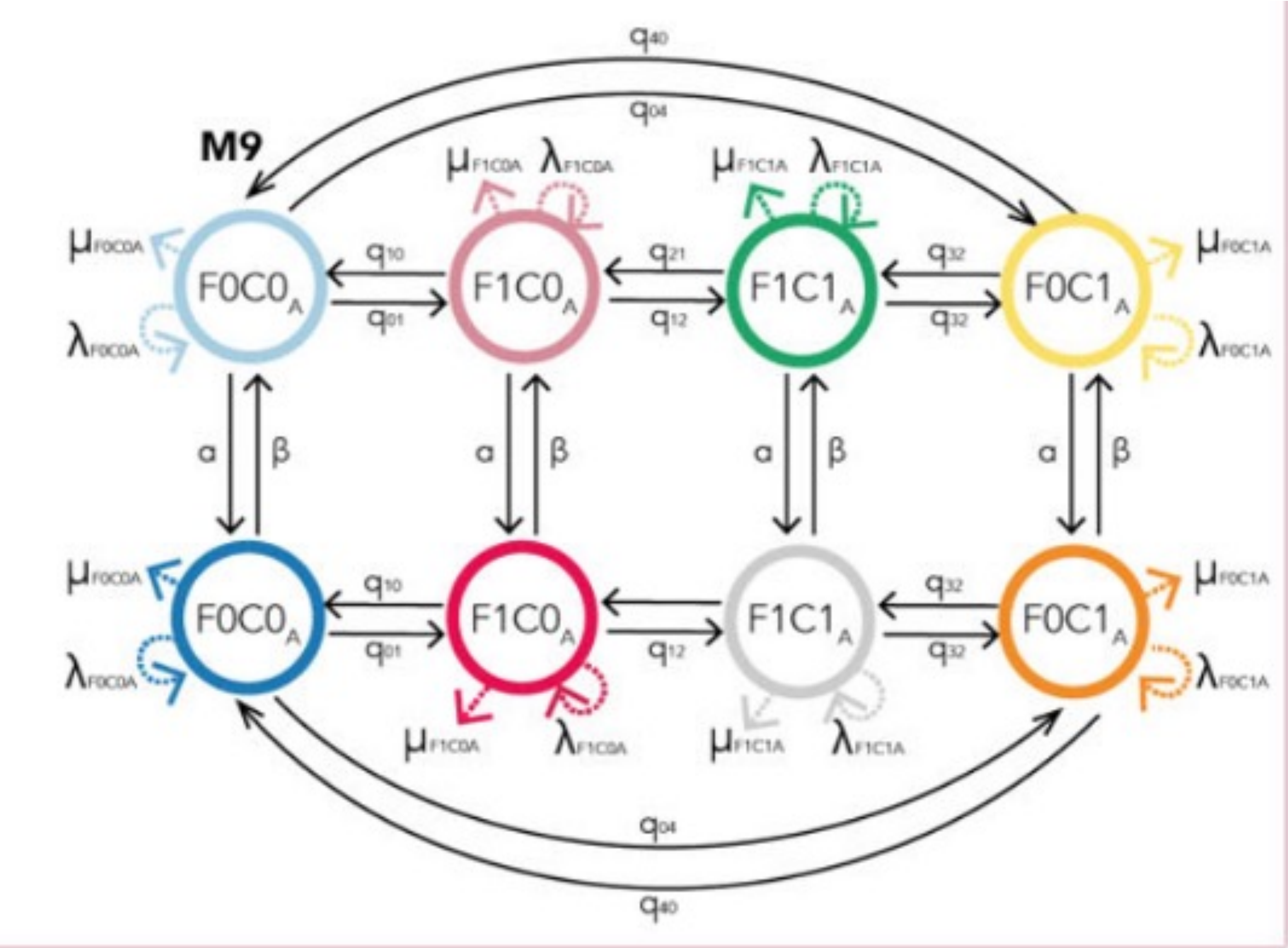
Verónica A. Rincón-Rubio, Rosana Zenil-Ferguson, Alejandro Gonzalez-Voyer. 2025. “The macroevolutionary consequences of the association between frugivory and carotenoid-dependent plumage coloration in passerine birds” Evolution, 2025, 79(8), 1643–1657
https://doi.org/10.1093/evolut/qpaf105

Class focus area: SSE and correlation

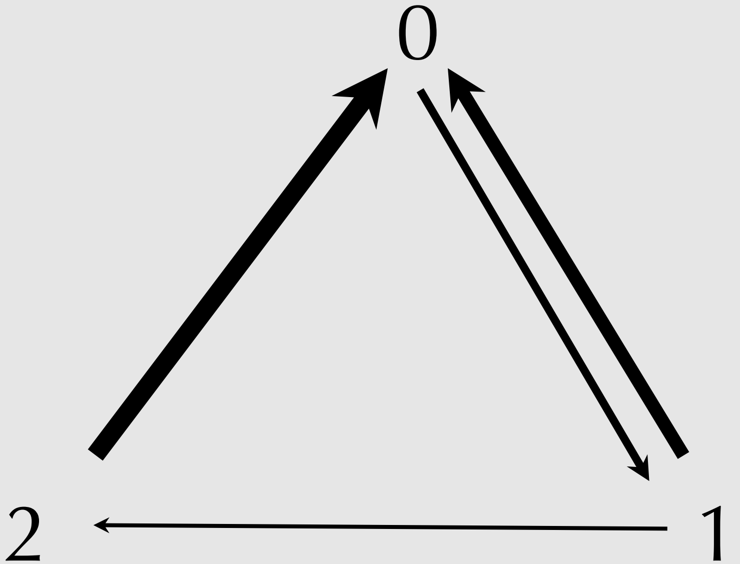
EEB603: Brian O’Meara

All quotes and images from the above paper unless otherwise noted

Photo from https://www.birdadvisors.com/northern-cardinal/



Well, this seems easy…


0
1
2

A, T, G, C

woody, herbaceous

susceptible, infected, recovered

herbivorous, omnivorous, carnivorous

0, 2, 4, 6, 8, ..., 100 legs

Per day:

Action	Bought by adult	Bought by child	Stolen
Probability	0.20	0.10	0.05

What is probability of it leaving the store that day?

If it leaves, what is the probability it was paid for?

What is the probability it stays in the store ≥ two days?

Per Δt:

Action	Bought by adult	Bought by child	Stolen
Probability	0.20 /scaling	0.10 /scaling	0.05 /scaling

Per Δt:

Action	Bought by adult	Bought by child	Stolen
Rate	r_{adult}	r_{child}	r_{stolen}

Per Δt:

From \ To	Store	Adult	Child	Thief
Store	-	$r_{\text{store-adult}}$	$r_{\text{store-child}}$	$r_{\text{store-thief}}$

Per Δt:

From \ To	Store	Adult	Child	Thief
Store	-	$r_{\text{store-adult}}$	$r_{\text{store-child}}$	$r_{\text{store-thief}}$
Adult				
Child				
Thief				

Per Δt:

From \ To	Store	Adult	Child	Thief
Store	-	$r_{store\text{-}adult}$	$r_{store\text{-}child}$	$r_{store\text{-}thief}$
Adult	$r_{adult\text{-}store}$	-	$r_{adult\text{-}child}$	$r_{adult\text{-}thief}$
Child	$r_{child\text{-}store}$	$r_{child\text{-}adult}$	-	$r_{child\text{-}thief}$
Thief	$r_{thief\text{-}store}$	$r_{thief\text{-}adult}$	$r_{thief\text{-}child}$	-

From \ To	Store	Adult	Child	Thief
Store	-	$r_{\text{store-adult}}$	$r_{\text{store-child}}$	$r_{\text{store-thief}}$
Adult	$r_{\text{adult-store}}$	-	$r_{\text{adult-child}}$	$r_{\text{adult-thief}}$
Child	$r_{\text{child-store}}$	$r_{\text{child-adult}}$	-	$r_{\text{child-thief}}$
Thief	$r_{\text{thief-store}}$	$r_{\text{thief-adult}}$	$r_{\text{thief-child}}$	-

Does the store ever get Twinkies back?
[Do people return Twinkies for a refund?]

$$H_0\text{: } r_{*\text{-store}} = 0$$
$$H_1\text{: } r_{*\text{-store}} > 0$$

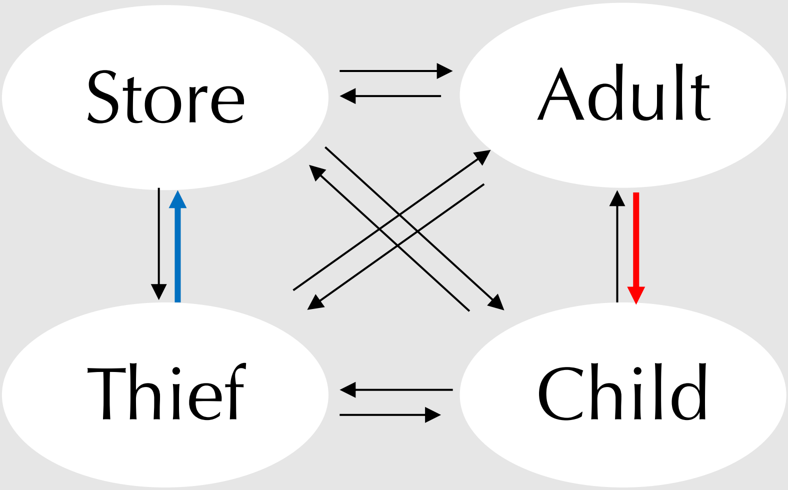
From \ To	Store	Adult	Child	Thief
Store	-	$r_{\text{store-adult}}$	$r_{\text{store-child}}$	$r_{\text{store-thief}}$
Adult	$r_{\text{adult-store}}$	-	$r_{\text{adult-child}}$	$r_{\text{adult-thief}}$
Child	$r_{\text{child-store}}$	$r_{\text{child-adult}}$	-	$r_{\text{child-thief}}$
Thief	$r_{\text{thief-store}}$	$r_{\text{thief-adult}}$	$r_{\text{thief-child}}$	-

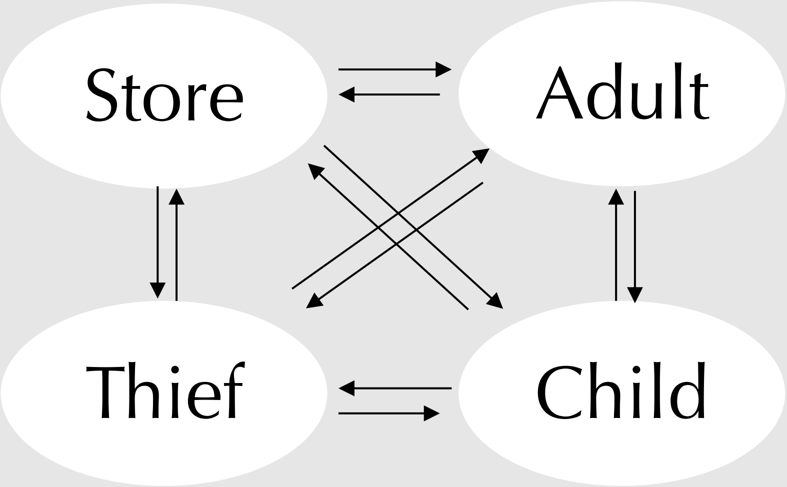
Do adults give to kids at the same rate kids give to adults?

$$H_0: r_{\text{child-adult}} = r_{\text{adult-child}}$$

$$H_1: r_{\text{child-adult}} \neq r_{\text{adult-child}}$$

From \ To	Store	Adult	Child	Thief
Store	-	$r_{\text{store-adult}}$	$r_{\text{store-child}}$	$r_{\text{store-thief}}$
Adult	$r_{\text{adult-store}}$	-	$r_{\text{adult-child}}$	$r_{\text{adult-thief}}$
Child	$r_{\text{child-store}}$	$r_{\text{child-adult}}$	-	$r_{\text{child-thief}}$
Thief	$r_{\text{thief-store}}$	$r_{\text{thief-adult}}$	$r_{\text{thief-child}}$	-



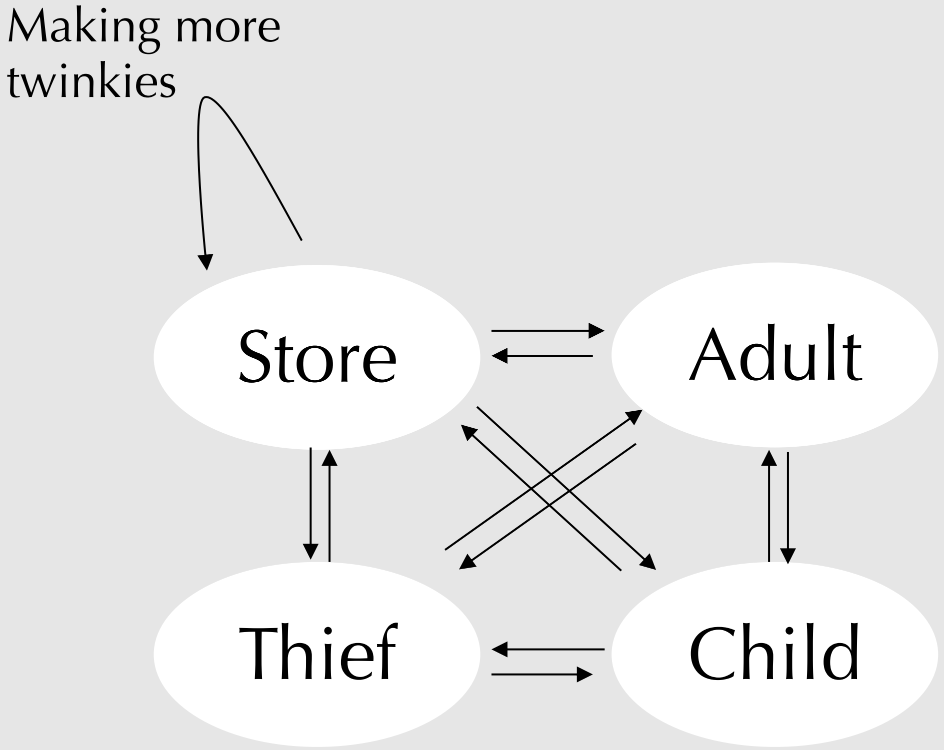


Store

Adult

Thief

Child



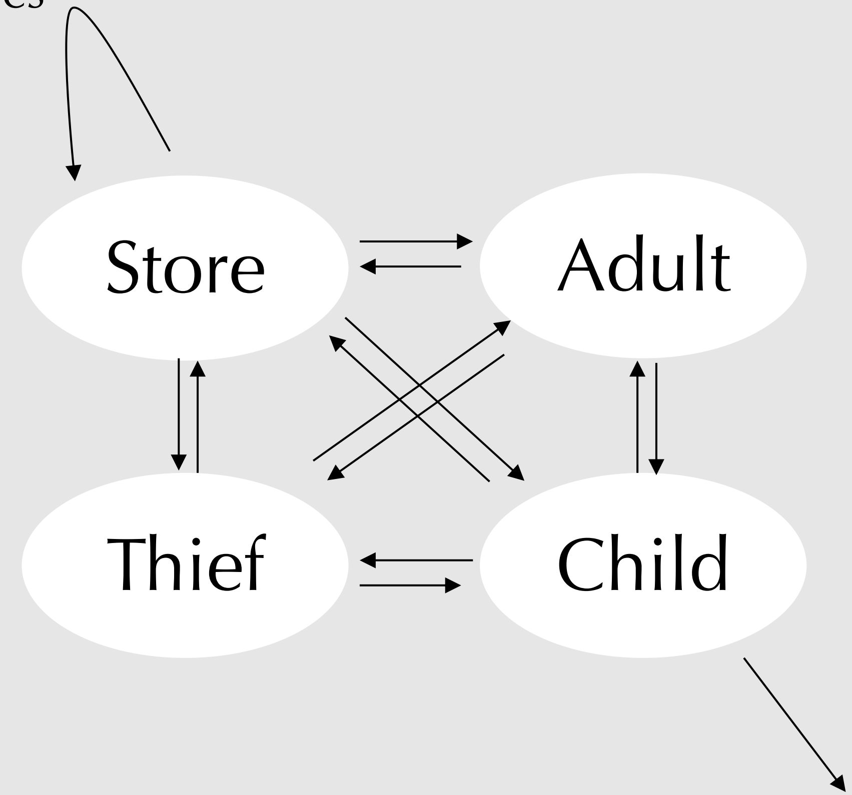
Making more twinkies

Store

Adult

Thief

Child



Making more twinkies

Store

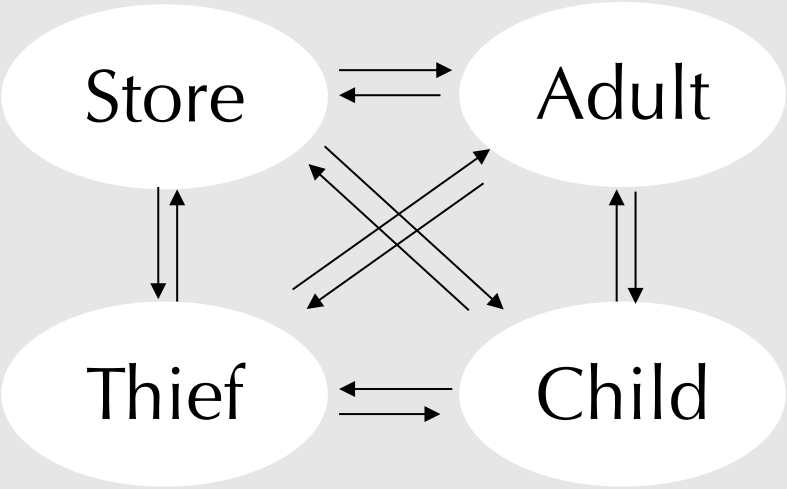
Adult

Thief

Child

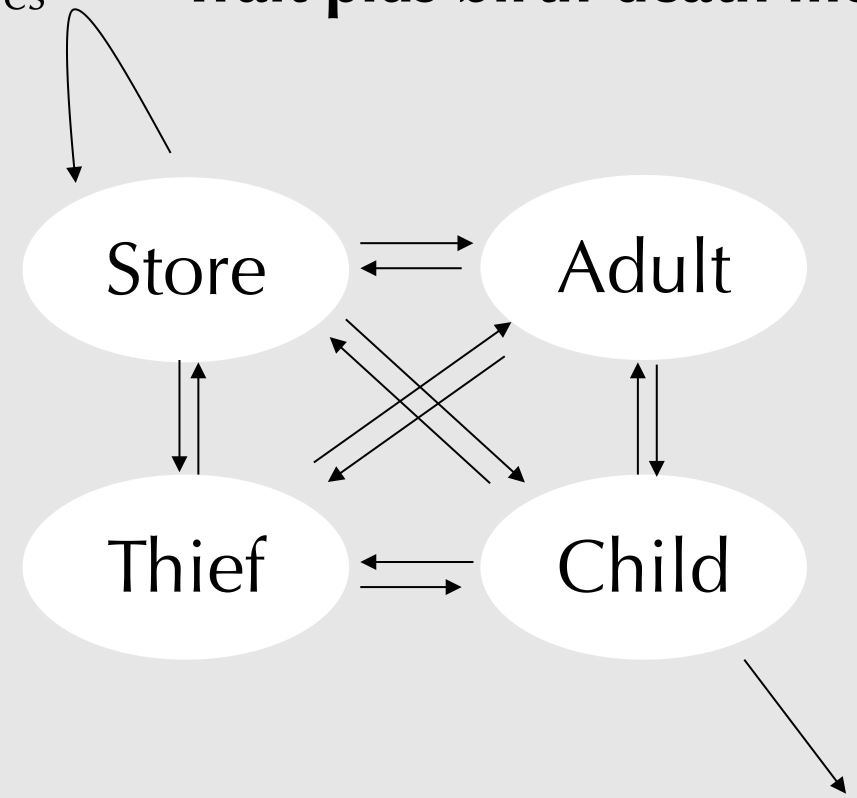
Eating twinkies

Trait only, assumes zero differential effect on birth or death



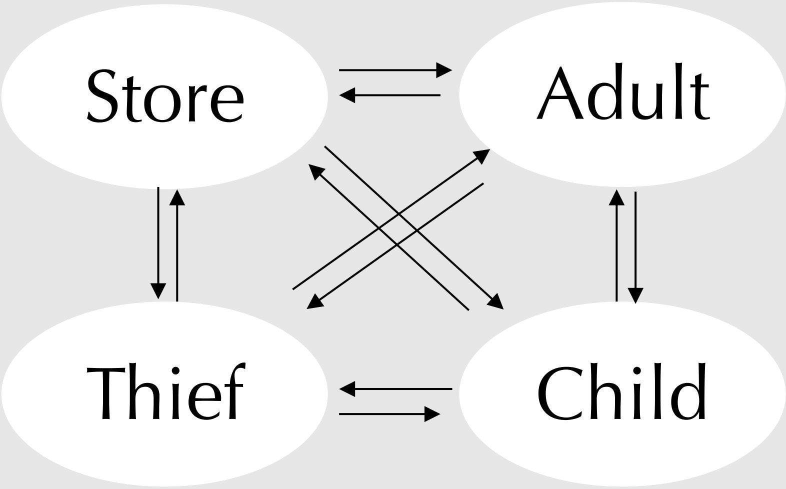
Trait plus birth-death model

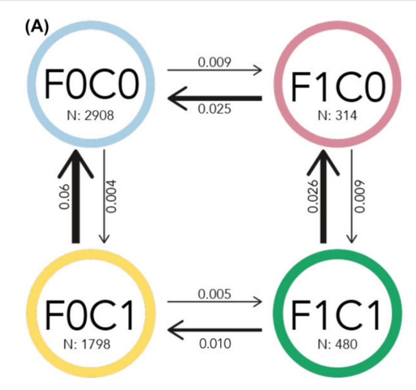
Making more twinkies



Eating twinkies

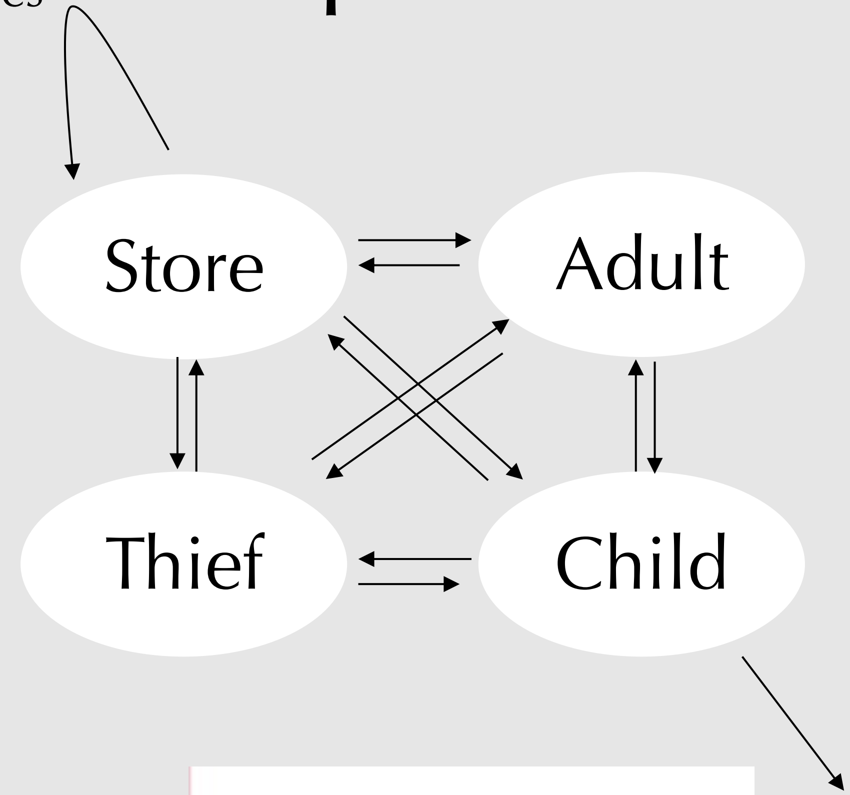
Trait only, assumes zero differential effect on birth or death

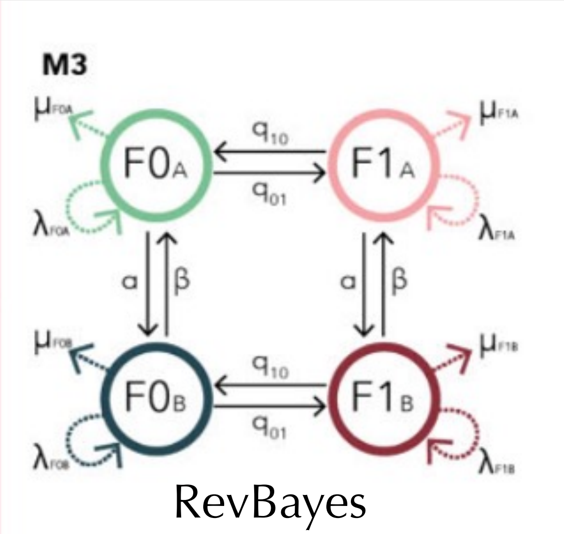




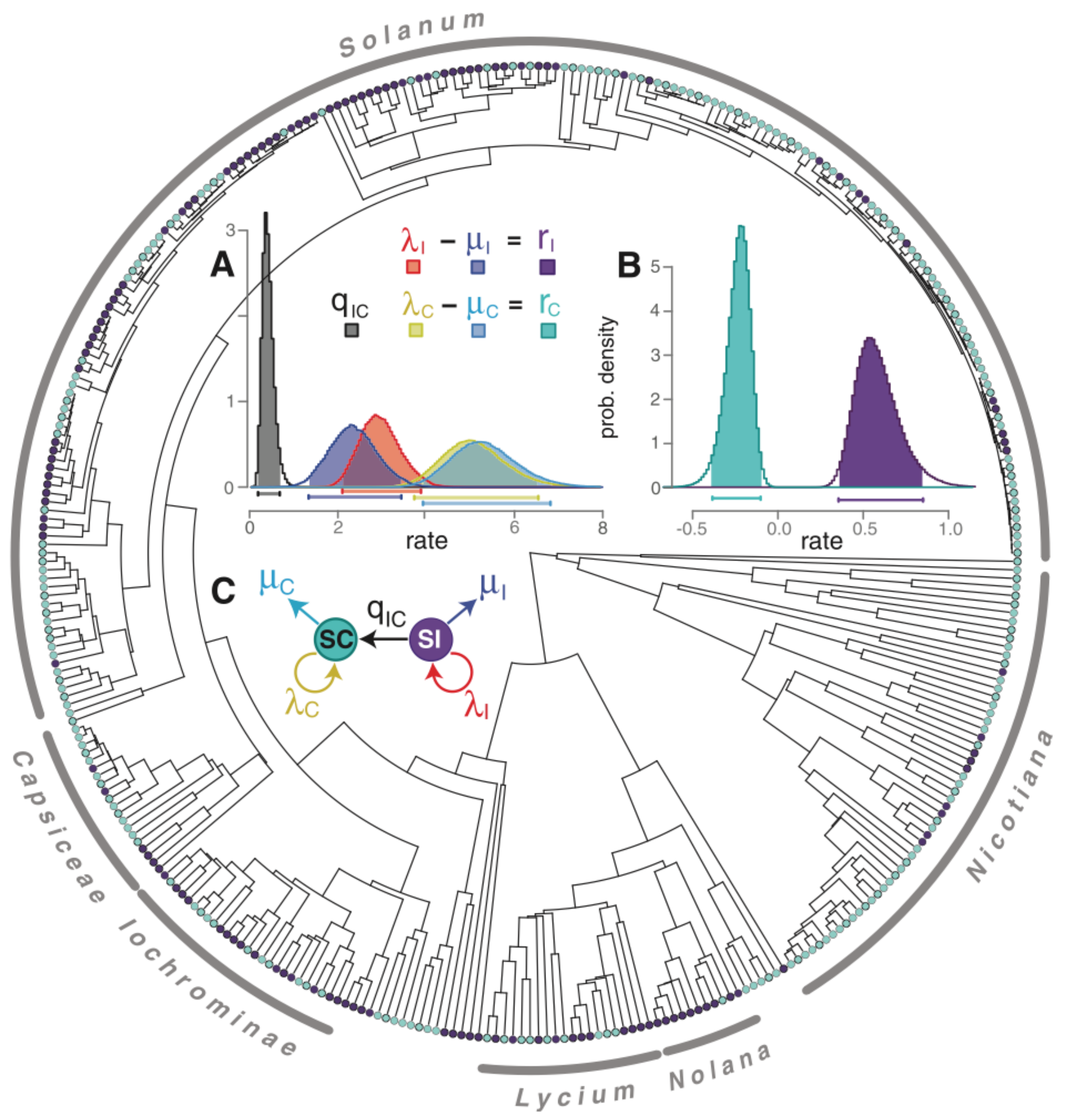
BayesTraits

Trait plus birth-death model

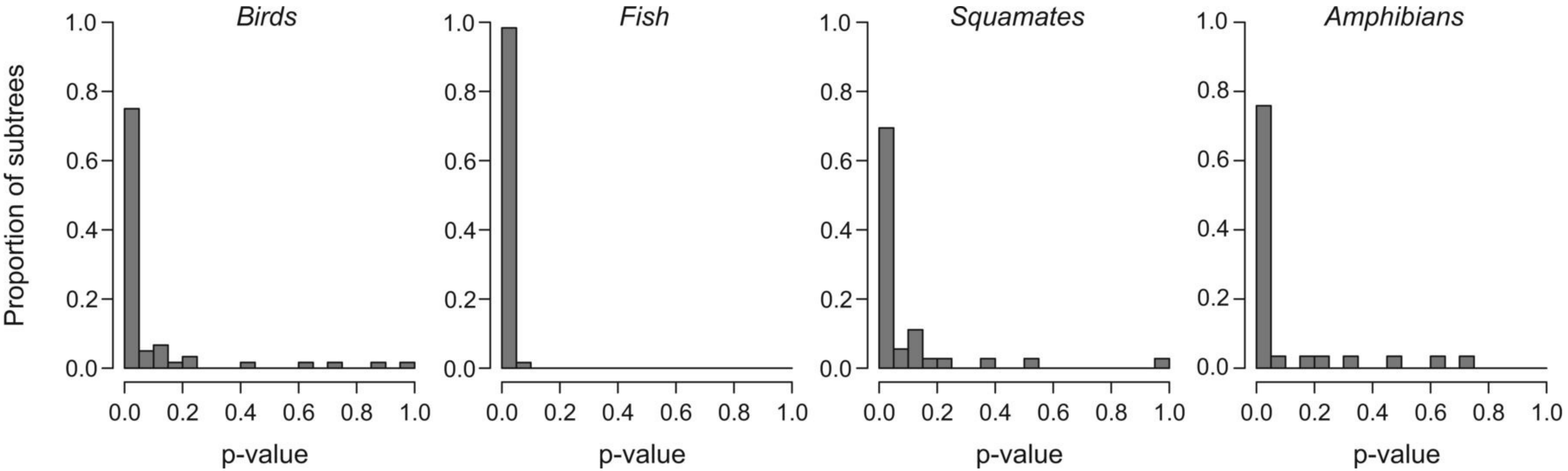




RevBayes

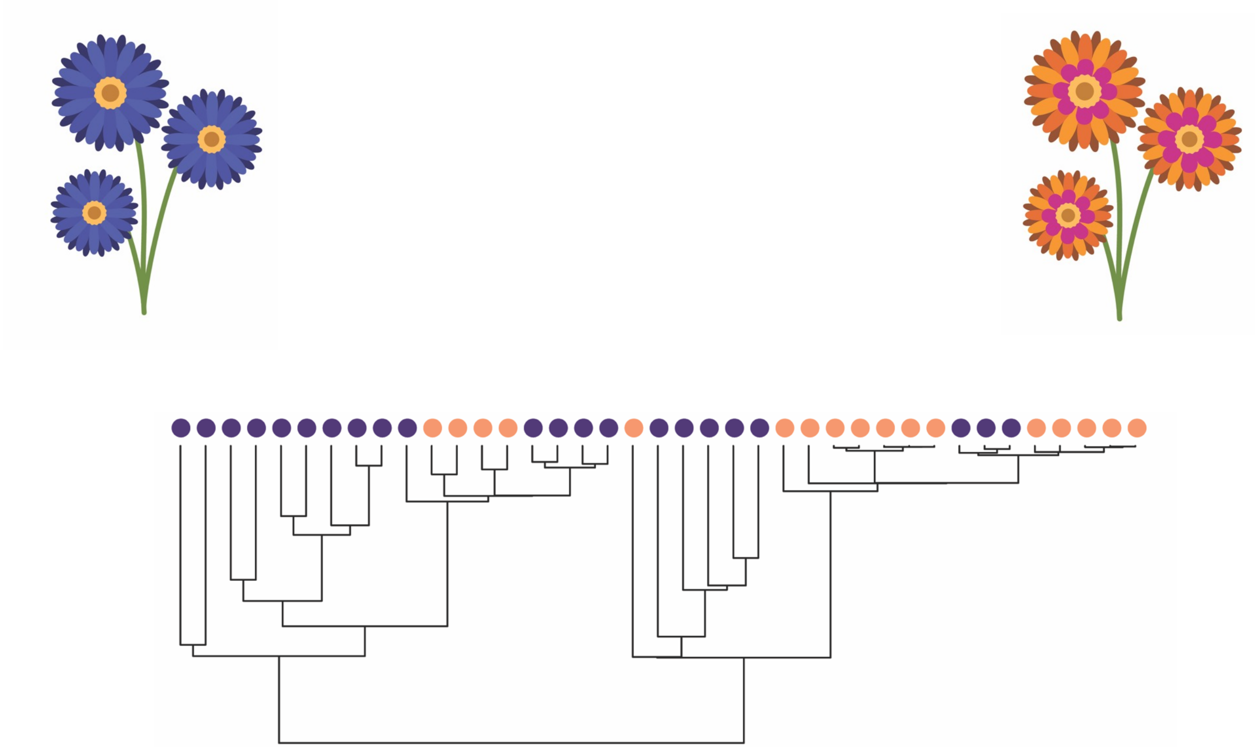


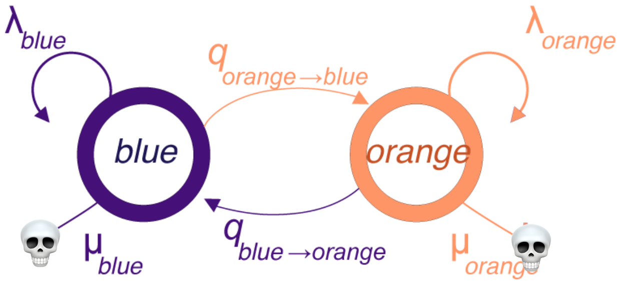
Goldberg et al. 2010



In the second exercise, we analyzed the effect of a purely arbitrary character on speciation rates across the 200–500 taxon subtrees drawn from the four vertebrate clades described above. We tested whether taxon name length—the number of letters in the Latin binominal for each taxon—was associated with speciation rate. We counted the number of letters in each taxon name and scored each species as “short” or “long” depending on whether the taxon name length was less than or greater than the median name length for taxa in each subtree. This character exhibits some phylogenetic signal as would an evolving trait, owing to the correlation in name lengths between congeners. For example, within the 60 bird subtrees, we found that 44 trees (73%) showed significant ($p<0.05$) phylogenetic signal in taxon name length, as assessed by computing the K-statistic (Blomberg et al. 2003) for each data set and determining significance via tip randomization. Name length of course cannot plausibly be considered a driver of speciation, although species richness could be reflected in linguistic or taxonomic practices. We fitted the four- and five-parameter BiSSE models described above to each subtree.

Rabosky & Goldberg 2015





λ_{blue}

$q_{orange \rightarrow blue}$

λ_{orange}

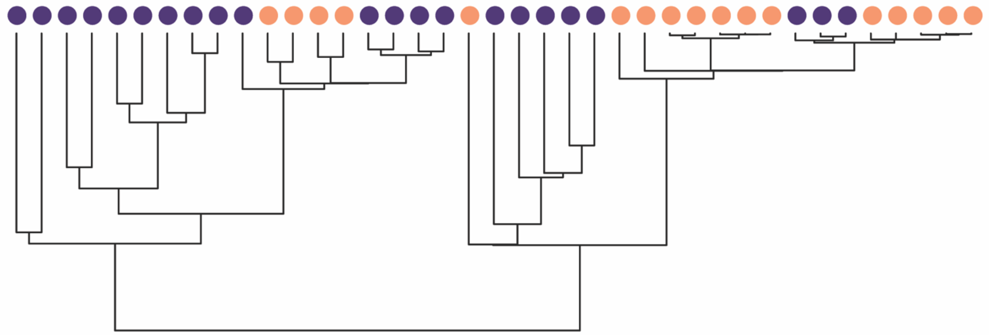
blue

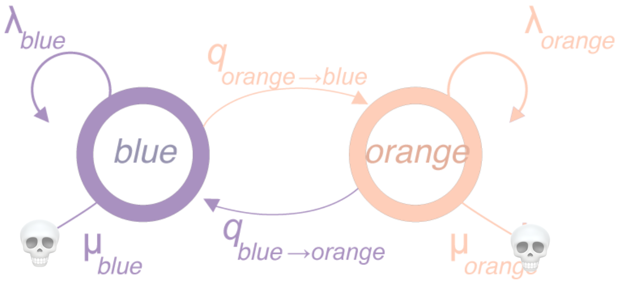
orange

μ_{blue}

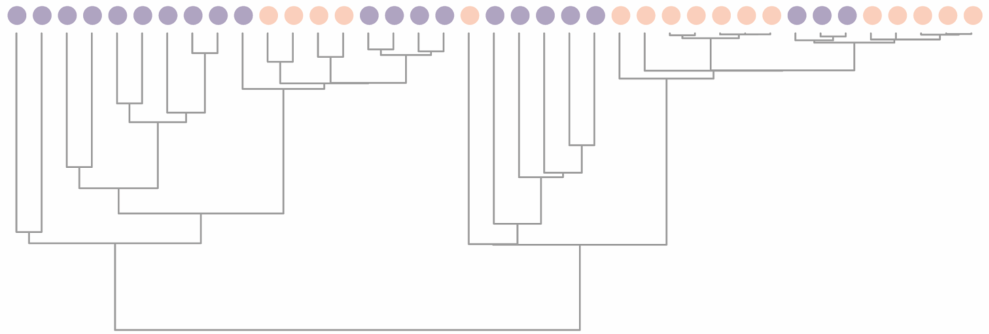
$q_{blue \rightarrow orange}$

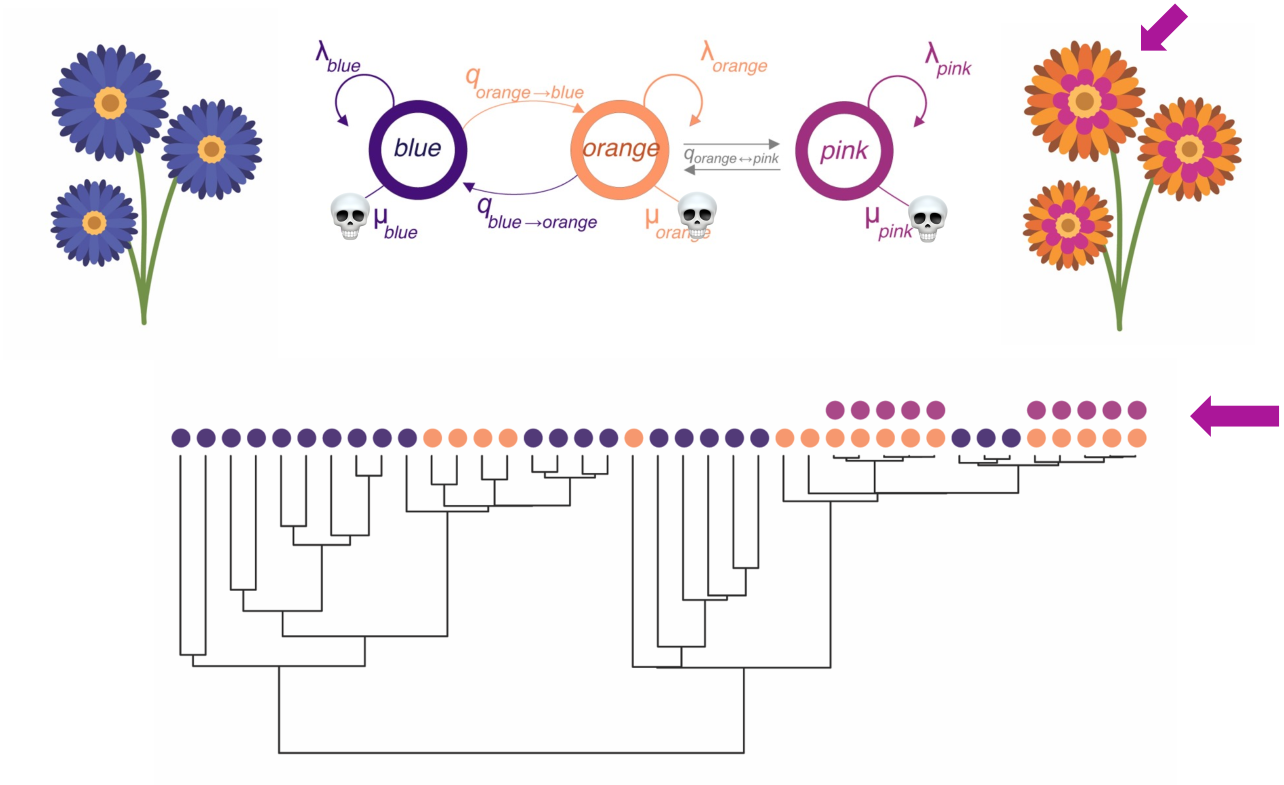
μ_{orange}

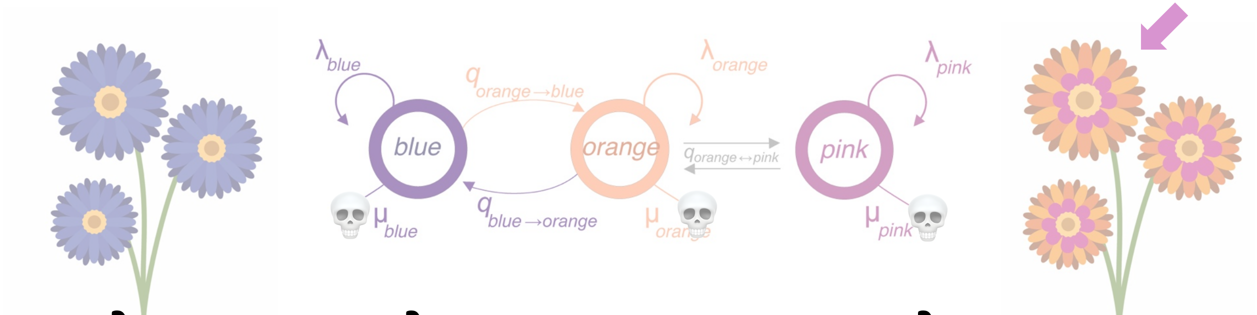




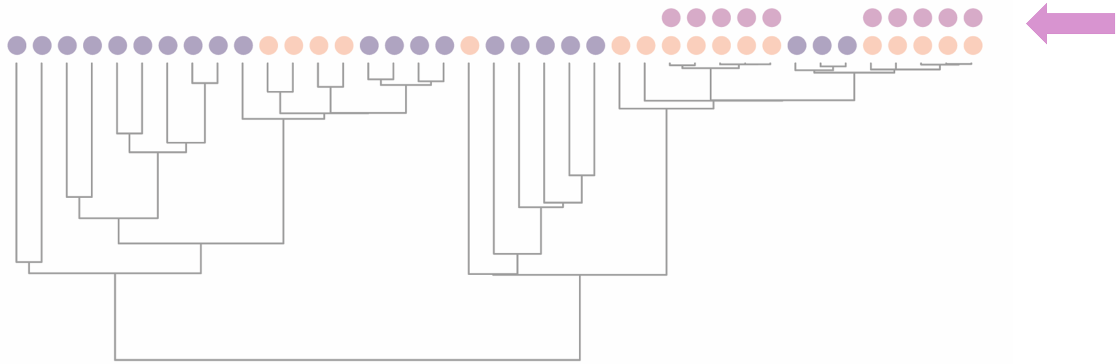
$$\lambda_{\text{blue}} < \lambda_{\text{orange}}$$

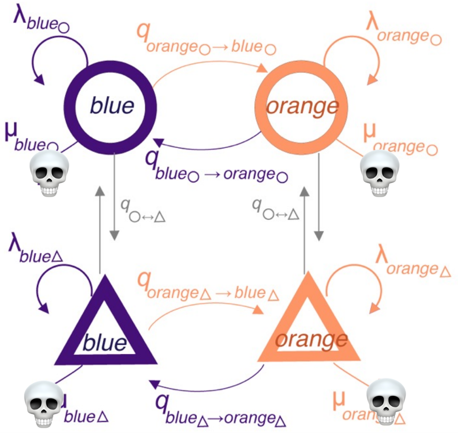


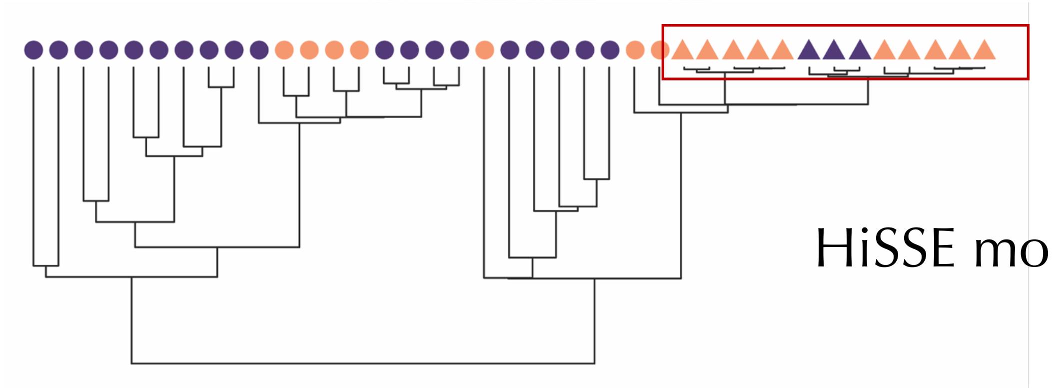

λ_{blue}
$q_{orange \to blue}$
λ_{orange}
λ_{pink}
blue
orange
$q_{orange \leftrightarrow pink}$
pink
μ_{blue}
$q_{blue \to orange}$
μ_{orange}
μ_{pink}



$\lambda_{\text{blue}} < \lambda_{\text{orange wo/ pink}} < \lambda_{\text{orange w/ pink}}$







HiSSE model

Beaulieu & O'Meara 2016 *Systematic Biology*

How do frugivory and/or carotenoids evolve with each other and affect diversification?

↓

Test for effect on diversification (*SSE in RevBayes): there are different rates, but not linked to these traits

↓

Ignore diversification, use just BayesTraits

F1: frugivory yes
F0: frugivory no
C1: carotenoids yes
C0: carotenoids no

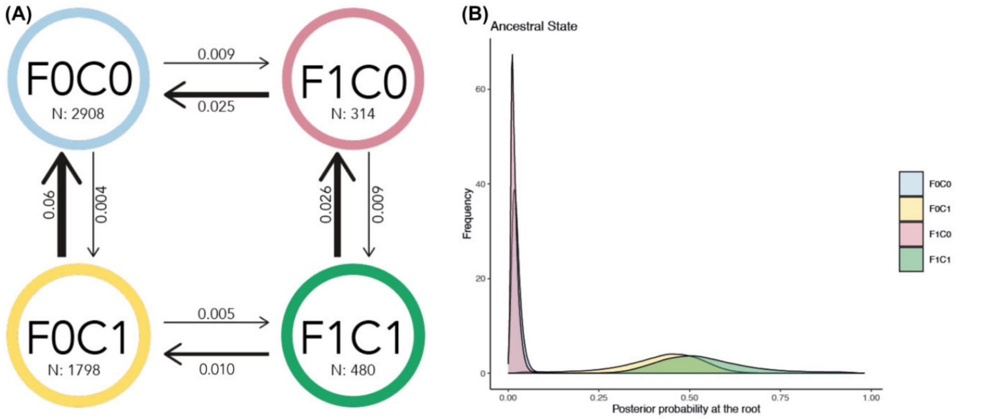


Figure 2. Correlated evolution of frugivory and carotenoid-dependent plumage coloration. (A) Summary diagram of the transition rates across the four combinations of character states inferred from the reversible-jump discrete dependent model of evolution. The sample sizes for each combination of character states are reported; the arrows are scaled to reflect the magnitude of median transition rates from the posterior distribution. (B) Joint posterior distribution of each state showing that the most likely probability at the root of the phylogeny includes both F1 C1 and F0 C1 as plausible roots.

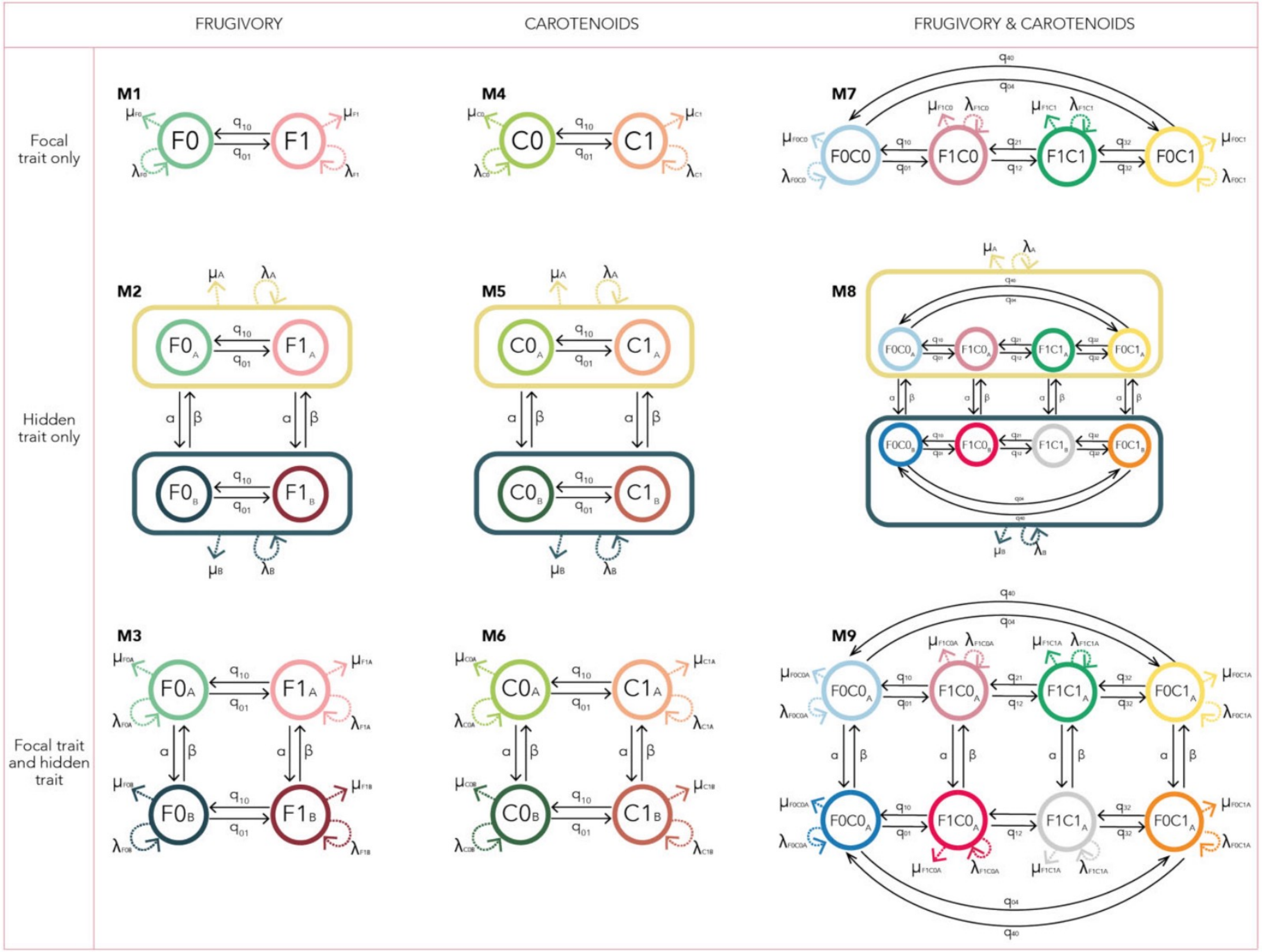
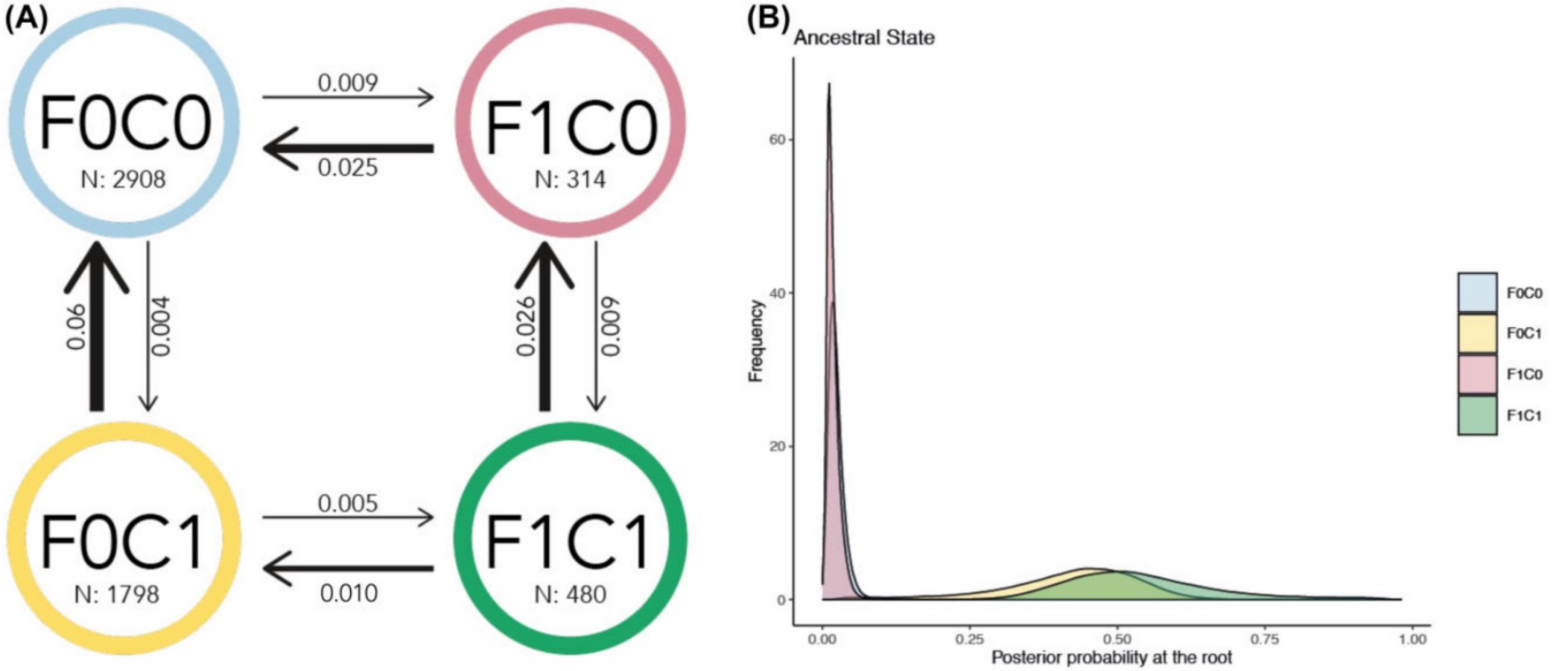


Figure 1. Models of diversification for frugivory, carotenoid-dependent plumage coloration, and hidden diversification factors. This figure presents nine state-dependent speciation and extinction (SSE) models (M1–M9), each testing the impact of frugivory, carotenoid-based coloration, and hidden traits on diversification rates. The models use the SSE framework to explore whether diversification is best explained by frugivory alone, carotenoid coloration alone, a combination of both, or unobserved factors (hidden traits). Different colors represent unique states of each trait, with arrows indicating potential evolutionary transitions between these states. Models incorporating hidden traits (all except models M1 and M4) allow for the possibility of unobserved influences on diversification rates. Each model variation includes distinct combinations of speciation (λ) and extinction (μ) rates, providing a structured approach to examine how both visible and hidden factors may drive evolutionary diversification.



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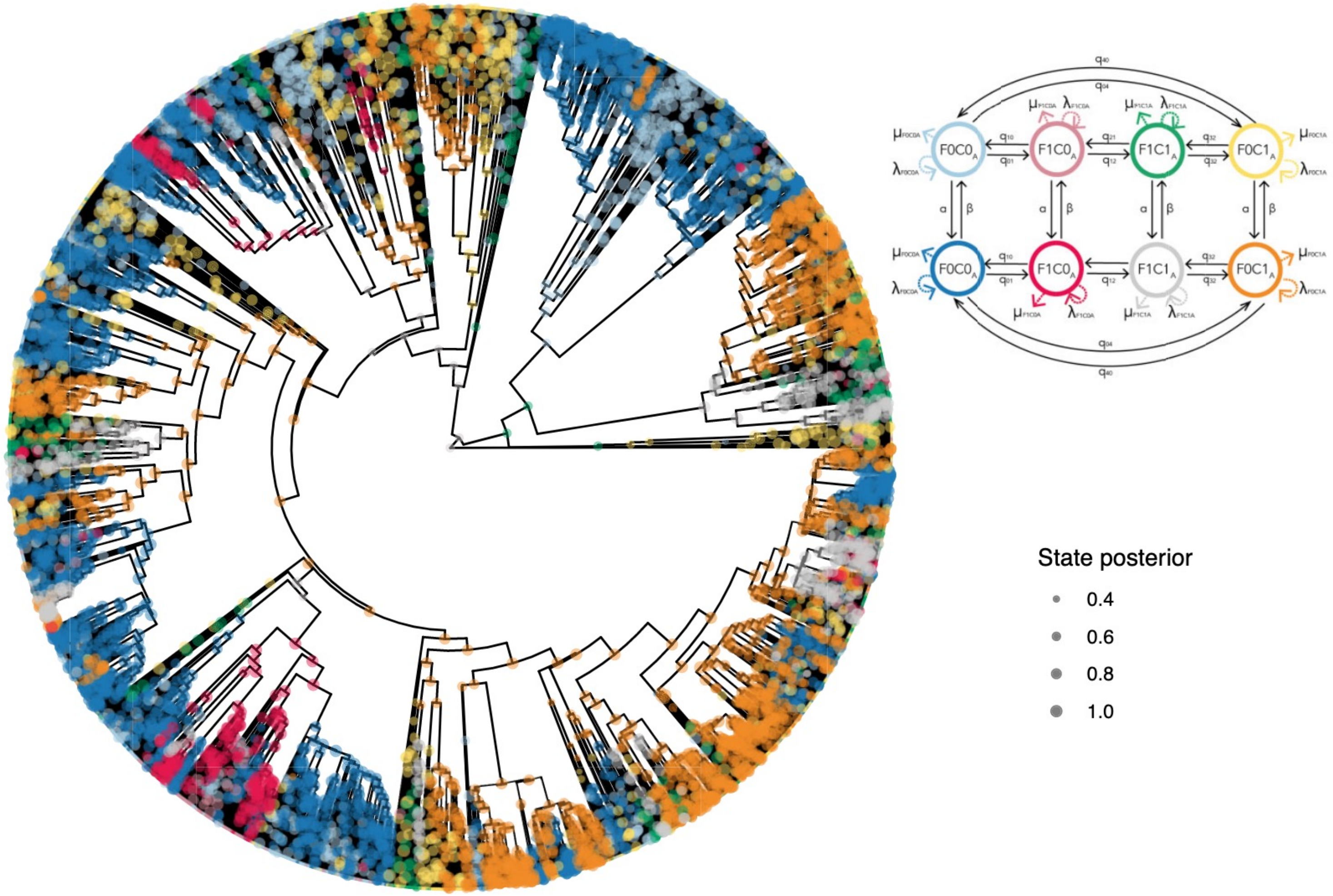


Figure 3. Ancestral state estimation showing the maximum a posteriori estimates of the marginal probability distributions for each node of the M9. F0 C0/F1 C0/F1 C1/F0 C1 + A/B model. The size of a node represents the posterior probability value of the estimated ancestral state. The color of the node represents the trait state.

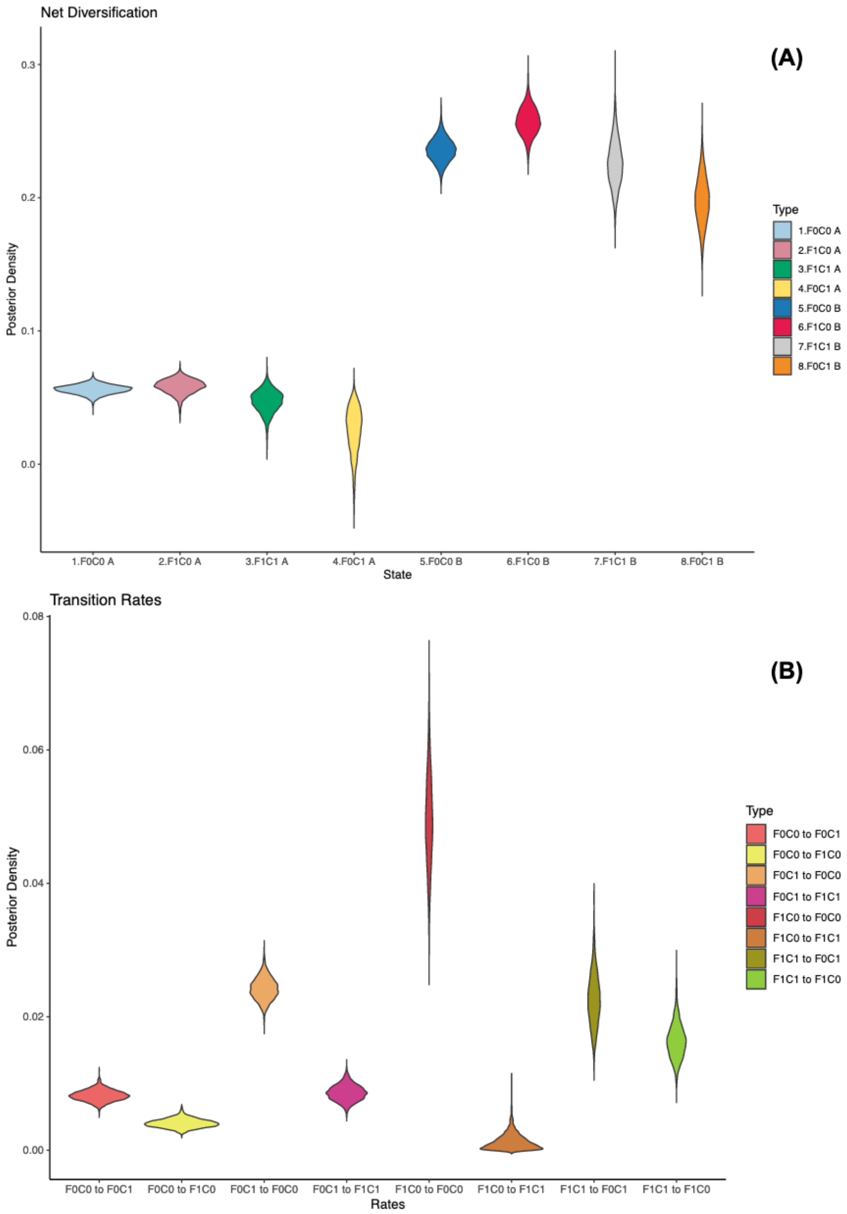


Figure 4. (A) Posterior distribution for each of the parameters in the frugivory and carotenoid-dependent plumage coloration model of focal traits with a hidden state: M9. F0 C0/F1 C0/F1 C1/F0 C1 + A/B. The width of each plot indicates the relative probability density for specific state value, with broader sections signifying higher density, hence more likely values. The MuHiSSE models show a greater diversification linked to a hidden state and not to either of the focal traits. (B) Posterior density distribution of the estimated transition rates between frugivory and carotenoid-dependent plumage coloration states across passerine species. Each violin plot represents the posterior density for a specific evolutionary transition (e.g., from F0 C0 to F0 C1), illustrating the probability distribution of each rate based on the posterior samples.

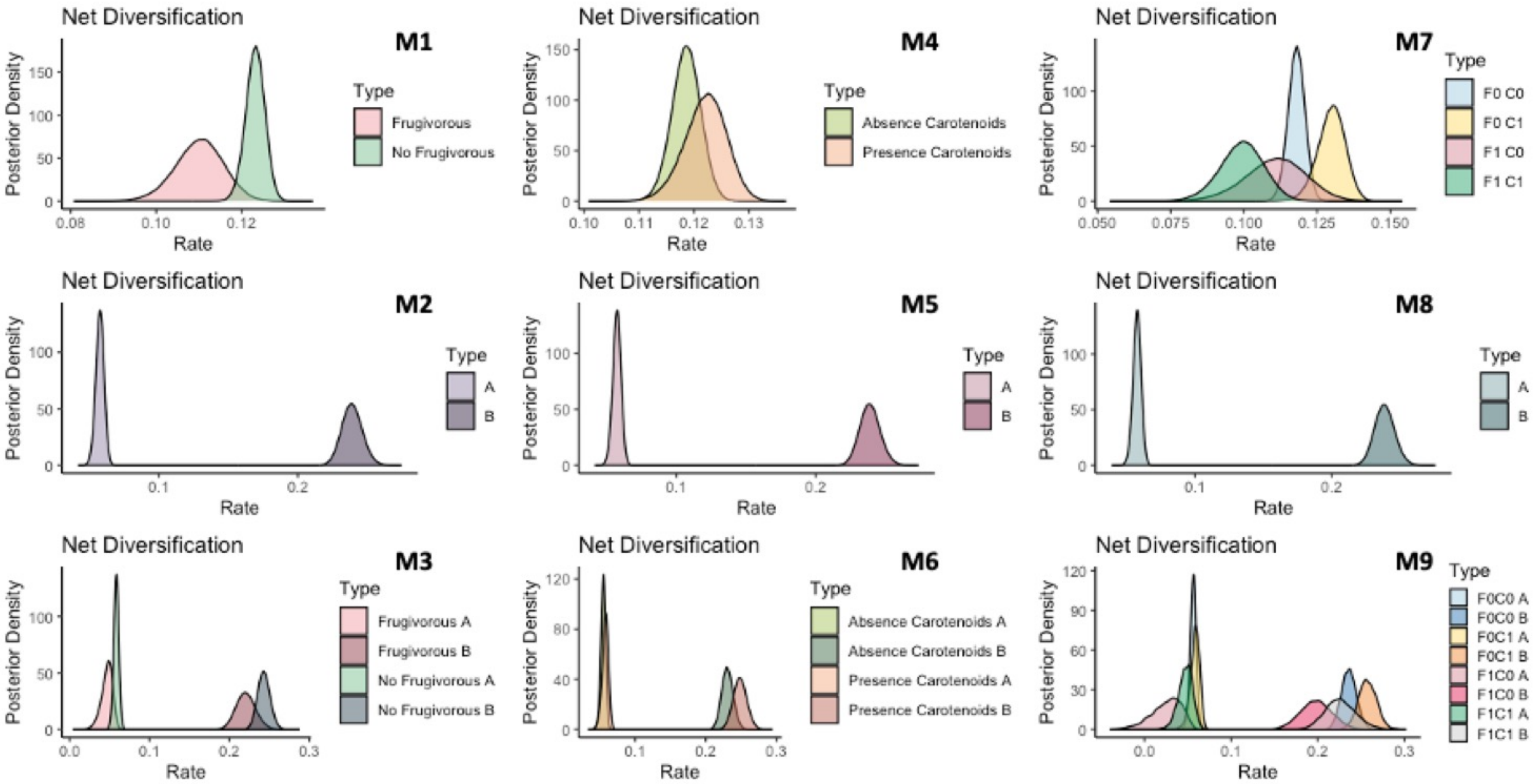


Figure S1. Net diversification rates for SSE models of focal traits with or without a hidden state. Each panel contains a graphical summary of estimated model parameters and displays posterior distributions for net diversification estimates.

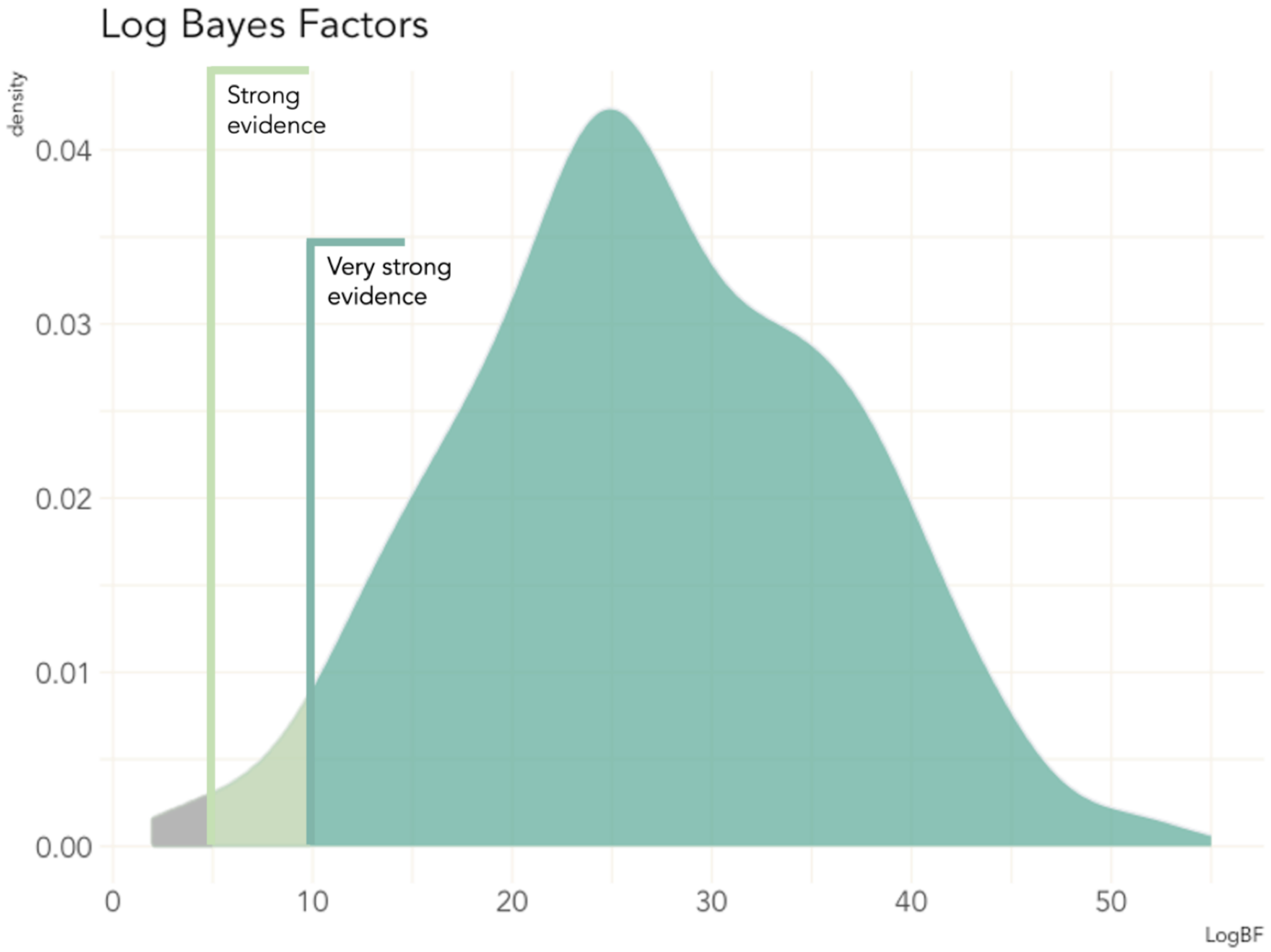


Figure S2. Distribution of Log Bayes factors obtained from the comparison between BayesTraits correlated evolution models for each sampled phylogenetic tree. The graph shows mostly very strong support for the dependent model.

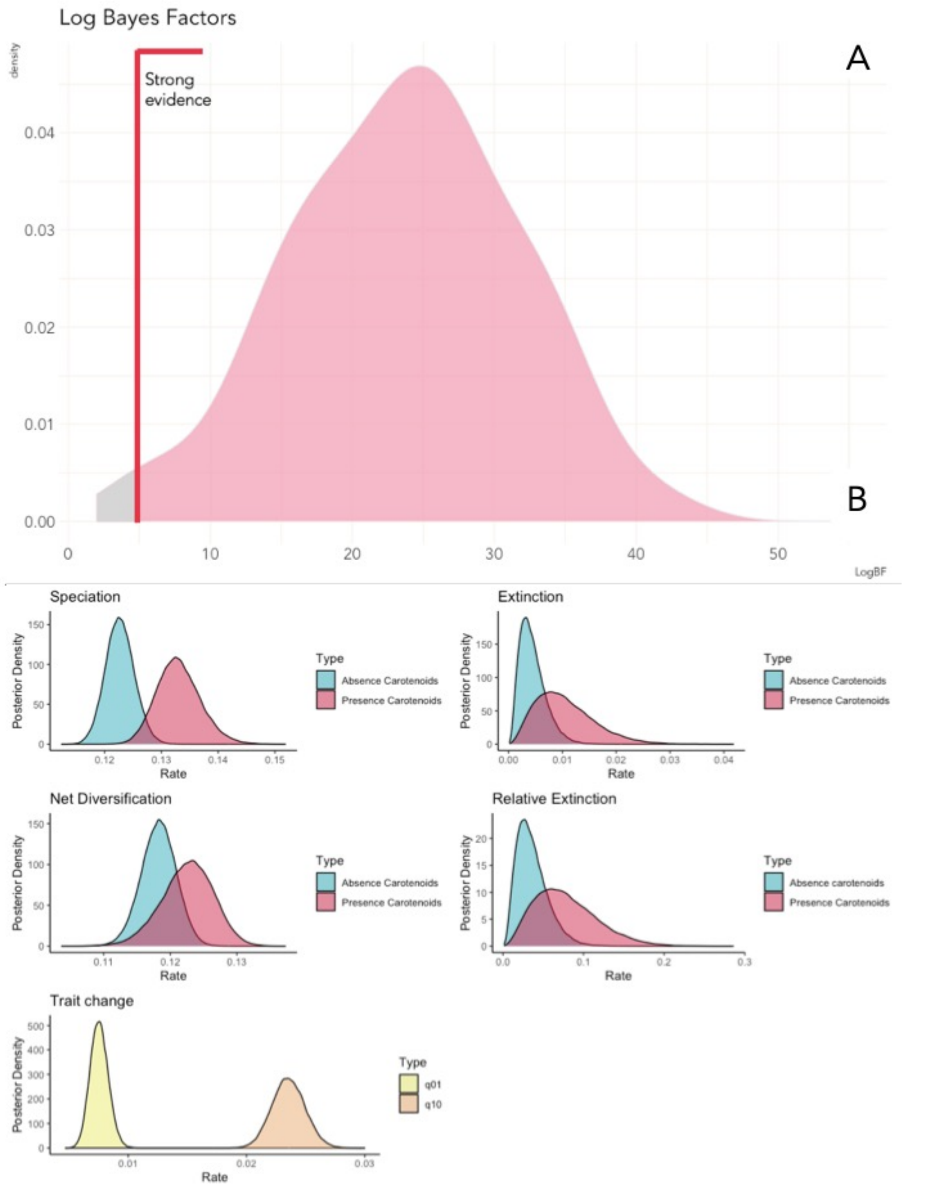
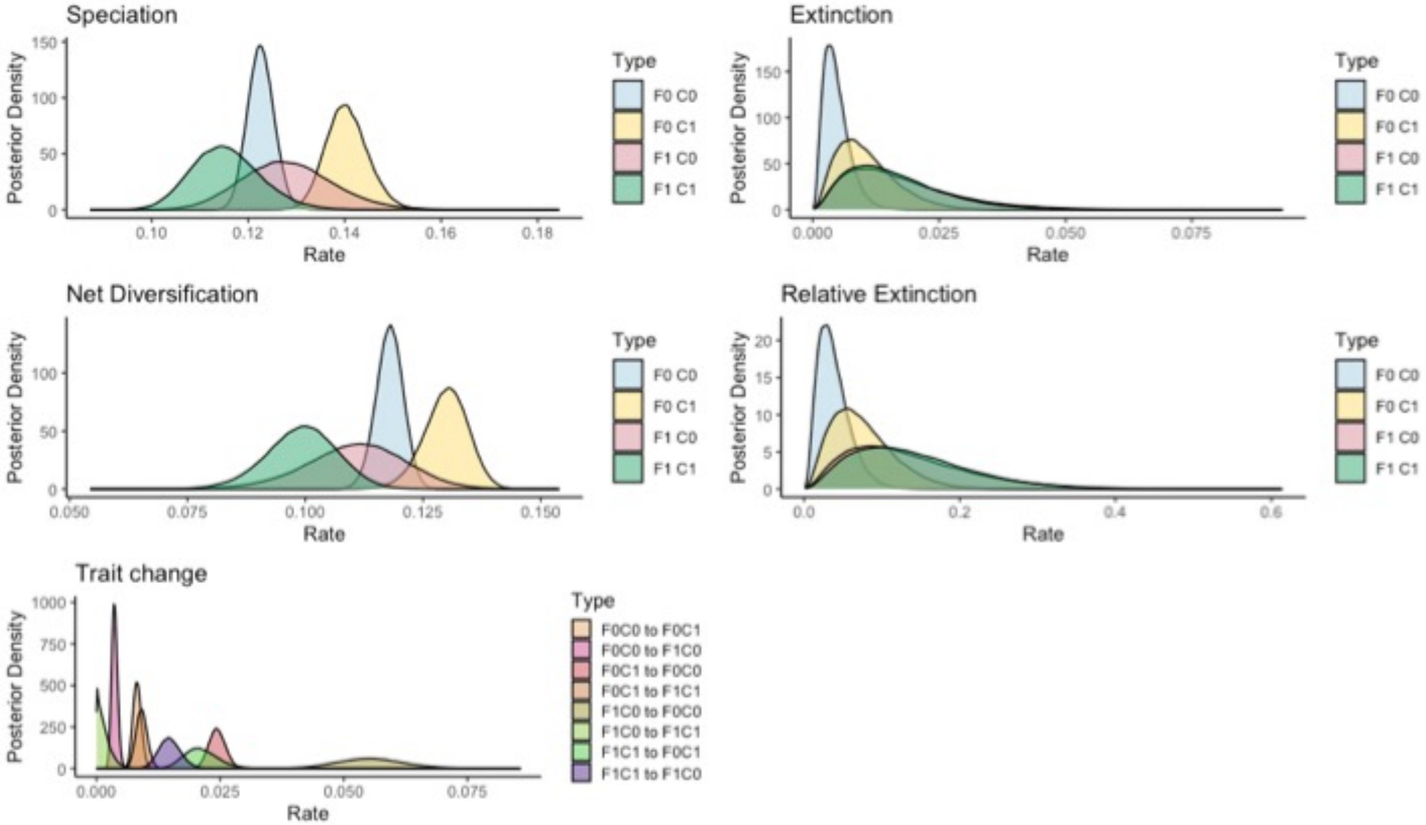


Figure S3. A) Distribution of Log Bayes factors obtained from the comparison between BayesTraits correlated evolution models with the species with conflicting classification from Delhey et al. (2022). The graph shows mostly very strong support for the dependent model. B) Speciation, extinction, and net diversification rates for SSE models of carotenoids with the species with conflicting classification from Delhey et al. (2022).



Speciation

Extinction

Net Diversification

Relative Extinction

Trait change

Figure S4. Speciation, extinction, and net diversification rates for State-dependent Speciation and Extinction models (SSE) of carotenoid-dependent coloration and frugivory (M7; MuSSE). Speciation and extinction rates are also presented to demonstrate the relative contribution of each process to overall diversification patterns.

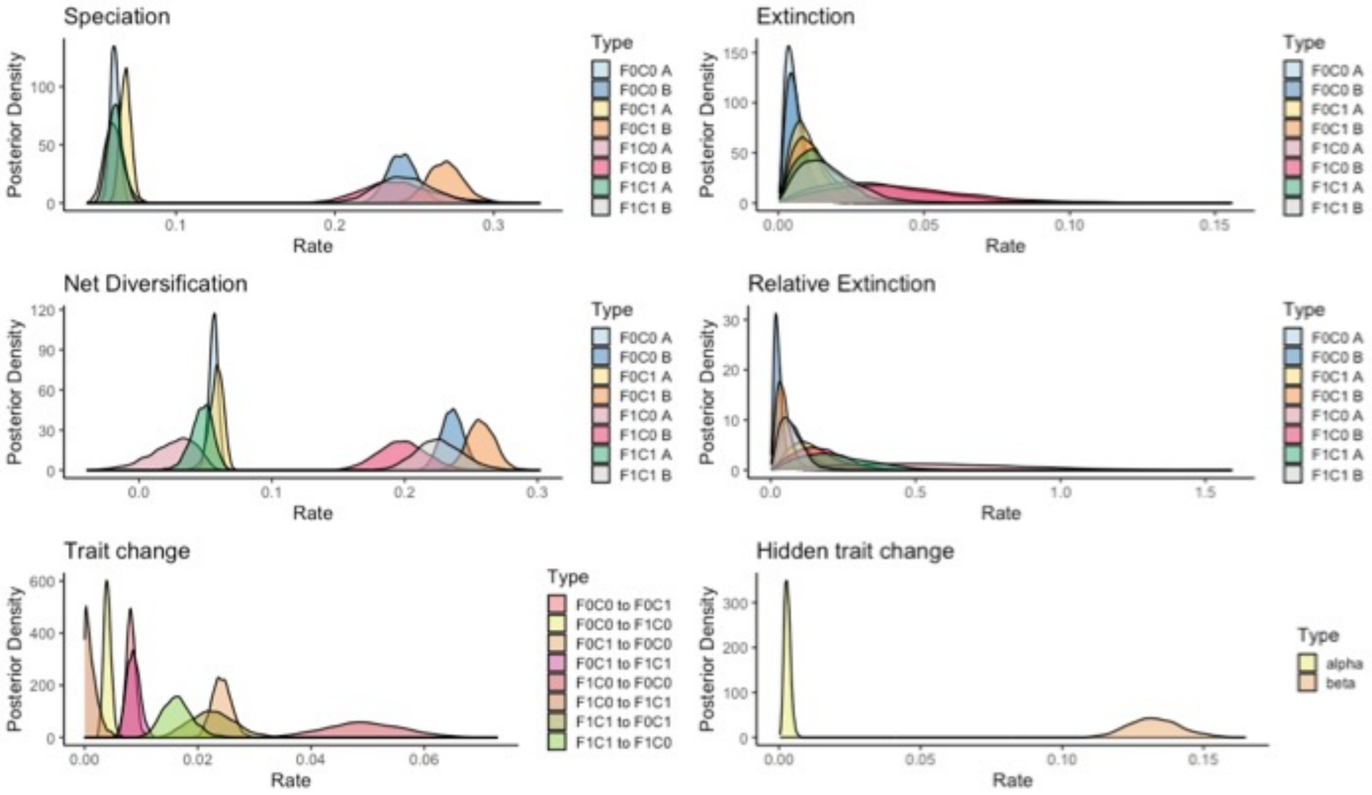


Figure S5. Speciation, extinction, and net diversification rates for Multi-State Hidden State Speciation and Extinction (MuHiSSE) models analyzing carotenoid-dependent plumage coloration, frugivory, and hidden diversification factors (M9; MuHiSSE). Speciation and extinction rates are also presented to demonstrate the relative contribution of each process to overall diversification patterns.

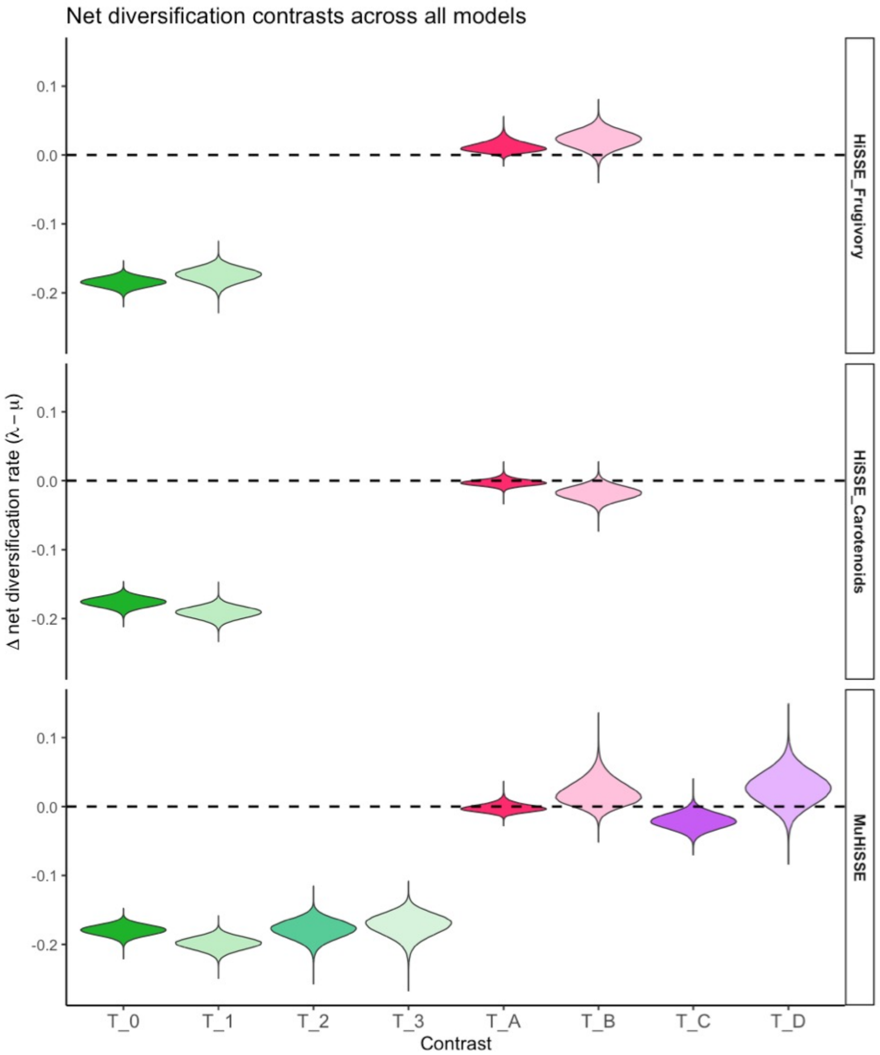


Figure S6. Net diversification contrasts across all models. Violin plots show the posterior distributions of net diversification rate contrasts (Δ = λ − μ) for different comparisons across the models incorporating hidden sates: HiSSE_Frugivory, HiSSE_Carotenoids, and MuHiSSE models. Contrasts labeled T_A to T_D represent differences between observed trait states, such as frugivory vs. non-frugivory or presence vs. absence of carotenoids. Contrasts labeled T_0 to T_3 reflect differences between hidden states while holding the observed trait constant. Distributions centered away from zero and whose 95% credible intervals do not include zero provide evidence for differences in diversification rates. The dashed horizontal line at zero marks the null expectation of no difference.

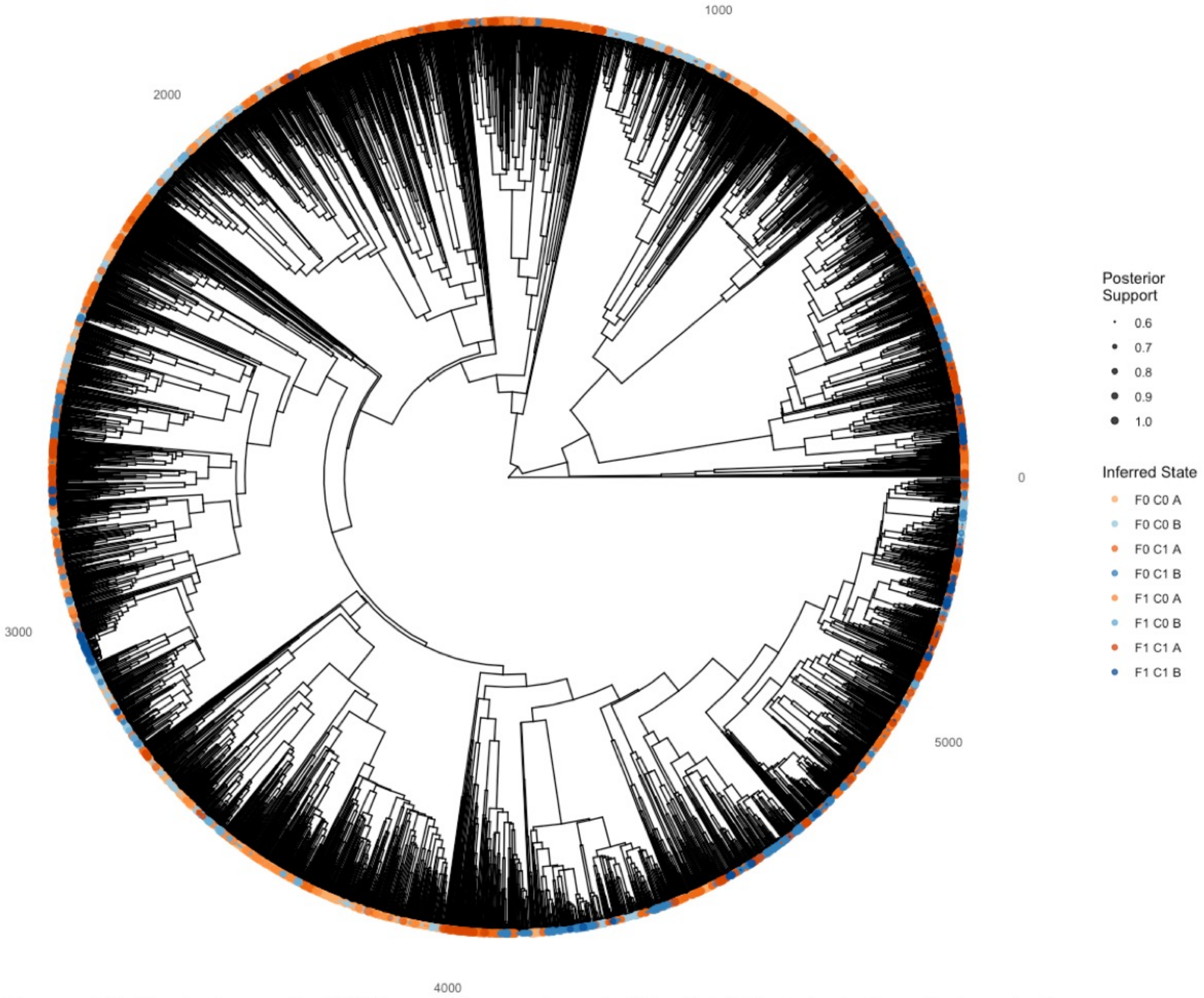


Figure S7. Posterior probabilities of the most probable (MAP) state inferred at each tip under the MuHiSSE model, summarizing support across 5,470 passerine species. Dot size reflects posterior probability for the most likely state at each tip.

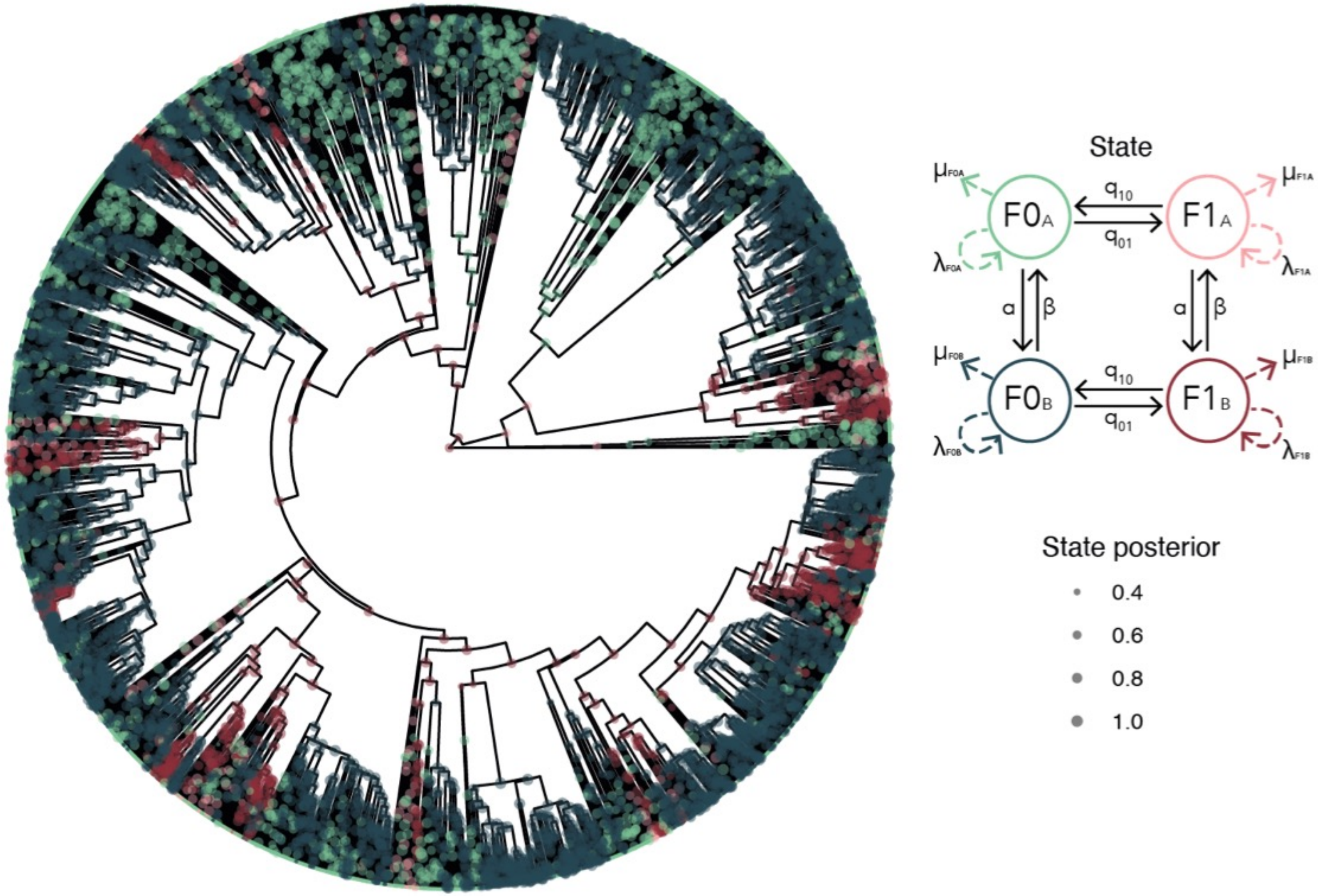


Figure S8. Ancestral state estimation using the maximum a posteriori for each node of model M2. F0/F1+A/B model. State posterior value shown at the root.

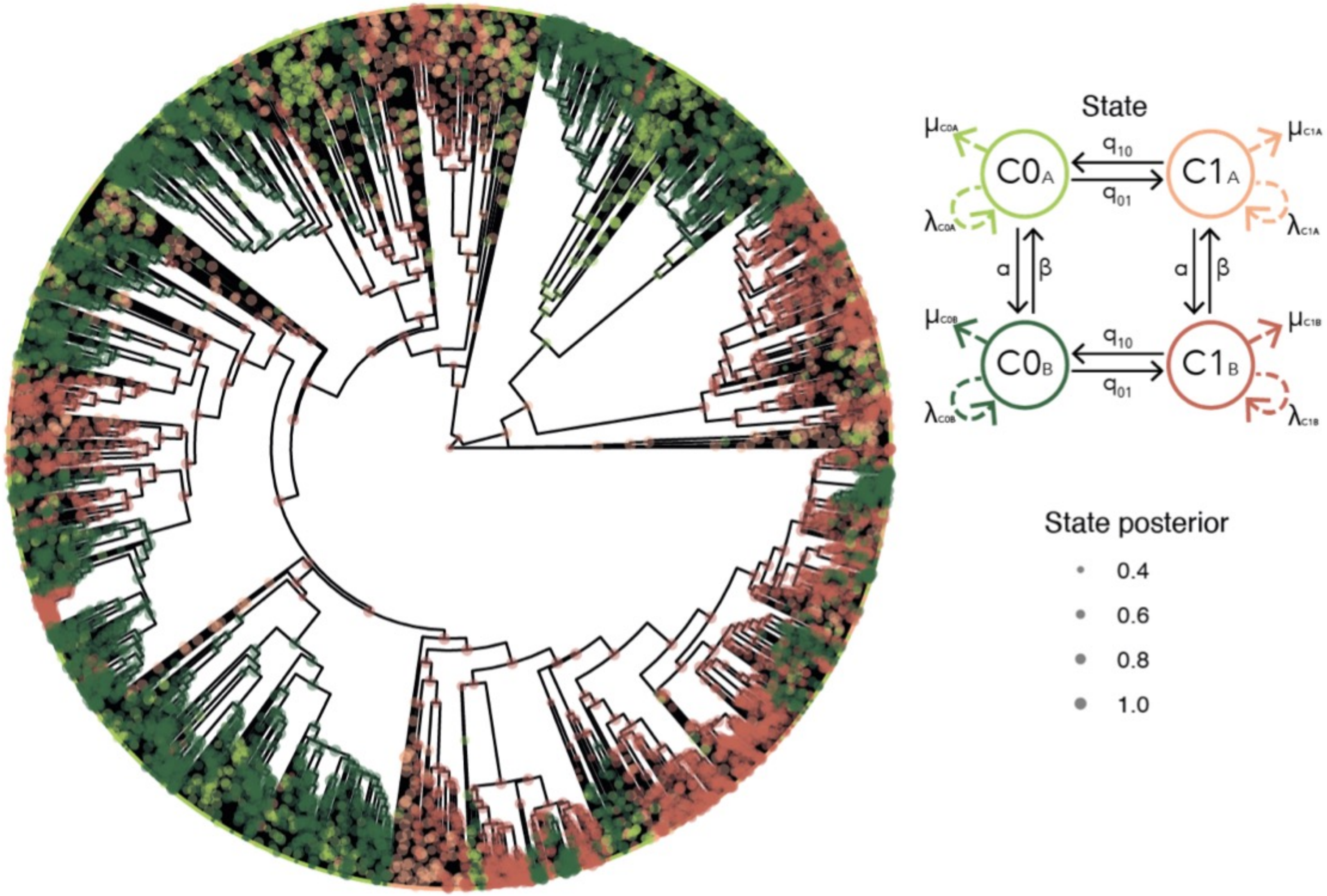


Figure S9. Ancestral state estimation using the maximum a posteriori for each node of model M5. C0/C1+A/B model. State posterior value shown at the root.

Table S1. Summary of transition rates between combinations of frugivory and carotenoid presence estimated under the RJ-MCMC Discrete Dependent model in BayesTraits. Values are based on 347,205 posterior samples. The median and interquartile range (IQR, 25th–75th percentile) describe the posterior distribution of each transition rate. The Z-score indicates the proportion of samples in which the rate was fixed to zero by the RJ algorithm — higher values suggest lower support for including that transition in the model.

Transition	Median	IQR (25%–75%)	Z-score
F0C0-F1C0	0.009	0.009–0.011	0
F0C0-F0C1	0.004	0.004–0.005	0
F1C0-F0C0	0.025	0.023–0.028	0
F1C0-F1C1	0.009	0.009–0.010	0
F0C1-F0C0	0.060	0.052–0.069	0
F0C1-F1C1	0.005	0.004–0.007	0.05
F1C1-F1C0	0.026	0.023–0.028	0
F1C1-F0C1	0.011	0.009–0.020	0

Table S2. Summary of net diversification contrasts between trait-states and between observed and hidden states for all hidden-state models.

Model	Diff	Contrast	Mean	2.50%	97.50%	Signif	Type
HiSSE_Frug	T_0	F0 A - F0 B	-0.185	-0.199	-0.172	≠ 0	Hidden state contrast
HiSSE_Frug	T_1	F1 A - F1 B	-0.174	-0.195	-0.155	≠ 0	Hidden state contrast
HiSSE_Frug	T_A	F1 A -F0 A	0.012	0.000	0.029	Includes 0	Observable contrast
HiSSE_Frug	T_B	F1 B - F0 B	0.023	-0.003	0.047	Includes 0	Observable contrast
HiSSE_Caro	T_0	C0 A - C0 B	-0.176	-0.191	-0.162	≠ 0	Hidden state contrast
HiSSE_Caro	T_1	C1 A - C1 B	-0.191	-0.208	-0.175	≠ 0	Hidden state contrast
HiSSE_Caro	T_A	C1 A - C0 A	-0.003	-0.012	0.007	Includes 0	Observable contrast
HiSSE_Caro	T_B	C1 B - C0 B	-0.018	-0.037	0.001	Includes 0	Observable contrast
MuHiSSE	T_0	F0C0 A - F0C0 B	-0.180	-0.195	-0.165	≠ 0	Hidden state contrast
MuHiSSE	T_1	F1C0 A - F1C0 B	-0.199	-0.217	-0.182	≠ 0	Hidden state contrast
MuHiSSE	T_2	F0C1 A - F0C1 B	-0.179	-0.206	-0.154	≠ 0	Hidden state contrast
MuHiSSE	T_3	F1C1 A - F1C1 B	-0.172	-0.206	-0.144	≠ 0	Hidden state contrast
MuHiSSE	T_A	F0C0 A - F1C0 A	-0.002	-0.013	0.011	Includes 0	Observable contrast
MuHiSSE	T_B	F0C1 A - F1C1 A	0.020	-0.011	0.061	Includes 0	Observable contrast
MuHiSSE	T_C	F0C0 B - F1C0 B	-0.021	-0.043	0.001	Includes 0	Observable contrast
MuHiSSE	T_D	F0C1 B - F1C1 B	0.027	-0.019	0.074	Includes 0	Observable contrast

This table presents posterior means, and 95% credible intervals for net diversification rate differences ($\Delta = \lambda - \mu$) across HiSSE_Frugivory, HiSSE_Carotenoids, and MuHiSSE models. Each contrast represents either a comparison between observed trait states (T_A–T_D) or between hidden states (T_0–T_3). Contrasts whose credible intervals exclude zero are highlighted and indicate strong evidence of differences in diversification rates.

1. What are Bayes factors?
2. What is reversible jump MCMC?
3. Why did they binarize frugivory and coloration. Although they do talk about this in the discussion, I think it would have been more interesting to look at continuous traits. So that makes me think what even the point of the paper was if they made such a categorization. It does give a foundation for further studies. On that note, my question is how do we look at continuous traits without categorization?
4. In the methods at the top of the right side of page 1645, the authors state that they conservatively classified "species where fruit consumption was mentioned without quantitative detail (e.g., “fruits and insects”) as nonfrugivorous, as these descriptions did not specify the proportion of fruits in their diet." It seems to me that the most conservative option would be to remove these species from the analysis altogether, as they did with species without enough information on diet. Why did they choose to include species without quantative information
5. ."We obtained a distribution of 1,000 trees with different topologies from the pseudo-posterior distribution for the Hackett backbone (Jetz et al., 2012). These trees allowed us to account for phylogenetic uncertainty by sampling across a range of topologies". If that interpretation is right, how common is it to do this?
6. Is there a specific reason they chose these numbers or do you just want a big enough itteration in the MCMC process? "MCMC chains were run for 1,010,000 iterations for each topology, totaling 505,000,000 iterations, with 10,000 iterations as burn-in and sampling every 1,000 iterations.”
7. Philosophically, is there a point at which your trees are so big and you have so many traits, does it make sense to plot everything on the tree? Like figure 3 is a choice, it is pretty to look at, but it is hard for me to extract meaningful information from it at the tip
8. Also, is there a historical reason why birds have so many resources like BirdTree.org, eBird.org, etc? Or do people really just like birds?
9. Why do we need to incorporate speciation and extinction into the models?