

The onset of the Neanderthal world: Exploring ecological niche dynamics and technological variability across Marine Isotope Stages 12, 11 and 10

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Abstract

Following the intense MIS 12 glacial is situated an important period of human evolution contemporaneous with the appearance of Neanderthal anatomical features, around 430,000 years ago, that is commonly described as a threshold for behavioural change in Western Europe. Specifically, we observe an increase in the number of well-preserved archaeological occupations, the appearance of technological innovations, and new subsistence behaviours in certain regions of Europe. This pattern suggests the emergence of regional cultural traditions, although the factors behind the appearance of certain technological innovations, such as the Levallois method, during this period of climatic amelioration remain unexplored. We employ ecological niche modelling tools to examine Western Europe's archaeological record across Marine Isotope Stages (MIS) 12–10. Specifically, using ellipsoid models, we estimate basal Neanderthal ecological niches and their potential geographic ranges for each MIS, and two intervals within MIS 11. With these results, we evaluate the relationship between ecological niche characteristics, niche dynamics, environmental suitability and lithic technological variability. We find that the hominin ecological niche is spatiotemporally dynamic across the entire study period and exhibits a relatively large increase in volume for phases that follow MIS 12 – MIS 11 (split into MIS 11c and MIS11ab) and MIS 10. We find few clear relationships between environmental suitability and lithic technologies or innovations. Rather, early Neanderthals maintained a variety of lithic reduction methods within their behavioural repertoire and achieved culturally adaptive flexibility by employing varying combinations of them.

1. Introduction

Hominin groups were present in southern and western portions of Europe as early as ca. 1.5 million years ago (Ma) during the Lower Pleistocene. Despite a presence across these broad regions for a relatively long period of time, the archaeological record and modelling work indicate that occupation was not permanent and that Europe witnessed periods during which it was uninhabited [1, 2]. Reconstructions indicate a severe drop in habitat suitability around 1.1 Ma suggesting that hominin groups were unable to occupy Europe during and following the climatically severe conditions of Marine Isotope Stage (MIS) 34. This is supported by the paucity of material culture and human fossil remains until approximately MIS 25 (ca. 1 Ma), or even possibly as late as MIS 22: ca. 900 kiloanni ago (ka). These findings corroborate prior findings that Europe—or at least significant portions of it—had been depopulated after initial settlement [3–5] and contradict propositions that environmental conditions in certain regions would have allowed for a continuous human presence in Europe [6].

While a hominin presence may have been permanent as of MIS 22, not all regions were continuously occupied. Dennell et al. [7] propose that while some were occupied during certain climatic regimes, others, such as those at high latitudes, possessed environmental conditions that hunter-gatherer groups could not occupy with the technological adaptations they possessed [2]. It is proposed that the former served as 'sources' and the latter as 'sinks' [7], which is founded on the model proposed earlier in the field of ecology [8]. During rigorous climatic episodes, groups would not have necessarily retreated to more

persistently favourable areas (i.e., refugia), but rather went extinct. During a subsequent period of climatic amelioration, peripheral regions would have been repopulated by groups from source regions. Under such a scenario, the archaeological record does not reflect repeated contractions and expansions from regions of refugia, but rather a long-term pattern of repeated local extinctions and resettlement of peripheral areas synchronous with climatic and environmental fluctuations.

By MIS 13, hominins were present across much of Europe and occupied a diverse range of environments [9, 10], likely reflecting the resettlement of numerous regions from source populations. This source/sink pattern, though, appears to have changed by MIS 12, a long and severe glacial event. For example, during this period we observe a hominin presence at the site of Cargny-la-Garenne in present-day Northwestern France [11, 12]. Thus, by ca. 500 ka, hominin groups possessed technological adaptations that permitted them to exploit regions of Europe in which they previously did not persist during severe climatic episodes. It appears, though, that this ability had been acquired, at least to some degree, by as early as MIS 16 (ca. 650 ka) based on the assemblages recovered from the site of Moulin Quignon in Northwestern France [13, 14]. The continuous occupation of such regions would have been facilitated by, or was perhaps due to, the emergence of cumulative culture, proposed to have been present by at least 600 ka [15] and the resulting and maintained cultural innovations that would have permitted occupations in regions characterized by severe conditions. By MIS 11, which begins ca. 426 ka [16], we observe the emergence of Levallois core technology added to the basal Neanderthal technological repertoire. During this long warm climatic stage, hominin groups employed a broad range of technologies, many with a long history of use, in a diverse range of environments across large areas of Europe. An analysis of the Iberian archaeological record prior to, during and following MIS 11 indicates that basal Neanderthals occupied a broader ecological niche, i.e. a broader range of environmental conditions, following 426 ka [5]. This conclusion, though, is not supported by an analysis of paleoclimatic preferences across Europe during MIS 13 and 11, which concluded that the expanded archaeological record of MIS 11c was not due to an overall broadening of the hominin climatic niche but rather to the extended duration of this phase's mild conditions [17]. Both of these studies, however, point out that the hominin niche was likely characterized by regional variability [5, 17].

1.1. Paleoclimatic context

MIS 11 was a period of reduced global ice volume composed of a single interglacial and a number of interstadial and stadial events [18] (Fig. 1), and it followed one of the most extensive glaciations of the last 1 million years: MIS 12 [19]. A period of 20,000 years separates the end of MIS 12 and MIS 11's thermal maximum, the MIS 11c interglacial [18], which occurred between 415–405 ka [20]. Ice sheet wastage during MIS 11c was significant due to its extended duration, and minimum ice sheet volume and maximum sea-level occurred ca. 405 ka during the latter part of its thermal maximum [20].

An 'interglacial' climatic episode is a period during which terrestrial records are characterized by a percentage of arboreal pollen greater than that of grass and shrub pollen. Southwestern Europe witnessed the expansion of woodland environments at the onset of MIS 11c, while this trend was delayed

in Northern regions of Europe characterized until then by open landscapes [18, 20]. Consequently, Europe as a whole did not see full interglacial woodland conditions until the latter part of MIS 11c. Climatic and thus vegetation conditions were not stable and unchanging and data indicate abrupt shifts. Such variability occurred on millennial timescales, although evidence indicates that in Northern Europe it was even more rapid and occurred on centennial timescales [20]. In conjunction with vegetation variability are observed periods of weakening in the Atlantic meridional overturning circulation brought about by wasting of the Greenland ice sheet [20, 21].

After ca. 396 ka, which marks the end of the MIS 11c interglacial, conditions began to progressively cool during the MIS 11b stadial, which has a period of maximum cooling centered on 375 ka [18]. This stadial is followed by a brief, weakly expressed interstadial (MIS 11a) that briefly interrupted the general cooling trend prior to MIS 10. This cooling trend is a significant departure from the conditions present during the preceding MIS 11c interglacial.

1.2. MIS 12 – 10 lithic technological variability

The lithic technologies employed by early Neanderthals during MIS 11 were varied and do not show clear patterning. The broad lithic technocomplex of this period can be described as one that incorporated various methods for producing flake blanks via cores exhibiting differing degrees of preparation, unretouched and retouched flake tools, and the occasional incorporation of bifacial handaxes and cleavers [10]. Acheulean bifaces receive a great deal of attention when investigating hominin behaviours and adaptations, but flake technologies are always present and are the foundation of the broad lithic technocomplex present in Europe during MIS 11.

While formal Levallois technology is well in place by the end of MIS 9, this technological innovation for producing standardized flake blanks appears as early as MIS 12 (e.g., the site of Cagny-la-Garenne). In Western Europe, it appears to be the result of transformations of flake core technologies present in Acheulean and Lower Palaeolithic assemblages [26]. The appearance of Levallois reduction methods during MIS 12 and MIS 11 seems to have multiple modes of origin, which is supported by the regionalization of Levallois technical features during later periods [26]. This is not surprising considering that Acheulean bifaces begin to show regional stylistic differences in Northwestern Europe prior to MIS 12/11 [27]. This pattern is supported by the presence of regionalized suites of skeletal traits [7], as well as genetic data indicating that basal Neanderthals were present as largely isolated, local groups [28].

Although Levallois technology typically represents a minor component of lithic assemblages at individual archaeological levels, its presence provides important insights into technological organisation and variability. With its production of standardized, predetermined flake blanks, the addition of Levallois techniques to the broader technological repertoire would suggest hominins aimed to increase toolkit, and thus behavioural, flexibility. During MIS 11, there is an increase in light-duty toolkits, with Levallois flakes being more efficient compared to other tool production methods (e.g., discoidal), as they could be used without needing to be retouched or modified. This suggests that the presence of Levallois technology

may reflect activities or settlement and subsistence behaviours linked to specific portions of the basal Neanderthal ecological niche.

1.3. Study aims

The archaeological record covering MIS 12–10 is sparse and characterized by coarse chronological data and often-discontinuous paleoenvironmental records. The exhaustive archaeological database and ecological niche modelling approach that we employ make it possible to estimate accurately the existing fundamental ecological niche for hominin groups that shared a common cohesive adaptive system [29] across this period of climatic and technological variability. Furthermore, in so doing, it is possible to evaluate previous inferences of the early Neanderthal niche [16, 17]. More importantly, the increased corpus of archaeological data associated with MIS 11 makes it possible to examine whether certain lithic technologies or technological adaptations were associated with specific portions of the hominin ecological niche or regions characterized by elevated or low environmental suitability.

Via an approach that incorporates ecological niche modelling methods with a detailed examination of archaeological and lithic technological data [30, 31], this study targets two objectives. The first is to estimate the Western European basal Neanderthal ecological niche across the climatic variability of MIS 12 to MIS 10 and determine whether it significantly changed between MIS 12, the MIS 11 climatic optimum ca. 400 ka, and later cooler conditions (MIS 11 ab) prior to and during MIS 10 (Fig. 2). The second objective is to investigate whether specific lithic technologies, and specifically the Levallois innovation, were associated with particular environments or portions of the Neanderthal ecological niche.

With respect to the first objective, we expect any observed changes in the niche through time (e.g., contraction, expansion) will reflect differing ranges of climatic conditions for habitual Neanderthal territories as a result of shifts between interglacial and stadial conditions. This expectation is based on the distribution of archaeological occurrences for each of the periods that we examine, the concept of source and sink populations [7], and evidence to suggest that hominin groups were territorially stable through time [10]. The expectation of territoriality reflects patterns (e.g., limited circulation of lithic raw materials, regional artefact styles) observed in the archaeological records in numerous regions for this and preceding marine isotope stages [9, 10, 13, 26, 27] and assumes a deep history for the pattern observed for Neanderthals during a later period of the Middle Paleolithic in Western Europe [33]. With respect to technology, we hypothesize that Levallois core technology, a clear marker of technological, and thus cultural, innovation, will be associated with lower levels of habitat suitability, as has been observed during MIS 4 [33]. More precisely, we expect to see Levallois technology present in areas of the ecological niche characterized by lower environmental suitability, thereby resulting in a rejection of a null hypothesis of no relationship between the presence of Levallois and ecology.

2. Results

2.1. Ecological niche modelling

Hominin niche volume from MIS 12 (volume = 26.61) to MIS 11c (volume = 125.94) sees a large increase (Fig. 3A, Table 1). The niche then slightly contracts during cool MIS 11ab (volume = 87.95; Fig. 3A; Table 1) indicating that Neanderthal groups occupied a broader range of environmental conditions during the warmer part of MIS 11. A similar niche volume to MIS 11c, albeit slightly reduced, is observed for the MIS 10 glacial (volume = 119.02; Fig. 3A, Table 1). The expansion during MIS 11c is principally due to PC2 and PC3, reflecting a broader range of seasonality values being occupied (e.g. bio04 and bio15) while that during MIS 10 is principally due to PC1, expressed as an increase in the range of temperature values (especially in bio05 and bio10) (Figure S1; Supplementary Tables S2–S4).

Geographic projections of the ellipsoid niche models (Fig. 3A) indicate that the MIS 12 niche is spatially fragmented (Fig. 3B), which is supported by a highly disjointed accessible area M consisting of a core region of suitability in northern Europe and limited zones of occupation around isolated sites in Southwest France and Italy. This core region of suitability contracts when projected onto MIS 11c conditions to a limited zone in Northern France and Southeastern Britain (Fig. 3C). Niche expansion extends the zone of suitability southwards during MIS 11c (Fig. 3D). During temperate MIS 11c, areas of elevated suitability are situated in what is now Southeastern Great Britain as well as Northern and Western France, with more restricted areas of elevated suitability in portions of Northeastern Iberia and Southern Italy (Fig. 3D). When projecting the MIS 11c niche onto MIS 11ab conditions, its suitable areas fragment and shift southwards and northwards (Fig. 3E) indicating an extended but patchy geographic expression of its environmental conditions during these following cooler phases. The geographic areas of highest suitability for the MIS 11ab niche are observed in patches of Southern Italy and Northeastern Iberia, but there is no single continuous habitable zone during this period, reflecting the highly patchy M accessible area (Fig. 3F). When the MIS 11ab niche ellipsoid is projected geographically onto MIS 10 conditions, one observes a significantly smaller geographic expression of suitability, with suitable areas restricted to more southern and northern areas (Fig. 3G). In comparison, the geographic expression of the MIS 10 niche (Fig. 3H), exhibits highly suitable areas in Central France and a large portion of Iberia. This distribution differs considerably from the MIS 11ab niche projected onto MIS 10 conditions.

Despite these clear geographic differences in niche distribution through time, the MIS 12, MIS 11c, MIS 11ab and MIS 10 ellipsoids display a high degree of overlap (Fig. 3A; Fig. 4A), with only PC2 scores from MIS 12 and MIS 10 occupations showing significant differences (Supplementary Figure S1; Supplementary Table S5). Statistical comparisons of the raw climatic variables at the sites, however, do show statistically significant increases in annual temperature (bio01) and temperature extremes (bio06, bio10, bio11) from MIS 12 to MIS 11c, decreases in net primary productivity (npp) from MIS 11c to MIS 11ab, and decreases in temperature annual range (bio07) from MIS 11ab to MIS 10 (Supplementary Figure S1; Supplementary Table S5). Precipitation, on the other hand, shows much less variability with no significant differences between phases (Supplementary Figure S1; Supplementary Table S5).

Despite these significant changes in individual variables (particularly temperature) through time, when accounting for all environmental conditions available during each period, the differences in the Neanderthal niche between each phase are not greater than what would be expected by chance (Table 1).

Thus, the null hypothesis of no difference (overlap among niches) cannot be rejected for any of the comparisons (Table 1; Fig. 4B). Sensitivity testing employing resampling demonstrates these results to be robust to climatic variability within MIS phases (Supplementary Table S1).

Table 1

Niche overlap results. Statistically significant differences are denoted by (*) and represent $p < 0.05$.

MIS division	Ellipsoid volume	Overlap test	Total points	Overlapped points	Overlap	p-value	Volume ratio	Diachronic niche dynamic
MIS 12	26.61	—	—	—	—	—	—	—
MIS 11c	125.94	—	—	—	—	—	—	—
		MIS 12 vs MIS 11c	2072	565	0.27	0.47	4.73	Expansion
MIS 11ab	87.95	—	—	—	—	—	—	—
		MIS 11c vs MIS 11ab	2641	826	0.31	0.10	0.70	Slight contraction
MIS 10	119.02	—	—	—	—	—	—	—
		MIS 11ab vs MIS 10	2618	976	0.37	0.13	1.35	Slight expansion

Given that the overlap between MIS 12, MIS 11c, MIS 11ab and MIS 10 niches does not deviate from the null hypothesis of no difference, an ellipsoid model using the combined occurrence data captures the full range of environmental conditions occupied by basal Neanderthal populations in our study area throughout this period (Fig. 4C). Compared to other accessible areas outside of the niche (Fig. 4C), the final Neanderthal niche falls positively along PC1 and PC3, suggesting occupation of the warmer and drier areas of the landscape (Supplementary Table S2, Supplementary Table S4). Geographic projection of the final niche model suggests that during MIS 12 suitable areas were widespread, though concentrated in Central and southern Iberia, southern Italy and Central France (Fig. 4D). However, sites in some of the most optimal regions (according to the overall basal Neanderthal niche incorporating all phases) had limited *M* accessible area based on only the MIS 12 sites, suggesting potentially restricted mobility. During the MIS 11c interglacial, the most highly suitable areas were more concentrated in Northeastern France, Southern Britain and Northern Iberia (Fig. 4E). During MIS 11ab, much of Western Europe was highly suitable for occupation with the most suitable areas are present in Southwestern France and Northeastern Iberia (Fig. 4F). The geographic projection of the niche onto MIS 10 climatic

layers indicates a more fragmented distribution of suitable areas, with pockets of suitability in Southeastern Iberia, as well as much of Britain and Italy (Fig. 4G).

2.2. Technological analysis

We first explored differences in suitability scores (extracted from the final niche model) in assemblages based on presence/absence data of specific lithic technologies and tool types. We find almost no significant relationships with suitability, with the exception that assemblages with a predominance of scrapers ($p = 0.04$) are associated with lower suitability scores compared to sites where scrapers do not dominate (Supplementary Table S6, Supplementary Figure S2). While not reaching the threshold for significance, assemblages with non-diagnostic LCTs ($p = 0.07$) and Levallois reduction ($p = 0.09$) show some evidence of being associated with lower suitability areas compared to assemblages where these are absent. Similarly while not significant, the presence of fire ($p = 0.09$) is associated with areas of higher suitability.

We next compared environmental suitability within technological categories (lithic technocomplex, Levallois types, LCTs, biface types, flake tools, raw materials and platform preparation), specifically between assemblages in which each attribute is present. We found that Levallois is generally found in slightly lower suitability areas compared to other reduction methods, particularly orthogonal and unipolar reduction (Supplementary Figure S3), with preferential Levallois found in the lowest suitability areas compared to other types (Supplementary Figure S4). Non-diagnostic LCTs are associated with lower suitability compared to picks, bifaces and cleavers (Supplementary Figure S5), with few differences between biface types (Supplementary Figure S6). Supporting the presence vs absence tests, assemblages with primarily scrapers are found in lower suitability areas compared to assemblages with other flake tool compositions, particularly compared to those with more denticulates or notches (Supplementary Figure S7). Assemblages where limestone dominates tend to be in lower suitability areas compared to those with only flint or multiple raw materials (Supplementary Figure S8). Platform preparation tends to be found in slightly lower suitability areas compared to non-prepared platforms (Supplementary Figure S9). However, only one of these tests returned significant results, suggesting that the presence of specific attributes within each technological category is not correlated with environmental suitability (Supplementary Figures S3–S9).

We then considered multivariate relationships between suitability and MIS 12–10 technologies, using all of the archaeological data and different cultural and technological subsets (Fig. 5A). Results of the multiple correspondence analysis (MCA) for all technologies indicate that the presence of indistinct Levallois, as well as the absence of specific Levallois varieties, bifaces, the presence of prepared platforms, scrapers and denticulates, and the absence of unipolar reduction cluster positively along Dim.1 (representing 27.9% of variability in the data) and Dim.2 (11.6% of the total variation) and are associated with sites from Southern France and Iberia (Fig. 5A). British sites (and others primarily from Central and Northern France such as La Celle, Ferme de l'Épinette and Cagny la Garenne) cluster negatively along both dimensions, largely due to the presence of flint and the absence of other raw materials, platform preparation and centripetal Levallois reduction (Fig. 5A and B). The presence of picks

and cleavers contribute negatively to Dim.1 and positively to Dim.2, clustering with MIS 11c sites, such as Menez Dregan and Terra Amata.

Suitability is negatively correlated with Dim. 1 and positively correlated with Dim. 2 (Fig. 5B), though this relationship is not strong given the distribution of sites along the two axes and the measure indicated by the red arrow in Fig. 5B. This supports the statistical results demonstrating that the overall expression of technological variability during MIS12–10 is not significantly associated with ecological niche characteristics. Nonetheless, Fig. 5C highlights how the different chronological periods relate to these two dimensions constructed using technological data. All of the periods overlap considerably in terms of technology. Yet sites from MIS 12, MIS 11c, and to a lesser extent MIS 11ab, show substantial similarities, although MIS 11ab is more differentiated. In MIS 11ab, many assemblages fall negatively along Dim.2. and are characterized by the absence of bifaces and distinct Levallois variants, as well as the presence of picks and cleavers. This technological diversification during MIS 11ab, compared to MIS 11c, corresponds to a slight contraction in niche volume and is the inverse of the, albeit weak, relationship with suitability (arrow in Fig. 5B). MIS 10 assemblages conversely tend to fall more positively along both dimensions.

3. Discussion

MIS 11 is a period during which we observe the beginnings of ‘Neanderthalisation’ in the hominin lineage. Following the intense glacial of MIS 12, considered to be a major climatic crisis for both hominins and fauna [34, 35], there is an increase in the number of well-preserved occupation levels in Western Europe and the appearance of new subsistence behaviours and technological innovations in specific areas that later become fully expressed by Neanderthals during the Middle Paleolithic. It has been hypothesized that MIS 11’s relatively long interglacial may have been crucial for the regionalization of behaviour [16] by providing an increased opportunity for innovation [26, 36–38], and this by groups possessing the capacity for cumulative culture [15].

Our results indicate that hominins in Western Europe occupied a wider range of environments across the available landscape from the onset of MIS 11 into MIS 10. However, despite MIS 11 being a period of relative stability, areas considered to be the most suitable for hominin populations still fluctuated geographically as a result of temporal climatic variability. Southern areas became more ecologically suitable during the cooler conditions of MIS 11ab, supporting previous work [39]. Despite these shifts in suitable area, we highlight a broad maintenance of territories, particularly in Britain. Such territorial stability mirrors the pattern observed with Neanderthals in Western Europe later during the Middle Paleolithic [33] and demonstrates that basal Neanderthal groups during MIS 11 were capable of adapting to significant environmental variability without needing to alter their territories in order to follow the shifting footprint of their niche across a period of climatic cooling. Sites in Britain during cooler periods of MIS 11 are deemed suitable in our niche model, yet during MIS 12 sites in the same area are associated with lower suitability, suggesting that following this glacial period, hominins adaptation served to overcome the ‘overwintering problem’ even in relatively unproductive environments [40, 41]. We

find that the lithic technocomplexes observed at sites in Britain remain similar across these environmental shifts, consisting mainly of orthogonal and unipolar knapping methods (rooted in the past) and a large cutting toolkit composed primarily of bifaces. Biface morphology is, however, variable, [37, 42] thus supporting the hypothesis of localized, well delineated group territories and cultural traditions [38]. We propose that such variability in the use of broadly similar technological substrates reflects population-level plasticity in how technology was employed at different sites, with manufacturing traditions persisting through time and across space regardless of climate change [43]. Variability in hand-axe form also may reflect the arrival of new groups or the diffusion of new traditions, facilitated by periods of low sea levels and/or local cultural evolution.

Within southern regions, pollen-based climatic reconstructions in the Mediterranean show MIS 11 to have been a relatively warm, stable period [16]. Such a long-lasting interglacial after the severe MIS 12 glacial favoured the development of vegetation conducive to animal and human settlement in these areas, likely leading to higher population densities [44]. Our niche models confirm that areas of Southwestern France, Northeastern Iberia and Southern Italy became suitable for human occupation throughout cooler periods of MIS 11 and MIS 10, potentially supporting stable populations or demographic 'sources' [7]. Demographic stability is important for the emergence, maintenance and diffusion of cultural traits; the sustained presence of hominin groups is more likely in areas of higher suitability, thus providing the demographics necessary for the emergence and maintenance of novel cultural (e.g., technological) innovations [45].

We find few correlations between lithic technologies and environmental suitability measures of the hominin niche from MIS 12 to MIS 10. The absence of marked and robust links between ecological parameters and lithic technocomplex across the roughly 100,000-year period that we examine indicates a high level of flexibility in basal Neanderthal technologies and raw material procurement strategies. Our results demonstrate that lithic assemblage composition reflects cultural technological preferences, raw material availability, and site activities (i.e., specific technological needs) rather than the patterned exploitation of specific environmental conditions with a specific technology. Even though Levallois is generally associated with lower suitability scores more than other reduction methods, the relationship is not statistically significant. We, therefore, cannot reject the null hypothesis of no link between Levallois technology and habitat suitability within the basal Neanderthal niche.

The weak influence of ecological factors on the technological patterns that we observe from MIS 12 to MIS 10, and the technological behavioural flexibility that we infer, indicate that caution is warranted when evaluating relationships between ecology and individual lithic technologies during the Lower Paleolithic. In finding that ecology is not a strong predictor of technology and that combinations of lithic technologies could alternatively reflect regional cultural preferences, raw material availability, or technological needs during particular site occupations, examinations of culture-environment relationships that focus solely on a specific technological feature (e.g. Acheulean bifaces [46]) are unlikely to capture the full range of expressed cultural variability. Behavioural changes associated with 'Neanderthalisation' (i.e., 'the Acheulean package') become widespread across large portions of Europe

by MIS 13 [4] and are typically found in association with flake-based lithic reduction methods. The subsequent emergence and distribution of Levallois technology illustrates this technological flexibility, given its convergent appearance in multiple contexts across Europe [47], where it is not necessarily associated with complex centripetal or discoidal reduction strategies. This variability suggests that the presence of individual technological features should not be interpreted in isolation, but rather as part of broader technological systems shaped by multiple interacting factors.

The only technological signal we find to have a statistically significant relationship with ecological suitability is the presence of scrapers. Hosfield [17] proposes that the long period of relative climatic stability during MIS 11c allowed for the development of regional expressions of lithic technological behavioural packages. This hypothesis, however, implies that regional technological variability is linked to local ecological parameters. While our results suggest that some relationships may exist, they are more related to other processes rather than characteristics of the existing fundamental niche (i.e., ecological suitability). Therefore, we propose that the variability observed in the MIS 12 to MIS 10 archaeological record reflects more the influence of cultural factors and that these factors are likely linked to changes in cognition coincident with the appearance of Neanderthal anatomical features [48]. DNA evidence suggests that as early as 600 ka, among Heidelbergensis populations, there was substantial genetic drift [49, 50]. It is possible that one of the results of such drift was an increase in cognitive capacity as hominins began to acquire more Neanderthal features, one of which was increased cranial capacity. Certain cultural and technological behavioural changes, inferred from observed changes in material culture assemblages, appear prior to MIS 12. This trend continued into MIS 11 and MIS 10 when we see behavioural flexibility expressed by the large spectrum of employed technological combinations. In other words, basal Neanderthal populations possessed the behavioural, and thus cultural, flexibility necessary to adapt to environmental reorganizations resulting from climate variability.

4. Materials and Methods

4.1. Occurrence Data

Estimating past hominin ecological niches requires occurrence data (i.e., archaeological sites) indicating a human presence at a location at a particular point in time. We reviewed the available literature to compile a list of sites in our defined study area (see below) possessing archaeological levels and associated material culture assemblages that can be attributed to the period spanning MIS 12–10. To this corpus, we added our assemblage data [47]. We note that Rineau et al. [47] record the presence of Levallois at two UK sites (Barham and Scanscombe UMG); however, this is unpublished and the method used is unknown. Next, we examined the chronological attributions for each archaeological level in order to retain occurrence data that are reliably associated with MIS 12, MIS 11 and MIS 10. Chronological data from archaeological levels of this period, however, are relatively imprecise thereby often making it difficult to determine with certainty with which marine isotope stage, or specific portion of it, an assemblage is associated. We, therefore, also relied on various proxy data (e.g. fauna assemblage species composition, pollen, sedimentology, etc.) to assign 39 assemblages to one of the three targeted MIS (Supplementary

Data File S1). MIS 11 covers a period of roughly 60,000 years (ca. 425–370 ka) [18] and was marked by pronounced climatic variability, so we also refined the chronological placement of the occurrence data within this isotope stage by assigning them to either temperate (MIS 11c interglacial) or cool (MIS 11ab stadial) conditions. In instances for which no such data were available or for which they were ambiguous, we did not retain the site level in the final occurrence dataset (Supplementary Data File S1). The final dataset contains 30 archaeological sites with a total of 39 archaeological levels (Supplementary Data File S1). Duplicate occurrences—sites situated within the same raster pixel of the climate model time series—were removed for the modelling such that only one site was retained per grid square. The retained 22 occurrences for MIS 12 (n = 4), MIS 11c (n = 10), MIS 11ab (n = 6) and MIS 10 (n = 10), are contained in Supplementary Table S7. Since we aimed to examine potential relationships between lithic technology and environmental suitability across these phases, all chronologically attributable archaeological sites were retained for the technological analysis, regardless of the technological composition of their lithic assemblages. The reason being that individual archaeological levels during this period are often characterized by a high degree of technological variability and varying frequencies of innovations. This variability makes the examination of only a single type of technology or innovation, such as Levallois, and its relationship to environmental parameters potentially incomplete. The same holds true for bifacial technology, which is not always present in assemblages of our period of study. Furthermore, when present, it is always associated with differing frequencies of flake technologies. Our approach, therefore, differs from one focused on only a single technological characteristic [46].

4.2. Lithic technological data

In order to examine the possible relationships between ecology and the presence or absence of specific lithic technologies, we retained relevant characteristics of the archaeological site occurrences' lithic assemblages (Supplementary Data File S1). These include both behavioural innovations (fire, Levallois, core management), as well as data concerning debitage methods, raw materials, and large and light-duty tools that characterize the assemblages: (1) Fire evidence; (2) Lithic technocomplex : U (unifacial), C (centripetal), O (orthogonal-SSDA), M (Multifacial), D (Discoid), L (Levallois); (3) Levallois core technology: U (unipolar), C (centripetal), E (preferential flake), I (indet.); (4) Large Cutting Tools categories (LCT): B (bifaces), P (picks), C (cleavers), O (others); (5) Biface details: BO (oval bifaces), BP (pointed bifaces), BF (bifaces on flake); (6) Flake tools: S (scraper-dominated; scrapers >), D (denticulates/notches-dominated; denticulates-notches >), SD (both scrapers and denticulates/notches; scrapers-denticulates); (7) Raw materials: F (flint, chert and others), L (Limestone), M (multiple stones); and (8) Complexity in core technology: P (platform preparation), NP (no preparation), O (no information).

4.3. Paleoclimatic data

In light of this study's objectives, we defined four chronologically broad periods across MIS 12, 11 and 10, each associated with contrasting climatic and environmental conditions. The first captures MIS 12, which is situated between 470–425 ka, reflecting a long, severe glacial period. The second period reflects the temperate conditions present between 420–400 ka during the MIS 11c interglacial. We defined a third period between 395–375 ka to capture conditions during MIS 11bab and thus examine the human niche

during the stadial conditions that immediately followed the interglacial. Finally, the glacial period MIS 10 is captured by the interval from 370–335 ka.

We used the *pastclim* R package [51] and the Krapp et al. [32] simulations it provides to obtain paleoclimatic and paleoenvironmental data for these periods. We sequenced each of these periods by 1,000 year intervals for which we extracted paleoclimatic variables at a resolution of 0.5 degrees (raster pixels measuring ~ 55 km on a side) within our delimited geographic coverage of Western Europe (-15–20 ° longitude and 35–59 ° latitude). The 14 bioclimatic variables are: mean annual temperature (bio01), temperature seasonality (bio04), maximum temperature of the warmest month (bio05), minimum temperature of the coldest month (bio06), temperature annual range (bio07), mean temperature of the warmest quarter (bio10), mean temperature of the coldest quarter (bio11), annual precipitation (bio12), precipitation of the wettest month (bio13), precipitation of the driest month (bio14), precipitation seasonality (bio15), precipitation of the wettest quarter (bio16), precipitation of the driest quarter (bio17), and net primary productivity (npp).

Because our data are associated with broad time intervals due to the chronological imprecision of the archaeological records of these periods, we calculated the median value of each variable for each pixel from the collection of 1,000-year time slice outputs extracted for each of our temporal intervals. We then performed sensitivity testing of this approach via two procedures. Firstly, to evaluate the pertinence of these median environmental layers for capturing climatic conditions across each period adequately (MIS 12, MIS 11c, MIS 11bab and MIS 10), we employed a resampling procedure previously employed elsewhere [52]. This analysis consisted of randomly selecting (with replacement) a 1,000-year time interval from each of the chronological periods that we defined for this study (see above) using a uniform distribution. The resulting values from the climatic variables for that time slice and its associated archaeological occurrences are then used to generate an ellipsoid niche model. We then performed a statistical niche overlap analysis (see Section 4.4 ‘Ecological niche modelling’ below) of these four models (MIS 12, 11c, 11ab, and 10). This process represents a single iteration, and we performed 100. These overlap evaluations of niches created from randomly sampled time intervals and their associated environmental values consistently produced non-significant results, with only 1 of the 100 iterations showing significant differences for a single pair of niches (MIS 12 vs 11c; Supplementary Table S1). Additionally, we statistically compared the climatic values extracted from a period’s median environmental layer against individual randomly sampled layers from across the maximum and minimum of the corresponding period (Supplementary Tables S1 and S8). Analyses based on the PCs consistently identified no substantial differences between the resampled climatic data and the median layer, particularly for PC1 and PC2, for which the proportion of significant tests was ≤ 0.12 across periods and was typically 0. PC3 showed a slightly higher proportion of significant tests for MIS 12–11ab (0.33) and MIS 10 (0.39); however, these values are still relatively low, indicating that the median layer provides a robust representation of climatic conditions across each period (Supplementary Table S8). Comparisons of the raw bioclimatic variables likewise identified only limited differences between the resampled and median layers, with most periods showing no significant differences across the individual climatic variables (Supplementary Table S8).

Secondly, via randomization, we tested the assignment of the occurrences to each phase (i.e. MIS 12, MIS11c, MIS11ab and MIS10). We followed Raia et al.'s [53] approach, which involved randomly assigning occurrences either to the phase assigned in the study or to the proceeding/following period (or both for the case of MIS 11c and MIS11b) via a uniform distribution. Once all occurrences are assigned to a phase, overlap analysis is performed; as with the resampling procedure, this represents a single iteration and we performed 100. Across all pairwise comparisons, the overlap values obtained using our original assignment of occurrences fell within the range generated by randomization rather than appearing as statistical outliers (Supplementary Figure S10). Consistent with this, the vast majority of pairwise comparisons returned non-significant p-values across iterations (Supplementary Figure S11), indicating that the non-significant overlap patterns we report are not an artefact of how individual occurrences happened to be assigned to phases, but instead reflect a stable signal across plausible alternative assignments. Together, these analyses support the robustness of the niche models built from median environmental data layers using our assignment of occurrences to periods (see Results).

In order to work with numerous bioclimatic variables, some of which are correlated, we performed a Principal Component Analysis (PCA) on the variables of the temperate period using the Grinnell R package (PCA_raster function) [54]. This produces as many principal components as there are input variables. PCA is a dimension reduction procedure that helps deal with multicollinearity; because this process also results in less interpretable dimensions, we performed supplementary Kruskal Wallis tests and post-hoc Dunn statistical tests to compare the raw climatic values and PC scores extracted at sites between phases (Supplementary Figure S1). To ensure that all niche models were constructed with equivalent dimensions in multivariate space and to enable subsequent overlap analysis and niche comparison between phases, we projected the principal components (PCs) determined for MIS 11c (as this is the phase with the most occurrences) onto the other the periods' bioclimatic data. We then examined the proportion of variance values for the individual principal components resulting from the PCA of the temperate (termed Initial) period variables and retained the number of components necessary to explain 99% of the variance—the first five principal components (PC1–PC5). Once we defined the geographic extents of the accessible area (M) for each period (see below), we used them to mask the environmental principal component rasters used to construct the ellipsoid niche model for each period.

4.4. Ecological niche modelling

For estimating past hominin ecological niches, we employed the Biotic-Abiotic-Mobility (*BAM*) framework [55]. Due to our broad geographic scope, as well as the number and resolution of environmental variables employed, we assume that we indirectly take into account biotic interactions (referred to as the Eltonian Noise hypothesis [56]) that may have influenced the characteristics of the basal Neanderthal ecological niche. Therefore, our niche estimations correspond to the intersection between suitable environmental conditions (A) and accessible area (M)—an intersection that we consider to approximate the hominin existing fundamental niche across the successive phases that we examined.

Since our occurrence data sets are small, as well as the fact that using background data from an area that is relatively large (i.e., Western Europe) can be problematic when estimating ecological niches [57],

we chose to avoid methods that can produce complex, and potentially overfitted, ecological niche models. We, therefore, produced ellipsoids [58] because they are simple models that do not rely on the sampling of pseudopresences from a calibration area. We employed the covariance matrix (CVA) method of ellipsoid modelling [59]. These ellipsoids are based on the centroid and a covariance matrix derived from the variables' values associated with the occurrences. Sites associated with climatic conditions closer to the centroid are deemed to have higher suitability (closer to 1) whereas those on the periphery of the ellipsoid have lower suitability (closer to 0) [60, 61]. Data preparation for modelling, model development, and post-modelling analyses were performed with version 4.3.3 of R [62] and the `ellipsenm` R package [63].

For parameterization of each model, we performed the in-built model calibration procedure in `ellipsenm` to find the best combination of environmental dimensions (PCs) taking into account group sample sizes (Supplementary Table S9). Model performance was assessed based on statistical significance, low omission (proportion of testing data known to be suitable but deemed unsuitable), and low prevalence (proportion of environmental space predicted as suitable). These routines allowed us to identify PC1, PC2 and PC3 (together representing 88.8% of the total variance) as the best predictors for models.

We developed ellipsoid models for the four periods independently using the parameter settings selected during model calibration. Due to our reduced sample sizes, we produced up to 10 replicates of the ellipsoid models via jackknifing and retained the mean output. We then projected ellipsoid models for the four periods geographically; the MIS 12 ellipsoid in environmental space was projected geographically onto this period's paleoenvironmental principal components, as well as onto those of the subsequent temperate period, MIS 11c. Similarly, we projected the MIS 11c ellipsoid model onto its associated paleoenvironmental variables, as well as those of the subsequent cooler periods, MIS 11bab. The MIS 11ab ellipsoid was also projected onto its variables, as well as those of the following stage, MIS 10. Finally, the MIS 10 model was projected geographically onto MIS 10 paleoclimatic variables. These geographic projections allowed us to assess the extent of change of areas considered suitable through time.

To compare ellipsoid niches developed for distinct periods, we used the overlap analysis tool in `ellipsenm`. This method relies on background data (drawn from an area accessible for populations in each period) for the calculation of statistical significance via a randomization process. We determined areas accessible to hominin populations (*M* in the BAM framework [55]) in each period via a dispersal simulation employing the `grinnell` R package [54]. This method combines basic concepts of ecological niche modelling and dispersal events to generate a species' potential accessible area [55]. The simulation consists of capturing areas that populations access during a simulation of dispersal that starts from a subset of known localities. The simulation parameters are defined via a dispersal kernel and a number of dispersal events considered (See details in [54]). For this simulation, we took into consideration the technological characteristics of the European MIS 11 hominin archaeological record, which exhibits a marked contrast between regions of Western versus those of Central and Eastern Europe. The archaeological record of this period points to the regional development of particular technological

expressions within the broader lithic technocomplex. Lithic assemblages observed in Central Europe lack Acheulean-type bifacial elements observed in Western and Southern Europe. Central Europe was therefore likely developing separately from Western Europe with specific cultural features more related to North Caucasus and Central Asia. Furthermore, complexes with Levallois debitage do not appear in Central Europe prior to MIS 10 and there is no evidence that when they appear they have a Lower Palaeolithic origin [26]. It is possible that these differences are related to the lower population densities modelled for interior portions of the continent [44]. Based on these differences, we set up grinnell such that estimated calibration areas excluded the majority of Central and Eastern Europe (see Fig. 3). The parameters used in the simulation are as follows: normal dispersal kernel with a standard deviation of 1, a starting proportion of 1, 2 maximum number of dispersers, and 30 dispersal events; all other parameters were kept at default settings.

Niche overlap analyses compute the degree of overlap between ellipsoids constructed with occurrence records, and compare the observed value against a null distribution of overlap values generated via a randomization process. This process consists of comparing ellipsoids created with random samples from the background corresponding to each period, and repeating this analysis for 1000 times. The null hypothesis for the test is that the niches overlap. The null hypothesis cannot be rejected if the observed overlap value falls inside the upper 95% of the null distribution [64].

In situations in which ellipsoid models do not differ significantly from one another (see Results), the interpretation is that the niche has not evolved, and one can combine the occurrence datasets to generate a more complete characterization of the existing fundamental niche. We therefore combined the MIS 12, MIS 11c, MIS 11ab and MIS 10 occurrences into a single, composite occurrence data set to produce our final niche model. An ellipsoid model was created by using the PC values assigned to each occurrence point from its associated set of environmental data (Supplementary Tables S2–S4). We then geographically projected the combined occurrence ellipsoid niche model onto MIS12, MIS 11c, MIS 11ab and MIS 10 environmental layers in order to view the spatial extent of the hominin existing fundamental ecological niche through time.

4.5. Technological analyses

To assess the relationship between ecological niche dynamics across MIS 12–10 and observed archaeological lithic typo-technological variability, we performed a series of non-parametric statistical tests to identify possible independent and multivariate links between environmental suitability and different technological attributes, in a similar vein to examinations of more recent periods [33, 65]. Because we aimed to conduct tests on the most exhaustive dataset possible, we repopulated the site dataset with the duplicate occurrences removed for the ecological niche modelling (see above; 4 removed for MIS 11c, 1 removed for MIS 11ab, and 3 removed for MIS 12, see Supplementary Table S7). For these analyses, sites in close proximity to one another, or different assemblages from the same site within the same climatic phase, share the same suitability score.

To test whether shared technological attributes within a region are likely to share more similar environmental conditions compared to more distant sites, we performed Moran's I test using a cost path analysis to determine the physical distance between occurrences. We applied Tobler's Hiking Function, which is often used in cost-analyses to estimate the maximum hiking speed (s) given the slope of the terrain (m) [66]. It is preferred over just the slope as it accounts for anisotropy (the direction of movement has an impact on the cost) and non-linear cost estimation (the cost of travel can change far more rapidly than the linear change from one input to the next). The maximum speed of off-path hiking (in km/h) is calculated as:

$$s = 6e^{-3.5|m+0.05|}$$

Tobler's Hiking function is not symmetric around 0 because humans tend to walk faster on gently downward slopes ($m = -0.05$) than on flat terrain ($m = 0$). To compute a transition layer using the Hiking Function, we calculated the slope m of the terrain from the altitude (z) and the distance between cell centres (d) of each DEM for each pair of cells (i and j). This was performed using the `gdistance` [67] R package with major water bodies masked from the analysis.

$$m_{ij} = (z_j - z_i) / d_{ij}$$

We then used slope (m) to calculate the travel time (T) in hours of moving between cells of the DEM using the reciprocal of Tobler Hiking Function:

$$T = 0.6e^{3.5|m+0.05|}$$

Finally, we employed a correction procedure to take into account the distance between cell centres since, when travelling at the same speed, a diagonal connection between cells takes longer to cross than a straight connection. Using Moran's I , we found that none of our technological attributes show spatial autocorrelation nor do the suitability scores (Supplementary Table S10). These results justify our use of standard statistical tests.

We then applied a multiple correspondence analysis (MCA) to the entire dataset of technologies and individual sub-categories. We also conducted individual non-parametric Wilcoxon's signed-ranks tests for the presence/absence of each technological attribute to examine comparisons between suitability scores and different technological groups and subgroups: lithic technocomplexes, Levallois types, large cutting tools, biface types, flake tools, platform preparation and raw materials. We utilized the `imputeMCA` function within the `missMDA` package [68] for the imputation of the small number of missing values in order maximize the sites utilized in the MCA. We applied a standard threshold of 0.05 to determine statistical significance but do not entirely discount results that have p-values between 0.10 and 0.05. While the latter do not meet our threshold, they point to possible relationships worth future testing if and when additional data become available.

Declarations

Author Contribution

LHT, MEC and WEB performed the analyses, MHM and PGM collated the occurrence and archaeological data, LHT and WEB wrote the main manuscript text. All authors reviewed the manuscript.

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Data Availability

All R scripts and associated data files used to prepare the data necessary for the ecological niche modeling analyses (MIS11_Set_up), to estimate ecological niches and evaluate overlap between the ellipsoid models (MIS11_Models_and_Overlap), to perform sensitivity tests (MIS11_Sensitivity_Analysis) and to evaluate relationships between lithic technology and environmental suitability (MIS11_Technology_analysis) are provided. Also included are the files of archaeological site occurrences (...nodupes) used in the Set up and Modeling scripts, as well as a bathymetry model from The General Bathymetric Chart of the Oceans (GEBCO; https://www.gebco.net/data_and_products/gridded_bathymetry_data/) and the technological data employed in the technological analysis script. These files are available via the following URL: <https://data.indores.fr/dataset.xhtml?persistentId=doi:10.48579/PRO/GIQJDA>.

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Figures

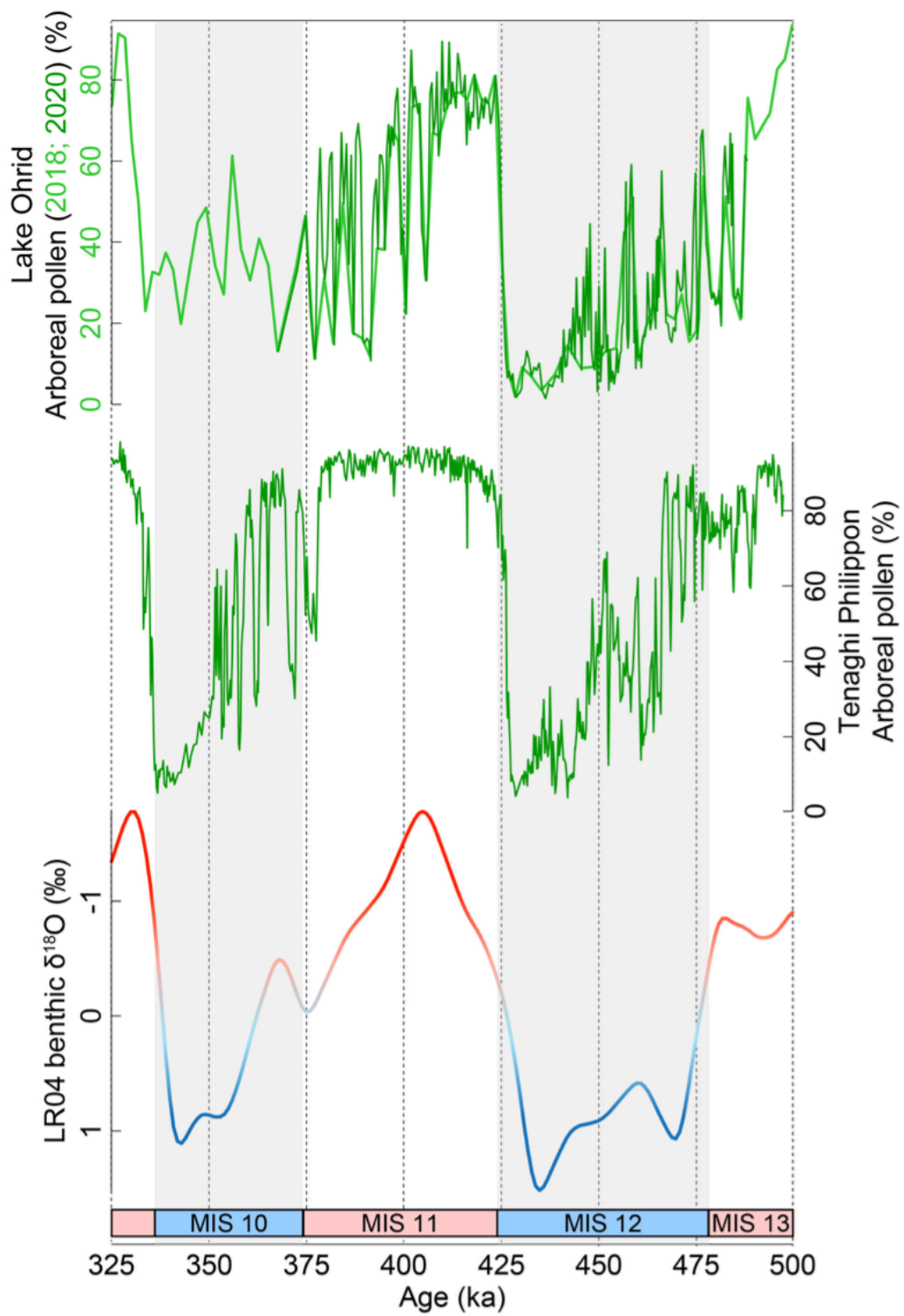


Figure 1

Climate variability across MIS 12, 11 and 10 illustrated by a number of climatic archives [22–25].

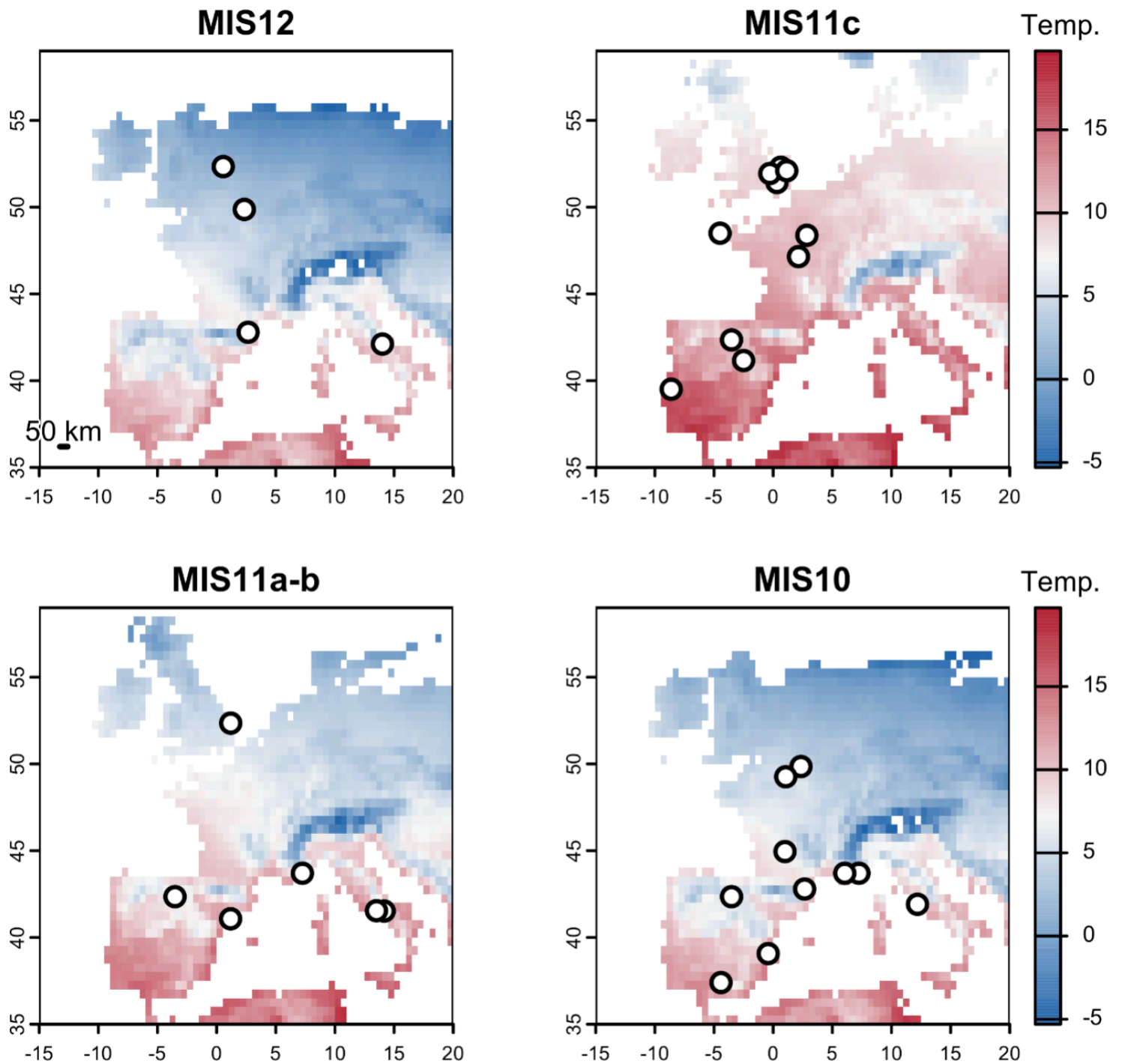


Figure 2

Maps depicting the geographic occurrences of archaeological sites attributed to the study periods within MIS 12–MIS 10 and used to estimate ecological niche. The map background is the calculated median for the variable bio1 (mean annual temperature) [32] across each study interval.

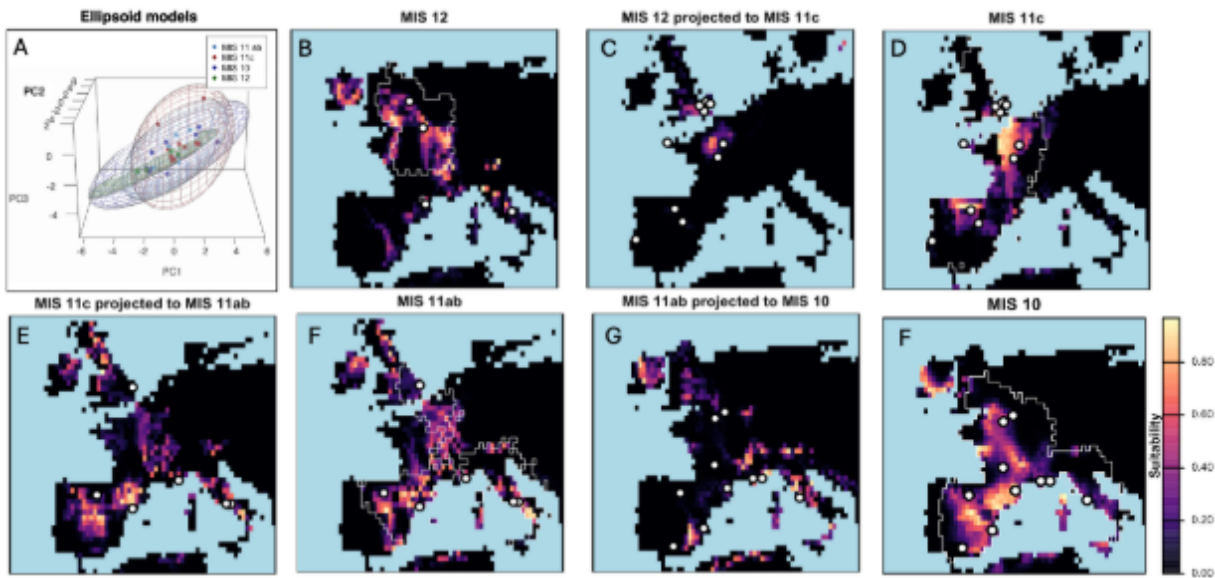


Figure 3

MIS 12–10 ellipsoid models and their geographic projections. A) Covariance matrix ellipsoid models for MIS 12 (green), MIS 11c (red), MIS 11ab (light blue), and MIS 10 (dark blue); B) MIS 12 ellipsoid model projected onto MIS 12 environmental conditions; C) MIS 12 ellipsoid model projected onto MIS 11c environmental conditions; D) MIS 11c ellipsoid model projected onto MIS 11c environmental conditions; E) MIS 11c ellipsoid model projected onto MIS 11ab environmental conditions; F) MIS 11ab ellipsoid model projected onto MIS 11ab environmental conditions; G) MIS 11ab ellipsoid model projected onto MIS 10 environmental conditions; H) MIS 10 ellipsoid model projected onto MIS 10 environmental conditions. Modelled accessible areas (*M*) are depicted with solid white lines for the four periods, and were used to calibrate their respective niche estimations. The predicted *M* for MIS 12 is fragmented and includes two small areas composed of only a small number of grid cells around the sites of Valle Guimentina (Italy) and Caune de l'Arago (Southern France).

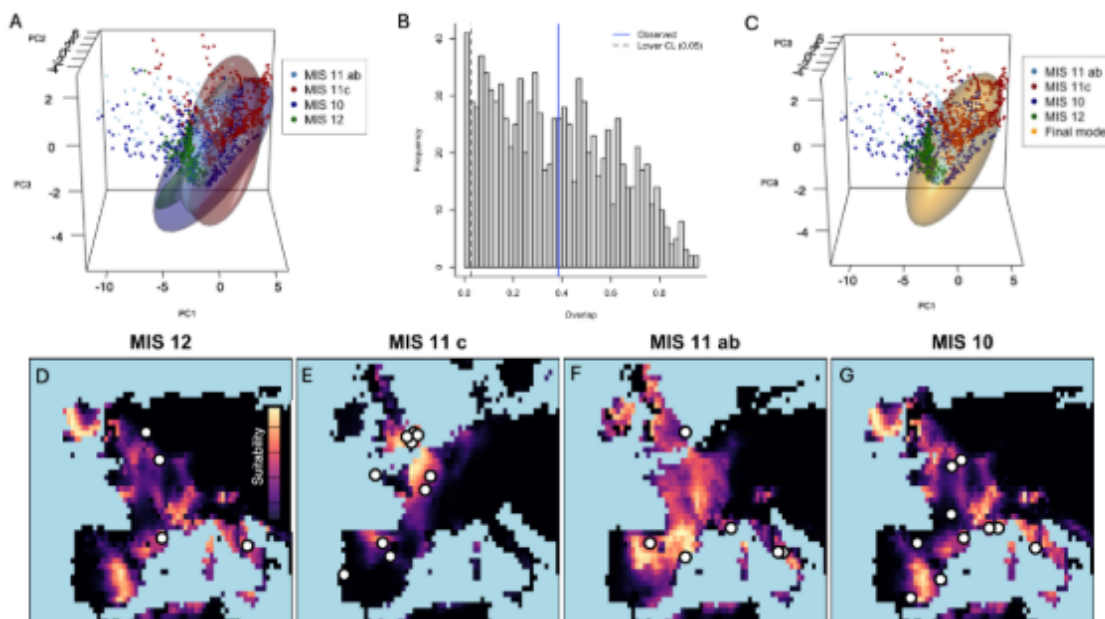


Figure 4

A) Overlap in environmental space of MIS 12 (green), MIS11c (red), MIS 11ab (light blue) and MIS 10 (dark blue) with environmental background from calibrated areas (*M*); B) An example of the results of the niche overlap analysis demonstrating no significant difference, here between the MIS 11c and MIS 11ab ellipsoids relative to random occurrences samples from the environmental background calibrated areas (*M*); C) Final ellipsoid model for combined occurrences against environmental background from each period's calibrated areas (*M*); D) Final combined ellipsoid model projected onto MIS 12 climatic conditions; E) Final combined ellipsoid model projected onto MIS 11c climate conditions; F) Final combined ellipsoid model projected onto MIS 11ab climate conditions; G) Final combined ellipsoid model projected onto MIS 10 climate conditions.

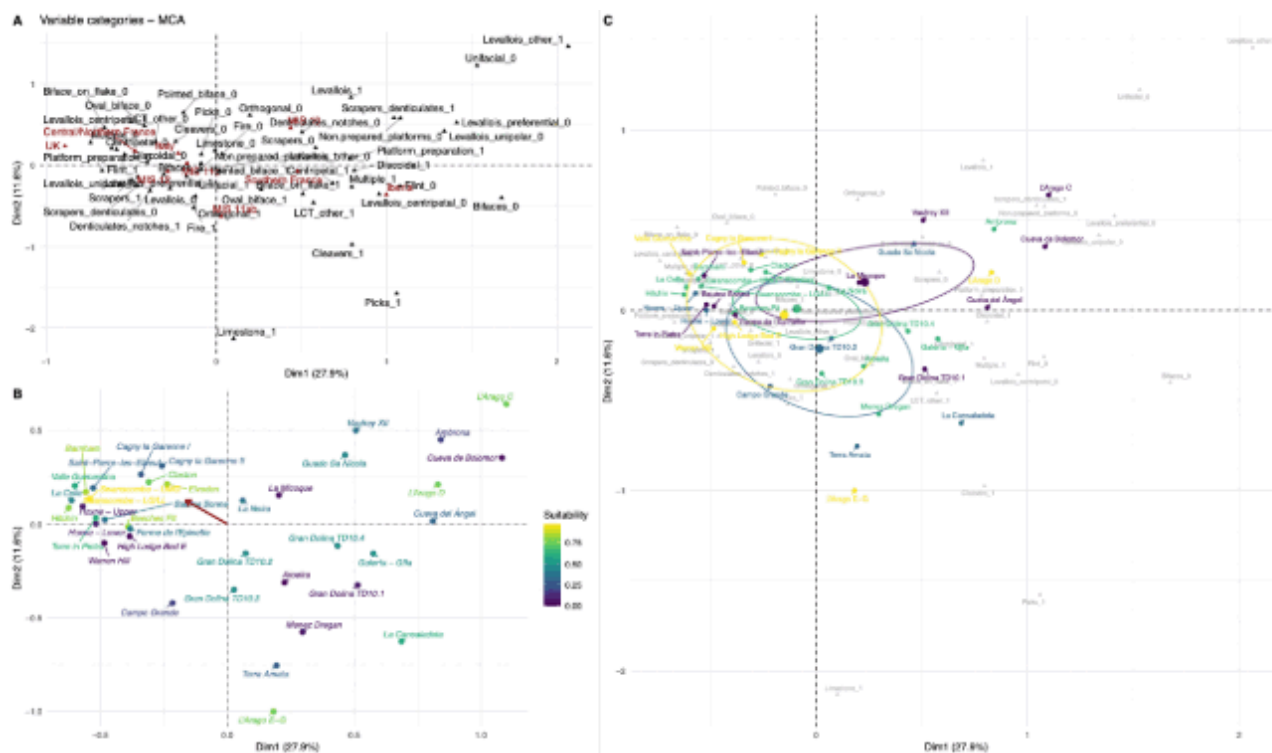


Figure 5

Results from multiple correspondence analysis (MCA) of the full dataset. A) MCA plot showing the relationship between all of the technologies studied (in black, 1 = present, 0 = absent) as well as supplementary qualitative variables – region and phase group (red). B) MCA Plot depicting sites coloured according to their suitability score. The red arrow shows the strength (length) and direction of the relationship between the two axes and suitability. C) MCA illustrating the technological attributes that contribute the most to the dimensions highlighted in grey. Sites are coloured according to their MIS attribution.

Supplementary Files

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