## Understanding global biodiversity patterns using the Tree of Life



#### Hélène Morlon Ecole Normale Supérieure

What explains species diversity across groups?



What explains species diversity across groups?

What explains species diversity across regions?





What explains species diversity across groups?

What explains species diversity across regions?





## What explains phenotypic diversity across groups and regions?



## Species richness results from speciation and extinction events, themselves influenced by various ecological and evolutionary processes

#### **Abiotic factors**



#### Phenotypic diversity results from character evolution, itself influenced by various ecological and evolutionary processes

#### **Abiotic factors**



Estimating rates of speciation, extinction, dispersal and trait evolution

Understanding how and why they vary across time, geographic regions, habitats, and taxonomic groups

## Fossil approaches for understanding diversification and trait evolution



Ezard et al. Science 2011

## Phylogenetic approaches for understanding diversification and trait evolution



4 510 mammal species Bininda-Edmond *et al. Nature* 2007



10 000 bird species Jetz et al. Nature 2012

## Phylogenetic approaches for understanding diversification and trait evolution

Stochastic models of cladogenesis

Stochastic models of trait evolution



trait value

We assume the phylogeny is known

Fit of models to data allows testing alternative scenarios of diversification and trait evolution and estimating relevant parameters

#### Stochastic models of trait evolution



## Choosing models, estimating parameters

- Likelihoods of continuous models are based on the multivariate normal distribution
  - Result of a continuous-time Markov process is a sum of multiple independent events central limit theorem

$$L = \frac{\exp\left\{-\frac{1}{2}\left[\mathbf{X} - \mathbf{E}(\mathbf{X})\right]'(\mathbf{V}^{-1})\left[\mathbf{X} - \mathbf{E}(\mathbf{X})\right]\right\}}{\sqrt{(2\pi)^N} * \det(\mathbf{V})}$$

Where:

X = vector of data

E(X) = vector of expected values (all the same in this case)

V = variance-covariance matrix

#### **Brownian motion**

- Named after Robert Brown, who described the motion of pollen grains in water in 1827
- First proposal for comparative analyses by Felsenstein (1985)
- Simplest model of character evolution
- Widely used (assumed) model for all types of analyses

#### **Brownian motion**

$$dX(t) = \sigma dB(t)$$
 where

$$dX(t)$$
 = change in  $X(t)$  in an  
instant of time  
 $\sigma$  = scale of change in  
 $X(t)$   
 $dB(t)$  = random variable of  
change in  $X(t)$ ,  
distributed as  
 $dB(t) \sim N(0, dt)$ 

Hansen and Martins 1996 Evolution



#### Brownian motion, phylogeny, and (co)variance

Format: branch lengths are proportional to... -Expected variance on diagonal -Expected covariance on off-diagonal

1	-ci	and acie	18 2 acit	3 aci	·····	8 <sup>5</sup> cie	e6 _cles1
_	spe	996-	6P6-	epe	696	596	596
species 1	1.44	1.26	0.20	0.20	0	0	0
species 2	1.26	1.44	0.20	0.20	0	0	0
species 3	0.20	0.20	1.44	1.42	0	0	0
species 4	0.20	0.20	1.44	1.44	0	0	0
species 5	0	0	0	0	1.44	0.07	0.07
species 6	0	0	0	0	0.07	1.44	1.21
specles 7	0	0	0	0	0.07	1.21	1.44

#### Brownian motion: summary

- "The" model of comparative biology, up to now
- What does this model mean in terms of our expected evolutionary model?
  - Drift: genetic or shifting selection optimum
- Does it actually work?
  - Most comparative datasets fit this model well (Freckleton et al. 2002, Blomberg et al. 2003)
  - Ancestral-state estimates based on this model fit well with known fossils (Polly 2001)



#### Ornstein-Uhlenbeck (OU)

- A process of drift towards an "optimum"
- First introduced for comparative methods by Hansen and Martins (1996), though its incorporation has been very slow
- Simplest model of selection (stabilizing) for modeling evolution along a phylogeny



#### Ornstein-Uhlenbeck (OU): the "rubber-band" model



When  $\alpha = 0$ , this collapses to Brownian motion

### **Ornstein-Uhlenbeck (OU): summary**

(1) Covariance: decays exponentially with time

$$V_{ij} = \frac{\sigma^2}{2\alpha} e^{-2\alpha(T-s_{ij})} (1 - e^{-2\alpha s_{ij}})$$

Where:

 $T = \max phylo.$  distance  $s_{ij} = \text{shared phylo.}$  distance between species *i* and *j* 

(2) Can apply multiple evolutionary optima ( $\theta$ )



Hansen and Martins, 1996, Evolution



#### Early-burst / ACDC

- Proposed by Blomberg et al. (2003), though actually very similar to an earlier idea (Pagel 1999)
- General idea: rate (σ) of change either accelerates (AC) or decelerates (DC) - previous models have assumed constant σ
- Later authors have used this to test for an early burst of evolution during adaptive radiation (i.e., deceleration of rate over time)

#### Early-burst / ACDC

- Effects on covariance
  - Acceleration (AC) : covariance increases more over time than under BM
  - Deceleration (DC) : covariance increases less over time than under BM

$$V_{ij} = \int_0^{s_{ij}} \sigma_0^2 e^{rt} dt$$

Where:

 $\sigma_0^2$  = base rate  $s_{ij}$  = shared phylo. distance between species *i* and *j r* = ACDC parameter

#### What drives phenotypic diversity? What is the role of shared ancestry versus local adaptation?

#### Anolis lizards in the Caribbean





Question 1: Have there been many independent microhabitat transitions in frogs?

### Phylogeny

•Topology: Pyron and Wiens 2011 Mol. Phylogenet. Evol.

•Branch lengths: BEAST (Drummond and Rambaut 2007 BMC Evol. Biol.)



We find many transitions:

- 11 Arboreal > 2 Torrent
- 8 Semi/Fully Aquatic ~ 5 Terrestrial
- 9 Burrowing



How repeatable is evolution? Might we see some convergent evolution but also a "footprint" of history?



How repeatable is evolution? Might we see some convergent evolution but also a "footprint" of history?

Collected additional data on functional morphology from 167 species across 10 sites



## Species (generally) cluster by microhabitat type



# How repeatable is evolution? Might we see some convergent evolution but also a "footprint" of history?

Collected additional data on functional morphology from 167 species over 10 sites

Developed novel tests of the effect of past adaptation to previous environments





#### Ornstein-Uhlenbeck models of adaptation



Tests of history versus convergent adaptation

Do different origins of similar microhabitat use lead to different morphology?

(A) Major clade?



Tests of history versus convergent adaptation

Do different origins of similar microhabitat use lead to different morphology?

(A) Major clade?

(B) All independent origins?



#### "Complete" convergence model







#### What drives phenotypic diversity?



Frog communities around the world converge towards similar evolutionary optima



... except burrowers for which different clades each have their own optimum

Ź







#### Moen, Morlon & Wiens, in press

#### **Stochastic models of cladogenesis**

1. the bases


### Phylogenetic approaches to diversification

Stochastic birth-death process

**Reconstucted phylogeny** 

The reconstructed evolutionary process

SEAN NEE, ROBERT M. MAY AND PAUL H. HARVEY

**PTB 1994** 



### Phylogenetic approaches to diversification

### Stochastic birth-death process

**Reconstucted phylogeny** 

1. compute the likelihood of the reconstructed phylogeny

2. apply maximum likelihood or bayesian methods to fit the model to empirical data



### birth-death model

stem age  $t_1$ speciation rate  $\lambda$ extinction rate  $\mu$ 

+

 $\lambda$  and  $\mu$  can vary over time sampling fraction f



### birth-death model

stem age  $t_1$  $\lambda$  and  $\mu$  can vary over time speciation rate  $\lambda$ + sampling fraction *f* extinction rate  $\mu$ probability that n species are sampled today  $f^n \Psi(t_2, t_1) \prod_{i=2}^n \lambda(t_i) \Psi(s_{i,1}, t_i) \Psi(s_{i,2}, t_i)$ t2  $\mathcal{L}(t_1,$ t3 t4

### birth-death model

stem age  $t_1$ speciation rate  $\lambda$ extinction rate  $\mu$ 

+

 $\lambda$  and  $\mu$  can vary over time sampling fraction f

probability that a lineage survives from  $t_1 \mbox{ to } t_2$  and leaves no descendant in the sample

$$\mathcal{L}(t_1,\ldots,t_n) = \frac{f^n \Psi(t_2,t_1) \prod_{i=2}^n \lambda(t_i) \Psi(s_{i,1},t_i) \Psi(s_{i,2},t_i)}{1 - \Phi(t_1)},$$



+

### birth-death model

stem age  $t_1$ speciation rate  $\lambda$ extinction rate  $\mu$ 

 $\lambda$  and  $\mu$  can vary over time sampling fraction f

probability that a lineage survives from  $t_1 \mbox{ to } t_2$  and lives no descendant in the sample

$$\mathcal{L}(t_1,\ldots,t_n) = \frac{f^n \Psi(t_2,t_1) \prod_{i=2}^n \lambda(t_i) \Psi(s_{i,1},t_i) \Psi(s_{i,2},t_i)}{1 - \Phi(t_1)},$$

probability of a speciation event at time t<sub>i</sub>



### birth-death model

stem age  $t_1$ speciation rate  $\lambda$ extinction rate  $\mu$ 

+

 $\lambda$  and  $\mu$  can vary over time sampling fraction f



birth-death modelstem age  $t_1$  $\lambda$  and  $\mu$  can vary over timebirth-death modelspeciation rate  $\lambda$ + $\lambda$  and  $\mu$  can vary over timeextinction rate  $\mu$ +sampling fraction f



 $\Phi(t) = \mathbb{P}\{\text{a lineage is } \textit{not in the sample} | \text{it was alive at the time } t\}$ 

$$\Phi(t + \Delta t) = \mu(t)\Delta t + (1 - \mu(t)\Delta t)\lambda(t)\Phi^{2}(t) + (1 - \mu(t)\Delta t)(1 - \lambda(t)\Delta t)\Phi(t) + o(\Delta t).$$

 $\Delta t \rightarrow 0$ 

$$\frac{d\Phi}{dt} = \mu(t) - (\lambda(t) + \mu(t))\Phi(t) + \lambda(t)\Phi^{2}(t)$$

$$\Phi(t) = 1 - \frac{e^{\int_0^t \lambda(u) - \mu(u)du}}{\frac{1}{f} + \int_0^t e^{\int_0^s \lambda(u) - \mu(u)du} \lambda(s)ds}$$



### birth-death model

stem age  $t_1$ speciation rate  $\lambda$ extinction rate  $\mu$ 

+

 $\lambda$  and  $\mu$  can vary over time sampling fraction f



### Support for a 4-shift rate model in the cetacean phylogeny



Table S2. Statistical support for rate shifts in the cetacean phylogeny

Model	nb	Description	LogL	AICc
No shift	1	Best fit model	-279.03	560.08
One shift	5	Best fit model: shift in the Delphinidae	-262.93*	536.22
Two shifts	6	Best fit model: shifts in the Delphinidae and Phocoenidae	-260.17 <sup>†</sup>	532.85
Three shifts	7	Best fit model: shifts in the Delphinidae, Phocoenidae and Ziphiidae	-256.13 <sup>‡</sup>	526.94
Four shifts	8	Best fit model: shifts in the Delphinidae, Phocoenidae, Ziphiidae, and Balaenopteridae	-250.13	517.14

## The resulting diversity curves show boom-then-bust diversity dynamics



## The resulting diversity curve is consistent with the fossil record



## Stochastic models of cladogenesis

## 2. environmental dependence



Species richness results from speciation and extinction events, themselves influenced by various biotic and abiotic processes

## **Abiotic factors** 0 10 20 Age (Ma) 30 40 50

60-

Geological

events

Panama

Acre

Pebas

System

GAAR

Pozo System

Δ

Global T (°C)

MM

CO

MECO

EECO

PETM

TEE

### **Biotic factors**









### Climate has been proposed as a major driver of diversification

Global surface temperature distribution

**Diversity gradients** 



# Kinetic effects of temperature on rates of genetic divergence and speciation

Andrew P. Allen\*\*, James F. Gillooly<sup>‡</sup>, Van M. Savage<sup>§</sup>, and James H. Brown<sup>+1</sup>

\*National Center for Ecological Analysis and Synthesis, 735 State Street, Suite 300, Santa Barbara, CA 93101; \*Department of Zoology, University of Florida, Gainesville, FL 32611; <sup>§</sup>Bauer Center for Genomics Research, Harvard University, Boston, MA 02138; and <sup>¶</sup>Department of Biology, University of New Mexico, Albuquerque, NM 87131

Contributed by James H. Brown, May 2, 2006

IAS

### Sea level may be a major determinant of diversity dynamics



## Macroevolutionary perspectives to environmental change

Condamine, Rolland & Morlon Ecology Letters (2013)



## How can we test the effect of abiotic factors on diversity dynamics using paleoenvironmental and phylogenetic data?



### **Macroevolutionary perspectives to environmental change**

Condamine, Rolland & Morlon Ecology Letters (2013)

# We derived the likelihood corresponding to a birth-death process in which:

the speciation rate  $\lambda$  can vary over time, lineages, and measured environmental variables E(t) the extinction rate  $\mu$  can vary over time, lineages, and measured environmental variables E(t) the extinction rate can exceed the speciation rate (periods of diversity decline) only a fraction f of extant species are sampled



## **Empirical application... under way**

- Phylogenetic trees spanning most of the tree of life
  - Amphibians
  - Angiosperms
  - Birds
  - Gymnosperms
  - Insects
  - Mammals
  - Reptiles



suggests the influence of temperature on diversification may explain the diversification slowdown observed in molecular phylogenies







## Stochastic models of cladogenesis

## 3. diversity- dependence





### Diversity-dependence brings molecular phylogenies closer to agreement with the fossil record

Rampal S. Etienne<sup>1,\*</sup>, Bart Haegeman<sup>2</sup>, Tanja Stadler<sup>3</sup>, Tracy Aze<sup>4</sup>, Paul N. Pearson<sup>4</sup>, Andy Purvis<sup>5</sup> and Albert B. Phillimore<sup>5</sup>

<sup>1</sup>Community and Conservation Ecology, Centre for Ecological and Evolutionary Studies,

## Louis DU PLESSIS tomorrow!

### **Stochastic models of cladogenesis**

### 4. testing hypotheses of equilibrium dynamics



## Inferring the Dynamics of Diversification: A Coalescent Approach

Hélène Morlon<sup>1</sup>\*, Matthew D. Potts<sup>2</sup>, Joshua B. Plotkin<sup>1</sup>\*

Is present-day species richness constrained by current ecological limits?



## We derived the likelihood of a reconstructed phylogeny corresponding to equilibrium dynamics



Morlon et al. PloS B 2010

## Likelihood derived from the coalescent process from population genetics

Likelihood of internode distances for the phylogeny of k randomly sampled species:

$$\Lambda(t_{1},t_{2},...,t_{k-1}) = \sum_{i=1}^{k-1} \log L(t_{i}) \qquad L(t_{i}) = \frac{i(i+1)}{2} \frac{2\lambda(v_{i})}{N(v_{i})} \exp \left[-\frac{i(i+1)}{2} \int_{v_{i}-t_{i}}^{v_{i}} \frac{2\lambda(t)}{N(t)} dt\right]$$



#### Morlon et al. PloS B 2010

# We used this likelihood to test the support for equilibrium dynamics across a wide range of phylogenies (289)

Morlon et al. PloS B 2010





Phillimore & Price PloSB 2008

McPeek AmNat 2008

**Expanding diversity** 



Model probability (Akaike weight)

Most phylogenies are consistent with the hypothesis that diversity is expanding with time- varying diversification rates

Morlon et al. PloS B 2010



Borrelia burgdorferi sensu lato

## **Consistent result for a bacterial clade**



assumed number of phylotypes

**Stochastic models of cladogenesis** 

### 5. protracted speciation (Rampal!)

6. age dependence



Combining models of trait evolution with models of cladogenesis : character-dependent diversification



#### **Binary trait** Estimating a Binary Character's Effect on Speciation and Extinction

WAYNE P. MADDISON,<sup>1,2,3,4</sup> PETER E. MIDFORD,<sup>1</sup> AND SARAH P. OTTO<sup>1,2</sup>

<sup>1</sup>Department of Zoology, University of British Columbia, Vancouver, BC V6T 1Z4, Canada; E-mail: wmaddisn@interchange.ubc.ca (W.P.M.) <sup>2</sup>Biodiversity Research Centre, University of British Columbia, Vancouver, BC V6T 1Z4, Canada <sup>3</sup>Department of Botany, University of British Columbia, Vancouver, BC V6T 1Z4, Canada <sup>4</sup>Wissenschaftskolleg zu Berlin, Wallotstraße 19, Berlin 14193, Germany



### **Quantitative trait**

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#### **Quantitative Traits and Diversification**

#### RICHARD G. FITZJOHN\*

Department of Zoology and Biodiversity Research Centre, University of British Columbia, Vancouver, BC V6T 1Z4, Canada \* Correspondence to be sent to: Department of Zoology, University of British Columbia, Vancouver, BC V6T 1Z4, Canada; E-mail: fitzjohn@zoology.ubc.ca.

> Received 24 December 2009; reviews returned 28 February 2010; accepted 9 August 2010 Guest Associate Editor: Daniel Rabosky

Abstract \_\_Quantitative traits have long been hypothesized to affect execution and extinction rates. For example, smaller

### **Geographic trait**

Syst. Bid. 60(4):451–465, 2011 (5) The Author(s) 2011. Published by Oxford University Press, on behalf of the Society of Systematic Biologists. All rights reserved. For Permissions, please email: journals.permissions@oup.com DOI:10.1093/sysbio/syr046 Advance Access publication on May 5, 2011

#### Phylogenetic Inference of Reciprocal Effects between Geographic Range Evolution and Diversification

EMMA E. GOLDBERG<sup>1,\*</sup>, LESLEY T. LANCASTER<sup>2</sup>, AND RICHARD H. REE<sup>3</sup>





PLOS BIOLOGY

### Faster Speciation and Reduced Extinction in the Tropics Contribute to the Mammalian Latitudinal Diversity Gradient

Jonathan Rolland<sup>1,2</sup>\*, Fabien L. Condamine<sup>1</sup>, Frederic Jiguet<sup>2</sup>, Hélène Morlon<sup>1</sup>\*

AB

ХF

1 CNRS, UMR 7641 Centre de Mathématiques Appliquées (Ecole Polytechnique), Palaiseau, France, 2 UMR 7204 MNHN–CNRS–UPMC Centre d'Ecologie et de Sciences de la Conservation, Museum National d'Histoire Naturelle, CP51, Paris, France

### range expansion into temperate regions

s

d

 $x_A$ 

range expansion into tropical regions

speciation rate in the tropics speciation rate in temperate regions

extinction rate in the tropics

speciation of widespread species

 $s_{AB}$ 

В

 $x_B$ 

by biome divergence

extinction rate in temperate regions



#### Rolland, Condamine, Jiguet & Morlon *PloS B* (2014)

### Trait change at cladogenetic event (Goldberg & Igic Evolution 2012)







#### Rolland, Jiguet, Jonsson, Condamine & Morlon PRSB (2014)
#### **Character + environmental dependence**



Cantalapiedra et al. PRSB 2013

**Developments under way** 



## **Testing the effect of biotic interactions on diversification**







Stochastic models of cladogenesis: Do we need a different approach?





-



(f) Protracted speciation





Stochastic models of cladogenesis: Models incorporating community assembly, range dynamics, population dynamics?



E-ARTICLE

## The Ecological Dynamics of Clade Diversification and Community Assembly

dynamics of species i in patch j

Mark A. McPeek<sup>\*</sup>  $N_{ij}(t+1) = N_{ij}(t) \exp\left(1 - \frac{\Sigma_j N_{ij}(t)}{K_{ij}}\right)$   $K_{ij} = K_{opt} \exp\left[-\left(\frac{E_j - E_i^*}{\omega}\right)^2\right]$ 



environmental gradient

#### The Shape and Temporal Dynamics of Phylogenetic Trees Arising from Geographic Speciation

ALEX L. PIGOT<sup>1,2,\*</sup>, ALBERT B. PHILLIMORE<sup>1,3</sup>, IAN P. F. OWENS<sup>1,3</sup>, AND C. DAVID L. ORME<sup>1,2</sup>

<sup>1</sup>Division of Biology, Department of Life Sciences, Imperial College London, Silwood Park, Ascot, Berkshire SL5 7PY, UK; <sup>2</sup>Grantham Institute for Climate Change, Imperial College London, South Kensington, London SW7 2AZ, UK; and <sup>3</sup>Natural Environment Research Council Centre for Population Biology, Imperial College London, Silwood Park, Ascot, Berkshire SL5 7PY, UK; \* Correspondence to be sent to: Division of Biology, Department of Life Sciences, Imperial College London, Silwood Park, Ascot, Berkshire SL5 7PY, UK; E-mail: alexander.pigot@imperial.ac.uk.

Syst. Biol. 2010



## Phylogenies arising from the Neutral Theory of Biodiversity (NTB)

The Unified Neutral Theory of BIODIVERSITY AND BIOGEOGRAPHY

STEPHEN P. HUBBELL



MANAGERANIS IN POPULATION BIOLOGY + 37

Hubbell 2001

#### Hubbell's model produces a species phylogeny



#### LETTER

### Inferring the parameters of the neutral theory of biodiversity using phylogenetic information and implications for tropical forests

#### Abstract

Franck Jabot\* and Jérôme Chave We develop a statistical method to infer the parameters of Hubbell's neutral model of



Phylogenies predicted by NTB have realistic imbalance...



Jabot & Chave *Eco. Lett.* 2008

## ... but unrealistic branch-length patterns



Davies et al. *Evolution* 2011

# The model of speciation by genetic differentiation





#### We relax a first limitation of NTB: constant total population size

We assume individuals give birth with rate *b* and die with rate *d b* and *d* can vary over time and we can have *b*<*d* 



We relax a second limitation of NTB: the point mutation mode of speciation

Speciation by genetic differentiation: A node is a speciation event only if *all individuals* of the two descendant populations are separated by *at least* one mutation



Phylogenies under SGD can be generated by a forward in time time-inhomogeneous branching process with three types



## Phylogenies under SGD have realistic branch-lengths and imbalance



#### Likelihoods of trees under SGD can be computed efficiently



taxon	p	$\log(b)$	b-d	$\nu$
bovinae	1	11.0	0.19	0.16
calomys	0.85	12.3	0.45	1.72
caprinae	0.89	10.7	0.40	0.39
dasyurid	0.92	10.8	0.20	0.23
dipodomys	0.95	11.2	0.05	0.30
duikers	0.83	11.2	0.38	0.30
genets	0.88	11.3	0.36	0.31
gibbon	1	8.8	0.53	0.32
howlerMonkey	0.91	11.5	0.20	0.39
macaca	0.95	6.4	0.42	0.76
microtus	0.69	6.9	1.84	1.05
mustelid	0.85	11.8	0.38	0.22
pikas	0.92	10.5	0.25	0.35
talpa	0.77	10.9	0.16	0.21

#### REVIEW AND SYNTHESIS

#### Phylogenetic approaches for studying diversification

#### Abstract

#### Hélène Morlon\*

Center for Applied Mathematics, Ecole Polytechnique, Palaiseau, Essonne, France

\*Correspondence: E-mail: helene. morlon@cmap.polytechnique.fr Estimating rates of speciation and extinction, and understanding how and why they vary over evolutionary time, geographical space and species groups, is a key to understanding how ecological and evolutionary processes generate biological diversity. Such inferences will increasingly benefit from phylogenetic approaches given the ever-accelerating rates of genetic sequencing. In the last few years, models designed to understand diversification from phylogenetic data have advanced significantly. Here, I review these approaches and what they have revealed about diversification in the natural world. I focus on key distinctions between different models, and I clarify the conclusions that can be drawn from each model. I identify promising areas for future research. A major challenge ahead is to develop models that more explicitly take into account ecology, in particular the interaction of species with each other and with their environment. This will not only improve our understanding of diversification; it will also present a new perspective to the use of phylogenies in community ecology, the science of interaction networks and conservation biology, and might shift the current focus in ecology on equilibrium biodiversity theories to non-equilibrium theories recognising the crucial role of history.

#### Keywords

Birth-death models, cladogenesis, diversity dynamics, extinction, speciation, stochastic biodiversity models.

Ecology Letters (2014)

### **Current and future developments**



## **Testing diversity-dependent effects in trait evolution**

# Quantifying the role of past adaptation on current morphological diversity



PC3 (+ foot webbing)





# We develop and use phylogenetic approaches to understand global biodiversity patterns, across the Tree of Life





Dan Moen



Jonathan Rolland

#### Fabien Condamine



Marc Manceau







**Amaury Lambert** 



**Frederic Jiguet** 













FRANCE BERKELEY FUND Funds France-Scaleday







Joshua Plotkin

- i "type 0" if it is a lineage from the underlying genealogy that has at least one descendant of same genetic type at present,
- ii "type 1" if it is a lineage from the underlying genealogy that has no descendant of same genetic type at present,
- iii "frozen" if there exists at least two individuals, one in each of the two subpopulations separated by the descending node in the underlying genealogy, of same genetic type. In this case, all the individuals from the descending nodes are collapsed into a single species, and the lineage is "frozen", in the sense that no further splitting or extinction events happen to this lineage up to the present.

A lineage of type 1 becomes of type 0 :

$$ho_{1 o 0}(t) = rac{
u(t)m(t)}{(1-m(t))}$$

A lineage of type 1 branches and gives rise to two descendant lineages of type 1 :

$$\rho_{1\rightarrow+1}(t) = g(t)(1-m(t))$$

A lineage of type 0 branches and gives rise to one descendant lineage of type 0 and one descendant lineage of type 1 :

$$\rho_{0 \to +1}(t) = 2g(t)(1 - m(t))$$

A lineage of type 0 "freezes", giving rise to a terminal branch in the phylogeny :

$$ho_{0
ightarrow arnothing}(t) = g(t)m(t)$$