

Olmec Pottery Production and Export in Ancient Mexico Determined Through Elemental Analysis

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The first Mesoamerican civilization, the Gulf Coast Olmec, is associated with hierarchical society, monumental art, and an internally consistent ideology, expressed in a distinct style and salient iconography. Whether the Olmec style arose in just one area or emerged from interactions among scattered contemporaneous societies remains controversial. Using elemental analysis, we determined the regional clay sources of 725 archaeological ceramic samples from across Mesoamerica. Exported Olmec-style ceramics originated from the San Lorenzo region of the Gulf Coast, supporting Olmec priority in the creation and spread of the first unified style and iconographic system in Mesoamerica.

More than 3000 years ago, the first civilization in ancient Mexico, the Olmec, coalesced along the Mexican Gulf Coast. Much of modern Mexico, along with Guatemala, Belize, Honduras, and El Salvador, constitutes the cultural region known as Mesoamerica (Fig. 1). Elements of the Olmec art style and associated iconography—the first coherent iconographic system in Mesoamerica—that emerged were depicted on stone monuments in the Gulf Coast, as well as on portable ceramic objects that have been found at sites throughout Mesoamerica (1, 2). Because this iconography has been linked with the dissemination of the social, political, and religious institutions of the Olmec, analyzing its origin and spread is central to understanding the development of complex society in Mesoamerica. The Olmec style's appearance at select sites outside the Gulf Coast has been used to argue that it arose in one area only and was exported or, alternatively, emerged from interactions among scattered regional chiefdoms (3). Here, we use instrumental neutron activation analysis (INAA) on archaeologically excavated or collected ceramics to fingerprint their provenience and exchange during the later half of the Early Formative period [~3450 to 2850 years before the present (yr B.P.), or 1500 to 900 B.C.E.].

The Olmec and Olmec style in Mesoamerica. Not all features referred to as the Olmec style may be linked with the archaeological Gulf Coast Olmec; thus, we distinguish between the terms Olmec culture and

Olmec style. Two views have emerged on the relationship of the Olmec with other contemporaneous cultures, characterized as the “mother culture” and “sister culture” perspectives (4). Proponents of the mother-culture perspective see the Olmec as more sociopolitically complex than coeval cultures, playing a central role in the dissemination of key elements of Mesoamerican civilization. Sister-culture advocates characterize the Olmec as at the same sociopolitical level as other contemporaneous chiefdoms; while engaged in competitive interaction, the Olmec had no priority in the development of the Olmec style and its distribution. Here, we endeavor to move beyond this dichotomy, which obscures understanding the complex nature of the Olmec and its relationships with its neighbors.

In terms of Early Formative complexity, recent investigations by Ann Cyphers and

her collaborators at the first Olmec capital, San Lorenzo, Veracruz (5), emphasize the higher sociopolitical level that the Olmecs achieved relative to contemporaneous groups in Mesoamerica (Fig. 1). While leaders, for example, at the emerging chiefdom of San José Mogote in the Valley of Oaxaca lived in somewhat better made wattle-and-daub huts than other villagers (6), San Lorenzo leaders probably lived in the so-called Red Palace, where they used basalt brought in from 60 km away to provide columns, step coverings, and drainage channels for their residence. Rather than engage in the typological argument as to whether the Olmec constituted a state or a chiefdom, we simply note the more complex level of sociopolitical organization achieved by the Olmec compared with that of other contemporaneous societies (7).

The “San Lorenzo horizon” from 3150 to 2800 yr B.P. (1200 to 850 B.C.E., or 1350 to 1000 calibrated B.C.E.) refers to the earliest spread of Olmec-style ceramic vessels and figurines across Mesoamerica (3, 8, 9). As defined at San Lorenzo (9), some Olmec ceramic types (such as Calzadas Carved pottery) have excised designs that may express ideological concepts through iconography (Fig. 2, A and B). Two additional San Lorenzo horizon pottery types have a fine kaolin clay body: Xochiltepec White and Conejo Orange-on-White (Fig. 2, C and D). Xochiltepec White has long been recognized as a possible export ware across Mesoamerica, although of uncertain provenance (6, 9).

The lack of the full repertoire of Olmec-style motifs at any one site and the apparent regional differences in expression of the Olmec style have been cited as evidence that each

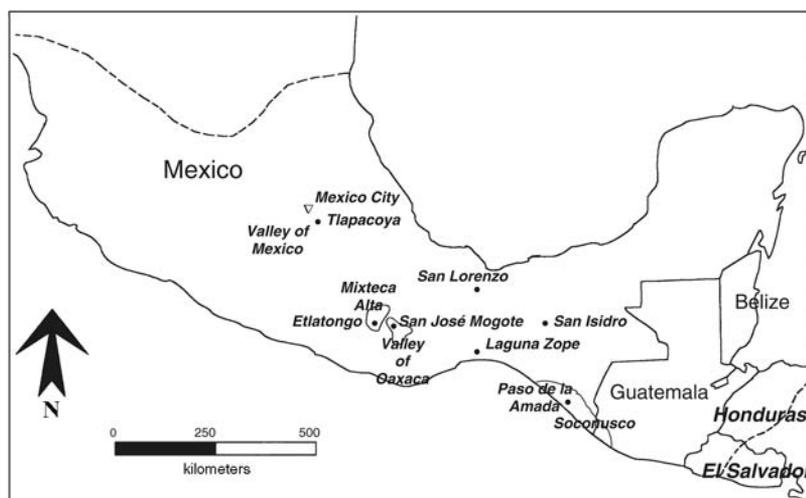


Fig. 1. Map of Early Formative regional centers, showing modern national borders and Mexico City for reference. Dashed lines show approximate boundaries of Mesoamerica.

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region contributed to the style, with no central origin of imagery (3). Ceramic data from Oaxaca have shaped this debate for the past 30 years, as archaeologists have used stylistic analysis, as well as limited microscopic study of select sherds, to assert that villagers created their own local set of Olmec-style symbols (6, 10). This model concludes that, rather than importing Gulf Coast pottery and iconography, Valley of Oaxaca potters produced and exported Olmec-style symbols made in distinctive gray-ware pottery, referred to as Delfina Fine Gray and Leandro Gray, across Mesoamerica; recipients of this Oaxaca-made pottery supposedly included the Gulf Coast Olmec (6, 11). To test this model, the first author excavated Early Formative ceramics at the site of Etlatongo, in the Nochixtlán Valley of the Mixteca Alta, northwest of the Valley of Oaxaca (Fig. 1). Previously explored by Roberto Zárate Morán, the site,

with little prior occupation, grew to be as large as contemporaneous San José Mogote during the San Lorenzo horizon, serving as the center of a small chiefdom comparable to that in the Valley of Oaxaca (7).

Ceramic data. Since the mid-1990s, a wide variety of Early Formative ceramic samples from regions of Mesoamerica have been submitted to the University of Missouri Research Reactor (MURR) for INAA (7, 12). Although the 80 samples detailed in table S1 come primarily from Etlatongo and San Lorenzo, the larger database includes a total of 725 sourced archaeological pottery samples from Tlapacoya (Basin of Mexico), San José Mogote and other Valley of Oaxaca sites, Laguna Zope (Pacific Coast, Isthmus of Tehuantepec), Paso de la Amada and other Mazatán area sites (Soconusco region, Pacific Coast of Chiapas), and San Isidro (Chiapas Central Depression) (table

S2). Samples of raw clay include 160 clay samples from San Lorenzo, 25 from Oaxaca (12–14), 203 from the Mazatán zone, 244 from the Basin of Mexico, and 196 samples of raw clay and modern/historic examples of pottery collected from pottery-making towns in the Valley of Oaxaca. Our data have been compared with an additional 527 archaeological samples from later sites in the Valley of Oaxaca.

Clays are useful in sourcing analysis because they reflect the composition of local geology. The clay available for pottery has been documented in the three regions on which we focus: San Lorenzo, the Valley of Oaxaca, and the Nochixtlán Valley (9, 13–16). Located in the Isthmian Saline Basin, San Lorenzo sits on a salt dome located in Miocene sedimentary rocks, adjacent to Pleistocene and Holocene alluvium deposited during flooding. The sedimentary rocks provide excellent pottery clays, including white-firing clay (kaolin). Precambrian metamorphic rock, Cretaceous limestone, and Miocene volcanic ignimbrite are exposed in the Valley of Oaxaca, along with Quaternary alluvium derived from these rocks. Clay was likely obtained from weathered Precambrian gneiss, schists, and the associated alluvium; kaolinite clays appear in scattered pockets (6). Similar rocks are exposed in the Nochixtlán Valley, although Cretaceous limestone is more abundant. Tertiary volcanic rocks, alluvial clays, and residual clays (with a high calcium carbonate content formed from the decomposition of limestone parent materials) are available in the Etlatongo vicinity.

All 80 pottery samples in table S1 have been recorded with photography and/or drawings, with all Etlatongo ($n = 42$) and San Lorenzo ($n = 21$) samples from well-documented archaeological contexts. Most of the ceramics in the larger database (table S2) have not been illustrated, and some lack archaeological provenience information (13). The sampling procedure was not random. Sherds were selected that would show both local production and possible imports, including samples similar to Xochiltepec White and Conejo Orange-on-White. Thus, Olmec-style sherds are overrepresented at most sites in the sample. In selecting samples from Etlatongo, special attention was paid to the gray wares that may have been exported by the Valley of Oaxaca (Fig. 3A).

Analysis. Sample preparation, INAA, and quantitative techniques (17, 18) are detailed in online materials (19). We used a variety of pattern-recognition techniques to discern compositionally homogeneous groups in the data and then tested the effectiveness of elemental discrimination between the groups by calculating individual ceramics and clay-sample Mahala-

Fig. 2. Profile and exterior views of Olmec pottery types produced at San Lorenzo. (A and B) Calzadas Carved pottery. [(A) is sample BLM060.] (C) Xochiltepec White (sample BLM042). (D) Conejo Orange-on-White (sample BLM041). Adapted from (9); drawings courtesy of M. Coe.

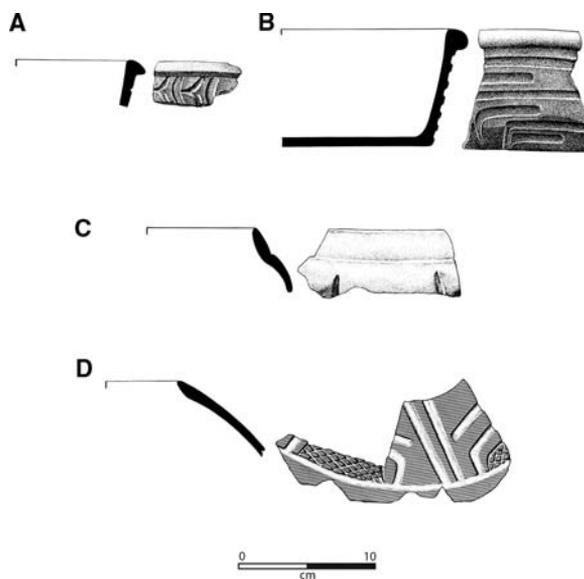
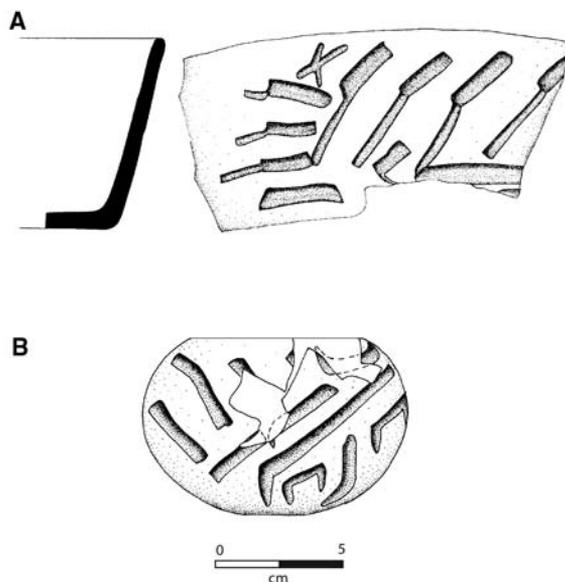


Fig. 3. Olmec-style pottery excavated at Etlatongo. (A) Profile and exterior of a bowl made with San Lorenzo clay (sample BLM003). (B) Reconstruction of a locally produced neckless jar (sample BLM006).



nobis distances from all group centroids. All Mahalanobis distances were cross-validated; that is, each specimen was removed from its presumed group before calculating its own Mahalanobis distance from the group's centroid (12, 20). This is a conservative approach to group evaluation that may exclude true group members but minimizes the chances of erroneous attribution. Such a conservative approach minimizes chances that Olmec-style sherds found outside the Gulf Coast will be incorrectly identified as imports rather than local production. Sherds that could fall into more than one group from the same region were not used in group definition (such as "San Lorenzo Local/White" in table S1); excluding them from specific group membership means that they play no role in defining the centroid and variance-covariance structure of those groups.

Production and consumption of Olmec-style ceramics. The majority ($n = 725$) of more than 1000 Early Formative archaeological and clay samples separate into 15 regionally specific compositional groups; the remainder fall into 3 unassigned groups (table S3). These 15 groups are discriminated well by the 32 elements retained for analysis according to the Mahalanobis distance-based probabilities of group membership. Several elements, such as chromium, thorium, tantalum, cesium, and calcium, are particularly useful as discriminators of ceramics made in different regions. For example, the Mazatán samples are all low in chromium, whereas the Tlapacoya samples are all enriched in chromium (Fig. 4).

Three groups—Etlatongo-1, Etlatongo-2, and Oaxaca-1—can be associated with highland Oaxaca production. Although we have numerous clay samples from the Valley of Oaxaca, local production at Etlatongo was primarily sampled by selecting highly friable utilitarian wares that would be in need of frequent replacement (7). The Etlatongo-1 and Etlatongo-2 groups represent the varied nature of the clays available in the Etlatongo vicinity. The data demonstrate that the same clays used for utilitarian vessels could also be used for serving vessels with Olmec-style motifs (Fig. 3B). Potters thus produced Olmec-style ceramics using local clays in both the Nochixtlán and Oaxaca Valleys.

Three groups—San Lorenzo White, San Lorenzo Local, and San Lorenzo Local/White—clearly derive from San Lorenzo region clays, even though the finished vessels are found at villages across Mesoamerica. The ceramics in the combined San Lorenzo Local/White group were produced with San Lorenzo region clays, but it was not possible to distinguish among these groups; a similar problem precludes sample BLM009 from being firmly placed in the San Lorenzo Local group. All examples of Conejo Orange-on-White, and

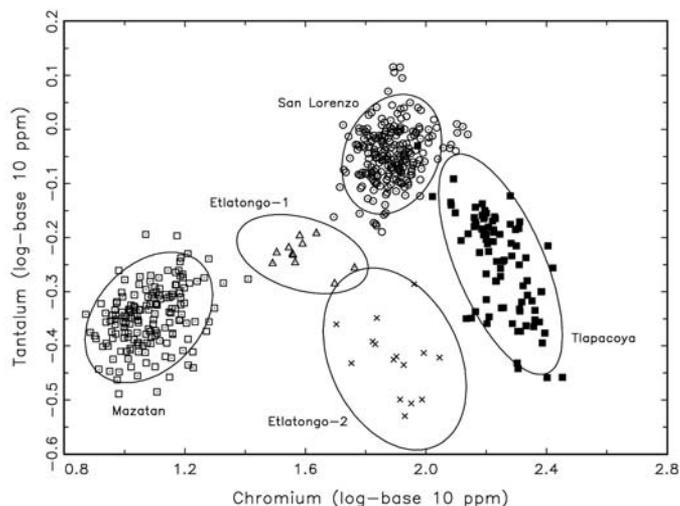


Fig. 4. Bivariate plot of chromium and tantalum concentrations in pottery samples assigned to five well-defined reference groups in the Early Formative pottery database. Ellipses represent 90% confidence level for group membership, with unique symbols for the samples of each group.

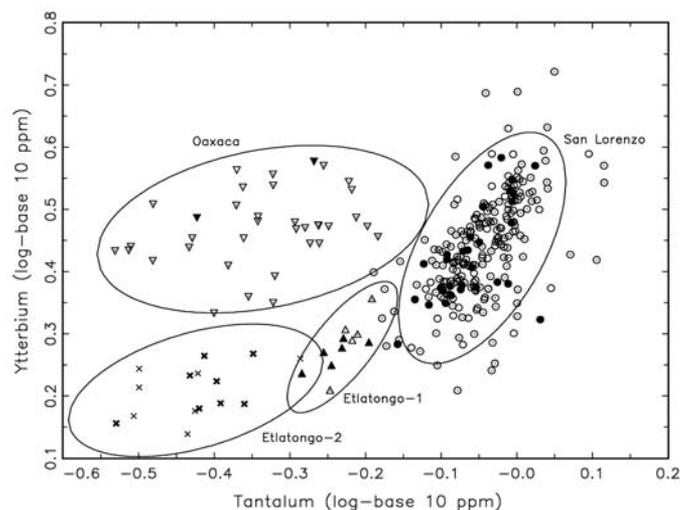


Fig. 5. Bivariate plot of tantalum and ytterbium shows the high concentration of tantalum in San Lorenzo samples. Shaded/bold symbols represent the samples detailed in table S1. Ellipses represent 90% confidence level for group membership, with unique symbols for the samples of each group.

virtually all Xochiltepec White and La Mina White ceramics in the sample, were evidently produced with San Lorenzo clay.

One white-ware group, White-2, cannot be associated with a specific region. All nine White-2 samples in table S3 appear similar to Xochiltepec White pottery or a similar type. The chemistry of Xochiltepec White pottery clearly indicates that it was produced in the Gulf Coast, but all White-2 group archaeological samples have been found in the Valley of Oaxaca. Although this occurrence could represent a kaolin source in the Valley of Oaxaca, approximately half of the specimens assigned to the group exceed 1% probability of membership in the San Lorenzo White group. Thus, there remains the possibility that the clay may be derived from slightly anomalous clays local to the San Lorenzo region.

The results of the INAA demonstrate that the Olmec produced luxury white wares, particularly Conejo Orange-on-White and Xochiltepec White, at San Lorenzo. Other regions included in the study evidently imported this pottery, which explains its

widespread distribution. Although some regions produced local variants, these were not exported between regions; no non-Gulf Coast-produced white ware was exported to San Lorenzo. Xochiltepec White, which first appears at San Lorenzo prior to the San Lorenzo horizon (9), and Conejo Orange-on-White were Olmec products exported to select sites throughout Mesoamerica.

In terms of decorated pottery, the San Lorenzo Local group contains most of the Olmec-style ceramics with iconography in the database, especially as expressed in gray-ware pottery. A problem did emerge early in the analysis in segregating pottery produced at San Lorenzo from certain Oaxaca gray wares. Generally, Gulf Coast clays contain low concentrations of calcium, whereas those from highland Oaxaca generally have high concentrations. Some samples of Gulf Coast pottery and clay, however, have calcium concentrations similar to examples of later Oaxacan gray wares, as well as ethnographic samples of Valley of Oaxaca pots and clay (12). A multivariate perspective resolves this problem; when all 32 elements retained from

Table 1. Secure regional assignments for Early Formative pottery

Archaeological context	Region as identified by INAA							Total
	Gulf Coast	Mazatán	Valley of Oaxaca	Nochixtlán Valley	Valley of Mexico	Chiapas Central Depression	Isthmus of Tehuantepec	
San Lorenzo (Gulf Coast)	203	0	0	0	0	0	0	203
Mazatán (various sites)	23	177	0	0	0	0	0	200
Valley of Oaxaca (various sites)	12	0	42	0	0	0	0	54
Etlatongo (Nochixtlán Valley)	35	0	0	26	0	0	0	61
Tlapacoya (Valley of Mexico)	17	0	0	0	87	0	0	104
San Isidro (Chiapas Central Depression)	1	0	0	0	0	41	0	42
Laguna Zope (Isthmus of Tehuantepec)	3	0	0	0	0	0	58	61
								725

the analysis are considered, the discrimination into groups is unambiguous. For example, just a bivariate plot of tantalum and ytterbium segregates archaeological samples from Oaxaca, Etlatongo, and San Lorenzo (Fig. 5).

In Oaxaca, Delfina and Leandro Gray pots with Olmec-style motifs have been interpreted as expressing local variants of the Olmec style manufactured in the Valley of Oaxaca and exported to other Formative centers (6, 11). Our data document the presence of compositionally different gray wares in the Valley of Oaxaca; it seems that both local manufacture and Olmec imports are represented at sites such as San José Mogote. Valley of Oaxaca-produced gray wares were not exported to the nearby Nochixtlán Valley; instead, Etlatongo imported Olmec-style gray wares from the more distant Gulf Coast (Fig. 3B). Indeed, all nonlocally produced Olmec-style gray pottery samples found outside the Gulf Coast appear to be San Lorenzo exports (Table 1).

The INAA data thus contradict the model that regional exports can be identified simply by style in assemblages of Olmec-style pottery (6). At least one supposed “Oaxaca-style” Calzadas Carved gray ware excavated at San Lorenzo (sample BLM050) was analyzed by INAA; it was produced with San Lorenzo clay.

The Olmec produced and exported a wide variety of Olmec-style iconography, often on gray-ware pottery, across Mesoamerica. Local production of Olmec-style motifs also occurred in all regions involved in this interaction. At Tlapacoya, a Basin of Mexico village known for pottery with elaborate profile views of cleft-headed creatures (21), Olmec-style designs occur on gray pottery with both San Lorenzo (BLM039) and local (BLM062) origins. Once again, none of the decorated and undecorated gray pottery analyzed from Tlapacoya was imported from Oaxaca.

Olmec and Early Formative interaction. The San Lorenzo Olmec produced both fine white-paste pottery and decorated Olmec-style ceramics. The Olmec exported this pottery to other regional centers across Mesoamerica, where many centers created local variants of it; indeed, we suspect Gulf Coast

Xochiltepec White served as the inspiration for local ceramic emulations throughout Mesoamerica. None of the locally produced Olmec-style pottery in the sample from the Valley of Oaxaca, the Nochixtlán Valley, the Valley of Mexico, the Isthmus of Tehuantepec, the Chiapas Central Depression, and the Mazatán region was exported to the Gulf Coast (Table 1). Contra to the sister-culture perspective, our analysis implies that the Olmec at San Lorenzo did not receive foreign-made variants of the Olmec style; the Olmec were its sole exporters. Despite the size of the San Lorenzo sample ($n = 203$), not a single analyzed sherd was imported. Rather than expressing regional styles from across Mesoamerica at San Lorenzo, the INAA data emphasize the diversity of Calzadas Carved pottery produced by the Olmec. Furthermore, the conservative approach used to assign members to the compositional groups may underestimate the numbers of San Lorenzo-derived specimens exported outside the Gulf Coast. Because sampling was not random, the data in Table 1 do not represent frequencies of imported pottery for each region.

Our data present several implications for understanding the Olmec and their relationships with contemporaneous groups. Olmec pottery and symbols associated with the Olmec were valued by elites at some of the largest chiefly centers in Early Formative Mesoamerica. It does not appear that these other regions contributed substantially to the assemblage of Olmec-style symbols employed beyond each region. Not only did the Olmec not import any foreign pottery with Olmec-style symbols, none of the regions in Table 1 exchanged pottery with each other. Etlatongo and San José Mogote, in adjacent regions of highland Oaxaca, received pottery from the more distant San Lorenzo rather than from each other. This appears to be a stark repudiation of the view of mutual exchange and production of these symbols, and it contradicts the claim that Oaxacan Delfina Fine gray pottery was as popular an export ware as Xochiltepec White (6). The regions outside the Gulf Coast appear to be primarily con-

sumers and emulators rather than exporters and innovators of Olmec-style motifs.

We propose that the San Lorenzo Olmec played a central role in synthesizing a distinct style and associated iconography, disseminating it across Mesoamerica. The mechanisms for exchange of Olmec-style pottery and symbols probably varied on a regional basis. Rather than being imposed by the Olmec, these symbols were received by people, probably leaders, at regional centers, who used, manipulated, and reproduced them in different ways. Exchange of these symbols formed an important component of communication and negotiation between communities on both intra- and interregional levels; non-Gulf Coast groups may have moved Olmec-produced objects between regions rather than locally produced pottery. The local impact of this interaction on communities varied. While this interaction may have had a transformative effect on the local population of the Mazatán region (22), the impact in the Nochixtlán Valley appears to be substantially different and less profound. Despite the high frequency of imported Olmec pottery in Table 1, the total quantity of Olmec-style pottery, both imported and locally made, probably never exceeded 5 to 10% of the total ceramic assemblage excavated at Etlatongo (7).

Olmec priority in the creation of the Olmec style emphasizes their important role in Early Formative social developments throughout much of Mesoamerica. Understanding the Olmec role in disseminating this style and associated iconography invokes more dynamic models of interregional interaction that explore the interests of both producers and consumers of Olmec-style pottery. This multifaceted interaction anticipates the increasingly complex nature of Olmec networks in the following Middle Formative Period, when La Venta became the Gulf Coast's largest Olmec center.

References and Notes

1. M. Coe, in *Handbook of Middle American Indians*, Vol. 3: *Archaeology of Southern Mesoamerica*, part 2, R. Wauchope, G. Willey, Eds. (Univ. Texas Press, Austin, 1965), pp. 739–775.
2. E. Benson, B. de la Fuente, Eds., *Olmec Art of Ancient Mexico* (National Gallery of Art, Washington, DC, 1996).

3. R. Sharer, D. Grove, Eds., *Regional Perspectives on the Olmec* (Cambridge Univ. Press, New York, 1989).
4. D. Grove, *J. World Prehistory* 11, 51 (1997).
5. A. Cyphers, in *Olmec to Aztec: Settlement Patterns in the Ancient Gulf Lowlands*, B. Stark, P. Arnold III, Eds. (Univ. of Arizona Press, Tucson, AZ, 1997), pp. 96–114.
6. K. Flannery, J. Marcus, *Early Formative Pottery of the Valley of Oaxaca, Mexico*, Memoirs of the Museum of Anthropology 27 (Univ. of Michigan, Ann Arbor, MI, 1994).
7. J. Blomster, *Etlatongo: Social Complexity, Interaction, and Village Life in the Mixteca Alta of Oaxaca, Mexico* (Wadsworth, Belmont, CA, 2004).
8. J. Blomster, *Ancient Mesoamerica* 9, 171 (1998).
9. M. Coe, R. Diehl, *In the Land of the Olmec*, Vol. 1: *The Archaeology of San Lorenzo Tenochtitlán* (Univ. of Texas Press, Austin, TX, 1980).
10. K. Flannery, in *Dumbarton Oaks Conference on the Olmec*, E. Benson, Ed. (Dumbarton Oaks, Washington, DC, 1968), pp. 79–117.
11. K. Flannery, J. Marcus, *J. Anthropol. Archaeol.* 19, 1 (2000).
12. H. Neff, M. Glascock, "Report on Instrumental Neutron Activation Analysis of Olmec Pottery" (Research Reactor Center, Univ. of Missouri, Columbia, MO, 2002).
13. R. Herrera, H. Neff, M. Glascock, J. Elam, *J. Archaeol. Science* 26, 967 (1999).
14. M. Thieme, in *Procesos de Cambio y Conceptualización del Tiempo: Memoria de la Primera Mesa Redonda de Monte Albán*, N. Robles García, Ed. (Instituto Nacional de Antropología e Historia, Mexico City, 2001), pp. 341–349.
15. J. Lorenzo, *Rev. Mex. Estud. Antropol.* 16, 49 (1960).
16. M. Kirkby, *The Physical Environment of the Nochihtlán Valley, Oaxaca*, Vanderbilt University Publications in Anthropology 2 (Vanderbilt Univ., Nashville, TN, 1972).
17. M. Glascock, in *Chemical Characterization of Ceramic Pastes in Archaeology*, H. Neff, Ed. (Prehistory Press, Madison, WI, 1992), pp. 11–26.
18. H. Neff, in *Modern Analytical Methods in Art and Archaeology*, E. Ciliberto, G. Spoto, Eds. (Wiley, New York, 2000), pp. 81–134.
19. Materials and methods are available as supporting material on Science Online.
20. R. Bishop, H. Neff, in *Archaeological Chemistry IV*, R. Allen, Ed. (American Chemical Society, Washington, DC, 1989), pp. 576–586.
21. P. Joralemon, *A Study of Olmec Iconography*, Studies in Pre-Columbian Art and Archaeology 7 (Dumbarton Oaks, Washington, DC, 1971).
22. J. Clark, M. Pye, in *Olmec Art and Archaeology in Mesoamerica*, J. Clark, M. Pye, Eds. (National Gallery of Art, Washington, DC, 2000), pp. 217–251.

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Supporting Online Material

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Materials and Methods

Tables S1 to S3

References

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Whole-Genome Patterns of Common DNA Variation in Three Human Populations

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Individual differences in DNA sequence are the genetic basis of human variability. We have characterized whole-genome patterns of common human DNA variation by genotyping 1,586,383 single-nucleotide polymorphisms (SNPs) in 71 Americans of European, African, and Asian ancestry. Our results indicate that these SNPs capture most common genetic variation as a result of linkage disequilibrium, the correlation among common SNP alleles. We observe a strong correlation between extended regions of linkage disequilibrium and functional genomic elements. Our data provide a tool for exploring many questions that remain regarding the causal role of common human DNA variation in complex human traits and for investigating the nature of genetic variation within and between human populations.

Single-nucleotide polymorphisms (SNPs) are the most abundant form of DNA variation in the human genome. It has been estimated that there are ~7 million common SNPs with a minor allele frequency (MAF) of at least 5% across the entire human population (1). Most common SNPs are to be found in most major populations, although the frequency of any allele may vary considerably between populations (2). An additional 4 million SNPs exist with a MAF between 1 and 5%. In addition, there are innumerable very rare

single-base variants, most of which exist in only a single individual.

The relationship between DNA variation and human phenotypic differences (such as height, eye color, and disease susceptibility) is poorly understood. Although there is evidence that both common SNPs and rare variants contribute to the observed variation in complex human traits (3, 4), the relative contribution of common versus rare variants remains to be determined. The structure of genetic variation between populations and its relationship to phenotypic variation is unclear. Similarly, the relative contribution to complex human traits of DNA variants that alter protein structure by amino acid replacement, versus variants that alter the spatial or temporal pattern of gene expression without altering protein structure, is unknown. In

some cases, these issues have been studied in limited genomic intervals, but comprehensive genomic analyses have not been possible.

Genome-wide association studies to identify alleles contributing to complex traits of medical interest are currently performed with subsets of common SNPs, and thus they rely on the expectation that a disease allele is likely to be correlated with an allele of an assayed SNP. Although studies have shown that variants in close physical proximity are often strongly correlated, this correlation structure, or linkage disequilibrium (LD), is complex and varies from one region of the genome to another, as well as between different populations (5, 6). Selection of a maximally informative subset of common SNPs for use in association studies is necessary to provide sufficient power to assess the causal role of common DNA variation in complex human traits. Although a large fraction of all common human SNPs are available in public databases, lack of information concerning SNP allele frequencies and the correlation structure of SNPs within and between human populations has made it difficult to select an optimal subset.

Here we examine the SNP allele frequencies and patterns of LD between 1,586,383 SNPs distributed uniformly across the human genome in unrelated individuals of European, African, and Asian ancestry. Our primary aim was to create a resource for further investigation of the structure of human genetic variation and its relationship to phenotypic differences.

A dense SNP map. To characterize a panel of markers that would be informative in whole-genome association studies, we selected a total of 2,384,494 SNPs likely to be common in individuals of diverse ancestry (7). We identified the majority (69%) of the SNPs by performing array-based resequencing

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