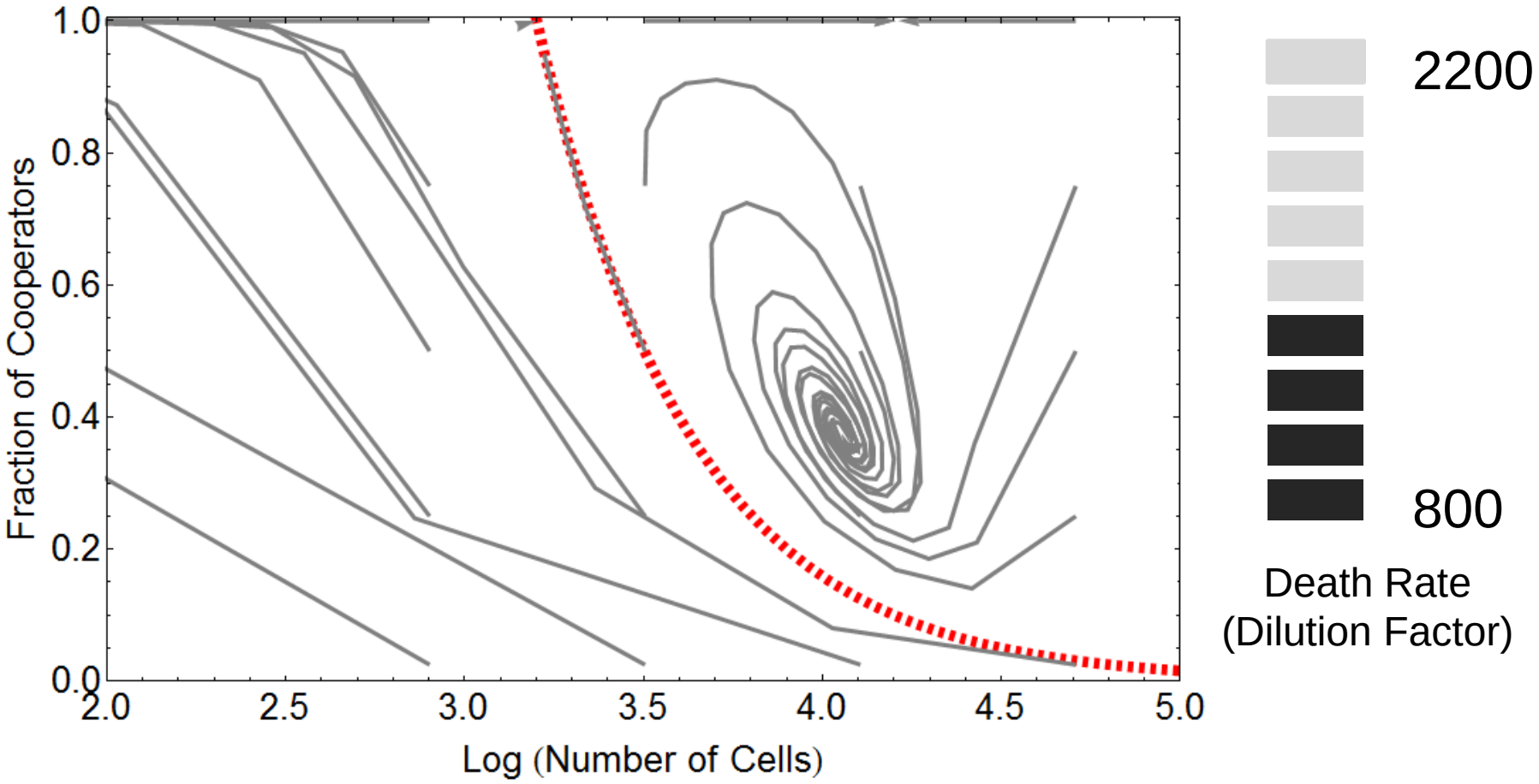
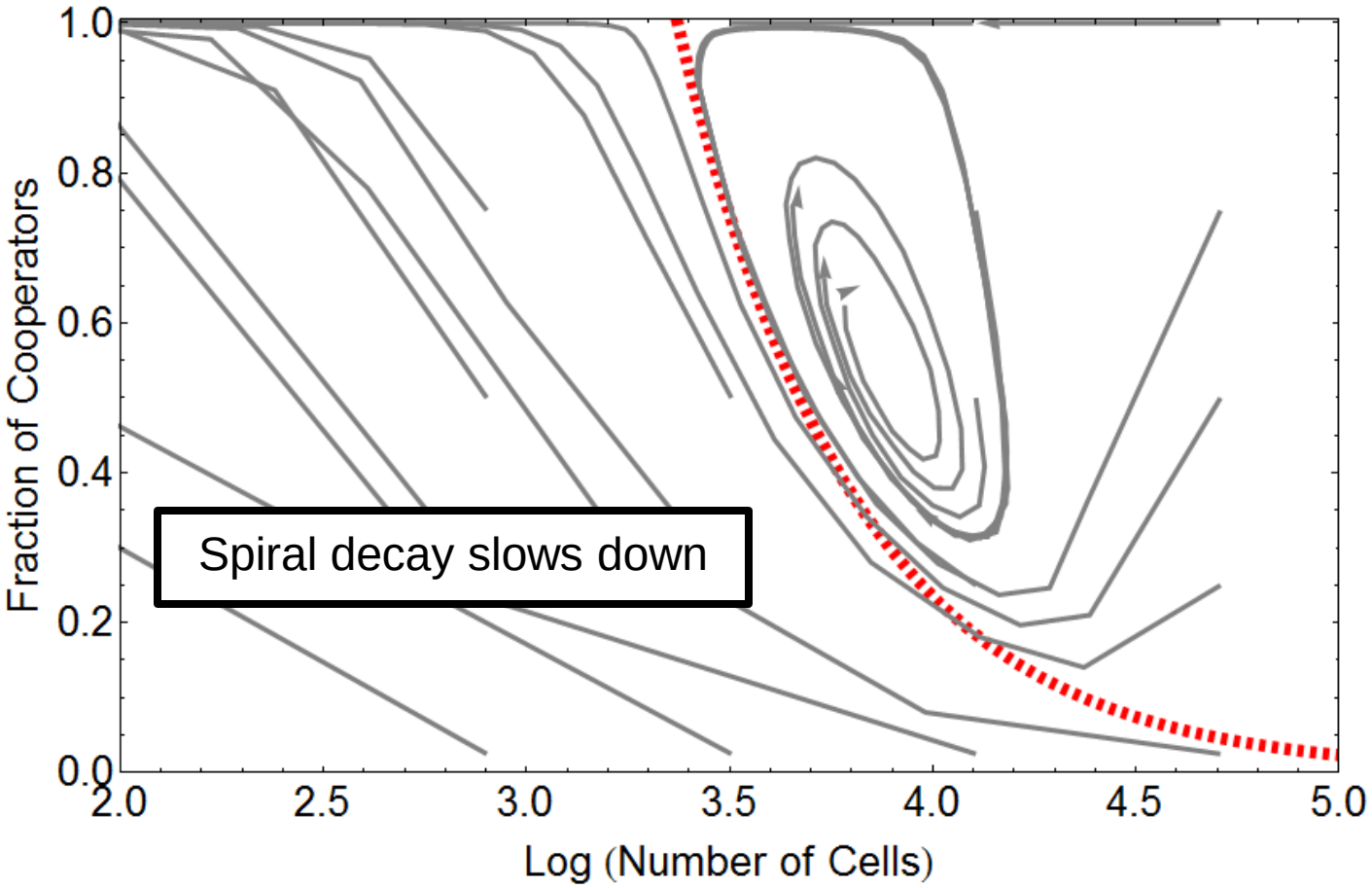


Chen, Sanchez, and Gore, *in preparation*

Fixed point loses stability as environment deteriorates



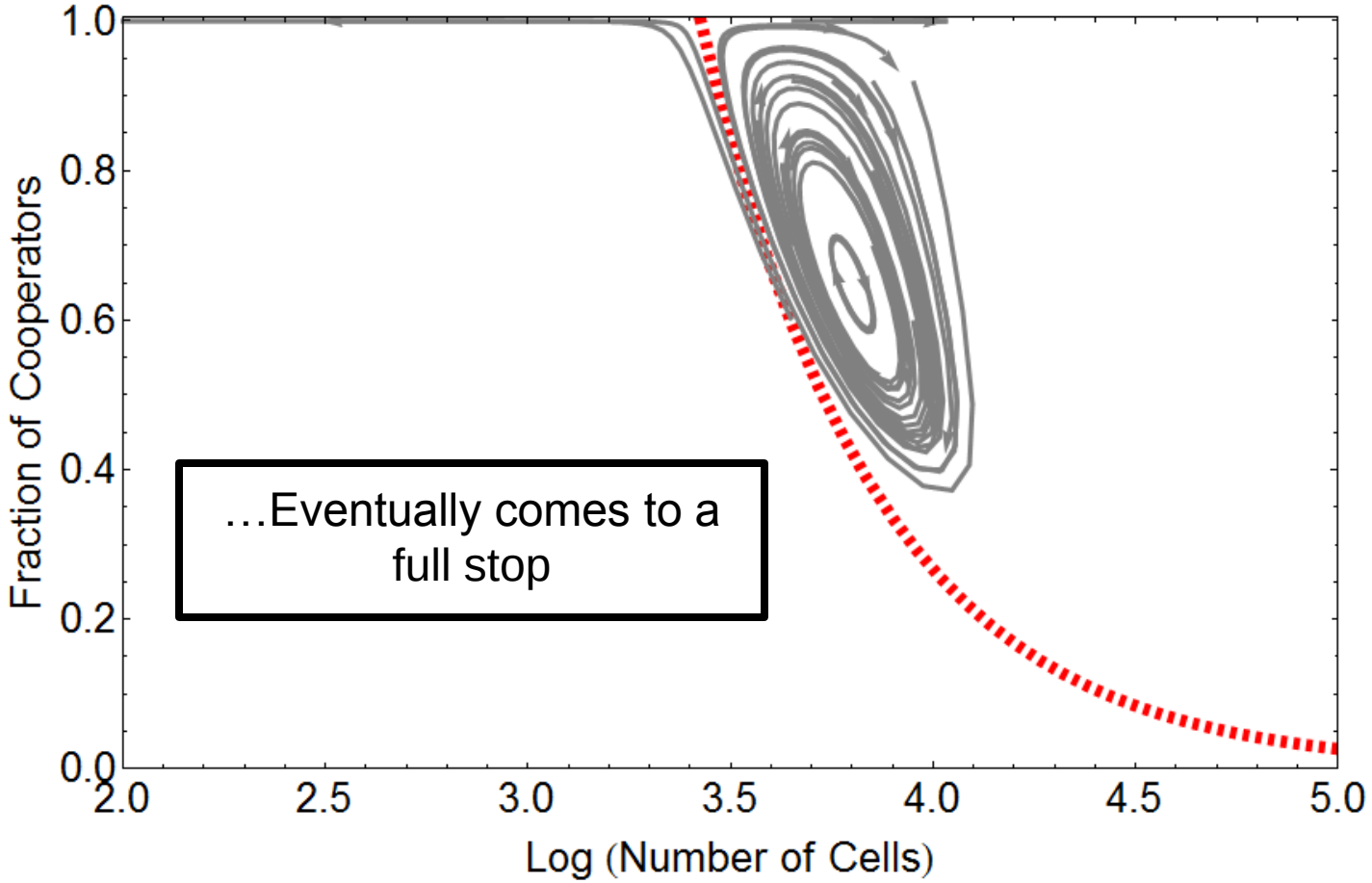
2200

800

Death Rate
(Dilution Factor)

Chen, Sanchez, and Gore, *in preparation*

Fixed point loses stability as environment deteriorates



2200

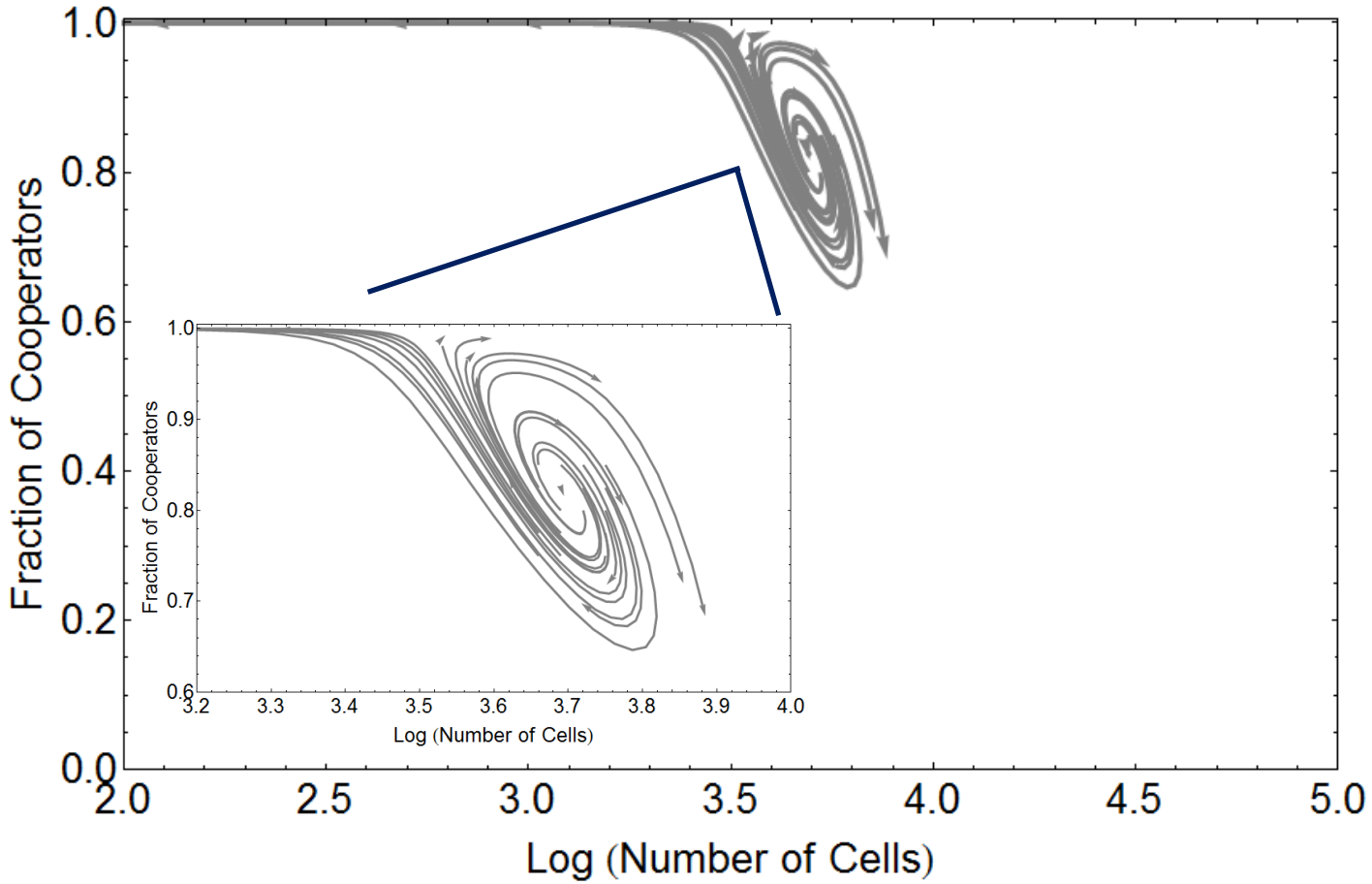
2100

800

Death Rate
(Dilution Factor)

Chen, Sanchez, and Gore, *in preparation*

Eventually the fixed point becomes unstable



2200

2125

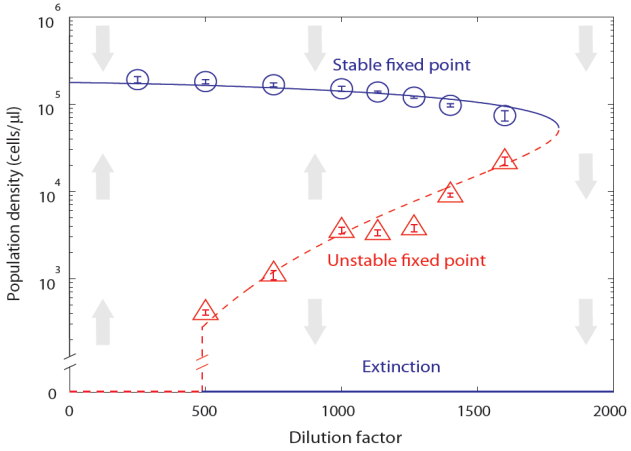
800

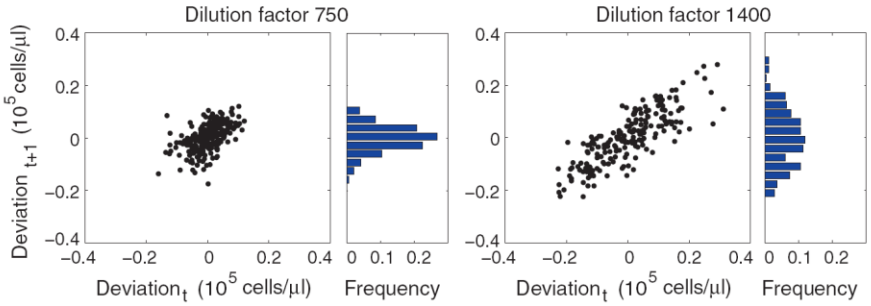
Death Rate
(Dilution Factor)

Chen, Sanchez, and Gore, *in preparation*

Summary

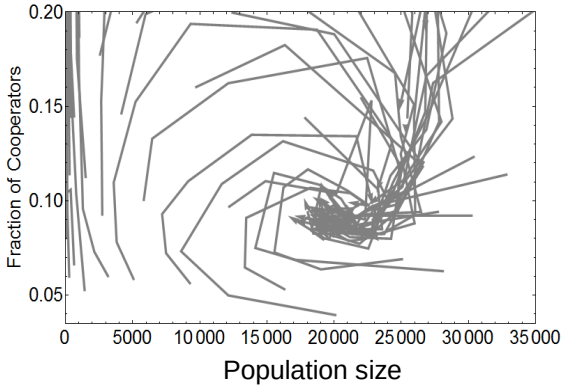
We have used cooperative growth of yeast to study catastrophic collapse

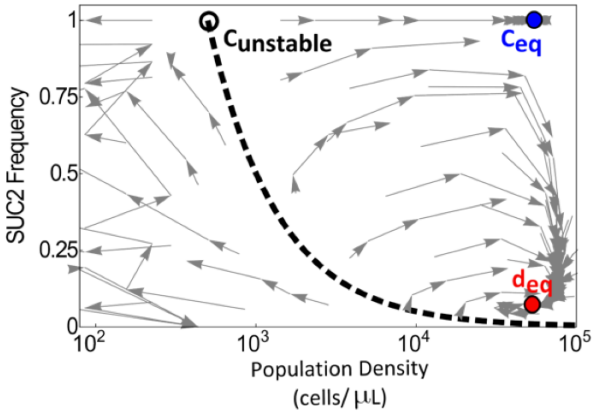




Both the size and timescale of population fluctuations increase before collapse

Cheater strategies invade, but there is coexistence and survival



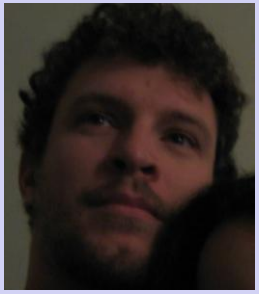


Insight obtained by visualizing the eco-evolutionary trajectories.

Acknowledgements

Postdocs

Alvaro Sanchez



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