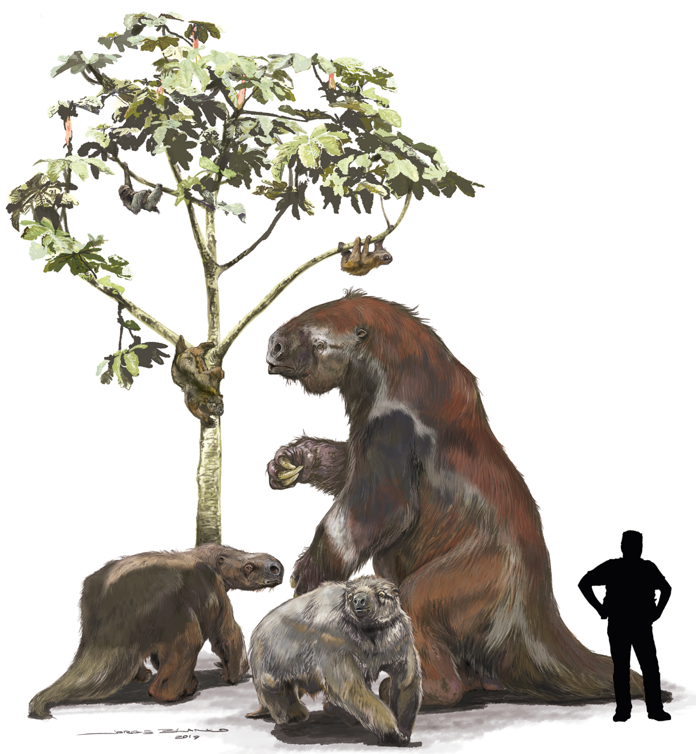
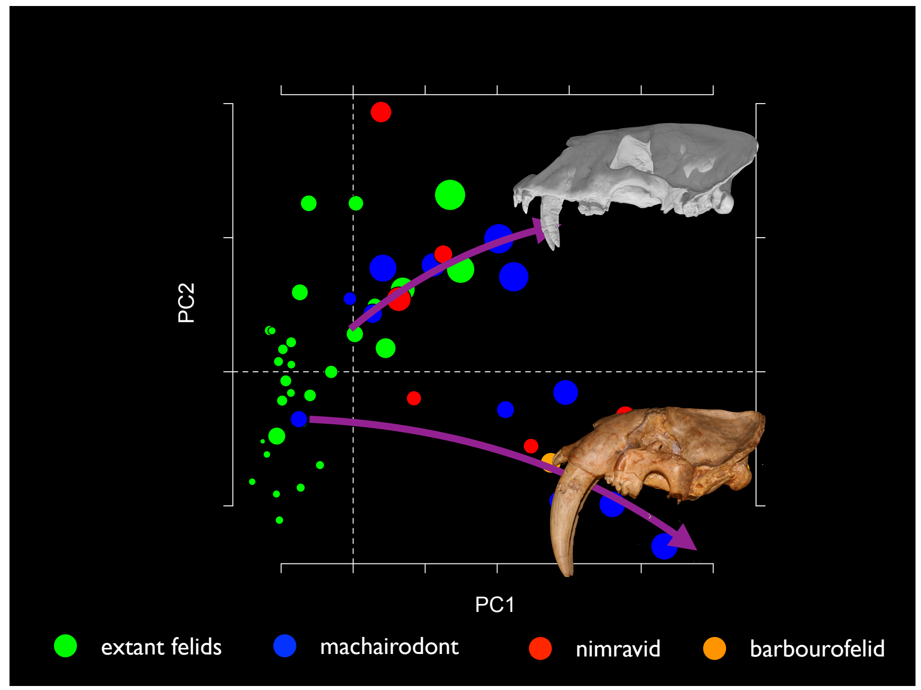
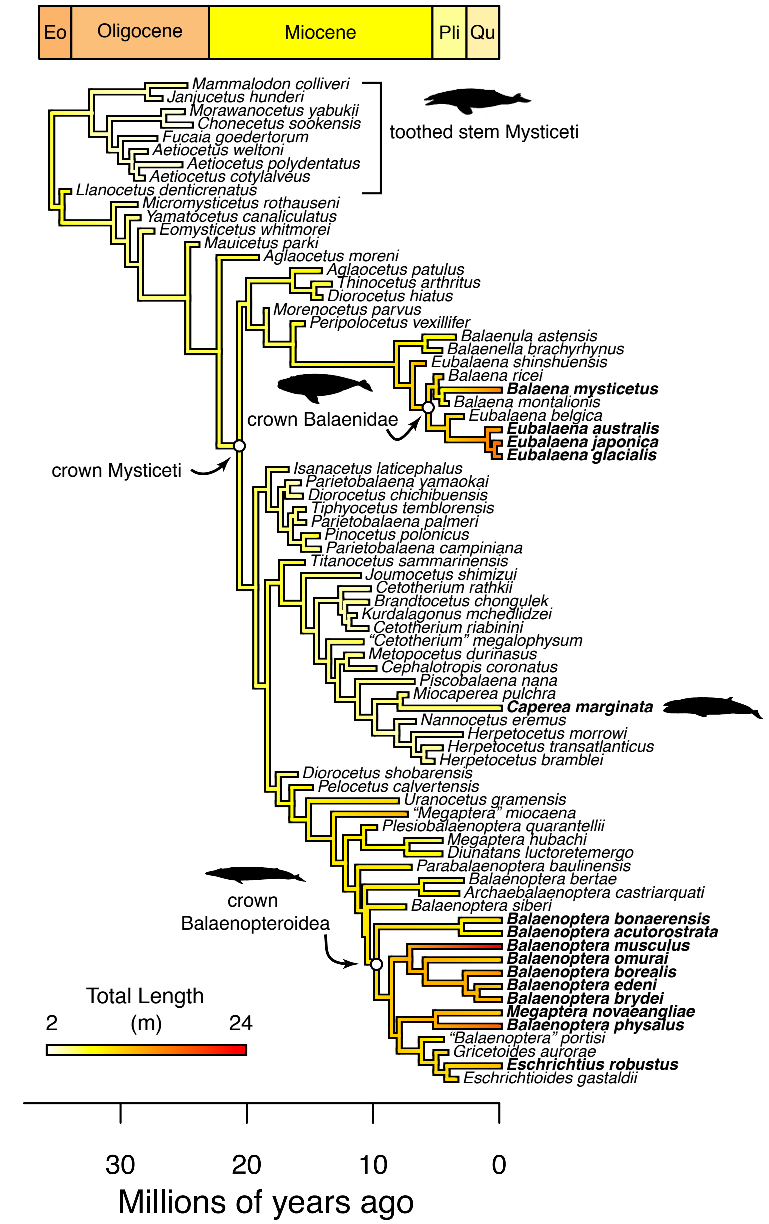
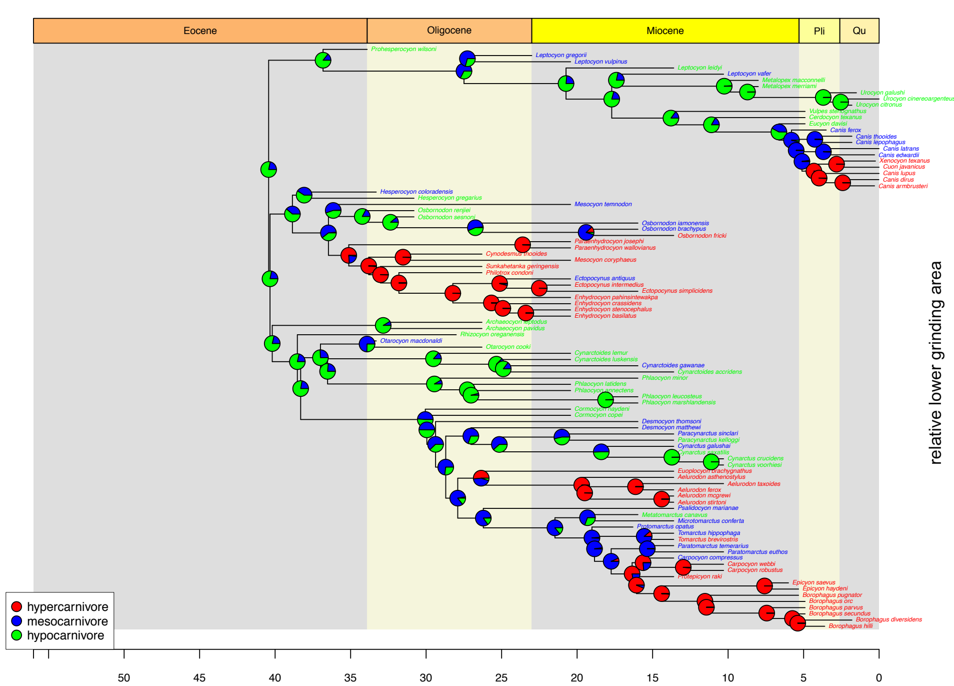
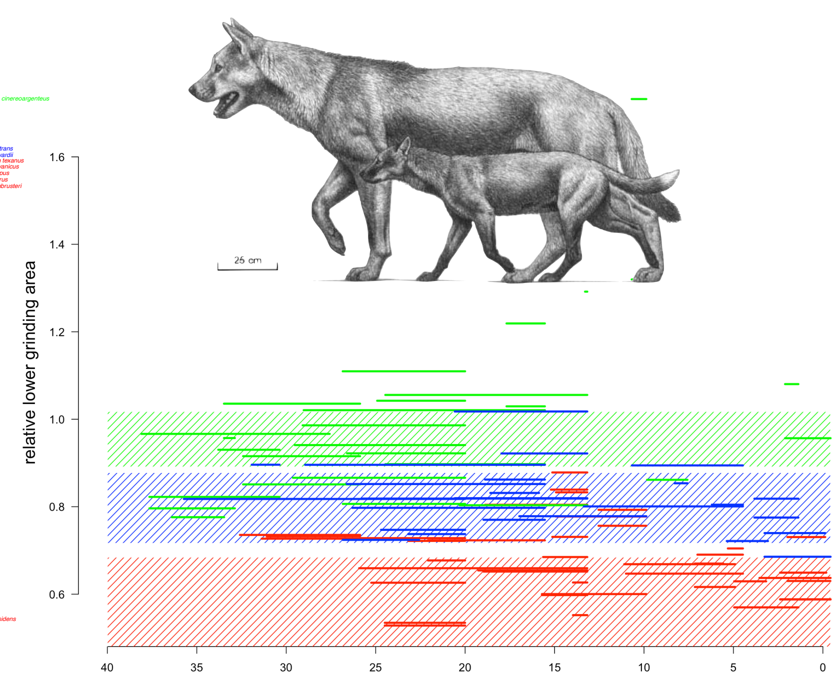
Graham Slater
University of Chicago
mammalian macroevolution

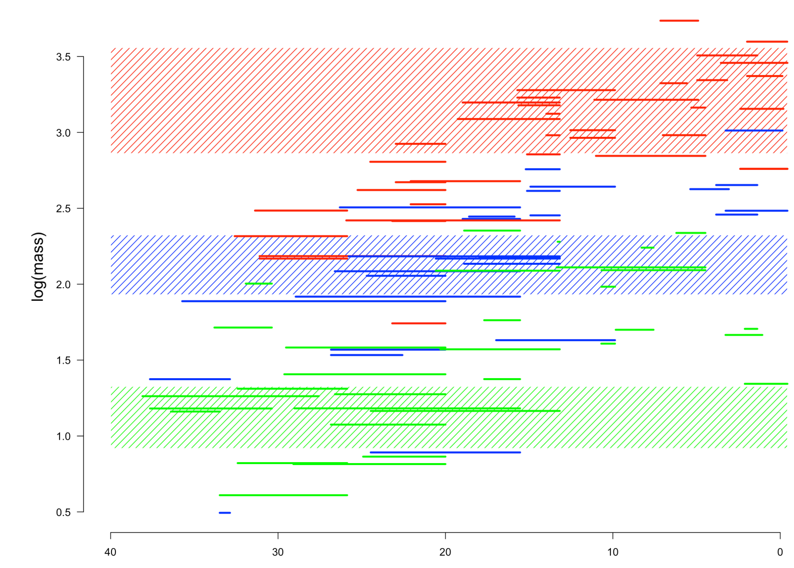












continuous trait evolution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+1


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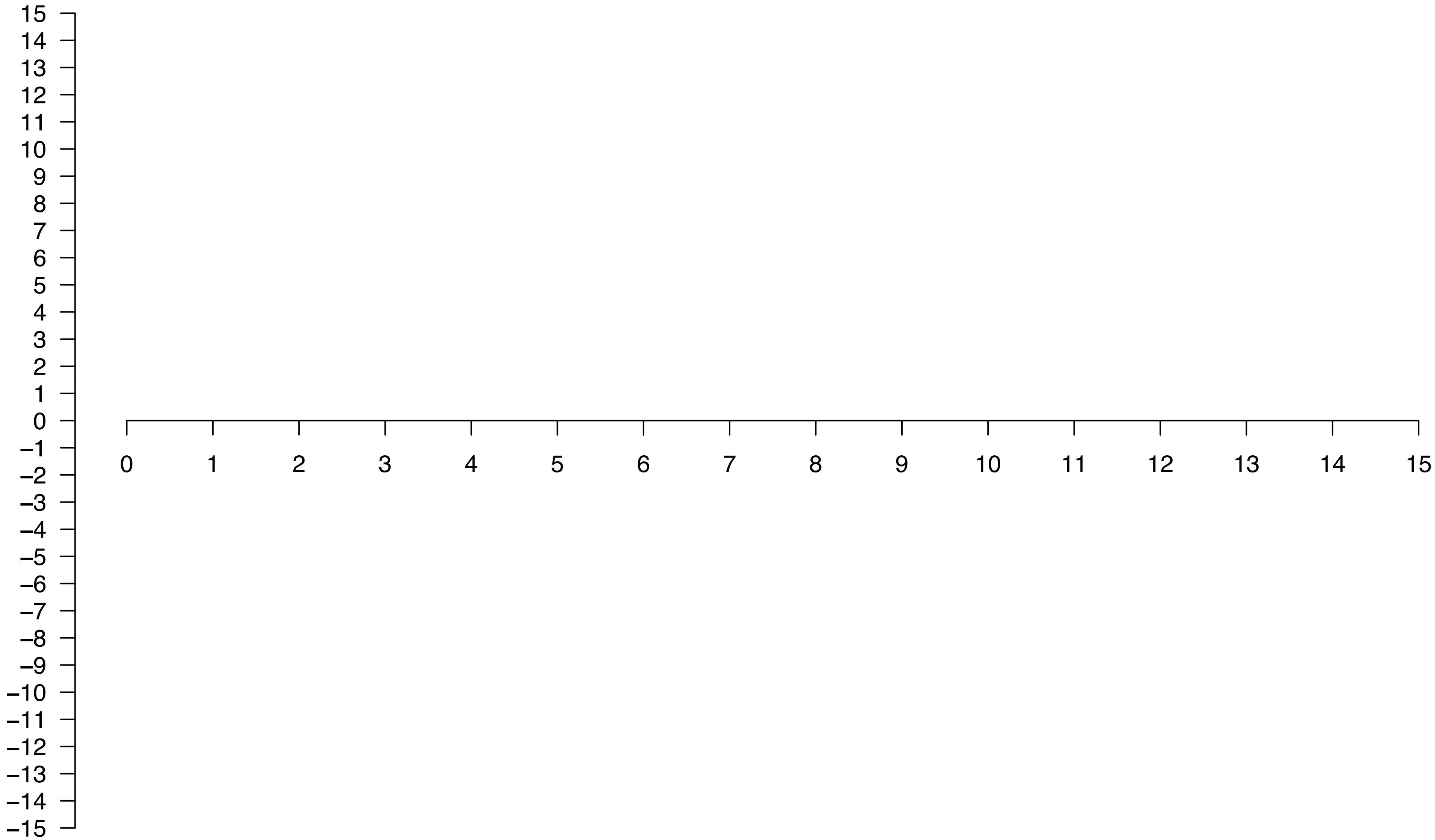
-1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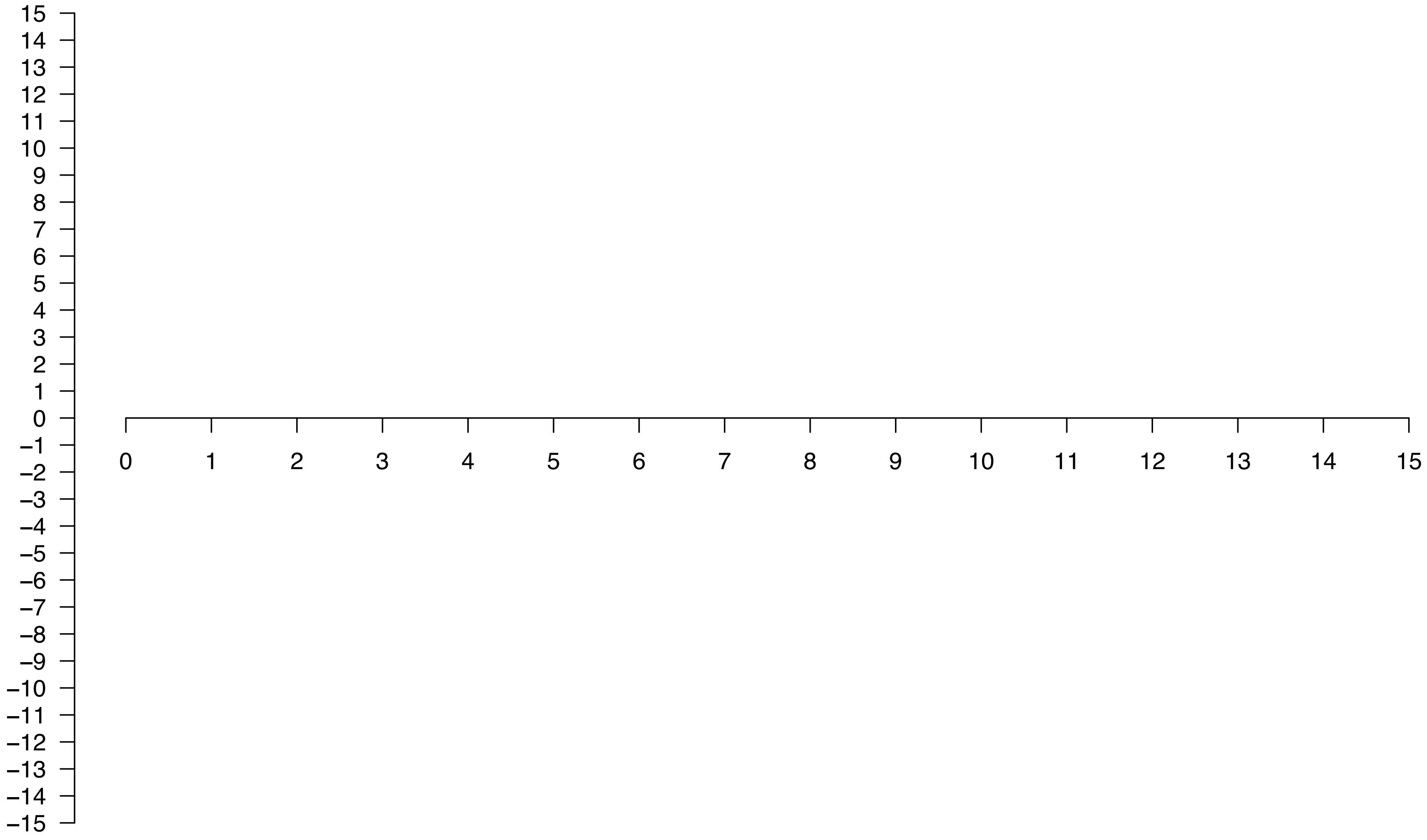
−14
−15
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15

$$F_n = 0 + X_1 + X_2 + ... + X_n$$



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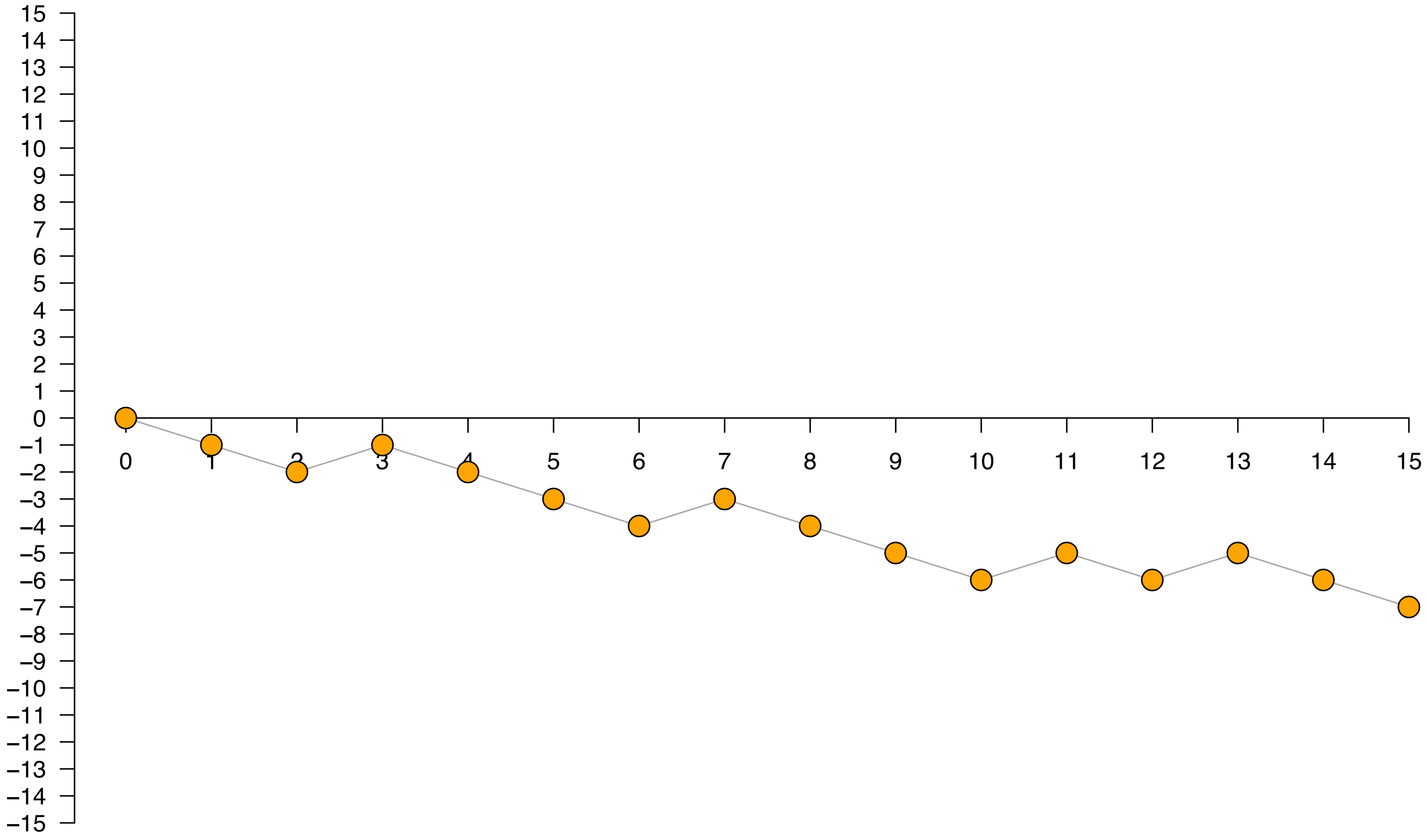

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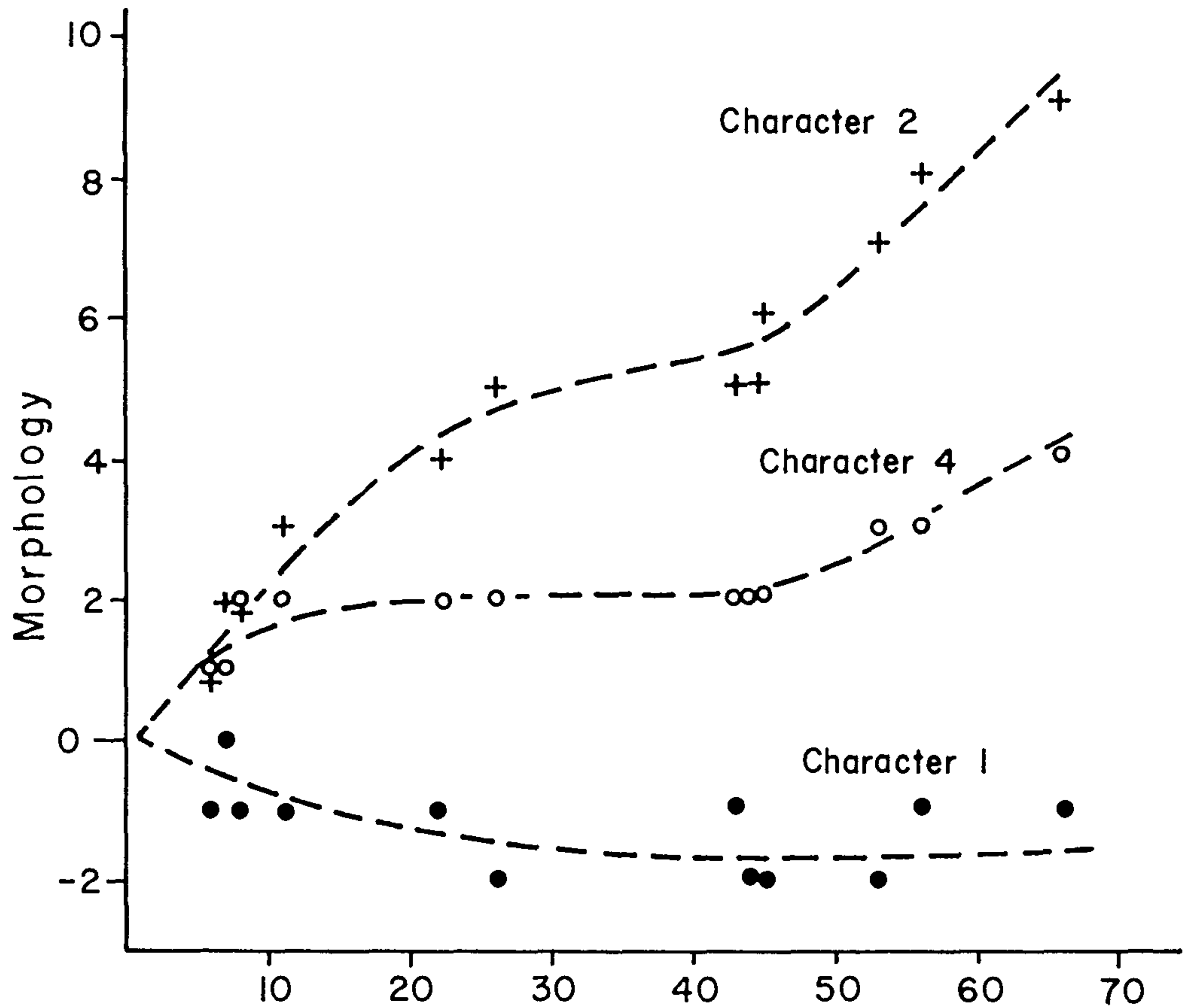
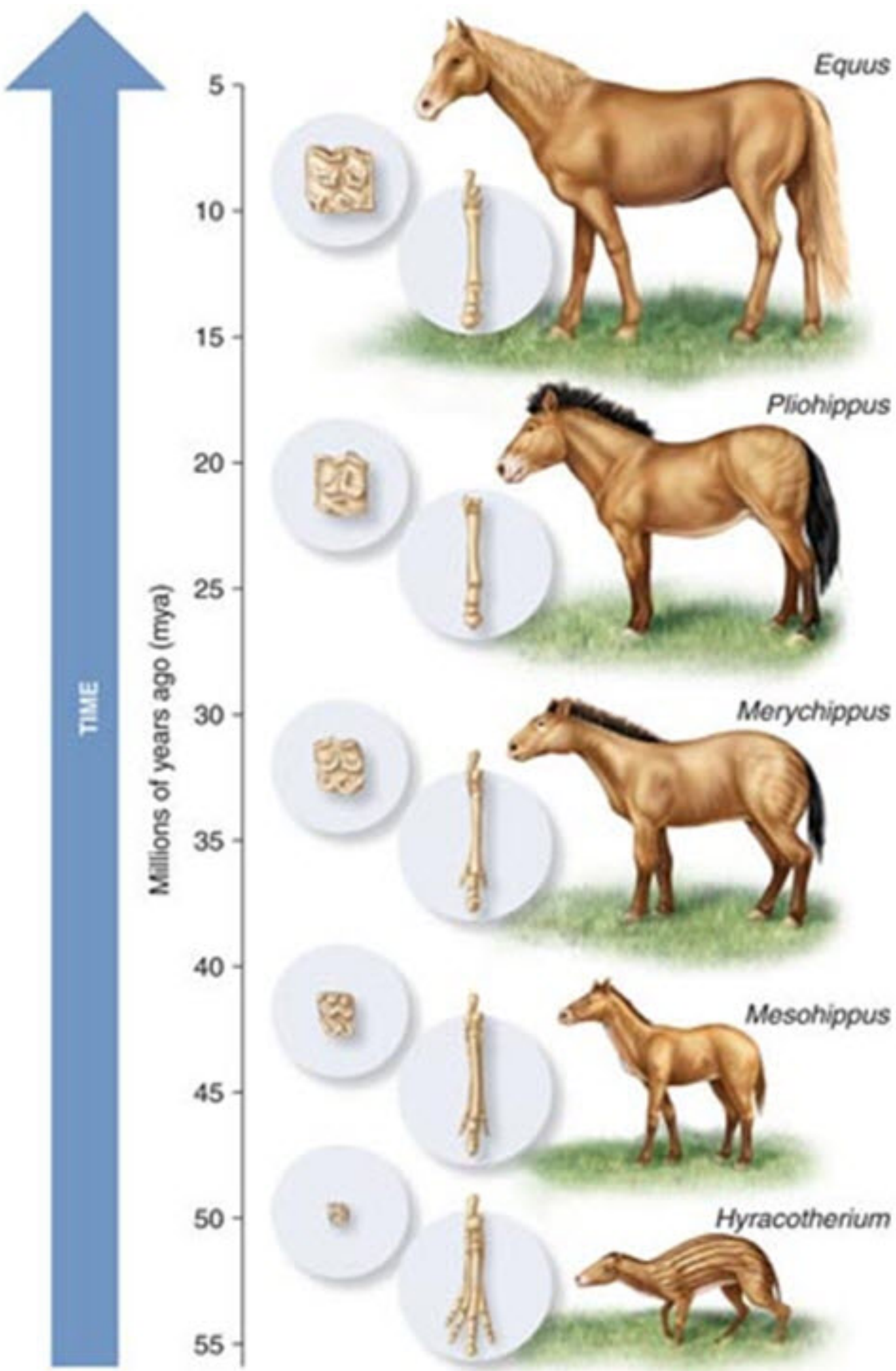
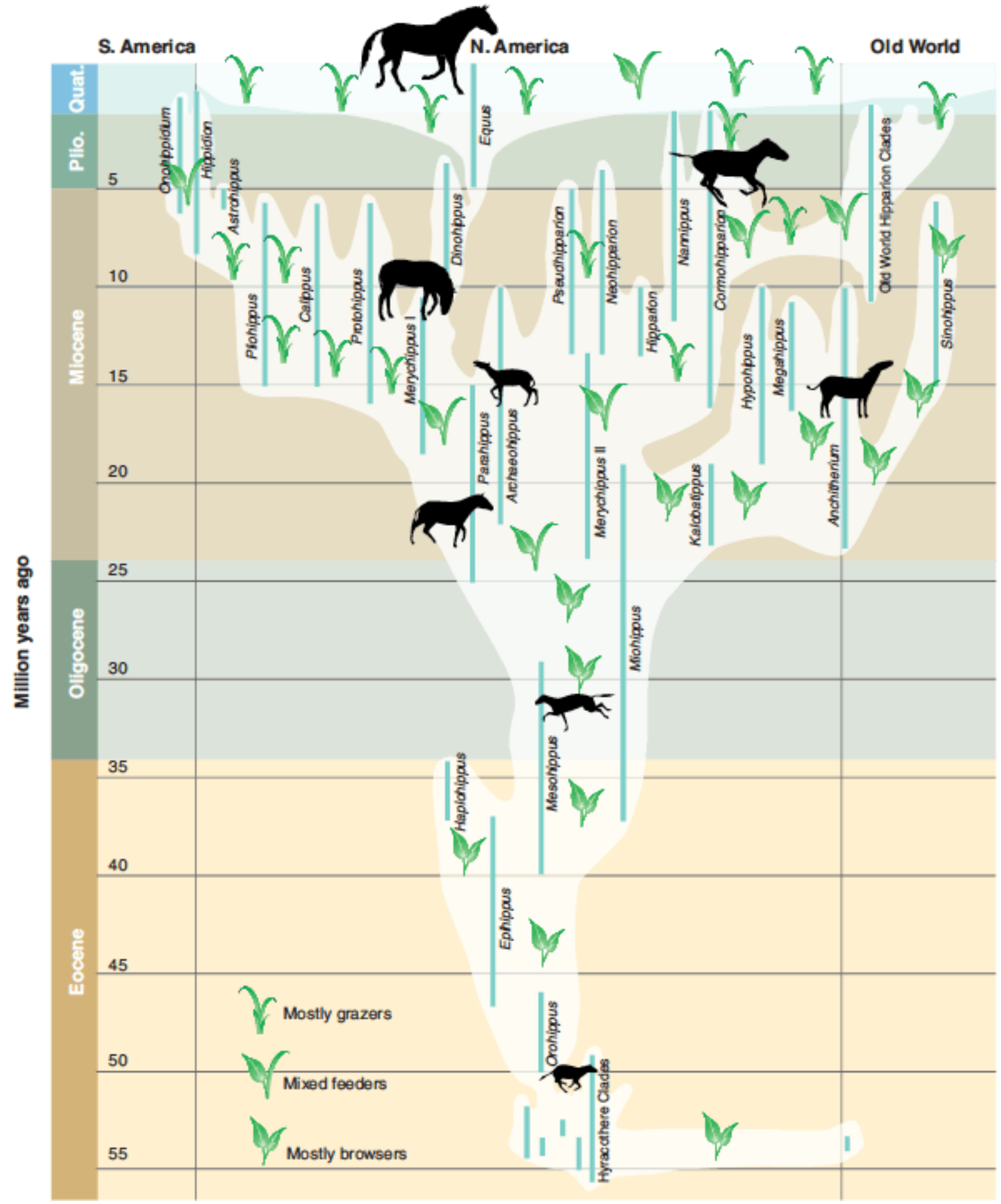


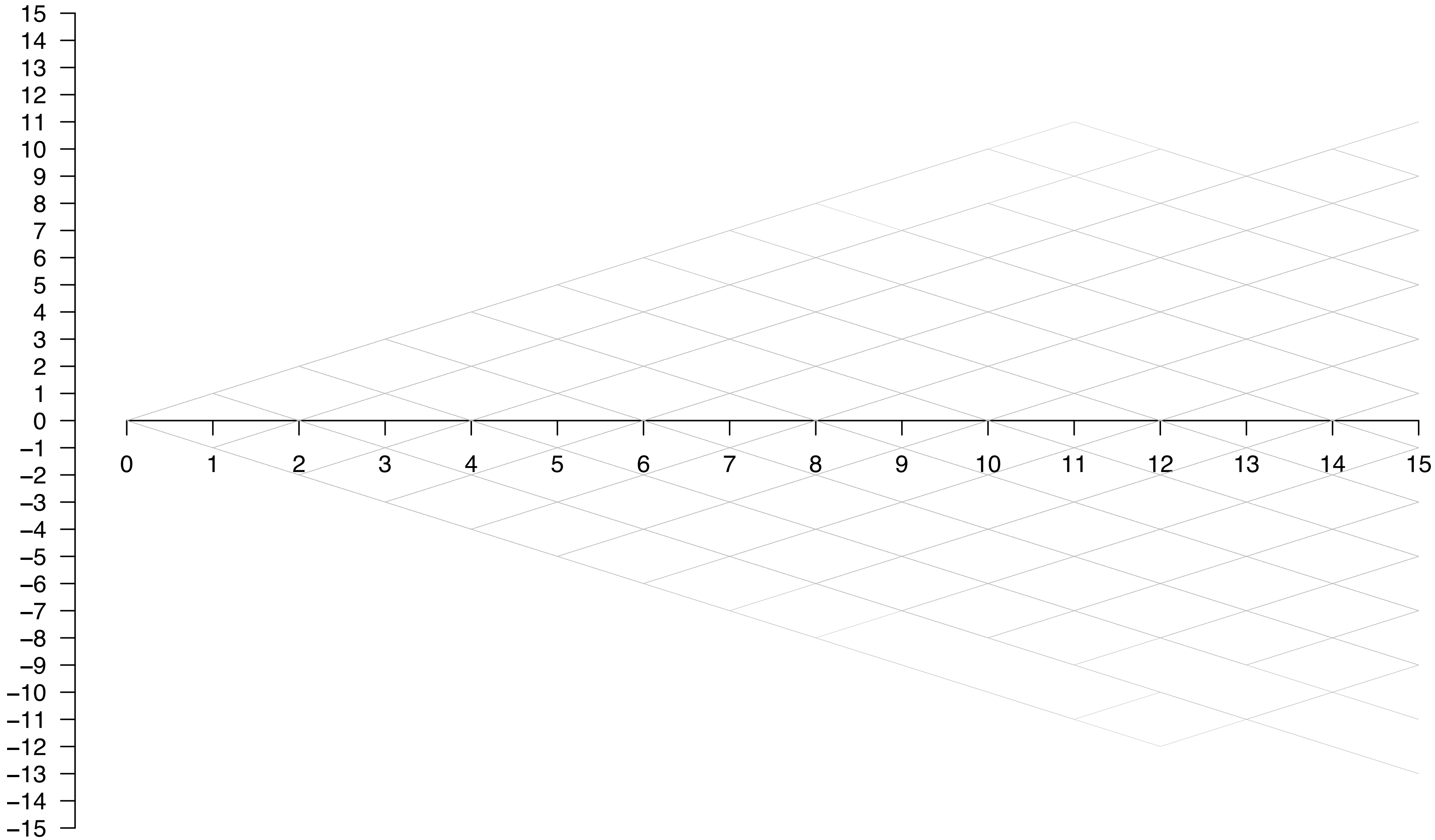
Raup and Gould 1974



TIME
Millions of years ago (mya)
5
10
15
20
25
30
35
40
45
50
55
Equus
Pliohippus
Merychippus
Mesohippus
Hyracotherium



S. America
N. America
Old World
Quat.
Plio.
Miocene
Oligocene
Eocene
Million years ago
5
10
15
20
25
30
35
40
45
50
55
Onohippidium
Hippidion
Astrohippus
Pliohippus
Calippus
Protohippus
Merychippus I
Dinohippus
Equus
Pseudhipparion
Neohipparion
Nannippus
Cormohipparion
Old World Hipparion Clades
Sinohippus
Hipparion
Hypohippus
Megahippus
Anchitherium
Kalobatippus
Parahippus
Archaeohippus
Merychippus II
Miohippus
Mesohippus
Haplohippus
Epihippus
Orohippus
Hyracothere Clades
Mostly grazers
Mixed feeders
Mostly browsers



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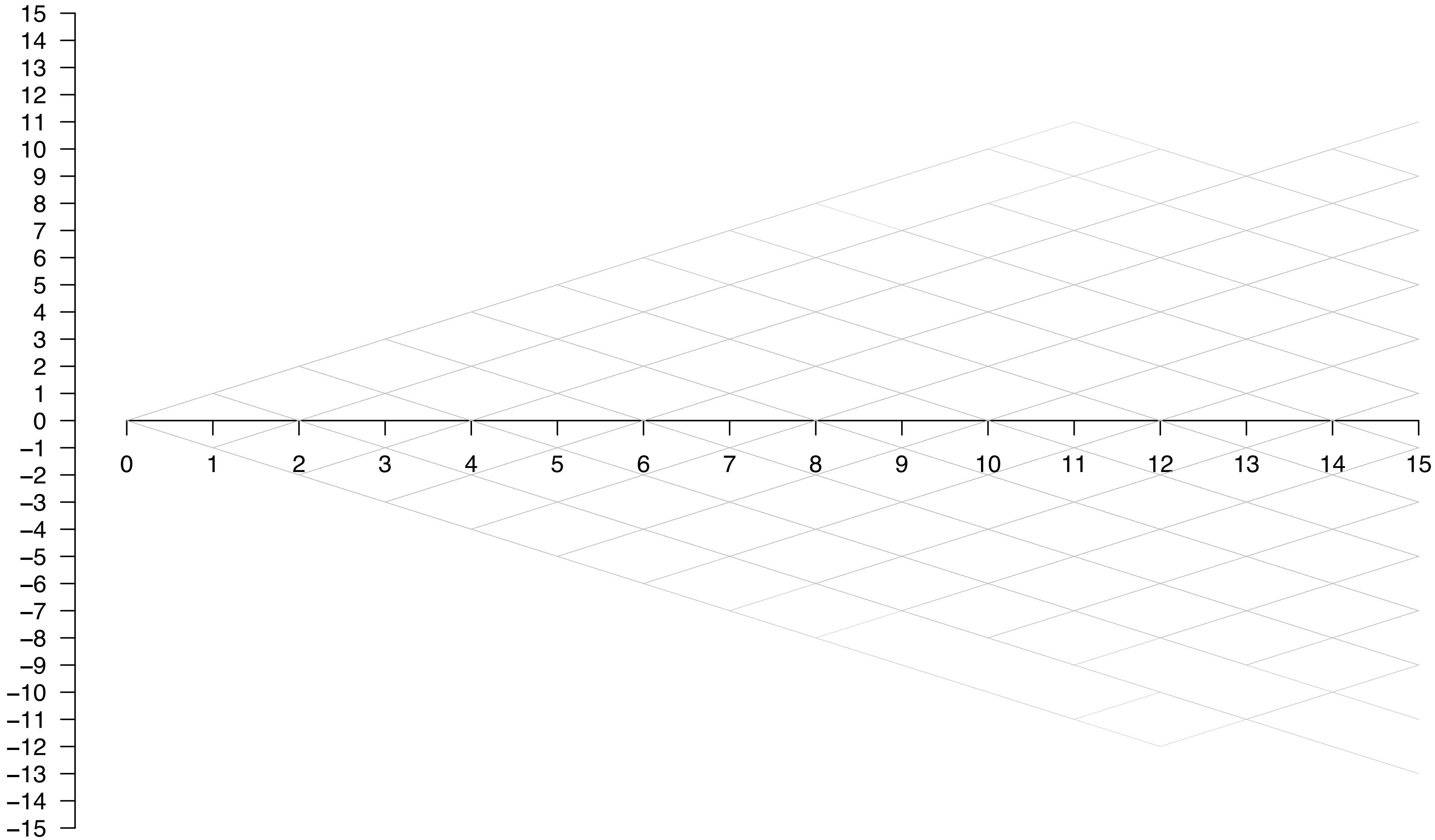
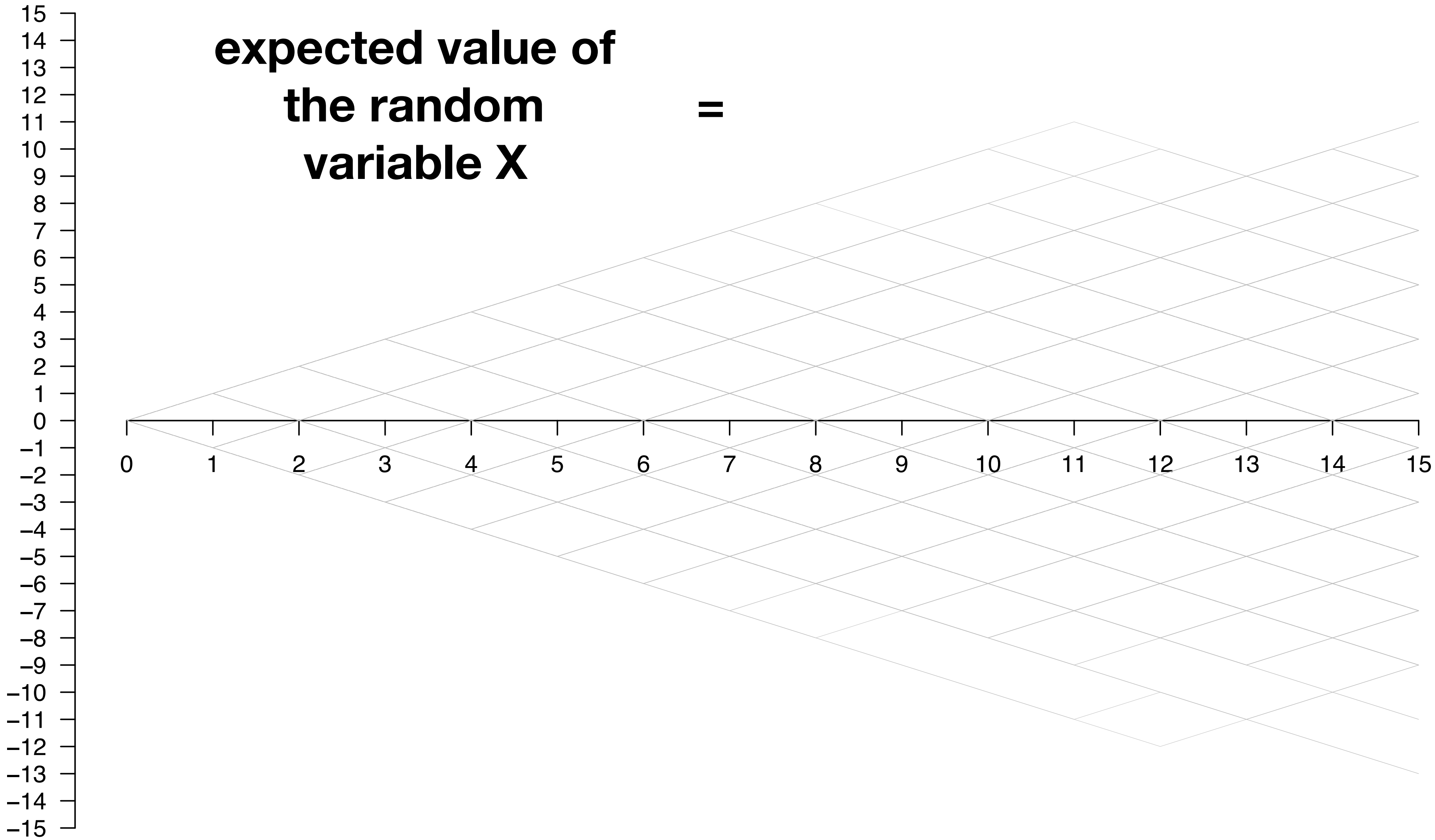
15

$$\mathbb{E}[X] = \sum_{i=1}^{n} x_i p_i$$

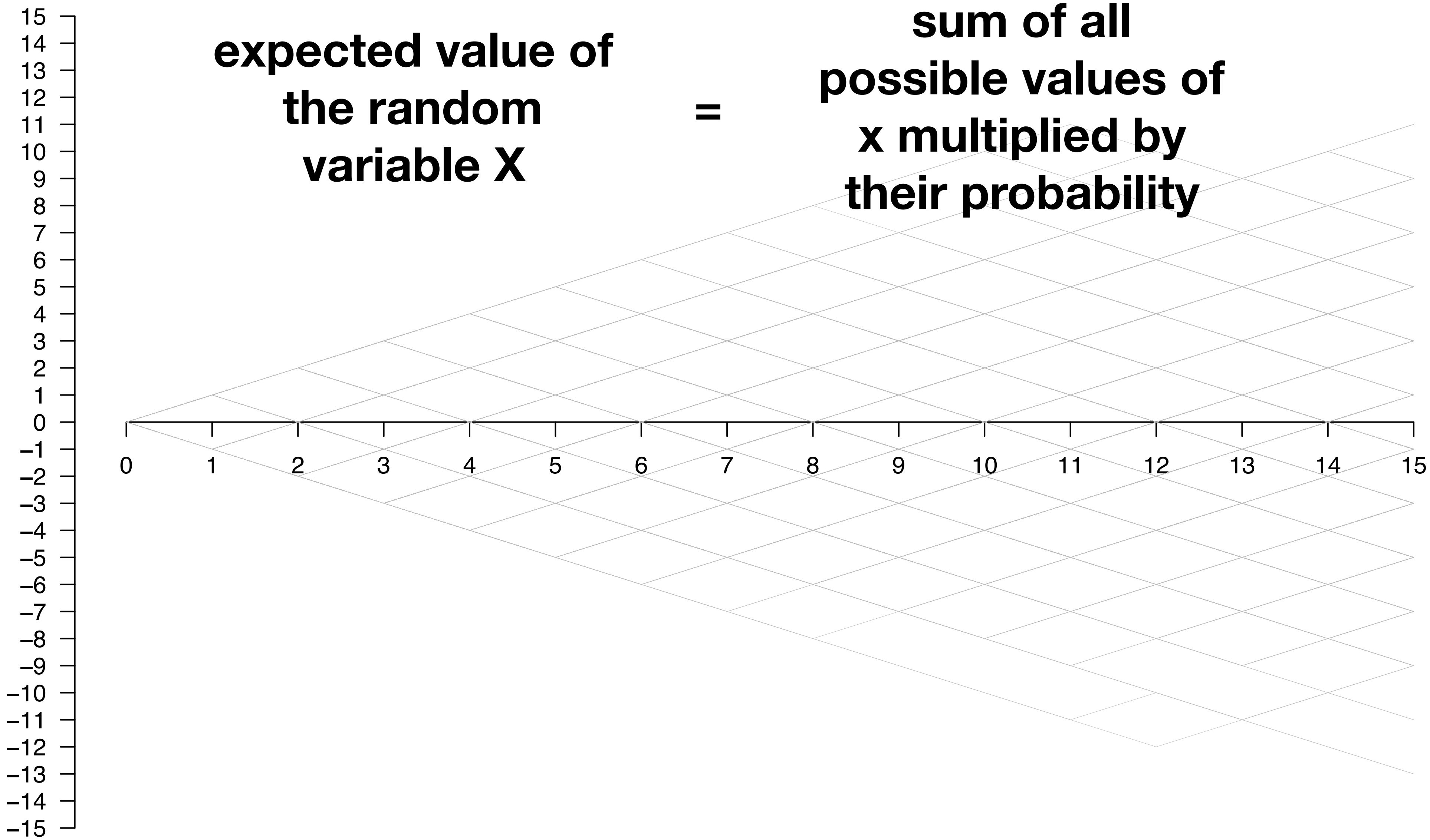


$$\mathbb{E}[X] = \sum_{i=1}^{n} x_i p_i$$

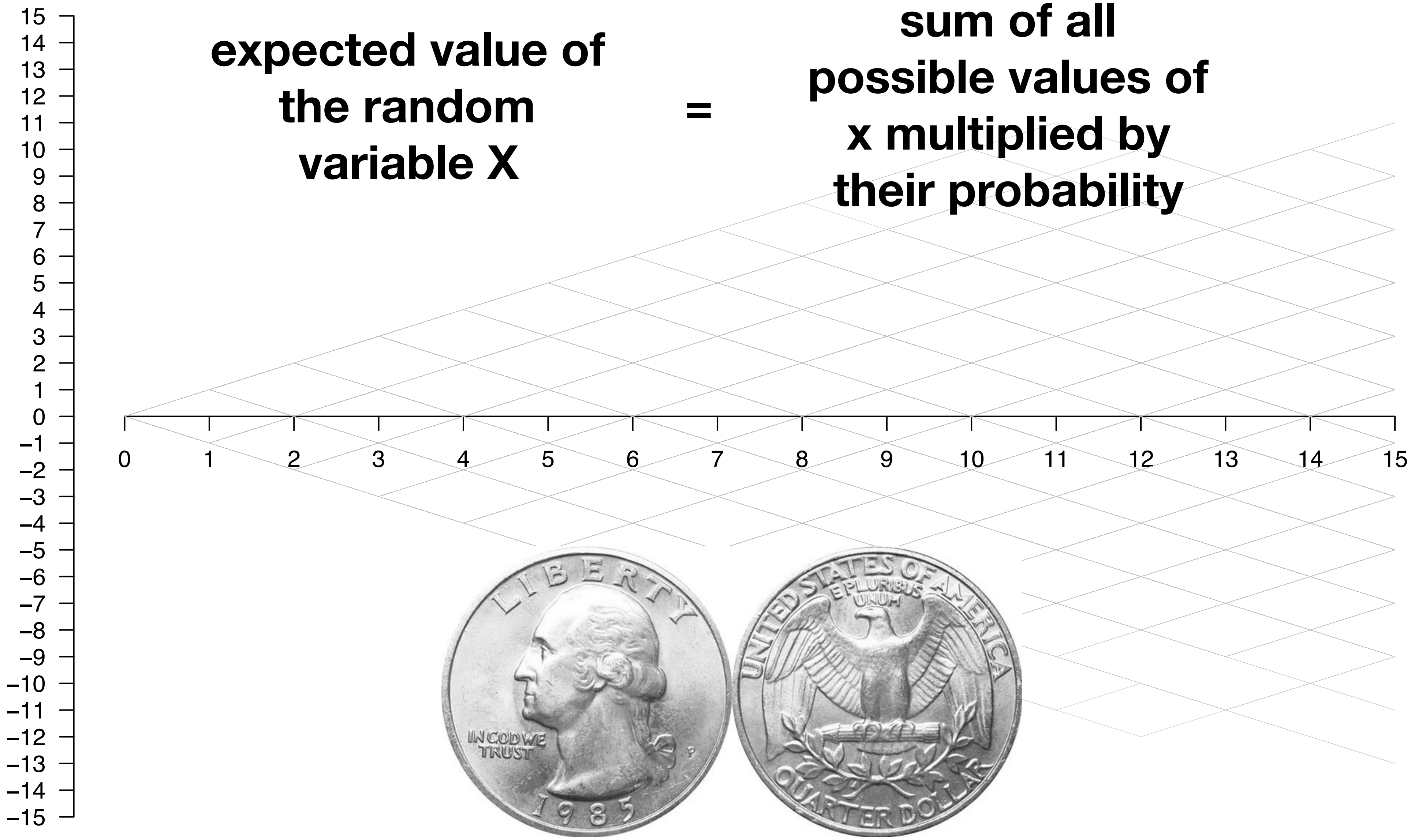


$$\mathbb{E}[X] = \sum_{i=1}^{n} x_i p_i$$

expected value of the random variable X **=** **sum of all possible values of x multiplied by their probability**

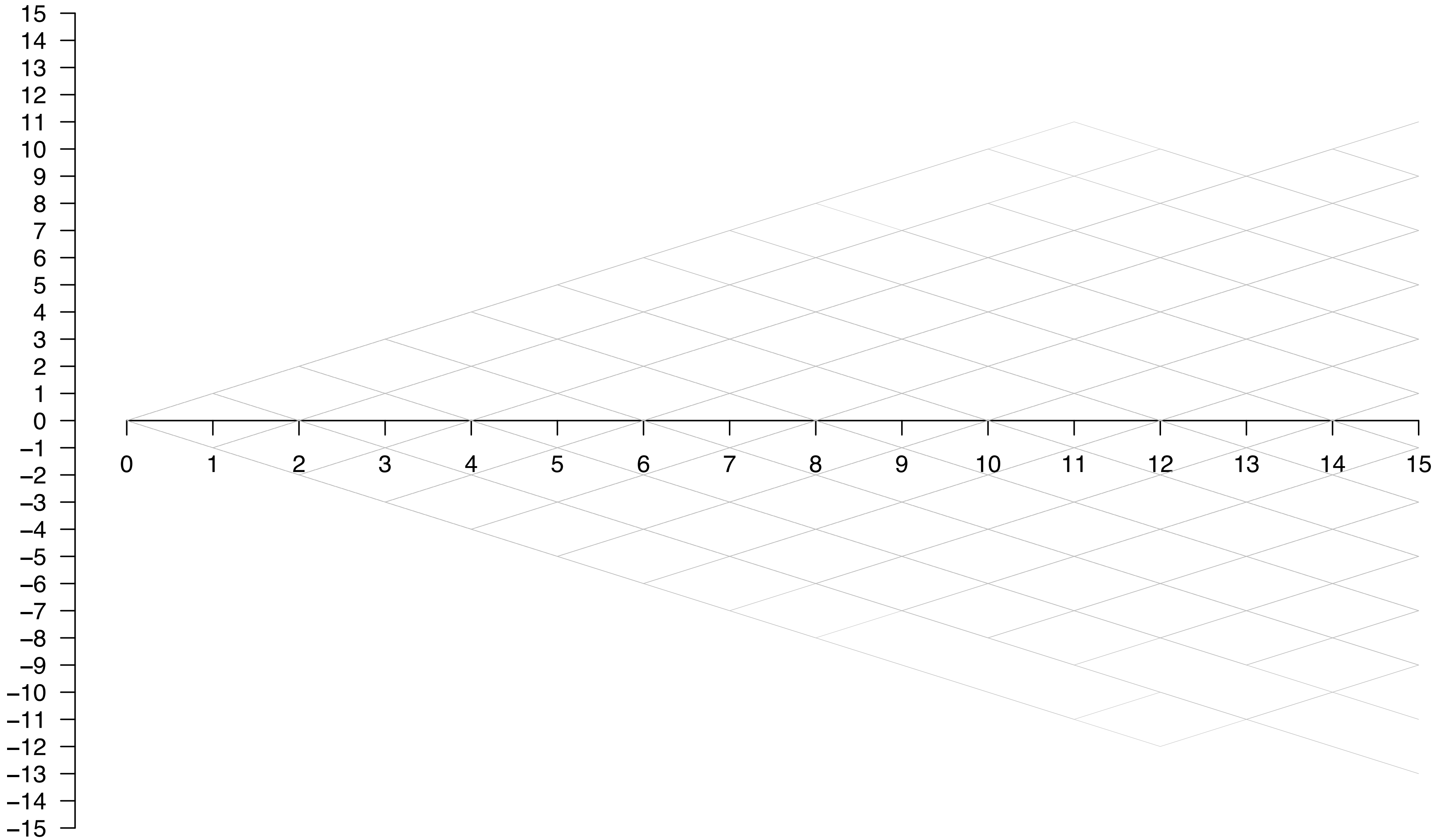


$$\mathbb{E}[X] = \sum_{i=1}^{n} x_i p_i$$



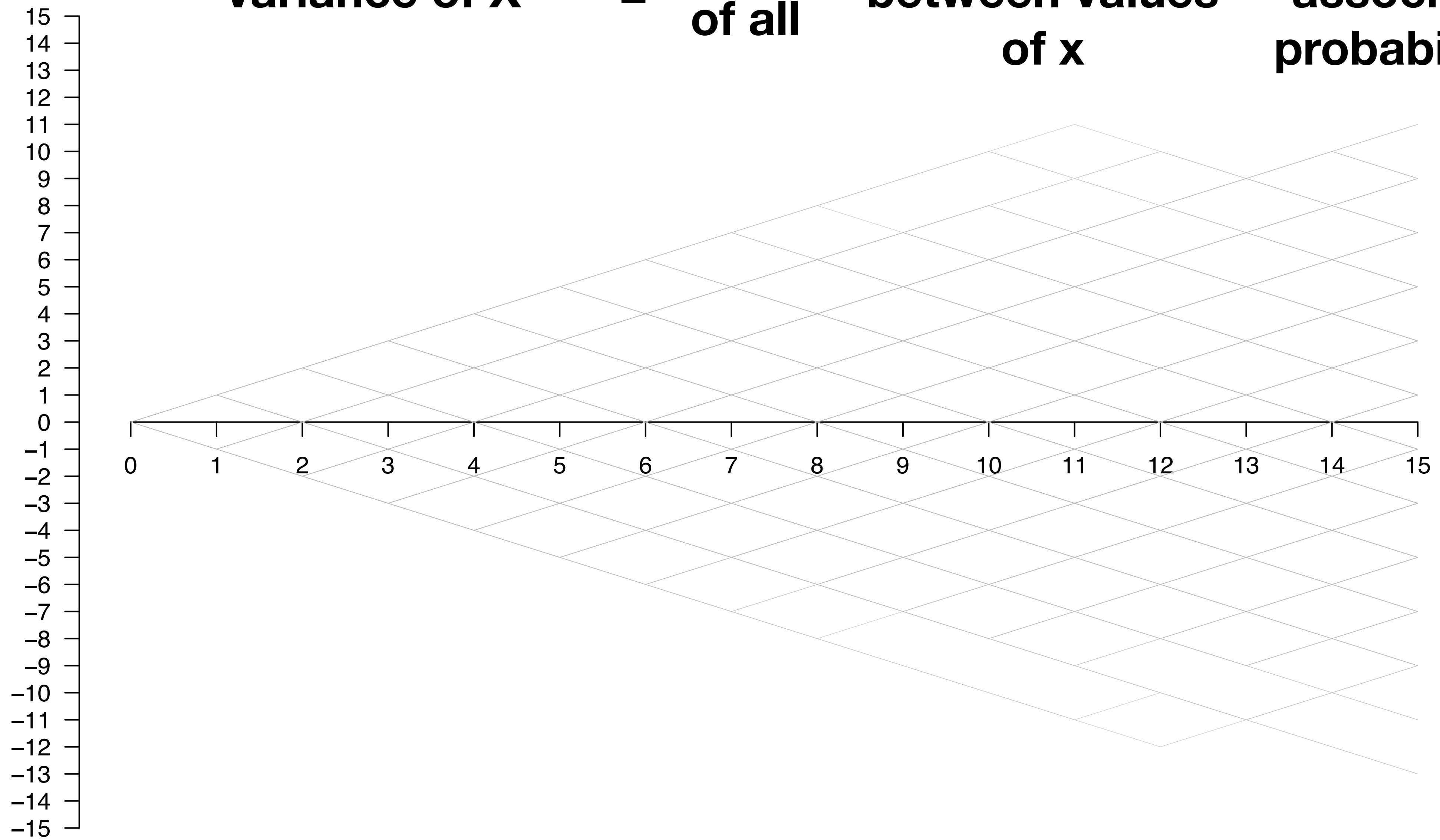
x	**+1**	**-1**
p	**0.5**	**0.5**

$$Var(X) = \sum_{i=1}^{n} (x_i - \mathbb{E}[X])^2 p_i$$



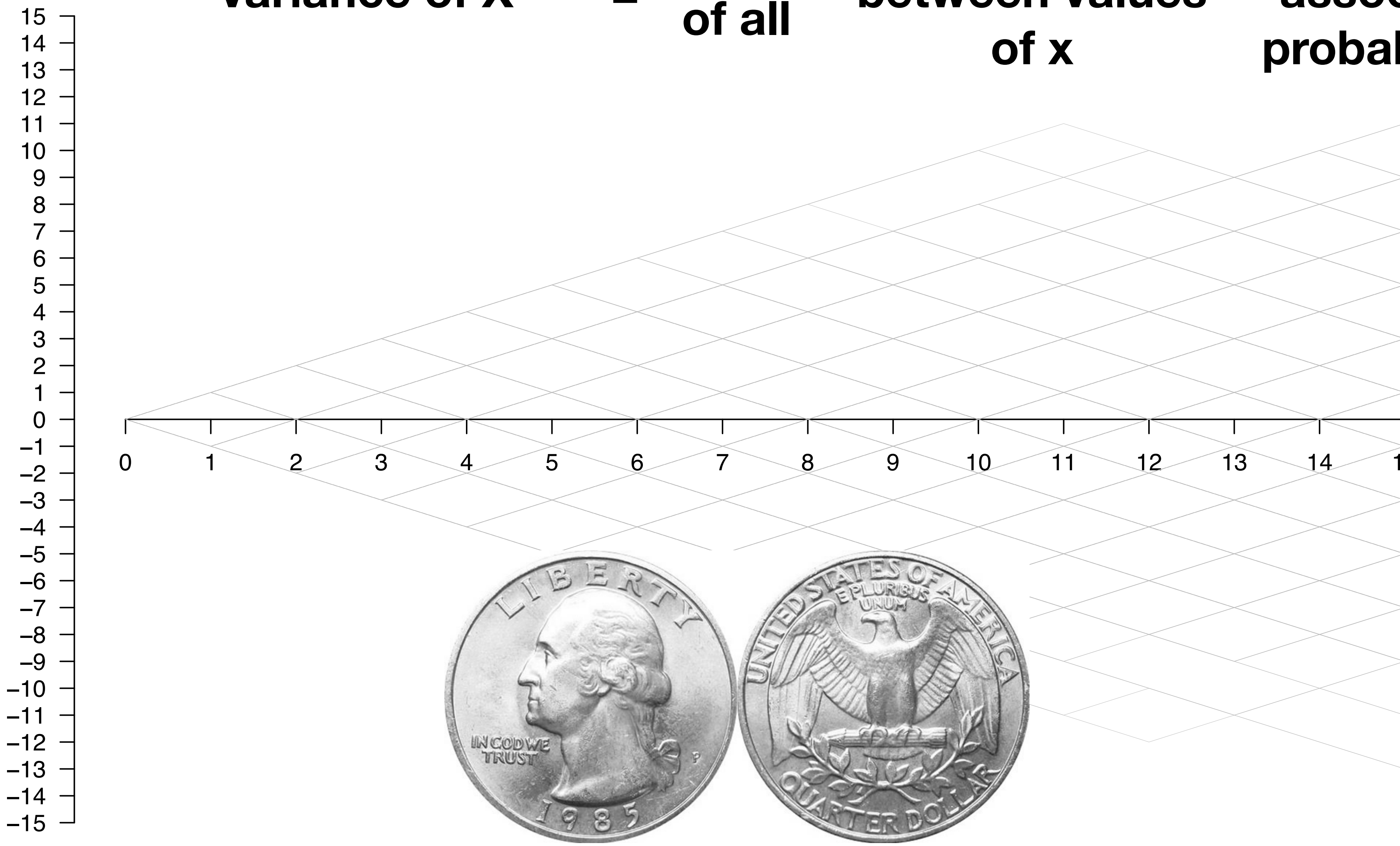
$$Var(X) = \sum_{i=1}^{n}(x_i - \mathbb{E}[X])^2 p_i$$

variance of X **=** **Sum of all** **squared diffs between values of x** **Multiplied by associated probabilities**



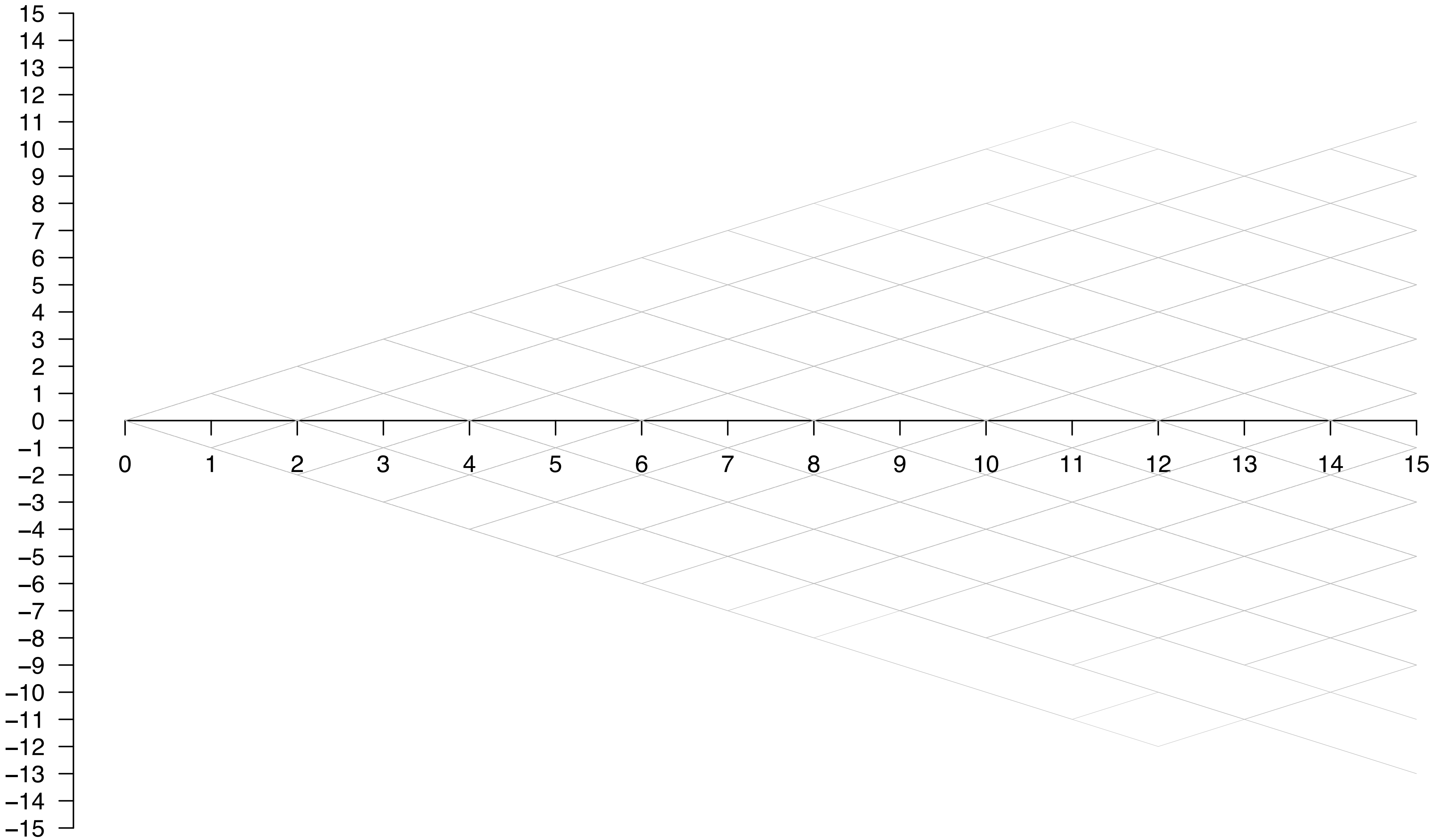
$$Var(X) = \sum_{i=1}^{n} (x_i - \mathbb{E}[X])^2 p_i$$

variance of X **=** **Sum of all** **squared diffs between values of x** **Multiplied by associated probabilities**



x	**+1**	**-1**
p	**0.5**	**0.5**

$$Var[X_1 + X_2 + ... + X_n] = Var[X_1] + Var[X_2] + ... + Var[X_n]$$

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+0.5


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-0.5

$$\mathbb{E}[X] = \sum_{i=1}^{n} x_i p_i$$

+0.5 **-0.5**

$$Var(X) = \sum_{i=1}^{n} (x_i - \mathbb{E}[X])^2 p_i$$

+0.5 **-0.5**


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+0.7


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-0.3

$$\mathbb{E}[X] = \sum_{i=1}^{n} x_i p_i$$

+0.7

-0.3

$$Var(X) = \sum_{i=1}^{n} (x_i - \mathbb{E}[X])^2 p_i$$

+0.7

-0.3

continuous random walks

likelihoods of random walks

likelihoods of random walks

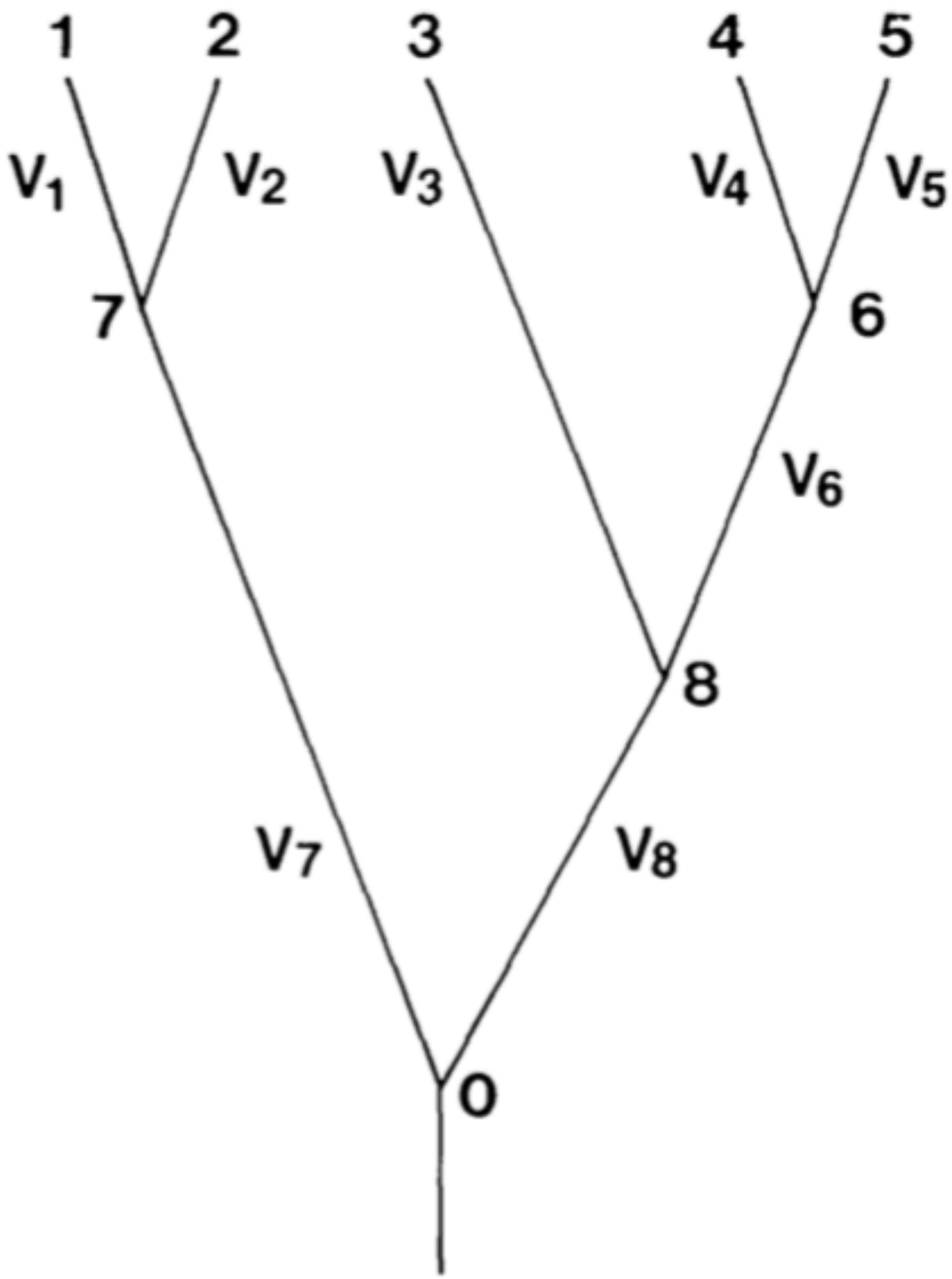
$$f(x|\mu,\sigma^2) = \frac{1}{\sqrt{2\pi\sigma^2}} e^{\frac{(x-\mu)^2}{2\sigma^2}}$$

likelihoods of random walks

$$f(x|\mu,\sigma^2) = \frac{1}{\sqrt{2\pi\sigma^2}} e^{\frac{(x-\mu)^2}{2\sigma^2}}$$

$$\mathcal{L}(X|\mu,\sigma^2) = \prod_{i=1}^{n} \frac{1}{\sqrt{2\pi\sigma^2}} e^{\frac{(x_i-\mu)^2}{2\sigma^2}}$$

Independent contrasts



THE FOUR CONTRASTS EXTRACTED FROM THE PHYLOGENY SHOWN IN FIGURE 9, EACH WITH ITS VARIANCE, ALL COMPUTED USING STEPS 1–4 IN THE TEXT

CONTRAST	VARIANCE
$X_1 - X_2$	$v_1 + v_2$
$X_4 - X_5$	$v_4 + v_5$
$X_3 - X_6$	$v_3 + v_6'$
$X_7 - X_8$	$v_7' + v_8'$

where

$$X_6 = \frac{v_4 X_5 + v_5 X_4}{v_4 + v_5}$$

$$v_6' = v_6 + v_4 v_5/(v_4 + v_5)$$

$$X_7 = \frac{v_2 X_1 + v_1 X_2}{v_1 + v_2}$$

$$v_7' = v_7 + v_1 v_2/(v_1 + v_2)$$

$$X_8 = \frac{v_6' X_3 + v_3 X_6}{v_3 + v_6}$$

$$v_8' = v_7' + v_3 v_6'/(v_3 + v_6')$$

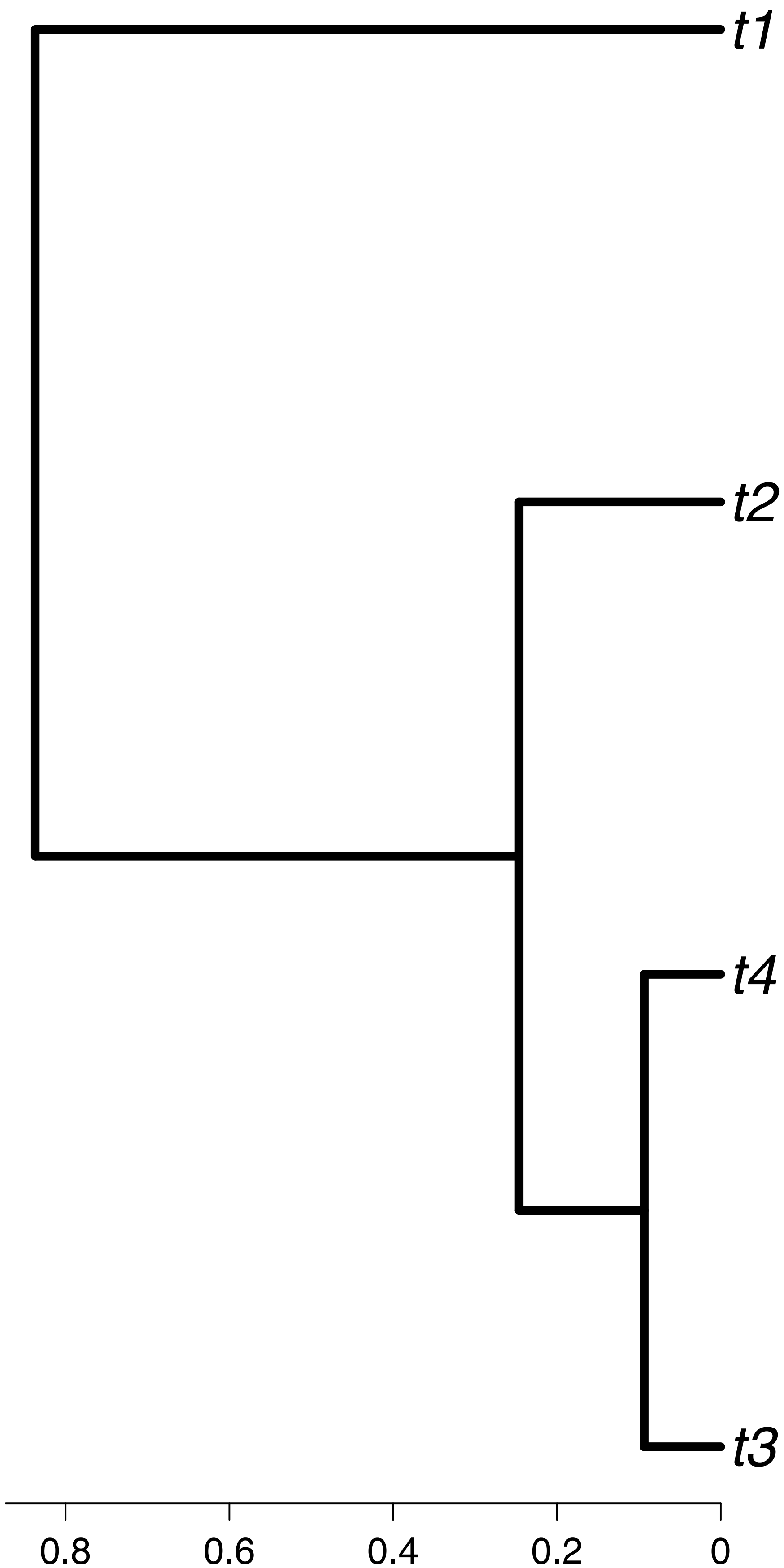
likelihoods of random walks with a covariance structure - the multivariate normal distribution

$$f(x_1, x_2, ..., x_k) = \frac{e^{-0.5[\mathbf{x}-\boldsymbol{\mu})^T \boldsymbol{\Sigma}^{-1}(\mathbf{x}-\boldsymbol{\mu})]}}{\sqrt{(2\pi)^k det(\boldsymbol{\Sigma})}}$$

likelihoods of random walks with a covariance structure - the multivariate normal distribution

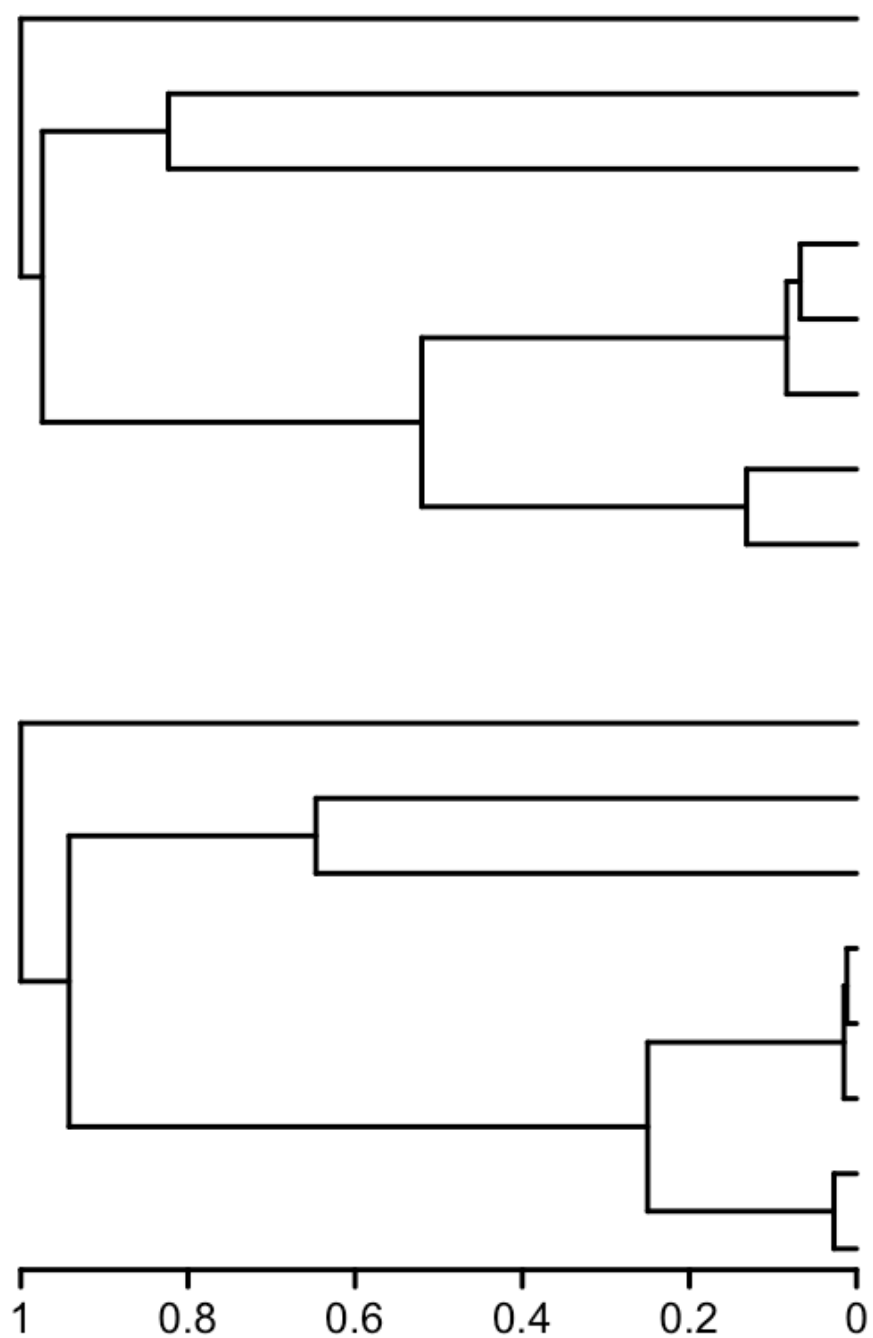
$$f(x_1, x_2, ..., x_k) = \frac{e^{-0.5[\mathbf{x}-\boldsymbol{\mu})^T \boldsymbol{\Sigma}^{-1}(\mathbf{x}-\boldsymbol{\mu})]}}{\sqrt{(2\pi)^k det(\boldsymbol{\Sigma})}}$$

$$f(x|\mu, \sigma^2) = \frac{1}{\sqrt{2\pi\sigma^2}} e^{\frac{(x-\mu)^2}{2\sigma^2}}$$

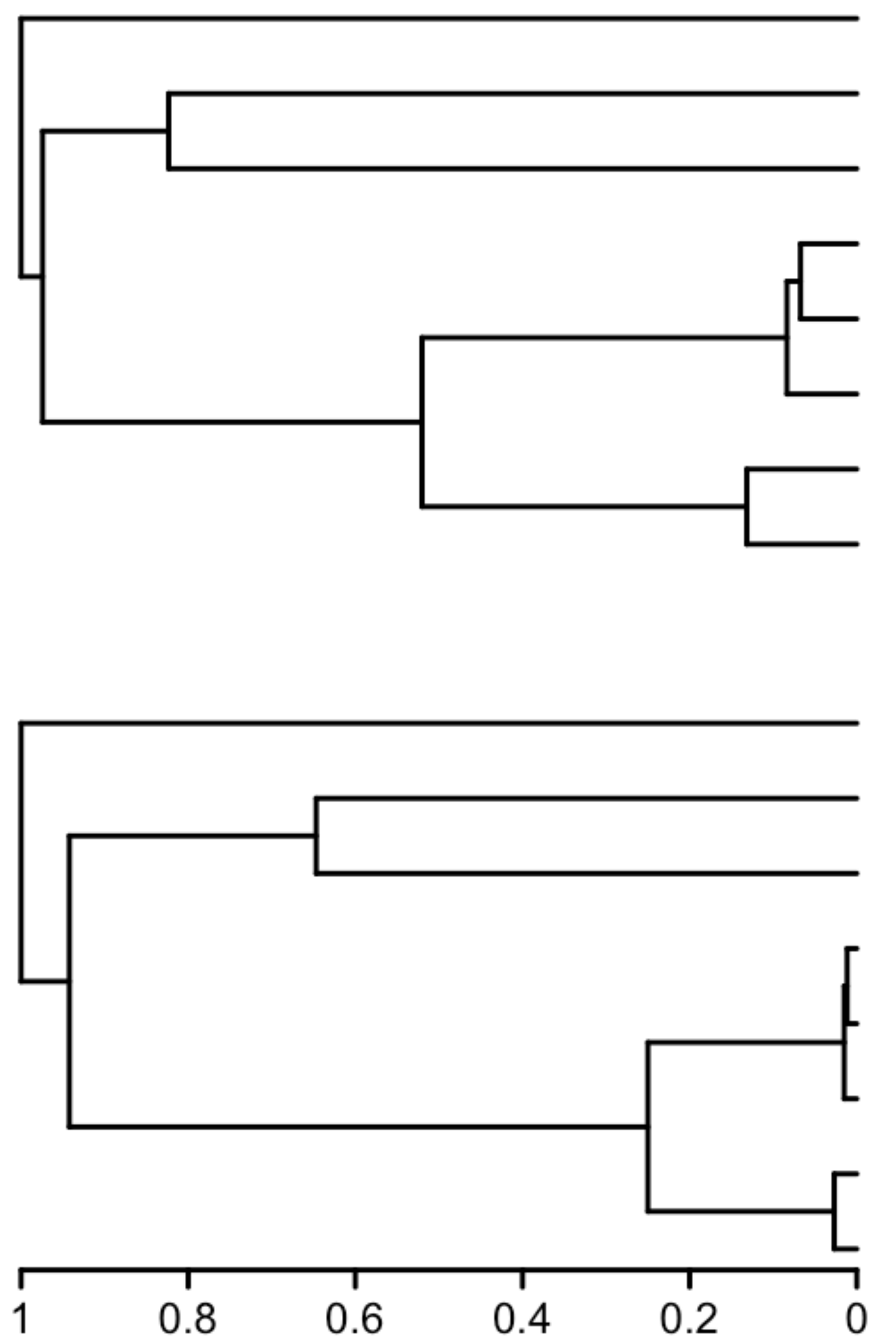


	t3	t4	t2	t1
t3	0.84	0.74	0.59	0.00
t4	0.74	0.84	0.59	0.00
t2	0.59	0.59	0.84	0.00
t1	0.00	0.00	0.00	0.84

O'Meara et al. (2006) Evolution

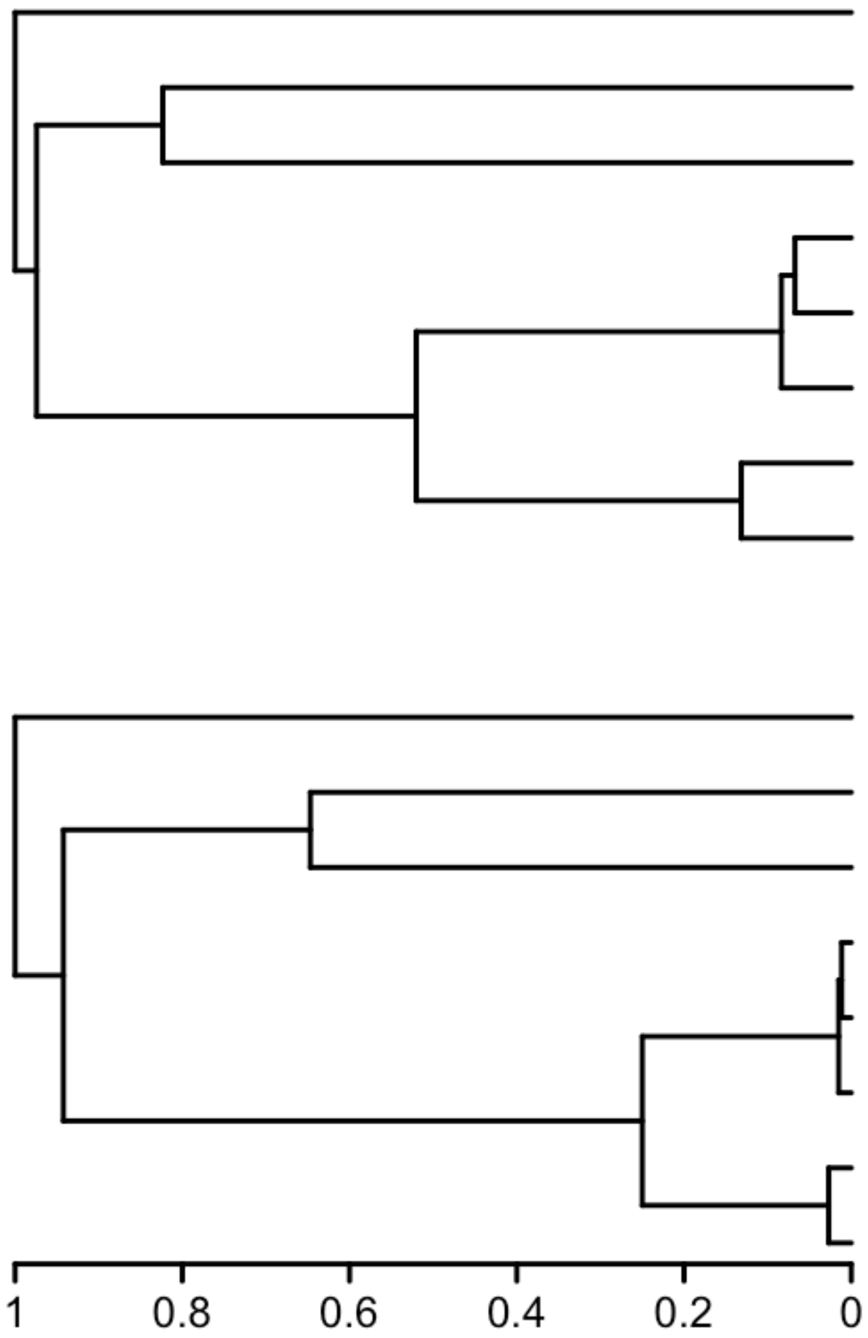


O'Meara et al. (2006) Evolution



$$\mathrm{E}(\text{disparity}) = \sigma^2\left[\frac{1}{N}\mathrm{tr}(\mathbf{C}) - \frac{1}{N^2}\mathbf{1}'\mathbf{C}\mathbf{1}\right]$$

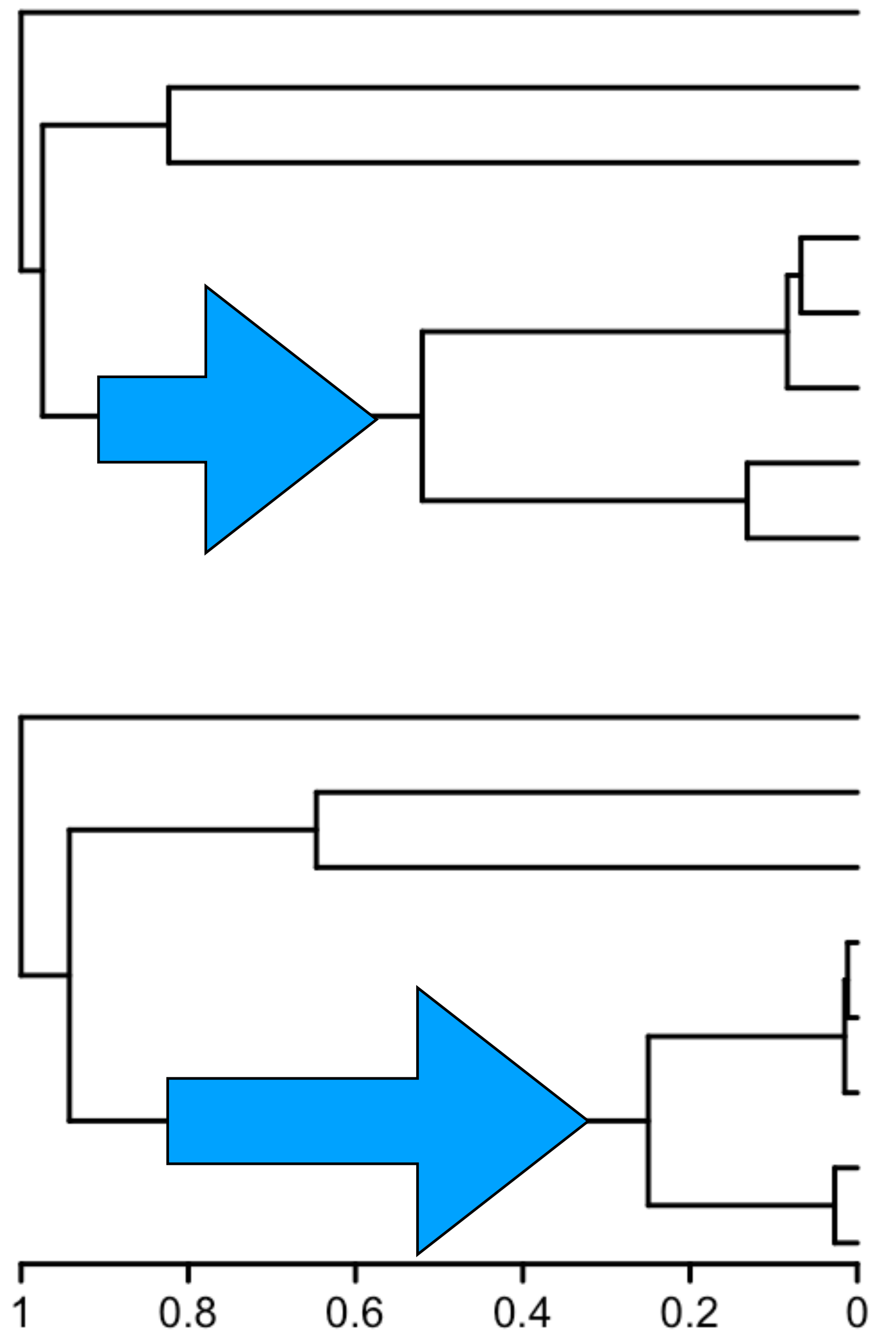
O'Meara et al. (2006) Evolution



rate * independent evolution

$$E(\text{disparity}) = \sigma^2\left[\frac{1}{N}\text{tr}(\mathbf{C}) - \frac{1}{N^2}\mathbf{1}'\mathbf{C}\mathbf{1}\right]$$

O'Meara et al. (2006) Evolution



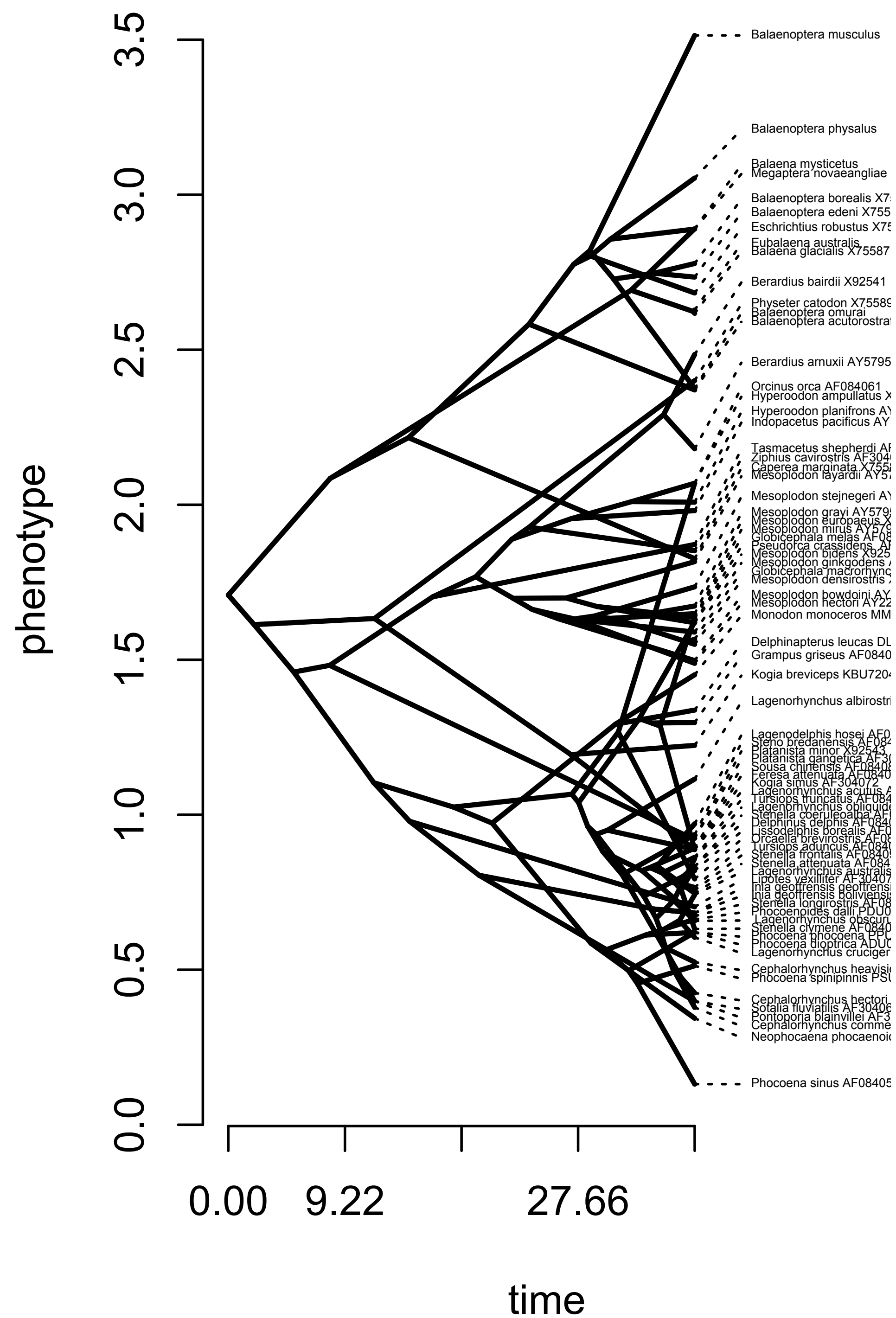
rate * independent evolution

$$E(\text{disparity}) = \sigma^2\left[\frac{1}{N}\text{tr}(\mathbf{C}) - \frac{1}{N^2}\mathbf{1}'\mathbf{C}\mathbf{1}\right]$$

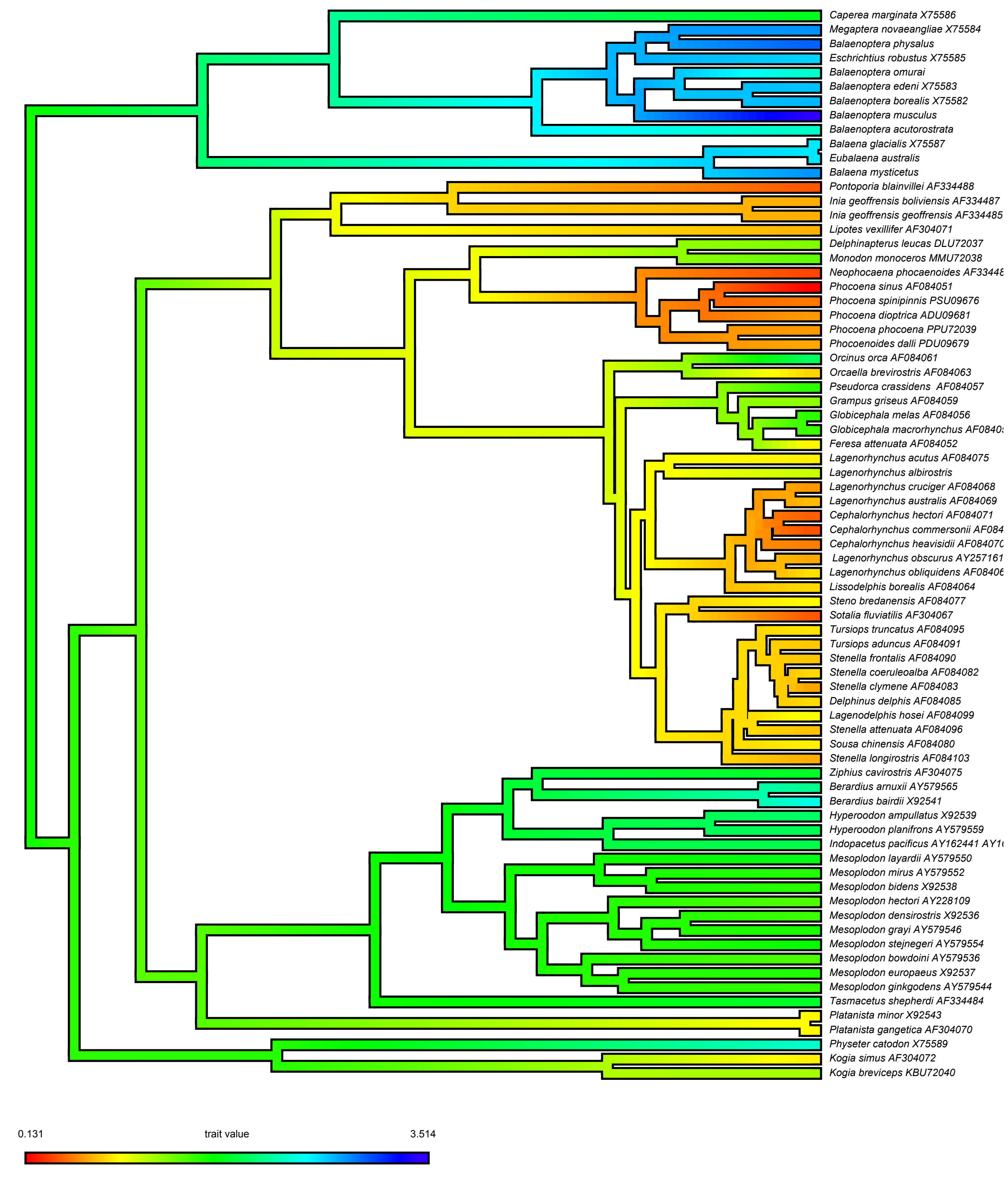
O'Meara et al. (2006) Evolution

fitting a Brownian motion model to phylogenetic data

ancestral states

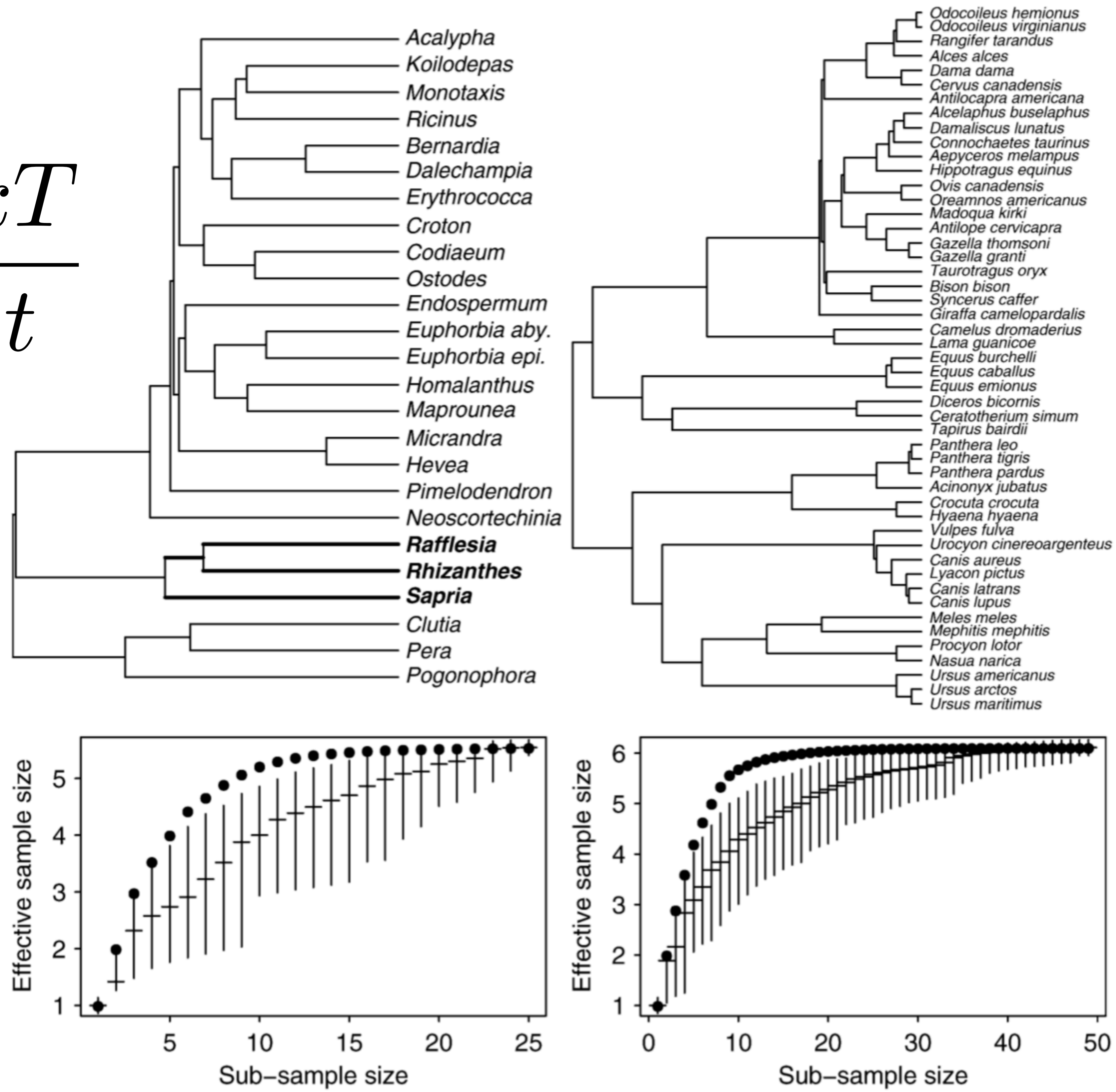


Phytools:::phenogram



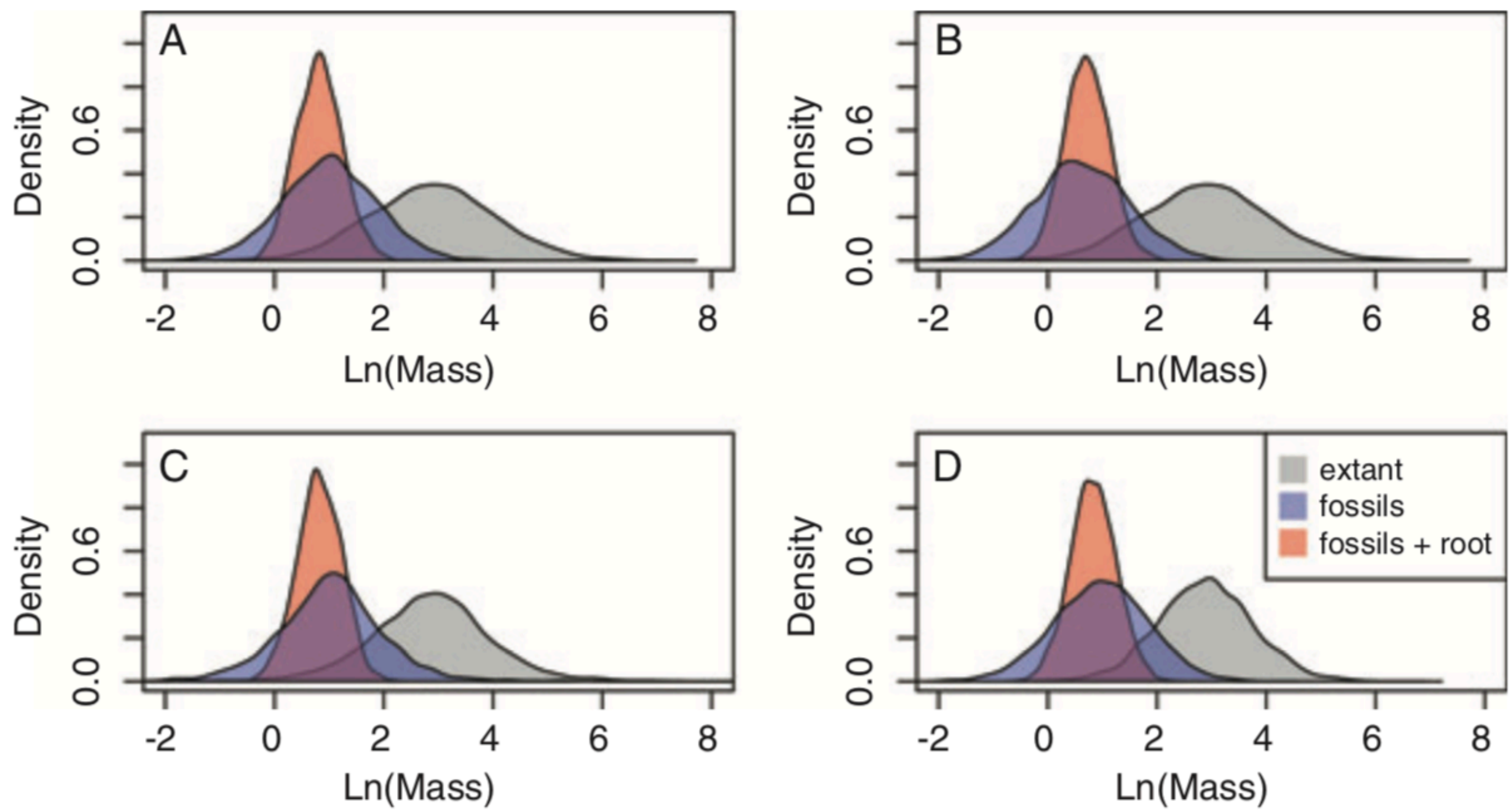
Phytools:::contmap

$$n_e \leq \frac{kT}{t}$$



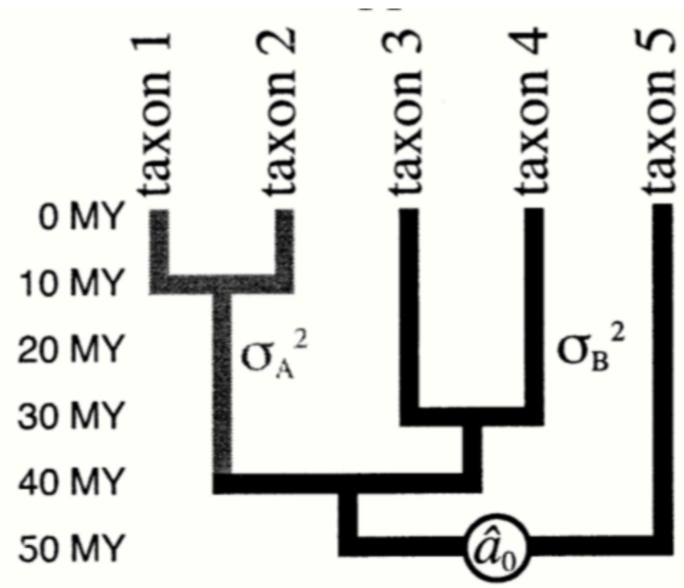
Ané 2008

fossil data improve ancestral state estimates



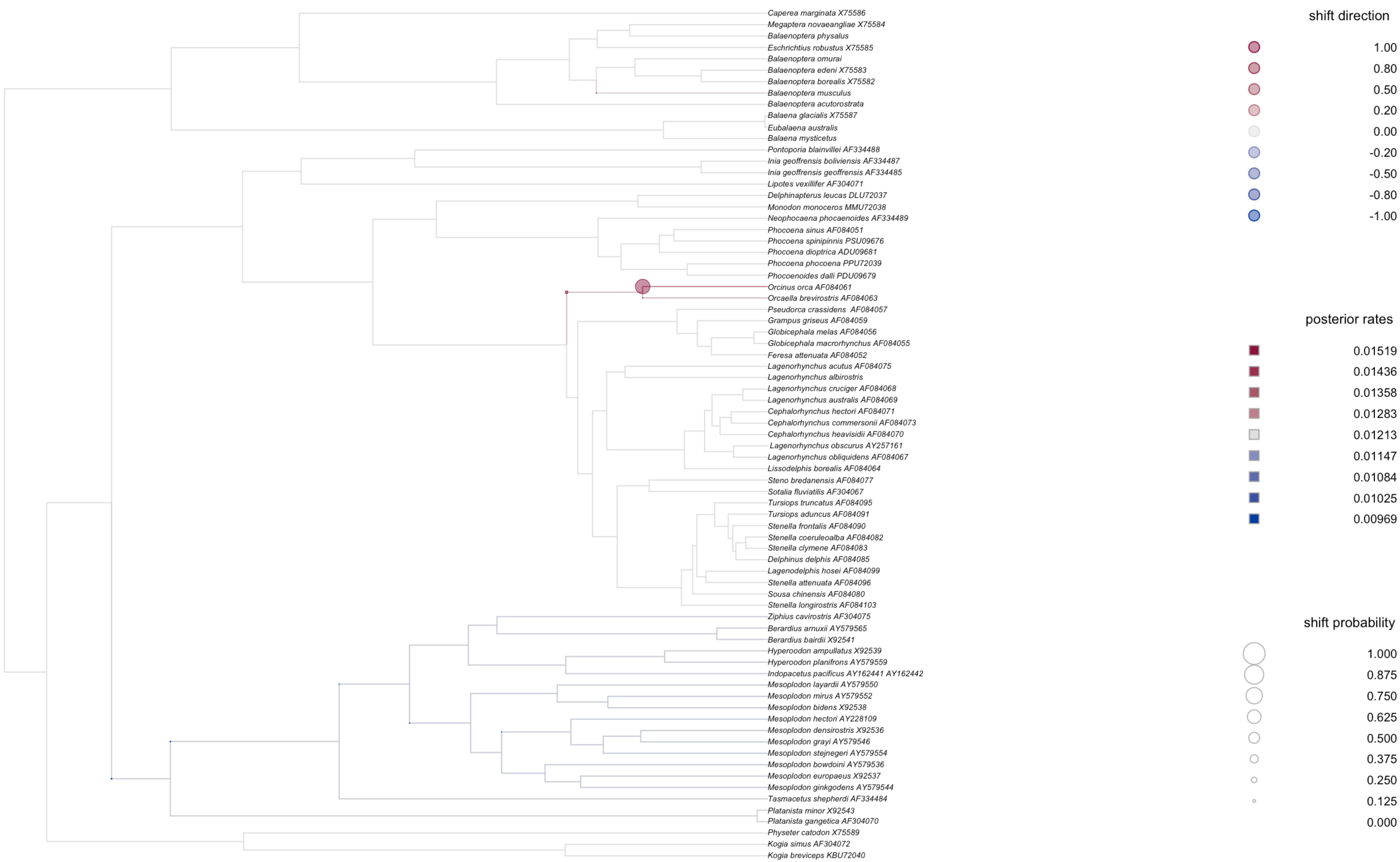
Slater et al (2012)

extending Brownian motion



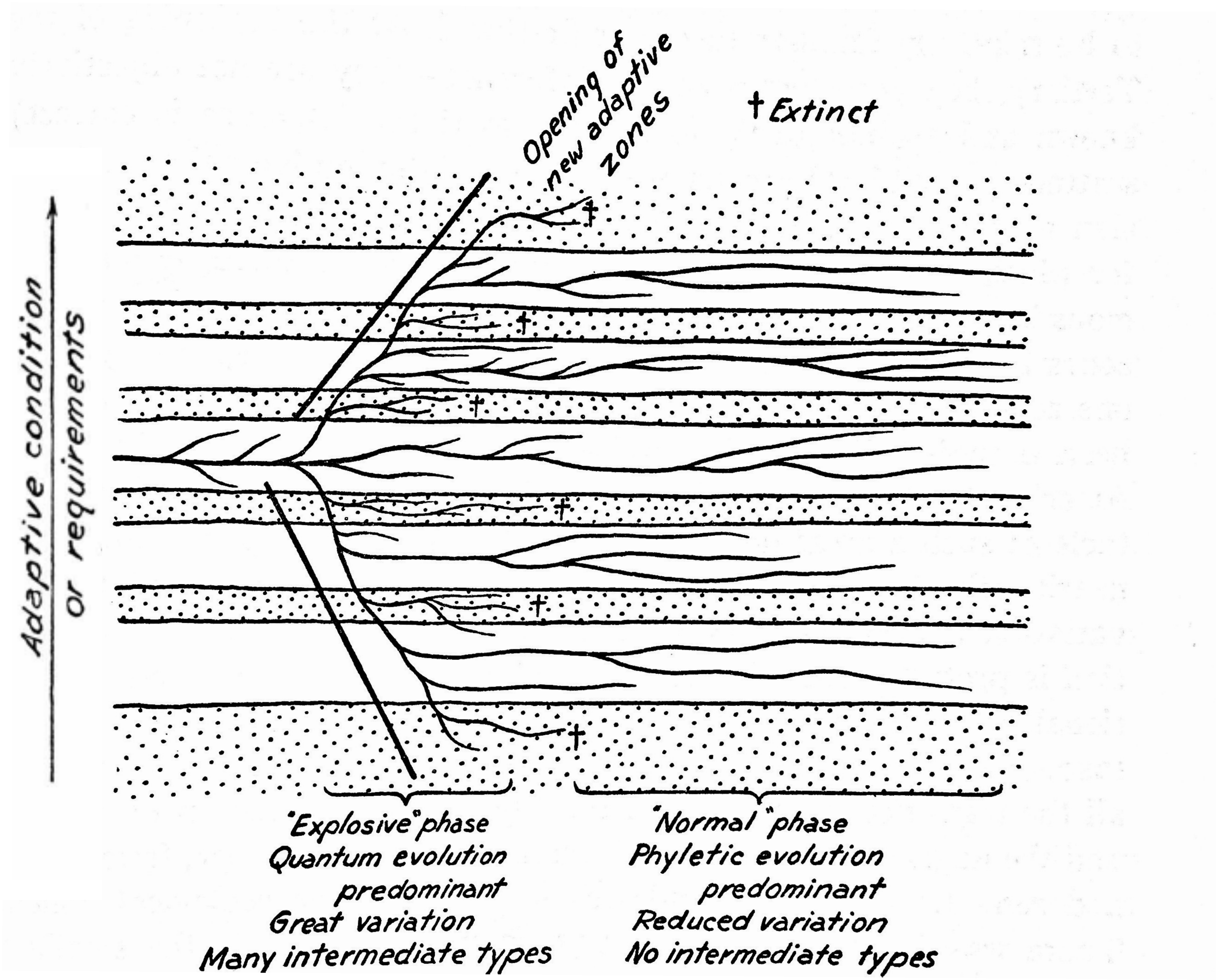
	taxon 1	taxon 2	taxon 3	taxon 4	taxon 5	E(**X**)
taxon 1	$40\sigma_A^2+10\sigma_B^2$	$30\sigma_A^2+10\sigma_B^2$	$10\sigma_B^2$	$10\sigma_B^2$	0	$\hat{a}_0$
taxon 2	$30\sigma_A^2+10\sigma_B^2$	$40\sigma_A^2+10\sigma_B^2$	$10\sigma_B^2$	$10\sigma_B^2$	0	$\hat{a}_0$
taxon 3	$10\sigma_B^2$	$10\sigma_B^2$	$50\sigma_B^2$	$20\sigma_B^2$	0	$\hat{a}_0$
taxon 4	$10\sigma_B^2$	$10\sigma_B^2$	$20\sigma_B^2$	$50\sigma_B^2$	0	$\hat{a}_0$
taxon 5	0	0	0	0	$50\sigma_B^2$	$\hat{a}_0$

O'Meara et al. 2006



geiger::auteur

Simpson's model of "Quantum Evolution"



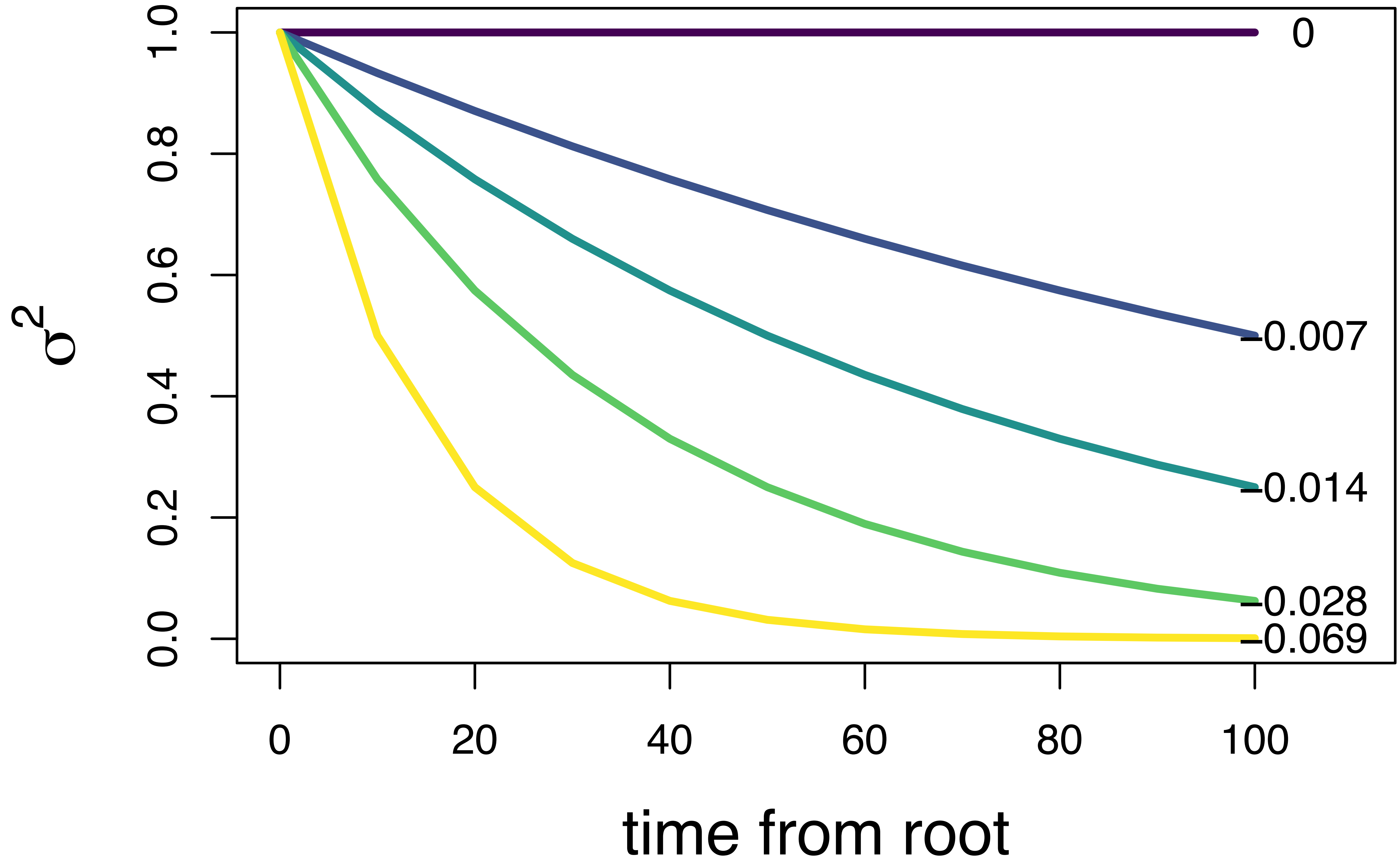
Simpson (1944) Temp and Mode in Evolution

Early Bursts

$$\sigma_t^2 = \sigma_0^2 e^{rt}$$

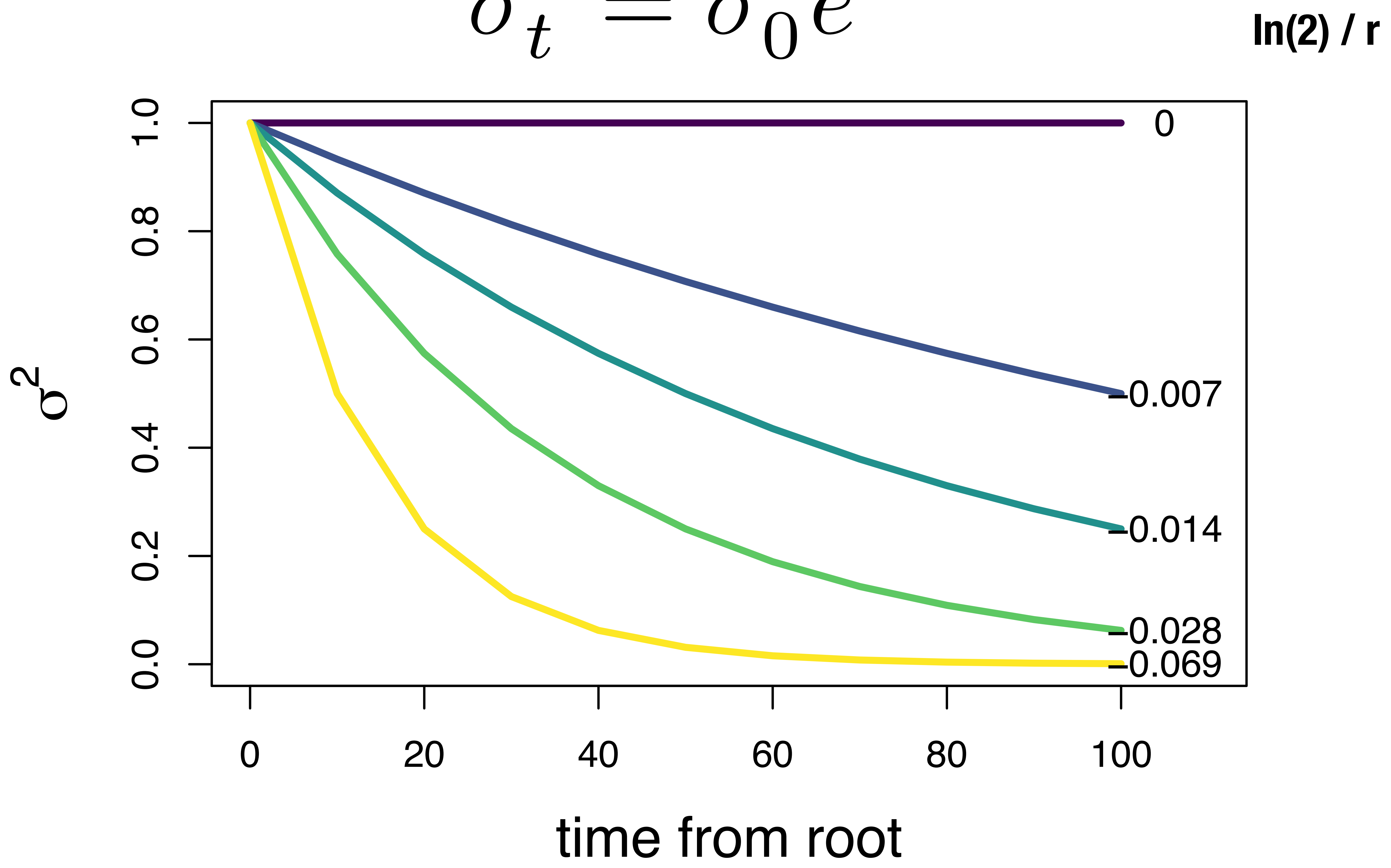
Early Bursts

$$\sigma_t^2 = \sigma_0^2 e^{rt}$$



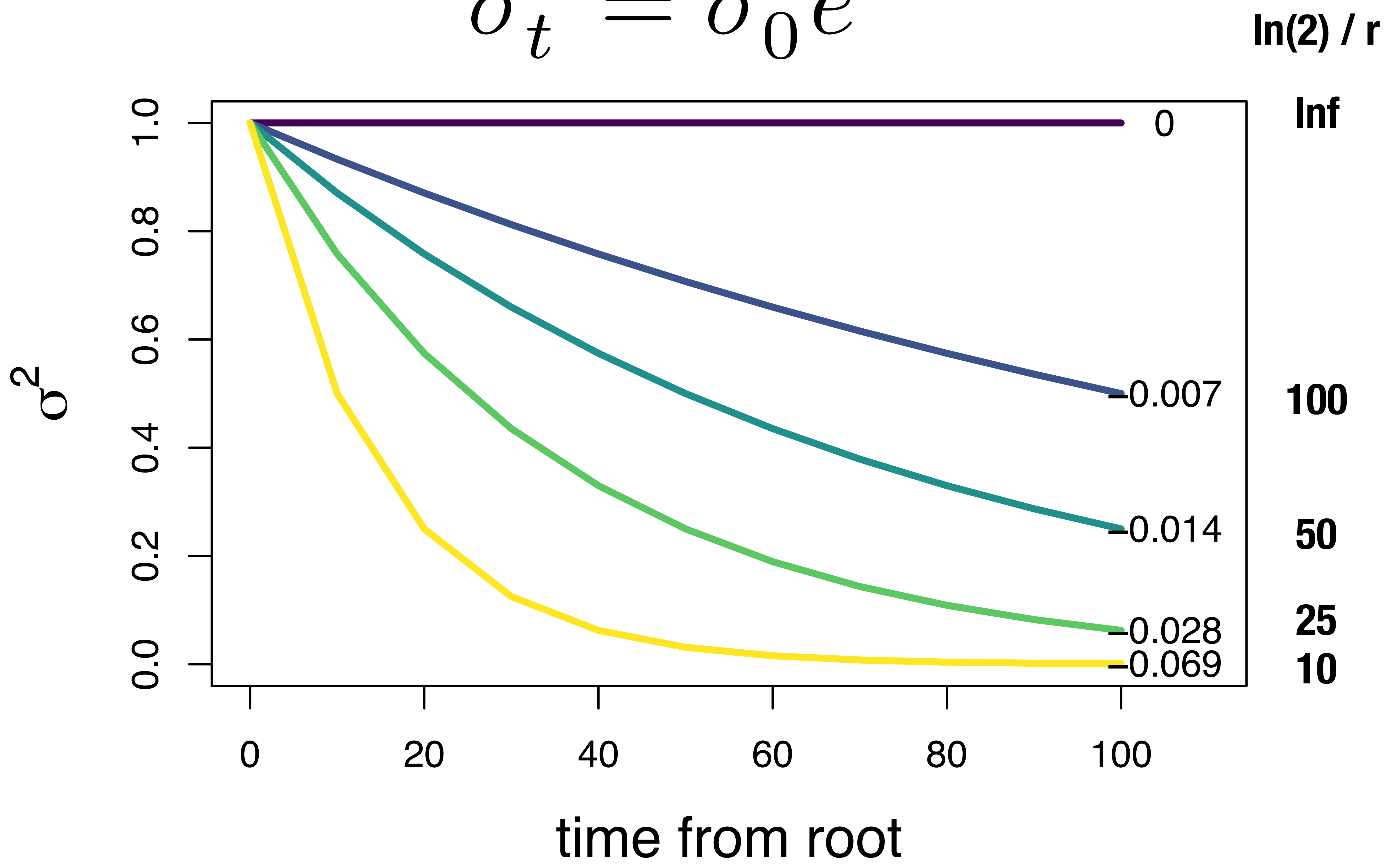
Early Bursts

$$\sigma_t^2 = \sigma_0^2 e^{rt}$$



Early Bursts

$$\sigma_t^2 = \sigma_0^2 e^{rt}$$



early bursts on trees

$$\mathbf{V}_{i,j} = \sigma_0^2 * \int_0^{\mathbf{C}_{i,j}} e^{rt} d(t)$$

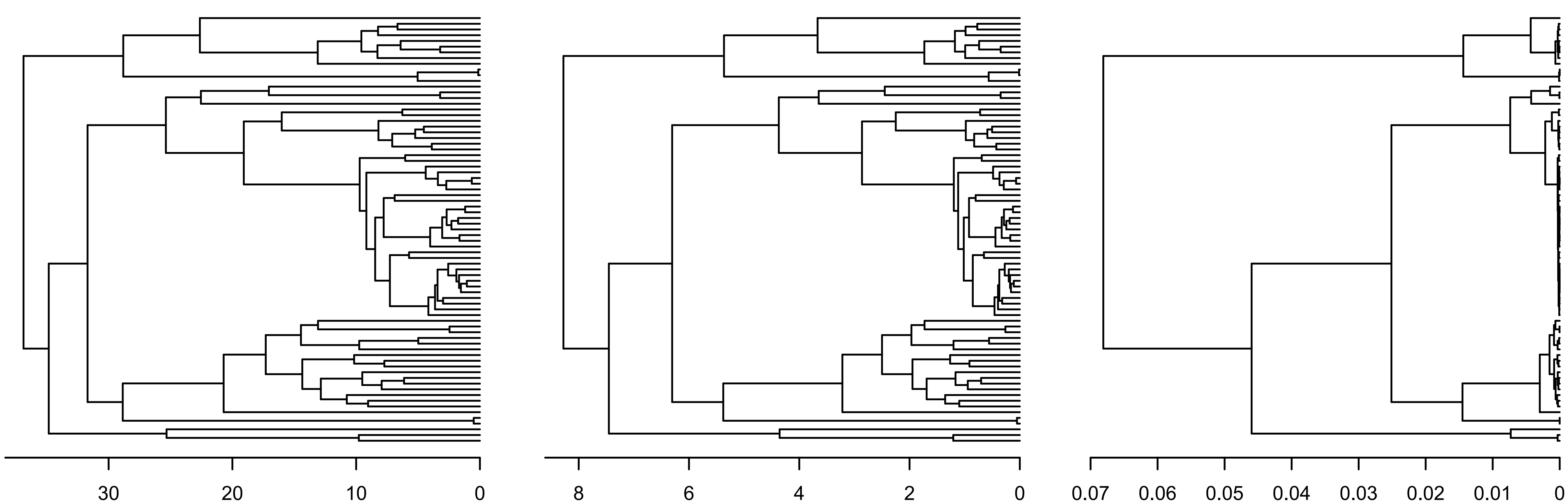
$$= \sigma_0^2 * \frac{e^{r\mathbf{C}_{i,j}} - 1}{r}$$

early bursts on trees

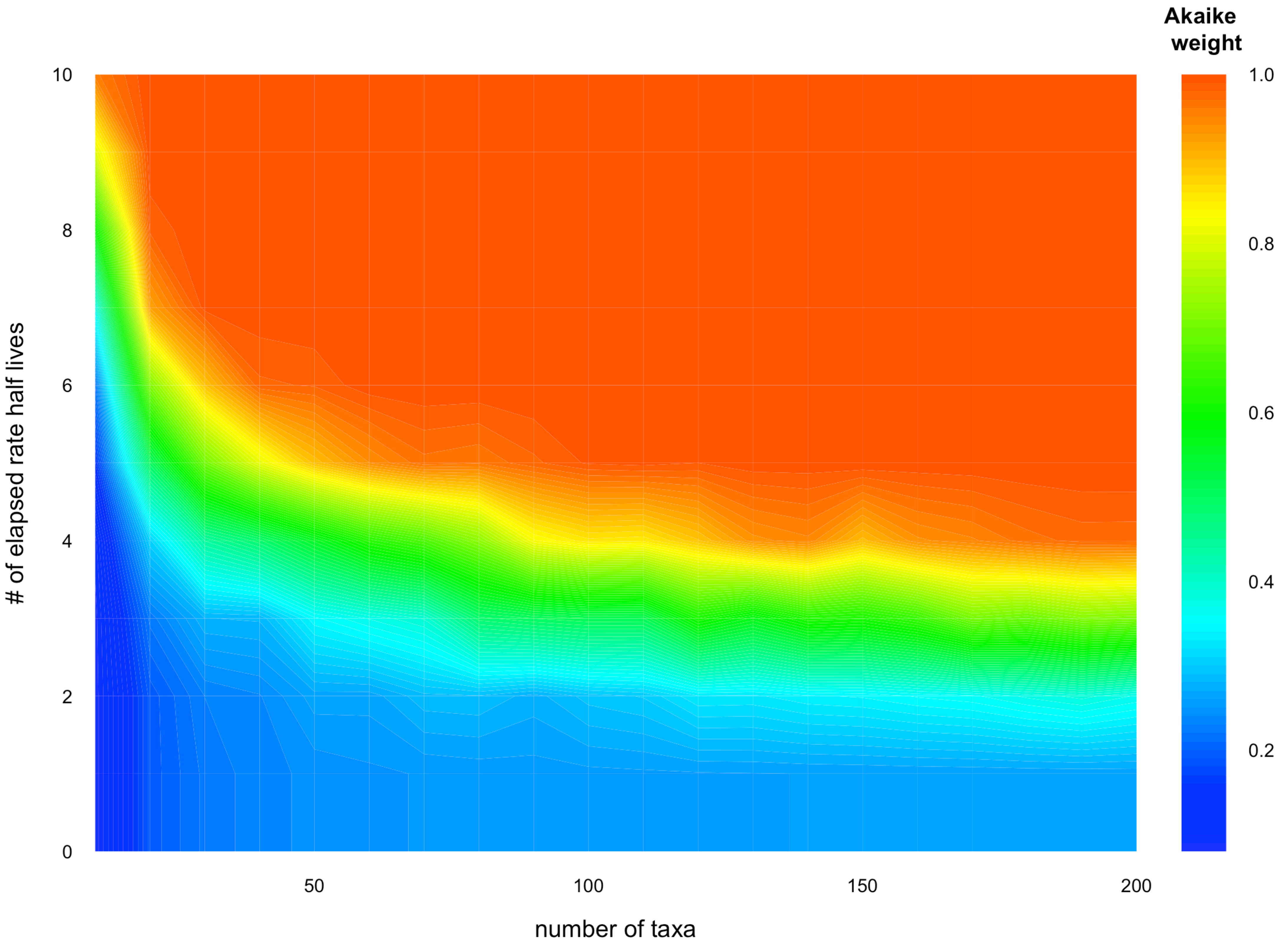
$$\mathbf{V}_{i,j} = \sigma_0^2 * \int_0^{\mathbf{C}_{i,j}} e^{rt} d(t)$$

$$= \sigma_0^2 * \frac{e^{r\mathbf{C}_{i,j}} - 1}{r}$$

BM | **1 rate half-life** | **10 rate half-life**



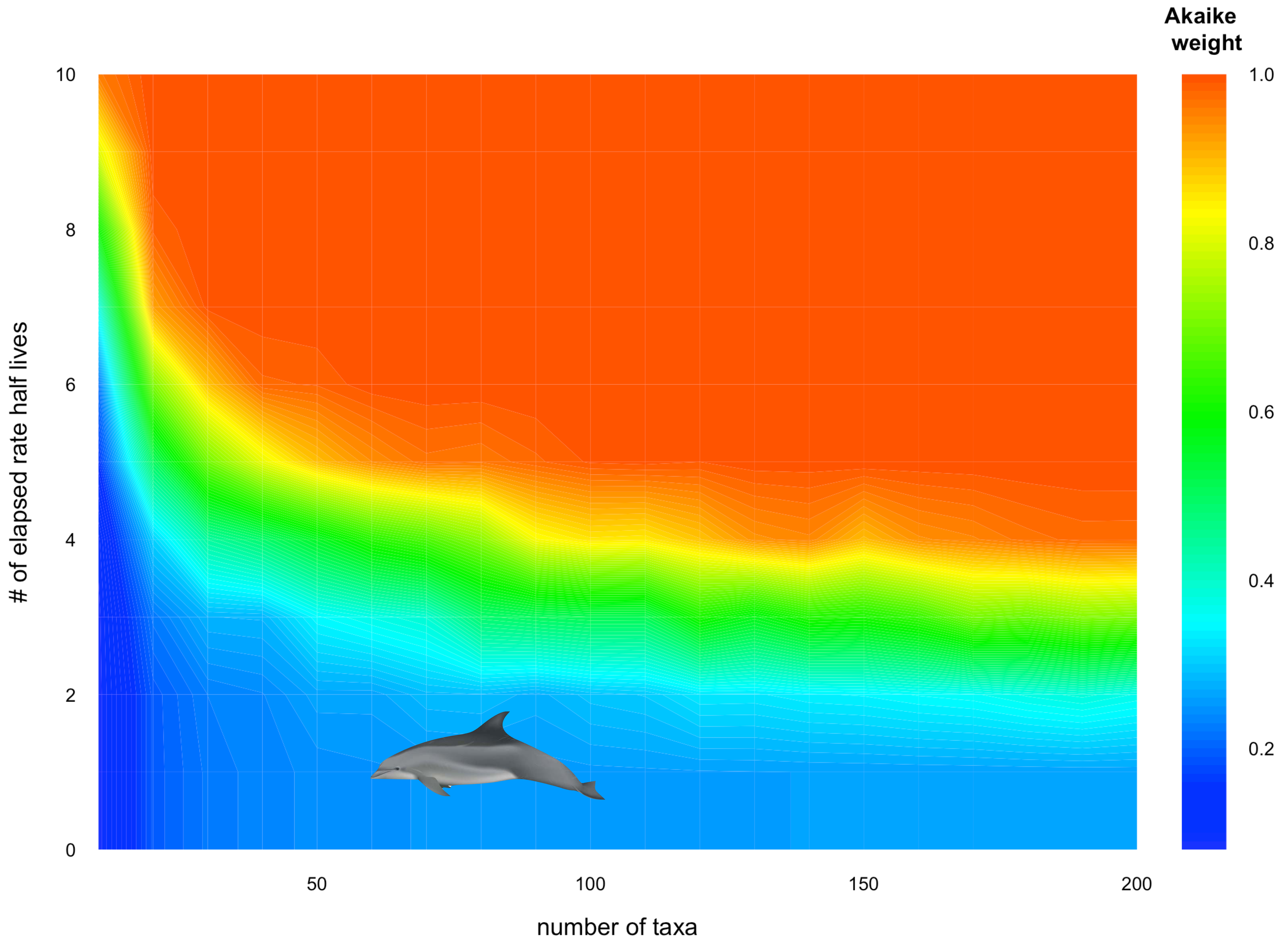
early bursts are difficult to detect*



*** when you only have extant taxa**

Slater and Pennell (2014) Systematic Biology

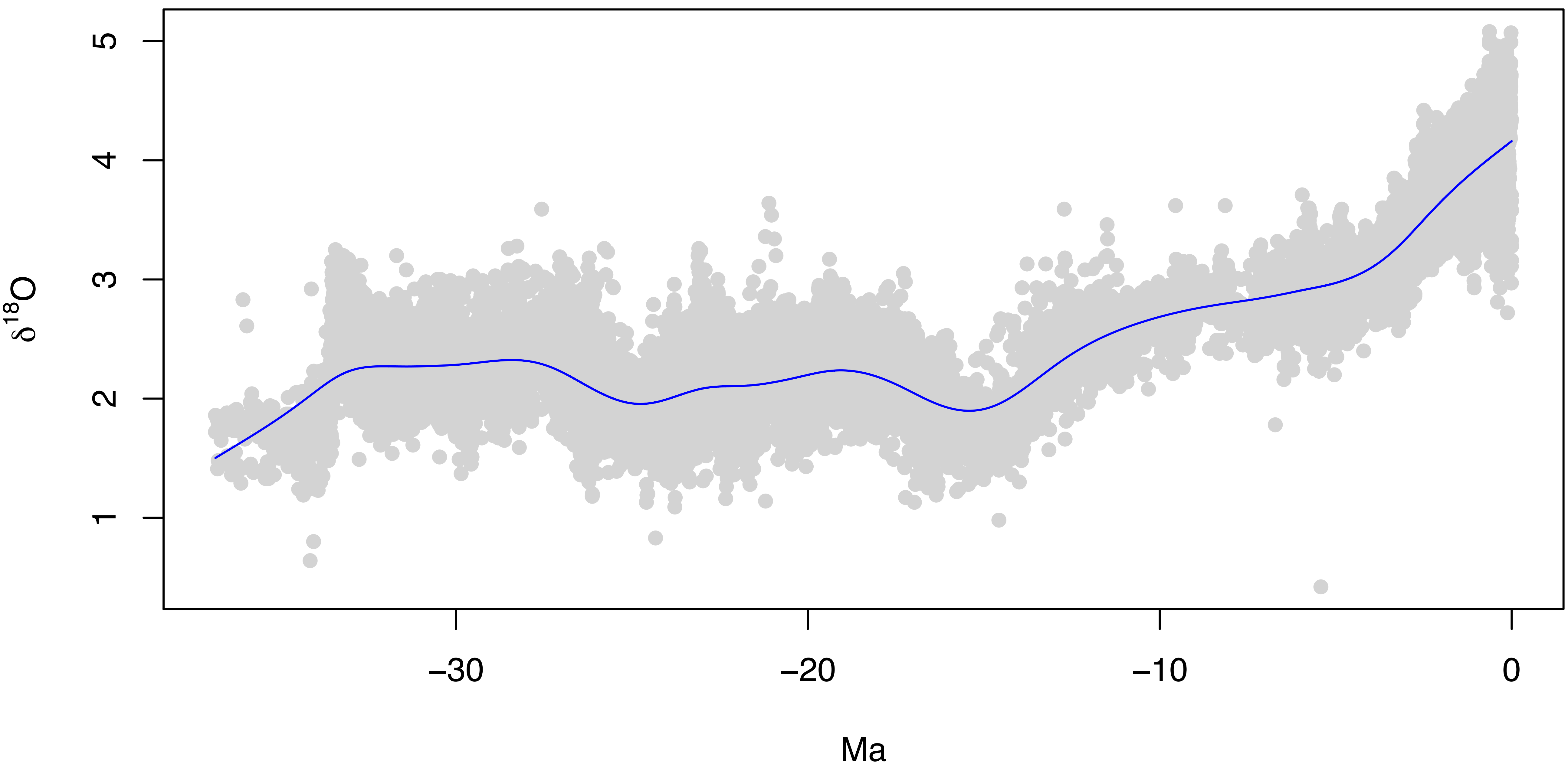
early bursts are difficult to detect*



*** when you only have extant taxa**

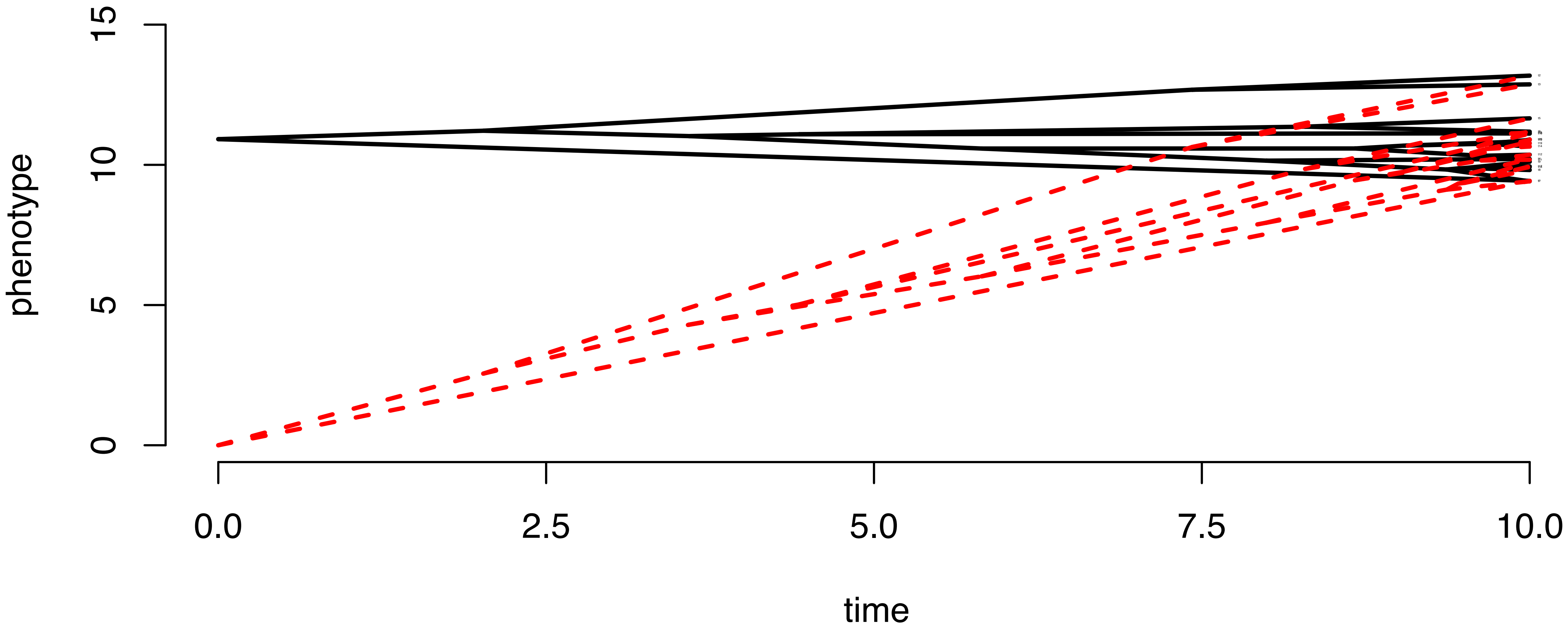
Slater and Pennell (2014) Systematic Biology

environmentally - determined rates



Data from Zachos et al 2008

trends screw up your ancestral states (and maybe your rates)



Model Selection!

Model Selection!

$$AIC = 2k - 2LnLk$$

Model Selection!

$$AIC = 2k - 2LnLk$$

$$AICc = 2k - 2LnLk + \frac{2k^2 + 2k}{n - k - 1}$$

Model Selection!

$$AIC = 2k - 2LnLk$$

$$AICc = 2k - 2LnLk + \frac{2k^2 + 2k}{n - k - 1}$$

$$\Delta AIC_i = AIC_i - AIC_{min}$$

Model Selection!

$$AIC = 2k - 2LnLk$$

$$AICc = 2k - 2LnLk + \frac{2k^2 + 2k}{n - k - 1}$$

$$\Delta AIC_i = AIC_i - AIC_{min}$$

$$AICW_i = \frac{e^{-0.5\Delta AIC_i}}{\sum_{j=1}^{n} e^{-0.5\Delta AIC_j}}$$

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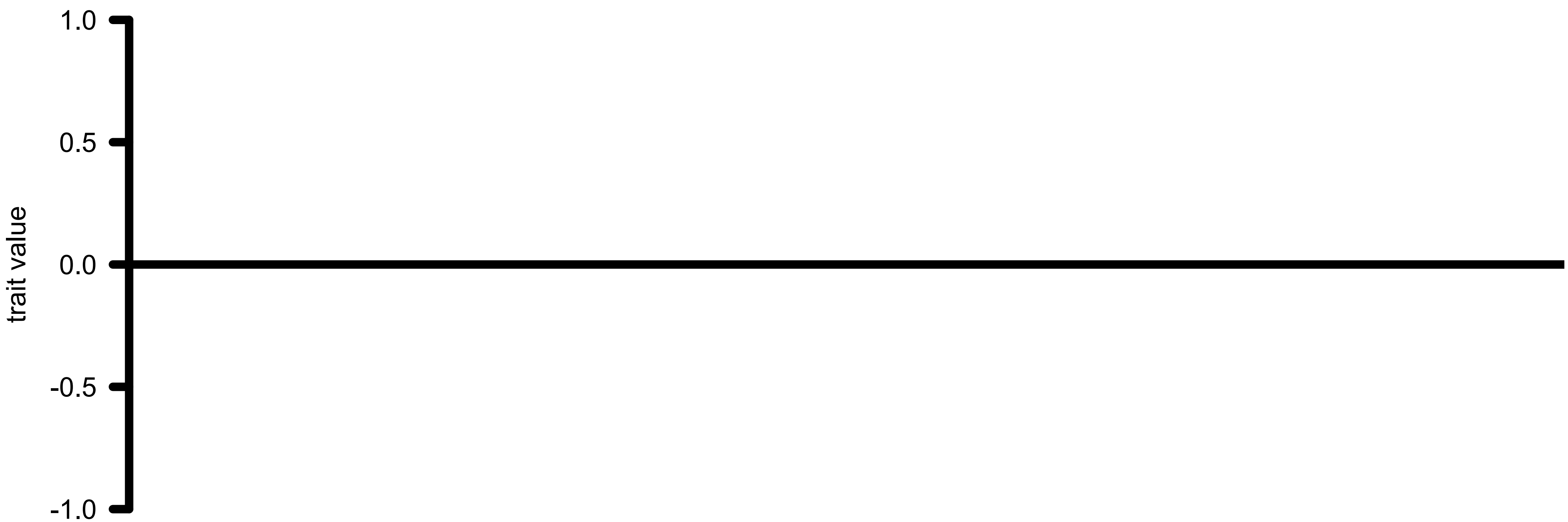

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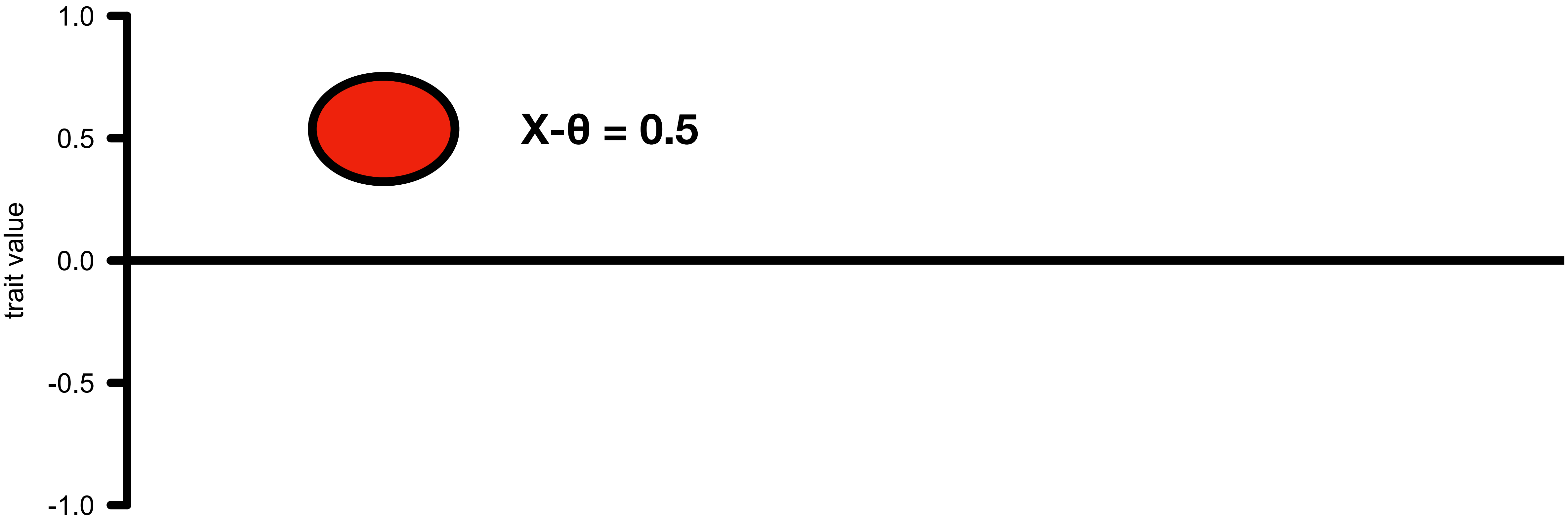

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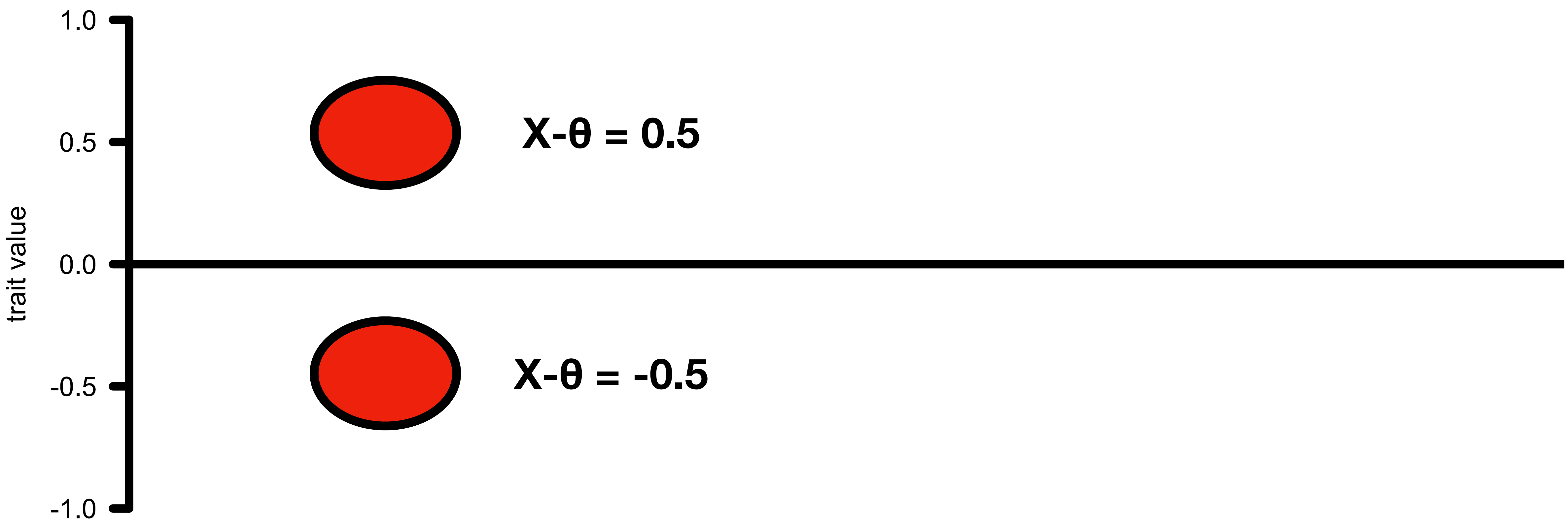

long term behavior of an OU process

$$\mathbb{E}[X_t|X_0] = [1 - e^{-\alpha t}]\theta + e^{-\alpha t}X_0$$

$$Var[X_t|X_0] = \frac{\sigma^2}{2\alpha}[1 - e^{-2\alpha t}]$$

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equilibrium variance

write an OU process simulator

1. what happens when the root state and θ are the same?

2. If the root state and θ differ and σ^2 =0.1, how strong does α have to be for the trait to get to θ in 10 time units? How about in 5? How about in 1?

2. Using the example above with any α that gets you to the optimum, what happens if you increase σ^2 once you ?

OU on trees

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$$\mathbf{V}_{ij} = \frac{\sigma^2}{2\alpha} e^{-\alpha t_{ij}} \left[1 - e^{-2\alpha \mathbf{C}_{ij}}\right]$$

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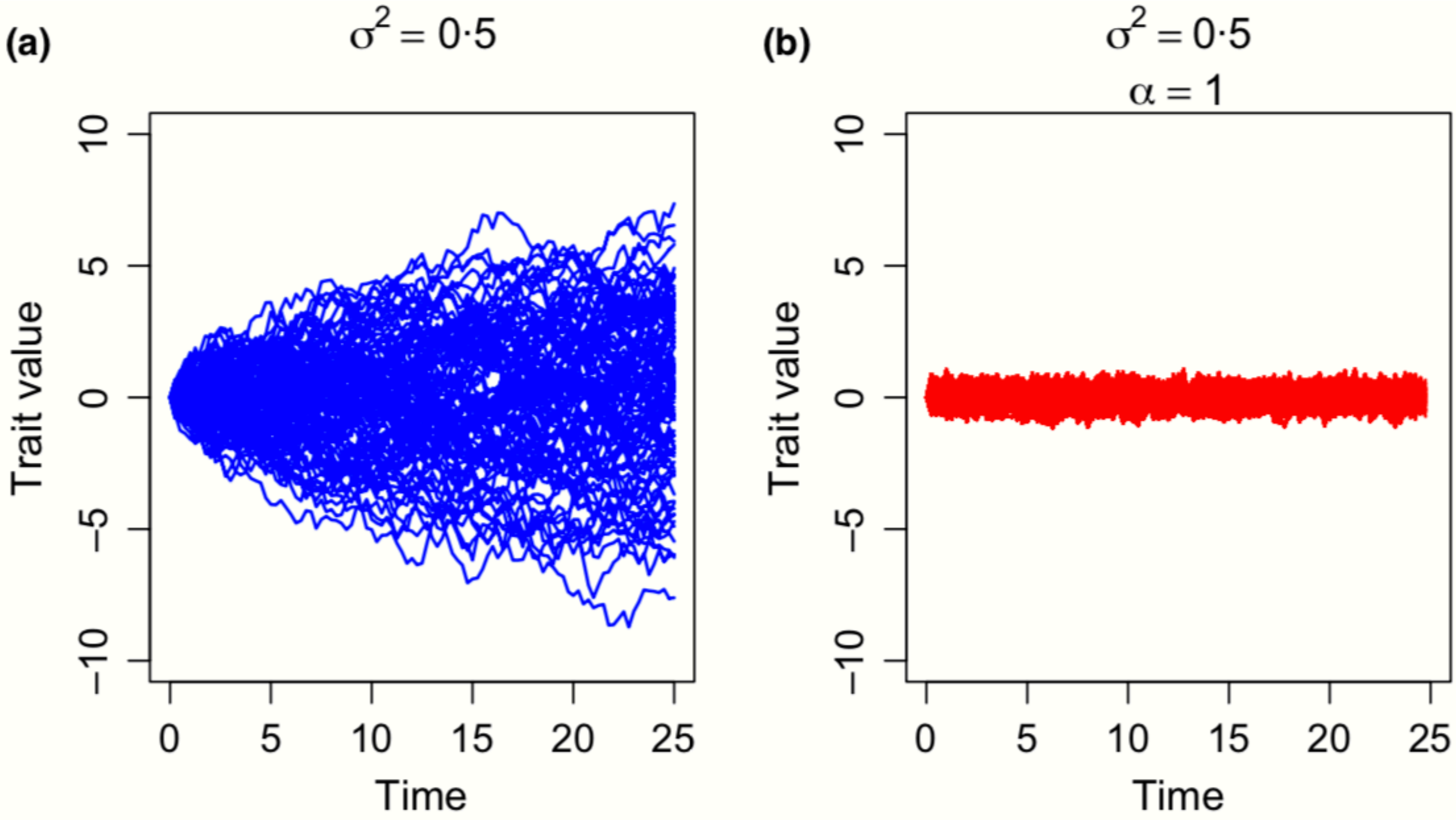
equilibrium variance

co-variance lost due to independent evolution

co-variance accumulated by the common ancestor



(a)
$\sigma^2 = 0{\cdot}5$
Trait value
10
5
0
−5
−10
0
5
10
15
20
25
Time
(b)
$\sigma^2 = 0{\cdot}5$
$\alpha = 1$
Trait value
10
5
0
−5
−10
0
5
10
15
20
25
Time

flavors of phylogenetic OU models

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- root state and θ are the same [aka single stationary peak] (geiger, mvMORPH)

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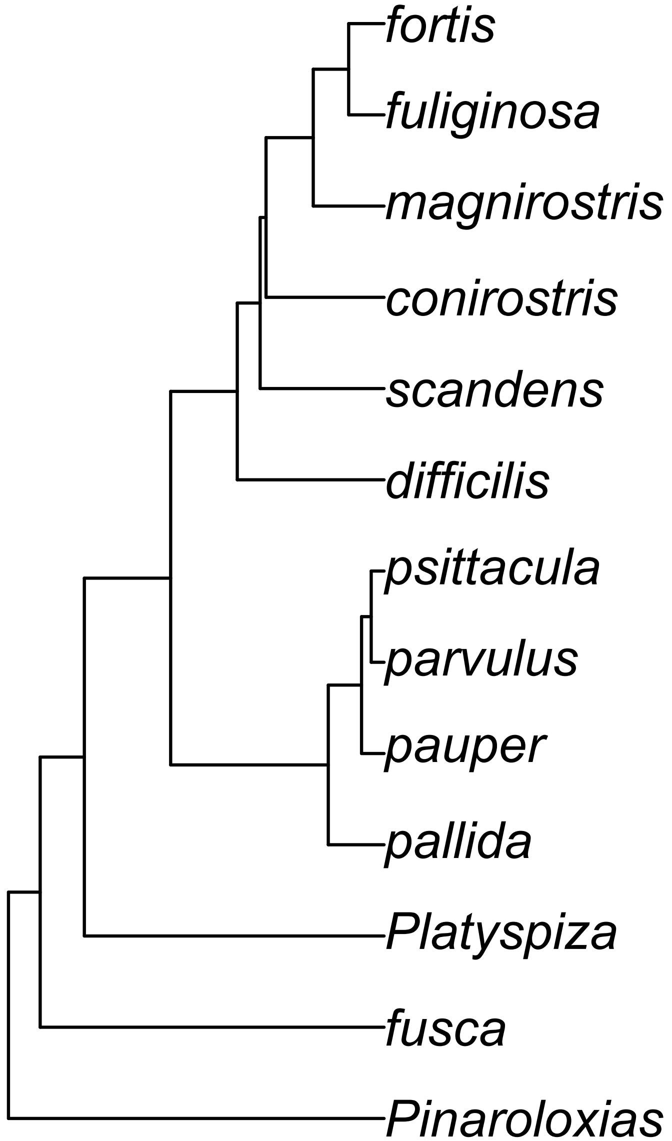
- **root state and θ are the different (maybe non-identifiable w/o fossil data)**
- **θ, α, and/ or σ^2 differ based on some user defined regimes (OUwie, OUCH, mvMORPH)**
- **θ, α, and/ or σ^2 differ based on regimes that are unknown a priori (bayou [rjMCMC], l1ou [lasso regression])**

multivariate data

multivariate data



	wingL	tarsusL	culmenL	beakD	gonysW
fuliginosa	4.13	2.81	2.09	1.94	1.85
fortis	4.24	2.89	2.41	2.36	2.22
magnirostris	4.40	3.04	2.72	2.82	2.68
conirostris	4.35	2.98	2.65	2.51	2.36
scandens	4.26	2.93	2.62	2.14	2.04
difficilis	4.22	2.90	2.28	2.01	1.93
pallida	4.27	3.09	2.43	2.02	1.95
parvulus	4.13	2.97	1.97	1.87	1.81
psittacula	4.24	3.05	2.26	2.23	2.07
pauper	4.23	3.04	2.19	2.07	1.96
Platyspiza	4.42	3.27	2.33	2.35	2.28
fusca	3.98	2.94	2.05	1.19	1.40
Pinaroloxias	4.19	2.98	2.31	1.55	1.63

multivariate data

$$\mathcal{L}(\mathbf{X}|\mathbf{R},\boldsymbol{\mu}) = \frac{e^{-0.5[\mathbf{X}-\boldsymbol{\mu}]^T\mathbf{V}^{-1}[\mathbf{X}-\boldsymbol{\mu}]}}{\sqrt{(2\pi)^{nr}det(\mathbf{V})}}$$

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V is the outer product R ⊗ C

multivariate data

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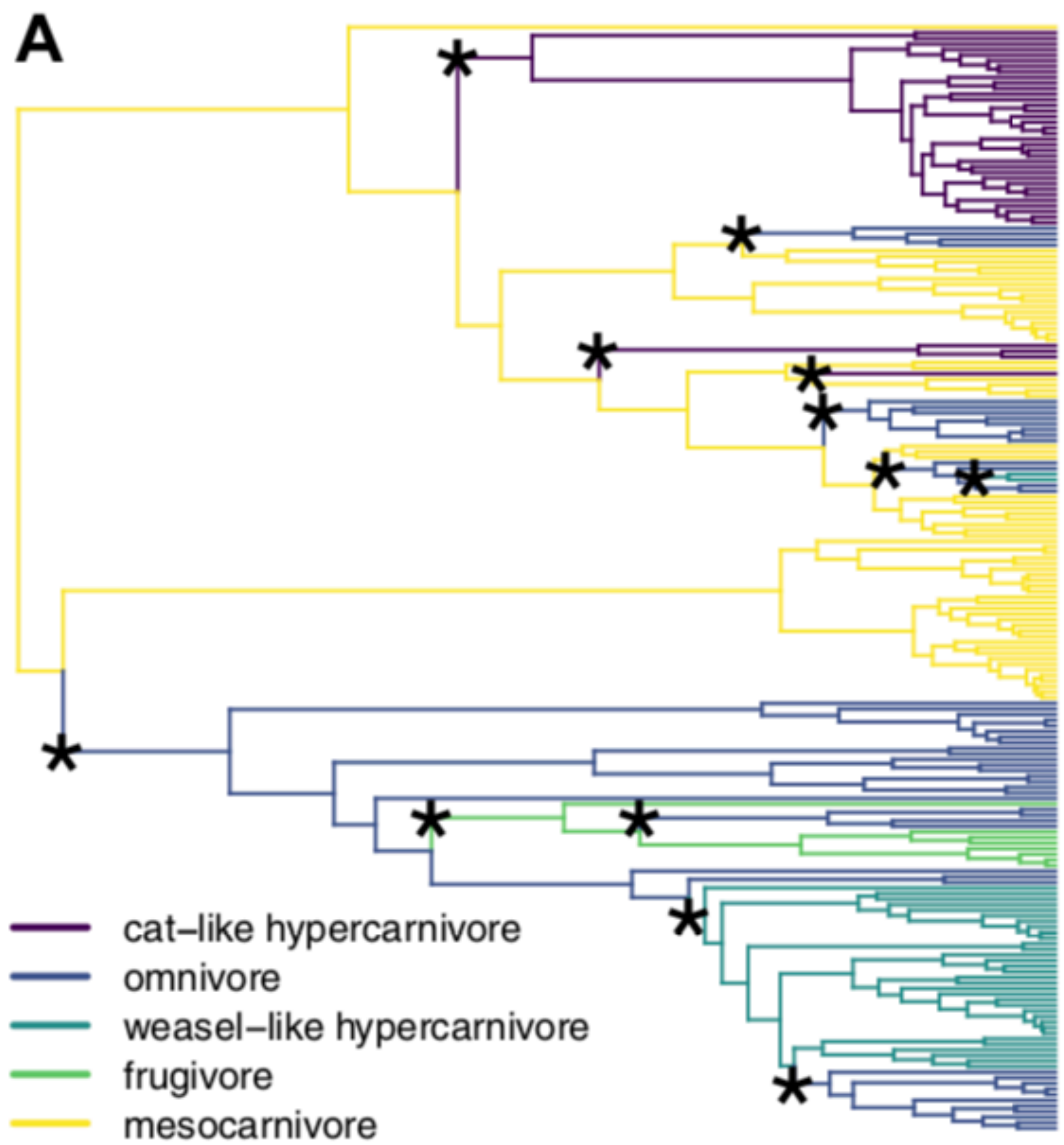
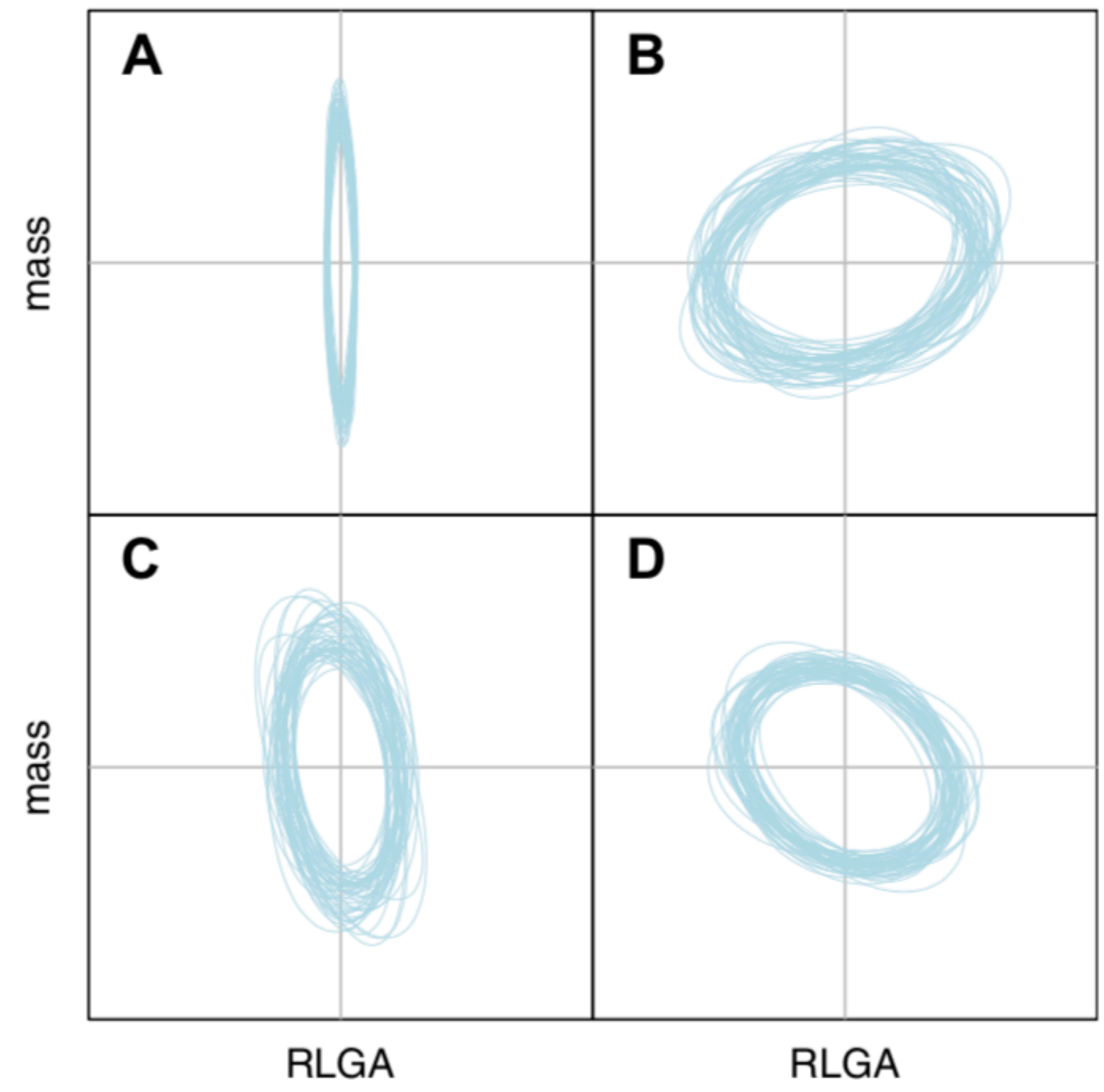
R is the "evolutionary rate matrix"

V is the outer product R $\otimes$ C



A
cat–like hypercarnivore
omnivore
weasel–like hypercarnivore
frugivore
mesocarnivore



A
B
C
D
mass
mass
RLGA
RLGA