SFI-CSSS
Week 3

Van Savage

"Sooner or later in life we all discover that perfect happiness is unrealizable, but few of us pause to consider the opposite: that so, too, is perfect unhappiness. The obstacles preventing the realization of both of these extreme states are of the same nature: they derive from our human condition, which is hostile to everything infinite. Our ever inadequate knowledge of the future opposes it, and this is called, in the one instance, hope and, in the other, uncertainty about tomorrow. The certainty of death opposes it, for death places a limit on every joy, but also on every sorrow. Our inevitable material cares oppose it, for, as they poison every lasting happiness, they just as assiduously distract us from our misfortunes, making our awareness of them intermittent and hence bearable."
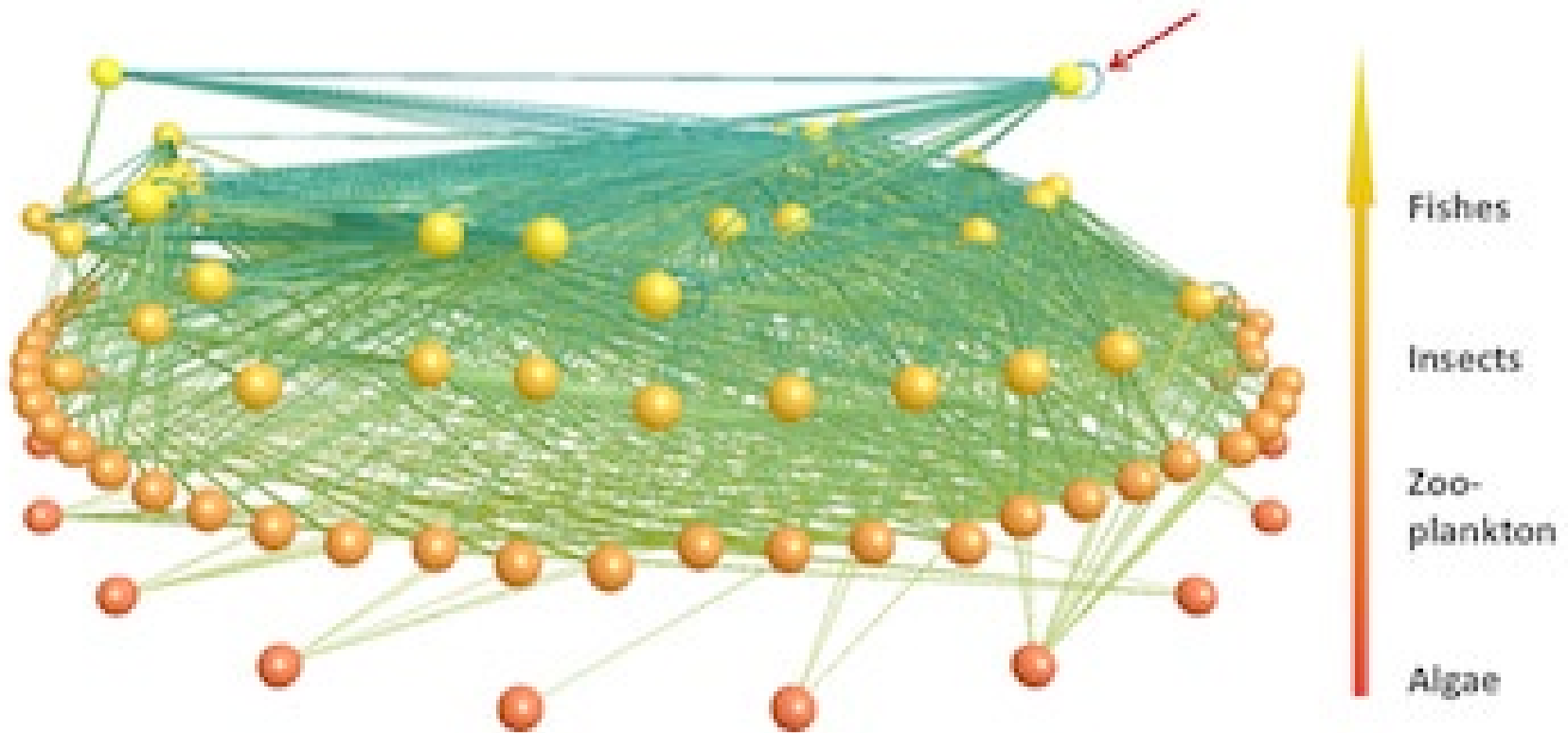
--Primo Levi

Complexity and Stability

Many biological systems and complex systems seem large, complex, and stable.

Do these features reinforce each other, tradeoff against each other, or do systems have to be special to achieve all of this?

Complexity and Stability—predator-prey food web

Little Rock Lake Food Web

Fishes

Insects

Zoo-plankton

Algae

92 species, 997 links, 11 links/species

In 1972, Robert May showed that randomly generated food webs decreased in stability as they increased in complexity. This result was paradoxical to many ecologists who experienced the opposite pattern in nature. This is the basis for the long-standing *diversity vs. stability* debate in ecology.

-Wilmers, Sinha, and Brede (SFI Summer School)
Oikos 2002

Review of May's model

May's dynamical equations on network

$$\dot{X}(t) = AX(t)$$

X—vector of population abundances at each node

A—Interaction matrix of strength of connections between nodes/species

Complexity-stability in May's model

n—number of species (or proteins or genes) determines size of matr

C=(number of links)/(number of possible pairs)
   realized connectance among parts and related to complexity
   determines number of non-zero entries in interaction matrix A

σ—standard deviation/width of normal distribution from which
   interactions are randomly sampled. Related to strength of
interaction.

μ—mean interaction strength=0 in May
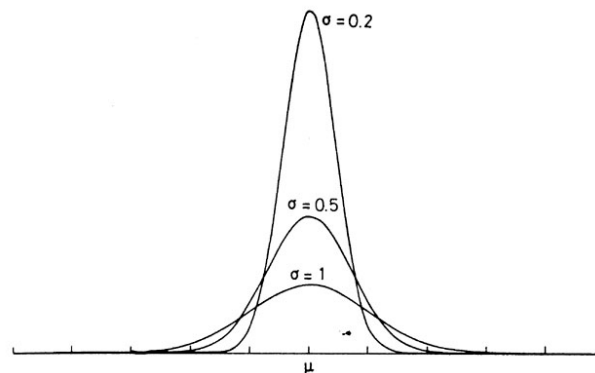
Stability analysis and eigenvalue theorem

Allow n to be large and non-diagonal entries into matrix are random. Seems difficult to calculate eigenvalues, but referred to theorem by Wigner semi-circle law. Numerically found that eigenvalues fall in circle centered at -1 that grows as $\sqrt{nC\sigma}$ and eventually crosses 0, implying instability.

(a) σ =0   (b) σ =0.016667

(c) σ =0.033333   (d) σ =0.05

Karl Nyman thesis
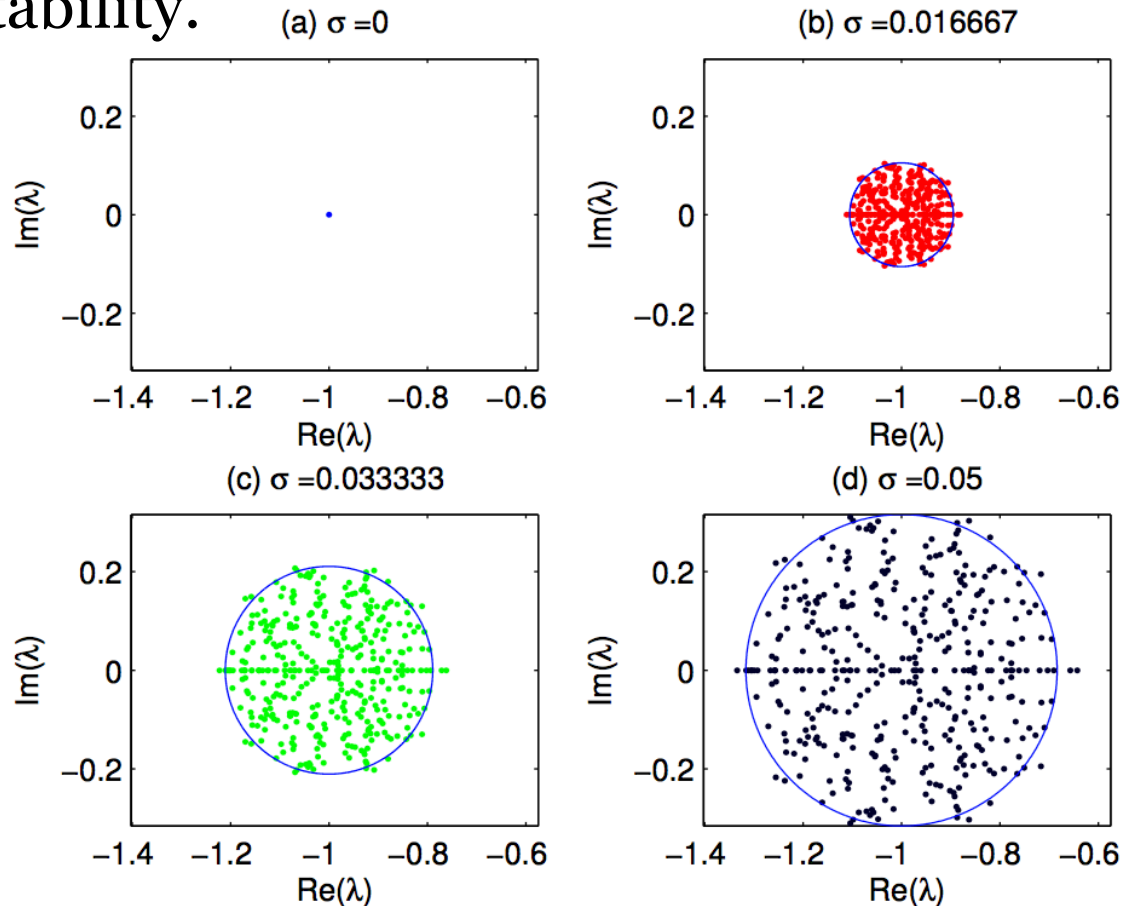
Seems counter to what we see in nature from genes to proteins to ecosystems.

Possible changes to assumptions

1. Refine what we mean by instability in mathematical system versus ecological system (e.g., Holling 1973 resilience paper).

1. Interaction matrices are not random. There is structure/hierarchy/modularity through all of these, and this is where a lot of the interesting biological processes enter.

3. How do realistic dynamical equations map onto May's definition of interaction matrix, A, and associated stability analysis.

4. Does not factor in environment (meaning body size, climate, diseases, etc.) can and how it changes over relevant time scales. Maybe never at equilibrium/fixed point to perturb away from.

Structured interaction matrices

Why ecological networks?

1950's Paradigm:

**Complex communities MORE
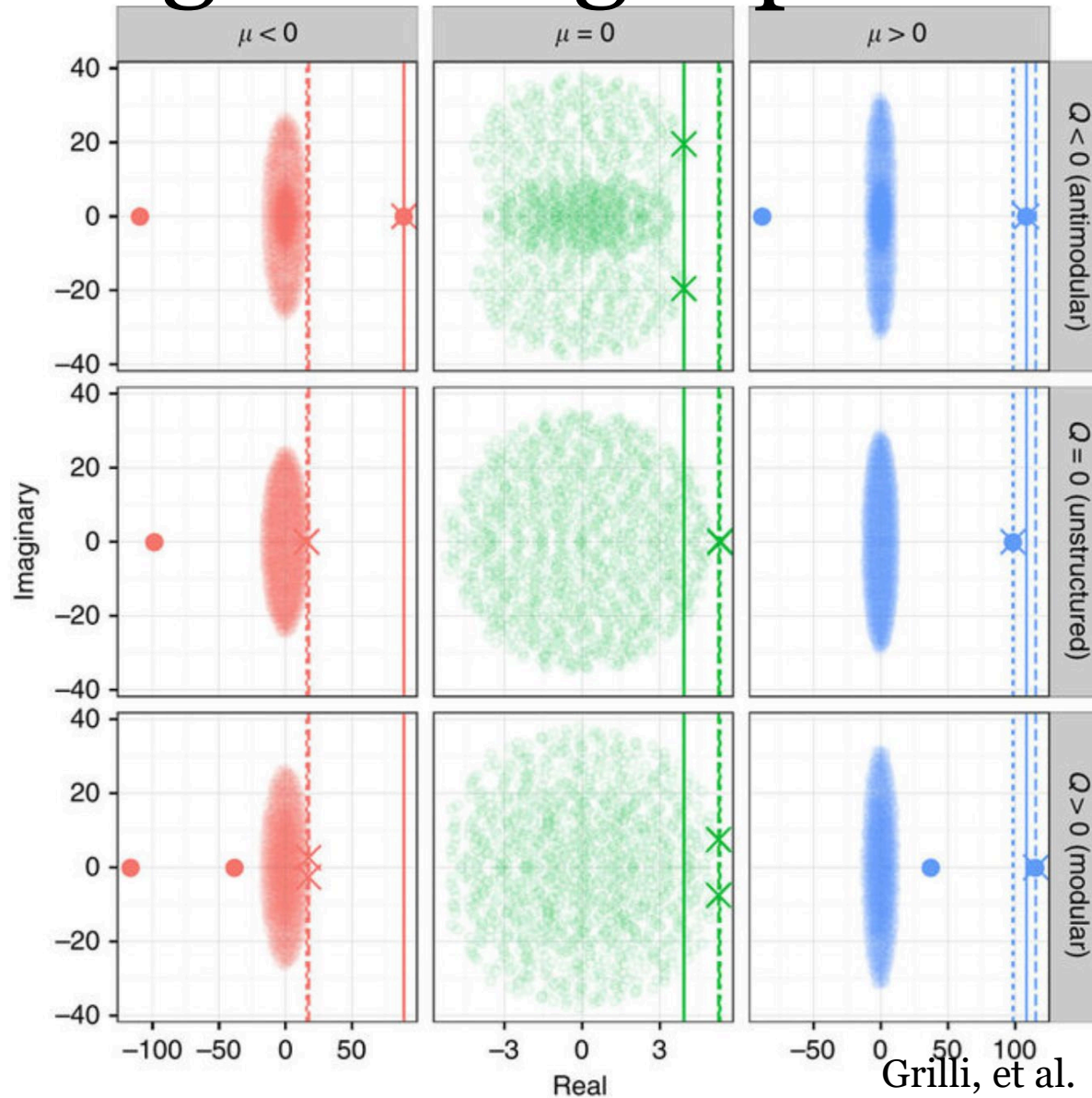stable than simple communities**

1970's Challenge:

**Complex communities LESS
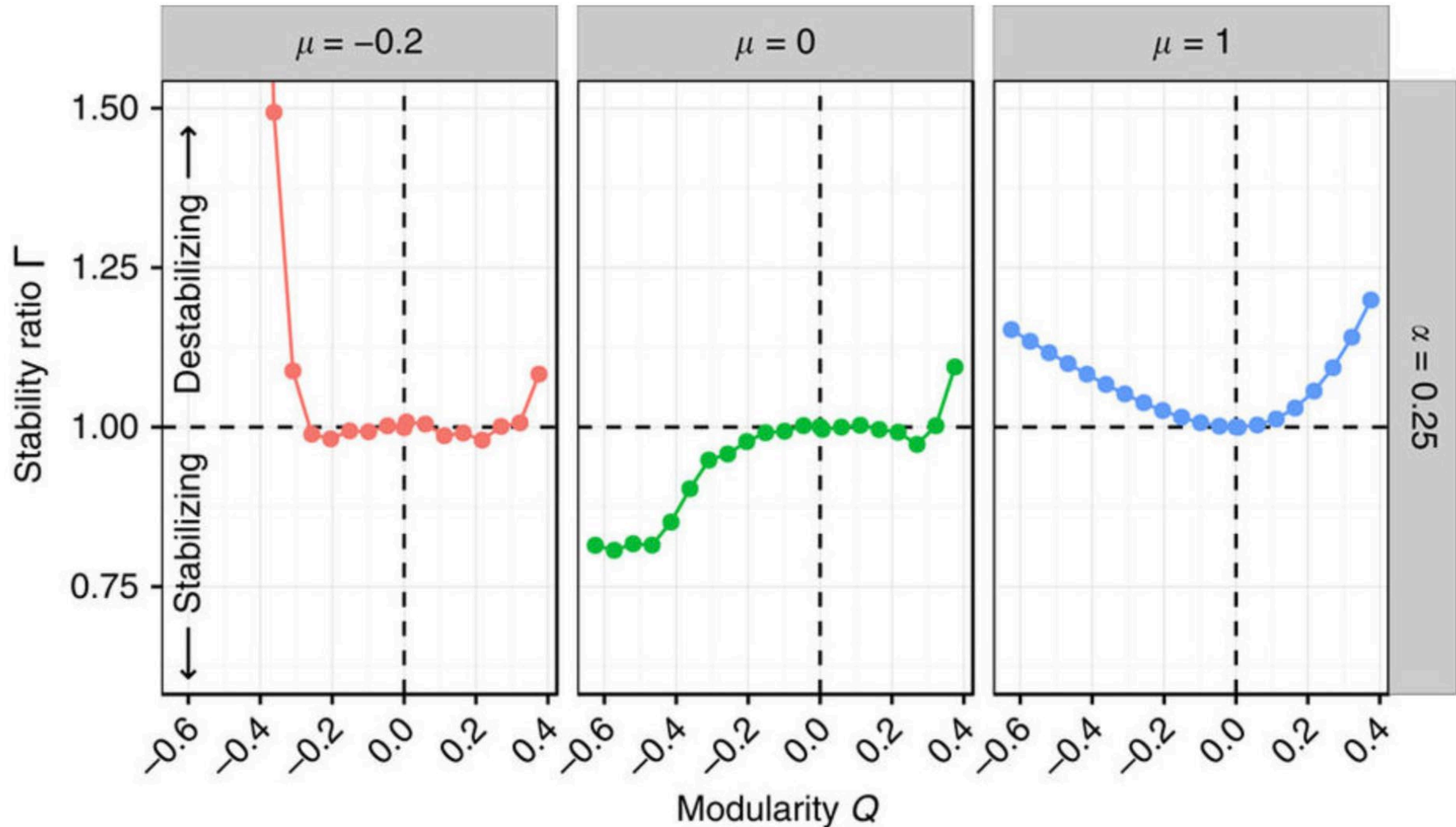stable than simple communities**

Current & Future Research:

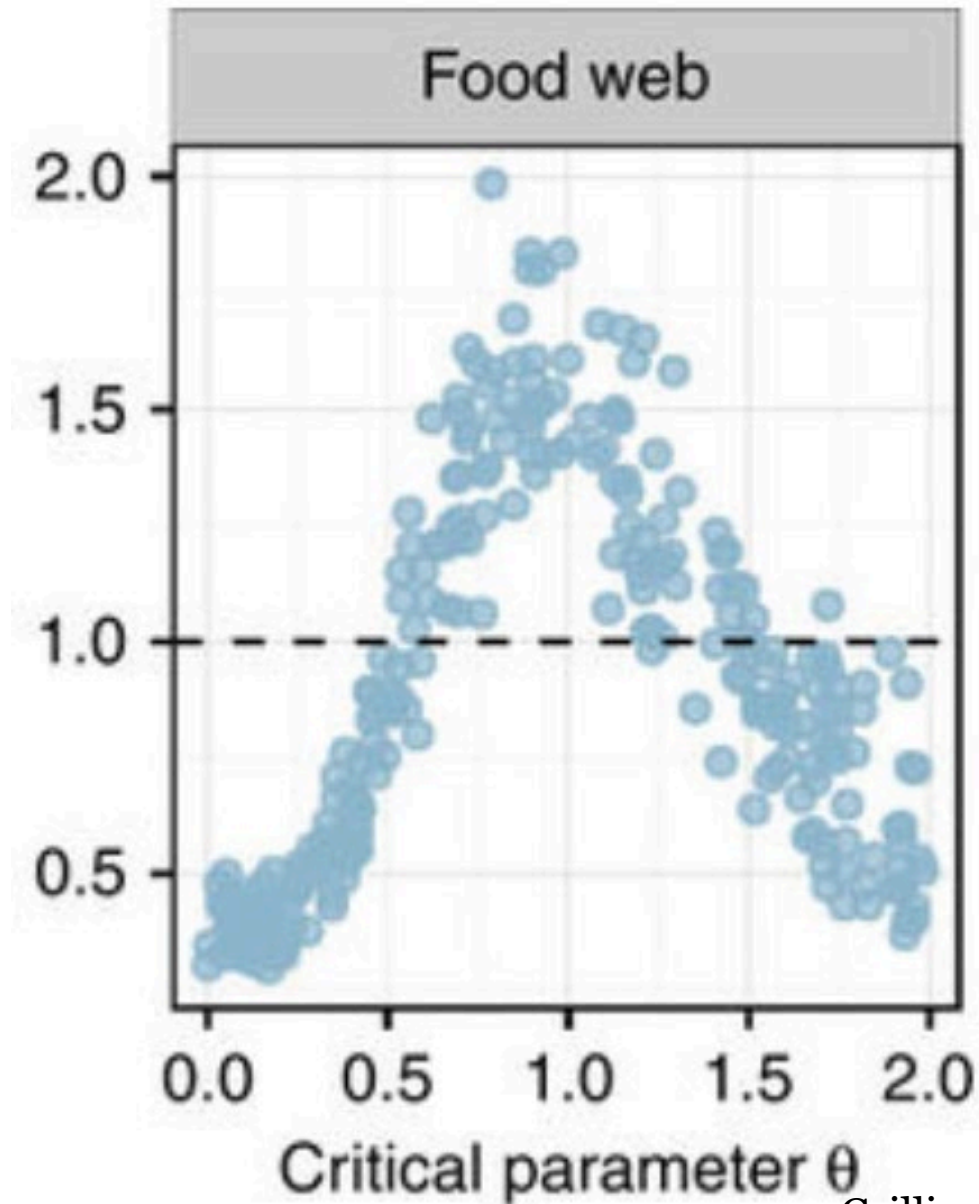**"Devious strategies" that promote
stability and species coexistence**

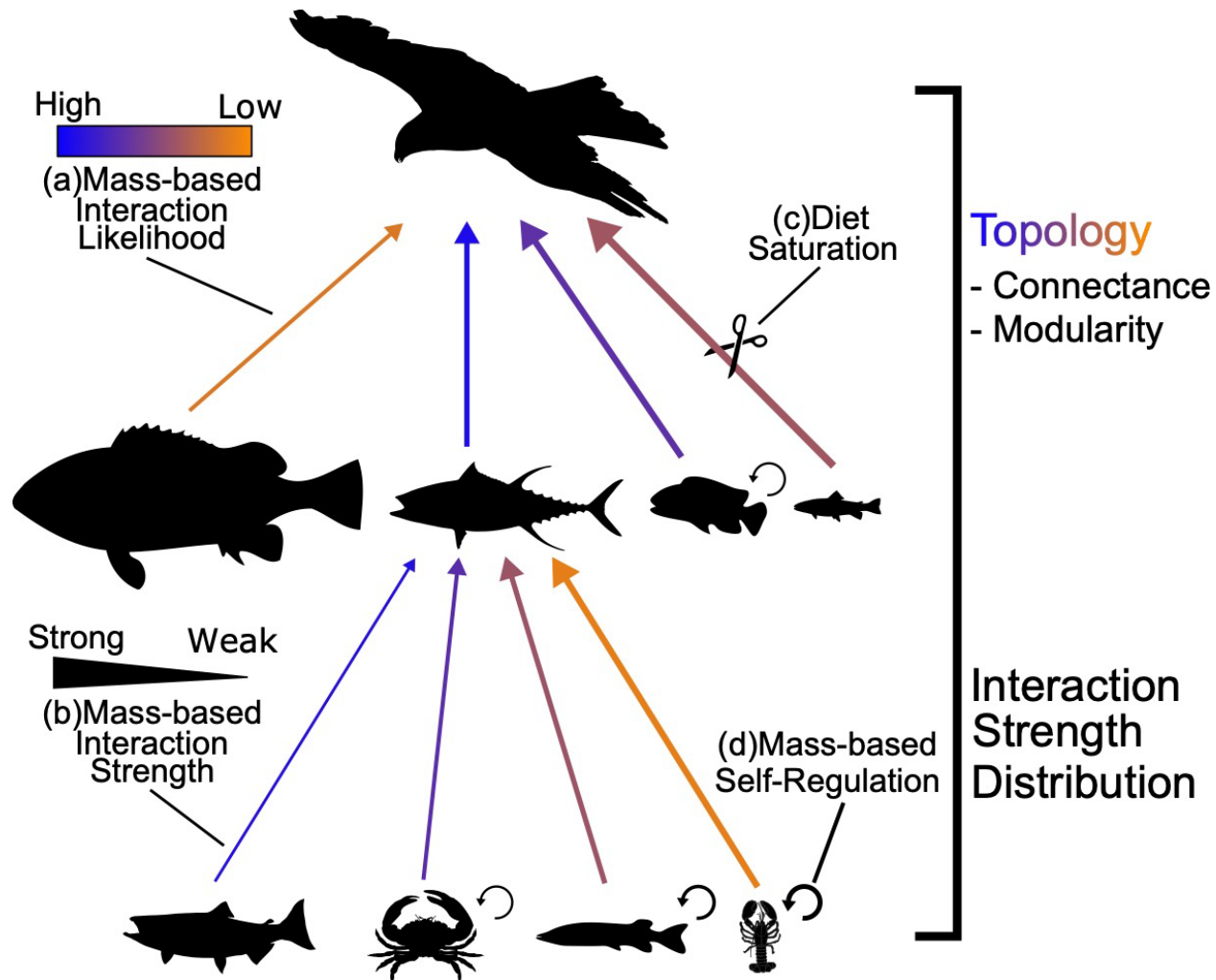# Modularity and mean interaction strength change spectrum

Grilli, et al. *Nat. Comm.*, 2016

Modularity and mean interaction strength change spectrum shape

Grilli, et al. *Nat. Comm.*, 2016

Positive vs. negative interactions

Grilli, et al. *Nat. Comm.*, 2016

Types of body mass constraints create modularity

High   Low

(a) Mass-based Interaction Likelihood

(c) Diet Saturation

Topology
- Connectance
- Modularity

Strong   Weak

(b) Mass-based Interaction Strength
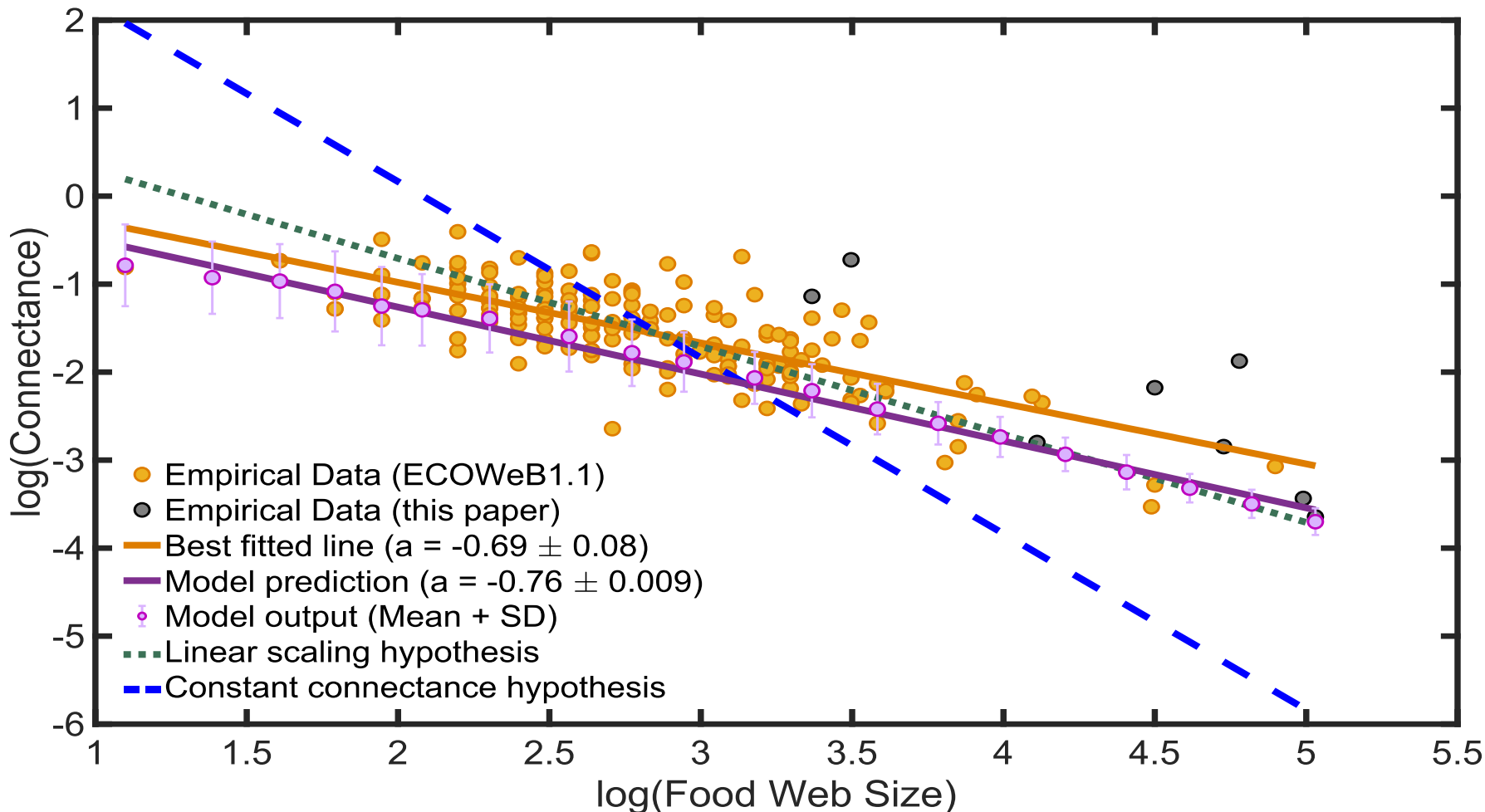
(d) Mass-based Self-Regulation

Interaction Strength Distribution

How does stability depend on each type of constraint?
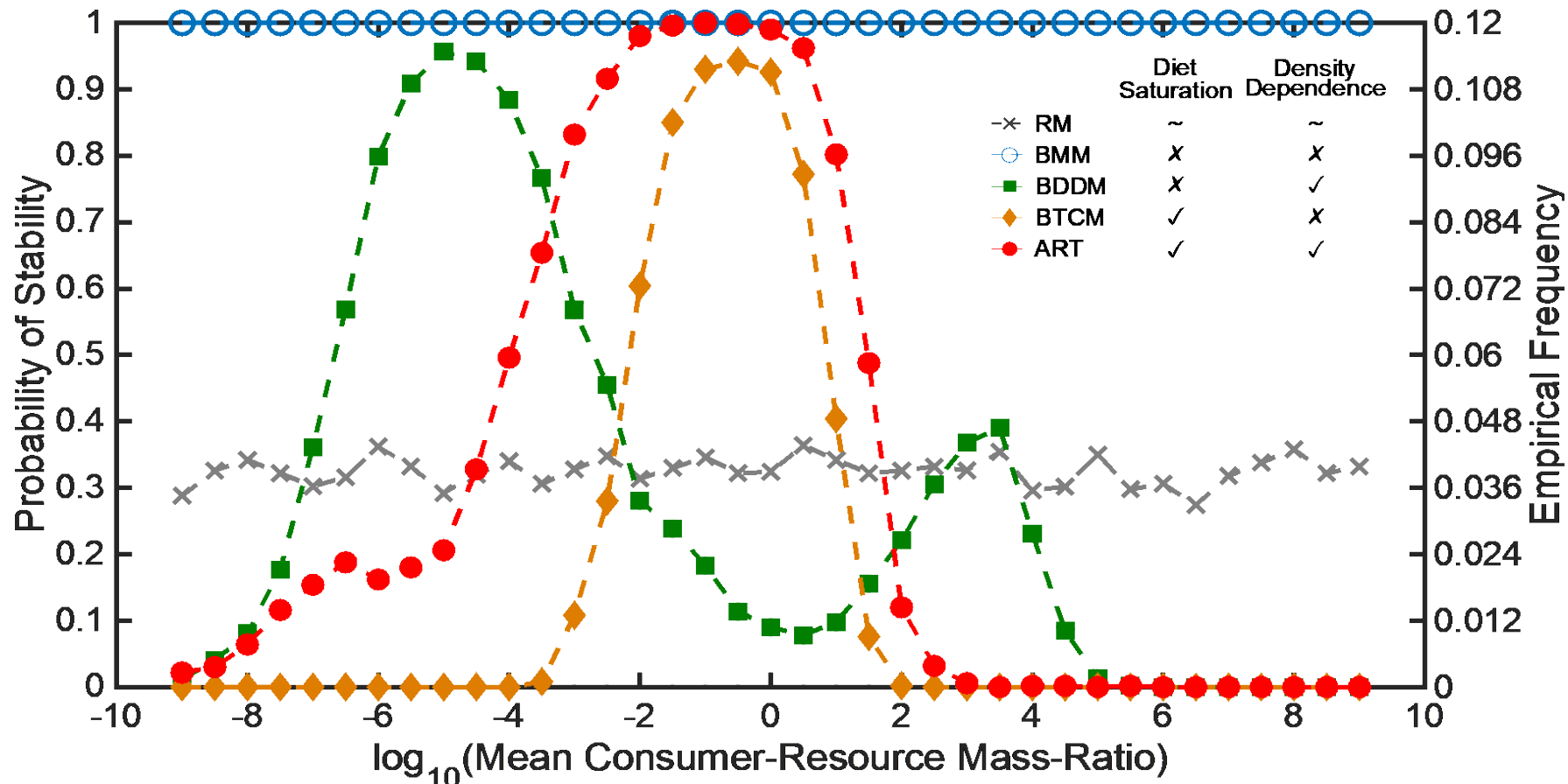
Consumption most crucial and relates to row-sum
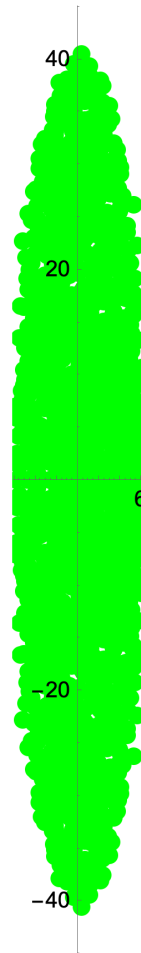
ART model correctly predicts connectance

Lin, Wieczynski, and Savage, submitted

Correlations across diagonal of matrix and
elliptical spectrum law

Correlation $\rho \Rightarrow$ Girko's elliptic law

$$A = \begin{array}{ccc} c & A_{12} & A_{13} \\ \rho A_{21} & c & A_{23} \\ \rho A_{31} & \rho A_{32} & c \end{array}$$
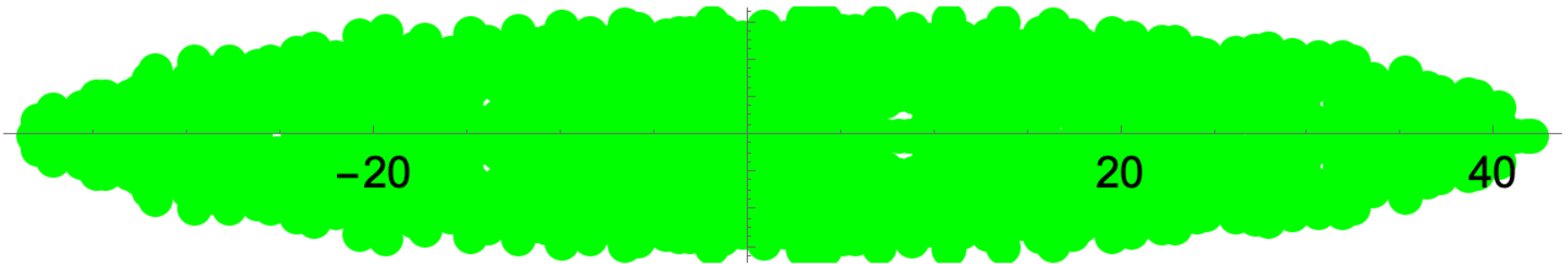
Correlation

$$\rho = -0.8$$

Correlation

$$\rho = 0.8$$

Food webs are
fractionally anti-symmetric

Ecological elliptic law $\rho = -\varepsilon$

$$A = \begin{matrix} c & A_{12} & A_{13} \\ -\varepsilon A_{21} & c & A_{23} \\ -\varepsilon A_{31} & -\varepsilon A_{32} & c \end{matrix}$$

$-\varepsilon$ equals correlation in last plots. Therefore, this structure will make spectrum an ellipse stretched out much more on imaginary axis than real axis, thus shrinking real axis and size of eigenvalues to make it more stable! Typically, $\varepsilon\sim0.1$, but if it were 1, we'd be infinitely stable. (Actually not surprising because that corresponds to a fully anti-asymmetric matrix.)

Ecological elliptic law $\rho = -\varepsilon$

$$A = \begin{array}{ccc} c & A_{12} & A_{13} \\ -\varepsilon A_{21} & c & A_{23} \\ -\varepsilon A_{31} & -\varepsilon A_{32} & c \end{array}$$

$\varepsilon = 1 \Rightarrow$ Purely anti-symmetric matrix (~stable)
$\varepsilon = -1 \Rightarrow$ Purely symmetric matrix (~unstable)
$\varepsilon = 0 \Rightarrow$ Purely triangular matrix (~c)

$\rho = 0 \Rightarrow$ Purely random matrix (~c)

Choice of dynamical equations
and
details of stability analysis

Add interactions

In matrix form

$$\dot{X}(t) = \left(\text{diag}(R) + \text{diag}(X(t))A \right) X(t)$$

No interactions means $\quad A_{ij} = 0$

Positive (increases growth) interactions means $\quad A_{ij} > 0$

Negative (decreases growth) interactions means $\quad A_{ij} < 0$

Interaction matrix to network

$$A = \begin{vmatrix} -r_1/K_1 & 0 & A_{13} \\ 0 & -r_2/K_2 & A_{23} \\ A_{31} & A_{32} & -r_3/K_3 \end{vmatrix}$$

Entries in interaction are where real biology and specifics of system come in. That is where lots of insight and knowledge and choices are made and data is confronted. Also in forming the terms in the equations to being with based on interactions. Here assumes standard random interactions among two things.

i=1

i=2

i=3
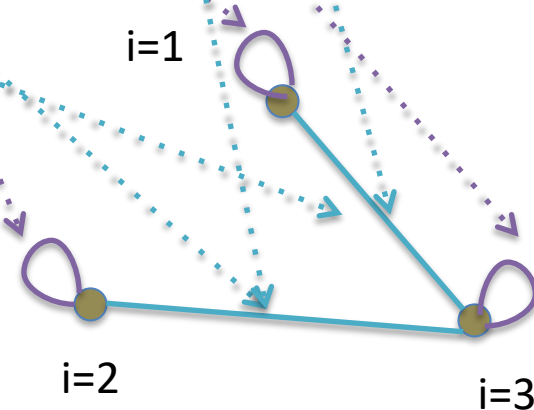
Calculate stability from Jacobian evaluated at fixed point

Perturbation, disturbance, etc

$$\frac{d(\delta X)}{dt} = J(X^*)\delta X + \sigma(\delta X^2)$$

Jacobian (change of coordinates); Gradient of interactions wrt each species

$$J(X^*) = \frac{d}{dX}\left[\left(\text{diag}(R) + \text{diag}(X(t))A\right)X(t)\right]\bigg|_{X=X^*}$$
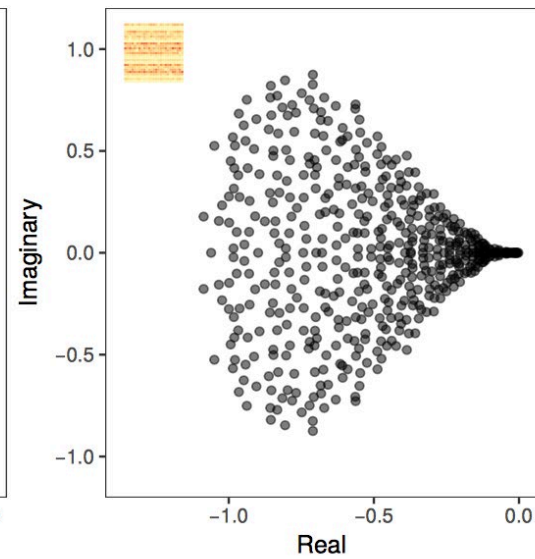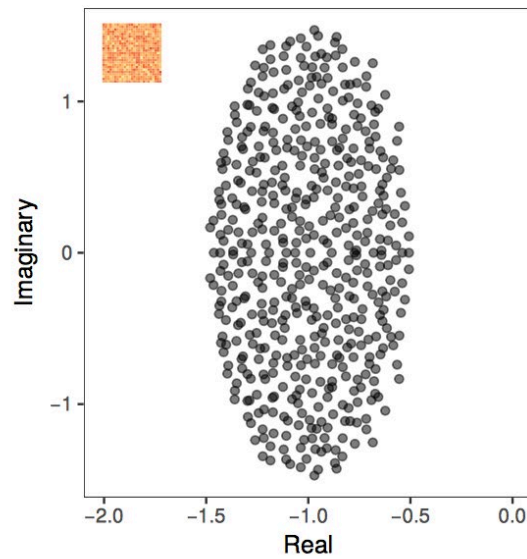
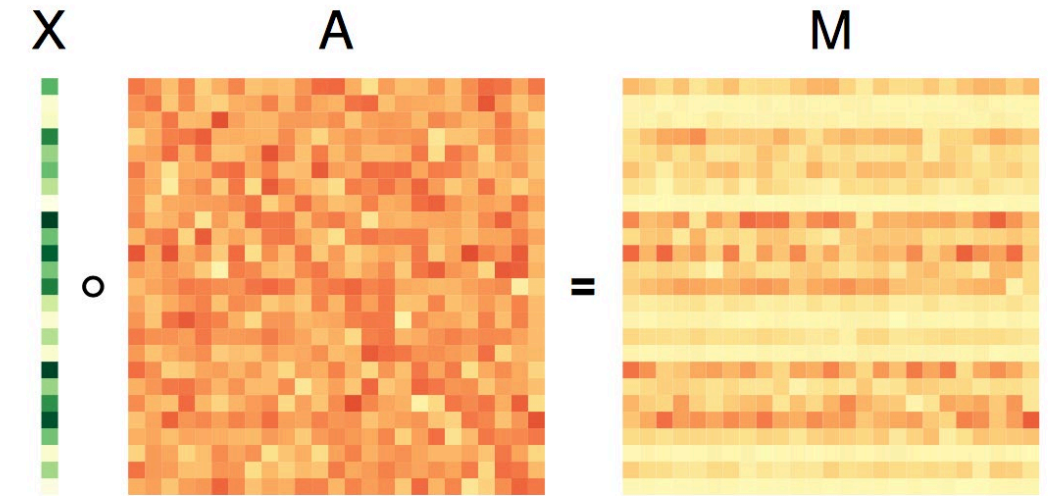$$\sim \text{diag}(R) + 2\text{diag}(X^*(t))A$$

What is the equilibrium or fixed point?

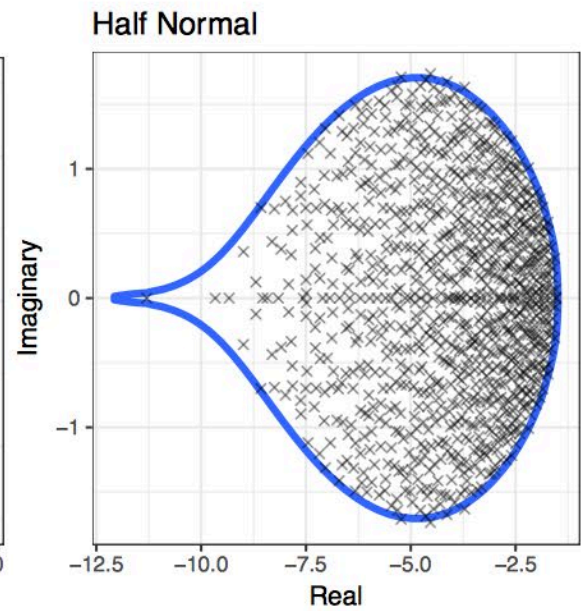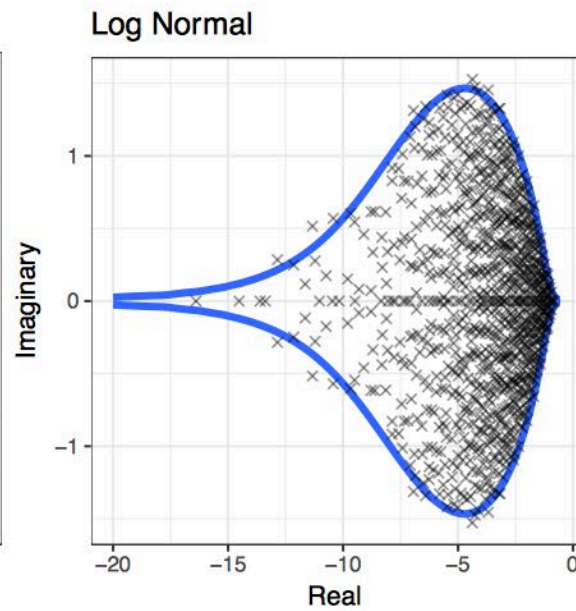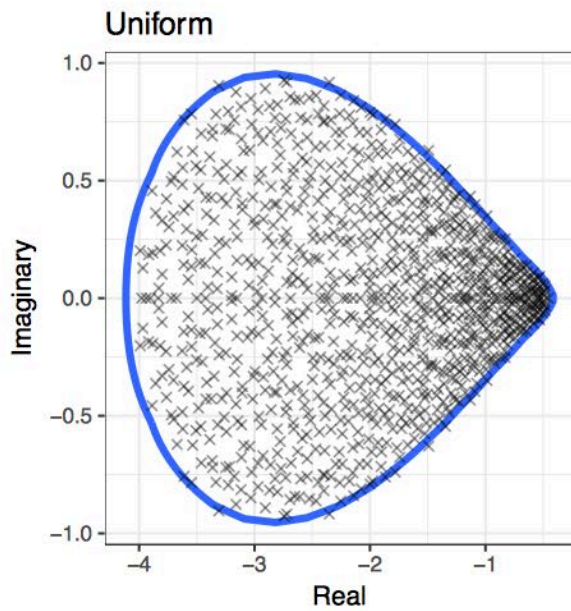$$0 = \dot{X}(t) = \left(\text{diag}(R) + \text{diag}(X(t))A \right) X(t)$$

because assumes things are no longer changing, meaning fixed

X* is solution to this equations. Interesting thing here is that this depends on X* itself and R and not just interactions that constrain equilibrium point of dynamics. Is this correct?

Change in spectrum using random X (population abundances at fixed point)

Different choices of randomness

Gibbs, Grilli, et al. arXiv, 2017

How else could we do this?

$$0 = \dot{X}(t) = f(X)X$$

and if X does not equal 0 (trivial solution) then
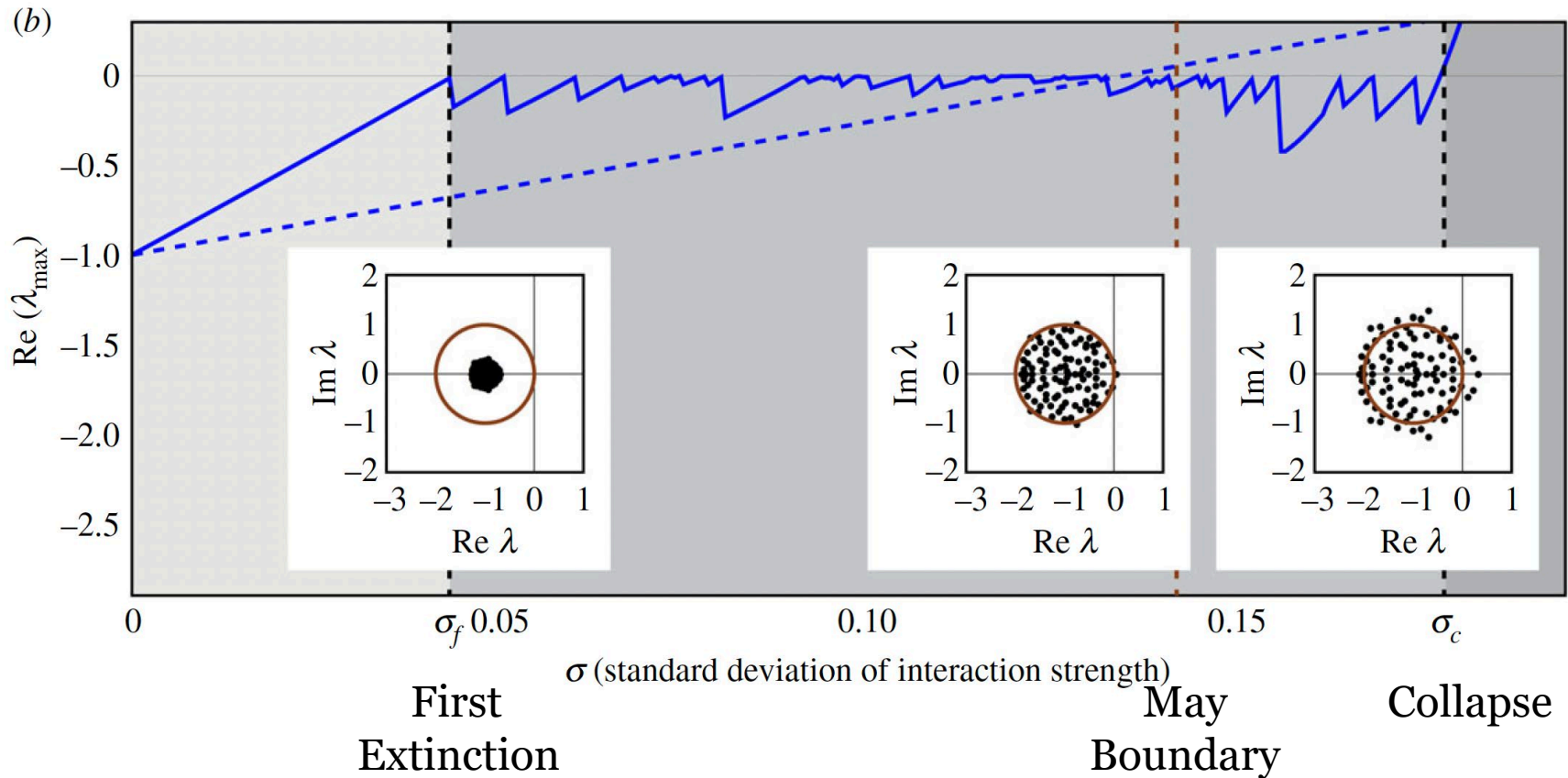
$$0 = f(X^*)$$

Still need to find J(x*) and diagonalize

$$\tilde{J}(x^*) = \frac{d}{dX}\left[\mathrm{diag(R)} + \mathrm{diag(X}(t))A\right]_{ij}\Bigg|_{X=X^*} \Rightarrow \tilde{J}(X^*) = A$$

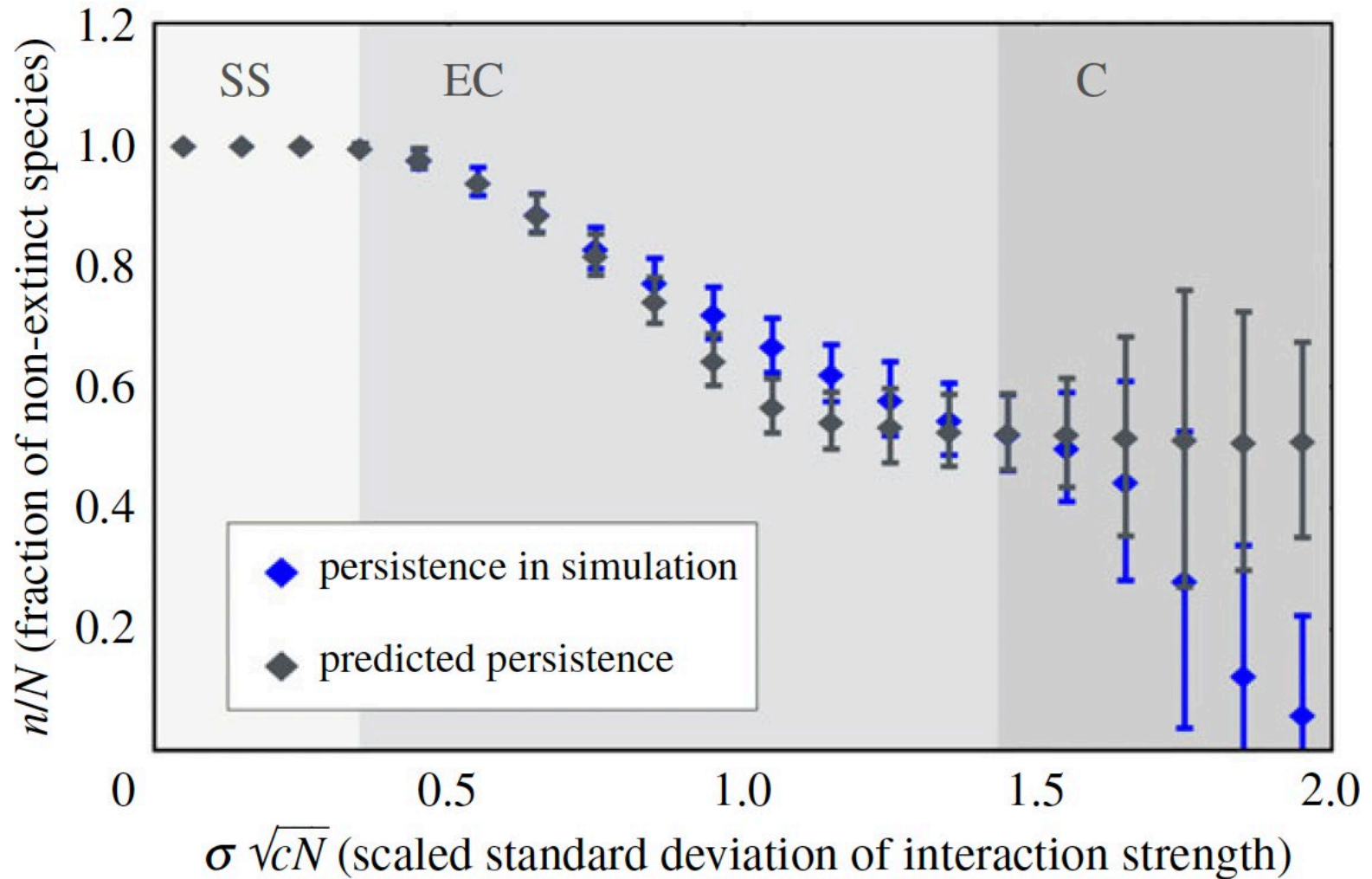Dependence on X^* is totally gone now. Only interaction matrix matters now.

This is basically what May did! But only works as long as no zero (trivial) abundances, i.e., extinctions.
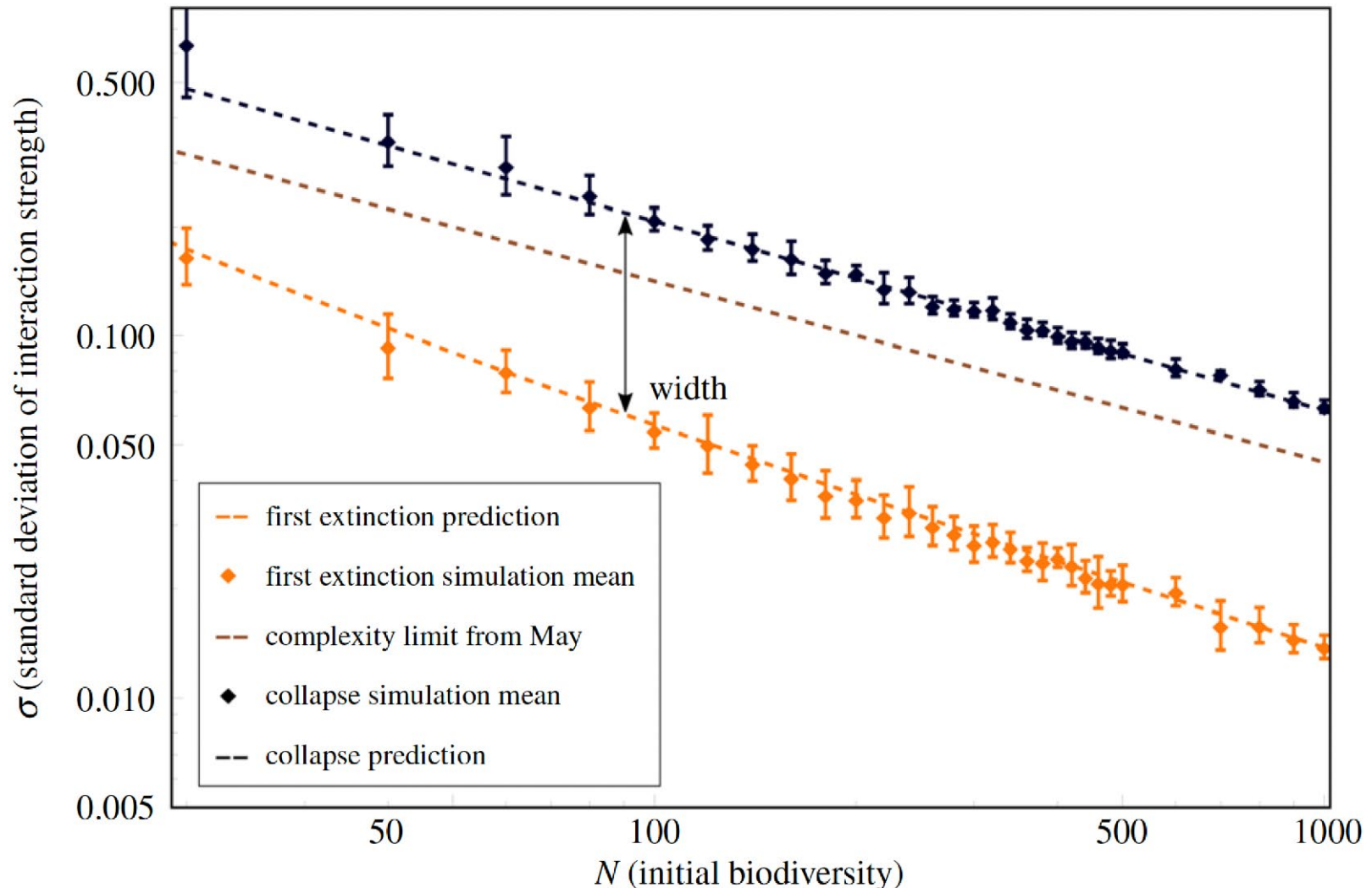
Analysis of complexity-stability continuum

Pettersson, Savage, Nilsson-Jacobi et al. *Roy. Soc. Interface,* 2021

Eigenvalue spectrum directly

(b)

Pettersson, Savage, Nilsson-Jacobi et al. *Roy. Soc. Interface,* 2021

Clarifying collapse

Pettersson, Savage, Nilsson-Jacobi et al. *Roy. Soc. Interface,* 2021

Diversity-Interaction Strength Tradeoff and Scaling Remains Roughly the Same

Pettersson, Savage, Nilsson-Jacobi et al. *Roy. Soc. Interface,* 2021

Calculating collapse

First zero of equation below defines σ_f

$$f_{\min}(x) = N(1 - F(x))^{N-1}f(x)$$

$$= \frac{Ne^{-(x-\mu_+)^2/2\sigma^2 cN}}{\sigma\sqrt{2\pi cN}}\left(\frac{1}{2} - \frac{1}{\sqrt{\pi}}\int_0^{(x-\mu_+)/\sigma\sqrt{2cN}} e^{-t^2}\,dt\right)^{N-1}$$

Collapse boundary defined by previous scaling like May but with different constant based on persistence
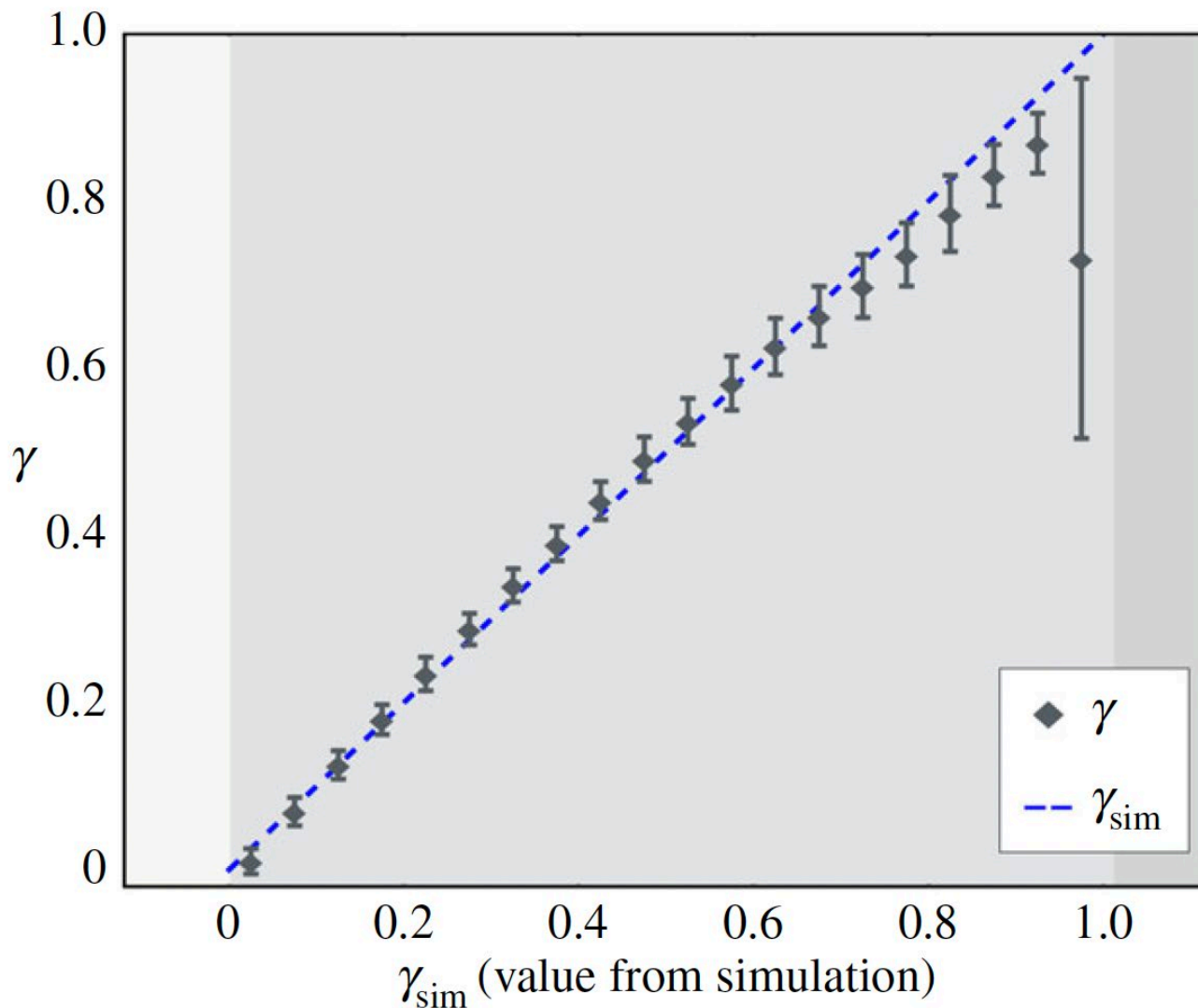
$$\sigma_c = \frac{1}{\sqrt{cNp_c}}.$$

Collapse metric

$$\gamma(n) = \frac{\sigma - \sigma_f(N_{\mathrm{pred}}(n))}{w(N_{\mathrm{pred}}(n))}$$

where $\omega = \sigma_c - \sigma_f$ and N_{pred} is estimated biodiversity based on empirical biodiversity n.

Pettersson, Savage, Nilsson-Jacobi et al. *Roy. Soc. Interface*, 2021

Collapse metric matches numerical solutions

Pettersson, Savage, Nilsson-Jacobi et al. *Roy. Soc. Interface*, 2021

Correlations within rows and columns of matrix:
row-sum, consumption, and Damuth's rule (EER)

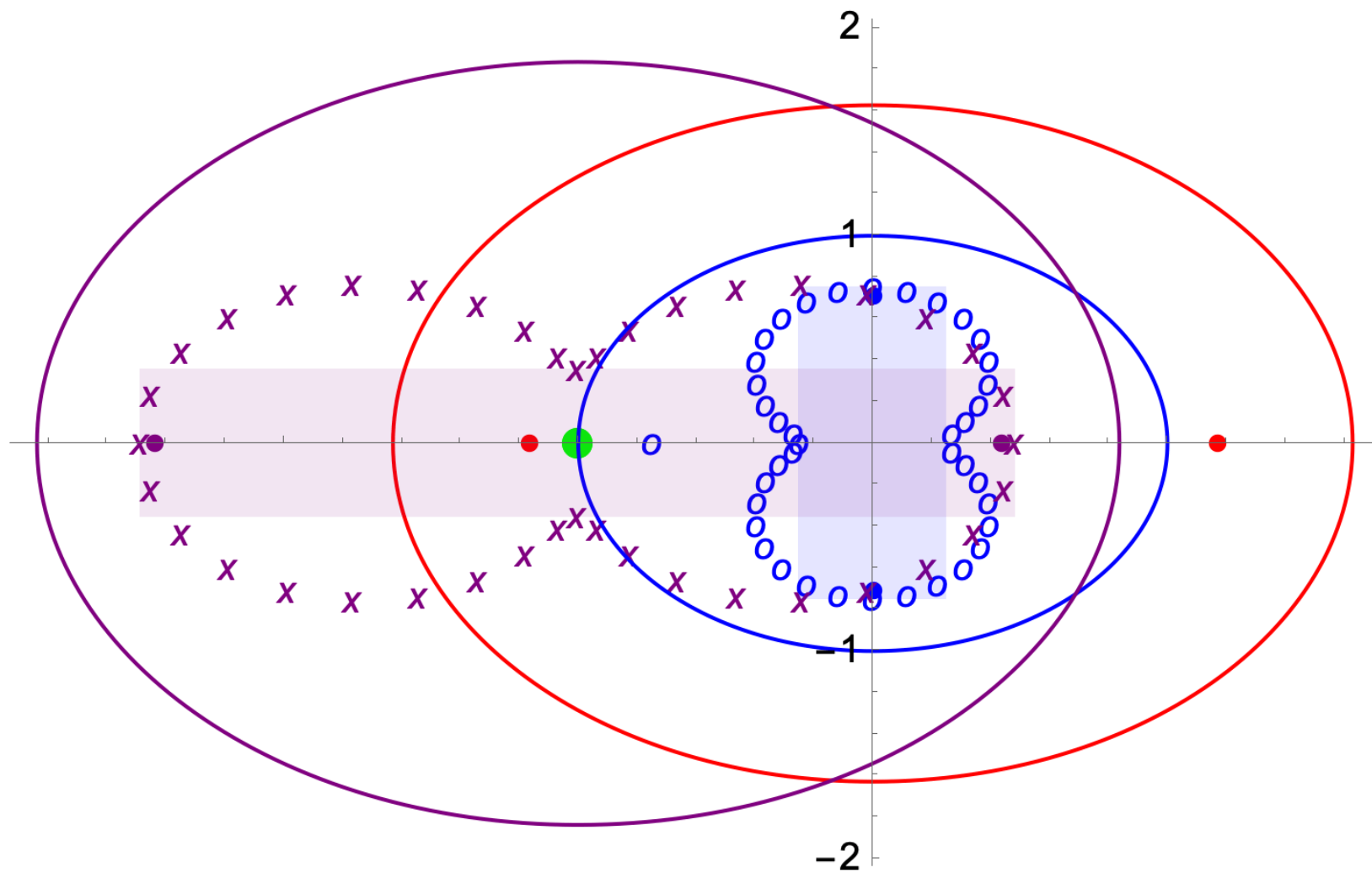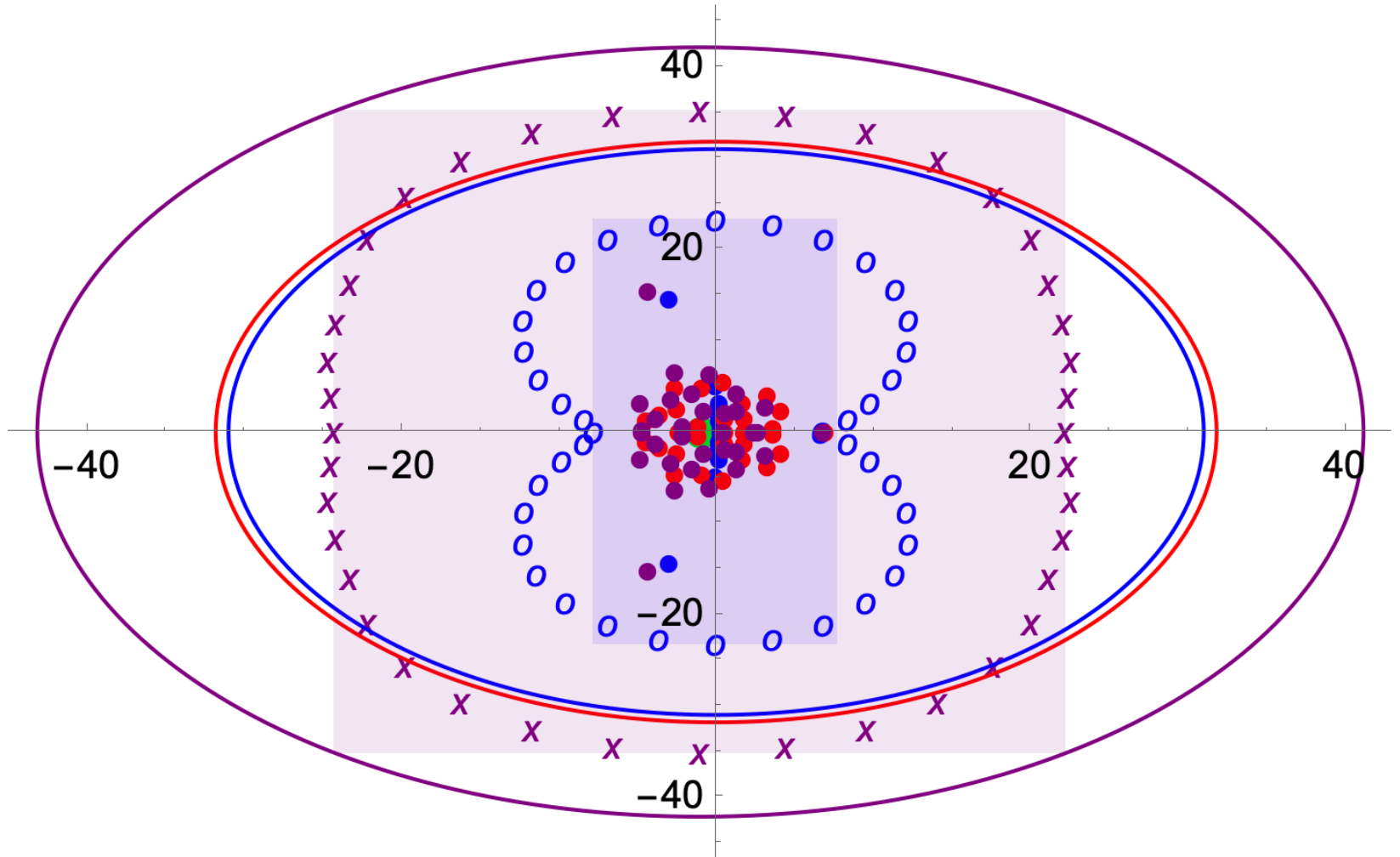# Row-sum variance and constraint relates to E-C width

Pettersson, Savage, Nilsson-Jacobi et al. *Phys. Rev. E,* 2022
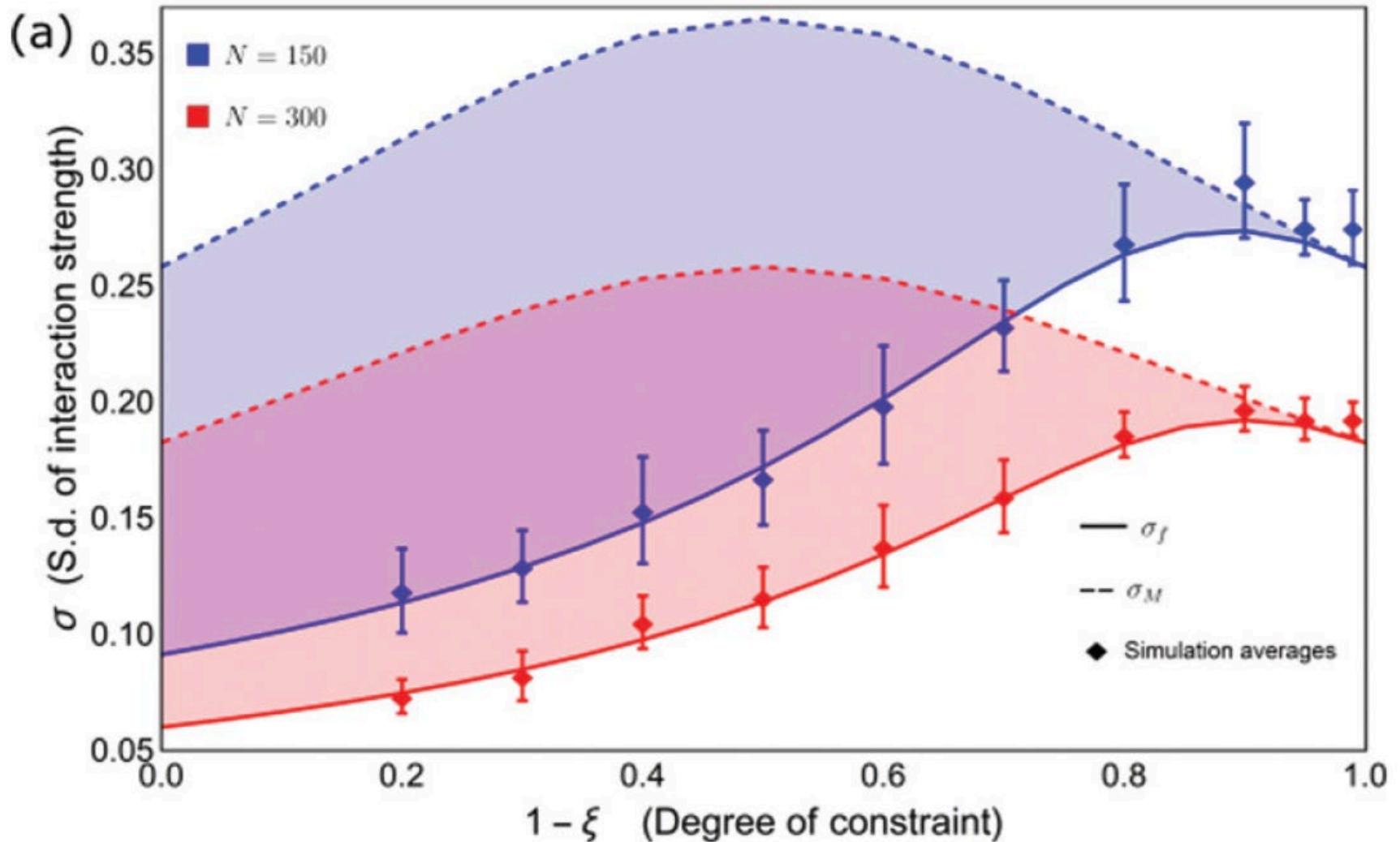
Better bounds

Gershgorin + Bendixson/Bromwich at board!

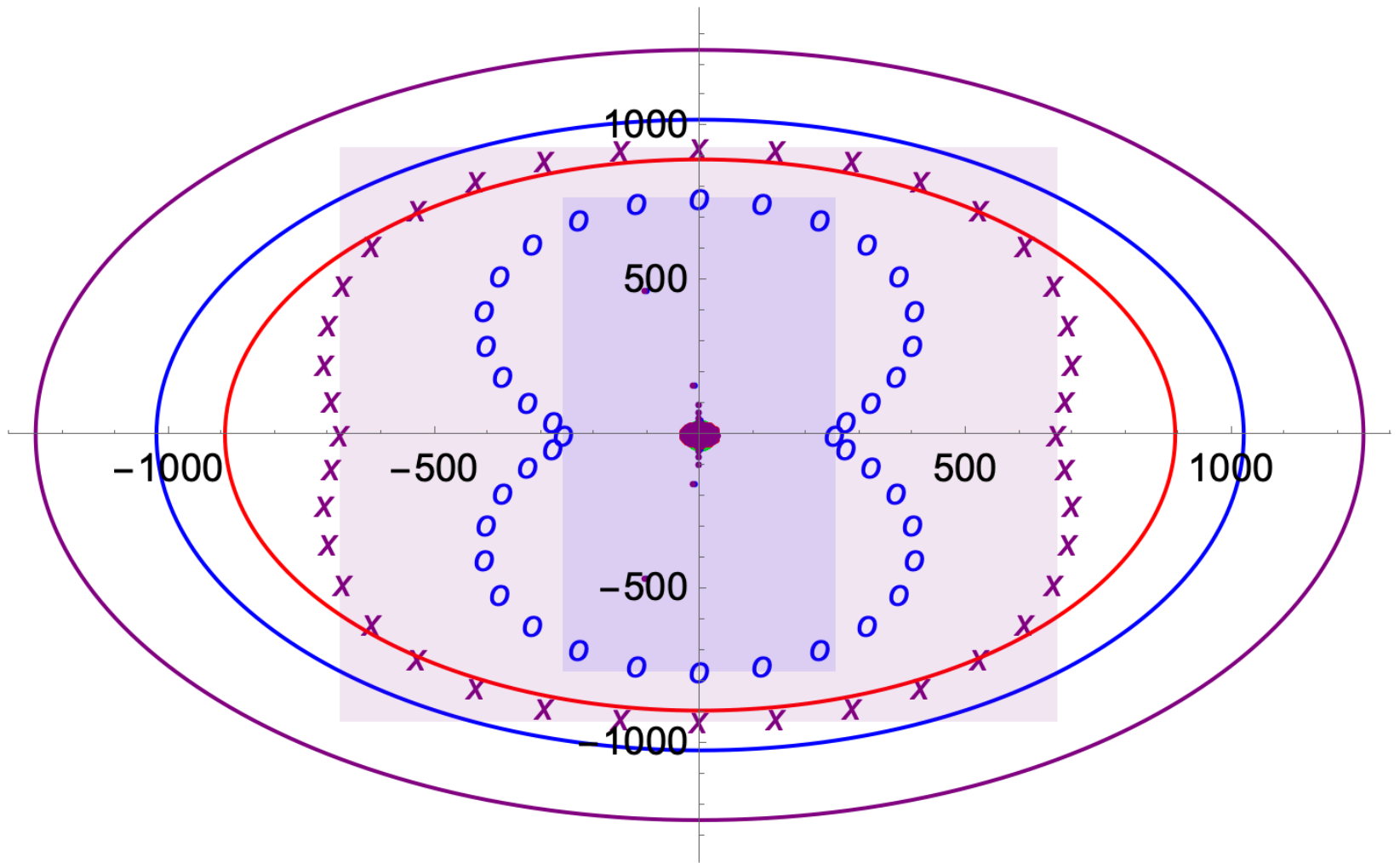Geometric interpretations of eigenvalue spectra

Examples

Examples

Examples

Conclusions

1. Can calculate collapse beyond just May stability criteria

2. Row-sum constraints matter for extinction-continuum and collapse

3. Row-sum constraints may relate to consumption constraints

4. Many ways to do row-sum constraint. Choices can be more or less biological or mathematically reasonable and have big influence on how spectrum and stability are affected. My focus now and finding some very interesting results and that it's very little studied.

People

Martin
Nilsson-Jacobi

Susanne Pettersson

Tianyun Lin

Ankit Vikrant

Daniel Wieczynski