Lesson 10: qpAdm

Friday July 27, 2018

9:00 – 11:30 am

Important D-statistic relationships in Haak et al. (2015)

- Class Discussion

Important D-statistic relationships in Haak et al. (2015)

- Three main categories we will focus on:
  - Early Neolithic
  - Middle Neolithic
  - Late Neolithic/Bronze Age

Early Neolithic (LBK)

- D(EUR, Esperstedt; LBK, Mbuti)<0 and D(EUR, LBK; Esperstedt, Mbuti)<0
  - Clade with Esperstedt relative to most EUR
- Clade with MN/EN relative to LN/HG
  - D(EN, LBK; HG, Mbuti)~0
  - D(MN, LBK; HG, Mbuti)>0

Middle Neolithic (Yamnaya)

- D(EUR, CW/Mot/Kar/Sam; Yamnaya, Mbuti)<0 and D(EUR no HG, Yamnaya; CW/Mot/Kar/Sam, Mbuti)<0
  - Yamnaya mostly clade with EHG and Corded_Ware
- D(EN/MN, LN; Yamnaya, Mbuti)<0 but most D(EN/MN, Yamnaya; LN, Mbuti)~0 (but Karsdorf <0 and some others)
  - D(LN, Yamnaya; EN/MN, Mbuti)>0
  - What is going on here?

Middle Neolithic (Esperstedt)

- D(EUR, SpainMN/EN/LBK; Esperstedt, Mbuti)<0 and D(EUR, Esperstedt; SpainMN/EN/LBK, Mbuti)<0
  - Esperstedt mostly groups with other MN and EN in Europe

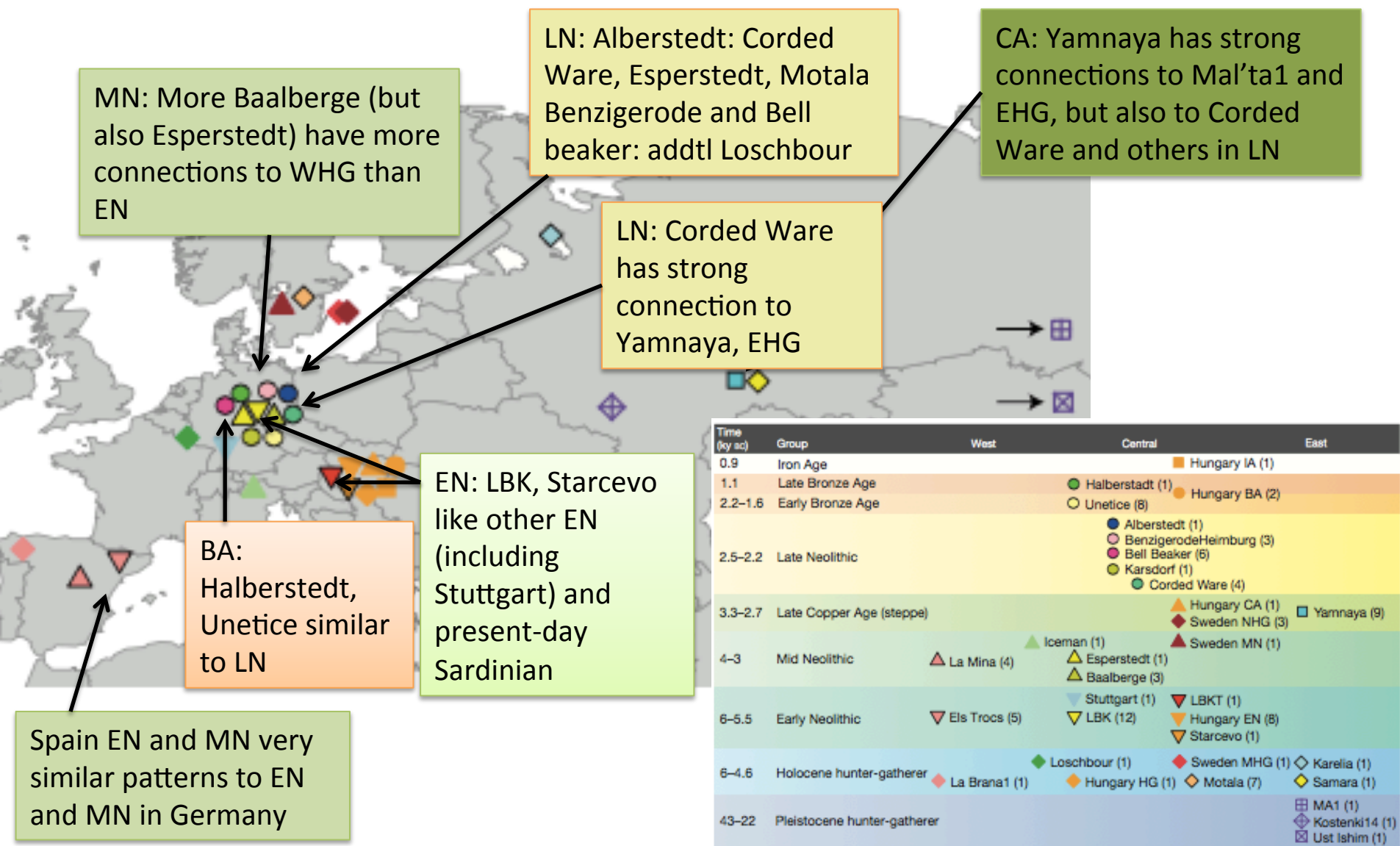# Late Neolithic/Bronze Age (Corded Ware)

- D(EUR, Yam/Mot/Kar/Sam; Corded_Ware, Mbuti)<0 and D(EUR no HG, Corded_Ware; Yam/Mot/Kar/Sam, Mbuti)<0
  - Corded_Ware mostly clade with EHG and Yamnaya
- See D(EUR, Esperstedt; Corded Ware, Mbuti)<0 but D(EUR, Corded Ware; Esperstedt, Mbuti) mostly >=0

Late Neolithic/Bronze Age (Alberstedt)

- D(EUR, CW/Esper/Mot; Alberstedt, Mbuti)<0 but D(EN/MN, Alberstedt; CW/Yam/Mot/Kar/Sam, Mbuti)<0
- CW connections (and thus, Yamnaya connections), but also MN connections

Comparing to Haak et al. (2015)

LN: Alberstedt: Corded Ware, Esperstedt, Motala Benzigerode and Bell beaker: addtl Loschbour

CA: Yamnaya has strong connections to Mal'ta1 and EHG, but also to Corded Ware and others in LN

MN: More Baalberge (but also Esperstedt) have more connections to WHG than EN

LN: Corded Ware has strong connection to Yamnaya, EHG

EN: LBK, Starcevo like other EN (including Stuttgart) and present-day Sardinian

BA: Halberstedt, Unetice similar to LN

Spain EN and MN very similar patterns to EN and MN in Germany

Time (ky ac)	Group	West	Central	East
0.9	Iron Age		■ Hungary IA (1)	
1.1	Late Bronze Age		● Halberstadt (1)	○ Hungary BA (2)
2.2–1.6	Early Bronze Age		○ Unetice (8)	
2.5–2.2	Late Neolithic		● Alberstedt (1) ● BenzigerodeHeimburg (3) ● Bell Beaker (6) ● Karsdorf (1) ● Corded Ware (4)	
3.3–2.7	Late Copper Age (steppe)		▲ Hungary CA (1) ◆ Sweden NHG (3)	■ Yamnaya (9)
4–3	Mid Neolithic	▲ La Mina (4)	▲ Iceman (1) ▲ Esperstedt (1) ▲ Baalberge (3)	▲ Sweden MN (1)
6–5.5	Early Neolithic	▽ Els Trocs (5)	▽ Stuttgart (1) ▽ LBKT (1) ▽ LBK (12) ▽ Hungary EN (8) ▽ Starcevo (1)	
6–4.6	Holocene hunter-gatherer	◆ La Brana1 (1)	◆ Loschbour (1) ◆ Hungary HG (1)	◆ Sweden MHG (1) ◇ Karelia (1) ◇ Motala (7) ◇ Samara (1)
43–22	Pleistocene hunter-gatherer			⊞ MA1 (1) ⊕ Kostenki14 (1) ⊠ Ust Ishim (1)

From the Haak et al. paper

instead, the Corded Ware are both the earliest and most strongly differentiated from the Middle Neolithic population.

'Outgroup' f_3 statistics[6] (Supplementary Information section 7), which measure shared genetic drift between a pair of populations (Extended Data Fig. 1), support the clustering of hunter-gatherers, Early/Middle Neolithic, and Late Neolithic/Bronze Age populations into different groups as in the PCA (Fig. 2a). We also analysed f_4 statistics, which allow us to test whether pairs of populations are consistent with descent from common ancestral populations, and to assess significance using a normally distributed Z score. Early European farmers from the Early and Middle Neolithic were closely related but not identical. This is reflected in the fact that Loschbour, a WHG individual from Luxembourg[4,] shared more alleles with post-4,000 BC European farmers from Germany, Spain, Hungary, Sweden and Italy than with early farmers of Germany, Spain, and Hungary, documenting an increase of hunter-gatherer ancestry in multiple regions of Europe during the course of the Neolithic. The two EHG form a clade with respect to all other present-day and ancient populations ($|Z| < 1.9$), and MA1 shares more alleles with them ($|Z| > 4.7$) than with other ancient or modern populations, suggesting that they may be a source for the ANE ancestry in present Europeans[4,12,22] as they are geographically and temporally more proximate than Upper Paleolithic Siberians. The Yamnaya differ from the EHG by sharing fewer alleles with MA1 ($|Z| = 6.7$) suggesting a dilution of ANE ancestry between 5,000–3,000 BC on the European steppe. This was likely due to admixture of EHG with a population related to present-day Near Easterners, as the most negative f_3 statistic in the Yamnaya (giving unambiguous evidence of admixture) is observed when we model them as a mixture of EHG and present-day Near Eastern populations like Armenians ($Z = -6.3$;

Supplementary Information section 7). The Late Neolithic/Bronze Age groups of central Europe share more alleles with Yamnaya than the Middle Neolithic populations do ($|Z| = 12.4$) and more alleles with the Middle Neolithic than the Yamnaya do ($|Z| = 12.5$), and have a negative f_3 statistic with the Middle Neolithic and Yamnaya as references ($Z = -20.7$), indicating that they were descended from a mixture of the local European populations and new migrants from the east. Moreover, the Yamnaya share more alleles with the Corded Ware ($|Z| \geq 3.6$) than with any other Late Neolithic/Early Bronze Age group with at least two individuals (Supplementary Information section 7), indicating that they had more eastern ancestry, consistent with the PCA and ADMIXTURE patterns (Fig. 2).

Modelling of the ancient samples shows that while Karelia is genetically intermediate between Loschbour and MA1, the topology that considers Karelia as a mixture of these two elements is not the only one that can fit the data (Supplementary Information section 8). To avoid biasing our inferences by fitting an incorrect model, we developed new statistical methods that are substantial extensions of a previously reported approach[4], which allow us to obtain precise estimates of the proportion of mixture in later Europeans without requiring a formal model for the relationship among the ancestral populations. The method (Supplementary Information section 9) is based on the idea that if a Test population has ancestry related to reference populations Ref_1, Ref_2, …, Ref_N in proportions α_1, α_2, …, α_N, and the references are themselves differentially related to a triple of outgroup populations A, B, C, then:
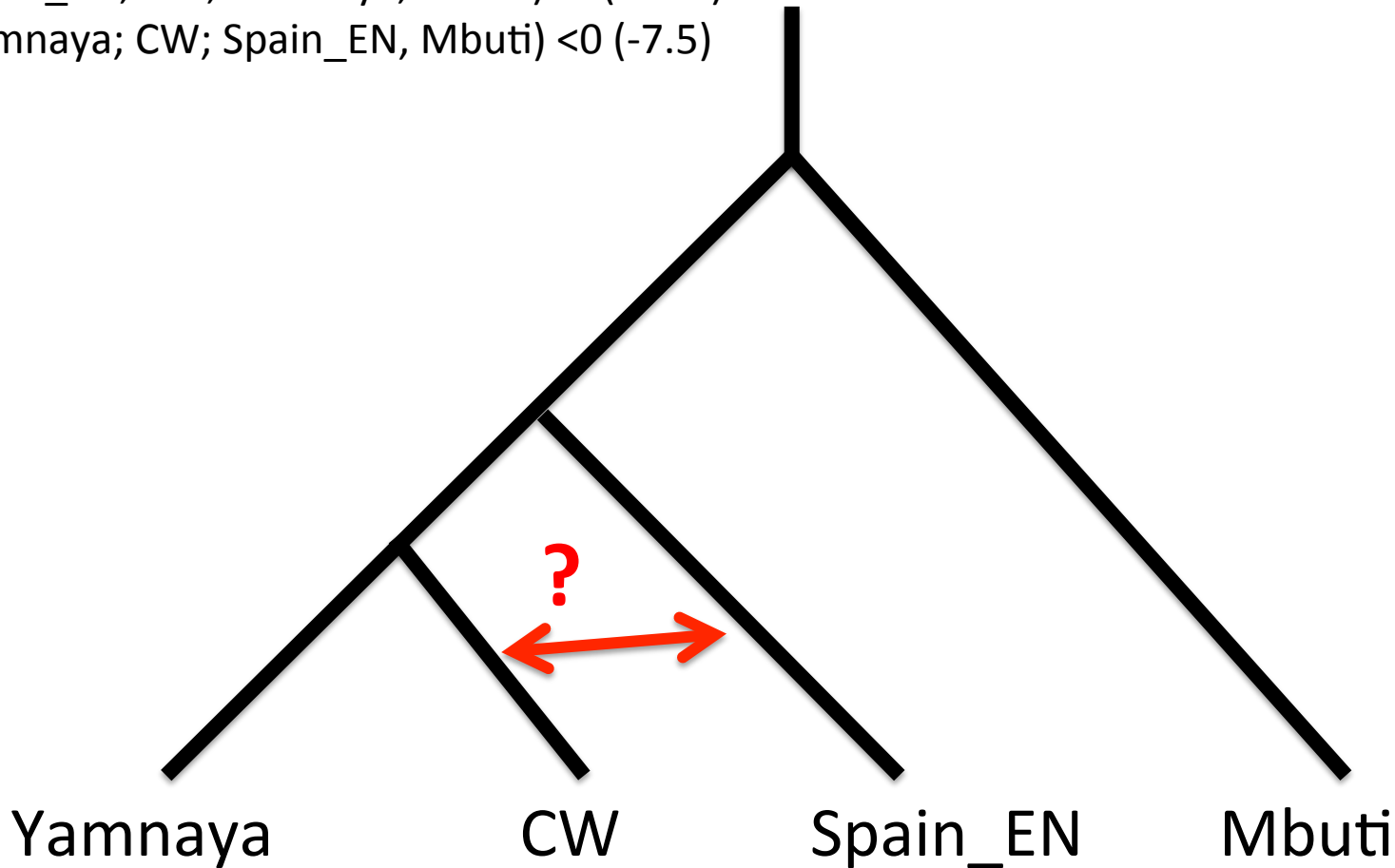
$$f_4(\text{Test}, A; B, C) = \sum_{i=1}^{N} a_i f_4(\text{Ref}_i, A; B, C)$$

Spain_EN, Yamnaya, Corded Ware

D(Spain_EN, Yamnaya; CW, Mbuti)<0 (-6.8)
D(Spain_EN, CW; Yamnaya, Mbuti)<0 (-14.3)
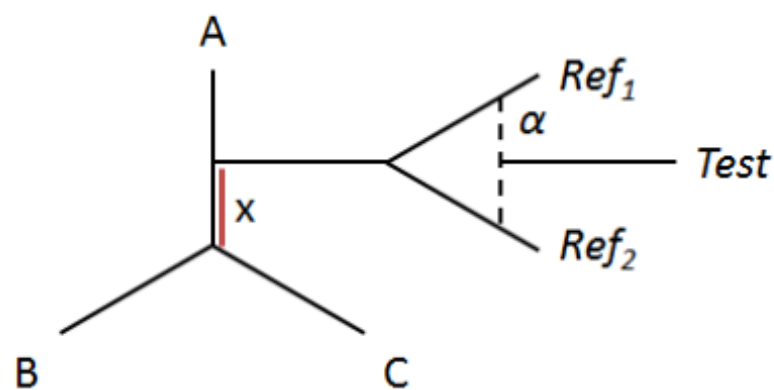D(Yamnaya; CW; Spain_EN, Mbuti) <0 (-7.5)

qpWave

Figure S9.1: If *Test* and *Ref*$_1$ form a clade with respect to the outgroups, then statistics involving either one of them and the outgroups are identical.
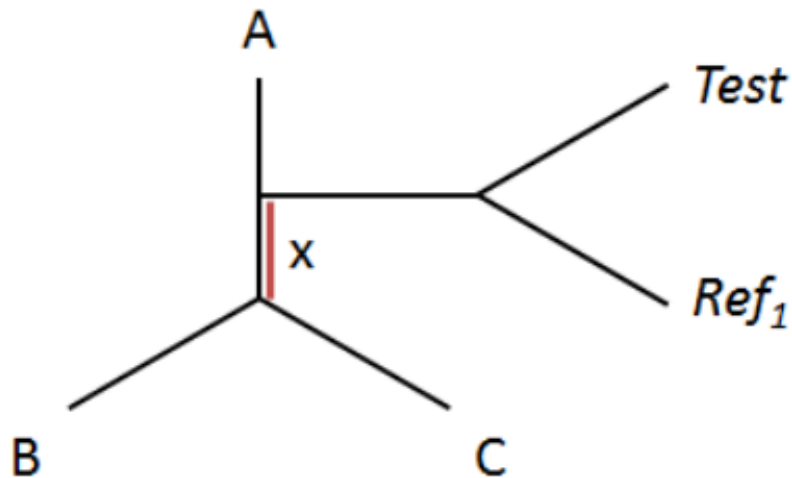
	X=Test	X=Ref$_1$
$f_4(X, A; B, C)$	0	0
$f_4(X, B; A, C)$	x	x
$f_4(X, C; A, B)$	x	x

f4(Test, A; B, C) = f4(Ref1, A; B, C)

(a)

$f_4(\text{Test or Ref}_1 \text{ or Ref}_2, A; B, C) = 0$
$f_4(\text{Test or Ref}_1 \text{ or Ref}_2, B; A, C) = x$
$f_4(\text{Test or Ref}_1 \text{ or Ref}_2, C; A, B) = x$

(b)

$f_4(Ref_1, A; B, C) = 0$ $f_4(Ref_2, A; B, C) = 0$
$f_4(Ref_1, B; A, C) = x+y$ $f_4(Ref_2, B; A, C) = y$
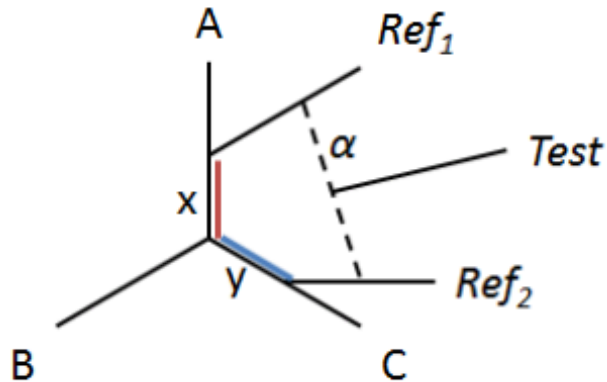$f_4(Ref_1, C; A, B) = x+y$ $f_4(Ref_2, C; A, B) = y$

$f_4(Test, A; B, C) = 0$
$f_4(Test, B; A, C) = y+\alpha x=(1-\alpha)\,f_4(Ref_2, B; A, C)+\alpha f_4(Ref_1, B; A, C)$
$f_4(Test, C; A, B) = y+\alpha x=(1-\alpha)\,f_4(Ref_2, C; A, B)+\alpha f_4(Ref_1, C; A, B)$

(c)
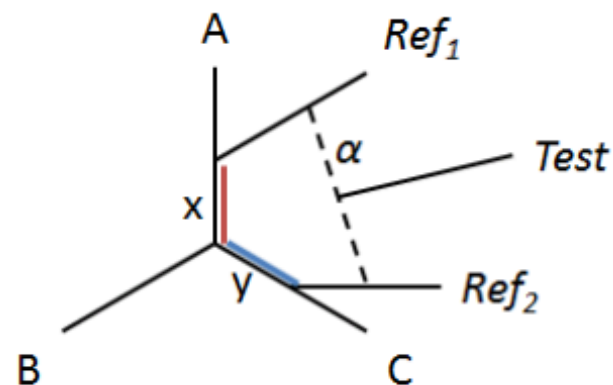
$f_4(Ref_1, A; B, C) = 0$ $f_4(Ref_2, A; B, C) = -y$
$f_4(Ref_1, B; A, C) = x$ $f_4(Ref_2, B; A, C) = -y$
$f_4(Ref_1, C; A, B) = x$ $f_4(Ref_2, C; A, B) = 0$

$f_4(Test, A; B, C) = -(1-\alpha)y = (1-\alpha)\,f_4(Ref_2, A; B, C)+\alpha f_4(Ref_1, A; B, C)$
$f_4(Test, B; A, C) = \alpha x-(1-\alpha)y = \alpha f_4(Ref_1, A; B, C)+(1-\alpha)f_4(Ref_2, A; B, C)$
$f_4(Test, C; A, B) = \alpha x = \alpha f_4(Ref_1, A; B, C)+(1-\alpha)\,f_4(Ref_2, A; B, C)$

(b)

$f_4(Ref_1, A; B, C) = 0$ $f_4(Ref_2, A; B, C) = 0$
$f_4(Ref_1, B; A, C) = x+y$ $f_4(Ref_2, B; A, C) = y$
$f_4(Ref_1, C; A, B) = x+y$ $f_4(Ref_2, C; A, B) = y$

$f_4(Test, A; B, C) = 0$
$f_4(Test, B; A, C) = y+\alpha x = (1-\alpha) f_4(Ref_2, B; A, C) + \alpha f_4(Ref_1, B; A, C)$
$f_4(Test, C; A, B) = y+\alpha x = (1-\alpha) f_4(Ref_2, C; A, B) + \alpha f_4(Ref_1, C; A, B)$

(c)

$f_4(Ref_1, A; B, C) = 0$ $f_4(Ref_2, A; B, C) = -y$
$f_4(Ref_1, B; A, C) = x$ $f_4(Ref_2, B; A, C) = -y$
$f_4(Ref_1, C; A, B) = x$ $f_4(Ref_2, C; A, B) = 0$
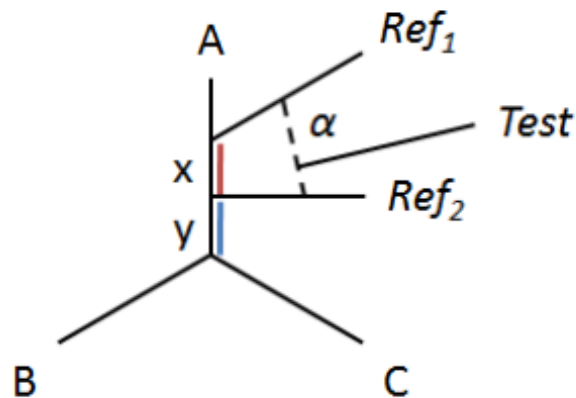
$f_4(Test, A; B, C) = -(1-\alpha)y = (1-\alpha) f_4(Ref_2, A; B, C) + \alpha f_4(Ref_1, A; B, C)$
$f_4(Test, B; A, C) = \alpha x - (1-\alpha)y = \alpha f_4(Ref_1, A; B, C) + (1-\alpha) f_4(Ref_2, A; B, C)$
$f_4(Test, C; A, B) = \alpha x = \alpha f_4(Ref_1, A; B, C) + (1-\alpha) f_4(Ref_2, A; B, C)$

f4(Test, A; B, C) = α f4(Ref1, A; B, C) + (1-α) f4(Ref1, A; B, C)

(b)

$f_4(Ref_1, A; B, C) = 0$ $f_4(Ref_2, A; B, C) = 0$
$f_4(Ref_1, B; A, C) = x+y$ $f_4(Ref_2, B; A, C) = y$
$f_4(Ref_1, C; A, B) = x+y$ $f_4(Ref_2, C; A, B) = y$

$f_4(Test, A; B, C) = 0$
$f_4(Test, B; A, C) = y+\alpha x = (1-\alpha) f_4(Ref_2, B; A, C) + \alpha f_4(Ref_1, B; A, C)$
$f_4(Test, C; A, B) = y+\alpha x = (1-\alpha) f_4(Ref_2, C; A, B) + \alpha f_4(Ref_1, C; A, B)$

(c)

$f_4(Ref_1, A; B, C) = 0$ $f_4(Ref_2, A; B, C) = -y$
$f_4(Ref_1, B; A, C) = x$ $f_4(Ref_2, B; A, C) = -y$
$f_4(Ref_1, C; A, B) = x$ $f_4(Ref_2, C; A, B) = 0$

$f_4(Test, A; B, C) = -(1-\alpha)y = (1-\alpha) f_4(Ref_2, A; B, C) + \alpha f_4(Ref_1, A; B, C)$
$f_4(Test, B; A, C) = \alpha x - (1-\alpha)y = \alpha f_4(Ref_1, A; B, C) + (1-\alpha) f_4(Ref_2, A; B, C)$
$f_4(Test, C; A, B) = \alpha x = \alpha f_4(Ref_1, A; B, C) + (1-\alpha) f_4(Ref_2, A; B, C)$

f4(Test, A; B, C) = α f4(Ref1, A; B, C) + (1-α) f4(Ref1, A; B, C)
More generally,

$$f_4(Test; A; B, C) \approx \sum_{i=1}^{N} \alpha_i f_4(Ref_i; A; B, C)$$

with $\sum_{i=1}^{N} \alpha_i = 1$ and $\alpha_i \geq 0, i = 1, \dots, N.$

F4(Test; A, B, C)

- A, B, and C are all outgroups, with m reference sets

- If n outgroups, then $n(n\text{-}1 \text{ choose } 2)$ arrangements.

- Matrix of $n(n\text{-}1 \text{ choose } 2)$ rows and m columns

$$f_4(Test; A; B, C) \approx \sum_{i=1}^{N} \alpha_i f_4(Ref_i; A; B, C)$$

with $\sum_{i=1}^{N} \alpha_i = 1$ and $\alpha_i \geq 0, i = 1, \ldots, N$. Given a set

$$t \approx R * \alpha^{\mathsf{T}}$$

$$
\begin{bmatrix}
F4(Test; A; B, C) \\
F4(Test; B; A, C) \\
F4(Test; C; A, B)
\end{bmatrix}
\approx
\begin{bmatrix}
F4(Ref_1; A; B, C) & F4(Ref_2; A; B, C) & \ldots & F4(Ref_m; A; B, C) \\
F4(Ref_1; B; A, C) & F4(Ref_2; B; A, C) & \ldots & F4(Ref_m; B; A, C) \\
F4(Ref_1; C; A, B) & F4(Ref_2; C; A, B) & \ldots & F4(Ref_m; C; A, B)
\end{bmatrix}
*
\begin{bmatrix}
\alpha_1 \\
\alpha_2 \\
. \\
. \\
. \\
\alpha_m
\end{bmatrix}
$$

$$f_4(Test; A; B, C) \approx \sum_{i=1}^{N} \alpha_i f_4(Ref_i; A; B, C)$$

with $\sum_{i=1}^{N} \alpha_i = 1$ and $\alpha_i \geq 0, i = 1, \dots, N$. Given a set

$$
\underset{t}{\begin{bmatrix} F4(Test; A; B, C) \\ F4(Test; B; A, C) \\ F4(Test; C; A, B) \end{bmatrix}}
\approx
\underset{R}{\begin{bmatrix} F4(Ref_1; A; B, C) & F4(Ref_2; A; B, C) \dots & F4(Ref_m; A; B, C) \\ F4(Ref_1; B; A, C) & F4(Ref_2; B; A, C) \dots & F4(Ref_m; B; A, C) \\ F4(Ref_1; C; A, B) & F4(Ref_2; C; A, B) \dots & F4(Ref_m; C; A, B) \end{bmatrix}}
\underset{*}{}
\underset{\alpha^{T}}{\begin{bmatrix} \alpha_1 \\ \alpha_2 \\ \vdots \\ \alpha_m \end{bmatrix}}
$$

This problem can be solved for α by least squares, minimizing $\|t - R\alpha^{T}\|_2^2$ subject to the constraint that α has non-negative elements and $\|a\|_1 = 1$. We use the implementation of least squares in the *lsqlin* function of Matlab (http://www.mathworks.com/help/optim/ug/lsqlin.html) which estimates the vector $\hat{\alpha}$ of the mixture proportions and also reports *resnorm* $= \|t - R\hat{\alpha}^{T}\|_2^2$, the squared 2-norm of the residuals.
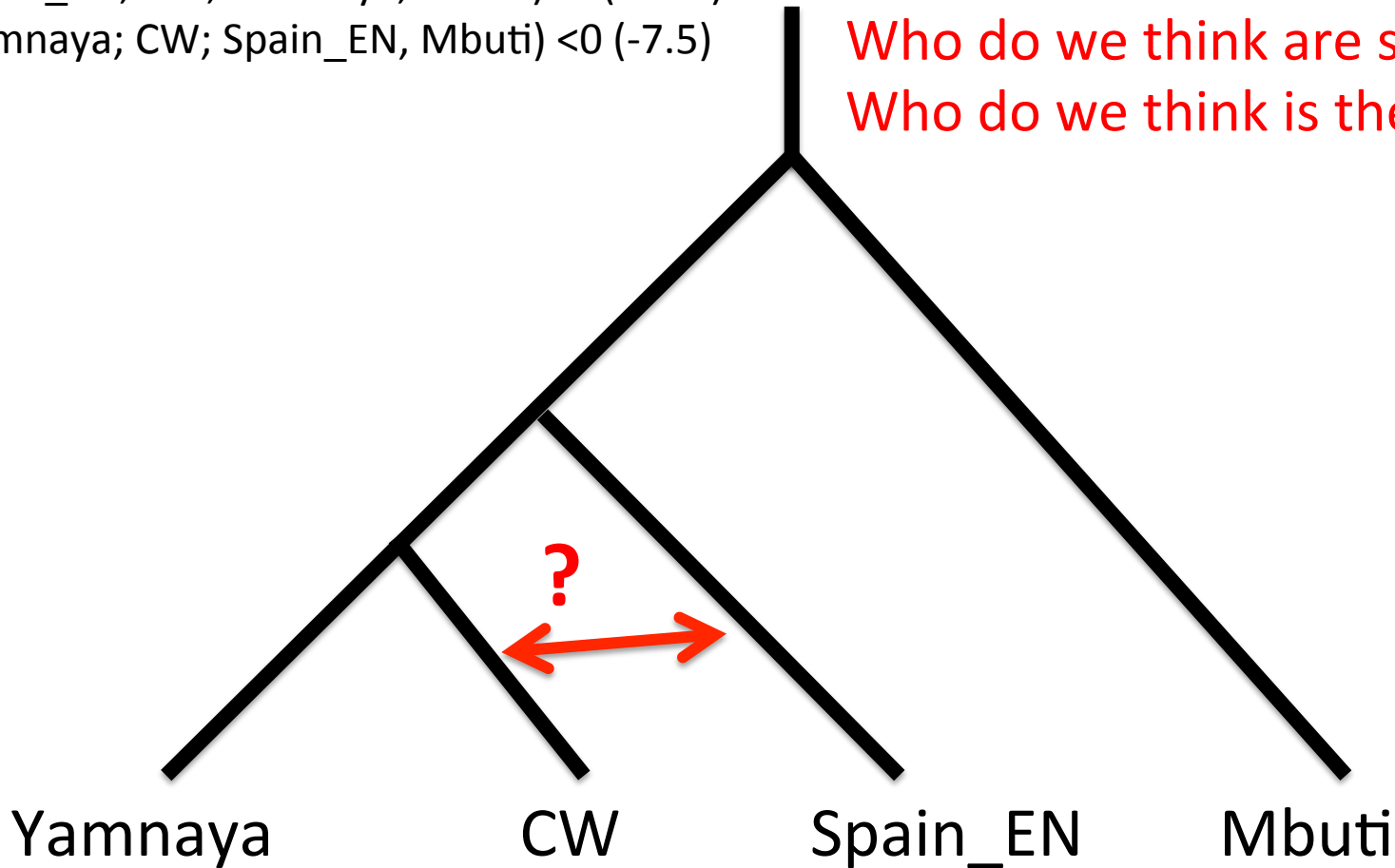
qpAdm: Some Thoughts

- Outgroup choice – very vital!
  - No need to know phylogenetic relationships BUT
  - Cannot all be from same population – if identically related to Test and References, then no leverage to find admixture proportion.
  - No recent admixture from outgroup to Test/Ref
  - Don't make this too big – computationally difficult and poor estimates result.
- qpWave important
  - Assume T=test, S={Ref1, Ref2,…,Refm}
  - qpWave(S) must have n streams of ancestry (r=n-1)
  - qpWave(T,S) should not increase rank (n streams of ancestry)
  - In practice, we can try qpAdm without necessarily knowing qpWave conditions (but need n-1 streams of ancestry).

Spain_EN, Yamnaya, Corded Ware

D(Spain_EN, Yamnaya; CW, Mbuti)<0 (-6.8)
D(Spain_EN, CW; Yamnaya, Mbuti)<0 (-14.3)
D(Yamnaya; CW; Spain_EN, Mbuti) <0 (-7.5)

Who do we think are sources?
Who do we think is the test?

?

Yamnaya   CW   Spain_EN   Mbuti

qpAdm software

- Just like qpWave, only ORDER MATTERS in the leftpop file.

TEST

REF1

REF2

```
Spain_EN
Corded_Ware_LN
Yamnaya
Haak01_leftpop.txt (END)
```
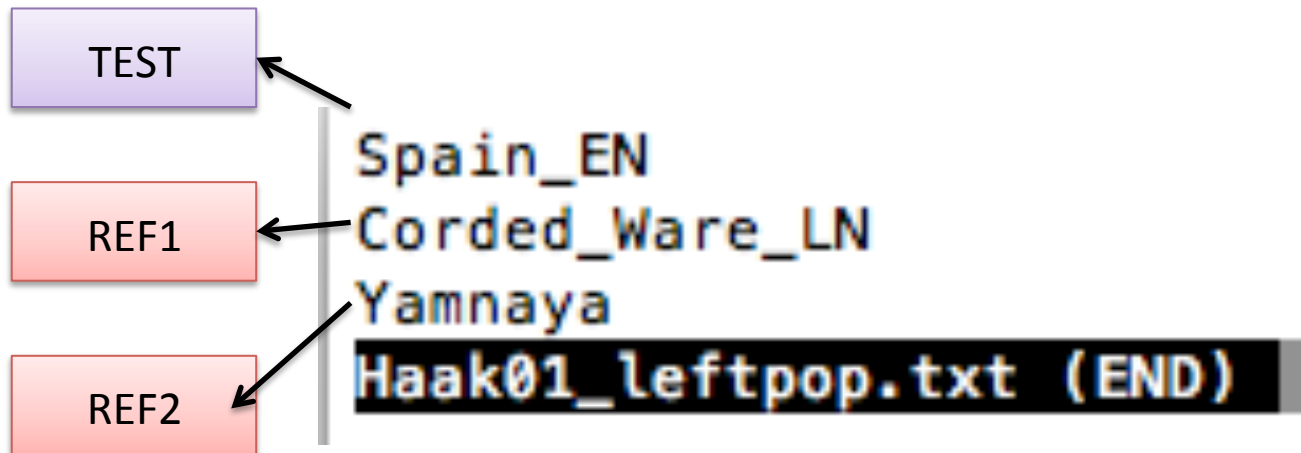
qpAdm software

- Just like qpWave, only ORDER MATTERS in the leftpop file.

What order do we want?
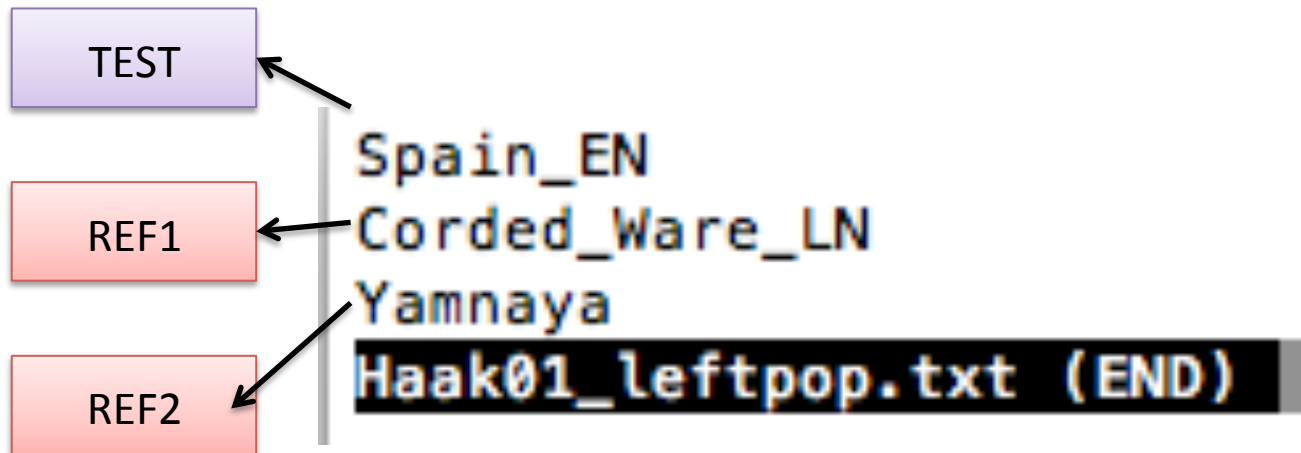
TEST

REF1

REF2

Spain_EN
Corded_Ware_LN
Yamnaya
Haak01_leftpop.txt (END)

Results

- ## qpAdm –p PARFILE > LOGFILE

```
Corded_Ware_LN
Spain_EN
Yamnaya
```

```
fixed pat  wt  dof      chisq         tail prob
          00  0   11     10.961         0.446573       0.233      0.767
          01  1   12    169.847     5.13073e-30        1.000     -0.000
          10  1   12     31.394        0.00171472      0.000      1.000
best pat:          00            0.446573              -   -
best pat:          10             0.00171472  chi(nested):    20.434 p-value for nested model:
6.17302e-06

    std. errors:      0.050      0.050
```

00 is the mixture case.
01 means all ancestry from Ref1
10 means all ancestry from Ref2

1. Look at "tail prob" – if p>0.05, then that model is possible.
2. If '00' is possible, then look at nested model – is '00' better than '01' or '10'?
     p-value for nested model (pnest) < 0.05, means you reject '10', so '00' is better than '10'.
3. Look at f1, f2 → 0.233 Spain_EN and 0.767 Yamnaya with SE=0.05
4. Is min(f1,f2)-SE>0?

Results

- ## qpAdm –p PARFILE > LOGFILE

```
Corded_Ware_LN
Spain_EN
Yamnaya
```

```
fixed pat   wt   dof      chisq        tail prob
        00   0    11      10.961        0.446573      0.233      0.767
        01   1    12     169.847     5.13073e-30      1.000     -0.000
        10   1    12      31.394        0.00171472    0.000      1.000
best pat:          00            0.446573                  -    -
best pat:          10            0.00171472  chi(nested):    20.434 p-value for nested model:
6.17302e-06
```

```
   std. errors:      0.050        0.050
```

00 is the mixture case.
01 means all ancestry from Ref1
10 means all ancestry from Ref2

Corded Ware seems to be a mixture of populations related to the Spain_EN and Yamnaya populations.

1. Look at "tail prob" – if p>0.05, then that model is possible.
2. If '00' is possible, then look at nested model – is '00' better than '01' or '10'?
     p-value for nested model (pnest) < 0.05, means you reject '10', so '00' is better than '10'.
3. Look at f1, f2 → 0.233 Spain_EN and 0.767 Yamnaya with SE=0.05
4. Is min(f1,f2)-SE>0?

Spain_EN or Yamnaya as Test?

```
Spain_EN
Corded_Ware_LN
Yamnaya
```

fixed pat	wt	dof	chisq	tail prob			
00	0	11	10.714	0.467501	4.298	-3.298	infeasible
01	1	12	169.762	5.34075e-30	1.000	-0.000	
10	1	12	344.858	0	0.000	1.000	

best pat: 00   0   - -
best pat: 01   5.34075e-30 chi(nested):   159.047 p-value for nested model:
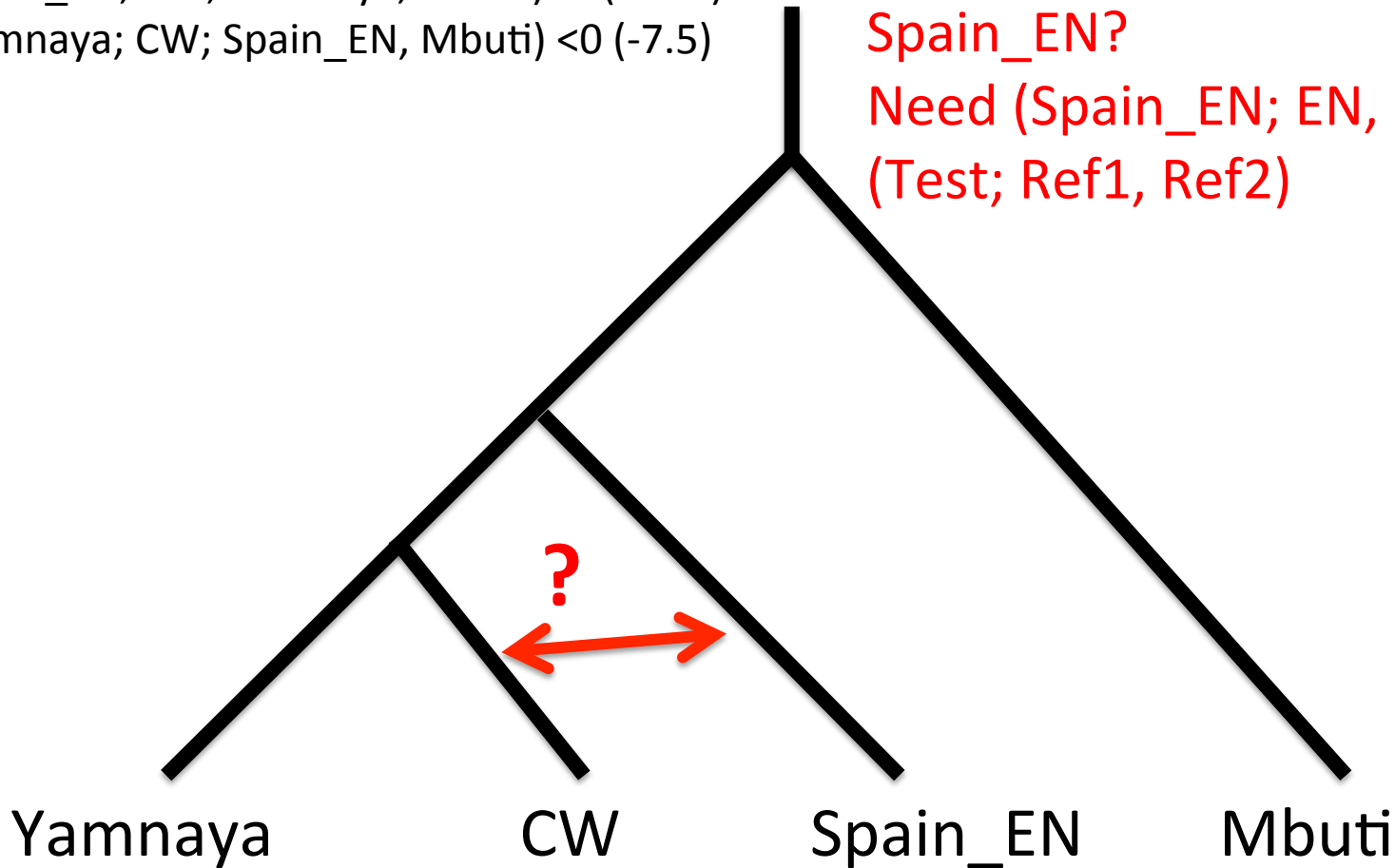   1.8271e-36

        std. errors: 0.925   0.925

```
Yamnaya
Spain_EN
Corded_Ware_LN
```

fixed pat	wt	dof	chisq	tail prob			
00	0	11	10.882	0.453196	-0.305	1.305	infeasible
01	1	12	345.393	0	1.000	-0.000	
10	1	12	31.453	0.00167982	0.000	1.000	

best pat: 00   0   - -
best pat: 10   0.00167982 chi(nested):   20.571 p-value for nested model:
5.74731e-06

        std. errors: 0.084   0.084

True reciprocal test

D(Spain_EN, Yamnaya; CW, Mbuti)<0 (-6.8)
D(Spain_EN, CW; Yamnaya, Mbuti)<0 (-14.3)
D(Yamnaya; CW; Spain_EN, Mbuti) <0 (-7.5)

We can find gene flow into CW.
What about gene flow into Spain_EN?
Need (Spain_EN; EN, CW) as (Test; Ref1, Ref2)

Gene flow into Spain_EN?

Test: Spain_EN
Ref1: Corded_Ware
Ref2: Spain_MN

Gene flow into Spain_EN?

Test: Spain_EN
Ref1: Corded_Ware
Ref2: Spain_MN

fixed pat	wt	dof	chisq	tail prob			
00	0	11	20.874	0.0346956	-0.084	1.084	infeasible
01	1	12	175.340	0	1.000	-0.000	
10	1	12	21.887	0.038804	0.000	1.000	

best pat: 00   0   - -
best pat: 10   0.038804 chi(nested):   1.013 p-value for nested model:
         0.314247

std. errors: 0.087   0.087

Should try more than one.
Maybe bad source population?
Either way, do not see gene flow into Spain_EN, and
with timing, geography, other populations, likely only
gene flow into Corded Ware and not other way around.

More intuition, maybe?
F4(Corded Ware, X/Y; Out, Out)

Tight positive – x and y clade relative to Corded Ware

Negative – admixture!

Loose positive – different relationship between x and y with Corded Ware
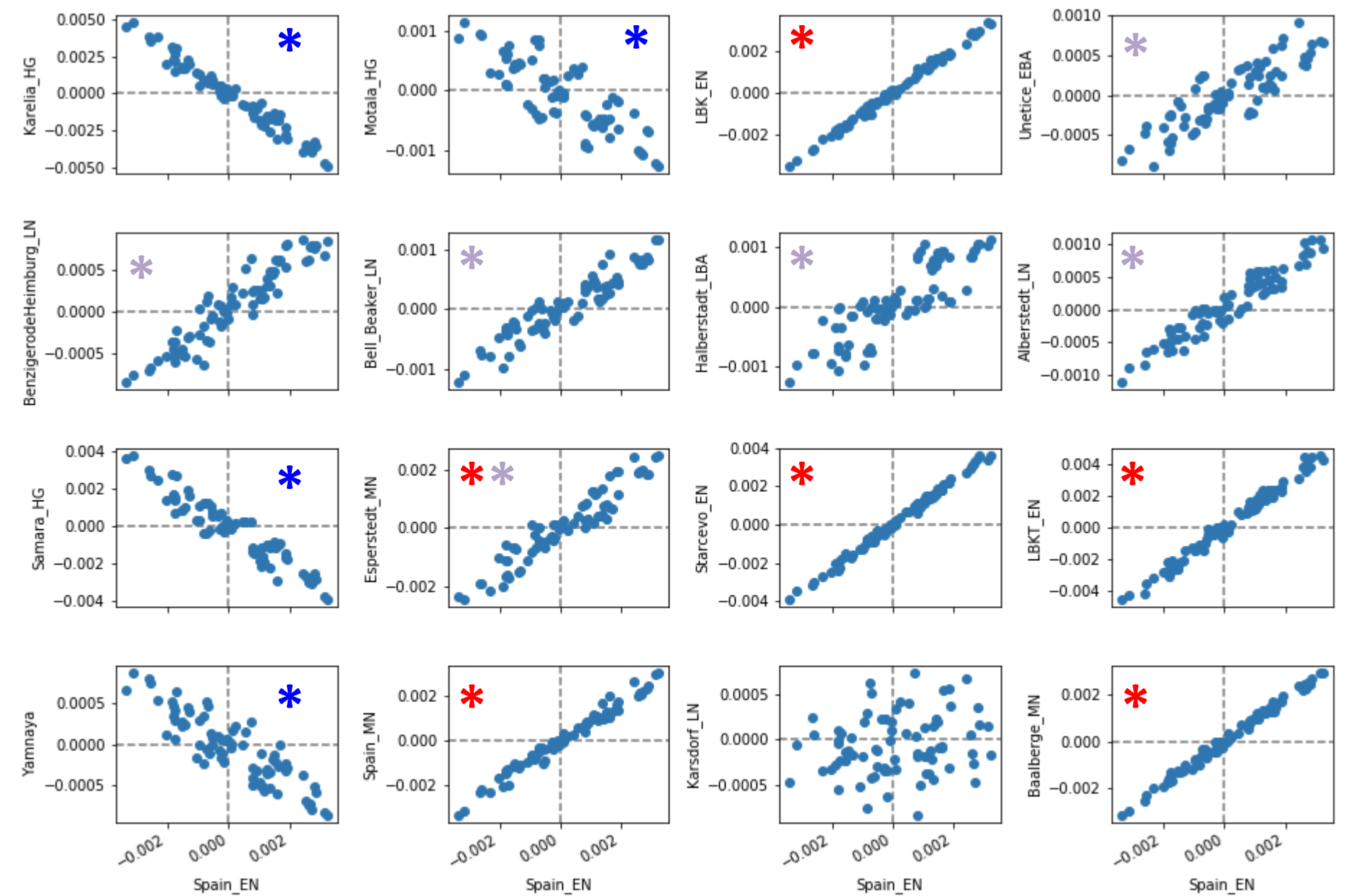
Class Activity – Try a three reference qpAdm test.

- What are the three sources of European ancestry?

Class Activity – Try a three reference qpAdm test.

- What are the three sources of European ancestry?

- Sources: LBK_EN, Loschbour, Yamnaya

- Test Spain_EN, Esperstedt_MN, Corded_Ware_LN, or Unetice_EBA
  - Try to see if you can figure out how to read the table in the log file for three populations!
  - How much of each type of ancestry do you find?

Three Source Case

```
fixed pat  wt   dof      chisq          tail prob
       000  0     10     12.930         0.227625      0.590      0.685     -0.275   infeasible
       001  1     11     14.080         0.228623      0.707      0.293      0.000
       010  1     11     16.819         0.113331      0.840     -0.000      0.160
       100  1     11     15.543         0.158965      0.000      2.144     -1.144   infeasible
       011  2     12     20.569         0.0570605     1.000     -0.000     -0.000
       101  2     12     34.297         0.000605429   0.000      1.000     -0.000
       110  2     12    111.478         3.05099e-18   0.000     -0.000      1.000
best pat:         000                   0                         -      -
best pat:         001            0.228623   chi(nested):      1.150 p-value for nested model:
    0.283597
best pat:         011            0.0570605  chi(nested):      6.489 p-value for nested model:
    0.0108521

     std. errors:      0.319      0.844      0.546
```

000 is the full mixture case.
010, 001, 100 means two source mixture model.
110, 011, 101 means all ancestry from one source

1. Look at "tail prob" – if p>0.05, then that model is possible.
2. If 000, 010, 001, 100 are possible, then look at nested model – is '000' better than two source models, better than the one source models??
    p-value for pnest < 0.05, means reject model in same line, preferring model in above line.
3. Look at f1, f2, f3.

qpAdm(Spain_EN; LBK_EN, Loschbour, Yamnaya)

```
 fixed pat   wt   dof      chisq          tail prob
       000   0    10       9.140          0.51884      0.936     0.093    -0.030   infeasible
       001   1    11       9.396          0.58539      0.948     0.052     0.000
       010   1    11       9.678          0.55954      0.973    -0.000     0.027
       100   1    11      23.096          0.0171314    0.000     2.491    -1.491   infeasible
       011   2    12       9.843          0.629774     1.000    -0.000    -0.000
       101   2    12      79.631          4.85302e-12  0.000     1.000    -0.000
       110   2    12     339.060                    0  0.000    -0.000     1.000
best pat:          000                  0               -    -
best pat:          001            0.58539  chi(nested):     0.256 p-value for nested model:
     0.613109
best pat:          011           0.629774  chi(nested):     0.447 p-value for nested model:
     0.503992

     std. errors:      0.076       0.163       0.111
```

qpAdm(Esperstedt_MN; LBK_EN, Loschbour, Yamnaya)

```
fixed pat   wt  dof     chisq         tail prob
        000  0   10     9.360        0.498287    0.679    0.421   -0.101  infeasible
        001  1   11    10.022        0.528452    0.707    0.293    0.000
        010  1   11    14.436        0.209782    0.846    0.000    0.154
        100  1   11    16.502        0.123488    0.000    1.871   -0.871  infeasible
        011  2   12    17.992        0.115945    1.000   -0.000   -0.000
        101  2   12    32.028       0.00137028   0.000    1.000    0.000
        110  2   12   121.960        2.5117e-20  0.000   -0.000    1.000
best pat:        000                    0            -    -
best pat:        001            0.528452  chi(nested):      0.661 p-value for nested model:
     0.41612
best pat:        011            0.115945  chi(nested):      7.970 p-value for nested model:
   0.00475557

    std. errors:      0.150       0.316      0.202
```

qpAdm(Corded_Ware_LN; LBK_EN, Loschbour, Yamnaya)

```
    fixed pat   wt   dof      chisq          tail prob
            000  0    10     10.210         0.422307      0.172      0.159      0.668
            001  1    11     24.316         0.0114639    -0.226      1.226     -0.000    infeasible
            010  1    11     11.094         0.435398      0.236     -0.000      0.764
            100  1    11     13.988         0.233652      0.000      0.440      0.560
            011  2    12    216.486              0         1.000     -0.000     -0.000
            101  2    12     25.256         0.0136574     0.000      1.000      0.000
            110  2    12     31.284         0.00178256    0.000     -0.000      1.000
best pat:        000          0.422307                   -  -
best pat:        010          0.435398   chi(nested):      0.885 p-value for nested model:
    0.346901
best pat:        101          0.0136574  chi(nested):     14.161 p-value for nested model:
0.000167793

      std. errors:      0.107       0.236       0.148
```

qpAdm(Unetice_LBA; LBK_EN, Loschbour, Yamnaya)

fixed pat	wt	dof	chisq	tail prob			
000	0	10	6.449	0.776267	0.275	0.303	0.422
001	1	11	17.490	0.0941965	0.048	0.952	0.000
010	1	11	15.390	0.165347	0.395	-0.000	0.605
100	1	11	15.209	0.173125	-0.000	0.848	0.152
011	2	12	225.464	0	1.000	-0.000	-0.000
101	2	12	16.072	0.187958	0.000	1.000	0.000
110	2	12	92.688	1.48661e-14	0.000	-0.000	1.000

best pat: 000   0.776267   -   -
best pat: 100   0.173125   chi(nested):   8.760 p-value for nested model:
   0.00307841
best pat: 101   0.187958   chi(nested):   0.863 p-value for nested model:
   0.352902

       std. errors: 0.063   0.129   0.087