RESEARCH PAPER

Niche dynamics of Palaeolithic modern humans during the settlement of the Palaearctic

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ABSTRACT

Aim During the Late Pleistocene (*c.* 126–10 ka), modern humans (*Homo sapiens*) expanded their geographical range across Eurasia and eventually colonized the Americas. Although the routes by which they migrated have been intensively analysed, the dynamics of their realized climatic niche are still largely unknown. We assess temporal changes in the climatic niche of modern humans, the geographical distribution of their climatic niche and whether niche dynamics correlate with the magnitude of climate change and cultural advances, between 46 and 11 ka.

Location Palaearctic.

Methods Using the radiocarbon dated archaeological record and spatial palaeoclimatic simulations, we quantify different parameters of the realized climatic niche of modern humans (niche overlap, niche breadth and climatic marginality) between consecutive 1000–2000 year intervals. Moreover, using climate envelope models, we map the potential distributions of modern humans for each time interval and identify the regions that remained more climatically suitable and stable for modern humans through time.

Results Between 46 and 22 ka the climatic niche of modern humans expanded, including periods of intense growth in niche breadth at 40 and 30 ka. Changes in seasonal water availability and technological innovations partly correlate with dynamics in niche parameters. We document a persistent climatically suitable mid-latitude belt in south Siberia linking western Europe to the Far East that may have facilitated human migration, and a potential climatic refugium in Beringia.

Main conclusions The climatic niche of modern humans changed across the Late Pleistocene, as the result of both climatic and cultural changes. These populations of hunter-gatherers occupied novel climatic conditions but also remained in previously occupied areas under changing climates during the settlement of the Palaearctic. Our approach can provide clues as to where early modern humans may have overlapped in geographical and environmental space with Neanderthals or Denisovans, as evidenced by their contribution to the genetic heritage of some current populations.

Keywords
Climate envelope models, climatic niche, climatic refugia, human expansion, Late Pleistocene, modern humans, niche dynamics.

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INTRODUCTION

Modern humans are believed to have originated in Africa approximately 200 ka (ka, thousand years ago) (Henn *et al.*, 2011). From there, they moved outward through Eurasia (*c.* 60 ka), crossing to the Americas through Beringia by at least 15 ka and finally populating South America (Waters *et al.*, 2011). During their journey through Europe and Asia they encountered changing climatic conditions (Muller *et al.*, 2011), topographic variability and diverse ecosystem types. There is an extensive overall agreement of the migration routes that modern humans used to expand their distribution and connect populations (Finlayson & Carrion, 2007) and on the areas where they managed to survive in periods of extreme conditions (Stewart & Stringer, 2012). The most commonly employed methods for investigating these issues are descriptions of the temporal concordance of archaeological findings with climatic changes (Nigst *et al.*, 2014), demographic patterns of human dispersal (Fort, 2012), linguistic variability across regions (Grollemund *et al.*, 2015) or genetic evidence of population differentiation (Tishkoff *et al.*, 2009) and introgression with other concurrent hominin populations (Huerta-Sanchez *et al.*, 2014).

Whereas the timing and routes of these dispersal events across geographical space have been intensively analysed and heavily disputed (Hoffecker *et al.*, 2014; Liu *et al.*, 2015; Pitulko *et al.*, 2016), less is known about the climatic niche dynamics of hunter-gatherer populations during this dispersal. Whether the realized niche of modern humans changed, and how it was distributed across the climatic space available during the settlement of the Palaearctic in the Late Pleistocene, is largely unknown. 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 realized species climatic niches, revealing changes in niche size (Nogues-Bravo, 2009; Veloz *et al.*, 2013), locations of refugia (Carnaval *et al.*, 2009) or extinction probability (Nogues-Bravo *et al.*, 2008; Metcalf *et al.*, 2014). These studies suggest that responses to climate change were species specific: some species tracked favourable climatic conditions as they shifted in space, while others remained in the same geographical regions by adapting to new climatic conditions or expanded their distributions into novel regions and climates (Lorenzen *et al.*, 2011). However, similar studies for humans are still in their infancy (Beeton *et al.*, 2014; Grollemund *et al.*, 2015; Benito *et al.*, 2016).

Here we take a macroecological perspective to capture broad temporal and spatial patterns of the occupancy of geographical and climatic space by modern humans during their expansion in the Palaearctic in the last part of the Late Pleistocene. We address three fundamental questions about the historical biogeography of modern human expansion across the Palaearctic, and the dynamics of their realized climatic niche during this period: (1) to what extent did the climatic niche of Palaeolithic modern humans remain stable through time; (2) where did the most suitable climatic conditions occur over time; and (3) how important are changes in climate and cultural periods in explaining climatic niche dynamics?

MATERIALS AND METHODS

Human occurrence data

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 3993 radiocarbon-dated remains from 46.5–10.5 ka. The majority were associated with Upper Palaeolithic (UP) archaeological sites (i.e. the third technological subdivision of the Stone Age, *c.* 50–10 ka) in western and central Europe, Siberia and China. We focused on this temporal extent because at *c.* 50 ka modern humans in Eurasia were largely restricted to the Near East and South/Southeast Asia (Atkinson *et al.*, 2008; Reyes-Centeno *et al.*, 2014), while by 11 ka they had completely occupied Eurasia, and had replaced or absorbed other hominins, particularly the Neanderthals (Vernot & Akey, 2014).

Occurrences of archaeological remains were collated from Ugan & Byers (2007) (all Eurasia), Hamilton & Buchanan (2010) (Siberia and northern China) and the International Union for Quaternary Research (INQUA) Radiocarbon Palaeolithic Database (v.13), excluding any data from North America or associated with *Homo neanderthalensis* remains or tool traditions. The data were standardized by excluding all specimen localities (1) not associated with lab codes, (2) without reported errors for ^{14}C determinations, (3) duplicate ^{14}C estimates or (4) with ^{14}C error $> 10\%$ of the mean age. To reduce the effect of the uneven distribution of the archaeological record across Europe and central-north Asia, two zones with contrasting fieldwork intensity in the last century, all palaeoclimatic data were gridded to $1° \times 1°$ resolution, and all occurrences within a grid cell were aggregated to a single occurrence.

Climatic variables

Palaeoclimatic conditions were simulated under the HadCM3 (Hadley Centre Coupled Model, version 3) Atmospheric–Ocean General Circulation Model (AOGCM) (Singarayer *et al.*, 2011). The simulations have a time step of 1000 years between 22 and 11 ka and of 2000 years before 22 ka, resulting in 24 intervals between 46 and 11 ka. To characterize the realized climatic niche of modern humans and model the potential distribution of their climatic niche, we utilized eight climatic variables including mean temperature (°C) and total precipitation (mm) for each season – spring (March–May), summer (June–August), autumn (September–November) and winter (December–February). Each climatic surface was cropped to the appropriate land surface area for that

time interval based on estimated changes in sea levels incorporated into the AOGCMs.

Estimation of realized climatic niche overlap, niche breadth and niche marginality

We estimated three parameters of the climatic niche of modern humans: temporal overlap, breadth and marginality (see Fig. 1 for a graphical representation of niche parameters). Firstly, we matched the distribution of dated human occurrences and local climatic conditions from palaeoclimatic simulations for each millennial and bimillennial time bin. To assign archaeological localities to the appropriate climatic millennial or bimillennial interval, we grouped all materials with a mean radiocarbon date ±500 years around that interval (e.g. localities assigned to the 21-ka climatic simulation had radiocarbon dates from 21.5 to 20.5 ka). To avoid associating localities to more than one palaeoclimatic simulation, we excluded all localities with radiocarbon standard error exceeding 500 calibrated years. Subsequently, we summarized the total available climatic space from 46 to 11 ka along the eight climatic variables in a two-dimensional space using a principal components analysis (PCA), and projected into this climatic space the human occurrences for each time interval to estimate the three niche parameters for each millennial/bimillennial time step (see Fig. S13 in the Supporting Information).

We quantified Schoener's D metric for niche overlap (Schoener, 1968; Broennimann et al., 2012) to measure the similarity in the realized climatic niche occupied by Palaearctic populations of modern humans between consecutive time intervals. This metric has been previously used to quantify niche overlap between sister species and between different (i.e. native and introduced) ranges of a single species, and to compare historical and current niches of different taxa (Veloz et al., 2012). The overlap (D) of the realized climatic niche between consecutive time intervals ranges from 0 (no overlap; niches are completely different) to 1 (complete overlap; niches are identical). This approach compares species niches directly in climatic rather than geographical space. The same PCA climatic space was subsequently used for estimating niche marginality and breadth. Niche overlap (D) was calculated in R (R Development Core Team) (see the section 'SI niche overlap') using the script by Broennimann et al. (2012) (Appendix S1).

We used the outlying mean index (OMI) to assess changes in niche breadth and niche marginality through time (Doledec et al., 2000). Using the location of dated human occurrences within the full climatic PCA space, we estimated the range of climatic conditions occupied by modern humans (niche breadth) and calculated the distance between the average environmental conditions they occupied (niche centroid) and the average conditions of the study area (niche marginality). OMI analyses were conducted in the R package 'ade4' (Dray & Dufour, 2007).

Climate envelope models

We used climate envelope models (CEMs) to reconstruct the geographical distribution of the climatic niche of modern humans in the Palaearctic for each time interval. Modelling was only performed for time intervals with at least $2n$ localities (n = number of predictor variables = eight seasonal climatic variables). The human occurrence data of each interval were randomly split to 70%–30%, using 70% of localities to calibrate the models and 30% to evaluate the models' predictive accuracy. This process was repeated 10 times for each time interval, and the final suitability map was constructed as the average of these 10 repetitions (Fig. S5). All CEMs were constructed using maximum entropy (MaxEnt; Phillips et al., 2006) in R (R Development Core Team, CRAN) and the package 'dismo'(Hijmans et al., 2011), using default settings.

To assess a model's ability to correctly predict human occurrences we used the continuous Boyce index ($B_{\text{cont(W)}}$), which does not require setting a threshold value for environmental suitability (Hirzel et al., 2006). $B_{\text{cont(W)}}$ varies from −1 to 1, with higher values of suitability indicating good model fit (evaluation localities are predicted in areas with high suitability), values close to zero indicating a model no better than random, and negative values indicating a poor model fit (evaluation localities are predicted in areas with low suitability). Model evaluation for each millennial or bimillennial time step was performed for the final average suitability surface across the 10 repetitions of each Maxent model per time interval.

To identify regions of long-term high climatic suitability across the time extent of the study, the cumulative climatic suitability per grid cell across all time intervals was divided by the number of intervals that grid cell was above sea level and not covered by ice. The regions of relatively high stability were identified as the 30% of grid cells with the highest average climatic suitability, following an approach similar to Graham et al. (2006).

Moreover, we estimated Schoener's D in geographical, rather than climatic, space (Warren et al., 2008) to quantify the degree of geographical overlap in climatic suitability (hereafter geographical overlap) between consecutive time intervals, as a proxy for changes in the distribution of modern humans. Following Broenimman et al. (2012) we combined the climatic conditions and fossil occurrences across all time intervals to estimate the 'total' realized climatic niche of modern humans. Subsequently we predicted the potential distribution of modern humans based on the climatic conditions of each time interval, projected it into the geographical space of the respective time interval and calculated the spatial overlap of these projections between consecutive intervals.

Cultural periods

We define cultural periods as a measure of advancement for modern humans that would enable them to survive in different environmental conditions. We used a broad classification
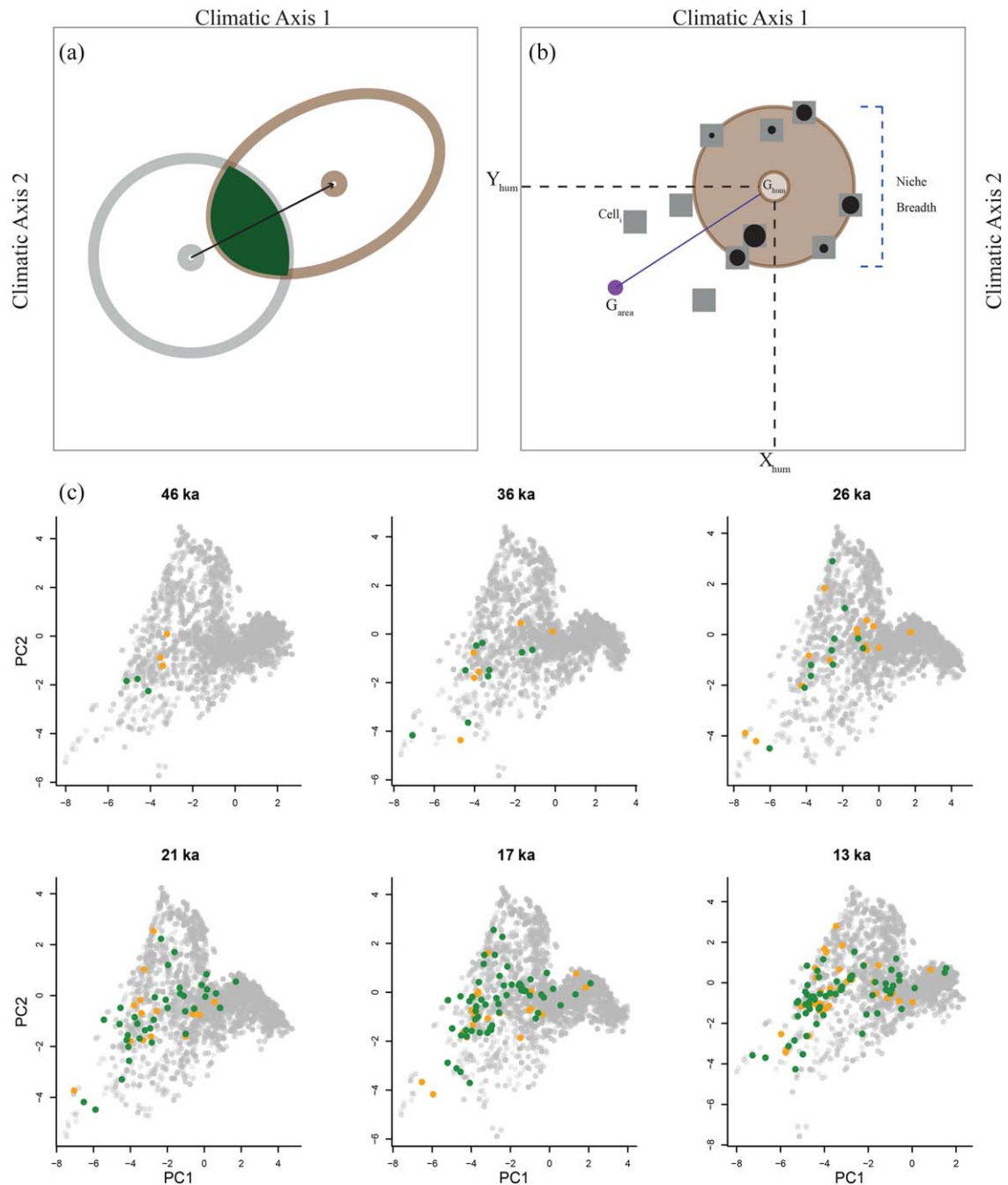
Figure 1 Theoretical representation of niche parameters in climatic space. (a) Change in the climatic niche (expansion and contraction along climatic axes) and in the position of the niche centroid (black line) between two time intervals. The grey and brown ovals represent the climatic niche at two different 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 palaeoclimatic 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} represents the centre of gravity of the total climatic space of the study area from 46 to 11 ka, while G_{hum} represents 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 interval. (c) Temporal distribution of occurrences in total climatic space available in the Late Pleistocene for six time intervals (46, 36, 26, 21, 17 and 13 ka). Axes represent principal component 1 (*x*-axis) and principal component 2 (*y*-axis) of the total climatic space. Grey circles represent background climatic conditions of the study area. Orange circles represent 'conserved' and green circles 'unique' sites in geographical space between time intervals.

of 'cultural periods' identified by lithic industries: Initial UP (45–40 ka); Aurignacian Europe/Early UP Siberia, 40–32 ka; Gravettian Europe/Middle UP Siberia, 32–24 ka; Glacial Maximum Europe/Middle UP Siberia, 24–17 ka; Late Glacial Europe/Late UP Siberia, 17–11 ka, partially modifying the chronological periods defined by Bocquet-Appel *et al.* (2005) for Europe. Although Siberia has three main cultural periods within the UP, they were divided into four based on the European archaeological record, where most of our fossil occurrences are found, permitting a common analysis of European and Asian data. Despite these regional differences, previous studies found that technological innovations spread quickly, suggesting population connections between central-south Siberia and central-eastern Europe (Goebel, 1999).

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 correlates of niche parameter dynamics and changes in the geographical distribution of the climatic niche of modern humans. To measure climate change, we quantified changes in the seasonal medians across the fossil localities between consecutive time intervals, for average temperature and total precipitation of each season. 'Cultural periods' were coded as a factor with five levels (one is the earliest cultural period while five is the most recent). We first estimated the explained deviance and *P*-value in niche overlap, breadth, marginality and geographical overlap of the climatic niche by the change in each seasonal climatic variable. Each GAM was run using each single climatic predictor separately because of the small number of time intervals relative to the number of climatic variables. We then measured the deviance explained in each of the four parameters by cultural periods alone (Tables S3–S5). Finally, we estimated changes in each parameter as the function of both changes in climate and 'cultural periods' (e.g. niche overlap as a dependent variable and summer temperature and cultural periods as independent variables).

RESULTS

Climatic niche dynamics

The realized climatic niche of modern humans changed extensively from 46 to 11 ka ($D = 0.271$), as indicated by varying levels of niche overlap across this period (low overlap is 0–0.3, medium overlap is 0.3–0.7 and high overlap is 0.7–1; Petitpierre *et al.*, 2012). Although the overall pattern of niche overlap through time shows a significant increase ($P = 0.006$; Fig. S10A) with changes occurring gradually over this 35,000-year span ($0.3 < D < 0.7$; Fig. 2A), niche overlap exhibits larger variability in the first period (46–26 ka) than in the second period (26–11 ka). However, estimates of niche overlap are sensitive to low sample sizes (Fig. S7C, Table S2), reducing the robustness of estimates of D for the first period

(before 26 ka). Thus we cannot exclude the possibility that the higher variability is due to small sample sizes.

Overall, the niche breadth of modern humans at 11 ka was 3.7 times larger than at 46 ka. Changes in niche breadth indicate expansion of the climatic niche ($P = 0.014$), with niche breadth increasing after 40 ka until reaching its largest extent at 22 ka ($P = 0.002$), with intermittent intervals of small contractions. Three intervals exhibited very rapid growth, as niche breadth expanded by 483% between 40 and 38 ka, and by 84% between 30 and 26 ka (Fig. 2B). Following the maximum niche breadth at 22 ka, the niche gradually contracted until the end of the Pleistocene at 11 ka (Figs 2B & S10C; $P < 0.001$).

Niche marginality declined throughout the study period (Figs 2B & S10D, E). This decrease through time is not significant ($P = 0.07$), but the results appear to be driven by the last large increase in marginality at 11 ka (excluding the last time interval, the overall pattern shows a significant decrease; $P = 0.002$). Two periods exhibited very rapid growth as niche marginality increased by 59% between 17 and 16 ka and by 74% between 13 and 11 ka, contributing to this pattern of increased marginality. The warmer and wetter conditions occupied by Palaearctic modern humans at the end of the Pleistocene were far from the average conditions for the time extent of our study (which were colder and drier), and were reflected in our results by a final large increase in niche marginality (45%). In contrast to niche overlap, estimates of niche breadth and niche marginality were largely unaffected by the differences in the number of occurrences used per time interval (Figs S7A, B).

Geographical dynamics of the climatic niches of modern humans

Changes in geographical overlap between consecutive time intervals showed no consistent pattern throughout the temporal extent of the study (Fig. S10B; $P = 0.461$), as levels of overlap varied between time intervals (partitioning of geographical overlap values follows that of niche overlap); most intervals (12 out of 23) exhibited medium to high overlap values ($0.6 < D < 0.7$) and four intervals had high overlap values ($D > 0.7$), indicating a stable distribution of suitable climatic conditions throughout the temporal extent of the study. Dividing the temporal extent into two periods (46–26 ka and 26–11 ka) indicated a significant decrease for the early period and no significant change during the second period; however, these patterns were mainly driven by a few medium to low values of geographical overlap (i.e. $D = 0.434$ between 26 and 24 ka and $D = 0.401$ between 12 and 11 ka) (Fig. 2A).

The geographical distribution of the climatic niche of modern humans for each time interval (Fig. S5) revealed the presence of a belt of consistently more suitable climatic conditions across south Siberia (suitability > 0.3) in comparison to the surrounding regions, beginning at 36 ka (Figs 3 & S5). Averaging climatic suitability values in each grid cell across
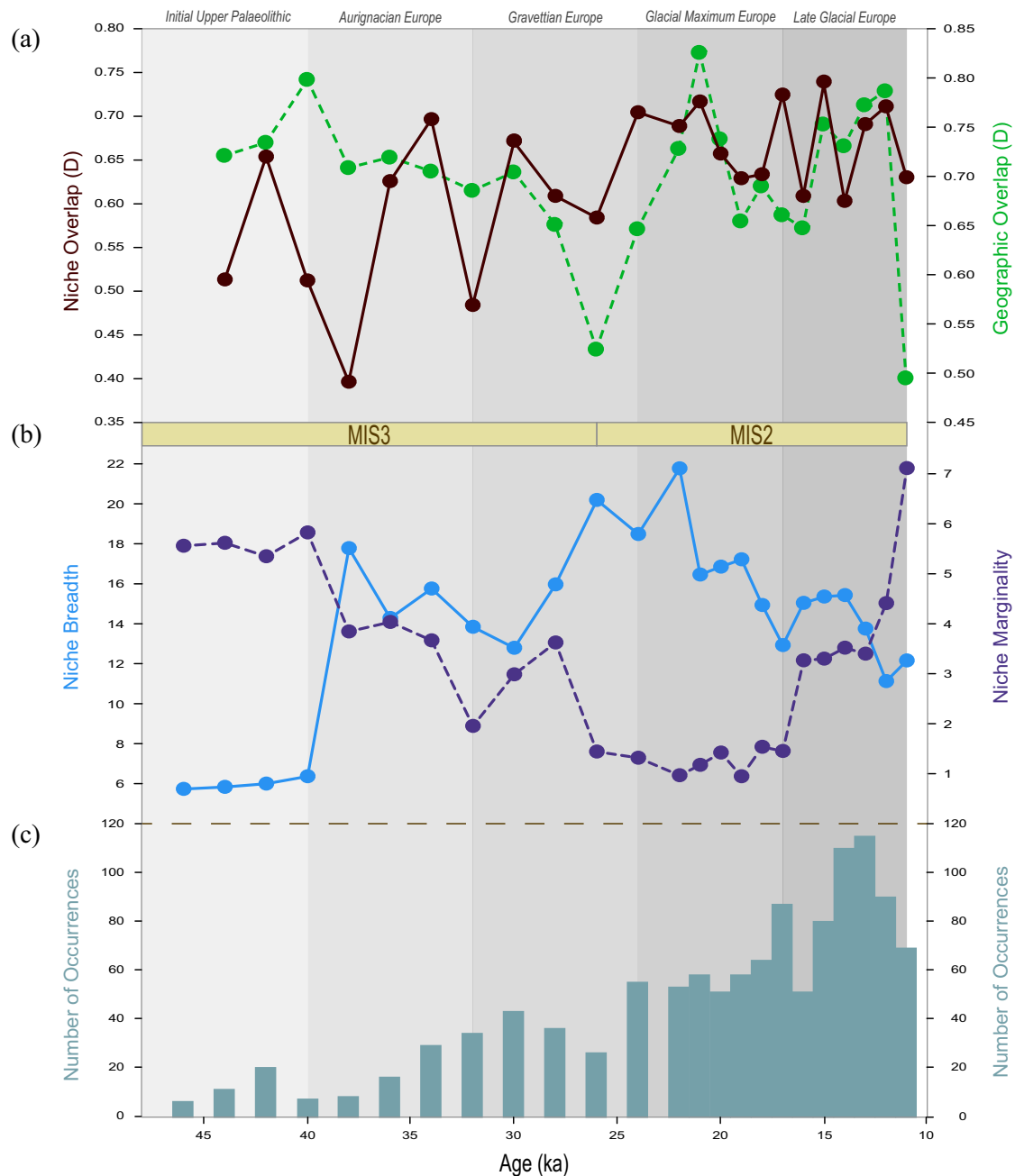
Figure 2 Temporal patterns of climatic niche parameters and geographical overlap between 46 and 11 ka. The upper panel (a) of the graph indicates overlap of the realized climatic niche (dashed brown line) and the geographical overlap of climatically suitable areas (light green line) between consecutive time intervals. The middle panel (b) represents the changes in niche breadth (dashed light blue line) and niche marginality (purple line). The lower panel (c) indicates the number of archaeological occurrences used per time interval for all analyses. Marine Isotope Stage 3 (MIS3) and MIS2 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).

all time intervals showed climatically more stable areas that are isolated from other patches of suitable conditions, occurring in present day east China, Japan, Korea, Kamchatka and submerged areas of Beringia (Fig. 3). Estimates of geographical overlap were not affected by the variability in the number of occurrences used per time interval (Fig. S7D, Table S2D).

Cultural and climatic correlates of niche dynamics

Changes in climate, particularly precipitation, were found to be the strongest correlate of the three niche parameters and of geographical overlap (Tables S4). Change in summer precipitation was the strongest predictor of niche overlap (deviance explained = 57.8%; $P = 0.001$). Changes in niche

breadth were correlated with changes in summer precipitation (deviance explained = 57%; $P = 0.001$), while changes in niche marginality were more strongly correlated with changes in winter precipitation (deviance explained = 52.8%; $P < 0.001$) closely followed by changes in spring precipitation (deviance explained = 49%; $P < 0.001$). Lastly, changes in
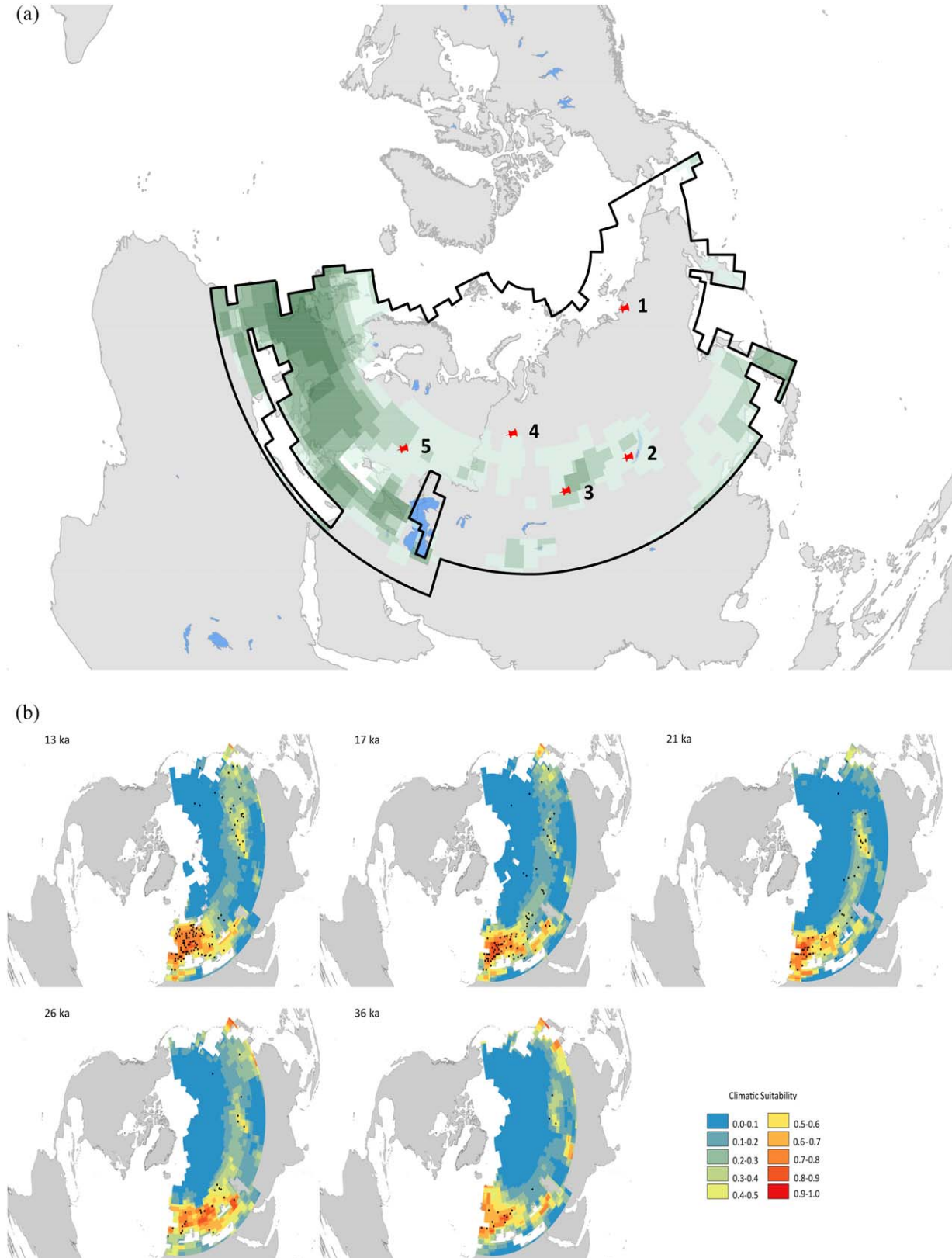
Figure 3 Geographical distribution of the climatic niche of modern humans. (a) Average climatic suitability through time. The coloured areas represent the 30% of the grid cells with the highest average suitability values between 46 and 11 ka. The black line outlines the maximum extent of the study area, including all grid cells above sea level for at least one time interval. Grey areas inside the black outline represent the remaining 70%. Red pins represent locations of Late Pleistocene modern human findings; 1, Yana RHS site; 2, Mal'ta; 3, Denisova cave; 4, Ust'-Ishim; 5, Kostyonki. (b) Potential geographical distribution of Palaearctic modern humans for five time intervals across the temporal extent of this study (36, 26, 21, 17 and 13 ka). All time periods are shown in Fig. S5. Warmer colours indicate higher climatic suitability, and archaeological occurrences (aggregated by grid cell) are indicated by black dots.

geographical overlap were correlated with autumn precipitation (deviance explained = 53.3%; $P < 0.03$). Explained deviance increased between 3% and 54.3% for all GAMs when changes in cultural periods were added to single-variable climatic models (Table S5); however, changes between cultural periods as a single predictor were not statistically significant for any of the niche parameters (Table S6).

DISCUSSION

The realized climatic niche of modern humans expanded as they colonized the Palaearctic, and both climate change and transitions between 'cultural periods' appear to have played a role in those changes. In addition, we found evidence of a region across south Siberia that retained more suitable climatic conditions dating back to 36 ka. During the oldest period, from 46 to 26 ka and roughly coinciding with Marine Isotope Stage 3(MIS3), modern humans expanded their distribution across much of the Palaearctic (Finlayson & Carrion, 2007). Evidence from archaeology 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 (Pitulko *et al.*, 2016). Our results reveal that from 46 to 22 ka, human expansion into new regions of Eurasia was accompanied by increased niche breadth, reflecting the growing variety of climatic conditions that modern humans were able to inhabit and exploit. Under the assumption that the amount of dated material is proportional to established modern human populations (Goldberg *et al.*, 2016), we consider differences in the spatial and temporal coverage of our database of Palaeolithic modern humans to be adequate proxy for estimating biogeographical patterns of *Homo sapiens*. However, estimates of niche overlap are sensitive to small sample sizes and the reported pattern for the first period (46–26 ka) should be interpreted with caution.

Changes in seasonal water availability appear to be a key driver of change in climate niche parameters (Table S4). During the cold and dry conditions of the Last Glacial Maximum (LGM), the rate of gross terrestrial primary productivity was about half that of the pre-industrial Holocene (Ciais *et al.*, 2011). 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 vital resources for hunter-gatherer populations, herbivores and food webs on which they may have depended (Meiri *et al.*, 2014; Graham *et al.*, 2016), consistent with the niche breadth

contraction and the possibly higher values of niche overlap between 26 and 11 ka.

However, our results indicate that transitions to more recent cultural periods also contributed, as a secondary driver, to the ability of modern humans to colonize new climatic conditions (Table S5). Hunter-gatherers during the Late Pleistocene 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 suggested to have been prompted by major episodes of unfavourable conditions (Ziegler *et al.*, 2013), population growth, intra- and inter-population interactions (Powell *et al.*, 2009) and subsistence practices (Stiner & Kuhn, 2006). Upper Palaeolithic hunting tools show considerable variation and diversified rapidly both in time and space, exhibited by the similarities in 'cultural periods' between distant Eurasian populations (Hoffecker, 2005). This tool diversification might stem from the variability of available resources, seasonality and demographic pressure. Modern humans may also have expanded their dietary niche (Hublin, 2015) in response to the need for more efficient resource uptake in the face of scarcity. Consequently, the 'cultural periods' used in our study may not reflect specific technological changes per se, but rather represent adaptations that would enable modern humans to survive in a variety of climatic conditions, thus increasing their realized climatic niche.

The existence of a persistent corridor of suitable climatic conditions 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 & S5). Our results indicate that this corridor linking Europe and Asia (Fig. S5) emerged *c.* 36 ka, in agreement with recent findings based on ancient DNA of European populations in the Middle Don River (Lazaridis *et al.*, 2014). Previous studies have also documented evidence of gene flow between Europeans and central Asian populations (Raghavan *et al.*, 2014). Despite the early emergence of this belt of suitable climatic conditions, it is only after 32 ka that this route remains nearly continuously suitable until 18 ka. Modern humans have been recorded in south Siberia as early as 45 ka (Fu *et al.*, 2014), and occupations have been detected at relatively low frequencies in this region since 36 ka, but with substantially increased frequency after 16 ka (Kuzmin & Keates, 2005). Recent genomic sequencing of ancient DNA from two individuals from north-eastern Siberia, dated at 24

and 17 ka, suggests that modern humans occupied this region throughout the LGM (Raghavan *et al.*, 2014). Whether this indicates continuous occupation or the region was mainly depopulated during the LGM is still debated (Goebel *et al.*, 2008). 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 (Hoffecker, 2005), suggesting, in light of our results (Fig. 3), that some pioneering human populations either survived in conditions of extremely unsuitable climate and low-productivity ecosystems (but see Allen *et al.*, 2010) or in micro-refugia at a spatial scale that is poorly reflected by the 2° spatial resolution of our palaeoclimatic simulations. Surprisingly, the area south of this mid-latitude belt in Asia (south of 48° latitude, apart from eastern China) also exhibited low climatic suitability for most time intervals of the analyses (Fig. S5). This could reflect the 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 (Boivin *et al.*, 2013).

Climate conditions in Europe were consistently more suitable than that of eastern Eurasia. 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. Beringia has already been proposed as a potential refugium for modern humans and other animal and plant species based on records from sea-floor sediments (Meiri *et al.*, 2014) and from the presence of similar ecosystems in analogous latitudes (Willerslev *et al.*, 2014).

Naturally, there are caveats associated with our analyses of the early biogeography of modern humans. First, our results are contingent on this particular occurrence dataset, and the 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 geographical 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 multiple dates among artefacts from a single site (Svenning *et al.*, 2011). To reduce the impact of these biases on our results, niche parameter and geographical distribution of the climatic niche 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 S2–S4). However, the estimates of niche overlap were shown to be sensitive to

sampling intensity, and we call for a careful interpretation of niche overlap dynamics. Second, while high-resolution climatic reconstructions vastly improve our ability to investigate the processes governing human range expansion, even 1000-year intervals cannot capture the abrupt climatic events (i.e. Heinrich events and Dansgaard–Oschger events; Singarayer *et al.*, 2011) which probably affected the distributions of humans and other species (Bradtmoller *et al.*, 2012), and the spatial resolution of 2° hampers the ability to detect refugia of small extent. However, even if the temporal resolutions of these reconstructions were higher, the precision of ^{14}C dating does not permit detailed interpretations. Our results may therefore underestimate the abrupt nature of climate niche dynamics. Third, our results are based on only one general circulation model (HadCM3). The variability among predictions of past rainfall and patterns by different GCMs can influence the output of niche estimates and/or CEMs and consequently the importance of specific climatic variables over others (Varela *et al.*, 2015), but the impact of GCM choice on model outputs has been shown to be of a secondary significance (Lorenzen *et al.*, 2011). Lastly, 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 multiple 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 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 palaeorecords in a unique quantitative framework, and reveals changes in the realized climatic niche of modern humans during their settlement across the Palaearctic. These methods provide insights that are distinct from, but complementary to, other modes of inference such as archaeology 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 evidence will allow exploration of the effects of climate change on genetic diversity, population size and genomic evolution in Palaearctic modern humans, as has been done for other species of megafauna (Lorenzen *et al.*, 2011; Metcalf *et al.*, 2014). We can also identify potential climatic refugia that may be targeted for future fieldwork exploration to find previously undiscovered settlement sites and human remains. Additionally, this approach can provide clues as to where early modern humans may have overlapped in geographical and/or environmental space with Neanderthals (Fu *et al.*, 2014; Nigst *et al.*, 2014) or Denisovans, as evidenced by their contribution to our genetic heritage (Huerta-Sanchez *et al.*, 2014; Vernot & Akey, 2014), and may shed new light on the mechanisms, such as competition for resources, underlying their

gradual geographical replacement and extinction during our global expansion.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site:

Figure S1 Modern human occurrences for all time intervals between 46 and 11 ka.

Figure S2 Changes in niche overlap between 46 and 11 ka, based on the number of occurrences used per time interval.

Figure S3 Changes in niche breadth between 46 and 11 ka.

Figure S4 Changes in niche marginality between 46 and 11 ka.

Figure S5 Maps of climatic suitability for modern humans in the Palaearctic between 42 and 11 ka.

Figure S6 Temporal changes in geographical overlap of climatic suitability using MaxEnt to construct Climate Envelope Models, between 46 and 11 ka.

Figure S7 Temporal changes in niche parameter and geographical overlap estimates between 46 and 11 ka, using different sample sizes of modern human occurrences for time intervals after 26 ka.

Figure S8 Changes in niche parameters and geographical overlap between 46 and 11 ka using bi-millennial (2000 year) time steps.

Figure S9 Box-plots of niche parameters and geographical overlap estimates using millennial versus bi-millennial time bins.

Figure S10 Linear regressions of niche parameters and geographical overlap versus time.

Figure S11 Number of occurrences per time interval used for all of the analyses.

Figure S12 Number of occurrences per time interval used for all of the analyses based on the grid cell coordinates.

Figure S13 Distribution of modern human remains per time interval in corresponding PCA climatic space, based on the grid cell coordinates.

Table S1 Results of the Monte Carlo randomization tests on modern human niche marginality through time.

Tables S2 Pearson's correlation coefficients (r) between original estimates of all niche parameters and median values of 100 subsamples using different values as sample sizes of modern human occurrences.

Table S3 Results of MaxEnt model evaluation for each time interval using the continuous Boyce index. Spearman's rho values correspond to the ability of each model to accurately predict true presences.

Table S4 Generalized additive models regressing each of the niche parameter changes and geographical overlap versus climatic changes.

Table S5 Generalized additive models regressing each of the niche parameter changes and geographical overlap versus climatic changes and changes between cultural periods as factor with five levels.

Tables S6 Generalized additive models regressing each of the niche parameter changes and geographical overlap versus changes between cultural periods as a factor with five levels.

BIOSKETCH

Konstantinos Giampoudakis's main research interest is to understand why and how *Homo sapiens* successfully spread across the planet and how they shaped ecosystems and communities during the Late Pleistocene. Using macroecological tools, fossil record and genetic data in a multi-temporal framework, he aims to answer questions that can improve our understanding about the ecology of humans and better anticipate future responses of species to anthropogenic climate change and habitat alteration.

Editor: Adam Algar