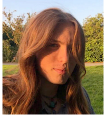
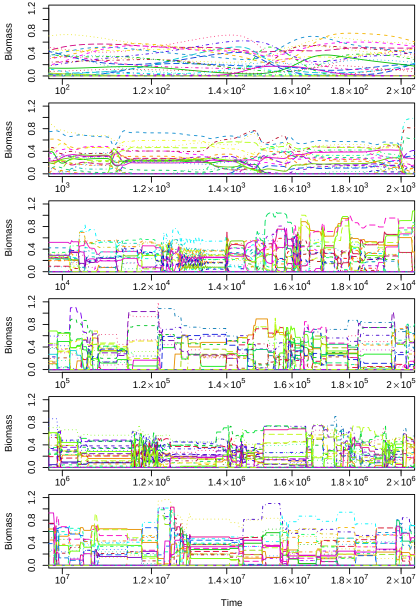
More Recent Evidence for Self-Organised Ecological Structural Instability in Nature


Axel G. Rossberg, Cillian Cockrell, Jacob D. O'Sullivan, etc.

Queen Mary University of London

Paris, 29 October 2024



Simulation of generic behaviour of random competitive LV models deeply inside the MA phase: heteroclinic networks (Hofbauer 1994, *Tatra Mountains Math. Publ.*).

$$\frac{dB_i}{dt} = \left[r_i - \sum_j^S A_{ij} B_j \right] B_i \qquad (1 \le i \le S)$$

$$S = 300$$

$$r_i = \mathcal{N}(1, 0.1)$$

$$A_{ij} = 0.5 \cdot \mathit{Bernoulli}(0.5) \quad (i \neq j)$$

$$A_{ii} = 1$$

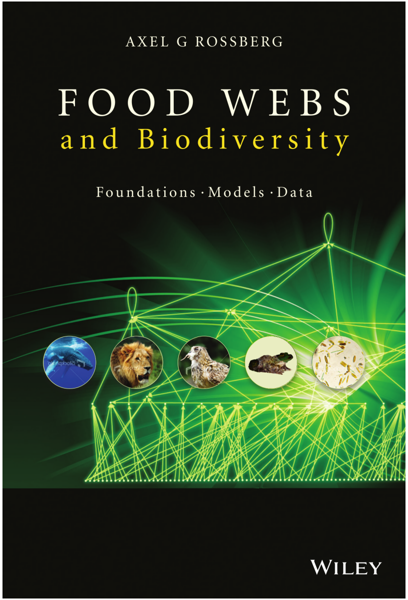
$$B_i = 0.001 \text{ at } t = 0$$

O'Sullivan, Terry, and Rossberg 2021, *Nat Commun*

First evidence that (ecological) structural instability controls natural community structure.

Wiley, 2013

PROSE award Biological Sciences 2013



Ecological Structural Instability

Consider the Lotka-Volterra competition model:

$$\frac{dB_j}{dt} = \left(1 - \sum_{k}^{S} G_{jk} B_k\right) B_j$$

G_{jk}: Competition (overlap) matrix
S: Species richness

- $G_{jj} = 1$
- G_{jk} = random i.i.d., mean μ, variance σ^2 ($j \neq k$).

What is the equilibrium distribution of biomasses B_j?

Ecological structural instability as amplification of indirect interactions

Equilibrium of population B_1:

$$\text{population growth rate} = 0 = 1 - \sum_k G_{jk} B_k \quad (1 \le j \le S)$$

For $j = 1$:

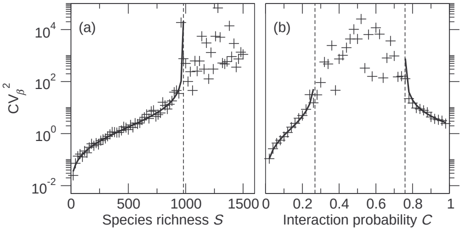
$$(1-\mu)^2 \operatorname{var} B_1 \approx S\sigma^2 \left[(\mathrm{E}B_{\text{other}})^2 + \operatorname{var} B_{\text{other}} \right]$$

$$(1-\mu)^2 \operatorname{var} B_1 \approx S\sigma^2 \left[(\mathrm{E}B_1)^2 + \operatorname{var} B_1 \right]$$

Solve for $\operatorname{var} B_1$:

$$\operatorname{var} B_1 = \ldots,$$

$$\mathrm{CV}_B^2 = \frac{S\sigma^2}{(1-\mu)^2 - S\sigma^2}.$$



Rossberg 2013, *Food Webs and Biodiversity*

→ Feedback amplification of $\operatorname{var} B_i$ through $S\sigma^2 \Longrightarrow$ singularity at $S = S_{\text{ESI}} = \frac{(1-\mu)^2}{\sigma^2}$!

History of self-consistency/mean-field/disordered-systems method

Diederich and Opper 1989, *Phys. Rev. A*	replicator model
Rieger 1989, *J. Phys. A: Math. Gen.*	various models
Tokita 2004, *Phys. Rev. Lett.*	replicator, various interaction patterns
Tokita 2006, *Ecol. Inform.*	symmetric replicator
Yoshino, Galla, and Tokita 2007, *J. Stat. Mech.*, Yoshino, Galla, and Tokita 2008, *Phys. Rev. E*	general replicator
Rossberg 2013, *Food Webs and Biodiversity*	LV assembly model, it's real!
Bunin 2017, *Phys. Rev. E*	general LV model
Tikhonov and Monasson 2017, *Phys. Rev. Lett.*	resource competition
Advani, Bunin, and Mehta 2018, *J. Stat. Mech.*	consumer-resource model
Dougoud et al. 2018, *PLoS Comput. Biol.*	strict proof
Pettersson, Savage, and Jacobi 2020, *Phys. Rev. E*	using von Neumann expansion

Assembly model!

The Lotka-Volterra competition model:

$$\frac{dB_j}{dt} = \left(1 - \sum_{k}^{S} G_{jk} B_k\right) B_j$$

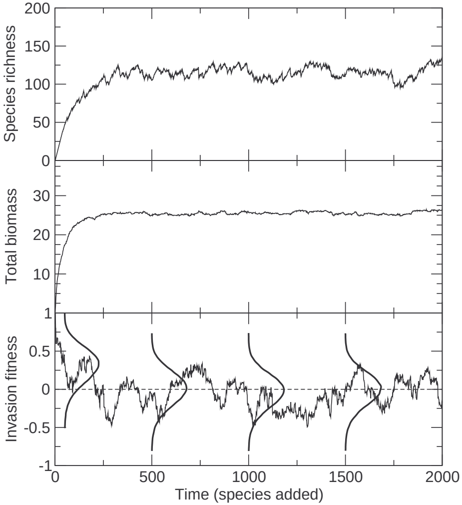
G_{jk}: *Competition (overlap) matrix*
S: *Species richness*

Here

- $G_{jj} = 1$
- $G_{jk} =$ random i.i.d., mean μ, variance σ^2 $(j \neq k)$.
- Add species one-by-one, simulate in between, remove those going extinct.

Gamarra et al. 2005, *Biological Invasions*

Community saturation in assembly models

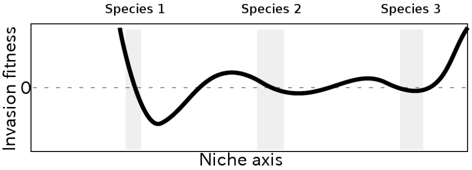


- Separate saturation of richness and biomass
- Community remains open to invasion
- Invasion fitness of ‘test species’ fluctuates

Solve this model?

Rossberg 2013, *Food Webs and Biodiversity*

Solving the model I (harvesting resistance)



From Metz et al. 1996, *Stochastic and Spatial Structures of Dynamical Systems* in *Stochastic and Spatial Structures of Dynamical Systems*

Harvesting resistance of a species:

$$h \stackrel{\text{def}}{=} -\left(\left. \frac{d \ln B(H)}{dH} \right|_{H=0} \right)^{-1}$$

where

H: Harvesting rate [1/Time]

$B(H)$: Equilibrium biomass of harvested species

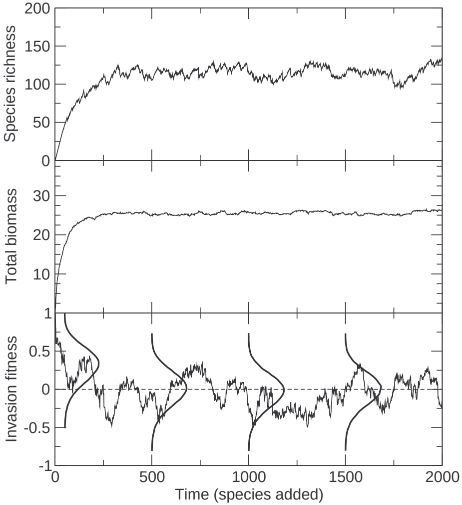
Important property:

$$(h \text{ after invasion}) \approx (\text{invasion fitness before invasion})$$

with '=' for Lotka-Volterra systems and close to extinction.

Furthermore, $h_j \approx \text{const.}\, B_j$ and $h_j \to 0$ at extinction.

Community saturation in assembly models



Now, consider interactions between:

- Fluctuations of invasion fitness
- Fluctuations of harvesting resistance
- Species turnover

Rossberg 2013, *Food Webs and Biodiversity*

Solving the model II (self-consistent assembly equilibrium)

Premises:

- Ecological community is in invasion-extinction quasi-equilibrium (Pawar 2009, *J. Theor. Biol.*) with S species on average.'
- Invasions and extinctions occur at rate 1 (defines time unit).
- As the community turns over, the invasion fitness r_i of a given potential invader i follows an Ornstein-Uhlenbeck process, i.e. a mean-reverting random walk, with identical parameters for all i.
- Harvesting resistance of residents j follows the same process, but with $h_j = r_i > 0$ at time of invasion, and extinction if $h_j = 0$.
- ~~Reversion rate of r_i is $1/S$.~~

Solve this self-consistency condition: the reversion rate (ρ) of r_i for potential invaders equals that of h_j for residents, while taking species turnover into account.

Some of the maths…

We now evaluate the relaxation rate of R_i using moment equations, denoting expectation values by brackets $\langle\cdot\rangle$. With our assumption of negligible correlations, suppressing the index i and abbreviating $Z = |\mathcal{A}|$, we can write $\langle R\rangle = \langle Z\rangle\langle y\rangle$, where the second factor is the expectation of y_i for a randomly chosen extant species. According to above considerations, $\langle R\rangle$ value changes over a small time interval $\delta T \geq 0$ to:

$$\begin{aligned}&\langle R(T+\delta T)\rangle \\ &\quad= \left\langle \sum_{j\in\mathcal{A}} y_j - \delta T \rho\big(y_j - \overline{y}\big) + \delta T C y^{\text{inv}} \right\rangle \qquad (9)\\ &\quad= \langle Z\rangle\langle y\rangle + \left[-\rho\langle Z\rangle(\langle y\rangle - \overline{y}) + C y^{\text{inv}}\right]\delta T,\end{aligned}$$

where y^{inv} denotes the mean associated with $P^{\text{inv}}(y)$. The sum above is over the extant species at time T. Extinctions of species can be disregarded at lowest order, because shortly before extinction their contribution to R is small. In the steady state the time-dependent term in Eq. (9) vanishes:

$$-\rho(\langle y\rangle - \overline{y})\langle Z\rangle + C y^{\text{inv}} = 0. \qquad (10)$$

Making use of Eq. (10), we similarly derive in Appendix the second moment

$$\begin{aligned}&\langle R(T)R(T+\delta T)\rangle = \\ &\quad \langle Z\rangle^2 \langle y\rangle^2 + \langle Z\rangle \langle y^2\rangle + \langle Z\rangle\, \rho\left(\langle y\rangle\overline{y} - \langle y^2\rangle\right)\delta T \qquad (11)\end{aligned}$$

Derivation of Eq. 11

We derive Eq. (11), making first use of Eq. (10) and then of the fact that $\operatorname{var} Z = \langle Z^2\rangle - \langle Z\rangle^2 = \langle Z\rangle$ on account of the Poisson distribution of Z:

$$\begin{aligned}
&\langle R(T)R(T+\delta T)\rangle \\
&= \left\langle \sum_{j,l\in\mathcal{A}} y_j(T) y_l(T+\delta T) + \sum_{j\in\mathcal{A}} y_j C y^{\text{inv}} \delta T \right\rangle \\
&= \left\langle \sum_{j,l\in\mathcal{A}} y_j \left[y_l - \rho(y_l - \overline{y})\delta T\right] \right\rangle + \langle y\rangle\langle Z\rangle C y^{\text{inv}}\delta T \\
&= \left\langle \sum_{\substack{j,l\in\mathcal{A}\\ j\neq l}} y_j \left[y_l - \rho(y_l - \overline{y})\delta T\right] \right\rangle \\
&\quad + \left\langle \sum_{j\in\mathcal{A}} y_j \left[y_j - \rho(y_j - \overline{y})\delta T\right] \right\rangle \\
&\quad + \langle y\rangle\langle Z\rangle C y^{\text{inv}}\delta T \\
&= \langle Z(Z-1)\rangle \left[\langle y\rangle^2 - \rho\left(\langle y\rangle^2 - \langle y\rangle\overline{y}\right)\delta T\right] \\
&\quad + \langle Z\rangle \left[\langle y^2\rangle - \rho\left(\langle y^2\rangle - \langle y\rangle\overline{y}\right)\delta T\right] \\
&\quad + \langle y\rangle\langle Z\rangle\rho(\langle y\rangle - \overline{y})\langle Z\rangle\delta T \\
&= \langle Z\rangle^2 \langle y\rangle^2 + \langle Z\rangle \langle y^2\rangle \\
&\quad + (\langle Z\rangle^2 - \langle Z^2\rangle)\rho\left(\langle y\rangle^2 - \langle y\rangle\overline{y}\right)\delta T \\
&\quad + \langle Z\rangle\,\rho\left(\langle y\rangle^2 - \langle y^2\rangle\right)\delta T \\
&= \langle Z\rangle^2 \langle y\rangle^2 + \langle Z\rangle \langle y^2\rangle \\
&\quad - \langle Z\rangle\,\rho\left(\langle y\rangle^2 - \langle y\rangle\overline{y}\right)\delta T \\
&\quad + \langle Z\rangle\,\rho\left(\langle y\rangle^2 - \langle y^2\rangle\right)\delta T \\
&= \langle Z\rangle^2 \langle y\rangle^2 + \langle Z\rangle \langle y^2\rangle \\
&\quad + \langle Z\rangle\,\rho\left(\langle y\rangle\overline{y} - \langle y^2\rangle\right)\delta T.
\end{aligned}$$

Combining the moment equations, we first evaluate

$$\operatorname{var} R = \langle R^2\rangle - \langle R\rangle^2 = \langle Z\rangle\langle y^2\rangle. \qquad (12)$$

Then we calculate the short-term autocorrelation function

$$\operatorname{cor}\left[R(T), R(T+\delta T)\right] = \frac{\operatorname{cov}\left[R(T), R(T+\delta T)\right]}{\operatorname{var} R} \qquad (13)$$

and from this, considering that for an Ornstein Uhlenbeck process $\operatorname{cor}[R(T), R(T+\delta T)] = \exp(-\tilde{\rho}|\delta T|)$, the relaxation rate of R as:

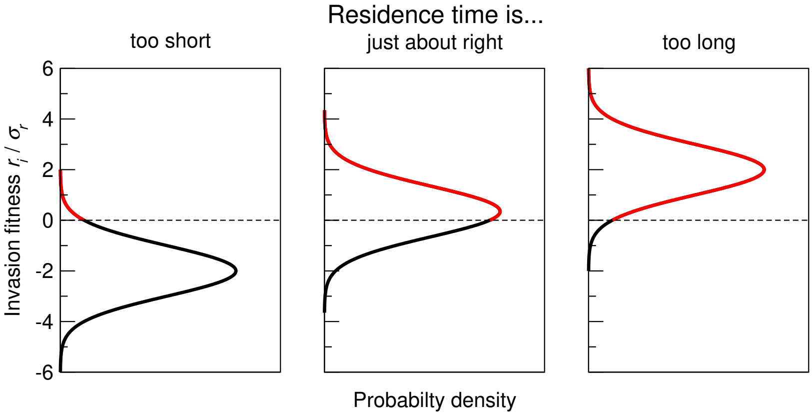
$$\begin{aligned}\tilde{\rho} &= -\lim_{\delta T\to 0^+} \frac{\mathrm{d}\operatorname{cor}\left[R(T), R(T+\delta T)\right]}{\mathrm{d}\delta T} \\ &= -\frac{\langle Z\rangle\,\rho\left(\langle y\rangle\overline{y} - \langle y^2\rangle\right)}{\langle Z\rangle\langle y^2\rangle} = -\frac{\rho\left(\langle y\rangle\overline{y} - \langle y^2\rangle\right)}{\langle y^2\rangle}. \qquad (14)\end{aligned}$$

Equating $\tilde{\rho}$ and ρ in Eq. (14) yields our self-consistency condition. It simplifies to

$$\overline{y} = 0, \quad \text{and so} \quad p_{\text{inv}} = \Phi(\overline{y}) = \frac{1}{2}, \qquad (15)$$

Cockrell, C., *et al.* (2024). Physical Review Research, 6(1), 013093.

Invasion probability (intuition)



- Previously: $\overline{r}/\sigma_r \approx 0.347$, invasion probability is 0.635.

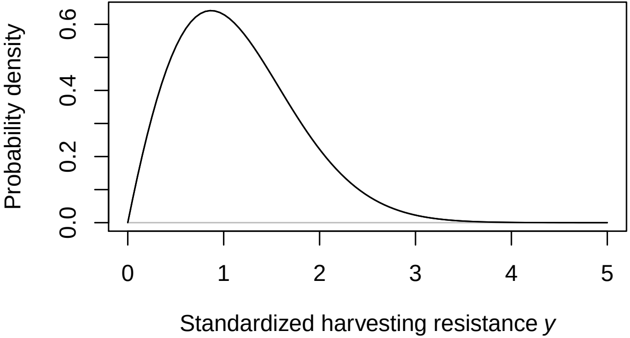
  Rossberg 2013, *Food Webs and Biodiversity*

- New: $\overline{r} = 0$, invasion probability is $1/2$.

  Cockrell et al. 2024, *Phys. Rev. Res.*

Solving the model III (distribution of scaled harvesting resistance)

$$0 = -\overbrace{\rho \frac{d[(0-y)P(y)]}{dy}}^{\text{mean reversion}} + \overbrace{\rho \frac{d^2 P(y)}{dy^2}}^{\text{diffusion}} + \overbrace{\sqrt{\frac{2}{\pi}} \exp\left(-\frac{y^2}{2}\right)}^{\text{invasions}}.$$



Solving the model IV (self-consistent community response)

To get S and the reversion rate, match parameters of Ornstein-Uhlenbeck process with elementary description of community-response to invasion. (Rossberg 2013, *Food Webs and Biodiversity*)

Compute the resident's response ΔB_k to an invader with biomass B_{inv} and interaction strengths γ_j from:

$$0 = \gamma_j B_{\text{inv}} + \sum_k G_{jk} \Delta B_k \quad (1 \le j \le S).$$

Problem is very similar to finding the equilibrium:

$$0 = 1 - \sum_k G_{jk} B_k \quad (1 \le j \le S).$$

This is where ESI enters the calculation. Negative ΔB_k are natural!

Analytic solution of species-rich LV assembly model

Let as above

$$\mu = \text{mean interspecific interaction},$$
$$\sigma^2 = \text{variance of interspecific interactions.}$$

In our model the singularity of Ecological Structural Instability occurs at richness

$$S_{\mathrm{ESI}} \stackrel{\text{def}}{=} \frac{(1-\mu)^2}{\sigma^2}.$$

Then, with

$$\langle y \rangle = 2^{1/2}\pi^{-1/2}\ln(2)^{-1} = 1.1511$$

and

$$\langle y^2 \rangle = 1 + \ln(4)^{-1} = 1.7213,$$

in the saturated LV assembly model,
species richness is

$$\langle S \rangle = \frac{S_{\mathrm{ESI}}}{\langle y^2 \rangle} \approx 0.58 S_{\mathrm{ESI}},$$

standard deviation of invasion fitness

$$\mathrm{SD}_r = \frac{\langle y^2 \rangle}{\langle y \rangle} \cdot \frac{\sigma^2}{\mu(1-\mu)},$$

and **relaxation rate** of a species' invasion fitness

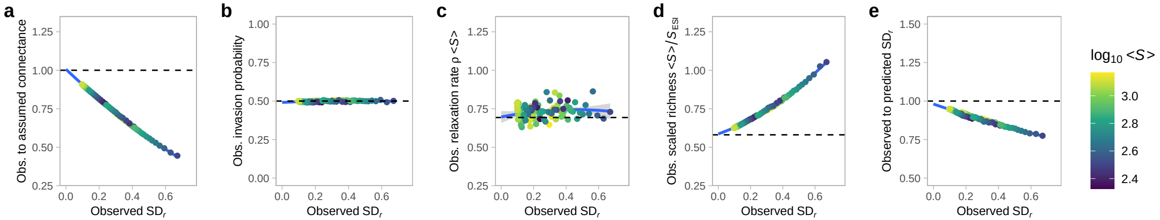
$$\rho = \frac{\ln 2}{\langle S \rangle} \text{ invasions.}$$

Invasion probability is $1/2$.

Cockrell et al. 2024, *Phys. Rev. Res.*

Numerical test of analytic solution

— — ——: universal analytic results Coloured: simulations



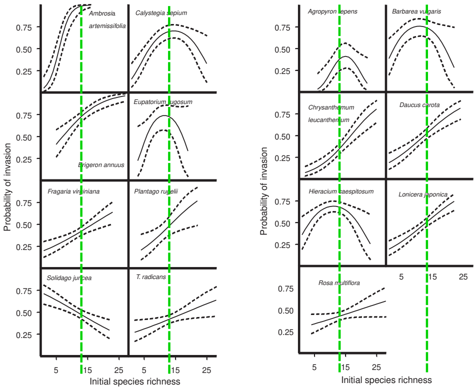
⟵ Limit of large and complex communities

Cockrell et al. 2024, *Phys. Rev. Res.*

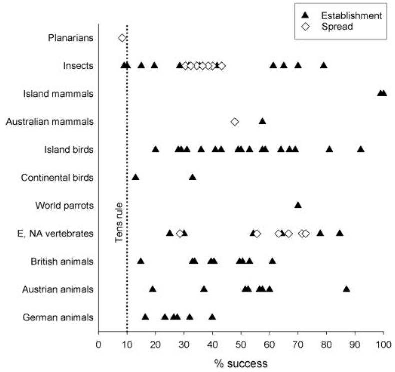
Empirical support for model predictions

Empirical invasion probabilities (1)

Plants in old fields



Europe & N.-America



"*Successional communities are model systems for the regulation of community invasibility because they are characterized by continuous species invasions, [...] While the proportion of exotic species has decreased over time, and field scale richness increased, species richness per plot has remained near 13 species per plot [...].*" (Meiners, Cadenasso, and Pickett 2004, *Ecol. Lett.*)

"*...we extract a median of* 51% *and an average of* 56 ± 5%" (Cockrell et al. 2024, *Phys. Rev. Res.*)

"*Mean establishment success [was]* 59.6 ± 11.6% *for introductions from Europe to North America and* 52.4 ± 11.9% *for the opposite direction* [...]"
meta-analysis by Jeschke and Strayer 2005, *PNAS*

Empirical invasion probabilities (2)

Hawaiian non-native birds

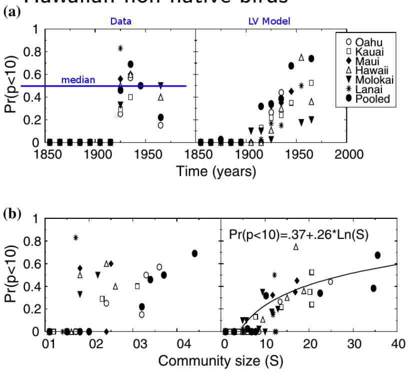
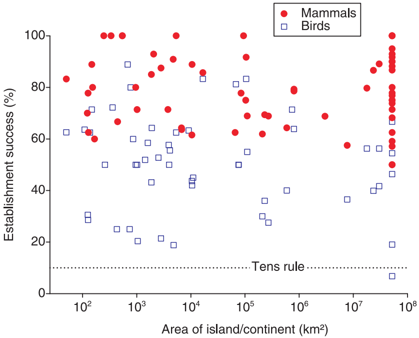


Figure 4. Species-specific probabilities of persisting less than 10 years in the islands as a function of (a) time, and (b) community size. Left: original field data. Right: LVM simulations. Observe the presence of marked thresholds in both analysis and the asymptotic behavior of these probabilities in islands with higher number of species.

(Gamarra et al. 2005, *Biological Invasions*)

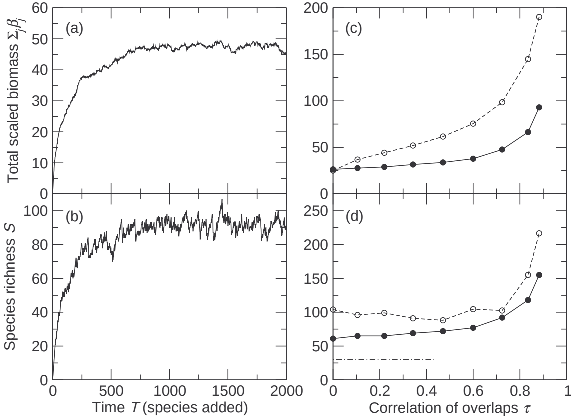
Mammals and Birds



"Establishment success was generally higher for mammals ($79 \pm 1.7\%$, mean $\pm$ standard error (SE), $n = 65$) than for birds ($50 \pm 2.6\%$, $n = 53$) [...]"

(Jeschke 2008, *Divers. Distrib.*)

Extension to partially symmetric interactions remains incomplete:

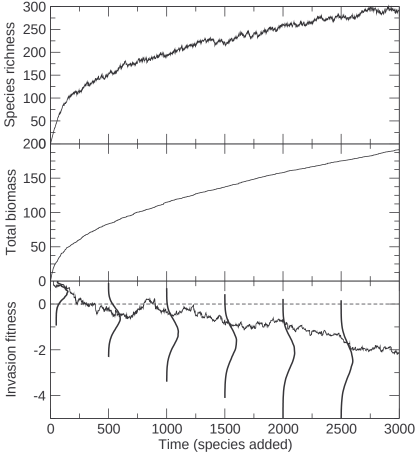


○: Analytic upper bounds

●: Numerical result

Increasing "competition avoidance" with increasing symmetry.

Singularity for perfect symmetry:



Rossberg 2013, *Food Webs and Biodiversity*

Dimensionless constants of nature in Physics:

For example the *dimensionless magnetic moment* of the electron:

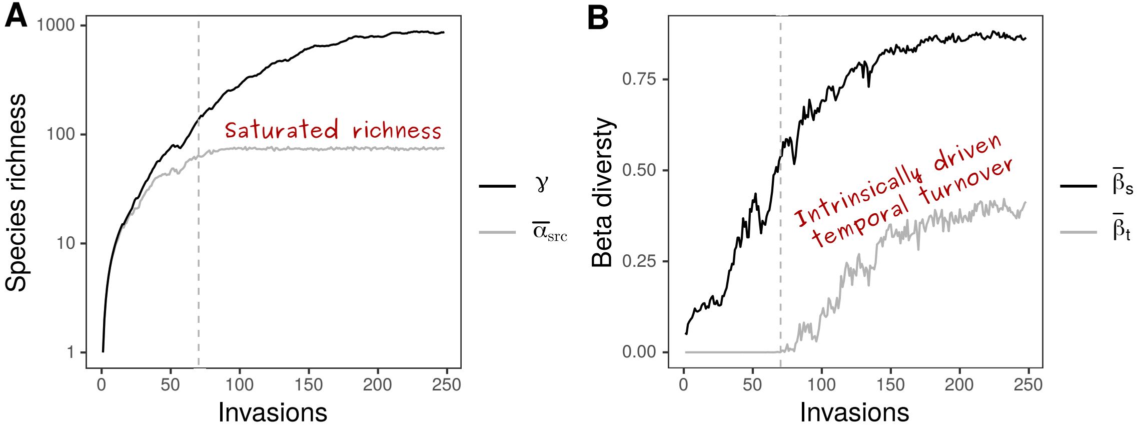
$g_\mathrm{e} = 2$	(1928, experiment)
$g_\mathrm{e} = 2$	(1928, theory: Dirac equation)
$g_\mathrm{e} = 2.00236$	(1948, experiment)
$g_\mathrm{e} = 2.00232$	(1948, theory: quantum electrodynamics)
$g_\mathrm{e} = 2.0023318416(13)$	(2006, experiment)
$g_\mathrm{e} = 2.0023318361(10)$	(2007, theory: standard model)

$\rightarrow$ New physics?

Ecological Structural Instability in Metacommunities

Species turnover caused by ecological structural instability

Simulations of Lotka-Volterra metacommunity model



O'Sullivan, Terry, and Rossberg 2021, *Nat Commun*

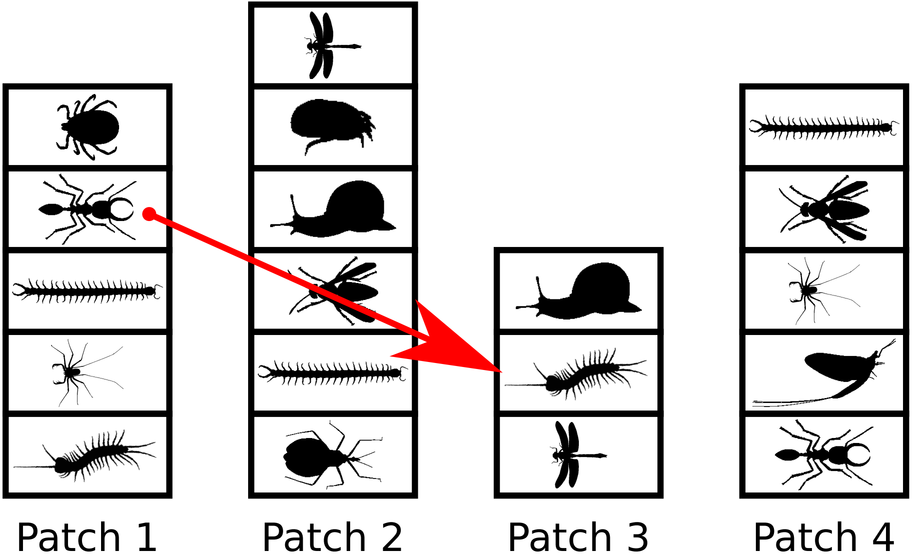
Assemblage Time Series Reveal Biodiversity Change but Not Systematic Loss

Maria Dornelas,[1*] Nicholas J. Gotelli,[2] Brian McGill,[3] Hideyasu Shimadzu,[1,4] Faye Moyes,[1] Caya Sievers,[1] Anne E. Magurran[1]

Dornelas et al. 2014, *Science*

The
Locally Saturated Patch Occupancy Model

The LSPOM (Locally Saturated Patch Occupancy Model)



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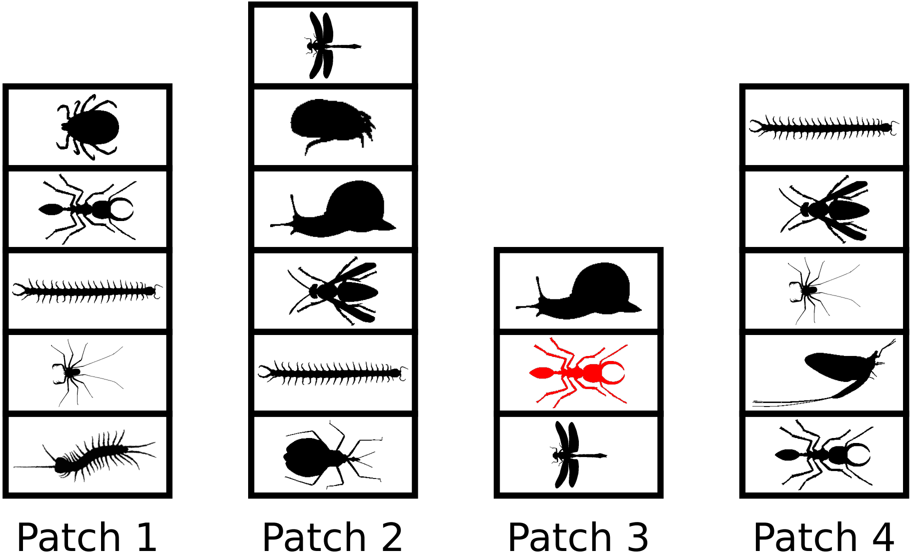

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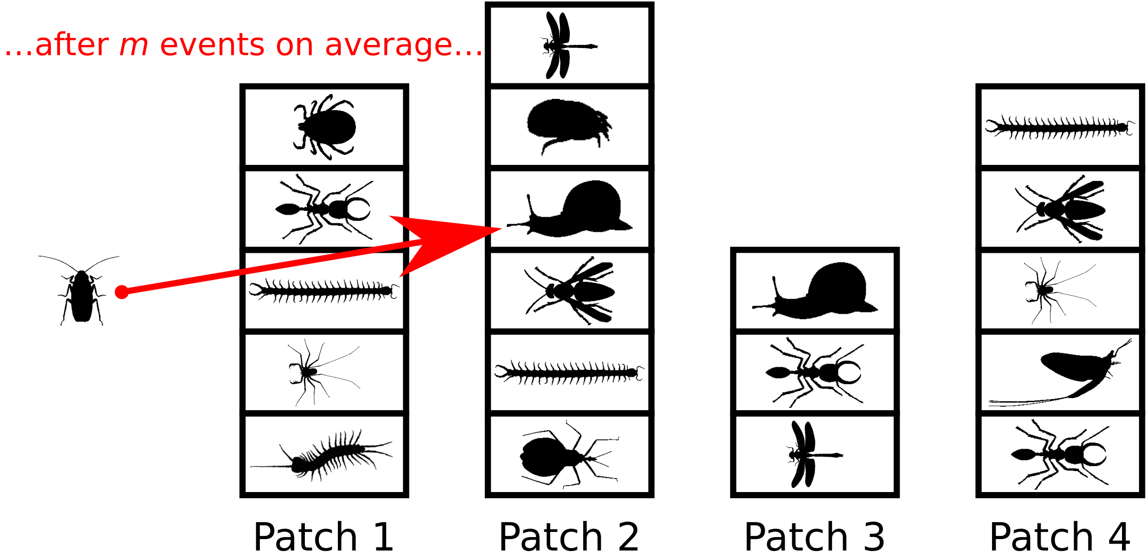

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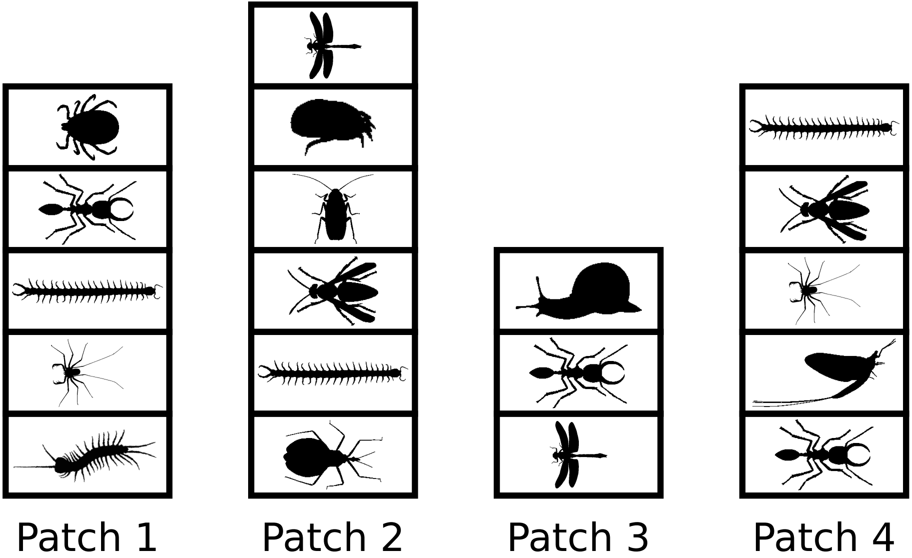

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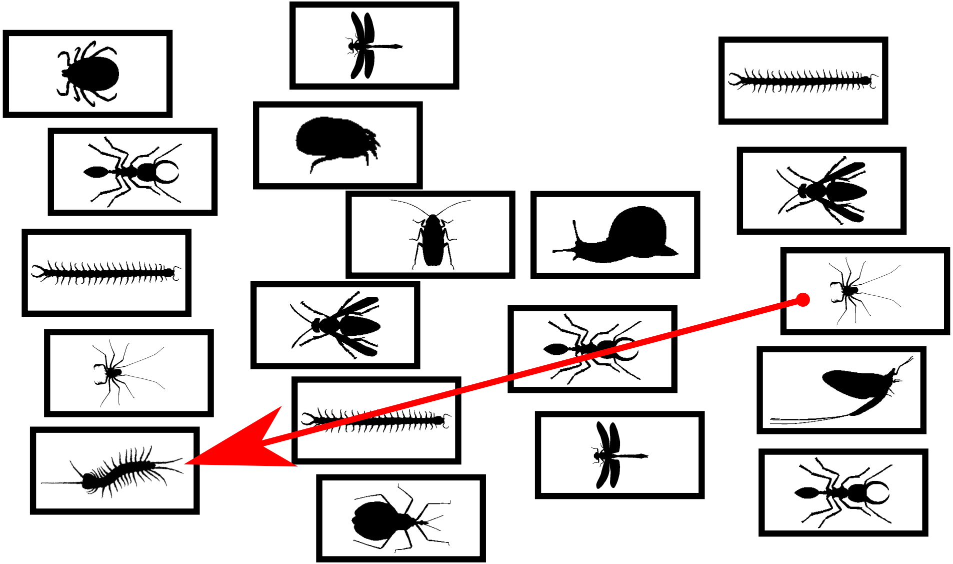


Macroecology: Occupancy Frequency Distributions

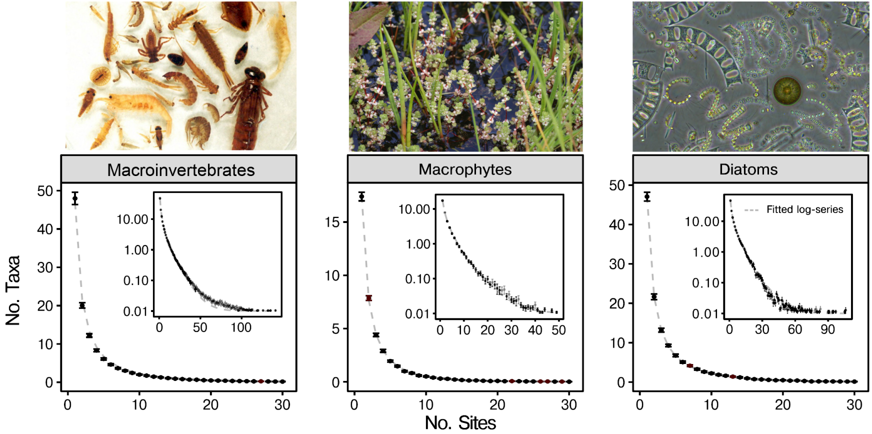
Log-series OFD:

$$(\text{number of taxa occupying } n \text{ sites}) \propto \frac{1}{n}\left(\frac{m}{m+1}\right)^n$$

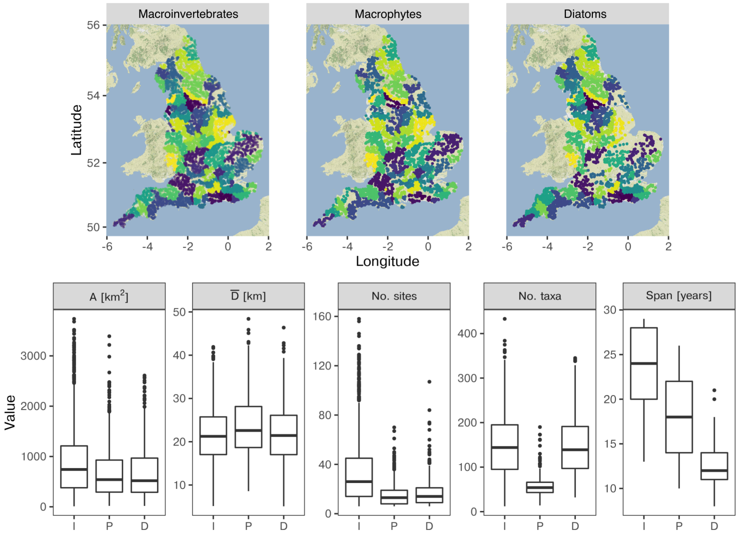
n: number of sites

m: mean number of colonisations per invasion

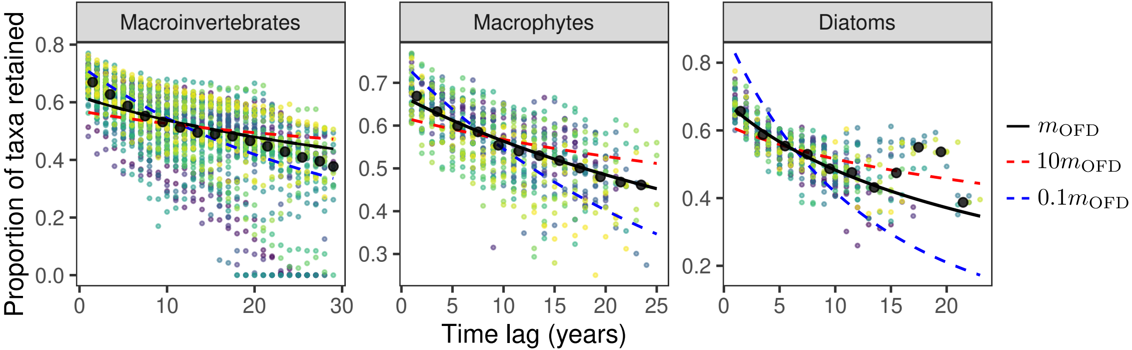
O'Sullivan, Terry, and Rossberg 2023, *Glob. Ecol. Biogeogr.*



Environmental Agency river surveys (Biosys)



Predicting Metacommunity-scale Turnover



Not bad!

O'Sullivan, Terry, and Rossberg 2023, *Glob. Ecol. Biogeogr.*
Pigolotti et al. 2005, Proc. Natl. Acad. Sci.

Take home messages

- The *asymmetric random Lotka-Volterra competition assembly model* and
- the *Locally Saturated Patch Occupancy Model (LSPOM)*

have both been solved analytically (in some limit). Their behaviour is well understood.

- Both models predicate empirically observed macroecological phenomena to high numerical accuracy.
- Both models invoke self-organised ESI.
- This adds to already strong empirical evidence for self-organised ESI from previous studies (Paris 2019).

→ Self-organised ESI is *the* mechanisms controlling complexity and stability of real-world ecological networks.

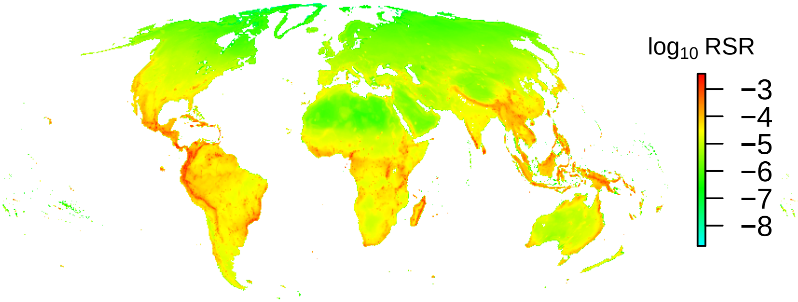
→ The fundamental principles governing 'complexity' and 'stability' of real-world ecological networks are understood. Let's take it from there!

---

1. Which structure in interaction matrices matters, and for what? What are appropriate "guilds" of species? (Barbier et al. 2018, *PNAS*)
2. How close is Nature to the UFP/MA transition?
3. Community assembly with environmental filtering and variability $[dB_j/dt = (s_j - \sum_k^S G_{jk} B_k) B_j]$.
4. Spatio-temporally explicit variants of LSPOM.
5. Species re-supply by allopatric speciation in long-separate lineages.
6. Spatially continuous models (maths of neutral theory?). Predict, e.g., global range-size rarity $(\mathrm{RSR}_j = \sum_{i \text{ at patch } j} |\text{patches occupied by } i|^{-1})$.

Range Size Rarity

Explain This!



Data: `https://www.iucnredlist.org/resources/other-spatial-downloads`

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