Limit Theorems for the Unified Neutral Theory of Biodiversity and Their Application to the Human Gut Microbiome

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Rencontre de la Chaire Modélisation Mathématique et Biodiversité
École Polytechnique
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Outline

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NEUTRAL *vs.* NICHE MODELS IN ECOLOGY

"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!"

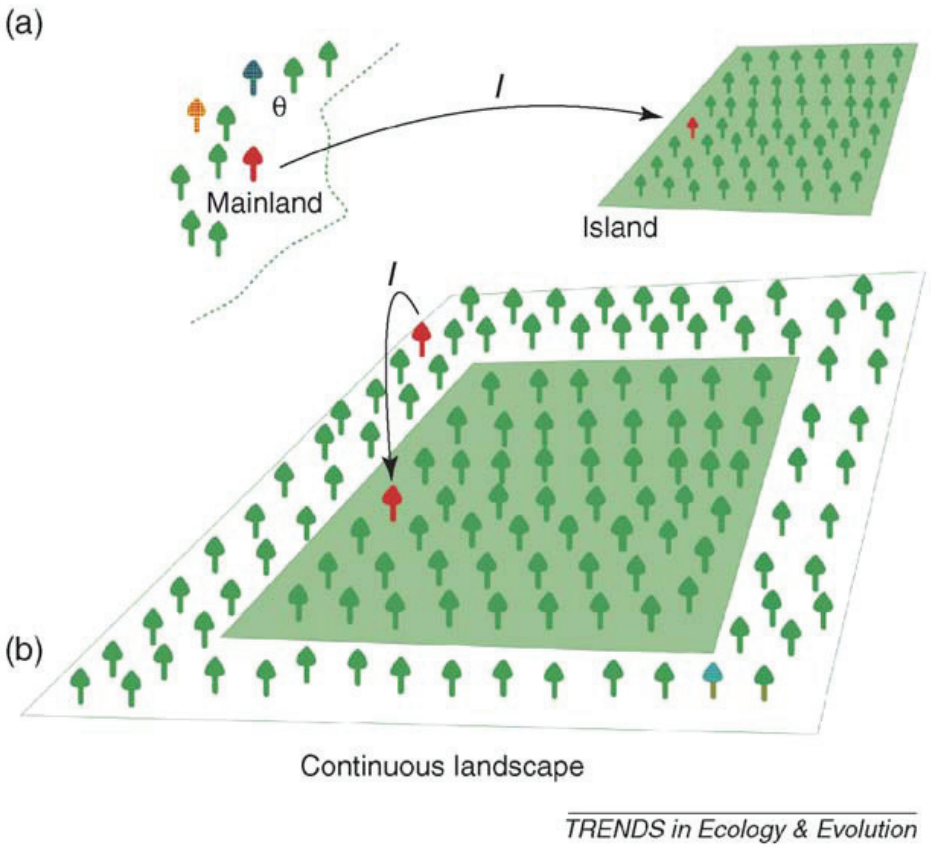
– Charles Darwin, *The Origin of Species*

NEUTRAL *vs.* NICHE MODELS IN ECOLOGY

After more than 25 years of research on the tropical forests of Barro Colorado Island, however, Stephen Hubbell controversially proposed exactly that. . . That random chance may in fact be the best explanation of the observed biodiversity.

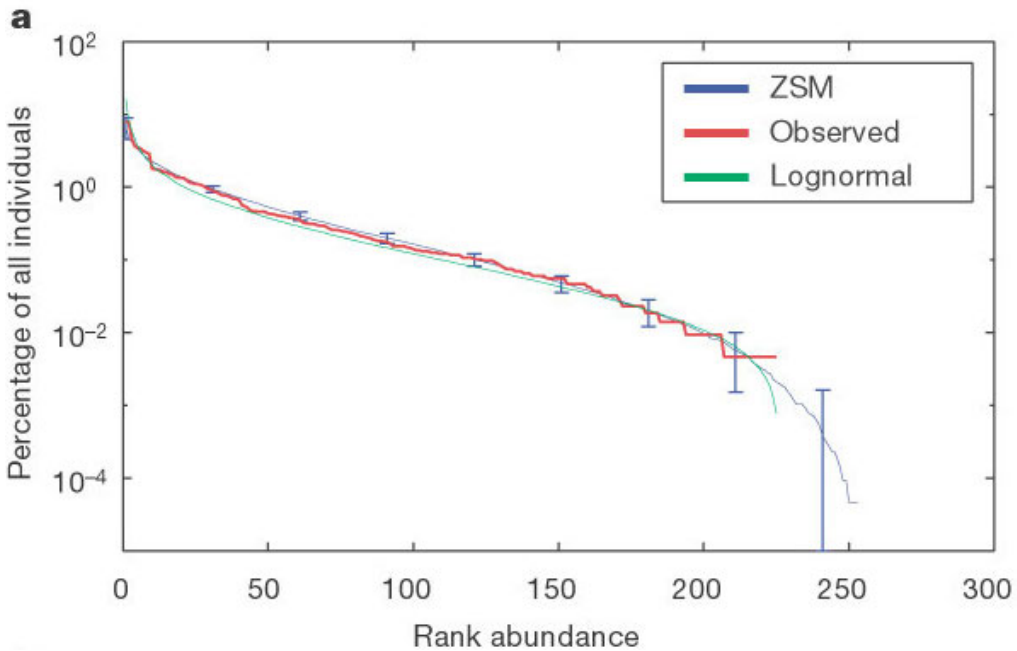
Gewin (2006)

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



Alonso, Etienne & McKane (2006).

RANK ABUNDANCE CURVES: EVIDENCE FOR THE UNTB?



McGill (2003).

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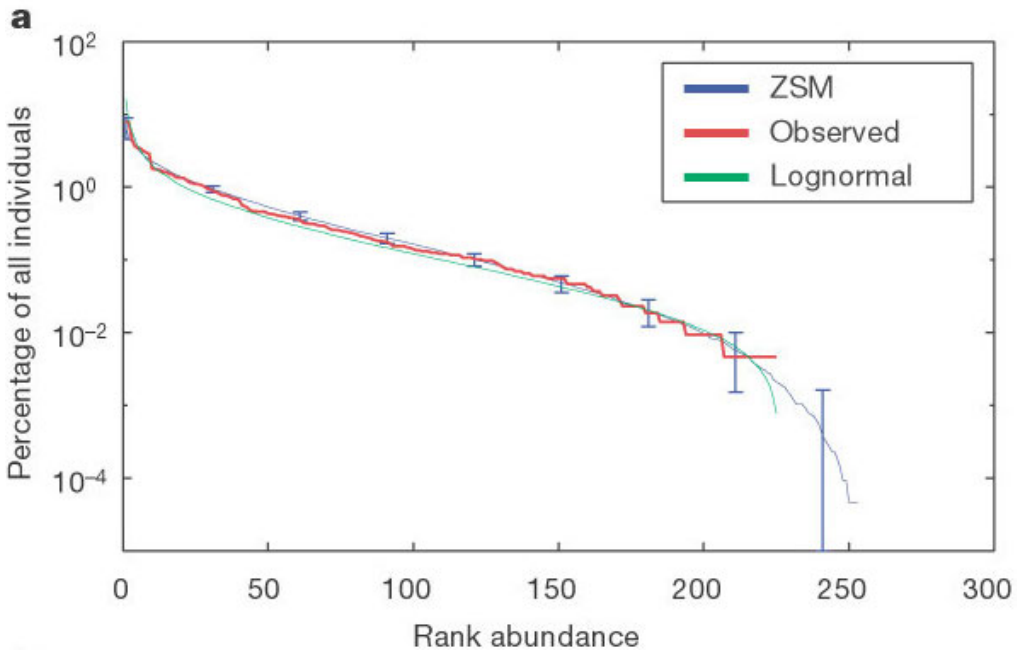

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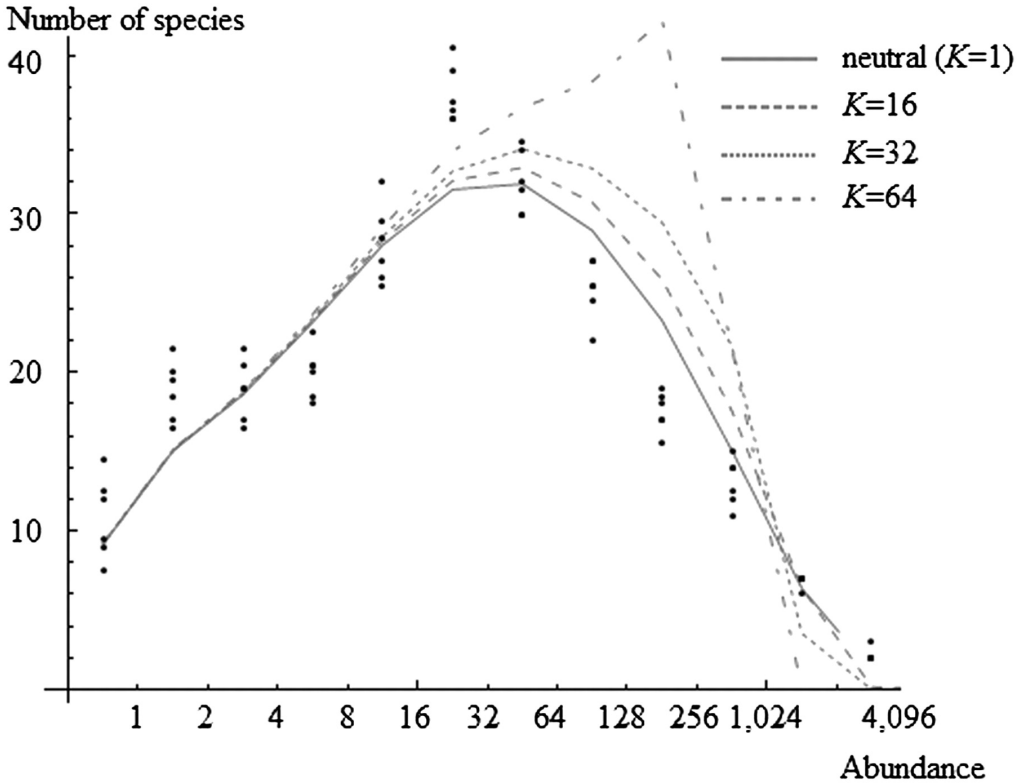
- Hubbell saw evidence for neutral assembly in a neutral model's accuracy in predicting species abundance distributions.
- Others took up the neutral theory, but in the same manner as neutral models in genetics, as a null model.

A REJECTABLE NULL?



Chisholme & Pacala (2010).

However, further modelling showed that niche-based models could produce species abundance curves almost identical to the neutral model.

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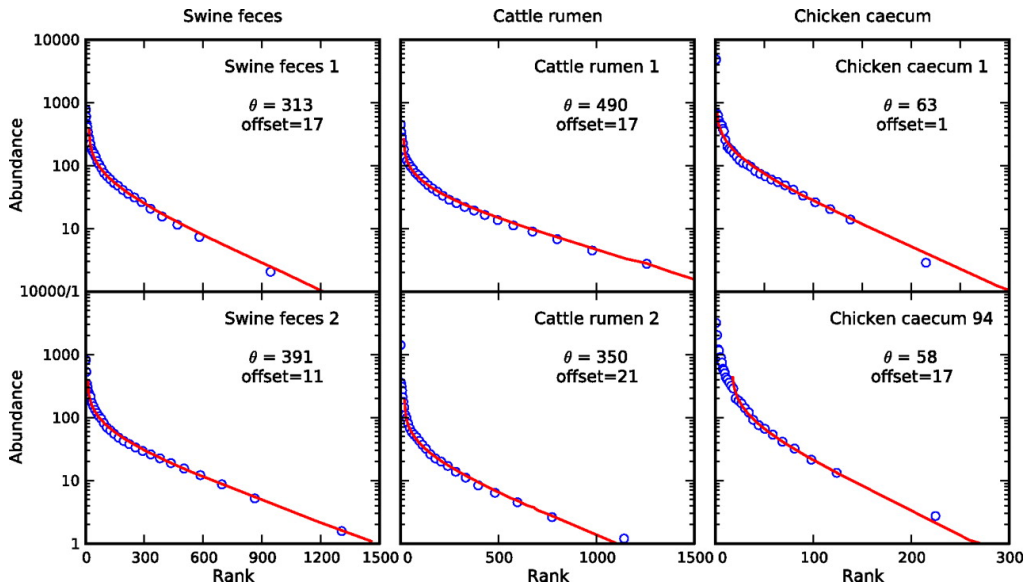

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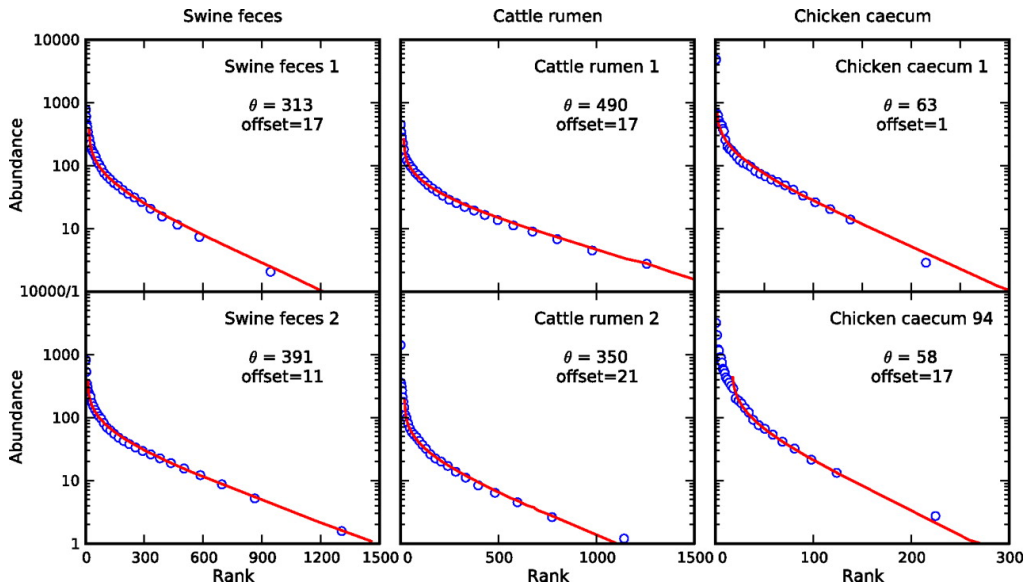

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- Moreover, species abundance curves fit from the neutral theory provide excellent matches to communities with known niches.
- Does this mean we need to reject the UNTB as even a null model?

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- To apply these tools to testing and possibly rejecting the neutral hypothesis for the assembly of the human gut microbiome.

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- *e.g.*, $(\nu_1, \ldots, \nu_N) \sim \text{Multinomial}\left(N, \frac{1}{N}\right)$ in the Wright-Fisher model.

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  - $\int f(y)\, P^{(N)}(x, dy) = \left(1 - c_{N_0} \frac{\theta}{2}\right) f(x) + c_{N_0} \frac{\theta}{2} \int f(y)\, dy + o(c_{N_0})$.

EXAMPLE: HUBBELL'S UNTB

- In Hubbell's original model, only a single individual is replaced in each deme at at each time step: $\nu_{ij} \in \{0, 1, 2\}$, with

$$(\nu_{i1}, \ldots, \nu_{iN_i}) = (1, \ldots, 1, 0, 1, \ldots, 1, 2, 1, \ldots, 1)$$

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- In Hubbell's model, immigrants are always from the mainland, which is assumed to have a fixed, stationary distribution (so that samples are distributed according to Ewens formula), and no mutations are assumed to occur on the islands.
- We will not need to make these assumptions, but will instead derive them (in the limit as $N \to \infty$) as a consequence of the relative size of the mainland and the islands.

Outline

ROBUSTNESS OF THE WRIGHT-FISHER DIFFUSION

- Möhle (2001) showed that if time is rescaled by c_N^{-1}, *i.e.*, by the effective population size, then the frequencies of types in a Cannings' model converge to those given by the Wright-Fisher diffusion, if and only if

$$\lim_{N\to\infty} \frac{\mathbb{E}\left[\nu_1(\nu_1-1)(\nu_1-2)\right]}{N\mathbb{E}\left[\nu_1(\nu_1-1)\right]} = 0.$$

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- We can thus say that the Wright-Fisher diffusion is a robust approximation to a broad class of neutral population genetic processes.
- We will see that a similar invariance principle exists for the class of Cannings' neutral community models, and moreover its stationary distribution is the Hierarchical Dirichlet Process (Teh, 2006)

INVARIANCE PRINCIPLE I: ISLANDS

- Let $X_{ij}(n) \in [0,1]$ be the type of the j^{th} individual in the i^{th} deme in the n^{th} generation, and let

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- Suppose that there exists a_N such that

$$\lim_{N\to\infty} \frac{c_{N_i}}{a_N} = \begin{cases} \gamma_i & \text{if } i \geq 1, \text{ and} \\ 0 & \text{otherwise.} \end{cases}$$

  exists for all i.

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INVARIANCE PRINCIPLE I: ISLANDS

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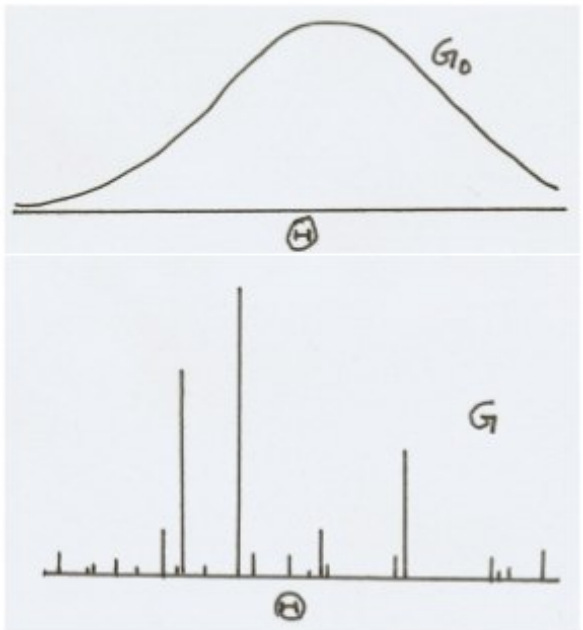
- Further, conditional on $G_0(0)$, the $G_i^{(N)}(0)$ are independent.

INVARIANCE PRINCIPLE I: STATIONARY DIRICHLET PROCESS

- As $t \to \infty$, the infinite alleles model with mutation rate θ and base measure μ tends to a stationary distribution with law $DP(\theta, \mu)$



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  - Let μ be a probability measure on a space Θ and let $X_i \sim \mu$ be i.i.d.
  - $\sum_{i=1}^{\infty} \beta_i \delta_{X_i}$ is a random variable with law $\text{DP}(\theta, \mu)$
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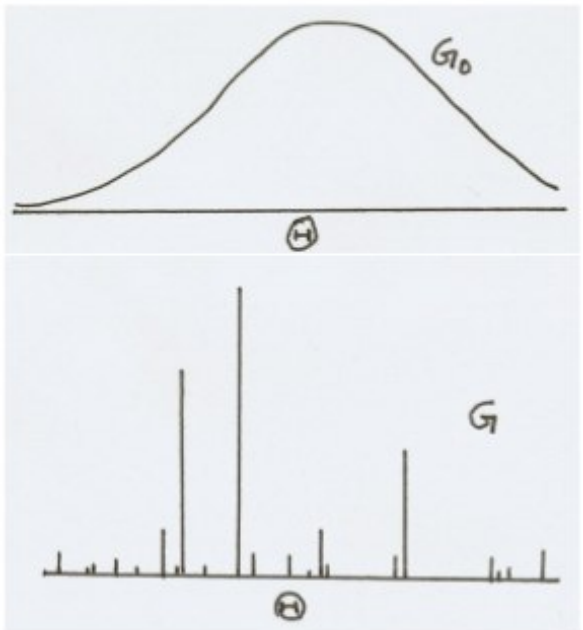

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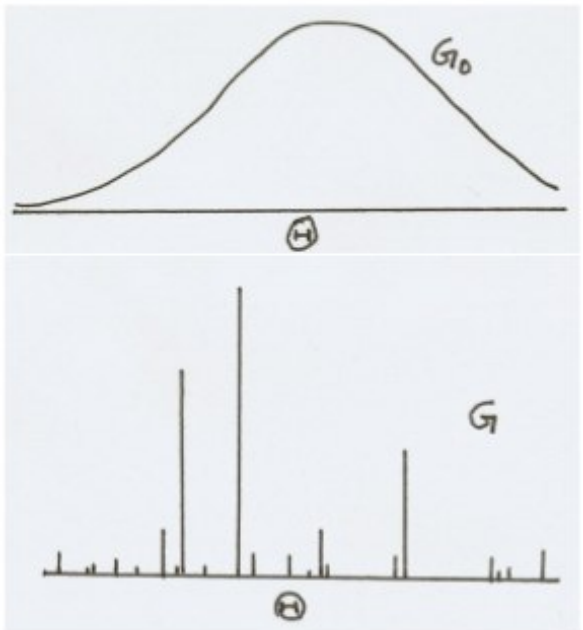
  - $\mathbb{E}\left[\sum_{i=1}^{\infty} \beta_i \delta_{X_i}\right] = \mu$.
- In particular, samples from a $\text{DP}(\theta, \mu)$ r.v. can be generated using Aldous' *Chinese restaurant process* and are distributed according to *Ewens' sampling formula*.



INVARIANCE PRINCIPLE II: MAINLAND

- Further, if we assume that $G_i^{(N)}(0) \stackrel{w}{\Longrightarrow} G_i(0)$, where $G_i(0) \sim \mathrm{DP}(I_i, G_0(0))$, *i.e.*, we assume that the islands are already at their stationary state, then

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- We can thus apply the extensive statistical machinery for the HDP developed in the machine learning literature.

Outline

An Efficient MCMC Algorithm

- The HDP lends itself very well to inference via a Gibbs sampler:
  - Gibbs sampling is a special case of Metropolis–Hastings.
  - Construct an ergodic discrete time Markov chain such that the joint probability distribution of the parameters, conditional on the observed data, is its stationary distribtution.
  - Parameters are the rescaled mutation and migration rates, θ and the I_i.
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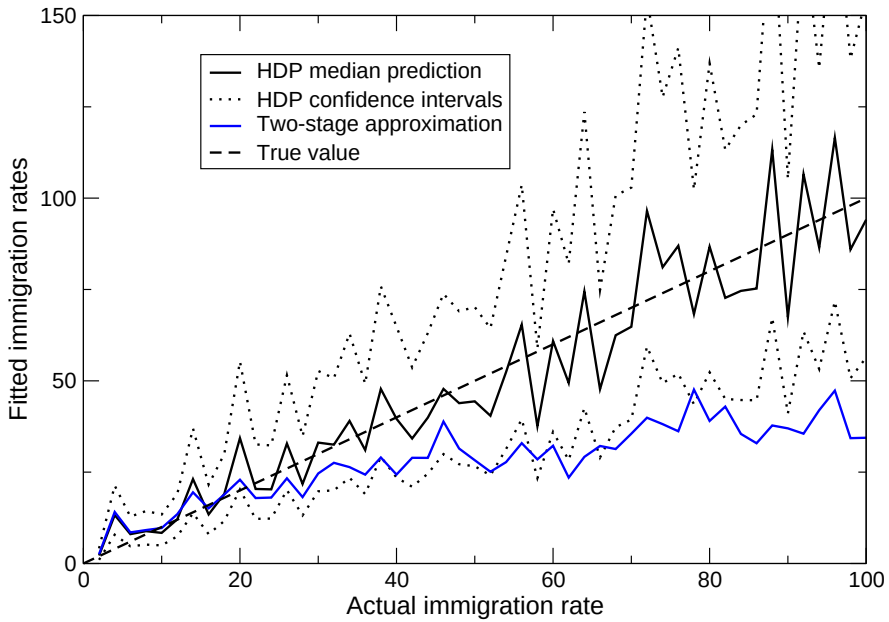
- Ergodicity of the Markov chain allows us to average over repeated samples to obtain expectations of arbitrary functions of the parameters.
  - The expected value of the parameters gives the Bayes' minimum square estimators (MSE), $\hat{\theta}$, $\hat{I}_i$.
  - We can easily determine the full posterior distribution or any related summary statistics.

TESTING THE GIBBS SAMPLER I: SIMULATED DATA



Estimated immigration rates vs. true values for the UNTB-HDP model fit to a neutral model simulation. Predictions are medians (solid line) from 25,000 posterior samples together with lower (2.5%) and upper (97.5%) Bayesian confidence intervals (dotted lines). The predictions from the two-stage approximation are also given (blue line).

TESTING THE GIBBS SAMPLER II: PANAMA CANAL ZONE DATASETS

Method	θ	I_{BCI}	I_C	I_S
Etienne fixed I	259	44.2	44.2	44.2
Etienne approx	342	53.7	30.8	33.9
Etienne exact	235 ± 23	65.3 ± 5.9	31.5 ± 3.9	35.7 ± 3.9
HDP approx	231 ± 22	65.5 ± 5.9	31.6 ± 3.8	35.8 ± 3.9

- Neutral parameter estimates for samples from three local tree communities (Sherman, BCI and Cocoli) in the Panama Canal Zone using previous approaches and the hierarchical Dirichlet process approximation. Standard errors are given for the methods where they are available.

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- HDP gives good agreement with exact methods.
- When we applied our HDP approach to 29 Panamanian tropical tree communities, we found a significant negative correlation between distance and estimated immigration rate – the latter are informative.

Outline

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- However, evidence of clustering of gut microbiota into different enterotypes (Arumugam et al., 2011; Holmes et al., 2012), which implies non- neutral structuring at the whole community level.
- We explored this by subdividing the species according to their taxa at multiple taxonomic levels; it should be increasingly the case that species in smaller clades occupy similar community roles and for neutrality we may only require this in the broadest sense, e.g., methanogens vs. sulphate reducers.

METHODS

- Used gut microbiome data from twins and their mothers (Turnbaugh et al., 2009): faecal samples from 154 individuals, characterized by family and body mass index (BMI), at two time points two months apart.
- The V2 hypervariable region of the 16S rRNA gene was amplified by PCR and then sequenced using 454 and de-noised using the AmpliconNoise pipeline (Quince et al., 2009, 2011).
- 570,851 reads split over 278 samples – sample size 53 to 10,580 with a median of 1,598.
- 19,647 unique sequences following noise removal, taxonomically classified using the RDP stand-alone classifier of Wang et al. (2007), split by phylum, using a cut-off of 70% bootstrap confidence
- Constructed 7,238 Operational Taxonomic Units (OTUs) at 3% sequence difference using average linkage clustering (Youssef et al., 2009)
- Fitted UNTB-HDP to each phylum, family and genus separately
- Only samples with > 100 representatives from a taxa were included, only fit to taxa with > 50 such samples.
- Used Monte Carlo significance test for neutrality from Etienne (2007): p_N metacommunity p-value; p_L 'local' p-value.

FITTING THE UNTB-HDP MODEL TO HUMAN GUT MICROBIOTA

Taxa	%age	#samples	#3% OTU	$\hat{\theta}$	$\hat{I}_i$	p_N	p_L
Bacteroidetes	29.9	249	585	151.32	1.46-5.57-13.52	0.0	0.0
Bacteroidaceae	23.6	221	224	50.79	0.85-3.33-7.70	0.0	0.05
Bacteroides	23.6	238	227	51.01	0.71-3.33-7.80	0.0	0.04
Rikenellaceae							
Alistipes	2.22	66	40	8.72	0.33-2.38-11.10	0.02	0.77
Firmicutes	66.1	277	4771	1383.38	21.44-44.82-80.81	0.0	0.0
Incertae Sedis XIV	7.56	124	217	47.75	2.16-9.88-27.42	0.0	0.06
Blautia	7.55	197	252	52.01	2.26-10.62-34.18	0.0	0.14
Lachnospiraceae	12.4	230	1076	314.66	6.57-13.28-23.91	0.0	0.0
Roseburia	2.61	87	124	38.21	0.40-2.41-7.12	0.0	0.18
Ruminococcaceae	24.2	257	1489	412.68	4.19-15.73-38.20	0.0	0.0
Faecalibacterium	12.1	236	369	84.27	0.66-6.87-21.46	0.0	0.01
Oscillibacter	1.90	58	72	19.33	0.84-3.23-8.16	0.068	0.34
Ruminococcus	1.74	60	35	10.99	0.00-0.38-1.94	0.013	0.65
Subdoligranulum	2.95	94	86	23.14	0.22-1.67-8.50	0.0	0.32

- $\hat{\theta}$: median over 25,000 Gibbs samples
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- The immigration rates are again informative: they are much lower for the Bacteroides than the Firmicutes, probably reflecting the fact that the latter are spore-forming.

IMMIGRATION RATES *vs.* BMI

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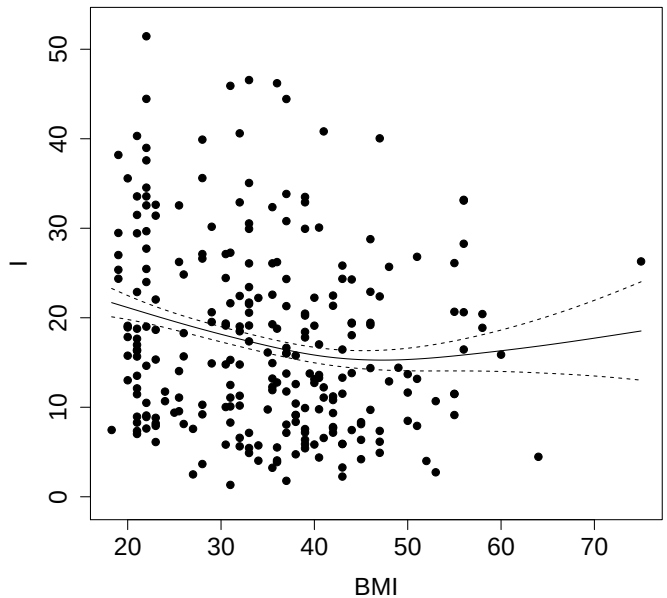

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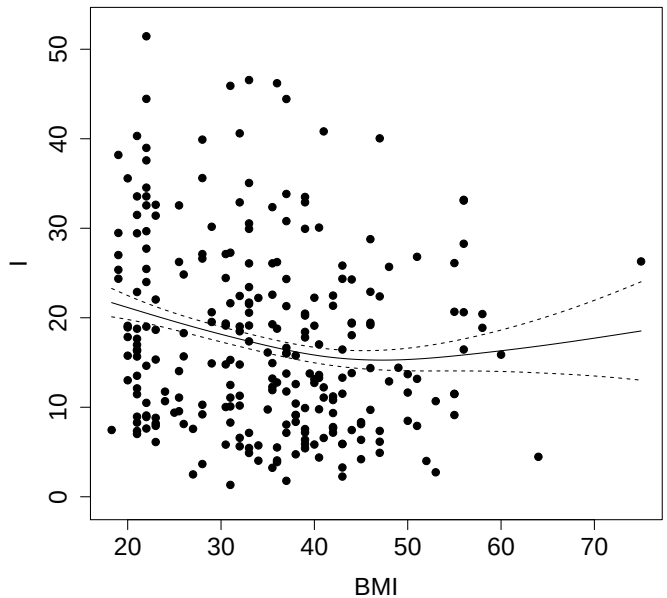

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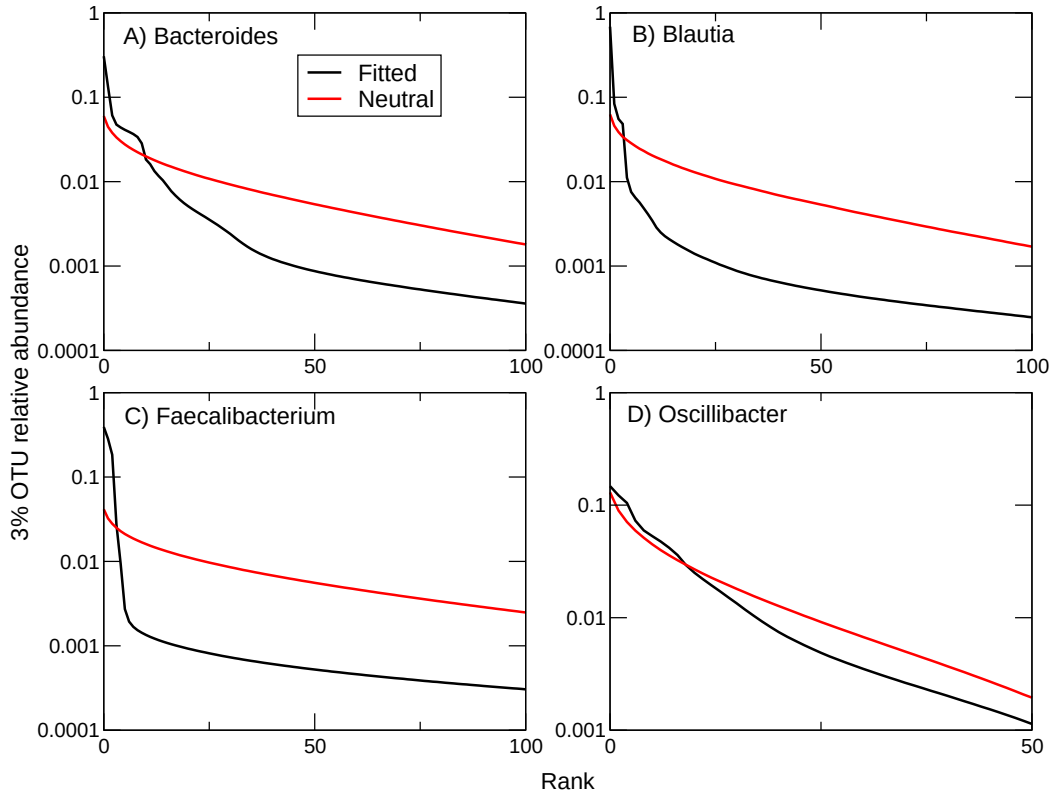
- Increasing nutrient supply counterintuitively reduces local biodiversity.

FITTED RANK-ABUNDANCE CURVES



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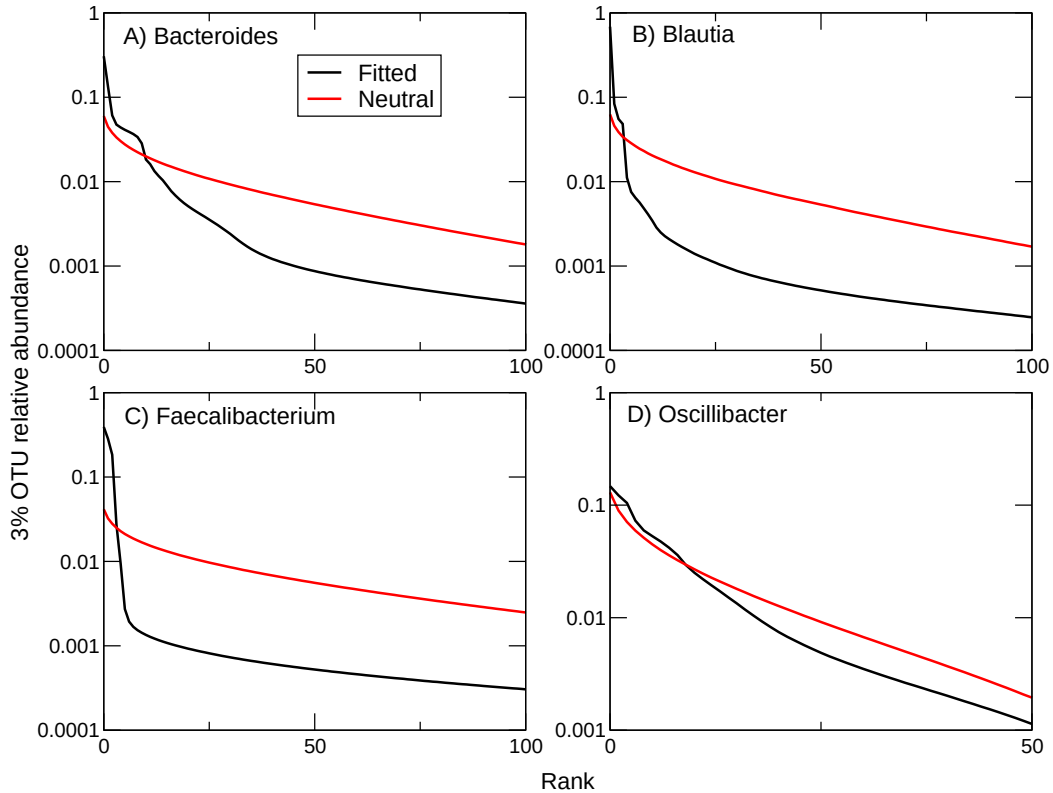

- Empricial metacommunity distributions (black line) and neutral metacommunity predictions (red line) for four genera: A) Bacteroides, B) Blautia, C) Faecalibacterium and D) Oscillibacter
- Unlike Jeraldo, *et. al.* (2012), when we fit the whole model, as opposed to the rank-abundance curve, we can reject the neutral hypothesis.

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- Moreover, we have formally linked a model from ecology, the UNTB, with a highly flexible model from machine learning, the hierarchical Dirichlet process; we hope that the connection we have made here will lead to further hierarchical Bayesian modelling in ecology.

Thank you!

Outline

A Community Model With Tradeoffs, No Fixed N

$$X_i^N(t) = \text{the number of individuals of species } i \text{ at time } t$$

Event	Rate
$X_i^N(t) \to X_i^N(t) + 1$	$\left(\beta_i X_i^N(t) + m_i\right)\left(\frac{N - \sum_{j=1}^K X_j^N(t)}{N} + \sum_{j=1}^K \kappa_{ij} \frac{X_j^N(t)}{N}\right)$
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- Individuals of species i give birth at per-capita rate β_i.

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Event	Rate
$X_i^N(t) \to X_i^N(t) + 1$	$\left(\beta_i X_i^N(t) + m_i\right)\left(\frac{N - \sum_{j=1}^K X_j^N(t)}{N} + \sum_{j=1}^K \kappa_{ij} \frac{X_j^N(t)}{N}\right)$
$X_i^N(t) \to X_i^N(t) - 1$	$\delta_i X_i^N(t)$

- Individuals of species i give birth at per-capita rate β_i.
- They die at rate δ_i.

$$X_i^N(t) = \text{the number of individuals of species } i \text{ at time } t$$

Event	Rate
$X_i^N(t) \to X_i^N(t) + 1$	$\left(\beta_i X_i^N(t) + m_i\right)\left(\frac{N - \sum_{j=1}^K X_j^N(t)}{N} + \sum_{j=1}^K \kappa_{ij} \frac{X_j^N(t)}{N}\right)$
$X_i^N(t) \to X_i^N(t) - 1$	$\delta_i X_i^N(t)$

- Individuals of species i give birth at per-capita rate β_i.
- They die at rate δ_i.
- Individuals of species i immigrate from the mainland at rate $m_i = \frac{\varpi_i}{N}$.

$$X_i^N(t) = \text{the number of individuals of species } i \text{ at time } t$$

Event	Rate
$X_i^N(t) \to X_i^N(t) + 1$	$\left(\beta_i X_i^N(t) + m_i\right)\left(\frac{N - \sum_{j=1}^K X_j^N(t)}{N} + \sum_{j=1}^K \kappa_{ij} \frac{X_j^N(t)}{N}\right)$
$X_i^N(t) \to X_i^N(t) - 1$	$\delta_i X_i^N(t)$

- Individuals of species i give birth at per-capita rate β_i.
- They die at rate δ_i.
- Individuals of species i immigrate from the mainland at rate $m_i = \frac{\varpi_i}{N}$.
- Individuals survive if they find an empty patch or if they out-compete an individual in an occupied patch.

For the community model with tradeoffs, long-term coexistence is only possible if $\kappa_{ij} \equiv \kappa$ and

$$\frac{\beta_i}{\delta_i} \equiv 1 - \nu.$$

For $t \in (\delta, \infty)$ for any fixed $\delta > 0$, the relative frequency process, $\mathbf{P}(t) = \frac{1}{\sum_{i=1}^{K} X_i(t)} \mathbf{X}(Nt)$ is a diffusion on the standard simplex with generator:

$$\begin{aligned}
\mathcal{L}f = \sum_{i=1}^{K-1} \frac{(1-\nu)(1-\kappa)}{\nu} \Bigg[\mu_i - \frac{\mu_. \beta_i p_i}{\sum_{k=1}^{K} \beta_k p_k} \\
+ \frac{\beta_i p_i}{\left(\frac{1}{\alpha} - 1\right) \left(\sum_{k=1}^{K} \beta_k p_k\right)_2} \sum_{k=1}^{K} (\beta_k - \beta_i) \beta_k p_k \Bigg] \partial_{p_i} f \\
+ \sum_{i=1}^{K-1} \sum_{j=1}^{K-1} \frac{(1-\nu)(1-\kappa)}{\nu} \beta_i p_i \left(\delta_{ij} - \frac{\beta_j p_j}{\sum_{k=1}^{K} \beta_k p_k} \right) \partial_{p_i} \partial_{p_j} f.
\end{aligned}$$

- The probability of having relative species abundances $(p_1, \ldots, p_K)$ is Dirichlet distributed:

$$\frac{\Gamma\left(\sum_{i=1}^{K} \frac{\varpi_i}{\beta_i}\right)}{\prod_{i=1}^{K} \Gamma\left(\frac{\varpi_i}{\beta_i}\right)} \prod_{i=1}^{K} p_i^{\frac{\varpi_i}{\beta_i} - 1}$$

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- This offers one potential explanation for the effectiveness of the UNTB in fitting real species abundance data: if we assume migration rates are proportional to birth rates ($\varpi_i = \beta_i \theta$,) then the abundance distribution under trade-offs is type independent.