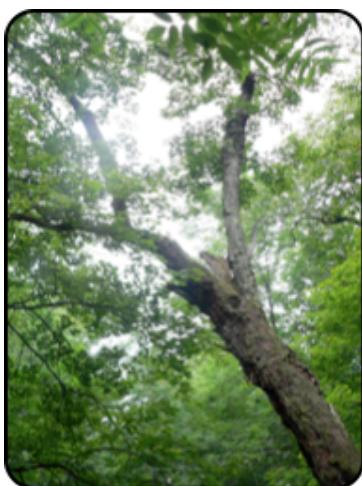
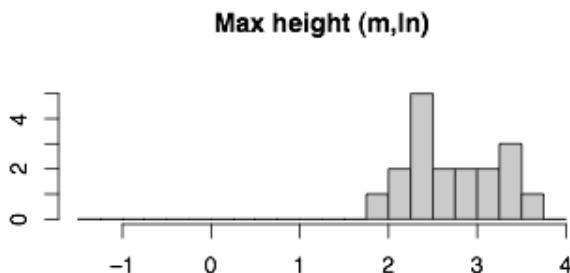


	Low rate of lineage diversification	High rates of lineage diversification
Ancestral trait innovation		
Low rate of trait diversification		
High rate of trait diversification		

	Low rate of lineage diversification	High rates of lineage diversification
Ancestral trait innovation	Evolutionary dead ends (e.g. specialization hypothesis)	Key innovation hypothesis for diversity
Low rate of trait diversification	Niche conservatism	
High rate of trait diversification	no special name? Adaptive divergence? Local adaptation?	Non-adaptive radiation Adaptive radiation

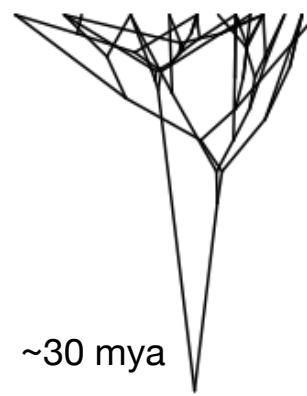
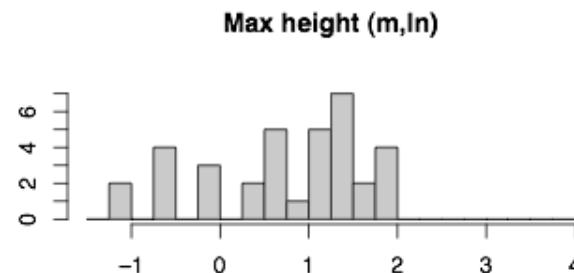
Diversification of height in maples, *Ceanothus* and silverswords

rate = 0.014 felsens

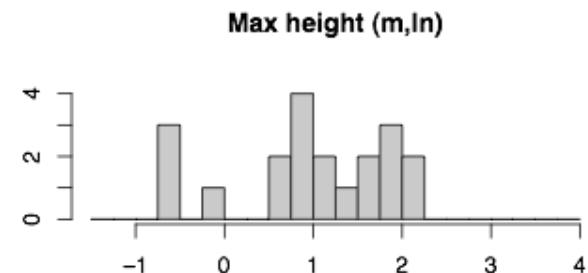


~45 mya

0.10 felsens



0.79 felsens



~5.2 mya



height data: Ackerly, unpubl., Hickman (1993), Wagner (1999)
phylogenies: Renner et al .(2008), Hardig et al. (2000), Baldwin & Sanderson (1998)



Nectar spurs in *Aquilegia*

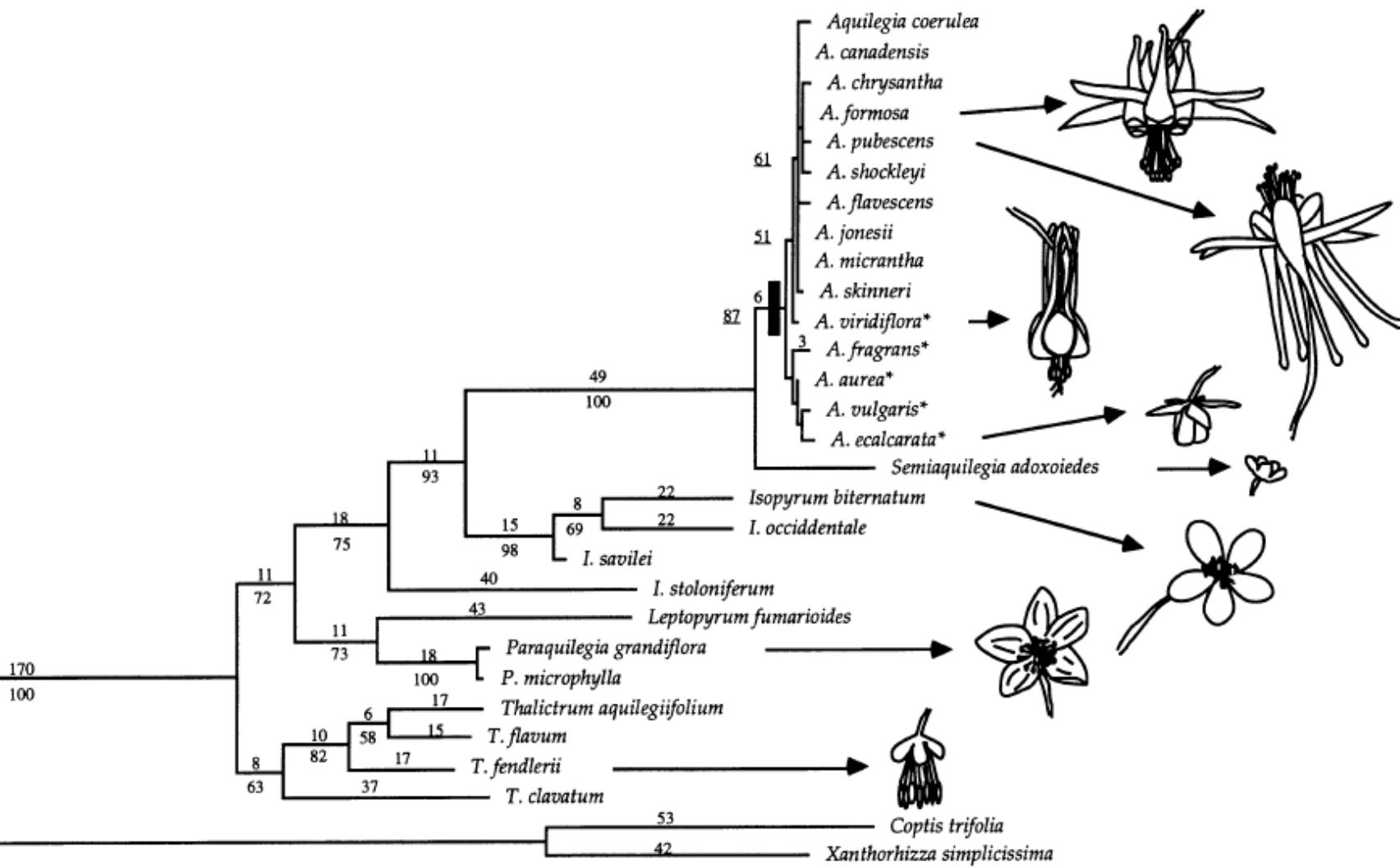


Table 2

NUMBER OF SPECIES IN GROUPS THAT HAVE INDEPENDENTLY EVOLVED FLORAL NECTAR SPURS AND THEIR INFERRED SISTER GROUPS (see references)

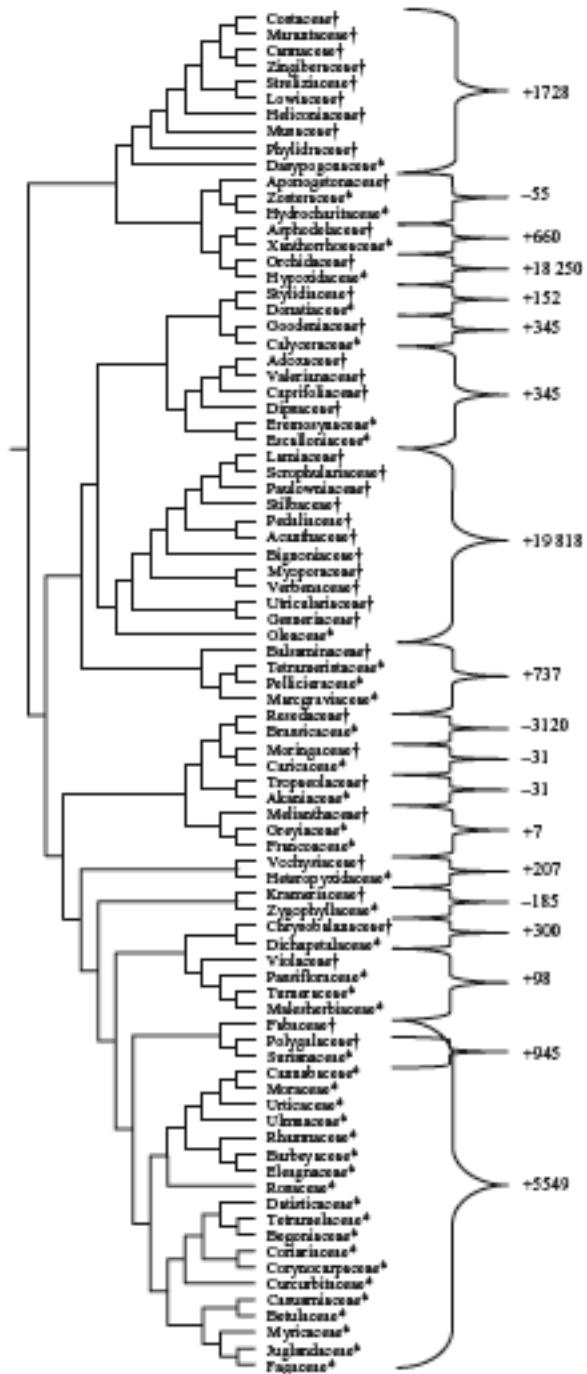
Spurred taxa	Nonspurred sister taxa	No. of spurred spp.: nonspurred spp.	P	References
<i>Aquilegia</i>	<i>Semiaquilegia</i>	70:1	0.014	Hodges and Arnold 1995
<i>Delphinium, Aconitum</i>	<i>Nigella</i>	350:14	0.039	Hoot 1991, 1995
	or	or	or	
<i>Delphinium, Aconitum</i>	<i>Nigella, Actaea, Cimicfuga</i>	350:37	0.095	Johansson and Jansen 1993
Fumariaceae	<i>Hypericum</i>	450:15	0.032	Hoot and Crane 1995
Tropaeolaceae	<i>Akaniaceae, Bretschneideraceae</i>	88:2	0.022	Chase et al. 1993; Rodman et al. 1993
<i>Anchiectia, Corynostylis</i>	<i>Agatea</i>	12:1	0.083	Hodges, Ballard, Arnold, and Chase, unpublished data
<i>Noisettia, Viola</i>	Subset of <i>Hybanthus</i>	401:<150	?	Hodges, Ballard, Arnold, and Chase, unpublished data
Lentibulariaceae	<i>Byblidaceae</i>	245:2	0.008	Olmstead et al. 1993; Bremer et al. 1994
<i>Pelargonium</i>	<i>Geranium, Erodium,</i> <i>Monsonia, Sarcocaulon</i>	280:399	0.588	Price and Palmer 1993

zygomorphic
laterally symmetric

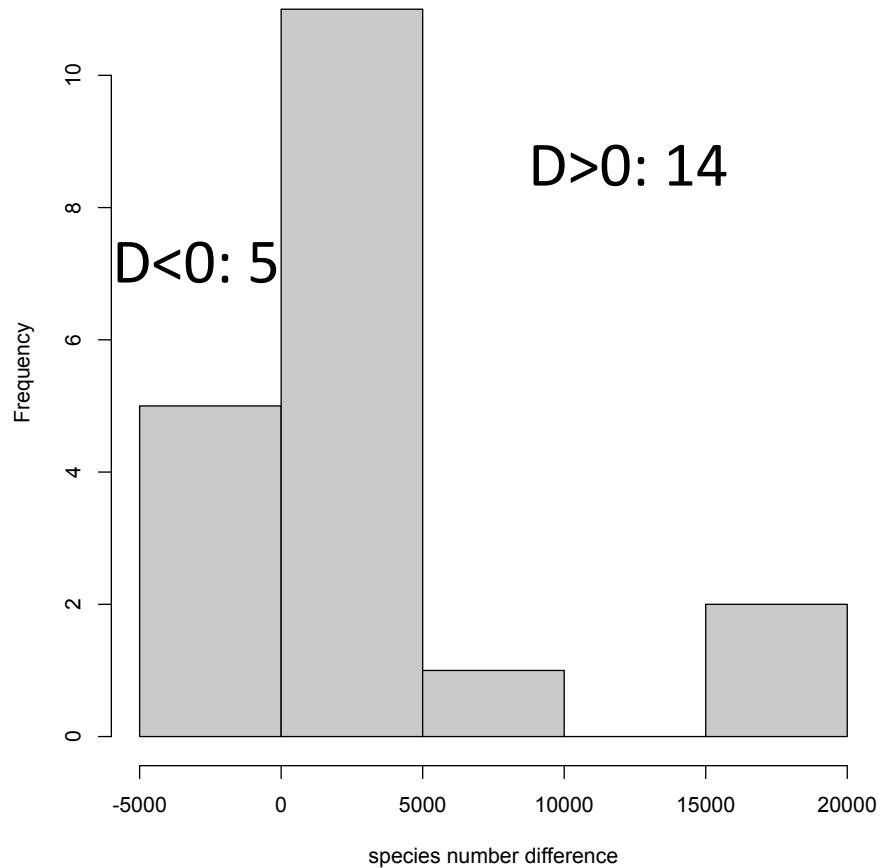


actinomorphic
radially symmetric





diversity of zygomorphic - actinomorphic clades



D>0: 14

D<0: 5

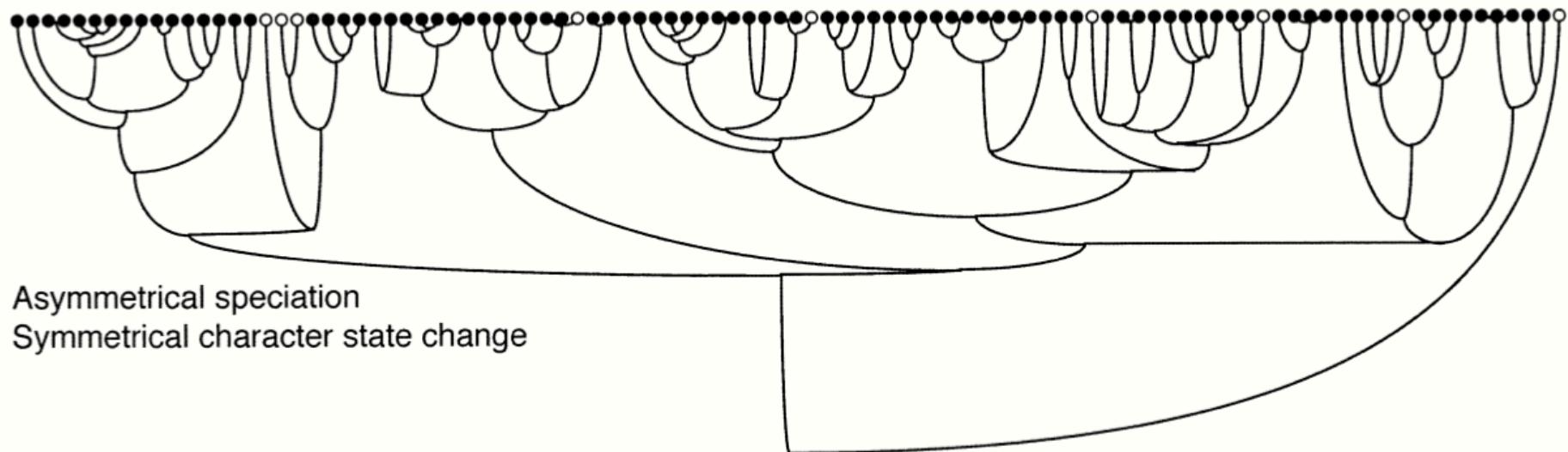


FIG. 1. An example tree and character distribution, simulated with biased speciation. Rate of speciation with state 1 (black) five times higher than rate of speciation with state 0 (white). States at internal nodes are parsimony reconstructions, not the actual ancestral states as simulated.

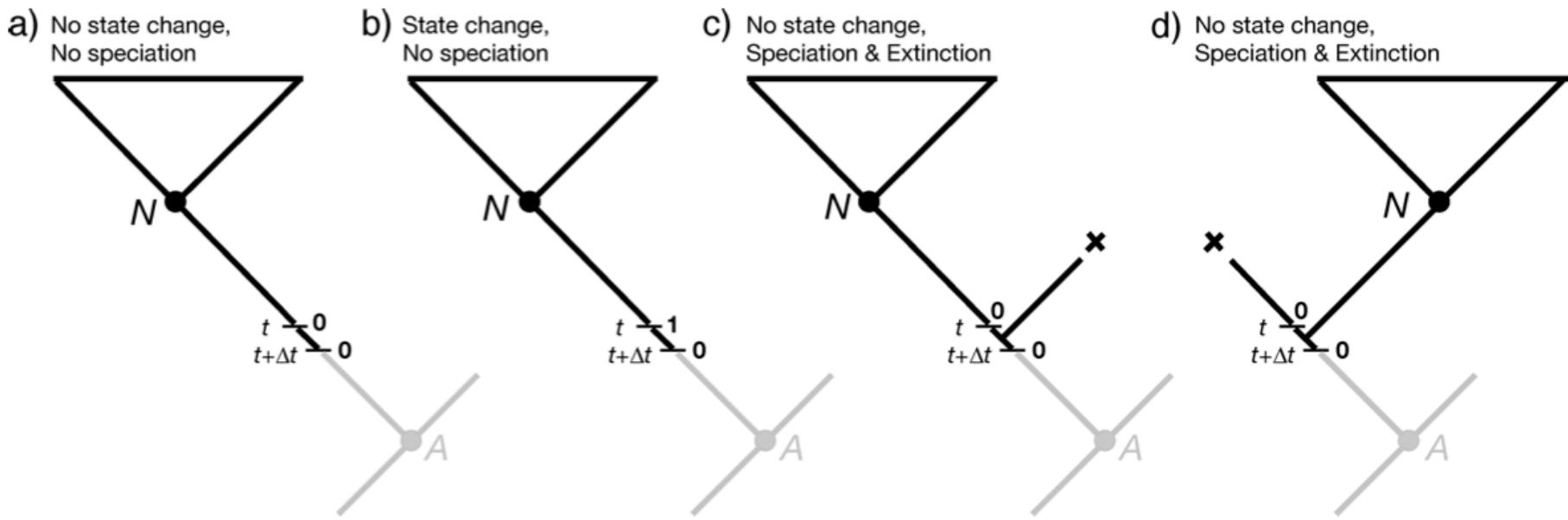
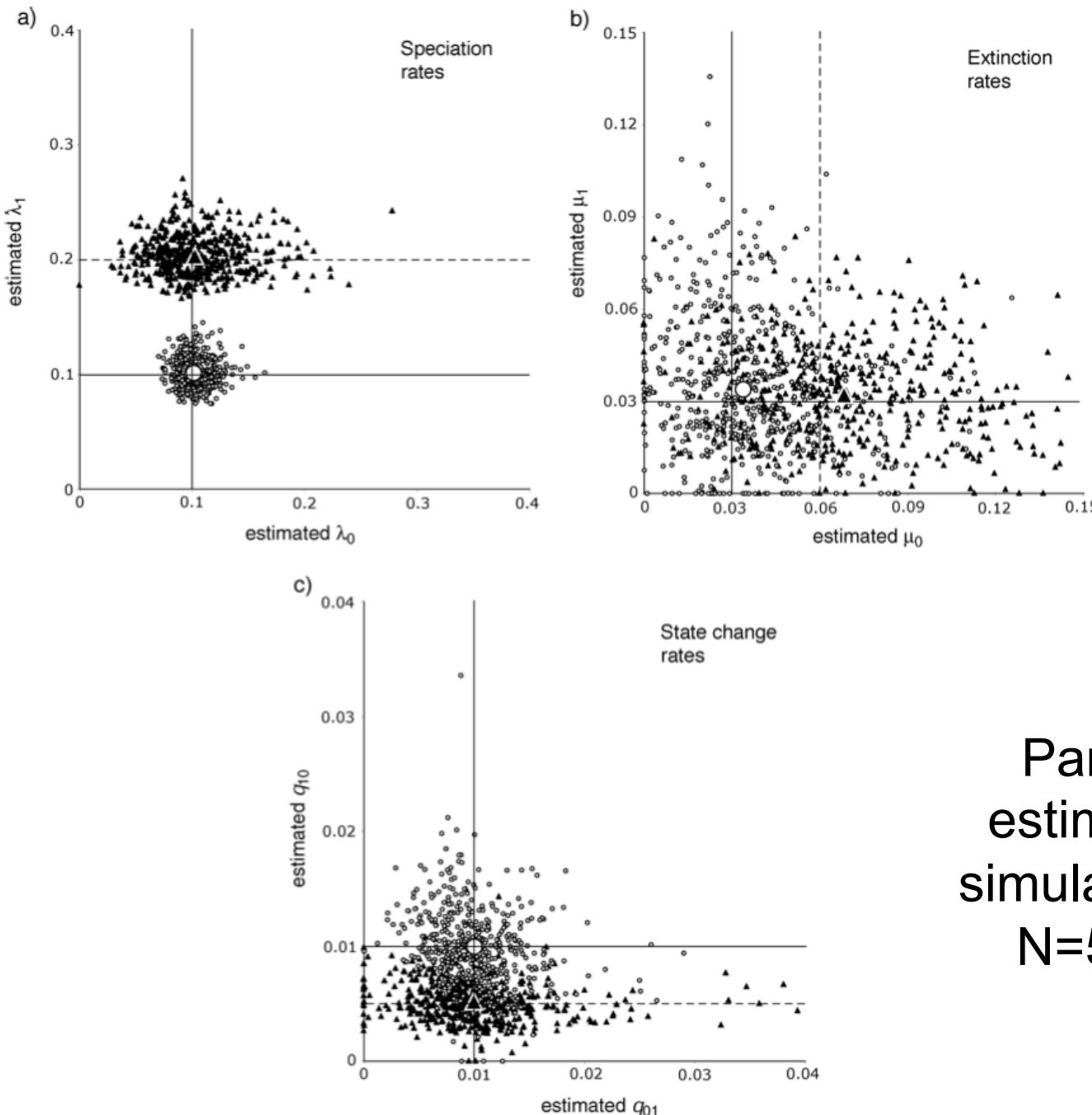


FIGURE 2. Alternative scenarios by which a lineage with state 0 at time $t + \Delta t$ on the branch might yield clade descended from node *N* but no other living descendants.



Parameter
estimation on
simulated trees,
 $N=500$ taxa

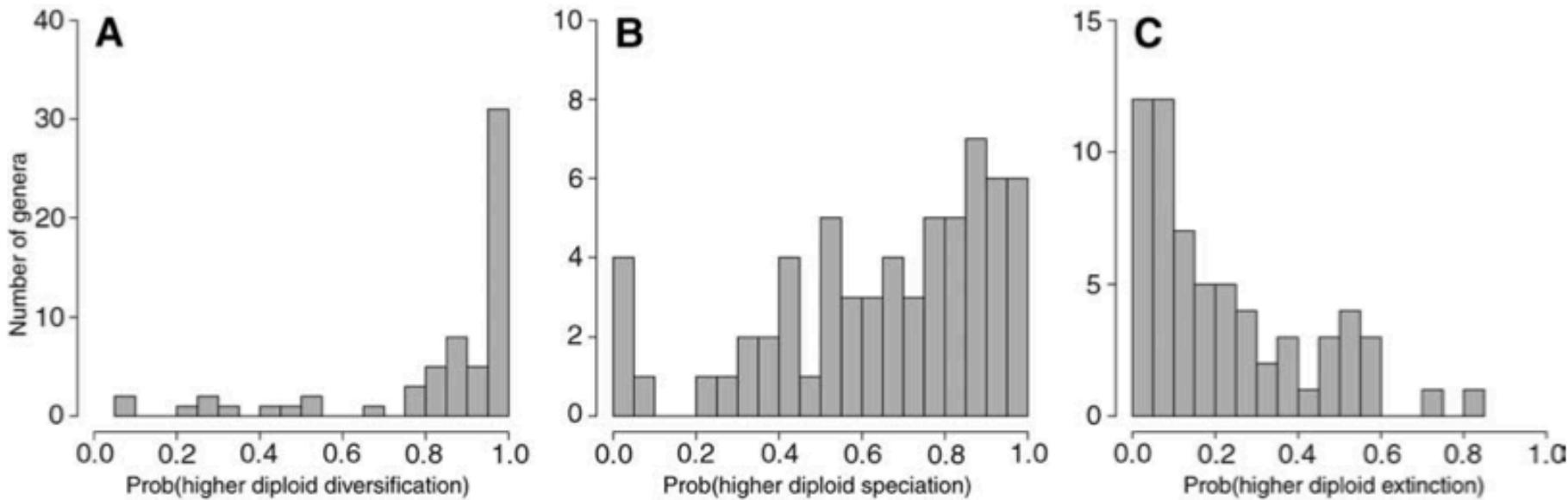
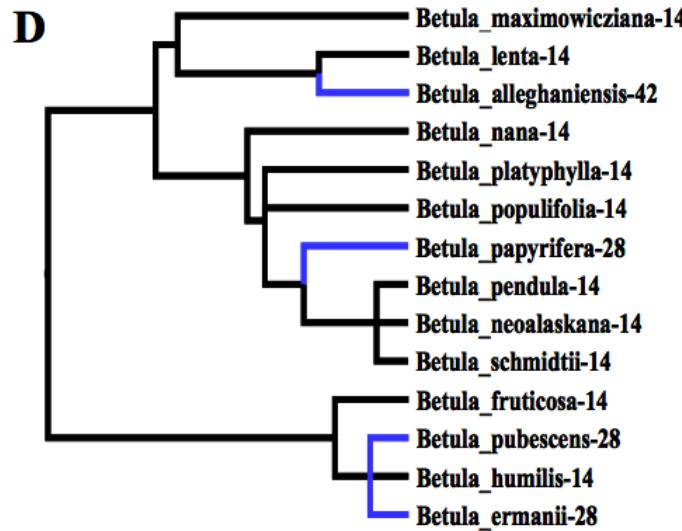
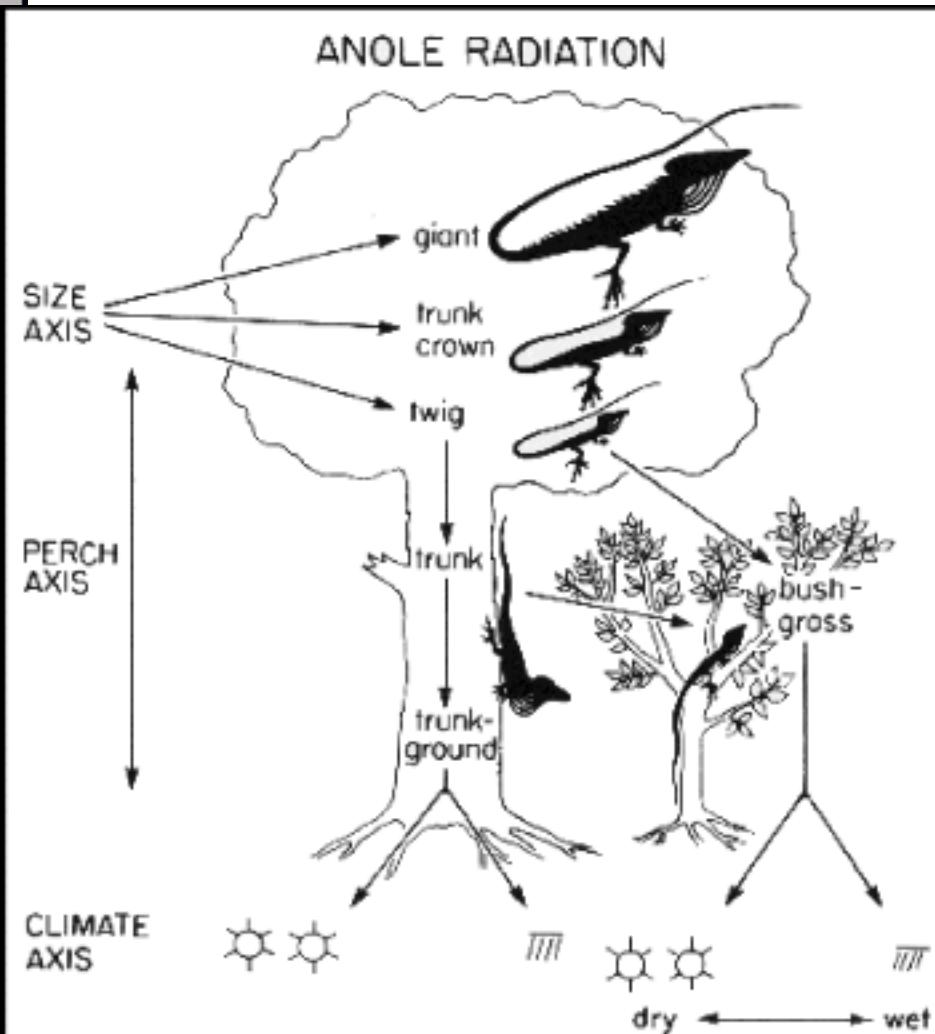
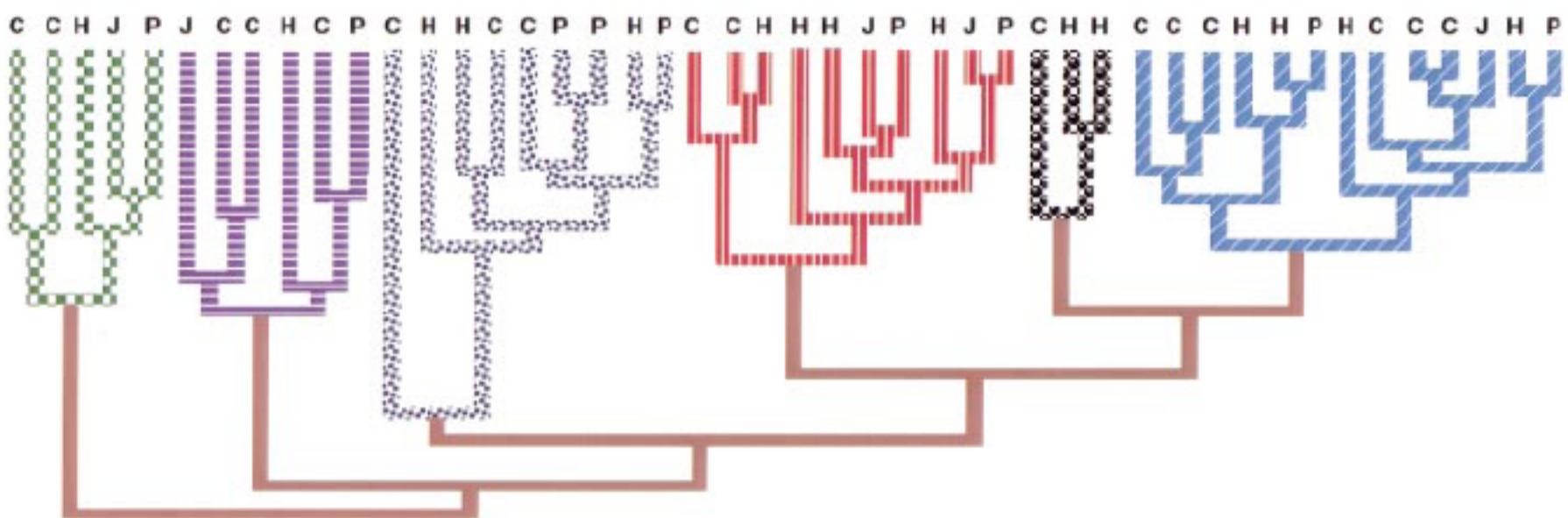
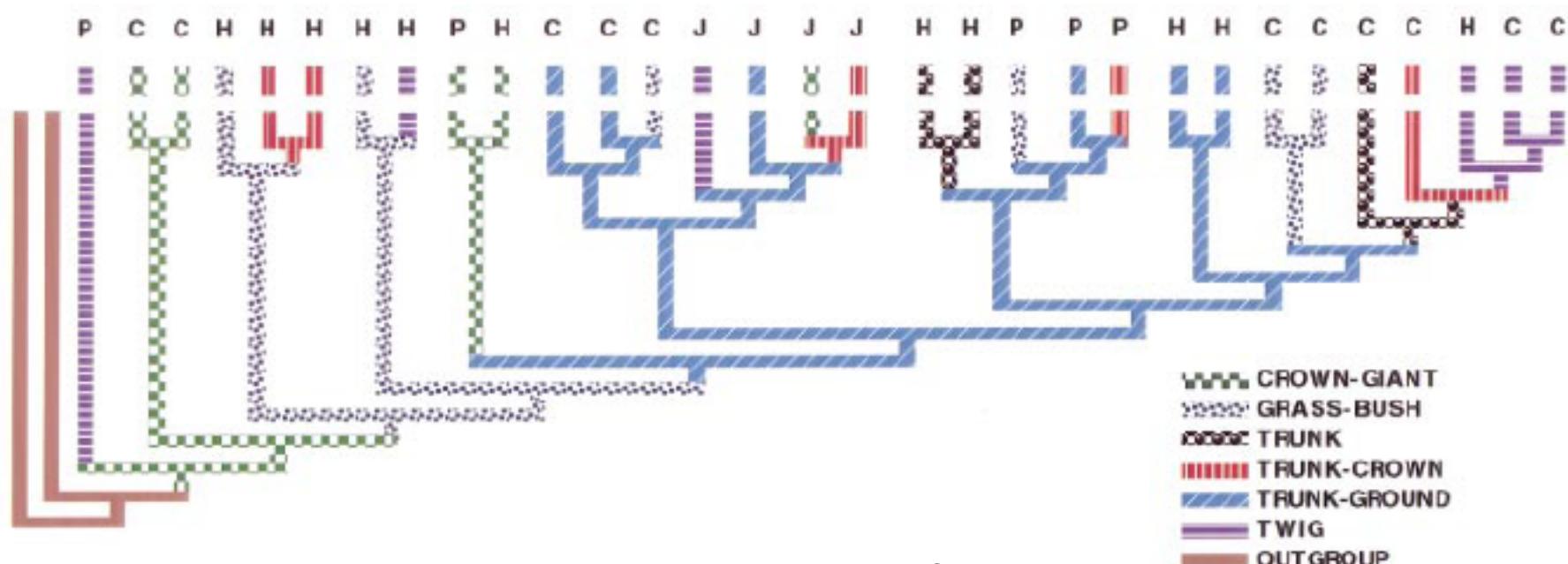
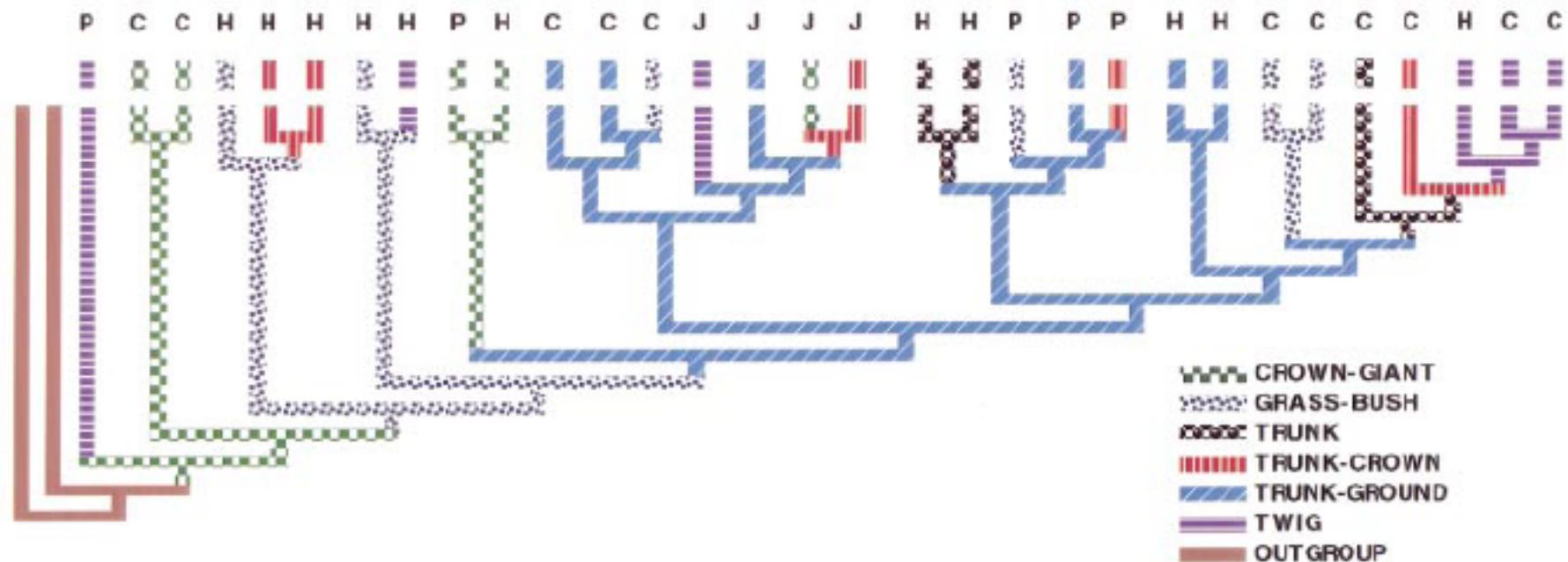
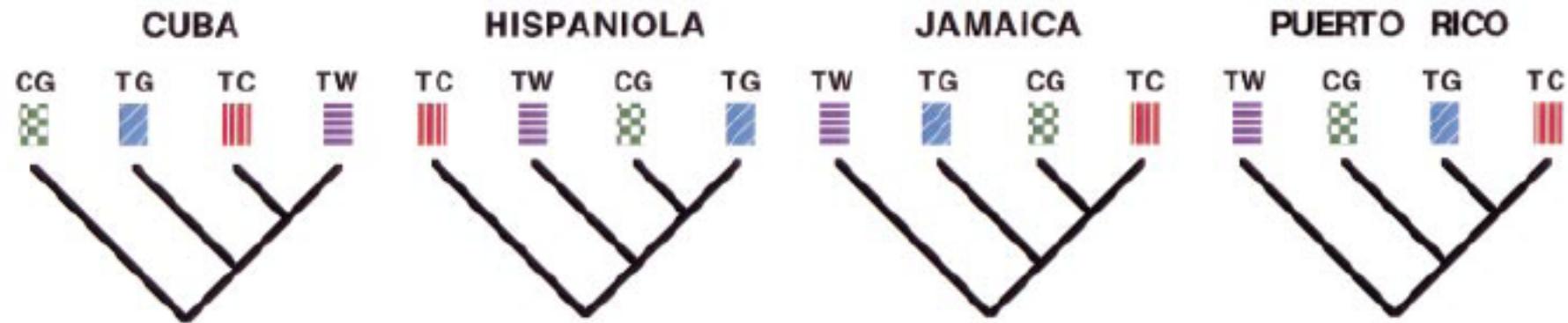


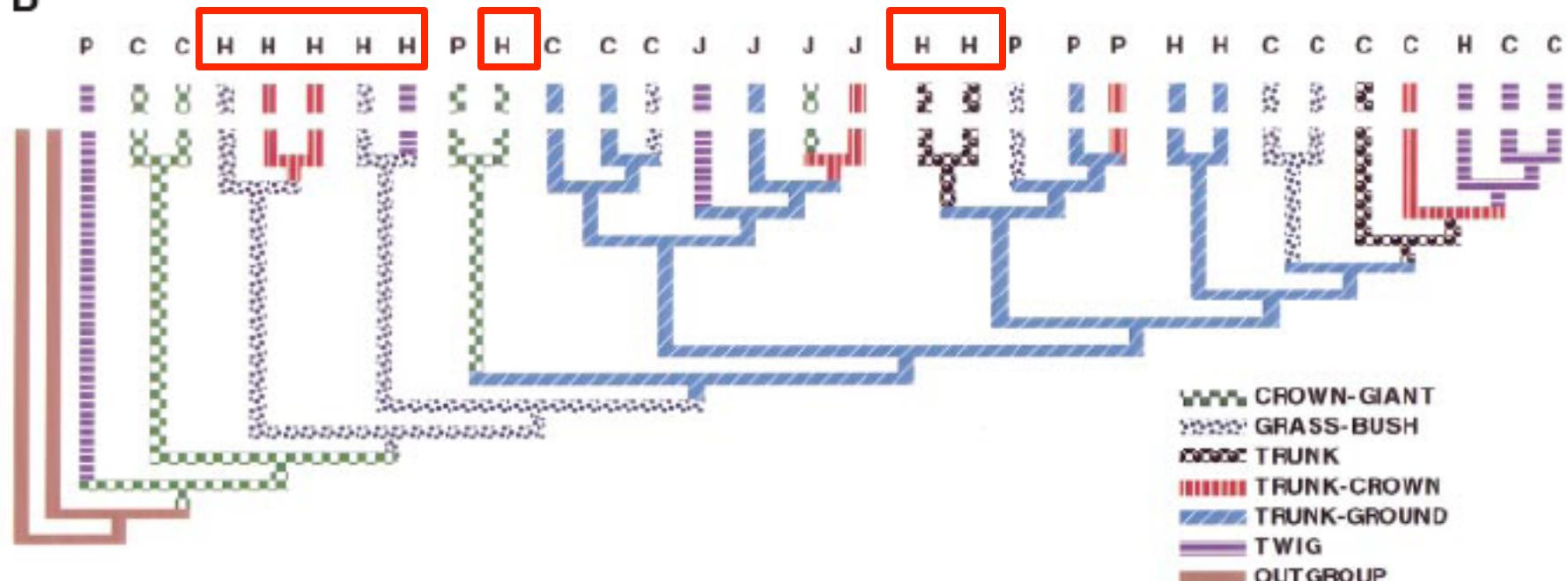
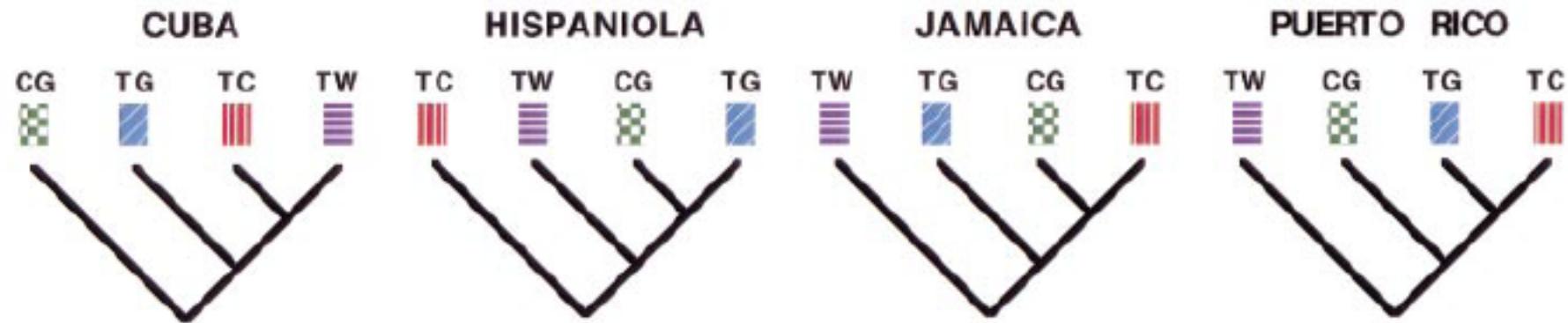
Fig. 1. The posterior probabilities that diploids exhibit higher rates of (A) diversification, (B) speciation, and (C) extinction than polyploids.

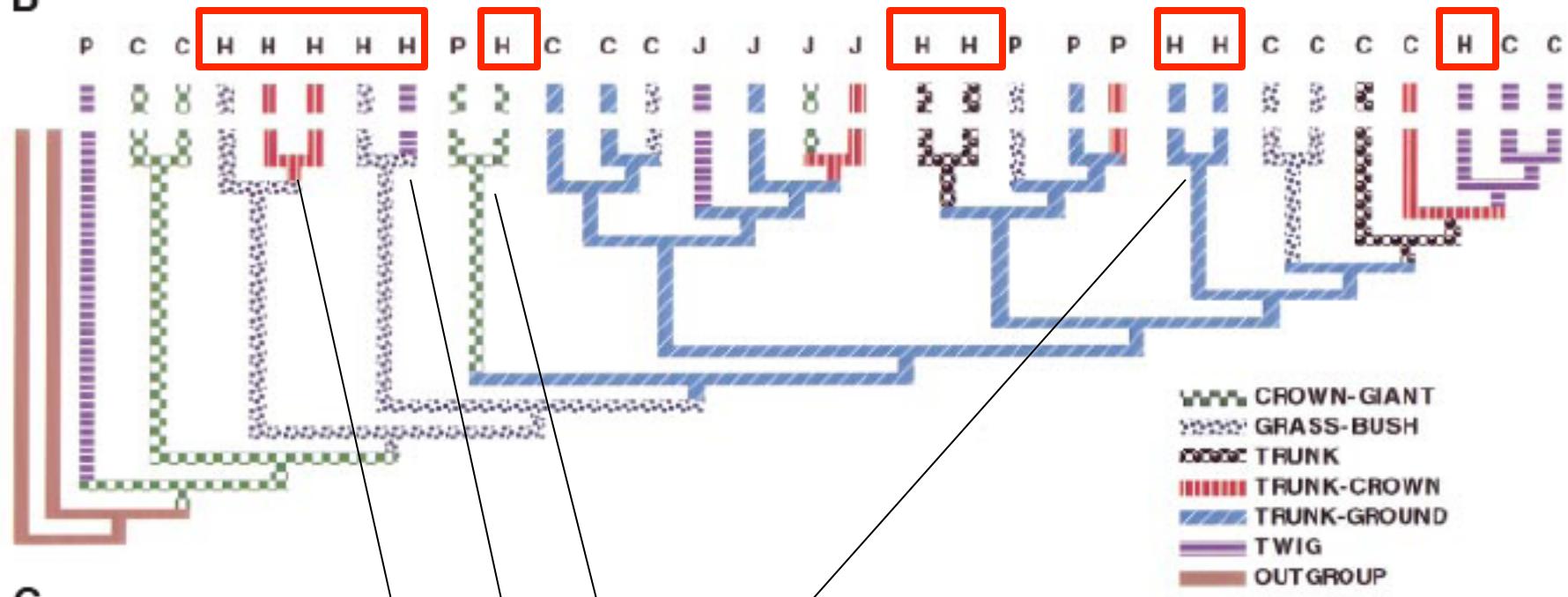
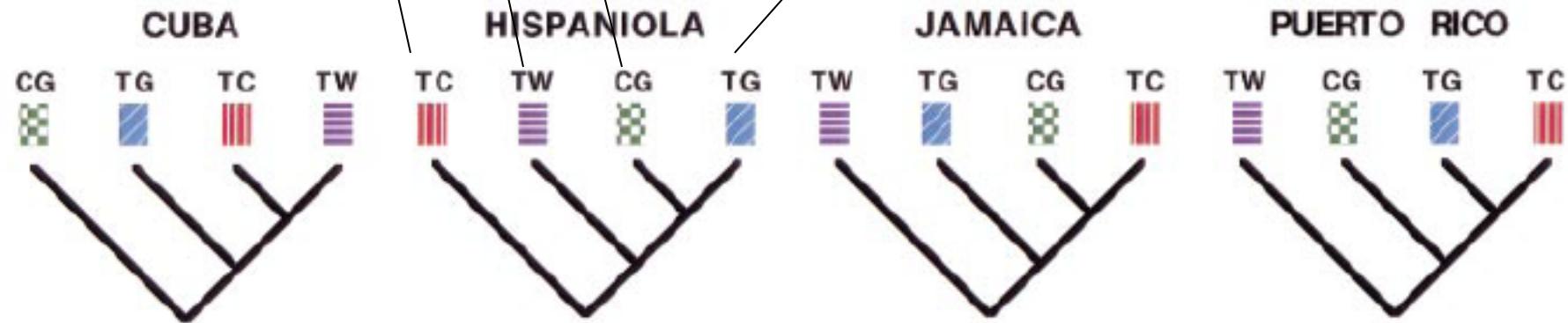
Anolis ecomorphs



A**B****C**

B**C**

B**C**

B**C**

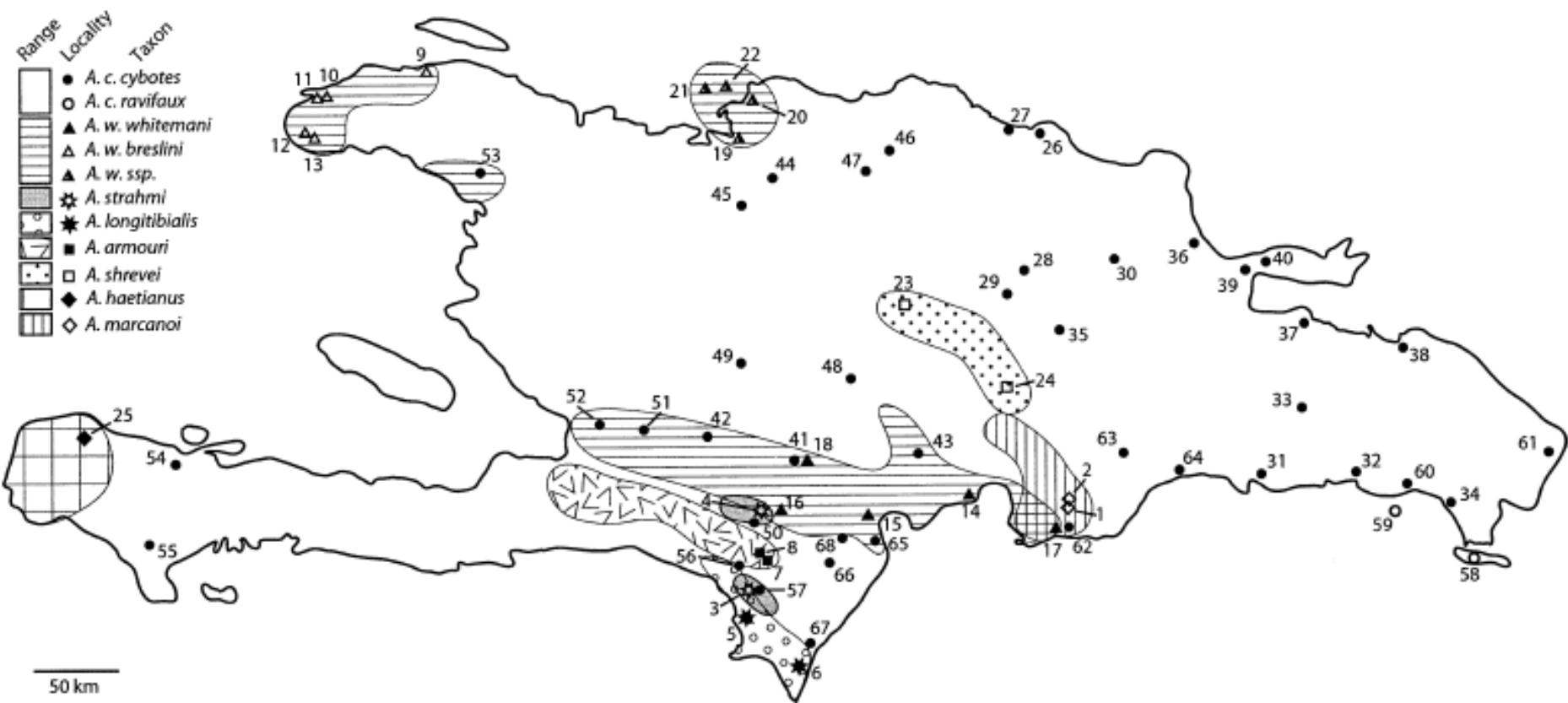
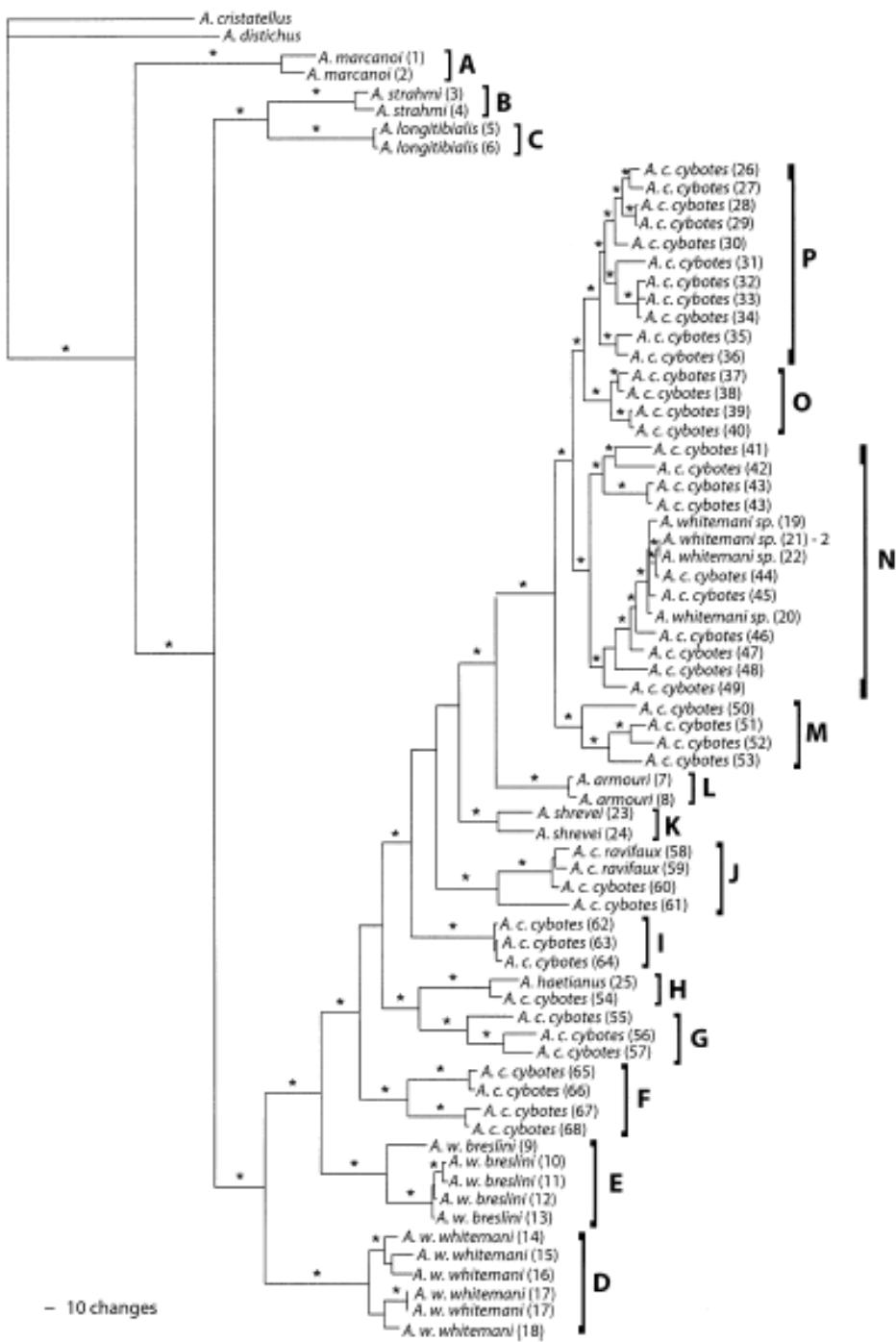


FIG. 1. Geographic ranges of cybotoid anoles based on maps of Schwartz and Henderson (1991) and sampling localities for populations included in our phylogenetic study. *Anolis cybotes cybotes* exists everywhere except high altitudes (above 1650 m) and extremely xeric regions in western Haiti and the southern Barahona Peninsula.



lineage diversity index = sum(obs – exp)
positive value = early accumulation of lineages

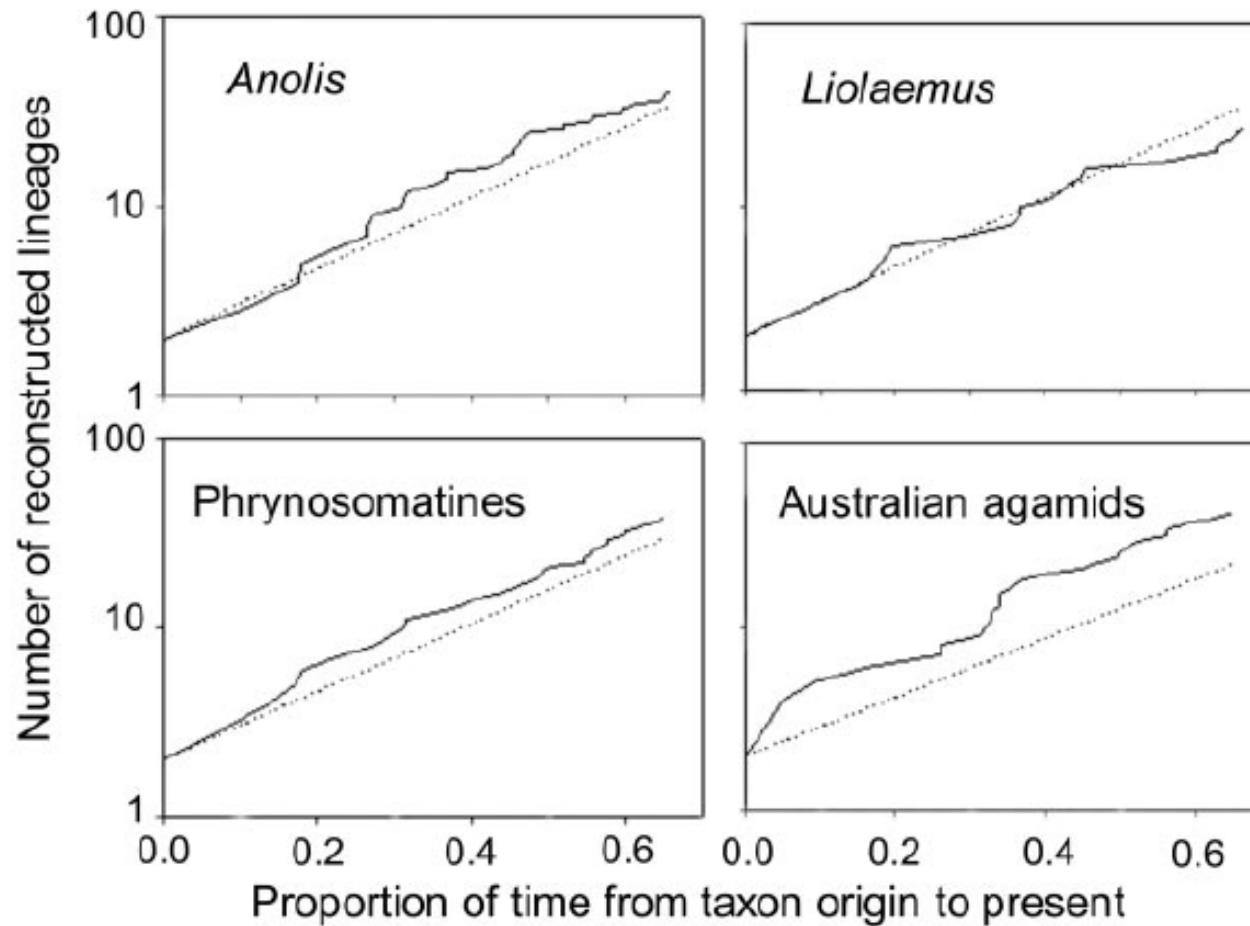


Fig. 1. Lineage accumulation curves for four lizard taxa compared with expectations under the null pure-birth model. Time is expressed as a proportion of the total time since the first cladogenetic event inferred for the taxon. Only the first two-thirds of each phylogeny is shown. Expected curves are obtained using an exponential model with the first branching in a clade set to time = 0 and the number of extant species (Table 1) set to time = 1. Solid line, actual number of reconstructed lineages for the clade; dashed line, expected number of lineages under the null pure-birth model.

Measuring niche conservatism - phylogenetic signal

Blomberg's K: measures degree of similarity among close relatives, relative to expectations based on Brownian motion

convergence

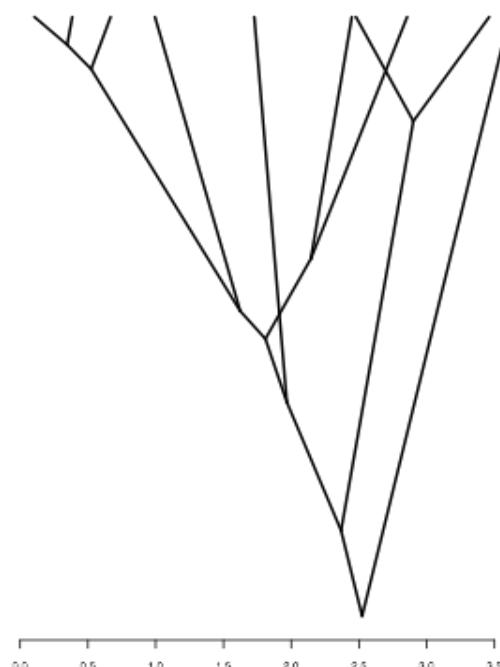
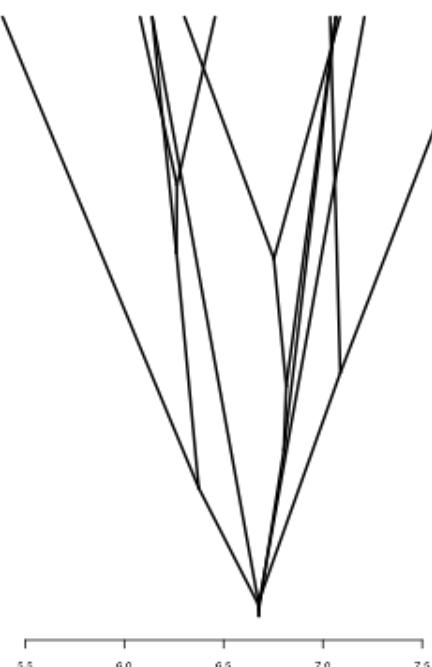
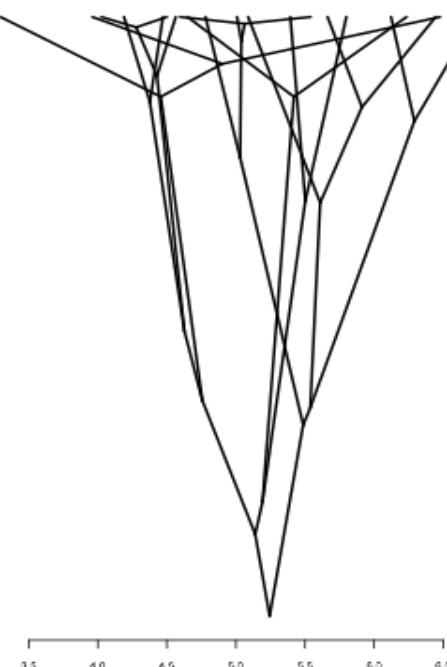
$$K \ll 1$$

brownian

$$K \sim 1$$

conserved

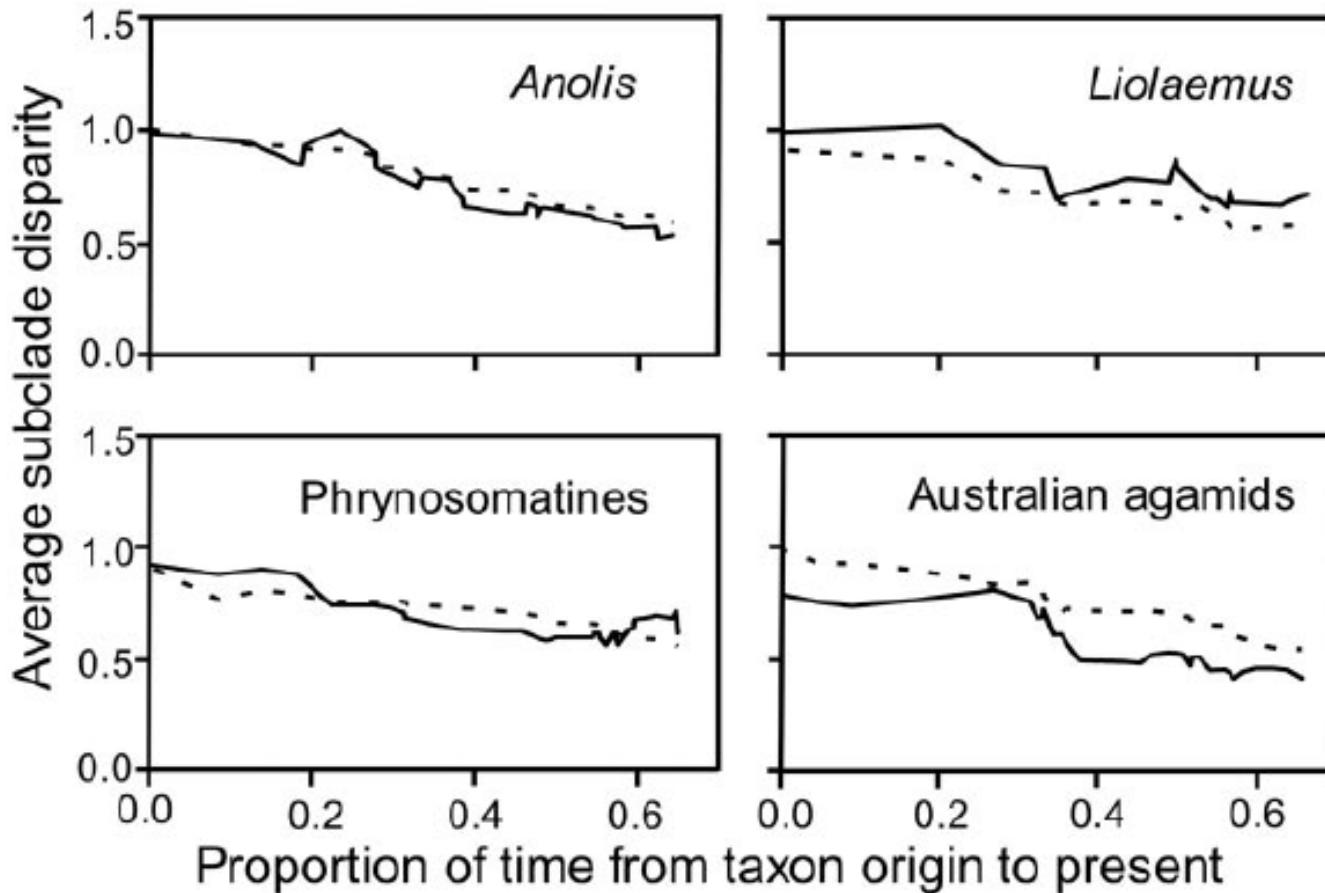
$$K \gg 1$$



mean subclade disparity/total disparity

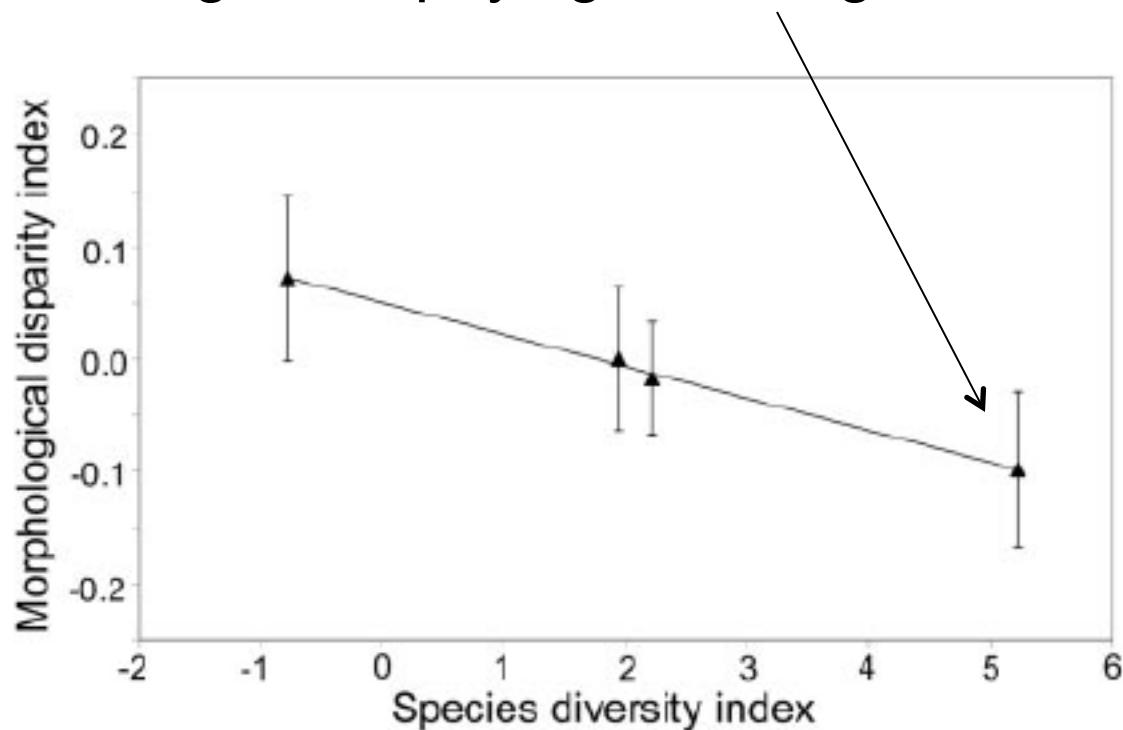
high values = high within group relative to among group variance = low phylo signal

Morphological disparity index = sum(obs-exp): positive values= deep clades span similar trait range, i.e. convergence across clades and low signal

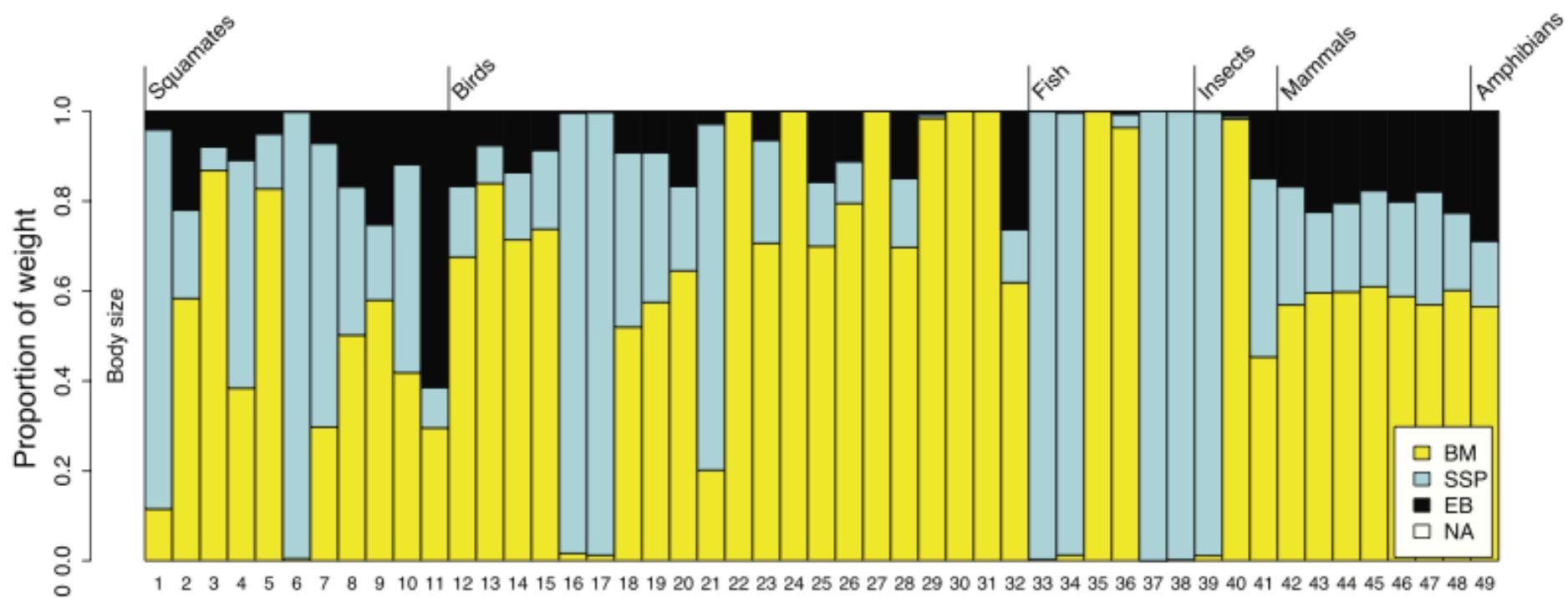


early diversification -> greater phylogenetic signal

Fig. 3. Relationship between LDI and MDI. Data show a highly significant negative correlation (19) ($r = -0.998, P = 0.004$). A variety of analyses indicate that the among-clade relationship between LDI and MDI is well-supported and robust to relaxation of assumptions concerning mode of character evolution, sampling, and extinction (19) (figs. S6 and S7; 95% confidence limits were established by calculating MDI separately for each of the 1000 simulations of character evolution that were used to calculate MDI for each clade). This result is also significant if γ (corrected for incomplete sampling by subtracting the mean of the γ values in the MCCR test simulations and dividing by the standard deviation of these simulation γ values) and δ values are used for each clade (standardized γ versus δ_{MLE} , $r = 0.97, P = 0.03$; in this analysis, the correlation is positive because more negative values of γ reflect a slowdown in diversification, corresponding to larger values of our LDI statistic).



Assign proportional weighting of alternative models that best fit data



Are there differences among clades in trait diversification (= disparification) rates

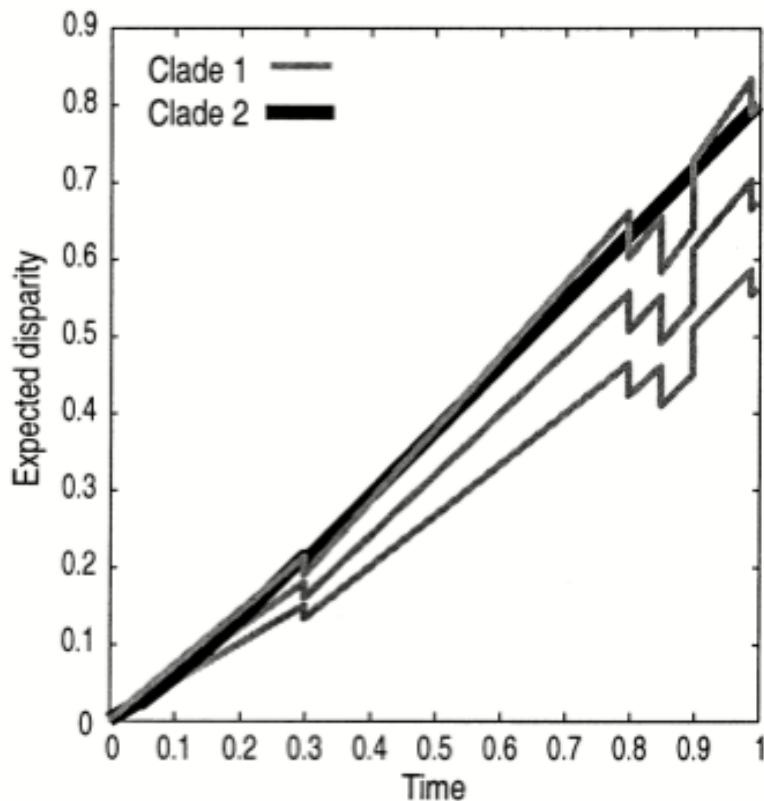


FIG. 1. Equation 1 was used to predict variance in terminal trait values within clade 1 and clade 2 through time. For clade 2, the Brownian rate parameter was always 1.0. For clade 1, the rate parameter took on values of 1.0 (the lowest line), 1.2 (the middle line), and 1.425 (the top line). Note that though the two clades have the same age and same number of taxa, clade 2 has a higher tip disparity when the rates of morphological evolution are equal and even when clade 1 has a 20% faster rate. Clade 1 has a greater amount of tip disparity when its rate is greater than 1.425 times that of clade 2.



Nested ML test:
Does a 2 rate model provide a
sufficiently better fit than a 1
rate model?

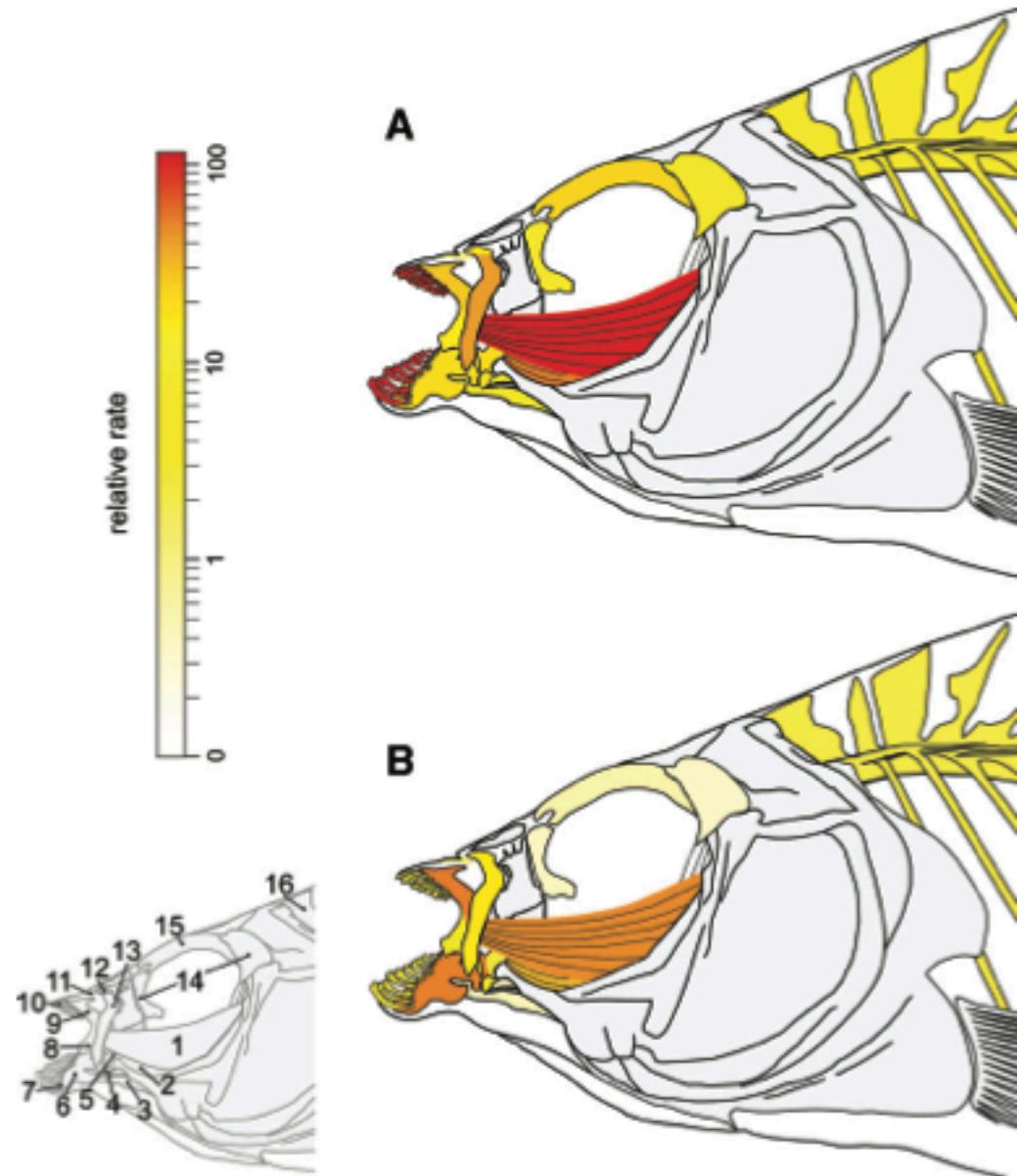


Figure 3. Cyprinodon heat map with colors indicating the rates of morphological diversification in the (A) Lake Chichancanab and (B) San Salvador Island clades relative to all other Cyprinodontidae for 16 functional traits (see Table 1). Numbered diagram corresponds to numbered descriptions of the traits in Methods.

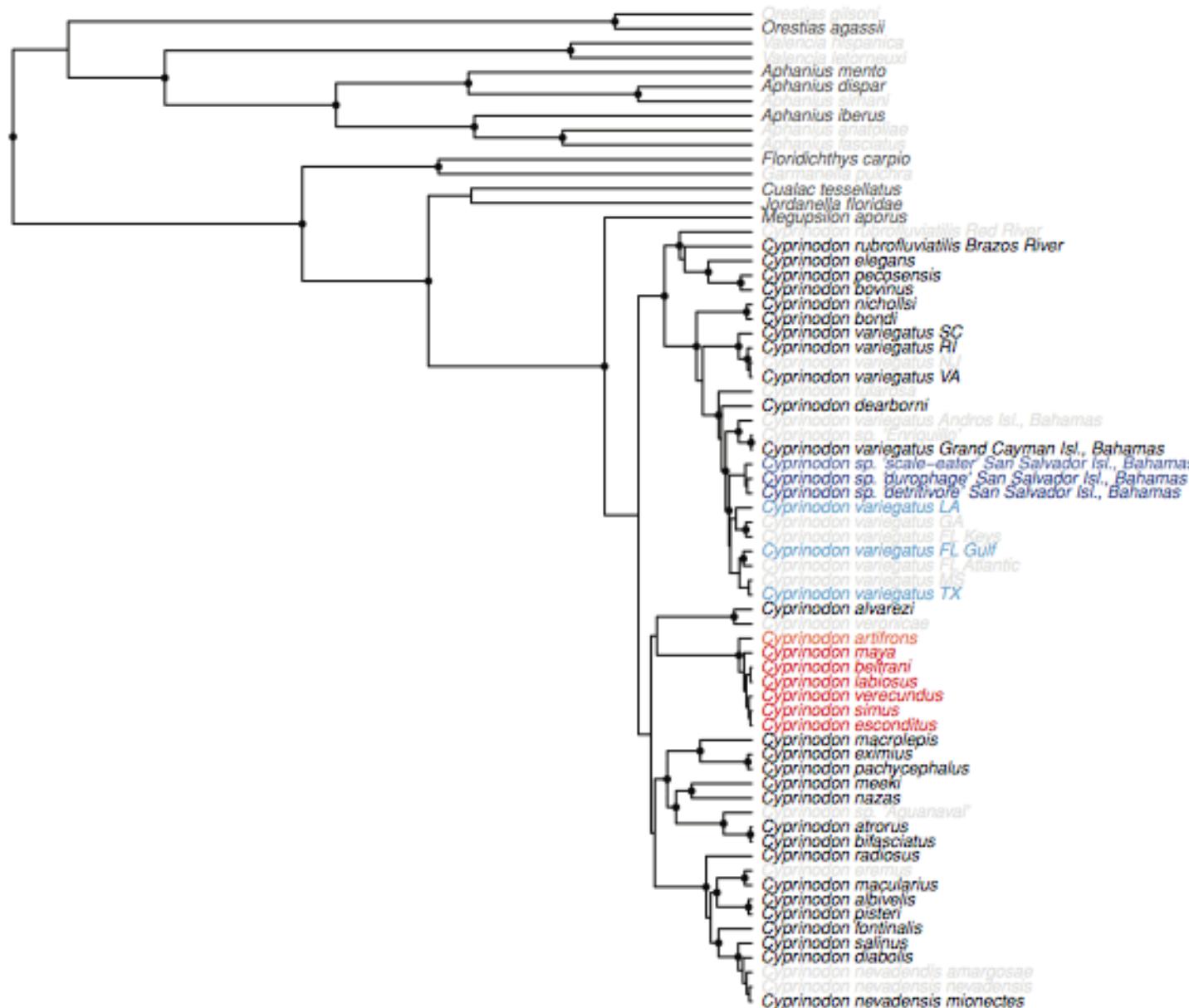


Figure 1. Maximum sum of credible clades phylogeny for the Cyprinodontidae with branch lengths in units of relative time. Nodes supported by a posterior probability ≥ 0.95 are indicated with a black dot. The Chichancanab clade is shown in red, the San Salvador clade in blue, the nearest allopatric sister species to each sympatric clade in lighter shades of red and blue, respectively, additional measured *Cyprinodon* in black, measured outgroups in dark gray, and unmeasured taxa included in phylogenetic analyses in light gray. Phylogenies were estimated under a relaxed molecular clock with a fixed mean clock rate using BEAST.

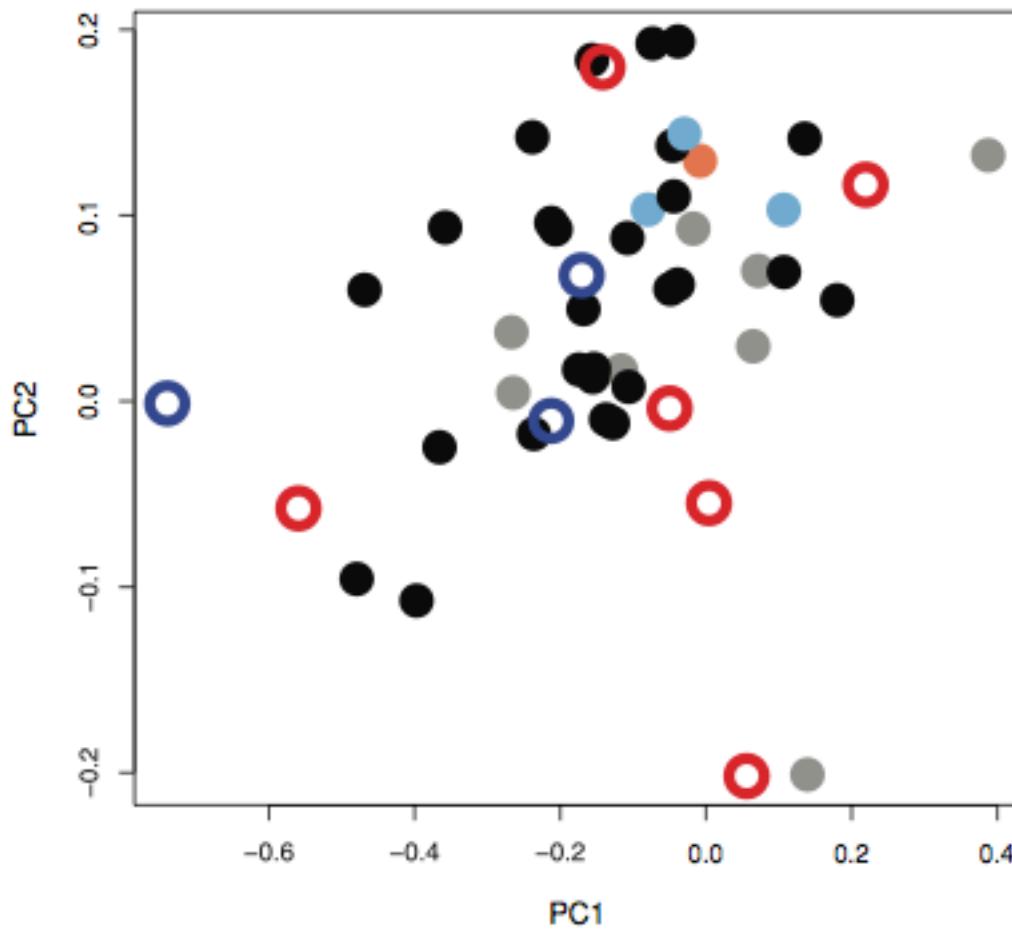


Figure 2. First two principal components of morphological variation (50.3% of total variation) in the phylogenetically corrected morphospace for 16 size-corrected traits among Cyprinodontidae, including the Lake Chichancanab radiation (○), San Salvador Island radiation (○), sister species to the Chichancanab clade (●), sister species to the San Salvador Island clade (●), all other *Cyprinodon* species (●), and outgroups (●).

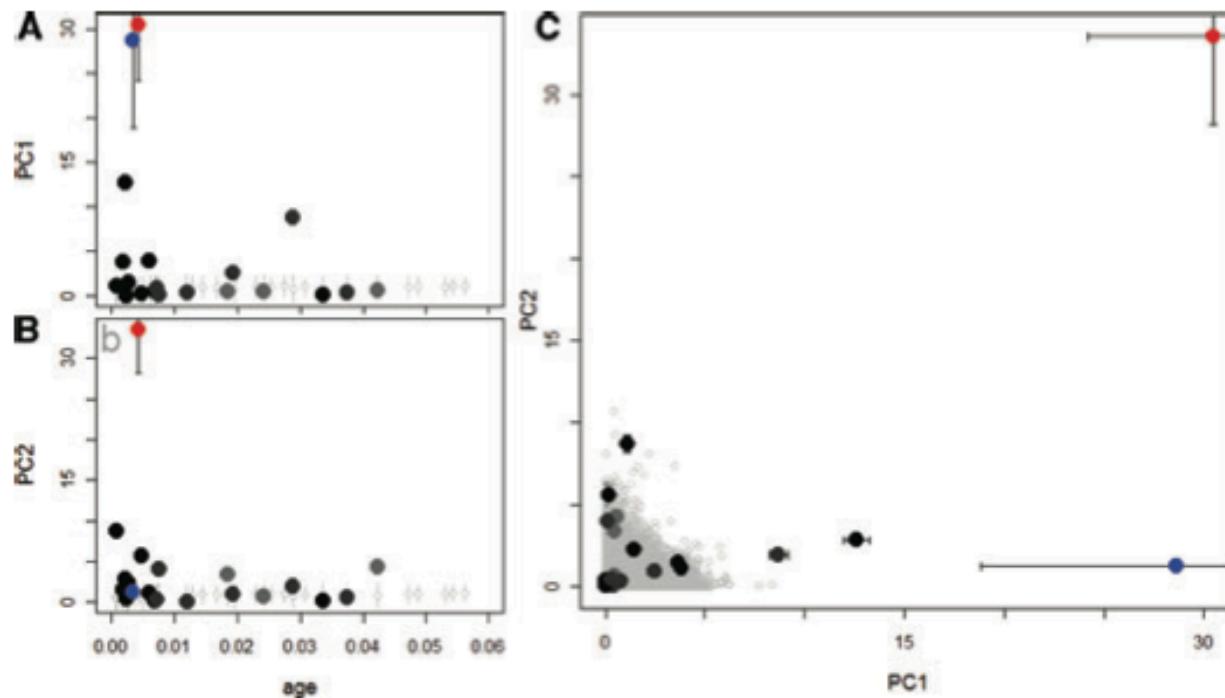
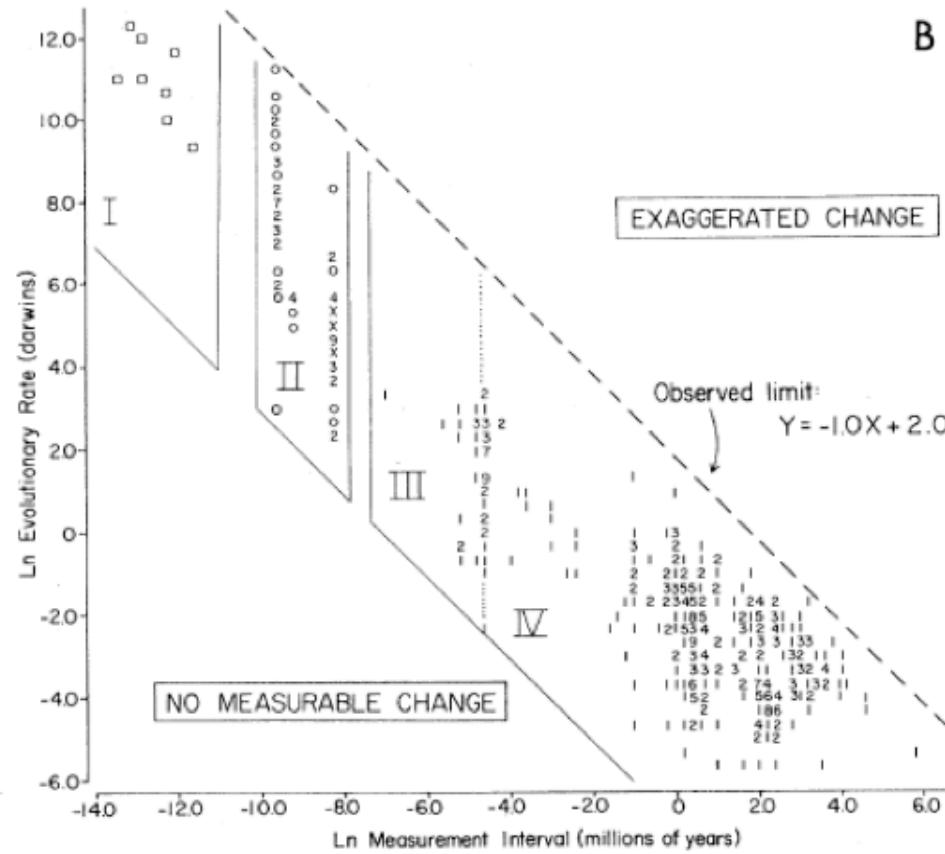


Figure 4. Relative rates of morphological diversification ($\text{mean} \pm \text{SE}$) on the (A) first and (B) second principal component axes relative to clade age. (C) The morphological diversification rate-space ($\text{mean} \pm \text{SE}$) on the first and second principal component axes. Observed rates are indicated for the Chichancanab (○) and San Salvador (●) clades, and all other two-species (●), three-species (●), and four-species (●) *Cyprinodon* clades measured; note that points are not statistically independent due to nested clade structure and shared histories. Means and standard errors were calculated by repeating rate analyses for 100 trees sampled from the stationary MCMC distribution. (A, B) Simulated relative rates of morphological diversification ($\text{mean} \pm 2\text{SD}$) under a Brownian motion model for 1000 iterations are shown in gray (●). (C) Each simulation is indicated by one point (●) in the morphological diversification rate-space.

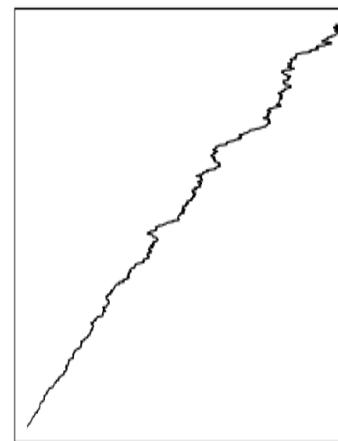
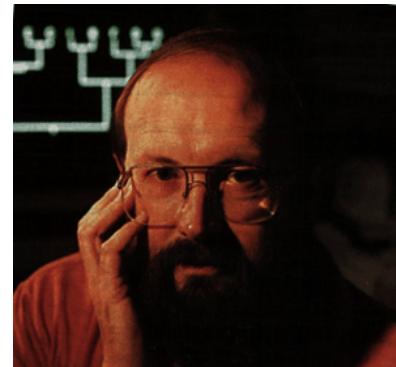
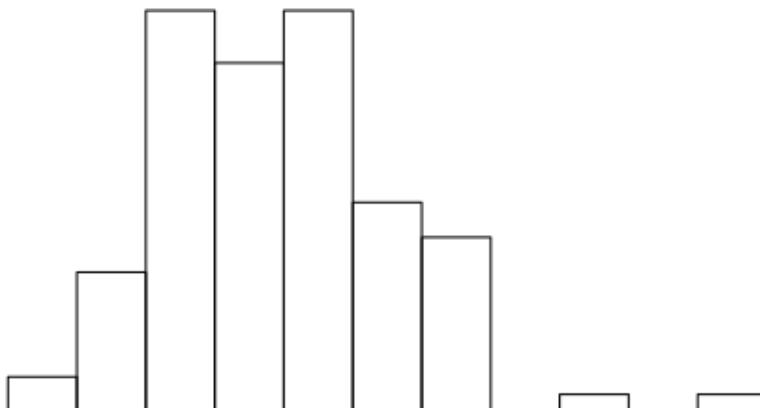
Quantifying rates of phenotypic evolution

$$1 \text{ darwin} = \frac{\text{change by factor of } e}{\text{million yrs}}$$



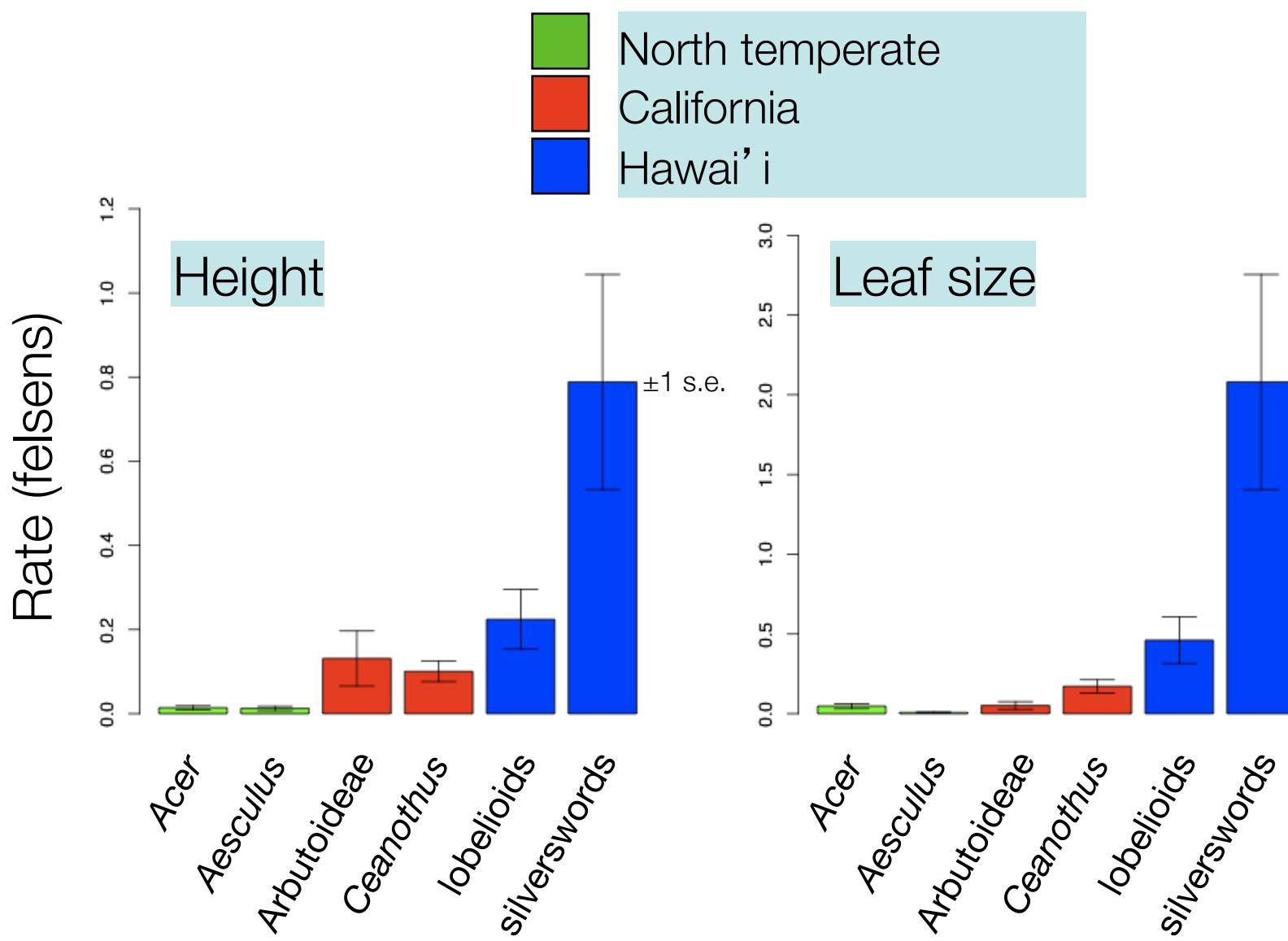
Rates of phenotypic diversification under Brownian motion

$$1 \text{ felsen} = \frac{1 \text{ Var}(\log_e(\text{trait}))}{\text{million yrs}}$$



var(x)

Rates of phenotypic diversification (estimated for Brownian motion model)

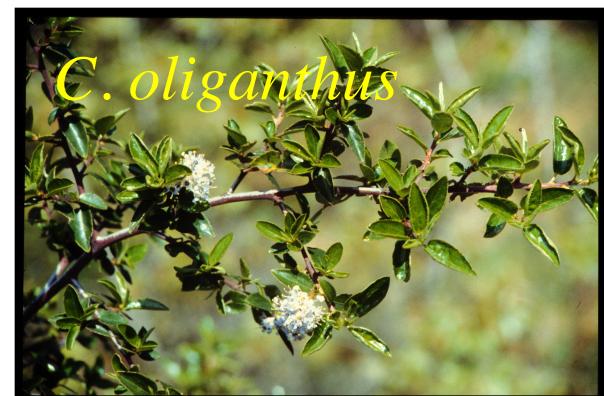
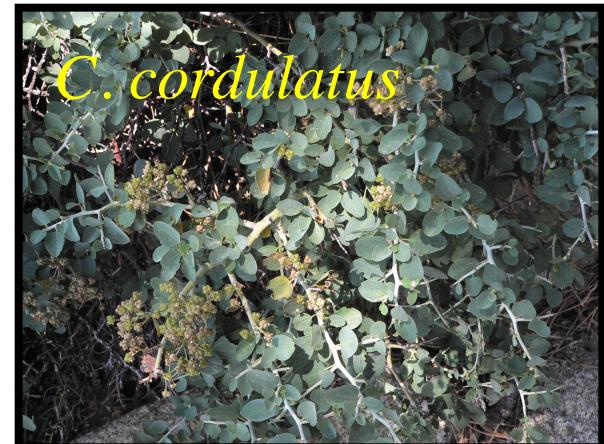
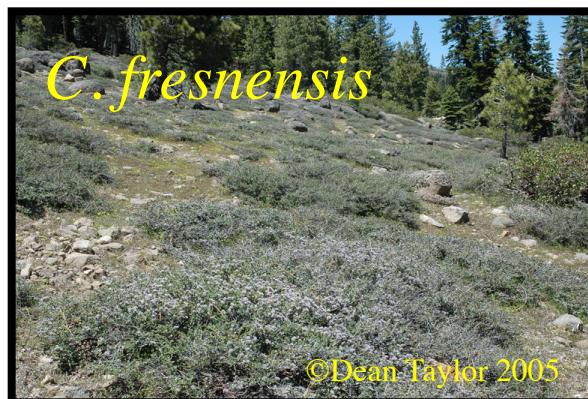


Ceanothus in California

Sierra pine
forest

β niche

Coastal and
foothill chaparral



high

sclerophyll

low

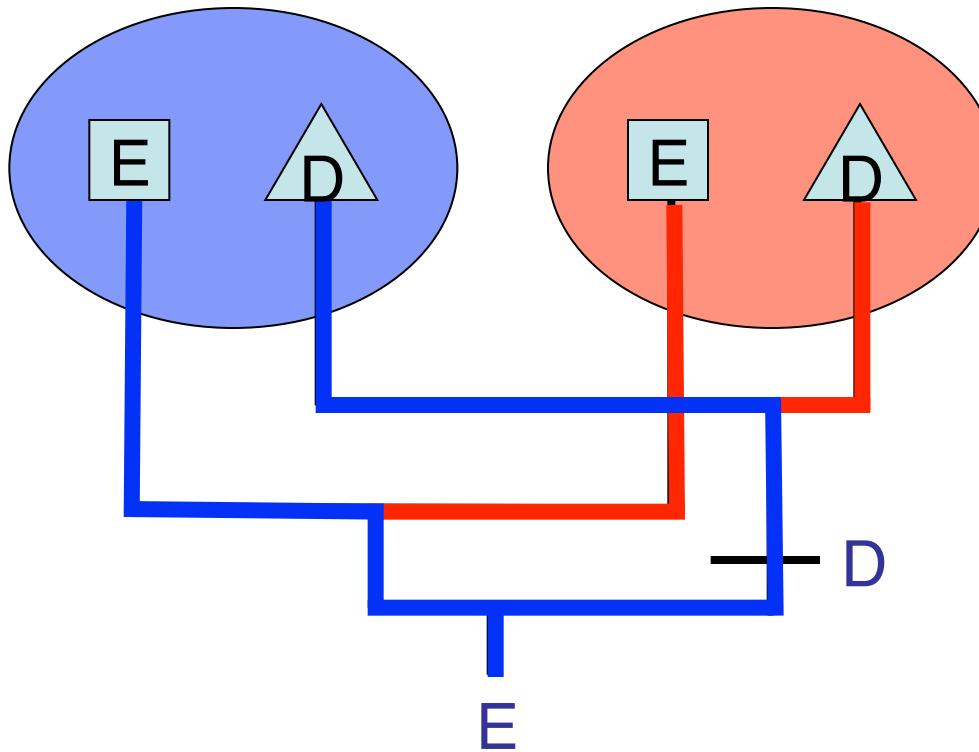
α niche

β :

cold

hot

α :



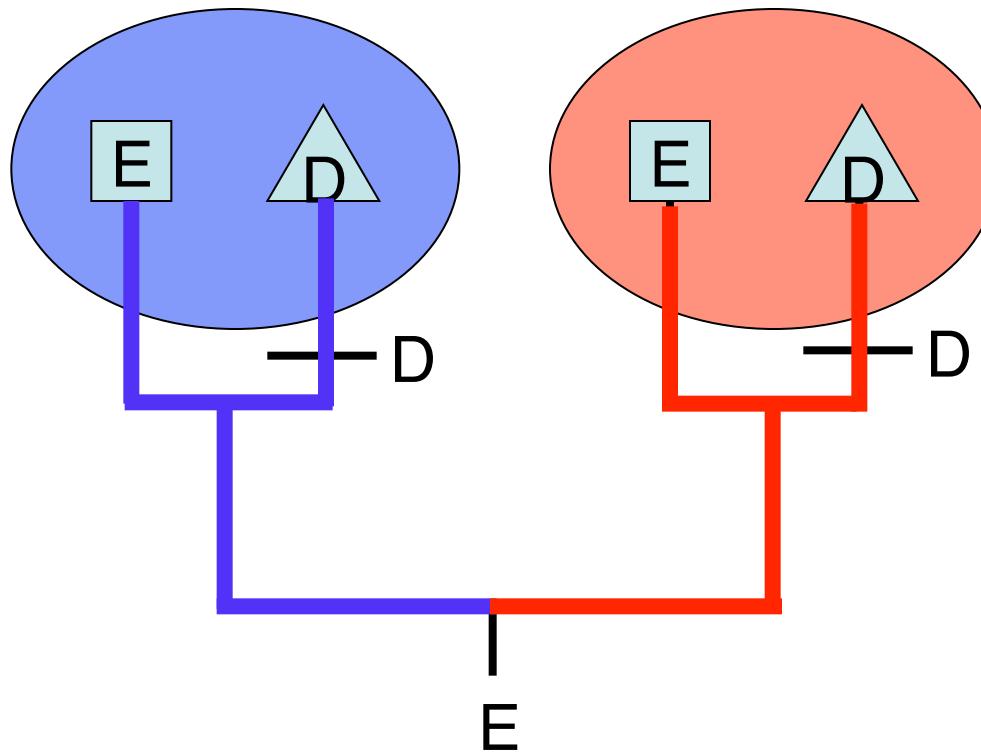
phylogenetic overdispersion = ‘ α first’

β :

cold

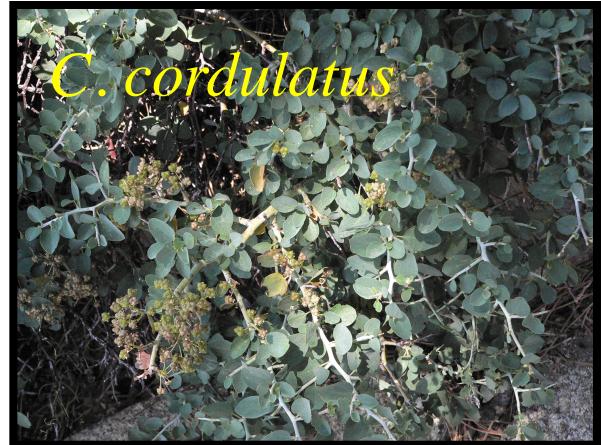
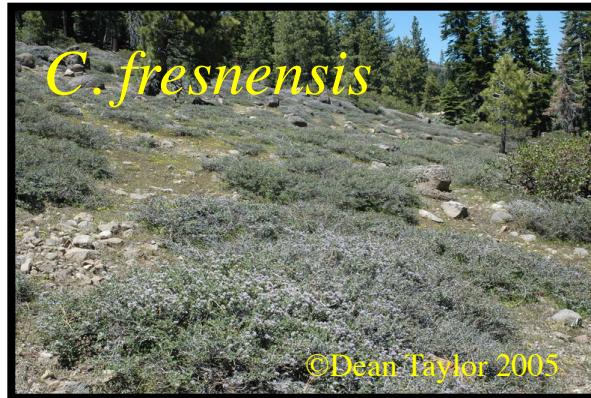
hot

α :



phylogenetic clustering = ‘ β first’

Sierra pine
forest



Coastal and
foothill chaparral



Cerastes

Euceanothus

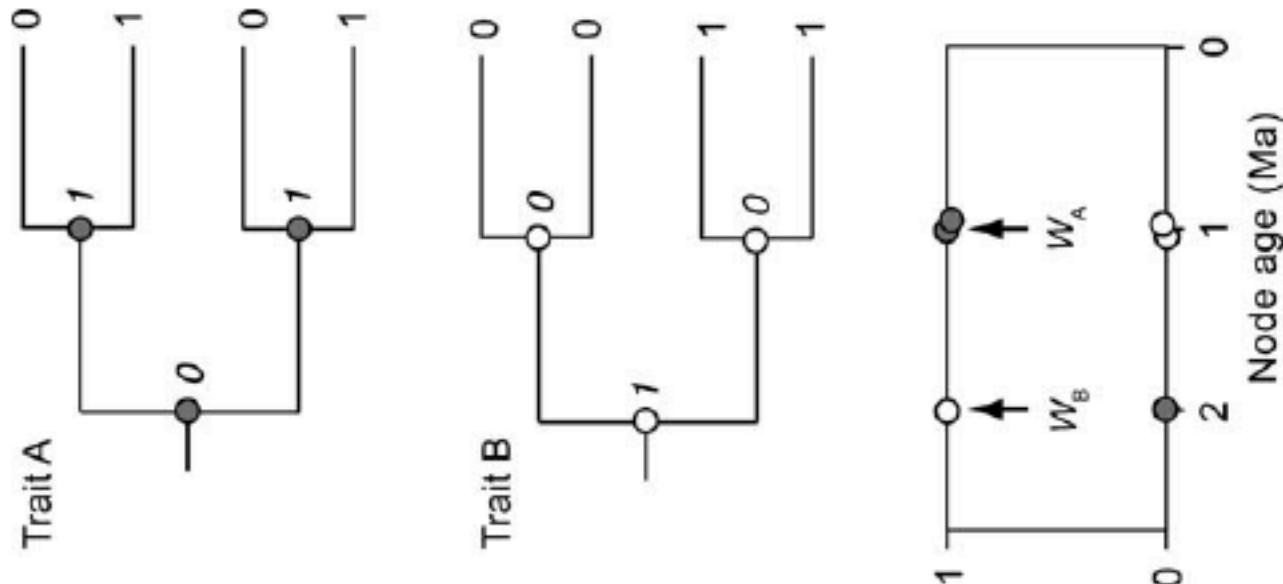
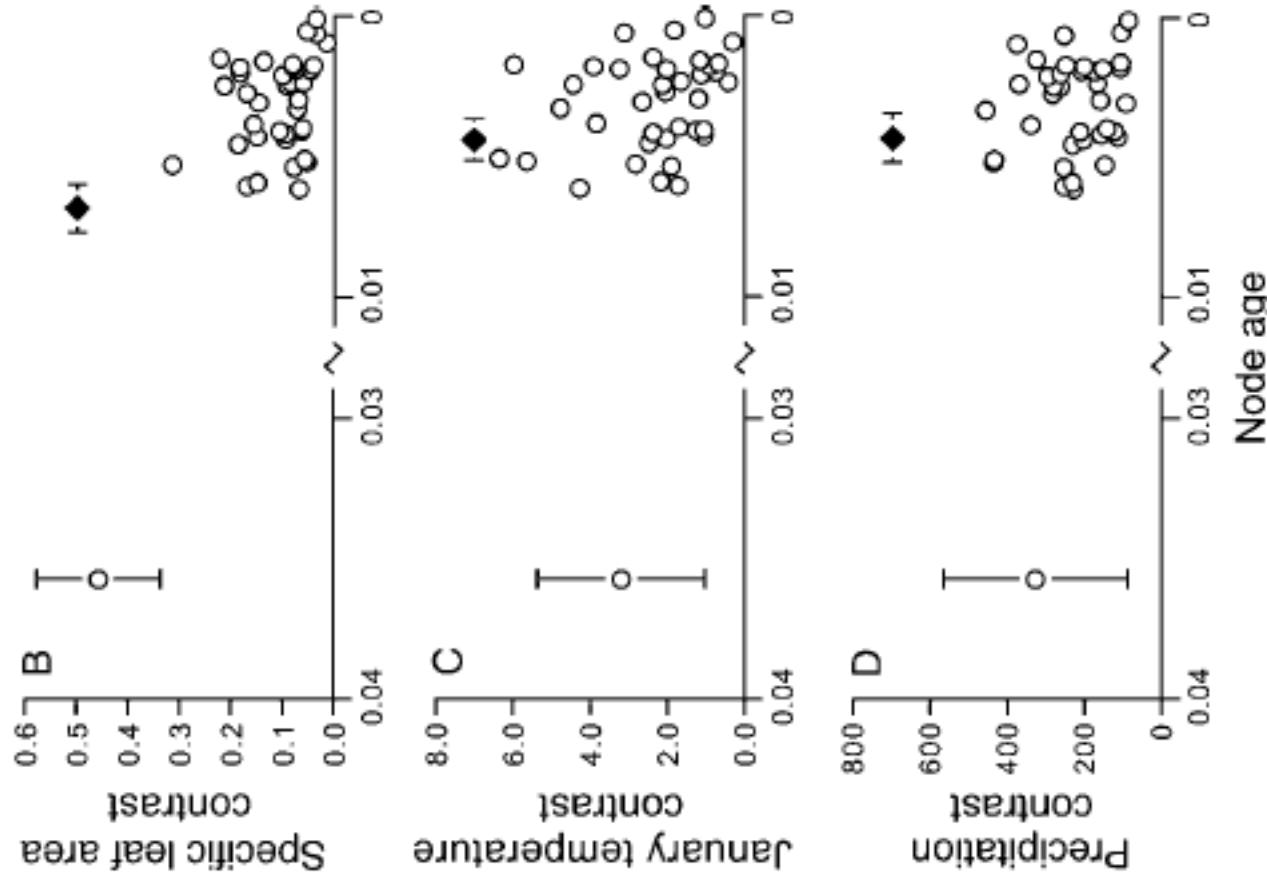
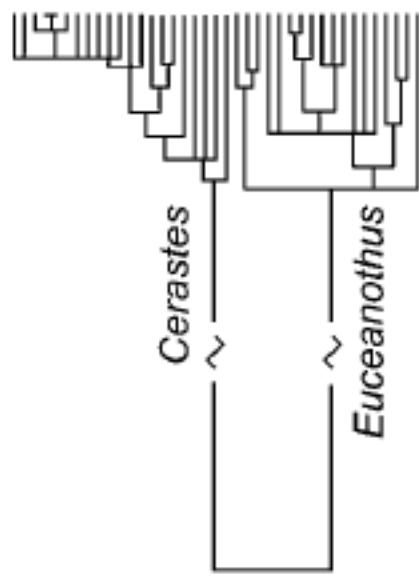
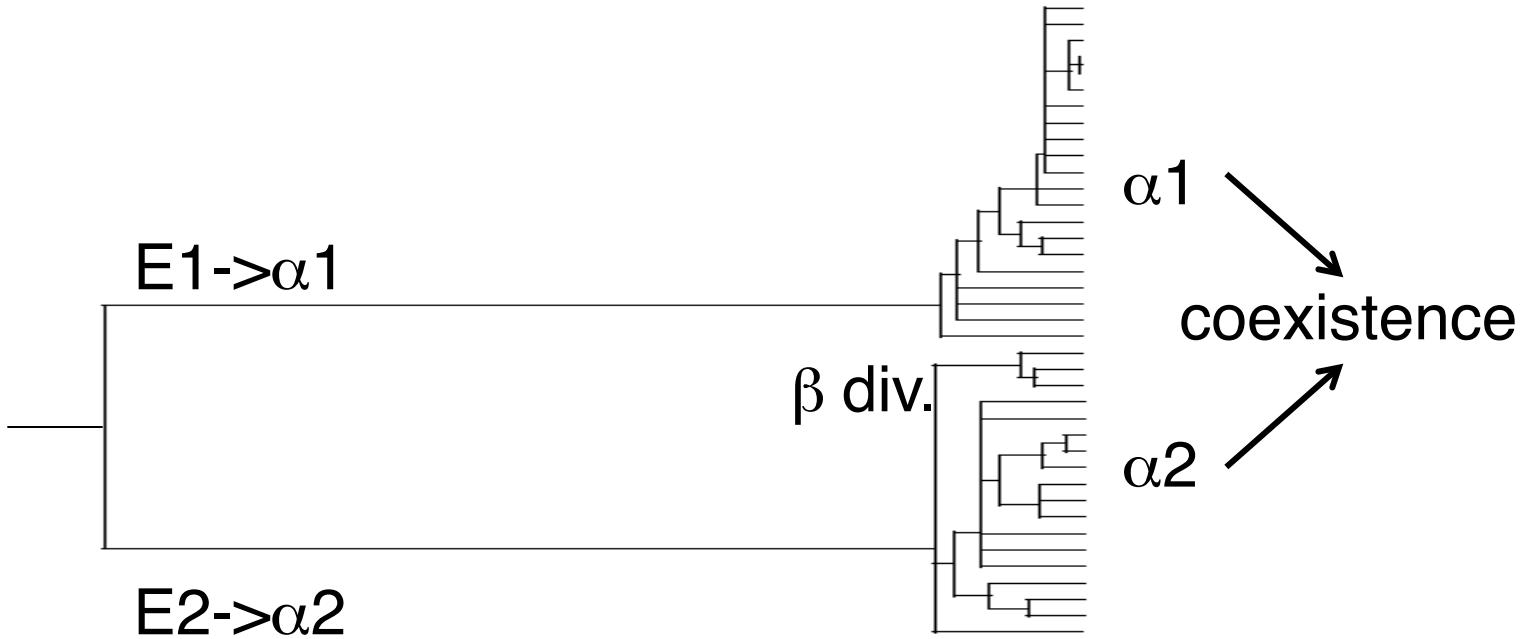


Fig. 1. Example of the divergence order test (DOT). Two patterns of trait divergence are illustrated on a simple phylogeny. Numbers at the tips of the phylogeny indicate two possible trait states, 0 or 1. Numbers at interior nodes (in italics) show the contrast for that node. Trait A (open circles) exhibits a pattern of late divergence, whereas Trait B (shaded circles) exhibits a pattern of early divergence. The lower panel plots contrast magnitude vs. age and shows the calculated weighted divergence age for Trait A ($W_A = 1$ Ma [i.e., 1 million years ago]) and Trait B ($W_B = 2$ Ma).

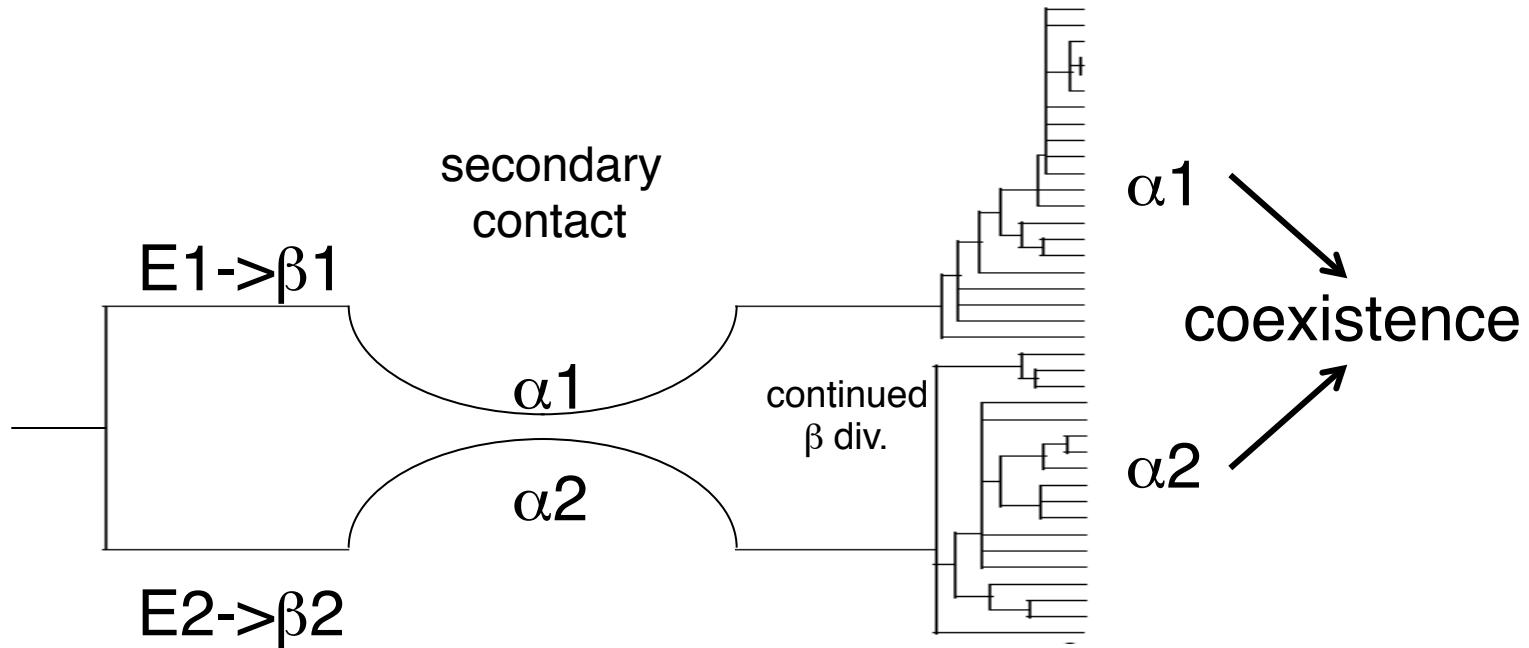
A





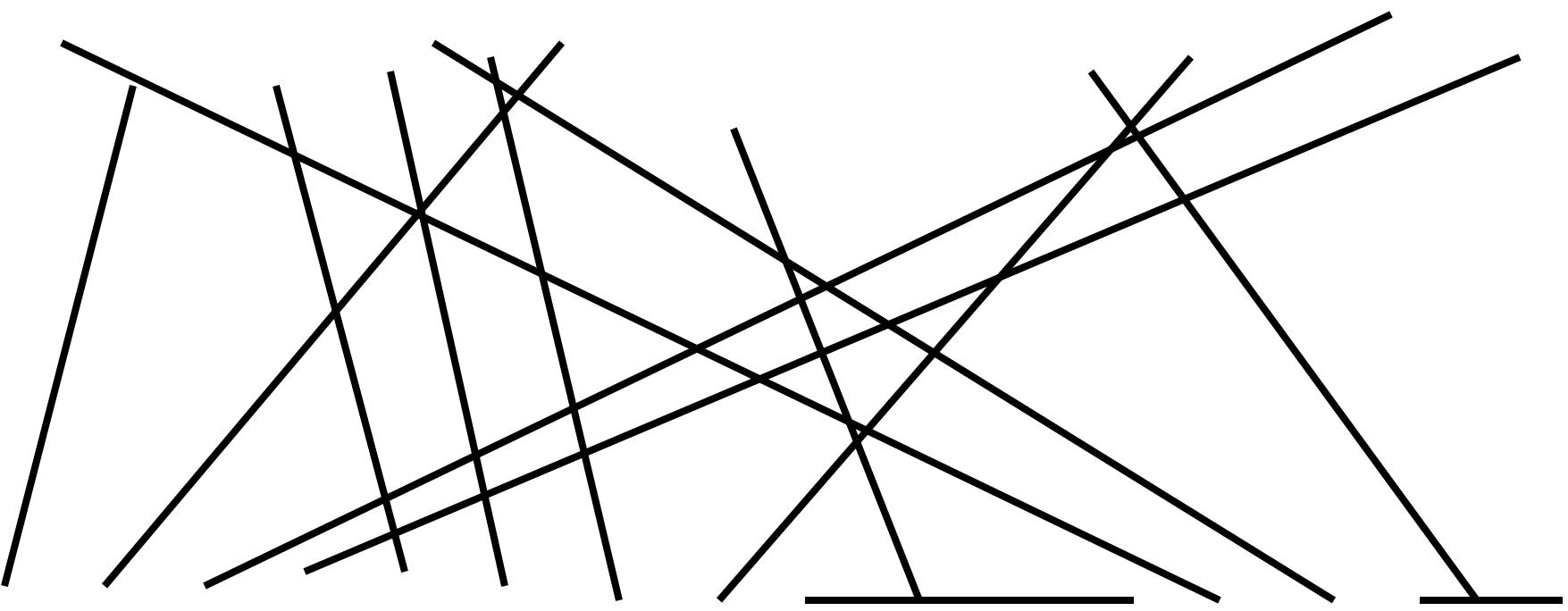
How do α -niche traits diverge during allopatric speciation?

- 1) alternative α states favored in 2 environments, coincidentally promote coexistence in modern communities.



How do α -niche traits diverge during allopatric speciation?

2) α differences evolved in secondary contact of sister taxa, prior to diversification of two clades; modern coexistence reflects ancestral character displacement; early habitat divergence undetectable due to rapid rates of evolution.



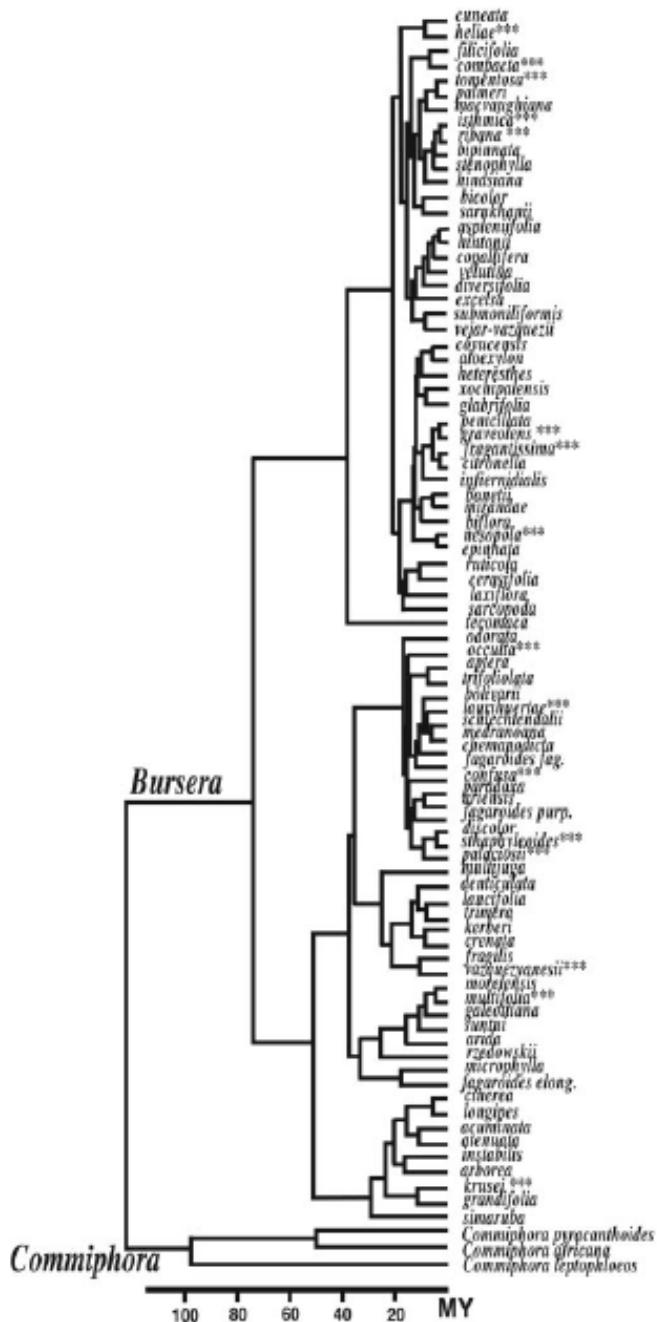


Fig. 2. Time-calibrated phylogeny of *Bursera* (modified from ref. 13). Asterisks indicate species that were added to the phylogeny on the basis of their taxonomic descriptions and for which divergence time is unknown.

Lineages-through-time (LTT) plot

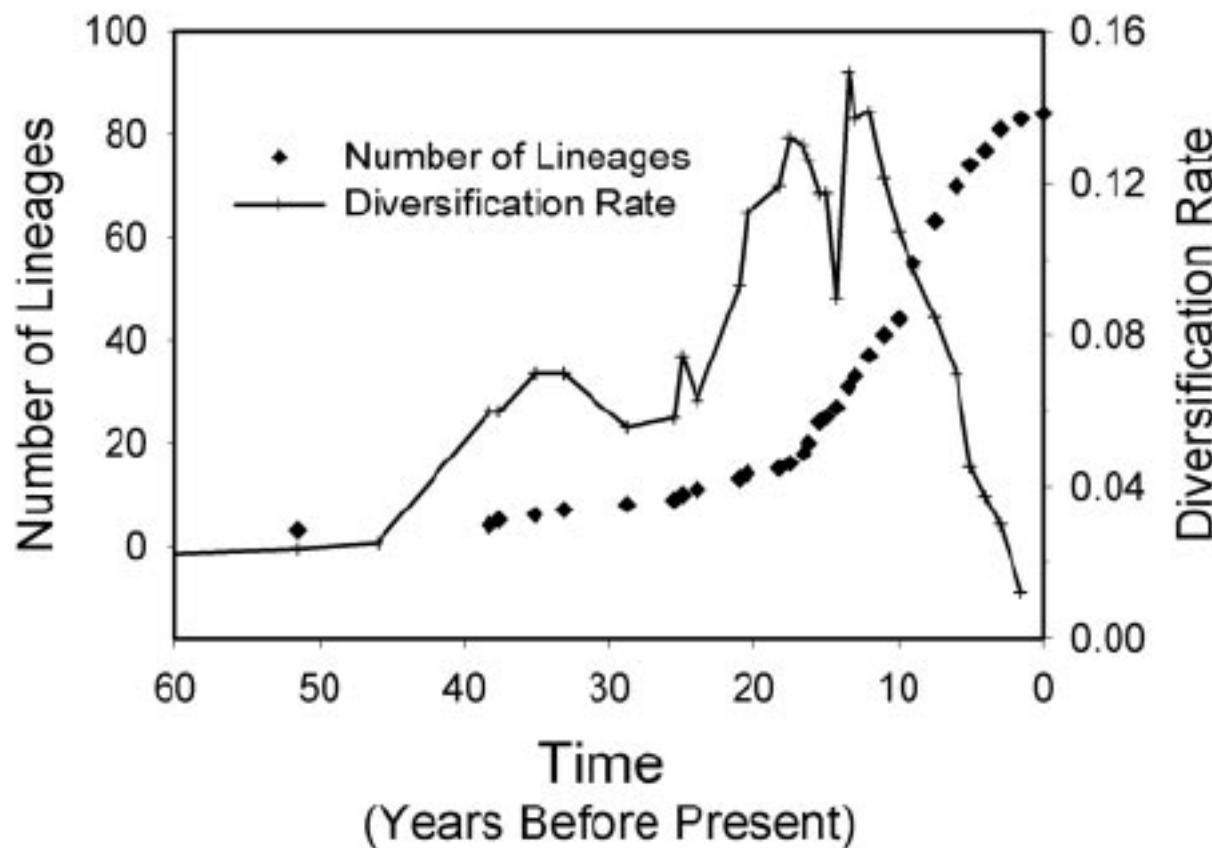


Fig. 3. Number of *Bursera* lineages through time and 10-MY average diversification rates at different times over the last 60 MY.

