Polya urn models for multivariate species abundances: properties and applications.

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June 20, 2024

Satistical context

- Object: Multivariate species abundances

  $\Leftrightarrow$ Multivariate count data

  $\boldsymbol{Y} = (Y_1, \ldots, Y_J) \in \mathbb{N}^J$ where J =number of species

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- Different modeling approaches
  1. Discrete copulas
     $\rightarrow$ Slar theorem does not hold ... copula is not unique !
  2. Poisson graphical model $Y_j \sim \mathcal{P}\left\{\exp(\eta_j)\right\}$, $\eta_j = \boldsymbol{y}_{-j}^T \beta_j$
     $\rightarrow$ implies negative constraint on predictors η_j ...
  3. Poisson log-normal: $\boldsymbol{Y} \sim \mathcal{PLN}(\boldsymbol{\mu}, \Sigma)$
     $\rightarrow$ dependences on latent variables $\boldsymbol{Z} \sim \mathcal{N}(\boldsymbol{\mu}, \Sigma)$
  4. Mixed multinomial $\boldsymbol{Y} \sim \mathcal{M}(n, \boldsymbol{\pi}) \underset{\boldsymbol{\pi}}{\wedge} \mathcal{D}(\boldsymbol{\theta})$
     $\rightarrow$ dependences on observed variable $\boldsymbol{Y}$

Outline

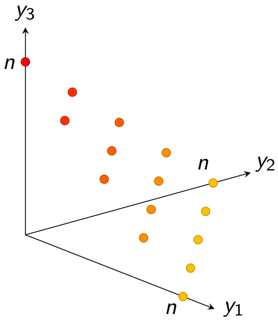
1. Polya splitting models
   - Singular distribution
   - Polya urn
   - Closure under thinning operation
   - Probabilistic graphical model
2. Neutral theory of biodiversity
   - State of the art
   - Link with Polya urn
3. Statistical point of view
   - Regression framework
   - Tree structure
   - Application on real data

Outline

Singular distributions

Definition

Multinomial distribution $\mathcal{M}(n, \boldsymbol{\pi})$ is supported on the discrete simplexe $\Delta_n = \{\boldsymbol{y} \in \mathbb{N}^J : |\boldsymbol{y}| = n\}$.



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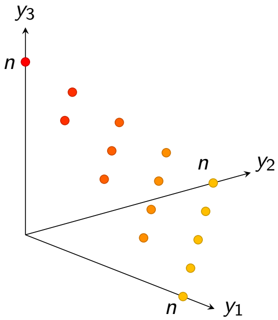

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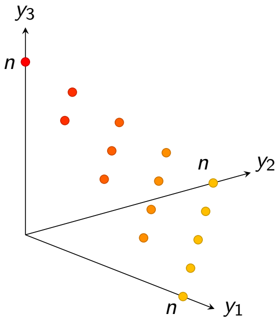

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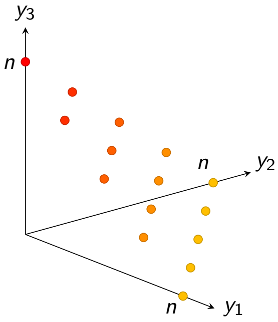


Problem

$\dim(\Delta_n) = J - 1$

Remark

compositional distribution	$\rightarrow$	singular distribution
continuous simplexe Δ		discrete simplexe Δ_n
$\boldsymbol{\pi} \sim \mathcal{D}$		$\mathcal{M}_{\Delta_n}(\boldsymbol{\pi}) \underset{\boldsymbol{\pi}}{\wedge} \mathcal{D}$

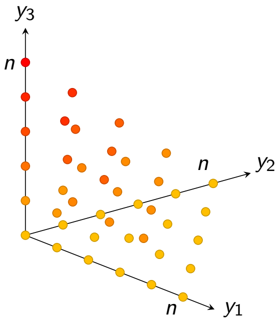
Non-singular version

Definition

$$\begin{array}{ll} & \boldsymbol{Y} \text{ follows non-singular multinomial} \\ \Leftrightarrow & (\boldsymbol{Y}, n - |\boldsymbol{Y}|) \text{ follows multinomial} \end{array}$$

Supported on the interior of Δ_n

$\blacktriangle_n = \left\{\boldsymbol{y} \in \mathbb{N}^J : |\boldsymbol{y}| \leq n\right\}$.



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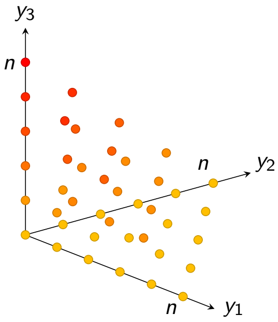

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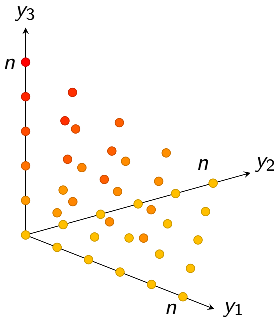

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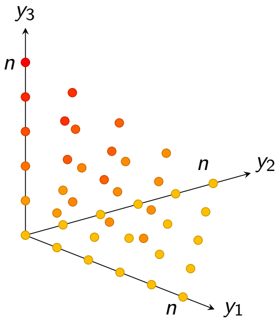

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$\dim(\blacktriangle_n) = J$

Problem

The support $\blacktriangle_n$ is bounded

Multinomial Splitting distribution

Definition

$\boldsymbol{Y}$ is said to follow a multinomial splitting distribution if

$$\begin{cases} |\boldsymbol{Y}| \sim \mathcal{L} & (sum) \\ \boldsymbol{Y} \text{ given } |\boldsymbol{Y}| = n \sim \mathcal{M}_{\Delta_n}(\boldsymbol{\pi}) & (split) \end{cases}$$

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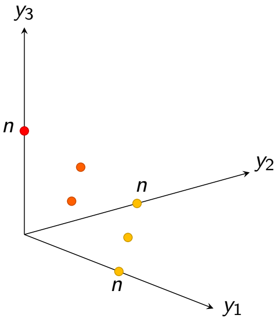

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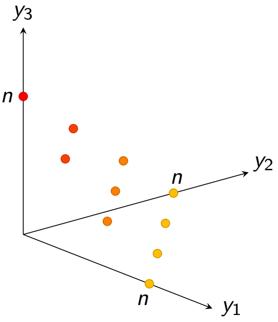

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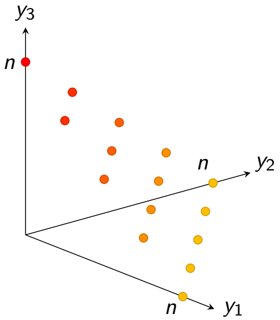

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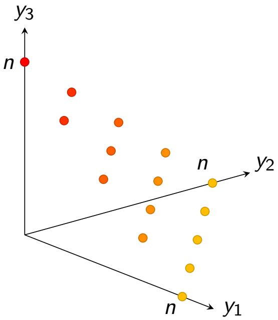

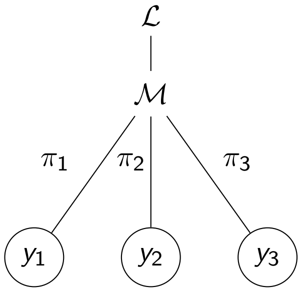

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$\mathcal{M}_{\Delta_n}(\boldsymbol{\pi}) \underset{n}{\wedge} \mathcal{L}$

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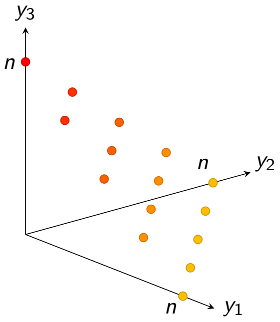

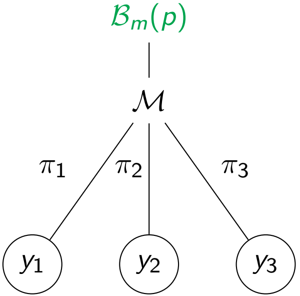

Non-singular multinomial

$\mathcal{M}_{\blacktriangle_m}(p \cdot \boldsymbol{\pi})$

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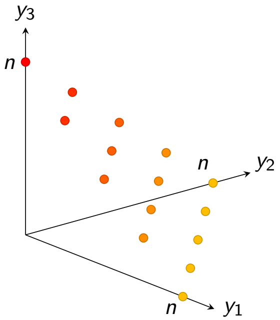
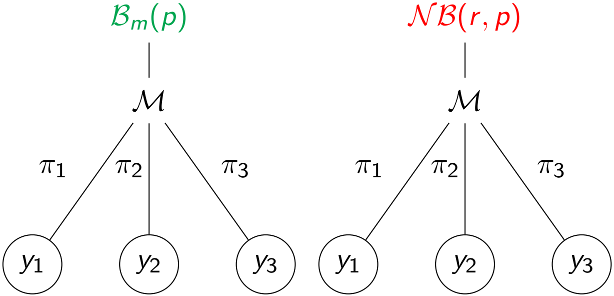




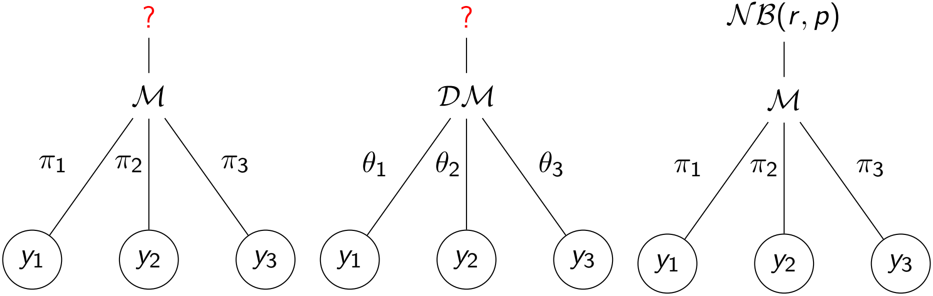
Non-singular multinomial
$\mathcal{M}_{\blacktriangle_m}(p \cdot \boldsymbol{\pi})$

Negative multinomial
$\mathcal{NM}(r, p \cdot \boldsymbol{\pi})$

Problem of models comparison . . .

Zhang et al. (2017)

They compared the **multinomial**, the **Dirichlet multinomial** and the **negative multinomial** regression models on RNA-seq dataset.



Multinomial (singular) | Dirichlet multinomial (singular) | Negative multinomial

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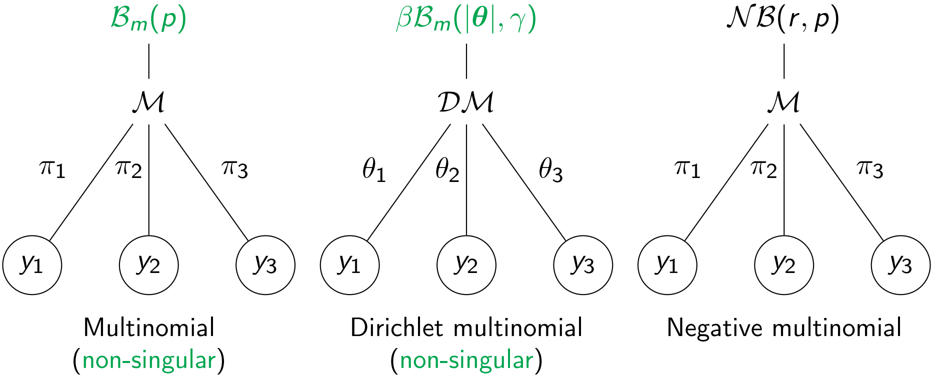
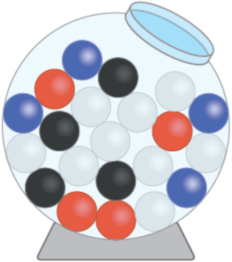


Outline

Pólya urn models

- The urn initially contains θ_j balls of the j^{th} color
- At each draw, one ball is drawn at random and then replaced with c "additional" balls of the same color ($c \in \{-1, 0, 1\}$).
- Focus on the count $\boldsymbol{y} = (y_1, \dots, y_J)$ of drawn balls after n draws

$$P_{|\boldsymbol{Y}|=n}(\boldsymbol{Y} = \boldsymbol{y}) = \binom{n}{\boldsymbol{y}} \frac{\prod_{j=1}^{J} \theta_j^{(y_j;c)}}{|\boldsymbol{\theta}|^{(n;c)}}, \quad \text{where } \theta^{(n;c)} := \prod_{k=0}^{n-1} (\theta + ck)$$



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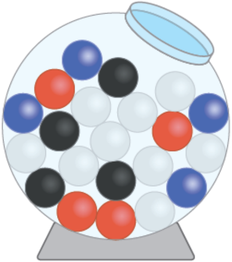

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   multivariate **hypergeometric**
2. $c = 0 \quad \leftrightarrow \quad$ with replacement (indep. draws)
   multinomial
3. $c = 1 \quad \leftrightarrow \quad$ with reinforcement
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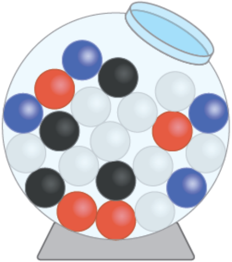

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Notation: $\boldsymbol{Y} \sim \mathcal{P}_{\Delta_n}^{[c]}(\boldsymbol{\theta}) \underset{n}{\wedge} \mathcal{L}$

General properties of Polya splitting

$$\boldsymbol{Y} \sim \mathcal{P}^{[c]}_{\Delta_n}(\boldsymbol{\theta}) \underset{n}{\wedge} \mathcal{L}$$

1. $Y_1, \ldots, Y_J$ are lineary free (random sum)
2. Log-likelihood decomposition (sum and split)

$$\mathcal{L} = \log p(|\boldsymbol{y}|) + \log p_{|\boldsymbol{y}|}(\boldsymbol{y})$$

3. Characteristics: pmf, expectation, co-variance

$$\mathrm{Cov}(Y_i, Y_j) = \frac{\theta_i \theta_j}{|\boldsymbol{\theta}|^2 (|\boldsymbol{\theta}| + c)} \left[\left(\mu_{(2)} - \mu_{(1)}^2\right) |\boldsymbol{\theta}| - c\mu_{(1)}^2 \right].$$

4. Marginal distribution (thinning operation)

$$Y_j \sim \mathcal{P}^{[c]}_{n}(\theta_j, |\boldsymbol{\theta}_{-j}|) \underset{n}{\wedge} \mathcal{L}$$

Pólya thinning operation

Let Y be an univariate count variable such that

$$Y \sim \mathcal{P}_n^{[c]}(\theta, \gamma) \underset{n}{\wedge} \mathcal{L}$$

Damage process

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Binomial thinning operation (Sprott, 1965)

Let n be the number of eggs and Y the number of **hatched** eggs

$$Y \sim \mathcal{B}_n(\pi) \underset{n}{\wedge} \mathcal{L}$$

It is equivalent to

$$Y = \sum_{i=1}^{n} Z_i, \quad n \sim \mathcal{L}, \quad Z_i \sim \mathcal{B}(\pi) \text{ i.i.d.}$$

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→ **How to choose the sum distribution $\mathcal{L}$?**

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Closure under thinning operation

Definition

A parametric distribution $\mathcal{L}(\psi)$ is said to be closed under the binomial thinning operation if there exists ψ' such that

$$\mathcal{B}_n(\pi) \underset{n}{\wedge} \mathcal{L}(\psi) = \mathcal{L}(\psi')$$

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Examples (Rao, 1965)

(1) $\mathcal{B}_n(\pi) \underset{n}{\wedge} \mathcal{B}_m(p) = \mathcal{B}_m(p')$ where $p' = \pi p$

(2) $\mathcal{B}_n(\pi) \underset{n}{\wedge} \mathcal{P}(\lambda) = \mathcal{P}(\lambda')$ where $\lambda' = \pi\lambda$

(3) $\mathcal{B}_n(\pi) \underset{n}{\wedge} \mathcal{NB}(r, b) = \mathcal{NB}(r, b')$ where $b' = \pi b$

Pmf of univariate Polya

Let $\theta^{(n;c)} = \prod_{k=0}^{n-1}(\theta + kc)$ denote the ascendent factorial. For $k = 0, \ldots, n$

$$P(X = k) = \binom{n}{k} \frac{\theta^{(k;c)}\gamma^{(n-k;c)}}{(\theta + \gamma)^{(n;c)}}$$

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Convolution identity

$$a_\theta^{[c]} * a_\gamma^{[c]} = a_{\theta+\gamma}^{[c]}$$

$\rightsquigarrow$ Vandermonde ($c = -1$), Newton ($c = 0$), Hagen-Rothe ($c = 1$)

(1) Polya distribution: $X \sim \mathcal{P}_n^{[c]}(\theta, \gamma)$

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	$c = -1$	$c = 0$	$c = 1$
$a_\theta^{[c]}(n)$	$\binom{\theta}{n}$	$\theta^n / n!$	$\binom{n+\theta-1}{n}$

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(3) Inverse Polya distribution: $X \sim \mathcal{IP}_n^{[c]}(r; \theta, \gamma)$

$$P(X = k) = \frac{r}{n+r} \frac{a_\theta^{[c]}(k) a_\gamma^{[c]}(r)}{a_{\theta+\gamma}^{[c]}(k+r)}, \quad k \in \mathbb{N}$$

	$c = -1$	$c = 0$	$c = 1$
$a_\theta^{[c]}(n)$	$\binom{\theta}{n}$	$\theta^n / n!$	$\binom{n+\theta-1}{n}$
(1)	hypergeometric	binomial	beta binomial

(1) Polya distribution: $X \sim \mathcal{P}_n^{[c]}(\theta, \gamma)$

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(2)	binomial	Poisson	negative binomial
(3)	beta binomial	negative binomial	beta negative binomial

Closure under Pólya thinning operation

Theorem 1 (Peyhardi, 2023)

(1) Pólya

$$\mathcal{P}_n^{[c]}(\theta,\gamma) \underset{n}{\wedge} \mathcal{P}_m^{[c]}(\boldsymbol{\theta}+\boldsymbol{\gamma},\lambda) = \mathcal{P}_m^{[c]}(\theta,\gamma+\lambda)$$

(2) Power series

$$\mathcal{P}_n^{[c]}(\theta,\gamma) \underset{n}{\wedge} \mathcal{PS}^{[c]}(\boldsymbol{\theta}+\boldsymbol{\gamma},\alpha) = \mathcal{PS}^{[c]}(\theta,\alpha)$$

(3) Inverse Pólya

$$\mathcal{P}_n^{[c]}(\theta,\gamma) \underset{n}{\wedge} \mathcal{IP}^{[c]}(r;\boldsymbol{\theta}+\boldsymbol{\gamma},\lambda) = \mathcal{IP}^{[c]}(r;\theta,\lambda)$$

	$c=-1$	$c=0$	$c=1$
$a_\theta^{[c]}(n)$	$\binom{\theta}{n}$	$\theta^n/n!$	$\binom{n+\theta-1}{n}$
(1)	hypergeometric	binomial	beta binomial
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(3)	beta binomial	negative binomial	beta negative binomial

Nine **multivariate** distributions

Split / Sum	Hypergeometric $c = -1$	Multinomial $c = 0$	Dirichlet multinomial $c = 1$
(1) Pólya	$\mathcal{H}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \mathcal{H}_m(\lvert\boldsymbol{\theta}\rvert, \gamma)$ (supp $= \blacktriangle_m \cap \blacksquare_{\boldsymbol{\theta}}$)	$\mathcal{M}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \mathcal{B}_m(p)$ (supp $= \blacktriangle_m$)	$\mathcal{DM}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \beta\mathcal{B}_m(\lvert\boldsymbol{\theta}\rvert, \gamma)$ (supp $= \blacktriangle_m$)
(2) Power series	$\mathcal{H}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \mathcal{B}_{\lvert\boldsymbol{\theta}\rvert}(p)$ (support $= \blacksquare_{\boldsymbol{\theta}}$)	$\mathcal{M}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \mathcal{P}(\lambda)$ (support $= \mathbb{N}^J$)	$\mathcal{DM}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \mathcal{NB}(\lvert\boldsymbol{\theta}\rvert, p)$ (support $= \mathbb{N}^J$)
(3) Inverse Pólya	$\mathcal{H}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \beta\mathcal{B}_{\lvert\boldsymbol{\theta}\rvert}(a, b)$ (support $= \blacksquare_{\boldsymbol{\theta}}$)	$\mathcal{M}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \mathcal{NB}(a, p)$ (support $= \mathbb{N}^J$)	$\mathcal{DM}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \beta\mathcal{NB}(\lvert\boldsymbol{\theta}\rvert, a, b)$ (support $= \mathbb{N}^J$)

Nine **multivariate** distributions

Sum \ Split	Hypergeometric $c=-1$	Multinomial $c=0$	Dirichlet multinomial $c=1$
(1) Pólya	$\mathcal{H}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \mathcal{H}_m(\lvert\boldsymbol{\theta}\rvert, \gamma)$ (supp $= \blacktriangle_m \cap \blacksquare_{\boldsymbol{\theta}}$)	$\mathcal{M}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \mathcal{B}_m(p)$ (supp $= \blacktriangle_m$)	$\mathcal{DM}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \beta\mathcal{B}_m(\lvert\boldsymbol{\theta}\rvert, \gamma)$ (supp $= \blacktriangle_m$)
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(3) Inverse Pólya	$\mathcal{H}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \beta\mathcal{B}_{\lvert\boldsymbol{\theta}\rvert}(a, b)$ (support $= \blacksquare_{\boldsymbol{\theta}}$)	$\mathcal{M}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \mathcal{NB}(a, p)$ (support $= \mathbb{N}^J$)	$\mathcal{DM}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \beta\mathcal{NB}(\lvert\boldsymbol{\theta}\rvert, a, b)$ (support $= \mathbb{N}^J$)

Closure under summation

$$\left.\begin{array}{l} Y_i \sim \mathcal{L}(\theta_i) \\ Y_j \sim \mathcal{L}(\theta_j) \end{array}\right\} \quad Y_i + Y_j \sim \mathcal{L}(\theta_i + \theta_j)$$

Nine **multivariate** distributions

Sum \ Split	Hypergeometric $c=-1$	Multinomial $c=0$	Dirichlet multinomial $c=1$
(1) Pólya Cov <0	$\mathcal{H}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \mathcal{H}_m(\lvert\boldsymbol{\theta}\rvert, \gamma)$ (supp $= \blacktriangle_m \cap \blacksquare_{\boldsymbol{\theta}}$)	$\mathcal{M}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \mathcal{B}_m(p)$ (supp $= \blacktriangle_m$)	$\mathcal{DM}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \beta\mathcal{B}_m(\lvert\boldsymbol{\theta}\rvert, \gamma)$ (supp $= \blacktriangle_m$)
(2) Power series Cov $=0$	$\mathcal{H}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \mathcal{B}_{\lvert\boldsymbol{\theta}\rvert}(p)$ (support $= \blacksquare_{\boldsymbol{\theta}}$)	$\mathcal{M}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \mathcal{P}(\lambda)$ (support $= \mathbb{N}^J$)	$\mathcal{DM}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \mathcal{NB}(\lvert\boldsymbol{\theta}\rvert, p)$ (support $= \mathbb{N}^J$)
(3) Inverse Pólya Cov >0	$\mathcal{H}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \beta\mathcal{B}_{\lvert\boldsymbol{\theta}\rvert}(a, b)$ (support $= \blacksquare_{\boldsymbol{\theta}}$)	$\mathcal{M}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \mathcal{NB}(a, p)$ (support $= \mathbb{N}^J$)	$\mathcal{DM}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \beta\mathcal{NB}(\lvert\boldsymbol{\theta}\rvert, a, b)$ (support $= \mathbb{N}^J$)

Closure under summation

$$\left.\begin{array}{l} Y_i \sim \mathcal{L}(\theta_i) \\ Y_j \sim \mathcal{L}(\theta_j) \end{array}\right\} \quad Y_i + Y_j \sim \mathcal{L}(\theta_i + \theta_j)$$

$$\mathrm{Cov}(Y_i, Y_j) = \frac{\theta_i \theta_j}{\lvert\boldsymbol{\theta}\rvert^2 (\lvert\boldsymbol{\theta}\rvert + c)} \left[\left(\mu_{(2)} - \mu_{(1)}^2\right) \lvert\boldsymbol{\theta}\rvert - c\mu_{(1)}^2 \right].$$

Outline

Sum \ Split	Hypergeometric $c=-1$	Multinomial $c=0$	Dirichlet multinomial $c=1$
(1) Pólya Cov <0	$\mathcal{H}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \mathcal{H}_m(\lvert\boldsymbol{\theta}\rvert,\gamma)$ (supp $= \blacktriangle_m \cap \blacksquare_{\boldsymbol{\theta}}$)	$\mathcal{M}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \mathcal{B}_m(p)$ (supp $= \blacktriangle_m$)	$\mathcal{DM}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \beta\mathcal{B}_m(\lvert\boldsymbol{\theta}\rvert,\gamma)$ (supp $= \blacktriangle_m$)
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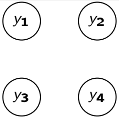
Theorem 2: characterization of PGM (Peyhardi, 2023)

The PGM of a Pólya splitting distribution $\mathcal{P}_n^{[c]}(\boldsymbol{\theta}) \underset{n}{\wedge} \mathcal{L}$ is:

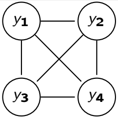
(A) empty **if and only if** $\mathcal{L} = \mathcal{PS}^{[c]}(\lvert\boldsymbol{\theta}\rvert,\alpha)$ (Power series)

(B) complete otherwise

(A)



(B)



Other applications . . .

Thm 2 $\Rightarrow$ Test of independence

Let $\boldsymbol{Y} \sim \mathcal{P}_{\Delta_n}^{[c]}(\boldsymbol{\theta}) \underset{n}{\wedge} \mathcal{L}$

$$H_0 : Y_1, \dots, Y_J \text{ independent} \quad \Leftrightarrow \quad H_0 : \mathcal{L} = \mathcal{PS}^{[c]}(|\boldsymbol{\theta}|, \alpha)$$

Moreover if $\mathcal{L} = \mathcal{PS}^{[c]}(\gamma, \alpha)$ then

$$H_0 : Y_1, \dots, Y_J \text{ independent} \quad \Leftrightarrow \quad H_0 : \gamma = |\boldsymbol{\theta}|$$

Other applications . . .

Thm 2 ⇒ Test of independence

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Thm 1 and Thm 2 ⇒ stationarity of INAR models (count time series)

$$X_t = \rho \circ X_{t-1} + \varepsilon_t$$

- $\rho \circ X | X = n \sim \mathcal{P}_n(\theta, \gamma)$
- $\varepsilon_t \sim \mathcal{PS}(\gamma, \alpha)$
- $X_0 \sim \mathcal{PS}(\theta + \gamma, \alpha)$

$$\Rightarrow \quad X_t \sim \mathcal{PS}(\theta + \gamma, \alpha)$$

Outline

Biological modeling framework (**Neutral Theory**)

- Biodiversity is not only determined by the number J of different entities, but also by the abundance of these entities $\boldsymbol{Y} = (Y_1, \ldots, Y_J)$.

- The neutral theory of biodiversity (Caswell, 1976) assumes
  - H_0: no biological interaction beetween species
    $\rightarrow$ challenges the traditional niche-based view of ecology
  - the multivariate species abundance distribution is the **stationary distribution** of a simple stochastic process
    H_0: null model

Mathematical modeling framework (**Neutral Theory**)

Let $\boldsymbol{Y}(t) = (Y_1(t), \ldots, Y_J(t))$ be a **multivariate** birth death process.

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Let $\boldsymbol{Y}(t) = (Y_1(t), \dots, Y_J(t))$ be a **multivariate** birth death process.

Jumping rates

$$\begin{aligned} q_j^+(\boldsymbol{y}) &:= m_j(\boldsymbol{y}) + y_j b_j(\boldsymbol{y}) \\ q_j^-(\boldsymbol{y}) &:= y_j d_j(\boldsymbol{y}) \end{aligned}$$

- $m_j(\boldsymbol{y})$: **immigration** rate of species j
- $b_j(\boldsymbol{y})$: per-individual **birth** rate of species j
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The master equation

$$\frac{\partial p_{\boldsymbol{y}}(t)}{\partial t} = \sum_{j=1}^{J} p_{\boldsymbol{y}-\boldsymbol{e}_j}(t) q_j^-(\boldsymbol{y}-\boldsymbol{e}_j) + p_{\boldsymbol{y}+\boldsymbol{e}_j}(t) q_j^+(\boldsymbol{y}+\boldsymbol{e}_j) - p_{\boldsymbol{y}+\boldsymbol{e}_j}(t) \left(q_j^-(\boldsymbol{y}) + q_j^+(\boldsymbol{y}) \right)$$

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Study the **stationary distribution** under neutral assumption on

$$q_j(\boldsymbol{y}) := \frac{q_j^+(\boldsymbol{y})}{q_j^-(\boldsymbol{y}+\boldsymbol{e}_j)}$$

Model I of Caswell (1976)

- Model
  - Speciation according to Poisson process
  - "New immigrant becomes the founder of a line of descendants generated by a linear birth-death process" ($b = d$)

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  2. Independence between species

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- Total abundance (at time t)

  $N_t \sim \mathcal{NB}$ with expectation $E[N_t] = t$

  Problem: "the total abundance grows without bound over time"

Model of Hubbell (2001)

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- Jumping rates

$$\begin{cases} q_j^+(\boldsymbol{y}) & = d\left(\frac{n - y_j}{n}\right)\left(\frac{y_j}{n-1}\right) \\ q_j^-(\boldsymbol{y}) & = d\left(\frac{y_j}{n}\right)\left(\frac{n - y_j}{n-1}\right) = q_j^+(\boldsymbol{y}) \end{cases}$$

$$\Rightarrow q_j(\boldsymbol{y}) = \frac{n+1}{n-1}\frac{y_j}{y_j+1}$$

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- Abundances **at equilibrium** $(t \to \infty)$

  $(y_1, \ldots, y_J) \sim \mathcal{DM}_{\Delta_n}$ (split)

Model of Haegeman and Etienne (2008)

- Assumptions
  1. **Neutrality** : functional equivalence among different species
     ~~**Zero sum game**~~ : total abundance is random !

- Jumping rates

$$\begin{cases} q_j^+(\boldsymbol{y}) & = m(|\boldsymbol{y}|)\pi_j + b(|\boldsymbol{y}|)y_j \\ q_j^-(\boldsymbol{y}) & = d(|\boldsymbol{y}|)y_j \end{cases}$$

$$\Rightarrow q_j(\boldsymbol{y}) = \frac{b(|\boldsymbol{y}|)}{d(|\boldsymbol{y}|+1)} \frac{\theta_j + y_j}{y_j + 1}$$

where $\theta_j := I\pi_j$ and $I = \frac{m(|\boldsymbol{y}|)}{b(|\boldsymbol{y}|)}$

- Abundances **at equilibrium** $(t \to \infty)$
  - $(y_1, \ldots, y_J)$ given $|\boldsymbol{y}| = n \sim \mathcal{DM}_{\Delta_n}(\boldsymbol{\theta})$ (split)

Model of Haegeman and Etienne (2008)

- Assumptions
  1. **Neutrality** : functional equivalence among different species
     ~~**Zero sum game**~~ : total abundance is random !
  2. **Independence** between species abundances
- Jumping rates

$$\begin{cases} q_j^+(\boldsymbol{y}) & = m(|\boldsymbol{y}|)\pi_j + b(|\boldsymbol{y}|)y_j \\ q_j^-(\boldsymbol{y}) & = d(|\boldsymbol{y}|)y_j \end{cases}$$

$$\Rightarrow q_j(\boldsymbol{y}) = \frac{b(|\boldsymbol{y}|)}{d(|\boldsymbol{y}|+1)} \frac{\theta_j + y_j}{y_j + 1}$$

where $\theta_j := I\pi_j$ and $I = \frac{m(|\boldsymbol{y}|)}{b(|\boldsymbol{y}|)}$
and $\frac{b(|\boldsymbol{y}|)}{d(|\boldsymbol{y}|+1)} = \alpha$ (constant)

- Abundances **at equilibrium** $(t \to \infty)$
  - $(y_1, \dots, y_J)$ given $|\boldsymbol{y}| = n \quad \sim \mathcal{DM}_{\Delta_n}(\boldsymbol{\theta})$ (split)
  - $|\boldsymbol{y}| \sim \mathcal{NB}(I, \alpha)$ (sum)

Outline

Model of Peyhardi et al. (2024)

- Assumptions
  1. Neutrality species are equivalent in immigration, birth and death rates
     ~~Zero sum game~~

- Jumping rates

$$\begin{cases} q_j^+(\boldsymbol{y}) & = m(|\boldsymbol{y}|)\pi_j + b(|\boldsymbol{y}|)y_j \\ q_j^-(\boldsymbol{y}) & = d(|\boldsymbol{y}|)y_j \end{cases}$$

$$\Rightarrow q_j(\boldsymbol{y}) = s(|\boldsymbol{y}|)\frac{\theta_j + y_j}{y_j + 1}$$

where $\theta_j := I\pi_j$ and $I = \frac{m(|\boldsymbol{y}|)}{b(|\boldsymbol{y}|)}$

- Abundances **at equilibrium** $(t \to \infty)$
  - $(y_1, \ldots, y_J)$ given $|\boldsymbol{y}| = n \sim \mathcal{DM}_{\Delta_n}(\boldsymbol{\theta})$ (split)
  - $|\boldsymbol{y}| \sim \mathcal{L}$ (sum)

Model of Peyhardi et al. (2024)

- Assumptions
  1. Neutrality species are equivalent in immigration, birth and death rates
     ~~Zero sum game~~
     ~~Independence~~
- Jumping rates

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where $\theta_j := I\pi_j$ and $I = \frac{m(|\boldsymbol{y}|)}{b(|\boldsymbol{y}|)}$

$s(|\boldsymbol{y}|) = \frac{1}{|\boldsymbol{\theta}|}\frac{m(|\boldsymbol{y}|)}{d(|\boldsymbol{y}|+1)}$ not necessary constant !

- Abundances **at equilibrium** $(t \to \infty)$
  - $(y_1, \ldots, y_J)$ given $|\boldsymbol{y}| = n \sim \mathcal{DM}_{\Delta_n}(\boldsymbol{\theta})$ (split)
  - $|\boldsymbol{y}| \sim \mathcal{L}$ (sum) $\leftrightarrow$ **any sum distribution**

Model of Peyhardi et al. (2024)

- Assumptions
  1. Neutrality species are equivalent in immigration, birth and death rates
     ~~Zero sum game~~
     ~~Independence~~
- Jumping rates (with possible density-dependent immigration)

$$\begin{cases} q_j^+(\boldsymbol{y}) & = m(|\boldsymbol{y}|)\,[\pi_j - Ky_j] + b(|\boldsymbol{y}|)y_j \\ q_j^-(\boldsymbol{y}) & = d(|\boldsymbol{y}|)y_j \end{cases}$$

$$\Rightarrow q_j(\boldsymbol{y}) = s(|\boldsymbol{y}|)\frac{\theta_j + \mathbf{c}y_j}{y_j + 1}$$

where $\theta_j := I\pi_j$ and $I = \frac{m(|\boldsymbol{y}|)}{b(|\boldsymbol{y}|)}$

$s(|\boldsymbol{y}|) = \frac{1}{|\boldsymbol{\theta}|}\frac{m(|\boldsymbol{y}|)}{d(|\boldsymbol{y}|+1)}$ not necessary constant !

- Abundances **at equilibrium** $(t \to \infty)$
  - $(y_1, \ldots, y_J)$ given $|\boldsymbol{y}| = n \sim \mathcal{P}^{[c]}_{\Delta_n}(\boldsymbol{\theta})$ (split) $\leftrightarrow$ **any Polya distribution**
  - $|\boldsymbol{y}| \sim \mathcal{L}$ (sum) $\leftrightarrow$ **any sum distribution**

Jumping rates → Polya splitting distrbutions (stationarity)

Sum \ Split	Hypergeometric $c = -1$	Multinomial $c = 0$	Dirichlet multinomial $c = 1$
(1) Pólya Cov < 0	$\mathcal{H}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \mathcal{H}_m(\|\boldsymbol{\theta}\|, \gamma)$ (supp $= \blacktriangle_m \cap \blacksquare_{\boldsymbol{\theta}}$)	$\mathcal{M}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \mathcal{B}_m(p)$ (supp $= \blacktriangle_m$)	$\mathcal{DM}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \beta\mathcal{B}_m(\|\boldsymbol{\theta}\|, \gamma)$ (supp $= \blacktriangle_m$)
(2) Power series Cov $= 0$	$\mathcal{H}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \mathcal{B}_{\|\boldsymbol{\theta}\|}(p)$ (support $= \blacksquare_{\boldsymbol{\theta}}$)	$\mathcal{M}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \mathcal{P}(\lambda)$ (support $= \mathbb{N}^J$)	$\mathcal{DM}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \mathcal{NB}(\|\boldsymbol{\theta}\|, p)$ (support $= \mathbb{N}^J$)
(3) Inverse Pólya Cov > 0	$\mathcal{H}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \beta\mathcal{B}_{\|\boldsymbol{\theta}\|}(a, b)$ (support $= \blacksquare_{\boldsymbol{\theta}}$)	$\mathcal{M}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \mathcal{NB}(a, p)$ (support $= \mathbb{N}^J$)	$\mathcal{DM}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \beta\mathcal{NB}(\|\boldsymbol{\theta}\|, a, b)$ (support $= \mathbb{N}^J$)

Jumping rates → Polya splitting distrbutions (stationarity)

Sum \ Split	Hypergeometric $c=-1$	Multinomial $c=0$	Dirichlet multinomial $c=1$
(1) Pólya Cov <0	$\mathcal{H}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \mathcal{H}_m(\lvert\boldsymbol{\theta}\rvert,\gamma)$ (supp $=\blacktriangle_m \cap \blacksquare_{\boldsymbol{\theta}}$)	$\mathcal{M}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \mathcal{B}_m(p)$ (supp $=\blacktriangle_m$)	$\mathcal{DM}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \beta\mathcal{B}_m(\lvert\boldsymbol{\theta}\rvert,\gamma)$ (supp $=\blacktriangle_m$)
(2) Power series Cov $=0$	$\mathcal{H}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \mathcal{B}_{\lvert\boldsymbol{\theta}\rvert}(p)$ (support $=\blacksquare_{\boldsymbol{\theta}}$)	$\mathcal{M}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \mathcal{P}(\lambda)$ (support $=\mathbb{N}^J$)	$\mathcal{DM}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \mathcal{NB}(\lvert\boldsymbol{\theta}\rvert,p)$ (support $=\mathbb{N}^J$)
(3) Inverse Pólya Cov >0	$\mathcal{H}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \beta\mathcal{B}_{\lvert\boldsymbol{\theta}\rvert}(a,b)$ (support $=\blacksquare_{\boldsymbol{\theta}}$)	$\mathcal{M}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \mathcal{NB}(a,p)$ (support $=\mathbb{N}^J$)	$\mathcal{DM}_n(\boldsymbol{\theta}) \underset{n}{\wedge} \beta\mathcal{NB}(\lvert\boldsymbol{\theta}\rvert,a,b)$ (support $=\mathbb{N}^J$)

Sum \ Split	Hypergeometric $c=-1$	Multinomial $c=0$	Dirichlet multinomial $c=1$
(1) Pólya	$\frac{m-\lvert\mathbf{y}\rvert}{\gamma-m+\lvert\mathbf{y}\rvert+1}$	$\frac{m-\lvert\mathbf{y}\rvert}{\gamma}$	$\frac{m-\lvert\mathbf{y}\rvert}{\gamma+m-\lvert\mathbf{y}\rvert-1}$
(2) Power series	α	α	α
(3) Inverse Pólya	$\frac{a+\lvert\mathbf{y}\rvert}{\lvert\boldsymbol{\theta}\rvert+b-\lvert\mathbf{y}\rvert-1}$	$\frac{a+\lvert\mathbf{y}\rvert}{\lvert\boldsymbol{\theta}\rvert+b}$	$\frac{b+\lvert\mathbf{y}\rvert}{\lvert\boldsymbol{\theta}\rvert+a+b+\lvert\mathbf{y}\rvert}$

Table: Parametric form of $s(\lvert\mathbf{y}\rvert)$ and thus of jumping rate $q_j(\mathbf{y}) = s(\lvert\mathbf{y}\rvert)\frac{\theta_j+cy_j}{y_j+1}$.

* The grey cells corresponds to the case of Haegeman and Etienne (2008).

Outline

Polya splitting **regression**

Let $x = (x_1, \dots, x_p) \in \mathbb{R}^p$ denotes the explanatory variables.

$$\boldsymbol{Y} \text{ given } x \sim \mathcal{P}^{[c]}_{\Delta_n}\{\boldsymbol{\theta}(x)\} \underset{n}{\wedge} \mathcal{L}\{\psi(x)\}$$

$$\Leftrightarrow \begin{cases} |\boldsymbol{Y}| \sim \mathcal{L}\{\psi(x)\} & \text{(sum regression)} \\ \boldsymbol{Y} \text{ given } |\boldsymbol{Y}| = n \text{ and } x \sim \mathcal{P}^{[c]}_{\Delta_n}\{\boldsymbol{\theta}(x)\} & \text{(split regression)} \end{cases}$$

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Example: negative multinomial regression

$$\boldsymbol{Y} \text{ given } x \sim \mathcal{M}_{\Delta_n}\{\boldsymbol{\pi}(x)\} \underset{n}{\wedge} \mathcal{NB}\{r, p(x)\}$$

$$\pi_j = \frac{\exp(x^t\beta_j)}{\sum_{k=1}^{J}\exp(x^t\beta_k)}\; j = 1, \dots, J \quad \text{and} \quad p = \frac{\exp(x^t\delta)}{1+\exp(x^t\delta)}$$

Maximum Likelihood Estimation (MLE)

Log-likelihood decomposition

$$\mathcal{L}(\{\beta_j\}, \delta; \boldsymbol{y}) = \mathcal{L}(\{\beta_j\}; \boldsymbol{y}) + \mathcal{L}(\delta; |\boldsymbol{y}|)$$

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separate estimation on sum and split

- estimate $\{\hat{\beta}_j\}$ on multivariate dataset $(\boldsymbol{y}_i, x_i)_{i=1,\ldots,n}$ (split)
- estimate $\hat{r}$ and δ on univariate dataset $(|\boldsymbol{y}_i|, x_i)_{i=1,\ldots,n}$ (sum)

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GLM properties

- concavity of log-likelihood for canonical link function
- simple formulation of Fisher's scoring algorithm
- asymptotic normality of MLE

Model selection

Time complexity

$$\left.\begin{array}{l} L \text{ models for the sum} \\ M \text{ models for the split} \end{array}\right\} \Rightarrow L \times M \text{ models}$$

with $\mathcal{O}(C + L)$ time complexity.

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Existing packages

- sum:
  - Poisson
  - Negative binomial
- split:
  - multinomial
  - Dirichlet multinomial

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Existing packages

- sum:
  - Poisson
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- split:
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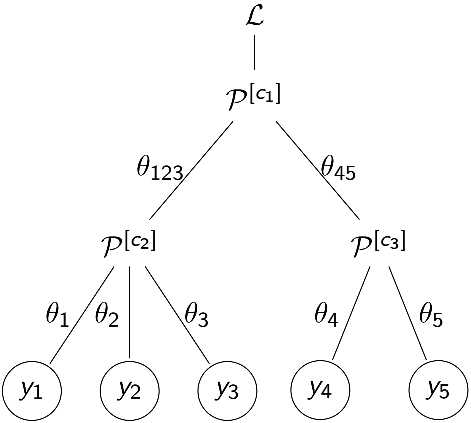
  - Dirichlet multinomial

Variables selection

LASSO, Ridge, step AIC, ...

Outline

Tree Polya splitting distribution

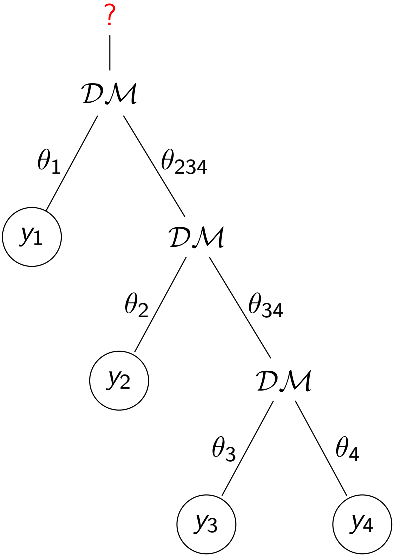


- decomposition of the likelihood

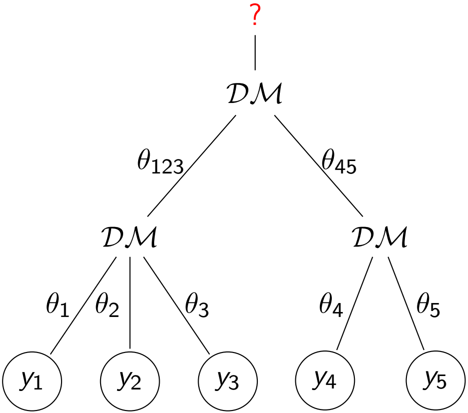
$$\mathcal{L} = \log p(|\mathbf{y}|) + \sum_{A \in \mathcal{I}} \log p_{|\mathbf{y}_A|}(\mathbf{y}_A)$$

  where $\mathcal{I}$ set of internal nodes
- more parameters $\rightarrow$ flexibility
- structured covariance
- includes DM, GDM, TDM as special cases

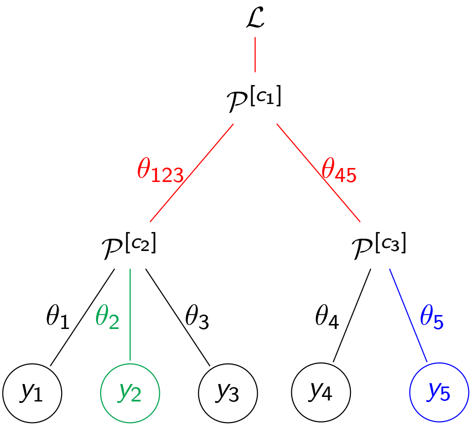
Generalization of GDM, TDM approaches



Generalized Dirichlet Multinomial

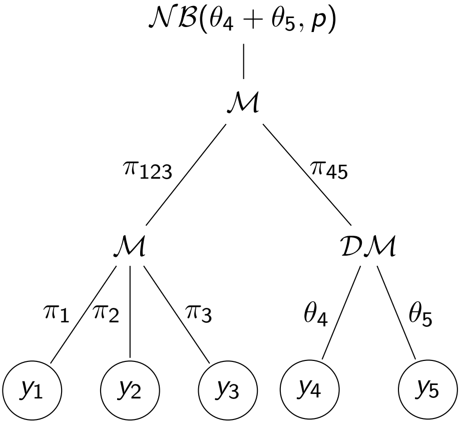


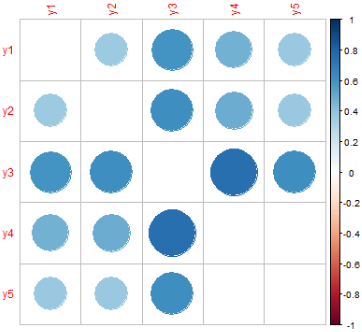
Tree Dirichlet Multinomial



$$\mathrm{Cov}(y_2, y_5) = \frac{\theta_2}{\theta_1 + \theta_2 + \theta_3} \frac{\theta_5}{\theta_4 + \theta_5} \mathrm{Cov}(y_1 + y_2 + y_3, y_4 + y_5)$$

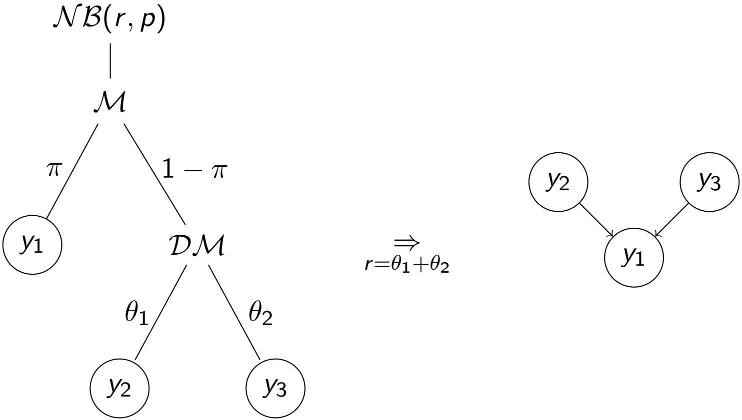
Example of structured covariance





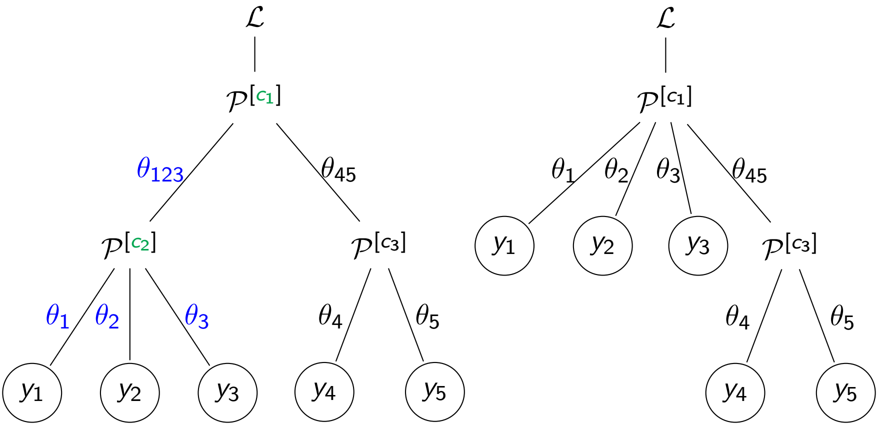
Probabilistic Graphical Model (V-structure)

If $r = \theta_1 + \theta_2$ then $p(y_1, y_2, y_3) = p(y_2)p(y_3)p(y_1|y_2 + y_3)$



- $y_2 \perp\!\!\!\perp y_3$
- $(y_2 + y_3) \nearrow \; \Rightarrow \; y_1 \nearrow$

Equivalent trees



Proposition

These two tree splitting models are equivalent **iff** $c_1 = c_2$ (same Polya) and $\theta_{123} = \theta_1 + \theta_2 + \theta_3$.

Outline

Trichoptera dataset description

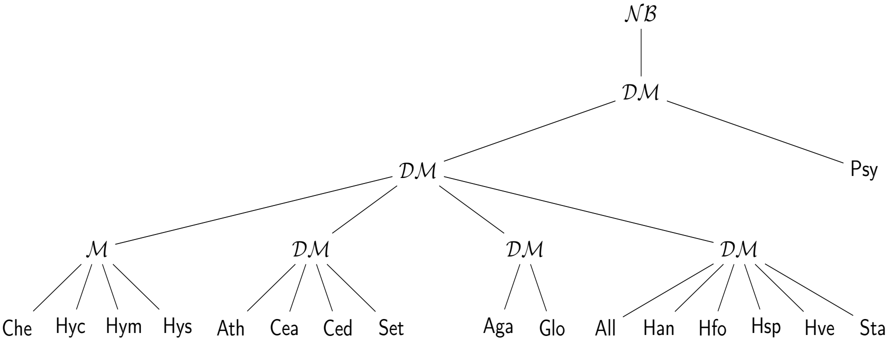
- Group of insects with aquatic larvae and terrestrial adults
- collected between 1959 and 1960 in Lyon
- available on R-package PLNmodels (Chiquet et al., 2021)

- $J = 17$ species abundances
  - Cheumatopsyche lepid (Che)
  - Hyctopsyche contuernglis (Hyc)
  - Hydropsyche mode (Hyd)

    $\vdots$
- $n = 49$ sites
- $p = 9$ covariates (meteorological factors)
  - temperature
  - Wind
  - Pressure

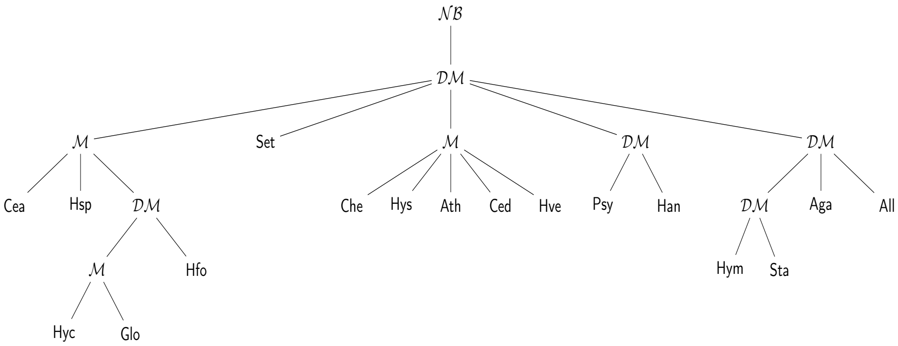
    $\vdots$

Partition tree according to families



Tree Pólya distribution (known tree)

Partition tree search



Tree Pólya distribution (unknown tree).

Models comparison (Trichoptera dataset)

Model	Log-likelihood	Nb. Param.	AIC	BIC
PLN full	-1130.05	170	2599.98	2921.71
PLN diagonal	-1187.97	34	**2443.95**	**2508.26**
PLN spherical	-1236.77	18	2509.55	2543.59

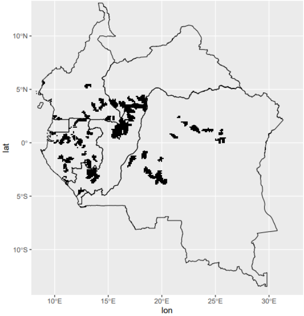
Table: Scores for different Poisson Log Normal (PLN) models

Model	Log-likelihood	Nb. Param.	AIC	BIC
DM	-1228.43	19	2494.87	2530.81
TP (known tree)	-1209.92	23	2465.85	2509.35
TP (unknown tree)	-1167.38	23	**2380.77**	**2424.28**

Table: Scores for different tree Polya (TP) models with NB sum distribution

Trees in Central Afric dataset (Fabrice Moudjeu)

- five countries : Cameroun, Gabon, Rep. of Congo . . .
- $n = 1571$ plots



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  with four families
  - Rosids
  - Asterids
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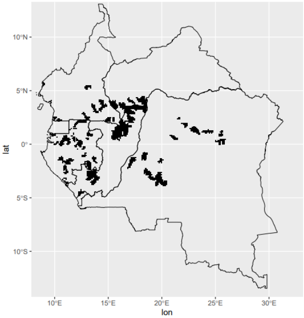
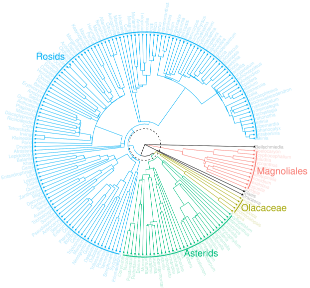
  - Magnoliales





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  with four families
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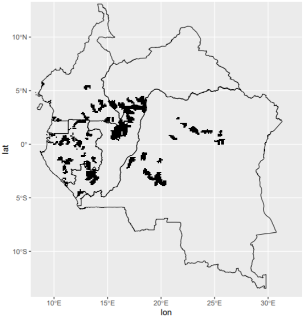
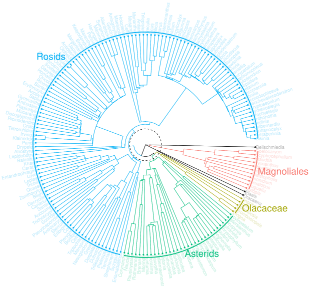
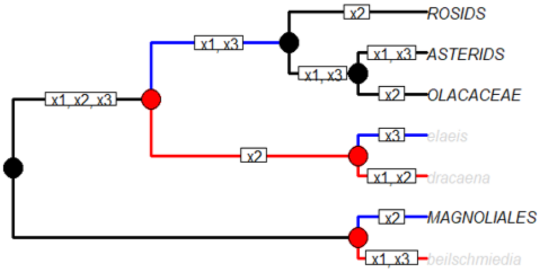
  - Magnoliales
- $p = 3$ covariates
  - x_1: evapotranspiration
  - x_2: seasonality
  - x_3: picks of temperature





Phylogeny and Zero inflation



- Phylogeny= binary tree

$$(Y_1, Y_2) \mid Y_1 + Y_2 = n \quad \sim \quad \mathcal{DM}_{\Delta_n}(\theta_1, \theta_2)$$

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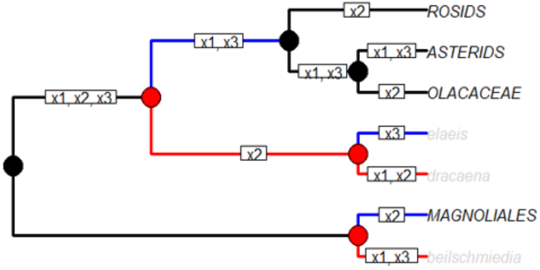

- Phylogeny= binary tree
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$$
\begin{aligned}
(Y_1, Y_2) \mid Y_1 + Y_2 = n &\sim \mathcal{DM}_{\Delta_n}(\theta_1, \theta_2) \\
\Leftrightarrow \quad Y_1 \mid Y_1 + Y_2 = n &\sim \beta\mathcal{B}_n(\theta_1, \theta_2)
\end{aligned}
$$

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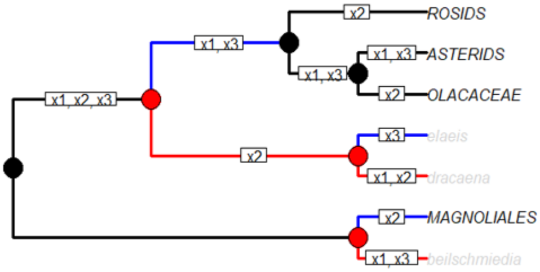

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\end{array}
$$

zero inflation

$$
Y_1 \mid Y_1 + Y_2 = n \sim \pi\delta_0 + (1-\pi)\beta\mathcal{B}_n(\theta_1, \theta_2)
$$

Conlusions and perspectives

Conclusions

- Multivariate extensions of usual count distributions (hypergeometric, binomial, beta binomial, negative binomial . . .)

  $\rightsquigarrow$ similar probabilistic properties

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  - decomposable score (log-likelihood, AIC, BIC)
  - regression + variables selection (existing packages)
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Perspectives

- Tree Polya $\longleftrightarrow$ neutral theory ?
- How measure deviance from neutral theory ?
- Search algorithm $\rightsquigarrow$ the best Tree

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Models for count time series

AR(1) model

$$X_t = \alpha + \rho \cdot X_{t-1} + \varepsilon_t$$

$(X_t)_{t\in\mathbb{N}}$ Markovian process with **continuous** state space $\mathcal{X} = \mathbb{R}$

INAR(1) model

$$X_t = \rho \circ X_{t-1} + \varepsilon_t$$

$(X_t)_{t\in\mathbb{N}}$ Markovian process with **discrete** state space $\mathcal{X} = \mathbb{N}$

The symbol $\circ$ denotes a stochastic operator that shrinks a random count variable into another one

Stationarity of Poisson INAR(1) model

Closure of Poisson distribution

$$X_t = \rho \circ X_{t-1} + \varepsilon_t$$

$$\left.\begin{array}{l} \bullet\ \rho \circ X | X = n \sim \mathcal{B}_n(\rho) \\ \bullet\ \varepsilon_t \sim \mathcal{P}((1-\rho)\lambda) \\ \bullet\ X_0 \sim \mathcal{P}(\lambda) \end{array}\right\} \Rightarrow \quad X_t \sim \mathcal{P}(\lambda)$$

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Closure under binomial thinning operator

$$\mathcal{B}_n(\rho) \underset{n}{\wedge} \mathcal{P}(\lambda) = \mathcal{P}(\rho\lambda)$$

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Closure under convolution

$$\mathcal{P}(\lambda) * \mathcal{P}(\mu) = \mathcal{P}(\lambda + \mu)$$

Stationarity of Power Series INAR(1) model

Closure of Power Series distribution

$$X_t = \rho \circ X_{t-1} + \varepsilon_t$$

- $\rho \circ X | X = n \sim \mathcal{P}_n(\theta, \gamma)$
- $\varepsilon_t \sim \mathcal{PS}(\gamma, \alpha)$
- $X_0 \sim \mathcal{PS}(\theta + \gamma, \alpha)$

$$\left.\begin{array}{l} \rho \circ X | X = n \sim \mathcal{P}_n(\theta, \gamma) \\ \varepsilon_t \sim \mathcal{PS}(\gamma, \alpha) \\ X_0 \sim \mathcal{PS}(\theta + \gamma, \alpha) \end{array}\right\} \Rightarrow \quad X_t \sim \mathcal{PS}(\theta + \gamma, \alpha)$$

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$$\Rightarrow \quad X_t \sim \mathcal{PS}(\theta + \gamma, \alpha)$$

Closure under Polya thinning operator

$$\mathcal{P}_n(\theta, \gamma) \underset{n}{\wedge} \mathcal{PS}(\theta + \gamma, \alpha) = \mathcal{PS}(\theta, \alpha)$$

Closure under convolution

$$\mathcal{PS}(\theta, \alpha) * \mathcal{PS}(\gamma, \alpha) = \mathcal{PS}(\theta + \gamma, \alpha)$$