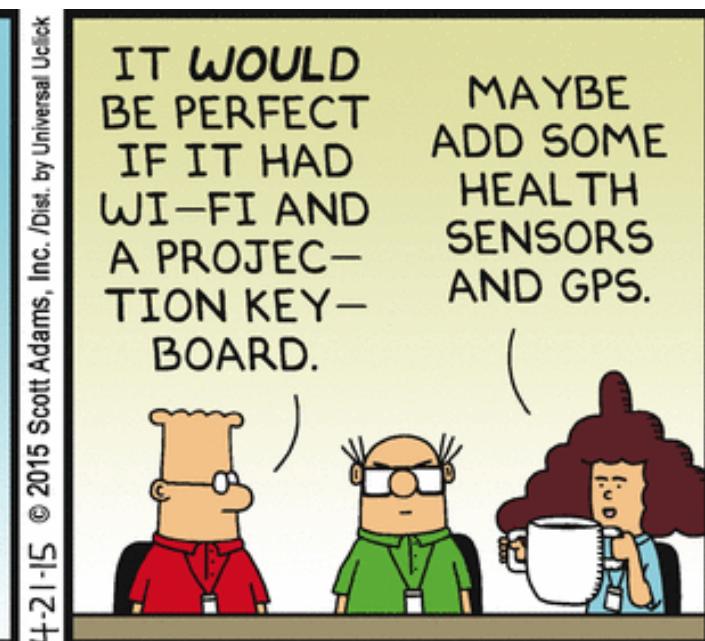
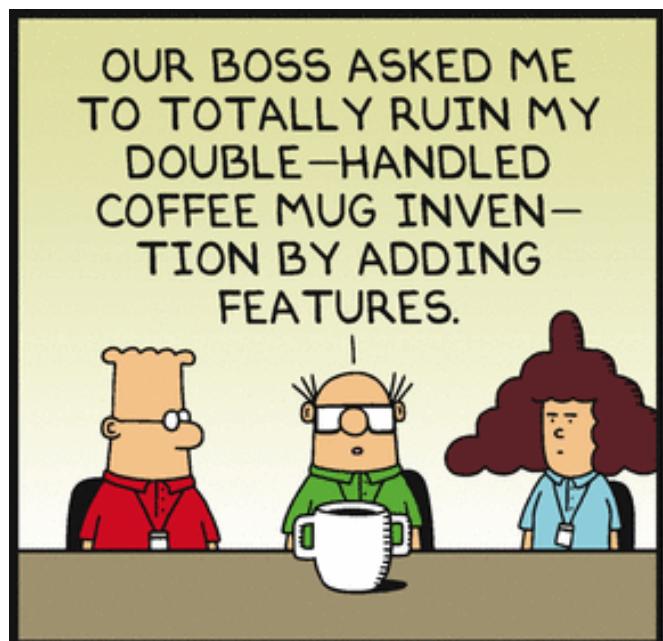
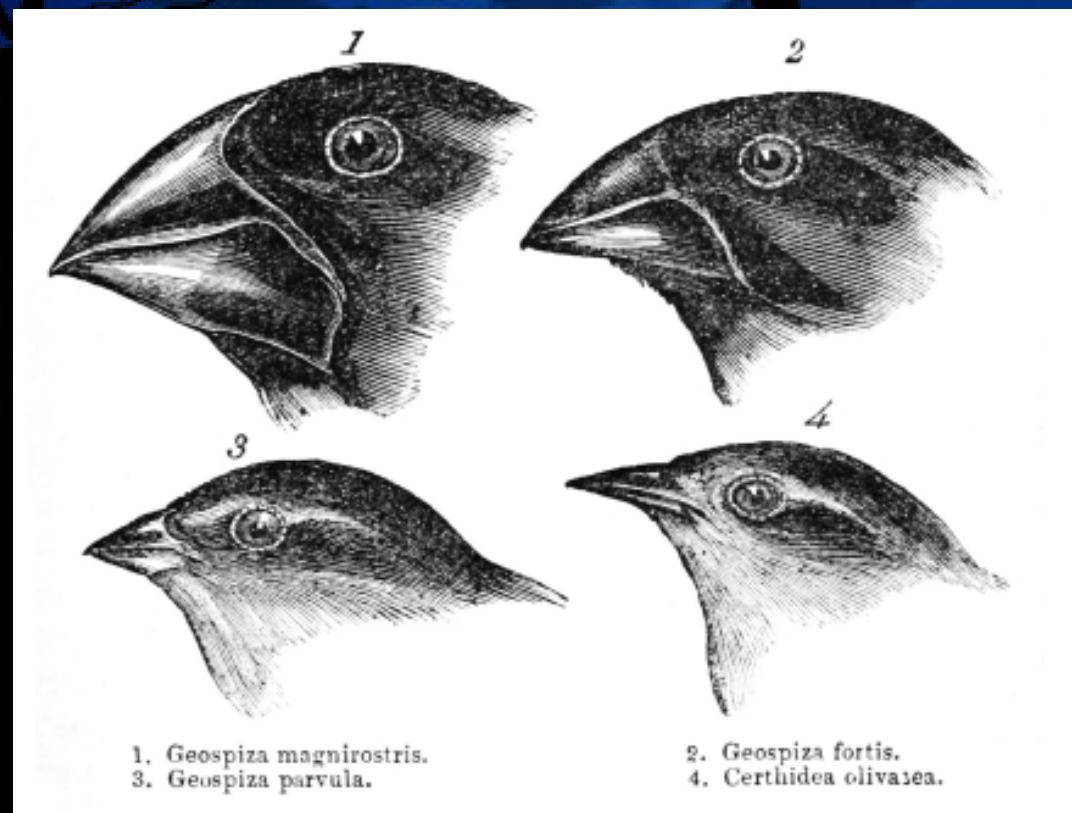
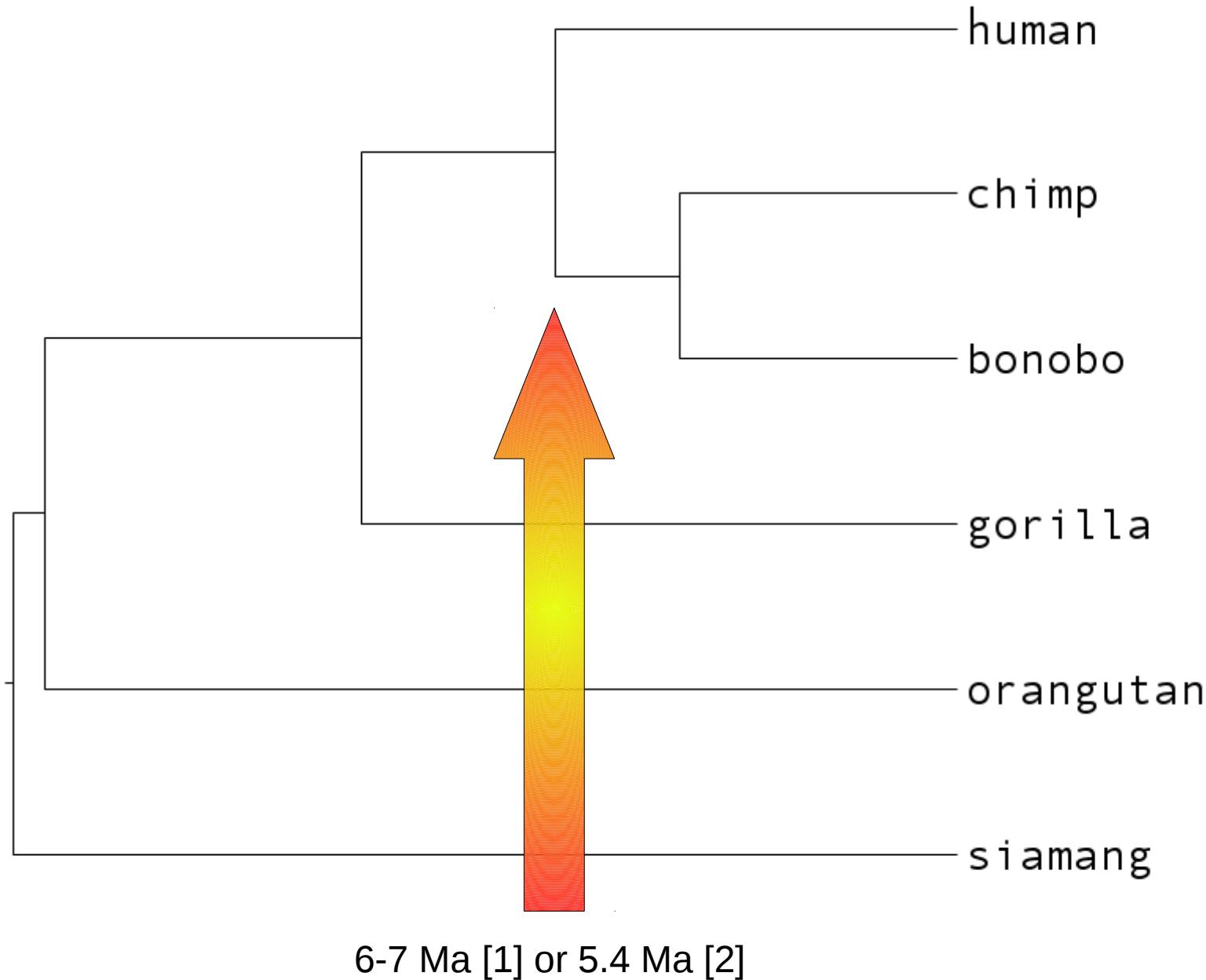


# Should protractedness be included in speciation models?

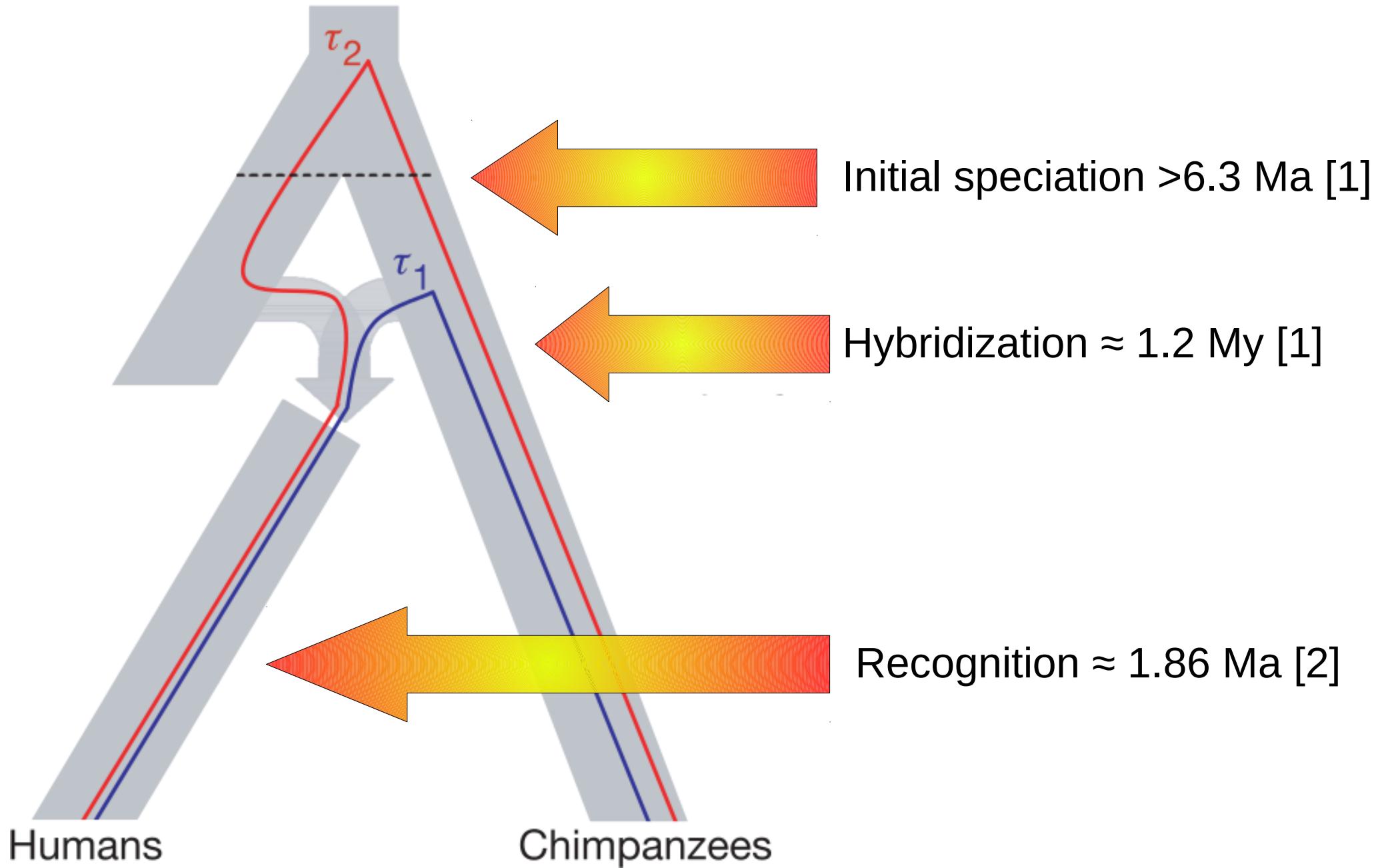
Richel Bilderbeek







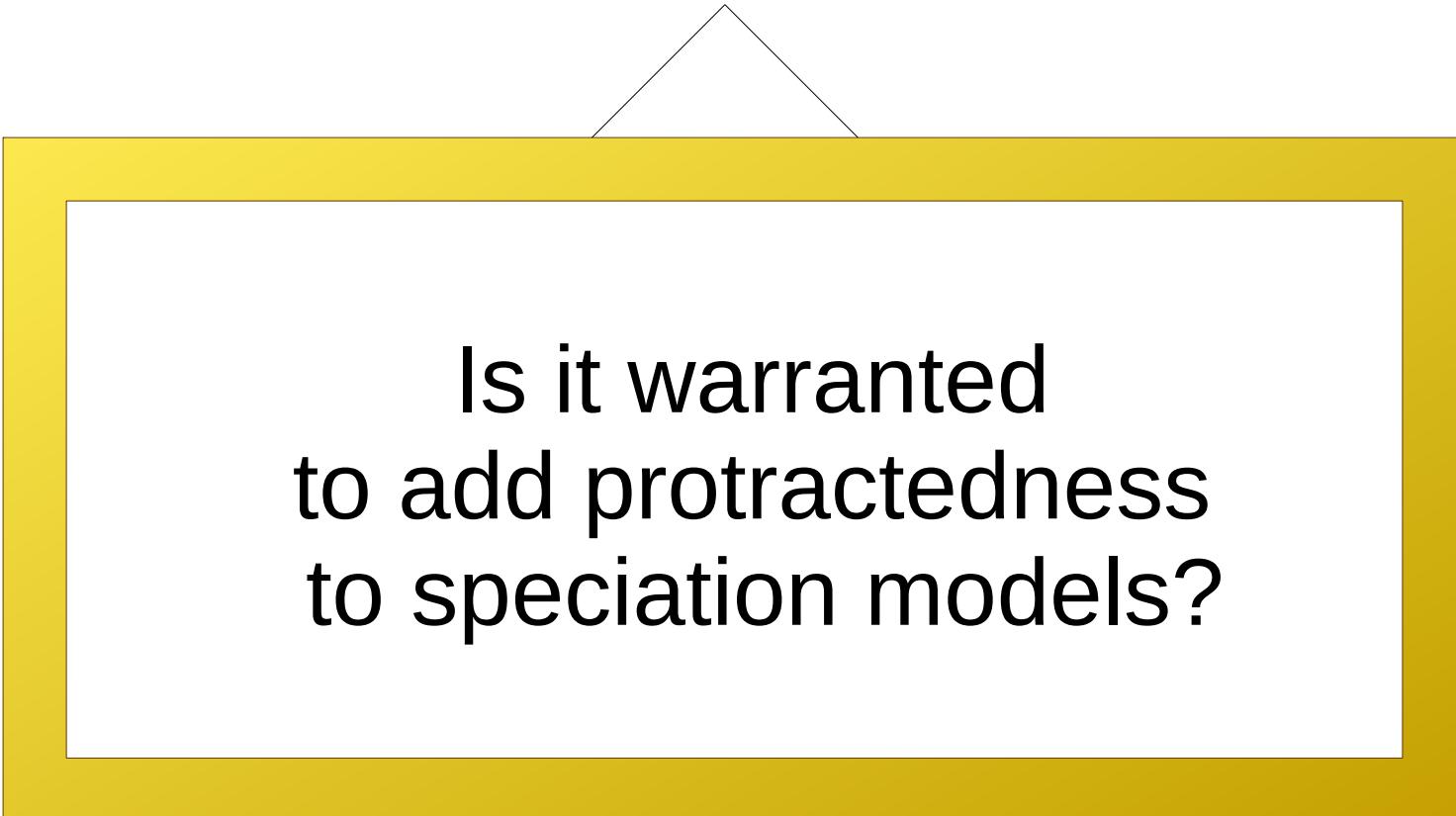
- [1] Brunet et al. A new hominid from the Upper Miocene of Chad, Central Afrika. 2002. Nature
- [2] Patterson et al. Genetic evidence for complex speciation of humans and chimpanzees. 2006. Nature



[1] Patterson et al. Genetic evidence for complex speciation of humans and chimpanzees. 2006. *Nature*

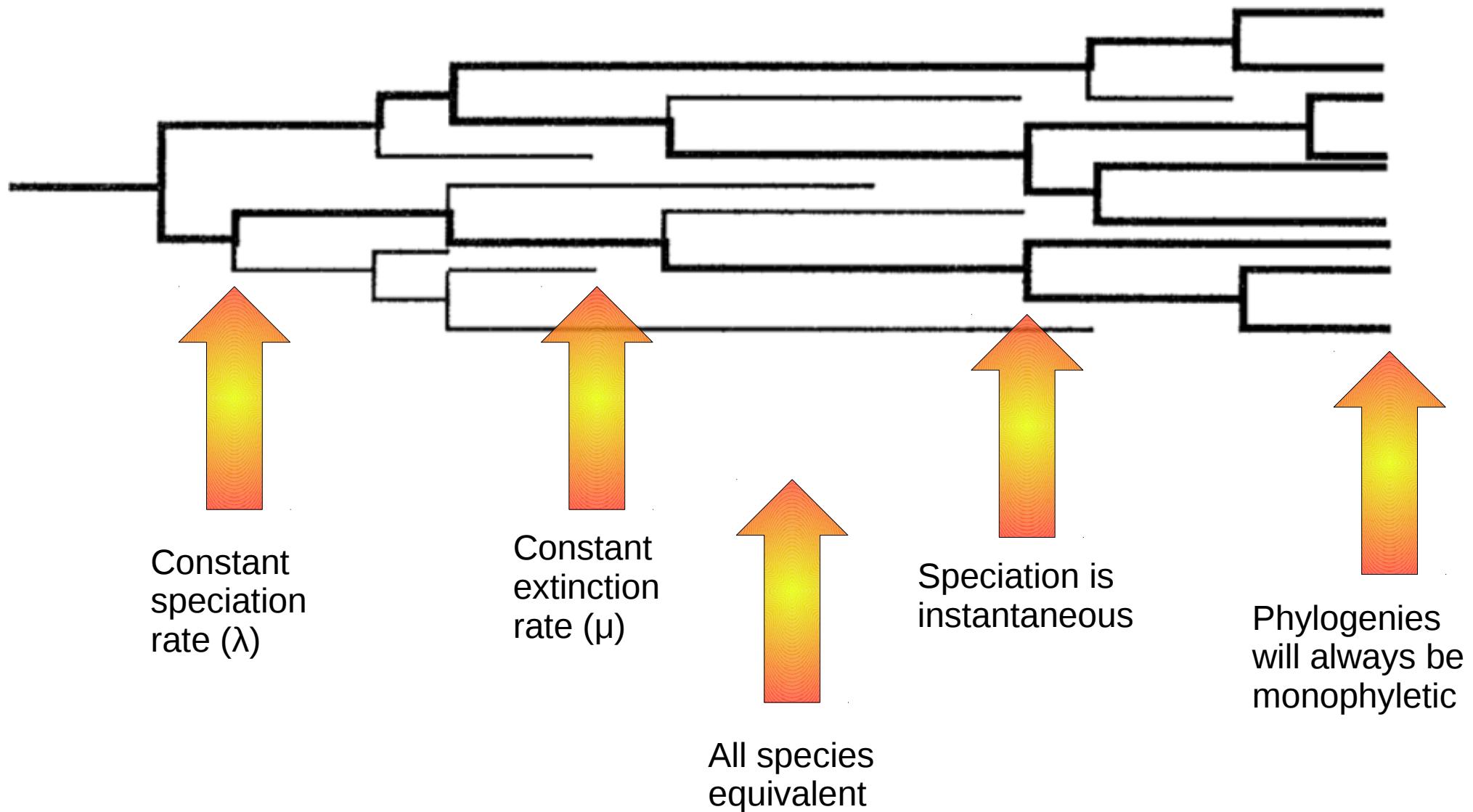
[2] Leakey et al. New fossils from Koobi Fora in northern Kenya confirm taxonomic diversity in early Homo. 2012. *Nature*

# Research question

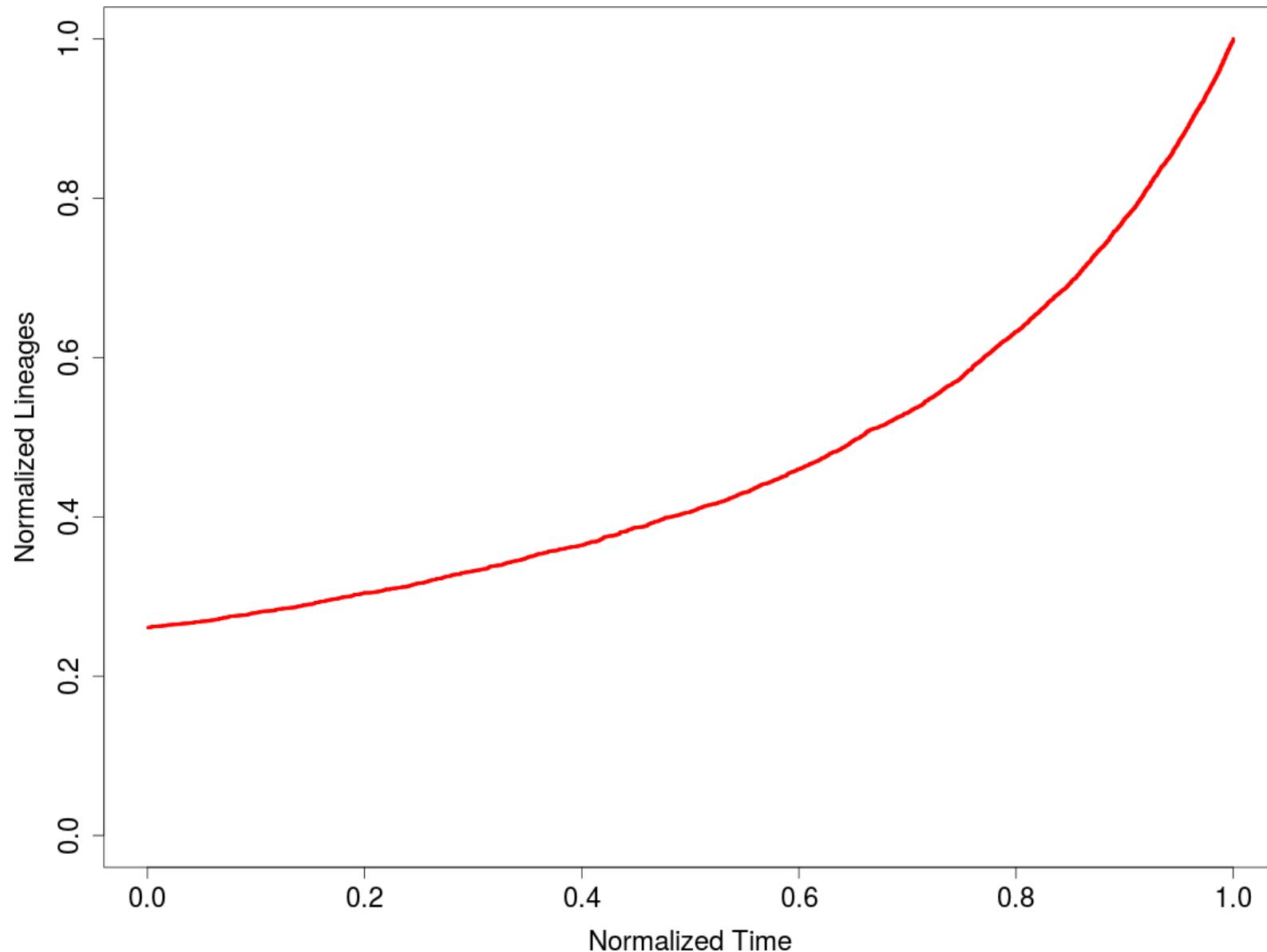


Is it warranted  
to add protractedness  
to speciation models?

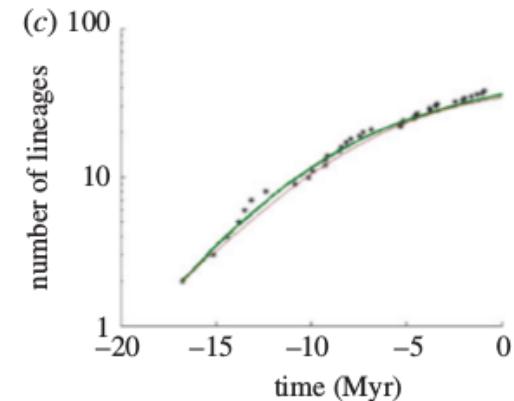
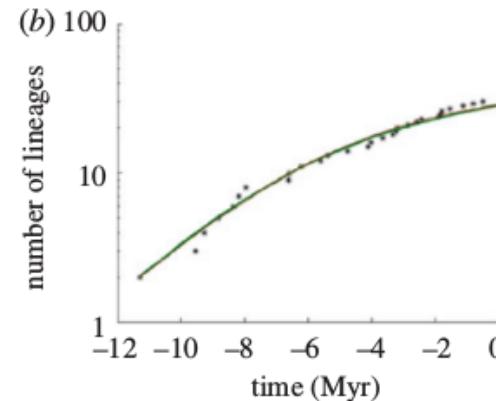
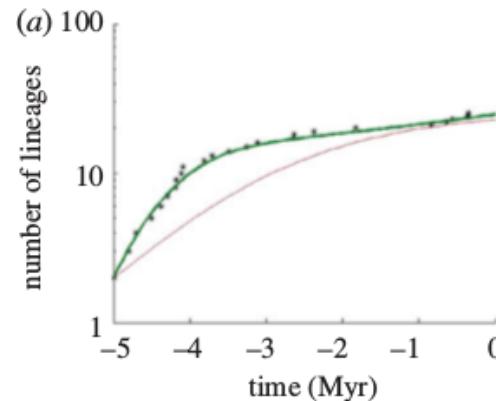
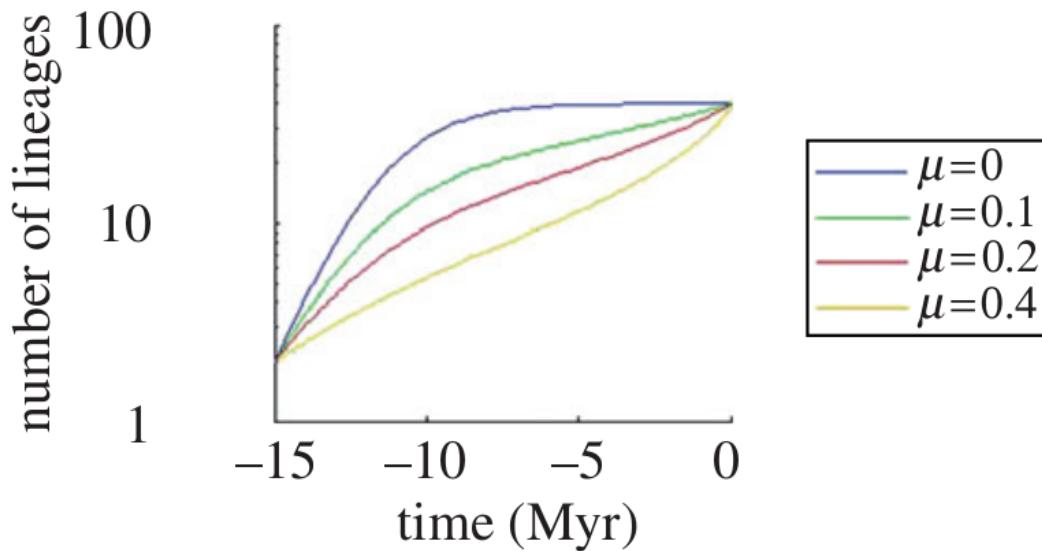
# Birth-death (BD) model



# Problem with BD model: exponential increase

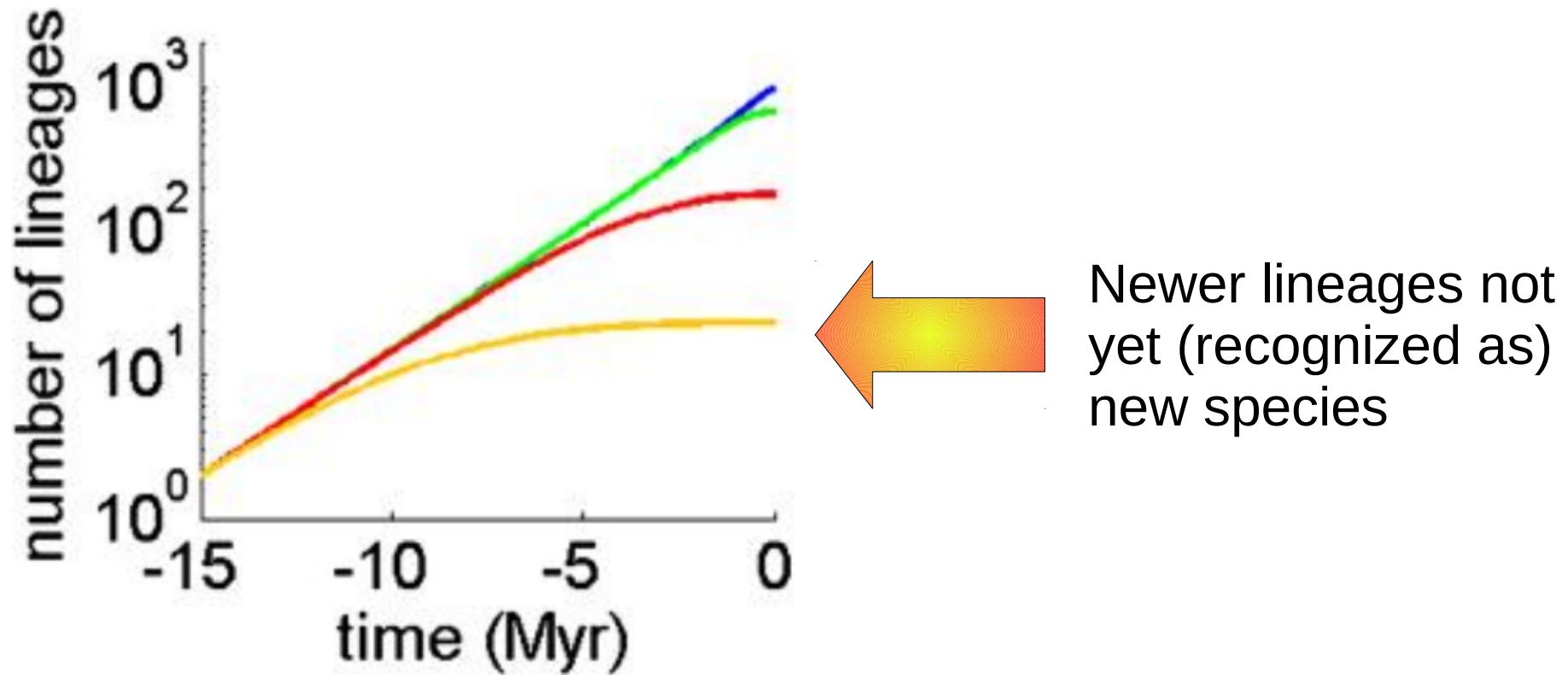


# Solutions

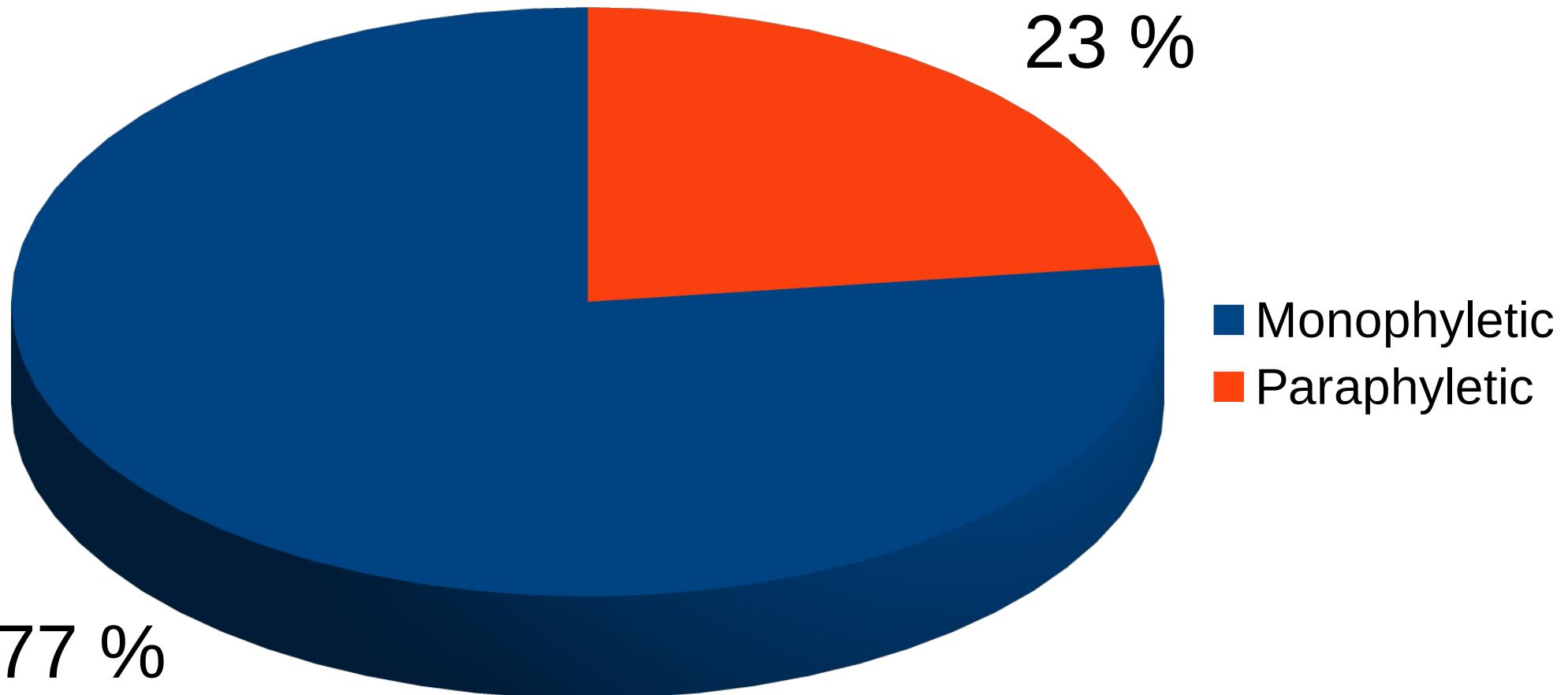


Etienne et al. Diversity-dependence brings molecular phylogenies closer to agreement with the fossil record. Proc. R. Soc. B. 2011

# Solutions



# Problems with BD model

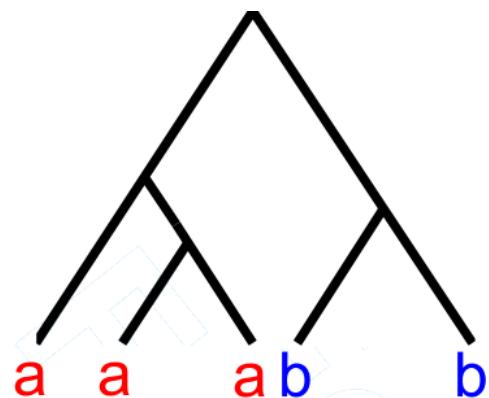


N = 2319 studies

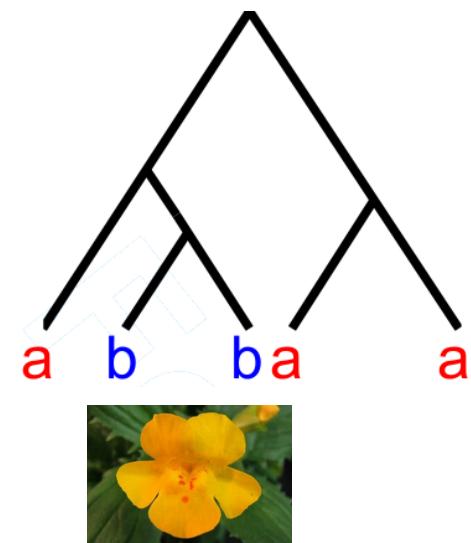
# Phyly

- Monophyly: a taxon of an ancestral species with its descendants (only)

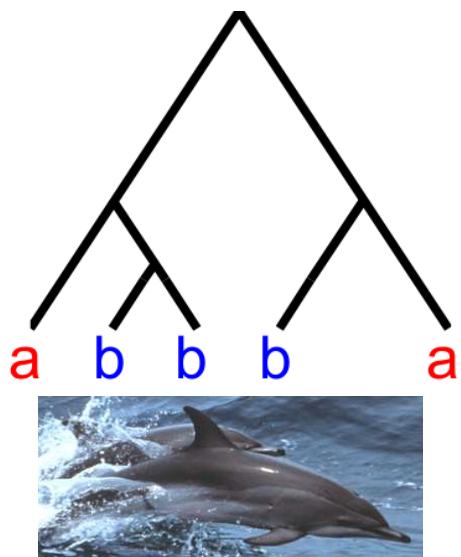
monophyly



paraphyly



polyphyly



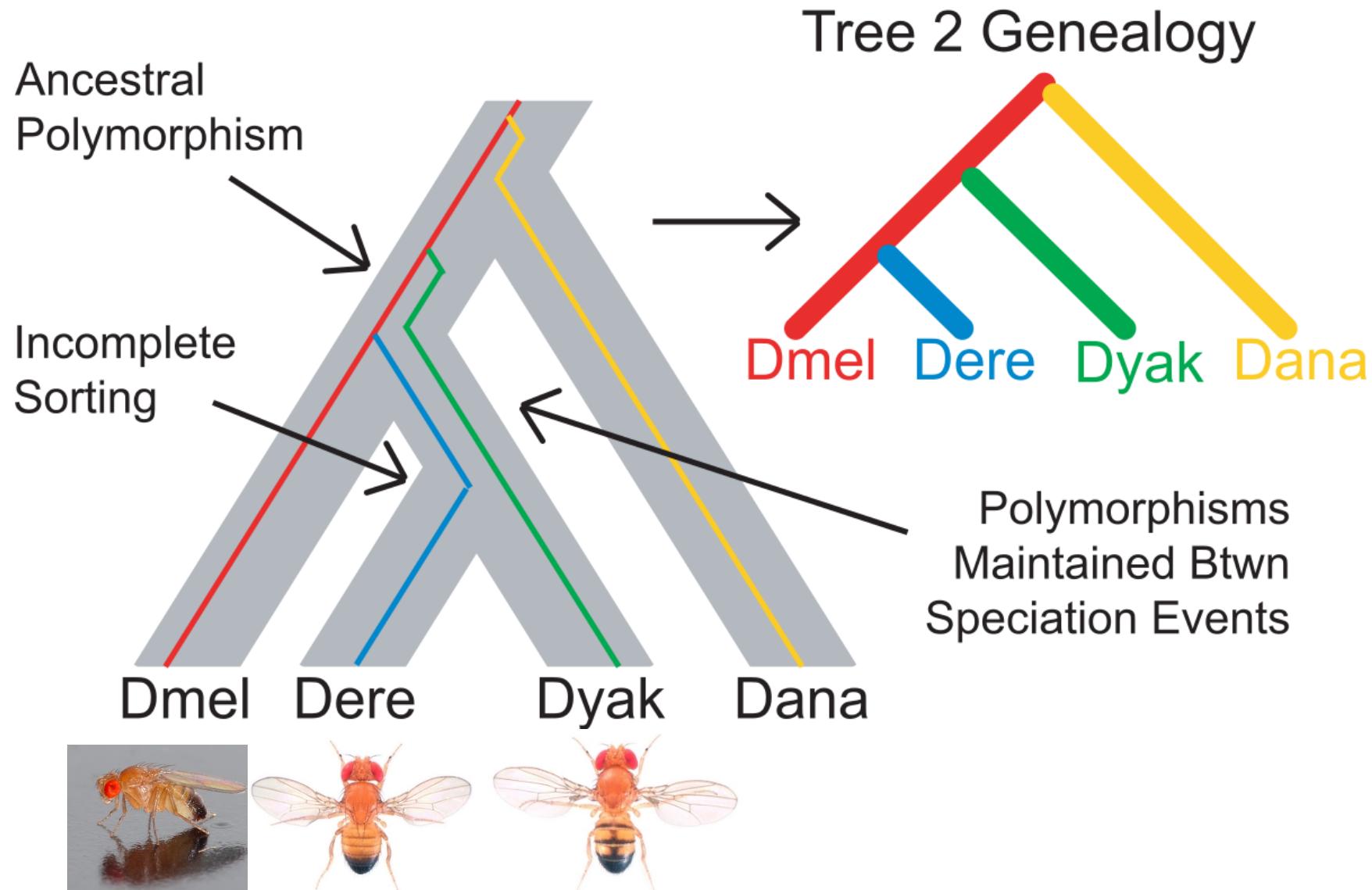
*Mimulus peregrinus*

*Stenella clymene*

Vallejo-Marín et al. Speciation by genome duplication. *Evolution*. 2015.

Amaral et al. Hybrid speciation in a marine mammal. *PloS one*. 2014

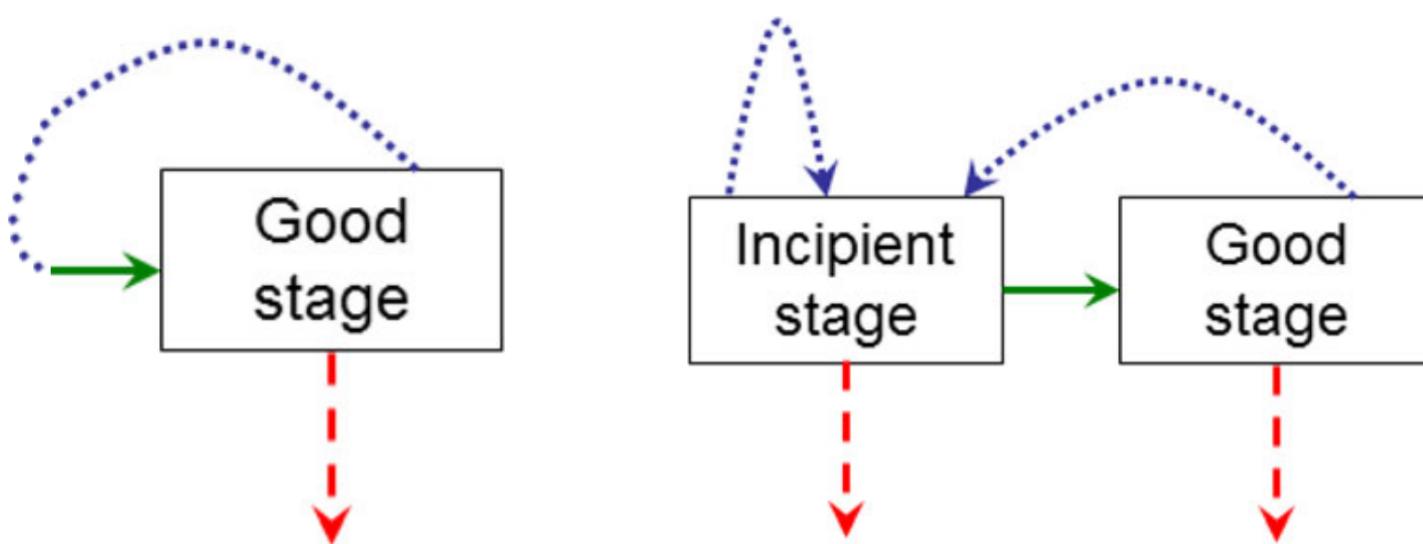
# Incomplete lineage sorting



Pollard et al. Widespread discordance of gene trees with species tree in *Drosophila*: evidence for incomplete lineage sorting. PLoS Genet

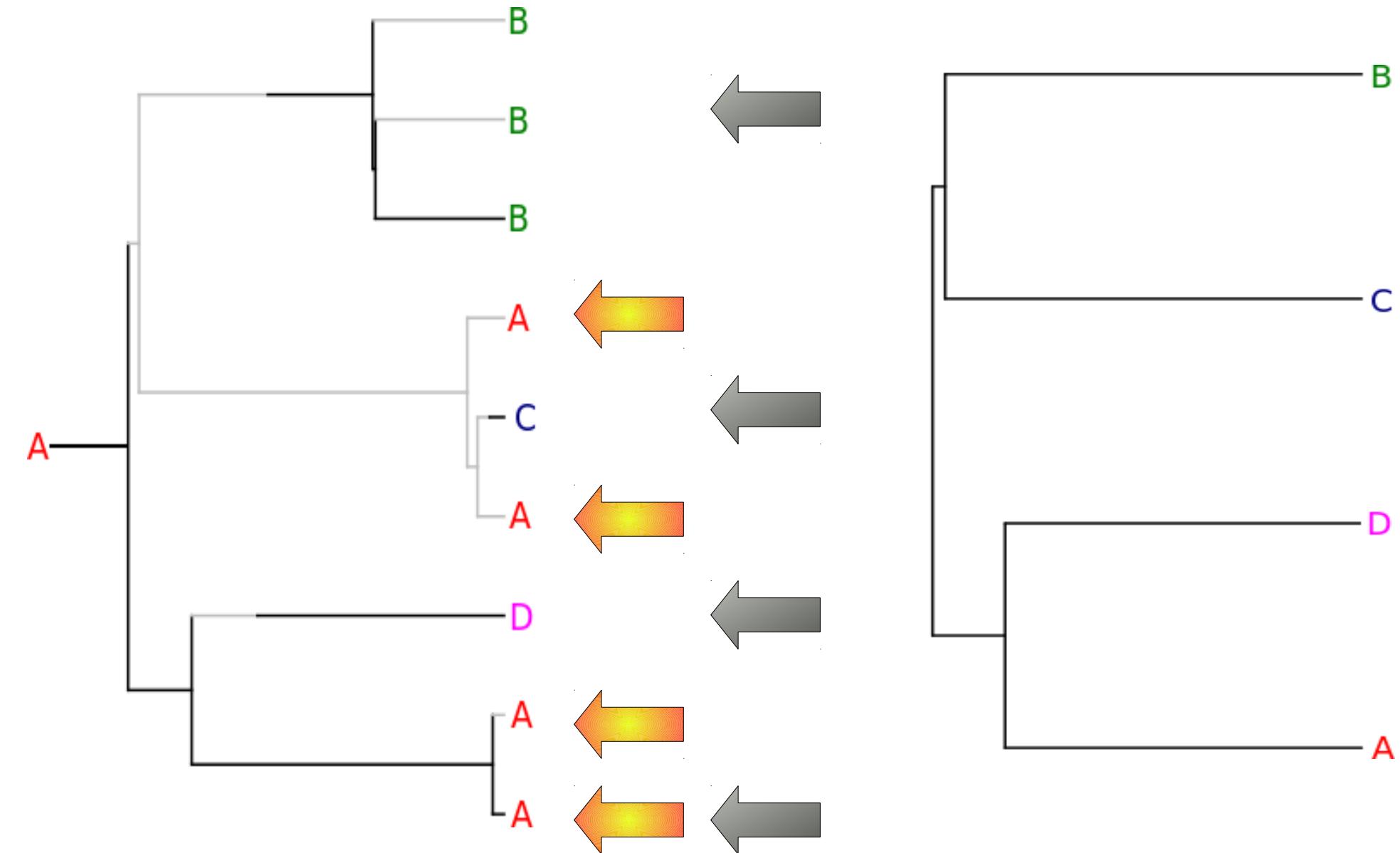
# Protracted speciation

- Speciation takes time



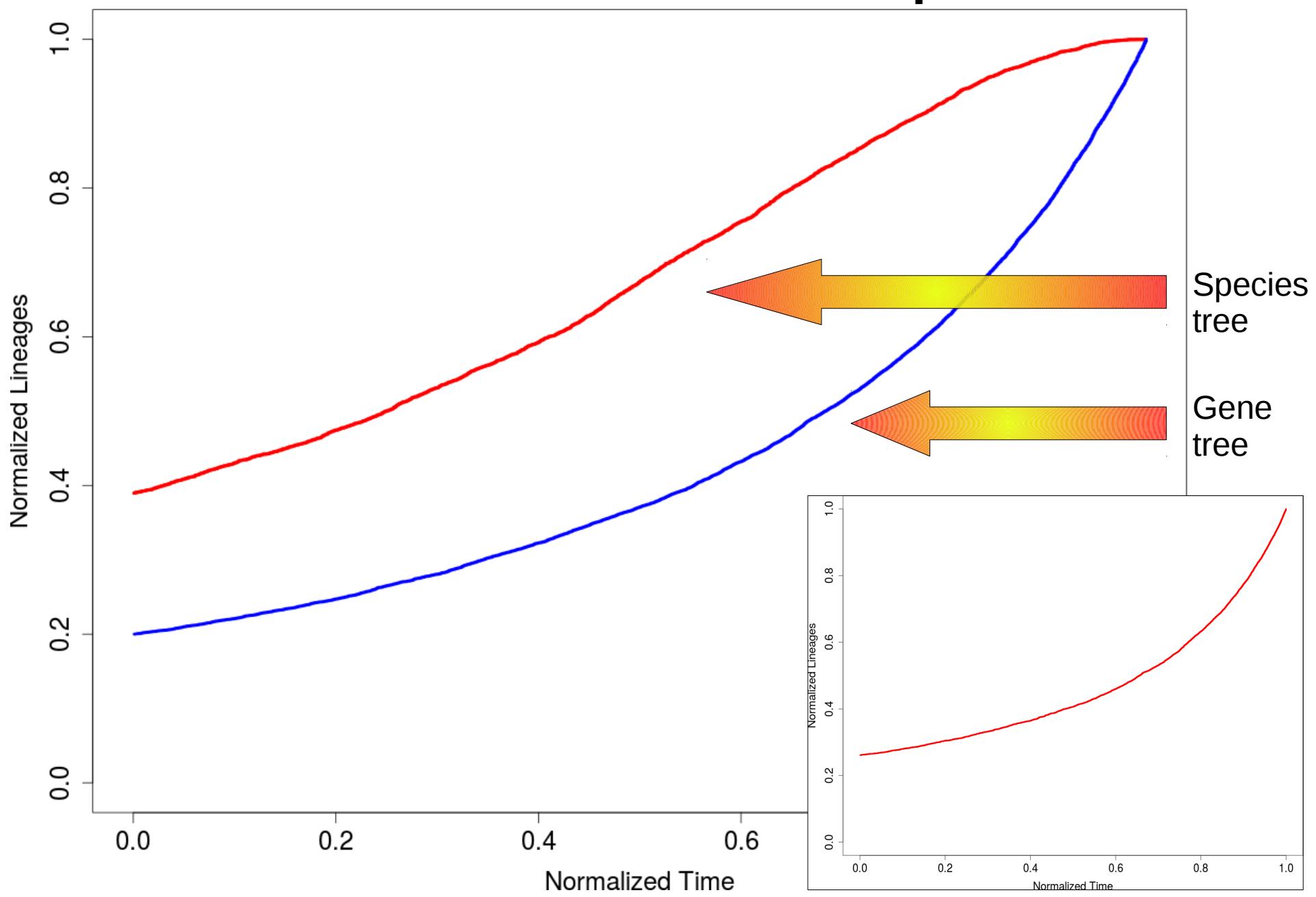
BD	PBD
Speciation rate	Speciation initiation rate
Extinction rate	Speciation completion rate Extinction rate

# Protracted speciation trees

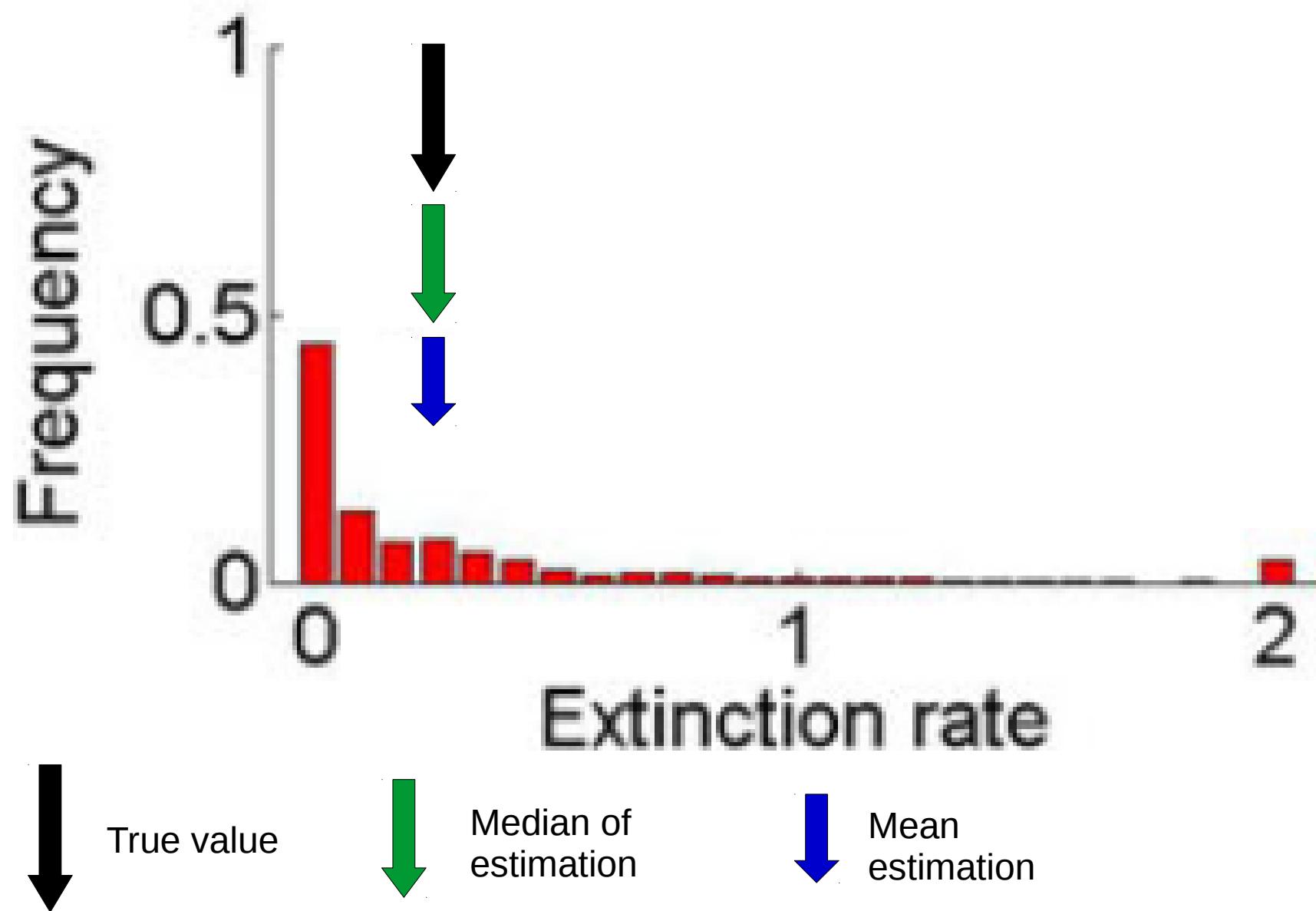


R package 'PBD', by Etienne

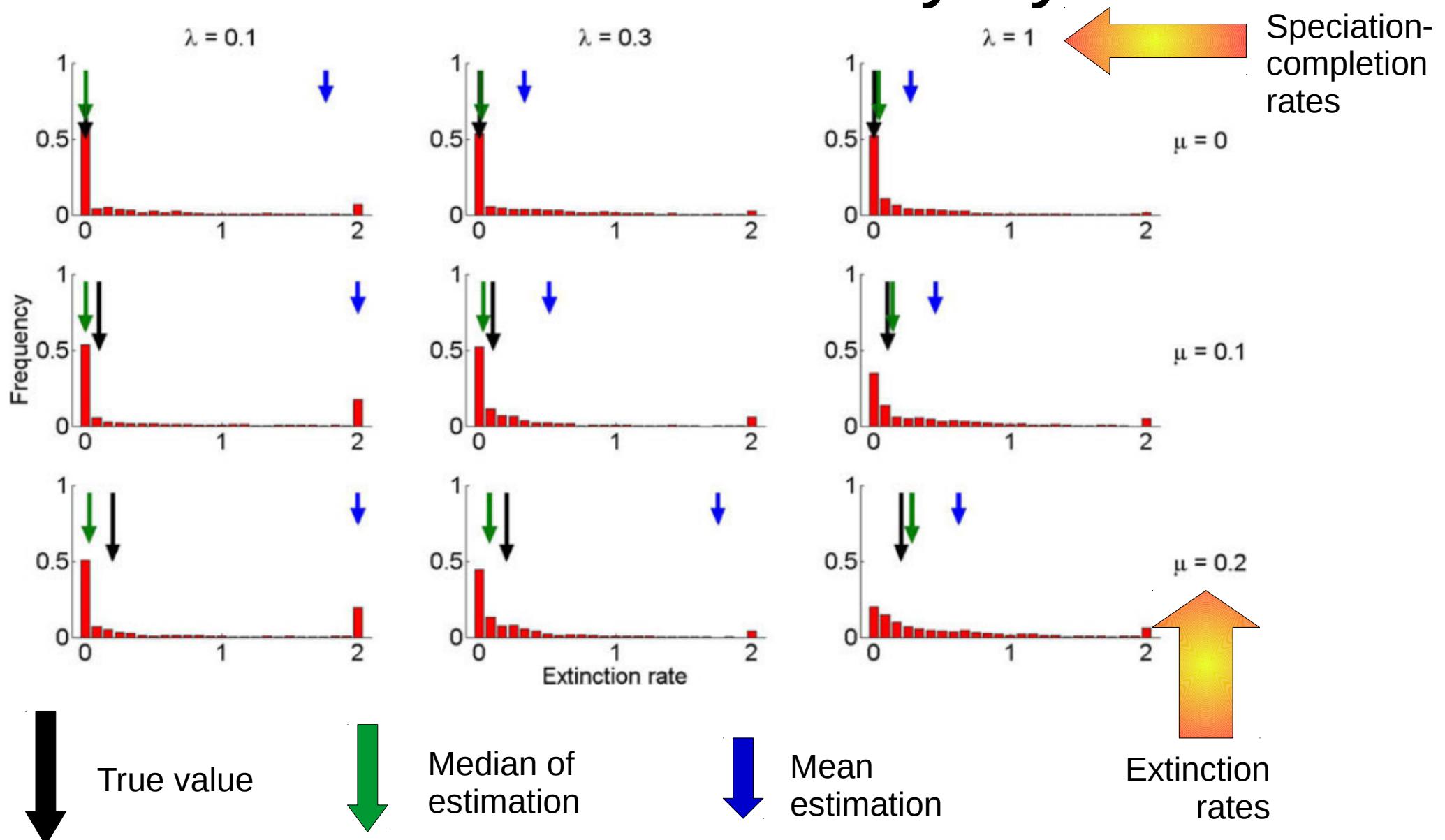
# Effect of PS on LTT plot



# Parameter recovery by ML

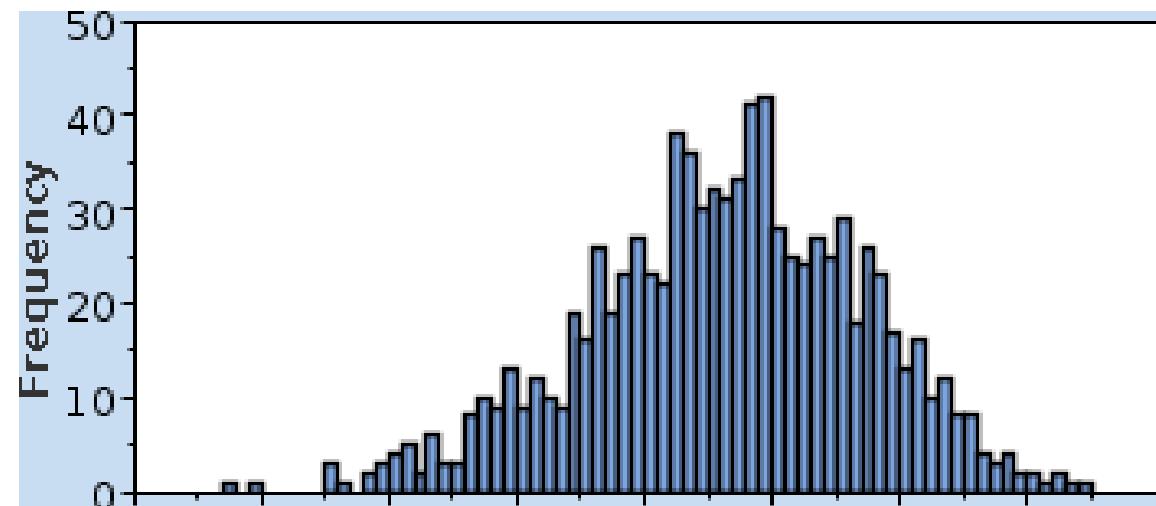
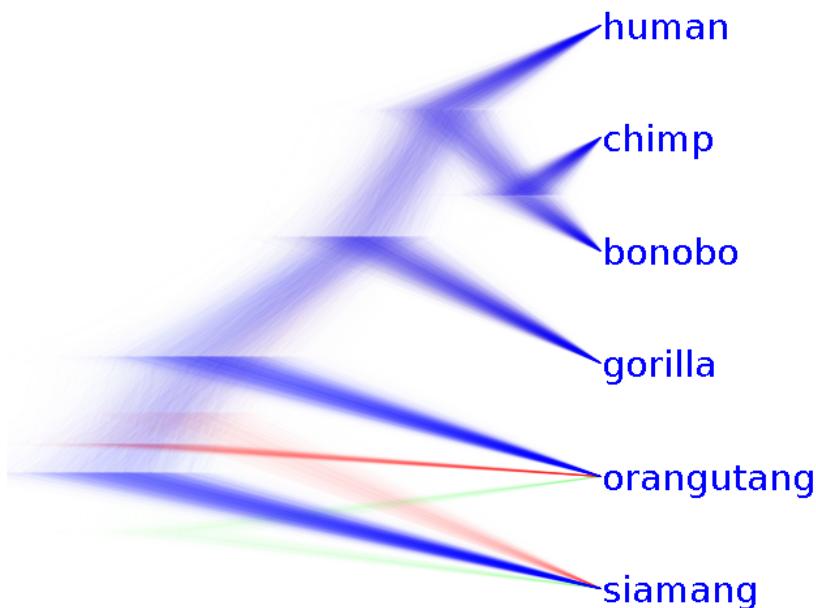


# Parameter recovery by ML



# Alternative

- Bayesian parameter estimation
- Phylogeny and parameters are jointly inferred



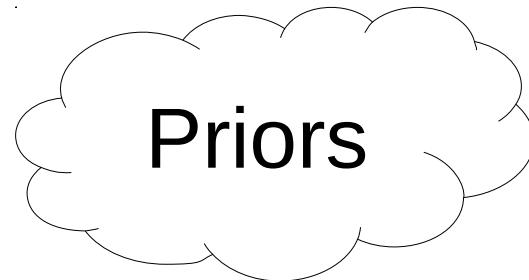
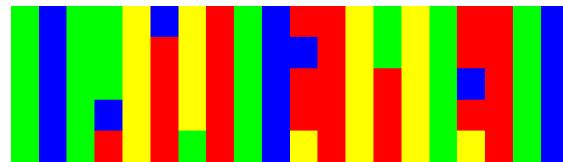
Höhna et al. Joint inference of phylogeny and diversification rates from molecular sequences does not outperform a 2-step approach. Unpublished

# BEAST 2

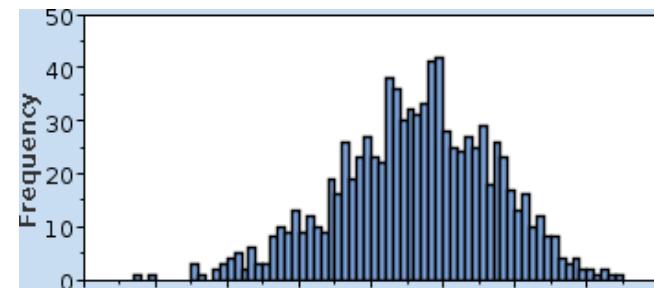
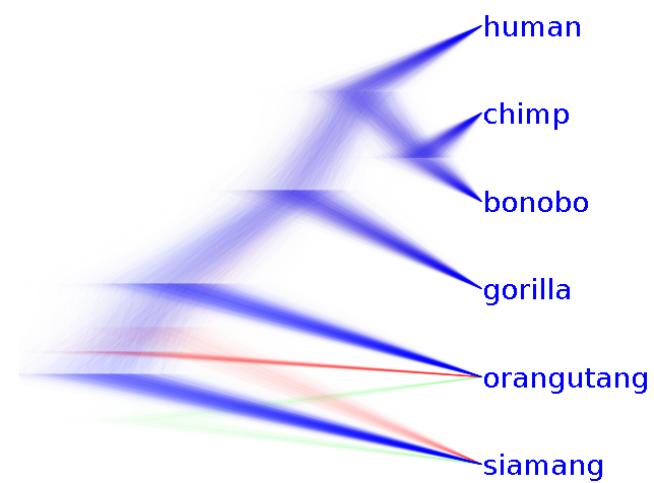
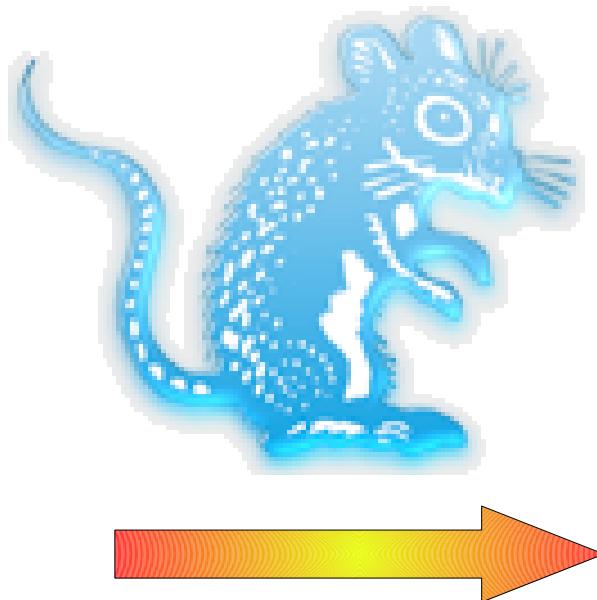
- Bayesian Evolutionary Analysis by Sampling Trees [1], heavily used [2]



One individual per species



Birth-Death prior

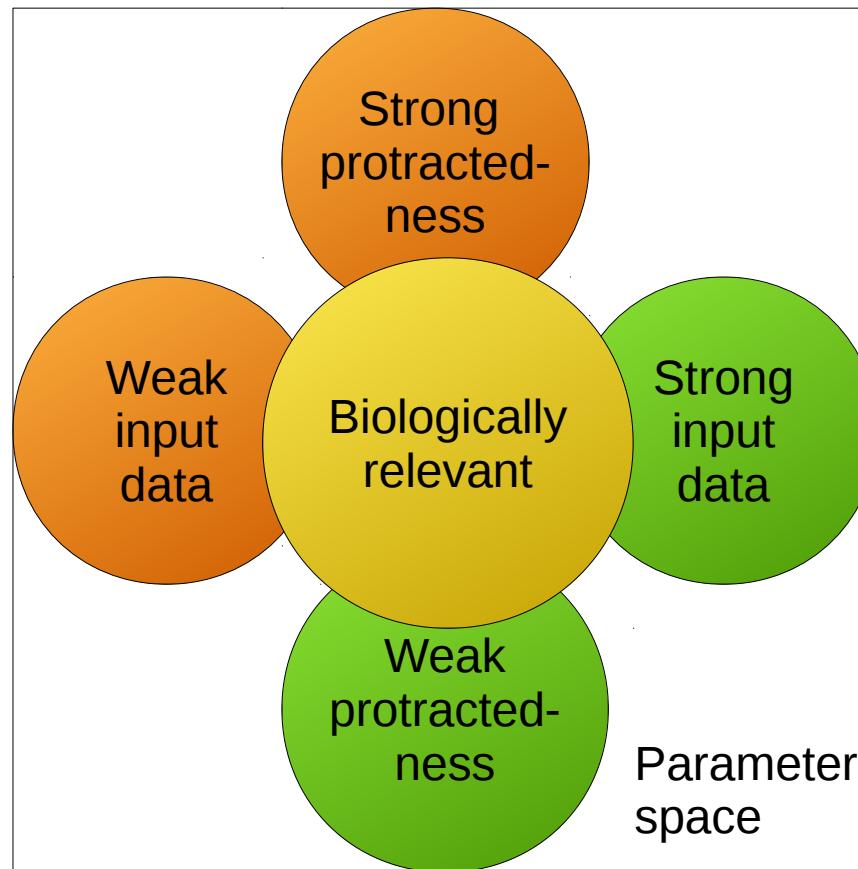


[1] Bouckaert, et al. BEAST 2: A Software Platform for Bayesian Evolutionary Analysis. 2014. PLoS

[2] BEAST 1: 5450 citations, BEAST 2: 126 citations (2015-11-19, [www.webofknowledge.com](http://www.webofknowledge.com))

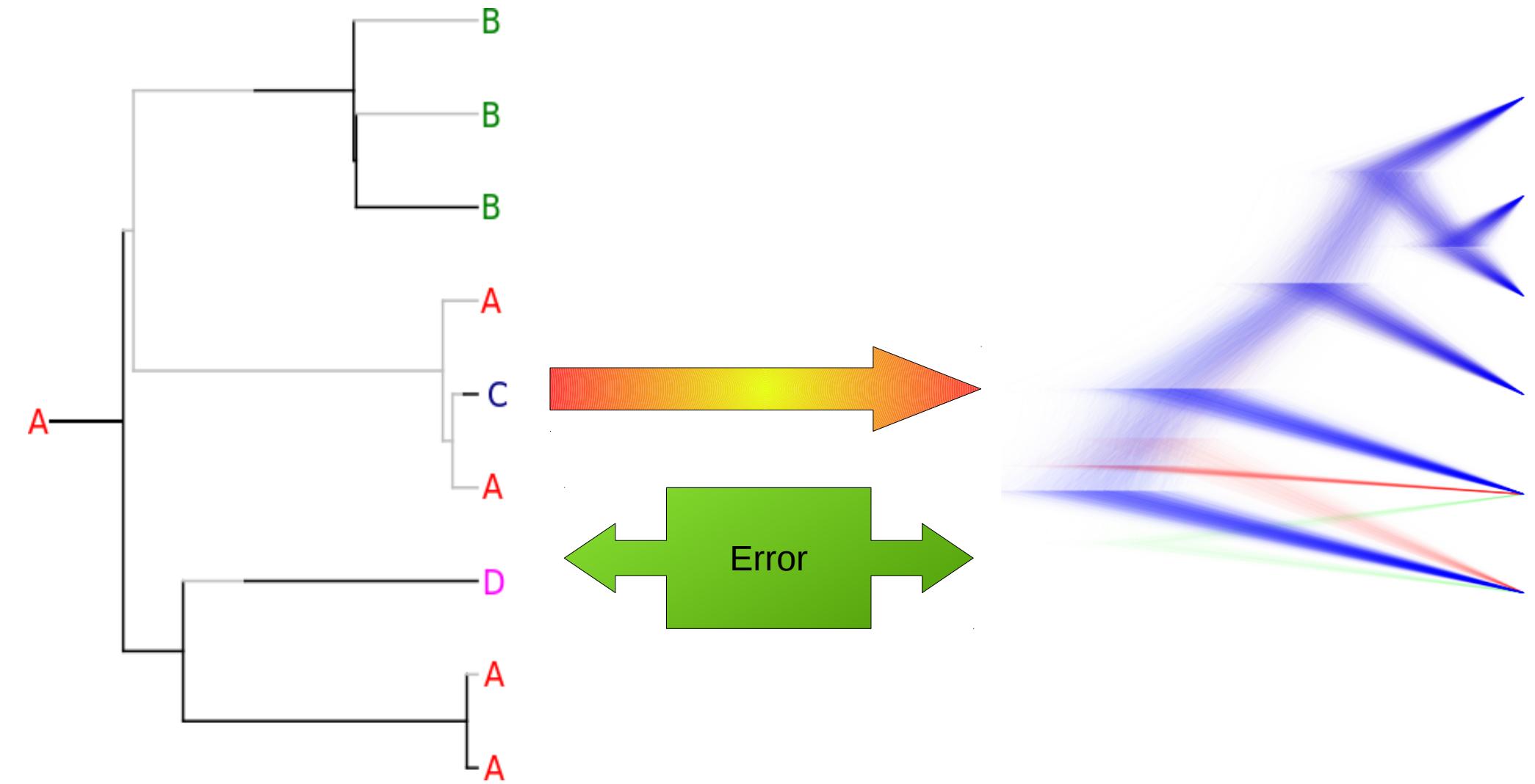
# This research question

- Under which conditions does BEAST2 suffice to recover a (simulated) protracted phylogeny using a BD tree prior?



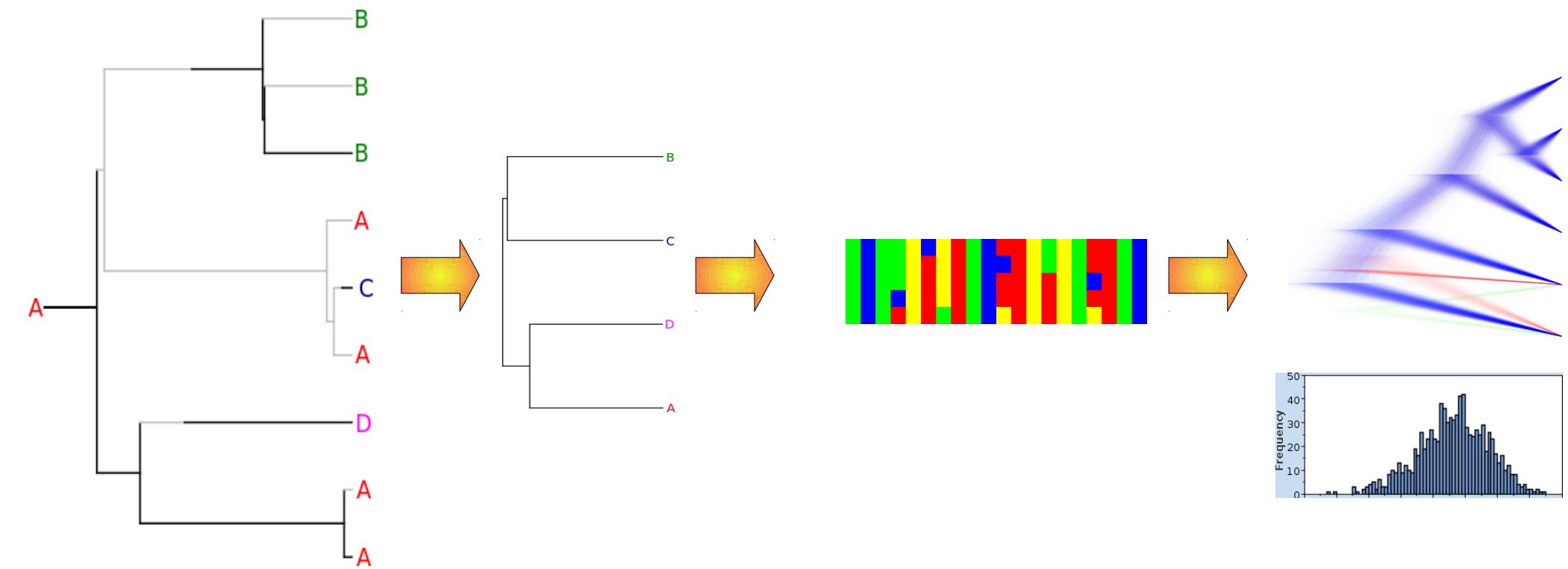
# Experiment

- Recover PBD phylogenies with BEAST2



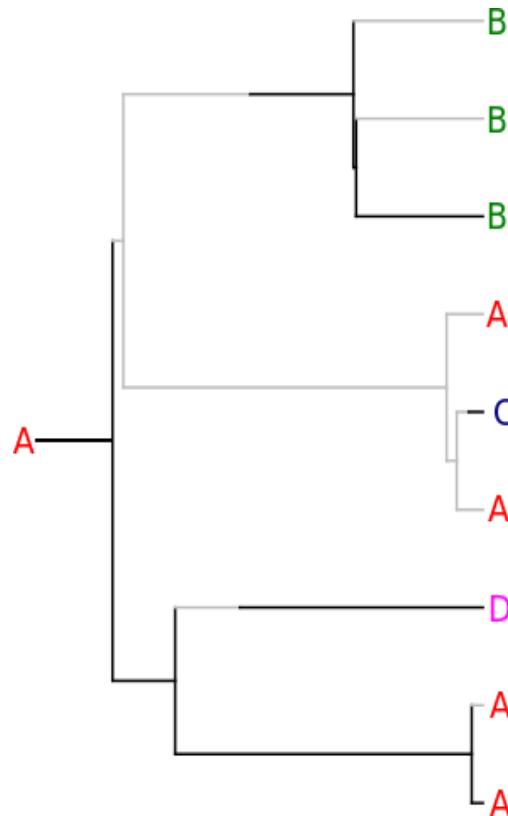
# Experiment

- Recover PBD phylogenies with BEAST2



# Step 1/5

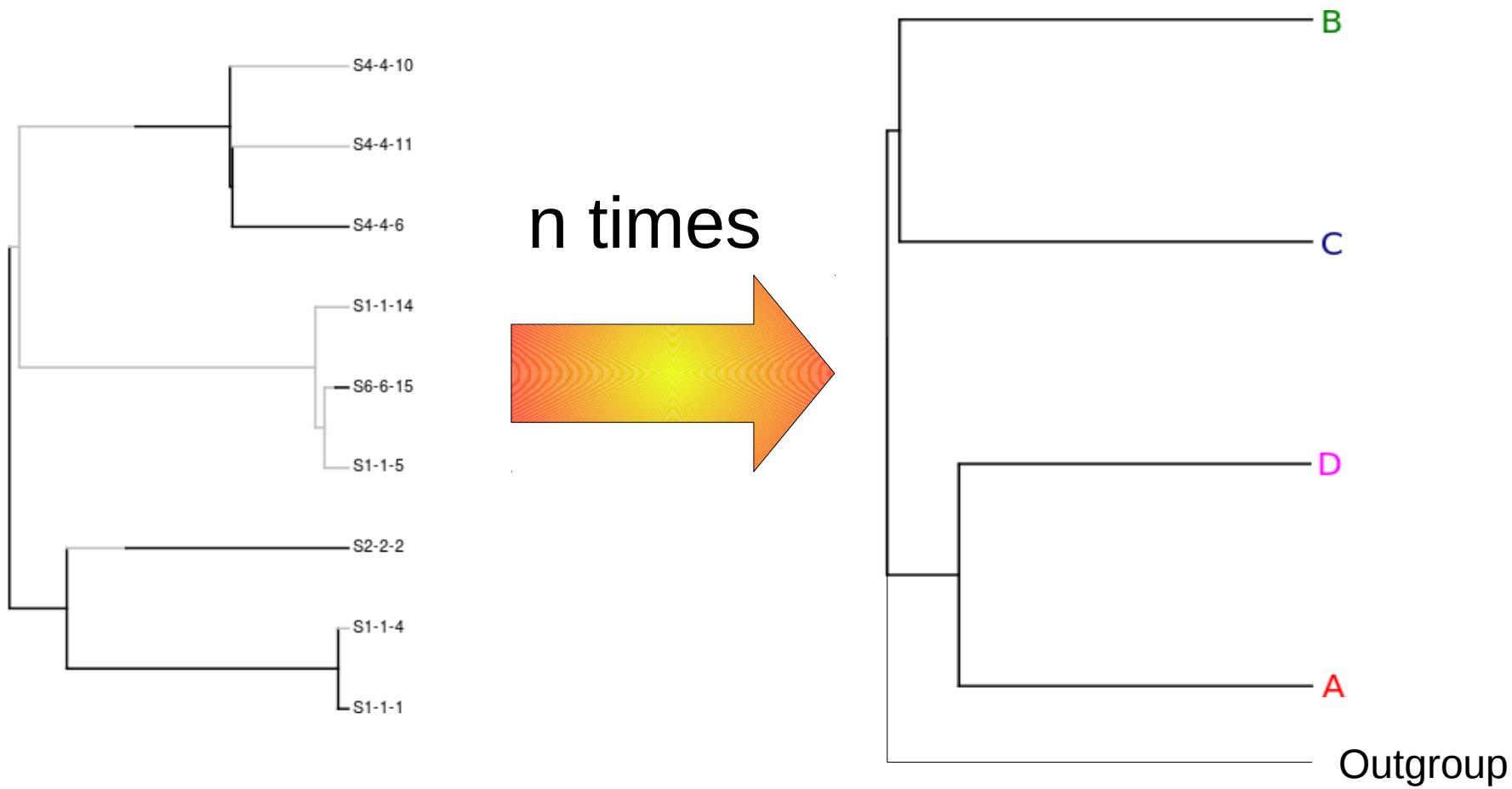
- Create a simulated 'true' protracted phylogeny (with possible paraphylies)



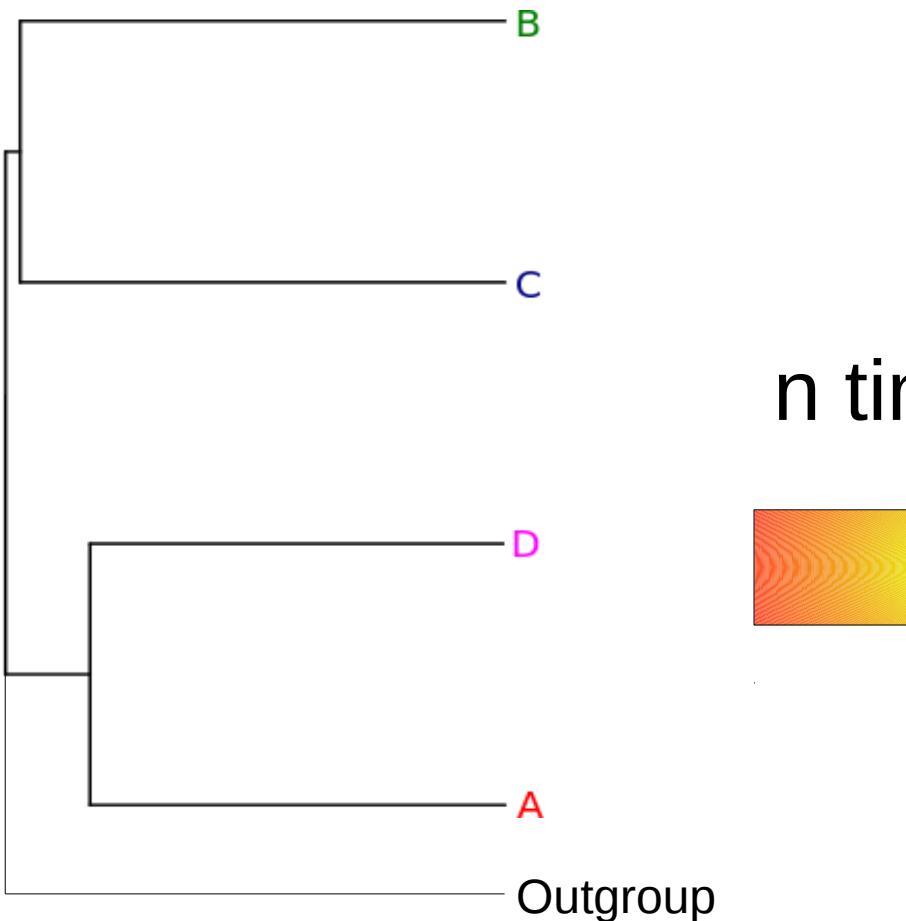
- Species initiation rate: {0.5} (as [1])
- Species completion rate: {0.1, 0.3, 1.0} (as [1]) and something big
- Extinction rate: {0.0, 0.1, 0.2} (as [1])
- Crown age: 15 My (as [1])

# Step 2/5

Sample a random (monophyletic) species tree,  
add an outgroup



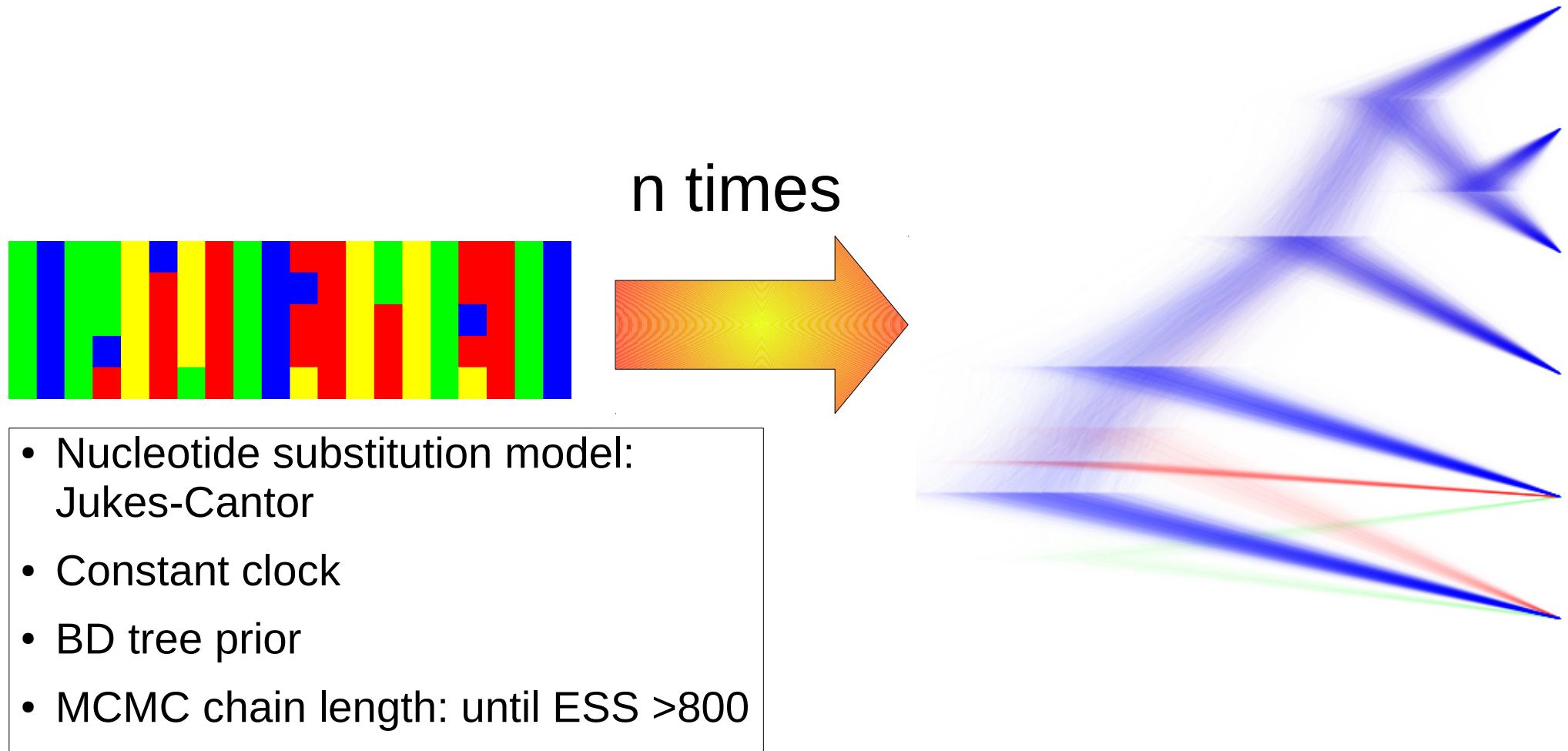
# Step 3/5



- mutation rate: {0.1, ? }
- sequence length: {1k, 10k, ? }
- Nucleotide substitution model: Jukes-Cantor

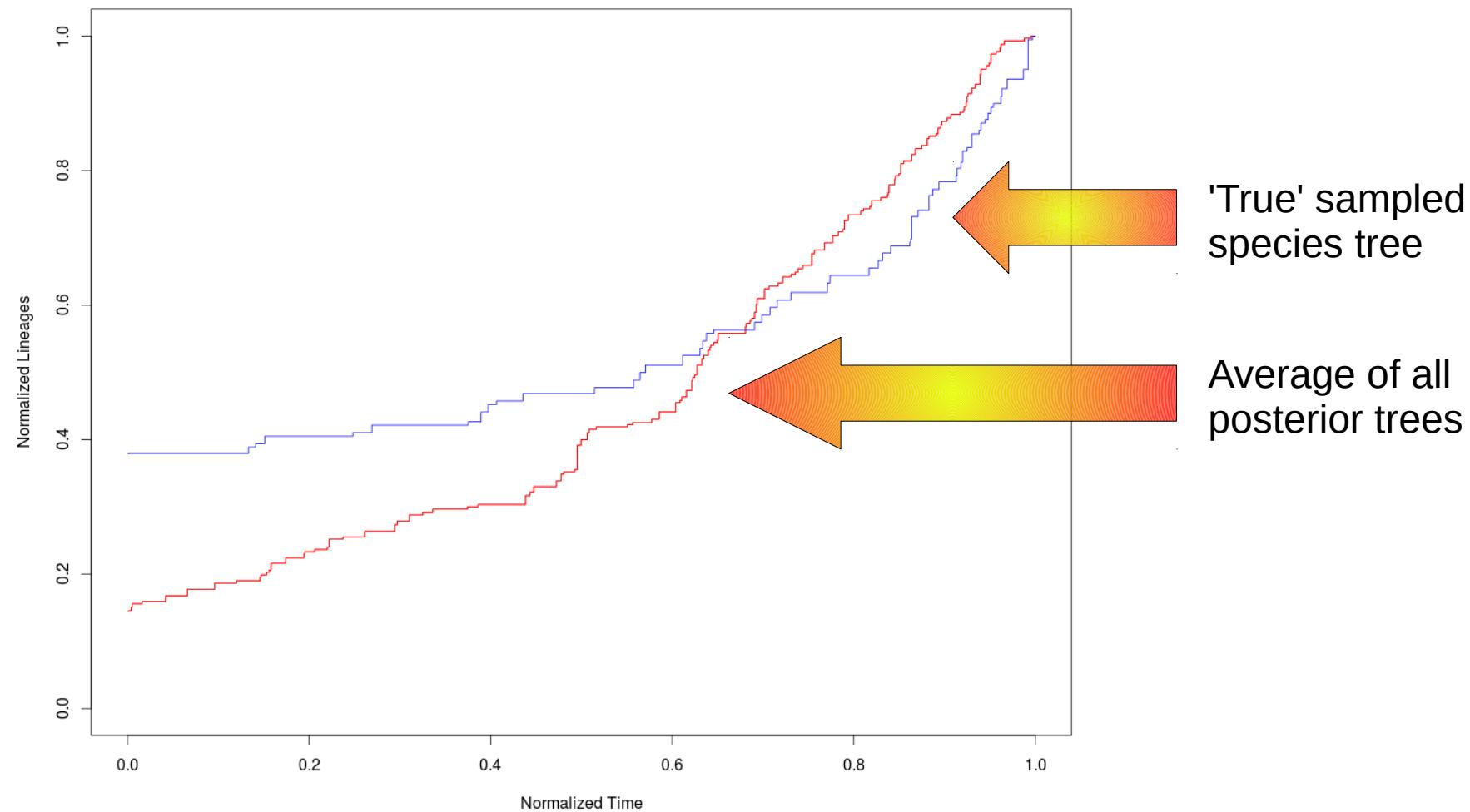
# Step 4/5

- Let BEAST2 infer a posterior



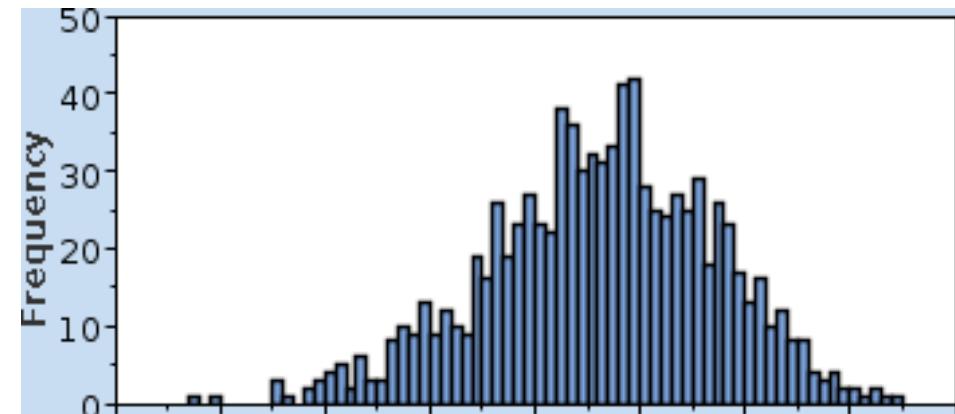
# Step 5/5

- Compare the sampled 'true' phylogeny with the posteriors



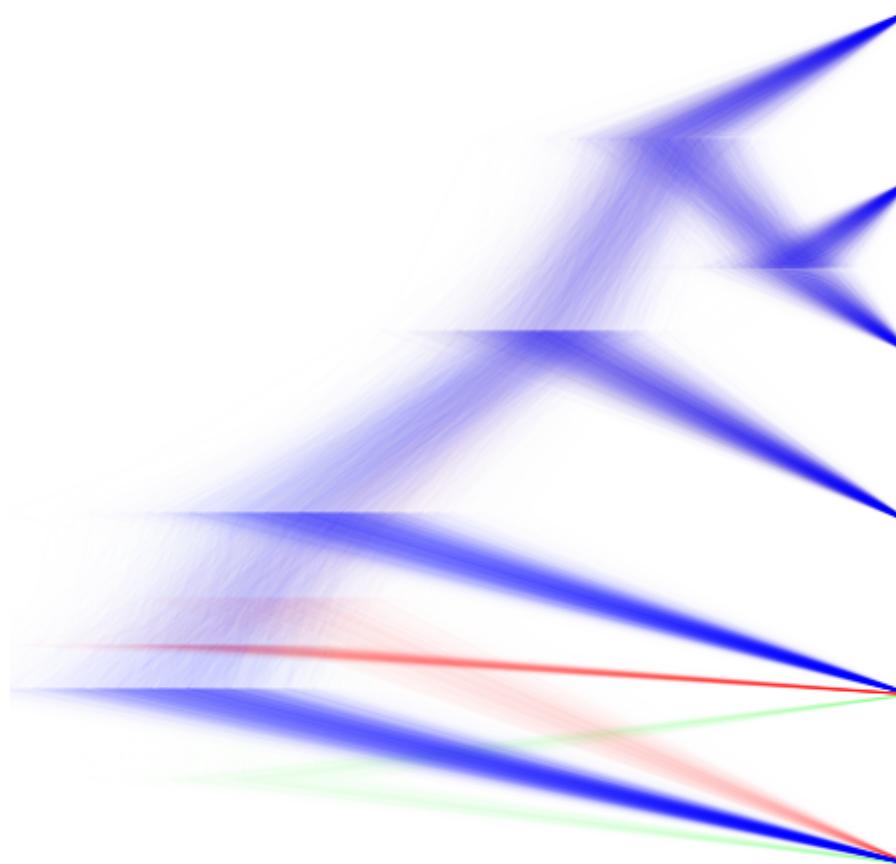
# Conclusion

- Unknown if protractness makes BEAST2 make incorrect predictions for biologically relevant parameters
- For sure: adding this to BEAST also allows to jointly infer parameters, especially the estimation of duration of speciation



# Implications

- Who-lived-when estimates may change
- Topology of phylogenies may change



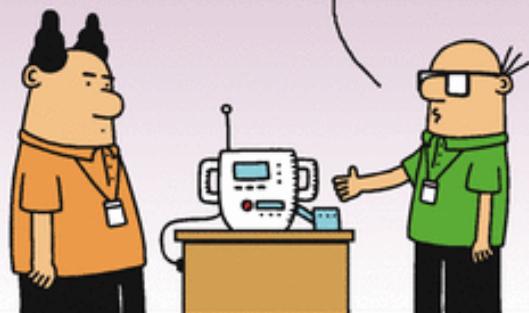
# Discussion

- Simple DNA substitution model
- Constant rate clock
- Processing the results



# Thanks

I ASKED THE OTHER  
ENGINEERS TO HELP ME  
DEVELOP MY DOUBLE-  
HANDLED COFFEE MUG  
INVENTION.



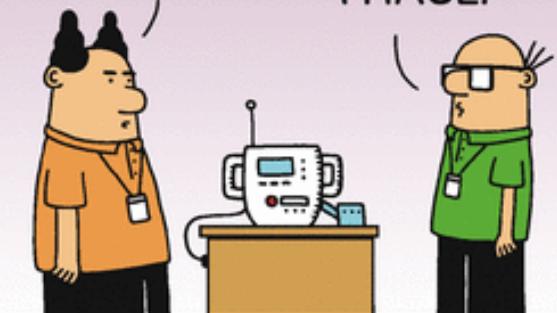
Dilbert.com DilbertCartoonist@gmail.com

NOW IT IS BLOATED  
WITH USELESS FEATURES  
AND NOT DISHWASHER  
SAFE. MAYBE YOU  
SHOULD CANCEL THE  
PROJECT.



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ARE  
YOU  
OKAY  
WITH  
THAT?



I'VE NEVER  
BEEN A BIG  
FAN OF THE  
IMPLEMENTA-  
TION  
PHASE.