

# Random Tree Shapes and the Future Loss of Phylogenetic Diversity

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# Outline

1. Introduction

2. Tree statistics

3. Lineage-Based Models

4. Individual-Based Models

5. Predict the Future ?

# Why trees ?

- ▶ **Phylogenetic tree** = Most basic pattern generated by (macro)evolutionary history

**Q1** : "Can we test the possibility that some aspects of the evolutionary record behave as stochastic variables ?" (Raup et al 1973)

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**Q2** : "Are there mathematically simple or biologically plausible stochastic models for phylogenetic trees whose realizations mimic actual trees ?" (Aldous 2001)

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**Q2** : "Are there mathematically simple or biologically plausible stochastic models for phylogenetic trees whose realizations mimic actual trees ?" (Aldous 2001)

- ▶ **Predict the future** of biodiversity : 'Noah's Ark problem' (Faller et al 2008)

**Q3** : "Can we predict how much evolutionary heritage will be lost in the face of current extinctions ?"

# Difficulty of characterizing trees

- ▶ Comparing two trees : distance ? Robinson-Foulds, Gromov-Hausdorff...
- ▶ Characterizing one tree : distance to some reference tree ?
- ▶ A distribution of trees : average tree ?
- ▶ Real functions of trees = statistic, likelihood
- ▶ Requires **stochastic models of trees**
  - ▶ Compare statistic to its distribution under null model (Q1)
  - ▶ Fit a non-null model (Q2)

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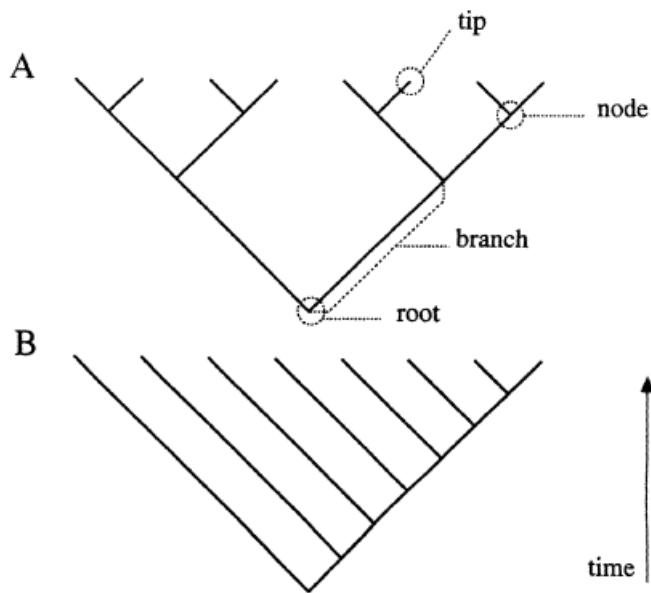
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## Perfectly Balanced Tree (A) vs Caterpillar Tree (B)





# Model-free statistics of trees I : Using topology only

See Shao & Sokal (1990), Kirkpatrick & Slatkin (1993), Mooers & Heard (1997)

## Local statistics

- ▶  $c_i = \#$  nodes on the path from tip  $i$  to the root
- ▶  $s_{\min}(v) = \#$  tips in smallest daughter clade of node  $v$
- ▶ Balance of node  $v = s_{\min}(v)/s_{\max}(v)$

## Global statistics

- ▶ Sackin index (Sackin1972)

$$\frac{1}{n} \sum_i c_i$$

- ▶ Colless index (Colless 1982)

$$\frac{2}{(n-1)(n-2)} \sum_v (s_{\max}(v) - s_{\min}(v))$$

# Model-free statistics of trees II : Using branch lengths also

## Local statistics

- ▶ 'Distinctiveness' = length of external edge of tip  $i$  (Redding et al 2008)
- ▶ Local Branching Index (Luksza & Laessig 2014, Neher et al 2014)

$$= \int_{\text{tree}} e^{-d(x,y)/\delta} dy$$

## Global statistics

- ▶ *Phylogenetic Diversity*  $PD$  = Total Length of Tree =  $\sum_{k=2}^n kg_k$   
with  $g_k$  = internode duration (Vane-Wright et al 1991, Faith 1992)
- ▶ Lineage-Through-Time plot
- ▶ Gamma (Cox & Lewis 1966, Pybus & Harvey 2000)

$$\gamma = \frac{\frac{1}{n-2} \sum_{i=2}^{n-1} \sum_{k=2}^i kg_k - \frac{PD}{2}}{PD / \sqrt{12(n-2)}}$$

# Understanding the origin of patterns

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- ▶  $H_0$  : 'pattern is not distinguishable from that generated by a Yule pure birth process'... vs key adaptations, adaptive radiations, etc.
- ▶ Root balance under the Yule model is uniform !  
"How different, then, is the real world from the stochastic system ?  
The answer would seem to be 'not very' — the outstanding feature of real and random clades is their basic similarity" (Gould et al 1977, Savage 1983)

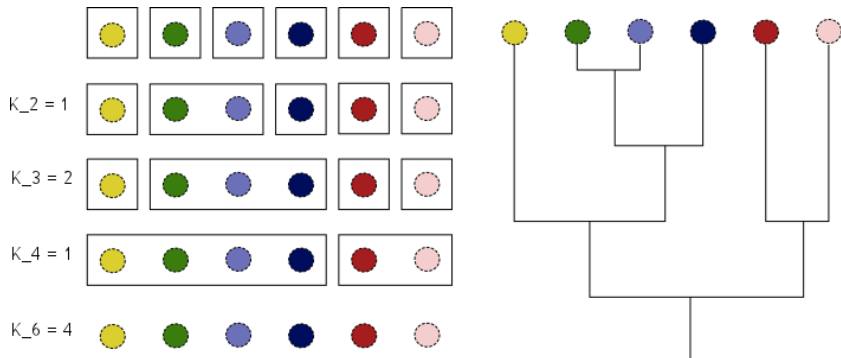
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- ▶ Empirical root balance  $\neq$  uniform (Slowinski 1990, Guyer & Slowinski 1991, 93)

# Aldous' Markov branching model on binary tree shapes

Aldous (1996, 2001)

- ▶ Assume we are given distributions  $q_n$  on  $\{1, \dots, n-1\}$ ,  $n \geq 2$
- ▶ Recursively split each subset of  $n$  balls according to  $q_n$  (r.v.'s  $K_n$  below)



- ▶  $q_n$  uniform yields the same tree shape as a Yule tree



# Sampling consistency

- ▶ A tree model is a family of probability distributions  $(P_n)$  on (exchangeably labelled) tree shapes with  $n$  tips
- ▶ Call  $T_n$  a random tree with law  $P_n$
- ▶ Call  $T'_n$  the tree obtained by removing one tip from  $T_{n+1}$  (say the tip labelled  $n + 1$ )
- ▶ The model is said **sampling consistent** if  $T_n$  and  $T'_n$  have the same distribution.
- ▶ Example : Kingman coalescent.

# Aldous' Markov branching model

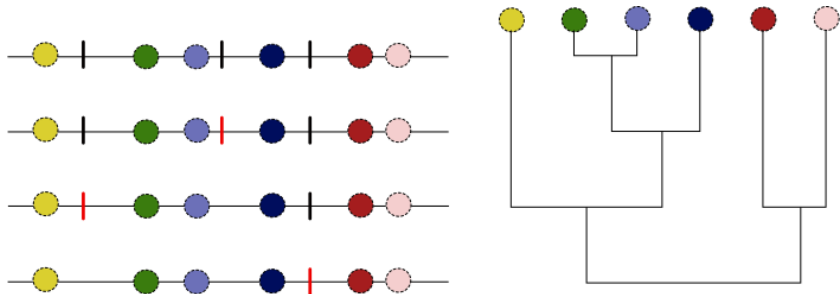
Theorem (Haas et al 2008, Lambert 2016)

A MB tree model is sampling-consistent *iff* there is a function  $f$  s.t.

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

## Construction

- ▶ Color dots are uniformly distributed in the interval
- ▶ Intervals are fragmented by r.v. with density  $\sim f$



# The $\alpha$ -splitting model

Ford 2005 (unpublished)

- ▶ Define the  $\alpha$ -splitting tree model recursively,  $\alpha \in [0, 1]$ .
- ▶ Conditional on a realization of the binary tree with  $n$  tips  $T_n$  :  
Give weight  $\alpha$  to every external edge of  $T_n$  and weight  $1 - \alpha$  to every internal edge, including the root edge.
- ▶ Generate  $T_{n+1}$  by choosing an edge in proportion to its weight and plant a new external edge in the middle of the chosen edge.
- ▶ The  $\alpha$ -model is sampling consistent.
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- ▶ The  $\alpha$ -model is sampling consistent.
- ▶ Imbalance increases with  $\alpha$
- ▶  $\alpha = 0$  : Yule ;  $\alpha = 1$  : caterpillar.

# The $\beta$ -splitting model

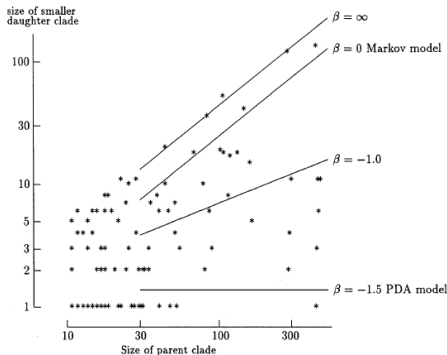
- ▶ The  $\beta$ -splitting model is for  $\beta \in (-2, \infty) : f(x) = cx^\beta(1-x)^\beta$
- ▶ Imbalance decreases with  $\beta$
- ▶ Q1 : distribution of MLE  $\hat{\beta}$  under the Yule model ?



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

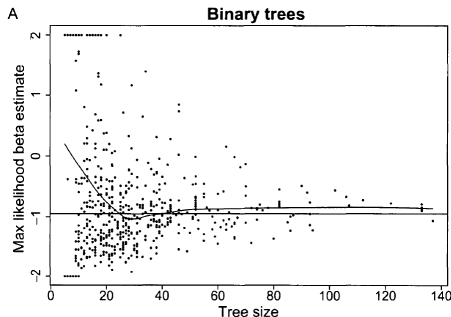
# Estimating $\beta$

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



MLE of  $\beta$

(Blum & François 2006)



$$\Rightarrow \beta \approx -1$$

Q2: "Why  $\beta \approx -1$ ?" or "Are there mathematically simple/biologically plausible stochastic models for phylogenetic trees whose realizations mimic actual trees?" (Aldous 2001)

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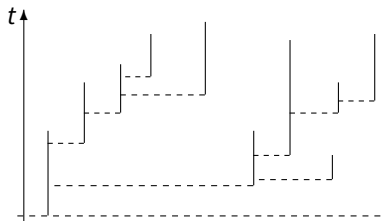
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# Birth-Death Model of Macroevolution (Nee 2006)

- ▶ Species seen as particles that can **split** (speciation) and **die** (extinction)
- ▶ Rates  $b(t, n, a, i)$  and  $d(t, n, a, i)$  may depend upon :

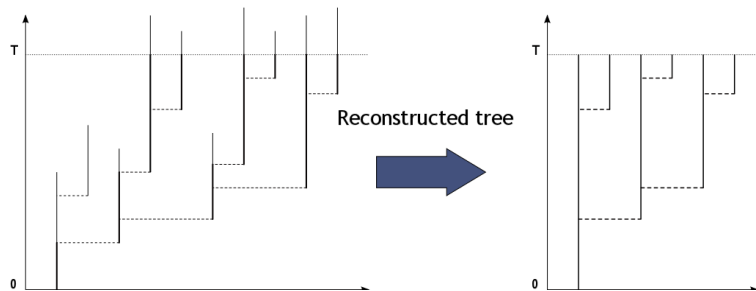


- ▶ **time  $t$**
- ▶ **number  $n$**  of standing particles
- ▶ **a non-heritable trait  $a$**  (e.g., age)
- ▶ **a heritable trait  $i$**
- ▶ Asymmetric birth =  
Mother keeps her trait
- ▶ Orientation =  
Daughter sprouts to the right

**Yule model** :  $b = \text{constant}$ ,  $d = 0$ .



# Reconstructed tree



- ▶ ‘Reconstructed tree’ or ‘reduced tree’ at height  $T$   
= remove all lineages **extinct** by  $T$  (fixed time).
- ▶ Q2 : Are there universal conditions on the rates for which the **reconstructed tree** has  $\beta \approx -1$ ?
- ▶ Q2' : What is the **law of the reconstructed tree** under the model ?  
Can we compute the **likelihood** of a given ultrametric (clock-like) phylogenetic tree under the model ?

# Characterizing lineage-based models

Lambert & Stadler "Birth–Death Models and Coalescent Point Processes : The Shape and Probability of Reconstructed Phylogenies" *TPB* (2013)

## ► A (partial) negative answer to Q2 :

Reconstructed trees always have the same topology in distribution as Yule trees ( $\beta = 0$ ) IFF  $b = b(t, n)$  and  $d = d(t, n, a)$

$\implies$  As soon as  $b = b(t, n)$  and  $d = d(t, n, a)$ , estimate  $\beta \approx 0$

## ► A (partial) positive answer to Q2' :

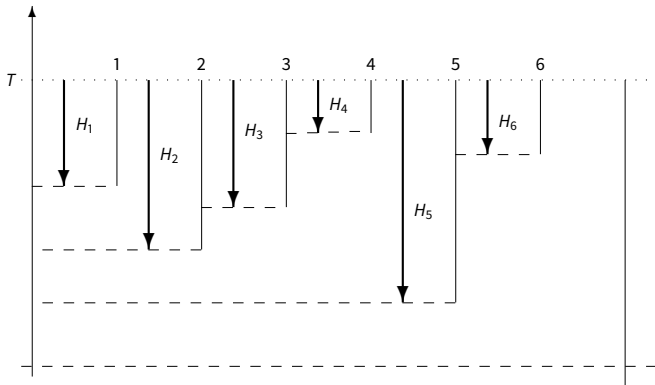
The likelihood of reconstructed trees always has an explicit product form IFF  $b = b(t)$  and  $d = d(t, a)$ .

$\implies$  The reconstructed tree is a ‘**coalescent point process**’...

# The CPP distribution

Rannala (1997), Popovic (2004), Aldous & Popovic (2005)

**CPP = Coalescent Point Process** = Oriented tree whose node depths  $H_1, H_2, \dots$ , form a sequence of **iid random variables** killed at its first value larger than  $T$ .



$b = b(t)$  and  $d = d(t, a)$  always produce CPP

Assume that  $b = b(t)$  **and**  $d = d(t, a)$ .

Set  $g(t, s)$  the density at time  $s$  of the extinction time of a species born at time  $t$ .

Theorem (Lambert & Stadler 2013)

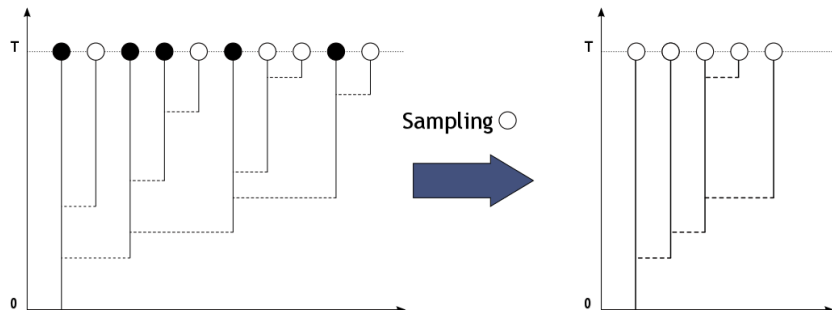
The **reconstructed (oriented) tree is a CPP** with typical node depth  $H$ , where the function  $F = 1/P(H > \cdot)$  is the *unique solution to the following linear integro-differential equation*

$$F'(t) = b(t) \left( F(t) - \int_{T-t}^T ds F(s) g(t, s) \right) \quad t \geq 0,$$

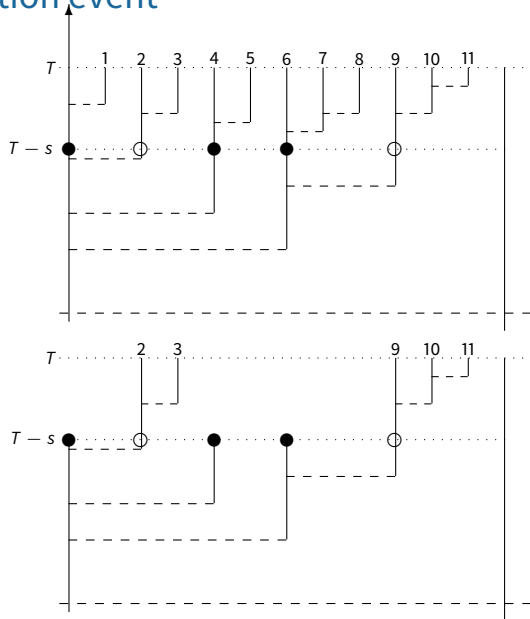
with initial condition  $F(0) = 1$ .

The result still holds with **missing species/mass extinction events** : each species is removed **independently with the same probability  $p$** .

# Missing species



# Mass extinction event



# Special cases

- If  $b = b(t)$  and  $d = d(t)$  (Kendall 1948, Nee et al 1994)

$$F(t) = 1 + \int_{T-t}^T ds b(s) e^{\int_s^T du (b-d)(u)}$$

- If  $b$  is constant and  $d = d(a)$ , then  $g(s, t) = g(t - s)$  [if  $a$  the age  $g(a) = d(a) e^{-\int_0^a ds d(s)}$ ] (Lambert 2010)

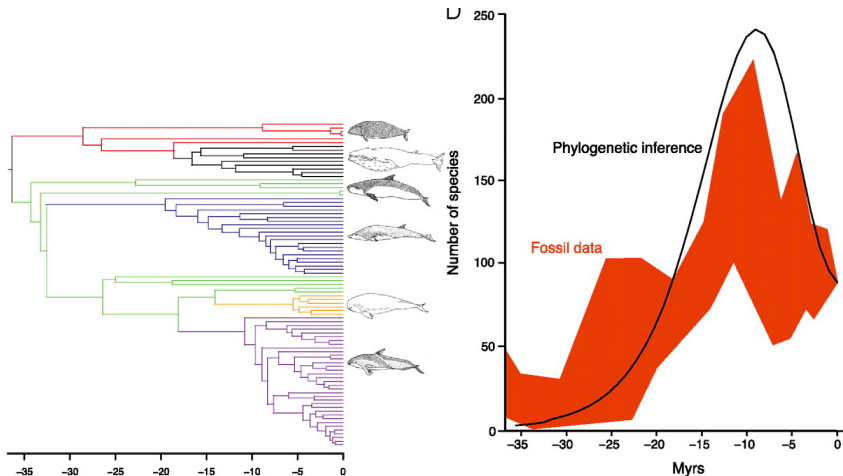
$$F' = b (F - F \star g),$$

- Mass extinction event with survival probability  $p$  at time  $T - s$

$$F_p(t) = \begin{cases} F(t) & \text{if } 0 \leq t \leq s \\ (1-p)F(s) + pF(t) & \text{if } s \leq t \leq T, \end{cases}$$

# Appl.1 Diversification of Cetaceans

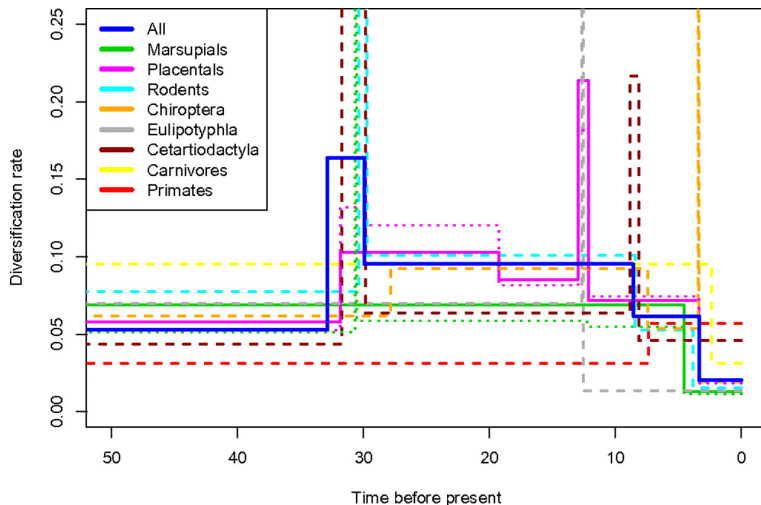
Morlon, Parsons & Plotkin "Reconciling Molecular Phylogenies with the Fossil Record" *PNAS* (2011)





# Appl.2 Diversification of Mammals

Stadler "Mammalian Phylogeny Reveals Recent Diversification Rate Shifts" *PNAS* (2011)



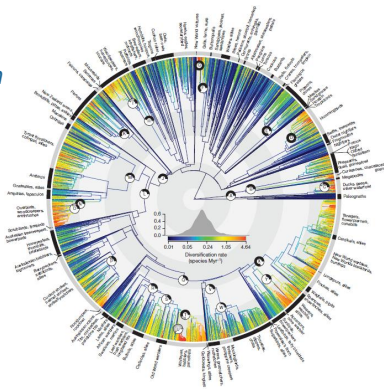
# Appl.3 Do species age ?

Alexander, Lambert & Stadler "Quantifying Age-dependent Extinction from Species Phylogenies"  
*Systematic Biology* (2015)

Gamma distributed lifetime ( $k, s > 0$ ), with mean  $m := ks$

$$g(a) = \Gamma(k)^{-1} s^{-k} a^{k-1} e^{-a/s}$$

- ▶ Test on simulations : accurate MLEs of  $b$  and  $m$
- ▶ MLE on *Aves* phylogeny = 9993 extant bird sp (Jetz et al 2012)
- ▶ Exponential model **rejected** ( $p = 10^{-15}$ )
- ▶ Shape parameter  $k \gg 1$  : extinction rate **increases with age**
- ▶ Average lifetime  $m = 15.26 \text{ My}$
- ▶ Speciation rate  $b = 0.108 \text{ My}^{-1}$

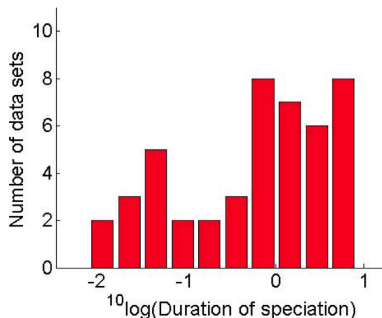


# Appl.4 How long does speciation take ?

Etienne, Morlon, Lambert "Estimating the Duration of Speciation from Phylogenies" *Evolution* (2014)

## Model of **Protracted Speciation** (Rosindell et al 2010, Etienne & Rosindell 2012)

- ▶ Species are ensembles of populations, each population gradually diverges from mother species
- ▶ Newborn populations are **incipient**, become **good** after some random time = **new species**
- ▶ **Speciation stage** = non-heritable trait



- ▶ **Duration of speciation** = Time before a good sp appears in the pop genealogy
- ▶ Test on simulations : efficient inference of duration of speciation
- ▶ Left : **duration of speciation** inferred in 46 bird clades (in My)

# Other lineage-based models of macro-evolution

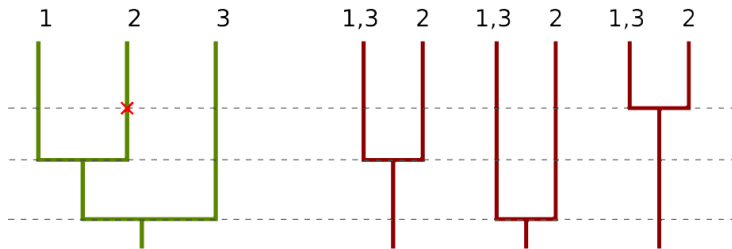
- ▶ **Diversity-dependent** diversification (Etienne et al *Proc B* 2012)
- ▶ **Trait-dependent** diversification : BiSSE, QuaSSE, GeoSSE... (Maddison et al *Syst Biol* 2007, FitzJohn *MEE* 2012...)

But see also Rabosky & Goldberg *Syst Biol* 2015...

- ▶ Reviews...
  - ▶ Ricklefs *TREE* (2007)
  - ▶ Pyron & Burbrink *TREE* (2013)
  - ▶ Stadler *JEB* (2013)
  - ▶ Morlon *Eco Lett* (2014)

## A positive answer to Q2 ?

- ▶ Phylogenetic method artifact ? (Huelsenbeck & Kirkpatrick *Evolution* 1996)
- ▶ Protracted speciation ? (Rosindell et al *Eco Lett* 2010)
- ▶ Neutral Biodiversity Theory ? (Jabot & Chave *Eco Lett* 2009, Davies et al *Evolution* 2012)
- ▶ Age-dependent speciation ? (Hagen et al *Syst Biol* 2015)



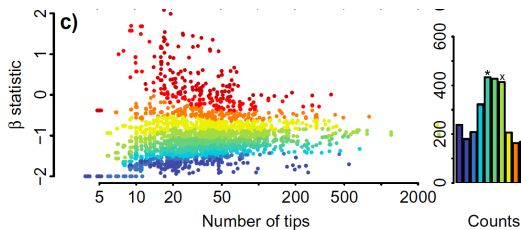
# A positive answer to Q2 ?

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

- ▶  $b = b(a)$  parameterized by

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

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



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

Q2 : "Why  $\beta \approx -1$ ?"

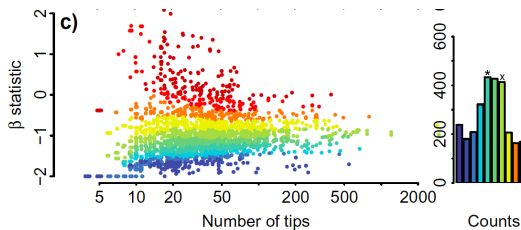
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— "Because  $\phi \approx 0.6$ " ;-)

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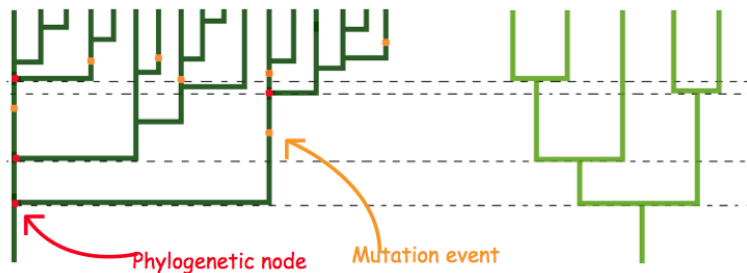
# Speciation by Genetic Differentiation (1)

Manceau, Lambert, Morlon "Phylogenies Support Out-of-Equilibrium Models of Biodiversity" *Ecology Letters* (2015)

- ▶ Start with a birth–death process (individual-based, constant rates  $b$  and  $d$ )
- ▶ Superimpose mutations at constant rate  $\theta$ , infinite-allele model
- ▶ **Species = minimal monophyletic taxon** such that any 2 tips with the same allele belong to the same species
- ▶ SGD = Speciation by genetic differentiation = individual-based version of protracted speciation

# Speciation by Genetic Differentiation (2)

Manceau, Lambert, Morlon "Phylogenies Support Out-of-Equilibrium Models of Biodiversity" *Ecology Letters* (2015)

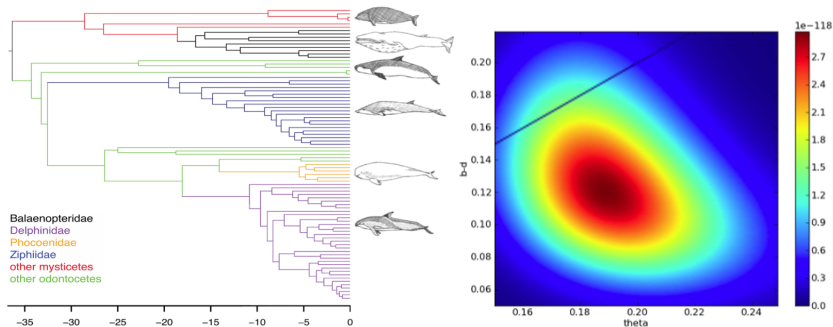


- ▶ A node on the genealogy is **phylogenetic** (= appears on the phylogeny) if
  - (i) The previous node is phylogenetic
  - (ii) All tips separated by this node carry different alleles
- ▶ The first node is phylogenetic if it satisfies (ii)

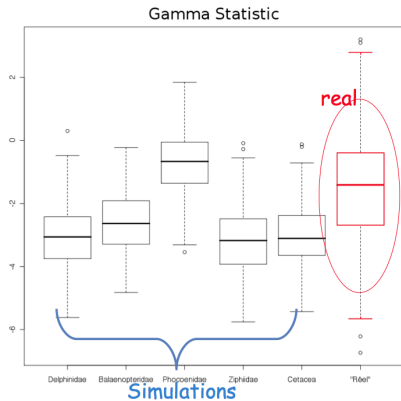
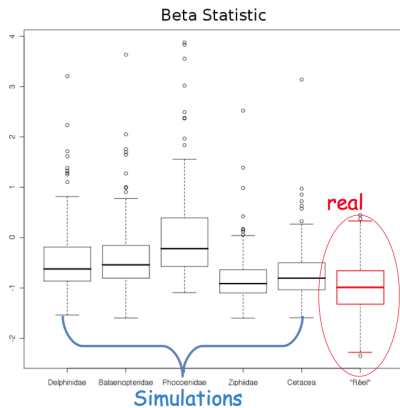
# Speciation by Genetic Differentiation (3)

Manceau, Lambert, Morlon "Phylogenies Support Out-of-Equilibrium Models of Biodiversity" *Ecology Letters* (2015)

- ▶ Multitype branching tree representation : fast simulation
- ▶ Likelihood computation by peeling algorithm, including the case of missing species
- ▶ Tests by simulations : accurate ML estimates of  $\theta$  and  $b - d$
- ▶ Inference from Cetaceans generates realistic values of  $\beta, \gamma$



# Speciation by genetic differentiation (4)



# An Individual-Based Model of Radiation (1)

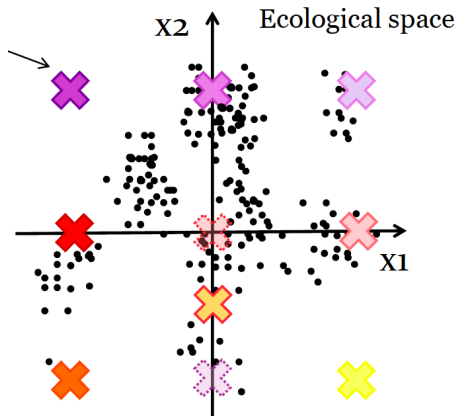
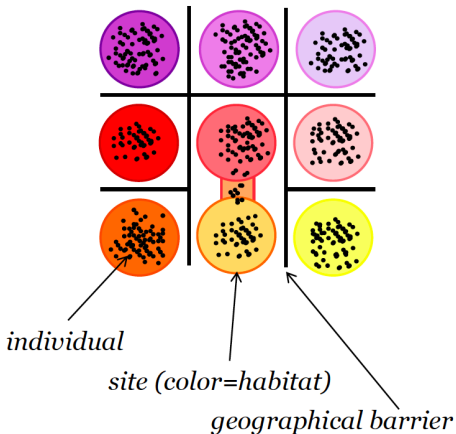
Aguilée, Claessen, Lambert "Adaptive Radiation Driven by the Interplay of Eco-Evolutionary and Landscape Dynamics" *Evolution* (2013)

- ▶ Individuals explicitly located in geographical/genotype space
- ▶ Ecological traits and choosiness trait are determined by  $L$  loci
- ▶ Assortative mating based on similarity in ecological traits and choosiness of parents
- ▶ Density- and phenotype-dependent competition for resources
- ▶ Selection can turn disruptive at ecological optimum
- ▶ Stabilizing selection + environmental stochasticity + character displacement

⇒ Rapid diversification

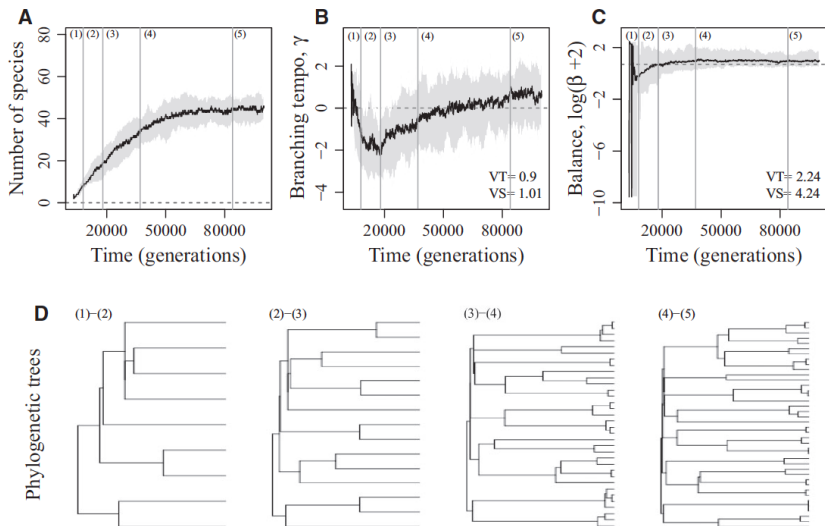
## An Individual-Based Model of Radiation (2)

Gascuel, Ferrière, Aguilée, Lambert "How Ecology and Landscape Dynamics Shape Phylogenetic Trees"  
*Systematic Biology* (2015)



# An Individual-Based Model of Radiation (3)

Gascuel, Ferrière, Aguilée, Lambert "How Ecology and Landscape Dynamics Shape Phylogenetic Trees" *Systematic Biology* (2015)



# An Individual-Based Model of Radiation (4)

Gascuel, Ferrière, Aguilée, Lambert "How Ecology and Landscape Dynamics Shape Phylogenetic Trees"  
*Systematic Biology* (2015)

- ▶ Phylogenies can be unbalanced for small phylogenies
  - ▶ In the initial phase of diversification
  - ▶ Under intense interspecific competition
- ▶ Ecological heterogeneity does not necessarily cause phylogenies to be unbalanced
- ▶ Contingency of landscape dynamics and resource distribution can cause wide variation in tree balance



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# The Loss of Phylogenetic Diversity

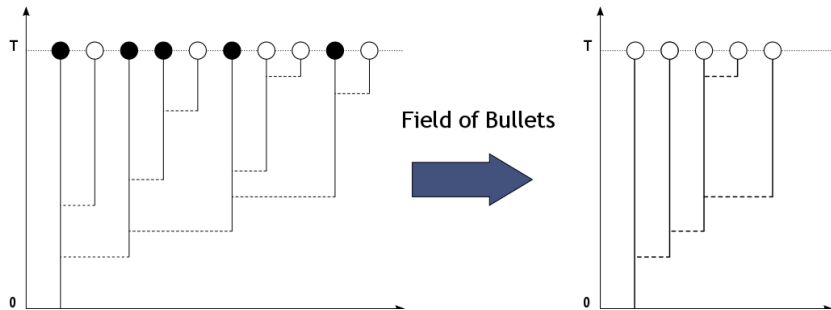
Q3 : "If a random, say 10% of species from some given clade were to disappear in the next 100 years due to current high rates of extinction, how much evolutionary heritage will be lost ?"

- ▶ **Field of Bullets** model : each species is removed independently, kept with probability  $p$
- ▶ Remaining PD  $S(p) = \text{Total Length of Tree spanned by surviving sp}$
- ▶ For a given tree,  $\mathbb{E}S(p)$  is **increasing and concave** (Faller, Pardi, Steel 2008)

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

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

# Field of Bullets



# Loss of PD in Random Trees

Remaining PD is...

- ▶ High for the **Kingman coalescent** (Nee & May *Science* 1997)  
Rule of thumb :  $S_n(1) \sim \log(n)$  so  $S_n(p)/S_n(1) \approx 1$
- ▶ **Lower in imbalanced trees** : more 'distinctive' sp
- ▶ **Low for the Yule tree** (Mooers, Gascuel, Stadler, Li, Steel *Syst Biol* 2011)  
Rule of thumb :  $S_n(1) \sim cn$  (recall CPP) so  $S_n(p)/S_n(1) < 1$

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

# Remaining PD for general Birth-Death Trees (1)

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

- ▶ As in a Coalescent Point Process, assume node depths  $H_i$  are i.i.d.
- ▶ Then conditional on  $n$  tips **before** FoB and  $K_n$  tips **after** FoB,

$$\text{With probability 1: } \lim_n \frac{S_n(p)}{S_n(1)} = p \frac{\mathbb{E}(B)}{\mathbb{E}(H)}$$

where

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

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

- ▶ Simple argument :
  - ▶ After FoB, the phylogenetic tree is a CPP with node depth  $B$
  - ▶ By the SLLN,  $S_n(1) \sim n\mathbb{E}(H)$  and  $S_n(p) \sim K_n\mathbb{E}(B)$
  - ▶ Conclude with  $K_n/n \rightarrow p$

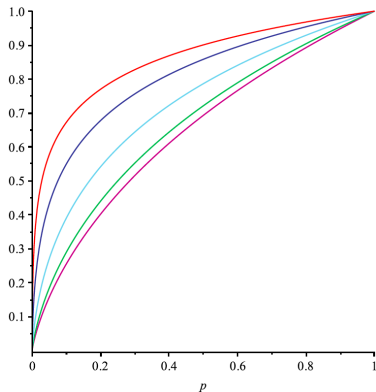
# Remaining PD for general Birth-Death Trees (2)

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

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

Remaining PD-to-old PD Ratio =

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

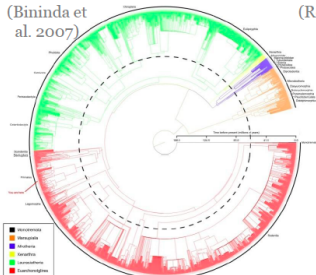


Right : Slow progression towards the unit step function (from pure birth to critical) :  $d/b = 0$  (the lowest curve) and then  $d/b = 0.5, 0.9, 0.99, 0.999$ .

# Remaining questions

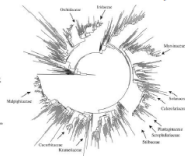
- ▶ What if poorer clades are older ?
- ▶ What if older clades carry more extinct-prone species ?
- ▶ If you're interested, listen to Odile Maliet's talk this afternoon ;-)

(Bininda et al. 2007)

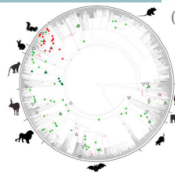


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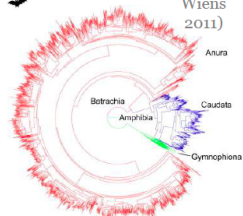
(Renner & Schaefer 2010)



(Purvis et al. 2011)

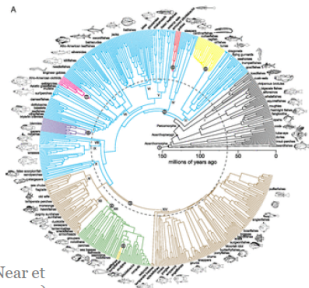


(Pyron & Wiens 2011)

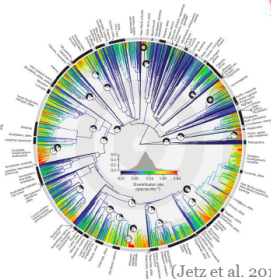


Thank you !

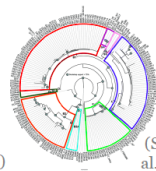
(Near et al. 2013)



(Jetz et al. 2012)



(Sahl et al. 2012)





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# SMILE : an interdisciplinary group in Paris



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SMILE = Stochastic Models for the Inference of Life Evolution