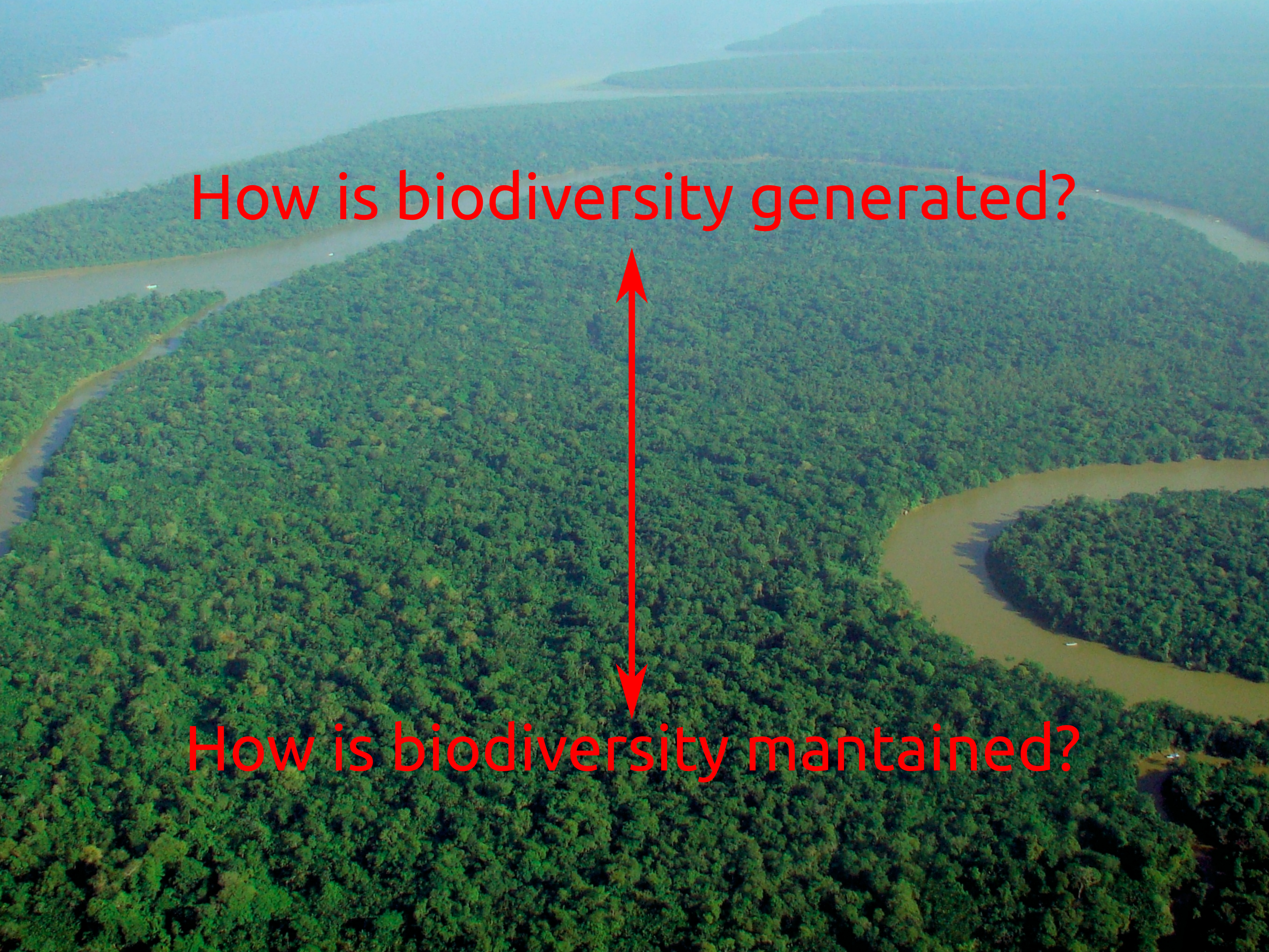
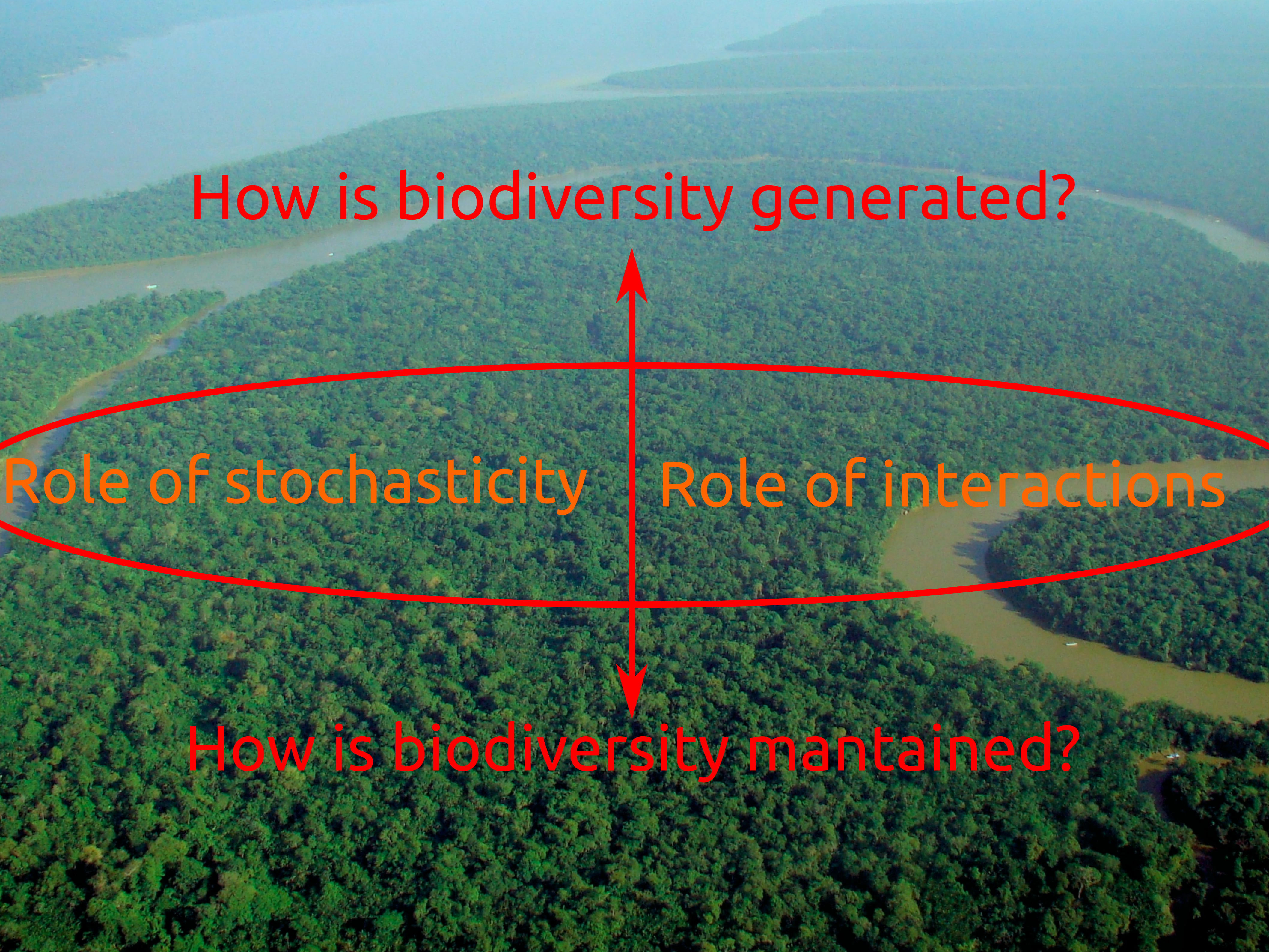
Higher-order interactions, stability and macroecological patterns

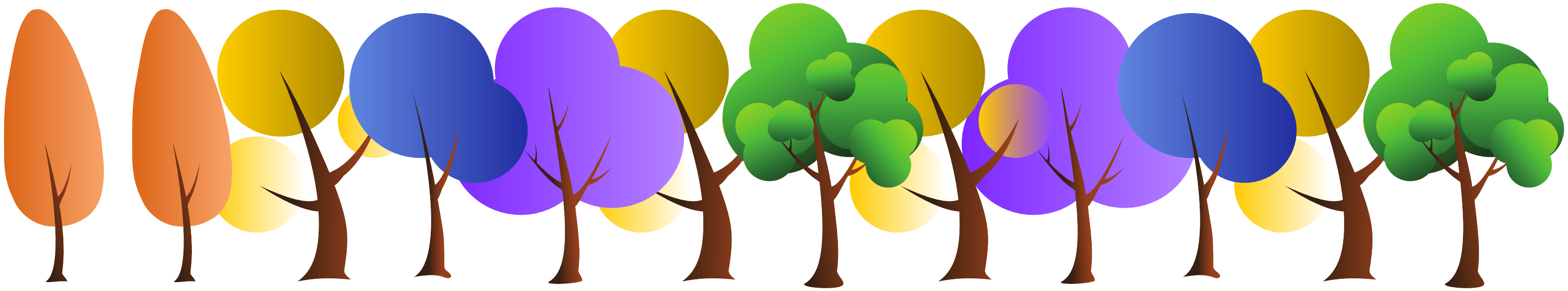
Jacopo Grilli

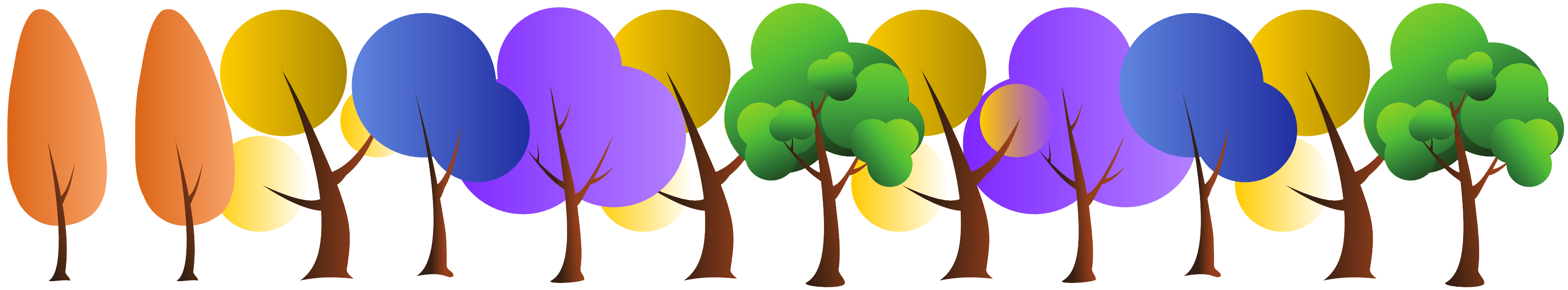
Santa Fe Institute

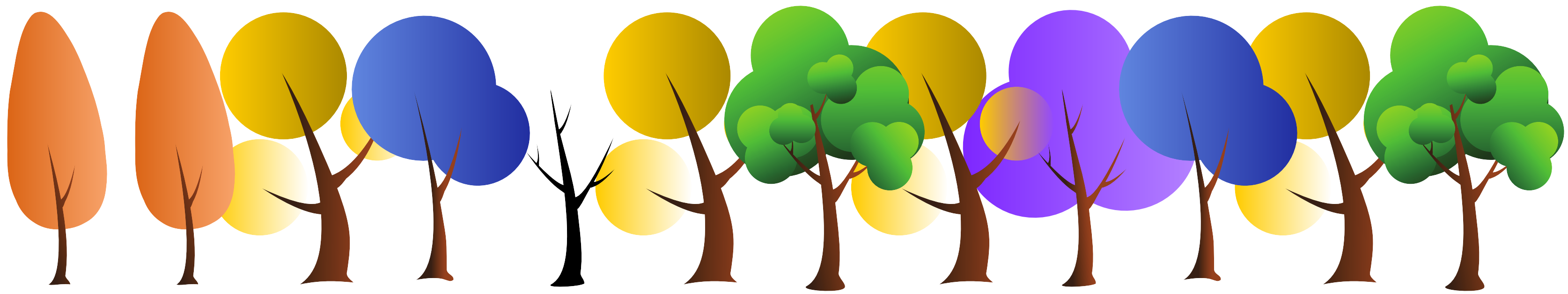
Jan 30, 2019 - WG Irreversibility in Ecology - SFI

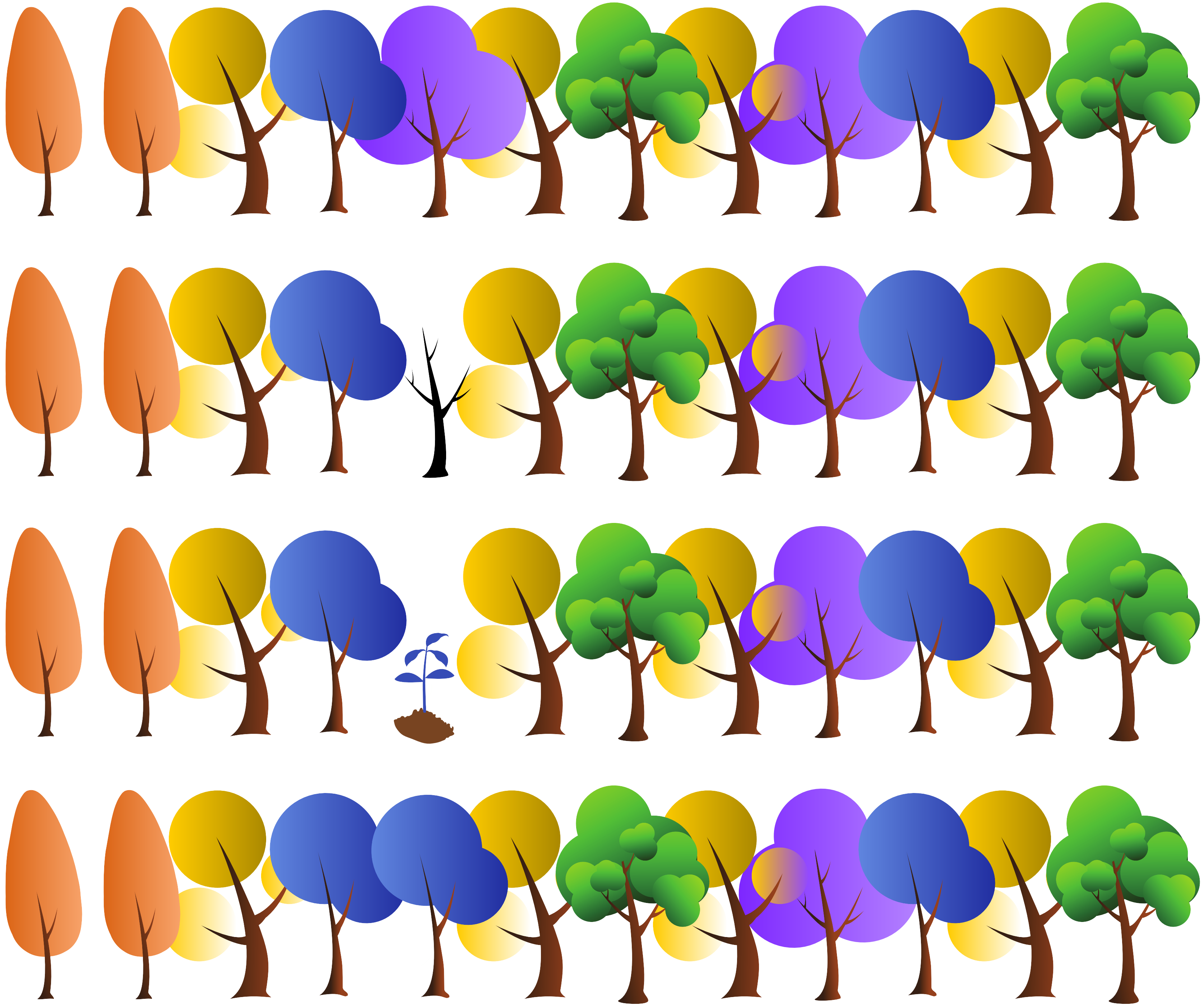

How is biodiversity generated?
How is biodiversity mantained?


How is biodiversity generated?
Role of stochasticity
Role of interactions
How is biodiversity mantained?

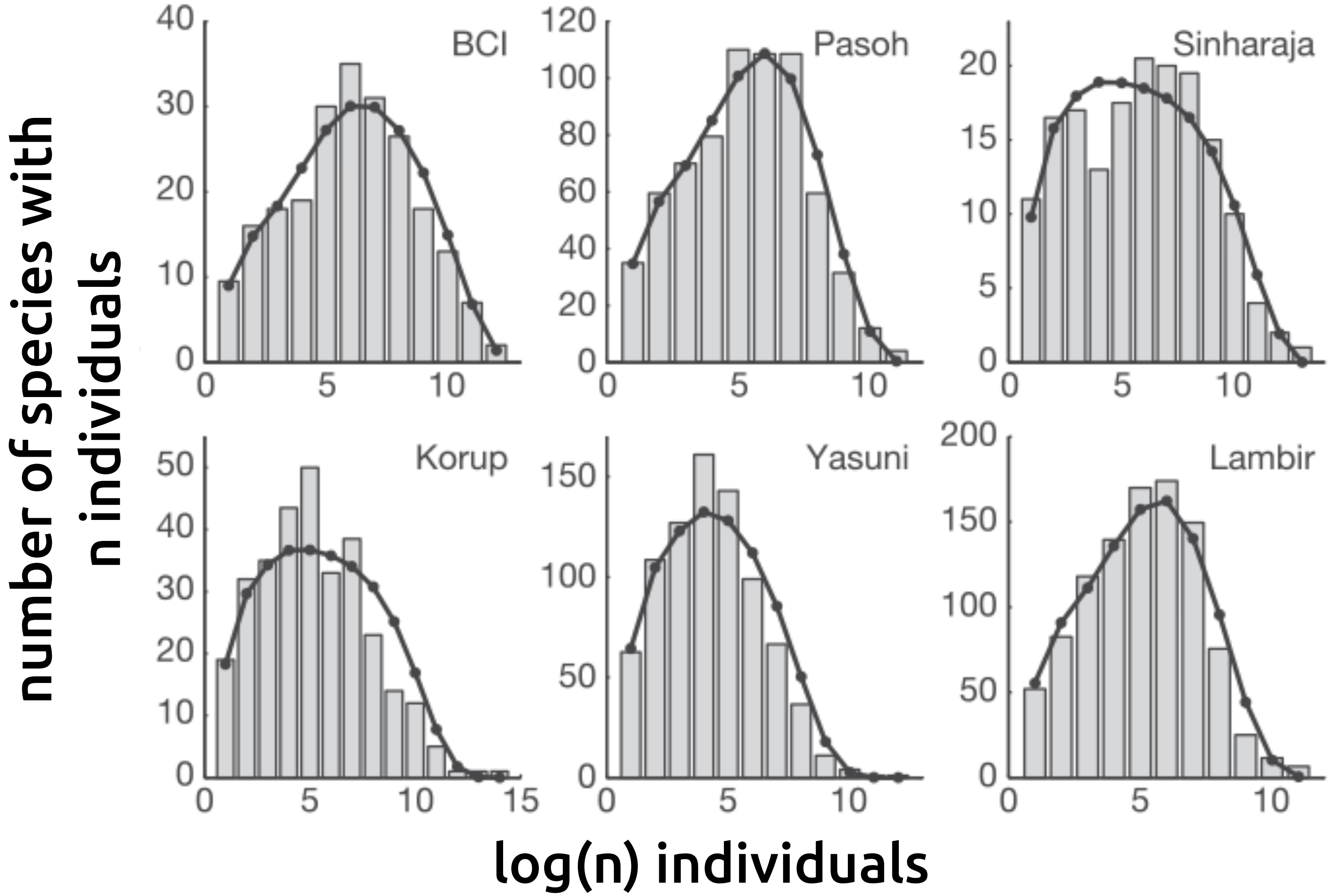








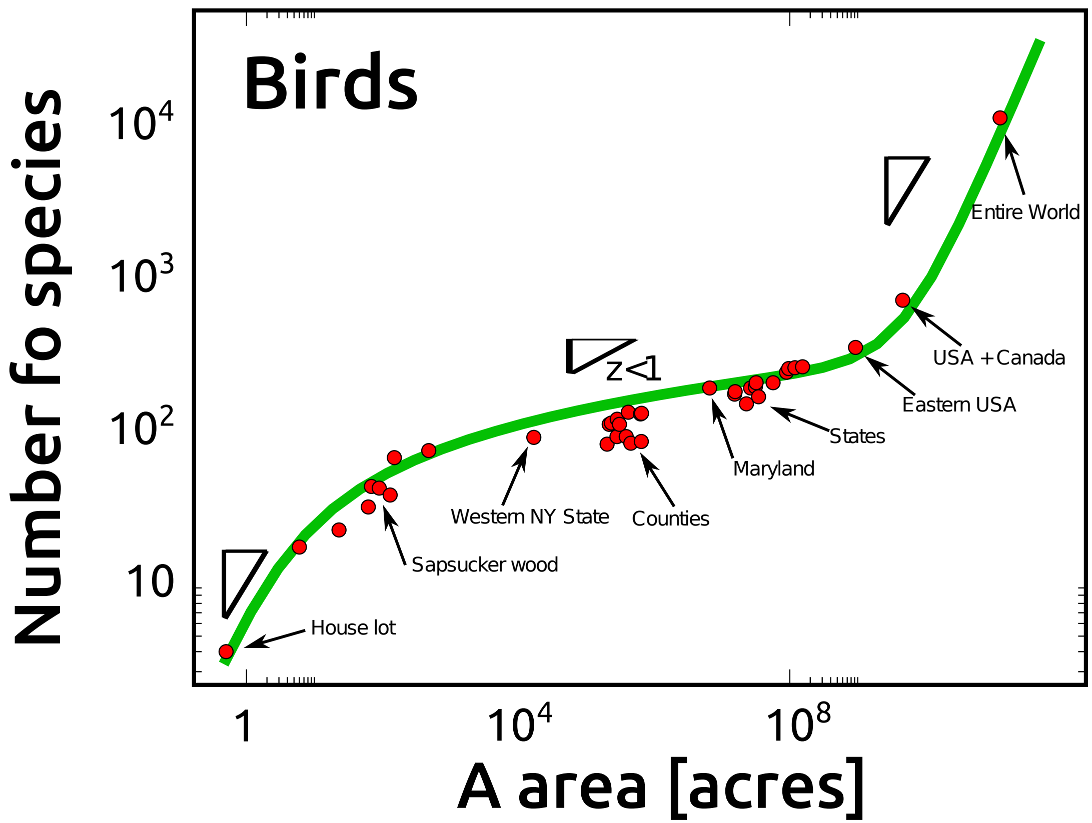
Neutral theory explains statical patterns observed across ecosystems



[Volkov, Maritan, Hubbel and Banavar, Nature 2003]

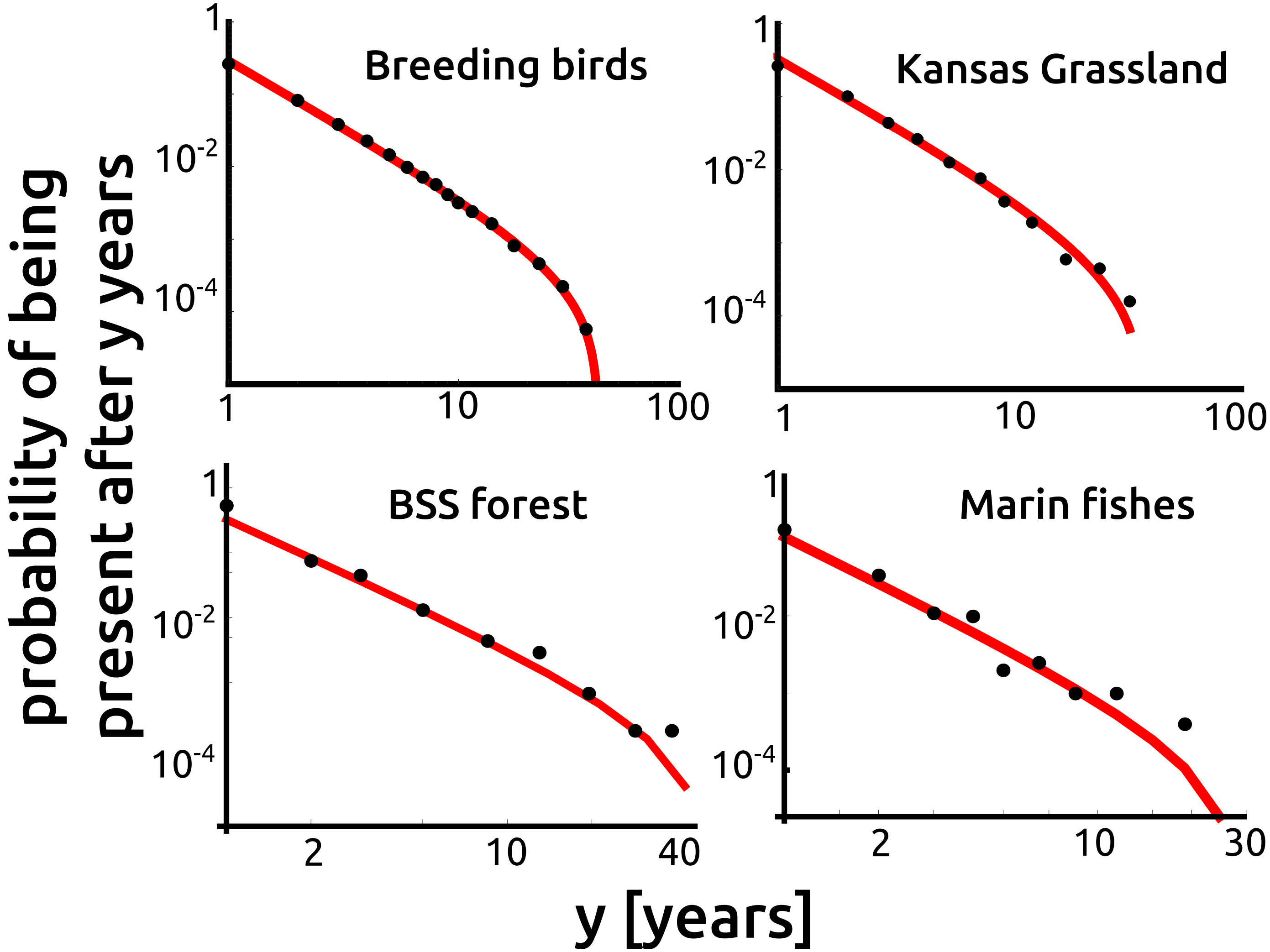
[Azaele, Suweis, Grilli, Volkov, Banavar and Maritan, Review of Modern Physics 2016]

Neutral theory explains spatial patterns observed across ecosystems



[Grilli, Azaele, Banavar and Maritan, JTB 2012]

Neutral theory explains dynamical patterns observed across ecosystems



[Bertuzzo, Suweis, Mari, Maritan and Rinaldo, PNAS 2011]

[Azaele, Suweis, Grilli, Volkov, Banavar and Maritan, Review of Modern Physics 2016]

What we do like about neutral theory

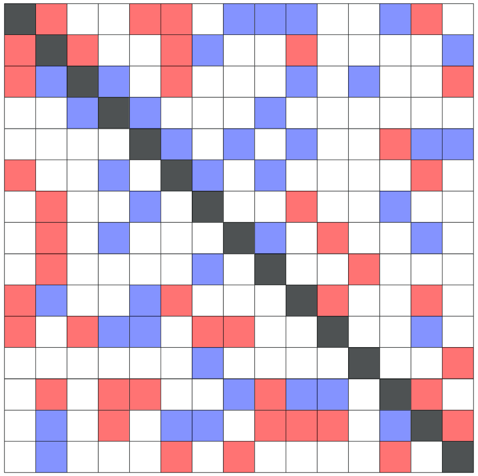
Reproduces and predicts macro-ecological patterns from minimal assumptions

High biodiversity "for free"

Simple and tractable

Biodiversity is not for free

Species interacting
at random



Stability decreases as biodiversity and/or interaction strenghts increase

[May, Will a large complex system be stable?, Nature 1972]

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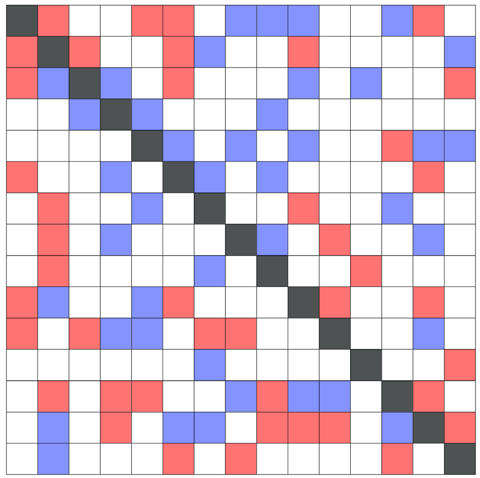

Stability decreases as biodiversity and/or interaction strenghts increase

[May, Will a large complex system be stable?, Nature 1972]

This argument still holds if you consider

Different interaction types
[Allesina & Tang, Nature 2012]

"Realistic" food web structure
[Allesina et al, Nat Comm 2015]

Modular structures
[Grilli et al, Nat Comm 2016]

Response to condition variability
[Grilli et al, Nat Comm 2017]

What we do like about neutral theory

Reproduces and predicts macro-ecological patterns from minimal assumptions

High biodiversity "for free"

Simple and tractable

What we do not like about neutral theory

Sensitivity to the hypothesis of ecological equivalence

Stability is only neutral

No interactions

Wrong species ages

Back-of-the-envelope calculation on species ages

number of generations of a species with relative abundance x

$$a(x) = 2N \frac{x}{1-x} |\log(x)|$$

[Kimura 1983]

Back-of-the-envelope calculation on species ages

number of generations of a species with relative abundance x

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[Kimura 1983]

Amazon rainforest

Total number of trees: $N \sim 10^{11}$

Most abundant species tree: $x \sim 10^{-2}$

Generation time of trees: ~ 30 years

Age of the most abundant species: $\sim 10^{11}$ years

Age of the universe: $\sim 10^{10}$ years , First tree: $\sim 10^{8}$ years ago

[Caveat: N is not constant. The effective N is the harmonic mean over time...]

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What next?

Strategy

1\.

Closed systems (no migration/speciation)

Deterministic analysis

2\.

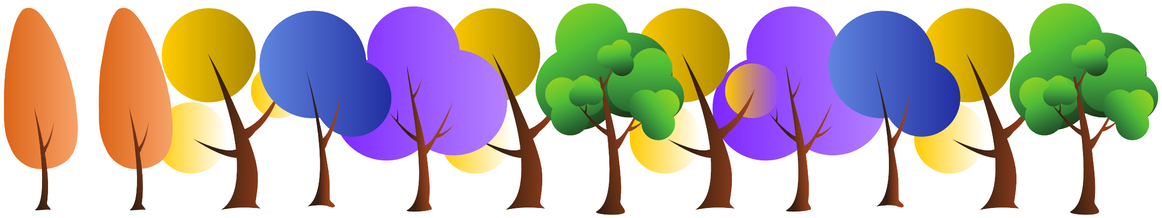
Closed systems (no migration/speciation)

Effect of stochasticity

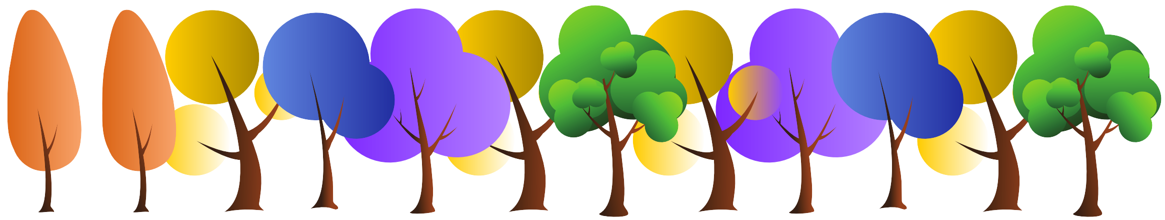
3\.

Open systems (migration/speciation)

Compare to neutral theory prediction

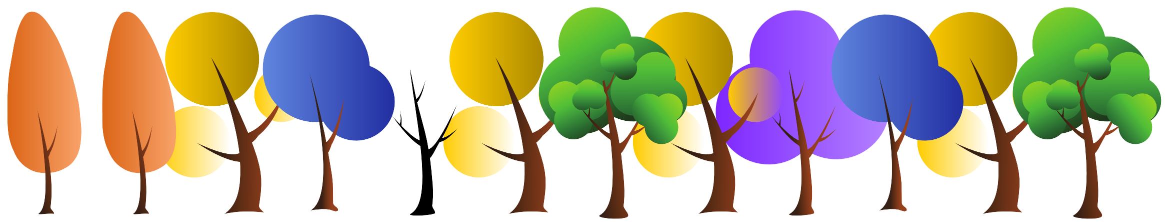
zero-sum  $\Sigma x_i=1$

zero-sum

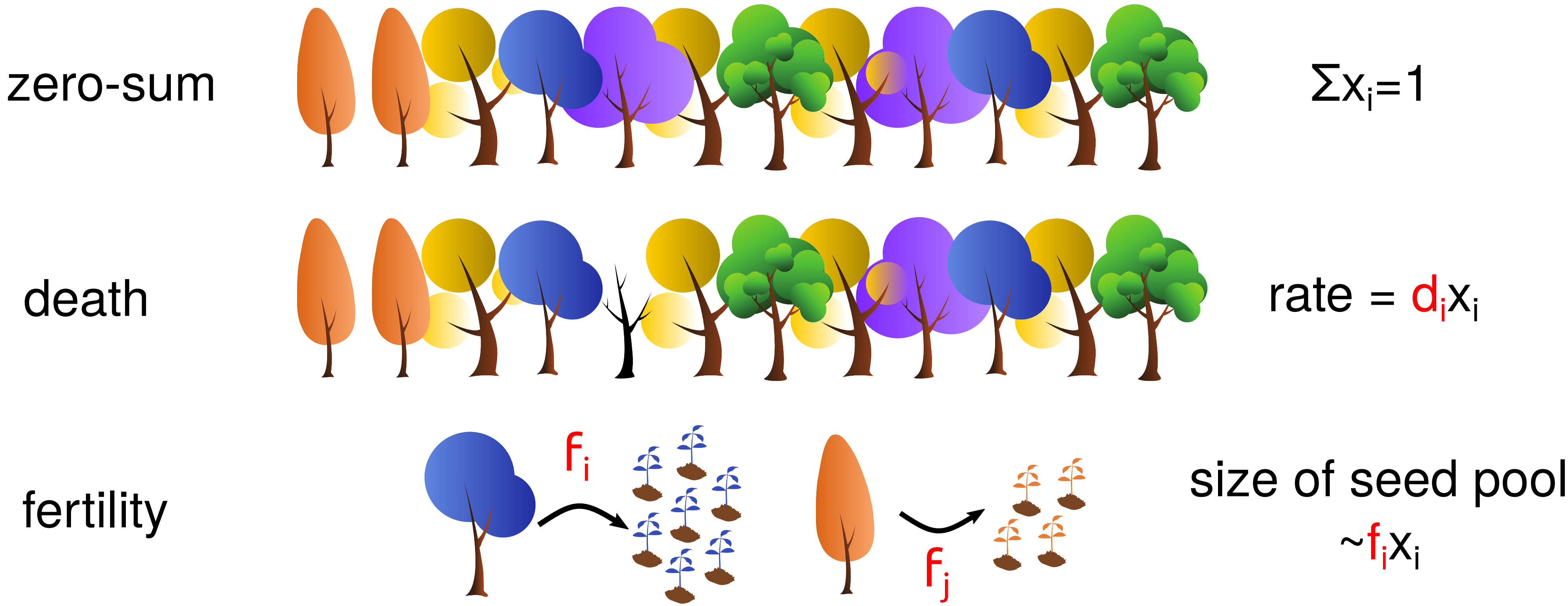


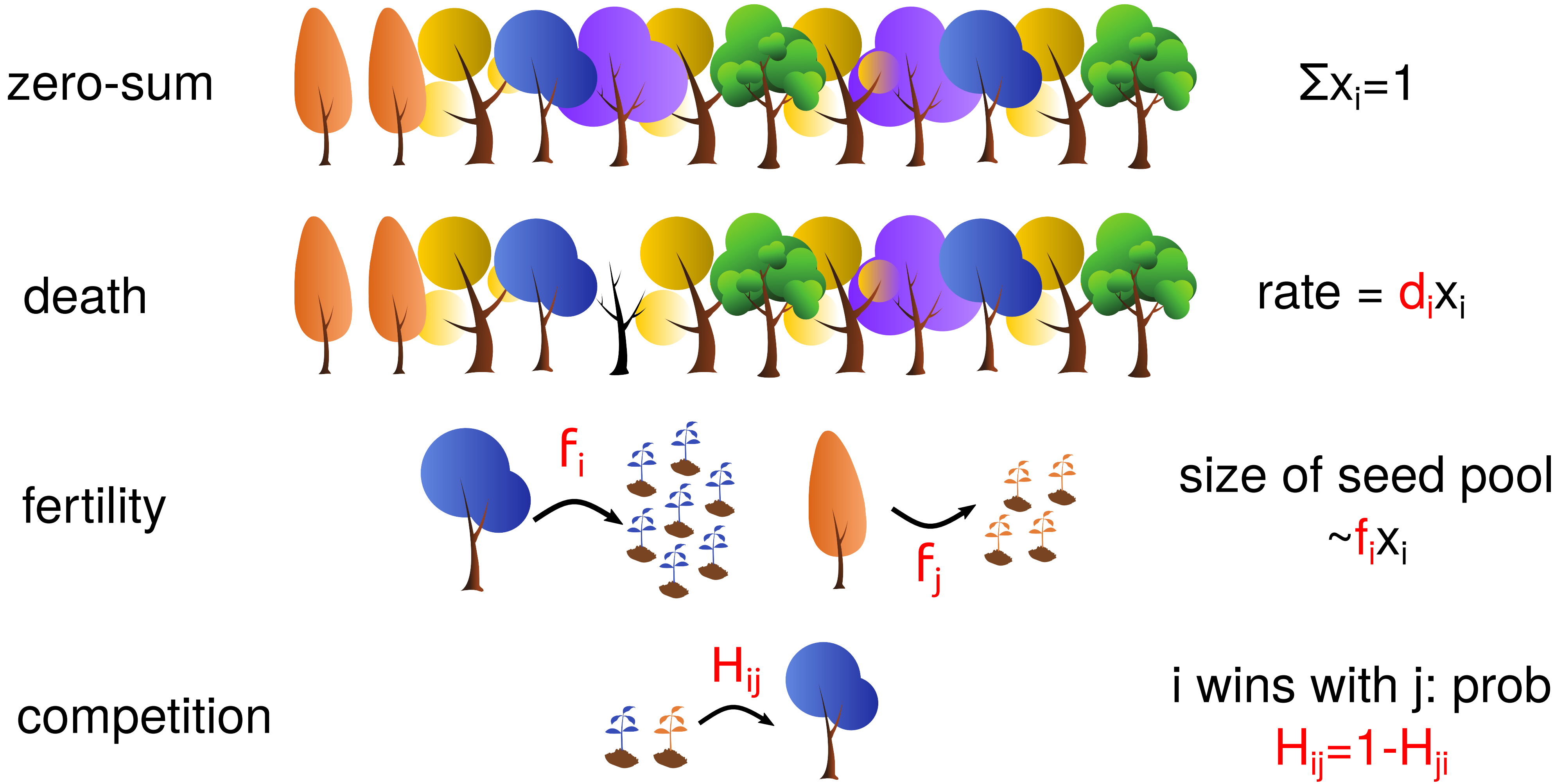
$\Sigma x_i=1$

death



rate = $d_i x_i$


zero-sum
$\Sigma x_i = 1$
death
rate = $d_i x_i$
fertility
f_i
f_j
size of seed pool
$\sim f_i x_i$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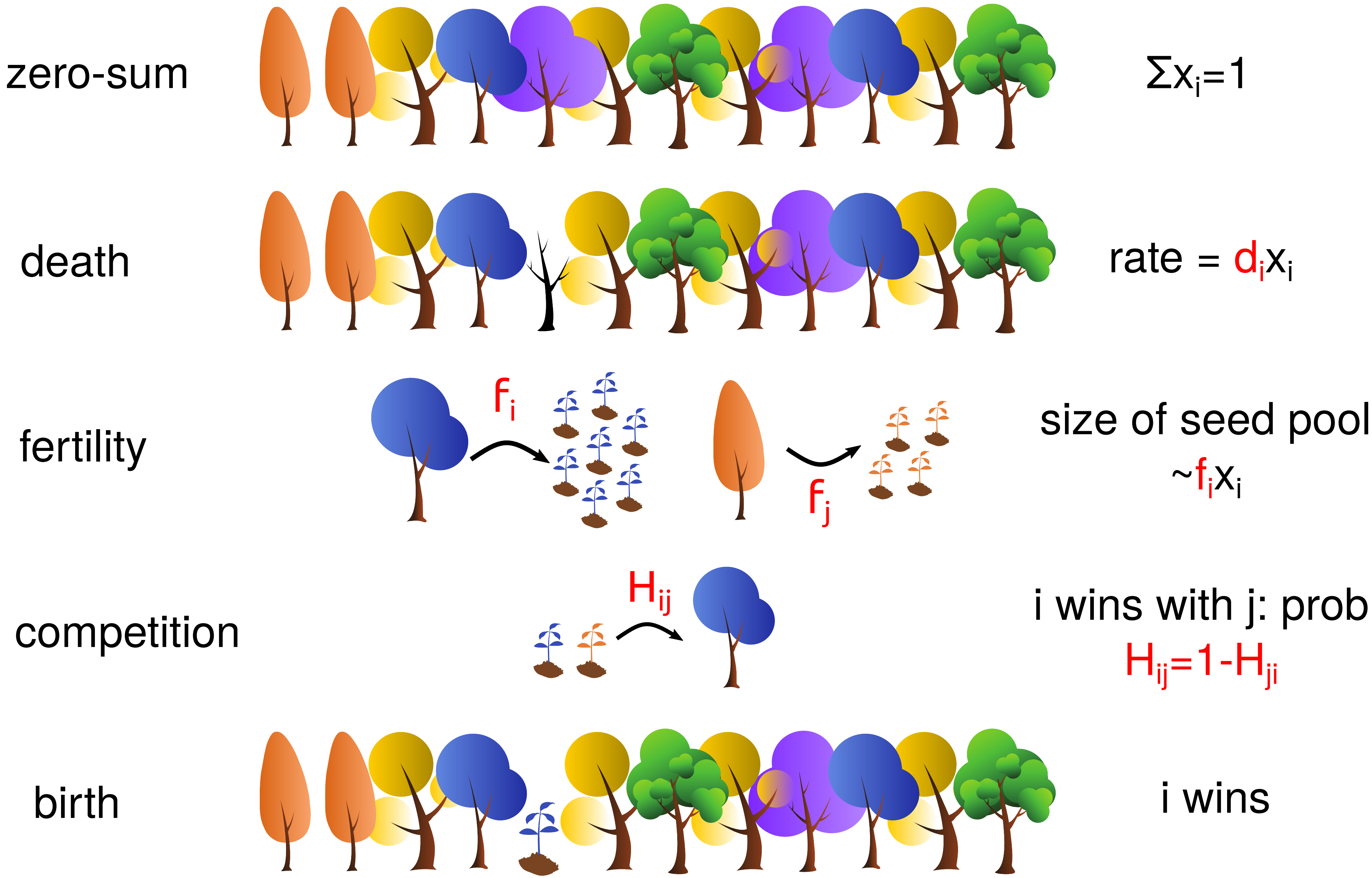
competition
H_{ij}
i wins with j: prob
$H_{ij}=1-H_{ji}$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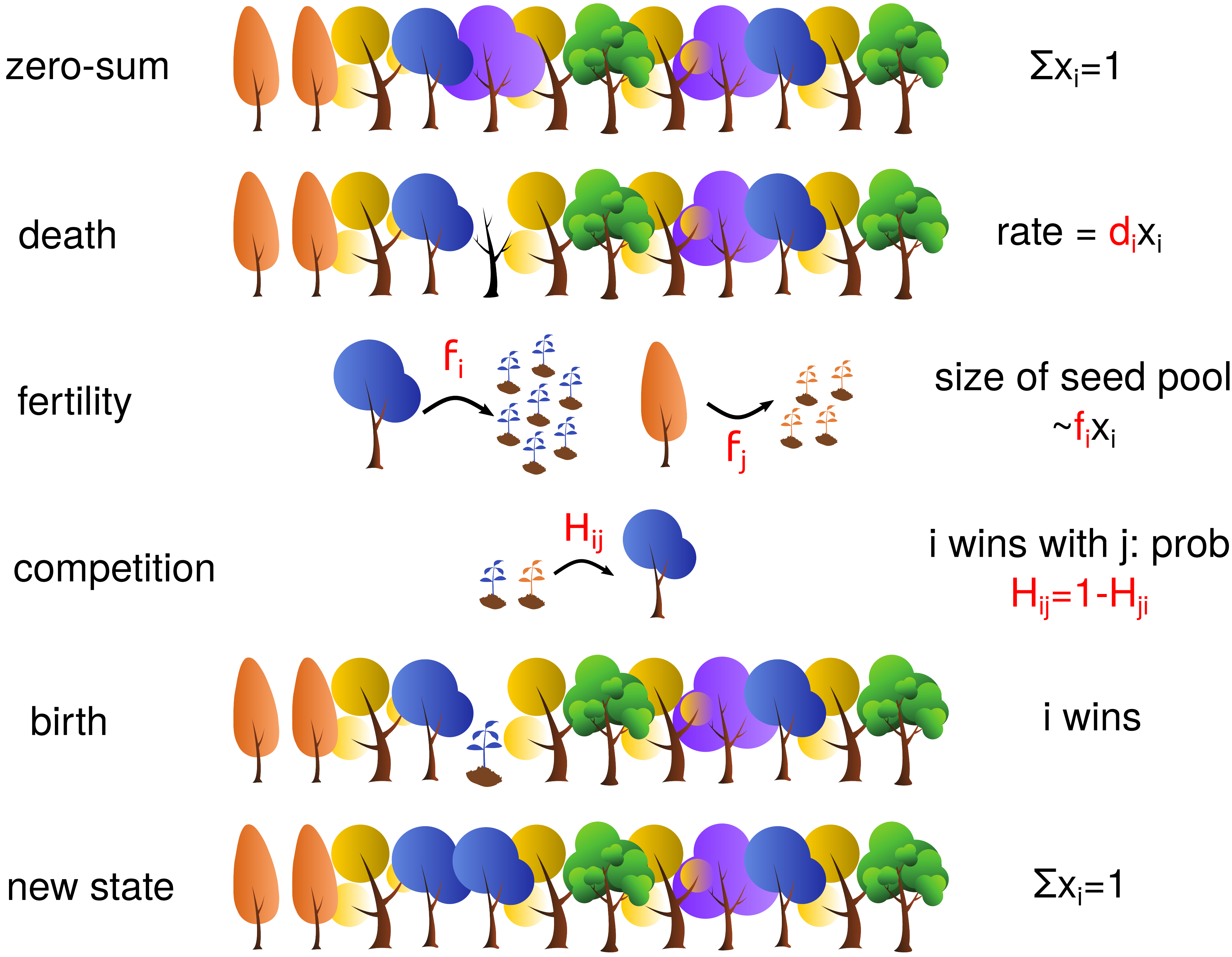
birth
i wins



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$H_{ij}=1-H_{ji}$
birth
i wins
new state
$\Sigma x_i=1$

Neutral theory

in the case of equal physiological rates $f_i = d_i = 1$
and equal competition abilities $H_{ij} = H_{ji} = 1/2$

Hypertournaments

in the case of equal physiological rates $f_i = d_i = 1$
and arbitrary $H_{ij} = 1 - H_{ji}$

Full model

Arbitrary physiological rates f_i, d_i and $H_{ij} = 1 - H_{ji}$

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$$\dot{x}_i = 2x_i \sum_j H_{ij} x_j - x_i$$

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equivalent to the replicator equation

$$\dot{x}_i = x_i \sum_j (H_{ij} - H_{ji}) x_j = x_i \sum_j P_{ij} x_j$$

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payoff of a symmetric game

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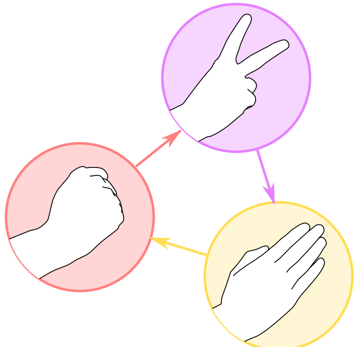

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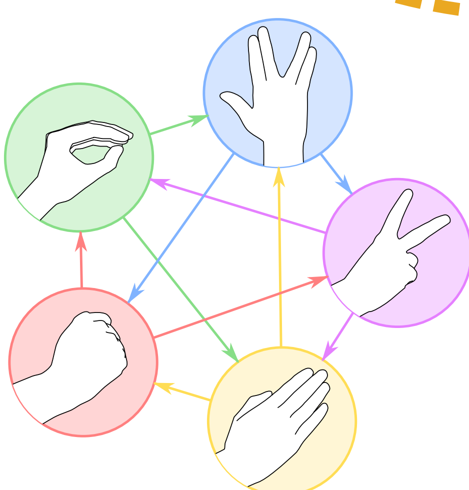

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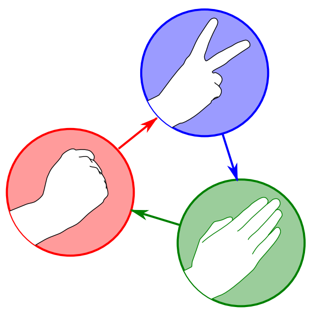
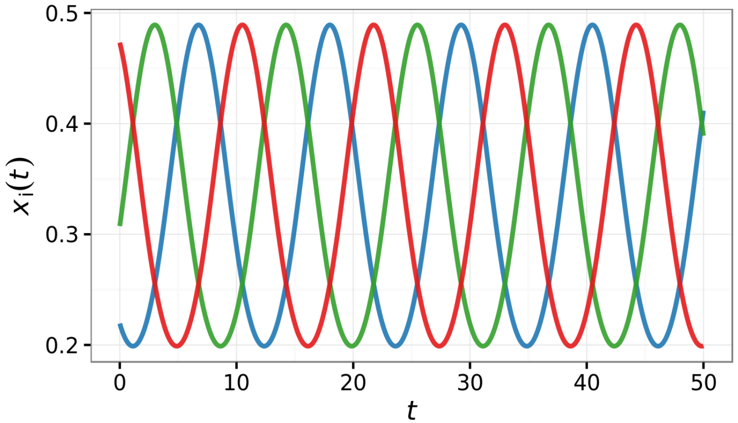
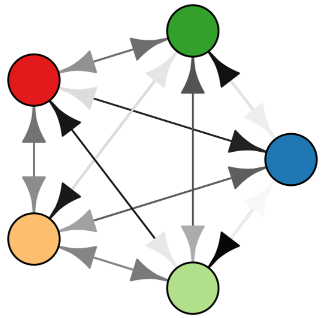
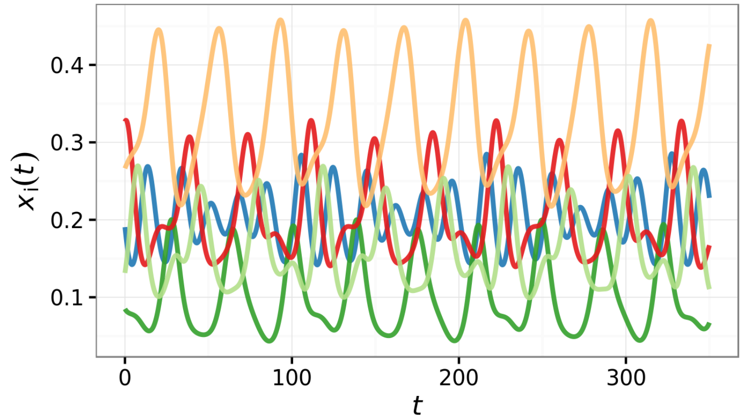
Always neutral cycles

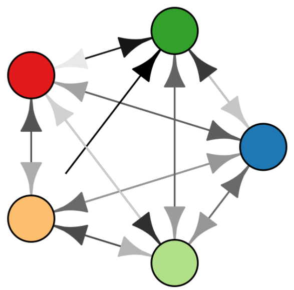
(if a fixed point exists)

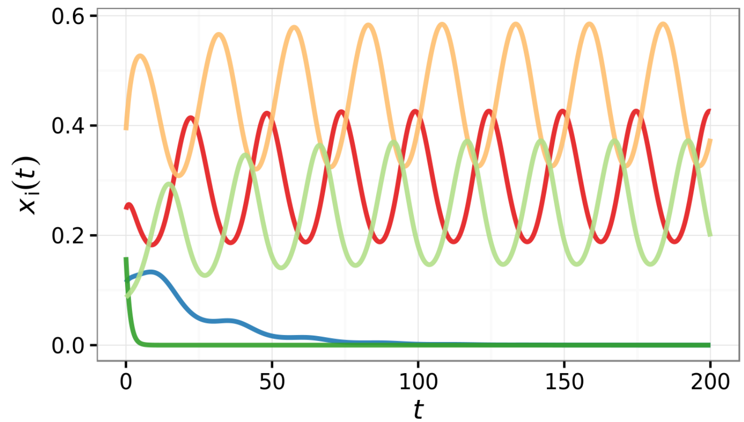






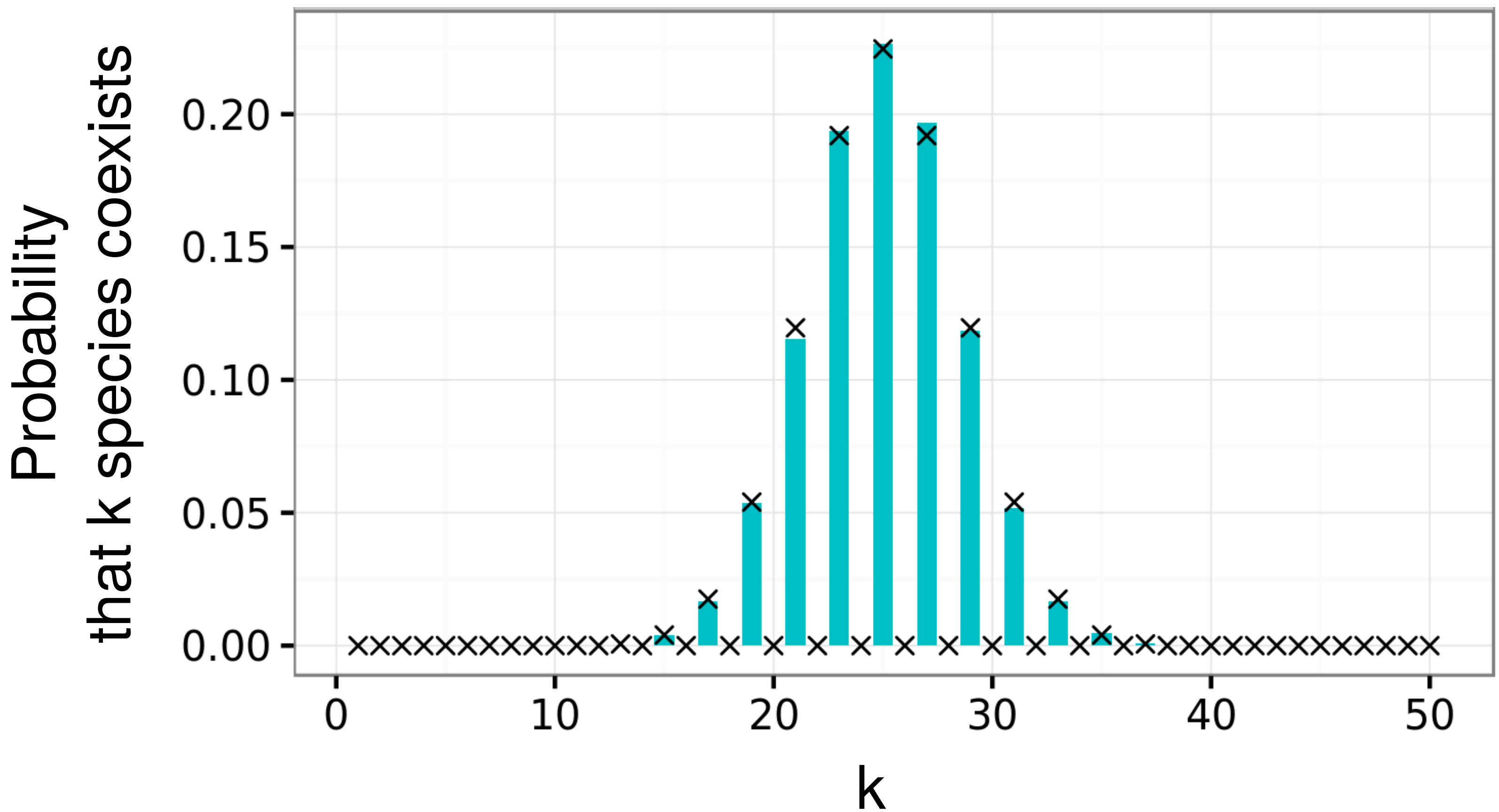






This model generates high biodiversity

Starting with 50 species and random interaction H



~ binomially distributed (only odd number of species)

On average half of the species survive

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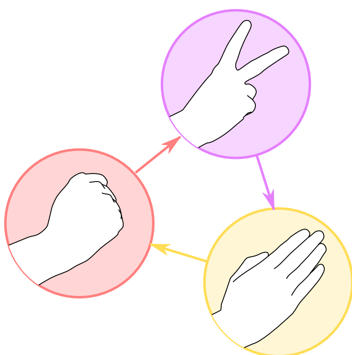
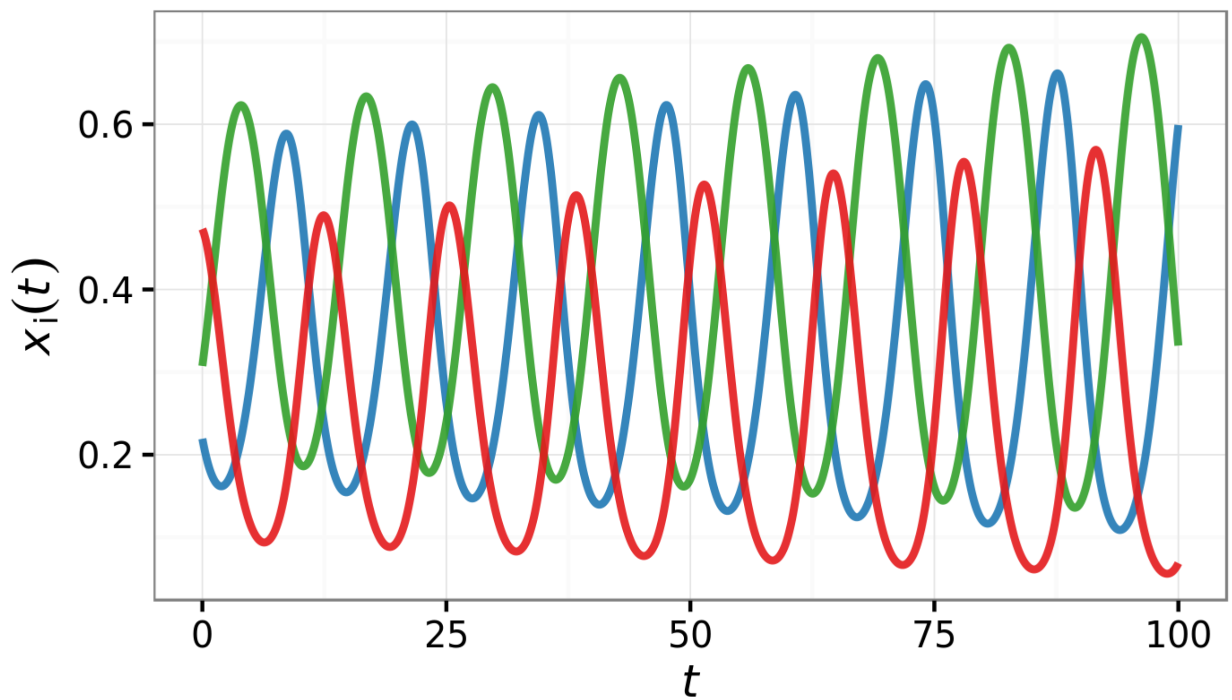
Variability of physiological rates inevitably leads to instability





The fixed point (if it exists) is unstable for **any** not fine tuned choice of physiological rates

Summary of results for pairwise interactions

Arbitrary H_{ij} and equal physiological rates

Neutral cycles around a fixed point

Random H_{ij}: on average half of the species coexist
[Brandl, working paper 2015]

Arbitrary H_{ij} and arbitrary physiological rates

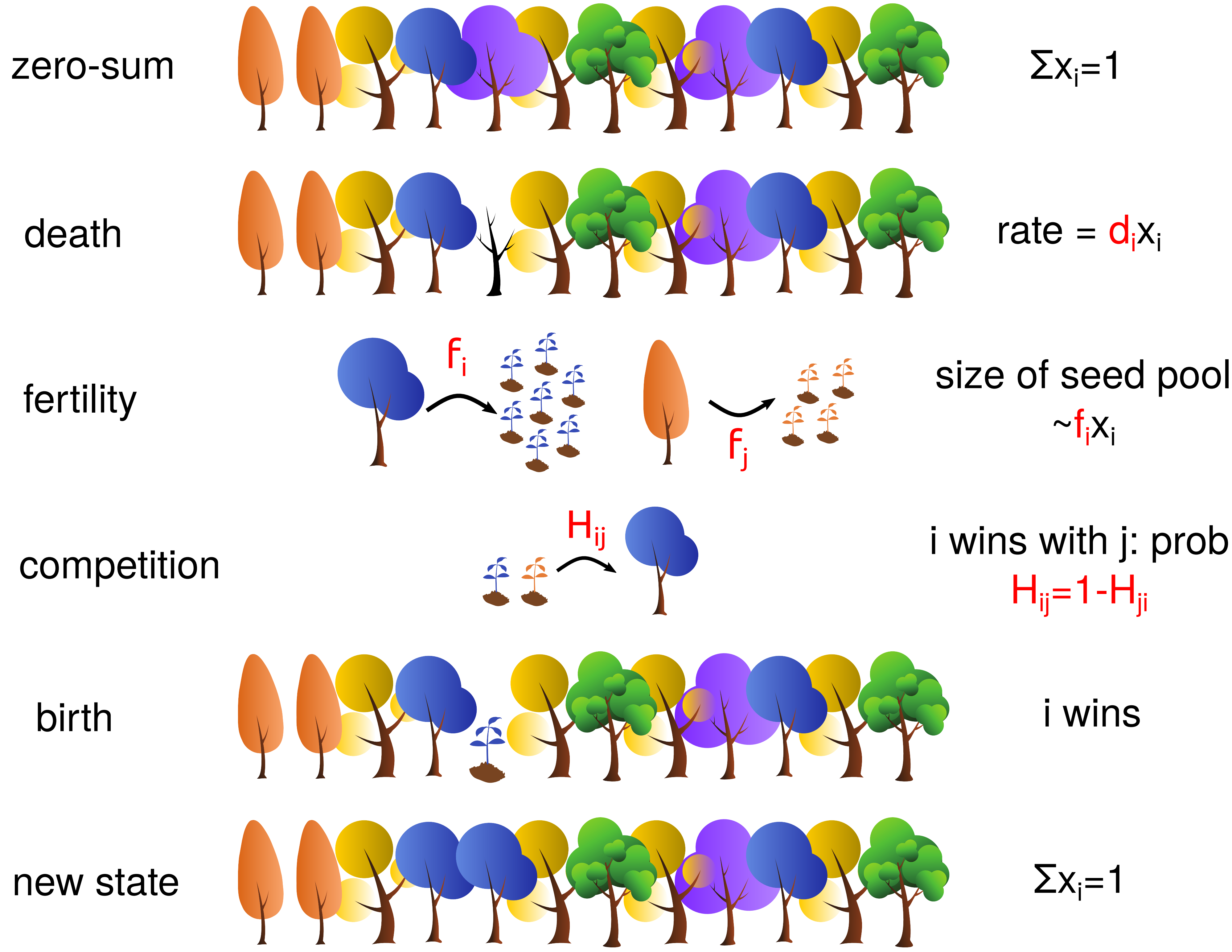
Fixed point is **always** unstable
[this work]

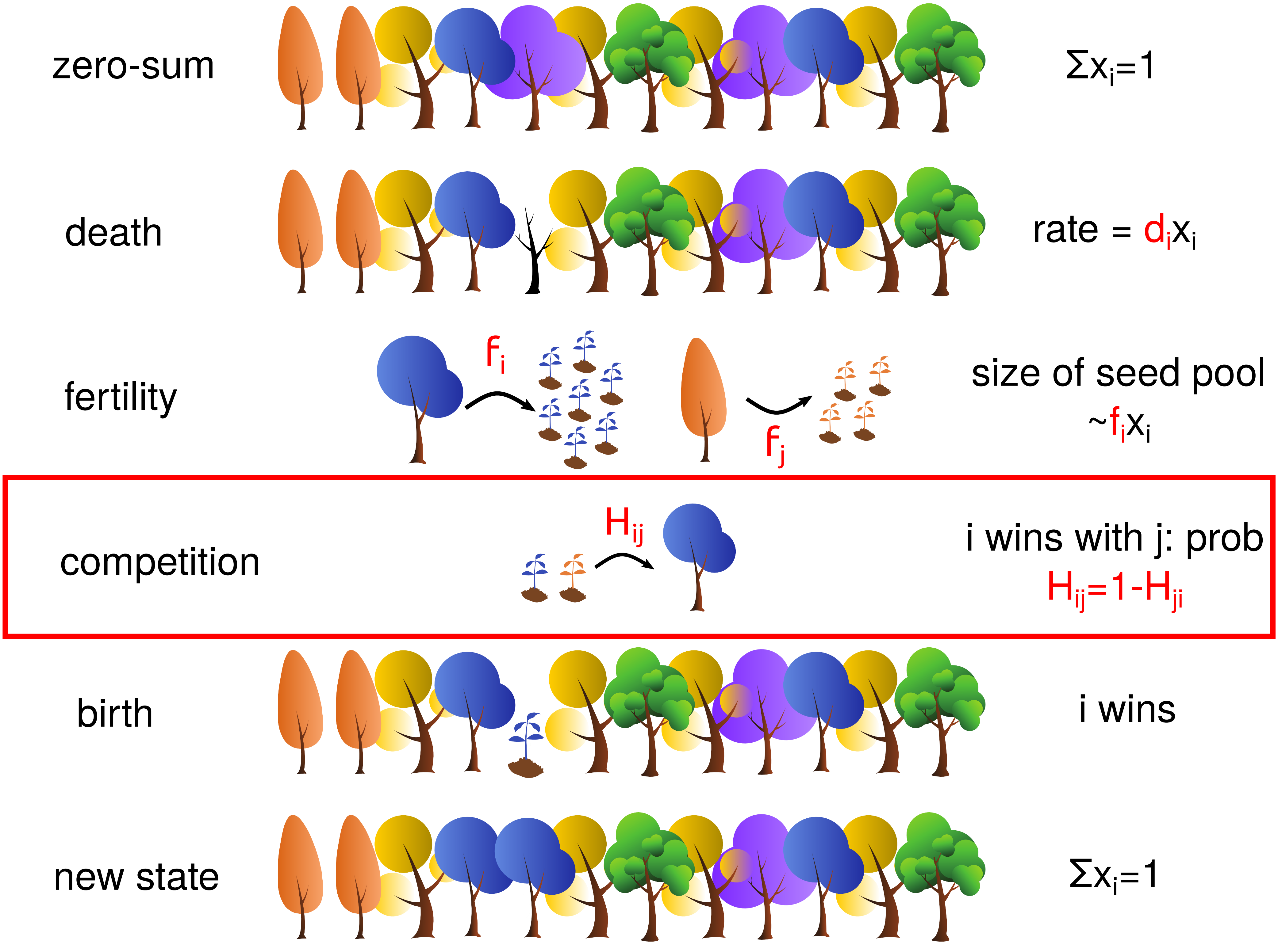
What we do not like about neutral theory

Sensitivity to the hypothesis of ecological equivalence

Stability is only neutral

No interactions


zero-sum
Σxi=1
death
rate = dixi
fertility
fi
fj
size of seed pool
~fixi
competition
Hij
i wins with j: prob
Hij=1-Hji
birth
i wins
new state
Σxi=1



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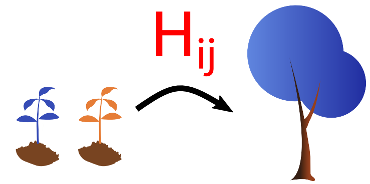
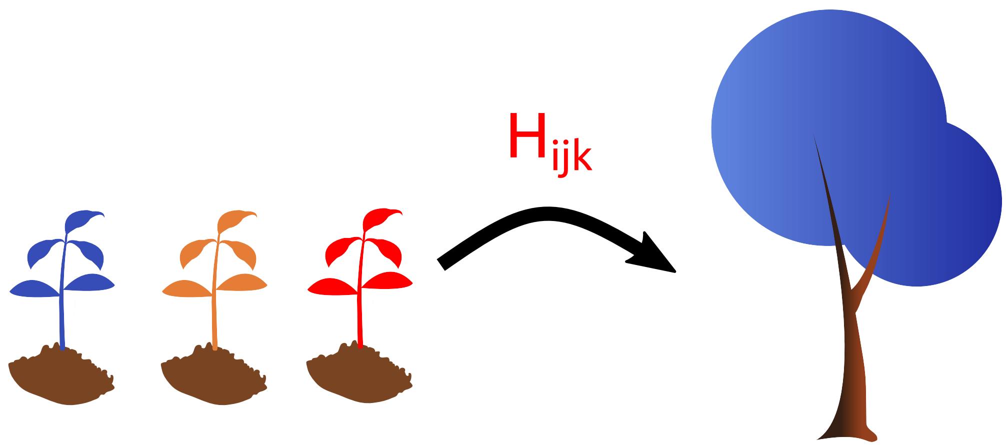


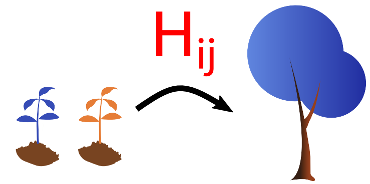
i wins with j: prob

$H_{ij}=1-H_{ji}$

Higher-order interactions



competition



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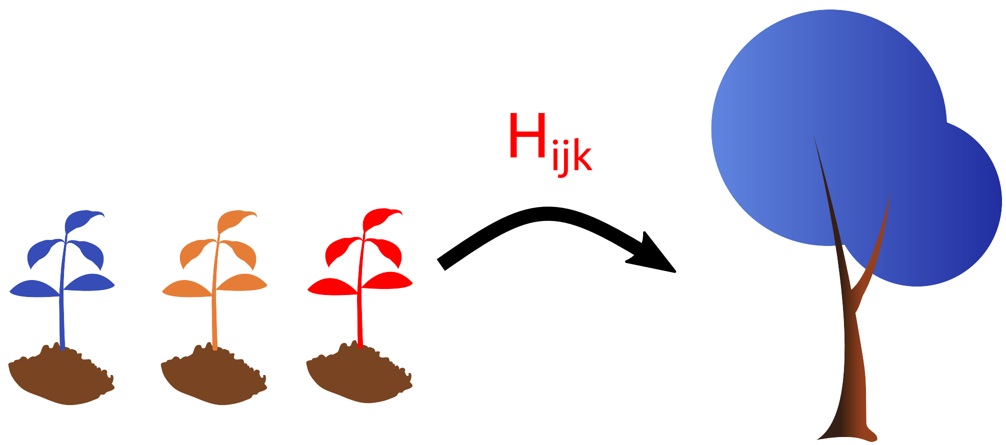
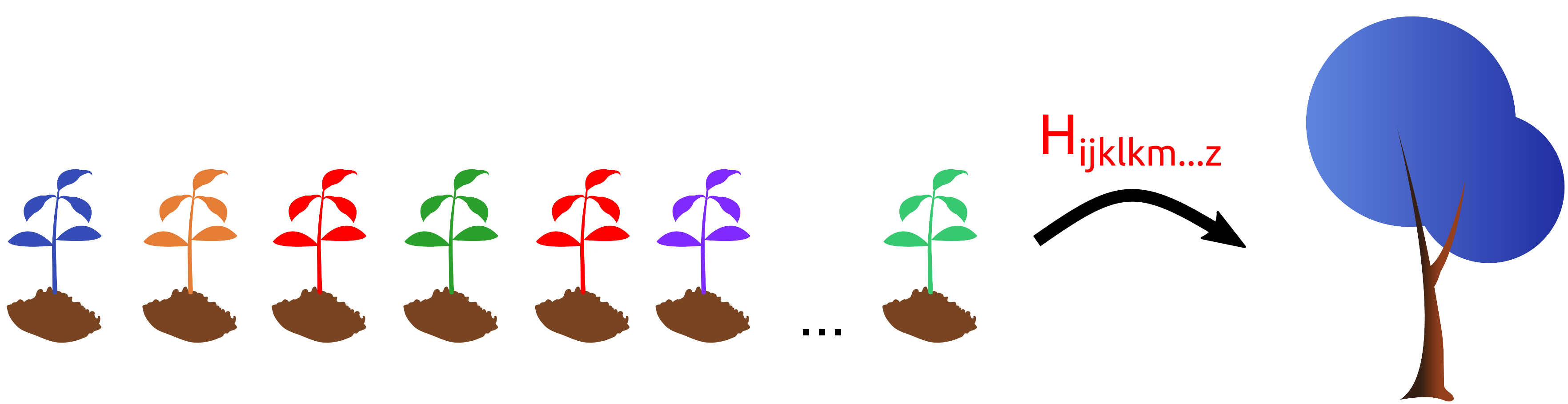


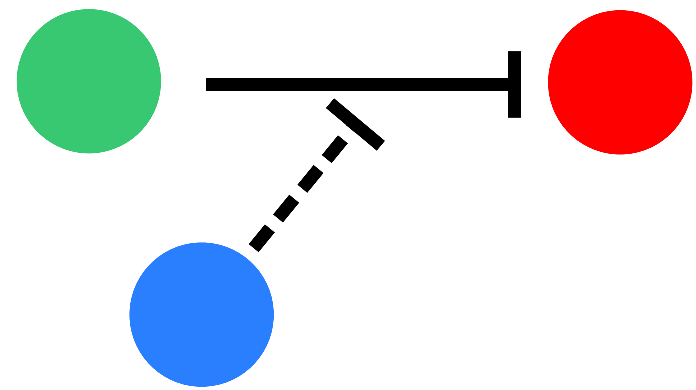


Higher-order interactions

● inhibts ●
producing an antibiotics

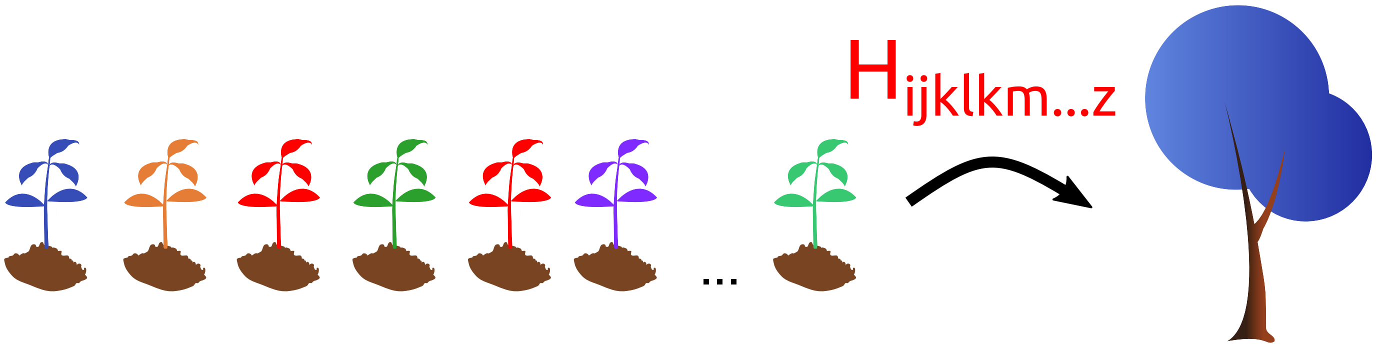
[Kelsic et al., Nature 2015]

● produces an enzyme that
degrades the antibiotic

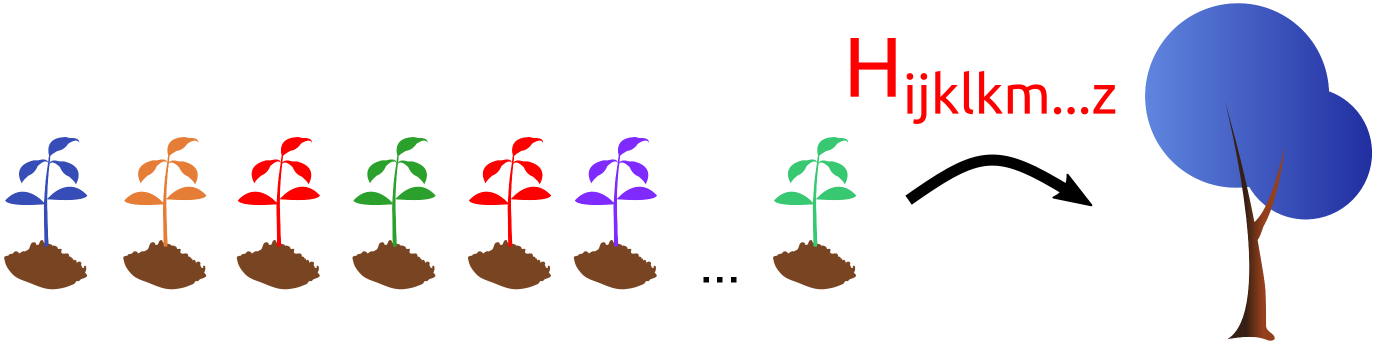


Strongly debated:

- their presence (common or rare?)
- their inference/measure
- their effect on community dynamics



A null parameterization of higher-order interactions



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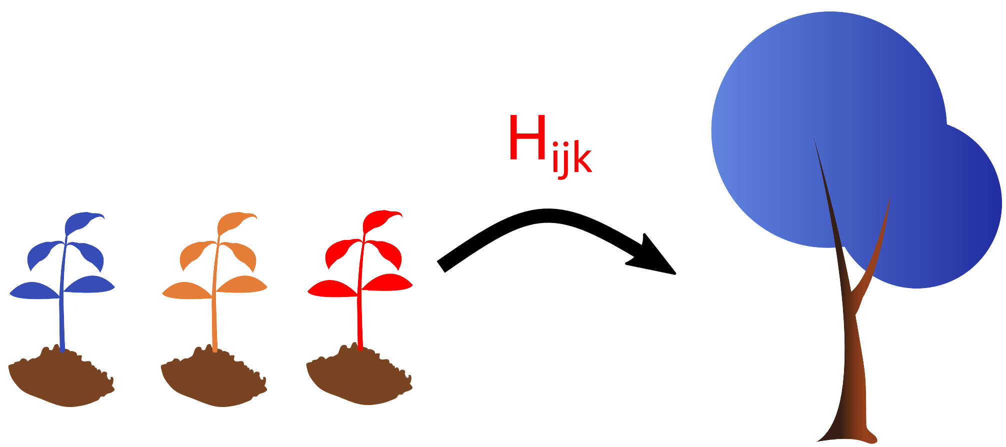

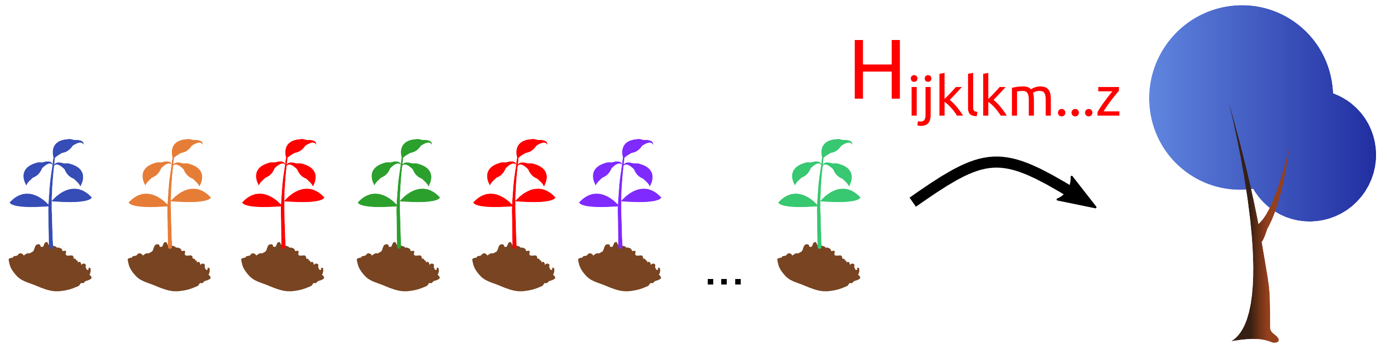

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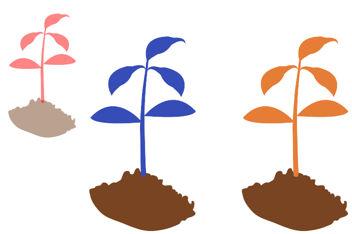

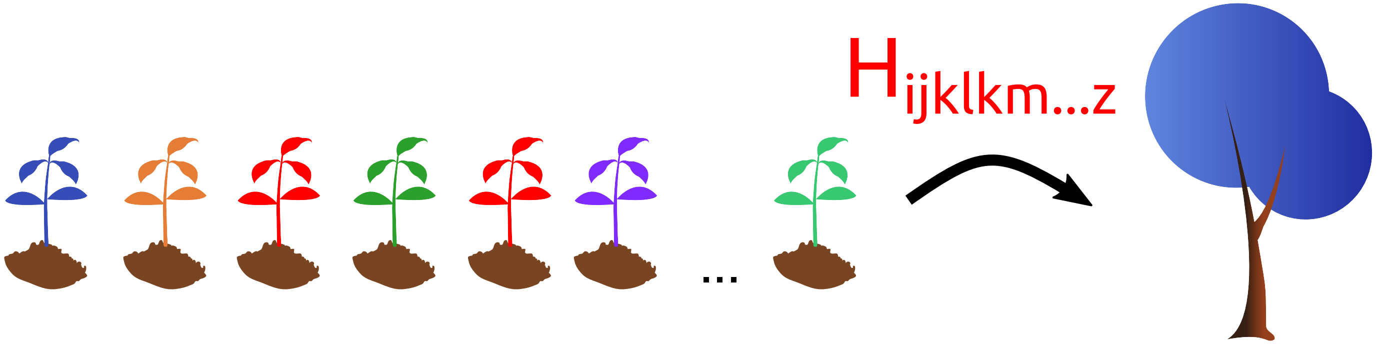

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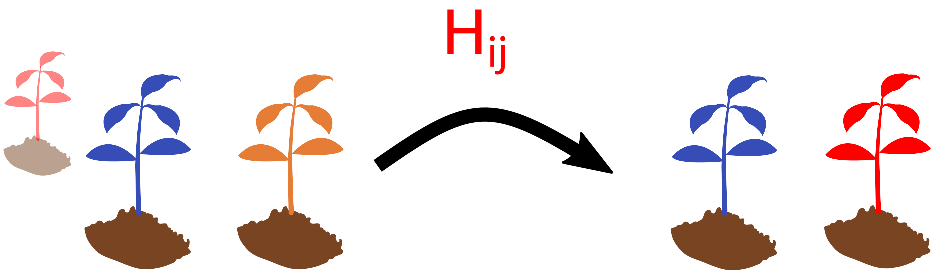

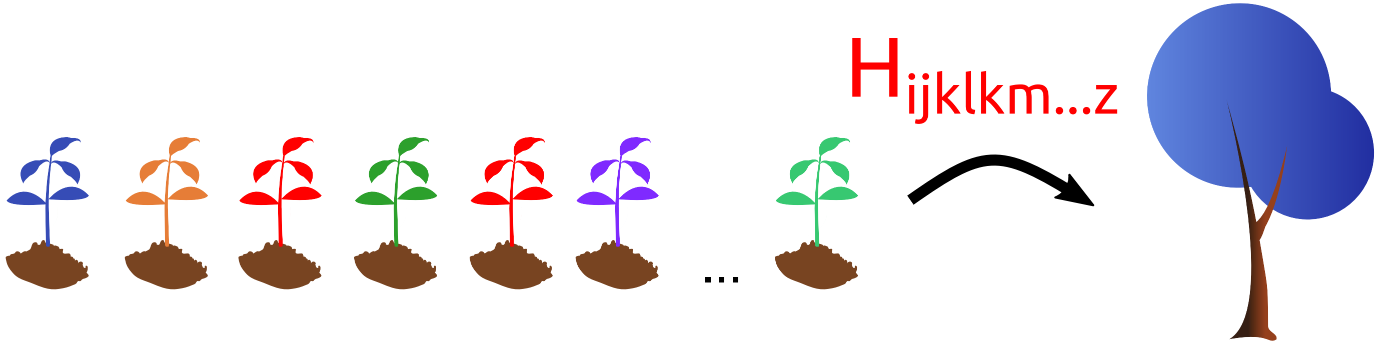

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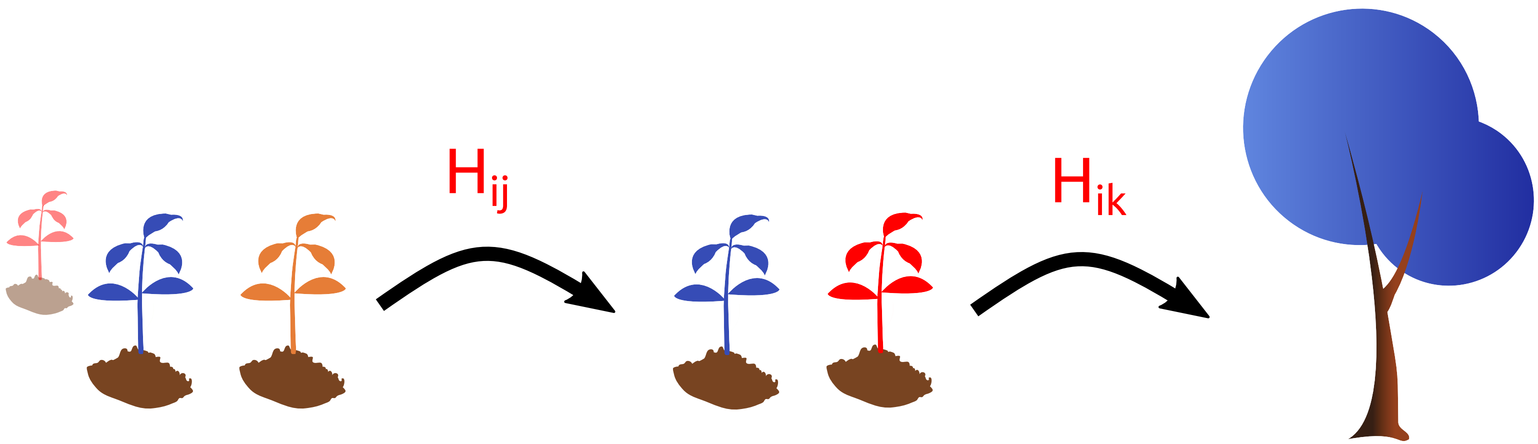
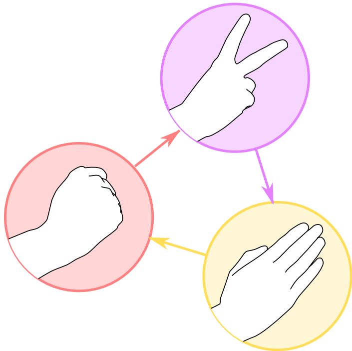


This parameterization makes sense

$$\dot{x}_i = x_i \sum_j (H_{ij} - H_{ji}) x_j = x_i \sum_j P_{ij} x_j$$

payoff of a symmetric game



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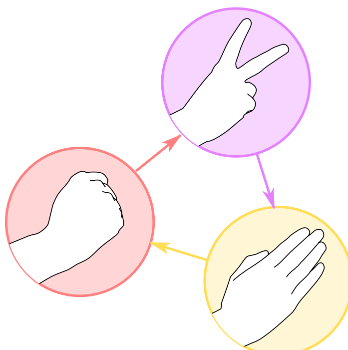
payoff of a symmetric game



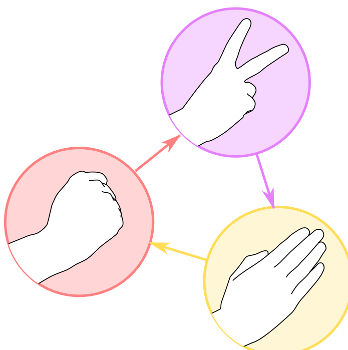
$$P = \begin{pmatrix} 0 & 1 & -1 \\ -1 & 0 & 1 \\ 1 & -1 & 0 \end{pmatrix} \quad H = \begin{pmatrix} \tfrac{1}{2} & 1 & 0 \\ 0 & \tfrac{1}{2} & 1 \\ 1 & 0 & \tfrac{1}{2} \end{pmatrix}$$

$$\dot{x}_i = x_i \sum_{jk} P_{ijk} x_j x_k$$

This parameterization makes sense

$$\dot{x}_i = x_i \sum_j (H_{ij} - H_{ji}) x_j = x_i \sum_j P_{ij} x_j$$

payoff of a symmetric game



$$P = \begin{pmatrix} 0 & 1 & -1 \\ -1 & 0 & 1 \\ 1 & -1 & 0 \end{pmatrix} \quad H = \begin{pmatrix} ½ & 1 & 0 \\ 0 & ½ & 1 \\ 1 & 0 & ½ \end{pmatrix}$$

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This parameterization makes sense

$$\dot{x}_i = x_i \sum_j (H_{ij} - H_{ji}) x_j = x_i \sum_j P_{ij} x_j$$

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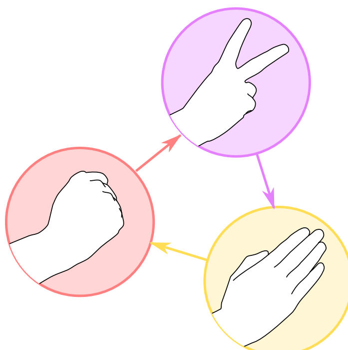

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$$\dot{x}_i = x_i \sum_{jk} P_{ijk} x_j x_k$$

Same form proposed for
>2 players versions of
rock-paper-scissor

Neutral theory
in the case of equal physiological rates $f_i = d_i = 1$
and equal competition abilities $H_{ij} = H_{ji} = 1/2$

Multi-player hypertournaments
in the case of equal physiological rates $f_i = d_i = 1$
and arbitrary $H_{ij} = 1 - H_{ji}$

Full model
Arbitrary physiological rates f_i, d_i and $H_{ij} = 1 - H_{ji}$

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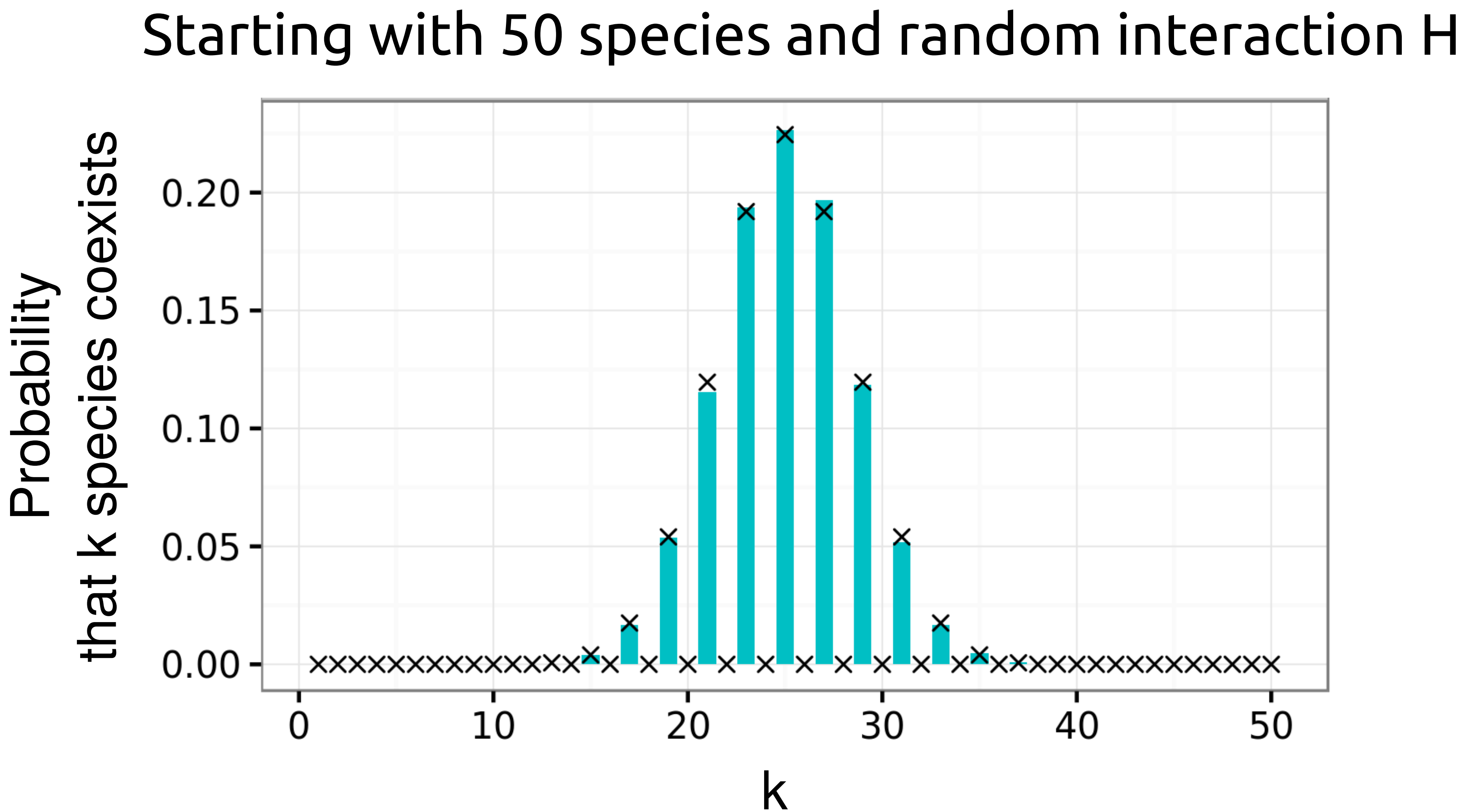
Full model

Arbitrary physiological rates f_i, d_i and $H_{ij} = 1 - H_{ji}$

This model generates high biodiversity

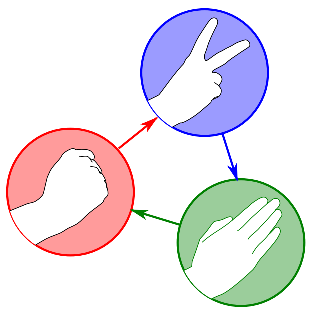


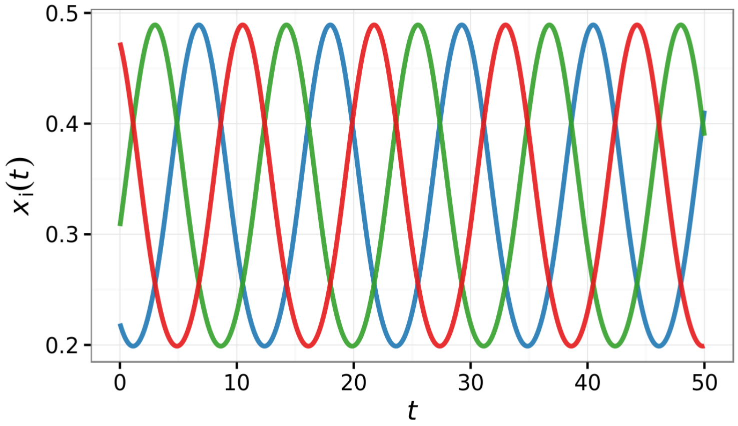
For equal physiological rates,
the fixed point is the same!

Neutral cycles for pairwise interactions

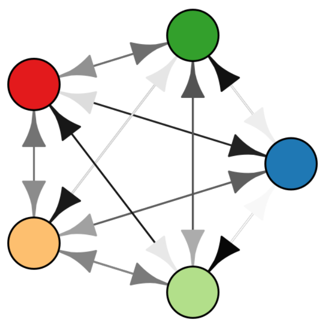
(if a fixed point exists)

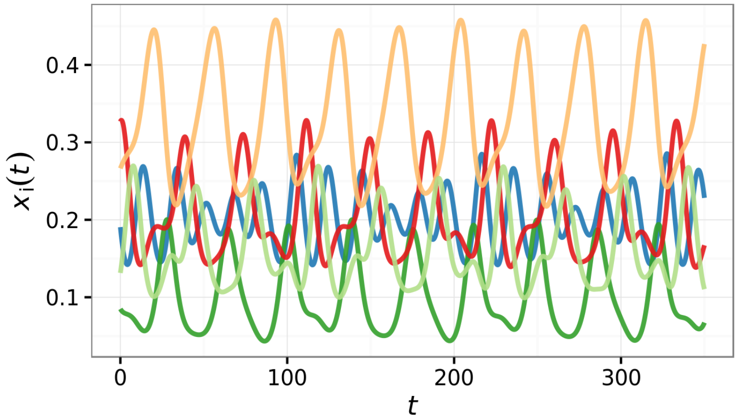
2 players



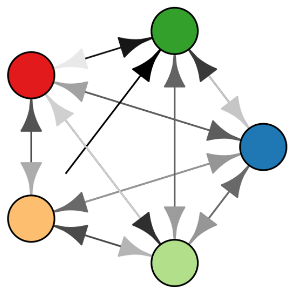


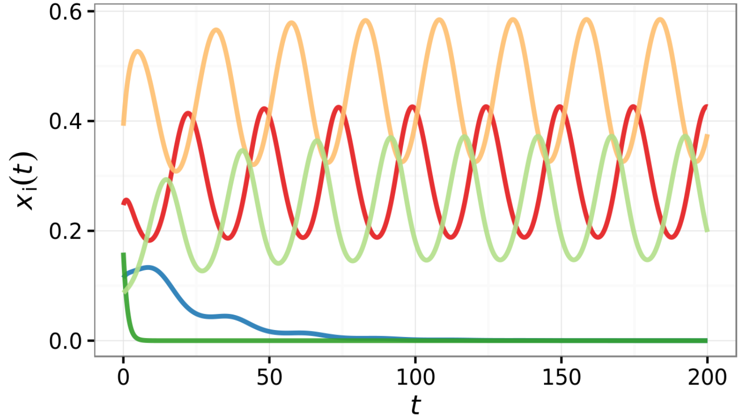
2 players





2 players

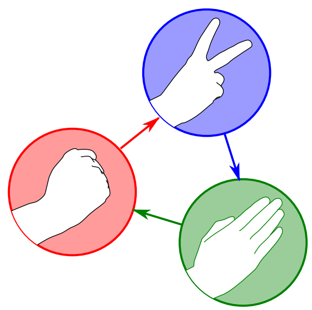


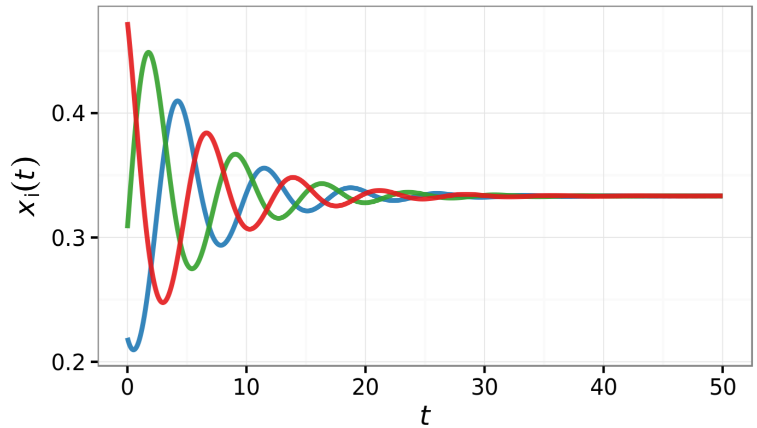


Always globally stable fixed point

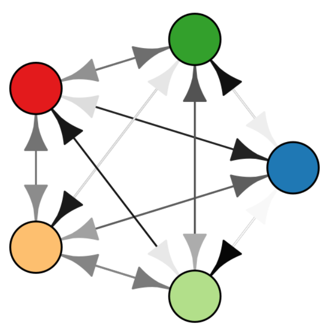
(if a fixed point exists)

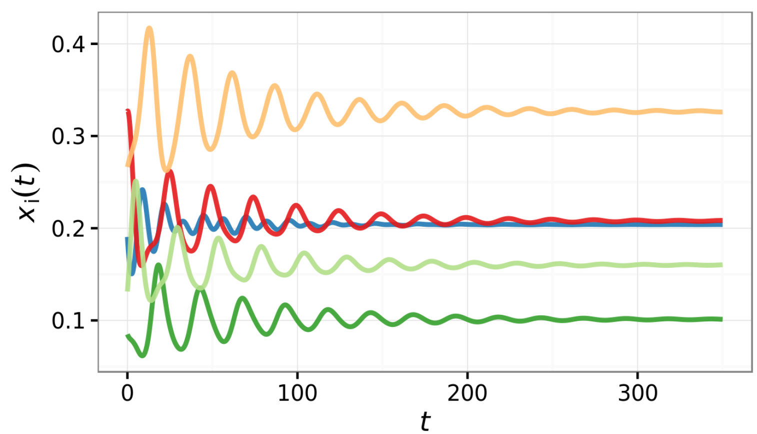
3 players



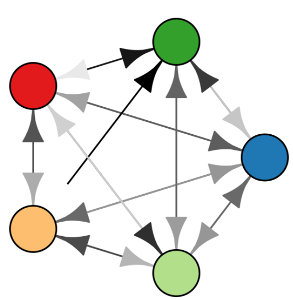


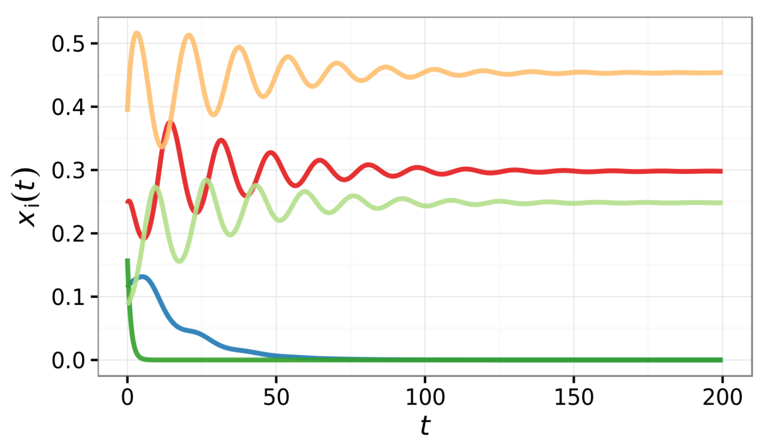
3 players





3 players





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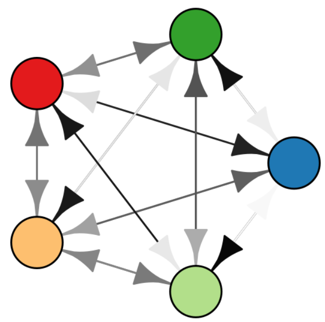
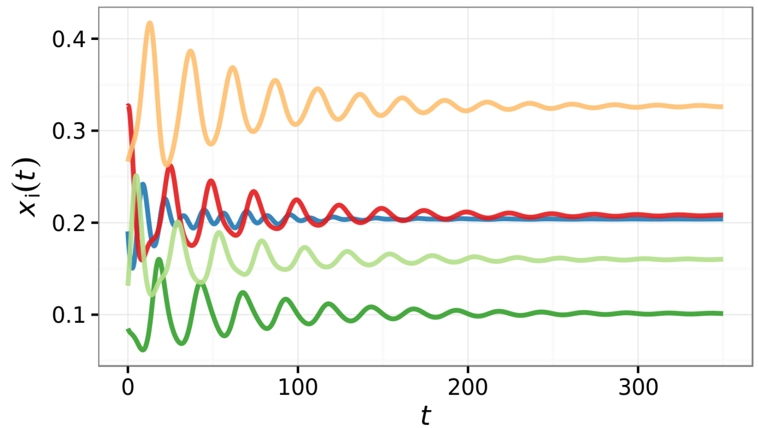
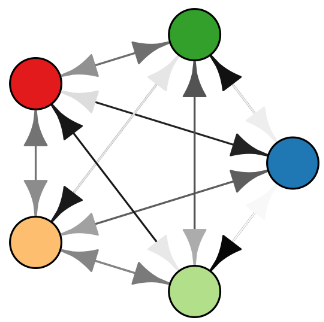
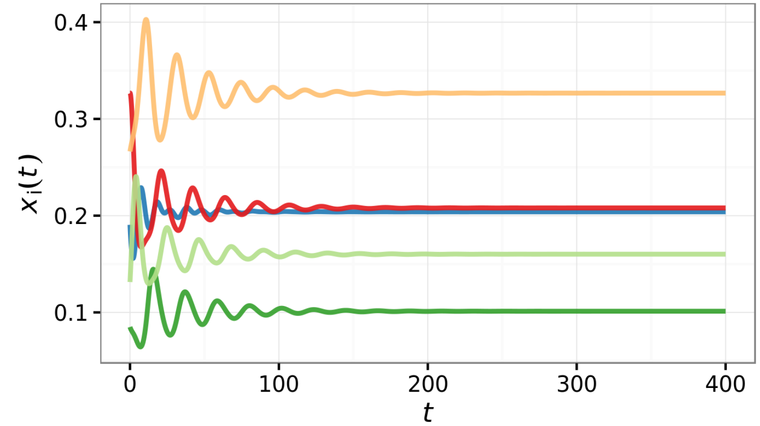


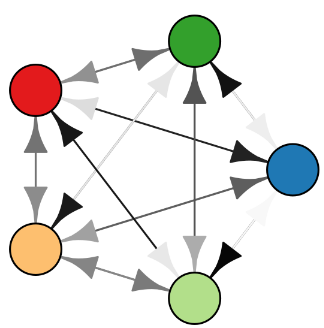


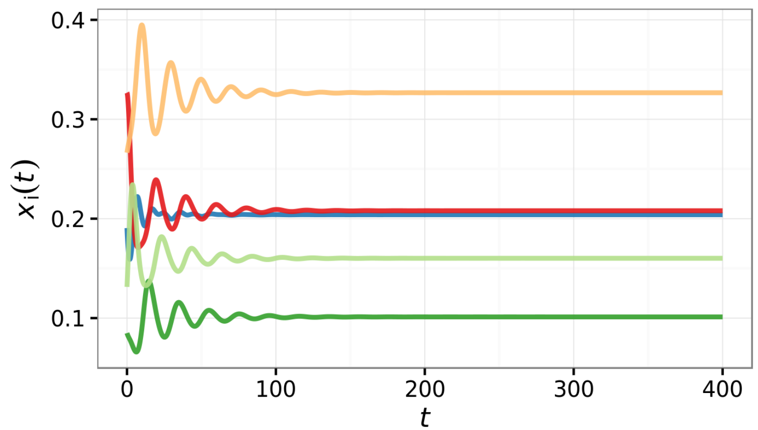
4 players





5 players





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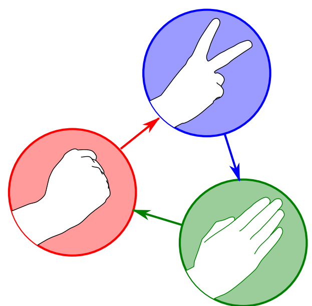
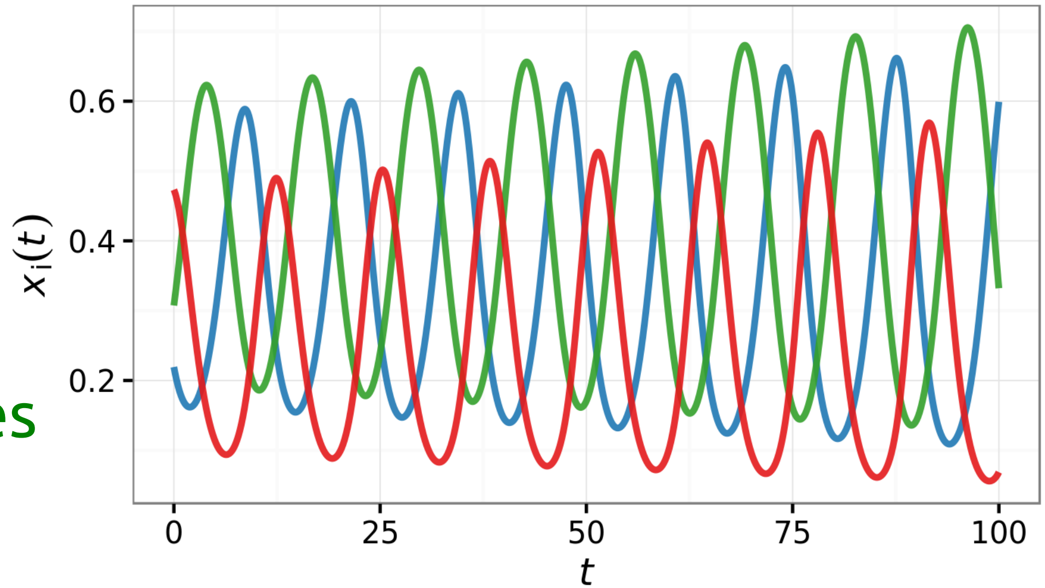
Full model

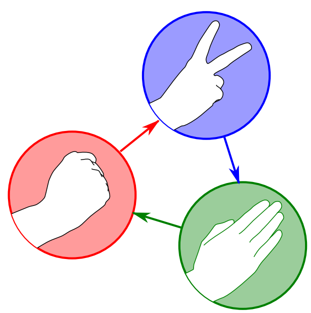
Arbitrary physiological rates f_i, d_i and H_{ij} =1- H_{ji}

Stable coexistence is possible w/o fine-tuning



2 players
different physiological rates





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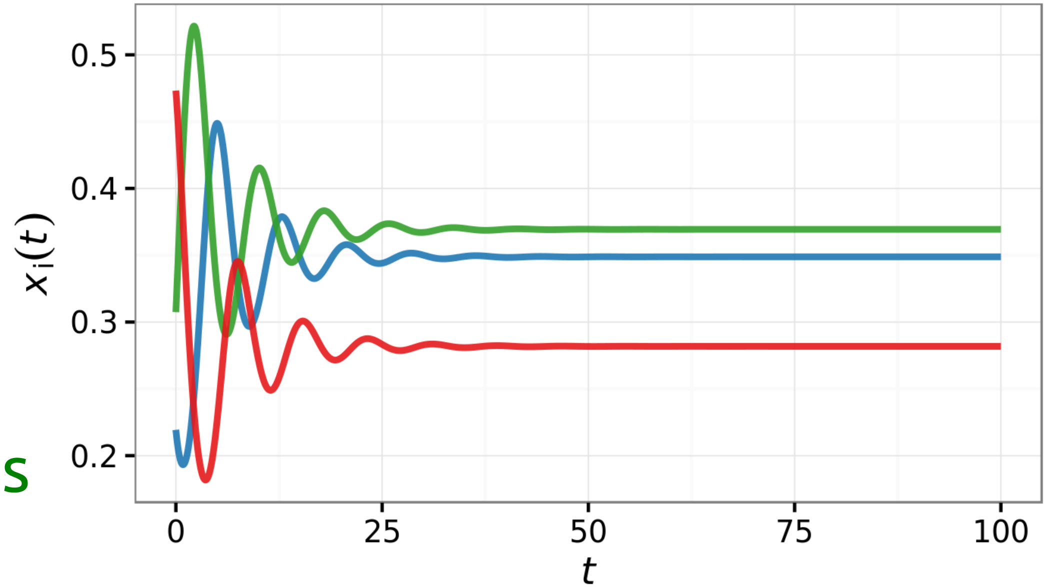


Summary of results for higher-order interactions

Arbitrary H_{ij} and equal physiological rates

Globally stable fixed point
[this work]

Random H_{ij}: on average half of the species coexist
[this work + Brandl, working paper 2015]

Arbitrary H_{ij} and arbitrary physiological rates

Fixed points still exist and they can be stable
[this work]

What we do not like about neutral theory

Sensitivity to the hypothesis of ecological equivalence

Stability is only neutral

No interactions

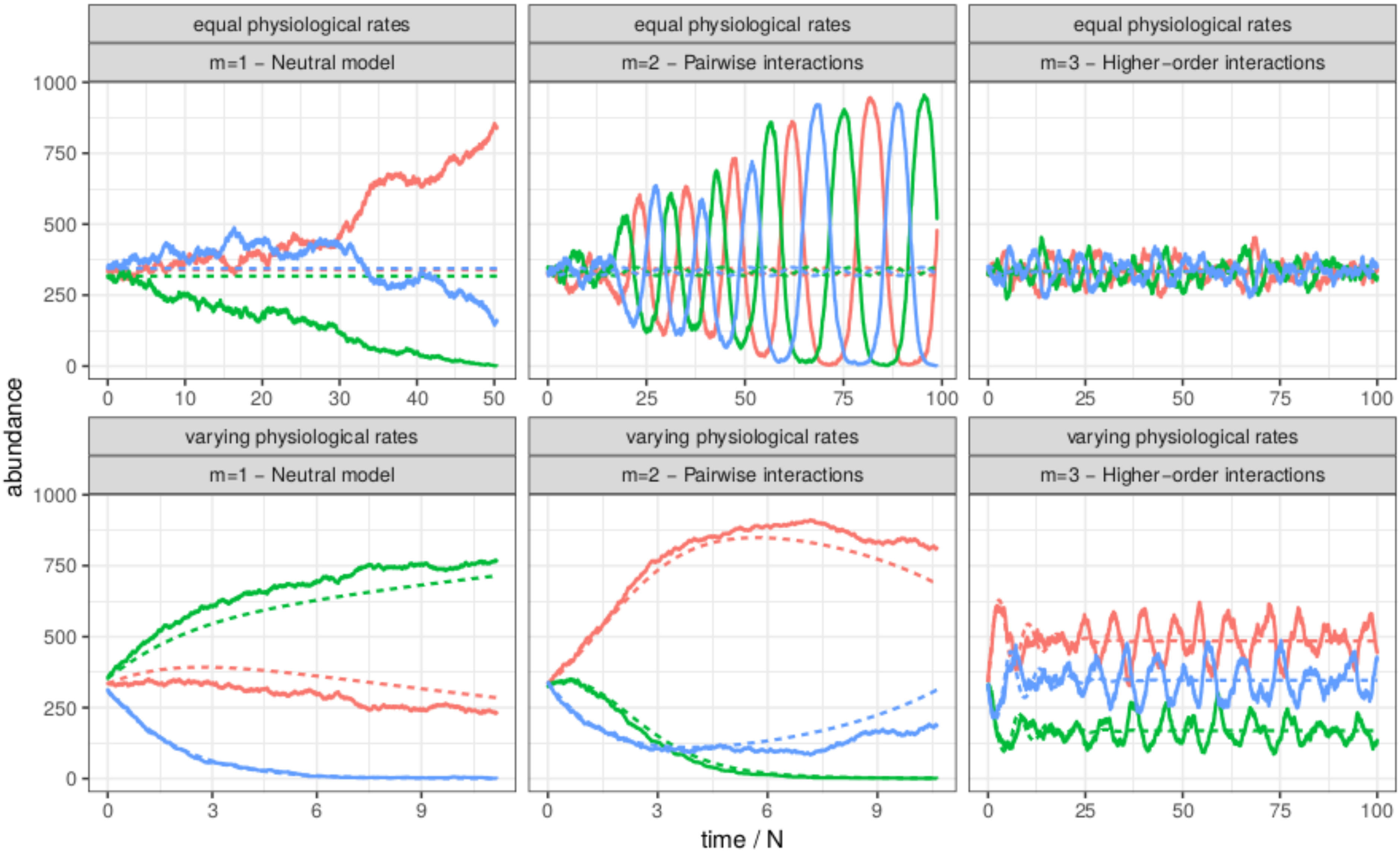
Strategy

1.
Closed systems (no migration/speciation)
Deterministic analysis

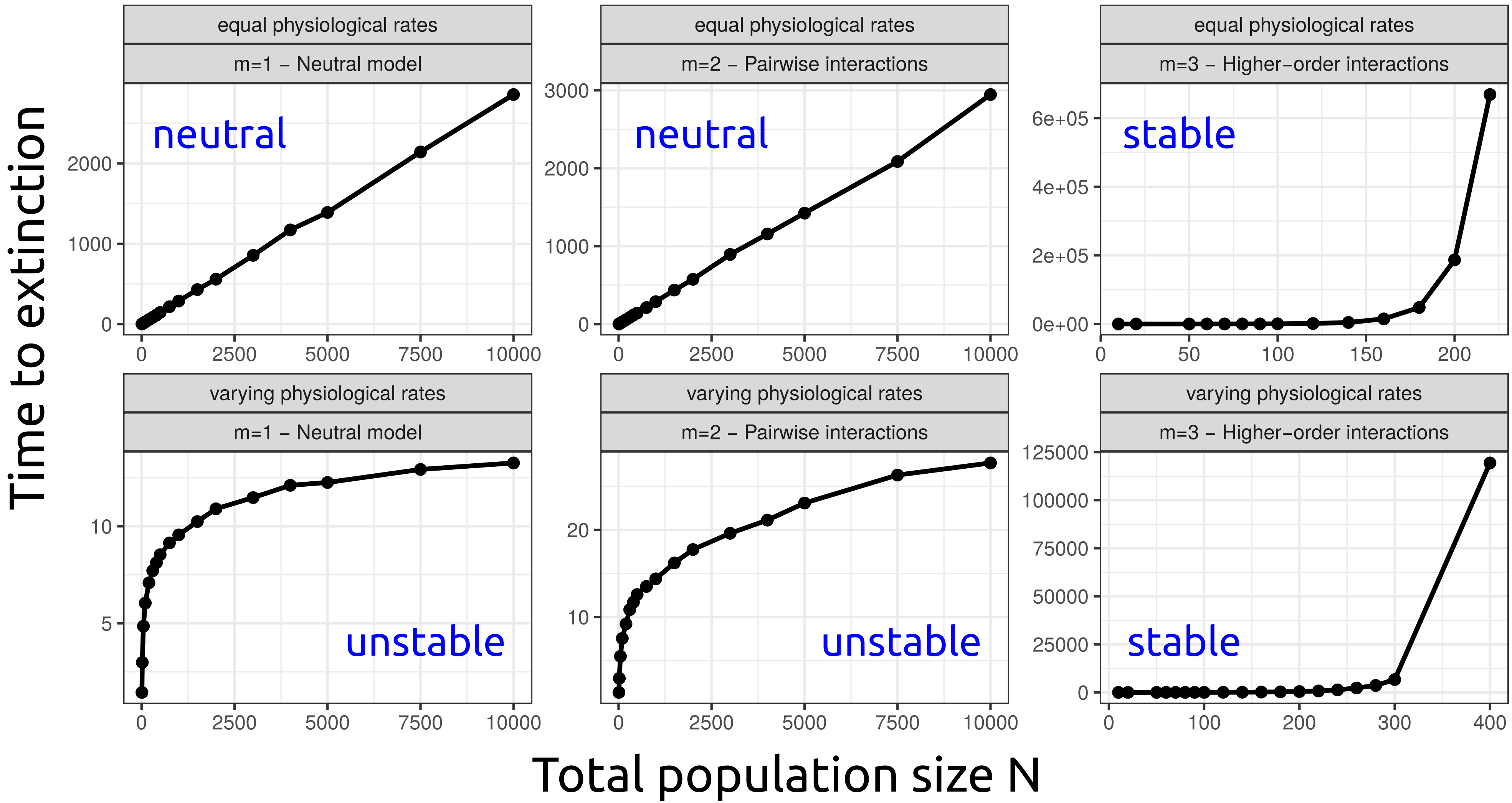
2.
Closed systems (no migration/speciation)
Effect of stochasticity

3.
Open systems (migration/speciation)
Compare to neutral theory prediction

Stochasticity does not change the message



Time to extinction depends on stability



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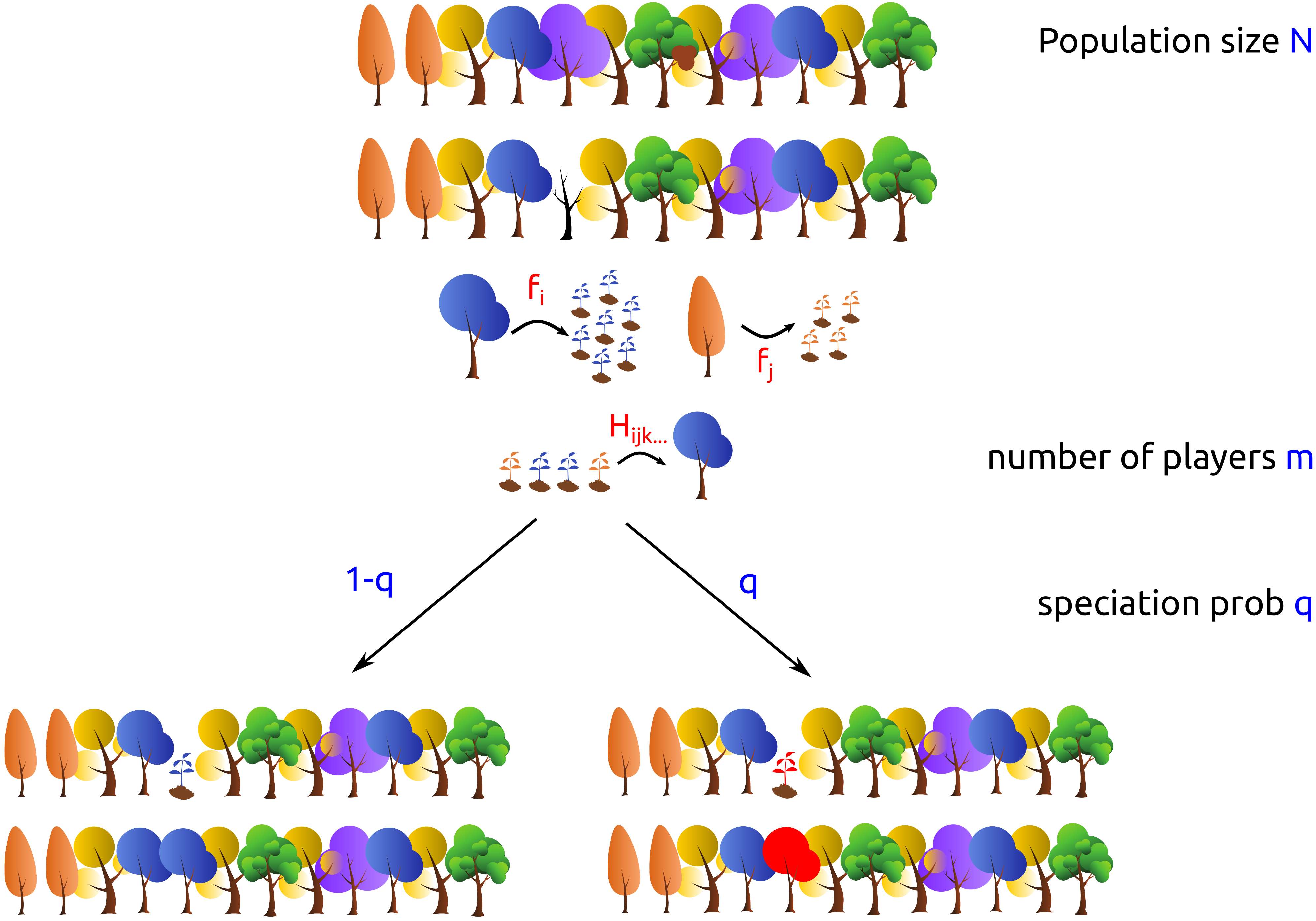
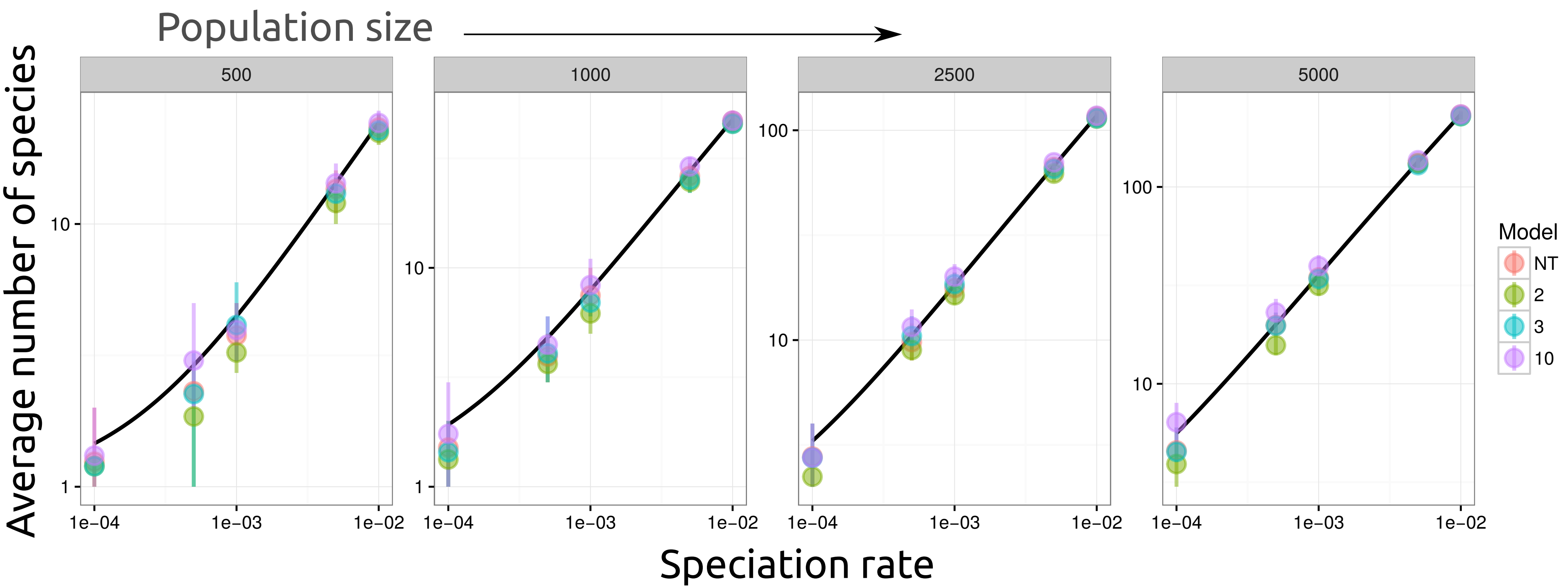


Population size N
f_i
f_j
$H_{ijk...}$
number of players m
1-q
q
speciation prob q

We recover neutral theory prediction on relative species abundances



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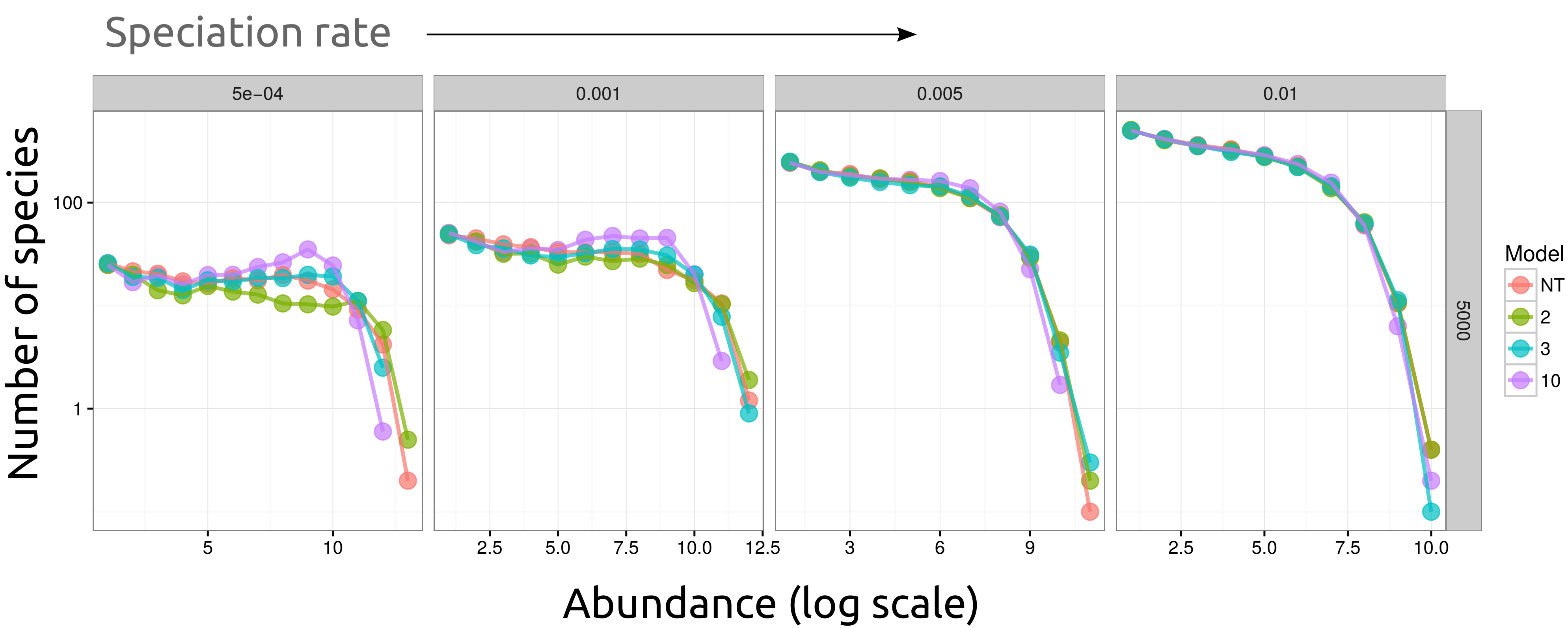
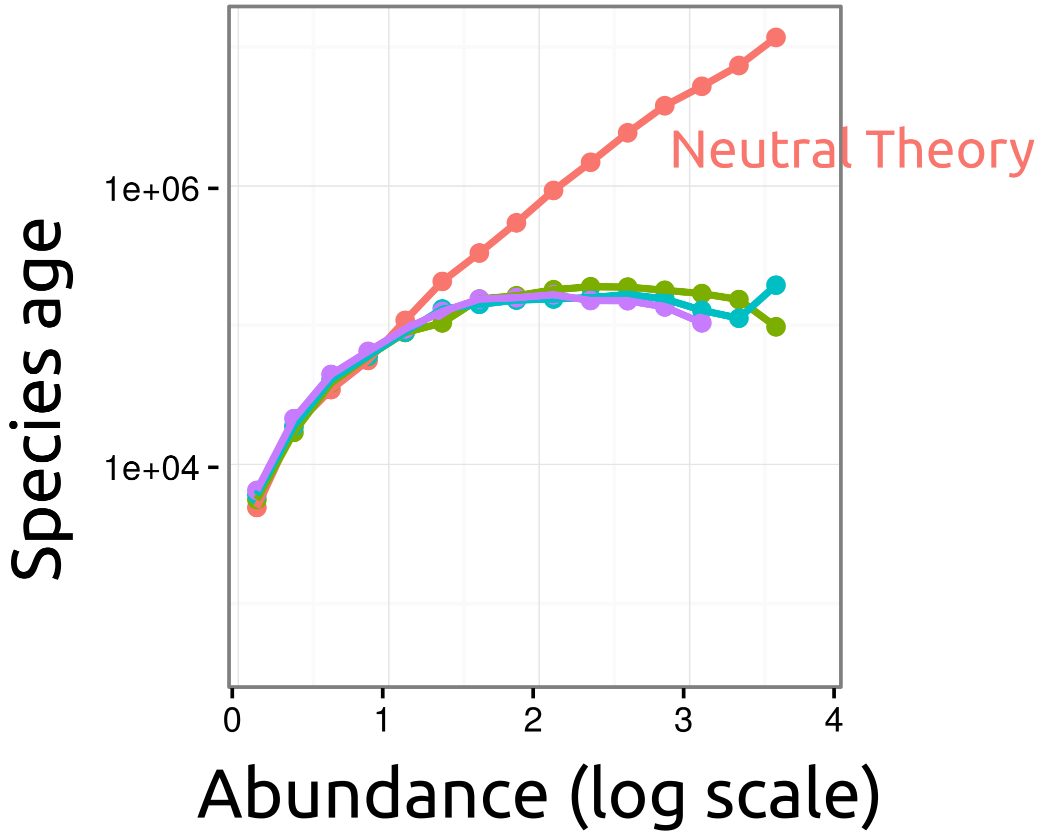


Better prediction on species ages



Three things I am confused about

#0 (the limiting factor)

Observables

What should we measure?

#1

Entropy vs Complexity

Is ecosystem complexity growing? Or not?

Is there a direction?

#2

Scales

[time, space, #individuals, diversity,...]

At what scales do we see ir(reversible) processes?

#3

Reversibility and reproducibility

Are reversible processes *less* reproducible?

Acknowledgments

Higher-order interactions

S. Allesina

M. Michalska-Smith

G. Barabás

Funding

HFSP

thank you!