Ranked Tree Shapes and the Future Loss of Phylogenetic Diversity

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joint works with M. Steel, F. Gascuel and O. Maliet

June 26, 2018
Luminy

Outline

Loss of Phylogenetic Diversity

- Q : "What fraction of the underlying evolutionary history survives when k of n species in a taxon are lost ?" (Nee & May 1997)

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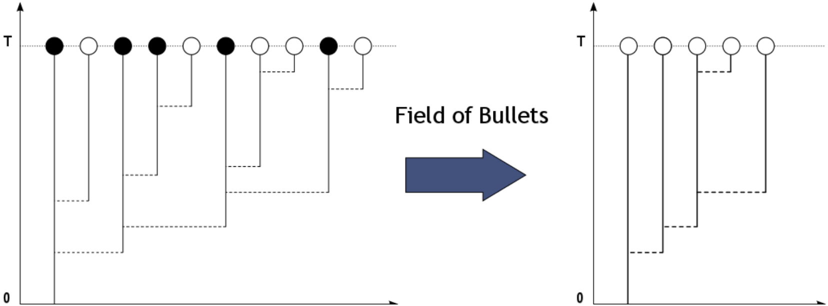
- Phylogenies as metric trees, carry a footprint of evolutionary history
- *Phylogenetic Diversity PD* $=$ Total Length of Tree (Faith 1992)
- Q becomes : "Can we predict how much Phylogenetic Diversity will remain in the face of present extinctions ?"

Field of Bullets Model (FoB)

- Take a phylogeny : tips = species
- Paint independently each tip in white w probability p, in black w probability $1 - p$
- White dot = extant/sampled
- Black dot = extinct/not sampled



The Loss of Phylogenetic Diversity

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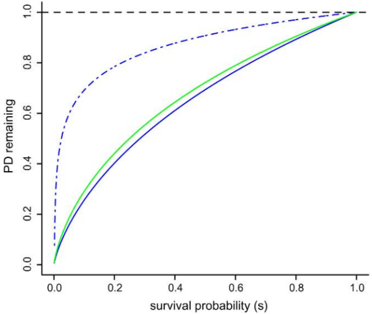

(Mooers, Gascuel, Stadler, Li, Steel 2011)

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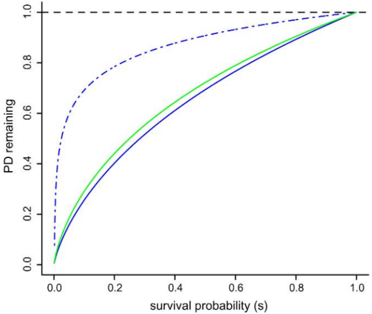

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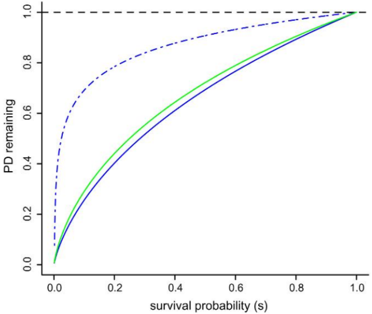
- Remaining PD $S(p)$ = total length of tree spanned by extant/sampled species
- For a given tree, $\mathbb{E}S(p)$ is increasing and concave (Faller, Pardi, Steel 2008)

$$\mathbb{E}S(p) = \sum_e \ell(e)\left(1-(1-p)^{n(e)}\right)$$

where :
$\ell(e)$ = length of edge e,
$n(e)$ = # tips descending from e



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Nee & May *Science* 1997

Extinction and the Loss of Evolutionary History

Sean Nee* and Robert M. May

Extinction episodes, such as the anthropogenic one currently under way, result in a pruned tree of life. But what fraction of the underlying evolutionary history survives when k of n species in a taxon are lost? This is relevant both to how species loss has translated into a loss of evolutionary history and to assigning conservation priorities. Here it is shown that approximately 80 percent of the underlying tree of life can survive even when approximately 95 percent of species are lost, and that algorithms that maximize the amount of evolutionary history preserved are not much better than choosing the survivors at random. Given the political, economic, and social realities constraining conservation biology, these findings may be helpful.

Nee & May *Science* 1997

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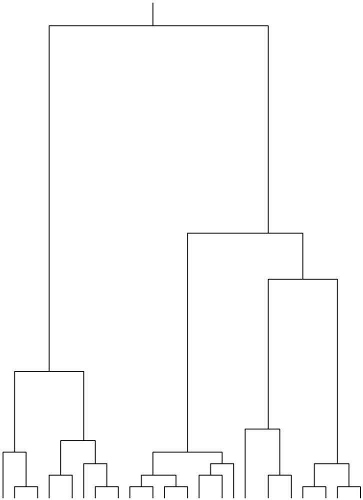
Rule of thumb :
$\mathbb{E}S_n(1) = \sum_{k=2}^{n} \frac{k}{\binom{k}{2}} \sim 2\log(n)$ so

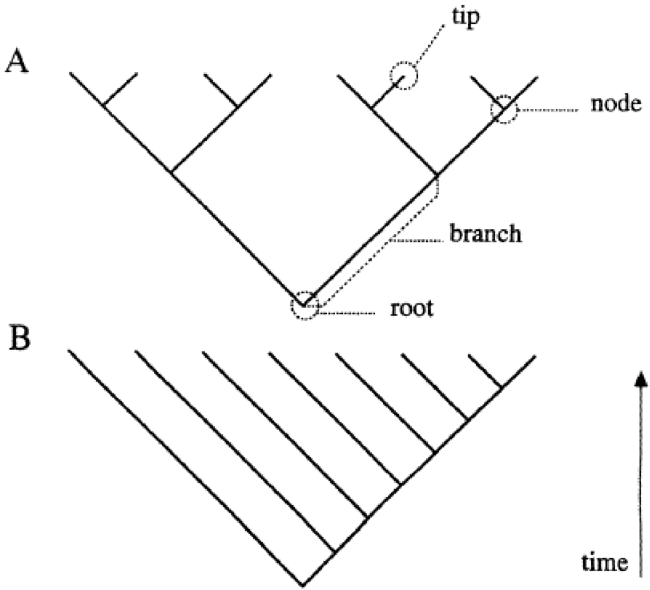
$$\frac{S_n(p)}{S_n(1)} \approx \frac{\log(pn)}{\log(n)} \approx 1$$

1. Field of Bullets
2. Very Small External Edges
3. Balanced



The Kingman Coalescent

Perfectly Balanced Tree (A) vs Caterpillar Tree (B)



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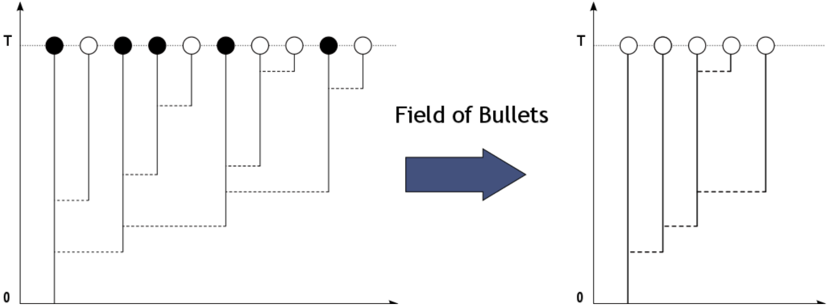
- High for the Kingman coalescent (Nee & May *Science* 1997)
- Lower for the Yule tree (Mooers, Gascuel, Stadler, Li, Steel *Syst Biol* 2011) :

$$\frac{\mathbb{E}S(p)}{\mathbb{E}S(1)} = \text{Ratio of expected remaining PD-to-Old PD} \approx -\frac{p \log p}{1-p}$$

Field of Bullets on a Birth-Death Tree

In a birth-death process stopped at time T, the **reduced tree** is a coalescent point process (CPP) : **node depths** are **i.i.d.**



Remaining PD for general Birth-Death Trees (1)

Lambert & Steel "Predicting the Loss of Phylogenetic Diversity under Non-Stationary Diversification Models" *JTB* 2013

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- Conditional on n tips **before** FoB,

$$\lim_n \frac{S_n(p)}{S_n(1)} = p\,\frac{\mathbb{E}(B)}{\mathbb{E}(H)}$$

where

$$B := \max_{i=1,\dots,G} H_i,$$

and G is a geometric r.v. with success probability p.

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  - Conclude with $K_n/n \to p$.

Remaining PD for general Birth-Death Trees (2)

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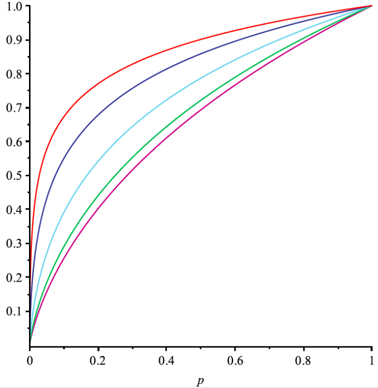
For a Birth-Death tree with sp rate b, ext rate d, div rate $r := b - d$

Remaining PD-to-old PD Ratio $= S(p)/S(1)$

$$= \begin{cases} \frac{dp}{bp-r}\frac{\ln(bp/r)}{\ln(b/r)} & \text{if } b > r \neq bp \\ -\frac{p\ln(p)}{1-p} & \text{if } b = r \\ -\frac{1-p}{\ln(p)} & \text{if } b > r = bp \end{cases}$$



Right : Slow progression towards the unit step function (from pure birth to critical) : $d/b = 0$ (the lowest curve) and then $d/b = 0.5, 0.9, 0.99, 0.999$.

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2. Node depths' rankings $\Longrightarrow \alpha =$ age-richness index
3. Abundances at tips $\Longrightarrow \eta =$ abundance-richness index

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Aldous' program

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1. What is a useful way to describe balance and imbalance in a general phylogenetic tree ?

2. Is there some particular region of the balance-imbalance spectrum containing most actual phylogenetic trees ?

3. If so, is there some mathematically simple and biologically plausible stochastic model for phylogenetic trees whose realizations mimic actual trees ?

Aldous' Markov branching model on binary tree shapes

Aldous (1996, 2001)

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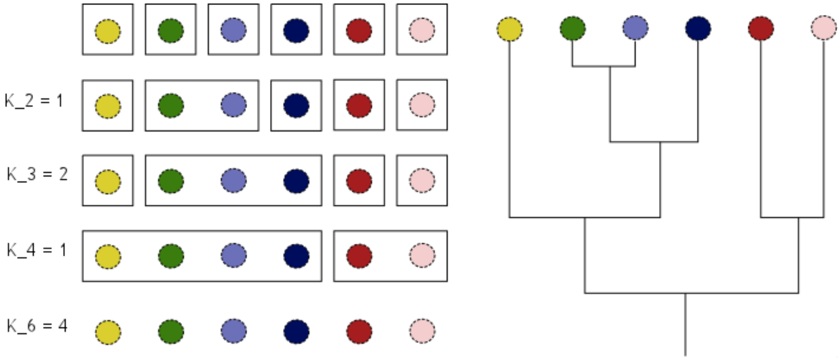

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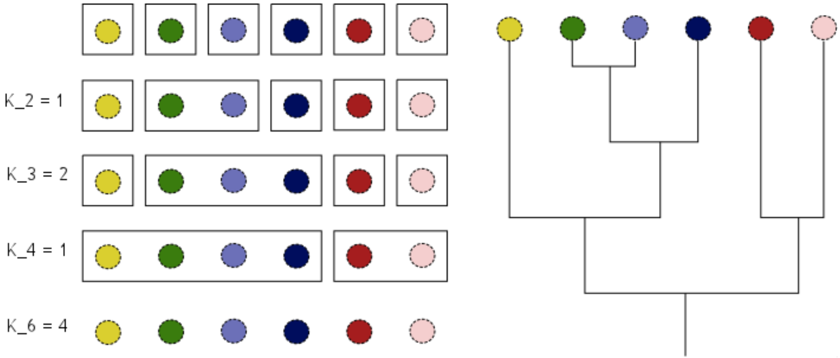

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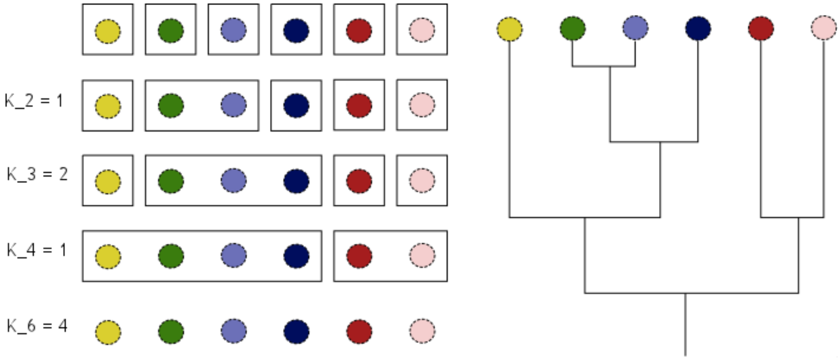

- Induces a law on **binary tree shapes with n labelled leaves**.
- q_n uniform yields the same tree shape as the reduced tree of any birth–death process (e.g., Yule tree)

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- Example : Kingman coalescent.

Aldous' Markov branching model (Mbm)

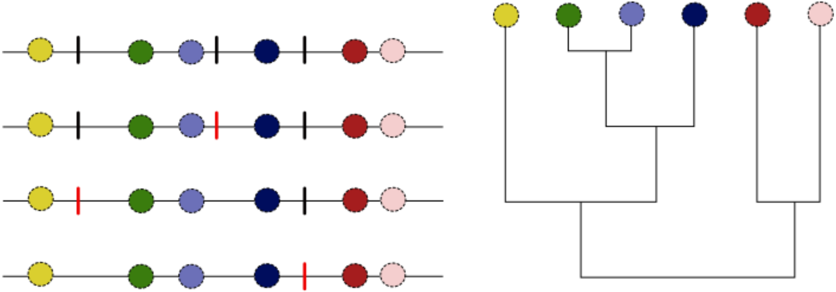
Theorem (Haas et al 2008, Lambert 2017)

A Mbm is sampling-consistent iff it there is a symmetric measure ν on $(0,1)$ s.t.

$$q_n(i) = a_n(\nu)^{-1} \binom{n}{i} \int_0^1 x^i (1-x)^{n-i} \nu(dx)$$

Construction

- Color dots are uniformly distributed in the interval
- Intervals are fragmented by r.v. R with law $\sim \nu$ (red dashes)



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- ...each block fragments into two blocks with frequencies dx and $1 - dx$ at rate $\nu(dx)$.
- The previous theorem states the one-to-one correspondence :

$$\text{Sampling-consistent Mbm} \iff \Pi_{|[n]} \text{ without fragmentation times}$$

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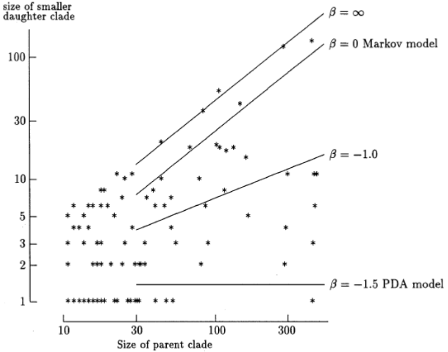
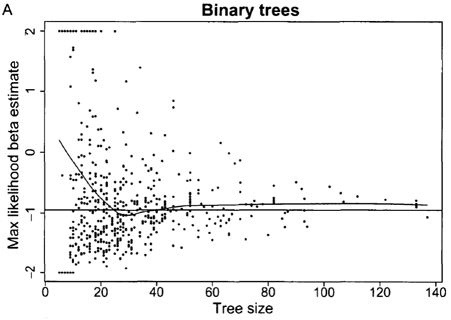
β	Description	Median split
-2	Completely unbalanced	1
-1.5	PDA model	1.5
-1	Unnamed	$\sqrt{m}$
0	Markov model	$m/4$
∞	An almost completely balanced model	$m/2$

Estimating β

S_{min} vs $S_{\text{min}} + S_{\text{max}}$ (Aldous 2001)



MLE of β (Blum & François 2006)



My favorite evolutionary conundrum : Why $\beta \approx -1$? (No answer here).

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Richness = Number of species in clade

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- Iteratively **split nodes** from root to tips **w/ proba prop. to** X^{α}
- Induces a sampling-consistent law on binary, **ranked** tree shapes with n labelled leaves.

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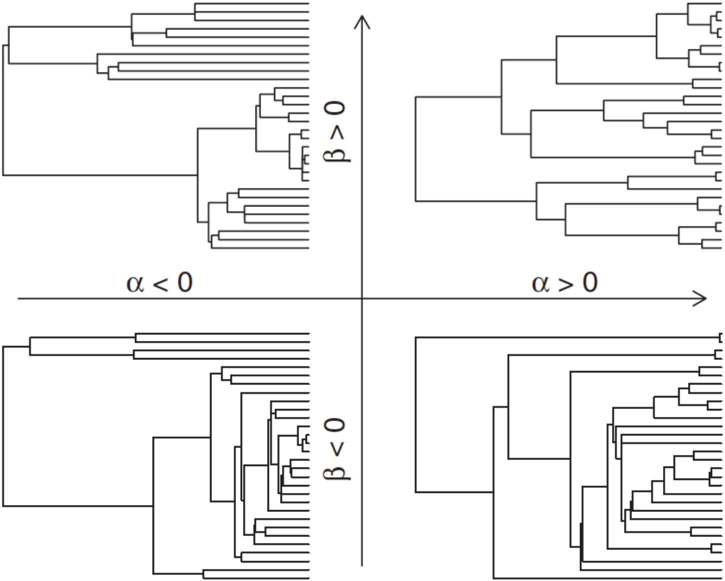
- See also : Sainudiin & Véber "A Beta-splitting model for evolutionary trees" *Royal Society Open Science* 2016



β > 0
α < 0
α > 0
β < 0

Self-similar fragmentation processes

Bertoin "Self-similar fragmentation processes" *Annales de l'IHP* 2002

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- Homogeneous fragmentation : $\alpha = 0$.
- Now $(\Pi^\alpha_{|[n]})$ is not Markov
- But $(\Pi_{|[n]}, R_n)$ is Markov, where R_n is the vector of n-tagged fragments = frequencies of blocks containing elements of $[n]$

SC Mbm w/ age-richness index $\alpha \iff \Pi^\alpha_{|[n]}$ w/ relative fragmentation times

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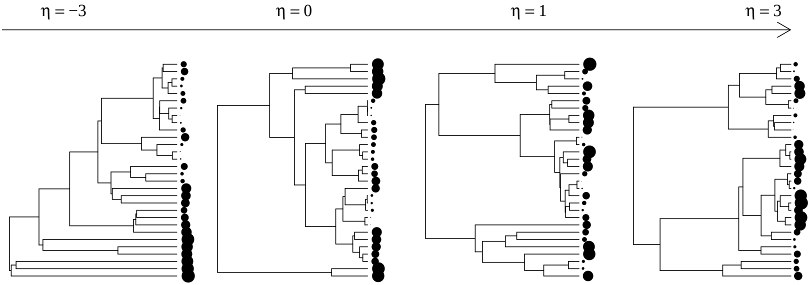
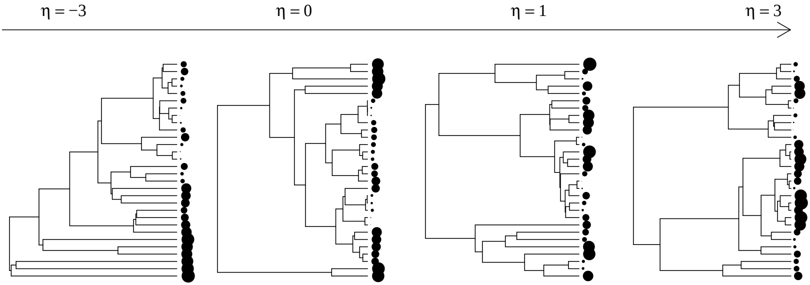
- **Sampling (keeping extant) in prop to abundance**

  $\approx$ Field of Bullets iff $\eta = 1$



- $\eta = -3$, rare species are all in large clades



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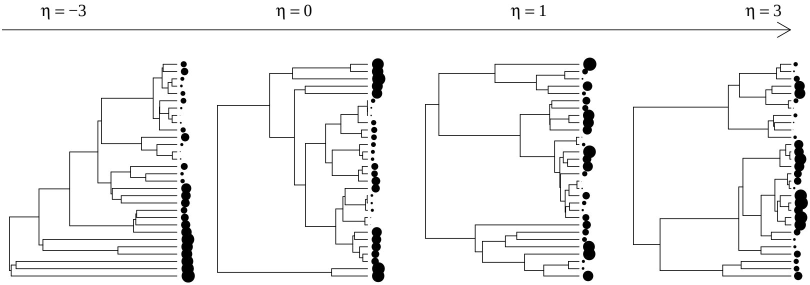

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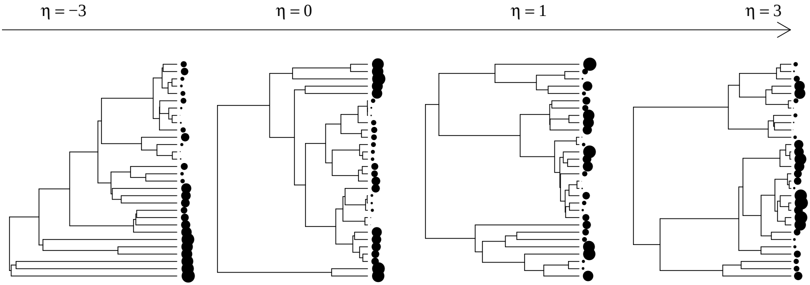


- $\eta = -3$, rare species are all in large clades
- $\eta = 0$, ‘equal-sharing’ measure (inv. prop. to number of splits)
- $\eta = 1$, species have equal abundances on average
- $\eta = 3$, the few species in poor clades are rare

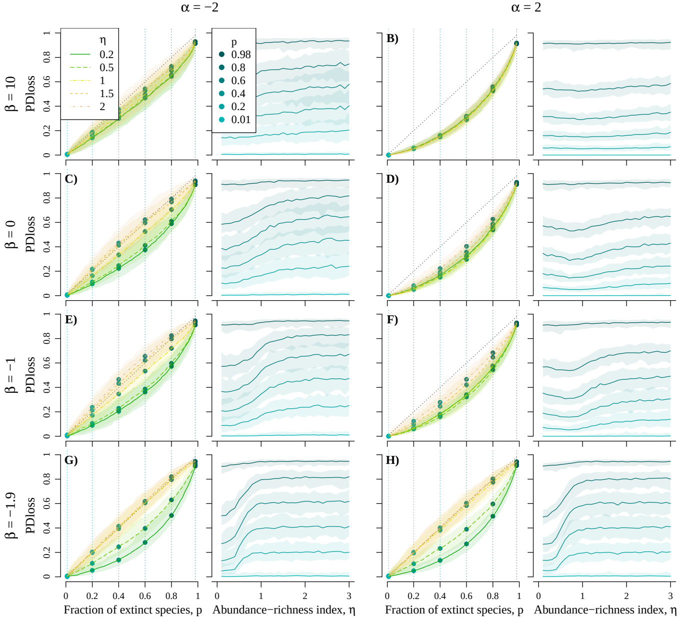
Warning!

The next slide represents $1 - S =$ PD loss...

...as a function of $1 - p =$ fraction of extinct species.

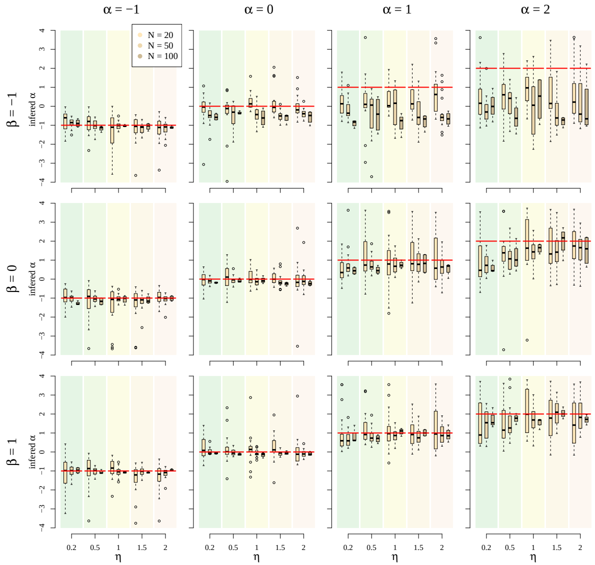
This function is expected to be increasing and convex in the FoB model.

'Danger zone' : $\alpha < 0, \eta > 1$

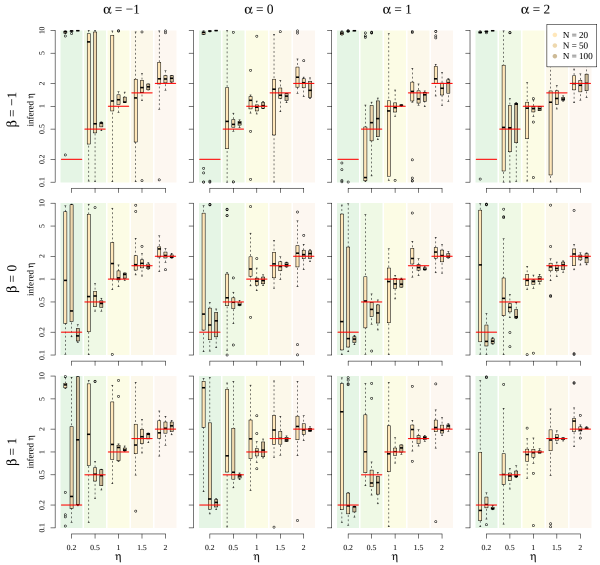


Outline

Inference of α

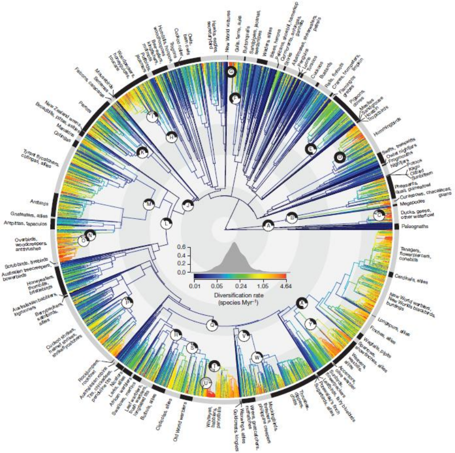


Inference of η



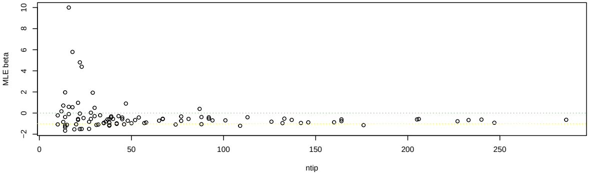
Data

Jetz et al "The global diversity of birds in space and time" *Nature* 2012

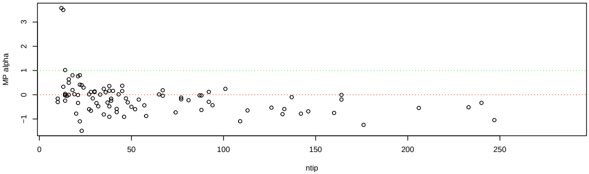


- Phylogenies of ≈ 100 clades in the class *Aves* (a.k.a. birds)
- Information used for inference :
  - Shapes of trees
  - Relative positions of nodes (but not the exact datation estimates)
  - Species range relative to sum of all species ranges.

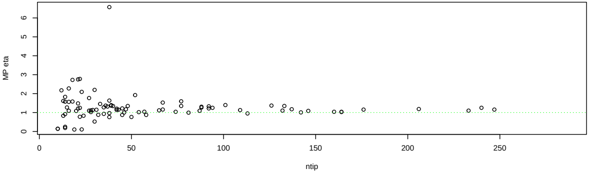
Inference from $\approx$ 100 bird clades



$\beta < 0$ and $\beta \approx -1$
(real trees are imbalanced)

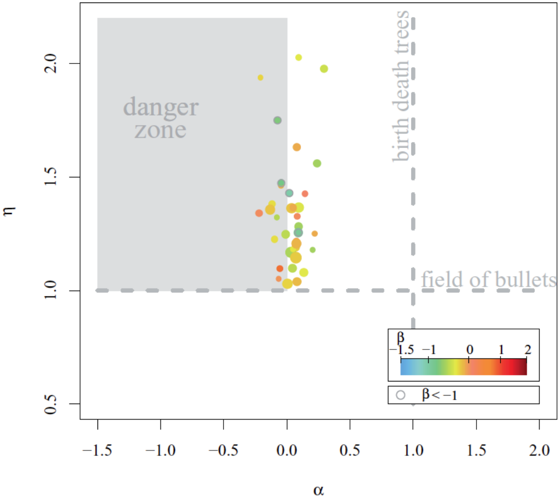


$\alpha < 0$
(deep nodes $\in$ small clades)



$\eta \geq 1$ and $\eta \approx 1$
(rare species $\in$ small clades)

Inference from ≈ 100 bird clades



Conclusion

Maliet, O., Gascuel, F., Lambert, A. (2018) "Ranked tree shapes, non-random extinctions and the loss of phylogenetic diversity" *Systematic Biology* (in press)

- New stochastic tree model with 3 parameters, tuning :
  - tree shape : $\beta =$ tree balance
  - ranked node depths : $\alpha =$ age-richness index
  - abundances at tips : $\eta =$ abundance-richness index
- Danger zone : $\beta < 0, \alpha < 0, \eta > 1$ = PD at risk
- Implemented in R-package *apTreeshape* (maintained by M.J. Blum)
- Large bird clades have $\beta \approx -1, \alpha < 0, \eta \approx 1$
- Bird clades in danger zone !

Perspectives

Maliet, O., Gascuel, F., Lambert, A. (2018) "Ranked tree shapes, non-random extinctions and the loss of phylogenetic diversity" *Systematic Biology* (in press)

- To extend the fragmentation process Π to a random fragmentation triple (Π, W, M) (Jean-Jil Duchamps, work in progress), where :

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- To confirm the last two findings with more data.

Collaborators

Fanny Gascuel (Institut Curie) . . . .

Odile Maliet (ENS) . . . .

Mike Steel (U Canterbury) . . . .

SMILE : an interdisciplinary group in Paris

SCIENCES SORBONNE UNIVERSITÉ

COLLÈGE DE FRANCE 1530

S.M.I.L.E

Stochastic Models for the Inference of Life Evolution

SMILE = Stochastic Models for the Inference of Life Evolution

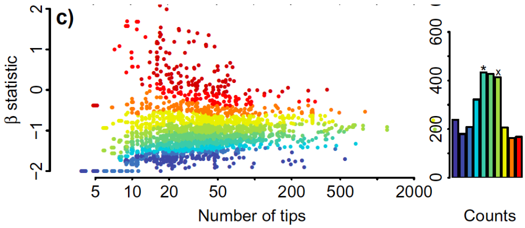
A positive answer to $\beta \approx -1$?

Hagen, Hartmann, Steel, Stadler "Age-Dependent Speciation Can Explain the Shape of Empirical Phylogenies" *Systematic Biology (2015)*

- Birth-death process with age-dependent birth rate $b = b(a)$ parameterized by

$$b(a) = ca^{\phi-1}$$

- Estimates of ϕ lie in $(0, 1)$: speciation rate decreases with age



For $\phi = 0.6$, the reconstructed tree has $\beta \approx -1$.

Q : "Why $\beta \approx -1$?"

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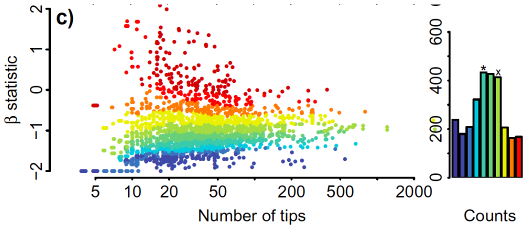

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— "Because $\phi \approx 0.6$" ;-)

Balance of incomplete trees

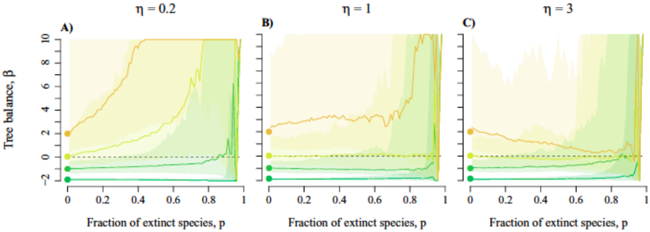

FIGURE 8. Effect of abundance-richness index η on the balance of phylogenetic trees after extinctions (Maximum Likelihood Estimate $\hat{\beta}$ of β). Initial tree balance β ranges from 10 (brown dots and lines, "bush trees") to -1.9 (green dots and lines, "caterpilar trees"). Extinction fraction p increases from 0.01 to 0.98 (from left to right). Results are based on 100 simulation replicates: plain lines give median values and light areas give 95% confidence intervals. Other parameter values: number of species $N = 100$, approximation parameter $\varepsilon = 0.001$, $\alpha = 0$.