A selection of ongoing work

Floral evolution

O'Meara*, Stacey Smith*, Armbruster, Harder, Hardy, Hileman, Hufford, Litt, Magallon, Stephen Smith, Stevens, Fenster, Diggle

Flexible trait evolution

O'Meara and Banbury[P]

Phylogeographic models

O'Meara, Jackson[P], Morales-Garcia, Carstens

* = equal lead authors
[P] = postdoc mentee

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NPS

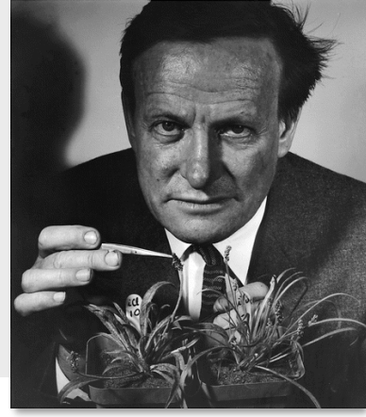


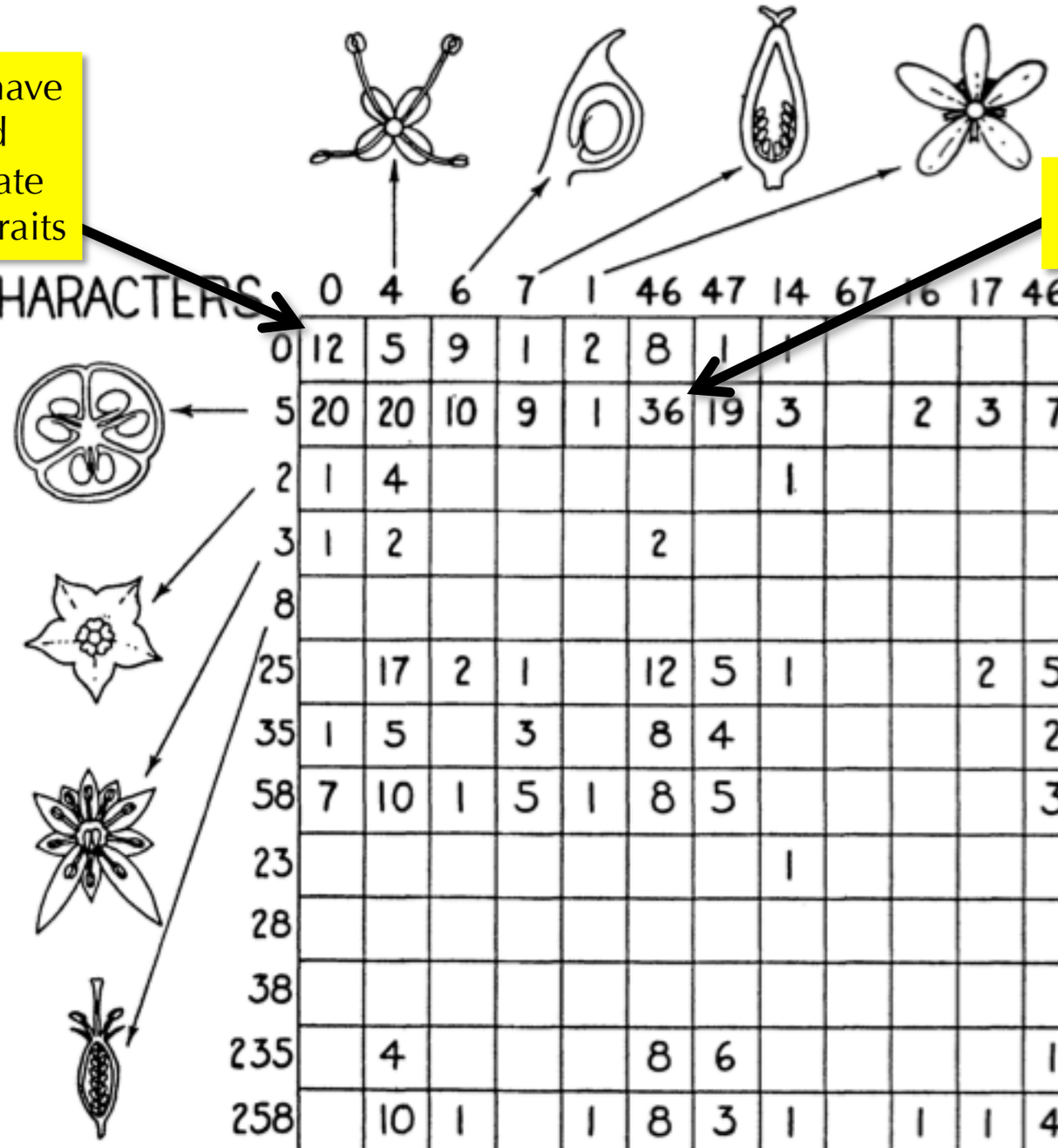
TABLE 1. *List of the eight characters used most frequently in the classification of the families of angiosperms*

Character: Primitive	Character: Advanced	Number in Chart
Calyx and corolla both present (dichlamydous).	Corolla or entire perianth absent (mono- or achlamydous).	1
Petals separate (polypetalous).	Petals (sepals in monochlamydous forms) united (sympetalous).	2
Calyx and corolla regular (actinomorphic).	Perianth irregular (zygomorphic).	3
Stamens more numerous than perianth members (polystemonous).	Stamens the same number as or fewer than perianth members (oligostemonous).	4
Carpels separate (apocarpous).	Carpels united (syncarpous).	5
Seeds more than one per carpel (many).	Seeds not more than one per carpel (few).	6
Placentation axial.	Placentation parietal, basal, or free central.	7
Carpels not united with the receptacle or perianth (hypogyny or perigyny).	Carpels united with receptacle, perianth, or both (epigyny).	8

Stebbins 1951

12 families have presumed ancestral state for all eight traits

36 families few stamens (4), fused carpels (5), and one seed per carpel (6)



CHARACTERS	0	4	6	7	1	46	47	14	67	16	17	467	146	147	167	1467
0	12	5	9	1	2	8	1	1					10			
5	20	20	10	9	1	36	19	3		2	3	7	8	3		24
2	1	4						1					1			
3	1	2				2										
8																
25		17	2	1		12	5	1			2	5	3	1		4
35	1	5		3		8	4					2	1	1		
58	7	10	1	5	1	8	5					3	1	1		5
23								1					1			
28																
38																
235		4				8	6					1				
258		10	1		1	8	3	1		1	1	4		3		6
358		7				2	1					1				
238																
2358		5				3	4	1				3				

No families have presumed derived state for all eight traits

Stebbins 1951

Stebbins (1951): Families are clumped in trait space, therefore "**combinations of characteristics** found in the larger, more successful families of flowering plants **evolved through the guidance of natural selection** because they represented particularly successful methods of solving problems of fertilization, seed dispersal or both."

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Continuing questions

- What is the mechanism? Natural selection for particular combinations? Differential diversification?

- Which traits matter most? Petal presence seems like it would be more important than position of the ovule inside a carpel.

- Is the pattern truly non-random?

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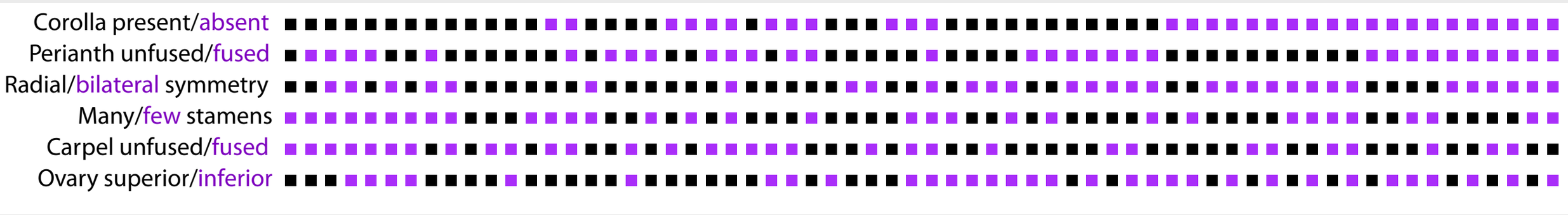
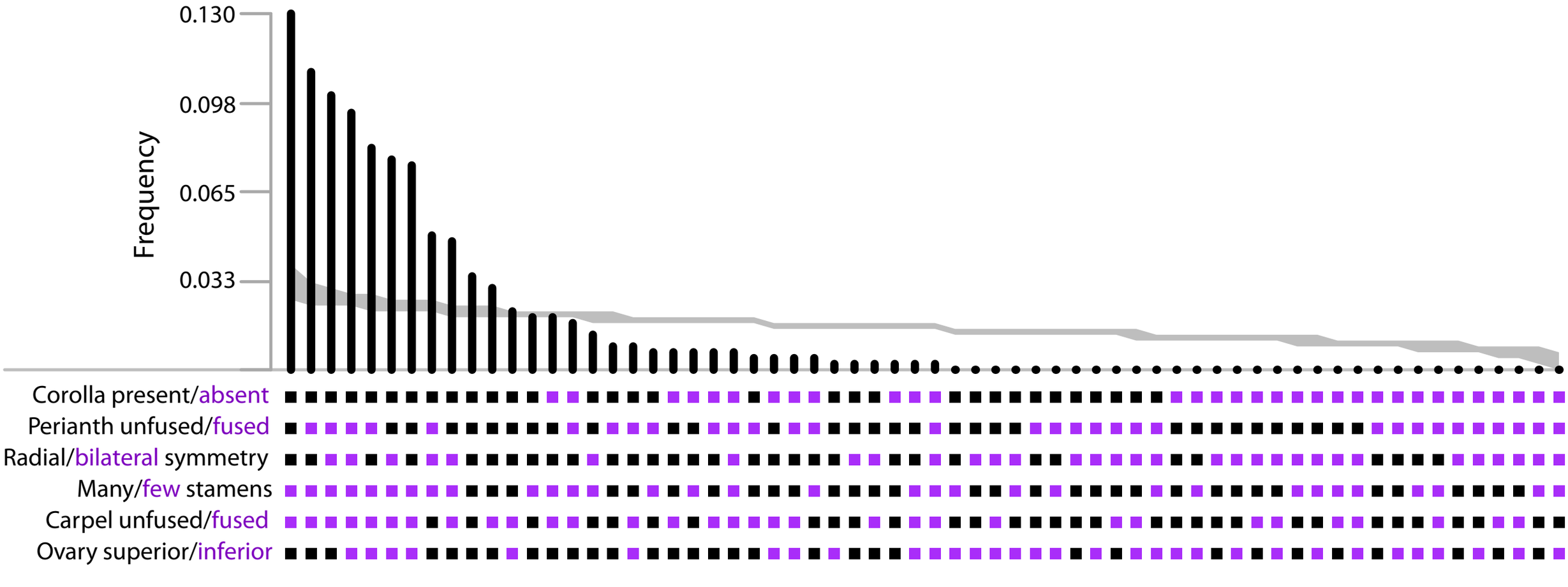
Stebbins 1951

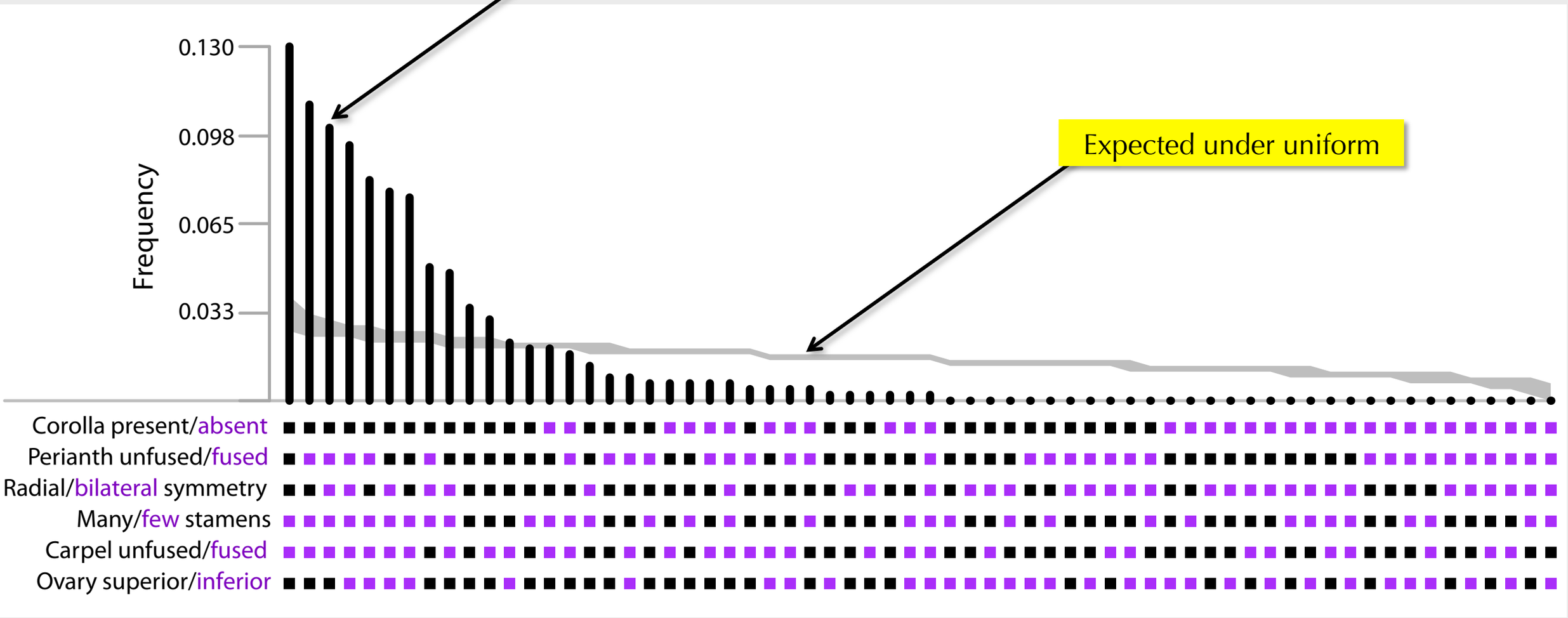
TABLE 1. *List of the eight characters used most frequently in the classification of the families of angiosperms*

Character	
Primitive	**Advanced**
Corolla present	Corolla absent
Perianth separate	Perianth fused
Radial symmetry	Bilateral symmetry
Many stamens	Few stamens
Carpels unfused	Carpels fused
Ovary superior	Ovary inferior

Stebbins 1951


Corolla present/absent
Perianth unfused/fused
Radial/bilateral symmetry
Many/few stamens
Carpel unfused/fused
Ovary superior/inferior


0.130
0.098
0.065
0.033
Frequency
Corolla present/absent
Perianth unfused/fused
Radial/bilateral symmetry
Many/few stamens
Carpel unfused/fused
Ovary superior/inferior


Actual frequencies
Expected under uniform
Frequency
0.130
0.098
0.065
0.033
Corolla present/absent
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Many/few stamens
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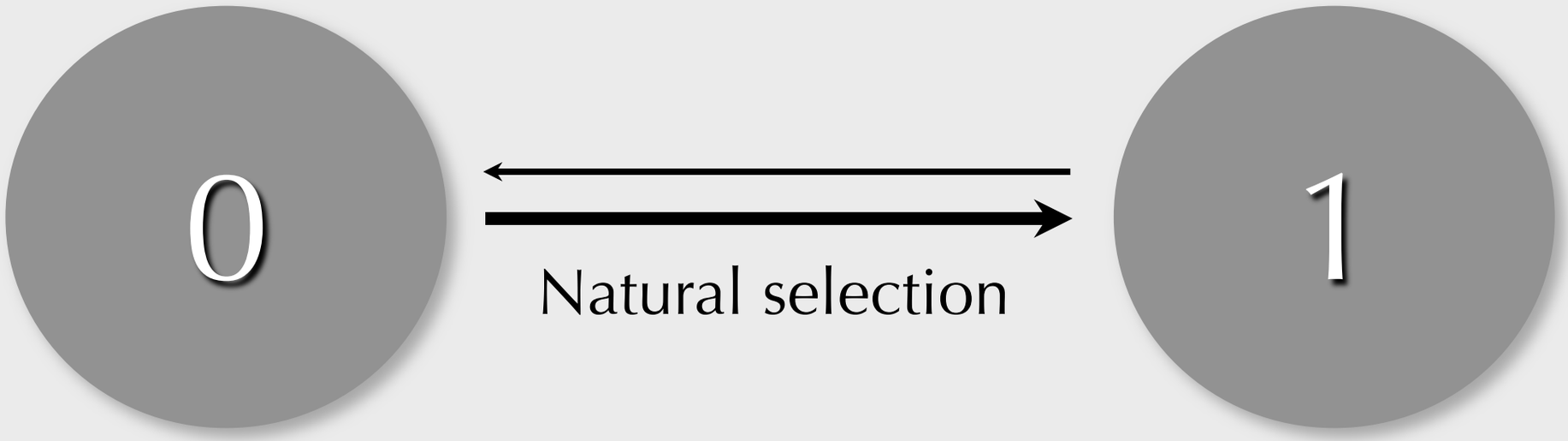
Actual frequencies

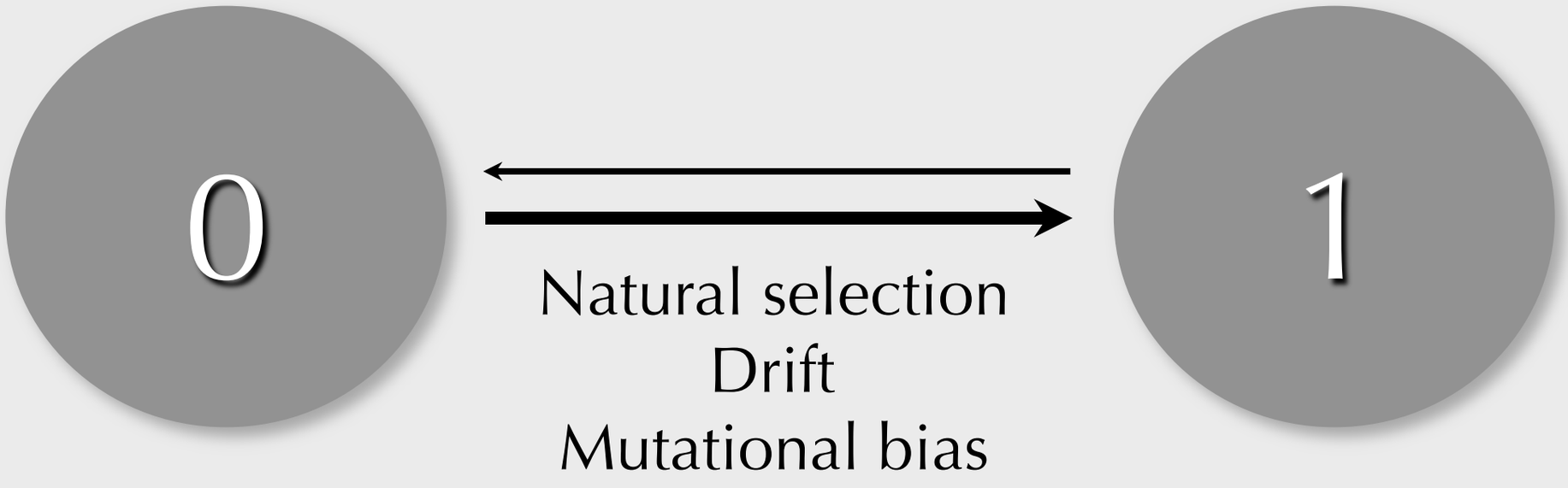
Expected under uniform

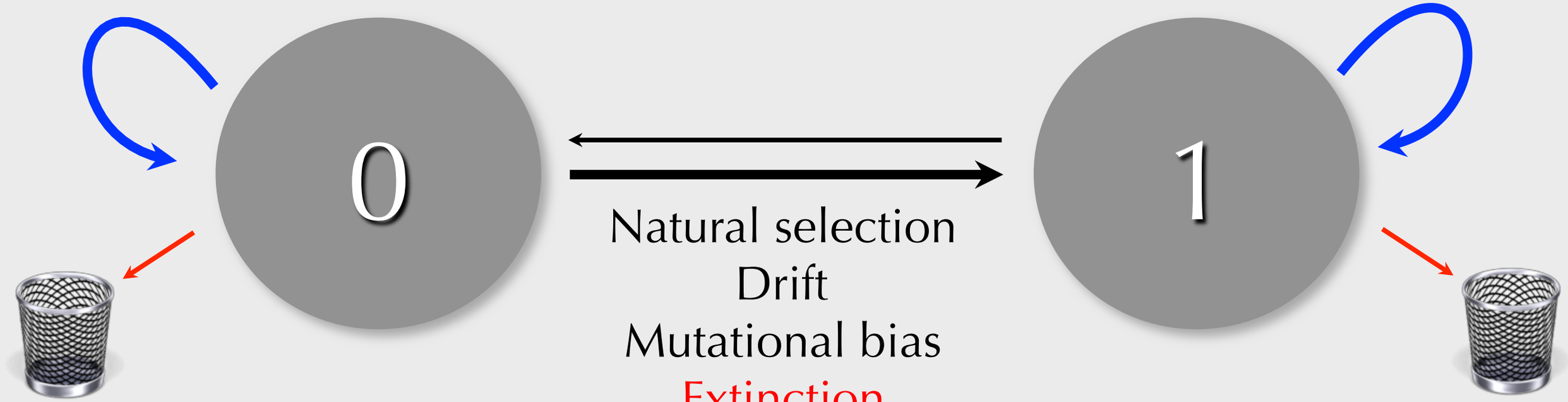
0.130
0.098
0.065
0.033
Frequency

Corolla present/absent
Perianth unfused/fused
Radial/bilateral symmetry
Many/few stamens
Carpel unfused/fused
Ovary superior/inferior

Presumed root state, still at high frequency


0
1
Natural selection


0
1
Natural selection
Drift
Mutational bias


0
1
Natural selection
Drift
Mutational bias
Extinction
Speciation

00

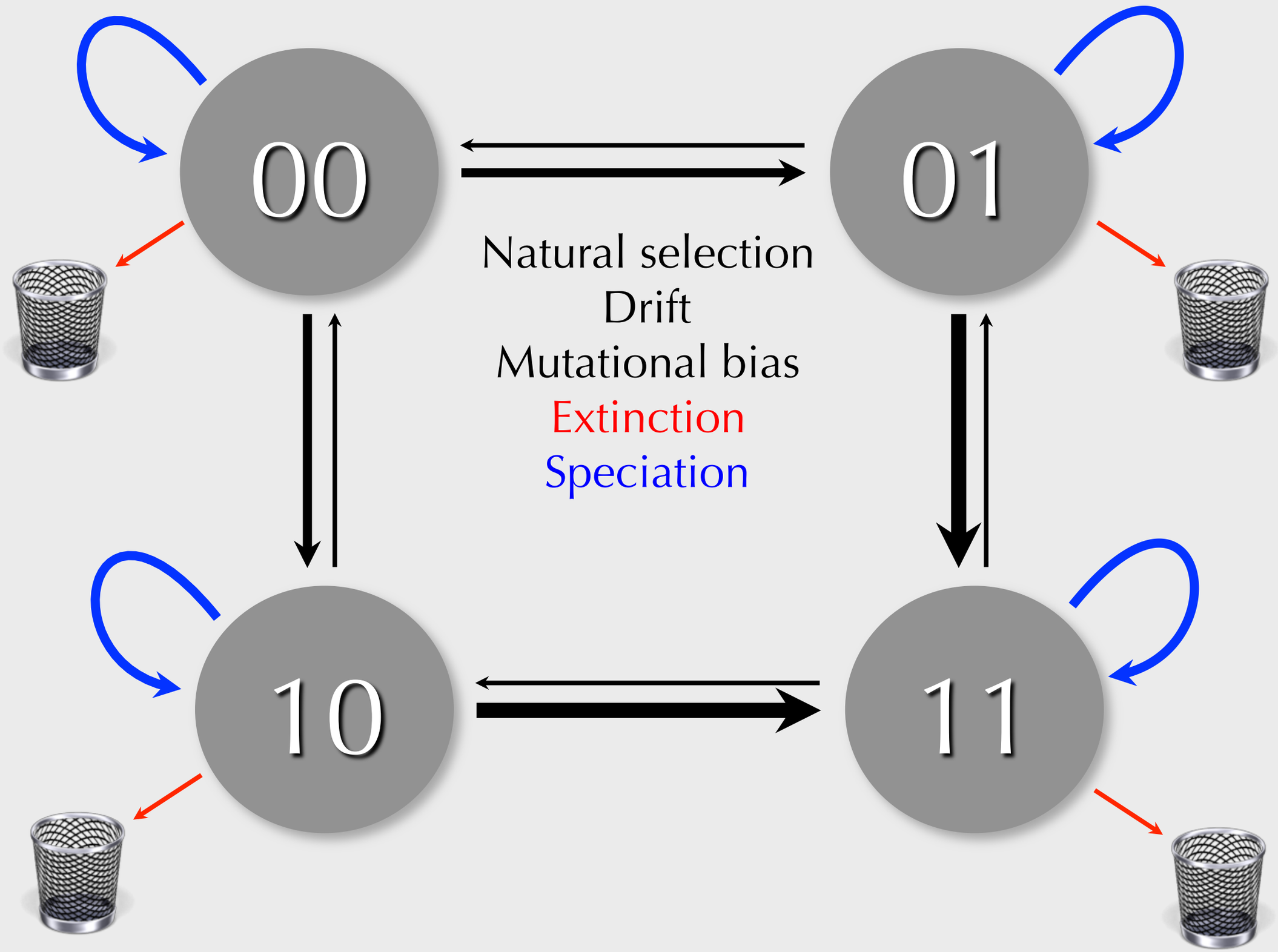
01

10

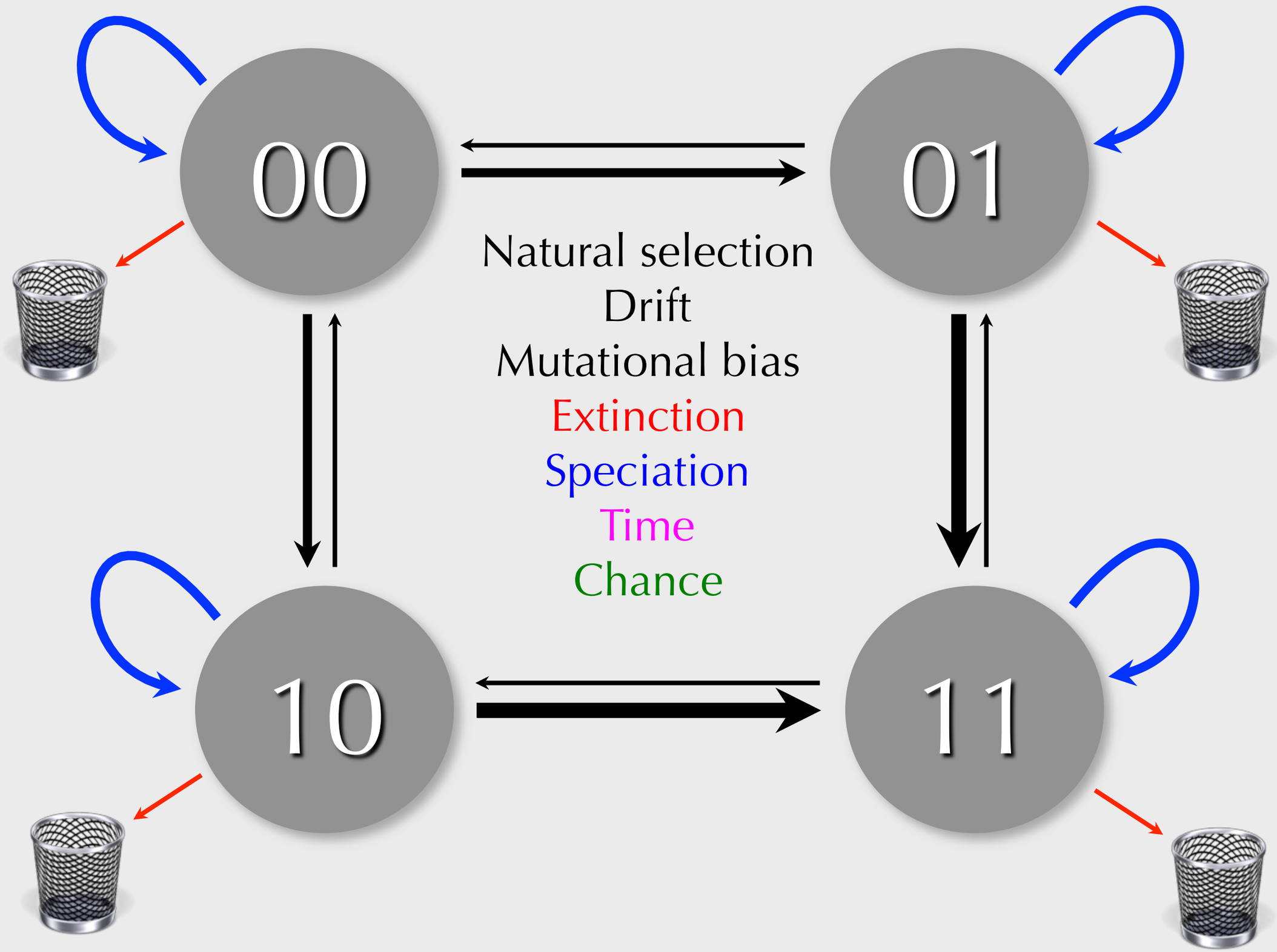
11

Natural selection
Drift
Mutational bias
Extinction
Speciation

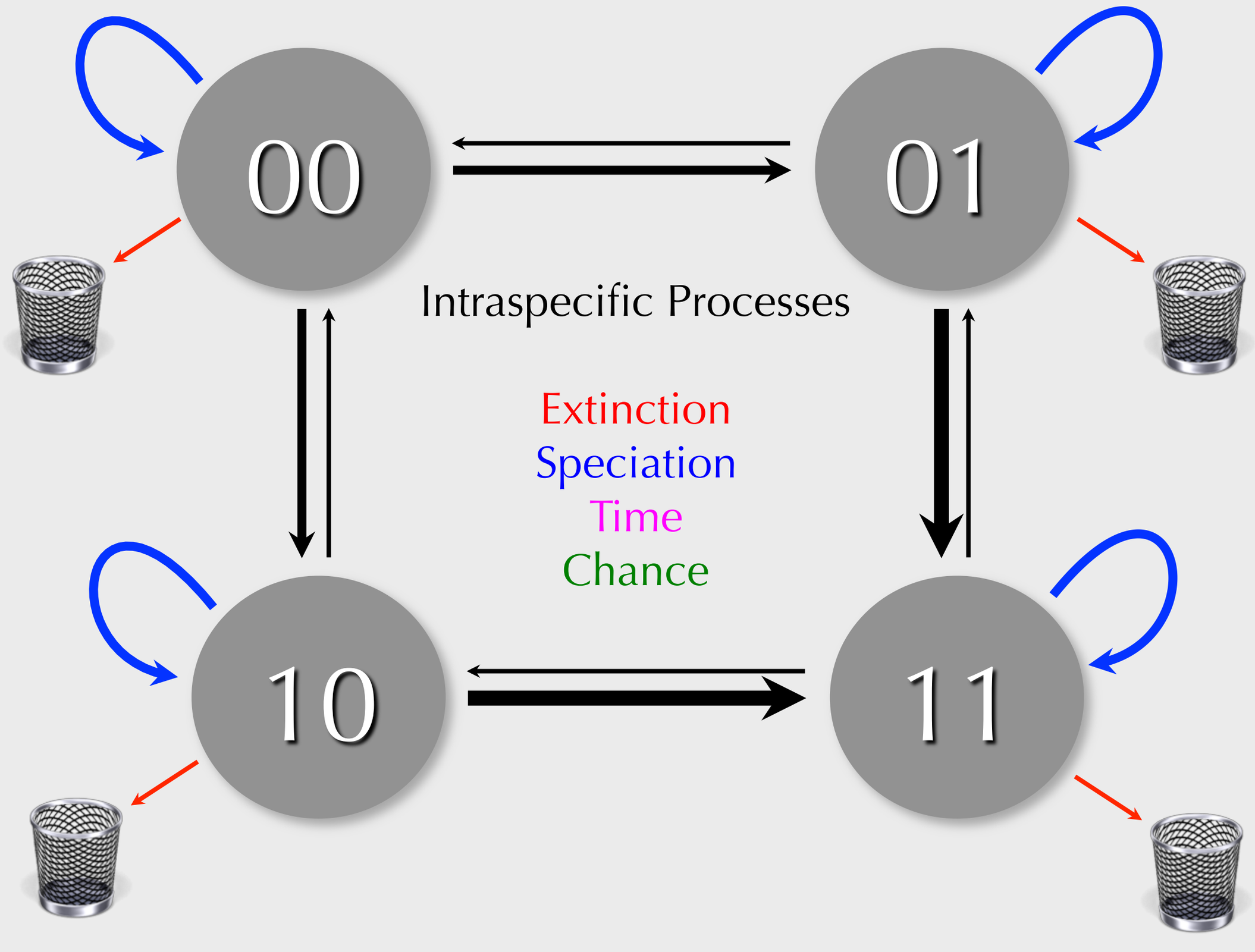
All the factors that lead to contemporary distributions?



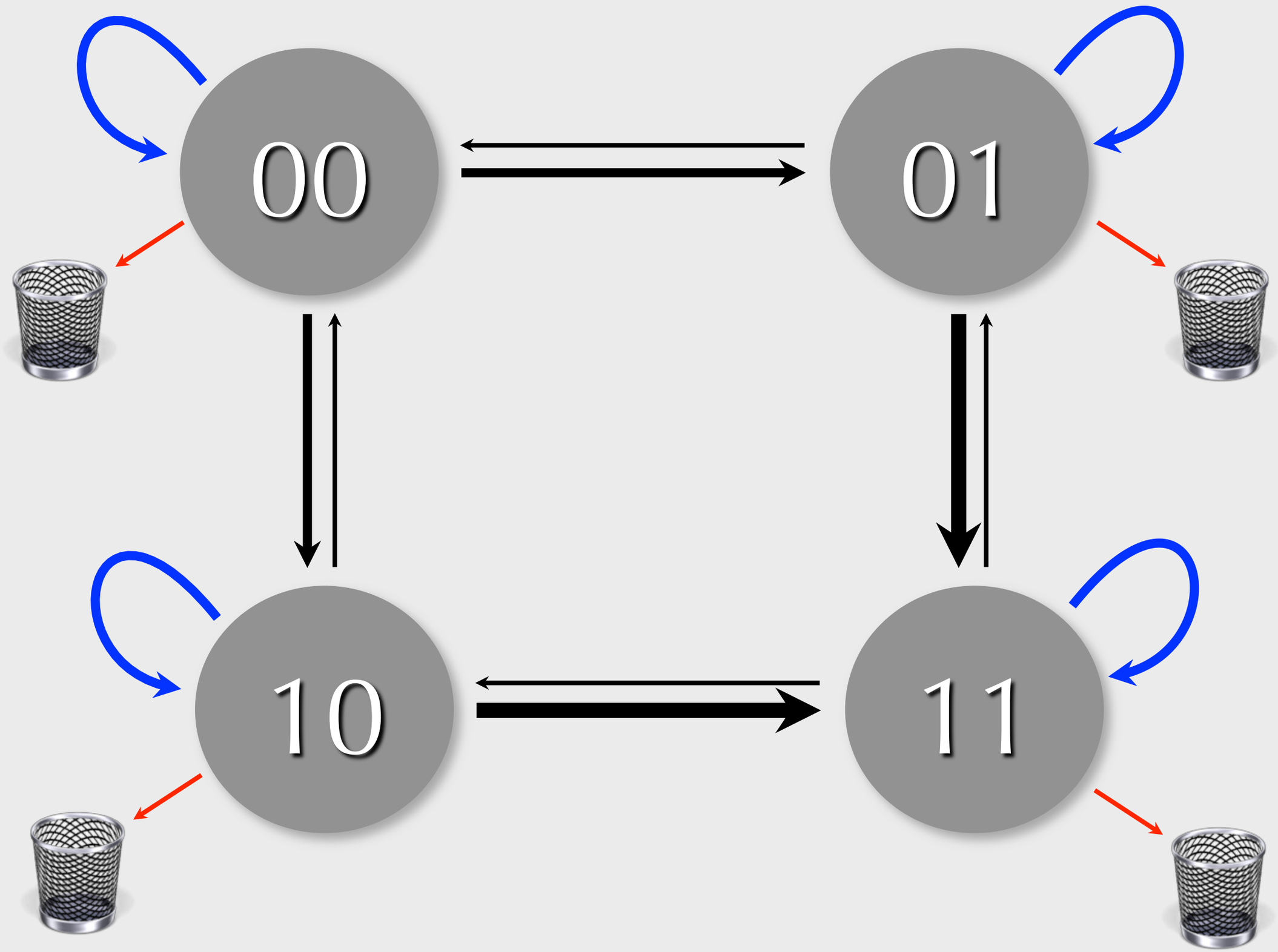
All the factors that lead to contemporary distributions?



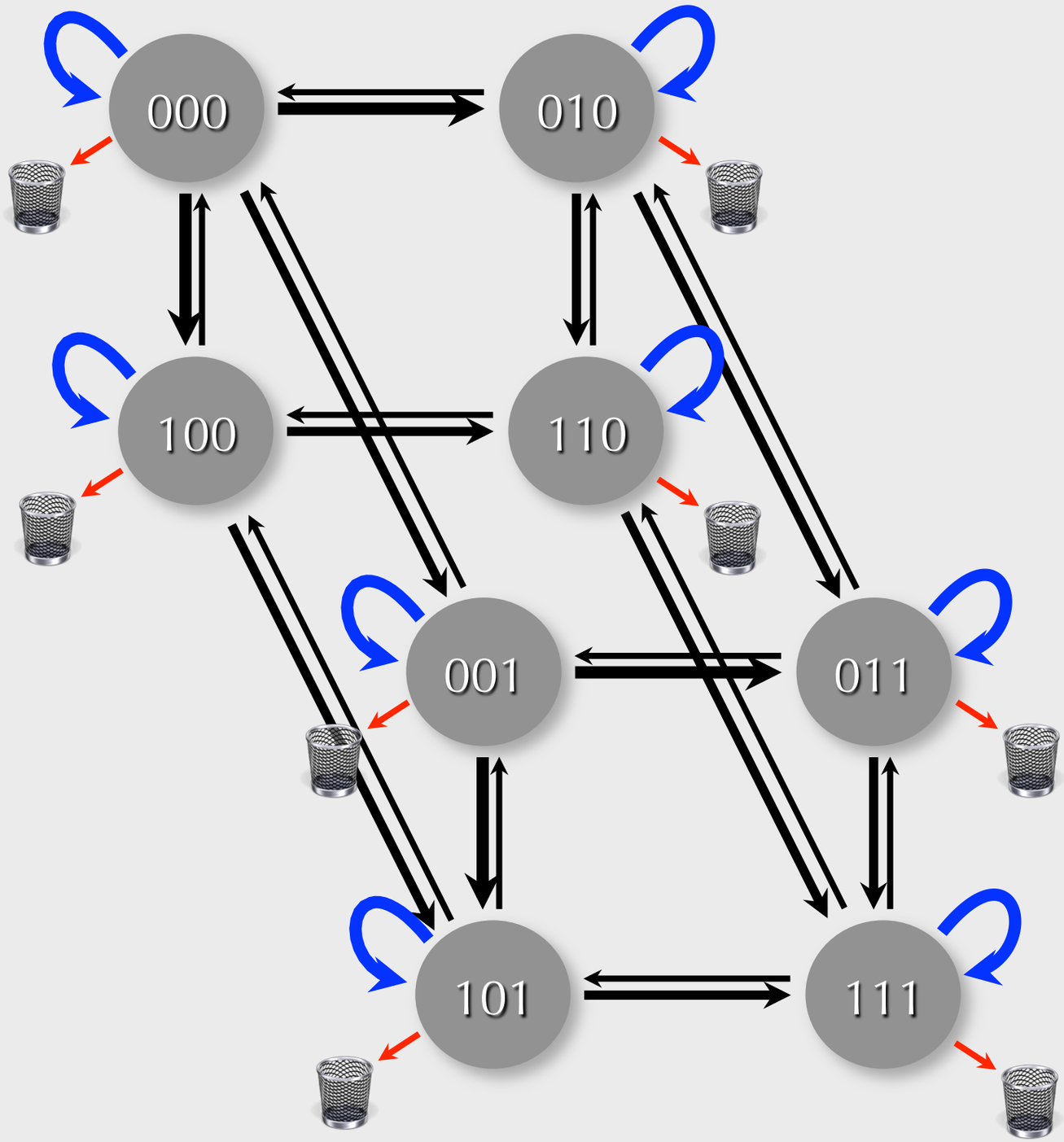
All the factors that lead to contemporary distributions?



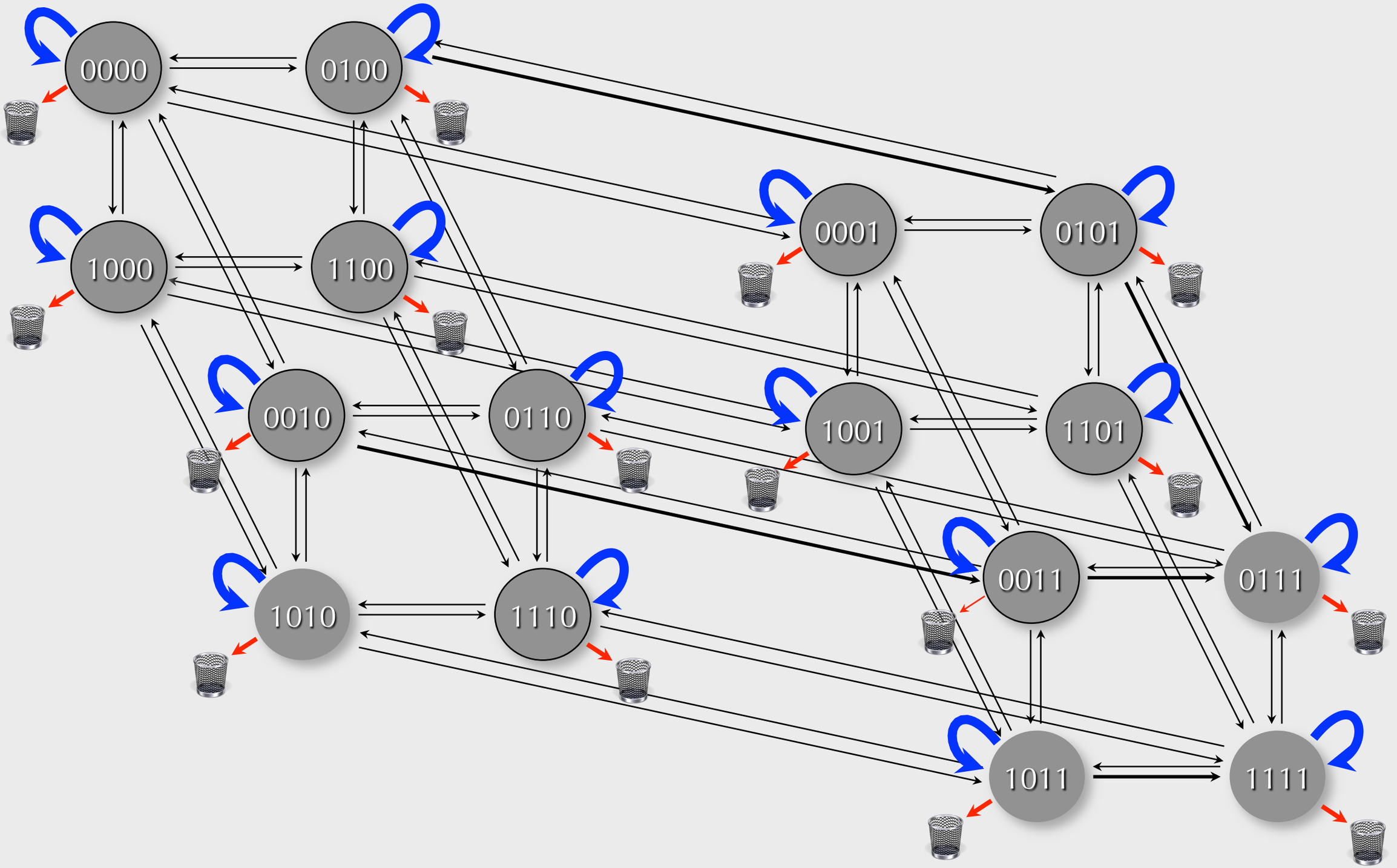
Two binary traits: 8 transitions, 4 birth, 4 death



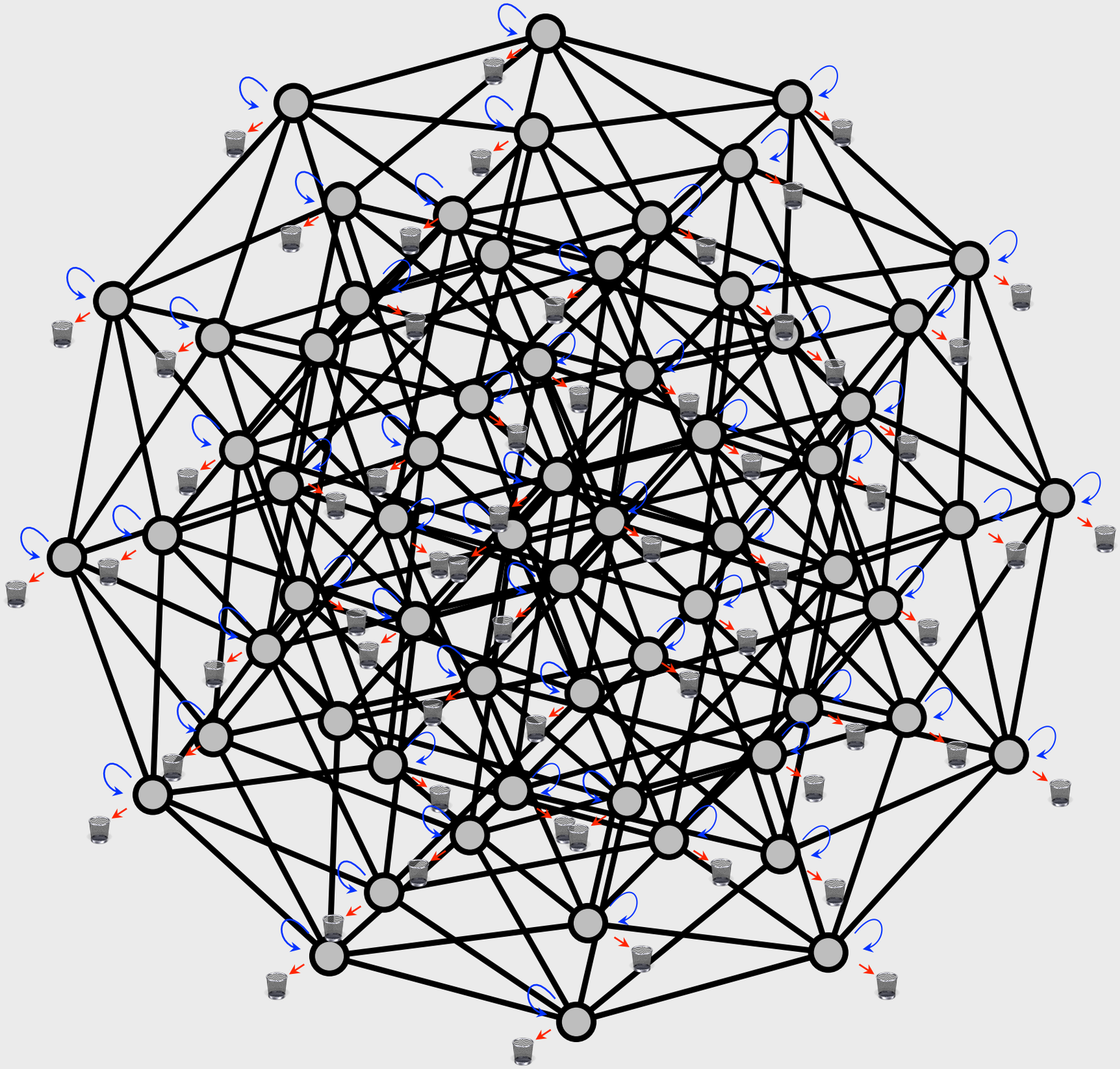
Three binary traits: 12 transitions, 8 birth, 8 death



Four binary traits: 64 transitions, 16 birth, 16 death

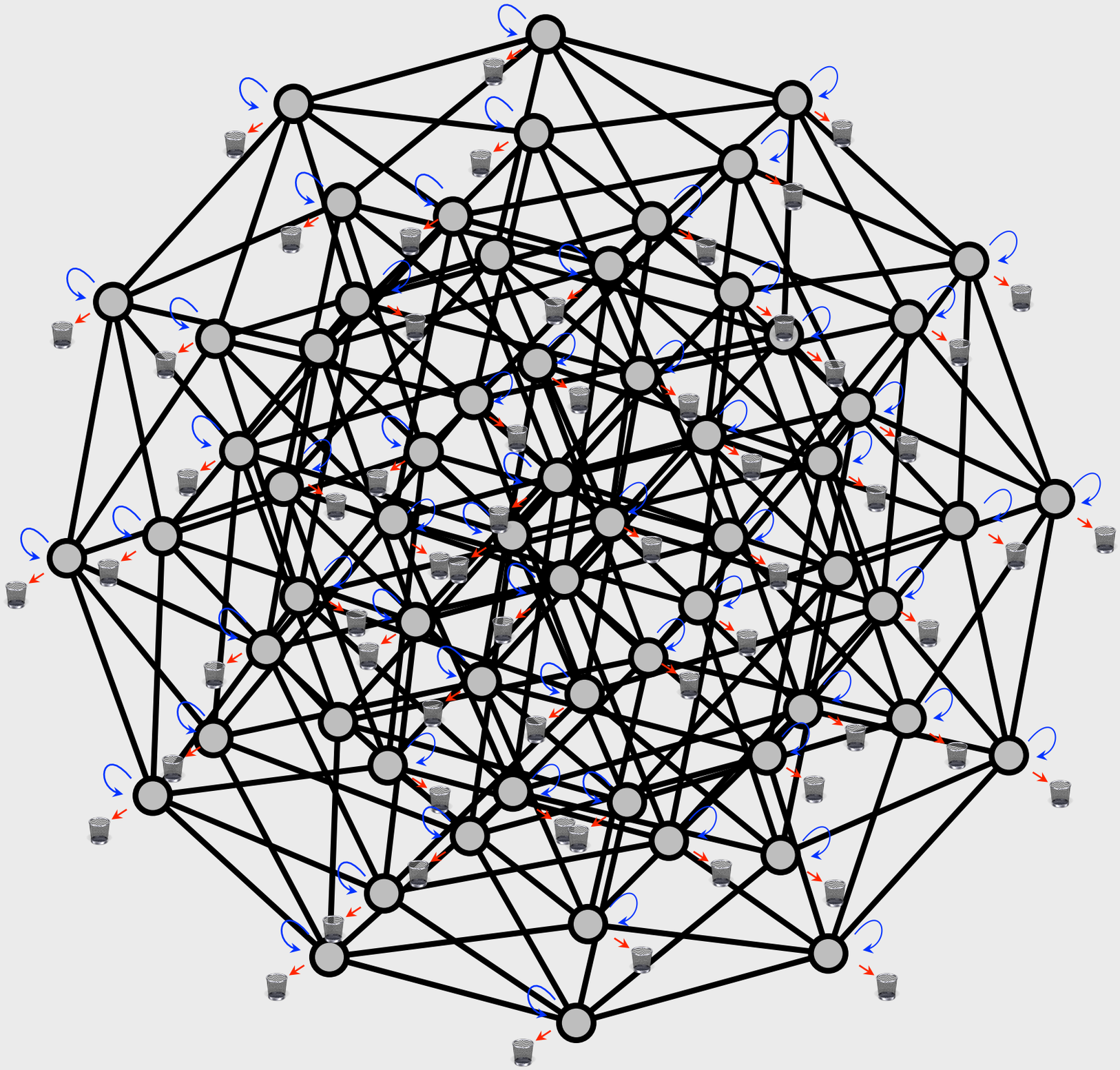


Six binary traits: 384 transitions, 64 birth, 64 death

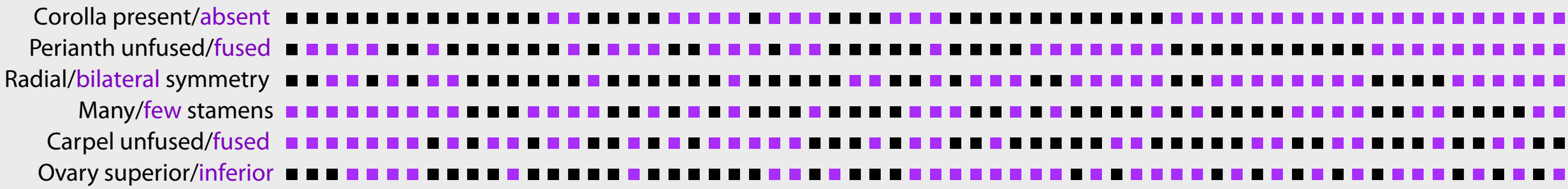


Six binary traits: 384 transitions, 64 birth, 64 death

Care about combinations, but can't estimate full model



Six binary traits: 384 transitions, 64 birth, 64 death
Solution: focal areas



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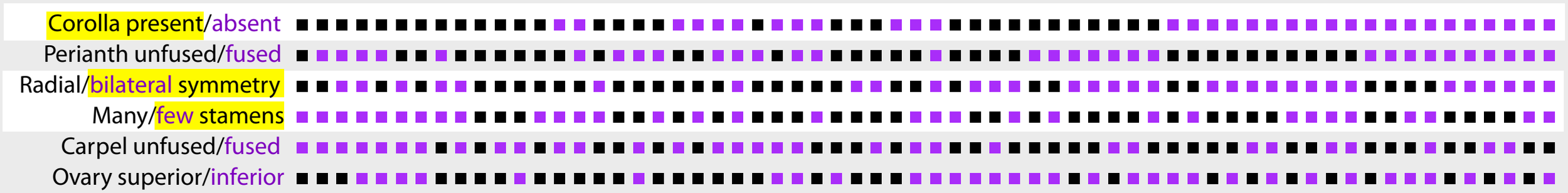

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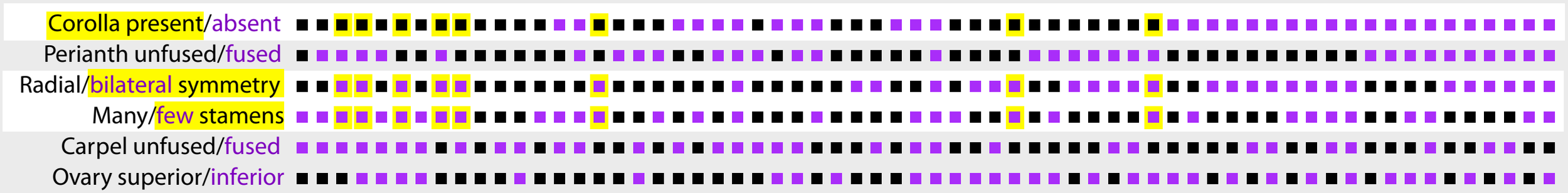

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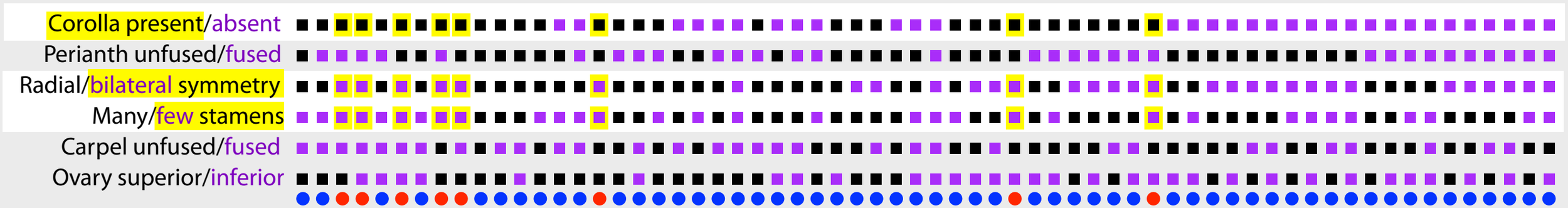

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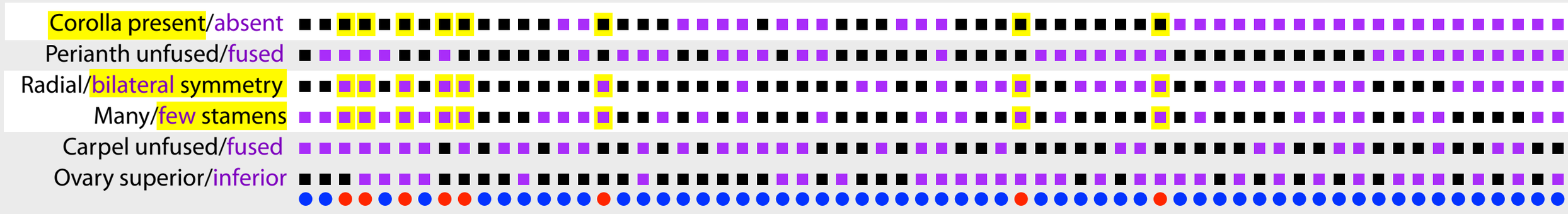

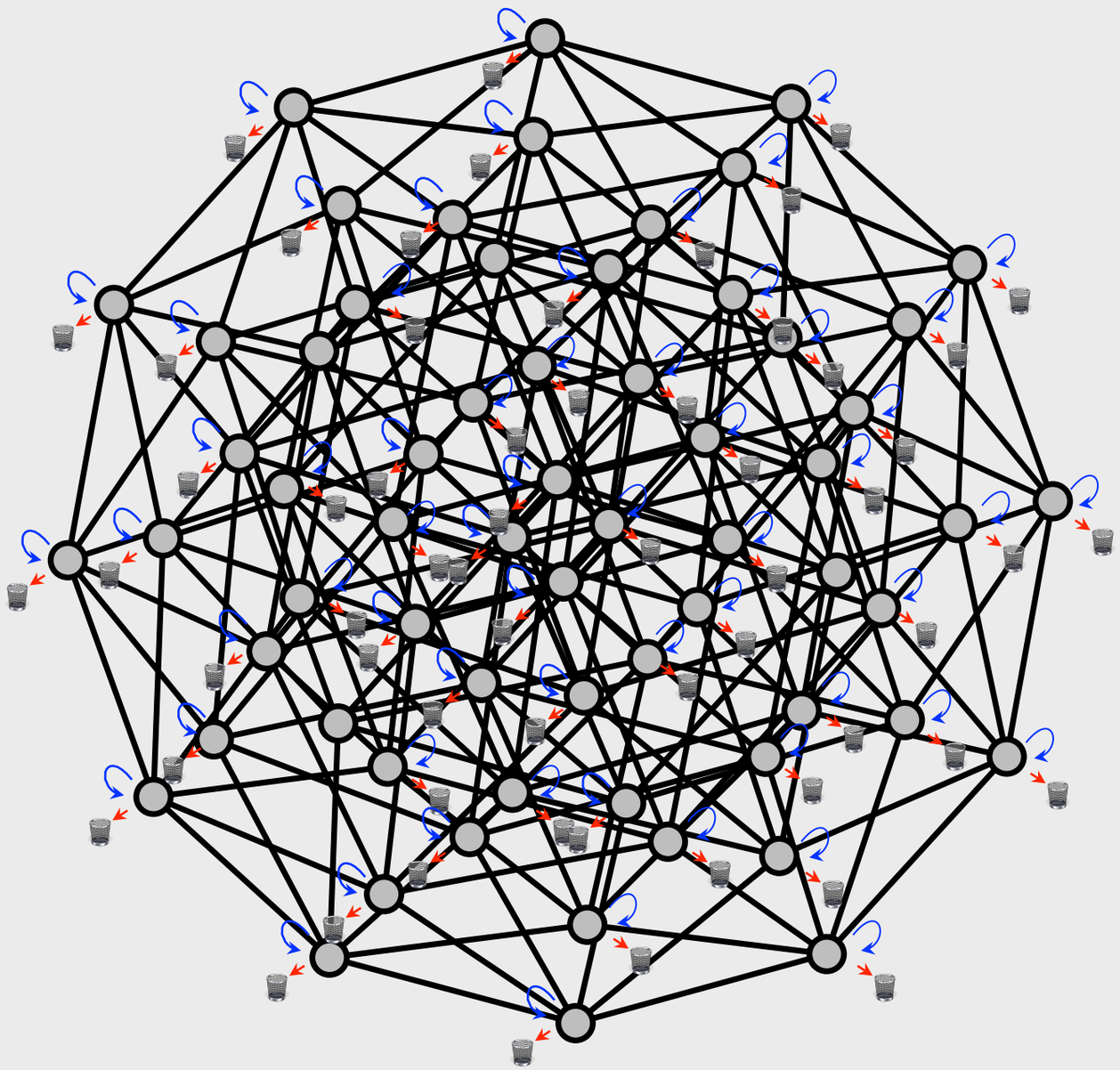

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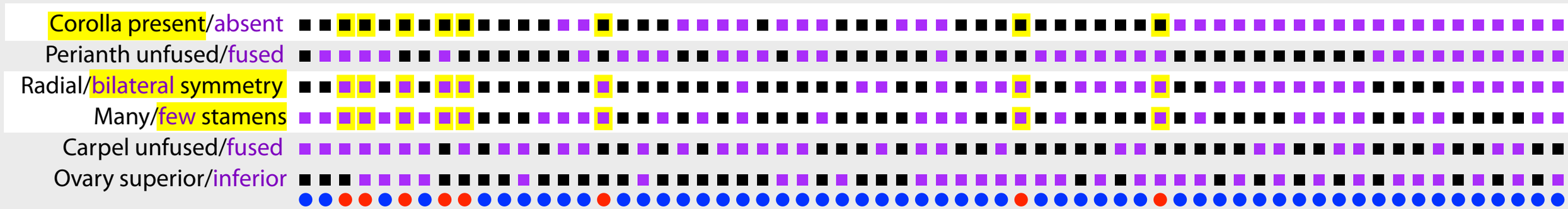

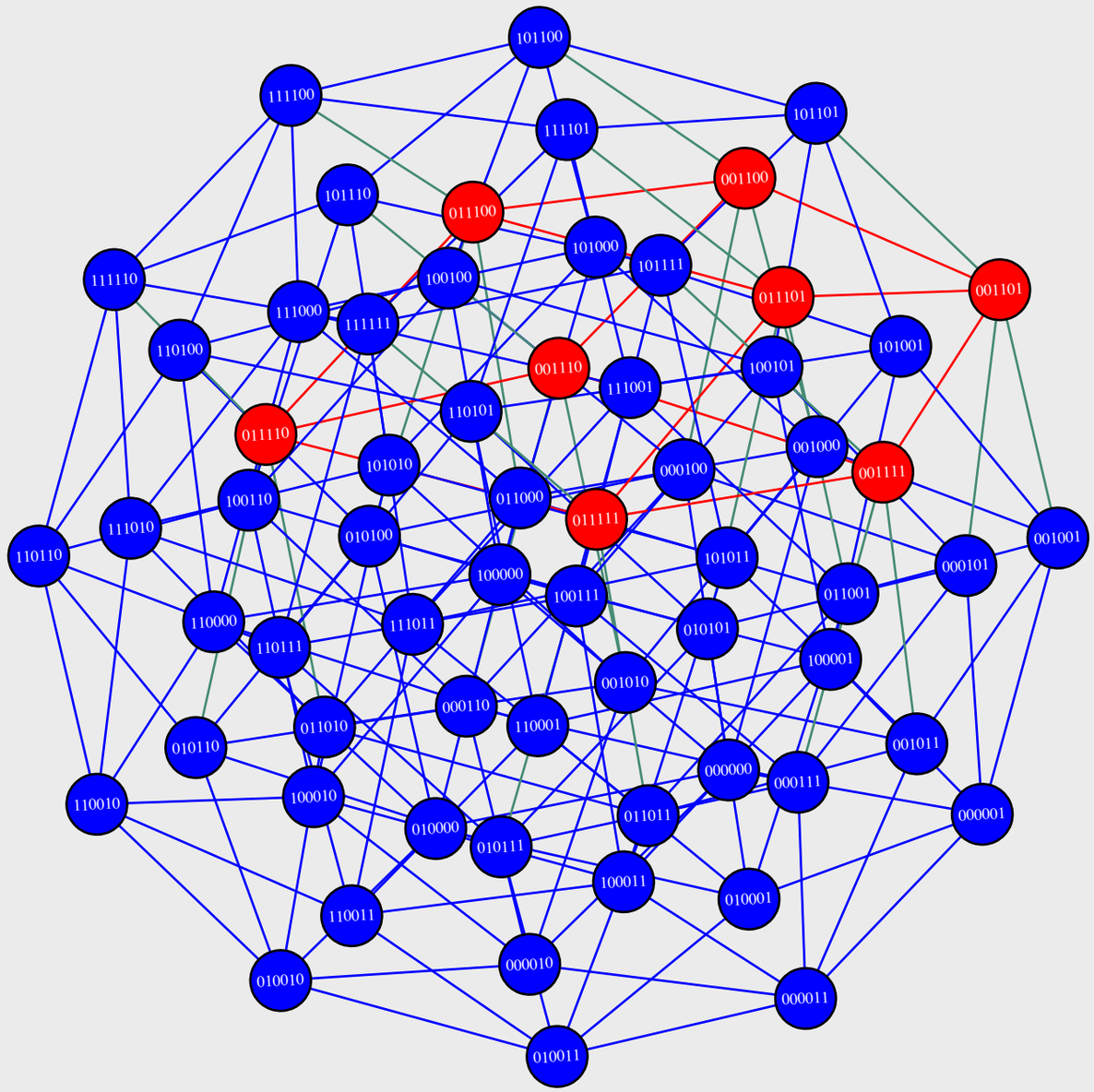

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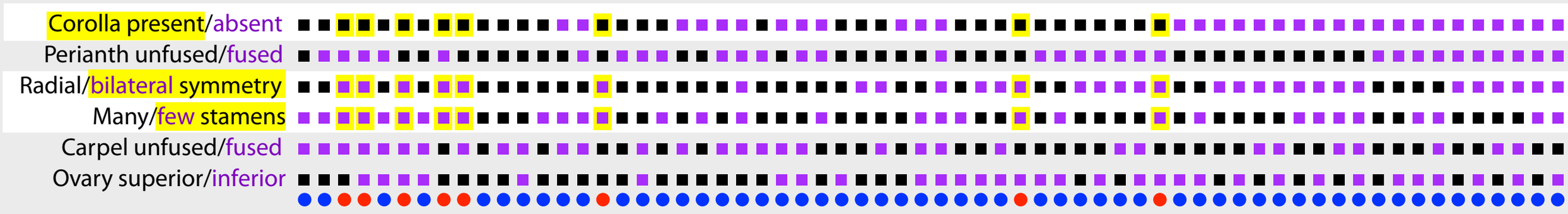
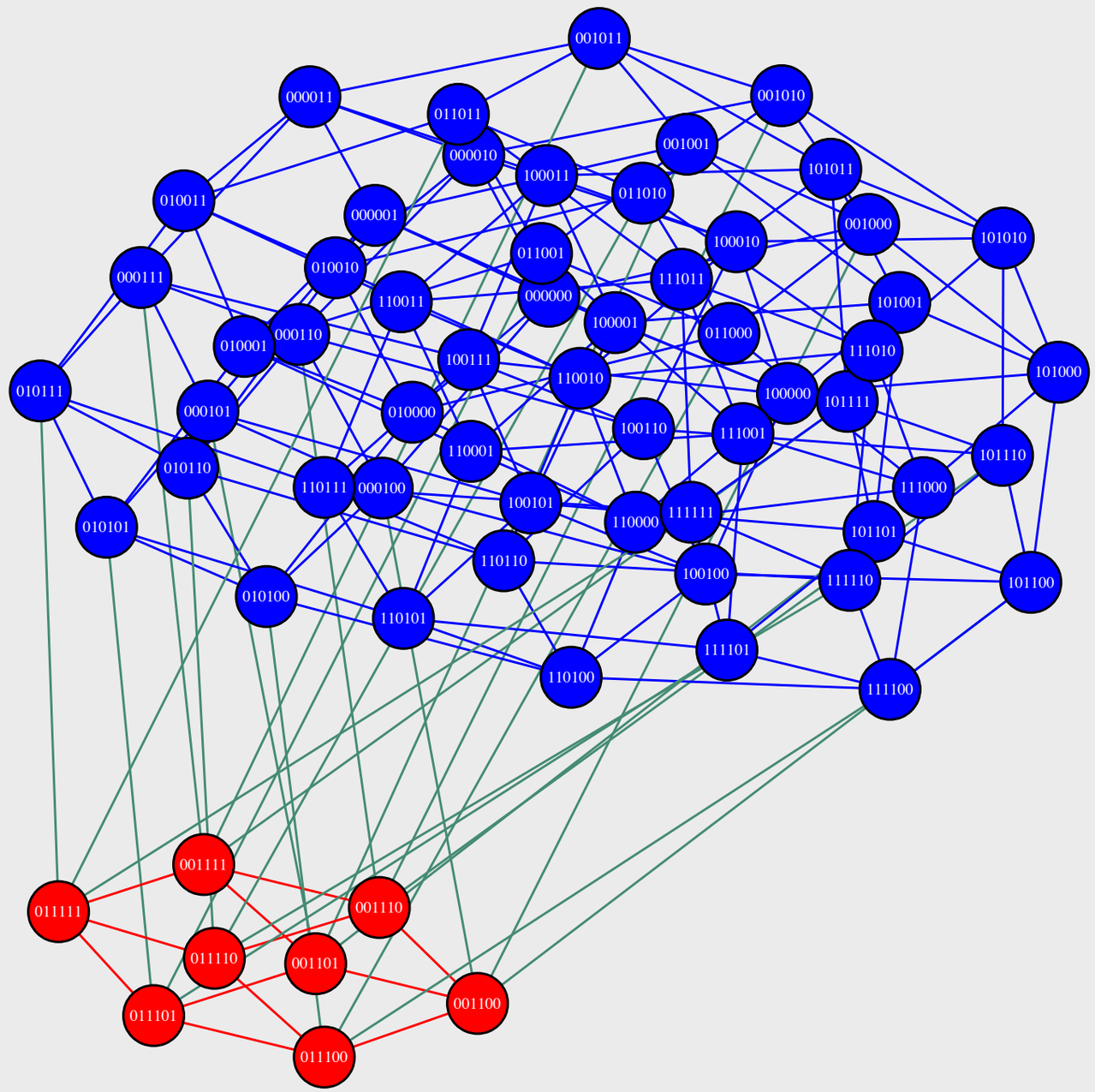
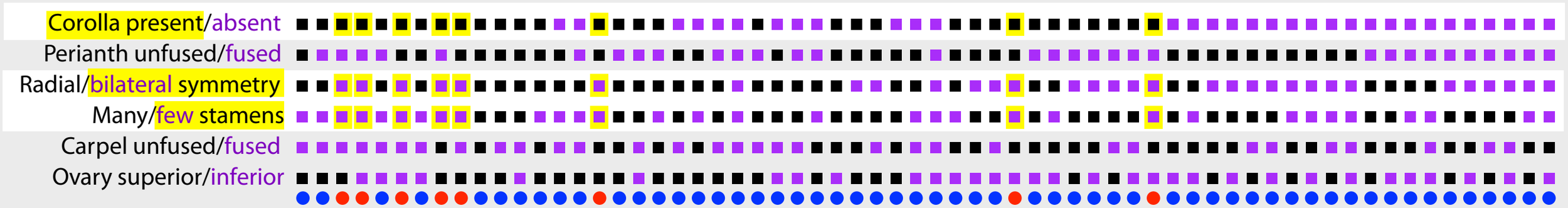




Six binary traits: *4 transitions, 2 birth, 2 death*
Solution: focal areas



$Birth_{focal}$

$Death_{focal}$

$Birth_{nonfocal}$

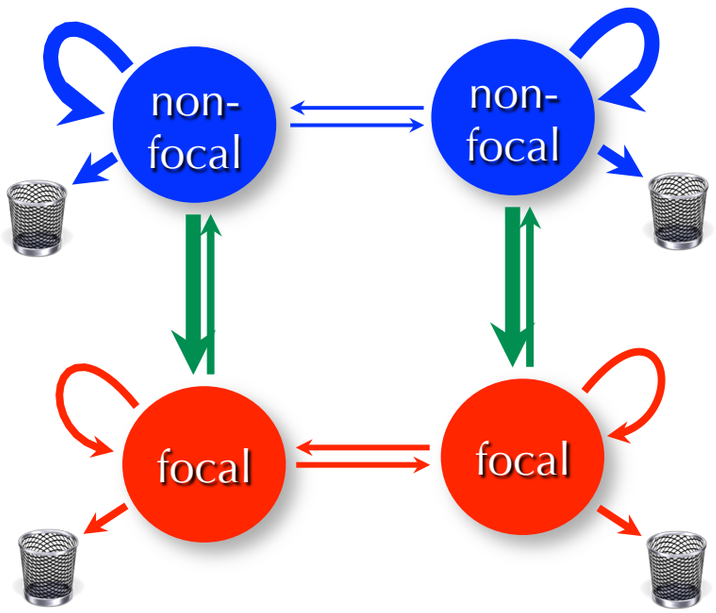
$Death_{nonfocal}$

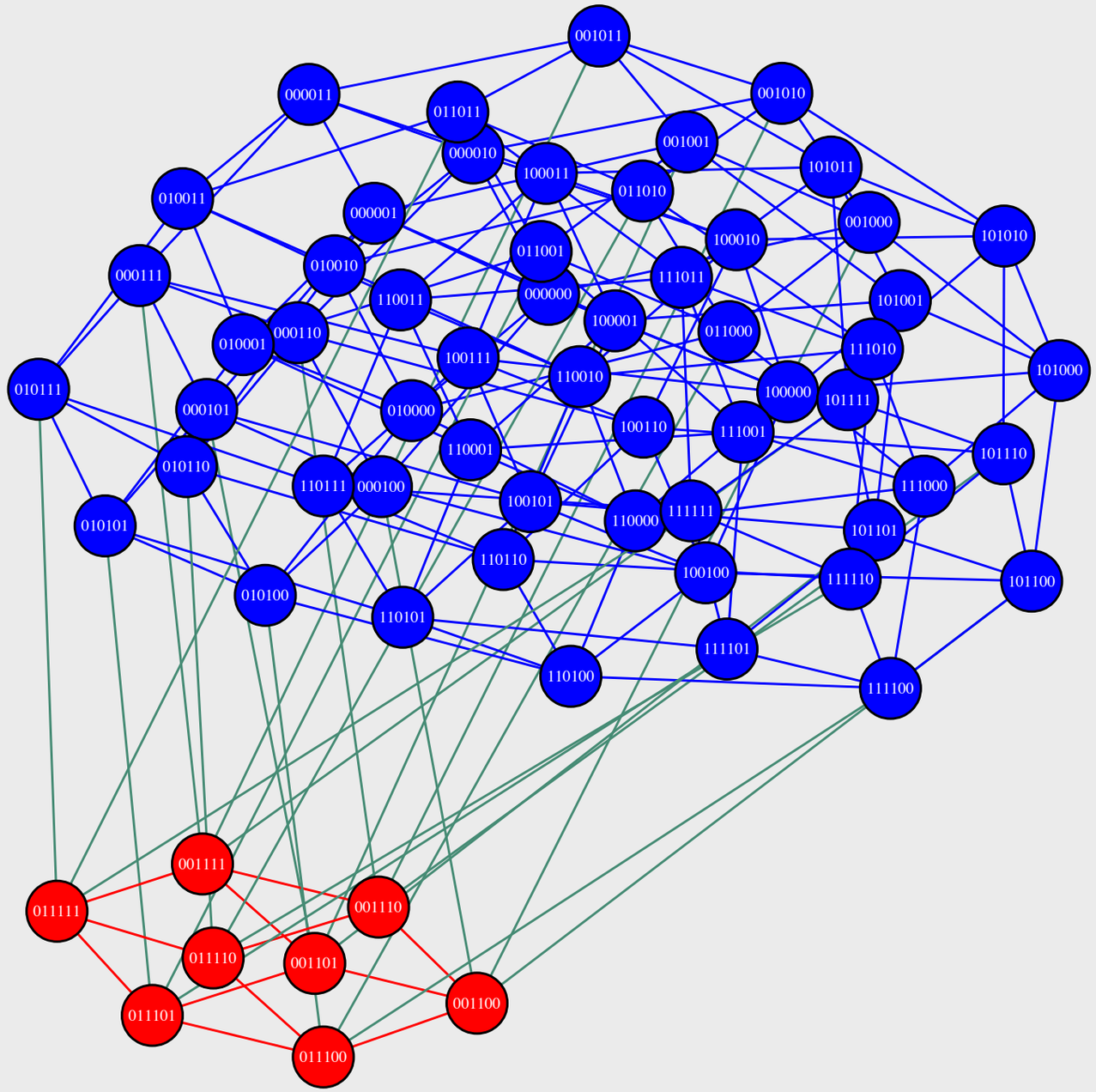
$Transition_{focal \rightarrow focal}$

$Transition_{nonfocal \rightarrow nonfocal}$

$Transition_{focal \rightarrow nonfocal}$

$Transition_{nonfocal \rightarrow focal}$

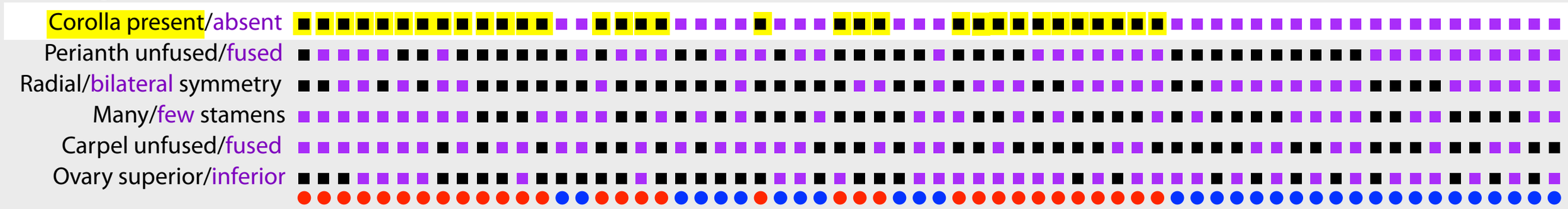




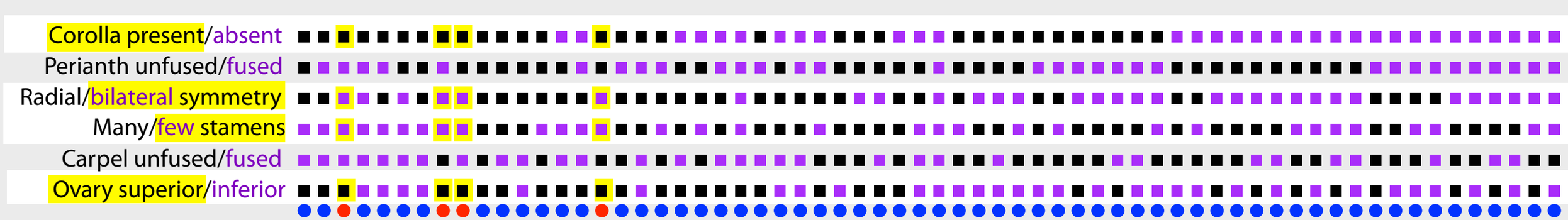
Variety of ways to assemble focal areas

(remember, just ways to group rates, so all models remain comparable)

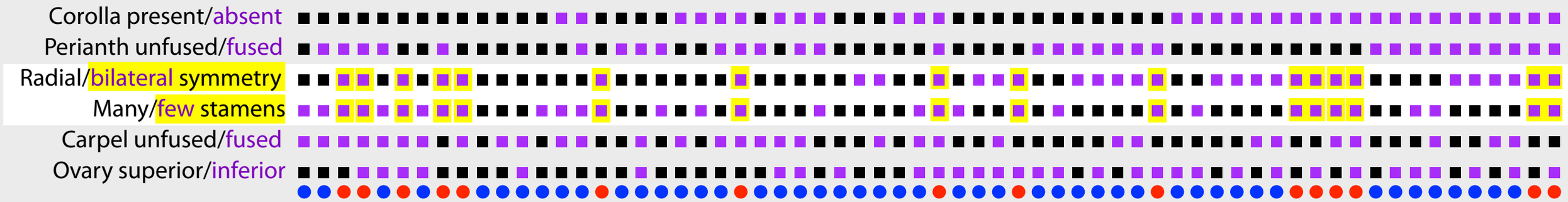
Single character: 0•••••



Four characters: 0•11•0



Pair of characters: ••11••



FaMuSSE: focal area MuSSE

- 5 transition models x 6 diversification models x 3^6 focal areas, minus models without enough data
- Total of 19,657 models evaluated
- Estimate likelihood using diversitree (Fitzjohn, 2012) and specified model
- Calculate AIC & Akaike weight

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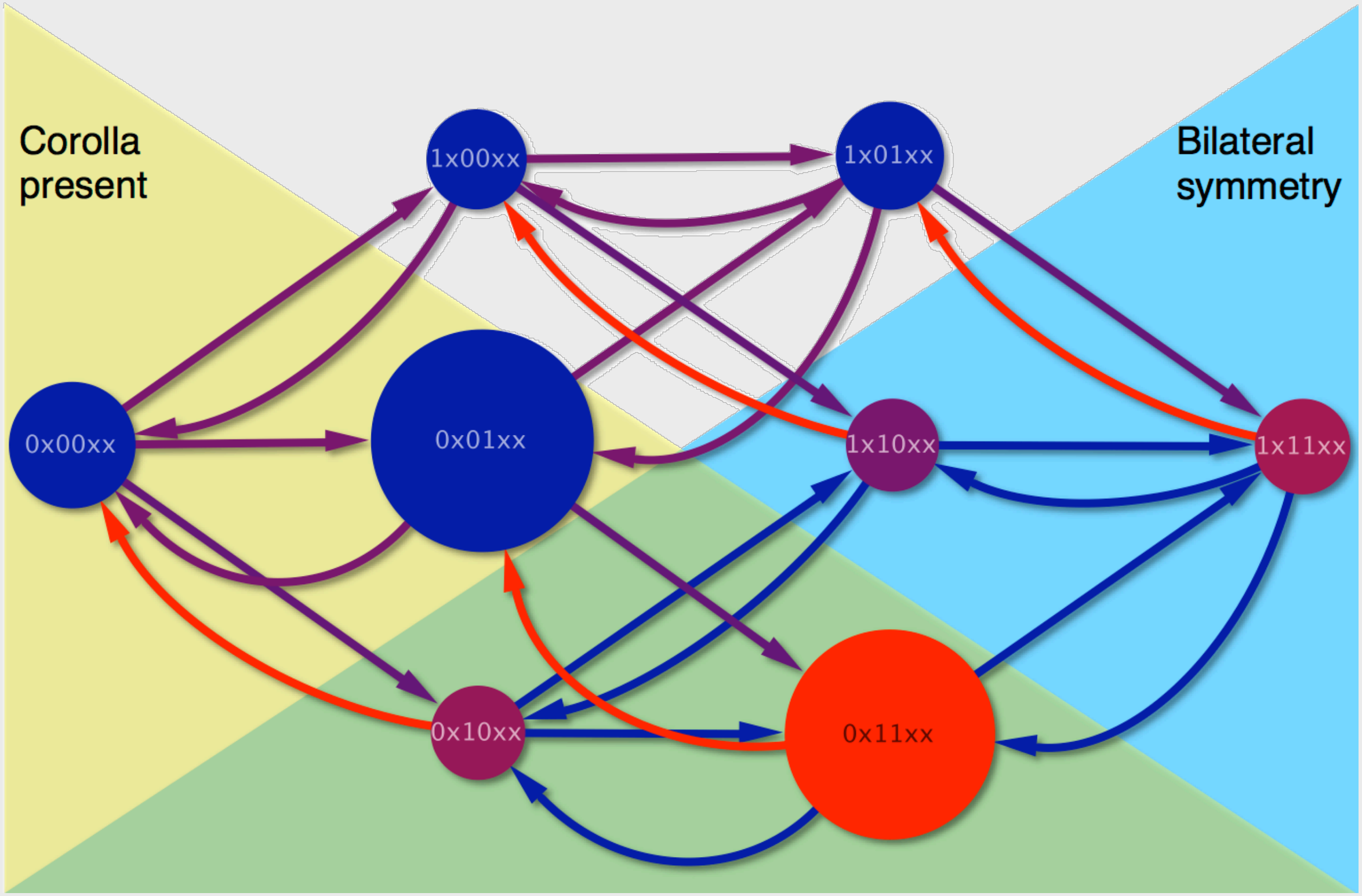
- Calculate AIC & Akaike weight

Akaike Weight	Cumulative Akaike Weight	Focal area	Diversification parameters	Transition parameters
0.274	0.274	Corolla present, bilateral symmetry, stamens few	4	1
0.245	0.519	Bilateral symmetry	4	4
0.202	0.721	Bilateral symmetry	4	1
0.128	0.849	Bilateral symmetry, stamens few	4	1
0.090	0.939	Corolla present, bilateral symmetry	4	1
0.024	0.963	Bilateral symmetry	4	2
0.014	0.977	Corolla present, bilateral symmetry, stamens few	4	2
0.009	0.985	Bilateral symmetry	3	4
0.003	0.988	Corolla present, bilateral symmetry	4	2
0.003	0.991	Corolla present, bilateral symmetry, stamens few	4	4

Model averaged results, looking at three characters that matter (corolla presence, bilateral symmetry, few stamens)



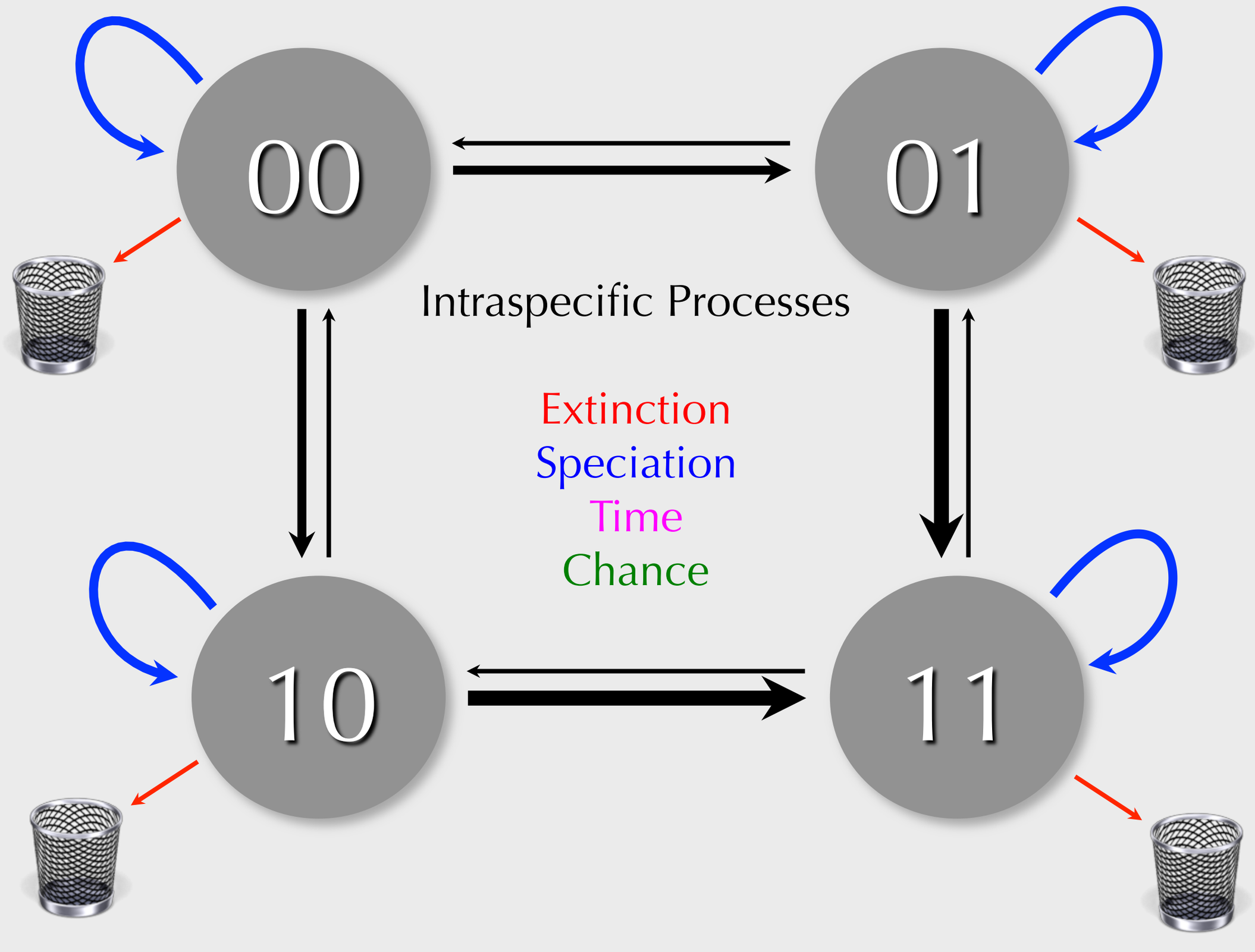
Summary:

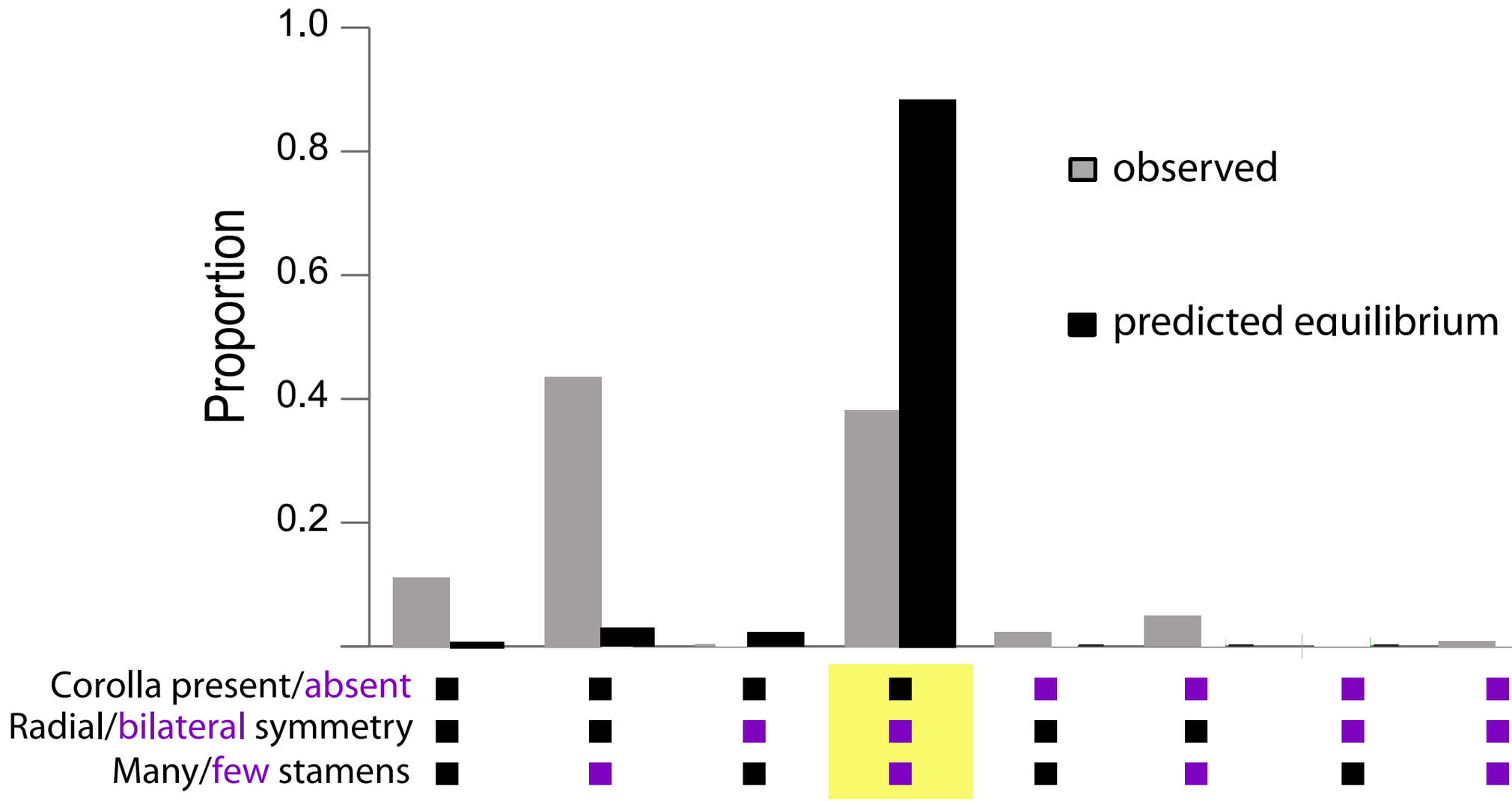
- Bilateral symmetry important for floral diversification, but so is having few stamens and having a corolla: character combinations matter

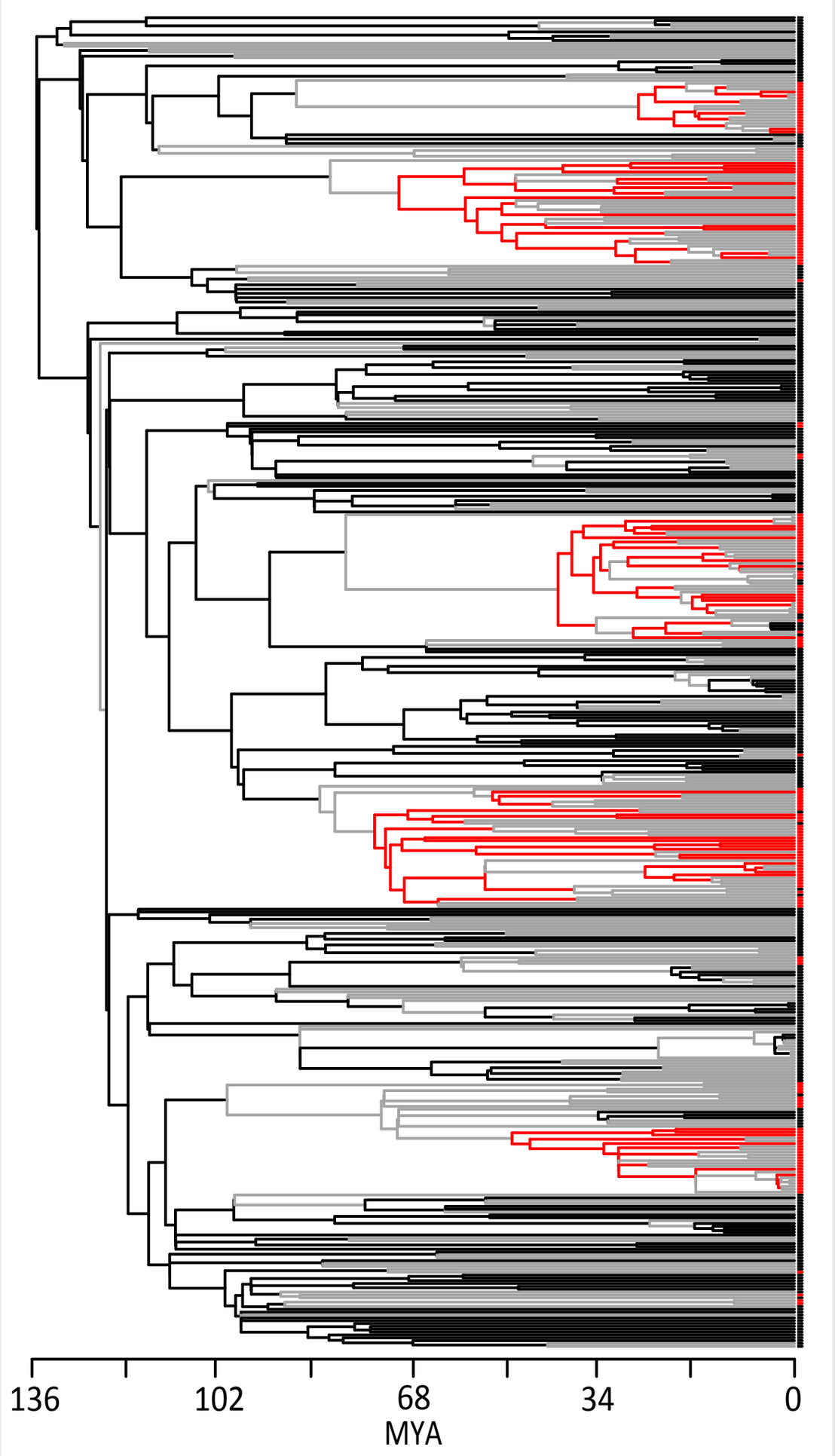
- All of these relate to precision of pollen placement: perhaps enable faster speciation?

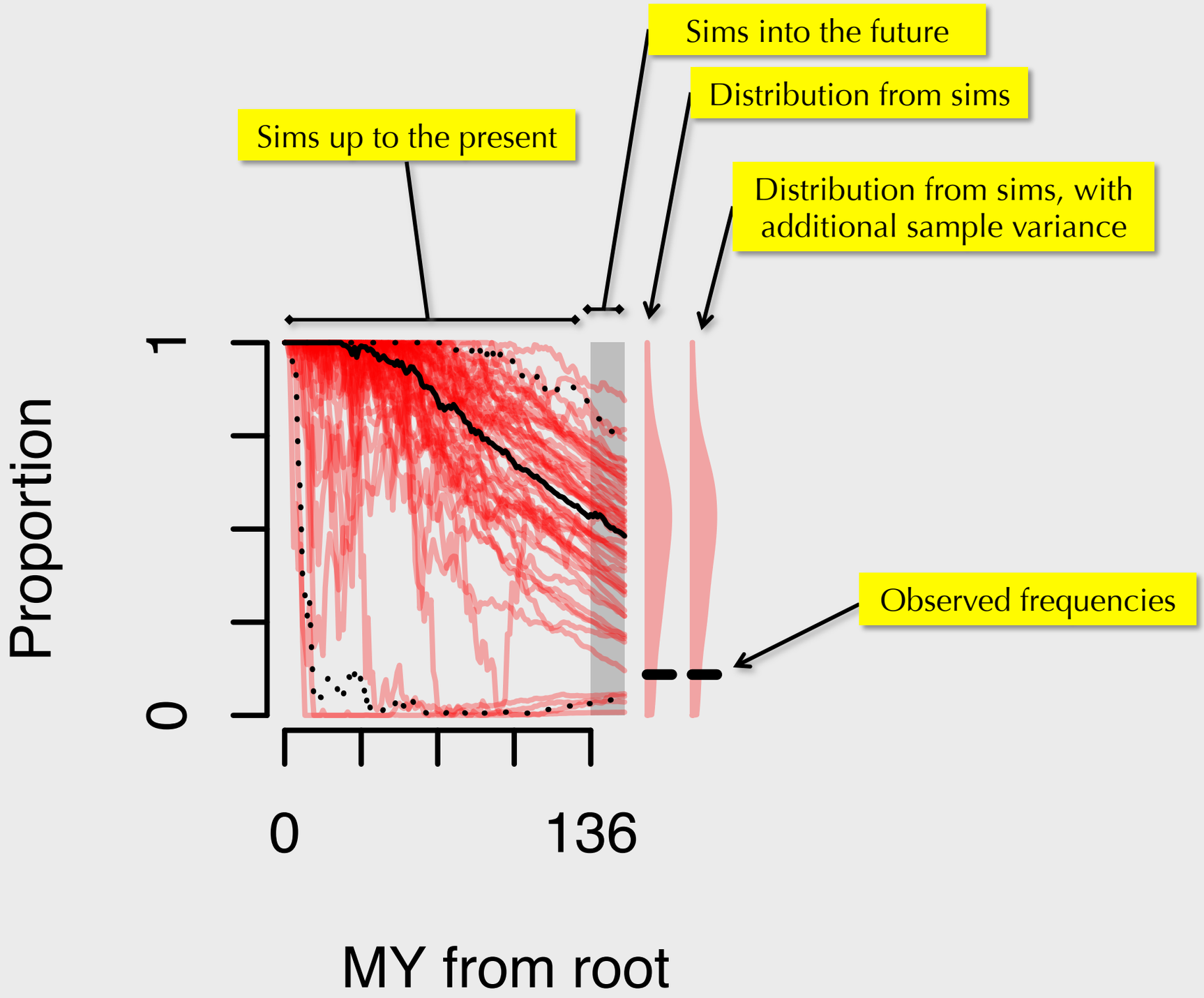
- Differential diversification rate ("species sorting") more important than differential transition rates (intraspecific natural selection, mutation, or drift)

All the factors that lead to contemporary distributions?

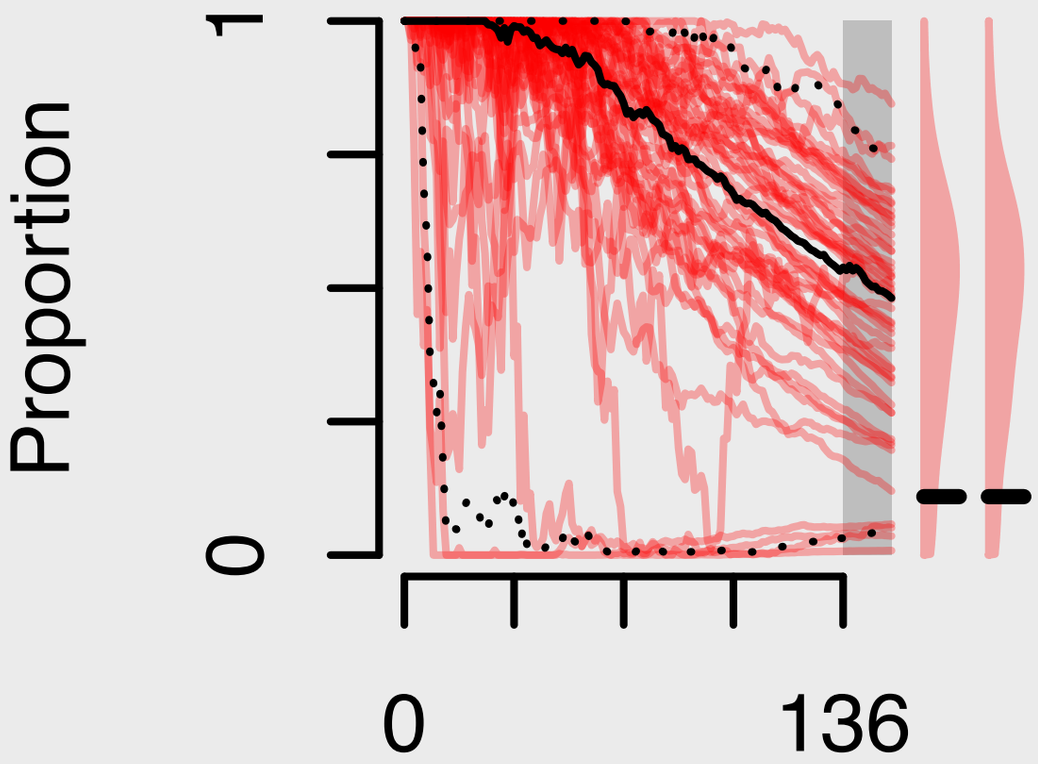



1.0
0.8
0.6
0.4
0.2
Proportion
observed
predicted equilibrium
Corolla present/absent
Radial/bilateral symmetry
Many/few stamens

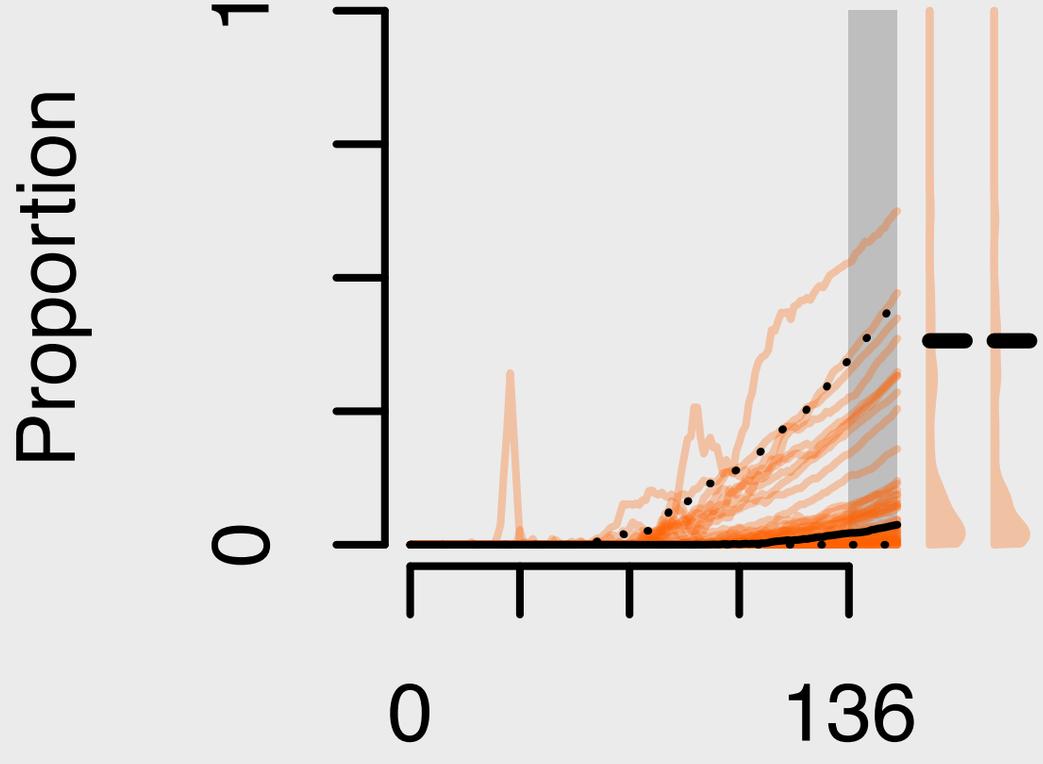

136
102
68
34
0
MYA

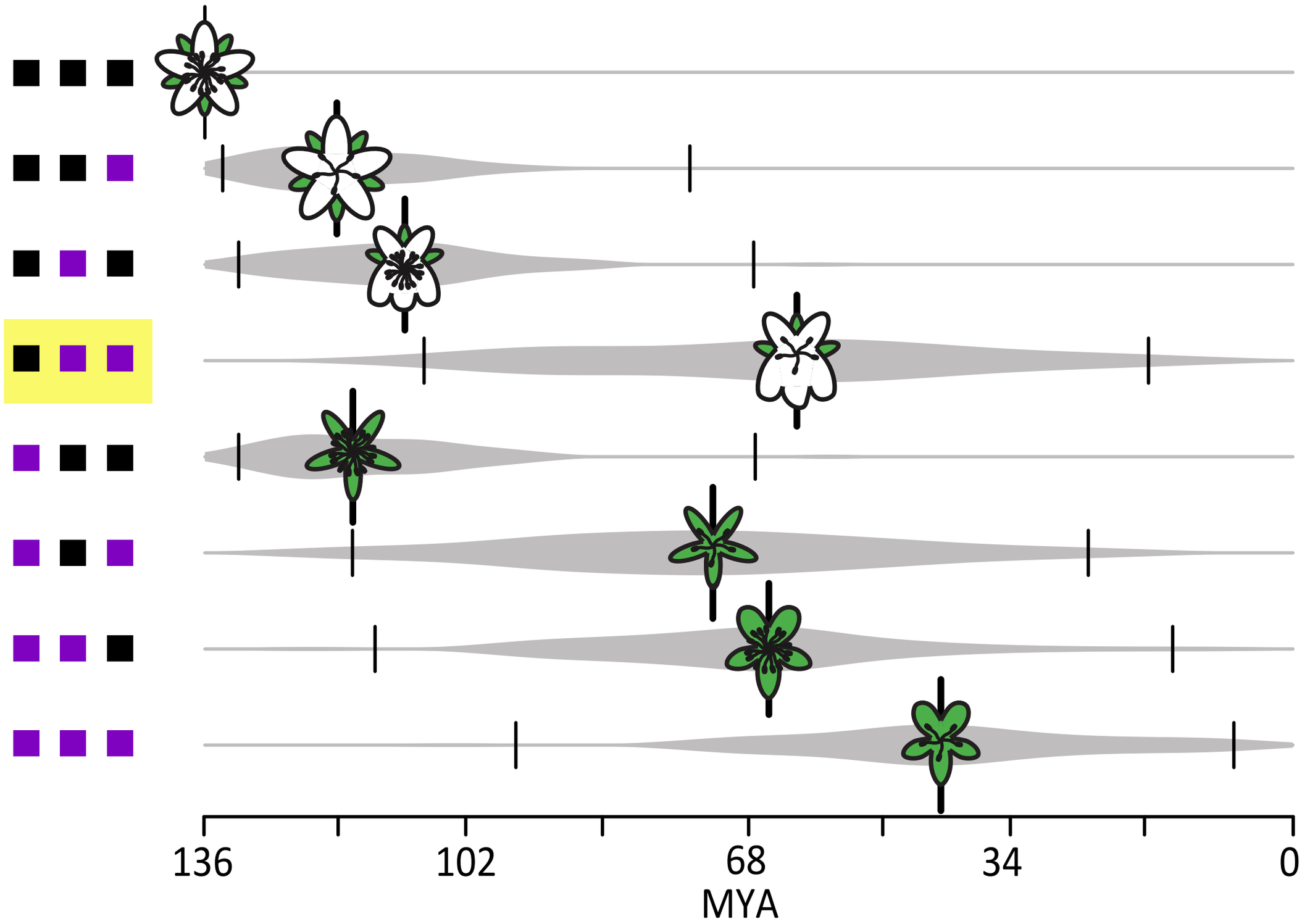

Sims into the future
Distribution from sims
Sims up to the present
Distribution from sims, with additional sample variance
Observed frequencies
Proportion
1
0
0
136
MY from root

Root combination (corolla present, radial symmetry, many stamens)



Fast combination (corolla present, bilateral symmetry, few stamens)




136
102
68
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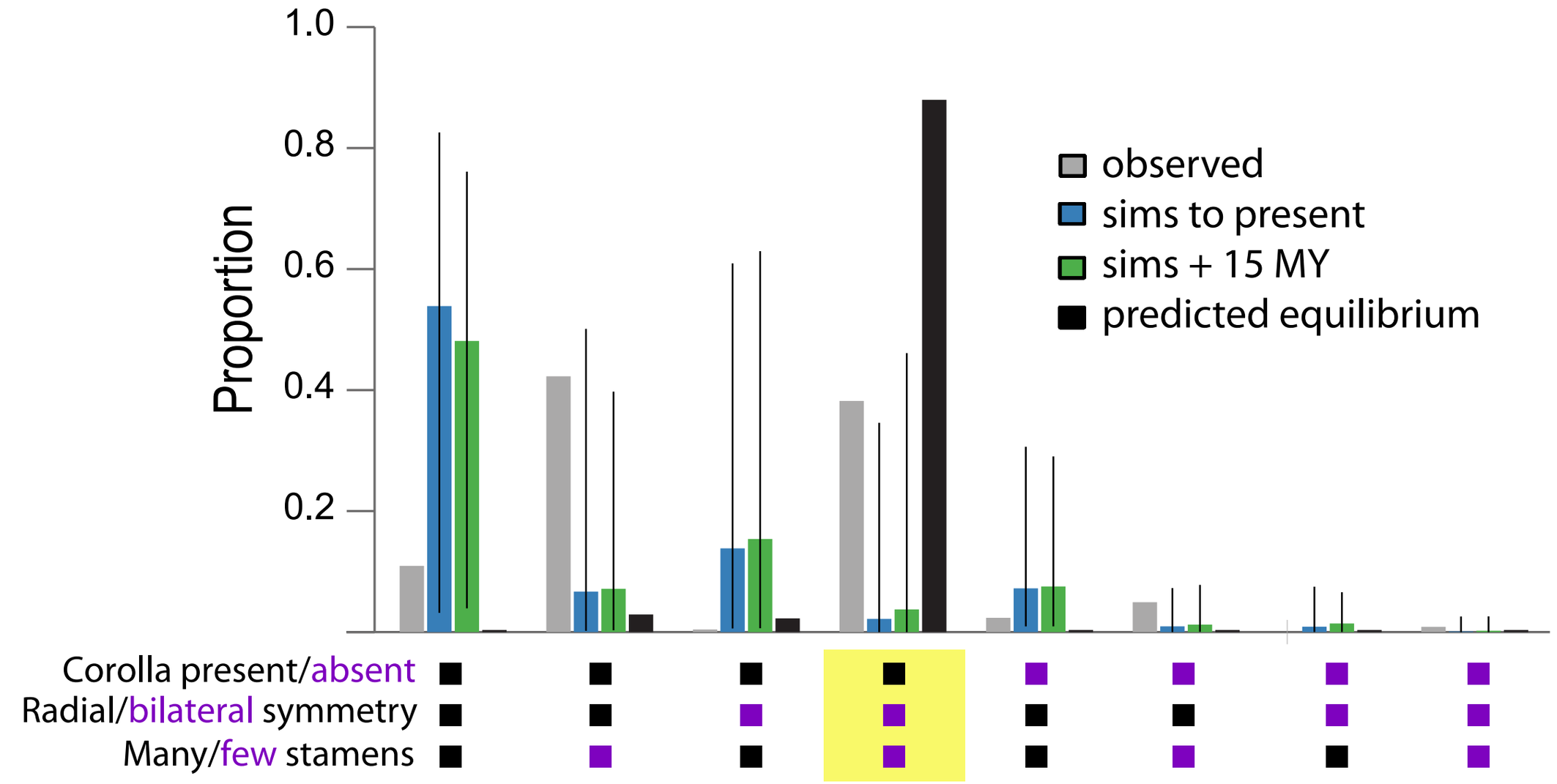
0
MYA


1.0
0.8
0.6
0.4
0.2
Proportion
observed
sims to present
sims + 15 MY
predicted equilibrium
Corolla present/absent
Radial/bilateral symmetry
Many/few stamens

Summary:

- Bilateral symmetry important for floral diversification, but so is having few stamens and having a corolla: character combinations matter

- All of these relate to precision of pollen placement: perhaps enable faster speciation?

- Differential diversification rate ("species sorting") more important than differential transition rates (intraspecific natural selection, mutation, or drift)

- Flowers aren't all at fastest diversifying combination because it took millions of years to evolve that

- Macroevolution limited by microevolutionary variation

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- Answer important questions