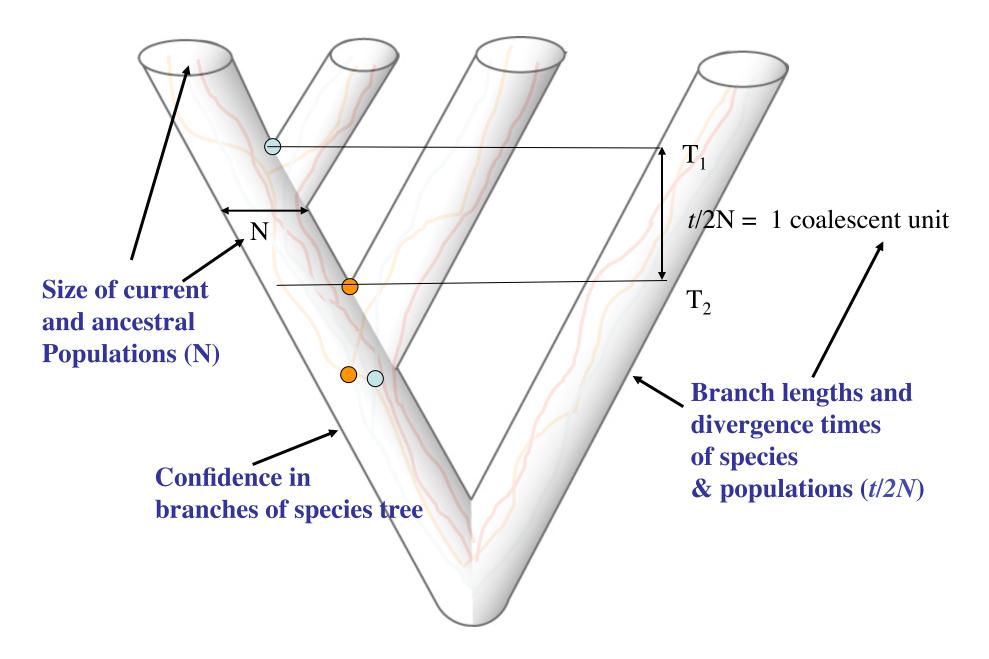
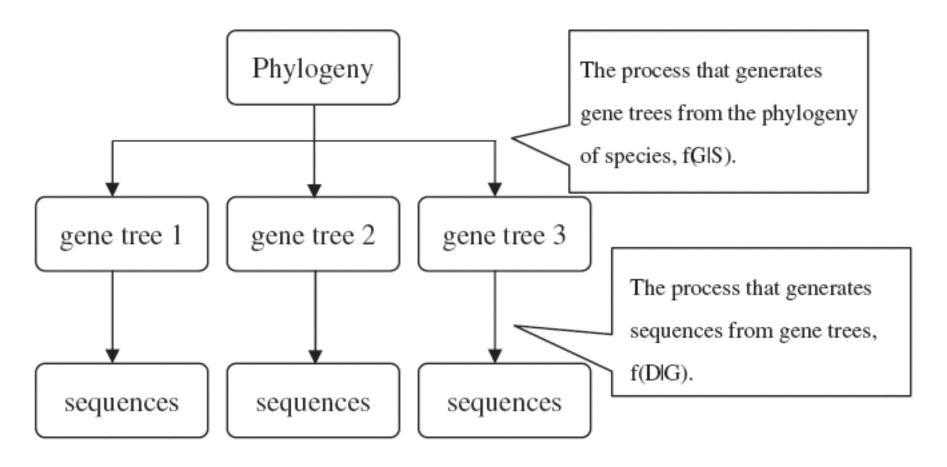
## Anatomy of a species tree



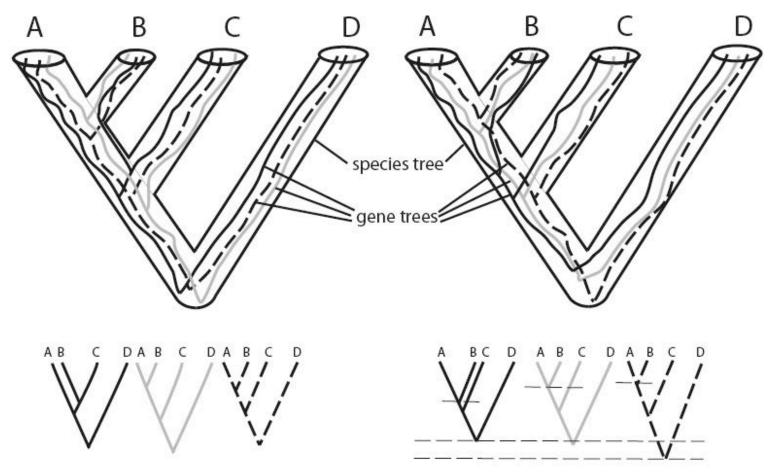
### Hierarchical nature of phylogeny



# Deep coalescence vs. branch length heterogeneity

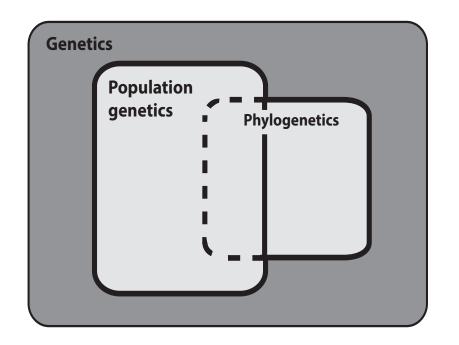
Deep coalescence

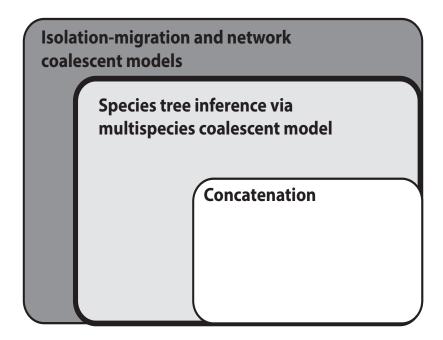
Branch length heterogeneity



Edwards 2009. Evolution 63:1-19

# The multispecies coalescent model in context

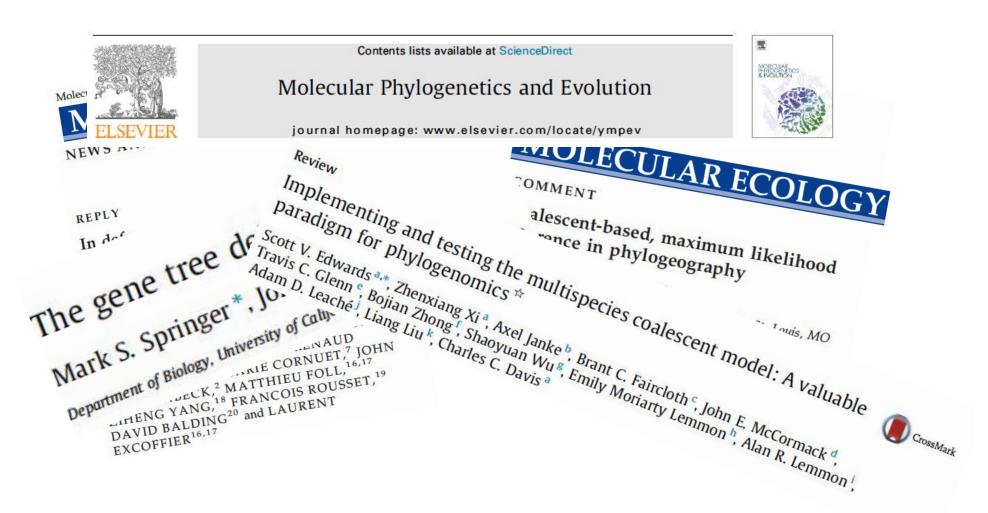




Key assumption of the MSC:
<a href="mailto:conditional independence">conditional independence</a> of loci
(mediated by recombination)

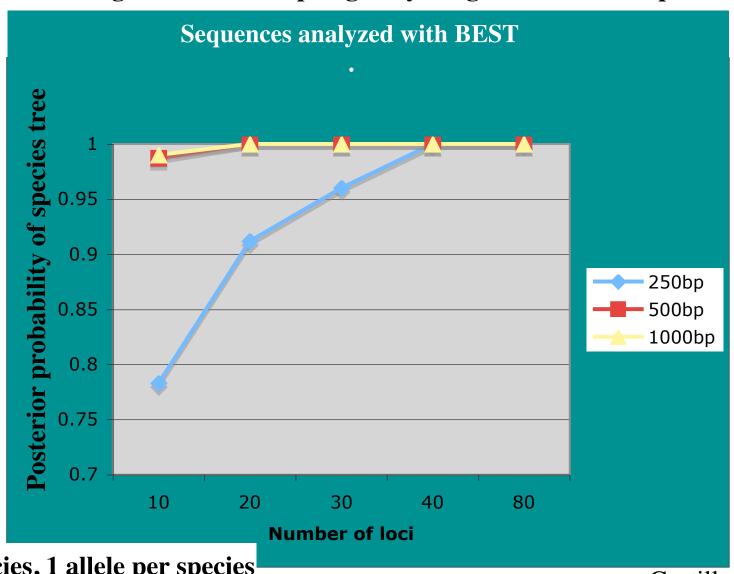
not presence of incomplete lineage sorting

# "Controversies" surrounding species tree methods



#### Do species tree methods require discordance of gene trees?

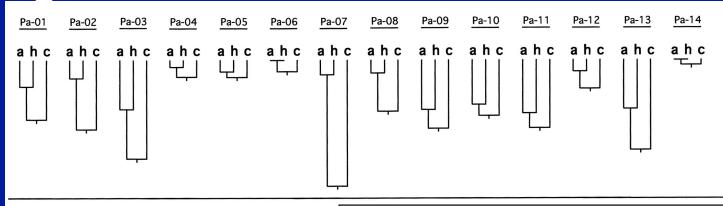
Simulation: all gene trees are topologically congruent with the species tree

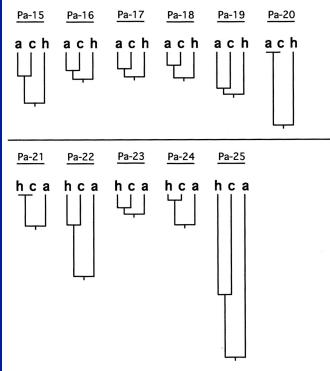


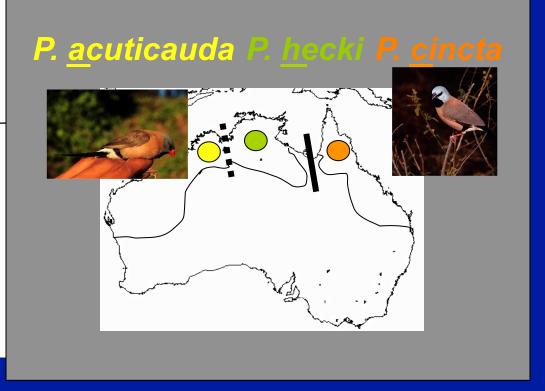
8 species, 1 allele per species

Castillo et al. 2010

#### 30 gene trees from Australian finches

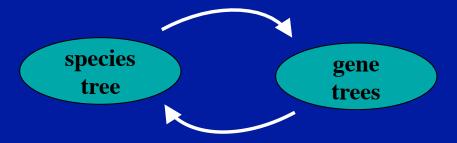






### Species trees from gene trees

Bayesian Estimation of Species Trees = The "BEST" method



- 1. Define an approximate species tree as a prior for gene trees
- 2. Estimate posterior of species tree f(S|D) using a birth-death prior on species tree and likelihoods of gene tree vectors from step 1 using coalescent theory.

Liu and Pearl. 2007. Species trees from gene trees: reconstructing posterior distributions of a species phylogeny using estimated gene tree distributions. *Syst. Biol.* 56 (May): 504 - 514. www.stat.osu.edu/~dkp/BEST

### Bayesian hierarchical model

(Liu and Pearl)

Bayesian Estimation of Species Trees = The "BEST" method (ha ha!)

Likelihood of sequence data given gene trees and substitution model

**Prior** on substitution parameters

birth-death prior on species tree

 $f(S,\mathbf{G},\lambda \mid D) = \frac{f(D \mid \mathbf{G},\lambda)f(\lambda)f(\mathbf{G} \mid S)f(S)}{f(D)}$ 

Estimated posterior of species tree

Likelihood of sequence data given gene trees and substitution model

Likelihood of gene tree distributions given species tree

Probability of the sequence data (impossible to know)

Liu, L. 2008. *Bioinformatics* 24: 2542–2543

#### **Australo-Papuan Fairy Wrens - Maluridae**



**Splendid Fairywren (Malurus)** 



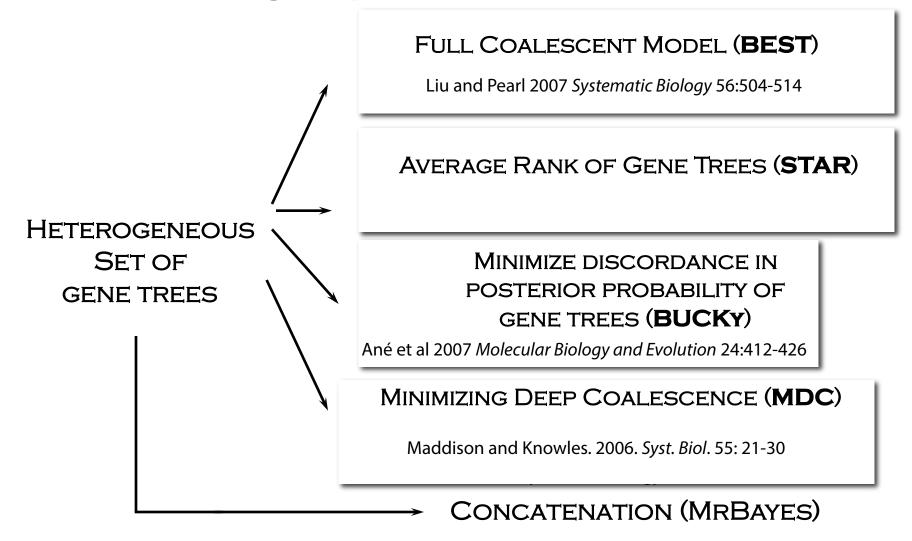


Superb Fairywren (*Malurus*)

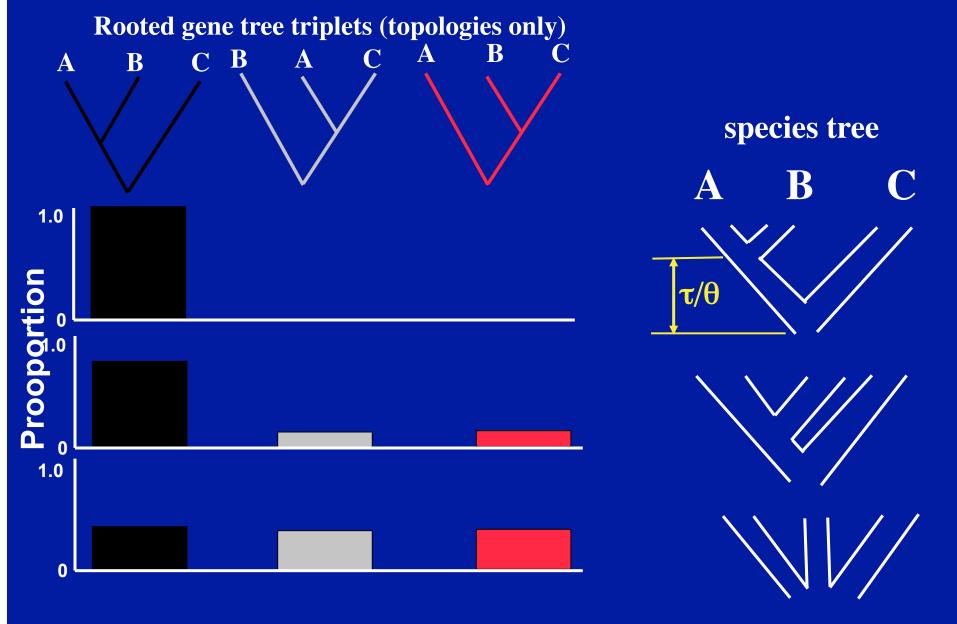


Southern Emu-wren (Stipiturus)

## Exploring incomplete lineage sorting through species tree methods

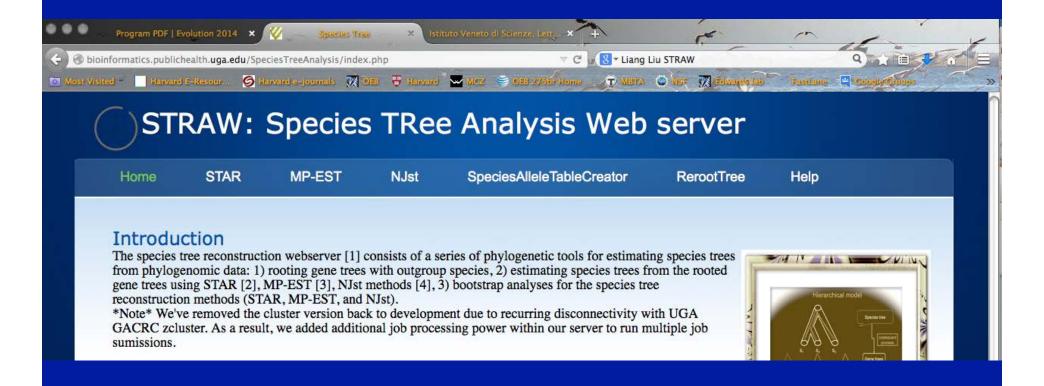


#### Maximum (pseudo) likelihood method for species trees



Liu, Li & Edwards. 2010. BMC Evol. Biol.

# Species Tree Web Server: STRAW



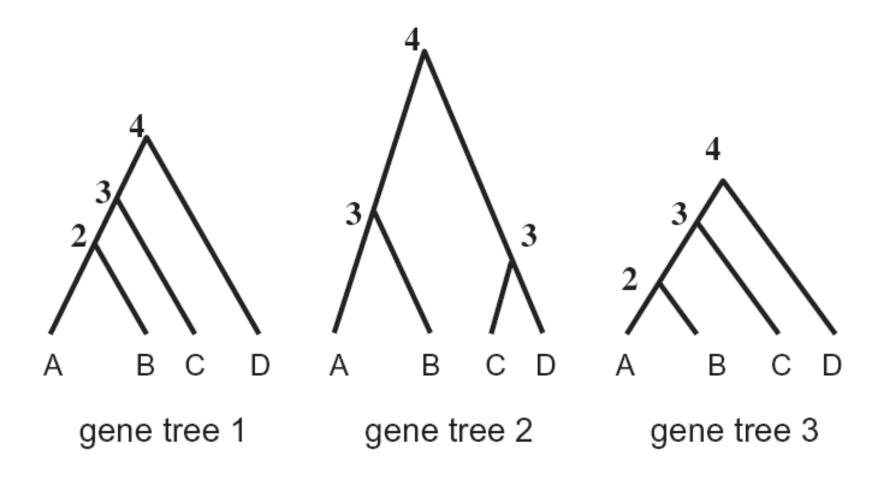
http://bioinformatics.publichealth.uga.edu/SpeciesTreeAnalysis/index.php

### Summarizing variation in gene trees

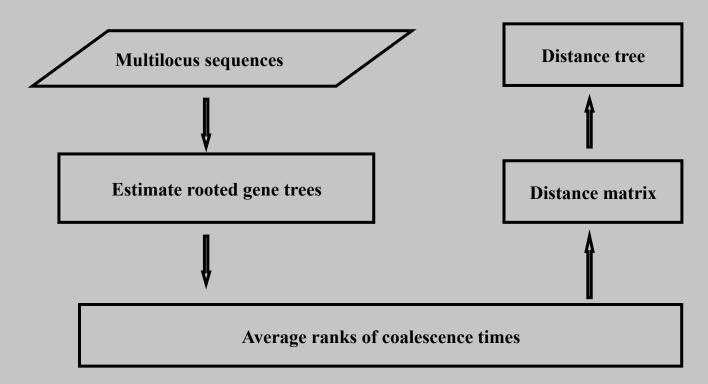
Compare taxon pairs via

1) Ranks

- 2) coalescence times 3) minimum divergences

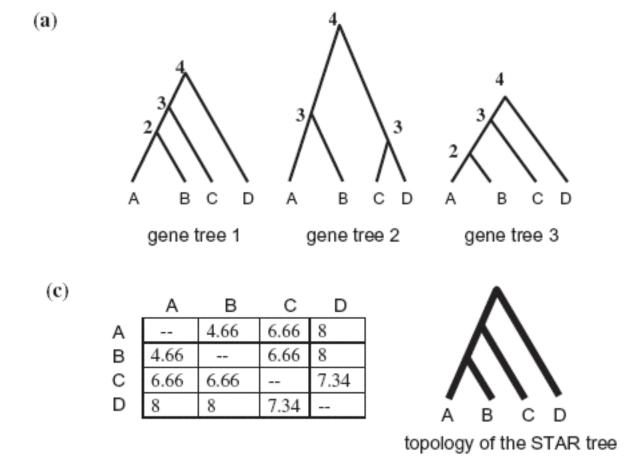


# Species Trees from Average Ranks of Coalescence Times (STAR)



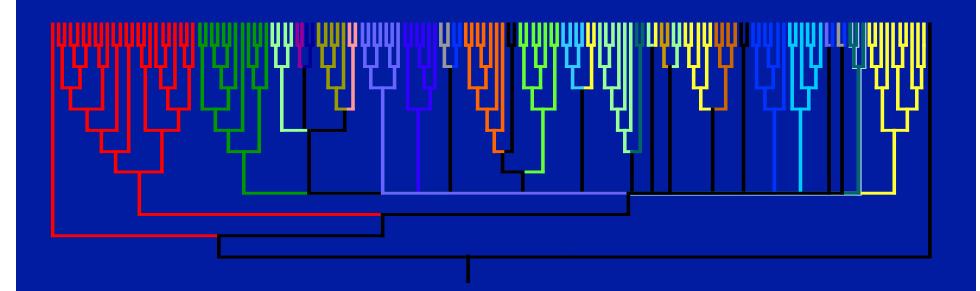
Liu, Yu, Pearl, Edwards (2009) Syst. Biol.doi:10.1093/sysbi

### Calculating a STAR tree



Liu, Yu, Kubatko, Pearl and Edwards 2009. Mol. Phyl. Evol. 53:320-328

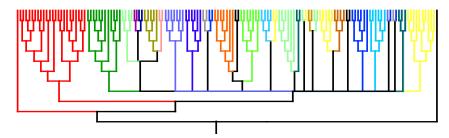
# PHYBASE: Constructing, manipulating and evaluating species trees



Liu & Yu. 2010. Bioinformatics 26: 962-963

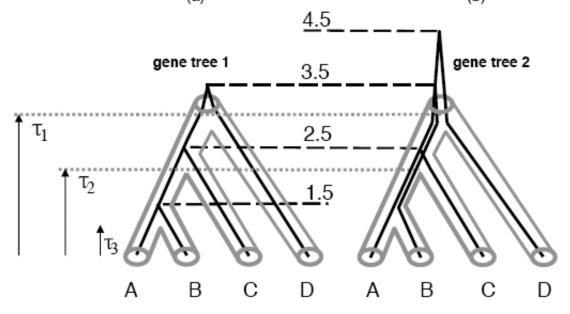
http://code.google.com/p/phybase/

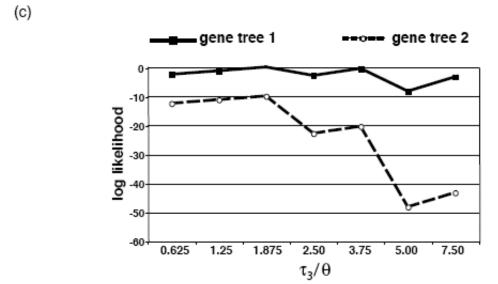
## Uses of phybase



- Conduct multilocus bootstrap
- •Estimate STAR, STEAC and Maximum Trees
- Calculate likelihood of species trees given gene trees
- Simulate gene trees (ultrametric and variable rates) and DNA sequences

#### Likelihood of gene trees given a species tree





Liu, Yu, Kubatko, Pearl and Edwards 2009. Mol. Phyl. Evol. 53: 320-328

### Multilocus bootstrap

Sample loci at random with replacement ...



Then sample sites within loci with replacement, just as in the normal bootstrap....



Seo, T.-K. 2008. Calculating Bootstrap Probabilities of Phylogeny Using Multilocus Sequence Data. *Mol. Biol. Evol.* 25:960-971.

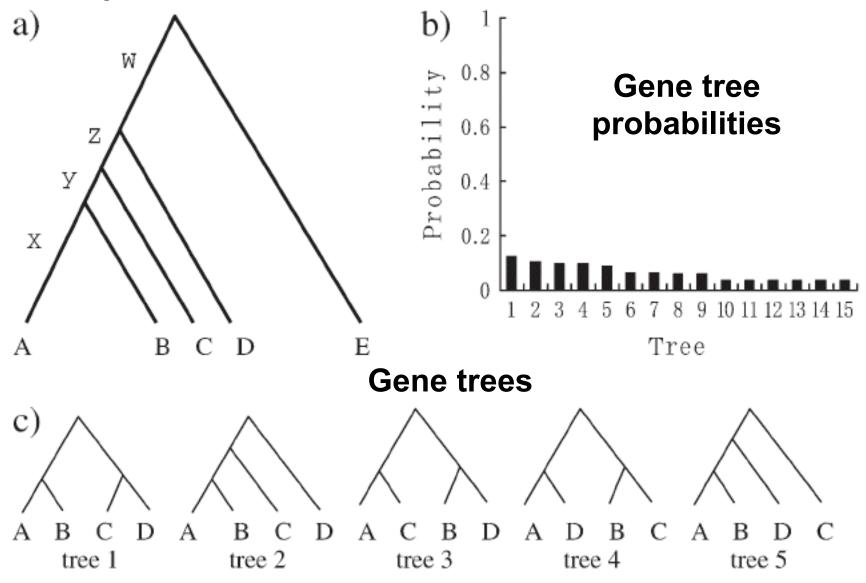
#### Pipeline for STAR/STEAC trees in phybase n species, l loci for each replicate **Phybase** Multilocus bootstrap (b replicates) phyml Make gene trees for all b\*l single gene matrices b replicates Make matrix **Phybase** of gene trees n gene trees Phybase or

other program

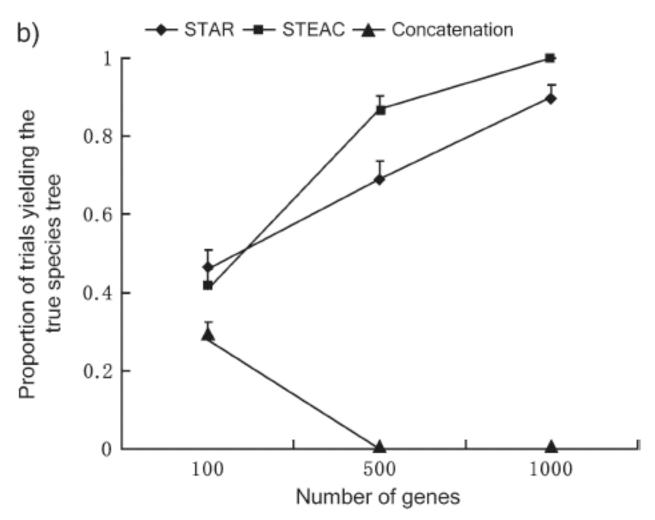
**Consensus STAR tree** 

### The anomaly zone

#### **Species tree**

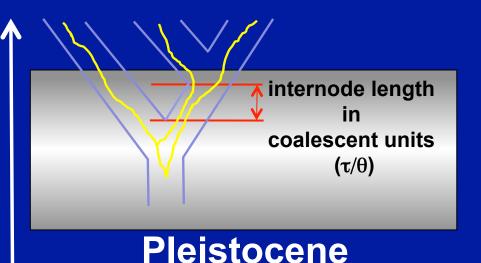


# Phylogenetic analysis in the anomaly zone



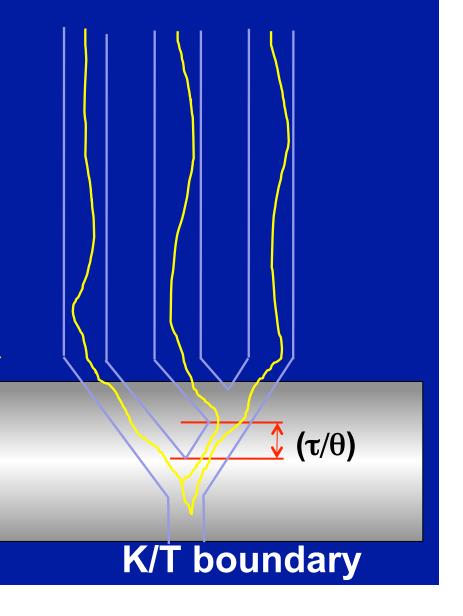
Liu, L., et al. 2009. Syst Biol 58:468-477.

# The multispecies coalescent applies to <u>ancient</u> as well as <u>recent</u> divergences



Probability of inconguence is the same in both cases!! Think: "short", not "recent"

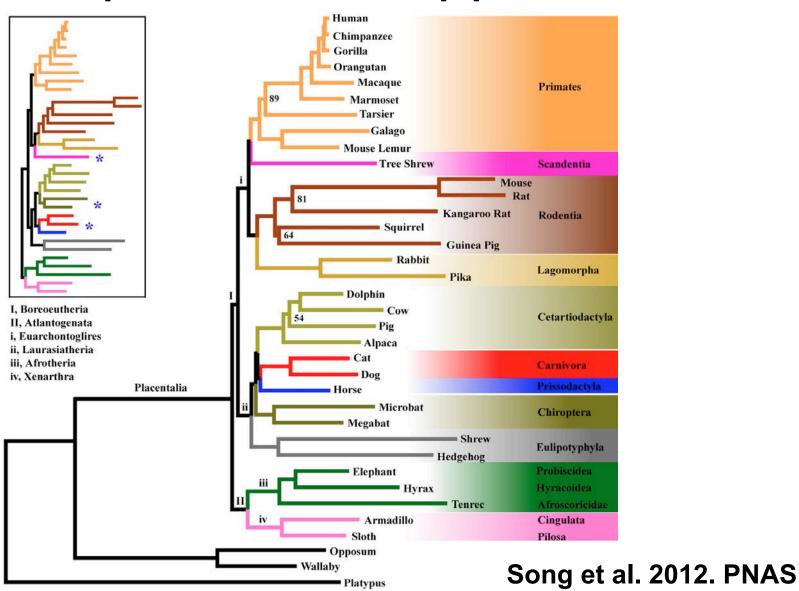
Absolute time in the past



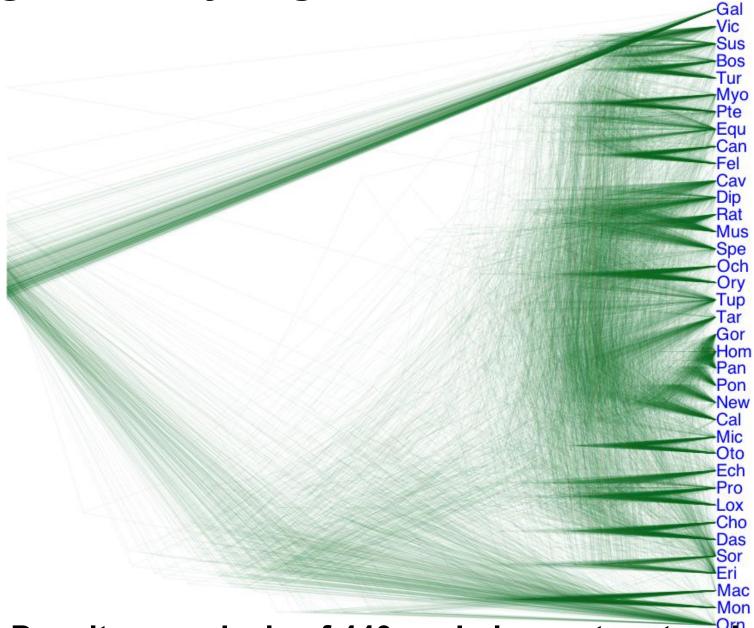
#### Mammal data set

- 37 ingroup taxa (placental mammals)
- 758 genes from Orthomam database
- 447 genes passed filtering
- Total ~1.38 Mb per species, avg. ~3.1 kb/gene
- Gene trees made via RaxML and best-fit substitution model
- MP-EST and STAR method
- ML and Bayesian supermatrix analysis

# Conflict between concatenation and species tree approaches

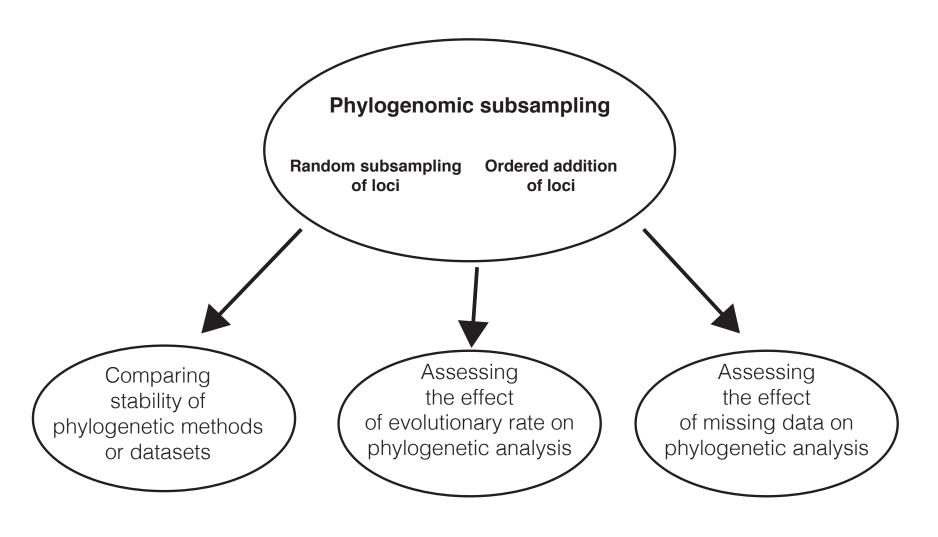


Large diversity of gene trees in mammal data set



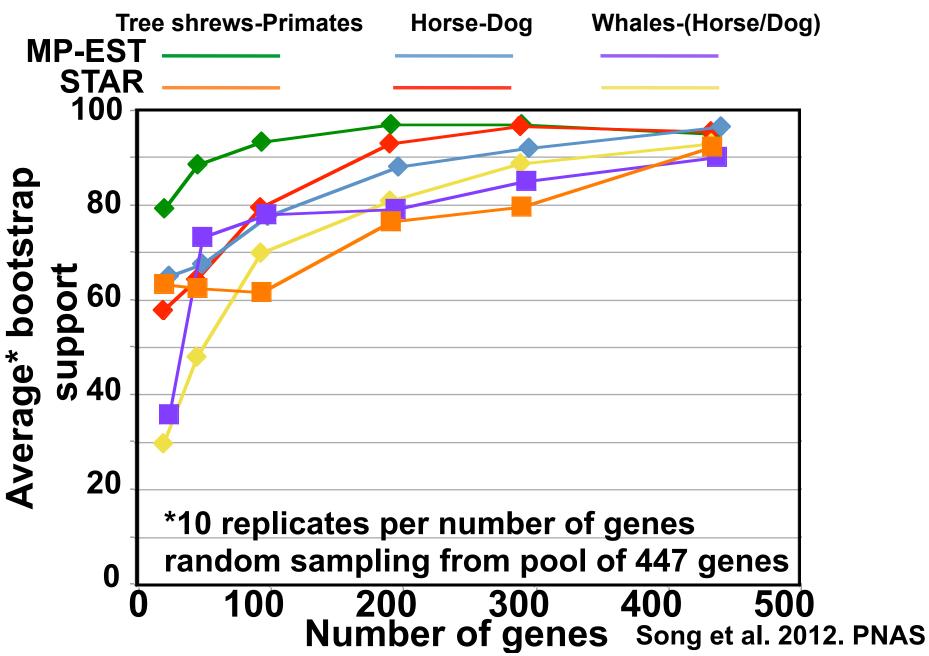
Densitree analysis of 440 scaled gene tree topologies

### Phylogenomic subsampling

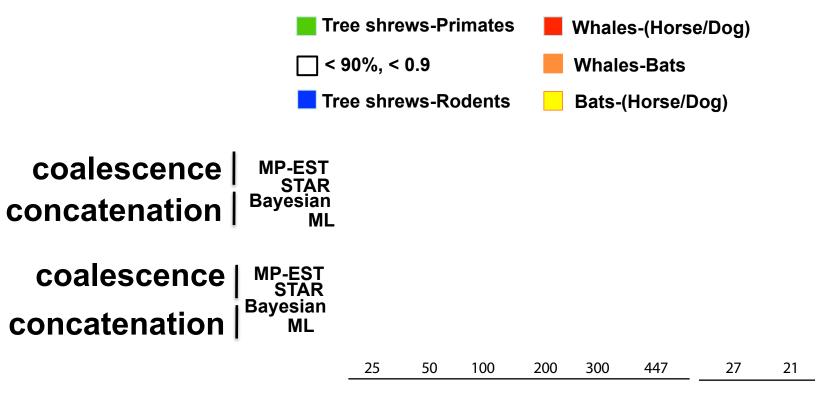


Edwards 2016 Zoologica Scripta

### More genes = more support



# Concatenation: more genes = strong but conflicting support for clades



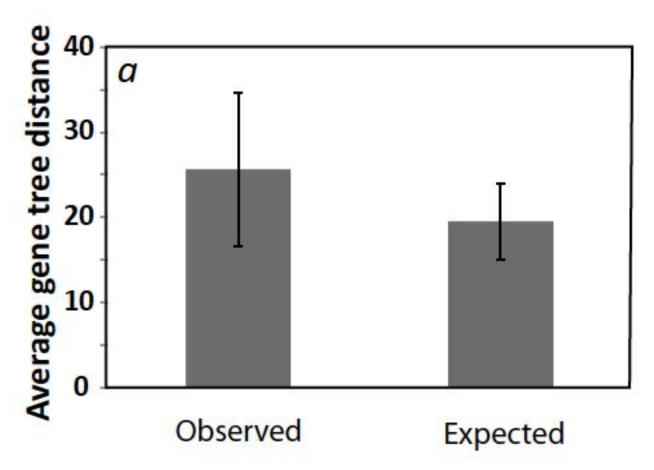
Number of genes Nu

Number of taxa

10 replicates (gene sets) per box, random sampling from pool of 447 genes

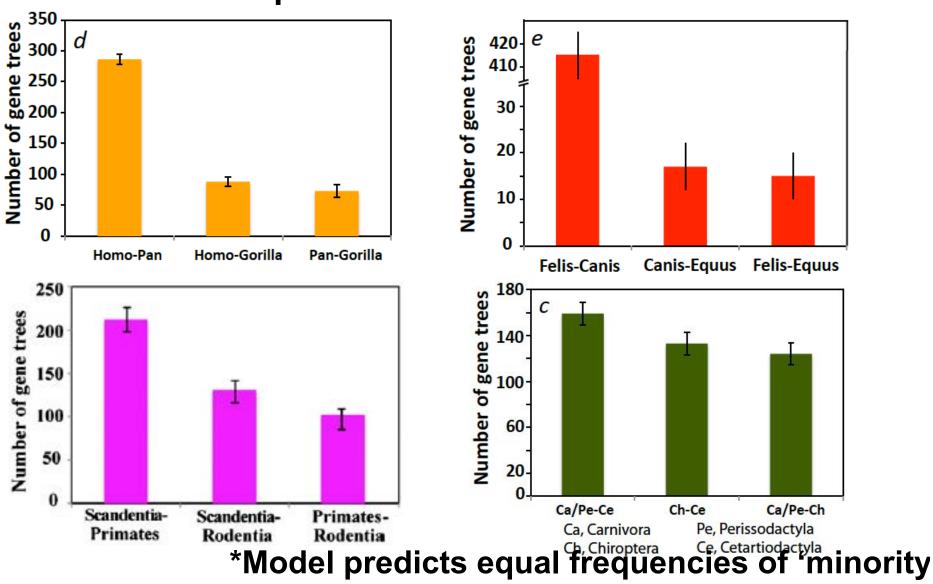
Song et al. 2012. PNAS

# Multispecies coalescent model explains ~77% of gene tree variation



Song et al. 2012. PNAS

# Gene tree distributions consistent with multispecies coalescent model\*



gang trace

## Misconceptions about "species tree" methods

 Species tree methods require discordance among gene trees \_ FALSE

- Species tree methods don't acknowledge gene tree estimation error – FALSE
- Species tree methods attribute all gene tree heterogeneity to incomplete lineage sorting
  - TRUE and FALSE