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# The Domestication of Pumpkins: Historical Perspectives and Modern Genetic Evidence

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**Abstract** The domestication of pumpkins (*Cucurbita* spp.) has a rich history that spans thousands of years, originating in the Americas and spreading globally. Understanding the genetic and evolutionary pathways of these crops provides insights into their domestication processes and the genetic diversity that has been shaped over millennia. This study synthesizes historical perspectives and modern genetic evidence to elucidate the domestication history of pumpkins, focusing on the genetic relationships between wild and domesticated species, and the impact of domestication on genetic diversity. Phylogenetic studies have revealed complex relationships among *Cucurbita* species, identifying novel connections and clarifying the genetic origins of domesticated taxa. Genomic analyses have uncovered structural variants and candidate domestication genes involved in growth regulation, plant defense, and seed development. Evidence suggests that domestication bottlenecks and gene flow between wild and domesticated subspecies have played significant roles in shaping genetic diversity. Additionally, the integration of archaeological and genomic data has provided a comprehensive understanding of the domestication timeline and the traits selected during early cultivation. The findings highlight the intricate genetic and evolutionary processes underlying pumpkin domestication. The identification of key genetic variants and the role of gene flow offer valuable insights for future breeding programs aimed at enhancing crop resilience and quality. Continued research integrating genomic and archaeological data is essential for a deeper understanding of the domestication and evolution of *Cucurbita* species.

**Keywords** Pumpkins (*Cucurbita* spp.); Pumpkin domestication; Phylogenetics; Genetic diversity; Ggene flow;, Structural variants; Archaeological genomics

## 1 Introduction

Pumpkin, a herbaceous plant of the genus *Cucurbita* in the Cucurbitaceae family, are significant both agriculturally and culturally across the globe. They are cultivated for their edible fruits and seeds, which are integral to various culinary traditions and agricultural practices (Devi et al., 2018). The economic importance of pumpkins is underscored by their diverse uses, ranging from food products to ornamental purposes (Kates, 2019). Additionally, pumpkins have been a staple in many cultures, particularly in the Americas, where they were first domesticated approximately 10,000 years ago (Paris, 2016). The seeds of pumpkins, especially those of *Cucurbita argyrosperma*, have been a crucial component of early Mesoamerican diets, highlighting their cultural and nutritional significance (Barrera-Redondo et al., 2020; Barrera-Redondo et al., 2021).

The domestication of pumpkins is a fascinating aspect of agricultural history, involving complex processes of human selection and genetic adaptation. The domestication of *Cucurbita* species began around 11,000 years ago in the New World, with early humans selecting for traits such as non-bitterness and increased fruit size (Chomicki et al., 2019). This process has led to significant genetic and morphological diversity among domesticated pumpkins and their wild relatives (Kates, 2021). The domestication of pumpkins has also been influenced by gene flow between wild and cultivated populations, which has helped maintain genetic diversity and adaptability (Barrera-Redondo et al., 2020; Barrera-Redondo et al., 2021). Phylogenetic studies have revealed intricate relationships between domesticated pumpkins and their wild ancestors, providing insights into the evolutionary history and domestication pathways of these crops (Kates et al., 2017).

This study comprehensively explores the domestication process of pumpkins by integrating historical perspectives and modern genetic evidence. It specifically explores the historical background and significance of pumpkin domestication, analyzes the genetic diversity and structure of domesticated pumpkins and their wild ancestors, and identifies genetic variations and structural changes associated with domestication traits. Additionally, it evaluates the impact of domestication on the breeding potential and agronomic characteristics of modern pumpkin varieties. By combining historical insights with modern genetic evidence, the study provides a comprehensive understanding of pumpkin domestication, revealing the complex interactions between human activities and plant evolution. This study offers valuable insights into the comprehensive understanding of pumpkin domestication, contributing to the conservation and improvement of this important crop.

## 2 Historical Perspectives on Pumpkin Domestication

### 2.1 Early evidence of pumpkin use by humans

The domestication of pumpkins (*Cucurbita* spp.) is deeply rooted in human history, with evidence suggesting that pumpkins were among the earliest crops cultivated by humans. The bitter flesh of wild *Cucurbita* species was generally inedible, leading early humans to initially consume the seeds, which were more palatable and nutritious (Lelley et al., 2009). Archaeological evidence indicates that pumpkins were first domesticated in the Americas around 10,000 years ago, making them one of the oldest domesticated crops from the Neolithic revolution (Paris, 2016; Barrera-Redondo et al., 2021).

These early humans likely gathered wild pumpkins for their seeds, which provided a valuable source of nutrition due to their high oil and protein content (Kistler et al., 2015). The consumption of pumpkin seeds and flesh is evidenced by phytoliths and starch grains found on ancient grinding tools and in human dental remains, indicating that pumpkins were an important part of the diet long before they were fully domesticated.

### 2.2 Archaeological findings of pumpkin cultivation

Archaeological discoveries have provided substantial insights into the early cultivation of pumpkins. Seeds and remnants of *Cucurbita* have been found in various archaeological sites across the Americas, dating back to approximately 10,000 years ago (Paris, 2016; Barrera-Redondo et al., 2021). These findings suggest that pumpkins were widely cultivated by indigenous peoples long before European contact. The presence of pumpkin seeds in mastodon dung deposits further supports the idea that these plants were part of the prehistoric landscape and were likely dispersed by large herbivores before their extinction (Kistler et al., 2015).

Archaeologists have discovered remnants of ancient farming systems, including irrigation channels and cultivated fields, indicating advanced agricultural practices involving pumpkins (Lombardo et al., 2020; Herrmann et al., 2023). The transition from wild to cultivated pumpkins involved selective breeding and careful cultivation, ultimately leading to the development of various domesticated varieties. Additionally, genomic studies have revealed that the domestication of pumpkins involved significant genetic changes, including the loss of bitterness, which made the fruits more palatable to humans (Chomicki et al., 2019; Kates et al., 2021).

### 2.3 Historical records and documentation

Historical records and documentation provide further evidence of the significance of pumpkins in human history. Indigenous peoples of the Americas, including the Maya, Aztec, and various Native American tribes, have long histories of cultivating and utilizing pumpkins. By the time of European contact in 1492, several cultivar groups of pumpkins and squashes had already been developed by indigenous American peoples (Paris, 2016). One notable historical document is the Florentine Codex, compiled in the 16th century by the Spanish friar Bernardino de Sahagún. This extensive work provides detailed descriptions of Aztec agriculture, including the cultivation and uses of pumpkins. These records, along with iconography and literature, highlight the widespread use and cultivation of pumpkins across different cultures and regions.

The dispersal of *Cucurbita* species to other continents following European contact underscores their global importance and adaptability (Paris, 2017). Modern genetic studies continue to shed light on the domestication processes and the genetic diversity of pumpkins, revealing complex histories of independent domestication events and gene flow between wild and domesticated populations (Barrera-Redondo et al., 2021; Kates et al., 2021).

The domestication of pumpkins is a testament to the ingenuity of early human societies and their ability to adapt and cultivate plants for their nutritional and cultural needs. The integration of archaeological, historical, and genetic evidence provides a comprehensive understanding of the domestication and evolution of this important crop.

## 3 Geographical Origins of Domesticated Pumpkins

### 3.1 Native regions of wild pumpkins

Wild pumpkins, belonging to the genus *Cucurbita*, are native to the Americas. The ancestral species of domesticated pumpkins were widely distributed across the New World. Evidence suggests that wild pumpkin species were once broadly spread across what is now the United States, Mexico, and Central America. The genus *Cucurbita* includes multiple species, among which zucchini (*Cucurbita pepo*) is one of the earliest domesticated species. These wild forms adapted to various ecological environments, often thriving in disturbed habitats created by large herbivores (Kistler et al., 2015; Kates et al., 2017; Chomicki et al., 2019).

Genetic and archaeological evidence indicates that the wild ancestors of domesticated pumpkins proliferated in the semi-arid and arid regions of these areas, growing alongside a diverse plant community. These wild pumpkins likely had small, bitter fruits, which were initially unappealing to humans, but due to their nutrient-rich seeds, they gradually came to be utilized by humans (Chomicki et al., 2019). Studies have found that two wild pumpkin species, *Cucurbita foetidissima* and *C. radicans*, which grow in the arid and semi-arid regions of Mexico and the United States, are nutritionally rich. *C. foetidissima* has larger fruits and a higher number of seeds, with seeds rich in non-polar compounds, while *C. radicans* has seeds with higher protein content (Mejía-Morales et al., 2021).

### 3.2 Spread of pumpkin cultivation in ancient times

The domestication of pumpkins began approximately 10,000 years ago in the Americas. As early human societies recognized the value of pumpkins and began selecting for larger, sweeter fruits with thinner rinds, pumpkin cultivation gradually spread beyond its native regions. The spread of pumpkin cultivation was driven by human migration and trade, and by the time Europeans made contact with the Americas in 1492, Indigenous peoples had already developed various cultivated pumpkin populations (Kistler et al., 2015; Paris, 2016).

Archaeological evidence, including seeds found in ancient fecal deposits and pictorial records, indicates that pumpkins were being cultivated in several regions of Central America, including present-day Mexico and Central America, between 8,000 and 10,000 years ago (Lombardo et al., 2020). The spread of pumpkin cultivation was closely linked to the rise of early agricultural societies, which facilitated the dissemination of pumpkin seeds and cultivation techniques across different ecological zones. As these early cultivators migrated or engaged in trade, pumpkins gradually spread northward into what is now the United States and southward into South America. The pumpkin's ability to adapt to a variety of climatic conditions provided favorable conditions for its widespread dissemination.

### 3.3 Key regions of early pumpkin domestication

Key regions for the early domestication of pumpkins include the lowlands of Jalisco, Mexico. Research indicates that *Cucurbita argyrosperma* was domesticated in the lowlands of Jalisco, Mexico, primarily for its edible seeds (Barrera-Redondo et al., 2021). *Cucurbita moschata*, another important species of pumpkin, is widely distributed in regions such as Mexico, the United States, and Peru. Studies have shown that *Cucurbita moschata* exhibits high genetic diversity, particularly among varieties found in Africa and South Asia (Lee et al., 2020). *Cucurbita* *maxima* was domesticated in the Andes region of South America, and research has pointed out that domesticated varieties from this region are well adapted to cold, high-altitude environments (López-Anido, 2021).

These regions offered the environmental conditions and cultural practices necessary to facilitate the domestication process. Genetic studies suggest that domestication events did not occur in isolation; there is evidence of gene flow between wild and domesticated populations, which helped maintain the genetic diversity and adaptability of domesticated pumpkins (Kistler et al., 2015; Kates et al., 2017; Barrera-Redondo et al., 2021).

## 4 Genetic Evidence of Pumpkin Domestication

### 4.1 DNA analysis of ancient pumpkin seeds

The analysis of ancient pumpkin seeds provides critical insights into the domestication process of pumpkins. High-throughput sequencing of complete plastid genomes from ancient, modern wild, and modern domestic *Cucurbita* samples has revealed independent domestication events in different regions, such as eastern North America and northeastern Mexico.

This sequencing also demonstrated the broad archaeological distribution of taxa currently unknown in the wild, suggesting a significant decline in wild-type populations coinciding with widespread domestication (Kistler et al., 2015). Additionally, the presence of pumpkin seeds in mastodon dung deposits indicates that large-bodied herbivores played a role in seed dispersal before their extinction, which may have influenced the domestication pathways of *Cucurbita* species (Kistler et al., 2015).

### 4.2 Genetic markers for domestication traits

Genetic markers have been instrumental in identifying domestication traits in pumpkins. For instance, the hull-less seed trait in *Cucurbita pepo*, controlled by a single recessive gene, has been mapped to a specific QTL on chromosome 12. This trait is highly valued in the industry as it eliminates the need for de-hulling seeds. Marker-assisted selection using SNP markers associated with this trait can significantly streamline breeding programs (Meru et al., 2022).

Furthermore, comparative genomic analyses of wild and domesticated *Cucurbita* argyrosperma have identified candidate domestication genes involved in growth hormone regulation, plant defense mechanisms, seed development, and germination. These findings highlight the genetic basis of key domestication traits and their potential for crop improvement (Barrera-Redondo et al., 2020; 2021).

### 4.3 Comparative genomics of wild and domesticated pumpkins

Comparative genomics has shed light on the genetic consequences of pumpkin domestication. Studies have shown that domesticated pumpkins exhibit reduced genetic diversity compared to their wild progenitors, although this reduction varies among species. For example, *Cucurbita argyrosperma* ssp. *argyrosperma* shows a significant reduction in genetic diversity relative to its wild counterpart, while other species like *Cucurbita maxima* do not exhibit the same pattern (Kates et al., 2021).

Research has explored the domestication process of *Cucurbita argyrosperma* by comparing its genome with that of its wild relative, *Cucurbita argyrosperma* subsp. *sororia*, revealing the impact of domestication on the genome and variations associated with domestication traits (Barrera-Redondo et al., 2020; 2021). The findings suggest that the domestication of *C. argyrosperma* likely originated in the lowlands of Jalisco, Mexico, and that there was gene flow between domesticated and wild populations during the domestication process, which helped alleviate the domestication bottleneck effect (Figure 1). Furthermore, phylogenetic studies using nuclear loci have further clarified the relationships between wild and domesticated species within the *Cucurbita* genus, revealing close relationships and providing new evolutionary insights, which are crucial for understanding the domestication history of these crops (Kates et al., 2017).

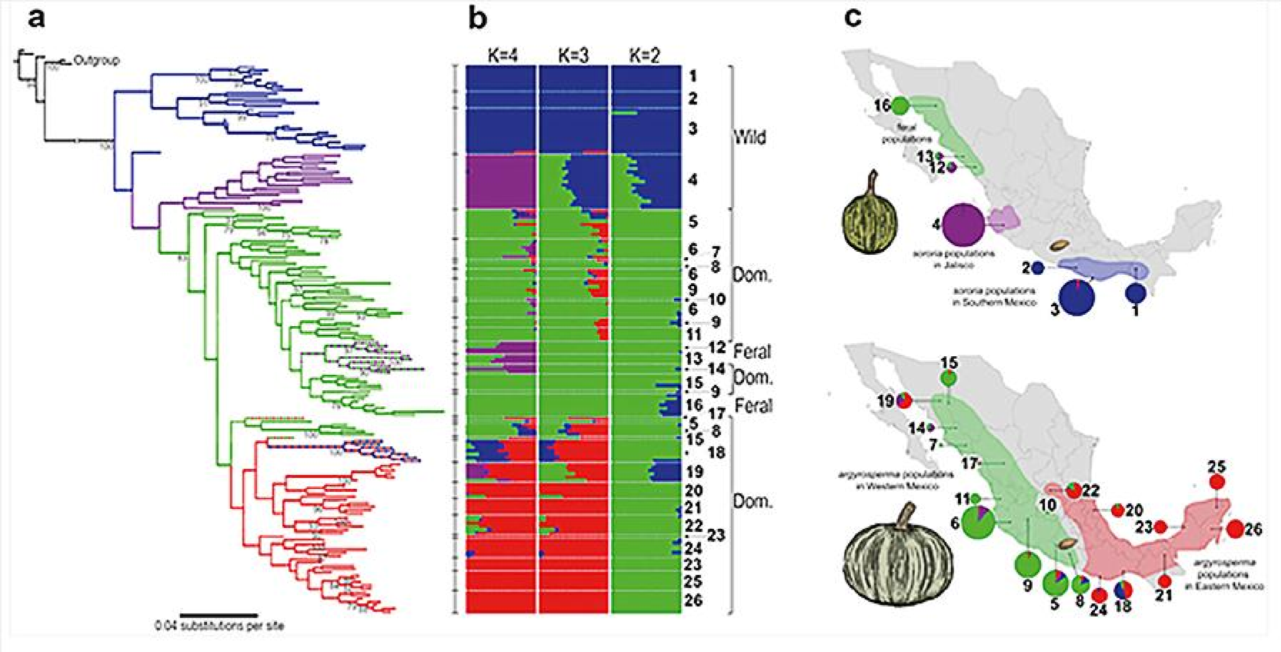


Figure 1 Genetic structure and phylogenetic relationships between the wild and domesticated populations of *Cucurbita argyrosperma* based on 2861 SNPs (Adopted from Barrera-Redondo et al., 2021)

Image caption: (a) shows the Maximum-Likelihood tree, indicating a monophyletic clade for all domesticated populations, suggesting a common domestication origin. (b) depicts the ADMIXTURE analysis, revealing genetic admixture between different populations, especially gene flow between wild and domesticated populations in the Jalisco region. (c) illustrates the geographic distribution of the genetic groups across Mexico. These results support the hypothesis that domesticated populations likely originated in the Jalisco region and have maintained connections with wild populations through gene flow (Adapted from Barrera-Redondo et al., 2021)

## 5 Morphological Changes During Domestication

### 5.1 Size and shape variations

The domestication of pumpkins has led to significant changes in the size and shape of the fruits. Wild *Cucurbita* species typically have smaller and more variable fruit sizes compared to their domesticated counterparts. Domesticated pumpkins, such as *Cucurbita maxima* and *Cucurbita pepo*, have been selectively bred for larger fruit sizes, which is a common trait favored by human cultivators (Paris, 2017; Kates et al., 2017). The genetic basis for these changes has been linked to specific quantitative trait loci (QTLs) that control fruit size, which were predominantly selected during the domestication process (Li et al., 2019). Additionally, the shape of the fruits has also been modified, with domesticated varieties exhibiting a wider range of shapes, from elongated to round, compared to the more uniform shapes of wild species (Paris, 2017).

### 5.2 Color and texture changes

Color and texture are other important morphological traits that have undergone significant changes during the domestication of pumpkins. Wild *Cucurbita* species often have fruits with green or mottled exteriors, while domesticated varieties display a wide array of colors, including orange, yellow, and white (Paris, 2017; Chomicki et al., 2019). These changes in color are associated with the accumulation of pigments such as lycopene and beta-carotene, which have been targeted during the domestication process to enhance the visual appeal and nutritional value of the fruits (Chomicki et al., 2019). The texture of the fruit flesh has also been improved, with domesticated pumpkins having a firmer and less fibrous texture compared to their wild relatives, making them more suitable for culinary uses (Paris, 2017).

### 5.3 Evolution of taste and nutritional content

The taste and nutritional content of pumpkins have evolved significantly through domestication. Wild *Cucurbita* species are known for their bitter taste, which is due to the presence of cucurbitacins, compounds that deter herbivory (Kistler et al., 2015). During domestication, non-bitterness was a favored trait, and selective breeding has led to the reduction or elimination of these bitter compounds in domesticated varieties (Kistler et al., 2015; Chomicki et al., 2019). This has made the fruits more palatable to humans and suitable for a variety of culinary applications. Additionally, the nutritional content of pumpkins has been enhanced, with increased levels of vitamins and minerals, particularly beta-carotene, which is a precursor to vitamin A (Paris, 2017; Chomicki et al., 2019). These improvements in taste and nutritional content have been achieved through both traditional breeding practices and modern genetic techniques (Hernández-Terán et al., 2017).

The domestication of pumpkins has resulted in significant morphological changes, including variations in size and shape, color and texture, and taste and nutritional content. These changes have been driven by human selection for traits that enhance the utility and appeal of the fruits, supported by genetic studies that have identified the underlying genetic mechanisms.

## 6 Agricultural Practices in Pumpkin Domestication

### 6.1 Traditional cultivation methods

Traditional cultivation methods for pumpkins have been shaped by centuries of agricultural practices. Historically, pumpkins have been grown in diverse ecological conditions, leading to the development of varieties with unique economic characteristics. For instance, in the Ararat Plain, different pumpkin varieties have been cultivated to adapt to local growing conditions, resulting in variations in phenophases, yield, and fruit quality (Sargsyan et al., 2022). Traditional methods often involve the use of open-pollinated varieties, which were predominant before the introduction of F1 hybrids in the 1980s (Loy et al., 2011). These methods have allowed for the natural selection of traits that are well-suited to specific climates and soil conditions, contributing to the wide range of pumpkin varieties available today.

### 6.2 Selection and breeding techniques

Selection and breeding techniques have played a crucial role in the domestication and improvement of pumpkins. Early breeding efforts focused on selecting plants with desirable traits such as fruit size, color, shape, and disease resistance. Techniques such as hybridization, inbreeding, and mutagenesis have been employed to develop new cultivars and hybrids (Elatskova, 2019). The pedigree system of breeding, which involves selecting and breeding individuals with desirable traits over multiple generations, has been widely adopted for pumpkins (Loy et al., 2011). Additionally, modern breeding strategies have incorporated molecular markers, genomics, and transcriptomics to better understand the inheritance of important traits and to facilitate the development of improved varieties (Kesh and Yadav, 2022). These advanced techniques have enabled breeders to create pumpkins with enhanced yield, nutritional value, and resistance to environmental stresses.

### 6.3 Impact of agricultural practices on genetic diversity

Agricultural practices have significantly impacted the genetic diversity of pumpkins. The domestication process often involves a genetic bottleneck, where only a subset of the wild genetic diversity is retained in the domesticated population. For example, studies have shown that genetic diversity relative to wild progenitors was reduced in domesticated subspecies of *Cucurbita argyrosperma*, although gene flow between wild and domesticated populations has helped to alleviate some of the effects of this bottleneck (Barrera-Redondo et al., 2021; Kates et al., 2021). The introduction of F1 hybrids and the focus on specific traits in breeding programs have also influenced genetic diversity. While these practices have led to the development of high-yielding and disease-resistant varieties, they may also reduce the overall genetic variability within cultivated pumpkin populations (Loy et al., 2011). Maintaining a balance between improving crop performance and preserving genetic diversity is essential for the long-term sustainability of pumpkin cultivation.

Traditional cultivation methods, selection and breeding techniques, and the impact of agricultural practices on genetic diversity have all played significant roles in the domestication and improvement of pumpkins. These practices have shaped the genetic landscape of pumpkins, leading to the development of a wide array of varieties that are well-suited to different growing conditions and consumer preferences.

## 7 Modern Genetic Techniques in Pumpkin Research

### 7.1 Genomic sequencing and analysis

Genomic sequencing has revolutionized our understanding of pumpkin domestication by providing detailed insights into the genetic variations between wild and domesticated species. For instance, targeted sequencing of approximately 15,000 SNPs in *Cucurbita argyrosperma* and *Cucurbita maxima* revealed significant differences in genetic diversity and structure between domesticated and wild progenitors. This study highlighted that only 1.5% of domestication features were shared between the two species, suggesting unique domestication pathways (Kates et al., 2021). Additionally, the genome of wild *Cucurbita argyrosperma* was sequenced, uncovering structural variants and candidate domestication genes involved in growth regulation, plant defense, and seed development. This genomic data indicated a monophyletic origin and gene flow between domesticated and wild subspecies, which likely mitigated the effects of domestication bottlenecks (Barrera-Redondo et al., 2021).

### 7.2 CRISPR and gene editing applications

CRISPR/Cas9 technology has emerged as a powerful tool for precision breeding in pumpkins, enabling targeted modifications to enhance desirable traits. The application of CRISPR/Cas9 in plant genome editing has been extensively reviewed, showcasing its potential to accelerate crop improvement by enabling targeted nucleotide substitutions and fine-tuning gene regulation (Chen et al., 2019). Although specific studies on pumpkins are limited, the successful de novo domestication of wild tomato using CRISPR/Cas9 demonstrates the potential of this technology. By editing six loci important for yield and productivity, researchers significantly improved fruit size, number, and nutritional value, paving the way for similar applications in pumpkins (Zsögön et al., 2018).

### 7.3 Future directions in genetic research of pumpkins

Future research in pumpkin genetics is poised to leverage advanced genomic and gene-editing technologies to further enhance crop traits and resilience. Expanding genomic sequencing efforts to include more wild and domesticated *Cucurbita* species will provide a comprehensive understanding of genetic diversity and evolutionary history (Kates et al., 2017). Additionally, integrating CRISPR/Cas9 with high-throughput mutant libraries and advanced delivery systems will facilitate the development of pumpkins with improved disease resistance, stress tolerance, and nutritional value (Chen et al., 2019). Continued exploration of gene flow between wild and domesticated species will also be crucial in maintaining genetic diversity and mitigating the effects of domestication bottlenecks (Barrera-Redondo et al., 2021). These advancements will not only enhance pumpkin breeding programs but also contribute to global food security by increasing the availability of nutritious and resilient crops.

## 8 Case Studies

### 8.1 Domestication of *Cucurbita pepo*

The domestication of *Cucurbita pepo* is one of the earliest examples of plant domestication in the Americas, with archaeological evidence indicating its cultivation history dates back to around 10,000 years ago in the region of Mexico. Castellanos-Morales et al. (2019) analyzed the genetic variation and structure of Mexican *Cucurbita pepo* ssp. *pepo* using two chloroplast regions and nine nuclear microsatellite loci to explore its domestication history. The study revealed that *Cucurbita pepo* ssp. *pepo* exhibits high genetic diversity, and *C. pepo* ssp. *fraterna* is likely its wild ancestor (Figure 2), although hybridization between the two complicates the definition of its ancestor.

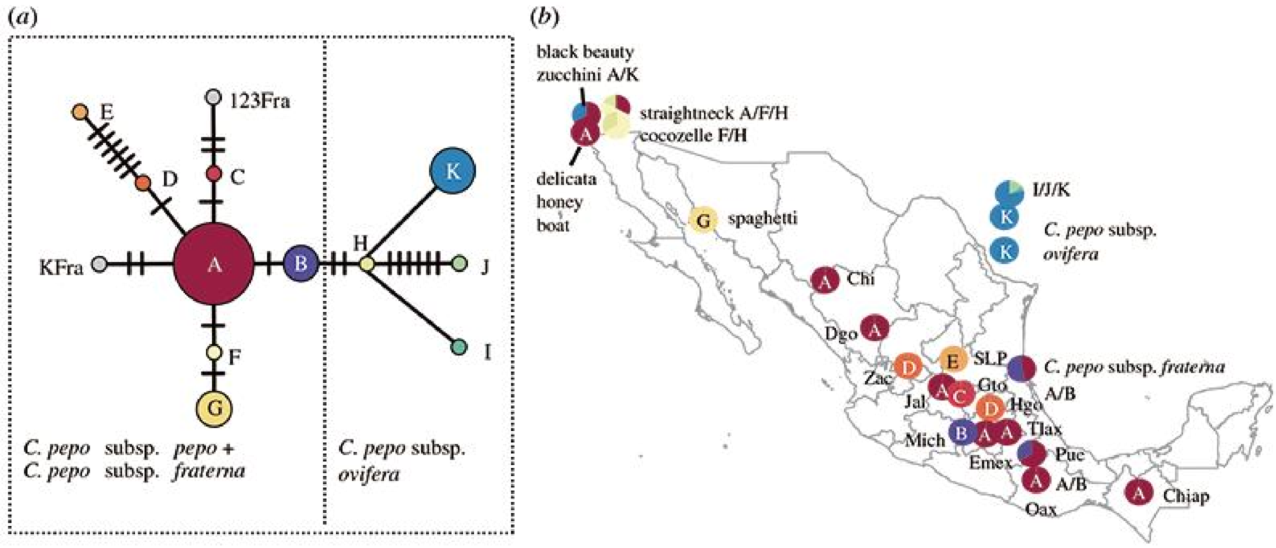


Figure 2 (a) Haplotype network for two concatenated chloroplast regions (*psbJ-petA* and *psbD-trnT*$^{(GGU)}$; 1724 bp) depicting the relationship between 11 haplotypes found in *C. pepo* ssp. *pepo*, *C. pepo* ssp. *fraterna* and *C. pepo* ssp. *ovifera* from the current study, plus data reported by Kistler et al. (2015), including *C. pepo* ssp. *fraterna* archaeological sample (123Fra) as well as *C. pepo* ssp. *fraterna* modern sample (KFra). (b) Geographical distribution of 11 haplotypes considered in the haplotype network for the individuals analysed in this study (Adopted from Castellanos-Morales et al., 2019)

The Approximate Bayesian Computation (ABC) analysis supported the hypothesis that *Cucurbita pepo* ssp. *pepo* originated through hybridization between *C. pepo* ssp. *fraterna* and *C. pepo* ssp. *ovifera*, although direct analysis suggested that *C. pepo* ssp. *fraterna* is more likely to be its ancestor. The study also revealed that the species underwent rapid population expansion and geographical diversification after domestication. This study provides important genetic evidence for understanding the domestication process of zucchini and its wild ancestors, offering valuable insights for future crop domestication studies.

### 8.2 Genetic diversity in pumpkin domestication

Research has examined the genetic consequences of domestication in two independently domesticated pumpkin species—*Cucurbita argyrosperma* and Indian pumpkin *Cucurbita maxima* (Kates et al., 2021). Through the analysis of 15,000 SNPs, covering wild, landrace, and improved varieties, the study found that *Cucurbita maxima* did not exhibit a significant reduction in genetic diversity following domestication, whereas *Cucurbita argyrosperma* showed a marked decline in genetic diversity (Figure 3).

This difference is primarily attributed to the distinct domestication processes of the two species and the varying degrees of gene flow between wild and cultivated populations. *Cucurbita maxima* was domesticated in South America and exhibits extensive morphological and genetic diversity, partly due to ongoing gene flow with its wild relatives. In contrast, *Cucurbita argyrosperma* was primarily domesticated in Mexico, with a more limited geographical distribution, and selection pressures were more focused on seed production rather than fruit diversity, leading to lower diversity and a significant genetic bottleneck.

*Cucurbita maxima* has untapped genetic diversity potential that could be utilized for crop improvement, whereas *Cucurbita argyrosperma* may require strategies to mitigate the impact of reduced diversity (Kates et al., 2021; Liu et al., 2022). The research indicates that domestication does not uniformly reduce crop genetic diversity; rather, the genetic consequences are largely dependent on the specific domestication history and practices involved.

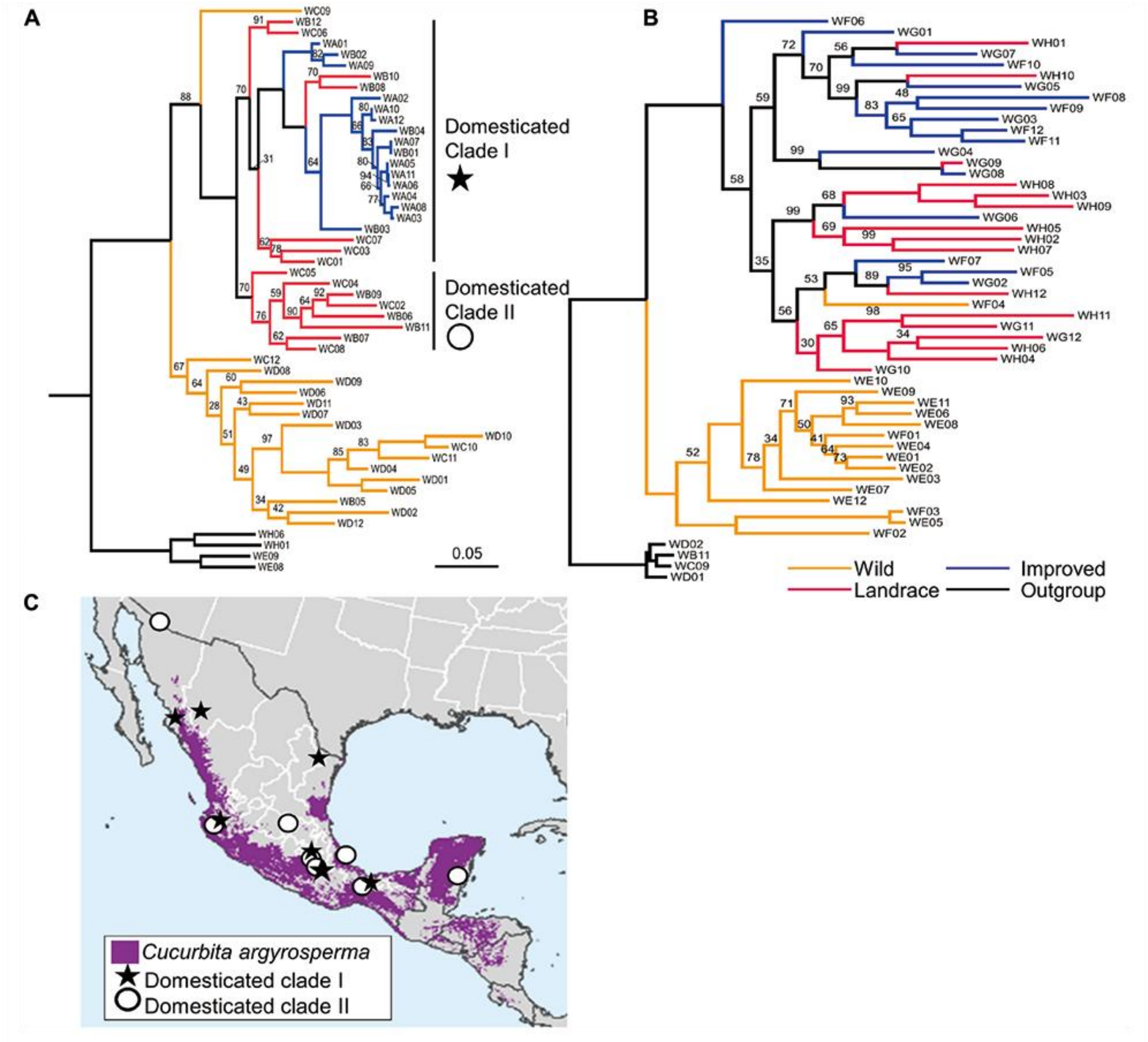


Figure 3 Results of phylogenetic analysis of (A) *Cucurbita argyrosperma* accessions and (B) *Cucurbita maxima* accessions (Adopted from Kates et al., 2021)

Image caption: The figure shows a clear separation between the wild and domesticated varieties of pumpkins, indicating that *Cucurbita argyrosperma* and *Cucurbita maxima* underwent significant genetic differentiation during domestication. Additionally, the domesticated *Cucurbita argyrosperma* is further divided into two subgroups, while the domesticated *Cucurbita maxima* exhibits a high level of consistency, with only one improved variety separating from the other domesticated varieties. This suggests that *Cucurbita argyrosperma* retained more genetic diversity during domestication, whereas the improved varieties of *Cucurbita maxima* are relatively more uniform and concentrated (Adopted from Kates et al., 2021)

## 9 Applications and Implications of Pumpkins

### 9.1 Agricultural benefits of domesticated pumpkins

Domesticated pumpkins offer several agricultural benefits, particularly in the context of sustainable farming practices. Pumpkins are highly adaptable to various soil and atmospheric conditions, making them a resilient crop in the face of climate change and other environmental challenges. They can thrive in low soil fertility and require less water compared to other staple crops, which is crucial in regions facing water scarcity (Hosen et al., 2021). Additionally, the genetic diversity within pumpkin species, as revealed by studies on their domestication, suggests that they have a robust potential for breeding programs aimed at improving crop resilience and yield

(Barrera-Redondo et al., 2021; Kates et al., 2021). The ability to hybridize and develop new varieties through modern breeding techniques further enhances their agricultural value, providing a means to increase productivity and address food security issues (Hosen et al., 2021).

### 9.2 Nutritional and health benefits

Pumpkins are not only agriculturally beneficial but also nutritionally rich, offering significant health benefits. They are a low-calorie food source packed with essential vitamins and minerals, making them an excellent addition to diets aimed at addressing nutritional deficiencies. Pumpkins are particularly high in vitamins A and C, potassium, and dietary fiber, which contribute to overall health and well-being (Hosen et al., 2021; Gomaa et al., 2023). Their seeds are also a valuable source of nutrients, including healthy fats, protein, and antioxidants, which have been linked to various health benefits such as improved heart health and reduced inflammation (Barrera-Redondo et al., 2021). The nutritional profile of pumpkins makes them an important crop for therapeutic nutrition, especially in regions with high rates of malnutrition and dietary disorders (Gomaa et al., 2023).

### 9.3 Economic impacts of pumpkin cultivation

The cultivation of pumpkins has significant economic implications, particularly for developing countries. As a versatile crop, pumpkins can be used in various forms, including fresh produce, processed foods, and seeds, providing multiple revenue streams for farmers. The economic traits of pumpkins, such as fruit yield and average fruit weight, are influenced by genetic and environmental factors, which can be optimized through selective breeding and improved agricultural practices (Gomaa et al., 2023). The increasing demand for pumpkins in both domestic and international markets highlights their economic potential. By investing in pumpkin cultivation, countries can enhance their agricultural productivity, create job opportunities, and boost their economies (Gomaa et al., 2023). Furthermore, the genetic studies on pumpkins provide valuable insights into their breeding potential, which can be leveraged to develop high-yielding and disease-resistant varieties, further enhancing their economic value (Barrera-Redondo et al., 2021; Kates et al., 2021).

The domestication and cultivation of pumpkins offer numerous benefits, from agricultural sustainability and nutritional health to economic growth. By harnessing the genetic diversity and adaptability of pumpkins, we can address some of the most pressing food security and nutritional challenges of our time.

## 10 Challenges and Opportunities

### 10.1 Technical challenges in pumpkin genetic research

Pumpkin genetic research faces several technical challenges that hinder the full exploitation of its genetic potential. One significant challenge is the limited understanding of the genomic impact of domestication and the identification of variants underlying domestication traits in *Cucurbita* species. Despite their economic importance, the genomic data for pumpkins and squashes are still lacking, which complicates efforts to identify and utilize beneficial genetic traits (Barrera-Redondo et al., 2020; 2021). Additionally, the genetic diversity of wild *Cucurbita* species is decreasing due to habitat loss and the extinction of megafaunal dispersers, which further limits the genetic pool available for research and breeding (Kates, 2019). Another technical challenge is the complexity of the genetic structure across different domestication statuses, as seen in the independent domestications of *Cucurbita argyrosperma* and *Cucurbita maxima*, which exhibit different patterns of genetic diversity and structure (Kates et al., 2021).

### 10.2 Opportunities for improving pumpkin varieties

Despite these challenges, there are numerous opportunities for improving pumpkin varieties. The genetic diversity present in wild *Cucurbita* species and their ability to cross with domesticated varieties offer a vast pool of untapped genetic variability. This genetic reservoir can be harnessed to develop disease-resistant cultivars and improve traits such as drought tolerance and nutritional content (Kates, 2019). Advances in biotechnology, including genetic engineering, mapping, genomics, and gene editing, present significant opportunities for the breeding and improvement of pumpkins and squashes. These technologies can help identify and manipulate genes related to growth hormones, plant defense mechanisms, seed development, and other important traits (Paris, 2018).

Additionally, the integration of archaeological and genomic data can provide deeper insights into the domestication processes and help identify traits that were selected for early in domestication, such as non-bitterness and fruit size (Chomicki et al., 2019).

### 10.3 Potential for sustainable pumpkin agriculture

Pumpkins have significant potential for contributing to sustainable agriculture. As a crop that is more adapted to low soil and atmospheric conditions than many other major crops, pumpkins can play a crucial role in achieving food and nutritional security, especially in regions facing agricultural challenges such as water shortage and extreme climatic conditions (Hosen et al., 2021). The diversification and development of hybrid pumpkin varieties through modern breeding techniques can enhance productivity and provide a balanced food source for malnourished and deprived populations (Hosen et al., 2021). Furthermore, the conservation of wild *Cucurbita* species through ex situ and in situ methods is essential for maintaining the genetic diversity necessary for future crop improvement and sustainability (Kates, 2019). By leveraging the genetic resources and modern technologies, pumpkins can be developed into a crop that not only meets current food demands but also contributes to a more sustainable and resilient agricultural system.

## 11 Concluding Remarks

The domestication of pumpkins, particularly within the *Cucurbita* genus, has been a complex process influenced by various genetic and environmental factors. Studies have shown that domestication has led to significant genetic changes, including reduced genetic diversity in some species, such as *Cucurbita argyrosperma*, while others like *Cucurbita maxima* have maintained more genetic variation. The domestication process has also been marked by gene flow between wild and domesticated subspecies, which has helped mitigate the effects of genetic bottlenecks. Additionally, the integration of archaeological and genomic data has provided insights into the domestication timeline and the traits selected for by early agricultural societies, such as non-bitterness and increased seed yield. Modern breeding practices continue to leverage this genetic diversity to develop new cultivars with desirable traits, such as drought tolerance and improved seed quality.

Future research should focus on further elucidating the genetic pathways involved in key domestication traits, such as fruit size, shape, and color, as well as resistance to environmental stresses. The identification of candidate genes and structural variants associated with these traits can provide valuable targets for genetic improvement. Additionally, understanding the role of gene flow and introgression in maintaining genetic diversity can inform breeding strategies aimed at enhancing crop resilience. There is also a need to explore the nutritional aspects of domesticated pumpkins, as current cultivars may have lower levels of key micronutrients and vitamins due to historical selection for traits like palatability and yield.

The prospects for pumpkin domestication studies are promising, given the advancements in genomic technologies and the increasing integration of multidisciplinary approaches. High-quality genome assemblies and population-level genomic data can facilitate the identification of domestication genes and the understanding of their evolutionary trajectories. Moreover, the development of new cultivars with improved traits, such as drought tolerance and disease resistance, can be accelerated through targeted breeding programs that utilize the genetic diversity present in both wild and domesticated populations. As climate change continues to impact agricultural productivity, the ability to breed pumpkins that are adaptable to a range of environmental conditions will be crucial for ensuring food security and sustainability.

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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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