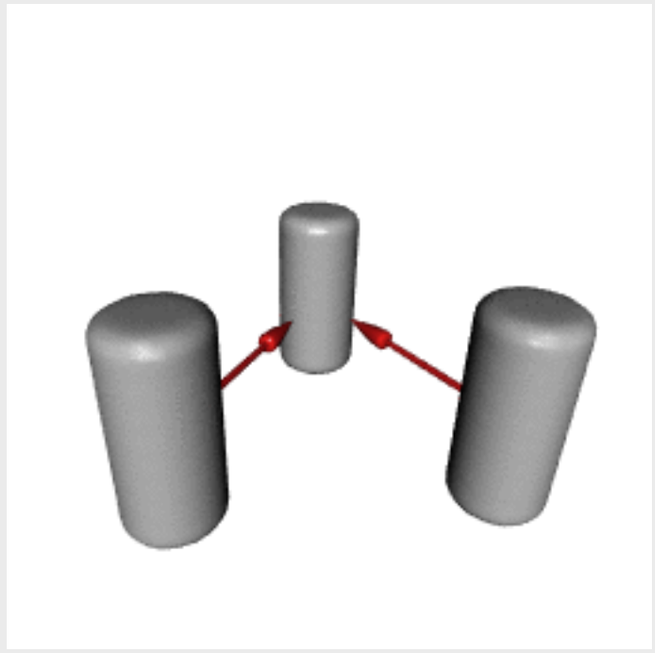
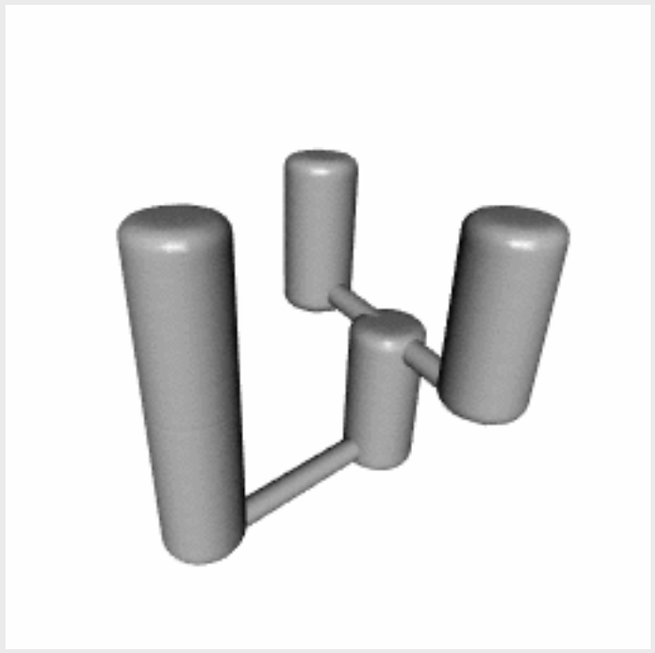
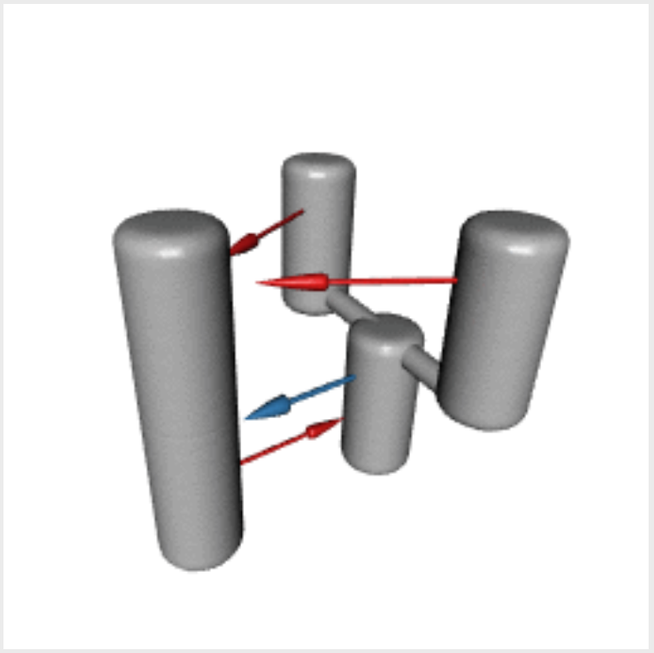
Simulated likelihood for species delimitation and phylogeography







Brian O'Meara
UT Knoxville

Bryan Carstens
Ohio State U


FORODWAITH
GREY MOUNTAINS
IRON HILLS
Erebor
BLUE MOUNTAINS
LINDON
Mithlond
THE SHIRE
Bree
Rivendell
ANDUIN
MIRKWOOD
Gulf of Lhûn
ERIADOR
MISTY MOUNTAINS
Moria
LÓRIEN
Dol Guldur
Tharbad
MINHIRIATH
Sea of Rhûn
RHOVANION
FANGORN
BROWN LANDS
ENEDWAITH
RHÛN
Isengard
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(South Gondor)
Bay of Belfalas
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The Great Sea
NEAR HARAD
UMBAR
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Miles
0
100
200
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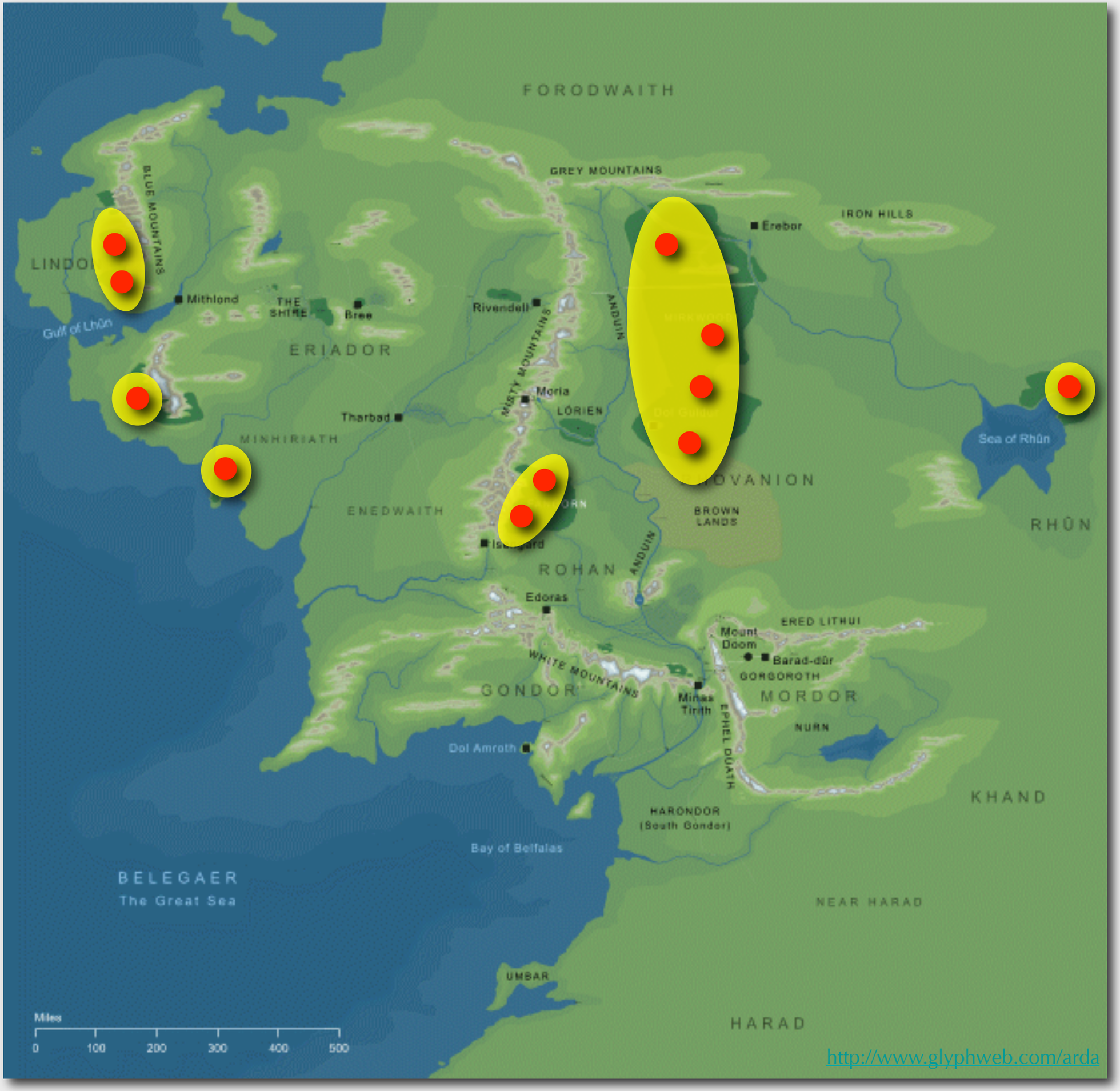
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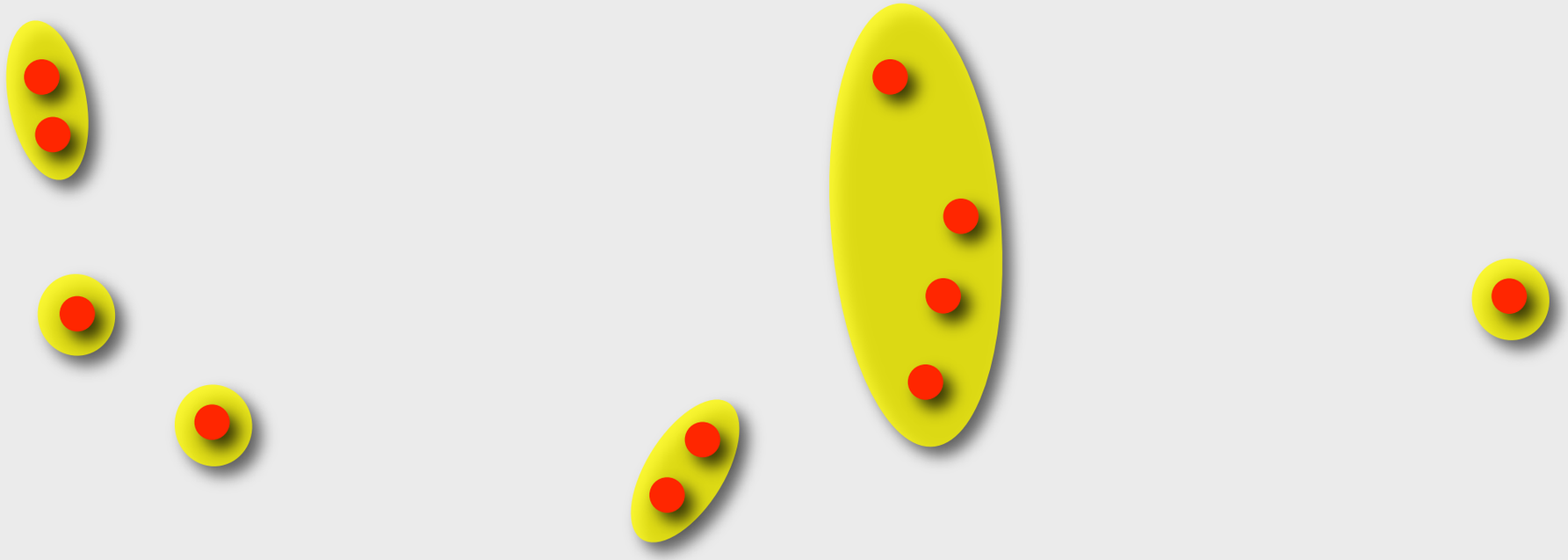
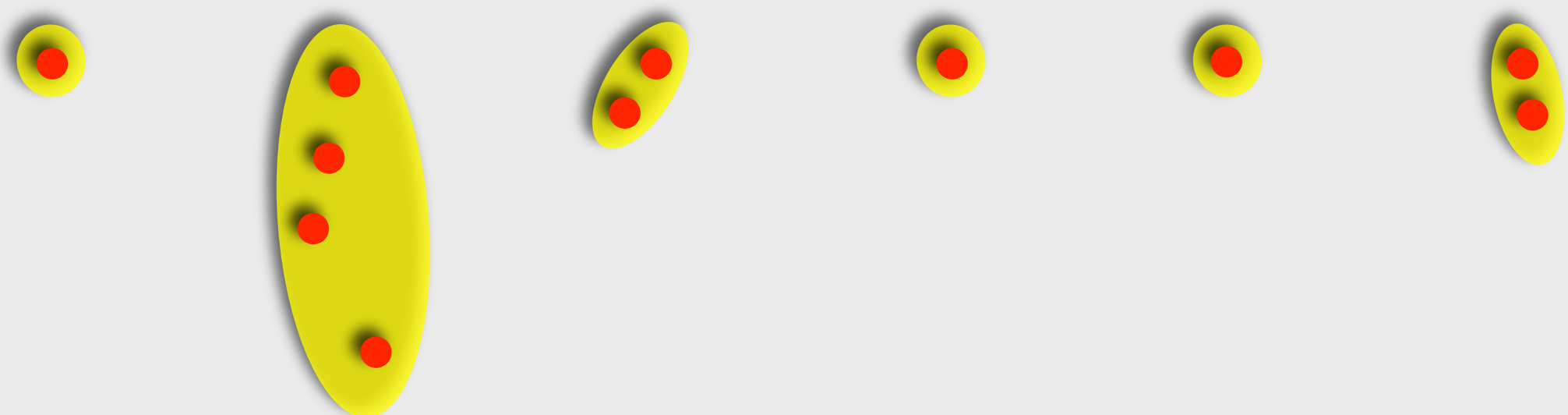
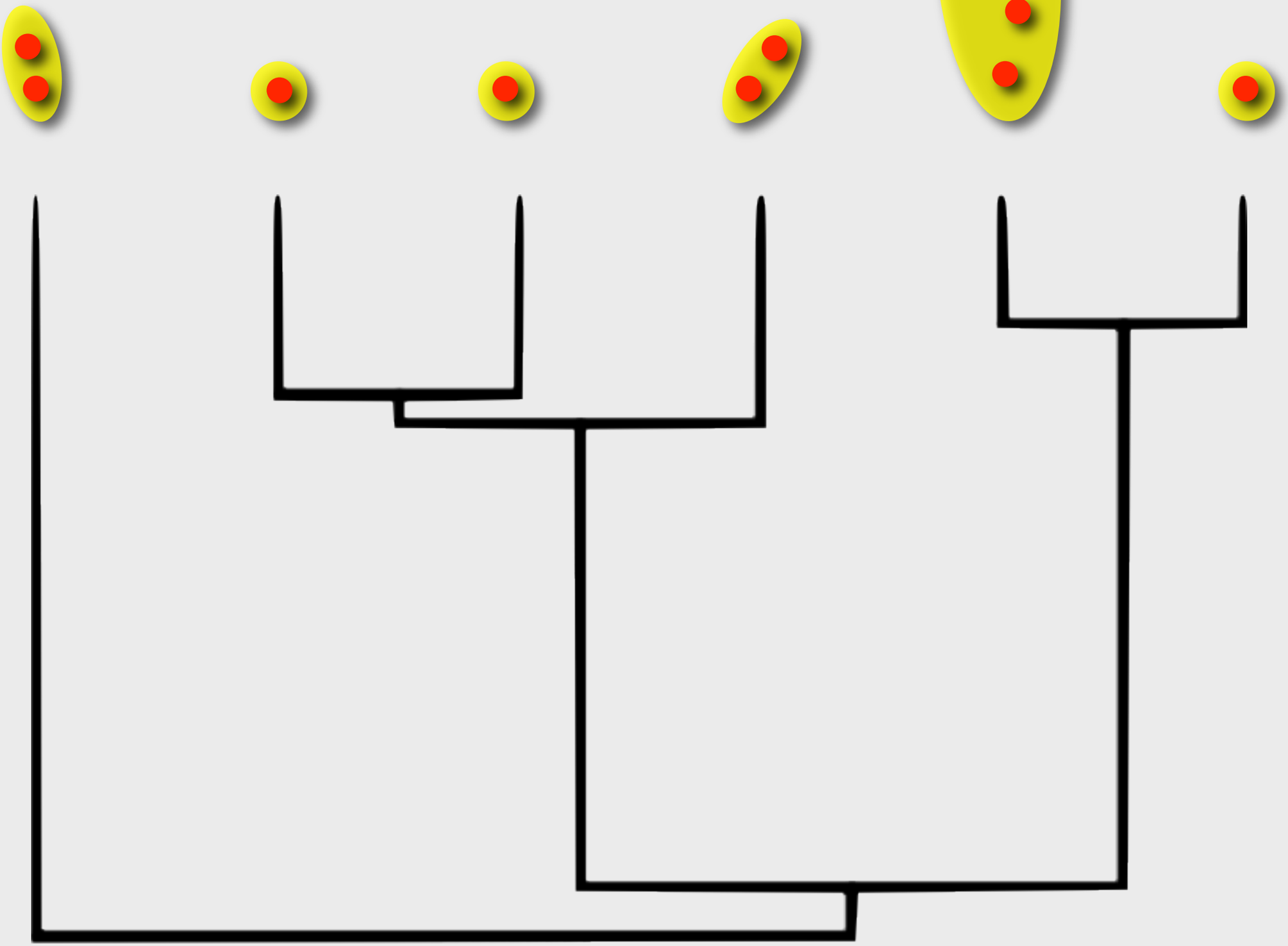
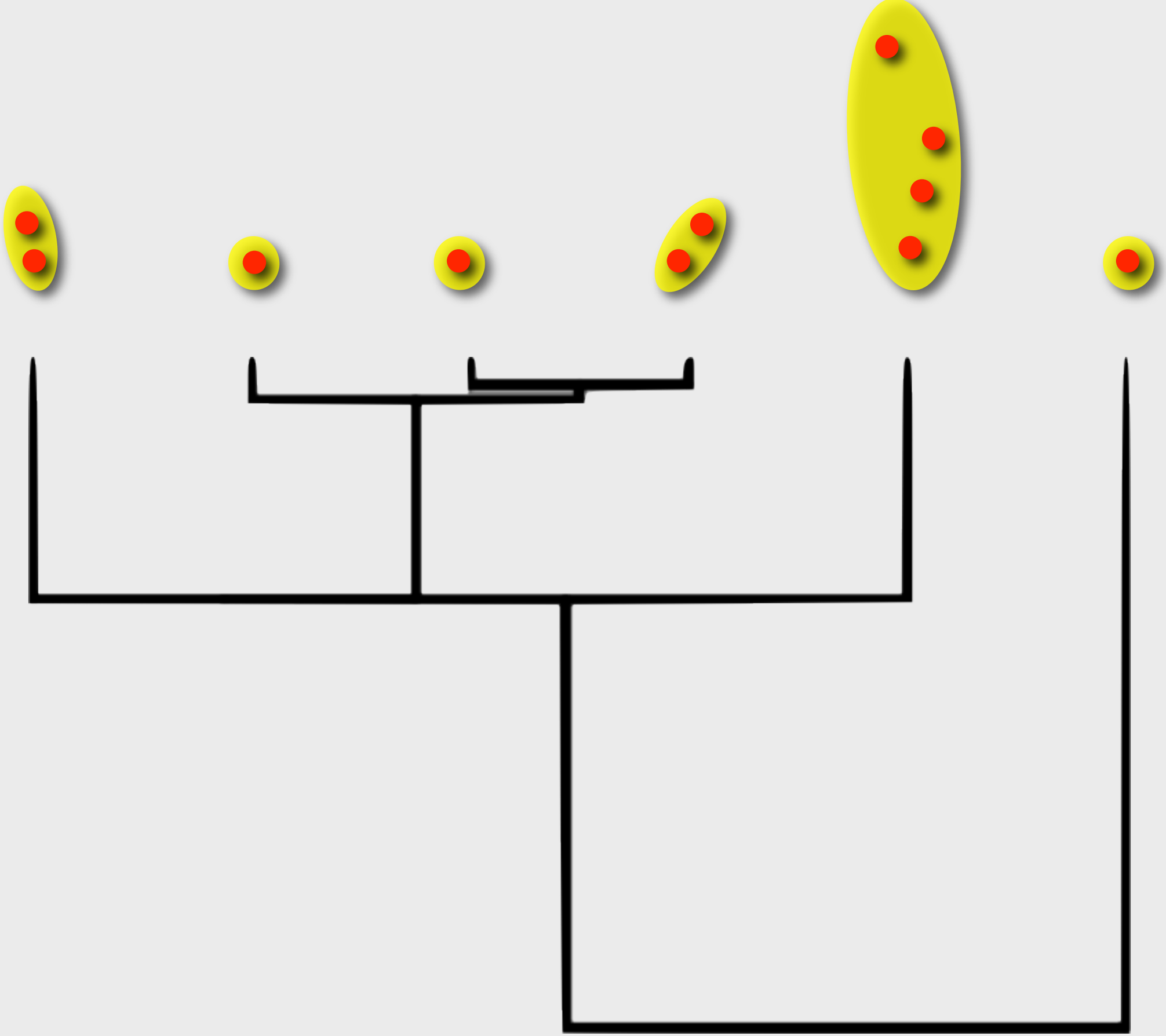
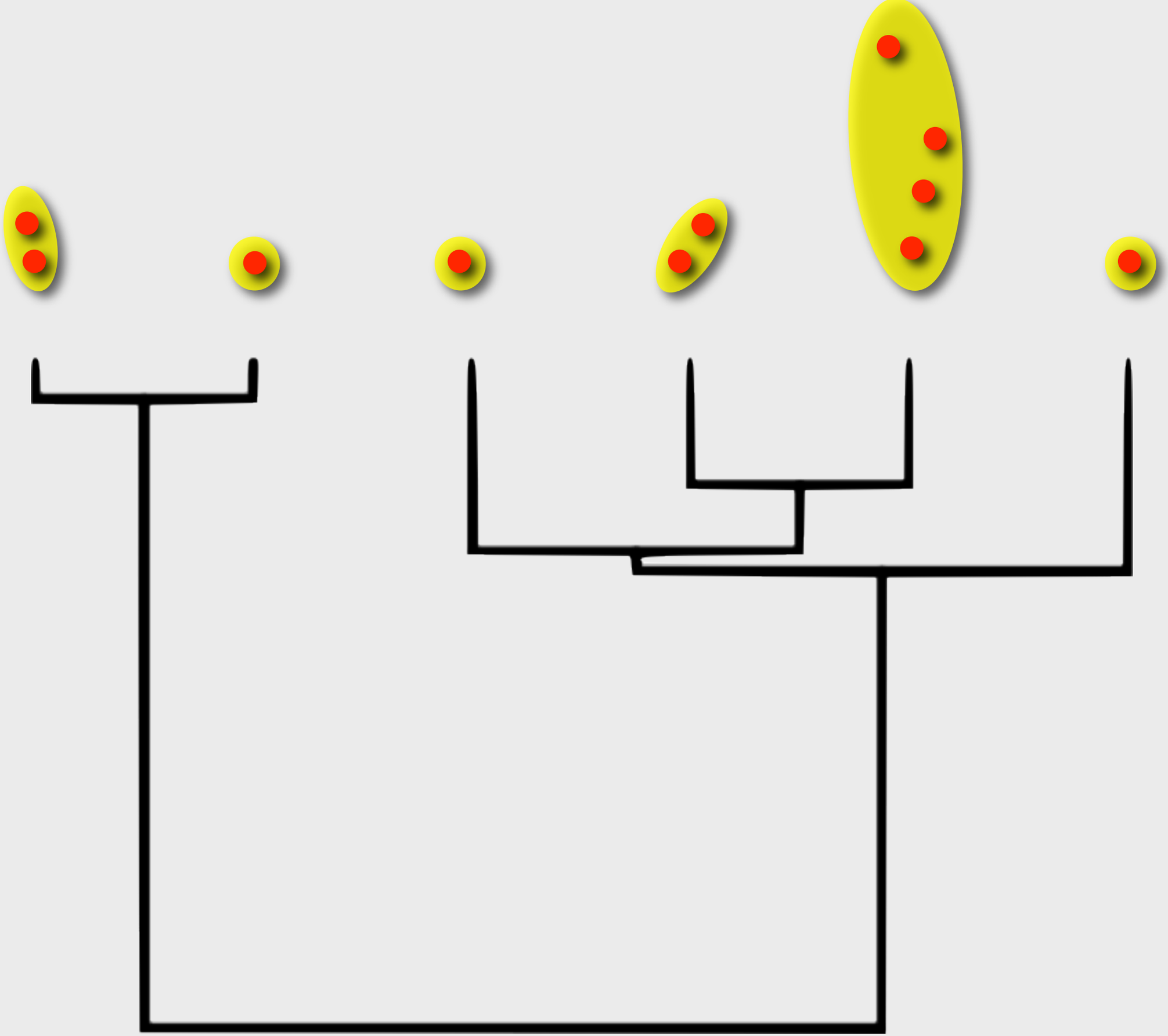
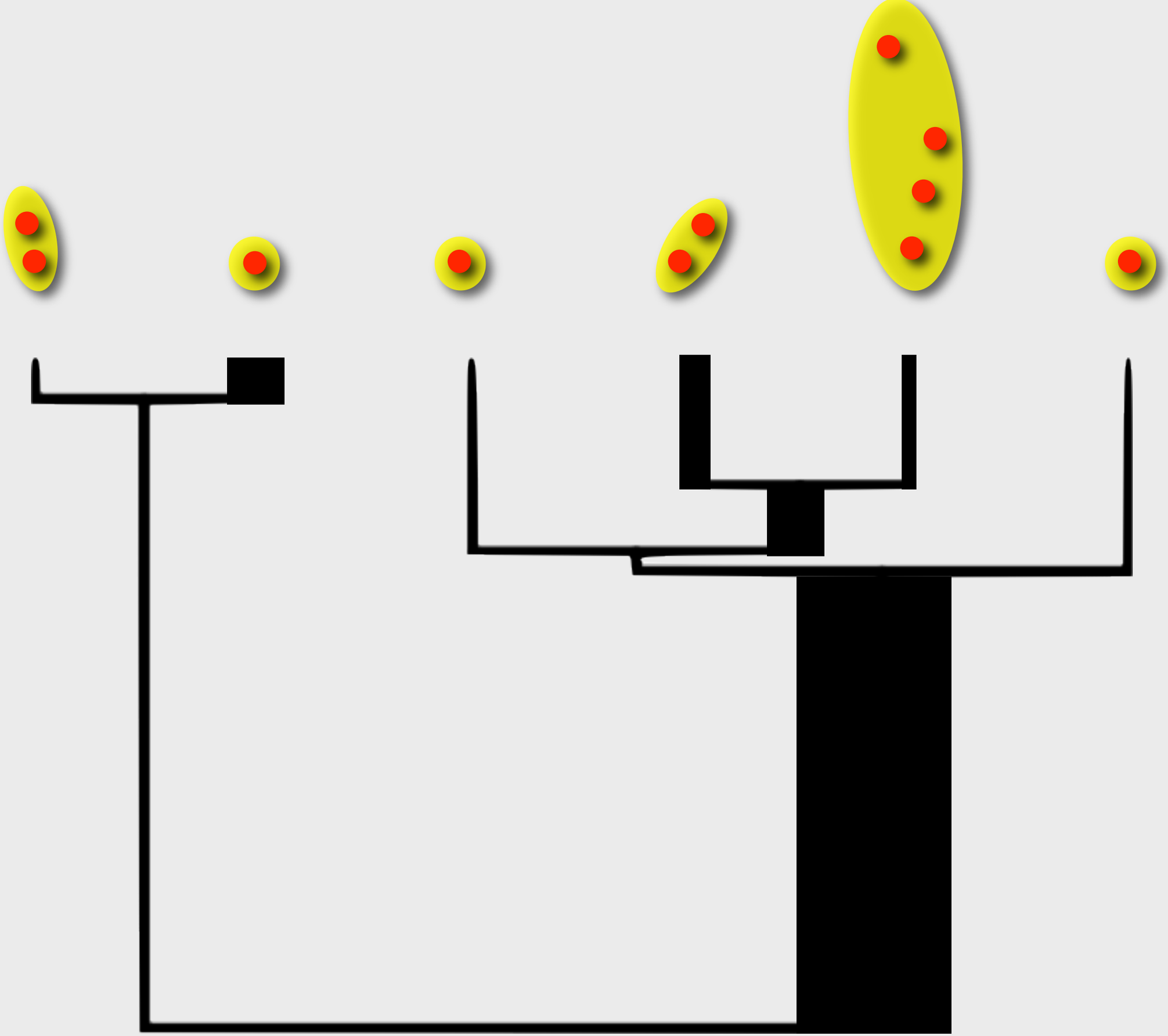


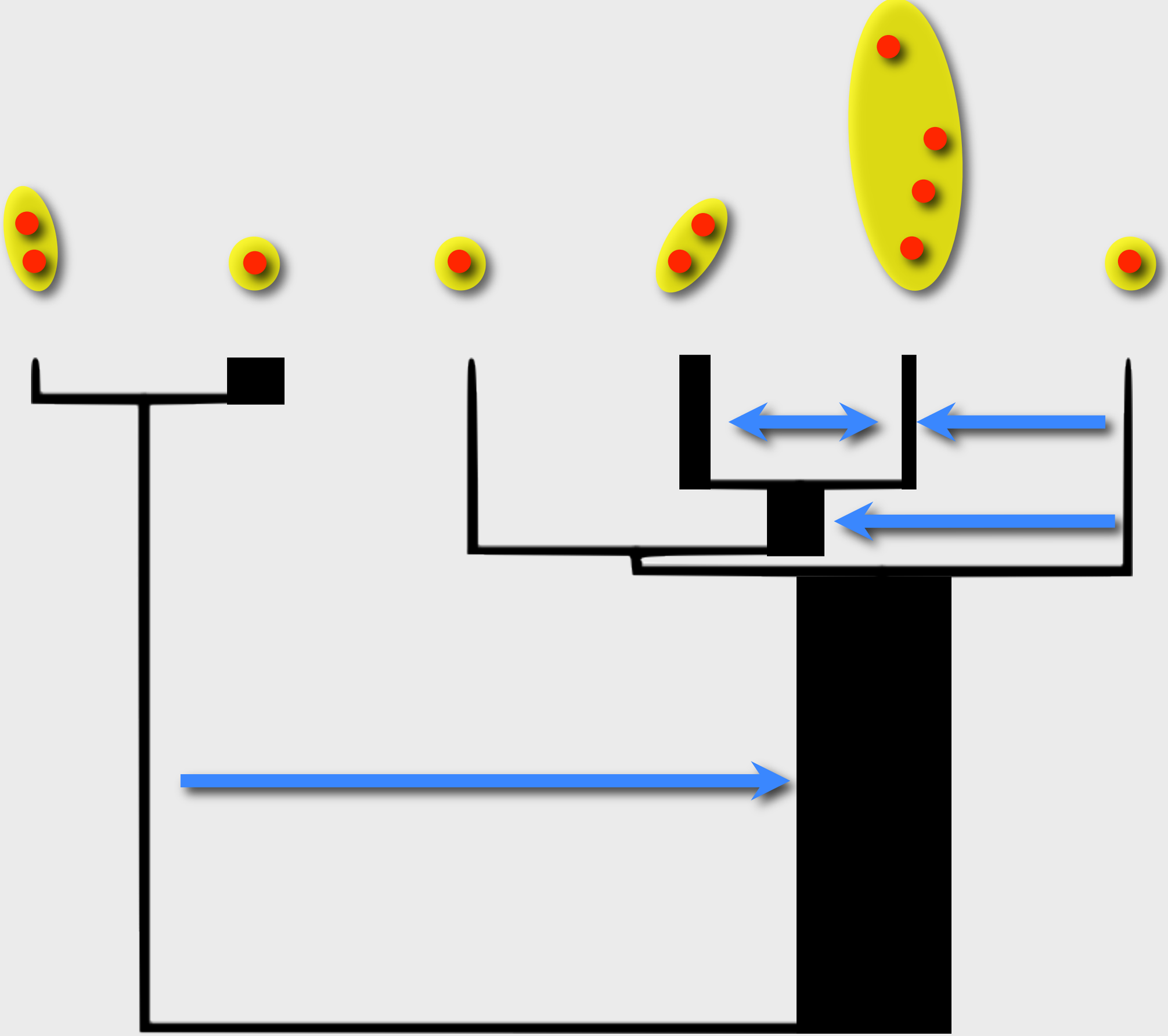


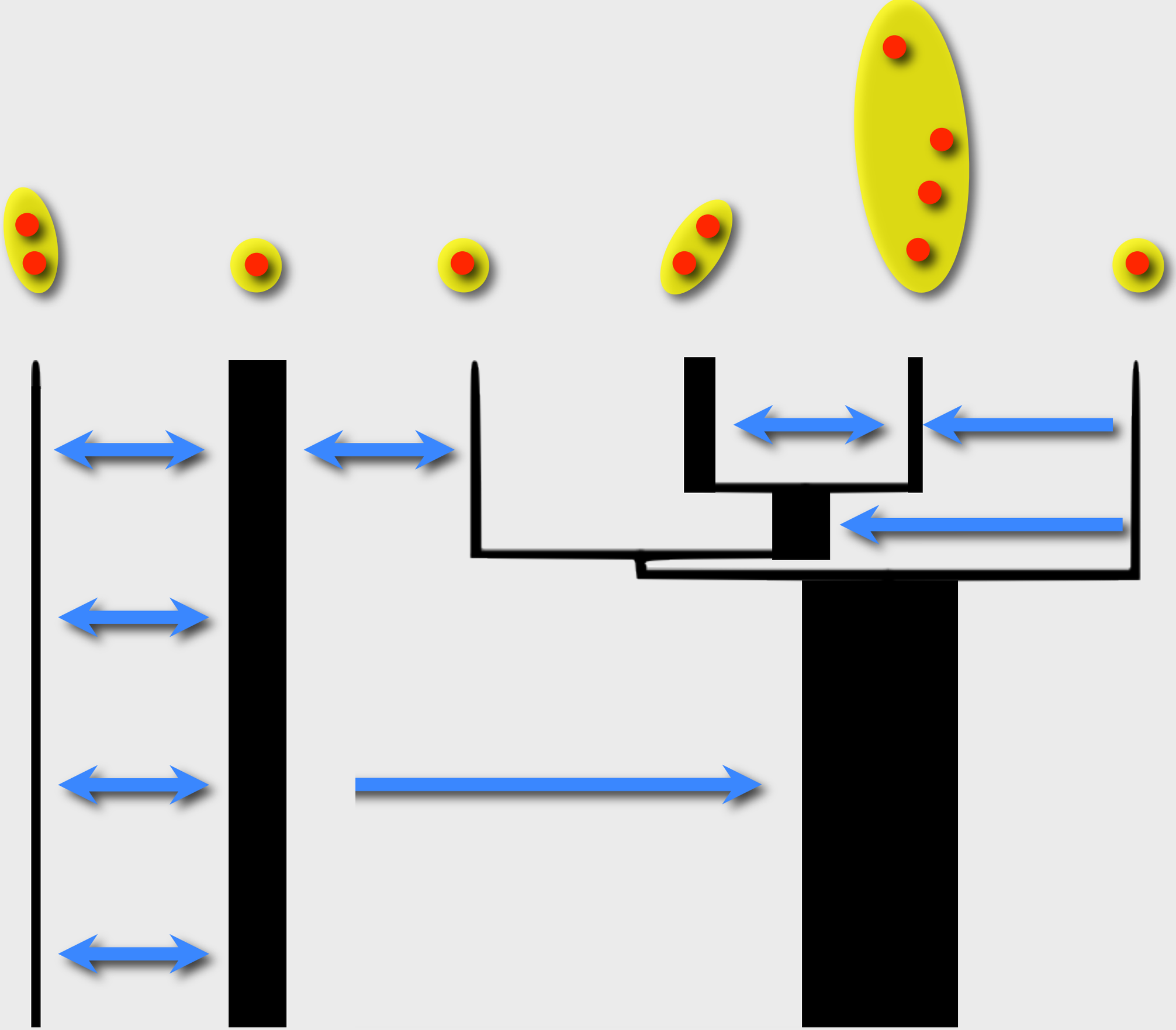


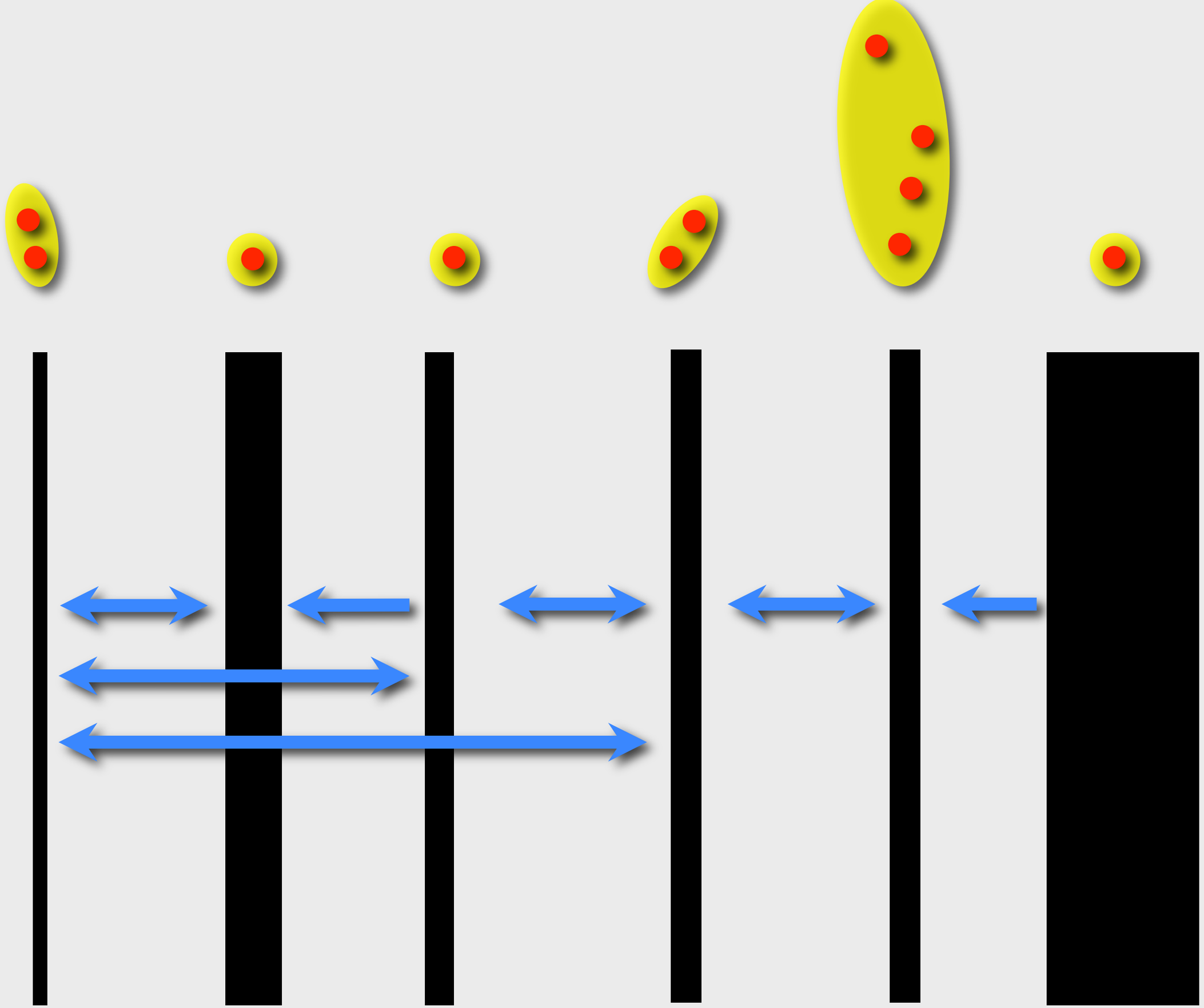












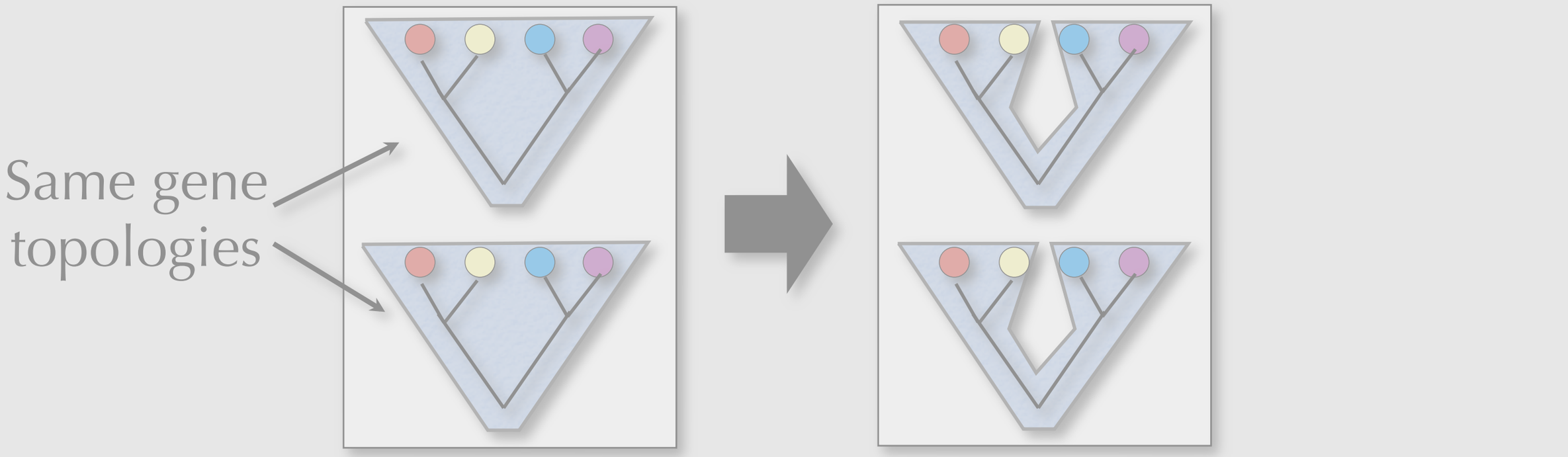
Brownie for species delim

```
Now starting the search proper.
A ">" before a score indicates that calculation of that score was aborted once the score for that move exceeded the best local score

Rep     Moves   #Spp    Type    Qual    CombScore           GTP          Struct          Local          Global      NTrees  Remaining
1       0       2               =G        770.620        52.000       1489.241        770.620        770.620       1       _aid_
1       1       2->3    i       *G         56.716       113.000          0.431         56.716         56.716       1       _aid_
1       2       3->2    d             >    56.716         0.000       > 113.432         56.716         56.716       1       _ai__
1       3       3->3    a             >    56.831       > 113.432       >   0.230         56.716         56.716       1       _ai__
1       4       3->3    a             >    56.831       > 113.432       >   0.230         56.716         56.716       1       _ai__
1       5       3->3    a             >    56.918       > 113.432       >   0.403         56.716         56.716       1       _ai__
1       6       3->4    i             >    56.831       > 113.432       >   0.230         56.716         56.716       1       _ai__
2       169     3->3    a             >    33.547       >  57.714       >   9.379         28.857         28.857       1       _a___
2       170     3->3    a             >    34.075       >  57.714       >  10.436         28.857         28.857       1       _a___
2       171     3->3    a             >    34.075       >  57.714       >  10.436         28.857         28.857       1       _a___
2       172     3->3    a                  35.954          54.000          17.907         28.857         28.857       1       _a___
2       173     3->3    a                  34.240          49.000          19.481         28.857         28.857       1       _____

Best trees overall

+-- (DpersimilisMather27,DpersimilisMather37,DpersimilisMather41,DpersimilisMatherB,DpersimilisMSH1,DpersimilisMSH3,DpersimilisMSH42,Dpersimilis
MSH7,DpersimilisSalem)
|
|+- (DbogotanaPotosi2,DbogotanaSusa3,DbogotanaSutatausa1,DbogotanaSutatausa3,DbogotanaToro4,DbogotanaToro6,DbogotanaToro7)
+|
 +- (DpseudoobscuraAF2,DpseudoobscuraAFC12,DpseudoobscuraAFC3,DpseudoobscuraAFC7,DpseudoobscuraMather48,DpseudoobscuraMSH32)
```

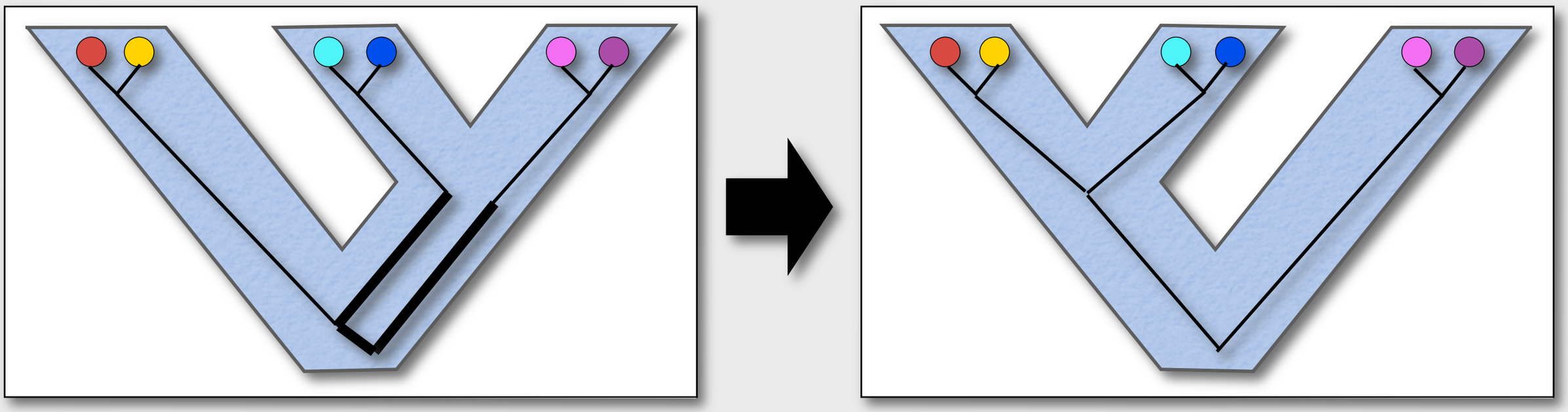
O'Meara 2010

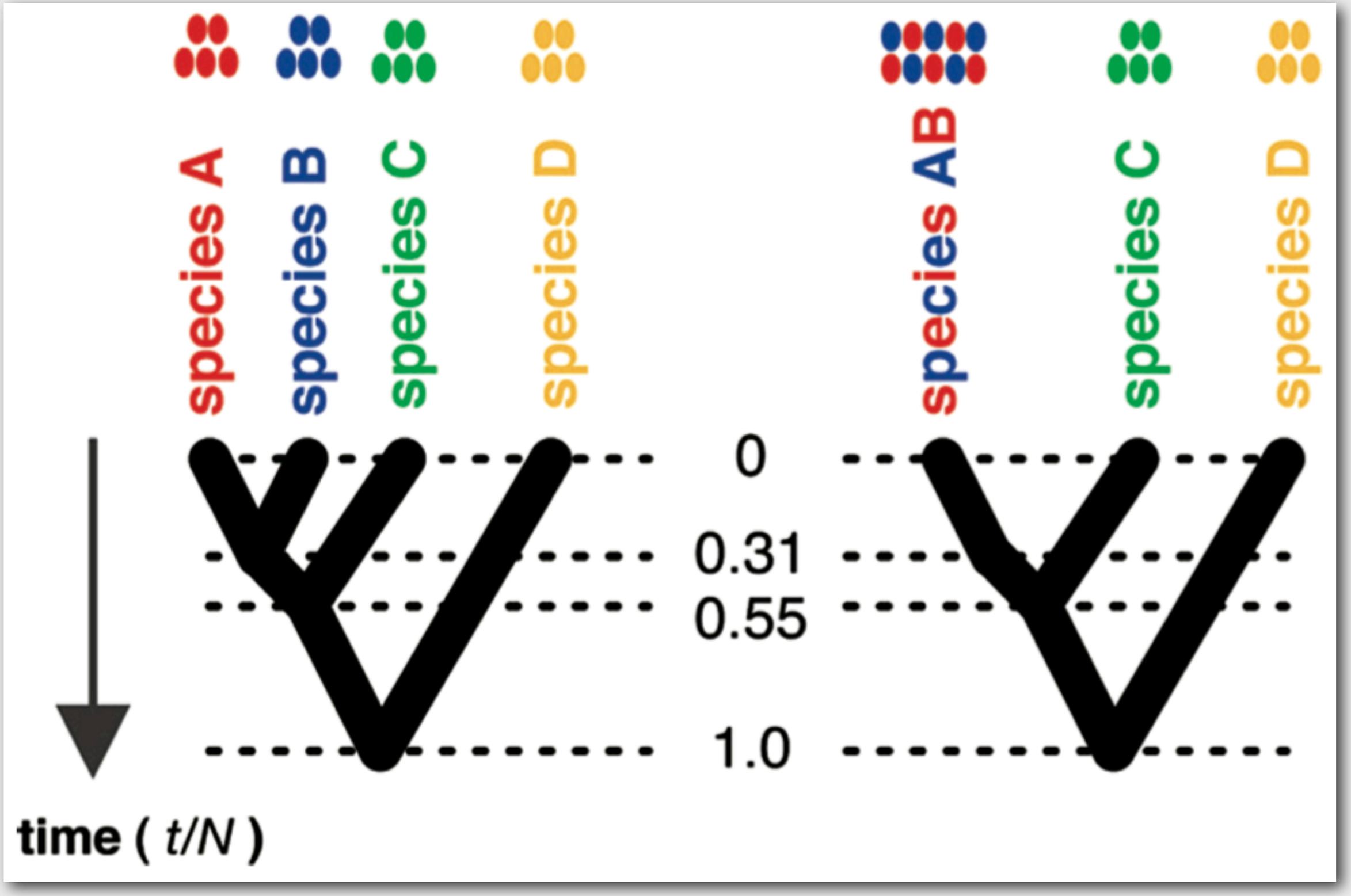
Infers species assignments and species tree simultaneously, using two approaches:

Minimize excess intraspecific structure



Minimize gene tree-species tree conflict





Knowles and Carstens 2007

Brownie for species delim

```
Now starting the search proper.
A ">" before a score indicates that calculation of that score was aborted once the score for that move exceeded the best local score

Rep     Moves   #Spp    Type    Qual    CombScore           GTP          Struct          Local          Global      NTrees  Remaining
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1       1       2->3    i       *G         56.716       113.000           0.431         56.716         56.716      1       _aid_
1       2       3->2    d               >  56.716         0.000        > 113.432         56.716         56.716      1       _ai__
1       3       3->3    a               >  56.831      > 113.432       >   0.230         56.716         56.716      1       _ai__
1       4       3->3    a               >  56.831      > 113.432       >   0.230         56.716         56.716      1       _ai__
1       5       3->3    a               >  56.918      > 113.432       >   0.403         56.716         56.716      1       _ai__
1       6       3->4    i               >  56.831      > 113.432       >   0.230         56.716         56.716      1       _ai__
2       169     3->3    a               >  33.547      >  57.714       >   9.379         28.857         28.857      1       _a___
2       170     3->3    a               >  34.075      >  57.714       >  10.436         28.857         28.857      1       _a___
2       171     3->3    a               >  34.075      >  57.714       >  10.436         28.857         28.857      1       _a___
2       172     3->3    a                  35.954         54.000          17.907         28.857         28.857      1       _a___
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|+- (DbogotanaPotosi2,DbogotanaSusa3,DbogotanaSutatausa1,DbogotanaSutatausa3,DbogotanaToro4,DbogotanaToro6,DbogotanaToro7)
+|
 +- (DpseudoobscuraAF2,DpseudoobscuraAFC12,DpseudoobscuraAFC3,DpseudoobscuraAFC7,DpseudoobscuraMather48,DpseudoobscuraMSH32)
```
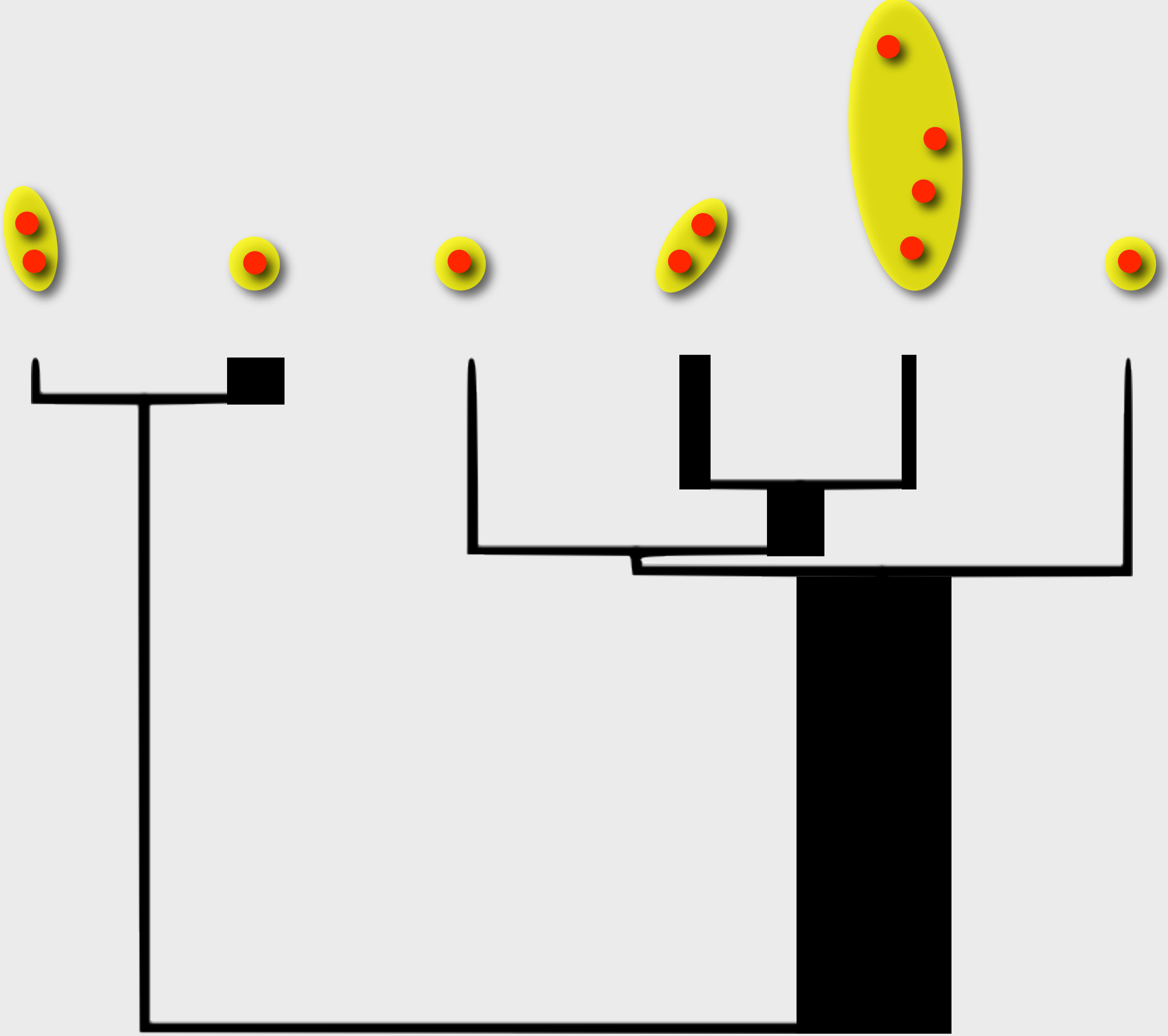

O'Meara 2010

Infers species assignments and species tree simultaneously. Returns a set of equally good trees.



Brownie

Single point estimate, no confidence

Tries a wide range of models

No migration

Many other approaches

Migration only (e.g. Migrate) or population coalescence only (e.g. BPP, gmyc)

Often specify two or a few models (backbone tree, specific ABC model, etc.)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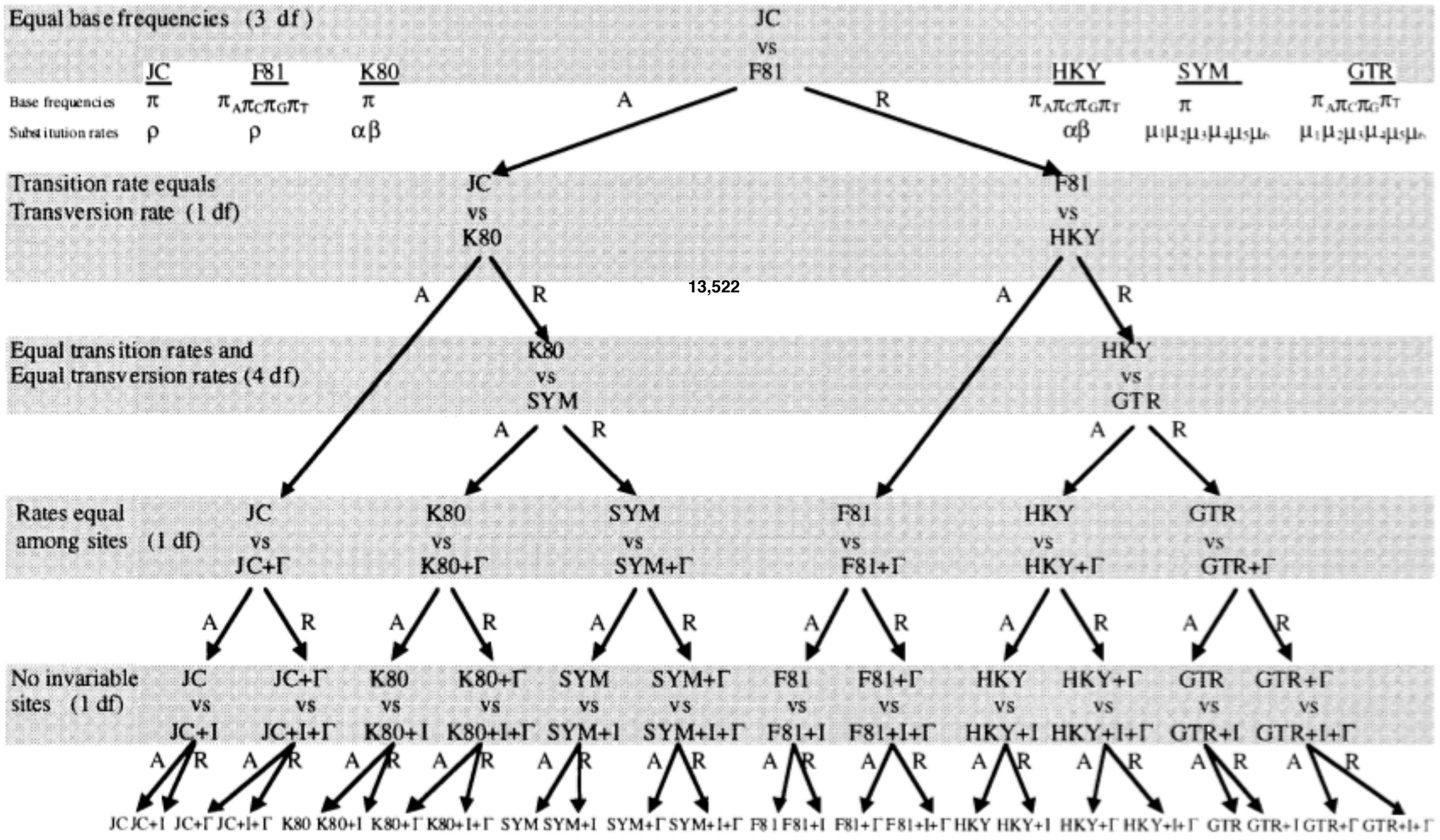
13,522 citations of first ModelTest paper (Posada and Crandall 1998) alone



Posada and Crandall 1998

Question	**Specified hypothesis method**	**Try all method**
DNA model	PAML	ModelTest
AA model	PAML	ProtTest
Continuous trait model	OUCH, Brownie (traits), OUWie	SURFACE, auteur
Diversification model	laser	Medusa
Phylogeographic	various ABC approaches	**phrapl**

phrapl

phylogeographic infe**r**ence using **ap**proximated **l**ikelihoods

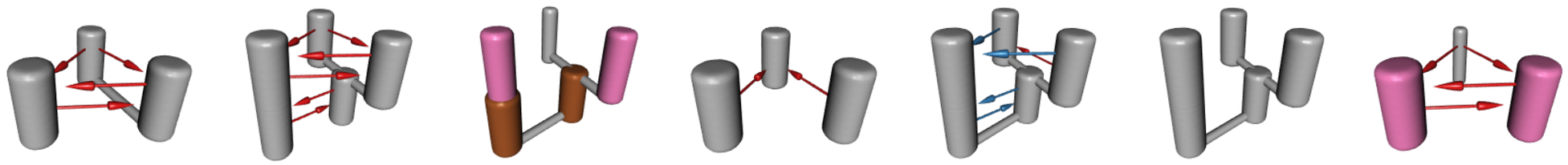
Input:
gene topologies
assignments of samples to populations

Jargon
N = number of populations
K = number of free parameters (as in AIC)

1

Generate all possible models

Given *N* populations, ≤*K* free parameters



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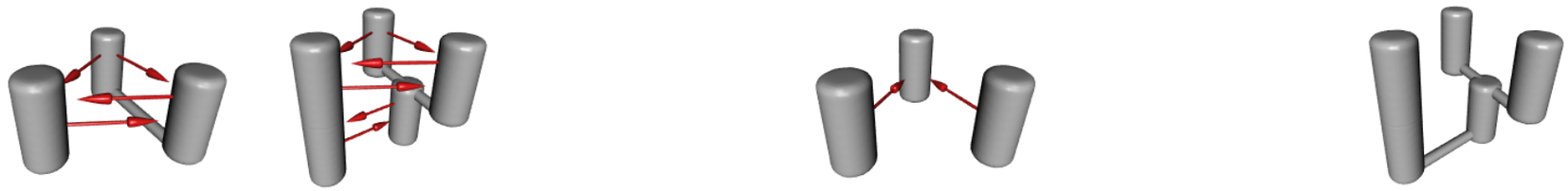
2

Filter

(only tree models, no more than two migration rates, etc.)



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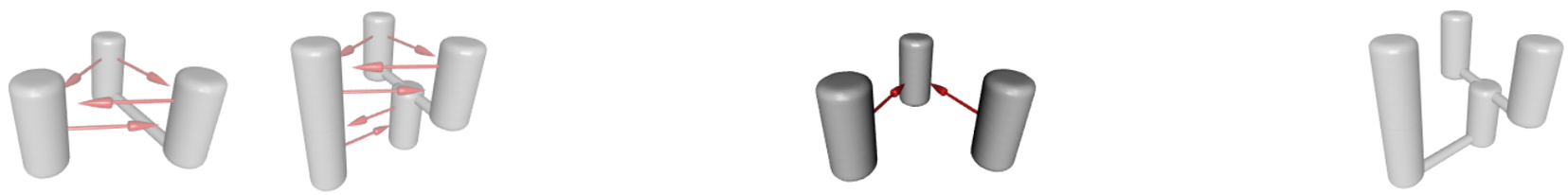
3

Analyze

(find best, find AIC for all



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Generate all possible models

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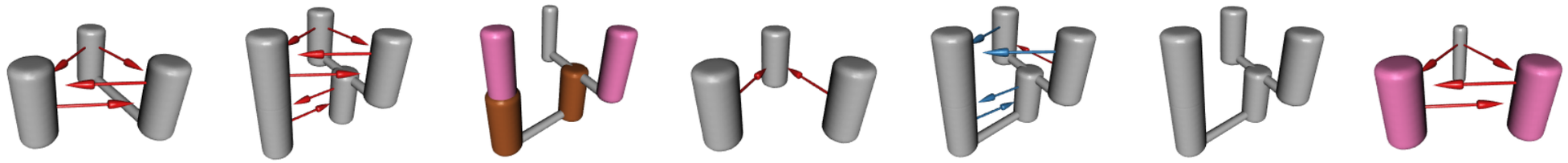

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2

Filter

(only tree models, no more than two migration rates, etc.)

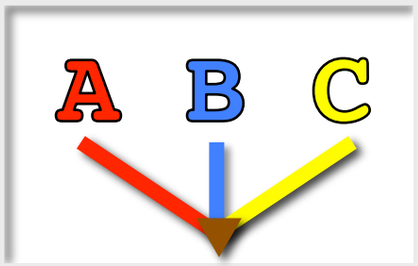
↓

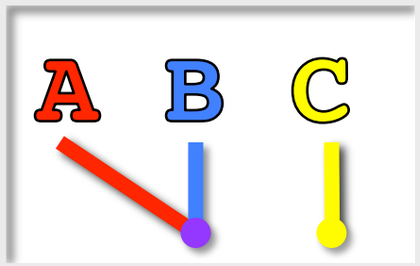
3

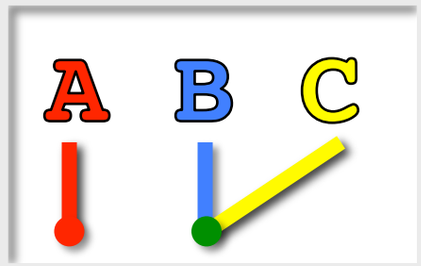
Analyze

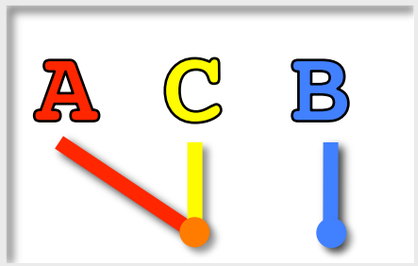
(find best, find AIC for all

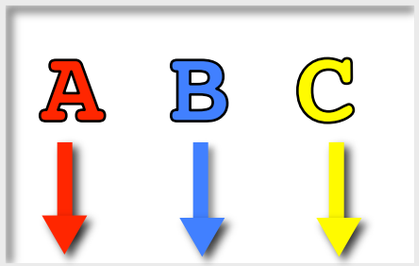
Coalescence of populations



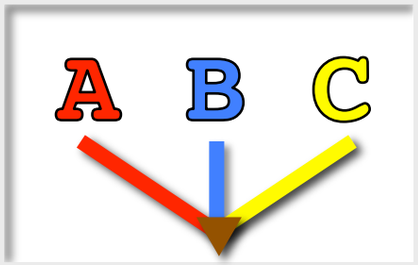


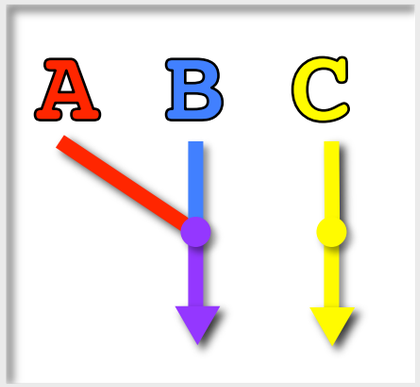


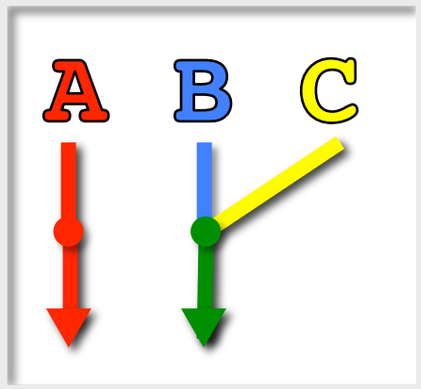


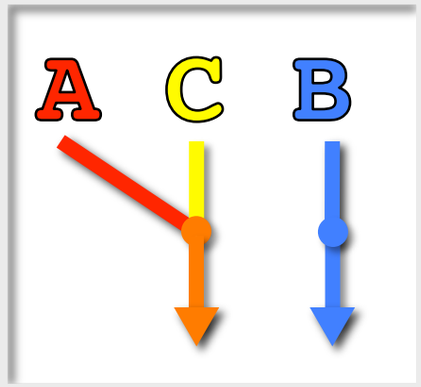


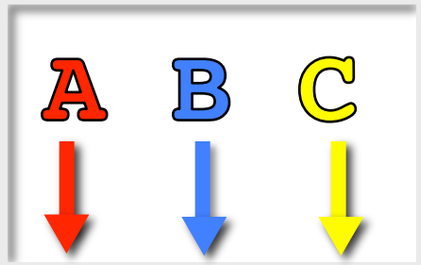
Coalescence of populations

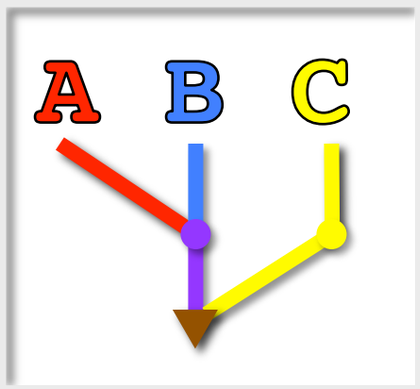


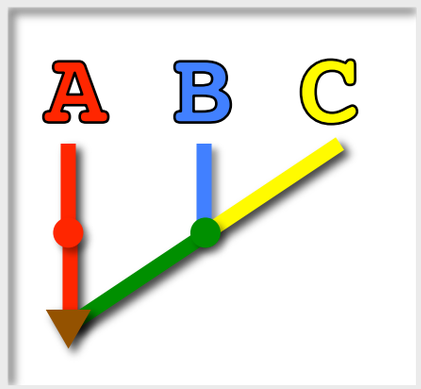


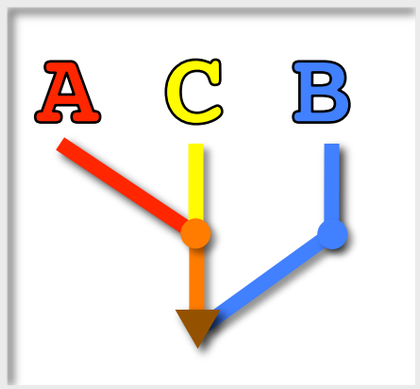












Coalescence of populations

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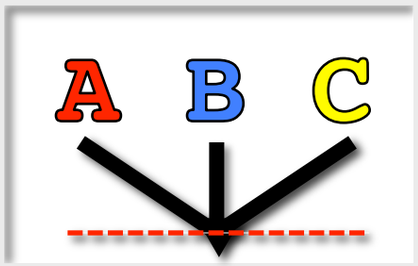
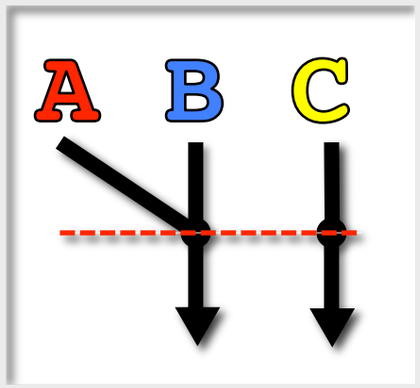


K=1



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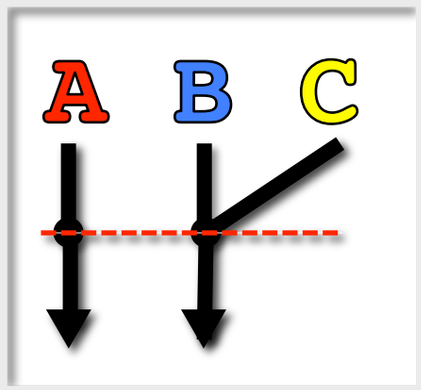
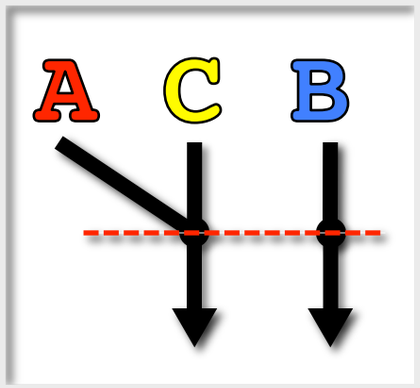
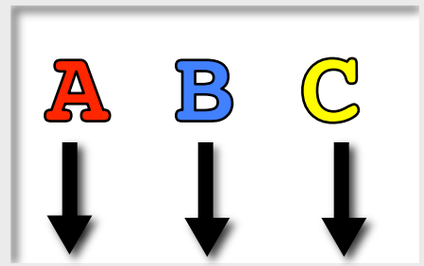


K=1



K=0



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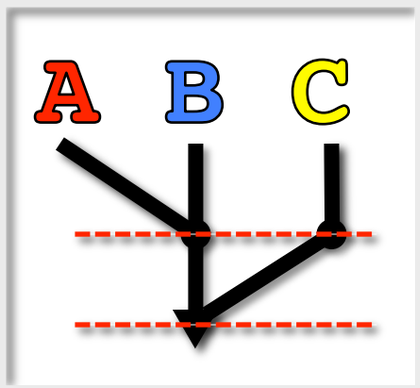

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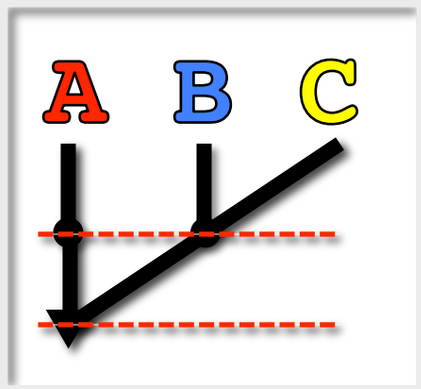

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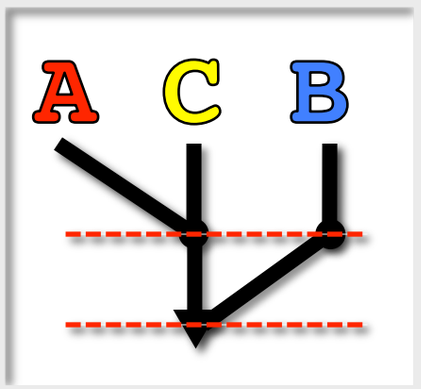
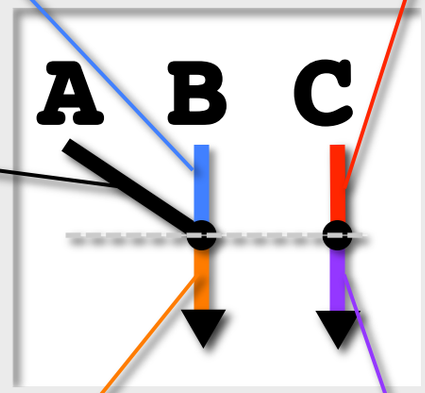


B: Same or different as A

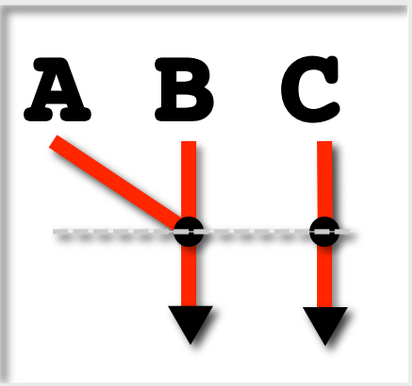
A: N_1



C1: Same or different as A and/or B and/or AB

AB: Same or different as A and/or B

C2: Same or different as A and/or B and/or AB and/or C1



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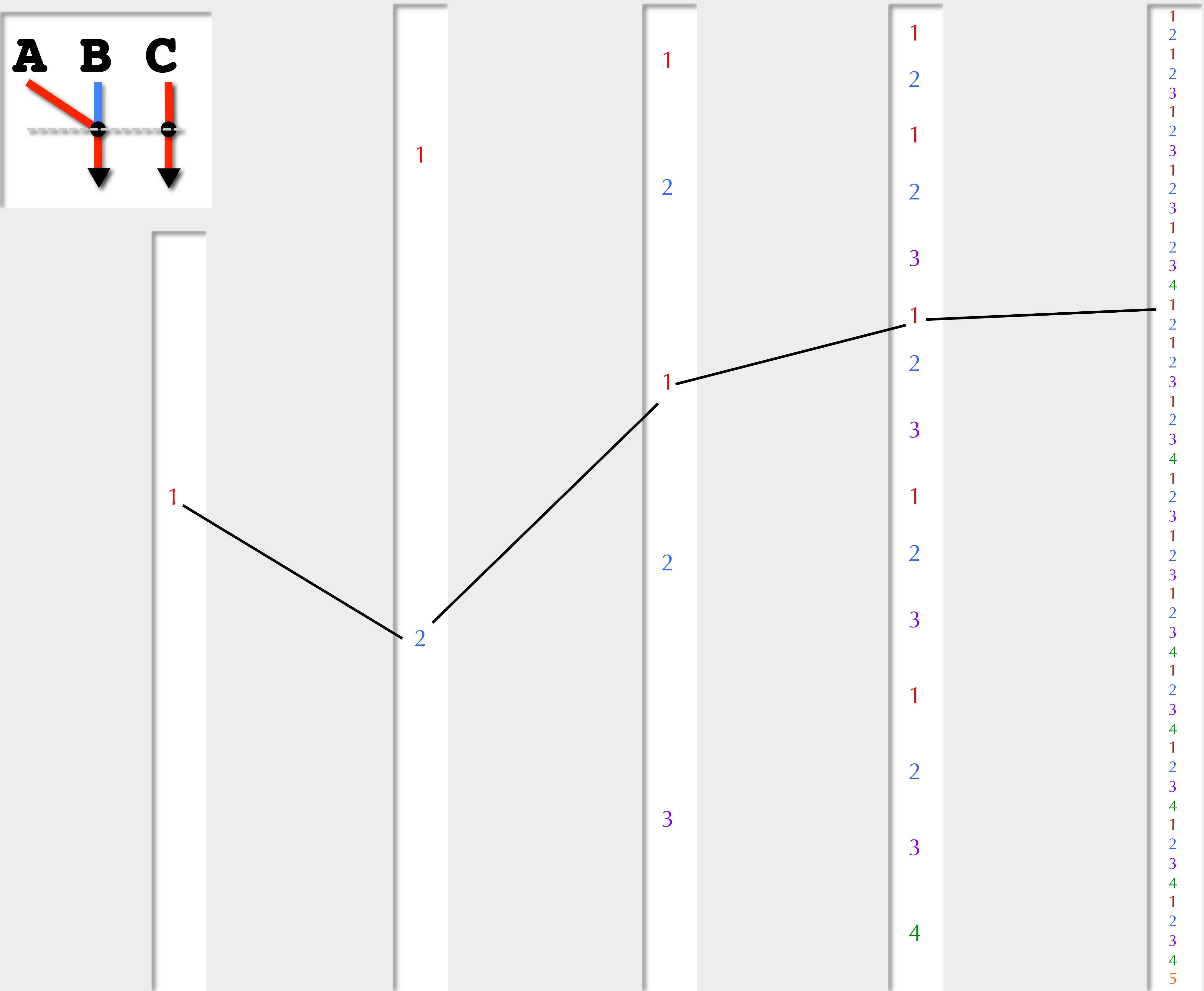
A
B
C
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1 2 1 2 3 1 2 3 1 2 3 1 2 3 4
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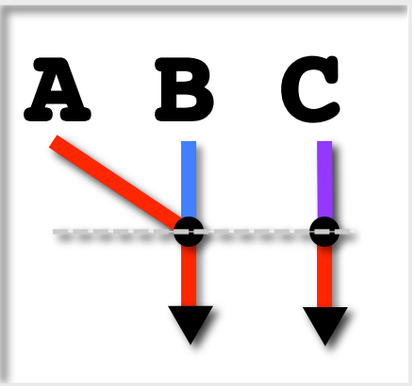

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1 2 3

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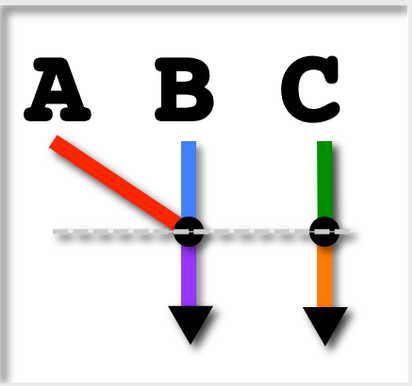

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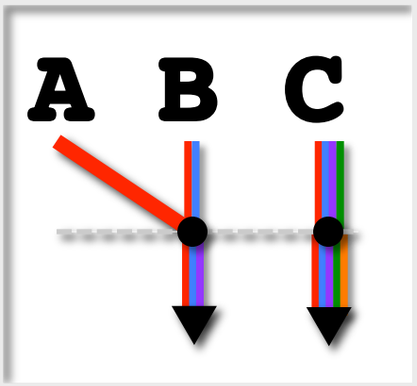
1 2 3 4

1 2 3 4

1 2 3 4 5


A
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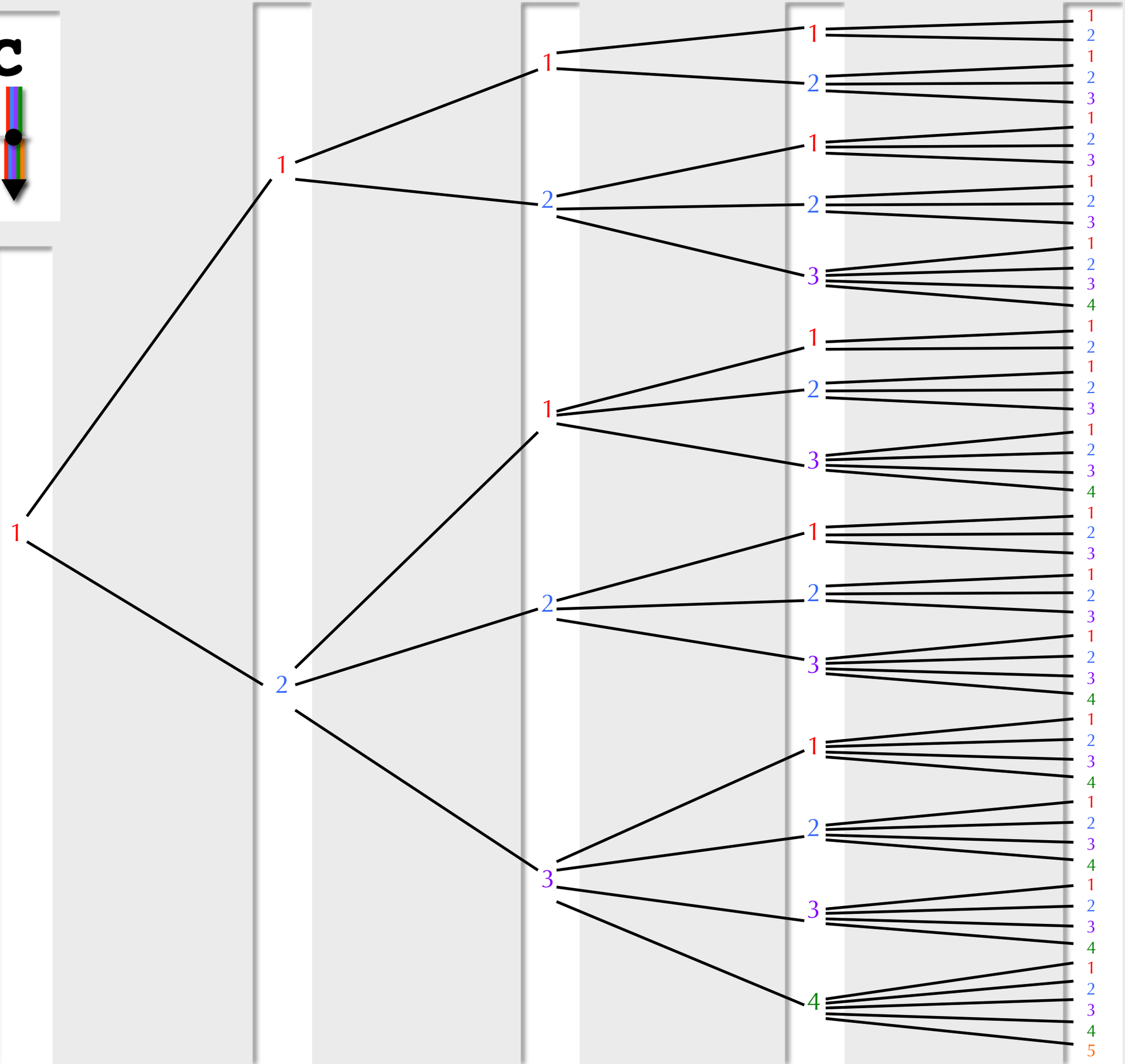
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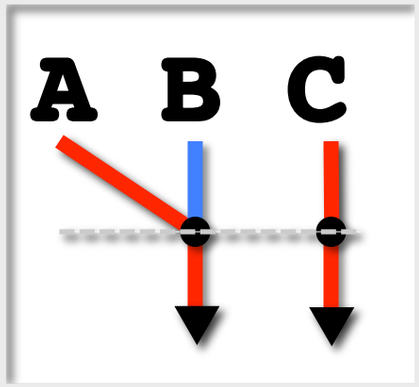
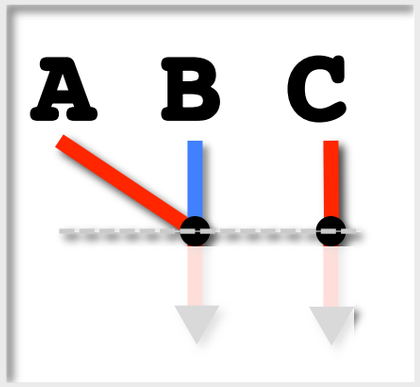


1 collapse parameter
2 population size parameters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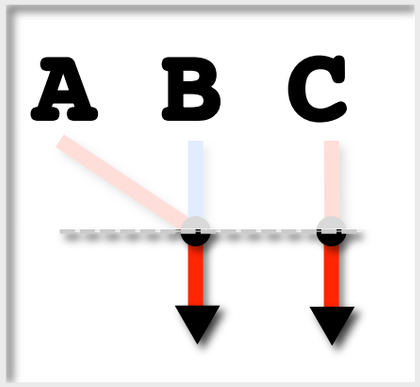
C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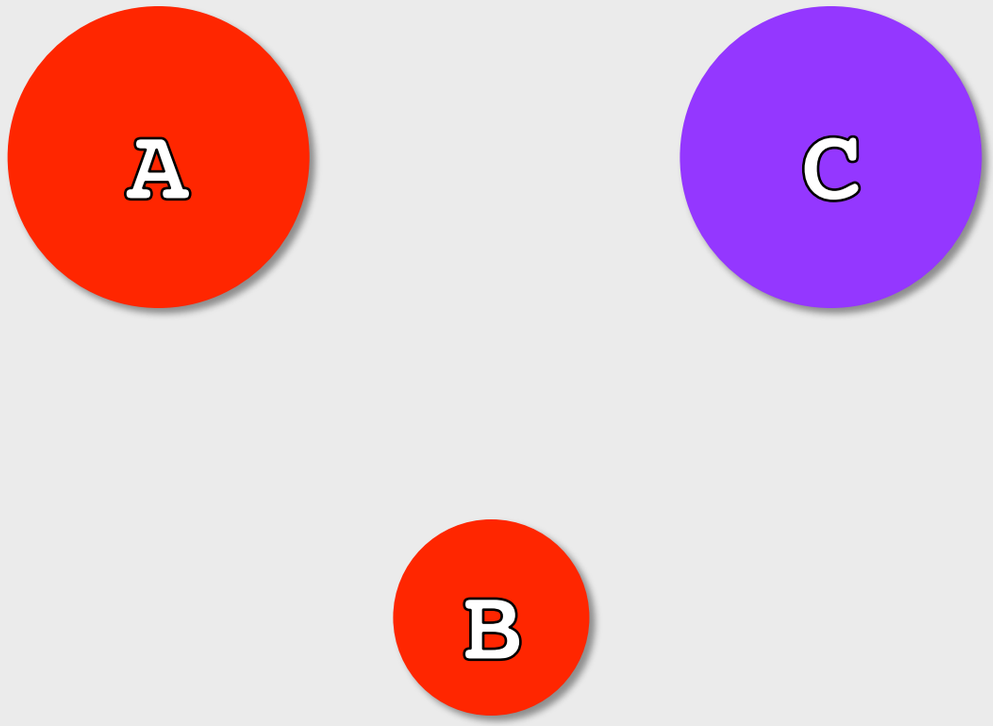
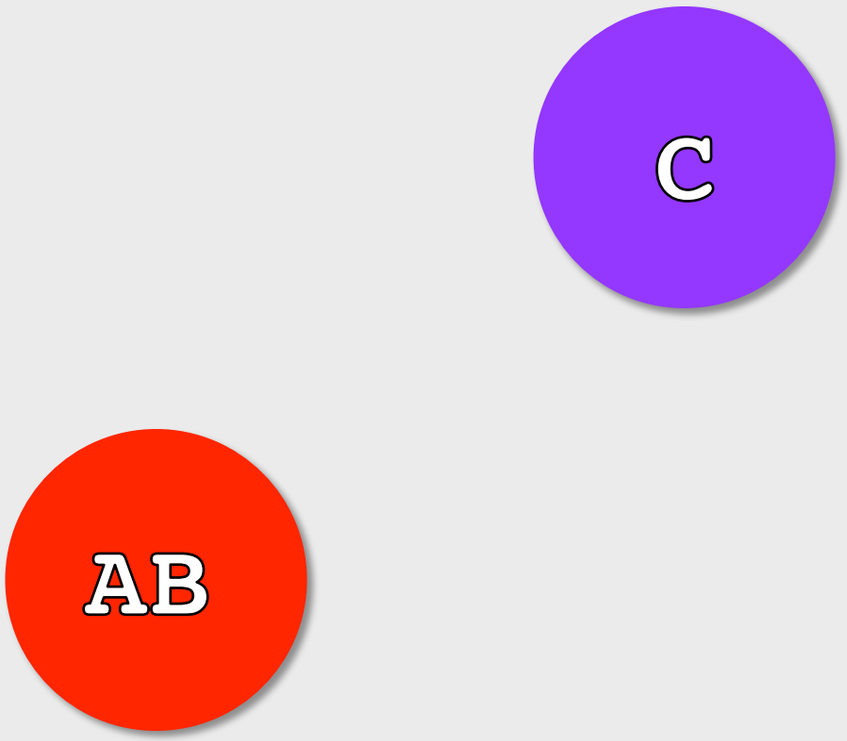
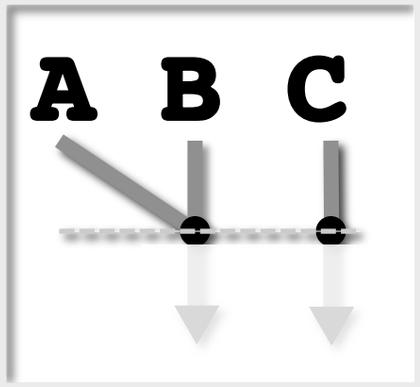
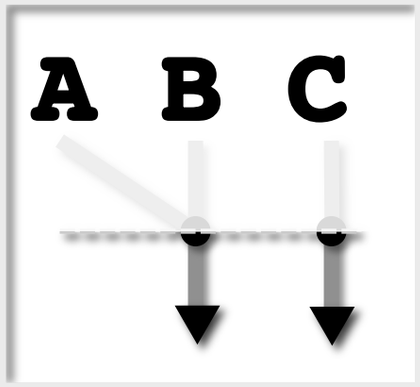
C


A
C
B


C
AB


A B C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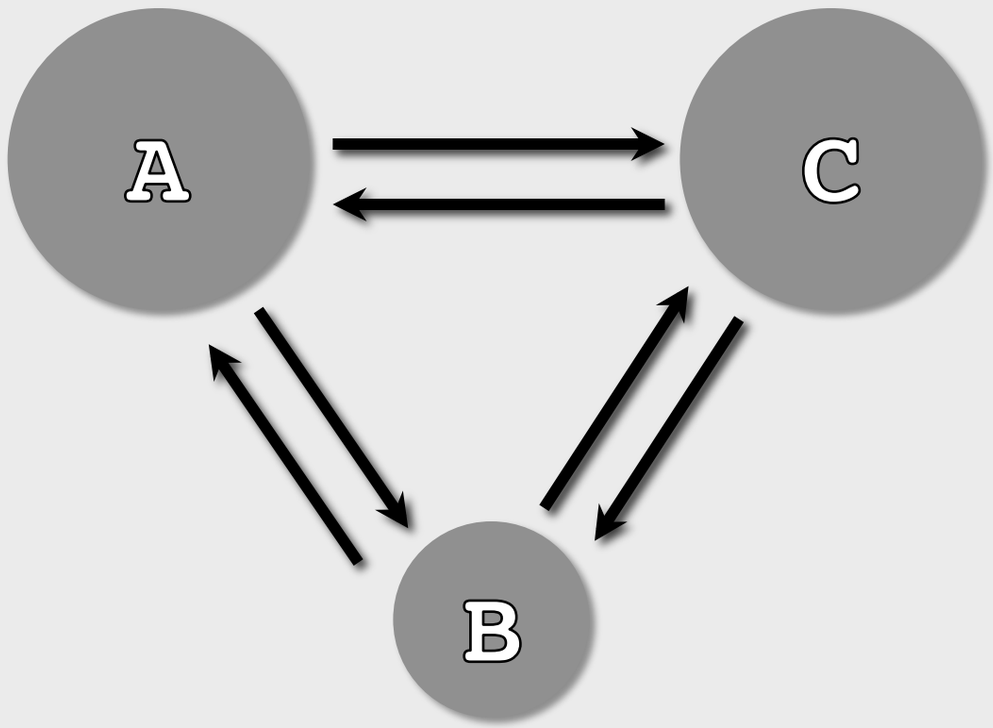
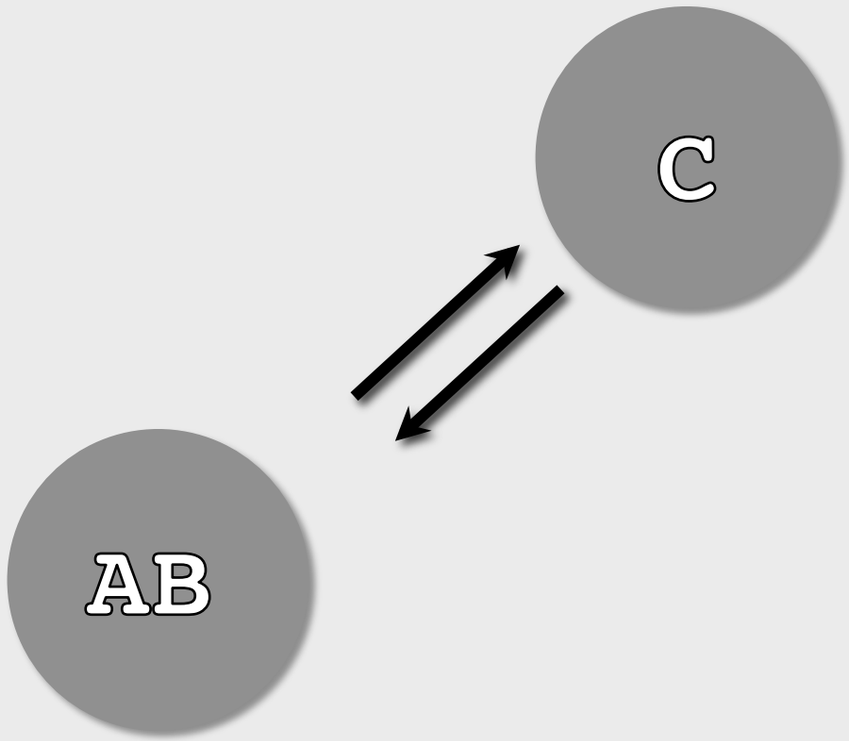

A
C
B


C
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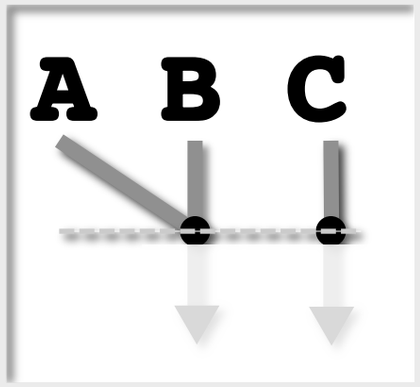
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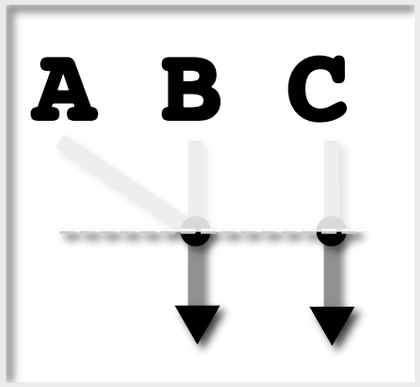
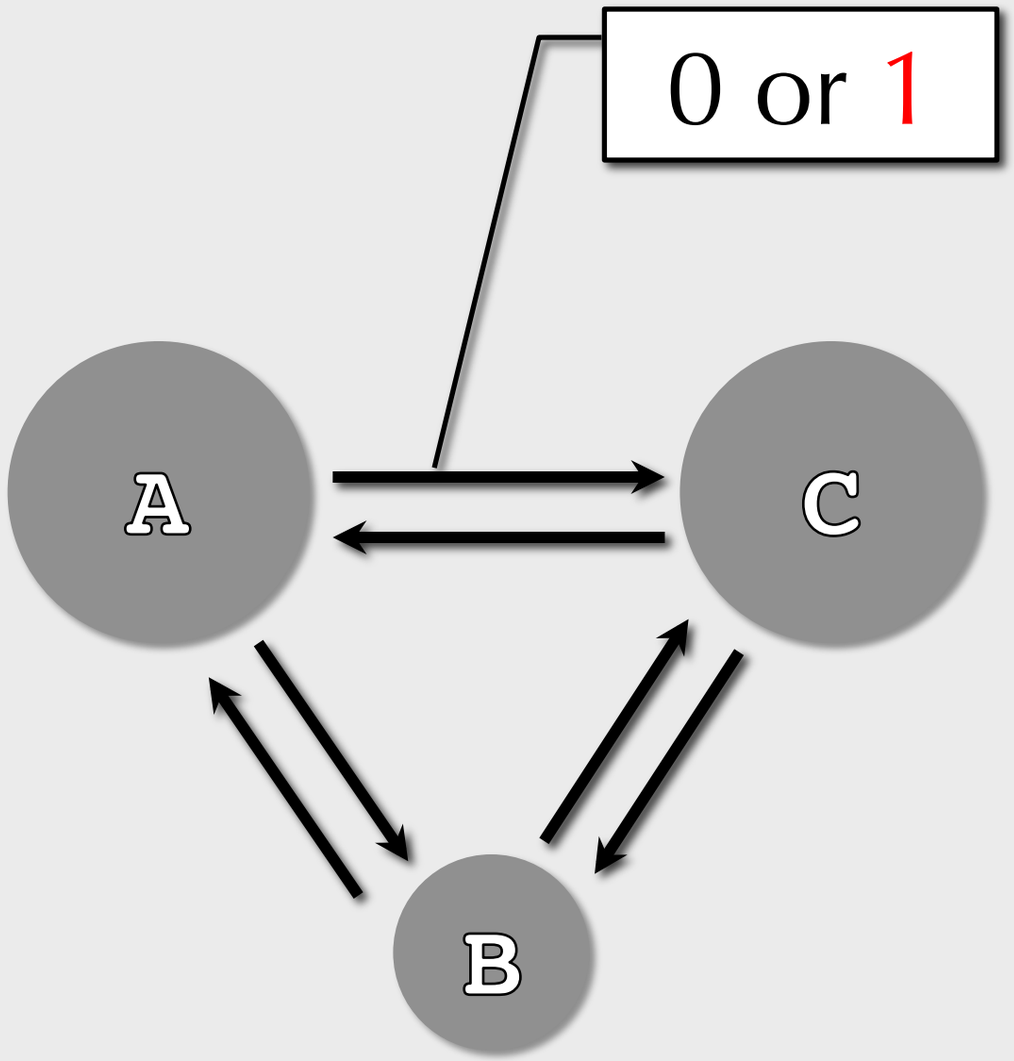
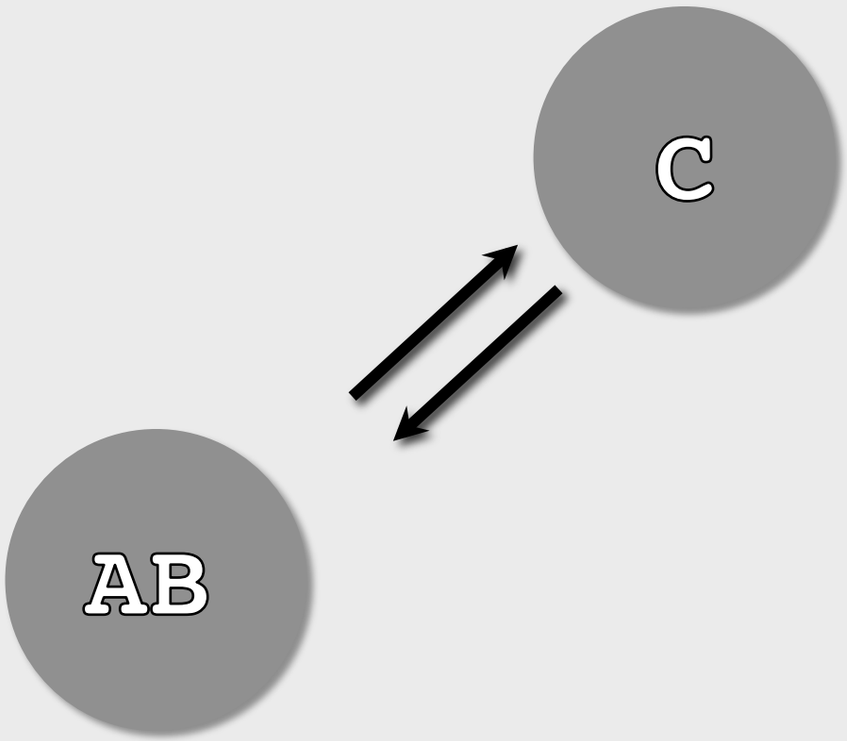
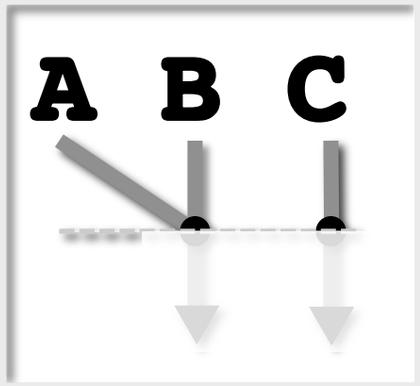
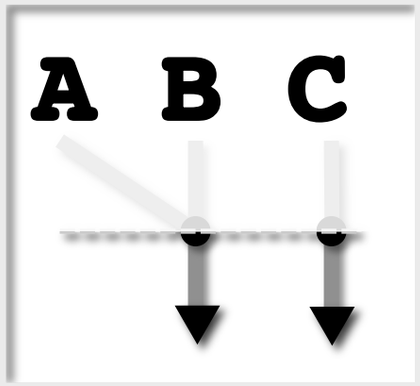
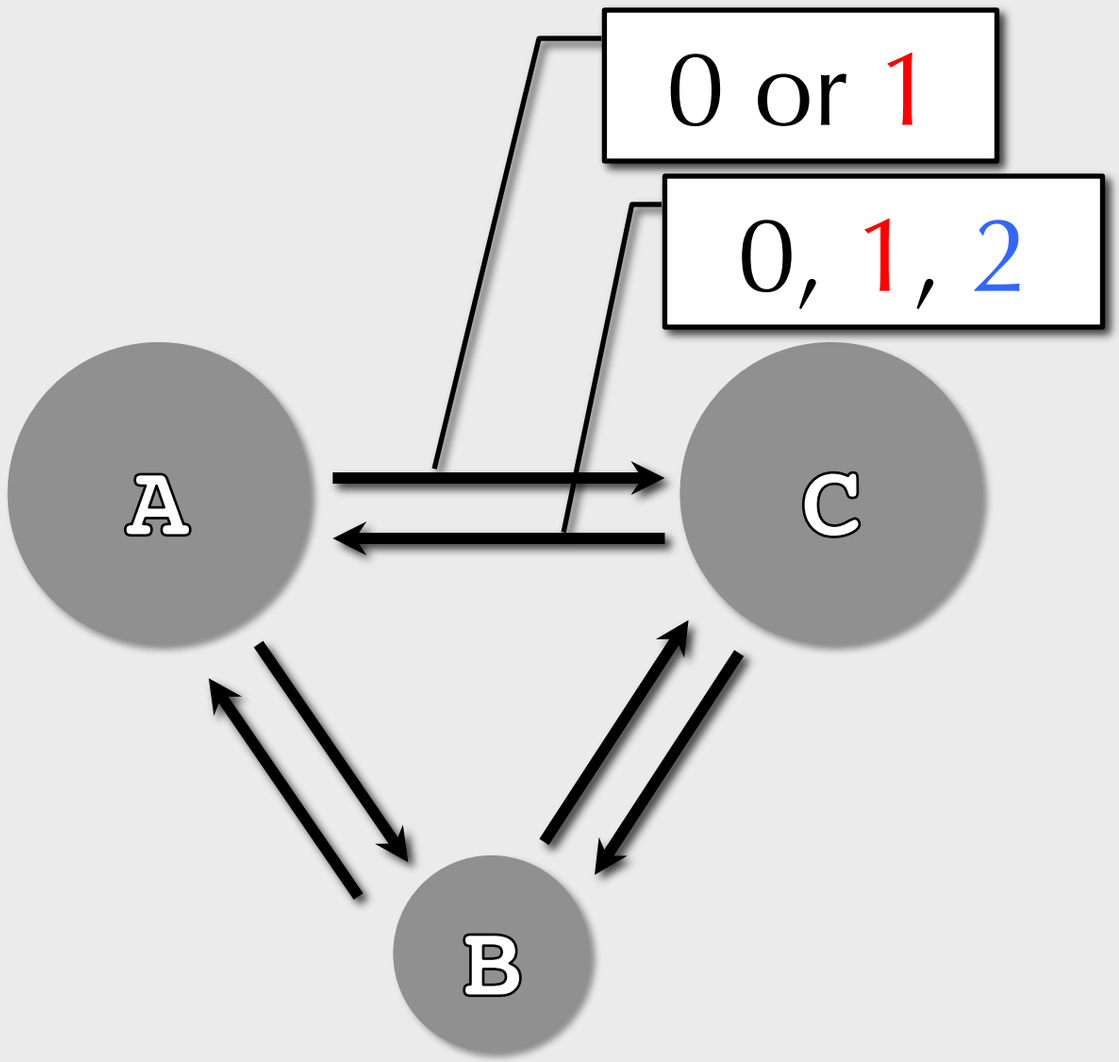

A B C

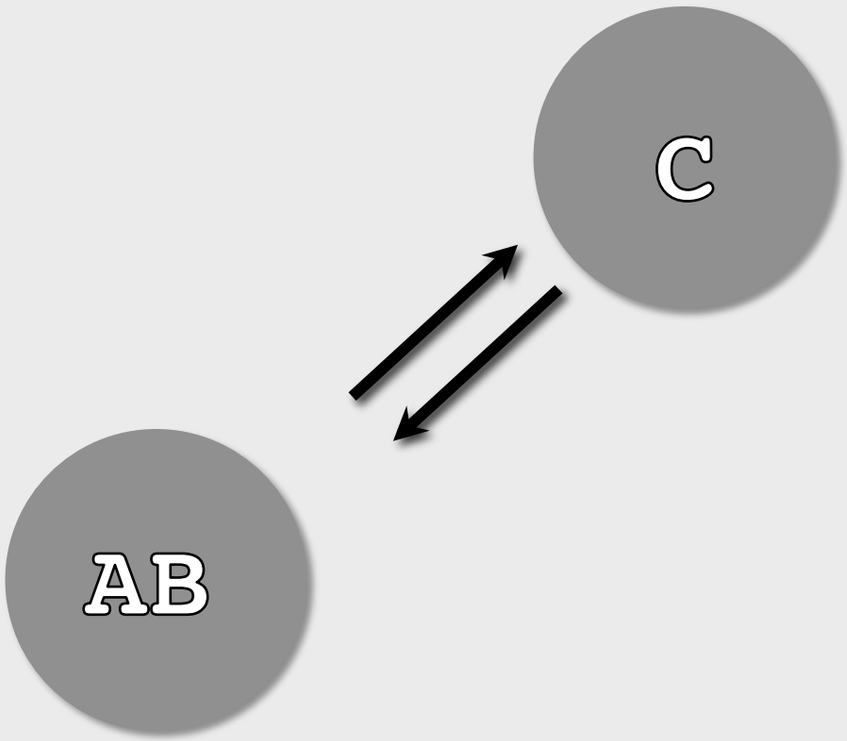

0 or 1
A
C
B


C
AB


A B C


A B C


0 or 1
0, 1, 2
A
C
B


C
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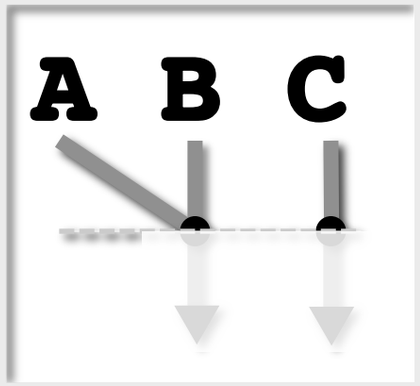
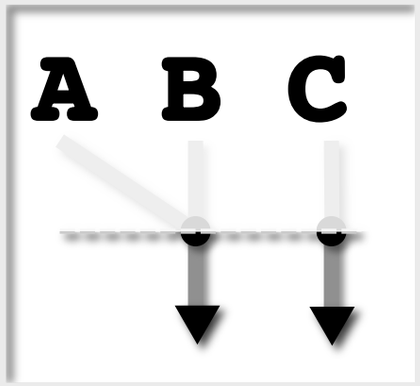
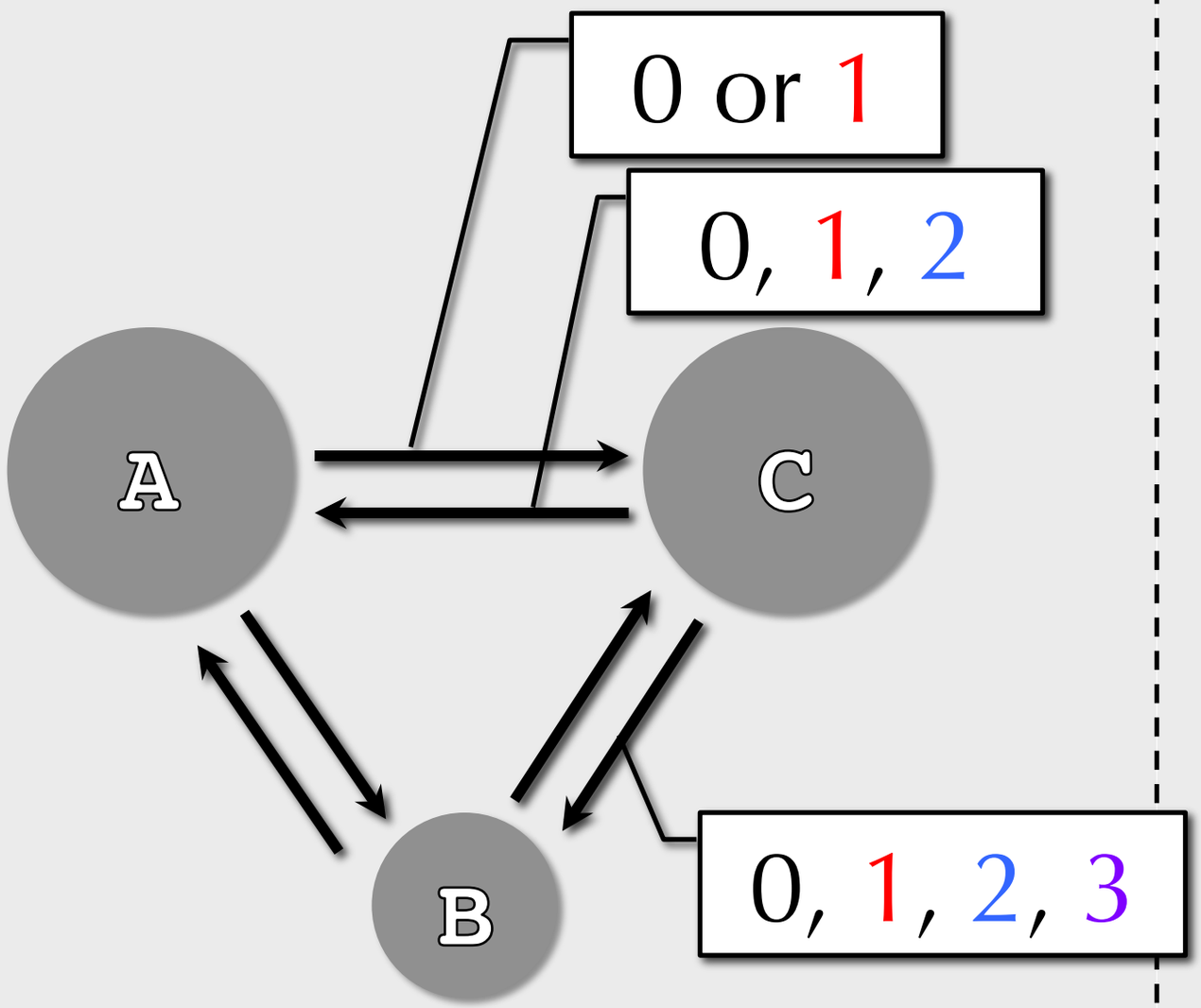
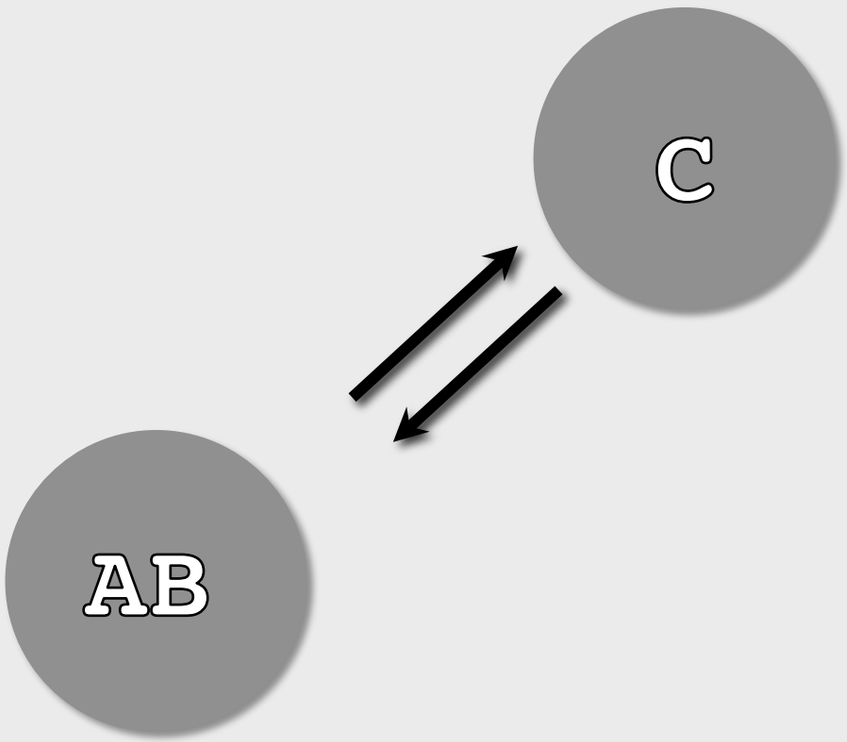

A B C


A B C


0 or 1
0, 1, 2
A
C
B
0, 1, 2, 3


C
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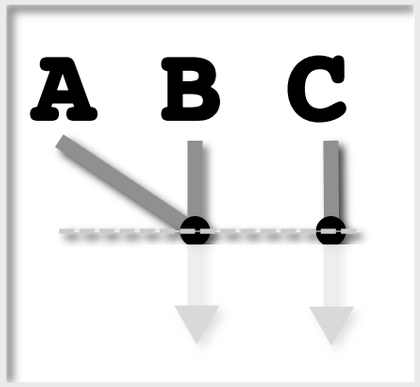
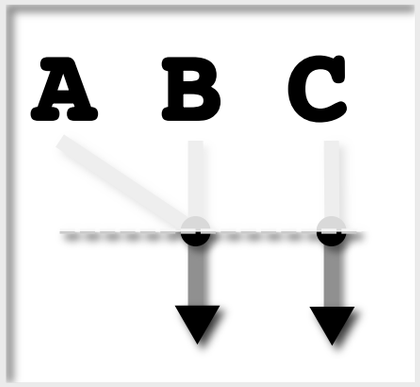
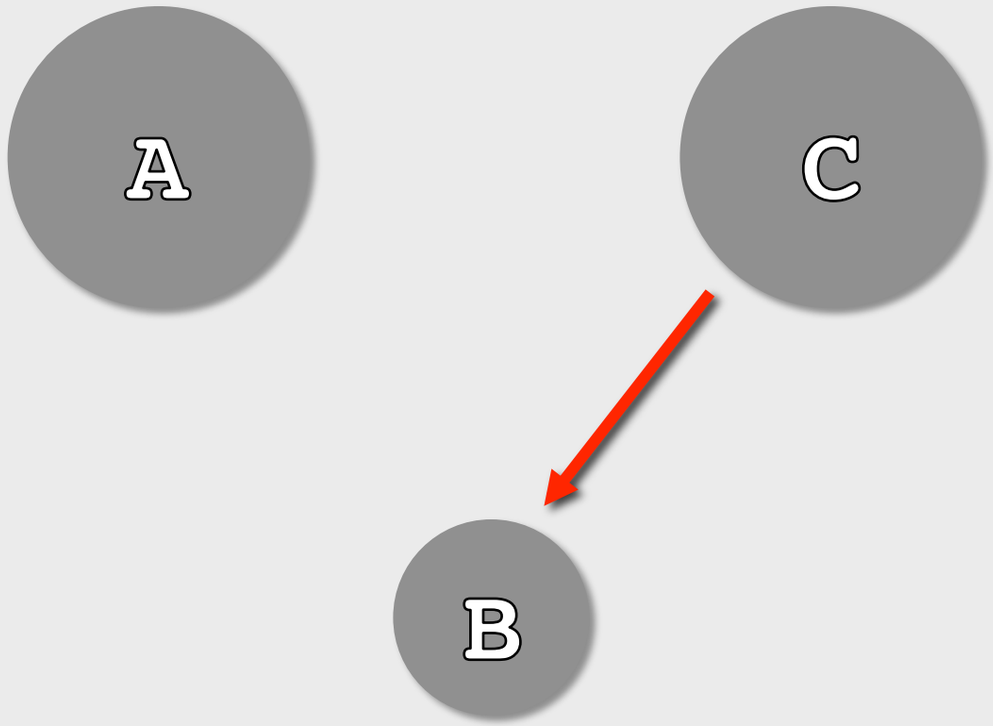
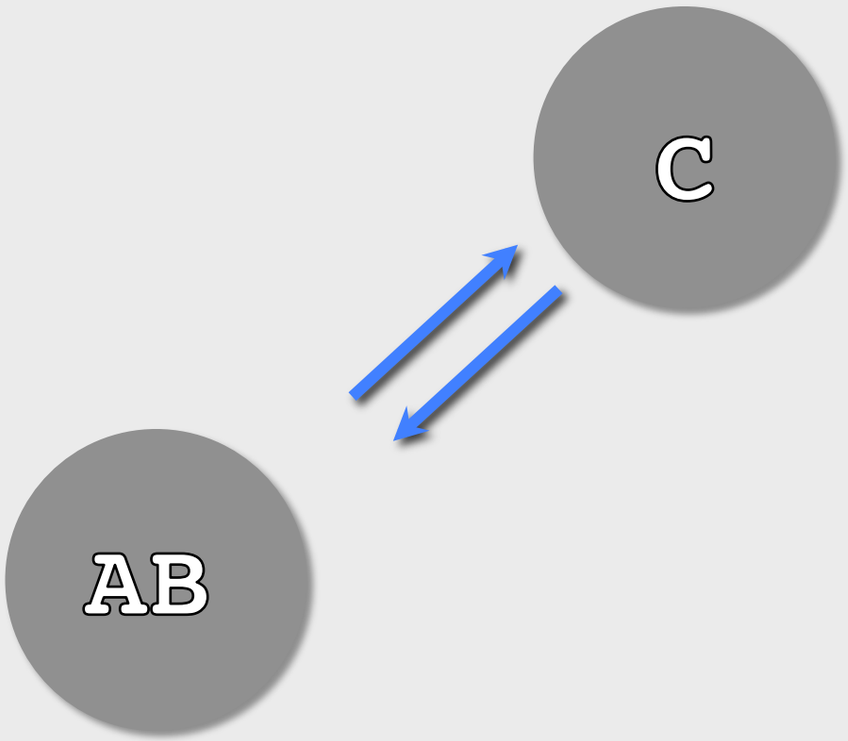
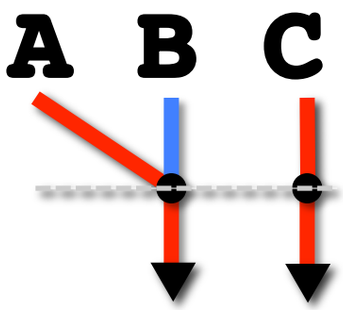

A B C

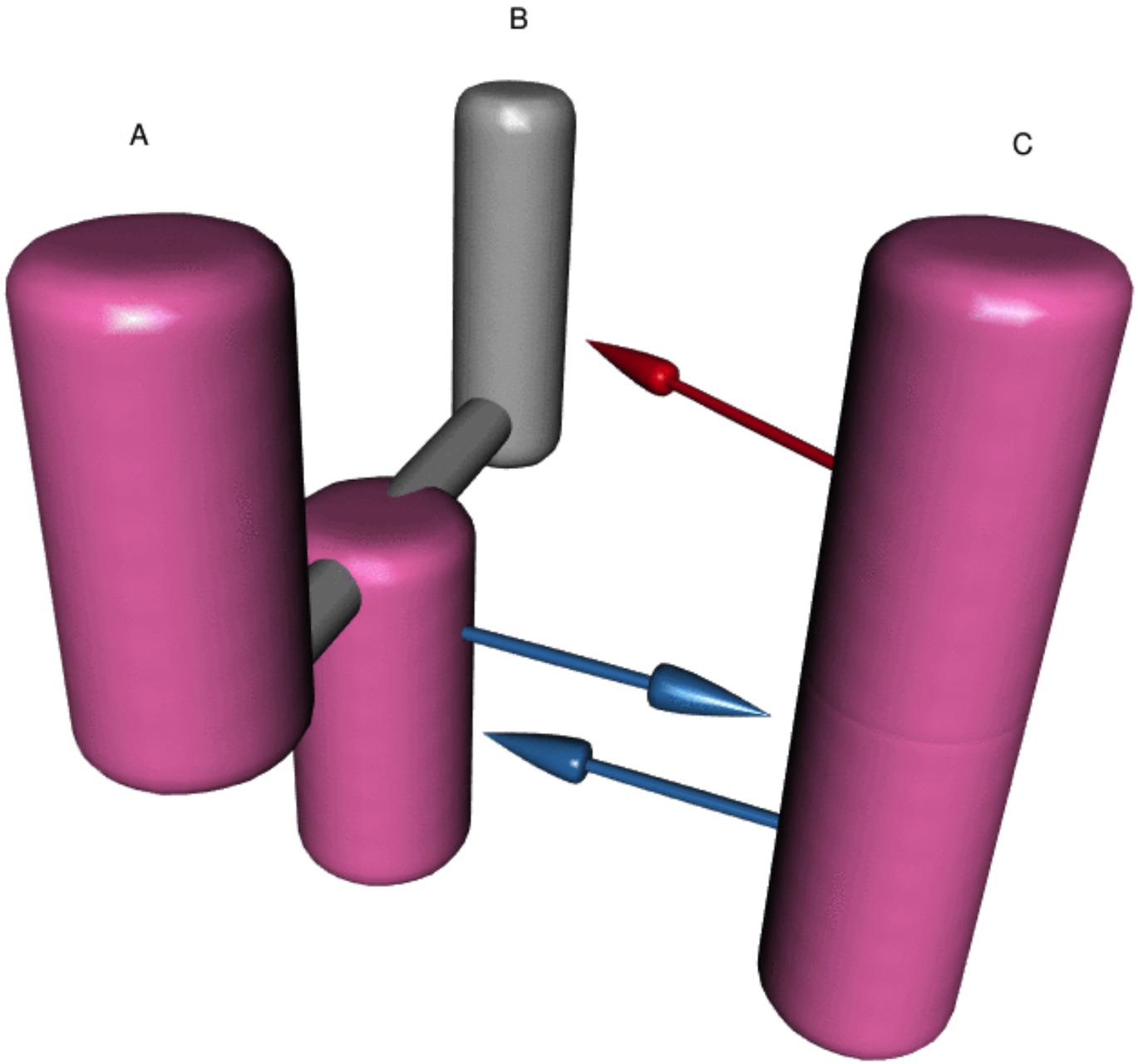

A B C

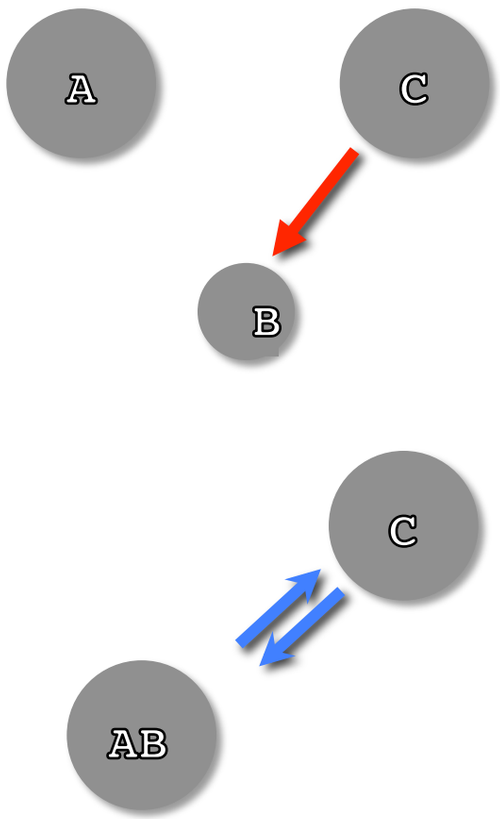

A
C
B

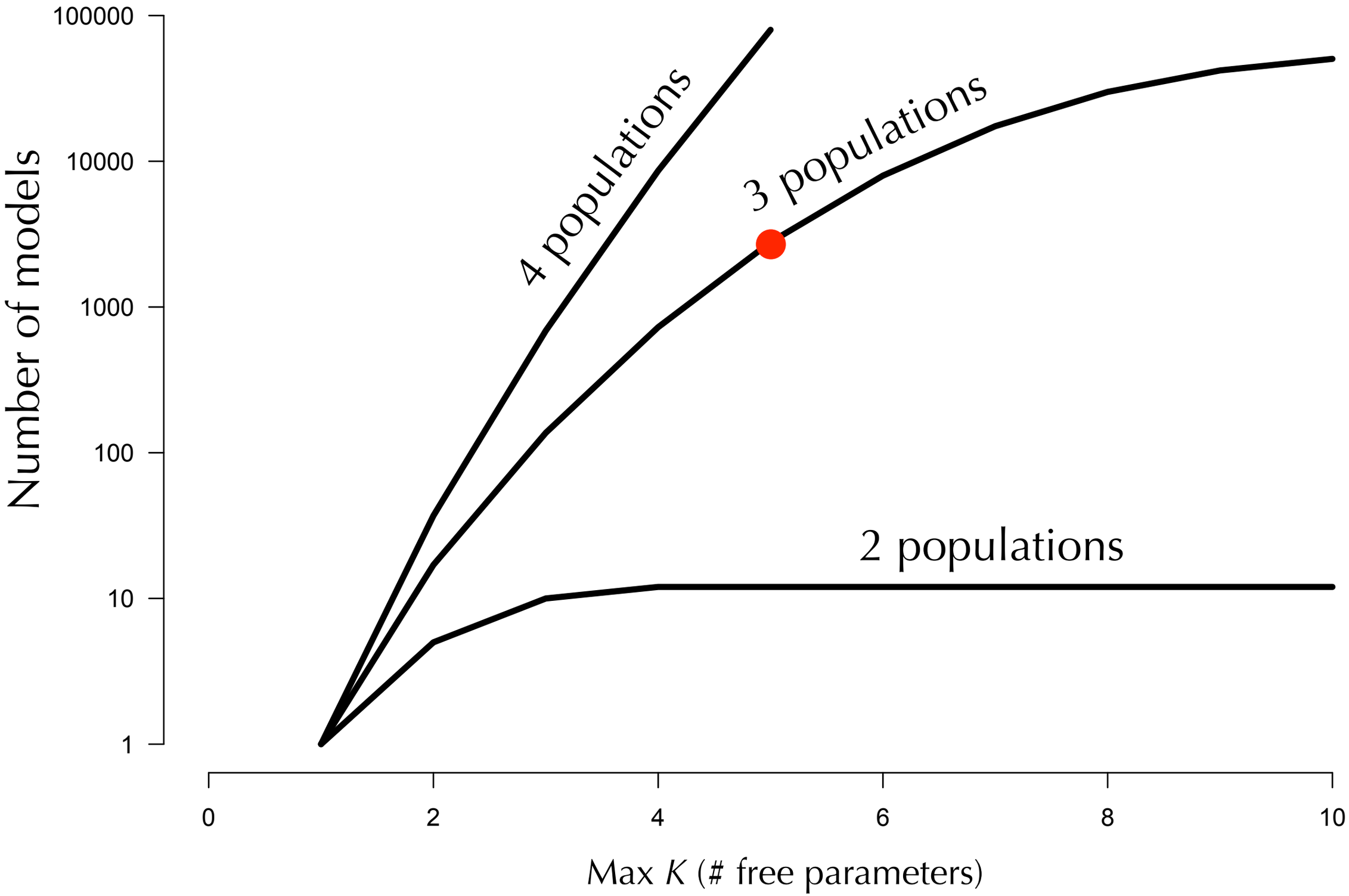

C
AB

1 collapse parameter
2 population size parameters
2 migration parameters

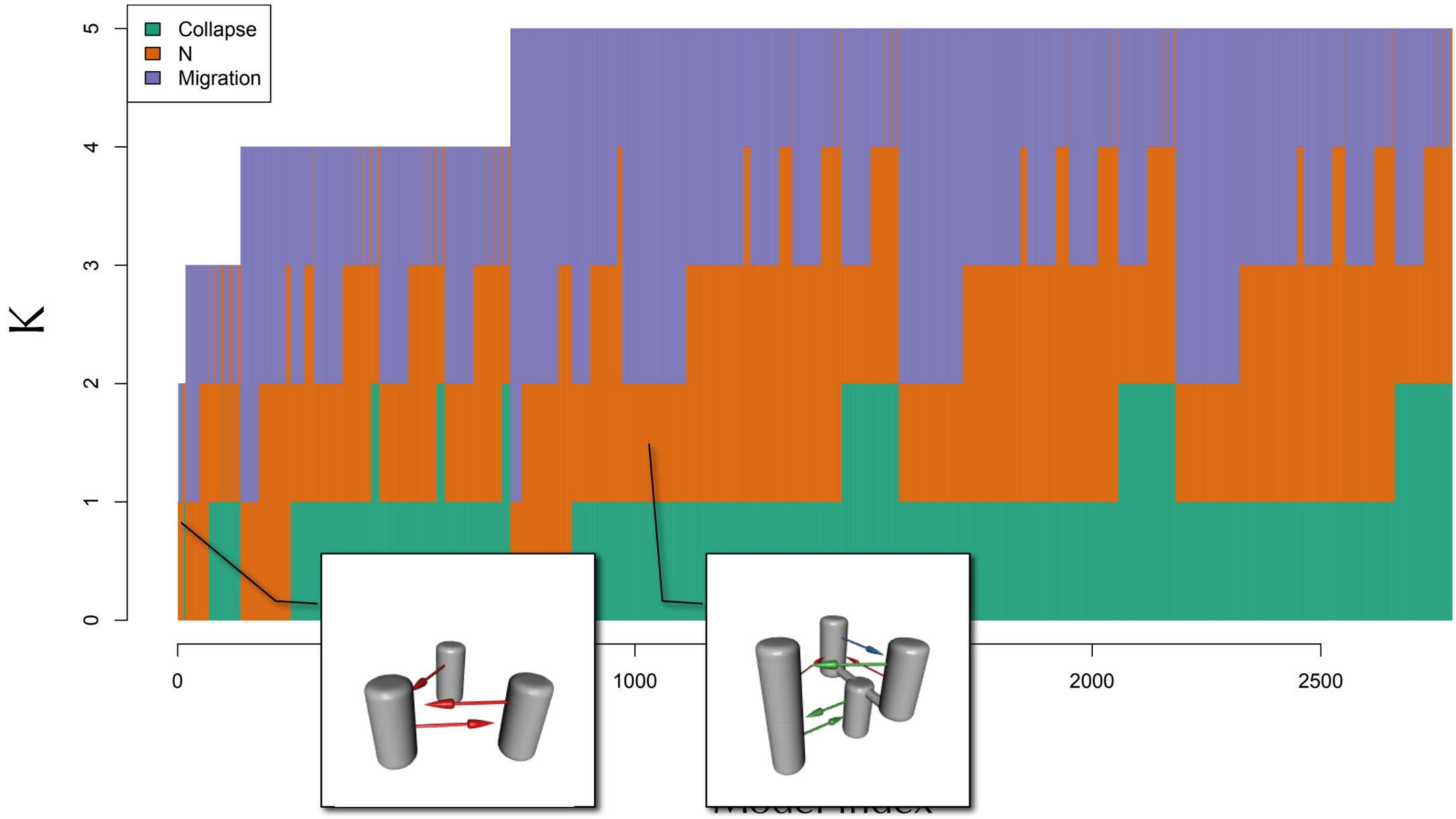







Number of models
100000
10000
1000
100
10
1
4 populations
3 populations
2 populations
0
2
4
6
8
10
Max K (# free parameters)

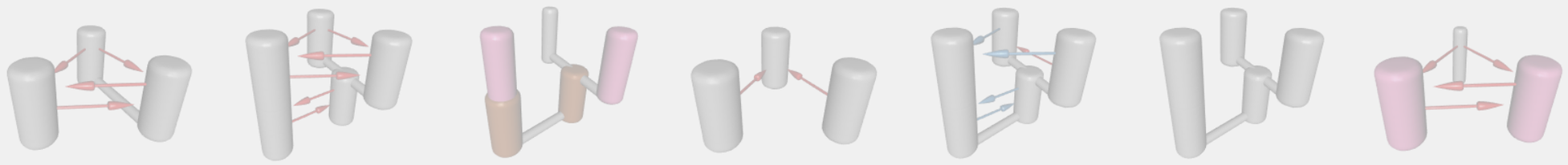
Model free parameters, three populations, max K=5



1

Generate all possible models

Given *N* populations, ≤*K* free parameters



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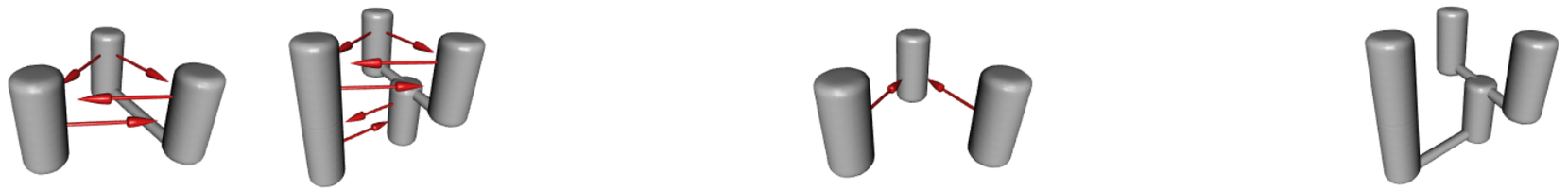
2

Filter

(only tree models, no more than two migration rates, etc.)



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3

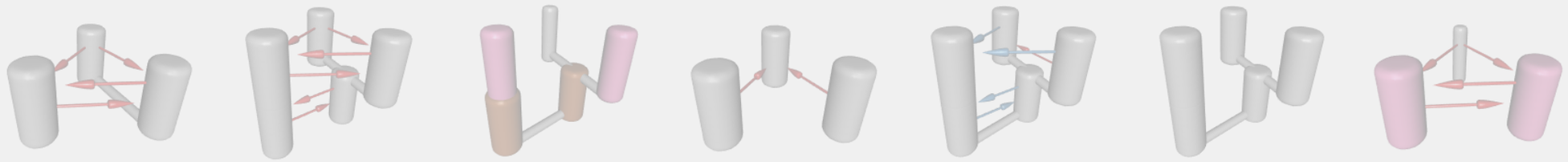
Analyze

(find best, find AIC for all

1

Generate all possible models

Given *N* populations, ≤*K* free parameters



↓

Filter

(only tree models, no more than two migration rates, etc.)

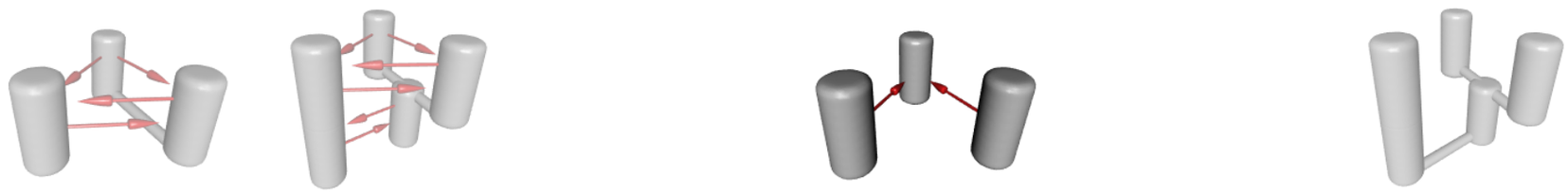
2

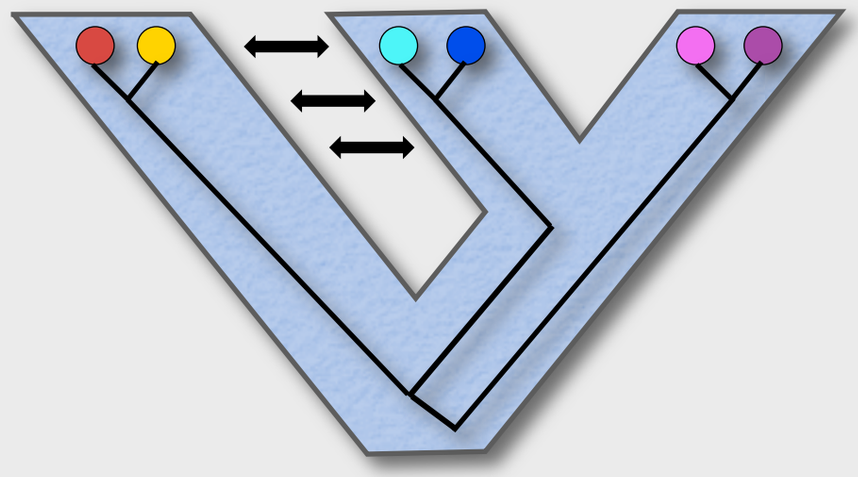
↓

3

Analyze

(find best, find AIC for all

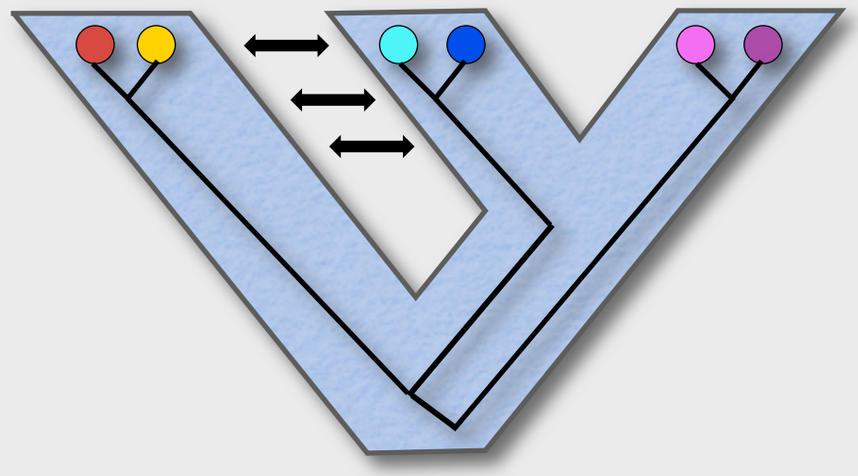




Exact likelihood: P(gene tree | population history)

COAL (Degnan and Salter 2005), STEM (Kubatko et al. 2009), BPP (Yang and Rannala 2010), IM (Nielsen and Wakely 2001), etc.

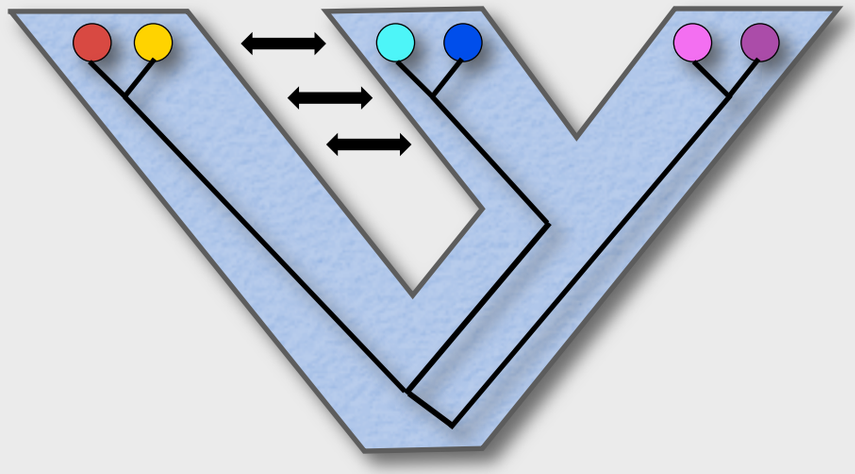
Issue: Not all models (currently) have analytical solutions, and it's always simpler to simulate (think of selection). But if it does work, can use it.



Approximate Bayesian Computation

Carmago et al. 2012, DIYABC (Cornuet et al. 2010), PopABC (Lopes et al. 2009)

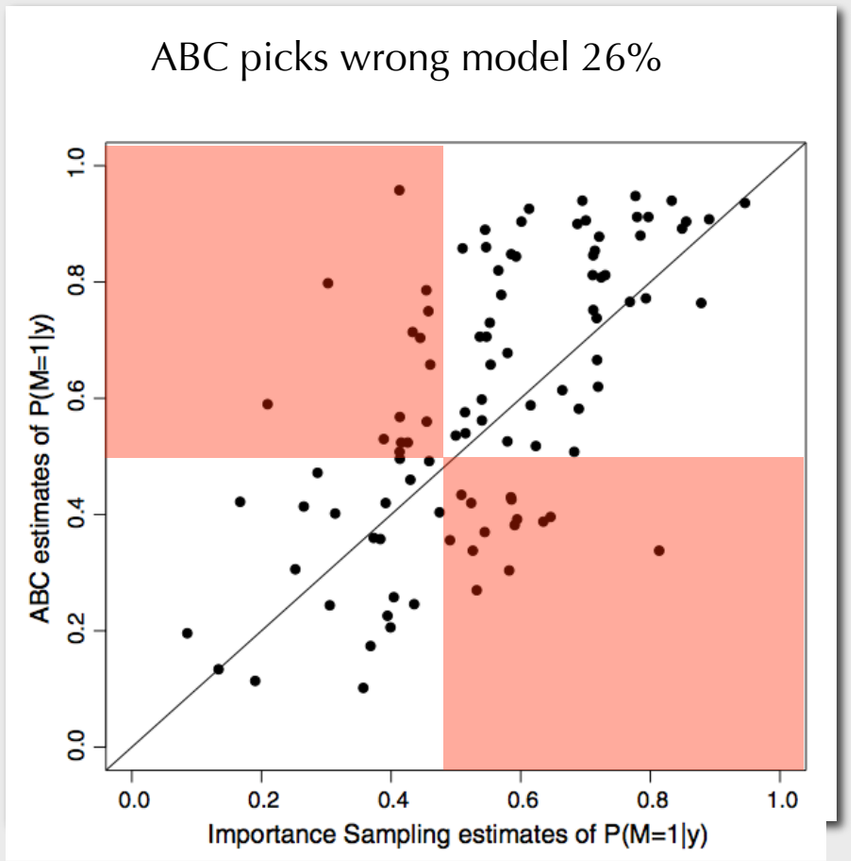
```
for (many reps) {
     sample parameters (or models) from prior
     simulate dataset using these parameters
     if (|(summary(dataset) – summary(observed)|< ε ){
          count as match, save these parameters
     }
}

plot(saved parameters) #or other way to summarize
```



Approximate Bayesian Computation

Model choice hard to do with ABC: can depend on summary stats, priors, ε

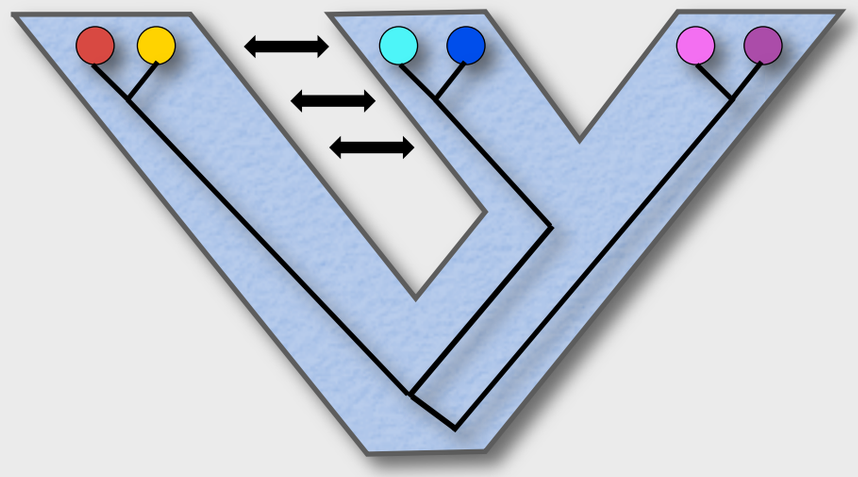
ABC picks wrong model 26%



Robert et al. 2011

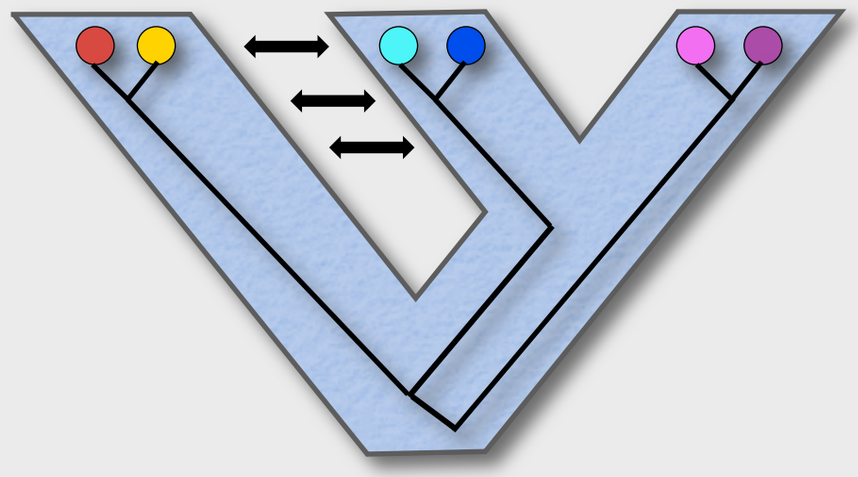
Use of priors itself

https://www.facebook.com/LizardProtest



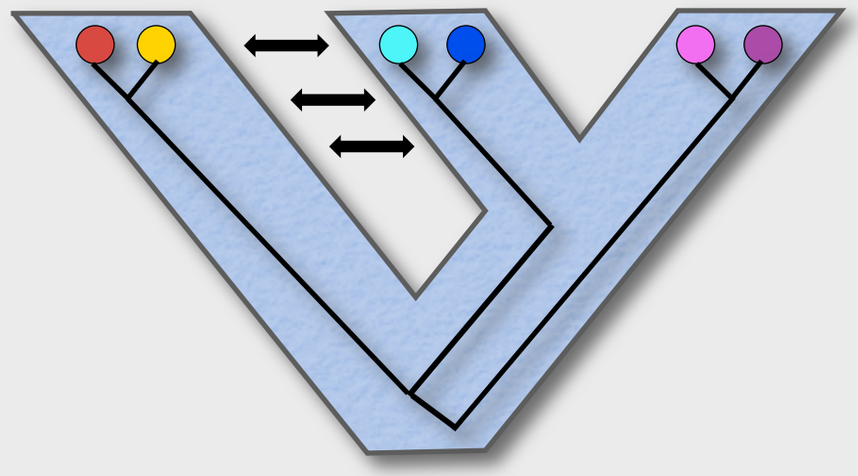
Approximate Likelihood

Estimate probability of data
counting exact matches



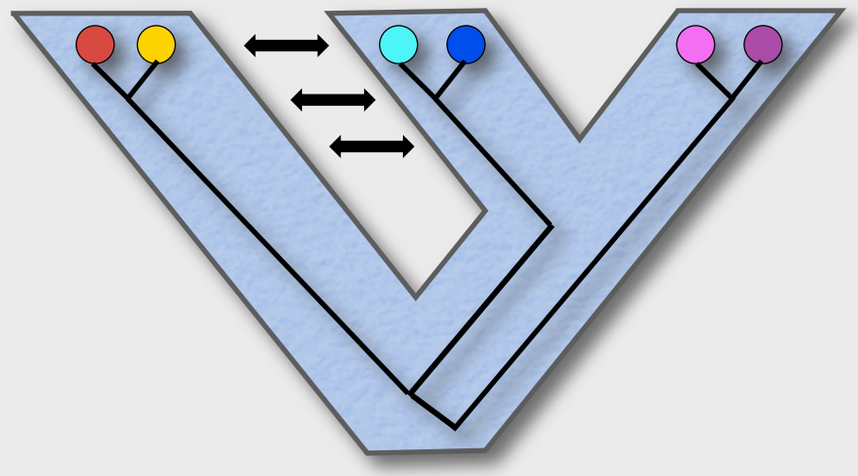
Approximate Likelihood

```
for (many reps) {
      sample parameters (or models) from prior
      simulate dataset using these parameters
      if (|(summary(dataset) – summary(observed)|< ε ){
            count as match, save these parameters
      }
}

plot(saved parameters) #or other way to summarize
```



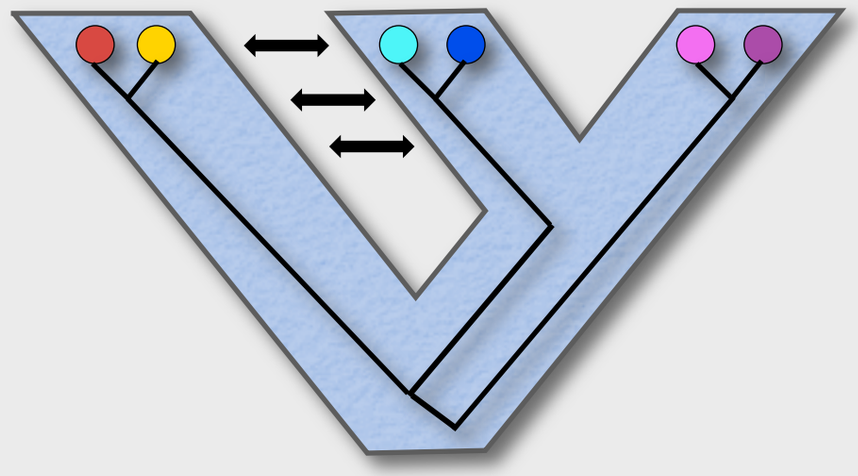
Approximate Likelihood

```
sample parameters (or models) from prior guesses
for (many reps) {
     sample parameters (or models) from prior
     simulate dataset using these parameters
     if (|(summary(dataset) – summary(observed)|< ε ){
          count as match, save these parameters
     }
}

plot(saved parameters) #or other way to summarize
```



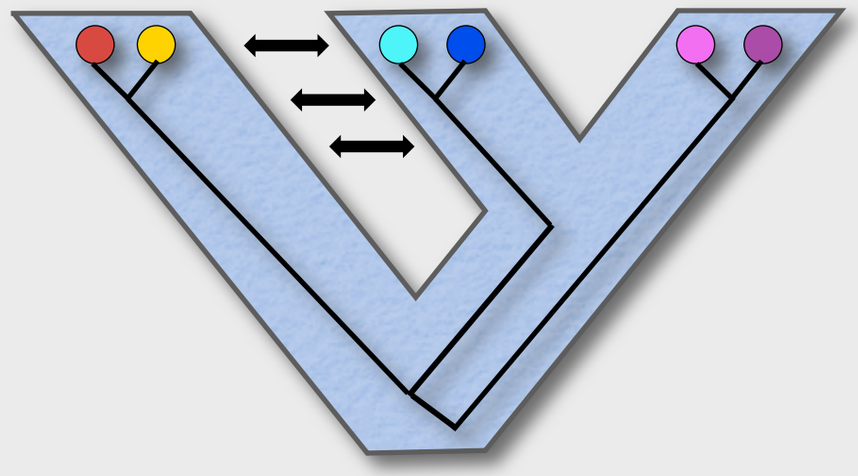
Approximate Likelihood

```
sample parameters (or models) from prior guesses
for (many reps) {
     sample parameters (or models) from prior
     simulate dataset using these parameters
     if (  topology(dataset) == topology(observed)  ){
          count as match, save these parameters
     }
}

plot(saved parameters) #or other way to summarize
```



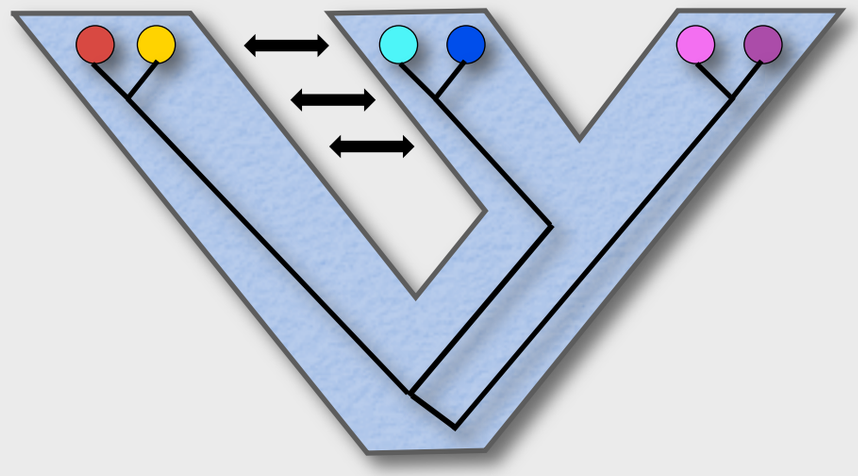
Approximate Likelihood

```
sample parameters ~~(or models)~~ from ~~prior~~ guesses
for (many reps) {
     ~~sample parameters (or models) from prior~~
     simulate dataset using these parameters
     if (  topology(dataset) == topology(observed)  ){
          count as match~~, save these parameters~~
     }
}

plot(saved parameters) #or other way to summarize
```



Approximate Likelihood

```
sample parameters (or models) from prior guesses
for (many reps) {
     sample parameters (or models) from prior
     simulate dataset using these parameters
     if (  topology(dataset) == topology(observed)  ){
          count as match, save these parameters
     }
}

Likelihood ≡ prob(topology(observed)| parameters)
```



Approximate Likelihood

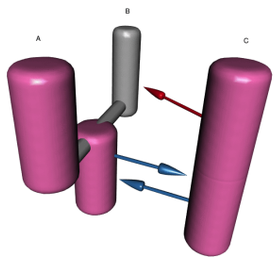
```
sample parameters (or models) from prior guesses
for (many reps) {
     sample parameters (or models) from prior
     simulate dataset using these parameters
     if (  topology(dataset) == topology(observed)  ){
          count as match, save these parameters
     }
}

Likelihood = prob(topology(observed)| parameters) ≈ #matches / #reps
```

Observed

		Summary	Match
Observed		4/7	NA
Sim 1		3/7	N
Sim 2		5/7	N
Sim 3		1/7	N
Sim 4		4/7	N
Sim 5		2/7	N
Sim 6		4/7	Y
Sim 7		5/7	N

		Summary	Match
Observed		4/7	NA
Sim 1		3/7 ✓	N
Sim 2		5/7 ✓	N
Sim 3		1/7	N
Sim 4		4/7 ✓	N
Sim 5		2/7	N
Sim 6		4/7 ✓	Y ✓
Sim 7		5/7 ✓	N

Approximate Bayesian Computation	**Approximate Likelihood**
Summary stats as functions of the data	Topologies (= the data)
Simulation	Simulation
Approximate match	Exact match
Priors	Starting values, but optimize
Integration	Maximum

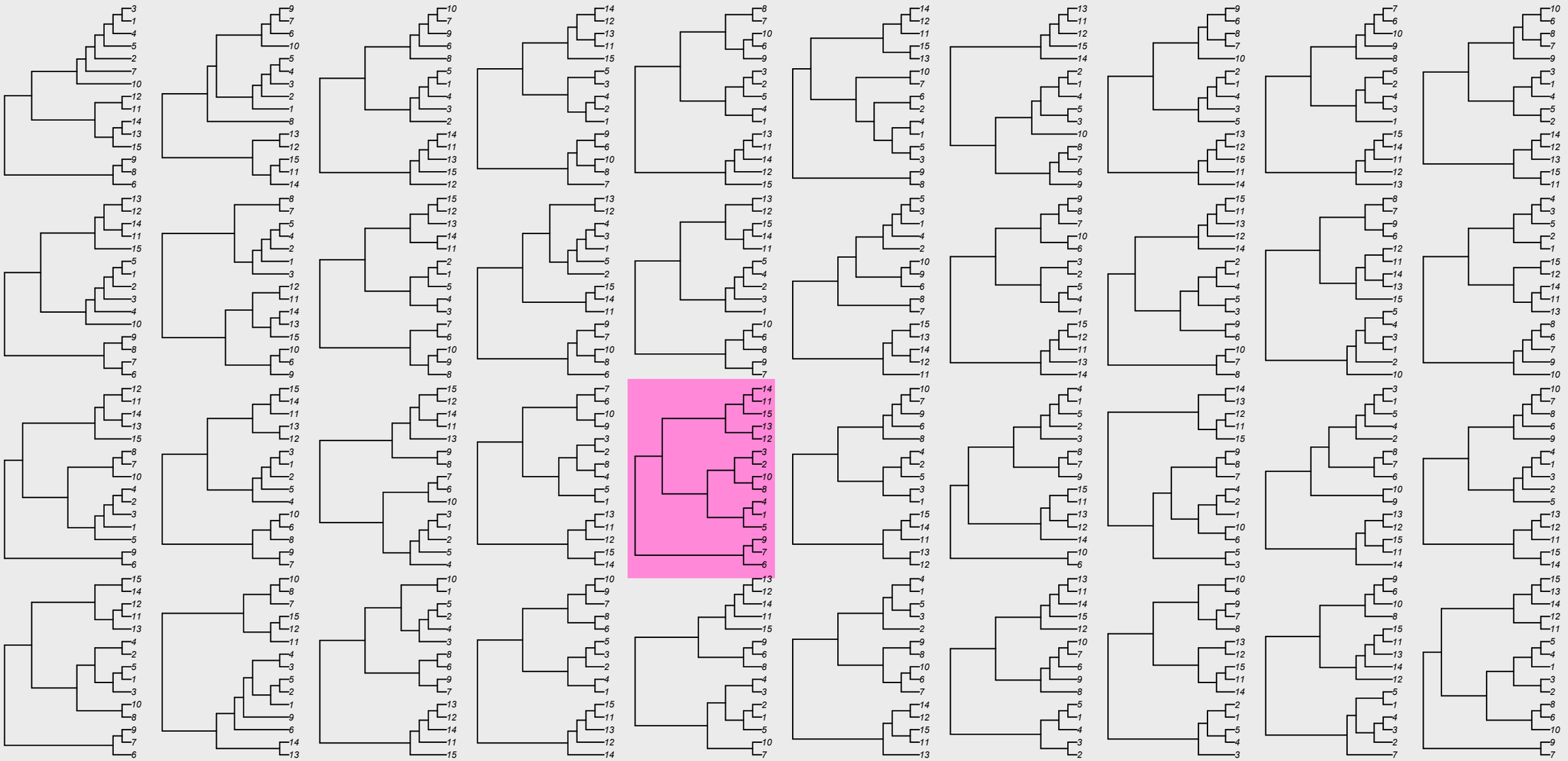


Collapse 1	Pop size 1	Pop size 2	Migration 1	Migration 2
4	1	3	0.2	0.6

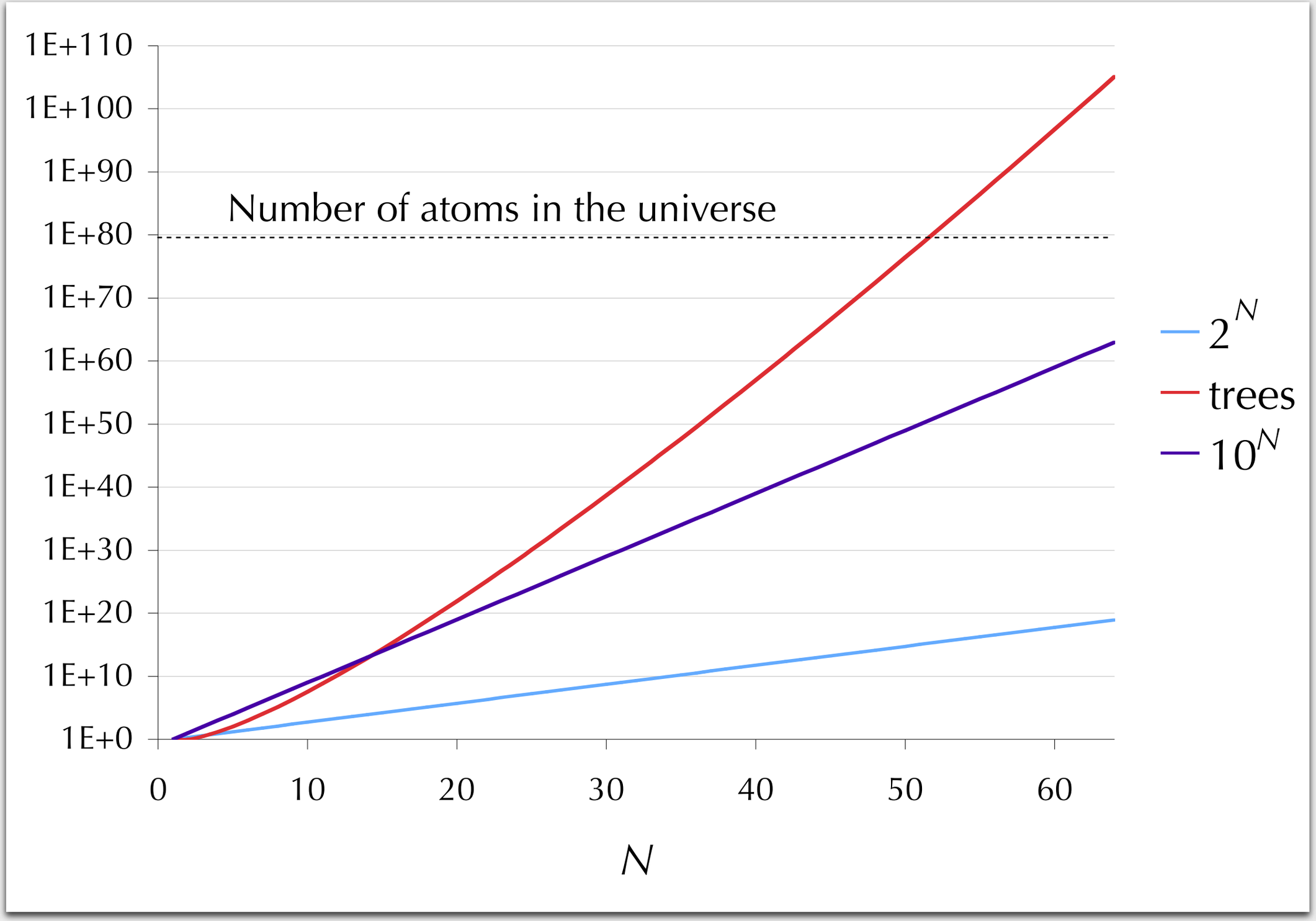
Generate 100,000 trees, three populations, five samples per population (~5 sec):

```
ms 15 100000 -T -I 3 5 5 5  -n 1 1.0 -n 2 3.0 -n 3 3.0 -ma x 0.0 0.0 0.2 x 0.0 0.0 0.0 x
        -ej 4.0 3 1 -en 4.0 1 3.0 -en 4.0 2 3.0 -em 4.0 1 2 0.6 -em 4.0 2 1 0.6
```

ms (Hudson 2002)

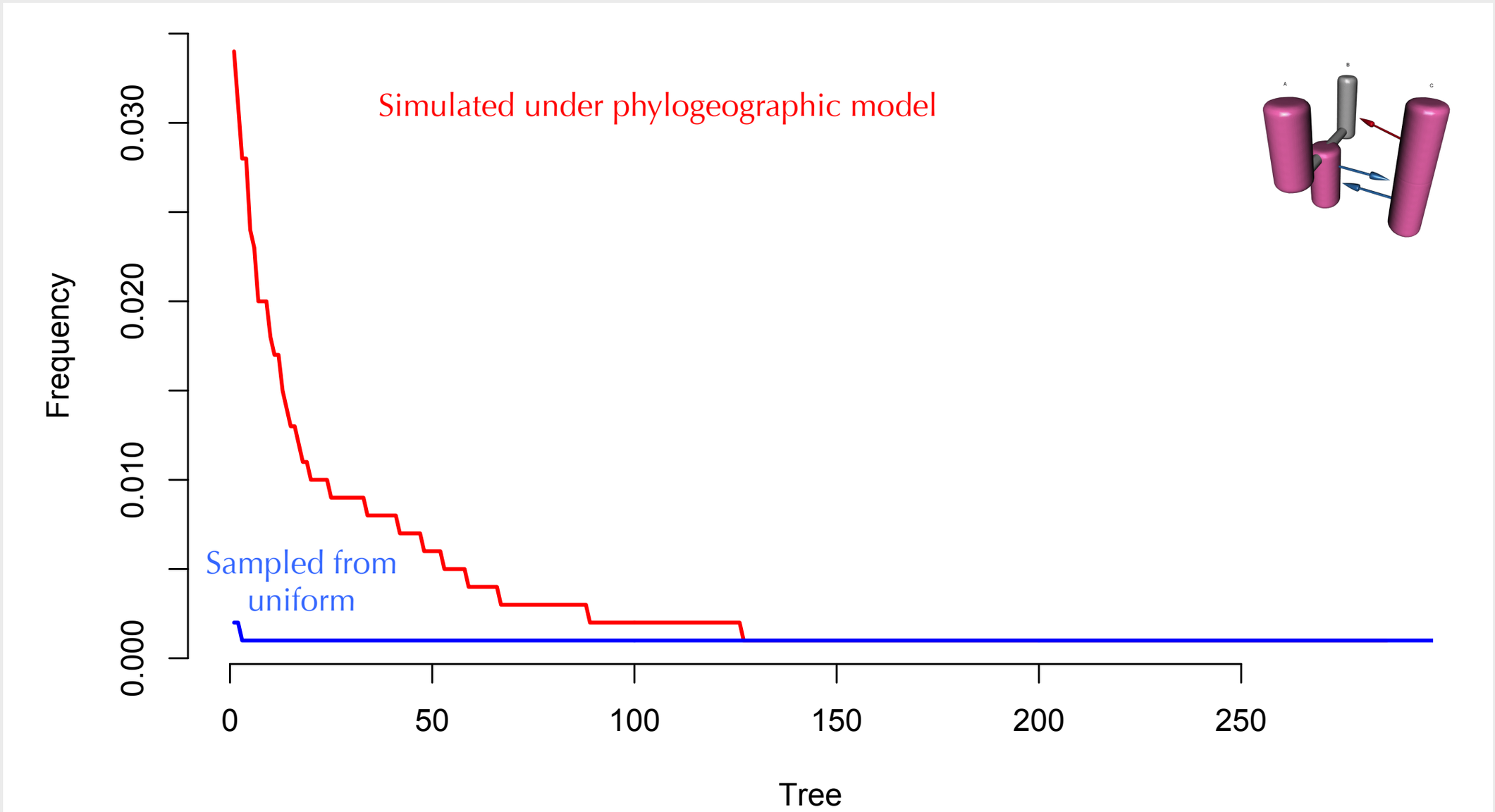


A dumb idea?


1E+110
1E+100
1E+90
1E+80
1E+70
1E+60
1E+50
1E+40
1E+30
1E+20
1E+10
1E+0
Number of atoms in the universe
0
10
20
30
40
50
60
N
2^N
trees
10^N

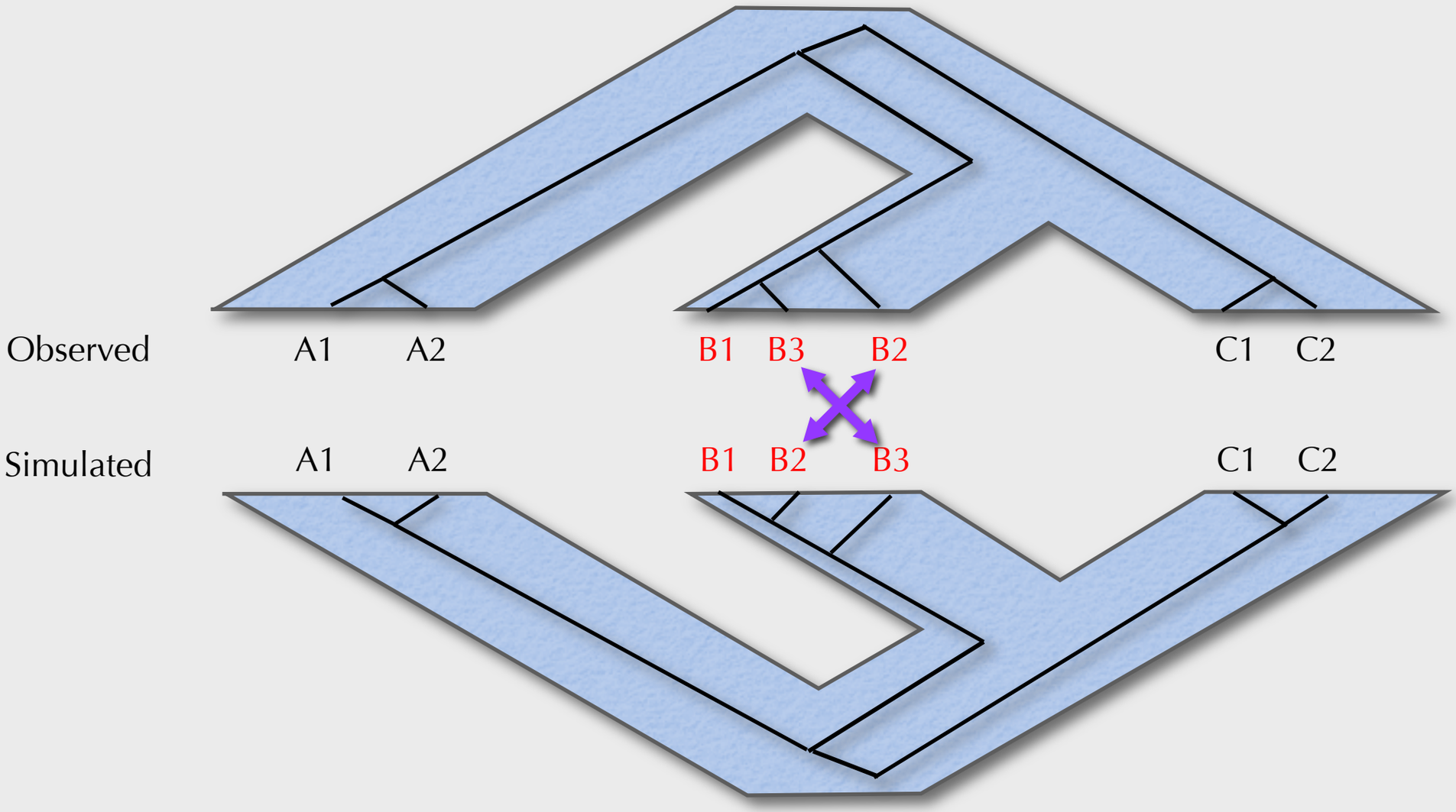
A dumb idea?

Tree probabilities not uniform (some trees *much* more likely than others)



A dumb idea?

Clever idea 1: Sample labels within populations arbitrary

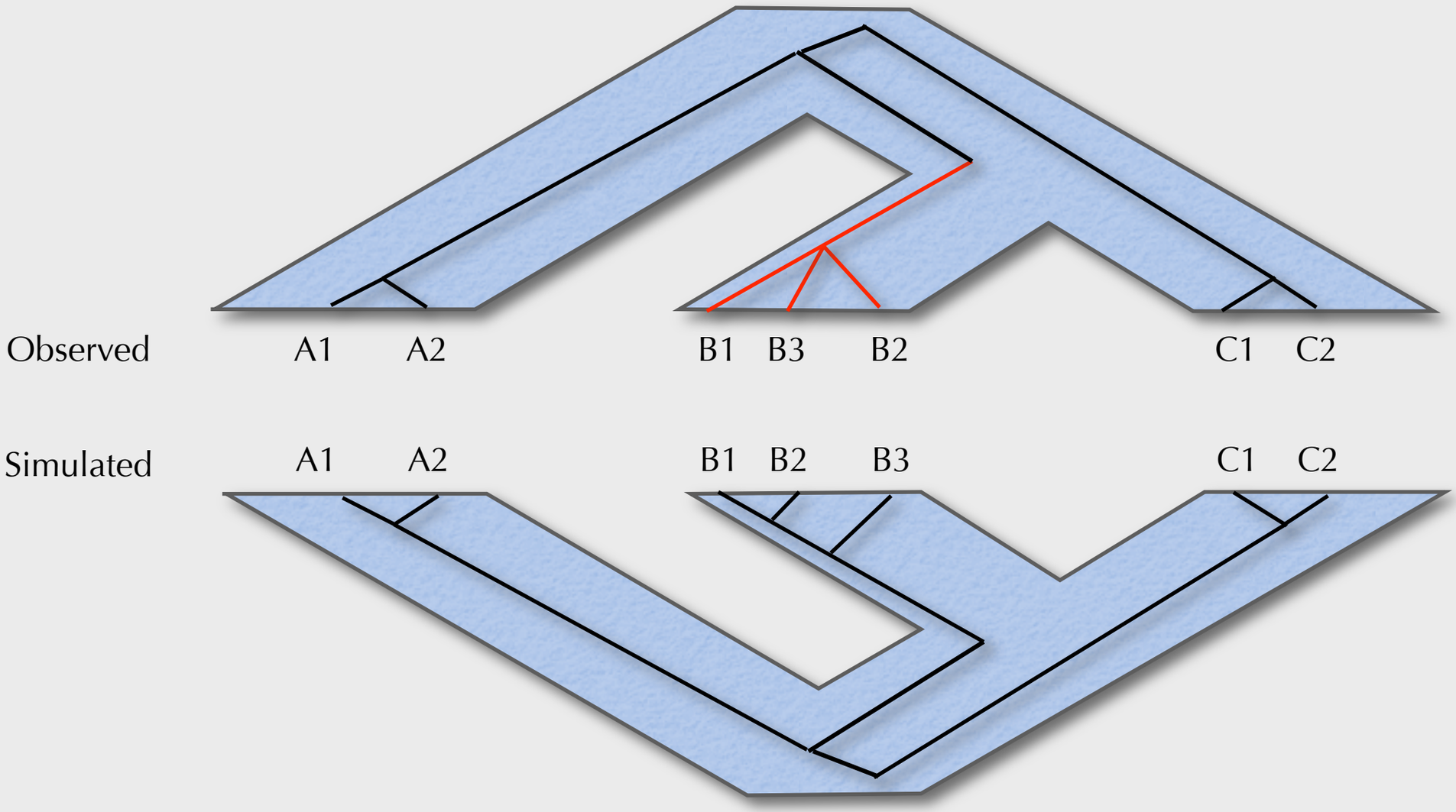


Match based on all possible labeling, then correct for this

i.e., three possible permutations, so if there is a match divide by 3 to get probability

A dumb idea?

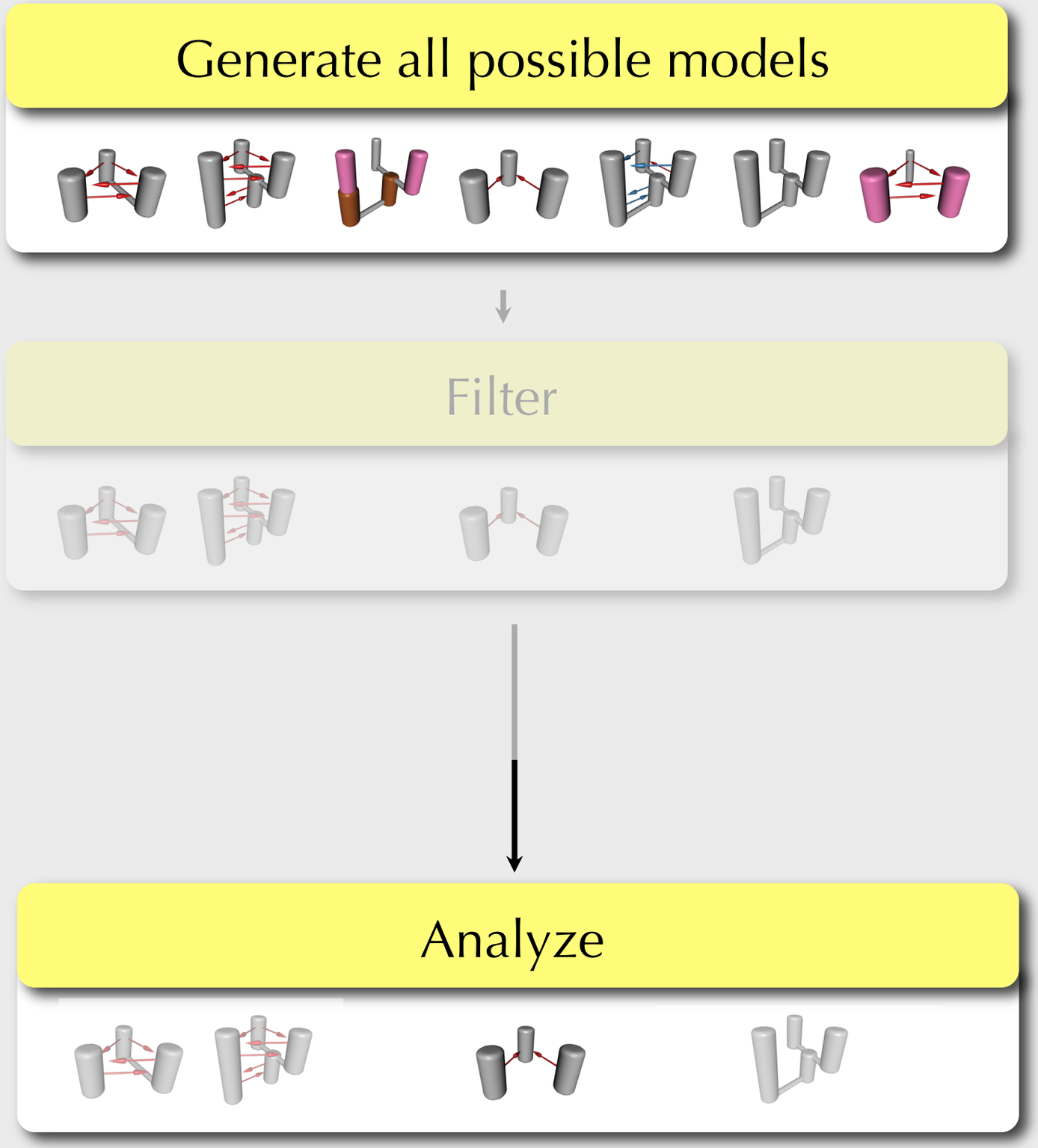
Clever idea 2: Polytomies are soft in gene trees (optional)

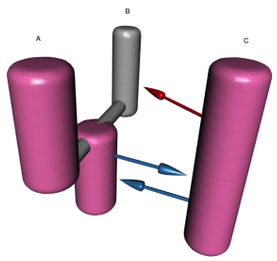


Match based on all possible resolutions, then correct for this

Grows (quickly) with number of populations

Grows quickly with number of samples per population, but only linearly with number of genes





Collapse 1	Pop size 1	Pop size 2	Migration 1	Migration 2
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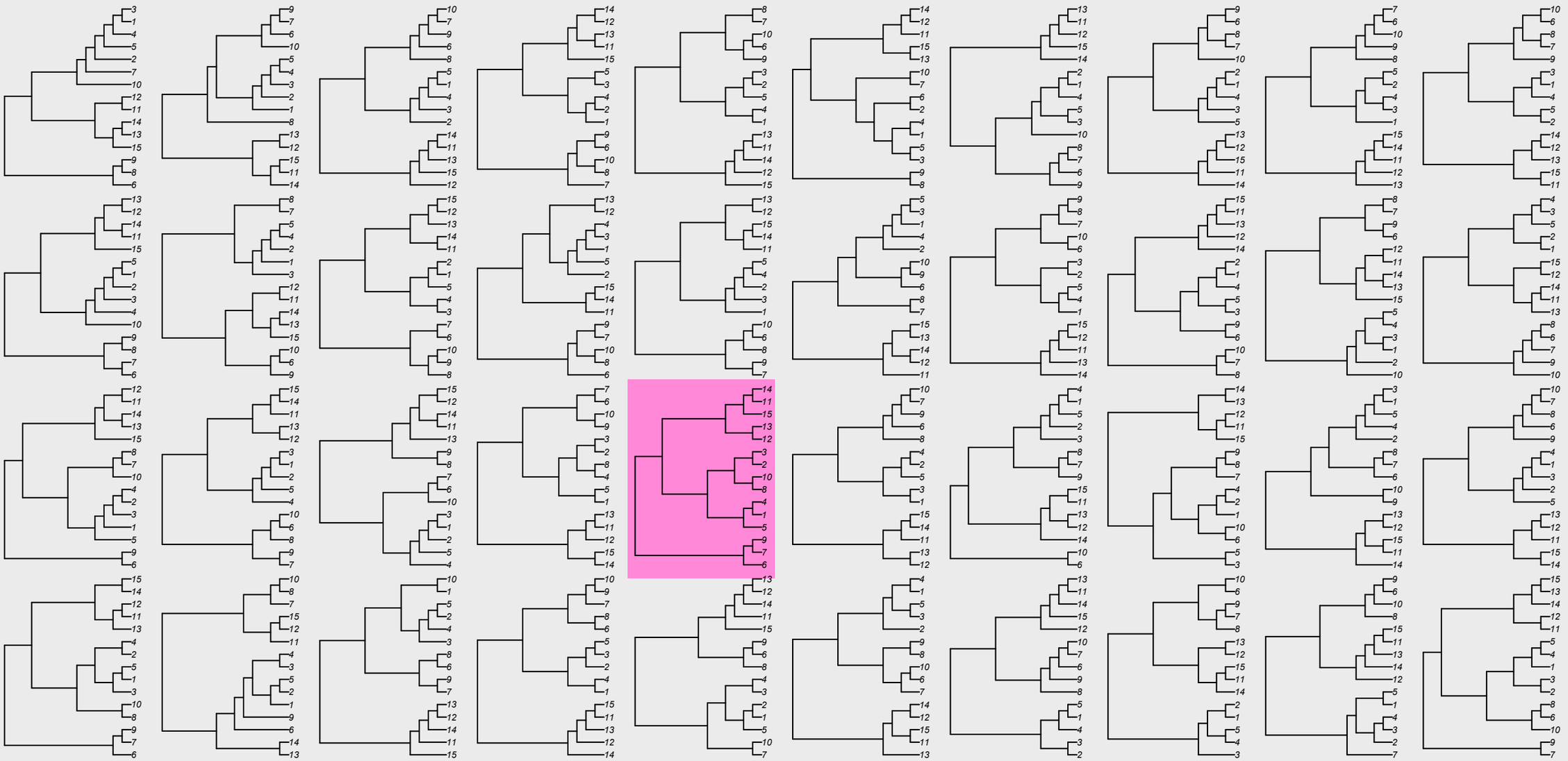
Generate 100,000 trees, three populations, five samples per population (~5 sec):

```
ms 15 100000 -T -I 3 5 5 5  -n 1 1.0 -n 2 3.0 -n 3 3.0 -ma x 0.0 0.0 0.2 x 0.0 0.0 0.0 x
        -ej 4.0 3 1 -en 4.0 1 3.0 -en 4.0 2 3.0 -em 4.0 1 2 0.6 -em 4.0 2 1 0.6
```

ms (Hudson 2002)

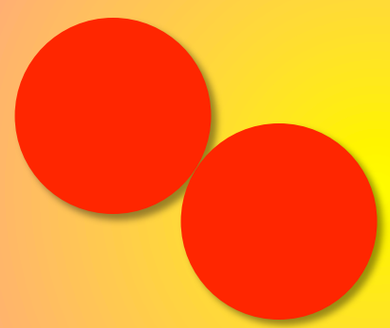


Optimization

Numerical parameters

Collapse 1	Pop size 1	Pop size 2	Migration 1	Migration 2
4	1	3	0.2	0.6



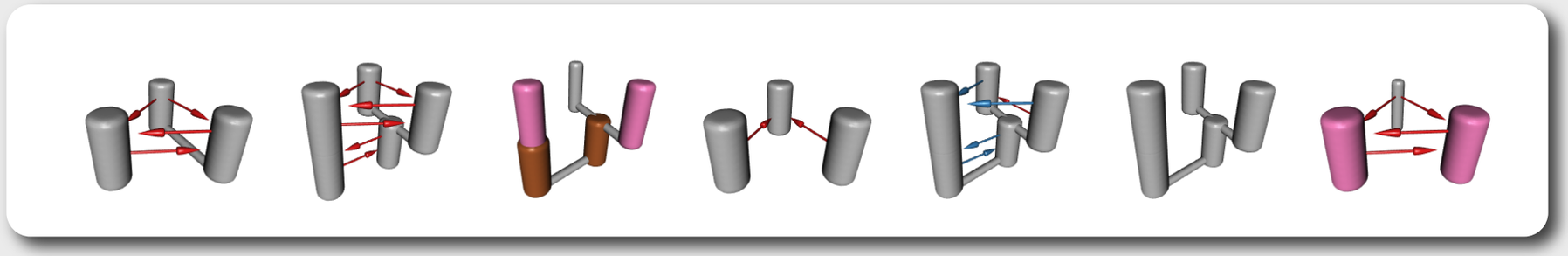



Optimization

Numerical parameters

Model

Exhaustive

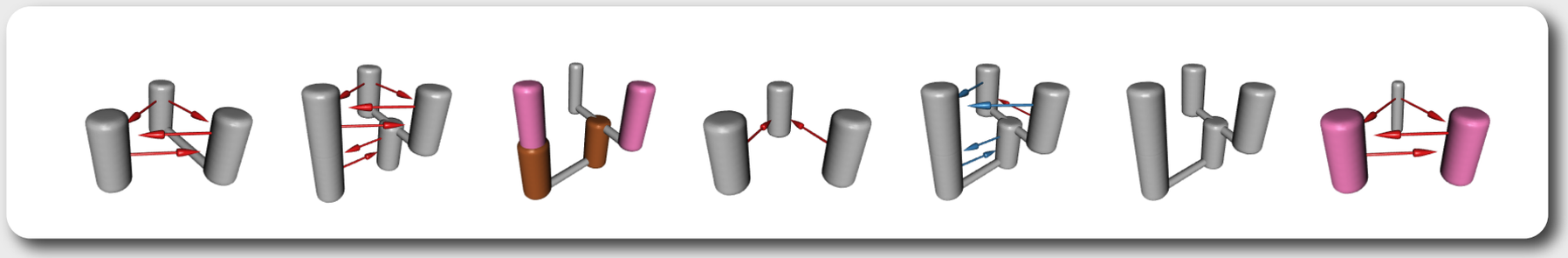


Optimization

Numerical parameters

Model

Exhaustive



Genetic

Break model into genes (one gene for collapse structure, one for migration structure, etc.)
Let them evolve, AIC is fitness

1.2

Collapse Model	Pop size Model	Migration Model	Continuous parameters
1	1	1	

0.0

Collapse Model	Pop size Model	Migration Model	Continuous parameters
2	1	3	

5.0

Collapse Model	Pop size Model	Migration Model	Continuous parameters
3	4	2	

20.5

Collapse Model	Pop size Model	Migration Model	Continuous parameters
1	2	1	

2.0

Collapse Model	Pop size Model	Migration Model	Continuous parameters
2	2	2	

⋮

1.2

Collapse Model	Pop size Model	Migration Model	Continuous parameters
1	1	1	...

0.0

Collapse Model	Pop size Model	Migration Model	Continuous parameters
2	1	3	...

5.0

Collapse Model	Pop size Model	Migration Model	Continuous parameters
3	4	2	...

20.5

Collapse Model	Pop size Model	Migration Model	Continuous parameters
1	2	1	...

2.0

Collapse Model	Pop size Model	Migration Model	Continuous parameters
2	2	2	...

1.2

Collapse Model	Pop size Model	Migration Model	Continuous parameters
1	1	1	...

0.0

Collapse Model	Pop size Model	Migration Model	Continuous parameters
2	1	3	...

Collapse Model	Pop size Model	Migration Model	Continuous parameters
			...

Collapse Model	Pop size Model	Migration Model	Continuous parameters
			...

2.0

Collapse Model	Pop size Model	Migration Model	Continuous parameters
2	2	2	...

1.2

Collapse Model	Pop size Model	Migration Model	Continuous parameters
1	1	1	...

0.0

Collapse Model	Pop size Model	Migration Model	Continuous parameters
2	1	3	...

Collapse Model	Pop size Model	Migration Model	Continuous parameters
2	1	1	...

2.0

Collapse Model	Pop size Model	Migration Model	Continuous parameters
2	2	2	...

```r
creteModelSpaceNLoptr<-function(migrationArrayMap, migrationArray, popVector, print.ms.string=FALSE, badAIC=100000000000000,
eterValue=100, nTrees=1,msLocation="/usr/local/bin/
areLocation="comparecladespipe.pl",assign="assign.txt",observed="observed.txt",unresolvedTest=TRUE, debug=FALSE,  method="nlminb",
itnmax=NULL,pop.size=50, print.results=FALSE, maxtime=0, maxeval=0, ...) {
  Domains<-matrix(ncol=2,nrow=3)
  Domains[1,]<-range(migrationArrayMap$collapseMatrix.number)
  Domains[2,]<-range(migrationArrayMap$n0multiplierMap.number)
  Domains[3,]<-range(migrationArrayMap$migrationArray.number)

  results<-genoud(searchContinuousModelSpaceNLoptr,nvars=3, max=FALSE,starting.values=c(1,1,1), MemoryMatrix=TRUE, boundary.enforcement=2,
data.type.int=TRUE, Domains=Domains, migrationArrayMap=migrationArrayMap, migrationArray=migrationArray, popVector=popVector,
print.ms.string=print.ms.string, badAIC=badAIC, maxParameterValue=maxParameterValue,
nTrees=nTrees,msLocation=msLocation,compareLocation=compareLocation,assign=assign,observed=observed,unresolvedTest=unresolvedTest,
debug=debug, method=method,itnmax=itnmax, pop.size=pop.size, print.results=print.results, maxtime=maxtime, maxeval=maxeval,
return.all=FALSE,...)
  return(results)
}
```

```perl
    sub returnclades {
        my ($intree, %localassignments) = @_;
        my @cladearray=();
        $intree=~s/:\d+\.?\d*e?\-?\d*//ig; #remove branch length (regex from Olaf Bininda-Emonds'
partitionmetric.pl script)
        while ($intree=~m/(\([\w\,]+\))/) {
            my $matchstring=$1;
            my $innermatch="";
            if ($matchstring=~m/\(([\w\,]+)\)/) {
                $innermatch=$1;
            }
            my @splitinner=split(/\,/,$innermatch);
            my @renamedinner=();
```

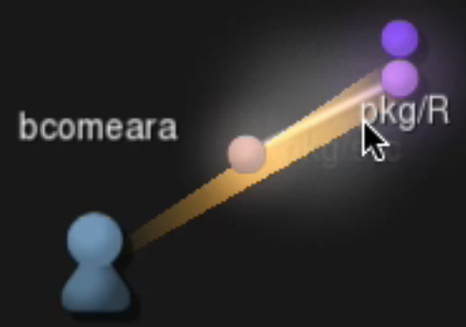
ms
Hudson
2002

When the option -T is used the trees representing the history of the sampled chromosomes are output. For example, the command line `ms 5 2 -T` results in the following output:

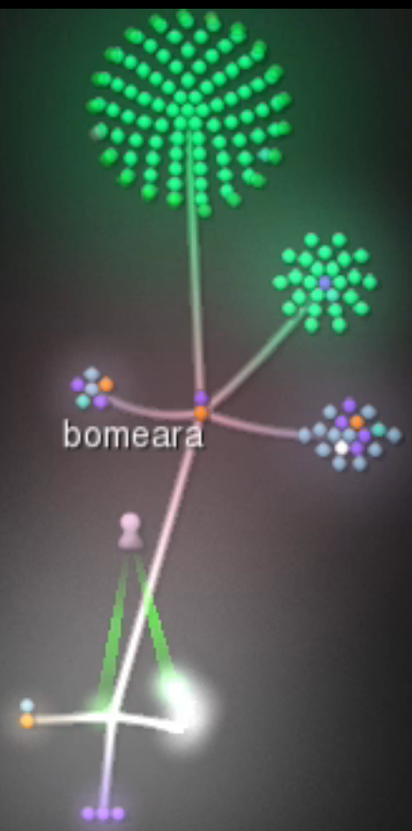
```
ms 5 2 -T
3579 27011 59243


//
((2:0.074,5:0.074):0.296,(1:0.311,(3:0.123,4:0.123):0.187):0.060);


//
(2:1.766,(4:0.505,(3:0.222,(1:0.163,5:0.163):0.059):0.283):1.261);
```

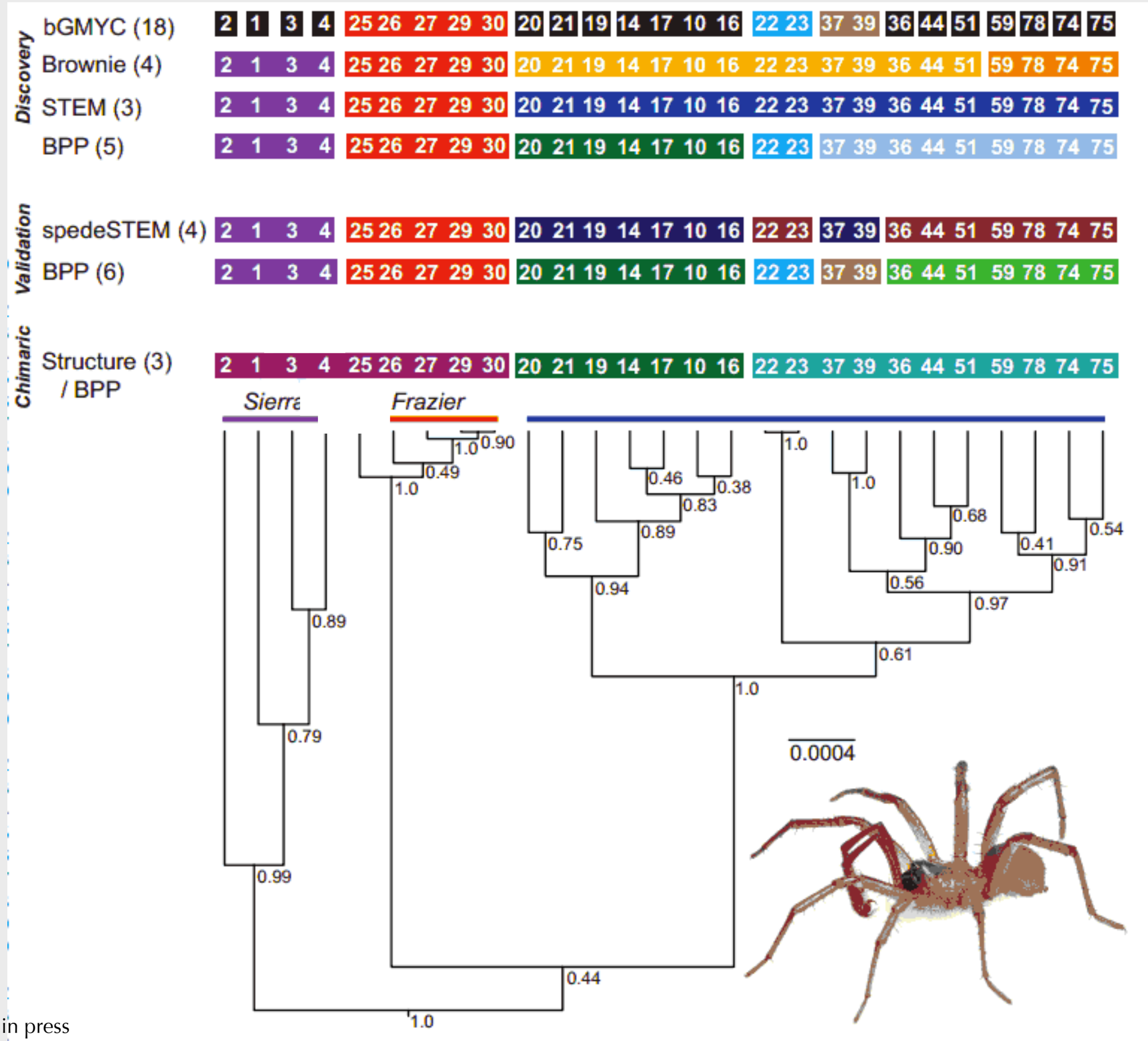
Code

11/27/11

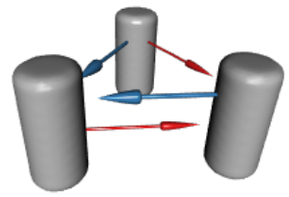
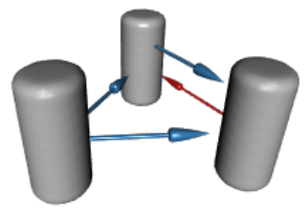
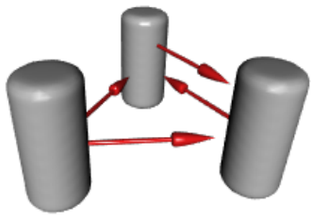
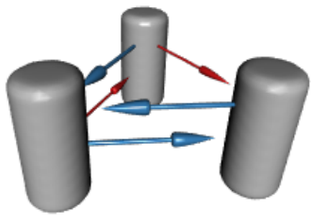
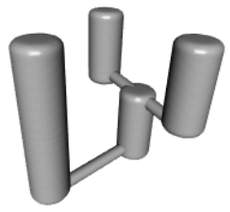


Analyses

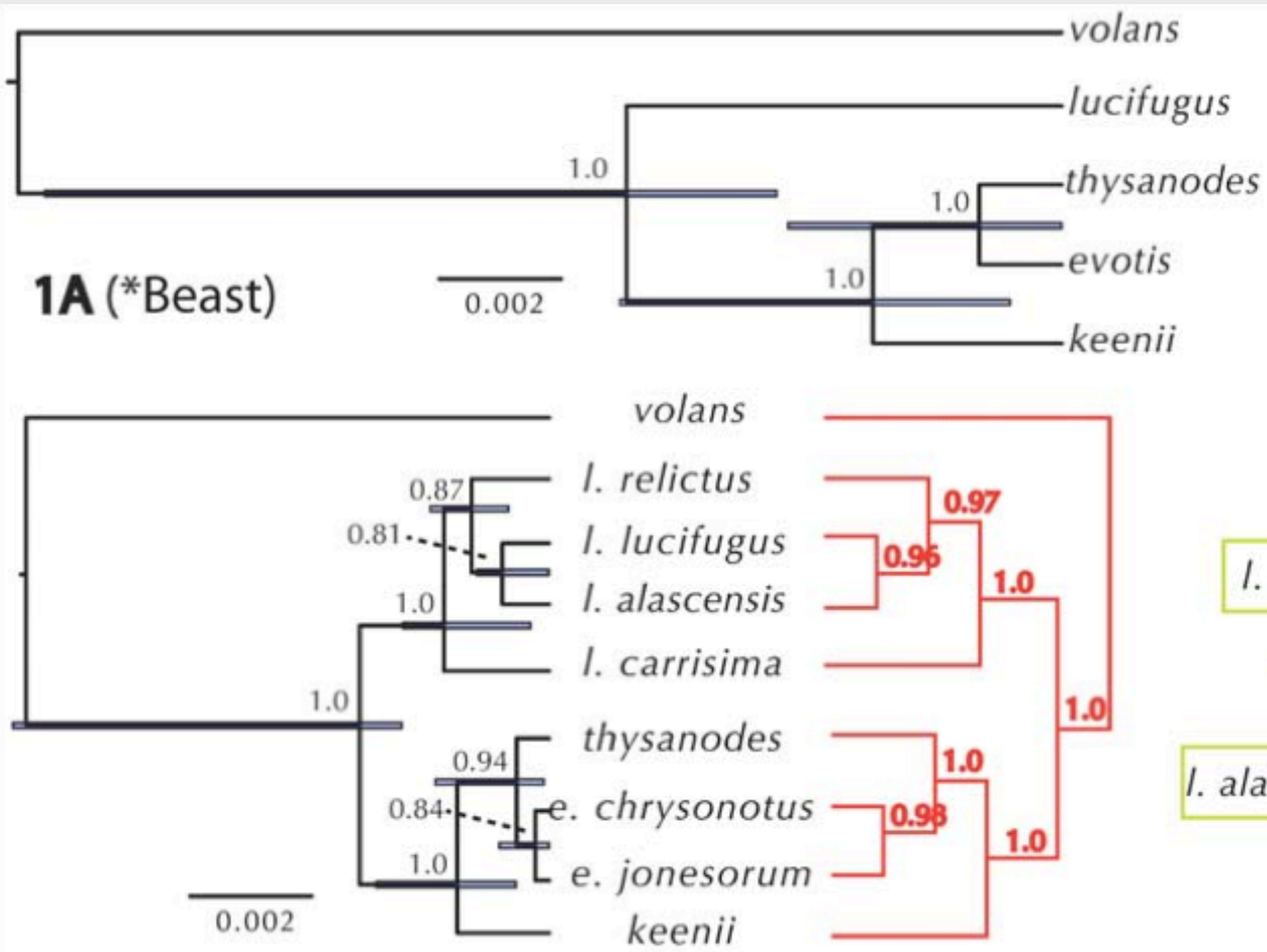




Satler et al. in press

ΔAIC	AIC weight	Model
0.0	0.954	
9.5	0.008	
9.6	0.008	
10.6	0.005	
135 other models		
261.8	0.000	

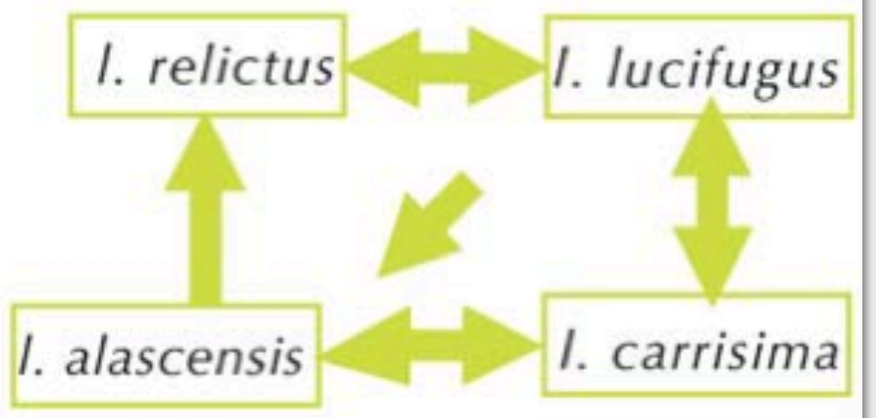
Kent McFarland



1A (*Beast)

1B (*Beast)

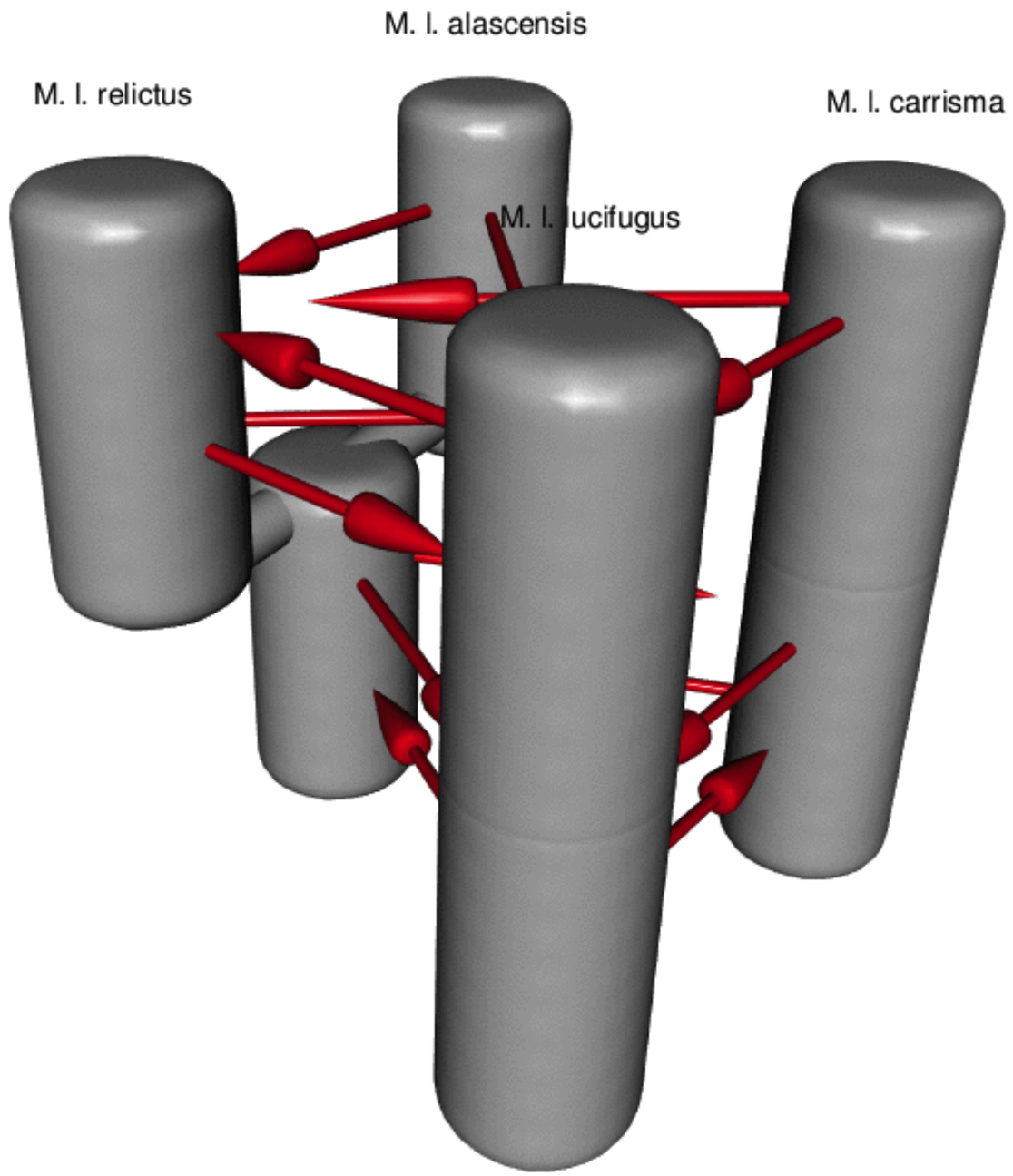
1C (BP&P)



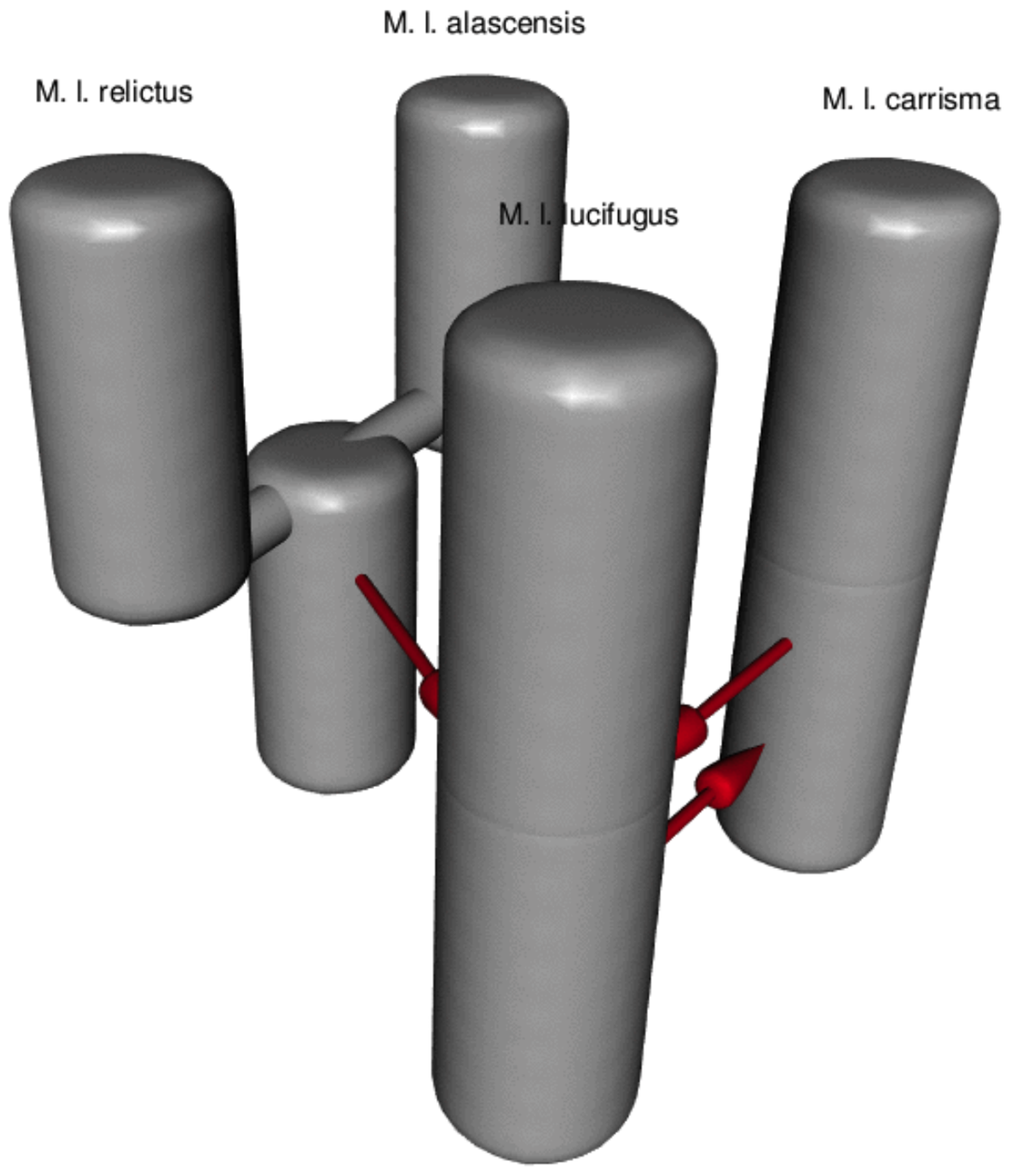
(p = 0.98)

1D (Migrate-n)

$\Delta AIC = 0$



$\Delta AIC = 5.6$

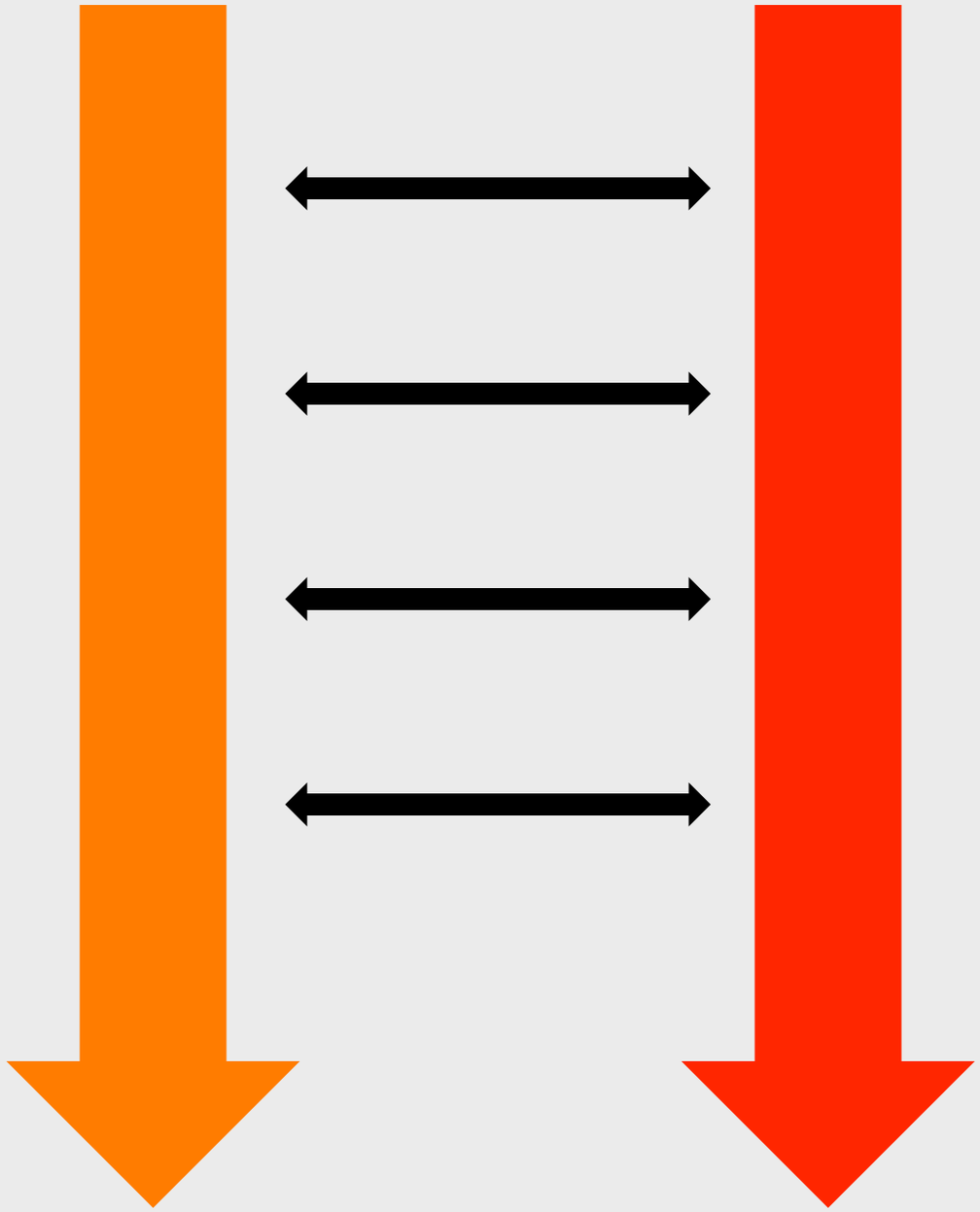


Summary

- Way to create many models
- Evaluate many models
- Prior free, but complementary with other approaches
- Should scale linearly with gene number

Present/Future

Coding
Brian O'Meara
Nathan Jackson



Empirical example,
use, documentation
Bryan Carstens
Ariana Morales

Present/Future

1. Better code (changing pop size, better algorithms), incl. more testing and comparison.
2. ~~Parameter estimation~~ (done)
3. Additional *Myotis* samples
4. Shortcuts (equivalent to ModelTest using a single NJ tree rather than tree search)
5. Sensitivity to tree uncertainty
6. Statistical phylogeography workshops (2014 & 2015)

Acknowledgements

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Note I am **looking for grad students**. Phylogeography, character evolution, diversification, etc. Five years guaranteed support.

End