Midterm Due Oct 3

12.5 points per question.

1. Sea levels are rising due to global warming. Imagine a rugged landmass that will then be subdivided due to ocean barriers. How will this affect A) speciation, B) extinction, and C) diversification rates? Why?
2. "We think early metazoan life was marine due to taphonomic bias," says your friend. Argue for or against this statement.
3. Describe Dobzhansky-Muller incompatibilities and their importance.
4. Describe a major event in earth history and how life would be different today had it not happened. It cannot be the KT extinction or the end Permian extinction.
5. Most groups of organisms are more diverse in the tropics than temperate areas. Frogs may be an exception. How could you A) find evidence to support this pattern and B) what might be the causes for this pattern, if it is true?
6. What would happen if Australia merged again with South America due to continental drift?
7. Give three examples of how we can use phylogenies to understand macroevolution.
8. There is a new method that lets you predict a speciation rate from the age of a species. How will you know if you can trust this?

Diversification

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EEB464 Fall 2018

Learning objectives

- Evidence for differential diversification
- Diversification models
- Patterns of diversification

How to Read the Circle of Life

Primordial life begins at the center and branches out in all directions, leading to the groups of species that exist today (*colored rings*)

Outer ring: Estimated proportion of all species*

Inner ring: Proportion of the groups named to date

Each black line represents at least 500 descendant species

Dark lines: Many species have been genetically sequenced

Light lines: Few species have been genetically sequenced

Nematodes (roundworms)

Lophotrocho-zoa (mollusks, segmented worms, brachiopods)

Deuterostomia (vertebrates, sea stars and urchins, certain worms)

Early diverging metazoa (cnidaria, comb jellies, sponges)

Many deuterostomia (*gold*) and plants (*dark green*) are already genetically sequenced (*dark lines*) because they are culturally or economically important (such as humans!)

Fungi

Plants

Early diverging archaeplastida (green algae, red algae)

Arthropods (insects, arachnids, crustaceans)

Scientists have identified about one million arthropods (*tan*); millions more remain undescribed

Experts expect that most new species to be discovered will be bacteria (*orange*) and archaea (*magenta*)

The first single-celled organism from which all life has descended arose 3.5 billion years ago

Archaea (single-celled micro-organisms that tolerate extreme conditions)

Bacteria

SARs† (diatoms, amoeboids, brown algae)

*Estimates vary widely; values shown are averages from multiple sources

†Stramenopiles, alveolates, Rhizaria

1 species

260,000 species

Same age, same starting diversity: why the difference?

TABLE 1

COMPARISON OF DIVERSITIES OF LINEAGES BEARING LATEX AND RESIN CANALS WITH SISTER GROUPS

Canal-bearing Taxon	No. of Species	Sister Group(s)	No. of Sister Group Species	Sign of Diversity Difference*	Age†
Pteridophyta (Marsileaceae, *Regnellidium*)[1]	1	*Marsilea* or *Pilularia*	60 6	−	45
Gnetales (Gnetaceae, *Gnetum*)[1]	30	*Welwitschia*	1	+	160
Coniferae (Pinaceae [250] + Cupressaceae [130] + Taxodiaceae [16] + Araucariaceae [38] + Podocarpaceae [125])[1]	559	Ginkgoaceae	1	+	180
Urticales (Urticaceae [700] + Moraceae [1,000] + Cannabaceae [3])[2]	1,703	Ulmaceae	150	+	93
Caryophyllales (Cactaceae, *Mammillaria*, sect. Mammillaria [110] + sect. Subhydrochylus [22])[5]	132	Ancistrocladae or Leptocladae	35 6	+	?
Theales (Dipterocarpaceae, Dipterocarpoidea)[1]	400	Monotoidea	35	+	60
Ebenales (Sapotaceae)[2]	800	Ebenaceae	450	+	67
Celastrales (Hippocrateaceae, *Hippocratea*)[1]	100	Celastraceae (*Lophopetalum*)	4	+	?

Nemonychidae(85)
Attelabinae(800)
Rhynchitinae(1200)
Antliarhininae(24)
Apioninae(1500)
Rhynchophoridae(1100)
Curculionidae(40502)
Oxycoryninae(10)
Allocoryninae(20)
Belinae(150)
Prioninae(770)
Aseminae(75)
Spondylinae(3)
Cerambycinae(10000)
Lamiinae(14000)
Lepturinae(1000)
Palophaginae(3)
Megalopodinae(350)
Zeugophorinae(50)
Orsodacninae(8)
Aulacoscelidinae(18)
Synetinae(11)
Eumolpinae(3200)
Megascelidinae(60)
Lamprosomatinae(190)
Chlamisinae(360)
Clytrinae(947)
Cryptocephalinae(2290)
Chrysomelinae(2000)
Galerucinae(5300)
Alticinae(8000)
Cassidinae(3000)
Hispinae(3000)
Donaciinae(165)
Criocerinae(1400)
Pachymerinae(77)
Amblycerinae(400)
Bruchinae(3000)

early Oligocene

Tr   Ju   Cr   Ter

Farrell. "Inordinate fondness" explained: Why are there so many beetles?. Science (1998) vol. 281 (5376) pp. 555-559

Table 1. Five independent contrasts of groups associated with gymnospermous seed plants versus angiosperms. All five contrasts yield a positive difference in favor of the hypothesis that angiosperm feeding is associated with enhanced diversity (one-tailed sign test, $P = 0.03$). Addition of the remaining (mostly weevil) subfamilies, not yet sequenced, will bring the total number of species to 135,000. For two comparisons, alternative topologies are three to four steps (combined changes in nucleotides and morphological characters) away (comparisons 3 and 5), but these alternatives yield the same conclusion of ancestral beetle associations with gymnosperms. Thus, for comparison 3 (the Cerambycidae), the closest alternative grouping (within four steps) is of the Spondylinae as sister to the angiosperm-associated clade, with Aseminae as sister to this assemblage. For comparison 5, the closest alternative (within three steps) is of Orsodacninae as sister to the angiosperm feeders.

Comparison	Primitively gymnosperm-associated taxon	Diversity	Primitively angiosperm-associated taxon	Diversity
1	Nemonychidae	85	Attelabinae-Rhynchitinae, Apioninae, and Curculionidae-Rhynchophoridae	44,002
2	Oxycoryninae-Allocoryninae	30	Belinae	150
3	Aseminae-Spondylinae	78	Lepturinae and Lamiinae-Cerambycinae	25,000
4	Palophaginae	3	Megalopodinae-Zeugophorinae	400
5	Orsodacninae-Aulacoscelidinae	26	Remaining Chrysomelidae	33,400

$$N(t) = N(0)e^{bt}$$

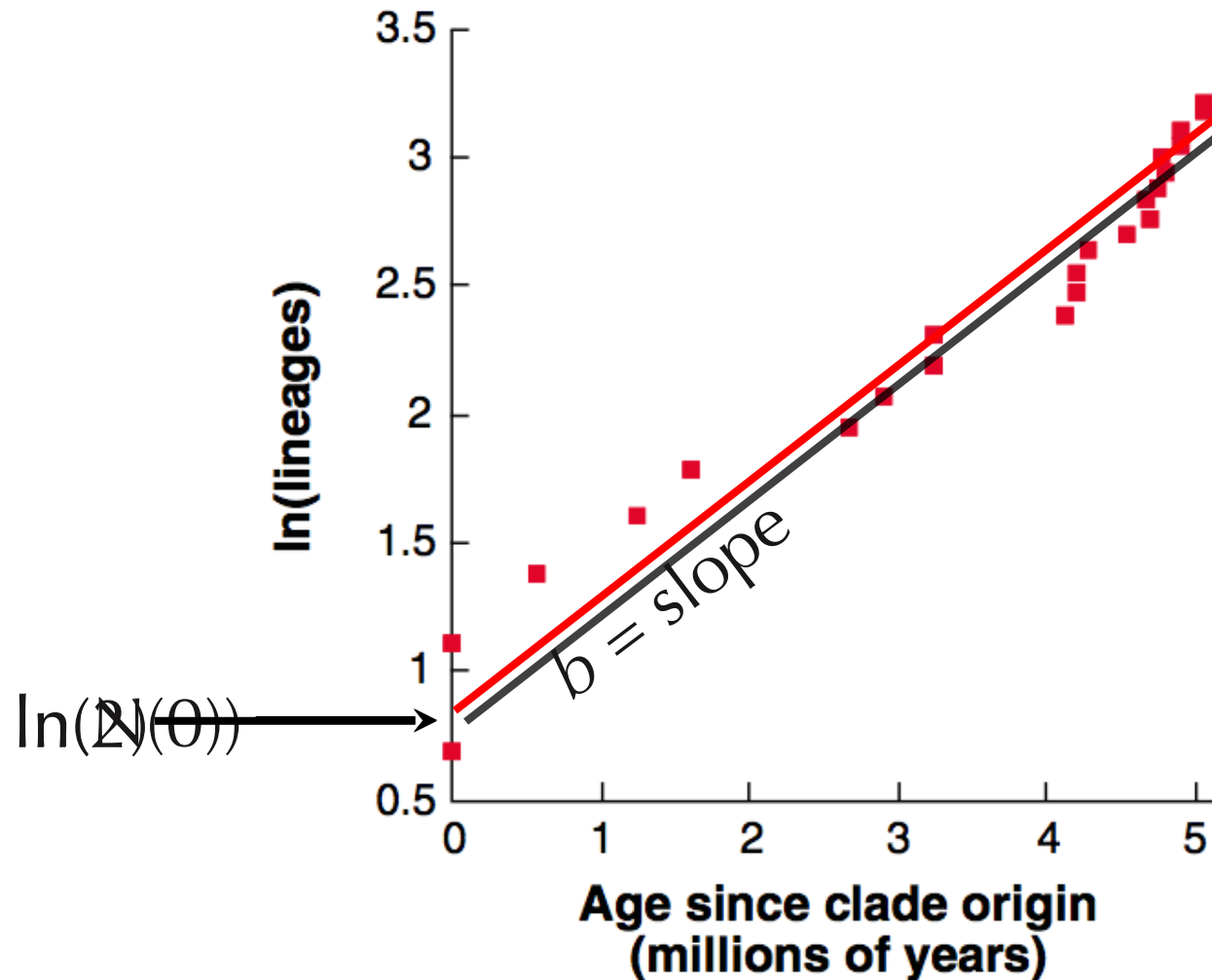$$N(t) = N(0)e^{bt} \qquad \ln(N(t)) = \ln(N(0)e^{bt}) = \ln(N(0)) + bt$$

Figure 2

Cumulative increase in the logarithm of the number of lineages in a dated molecular phylogeny of the Hawaiian silversword alliance. Data from Baldwin & Sanderson (1998).
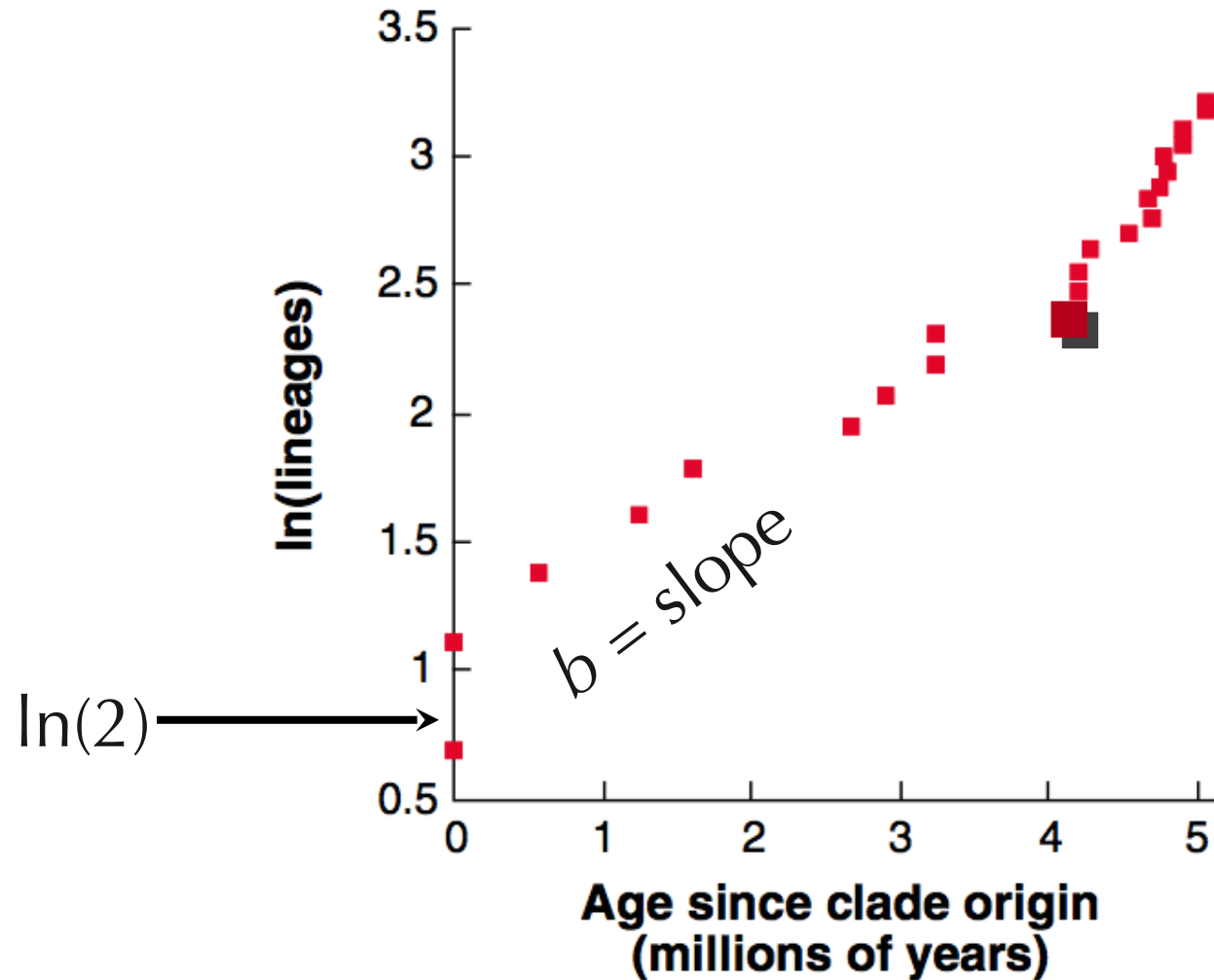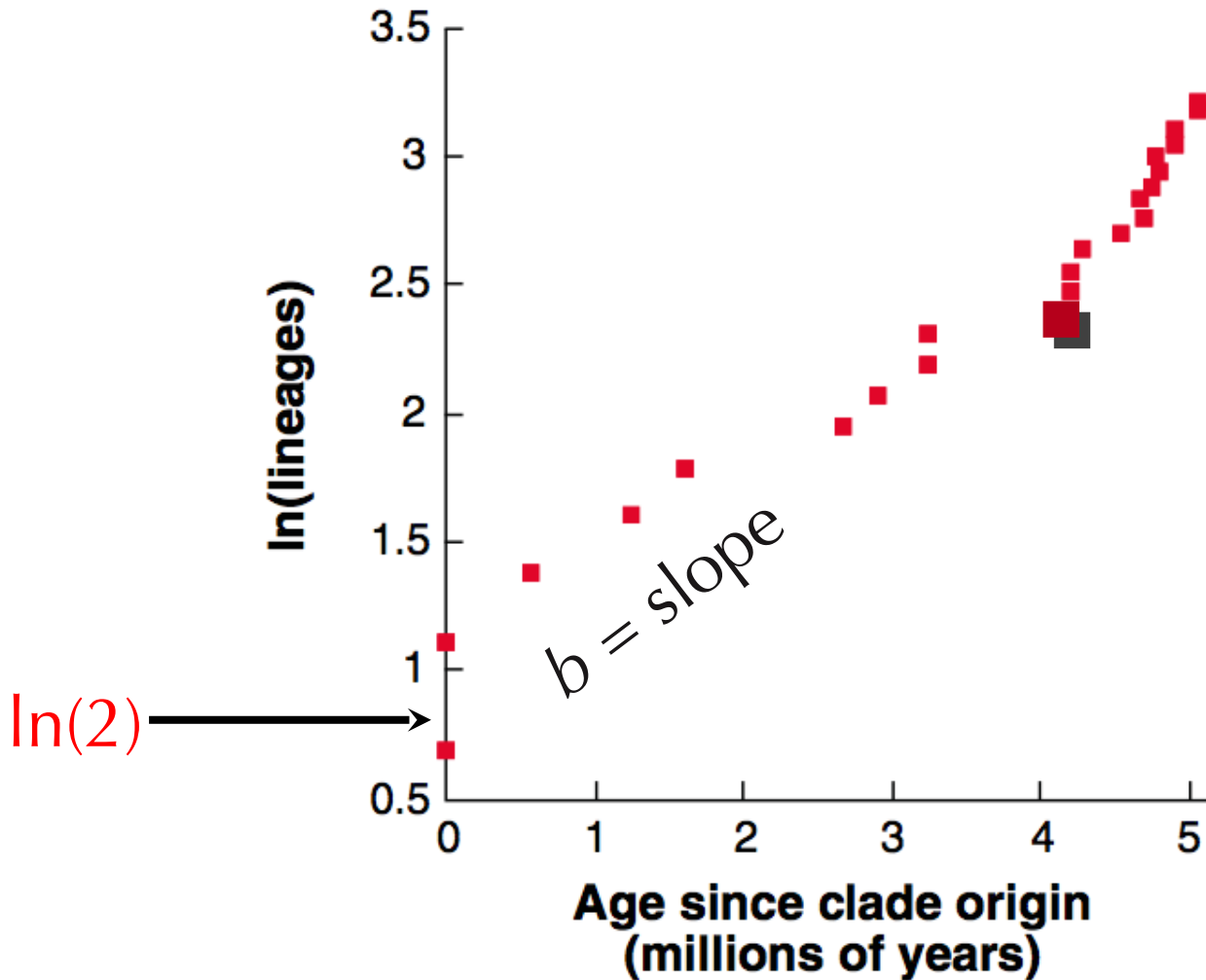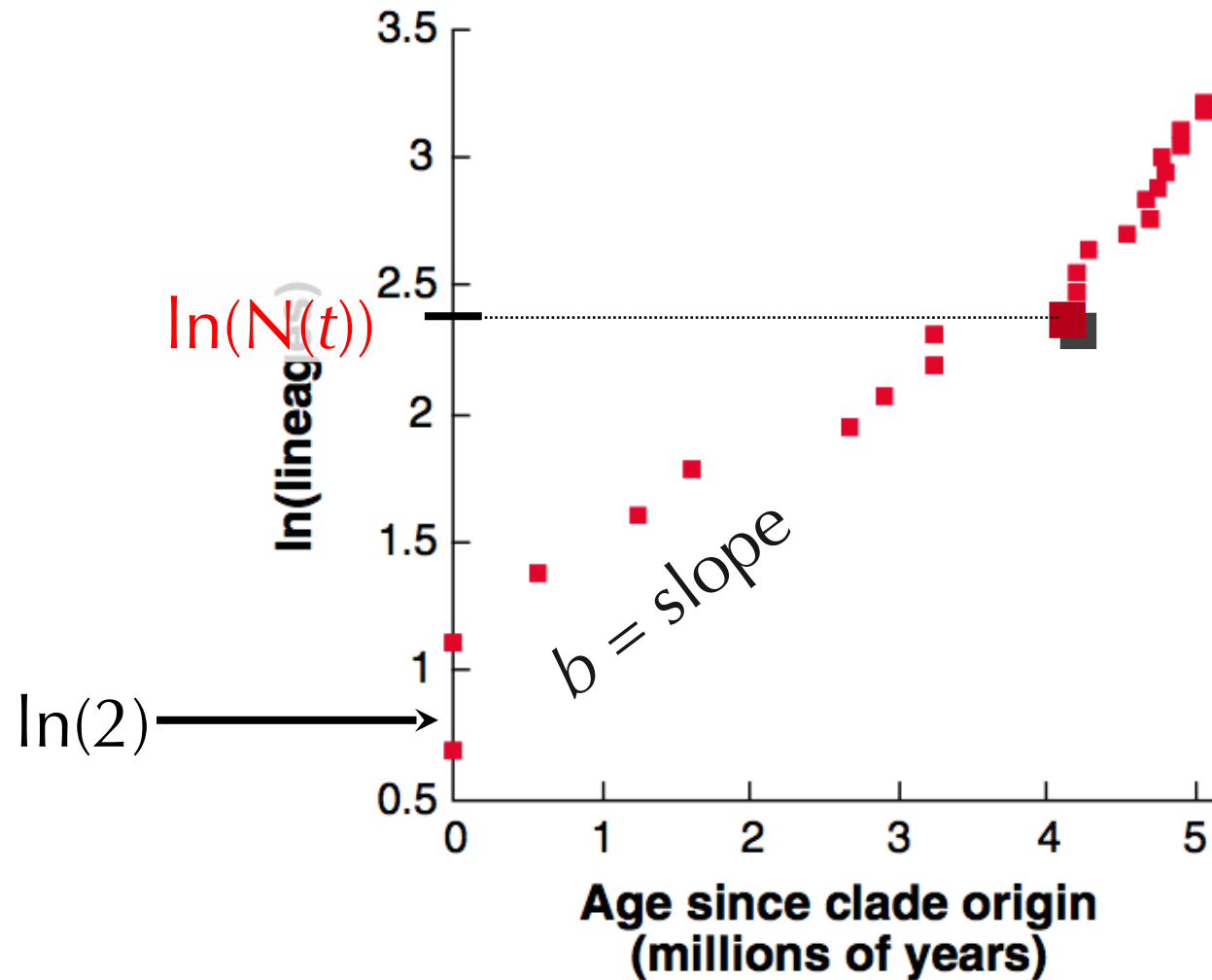
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Figure 2

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$$\ln(\mathrm{N}(t)) = \ln(2) + bt$$

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Nee. Birth-death models in macroevolution. Annu Rev Ecol Syst (2006) vol. 37 pp. 1-17
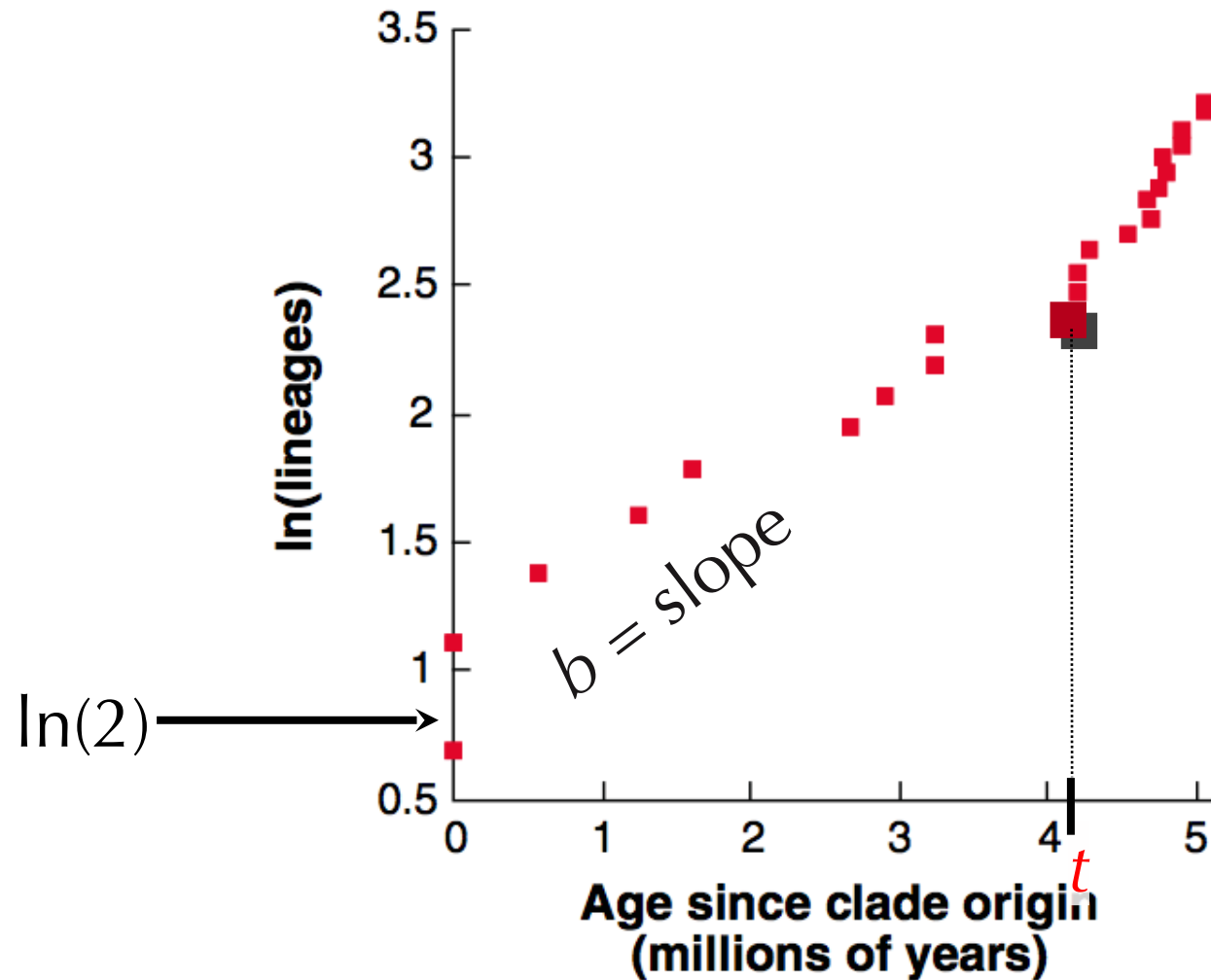
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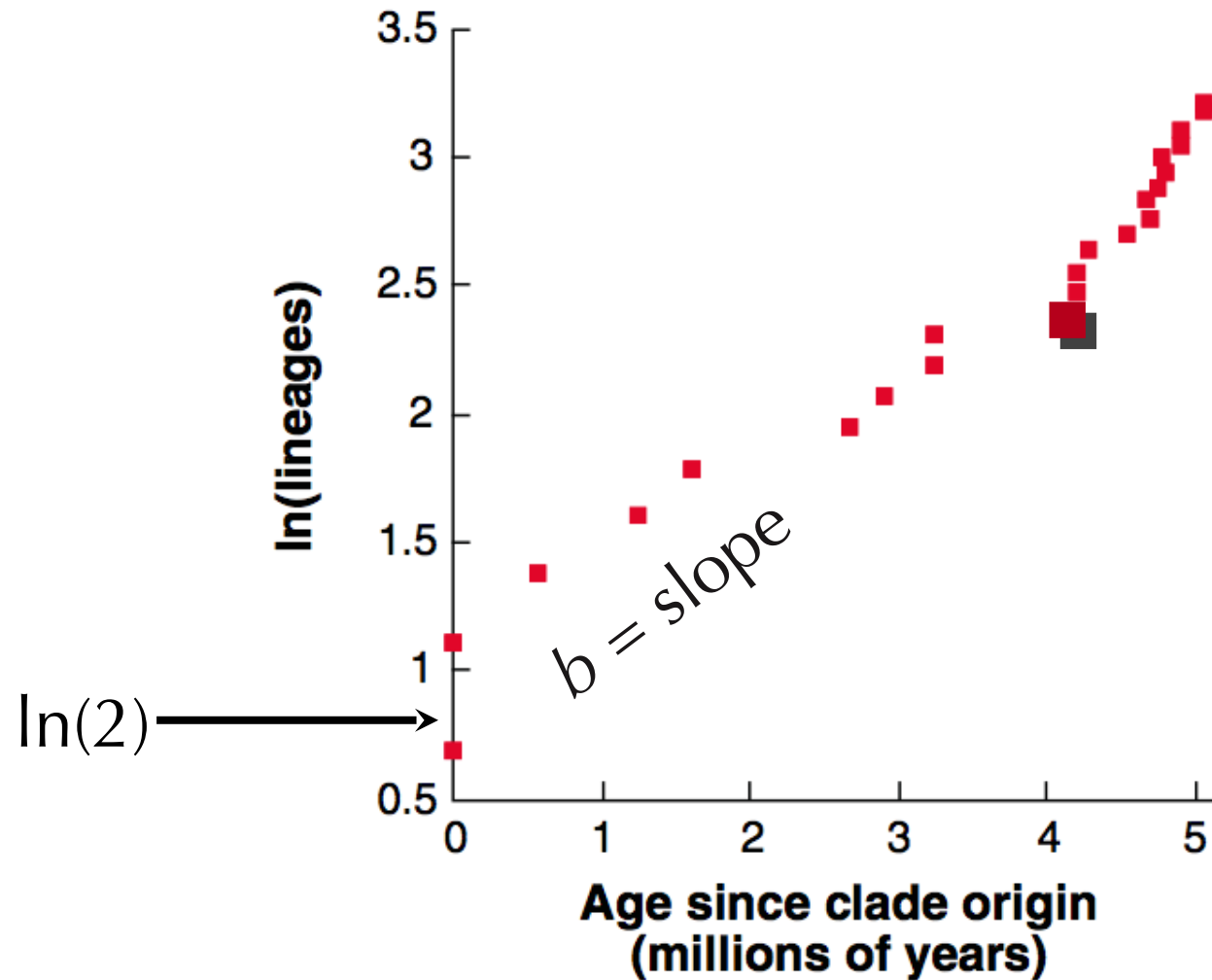
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$$\boldsymbol{b} = (\ln(N(t)) - \ln(2)) \div t$$

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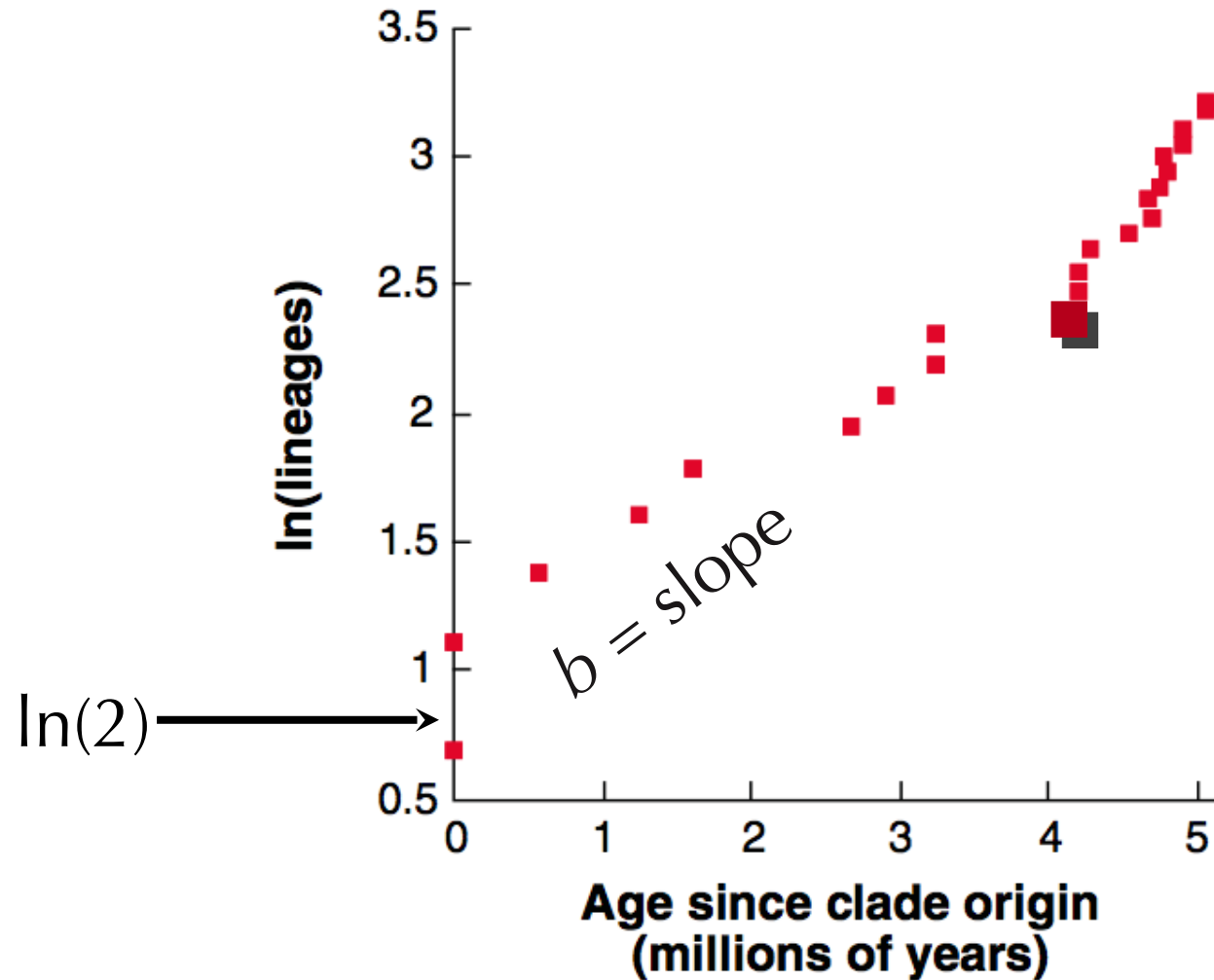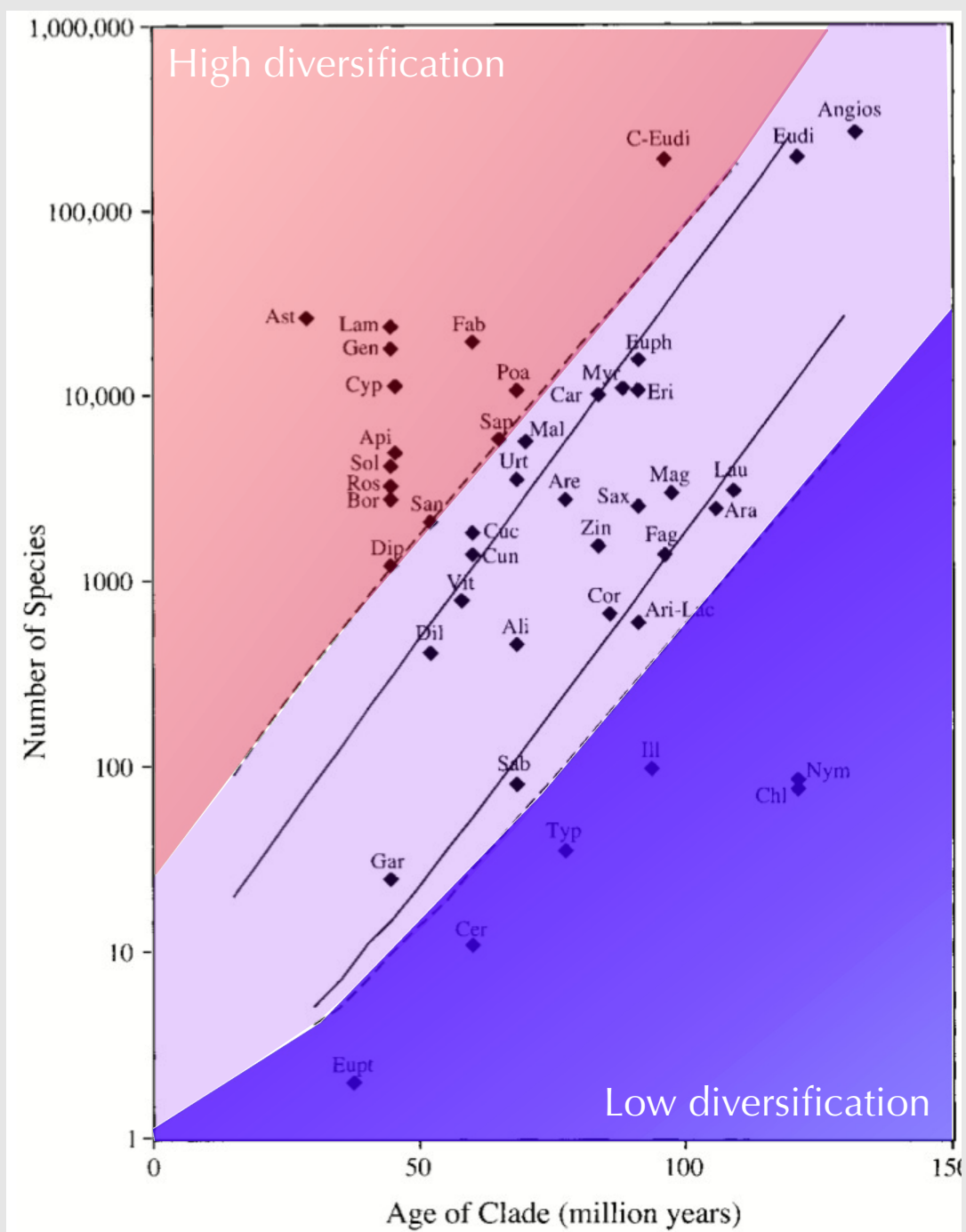
$$b = (\ln(N(t)) - \ln(2)) \div t$$

Magallón and Sanderson. Absolute diversification rates in angiosperm clades. Evolution (2001)

$$b = (\ln(N(t)) - \ln(2)) \div t$$

Clade	Abbr.	No. of species		Fossil record	Age
Angiosperms					
Angiosperm pollen grains (Incertae sedis angiosperms)	Angios	262,196	CG	late Valanginian–early Hauterivian	132
"magnoliids"					
Amborellaceae	x	1	—	no known fossil record	—
Aristolochiaceae-Lactoridaceae	Ari-Lac	601	CG	Turonian	91.2
Calycanthales	Cal	10	SG	early Albian	108.8
Canellaceae	x	16	—	no reliable fossil record	—
Ceratophyllaceae	Cer	11	CG	Paleocene	59.9
Chloranthaceae	Chl	75	CG	Barremian–Aptian	121.0
Illiciales	Ill	98	CG	Cenomanian–Turonian	93.5
Laurales	Lau	3094	CG	early Albian	108.8
Magnoliales	Mag	3016	SG	early Albian	108.8
Magnoliales	Mag	3016	CG	early Cenomanian	97.5
Nymphaeales	Nym	85	CG	Barremian–Aptian	121.0
Piperales	x	2107	—	no reliable fossil record	—
Winteraceae	Win	80	SG	late Barremian	122.5
Monocots					
Acorus	x	1	—	no known fossil record	—
Alismatiflorae	Ali	454	CG	Maastrichtian	68.1
Arales	Ara	2480	CG	Albian	105.5
Arecaceae	Are	2780	SG	Upper Santonian	84.0
Arecaceae	Are	2780	CG	Campanian	77.4
Asparagales[1]	x	6635	CG	Late Eocene	37.5
Bromeliaceae[2]	x	1600	CG	Late Eocene	37.5
Commelinaceae[3]	x	700	CG	Middle Miocene	13.8

Magallón and Sanderson. Absolute diversification rates in angiosperm clades. Evolution (2001)

$$b = (\ln(N(t)) - \ln(2)) \div t$$

Clade		$\epsilon = 00$
Eupteleaceae	CG	0.0000
Trochodendrales	SG	0.0066
Nelumbonaceae	SG	0.0068
Calycanthales	SG	0.0212
Platanaceae	SG	0.0212
Ceratophyllaceae	CG	0.0285
Chloranthaceae	CG	0.0300
Nymphaeales	CG	0.0310
Winteraceae	SG	0.0358
Typhales	CG	0.0370
Illiciales	CG	0.0416
Buxales	SG	0.0418
Triuridaceae	SG	0.0473
Sabiales	CG	0.0542
Nymphaeales	CG	0.0551
Garryaceae	CG	0.0571
Ari-Lac	CG	0.0626
Laurales	CG	0.0675
Arales	CG	0.0675
Cornales	CG	0.0678
Fagales	CG	0.0680
Proteaceae	SG	0.0723
Magnoliales	SG	0.0736
Magnoliales	CG	0.0751
Saxifragales	CG	0.0784
Alismatiflorae	CG	0.0797
Zingiberales	CG	0.0798
Angiosperms	**CG**	**0.0893**

Magallón and Sanderson. Absolute diversification rates in angiosperm clades. Evolution (2001)

Magallón and Sanderson. Absolute diversification rates in angiosperm clades. Evolution (2001)
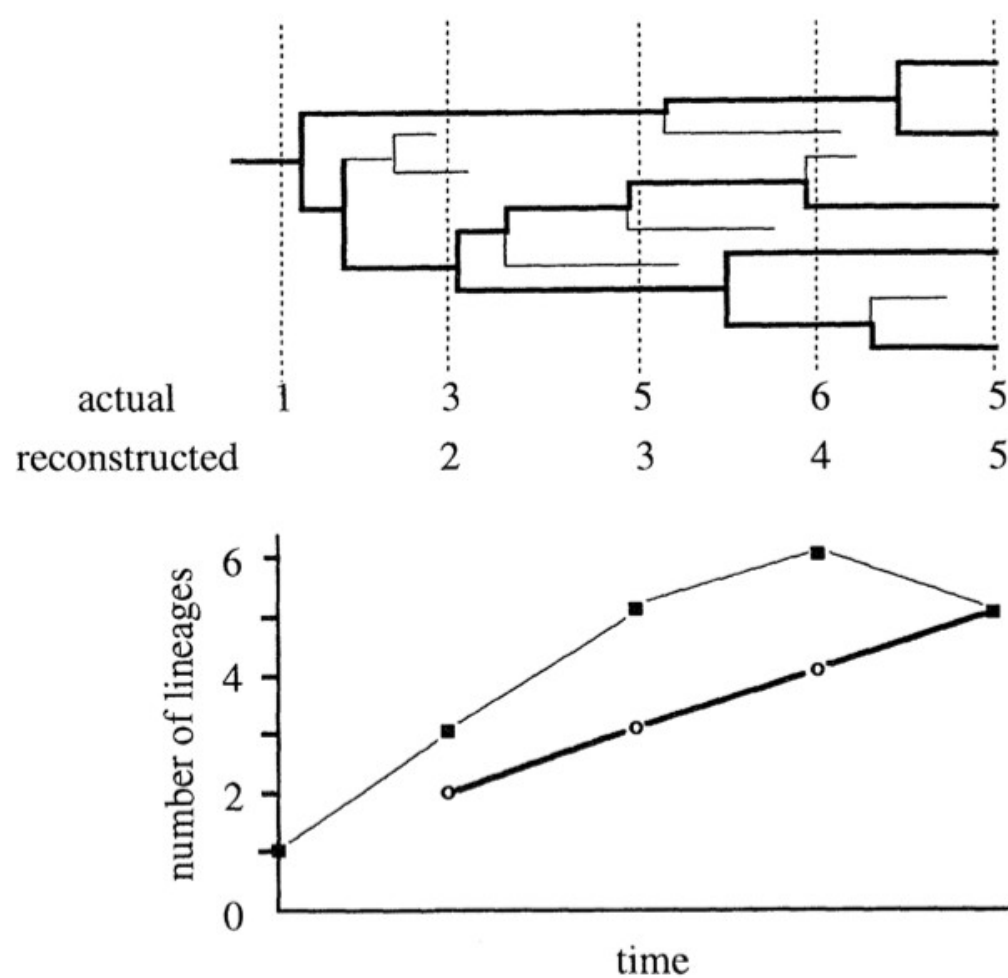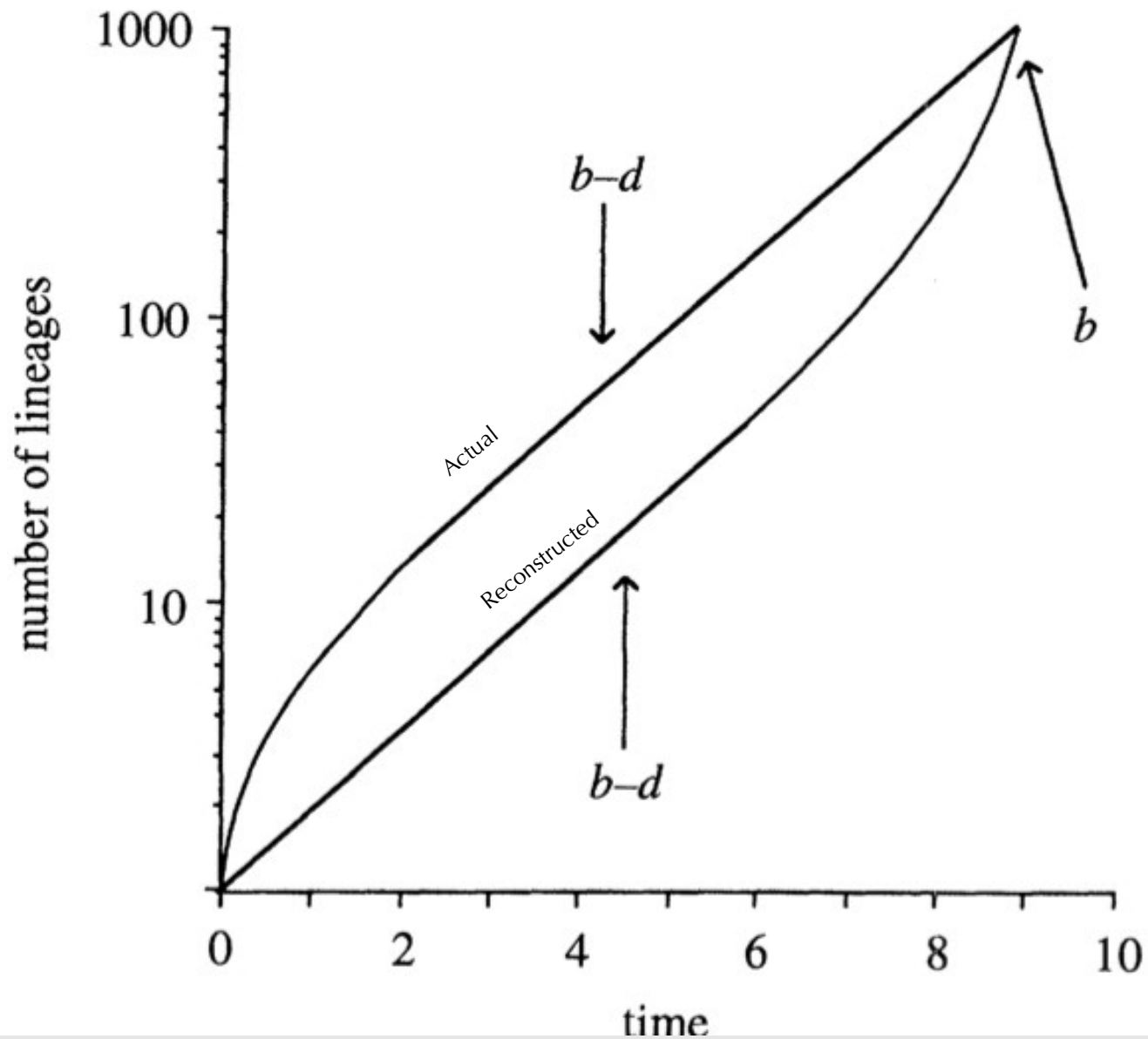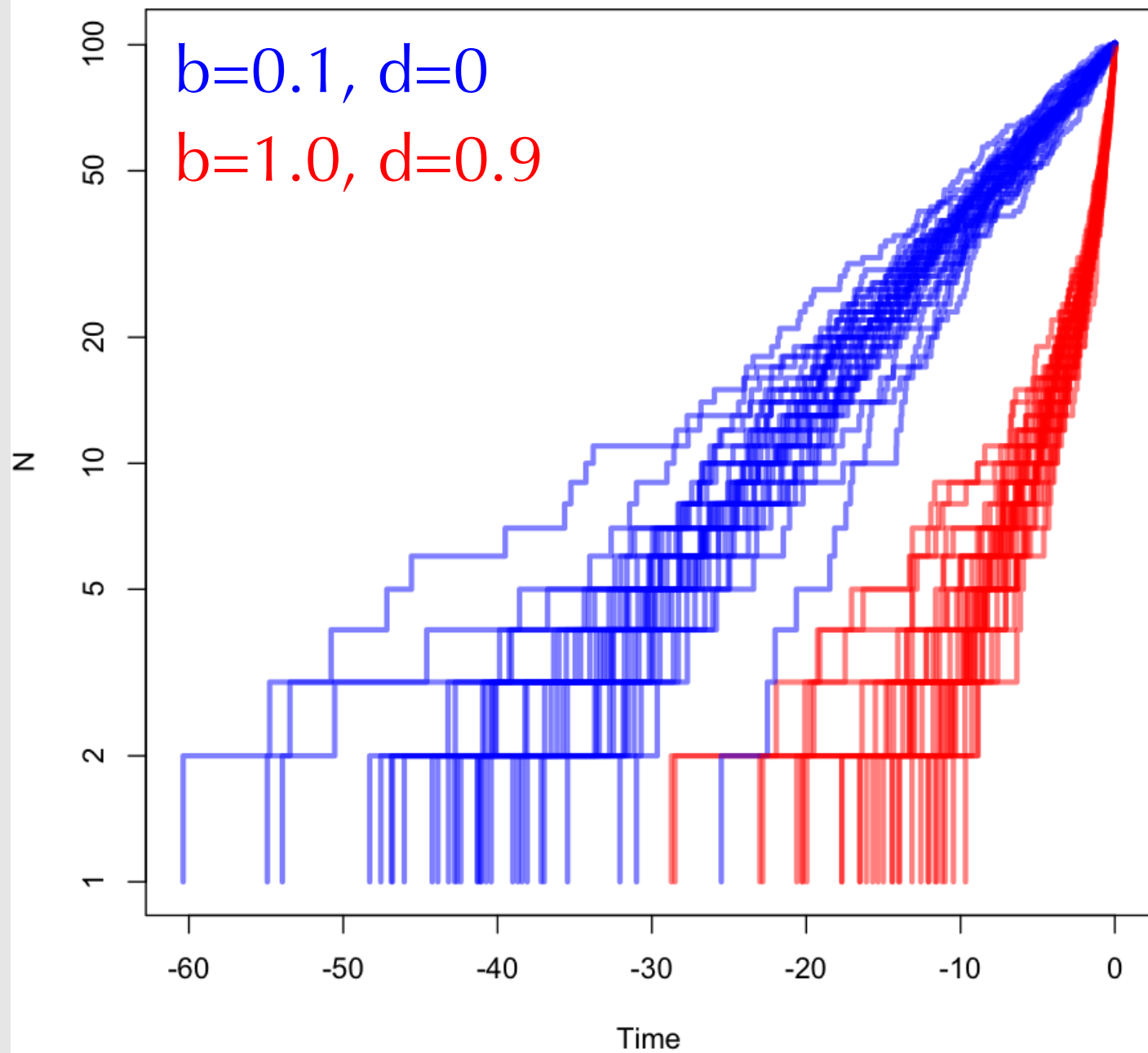
Figure 1. A hypothetical phylogeny as it would appear in a perfect fossil record. The bold lines represent those lineages which have some descendants at the present day and, so, would appear in a phylogeny reconstructed from molecular data. The numbers of lineages through time for the actual and reconstructed phylogenies are plotted at the bottom of the figure.
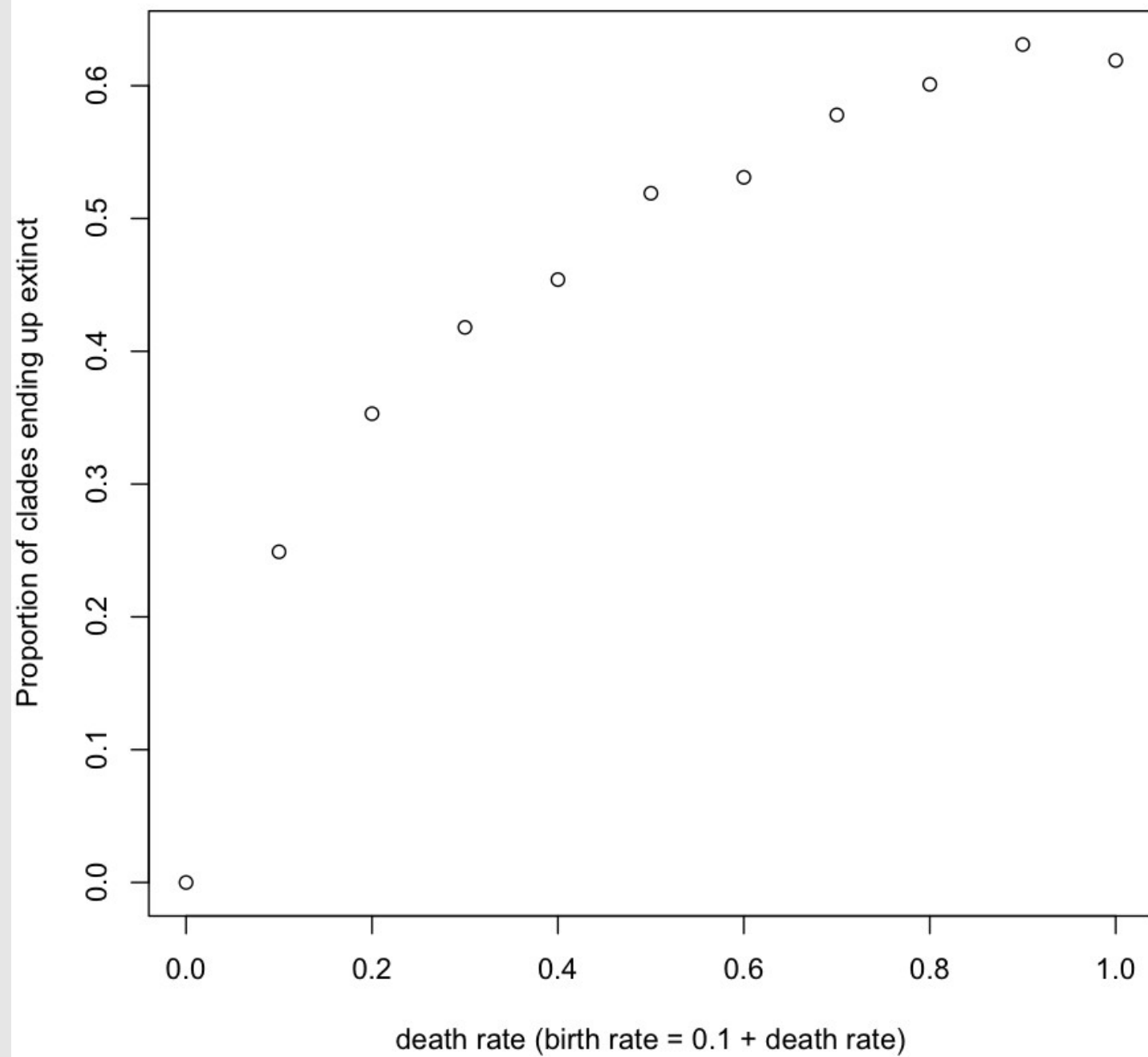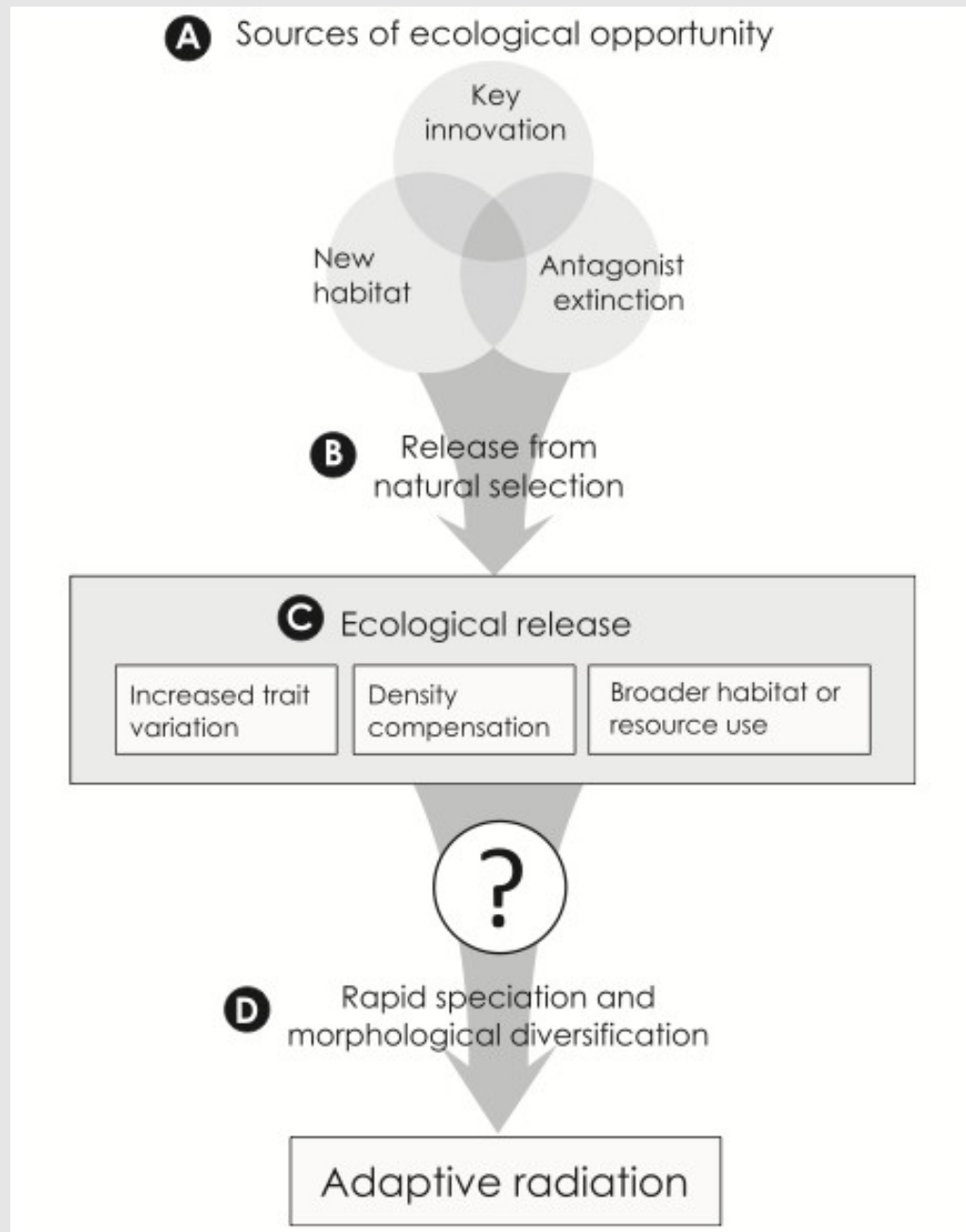
Nee et al. Extinction Rates can be Estimated from Molecular Phylogenies. Philosophical Transactions: Biological Sciences (1994) vol. 344 (1307) pp. 77-82

b=0.1, d=0
b=1.0, d=0.9

Fig. 1. Adaptive diversification in Caribbean *Anolis* lizards. On each island in the Greater Antilles, anoles have diversified to produce the same set of habitat specialists. Shown here (clockwise from top left) are *A. cybotes*, trunk-ground specialist, Hispaniola (photo: J. Losos); *A. pulchellus*, grass-bush, Puerto Rico (photo: J. Losos); *A. insolitus*, twig, Hispaniola (photo: L. Mahler); *A. chlorocyanus*, trunk-crown, Hispaniola (photo: M. Losos).

Fig. 2. Adaptive diversification in cichlids. Several examples of cichlids that use different habitats. (Upper left) *Gnathochromis permaxillaris* occurs in the deeper (>35 m) intermediate (rock-sand interface) habitat with sediment-rich bottoms in Lake Tanganyika. (Upper right) *Lethrinops furcifer* is found in sandy environments near beaches in Lake Malawi. (Center) *Hemitilapia oxyrhynchus*, which is found in shallow vegetated habitats in Lake Malawi. (Lower left) *Cyprichromis* sp. "Leptosoma Jumbo" (Nkondwe) occurs in open water in Lake Tanganyika. (Lower right) *Petrotilapia nigra* occurs in the upper part (>10 m) of the sediment-free rocky habitat of Lake Malawi. [Photographs by A. Konings]

Yoder et al. Ecological opportunity and the origin of adaptive radiations. Journal of Evolutionary Biology (2010) vol. 23 (8) pp. 1581-1596
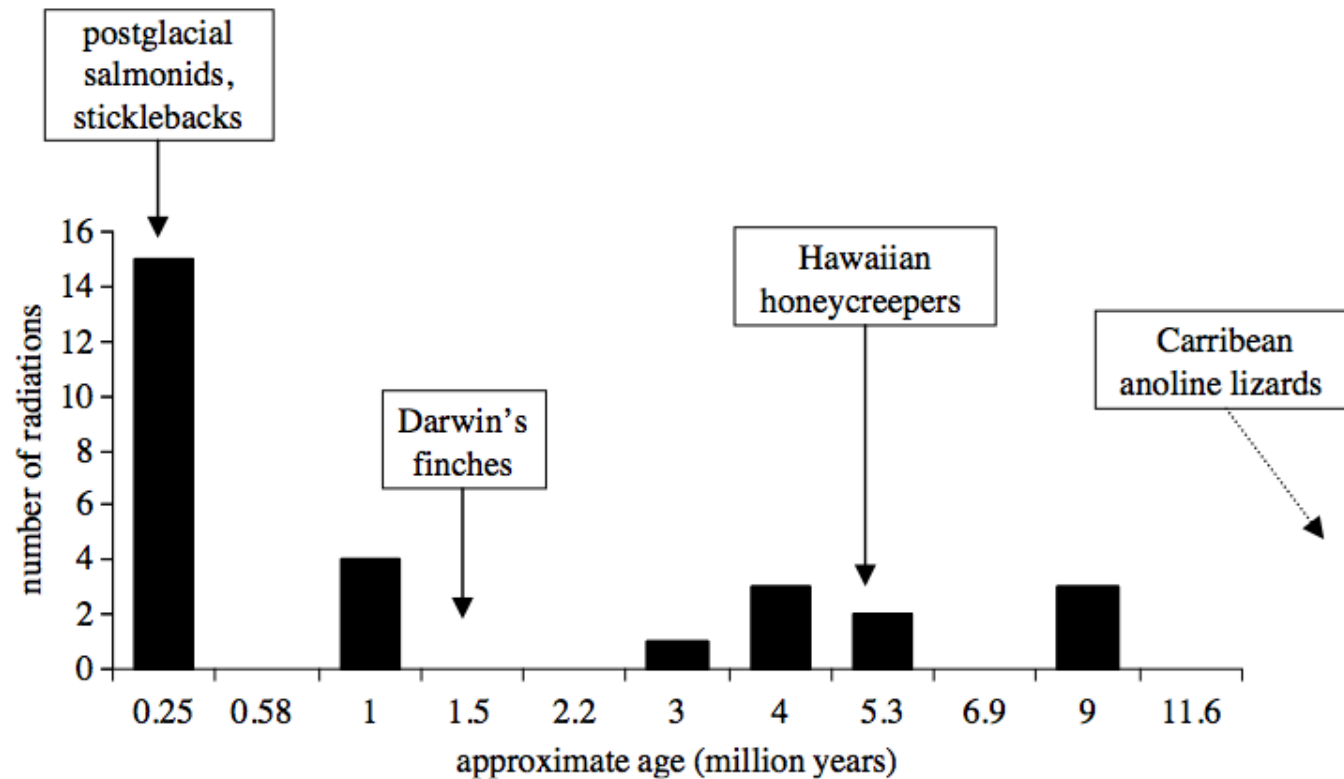
Figure 1. Frequency distribution of the age of African lacustrine cichlid fish radiations contrasted with approximate ages of other well-studied vertebrate adaptive radiations.
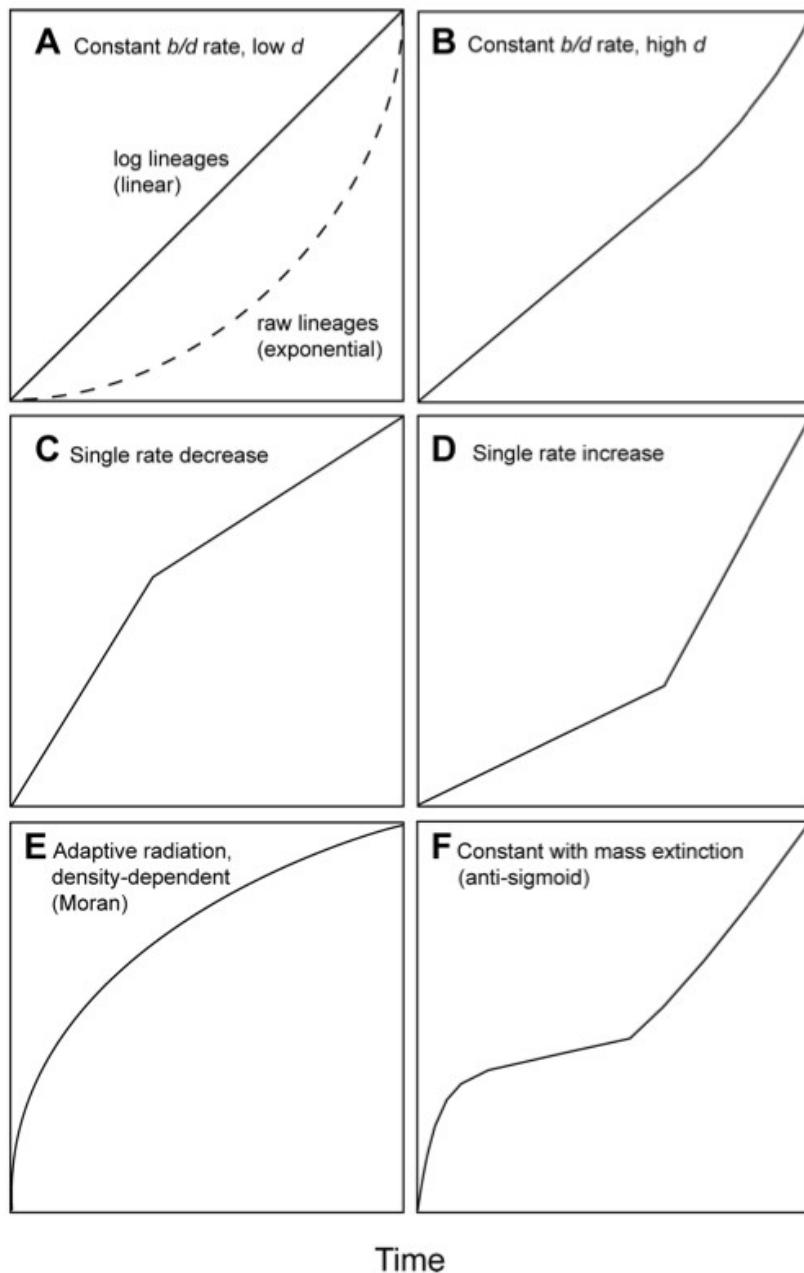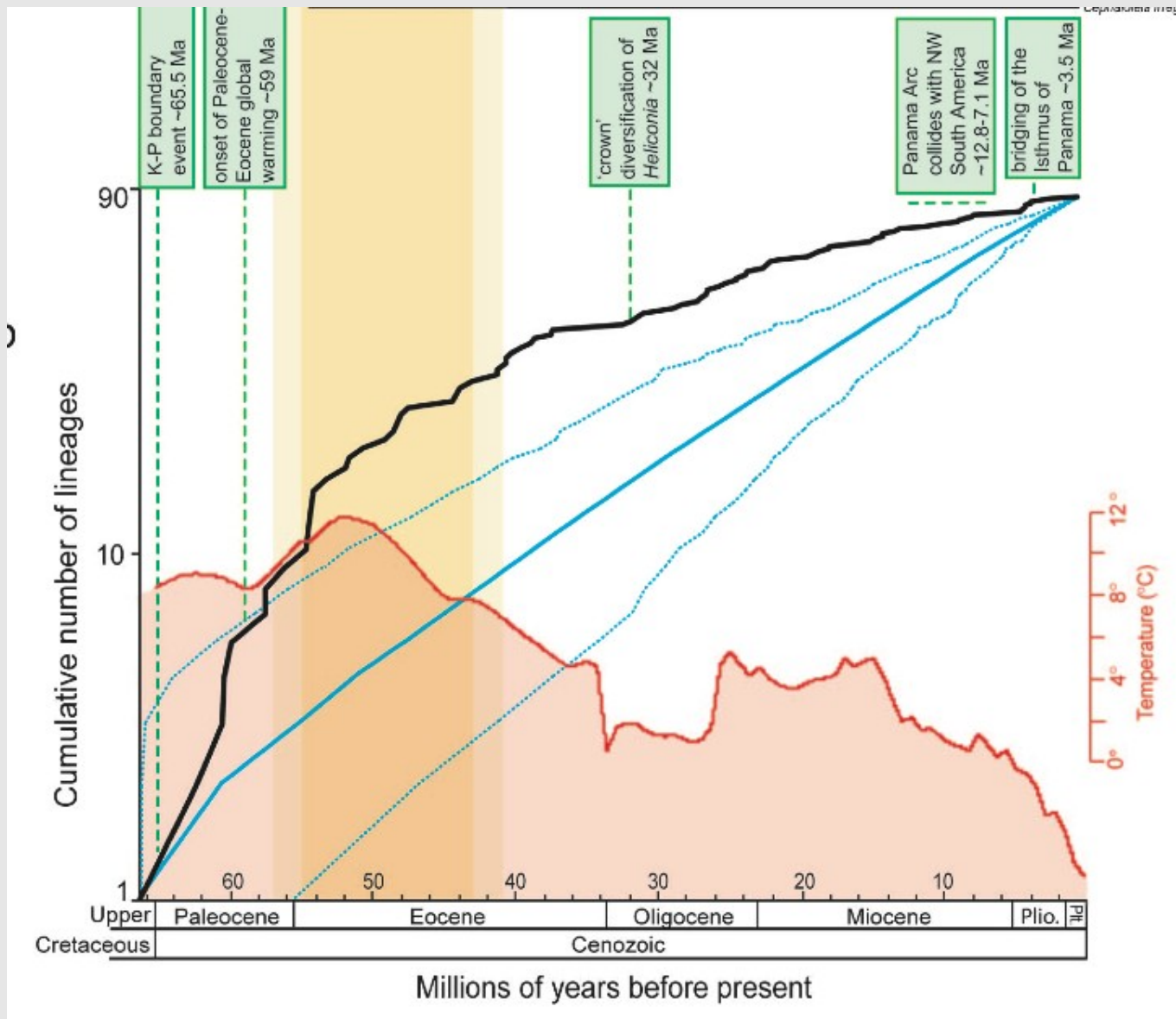
Figure 1. Theoretical lineages through time (LTT) plots. All *y*-axes have a log scale except the exponential curve in (A). (A) Constant birth (*b*) and death (*d*) rates give an exponential curve (broken line), which becomes a straight line in a log plot if the *d/b* ratio is low, for example, *d* = 0.5*b*. (B) If *d/b* is high (e.g., *d* = 0.8 *b*), the curve steepens toward the present because recent lineages are less likely to have become extinct. The following curves all assume a low *d/b* ratio. (C) Constant *b/d* with an abrupt rate decrease. (D) Constant *b/d* with an abrupt rate increase. (E) Adaptive radiation in which death rate depends on lineage density (Moran process: Harvey et al. 1994; Nee 2006; Ricklefs 2007). The curve is convex with an initially steep slope that decreases as niche space fills. (F) Antisigmoid curve from a mass extinction event—the plateau and subsequent sharp upturn in slope are caused entirely by the extinction and do not reflect any change in background *b* and *d* rates (Harvey et al. 1994).

McKenna and Farrell. Tropical forests are both evolutionary cradles and museums of leaf beetle diversity. Proceedings of the National … (2006)
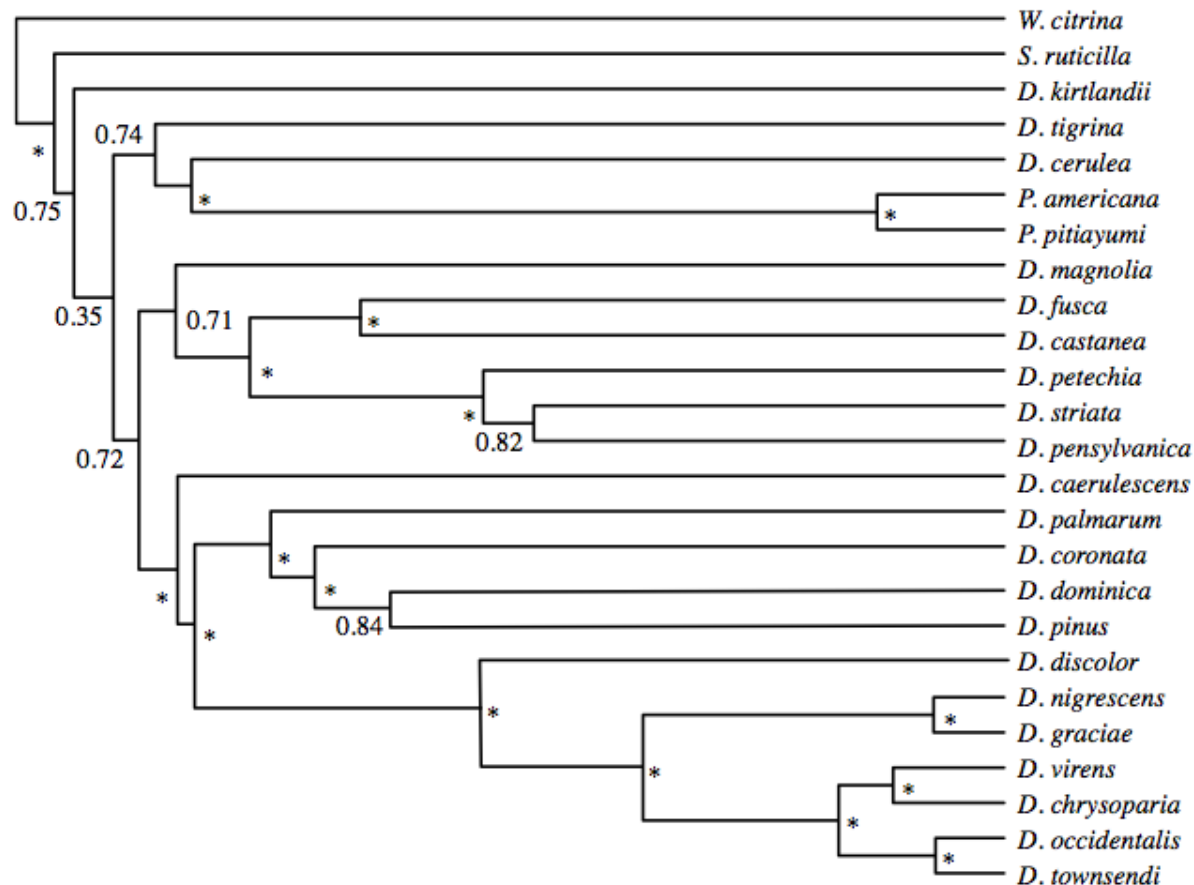
Figure 1. Maximum clade credibility (MCC) tree from Bayesian analysis of all continental North American *Dendroica* wood warbler species. Nodes marked with asterisks are supported by posterior probabilities of more than 0.95. Tree is based on more than 9 kb of mtDNA and nuclear intron sequence. Branch lengths are proportional to absolute time.

$$\lambda(t) = \lambda_0 N_t^{-x}$$

$$\lambda(t) = \lambda_0 \left(1 - \frac{N_t}{K} \right)$$

$$\lambda(t) = \lambda_0 \left(1 - \frac{t}{K} \right)$$

Rabosky and Lovette. Density-dependent diversification in North American wood warblers. Proceedings of the Royal Society of London (2008)

Table 1. Summary of diversification models fitted to the MCC tree (figure 1) for the North American *Dendroica* wood warbler radiation.

model	log likelihood	ΔAIC[a]
density-dependent, exponential	50.47	0
density-dependent, linear	48.42	4.09
linear	45.33	10.27
pure birth	40.45	18.03

[a] Difference in AIC scores between each model and the overall best-fit model.

$$\lambda(t) = \lambda_0 N_t^{-x}$$

$$\lambda(t) = \lambda_0 \left(1 - \frac{N_t}{K}\right)$$

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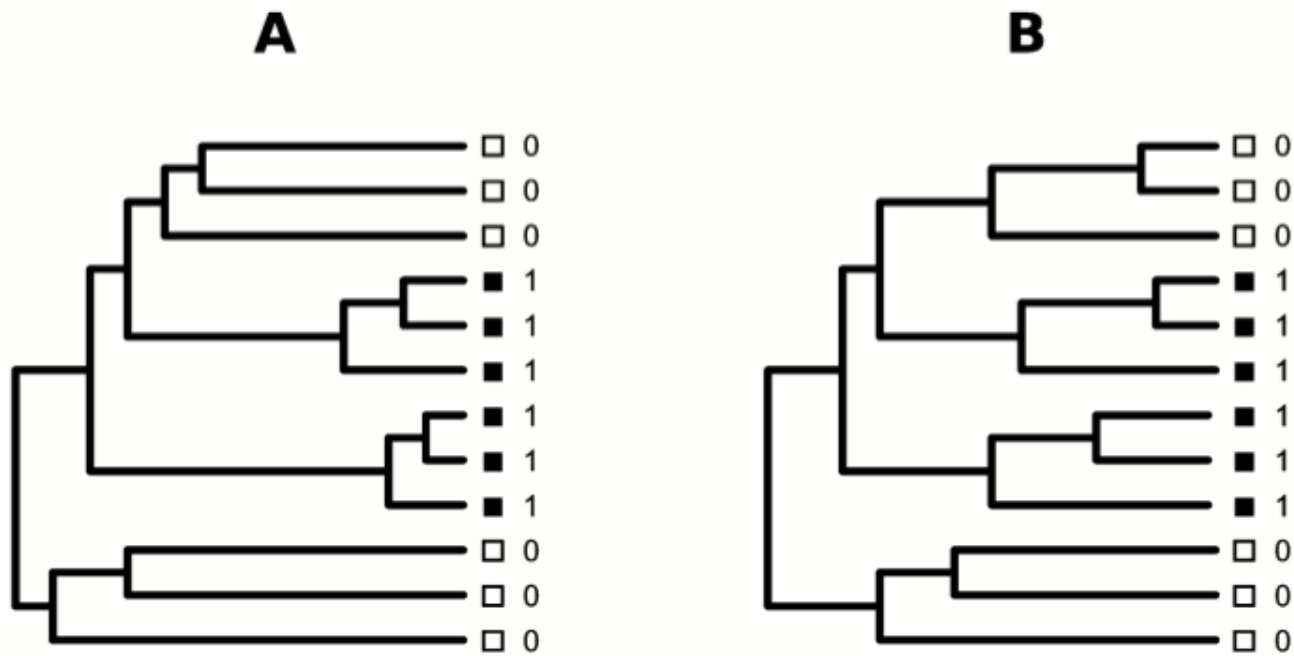
FIG. 1. Hypothetical phylogenies with a candidate key innovation (black boxes, state 1). Absence of the trait, state 0, is denoted by open boxes. The relative durations of terminal branches suggest that the character covaries with diversification rate in (A) but not in (B).
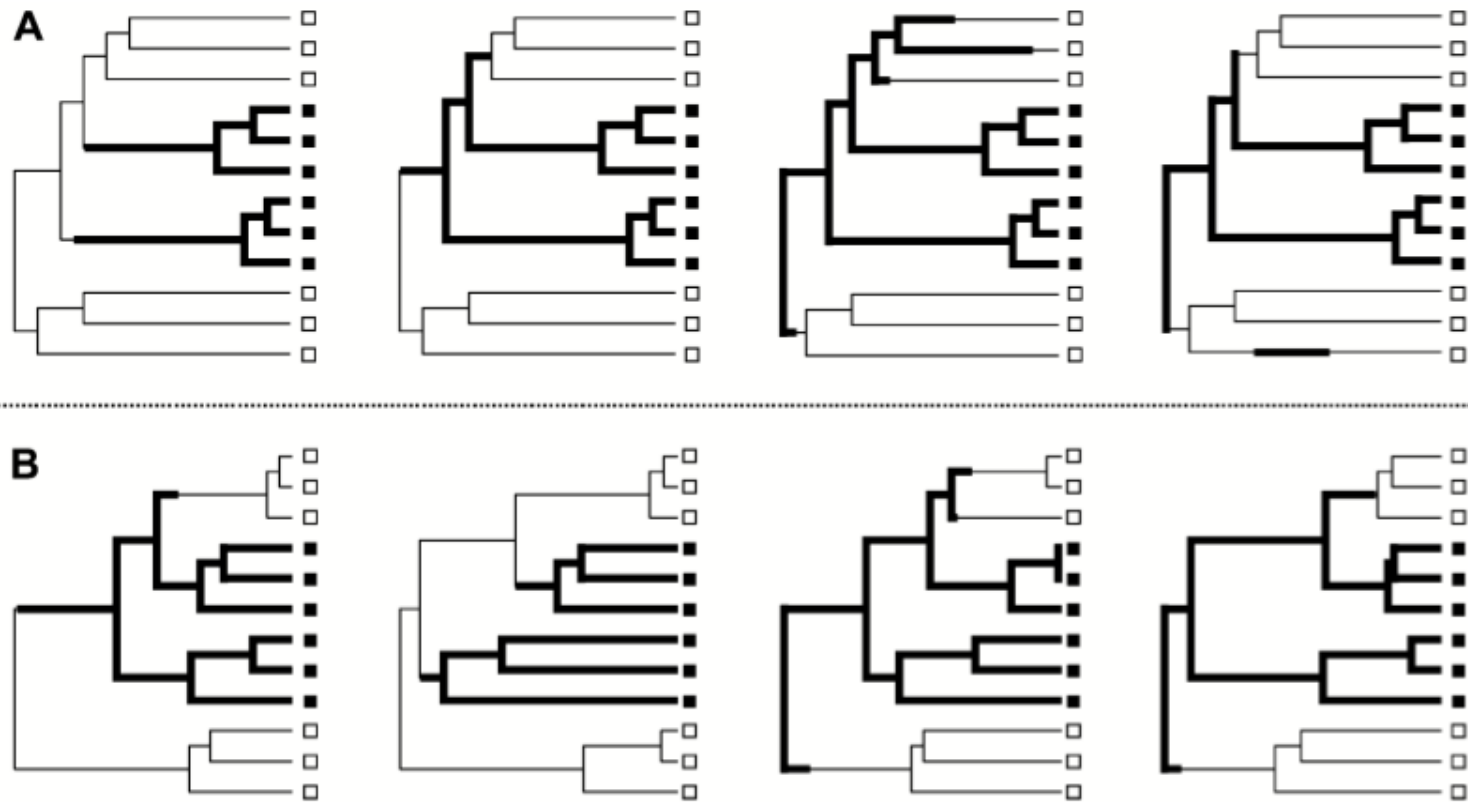
FIG. 2. Example character histories generated by stochastic mapping, with thick lines representing time spent in state 1 (black boxes). (A) Four simulated histories of the character on the tree shown in Figure 1A. (B) One history simulated on each of four different trees that are topologically identical to (A) but have random branch lengths as predicted by the Yule model of cladogenesis. Histories involving fewer character state changes are generated more frequently than those with more changes. For each history, the proposed test measures the state-specific diversification rate (λ_i) as the number of branching events associated with state i, divided by the amount of time spent in that state. Many histories such as those shown in (A) are used to obtain the the test statistic, d. To generate a null distribution of expected values of d, the procedure is repeated for many random sets of branch lengths and histories such as those shown in (B).

Alfaro et al. Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. P Natl Acad Sci Usa (2009) vol. 106 (32) pp. 13410-134