Introduction

David Goldstein

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Copenhagen phylolinguistics workshop

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The overarching question

- How do we draw inferences about the unobservable linguistic past from observable linguistic (and non-linguistic) data?

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- Provide a conceptual introduction to Bayesian phylogenetic inference

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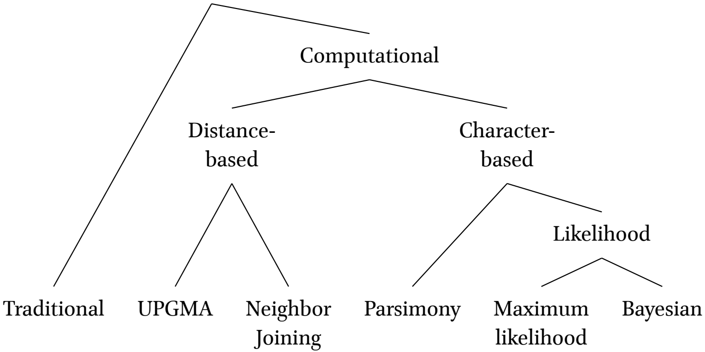
- Enable you to interpret some of the results of a Bayesian phylogenetic analysis

What are phylogenetic trees?

A phylogenetic tree is a hypothesis about the specific sequence of historical branching events leading from a common ancestor forwards in time to contemporary groupings, be they biological species or languages. (*Pagel 2017, p. 152*)

Overview of methods in linguistic phylogenetics



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- Character-based methods infer a tree on the basis of linguistic characters. In principle, these can be continuous or discrete, but in practice they are overwhelmingly discrete.
- Likelihood and Bayesian methods are probabilistic and assume stochastic models of linguistic change.

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- Flexibility—it's possible to create a wide array of models.
- Bayesian methods can build on traditional knowledge through the use of prior probability distributions.

Increasing prominence in the field

CLADE	LITERATURE
Iranian	Cathcart 2019, Cathcart 2020
Semitic	Kitchen et al. 2009
Dravidian	Kolipakam et al. 2018
Transeurasian	Robbeets and Bouckaert 2018
Pama-Nyungan	Bowern 2012, Bowern and Atkinson 2012, Bouckaert, Bowern, et al. 2018
Turkic	Savelyev and Robbeets 2020
Sino-Tibetan	Sagart et al. 2019, Zhang, Yan, et al. 2019, Zhang, Ji, et al. 2020
Japonic	Lee and Hasegawa 2011
Austronesian	Saunders 2005, Dunn et al. 2008, Gray, Drummond, et al. 2009, Greenhill and Gray 2009, Greenhill, Atkinson, et al. 2010
Indo-European	Gray and Atkinson 2003, Atkinson and Gray 2006, Bouckaert, Lemey, et al. 2012, Chang et al. 2015, Rama 2018
Slavic	Cathcart and Wandl 2020
Dene-Yeniseian	A. Sicoli and Holton 2014, Yanovich 2020
Bantu	Guillon and Mace 2016; Holden et al. 2005

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The representation of the data

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- Any heritable and potentially variable observable feature of a language. Characters states may be discrete or continuous.

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- DISCRETE CHARACTER: Any homologous or cross-linguistically comparable trait or feature whose possible states are finite.
- It is possible to carry out phylogenetic inference on continuous characters, but I'm not aware of any attempts to do this in a linguistic context.

Multistate character (Lexical cognates)

Language	‘father’	Class
Old English	*fæder*	1
Gothic	*fadar, atta*	1, 2
Old Norse	*faðir*	1
Latin	*pater*	1
Rumanian	*tată*	3
Greek	πατήρ	1
Sanskrit	*pitṛ́*	1
Old Irish	*athir*	1
Armenian	*hayr*	1
Hittite	*attas*	2?
Tocharian A	*pācar*	1
Tocharian B	*pācer*	1
Lithuanian	*tėvas*	4
OCS	отьць	5
Russian	отец	5

Binary character (Lexical cognates)

Language	'father'	1	2	3	4	5
Old English	*fæder*	1	0	0	0	0
Gothic	*fadar*, *atta*	1	1	0	0	0
Old Norse	*faðir*	1	0	0	0	0
Latin	*pater*	1	0	0	0	0
Rumanian	*tată*	0	0	1	0	0
Greek	πατήρ	1	0	0	0	0
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Partial cognates

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- See List 2016 if you're curious.

Let’s look at our dataset (the .nex file)

#NEXUS

BEGIN DATA;
DIMENSIONS NTAX=24 NCHAR=294;
FORMAT DATATYPE=STANDARD MISSING=? GAP=- INTERLEAVE=NO
symbols=“01”;
MATRIX
Hittite ?00000000000000000000001000000
Armenian 10001110000000000000000010000

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- This term is slightly misleading, because it conceals the intervention of the researcher. The data have not simply been “observed,” they’ve been *selected*!
- Bayesian methods are amazing, but they are not pixie dust: posterior inferences can only be as good as the data on which they are based. There never has been and never will be an exception to this truth.

Let's look at our RevBayes script

- Open `copenhagen-ringe-mk-ard-cc-prior.Rev`

Bayesian inference

The fundamental idea

Informal statement

- What is the probability of something unobserved or unobservable (such as a phylogenetic tree) given data that we can observe?

Bayes' Theorem

Bayes' Theorem

$$p(\theta|y) = \frac{p(y|\theta) \cdot p(\theta)}{p(y)}$$

y	"Observed data"
θ	Unobserved parameter
$p(\theta\|y)$	Posterior probability
$p(y\|\theta)$	Likelihood
$p(\theta)$	Prior probability
$p(y)$	Marginal likelihood

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- How probable is it that a player will draw a card from a particular suit? $13/52 = 0.25$.
- Now suppose that the player draws a spade. What is the probability that he will draw a second spade?
- Since one spade has already been drawn, only 12 remain. Since one card has already been drawn, the total number of cards in the deck is 51. $P(\text{Draw spade}|\text{First draw a spade}) = 12/51 = 0.24$.

Bayes' Theorem restated

Bayes' Theorem without the normalizing constant (i.e., as an unnormalized density)

$$p(\theta|y) \propto p(y|\theta) \cdot p(\theta)$$

Bayes' Theorem in a phylogenetic context

Bayes' Theorem in phylogenetics

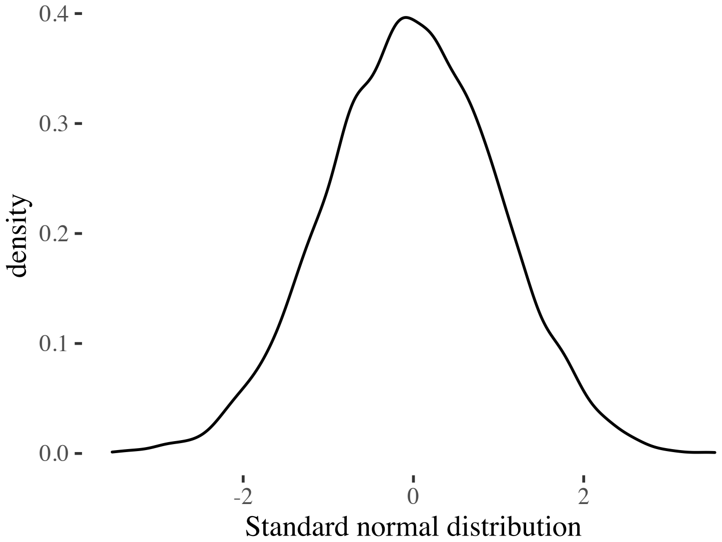
$$p(\Phi, \nu, \Phi | y) \propto p(y | \Psi, \nu, \Phi) \times p(\Psi, \nu, \Phi)$$

- Φ Tree topology
- ν Branch lengths
- Φ Parameters associated with transition model
- y Observed data

Excursus: Uniform distribution $\theta \sim \mathcal{U}(0, 4)$

Excursus: Standard normal distribution

$$\theta \sim \mathcal{N}(\mu = 0, \sigma = 1)$$



Bayesian analyses yield posterior distributions

- Phylogenetic trees

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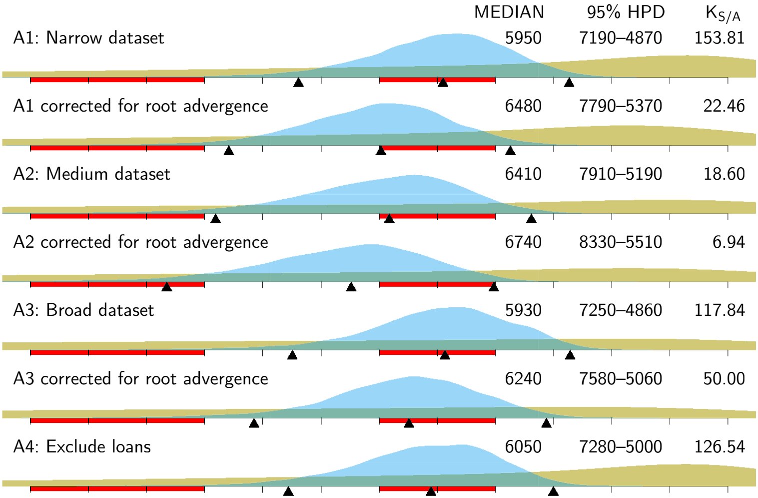
Bayesian analyses yield posterior distributions

- Phylogenetic trees
- Rates of change
- Branch lengths
- Ancestral states

Posterior distributions for root age (Chang et al. 2015)



An illustration of Bayesian inference

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- This value is a parameter—it controls the rate at which heads and tails show up.

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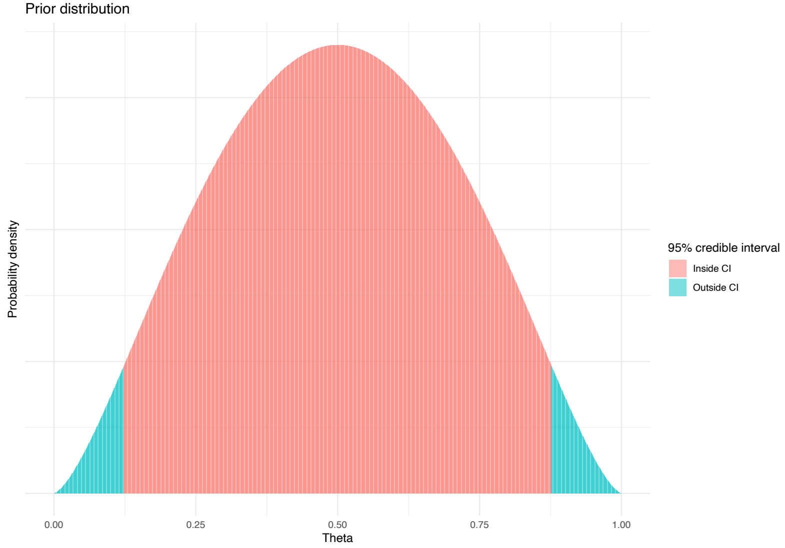
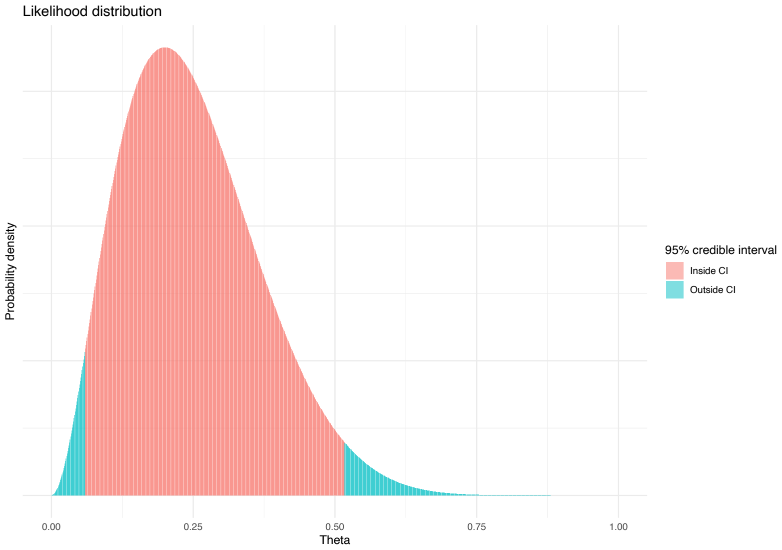
- Let's say we really have no idea—the mint could produce anything.
- We flip the coin 10 times, and heads comes up twice.

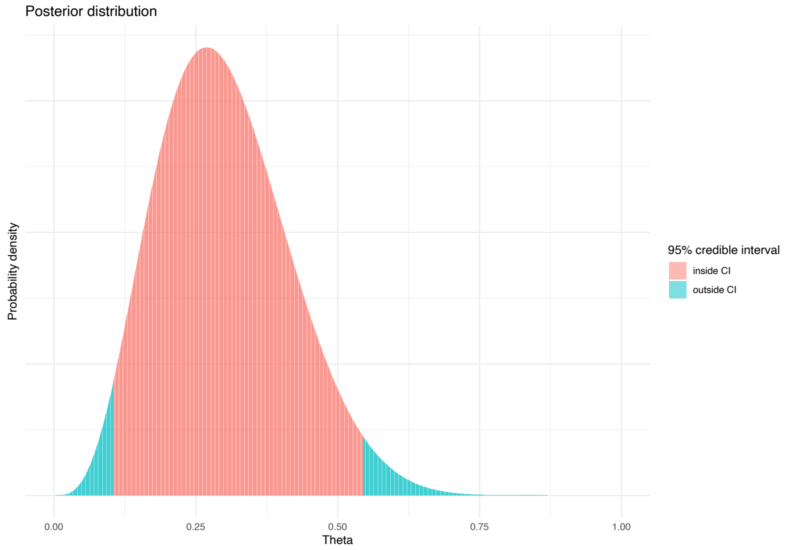
Prior probability distribution



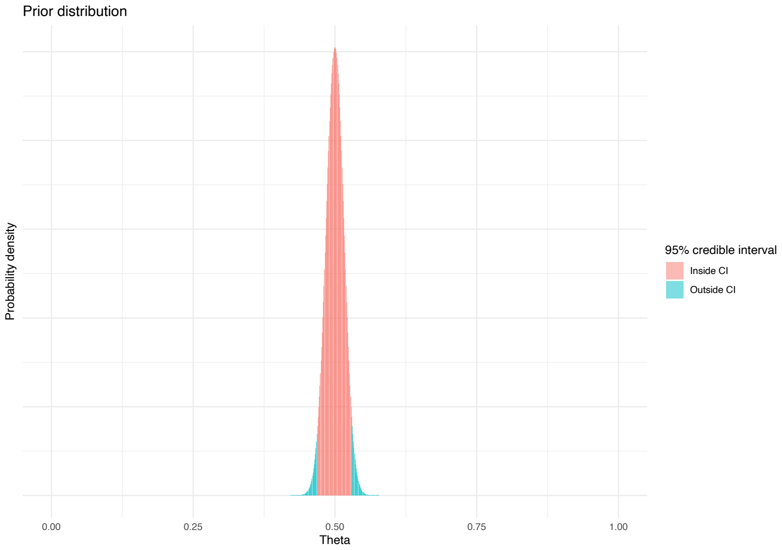
Likelihood $p(y|\theta)$



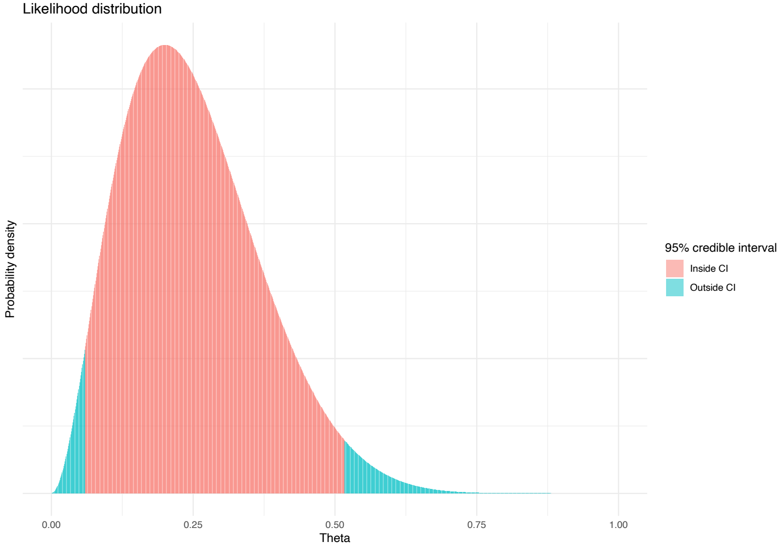
Posterior distribution



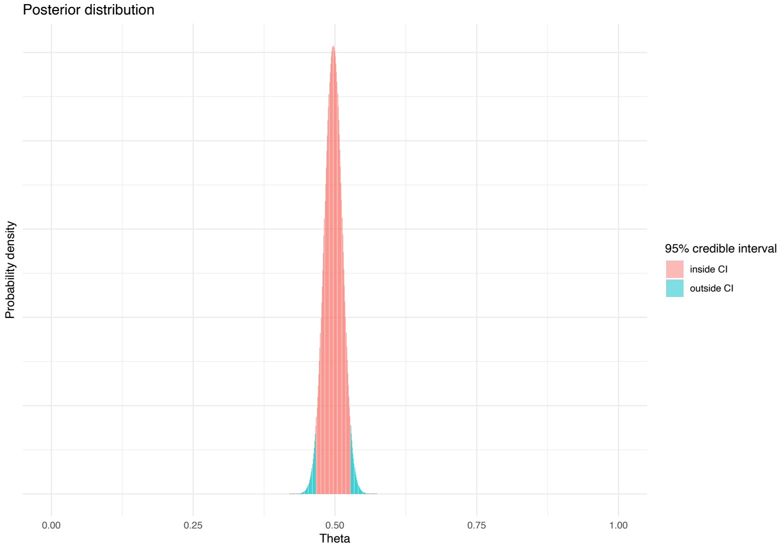
Now let’s change our prior beliefs



Likelihood $p(y|\theta)$ (no change)



Posterior is a compromise between the data and the priors



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- Priors are a non-trivial aspect of Bayesian inference.
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- The less observed data you have, the greater their impact on the posterior.
- Priors have been hugely controversial in the history of Bayesian inference.
- Priors should be explicit and justifiable. If we can justify informative priors, then we should use them.

Coming back to phylogenetics

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- We ultimately want to calculate $p(\Psi|y)$, but to do that we need to be calculate the likelihood $p(y|\Psi)$.

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- We ultimately want to calculate $p(\Psi|y)$, but to do that we need to be calculate the likelihood $p(y|\Psi)$.
- That is, we need a way to calculate the likelihood of a particular sequence at the tips of the tree given a particular tree.

Calculating likelihood of a sequence

Two fundamental notions of probability theory

Independence

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$P(X \cap Y) = P(X) \cdot P(Y)$ iff $P(Y|X) = P(Y)$

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- Multiple flips of a coin are independent.
- The result of an earlier flip does not influence the probability of the current flip.

Mutually exclusive events

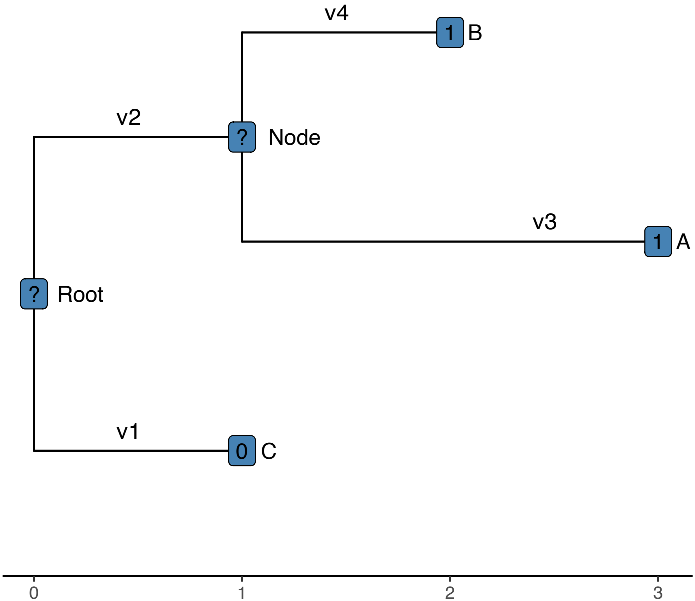
Probability of mutually exclusive (bzw. disjoint) events

When two events X and Y are mutually exclusive,

$$P(X \cup Y) = P(X) + P(Y)$$

We're going to use this concept to take into account uncertainty at interior nodes.

Hypothetical tree



What is the likelihood of our observed sequence?

- What is the likelihood of 110 at the tips given the above tree and its associated branch lengths?

$$p(y|\Psi,\nu) = \pi_0 \cdot p_{00}(\nu 1) \cdot p_{00}(\nu 2) \cdot p_{01}(\nu 3) \cdot p_{01}(\nu 4)$$

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$p_{ij}(\nu_k) = p(i|j,\nu_k)$: Transition probability

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- If we knew the states at the root and an interior node and if we could assume that all transitions were independent, we could simply do a lot of multiplication.
- If the values at the root and interior node were both zero, for instance:

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The idea behind maximum likelihood

- Find the tree and branch lengths that yield the maximum likelihood for the observed data
- In other words, what values of Ψ and ν yield the highest value for $p(C = 0, A = 1, B = 1|\Psi, \nu)$?
- In a Bayesian context, we do more than search for the maximum-likelihood tree (and branch lengths) because the likelihood values are all multiplied by a prior distribution.

How do we calculate transition probabilities?

- We do this with a transition model

Transition models

Deterministic vs. stochastic processes

- DETERMINISTIC PROCESS The same output is always produced from a given input. (Dowbrow 2016, p. 1)

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- What are some examples of stochastic processes?
- Whether or not it will rain tomorrow, how many text messages you’ll receive in a given day, how long you’re going to have to wait in line...

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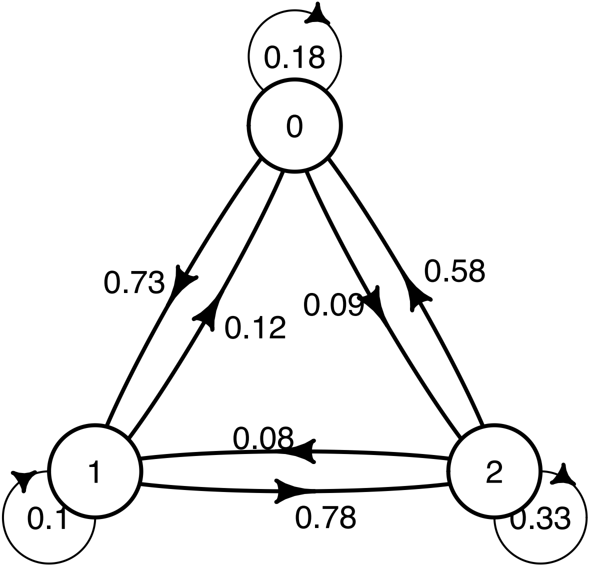
Markov chain

- A MARKOV CHAIN is a stochastic model describing a sequence of possible events in which the probability of each event depends only on the state attained in the previous event.

Markov chain as transition graph



Markov chain as matrix

$$
\begin{array}{cc}
 & \begin{array}{ccc} 0 & 1 & 2 \end{array} \\
\begin{array}{c} 0 \\ 1 \\ 2 \end{array} & \begin{bmatrix} 0.6 & 0.2 & 0.2 \\ 0.4 & 0.5 & 0.1 \\ 0.3 & 0.3 & 0.4 \end{bmatrix}
\end{array}
$$

- Each row in the above matrix sums to 1. Why?

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- Given a branch of a specific length, the CTMC provides us with probabilities for transitions among the possible states.

Continuous-time Markov Chain (CTMC)

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- Likelihood and Bayesian methods model the history of characters on a phylogenetic tree as a MARKOV PROCESS.
- CTMCs are the basis of most computational phylogenetic methods (Warnow 2018, p. 147).

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  Transitions are independent (what happens in one region of the tree is assumed to be independent of what happens elsewhere in the tree).
- *Constant rate*
  For each rate parameter, a single rate is estimated for the entire tree, i.e., we're not going to allow rates to speed up or slow down along the tree.

Transition probability matrix $\mathbf{P}$

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- There are many different varieties of rate matrices (or transition models).
- Different transition models allow us to make different assumptions about linguistic change.

Equal-rate (ER) model

$$
\begin{array}{c c}
 & \begin{array}{cc} 0 & 1 \end{array} \\
\begin{array}{c} 0 \\ 1 \end{array} & \begin{bmatrix} -q & q \\ q & -q \end{bmatrix}
\end{array}
$$

- q_1 = rate at which character changes from 0 to 1 over a short interval dt

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$$

- q_1 = rate at which character changes from 0 to 1 over a short interval dt
- q_2 = rate at which character changes from 1 to 0 over a short interval dt

Equal-rate (ER) model

$$
\begin{array}{cc}
 & \begin{array}{cc} 0 & 1 \end{array} \\
\begin{array}{c} 0 \\ 1 \end{array} & \begin{bmatrix} -q & q \\ q & -q \end{bmatrix}
\end{array}
$$

- q_1 = rate at which character changes from 0 to 1 over a short interval dt
- q_2 = rate at which character changes from 1 to 0 over a short interval dt
- The elements on the diagonal are determined by summing the non-diagonal elements in the row and negating them.

All-rates-different (ARD) model

$$
\begin{array}{cc}
 & \begin{array}{cc} 0 & \quad 1 \end{array} \\
\begin{array}{c} 0 \\ 1 \end{array} & \begin{bmatrix} -q_1 & q_1 \\ q_2 & -q_2 \end{bmatrix}
\end{array}
$$

The Mk model

- M stands for Markov

The Mk model

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- k is a variable over discrete character states

Other transition models

- F81

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- F81
- HKY

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- F81
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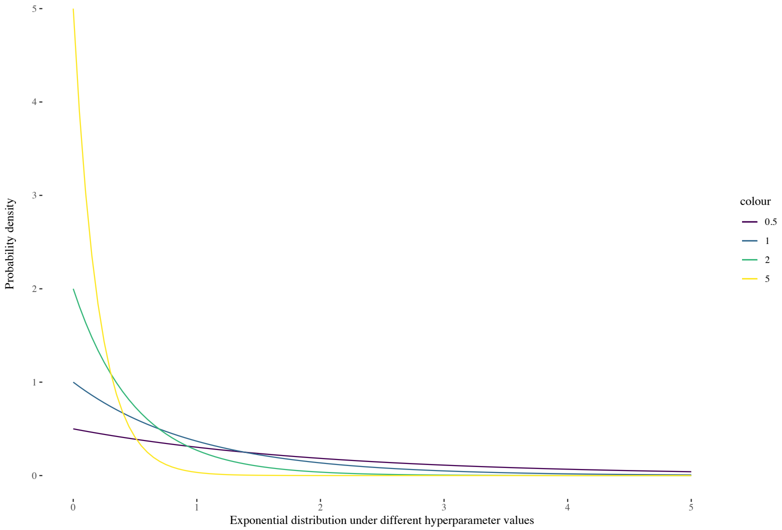
- GTR

Other transition models

- F81
- HKY
- GTR
- Covarion

Prior distribution for the rates

Exponential distribution ($q_{ij} \sim \text{Exp}(\lambda)$)



Let's look at our .Rev script again

- Look at the code for the rate matrix Q

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