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The Spread of Maize from Southern Mexico: Genetic and Archaeological Perspectives

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Abstract Maize (*Zea mays*), domesticated from its wild ancestor teosinte in southern Mexico around 9 000 years ago, has become one of the most important staple crops globally. This research integrates genetic and archaeological data to trace the domestication, dissemination, and impact of maize. Genetic evidence pinpoints the Balsas River Valley as the center of domestication, with subsequent spread facilitated by genetic diversity and adaptive introgression with local teosinte populations. Archaeological findings corroborate these genetic insights, revealing early cultivation sites and trade routes that enabled maize to adapt to diverse environments across the Americas. The spread of maize significantly influenced ancient agricultural practices, economic structures, and cultural rituals, underlining its role in shaping complex societies. Modern implications emphasize the importance of genetic diversity for breeding resilient maize varieties and the need for interdisciplinary research to address contemporary agricultural challenges. This research highlights the transformative journey of maize from its origin to its current global significance, providing a comprehensive understanding of its past, present, and future.

Keywords Maize domestication; Genetic diversity; Archaeological evidence; Crop adaptation; Agricultural practices

1 Introduction

Maize (*Zea mays*), commonly known as corn, stands as one of the most vital crops in global agriculture. It serves not only as a staple food for millions of people but also as a fundamental component in animal feed, biofuel production, and numerous industrial applications (Ramos-Madrigal et al., 2016; Smith et al., 2018). The versatility of maize and its adaptability to diverse climatic conditions have allowed it to become a cornerstone of food security and economic stability in many regions across the world. Its high yield potential and significant nutritional value further underline its critical role in sustaining the growing global population (Tenaillon and Charcosset, 2011; Galvan et al., 2019).

Understanding the origins and spread of maize is crucial for several reasons. Firstly, it provides insights into the processes of domestication and crop evolution, which are fundamental to improving current agricultural practices and developing more resilient crop varieties (Aguirre-Liguori et al., 2016; Zahn et al., 2018). Tracing the historical pathways of maize dispersal helps elucidate the cultural and economic exchanges among ancient civilizations, highlighting the role of maize in the development of complex societies (Kistler er al., 2018; 2020). Finally, knowledge of maize's genetic diversity and adaptation mechanisms is essential for addressing contemporary challenges such as climate change, food security, and sustainable agriculture (Orozco-Ramírez et al., 2016; Lohse et al., 2022).

This study aims to synthesize genetic and archaeological evidence to provide a comprehensive overview of the genetic diversity within the genus *Zea*, with a particular focus on the domestication and dissemination of maize from its origin in southern Mexico. By integrating findings from diverse fields, this paper seeks to elucidate the complex interplay between human activity and genetic evolution that has driven the expansion of maize. The significance of this work lies in its potential to inform current and future efforts in maize conservation and improvement. By understanding the genetic underpinnings and historical trajectories of maize, researchers and agriculturalists can better address contemporary challenges in food security and crop sustainability.

2 Origins of Maize in Southern Mexico

2.1. Genetic evidence for the domestication of maize

The genetic evidence for the domestication of maize points to a single origin in southern Mexico, where its wild ancestor, teosinte (*Zea mays* ssp. *parviglumis*), was domesticated (Heerwaarden et al., 2010; Panda et al., 2020). Genetic studies have consistently supported this theory, indicating that maize underwent a domestication event approximately 9 000 years ago in this region. Molecular analyses, including those of isozymes and chloroplast DNA, provide strong support for the hypothesis that teosinte is ancestral to maize. These studies have shown that populations of teosinte from the central Balsas River Valley in Mexico exhibit the closest genetic relationship to modern maize (Doebley, 1990).

Further research has revealed that during domestication, a significant genetic bottleneck occurred, reducing genetic diversity in maize compared to its wild relatives. This bottleneck is evidenced by the reduced genetic variability observed in domesticated maize when compared to teosinte (Vallebueno-Estrada et al., 2016). Genomic studies also highlight the role of artificial selection in shaping maize's genetic makeup, with approximately 2% of maize genes showing signs of artificial selection, primarily related to traits advantageous for cultivation and yield (Yamasaki et al., 2007).

2.2 Archaeological findings related to early maize cultivation

Archaeological evidence supports the genetic findings by indicating early maize cultivation in southern Mexico. Macro- and microbotanical evidence, including maize pollen and phytoliths, has been found in sediment layers dating back to approximately 8 700 years ago. These findings suggest that maize was one of the first domesticated crops in the region and played a crucial role in the development of early agricultural societies.

Significant archaeological sites such as Guilá Naquitz and San Marcos Cave have yielded early maize cobs and other botanical remains, which provide concrete evidence of early cultivation practices. These sites illustrate the transition from wild to domesticated maize, highlighting the gradual process of selecting for desirable traits over generations (Aguirre-Liguori et al., 2016).

2.3 The role of Southern Mexico in the initial domestication process

Southern Mexico, particularly the Balsas River Valley, is recognized as the primary center of maize domestication. This region's unique environmental conditions and the presence of wild teosinte provided the ideal setting for the initial domestication process. Genetic evidence indicates that the domestication of maize was a single event rather than multiple independent events, underscoring the significance of southern Mexico in this agricultural milestone (Doebley, 1990).

The role of southern Mexico in maize domestication is further emphasized by studies on genetic introgression. As domesticated maize spread to different regions, it occasionally hybridized with local wild teosinte populations, incorporating beneficial traits that allowed maize to adapt to diverse environments. This genetic exchange facilitated the spread of maize to higher elevations and different climatic zones, demonstrating the adaptability and resilience of this crop (Aguirre-Liguori et al., 2016).

The genetic and archaeological evidence converges on southern Mexico as the cradle of maize domestication. The genetic data indicate a single domestication event in this region, while archaeological findings provide tangible proof of early cultivation practices. The initial domestication process in southern Mexico set the stage for maize to become a globally significant crop, underlining the importance of this region in agricultural history.

3 Genetic Perspectives on Maize Spread

3.1 Analysis of maize genetic diversity and its implications

Maize (*Zea mays*) exhibits significant genetic diversity, which has profound implications for its cultivation, adaptation, and improvement. The genetic diversity within maize is a product of both its domestication history and subsequent breeding practices. This diversity is critical for the crop's ability to adapt to various environmental stresses and changing climatic conditions.

Genetic analyses have demonstrated that maize possesses high levels of allelic variation, particularly between different landraces and wild relatives such as teosinte. This variation is evident in traits related to yield, disease resistance, and environmental adaptability (Doebley, 1990). The genetic diversity within maize is essential for maintaining its resilience against pests and diseases, such as Maize Lethal Necrosis Disease (MLND), which poses a significant threat to maize production in regions like Eastern Africa (Ndakidemi et al., 2016).

Furthermore, genetic diversity is vital for ongoing breeding programs. By utilizing the diverse genetic pool available in both cultivated and wild maize populations, breeders can develop varieties that are more productive, nutritionally enhanced, and better suited to specific growing conditions. This genetic richness provides the foundation for future improvements in maize, ensuring the crop remains viable and productive in the face of environmental challenges (Figure 1) (Yamasaki et al., 2007).

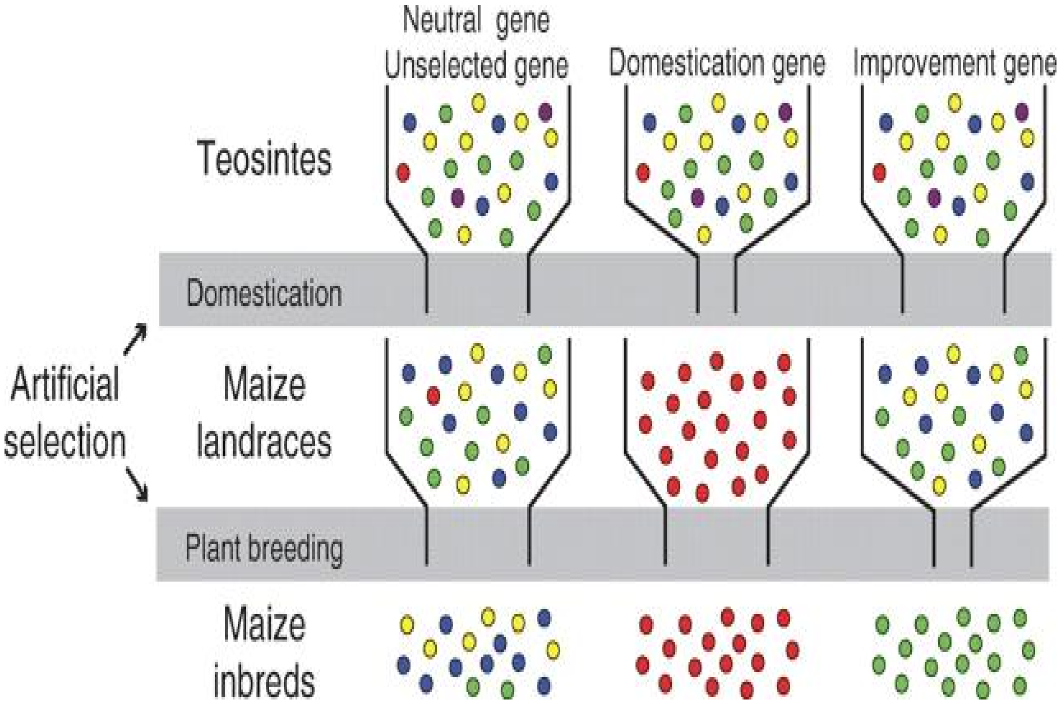

Figure 1 Effect of artificial selection on the genetic diversity of maize genes (Adopted from Yamasaki et al., 2007).
Image caption: Artificial selection in maize can be divided into two stages: domestication and improvement (plant breeding). The coloured circles represent different alleles. The shaded areas indicate bottleneck effects placed on all genes by the processes of domestication and improvement. The model assumes that there will be three types of genes; neutral (unselected) genes that show reduction of diversity by the general bottleneck effects, domestication genes in which diversity is greatly reduced by selection between the teosintes and landraces, and improvement genes in which diversity is greatly reduced by selection between the landraces and inbreds (Adapted from Yamasaki et al., 2007).).

3.2 Genomic studies tracing the migration of maize populations

Genomic studies have played a crucial role in tracing the migration and spread of maize from its center of domestication in southern Mexico. These studies leverage advanced genomic technologies to analyze the DNA of ancient and modern maize samples, providing insights into how maize populations have moved and adapted over time.

One significant finding from genomic research is the identification of genetic markers that indicate the pathways through which maize spread across the Americas and eventually to other parts of the world. For instance, maize spread northward into the southwestern United States and southward into Central and South America. Genetic evidence suggests that as maize migrated, it hybridized with local teosinte populations, incorporating beneficial traits that enhanced its adaptability to diverse environments (Aguirre-Liguori et al., 2016; Kistler et al., 2020).

Additionally, genomic studies have highlighted the role of human selection in shaping the genetic landscape of maize. Artificial selection for desirable traits such as yield, taste, and hardiness has resulted in a variety of landraces adapted to specific regions and uses. This selection pressure has left distinct genetic signatures in the maize genome, which researchers can trace to understand the historical development and spread of different maize varieties (Yamasaki et al., 2007).

3.3 Insights from genetic markers and phylogenetic studies

Genetic markers and phylogenetic studies provide critical insights into the evolutionary history and genetic relationships of maize. These tools enable scientists to construct detailed phylogenetic trees that illustrate the genetic connections between different maize varieties and their wild relatives.

Isozyme and chloroplast DNA studies have been particularly instrumental in understanding the genetic evolution of maize. These studies confirm that teosinte, particularly *Zea mays* ssp. *parviglumis*, is the closest wild relative of domesticated maize. This relationship is evident in the genetic similarities observed in isozyme and chloroplast DNA profiles between teosinte and maize (Doebley, 1990).

Moreover, molecular markers such as single nucleotide polymorphisms (SNPs) have been used to trace the genetic diversity and adaptation of maize. SNP analysis helps identify regions of the genome that have undergone selection pressures, providing clues about the traits that were crucial for maize's adaptation to new environments (Aguirre-Liguori et al., 2016; Costa et al., 2022).

Phylogenetic studies also reveal the complex interplay between maize and its environment. As maize spread to different regions, it encountered various environmental challenges, leading to genetic adaptations that enhanced its survival and productivity. These adaptations are reflected in the genetic diversity seen across different maize populations, highlighting the importance of genetic research in understanding and leveraging this diversity for future crop improvement (Doebley, 1990).

The genetic diversity of maize, its migration patterns traced through genomic studies, and the insights gained from genetic markers and phylogenetic analyses all contribute to a comprehensive understanding of maize's spread and adaptation. These findings not only illuminate the past but also guide future efforts in maize breeding and conservation, ensuring the continued success of this vital crop.

4 Archaeological Evidence for the Spread of Maize

4.1 Key archaeological sites with maize remnants

The spread of maize from its origin in southern Mexico is documented through various key archaeological sites that provide substantial evidence of early maize cultivation and usage. One such significant site is Guilá Naquitz Cave in Oaxaca, Mexico, where maize cobs dating back to approximately 6 250 years ago were discovered, marking some of the earliest evidence of domesticated maize (Hart and Lovis, 2013).

Another crucial site is San Marcos Cave, also in Oaxaca, where botanical remains including maize cobs and kernels have been dated to around 4 500 years ago. These findings provide insights into the early stages of maize domestication and its initial cultivation practices (Doebley, 1990).

In the southwestern United States, the Bat Cave in New Mexico revealed maize cobs dated to about 3 000 years ago, indicating the northward spread of maize agriculture. This site, among others in the region, showcases the adaptation and expansion of maize cultivation into different environmental zones (Hart and Lovis, 2013).

4.2 Radiocarbon dating and other dating methods used in maize studies

Radiocarbon dating is a pivotal method for establishing the chronological framework of maize domestication and spread. This technique measures the decay of carbon-14 isotopes in organic material, providing age estimates for archaeological samples. The radiocarbon dating of maize remains from Guilá Naquitz and San Marcos Caves has been instrumental in tracing the timeline of early maize cultivation (Piperno, 2016).

Phytolith analysis, another dating method, involves examining silica structures formed in plant cells that remain preserved in soil long after the plants have decayed. Phytoliths specific to maize can be identified and dated, providing additional evidence of maize presence in ancient soils. This method has corroborated radiocarbon dating results in several key sites, enhancing the understanding of maize's spread (Piperno, 2016; Smith, 2017).

Stable isotope analysis of carbon and nitrogen in human and animal bones from archaeological sites offers further insights into ancient diets and agricultural practices. This technique can distinguish between different types of plants consumed, including maize, by analyzing the isotopic signatures left in the bones. Studies using stable isotope analysis have confirmed the significant role of maize in ancient diets across various regions (Schoeninger and Moore, 1992).

4.3 Evidence of maize use and cultivation in different regions

The archaeological record provides extensive evidence of maize use and cultivation across different regions, illustrating its spread from southern Mexico to various parts of the Americas and beyond. In the northeastern United States, maize remains found in sites such as the Finger Lakes region of New York indicate that maize agriculture was established by around 1,000 AD. These findings suggest that maize played a crucial role in the development of settled village life and agricultural systems in the region (Hart and Lovis, 2013).

In South America, evidence from sites in Peru, such as the archaeological remains at Huaca Prieta, show that maize was cultivated and used extensively by around 3 000 years ago. The presence of maize in these sites highlights its importance in the diet and economy of pre-Columbian societies in the region (Dunn, 1979).

Further afield, the introduction of maize into Europe is well-documented, with archaeological evidence showing that maize reached the continent by the late 15th century. The spread of maize across Europe was rapid, and it soon became a staple crop in many regions. Genetic studies of European maize landraces indicate a high level of diversity, reflecting the various introductions and adaptations of maize to different European environments (Gouesnard et al., 2005; Kistler et al., 2020).

The archaeological evidence, supported by advanced dating methods, paints a comprehensive picture of the spread of maize from its origin in southern Mexico to various parts of the world. The continuous discovery and analysis of maize remnants at key archaeological sites underscore the significance of this crop in ancient agricultural systems and its enduring impact on human societies.

5 Routes and Mechanisms of Maize Dissemination

5.1 Proposed routes of maize spread from southern mexico

The spread of maize from its origin in southern Mexico followed several key routes that facilitated its dissemination across the Americas and eventually to other parts of the world. Initially, maize spread northward into the southwestern United States and southward into Central and South America. Genetic and archaeological evidence supports these pathways, showing that as maize moved, it adapted to diverse environments and incorporated beneficial traits from local teosinte populations (Aguirre-Liguori et al., 2016).

One of the major routes of maize spread into the southwestern United States was through the highlands of Mexico, where it adapted to cooler climates and higher altitudes. This route is evidenced by early maize remains found in sites such as Bat Cave in New Mexico, dating back to approximately 3 000 years ago (Hart and Lovis, 2013).

Southward, maize spread through the Isthmus of Tehuantepec into Central America and further into South America. This route is supported by archaeological findings in Peru, where maize was present as early as 3 000 years ago. The spread of maize into South America involved both coastal and inland routes, adapting to various climatic and environmental conditions along the way (Doebley, 1990).

5.2 Cultural and trade exchanges facilitating maize dissemination

The dissemination of maize was significantly facilitated by cultural and trade exchanges among ancient civilizations. Maize was not only a staple crop but also a commodity traded extensively across regions, spreading agricultural practices and crop varieties. These exchanges occurred through established trade networks that connected different Mesoamerican cultures and beyond.

In Mesoamerica, the trade networks established by the Olmecs, Mayans, and Aztecs played a crucial role in the spread of maize. These civilizations traded maize as a valuable commodity, along with other goods, facilitating its spread to new areas and the exchange of agricultural knowledge. The Mayan civilization, in particular, is noted for its advanced agricultural techniques and extensive maize cultivation, which influenced surrounding regions (Orozco-Ramírez and Solís-Castillo, 2019).

Further north, maize cultivation spread into the southwestern United States through trade and cultural interactions with indigenous groups. The Ancestral Puebloans, known for their sophisticated agricultural systems, adopted maize cultivation, which became a central component of their diet and culture. Trade routes such as the Chacoan roads facilitated the movement of maize and agricultural knowledge across the region (Hart and Lovis, 2013).

In South America, the spread of maize was influenced by the Andean civilizations, such as the Inca, who developed extensive agricultural terraces and irrigation systems. Maize was a staple crop in the Andean region and was traded extensively, contributing to its spread throughout the continent (Dunn, 1979).

5.3 Environmental and ecological factors influencing the spread

Environmental and ecological factors played a critical role in the dissemination of maize. The adaptability of maize to various climatic conditions and its ability to thrive in diverse ecological zones were key factors in its widespread cultivation. Maize's genetic diversity allowed it to be cultivated in a range of environments, from arid regions to high-altitude areas (Tenaillon and Charcosset, 2011).

One significant environmental factor was the adaptability of maize to different altitudes and climates. In the highlands of Mexico and the Andes, maize adapted to cooler temperatures and shorter growing seasons. Genetic studies have shown that maize incorporated traits from local teosinte populations, which helped it thrive in these environments (Aguirre-Liguori et al., 2016)

Soil fertility and water availability were also crucial in the spread of maize. Regions with fertile soils and reliable water sources, such as river valleys, supported intensive maize cultivation. The development of irrigation systems and agricultural terraces in regions like the Andean highlands further facilitated maize cultivation in areas with less natural water availability (Hart and Lovis, 2013)

Additionally, human-induced environmental changes, such as deforestation and land modification for agriculture, created new habitats for maize cultivation. The clearing of forests and the development of agricultural fields expanded the areas where maize could be grown, supporting larger populations and more complex societies.

The spread of maize from southern Mexico was facilitated by a combination of proposed routes, cultural and trade exchanges, and environmental factors. These elements collectively contributed to the widespread dissemination and adaptation of maize, making it one of the most important crops in human history.

6 Integration of Genetic and Archaeological Data

6.1 Correlating genetic data with archaeological findings

Integrating genetic and archaeological data provides a comprehensive understanding of maize's domestication and spread. Genetic studies offer insights into the evolutionary history and genetic diversity of maize, while archaeological findings provide physical evidence of cultivation and usage patterns. By correlating these data sets, researchers can trace the geographical and temporal pathways of maize dissemination.

Genetic evidence indicates that maize was domesticated from its wild ancestor, teosinte, in the Balsas River Valley of southern Mexico around 9 000 years ago (Doebley, 1990). This genetic information aligns with archaeological discoveries of early maize remains at sites such as Guilá Naquitz Cave and San Marcos Cave in Oaxaca, which date back to approximately 6 250 and 4 500 years ago, respectively (Hart and Lovis, 2013).

Further genetic analyses show a reduction in genetic diversity during domestication, which corresponds with archaeological evidence of selective breeding and cultivation practices. For example, genetic studies have identified specific alleles in maize that were selected for traits such as increased cob size and kernel number, traits that are evident in the larger, more productive maize cobs found at later archaeological sites (Aguirre-Liguori et al., 2016).

6.2 Case studies showcasing the integration of both data types

One notable case study is the integration of genetic and archaeological data from the southwestern United States. Genetic analyses of ancient maize samples from sites such as Bat Cave in New Mexico, dating back to around 3 000 years ago, reveal genetic markers indicative of adaptation to the arid conditions of the region. This genetic information complements archaeological findings of irrigation and dry farming techniques used by the Ancestral Puebloans to cultivate maize (Hart and Lovis, 2013)

Another case study involves the Andean region of South America, where maize was present by approximately 3 000 years ago. Genetic studies of Andean maize show introgression from local teosinte populations, which likely contributed to its adaptation to high-altitude environments. Archaeological evidence from sites such as Huaca Prieta in Peru supports this, showing early agricultural terraces and irrigation systems that facilitated maize cultivation in these challenging environments (Dunn, 1979).

6.3 Benefits and challenges of interdisciplinary research in maize studies

The integration of genetic and archaeological data in maize studies offers several benefits. It provides a holistic view of maize domestication and spread, combining genetic evidence of evolutionary changes with archaeological context. This interdisciplinary approach can reveal how ancient agricultural practices influenced genetic diversity and how genetic adaptations facilitated maize's spread to diverse environments.

One significant benefit is the ability to cross-validate findings. Genetic data can confirm hypotheses generated from archaeological evidence and vice versa. For instance, genetic markers indicating drought tolerance in ancient maize can be linked to archaeological evidence of irrigation systems in arid regions, providing a fuller picture of ancient agricultural strategies (Aguirre-Liguori et al., 2016).

However, integrating these data types also presents challenges. One major challenge is the difference in temporal resolution. Genetic data can provide continuous records over long periods, while archaeological evidence is often discrete and dependent on site preservation and excavation quality. Additionally, the spatial resolution of archaeological data can be limited to specific sites, whereas genetic data can cover broader geographical ranges.

Another challenge is the interdisciplinary nature of the research, which requires collaboration between geneticists, archaeologists, and other specialists. Differences in methodologies, terminologies, and research priorities can complicate collaboration. Effective interdisciplinary research necessitates clear communication and a willingness to integrate diverse perspectives and techniques.

Integrating genetic and archaeological data enriches our understanding of maize domestication and spread, offering comprehensive insights that neither discipline could achieve alone. Despite the challenges, the benefits of interdisciplinary research are substantial, providing a more detailed and accurate picture of maize's history and its impact on human societies.

7 Impacts of Maize Spread on Ancient Societies

7.1 Agricultural practices and societal changes driven by maize cultivation

The introduction and widespread cultivation of maize had profound effects on agricultural practices and societal structures in ancient civilizations. Initially domesticated in southern Mexico, maize's adaptability to diverse climates and soils facilitated its spread to various regions, leading to significant agricultural innovations. The cultivation of maize required the development of new farming techniques, such as crop rotation and irrigation, which improved agricultural productivity and sustainability.

In Mesoamerica, maize cultivation supported the growth of complex societies, including the Olmecs, Mayans, and Aztecs. These civilizations developed advanced agricultural systems, including terracing and chinampas (floating gardens), which allowed them to cultivate maize in a variety of environmental conditions. The increased agricultural productivity from maize cultivation enabled population growth and urbanization, leading to the development of large, centralized states with sophisticated political and social structures (Tuxill et al., 2010; Hart and Lovis, 2013; Kistler et al., 2020).

Maize also played a crucial role in the development of settled agricultural communities in the southwestern United States. The Ancestral Puebloans, for example, relied heavily on maize cultivation, which supported the establishment of permanent settlements and the construction of large, communal structures. These changes in agricultural practices and settlement patterns were directly linked to the introduction and expansion of maize agriculture (Doebley, 1990).

7.2 Economic and nutritional impacts on ancient populations

Maize's high nutritional value and versatility had significant economic and nutritional impacts on ancient populations. As a staple crop, maize provided a reliable source of calories, carbohydrates, and essential nutrients, contributing to improved dietary diversity and food security. The cultivation of maize allowed for surplus production, which could be stored and traded, fostering economic growth and inter-regional trade networks.

In Mesoamerican societies, maize was not only a staple food but also a key commodity in trade. The surplus maize produced through advanced agricultural techniques was traded for other goods, such as pottery, textiles, and jade, facilitating economic exchange and cultural interaction across the region. This trade network contributed to the economic prosperity and political power of maize-cultivating societies (Hart and Lovis, 2013).

Nutritionally, maize provided essential vitamins and minerals, such as vitamin A, iron, and zinc. The introduction of maize-based diets improved overall health and reduced the incidence of malnutrition-related diseases. Biofortification efforts, both ancient and modern, have further enhanced the nutritional profile of maize, addressing deficiencies in essential nutrients (Table 1) (Shah et al., 2016).

Table 1 Concentration of major phytochemical compounds of maize per 100 gm (Adopted from Shah et al., 2016)

Compounds	Concentration (mg/100gm)
(1) Caroteniods	-
(a) Carotene	2.2
(b) Xanthophylls	2.07
(i) Lutein	1.5
(ii) Zeaxanthin	0.57
(2) Phenolic compounds	-
(a) Ferulic acid (FA)	174
(b) Anthocyanins	141.7
(3) Phytosterols	14.83
(a) Sitosterol	9.91
(b) Stigmasterol	1.52
(c) Campesterol	3.4

Table caption: Table 1 provides a detailed analysis of the concentration of major phytochemical compounds in maize, measured per 100 grams. Carotenoids are present in notable amounts, with carotene at 2.2 mg and xanthophylls at 2.07 mg, which includes lutein at 1.5 mg and zeaxanthin at 0.57 mg. Phenolic compounds are significantly higher, with ferulic acid (FA) at 174 mg and anthocyanins at 141.7 mg. Phytosterols are also represented, totaling 14.83 mg, with sitosterol at 9.91 mg, stigmasterol at 1.52 mg, and campesterol at 3.4 mg. This table highlights the rich nutritional profile of maize, particularly its strong presence of antioxidant phenolic compounds and carotenoids, which are essential for human health (Adopted from Shah et al., 2016)

7.3 Maize in the context of cultural and ritual practices

Maize held significant cultural and ritual importance in many ancient societies. In Mesoamerica, maize was not only a staple food but also a central element in mythology, religion, and daily life. The Mayans, for example, revered maize as a sacred crop, believing it was a gift from the gods. Maize was integral to various religious ceremonies and rituals, symbolizing life, fertility, and sustenance.

The Popol Vuh, a sacred Mayan text, describes the creation of humans from maize dough, highlighting the crop's fundamental role in Mayan cosmology and cultural identity. Similarly, the Aztecs worshipped Centeotl, the maize god, and conducted elaborate rituals to ensure a bountiful maize harvest. These cultural practices underscored the deep spiritual connection between maize and the societies that cultivated it (Hart and Lovis, 2013).

In the southwestern United States, maize was central to the cultural and ceremonial life of the Ancestral Puebloans and other indigenous groups. Maize was used in various ceremonies, including planting and harvest rituals, to honor the earth and seek blessings for a successful crop. The significance of maize in these cultural practices reinforced its importance in the social and spiritual fabric of these communities (Lantos et al., 2015).

In conclusion, the spread of maize from southern Mexico had profound impacts on ancient societies, driving agricultural innovations, economic growth, and cultural development. The integration of maize into agricultural systems and cultural practices highlights its enduring significance and transformative role in shaping the history and development of civilizations across the Americas.

8 Modern Implications and Future Research Directions

8.1 Lessons learned from the historical spread of maize

The historical spread of maize provides valuable lessons that can inform modern agricultural practices and crop management strategies. One key lesson is the importance of genetic diversity in ensuring the adaptability and resilience of maize to various environmental conditions. As maize spread from its origin in southern Mexico to different regions, it incorporated beneficial traits from local teosinte populations, which enhanced its adaptability to new climates and agricultural systems (Aguirre-Liguori et al., 2016; Kistler et al., 2016; Zahn et al., 2018)

Another critical lesson is the role of human intervention and selective breeding in shaping the genetic makeup of maize. Ancient agricultural societies selected for traits that improved yield, disease resistance, and adaptability, laying the foundation for the diverse maize varieties we have today. This historical perspective underscores the ongoing need for targeted breeding programs to address contemporary agricultural challenges, such as climate change and food security (Doebley, 1990).

8.2 Implications for modern maize breeding and agricultural practices

The insights gained from the historical spread and adaptation of maize have significant implications for modern breeding and agricultural practices. One major implication is the necessity of maintaining and expanding genetic diversity within maize breeding programs. Modern maize breeding often focuses on increasing yield and stress resistance through advanced genetic techniques, such as marker-assisted selection and genomic selection. These methods can help identify and incorporate beneficial traits from diverse genetic sources, ensuring that new maize varieties are resilient and high-yielding (Gazal et al., 2015).

Incorporating lessons from historical spread, modern breeding programs also emphasize the importance of adaptability to different environmental conditions. This involves developing maize varieties that can thrive under diverse climatic conditions and resist various biotic and abiotic stresses. For example, recent advances in molecular breeding have facilitated the development of maize hybrids that are more tolerant to drought and heat, addressing the challenges posed by climate change (Hake and Ross-Ibarra, 2015; Benavente and Giménez, 2021; Zhao et al., 2022).

8.3 Future research opportunities in genetic and archaeological studies of maize

Future research in maize studies can benefit from an interdisciplinary approach that integrates genetic, archaeological, and ecological data. One promising area of research is the continued exploration of maize's genetic diversity using advanced genomic tools. Techniques such as genome-wide association studies (GWAS) and high-throughput sequencing can help identify genetic variants associated with desirable traits, providing a deeper understanding of maize's genetic architecture and evolutionary history (Table 2) (Medeiros et al., 2021).

Table 2 Genetic mapping studies on metabolic traits in maize (Adopted from Medeiros et al., 2021)

Trait	Measurement	Candidate gene, locus, or encoding enzyme	Analysis
Carotenoids in kernels	LC	*y1*, *vp5*, and QTL	Linkage mapping
Maysin and chlorogenic acid in silks	LC	*p*, *a1*, *c2*, and *whp1*	Linkage mapping
Oleic acid in kernels	GC	*fad2*	Linkage mapping
Carotenoid composition and content in kernels	LC	*lcyE*	Association and linkage mapping
Oil content and fatty acid composition in seeds and embryos	NMR and GC	*dgat1-2*	QTL mapping
β-carotene in grains	LC	*lcyE* and *crtRB1*	QTL and linkage mapping
Oil content and fatty acid composition in kernels	GC	Multiple candidate genes	QTL and linkage mapping
Palmitic acid content in kernels	GC	*fatb*	QTL, association, and linkage mapping
Carbohydrates and ABA metabolites during stress in ears, silks, and leaves	ELISA and spectrophotometry	Multiple candidate genes	Association mapping
Anthocyanin in kernels	LC	*f3'h1*	Linkage mapping
Oil content and fatty acid composition in kernels	NMR and GC	*dgat1-2*	Linkage mapping
Starch, protein, and oil content in kernels	NIRS	Multiple candidate genes	Linkage mapping and GWAS
α-tocopherol content in kernels	LC	*vte4*	Linkage mapping and GWAS
Leaf metabolome	GC-MS	Multiple candidate genes	GWAS
α-carotene in kernels	LC	*crtRB3*	QTL and linkage mapping
Carotenoid content in grains	LC	*psy1*	QTL and linkage mapping
Carotenoid composition and concentration in grains	LC	Multiple candidate genes	QTL and linkage mapping
Oil biosynthesis in kernels	GC	Multiple candidate genes	Linkage mapping and GWAS
Tocochromanols in grains	LC	*hggt1* and GRMZM2G437912	GWAS
Aphid resistance/benzoxazinoid content in leaves	LC-MS	*bx10a*, *bx10b*, and *bx10c*	QTL and association mapping
Leaf lipidome	LC-MS	Multiple candidate genes	GWAS
Carotenoids in kernels	LC	Multiple candidate genes	GWAS
Metabolic diversity of kernels	LC-MS	Multiple candidate genes	Linkage mapping and GWAS
Carotenoids in kernels	LC	Multiple candidate genes	GWAS
Primary metabolism in leaves and kernels	GC-MS	Multiple candidate genes	QTL and linkage mapping
Carbon and nitrogen metabolism in leaves	Spectrophotometry	Multiple candidate genes	Linkage mapping and GWAS
Ratio of tocotrienolsa	LC	*vte1*	GWAS
Starch content in kernels	NIRS	Multiple candidate genes	GWAS
Metabolic diversity in mature kernels	LC-MS	Multiple candidate genes	QTL, linkage mapping, and GWAS
Carbohydrates and ABA metabolites during stress in ears, silks, and leavesb	ELISA and LS	Multiple candidate genes	GWAS
Amino acids in kernels	CEC and spectrophotometry	Multiple candidate genes	QTL, linkage mapping, and GWAS

Archaeological studies can complement genetic research by providing context for the domestication and spread of maize. Future archaeological research can focus on uncovering more ancient maize cultivation sites and employing advanced dating techniques to build a more detailed timeline of maize domestication and migration. This can help trace the interactions between ancient human societies and their agricultural practices, shedding light on how cultural and environmental factors influenced maize cultivation (Piperno, 2016).

Another critical area for future research is the impact of modern agricultural practices on maize genetic diversity. As agricultural systems become more intensive and reliant on a narrower range of high-yielding hybrids, there is a risk of reducing genetic diversity, which can make crops more vulnerable to pests, diseases, and environmental changes. Research should focus on developing sustainable agricultural practices that maintain or enhance genetic diversity, such as agroforestry and polyculture systems (Domiciano et al., 2021).

Tthe integration of genetic and archaeological data provides a comprehensive understanding of maize's past, present, and future. By learning from historical spread and adaptation, modern breeding programs can develop resilient and high-yielding maize varieties. Future research should continue to explore genetic diversity and sustainable agricultural practices to ensure the long-term viability and productivity of maize.

9 Concluding Remarks

The systematic research of genetic and archaeological perspectives on the spread of maize from southern Mexico highlights several critical findings. Genetic evidence indicates that maize was domesticated from its wild ancestor, teosinte, approximately 9 000 years ago in the Balsas River Valley. Archaeological data support this by revealing early maize cultivation sites in southern Mexico and beyond, illustrating the crop's initial domestication and subsequent dissemination. Genetic diversity studies underscore the adaptability of maize, which incorporated beneficial traits from local teosinte populations as it spread to various regions.

The research also outlines the routes of maize spread, facilitated by cultural and trade exchanges among ancient civilizations. The economic and nutritional impacts of maize were significant, providing a reliable food source and promoting economic growth through trade. Additionally, maize held cultural and ritual importance in many societies, integrating deeply into their social and spiritual practices.

The findings from this research have several implications for researchers, archaeologists, and agricultural scientists. For researchers, the integration of genetic and archaeological data provides a more comprehensive understanding of maize's domestication and spread. This interdisciplinary approach can be applied to other crops to gain similar insights into their historical development and genetic diversity. Archaeologists can benefit from the genetic data that offer timelines and migration patterns of maize cultivation, helping to identify and interpret archaeological sites. Understanding the genetic makeup of ancient maize samples can provide clues about past agricultural practices and human interactions with the environment.

For agricultural scientists, the historical lessons of maize domestication and spread emphasize the importance of maintaining genetic diversity in modern breeding programs. This diversity is crucial for developing resilient maize varieties that can withstand environmental stresses and adapt to changing climates. Additionally, the historical success of maize as a staple crop highlights its potential for addressing current and future food security challenges.

The research underscores the need for continued interdisciplinary research and collaboration to fully understand the complexities of maize domestication and its impacts on ancient and modern societies. Integrating genetic, archaeological, and ecological data provides a holistic view of maize's history and its future potential. Such collaboration can lead to innovative solutions for current agricultural challenges, including climate change, food security, and sustainable farming practices. Future research should focus on expanding the genetic and archaeological databases of maize, employing advanced genomic and dating techniques to uncover more detailed insights. Collaborative efforts between geneticists, archaeologists, agronomists, and ecologists will be essential to build a comprehensive understanding of maize and other critical crops。

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Conflict of Interest Disclosure

The author affirms that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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