

## Role of Transposable Elements in the Evolution of the *Triticeae* Genome

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**Abstract** Transposable elements (TEs) are ubiquitous components of genomes and play a significant role in the evolution and diversification of the *Triticeae* tribe, which includes important cereal crops such as wheat, barley, and rye. This research examines the impact of TEs on *Triticeae* genome evolution, exploring their contribution to genome size, structure, and genetic diversity. We discuss the classification and mechanisms of TEs, focusing on their role in genome expansion, gene regulation, and the creation of new regulatory networks. Case studies in *Triticeae* species highlight the dynamic nature of TEs and their influence on genomic architecture and evolutionary adaptation. Advances in sequencing technologies and bioinformatics tools have enhanced our understanding of TE diversity and activity, paving the way for new discoveries and potential applications in crop improvement. This research underscores the importance of continued research into TEs to fully elucidate their roles and harness their potential for agricultural and biotechnological advancements.

**Keywords** Transposable elements; *Triticeae* genome; Genome evolution; Retrotransposons; Genetic diversity

The *Triticeae* tribe, belonging to the Poaceae family, encompasses some of the most agriculturally significant cereal crops, including wheat (*Triticum* spp.): barley (*Hordeum* spp.): and rye (*Secale* spp.). The *Triticeae* tribe is characterized by its genetic diversity and adaptability, which have enabled these species to thrive in various environmental conditions. These crops are foundational to global agriculture, supplying staple food sources for human consumption and livestock feed, thereby significantly contributing to food security and the agricultural economy worldwide (Li et al., 2004).

The genomes of *Triticeae* species are notably large and complex, with a significant portion composed of repetitive sequences. This genetic diversity, driven by polyploidization, mutations, and the activity of transposable elements (TEs): is vital for the adaptability and resilience of these crops, enabling them to withstand diverse environmental conditions and resist various biotic and abiotic stresses (Middleton et al., 2013). For instance, the wheat genome, one of the largest among *Triticeae*, is approximately 15 Gb in size and is predominantly hexaploid, containing three sets of homologous chromosomes (AABBDD) (Papon et al., 2023). A striking feature of these genomes is the high proportion of transposable elements (TEs): which constitute over 80% of the wheat genome (Wicker et al., 2018; Zhang et al., 2021). This extensive presence of TEs contributes to the genetic diversity and evolutionary dynamics of *Triticeae* species.

Transposable elements (TEs) are DNA sequences that can change their position within the genome, thereby creating or reversing mutations and altering the cell's genetic identity. They are categorized into two main types: Class I elements, or retrotransposons, which move via an RNA intermediate, and Class II elements, or DNA transposons, which operate through a "cut-and-paste" mechanism. Retrotransposons include long terminal repeat (LTR) elements and non-LTR elements, while DNA transposons can be autonomous, carrying the necessary machinery for their movement, or non-autonomous, relying on external transposase enzymes for transposition (Thiyagarajan et al., 2022). Within these classes, TEs are further divided into various families based on their structural characteristics and mechanisms of transposition. In *Triticeae* genomes, TEs constitute a significant portion, with retrotransposons like LTRs being particularly abundant (Sabot and Schulman, 2009).

The study of TEs in plant genomes has a rich history, dating back to the pioneering work of Barbara McClintock in the 1940s, who discovered "jumping genes" in maize. Since then, TEs have been recognized as major players in genome evolution, contributing to genetic variation, genome size expansion, and regulatory network modifications. In *Triticeae*, advances in genomic technologies have allowed for the detailed identification and characterization of numerous TE families, enhancing our understanding of their roles in genome evolution, gene regulation, and adaptability (Wicker et al., 2018). Recent studies have highlighted the significant role of TEs in shaping the genome structure and function, influencing gene expression, and facilitating adaptation to environmental changes (Zhang et al., 2021; Papon et al., 2023).

This study aims to elucidate the role of transposable elements in the evolution of the *Triticeae* genome. By synthesizing current research findings, we seek to provide a comprehensive understanding of how TEs contribute to genetic diversity, genome evolution, and the adaptive potential of *Triticeae* species. This study will explore the mechanisms by which TEs influence genome dynamics, the evolutionary implications of TE activity, and the potential applications of this knowledge in crop improvement and breeding programs.

## **1 Types and Mechanisms of Transposable Elements in *Triticeae***

### **1.1 Classification of transposable elements**

Transposable elements (TEs) in the *Triticeae* genomes are broadly classified into two main classes based on their mechanisms of transposition: Class I elements, or retrotransposons, and Class II elements, or DNA transposons. Class I elements, also known as retrotransposons, move via an RNA intermediate. These are further subdivided into Long Terminal Repeat (LTR) retrotransposons and non-LTR retrotransposons. LTR retrotransposons, such as Ty1-copia and Ty3-gypsy, are particularly prevalent in the *Triticeae* genomes and are characterized by their long terminal repeats which flank the coding regions of the transposon (Sabot and Schulman, 2009). Non-LTR retrotransposons include LINES (Long Interspersed Nuclear Elements) and SINEs (Short Interspersed Nuclear Elements) (Klein and O'Neill, 2018; Colonna Romano and Fanti, 2022): where LINES are autonomous and SINEs depend on the enzymatic machinery of LINES for their movement (Wicker et al., 2013).

Class II elements, or DNA transposons, move through a "cut-and-paste" mechanism. Examples include the Tn3 family transposons, which utilize a replicative transposition mechanism (Lima-Mendez et al., 2020). These are categorized into several superfamilies such as CACTA transposons and MITEs (Miniature Inverted-repeat Transposable Elements). CACTA transposons, like the Caspar family, are significantly present in the *Triticeae* genomes and play a critical role in genome organization (Wicker et al., 2003). MITEs, being non-autonomous elements, rely on the transposase enzymes of other transposons for their movement and are often associated with gene regions, impacting their regulation and evolution (Wicker et al., 2001).

### **1.2 Mechanisms of transposition**

The transposition mechanisms of TEs differ between Class I and Class II elements (Figure 1). Retrotransposons (Class I elements) utilize a copy-and-paste mechanism (Figure 1a and Figure 1b). This process begins with the transcription of the retrotransposon into RNA, which is then reverse transcribed into DNA by the enzyme reverse transcriptase. The newly synthesized DNA is subsequently integrated into a new location in the genome by the integrase enzyme (Sabot and Schulman, 2009). This process can lead to an increase in the number of copies of the element within the genome (Klein and O'Neill, 2018; Ali et al., 2021). In contrast, DNA transposons (Class II elements) follow a cut-and-paste mechanism (Figure 1c). Here, the transposon is first excised from its original location in the genome by the transposase enzyme. The excised DNA element is then inserted into a new genomic location, completing the transposition process (Wicker et al., 2003). Some DNA transposons can also mediate duplications via transposition-independent mechanisms, such as gap filling, or transposition-dependent mechanisms, such as replication fork switching (Lima-Mendez, 2020; Tan et al., 2021).

### **1.3 Distribution and abundance in *Triticeae* genomes**

The distribution and abundance of TEs in *Triticeae* genomes are highly variable and significant. TEs constitute a substantial portion of the *Triticeae* genomes, with LTR retrotransposons alone accounting for 55%~70% of the

genome (Sabot and Schulman, 2009). This high abundance underscores the impact of TEs on genome size and structure.

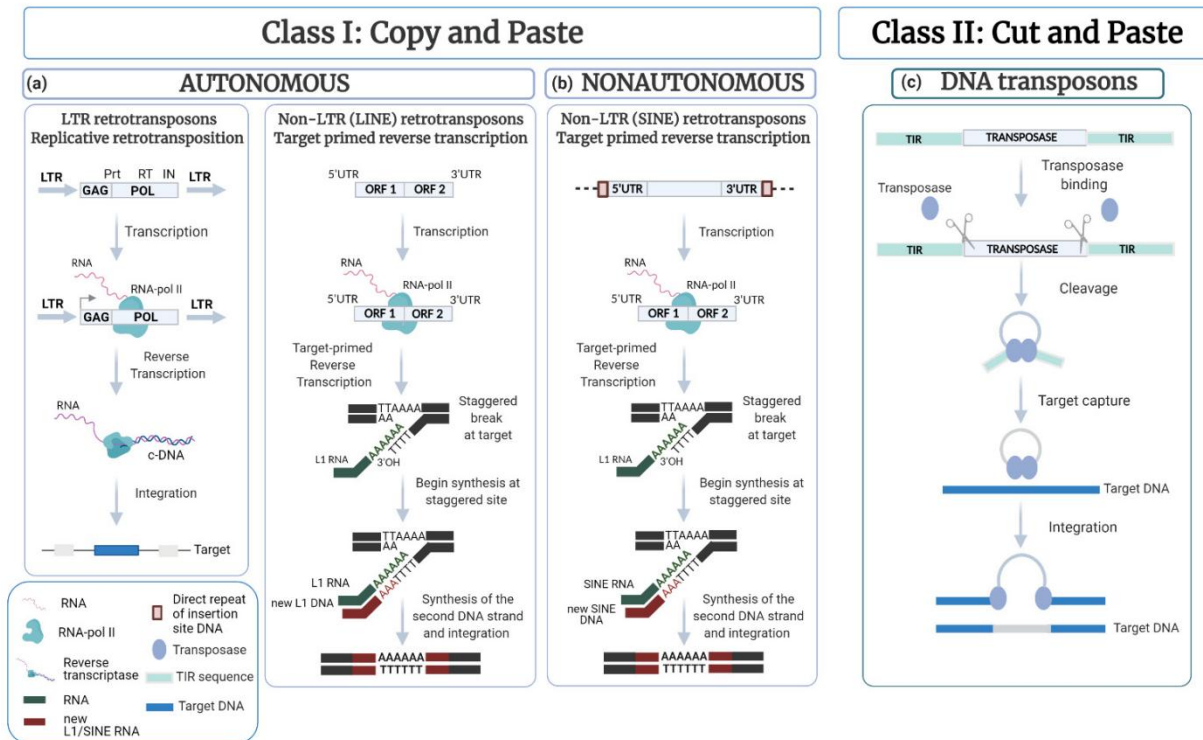


Figure 1 Mechanisms schematic representation of Class I and Class II TEs (Adapted from Colonna Romano and Fanti, 2022)

The distribution of TEs within the genome is influenced by various factors, including the genomic context and the presence of specific regulatory mechanisms that control TE activity. For instance, TEs can be silenced through epigenetic modifications, but they can also be reactivated under certain conditions, such as environmental stress or during specific developmental stages (Ali et al., 2021; Colonna Romano and Fanti, 2022). The dynamic nature of TEs and their ability to induce genetic variability make them crucial players in the evolution of the *Triticeae* genome.

TEs are not evenly distributed within the genome; they tend to cluster in specific regions such as near centromeres and telomeres, and are often less prevalent in gene-rich areas. For instance, CACTA elements are frequently associated with gene regions, contributing to their regulation and evolutionary significance (Wicker et al., 2003). Additionally, the composition and dynamics of TEs vary among different *Triticeae* species. The BARE1 element, for example, is a significant contributor to the genomes of several *Triticeae* species, including wheat and barley, and shows considerable variation in its abundance and activity between species (Middleton et al., 2013).

## 2 Transposable Elements and Genetic Diversity

### 2.1 Contribution to genetic variation

Transposable elements (TEs) significantly contribute to genetic variation genomes by introducing novel insertions that can disrupt or alter gene functions (Figure 2). This insertional mutagenesis can generate genetic diversity and impact various traits, influencing adaptation and evolution. Recent studies have shown that TEs in *Triticeae*, such as in *Thinopyrum intermedium* and its diploid relatives, display considerable variation in copy number and abundance, highlighting their role in creating genetic diversity (Divashuk et al., 2019). Furthermore, the novel non-autonomous DNA transposon identified in the *DRF1* gene in *Triticum durum* and other *Triticeae* species suggests recent evolutionary activity contributing to genetic variability (Thiyagarajan et al., 2022).

### 2.2 Role in gene and genome evolution

TEs are integral to gene and genome evolution, facilitating the emergence of new gene functions and regulatory

networks. They can act as sources of genetic innovation by promoting gene duplications, creating new regulatory elements, and influencing gene expression. For instance, the study of TEs in fungal wheat pathogens has shown that TEs can shape genome architecture and affect gene regulation, particularly in relation to pathogenicity (Lorrain et al., 2021). Additionally, the genomic ecosystem of maize highlights how TEs contribute to the diversification of gene regulation and phenotypic traits, emphasizing their evolutionary impact (Stitzer et al., 2021).

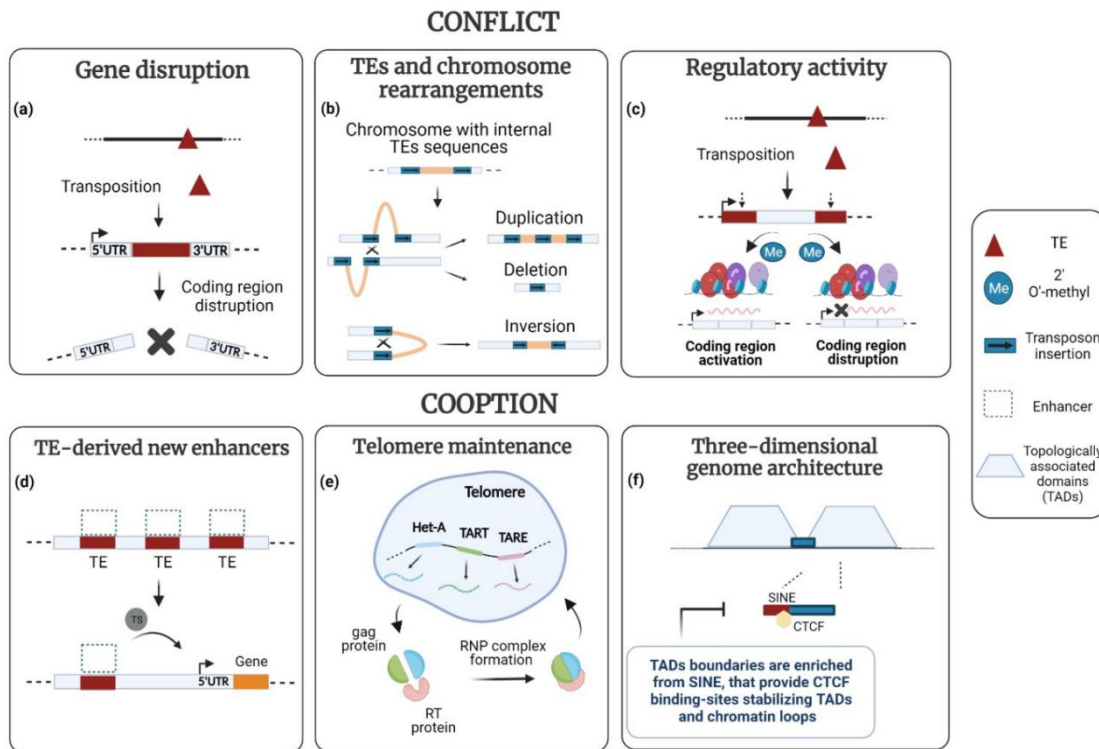


Figure 2 The role of transposons (TEs) in the genome (Adapted from Colonna Romano and Fanti, 2022)

Image caption: Transposable elements (TEs) can exert various deleterious effects on the host genome: (a) Insertion into coding exons causes frameshift mutations, disrupting protein function; (b) They serve as substrates for chromosomal rearrangements, leading to duplication, deletion, inversion, and translocation; (c) Insertion into regulatory regions triggers epigenetic modifications, improperly activating or suppressing gene expression. TEs can be domesticated by the host genome, producing new regulatory signals or coding sequences: (d) Providing new enhancer sequences, altering the spatiotemporal regulation of gene expression; (e) After losing telomerase, non-LTR family retrotransposons participate in telomere maintenance; (f) By offering binding sites for CTCF protein, they help maintain genomic structure (Adapted from Colonna Romano and Fanti, 2022)

### 2.3 Influence on genome structure

TEs profoundly influence genome structure in *Triticeae* by contributing to genome size variation, chromosomal rearrangements, and the creation of gene-rich regions. The high TE content in *Triticeae* genomes, as observed in *Aegilops speltoides*, underlies extensive genome reshuffling and intraspecific diversification (Raskina, 2018). Moreover, recent research has demonstrated that TEs can lead to major chromosomal rearrangements and affect gene expression, contributing to phenotypic variation and adaptation. For example, the reactivation of the Styx element in fungal wheat pathogens triggered significant chromosomal rearrangements, illustrating the dynamic nature of TEs in shaping genome structure (Badet et al., 2023).

## 3 Methodological Approaches to Study TEs in *Triticeae*

### 3.1 Genomic sequencing and annotation

Genomic sequencing has been fundamental in advancing our understanding of transposable elements (TEs) in the *Triticeae* genome. High-throughput sequencing technologies such as Illumina, PacBio, Next Generation Sequencing (NGS); and Oxford Nanopore have enabled researchers to obtain comprehensive genomic data, facilitating the identification and annotation of TEs. For instance, NGS has been instrumental in uncovering the

sophisticated transcriptional responses governed by TEs in various organisms, highlighting their regulatory roles in health and disease (Marasca et al., 2020). Additionally, the development of specific pipelines, such as PiRATE, has facilitated the accurate annotation of TEs by combining multiple detection and classification tools, as demonstrated in the microalga *Tisochrysis lutea* (Bertheliet al., 2018). These methodologies are crucial for generating detailed TE libraries and understanding their distribution, activity, and evolutionary impact.

In the study of Wicker et al. (2018): the sequencing of the hexaploid bread wheat genome provided a detailed view of TE dynamics, revealing that TEs comprise approximately 85% of the wheat genome and play significant roles in genome organization and evolution (Wicker et al., 2018). The accurate annotation of TEs involves identifying their sequences, classifying them into families and subfamilies, and determining their insertion sites within the genome. This process is supported by databases such as Repbase and tools like Repeat Masker, which provide curated sequences of known TEs for comparison (Wells and Feschotte, 2020).

### **3.2 Bioinformatics tools and techniques**

Bioinformatics tools are crucial for analyzing the vast amounts of data generated by genomic sequencing. Programs like RepeatMasker and CENSOR are widely used for detecting and masking repetitive elements, including TEs, in genomic sequences (Zhang et al., 2021). These tools compare genomic sequences against databases of known repetitive elements to identify TEs. Additionally, bioinformatics pipelines such as TEAnnotator integrate multiple tools for a comprehensive analysis of TEs, including their identification, classification, and annotation. Comparative genomics and phylogenetic analysis are also employed to study the evolutionary dynamics of TEs. Comparative genomics allows researchers to identify conserved and lineage-specific TEs by comparing genomes of different *Triticeae* species, providing insights into TE diversity and evolutionary history (Oggenfuss et al., 2021).

### **3.3 Experimental approaches**

Experimental approaches complement genomic and bioinformatics studies by providing functional insights into TEs. Techniques such as PCR-based methods and Southern blotting are used to study the insertion patterns and copy numbers of TEs in the genome (Thiyagarajan et al., 2022). Transposon display, a variation of the PCR technique, allows for the visualization of TE insertions across different genomic backgrounds. In situ hybridization is another powerful technique used to determine the chromosomal locations of TEs. This method involves hybridizing labeled DNA probes specific to TE sequences to chromosomes, allowing for the visualization of TE distribution and abundance within the genome (Raskina, 2018). Additionally, RNA-seq is utilized to study the expression profiles of TEs under various conditions, providing insights into their regulatory roles and responses to environmental stresses (Lorrain et al., 2021).

## **4 Evolutionary Impact of Transposable Elements on *Triticeae***

TEs are crucial elements in the evolution of the *Triticeae* genome, influencing genome size, creating new regulatory elements, and contributing to adaptation. Their dynamic nature and ability to generate genetic diversity make them key players in the evolutionary processes shaping the *Triticeae* and other species.

### **4.1 Genome expansion and contraction**

Transposable elements (TEs) are significant contributors to the dynamic nature of the *Triticeae* genome, influencing both its expansion and contraction. In wheat, for instance, TEs constitute more than 80% of the genome, acting as major drivers of genome evolution (Zhang et al., 2021). The insertion and proliferation of TEs can lead to genome expansion by adding repetitive sequences. Conversely, the removal through recombination and other mechanisms or silencing of TEs can contribute to genome contraction (Oggenfuss et al., 2021). The balance between these processes is crucial for maintaining genome stability and functionality. The rapid expansion of TEs, as observed in other species like sea kraits, can lead to significant genomic changes, including insertions into introns and regulatory regions, which may alter gene expression and contribute to adaptation (Galbraith et al., 2021).

## 4.2 Regulatory element creation

TEs are instrumental in the creation of new regulatory elements within the *Triticeae* genomes. These elements can introduce novel promoters, enhancers, and other regulatory sequences that influence gene expression and regulation. In wheat, for example, TEs have been found to contribute significantly to the regulatory evolution by embedding themselves in transcription factor binding sites, thus affecting the transcriptional regulatory network (Zhang et al., 2021). This phenomenon is not unique to *Triticeae*; in humans, TEs have been shown to contribute to the evolution of regulatory networks by providing binding sites for transcription factors and creating new enhancers (Glinsky, 2018; Ali et al., 2021). The exaptation of TE sequences into functional regulatory elements is a common theme across different species, highlighting their role in driving regulatory innovations (Joly-Lopez and Bureau, 2018). This insertion can result in the modification of gene expression patterns, potentially providing adaptive advantages in response to environmental changes.

## 4.3 Contribution to adaptation

TEs significantly contribute to the adaptability of *Triticeae* species by inducing genetic variations that can be beneficial under specific environmental conditions. The activation of TEs can lead to the generation of genetic diversity, which is essential for adaptation to new or changing environments. For example, the activity of TEs in the fungal wheat pathogen *Zymoseptoria tritici* has been linked to chromosomal rearrangements and the creation of new gene regulatory networks, aiding in the pathogen's adaptation and survival (Lorrain et al., 2021). Similarly, the reactivation of TEs in wheat can result in structural changes that enhance the plant's ability to respond to biotic and abiotic stresses (Oggenfuss and Croll, 2023).

## 5 Case Studies in *Triticeae* Genome

### 5.1 Wheat (*Triticum aestivum*)

Wheat, as a primary staple crop, has undergone extensive genomic studies to understand the role of transposable elements (TEs) in its genome evolution (Figure 3). The wheat genome is hexaploid, comprising three subgenomes (A, B, and D): which adds complexity to its study. Recent research has highlighted that TEs have massively proliferated in these subgenomes, contributing to the genome's size and structural diversity. No significant TE bursts were observed after polyploidization events, indicating a steady state of TE activity (Wicker et al., 2018).

Wicker et al. (2018) revealed the variability and similarities of transposable elements (TEs) in the three subgenomes (AA, BB, DD) of wheat. Sequence alignment of the homologous regions of chromosomes 3A, 3B, and 3D demonstrated highly conserved genes but inconsistent positions of TEs, suggesting independent insertions (Figure 3a). In the hexaploid wheat genome, the distribution ratios of the 20 most abundant TE families varied across the A, B, and D subgenomes (Figure 3b): reflecting the diversity of each subgenome. K-mer analysis further revealed the proportions of repetitive sequences at different frequencies, with the D genome showing the highest proportion of 60-mer repetitive sequences, while the B genome had the lowest, indicating a possible higher abundance of repetitive sequences in the D genome that could impact its genomic structure and function (Figure 3c). The distribution of 20-mer frequencies on physical chromosomes confirmed the characteristic of fewer repetitive sequences in the B genome (Figure 3d). These findings highlight the complex insertion patterns of TEs in the wheat genome and the significant differences between subgenomes, which are crucial for understanding the structural and functional diversity of the wheat genome.

Recent advances have shed light on the dynamic nature of TEs in wheat. The presence of high-copy transposons, such as miniature inverted-repeat transposable elements (MITEs): has been shown to significantly influence the wheat genome. Miniature inverted-repeat transposable elements (MITEs) are particularly abundant in wheat, with the Stowaway superfamily accounting for about 80% of the MITE insertions. These elements are distributed across the seven homologous chromosomes of wild emmer and bread wheat, with a significant proportion located near coding genes, suggesting a potential impact on gene expression (Keidar-Friedman et al., 2018). These elements contribute to genetic diversity and evolutionary adaptations, with studies indicating that MITE insertions are associated with functional variations in wheat genes (Ubi et al., 2022). Moreover, TEs play a crucial role in the

wheat transcriptional regulatory network, where lineage-specific TEs have been shown to drive regulatory innovations, particularly in response to environmental stressors (Zhang et al., 2021).

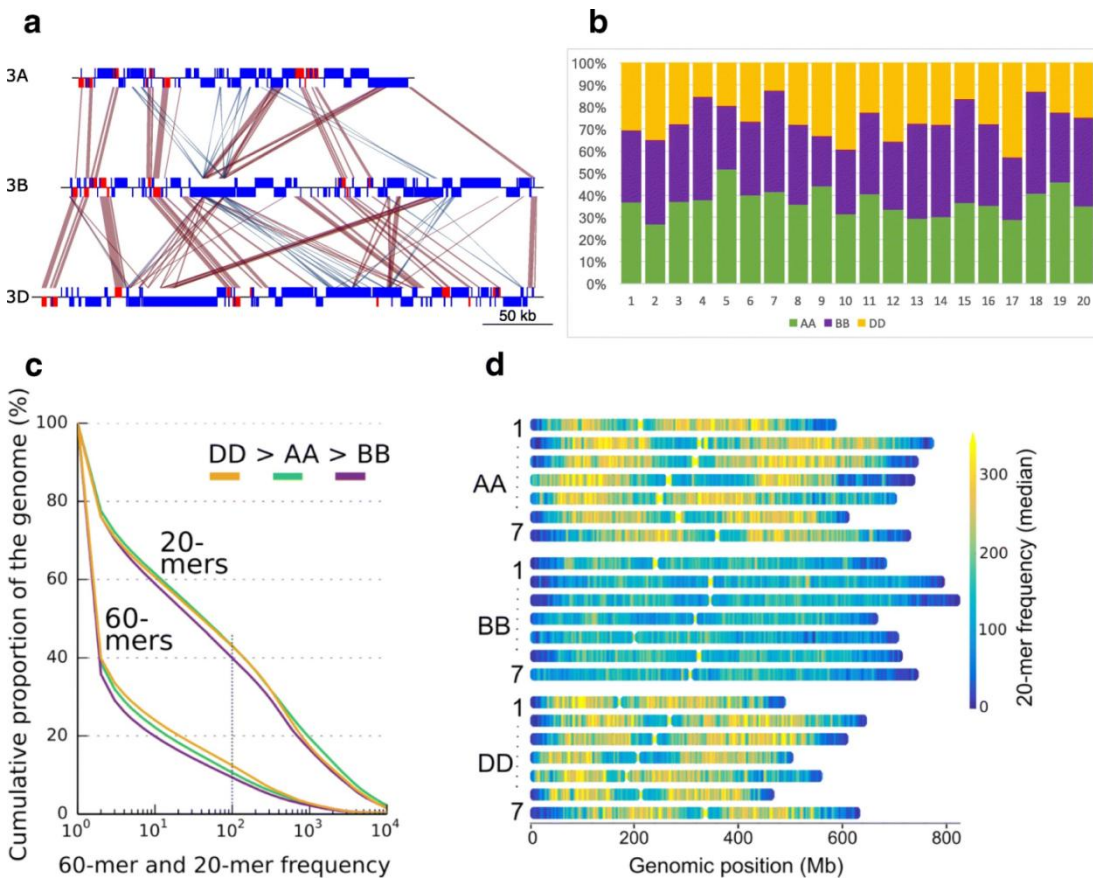


Figure 3 Variability and similarity of the three subgenomic repeat compositions in wheat (Adapted from Wicker et al., 2018)

Image caption: (a) shows the sequence alignment of approximately 300 kb homologous regions on chromosomes 3A, 3B, and 3D, where red and blue areas indicate regions with high sequence homology, demonstrating the high conservation of genes and the collinearity among the A-B-D genomes, but TEs are absent at the homologous positions.; (b) displays the proportions of the 20 most abundant TE families in the A, B, and D genomes of the hexaploid wheat genome; (c) presents the proportion of repetitive sequences defined by k-mers at different frequencies, showing the D genome has the highest proportion of 60-mer repeats, while the B genome has the lowest; (d) illustrates the distribution of 20-mer frequencies across the physical chromosomes, with the B genome having the lowest proportion of repeats (Adapted from Wicker et al., 2018)

## 5.2 Barley (*Hordeum vulgare*)

Barley, another vital cereal crop within the *Triticeae* tribe, shares a close evolutionary relationship with wheat and other *Triticeae* species, has a genome that is heavily influenced by TEs, similar to wheat. The study of TEs in barley has provided insights into the evolutionary dynamics of these elements within the *Triticeae* tribe. For instance, the presence of specific TE families, such as Sabrina and Angela-A, has been observed in both barley and its diploid relatives, indicating their role in genome evolution and speciation. TEs in barley account for a substantial portion of the genome, predominantly consisting of LTR retrotransposons. The BARE1 element, a type of LTR retrotransposon, is highly prevalent in the barley genome and contributes significantly to its genetic composition (Middleton et al., 2013).

Research has shown that the dynamics of TE proliferation in barley are linked to environmental stress and adaptation processes. The adaptive response facilitated by TEs is crucial for barley's survival and evolution under varying environmental conditions. This adaptive capacity is partly due to the ability of TEs to generate genetic variation, which is beneficial for coping with environmental changes (Middleton et al., 2013). The presence of lineage-specific TEs, such as the novel non-autonomous DNA transposon identified in the DRF1 gene, suggests

that TEs contribute to the unique genomic features of barley and other *Triticeae* species (Thiyagarajan et al., 2022). Comparative genomic analyses between barley and other *Triticeae* genomes have provided valuable insights into the evolutionary mechanisms driving genome diversification within this group.

### 5.3 Rye (*Secale cereale*)

Rye, known for its resilience and ability to grow in poor soil conditions, also exhibits a genome significantly shaped by TEs. Comparative studies have highlighted that TEs in rye contribute to its large genome size and genetic diversity. The genome of rye contains a substantial proportion of Class I retrotransposons, which play a key role in shaping its genomic structure and evolutionary trajectory (Markova and Mason-Gamer, 2015).

Comparative studies of TE abundance in rye and its relatives have revealed significant differences in the distribution and composition of these elements. For example, the TE family Sabrina is highly abundant in rye, similar to other *Triticeae* species, suggesting a conserved role in genome evolution (Divashuk et al., 2019). The study of TEs in rye has also provided insights into the mechanisms of polyploidization and speciation within the *Triticeae* tribe (Figure 4). The relationships between the genomes of rye and other *Triticeae* species, based on TE abundance, highlight the role of these elements in the evolutionary history of the tribe.

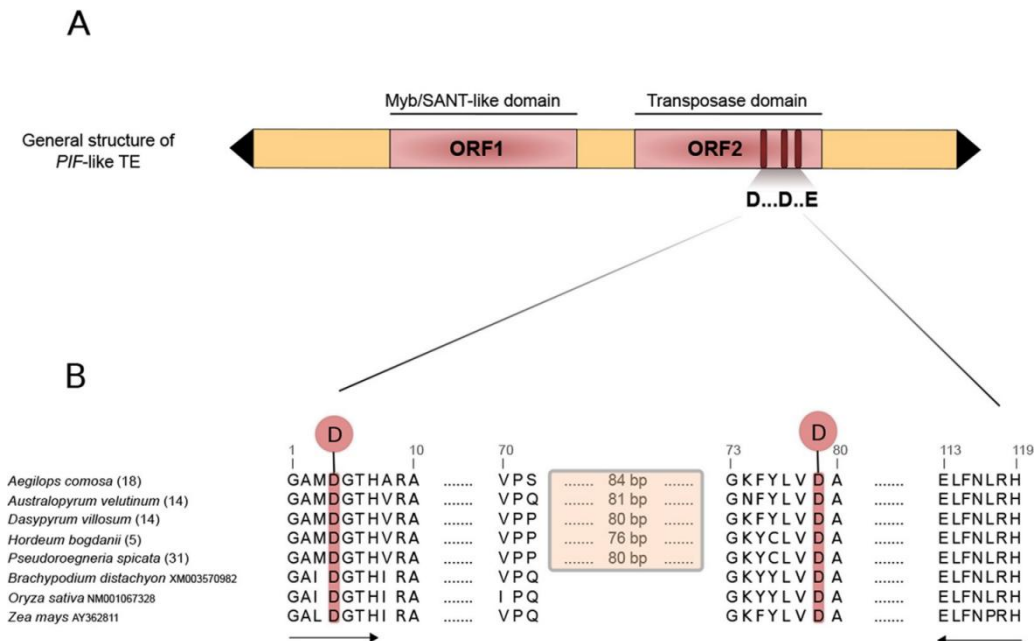


Figure 4 Overall structure of PIF-like transposons and their conserved transposase domains (Adapted from Markova and Mason-Gamer, 2015)

Image caption: (A) PIF-like transposons contain two open reading frames (ORFs): where ORF2 includes a "DDE" motif composed of three conserved amino acids, essential for the function of the transposase, Black triangles represent terminal inverted repeat sequences (TIRs): and pink rectangles indicate the open reading frames; (B) Comparison of the conserved transposase domains and their corresponding "DD" parts from *Brachypodium*, *Oryza*, *Zea*, and five representative *Triticeae* species. Shaded rectangles represent intron regions, bold arrows indicate the location of ORF2 amplification primers; numbers denote specific clone sequences within each cereal species (Adapted from Markova and Mason-Gamer, 2015)

Markova and Mason-Gamer (2015) found that the ORF2 of PIF-like transposons contains a critical "DDE" motif (Figure 4A). After comparing conserved transposase domain sequences across multiple species, the "DD" part showed high conservation, but there were variations in intron length (Figure 4B). This indicates the conservation of core functional areas and the variability of non-coding regions in PIF-like transposons, suggesting that these transposons have similar functions across different species while also adapting to various genomic environments. Rye has been particularly useful in studying horizontal transfer of TEs among *Triticeae* species. Evidence indicates that certain TE families have been transferred horizontally between rye and other *Triticeae* members,



suggesting a complex evolutionary history involving both vertical inheritance and horizontal gene transfer (Markova and Mason-Gamer, 2015). This highlights the role of TEs not only in genome expansion but also in facilitating genetic exchange and diversity within the *Triticeae* tribe, making rye a key species for understanding TE dynamics and their impact on genome evolution.

## **6 Challenges and Future Directions**

### **6.1 Current limitations in TE research**

Research on transposable elements (TEs) in the *Triticeae* genome faces several significant challenges. One of the primary limitations is the complexity and size of the *Triticeae* genomes, which are often large and polyploid, making it difficult to accurately map and characterize TEs. Additionally, the high sequence similarity among TE families complicates the identification and classification of individual elements (Quesneville, 2020; Wells and Feschotte, 2020). Another challenge is the limited availability of comprehensive and high-quality genome assemblies for many *Triticeae* species, which hinders the ability to perform detailed comparative analyses (Ibrahim et al., 2021). Furthermore, the dynamic nature of TEs, including their ability to transpose and generate new insertions, adds another layer of complexity to studying their evolutionary impact (Lanciano and Cristofari, 2020; Bhat et al., 2022).

### **6.2 Emerging technologies and methods**

Despite these challenges, several emerging technologies and methods hold promise for advancing TE research in the *Triticeae* genome. High-throughput sequencing technologies, such as long-read sequencing, are improving the resolution and accuracy of genome assemblies, enabling better identification and characterization of TEs (Ibrahim et al., 2021). Advances in bioinformatics tools and computational methods are enhancing the ability to analyze TE sequences and their regulatory impacts on gene expression (Lanciano and Cristofari, 2020; Ali et al., 2021). Techniques such as CRISPR/Cas9 genome editing are also being explored to study the functional roles of TEs by enabling targeted manipulation of TE sequences (Drongitis et al., 2019). Moreover, the integration of multi-omics approaches, including transcriptomics and epigenomics, is providing deeper insights into the regulatory networks involving TEs (Ali et al., 2021; Amorim et al., 2021).

### **6.3 Potential applications in crop improvement**

TEs can drive genetic diversity, which is crucial for the development of new traits and adaptation to changing environments. For example, TEs have been linked to the regulation of genes involved in stress responses, suggesting their potential use in breeding programs aimed at enhancing crop resilience (Zhang et al., 2021).

Additionally, TEs can be harnessed as molecular markers in marker-assisted selection, facilitating the identification of desirable traits and accelerating the breeding process. The use of TEs as markers has been demonstrated in various studies, highlighting their utility in improving crop yield, disease resistance, and quality (Ventimiglia et al., 2023).

Furthermore, biotechnological approaches that manipulate TEs could be employed to introduce new genetic variations into *Triticeae* genomes. Techniques such as transposon tagging and targeted TE activation may enable the creation of novel phenotypes, providing a powerful tool for crop genetic enhancement and adaptation (Thiyagarajan et al., 2022).

While current limitations pose challenges to TE research, emerging technologies and methodologies offer promising solutions. The insights gained from studying TEs not only advance our understanding of genome evolution but also pave the way for innovative applications in crop improvement, addressing the urgent need for sustainable agricultural practices in the face of global challenges.

## **7 Concluding Remarks**

The core findings of recent research underscore the significant role that transposable elements (TEs) occupy in the wheat genome. Particularly notable are the Class I retrotransposons, especially the long terminal repeat (LTR)

retrotransposons, which form a crucial part of the genome's repetitive DNA sequences. These genetic elements not only profoundly impact the expansion of the genome size but also play an indispensable role in the regulation of gene expression and the formation of new regulatory networks. Furthermore, TEs significantly drive the creation of genetic diversity and the flexibility of the genome, providing species with strong support to adapt to environmental changes and evolve. These discoveries not only enrich our understanding of the wheat genome structure but also offer new insights and directions for future agricultural genetic improvements and breeding practices.

In-depth and sustained research on transposable elements (TEs) is crucial, as understanding how TEs impact the structure and function of genomes will provide valuable insights into the fundamental processes of genomic evolution and adaptation. This knowledge is key for improving crop varieties through methods such as genetic engineering and selective breeding. TEs not only serve to create genetic diversity but also introduce traits beneficial for agricultural production, offering new possibilities for crop improvement. With the rapid development of sequencing technologies and bioinformatics tools in recent years, we now have unprecedented opportunities to explore the diversity and activity of TEs in cereal genomes. These advanced tools and techniques enable us to annotate TEs more precisely and conduct in-depth analysis of their functions. Such achievements lay a solid foundation for further exploration of the roles and impacts of TEs in areas like genomic regulation and evolution, potentially paving new paths for future agricultural science research.

Transposable elements are dynamic and influential components of the *Triticeae* genome, driving genetic innovation and facilitating adaptation. The extensive presence and activity of TEs in *Triticeae* species, particularly in wheat, underscore their critical role in shaping genomic architecture and evolutionary trajectories. Continued research into TEs will not only enhance our understanding of genome evolution but also open up new avenues for crop improvement and adaptation strategies. As we advance our knowledge and tools, the potential to harness the power of TEs for agricultural and biotechnological applications becomes increasingly tangible.

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### **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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