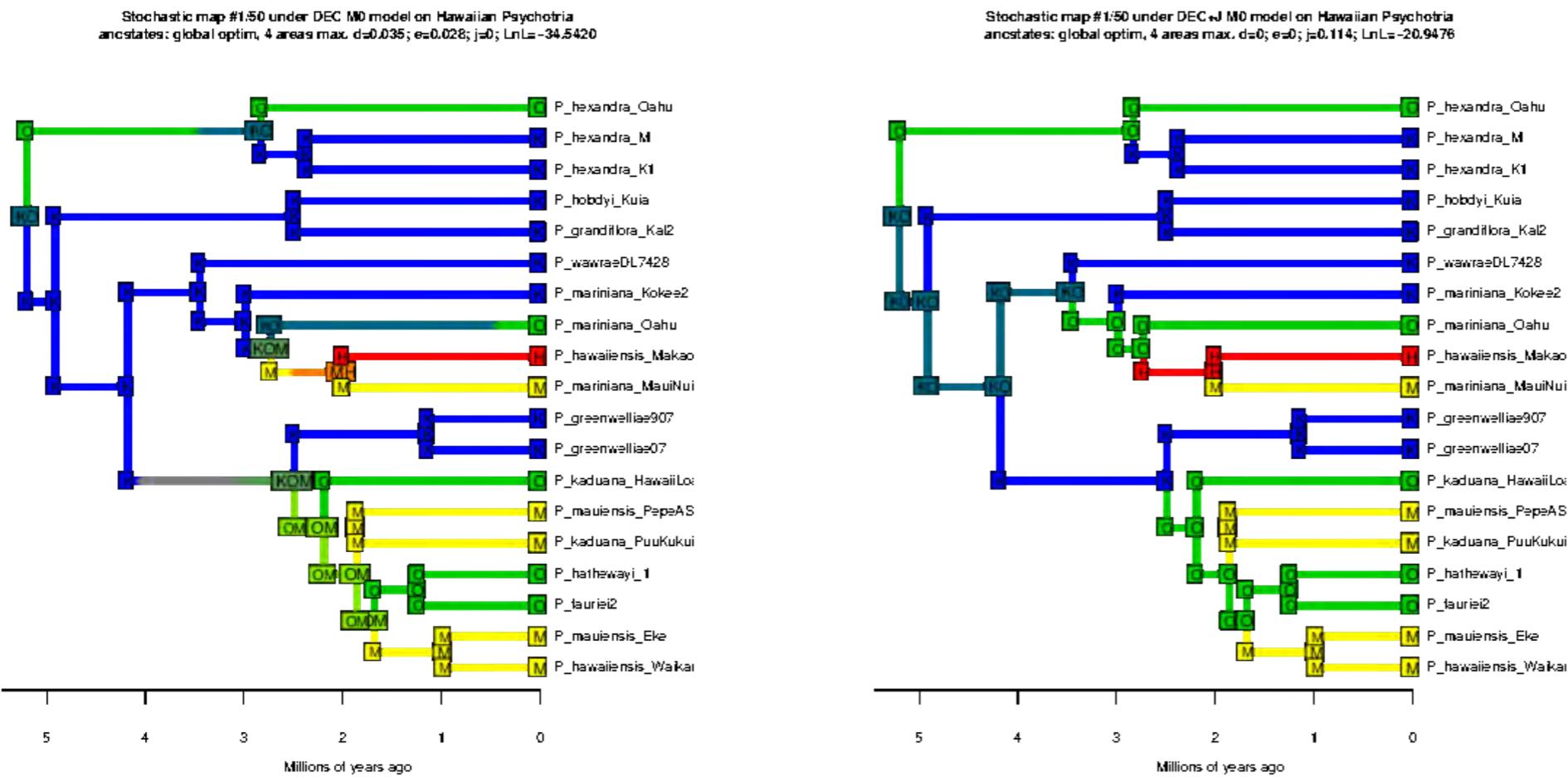


# Trait-dependent dispersal models in phylogenetic biogeography: theory and application in ants, crocs, lizards and kauri

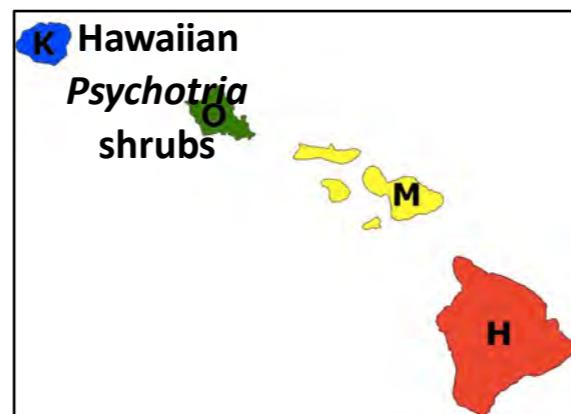


**Nicholas J. Matzke  
Senior Lecturer, SBS**

School of Biological Sciences,  
University of Auckland

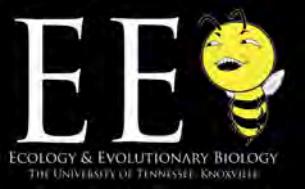
[phylo.wikidot.com/nicholas-j-matzke](http://phylo.wikidot.com/nicholas-j-matzke)

# possible histories (DEC model)



## possible histories (DEC+J model)

Thanks for support from:



# **Historical biogeography methods**

- 1. Estimate a dated phylogeny**
- 2. Put the geographic ranges at the tips**
- 3. Assume some process(es)**
- 4. Conduct inference**

# **Summary of previous lectures:**

**Different authorities have different assumptions about what processes matter!**

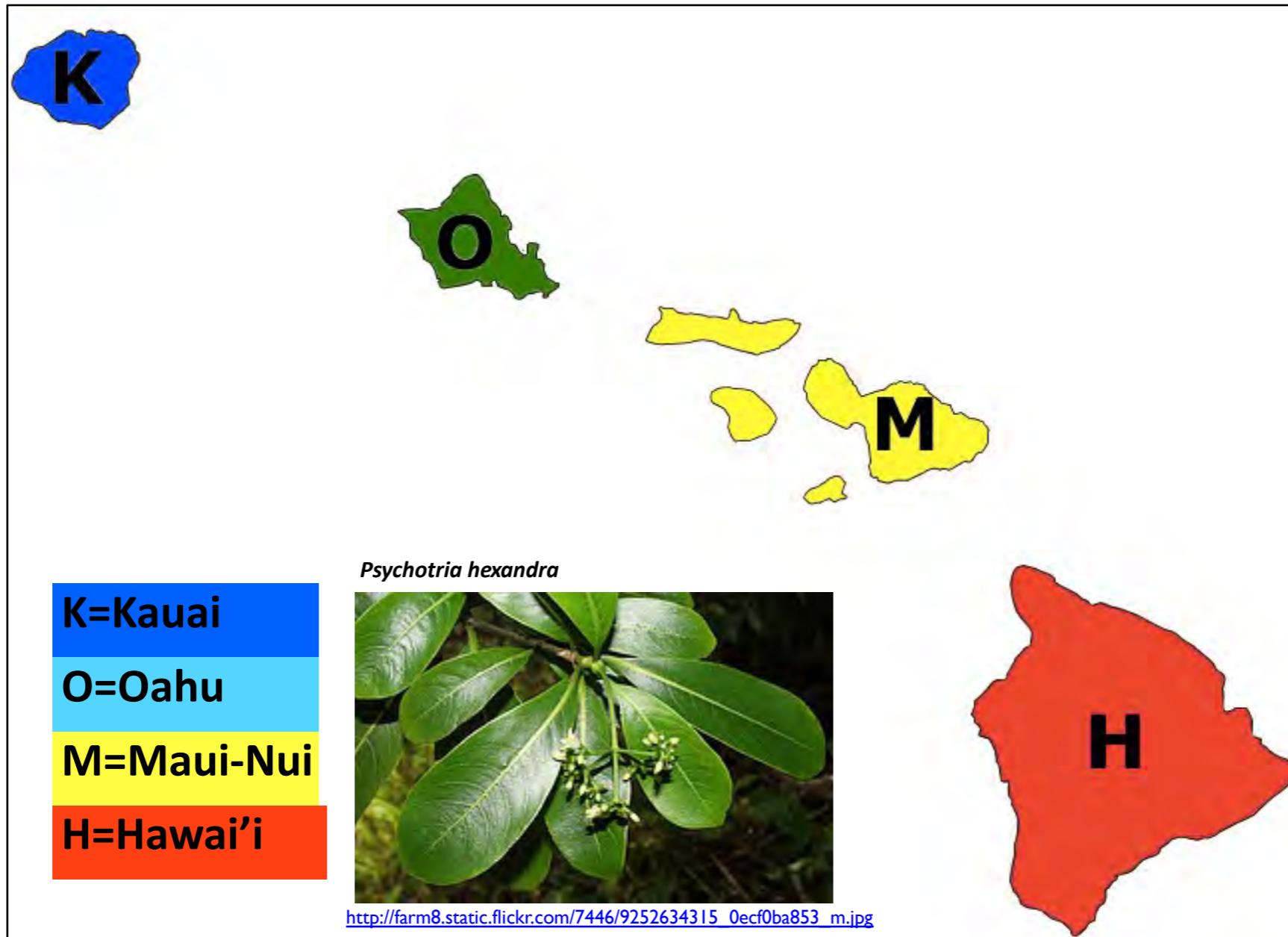
**Your inferences will depend on your assumptions**

Vicariance: deterministic vision where geology determines ranges

Dispersal: “unpredictable” “chance events”

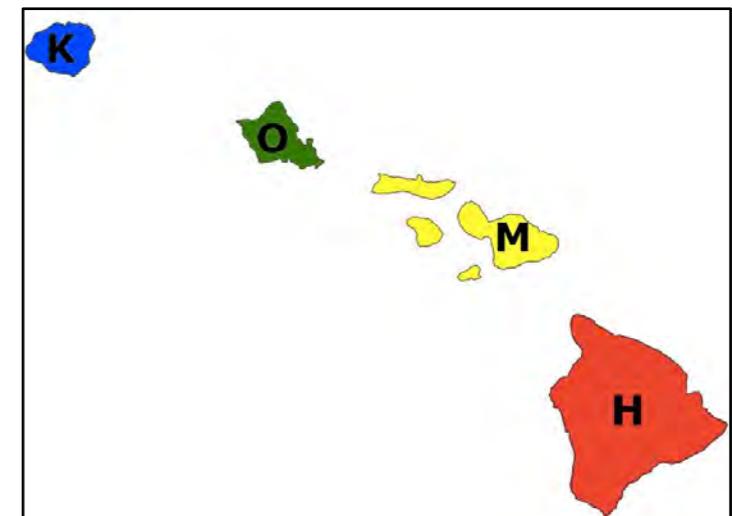
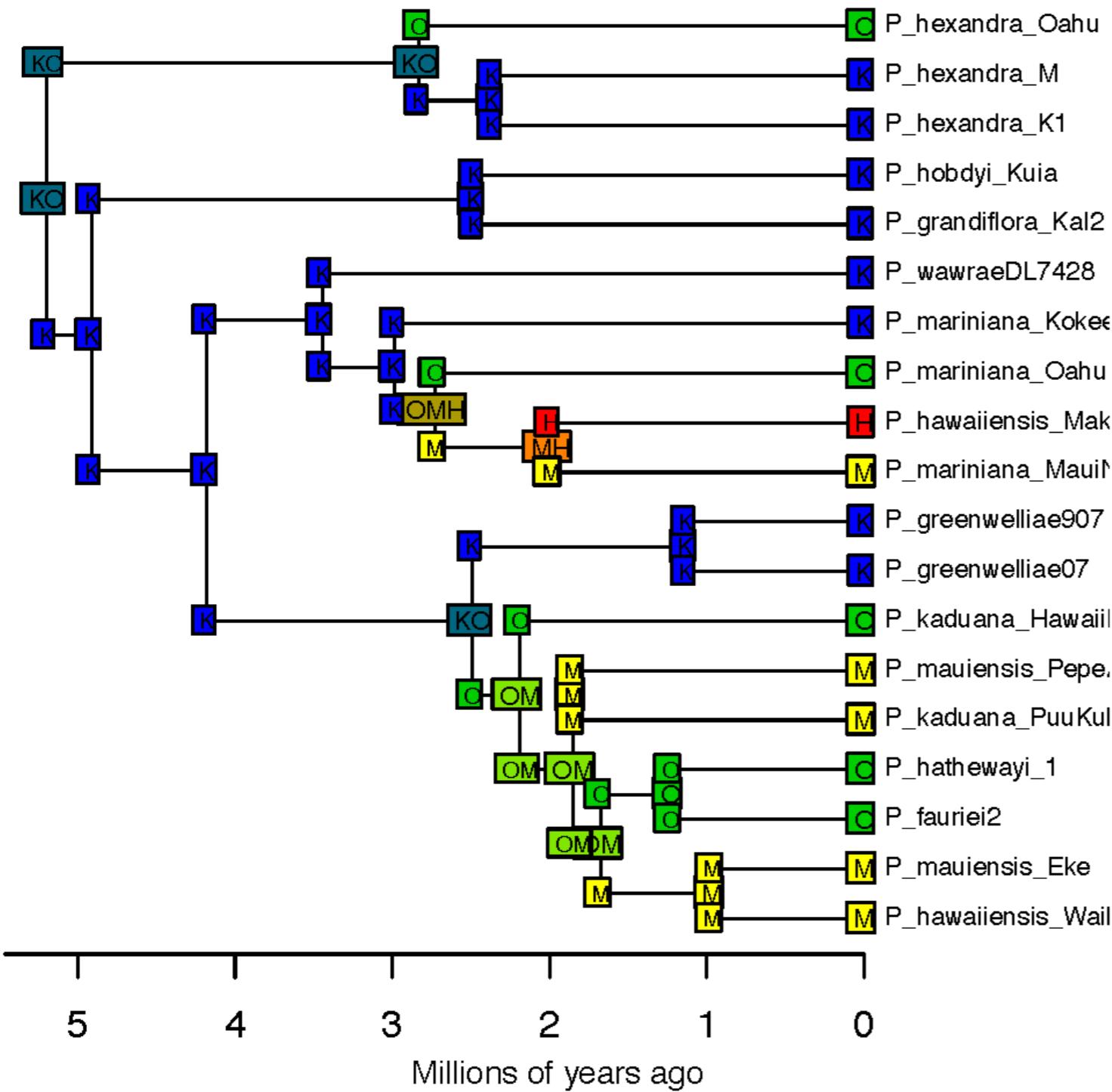
Me: “Unpredictable” doesn’t mean intractable – we can address using probabilistic models

# Results of different biogeography models on same dataset:



# Example of biogeographic history: *Psychotria*

## Model: DEC



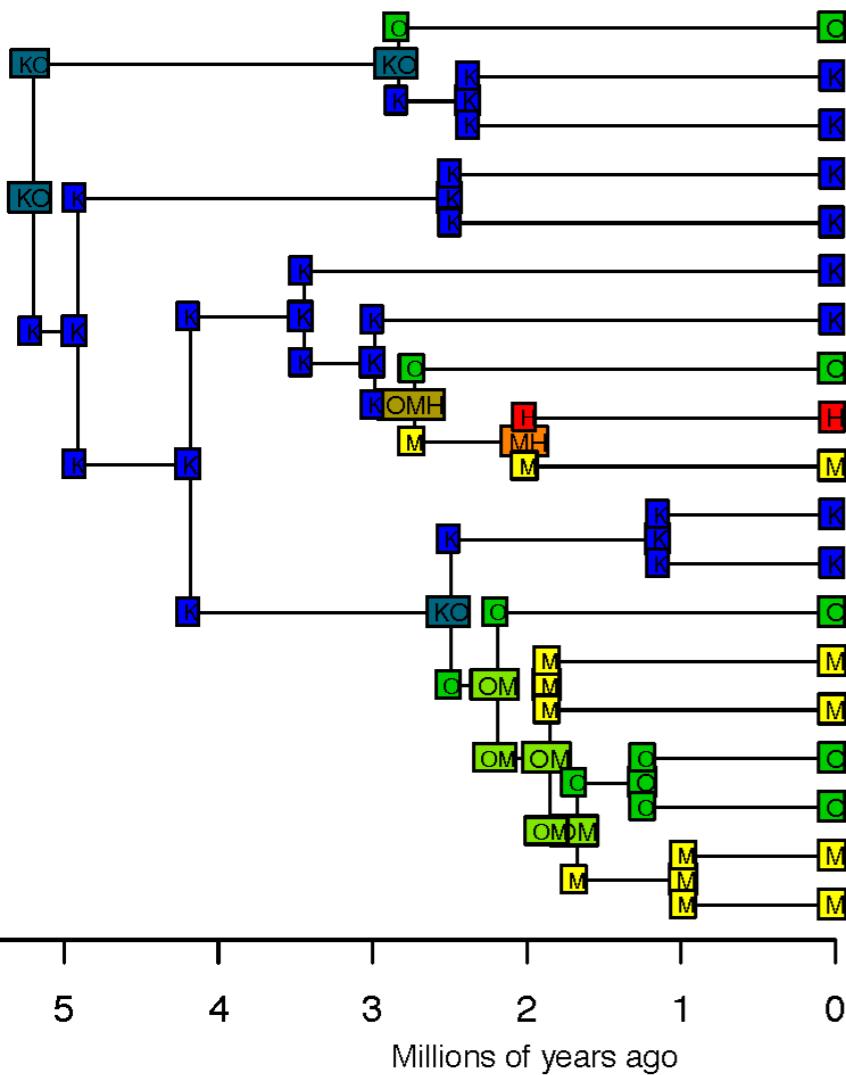
K=Kauai  
O=Oahu  
M=Maui-Nui  
H=Hawai'i



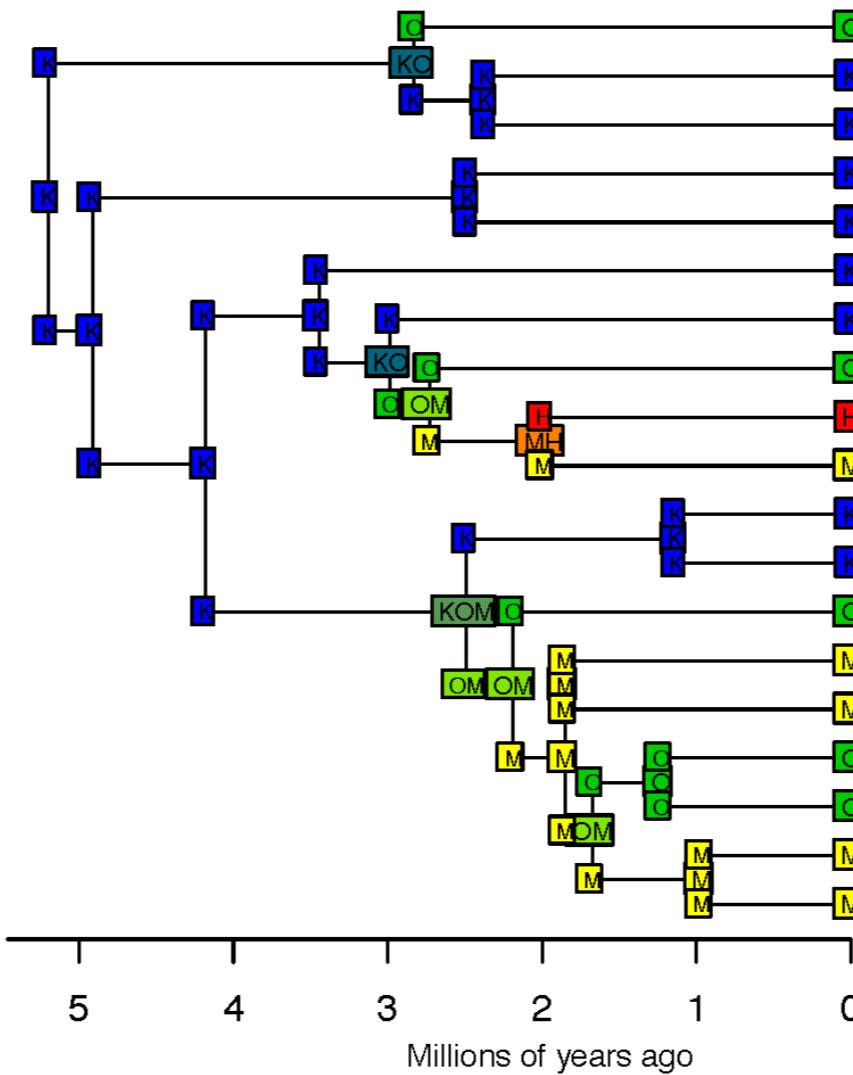
[http://farm8.static.flickr.com/7446/9252634315\\_0ecf0ba853\\_m.jpg](http://farm8.static.flickr.com/7446/9252634315_0ecf0ba853_m.jpg)

# Comparison: 3 models

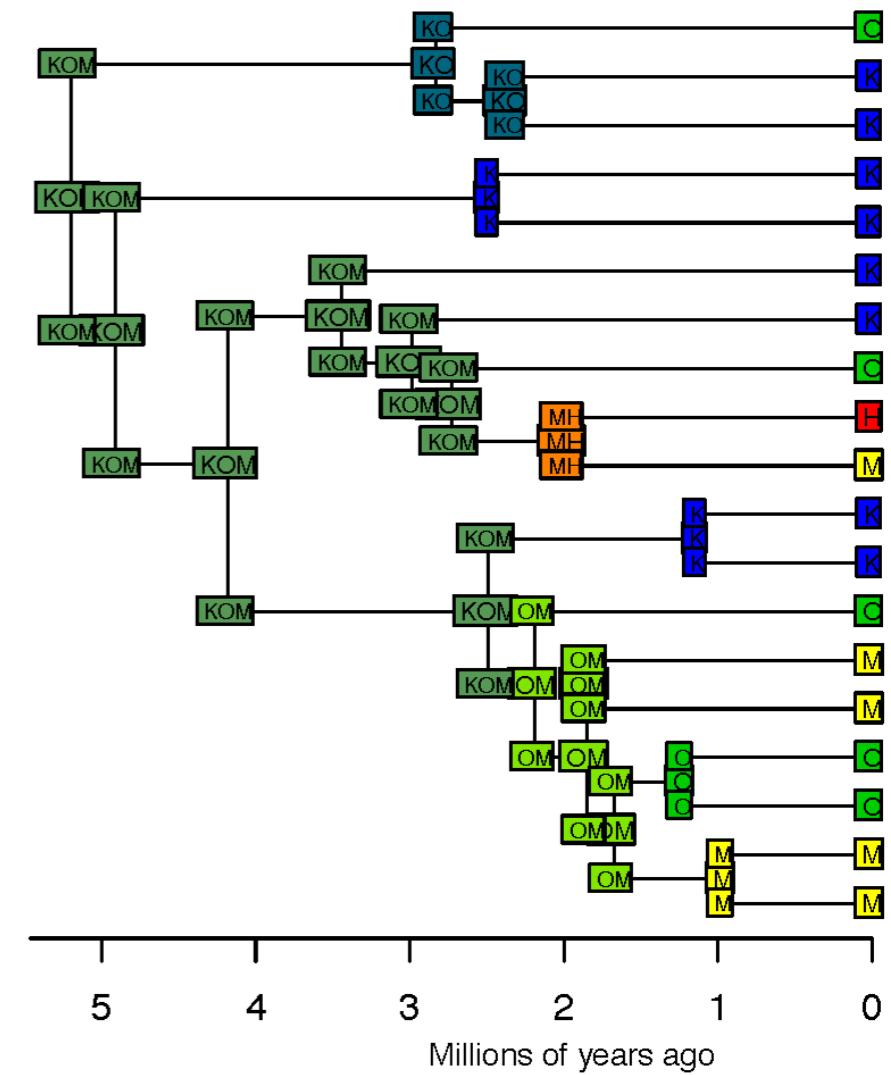
**Model: DEC**



**Model: DIVA**



**Model: BayArea**



*Psychotria hexandra*

- K=Kauai
- O=Oahu
- M=Maui-Nui
- H=Hawai'i



[http://farm8.static.flickr.com/7446/9252634315\\_0ecf0ba853\\_m.jpg](http://farm8.static.flickr.com/7446/9252634315_0ecf0ba853_m.jpg)

**I think we should use  
statistical model choice  
in biogeography**

**Comparison of two models:**

- 1. model without founder-event speciation**
- 2. model with founder-event speciation**

	Process	Ranges Before	Ranges After	Character mapping	DIVA	DEC (LAGRANGE)	BayArea, BBM (RASP)
Anagenetic	Dispersal				✓	✓	✓
	Extinction				✓	✓	✓
	Range-switching				✓		
Cladogenetic	Sympatry (narrow)				✓	✓	✓
	Sympatry (widespread)						✓
	Sympatry (subset)					✓	
	Vicariance (narrow)				✓	✓	
	Vicariance (widespread)					✓	
	Founder						

Which model should we use?

What about founder-event speciation?

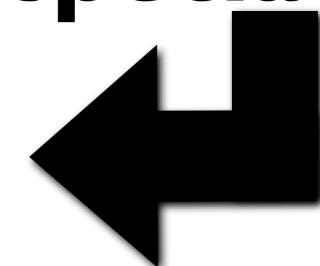
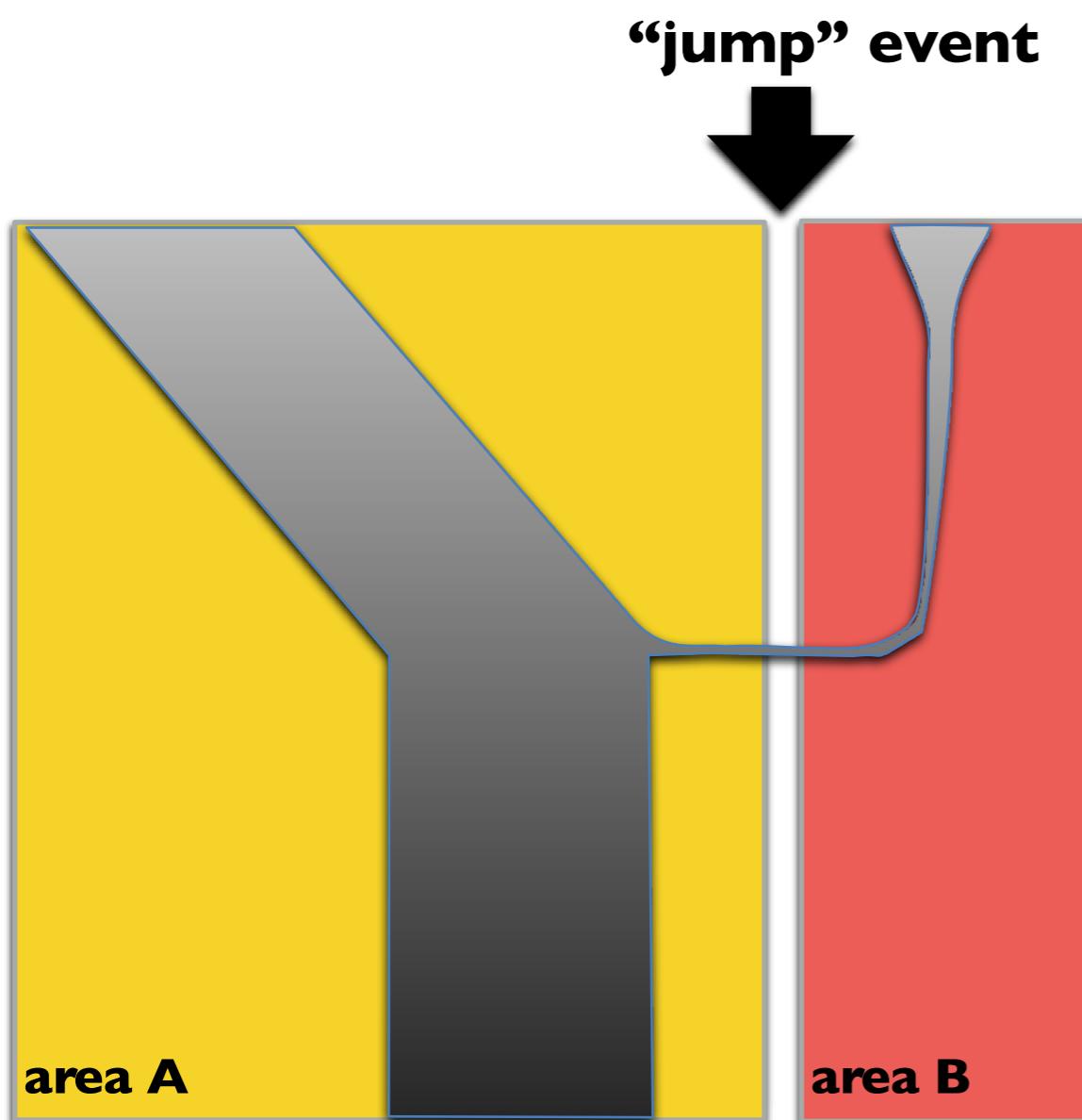


Figure 1, Matzke 2013, *Frontiers of Biogeography*

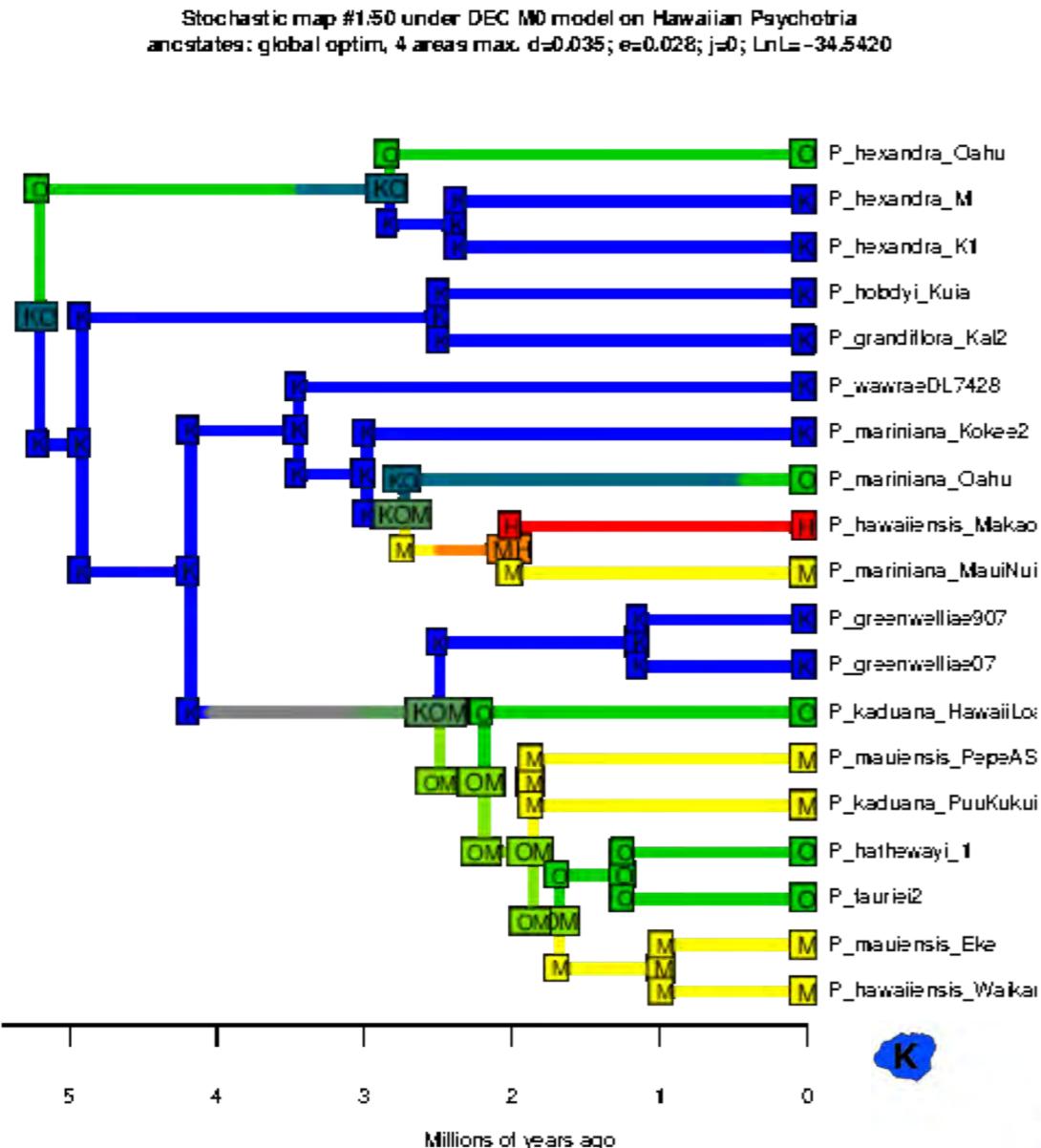
# Founder-event speciation



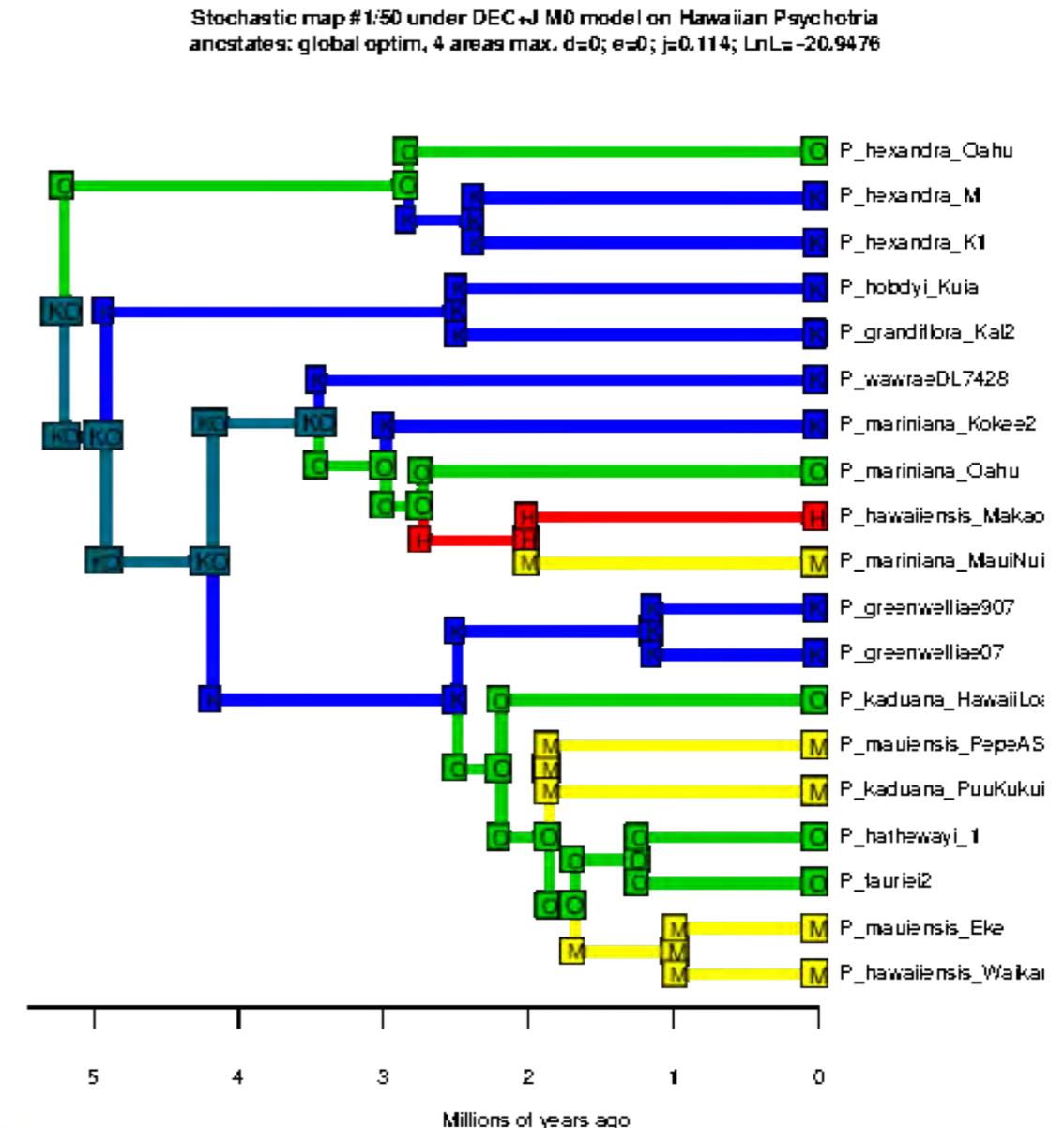
- In founder-event speciation, a rare dispersal event “instantaneously” establishes a geographically isolated new lineage with one or a few individuals
- Widely discussed in population genetics, speciation literature, island biogeography
- However, ignored in traditional historical biogeography computer models

# Example stochastic map

## ML DEC model



## ML DEC+J model



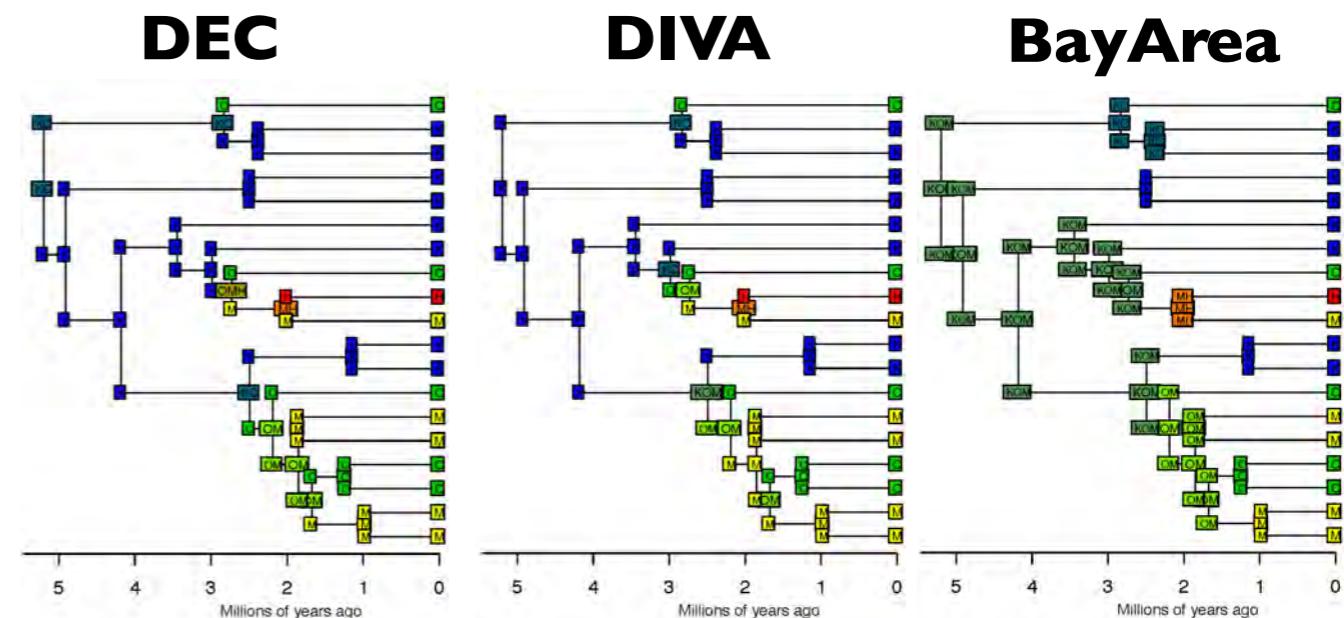
(under model M0: no geology)

# Historical biogeography methods

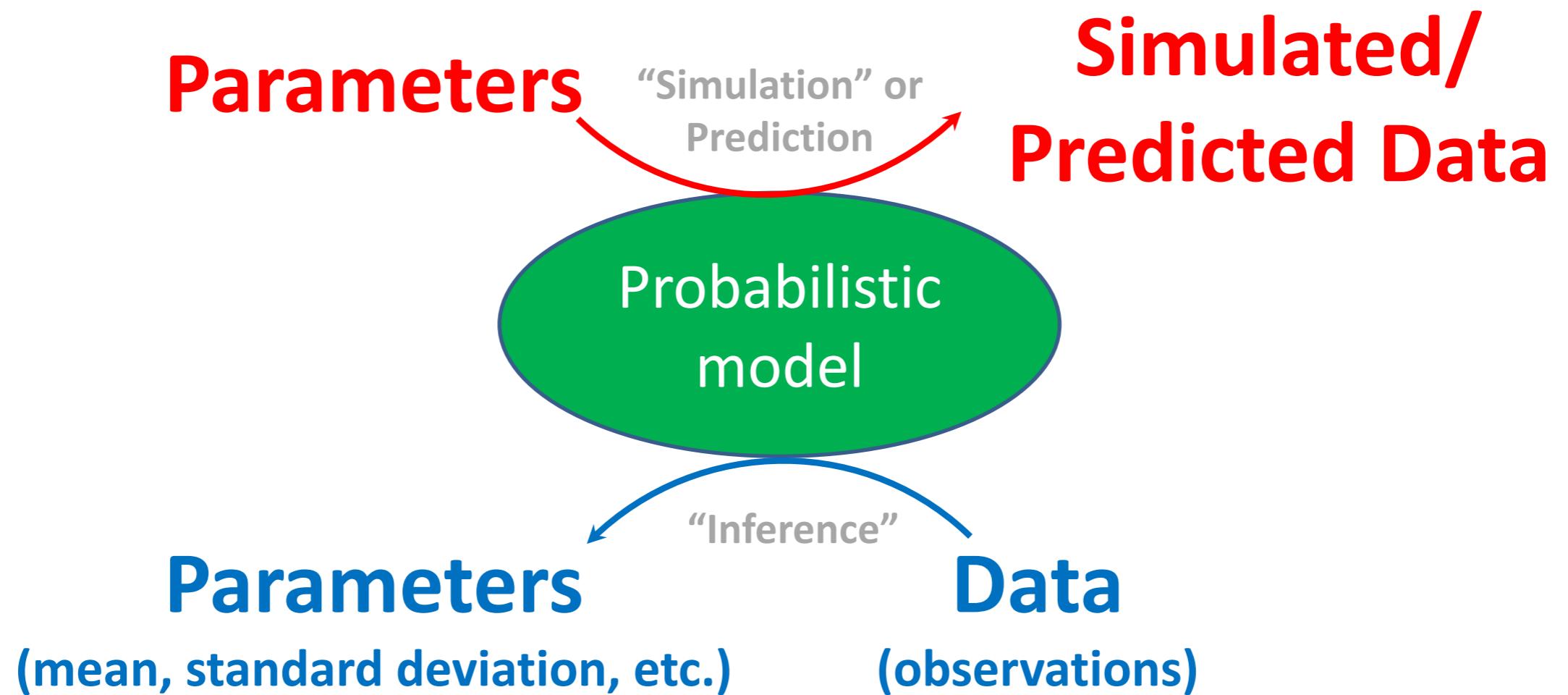
1. Estimate a dated phylogeny
2. Put the geographic ranges at the tips

## 3. Assume some process(es)

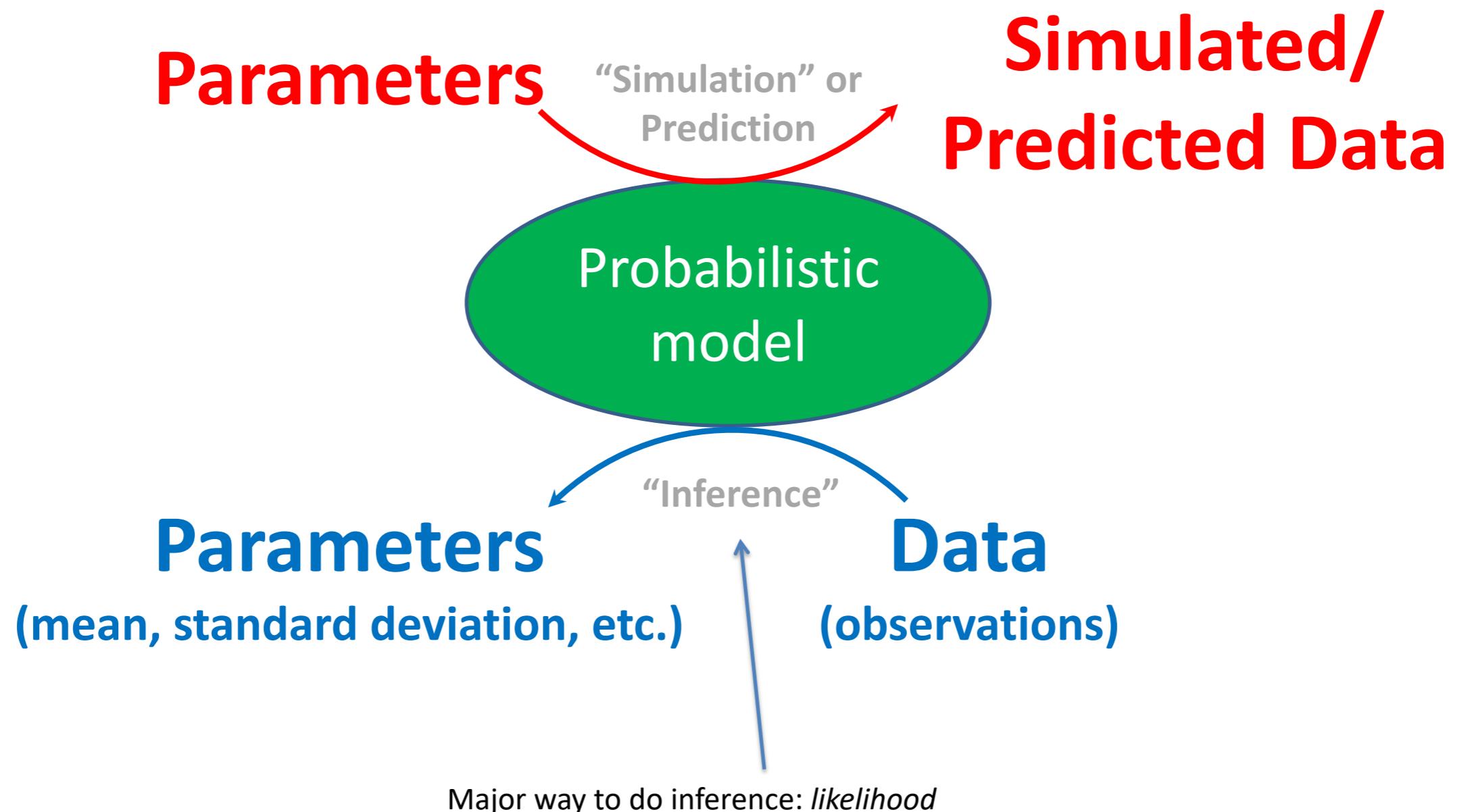
## 4. Conduct inference



# Review: Models, parameters, and data



# Review: Models, parameters, and data



# **Likelihood: the key concept**

**Likelihood = probability of the data,  
given a model**

**Likelihood =  $P(\text{data} \mid \text{model})$**

$$L = P(D \mid M)$$

$$\ln L = \log(P(D|M))$$

**$\ln L$  = natural logarithm of the likelihood**

# What is likelihood?

**Likelihood = Prob(data | model)**

A conditional probability

**Likelihood is a fundamental concept in statistics and inference**

**The inference method of Maximum Likelihood is ubiquitous in parametric statistics**

**Statistics like the mean, or linear regression, can be justified through ML**

# Key concepts

**Likelihood = Prob(data | model)**

A conditional probability

**Data: some observations (numbers) you have collected – considered unchanging for the purposes of your statistical analysis**

**Model: some process that you postulate could have produced the data; it is an equation giving the likelihood**

**“Models put probabilities on data.”**

**Parameters: Numbers in the model that can be changed / learned (e.g., the probability of heads, the rate of change)**

# **Maximum Likelihood Inference**

**Likelihood = probability of the data,  
assuming a model**

**Maximum Likelihood (ML): find the  
parameter values that maximize the  
probability of the data**

# Maximum Likelihood Inference

Likelihood = probability of the data, assuming a model

**Maximum Likelihood (ML): find the parameter values that maximize the probability of the data**

For example: coin-flipping

Data: HHHHHHHHTTT -- 7 Heads, then 3 Tails



# Maximum Likelihood Inference



Likelihood = probability of the data, assuming a model

**Maximum Likelihood (ML):** find the parameter values that maximize the probability of the data

For example: coin-flipping

Data: HHHHHHHHTTT -- 7 Heads, then 3 Tails

Model	Parameter	Calculation	Prob(data)	Ln(prob)	Prob. ratio	ML says
Fair coin	prob(Heads) = 0.5	$0.5^7 \times 0.5^3$	0.000977	-6.93	1	worse
Biased coin	prob(Heads) = 0.7	$0.7^7 \times 0.3^3$	0.00222	-6.11	2.28	better

# We can calculate likelihood or lnL for many different possible parameter values

Data/observations are fixed: we observed 7 Heads, 3 Tails. Which parameter value is best?

Name of free parameter is  
“*ProbHeads*”

“raw likelihood”

log-likelihood

<i>probHeads</i>	Likelihood	$\log_e(L)$	LnL
0.0	0.0	$\log(0.0)$	-Inf
0.1	0.0000000729	$\log(0.0000000729)$	-16.434177
0.2	0.0000065536	$\log(0.0000065536)$	-11.935496
0.3	0.0000750141	$\log(0.0000750141)$	-9.497834
0.4	0.0003538944	$\log(0.0003538944)$	-7.946512
0.5	0.0009765625	$\log(0.0009765625)$	-6.931472
0.6	0.0017915904	$\log(0.0017915904)$	-6.324652
0.7	0.0022235661	$\log(0.0022235661)$	-6.108643
0.8	0.0016777216	$\log(0.0016777216)$	-6.390319
1.0	0.0	$\log(0.0)$	-Inf

Parameter values to try

Plot a likelihood curve from these

# Likelihood profile curve

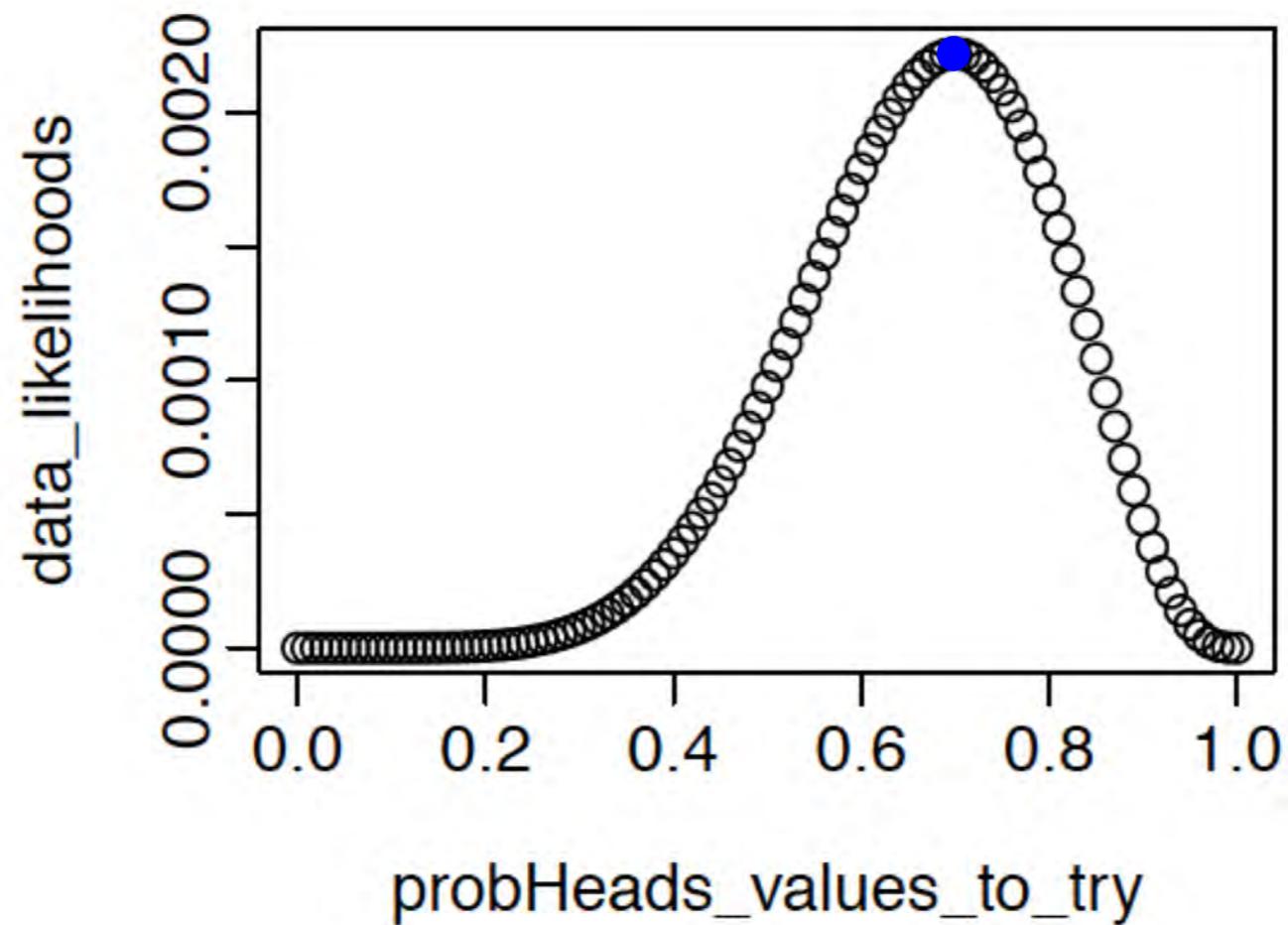


Figure 3: The likelihood of the coinflip data (7 Heads, 3 Tails), under 101 possible values of the parameter *probHeads*.

# Log-likelihood (lnL)

The log-likelihood (always the NATURAL log) is

1. An easy way to represent very small numbers
2. Helps the computers avoid numeric underflow problems
  - Multiplication in becomes addition in log-space  
(also makes calculus easier)
  - E.g., in R, 0.1 times itself 300 times:  $0.1^{300} = 1e-300$   
But  $(0.1^{300}) * (0.1^{300}) = 0.0$ , which is wrong (underflow rounds down to 0.0)
  - In log space:  $\log(0.1^{300}) = 300 * \log(0.1) = 300 * -2.3026 = -690.78$   
 $\log((0.1^{300}) * (0.1^{300})) = 300 * \log(0.1) + 300 * \log(0.1) = 600 * \log(0.1) =$   
 $= 1381.55 = 2 * -690.78$
3. Important in Information Theory
4. Maximizing the lnL finds the same parameters as maximizing the likelihood

Note: reverse the log() operation with exp():  $\log(0.1) = -2.3026$ ,  $\exp(-2.3026) = 0.1$   
 $\exp(1) = 2.718282\dots$ , which is known as Euler's number,  $e$ , the base of the natural log

# The maximum likelihood and log-likelihood (lnL) give the same parameter estimate

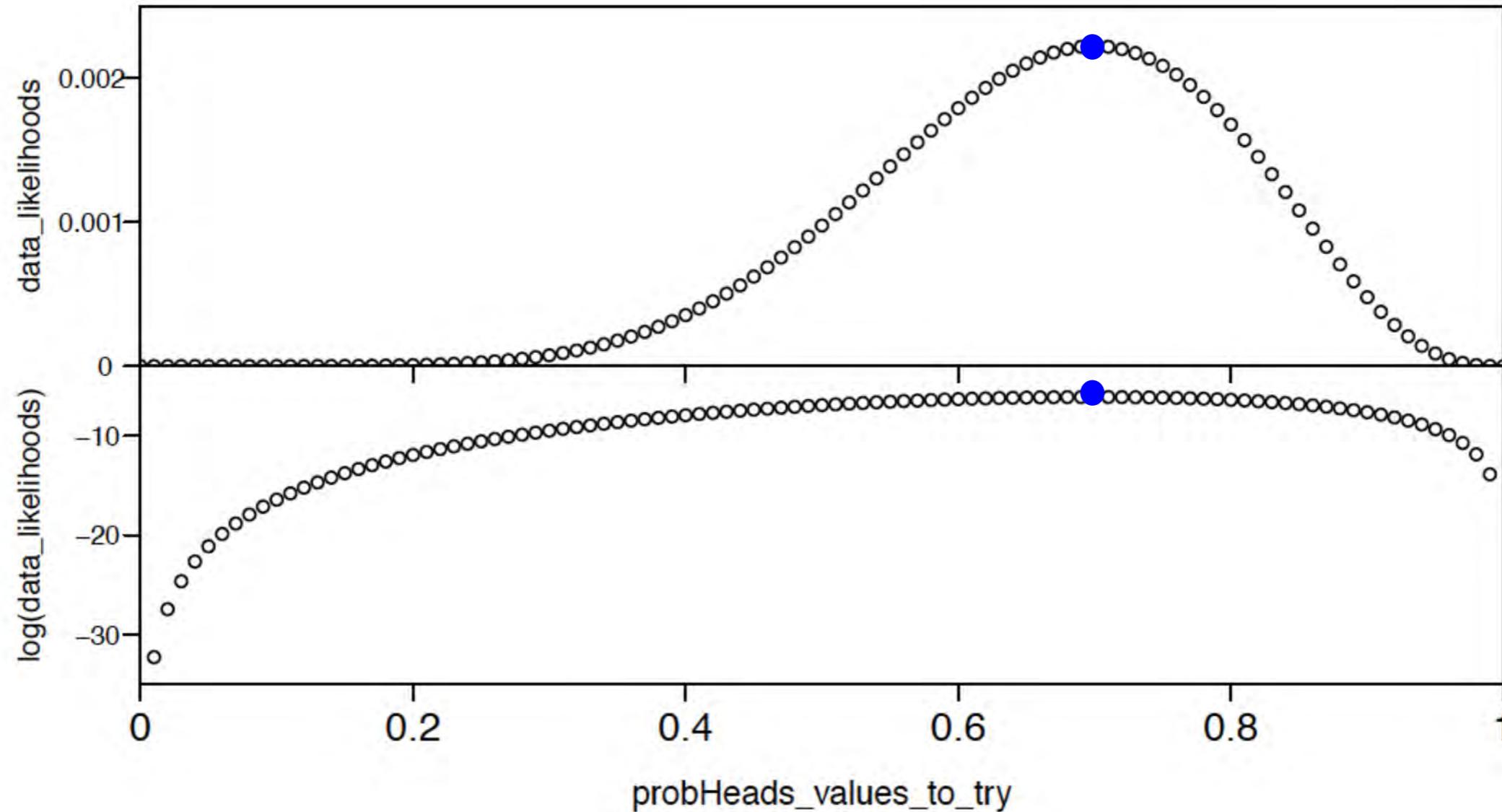


Figure 5: Comparison of the likelihood and log-likelihood of the coinflip data (7 Heads, 3 Tails), under 101 possible values of the parameter `probHeads`.

# What is our best estimate of the parameter?

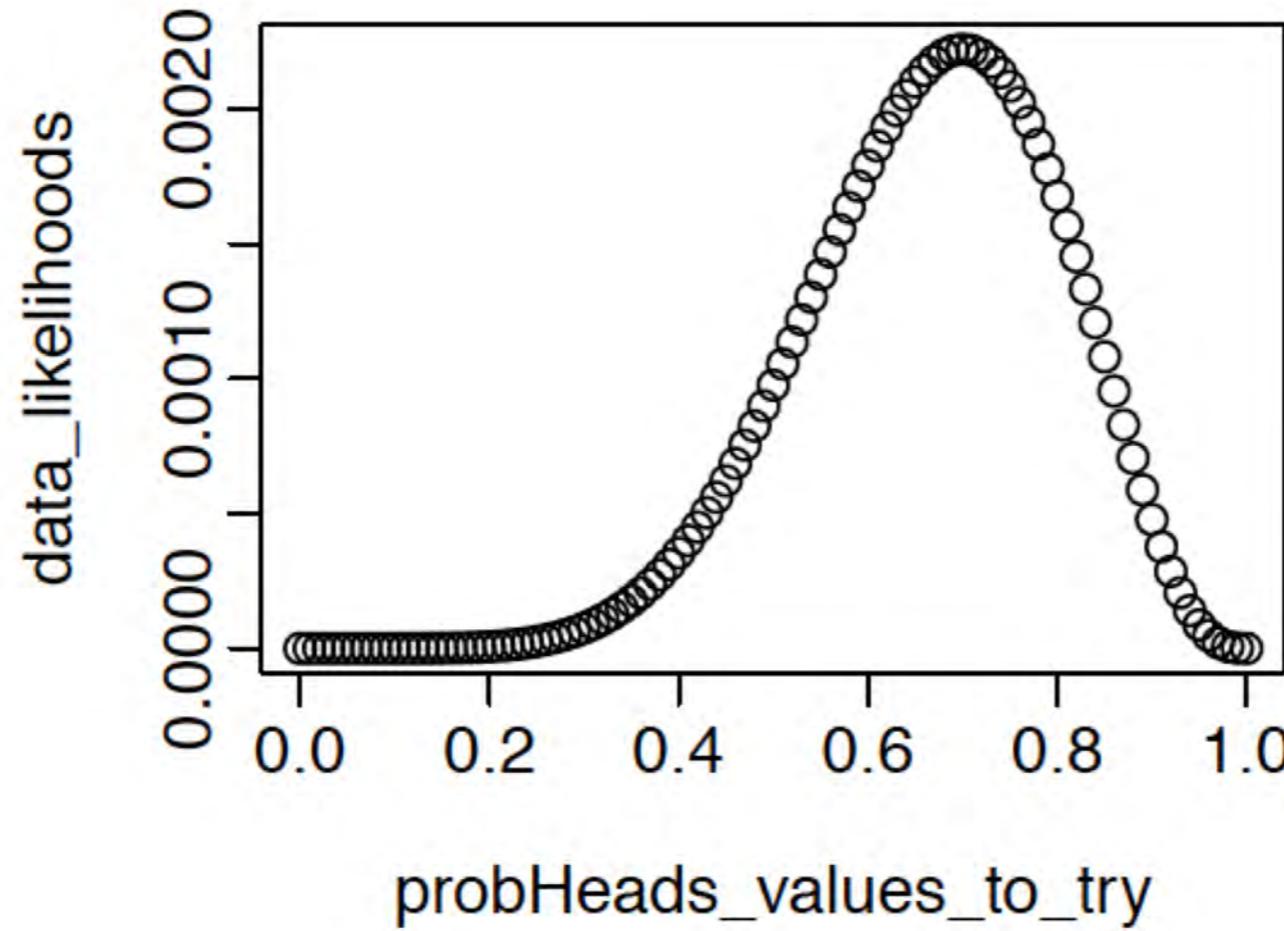


Figure 3: The likelihood of the coinflip data (7 Heads, 3 Tails), under 101 possible values of the parameter *probHeads*.

# What is our best estimate of the parameter?

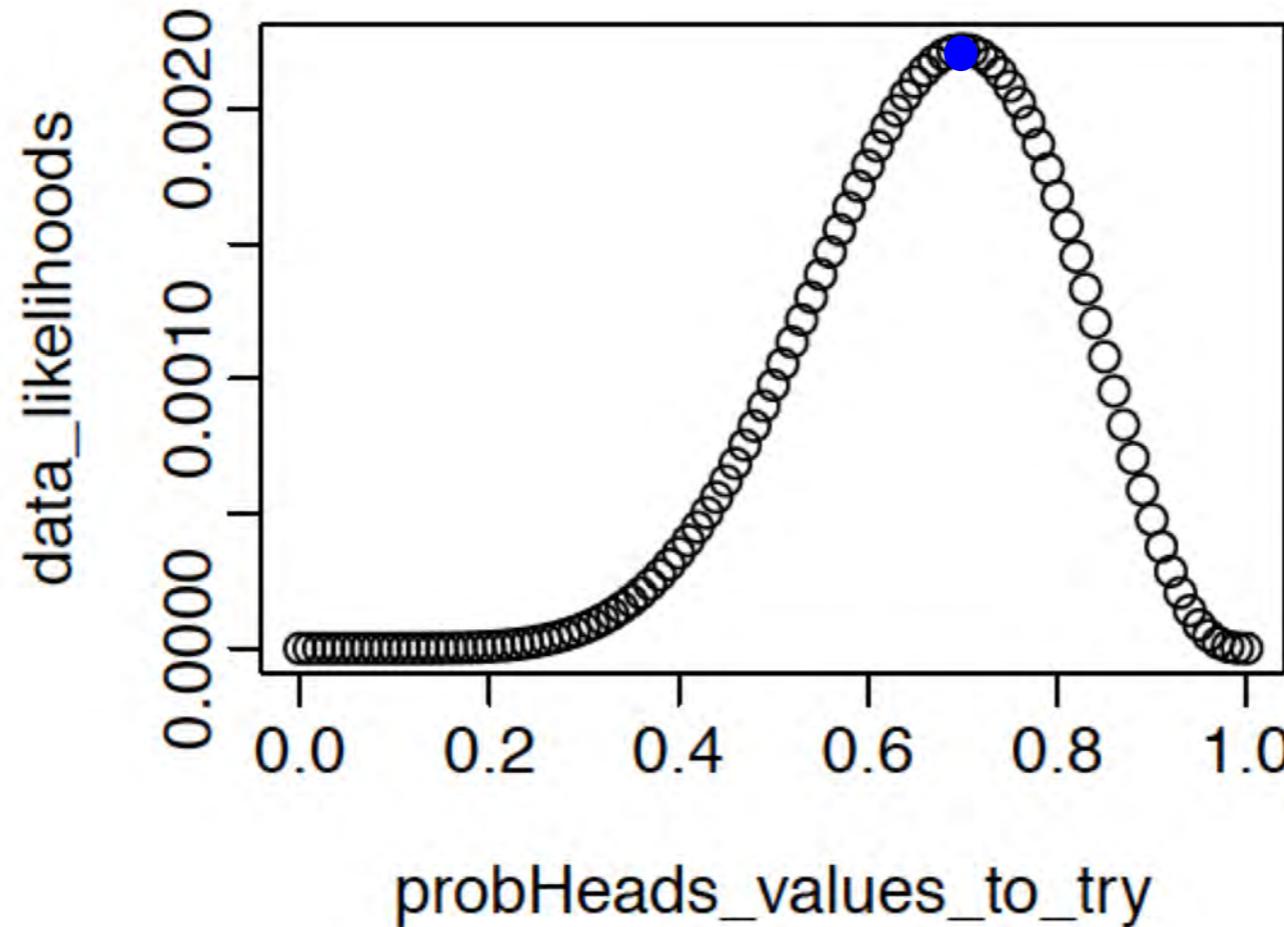


Figure 3: The likelihood of the coinflip data (7 Heads, 3 Tails), under 101 possible values of the parameter *probHeads*.

# What is our best estimate of the parameter?

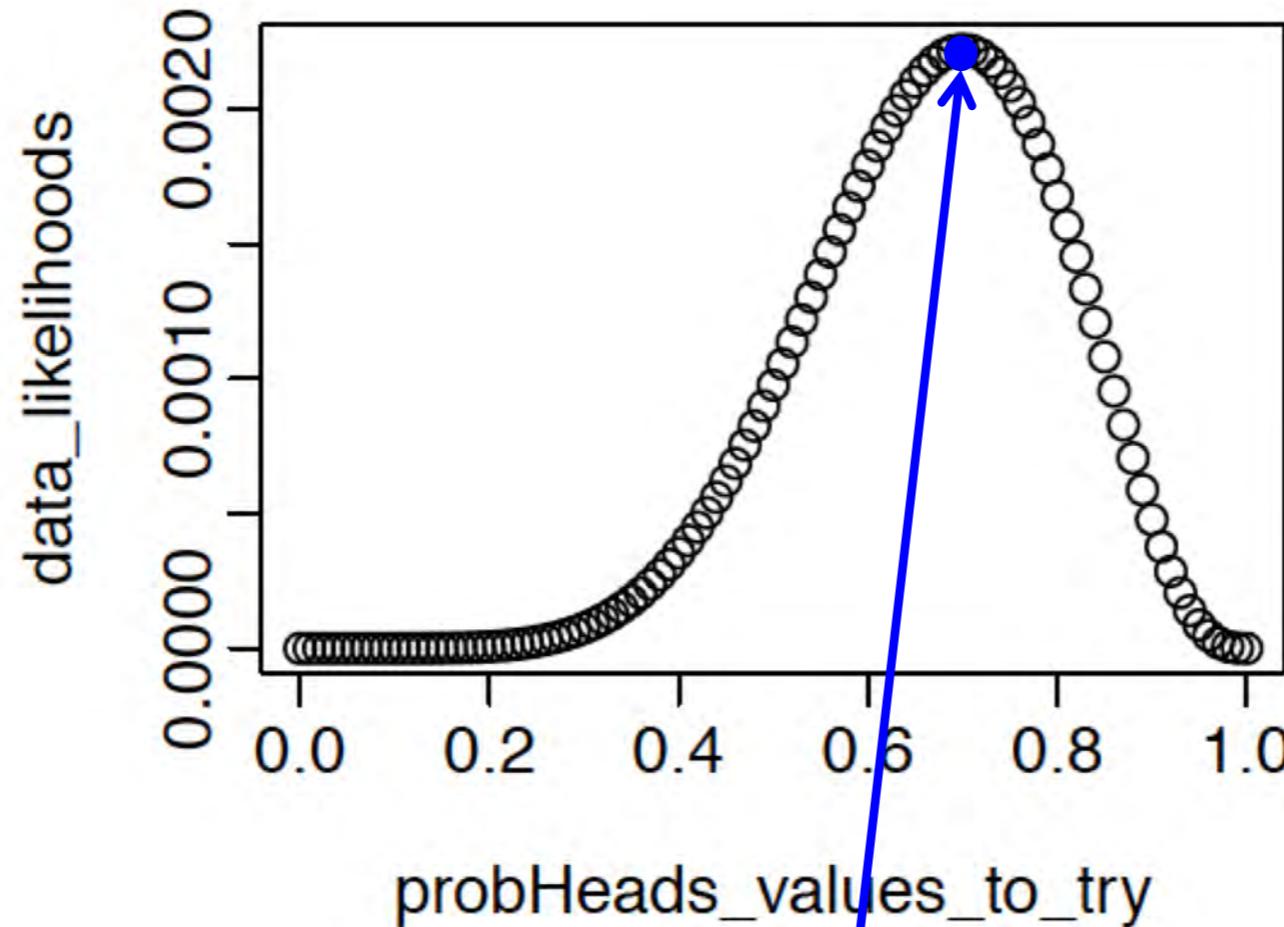


Figure 3: The likelihood of the coinflip data (7 Heads, 3 Tails), under 101 possible values of the parameter *probHeads*.

# What is our best estimate of the parameter?

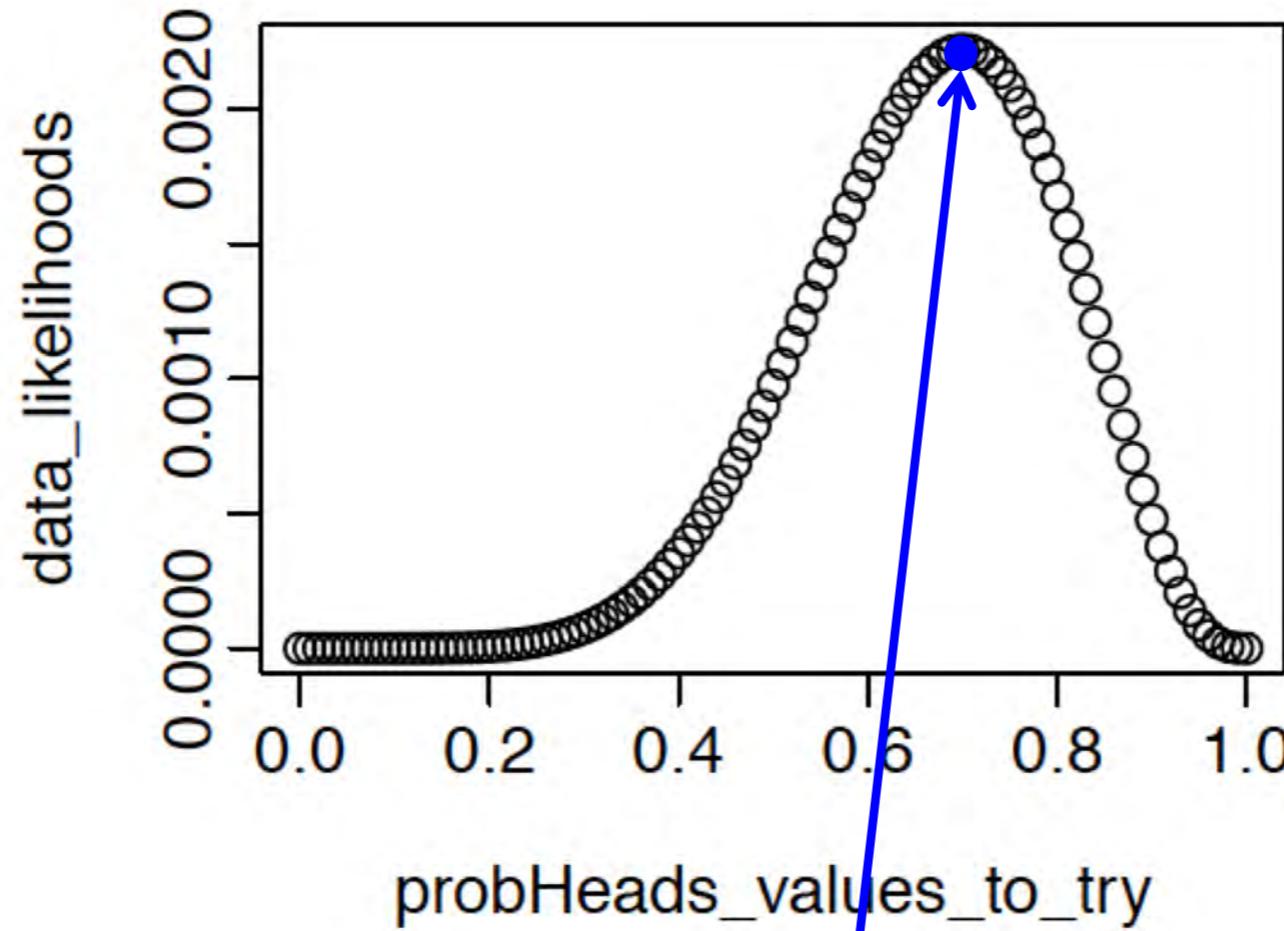


Figure 3: The likelihood of the coinflip data (7 Heads, 3 Tails), under 101 possible values of the parameter *probHeads*.

**The parameter value that  
Maximizes the Likelihood (ML)**

# How to find the maximum of the likelihood?

Several possible methods:

1. Intuition
2. Calculus to get an analytic solution
3. Exhaustive search “grid search”
4. Optimization / hill-climbing

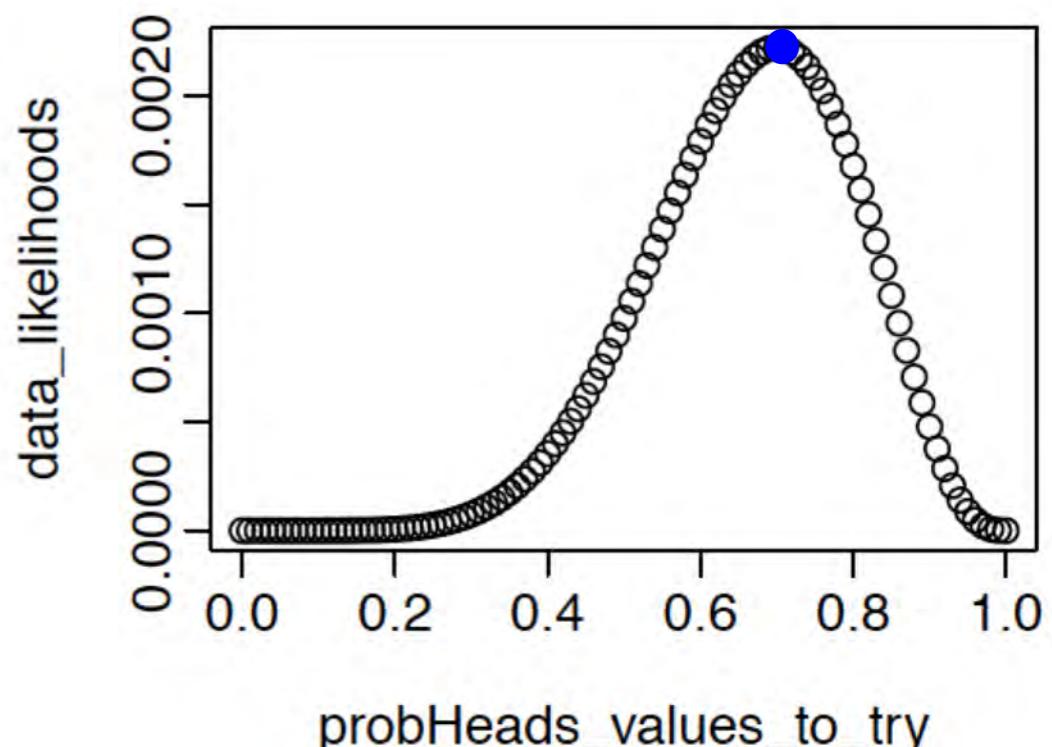


Figure 3: The likelihood of the coinflip data (7 Heads, 3 Tails), under 101 possible *probHeads*.

# How to find this maximum?

Method 1: intuition

In very simple cases, like coin-flipping, you can guess that the average of your data provides the best estimate.

(But: your intuition can betray you, e.g. if you think about your prior experience that most coins are fair)

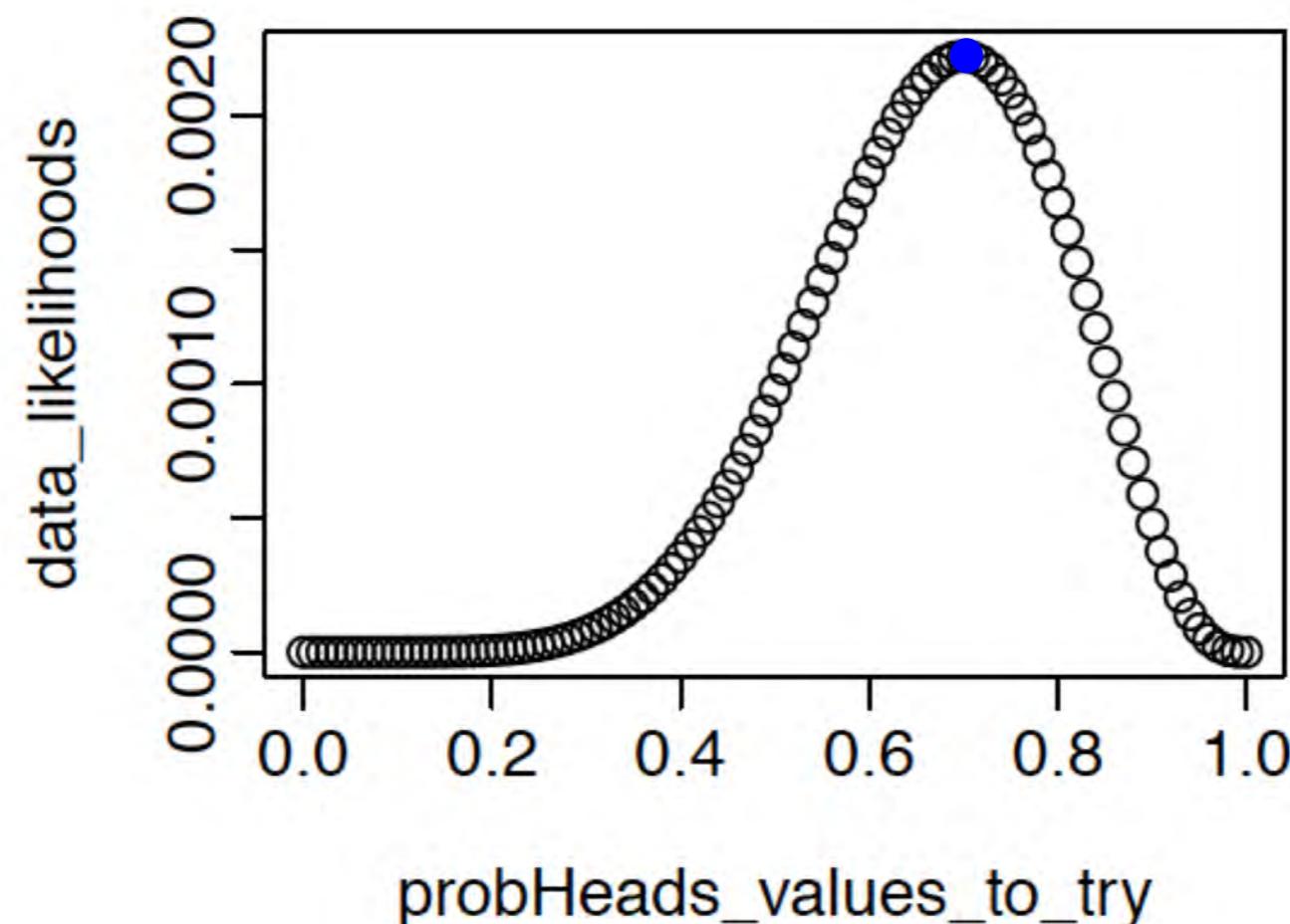


Figure 3: The likelihood of the coinflip data (7 Heads, 3 Tails), under 101 possible values of the parameter *probHeads*.

# The parameter value that Maximizes the Likelihood (ML)

Method 2: calculus

Short-short version:

- (1) Taking the first derivative of a function provides an equation giving the slope at each point
- (2) The slope will be 0.0 at the maximum of the curve
- (3) Setting the derivative to 0.0 and solving gives a formula for the Maximum Likelihood.

This is known as an “analytic solution”.

Analytic solutions are very fast, and are the basics of a lot of the “cookbook” formulas that get taught.

But they often aren’t available for complex models.

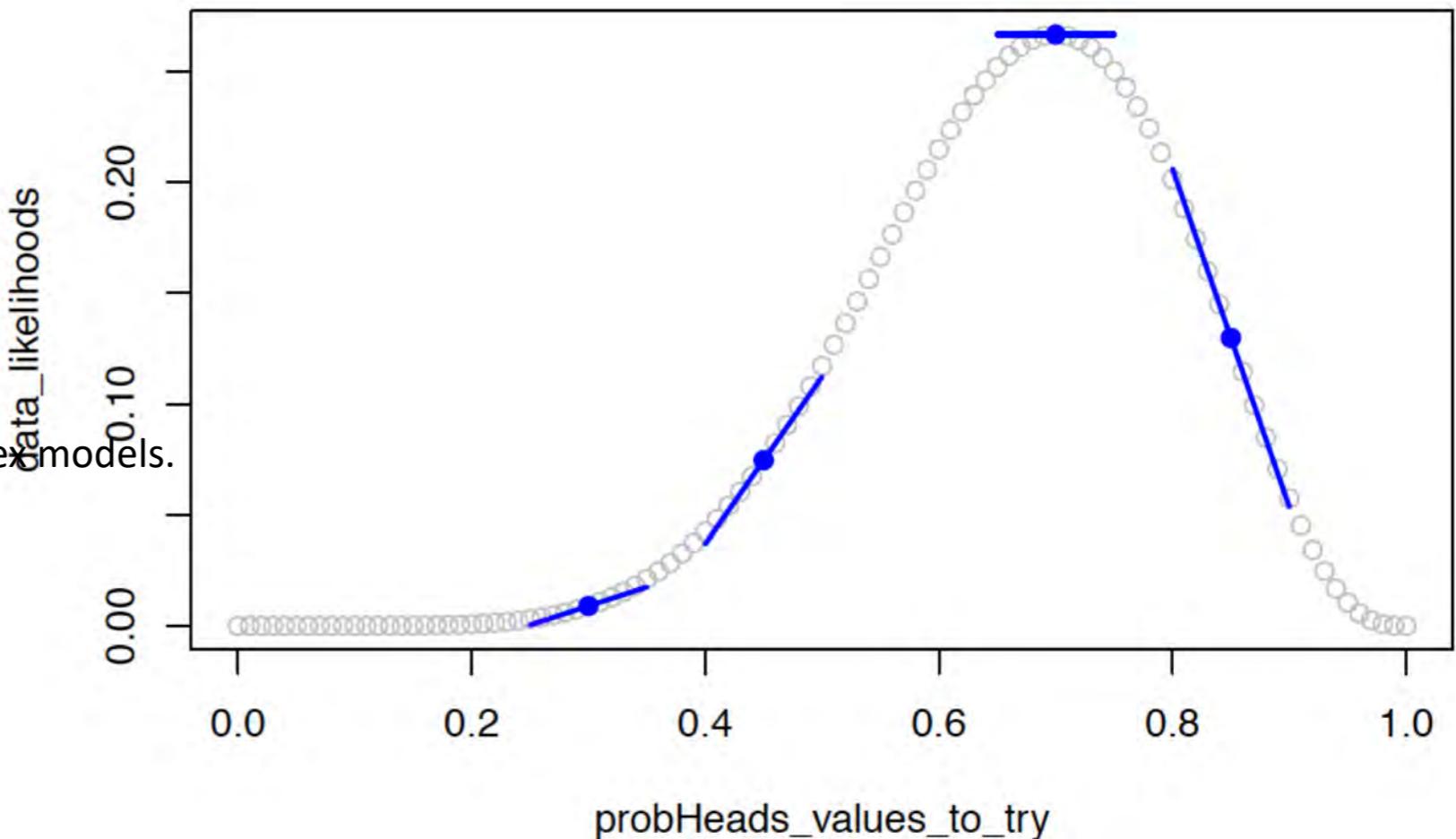


Figure 4: The coinflip likelihood curve, with slopes (first derivative) plotted when  $probHeads=0.3, 0.45, 0.7$ , and  $0.85$ .

# The parameter value that Maximizes the Likelihood (ML)

Method 2: calculus

E.g., here's the proof (not examinable) showing that the likelihood is maximized at

(Number of Heads) / (Total number of coinflips)

<https://stats.stackexchange.com/questions/181035/how-to-derive-the-likelihood-function-for-binomial-distribution-for-parameter-es>

(not examinable)

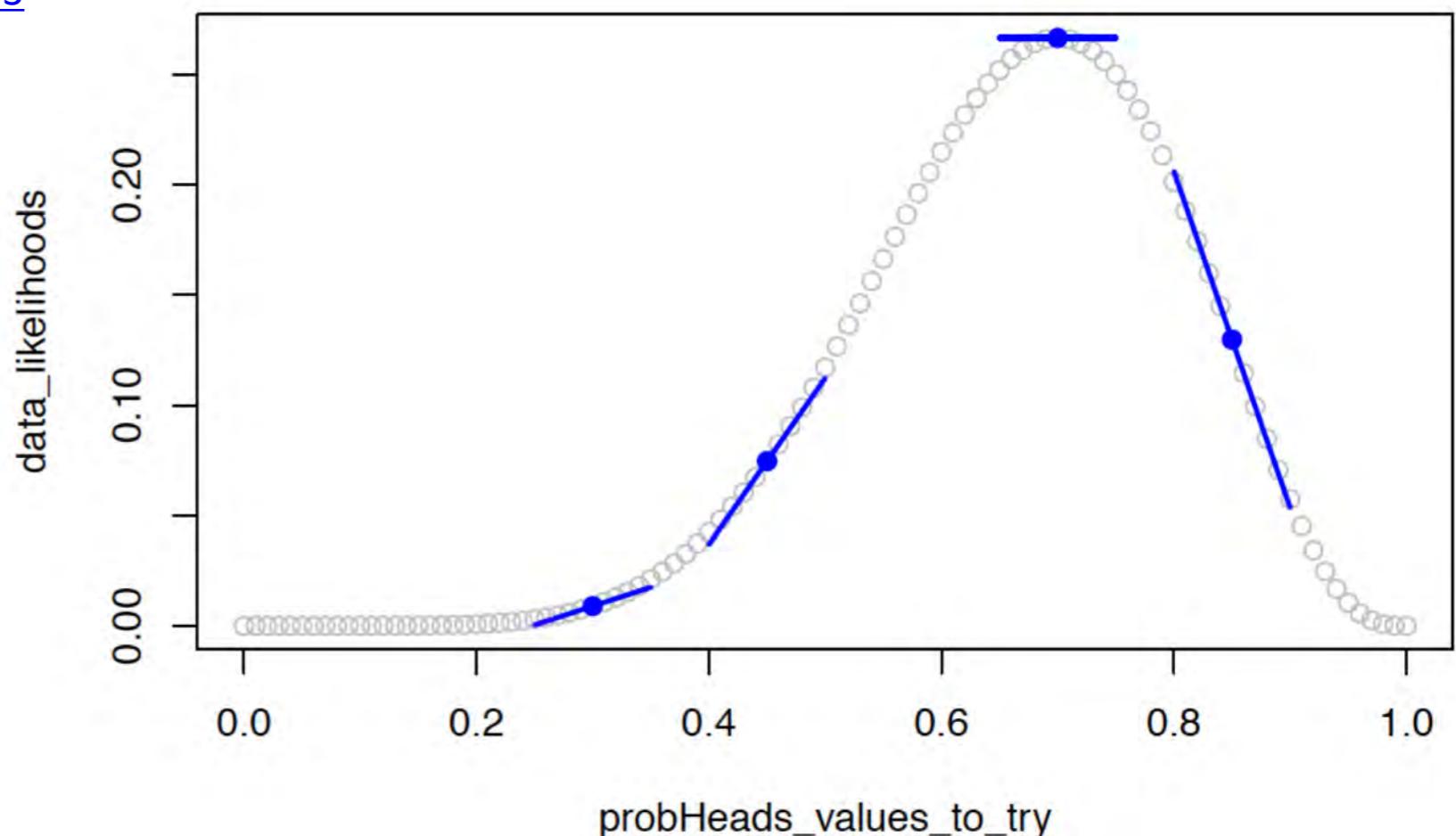


Figure 4: The coinflip likelihood curve, with slopes (first derivative) plotted when  $probHeads=0.3, 0.45, 0.7$ , and  $0.85$ .

# How to find this maximum?

Method 3: exhaustive search (or “gridded search”).

- (1) pick a bunch of parameter values that cover the parameter space
- (2) choose the parameter value that maximizes the likelihood

Problem: can only be done easily for 1 or 2 parameters.

More parameters = more “dimensions” = explosion of number of calculations

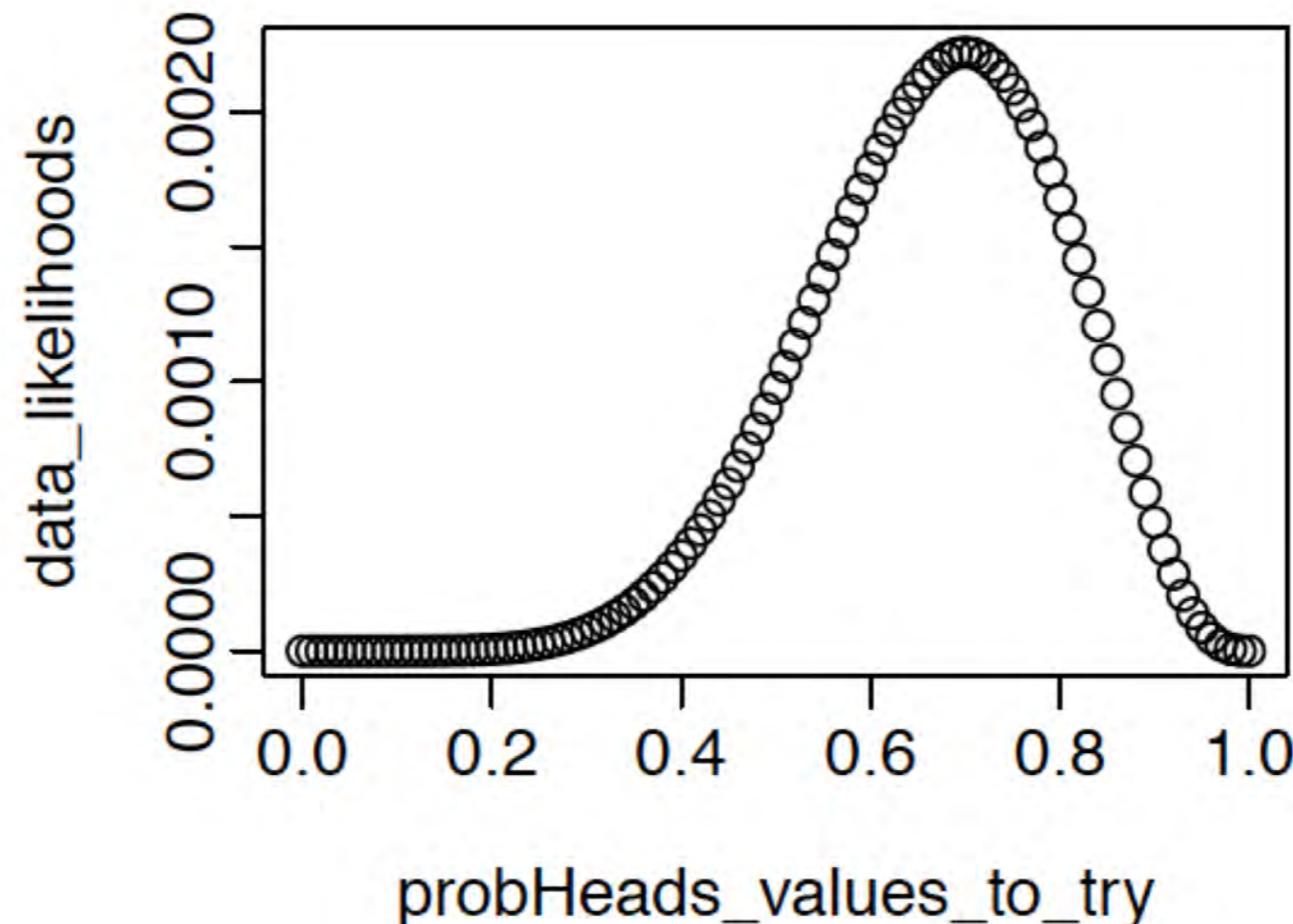


Figure 3: The likelihood of the coinflip data (7 Heads, 3 Tails), under 101 possible values of the parameter *probHeads*.

# How to find this maximum?

Advantage of optimization/hill-climbing: extremely flexible, can be used on all sorts of complex models

Disadvantages of optimization/hill-climbing: much slower than analytic solutions; no absolute guarantee the search will actually find the true peak

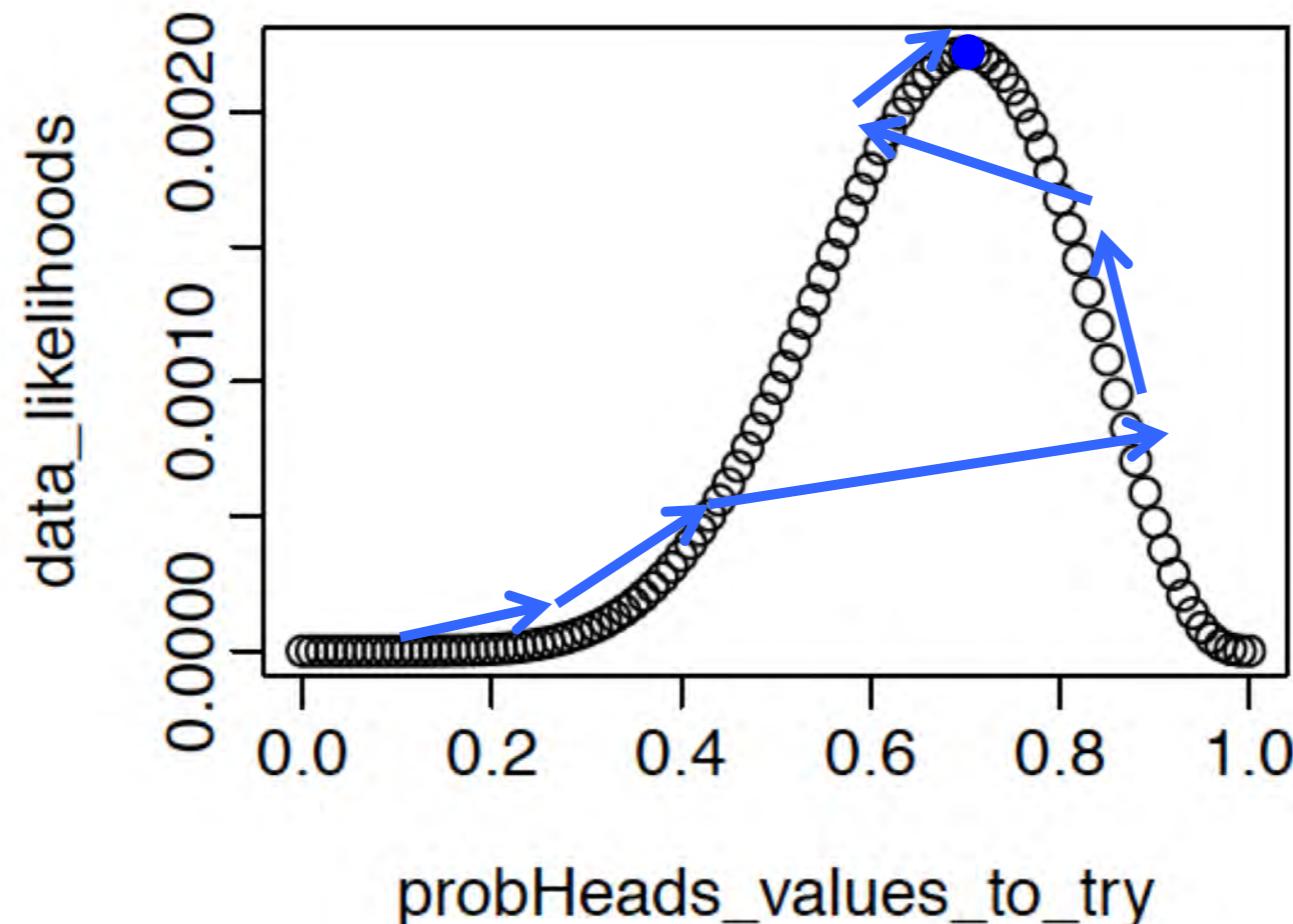
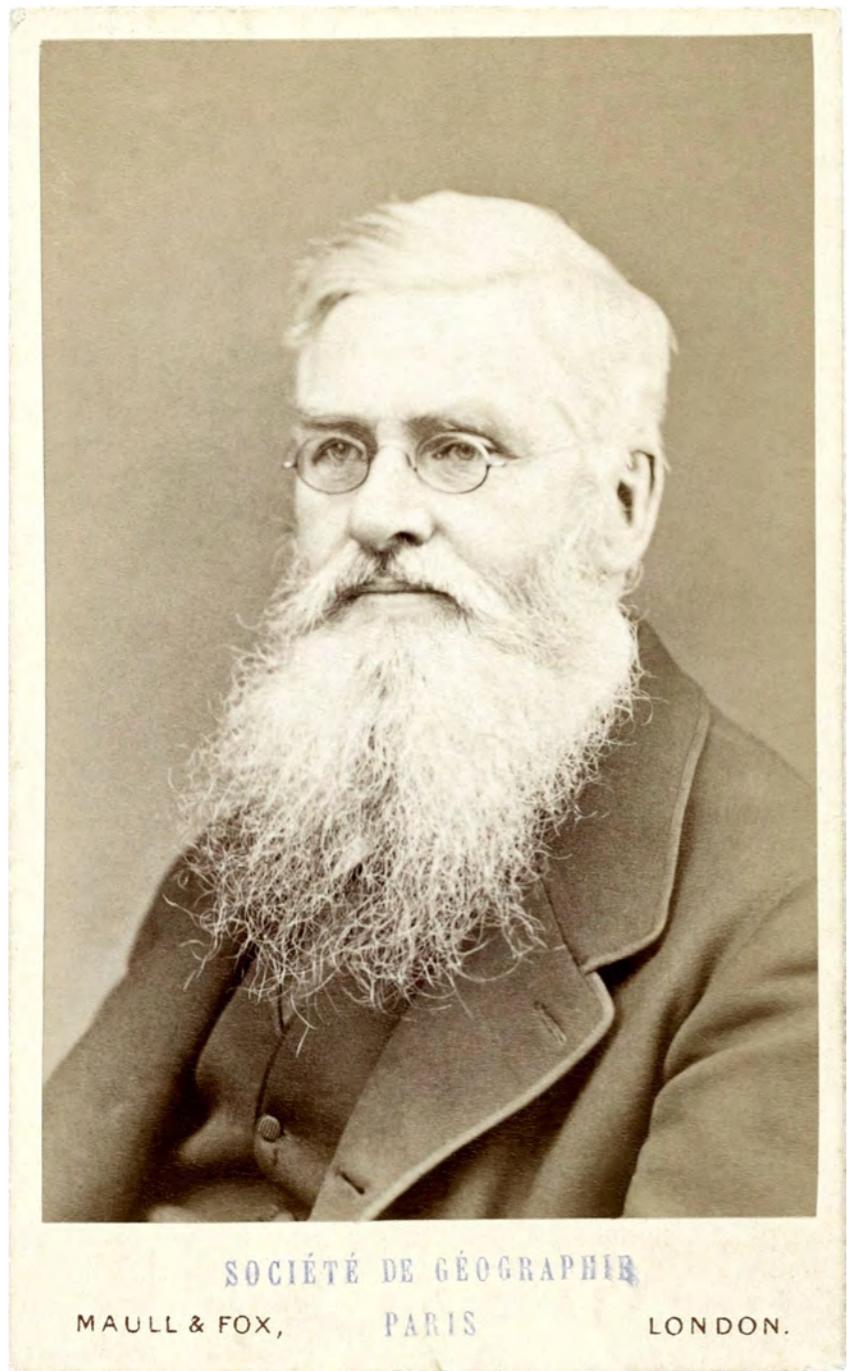


Figure 3: The likelihood of the coinflip data (7 Heads, 3 Tails), under 101 possible values of the parameter `probHeads`.

**Can we measure the  
importance of distance  
in biogeography?**

# Historical biogeography: Wallace and Darwin

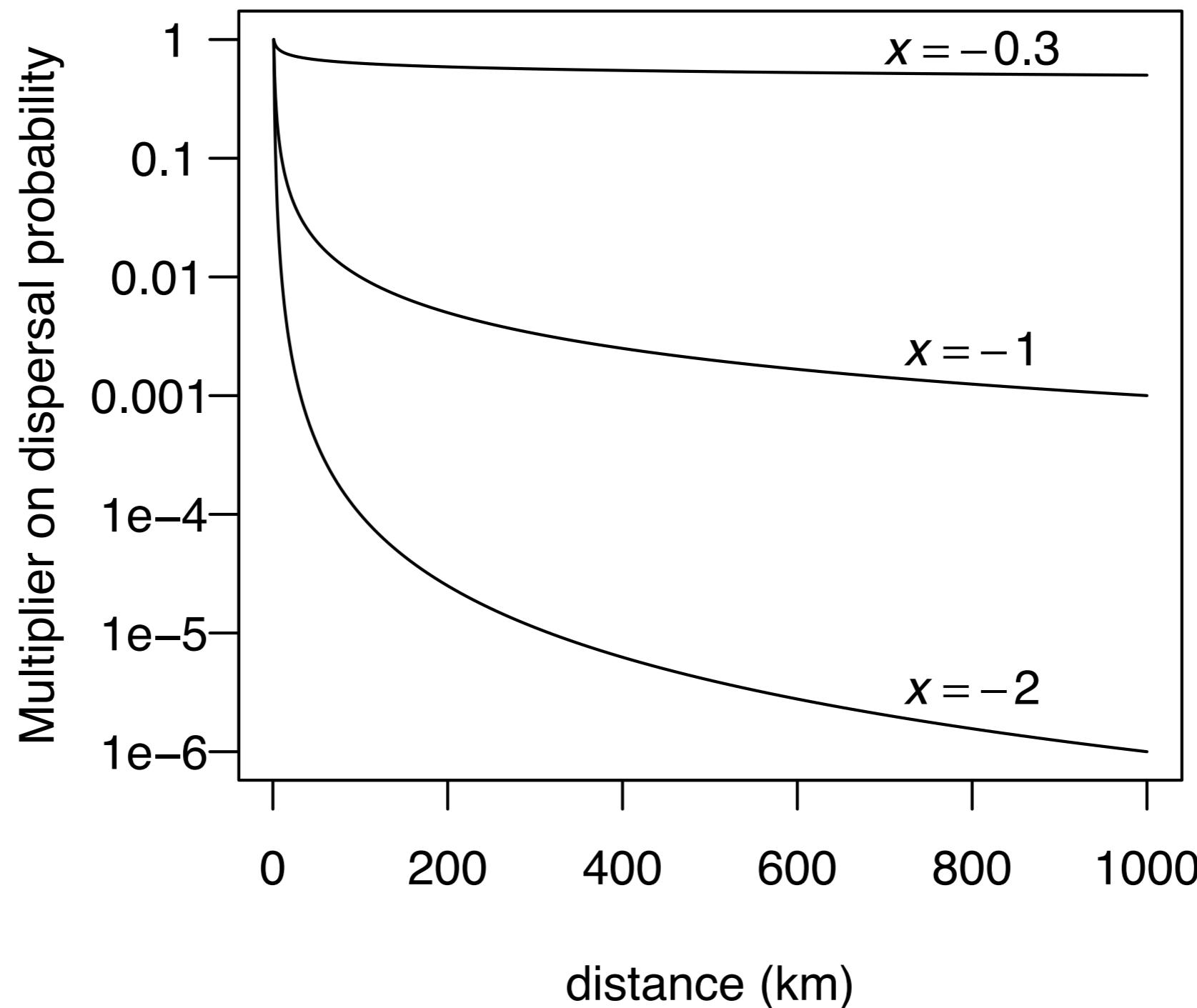


**Wallace (1855): “Every species has come into existence coincident both in space and time with a pre-existing closely allied species.”**



**Darwin (1859): “the more nearly any two forms are related in blood, the nearer they will generally stand to each other in time and space”.**

# The “+x” model: modify dispersal probability by distance<sup>x</sup>





ORIGINAL  
ARTICLE



# Bayesian estimation of the global biogeographical history of the Solanaceae

Julia Dupin<sup>1\*</sup>, Nicholas J. Matzke<sup>2</sup>, Tiina Sarkinen<sup>3</sup> Sandra Knapp<sup>4</sup>,  
Richard G. Olmstead<sup>5</sup>, Lynn Bohs<sup>6</sup> and Stacey D. Smith<sup>1</sup>

,

---



ORIGINAL  
ARTICLE

# Bayesian estimation of the global biogeographical history of the Solanaceae

Julia Dupin<sup>1\*</sup>, Nicholas J. Matzke<sup>2</sup>, Tiina Särkinen<sup>3</sup>, Sandra Knapp<sup>4</sup>,  
Richard G. Olmstead<sup>5</sup>, Lynn Bohs<sup>6</sup> and Stacey D. Smith<sup>1</sup>





# Bayesian estimation of the global biogeographical history of the Solanaceae

Julia Dupin<sup>1\*</sup>, Nicholas J. Matzke<sup>2</sup>, Tiina Särkinen<sup>3</sup>, Sandra Knapp<sup>4</sup>,  
Richard G. Olmstead<sup>5</sup>, Lynn Bohs<sup>6</sup> and Stacey D. Smith<sup>1</sup>

50 to 24 Ma



24 to 10 Ma



10 Ma to Present



T  
i  
m  
e



	SAm	CAm	Car	NAm	AF	EU	OZ
SAm	1	0.4	0.4	0.2	0.1	0.1	0.1
CAm	0.4	1	0.7	0.4	0.1	0.1	0.1
Car	0.4	0.7	1	0.4	0.1	0.1	0.1
NAm	0.2	0.4	0.4	1	0.7	1	0.3
AF	0.1	0.1	0.1	0.7	1	0.7	0.3
EU	0.1	0.1	0.1	0.8	0.7	1	0.3
OZ	0.1	0.1	0.1	0.3	0.3	0.3	1

	SAm	CAm	Car	NAm	AF	EU	OZ
SAm	1	0.6	0.5	0.5	0.1	0.2	0.1
CAm	0.6	1	0.7	0.6	0.1	0.1	0.1
Car	0.5	0.7	1	0.5	0.1	0.1	0.1
NAm	0.5	0.6	0.5	1	0.4	0.5	0.1
AF	0.1	0.1	0.1	0.4	1	1	0.3
EU	0.2	0.1	0.1	0.5	1	1	0.5
OZ	0.1	0.1	0.1	0.1	0.3	0.5	1

	SAm	CAm	Car	NAm	AF	EU	OZ
SAm	1	1	0.75	1	0.1	0.2	0.1
CAm	1	1	0.7	1	0.1	0.1	0.1
Car	0.75	0.7	1	0.8	0.1	0.1	0.1
NAm	1	1	0.8	1	0.1	0.2	0.1
AF	0.1	0.1	0.1	0.1	1	1	0.7
EU	0.2	0.1	0.1	0.2	1	1	0.7
OZ	0.1	0.1	0.1	0.1	0.7	0.7	1

# Global Solanaceae: distance, Biogeographical Stochastic Mapping

	Models	Dispersal multipliers	Free parameters					Log-Likelihood	AIC	Δ AIC	AIC weights
			Number	$d^{(1)}$	$e^{(2)}$	$j^{(3)}$	$w^{(4)}$				
#	<b>Basic Models</b>										
1	DEC_NonTS	Non-TS	2	0.011	0.000	0.000	1.000	-1341.413	2686.826	317.604	0.000
2	DIVALIKE_NonTS	Non-TS	2	0.013	0.000	0.000	1.000	-1401.936	2807.871	438.648	0.000
3	BayAreaLIKE_NonTS	Non-TS	2	0.009	0.049	0.000	1.000	-1528.828	3061.656	692.433	0.000
	<b>Time-Stratified Models</b>										
4	DEC_TS	TS	2	0.025	0.000	0.000	1.000	-1210.832	2425.663	56.441	0.000
5	DIVALIKE_TS	TS	2	0.029	0.000	0.000	1.000	-1252.831	2509.661	140.438	0.000
6	BayAreaLIKE_TS	TS	2	0.023	0.044	0.000	1.000	-1430.614	2865.227	496.004	0.000
	<b>+j Models</b>										
7	DEC_NonTS_j	Non-TS	3	0.010	0.000	0.003	1.000	-1324.525	2655.050	285.828	0.000
8	DIVALIKE_NonTS_j	Non-TS	3	0.011	0.000	0.003	1.000	-1387.768	2781.536	412.313	0.000
9	BayAreaLIKE_NonTS_j	Non-TS	3	0.007	0.004	0.009	1.000	-1335.728	2677.457	308.234	0.000
10	DEC_TS_j	TS	3	0.022	0.000	0.008	1.000	-1191.907	2389.813	20.590	0.000
11	DIVALIKE_TS_j	TS	3	0.025	0.000	0.007	1.000	-1239.123	2484.246	115.024	0.000
12	BayAreaLIKE_TS_j	TS	3	0.015	0.001	0.020	1.000	-1213.992	2433.984	64.762	0.000
	<b>+w Models</b>										
13	DEC_TS_w	TS	3	0.026	0.000	0.000	1.114	-1204.980	2415.960	46.738	0.000
14	DIVALIKE_TS_w	TS	3	0.032	0.000	0.000	1.201	-1250.615	2507.231	138.008	0.000
15	BayAreaLIKE_TS_w	TS	3	0.026	0.045	0.000	1.307	-1425.518	2857.036	487.813	0.000
	<b>+j +w Models</b>										
16	DEC_TS_j_w	TS	4	0.029	0.000	0.009	1.887	-1180.611	2369.223	0.000	0.999
17	DIVALIKE_TS_j_w	TS	4	0.027	0.000	0.007	1.344	-1221.864	2451.729	82.506	0.000
18	BayAreaLIKE_TS_j_w	TS	4	0.016	0.001	0.021	1.117	-1210.247	2428.494	59.271	0.000

# Global Solanaceae: distance, Biogeographical Stochas3c Mapping

	Models	Dispersal multipliers	Free parameters					Log-Likelihood	AIC	$\Delta AIC$	AIC weights
			Number	$d^{(1)}$	$e^{(2)}$	$j^{(3)}$	$w^{(4)}$				
#	<b>Basic Models</b>										
1	DEC_NonTS	Non-TS	2	0.011	0.000	0.000	1.000	-1341.413	2686.826	317.604	0.000
2	DIVALIKE_NonTS	Non-TS	2	0.013	0.000	0.000	1.000	-1401.936	2807.871	438.648	0.000
3	BayAreaLIKE_NonTS	Non-TS	2	0.009	0.049	0.000	1.000	-1528.828	3061.656	692.433	0.000
	<b>Time-Stratified Models</b>										
4	DEC_TS	TS	2	0.025	0.000	0.000	1.000	-1210.832	2425.663	56.441	0.000
5	DIVALIKE_TS	TS	2	0.029	0.000	0.000	1.000	-1252.831	2509.661	140.438	0.000
6	BayAreaLIKE_TS	TS	2	0.023	0.044	0.000	1.000	-1430.614	2865.227	496.004	0.000
	<b>+j Models</b>										
7	DEC_NonTS_j	Non-TS	3	0.010	0.000	0.003	1.000	-1324.525	2655.050	285.828	0.000
8	DIVALIKE_NonTS_j	Non-TS	3	0.011	0.000	0.003	1.000	-1387.768	2781.536	412.313	0.000
9	BayAreaLIKE_NonTS_j	Non-TS	3	0.007	0.004	0.009	1.000	-1335.728	2677.457	308.234	0.000
10	DEC_TS_j	TS	3	0.022	0.000	0.008	1.000	-1191.907	2389.813	20.590	0.000
11	DIVALIKE_TS_j	TS	3	0.025	0.000	0.007	1.000	-1239.123	2484.246	115.024	0.000
12	BayAreaLIKE_TS_j	TS	3	0.015	0.001	0.020	1.000	-1213.992	2433.984	64.762	0.000
	<b>+w Models</b>										
13	DEC_TS_w	TS	3	0.026	0.000	0.000	1.114	-1204.980	2415.960	46.738	0.000
14	DIVALIKE_TS_w	TS	3	0.032	0.000	0.000	1.201	-1250.615	2507.231	138.008	0.000
15	BayAreaLIKE_TS_w	TS	3	0.026	0.045	0.000	1.307	-1425.518	2857.036	487.813	0.000
	<b>+j +w Models</b>										
16	DEC_TS_j_w	TS	4	0.029	0.000	0.009	1.887	-1180.611	2369.223	0.000	0.999
17	DIVALIKE_TS_j_w	TS	4	0.027	0.000	0.007	1.344	-1221.864	2451.729	82.506	0.000
18	BayAreaLIKE_TS_j_w	TS	4	0.016	0.001	0.021	1.117	-1210.247	2428.494	59.271	0.000

# Akaike Information Criterion

“True model”

Better fit

- distance from truth

AIC =  
estimator of  
relative distance  
from true model

Worse fit

higher AIC = higher distance

lower AIC = lower distance

higher data  
log-likelihood  
(LnL)

fewer  
free  
parameters

**Akaike Information  
Criterion (AIC) =**  
$$-2(\text{LnL} - \# \text{ of parameters})$$

lower data  
log-likelihood  
(LnL)

more  
free  
parameters

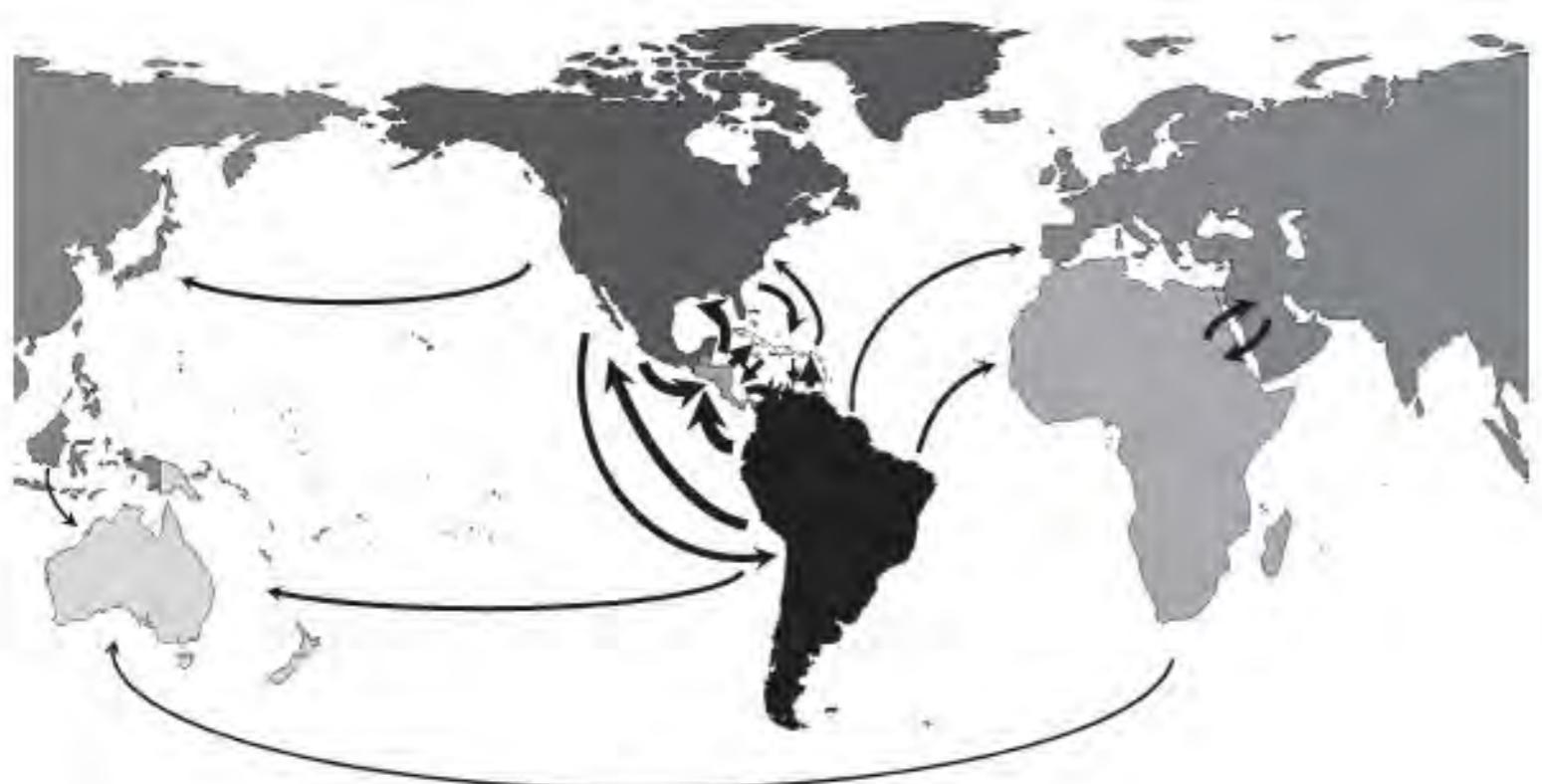
# Global Solanaceae: distance, Biogeographical Stochastic Mapping

	Models	Dispersal multipliers	Free parameters					Log-Likelihood	AIC	$\Delta$ AIC	AIC weights
			Number	$d^{(1)}$	$e^{(2)}$	$j^{(3)}$	$w^{(4)}$				
#	<b>Basic Models</b>										
1	DEC_NonTS	Non-TS	2	0.011	0.000	0.000	1.000	-1341.413	2686.826	317.604	0.000
2	DIVALIKE_NonTS	Non-TS	2	0.013	0.000	0.000	1.000	-1401.936	2807.871	438.648	0.000
3	BayAreaLIKE_NonTS	Non-TS	2	0.009	0.049	0.000	1.000	-1528.828	3061.656	692.433	0.000
	<b>Time-Stratified Models</b>										
4	DEC_TS	TS	2	0.025	0.000	0.000	1.000	-1210.832	2425.663	56.441	0.000
5	DIVALIKE_TS	TS	2	0.029	0.000	0.000	1.000	-1252.831	2509.661	140.438	0.000
6	BayAreaLIKE_TS	TS	2	0.023	0.044	0.000	1.000	-1430.614	2865.227	496.004	0.000
	<b>+j Models</b>										
7	DEC_NonTS_j	Non-TS	3	0.010	0.000	0.003	1.000	-1324.525	2655.050	285.828	0.000
8	DIVALIKE_NonTS_j	Non-TS	3	0.011	0.000	0.003	1.000	-1387.768	2781.536	412.313	0.000
9	BayAreaLIKE_NonTS_j	Non-TS	3	0.007	0.004	0.009	1.000	-1335.728	2677.457	308.234	0.000
10	DEC_TS_j	TS	3	0.022	0.000	0.008	1.000	-1191.907	2389.813	20.590	0.000
11	DIVALIKE_TS_j	TS	3	0.025	0.000	0.007	1.000	-1239.123	2484.246	115.024	0.000
12	BayAreaLIKE_TS_j	TS	3	0.015	0.001	0.020	1.000	-1213.992	2433.984	64.762	0.000
	<b>+w Models</b>										
13	DEC_TS_w	TS	3	0.026	0.000	0.000	1.114	-1204.980	2415.960	46.738	0.000
14	DIVALIKE_TS_w	TS	3	0.032	0.000	0.000	1.201	-1250.615	2507.231	138.008	0.000
15	BayAreaLIKE_TS_w	TS	3	0.026	0.045	0.000	1.307	-1425.518	2857.036	487.813	0.000
	<b>+j +w Models</b>										
16	DEC_TS_j_w	TS	4	0.029	0.000	0.009	1.887	-1180.611	2369.223	0.000	0.999
17	DIVALIKE_TS_j_w	TS	4	0.027	0.000	0.007	1.344	-1221.864	2451.729	82.506	0.000
18	BayAreaLIKE_TS_j_w	TS	4	0.016	0.001	0.021	1.117	-1210.247	2428.494	59.271	0.000

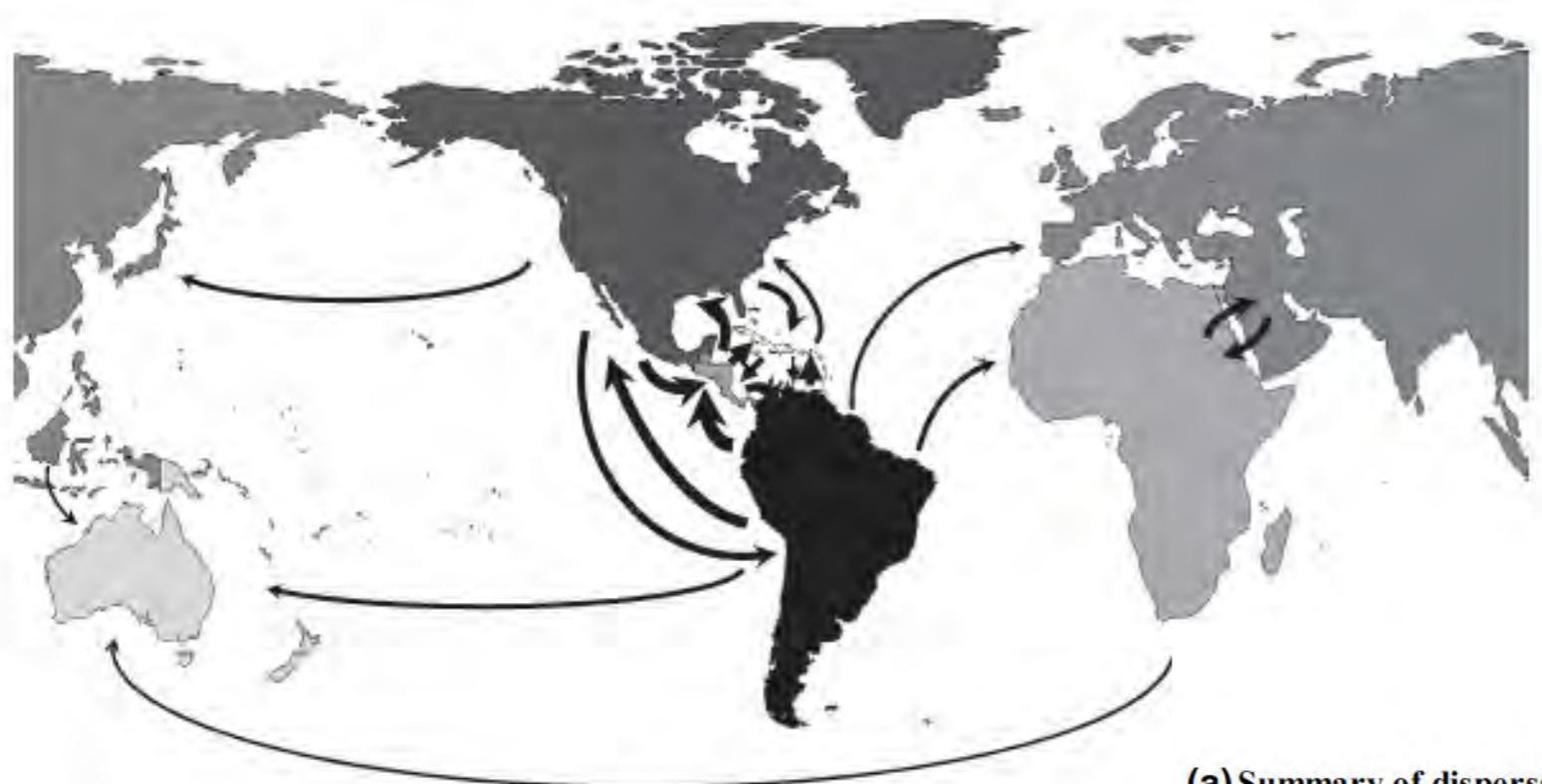
# Global Solanaceae: distance, Biogeographical Stochastic Mapping

#	Models	Dispersal multipliers	Free parameters					Log-Likelihood	AIC	$\Delta$ AIC	AIC weights
			Number	$d^{(1)}$	$e^{(2)}$	$j^{(3)}$	$w^{(4)}$				
1	DEC_N									317.604	0.000
2	DIVAL									438.648	0.000
3	BayArea Time-Space									692.433	0.000
4	DEC_TS									56.441	0.000
5	DIVAL_TS									140.438	0.000
6	BayArea +j Model									496.004	0.000
7	DEC_TS_w									285.828	0.000
8	DIVAL_TS_w									412.313	0.000
9	BayArea_TS_w									308.234	0.000
10	DEC_TS_j									20.590	0.000
11	DIVAL_TS_j									115.024	0.000
12	BayArea_TS_j									64.762	0.000
13	DEC_TS_j_w									46.738	0.000
14	DIVAL_TS_j_w									138.008	0.000
15	BayAreaLIKE_TS_w	TS	3	0.026	0.045	0.000	1.307	-1425.518	2857.036	487.813	0.000
	+j +w Models										
16	<b>DEC_TS_j_w</b>	TS	4	<b>0.029</b>	<b>0.000</b>	<b>0.009</b>	<b>1.887</b>	<b>-1180.611</b>	<b>2369.223</b>	<b>0.000</b>	<b>0.999</b>
17	DIVALIKE_TS_j_w	TS	4	0.027	0.000	0.007	1.344	-1221.864	2451.729	82.506	0.000
18	BayAreaLIKE_TS_j_w	TS	4	0.016	0.001	0.021	1.117	-1210.247	2428.494	59.271	0.000

# Global Solanaceae: distance, Biogeographical Stochastic Mapping



# Global Solanaceae: distance, Biogeographical Stochastic Mapping



Bayesian estimation of Solanaceae biogeography

(a) Summary of dispersal events counts (and standard deviations)

	SAm	CAm	Car	NAm	AF	EU	OZ	
SAm	-	48.6 (2.63)	15.13 (1.62)	41.65 (2.83)	5.67 (0.89)	5.03 (1.14)	3.58 (0.77)	119.66 47%
CAm	11.35 (2.32)	-	10.12 (1.41)	23.26 (4.21)	0.22 (0.19)	0.35 (0.34)	0.32 (0.31)	45.62 18%
Car	1.21 (0.94)	4.20 (1.14)	-	3.09 (1.02)	0.22 (0.27)	0.11 (0.17)	0.14 (0.08)	8.97 4%
NAm	9.12 (1.51)	32.44 (4.01)	7.39 (1.20)	-	0.59 (0.29)	2.33 (0.78)	1.34 (0.52)	53.21 20%
AF	0.03 (0.21)	0.04 (0.22)	0.07 (0.33)	0.13 (0.31)	-	10.15 (1.39)	3.89 (0.83)	14.31 6%
EU	0.09 (0.22)	0.08 (0.32)	0.11 (0.21)	1.17 (0.32)	8.28 (1.32)	-	1.78 (0.37)	11.51 4%
OZ	0.06 (0.12)	0.04 (0.21)	0.04 (0.11)	0.12 (0.34)	1.39 (0.71)	0.88 (0.27)	-	2.53 1%
	21.86 9%	85.4 33%	32.86 13%	69.42 27%	16.37 6%	18.85 8%	11.05 4%	255.81 100%

# **What if dispersal ability depends on an evolving trait?**

# What if dispersal ability depends on an evolving trait?



Fence or snake-eyed skink (*Cryptoblepharus virgatus*) photographed in Sydney, Australia.  
[https://en.wikipedia.org/wiki/Cryptoblepharus\\_virgatus#/media/File:Cryptoblepharus\\_virgatus.jpg](https://en.wikipedia.org/wiki/Cryptoblepharus_virgatus#/media/File:Cryptoblepharus_virgatus.jpg)

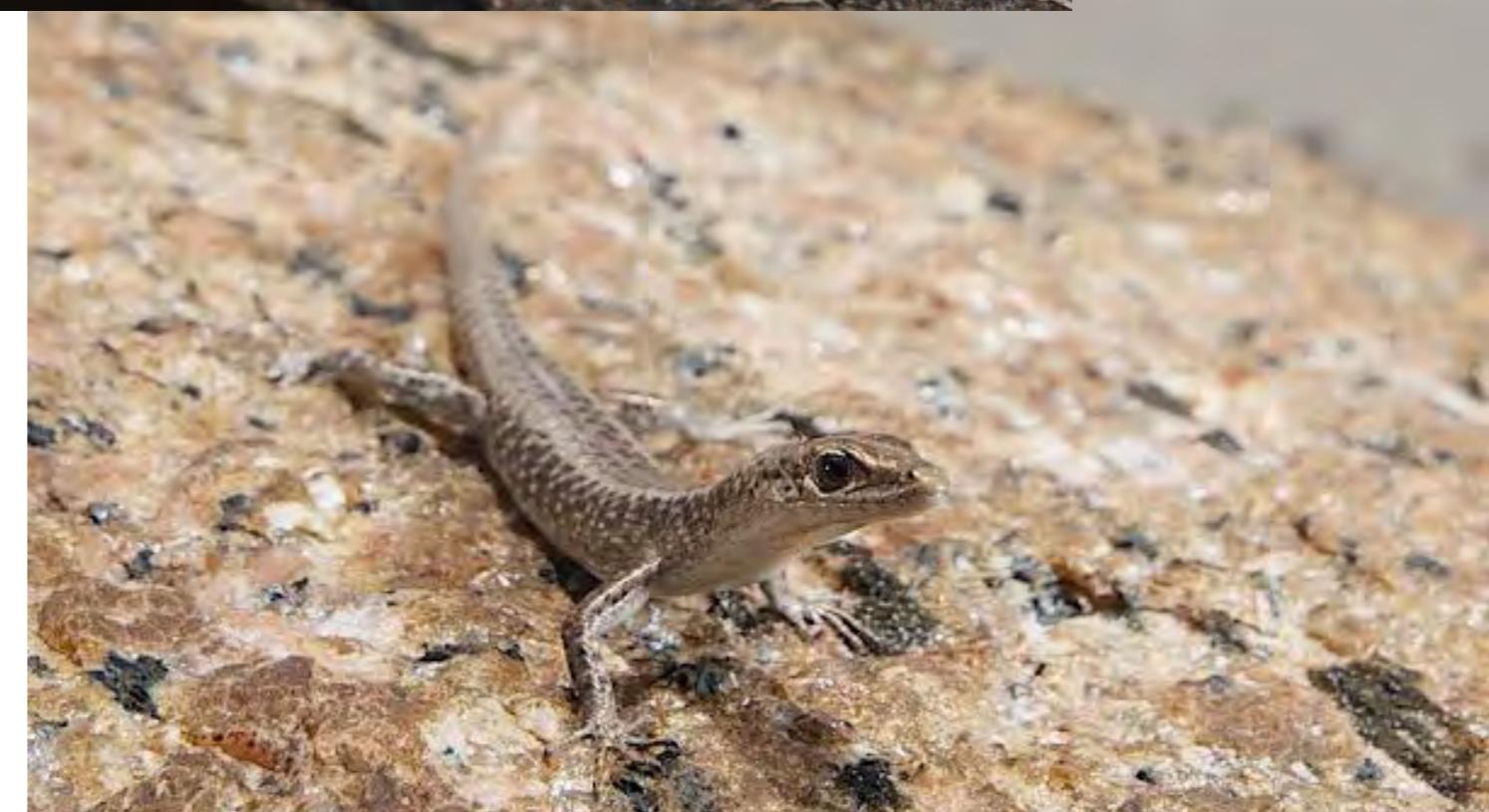
# ***Cryptoblepharus* lizards (with Moos Blom, ANU)**



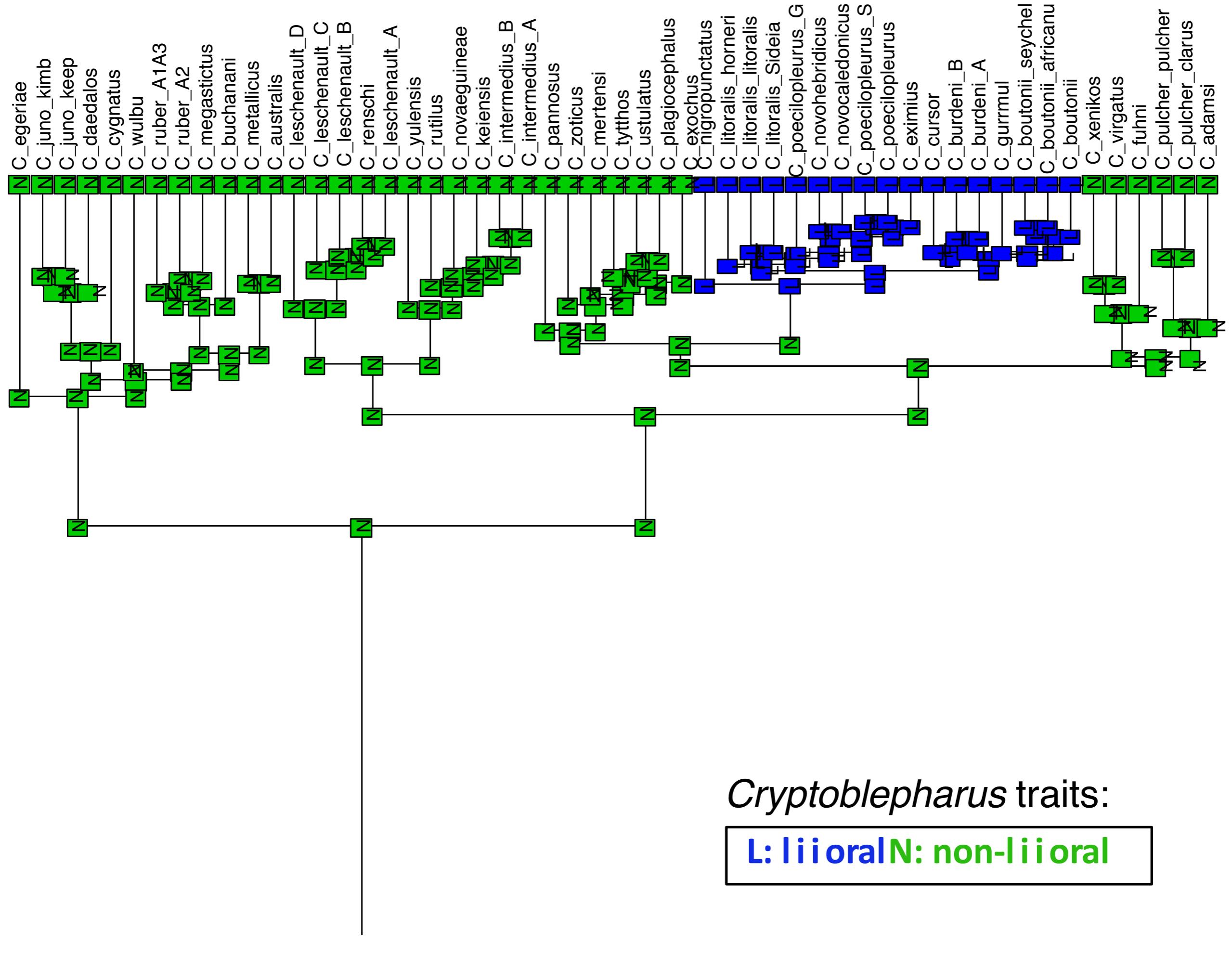
**rock-dwelling species**



**arboreal  
species**

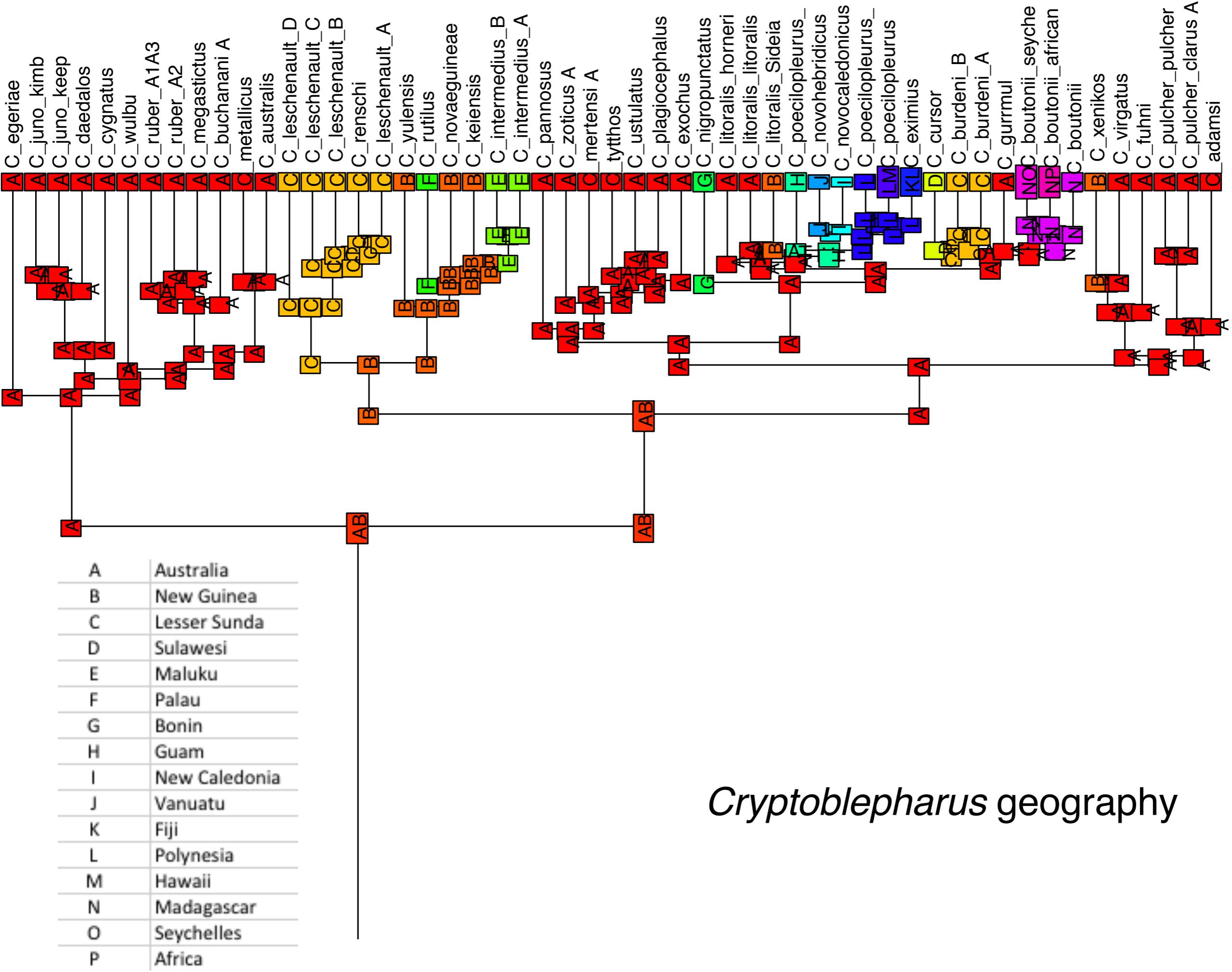


**littoral (beach)  
species**



*Cryptoblepharus* traits:

**L: litoral** **N: non-litoral**



# Trait-dependent DEC model

Traditional:

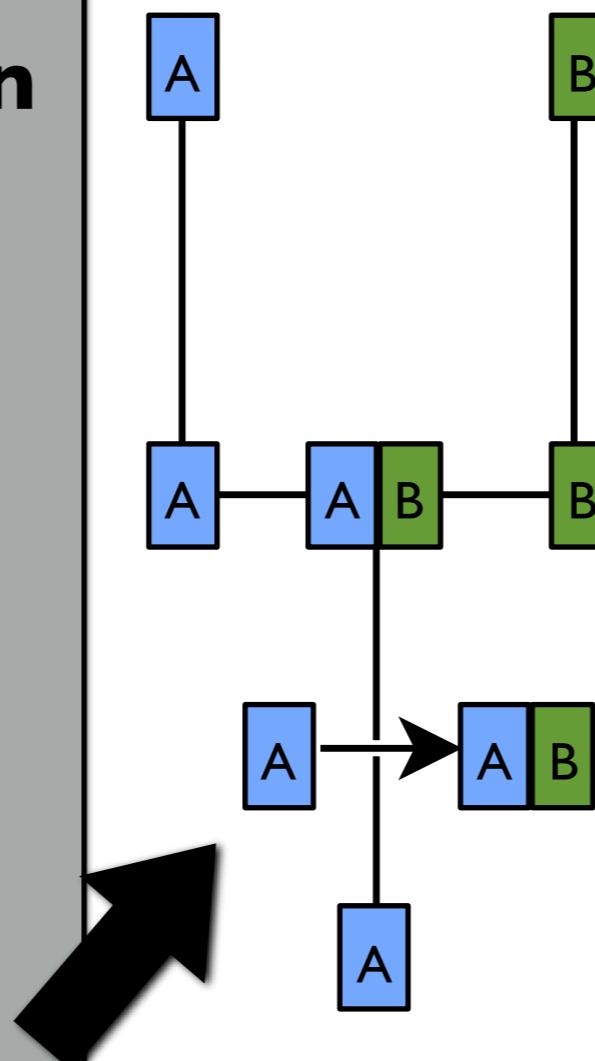
## Dispersal-Extinction (on branches)

$d$  = rate of “dispersal”  
(range expansion)

$e$  = rate of “extinction”  
(range contraction /  
local extirpation)

Rate matrix:

	null	A	B	AB
null	-			
A	$e$	-		$d$
B	$e$	-		$d$
AB		$e$	$e$	-



Trait-dependent:

Rate matrix:

	FLY	NOT
FLY	-	$t_{12}$
NOT	$t_{21}$	-

descendant range

	null	A	B	AB
null	-			
A	$e$	-		$d$
B	$e$	-	-	$d$
AB		$e$	$e$	-

ancestor  
range

ancestor  
range

## Trait matrix (anagenetic):

		descendant trait	
		state 1	state 2
ancestor trait	state 1	-	$t_{12}$
	state 2	$t_{21}$	-

## Geography transition matrix (anagenetic):

+

		descendant range			
ancestor range	null	A	B	AB	
	null	-			
A	e	-		$d$	
B	e		-	$d$	
AB		e	e	-	

==

## Combined trait + geography matrix (anagenetic):

		descendant trait+geographic range							
ancestor trait+geographic range	1,null	1,A	1,B	1,AB	2,null	2,A	2,B	2,AB	
	1,null	-				$t_{12}$			
1,A	e	-			$m_{1d}$		$t_{12}$		
1,B	e		-		$m_{1d}$			$t_{12}$	
1,AB		e	e	-					$t_{12}$
2,null	$t_{21}$					-			
2,A		$t_{21}$				e	-		$m_{2d}$
2,B			$t_{21}$		e		-		$m_{2d}$
2,AB				$t_{21}$	e	e	-		

**Table D.** Statistical model comparison with sample-size corrected AIC (AICc).

Model	LnL	# of free parameters AICc	AICc model weight	Percentage model weight
<b>1.</b> DEC+J, with trait transitions	-106.5	5	224.2	0.000
<b>2.</b> DEC+J+x (distance-based dispersal), with trait transitions	-98.8	6	211.5	0.000
<b>3.</b> DEC+J, with trait transitions, and <u>dispersal multiplier for trait 'littoral'</u>	-95.5	6	204.8	0.002
<b>4.</b> DEC+J+x (distance-based dispersal), with trait transitions, and dispersal multiplier for trait 'littoral'	-88.0	7	192.6	0.998

**Table D.** Statistical model comparison with sample-size corrected AIC (AICc).

Model	LnL	# of free parameters	AICc	AICc model weight	Percentage model weight
1. DEC+J, with trait transitions	-106.5	5	224.2	0.000	0.00%
2. DEC+J+x (distance-based dispersal), with trait transitions	-98.8	6	211.5	0.000	0.01%
3. DEC+J, with trait transitions, and dispersal multiplier for trait 'littoral'	-95.5	6	204.8	0.002	0.22%
4. DEC+J+x (distance-based dispersal), with trait transitions, and dispersal multiplier for trait 'littoral'	-88.0	7	192.6	0.998	99.77%

**Table B.** Maximum-likelihood estimates of parameters inferred with BioGeoBEARS for the DEC+J model, with and without distance-based dispersal (+x) and trait-based dispersal (+m2).

Model	Parameters (defined)							
	d	e	j	x	t12	t21	m1	m2
1. DEC+J, with trait transitions	0.0017	0	0.012	0	0.0071	0	1	1
2. DEC+J+x (distance-based dispersal), with trait transitions	0.0244	0	0.174	-1.23	0.0071	0	1	1
3. DEC+J, with trait transitions, and dispersal multiplier for trait 'littoral'	0.0007	0	0.005	0	0.0070	0	1	8.51
4. DEC+J+x (distance-based dispersal), with trait transitions, and dispersal multiplier for trait 'littoral'	0.0125	0	0.095	-1.23	0.0070	0	1	6.12
						(parameter is fixed)		

**Table B.** Maximum-likelihood estimates of parameters inferred with BioGeoBEARS for the DEC+J model, with and without distance-based dispersal (+x) and trait-based dispersal (+m2).

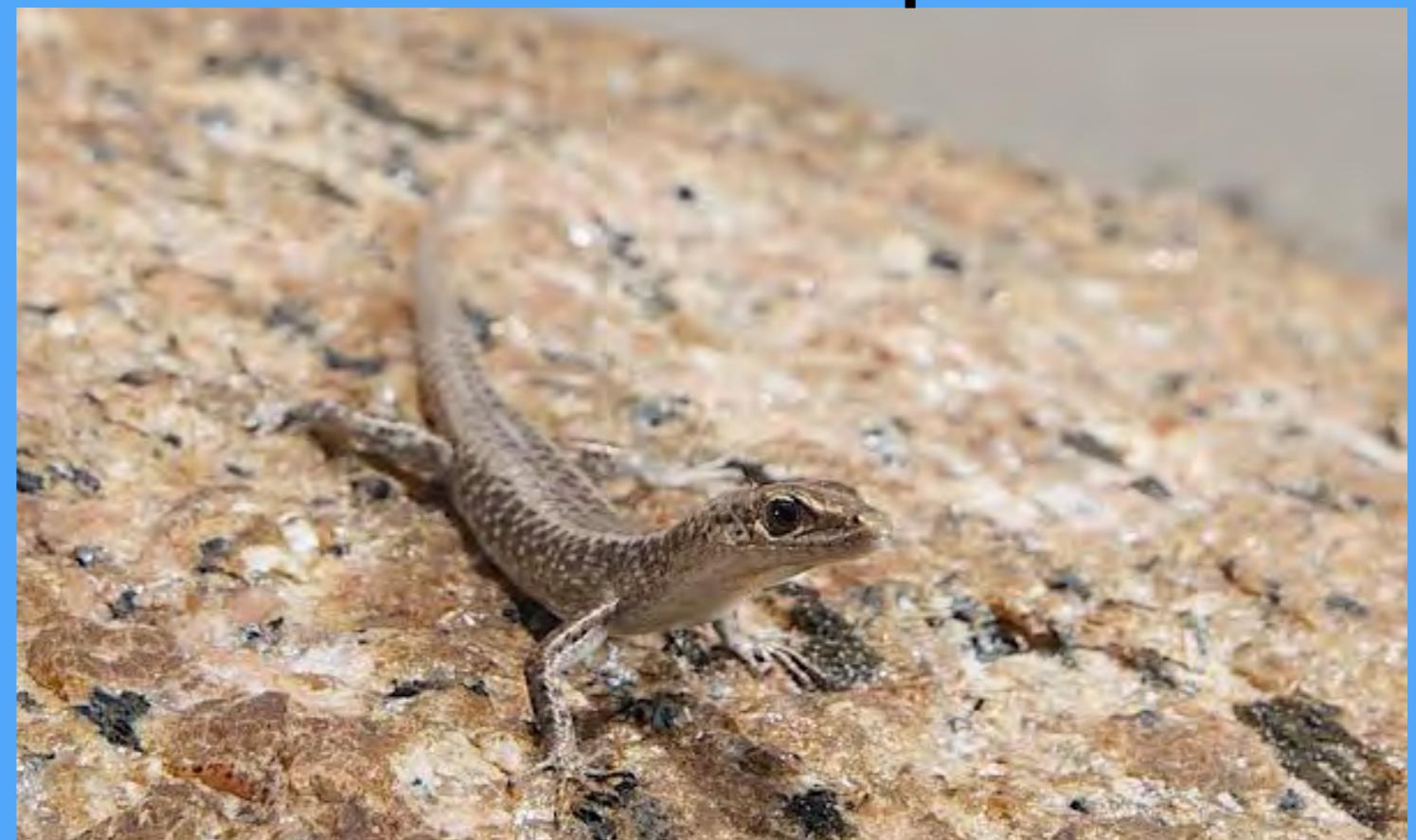
Model	Parameters (defined)							
	d	e	j	x	t12	t21	m1	m2
1. DEC+J, with trait transitions	0.0017	0	0.012	0	0.0071	0	1	1
2. DEC+J+x (distance-based dispersal), with trait transitions	0.0244	0	0.174	-1.23	0.0071	0	1	1
3. DEC+J, with trait transitions, and dispersal multiplier for trait 'littoral'	0.0007	0	0.005	0	0.0070	0	1	8.51
4. DEC+J+x (distance-based dispersal), with trait transitions, and dispersal multiplier for trait 'littoral'	0.0125	0	0.095	-1.23	0.0070	0	1	6.12
					(parameter is fixed)			

Tabl  
disp

*Cryptoblepharus* lizards:  
littoral species have a dispersal  
rate ~6 times higher over  
evolutionary time

1. D  
2. D  
disp  
3.D  
disp  
4.D  
disp  
disp

littoral (beach)  
species



# Trait-dependent dispersal in Podocarpaceae+Araucariaceae (with Kristina Klaus, Univ. of Bochum)



**Figure 1.** Seed cone variability in the Podocarpaceae. **a** *Podocarpus macrophyllus*, **b** *Podocarpus nivalis*, **c** *Phyllocladus aspleniifolius*, **d** *Microcachys tetragona*, **e** *Dacrycarpus dacrydioides* **f** *Podocarpus elatus*, **g** *Afrocarpus falcatus*, **h** *Saxeothaea conspicua*, **i** *Prumnopitys amara*.

# Trait-dependent dispersal in Podocarpaceae+Araucariaceae (with Kristina Klaus, Univ. of Bochum)



**Hypothesis:**

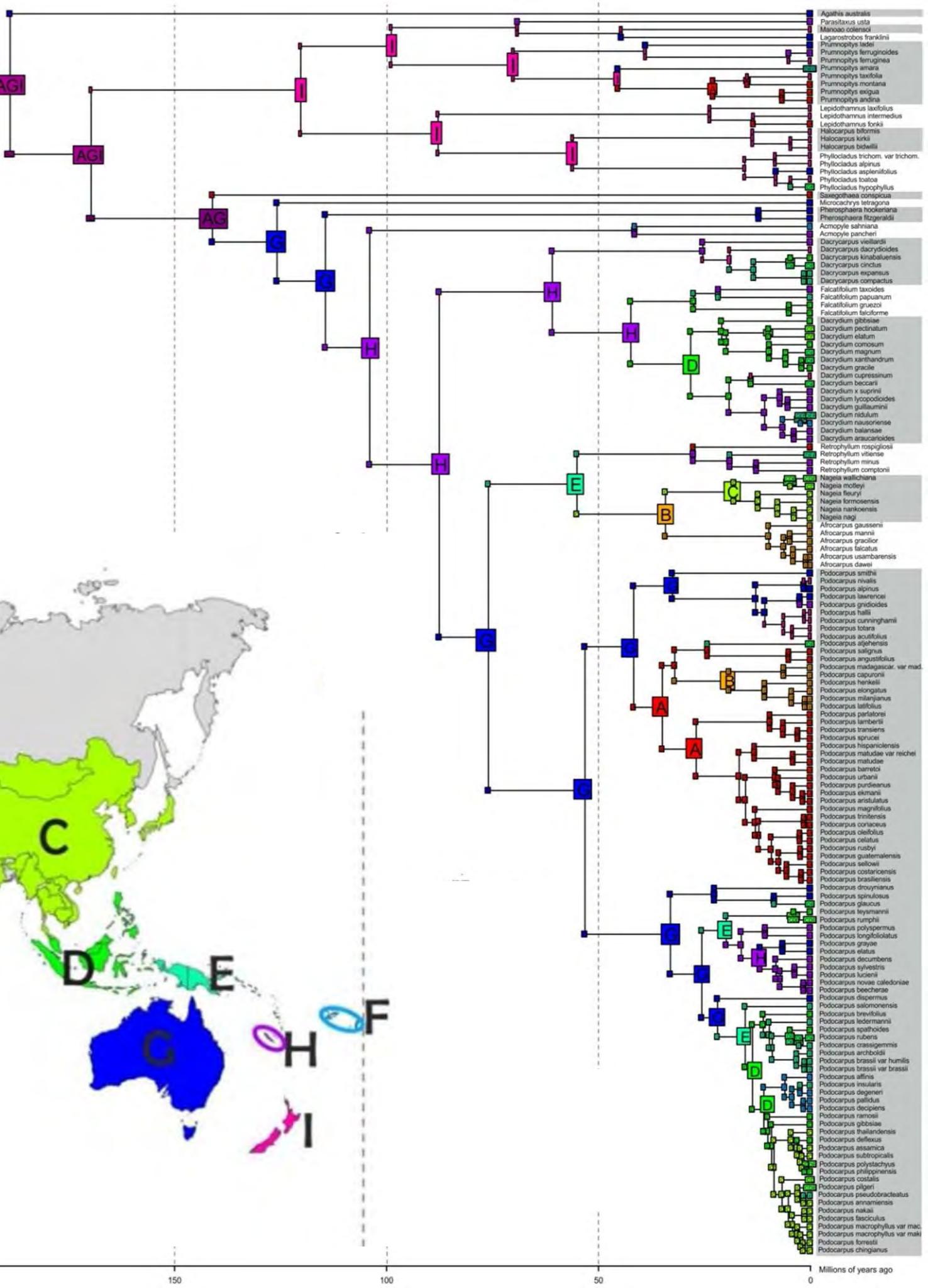
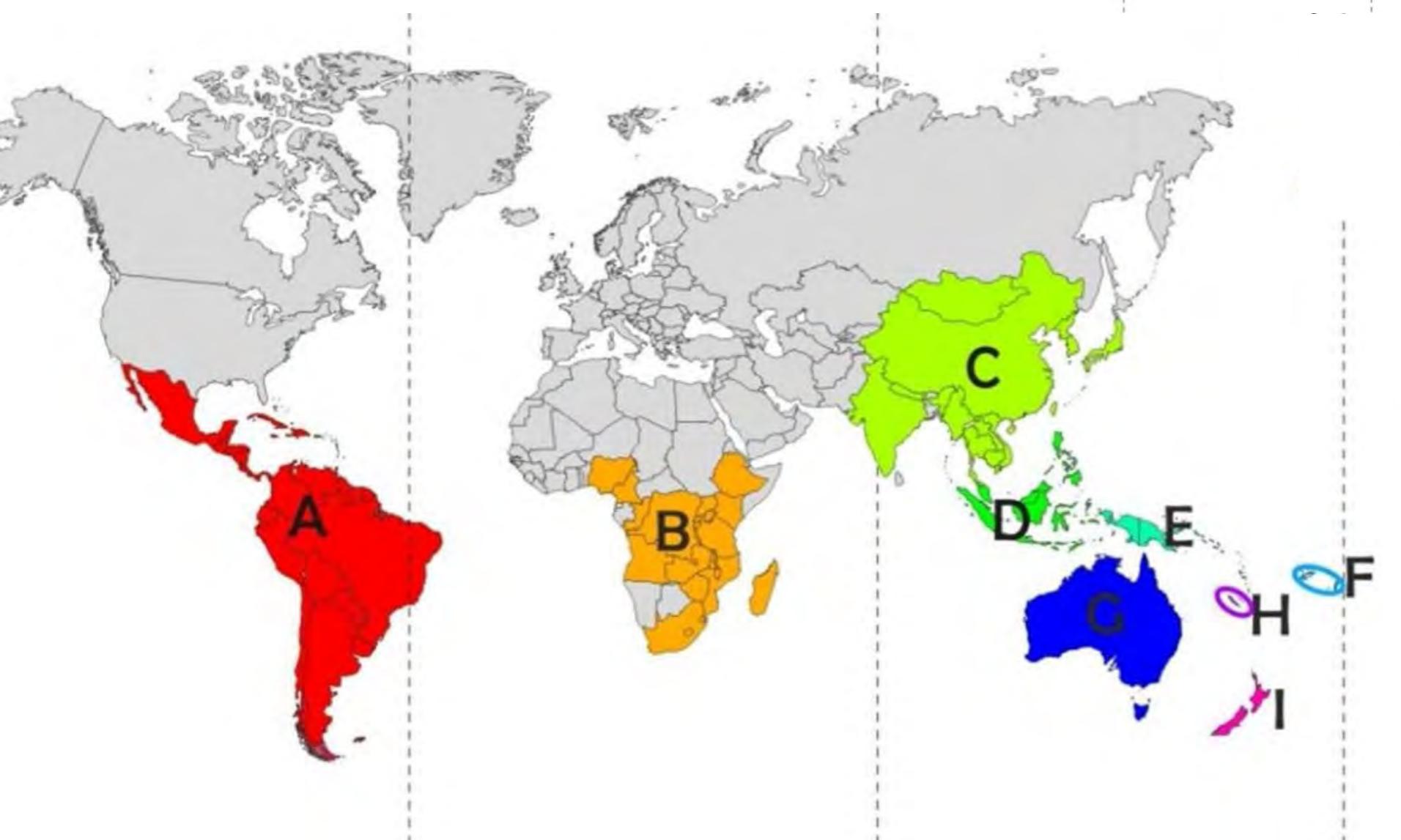
**fleshy cones  
will be better  
dispersers**

**Figure 1.** Seed cone variability in the Podocarpaceae. **a** *Podocarpus macrophyllus*, **b** *Podocarpus nivalis*, **c** *Phyllocladus aspleniifolius*, **d** *Microcachys tetragona*, **e** *Dacrycarpus dacrydioides* **f** *Podocarpus elatus*, **g** *Afrocarpus falcatus*, **h** *Saxegothaea conspicua*, **i** *Prumnopitys amara*.

# Podocarpaceae

## DEC+j+x+traits model:

### Biogeography



# Podocarpaceae

## DEC+ $j$ + $x$ +traits model:

### Traits



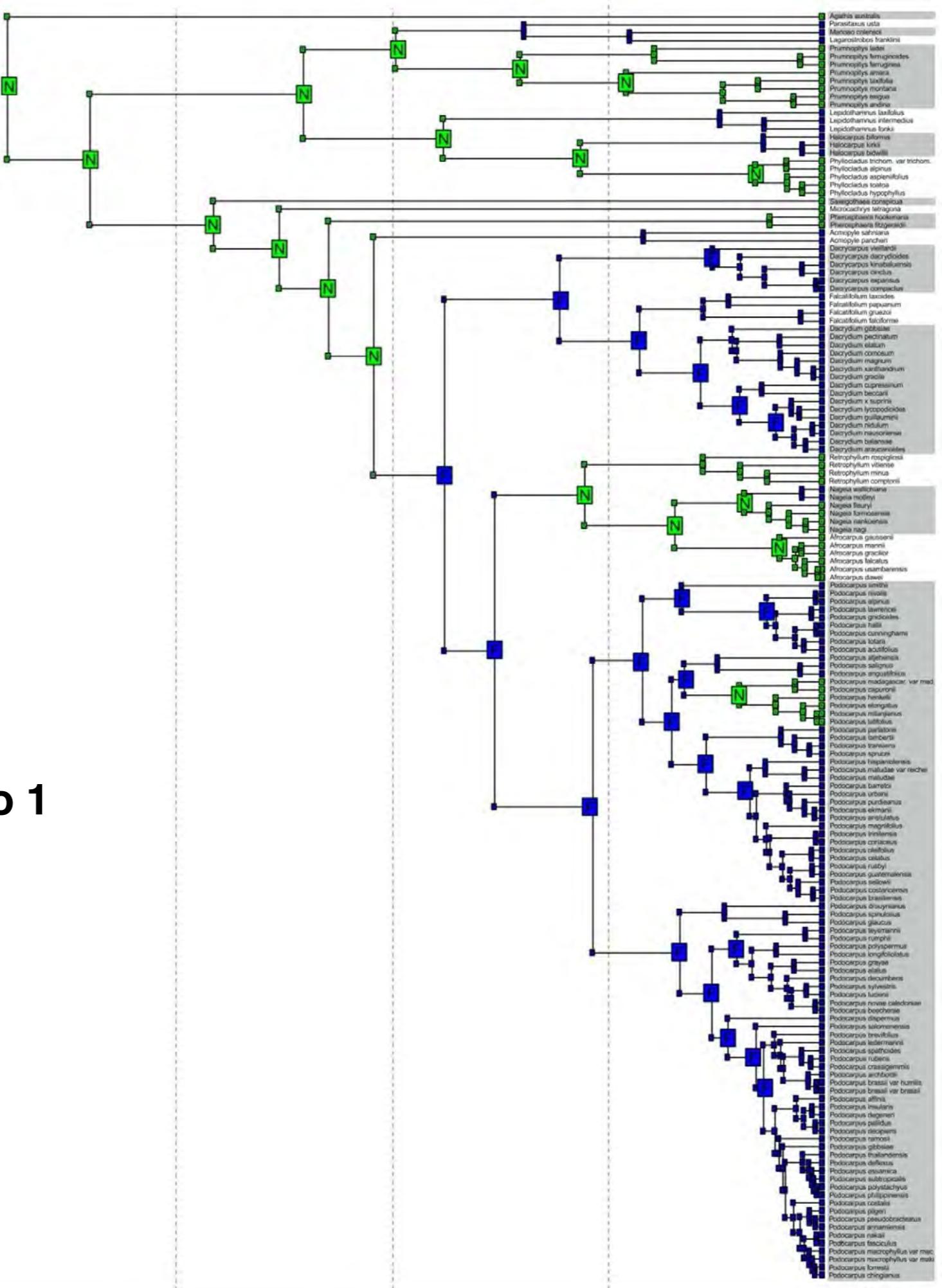
### Fleshy cones

- Dispersal multiplier  $m_1$  fixed to 1



### Non-fleshy cones

- Dispersal multiplier  $m_2 = 0.5$



# Trait-dependent model results

# Trait-dependent model results

TABLE 1. Testing for the influence of trait state, distance, and changing geography on dispersal rates

Model category	Time-stratification	Base model	geog lnL	trait lnL	joint lnL	np	Parameters							LRT on pairs of nested models				
							d	e	j	x	t <sub>12</sub>	t <sub>21</sub>	m <sub>1</sub>	m <sub>2</sub>	AICc weight	adding j P-value	adding x P-value	adding m <sub>2</sub> P-value
Distance-indep. Constant trait-indep. geography		DEC+t <sub>12</sub> +t <sub>21</sub>	-427.11	-25.1	-452.2	4	0.0049	0.0072	0	0.0054	0.0016	1	1	0.0%				
		DEC+j+t <sub>12</sub> +t <sub>21</sub>	-416.15	-25.1	-441.2	5	0.0024	9E-07	0.015	0	0.0054	0.0016	1	1	0.0%	2.8E-06***		
		DIVALIKE+t <sub>12</sub> +t <sub>21</sub>	-450.85	-25.1	-475.9	4	0.0064	0.0087	0	0	0.0054	0.0016	1	1	0.0%			
		DIVALIKE+j+t <sub>12</sub> +t <sub>21</sub>	-424.93	-25.1	-450.0	5	0.0027	1E-06	0.016	0	0.0054	0.0016	1	1	0.0%	6.0E-13***		
		BAYAREALIKE+t <sub>12</sub> +t <sub>21</sub>	-535.53	-25.1	-560.6	4	0.01	0.0555	0	0	0.0054	0.0016	1	1	0.0%			
		BAYAREALIKE+j+t <sub>12</sub> +t <sub>21</sub>	-440.95	-25.1	-466.0	5	0.0014	0.0081	0.026	0	0.0054	0.0016	1	1	0.0%	4.8E-43***		
Distance-indep. Constant trait-dep. geography		DEC+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-450.1	5	0.006	0.004	0	0	0.0037	0.0044	1	0.419	0.0%		0.041*			
		DEC+j+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-439.8	6	0.003	0.000	0.017	0	0.0034	0.0044	1	0.528	0.0%	5.6E-06***	0.091ns			
		DIVALIKE+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-468.1	5	0.009	0.000	0	0	0.0035	0.0048	1	0.279	0.0%		7.2E-05***			
		DIVALIKE+j+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-446.0	6	0.004	0.000	0.019	0	0.0035	0.0044	1	0.404	0.0%	3.2E-11***	0.005**			
		BAYAREALIKE+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-559.7	5	0.012	0.055	0	0	0.0054	0.0013	1	0.698	0.0%		0.177ns			
		BAYAREALIKE+j+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-465.9	6	0.001	0.008	0.027	0	0.0054	0.0016	1	0.866	0.0%	1.1E-42***	0.618ns			
Distance-dep. Constant trait-indep. geography		DEC+x+t <sub>12</sub> +t <sub>21</sub>	-398.13	-25.1	-423.2	5	0.0692	0.0069	0	-0.87	0.0054	0.0016	1	1	0.0%		3E-14***	
		DEC+x+j+t <sub>12</sub> +t <sub>21</sub>	-384.42	-25.1	-409.5	6	0.030	3E-07	0.287	-0.88	0.0054	0.0016	1	1	8.6%	0.000***	2E-15***	
		DIVALIKE+x+t <sub>12</sub> +t <sub>21</sub>	-409.14	-25.1	-434.2	5	0.1071	0.0064	0	-0.96	0.0054	0.0016	1	1	0.0%		7E-20***	
		DIVALIKE+x+j+t <sub>12</sub> +t <sub>21</sub>	-385.22	-25.1	-410.3	6	0.0338	1E-07	0.210	-0.84	0.0054	0.0016	1	1	3.9%	0.000***	5E-19***	
		BAYAREALIKE+x+t <sub>12</sub> +t <sub>21</sub>	-511.0	-25.1	-536.1	5	0.1186	0.058	0	-0.79	0.0054	0.0016	1	1	0.0%		2E-12***	
		BAYAREALIKE+x+j+t <sub>12</sub> +t <sub>21</sub>	-405.85	-25.1	-430.9	6	0.020	0.004	0.330	-0.87	0.0054	0.0016	1	1	0.0%	1.2E-47***	5E-17***	
Distance-dep. Constant trait-dep. geography		DEC+x+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-421.5	6	0.086	0.007	0	-0.88	0.0057	0.0014	1	0.575	0.0%		4E-14***	0.066ns		
		DEC+x+j+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-408.7	7	0.048	0.000	0.404	-0.93	0.0028	0.0040	1	0.590	6.8%	4.0E-07***	2E-14***	0.196ns		
		DIVALIKE+x+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-429.6	6	0.139	0.004	0	-0.92	0.0035	0.0048	1	0.367	0.0%		2E-18***	0.002**		
		DIVALIKE+x+j+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-406.5	7	0.063	0.000	0.273	-0.86	0.0044	0.0051	1	0.373	58.8%	1.1E-11***	6E-19***	0.006**		
		BAYAREALIKE+x+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-535.0	6	0.137	0.058	0	-0.78	0.0054	0.0013	1	0.683	0.0%		2E-12***	0.141ns		
		BAYAREALIKE+x+j+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-430.0	7	0.026	0.003	0.408	-0.91	0.0055	0.0016	1	0.640	0.0%	1.4E-47***	2E-17***	0.161ns		
Distance-dep. Constant trait-dep. all areas extant		DEC+x+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-421.2	6	0.089	0.007	0	-0.88	0.0058	0.0013	1	0.522	0.0%		3E-14***			
		DEC+x+j+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-408.7	7	0.037	0.000	0.279	-0.82	0.0039	0.0040	1	0.486	6.5%	5.7E-07***	2E-14***			
		DIVALIKE+x+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-429.6	6	0.139	0.005	0	-0.92	0.0035	0.0047	1	0.389	0.0%		2E-18***			
		DIVALIKE+x+j+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-407.8	7	0.046	0.000	0.241	-0.80	0.0071	0.0054	1	0.498	15.4%	4.5E-11***	2E-18***			
		BAYAREALIKE+x+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-534.4	6	0.147	0.059	0	-0.81	0.0054	0.0013	1	0.677	0.0%		1E-12***			
		BAYAREALIKE+x+j+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-430.3	7	0.025	0.004	0.372	-0.88	0.0055	0.0016	1	0.650	0.0%	3.1E-47***	3E-17***			
Distance-dep. Changing distances, New Caledonia rises at 37 Ma		DEC+x+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-425.7	6	0.084	0.008	0	-0.85	0.0057	0.0013	1	0.556	0.0%					
		DEC+x+j+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-413.9	7	0.041	0.002	0.266	-0.81	0.0040	0.0040	1	0.567	0.0%	1.2E-06***				
		DIVALIKE+x+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-434.0	6	0.140	0.006	0	-0.91	0.0036	0.0046	1	0.403	0.0%					
		DIVALIKE+x+j+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-413.6	7	0.058	0.000	0.247	-0.84	0.0031	0.0045	1	0.457	0.0%	1.8E-10***				
		BAYAREALIKE+x+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-536.8	6	0.158	0.060	0	-0.83	0.0054	0.0013	1	0.678	0.0%					
		BAYAREALIKE+x+j+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-432.4	7	0.027	0.005	0.360	-0.87	0.0056	0.0015	1	0.623	0.0%	2.4E-47***				
Distance-dep. Changing distances, New Caledonia+ New Zealand rise at 37 Ma		DEC+x+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-436.4	6	0.082	0.014	0	-0.74	0.0057	0.0011	1	0.522	0.0%					
		DEC+x+j+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-429.6	7	0.050	0.009	0.161	-0.73	0.0056	0.0012	1	0.572	0.0%	0.000***				
		DIVALIKE+x+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-446.5	6	0.130	0.015	0	-0.81	0.0056	0.0013	1	0.479	0.0%					
		DIVALIKE+x+j+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-432.2	7	0.072	0.009	0.191	-0.80	0.0056	0.0013	1	0.514	0.0%	0.000***				
		BAYAREALIKE+x+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-539.4	6	0.173	0.062	0	-0.85	0.0054	0.0013	1	0.672	0.0%					
		BAYAREALIKE+x+j+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-446.7	7	0.030	0.012	0.279	-0.78	0.0055	0.0014	1	0.642</						

# Trait-dependent model results

TABLE 1. Testing for the influence of trait state, distance, and changing geography on dispersal rates

Model category	Time-stratification	Base model	Parameters										LRT on pairs of nested models					
			geog lnL	trait lnL	joint lnL	np	d	e	j	x	t <sub>12</sub>	t <sub>21</sub>	m <sub>1</sub>	m <sub>2</sub>	AICc weight	adding j P-value	adding x P-value	adding m <sub>2</sub> P-value
Distance-indep. Constant trait-indep. geography		DEC+t <sub>12</sub> +t <sub>21</sub>	-427.11	-25.1	-452.2	4	0.0049	0.0072	0	0.0054	0.0016	1	1		0.0%			
		DEC+j+t <sub>12</sub> +t <sub>21</sub>	-416.15	-25.1	-441.2	5	0.0024	9E-07	0.015	0	0.0054	0.0016	1	1		0.0%	2.8E-06***	
		DIVALIKE+t <sub>12</sub> +t <sub>21</sub>	-450.85	-25.1	-475.9	4	0.0064	0.0087	0	0	0.0054	0.0016	1	1		0.0%		
		DIVALIKE+j+t <sub>12</sub> +t <sub>21</sub>	-424.93	-25.1	-450.0	5	0.0027	1E-06	0.016	0	0.0054	0.0016	1	1		0.0%	6.0E-13***	
		BAYAREALIKE+t <sub>12</sub> +t <sub>21</sub>	-535.53	-25.1	-560.6	4	0.01	0.0555	0	0	0.0054	0.0016	1	1		0.0%		
		BAYAREALIKE+j+t <sub>12</sub> +t <sub>21</sub>	-440.95	-25.1	-466.0	5	0.0014	0.0081	0.026	0	0.0054	0.0016	1	1		0.0%	4.8E-43***	
Distance-indep. Constant trait-dep. geography		DEC+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-450.1	5	0.006	0.004	0	0	0.0037	0.0044	1	0.419		0.0%		0.041*		
		DEC+j+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-439.8	6	0.003	0.000	0.017	0	0.0034	0.0044	1	0.528		0.0%	5.6E-06***	0.091ns		
		DIVALIKE+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-468.1	5	0.009	0.000	0	0	0.0035	0.0048	1	0.279		0.0%		7.2E-05***		
		DIVALIKE+j+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-446.0	6	0.004	0.000	0.019	0	0.0035	0.0044	1	0.404		0.0%	3.2E-11***	0.005**		
		BAYAREALIKE+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-559.7	5	0.012	0.055	0	0	0.0054	0.0013	1	0.698		0.0%		0.177ns		
		BAYAREALIKE+j+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-465.9	6	0.001	0.008	0.027	0	0.0054	0.0016	1	0.866		0.0%	1.1E-42***	0.618ns		
Distance-dep. Constant trait-indep. geography		DEC+x+t <sub>12</sub> +t <sub>21</sub>	-398.13	-25.1	-423.2	5	0.0692	0.0069	0	-0.87	0.0054	0.0016	1	1		0.0%	3E-14***	
		DEC+x+j+t <sub>12</sub> +t <sub>21</sub>	-384.42	-25.1	-409.5	6	0.030	3E-07	0.287	-0.88	0.0054	0.0016	1	1		8.6%	0.000***	2E-15***
		DIVALIKE+x+t <sub>12</sub> +t <sub>21</sub>	-409.14	-25.1	-434.2	5	0.1071	0.0064	0	-0.96	0.0054	0.0016	1	1		0.0%	7E-20***	
		DIVALIKE+x+j+t <sub>12</sub> +t <sub>21</sub>	-385.22	-25.1	-410.3	6	0.0338	1E-07	0.210	-0.84	0.0054	0.0016	1	1		3.9%	0.000***	5E-19***
		BAYAREALIKE+x+t <sub>12</sub> +t <sub>21</sub>	-511.0	-25.1	-536.1	5	0.1186	0.058	0	-0.79	0.0054	0.0016	1	1		0.0%	2E-12***	
		BAYAREALIKE+x+j+t <sub>12</sub> +t <sub>21</sub>	-405.85	-25.1	-430.9	6	0.020	0.004	0.330	-0.87	0.0054	0.0016	1	1		0.0%	1.2E-47***	5E-17***
Distance-dep. Constant trait-dep. geography		DEC+x+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-421.5	6	0.086	0.007	0	-0.88	0.0057	0.0014	1	0.575		0.0%		4E-14***	0.066ns	
		DEC+x+j+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-408.7	7	0.048	0.000	0.404	-0.93	0.0028	0.0040	1	0.590		6.8%	4.0E-07***	2E-14***	0.196ns	
		DIVALIKE+x+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-429.6	6	0.139	0.004	0	-0.92	0.0035	0.0048	1	0.367		0.0%		2E-18***	0.002**	
		DIVALIKE+x+j+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-406.5	7	0.063	0.000	0.273	-0.86	0.0044	0.0051	1	0.373		58.8%	1.1E-11***	6E-19***	0.006**	
		BAYAREALIKE+x+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-535.0	6	0.137	0.058	0	-0.78	0.0054	0.0013	1	0.683		0.0%		2E-12***	0.141ns	
		BAYAREALIKE+x+j+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-430.0	7	0.026	0.003	0.408	-0.91	0.0055	0.0016	1	0.640		0.0%	1.4E-47***	2E-17***	0.161ns	
Distance-dep. Constant trait-dep. all areas extant		DEC+x+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-421.2	6	0.089	0.007	0	-0.88	0.0058	0.0013	1	0.522		0.0%		3E-14***		
		DEC+x+j+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-408.7	7	0.037	0.000	0.279	-0.82	0.0039	0.0040	1	0.486		6.5%	5.7E-07***	2E-14***		
		DIVALIKE+x+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-429.6	6	0.139	0.005	0	-0.92	0.0035	0.0047	1	0.389		0.0%		2E-18***		
		DIVALIKE+x+j+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-407.8	7	0.046	0.000	0.241	-0.80	0.0071	0.0054	1	0.498		15.4%	4.5E-11***	2E-18***		
		BAYAREALIKE+x+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-534.4	6	0.147	0.059	0	-0.81	0.0054	0.0013	1	0.677		0.0%		1E-12***		
		BAYAREALIKE+x+j+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-430.3	7	0.025	0.004	0.372	-0.88	0.0055	0.0016	1	0.650		0.0%	3.1E-47***	3E-17***		
Distance-dep. Changing distances, New Caledonia rises at 37 Ma		DEC+x+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-425.7	6	0.084	0.008	0	-0.85	0.0057	0.0013	1	0.556		0.0%				
		DEC+x+j+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-413.9	7	0.041	0.002	0.266	-0.81	0.0040	0.0040	1	0.567		0.0%	1.2E-06***			
		DIVALIKE+x+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-434.0	6	0.140	0.006	0	-0.91	0.0036	0.0046	1	0.403		0.0%				
		DIVALIKE+x+j+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-413.6	7	0.058	0.000	0.247	-0.84	0.0031	0.0045	1	0.457		0.0%	1.8E-10***			
		BAYAREALIKE+x+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-536.8	6	0.158	0.060	0	-0.83	0.0054	0.0013	1	0.678		0.0%				
		BAYAREALIKE+x+j+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-432.4	7	0.027	0.005	0.360	-0.87	0.0056	0.0015	1	0.623		0.0%	2.4E-47***			
Distance-dep. Changing distances, New Caledonia+ New Zealand rise at 37 Ma		DEC+x+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-436.4	6	0.082	0.014	0	-0.74	0.0057	0.0011	1	0.522		0.0%				
		DEC+x+j+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-429.6	7	0.050	0.009	0.161	-0.73	0.0056	0.0012	1	0.572		0.0%	0.000***			
		DIVALIKE+x+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-446.5	6	0.130	0.015	0	-0.81	0.0056	0.0013	1	0.479		0.0%				
		DIVALIKE+x+j+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-432.2	7	0.072	0.009	0.191	-0.80	0.0056	0.0013	1	0.514		0.0%	0.000***			
		BAYAREALIKE+x+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-539.4	6	0.173	0.062	0	-0.85	0.0054	0.0013	1	0.672		0.0%				
		BAYAREALIKE+x+j+t <sub>12</sub> +t <sub>21</sub> +m <sub>2</sub>	-446.7	7	0.030	0.012	0.279	-0.78	0.0055	0.0014	1	0.642		0.0%	3.2E-42***			
Distance-dep. Changing distances, New Caledonia sunken from 52-																		

# Trait-dependent model results

- \* 87.5% AICc weight for trait-dependent models
  - \* Lineages with nonfleshy cones have a dispersal rate about  $m_2=0.49$  lower than fleshy cone lineages

# Distance effect: $x=-0.86$

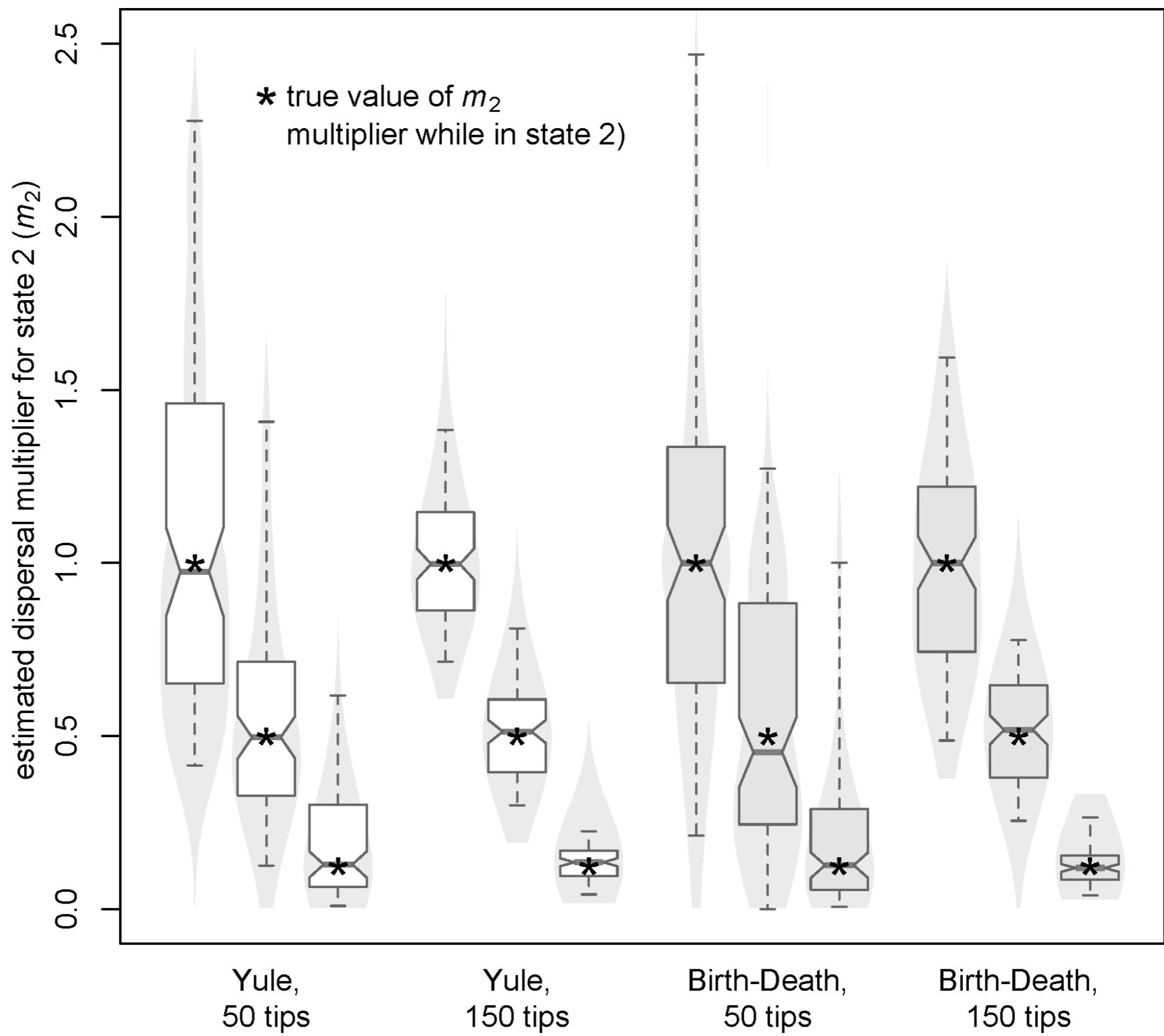


# Trait-dispersal modifiers: $m_1=1.0$

$m_2=0.49$

# Simulation test for inference of $m_2$ :

- strong vs. weak effects
- dataset size



# Ecology-dependent dispersal in Indo-Pacific trap-jaw ants (*Odontomachus*)

ORIGINAL ARTICLE

WILEY MOLECULAR ECOLOGY

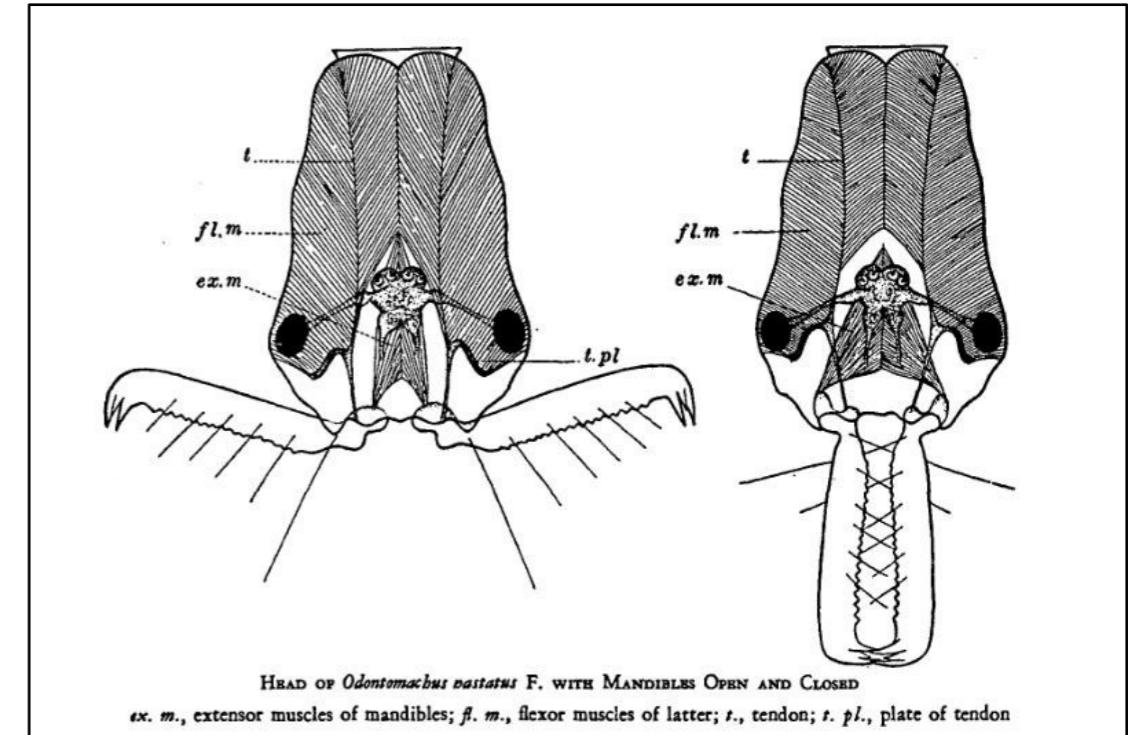
Taxon cycle predictions supported by model-based inference in Indo-Pacific trap-jaw ants (Hymenoptera: Formicidae: *Odontomachus*)

Pável Matos-Maraví<sup>1,2,3,4</sup>  | Nicholas J. Matzke<sup>5,6</sup> | Fredrick J. Larabee<sup>7,8</sup> |  
Ronald M. Clouse<sup>9</sup> | Ward C. Wheeler<sup>9</sup> | Daniela Magdalena Sorger<sup>10,11,12</sup> |  
Andrew V. Suarez<sup>8</sup> | Milan Janda<sup>1,13</sup>

With:

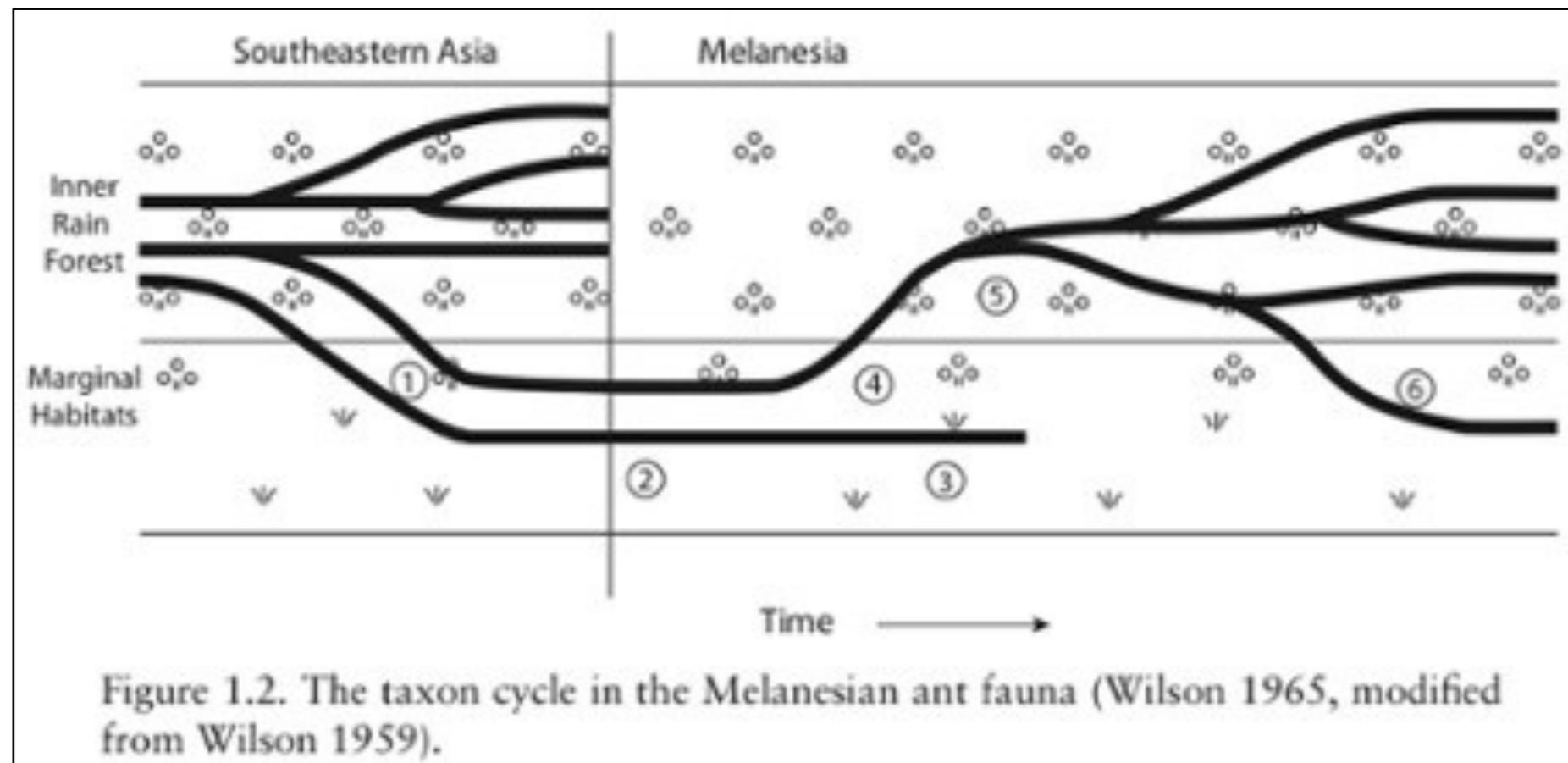


Pavel Matos-Maravi



Wheeler, W.M. (1927): The physiognomy of insects. *Quarterly Review of Biology* 2: 1-36.  
<https://en.wikipedia.org/wiki/File:OdontomachusHeadWheeler.jpg>

# The Taxon Cycle Hypothesis

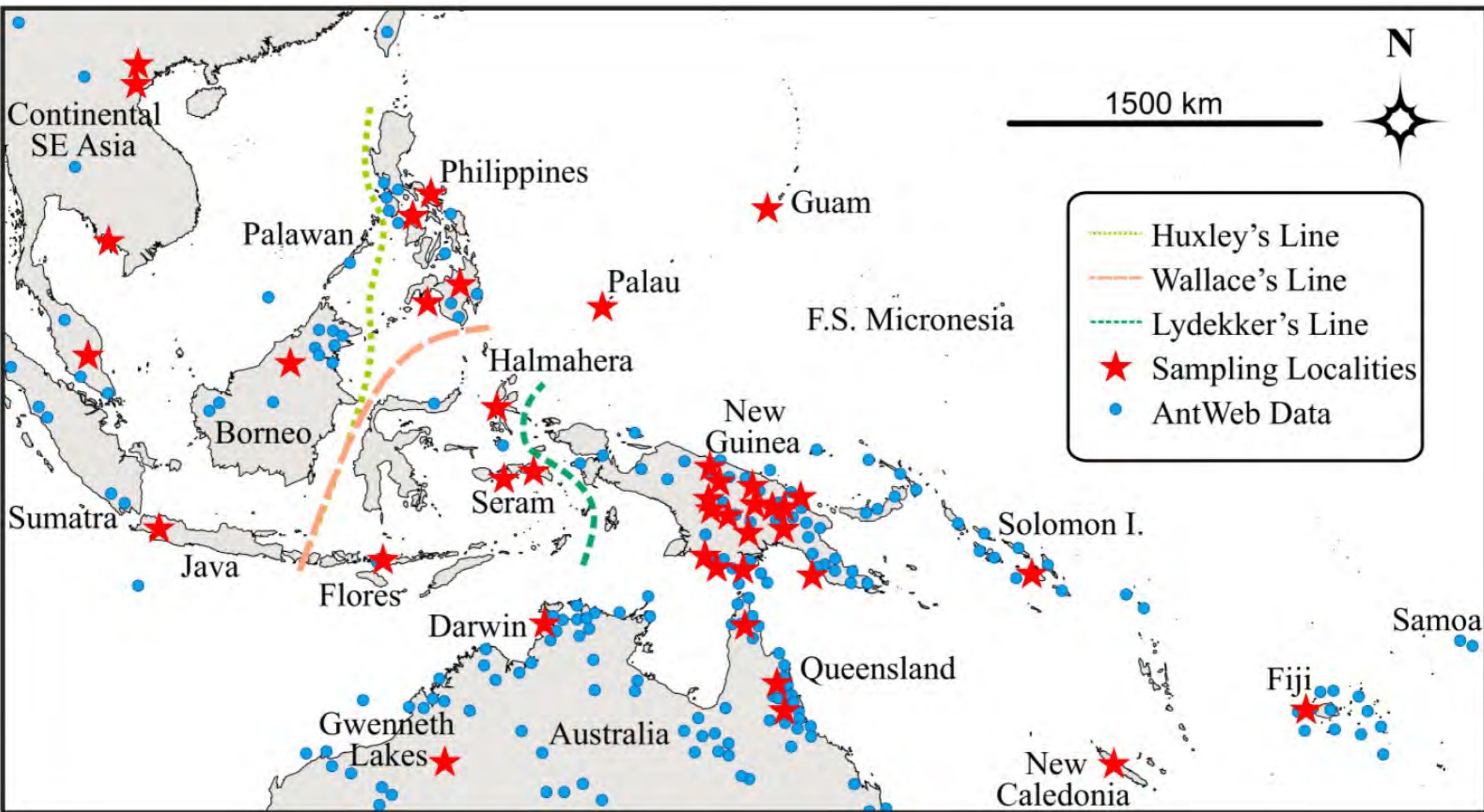


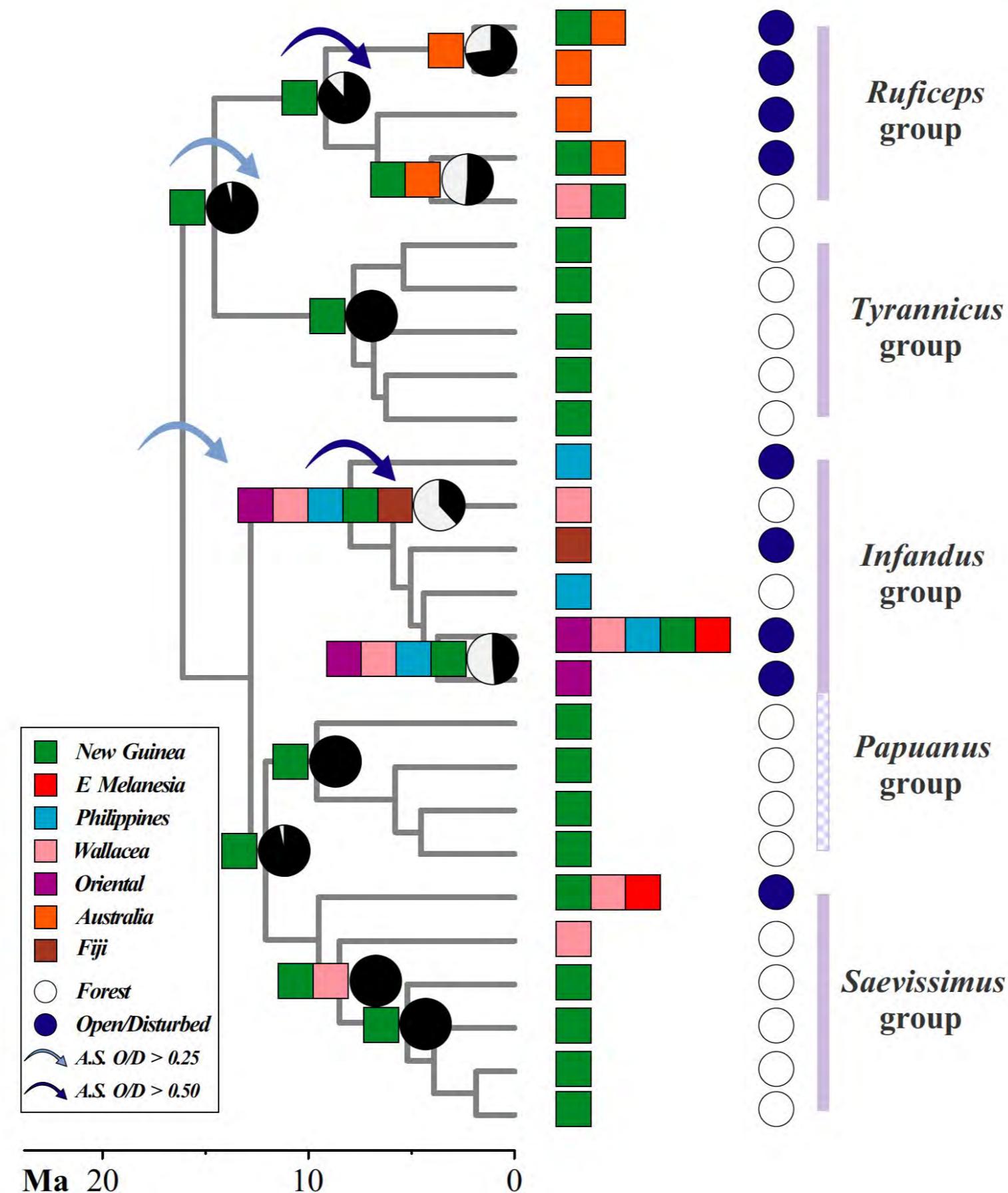
<http://www.ourdailyread.com/2015/04/island-biogeography-revisited-online-book-club-chapter-one/>

**Our biogeographical models  
don't test all aspects of the  
Taxon Cycle idea  
(which is quite complex)**

**But: we can test the  
dispersal part of it: do  
marginal-habitat ants have  
a higher dispersal rate?**

# *Odontomachus* in the Indo-Pacific





Matos-Mara **FIGURE 4** Ancestral area inference on the Indo-Pacific clade using a trait-dependent dispersal model implemented in BioGeoBEARS. The

# *Odontomachus* in the Indo-Pacific

**TABLE 5** BioGeoBEARS analyses of biogeography + trait data (comparing models with trait-independent dispersal and trait-dependent dispersal), at a fine geographical scale (the Indo-Pacific clade, 26 extant tips)

Biogeographical models	d	e	j	t <sub>12</sub>	t <sub>21</sub>	m <sub>2</sub>	loglik	AICc	df	Akaike weights
DEC + 2rates, m <sub>2</sub> = 1	0.007	0.000	0.000	0.074	0.000	1.000	-67.167	144.238	4	0.02
DEC + J + 2rates, m <sub>2</sub> = 1	0.007	0.000	0.006	0.074	0.000	1.000	-66.547	146.094	5	0.01
DEC + 2rates + m <sub>2</sub>	0.016	0.000	0.000	0.072	0.000	0.000	-61.883	136.767	5	0.66
DEC + J + 2rates + m <sub>2</sub> , run1	0.014	0.000	0.035	0.074	0.000	0.000	-60.941	138.302	6	0.31
DIVA + 2rates, m <sub>2</sub> = 1	0.012	0.000	0.000	0.074	0.000	1.000	-75.615	161.136	4	0.00
DIVA + J + 2rates, m <sub>2</sub> = 1	0.009	0.000	0.021	0.074	0.000	1.000	-73.756	160.513	5	0.00
DIVA + 2rates + m <sub>2</sub>	0.024	0.000	0.000	0.072	0.000	0.000	-66.810	146.620	5	0.00
DIVA + J + 2rates + m <sub>2</sub> , run1	0.017	0.000	0.069	0.073	0.000	0.000	-64.327	145.076	6	0.01
BAYAREA + 2rates, m <sub>2</sub> = 1	0.006	0.076	0.000	0.074	0.000	1.000	-79.442	168.789	4	0.00
BAYAREA + J + 2rates, m <sub>2</sub> = 1	0.007	0.000	0.038	0.074	0.000	1.000	-78.110	169.220	5	0.00
BAYAREA + 2rates + m <sub>2</sub>	0.013	0.075	0.000	0.072	0.000	0.000	-75.434	163.869	5	0.00
BAYAREA + J + 2rates + m <sub>2</sub> , run2	0.014	0.000	0.131	0.074	0.000	0.000	-68.018	152.456	6	0.00

# *Odontomachus* in the Indo-Pacific

Indo-Pacific *Odontomachus* (26 species)

\* Lineages in closed forest habitat are inferred  
to have 0 dispersal in this dataset

Trait-dispersal modifiers:  $m_1=1.0$        $m_2=0.0$

DIVA + 2rates + $m_2$	0.024	0.000	0.000	0.072	0.000	0.000	-66.810	146.620	5	0.00
DIVA + J + 2rates + $m_2$ , run1	0.017	0.000	0.069	0.073	0.000	0.000	-64.327	145.076	6	0.01
BAYAREA + 2rates, $m_2 = 1$	0.006	0.076	0.000	0.074	0.000	1.000	-79.442	168.789	4	0.00
BAYAREA + J + 2rates, $m_2 = 1$	0.007	0.000	0.038	0.074	0.000	1.000	-78.110	169.220	5	0.00
BAYAREA + 2rates + $m_2$	0.013	0.075	0.000	0.072	0.000	0.000	-75.434	163.869	5	0.00
BAYAREA + J + 2rates + $m_2$ , run2	0.014	0.000	0.131	0.074	0.000	0.000	-68.018	152.456	6	0.00

# ***Odontomachus* in the Indo-Pacific**

The dataset size is very small for such a complex model

Check on simulated 25-species datasets, for sanity:

# *Odontomachus* in the Indo-Pacific

The dataset size is very small for such a complex model

Check on simulated 25-species datasets, for sanity:

Lineage extinction rate	True value of $m_2$ for the simulation	Inferred $m_2$
0.0	1.0	1.8551 (0.2675, 4.0947)
0.0	0.1	0.5024 (0, 1.1932)
0.0	0.0	0.0752 (0, 0.0523)
0.05	1.0	1.6125 (0.2621, 3.9574)
0.05	0.1	0.5092 (0, 1.0003)
0.05	0.0	0.0589 (0, 0.0598)

# *Odontomachus* in the Indo-Pacific

The dataset size is very small for such a complex model

Check on simulated 25-species datasets, for sanity:

Lineage extinction rate	True value of $m_2$ for the simulation	Inferred $m_2$
0.0	1.0	1.8551 (0.2675, 4.0947)
0.0	0.1	0.5024 (0, 1.1932)
0.0	0.0	0.0752 (0, 0.0523)
0.05	1.0	1.6125 (0.2621, 3.9574)
0.05	0.1	0.5092 (0, 1.0003)
0.05	0.0	0.0589 (0, 0.0598)

# **Conclusions and cautions**

**Computational challenges**

**Model limitations**

# Computation speed problem:

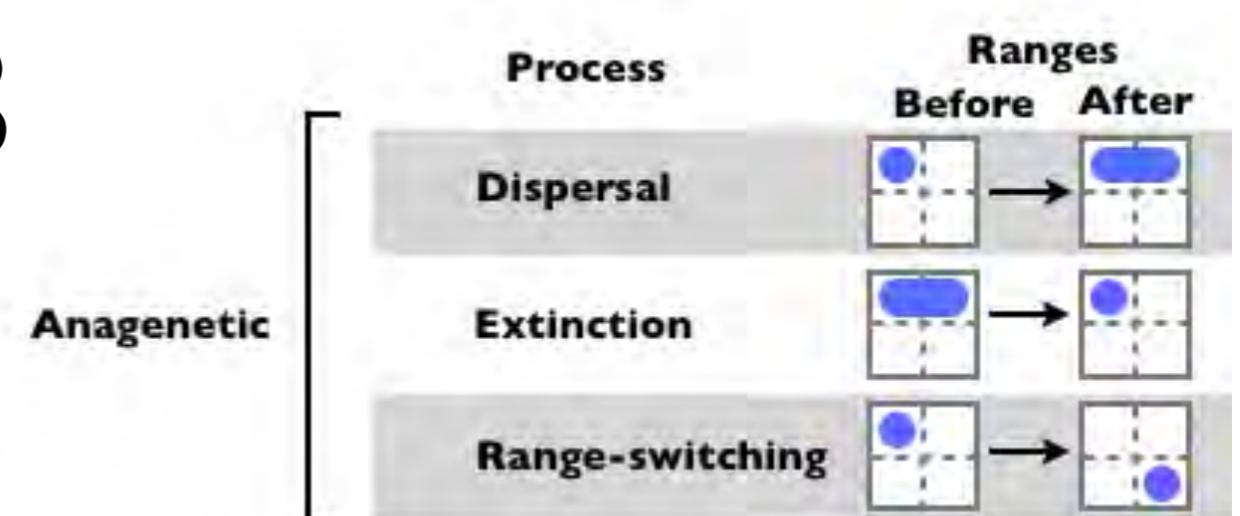
(number of ranges) =  $2^{(\text{number of areas})}$

2 areas = 4 states

4 areas = 16 states

10 areas = 1024 states

11 areas = 2048



# **DEC model**

**(Dispersal-Extinction-Cladogenesis; Ree & Smith 2008)**

# **DNA model**

**Rate matrix:**

		descendant state			
		A	C	G	T
ancestor state	A	-	r	r	r
	C	r	-	r	r
	G	r	r	-	r
	T	r	r	r	-

**(Jukes-Cantor, JC69)**

# DEC model

(Dispersal-Extinction-Cladogenesis; Ree & Smith 2008)

## DNA model

Rate matrix:

		descendant state			
		A	C	G	T
ancestor state	A	-	r	r	r
	C	r	-	r	r
	G	r	r	-	r
	T	r	r	r	-

(Jukes-Cantor, JC69)

## DEC model, 2 areas

Rate matrix:

		descendant range			
		null	A	B	AB
ancestor range	null	-			
	A	e	-	d	
	B	e	-	d	
	AB		e	e	-

d=rate of “dispersal” (range expansion)

e=rate of “extinction” (range loss)

# DEC model, 12 areas = $2^{12} = 4096$ states

4x4 rate matrix

4096 descendant ranges →

→ 4096 ancestor ranges

	null	A	B	AB
null	-			
A	e	-		d
B	e	-	-	d
AB		e	e	-

## **DEC model, 12 areas = $2^{12} = 4096$ states**

4x4 rate matrix

4096 descendant ranges →

	null	A	B	AB
null	-			
A	e	-		d
B	e		-	d
AB		e	e	-

→ 4096 ancestor ranges

**A 4096 x 4096 rate matrix is  
very big and makes the  
probability calculations very slow**

# **DEC model, 12 areas = $2^{12} = 4096$ states**

4x4 rate matrix

4096 descendant ranges →

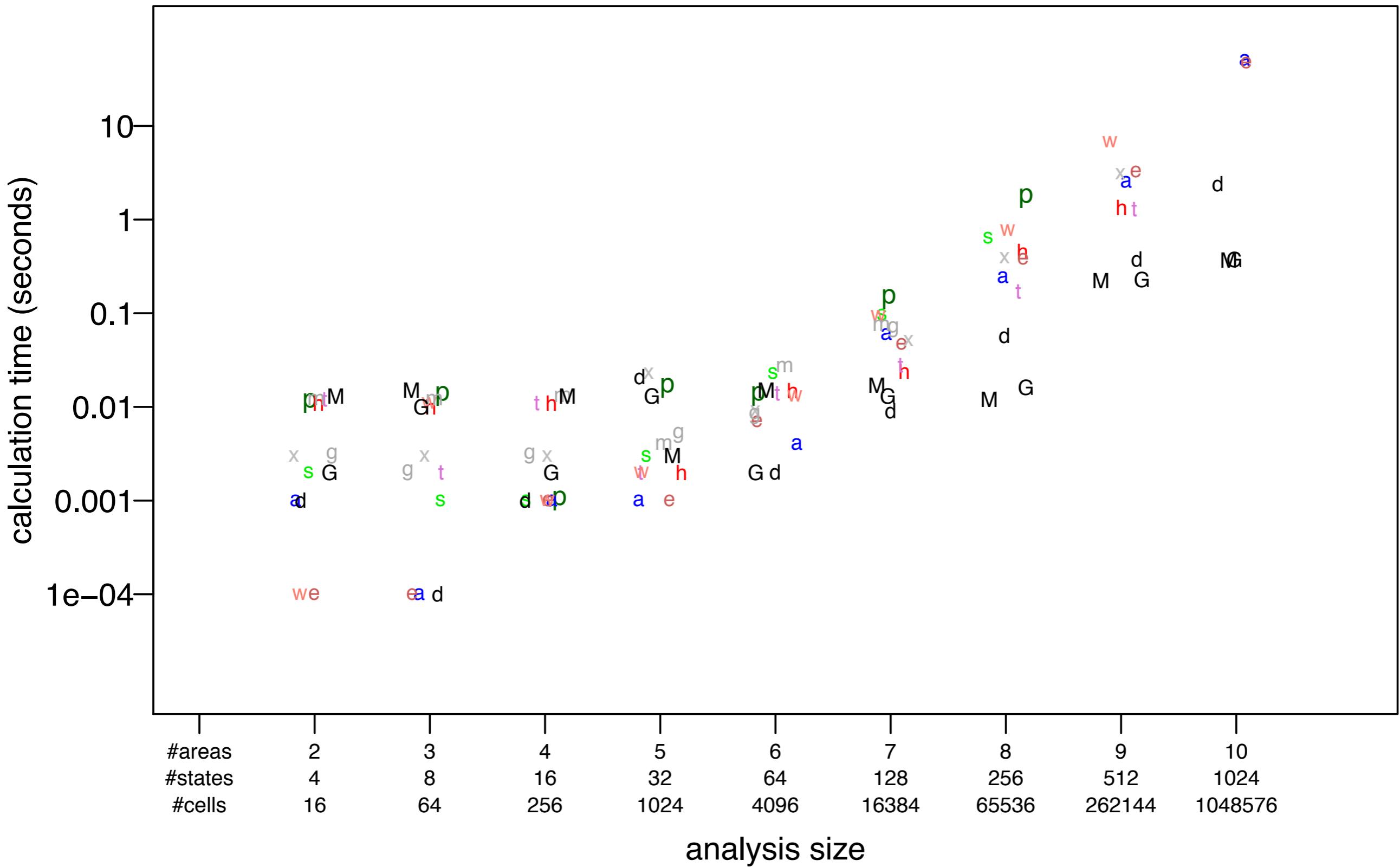
	null	A	B	AB
null	-			
A	e	-		d
B	e		-	d
AB		e	e	-

↓ 4096 ancestor ranges

**A 4096 x 4096 rate matrix is  
very big and makes the  
probability calculations very slow**

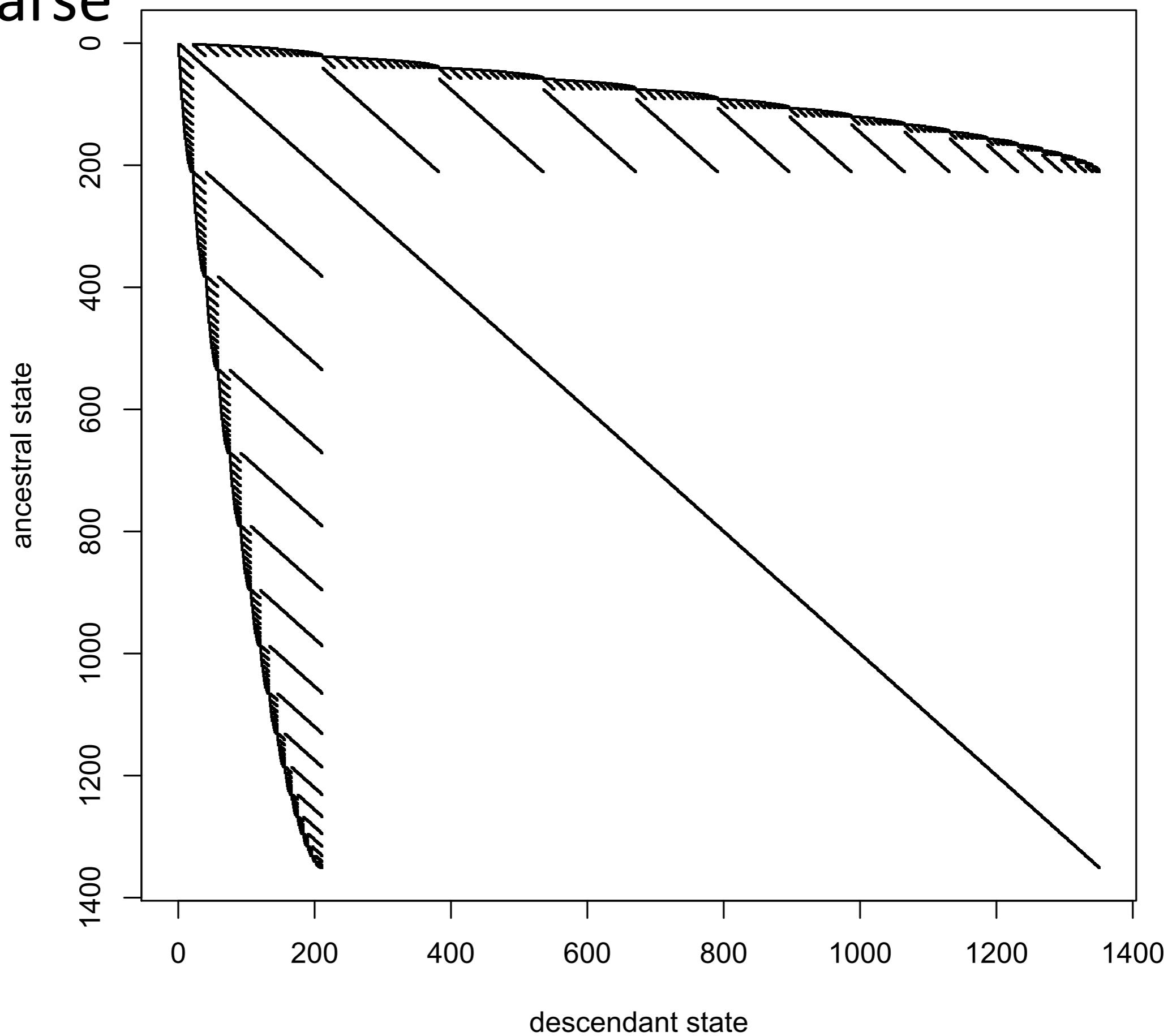
**I use C++ and parallel processing  
to speed it up**

# Speed comparison of R matrix exponentiation commands

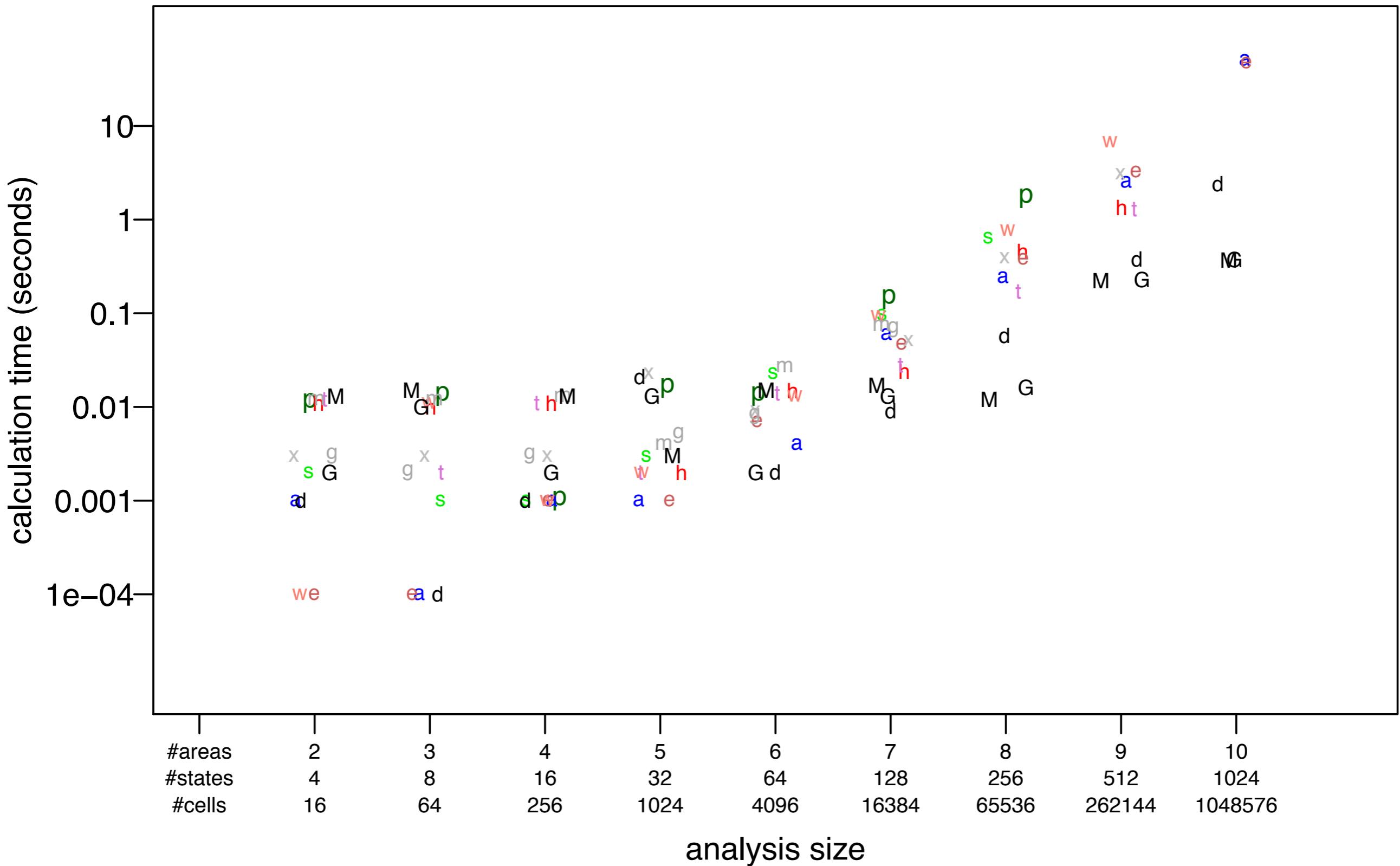


Q Matrices  
are sparse

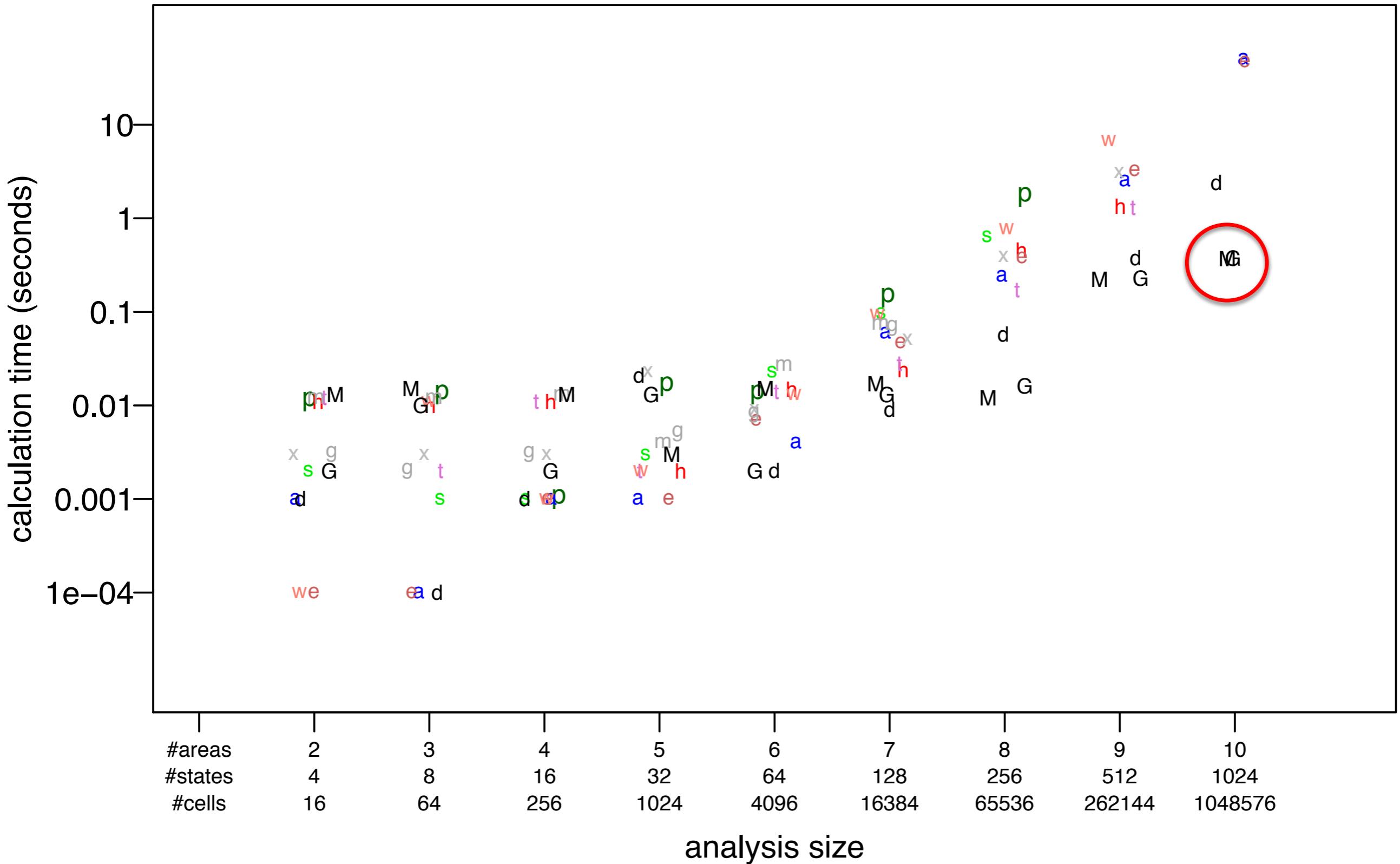
1351x1351 biogeography Q matrix  
(20 areas, 3 max per range)



# Speed comparison of R matrix exponentiation commands



# Speed comparison of R matrix exponentiation commands



# Anagenetic Problem:

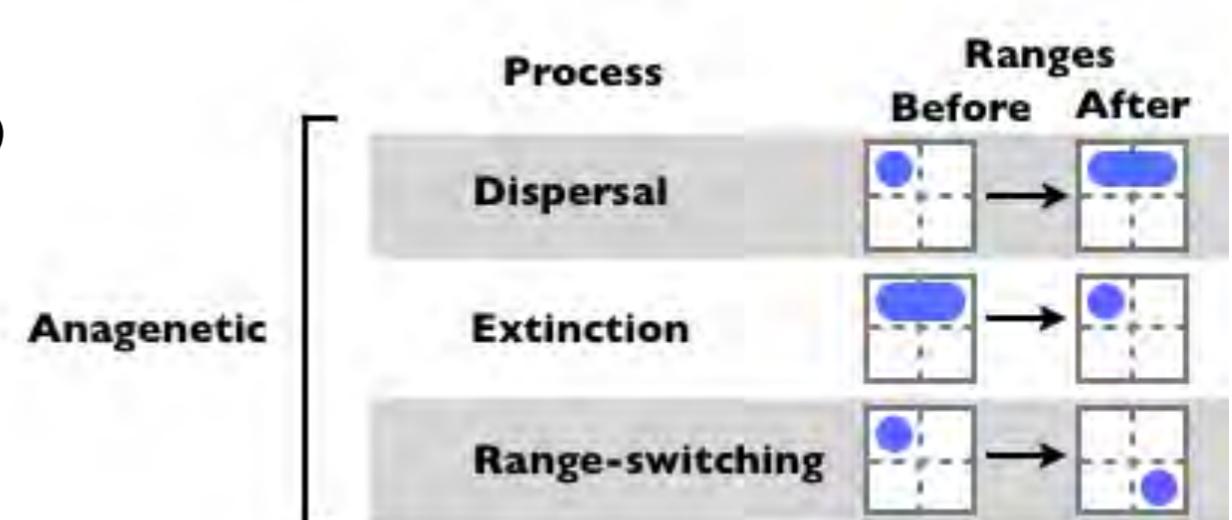
# of ranges =  $2^{(\# \text{ of areas})}$

2 areas = 4 states

4 areas = 16 states

10 areas = 1024 states

11 areas = 2048



# Cladogenetic Problem:

# of transitions =

$$(\# \text{ ranges})^3$$

2 areas = 4 states = 64 triplets

4 areas = 16 states = 4096 triplets

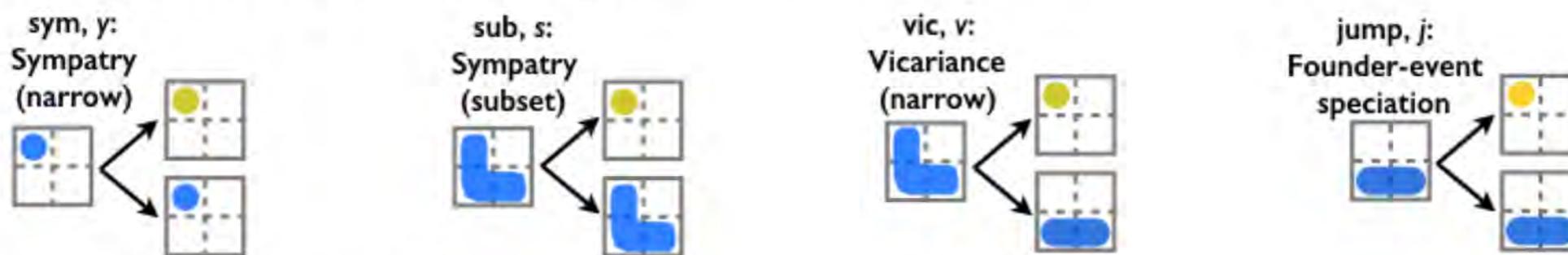
10 areas = 1024 states = 1 billion+

11 areas = 2048 states = 8.6 billion+

# Cladogenetic range change transition matrix

## Standard DEC+J model: cladogenetic processes

### **Cladogenetic range-change events:**

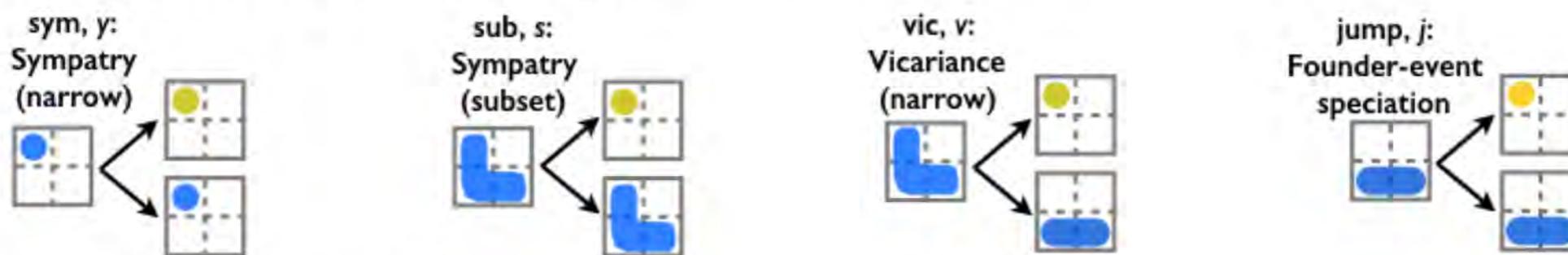


## Cladogenetic transition matrix:

# Cladogenetic range change transition matrix (mostly 0s)

## Standard DEC+J model: cladogenetic processes

## Cladogenetic range-change events:



## Cladogenetic transition matrix:

**Tricks to speed things up:**

- 1. Sparse representations (exclude 0s)**
- 2. C++ backend**
- 3. Parallel processing**
- 4. Exclude unlikely ranges**

**More complex problems:**

- 1. Trait-linked dispersal**
- 2. Include speciation/extinction**

# Trait-linked dispersal

# Trait-linked dispersal

Rate matrix for a standard discrete trait model (e.g.  $M_k$ ), and the anagenetic portion of a standard DEC-type model

Anagenetic portion of the trait-based dispersal model variant

Trait matrix

descendant trait

ancestor trait	state	state
	1	2
state 1	-	$t_{12}$
state 2	$t_{21}$	-

Geography matrix

descendant range

ancestor range	null	A	B	AB
	null	-		
A	e	-	$d$	
B	e	-	$d$	
AB	$e$	$e$	-	



Combined trait + geography matrix

$t_{12}$

$t_{21}$

	null	A	B	AB
	null	-		
A	e	-	$m_1 d$	
B	e	-	$m_1 d$	
AB	$e$	$e$	-	

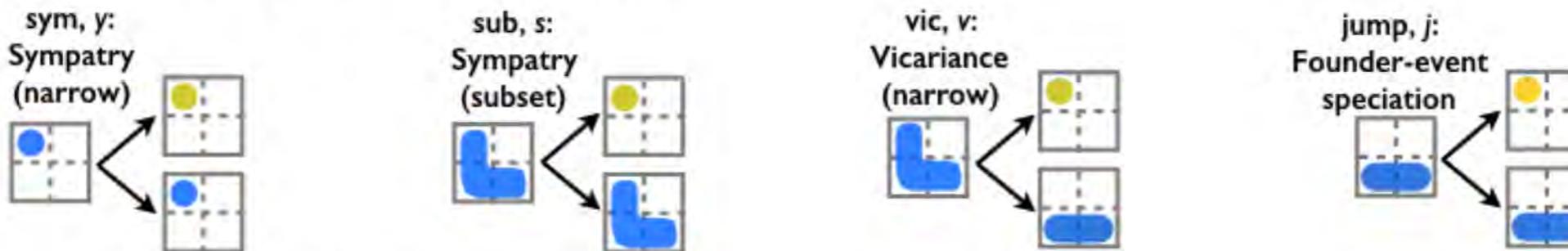
$t_{12}$

	null	A	B	AB
	null	-		
A	e	-	$m_2 d$	
B	e	-	$m_2 d$	
AB	$e$	$e$	-	

	null	A	B	AB
	null	-		
A	e	-	$m_2 d$	
B	e	-	$m_2 d$	
AB	$e$	$e$	-	

# Standard DEC+J model: cladogenetic processes

## Cladogenetic range-change events:



## Cladogenetic transition matrix:

# Trait-based DEC+J model: cladogenetic processes

## Cladogenetic transition matrix while in trait state #1:

## Cladogenetic transition matrix while in trait state #2:

**Biggest problem with all  
of these biogeography  
models: EXTINCTION**

# Biggest problem with all of these biogeography models: EXTINCTION

nature  
ecology & evolution

PERSPECTIVE

PUBLISHED: 23 MAY 2017 | VOLUME: 1 | ARTICLE NUMBER: 0165

## Five palaeobiological laws needed to understand the evolution of the living biota

Charles R. Marshall

The foundations of several disciplines can be expressed as simple quantitative laws, for example, Newton's laws or the laws of thermodynamics. Here I present five laws derived from fossil data that describe the relationships among species extinction and longevity, species richness, origination rates, extinction rates and diversification. These statements of our palaeobiological knowledge constitute a dimension largely hidden from view when studying the living biota, which are nonetheless crucial to the study of evolution and ecology even for groups with poor or non-existent fossil records. These laws encapsulate: the critical fact of extinction; that species are typically geologically short-lived, and thus that the number of extinct species typically dwarfs the number of living species; that extinction and origination rates typically have similar magnitudes; and, that significant extinction makes it difficult to infer much about a clade's early history or its current diversity dynamics from the living biota alone. Although important strides are being made to integrate these core palaeontological findings into our analysis of the living biota, this knowledge needs to be incorporated more widely if we are to understand their evolutionary dynamics.

**Biggest problem with all  
of these biogeography  
models: EXTINCTION**

In biogeography: missing  
speciation events might  
change ranges!

**Biggest problem with all  
of these biogeography  
models: EXTINCTION**

**Possible solution:  
ClasSE model, but it is slow!**

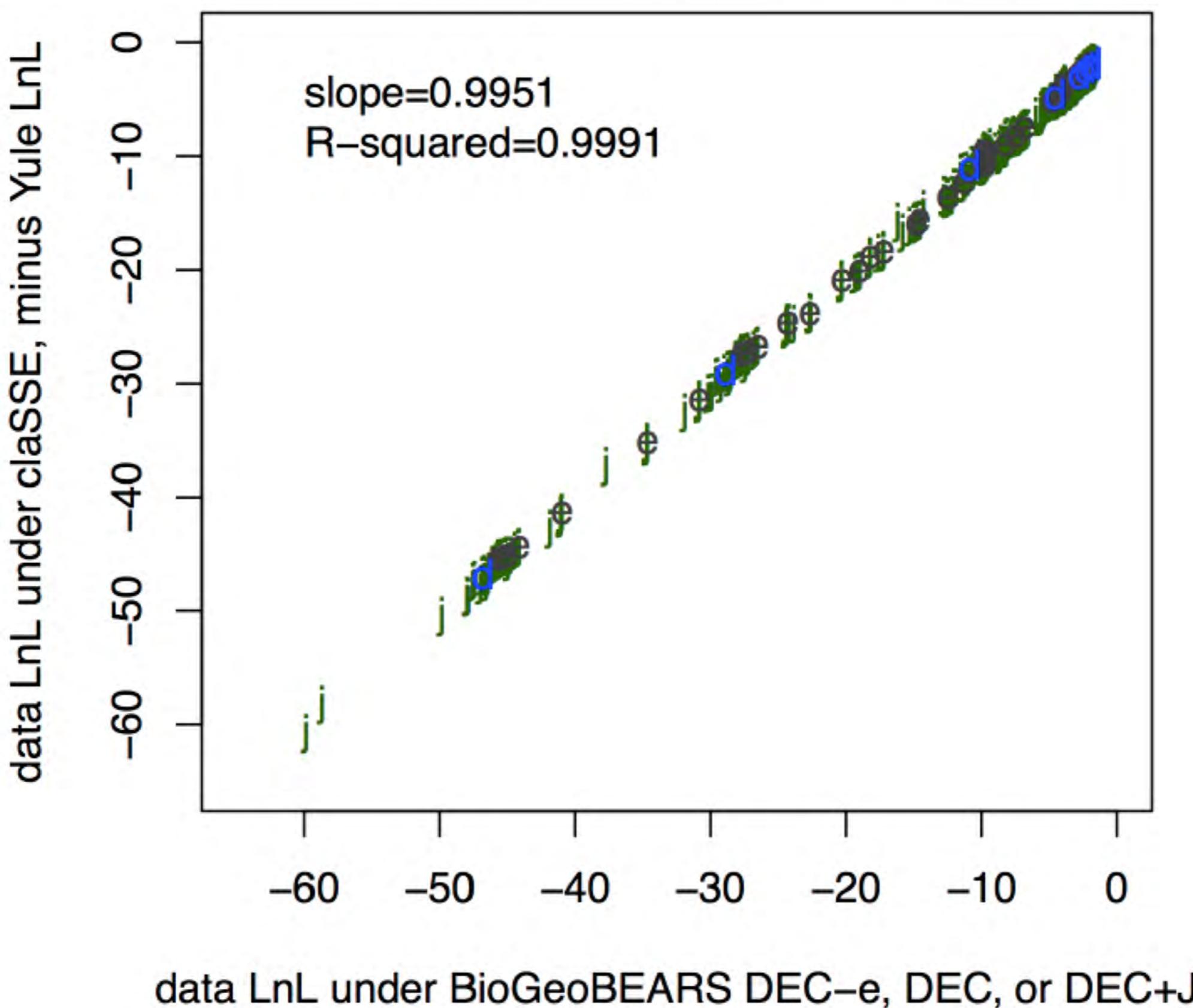
Biogeography models are just  
special cases of ClasSE:

Extinction = 0 (Yule process)

Flat root state frequencies

State-dependent range-change  
at cladogenesis

# BioGeoBEARS log-likelihoods vs. claSSE log-likelihoods (all)

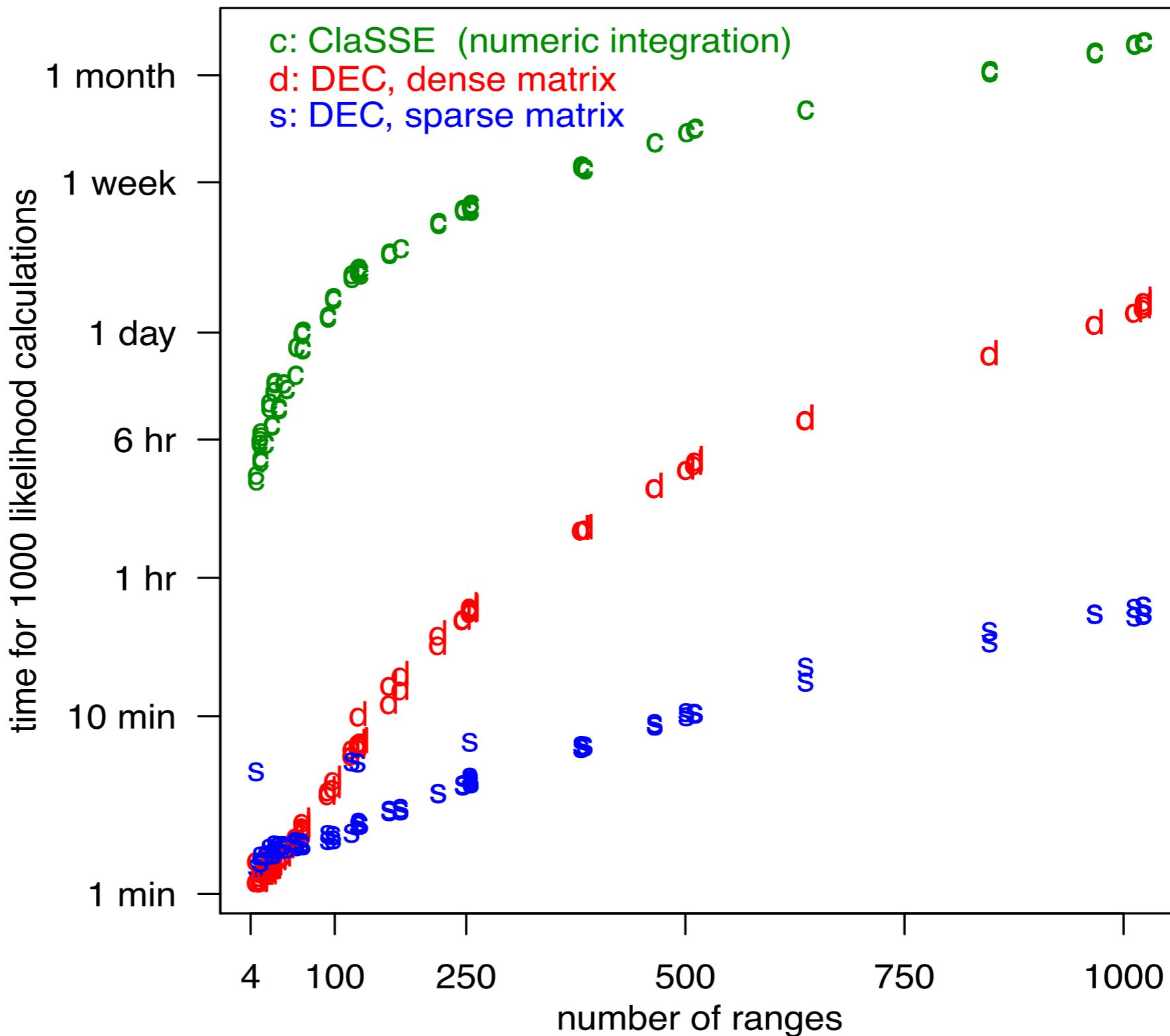


# **Problem with ClasSE:**

**Numeric integration used to  
approximate the likelihood**

**Even slower than matrix  
exponentiation!**

# Problem with ClasSE:



# Julia to the rescue?

Julia 1.0 released in early 2019, after many years <1.0

Core developers at MIT

Aims to have R/Python-like usage

But compiles to C-like speeds

KEY advantage: DifferentialEquations.jl library



TOOLBOX · 30 JULY 2019

# Julia: come for the syntax, stay for the speed

Researchers often find themselves coding algorithms in one programming language, only to have to rewrite them in a faster one. An up-and-coming language could be the answer.

Jeffrey M. Perkel



# Julia to the rescue?

KEY advantage: *DifferentialEquations.jl* library  
by Chris Rackauckas

Comparison Of Differential Equation Solver Software				Performance Metrics											
Subject/Item	MATLAB	SciPy	deSolve	DifferentialEquations.jl	Sundials	Hairer	ODEPACK/Neltib/NAG	JiCODE	PyDSTool	FATODE	GSL	BOOST	Mathematica	Maple	
Language	MATLAB	Python	R	Julia	C++ and Fortran	Fortran	Fortran	Python	Python	Fortran	C	C++	Mathematica	Maple	
Selection of Methods for ODEs	Fair	Poor	Fair	Excellent	Good	Good	Good	Poor	Poor	Good	Poor	Fair	Fair	Fair	
Efficiency*	Poor	Poor	Poor	Excellent	Excellent	Good	Good	Good	Good	Good	Fair	Fair	Fair	Good	
Tweakability	Fair	Poor	Good	Excellent	Excellent	Good	Good	Fair	Fair	Fair	Fair	Fair	Good	Fair	
Event Handling	Good	Good	Fair	Excellent	Good**	None	Good**	None	Fair	None	None	None	Good	Good	
Symbolic Calculation of Jacobians and Autodifferentiation	None	None	None	Excellent	None	None	None	None	None	None	None	None	Excellent	Excellent	
Complex Numbers	Excellent	Good	Fair	Good	None	None	None	None	None	None	Good	Excellent	Excellent		
Arbitrary Precision Numbers	None	None	None	Excellent	None	None	None	None	None	None	Excellent	Excellent	Excellent		
Control Over Linear/Nonlinear Solvers	None	Poor	None	Excellent	Excellent	Good	Depends on the solver	None	None	None	None	Fair	None		
Built-in Parallelism	None	None	None	Excellent	Excellent	None	None	None	None	None	Fair	None	None		
Differential-Algebraic Equation (DAE) Solvers	Good	None	Good	Excellent	Good	Excellent	Good	None	Fair	Good	None	None	Good	Good	
Implicitly-Defined DAE Solvers	Good	None	Excellent	Fair	Excellent	None	Excellent	None	None	None	None	None	Good	None	
Constant-Lag Delay Differential Equation (DDE) Solvers	Fair	None	Poor	Excellent	None	Good	Fair (via DDVERK)		None	None	None	None	Good	Excellent	
State-Dependent DDE Solvers	Poor	None	Poor	Excellent	None	Excellent	Good	None	None	None	None	None	None	Excellent	
Stochastic Differential Equation (SDE) Solvers	Poor	None	None	Excellent	None	None	None	Good	None	None	None	Fair	Poor		
Specialized Methods for 2nd Order ODEs and Hamiltonians (and Symplectic Integrators)	None	None	None	Excellent	None	Good	None	None	None	None	Fair	Good	None		
Boundary Value Problem (BVP) Solvers	Good	Fair	None	Good	None	None	Good	None	None	None	None	Good	Fair		
GPU Compatibility	None	None	None	Excellent	Good	None	None	None	None	None	None	Good	None	None	
Analysis Addons (Sensitivity Analysis, Parameter Estimation, etc.)	None	None	None	Excellent	Excellent	None	Good (for some methods like DASPK)	None	Poor	Good	None	None	Excellent	None	

\*Efficiency takes into account not only the efficiency of the implementation, but the features of the implemented methods (advanced timestepping controls, existence of methods which are known to be more efficient, Jacobian handling).

\*\*Event handling needs to be implemented yourself using basic rootfinding functionality.

For more detailed explanations and comparisons, see the following blog post:

Scale

None	Poor	Fair	Good	Excellent
------	------	------	------	-----------

<http://www.stochastictest.com/a-comparison-between-differential-equation-solver-sules-in-matlab-r-julia-python-c-and-fortran>

Explanation

Functionality does not exist	Functionality exists, but is feature-incomplete	The basic features exist	The basic features exist and some extra tweakability exists. May include extra methods for efficiency.	Has all of the basic features and more. Extra features for flexibility and efficiency.
------------------------------	---	--------------------------	--	--

<https://github.com/JuliaDiffEq/DifferentialEquations.jl>

# MIT News: New climate model to be built from the ground up

*December 12, 2018*

Our group collaborates in a new Climate Modeling Alliance to advance climate modeling and prediction. You can read about the overall project in a [press release](#) issued by Caltech, in partnership with the MIT School of Science, the Naval Postgraduate School, and the Jet Propulsion Laboratory. We also have a brand [new website](#) with more details.

The MIT team's role in CliMA is described in an [article](#) published on the PAOC's website and reproduced here:

At MIT, Professors [Raffaele Ferrari](#) and [John Marshall](#), both Cecil and Ida Green Professors of Oceanography and members of the Program in Atmospheres, Oceans and Climate (PAOC), will develop the ocean and sea-ice component of the CliMa climate model, leveraging their expertise in the development of ocean models (the MITgcm was spearheaded by Marshall, with [Chris Hill](#) and [Jean Michel Campin](#) as key developers) and in the representation of sub-gridscale mixing processes in the ocean (Ferrari and Marshall).

To take advantage of new computer architectures, languages, and machine learning techniques, the team has partnered with [Alan Edelman](#)'s group in CSAIL at MIT, who will help write the new generation climate model in the [Julia](#) computing language developed by the group. This will enable the MIT team to target GPUs, CPUs, and evolving computer architectures within one code

# ClaSSE model in *Julia*

## Methods:

1. Made basic calculation as fast as possible in Julia
  - fully used sparsity
  - all parameter arrays & indexing pre-allocated
  - minimized Garbage Collection with `@benchmark` & advice from `DifferentialEquations` help forum (including Rackauckas)
2. Precalculate “Es” (conditional extinction probabilities) once, then interpolate for “Ds” (observed data probabilities)

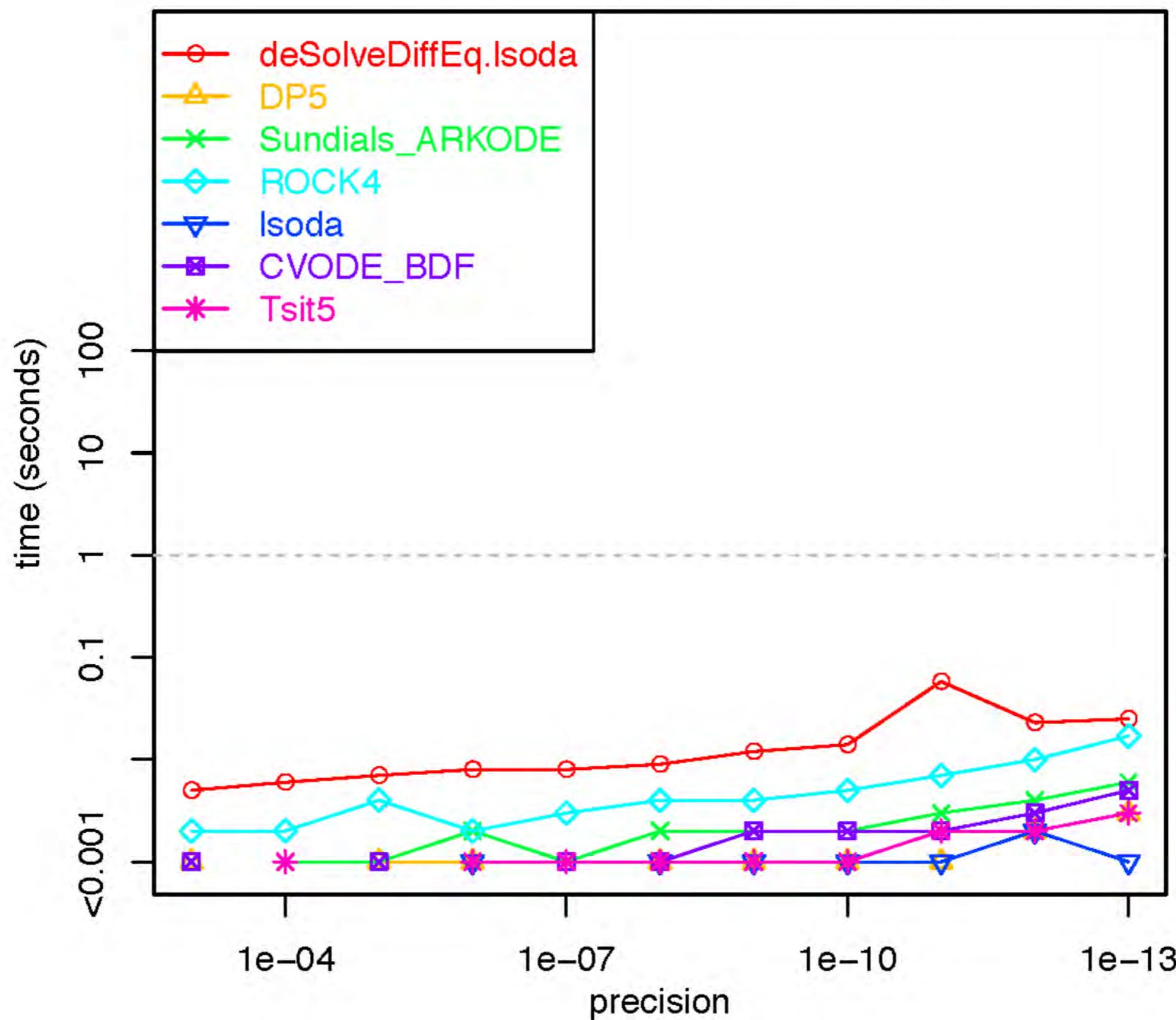
# ClaSSE model in *Julia*

## Methods:

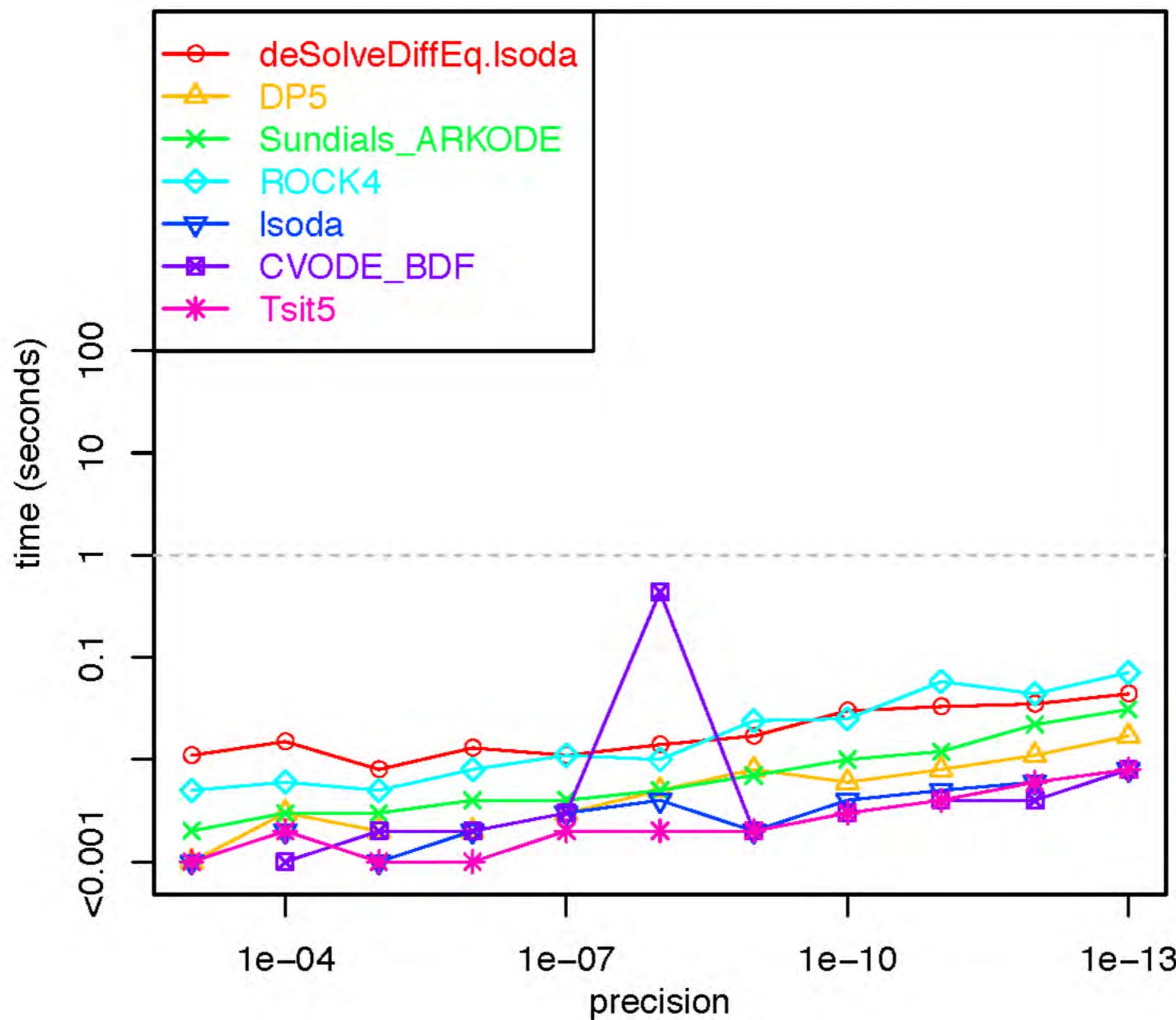
3. Compare Julia's many available differential equation solvers with Work-Precision diagrams

- from 2-11 areas
- i.e. from 4-2048 states (geographic ranges)
- i.e. systems of 8-4048 differential equations

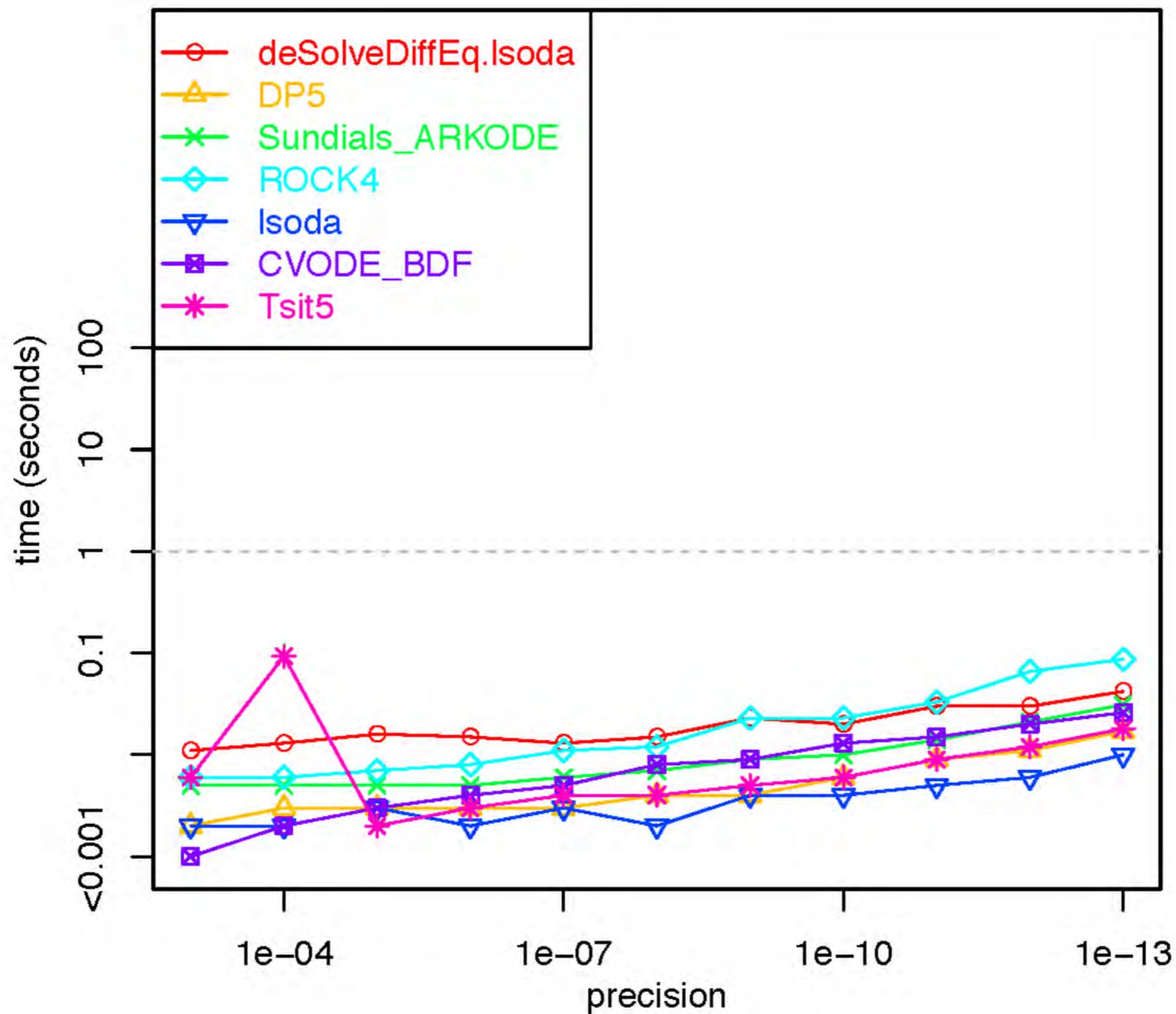
## Work–precision diagram, 2 areas, 4 states



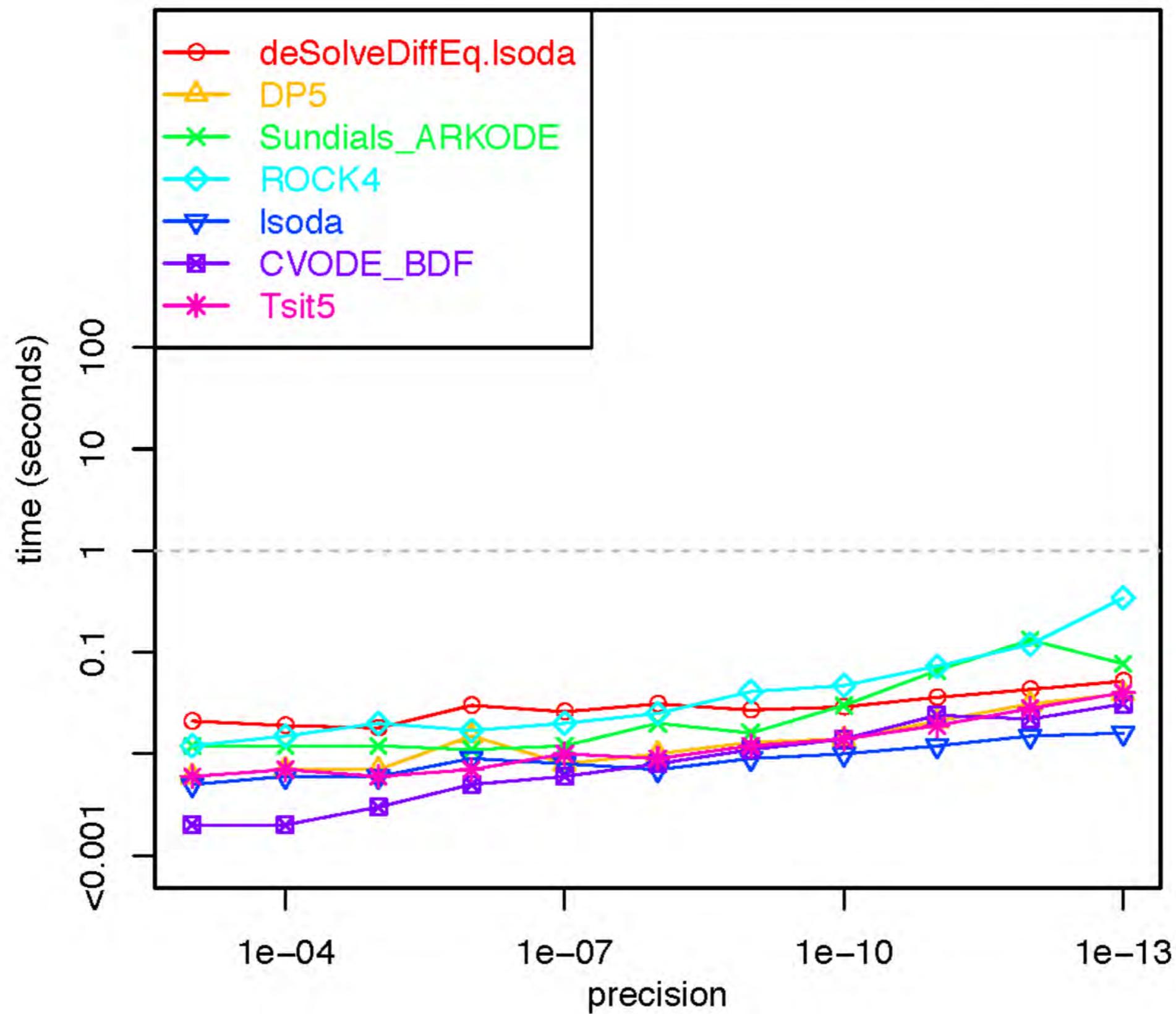
## Work–precision diagram, 3 areas, 8 states



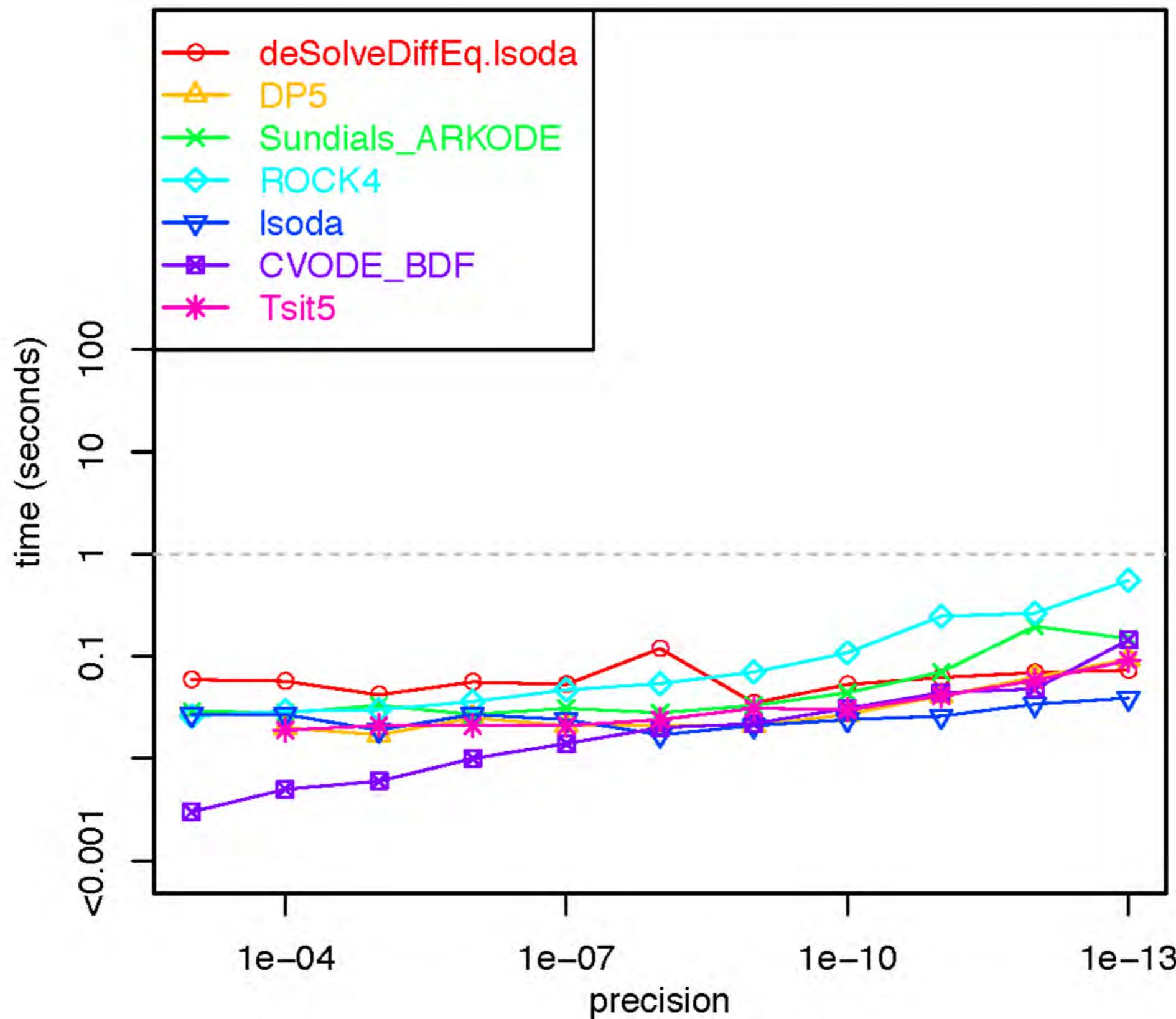
## Work–precision diagram, 4 areas, 16 states



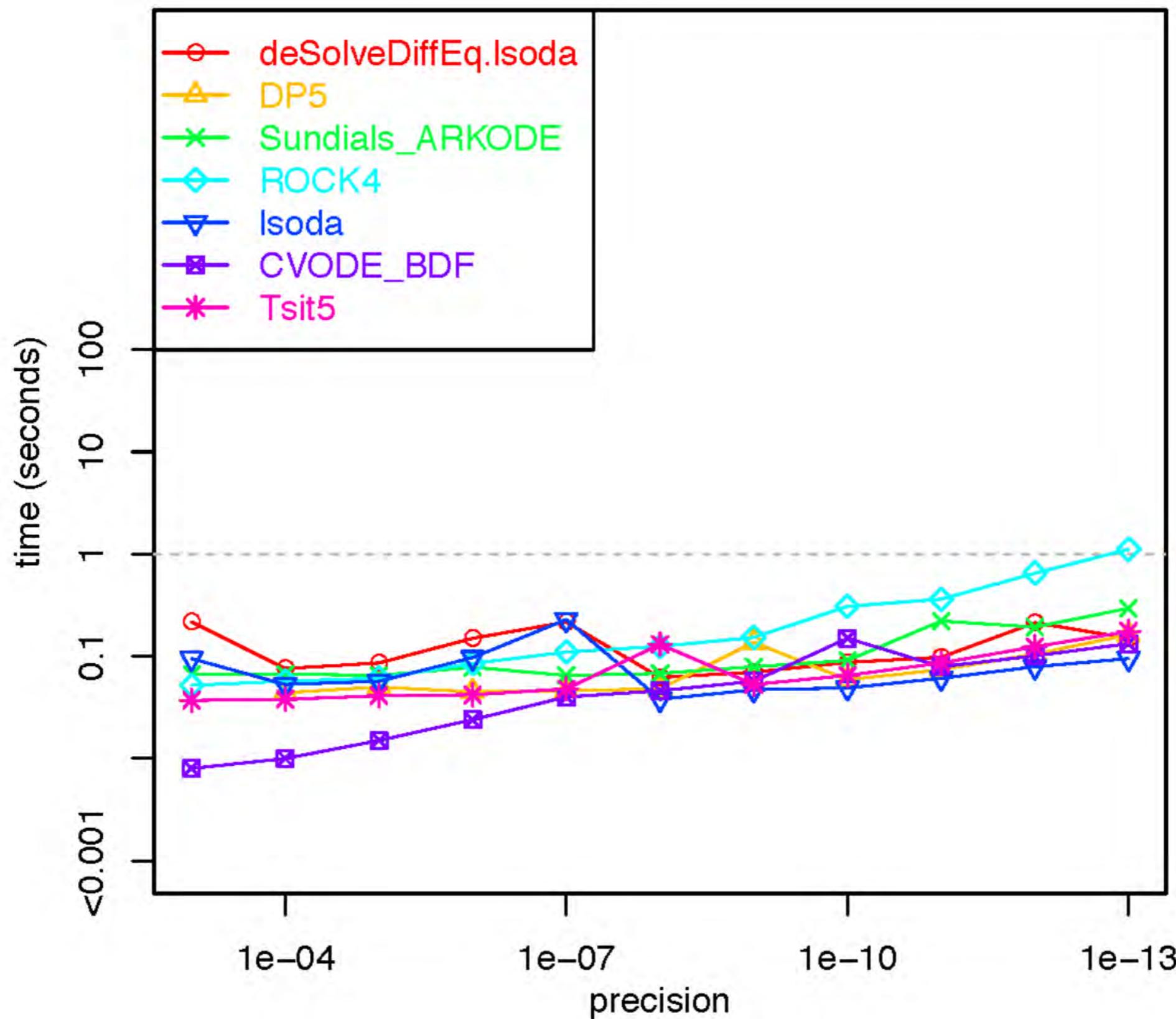
## Work–precision diagram, 5 areas, 32 states



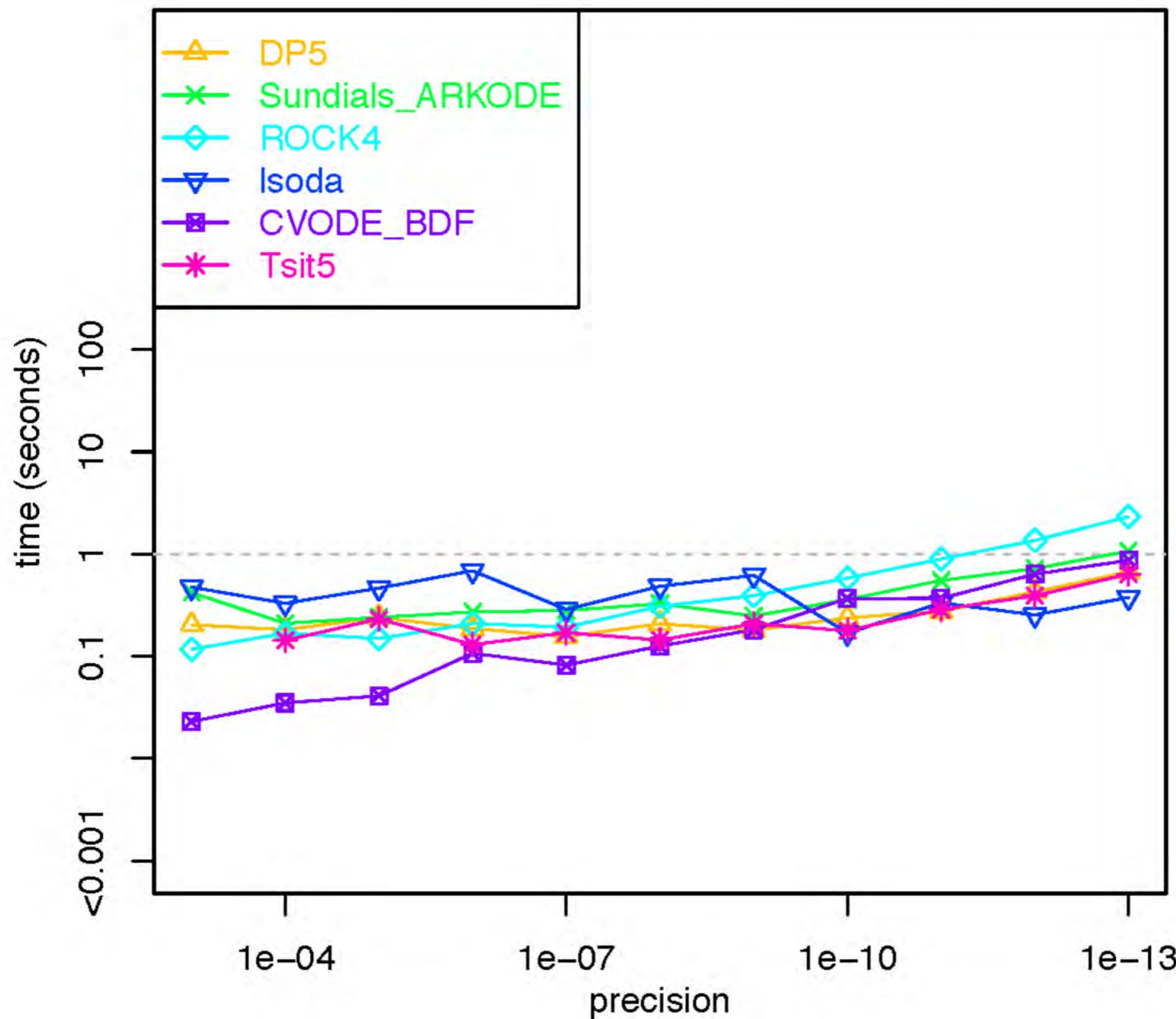
## Work–precision diagram, 6 areas, 64 states



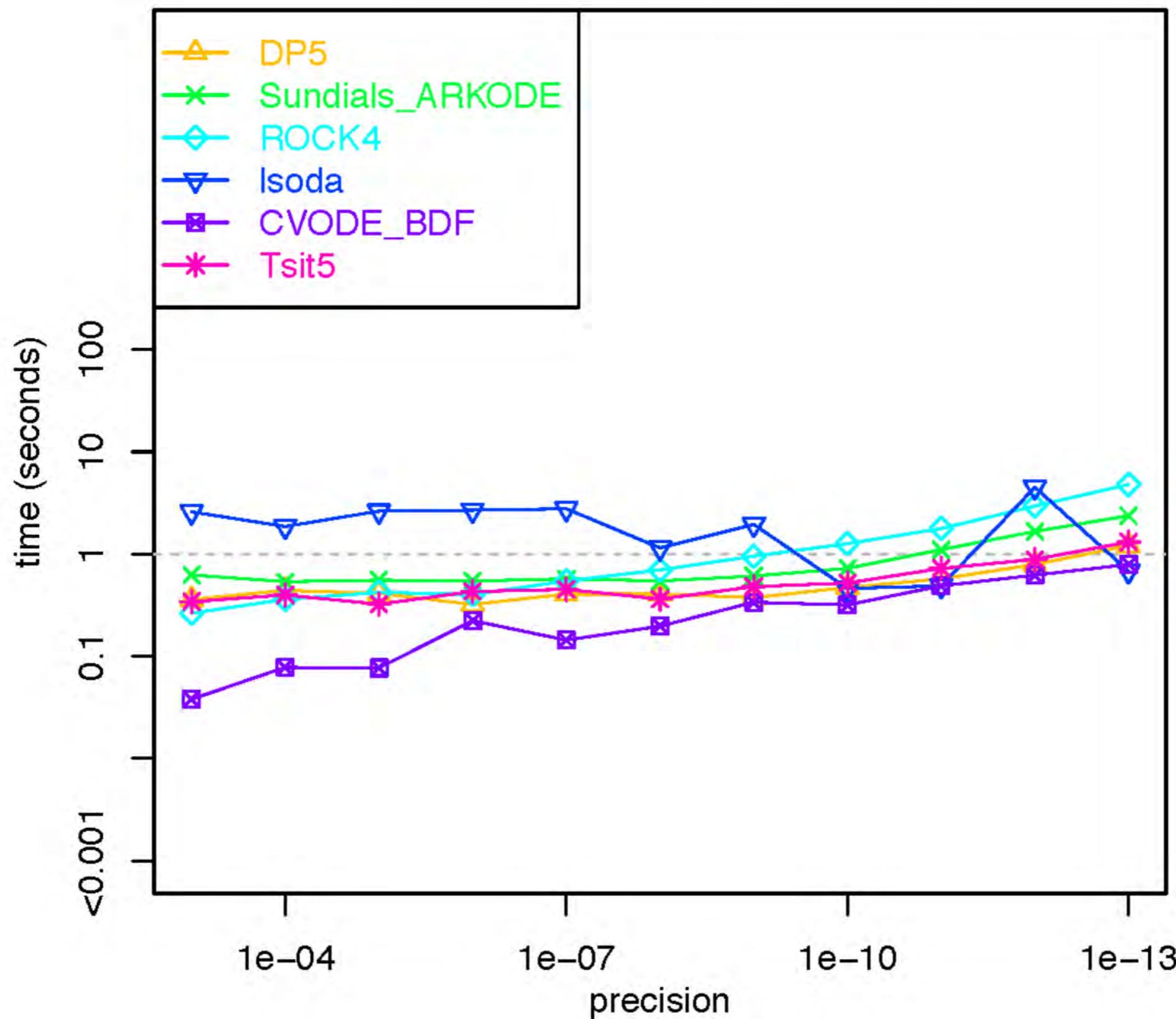
## Work–precision diagram, 7 areas, 128 states



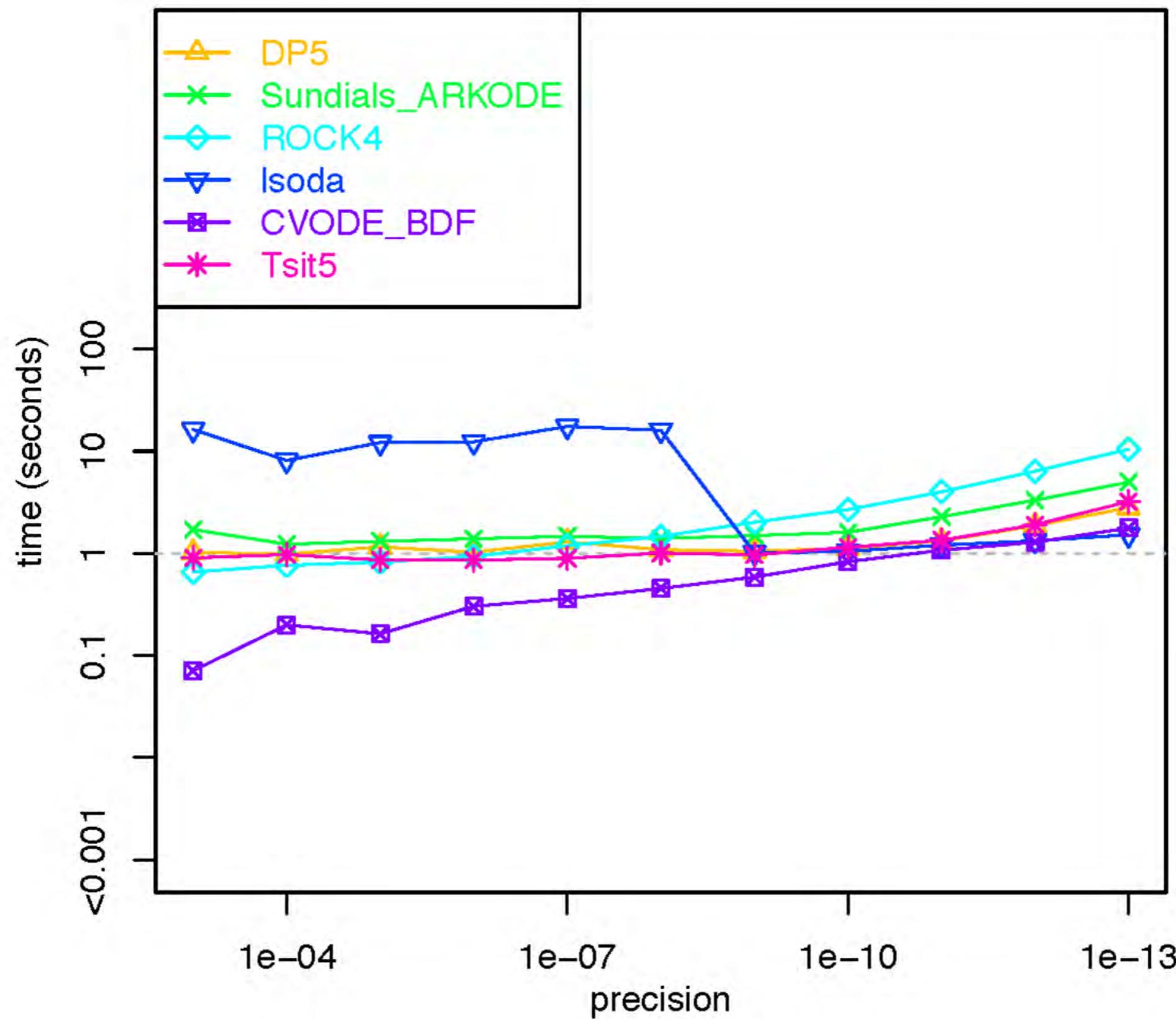
## Work–precision diagram, 8 areas, 256 states



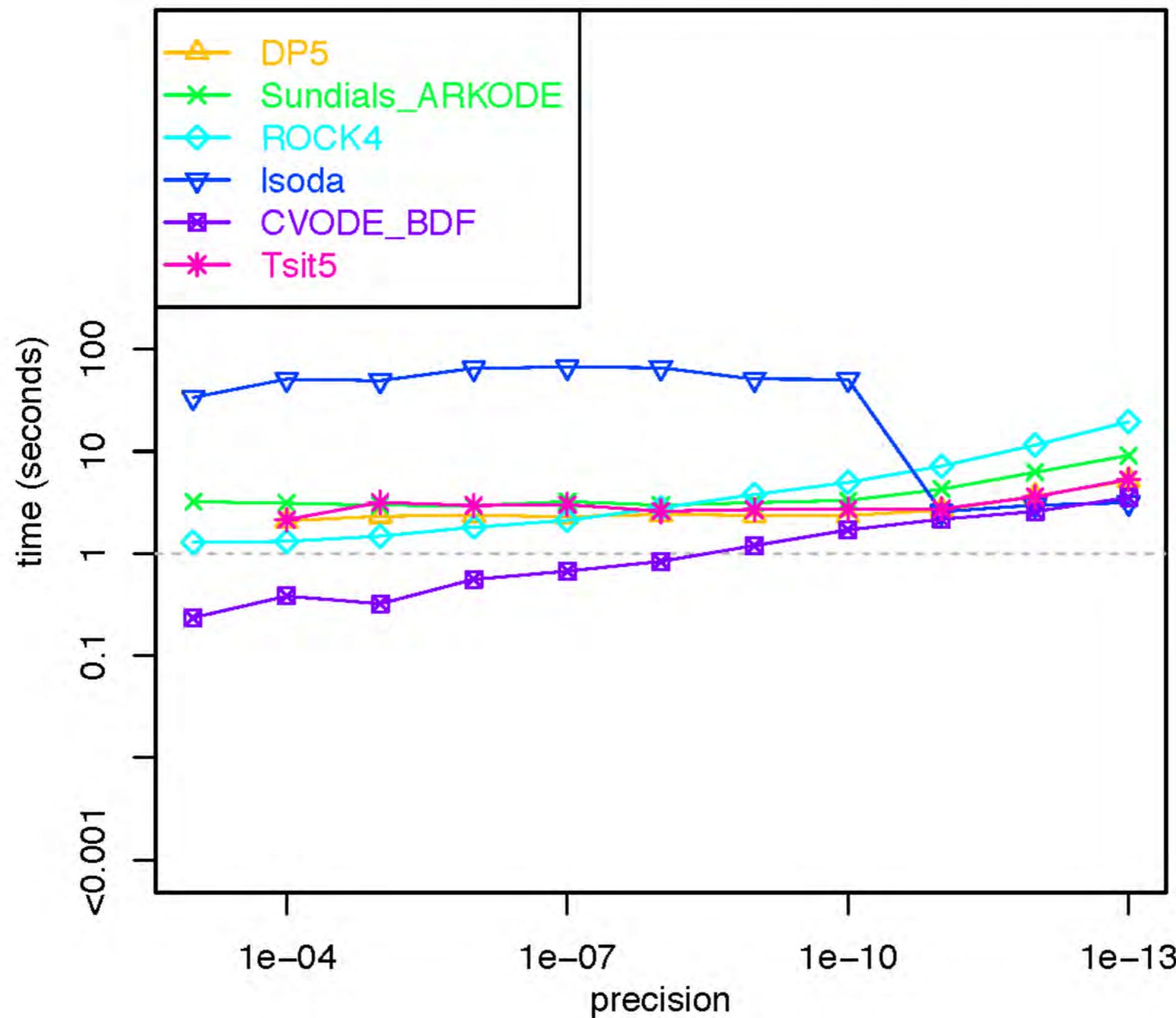
## Work–precision diagram, 9 areas, 512 states



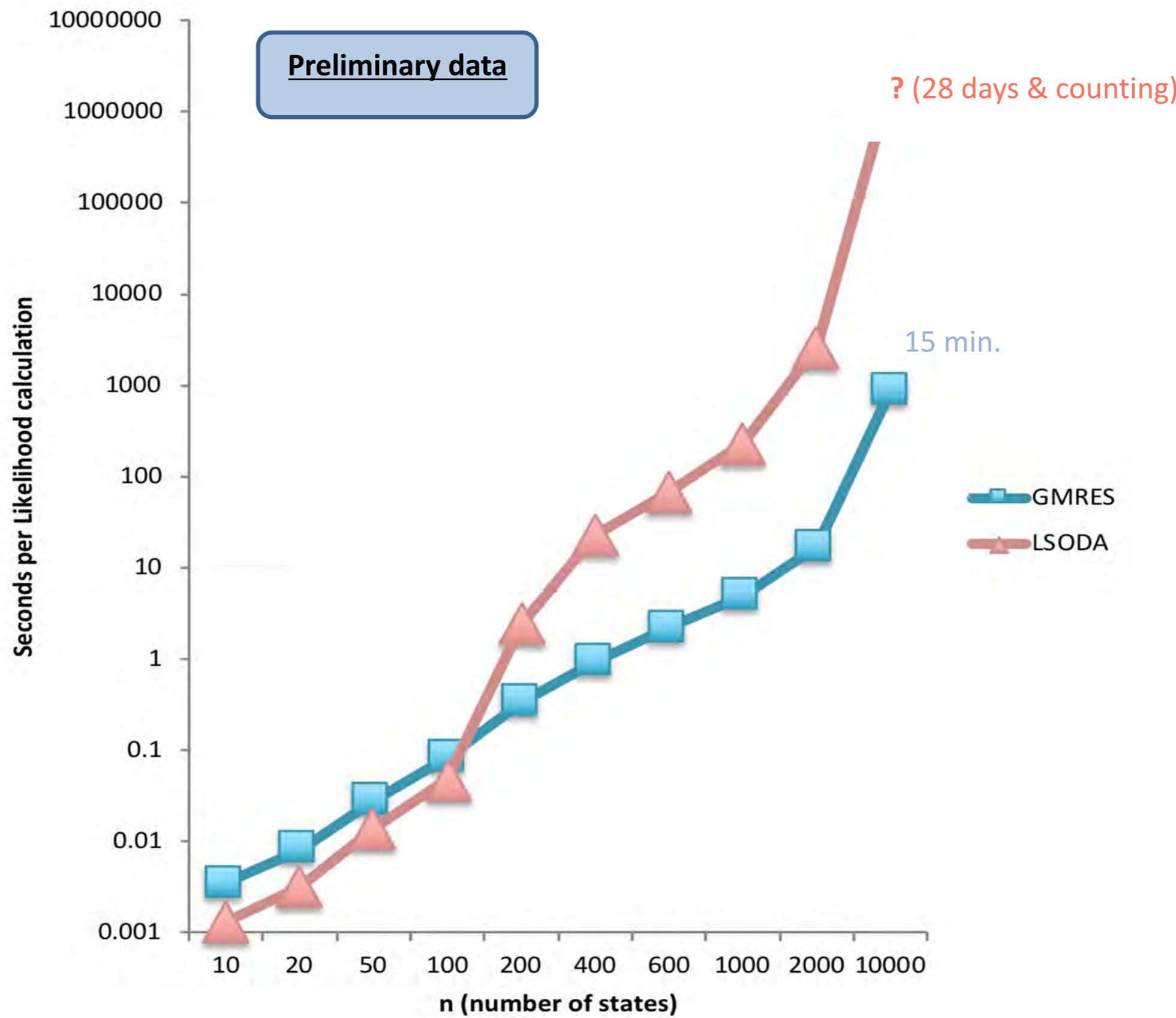
## Work-precision diagram, 10 areas, 1024 states



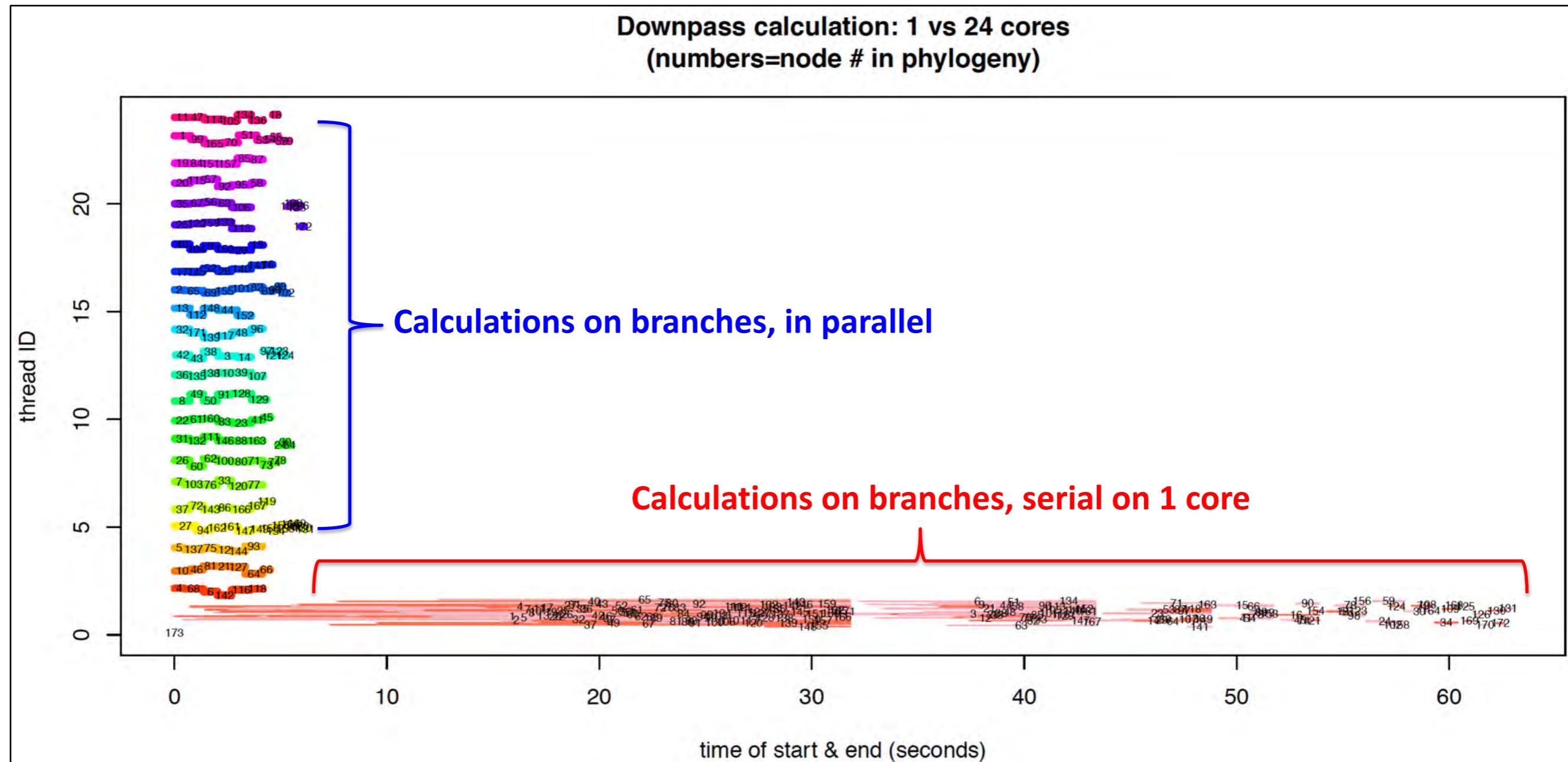
## Work-precision diagram, 11 areas, 2048 states



# How far could we push this?



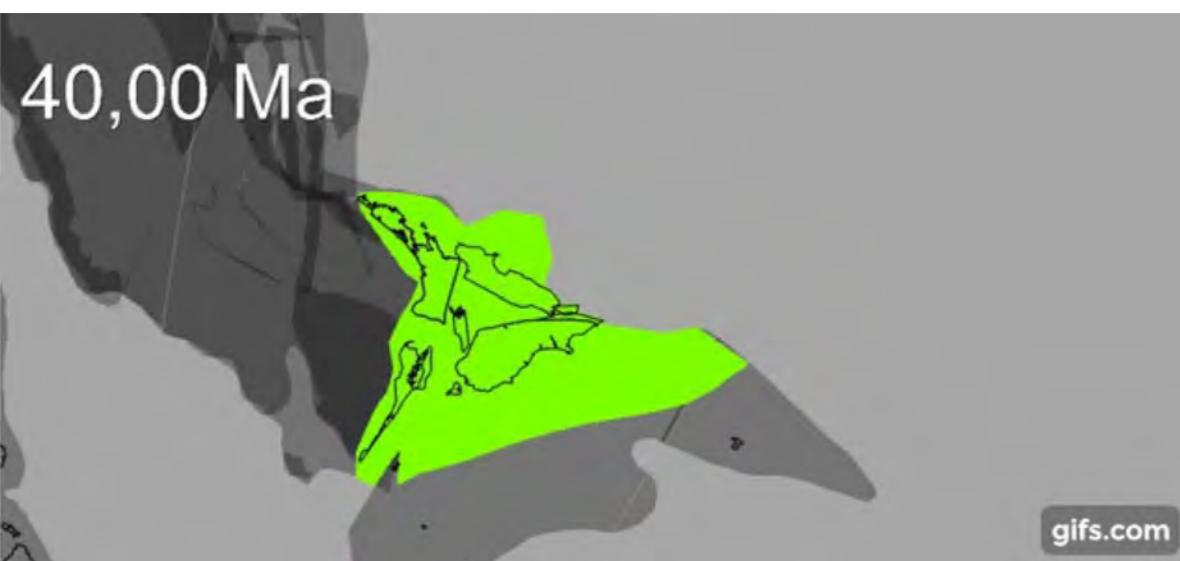
# Serial vs. Parallel - speeding up SSE calculations



# *BioGeoJulia*: complexifying biogeography

Integrate *BioGeoJulia* with  
*GPlates* for continuous  
palaeogeography

*GPlates* animation: Zealandia crustal thickness



Müller, Zahirovic et al. (2018), U. Sydney "Modelling and visualising distributed crustal deformation of Australia and Zealandia using *GPlates* 2.0." <https://www.youtube.com/watch?v=iKkCldZ6oaE>

*BioGeoJulia*: extract & use  
continuous estimates of  
areas, distances



Sabin Zahirovic, *GPlates*  
coauthor, U. Sydney

## Comparison of model features

Features of biogeographical models:	Models in use:					This Proposal ( <i>BioGeoJulia</i> )
	<i>Markov-k</i> (and e.g. DNA models) Lewis (2001)	<i>Lagrange / DEC</i> (Python)	<i>Ree &amp; Smith (2008)</i> <i>BioGeoBEARS / DEC+J etc.</i> (R package)	<i>Matzke (2013, 2014)</i>	<i>ClassSE</i> ( <i>diversitree</i> R package) Goldberg & Igić (2012)	
Probabilistic model of range evolution	X	X	X	X	X	X
Ranges can occupy multiple areas	X	X	X	X	X	X
Range expansion/contraction	X	X	X	X	X	X
Vicariance (large range can divide at speciation)	X	X	X	X	X	X
Plate tectonics/paleogeography (by hand)	X	X	X	X	X	X
Jump dispersal		X	X	X	X	X
Statistical comparison of multiple models		X	X	X	X	X
Distance-dependent dispersal		X	X	X	X	X
Trait-dependent dispersal			X	X	X	X
Speciation rate depends on region				X	X	X
Lineage extinction				X	X	X
Incomplete sampling in some subclades					X	X
Fossil sampling					X	X
Plate tectonics/paleogeography (using <i>GPlates</i> software)					X	X
Speed						
Sparse matrix library to speed up large matrices				X		X
Example number of areas	20	11	11	6		11
State space (maximum number of possible ranges in a typical analysis)	20	2048	2048	31		2047
Calculation strategy			matrix exponentiation		numeric integration	
Analysis time	10 min.	1 week	3 hr	1 week+	<1 day	

X=possible, but not implemented

# Conclusions

1. Large ClaSSE models will probably never be super-fast – but Julia versions should be fast enough for e.g. Maximum Likelihood
2. The number of free parameters explodes to meaninglessness quickly. So model (parametric) complexity has to be carefully controlled by carefully thinking about, and designing, meaningful models controlled by a small number of parameters (as in e.g. standard biogeography models)
3. Julia's DifferentialEquations solvers are *very* flexible, suggesting that more interesting models could be designed in this framework (regional carrying capacity, interpolating in the impact of external forcers like changing geography & climate, etc.)

Acknowledgements: Marsden grant no. 18-UOA-34



# Cautions

“All models are wrong, but some models are useful.”

-- George Box



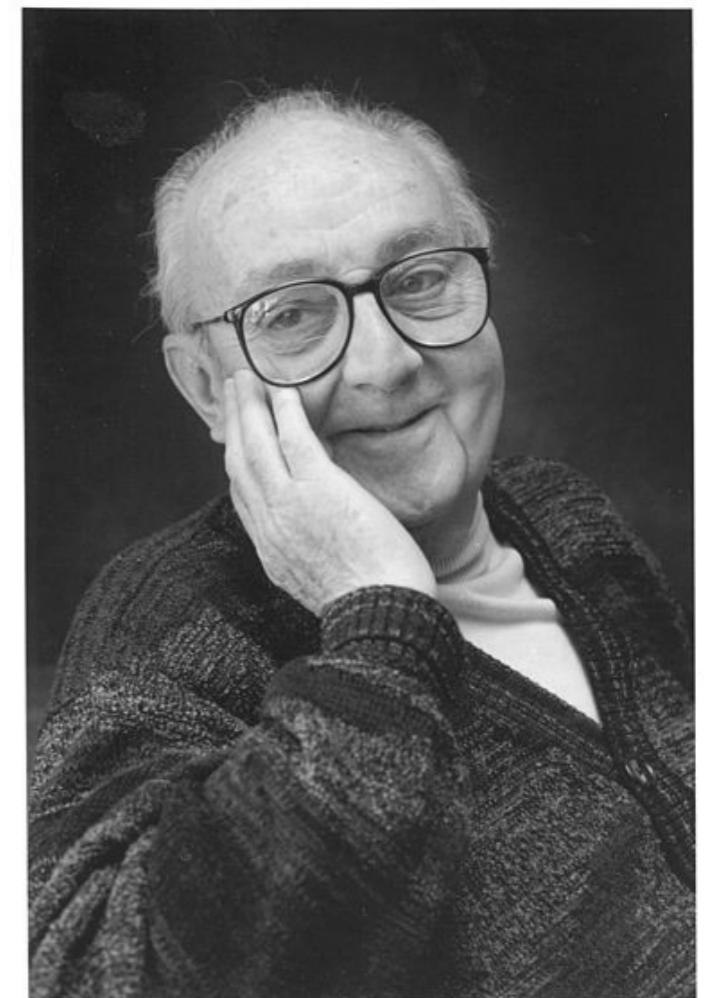
George E. P. Box  
(1919-2013)

I say: we'll never know the usefulness / misleading qualities unless we do statistical model comparison.

# Cautions

“All models are wrong, but some models are useful.”

-- George Box



George E. P. Box  
(1919-2013)

Current grant proposals to:

1. Include lineage extinction
2. Include *GPlates* (open-source plate tectonics)
3. Do calculations in reasonable time

# Summary

1. Model choice **matters** in historical biogeography! We should **always** do it!
2. Distance **matters** in historical biogeography!  
We should **always** test distance!
3. Traits also often matter! We should test for this wherever possible!
4. We can test models by comparing log-likelihoods, or penalized log-likelihoods (AIC)

Interested in evolution & biogeography? Come work with me! Questions/comments/collaborations at:

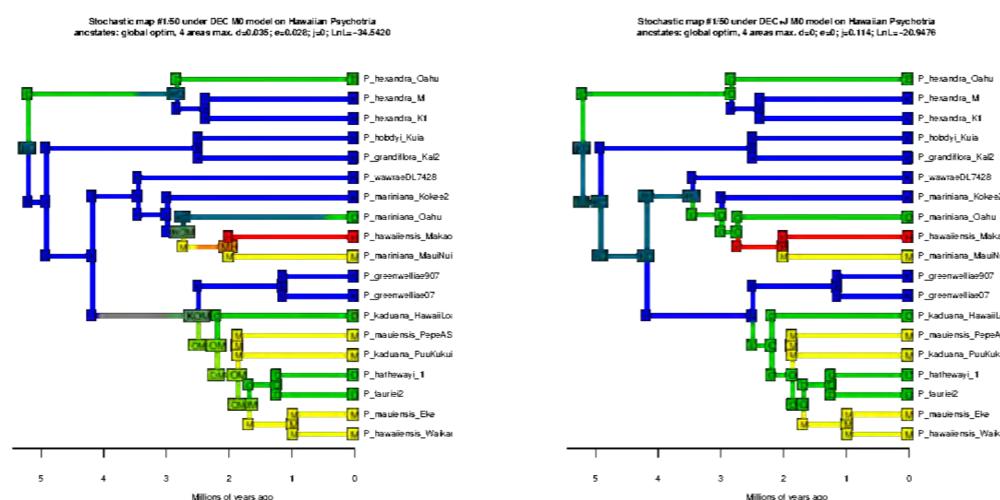
[n.matzke@auckland.ac.nz](mailto:n.matzke@auckland.ac.nz)



Senior Lecturer  
University of Auckland  
[phylo.wikidot.com/nicholas-j-matzke](http://phylo.wikidot.com/nicholas-j-matzke)

The screenshot shows the PhyloWiki BioGeoBEARS page. At the top, there's a header with the PhyloWiki logo and the text "Assisting research and education in phylogenetics and evolution". Below the header is a navigation bar with links for "example menu" and "contact". The main content area is titled "BioGeoBears" and includes a "Table of Contents" section with a dashed border containing a list of updates from May 2014 to December 2013. On the left, there's a sidebar with links for "Welcome page", "What is a Wiki Site?", "How to edit pages?", "How to join this site?", "Site members", "Recent changes", "List all pages", "Page Tags", and "Site Manager". Below that is a "Page tags" section with "start" and "free icons" buttons, and a "Add a new page" section with a text input field, a "new page" button, and an "edit this panel" link.

TRY BioGeoBEARS AT:  
<http://phylo.wikidot.com/biogeobears>



Funding: NIMBioS  
University of Auckland  
Marsden Fast-Start

Thanks for support from:

