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Phylogenomic Studies in *Zea*: Evolutionary Relationships and Species Divergence

Jiansheng Li
Sanya Institute of China Agricultural University, Sanya, 572025, Hainan, China
Corresponding email: lijiansheng@cau.edu.cn

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Abstract Phylogenomic studies have significantly advanced our understanding of the evolutionary relationships and species divergence within the genus *Zea*. By analyzing complete plastid genomes from five *Zea* species (*Zea diploperennis, Zea perennis, Zea luxurians, Zea nicaraguensis,* and *Zea mays* subsp. *huehuetenangensis*), this study investigates the rates and patterns of microstructural changes, including inversions and insertion/deletion mutations (indels). The findings reveal 193 indels and 15 inversions, with tandem repeat indels being the most prevalent. Divergence times were estimated using a noncorrelated relaxed clock method, indicating that the stem lineage of all *Zea* species diverged approximately 176 000 years before present (YBP). The mutation rates for the genus ranged from 1.7E-8 to 3.5E-8 microstructural changes per site per year, highlighting non-uniform rates of change despite close taxonomic relationships. These results corroborate previous studies on *Zea* mitochondrial and nuclear data, providing a comprehensive phylogenomic framework for understanding the evolutionary history and diversification of *Zea* species.

Keywords Maize (*Zea mays*); Phylogenomics; *Zea* species; Microstructural changes; Divergence times; Plastid genomes

1 Introduction

The genus *Zea*, belonging to the grass family Poaceae, is of significant agronomic and scientific importance. It includes several species, with maize (*Zea mays*) being the most prominent. Maize is not only a staple food crop but also a model organism for genetic and genomic research due to its extensive genetic diversity and well-characterized genome (Strable and Scanlon, 2009; Vincent, 2012). The genus *Zea* also includes wild relatives known as teosintes, which are crucial for understanding the evolutionary history and domestication of maize (Dermastia et al., 2009; Hufford et al., 2012a). The evolutionary study of *Zea* provides insights into plant domestication, adaptation, and the genetic basis of important agronomic traits (Kellogg and Birchler, 1993; Hilton and Gaut, 1998).

Phylogenomics, the intersection of phylogenetics and genomics, is a powerful tool in evolutionary biology. It involves the analysis of genome-wide data to infer evolutionary relationships and understand the genetic basis of phenotypic diversity (Kellogg and Birchler, 1993). In the context of *Zea*, phylogenomic studies have elucidated the evolutionary relationships among different species and subspecies, shedding light on the processes of speciation and domestication (Hilton and Gaut, 1998; Ross-Ibarra et al., 2009). These studies are crucial for understanding the genetic mechanisms underlying important traits such as disease resistance, yield, and environmental adaptability (Strable and Scanlon, 2009; Mounika et al., 2018). By integrating phylogenetic and genomic data, researchers can gain a comprehensive understanding of plant evolution and the factors driving genetic diversity (Kellogg and Birchler, 1993; Curry 2020).

This study investigates the evolutionary relationships within the genus *Zea* using phylogenomic approaches. This includes understanding the divergence times, gene flow, and adaptive evolution among different *Zea* species and subspecies. The study aims to contribute to the broader field of plant science by providing insights into the genetic basis of important agronomic traits and the evolutionary processes shaping plant diversity. Additionally, this research will inform conservation strategies for wild relatives of maize and guide breeding programs aimed at improving crop resilience and productivity.

2 Methodological Approaches in Phylogenomics

2.1 Genomic data acquisition

In phylogenomic studies of the genus *Zea*, various types of genomic data are utilized, including whole genome sequences and transcriptomic data. Whole genome sequencing, such as the sequencing of complete plastid genomes (plastomes), provides comprehensive data that can be used to analyze microstructural changes like inversions and indels (Orton et al., 2017) Transcriptomics, which involves sequencing RNA to study gene expression, is another valuable source of data. For instance, RNA sequencing has been used to assemble large and accurate phylogenomic datasets, as demonstrated in studies of jawed vertebrates (Irisarri et al., 2017).

The methods for collecting and curating genomic data are diverse. Whole genome sequencing can be performed using next-generation sequencing technologies, which allow for the sequencing of entire genomes at a relatively low cost (Allio et al., 2019). Transcriptomic data can be obtained through RNA sequencing, which involves extracting RNA, converting it to cDNA, and then sequencing the cDNA (Irisarri et al., 2017). Data curation involves filtering and assembling the raw sequence data to ensure accuracy and completeness. For example, in the study of swallowtail butterflies, orthologous coding sequences were identified from whole-genome shotgun sequences, and these sequences were then used for phylogenomic analyses (Allio et al., 2019).

2.2 Phylogenomic analysis techniques

Phylogenomic analysis involves several bioinformatics tools and techniques for alignment and phylogenetic tree construction. Tools such as IQ-TREE and PhyloBayes are commonly used for maximum-likelihood and Bayesian mixture model analyses, respectively (Allio et al., 2019). These tools help in constructing phylogenetic trees by aligning sequences and estimating evolutionary relationships based on the aligned data.

Models of molecular evolution are crucial in phylogenomic analyses. These models describe how sequences evolve over time and are used to infer phylogenetic relationships. For instance, the noncorrelated relaxed clock method is used to estimate divergence times by allowing different parts of the genome to evolve at different rates (Orton et al., 2017). Other models, such as the uncorrelated lognormal (UCLN) model, are used to account for rate heterogeneity across genes and lineages (Smith et al., 2018).

2.3 Addressing methodological challenges

Phylogenomic studies face several methodological challenges, including incomplete lineage sorting and hybridization. Incomplete lineage sorting occurs when the gene tree does not match the species tree due to ancestral polymorphisms. This issue can be addressed using multispecies coalescent methods, which consider the coalescent process of gene lineages within species (Koenen et al., 2019). Hybridization, which involves the mixing of genetic material from different species, can confound phylogenetic analyses. Techniques such as the D-statistic (ABBA-BABA test) are used to detect introgression and hybridization events (Vargas et al., 2017).

Managing large genomic datasets is another significant challenge. Phylogenomic datasets can be vast, making it difficult to perform analyses on the entire dataset. One approach to manage this issue is "gene shopping," where a subset of genes with desirable properties (e.g., clock-likeness, reasonable tree length, and minimal topological conflict) is selected for analysis (Smith et al., 2018). This method helps reduce errors associated with model mis-specification and makes divergence-time estimation more efficient.

3 Evolutionary Relationships within *Zea*

3.1 Phylogenetic trees of *Zea* species

The construction and interpretation of phylogenetic trees are fundamental to understanding the evolutionary relationships within the genus *Zea*. Phylogenetic trees are graphical representations that depict the evolutionary pathways and relationships among different species based on genetic data. In the context of *Zea*, complete plastid genomes (plastomes) have been utilized to construct these trees, providing insights into the microstructural changes such as inversions and insertion or deletion mutations (indels) that have occurred over time (Orton et al., 2017).

The major evolutionary relationships revealed among *Zea* species indicate that despite the close genetic relationships, there are significant variations in mutation rates. For instance, the study of five *Zea* species, including *Zea diploperennis, Zea perennis, Zea luxurians, Zea nicaraguensis,* and *Zea mays* subsp. *huehuetenangensis*, showed that tandem repeat indels were the most common type of microstructural change observed. These findings are consistent with previous studies that have examined mitochondrial and nuclear data, confirming the robustness of the phylogenetic trees constructed using plastome alignments (Orton et al., 2017).

3.2 Divergence time estimation

Estimating divergence times within the *Zea* genus involves sophisticated methods that model rate variation among lineages. One effective approach is the noncorrelated relaxed clock method, which allows for the estimation of divergence dates without assuming a constant rate of evolution across all branches of the phylogenetic tree. This method has been applied to calculate divergence times for specific nodes within Zea, revealing that the stem lineage of all *Zea* species diverged approximately 176 000 years before present (YBP) (Orton et al., 2017).

Key divergence events within the *Zea* genus include the separation of subspecies around 38 000 YBP and the divergence of section Luxuriantes around 23 000 YBP. These temporal contexts provide a framework for understanding the evolutionary history and speciation events within the genus. The calculated mutation rates for *Zea*, ranging from 1.7E-8 to 3.5E-8 microstructural changes per site per year, highlight the non-uniformity of evolutionary rates despite the close relationships among taxa (Orton et al., 2017).

3.3 Evolutionary history of major *Zea* species

The evolutionary pathways of major *Zea* species, such as maize (*Zea mays*), are shaped by a combination of genetic, environmental, and ecological factors. Maize, in particular, has undergone significant evolutionary changes that have been well-documented through phylogenomic studies. The use of complete plastid genomes has provided a detailed understanding of the microstructural changes and divergence times within the genus (Figure 1) (Orton et al., 2017).

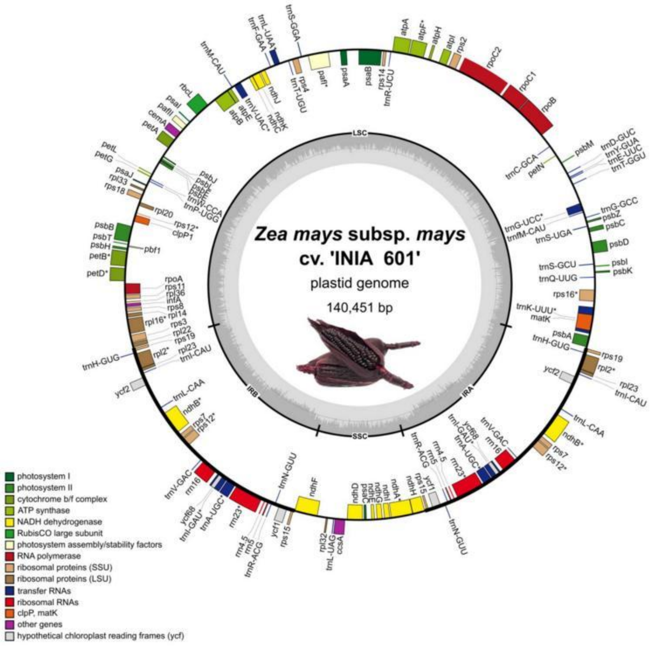

Figure 1 Plastid genome of *Zea mays* subsp. *mays* cv. ‘INIA 601’(Adopted from Orton et al., 2017)

Image caption: The thick lines indicate the IR1 and IR2 regions, which separate the SSC and LSC regions. Genes inside the circle are transcribed in the clockwise direction and genes outside the circle in the counterclockwise direction. Colors of genes indicate their function as shown in the legend. Genes containing introns are marked with an asterisk (*) (Adopted from Orton et al., 2017)

Factors influencing speciation within *Zea* include genetic mutations, environmental pressures, and hybridization events. The study of plastid genomes has revealed that tandem repeat indels are a common type of mutation, suggesting that these genetic changes play a crucial role in the evolutionary divergence of *Zea* species. Additionally, the non-uniform mutation rates observed across different species indicate that evolutionary pressures may vary significantly within the genus (Orton et al., 2017).

4 *Zea* Species Divergence and Genetic Adaptation

4.1 Genetic differentiation among *Zea* species

Genetic differentiation among *Zea* species is a complex process influenced by various evolutionary forces, including gene flow, natural selection, and genetic drift. Studies have shown that divergence in *Zea* species, such as *Zea mays* ssp. *parviglumis* and *Zea mays* ssp. *mexicana*, has occurred despite continuous gene flow, suggesting that local adaptation plays a significant role in maintaining species boundaries. The identification of key genes involved in species differentiation has been facilitated by genome-wide scans, which have revealed significant SNP associations with environmental variables like temperature and soil phosphorus concentration (Aguirre-Liguori et al., 2019). These findings indicate that specific genomic regions, possibly including putative inversions, contribute to reduced gene flow and increased genetic differentiation between locally adapted populations.

In addition to local adaptation, historical gene flow has also played a crucial role in the divergence of *Zea* species. For instance, sequence polymorphism data from 26 nuclear loci have provided evidence for adaptive and purifying selection at nonsynonymous sites, highlighting the role of gene flow in the evolutionary history of *Zea mays* ssp. *mays* and three wild *Zea taxa*. This study estimated divergence times and suggested rapid diversification of lineages within *Zea* in the last~150 000 years, further emphasizing the importance of gene flow in shaping genetic differentiation (Ross-Ibarra et al., 2009).

4.2 Natural selection and adaptive traits

Natural selection is a driving force in shaping adaptive traits in *Zea* species. The role of natural selection in adaptive divergence is evident from studies on other taxa, such as Acrossocheilus, where positive selection on mitochondrial genes has been linked to adaptation to different habitats (Zhao et al., 2022). Similarly, in *Zea* species, natural selection has likely played a crucial role in the evolution of adaptive traits that confer ecological advantages in specific environments.

Case studies of adaptive traits in *Zea* species have highlighted the importance of environmental factors in shaping genetic variation. For example, the divergence between *Zea mays* ssp. *parviglumis* and *Zea mays* ssp. *mexicana* has been associated with adaptation to temperature and soil phosphorus concentration. Genome-wide scans have identified outlier SNPs linked to these environmental variables, suggesting that natural selection has targeted specific genomic regions to drive adaptive divergence (Aguirre-Liguori et al., 2019).

Moreover, the study of genetic differentiation in other species, such as Daphnia pulex, has shown that regions of high gene density and recombination are more divergent, indicating that selection on genes related to local adaptation shapes genome-wide patterns of differentiation (Wersebe et al., 2022). These findings underscore the role of natural selection in driving adaptive traits and genetic differentiation in *Zea* species.

4.3 Hybridization and its evolutionary Impact

Hybridization has played a significant role in the evolution of *Zea* species, contributing to genetic diversity and adaptive potential. Gene flow between hybridizing taxa can lead to heterogeneous genomic divergence, as observed in the teosinte subspecies *Zea mays* ssp. *parviglumis* and *Zea mays* ssp. *mexicana*. The continuous gene flow and secondary contact between these subspecies have resulted in genomic regions of high differentiation, likely driven by adaptive divergence and reduced gene flow in locally adapted populations (Aguirre-Liguori et al., 2019).

Historical gene flow has also been a key factor in the divergence of *Zea* species. For instance, cultivated maize (*Zea mays* ssp. *mays*) may serve as a bridge for gene flow among otherwise allopatric wild taxa, facilitating the exchange of genetic material and promoting genetic diversity. This historical gene flow has likely contributed to the rapid diversification of lineages within *Zea*, as evidenced by the consistent estimates of divergence times from various markers (Ross-Ibarra et al., 2009).

Case examples of gene flow between *Zea* species and its consequences can be seen in the study of pea aphid host races, where genomic hotspots of differentiation have been identified in regions associated with reproductive isolation and host-plant specialization (Nouhaud et al., 2018). These findings suggest that hybridization and gene flow can lead to the emergence of new adaptive traits and contribute to the evolutionary dynamics of *Zea* species.

5 Implications for Crop Improvement

5.1 Contributions to maize breeding programs

The application of phylogenomic insights has significantly enhanced maize breeding programs by providing a deeper understanding of the genetic basis of important traits. For instance, the comprehensive assessment of maize evolution through genome-wide resequencing has identified numerous genes with strong signals of selection, which are crucial for major morphological changes in maize (Figure 2) (Hufford et al., 2012b). This information is invaluable for breeders aiming to develop new varieties with improved traits.

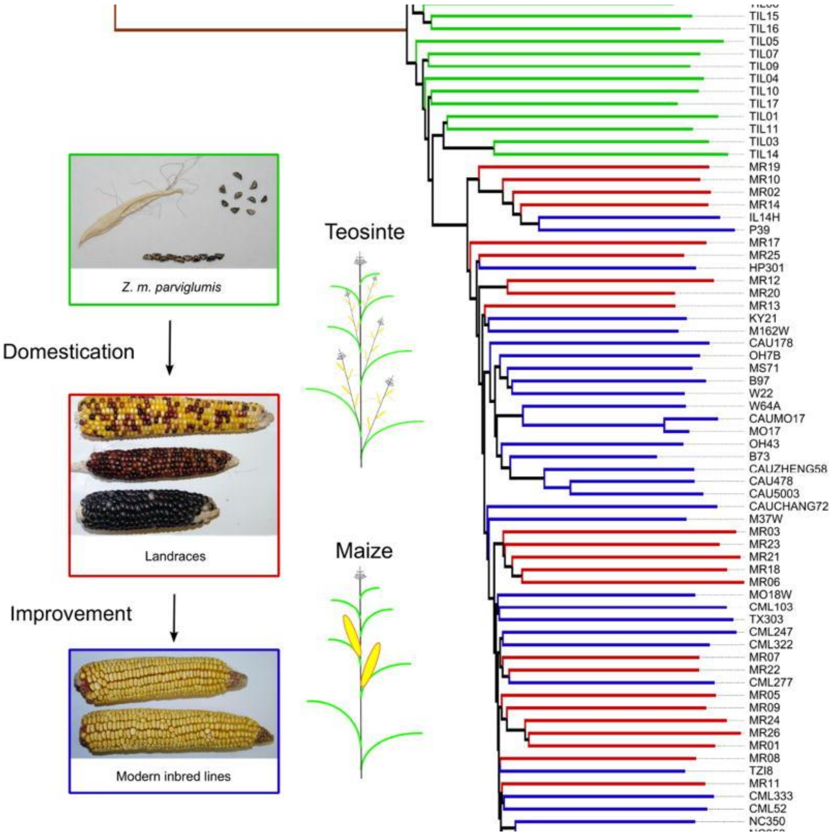

Figure 2 Neighbor-joining tree and changing morphology of domesticated maize and its wild relatives (Adopted from Hufford et al., 2012b)

Image caption: Taxa in the neighbor-joining tree (right) are represented by different colors: parviglumis (green), landraces (red), improved lines (blue), mexicana (yellow), and Tripsacum (brown). Morphological changes (left) are shown for female inflorescences and plant architecture during domestication and improvement (Adopted from Hufford et al., 2012b)

Moreover, the integration of genomic prediction methods, such as GBLUP and BayesB, has facilitated more accurate predictions of hybrid performance, thereby optimizing the selection process in breeding programs (Technow et al., 2014). This approach allows breeders to focus on the performance of experimental hybrids rather than solely on parental lines, enhancing the efficiency of breeding strategies.

Additionally, the identification of specific genetic loci associated with ear traits through GWAS and QTL mapping has provided targets for improving maize yield (Dong et al., 2023). By leveraging these genetic insights, breeders can develop maize varieties with enhanced ear traits, contributing to higher productivity.

5.2 Conservation of wild relatives

Conserving the genetic diversity of wild *Zea* species is crucial for maintaining a reservoir of beneficial traits that can be integrated into cultivated maize. The domestication of maize from its wild ancestor, teosinte, involved significant metabolic divergence, with distinct sets of metabolites being targeted during different stages of maize evolution (Xu et al., 2019). This highlights the importance of preserving wild relatives to ensure the availability of diverse genetic resources.

Strategies for integrating wild genetic resources into crop breeding include the use of genomic screening to identify genes affected by artificial selection during domestication and improvement (Yamasaki et al., 2007). By understanding the genetic basis of traits in wild relatives, breeders can introgress these beneficial alleles into cultivated maize, enhancing its adaptability and resilience.

Furthermore, the use of temperate germplasm to improve tropical germplasm has shown potential in enhancing heterosis in grain yields (Wen et al., 2012). This approach involves incorporating unique alleles from temperate lines into tropically adapted lines, thereby increasing genetic diversity and improving crop performance.

5.3 Utilizing genetic diversity for agriculture

Leveraging phylogenomic data to identify beneficial traits is a key strategy for improving agricultural productivity. For example, the identification of candidate genes contributing to metabolic divergence between maize and teosinte has provided insights into domestication-associated changes in metabolism (Xu et al., 2019). These findings can be used to develop maize varieties with enhanced metabolic traits, improving their nutritional quality and stress tolerance.

Practical applications of phylogenomic findings in agriculture include the development of novel structural features in maize plants to increase yield and adaptability (Li et al., 2021). By understanding the phenotypic trait panorama, breeders can select for traits that enhance the structural efficiency of maize, such as improved nutrient transfer and epigenetic memory.

Additionally, the integration of digital technologies and physiological knowledge into breeding programs has shown promise in hastening genetic gain (Diepenbrock et al., 2021). By combining crop growth models with whole genome prediction, breeders can more accurately predict the performance of untested genotypes in diverse environments, thereby accelerating the development of high-yielding maize varieties.

6 Future Directions in *Zea* Phylogenomics

6.1 Advances in genomic technologies

The advent of cutting-edge genomic technologies such as CRISPR and long-read sequencing has revolutionized the field of phylogenomics, offering unprecedented opportunities to delve deeper into the evolutionary relationships and species divergence within the genus *Zea*. Long-read sequencing technologies, for instance, have significantly enhanced our ability to sequence entire genomes with high accuracy, thereby providing a more comprehensive understanding of genetic variations and evolutionary patterns (McKain et al., 2018; Koenen et al., 2019; Guo et al., 2022). These technologies facilitate the identification of orthologous genes and the construction of more accurate phylogenetic trees, which are crucial for resolving complex evolutionary histories (Delsuc et al., 2005; Allio et al., 2019).

CRISPR technology, on the other hand, offers the potential to manipulate specific genes and observe the resultant phenotypic changes, thereby providing insights into gene function and evolutionary adaptations (Guo et al., 2022; Chen et al., 2024). The integration of CRISPR with phylogenomic studies could enable researchers to experimentally validate hypotheses about gene function and evolutionary processes, thus bridging the gap between genomics and functional biology.

Future prospects for using these technologies in *Zea* studies are promising. For instance, long-read sequencing could be employed to sequence the genomes of lesser-studied *Zea* species, thereby filling gaps in our current genomic databases and providing a more complete picture of the genus's evolutionary history (Orton et al., 2017). Additionally, CRISPR could be used to investigate the functional roles of specific genes identified through phylogenomic analyses, thereby enhancing researchers understanding of the genetic basis of key traits such as drought tolerance and disease resistance.

6.2 Integrating phylogenomics with other disciplines

The integration of phylogenomics with other scientific disciplines such as ecology, physiology, and environmental science holds great potential for advancing researchers understanding of *Zea* evolution. By combining genomic data with ecological and physiological information, researchers can gain a more holistic view of how environmental factors and physiological adaptations have shaped the evolutionary trajectories of *Zea* species (Siepel, 2009; Fu et al., 2024).

For example, ecological data on habitat preferences and environmental conditions can be used to contextualize phylogenomic findings, thereby providing insights into how different *Zea* species have adapted to their respective environments. Similarly, physiological studies on traits such as photosynthetic efficiency and water use can help elucidate the genetic basis of these adaptations and their evolutionary significance (Koenen et al., 2019).

An interdisciplinary approach can also facilitate the identification of key genes and pathways involved in important traits, thereby informing breeding programs aimed at improving crop resilience and productivity. For instance, integrating phylogenomic data with physiological studies on drought tolerance could help identify candidate genes for genetic improvement, thereby contributing to the development of more resilient *Zea* varieties (Orton et al., 2017; McKain et al., 2018).

6.3 Addressing knowledge gaps

Despite significant advances in *Zea phylogenomics*, several knowledge gaps remain. One major gap is the limited genomic data available for many *Zea* species, particularly those that are less economically important than *Zea mays*. This lack of data hampers researchers ability to construct comprehensive phylogenies and understand the full extent of genetic diversity within the genus (Orton et al., 2017; McKain et al., 2018).

Another gap is the incomplete understanding of the evolutionary processes that have shaped the genetic diversity of *Zea* species. For instance, the roles of hybridization, introgression, and incomplete lineage sorting in *Zea* evolution are not fully understood and warrant further investigation (Vargas et al., 2017; Guo et al., 2022). Addressing these gaps will require the application of advanced genomic technologies and interdisciplinary approaches, as well as the generation of new genomic data for under-studied species.

Proposed research directions to fill these gaps include the sequencing of additional *Zea* genomes using long-read technologies, which will provide more complete and accurate genomic data for phylogenetic analyses (Orton et al., 2017; McKain et al., 2018). Additionally, studies investigating the roles of hybridization and introgression in *Zea* evolution could provide valuable insights into the genetic mechanisms underlying species divergence and adaptation (Vargas et al., 2017).

7 Concluding Remarks

The phylogenomic studies within the genus *Zea* have provided significant insights into the evolutionary relationships and species divergence. The analysis of complete plastid genomes (plastomes) across five *Zea* species revealed substantial microstructural changes, including 193 indels and 15 inversions, with tandem repeat indels being the most common. Divergence times were estimated, indicating that the stem lineage of all *Zea* species diverged approximately 176 000 years before present (YBP), with more recent divergence events occurring between 38 000 and 23 000 YBP. Additionally, the study confirmed previous findings from mitochondrial and nuclear data, reinforcing the robustness of the phylogenomic approach. Another study highlighted the role of gene flow in the evolutionary history of *Zea*, showing that gene flow has been a significant factor in population divergence and speciation within the genus. This study also provided consistent estimates of divergence times, suggesting rapid diversification within the last 150 000 years.

Building on these findings, several potential areas of investigation emerge. Further exploration of the rates and patterns of microstructural changes across a broader range of *Zea* species could provide deeper insights into the mechanisms driving genomic evolution in this genus. Additionally, investigating the role of gene flow in more detail, particularly how cultivated maize may facilitate gene flow among wild taxa, could enhance understanding of the evolutionary dynamics within *Zea*. Another promising area is the examination of adaptive and purifying selection at nonsynonymous sites across different *Zea* species, which could shed light on the selective pressures shaping the genomes of these plants. Integrating data from nuclear, mitochondrial, and plastid genomes in a comprehensive phylogenomic framework could offer a more holistic view of the evolutionary history and relationships within *Zea*.

Continued research in *Zea phylogenomics* is crucial for several reasons. Understanding the evolutionary relationships and divergence within this genus not only provides insights into the history and adaptation of these species but also has practical implications for agriculture and conservation. As *Zea mays* (maize) is a staple crop worldwide, knowledge of its genetic diversity and evolutionary history can inform breeding programs aimed at improving crop resilience and productivity. Moreover, studying the wild relatives of maize can reveal valuable genetic resources that may be harnessed for crop improvement. The findings from phylogenomic studies also contribute to the broader understanding of plant evolution and the processes driving speciation and adaptation. Therefore, continued research in this field is essential for advancing both basic and applied plant sciences.

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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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