Rescuing metacommunity ecology using random matrix theory

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with Dominique Gravel & Mathew Leibold

The initial question

Will a Large Complex System be Stable?

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Received January 10, 1972.

Formalization

Assume a feasible equilibrium X^* of

$$\frac{d\mathbf{X}}{dt} = \mathbf{G}(\mathbf{X})$$

where X denotes the abundance vector for all the *S* species and vector G(X) represents the dynamics of the system (competition, predation, mutualism…)

Linearization

Assume a feasible equilibrium X*

Linearize the dynamics around the equilibrium

$$\frac{d(\mathbf{X}-\mathbf{X}^*)}{dt} \approx \underbrace{\partial\mathbf{G}(\mathbf{X}^*)}_{\text{Jacobian matrix J}}.(\mathbf{X}-\mathbf{X}^*)$$

The Jacobian matrix

Assume that the system is “random” and properly scaled, i.e. the Jacobian looks like

$$\mathbf{J} = \begin{bmatrix} -m & & B(c)\times\mathcal{N}\left(0,\sigma^2\right) & \\ & -m & & \\ B(c)\times\mathcal{N}\left(0,\sigma^2\right) & & \ddots & \\ & & & -m \end{bmatrix}$$

where $B(c)$ = Bernoulli distribution

$N(0,\sigma^2)$ = Gaussian distribution

The result of May (1972)

(from Wigner 1959; rewritten by Allesina & Tang 2012)

For large *S*, the system is stable if and only if

$$\sigma\sqrt{c(S-1)} < m$$

- σ: Interaction sd
- c: Connectance of the interaction matrix
- S: Species richness
- m: Feedback of a species on itself

General question

May’s result proves that, all else being equal, a system with many (S) interacting (c) species, with “intense” interactions (σ) is very likely to be unstable

Q: What are the missing elements that would allow for many-species stable ecological systems?

Sequels to May's paper

Three main lines of investigation:

1. Rephrasing the "stability" criterion

2. Jointly studying feasibility & stability

3. Extending May's approach to more detailed cases

A recent example

Stability criteria for complex ecosystems

Stefano Allesina[1,2] & Si Tang[1]

Following line (3) : dissected May's arguments by interaction type

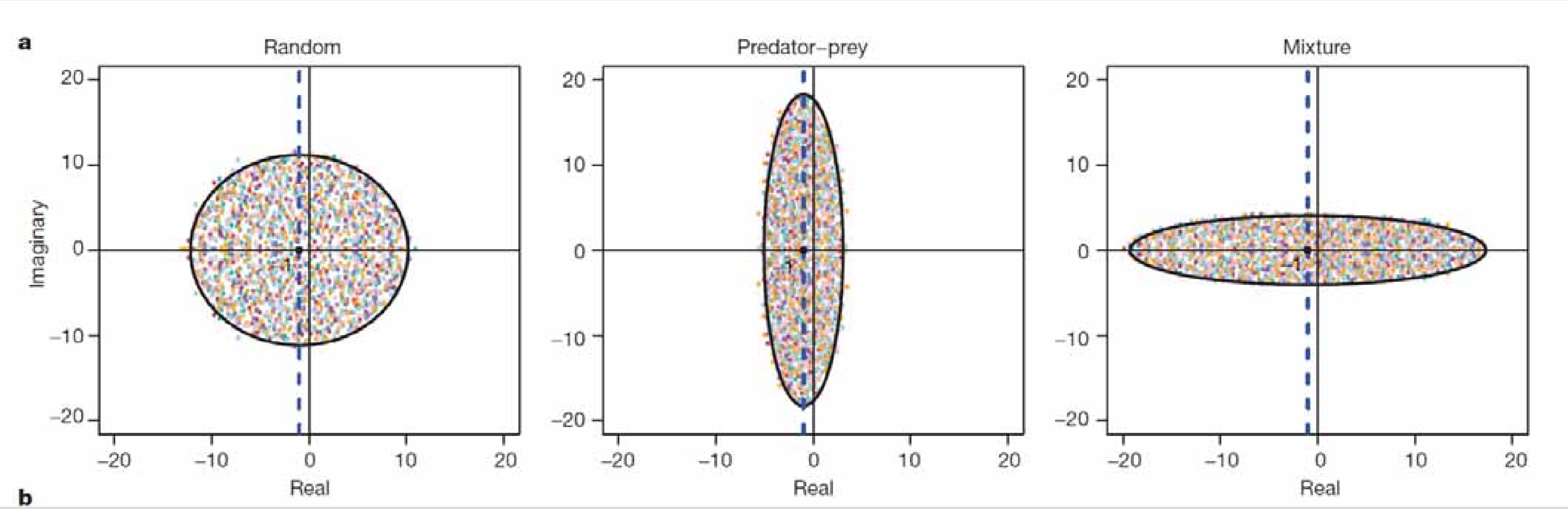
- predation (-/+)
- mutualism (+/+)
- competition (-/-)

Allesina & Tang 2012

A recent example

Main result from Allesina & Tang

Empirical spectral distribution (ESD) changes by interaction type



Allesina & Tang 2012

Specific question

Spatial structure and dispersal are often invoked as determinants of stability/instability

Q: What happens in May's model with spatial structure?

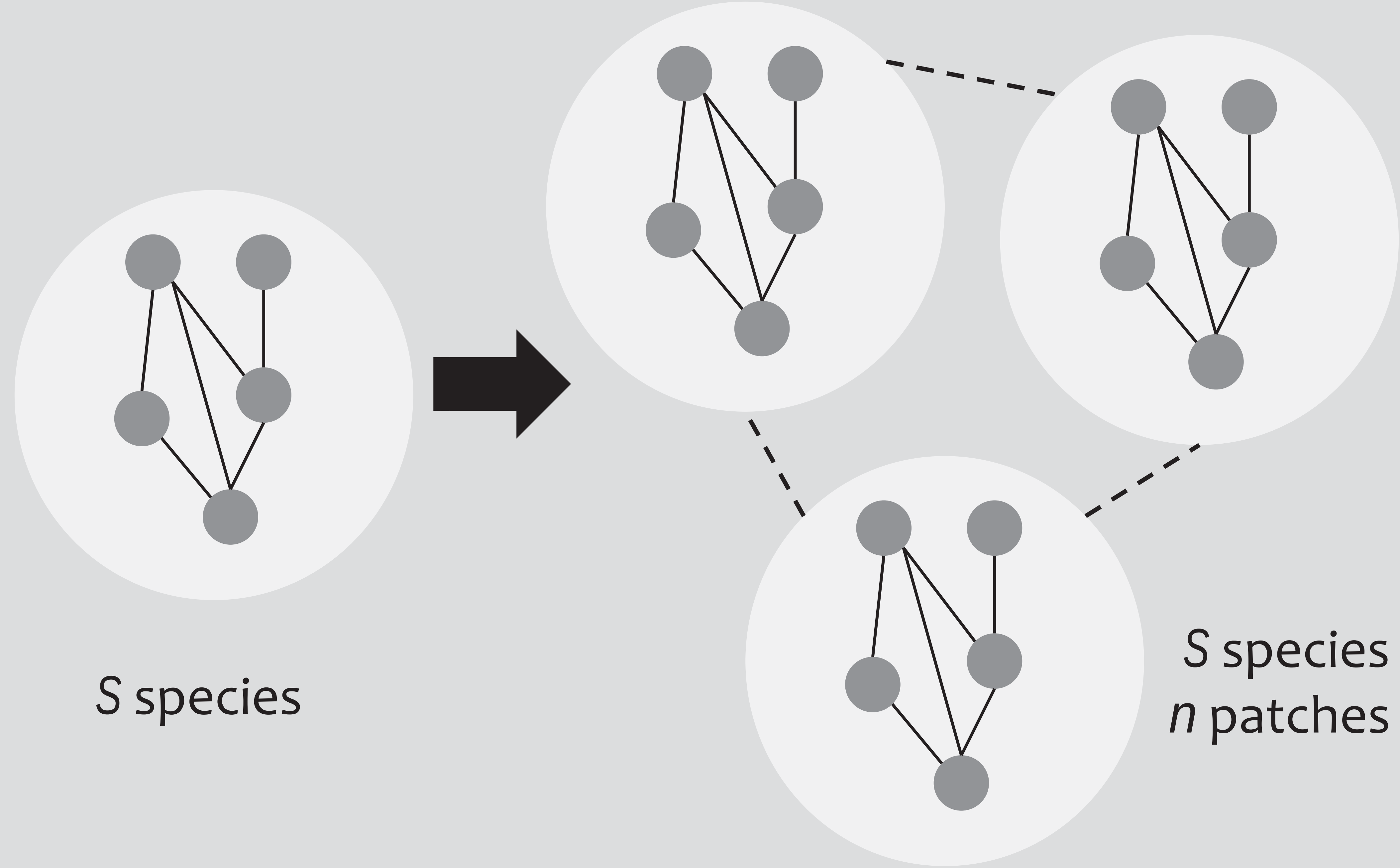
Our own sequel

1. ~~Rephrasing the "stability" criterion~~

2. Jointly studying feasibility & stability

3. Extending May's approach to more detailed cases

Conceptual model



Principle of the analysis

$$\underbrace{\sigma\sqrt{c(S-1)}}_{\text{Random part}} < \underbrace{m}_{\text{Deterministic part}}$$

Random part

= square root of variance x system size

Deterministic part

= min |λ| from the deterministic ESD

Principle of the analysis

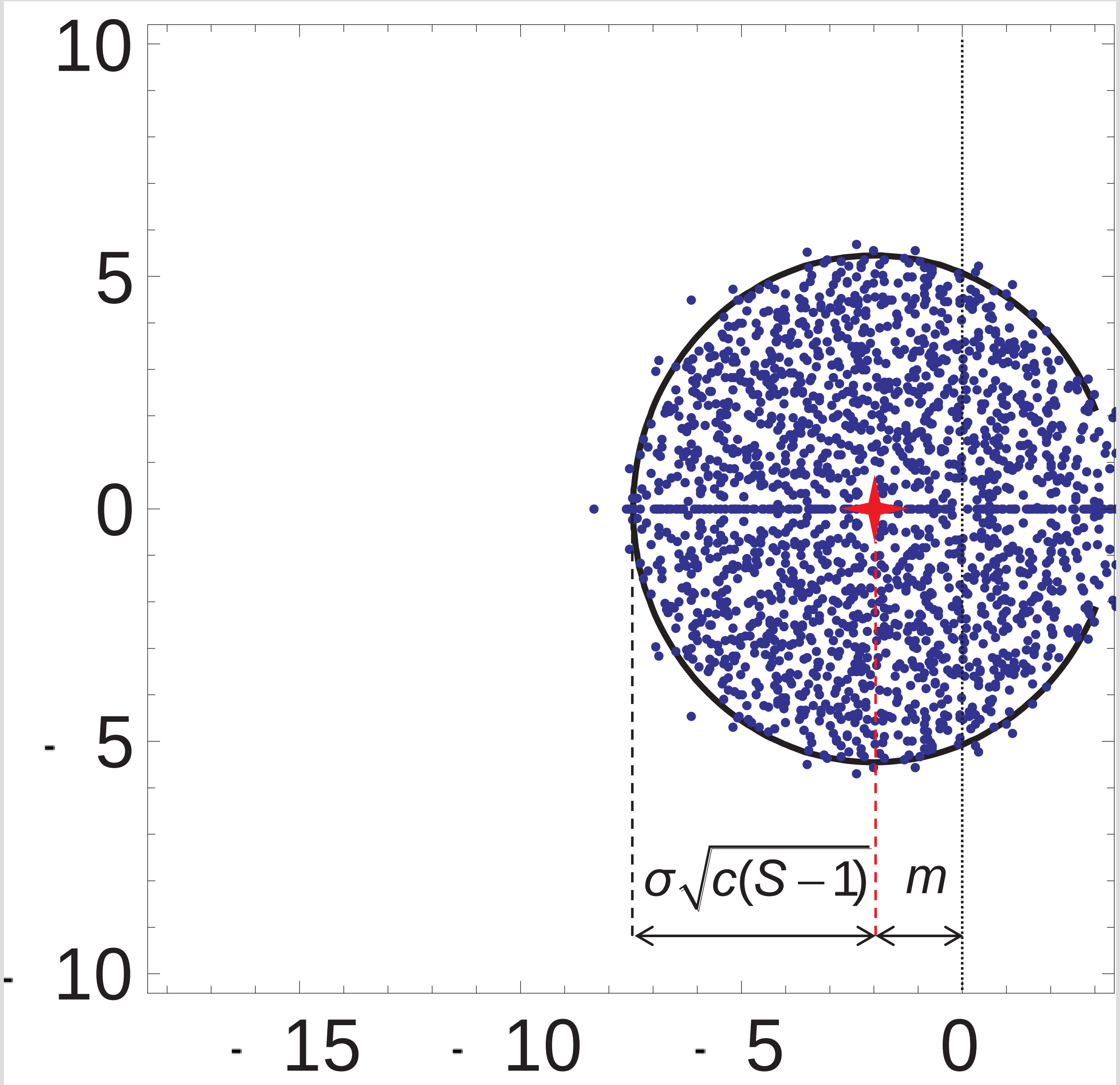
$$\sigma\sqrt{c(S-1)} < m$$

Random part	Deterministic part
= square root of variance x system size	= min |λ| from the deterministic ESD

What we need!

"Radius" of the ESD subset of J that stands closest to positive values	Center of the ESD subset of J that stands closest to positive values

Principle of the analysis



Principle of the analysis

Support of the ESD of X = A + B (size = n) with

- A random, mean = 0, sd = σ
- B deterministic, ESD = μ_B

= z's that verify

$$\int \frac{\mu_{B/\sigma\sqrt{n}}(du)}{|z-u|^2} \geq 1$$

Tao *et al*. 2010

Spatial structure in the Jacobian

$$
\mathbf{J} = \begin{bmatrix}
-m-d & & (a_{ij}^{1}) & & d/(n-1) & 0 & \cdots & 0 & d/(n-1) & 0 & \cdots & 0 \\
 & -m-d & & & 0 & d/(n-1) & \ddots & \vdots & 0 & d/(n-1) & \ddots & \vdots \\
(a_{ij}^{1}) & & \ddots & & \vdots & \ddots & \ddots & 0 & \vdots & \ddots & \ddots & 0 \\
 & & & -m-d & 0 & \cdots & 0 & d/(n-1) & 0 & \cdots & 0 & d:(n-1) \\
d/(n-1) & 0 & \cdots & 0 & \ddots & & (a_{ij}^{k}) & & & & & \\
0 & d/(n-1) & \ddots & \vdots & & \ddots & & & & & & \\
\vdots & \ddots & \ddots & 0 & (a_{ij}^{k}) & & \ddots & & & & & \\
0 & \cdots & 0 & d/(n-1) & & & & \ddots & & & & \\
d/(n-1) & 0 & \cdots & 0 & & & & & -m-d & & (a_{ij}^{n}) & \\
0 & d/(n-1) & \ddots & \vdots & & & & & & -m-d & & \\
\vdots & \ddots & \ddots & 0 & & & & & (a_{ij}^{n}) & & \ddots & \\
0 & \cdots & 0 & d/(n-1) & & & & & & & & -m-d
\end{bmatrix}
$$

Among patches

Within patches

Spatial structure in the Jacobian

$-(m+d)\mathbf{I}+\mathbf{A}_1$	$\left(d/(n-1)\right)\mathbf{I}$	$\left(d/(n-1)\right)\mathbf{I}$
$\left(d/(n-1)\right)\mathbf{I}$	$-(m+d)\mathbf{I}+\mathbf{A}_k$	$\left(d/(n-1)\right)\mathbf{I}$
$\left(d/(n-1)\right)\mathbf{I}$	$\left(d/(n-1)\right)\mathbf{I}$	$-(m+d)\mathbf{I}+\mathbf{A}_n$

Among patches

Within patches

Deterministic part of the Jacobian

$-(m+d)\mathbf{I}$	$\left(d/(n-1)\right)\mathbf{I}$	$\left(d/(n-1)\right)\mathbf{I}$
$\left(d/(n-1)\right)\mathbf{I}$	$-(m+d)\mathbf{I}$	$\left(d/(n-1)\right)\mathbf{I}$
$\left(d/(n-1)\right)\mathbf{I}$	$\left(d/(n-1)\right)\mathbf{I}$	$-(m+d)\mathbf{I}$

Among patches

Within patches

Deterministic part of the Jacobian

Eigenvalues of the deterministic part of the Jacobian change from

$$\underbrace{(-m,-m,\ldots,-m)}_{S\text{ times}}$$

to

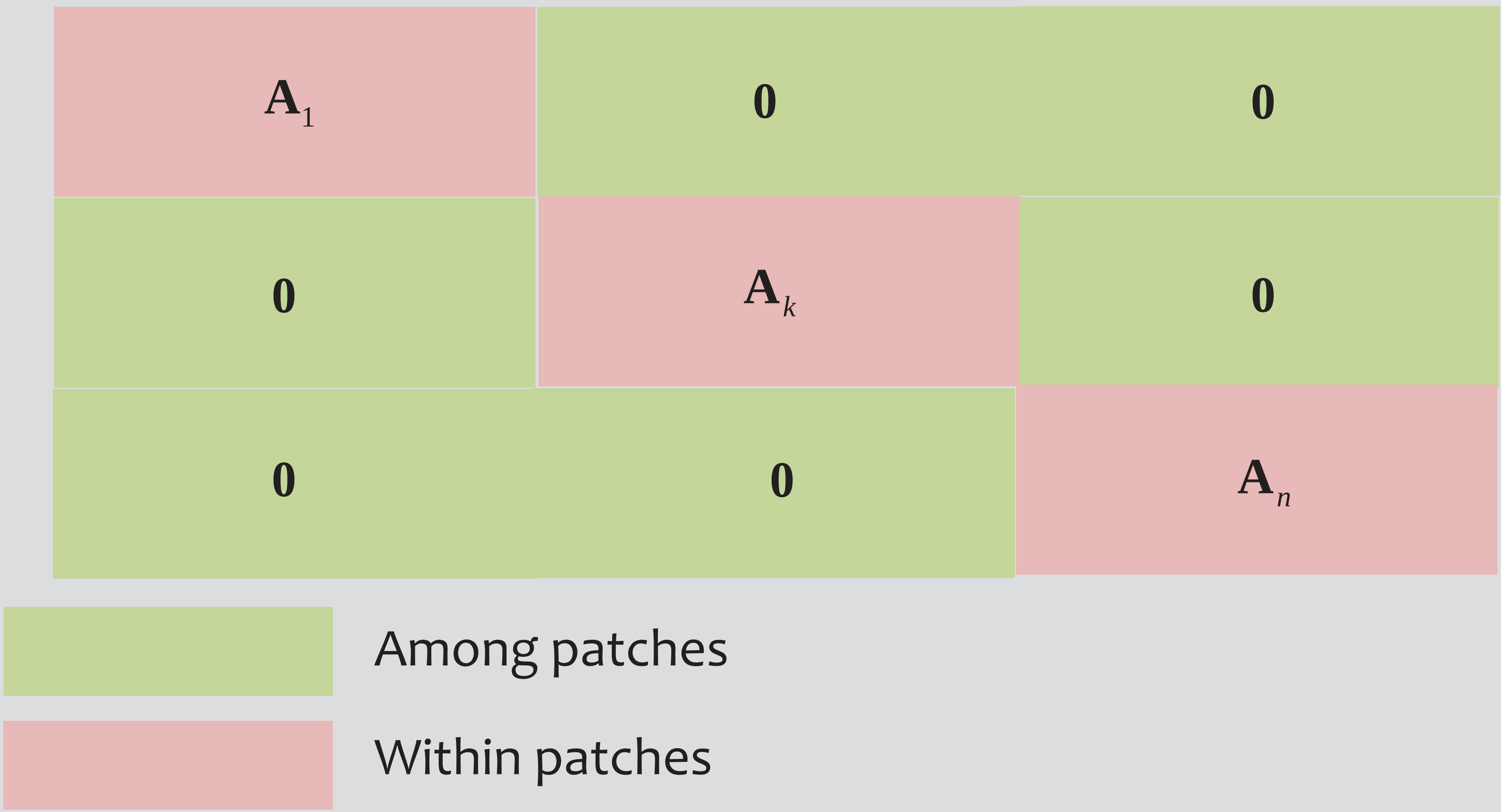
$$(\underbrace{-m,-m,\ldots,-m,}_{S\text{ times}}\underbrace{-m-dn/(n-1),\ldots,-m-dn/(n-1)}_{(n-1)S\text{ times}})$$

→ The deterministic effect of d is to "push" a fraction of the ESD to the left of the complex plane

Random part of the Jacobian

With only one patch… (May's model)

Random part of the Jacobian



Random part of the Jacobian

- Connectance goes from c to c/n
- System size goes from S to nS
- Variance?

Random part of the Jacobian

- Connectance goes from c to c/n
- System size goes from S to nS
- Variance

  For large d, changes from $\mathrm{V}\left[\mathbf{A}\right]$

  to $\mathrm{V}\left[\overline{\mathbf{A}}\right] = \mathrm{V}\left[\frac{1}{n}\sum_i \mathbf{A}_i\right]$

Heterogeneous random parts

Computing the variance:

when all A_i are independent (heterogeneous case)

$$\mathrm{V}\left[\overline{\mathbf{A}}\right] = \mathrm{V}\left[\frac{1}{n}\sum_i \mathbf{A}_i\right] = \frac{1}{n^2}\sum_i \mathrm{V}\left[\mathbf{A}_i\right] = \frac{1}{n}\mathrm{V}\left[\mathbf{A}\right]$$

→ With heterogeneous random parts, high dispersal among patches leads to a less stringent criterion for stability

$$\sigma\sqrt{c(S-1)/n} < m$$

Homogeneous random parts

Computing the variance:

when all A_i are equal (homogeneous case)

$$V\left[\overline{\mathbf{A}}\right] = V[\mathbf{A}]$$

$\rightarrow$ With homogeneous random parts, spatial structure has no effect on stability

$$\sigma\sqrt{c(S-1)} < m$$

General case (large *d*)

Computing the variance:

general case (depends on the correlation ρ among A's)

$$\mathsf{V}\left[\overline{\mathbf{A}}\right] = \mathsf{V}[\mathbf{A}] / n_e$$

$$n_e = n / \left[1 + (n-1)\rho\right]$$

$$\sigma\sqrt{c(S-1)/n_e} < m$$

General case (small ***d***)

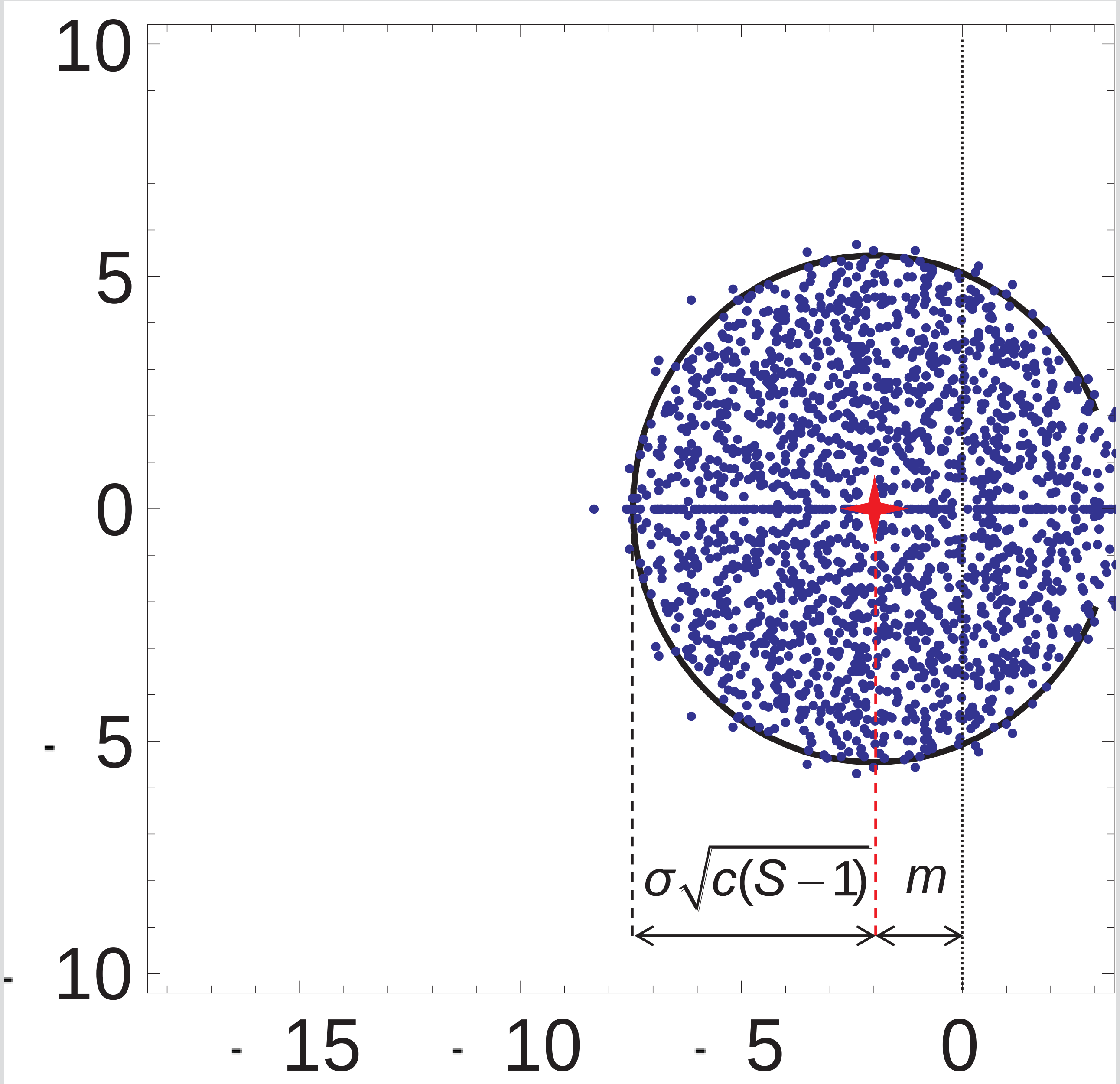
When *d* is small, a different approximation:

$$\sigma\sqrt{c\left(S-1\right)} < m+d$$

valid whatever the value of ρ

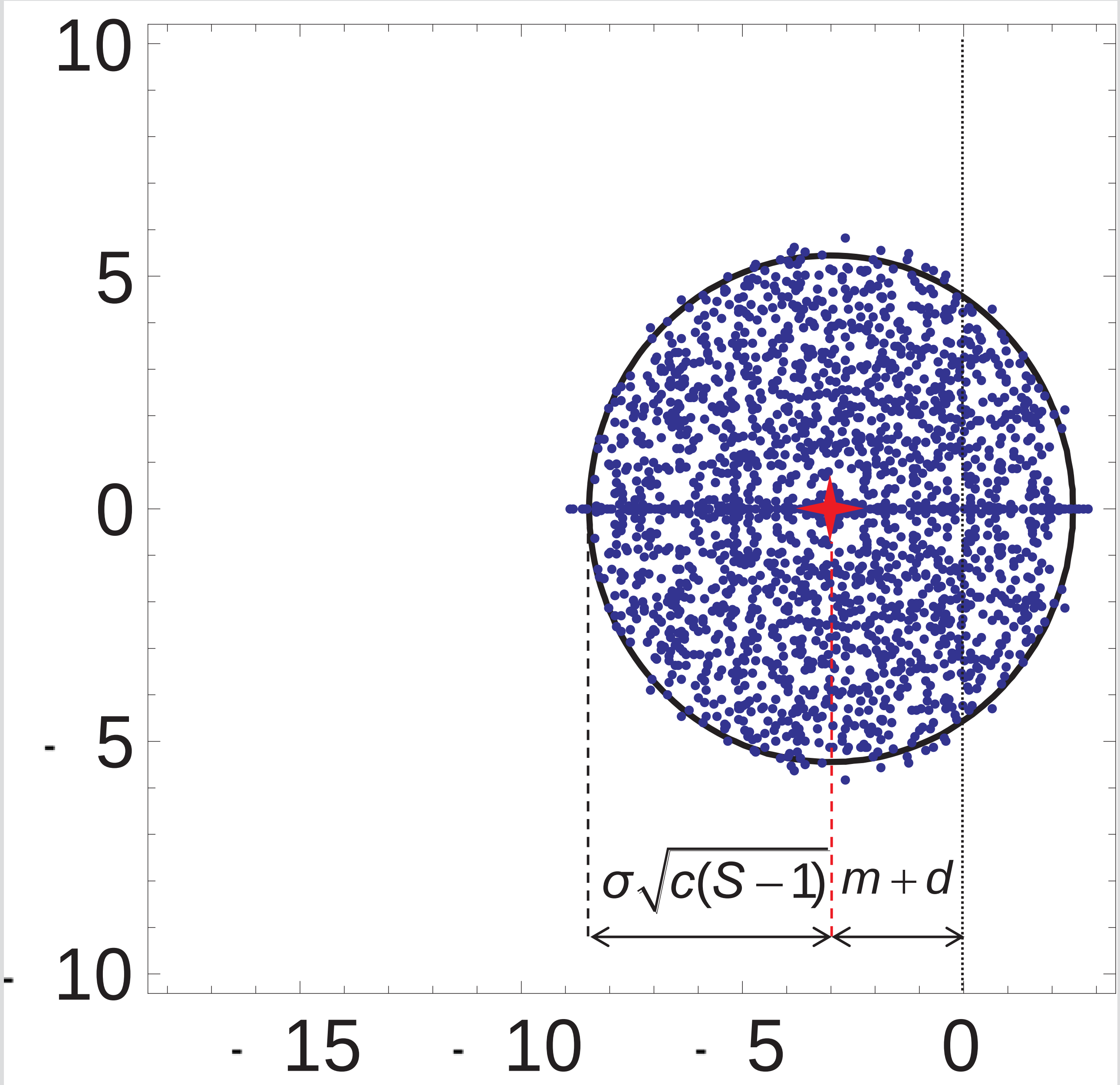
What it looks like…

$d = 0$
$n = 20$
$S = 100$
$m = 2$
$\rho = 0$



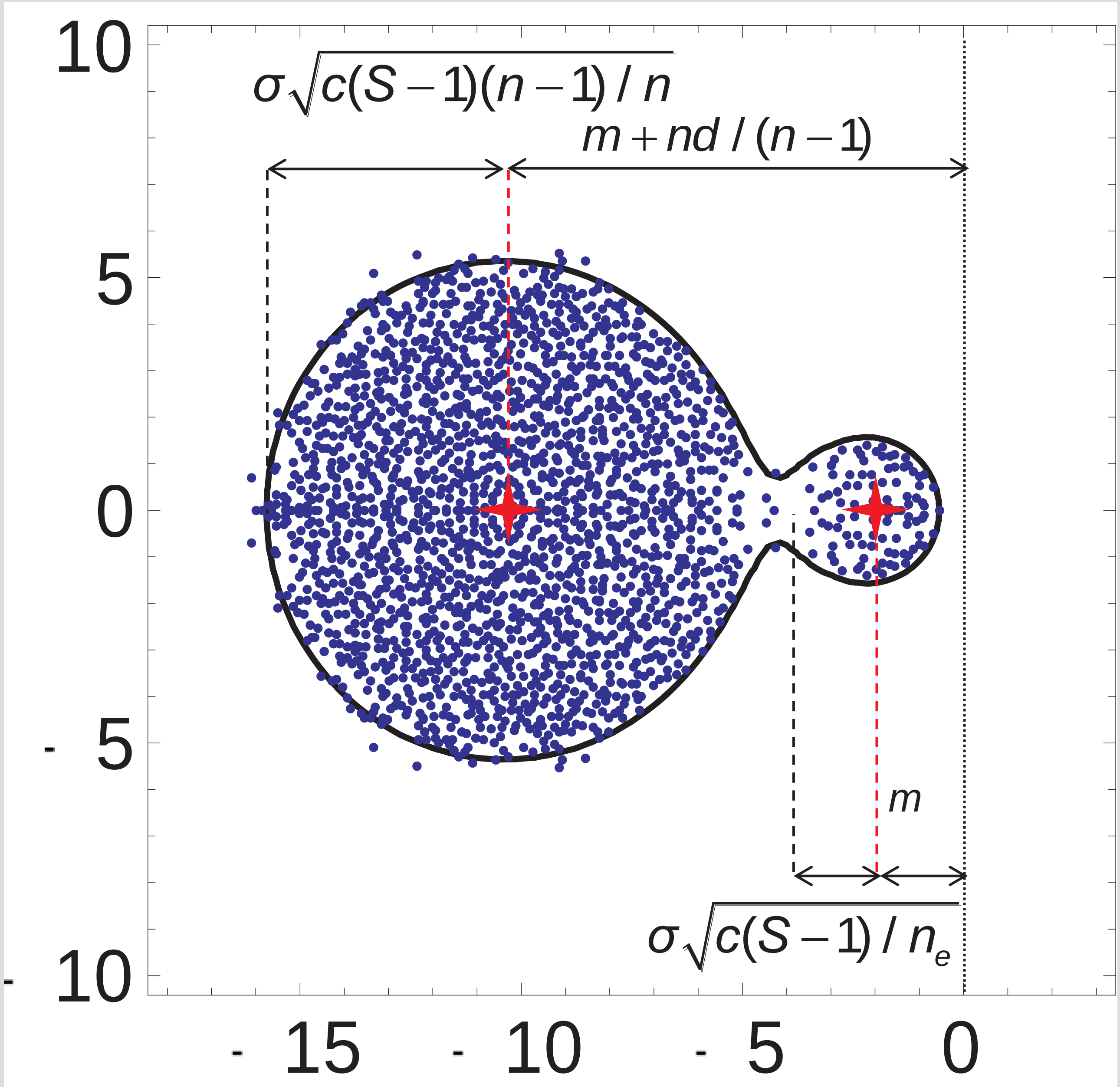
What it looks like…

$d = 1$
$n = 20$
$S = 100$
$m = 2$
$\rho = 0$



What it looks like…

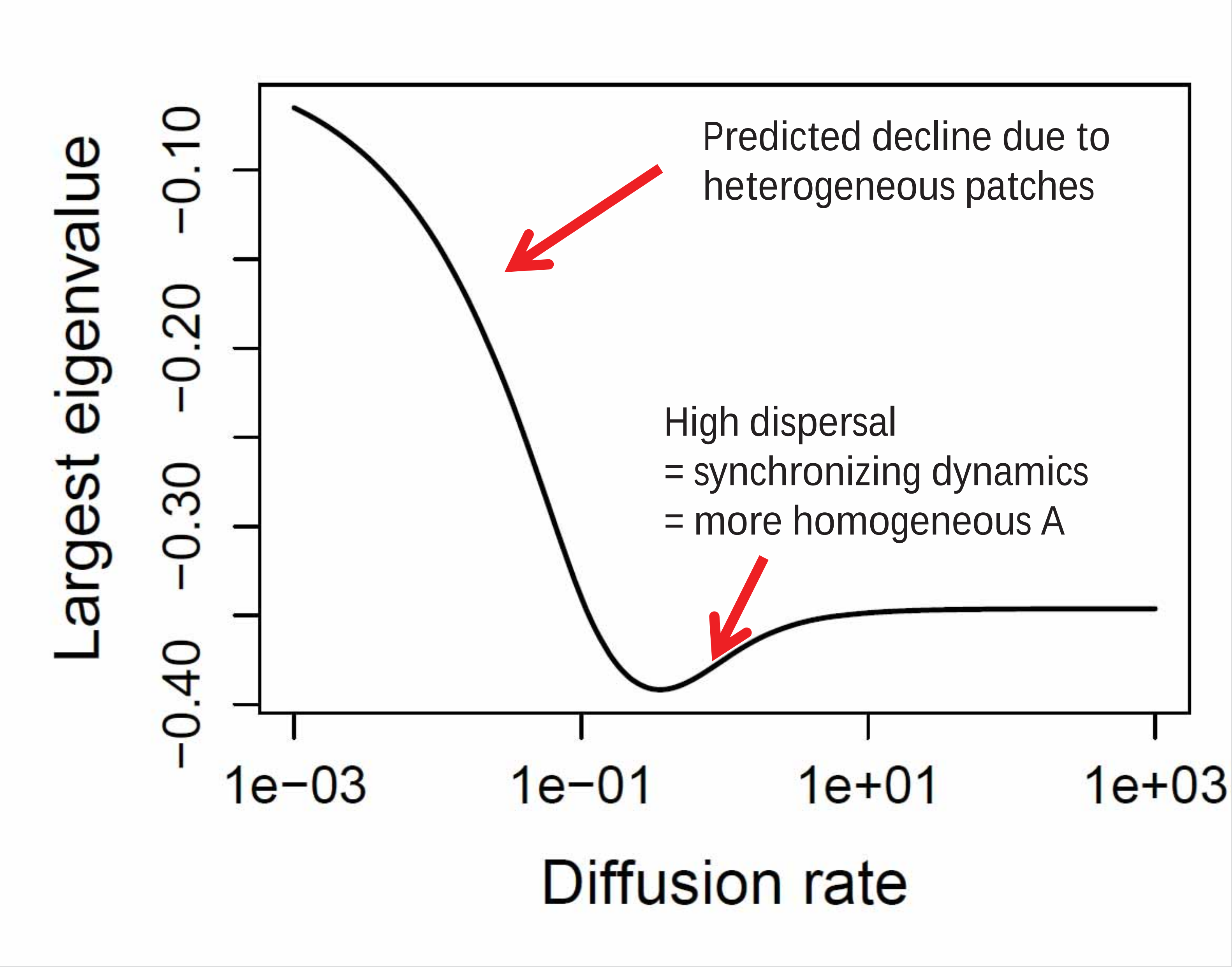
$d = 8$
$n = 20$
$S = 100$
$m = 2$
$\rho = 0$



Extensions

- Works with non-complete spatial graphs
- Works with species-specific dispersal rates
- Simulations (with feasibility constraints) show the same results
- One thing you can't study from J alone is the feedback between *d* and the homogeneity of A

Feedback between ***d*** and A



Take-home messages

1. Stabilization requires heterogeneity of Jacobians
2. Dispersal effectively splits the ESD into diverging disks, and the disk closest to R^+ has weight = 1/*n*
3. Dispersal can feed back on the homogeneity of the random parts → intermediate dispersal rates are better at stabilizing

Perspectives

- dispersal when not diffusive
  - density-dependent dispersal
- putting together dispersal at different scales (non trans-specific definition of patches)
- explicit link between feasibility conditions and stability conditions (like Bastolla et al. 2005)

Thank you!

NIMBioS
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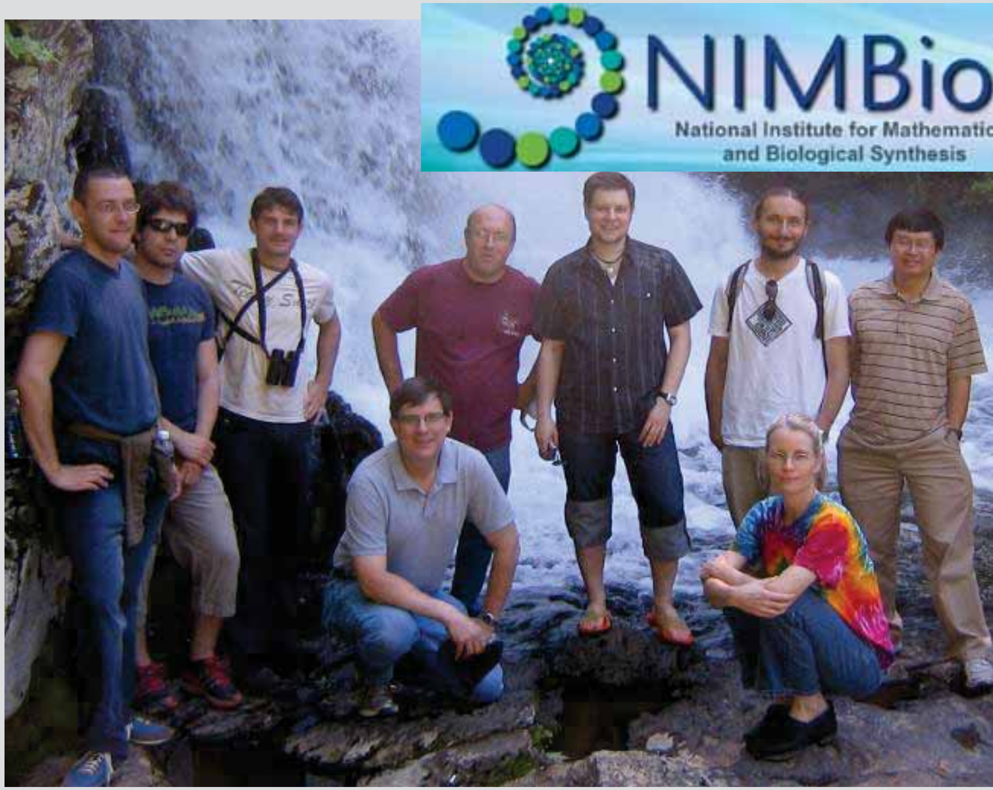

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