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

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ABSTRACT

The population dynamics that followed the out of Africa expansion (OoA) and ultimately led to the formation of Oceanian, West and East Eurasian macro populations have long been debated [1–4]. Furthermore, with the OoA being dated between 70 kya [1,4,5] and 65 kya [6] and the earliest splits between West and East Eurasian populations being inferred not earlier than 43 kya from modern DNA data [1,4,7], an additional question concerns the whereabouts of the early migrants out of Africa before those differentiations.

Shedding light on these population dynamics may, in turn, provide clues to better understand cultural evolution in Eurasia between 50 kya and 35 kya, where the development of new technologies may be correlated to parallel independent evolution paths, to the arrival of new populations, or to long-term processes of cultural and biological exchanges.

Here we jointly re-analyze Eurasian Paleolithic DNA available to date in light of material culture, and provide a comprehensive population model with minimal admixture events. Our integrated approach i) maintains Zlatý Kůň genetically as the most basal out of Africa human lineage sequenced to date, also in comparison to Oceanians and putatively links it with non-Mousterian material cultures documented in Europe 48-43 kya; ii) infers the presence of an OoA population Hub from which a major wave broadly associated with Initial Upper Paleolithic lithic industries emanated to populate West and East Eurasia before or around 45 kya, and of which Ust'Ishim, Bacho Kiro and Tianyuan were unadmixed descendants; iii) proposes a parsimonious placement of Oase1 as an individual related to Bacho Kiro who experienced additional Neanderthal introgression; and iv) explains the East/West Eurasian population split as a longer permanence of the latter in the OoA Hub, followed by a second population expansion (before 37 kya), broadly associated with Upper Paleolithic industries, that largely

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replaced pre-existing humans in Europe, and admixed with the previous wave to form Yana and Mal'ta in Siberia and, to a greater extent, GoyetQ116-1 in Belgium.

Main Text

Disentangling the processes underlying population and technological shifts between ~50 kya and ~35 kya in Eurasia is critical to explain the formation of current *H. sapiens* macro populations and to understand if cultural change documented in the archaeological record can be attributed to population movements, human interactions, convergence or any intermediate mechanism of biocultural exchange. This time interval is characterised by the appearance and turnover of several techno-complexes which, based on technological characteristics we divide into: i) production of blades using volumetric and levallois methods here extensively defined as Initial Upper Paleolithic (IUP) [8–10] ; ii) lithic industries characterized by the production of blades and bladelets often together with ornaments and bone tools and here inclusively defined as Upper Paleolithic (UP) ; iii) non-Mousterian and non-IUP technologies appeared during the Middle to Upper Palaeolithic transition, comprising Uluzzian, Châtelperronian , Szeletian and Lincombian-Ranisian-Jermanowician (LRJ) (Supplementary Section 1). Only a few contexts present with both material culture and stratigraphically related human remains for which aDNA is available, which leads to many possible scenarios of association between cultural change and human migration, as well as with inter- and intra-specific human interaction.

From a genetic perspective, two recent studies found that around 45 kya, nearby European territories were occupied by either a human population basal to all Eurasians [11] or by a human population that is closer to ancient and contemporary East Asians than to later and contemporary Europeans [12], which triggers the question of where and how the European component, later represented by Kostenki14 (37 kya), differentiated after separating from East Asia. We then started (Supplementary Section **2**) with the simple population tree proposed by Prufer and colleagues [11] and tried to add Bacho Kiro in different positions without invoking additional admixture events, with the exception of the extra Neanderthal introgression already documented for the Bacho Kiro samples [12] (Figure S1, Supplementary Section 3). To allow the likely European Neanderthal population that admixed with the ancestors of Bacho Kiro to be different from the Neanderthal population that admixed with the ancestors of all non Africans shortly after the Out of Africa, we modeled it as a different node closer to the Neanderthal from Vindija (Croatia); if it was indeed the same Neanderthal population the inferred drift between the two nodes would be 0. Additionally, to avoid our results to be driven by later population interaction between Eurasia and Western Africa [13] or by the putative admixture of Mbuti pygmies with an archaic ghost hominin [14–16] we used four ancient South African hunter-gatherers [17,18] (Table S1) instead of Mbuti, and found the best placement of

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Bacho Kiro as a sister of Tianyuan (Figure S1.C, Supplementary Section 3.2). This placement is different from the one proposed by [12] and we speculate this may be due to the ready presence of Neanderthal at the initial stages of our qpGraph modelling or to the availability of Zlatý Kůň, who may provide a good guidance to the basal OoA genetic landscape. After adding Kostenki14 as a key ancient European sample, we found that Ust'Ishim would fit better as a basal split along the branch leading to Tianyuan and Bacho Kiro (Supplementary Section **3.3**) (Figure S2).

The scenario emerging from our proposed tree (Figure 1A, Figure S2.B) depicts Zlatý Kůň as a population basal to all subsequent splits within Eurasia. Downstream of Zlatý Kůň, the separation of Ust'Ishim and other ancient samples (Bacho Kiro and Tianyuan, genetically East Asians, in red in Figure 1A) from the branch eventually leading to Kostenki and Sunghir (genetically West Eurasians with a deep shared genetic drift - 49 units -, in blue in Figure 1A) defines the first major subdivision of Eurasian genetic components. Significantly, this structure is broadly matched by the spatiotemporal distribution of material cultural evidence at a cross-continental scale, according to the present state of archaeological knowledge. From a chronological point of view the right branch (red) of Figure 1A presents samples dated ~45/40 kya, while the left (blue) one is instead characterised by a younger date of the Kostenki and Sunghir samples (37 and 34 kya respectively). The structure emerging from genetic distances is also supported and confirmed by technological evidence. The earlier, red branch is consistently populated by contexts either directly showing or surrounded by geographic and temporal proxies exhibiting IUP technology (Table S1, Table S2). The later, blue branch is instead predominantly characterised by contexts with UP technology (Table S1, Table S2). Finally, the basal Zlatý Kůň is coeval to Eastern European sites exhibiting Mousterian, non-Mousterian and IUP technologies (Table S1, Table S3).

Notably, Oase1, which has so far been regarded as a lineage unrelated to extant Eurasians [19], can be modeled as an additional admixture between Bacho Kiro and Neanderthals (Figure 1A, Supplementary Section 3.4). This result is coherent from a geographical and chronological perspective, being Oase1 dated to around 5 ky later with respect to Bacho Kiro and being located just a few hundred kilometers away. Incidentally, the proposed placement of Oase1 on the graph provides support for the claim made in the original Oase1 publication [19] about an additional pulse of Neanderthal admixture experienced by the Oase1 ancestors between the one shared by all non Africans and the one that occurred 4-6 generations before it lived. We here propose that such an event may be shared with the Bacho Kiro population or with a closely related one, which could be seen as ancestral to Oase1. This is also consistent with the reported East Asian genetic affinities for another sample from the same site (Oase2, Supplementary Section 3.4).

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Our model would then explain Ust'Ishim as the result of early IUP movements towards Siberia [20], and the presence of Bacho Kiro-like populations in Europe at least from 45kya as part of a broader peopling event that reached as far East as Tianyuan (40kya) with little or no interaction with pre-existing Zlatý Kůň-like groups (Figure S4, Supplementary Section 3.5) but with occasional contacts with Neanderthals [12,19]. The UP branch in the model would have then emerged from a putative OoA Hub well after 45kya, a scenario that finds support in the previously hypothesised appearance of the UP techno-complexes in Europe (with specific reference to the Aurignacian) as at least partly triggered by migration rather than as local developments of pre-existing technologies [21–31]. As far as Northern Asia is concerned, the UP legacy may be responsible for the West Eurasian components already reported in ancient Siberian samples dated between 34kya (Salkhit, [32]), 31kya (Yana1, [33]) and 24kya (Mal'ta, [34]). Admixture events in varying proportions between sister groups of Sunghir and Tianyuan can indeed explain this observation (Figure 1A, purple leaves; Figure S5, Supplementary Section 3.6). This is further supported by the younger chronology for these two sites which is compatible with a stepwise arrival of West Eurasian components in Siberia following the UP exit from the Hub sometime before 37 kya. The lack of West Eurasian components in Tianyuan and in subsequent East Asian individuals may provide clues on the resistance of those groups to the incoming UP population movements, or on subsequent re-expansion from a genetically IUP-like population reservoir.

West Eurasian IUP populations, on the other hand, likely declined and ultimately disappeared, as suggested by the fact that our population tree is compatible with the arrival in Europe of UP groups who experienced no further admixture with pre-existing IUP or Neanderthals, with the exception of human groups like GoyetQ116-1. The East Asian component carried by this sample [35] can be described as an interaction between pre-existing Bacho Kiro-like and incoming UP groups in West Europe with an additional Tianyuan-like component. Such a variegated East Asian substrate found in the otherwise West Eurasian GoyetQ116-1 sample accounts for yet undescribed complexities within the IUP population branch (Figure S6, Supplementary Section 3.7).

Given the relatively simple population tree needed to explain the post OoA Eurasian population movements using aDNA samples available to date, and benefiting from the basal position of Zlatý Kůň, we tried to model Oceanian populations (modern Papuans) within the emerging picture to resolve a long lasting debate on their topological position with respect to East and West Eurasians. Starting from the topologies proposed in [1,2] we first tried to place Papuans as the most basal branch along the non-African sub-tree, allowing for the documented Denisova admixture [36,37]. We avoided including the sampled Denisova aDNA within the population tree to eliminate attractions from yet uncharacterized, deep splits along the hominin branch, and opted for a surrogate ghost split along the archaic human lineage.

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Simply placing Papuans in a basal position (either before or after the split of Zlatý Kůň) was rejected and highlighted a notable attraction between them and Tianyuan. We then modelled Papuans as sister of Tianyuan (Figure 1.B, Figure S7.A) [3], a solution that yielded only two marginal outliers that could be resolved when taking all the SNPs into account (Supplementary Section 3.8). This topology could be marginally improved when allowing for a contribution of a basal lineage, whose magnitude decreased the deeper was its position along and beyond the OoA tree: 94% as the ancestor of Bacho Kiro and Tianyuan (Figure S7.B) or 53% as the most basal IUP lineage (Figure S7.C), 40% before the West/East Eurasia split (Figure S7.D), 2% before the Zlatý Kůň lineage, along the OoA path (Figure S7.E) and 2% as an extinct OoA (xOoA, Figure S7.F) as proposed by Pagani and colleagues [7]. Notably, all the acceptable solutions for the placement of Papua within the broader OoA tree confirm Zlatý Kůň as the most basal human genome among the ones ever found Out of Africa. Taken together with a lower bound of the final settlement of Sahul at 37 kya (the date of the deepest population splits estimated by [1]) it is reasonable to describe Oceanians as either an almost even mixture between East Asians and a lineage basal to West and East Asians occurred sometimes between 45 and 37kya, or as a sister lineage of East Asians with or without a minor basal OoA or xOoA contribution. We here chose to parsimoniously describe Papuans as a simple sister group of Tianyuan, cautioning that this may be just one out of five equifinal possibilities.

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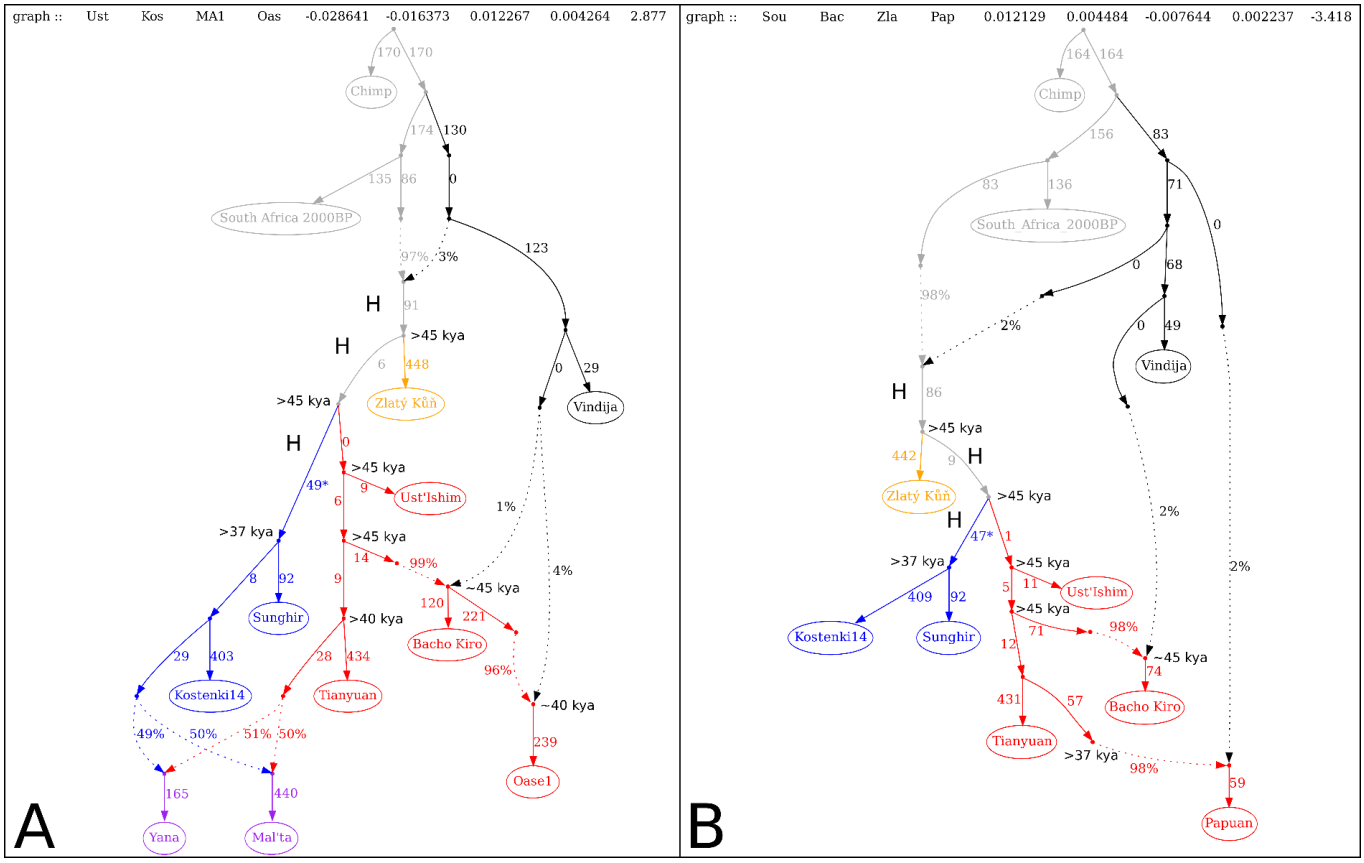

Figure 1 qpGraph models for Paleolithic Eurasia. **Panel A:** Best fit population model that recapitulates the major population streams from an Out of Africa hub, colored according to the most parsimonious lithic culture affiliation (Transitional complexes: yellow; Initial Upper Paleolithic, IUP: red; Upper Paleolithic, UP: blue). See Supplementary Sections 1 and 3 for more details on the qpGraph generation and on the material culture labels. **Panel B:** Modern Papuans can be modelled as a terminal branch of the Paleolithic expansion that was associated with IUP in Eurasia. Such a model is just one of the five equiprobable possibilities we identified (Figure S5) and is reported here just on the basis of its parsimonious nature.

Nodes labelled with "H" represent population differentiation inferred to have happened inside the population hub out of Africa. Asterisk indicate genetic drift putatively occurred inside the hub, which differentiates the West and East Eurasian genetic components.

In conclusion, via introducing the concept of post OoA population Hub, our model provides a robust, elegant and parsimonious framework to explain the relationships between the most representative ancient human DNA available to date between 60 and 24kya across Eurasia, which can be accommodated within just three expansions out of a putative OoA Hub (Figure 2, Supplementary Section 4). Zlatý Kůň may represent an early expansion, which left little to no traces in subsequent Eurasians and occurred before 45kya (Figure 2A). We speculate this population movement might be linked to non-Mousterian and non-IUP lithic techno-complexes that appeared in Central and Eastern Europe between 48-44kya (e.g., Szeletian, LRJ) [38,39]. A subsequent expansion (linked to IUP in Eurasia) can be dated to around

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45kya as proposed by Zwyn and colleagues [20], and here we propose it to be a wider phenomenon that populated the broad geographic area between Mediterranean Levant [40–44], East Europe [45–47], Siberia-Mongolia [10,20,48–51] and East Asia [9,52,53] in less than 5ky, reaching as far South as Oceania before 37kya, and which eventually died out in Europe after repeated admixtures with Neanderthals (Bacho Kiro and Oase1 being two notable examples) **(**Figure 2.B**)**. In Western Europe, in the same timeframe, this interaction has been suggested as a trigger for the development of Chatelperronian material culture [54], while the Uluzzian techno-complex in Mediterranean Europe might be better explained by an additional, yet uncharacterized expansion from the Hub [55,56].

The last major expansion needed to explain the observed data (UP) took place later than 45 kya and before 37kya and repopulated (Kostenki, Sunghir), or interacted with, pre-existing human groups (GoyetQ116-1, Figure S6) in Europe, and admixed with members of the previous wave in Siberia (Yana, Mal'ta and perhaps Salkhit) as it moved East in the subsequent 5-10kya (Figure 2.C). The split time between East and West Eurasians estimated at ~40 kya [1] from modern genomes and the differentiation of these two macro-populations can therefore be explained by the inferred timing of the IUP exit from the Hub, followed by subsequent diversification within the Hub of the ancestors of West Eurasians, later mitigated by ongoing cross-Eurasian gene flow.

In this paper, we used extensive cultural categories that are in agreement with the demic movements at the present, coarse scale of analysis. The general trends observed here emerge from a broad perspective, and further work is needed to test specific hypotheses concerning actual processes of branching, local adaptation, cultural transmission and convergence [10,57]. Similarly, we remain oblivious about the precise location of the inferred population Hub. More ancient genomes are needed, as well as a better understanding of the role of South and SouthEast Asia, for which currently known material culture suggests complex trajectories [58–68].

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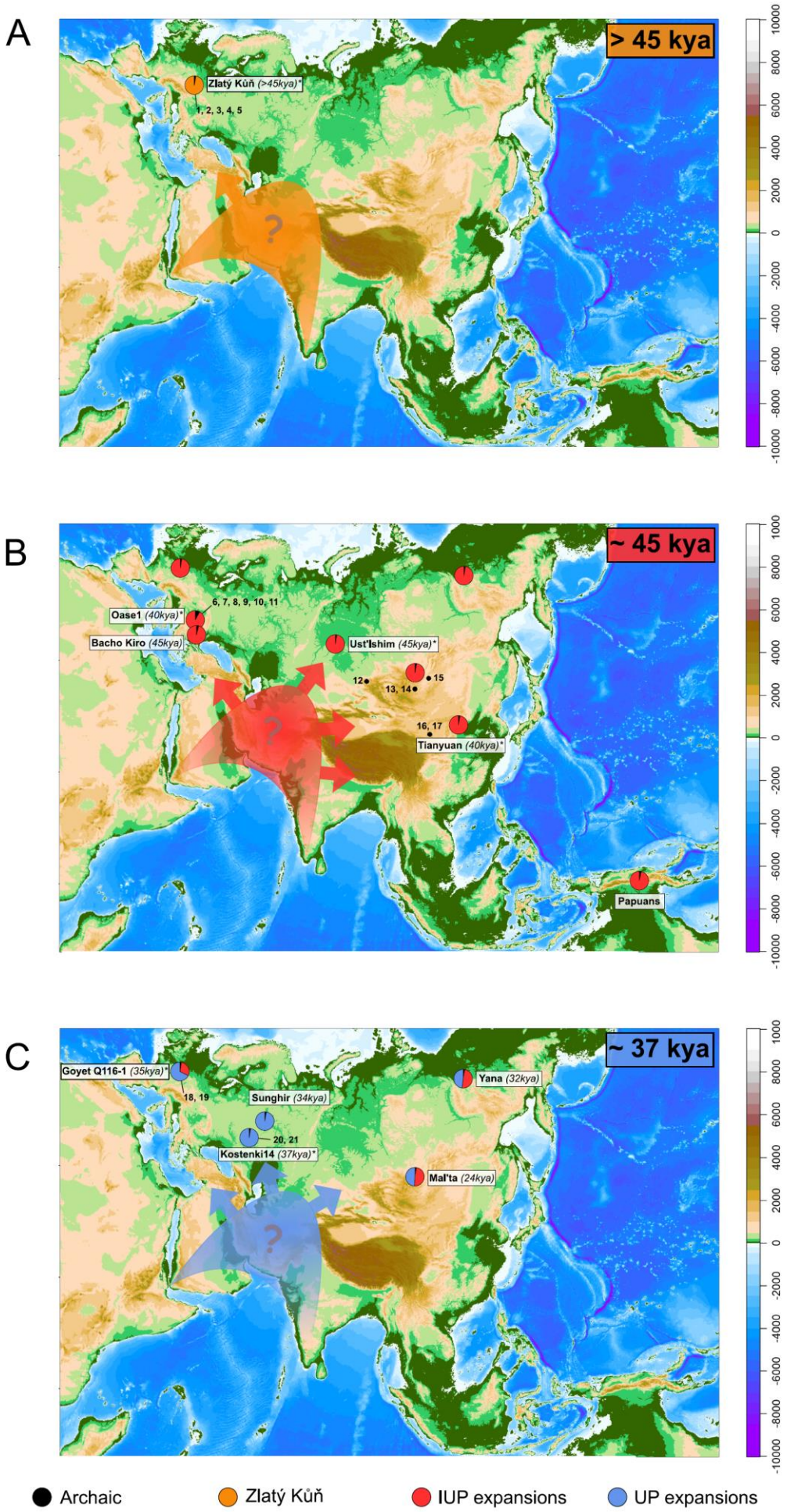

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Figure 2 Subsequent expansions into Eurasia from a population hub out of Africa. **Panel A**: Zlatý Kůň can be described as a putative early expansion from the population formed after the major expansion Out of Africa and hybridization with Neanderthals, and could be linked with transitional cultures found in Europe 48-45 kya. **Panel B:** Representative samples dated between 45 kya and 40 kya across Eurasia can be ascribed to a population movement with uniform genetic features and material culture consistent with an Initial Upper Palaeolithic affiliation and which can also explain Oase1 after allowing for additional Neanderthal contributions; modern Papuans may be genetically seen as an extreme extension of this movement. **Panel C:** following local genetic differentiation, a subsequent population expansion could explain the genetic components found in ancient samples <37kya which contain it in unadmixed form (Kostenki14, Sunghir) or admixed with pre-existing IUP components (Goyet Q116-1, Yana1, Mal'ta).

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

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

Data and Code Availability

No new data or software was generated for this study. All software, lithic information and genomes are publicly available from the published sources.

Allen ancient DNA resource data repository: https://reich.hms.harvard.edu/allen-ancient-dna-resource-aadr-downloadable-genotypes-present-day-and-ancient-dna-data

European Nucleotide Archive (accession numbers PRJEB39134**;** PRJEB39040)

Palaeoenvironmental data: https://www.ncei.noaa.gov/

Software: https://github.com/DReichLab/AdmixTools, qpGraph version: 7365

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Authors Contribution:

Conceptualization: L.V, L.P; Data Analyses: L.V., G.M, E.B, S.A.; Drafting of the manuscript: L.V., G.M, E.B, L.P.; Interpretation of Results: T.P, S.B., L.P.; Revision of the manuscript: all authors.

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