Stability, dispersal and ecological networks

François Massol

June 1st 2015

General theme

Evolutionary ecology of fluxes

- Evolution & ecology of dispersal
- Spatial structure, networks of populations
- Food webs & other interaction networks

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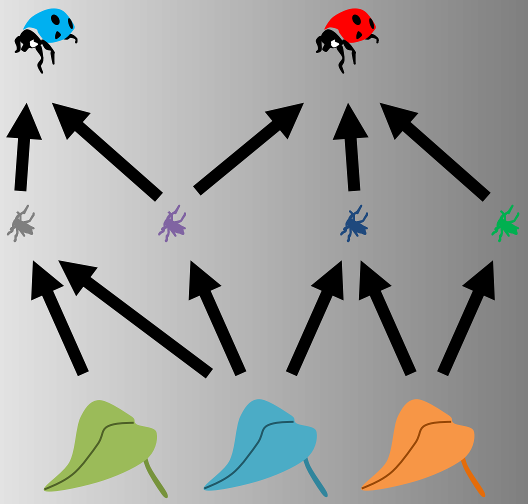
Evolutionary ecology of fluxes

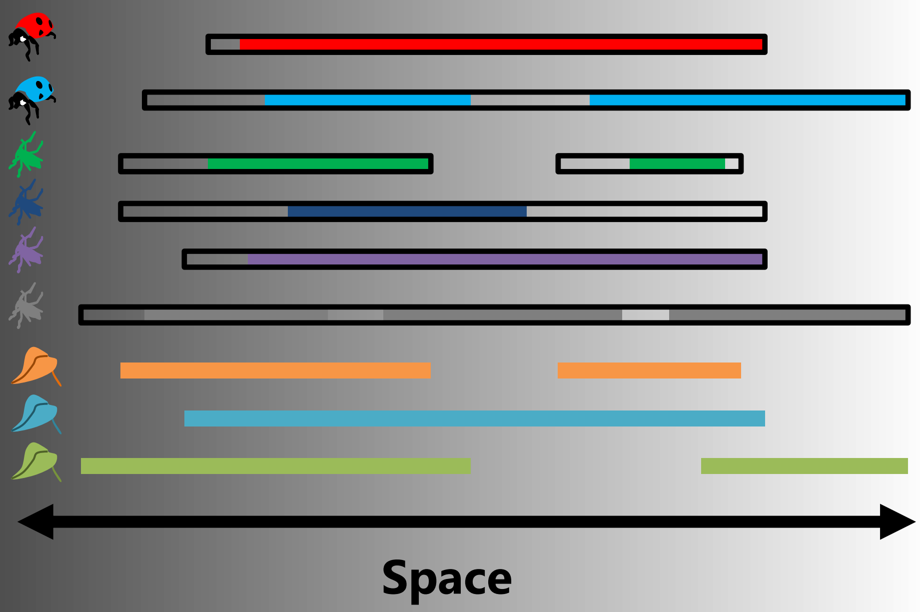
- Evolution & ecology of dispersal
- Spatial structure, networks of populations
- Food webs & other interaction networks

- Ultimately: (spatial) network of (interaction) networks

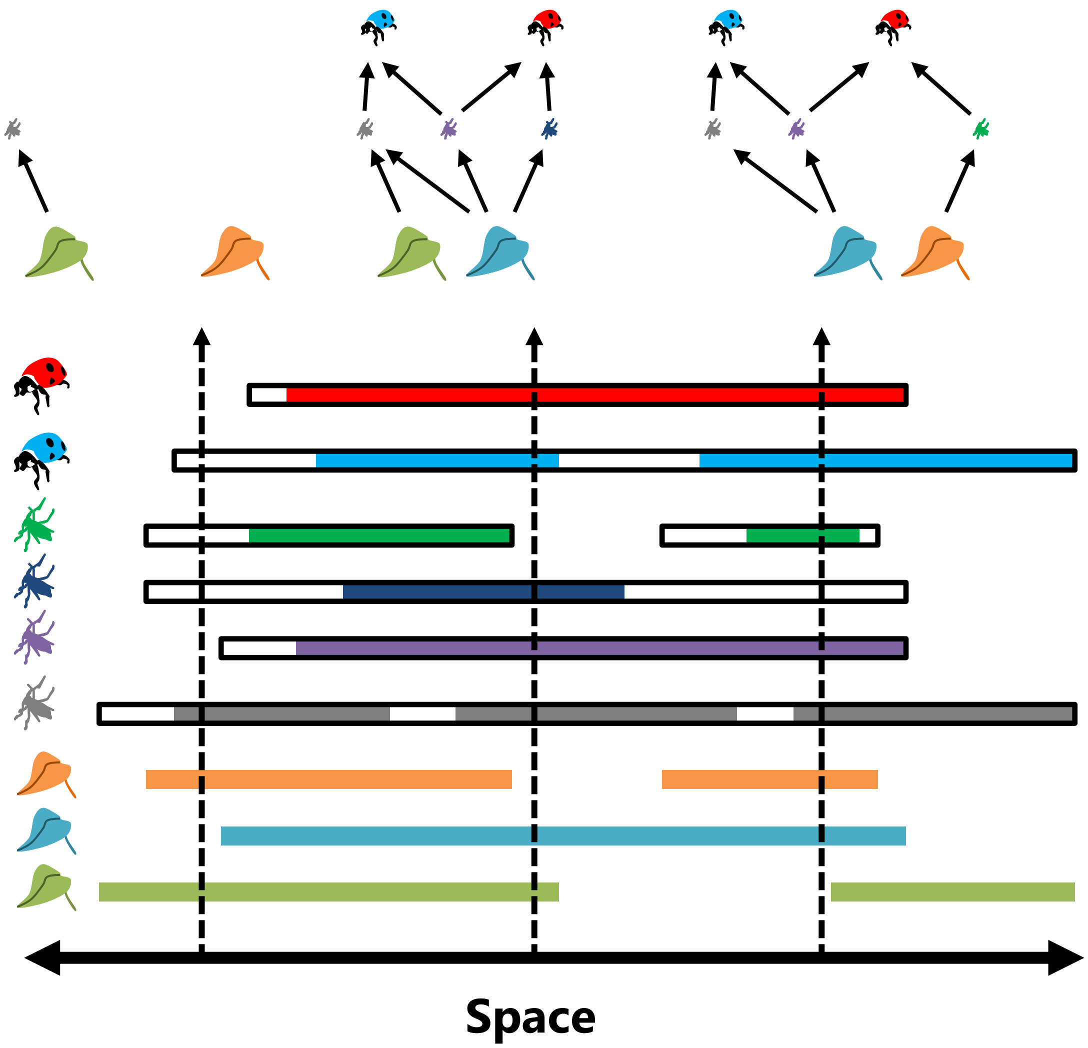
Spatially structured networks



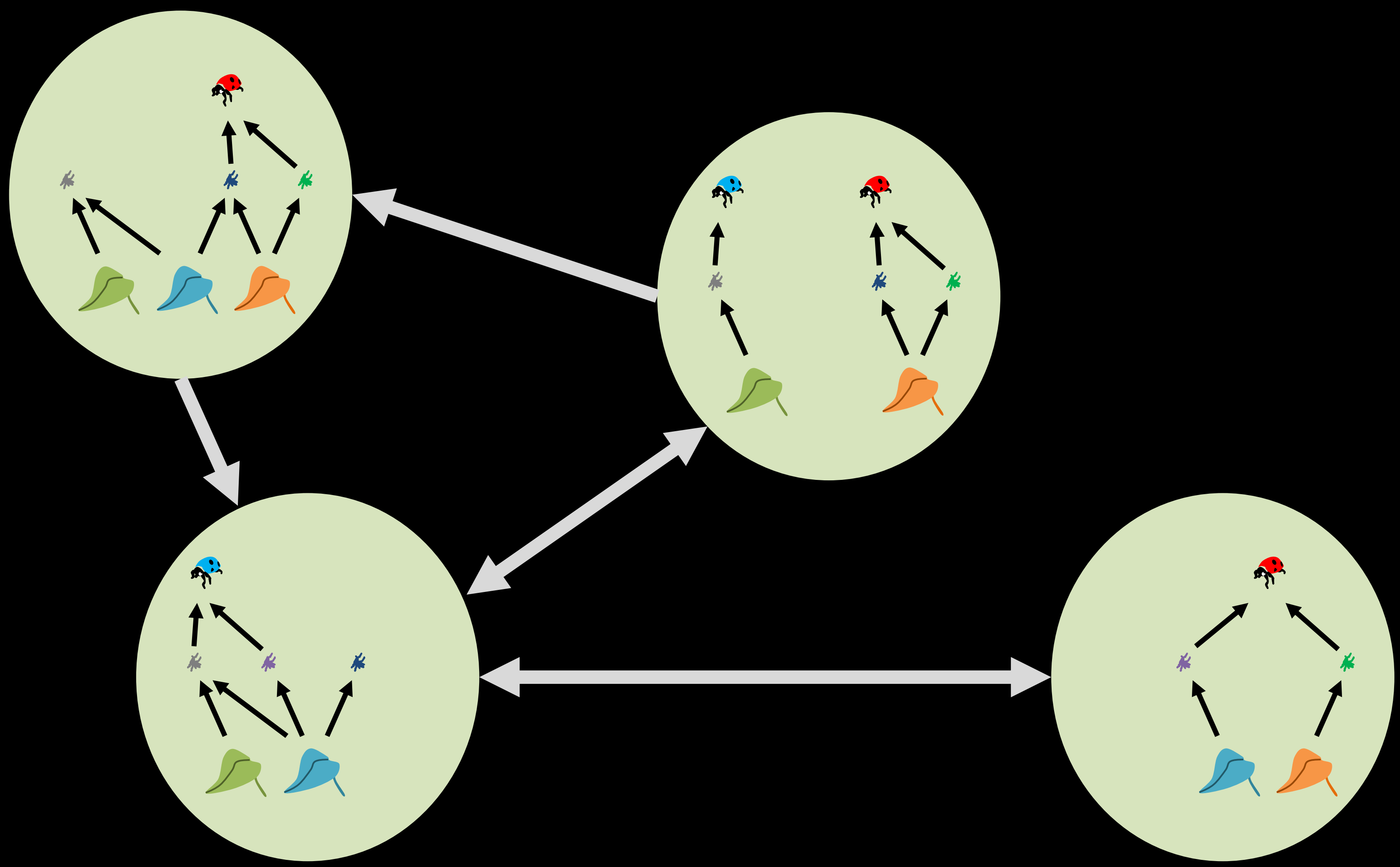
Spatially structured networks



Spatially structured networks



Spatially structured networks



Today's outline

CONSEQUENCES OF DISPERSAL IN ECOSYSTEMS

1. **Ecosystem stability**

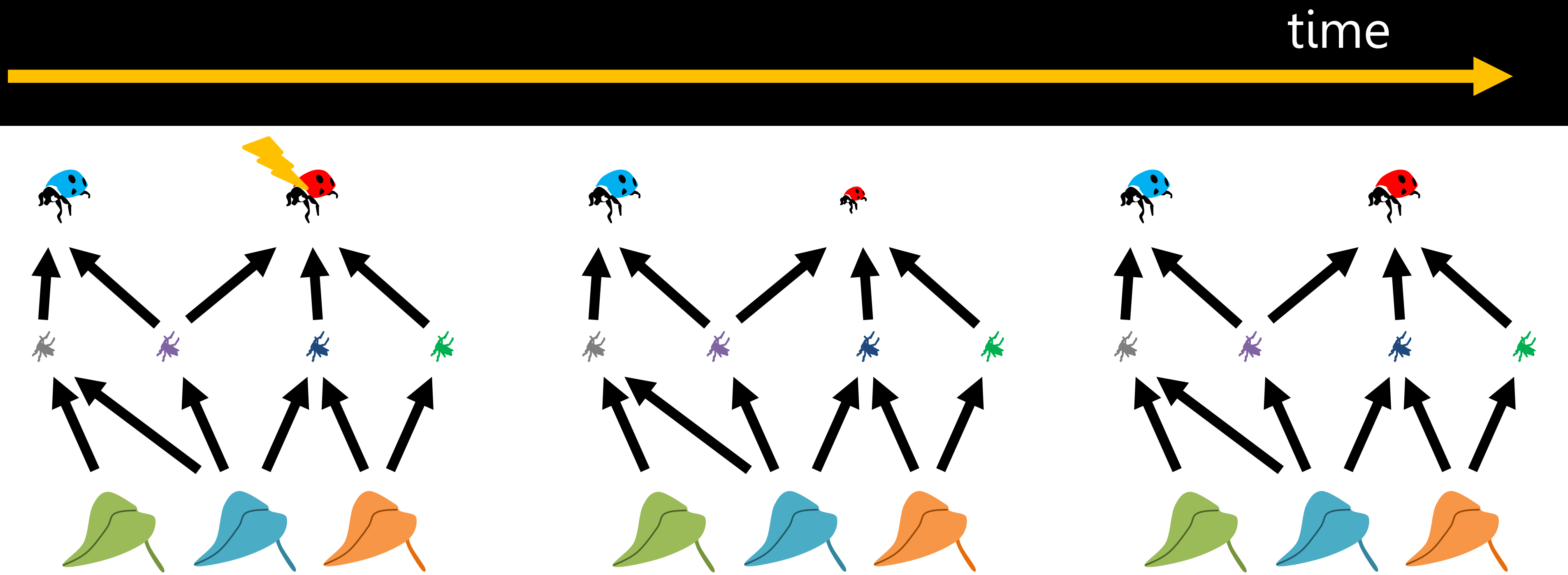
2. **Patch dynamics on networks**

ECOSYSTEM STABILITY

Ecosystem stability

The question:

Does species diversity and the variability of species interactions stabilize ecosystems?

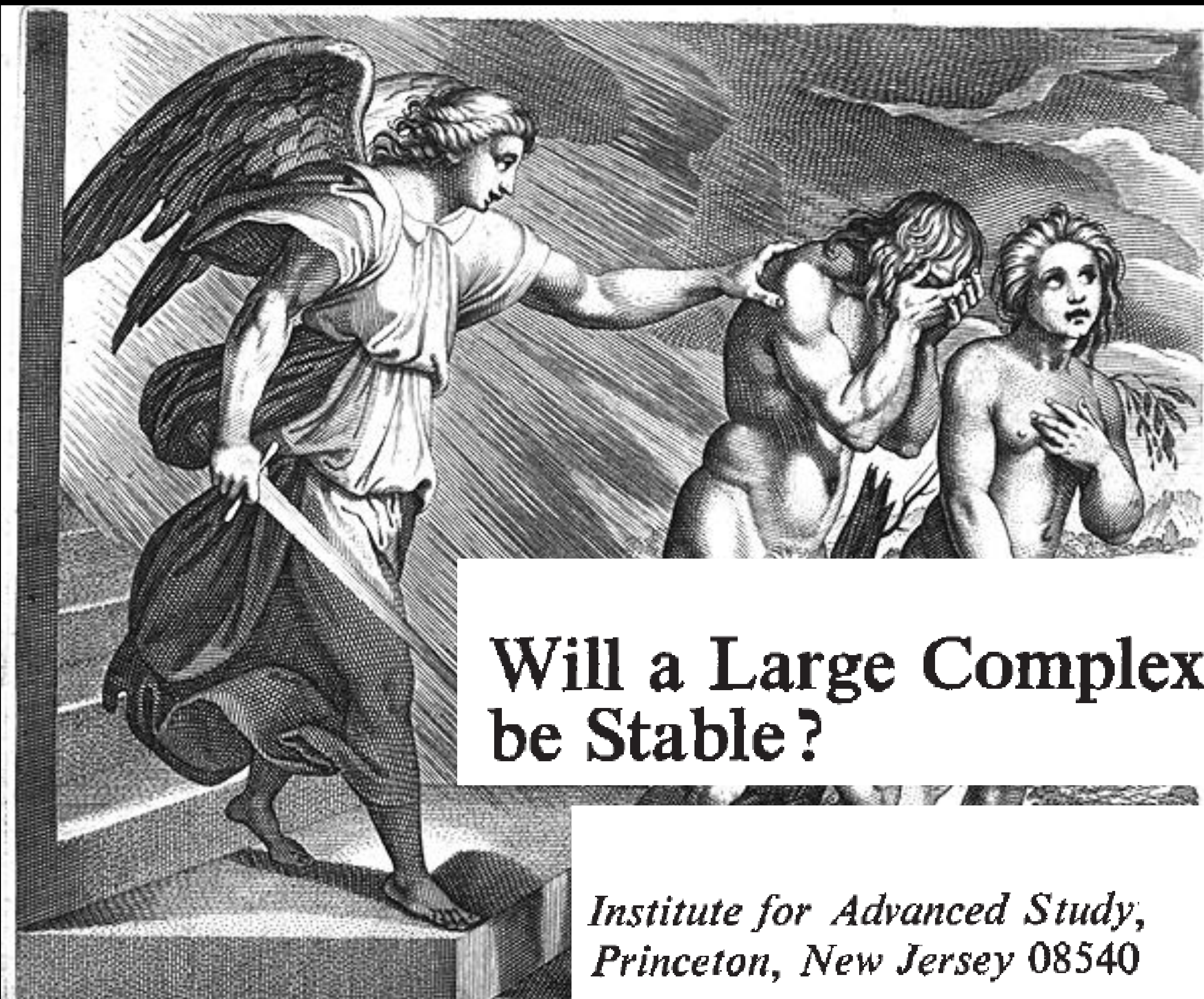


Diversity stabilizes ecosystems…

Dominant view until the 70's

"a larger number of paths through each species is necessary to reduce the effects of overpopulation of one species" – MacArthur 1955

… or does it?



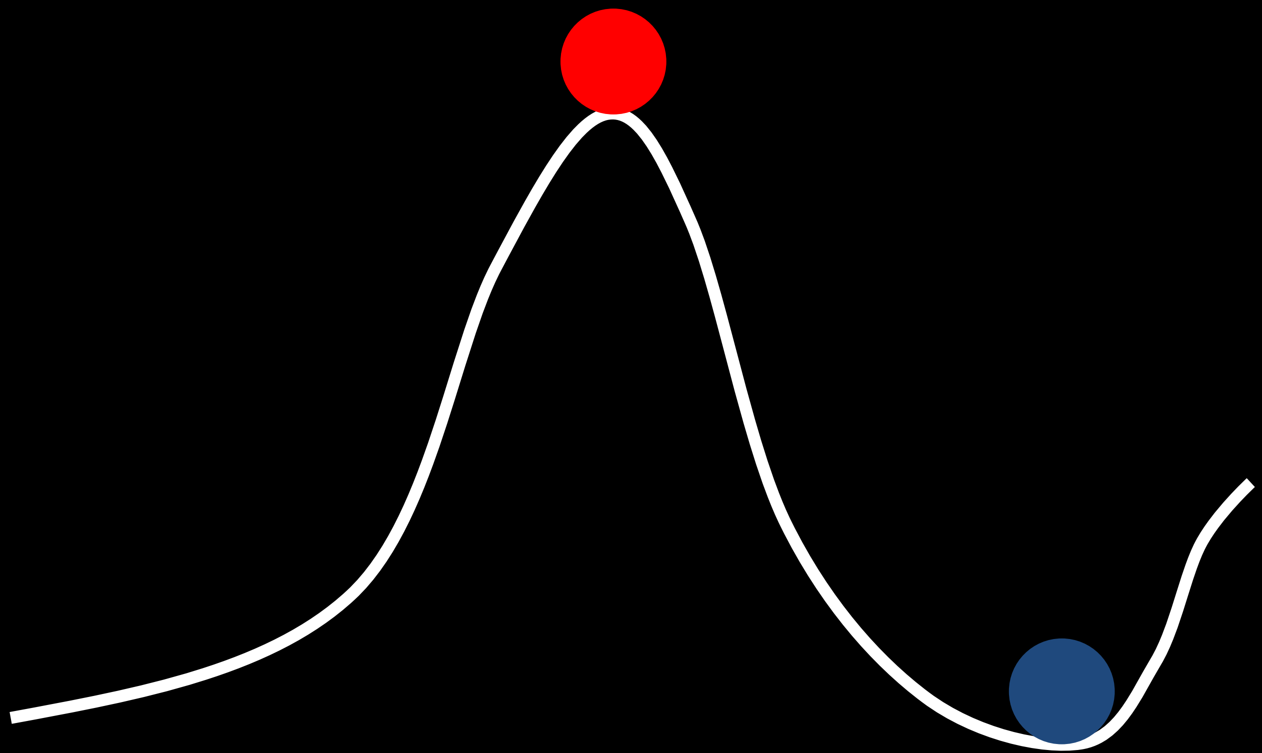
Will a Large Complex System be Stable?

ROBERT M. MAY*

Institute for Advanced Study, Princeton, New Jersey 08540

Received January 10, 1972.

Mathematical stability



Formalization

Assume a feasible equilibrium $\mathbf{X}^*$ of

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

where

$\mathbf{X}$ =abundance vector for all the S species

$\mathbf{G}(\mathbf{X})$ = dynamics of the system (competition, predation, mutualism...)

Linearization

Assume a feasible equilibrium $\mathbf{X}^*$

Linearize the dynamics around the equilibrium

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

Stable equilibrium (locally) $\Longleftrightarrow$ All eigenvalues of $\mathbf{J}$ have negative real parts

The Jacobian matrix of a random ecosystem

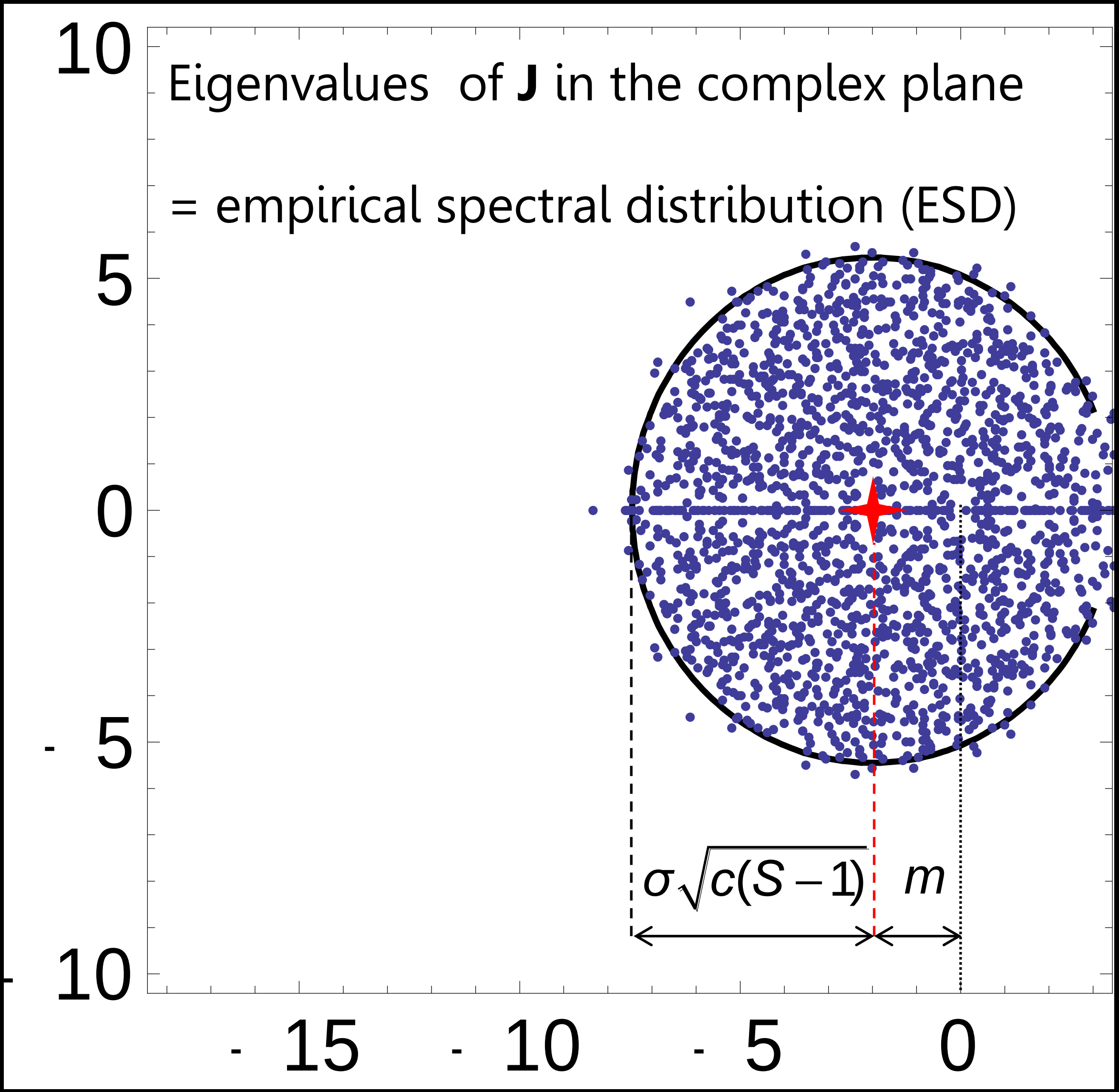
Assume that the system is "random" and properly scaled, *i.e.* the Jacobian looks like

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

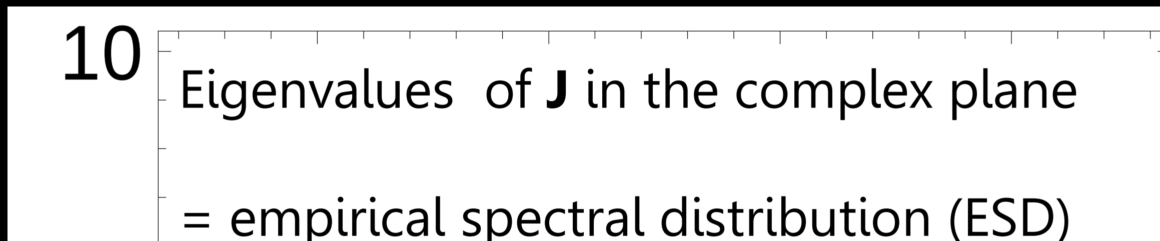
where $\mathcal{B}(c)$ = Bernoulli distribution

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

Empirical spectral distribution



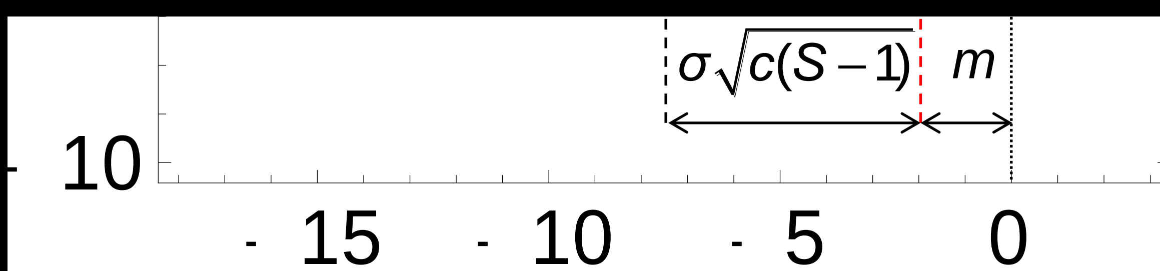
Empirical spectral distribution



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

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

May 1972



Sequels to May’s paper

Three “classic” lines of investigation after “May’s paradox”:

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

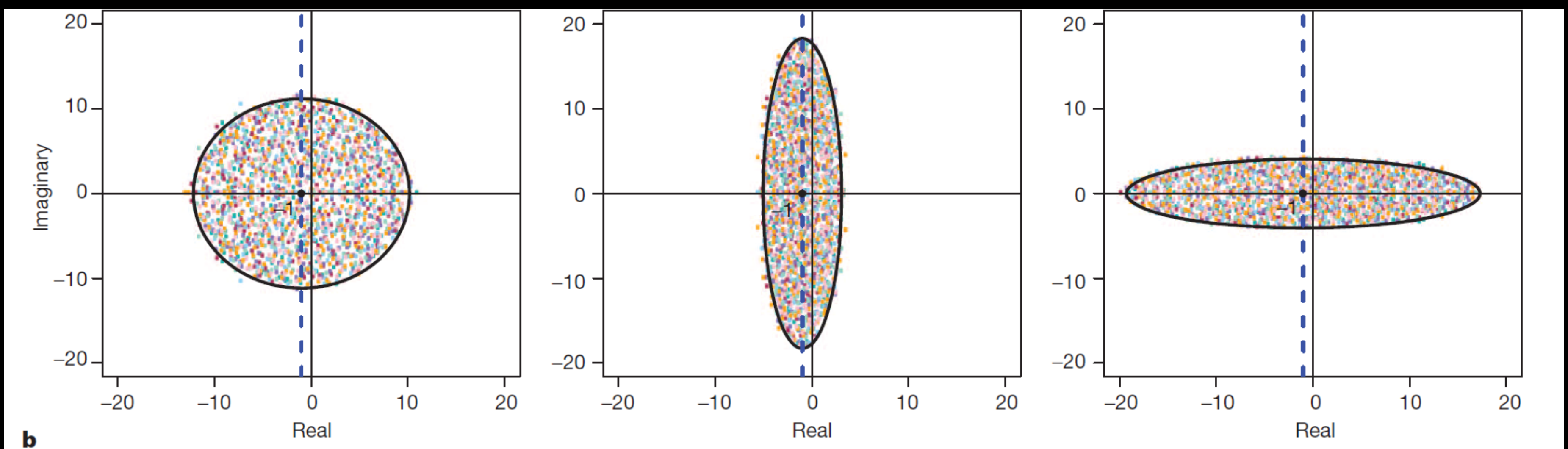
- predation (-/+)
- mutualism (+/+)
- competition (-/-)

Allesina & Tang 2012

A recent example

Main result from Allesina & Tang

Empirical spectral distribution (ESD) changes by interaction type

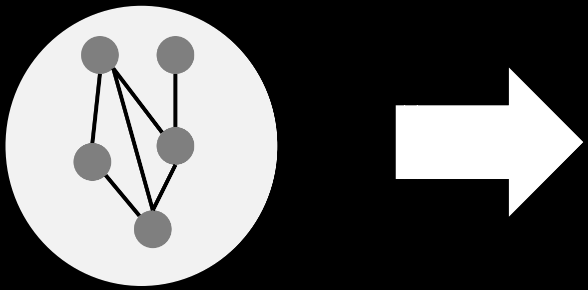


Allesina & Tang 2012

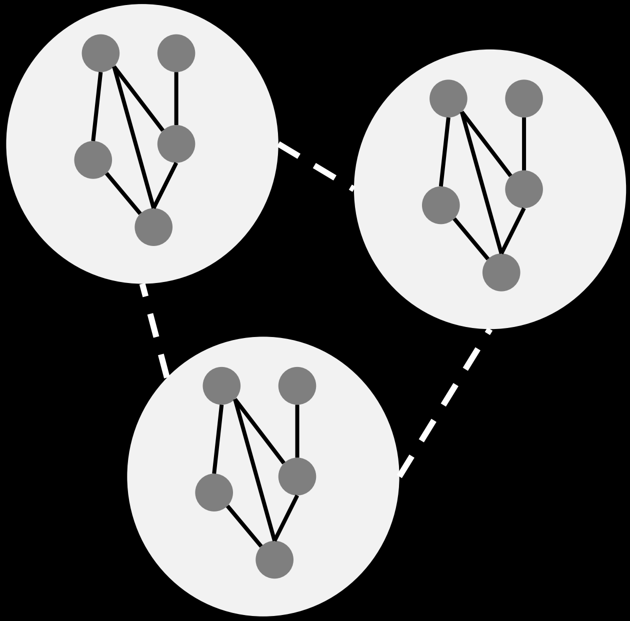
Our own sequel

Dominique Gravel

Mathew Leibold

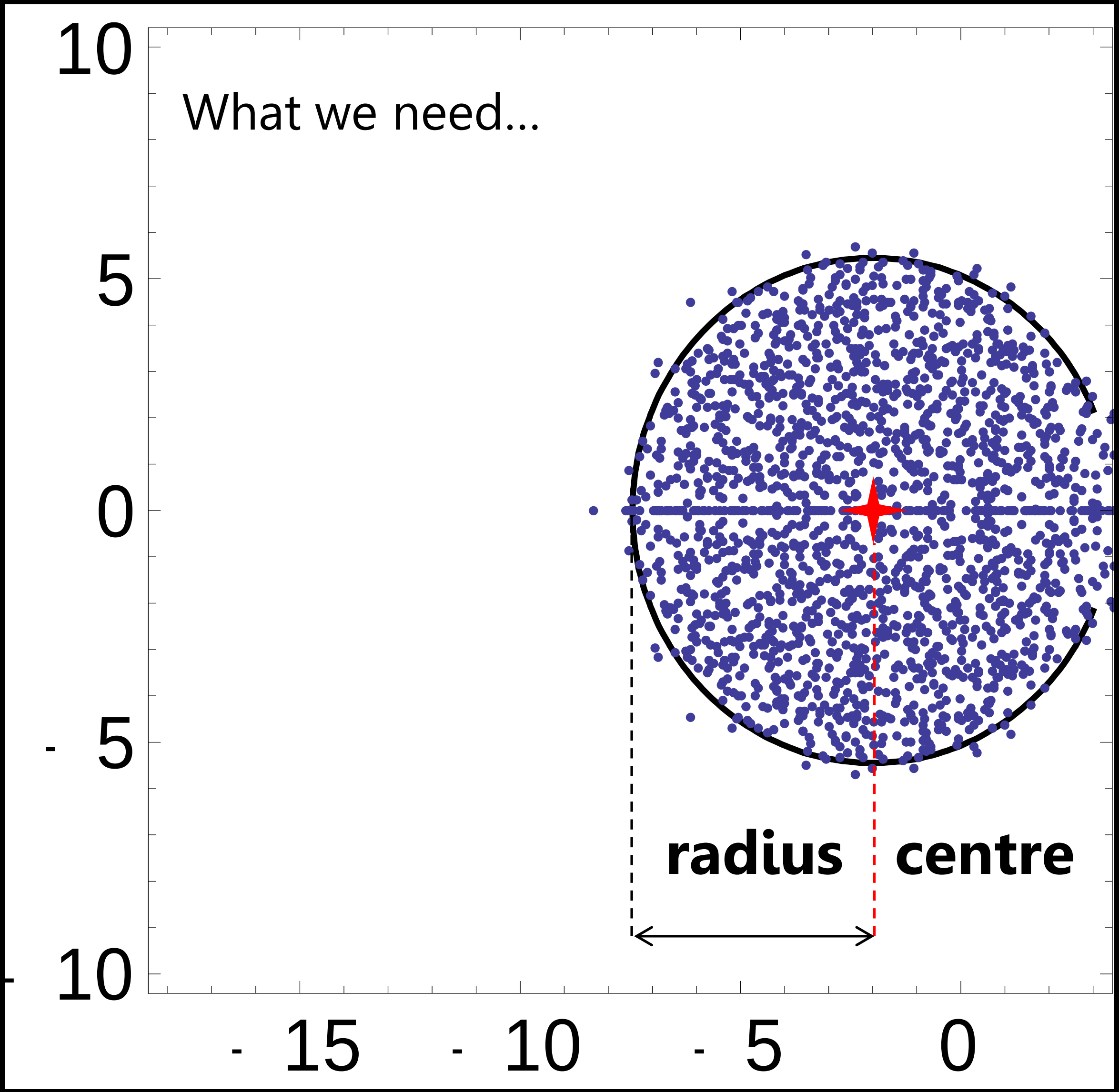


S species

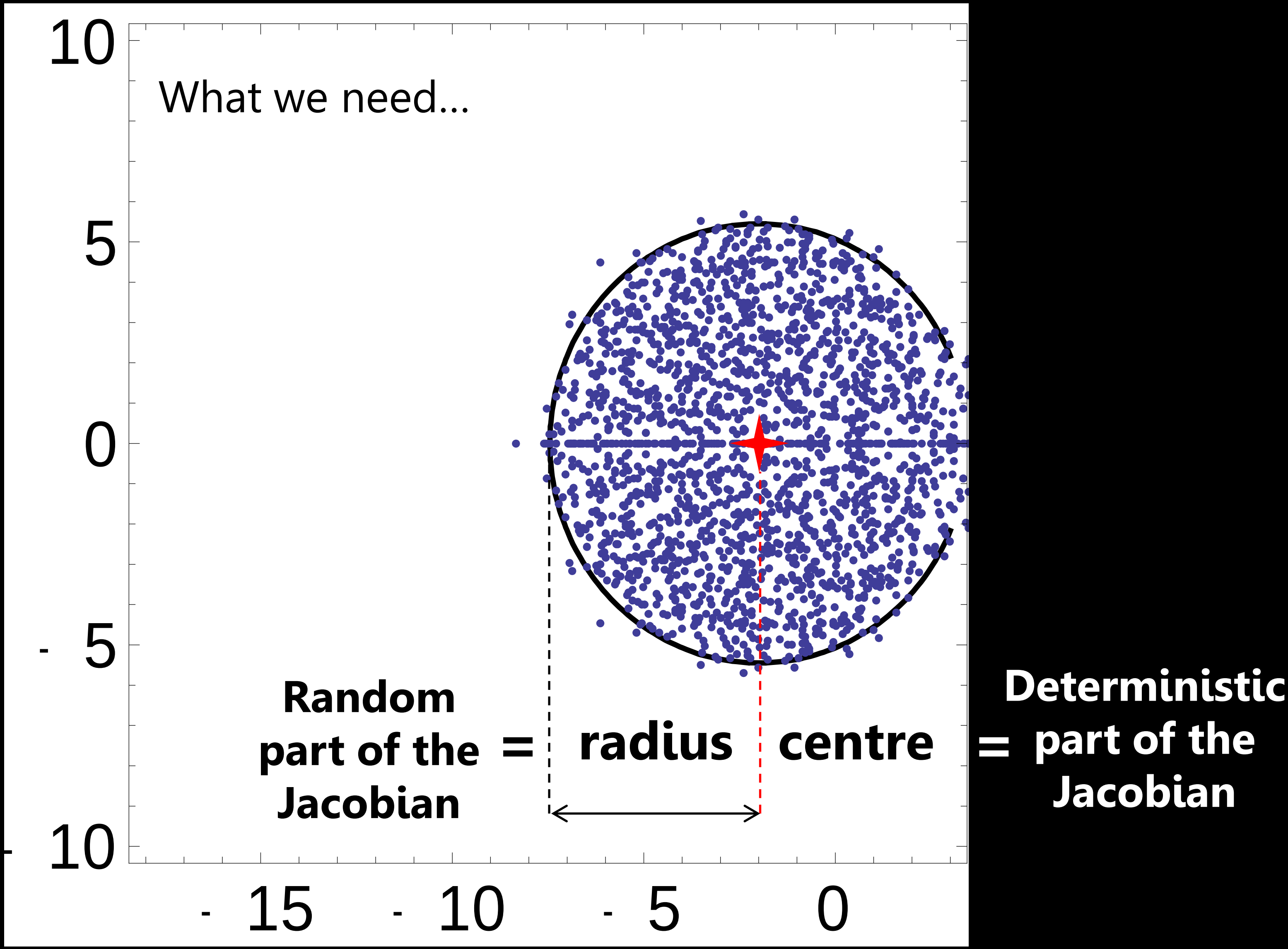


S species
n patches
dispersal among patches

Principle of the analysis



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

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

Tao *et al*. 2010

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

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

Deterministic part

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

Green: Among patches

Pink: Within patches

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

Deterministic part

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

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

$\mathbf{A}_1$	$\mathbf{0}$	$\mathbf{0}$
$\mathbf{0}$	$\mathbf{A}_k$	$\mathbf{0}$
$\mathbf{0}$	$\mathbf{0}$	$\mathbf{A}_n$

Among patches

Within patches

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

Random part

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

Computing the variance: large *d*

Depends on the correlation ρ among **A**'s

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

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

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

Computing the variance: small *d*

No change in variance, but change in ESD centre

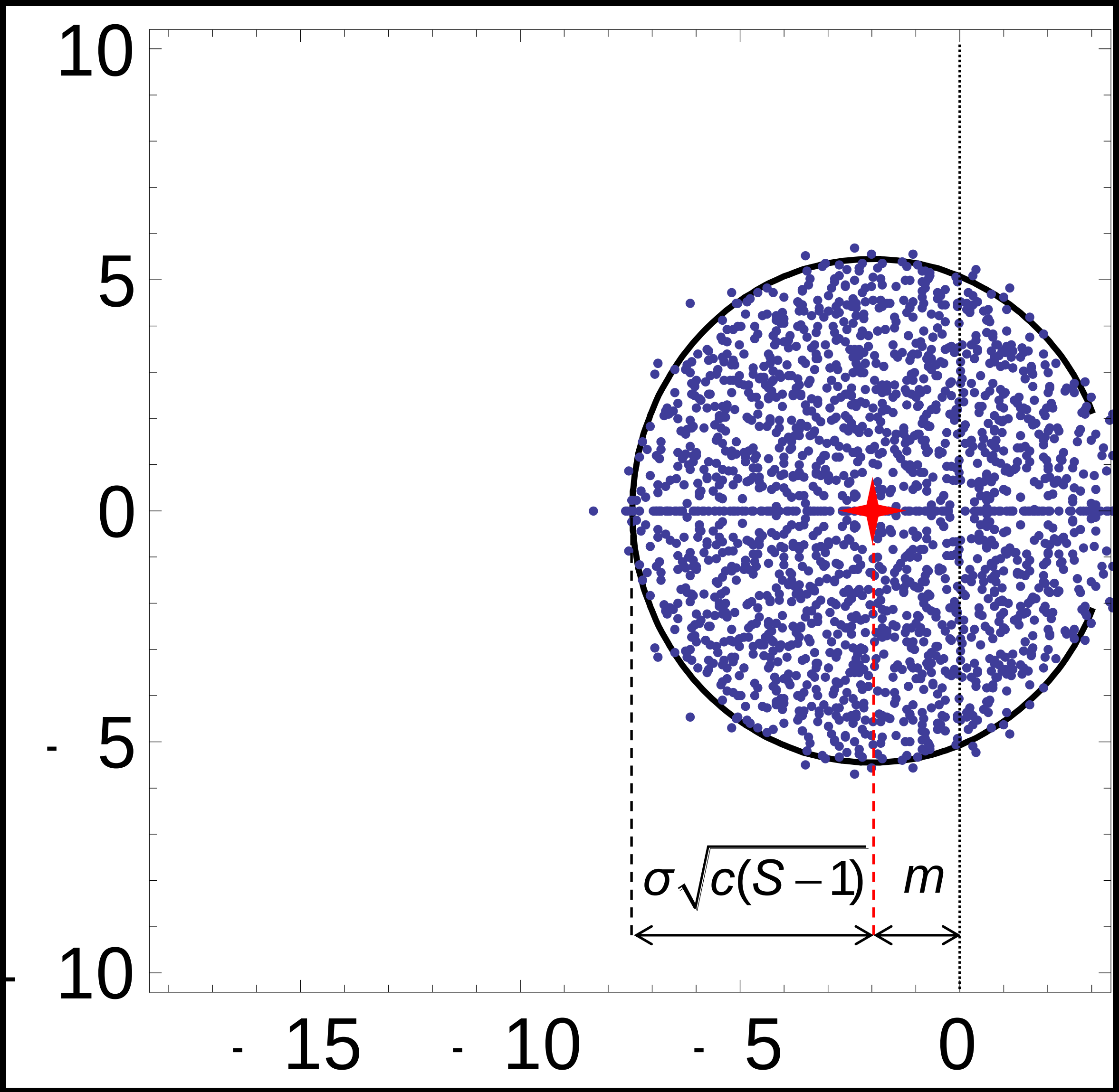
When *d* is small, a different approximation:

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

approximately valid whatever the value of ρ

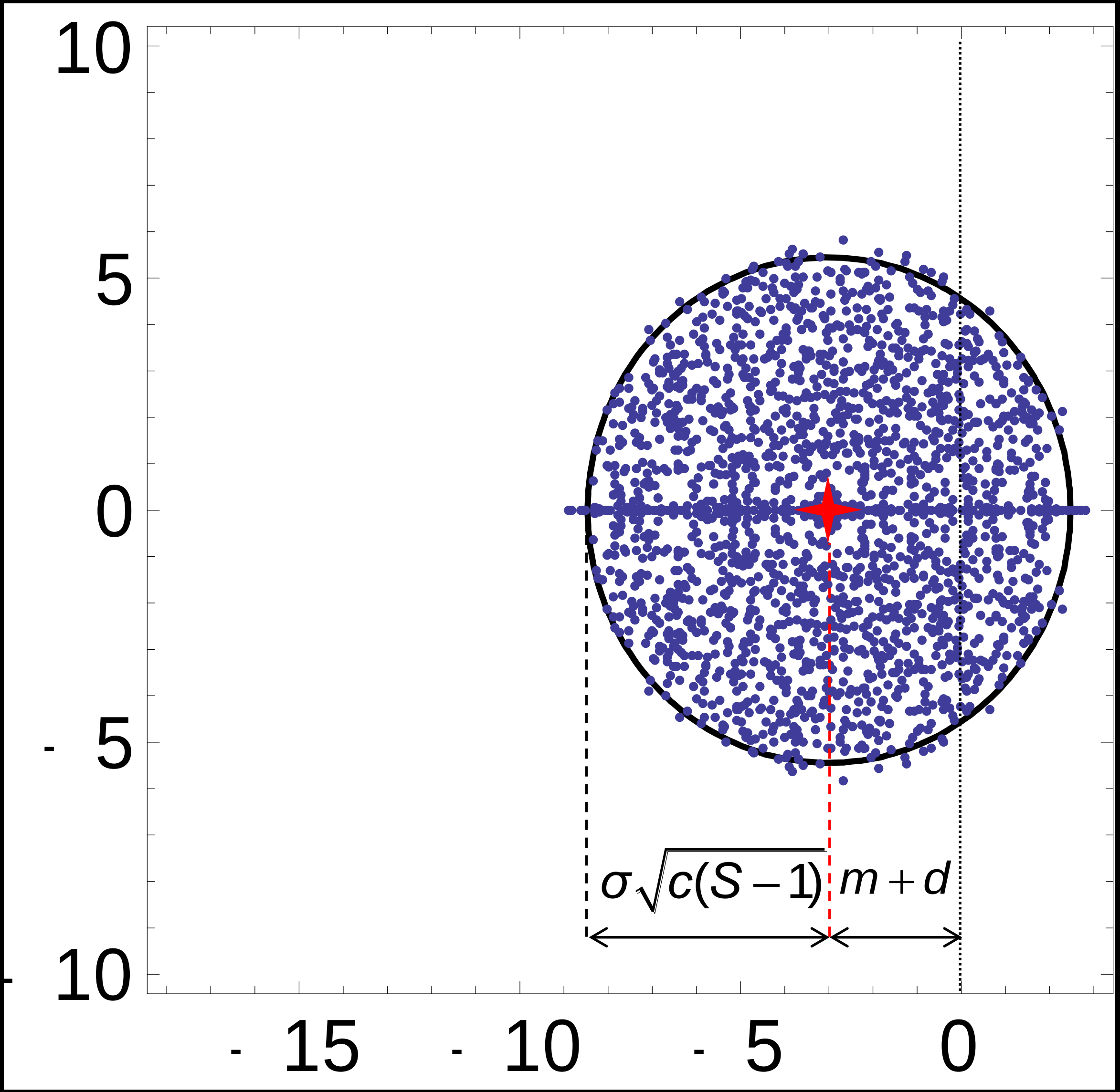
What it looks like…

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



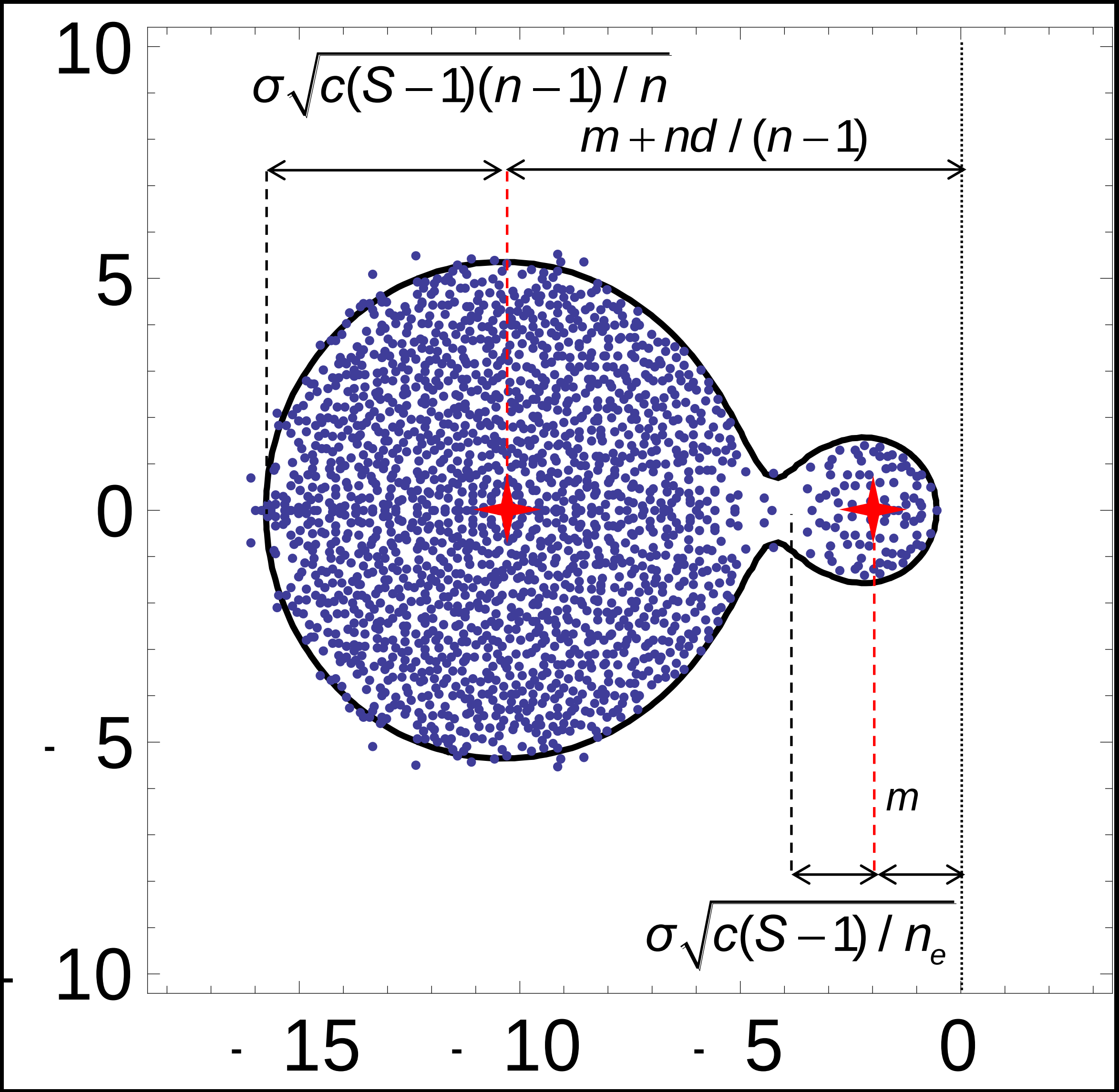
What it looks like...

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



What it looks like…

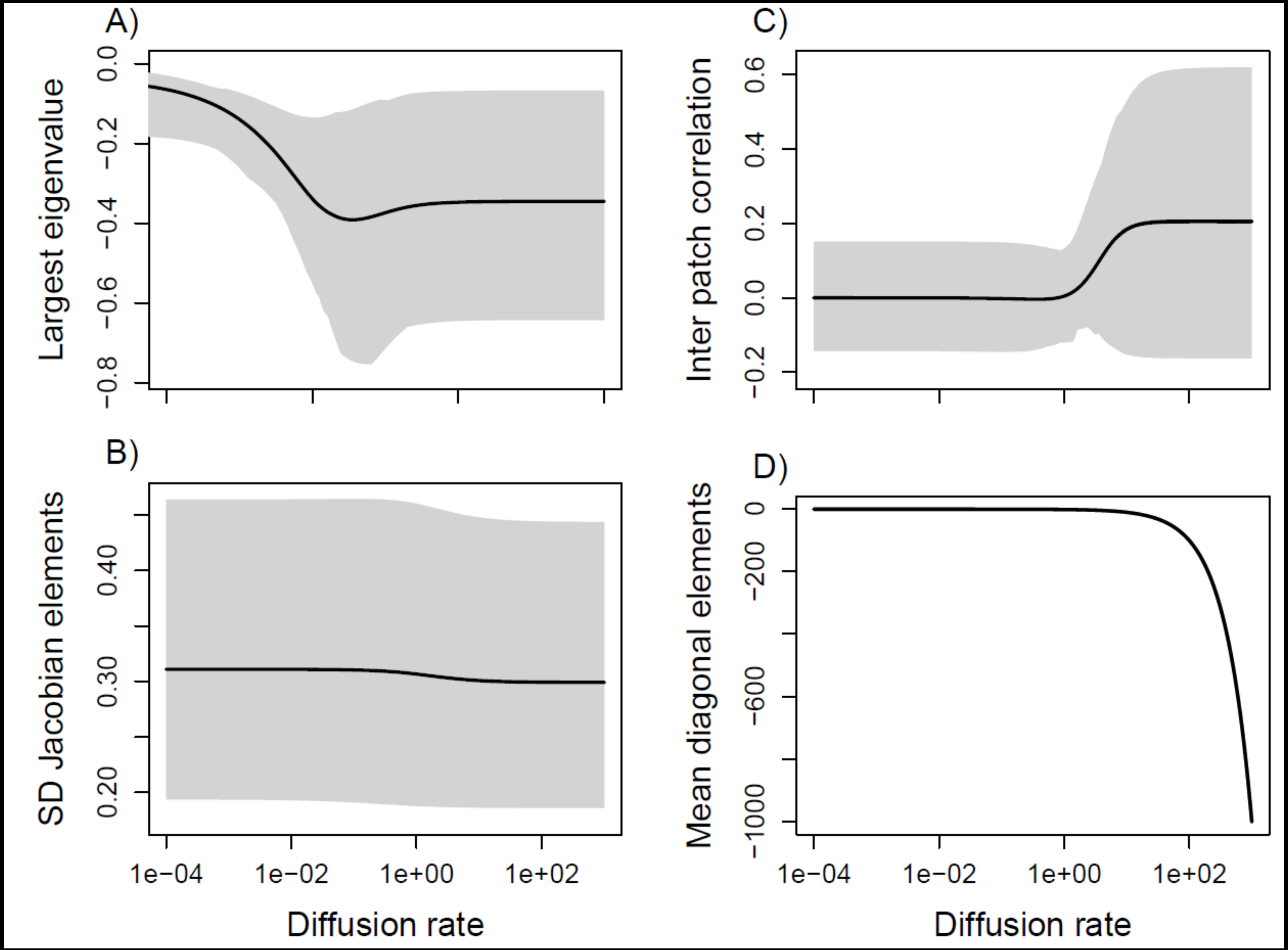
$d = 8$
$n = 20$
$S = 100$
$m = 2$
$\rho = 0$



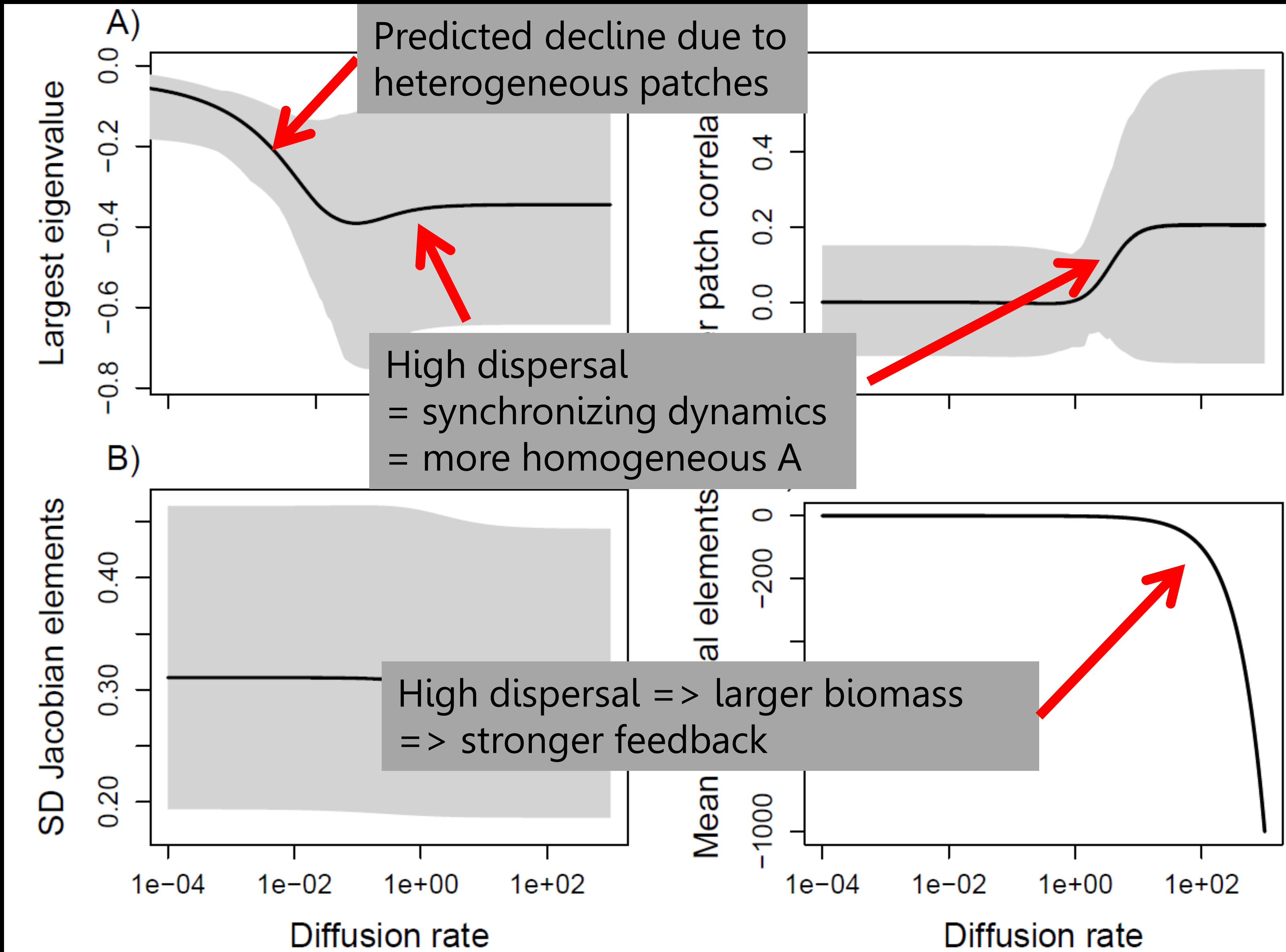
Extensions

- Works with non-complete (but regular) 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



Feedback between *d* and A



Take-home messages

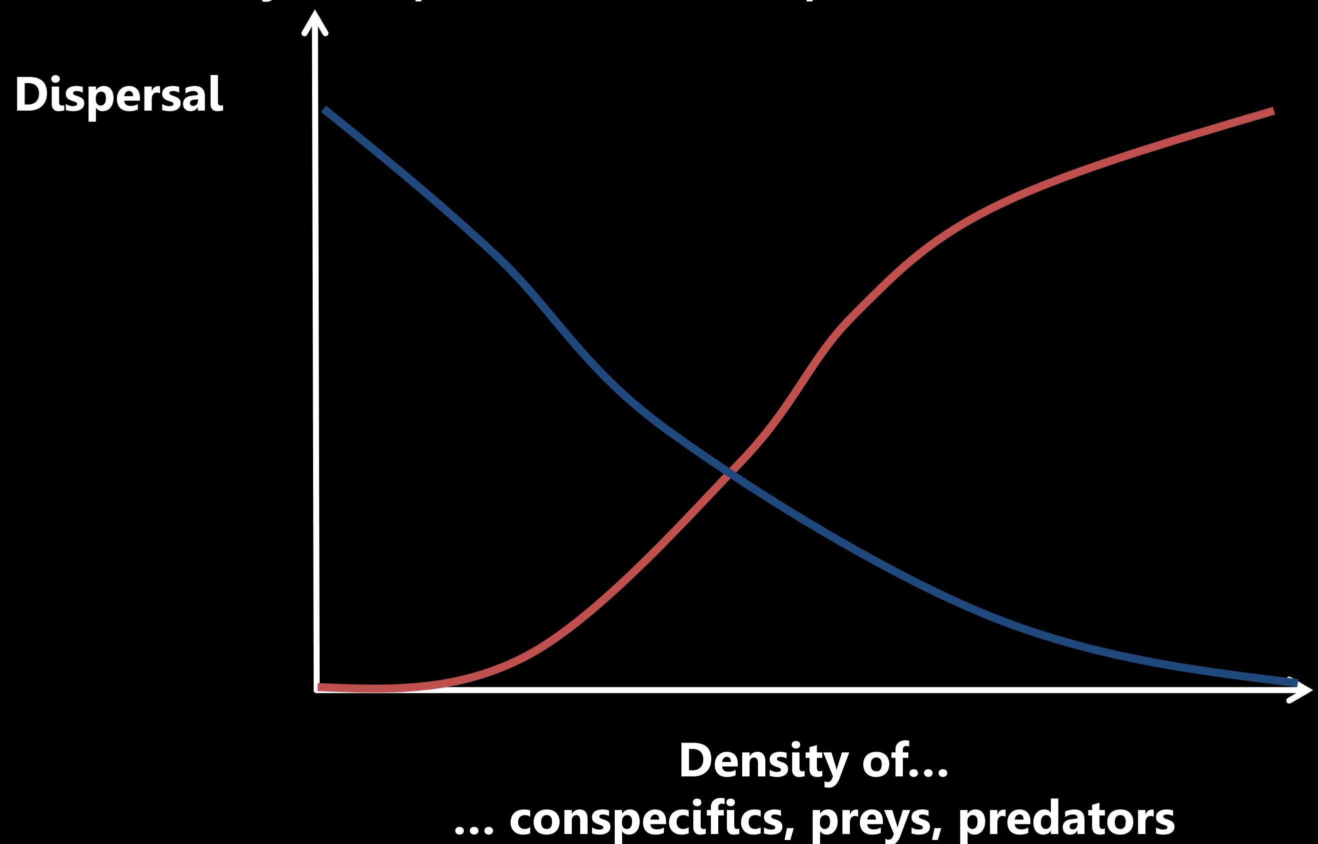
1. Stabilization requires heterogeneity of feedbacks among patches and dispersal

2. Dispersal can homogenize feedbacks

3. Optimal stability is achieved at intermediate dispersal rates

Perspectives

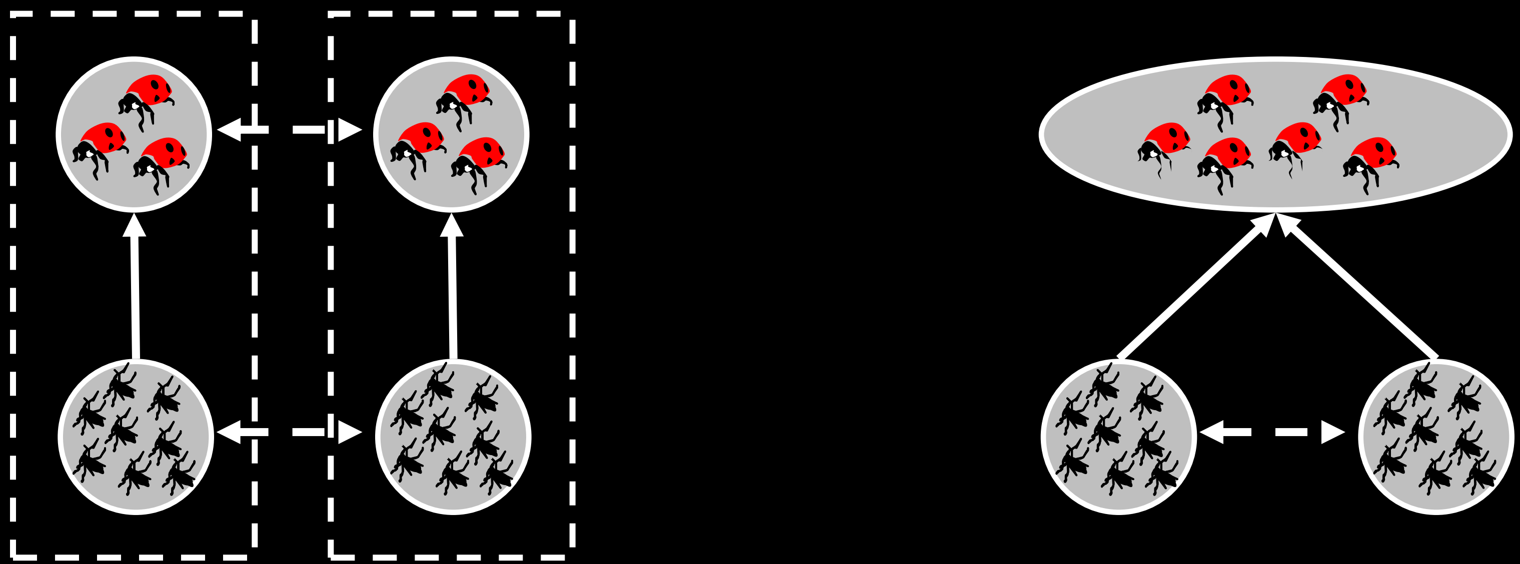
- dispersal when not diffusive
  - density-dependent dispersal



Perspectives

- dispersal when not diffusive
  - density-dependent dispersal

- putting together dispersal at different scales (non trans-specific definition of patches)



Perspectives

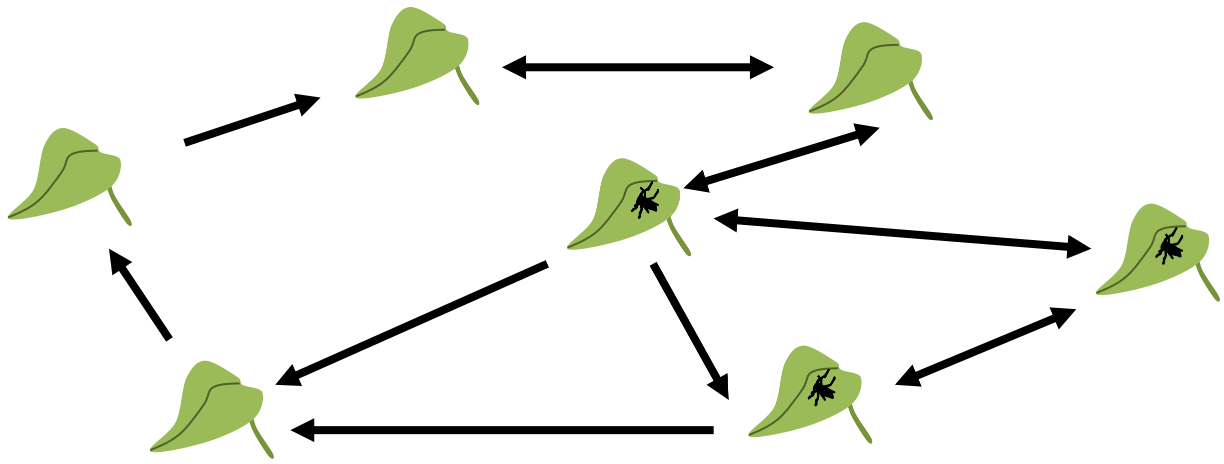
- dispersal when not diffusive
  - density-dependent dispersal
- putting together dispersal at different scales (non trans-specific definition of patches)
- explicit link between feasibility and stability
- random network of patches (not regular)

PATCH DYNAMICS ON NETWORKS

Patch dynamics on networks

The question:

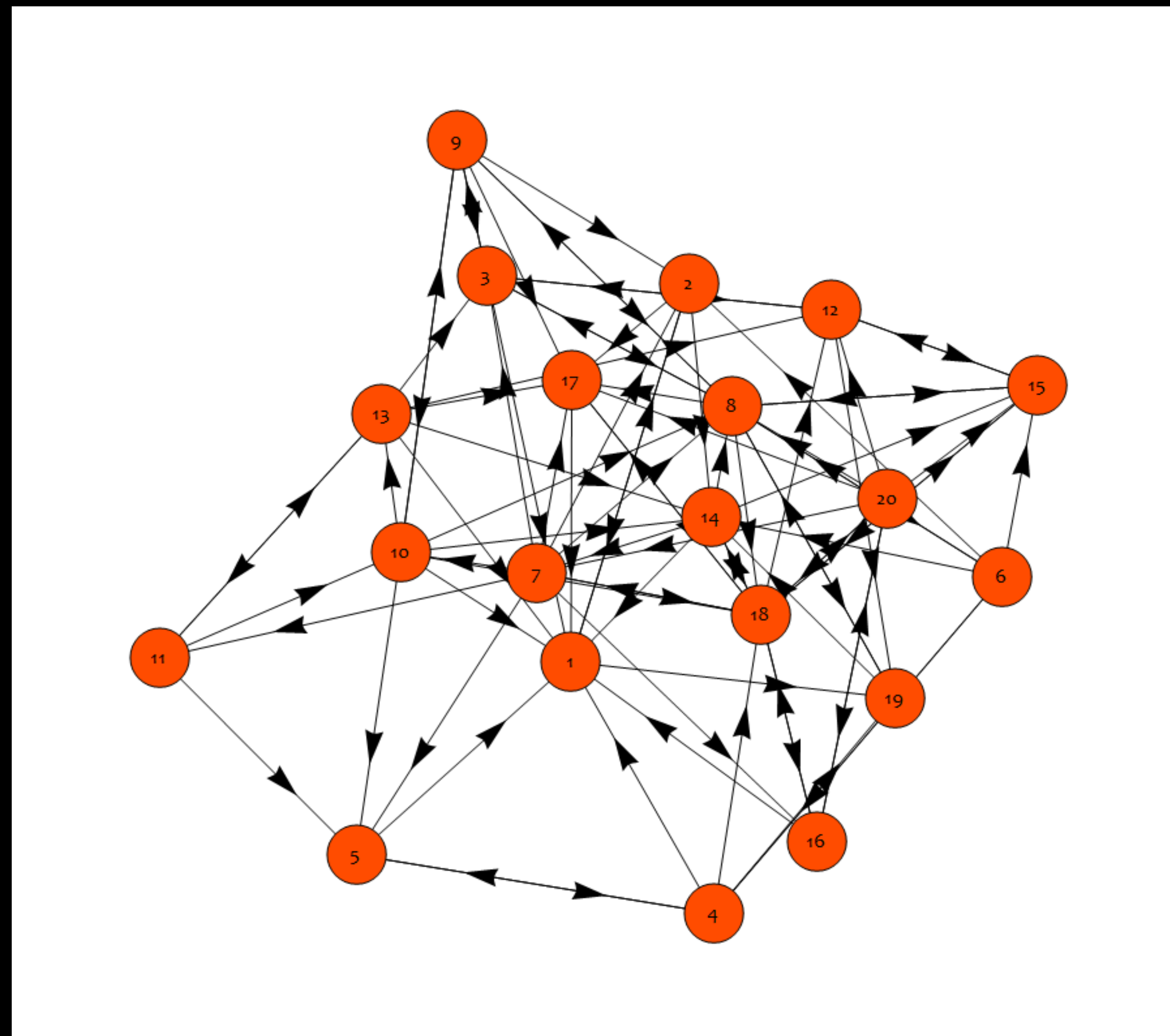
Does metapopulation network structure affect species occupancy?



The initial problem: a model for seed exchange networks


Doyle McKey


Francisco Laso



A model for seed exchange networks

- Simplest model to capture specificities of seed exchange networks
- Dynamic processes:
  - extinction of variety in farmer's fields,
  - diffusion of variety through exchange between farmers,
  - background diffusion (getting the variety from NGOs, markets, nature, etc.)
- On a directed network

Parallel with metapopulations

- Seed exchange = colonisation
- Extinction of variety = extinction of population
- Background diffusion = external source of propagules

Spatial network structure and metapopulation persistence

Luis J. Gilarranz *, Jordi Bascompte

Integrative Ecology Group, Estación Biológica de Doñana, CSIC, C/Américo Vespucio s/n, E-41092 Sevilla, Spain

Parallel with epidemics

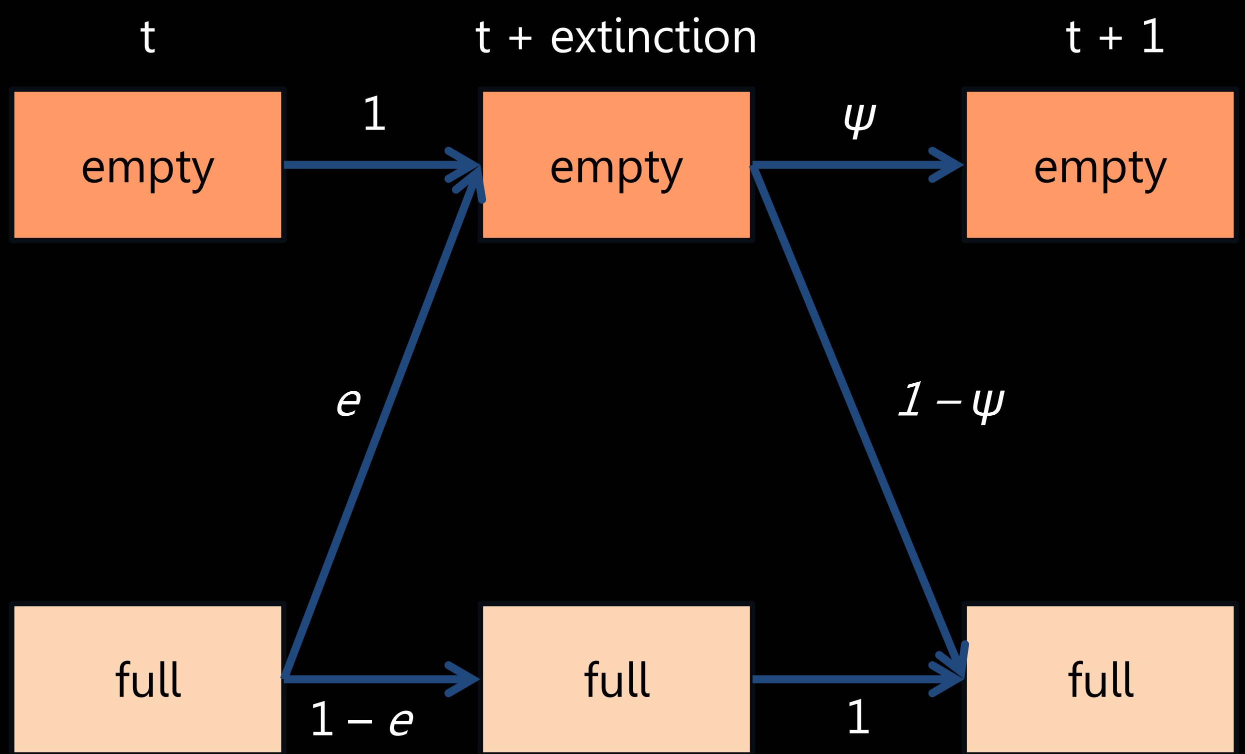
- Seed exchange = infection by contact
- Extinction of variety = patient recovery
- Background diffusion = self-infection

Epidemics in networks with nodal self-infection and the epidemic threshold

Piet Van Mieghem* and Eric Cator
Delft University of Technology, Faculty of Electrical Engineering, Mathematics and Computer Science, P.O Box 5031, 2600 GA Delft, The Netherlands
(Received 10 May 2012; published 30 July 2012)

Modeling approach

Three processes: extinction (*e*), background diffusion (*d*), diffusion through exchange (*c*)



$$\psi = (1-d)(1-c)^{\#\,occupied\,neighbours}$$

An approximation for occupancy

Method: the N-intertwined model

What does this mean?

= take expectation after extinction

& take expectation after colonization

(i.e. not computing full proba of having *n* occupied nodes at time *t*+1 as a function of having *k* infected nodes at time *t*)

Deriving the approximation

First, consider a complete graph of size *N* (i.e. all nodes are linked)

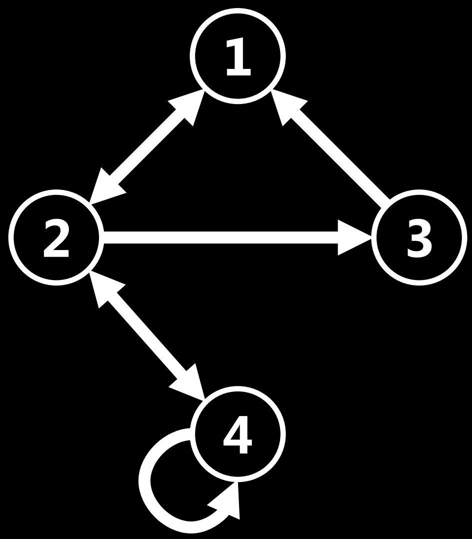
$$p_{t+1} = \underbrace{(1-e)p_t}_{\text{probability that an occupied patch stays occupied}} + \underbrace{\left[1-(1-e)p_t\right]}_{\text{probability that a patch ends up empty after extinction episode (already empty or goes extinct)}} \underbrace{\left\{1-(1-d)(1-c)^{N(1-e)p_t}\right\}}_{\text{probability that the empty patch is colonized, either through } c \text{ or } d}$$

probability that an occupied patch stays occupied

probability that the empty patch is colonized, either through *c* or *d*

probability that a patch ends up empty after extinction episode (already empty or goes extinct)

A network = a matrix



Network representation

out of

to	N1	N2	N3	N4
N1	0	1	1	0
N2	1	0	0	1
N3	0	1	0	0
N4	0	1	0	1

Adjacency matrix

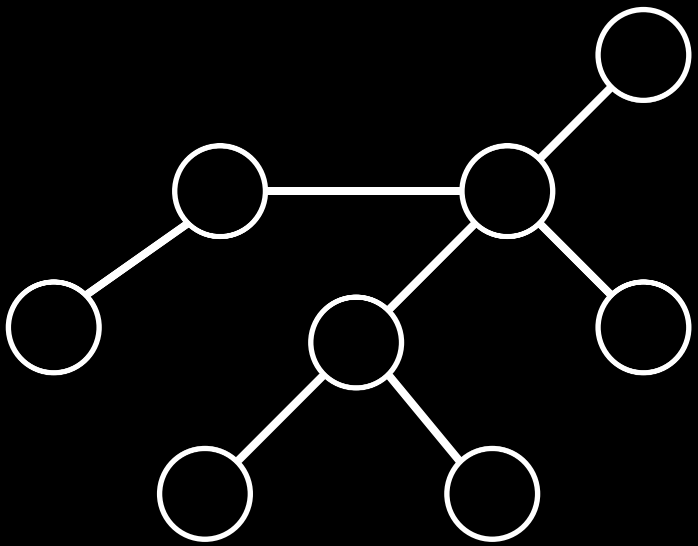
From complete graphs to a more general model

N in a complete graph ≈ # of neighbours

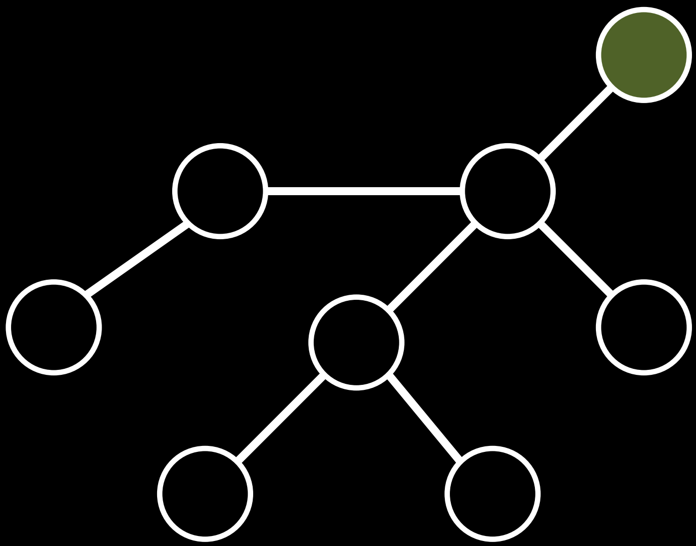
→ average degree in general?

But… the average degree experienced by a particle diffusing on a network
≠ the expectation of the degree among nodes!

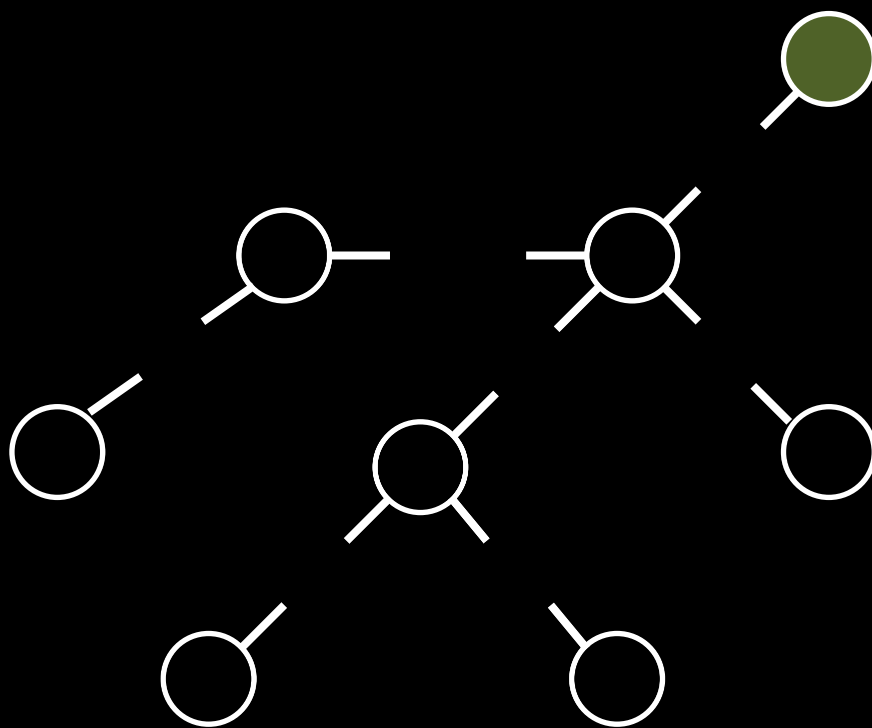
The “average degree”



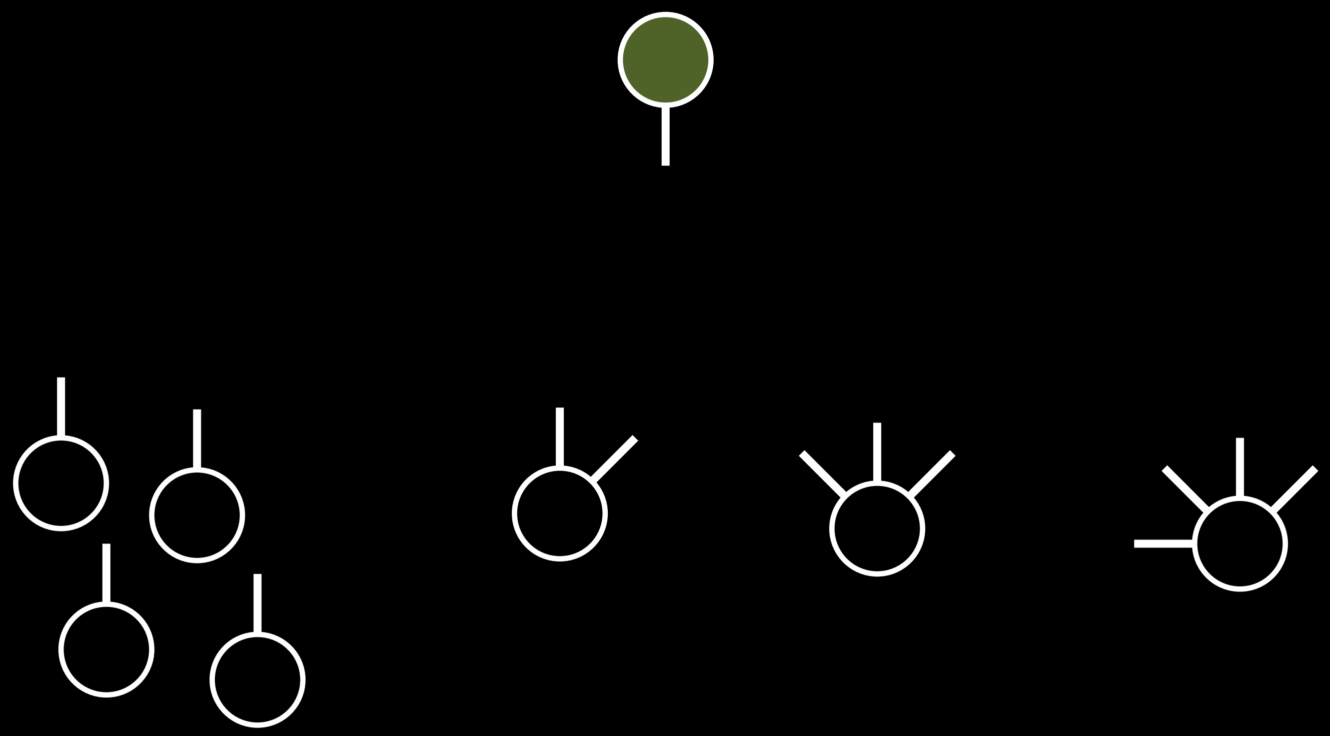
The “average degree”



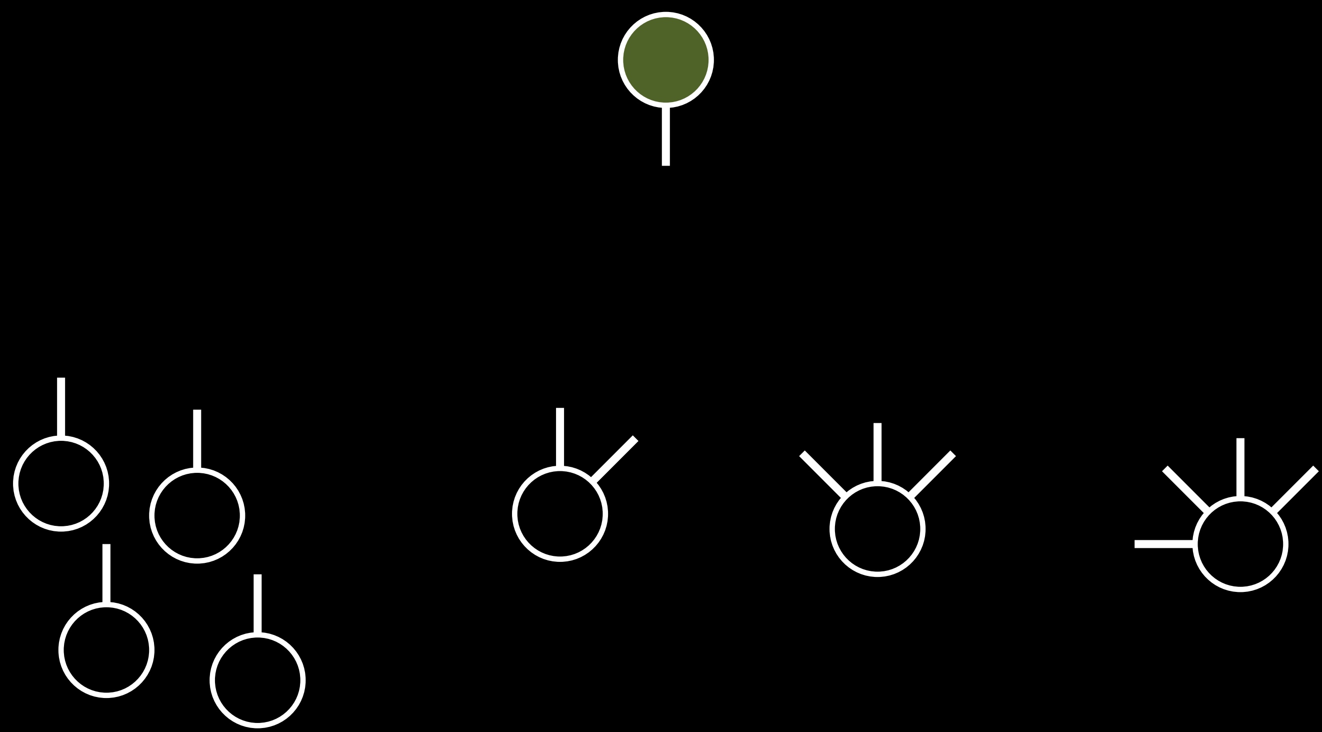
The “average degree”



The "average degree"

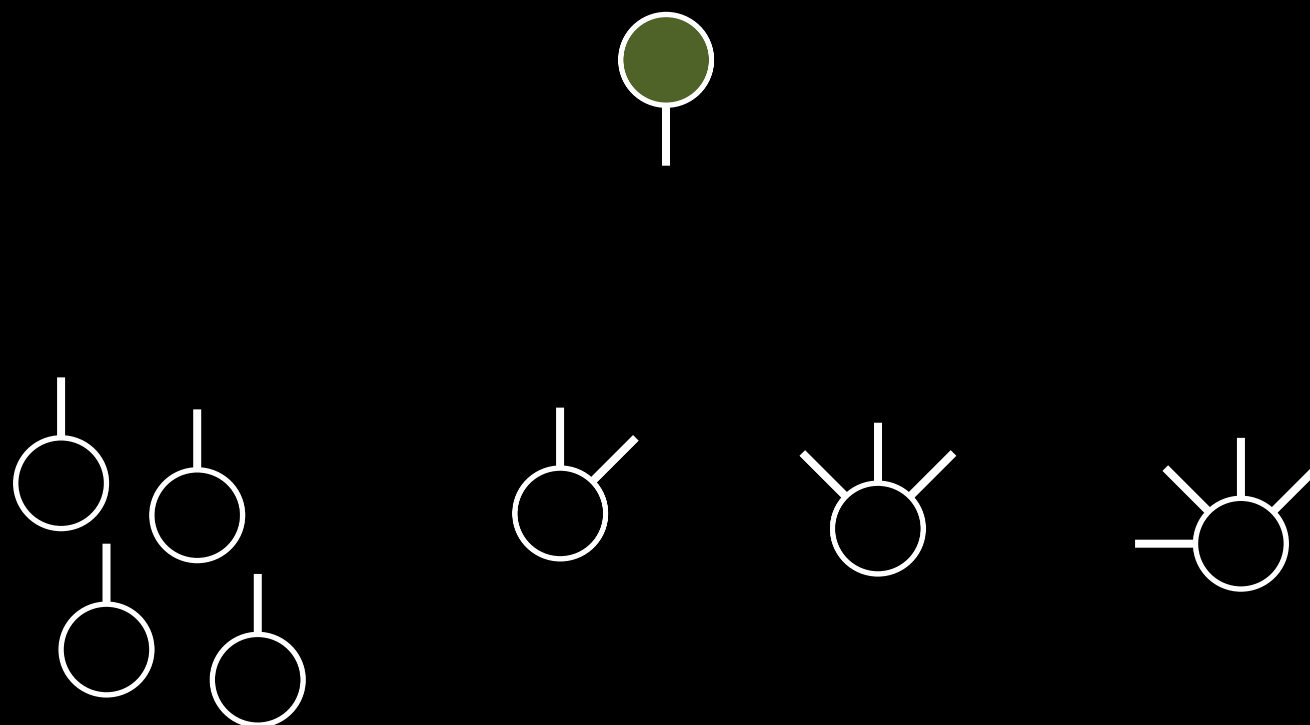


The “average degree”



				“average degree”
proba in network	4/7	1/7	1/7	1/7	13/7 ≈ 1.86

The “average degree”



					“average degree”
proba in network	4/7	1/7	1/7	1/7	$13/7 \approx 1.86$
proba among edges	4/13	2/13	3/13	4/13	$33/13 \approx 2.53$

The “average degree”

- This demonstration = what happens from one node to the next (i.e. the relevant quantity is the expected squared degree)
- Taking paths of infinite length within the network, what matters is the dominant eigenvalue / spectral radius of the adjacency matrix

Deriving the approximation

Now consider that N can be replaced by the spectral radius ρ

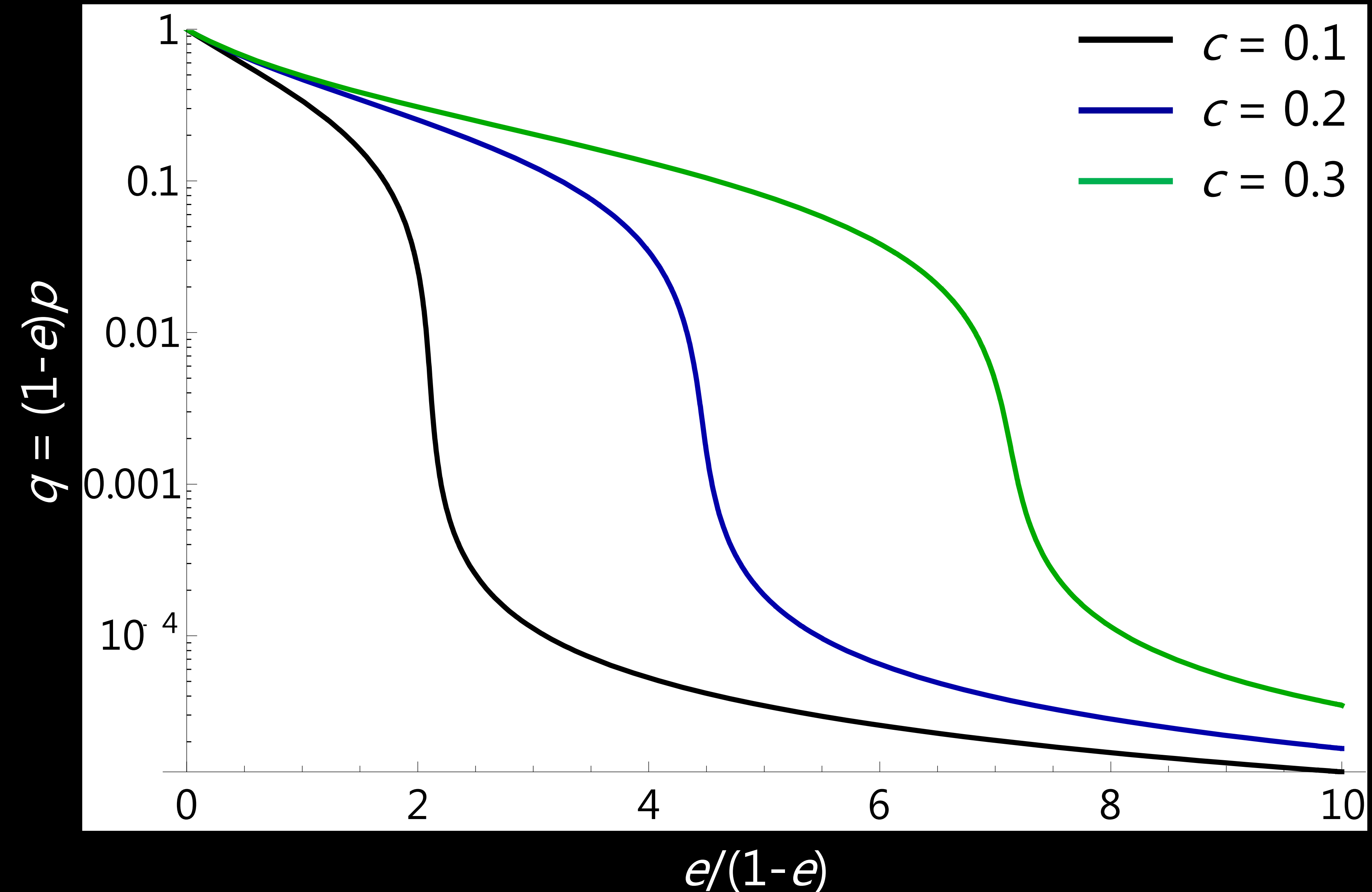
$$p_{t+1} = (1-e)p_t + \left[1-(1-e)p_t\right]\left\{1-(1-d)(1-c)^{N(1-e)p_t}\right\}$$

⬇

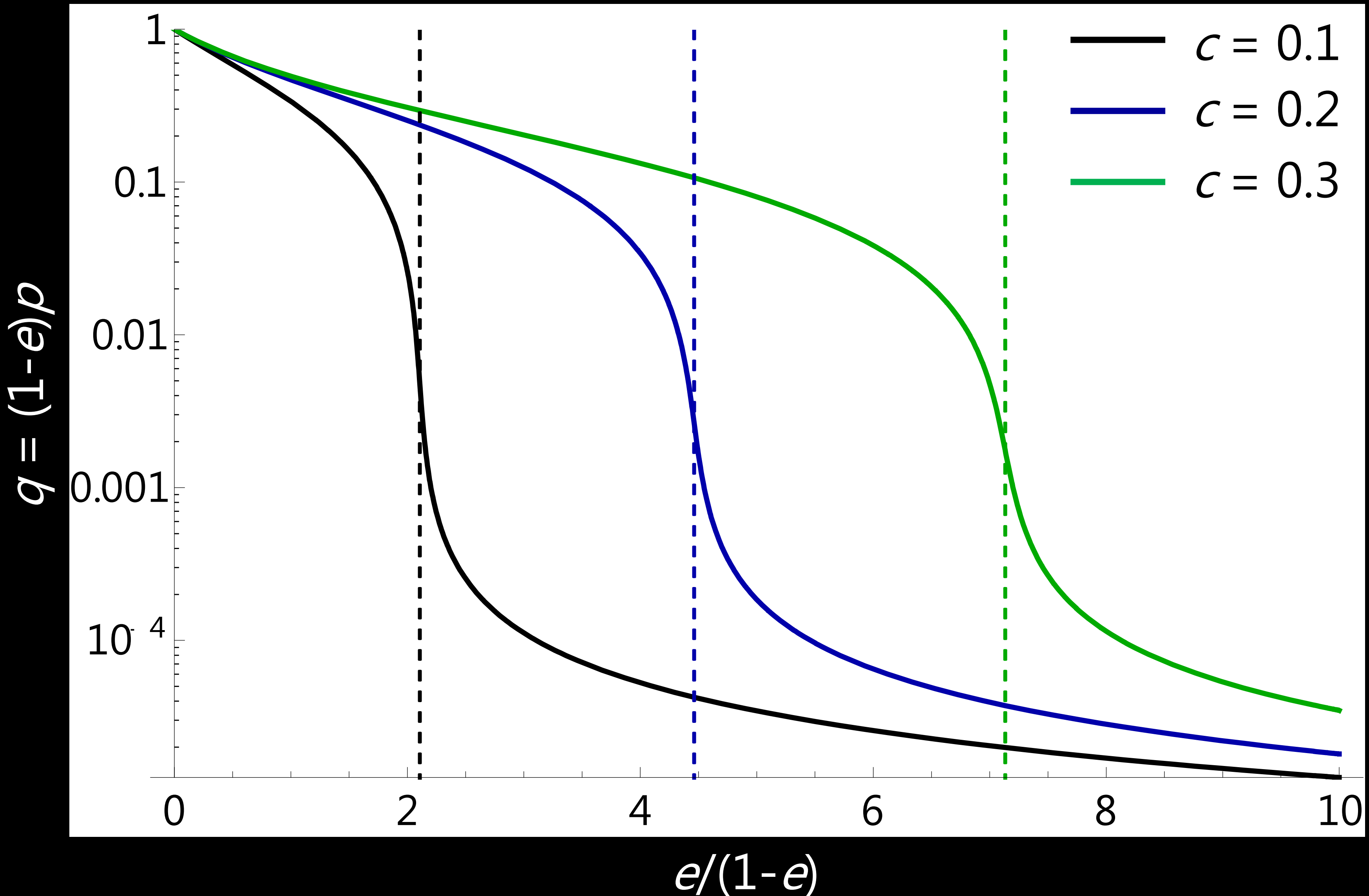
$$p_{t+1} = (1-e)p_t + \left[1-(1-e)p_t\right]\left\{1-(1-d)(1-c)^{\rho(1-e)p_t}\right\}$$

In principle, occupancy could be deduced from the knowledge of c, d, e and ρ

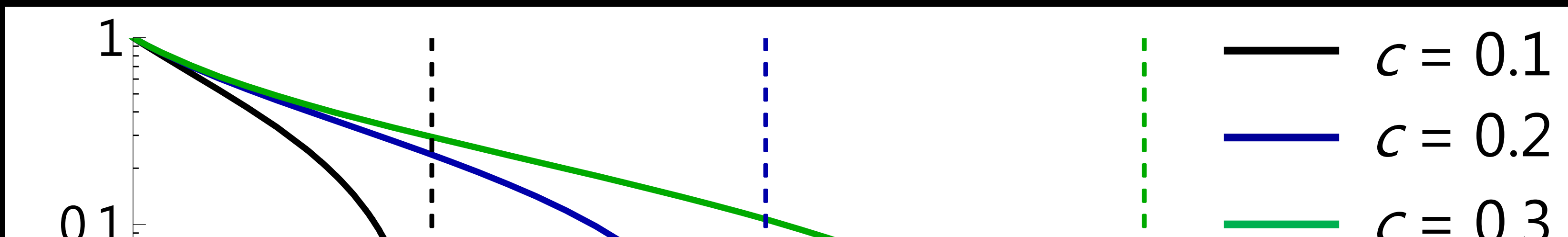
What does this approximation say?



What does this approximation say?

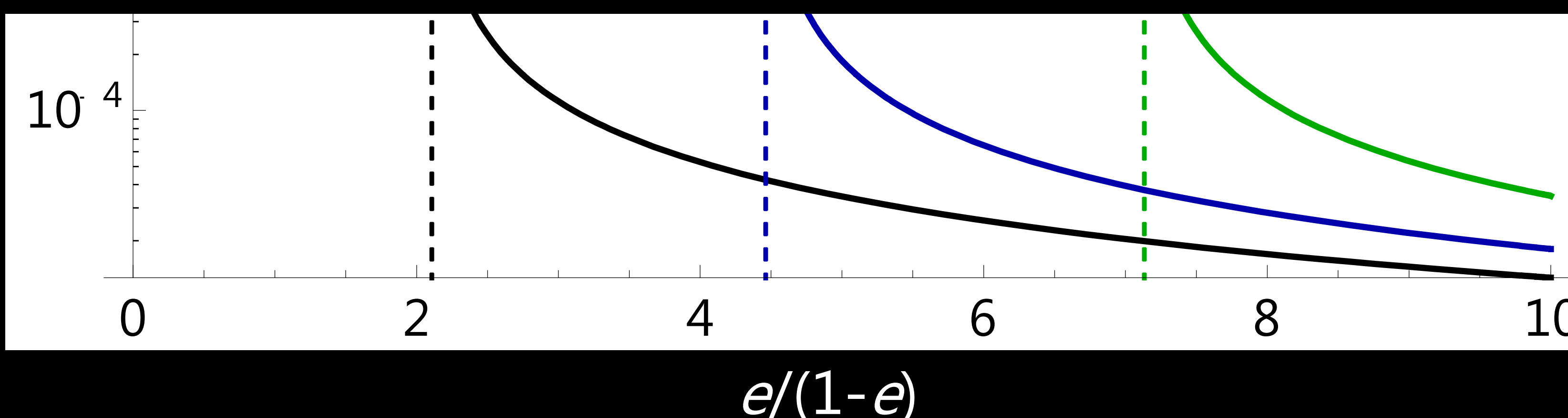


What does this approximation say?



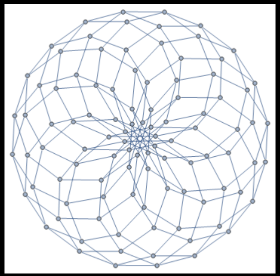
Inflexion point at $\frac{e}{1-e} = -\rho \log(1-c)$

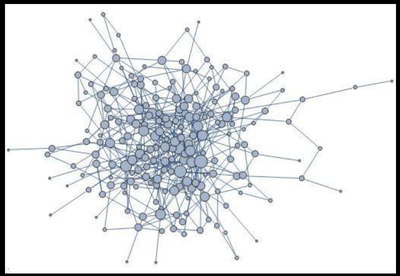
= two regimes (driven by *c* vs. driven by *d*)

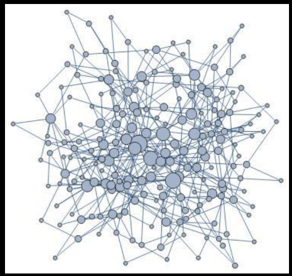


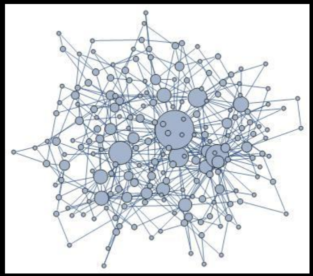
Does the approximation work?

Maxime Dubart's MSc 1 internship





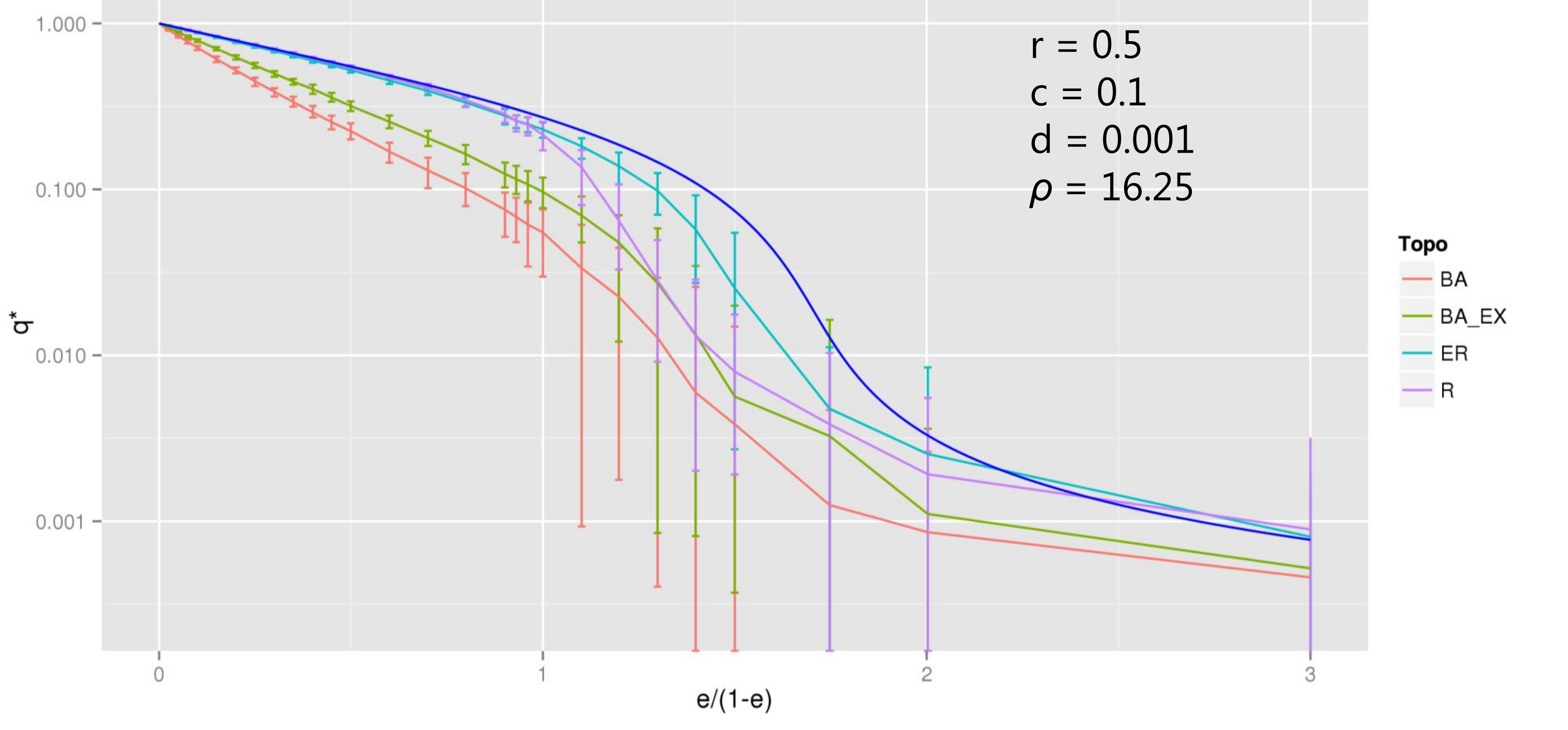




- Topologies: regular, E-R, exponential, scale-free
- Set *d* and *c* at given values
- Vary reciprocity at a given ρ

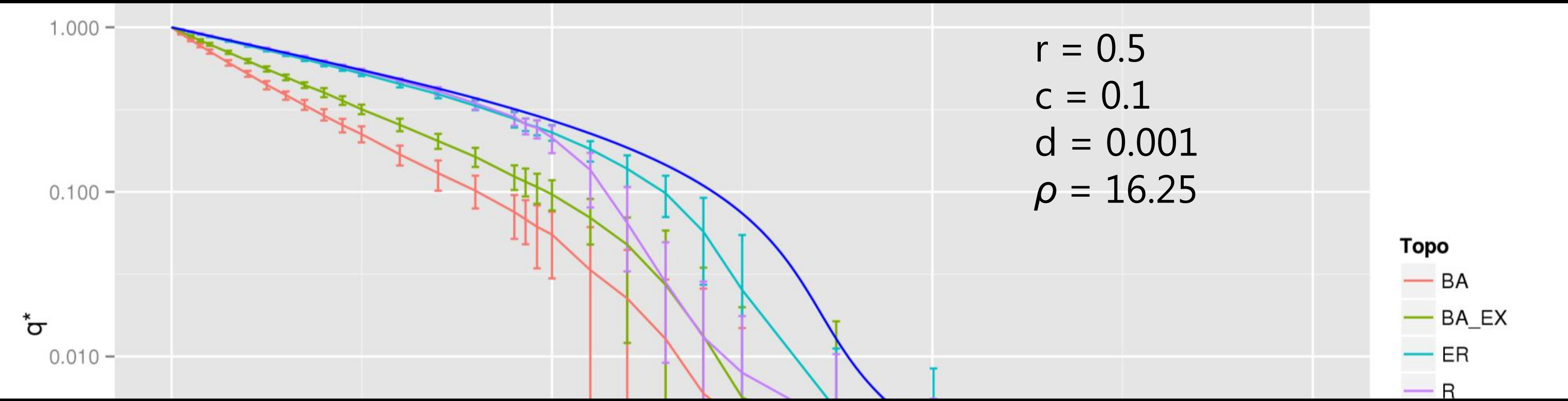
- Patterns of *q* as a function of *e*/(1-*e*)

General fit



r = 0.5
c = 0.1
d = 0.001
ρ = 16.25
1.000
0.100
0.010
0.001
q*
0
1
2
3
e/(1-e)
Topo
BA
BA_EX
ER
R

General fit

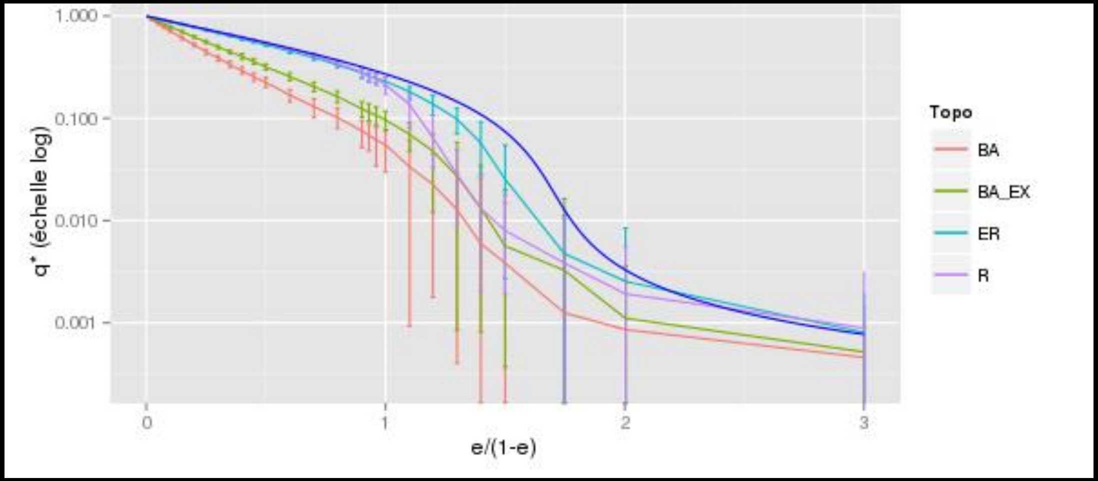


The approximation overestimates *q*

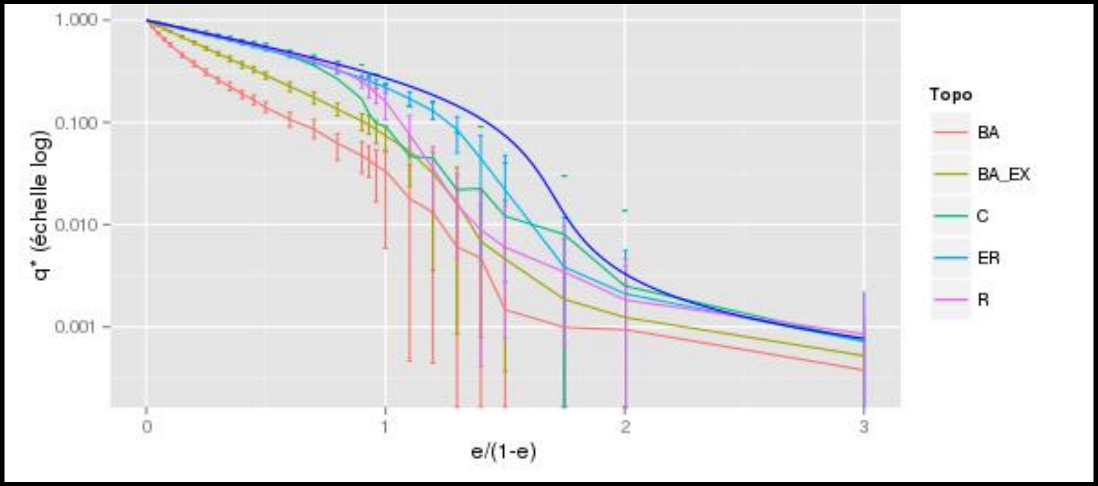
However, comparing topologies at fixed *ρ* yields a consistent ranking (≠ at fixed average degree)

Effect of reciprocity

r = 0.5
c = 0.1
d = 0.001
ρ = 16.25

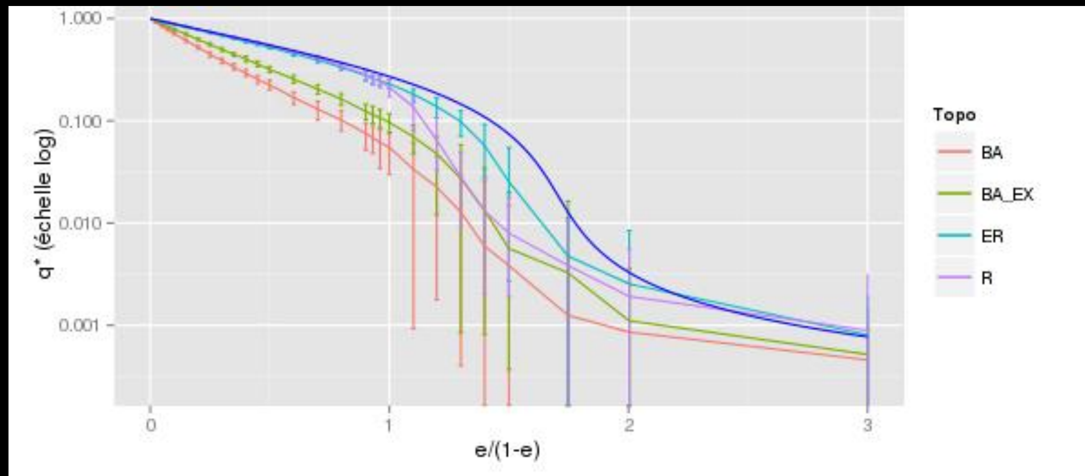


r = 1
c = 0.1
d = 0.001
ρ = 16.25

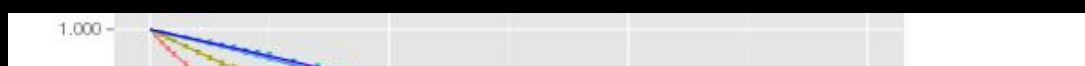


Effect of reciprocity

r = 0.5
c = 0.1
d = 0.001
ρ = 16.25



r = 1



When controlling for ρ, independent of reciprocity

Take-home messages

1. Two phases for occupancy: *c* and *d*-driven

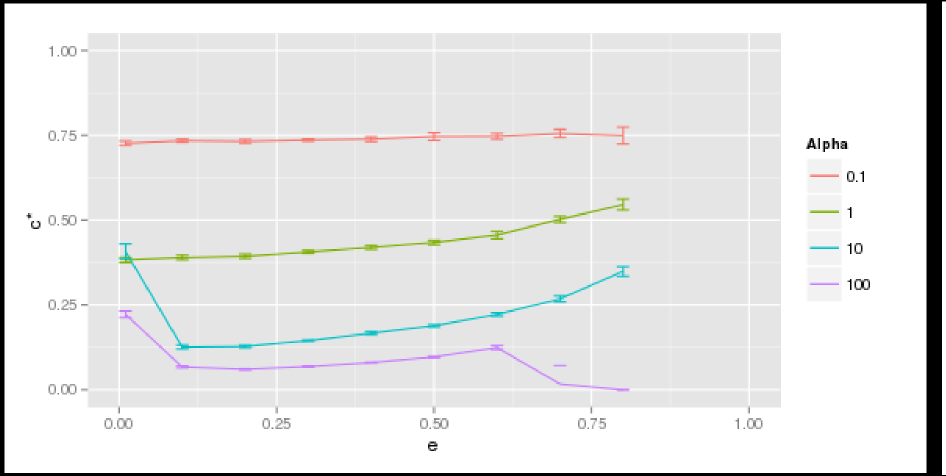
2. Networks with same ρ but different reciprocities yield similar occupancies

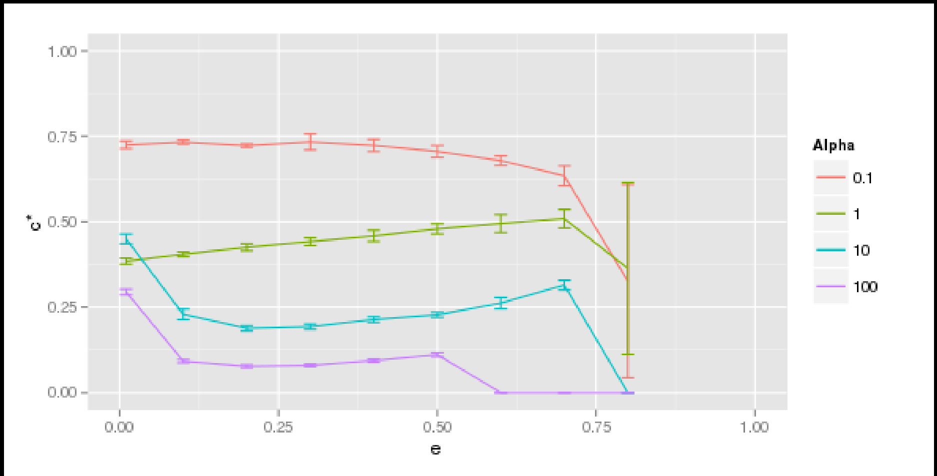
3. Networks with same ρ but different average degrees yield similar occupancies

4. At given ρ, consistent ranking of topologies (Erdős-Rényi > Exponential > Scale-free)

Immediate perspective

Evolution of colonization capacity under the competition-colonization trade-off





Erdős-Rényi

Scale-free

Thank you!

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Working groups on networks

Réseau National des Systèmes Complexes (RNSC)

MIRES & DyBRES