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 maintained?
How is biodiversity generated?

Role of stochasticity

Role of interactions

How is biodiversity maintained?
Neutral theory explains statical patterns observed across ecosystems

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

[May, Will a large complex system be stable?, Nature 1972]
Biodiversity is not for free

Species interacting at random

Stability decreases as biodiversity and/or interaction strengths 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 $x$

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

[Kimura 1983]
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]

Amazon rainforest

Total number of trees: $N \sim 10^{11}$
Most abundant species tree: $x \sim 10^{-2}$
Generation time of trees: $\sim 30$ 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...]
What we do not like about neutral theory

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No interactions

Wrong species ages
What we do not like about neutral theory

Sensitivity to the hypothesis of ecological equivalence

Stability is only neutral

No interactions

Wrong species ages

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 $\sum_{i=1}^{\Sigma} x_i = 1$
zero-sum \[ \sum x_i = 1 \]

dead rate \[ d_i x_i \]
zero-sum

\[ \sum x_i = 1 \]

death

rate = \( d_i x_i \)

fertility

size of seed pool

\[ \sim f_i x_i \]
zero-sum

\[ \sum x_i = 1 \]

death

rate = \( d_i x_i \)

fertility

size of seed pool

\( \sim f_i x_i \)

competition

i wins with j: prob

\[ H_{ij} = 1 - H_{ji} \]
zero-sum

\[ \sum x_i = 1 \]

density

\[ \text{rate} = d_i x_i \]

fertility

size of seed pool

\[ \sim f_i x_i \]

competition

i wins with j: prob

\[ H_{ij} = 1 - H_{ji} \]

birth

i wins
zero-sum \[ \Sigma x_i = 1 \]

death \[ \text{rate} = d_i x_i \]

fertility \[ \text{size of seed pool} \sim f_i x_i \]

competition \[ i \text{ wins with } j: \text{ prob } H_{ij} = 1 - H_{ji} \]

birth \[ i \text{ wins} \]

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

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

Deterministic limit

$$\dot{x}_i = 2x_i \sum_j H_{ij} x_j - x_i$$
Hypertournaments
in the case of equal physiological rates $f_i=d_i=1$
and arbitrary $H_{ij}=1-H_{ji}$

Deterministic limit

$$\dot{x}_i = 2x_i \sum_j H_{ij} x_j - x_i$$
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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in the case of equal physiological rates $f_i=d_i=1$
and arbitrary $H_{ij}=1-H_{ji}$

Deterministic limit

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equivalent to the replicator equation

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

payoff of a symmetric game
Hypertournaments
in the case of equal physiological rates $f_i = d_i = 1$
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$$\dot{x}_i = x_i \sum_j (H_{ij} - H_{ji}) x_j = x_i \sum_j P_{ij} x_j$$

payoff of a symmetric game

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

in the case of equal physiological rates \( f_i = d_i = 1 \)

and arbitrary \( H_{ij} = 1 - H_{ji} \)

Deterministic limit

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

equivalent to the replicator equation

\[
\dot{x}_i = x_i \sum_j \left( H_{ij} - H_{ji} \right) x_j = x_i \sum_j \left( P_{ij} x_j \right)
\]

payoff of a symmetric game

\[
P = \begin{pmatrix}
0 & 1 & -1 & 1 & -1 \\
-1 & 0 & 1 & -1 & 1 \\
1 & -1 & 0 & 1 & -1 \\
-1 & 1 & -1 & 0 & 1 \\
1 & -1 & 1 & -1 & 0
\end{pmatrix} \\
H = \begin{pmatrix}
\frac{1}{2} & 1 & 0 & 1 & 0 \\
0 & \frac{1}{2} & 1 & 0 & 1 \\
1 & 0 & \frac{1}{2} & 1 & 0 \\
0 & 1 & 0 & \frac{1}{2} & 1 \\
1 & 0 & 1 & 0 & \frac{1}{2}
\end{pmatrix}
\]
Always neutral cycles
(if a fixed point exists)
This model generates high biodiversity

Starting with 50 species and random interaction $H$

$\sim$ binomially distributed (only odd number of species)

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

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in the case of equal physiological rates $f_i = d_i = 1$
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Full model
Arbitrary physiological rates $f_i, d_i$ and $H_{ij} = 1 - H_{ji}$
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

\[ \sum x_i = 1 \]

dead:

rate = \( d_i x_i \)

fertility:

size of seed pool \( \sim f_i x_i \)

competition:

i wins with j: prob \( H_{ij} = 1 - H_{ji} \)

birth:

i wins

new state:

\[ \sum x_i = 1 \]
zero-sum

death

fertility

size of seed pool

competition

birth

new state

Birth i wins

\[ \Sigma x_i = 1 \]

Death rate = \[ d_i x_i \]

\[ \Sigma x_i = 1 \]

Fertility size of seed pool

\[ \sim f_i x_i \]

\[ f_j \]

}\[ \text{competition} \]

i wins with j: prob

\[ H_{ij} = 1 - H_{ji} \]

\[ \Sigma x_i = 1 \]

\[ \Sigma x_i = 1 \]
competition

Higher-order interactions

H_{ij} = 1 - H_{ji}

i wins with j: prob

H_{ijk}
competition

i wins with j: prob \( H_{ij} = 1 - H_{ji} \)

Higher-order interactions

\( H_{ijk} \)

\( H_{ijklkm...z} \)
Higher-order interactions

- inhibts producing an antibiotics
- produces an enzyme that degrades the antibiotic

[Strongly debated:
  - their presence (common or rare?)
  - their inference/measure
  - their effect on community dynamics]

[Kelsic et al., Nature 2015]
A null parameterization of higher-order interactions
A null parameterization of higher-order interactions
A null parameterization of higher-order interactions
A null parameterization of higher-order interactions
A null parameterization of higher-order interactions
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} \frac{1}{2} & 1 & 0 \\ 0 & \frac{1}{2} & 1 \\ 1 & 0 & \frac{1}{2} \end{pmatrix}
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This parameterization makes sense

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

payoff of a symmetric game

\[
\begin{pmatrix}
0 & 1 & -1 \\
-1 & 0 & 1 \\
1 & -1 & 0
\end{pmatrix}
\]

\[
\begin{pmatrix}
\frac{1}{2} & 1 & 0 \\
0 & \frac{1}{2} & 1 \\
1 & 0 & \frac{1}{2}
\end{pmatrix}
\]

\[ \dot{x}_i = x_i \sum_{j,k} P_{ijk} x_j x_k \]
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

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\end{pmatrix}
\quad H = \begin{pmatrix}
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\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

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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 $H_{ij} = 1 - H_{ji}$
Neutral theory
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Full model
Arbitrary physiological rates $f_i$, $d_i$ and $H_{ij} = 1 - H_{ji}$
This model generates high biodiversity

Starting with 50 species and random interaction $H$

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
Always globally stable fixed point
(if a fixed point exists)

3 players

4 players

5 players
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 $H_{ij} = 1 - H_{ji}$
Stable coexistence is possible w/o fine-tuning

2 players
different physiological rates

3 players
different physiological rates
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

![Graphs showing the relationship between time to extinction and total population size N.](image_url)
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
Population size $N$

Number of players $m$

Speciation probability $q$

$1-q$ and $q$ probabilities.
We recover neutral theory prediction on relative species abundances

![Graph showing the relationship between population size and speciation rate, with average number of species on the y-axis and speciation rate on the x-axis. The graphs display data for population sizes of 500, 1000, 2500, and 5000, with the model NT2, 3, and 10 indicated for each population size.]
We recover neutral theory prediction on relative species abundances.
Better prediction on species ages

![Graph showing species age vs. abundance with a log scale, labeled "Neutral Theory".]
Three things I am confused about
#0 (the limiting factor)

Observables

What should we measure?
Entropy vs Complexity
Is ecosystem complexity growing? Or not?
Is there a direction?
Scales

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

At what scales do we see ir(reversible) processes?
Reversibility and reproducibility
Are reversible processes *less* reproducible?
Acknowledgments

Higher-order interactions
S. Allesina
M. Michalska-Smith
G. Barabás