Geometric signs reveal changes in social structures and networks during the Western Eurasian Aurignacian

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Abstract

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Archaeological evidence from the Upper Paleolithic period indicates increasingly complex social organization across Europe1. Archaeologists have frequently used ancient art, the abundance of which is distinctive quality of the period, as a proxy for cultural difference in order to understand the shifting patterns of social organization and diversity of the Upper Paleolithic2–7. Considered to be the starting point of the Upper Paleolithic, the Aurignacian technocomplex (ca. 43 - 30 k BP) is often linked to the dispersal of *Homo sapiens* across Western Eurasia, and is characterized by lithic and osseus markers8,9, some of which are decorated with geometric signs10. In this paper we investigate Aurignacian social organization dynamics implied by the distribution and variation of geometric sign types found on mobile objects in Europe across four phases of the Aurignacian period.

## Cultural group identification in the Upper Paleolithic

Previous work has fruitfully explored social organization dynamics of the Upper Paleolithic using statistical analyses of objects to understand patterns of cultural groups. Multivariate analyses of beads from the Gravettian technocomplex suggests an east to west cline of nine cultural groups3. Seriation analysis, PCoA, and network analysis were used to identify groups from 134 discrete bead types recovered from both burial and occupation sites. To validate their claims of cultural groups,3 used a Mantel test to evaluate an isolation-by-distance hypothesis, which proposes that cultural difference can be primarily explained by geographic distance. They found that geographic distance alone did not solely account for the bead distribution. The nine geographically discrete groups encompass the regions of eastern, northwestern and central Europe, the northern and southern Iberian peninsula, southern and northern Italy, and the eastern and western Mediterranean regions.

Similar analyses of personal ornament types from the Aurignacian identified fourteen geographically cohesive groups6. Drawing on ethnographic studies that show how body decoration and ornamentation indicate ethno-linguistic identity,6 used Aurignacian personal ornamentation as a proxy for ethno-linguistic diversity. The variation in personal ornament types is interpreted as evidence of long-lasting cultural differences and as robustly establishing the ethno-linguistic diversity of the Aurignacian period. Seriation, correspondence, and GIS analyses of 157 distinct ornament types from 98 Aurignacian sites in Europe and the Near East identified geographically cohesive groups sharing similar ornament type associations. These groups sweep counter-clockwise throughout western France, northern Spain, the Pyrenees, and the Mediterranean region.

Cultural groups have also been identified from forty-two quadrilateral geometric signs from four cave sites in the Cantabrian region of Spain, likely associated with the Magdalenian period, spanning a distance of 30 kilometers4. Multivariate analysis of 45 morphological characteristics of the signs revealed two clusters. To interpret these clusters,4 drew on case studies of geometric signs as identity markers, including South African engraved ostrich shells from 60 k BP, maker’s marks on Gallo-Roman pottery, and 19th century French craft guild members’ personal marks. Using these case studies as analogies,4 interpreted the Magdalenian geometric signs as identity markers, and the two clusters as representative of two cultural groups.

In this study, we extend this previous work using geometric signs as identity markers to investigate cultural group dynamics in the Aurignacian period, providing a novel approach to understanding how early groups of *Homo sapiens* interacted with each other and their environments. Our archaeological and modelling results support the view that geometric signs are reliable proxies for reconstructing past cultural diversity and correlate with past population dynamics.

## The Aurignacian

The Aurignacian period (43-30 k BP) is largely characterized by material culture indicators such as carinated scrapers, small-flake tools and split-based bone and ivory tools, as well as an ongoing evolutionary shift from Neanderthals to early modern humans11.12 divided the Aurignacian into two main phases, Aur-P1 (Proto/Early, 43–37 k BP), and Aur-P2 (Evolved/Late, 37-32 k BP).13 used Bayesian modeling methods to further divide Aur-P1 into the Proto and Early Aurignacian, placing the Proto-Aurignacian at 41.5 - 39.9 k BP, and the early Aurignacian at 39.8 - 37.8 k BP. They found that the Proto-Aurignacian occurs during the Greenland Interstadials (GI) 9 and 10, periods of climatic amelioration, while the Early Aurignacian began with the Henrich Stadial, which is characterized by dry and arid conditions, and ends with GI 8. Similar to13, we divide the Aurignacian into four phases based on material culture changes; Proto, Early, Evolved, and Late Aurignacian14, as summarised in [Table 1](#tbl-aur-table).

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| | Time Period Name | Dates (k cal BP) | Material Culture Markers | Environmental Context | | --- | --- | --- | --- | | Transitional | 43 - 41.5 | Sidescrapers, bladelets, split-base points, flake production scheme, Mousterian influences still present | Preceeded by Greenland Stadial 12, ends with GI 11 | | Proto-Aurignacian | 41.5 - 39.8 | Large, straight bladelets from prismatic and pyrimidal cores | GI 9 and 10 | | Early Aurignacian | 39.8 - 37.8 | Twisted bladelets produced from carinated cores | Begins with Henrich Stadial 4, ends with GI 8 | | Evolved/Late Aurignacian | 37.8 - 32 | Backed microblade, more varied tool kits, beginnings of Gravettian influence | GI 8 - 6 |   Table 1: Summary of chronological, cultural and environmental characteristics of Aurignacian periods11–13,15 |

We hypothesize that these phases, and the environmental changes across the them, may correspond to changes in dynamics of cultural groups, as represented by patterns in the distribution of geometric signs. We aim to address the following questions: How do grouping dynamics of geometric signs change across the four phases of the Aurignacian? How do the groupings vary in diversity, size, connectivity, and distribution? What do these patterns tell us about dynamics of social organization throughout the Aurignacian? To answer these questions we use seriation analysis, network analysis, and PerMANOVA tests.

## Geometric signs from the Aurignacian

Our data comes from SignBase 1.0, an open-access collection of geometric signs on mobile objects from Upper Paleolithic Europe. SignBase 1.0 is a record of objects noting only the presence or absence of each sign on the object, without details of the quantity or sequence of individual signs on a given object. We used the identification of sign types provided by SignBase’s curators10. The data set consists of 531 objects found at 65 sites in 13 countries, and records 55 geometric sign types. We excluded signs classified by10 as “other”. To improve the quality of our data we excluded seven sites from the sample: only Willendorf (one sign present); Riparo di Fontana Nuova, Muralovka, Shanidar Cave, and Hayonim Cave (extreme geographic distance from the other sites); Grotte De La Princesse Pauline and Šandalja II (dated much later than the rest of the assemblages). This resulted in a sample of 438 objects found at 30 sites in 7 countries, and 54 sign types used in this study ([Figure 1](#fig-site-map)).

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| Figure 1: A: Map of sites in each Aurignacian phase that contain geometric signs on mobile objects. B: Abundance of signs over time, phases indicated by colours. C. Distribution of object count by site |

The distribution of objects across sites is highly skewed, as seen in [Figure 1](#fig-site-map) C. To minimize the influence of this skewed distribution, we followed16 in using presence/absence data for each sign at each site, reducing the effect of variation in object count between sites. We used Mantel tests with a Euclidean object abundance distance matrix and a Jaccard distance matrix of sign types. The test seeks to determine the level of correspondence between the matrices through permutational evaluation of the null distribution17, (here 1000 permutations), producing a Mantel R statistic and a p-value. The R statistic falls between -1, meaning a strong negative correlation, and 1, meaning a strong positive correlation, while a value of 0 means no correlation. The p-value estimates the probability of obtaining the observed correlation if the null hypothesis of no correlation were true (we use an alpha value of 0.05 for the threshold of statistical significance). The Mantel tests were performed using the vegan package18. The test indicated that there was no significant correlation between object abundance and sign type distribution (R = 0.078, p = 0.092), validating our decision to use presence/absence data.

Ages of the objects were determined by calibrating the uncalibrated ages provided by SignBase using the rcarbon package19. The calibrated radiocarbon dates of the sampled data range from approximately 32,893 BP to 44,778 BP, spanning an overall time range of 11,885 years. We assigned each object to a chronological phase following the date ranges recorded in [Table 1](#tbl-aur-table). The Transitional phase has 6 sites and 11 sign types, the Proto-Aurignacian has 10 sites and 23 sign types, the Early Aurignacian has 9 sites and 18 sign types, and the Evolved Aurignacian has 9 sites and 19 sign types. A Mantel test to evaluate the correlation between distance in time and distribution of sign types found a statistically significant correlation (R = 0.06, p = 0.01). This confirms that our assumption that a meaningful change in sign types occurs over time during the Aurignacian period.

If the distribution of sign types can be mostly explained by geographic distance, then we would see similarity in sign type distribution decreasing as geographic distance increases20,21. This relationship can be investigated using the isolation-by-distance framework, which proposes that cultural difference can be primarily explained by geographic distance16. To confirm that the distribution of sign types is influenced by cultural factors rather than geographic distance, we calculated the correlation between sign type distribution and geographic distance for each phase. We used Mantel tests with a geographic distance matrix and a Jaccard similarity matrix, with the results shown in [Table 2](#tbl-mantel-table). None of the phases have a statistically significant correlation between sign type distribution and geographical distance, so we reject the isolation-by-distance hypothesis as a primary explanation for variation in sign type distribution.

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| | Aurignacian phase | Mantel R | Mantel p | | --- | --- | --- | | Transitional | 0.421 | 0.081 | | Proto-Aurignacian | -0.188 | 0.872 | | Early Aurignacian | 0.259 | 0.075 | | Evolved Aurignacian | -0.055 | 0.589 |   Table 2: Table of the results per phase for the Mantel test between a Jaccard matrix of sign type diversity and a geographic distance matrix |

# Results

## Cultural Group Detection

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| Figure 2: Seriation analysis of the data, with group membership indicated by color. Restricted group is in yellow, broader group is in blue. |

For each of the phases, our seriation analysis identifies two groups, one with a restricted range of sign types (1-3 types), which tend to be visually simpler signs, and one with a broader range (up to 14 types), which include more complex signs. Simpler signs composed of fewer components, like line and notch, are the most prevalent across all time periods. Overall, across the four phases, the number of sites in the restricted range group tends to be less than or equal to the number of sites in the broader range group, with the exception of the final Evolved phase.

In the Transitional phase, there is a relatively small range of sign types compared to other phases. The restricted range group consists of Fumane, Pod Hradem, and Geissenklösterle, two of which only have a notch, and one of which has a notch and circumnotch. The broader range group consists of Labeko Koba, Hohle Fels, and El Castillo, which vary in their sign composition and have only the line and oblique line (obline) signs in common.

In the Proto-Aurignacian we see an expansion in both the number of sites and range of signs, with no overlap in sites from the Transitional phase, except for Geissenklösterle, which is present in both phases. The restricted range group consists of Abri Pataud, Hohlenstein-Stadel, and Mladeč, which only have notches and lines, and Gatzarria which also has a dashline. The broader range group consists of Geissenklösterle, Spy, Vogelherd, Grotte du Renne, La Ferrassie, and Les Cottés, where we see a more consistent pattern of a more diverse range of signs, compared to the broader range group of the Transitional phase. In addition to line and notch, the obline, radial notch (radnotch), cross, hatching, and circumferential notch (circumnotch) are also frequently found in the broader range group.

In the Early Aurignacian, we see appearance of completely new sites with no overlap with the Proto-Aurignacian sites, as well as increased diversity of patterns within the groups. The restricted range group consists of Grottes de Fonds-de-Forêt (radnotch and notch), Riparo Bombrini (notch), and Grotte de la Verpillière I (notch and line). The broader range group consists of Solutré, Hohle Fels, Castanet, Cellier, Blanchard, and Trou al’Wesse, which contain a wide range of signs in a variety of combinations. In addition to line and notch, the obline, dot and vulva are also frequently found in the broader range group.

Finally, in the Evolved Aurignacian, we see slightly more consistent groups, again with new sites with no overlap with the Early Aurignacian sites, except for Hohle Fels, which also appears in the Transitional phase. Vogelherd also reappears, having appeared earlier in the Proto-Aurignacian. The restricted range group consists of Les Rois, Gargas, La Viña, Sirgenstein Cave, and Vindija Cave, with the line, notch, and and obline signs. The broader range group consists of Trou Magrite, Bockstein-Törle, Vogelherd, and Hohle Fels. Along with line, notch, and obline, the hatching, and oblique notch (obnotch) signs are also frequently found in the broader range group.

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| Figure 3: Network analysis of the data |

The results of the network analysis supports the restricted-broad groupings identified in [Figure 2](#fig-seriation), and provide additional insights into the evolution of connectivity between groups. In the Transitional phase, the network analysis reveals one distinct and one disconnected group. The restricted range group consists of Geissenklösterle, Fumane, and Pod Hradem, and the broad range group consists of Hohle Fels, El Castillo, and Labeko Koba, with no connections between the groups. The Proto-Aurignacian phase also shows two clearly defined groups, the broad range group consisting of Geissenklösterle, Spy, Vogelherd, and Grotte du Renne, and the restricted range group consisting of Mladeč, Hohlenstein-Stadel, Gatzarria, and Abri Pataud. However, it also displays some connectivity between the two groups of sites, with La Ferrassie connected to both groups. Les Cottés stands out with no connections to either group. The Early Aurignacian shows more strongly inter-connected groups – although the shape still suggests two main groups – with Grotte de la Verpillière I in particular having multiple strong connections to both groups. Lastly, the Evolved Aurignacian again shows two main groups, although intra-group connectivity has decreased, with the broad range group consisting of Hohle Fels, Trou Magrite, Vogelherd, and Bockstein-Törle, and the restricted range group consisting of Gargas, La Viña, Sirgenstein Cave, Vindija Cave, and Les Rois. As for the Early Aurignacian, inter-connectivity between groups continues to be evident in the Evolved Aurignacian, with connections between Trou Magrite, Gargas, and Vindija Cave, and Bockstein-Törle and Gargas, however the strength of inter-connectivity is weaker than in the Early Aurignacian.

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| Figure 4: Map of sites faceted by time period and colored by group type |

While th results of the seriation and network analyses point to two main groups of sites within each phase, spatial clusters of sites are not highly evident in these groups, in part due to the small numbers of sites in each phase ([Figure 4](#fig-group-map)). In the Transitional phase, sites are widely spread out across Western Europe. This wider distribution may be a factor in weak connections seen in [Figure 3](#fig-neighbor-net). In the Proto-Aurignacian, we see a slightly narrower geographic distribution of sites westward but a spread northward, and more overlapping of sites between groups, which may be associated with the slightly stronger connectivity seen there. This phase is also associated with an increase in sites and sign types, which may be correlated with the increased proximity and population density. In the Early Aurignacian, we see a reduced distribution, with sites clustered closer together, which may be associated with the increased connectivity in that phase. In the Evolved Aurignacian, we see a wider distribution and more distance between sites, which may be associated with the reduced connectivity seen in that phase. The Mantel tests, as shown in [Table 2](#tbl-mantel-table), tell us that the sign distribution in the Proto-Aurignacian experiences the lowest correlation with geographic distance, while the Early Aurignacian has the highest correlation.

## Cultural Connection Strength

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| | Aurignacian phase | PerMANOVA R2 | PerMANOVA F | PerMANOVA p | | --- | --- | --- | --- | | Transitional | 0.452 | 3.305 | 0.100 | | Proto-Aurignacian | 0.274 | 3.021 | 0.012 | | Early Aurignacian | 0.215 | 1.915 | 0.013 | | Evolved Aurignacian | 0.224 | 2.020 | 0.022 |   Table 3: Table of the results per phase for the perMANOVA |

The perMANOVA R2 statistic shows the proportion of sign variation that can be explained by group membership. The Transitional period has the highest score of 0.452 while the Early Aurignacian has the lowest score of 0.215. We see a large decline in scores between the Transitional and the Proto-Aurignacian periods, before a slight increase in between the Early and Evolved Aurignacian periods. The pseudo-F statistic quantifies the difference between groups, with the Transitional phase having the highest value of 3.305, and the Early Aurignacian having the lowest value of 1.915. Similar to the R2 statistic, we see a decline in values between the Transitional and the Proto-Aurignacian periods, before a slight increase in between the Early and Evolved Aurignacian period. The perMANOVA p-value indicates a statistically significant difference in the distribution of signs between the restricted and broad range groups for the Proto , Early, and Evolved Aurignacian phases, but not the Transitional phase (p = 0.1).

# Discussion

## Grouping Dynamics Across the Four Phases of the Aurignacian

Our first aim was to determine how the grouping dynamics of geometric signs changed across four phases of the Aurignacian, specifically in terms of diversity, size, connectivity, and distribution. The results from [Figure 2](#fig-seriation) show that each phase can be divided into two main cultural groups, with sign type number and diversity serving as a major dividing factor, and that group size varied from phase to phase, with a large increase in between the Transitional phase and the Proto-Aurignacian. [Figure 3](#fig-neighbor-net) shows that group inter-connectivity and intra-connectivity varies from phase to phase, with weak intra-group connections and no inter-group connections in the Transitional phase, to stronger intraconnections and interconnections starting to form in the Proto-Aurignacian, to very strong connections (both between and within groups) in the Early Aurignacian, to weaker connections in the Evolved Aurignacian. The perMANOVA tests show that the changes between the the Proto, Early, and Evolved Aurignacian phases are statistically significant, that the Transitional period experiences the highest level of difference between groups, while the Early Aurignacian has the least.

One consistent grouping dynamic throughout all four phases is the restricted/broader range group divide, which may be influenced by variation in social structure. Variation in hunter-gatherer social structures is well-known from ethnographic and archaeological research22–29. Studies have established how variation in ornamentation and other forms of material culture can be used to communicate information about the numbers and types of social roles and statuses within groups4,29–40. Drawing on this work, we interpret the broader/restricted range grouping in the geometric sign data as indicating variation in social structure. The broader range groups, with higher variety of signs and more visually complex signs, indicates communities with a greater variety of formalized social roles. Conversely, the sites with a restricted range of signs indicate communities with fewer formalized social roles. A single larger community could have both of these groups as sub-sets, rather than the restricted/broader range groups being distinct, non-overlapping cultural groups.

The connectivity between sites represented in [Figure 3](#fig-neighbor-net) may reflect non-utilitarian mobility among these larger communities. Previous studies have shown a range of variation in magnitudes and types of mobility among hunter-gatherer groups27,28,41–43. Non-utilitarian mobility establishes regional social networks which facilitate the spread of information and the survival of hunter-gatherers in uncertain environments44–48. The exchange and production of decorative items, such as objects with geometric signs, has been associated with non-utilitarian mobility and recognized as an indicator of social contact44,49–52. We can divide the connections depicted in [Figure 3](#fig-neighbor-net) into shorter-term information exchange and longer-term residential movement.

One form of longer-term residential movement that may be related to non-utilitarian mobility are aggregation/dispersion patterns, which are defined by53 as a type of hunter-gather settlement pattern in which groups both break off in dispersed fragments and congregate in large groups, typically for subsistence or social reasons. Aggregation sites, associated with high degrees of connectivity, are the places where those group fragments or individuals congregate. Some archaeological indicators of aggregation sites include proximity to certain environmental resources, as well as a more diverse artifact assemblage53, including, in some cases, decorative objects49. Previous studies have also identified evidence of aggregation/dispersion patterns among the early modern humans of the Upper Paleolithic2,54,55,55–60.

Following this previous work, we identify aggregation sites as those with a higher than expected sign diversity index. [Figure 5](#fig-div-plot) plots the expected Shannon-Weaver diversity index61 for a given sample size against the actual diversity index per site62. The plot identifies multiple sites with a higher than expected diversity of signs, such as Hohle Fels in the Transitional phase, Spy, La Ferrassie, and Les Cottés in the Proto-Aurignacian, Solutré, Hohle Fels, and Grottes de Fonds-de-Forêt in the Early Aurignacian, and Vogelherd, Bockstein-Törle, and Vindija Cave in the Evolved Aurignacian. Notably, most of these sites are not shown as having connections between groups in [Figure 3](#fig-neighbor-net), except for La Ferrassie in the Proto-Aurignacian. This suggests a distinction between shorter-term information exchange (e.g. the highly interconnected sites in [Figure 3](#fig-neighbor-net)) and longer-term residential movement for aggregation (e.g. the sites with higher than expected diversity in [Figure 5](#fig-div-plot)).

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| Figure 5: Plots of expected versus actual diversity of signs for each site by time period. The blue line is the expected Heterogeneity value under the null model (simple increase in sample size means simple increase in diversity of sign types. The upper red line is the upper 95% confidence interval, if a site is near or above that line, it has a much higher diversity of signs than expected under the null model.The lower red line is the lower 95% confidence interval, if a site is near or below that line, it has a much lower diversity of signs than expected under the null model. |

## Social Organization Dynamics Throughout the Aurignacian

The second aim was to determine what these patterns reveal about the dynamics of social organization throughout the Aurignacian. The results suggest that the Transitional phase was sparsely populated, with minimal interaction between loosely connected groups. For the Proto-Aurignacian, the results suggest a large expansion in social interaction within groups, as well as some degree of interaction between groups, with geographic distance having the least influence on sign distribution [Table 2](#tbl-mantel-table). The Early Aurignacian experiences a large surge in interaction between groups, as well as interaction within groups, and an increase in the correlation with geographic distance. The Evolved Aurignacian experiences a decline in between-group interaction, although it maintains within-group interaction.

These results are consistent with previous work on the environmental and population change during these phases. From 45 - 43.25 k BP, the population density in Europe was extremely low, due to the unfavorable environmental conditions of Greenland Stadial 12 (44 k BP) and the slow westward expansion of early modern humans63. This was followed by rapid expansion from 43.25-41 k BP (Transitional/Proto), with the maximum extent of Proto/Early Aurignacian settlement being reached around 41 k BP. This rapid population expansion could be what stimulated the emergence of signs as a marker of group membership. Other studies have also found similar associations in other regions and time periods between increases in quantity and diversity of art, and increases in population density64–72.

Our results are consistent with13 who used eco-cultural niche modeling to show that the Heinrich Stadial 4 (HS4) at the very beginning of the Early Aurignacian resulted in a expansion of people into new environmental niches, which they hypothesize was associated with an expansion of social networks both within and between populations. This correlates with our results which show a large increase in both inter-connectivity and intra-connectivity strength in the Early Aurignacian, as well as the increased sign type correlation with geographic distance. Similarly,12 developed a human-existence probability model for the Aurignacian, finding an expanded, more dispersed settlement area for Evolved/Late Aurignacian theorizing that the environmental changes of HS4 lead to humans better adapted to survive in a broader range of climate conditions.63 also finds an increase in expansion marking the beginning of the Evolved Aurignacian. This geographic expansion may explain our results, where we find weaker, more dispersed connections in the Evolved Aurignacian.

# Conclusion

This study adds to our knowledge of social networks within the Aurignacian period, as our results document dynamic patterns of social exchange and connection. Previous work3,55,73–76 has used material culture analysis to reconstruct Upper Paleolithic social networks, which have been argued to be a driver of cultural and evolutionary change2,48,77–81.82 places the emergence of complex inter-group connectivity at around 30 k BP, however, our results show evidence of inter-connectivity beginning at around 41 k BP, perhaps suggesting an earlier emergence of complex inter-connectivity than previously predicted. We attempted to rectify the low temporal resolution that tends to affect network analysis results when analyzing older, more time-averaged data sets83 by dividing the data up into smaller time periods. Additionally, by focusing on change over time, we are able to see social networks as fluid and dynamic, rather than static and bounded54.

One limitation is the potential ambiguity that arises with some of the sign types. While84 argues in favor of Aurignacian geometric signs as symbolic expression, potential ambiguity still remains over whether function is consistent across all sign type occurrences, particularly in regards to the simpler sign types composed from fewer elements. We included the more ambiguous sign types because similar sign occurrence may still serve as evidence of cultural connectivity regardless of function, even if it is random copying20, and additionally, greater quantities of included sign types serves to establish stronger connections83. This ambiguity may be addressed in the future through the usage of the data recently released in SignBase 2.0 covering sites in Germany, which contains more detailed information on the specific order and patterns in which signs occurred on individual objects.

# Methods

## Cultural Group Detection Using Seriation and Network Analysis

Seriation analysis is the arrangement of data into a linear order to reveal patterns85. We used the Brower-Kile86 seriation algorithm from the seriation package87, in which a unidimensional sequence is generated by reordering the rows and columns to group the presences along the diagonal. To investigate connectivity among clusters of sites in the seriation solution, we used network analysis to represent and quantify the relationship between sites88. Each node is a site, and each edge is a measure of sign type distribution similarity, as computed by the Jaccard similarity algorithm. To avoid cluttering the graph, all edges below the value of 0.2 were removed. Results were plotted with the Fruchterman-Reingold layout89, a force-directed graph layout for uniform edge lengths, and network analysis was performed using the vegan18, statnet90 and igraph91 packages.

## PerMANOVA for Cultural Connection Strength

PerMANOVA quantifies the level of variation between groups versus the level of variation within groups92,93. The results are expressed by an R2 statistic, which quantifies how much of the variation in sign distribution can be explained by group membership, a pseudo-F statistic, and a p-value. The pseudo-F statistic compares the total sum of squared dissimilarities between groups to total sum of squared dissimilarities within groups. Larger pseudo-F statistics indicate more separation between groups. The p-value quantifies the probability of obtaining the observed difference if the null hypothesis were true (we use an alpha value of 0.05 for the threshold of statistical significance). The perMANOVA was performed using the vegan18 and igraph91 packages.

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