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Genetic Structure and Diversity in *Zea Genus*: Implications for Conservation and Breeding

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Abstract The *Zea genus*, encompassing vital crop species like maize, holds significant genetic diversity essential for agricultural sustainability and food security. This study aims to elucidate the genetic structure and diversity within *Zea* species, underscore the importance of conserving these genetic resources, and highlight their implications for breeding programs. The phylogenetic relationships within *Zea*, genetic variation, and methods for assessing genetic structure are explored to provide a comprehensive understanding of the genus's genetic framework. The study also examines molecular markers, geographic distribution, and factors influencing genetic diversity, emphasizing the need for robust conservation strategies. Threats to genetic diversity are identified, alongside conservation efforts including the role of gene banks, ex situ, and in situ conservation. The utilization of genetic diversity in breeding programs is discussed, focusing on stress resistance, adaptability, yield enhancement, and modern breeding techniques such as genomic selection. Case studies of successful breeding programs and conservation projects illustrate practical applications and challenges. Future directions highlight advances in genomic tools, integrating conservation with breeding efforts, and policy considerations. This study underscores the critical need for continued research and strategic conservation to harness the full potential of *Zea* genetic resources for future agricultural innovation.

Keywords *Zea genus*; Genetic diversity; Conservation; Breeding programs; Genomic tools

1 Introduction

The genus *Zea*, belonging to the Poaceae family, encompasses a range of species including the domesticated maize (*Zea mays* ssp. *mays*) and its wild relatives commonly known as teosintes. These species are indigenous to Central and South America and exhibit significant genetic diversity and evolutionary history. The genus *Zea* is divided into two sections: *Zea* and *Luxuriantes*, with the former including the domesticated maize and its closest wild relatives, and the latter comprising more distantly related species such as *Zea luxurians* and *Zea nicaraguensis* (Tiffin and Gaut, 2001; Orton et al., 2017). The evolutionary trajectory of *Zea* has been shaped by processes such as polyploidy, speciation, and domestication, which have contributed to the genetic complexity observed within this genus (Tiffin and Gaut, 2001; Orton et al., 2017).

Genetic diversity within the genus *Zea* is crucial for several reasons. Firstly, it provides a reservoir of alleles that can be utilized for crop improvement and adaptation to changing environmental conditions. For instance, the wild progenitors of maize, such as *Zea mays* ssp. *parviglumis*, harbor a substantial amount of genetic variation that can be harnessed for breeding programs aimed at enhancing traits like disease resistance, drought tolerance, and yield (Gasca-Pineda et al., 2020; Chen et al., 2021). Secondly, understanding the genetic structure and diversity of *Zea* species is essential for conservation efforts. The loss of genetic diversity in certain populations, particularly those of wild teosintes, underscores the need for both in situ and ex situ conservation strategies to preserve these valuable genetic resources (Gasca-Pineda et al., 2020; Rivera-Rodríguez et al., 2023). Lastly, the study of genetic diversity in *Zea* provides insights into the evolutionary processes that have shaped the current distribution and adaptation of these species, thereby informing strategies for their sustainable management and utilization (Xia et al., 2004; Ross-Ibarra et al., 2009; Orton et al., 2017).

This study comprehensively assess the genetic structure and diversity within the genus *Zea*, with a particular focus on both domesticated maize and its wild relatives. This includes evaluating the levels of genetic variation across different species and subspecies, and understanding the factors that have influenced this diversity. explore the implications of genetic diversity for the conservation and breeding of *Zea* species. This involves identifying key genetic resources that can be leveraged for crop improvement and developing strategies to mitigate the loss of genetic diversity in wild populations. Synthesize current knowledge on the evolutionary history and gene flow within the genus *Zea*, thereby providing a framework for future research and conservation efforts. By addressing these objectives, this study aims to contribute to the broader understanding of the genetic landscape of *Zea* and its significance for both agricultural and ecological contexts.

2 Genetic Structure of *Zea genus*

2.1 Phylogenetic relationships within *zea*

The genus *Zea*, which includes both domesticated maize (*Zea mays* ssp. *mays*) and its wild relatives (teosintes), exhibits complex phylogenetic relationships shaped by historical gene flow and divergence events. Studies have shown that the diversification of *Zea* lineages occurred relatively rapidly within the last 150 000 years, with significant gene flow among taxa, including between domesticated maize and wild teosintes (Ross-Ibarra et al., 2009). This gene flow has played a crucial role in the evolutionary history of *Zea*, contributing to the genetic diversity observed within the genus.

2.2 Genetic variation and population structure

Genetic variation within *Zea* is substantial, with different studies highlighting the diversity present in various populations and breeding lines. For instance, SSR marker analysis of CIMMYT maize inbred lines revealed an average of 7.4 alleles per marker, indicating high genetic diversity (Xia et al., 2004). Similarly, SNP analysis of maize inbred lines from Sichuan province, China, identified significant genetic variation and population structure, with lines clustering into distinct groups based on their genetic backgrounds (Leng et al., 2019). The genetic diversity within and among CIMMYT maize populations was also confirmed by SSR markers, with most molecular variation found within populations rather than between them (Reif et al., 2004).

In addition, the genetic structure of maize germplasm in the China Summer maize ecological region was characterized using over 525 000 SNPs, revealing large genetic diversity and distinct heterotic groups (Shu et al., 2021). This diversity is crucial for breeding programs as it provides a broad genetic base for developing new hybrids with desirable traits.

2.3 Methods for assessing genetic structure

Various molecular markers and techniques have been employed to assess the genetic structure of *Zea*. Simple sequence repeat (SSR) markers have been widely used due to their high polymorphism and ability to reveal genetic relationships among inbred lines (Enoki et al., 2002; Reif et al., 2004; Xia et al., 2004). Genotyping by sequencing (GBS) has also been utilized to generate large numbers of SNPs, providing detailed insights into genetic diversity and population structure (Leng et al., 2019; Shu et al., 2021). Additionally, techniques such as quantitative hybridization and slot blotting have been used to measure the variation in repetitive sequences within the maize genome, further elucidating the genetic structure of different maize strains.

These methods have enabled researchers to identify genetic clusters, assess linkage disequilibrium, and understand the genetic basis of important agronomic traits. For example, the MAGIC maize population, a multi-parental population derived from eight diverse founder lines, has been developed to facilitate high-resolution QTL mapping and the identification of candidate genes for complex traits (Figure 1) (Dell’Acqua et al., 2015) . This population provides a valuable resource for studying the genetic architecture of maize and improving breeding strategies.

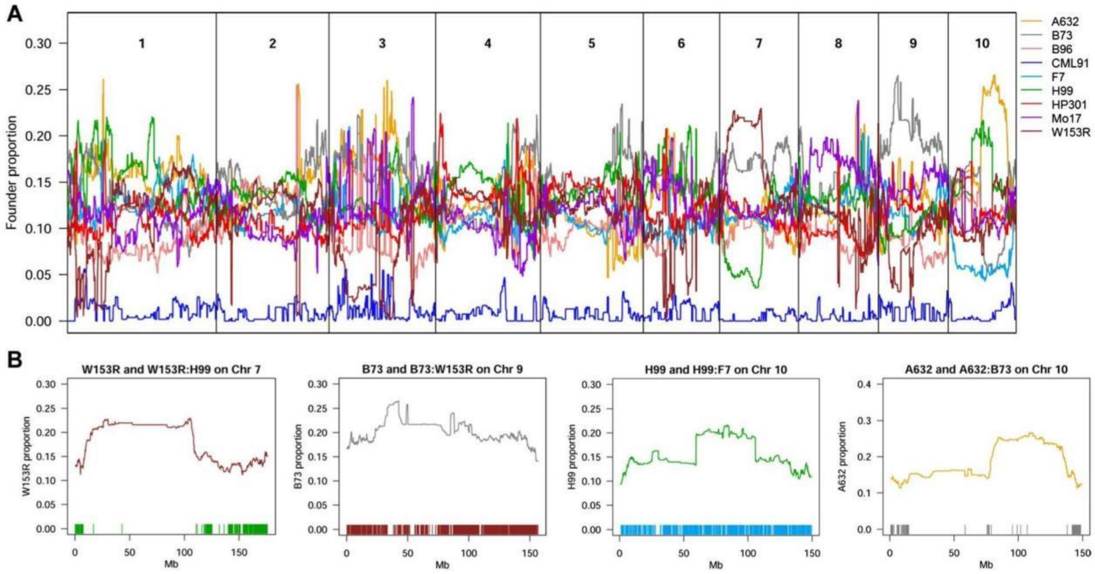

Figure 1 Locus-based founders contribution to the MM genomes (Adopted from Dell'Acqua et al., 2015)

Image caption: Panel a shows that founders' contribution to MM lines genomes is close to 12.5%, except for CML91, seldom introduced. Because of this, CML91 was excluded from QTL analyses. Some regions still show significant deviation from the expected one-eighth. Regions of Chr 7, 9, and 10 in which founder proportions are distorted are shown in panel (b). Each line depicts the contribution of the founder that is over-represented. Below the line, each tick (colored according to legend in panel (a) indicates a polymorphism between the over-represented and the under-represented founder. The allelic distortion on Chr 7, 10 (for A632 vs. B73), and partially 9 can be related with IBS regions in which the haplotype model cannot distinguish between the two founders (Adopted from Dell'Acqua et al., 2015)

3 Diversity within *Zea* Species

3.1 Molecular markers and genetic diversity

Molecular markers have been extensively used to assess genetic diversity within *Zea* species. Simple sequence repeat (SSR) markers, for instance, have been employed to investigate the genetic diversity among tropical lowland inbred lines of maize. The study revealed an average of 7.4 alleles per marker, indicating substantial genetic variation within the germplasm (Xia et al., 2004). Another study using SSR markers on CIMMYT maize populations found that most molecular variation was within populations, with significant deviations from Hardy-Weinberg equilibrium due to an excess of homozygosity (Reif et al., 2004). Additionally, nuclear microsatellite loci have been used to examine genetic diversity in wild maize (teosinte), revealing significant genetic structure among populations and variable levels of diversity within subspecies (Gasca-Pineda et al., 2020).

3.2 Geographic distribution of genetic diversity

The geographic distribution of genetic diversity in *Zea* species is influenced by both historical and contemporary factors. For example, the genetic diversity of teosinte has been shaped by past climate fluctuations during the Holocene and Pleistocene, as well as local adaptation and genetic isolation (Gasca-Pineda et al., 2020). In cultivated maize, genetic diversity patterns often reflect the origins and breeding histories of the germplasm. A study on cultivated lentil, which can be paralleled to maize, showed that genetic diversity clusters prominently reflected geographical origins, indicating that similar patterns might be expected in maize (Khazaei et al., 2016). Furthermore, the genetic structure of maize populations adapted to different megaenvironments (tropical, subtropical, and temperate) supports the idea that geographic distribution plays a crucial role in shaping genetic diversity (Reif et al., 2004).

3.3 Factors influencing genetic diversity

Several factors influence genetic diversity within *Zea* species. Local adaptation and historical environmental shifts are significant contributors, as seen in the genetic diversity of teosinte, which is influenced by both contemporary factors and historical climate fluctuations (Gasca-Pineda et al., 2020). The breeding system and colonizing ability also play a role, as demonstrated in a study on wild orchids, where different breeding systems led to varying levels of genetic variation and population structure (Sun and Wong, 2001) Additionally, species traits related to parental investment, such as longevity and fecundity, have been shown to predict genetic diversity levels, with long-lived or low-fecundity species being less genetically diverse (Romiguier et al., 2014). These findings highlight the complex interplay of ecological, environmental, and biological factors in shaping the genetic diversity of *Zea* species.

4 Conservation of *Zea* Genetic Resources

4.1 Threats to genetic diversity in *Zea*

The genetic diversity of *Zea* species, including maize and its wild relatives, faces several threats. One significant threat is the economic pressure favoring genetic monocultures to maximize short-term agricultural gains, which reduces genetic variability and increases vulnerability to pests and climatic extremes. Additionally, the loss of traditional farming practices and the adoption of high-yielding crop cultivars contribute to the erosion of landraces, which are crucial reservoirs of genetic diversity. Habitat destruction and environmental changes further exacerbate the loss of genetic diversity in wild *Zea* populations.

4.2 Strategies for conservation

To mitigate these threats, a combination of in situ and ex situ conservation strategies is essential. In situ conservation involves maintaining genetic resources in their natural habitats, which allows for the preservation of not only the genetic material but also the ecological and evolutionary processes that shape it. Ex situ conservation, on the other hand, involves preserving genetic material in gene banks, seed banks, and other repositories, providing a backup against the loss of genetic diversity in the wild. Both strategies are complementary and necessary for a comprehensive conservation approach.

4.3 Role of gene banks and ex situ conservation

Gene banks play a critical role in the ex situ conservation of *Zea* genetic resources. They provide a secure environment for the long-term storage of genetic material, ensuring that it remains available for future breeding and research efforts. Ex situ collections can capture a significant portion of the genetic diversity found in natural populations, although they may under-represent some rare alleles (Kallow et al., 2021). Regular evaluation and regeneration of gene bank accessions are necessary to maintain genetic diversity and prevent genetic drift (Hintum et al., 2007). Additionally, incorporating genetic material from wild populations into gene banks can enhance the genetic representation and resilience of ex situ collections.

4.4 In situ conservation efforts

In situ conservation efforts focus on preserving *Zea* genetic resources within their natural habitats. This approach maintains the dynamic processes of natural selection and adaptation, which are crucial for the long-term survival and evolution of species. In situ conservation can be achieved through the establishment of genetic reserves, protected areas, and the promotion of traditional farming practices that maintain landrace diversity. For example, the ongoing maintenance of maize landraces by farmers in southern Mexico demonstrates the potential for in situ conservation to coexist with modern agricultural practices. Mapping the geographical distribution of genetic variation can also help identify areas of high diversity and guide conservation efforts.

5 Implications for Breeding

5.1 Utilization of genetic diversity in breeding programs

The genetic diversity present in *Zea* species, including both domesticated maize and its wild relatives, offers a rich reservoir of alleles that can be harnessed for breeding programs. The extensive genetic variation found in maize, as well as in its wild relatives such as teosinte, provides opportunities to introduce novel traits and enhance the genetic base of elite breeding materials (Whitt et al., 2002; Abdoul-Raouf et al., 2017). For instance, the incorporation of alleles from wild relatives has been shown to improve stress tolerance and yield in maize (Abdoul-Raouf et al., 2017). This genetic diversity is crucial for developing new varieties that can adapt to changing environmental conditions and meet the growing food demands (Chen et al., 2021).

5.2 Breeding for stress resistance and adaptability

Breeding for stress resistance and adaptability is essential for ensuring the sustainability of maize production under various environmental stresses. Studies have identified specific genes and pathways that confer resistance to biotic and abiotic stresses, such as drought, low nitrogen, soil acidity, and pest and disease resistance (Wen et al., 2011; Abdoul-Raouf et al., 2017). For example, the use of wild relatives like teosinte and Tripsacum has been instrumental in introducing genes that confer tolerance to chlorotic dwarf virus, downy mildew, Fusarium, Striga hermonthica, rootworms, drought, and flooding (Abdoul-Raouf et al., 2017). Additionally, genomic studies have revealed signatures of selection for traits like heat tolerance and tick resistance in African cattle, which can be analogous to similar efforts in maize breeding (Kim et al., 2017).

5.3 Enhancing yield and nutritional quality

Improving grain yield and nutritional quality remains a primary goal in maize breeding. The genetic architecture of maize ear traits, which significantly influence yield, has been dissected using multiple populations and high-density markers. This approach has identified numerous quantitative trait loci (QTLs) that can be targeted for yield improvement. Furthermore, the genetic diversity within maize and its wild relatives can be exploited to enhance nutritional quality by introducing alleles that improve the content of essential nutrients (Whitt et al., 2002; Chen et al., 2021). The integration of these diverse genetic resources into breeding programs can lead to the development of high-yielding and nutritionally superior maize varieties.

5.4 Genomic selection and modern breeding techniques

Genomic selection and other modern breeding techniques have revolutionized maize breeding by increasing selection intensity and accelerating the breeding cycle. Genomic prediction models, which use marker effects to predict hybrid performance, have shown promise in improving traits such as grain yield, anthesis date, and anthesis-silking interval (Windhausen et al., 2012). However, the effectiveness of these models depends on the genetic relationship between the training and validation sets, as well as the population structure (Windhausen et al., 2012). Additionally, the use of high-density genomic variation maps and genome-wide association studies (GWAS) can facilitate the identification of adaptive variants and the fine mapping of QTLs, thereby enhancing the precision and efficiency of breeding programs (Chen et al., 2021).

In conclusion, the genetic diversity within *Zea* species provides a valuable resource for maize breeding programs. By leveraging this diversity, breeders can develop new varieties with improved stress resistance, adaptability, yield, and nutritional quality. Modern breeding techniques, including genomic selection and GWAS, further enhance the potential for achieving these goals, ultimately contributing to the sustainability and productivity of maize agriculture.

6 Case Studies

6.1 Successful breeding programs utilizing *zea* genetic diversity

Several breeding programs have successfully utilized the genetic diversity of *Zea* to enhance crop performance and resilience. For instance, the breeding program in Sichuan province, Southwest China, has leveraged the genetic diversity and population structure of 157 elite maize inbred lines to improve hybrid production. This program identified four distinct genetic groups, which facilitated the strategic use of germplasm in hybrid breeding, leading to better exploitation of heterotic patterns (Leng et al., 2019). Similarly, the International Maize and Wheat Improvement Center (CIMMYT) has investigated the genetic diversity among tropical lowland inbred lines using SSR markers. This study revealed a lack of structure within the germplasm, which can be attributed to the mixed origin of the populations used. The findings support the choice of representative testers for evaluating inbred lines, thereby enhancing the exploitation of genetic diversity in hybrid breeding (Xia et al., 2004).

6.2 Conservation projects in different regions

Conservation projects across various regions have focused on preserving the genetic diversity of *Zea* species. In Mexico, the genetic diversity of wild maize (teosinte) has been studied to understand the effects of historical climate fluctuations on genetic diversity. This research highlighted the significant genetic structure among populations and the influence of local adaptation and genetic isolation on current genetic diversity (Figure 2)

(Gasca-Pineda et al., 2020). Additionally, the genetic diversity of cultivated lentil (Lens culinaris Medik.) has been assessed to support conservation and crop genetic enhancement strategies. This study categorized accessions into three major groups based on geographical origin, reflecting the world's agro-ecological zones, and emphasized the need for continued conservation efforts to maintain genetic diversity (Khazaei et al., 2016).

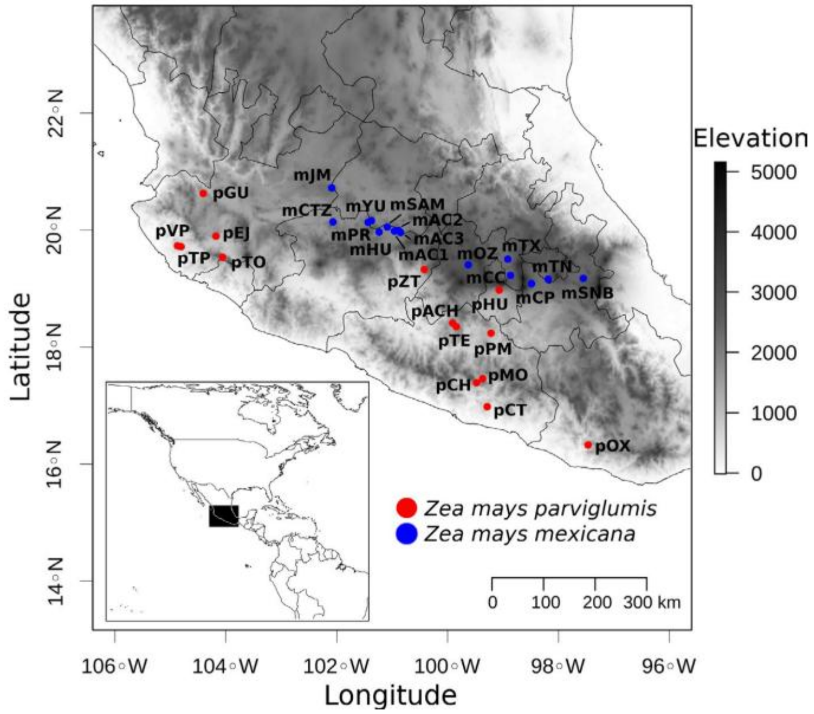

Figure 2 Teosinte analyzed populations and elevation (Adopted from Gasca-Pineda et al., 2020)

Image caption: In red, *Zea mays* subsp. *parviglumis*; in blue, *Zea mays* subsp. *Mexicana* (Adopted from Gasca-Pineda et al., 2020)

6.3 Challenges and solutions in *zea* breeding and conservation

Breeding and conservation of *Zea* face several challenges, including genetic bottlenecks, low genetic diversity in critical genes, and environmental stressors. For example, the genetic diversity in the maize starch pathway has been found to be unusually low due to strong artificial selection, suggesting that future breeding may need to incorporate alleles from wild relatives to overcome this limitation (Whitt et al., 2002). In the sub-tropics, maize breeding programs face challenges such as drought stress and aflatoxin contamination. A genome-wide association study identified quantitative trait variants associated with yield and aflatoxin resistance, demonstrating the potential of genetic diversity to improve breeding outcomes under these conditions (Farfan et al., 2015). Conservation efforts also need to address the genetic structure and differentiation within populations, as seen in the study of wild orchids with contrasting breeding systems, which highlighted the need for tailored conservation strategies based on genetic variation and population structure (Sun and Wong, 2001).

By understanding and addressing these challenges, breeding programs and conservation projects can better utilize the genetic diversity of *Zea* to enhance crop performance and ensure the long-term sustainability of these valuable genetic resources.

7 Future Directions

7.1 Advances in genomic tools and technologies

The rapid advancement in genomic tools and technologies holds significant promise for enhancing our understanding of genetic diversity and structure within the genus *Zea*. High-density genomic variation maps, such as those developed from ~700 genomes encompassing maize and all wild taxa of *Zea*, have identified over 65 million single nucleotide polymorphisms (SNPs), 8 million Insertion/Deletion (InDel) polymorphisms, and numerous novel inversions (Chen et al., 2021). These comprehensive genomic datasets enable the identification of adaptive variants and provide insights into evolutionary processes, which are crucial for both conservation and breeding programs. Future research should focus on leveraging these genomic resources to develop novel mutant alleles and to explore the genetic basis of important traits such as flowering time and highland adaptation (Chen et al., 2021).

7.2 Integrating conservation and breeding efforts

Integrating conservation and breeding efforts is essential for maintaining the genetic diversity of *Zea* species. The conservation of genetic diversity, both among and within breeds, is a costly process that requires strategic choices between breeds and individual animals (Oldenbroek, 2021). Genomic information can play a pivotal role in this integration by accurately measuring genetic distances among breeds and relationships within breeds. This information can be used to detect valuable rare alleles and haplotypes, facilitating their conservation either in vitro (gene banks) or in vivo (maintaining small populations alive) (Oldenbroek, 2021). Additionally, the genetic variability observed in locally adapted breeds, such as the significant differentiation between taurine and zebu breeds in Brazil, highlights the potential for using this variability in breeding programs to enhance the resilience and productivity of *Zea* species (Campos et al., 2017).

7.3 Policy and regulatory considerations

Effective conservation and breeding strategies for *Zea* species require supportive policy and regulatory frameworks. Policymakers must recognize the importance of genetic diversity and implement regulations that promote the conservation of both wild and domesticated *Zea taxa*. This includes establishing gene banks and protected areas, as well as providing incentives for farmers and breeders to maintain diverse genetic resources. Furthermore, international collaboration and data sharing are crucial for the success of these efforts. The development of standardized genomic tools and protocols can facilitate the exchange of information and resources across borders, ensuring that the genetic diversity of *Zea* is preserved for future generations.

8 Concluding Remarks

The genetic structure and diversity within the genus *Zea*, particularly maize (*Zea mays* L.), have significant implications for both conservation and breeding programs. Several studies have highlighted the extensive genetic variation present within and among different maize populations and their wild relatives.

Genetic Diversity in Maize Populations: Research using simple sequence repeat (SSR) markers has shown that most genetic variation is found within populations rather than between them. This suggests that intra-population diversity is a critical resource for breeding programs.

Genetic Differentiation and Population Structure: Studies have demonstrated that maize populations adapted to different megaenvironments (MEs) cluster together, indicating a clear genetic structure based on environmental adaptation. This clustering supports the idea that local adaptation plays a significant role in shaping genetic diversity.

Wild Relatives of Maize: The genetic diversity in wild relatives of maize, such as teosinte, has been extensively mapped, revealing millions of single nucleotide polymorphisms (SNPs) and other genetic variations. These wild relatives possess unique adaptations, such as perenniality and regrowth, which are valuable for breeding programs aimed at improving maize resilience and productivity.

(1) Expand Genetic Mapping: Future research should continue to expand the genetic mapping of both cultivated maize and its wild relatives. High-density genomic variation maps can uncover novel genetic variants that are crucial for breeding programs. This includes focusing on underexplored genetic regions and wild taxa within the genus *Zea.*

(2) Utilize Wild Relatives for Breeding: Breeding programs should leverage the genetic diversity found in wild relatives of maize. The unique adaptations present in these wild species, such as those related to highland and high latitude environments, can be introduced into cultivated maize to enhance its adaptability and resilience.

(3) Conservation of Genetic Resources: Conservation efforts should prioritize maintaining the genetic diversity within and among maize populations. This includes preserving both cultivated varieties and wild relatives to ensure a broad genetic base for future breeding efforts. Strategies such as in situ and ex situ conservation can be employed to achieve this goal.

(4) Investigate Hormone and Flowering Pathways: Further research is needed to understand the specific genetic pathways involved in key adaptations, such as hormone-related pathways for highland adaptation and flowering time pathways for high latitude adaptation. Identifying and characterizing these pathways can provide targeted approaches for breeding programs.

(5) Monitor Genetic Purity: It is essential to monitor the genetic purity of locally adapted breeds and populations. Introgression from other breeds or species can dilute unique genetic traits. Regular genetic assessments using markers like SNPs can help maintain the integrity of these populations.

By addressing these recommendations, future research and breeding programs can effectively utilize the genetic diversity within the genus *Zea* to enhance maize productivity, adaptability, and conservation.

Conflict of Interest Disclosure

The authors affirm 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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