Robust coexistence in ecological competitive communities

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Based on the preprint

Robust coexistence in ecological competitive communities

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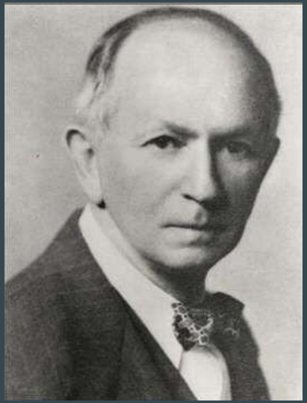
What are the typical dynamics of highly-diverse systems?

Do dynamics become more complex as the systems become more diverse?

Competitive Lotka-Volterra systems

Lotka 1920
Volterra 1926



n populations growing together and competing for resources

$$\frac{dx_i}{dt} = r_i x_i \left(1 - \sum_j A_{ij} x_j\right)$$

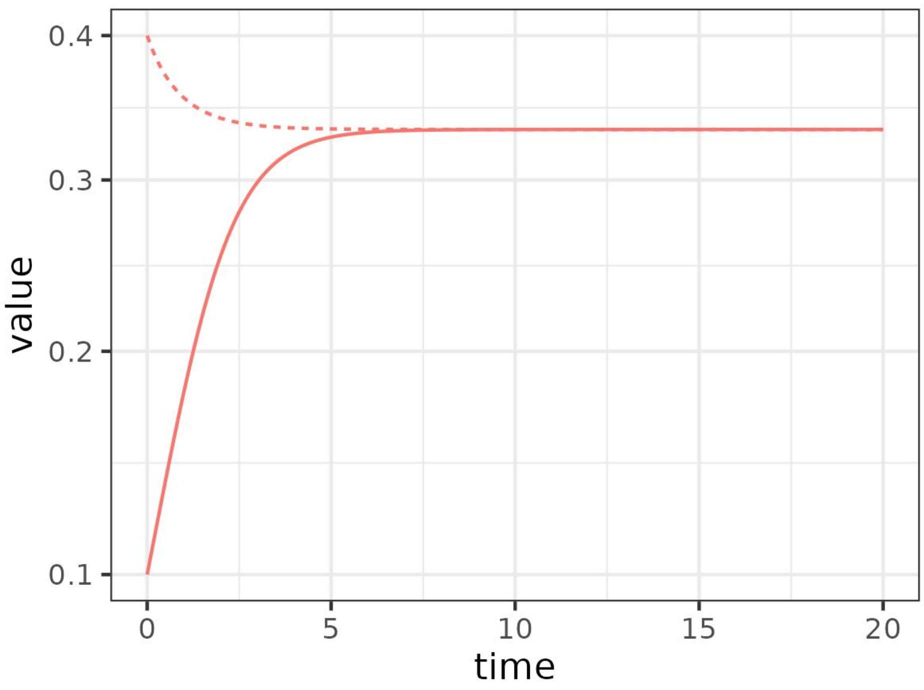
$r_i > 0$ growth rates

A_{ij} reduction in growth of i due to j

Assume that **on average, species compete**

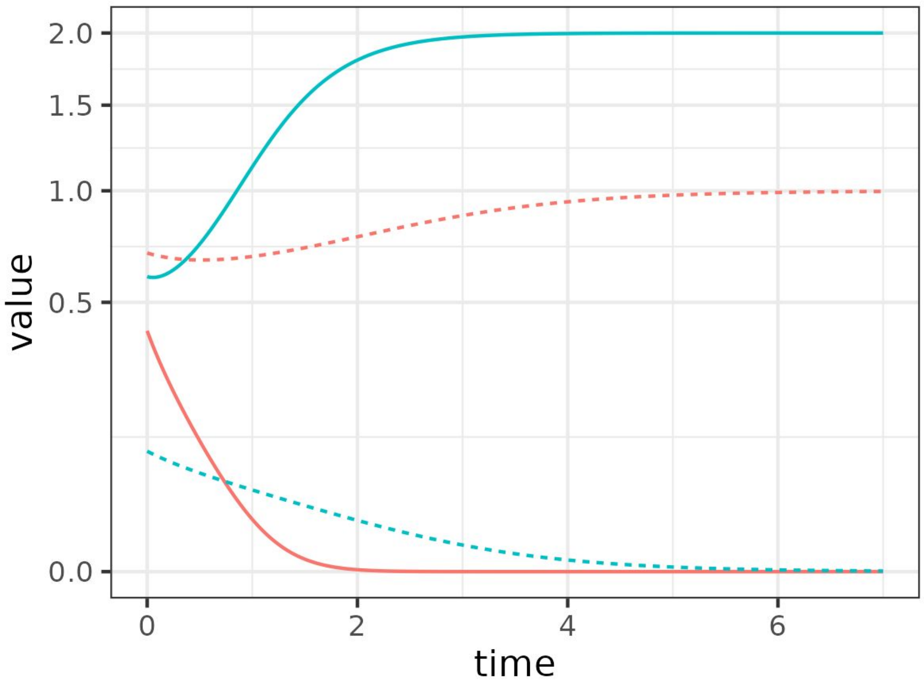
1 population

Stable equilibrium



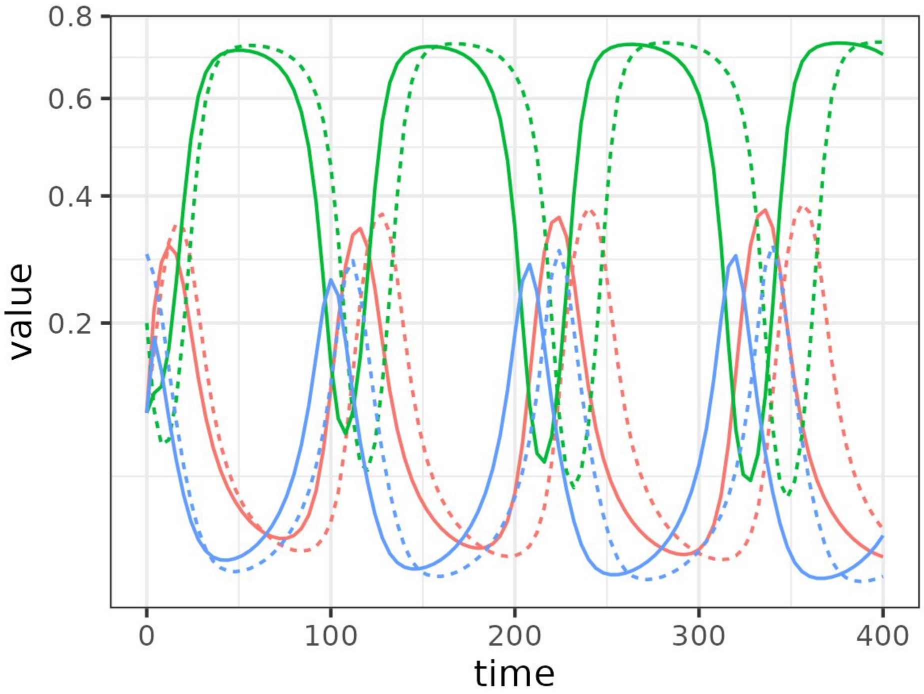
2 populations

Priority effects/bistability



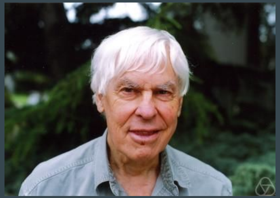
3 populations

Limit cycles

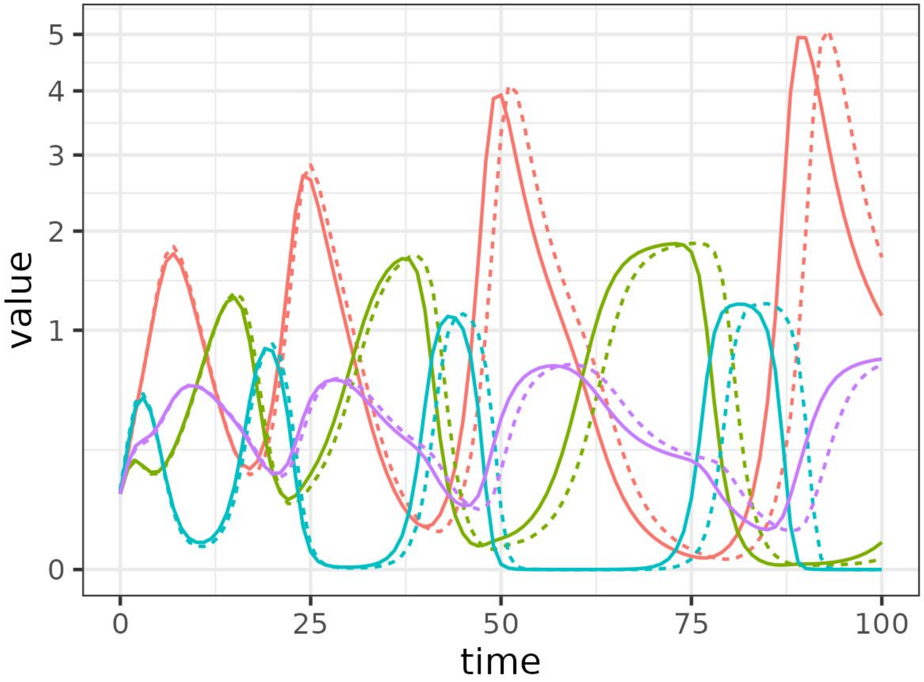


4 populations

Chaos



Stephen Smale, J Math Bio, 1976



Feasible Equilibrium

Out-of-equilibrium coexistence requires a feasible equilibrium, which is the time-average of the dynamics

$$\frac{dx_i}{dt} = r_i x_i \left(1 - \sum_j A_{ij} x_j\right)$$

$$Ax = 1$$

$$x = A^{-1} 1 > 0$$

Effect of intraspecific competition

We consider the effects on coexistence when we increase intraspecific competition

$$A = \alpha I + B$$

Stability of equilibria in competitive systems

A sufficiently strong intraspecific competition α_s guarantees global stability of dynamics

IF $A + A^T$ IS P.D.

$x(t) \to \bar{x}$ AS $t \to \infty$

$\bar{x} = \begin{pmatrix} y^* \\ 0 \end{pmatrix}$ ← COEXISTING; ← EXTINCT, CANNOT INVADE

$2\alpha I + B + B^T$

$\alpha > \alpha_s$ ONLY EQUILIBRIA

General systems

Effect of average interaction strength

Transitions to and from feasibility

Canonical matrix for competitive systems

Adding positive constants to each column does not change the feasibility of the equilibrium

$$A = \alpha I + B \qquad \frac{1}{n} B^T \mathbb{1} = m$$

$$A = \alpha I + C + \mathbb{1} m^T \quad \text{WITH} \quad C^T \mathbb{1} = 0$$

CONSIDER

$$Ax = \mathbb{1} \quad (\alpha I + B) x = \mathbb{1} \quad (\alpha I + C + \mathbb{1} m^T) x = \mathbb{1}$$

AND

$$(\alpha I + C) y = \mathbb{1}$$

THEN

$$x = \frac{1}{1 + m^T y} y$$

Canonical matrix for competitive systems

Adding positive constants to each column does not change the feasibility of the equilibrium

$$x = \frac{1}{1 + u^T y} y$$

$$\text{BUT} \quad 1^T(\alpha I + C) y = 1^T 1$$

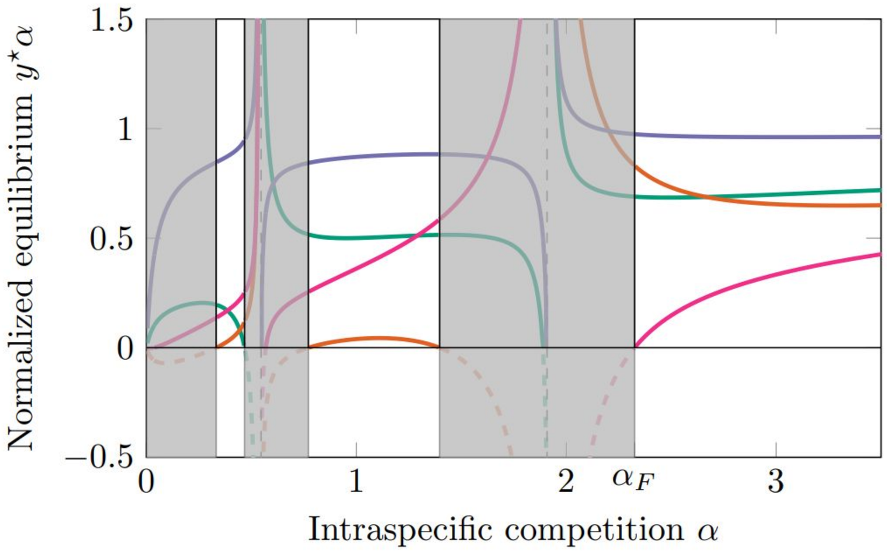
$$\alpha 1^T y = n$$

$$\frac{1}{n} 1^T y = \frac{1}{\alpha}$$

Transitions to and from feasibility

As we increase α, the solution can gain or lose feasibility

There is a critical value α_F at which:
- The solution is feasible
- It remains feasible for $\alpha > \alpha_F$



The existence of α_F can be proven using Perron-Frobenius theorem

Transitions to and from feasibility

We want to find α_F

$$y_i(\alpha) = \frac{|Q_i|}{|Q|}$$

$$Q = \alpha I + C$$

$$Q_i = \begin{pmatrix} \alpha \check{I} + \check{C} & \vdots \\ c^T & \vdots \end{pmatrix}$$

Transitions to and from feasibility

We want to find α_F:

- α_0 largest value of α leading to divergence

$$y_i(\alpha) = \frac{|Q_i|}{|Q|} \qquad Q = \alpha I + C$$

$$Q_i = \begin{pmatrix} \alpha \check{I} + \check{C} & \vdots \\ c^T & \end{pmatrix}$$

$|Q| = 0 \Rightarrow C$ HAS REAL, NEGATIVE EIGENVALUE λ

$$\alpha = -\lambda$$

IF $\lim_{\alpha \to -\lambda} |Q_i| \neq 0$ SOLUTIONS DIVERGE TO $\pm\infty$ (NO FEASIBILITY)

α_0 = LARGEST α LEADING TO DIVERGENCE

If there are no divergences, $\alpha_0 = 0$

Transitions to and from feasibility

We want to find α_F:

- α_0 largest value of α leading to divergence

$$|Q_i| = \left|\begin{array}{c|c} \alpha \hat{I} + \check{C} & \begin{matrix}1\\ \vdots \\ 1\end{matrix} \\ \hline c^T & 1 \end{array}\right| =$$

$$\left|\begin{array}{c|c} \alpha \hat{I} + \hat{C} - 1c^T & \begin{matrix}0\\ \vdots \\ 0\end{matrix} \\ \hline c^T & 1 \end{array}\right| = |\alpha \hat{I} + \hat{C} - 1c^T|$$

$$= |\alpha \hat{I} + \hat{B} - 1b^T|$$

Transitions to and from feasibility

We want to find α_F:

- α_0 largest value of α leading to divergence
- $\alpha_i > \alpha_0$ largest value of α leading to $y_i(\alpha_i)=0$

$$|Q_i| = \left|\begin{matrix} \alpha\hat{I}+\check{C} & \vdots \\ c^T & \end{matrix}\right| = |\alpha\hat{I} + \hat{B} - 1b^T|$$

$|Q_i|=0 \Rightarrow \check{C} - 1c^T$ OR $\hat{B} - 1b^T$ HAS A NEGATIVE REAL EIGENVALUE λ AND $\alpha = -\lambda$

i.e. $y_i(\alpha)=0$

IF $|Q| \neq 0$

$\alpha_i = \max \alpha$ S.T. $|Q_i|=0$

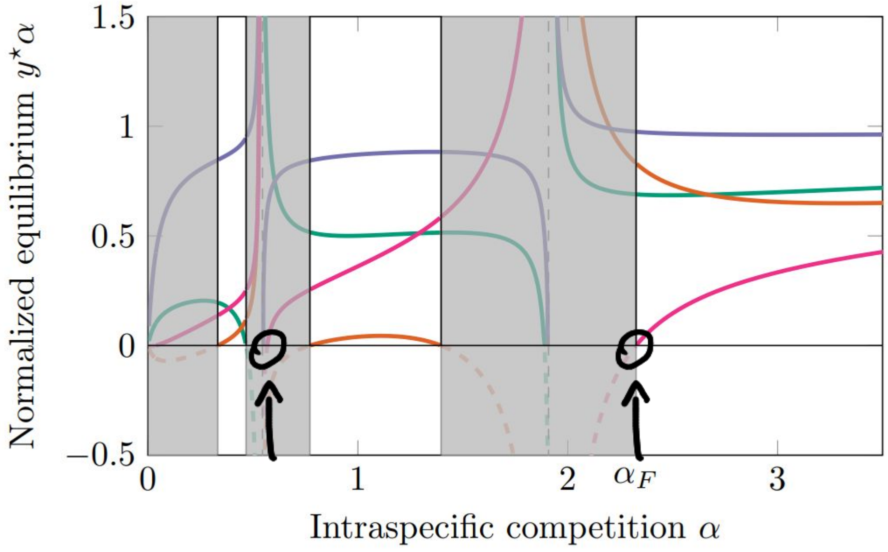
AT THIS POINT $y_i(\alpha_i)$ MUST TRANSITION TO POSITIVE (BECAUSE $y_i(\alpha_F)>0$)

If there are no real, negative eigenvalues, or transitions appear before α_0, set $\alpha_i = 0$

Transitions to and from feasibility

We want to find α_F:

- α_0 largest value of α leading to divergence
- $\alpha_i > \alpha_0$ largest value of α leading to $y_i(\alpha_i)=0$

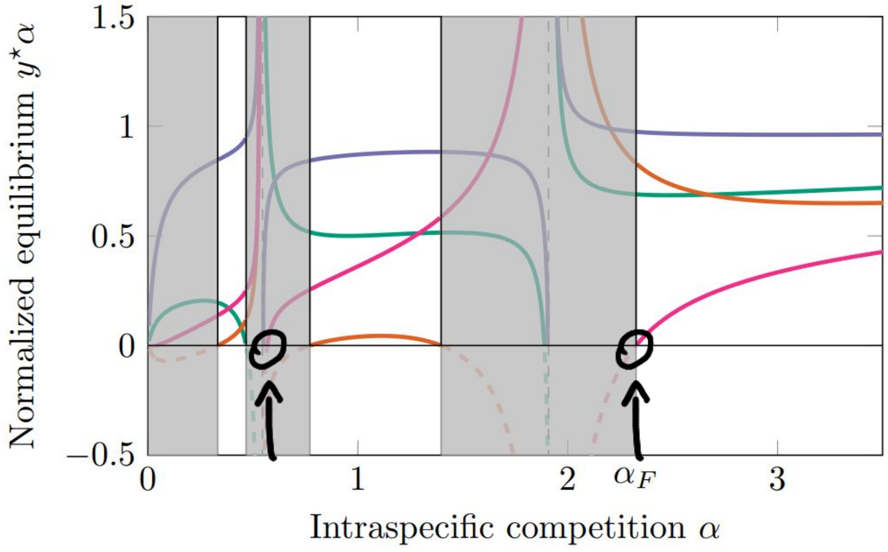


Example transitions for pink population. $\tilde{B} - 1b^T$ has two negative, real eigenvalues.

Transitions to and from feasibility

We want to find α_F:

- α_0 largest value of α leading to divergence
- $\alpha_i > \alpha_0$ largest value of α leading to $y_i(\alpha_i)=0$
- $\alpha_F = \max(\alpha_0, \alpha_1, \alpha_2, ..., \alpha_n)$



Example transitions for pink population. $\tilde{B} - 1b^T$ has two negative, real eigenvalues.

Random systems

We now turn to systems with random coefficients

We examine cases in which populations are statistically equivalent

Random interactions (elliptic law)

$$B' = B + \mu \mathbf{1}\mathbf{1}^T$$

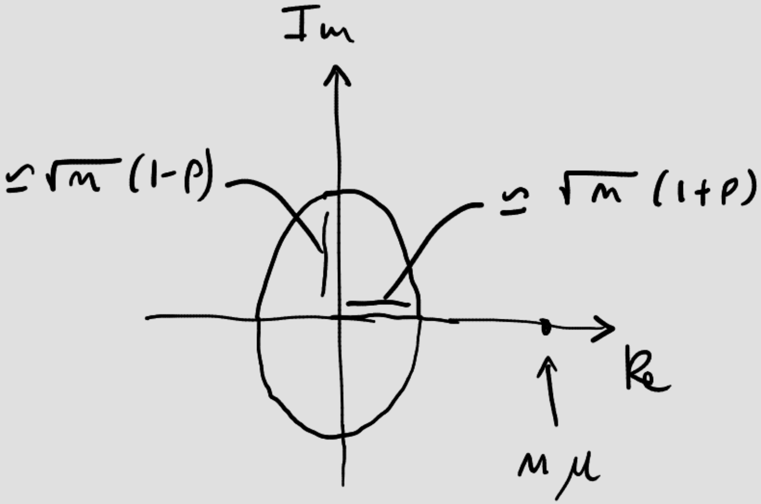
$$\mu > 0$$

$$(B_{ij}, B_{ji}) \sim \text{BIVARIATE DISTRIBUTION}$$

$$\mathbb{E}(B_{ij}) = 0$$

$$\mathbb{E}(B_{ij}^2) = 1$$

$$\mathbb{E}(B_{ij} B_{ji}) = \rho$$



Allesina & Tang, 2012

Random interactions (elliptic law)

$B' = B + \mu 1 1^T$

$\mu > 0$

$(B_{ij}, B_{ji}) \sim$ BIVARIATE DISTRIBUTION

$\mathbb{E}(B_{ij}) = 0$

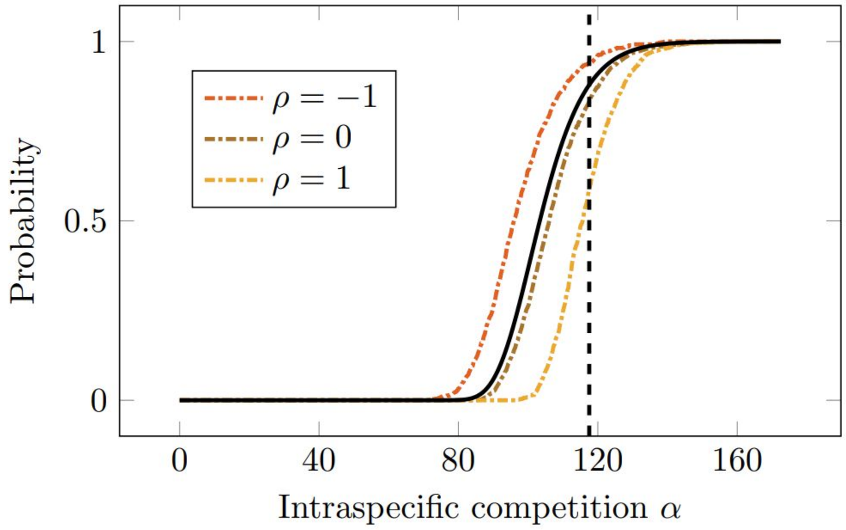
$\mathbb{E}(B_{ij}^2) = 1$

$\mathbb{E}(B_{ij} B_{ji}) = \rho$

BUT B' AND B HAVE SAME FEASIBILITY

W.L.O.G. $\mu = 0$

Many results available!



Roberts, 1974. Probability of stability given feasibility is high, and increases with n

Stone, 1988 (and 2016). Computes $p_F(a)$ for ρ=0

Bizeul & Najim, 2021. For ρ=0
$p_F(a) \cong 0$ if $a \ll (2\ n \log n)^{1/2}$ and
$p_F(a) \cong 1$ if $a \gg (2\ n \log n)^{1/2}$

Clenet et al., 2022. Different values of ρ do not alter substantially the critical value; feasibility implies stability.

Liu et al. 2023, Marcus et al. 2024, and many others

Using small-rank perturbations

$\alpha_F = \max(\alpha_0, \alpha_1, \alpha_2, \ldots, \alpha_m)$

FOR LARGE RANDOM MATRICES $\alpha_0 \cong \sqrt{m}\,(1+\rho)$

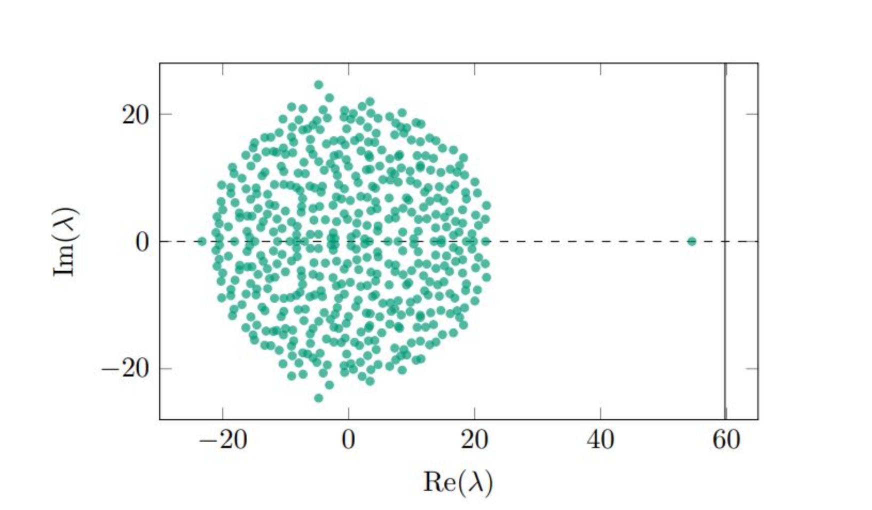
Using small-rank perturbations

$$\alpha_F = \max(\alpha_0, \alpha_1, \alpha_2, \ldots, \alpha_m)$$

α_i = LARGEST REAL EIGENVALUE OF

$$\mathbb{1} b^{(i)T} - \widehat{B}^{(i)}$$

(IF LARGER THAN α_0)



Using small-rank perturbations

α_i = LARGEST REAL EIGENVALUE OF

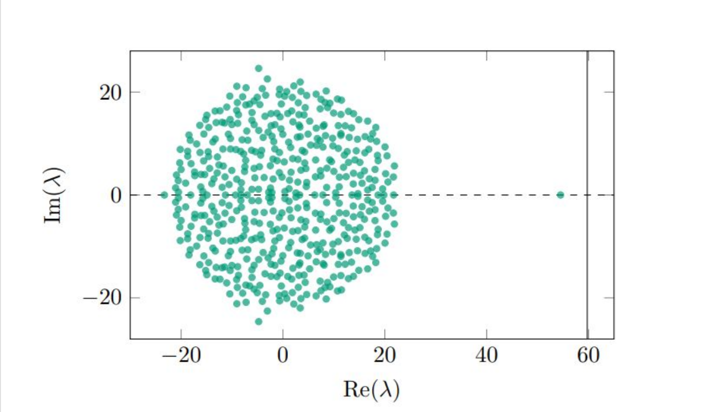
$$\mathbb{1}b^{(i)^T} - \hat{B}^{(i)}$$

(IF LARGER THAN α_0)

OUTLIER EIGENVALUE OF

$$\lambda_0^{(i)}\left(\frac{1}{\sqrt{M-1}}\left(\mathbb{1}b^{(i)^T} - \hat{B}^{(i)}\right)\right) = \gamma_i + \frac{\rho}{\gamma_i} + o(1)$$

$$\gamma_i = \lambda\left(\frac{1}{\sqrt{M-1}}\mathbb{1}b^{(i)^T}\right) = \frac{1}{\sqrt{M-1}}\sum_j b_j^{(i)} = \frac{1}{\sqrt{M-1}}\sum_j B_{ij} = i^{TH} \text{ ROW SUM}$$



A single outlier ⟶ a single transition

Using small-rank perturbations

α_i = LARGEST REAL EIGENVALUE OF

$$\mathbb{1} b^{(i)T} - \tilde{B}^{(i)}$$

(IF LARGER THAN α_0)

$$\alpha_i \simeq \sqrt{m-1}\left(\gamma_i + \frac{\rho}{\gamma_i}\right)$$

$$\alpha_F = \max(\alpha_0, \alpha_1, \alpha_2, \ldots, \alpha_m)$$

α_F (TYPICALLY) ASSOCIATED WITH <u>LARGEST ROW SUM</u>

Using small-rank perturbations

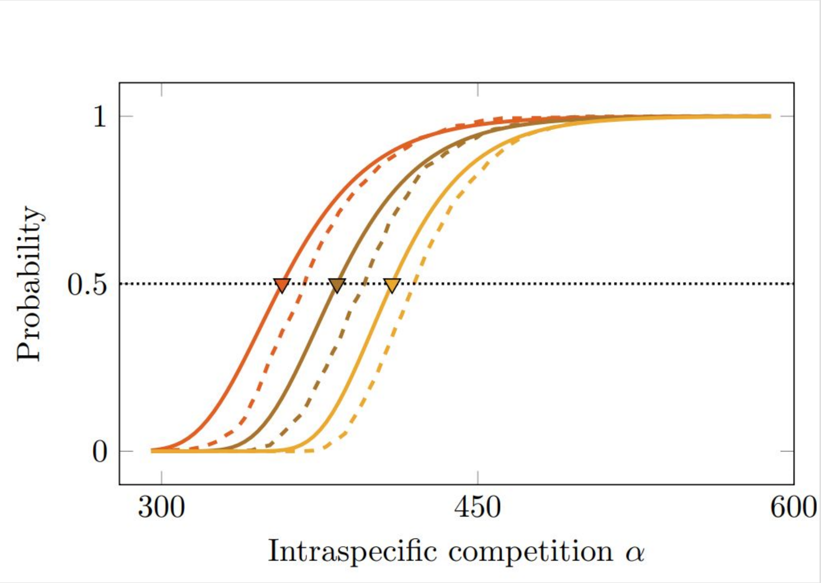
ASSUMING

$\gamma_i \sim N(0,1)$

$P(\max_i \gamma_i) \xrightarrow[n \to \infty]{}$ GUMBEL DISTRIBUTION (BIZEUL & NAJIM)

$$P_F(\alpha) = e^{-e^{-x}} \quad x = \left(\frac{\tilde{\alpha} + \sqrt{\tilde{\alpha}^2 - 4\rho}}{2} - b_n\right) b_n$$

$$\tilde{\alpha} = \frac{\alpha}{\sqrt{n-1}} \quad b_n = \sqrt{W_0} \simeq \sqrt{\log \frac{n^2}{2\pi}}$$



Recover spacing between curves; persistent effect of ρ; universal

Statistically-equivalent populations

$$\left(\sum_j y_j^\star\right)^2 = \frac{n^2}{\alpha^2}$$

$$\sum_j (y_j^\star)^2 + \sum_i \sum_{j \neq i} y_i^\star y_j^\star = \frac{n^2}{\alpha^2}$$

$$n\mathbb{E}((y_i^\star)^2) + n(n-1)\mathbb{E}(y_i^\star y_j^\star) = \frac{n^2}{\alpha^2}$$

$$\mathbb{V}(y_i^\star) + \mathbb{E}(y_i^\star)^2 + (n-1)\left(\mathbb{C}\text{ov}(y_i^\star, y_j^\star) + \mathbb{E}(y_i^\star)\mathbb{E}(y_j^\star)\right) = n\mathbb{E}(y_i^\star)^2$$

$$\mathbb{V}(y_i^\star) + \mathbb{E}(y_i^\star)^2 + (n-1)\left(\mathbb{C}\text{ov}(y_i^\star, y_j^\star) + \mathbb{E}(y_i^\star)^2\right) = n\mathbb{E}(y_i^\star)^2$$

$$\mathbb{V}(y_i^\star) + (n-1)\mathbb{C}\text{ov}(y_i^\star, y_j^\star) = 0$$

The model is closed under relabeling of the populations

There is no special structure making one population behave differently from the rest

But then all components have the same expectation, variance, and correlation

Statistically-equivalent populations

$$y^\star \sim n\left(\frac{1}{\alpha}\mathbb{1}, \sigma_{y^\star}^2\left(\frac{n}{n-1}I - \frac{1}{n-1}\mathbb{1}\mathbb{1}^T\right)\right)$$

$$p_F(n, \alpha, \sigma_{y^\star}^2) \approx \Phi\left(\frac{1}{\alpha\sigma_{y^\star}}\right)^n$$

If we assume that y is approximately normally-distributed, then we just need to determine the variance

All the complications of the random model will be absorbed in the variance term

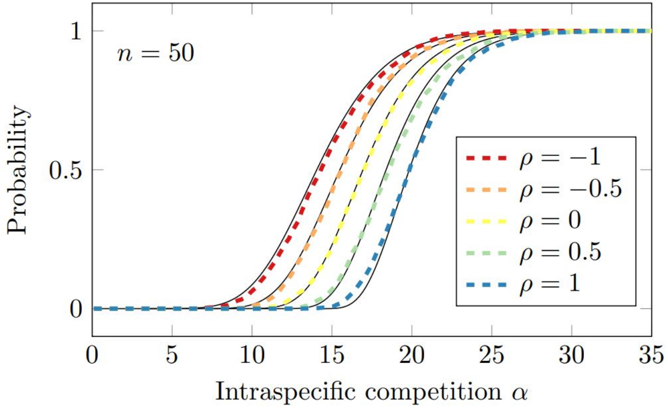
Further, if we assume independence, we can compute p_F

Computing the variance

$$G(z) = \mathbb{E}\left((zI + B)^{-1}\right)$$

↑ COMPLEX

$$\frac{1}{(\alpha \sigma_y)^2} \approx \frac{\alpha^2 + \alpha\sqrt{\alpha^2 - 4\rho(m-1)}}{2(m-1)} - (1+\rho)$$



Computing the variance can be accomplished in different ways

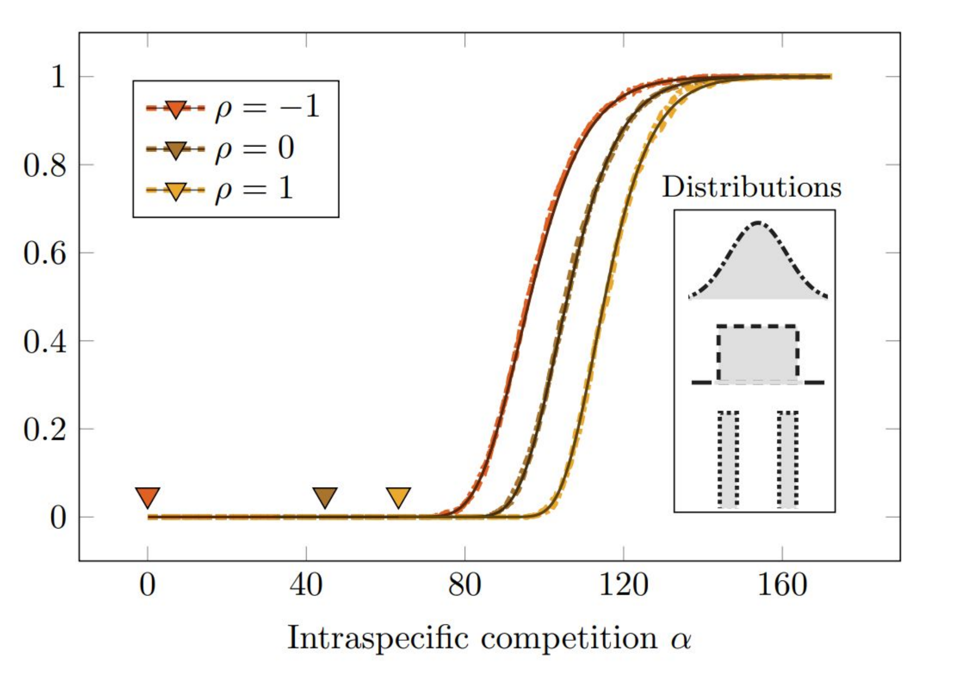
One that works very well is using the theory of resolvents (ht José Capitán)

We recover extremely precise approximation even for small *n*

Alternatively---use iterative solution of linear systems (following Stone 1988)

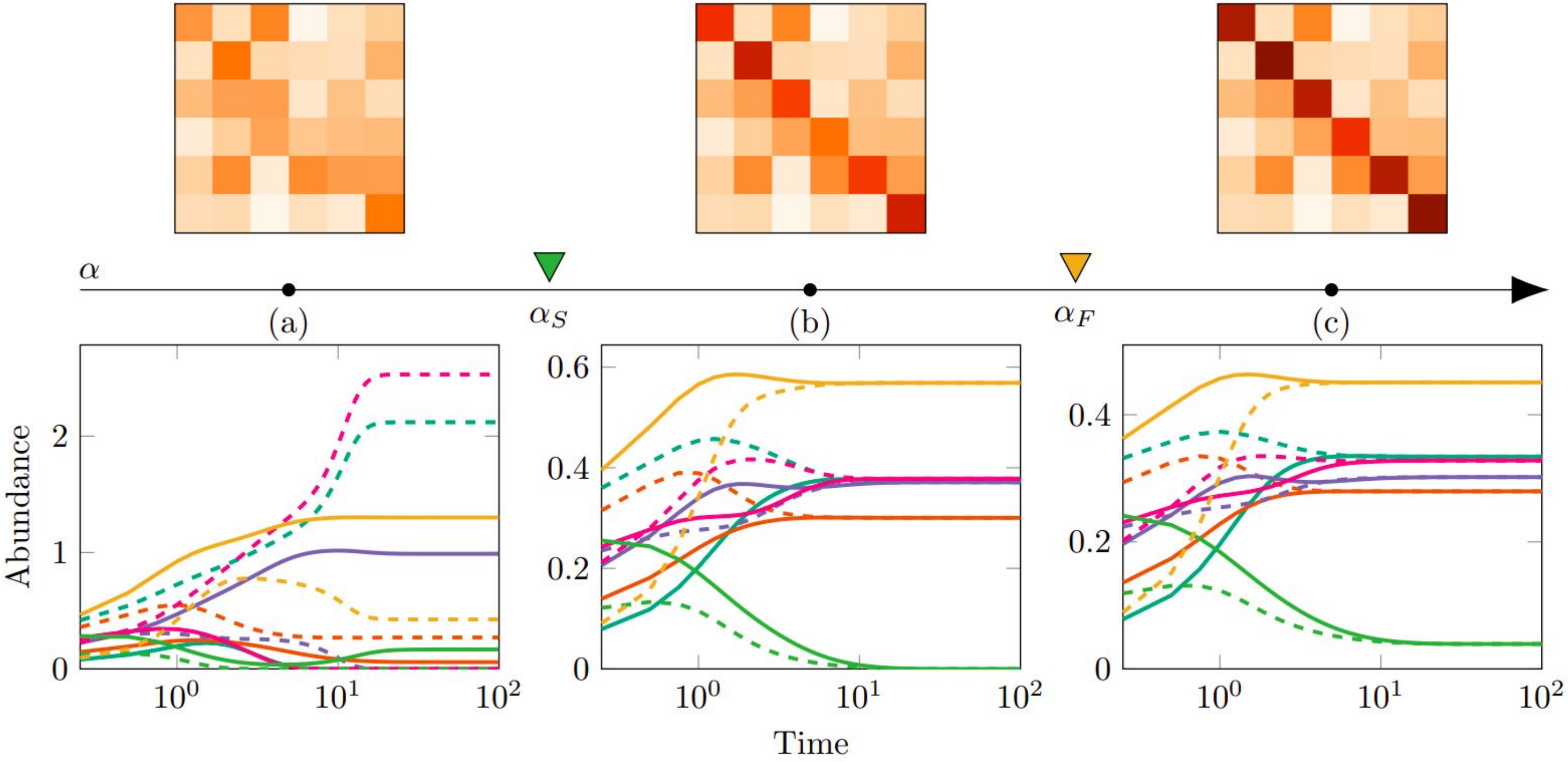
Consequences for dynamics

Robust coexistence of surviving sub-community

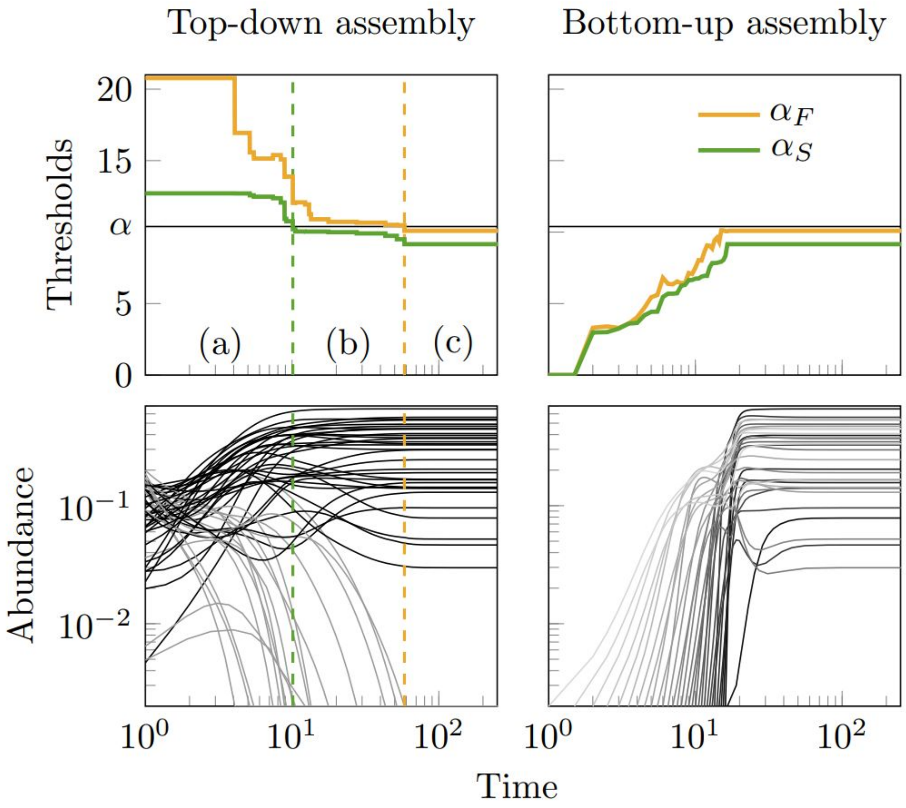


Feasibility implies stability

Three scenarios



Top-down vs bottom-up assembly



Summary

General systems

For "competitive" GLV, average interaction strength has no effect of feasibility

Many transitions

Exists critical value α_F

Random systems

A single transition

Universality

Statistically-equivalent populations → only variance changes

Conclusions

“Competitive” GLV: intraspecific competition can guarantee feasibility and stability (key: $r > 0$)

For large random systems, generically $\alpha_S < \alpha_F$ and thus we observe only equilibria (no cycles or chaos)

Experiments: documented examples of cycles and chaos in food webs or structured populations

Conclusions

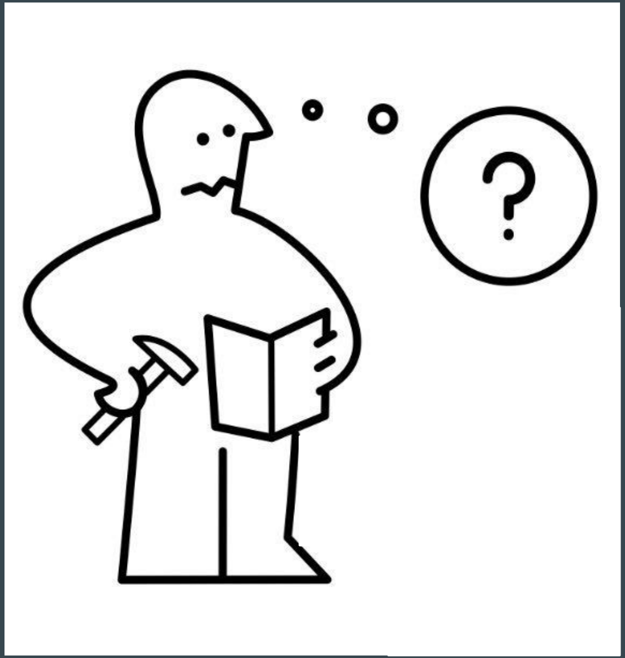
Populations will settle at a saturated equilibrium, as found for consumer-resource models and GLV with symmetric interactions (e.g., based on similarity)

Globally-stable dynamics for the surviving species, lack of invasibility for those that go extinct (up to a point), the system can be built via successive invasions

The epitome of robust coexistence

Thank you!

Comments? Questions?



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Extra: existence of α_F

$$\left(I + \frac{1}{\alpha}C\right) y = \frac{1}{\alpha}\mathbb{1}$$

$$y^T \mathbb{1} = \frac{m}{\alpha} \qquad 1 = \frac{\alpha}{m}\mathbb{1}^T y$$

$$\left(I + \frac{1}{\alpha}C\right) y = \frac{1}{m}\mathbb{1}\mathbb{1}^T y$$

$$\left(\frac{1}{m}\mathbb{1}\mathbb{1}^T - \frac{1}{\alpha}C\right) y = y$$

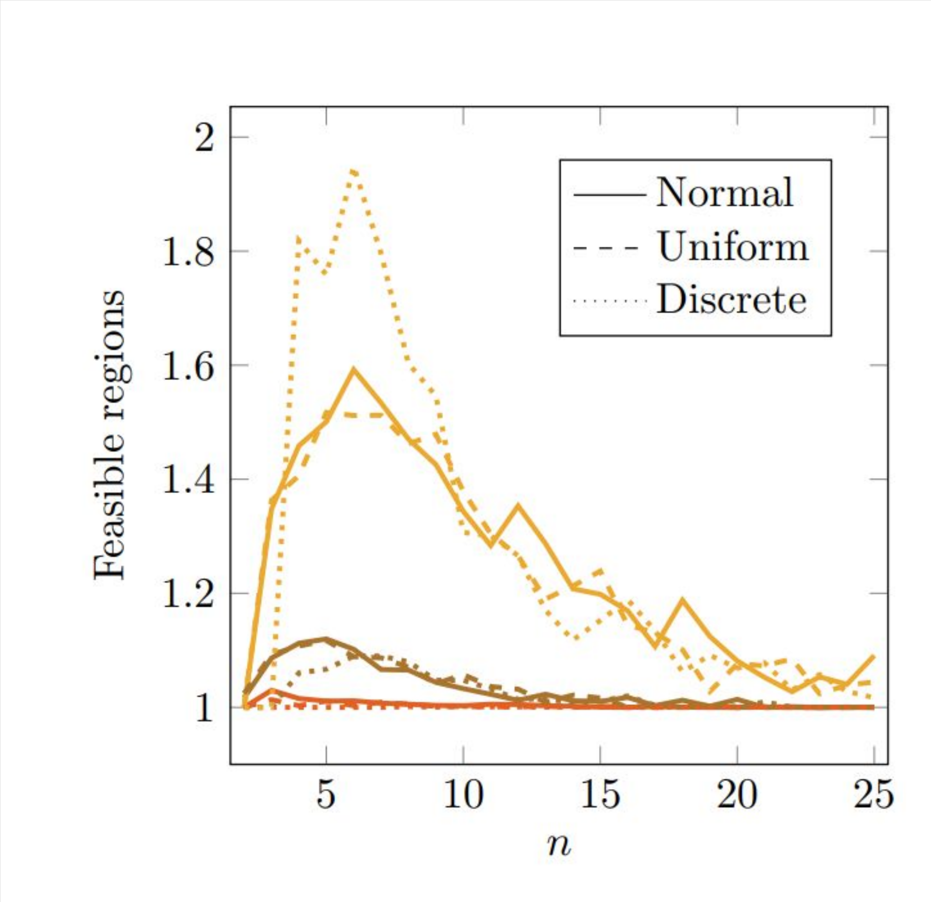
IF $\alpha = \alpha_\infty > \max_{i,j} C_{ij}\, m$

THEN $\left(\frac{1}{m}\mathbb{1}\mathbb{1}^T - \frac{1}{\alpha}C\right)_{ij} > 0 \quad \forall i, j$

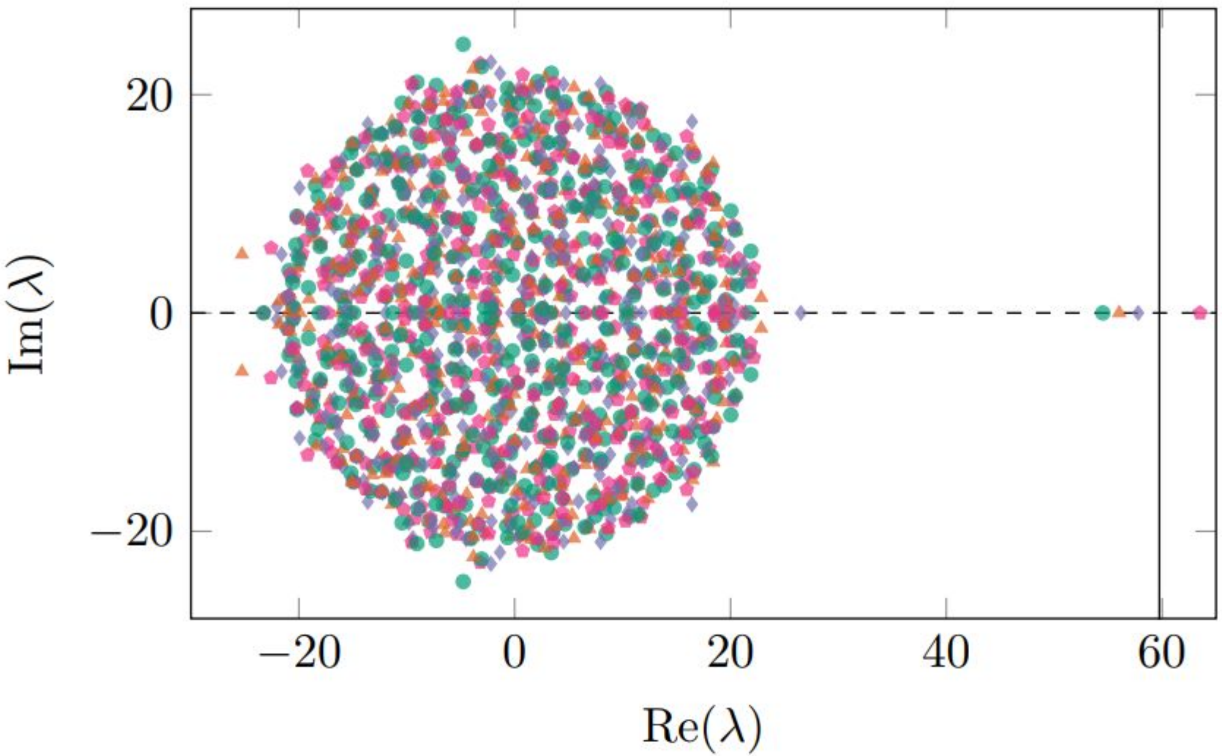
COL SUM $= 1 \Rightarrow$ S.R. $= 1$

$\Rightarrow$ PERRON–FROBENIUS

Extra: number of transitions



Extra: outliers vs row sums



Extra: assembly