

1 Genetics and material culture support repeated expansions into 2 Paleolithic Eurasia from a population hub out of Africa

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10 Abstract

11 The population dynamics that followed the out of Africa expansion (OoA) and the
12 whereabouts of the early migrants before the differentiation that ultimately led to the
13 formation of Oceanian, West and East Eurasian macro populations have long been debated.
14 Shedding light on these events may, in turn, provide clues to better understand cultural
15 evolution in Eurasia between 50kya and 35kya.

16 Here we analyze Eurasian Paleolithic DNA evidence to provide a comprehensive population
17 model and validate it in light of available material culture. Leveraging on our integrated
18 approach we propose the existence of a Eurasian population Hub, where *Homo sapiens*
19 lived between the OoA and the broader colonization of Eurasia, which was characterized by
20 multiple events of expansion and local extinction. A major population wave out of Hub, of
21 which Ust'Ishim, Bacho Kiro and Tianyuan are unadmixed representatives, is broadly
22 associated with Initial Upper Paleolithic lithics and populated West and East Eurasia before
23 or around 45 kya, before getting largely extinct in Europe. In this light, we suggest a
24 parsimonious placement of Oase1 as an individual related to Bacho Kiro who experienced
25 additional Neanderthal introgression. Another expansion, started before 38 kya, is broadly
26 associated with Upper Paleolithic industries and repopulated Europe with sporadic
27 admixtures with the previous wave (GoyetQ116-1) and more systematic ones while moving
28 through Siberia (Yana, Mal'ta).

29 Introduction

30 Several layers of genetic, palaeoanthropology and palaeoclimatology evidence point to 70-
31 60 kya as the most likely time window for the major colonization of Eurasia by *Homo*
32 *sapiens*. For several millennia, however, the human population Out of Africa (OoA) did not
33 expand much from a demographic perspective, with the divergence between Eastern and
34 Western Eurasian populations inferred not earlier than 45-40 kya ago from modern DNA
35 data(Bergström et al., 2020; Choin et al., 2021; Malaspinas et al., 2016; Pagani et al., 2015,
36 2016; Schiffels & Durbin, 2014; Soares et al., 2012). We can imagine that, after leaving
37 Africa(Pagani, 2019), the ancestors of all non Africans lived somewhere on the new
38 continent, interbred with Neanderthals(Green et al., 2010) and persisted as a single
39 population for at least 15 thousand years (conservatively, the time between the OoA
40 bottleneck and the split between European and East Asian populations, marking the
41 beginning of a broader expansion) and later expanded from this “population Hub” ultimately

42 colonizing all of Eurasia and further.
43 Disentangling the processes underlying population and technological shifts between ~50 kya
44 and ~35 kya during the broader colonization of Eurasia is critical to explain the shaping of
45 current *H. sapiens* genetic diversity out of Africa, and to understand if cultural change
46 documented in the archaeological record can be attributed to population movements, human
47 interactions, convergence or any intermediate mechanism of biocultural exchange. This time
48 interval is characterised by the appearance and turnover of several techno-complexes
49 which, based on technological characteristics, we divide into: i) production of blades using
50 volumetric and levallois methods here extensively defined as Initial Upper Paleolithic (IUP)
51 (E. Boëda et al., 2013; Kuhn, 2019; Kuhn & Zwyns, 2014) ; ii) lithic industries characterized
52 by the production of blades and bladelets often together with ornaments and bone tools and
53 here inclusively defined as Upper Paleolithic (UP) ; iii) non-Mousterian and non-IUP
54 technologies appeared during the Middle to Upper Palaeolithic transition, comprising
55 Uluzzian, Châtelperronian, Szeletian and Lincombian-Ranisian-Jermanowician (LRJ) (see
56 Supplementary Section 1 for an in-depth definition of these material culture labels). Only a
57 few contexts present with both material culture and stratigraphically related human remains
58 for which aDNA is available (Table 1, Table S1), which leads to many possible scenarios of
59 association between cultural change and human migration, as well as with inter- and intra-
60 specific human interaction.

61 From a genetic perspective, two recent studies found that around 45 kya, nearby European
62 territories were occupied by either a human population basal to all Eurasians: Zlatý
63 Kůň(Prüfer et al., 2021), or by a human population that is closer to ancient and
64 contemporary East Asians than to later and contemporary Europeans(Hajdinjak et al., 2021),
65 which triggers the question of where and how the European component, later represented by
66 Kostenki14 (38 kya), differentiated after separating from East Asians.

67 **Table 1** Summary of Paleolithic individuals used for qpGraph modeling, see table S1 for full details

Sample	Techno-complex	Country	Date(kya)	Reference
Zlatý Kůň	Szeletian/IUP ^a	Czech Republic	>45	(Prüfer et al., 2021)
Ust'Ishim	IUP ^a	Russia	45	(Fu et al., 2014)
Bacho Kiro	IUP	Bulgaria	45	(Hajdinjak et al., 2021)
Oase1	IUP/UP ^a	Romania	40	(Fu et al., 2015)
Tianyuan	IUP ^a	China	40	(Yang et al., 2017)
Kostenki14	UP ^a	Russia	38	(Fu et al., 2016)
GoyetQ116-1	UP ^a	Belgium	35	(Fu et al., 2016)
Sunghir	UP	Russia	34	(Sikora et al., 2017)
Yana	UP	Russia	32	(Sikora et al., 2019)
Mal'ta	UP	Russia	24	(Raghavan et al., 2014)

68 a: attribution based on nearby coeval sites

69 **Results**

70 We used Treemix(Pickrell & Pritchard, 2012) for a preliminary, unsupervised exploration of
71 the genetic relationships among the crucial samples listed in Table 1 and, after adding up to
72 5 admixture events we found that it fails in identifying well known events such as the
73 Neanderthal admixture shared by all Eurasians that is instead monopolized by Bacho Kiro,
74 and noted high residuals in any solution offered by this method (results not shown). Despite
75 known limitations involved in its reliance on initial topologies based on the operator's
76 assumptions, we resorted to qpGraph (Supplementary Section 2), implementing the simple
77 population tree proposed by Prüfer and colleagues(Prüfer et al., 2021) and proceeded
78 step-wise to minimize the aforementioned issues. We tried to add Bacho Kiro in all plausible
79 positions without invoking additional admixture events, with the exception of the extra
80 Neanderthal introgression already documented for the Bacho Kiro samples(Hajdinjak et al.,
81 2021) (Figure S1, Supplementary Section 3). To allow the likely European Neanderthal
82 population that admixed with the ancestors of Bacho Kiro to be different from the
83 Neanderthal population that admixed with the ancestors of all non Africans shortly after the
84 Out of Africa, we modeled it as a different node closer to the Neanderthal from Vindija
85 (Croatia); if it was indeed the same Neanderthal population the inferred drift between the two
86 nodes would be 0. Additionally, to avoid our results to be driven by later population
87 interaction between Eurasia and Western Africa(Chen et al., 2020) or by the putative
88 admixture of Mbuti pygmies with an archaic ghost hominin(Hammer et al., 2011; Hsieh et al.,
89 2016; Lipson et al., 2020) we used four ancient South African hunter-gatherers(Schlebusch
90 et al., 2017; Skoglund et al., 2017) (Table S1) instead of Mbuti, and found the best
91 placement of Bacho Kiro as a sister group of Tianyuan (Figure S1.C, Supplementary Section
92 3.2). This placement is different from the one proposed by(Hajdinjak et al., 2021) and we
93 found little support for a model placing Bacho Kiro as an early branch among the Out of
94 Africa lineage (Figure S1.A) when immediately accounting for its higher Neanderthal
95 ancestry, possibly also thanks to the availability of Zlatý Kůň, who may provide a good
96 guidance to the basal OoA genetic landscape. After adding Kostenki14 as a key ancient
97 European sample, we found that Ust'Ishim would fit better as a basal split along the branch
98 leading to Tianyuan and Bacho Kiro (Supplementary Section 3.3) (Figure S2).

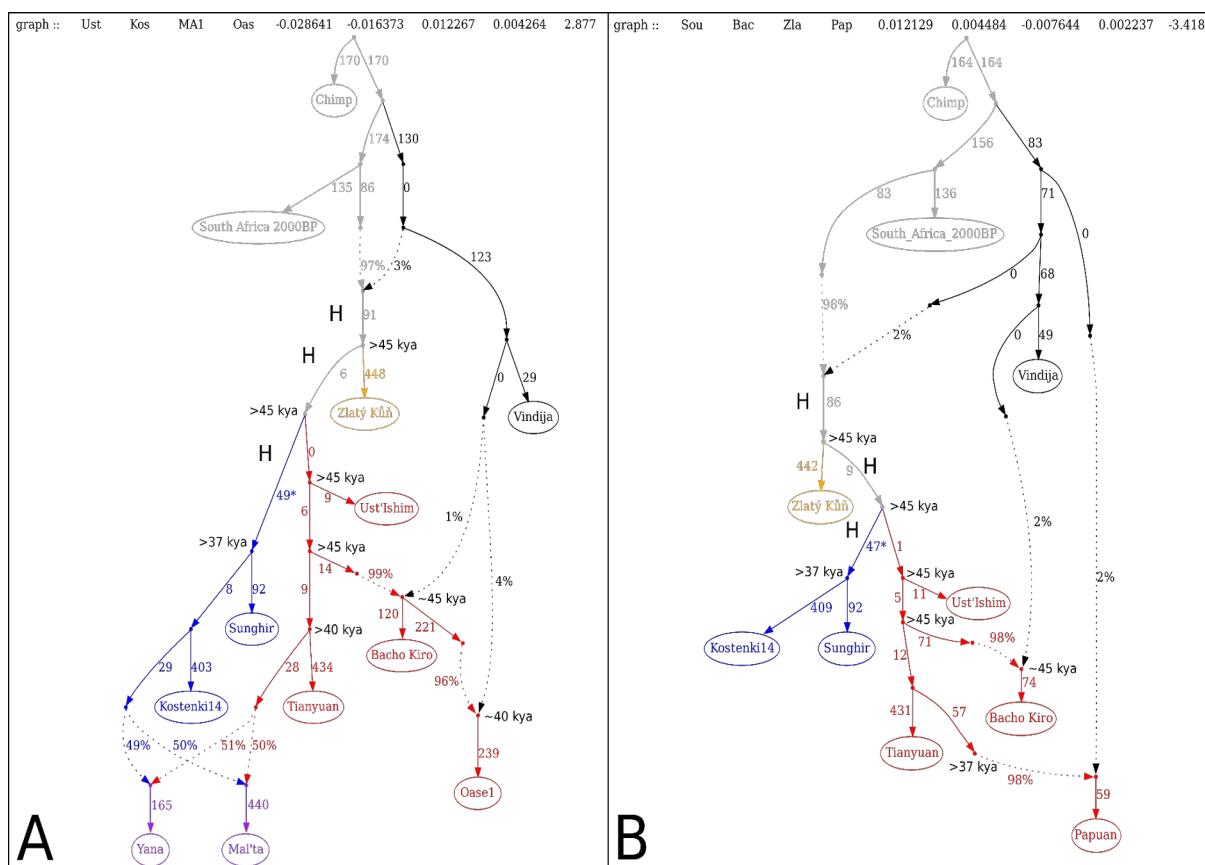
99 The scenario emerging from our proposed tree (Figure 1A, Figure S2.B) depicts Zlatý Kůň
100 as a population basal to all subsequent splits within Eurasia. Downstream of Zlatý Kůň, the
101 separation of Ust'Ishim and other genetically East Asian ancient samples (Bacho Kiro and
102 Tianyuan, red in Figure 1A) from the branch eventually leading to Kostenki and Sunghir
103 (genetically West Eurasians with a deep shared genetic drift - 49 units -, in blue in Figure 1A)
104 defines the first major subdivision of Eurasian genetic components. Although this represents
105 only one of several otherwise unexplored possible trees, its topology is broadly matched by
106 the spatiotemporal distribution of material cultural evidence at a cross-continental scale,
107 according to the present state of archaeological knowledge. From a chronological point of
108 view the right branch (red) of Figure 1A presents samples dated ~45/40 kya, while the left
109 (blue) one is instead characterised by a younger date of the Kostenki and Sunghir samples
110 (38 and 34 kya respectively). The structure emerging from genetic distances is also
111 supported and confirmed by technological evidence. The earlier, red branch is consistently
112 populated by contexts either directly showing or surrounded by geographic and temporal
113 proxies exhibiting IUP technology (Table S1, Table S2). The later, blue branch is instead
114 predominantly characterised by contexts with UP technology (Table S1, Table S2). Finally,
115 the basal Zlatý Kůň is coeval to Eastern European sites exhibiting Mousterian, non-
116 Mousterian and IUP technologies (Table S1, Table S3).

117 Notably, Oase1, which has so far been regarded as a lineage unrelated to extant
118 Eurasians(Fu et al., 2015), can be modeled as an additional admixture between the Bacho
119 Kiro population, or a closely related one, and Neanderthals (Figure 1A, Supplementary
120 Section 3.4). This result is coherent from a geographical and chronological perspective,
121 being Oase1 dated to around 5 ky later with respect to Bacho Kiro and being located just a
122 few hundred kilometers away. Incidentally, the proposed placement of Oase1 on the graph
123 provides support for the claim made in the original Oase1 publication(Fu et al., 2015) about
124 an additional pulse of Neanderthal admixture experienced by the Oase1 ancestors between
125 the one shared by all non Africans and the one that occurred 4-6 generations before it lived.
126 We here propose that such an event may be shared with the Bacho Kiro population or with a
127 closely related one, which could be seen as ancestral to Oase1. To rule out the possibility
128 that Oase1 attraction to Bacho Kiro is driven by the excess of Neanderthal ancestry they
129 share, we masked the most recent Neanderthal introgressed segments of Oase1 and re-run
130 the analysis: Oase1 holds its position and can be modeled without the last admixture event
131 with Neandethal hence confirming its genuine affinity with Bacho Kiro (Figure S3.D,
132 Supplementary section 3.4). Finally, this placement for Oase1 is consistent with the reported
133 East Asian genetic affinities for another sample from the same site (Oase2, Supplementary
134 Section 3.4).

135 Our model inferred by genetic data and supported by material culture, would then explain
136 Ust'Ishim as the result of early IUP movements towards Siberia(Nicolas Zwyns, 2021;
137 Nicolas Zwyns et al., 2019), and the presence of Bacho Kiro-like populations in Europe at
138 least from 45kya as part of a broader peopling event that reached as far East as Tianyuan
139 (40kya) with little or no interaction with pre-existing Zlatý Kůň-like groups (Figure S4,
140 Supplementary Section 3.5) but with occasional contacts with Neanderthals(Fu et al., 2015;
141 Hajdinjak et al., 2021). The UP branch in the model would have then emerged from a
142 putative OoA population Hub well after 45kya, a scenario that finds support in previous
143 hypotheses on the appearance of UP techno-complexes (e.g. Aurignacian) in Europe,
144 although the role of migrations and exchange between Europe, and Western Asia and the
145 Levant is still debated(Bataille et al., 2020; Conard, 2002; Davies, 2007; Falcucci et al.,
146 2020; Hessecker, 2009; Hublin, 2015; Le Brun-Ricalens et al., 2009; Mellars, 2006; Nigst et
147 al., 2014; Teyssandier, 2006; Zilhão, 2014) . The origin and spatiotemporal development of
148 later UP techno-complexes (e.g. Gravettian) are also still debated, and are currently
149 interpreted as the outcome of mixed processes involving regional adaptation, functional
150 convergence, and exchange between populations which took place in Europe(Kozłowski,
151 2015; Moreau, 2012; M. Otte, 2013; Marcel Otte, 2017; Pesesse, 2010) after the putative
152 split from the OoA hub. As far as Northern Asia is concerned, the UP legacy may be
153 responsible for the West Eurasian components already reported in ancient Siberian samples
154 dated between 34kya (Salkhit(Massilani et al., 2020)), 31kya (Yana1(Sikora et al., 2019))
155 and 24kya (Mal'ta(Raghavan et al., 2014)). Admixture events in varying proportions between
156 sister groups of Sunghir and Tianyuan can indeed explain this observation (Figure 1A,
157 purple leaves; Figure S5, Supplementary Section 3.6). This is further supported by the
158 younger chronology for these two sites which is compatible with a stepwise arrival of West
159 Eurasian components in Siberia following the UP exit from the Hub sometimes before 38
160 kya. The lack of West Eurasian components in Tianyuan and in subsequent East Asian
161 individuals may provide clues on the resistance of those groups to the incoming UP
162 population movements, or on subsequent re-expansion from a genetically IUP-like
163 population reservoir.

164 West Eurasian IUP populations, on the other hand, likely declined and ultimately
165 disappeared, as suggested by the fact that our population tree is compatible with the arrival
166 in Europe of UP groups who experienced no further admixture with pre-existing IUP or
167 Neanderthals, with the exception of GoyetQ116-1. The East Asian component carried by this
168 sample(Fu et al., 2016) can be described as an interaction between pre-existing Bacho Kiro-
169 like and incoming UP groups in West Europe with an additional Tianyuan-like component.
170 Such a variegated East Asian substrate found in the otherwise West Eurasian GoyetQ116-1
171 sample accounts for yet undescribed complexities within the IUP population branch (Figure
172 S6, Supplementary Section 3.7). Interestingly, the fate of the IUP populations in Europe
173 coincides with the extinction of the last Neanderthals(Hajdinjak et al., 2018).

174 Given the relatively simple population tree needed to explain the post OoA Eurasian
175 population movements using aDNA samples available to date, and benefiting from the basal
176 position of Zlatý Kůň, we tried to model Oceanian populations (using modern Papuans)
177 within the emerging picture to resolve a long lasting debate on their topological position with
178 respect to East and West Eurasians. Starting from the topologies proposed in(Choin et al.,
179 2021; Malaspinas et al., 2016) we first tried to place Papuans as the most basal branch
180 along the non-African sub-tree, allowing for the documented Denisova admixture(Meyer et
181 al., 2012; Reich et al., 2011). We avoided including the sampled Denisova aDNA within the
182 population tree to eliminate attractions from yet uncharacterized, deep splits along the
183 hominin branch(Hajdinjak et al., 2021), and opted for letting qpGraph infer Denisova as a
184 basal split along the archaic human lineage. Simply placing Papuans in a basal position
185 (either before or after the split of Zlatý Kůň) was rejected and highlighted a notable attraction
186 between them and Tianyuan. We then modelled Papuans as sister of Tianyuan (Figure 1.B,
187 Figure S7.A)(Wall, 2017), a solution that yielded only two marginal outliers that could be
188 resolved when taking all the SNPs into account (Supplementary Section 3.8). This topology
189 could be further improved when allowing for a contribution of a basal lineage, whose
190 magnitude decreased the deeper was its position along and beyond the OoA tree: 94% as
191 the ancestor of Bacho Kiro and Tianyuan (Figure S7.B) or 53% as the most basal IUP
192 lineage (Figure S7.C), 40% before the West/East Eurasia split (Figure S7.D), 2% before the
193 Zlatý Kůň lineage, along the OoA path (Figure S7.E) and 2% as an extinct OoA (xOoA,
194 Figure S7.F) as proposed by Pagani and colleagues(Pagani et al., 2016). Notably, all the
195 acceptable solutions for the placement of Papuans within the broader OoA tree encompass
196 a Denisova contribution and confirm Zlatý Kůň as the most basal human genome among the
197 ones ever found Out of Africa. Taken together with a lower bound of the final settlement of
198 Sahul at 37 kya (the date of the deepest population splits estimated by(Malaspinas et al.,
199 2016)) it is reasonable to describe Papuans as either an almost even mixture between East
200 Asians and a lineage basal to West and East Asians occurred sometimes between 45 and
201 38kya, or as a sister lineage of East Asians with or without a minor basal OoA or xOoA
202 contribution. We here chose to parsimoniously describe Papuans as a simple sister group of
203 Tianyuan, cautioning that this may be just one out of six equifinal possibilities.



204 **Figure 1** qpGraph models for Paleolithic Eurasia. **Panel A:** Best fit population model that
 205 recapitulates the major population streams from an Out of Africa hub, colored according to the most
 206 parsimonious lithic culture affiliation (Transitional complexes: yellow; Initial Upper Paleolithic, IUP: red;
 207 Upper Paleolithic, UP: blue). See Supplementary Sections 1 and 3 for more details on the qpGraph
 208 generation and on the material culture labels. The tree proposed here is based on 71539 SNPs due to
 209 the presence of Oase1, but its significance holds with a greater number of SNPs (302476) when
 210 Oase1 is removed (Figure S5.C). **Panel B:** Modern Papuans can be modelled as a terminal branch of
 211 the Paleolithic expansion that was associated with IUP in Eurasia. Such a model, based on 417400
 212 SNPs, is just one of the six acceptable possibilities we identified (Figure S7) and is reported here just
 213 on the basis of its parsimonious nature.
 214 Nodes labelled with "H" represent population differentiation inferred to have happened inside the
 215 population hub out of Africa. Asterisks indicate genetic drift putatively occurred inside the hub, which
 216 differentiates the West and East Eurasian genetic components.

217 **Discussion**

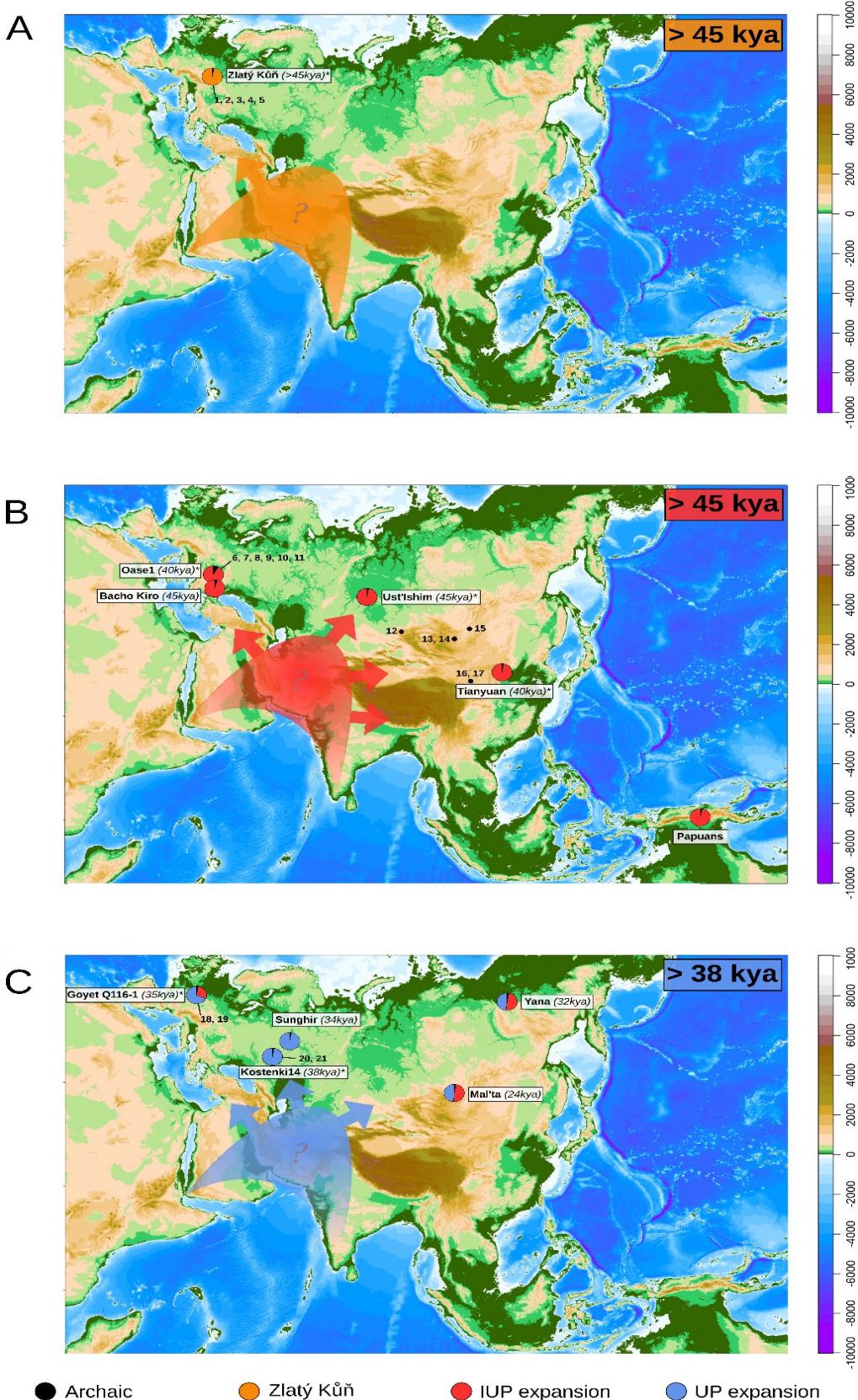
218 In conclusion, via introducing the concept of post OoA population Hub, our model provides a
219 robust, elegant and parsimonious framework to explain the relationships between the most
220 representative ancient human DNA available to date between 60 and 24kya across Eurasia,
221 which can be accommodated within just three expansions out of a putative OoA Hub (Figure
222 2, Supplementary Section 4). Zlatý Kůň may represent an early expansion, which left little to
223 no traces in subsequent Eurasians and occurred before or around 45kya (Figure 2A). We
224 speculate this population movement might be linked either to IUP(Richter et al., 2008;
225 Tostevin, 2003) or to non-Mousterian and non-IUP lithic techno-complexes that appeared in
226 Central and Eastern Europe between 48-44kya (e.g., Szeletian, LRJ)(Nejman et al., 2017;
227 Svoboda, 2000).

228 A subsequent expansion (linked to IUP in Eurasia) can be dated earlier than 45kya as
229 proposed by Zwyn and colleagues(Nicolas Zwyns et al., 2019), and here we propose it to be
230 a wider phenomenon that populated the broad geographic area between Mediterranean
231 Levant(Eric Boëda & Bonilauri, 2006; Kadowaki et al., 2021; Kuhn et al., 2009; Leder, 2017;
232 Marks & Kaufman, 1983), East Europe(Fewlass et al., 2020; Hublin et al., 2020; Richter et
233 al., 2008), Siberia-Mongolia(Derevianko et al., 2013; Kuhn, 2019; Rybin et al., 2020; N.
234 Zwyns et al., 2012; Nicolas Zwyns et al., 2019; N. Zwyns & Lbova, 2019) and East Asia(E.
235 Boëda et al., 2013; Morgan et al., 2014; Peng et al., 2020) in less than 5ky, reaching as far
236 South as Papua New Guinea before 38kya, and which eventually died out in Europe after
237 repeated admixtures with Neanderthals (Bacho Kiro and Oase1 being two notable
238 examples) (Figure 2.B). In Western Europe, in the same timeframe, this interaction has been
239 suggested as a trigger for the development of Chatelperronian material culture(Roussel et
240 al., 2016), while the Uluzzian techno-complex in Mediterranean Europe may tentatively be
241 better explained by an additional, yet uncharacterized expansion from the Hub(Benazzi et
242 al., 2011; Marciani et al., 2020) although genomic data from Uluzzian strata is still lacking.
243 The Uluzzian technocomplex is indeed characterized by unprecedented versatility and
244 efficient management of production costs, considerably lower standardisation in design
245 compared to Mousterian industries, lower time and energy expenditure for initialisation and
246 management of volumes, and a much shorter response time to change in raw material or
247 environmental conditions(Arrighi, Marciani, et al., 2020; Collina et al., 2020; Marciani et al.,
248 2020; Moroni et al., 2013, 2018; Peresani et al., 2019; Riel-Salvatore, 2007, 2009, 2010;
249 Silvestrini et al., 2021). In addition, this technological change is linked to the appearance of
250 complementary tools(Haidle et al., 2015)^(Sano et al., 2019), innovations in hunting
251 strategies(Boscato & Crezzini, 2012; Romandini et al., 2020), and a shared package of
252 symbolic artefacts(Arrighi, Bortolini, et al., 2020; Arrighi, Moroni, et al., 2020). All these
253 almost unique and distinctive elements make it very difficult to infer heritable continuity with
254 local Mousterian material culture, or preferential technological proximity with any other
255 IUP/UP Eurasian technology, and support the hypothesis of an independent population
256 expansion.

257 The last major expansion needed to explain the observed data (UP) took place later than 45
258 kya and before 38kya and repopulated (Kostenki, Sunghir), or interacted with, pre-existing
259 human groups (GoyetQ116-1, Figure S6) in Europe, and admixed with members of the
260 previous IUP wave in Siberia (Yana, Mal'ta and perhaps Salkhit) as it moved East in the
261 subsequent 5-10kya (Figure 2.C). The split time between East and West Eurasians
262 estimated at ~40 kya(Malaspina et al., 2016) from modern genomes and the differentiation
263 of these two macro-populations can therefore be explained by the inferred timing of the IUP

264 exit from the Hub, followed by subsequent diversification within the Hub of the ancestors of
265 West Eurasians, later mitigated by ongoing cross-Eurasian gene flow. Importantly, the
266 qpGraph results that form the basis for this emerging picture describe only one of the many
267 possible arrangements of the genetic data we explored and, by itself, it shouldn't be
268 interpreted as the only or best outcome. Remarkably though, the arrangement described
269 here matches and simplifies scenarios inferred from material culture evidence, and provides
270 a framework for placing genetic and cultural data onto a coherent landscape.

271 In this paper, we used extensive cultural categories that are in agreement with the demic
272 movements at the present, coarse scale of analysis. The general trends observed here
273 emerge from a broad perspective, and further work is needed to test specific hypotheses
274 concerning actual processes of branching, local adaptation, cultural transmission and
275 convergence(Groucutt, 2020; Kuhn, 2019). Similarly, we remain oblivious about the precise
276 location of the inferred population Hub, although North Africa or West Asia seem the most
277 plausible candidates. More ancient genomes are needed, as well as a better understanding
278 of the role of South and SouthEast Asia, for which currently known material culture suggests
279 complex trajectories(Allen & O'Connell, 2014; Bird et al., 2019; Bradshaw et al., 2021;
280 Clarkson et al., 2017; Dennell & Petraglia, 2012; Michel et al., 2016; O'Connell et al., 2018;
281 Petraglia et al., 2010; Shackelford et al., 2018; Sun et al., 2021; Westaway et al., 2017).



282 **Figure 2** Subsequent expansions into Eurasia from a population hub out of Africa. **Panel A:** Zlatý Kůň
 283 can be described as a putative early expansion from the population formed after the major expansion
 284 Out of Africa and hybridization with Neanderthals, and could be linked with transitional cultures found
 285 in Europe 48-45 kya. **Panel B:** Representative samples dated between 45 kya and 40 kya across
 286 Eurasia can be ascribed to a population movement with uniform genetic features and material culture

287 consistent with an Initial Upper Palaeolithic affiliation and which can also explain Oase1 after allowing
288 for additional Neanderthal contributions; modern Papuans may be genetically seen as an extreme
289 extension of this movement. **Panel C:** following local genetic differentiation, a subsequent population
290 expansion could explain the genetic components found in ancient samples <38 kya which contain it in
291 unadmixed form (Kostenki14, Sunghir) or admixed with pre-existing IUP components (Goyet Q116-1,
292 Yana1, Mal'ta).

293 The dates at the top right of each map provide a lower bound, based on the C14 of the earliest
294 available sample for the inferred population wave.

295 * indicate sites for which material culture was not available in direct association. For these sites the
296 nearest spatio-temporal proxies were used, as indicated in Table S1. Numbers on the map refer to the
297 position of relevant proxies: 1: Szeleta (S); 2: Pod_Hradem (S); 3: Moravský_Krumlov_IV (S); 4:
298 Stranska_Skala_III-IIIC (IUP); 5: Brno-Bohunice (IUP); 6: Bacho_Kiro_IUP_layer_11 (IUP); 7:
299 Ořechov_IV_-Kabáty (IUP); 8: Brno-Bohunice (IUP); 9: Românesti-Dumbravita (UP); 10: Cosava
300 (UP); 11: Tincova (UP); 12: Kara_Bom_OH_5_OH6 (IUP); 13: Tolbor-4_layer_4-5-6 (IUP); 14: Tolbor-
301 16_layer_6 (IUP); 15: Kamenka_A (IUP); 16: Suindonggou_1 (IUP); 17: Suindonggou_2 (IUP); 18:
302 Maisières-Canal (UP); 19: Spy_Ossiferous_Horizon_2 (UP); 20: Kostenki_12_Vokov (UP); 21:
303 Kostenki_1 (UP).

304 **Material and Methods**

305 We downloaded the aligned sequences for the IUP Bacho Kiro individuals from the
306 European Nucleotide Archive (accession number [PRJEB39134](#)), and merged files from the
307 same individual. We clipped 3 bases off the ends of each read to avoid excess of aDNA
308 damage using trimBam (https://genome.sph.umich.edu/wiki/BamUtil:_trimBam) and then
309 generated pseudo-haploid calls with the genotype caller pileupCaller
310 (<https://github.com/stschiff/sequenceTools/tree/master/src-pileupCaller>) using the
311 majorityCall option that, for each locus, either chooses the allele supported by the highest
312 number of reads or picks one randomly if the number is the same. Only positions with base
313 quality and read quality higher than 30 were considered. The processed Eigenstrat files of
314 the Zlatý Kůň individual were kindly provided by Prof. Cosimo Posth and Dr. He Yu.

315 We merged the files with the 1240K “Allen Ancient DNA Resource” v44.3 database
316 (<https://reich.hms.harvard.edu/allen-ancient-dna-resource-aadr-downloadable-genotypes-present-day-and-ancient-dna-data>)(Bergström et al., 2020; Skoglund et al., 2015), then kept
317 only autosomal SNPs (1,150,639) using Plink 1.9(Chang et al., 2015) and then converted
318 back to Eigenstrat format using Admixtools convertf(Patterson et al., 2012).
319

320 We ran Admixtools qpGraph(Patterson et al., 2012),
321 <https://github.com/DReichLab/AdmixTools>, qpGraph version: 7365) with the following
322 parameters: outpop: NULL, blgsize: 0.05, lsqmode: YES, diag: .0001, useallsnps: NO,
323 bigter: 6, forcezmode: YES, initmix: 10000, precision: .0001, zthresh: 3.0, terse: NO, hires:
324 YES.

325 **Data and Code Availability**

326 No new data or software was generated for this study. All software, lithic information and
327 genomes are publicly available from the published sources.
328 Allen ancient DNA resource data repository: <https://reich.hms.harvard.edu/allen-ancient-dna-resource-aadr-downloadable-genotypes-present-day-and-ancient-dna-data>
329

330 European Nucleotide Archive (accession numbers [PRJEB39134](#); [PRJEB39040](#))
331 Palaeoenvironmental data: <https://www.nciei.noaa.gov/>
332 Software: <https://github.com/DReichLab/AdmixTools>, qpGraph version: 7365

333 **Acknowledgements**

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345 **Competing interests**

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