Hurray! - Ecological structural instability is everywhere

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What is ecological structural instability?

Definition: *Ecological structural instability* is a sensitivity of ecological communities to press perturbations that is so large that this easily leads to extinctions.

Bastolla et al. 2009, *Nature*
Rossberg 2013, *Food Webs and Biodiversity*
O'Sullivan, Knell, and Rossberg 2019, *Ecol. Lett.*

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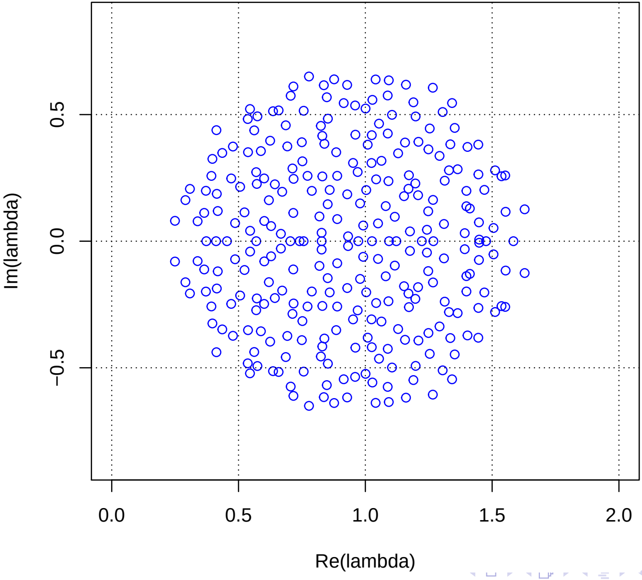
Formal operationalisation: An LV competition model of the form

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

is ecologically structurally unstable when the interaction matrix **G** has eigenvalues close to zero.

Rossberg 2013, *Food Webs and Biodiversity*

How close?

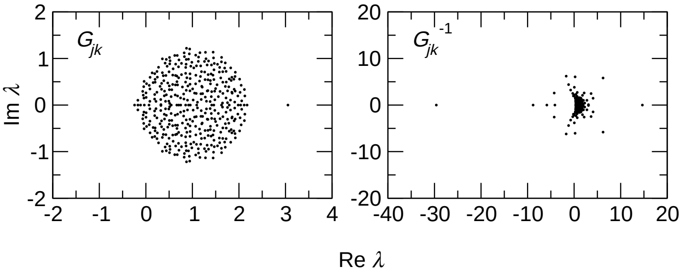


Structural instability through ill-conditioned competition

Prediction of equilibria:

$$\frac{dB_j}{dt} = 0 = \left(r_j - \sum_k^S G_{jk} B_k \right) B_j \quad \Longrightarrow \quad B_k = \sum_j^S G_{kj}^{-1} r_j .$$

$$\mathbf{G} \leftrightarrow \mathbf{G}^{-1} \quad \Longleftrightarrow \quad \lambda \leftrightarrow \lambda^{-1}$$



Ecological structural instability is what engineers call “ill conditioned”.

A simple model

The Lotka-Volterra competition model:

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

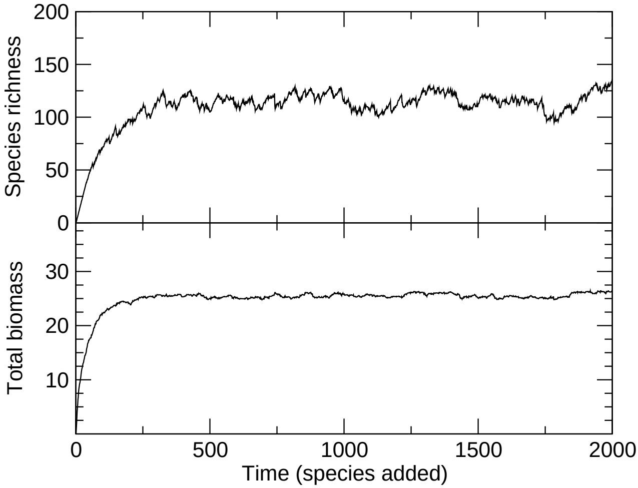
G_{jk}: Competition (overlap) matrix
S: Species richness

Here

- Add species one-by-one, remove those going extinct.
- $G_{jj} = 1$
- $G_{jk} = \begin{cases} 0.2 & \text{with probability } 0.2, \\ 0 & \text{otherwise} \end{cases} \qquad (j \neq k).$

Gamarra et al. 2005, *Biological Invasions*

Community saturation



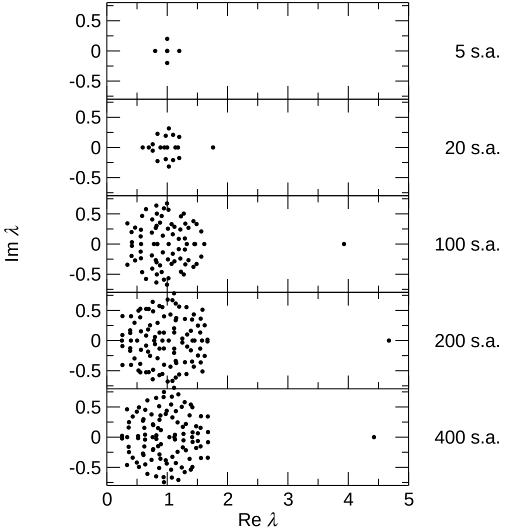
- Community saturation
- Ongoing invasions & extinctions

("stochastic species packing")

Rossberg 2013, *Food Webs and Biodiversity*

The spectrum of G

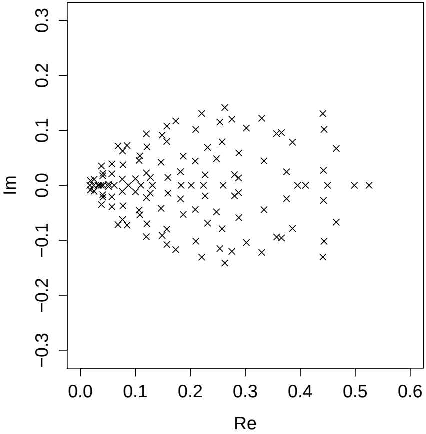
Spectra of G_{ij} during assembly.



- Expansion of distribution...
- ... but stops when approaching zero.

Rossberg 2013, *Food Webs and Biodiversity*

Community matrix of simple assembly model



Spectrum of $-\mathbf{J} = \color{red}{\mathbf{B}} \circ \mathbf{G}$.

See also Stone 2018, *Sci. Rep.*

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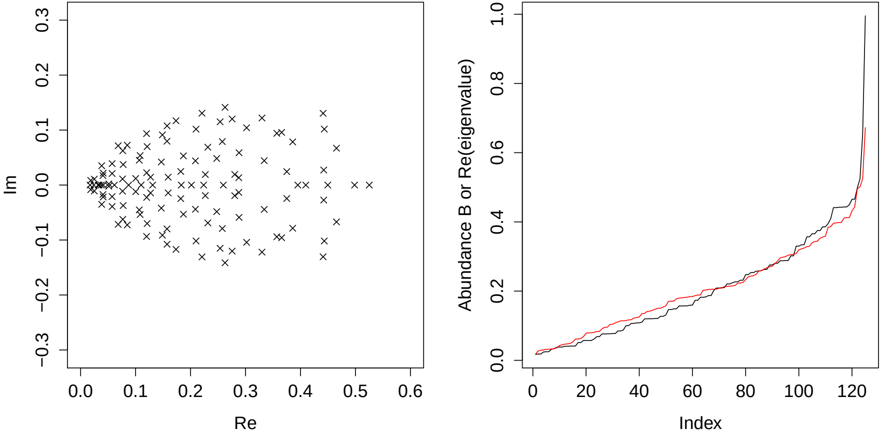

Spectrum of $-\mathbf{J} = \mathbf{B} \circ \mathbf{G}$, in relation to entries of $\mathbf{B}$.

See also Stone 2018, *Sci. Rep.*

Differences between random-matrix stability- and competition theory

	Stability theory	Competition theory
	May 1972	Rossberg 2013
Problem:	linear stability	structural stability
Relevant matrix:	Jacobian (community matrix)	competitive overlaps
Criterion on eigenvalues:	positive real parts	values near zero
1s on diagonal by:	assumption (dodgy)	construction
Interactions:	mostly feeding	competition
Food-web sparseness:	troublesome	essential fact
Verifiable prediction:	bounded link density	structural instability bounded richness ratio
Prediction holds:	not in simulations	yes
Related bifurcation:	bif-*what*?	transcritical

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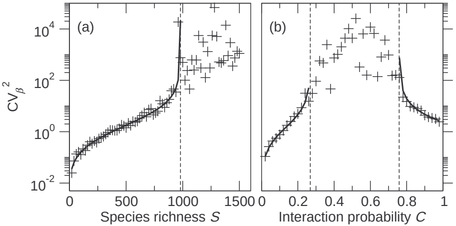
Solve for $\operatorname{var} B_1$:

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

$$\mathrm{CV}_B^2 = \frac{S \operatorname{var} G_{12}}{(1 - \mathrm{E}G_{12})^2 - S \operatorname{var} G_{12}}.$$

Rossberg 2013, *Food Webs and Biodiversity*



(see also Jansen and Kokkoris 2003, *Ecol. Lett.*)

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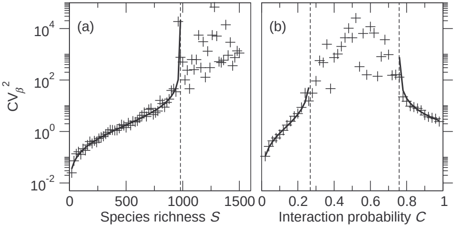

Rossberg 2013, *Food Webs and Biodiversity*

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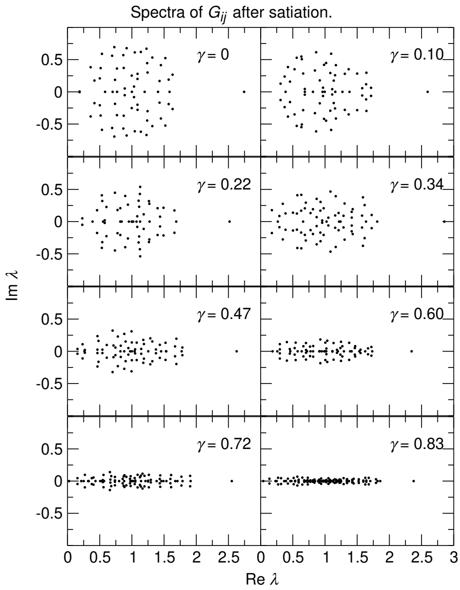
$\rightarrow$ Feedback amplification of $\operatorname{var} B_i$ through $\operatorname{var} G_{ij}$ $\rightarrow$ singularity!

Partially symmetric variants



- Shape of clouds depends on symmetry of G_{ij} [$\gamma = \mathrm{corr}(G_{jk}, G_{kj})$].
- Few EV < 0, some EV near 0 (especially for large γ).
- By random matrix theory,

$$(\text{length of cloud}) = 2S^{1/2}(1+\gamma)\ \mathrm{std}\ G_{12}$$

Sommers et al. 1988, *Phys. Rev. Lett.*

- Structural instability when

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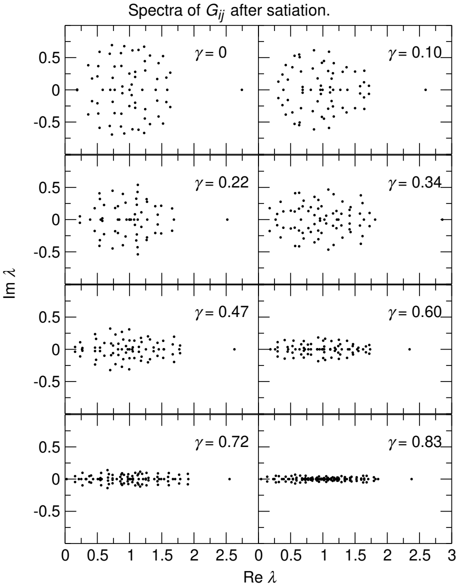

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UFP $\leftrightarrow$ MA transition is due to structural instability!

Effective self-regulation:

$$u := \frac{1 - \mathrm{E}G_{12}}{S_{\text{pool}}^{1/2}\,\mathrm{std}\,G_{12}}$$

With

$$v = \frac{S}{S_{\text{pool}}}\frac{1}{u - \gamma v} = \phi\frac{1}{u - \gamma v},$$

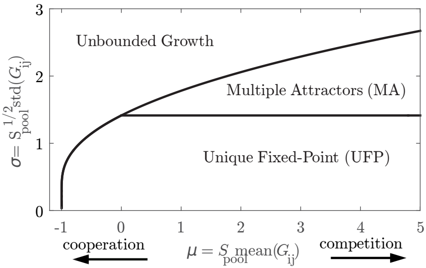
that is

$$v = \frac{1}{2\gamma}\left(u - \sqrt{u^2 - 4\gamma\phi}\right),$$

the condition for UFP $\leftrightarrow$ MA is

$$(u - \gamma v)^2 - \phi = 0. \qquad (1)$$

Bunin 2017, *Phys. Rev. E*



Eq. (1) is equivalant to

$$\phi = \frac{u^2}{(1+\gamma)^2} \Leftrightarrow S = \frac{(1 - \mathrm{E}G_{12})^2}{(1+\gamma)^2\,\mathrm{var}\,G_{12}}$$

Rossberg 2013, *Food Webs and Biodiversity*

for any $u > 0$ and $-1 < \gamma < 1$.

Dynamics in the MA phase

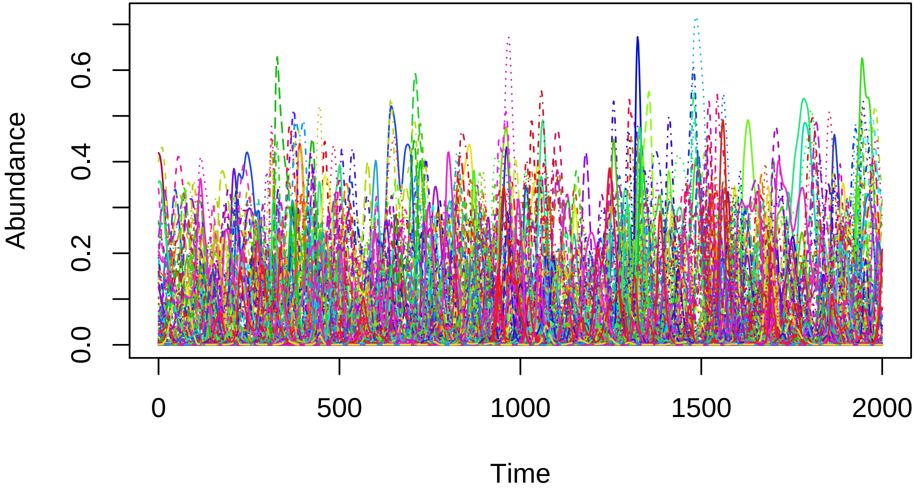
Let's simulate MA phase, regularising model.

$$\frac{dB_j}{dt} = \left(1 - \sum_{k}^{S_{\text{pool}}} G_{jk} B_k\right) B_j + \epsilon$$

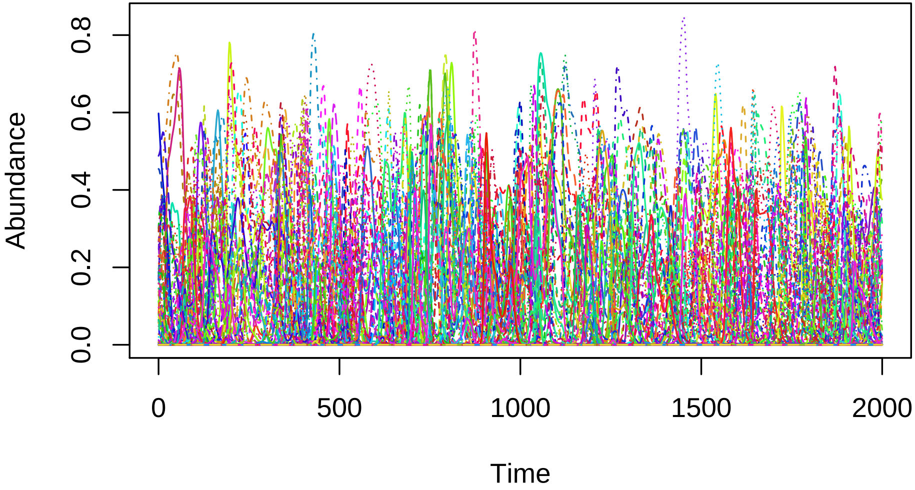
Set

- $S_{\text{pool}} = 400$
- $G_{jj} = 1$
- $G_{jk} = \begin{cases} 0.5 & \text{with probability } 0.5, \\ 0 & \text{otherwise} \end{cases} \qquad (j \neq k).$

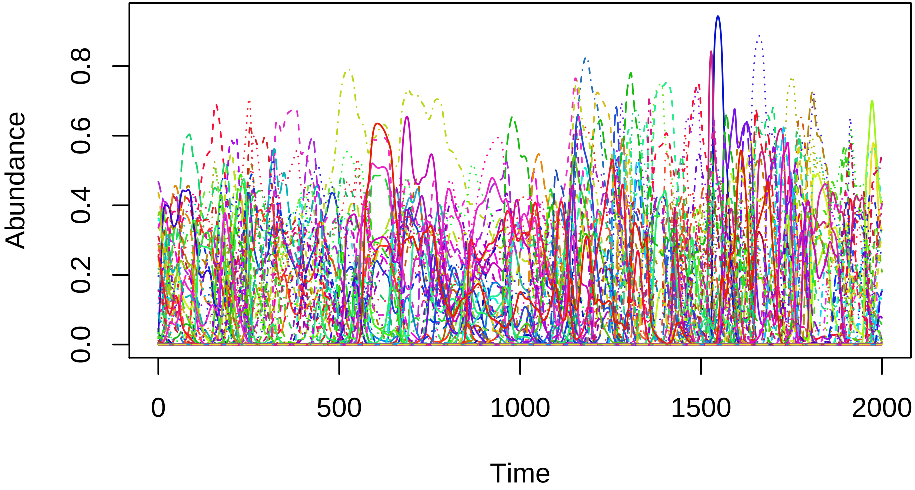
Steady state of MA phase: $\epsilon = 10^{-4}$



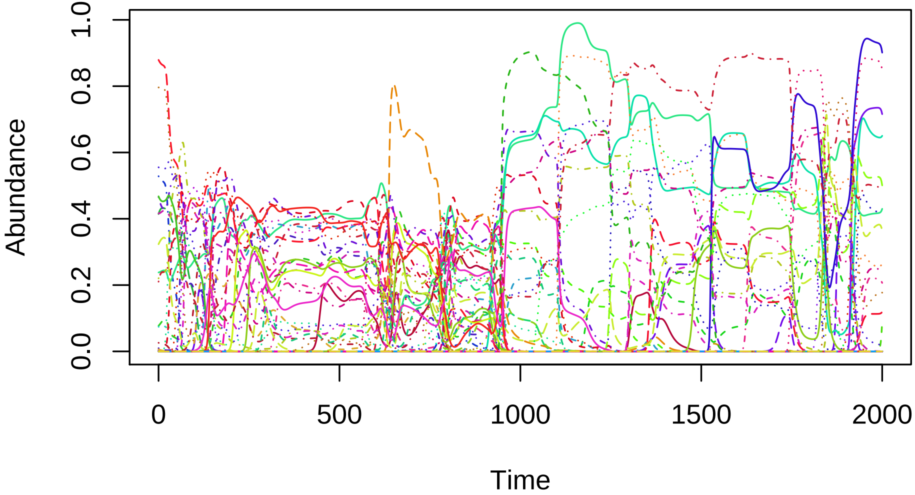
Steady state of MA phase: $\epsilon = 10^{-10}$



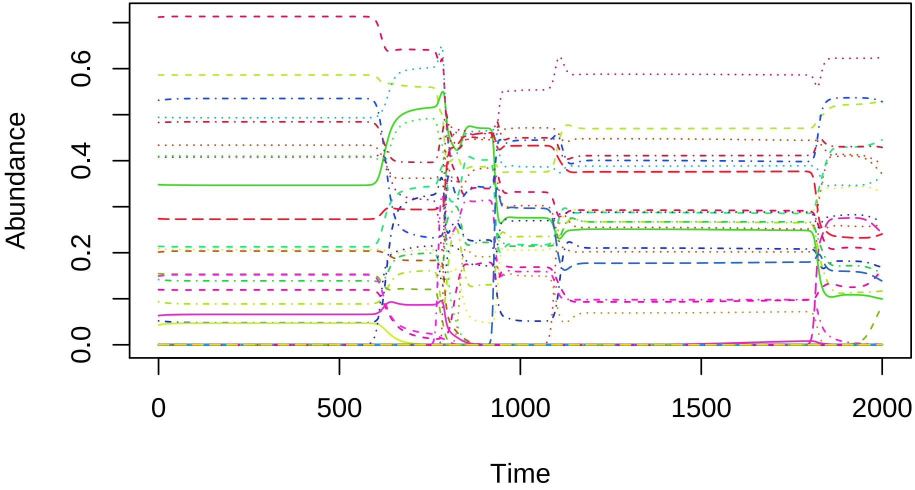
Steady state of MA phase: $\epsilon = 10^{-20}$



Steady state of MA phase: $\epsilon = 10^{-200}$



Steady state of MA phase: $\epsilon = 10^{-2000}$



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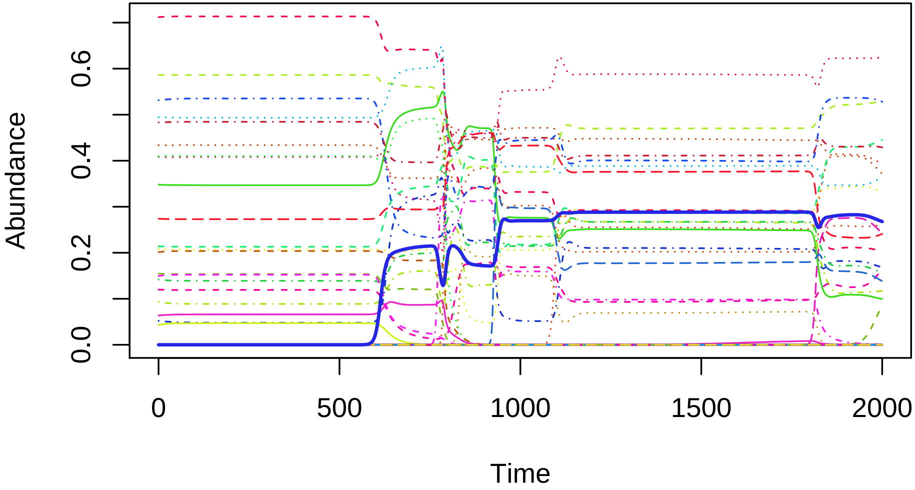

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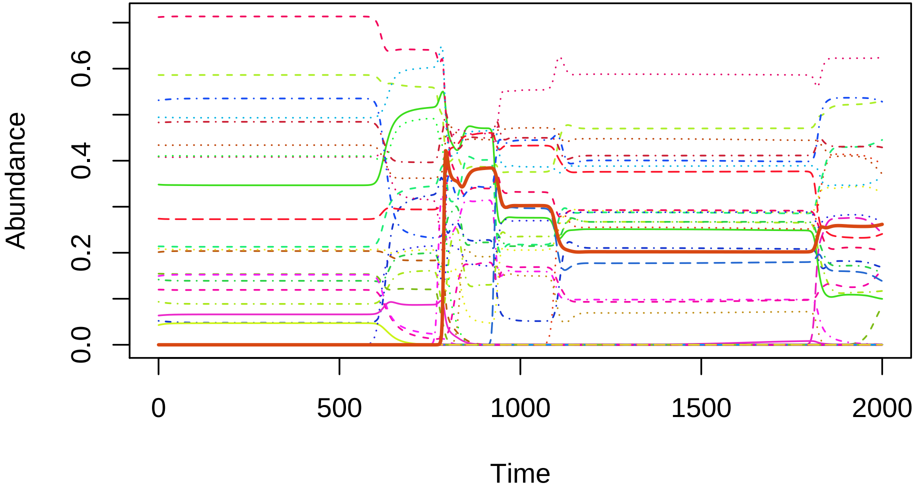

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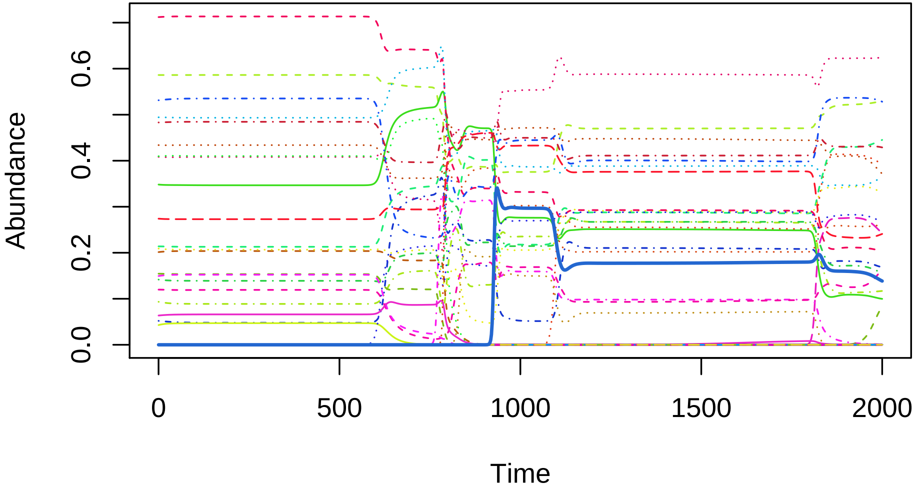

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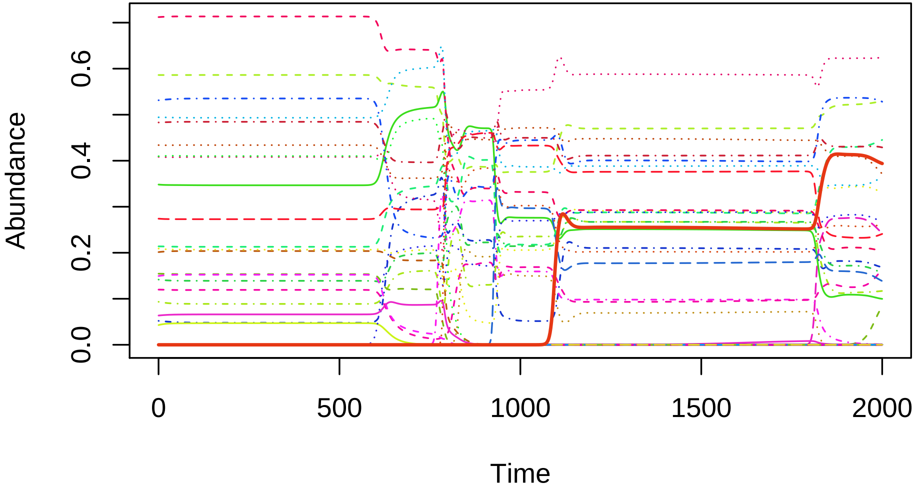

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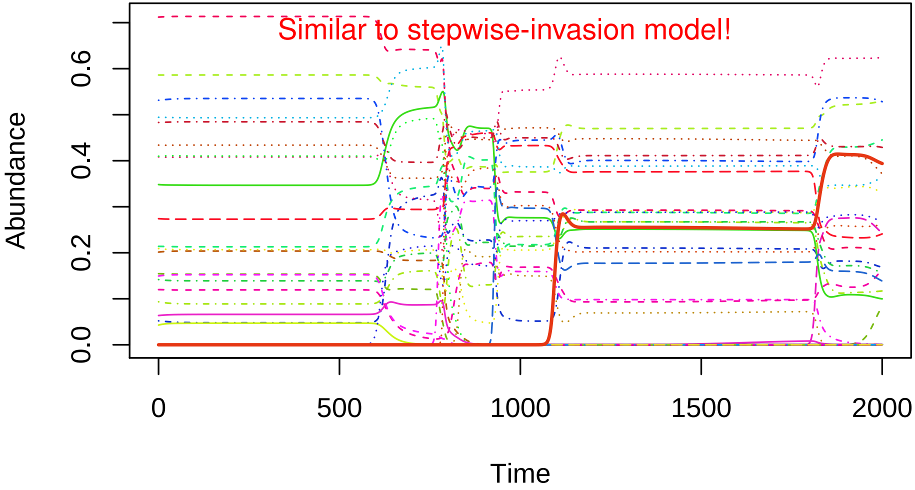

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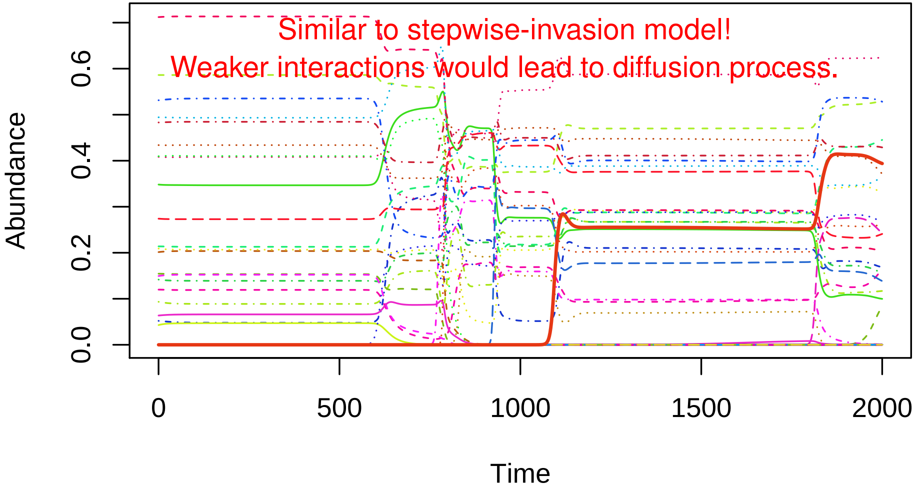

‘MA’ steady-state in limit of weak interactions

The distribution $P_B(B) = cP(cB) = cP(x)$ of abundances B_i is, up to a constant $c = x_i/B_i$, given by the Fokker-Planck Equation:

$$0 = \overbrace{\frac{e^{-(x-x_0)/2}}{\sqrt{2\pi}\Phi(x_0)}}^{\text{invasion}} + \overbrace{\frac{d^2}{dx^2}P(x)}^{\text{diffusion}} + \overbrace{\frac{d}{dx}\left[(x-x_0)P(x)\right]}^{\text{reversion}}$$

with *absorbing* boundary condition $P(0) = 0$, $P'(0) = 1$.

– $x_0 \approx 0$ is a constant determined e.g. by shooting method.
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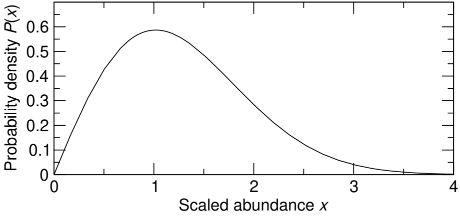
– With $\gamma \neq 0$ *competition avoidance* complicates the picture further.



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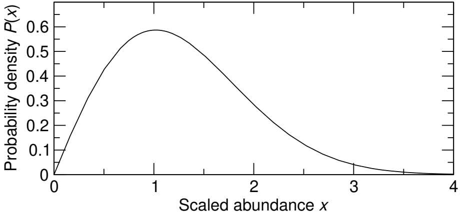

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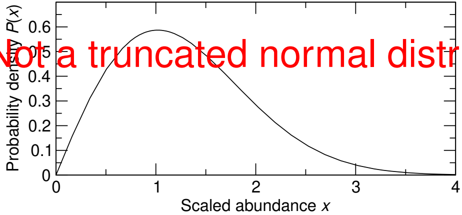

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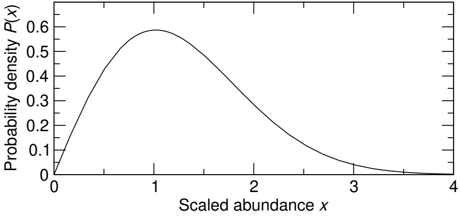

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Empirical invasion probabilities

Hawaiian non-native birds

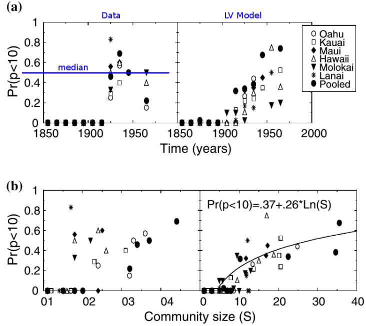
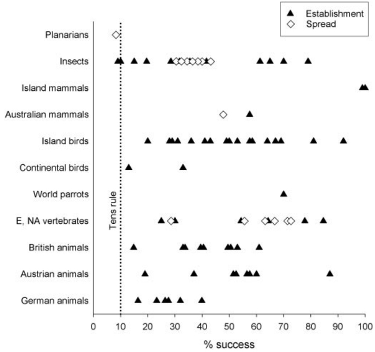


Figure 4. Species-specific probabilities of persisting less than 10 years in the islands as a function of (a) time, and (b) community size. Left: original field data. Right: LVM simulations. Observe the presence of marked thresholds in both analysis and the asymptotic behavior of these probabilities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

Gamarra et al. 2005, *Biological Invasions*

Europe & N.-America



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

Rossberg, Caskenette, and Bersier 2017, *Adaptive Food Webs: Stability and Transitions of Real and Model Ecosystems*

Strength of indirect effects

INDIRECT EFFECTS IN MARINE ROCKY INTERTIDAL INTERACTION WEBS: PATTERNS AND IMPORTANCE[1]

Two methods of analysis suggested that indirect effects accounted for ≈40% of the change in community structure resulting from manipulations, with a range of 24–61%. The proportion of change due to indirect effects was constant with web species richness, in-

Menge 1995, *Ecological Monographs*

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corresponds to the direct impact of the invader on resident species. The denominator $(1 - \mathrm{E}\alpha_{12})^2 - S \operatorname{var} \alpha_{12}$ describes the amplification of the invader's perturbation through indirect interactions with other species. The remaining term $\mathrm{E}y^2$ is a conversion factor. Considering the limiting case $\mathrm{E}\alpha_{12} = 0$ for simplicity, so that $S \approx 0.5/\operatorname{var} \alpha_{12}$, **one sees that** through the indirect interactions the strength of the direct effect is approximately doubled. In other words, direct and indirect interactions contribute roughly equal parts to the disturbances of residents by invaders. On the premise that, in prac-

Rossberg 2013, *Food Webs and Biodiversity*

Rossberg, Caskenette, and Bersier 2017, *Adaptive Food Webs: Stability and Transitions of Real and Model Ecosystems*

No equilibirum in the real world

1. Evidence from long-term censuses suggests that few natural populations or communities persist at or near an equilibrium condition on a local scale (37). There is no clear demarcation between assemblages in an equilibrium state and those that are not.

Sousa 1984, *Annual Review of Ecology and Systematics*

Rossberg, Caskenette, and Bersier 2017, *Adaptive Food Webs: Stability and Transitions of Real and Model Ecosystems*

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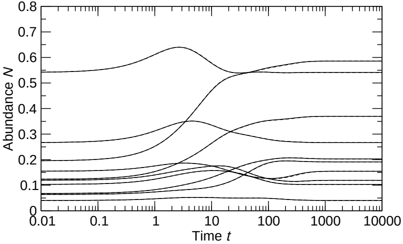


Structurally unstable community responds to perturbation, 10 sample species out of 170.

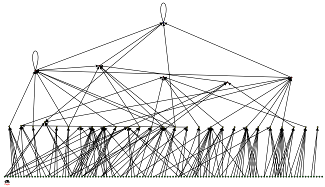
Rossberg and Farnsworth 2011, *Theor. Ecol.*

Rossberg, Caskenette, and Bersier 2017, *Adaptive Food Webs: Stability and Transitions of Real and Model Ecosystems*

The competitive overlap matrix $\mathbf{G}$ for food webs

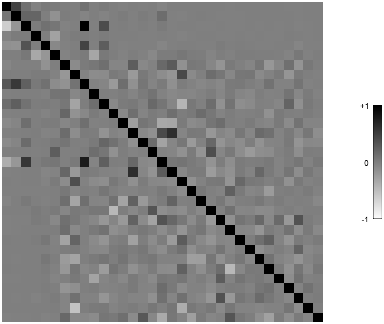
Compute *effective competition matrix* $\hat{\mathbf{C}}$ from *interaction matrices* $\mathbf{A}$ (eating), $\mathbf{A}'$ (being eaten) and *direct competition matrix* $\mathbf{C}$:

$$\hat{\mathbf{C}} = \epsilon \mathbf{A}^{\mathrm{T}} \hat{\mathbf{C}}^{-1} \mathbf{A}' + \mathbf{C}.$$



Compute *competitive overlap matrix* $\mathbf{G}$:

$$G_{ij} = \frac{\hat{C}_{ij}}{\sqrt{\hat{C}_{ii}\hat{C}_{jj}}}.$$



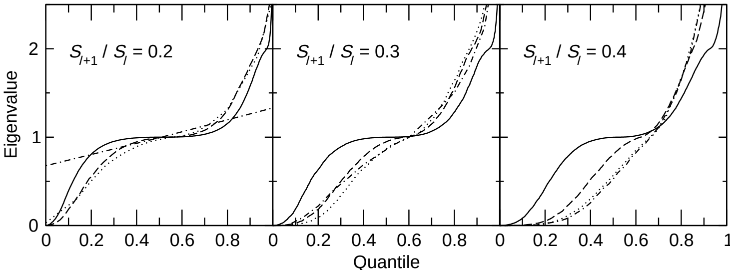
G

Rossberg 2013, *Food Webs and Biodiversity*

Multi-level food webs

Eigenvalues of competition matrices

Eigenvalues of resource overlap (competition) matrices in layered, random, sparse food webs:



Rossberg 2013, *Food Webs and Biodiversity*

Richness by trophic level (data)

Marine ecosystems:

Vol. 240: 11–20, 2002 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published September 12

Use of size-based production and stable isotope analyses to predict trophic transfer efficiencies and predator-prey body mass ratios in food webs

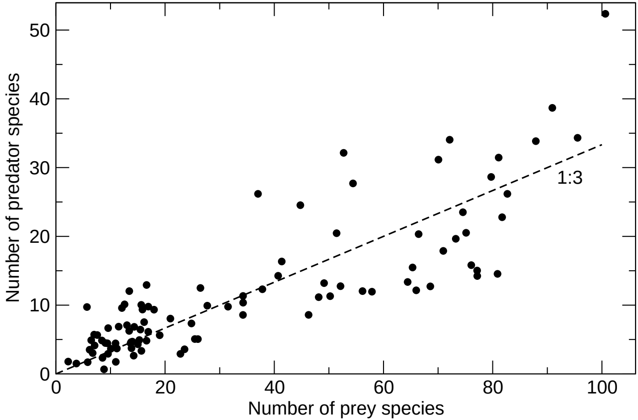
Simon Jennings*, **Karema J. Warr**, **Steve Mackinson**

Centre for Environment, Fisheries & Aquaculture Science, Lowestoft Laboratory, Suffolk NR33 0HT, United Kingdom

quantify trophic transfer efficiency, mean predator-prey body-mass ratios and the mean ratio of the number of predator to prey species in marine food webs. We applied these methods to the central North Sea, and estimated transfer efficiencies of 3.7 to 12.4 %, a mean predator-prey body-mass ratio of 109:1 and a mean ratio of the number of predator to prey species of 0.34. We conducted sensitivity analyses to show how differences in the fractionation of $\delta^{15}N$ and changes in the slope of the rela-

Richness by trophic level (data)

Freshwater ecosystems (I):

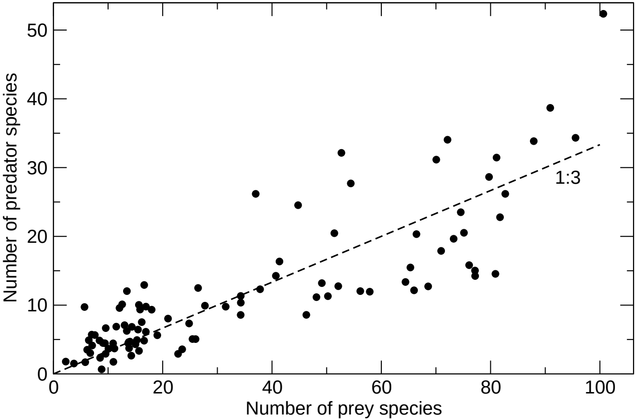


"'Prey' species are detrivores, herbivores and fungivores; 'predators' eat 'prey' species [...]"

UK and US freshwater habitats, Jeffries and Lawton 1985, *Freshw. Biol.*

Richness by trophic level (data)

Freshwater ecosystems (I):

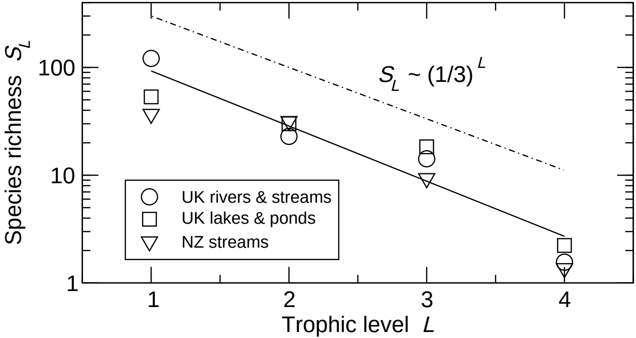


"'Prey' species are detrivores, herbivores and fungivores; 'predators' eat 'prey' species [...]"

UK and US freshwater habitats, Jeffries and Lawton 1985, *Freshw. Biol.*

Richness by trophic level (data)

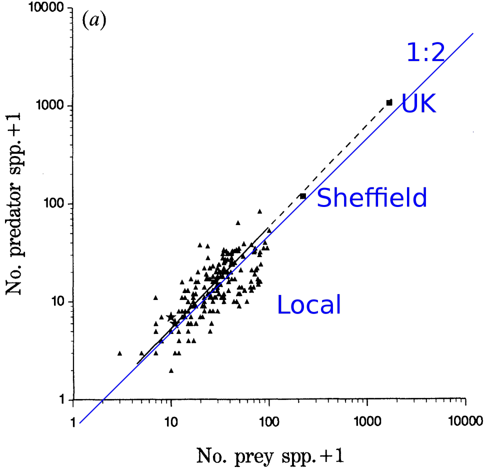
Freshwater ecosystems (II):



After Petchey et al. 2004, *Oikos*. UK: $n = 123$, NZ: $n = 18$

Richness ratios across scales

UK freshwater communities



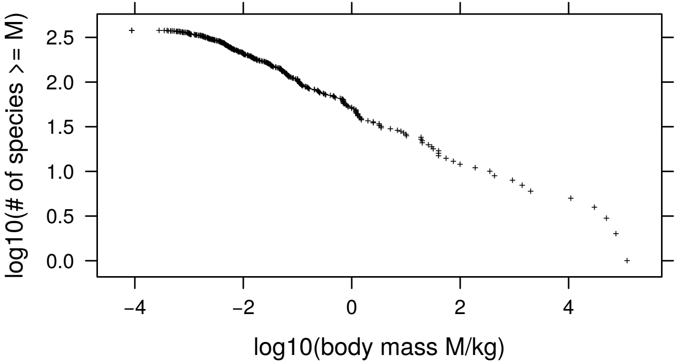
'prey' are [...] non-carnivorous consumers.
[...] 'predators' [...] are carnivores [...]

Note:

$$\frac{1}{3} + \frac{1}{3^2} + \frac{1}{3^3} + \ldots = \frac{1}{2}$$

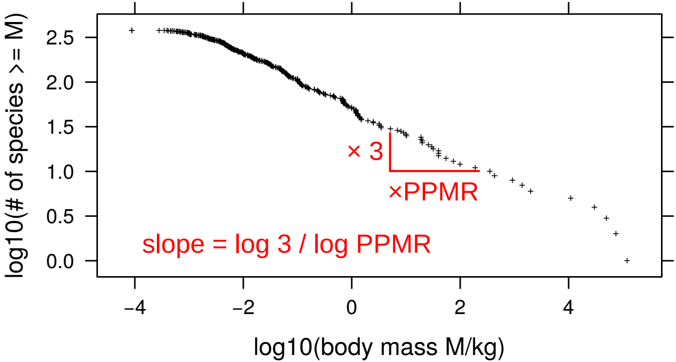
Warren and Gaston 1992, *Philos. Trans. R. Soc. Lond. B Biol. Sci.*

Species-size distribution — Barents Sea



ICES 2013, *Report of the Working Group on the Ecosystem Effects of Fishing Activities (WGECO)*

Species-size distribution — Barents Sea



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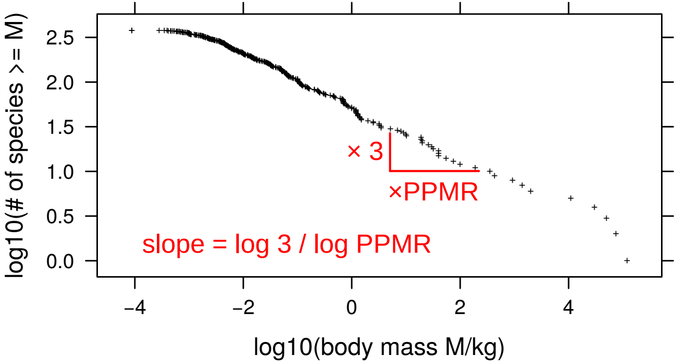
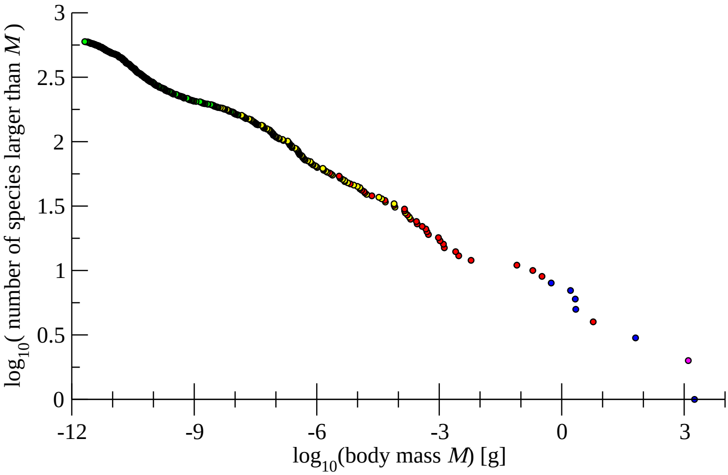
Species-size distribution — Barents Sea



ICES 2013, *Report of the Working Group on the Ecosystem Effects of Fishing Activities (WGECO)*

With PPMR = 30 - 1000, slope = 0.3 - 0.16, typically 0.2.

Simulated species size distributions (PDMM)



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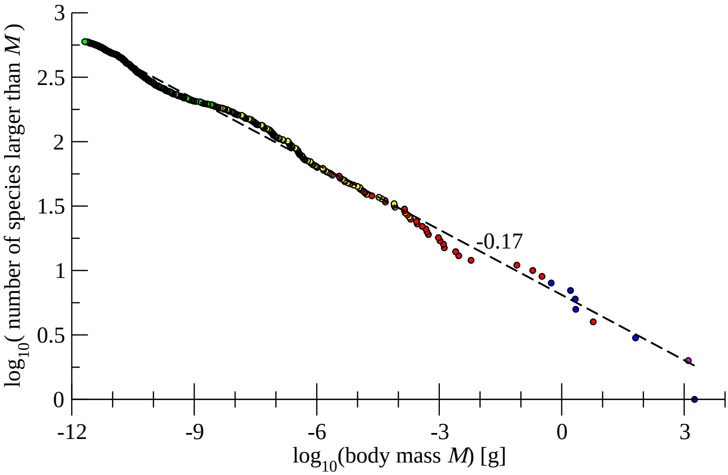
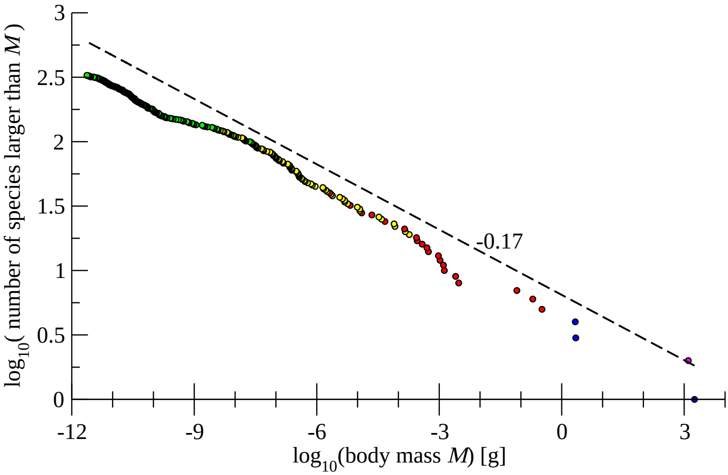
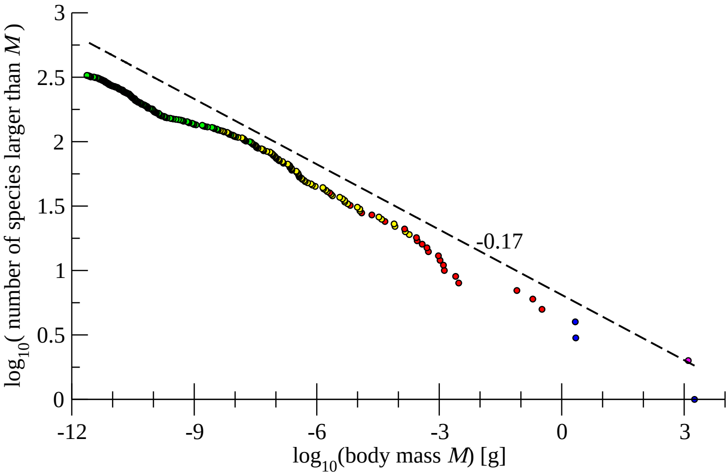


Simulated species size distributions (PDMM)



Simulated species size distributions (PDMM)

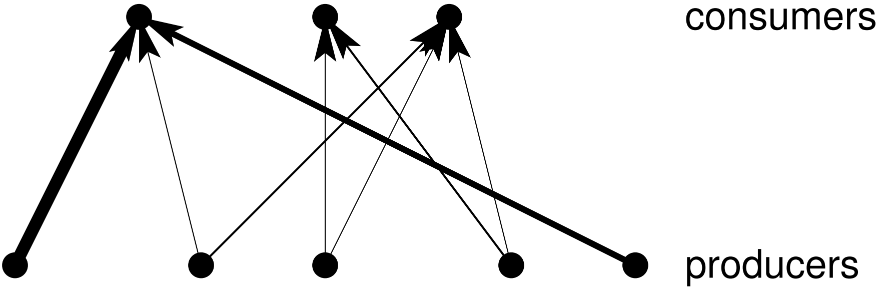


Conserve low-level biodiversity!

Two-level food webs

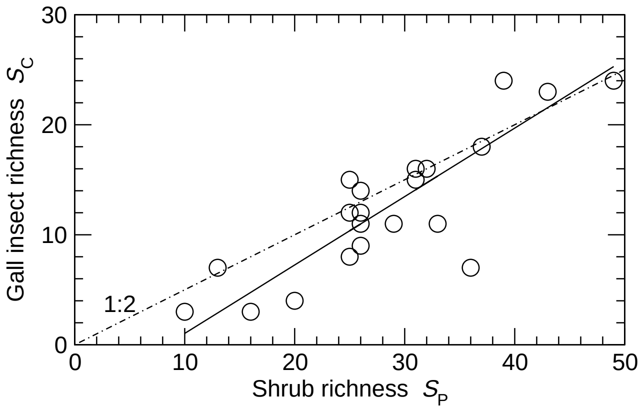
Gall-forming insects

Two-level food webs



Predicted consumer:producer richness ratio = 1:2

Two-level food webs (I)

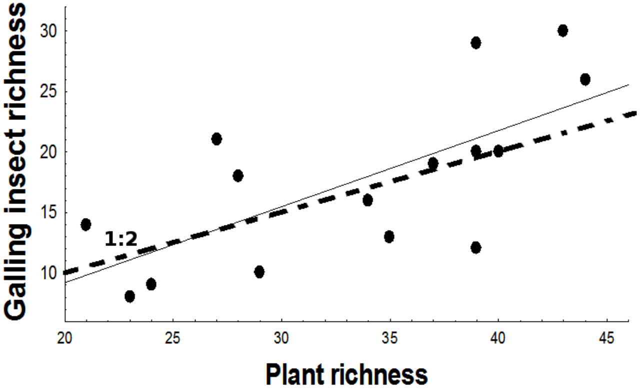


After Wright and Samways 1998, *Oecologia*

Cape Floristic Region

MA-regression: $S_C = 0.62\, S_P - 5.2$

Two-level food webs (II)



Santos de Araújo 2011, *Trop. Conserv. Sci.*

Brazilian Cerrado

Regression: $S_C = 0.62\, S_P - 3.4$

The LV Metacommunity model (LVMCM)

We study a metacommunity of coupled LV models

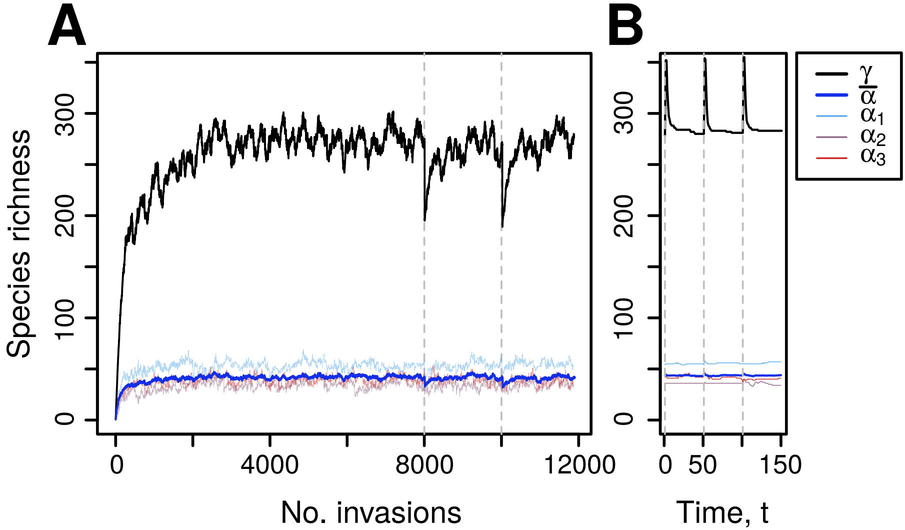
$$\frac{db_{ix}}{dt} = b_{ix}\left(r_{ix} - \sum_{j=1}^{S} \mathbf{A}_{ij}\, b_{jx}\right) - e\, b_{ix} + \sum_{y \in \mathcal{N}(x)} \frac{e}{k_y} \exp\left(-d_{xy}\ell^{-1}\right) b_{iy},$$

or in matrix form

$$\frac{d\mathbf{B}}{dt} = \mathbf{B} \circ (\mathbf{R} - \mathbf{AB}) + \mathbf{BD}.$$

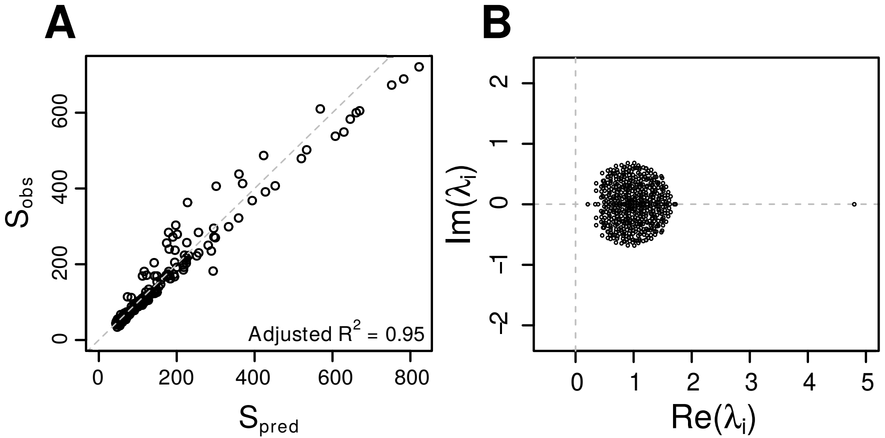
O'Sullivan, Knell, and Rossberg 2019, *Ecol. Lett.*

Community assembly



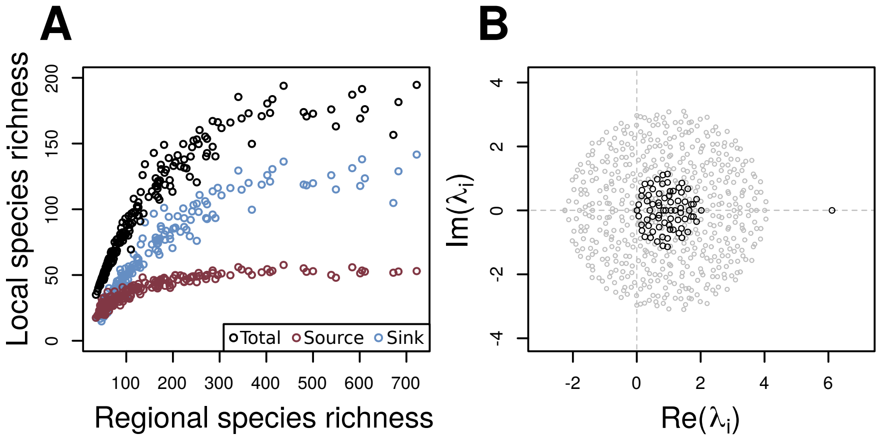
O'Sullivan, Knell, and Rossberg 2019, *Ecol. Lett.*

Regional Structural Instability



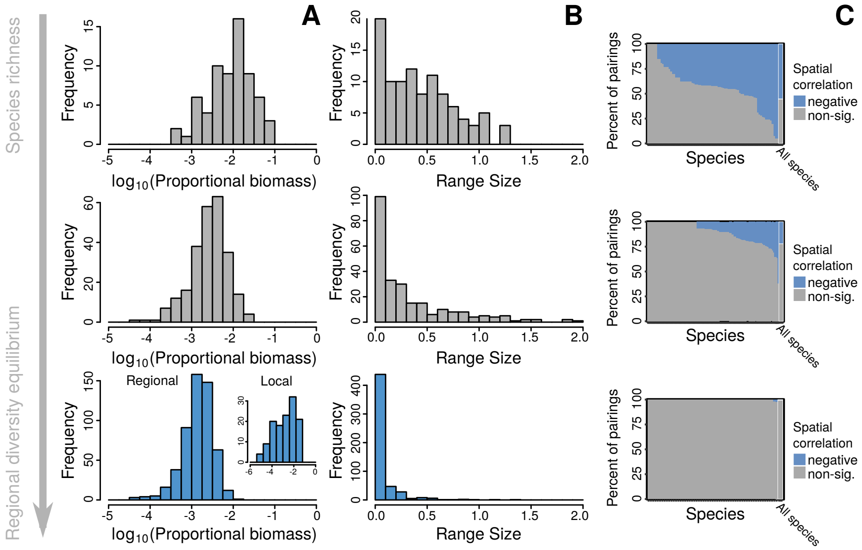
O'Sullivan, Knell, and Rossberg 2019, *Ecol. Lett.*

Local Structural Instability



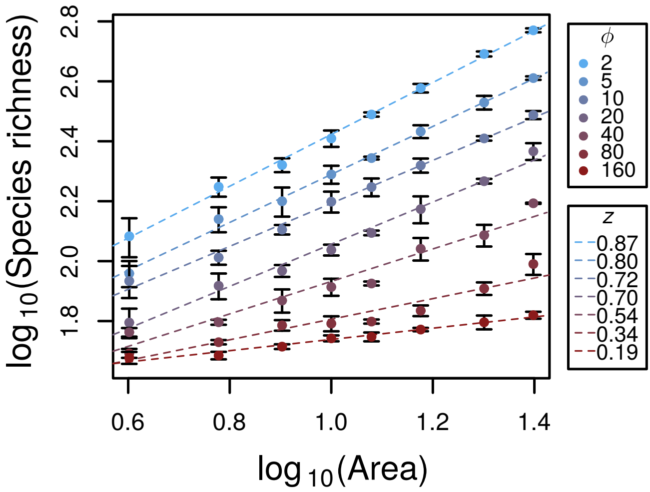
O'Sullivan, Knell, and Rossberg 2019, *Ecol. Lett.*

Macroecological patterns I: abundances & ranges



Simulation by O'Sullivan, Knell, and Rossberg 2019, *Ecol. Lett.*
Patterns identified as fundamental by McGill 2010.

Biodiversity patterns II: species-area relations



Predicted by McGill 2010 as consequence of patterns I.

O'Sullivan, Knell, and Rossberg 2019, *Ecol. Lett.*
McGill 2010, *Ecology Letters*

Hurray!
Structural instability is real!

Long live theoretical ecology — let's apply it to the real world!

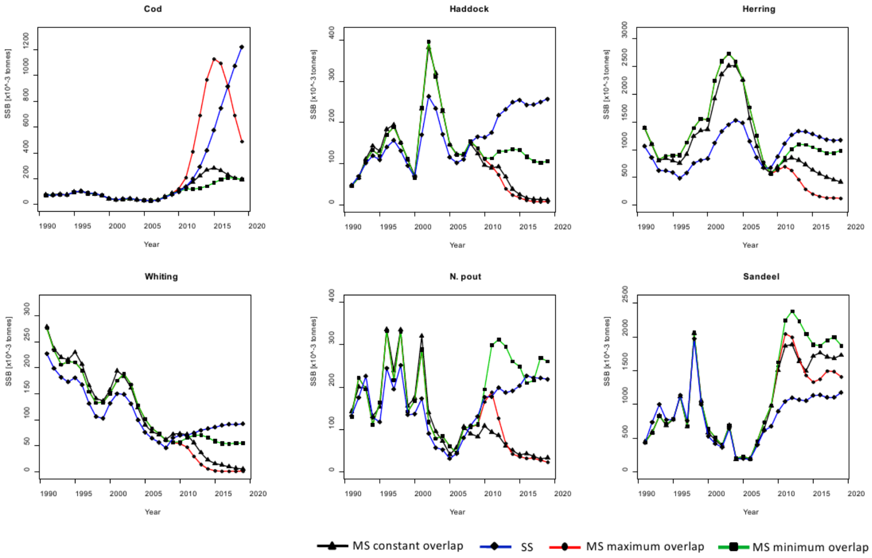
Sensitivity to pressures and parameters

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

$\rightarrow$ response by species i to applying pressures F_j given by

$$\Delta B_i = -\sum_j G_{ij}^{-1} F_j$$

Model are difficult to parameterize



North Sea SMS, ICES (WGSAM), 2009

ICES Journal of
Marine Science

International Council for the Exploration of the Sea
Conseil International pour l'Exploration de la Mer

ICES Journal of Marine Science (2016), 73(10), 2499–2508. doi:10.1093/icesjms/fsw113

Original Article

Maximum sustainable yield from interacting fish stocks in an uncertain world: two policy choices and underlying trade-offs

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[2]*Queen Mary University of London, School of Biological and Chemical Sciences, 327 Mile End Rd, London E1 4NS, UK*

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Farcas, A. and Rossberg, A. G.' Maximum sustainable yield from interacting fish stocks in an uncertain world: two policy choices and underlying trade-offs. – ICES Journal of Marine Science, 73: 2499–2508.

Received 26 December 2015; revised 26 May 2016; accepted 1 June 2016; advance access publication 28 July 2016.

PDMM aquatic food webs

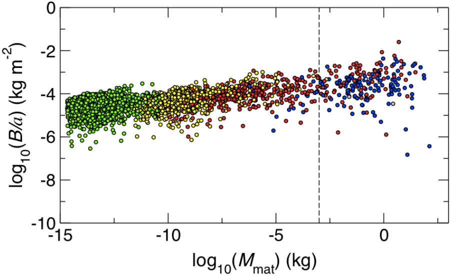

Table 1 | Validation of model food webs.

Property	Range of model values	Range of empirically derived values
Phytoplankton species richness	2,559-2,961	268-1,700
Fish species richness	148-280	192-314
Dietary diversity of fish species	6.17-8.05	6-14
Diet-partitioning exponent for fish species[36]	0.509-0.644	0.21-0.66
Maturation body mass of phytoplankton species (kg)	$10^{-14.7}$-$10^{-9.01}$	10^{-15}-$10^{-8.69}$
Maturation body mass of fish species (kg)	$10^{-3.0}$-$10^{2.47}$	$10^{-3.0}$-$10^{2.54}$
Trophic level of fish species	2.03-5.53	2-4.53
Slope of diversity spectrum	0.149-0.491	0.163-0.460
Slope of biomass size-spectrum	−0.536-0.0234	−0.25-0.025
Biomass density of fish species (kg m^{-2})	$10^{-13.0}$-$10^{-1.60}$	$10^{-10.1}$-$10^{-2.28}$

Range of values of 10 key properties for the 20 PDMM food webs used, compared with empirically derived ranges pertaining to temperate shelf communities. In calculating the slopes of the diversity spectra, a lower bound of 1 kg was used for 16 of the 20 food webs, whereas a lower bound of 3-35 kg was used for the remaining four webs.

Fung et al. 2015, *Nat Commun*

Strategies to overcome structural instability

Example: Management for Maximum Sustainable Yield

Harvest Control Rule	Regulari-sation	% of theoretical maximum sustainable total yield
Pressure (‘F’) Target Control	none	33.9
	standard	55.9
State (‘B’) Target Control	none	57.0
	standard	84.8
Singe Species Control		51.7

Policy changes recommended to European Commission:

Farcas and Rossberg 2016, *ICES J. Mar. Sci.*

Strategies to overcome structural instability

Example: Management for Maximum Sustainable Yield

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Policy changes recommended to European Commission:

- Regularise matrix inversions

Farcas and Rossberg 2016, *ICES J. Mar. Sci.*

Strategies to overcome structural instability

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Policy changes recommended to European Commission:

- Regularise matrix inversions
- State targets,

$$\text{yield} = \hat{\mathbf{B}}_{\text{MSY}}^{\mathrm{T}} \left(\mathbf{r} - \mathbf{G} \hat{\mathbf{B}}_{\text{MSY}} \right) ,$$

not pressures targets

$$\text{yield} = \hat{\mathbf{F}}_{\text{MSY}}^{\mathrm{T}} \mathbf{G}^{-1} \left(\mathbf{r} - \hat{\mathbf{F}}_{\text{MSY}} \right) .$$

Farcas and Rossberg 2016, *ICES J. Mar. Sci.*

Conclusions

- Structural instability controls the structure of large model communities.
- There is overwhelming *indirect* evidence that most natural ecological communities (at all scales) are structurally unstable.
- **Let's develop the real-world applications of these insights.**

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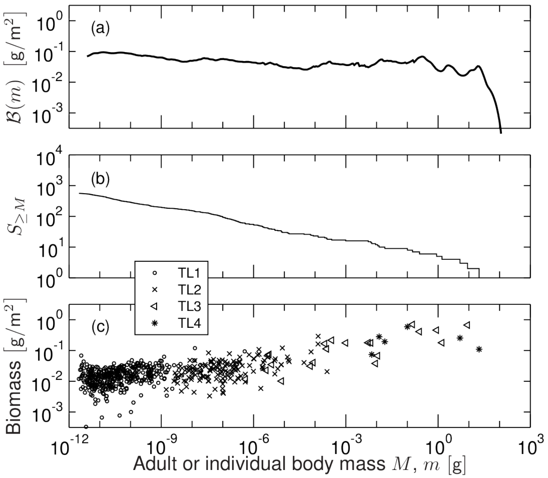
Three allometries

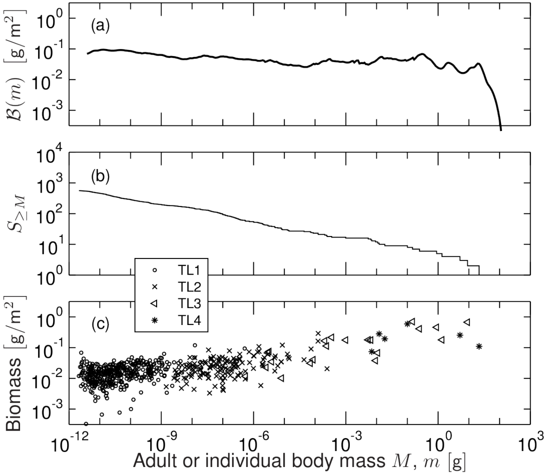


$$\text{slope} = \frac{\log \tau}{\log \text{PPMR}} + \frac{1}{4}$$
$$\approx 0$$

$$\text{slope} = \frac{\log 1/3}{\log \text{PPMR}}$$
$$\approx -0.2$$

Rossberg 2013, *Food Webs and Biodiversity*

Three allometries



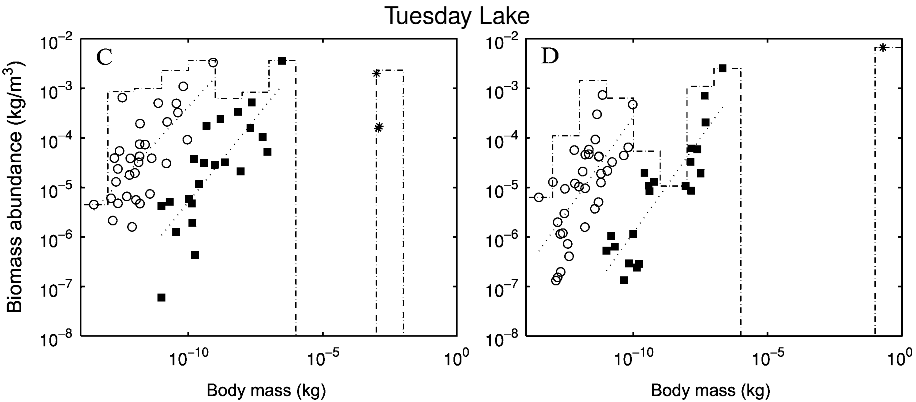
$$\text{slope} = \frac{\log \tau}{\log \text{PPMR}} + \frac{1}{4} \approx 0$$

$$\text{slope} = \frac{\log 1/3}{\log \text{PPMR}} \approx -0.2$$

$$\text{slope} = \frac{\log 3\tau}{\log \text{PPMR}} + \frac{1}{4} \approx -\frac{\log 1/3}{\log \text{PPMR}} \approx 0.2$$

Rossberg 2013, *Food Webs and Biodiversity*

Biomass by body mass (data)

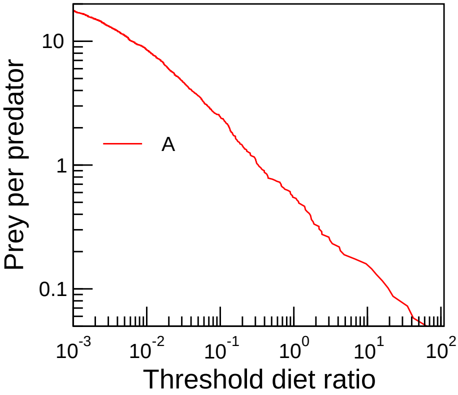


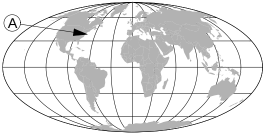
overall slope: 0.17

overall slope: 0.26
(with largemouth bass)

Jonsson, Cohen, and Carpenter 2005, *Adv. Ecol. Res.*

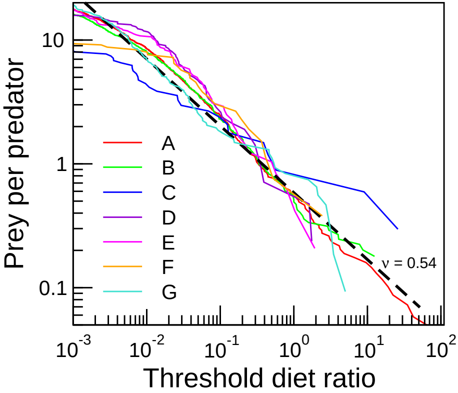
Narrow diets of fish

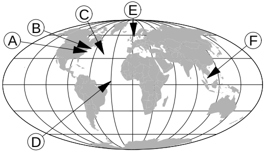


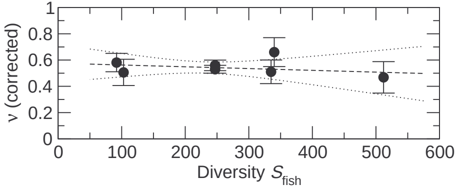


Rossberg, Farnsworth, et al. 2011, *Proceeding R. Soc. B*

Narrow diets of fish

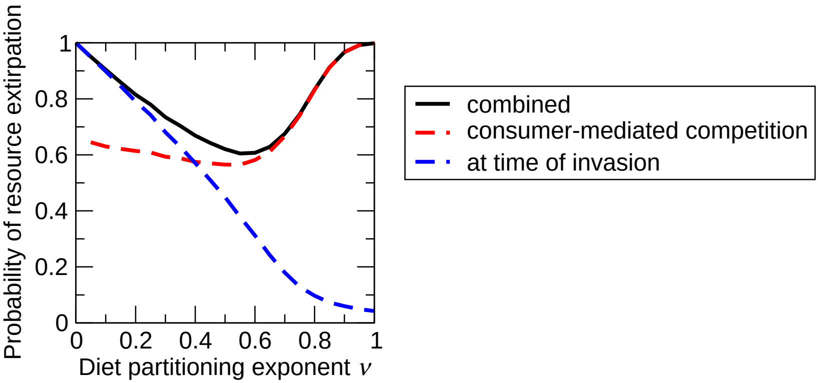






Rossberg, Farnsworth, et al. 2011, *Proceeding R. Soc. B*

Optimisation of dietary diversity



Rossberg 2013, *Food Webs and Biodiversity*