The Role of Migration in Cultural Changes during the Chalcolithic period in the Levant

Éadaoin Harney[*1], Hila May[*2], Israel Hershkovitz[2], Dina Shalem[3], Nadin Rohland[4], Swapan Mallick[4], Iosif Lazaridis[4], Nick Patterson[4,5] and David Reich[4,5,6]
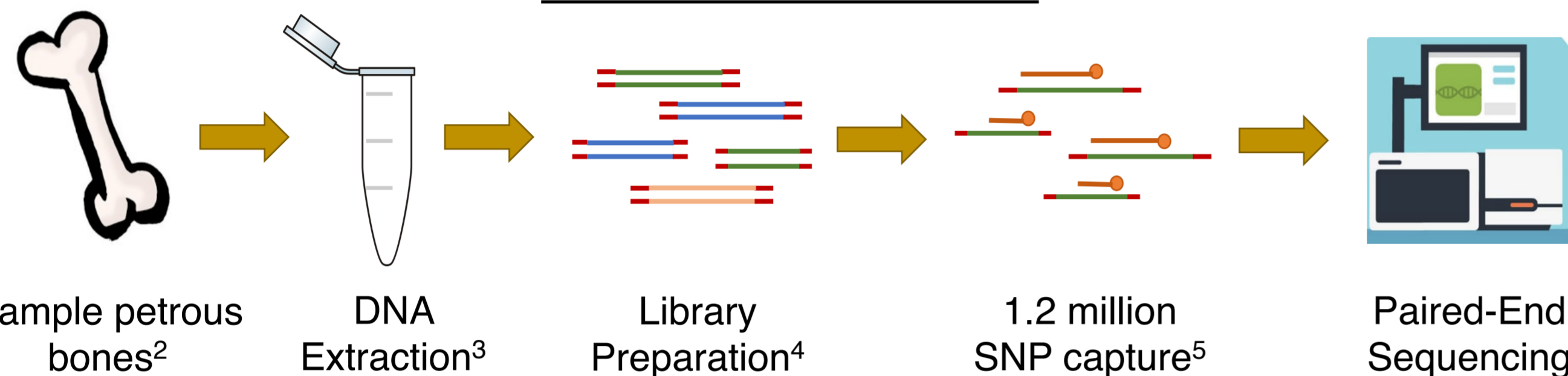
[1]Organismic and Evolutionary Biology, Harvard University [2]Anatomy and Anthropology, Tel Aviv University [3]The Institute for Galilean Archaeology [4]Genetics, Harvard University [6]Howard Hughes Medical Institute

Background and Aims

We report on the genetic history of a Chalcolithic population from Peqi'in Cave in Northern Israel, dating to 4,500-3,500 BCE. Archaeological excavations at Peqi'in Cave revealed dozens of large ossuaries, containing an estimated total of 600-1,000 individuals[1]. A number of the artifacts in Peqi'in are unique to this site, but there are also similarities in the artifact styles to contemporary and earlier cultures from Anatolia and Iran, and differences from earlier Levantine sites. This study aims to:

- **Determine the genetic relationships between the individuals buried in Peqi'in Cave and other ancient groups.**
- **Test the hypothesis that the Chalcolithic culture of the Levant may have been affected by movements of people from outside the region.**


Sampling locations for all data

Peqi'in Cave, Israel

Artifacts from Peqi'in Cave

Data Generation

Sample petrous bones[2] → DNA Extraction[3] → Library Preparation[4] → 1.2 million SNP capture[5] → Paired-End Sequencing

Ancient DNA data from 22 individuals from Peqi'in Cave was recovered.
- Population name: Levant_ChL
- Average of 0.65x coverage & 340,047 SNPs hit at least once
- 1 sample excluded due to IBD
- Combined with the dataset from [6]

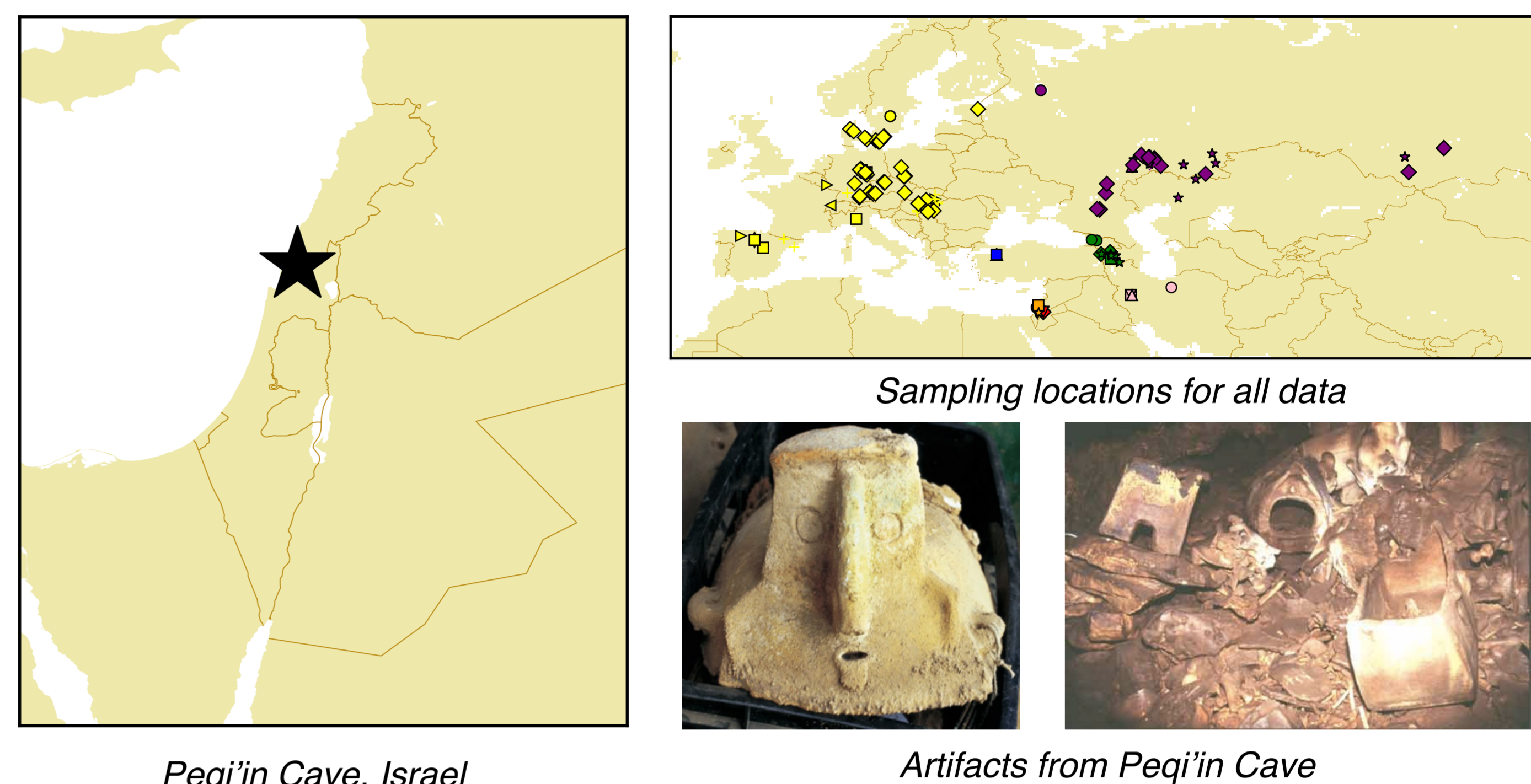## PCA shows Levant_ChL falls on genetic cline
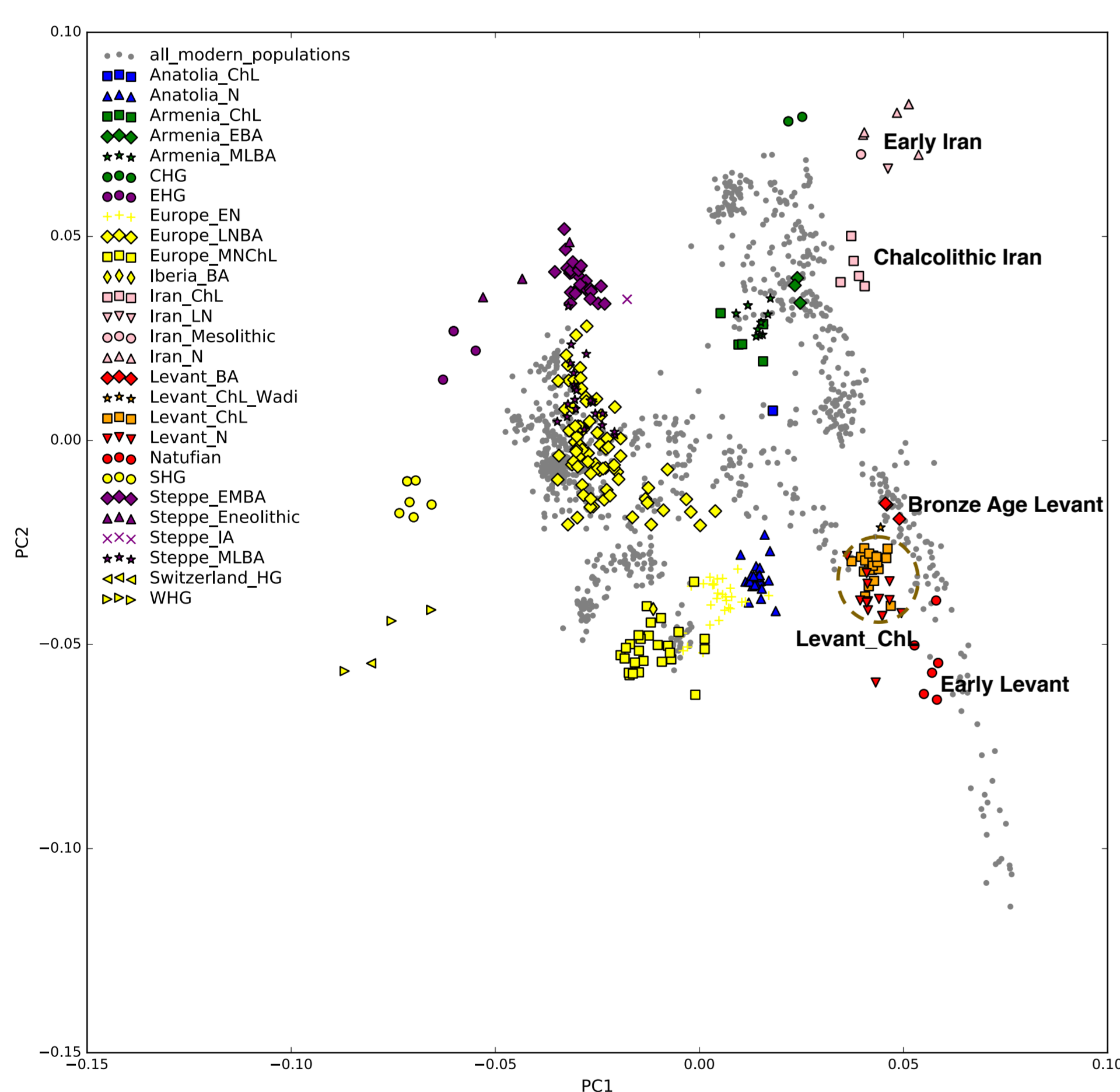
Levant_ChL falls along a gradient of populations from Early Levant to Early Iran. This may reflect an admixture event, as the Levant Bronze Age (Levant_BA) has been shown to be admixed between Levant Neolithic (Levant_N) and Iran Chalcolithic (Iran_ChL) like populations[6].

f-statistics indicate Levant_ChL is admixed
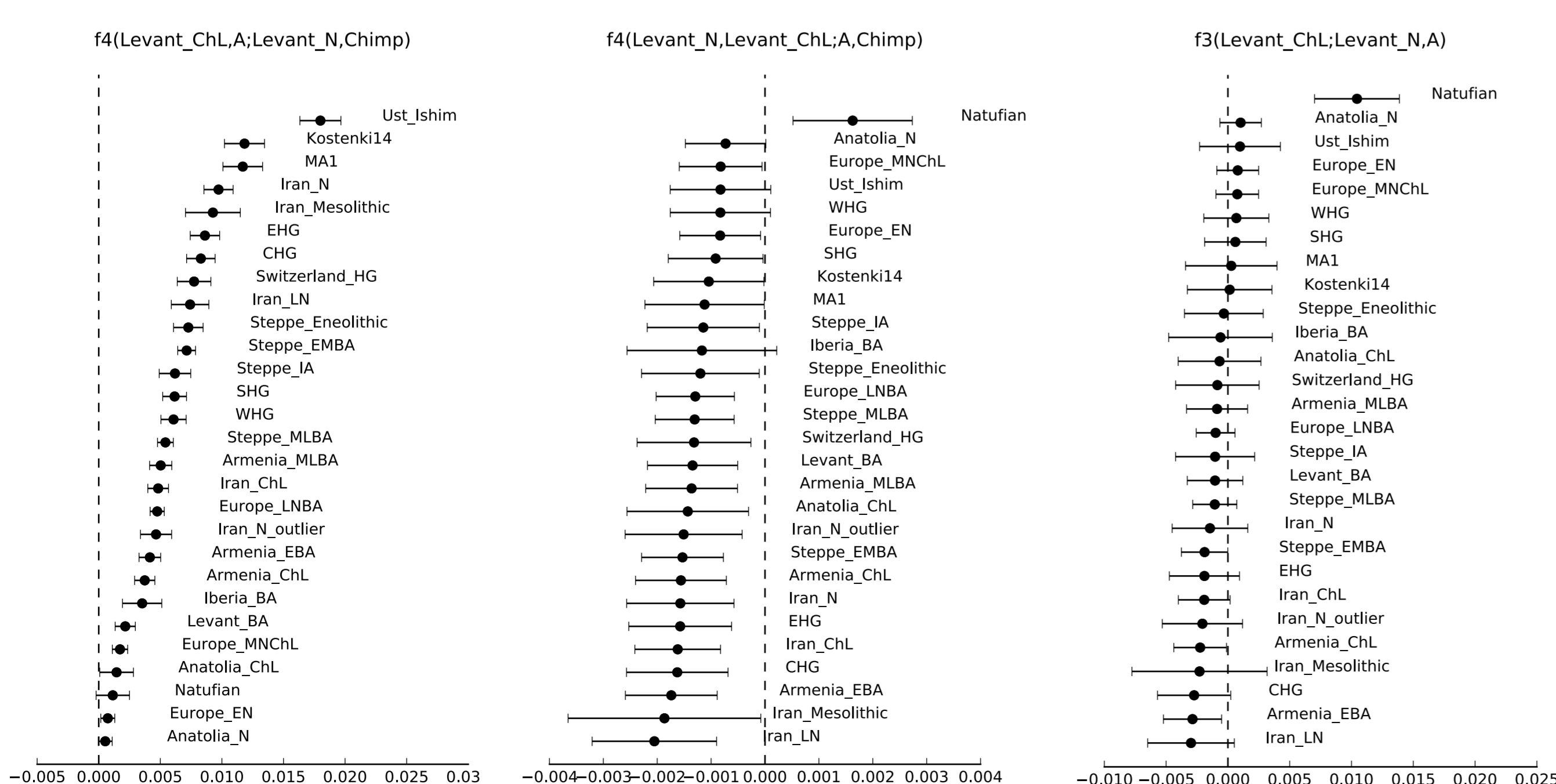
f_4-statistics indicate that Levant_ChL and Levant_N are closely related (left), but that Levant_ChL possesses additional ancestry related to non-Levantine populations (middle). Negative f_3-statistics confirm that Levant_ChL is admixed (right).
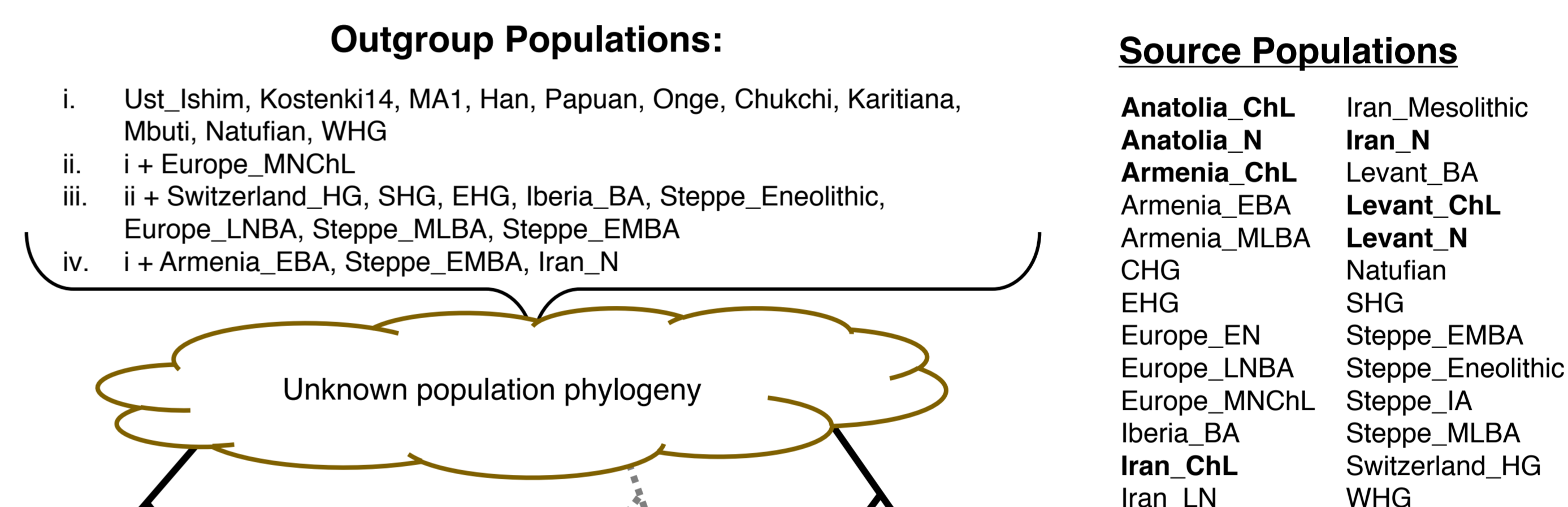
qpAdm identifies plausible admixture models

qpAdm is used to identify plausible admixture models and estimate admixture proportions for Levant_ChL. Additionally, we attempt to model the Levant_BA population as descended from Levant_ChL.

Outgroup Populations:
i. Ust_Ishim, Kostenki14, MA1, Han, Papuan, Onge, Chukchi, Karitiana, Mbuti, Natufian, WHG
ii. i + Europe_MNChL
iii. ii + Switzerland_HG, SHG, EHG, Iberia_BA, Steppe_Eneolithic, Europe_LNBA, Steppe_MLBA, Steppe_EMBA
iv. i + Armenia_EBA, Steppe_EMBA, Iran_N

Source Populations

Anatolia_ChL	Iran_Mesolithic
Anatolia_N	**Iran_N**
Armenia_ChL	Levant_BA
Armenia_EBA	**Levant_ChL**
Armenia_MLBA	**Levant_N**
CHG	Natufian
EHG	SHG
Europe_EN	Steppe_EMBA
Europe_LNBA	Steppe_Eneolithic
Europe_MNChL	Steppe_IA
Iberia_BA	Steppe_MLBA
Iran_ChL	Switzerland_HG
Iran_LN	WHG

*For 3-way admixture models, source population combinations are restricted to those that contain at least 2 bolded populations.

Unknown population phylogeny

Source Pop 1 — Target — Source Pop 3 — Source Pop 2

Target: Levant_ChL

Levant_ChL is modeled as the result of a 2- or 3-way* admixture between all combinations source populations, with i outgroup populations

Target	Source 1	Source 2	Source 3	Outgroup Pops	p-value rank = 2	Source 1	Source 2	Source 3
Levant_ChL	Levant_N	Iran_ChL	Anatolia_N	i	0.0578	0.60±0.04	0.16±0.03	0.24±0.05
Levant_ChL	Levant_N	Iran_ChL	Anatolia_N	ii	0.087742	0.60±0.03	0.16±0.03	0.25±0.03
Levant_ChL	**Levant_N**	**Iran_ChL**	**Anatolia_N**	iii	0.181919	0.58±0.03	0.17±0.02	0.25±0.03
Levant_ChL	Levant_N	Iran_ChL	Europe_EN	i	0.079538	0.64±0.03	0.19±0.03	0.17±0.03
Levant_ChL	Levant_N	Iran_ChL	Europe_EN	ii	0.044794	0.64±0.03	0.16±0.02	0.20±0.03

2-way models: all rejected
3-way models: 2 plausible
- Additional outgroups are included to identify best model

Target: Levant_BA

Levant_BA is modeled as the result of a 2-way admixture between either Levant_N or Levant_ChL and another source, with i outgroup populations.

Target	Source 1	Source 2	Outgroup Pops	p-value rank=1	Source 1	Source 2
Levant_BA	Levant_N	Iran_ChL	i	0.987662	0.55±0.03	0.451±0.03
Levant_BA	**Levant_N**	**Iran_ChL**	iv	0.513973	0.57±0.03	0.43±0.03
Levant_BA	Levant_ChL	Iran_ChL	i	0.238498	0.71±0.04	0.29±0.04
Levant_BA	Levant_ChL	Iran_ChL	iv	0.014983	0.73±0.03	0.27±0.03

Best plausible model for each case shown
- Inclusion of additional outgroups excludes all Levant_ChL models

qpWave supports 3 sources of ancestry in the Levant

qpWave is applied to determine the number of source populations required to model Levant_N, Levant_ChL, and Levant_BA with i outgroups

rank	DoF	χ^2	p-value
0	20	199.278	0.000
1	9	35.155	0.000
2	0	0.000	1.000

A minimum of three source populations (rank = 2) are required

Conclusions

We find that the individuals from Peqi'in derive ~58% of their ancestry from populations related to those of the local Levant Neolithic, ~17% from populations related to the Iran Chalcolithic, and ~25% related to the Anatolian Neolithic, supporting the hypothesis that this population was formed in part by migration from the North. We show that population turnover continued after the Chalcolithic, as the population from Peqi'in did not contribute to later Levantine populations from the Bronze Age.

References

(1) Gal et al., *Atiqot*, **1999**, 37(1):16   (2) Pinhasi et al., *PLOS ONE*, **2015**, 10(6)   (3) Dabney et al., *PNAS*, **2013**, 110(39):15758-15763   (4) Rohland et al., *Phil. Trans. R. Soc.* B, **2015**, 370(1660):20130624   (5) Mathieson et al., *Nature*, **2016**, 528(7583):499-503   (6) Lazaridis et al., *Nature*, **2016**, 536.7617:419-424