## Mixture Models

## Classic Mixture Models

- Proportion of invariable sites model

$$
(L)=p_{\text {invar }} L_{\mathrm{invar}}+\left(1-p_{\mathrm{invar}}\right) L_{\text {variable }}
$$

- Discrete gamma among-site rate het. model

$$
L=\underbrace{\left(\frac{1}{4}\right) L_{r_{1}}}_{\text {(Number of categories } k=4 \text { in this case) }}+\left(\frac{1}{4}\right) L_{r_{2}}+\left(\frac{1}{4}\right) L_{r_{3}}+\left(\frac{\Upsilon}{4}\right) L_{r_{4}}
$$

## Pagel and Meade's 2004 mixture model



Base frequencies are common to all $Q$ matrices.
(BayesPhylogenies software at http://www.evolution.reading.ac.uk/SoftwareMain.html)

## Pagel-Meade 2004 mixture model



## Heterotachy

## Heterotachy



Kolaczkowski and Thornton (2004)

## Kolaczkowski \& Thornton's (2008) heterotachy model



Each $b_{i}$ represents an entire set of 5 branch lengths.
This model potentially adds a lot of parameters (if the tree is large)

Kolaczkowski and Thornton (2008)


## Heterotachy



Kolaczkowski and Thornton (2008)


# riMCMC heterotachy model 

Red edges have prob. > 0.5 of having 2 edges

Pagel and Meade (2008)

## rjMCMC heterotachy model



Software: http://www.evolution.reading.ac.uk/BayesPhyHeterotachy.html
Pagel and Meade (2008)

## Covarion Models

## Covarion Hypothesis

"...at any one point in time only a very restricted number of positions can fix mutations but that as mutations are fixed the positions capable of accepting mutations also change so that examination of a wide range of species reveals a wide range of altered positions. We define this restricted group as the concomitantly variable codons. "

Fitch and Markowitz (1970)

## Covarion Hypothesis



Extreme form of heterotachy

Fitch and Markowitz (1970)

## Covarion Model



## Covarion Model

Pretend there are 10 presence/absence characters, each of which can be in an on or off state at any point in time.. Consider only site 7 for the moment (bold boxes)...


## Covarion Mixture Model

Note that some sites switch from off to on (or vice versa) often (e.g. site 7)...


## Covarion Mixture (CM) Model

Note that some sites switch from off to on (or vice versa) often (e.g. site 7), while other sites rarely switch (e.g. site 1).


Zhou et al. 2010 suggest using a Dirichlet procesc prior model to allow groups ot sites to have distinct $S_{01}$ and $s_{10}$ parameter values.

Zhou et al. (2010)

