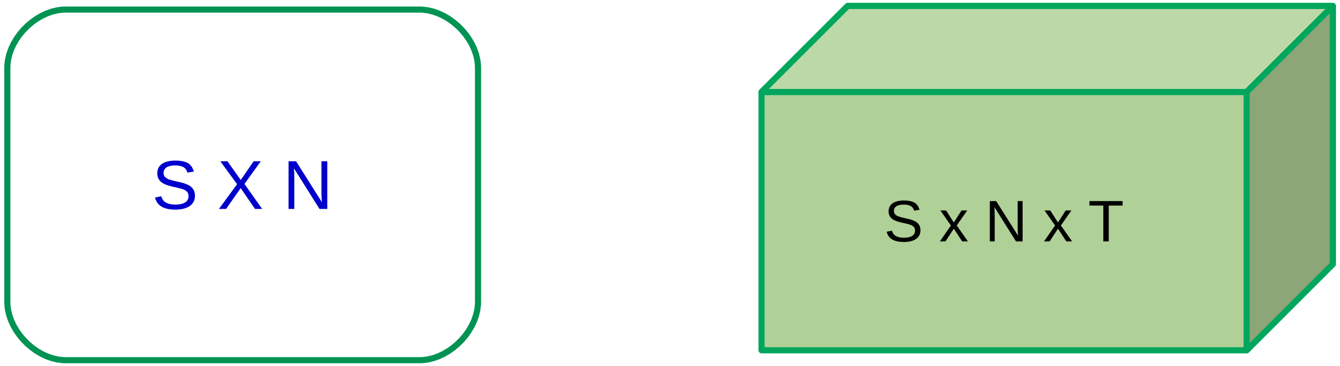
Time

Tasks

Model
Diagnose
Predict
Manipulate



Cross-sectional cohort

Longitudinal cohort

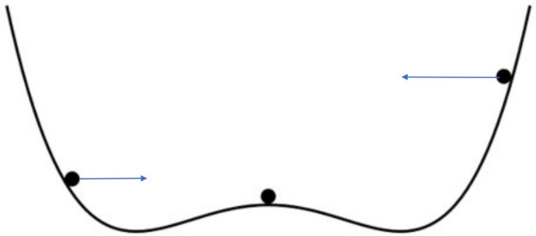
Taxonomic
units

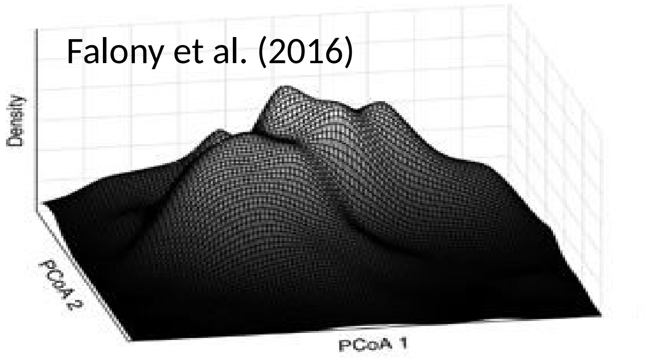
S X N

S x N x T

Towards a dynamic landscape model of the gut microbiome

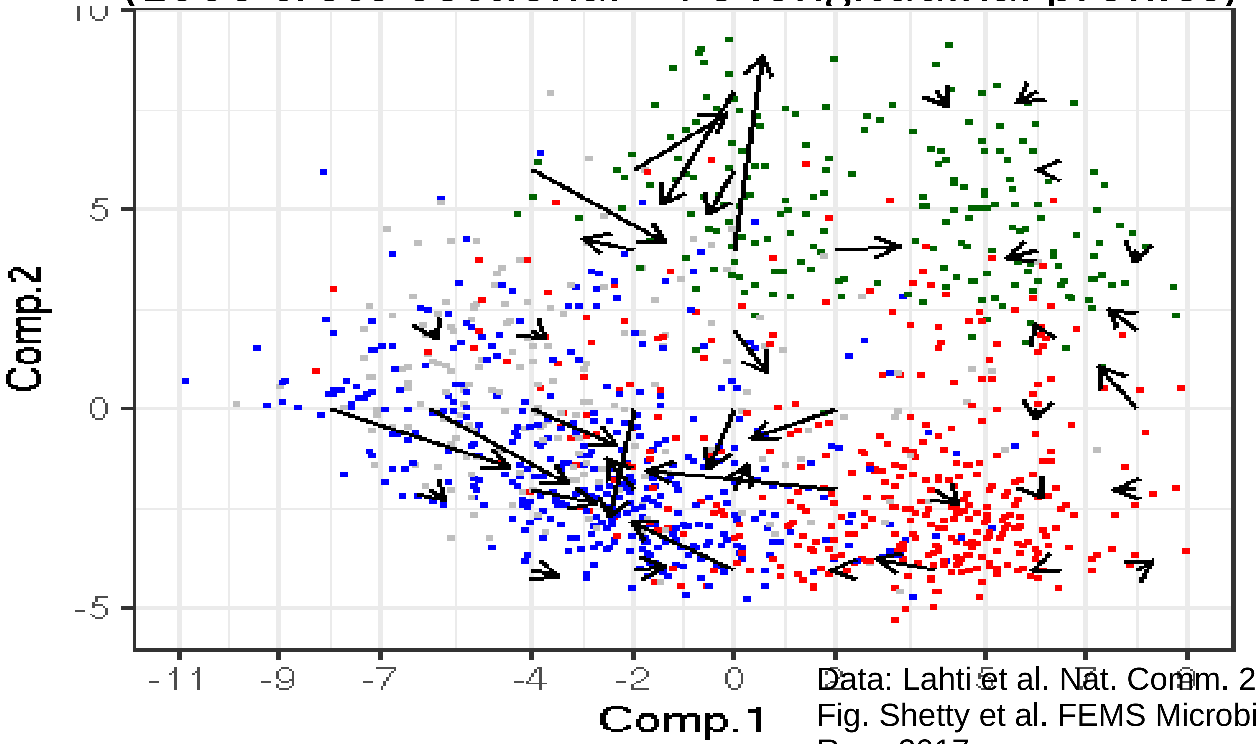
Prior info from background cohorts & pooling evidence across individuals





Falony et al. (2016)

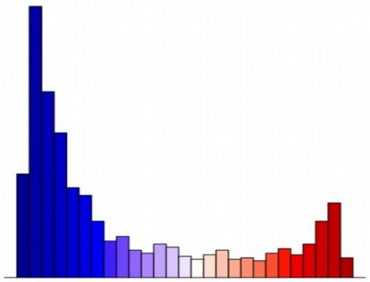
Gradients of change on HITChip PCA landscape (1006 cross-sectional + 78 longitudinal profiles)

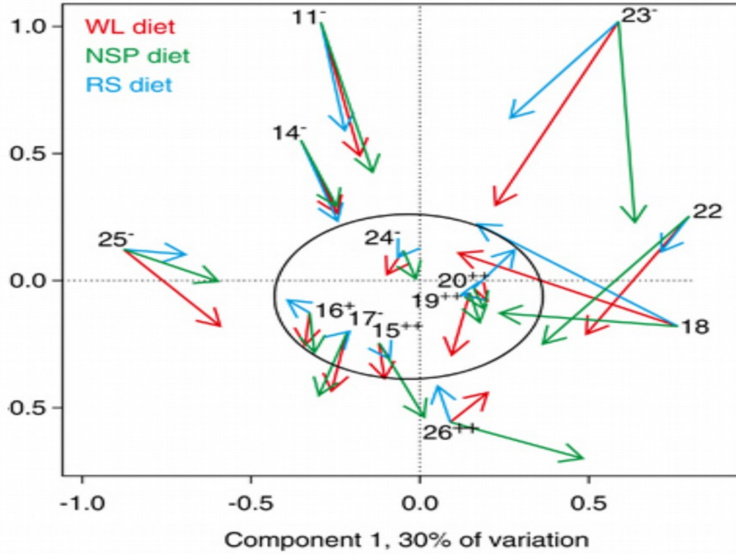


Data: Lahti et al. Nat. Comm. 2014
Fig. Shetty et al. FEMS Microbiol Rev.. 2017

Challenge for manipulation:
- individual responses !

Responders vs.
non-responders
- personalized treatment ?





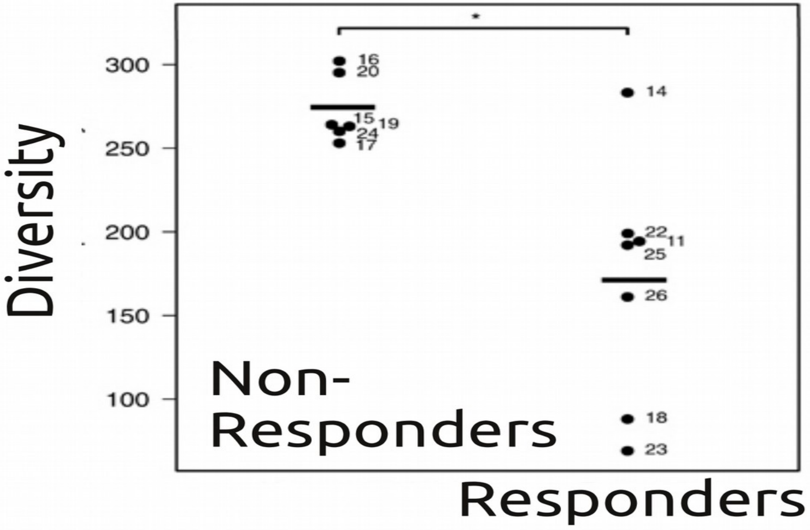
The ISME Journal , (24 April 2014) | doi:10.1038/ismej.2014.63

Impact of diet and individual variation on intestinal microbiota composition and fermentation products in obese men

Anne Salonen, Leo Lahti, Jarkko Salojärvi, Grietje Holtrop, Katri Korpela, Sylvia H Duncan, Priya Date, Freda Farquharson, Alexandra M Johnstone, Gerald E Lobley, Petra Louis, Harry J Flint and Willem M de Vos

Lahti et al. Nat. Comm. 5:4344, 2014

Korpela et al. PLoS ONE 9(3): e90702, 2014



Microbial communities as dynamical systems

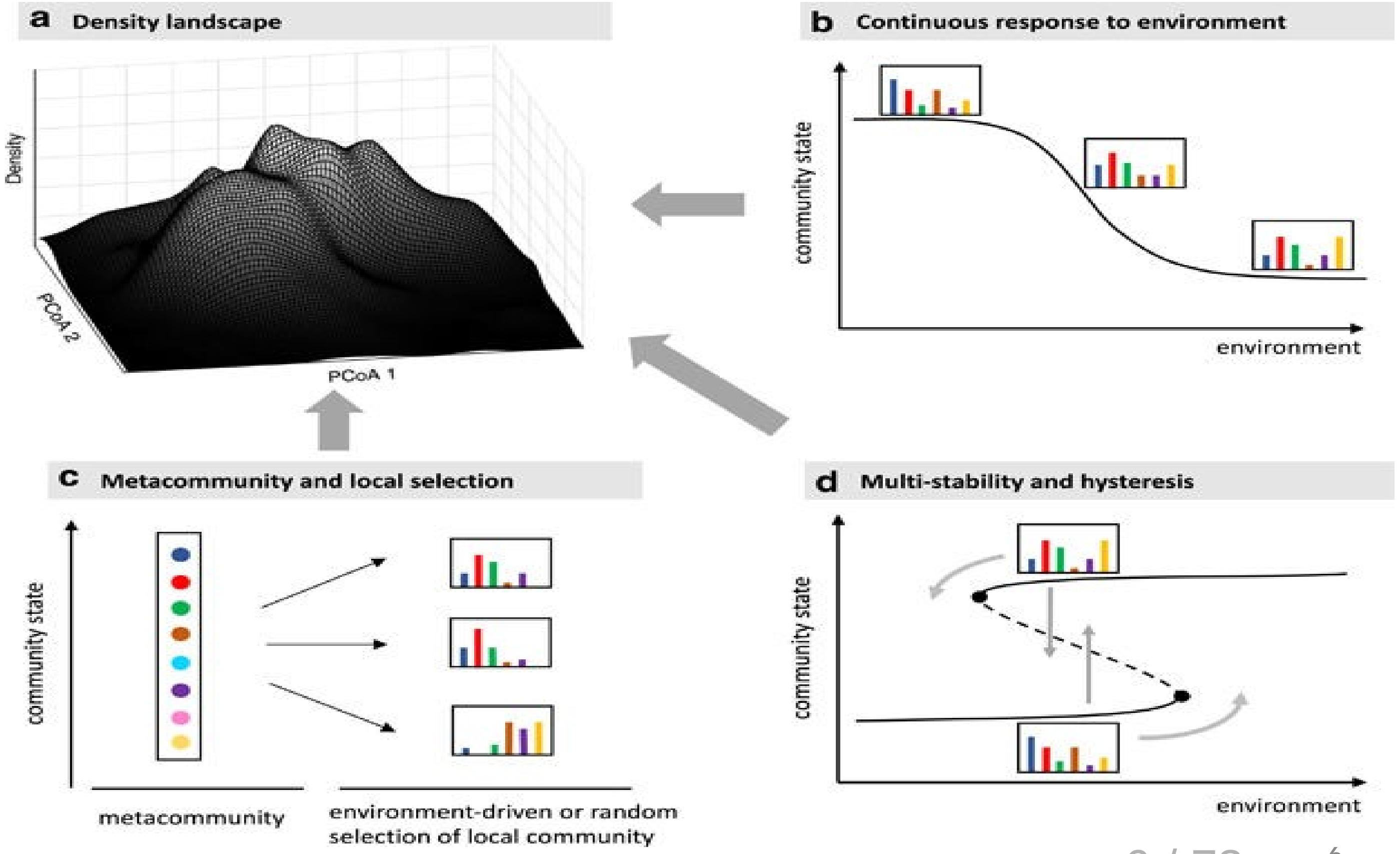
Didier Gonze [1, 2], Katharine Z Coyte [3, 4], Leo Lahti [5, 6, 7], Karoline Faust [5]

External perturbations (push & pulse)

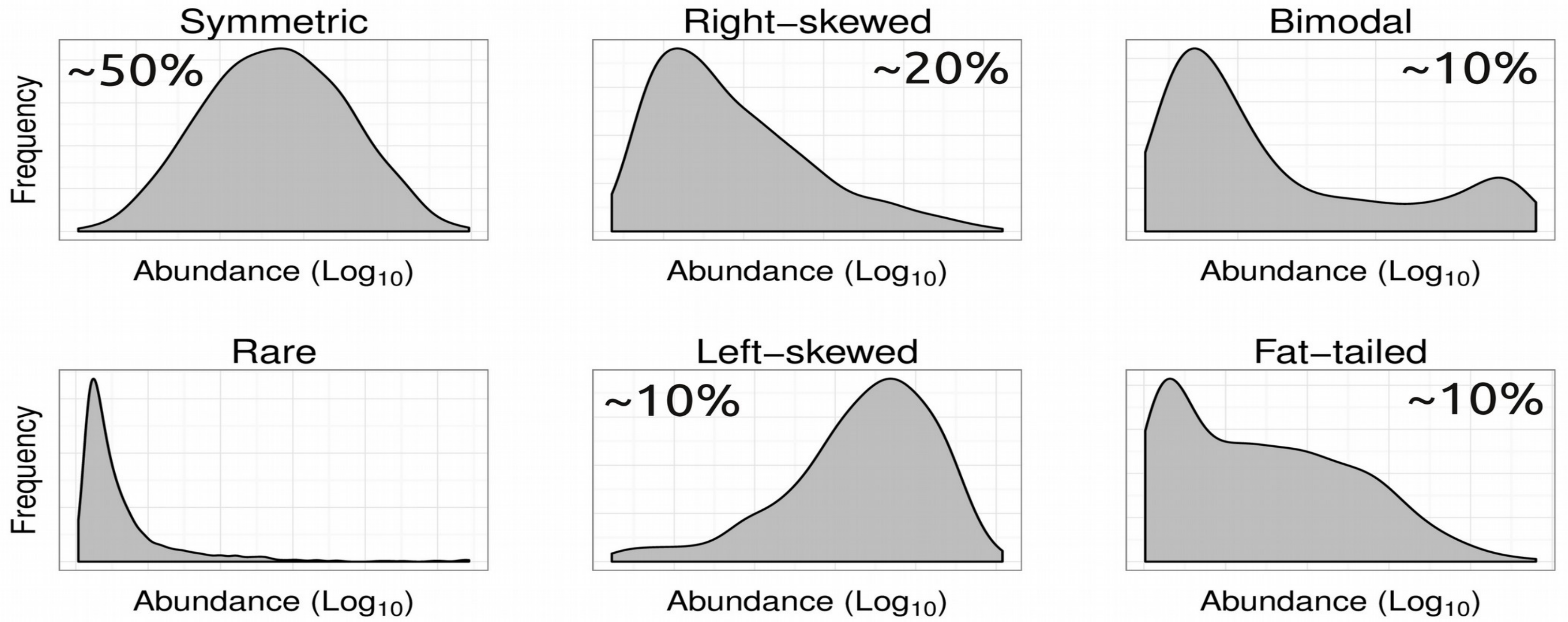
Internal dynamics and multi-stability

Immigration

Stochasticity



Abundance types break Gaussian assumptions



Lahti et al. Nat. Comm. 5:4344, 2014

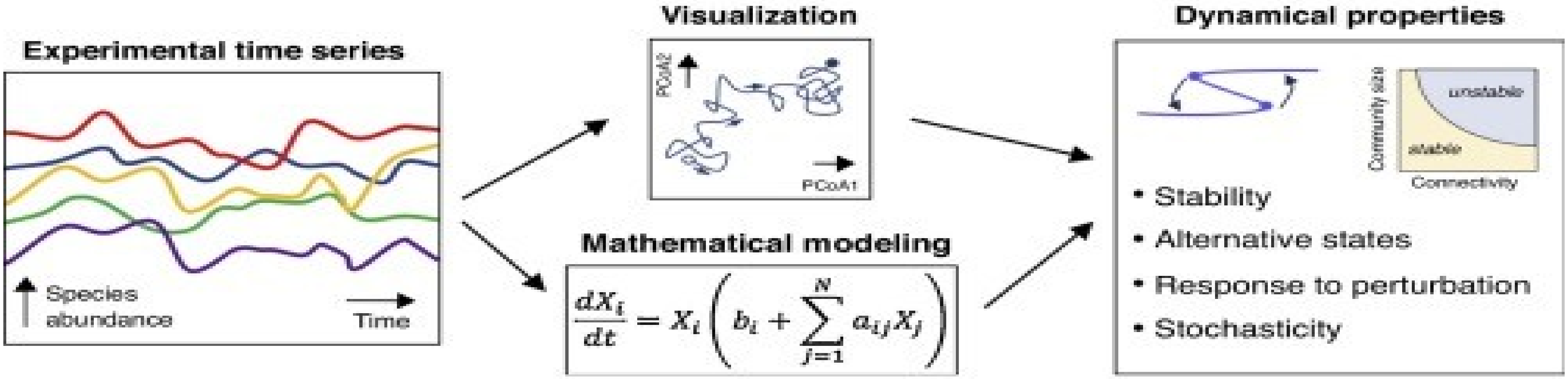
Neutral model

Interaction models

Immigration

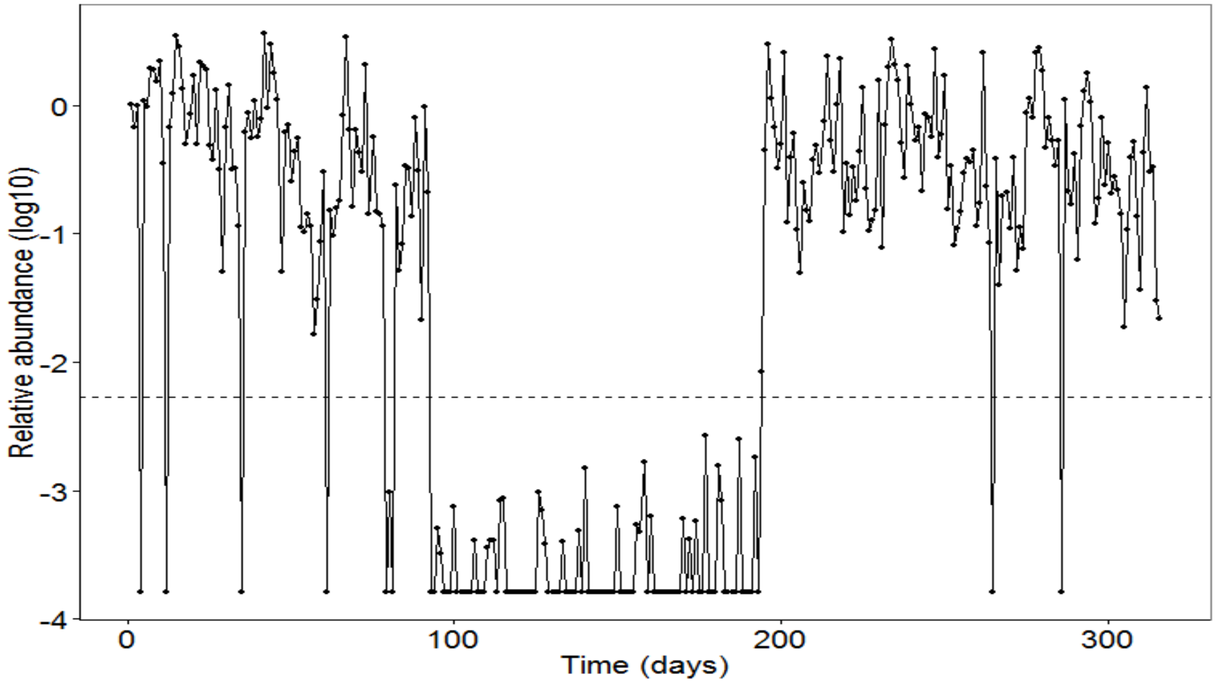
Stochastic variation

Choose the model, estimate parameters



Long and dense time series

1 individual & 300+ days

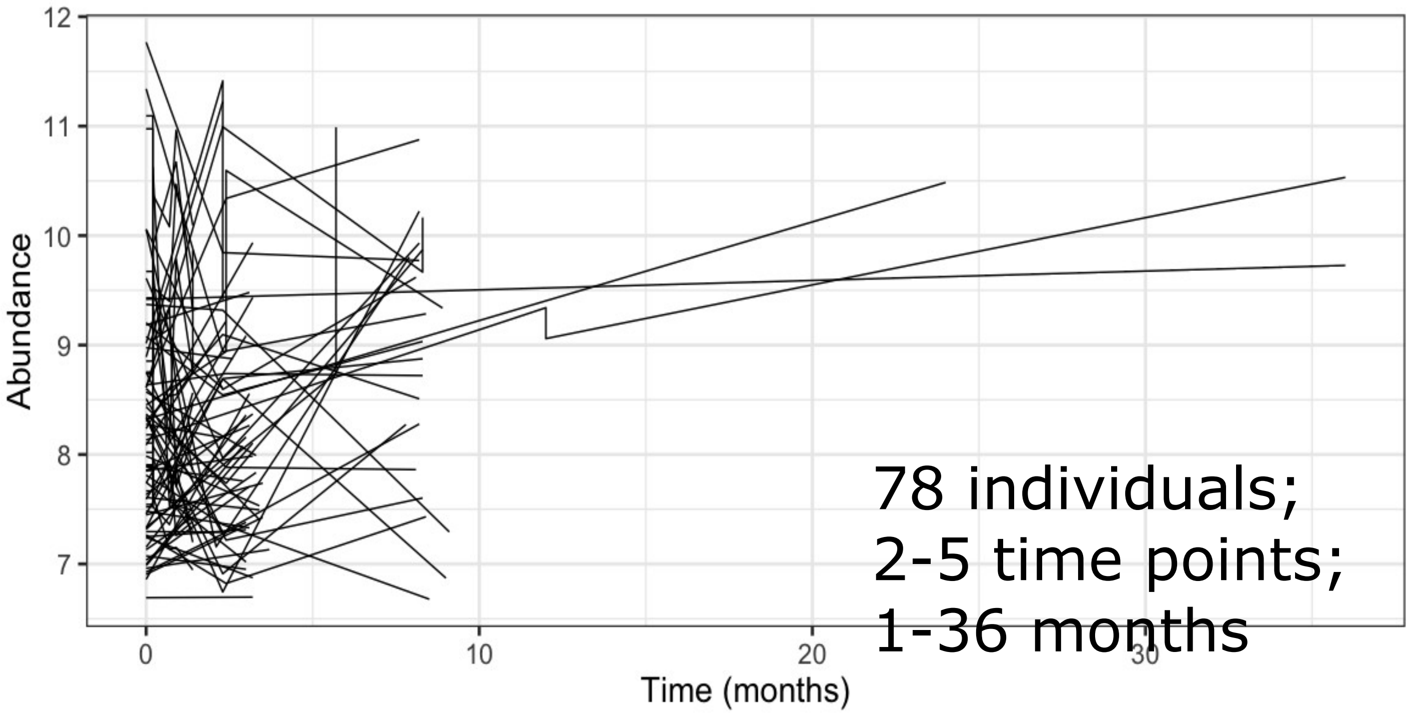


Data: David et al (2012)

Raes Lab / Flemish Gut Flora project now collecting dense time series for hundreds of individuals 150+ days!

Typical microbiome time series: short, sparse, noisy

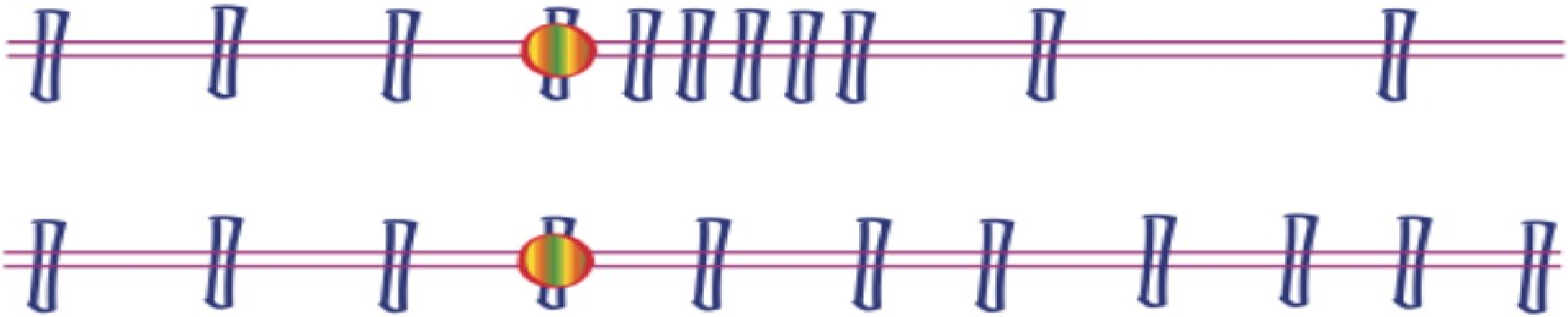
→ challenge for fitting parametric models



78 individuals;
2-5 time points;
1-36 months

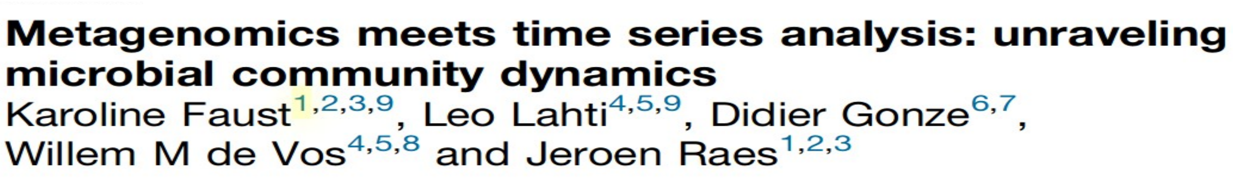
Data:
HITChip Atlas
Lahti et al (2014)

Longitudinal Data Analyses



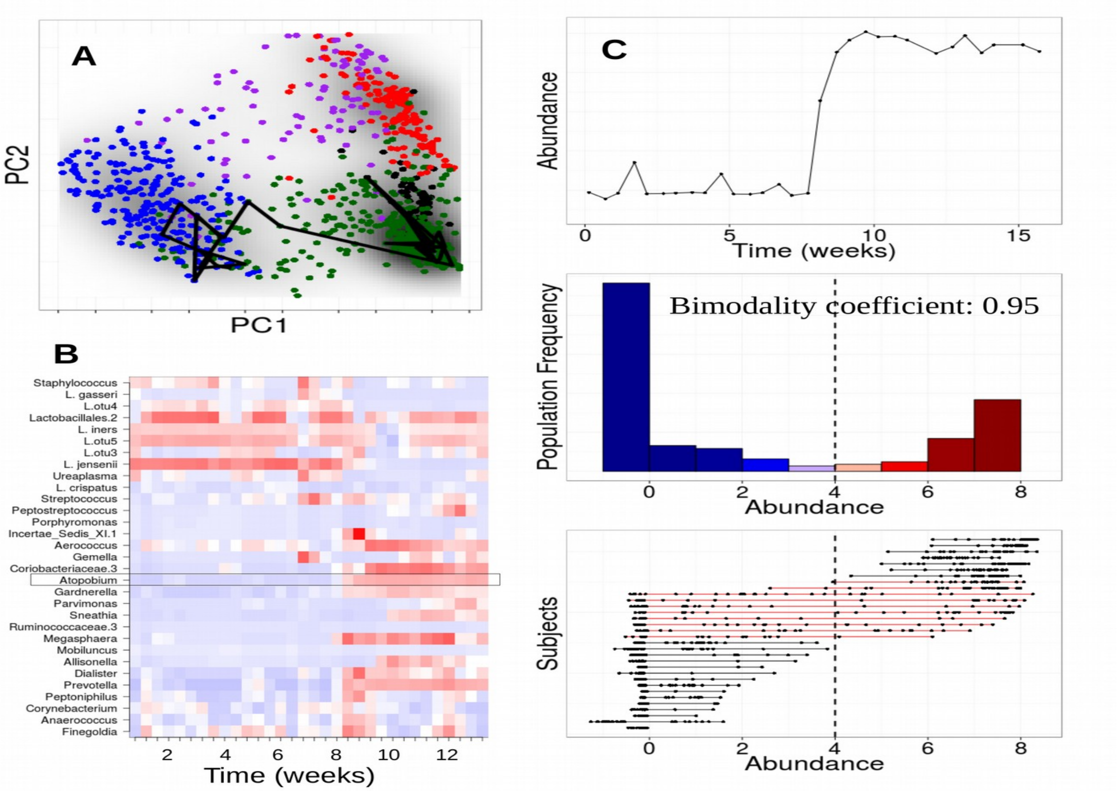
Source: Susan Holmes | http://web.stanford.edu/class/bios221/Short-Phyloseq-Resources.html

Neutral variation



Metagenomics meets time series analysis: unraveling microbial community dynamics

Karoline Faust[1,2,3,9], Leo Lahti[4,5,9], Didier Gonze[6,7],
Willem M de Vos[4,5,8] and Jeroen Raes[1,2,3]



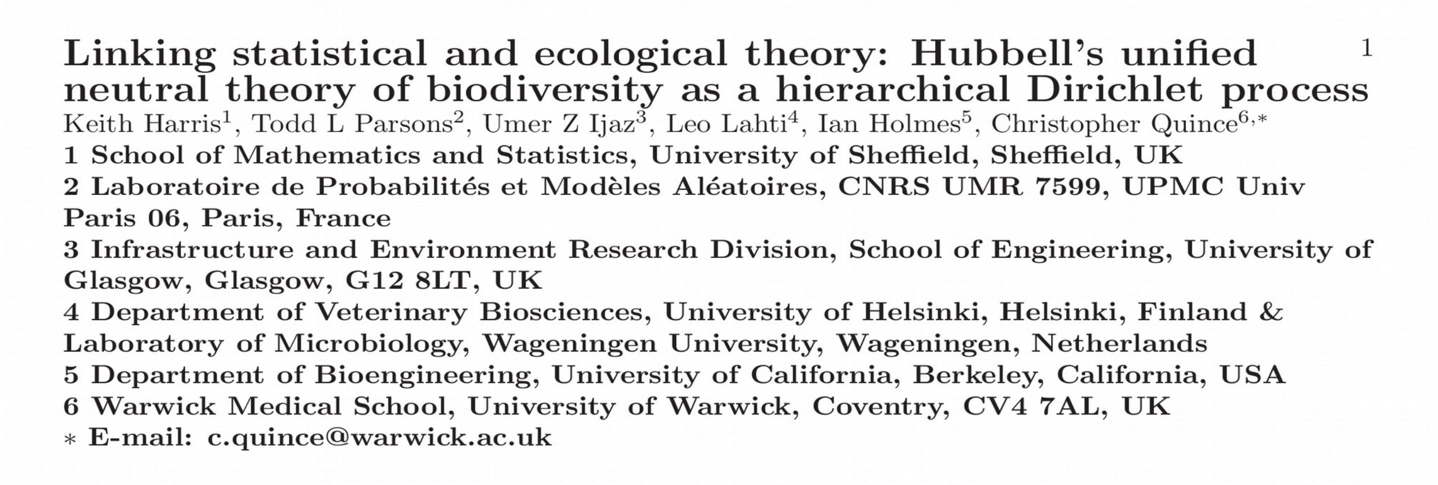
Data: Vaginal microbiota time series from 32 women. Gajer *et al. 2012*

Starting point: no dependence in time?

- For instance, sample data from a distribution that emphasizes the dominance of certain species

  → Communities look similar in all time points even if they are independent, given the model

Can random chance explain the observed diversity of the human gut microbiomes ?



Linking statistical and ecological theory: Hubbell's unified neutral theory of biodiversity as a hierarchical Dirichlet process 1

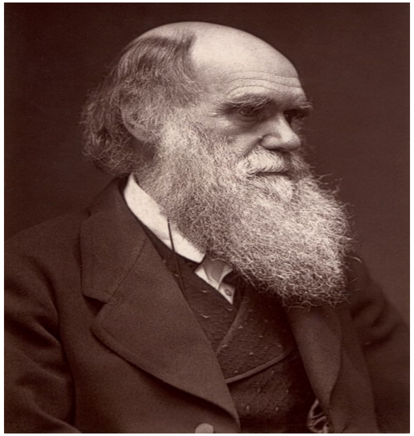
Keith Harris[1], Todd L Parsons[2], Umer Z Ijaz[3], Leo Lahti[4], Ian Holmes[5], Christopher Quince[6,*]
1 School of Mathematics and Statistics, University of Sheffield, Sheffield, UK
2 Laboratoire de Probabilités et Modèles Aléatoires, CNRS UMR 7599, UPMC Univ Paris 06, Paris, France
3 Infrastructure and Environment Research Division, School of Engineering, University of Glasgow, Glasgow, G12 8LT, UK
4 Department of Veterinary Biosciences, University of Helsinki, Helsinki, Finland & Laboratory of Microbiology, Wageningen University, Wageningen, Netherlands
5 Department of Bioengineering, University of California, Berkeley, California, USA
6 Warwick Medical School, University of Warwick, Coventry, CV4 7AL, UK
∗ E-mail: c.quince@warwick.ac.uk

- Unified Neutral Theory of Biodiversity
- Connection to Hierarchical Dirichlet Process
- Validation & Experiments

How to explain the observed variation –classical niche model:

”When we look at the plants and bushes clothing an entangled bank, we are tempted to attribute their proportional numbers and kinds to what we call chance. But how false a view is this!”

– Charles Darwin, The Origin of Species.



Neutral vs. niche models in ecology ?

After >25 years on the Barro Colorado Island tropical forests, Hubbell controversially proposed that.. random chance may in fact be the best explanation of the observerd biodiversity (Hubbell 2001).

Functional equivalence hypothesis

Differences between individuals are neutral in terms of fitness, regardless of their species -> Identical *per capita* demographic rates (birth, death) - At least within specific taxonomic guild.

-> No competition but stochastic fluctuations !

How much niche differences affect community assembly, stability and resilience ?

Hubbell:
Is there a limiting niche similarity for species in functional groups? –> *No evidence in the investigated tree communities*

How many coexisting tree species can be classified in the same functional group? -> *Arbitrarily many*

Mainland – Island model

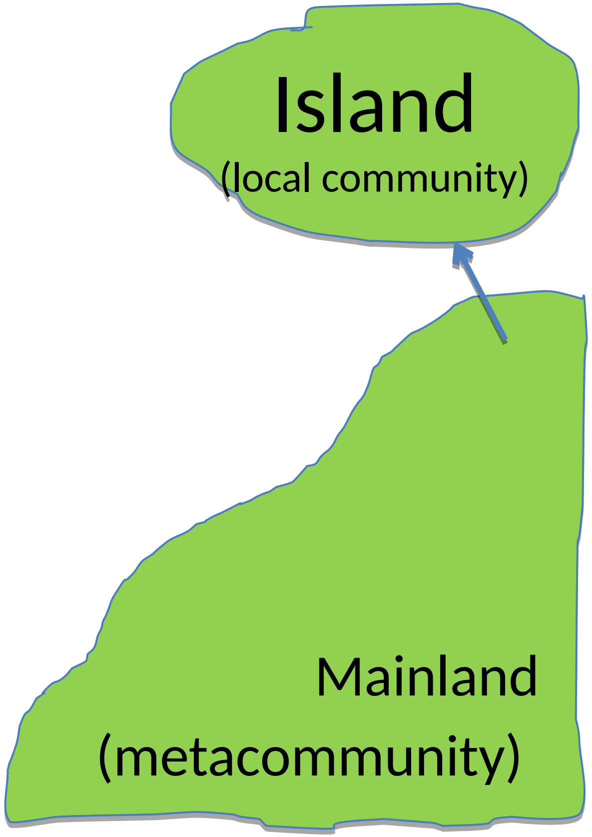
Metacommunity (‘mainland’): diversity affected by size, speciation and extinction rates

Local community (‘island’) -> immigration rate?

Caswell 1976: single local community + migration

Hubbell 2001: many local communities + neutrality

Etienne 2004: exact likelihood for single-site model



Limitations with the standard models:

- Single site not sufficient for reliable model fit
- Niche models can generate identical predictions
- Complexity of the full model: many islands; varying immigration rates & population sizes (two-stage approximations proposed by Etienne 2007-2009)
- Fixed metacommunity vs. potentially infinite species pool
- Limited scalability
- Lack of tractable and accurate algorithms for the full multi-

Community with J individuals from two species

Neutral model of local community dynamics

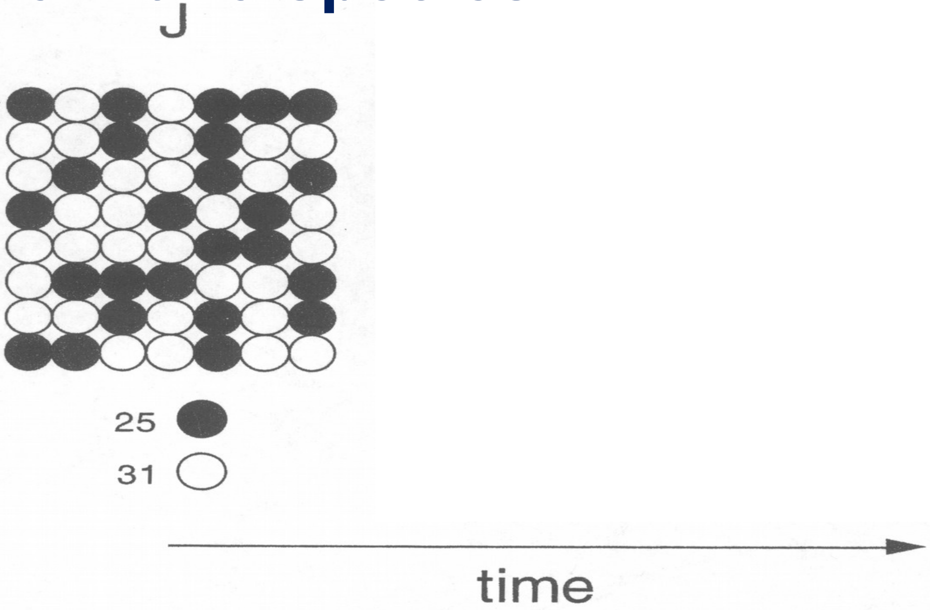


FIG. 4.1. Cartoon of one disturbance cycle in a model community undergoing zero-sum ecological drift. At the beginning of the cycle are two species whose individuals occupy all sites or resources (*left*).

Figure: Hubbell (2001)

Disturbance removes D individuals

Neutral model of local community dynamics

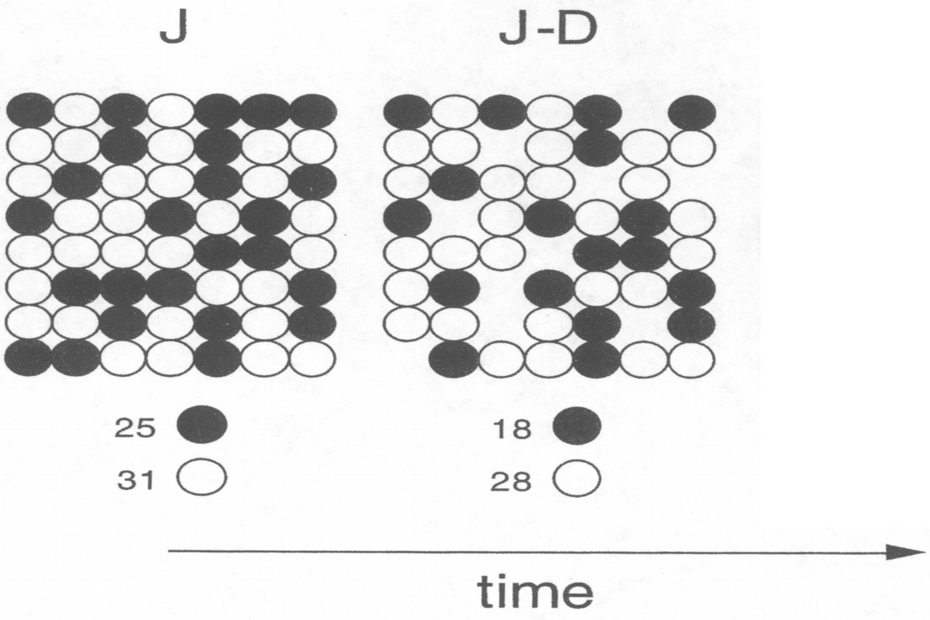


FIG. 4.1. Cartoon of one disturbance cycle in a model community undergoing zero-sum ecological drift. At the beginning of the cycle are two species whose individuals occupy all sites or resources (*left*). Immediately after the disturbance, which killed several individuals of both species, vacant sites or unutilized resources are opened up (*middle*).

Figure: Hubbell (2001)

Neutral model: random drift + immigration

Community dynamics:

1. Stochastic birth/death dynamics: random drift
2. Random immigration from metacommunity

Assumptions:

- Species ecologically equivalent on *per capita* basis
- Zero sum game: fixed community size ("large landscapes are always saturated with individuals")

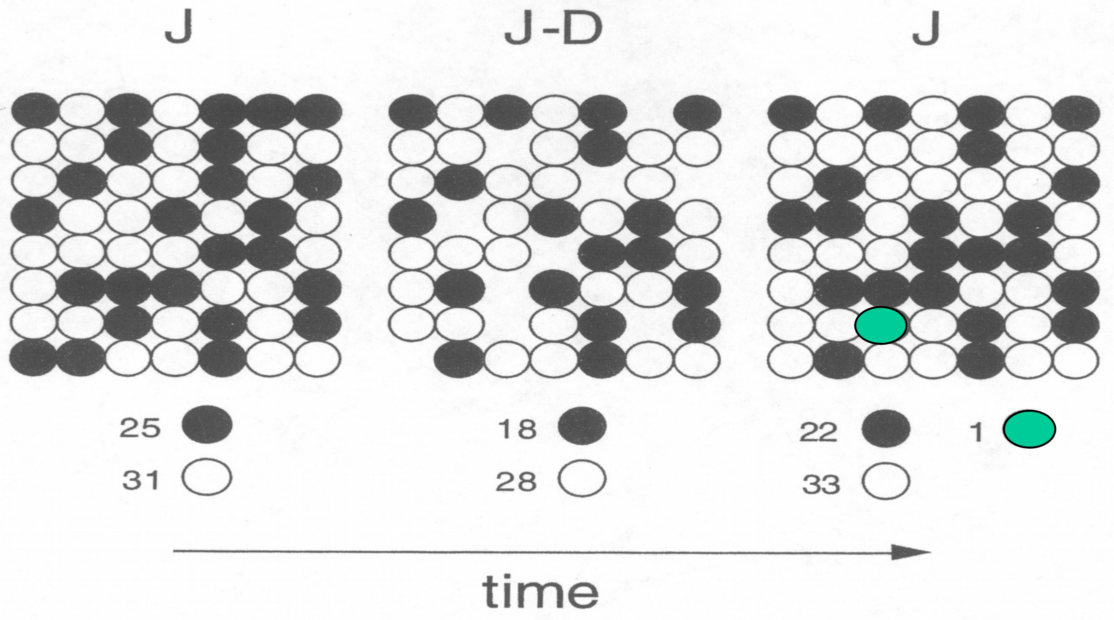
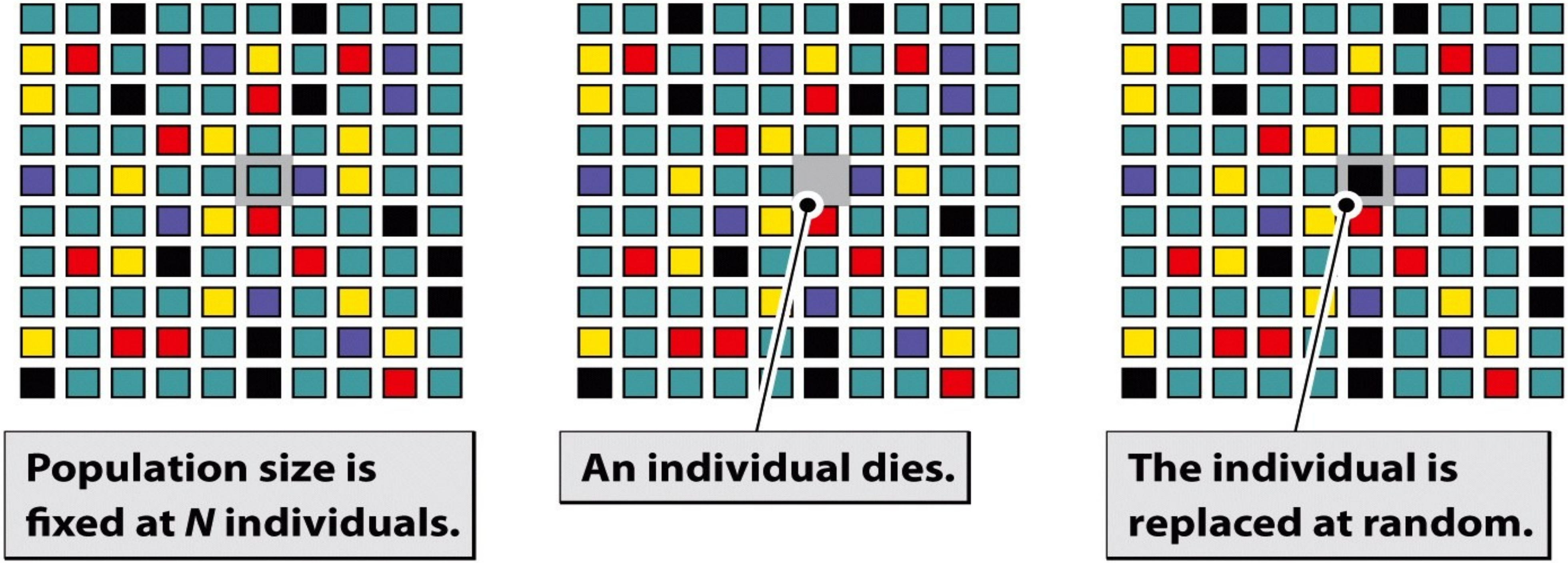


FIG. 4.1. Cartoon of one disturbance cycle in a model community undergoing zero-sum ecological drift. At the beginning of the cycle are two species whose individuals occupy all sites or resources (*left*). Immediately after the disturbance, which killed several individuals of both species, vacant sites or unutilized resources are opened up (*middle*). These are occupied by recruits from the two species in the local community, and by an immigrant individual of a third species from the metacommunity source area (*right*).

Figure: Hubbell (2001)

Random drift in community assembly



Population size is fixed at *N* individuals.

An individual dies.

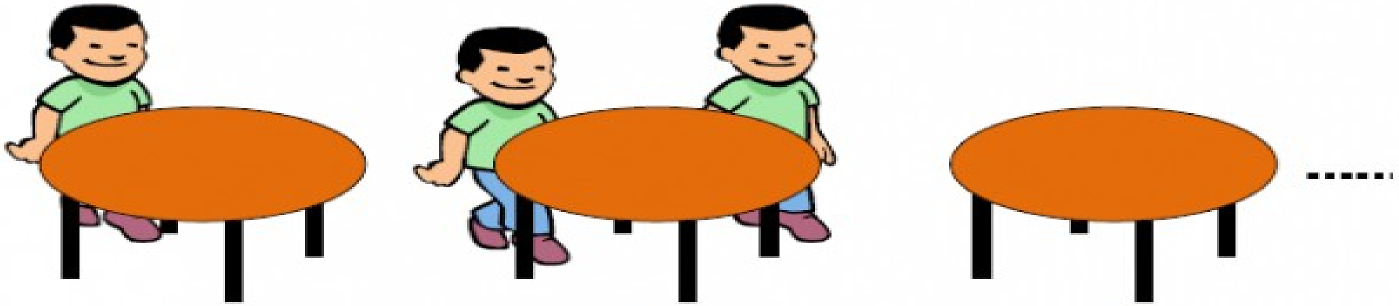
The individual is replaced at random.

Figure 20.26
***The Economy of Nature*, Sixth Edition**
© 2010 W. H. Freeman and Company

DP as Chinese Restaurant Process (CRP)

Future samples derive from new species (table) with prob. proportional to θ and join existing species (table) with prob. proportional to their size

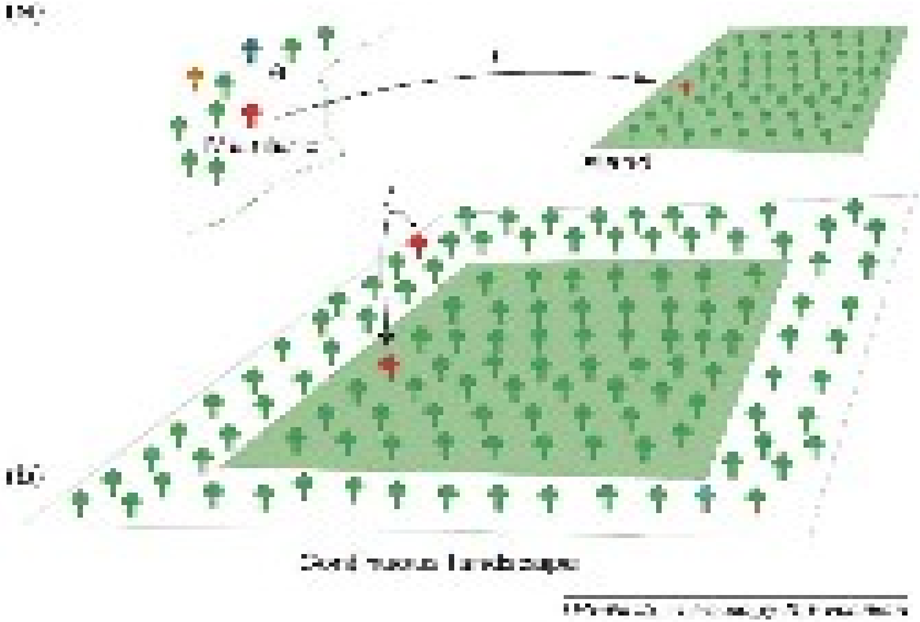
Generates conditional samples marginalised over GEM



$P(z_i = c \mid c_{-i}) =$	1	0	0
	$\frac{1}{1+\theta}$	$\frac{\theta}{1+\theta}$	0
	$\frac{1}{2+\theta}$	$\frac{1}{2+\theta}$	$\frac{\theta}{2+\theta}$
	$\frac{1}{3+\theta}$	$\frac{2}{3+\theta}$	$\frac{\theta}{3+\theta}$

blog.datumbox.com/the-dirichlet-process-the-chinese-restaurant-process-and-other-representations/

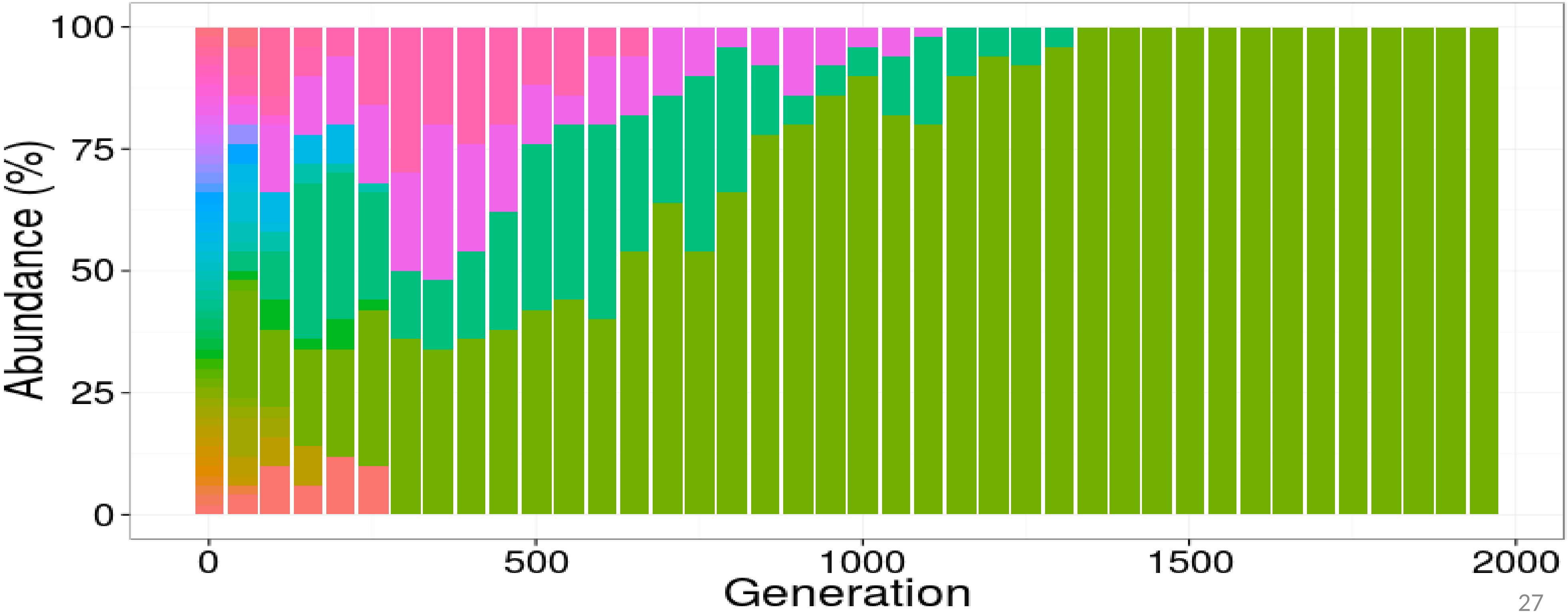
HUBBELL'S UNIFIED NEUTRAL THEORY OF BIODIVERSITY AND BIOGEOGRAPHY (UNTB)



Alonso, Etienne & McKane (2006).

Single-species dominance also from random walk !

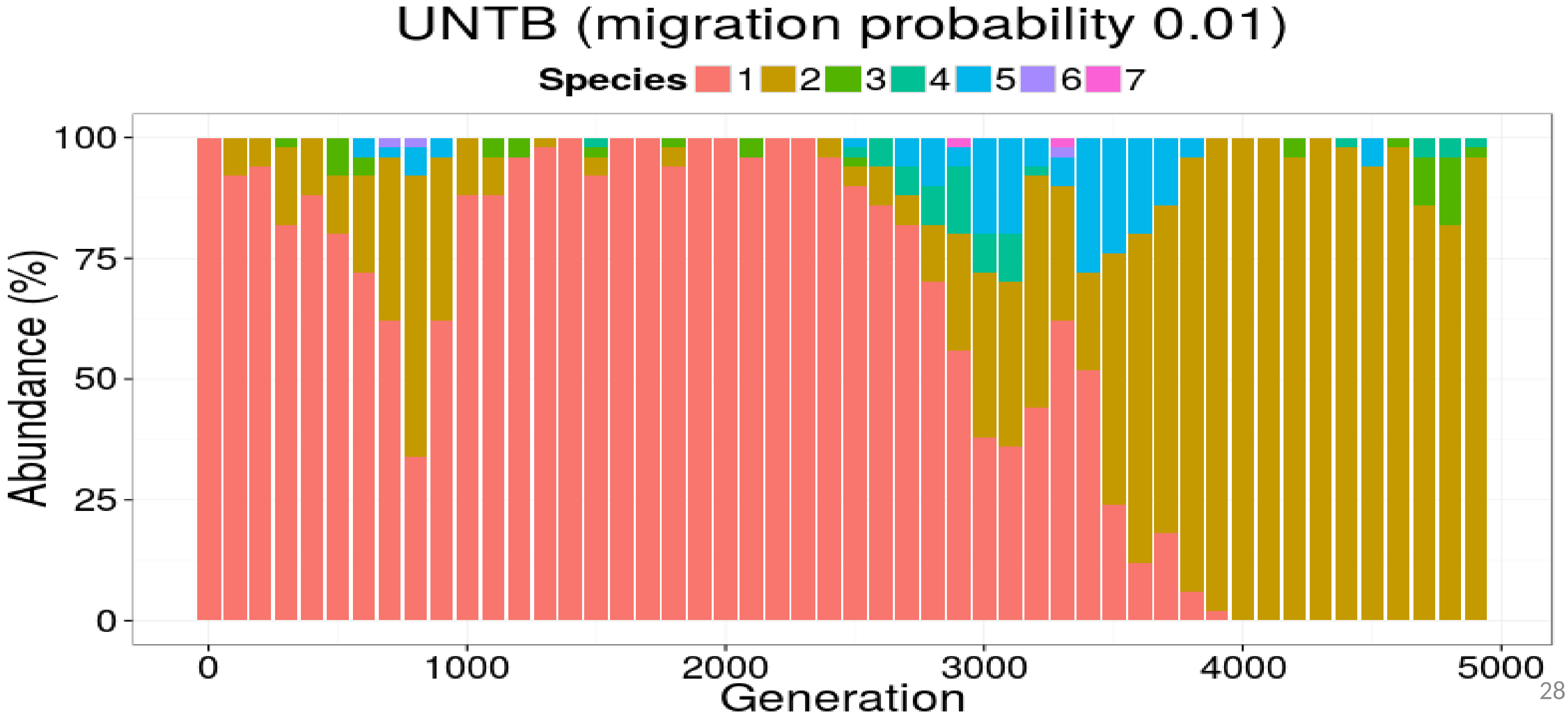
Random drift + No migration + Fixed community size



Random migration as ecological driver ?

Random drift + **Small migration / speciation** + Fixed community size

Drastic shifts in community dominance by different species !



Testing the model: rank-abundance curves

Neutral Theory: predicted species abundance distributions (SAD) match real observations

Fundamental biodiversity parameter: $\theta = 2J\nu$
J = metacommunity size
ν = speciation rate

Problems with single-site model:

- Single site not sufficient for reliable model fit
- Niche models can generate identical SADs (Chisholm & Pacala 2010).

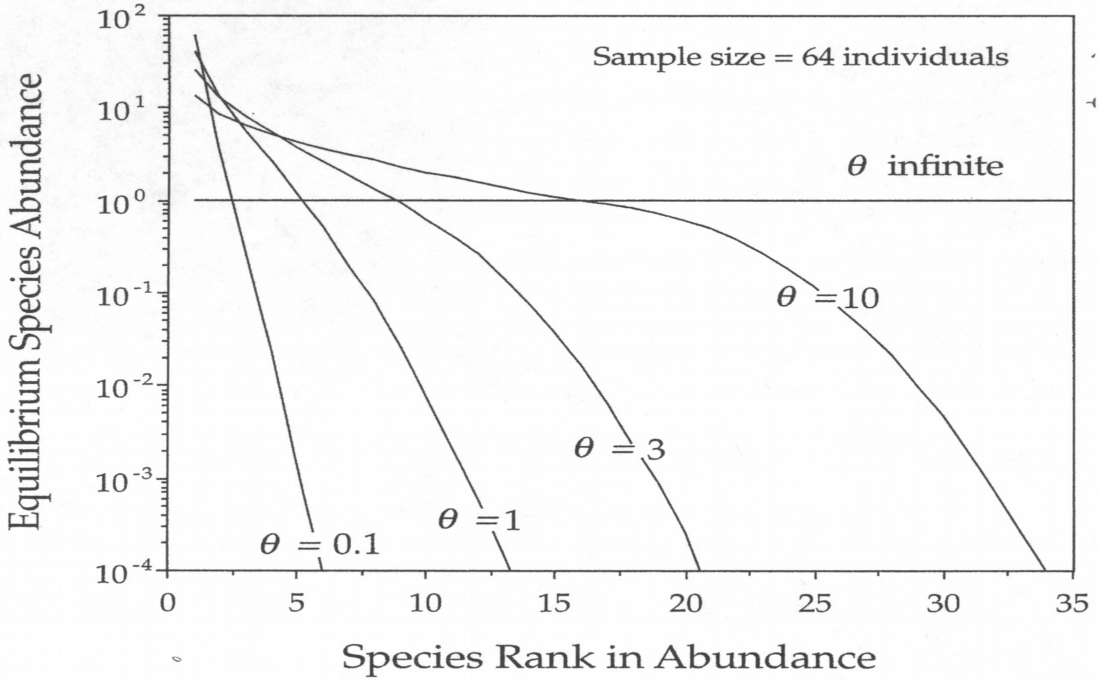


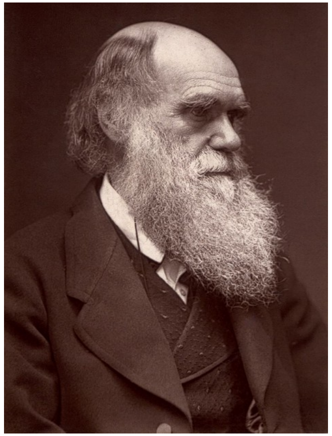
FIG. 5.2. Expected metacommunity dominance-diversity distributions for a sample of 64 individuals, for various values of the parameter, θ. When θ is small, the expected dominance-diversity curve is geometric-like. As θ becomes larger, the expected dominance-diversity curve becomes lognormal-like. As $\theta \to \infty$, the distribution approaches a horizontal line. In the limit, when θ is infinite, every individual in the sample is a new and different species, however large a sample is taken.

Figure: Hubbell 2001

Neutral model of biodiversity suggests no interaction: could random chance explain microbiome variation?

Niche model ”When we look at the plants and bushes clothing an entangled bank, we are tempted to attribute their proportional numbers and kinds to what we call chance. But how false a view is this!” (**Darwin**, *The Origin of Species)*

Neutral model After >25 years on the Barro Colorado Island tropical forests, **Hubbell** proposed that.. random variation could in fact best explain observed biodiversity (Hubbell 2001).



Microbiomics data

- Microbial community data in a frequency matrix:

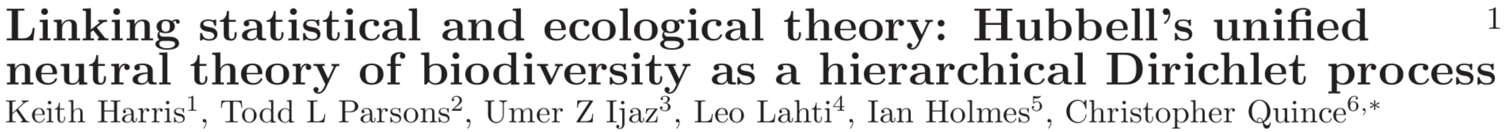
n indexes samples s indexes taxa

$$\mathbf{X} x_{n,s} n = 1, \ldots, N s = 1, \ldots, S$$

	Taxa1	Taxa2	Taxa3	Taxa4
Sample1	111	52	22	98
Sample2	50	10	0	30
Sample3	0	45	65	0
Sample4	0	100	40	0

- Discrete, sparse, variable sample size
- Up to thousands of sites; millions of individuals
- Tens of thousands of individuals per site

-> Principled approaches needed to fit such models efficiently !



Linking statistical and ecological theory: Hubbell's unified neutral theory of biodiversity as a hierarchical Dirichlet process

Keith Harris[1], Todd L Parsons[2], Umer Z Ijaz[3], Leo Lahti[4], Ian Holmes[5], Christopher Quince[6,*]

$$X_i \mid N_i, p_i \sim MN(N_i, p_i)$$
$$p_i \mid I_i, \beta \sim DP(I_i, \beta)$$
$$\beta \mid \theta \sim Stick(\theta) \sim DP(\theta, 1)$$

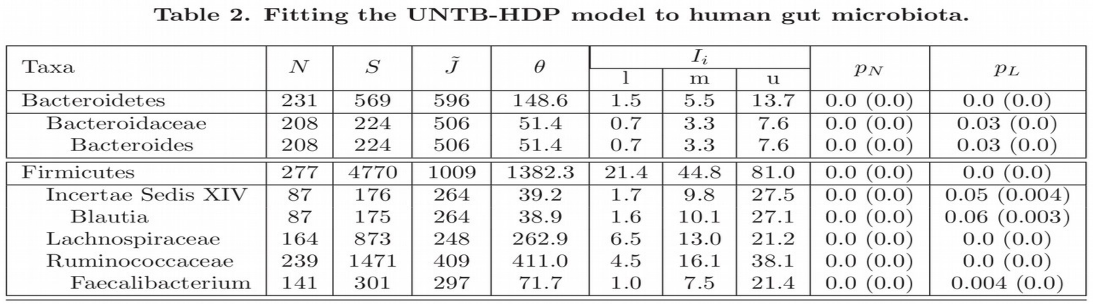
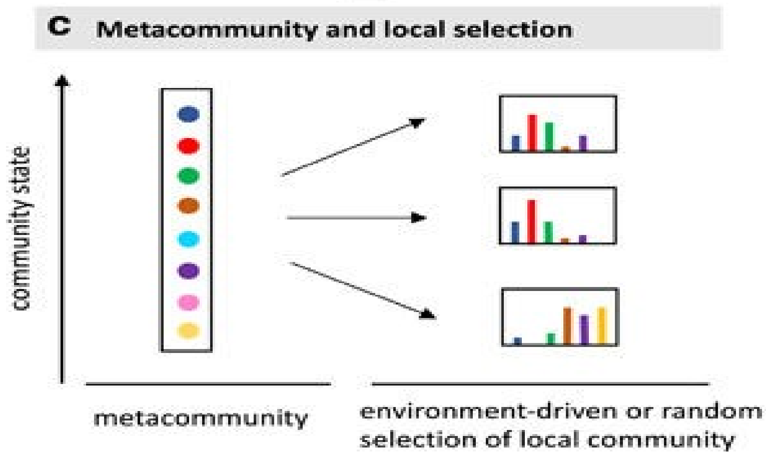


Table 2. Fitting the UNTB-HDP model to human gut microbiota.

Taxa	N	S	$\tilde{J}$	θ	I_i			p_N	p_L
					l	m	u		
Bacteroidetes	231	569	596	148.6	1.5	5.5	13.7	0.0 (0.0)	0.0 (0.0)
Bacteroidaceae	208	224	506	51.4	0.7	3.3	7.6	0.0 (0.0)	0.03 (0.0)
Bacteroides	208	224	506	51.4	0.7	3.3	7.6	0.0 (0.0)	0.03 (0.0)
Firmicutes	277	4770	1009	1382.3	21.4	44.8	81.0	0.0 (0.0)	0.0 (0.0)
Incertae Sedis XIV	87	176	264	39.2	1.7	9.8	27.5	0.0 (0.0)	0.05 (0.004)
Blautia	87	175	264	38.9	1.6	10.1	27.1	0.0 (0.0)	0.06 (0.003)
Lachnospiraceae	164	873	248	262.9	6.5	13.0	21.2	0.0 (0.0)	0.0 (0.0)
Ruminococcaceae	239	1471	409	411.0	4.5	16.1	38.1	0.0 (0.0)	0.0 (0.0)
Faecalibacterium	141	301	297	71.7	1.0	7.5	21.4	0.0 (0.0)	0.004 (0.0)



Gut microbiome (500k seqs; 278 subjects)

Neutrality depends on taxonomic level

Bacteroidetes have less immigration than spore-forming Firmicutes

Applications (Harris et al. PIEEE 2017)

- Classical tropical trees data set (classical example)
- Human gut microbiome (570,851 sequences; 278 subjects)

Gut microbiome neutrality ?

- Depends on taxonomic level
- Bacteroidetes have lower immigration than the spore-forming Firmicutes

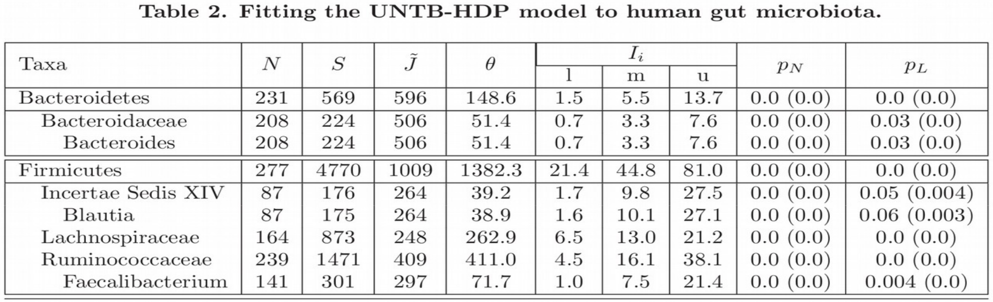


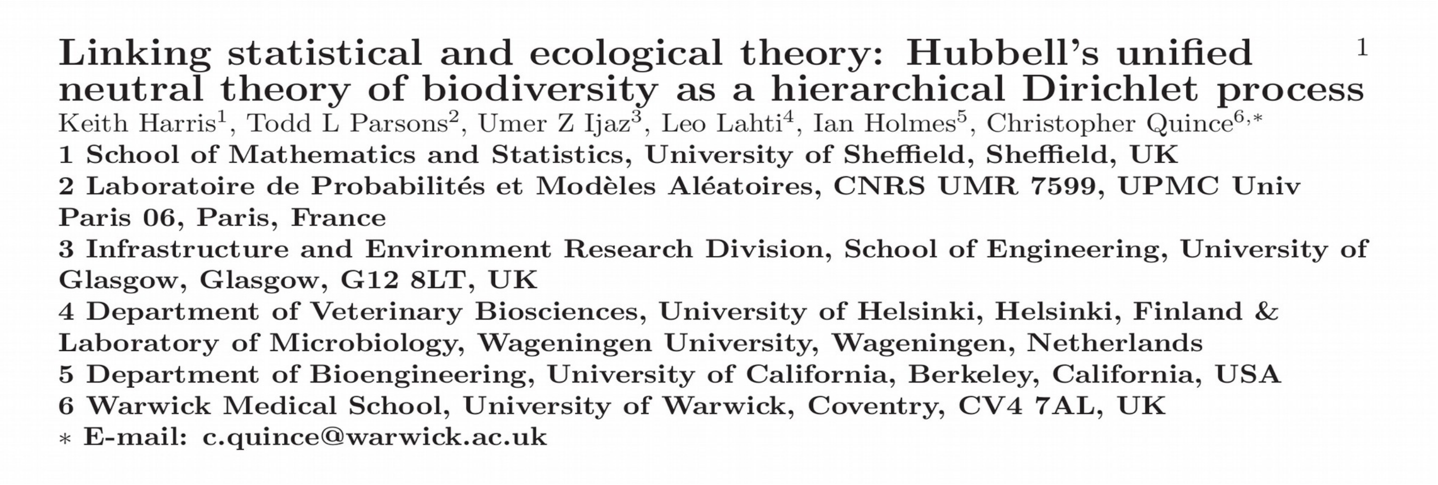
Table 2. Fitting the UNTB-HDP model to human gut microbiota.

Taxa	N	S	$\tilde{J}$	θ	I_i			p_N	p_L
					l	m	u		
Bacteroidetes	231	569	596	148.6	1.5	5.5	13.7	0.0 (0.0)	0.0 (0.0)
Bacteroidaceae	208	224	506	51.4	0.7	3.3	7.6	0.0 (0.0)	0.03 (0.0)
Bacteroides	208	224	506	51.4	0.7	3.3	7.6	0.0 (0.0)	0.03 (0.0)
Firmicutes	277	4770	1009	1382.3	21.4	44.8	81.0	0.0 (0.0)	0.0 (0.0)
Incertae Sedis XIV	87	176	264	39.2	1.7	9.8	27.5	0.0 (0.0)	0.05 (0.004)
Blautia	87	175	264	38.9	1.6	10.1	27.1	0.0 (0.0)	0.06 (0.003)
Lachnospiraceae	164	873	248	262.9	6.5	13.0	21.2	0.0 (0.0)	0.0 (0.0)
Ruminococcaceae	239	1471	409	411.0	4.5	16.1	38.1	0.0 (0.0)	0.0 (0.0)
Faecalibacterium	141	301	297	71.7	1.0	7.5	21.4	0.0 (0.0)	0.004 (0.0)

Novel Covariance-Based Neutrality Test of Time-Series Data Reveals Asymmetries in Ecological and Economic Systems

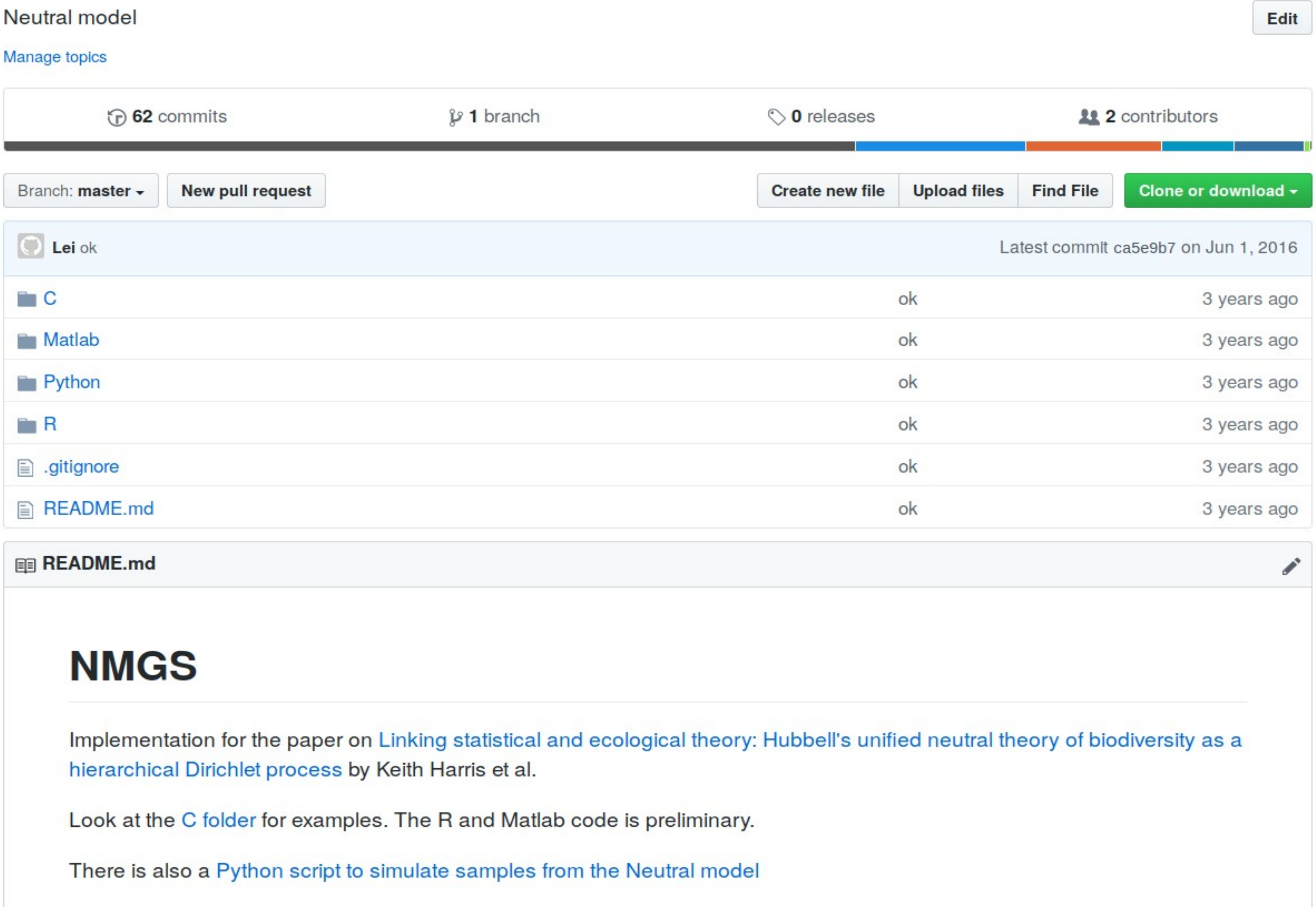
Alex D. Washburne, Joshua W. Burby, Daniel Lacker

Published: September 30, 2016 • https://doi.org/10.1371/journal.pcbi.1005124 • >> See the preprint



Linking statistical and ecological theory: Hubbell's unified neutral theory of biodiversity as a hierarchical Dirichlet process

Keith Harris[1], Todd L Parsons[2], Umer Z Ijaz[3], Leo Lahti[4], Ian Holmes[5], Christopher Quince[6,*]
1 School of Mathematics and Statistics, University of Sheffield, Sheffield, UK
2 Laboratoire de Probabilités et Modèles Aléatoires, CNRS UMR 7599, UPMC Univ Paris 06, Paris, France
3 Infrastructure and Environment Research Division, School of Engineering, University of Glasgow, Glasgow, G12 8LT, UK
4 Department of Veterinary Biosciences, University of Helsinki, Helsinki, Finland & Laboratory of Microbiology, Wageningen University, Wageningen, Netherlands
5 Department of Bioengineering, University of California, Berkeley, California, USA
6 Warwick Medical School, University of Warwick, Coventry, CV4 7AL, UK
∗ E-mail: c.quince@warwick.ac.uk



Neutral model

Lei ok

Latest commit ca5e9b7 on Jun 1, 2016

C	ok	3 years ago
Matlab	ok	3 years ago
Python	ok	3 years ago
R	ok	3 years ago
.gitignore	ok	3 years ago
README.md	ok	3 years ago

README.md

NMGS

Implementation for the paper on Linking statistical and ecological theory: Hubbell's unified neutral theory of biodiversity as a hierarchical Dirichlet process by Keith Harris et al.

Look at the C folder for examples. The R and Matlab code is preliminary.

There is also a Python script to simulate samples from the Neutral model

Interaction models

Bistable system

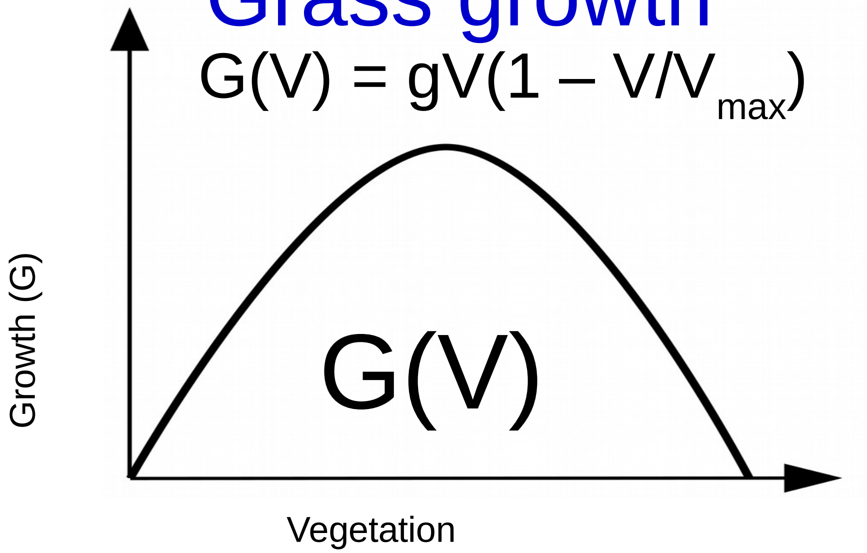
$$\frac{dV}{dt} = G(V) - c(V)H$$

Noy-Meir 1975
V : Vegetation
G(V) : Growth per unit time

c(V) : Consumption of vege
H : Sheep

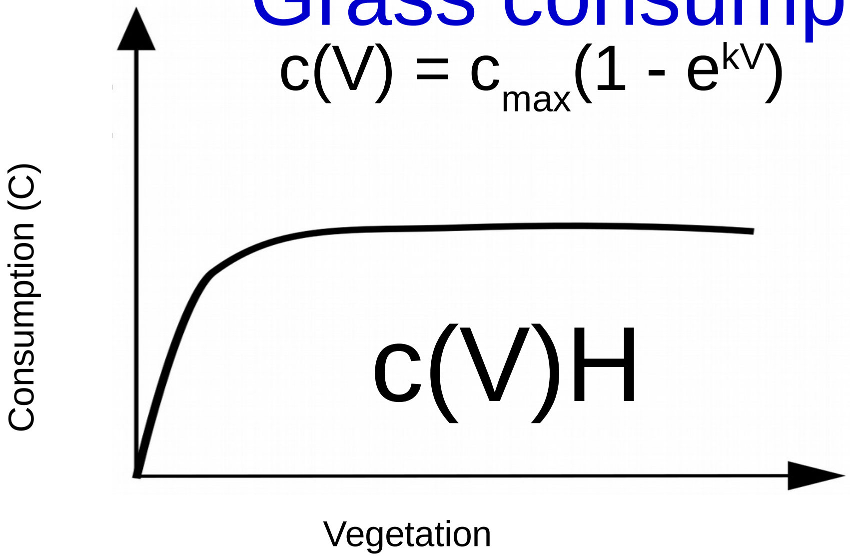
Grass growth

$G(V) = gV(1 – V/V_{max})$



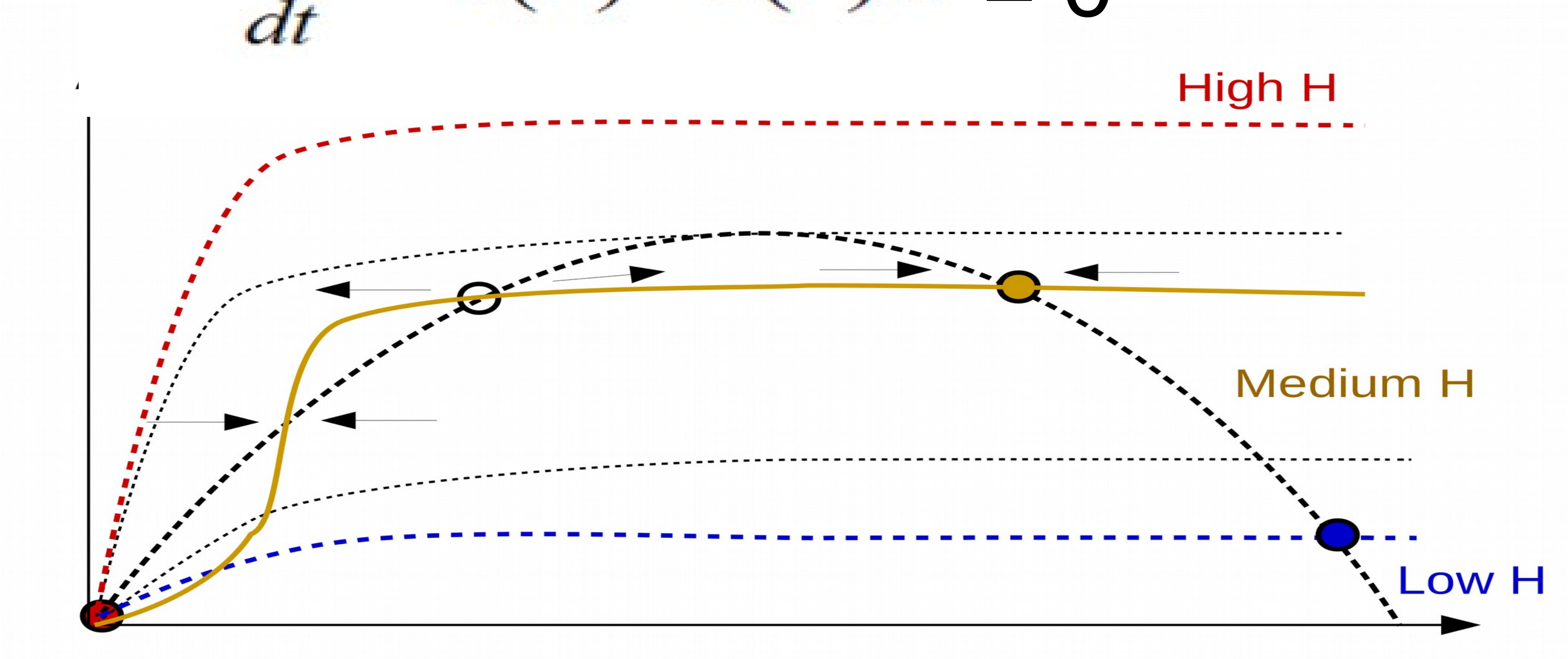
Grass consumption

$c(V) = c_{max}(1 - e^{kV})$



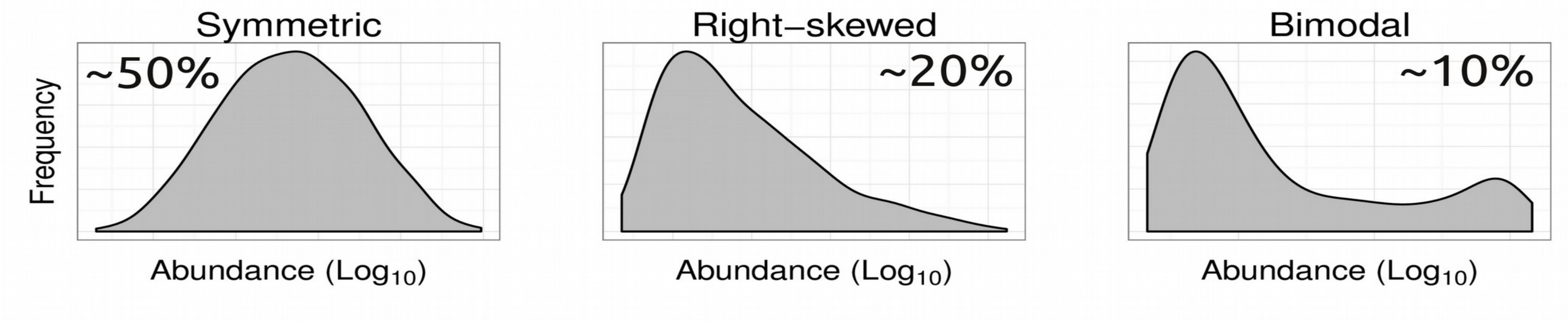
Equilibrium (Growth ~ Consumption):

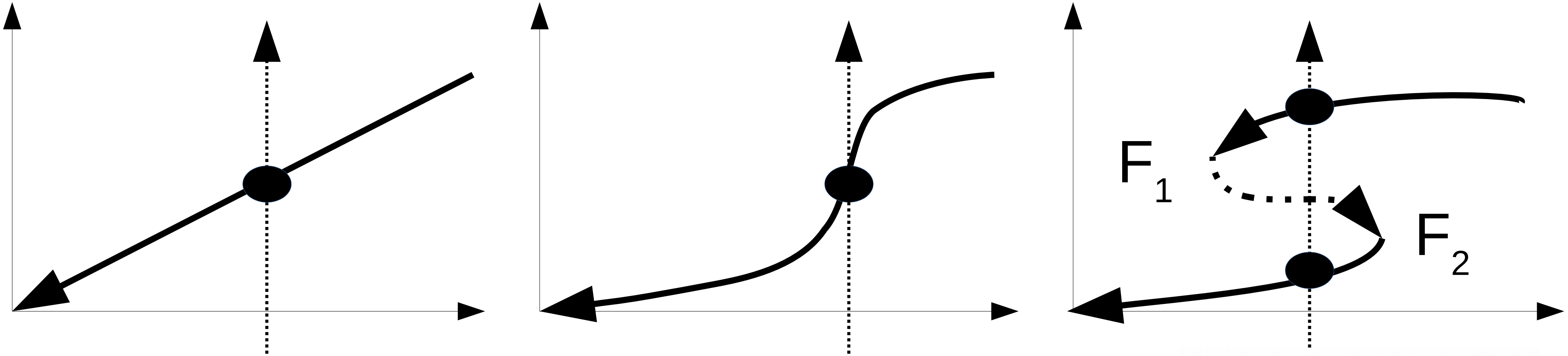
$$\frac{dV}{dt} = G(V) - c(V)H = 0$$



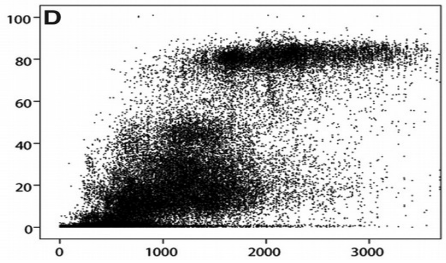
Growth (G) and

Vegetation (V)





Environmental variation

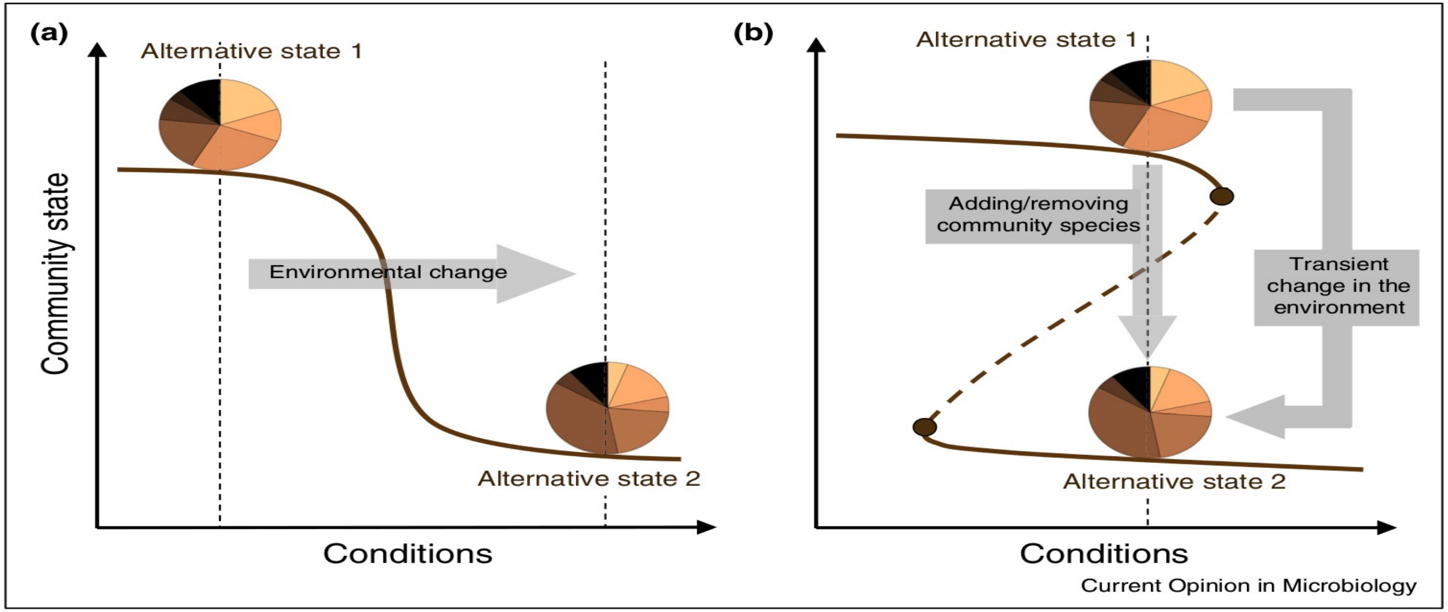


Alternative (stable) states

Diversity ?

State induced by
external factors

Intrinsic stability:
robust to external factors



Environmental or host factor (e.g. body-mass index)

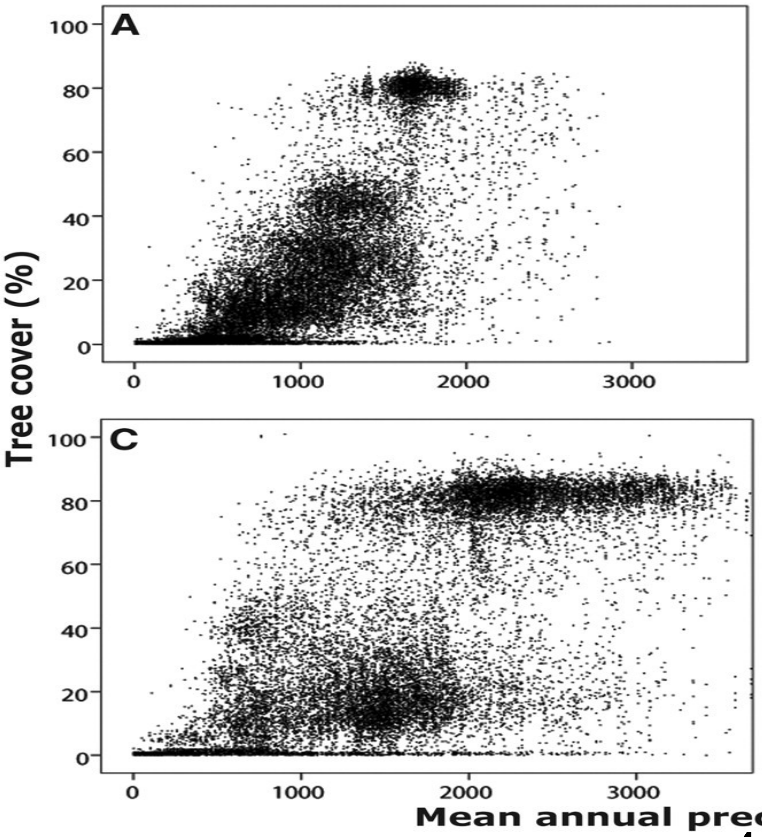
Faust et al. Curr. Op. Microbiol. 2015

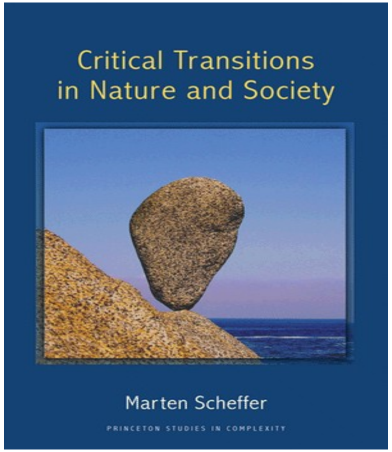
Science 14 October 2011:
Vol. 334 no. 6053 pp. 232-235
DOI: 10.1126/science.1210657

REPORT

Global Resilience of Tropical Forest and Savanna to Critical Transitions

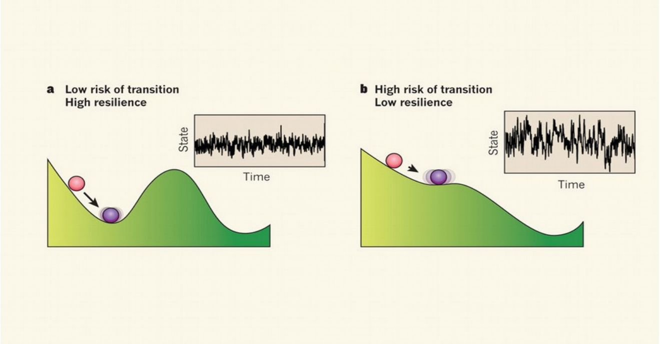
Marina Hirota[1], Milena Holmgren[2,*], Egbert H. Van Nes[1], Marten Scheffer[1]





Fecal transplant induced ecosystem level state shift

Efficient treatment in C. difficile infected patients. Shift from Bacilli- and Proteobacteria-dominated state to a healthy state dominated by Bacteroides and many butyrate producing taxa



Better than antibiotics !

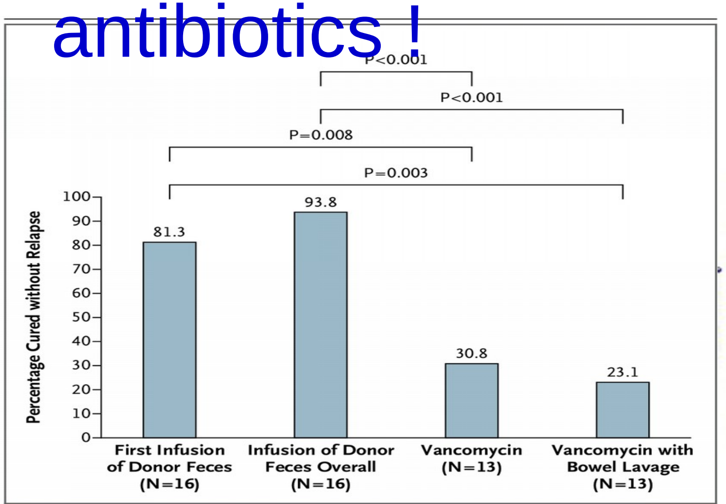
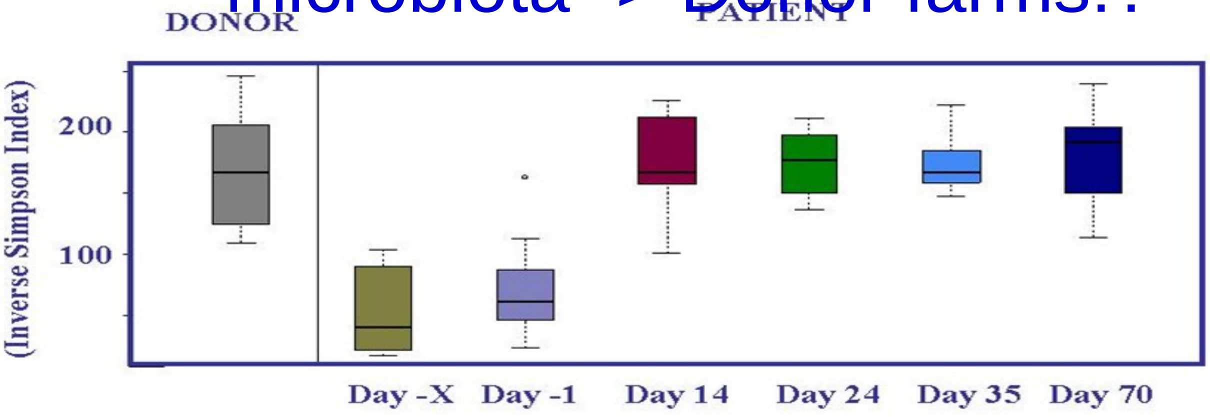


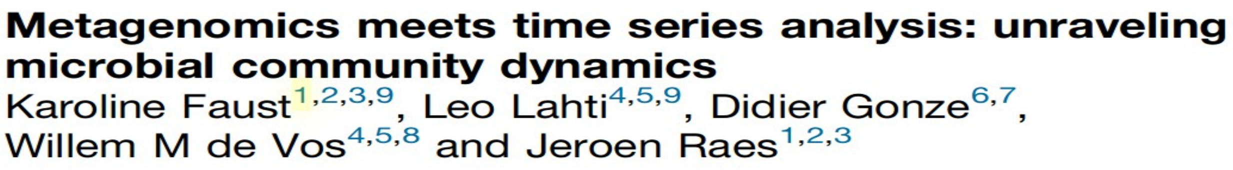
Figure 2. Rates of Cure without Relapse for Recurrent *Clostridium difficile* Infection.

Shown are the proportions of patients who were cured by the infusion of donor feces (first infusion and overall results), by standard vancomycin therapy, and by standard vancomycin therapy plus bowel lavage.

Patient gets donor microbiota -> Donor farms!?



Els van Nood et al., NEJM 368(5) 2013
Fuentes et al. ISME J, 8:1621-33, 2014

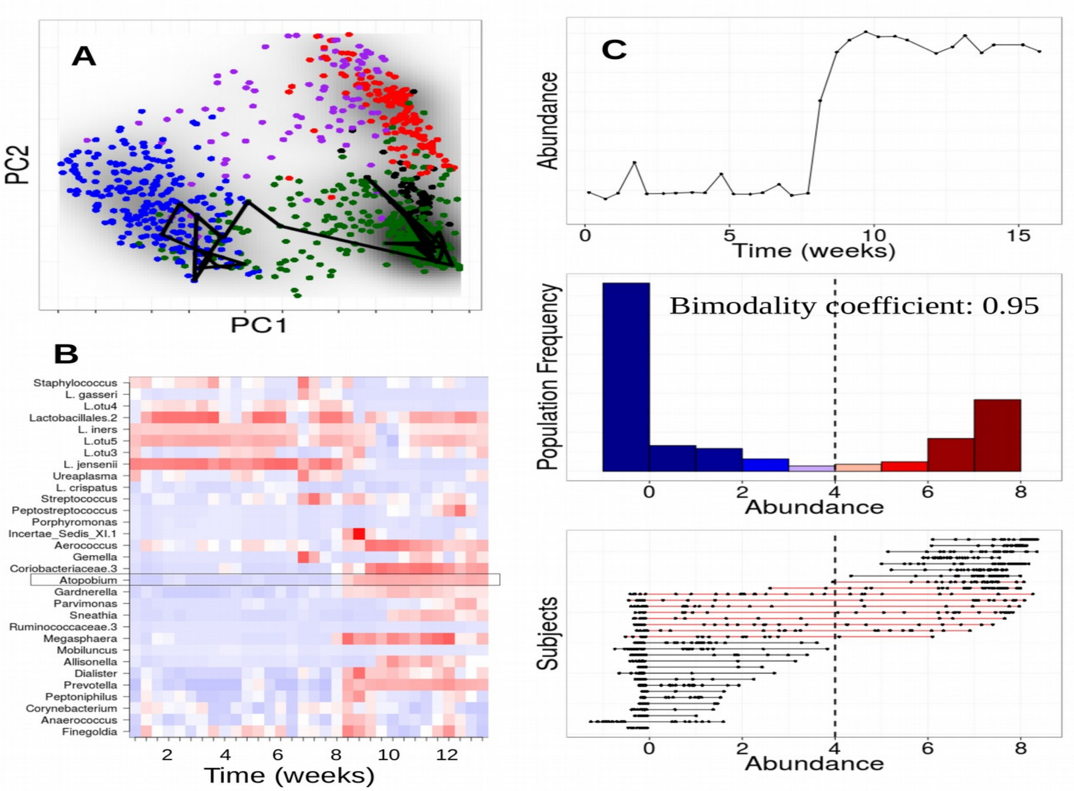


Metagenomics meets time series analysis: unraveling microbial community dynamics

Karoline Faust[1,2,3,9], Leo Lahti[4,5,9], Didier Gonze[6,7], Willem M de Vos[4,5,8] and Jeroen Raes[1,2,3]

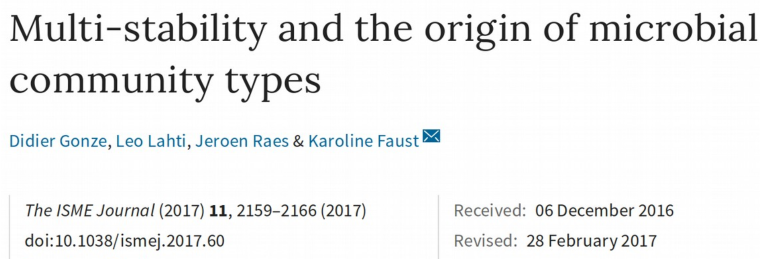
Variation:

- cross-sectional
- spatial
- temporal



Data: Vaginal microbiota time series from 32 women. Gajer *et al.* 2012

Interaction models yield more complex dynamics and predict alternative stable states



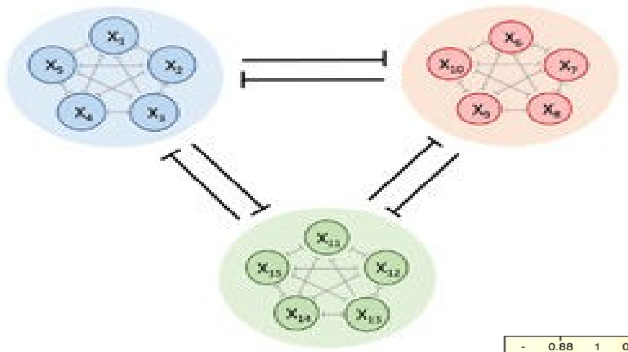
Multi-stability and the origin of microbial community types

Didier Gonze, Leo Lahti, Jeroen Raes & Karoline Faust

The ISME Journal (2017) **11**, 2159–2166 (2017)
doi:10.1038/ismej.2017.60

Received: 06 December 2016
Revised: 28 February 2017

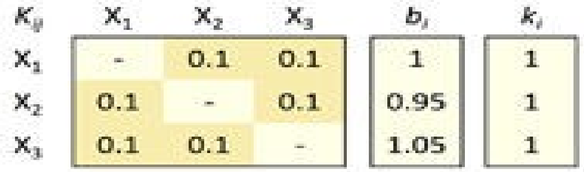
Inter-group inhibition stronger than intra-group inhibition (the smaller the stronger)



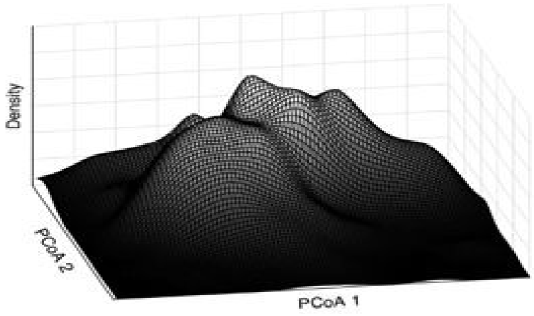
b

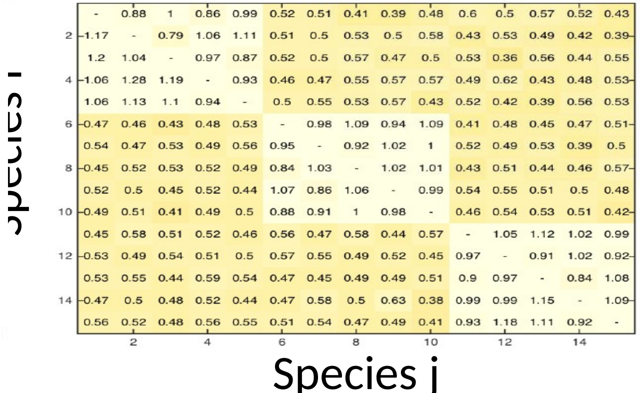
$$\frac{dX_i}{dt} = X_i(b_i f_i(\{X_k\}) - k_i X_i)$$

$$f_i(\{X_k\}) = \prod_{\substack{k=1 \\ k \neq i}}^{N} \frac{K_{ik}^n}{K_{ik}^n + X_k^n}$$



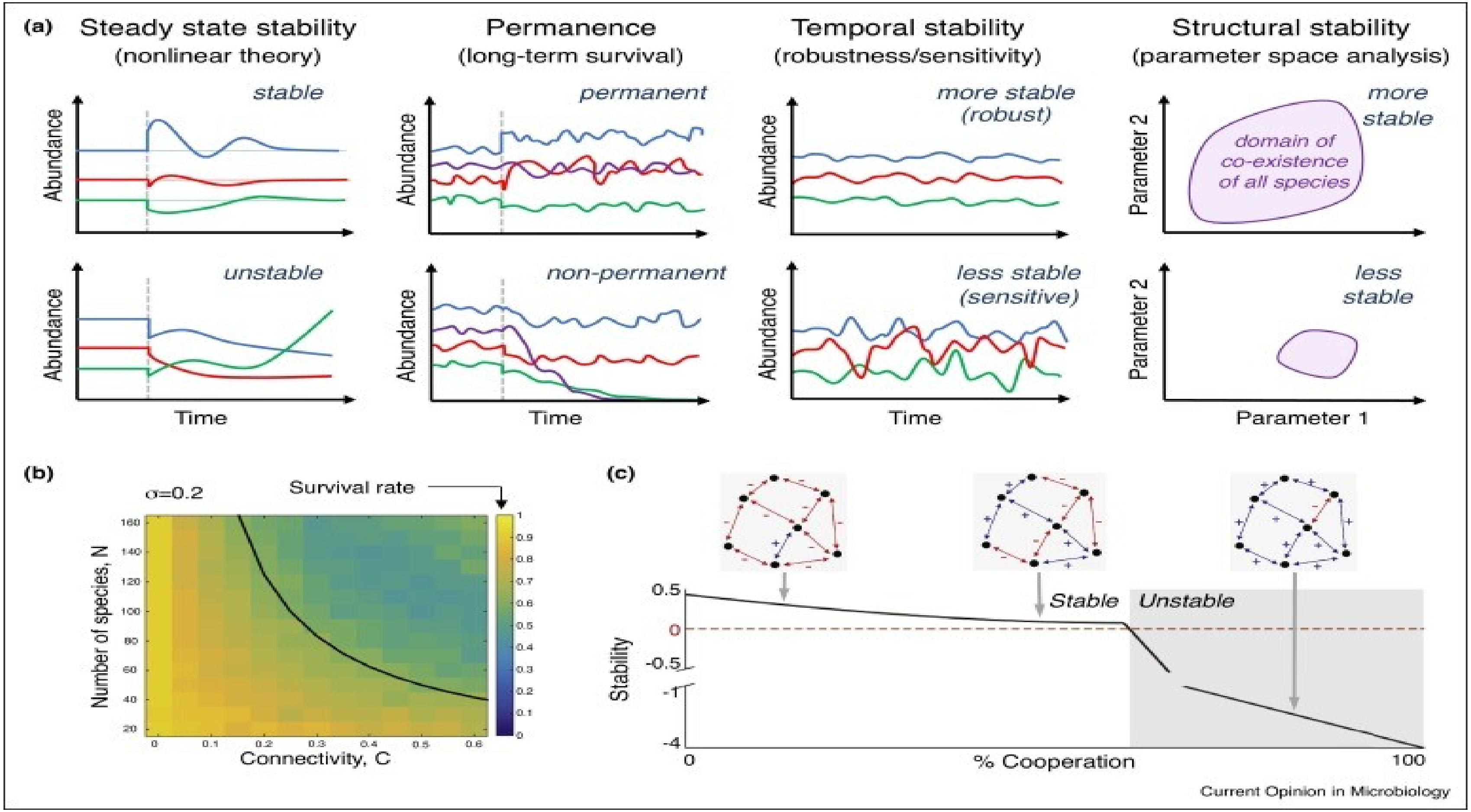
K_{ij}	X_1	X_2	X_3	b_i	k_i
X_1	-	0.1	0.1	1	1
X_2	0.1	-	0.1	0.95	1
X_3	0.1	0.1	-	1.05	1





		2		4		6		8		10		12		14	
	-	0.88	1	0.86	0.99	0.52	0.51	0.41	0.39	0.48	0.6	0.5	0.57	0.52	0.43
2	1.17	-	0.79	1.06	1.11	0.51	0.5	0.53	0.5	0.58	0.43	0.53	0.49	0.42	0.39
	1.2	1.04	-	0.97	0.87	0.52	0.5	0.57	0.47	0.5	0.53	0.36	0.56	0.44	0.55
4	1.06	1.28	1.19	-	0.93	0.46	0.47	0.55	0.57	0.57	0.49	0.62	0.43	0.48	0.53
	1.06	1.13	1.1	0.94	-	0.5	0.55	0.53	0.57	0.43	0.52	0.42	0.39	0.56	0.53
6	0.47	0.46	0.43	0.48	0.53	-	0.98	1.09	0.94	1.09	0.41	0.48	0.45	0.47	0.51
	0.54	0.47	0.53	0.49	0.56	0.95	-	0.92	1.02	1	0.52	0.49	0.53	0.39	0.5
8	0.45	0.52	0.53	0.52	0.49	0.84	1.03	-	1.02	1.01	0.43	0.51	0.44	0.46	0.57
	0.52	0.5	0.45	0.52	0.44	1.07	0.86	1.06	-	0.99	0.54	0.55	0.51	0.5	0.48
10	0.49	0.51	0.41	0.49	0.5	0.88	0.91	1	0.98	-	0.46	0.54	0.53	0.51	0.42
	0.45	0.58	0.51	0.52	0.46	0.56	0.47	0.58	0.44	0.57	-	1.05	1.12	1.02	0.99
12	0.53	0.49	0.54	0.51	0.5	0.57	0.55	0.49	0.52	0.45	0.97	-	0.91	1.02	0.92
	0.53	0.55	0.44	0.59	0.54	0.47	0.45	0.49	0.49	0.51	0.9	0.97	-	0.84	1.08
14	0.47	0.5	0.48	0.52	0.44	0.47	0.58	0.5	0.63	0.38	0.99	0.99	1.15	-	1.09
	0.56	0.52	0.48	0.56	0.55	0.51	0.54	0.47	0.49	0.41	0.93	1.18	1.11	0.92	-

Stability



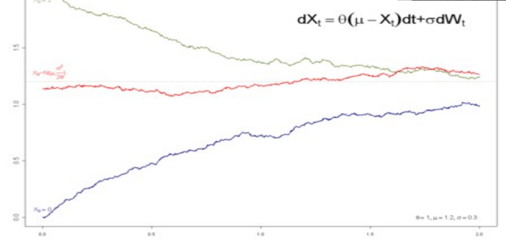
Current Opinion in Microbiology

Deterministic vs. stochastic models

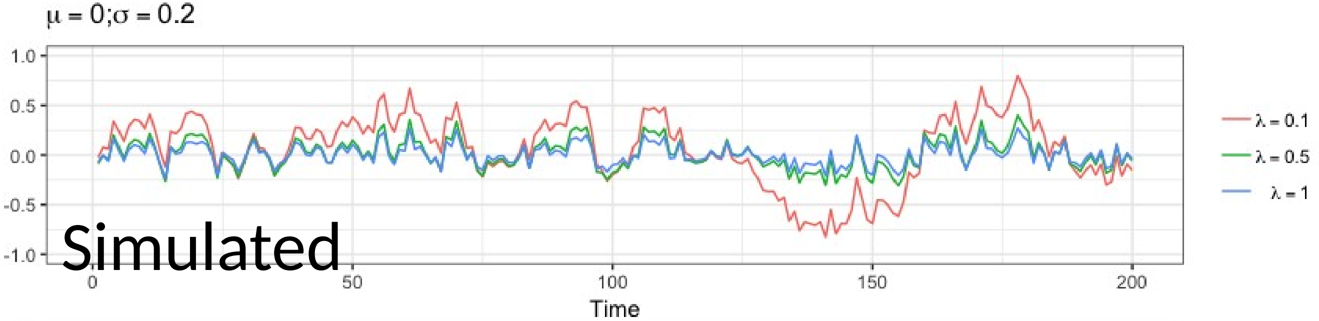
randomness is essential for the system dynamics

Quantifying resilience & stochasticity

Ornstein-Uhlenbeck Process (OUP) quantifies key properties of a stable state:



$$dX = \lambda(\mu - X)dt + \sigma dS$$



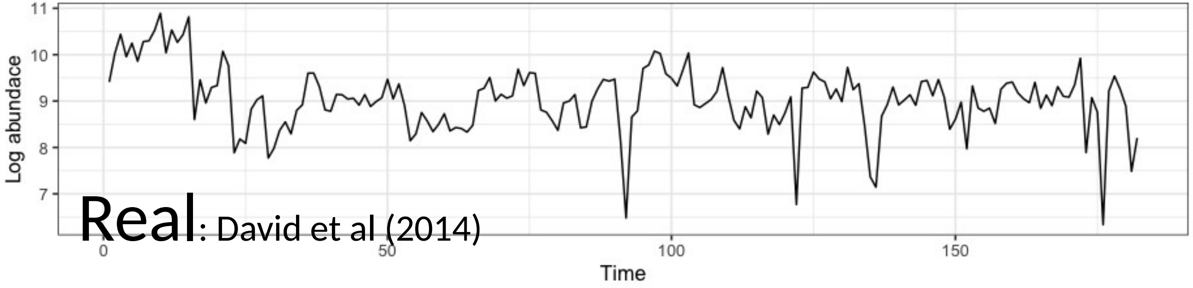
Simulated

$\lambda =$ mean reversion rate

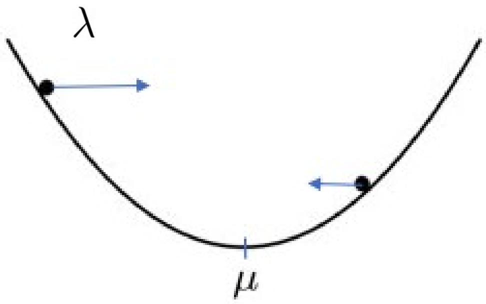
$\mu =$ long-term mean

$\sigma =$ stochasticity level

$S =$ stochastic process

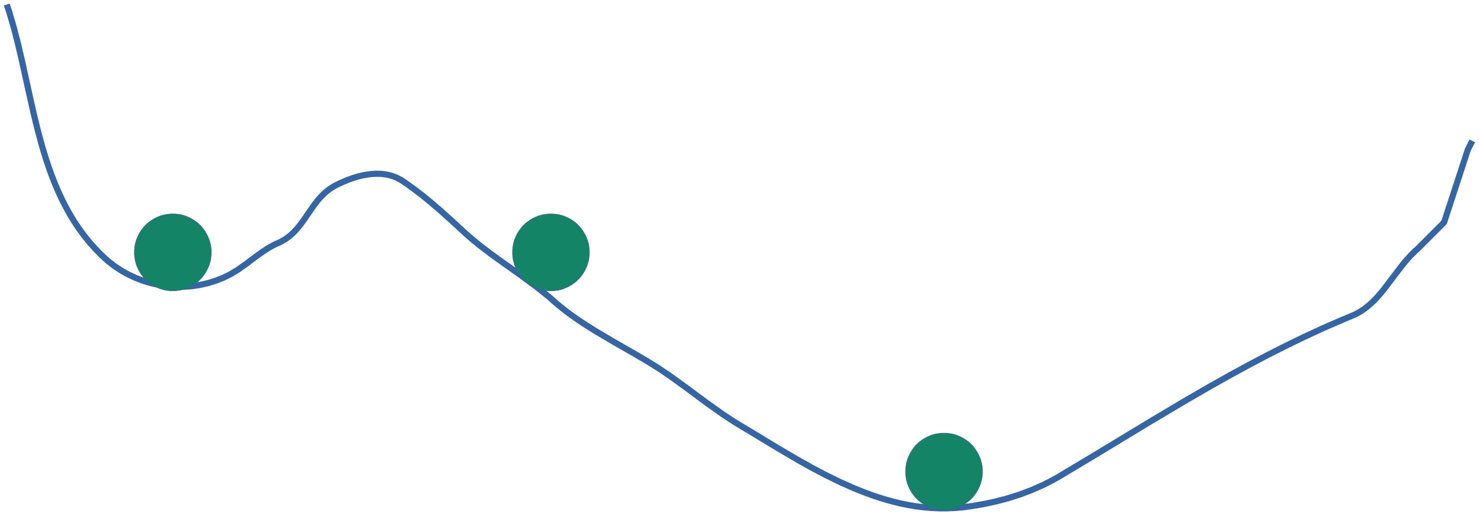


Real: David et al (2014)



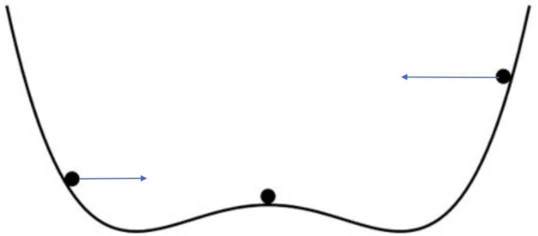
Laitinen & Lahti: StanCon 2018 Helsinki &
Advances in Intelligent Data Analysis XVII, 2018

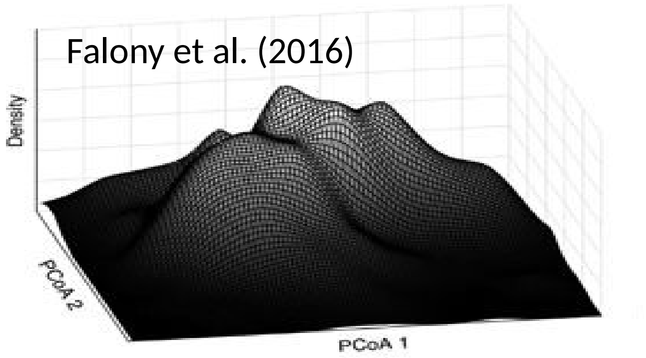
Resilience



Towards a dynamic landscape model of the gut microbiome

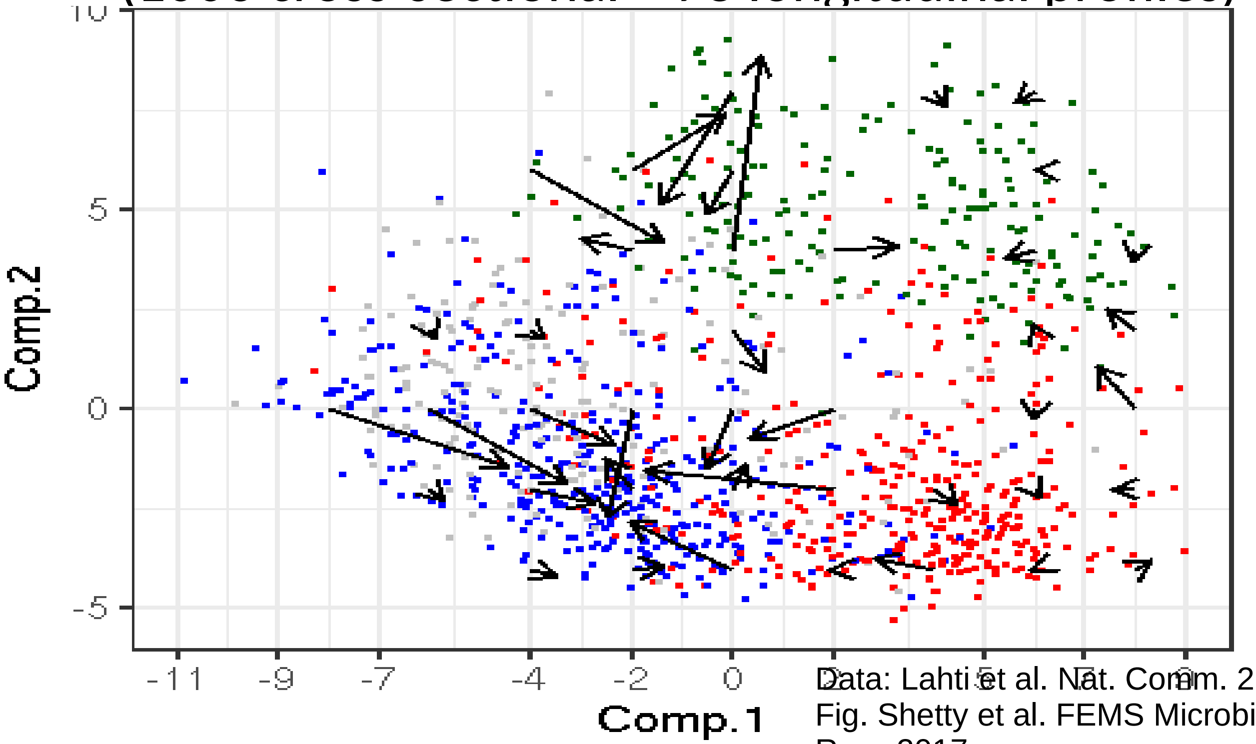
Prior info from background cohorts & pooling evidence across individuals



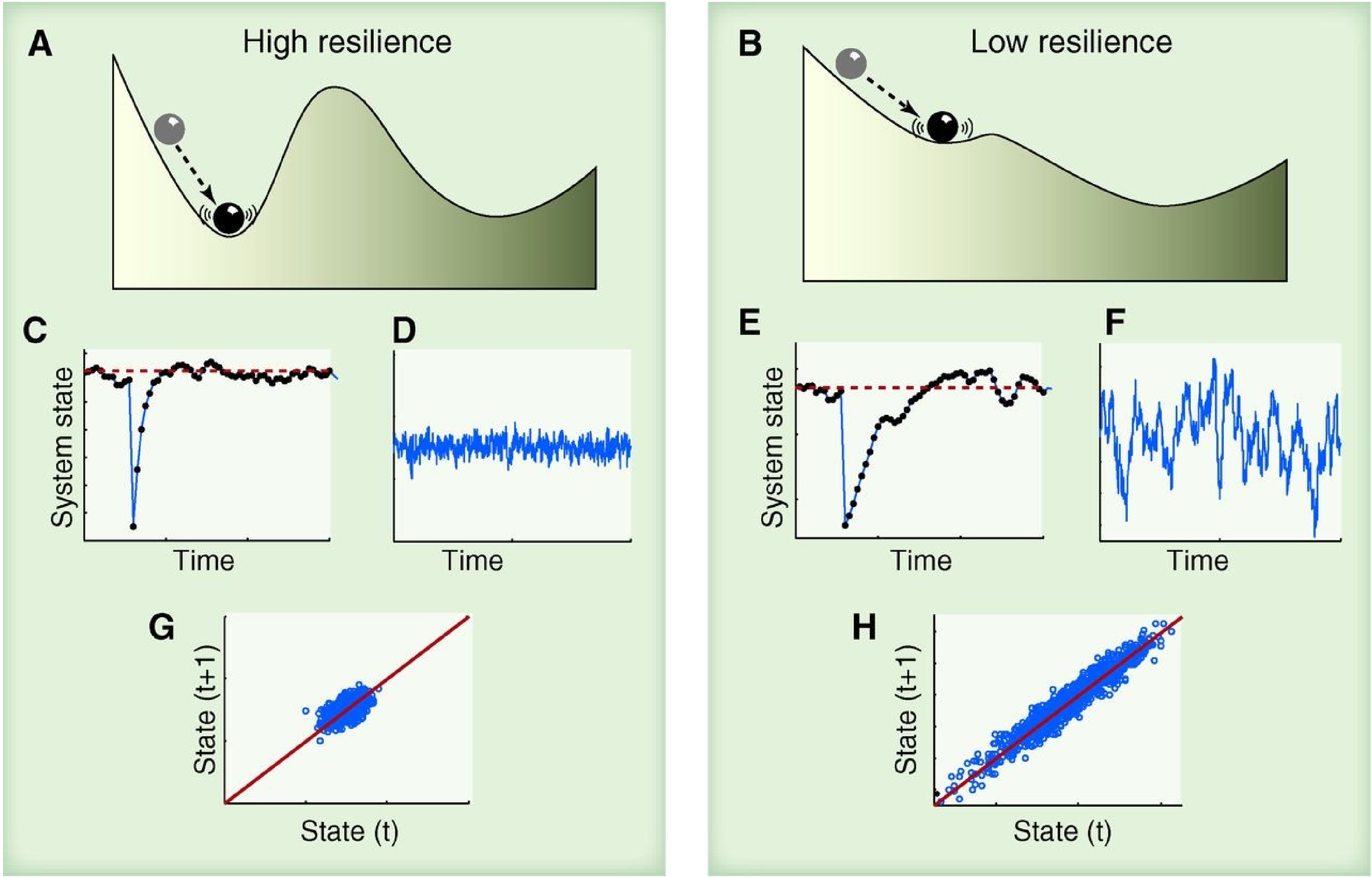


Falony et al. (2016)

Gradients of change on HITChip PCA landscape (1006 cross-sectional + 78 longitudinal profiles)

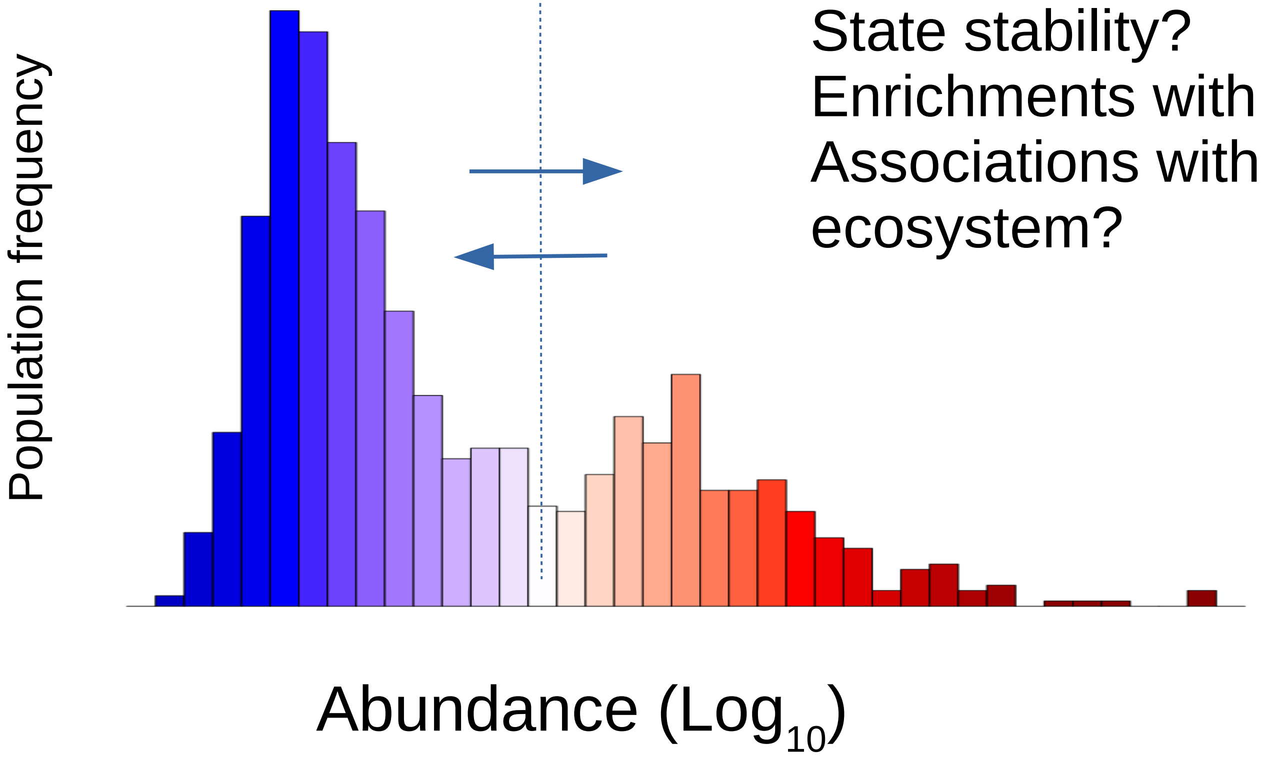


Data: Lahti et al. Nat. Comm. 2014
Fig. Shetty et al. FEMS Microbiol Rev.. 2017


A
High resilience
B
Low resilience
C
System state
Time
D
Time
E
System state
Time
F
Time
G
State (t+1)
State (t)
H
State (t+1)
State (t)

Alternative states in specific bacterial groups ?
→ Bimodal population distribution is one indicator

Dialister spp. (N = 1006)



State stability?
Enrichments with diet / health / etc.?
Associations with the overall ecosystem?


nature COMMUNICATIONS

ARTICLE

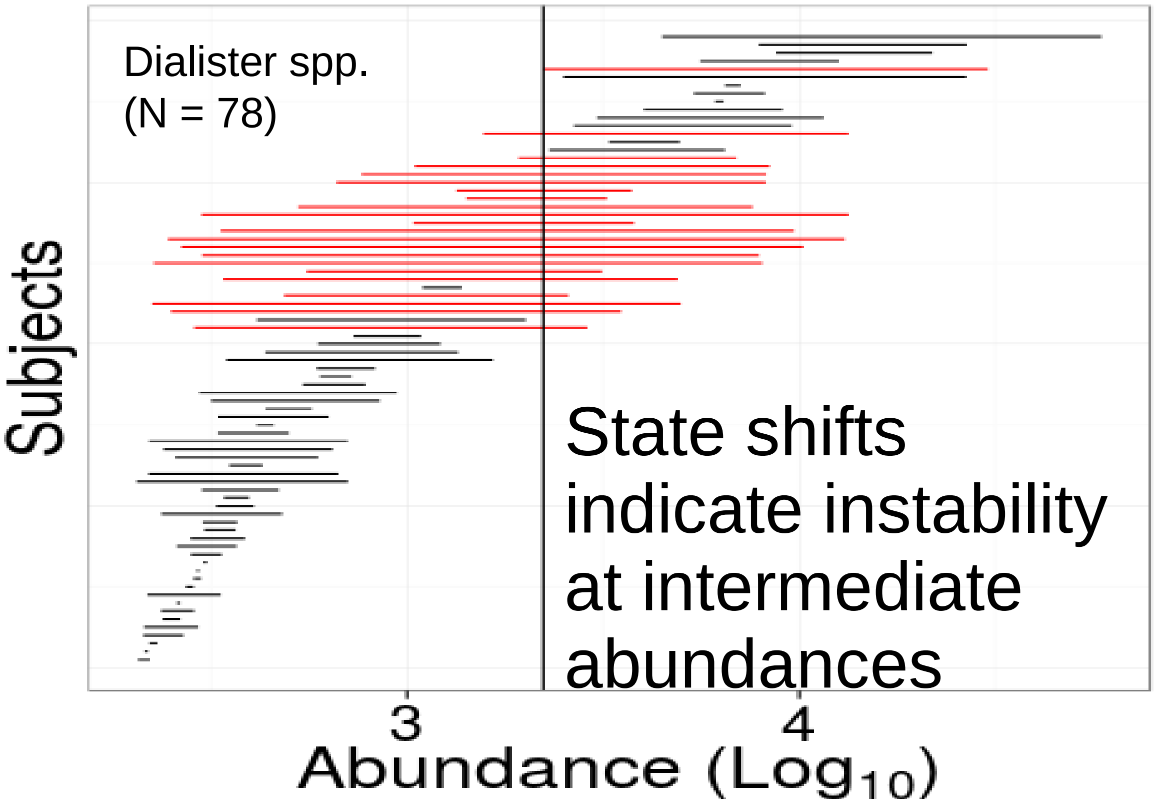
Received 23 Jan 2014 | Accepted 9 Jun 2014 | Published 8 Jul 2014 DOI: 10.1038/ncomms5344 OPEN

Tipping elements in the human intestinal ecosystem

Leo Lahti[1,2], Jarkko Salojärvi[1,*], Anne Salonen[3,*], Marten Scheffer[4] & Willem M. de Vos[1,2,3]

Bi-stability analysis with many short time series

Non-parametric potential analysis & Fokker-Planck dynamics



State shifts indicate instability at intermediate abundances

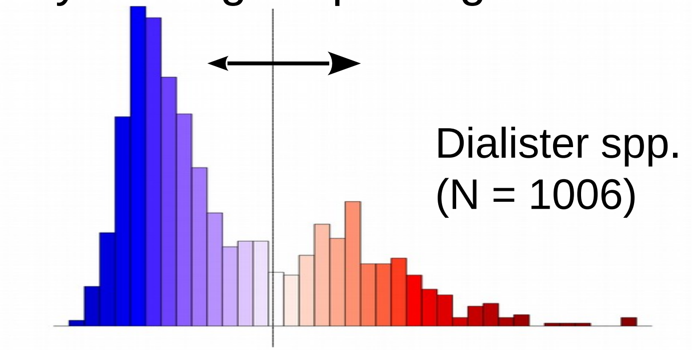
System state described by a stochastic process:

$$dz = -U(z)dt + \sigma\, dW$$

ation density:

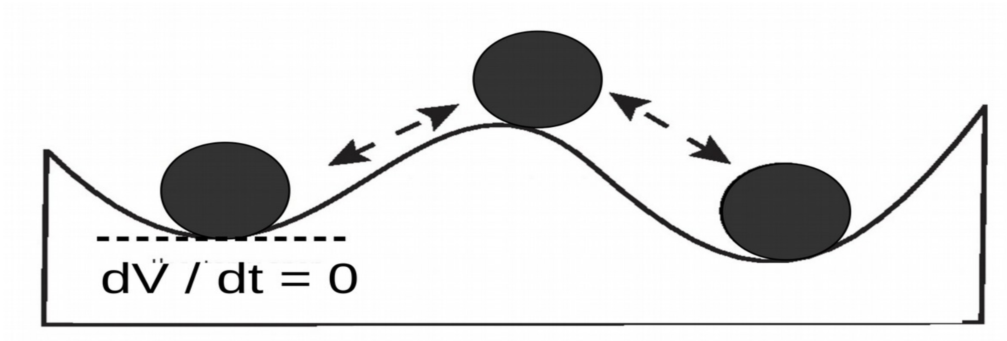
$$U(z) = -\frac{\sigma^2}{2} log P(z)$$

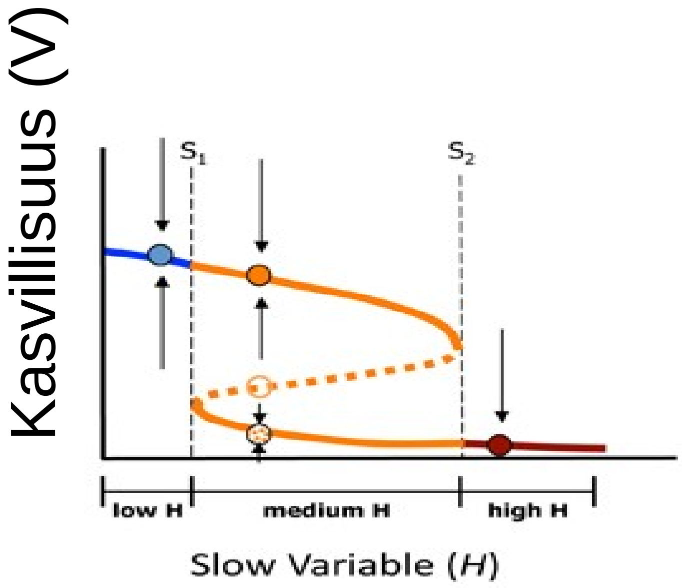
Used in climatology and ecology.
earlywarnings R package

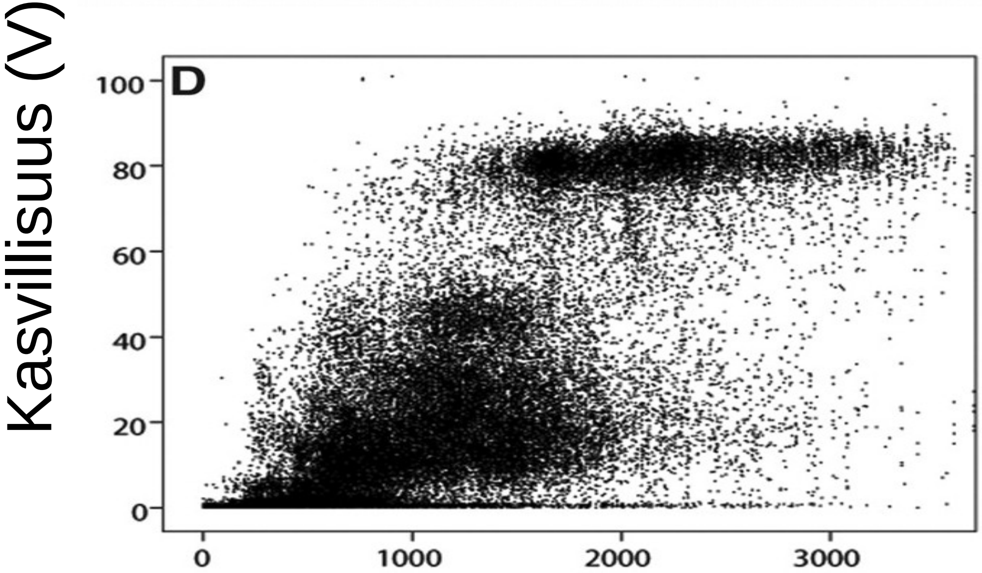


Lahti et al. Nat. Comm 2014
Hirota et al. Science 2011
Livina et al. Clim Past. 2010

Tipping point



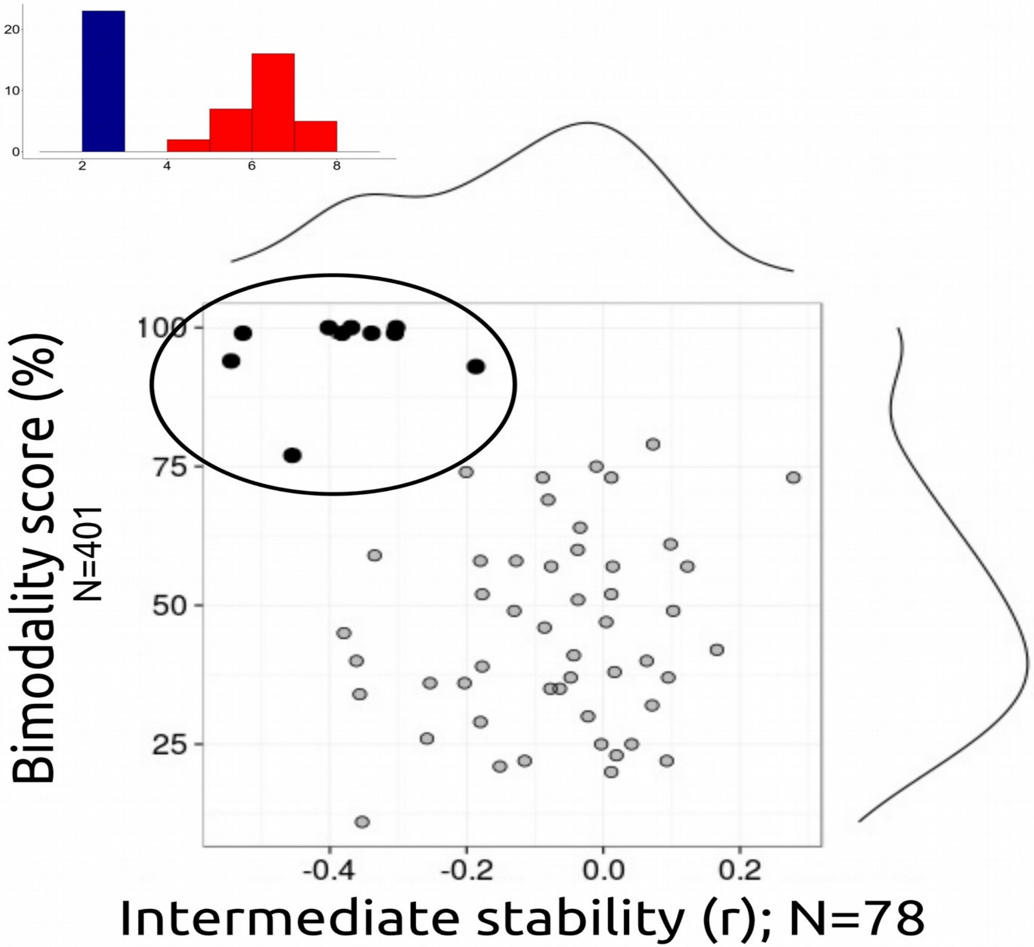




Bi-stable taxa:

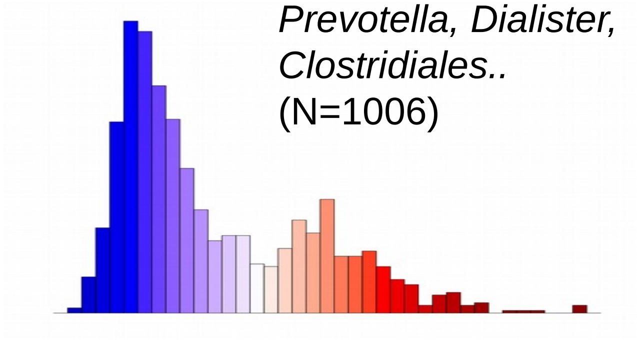
- Prevotella groups
  (oralis & melaninogenica)
- Dialister spp.
- Uncultured Clostridiales I-II
- B. fragilis group
- Uncultured Mollicutes
- Clostridium groups
  (difficile, colinum,
  sensu stricto)
- Lactobacillus plantarum

+ methanogenic archaea



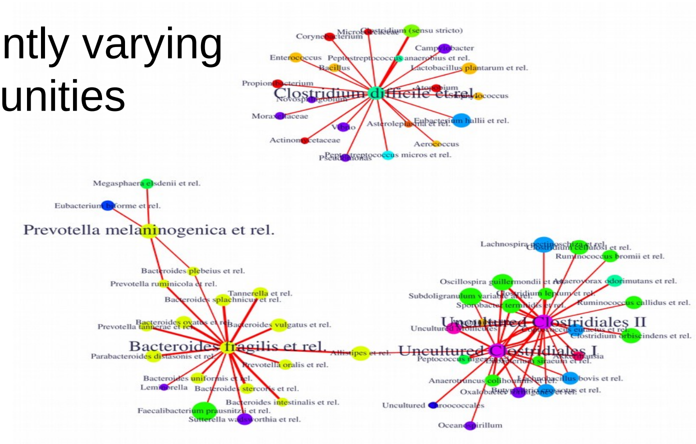
Lahti et al. Nat. Comm. 5:4344, 2014

Subject stratification into community types could reduce complexity



Bistable taxa:
Prevotella, Dialister, Clostridiales..
(N=1006)

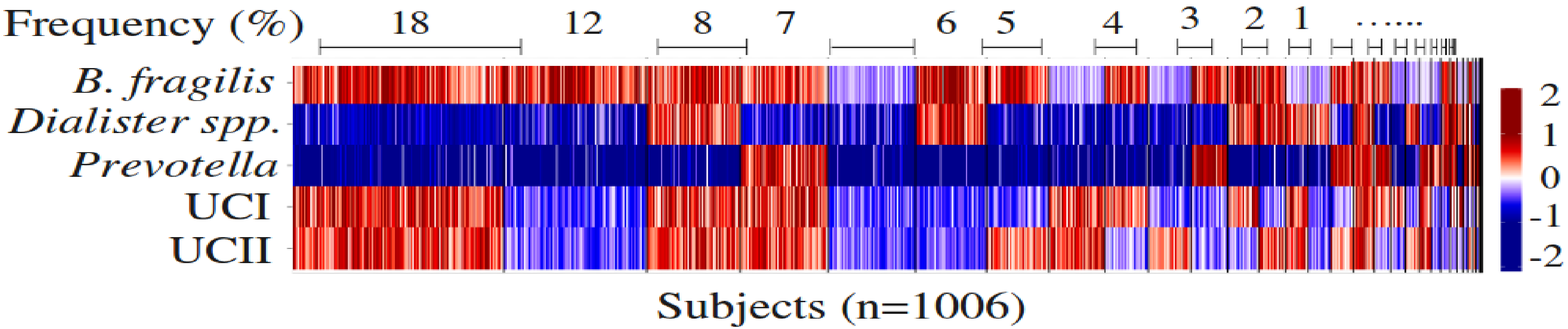
Independently varying
sub-communities



Ecosystem states are rich combinations

of independent tipping elements ?

Lahti et al. Nat. Comm. 2014



Early warning signals

Early warning signals to predict state shifts ?

Early warning signals for a critical transition in a time series generated by a model of a harvested population[77] driven slowly across a bifurcation.

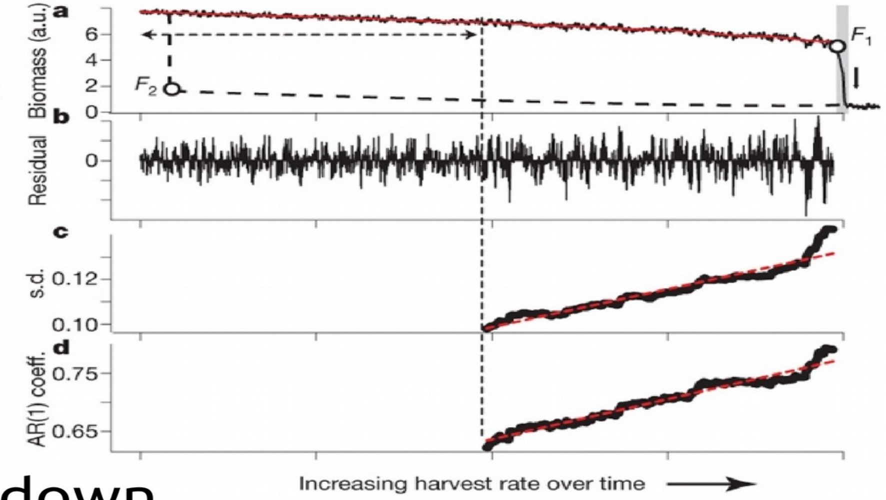
Autocorrelation

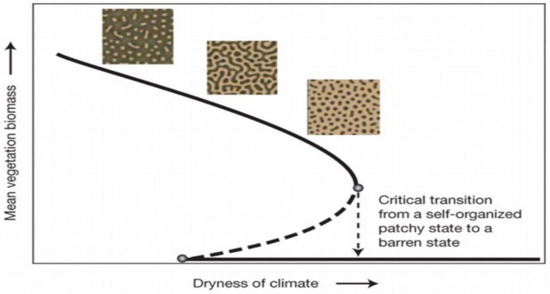
Variance

Skewness

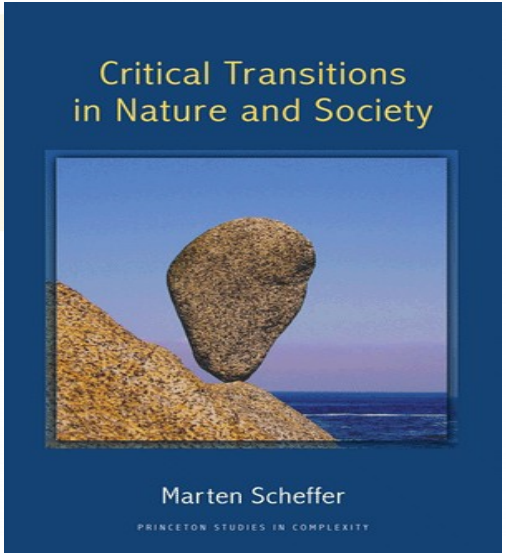
Flickering

Critical slowing down





M Scheffer *et al.* *Nature* **461**, 53-59 (2009) doi:10.1038/nature08227

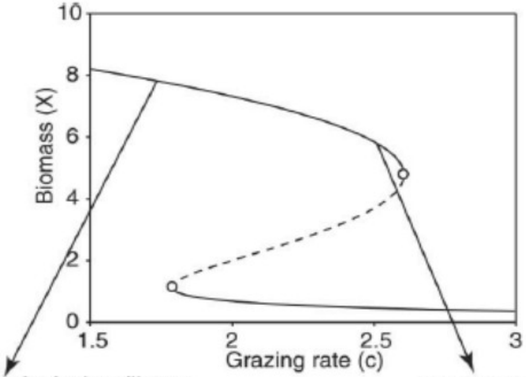


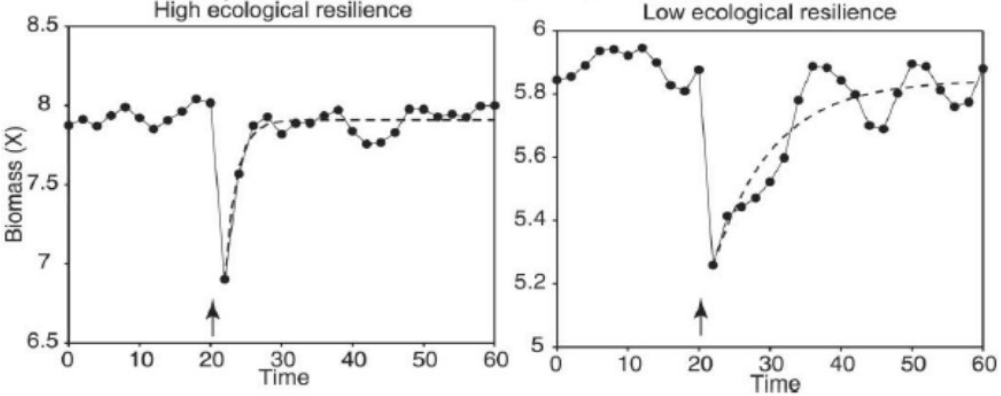
CRAN: earlywarnings R package

V. Dakos & L. Lahti

recovery time after a temporal perturbation

underexploited





overexploited

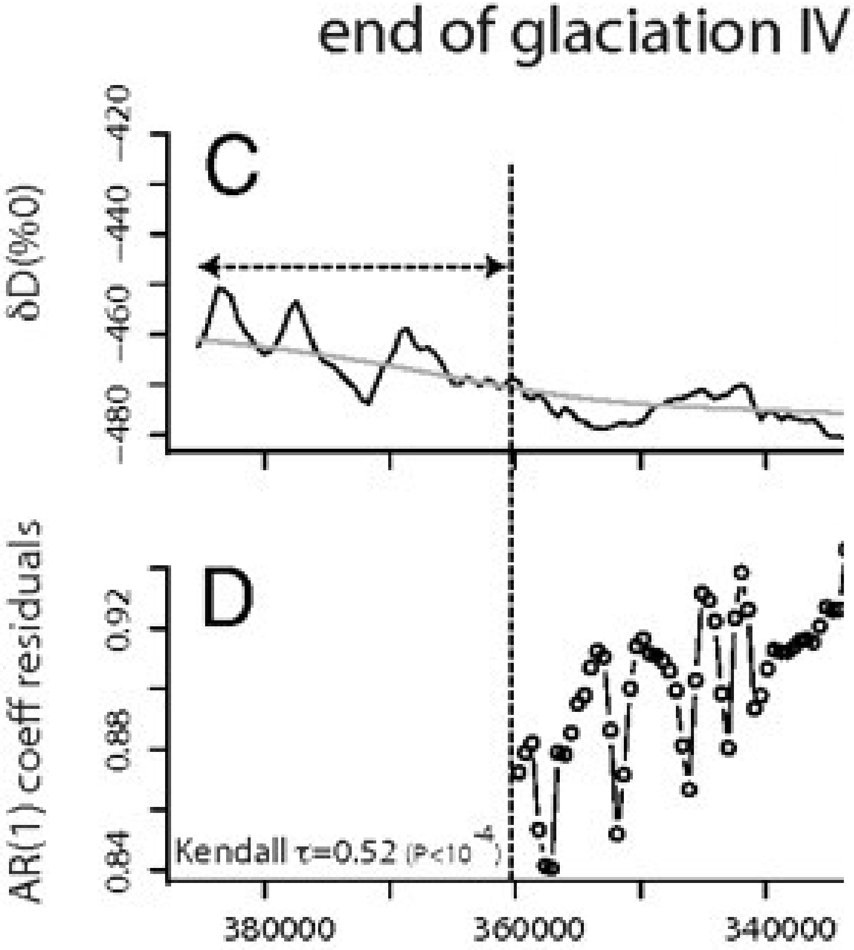
REVIEW

Anticipating Critical Transitions

Marten Scheffer[1,2,*], Stephen R. Carpenter[3], Timothy M. Lenton[4], Jordi Bascompte[5], William Brock[6], …

+ See all authors and affiliations

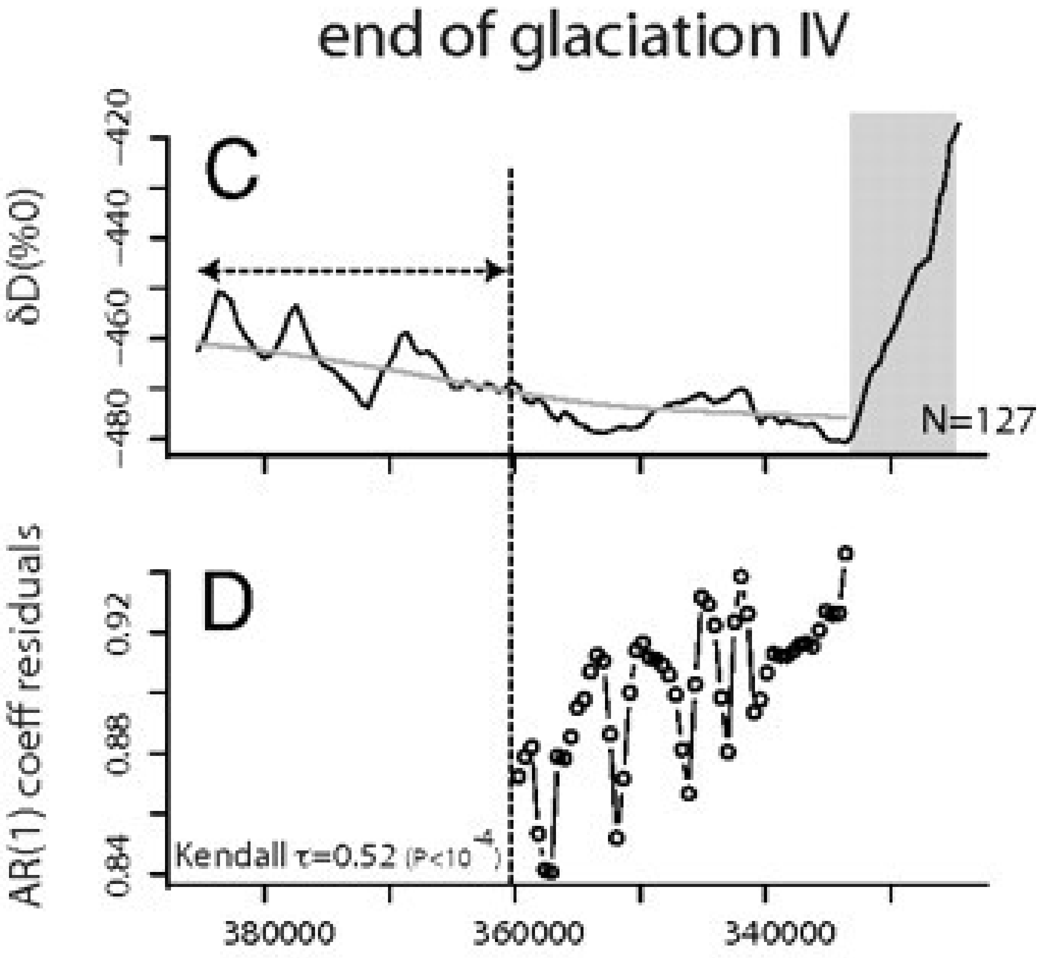
Science 19 Oct 2012:
Vol. 338, Issue 6105, pp. 344-348
DOI: 10.1126/science.1225244



Slowing down as an early warning signal for abrupt climate change

Vasilis Dakos, Marten Scheffer, Egbert H. van Nes, Victor Brovkin, Vladimir Petoukhov, and Hermann Held

PNAS September 23, 2008 105 (38) 14308-14312; https://doi.org/10.1073/pnas.0802430105



Slowing down as an early warning signal for abrupt climate change

Vasilis Dakos, Marten Scheffer, Egbert H. van Nes, Victor Brovkin, Vladimir Petoukhov, and Hermann Held

PNAS September 23, 2008 105 (38) 14308-14312; https://doi.org/10.1073/pnas.0802430105

Memory

Time points are dependent

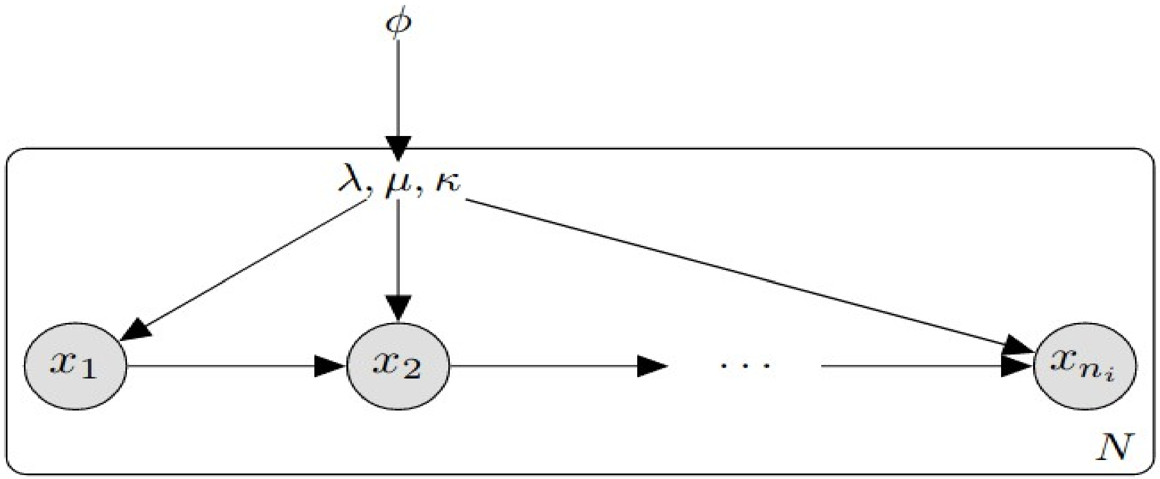
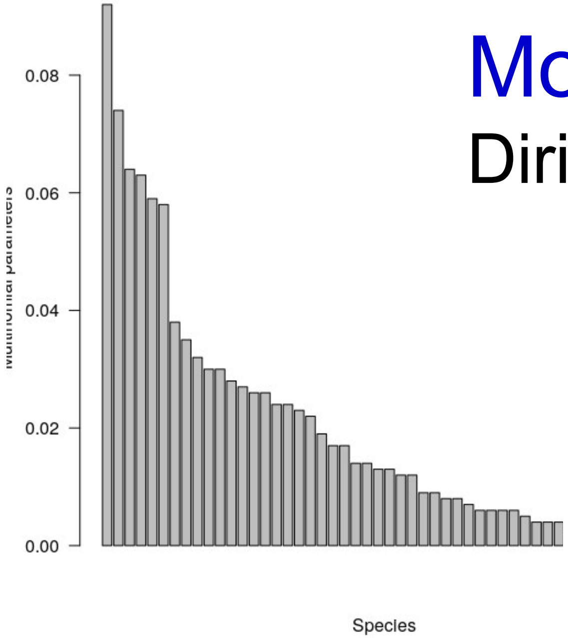
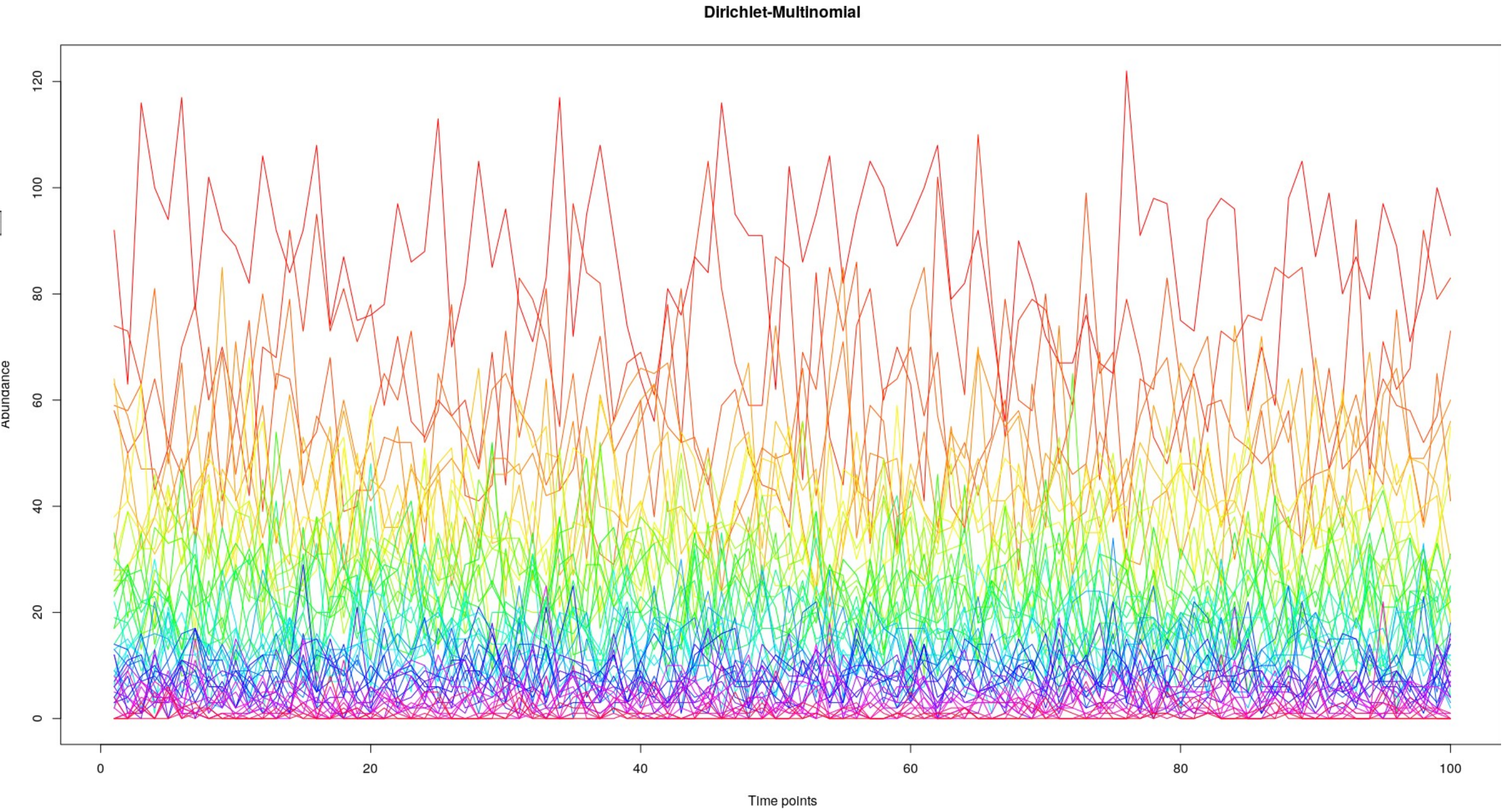


Fig. 2: Bayesian graph representation of the hierarchical OU process. Hyperparameters are denoted with ϕ.

Model with independent time points

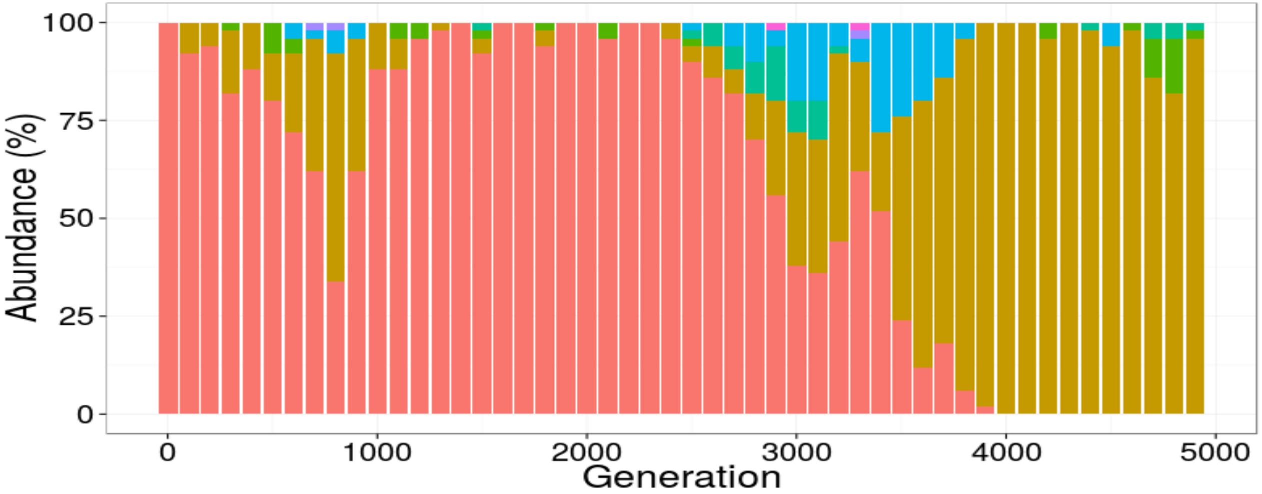
Dirichlet-Multinomial: no memory, no dependence

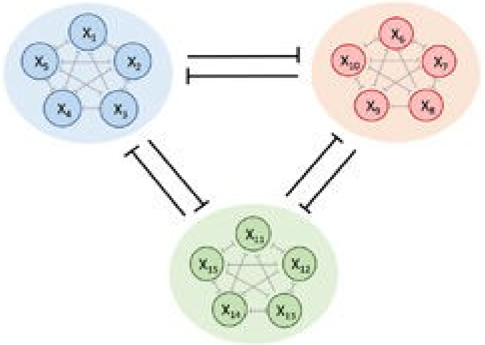




Time points depend (only) on the previous state

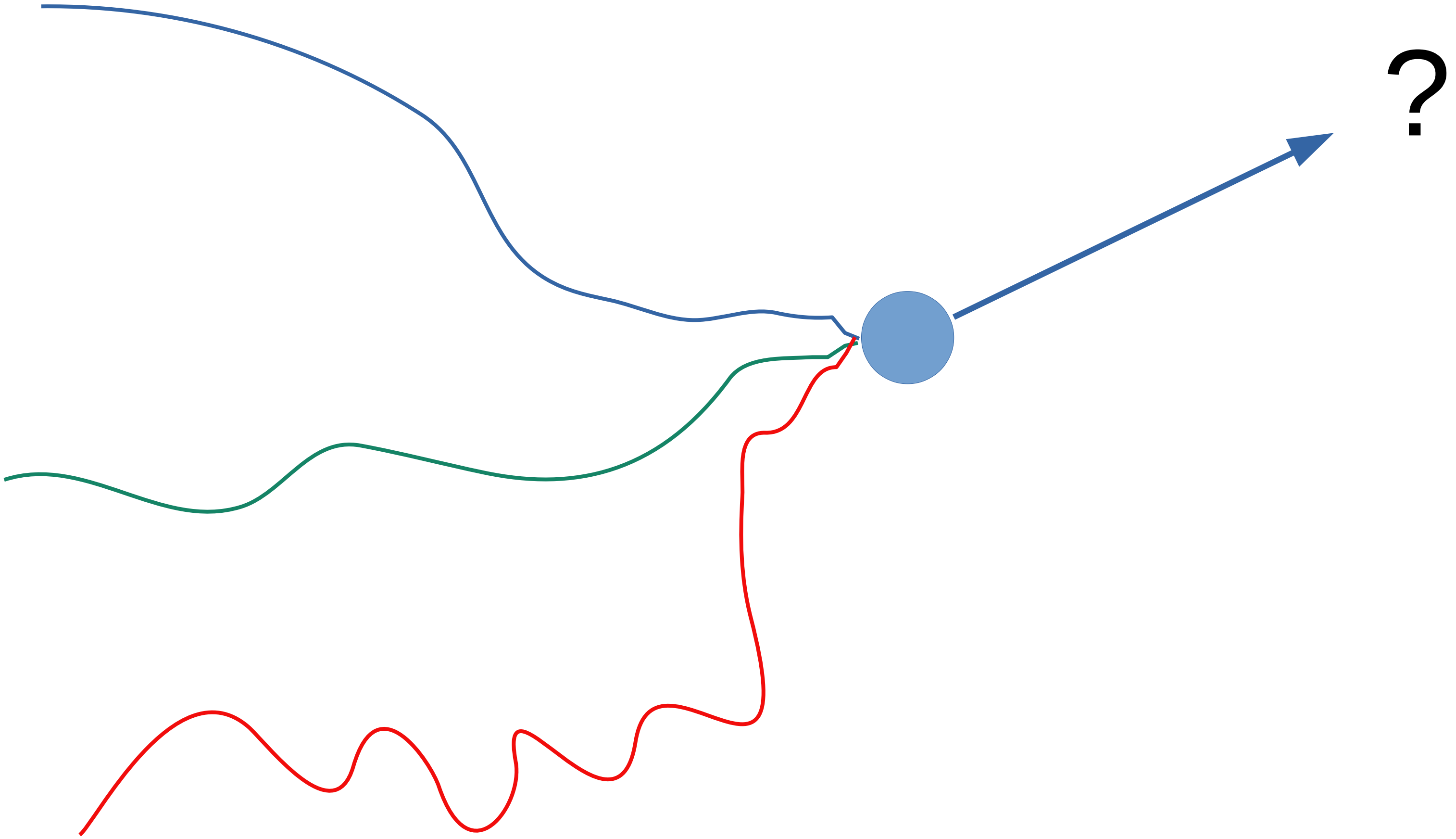
Neutral model, Lotka-Volterra & many interaction models





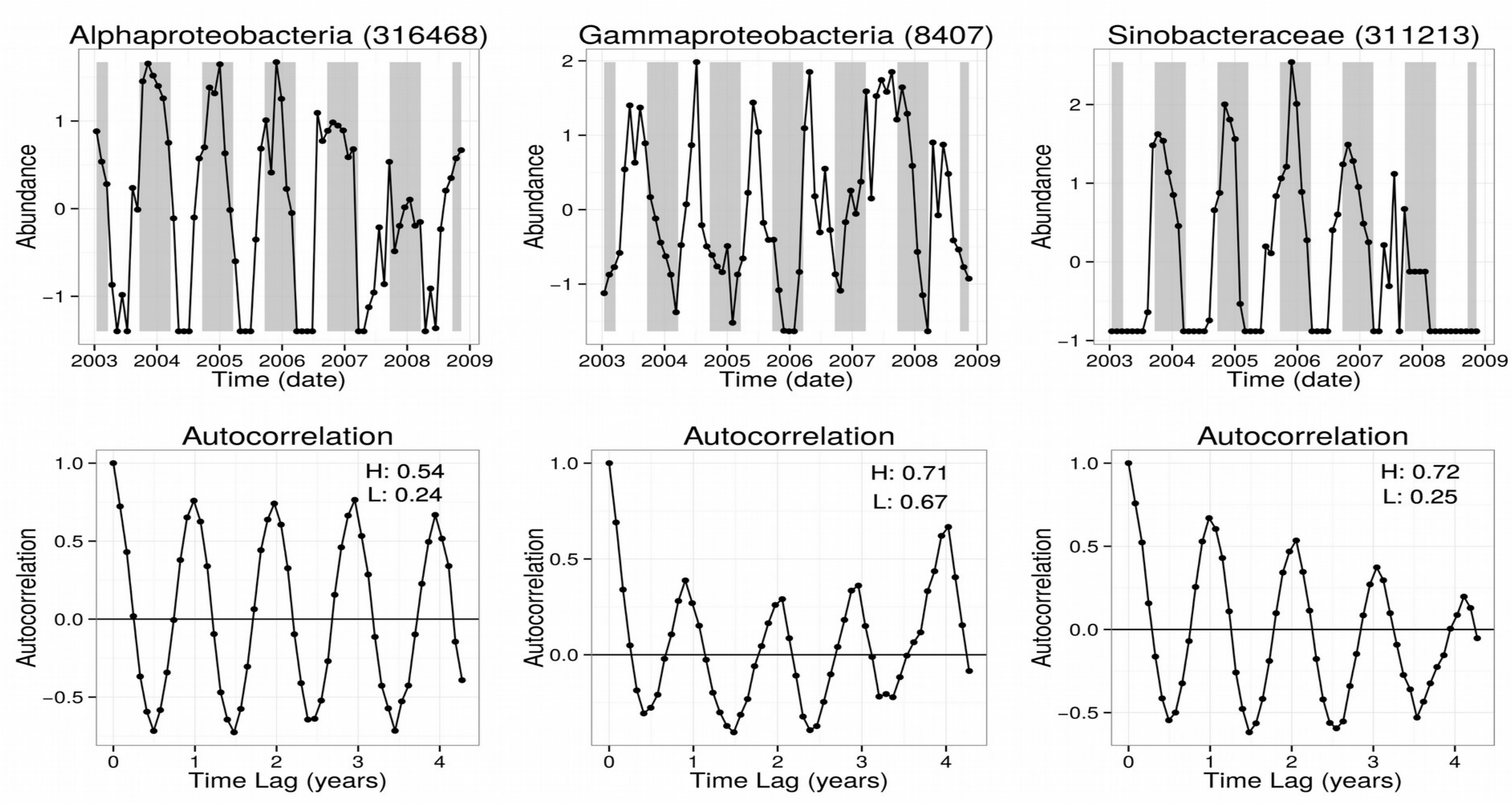
$$\frac{dX_i}{dt} = X_i(b_i f_i(\{X_k\}) - k_i X_i)$$

Memory: past trajectories influencing future choices?



Periodicity

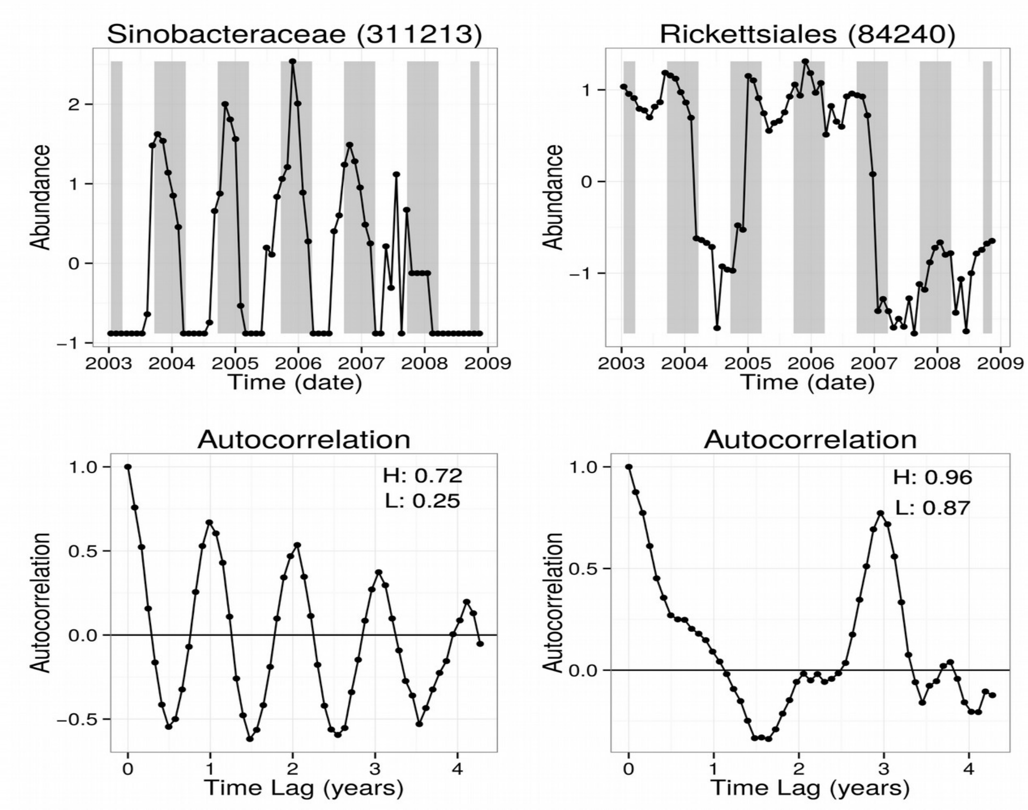
Hurst exponent quantifies periodicity and persisting trends



Faust et al. 2015

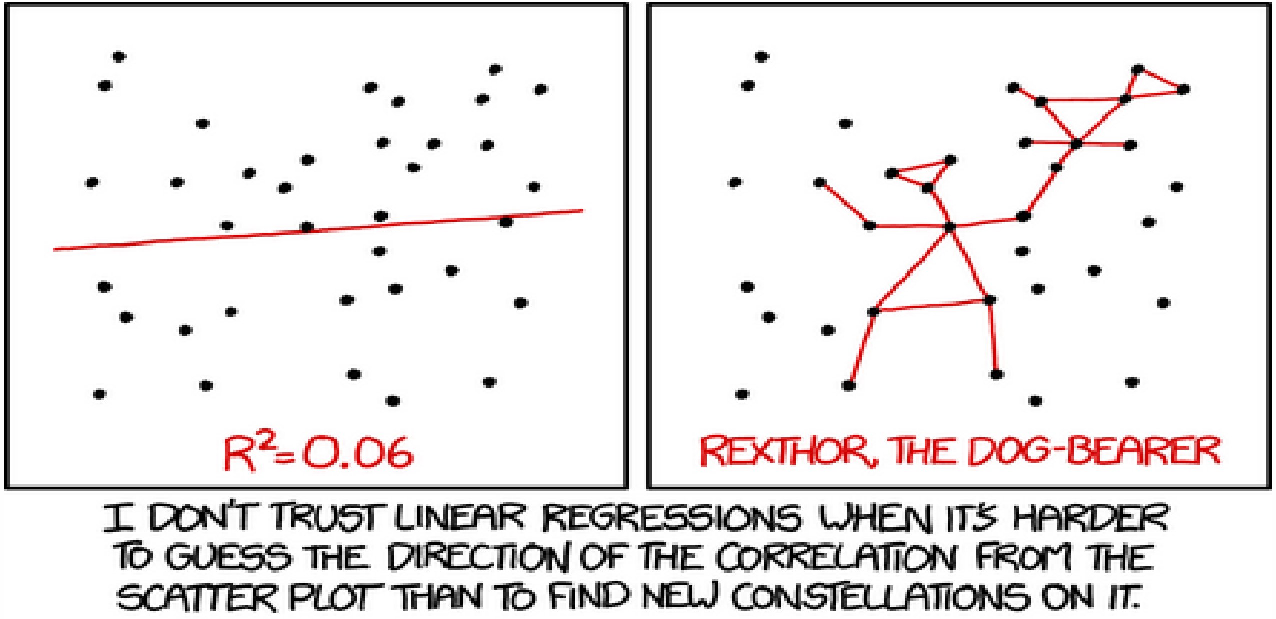
Chaos

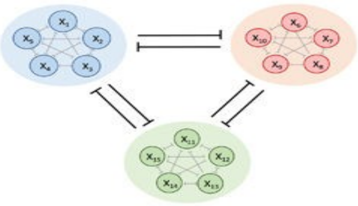
Lyapunov exponent quantifies chaos



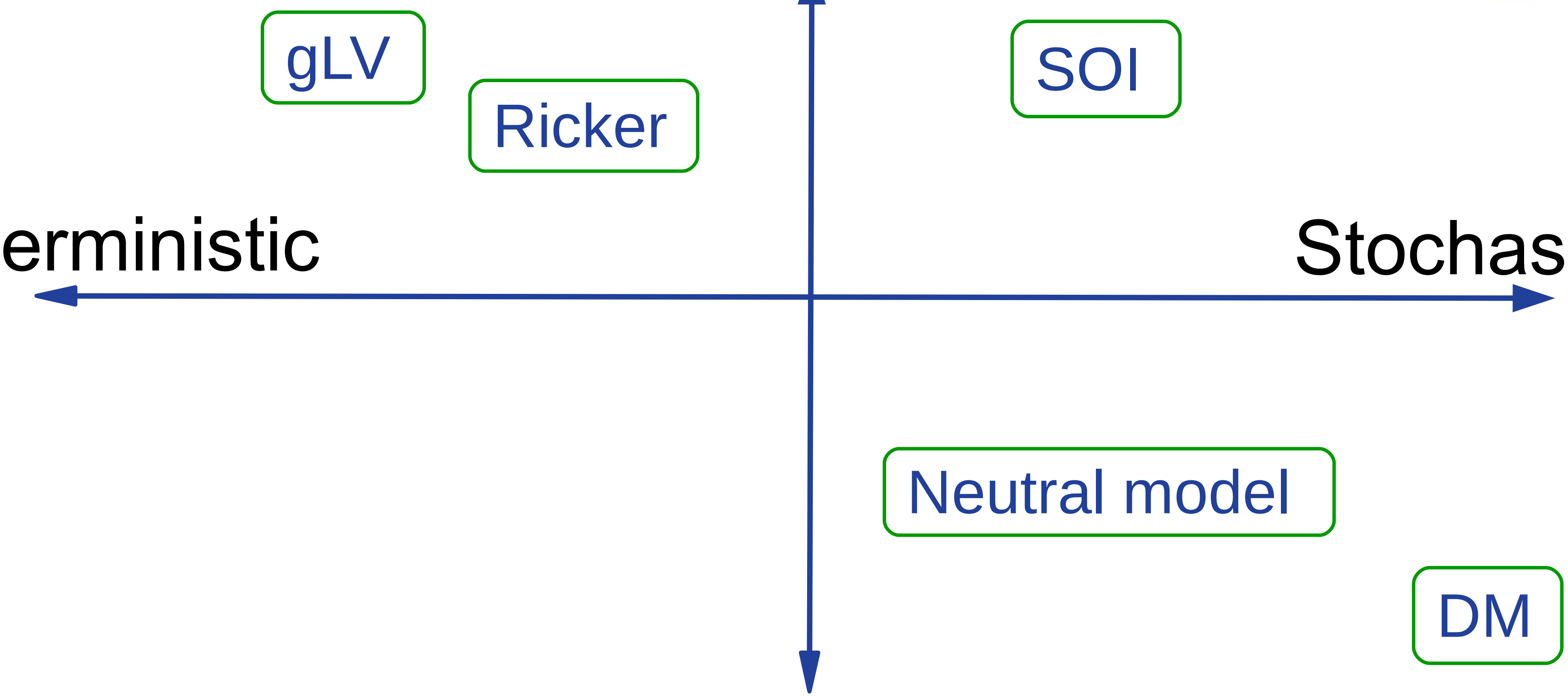
Faust et al. 2015

How we choose which model to apply?





Species Interactions



Deterministic

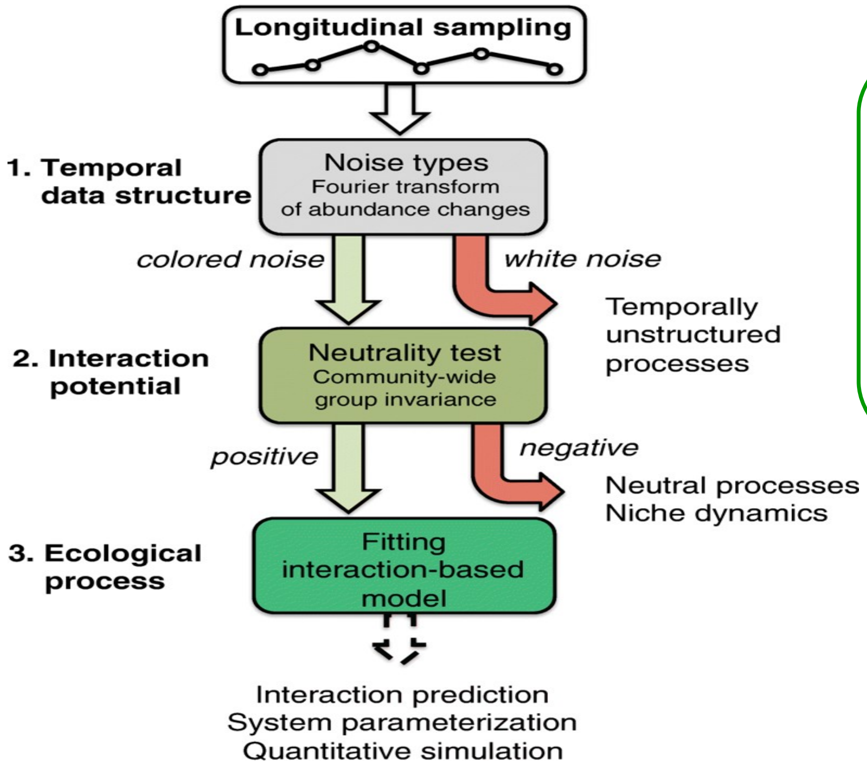
Stochastic

No interactions

“Colors of noise” hint at ecological mechanisms

Signatures of ecological processes in microbial community time series

Karoline Faust[1*], Franziska Bauchinger[2], Béatrice Laroche[3], Sophie de Buyl[4,5], Leo Lahti[1,6,7], Alex D. Washburne[8,9], Didier Gonze[5,10] and Stefanie Widder[11,12,13*]

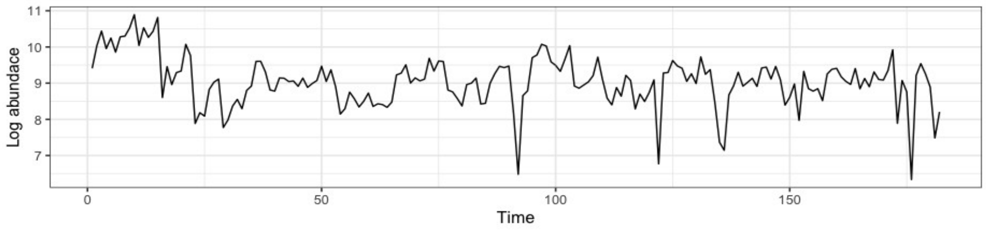


White noise → Unstructured

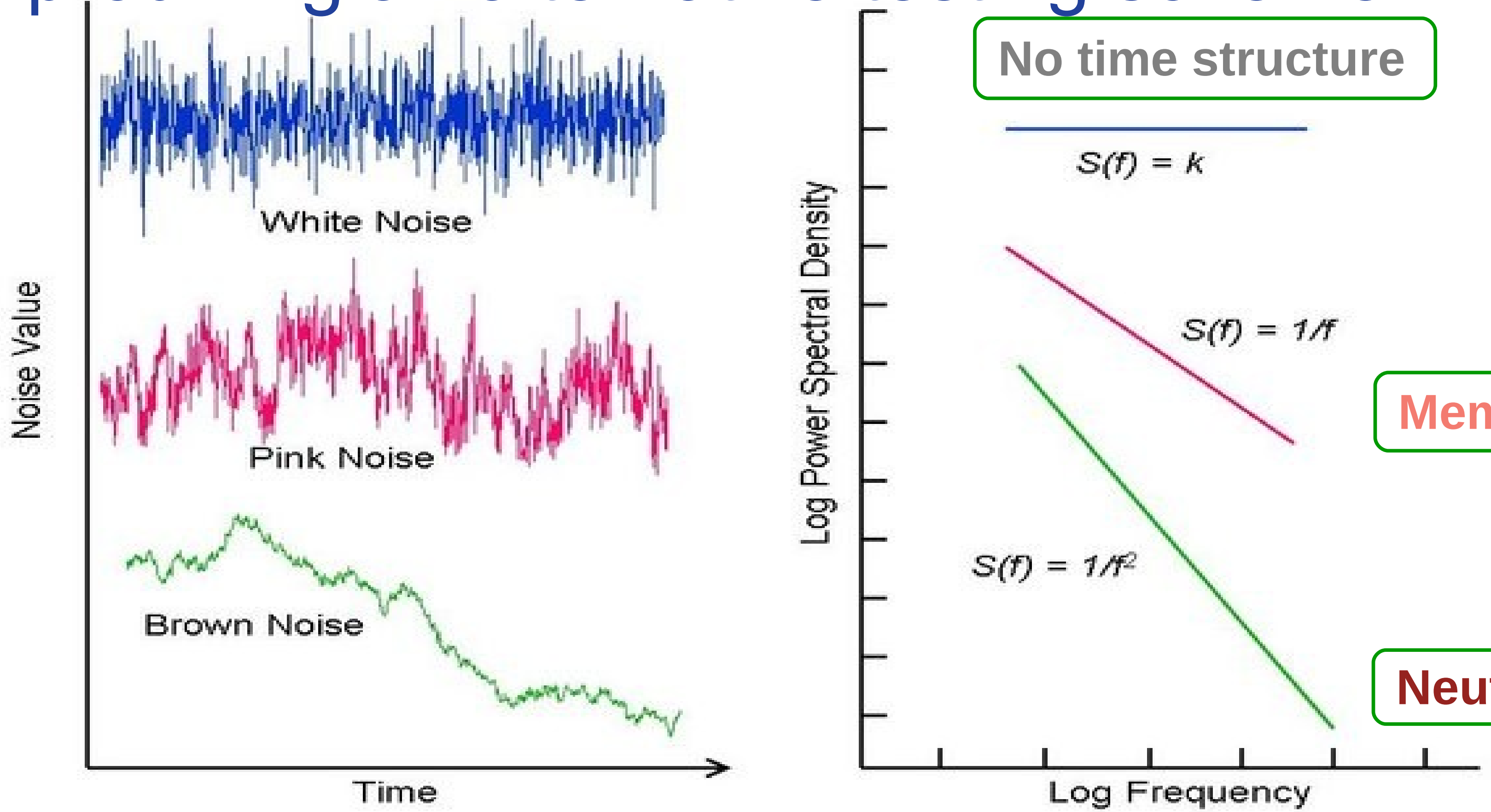
Pink noise → Time dependence

Brown noise → Neutrality

Black noise → Interactions



“Colors of noise” characterize time series, prodiving an alternative testing scheme

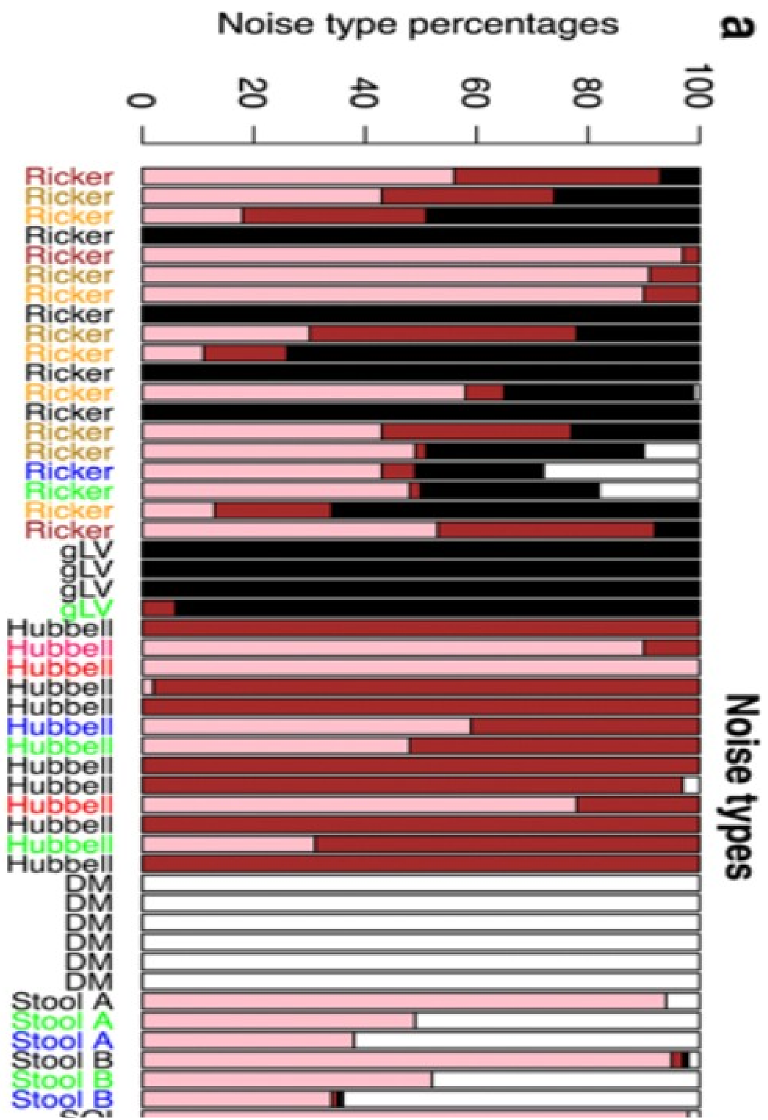


No time structure

Memory in time

Neutral variation

http://www.scholarpedia.org/article/1/f_noise



Distinct noise profiles of ecological processes confirmed in simulations

White noise → Unstructured

Pink noise → Time dependence

Brown noise → Neutrality

Black noise → Interactions

Key sources of microbial ecosystem variation

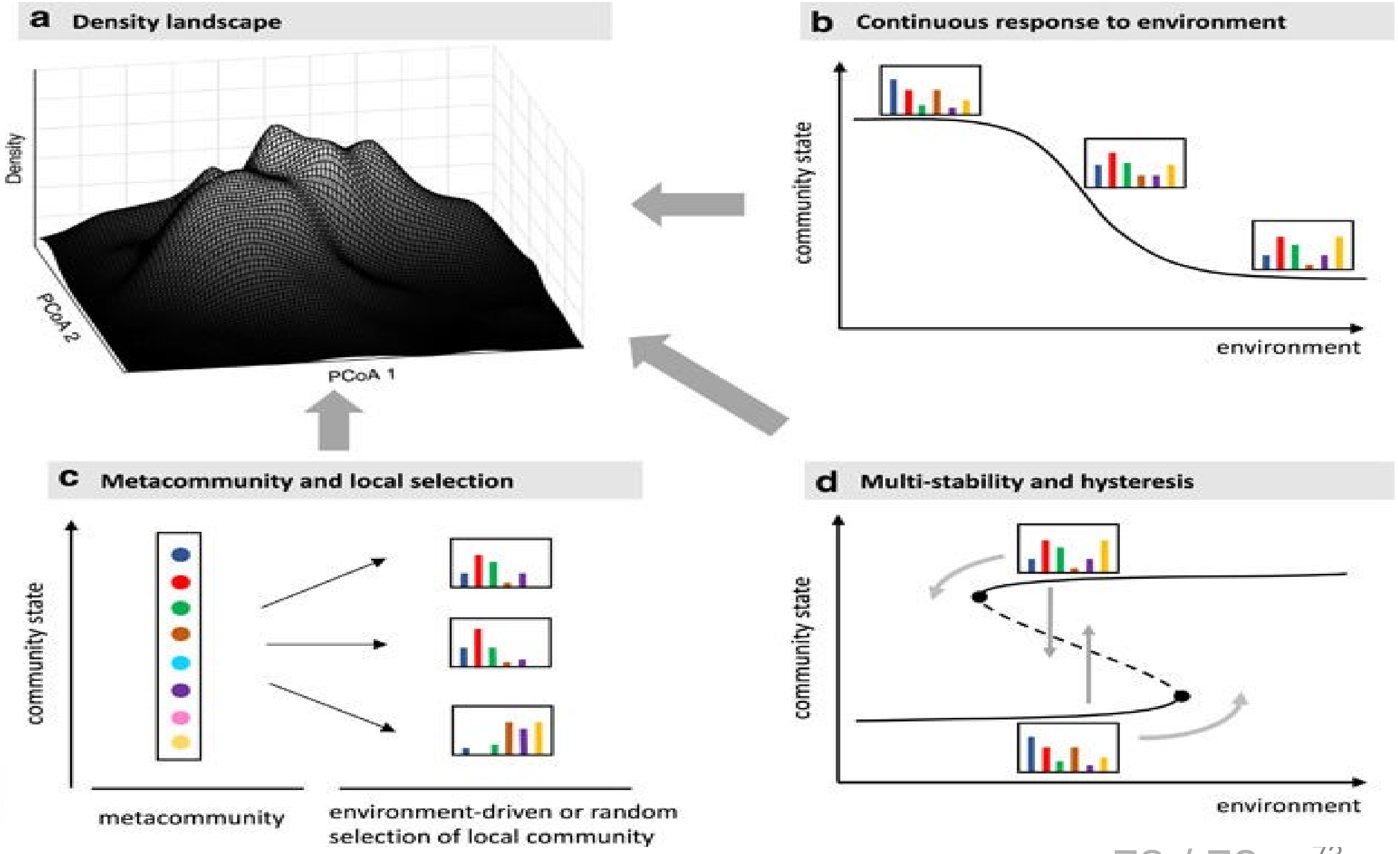
External perturbations (push & pulse)

Internal dynamics and multi-stability

Immigration

Stochasticity

Memory




Microbial communities as dynamical systems

Didier Gonze [1, 2] ✉, Katharine Z Coyte [3, 4], Leo Lahti [5, 6, 7], Karoline Faust [5] ✉