

On the relative importance of demic and cultural diffusion in the Neolithic spread in Europe

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***Neonet seminar 2025,
Madrid, 15 Mayo 2025***



Academia Grant 2022-2026



Grant PID2023-150978NB-C22



Grant 2021-SGR-00190

Esta charla tiene 2 partes:

- 1ª parte: resultados recientes de investigación de nuestro grupo.
- 2ª parte: evidencias directas de transmisión cultural entre neolíticos y cazadores-recolectores.

Ammerman and Cavalli-Sforza (1984)

$$\text{spread rate} = s = 2\sqrt{aD}$$

where

a = initial growth rate

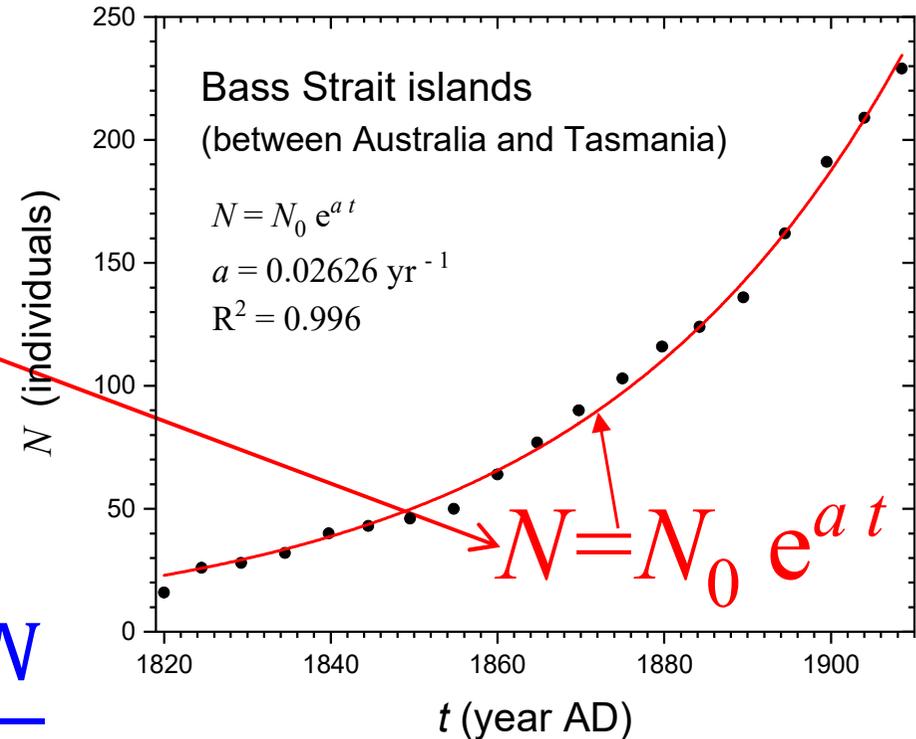
D = diffusion coefficient:

$$D = \frac{(r_1^2 + r_2^2 + \dots + r_N^2)/N}{4T}$$

with

r_1, r_2, \dots, r_N = intergenerational distance of individual 1, 2, ..., N .

T = generation time. What kind of distances?



Strictly, the correct distances are:

B distances = between birthplaces of parent and child

But very difficult to find. So 2 other distances have been used:

M distances = between birthplaces of spouses (M=mating)

R distances = between birthplace and place of residence

Pre-industrial farming population	probabilities $\{p_1, p_2, p_3, \dots\}$	distances $\{r_1, r_2, r_3, \dots\}$
Majangir R ETHIOPIA. Amm. & C-S (1984)	{0.40, 0.17, 0.17, 0.26}	{2.4, 14.5, 36.2, 60.4} km
Issongos M CENTRAL AFRICAN REPUBLIC Ammerman & C-S (1984)	$\left\{ \begin{array}{l} 0.42, 0.23, 0.16, 0.08, 0.07, \\ 0.02, 0.01, 0.01 \end{array} \right\}$	$\left\{ \begin{array}{l} 2.3, 7.3, 15, 25, 35, \\ 45, 55, 100 \end{array} \right\}$ km
Markazi B IRAN. Cobo et al. (2019)	$\left\{ \begin{array}{l} 0.799, 0.041, 0.022, 0.025, 0.064, \\ 0.004, 0.009, 0.021, 0.015 \end{array} \right\}$	$\left\{ \begin{array}{l} 0.5, 5.5, 15, 25, 35, \\ 50.03, 57.20, 60.51, 97.65 \end{array} \right\}$ km
Bihar M INDIA. Cobo et al. (2019)	$\left\{ \begin{array}{l} 0.018, 0.081, 0.105, 0.129, 0.14, 0.125, \\ 0.107, 0.079, 0.068, 0.057, 0.036, 0.025, 0.03 \end{array} \right\}$	$\left\{ \begin{array}{l} 2.5, 7.5, 12.5, 17.5, 22.5, 27.5, \\ 32.5, 37.5, 42.5, 47.5, 52.5, 57.5, 62.5 \end{array} \right\}$ km
Chandauli M INDIA. Cobo et al. (2019)	$\left\{ \begin{array}{l} 0.058, 0.122, 0.191, 0.256, 0.168, \\ 0.101, 0.069, 0.023, 0.012 \end{array} \right\}$	$\left\{ \begin{array}{l} 4, 12, 20, 28, 36, \\ 44, 52, 60, 68 \end{array} \right\}$ km

Two problems

- How can we test if the 3 kinds of distances give similar results?
- Histograms may not yield accurate spread rates, specially for long distances. Can we use lists of distances?

There is only one census with individual data (as far as we know), such that we can calculate B, M and R distances for the same population (Yanomamö, from Brazil and Venezuela):

Biella, P., Chagnon, N.A. & Seaman, G., *Yanomamö Interactive. The Ax Fight (CD-ROM)*, Orlando: Hartcourt Brace & Co. (1997).

We used this census to calculate lists (not histograms) of B, M and R distances (next slide)

Table S1 to Bancells & Fort, *Archaeol. Anthropol. Sci.* (2024)

B distances (i.e., between the birthplaces of parent and child)

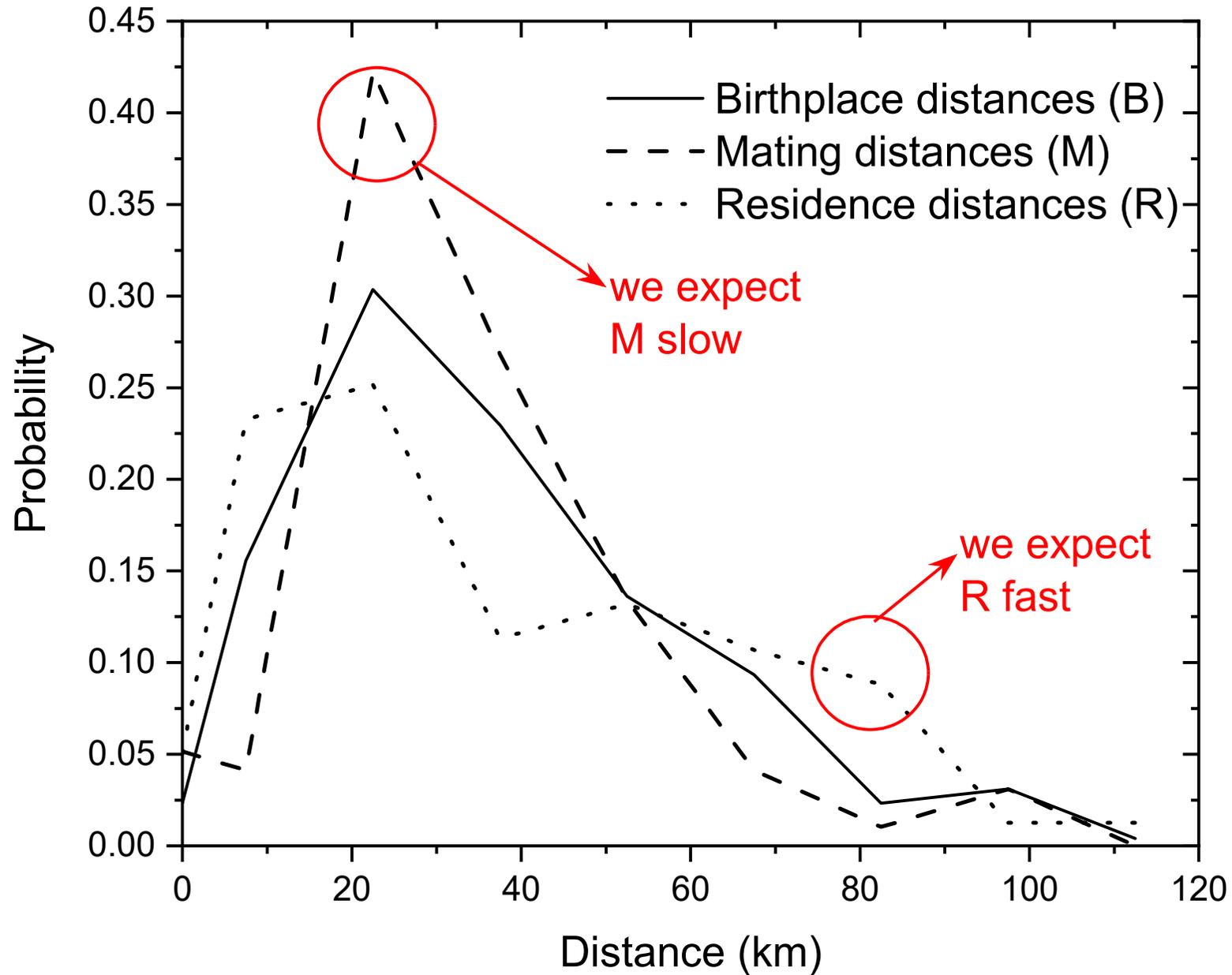
person	person	person	person	parent	parent	parent	parent	B distance
ID	POB. ID	POB. latitude	POB. longitude	ID FA/MO	POB. ID FA/MO	POB. FA/MO latitude	POB. FA/MO longitude	DIST. FA/MO
		° N	° W			° N	° W	km
227	145	1.98	64.57	777	145	1.98	64.57	0.00
1022	126	1.60	65.27	651	126	1.60	65.27	0.00
1246	124	1.78	65.15	1929	124	1.78	65.15	0.00
1795	145	1.98	64.57	777	145	1.98	64.57	0.00
2384	128	1.68	65.27	1046	128	1.68	65.27	0.00
2531	126	1.60	65.27	522	126	1.60	65.27	0.00
2518	9	1.55	65.37	1834	113	1.55	65.38	1.85
159	126	1.60	65.27	2130	118	1.62	65.30	4.14
951	126	1.60	65.27	950	118	1.62	65.30	4.14
1125	126	1.60	65.27	1509	118	1.62	65.30	4.14
2380	126	1.60	65.27	1568	118	1.62	65.30	4.14
2398	126	1.60	65.27	950	118	1.62	65.30	4.14

In this way we found **257 B distances**.

Similarly, we found
159 R distances and
97 M distances

We admit that the Yanomamö are a single population of horticulturalists living in the Amazonian forest. So we need more data, ideally from Neolithic Europe (using aDNA). Or at least censuses for other populations of pre-industrial farmers. If you know one, please let me know! This is only a first step.

Yanomamö



Simulations

Each generation ($t = 1, 2, 3, \dots$) :

- 1) Reproduction (logistic, with a and T from ethnography)
- 2) Dispersal, using the **list of B, R or M distances**
- 3) Interbreeding: $P_N = \text{farmers/km}^2$, $P_{HG} = \text{HGs/km}^2$

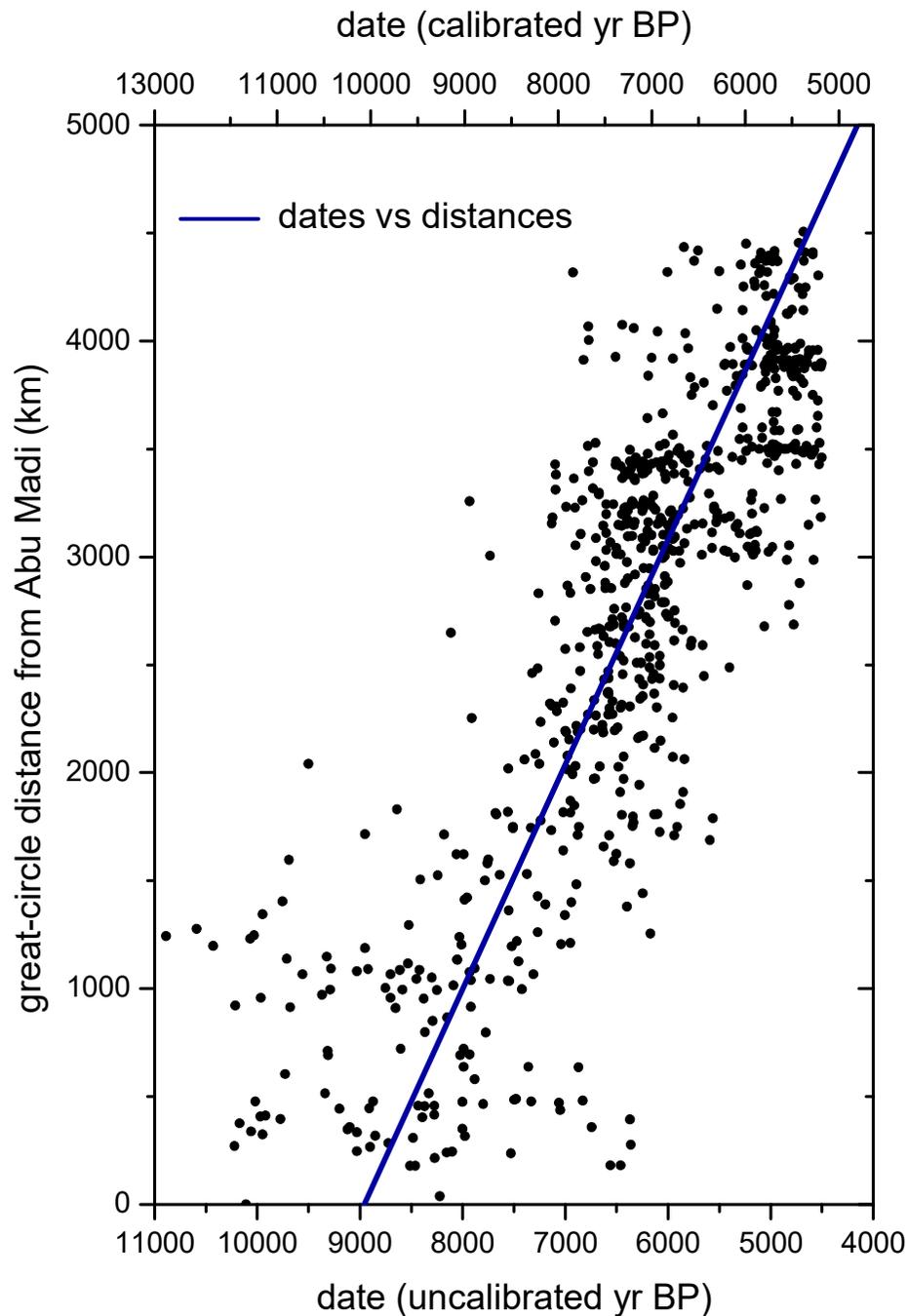
$$P_N(t + 1, x, y) - P_N(t, x, y) = C \frac{P_{HG} P_N}{P_{HG} + P_N} \approx C P_N \text{ if } P_N \ll P_{HG}$$

$$P_{HG}(t + 1, x, y) - P_{HG}(t, x, y) = C \frac{P_{HG} P_N}{P_{HG} + P_N} \approx -C P_N$$

$C =$ fraction of early farmers who interbreed with a HG.

For acculturation we can use the same Eqs. Then:

$C =$ number of HGs acculturated by an early farmer.



To apply this model we
need a range for the
spread rate from
archaeological data

0.9-1.3 km/yr

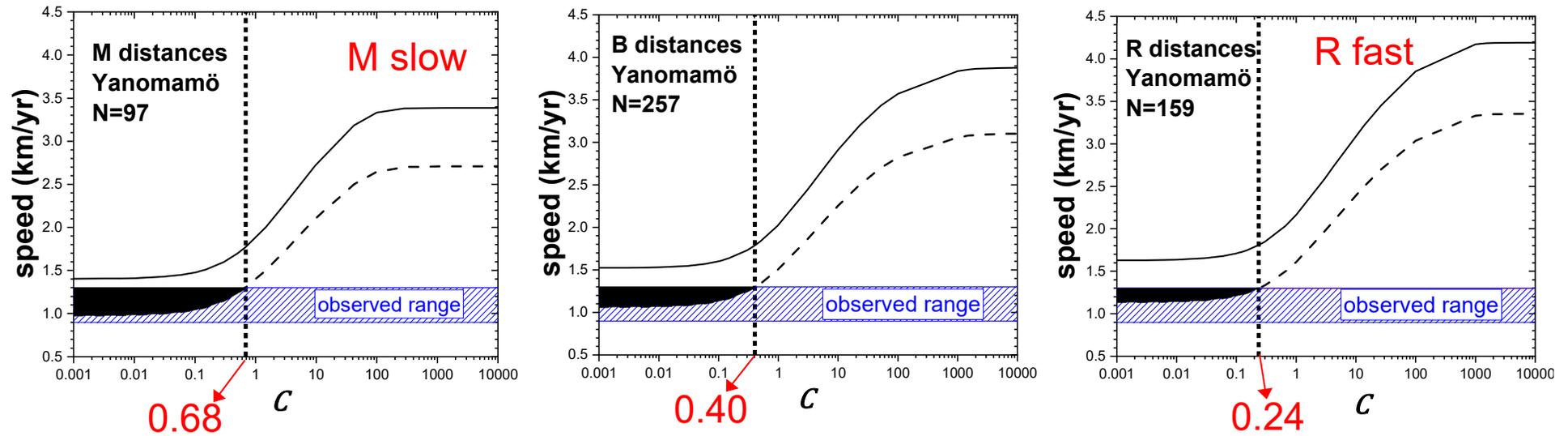
great circles & shortest paths

$$r = 0.83$$

(for both highest- r origins)

735 sites in Europe & Near East

Pinhasi, Fort & Ammerman,
PLoS Biol. (2005)



The 3 distances lead to similar curves (and consistent with the observed range).

From these figs., we can find ranges for C :

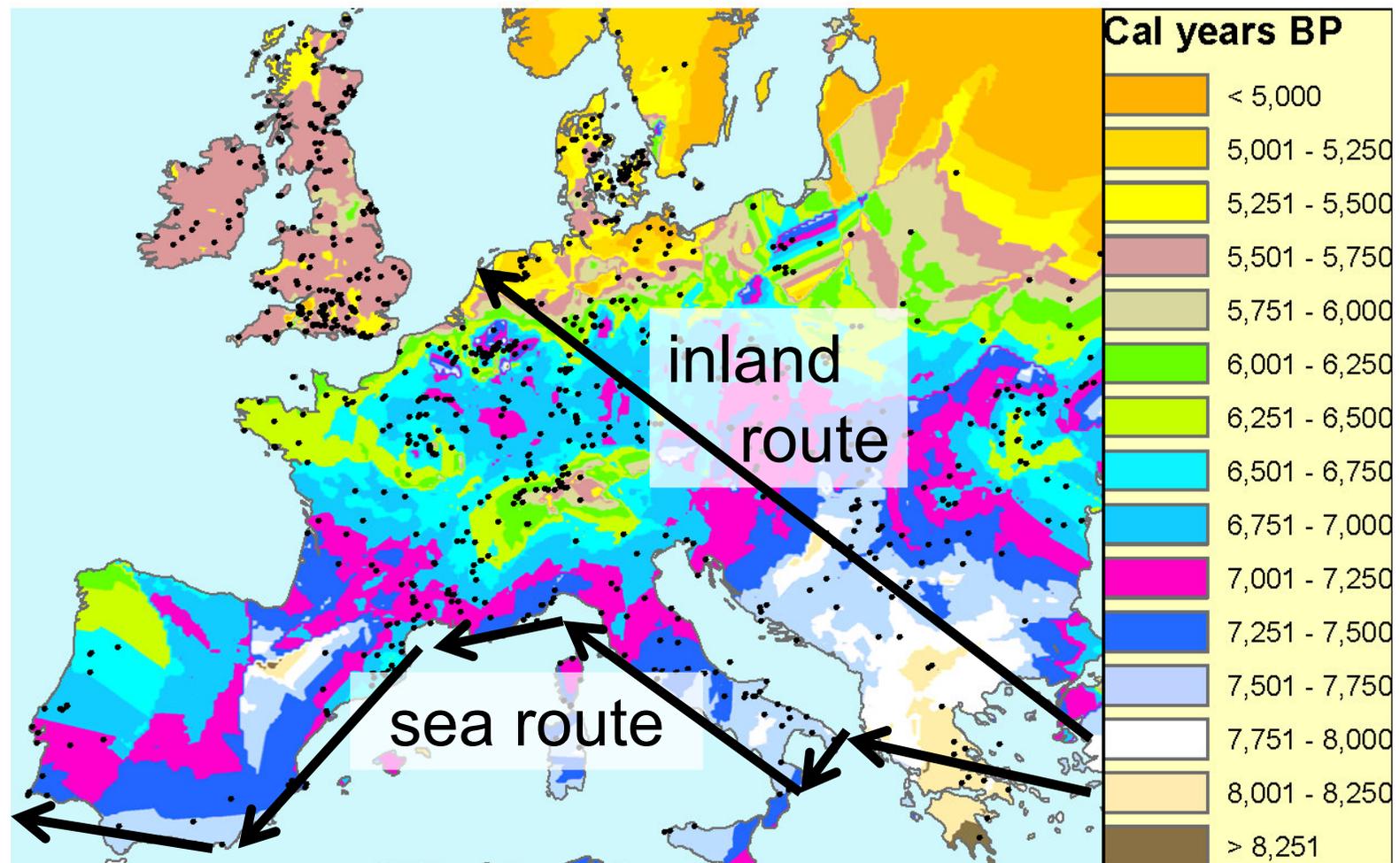
$0 < C < 0.68$ (M distances)

$0 < C < 0.40$ (B distances, the most reliable ones)

$0 < C < 0.24$ (R distances)

Therefore, Archaeology implies that **$0 < C < 0.40$ (B distances)**, i.e. the percentage of early farmers who interbred with a HG or acculturated one of them was **between 0% and 40%**.

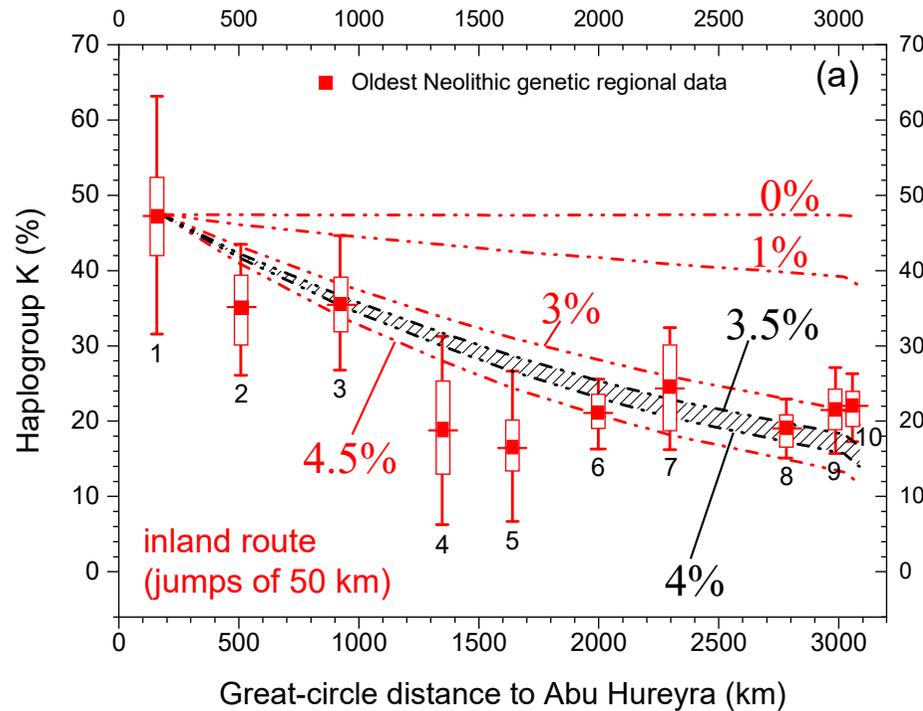
Ancient DNA along two routes



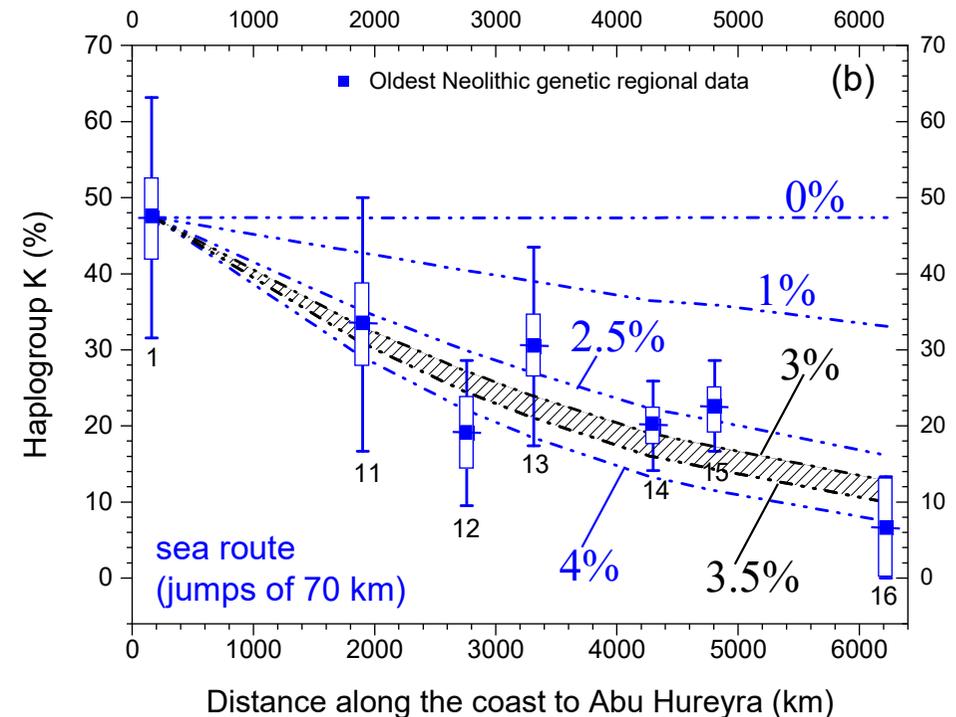
Interpolation from Fort, *J. R. Soc. Interface* (2015)

Mitochondrial haplogroup K is the most frequent one in farmers. It is essentially absent in HGs

Inland route



Sea route



Best fits: 3.5% - 4%

Best fits: 3% - 3.5%

The percentage of early farmers who interbred with HGs was essentially the same (~3.5%)!

Previous slide:

~3.5% of early farmers interbred with
a HG

Taking into account the uncertainties in the
parameter values and in the initial
frequencies of haplogroup K:

1% - 8% of early farmers interbred with a HG

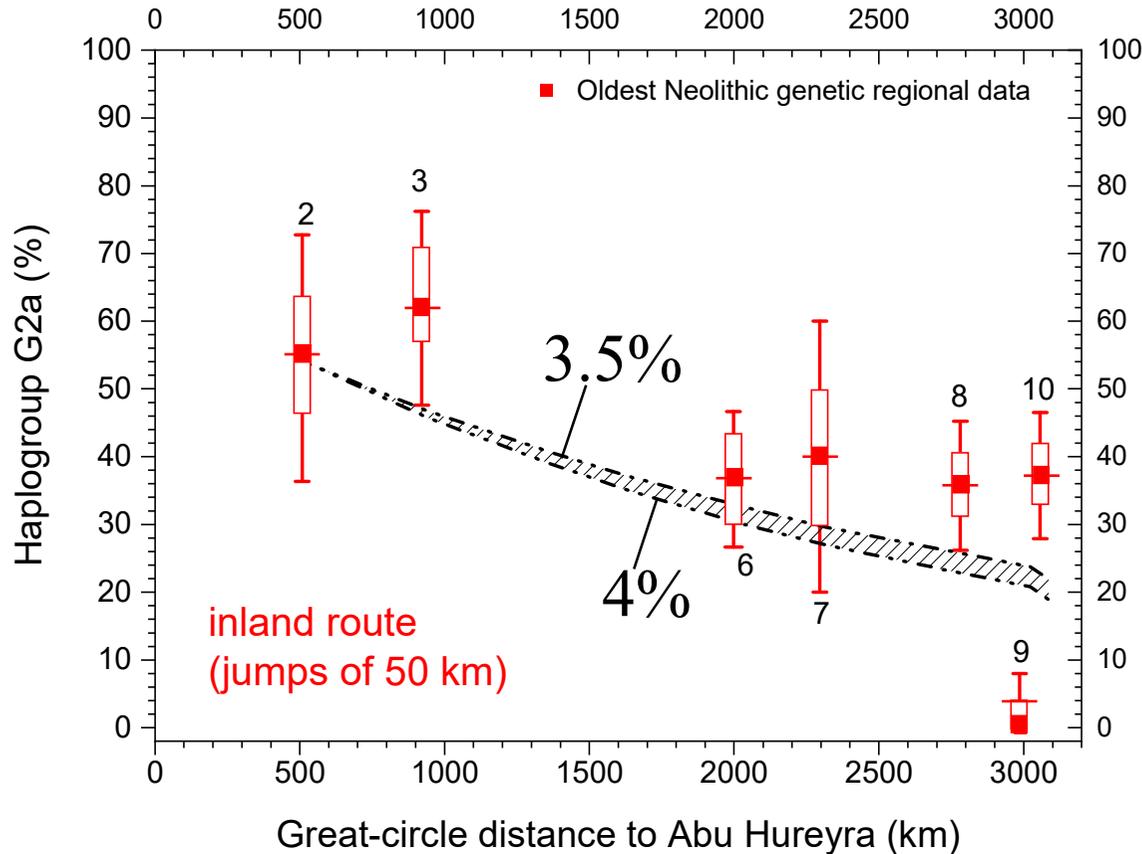
New results (unknown 1 year ago):

- Y chromosome
- whole genome

(next slides)

Y chromosome

Haplogroup G2a is the most frequent one in farmers.
It is essentially absent in hunter-gatherers

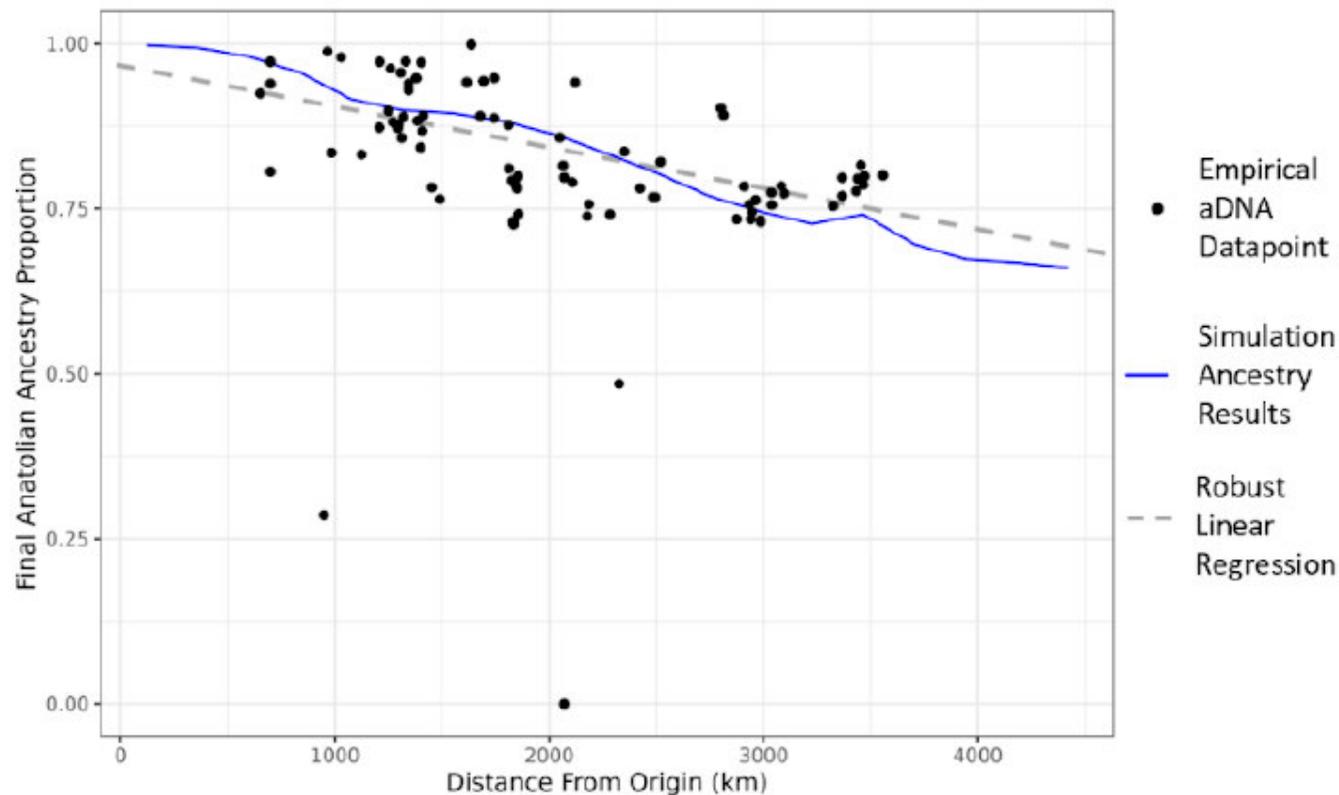


We obtain again ~3.5%, in agreement with the mt DNA results

For the sea route there are not enough data yet.

Fort & Pérez-Losada, *Nature Comm.* (2024)

Whole genome



LaPolice,
Williams
& Huber,
bioRxiv
(2024)

Blue line assumes that 0.1% of early farmers acculturated a HG per year, i.e. about $0.1\% \cdot 32 \text{ yr} = 3.2\%$ per generation.

This is consistent with our estimation that 1% - 8% of early farmers interbred with a HG or acculturated him/her.

Conclusiones de la 1ª parte

- B, R and M distances are reliable according to the data available.
- **Archaeology** implies that the percentage of early farmers who interbred with a HG or acculturated one of them was **between 0% and 40%**
- **Ancient DNA: 3 different kinds of data** (mtDNA, Y-chromosome and the whole genome) lead to the same result: **between 1% and 8%** of early farmers interbred with a HG or acculturated him/her.
- The range from **ancient DNA** is much more accurate than that from **Archaeology**.

2^a parte

· Ammerman & Cavalli-Sforza (1973): $s = 2\sqrt{aD}$ (demic).

No direct evidence of Neolithic cultural transmission.

· Fort & Méndez (1999): $s = \frac{2\sqrt{aD}}{1 + \frac{aT}{2}}$ (demic).

No direct evidence of Neolithic cultural transmission.

· What is the situation today?

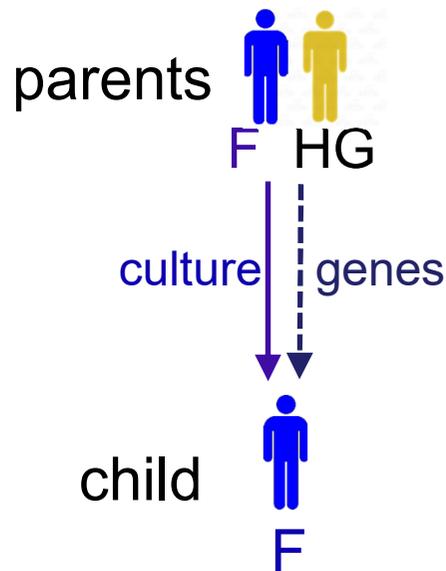
Ancient DNA has yielded direct evidence of cultural transmission.

We review it in the next slides.

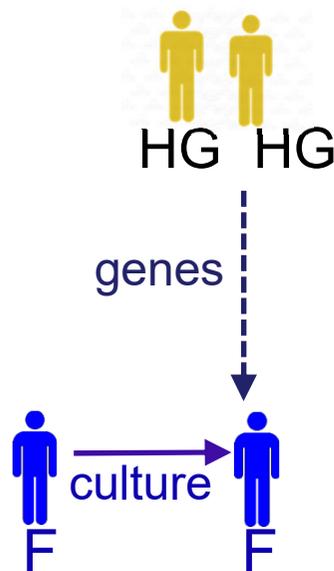
Cultural transmission

3 types

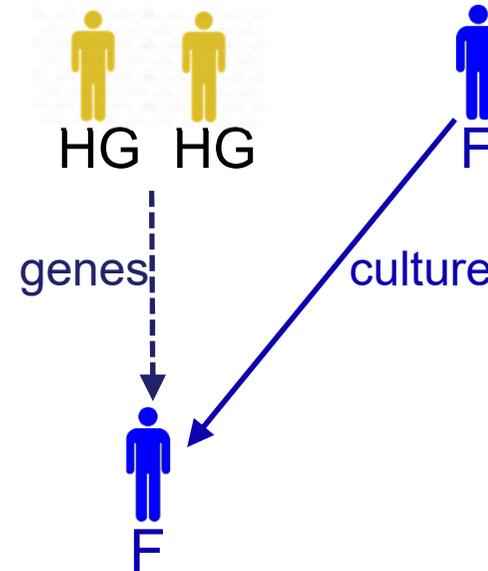
1) vertical
[interbreeding]



2) horizontal
[acculturation]



3) oblique
[acculturation]

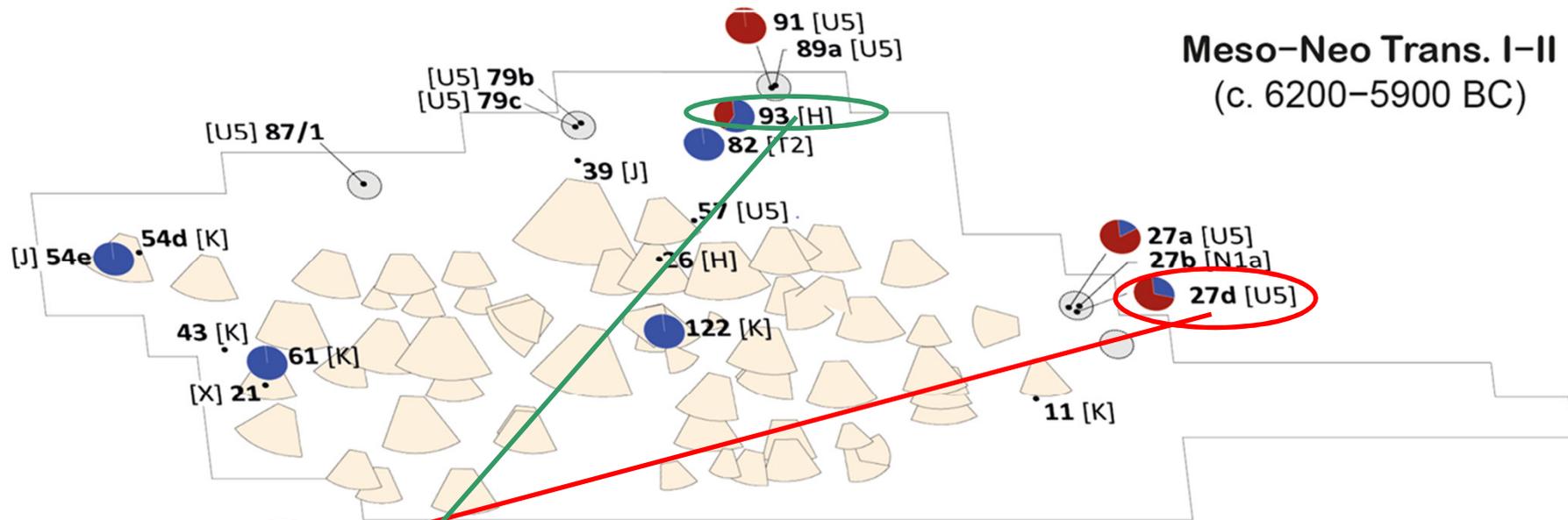


Cavalli-Sforza & Feldman, *Cultural transmission and evolution*, Princeton Univ. Press (1981). **Then no direct evidence of Neolithic cultural transmission.**

In the next 2 slides, we will see that today we have such direct evidence.

Vertical cultural transmission

Brami, ..., & Burger, Was the fishing village of Lepenski Vir [Serbia] built by Europe's first farmers? *J. World Prehist.* (2022)



- Individual 27d has 75% HG ancestry and 25% Aegean ancestry on the autosomes, so he had 1 genetically Aegean and 3 HG grandparents.”
- Individual 93 had 1 genetically HG and 3 Aegean grandparents (Hofmanová et al., bioRxiv 2022).

In both cases, there is an admixed parent, who was son/daughter of a genetically HG and a genetically Aegean.

This is direct evidence for interbreeding (vertical transmission).

Horizontal cultural transmission

A HGs that became a farmer: Vittrup (Denmark)

~30 year-old male. Violent death: 8 impacts in the cranium.

Genomically different from farmers (Funnel Beaker) and closely related to HGs from Norway and Sweden (Pitted ware).

Isotopic analyses demonstrate a fisher-hunter way of life in his childhood and a diet typical of farmers later on.

A dietary isotopic transect of one of his teeth shows that the transfer between societies of foragers and farmers took place before 9-12 years. The distance covered was >75 km by sea.

Fischer et al., Vittrup Man-the life-history of a genetic foreigner in Neolithic Denmark. *PLoS One* (2024).

Another HG that became a farmer: Svinninge Vejle (Denmark)

Allentoft et al., Population genomics of post-glacial western Eurasia. *Nature* (2024).

This is direct evidence for acculturation (oblique/horiz. transmission). 21