Biological Sciences; Ecology

Climatic niche shifts drove rapid expansion of Paleolithic Modern Humans

Giampoudakis K.[a,1], Marske K.A.[a], Borregaard M.K.[a] , Ugan A.[b,c], Singarayer J.[d], Valdes P.[e], Rahbek C.[a,f] & Nogués-Bravo D.[a]

a: Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, Universitetsparken 15, 2100 Copenhagen Ø, Denmark
b: Department of Anthropology, 270 S. 1400 East Room 102 ,University of Utah, Salt Lake City, UT 84112, USA
c: Far Western Anthropological Research Group, 2727 Del Rio Place, Davis, CA 95618, USA
d: Department of Meteorology, University of Reading, Earley Gate, Reading, RG6 6BB, UK
e: School of Geographical Sciences, University of Bristol, University Road, Clifton, Bristol BS8 1SS, UK
f: Imperial College London, Silwood Park Campus, Ascot, Berkshire SL5 7PY, UK

[1] *Corresponding author*: Konstantinos Giampoudakis, Universitetsparken 15, 2100 Copenhagen Ø, Denmark, +4581710568 *konstantinosg@snm.ku.dk*

Abstract

The routes by which Palearctic modern humans expanded their geographic ranges across Eurasia to colonize the Americas during the Late Pleistocene have been intensively analyzed. Whether this geographic expansion occurred as a result of tracking a specific set of favourable climatic conditions, or via concurrent colonization of novel climates, remains unclear. Analyses of the ecological niche linking archeological and paleoclimatic data revealed that Palearctic hunter-gatherers significantly altered their climatic niche during the last phase of the Late Pleistocene, colonizing novel climatic as well as geographic space between 46ka-26ka. In contrast, from 26ka-11ka, the climatic niche was more stable, even as humans dispersed to different geographic regions. This dispersal was facilitated by a persistent climatically suitable 'corridor' linking Western Europe to Far East Asia beginning 32ka, via a mid-latitude belt in South Siberia. Other areas with suitable climates over long periods included Kamchatka and regions of Beringia which are currently submerged. Niche dynamics were controlled by changes in seasonal water availability and Upper Paleolithic technological innovations associated with transitions between cultural periods.

Keywords: Late Pleistocene; modern humans; climatic niche; climatic refugia

Significance Statement

Humans have successfully colonized every continent except Antarctica and live in nearly every ecosystem, from the wet tropics to the high arctic. However, at some point in our history, our suvival was dependent upon a much more constrained set of climatic conditions. We explore how changes in the environmental conditions in which early humans were able to persist, as well as changes in cultural periods, facilitated human expansion through Eurasia during the Late Pleistocene. Using a unique framework that integrates paleo-information sources with macroecology we show that humans expanded their ability to survive in more diverse climatic conditions until ~26ka while afterwards tracked specific types of climates, probably due to the adverse conditions around the Last Glacial Maximum.

Introduction

Anatomically Modern Humans (AMHs), hereafter modern humans, are believed to have originated in Africa approximately 200ka (ka= thousand years ago). From there, they moved outward through Eurasia (~60ka) (but see 1), crossing to the Americas through Beringia by at least 15ka, and finally populating South America (2-4). The spread and colonization of modern humans throughout Europe and Asia occurred during a period of intense climate change, and these changing conditions may have driven humans to colonize new regions via specific dispersal routes (5-7).

Whereas the timing and routes of these dispersal events across geographical space have been intensively analysed and heavily disputed (1, 8-10) less is known about the niche dynamics of hunter-gatherers populations during this dispersal. A fundamental question is whether modern humans colonised novel climatic conditions as they expanded their geographic distribution, or tracked a specific set of climates in which they were able to persist. In comparison, the responses of other iconic glacial-era species to the climatic changes of this period are relatively well investigated. Macroecological approaches have successfully reconstructed the Late Pleistocene biogeography of numerous animal and plant species by quantifying species' climatic niches (11), revealing changes in niche size (12, 13), locations of refugia (14, 15) or extinction probability (16-18). These studies suggest that climate change responses were species-specific: some species tracked favorable climatic conditions as they shifted in space, while others remained in the same geographic regions by adapting to new climatic conditions or expanded their distributions into novel regions and climates (16, 17). However, similar studies for modern humans are still in their infancy (but see 19-21).

Here, we present evidence that modern humans shifted and expanded their niche into new climatic conditions, in response to the magnitude of climate change and transitions between cultural periods from 46ka until 11ka. Moreover, we provide evidence for a continuous corridor across South Siberia that maintained relatively stable climatic conditions suitable for dispersal by modern humans between Europe and central Asia. We also demonstrate a unique quantitative framework that integrates a suite of paleo-information sources with macroecological and community ecological tools for identifying the responses of modern humans to past climatic changes.

We quantified changes in the climatic niche, or the set of climatic conditions occupied by modern human from Europe and central and north Asia, between 46ka and 11ka. We used 3,993 Eurasian Paleolithic radiocarbon-dated occurrences and 25 paleoclimatic simulations at intervals of 1,000/ 2,000-years, to calculate changes in three niche parameters: i) niche overlap, defined as the amount of climate space continuously occupied by modern humans in two consecutive time intervals (22); ii) niche breadth, or the range of climatic conditions inhabited at each interval, and iii) niche marginality, measured as the distance between the average climatic conditions inhabited by modern humans within each interval and the average climatic conditions of the study area across all 25 climatic intervals (23-25) (Fig.1). In addition, we estimated the geographical distribution of modern humans' suitable climatic conditions in each time interval using Climatic Envelope Models (CEMs) (26-28). We used the resulting maps of climatic suitability (as in 29) to quantify changes in the distribution of modern humans and to identify areas with consistently high climatic suitability throughout the study period (14). Finally, we implemented Generalized Additive Models (GAMs) to separate the effects of climate change versus technological/cultural transitions as potential drivers of the observed changes in niche parameters.

We provide answers to three fundamental questions about the historical biogeography of modern human expansion across Eurasia: i) to what extent did this expansion occur via colonization of novel climatic conditions versus dispersal to novel regions following a specific set of climate conditions; ii) how important are changes in climate versus cultural periods in explaining niche dynamics; and iii) what was the most plausible route, and over which time periods, connecting modern humans from Europe and central and northeast Asia?

Results

Climatic niche dynamics

The climatic niche of modern humans changed extensively from 46ka to 11ka, as indicated by varying levels of niche overlap between intervals across this period (D= 0.271; with 0 being no overlap and 1 complete overlap; low overlap is 0-0.3, medium overlap is 0.3-0.7 and high overlap is 0.7-1; these categories follow 22, 30). Changes in the climatic niche happened gradually over this 35,000 year time period ($0.3<D<0.7$, Fig. 2A), punctuated by brief periods of rapid niche change. The episodes of rapid change were concentrated in the first half of the study period, as indicated by large differences in niche overlap for some consecutive periods occurring before 26ka. Following 26ka, the climatic niche of modern humans showed consistently higher niche overlap.

Analysis of niche breadth indicate that these changes reflect expansion of the climatic niche, with niche breadth consistently increasing from 40ky until reaching its largest extent at 22ka, with some intermittent periods of small contractions. Two time intervals exhibited very rapid growth, as niche breadth expanded by 483% between 40ka and 38ka, and by 83%

between 30ka and 26ka (Fig. 2B). Following the maximum niche breadth at 22ka, the niche contracted gradually until the end of the Pleistocene at 11ka (Fig. 2B).

In contrast to niche breadth, niche marginality, or the distance between the average climatic conditions occupied by modern humans in each time interval and the average conditions from 46ka to 11ka of the study area, roughly declined throughout the study period (Fig. 2B). As modern humans expanded their niche into new climatic conditions, the centroid of their climatic niche approached the mean climatic conditions of the geographical study area across the 25 climatic simulation intervals. Modern humans' climatic niche became progressively less marginal relative to the available climate space (i.e. people occupied a larger fraction of the climatic zones available across Eurasia) until 26ka, succeeded by a period of consistently low marginality until 16ka. After 16ka, the climatic niche of modern humans became increasingly marginal relative to the average climatic conditions 46ka-11ka (Fig. 2B). The warmer and wetter conditions occupied by Palearctic modern humans at the end of the Pleistocene are far from the average conditions for the time extent of our study, which was colder and dryer during most of the time, reflected in our results by a final large increase in niche marginality.

Trends across all niche parameters roughly divide the 35,000 year temporal extent of our study into two main periods: a period of niche change associated with niche expansion from the beginning of the study, 46ka, until ~26ka and a period of larger niche stability associated with gradual niche contraction from ~26ka through the end of the Pleistocene, ~11ka. These periods partially coincide with two distinct paleoclimatic periods: Marine Isotope Stage 3 (MIS3; ~60ka-27ka), which was warmer than MIS2, and Marine Isotope Stage 2 (MIS2; ~27ka-11ka), which was characterized by cold and arid conditions throughout most of its extent, including the Last Glacial Maximum (~21ka: LGM) (31-32). The variances of niche overlap ($P=0.026$) and niche breadth ($P=0.041$) are significantly different between periods, and the variance of niche marginality is nearly so ($P=0.054$).

Cultural and climatic drivers of niche dynamics

Changes in climate, particularly precipitation, were found to be the strongest driver of niche parameters (see *Materials and Methods* and *SI Results*). Change in summer precipitation was the strongest predictor of niche overlap (deviance explained=*57.8%*; P =0.001). Niche breadth change was correlated with change in summer precipitation (deviance explained=57%; P =0.001). Niche marginality change was most strongly correlated with change in winter precipitation (deviance explained=*52.8%*; P <0.001) closely followed by change in spring precipitation (deviance explained=*49%*; P <0.001) (Table S3). Deviance explained increased from 5%-40% for all models when changes in cultural periods were added to single-variable climatic models as a categorical factor with 5 levels (see *Materials and Methods* and Table S4). Changes between cultural periods as a single predictor of the three niche parameters were not statistically significant (Table S5).

Geographic overlap of climatically suitable areas

Changes in geographic overlap of climatically suitable areas (herafter geographic overlap) between consecutive time intervals are consistent with the patterns for niche overlap, breadth and marginality in that the results rougly indicate two periods (46ka-26ka and 26ka-11ka) differing both in direction and magnitude of change (Fig. 2A). There was a general tendency for decreasing geographic overlap until 26ka, followed by a tendency for increase until 11ka. Apart from this general trend, medium to large overlap within discrete intervals during these two periods suggest short intervals of relative stability in the geographic distribution of suitable climatic conditions (Fig. 2A).

Comparing the geographic distribution of climatically suitable areas across all intervals (Fig. 3) indicates that a belt of consistently suitable climatic conditions across South Siberia (5) may have allowed modern humans to disperse across western Eurasia and Northeastern Eurasia/Beringia (33). We also found climatically stable areas that are isolated from other patches of suitable conditions, which may have acted as potential climatic refugia (34), occuring in present day East China, Japan, Korea, Kamchatka and submerged areas of Beringia (Fig. 3).

Discussion

We document the extent to which the expansion of modern humans across Eurasia occurred via colonization of novel climatic conditions or by tracking specific climate conditions into new regions, along 35,000 years of climate change. We found that modern humans followed both strategies: from 46ka to 26ka, changes in geographic distribution coincided with expansion of the climatic niche, but after 26ka, they began to track a similar set of suitable conditions during the extreme cold and arid conditions of the Last Glacial Maximum. The combined effect of both climate change and changes between cultural periods are significant predictors of the shifts in the climatic niche of modern humans. In addition, we present evidence of a potential dispersal route across South Siberia which retained suitable climatic conditions dating back to 32ka and persisting until 18 ka, when this belt became more unsuitable, suggesting reduced potential for dispersal across a vast space of harsh climate immediately following the onset of the LGM (5, 33, 35, 36). Our results are robust to the number of occurrences of modern humans and to the temporal resolution of millennial versus bimillennial time periods (see *SI Results*).

During the niche-expansion phase, from 46ka to 26ka and roughly coinciding with MIS3, modern humans expanded their distribution across much of the Palearctic (6); evidence from archeology and human genetics show that modern humans had already reached parts of south-central Siberia -although there is also evidence for occupation of more northerly sites (2, 33, 37, 38). Our results reveal that from 46ka to 26ka, human expansion into new regions of Eurasia was accompanied by increased niche breadth and low niche overlap between intervals, reflecting the growing variety of climatic conditions that modern humans were able to inhabit and exploit.

In contrast, during MIS2, 26ka-11ka, the climatic niche of modern humans was more stable. During this period populations dispersed to and inhabited regions with similar climatic conditions; that is, modern humans entered a climate tracking phase, as suggested by higher niche overlap, lower niche expansion and higher geographical overlap between intervals (Fig. 2) than during the MIS3. These findings indicate that modern humans adjusted their geographical distribution to colonize suitable climatic conditions rather than expanding to fill new ones. There is evidence that human populations in high latitudes persisted in some pockets of suitable climate (33, 39) during MIS2. Coinciding with the LGM, modern humans experienced a decline in niche breadth. We presume that this decline reflects the decrease in the geographical availability of climatic conditions supporting the minimum levels of ecosystem productivity required to maintain viable populations of hunter-gatherers. Changes in seasonal water availability appear to be the key driver of change in climate niche parameters. In temperate and cold areas, the level of precipitation during the growing season could have played a critical role in plant productivity, driving the availability of a vital resource for hunter-gatherer populations, herbivores and food webs on which they may have depended (40-42). Climatic conditions have been used to predict Net Primary Productivity levels (43) for this period (36) with higher productivity associated with warmer and wetter conditions. During the cold and dry conditions of the LGM, the rate of gross terrestrial primary productivity was about 40±10 $PgCyr^{-1}$, half of the pre-industrial Holocene (44).

However, our results suggest also that transitions to more modern cultural periods also contributed, as a secondary factor, to the ability of modern humans to colonize new climatic conditions. Hunter-gatherers during the Late Pleistoce demonstrated a remarkable variety of cultural adaptations concurrent with a period of climatic and environmental changes, which may have played a key role in ensuring their survival and population growth. Cultural evolution is indeed suggested to have been affected by major episodes of unfavourable conditions (45, 46), population growth, intra and inter-population interactions (47) and subsistence practices (48). Upper Paleolithic hunting tools show a considerable variance and diversified rapidly both in time and space (48) exhibited by the simialrities in ‘cultural periods’ between far apart Eurasian populations (49-51). This diversification might stem from the different carrying capacities of ecosystems, variability of resources, seasonality and demographic pressure. As a result, modern humans may have increased their dietary niche (52) and respectively the need for more efficient resource uptake. The ‘cultural periods’ used in our study do not reflect specific technological changes per se, but rather represent adaptations that would enable them to survive in a variety of climatic conditions, thus increasing their climatic niche.

Existence of a persistent corridor with suitable climate across Southern Siberia suggests that modern human populations inhabiting Europe and central-north Asia may have remained connected via dispersal along this route (Figs. 3 and S7). Our results indicate that this corridor linking Europe and Asia emerged ~36ka, in agreement with recent findings based on ancient DNA of European populations in the Middle Don River (53). Previous studies have also documented evidence of gene flow between Europeans and central Asian populations (5, 53, 54). Despite the early emergence of this relatively continuous belt of suitable climatic conditions surrounded by highly unsuitable areas, it is after 32ka that this route remains highly suitable until 18ka. Modern humans have been recorded in south Siberia as early as 45ka (55), and occupations have been detected at relatively low frequencies in this region through 36ka, but with substantially increased frequency after 16ka (39). Recent genomic sequencing of ancient DNA from two individuals from northeastern Siberia, dated 24ka and 17ka, suggests that this region was occupied throughout the Last Glacial Maximum (54). Whether this indicates continuous occupation or the region was mainly depopulated during the LGM is still debated (2, 37, 49). However, the climatic suitability along this corridor was much lower than that of Western Europe, suggesting that the modern human populations within central Siberia may have dispersed, occupied and survived in lower productivity ecosystems and lower population sizes than in Western Europe. All regions above 61° latitude showed consistently low climatic suitability across the time extent of the study, although the models include some archaeological localities from that latitudinal band. These localities have been reported in previous studies (33, 37, 49, 50), suggesting, in light of our results, that some pioneering human populations either survived in conditions of extremely unsuitable climates and low productivity ecosystems, or in micro-refugia at a spatial scale that is poorly reflected by the 2-degree spatial resolution of our paleoclimatic simulations. Surprisingly, the area south of this mid-latitude belt in Asia (south of 48 ° latitude, apart from East China) also exhibited low climatic suitability for most time intervals of the analyses (Fig. S7). This is due to a lack of well dated human occurrences for South Asia in our database. To more fully understand the movement patterns of modern humans during the Late Pleistocene, key regions like the Arabian Peninsula, South Asia, East Asia and Southeast Asia need to be more intensively surveyed and studied (56).

While all regions of our study area were affected to some extent by climate change, western and eastern Europe have numerous archaeological sites from the period (33, 57-59) and were probably continuously inhabited by modern humans (Fig. S7). Our results show that the climate of this region was consistently more suitable than that of eastern Eurasia, suggesting that the ecosystems had levels of primary productivity able to support dense modern human populations. Outside Western Europe and the Middle East, however, the presence of suitable climatic conditions in East China, Japan, Korea, Kamchatka and Beringia over lengthy periods suggests that these regions may have served as climatic refugia for modern humans. High latitude climatic refugia have been frequently reported for woolly rhinos, woolly mammoths, horses, reindeer, elk musk ox (16, 60-64) and small mammals (65-67). Furthermore, Beringia has been proposed as a potential refugium for modern humans and other animal and plant species based on records from sea-floor sediments (10, 40, 41) and from the presence of similar ecosystems in analogous latitudes (68-70).

Naturally, there are caveats associated with our analyses of the early biogeography of modern humans. First, our results are contingent on this particular data set, spatial resolution and temporal extent of the analyses. The addition of localities recording human presence across southern Asia, for example, would expand the area of suitable climatic conditions from the South Siberian belt towards these regions. In addition, the archaeological record may not accurately reflect the full geographic range of early humans within a particular time interval because of differences in sampling intensity among regions, taphonomic potential among sites, settlement size and potential for detection, or the existence of mulitple dates among artifacts from a single site (71, 72). To reduce the impact of these biases on our results, niche parameter and climatic suitability estimates counted each occupied climatic grid cell only once per time interval regardless of the number of dated remains therein, avoiding the artificial weighting of a subset of climatic conditions toward that of a few well-sampled grid cells (Figs. S4-S6). The algorithm to estimate the climatic niche uses a kernel density function, reducing the impact of differences in sample size. Second, while high resolution climatic reconstructions vastly improve our ability to investigate the processes governing human range expansion, even 1,000 year intervals cannot capture the abrupt climatic events (i.e. Heinrich events and Dansgaard-Oschger events; 73) which likely affected the distributions of humans and other species (59), and the spatial resolution of 2 degrees hampers the ability for detecting refugia of small extent. However, even if the temporal resolutions of these reconstructions were higher, the precision of ^{14}C dating does not permit more detailed interpretations. Our results may therefore underestimate the abrupt nature of climate niche dynamics. Third, while each techno-cultural transition was implemented in our analysis as a single event, transitions were in reality more gradual, reaching different parts of Eurasia at different times, while mulitple lithic industries existed simultaneously even within Europe (e.g. Solutrean in the Atlantic side and Lower Magdalenian in the rest of Europe). Nevertheless, we used a broad classification of cultural periods (see *Results*), as a proxy for cultural and technological advancement, and including more complex variables to estimate niche construction using technological developments may fine-tune our findings in the future.

Despite these caveats, our approach pulls together complementary sources of paleo records in a unique quantitative framework, and reveals significant changes to the climatic niche during modern human dispersal across Eurasia under severe climate change. These methods provide insights which are distinct from, but complementary to, other modes of inference such as arcehology or population genetics: for example, the timing and magnitude of changes in the ecological niche and geographical range could be used to inform population genetic hypotheses. Linking our framework to genetic evidences will allow exploring the effects of climate change on genetic diversity, population size and genomic evolution in Palearctic modern humans as has been done for other megafauna species (17, 18). We can also identify potential climatic refugia that may be targeted for future field work exploration to find previously undiscovered settlement sites and human remains.

Additionally, this approach can provide further clues as to where early modern humans may have overlapped in geographic and/or environmental space with archaic populations, such as Neanderthals (55, 74, 75) or Denisovans, as evidenced by their contribution to our genetic heritage (76-78), and may shed new light on the mechanisms, such as competition for resources, underlying their gradual geographical replacement and extinction during our global expansion.

Materials and methods

Human occurrences

Localities of fossils and other archaeological remains span Eurasia, from western Europe to western Beringia (north of 31° and 38° N latitude for Europe and Asia, respectively) , and include 3,993 radiocarbon dated finds from 46.5ka-10.5ka. The majority were associated with Upper Paleolithic archaeological sites in western and central Europe, Siberia, and China. We focused on this temporal extent because at ~50ka Anatomically Modern Humans in Eurasia were largely restricted to the Near East (but see 1, 9, 79), while by 11ka they had completely occupied Eurasia, and had replaced or absorbed all archaic populations, particularly the Neanderthals (5, 80).

Localities of archaeological remains were collated from Ugan & Byers (81) (all Eurasia), Hamilton & Buchanan (33) (Siberia and northern China) and the International Union for Quaternary Research (INQUA) Radiocarbon Paleolithic Database, v.13, excluding any data from North America or associated with *Homo neanderthalensis* remains or tool traditions. The data were standarised by excluding all specimen localities i) not associated with lab codes, ii) without reported errors for ^{14}C determinations, iii) duplicate ^{14}C estimates or iv) with ^{14}C error >10% of the mean age.

Climatic Data

Paleoclimatic conditions were simulated under the HadCM3 (*Hadley Centre Coupled Model, version 3*) Atmospheric-Ocean coupled General Circulation Model (AOGCM). The model was driven by changes to incoming solar insolation due to variation in orbital configuration, atmospheric greenhouse gas changes derived from ice core records and ice-sheet and sea level changes. The simulations have a time step of 1,000 years between 22ka and 11ka and of 2,000 years before 22ka, resulting in 25 intervals between 11ka-46ka (see 73, 82 for further details of experimental details).

The climatic niche was characterised on the basis of mean temperature (°C) and total precipitation (mm) during the spring, summer, fall, and winter seasons. Seasonal variables were used because they are more likely than annual means to capture the climatic boundaries of a species' niche. Previous studies have used seasonal variables that captured climatic variability, rather than annual means, to model the climatic niches of other megafauna species (16). Each climatic surface was cropped to the appropriate land surface area for that period based on estimated changes in sea level and land surface incorporated into the AOGCMs. Study area is shown in Fig. 3.

Climatic niche overlap, niche breadth and niche marginality

An adaptation of Schoener's D metric for niche overlap (83) from Broennimann and colleagues (22) was implemented to measure the similarity in climatic niche occupied by Palearctic populations of modern humans between consecutive time periods. This metric has been previously used to quantify niche overlap between sister species or between different (i.e., native and introduced) ranges of a single species. D ranges from 0 (no overlap; niches are completely different) to 1 (complete overlap; niches are identical). This framework compares species' niches directly in climatic, rather than geographic, space, and uses a kernel density function to determine the 'smoothed' density of occurrences in each cell in the niche space (22). Consequently, it reduces the effects of an uneven distribution of archaeological localities relative to the human climatic niche and the uneven availability of environmental conditions between the range between time periods (i.e., a particular set of conditions may occur over extensive geographic space during one period but occupy significantly less space during the subsequent period). Niche overlap (D) was calculated in R (R Development Core Team).

The Outlying Mean Index (OMI), an ordination technique, was used to assess changes in niche breadth and niche marginality through time (23), utilising the package ade4 in R (R Development Core Team, CRAN) (84). OMI is used to assess the niche separation and breadth of species assemblages or closely related species across the main environmental axes (24) (see *SI Outlying Mean Index*) but it was applied here to the climatic niche of modern humans across time. OMI quantifies the environmental conditions occupied by each species (niche breadth) and calculates the distance between the average environmental conditions occupied by each species (i.e. niche centroid) and the average conditions of the study area, or niche marginality. In this study we used a climatic niche space that encompasses all the available climatic conditions across the 25 climatic simulation intervals.

Climate envelope models

Climatic Envelope Models (CEMs) were used to reconstruct the distribution of climatic suitability for Paleolithic modern humans in the Palearctic for each time interval, and to identify areas of relative climatic stability across the time extent of the study. CEMs were constructed using Maximum Entropy (MaxEnt*;* 85, 86) in R (R Development Core Team, CRAN) and the package Dismo (87). Modeling was only performed for time intervals with at least 2n localities (n= number of predictor climatic variables). All other parameters for the models were implemented as the default settings. The human occurrence data were randomly split to 70%-30%, using 70% of localities to calibrate the models, and 30% as a validation dataset to evaluate the models' predictive accuracy (but see 88). This process was repeated 10 times for each time interval, and as the final suitability map is the average of these 10 repetitions.

CEMs were validated using the Continuous Boyce Index ($B_{cont(W)}$), which does not require setting a threshold value for environmental suitability, following the implementation by Hirzel and colleagues (89). After partitioning the climatic suitability range into 10 evenly spaced bins, the *predicted frequencies* of archaeological localities for each climatic suitability bin were correlated with the *expected frequency* based on the relative geographic area within each bin. The Spearman rank correlation of *predicted/expected* frequencies against the mean climatic suitability of each bin provides the Boyce index. The $B_{cont(W)}$ varies from -1 to 1, with higher values of suitability indicating good model fit (validation localities are predicted in areas with high suitability values), values close to 0 indicating a model no better than random, and negative values indicating a poor model (validation localities are predicted in areas with low suitability values). Model validation was performed for the average model per time period.

Schoener's D metric as implemented by Warren et al (29) (i.e., in geographic, rather than climatic, space), was used to quantify the degree of geographic overlap in climatically suitable areas between consecutive time intervals. To define regions of long-term high climatic suitability, the cumulative climatic suitability per grid cell across all time intervals was divided by the number of intervals each grid cell was above sea level and not covered by ice. The regions of consistently high climatic suitability were measured as the 30% of grid cells with the highest mean climatic suitability, following an approach similar to Graham et al (90).

Cultural and climatic drivers of niche dynamics

Generalized Additive Models (GAMs) were used to assess the effects of climate change and transitions between 'cultural periods' as drivers of niche parameters and distribution changes in climatic suitability of Palearctic modern humans. Changes in the seasonal medians across fossil localities between consecutive time intervals for temperature and total precipitation were employed as single climatic predictors. Each GAM was run using a single climatic predictor because of the small number of time periods relative to the number of climatic variables. This was performed both including and excluding changes between 'cultural periods', which were measured as a factor with 5 levels (1 is the earliest cultural period while 5 is the most recent). Lastly, a series of GAMs was run using cultural changes as a single predictor.

Cultural Periods

We used a broad classification of 'cultural periods' identified by lithic industries: Initial Upper Paleolithic (UP) (45ka-40ka); Aurignacian Europe/ Early UP Siberia, 40ka-32ka; Gravettian Europe /Middle UP Siberia, 32ka-24ka; Glacial Maximum Europe/Middle UP Siberia, 24ka-17ka; Late Glacial Europe/Late UP Siberia, 17ka-11ka, partially modifying the chronological periods defined by (35) for the European part. Even though Siberia has three main cultural periods within the UP, they were divided into four based on the European archaeological record, where most of the fossil occurrences of our database are found, permiting a common analysis of European and Asian data. Despite these differences between regions of Eurasia, previous studies state that technological innovations spread quickly, suggesting population connections between central-South Siberia and central-Eastern Europeans (49-51).

Acknowledgments

We acknowledge the Danish National Research Foundation for their financial support to the Center for Macroecology, Evolution and Climate. DNB thanks 'Det Frie Forskningsrads Forskerkarriere Program Sapere Aude' and KAM thanks the

Villum Foundation Young Investigator's Programme. We finally thank Zhiheng Wang and Ben Holt for assistance with R and Nathan Sanders for discussion and critiques on the manuscript.

References

1. Reyes-Centeno H et al. (2014) Genomic and cranial phenotype data support multiple modern human dispersals from Africa and a southern route into Asia. *Proc Natl Acad Sci U S A* 111:7248–53.
2. Goebel T, Waters MR, O'Rourke DH (2008) The late Pleistocene dispersal of modern humans in the Americas. *Science* 319:1497–502.
3. Waters MR et al. (2011) The Buttermilk Creek complex and the origins of Clovis at the Debra L. Friedkin site, Texas. *Science* 331:1599–603.
4. Waters MR et al. (2011) Pre-Clovis mastodon hunting 13,800 years ago at the Manis site, Washington. *Science* 334:351–3.
5. Finlayson C (2005) Biogeography and evolution of the genus Homo. *Trends Ecol Evol* 20:457–63.
6. Finlayson C, Carrión JS (2007) Rapid ecological turnover and its impact on Neanderthal and other human populations. *Trends Ecol Evol* 22:213–22.
7. Müller UC et al. (2011) The role of climate in the spread of modern humans into Europe. *Quat Sci Rev* 30:273–279.
8. Cooper A, Stringer CB (2013) Paleontology. Did the Denisovans cross Wallace's Line? *Science* 342:321–3.
9. Rasmussen M et al. (2011) An Aboriginal Australian genome reveals separate human dispersals into Asia. *Science* 334:94–8.
10. Hoffecker JF, Elias SA, O'Rourke DH (2014) Anthropology. Out of Beringia? *Science* 343:979–80.
11. Peterson AT, Soberón J, Pearson RG, Anderson RP, Martínez-Meyer E, Nakamura M and Araújo MB (2011). Ecological Niches and Geographic Distributions. Princeton University Press, Princeton.
12. Nogués-Bravo D (2009) Predicting the past distribution of species climatic niches. *Glob Ecol Biogeogr* 18:521–531.
13. Veloz S, Nur N, Salas L, Jongsomjit D (2013) Modeling climate change impacts on tidal marsh birds: Restoration and conservation planning in the face of uncertainty. *Ecosphere* 4:art49.
14. Carnaval A, Hickerson M (2009) Stability predicts genetic diversity in the Brazilian Atlantic forest hotspot. *Science* 323:785–789.
15. Nogués-Bravo D, Ohlemüller R, Batra P, Araújo MB (2010) Climate predictors of late quaternary extinctions. *Evolution* 64:2442–9.

16. Nogués-Bravo D, Rodríguez J, Hortal J, Batra P, Araújo MB (2008) Climate change, humans, and the extinction of the woolly mammoth. *PLoS Biol* 6:e79.
17. Lorenzen ED et al. (2011) Species-specific responses of Late Quaternary megafauna to climate and humans. *Nature* 479:359–64.
18. Metcalf JL et al. (2014) Integrating multiple lines of evidence into historical biogeography hypothesis testing: a Bison bison case study. *Proc Biol Sci* 281:20132782.
19. Banks W, D'Errico F, Dibble H (2006) Eco-cultural niche modeling: new tools for reconstructing the geography and ecology of past human populations. *PaleoAnthropology* 2006:68–83.
20. Banks WE et al. (2008) Human ecological niches and ranges during the LGM in Europe derived from an application of eco-cultural niche modeling. *J Archaeol Sci* 35:481–491.
21. Beeton TA, Glantz MM, Trainer AK, Temirbekov SS, Reich RM (2014) The fundamental hominin niche in late Pleistocene Central Asia: a preliminary refugium model. *J Biogeogr* 41:95–110.
22. Broennimann O et al. (2012) Measuring ecological niche overlap from occurrence and spatial environmental data. *Glob Ecol Biogeogr* 21:481–497
23. Dolédec S, Chessel D, Gimaret-Carpentier C (2000) Niche separation in community analysis: a new method. *Ecology* 81:2914–2927.
24. Hof C, Rahbek C, Araújo MB (2010) Phylogenetic signals in the climatic niches of the world's amphibians. *Ecography (Cop)* 33:242–250.
25. Thuiller W, Lavorel S, Midgley G, Lavergne S, Rebelo T (2004) RELATING PLANT TRAITS AND SPECIES DISTRIBUTIONS ALONG BIOCLIMATIC GRADIENTS FOR 88 LEUCADENDRON TAXA. *Ecology* 85:1688–1699.
26. Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. *Ecol Modell* 135:147–186.
27. Engler R, Guisan A, Rechsteiner L (2004) An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. *J Appl Ecol* 41:263–274.
28. Araújo MB, Peterson AT (2012) Uses and misuses of bioclimatic envelope modeling. *Ecology* 93:1527–1539.
29. Warren DL, Glor RE, Turelli M (2008) Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution* 62:2868–83.

30. Petitpiere B et al. (2012) Climatic Niche Shifts Are Rare Among Terrestrial Plant Invaders. *Science* 335: 1344-1348
31. Hetherington R & Reid RGB (2010) The climate connection, Cambridge University Press, Cambridge
32. Clark PU et al. (2009) The Last Glacial Maximum. *Science* 325:710-714
33. Hamilton MJ, Buchanan B (2010) Archaeological support for the three-stage expansion of modern humans across northeastern Eurasia and into the Americas. *PLoS One* 5:e12472
34. Gavin DG et al. (2014) Climate refugia: joint inference from fossil records, species distribution models and phylogeography. *New Phytol* 204:37–54.
35. Bocquet-Appel JP, Demars PY, Noiret L, Dobrowsky D (2005) Estimates of Upper Palaeolithic meta-population size in Europe from archaeological data. *J Archaeol Sci* 32:1656–1668.
36. Eriksson A et al. (2012) Late Pleistocene climate change and the global expansion of anatomically modern humans. *Proc Natl Acad Sci USA* 109:16089–94.
37. Pitulko VV et al. (2004) The Yana RHS site: humans in the Arctic before the last glacial maximum. *Science* 303:52–56.
38. Gibbons A (2014) Human evolution. Oldest Homo sapiens genome pinpoints Neanderthal input. Science 343:1417
39. Kuzmin YV., Keates SG (2005) Dates Are Not Just Data: Paleolithic Settlement Patterns in Siberia Derived from Radiocarbon Records. *Am Antiq* 70:773.
40. Meiri M et al. (2014) Faunal record identifies Bering isthmus conditions as constraint to end-Pleistocene migration to the New World. *Proc Biol Sci* 281:20132167.
41. Elias S, Crocker B (2008) The Bering Land Bridge: a moisture barrier to the dispersal of steppe–tundra biota? *Quat Sci Rev* 27:2473–2483.
42. Willis K, Van Andel T (2004) Trees or no trees? The environments of central and eastern Europe during the Last Glaciation. *Quat Sci Rev* 23:2369–2387.
43. Del Grosso S et al. (2008) GLOBAL POTENTIAL NET PRIMARY PRODUCTION PREDICTED FROM VEGETATION CLASS, PRECIPITATION, AND TEMPERATURE. *Ecology* 89:2117–2126.
44. Ciais P et al. (2011) Large inert carbon pool in the terrestrial biosphere during the Last Glacial Maximum. *Nat Geosci* 5:74–79.

45. Munoz SE, Gajewski K, Peros MC (2010) Synchronous environmental and cultural change in the prehistory of the northeastern United States. *Proc Natl Acad Sci U S A* 107:22008–13.
46. Ziegler M et al. (2013) Development of Middle Stone Age innovation linked to rapid climate change. *Nat Commun* 4:1905.
47. Powell A, Shennan S, Thomas MG (2009) Late Pleistocene demography and the appearance of modern human behavior. *Science* 324:1298–301.
48. Stiner MC, Kuhn SL (2006) Changes in the “Connectedness” and Resilience of Paleolithic Societies in Mediterranean Ecosystems. *Hum Ecol* 34:693–712.
49. Goebel T (1999) Pleistocene human colonization of Siberia and peopling of the Americas: An ecological approach. *Evol Anthropol Issues, News, Rev* 8:208–227
50. Hoffecker JF (2005) Innovation and technological knowledge in the Upper Paleolithic of Northern Eurasia. *Evol Anthropol Issues, News, Rev* 14:186–198
51. Ambrose SH (2001) Paleolithic Technology and Human Evolution. *Science* 291:1748–1753.
52. Hublin JJ & Richards MP (2009) The evolution of hominin diets: Integrating approaches to the study of Palaeolithic subsistence. Dordrecht: Springer.
53. Lazaridis I et al. (2014) Ancient human genomes suggest three ancestral populations for present-day Europeans. *Nature* 513:409–413.
54. Raghavan M et al. (2014) Upper Palaeolithic Siberian genome reveals dual ancestry of Native Americans. *Nature* 505:87–91.
55. Fu Q et al. (2014) Genome sequence of a 45,000-year-old modern human from western Siberia. *Nature* 514:445–49
56. Boivin N, Fuller DQ, Dennell R, Allaby R, Petraglia MD (2013) Human dispersal across diverse environments of Asia during the Upper Pleistocene. *Quat Int* 300:32–47.
57. Bocquet-Appel JP, Demars PY (2000) Population Kinetics in the Upper Palaeolithic in Western Europe. *J Archaeol Sci* 27:551–570.
58. Hoffecker J (2009) The spread of modern humans in Europe. *Proc Natl Acad Sci USA* 106:16040–5.
59. Bradtmöller M, Pastoors A, Weninger B, Weniger GC (2012) The repeated replacement model – Rapid climate change and population dynamics in Late Pleistocene Europe. *Quat Int* 247:38–49.

60. Kuzmin Y, Orlova L (2004) Radiocarbon chronology and environment of woolly mammoth (Mammuthus primigenius Blum.) in northern Asia: results and perspectives. *Earth-Science Rev* 68:133–169.

61. Orlova L, Kuzmin Y, Dementiev V (2004) A REVIEW OF THE EVIDENCE FOR EXTINCTION CHRONOLOGIES FOR FIVE SPECIES OF UPPER PLEISTOCENE MEGAFAUNA IN SIBERIA. *Radiocarbon* 46:301–314.

62. Forman SL, Weihe RR (2000) The Holocene occurrence of reindeer on Franz Josef Land, Russia. *The Holocene* 10:763–768.

63. Barnes I et al. (2007) Genetic structure and extinction of the woolly mammoth, Mammuthus primigenius. *Curr Biol* 17:1072–5.

64. Cook JA et al. (2005) Beringia : Intercontinental exchange and diversification of high latitude mammals and their parasites during the Pliocene and Quaternary. *New Phytol* 44:33–44.

65. Stewart JR, Lister AM (2001) Cryptic northern refugia and the origins of the modern biota. *Trends Ecol Evol* 16:608–613.

66. Wójcik JM, Ratkiewicz M, Searle JB (2002) Evolution of the common shrew Sorex araneus : chromosomal and molecular aspects. *Acta Theriol (Warsz)* 47:139–167.

67. Jaarola M, Searle JB (2002) Phylogeography of field voles (Microtus agrestis) in Eurasia inferred from mitochondrial DNA sequences. *Mol Ecol* 11:2613–21.

68. Willerslev E et al. (2014) Fifty thousand years of Arctic vegetation and megafaunal diet. *Nature* 506:47–51.

69. Parducci L et al. (2012) Glacial survival of boreal trees in northern Scandinavia. *Science* 335:1083–1086.

70. Tzedakis PC, Emerson BC, Hewitt GM (2013) Cryptic or mystic? Glacial tree refugia in northern Europe. *Trends Ecol Evol* 28:696–704.

71. Varela S, Lobo JM, Hortal J (2011) Using species distribution models in paleobiogeography: A matter of data, predictors and concepts. *Palaeogeogr Palaeoclimatol Palaeoecol* 310:451–463.

72. Svenning JC, Fløjgaard C, Marske KA, Nógues-Bravo D, Normand S (2011) Applications of species distribution modeling to paleobiology. *Quat Sci Rev* 30:2930–2947.

73. Singarayer, JS, Valdes, PJ (2010) High-latitude climate sensitivity to ice-sheet forcing over the last 120kyr. *Quat Sci Rev*

74. Mellars P (2004) Neanderthals and the modern human colonization of Europe
75. Nigst PR et al. (2014) Early modern human settlement of Europe north of the Alps occurred 43,500 years ago in a cold steppe-type environment. *Proc Natl Acad Sci U S A 111:* 14394-99
76. Sankararaman S et al. (2014) The genomic landscape of Neanderthal ancestry in present-day humans. *Nature* 507:354–7.
77. Vernot B, Akey JM (2014) Resurrecting surviving Neandertal lineages from modern human genomes. *Science* 343:1017–21.
78. Huerta-Sánchez E et al. (2014) Altitude adaptation in Tibetans caused by introgression of Denisovan-like DNA. *Nature* 512:194-197
79. Pope KO, Terrell JE (2007) Environmental setting of human migrations in the circum-Pacific region. *J Biogeogr* 35:1-21
80. Mellars P (2006) Going east: new genetic and archaeological perspectives on the modern human colonization of Eurasia. *Science* 313:796–800.
81. Ugan A, Byers D (2007) Geographic and temporal trends in proboscidean and human radiocarbon histories during the late Pleistocene. *Quat Sci Rev* 26:3058–3080.
82. Singarayer JS, Valdes PJ, Friedlingstein P, Nelson S and Beerling DJ (2011) Late Holocene methane rise caused by orbitally controlled increase in tropical sources. *Nature* 470:82-85
83. Schoener TW (1968) The Anolis Lizards of Bimini: Resource Partitioning in a Complex Fauna. *Ecology* 49:704.
84. Dray S and Dufour AB (2007) The ade4 package: implementing the duality diagram for ecologists. Journal of Statistical Software. 22(4): 1-20.
85. Phillips S, Dudík M, Schapire R (2004) A maximum entropy approach to species distribution modeling. *Proceedings of the twenty-first Intern Conf on Machine-Learning*: 655–662.
86. Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. *Ecol Modell* 190:231–259.
87. Hijmans RJ, Phillips S, Leathwick J and Elith J (2011), Package 'dismo'.
88. Araujo MB, Pearson RG, Thuiller W, Erhard M (2005) Validation of species-climate impact models under climate change. *Glob Chang Biol* 11:1504–1513.

89. Hirzel AH, Le Lay G, Helfer V, Randin C, Guisan A (2006) Evaluating the ability of habitat suitability models to predict species presences. *Ecol Modell* 199:142–152.

90. Graham (2006) Habitat history improves prediction of biodiversity in rainforest fauna. *Proc Natl Acad Sci U S A* 103:632-36.

Figures

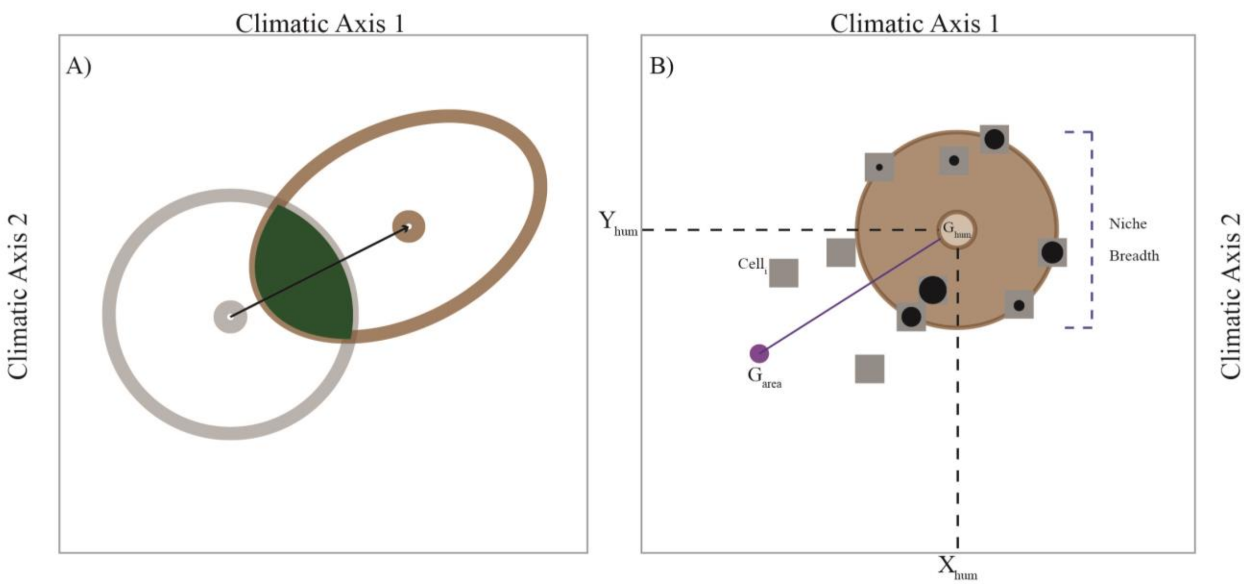

Fig.1: Theoretical representation of niche parameters in climatic space. A) Change in the climatic niche (expansion and contraction along climatic axes) and in the position of the niche centroid (black line) between two time periods. The grey and brown ovals represent the climatic niche at two different time intervals, while the overlap between intervals is shown in green. B) The brown circle represents the climatic niche in one time interval. Grey rectangles represent climatic conditions of individual grid cells in paleoclimatic maps, while black dots and their relative sizes indicate the presence and abundance of human occurrences within a particular set of climate conditions. G_{area} is the center of gravity of the total climatic space from 46ka to 11ka of the study area, while G_{hum} is the average climatic conditions of the climatic niche of modern humans, and the purple line represents the niche marginality, or the distance between these two points. The blue dashed line represents the niche breath or the total climatic conditions occupied by modern humans in a time period.

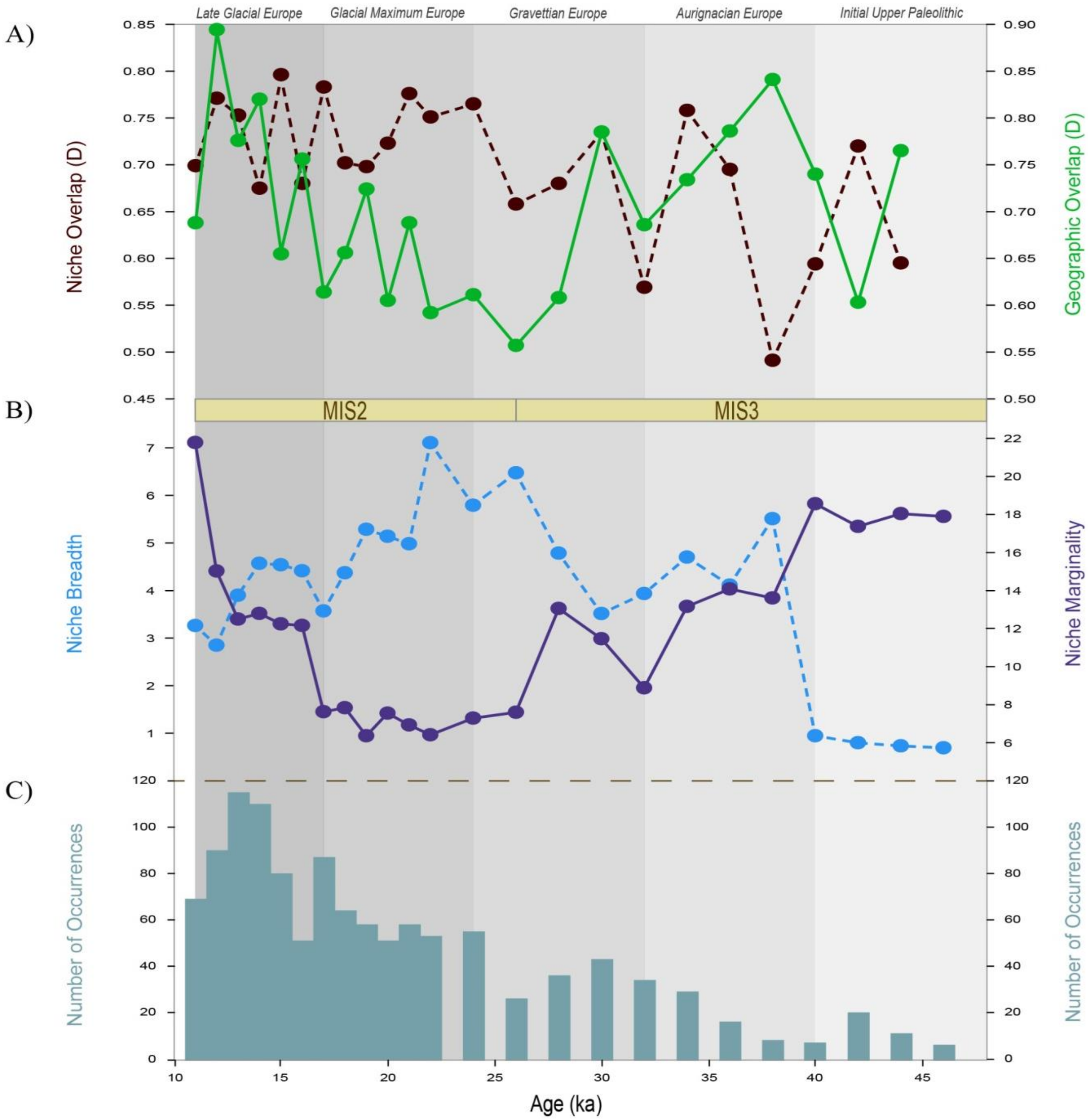

Fig. 2: Temporal trends of climatic niche parameters for Anatomically Modern Humans between 46-11ka. The upper panel (2A) of the graph indicates overlap of the climatic niche (dashed brown line) and the geographic overlap of climatically suitable areas (light green line) between consecutive time intervals. The middle panel (2B) represents the changes in niche breadth (dashed light blue line) and niche marginality (purple line). The lower panel (2C) indicates the number of fossil occurrences used per time interval for all analyses. The climatic periods Marine Isotope Stage 3 and Marine Isotope Stage are indicated by a yellow bar, while different cultural periods are indicated by the grey bars behind the three panels (names are shown at the top).

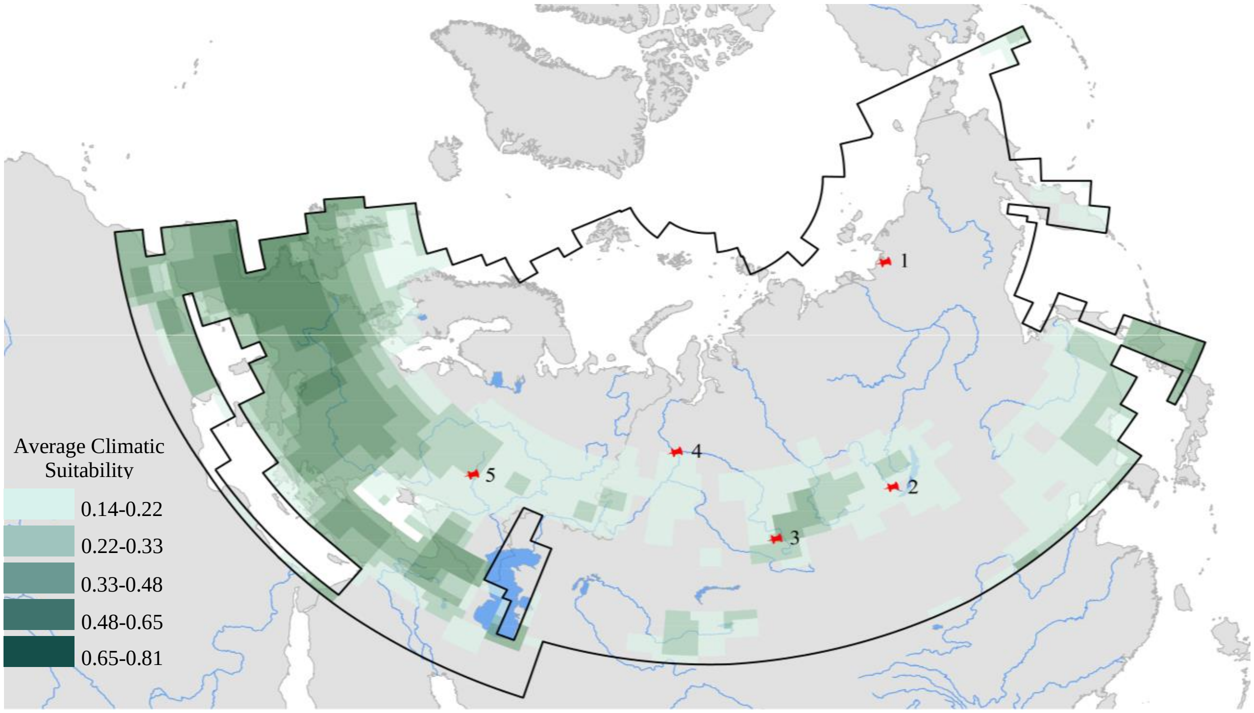

Fig. 3**:** Suitable climatic corridor for potential dispersal across Eurasia. The maximum extent of the study area, including all grid cells above sea level for at least one time interval, is outlined in black. The colored areas represent the 30 percent of the grid cells with the highest average suitability values across time bins between 46ka and 11ka. Grey areas inside the black outline represent the remaining 70 percent. Red pins represent locations of Late Pleistocene human findings; 1 - Yana RHS site, 2 - Mal'ta, 3 - Denisova cave, 4 - Ust'-Ishim, 5 - Kostyonki.