

## Impact of Transposons and Structural Variations on the Adaptation and Diversification of the *Oryza* Species

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**Abstract** Transposons, as mobile genetic elements in the genome, play a crucial role in genetic innovation and genome reconstruction of rice. Structural variation (including deletion, duplication, inversion, and translocation) greatly alters the genome structure and function, thereby affecting the phenotypic characteristics of rice and its ability to adapt to the environment. Both of them have important contributions to rice seed breeding. In this study, we reviewed the effects of transposon and structural variation on the adaptability and diversity of *Oryza* species, and discussed in detail how these genetic variants promote the adaptability and biodiversity of *Oryza* species by altering gene expression, regulating physiological and biochemical pathways, and adapting to environmental stress. Technical challenges and advances in studying the role of transposons and structural variation in rice were also discussed, and potential applications of these genetic mechanisms in future rice breeding and ecological conservation were pointed out. Through a systematic analysis of the existing literature, this study highlights the importance of understanding the role of these genetic elements in the adaptation and diversification of rice, and provides references for future research directions.

**Keywords** *Oryza* species; Transposon; Structural variation; Genetic diversity; Adaptability

### 1 Introduction

Rice (*Oryza sativa*) is one of the most important cereal crops globally, serving as a staple food for more than half of the world's population. Its genetic diversity and adaptability to various environments have been subjects of extensive research, given its significance for food security and agriculture. Within the genomic landscape of rice and other organisms, transposable elements (TEs) and structural variations play a pivotal role in shaping genetic diversity and facilitating adaptation and speciation.

Transposable elements, often referred to as “jumping genes”, are DNA sequences capable of changing their position within the genome. This mobility can lead to a wide range of genomic alterations, including insertions, deletions, and rearrangements, collectively known as structural variations. These genomic changes can have profound effects on gene expression, phenotypic diversity, and the evolutionary trajectory of species. For instance, the recent activity of retrovirus-like retrotransposons in flycatcher species suggests a rich source of structural variation that may contribute to phenotypic consequences and diversification in birds (Suh et al., 2018). Similarly, in the rice blast fungus *Magnaporthe Oryzae*, dynamic transposition of TEs has been shown to significantly impact genome stability, gene expression, and virulence, driving rapid evolution and population divergence (Lin et al., 2023).

This study investigated the effects of transposon and structural variation on adaptation and diversity of rice species, aimed at synthesizing knowledge of how these genetic elements contribute to the evolutionary process of rice. This study will cover the mechanisms by which TEs induce genomic changes, their effects on gene expression and adaptation, and broader implications for the evolution of rice species. Through this comprehensive analysis, this study seeks to gain insight into the genomic basis of rice adaptation and the potential to harness the power of TE and structural variation for breeding and conservation strategies.

## 2 Transposons in the Rice Genome

### 2.1 Classification and characteristics of transposons in *Oryza*

Transposable elements (TEs) are ubiquitous genomic entities that can insert themselves into various locations within a host genome (such as *Oryza* rice (Figure 1), potentially influencing gene expression and genomic stability. In the genus *Oryza*, a novel LTR retrotransposon named RTPOSON has been identified, which belongs to the Ty1-copia group of retrotransposons. RTPOSON is characterized by its long terminal repeats (LTRs) and the presence of open reading frames encoding for proteins such as UBN2\_2 and zinc knuckle. The RTPOSON elements have been found to be abundant in *Oryza* genomes, with more than 700 identified instances. These elements have proliferated within the last 8 million years, with notable bursts of activity within the last 1.5~5.0 million years, suggesting their significant role in the recent genomic evolution of rice species (Hsu et al., 2016).

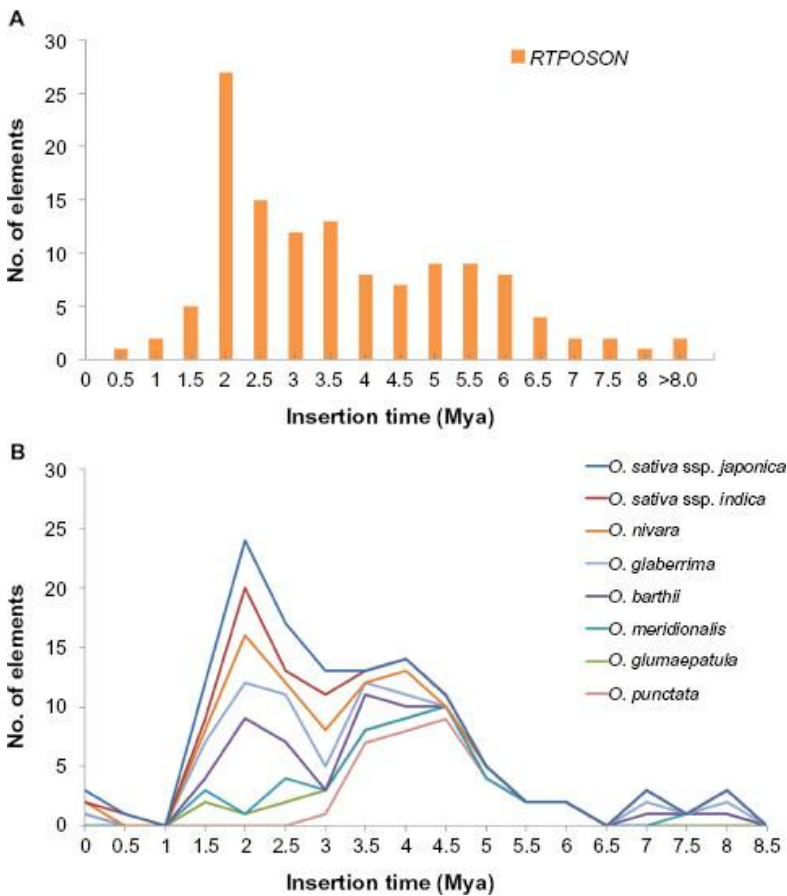


Figure 1 The estimated insertion times of RTPOSON elements in *Oryza* rice (Adopted from Hsu et al., 2016)

Image caption: (A) The 127 intact elements from *Oryza* were used to estimate the insertion times of RTPOSON; Kimura distances were converted to millions of years ago using the substitution rate of  $1.3 \times 10^{-8}$  (B) Insertion times of intact RTPOSON from eight *Oryza* species (Adopted from Hsu et al., 2016)

### 2.2 A historical review of the discovery and study of transposons in rice

The study of transposons in rice has revealed their profound impact on genome evolution and diversification. While the reference provided does not directly discuss the historical discovery of transposons in rice, it is known that the research on transposons has evolved from merely identifying these elements to understanding their role in shaping the genome. The discovery of RTPOSONs and their classification into subgroups based on structural diversity exemplifies the ongoing efforts to characterize the transposon landscape in rice. The identification of orthologous insertions of RTPOSONs in different rice subspecies indicates that transposons have been an integral part of the rice genome's history, contributing to the divergence of indica and japonica subspecies (Hsu et al., 2016).

### 2.3 The role of transposons in genome evolution and functional genomics

Transposons play a critical role in genome evolution by inducing structural variations that can lead to gene disruptions, exon shuffling, and alterations in gene expression. In the context of functional genomics, RTPOSON elements have been shown to integrate preferentially in genic regions, which might have implications for genic innovation and genetic variation in rice. The presence of intact RTPOSONs and their homologous fragments in these regions suggests that they may contribute to the functional diversification of the rice genome. Furthermore, the proliferation of RTPOSONs after the divergence of indica and japonica rice subspecies points to their potential role in the adaptive evolution of these groups (Hsu et al., 2016).

The impact of transposons on genome evolution is not limited to plants but is also observed in other organisms. For instance, in the rice blast fungus *Magnaporthe Oryzae*, transposable elements have been shown to significantly influence genome stability, gene expression, and virulence. The dynamic transposition of TEs in *M. Oryzae* contributes to the rapid evolution and diversification of this pathogen, with TE insertions being highly concordant with population divergence on different rice cultivars (Figure 2) (Lin et al., 2023). This highlights the broader significance of transposons as agents of rapid adaptation and diversification across various species.

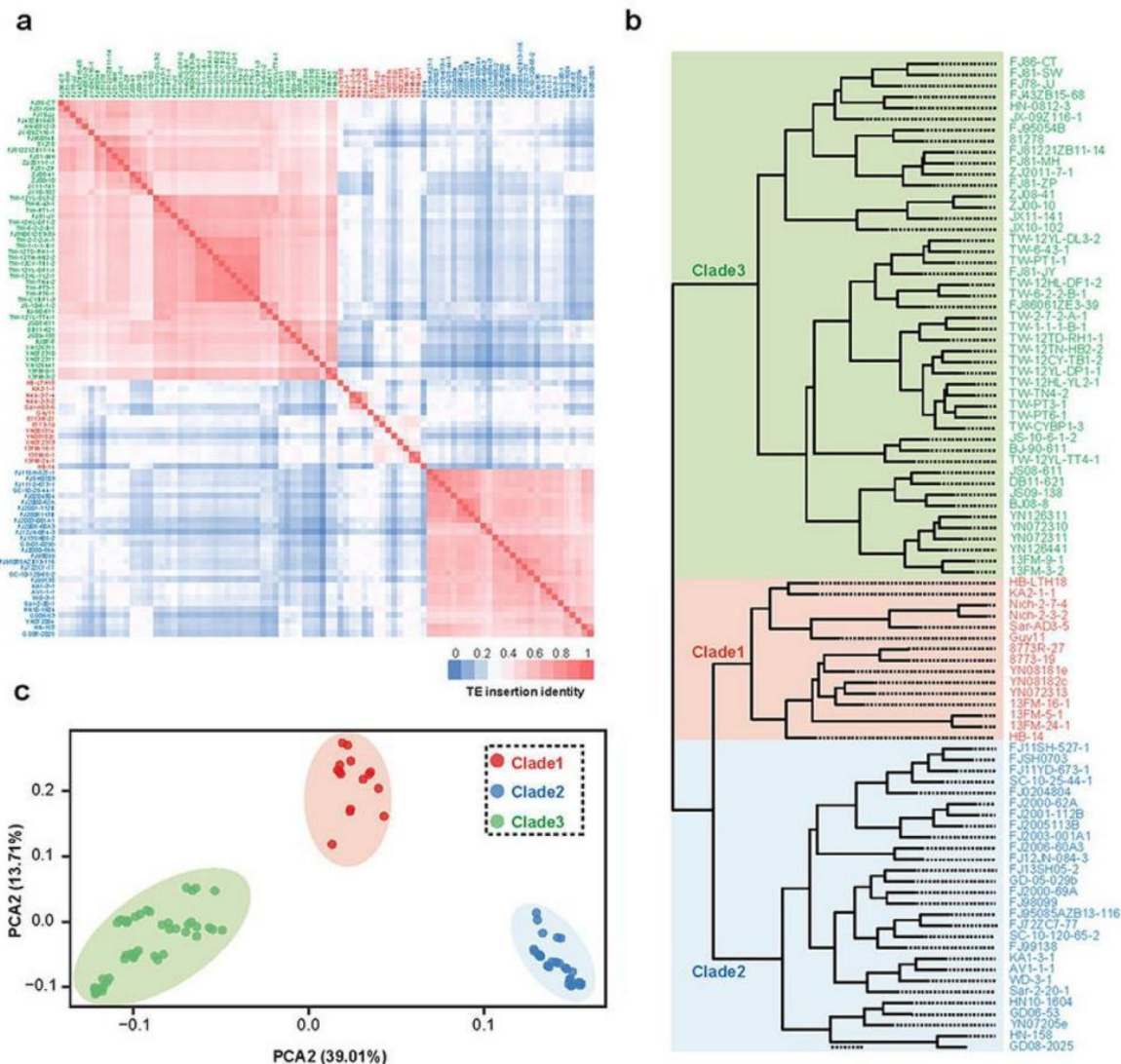


Figure 2 TE insertion was associated with the divergence of *M. Oryzae* rice population (Adopted from Lin et al., 2023)  
 Image caption: a) The heatmap showing the identity of TE insertion site between each two isolates; b) The hierarchical tree built by using the TE insertion sites of *M. Oryzae* population; Three distinct clades were marked in red, blue and green colors respectively; c) Principal component analysis using the TE insertion sites (Adopted from Lin et al., 2023)

### 3 Structural Variation of *Oryza* Species

#### 3.1 Definition and type of structural variation

Structural variation (SV) in the context of genomic research refers to large-scale alterations in the genome that can encompass a variety of changes such as insertions, deletions, copy number variations, inversions, and translocations. These variations can range from a few base pairs to large segments of the genome, and they contribute significantly to the genetic diversity and evolution of species. In rice (*Oryza* species), structural variations are particularly influenced by transposable elements (TEs), which are sequences of DNA that can change their position within the genome. TEs can be classified into two major classes: Class I retrotransposons, which transpose through an RNA intermediate, and Class II DNA transposons, which move directly as DNA (Zuccolo et al., 2007; Wicker et al., 2016).

#### 3.2 Methods for detection and identification of structural variation in *Oryza* species genome

The detection and identification of structural variations within the *Oryza* species genome are achieved through various genomic techniques. Advances in sequencing technologies have enabled the construction of genomic libraries from representative *Oryza* species, allowing for a comprehensive study of repetitive element composition and distribution (Zuccolo et al., 2007). Comparative genomic approaches have been utilized to identify transposon insertion polymorphisms (TIPs) between different rice cultivars, providing insights into intraspecific variation (Huang et al., 2008). These methods are crucial for understanding the dynamics of genome size variation and the role of transposons in shaping the rice genome.

#### 3.3 Example of structural variations that contribute to phenotypic traits associated with adaptation

Transposable elements have been shown to play a significant role in the phenotypic diversity and environmental adaptation of rice. For instance, TE-induced epigenetic alterations and the modification of gene expression contribute to phenotypic variation and adaptation to geography or stress (Song and Cao, 2017). The proliferation of Long Terminal Repeat (LTR) retrotransposons in various *Oryza* species has led to genome size variation, which is a key factor in the adaptation and diversification of the genus (Piégu et al., 2006; Zuccolo et al., 2007). Moreover, DNA transposon activity has been associated with increased mutation rates in genes, potentially leading to adaptive phenotypic traits (Wicker et al., 2016). These structural variations, driven by transposons, are a testament to the dynamic nature of the rice genome and its ability to adapt to different environmental conditions.

### 4 Effects of Transposon and Structural Variation on Adaptation

#### 4.1 Mechanisms of transposon and structural variation affecting adaptive traits

Transposable elements (TEs) have been identified as significant contributors to phenotypic variation and adaptation. In *Capsella rubella*, TEs are enriched in gene promoter regions and are associated with changes in gene expression, particularly affecting flowering-time variation, a trait correlated with fitness and adaptation (Niu et al., 2019). Similarly, in *Arabidopsis thaliana*, DNA methylation variation, particularly in transposons, is influenced by temperature and associated with genetic variants, suggesting a genetic basis for epigenome modulation as a response to environmental changes (Dubin et al., 2015). The study of cis-acting regulatory modifications in the *Arabidopsis* genus has revealed that polygenic adaptation can reshape distinct molecular functions, such as metal transport and homeostasis in *Arabidopsis halleri* and transcriptional response to cold stress in *Arabidopsis lyrata* (He et al., 2016).

#### 4.2 Case studies in which transposon or structural variation enhances tolerance or adaptability to environmental change

The role of TEs in environmental adaptability is exemplified by the ONSEN retrotransposon in *Arabidopsis*, which, when activated by heat stress, can induce an ABA-insensitive phenotype, suggesting a mechanism for stress tolerance (Ito et al., 2016). In *Drosophila melanogaster*, the insertion of an Accord transposable element upstream of the *Cyp6g1* gene has been associated with resistance to DDT, with the most resistant allele contributing significantly to the phenotypic variation in resistance (Schmidt et al., 2010). Additionally, the

RWG LTR retrotransposon family in the genus *Oryza* has been shown to cause genome size expansion and organization changes, which may have implications for adaptation (Ammiraju et al., 2007).

#### **4.3 The role of mobile genetic elements in creating genetic novelty and adaptive potential**

Mobile genetic elements, such as TEs, are a source of genetic novelty that can drive genome evolution. In *Caenorhabditis elegans*, the distribution and abundance of TEs across wild strains suggest that TEs contribute to phenotypic variation and may be regulated by piwi-interacting RNAs and chromatin factors (Laricchia et al., 2017). The genetic variation at the *Cyp6g1* locus in *Drosophila melanogaster* demonstrates how multiple adaptive steps at a single locus can occur in rapid succession, contributing to the organism's ability to adapt to insecticides (Schmidt et al., 2010). In songbirds, the abundance of recent activity of retrovirus-like retrotransposons implies a rich source of structural variation that may have phenotypic consequences for the diversification of these species (Suh et al., 2018).

### **5 The Role of Transposons and Structural Variation in Rice Variety Diversification**

#### **5.1 Contributions of transposons and structural variation to genetic diversity and speciation in rice**

Transposable elements (TEs) have been recognized as significant contributors to genomic novelty and diversity in plants, including rice (*Oryza sativa*). TEs, once considered 'selfish DNA', are now understood to play a role in phenotypic variation and adaptation to environmental conditions through epigenetic regulation and gene expression modification (Song and Cao, 2017). The differentiation between Indica and Japonica rice, two major subspecies, has been partly attributed to the activity of TEs, particularly the insertion events of Ty3/Gypsy elements, which have been shown to cause genome structural variations (Wu et al., 2022). Moreover, TEs have been implicated in the speciation process by generating reproductive isolation through hybrid defects and altering regulatory networks (Qin et al., 2021).

#### **5.2 Effects of gene flow and reproductive isolation between different *Oryza* species**

The role of TEs in speciation is further emphasized by their association with hybrid defects that can lead to reproductive isolation between emerging species (Qin et al., 2021). The genomic diversity within rice species, as revealed by the presence of transposon insertion polymorphisms (TIPs), suggests that TEs have been a significant source of genetic variation, potentially influencing gene flow and reproductive isolation (Chen et al., 2020). The burst of a transposable element in a rice population has been shown to generate genomic variations that could affect selection and adaptation, further contributing to the diversification of rice varieties (Nakazaki et al., 2003).

#### **5.3 Insights from comparative genomic studies of different species and subspecies of *Oryza* species**

Comparative genomic studies have provided insights into the impact of structural variations (SVs) and gene copy number variations (gCNVs) on rice evolution and domestication. A pan-genome analysis of diverse rice accessions revealed hidden genomic variations, including SVs and gCNVs, which have shaped rice environmental adaptation and domestication (Huang et al., 2008). The genomic variation among Asian cultivated rice genomes also underscores the importance of TEs in creating within- and between-population variation, with novel genes and presence-absence variations contributing to the complexity of rice genomes (Wang et al., 2018). Additionally, the evolution and diversification of centromeres among closely related rice species have been influenced by transposons, with recent insertions leading to rapid divergence (Gao et al., 2015).

### **6 Challenges and Future Directions**

#### **6.1 Technical and methodological challenges in studying transposon and structural changes**

The study of transposons and structural variations presents several technical and methodological challenges. Transposable elements (TEs) are ubiquitous genomic components that can insert into various locations within the genome, affecting gene expression, DNA methylation, and genomic stability (Suh et al., 2018). The identification and characterization of these elements, particularly retrovirus-like LTR retrotransposons, require comprehensive repeat annotation and whole-genome resequencing (Suh et al., 2018). However, the density and

heterogeneity of these elements, as seen in the flycatcher species, can complicate analyses due to the presence of polymorphic TE insertions that vary within and among species (Suh et al., 2018). In the genus *Oryza*, the variation in genome size, which is partly attributed to the proliferation of TEs, further complicates the study as different species exhibit different extents of TE proliferation (Zuccolo et al., 2007). The dynamics of retrotransposition-driven genomic expansions, as observed in *Oryza australiensis*, are not fully understood, and the rapid increase in genome size poses additional challenges for genomic analysis (Piégu et al., 2006).

### 6.2 New genomic technologies open up future research opportunities

Advancements in genomic technologies have the potential to overcome some of the challenges faced in studying TEs and structural variations. High-throughput sequencing and improved bioinformatics tools can facilitate the detection and quantification of TEs across various *Oryza* species. These technologies can also aid in understanding the phylogenetic relationships among species based on TE distribution and abundance (Zuccolo et al., 2007). Furthermore, the study of DNA transposons in organisms like rotifers has revealed diverse superfamilies and structural organizations, which can be explored in greater depth with new genomic tools (Arkhipova and Meselson, 2005). These advancements will enable researchers to dissect the complex interactions between TEs and their host genomes, leading to a better understanding of their role in genome size variation and species diversification.

### 6.3 Potential application of transposon and structural variation knowledge in breeding programs

The knowledge gained from studying transposons and structural variations has significant implications for breeding programs, particularly in crop species like rice. TEs have been shown to contribute to phenotypic diversity and environmental adaptation in rice by regulating gene expression and creating new genes. Understanding the epigenetic regulation mediated by TEs can provide insights into how phenotypic variation arises and how it can be harnessed for crop improvement (Song and Cao, 2017). By identifying TEs associated with desirable traits, breeders can potentially develop new rice varieties that are better adapted to changing environmental conditions or that have improved agronomic characteristics. The integration of TE knowledge into breeding strategies represents a promising avenue for enhancing the adaptability and diversity of the *Oryza* species.

## 7 Concluding Remarks

The genus *Oryza*, which includes the world's most important food crop-rice (*Oryza sativa*), exhibits a remarkable diversity in genome size across its species, ranging from 357 Mbp to 1 283 Mbp. This variation is largely attributed to the activity of transposable elements (TEs), particularly Long Terminal Repeat retrotransposons (LTRs), which have proliferated to varying extents in different species. The distribution and abundance of these elements are not random but are a result of their significant role in shaping the genomes of the *Oryza* species. For instance, two families of *Ty3-gypsy* elements, *RIRE2* and *Atlantys*, have been identified as major contributors to the genome size variations within the genus.

In addition to genome size variation, TEs have been implicated in the generation of genomic novelty and diversity, which are essential for phenotypic variation and environmental adaptation in rice. DNA transposons, a class of TEs, are scattered throughout the rice genome and are known to modulate gene expression and create new genes, contributing to the phenotypic diversity and adaptation to different geographical locations and stress conditions. This highlights the dual role of TEs as both genomic parasites and sources of genomic diversity.

The understanding of TEs and their impact on genome structure and function has profound implications for future research and practical applications. There is a need for comprehensive studies to elucidate the mechanisms by which TEs contribute to gene regulation and the creation of new genes, as well as their overall impact on the adaptability and resilience of rice species. Such knowledge could pave the way for the development of rice varieties with enhanced adaptability to changing environmental conditions and stress factors, which is crucial for sustainable agriculture and food security.

Moreover, the conservation of genetic diversity within the *Oryza* genus is of paramount importance, not only for the preservation of natural biodiversity but also for the potential it holds for breeding programs. Understanding the role of TEs in generating this diversity can inform conservation strategies and ensure the maintenance of a rich genetic pool, which is essential for the continued evolution and adaptation of rice species in the face of global climate change. TEs and structural variations play a pivotal role in the adaptation and diversification of rice species. Future research should focus on unraveling the complex interactions between TEs and the host genome, which will undoubtedly enhance our ability to harness this knowledge for the improvement of rice cultivation and the conservation of its genetic diversity.

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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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