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Geographical Migration and Domestication of *Oryza* Species: Tracing the Roots

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Abstract This study examines the geographical migration and domestication of *Oryza* species, focusing on *Oryza sativa* (Asian rice) and *Oryza glaberrima* (African rice). By synthesizing genetic and archaeological evidence, it traces the evolutionary paths and dispersal of these crops from wild ancestors to cultivated forms. This study highlights the complex selection processes tailored to diverse environments, which have been crucial in the adaptation and spread of rice cultivation. Studying rice's migration and domestication is essential for understanding agricultural history and genetic diversity, aiding breeding programs aimed at enhancing yield, disease resistance, and adaptability. This study also discusses the impact of independent domestication events across various regions on the genetic diversity of modern rice varieties. This study provides insights into the domestication events that have shaped one of the world's staple crops, contributing to global food security initiatives amidst changing climatic conditions.

Keywords Rice origins; Geographical migration; Domestication; *Oryza sativa*; *Oryza glaberrima*

1 Introduction

The genus *Oryza*, which includes both wild and cultivated rice species, is of paramount importance to global agriculture. Rice (*Oryza sativa* L.) is a staple food for more than half of the world's population, making it a critical crop for food security (Londo et al., 2006). The genus comprises two primary cultivated species: *Oryza sativa*, commonly known as Asian rice, and *Oryza glaberrima*, known as African rice. While *Oryza sativa* has been extensively studied and is well understood, the origins and domestication processes of *Oryza glaberrima* remain subjects of ongoing research and debate (Wang et al., 2014; Veltman et al., 2019). The domestication of these species from their wild progenitors, such as *Oryza rufipogon* for Asian rice and *Oryza barthii* for African rice, involved complex processes of selection and adaptation to diverse environments (Nabholz et al., 2014; Chen et al., 2019; Zheng et al., 2021).

Understanding the migration and domestication of *Oryza* species is crucial for several reasons. Firstly, it provides insights into the evolutionary history and genetic diversity of these crops, which is essential for breeding programs aimed at improving yield, disease resistance, and environmental adaptability (Londo et al., 2006; Chen et al., 2019). Secondly, studying the geographical migration patterns helps in tracing the spread of rice cultivation and the cultural exchanges that accompanied it, thereby enriching our knowledge of human agricultural history (Cívan̆ et al., 2015). Additionally, recognizing the independent domestication events and the genetic adaptations that occurred in different regions can inform strategies to mitigate the impacts of climate change on rice production (Wang et al., 2014; Zheng et al., 2021). For instance, the unique adaptations of African rice to harsh environments such as drought can be leveraged to develop more resilient rice varieties (Nabholz et al., 2014).

This study aims to achieve the following objectives: to synthesize current knowledge on the origins and domestication processes of *Oryza* species, with a focus on both Asian and African rice; to examine the genetic and archaeological evidence supporting various hypotheses of rice domestication and migration, including centric, non-centric, and polycentric models; to explore the genetic adaptations that have enabled rice to thrive in diverse geographical regions and environmental conditions; to highlight the implications of these findings for rice breeding and agricultural sustainability in the face of global challenges such as climate change and food security By addressing these objectives, this study will provide a comprehensive understanding of the geographical migration and domestication of *Oryza* species, tracing the roots of one of the world’s most important crops.

2 Origins and Early Evolution of *Oryza* Species

2.1 Phylogenetic overview

The genus *Oryza*, which includes both domesticated and wild rice species, has a complex phylogenetic history. Molecular phylogenetic studies using DNA sequences from chloroplast, mitochondrial, and nuclear genomes have shown that the rice tribe (*Oryzeae*) is monophyletic and can be divided into two main clades corresponding to traditionally recognized subtribes. The divergence of *Oryza* and *Leersia* from other genera in the *Oryzeae* tribe is estimated to have occurred around 20 million years ago (mya), with *Oryza* and *Leersia* themselves diverging approximately 14 mya (Guo and Ge, 2005). This long evolutionary history has been marked by significant genetic conservation, turnover, and innovation across the genus, as evidenced by the study of 13 reference genomes spanning the *Oryza* species tree (Figure 1) (Stein et al., 2018).

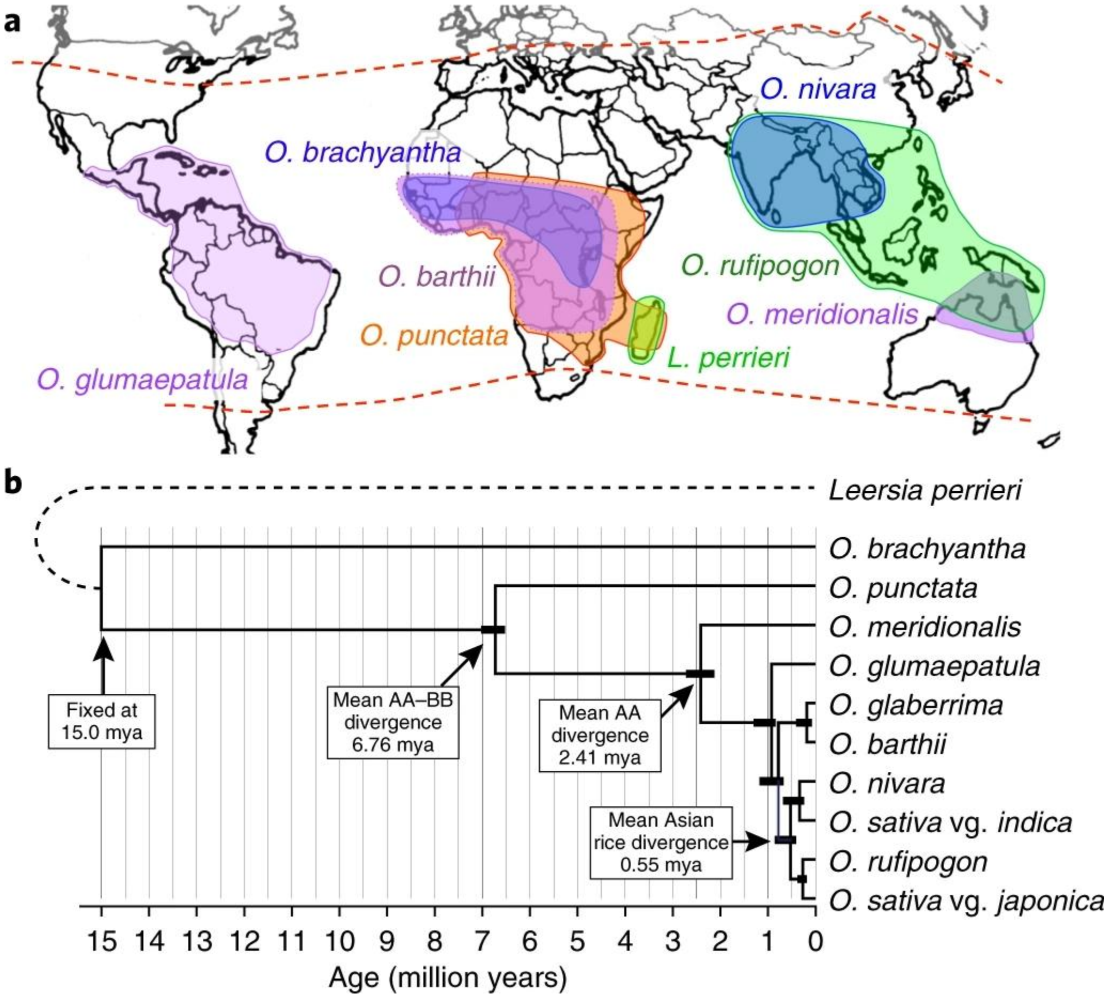

Figure 1 Geographic distribution and phylogenetic reconstruction of wild species of *Oryza* and *Leersia* (Adopted from Stein et al., 2018)

Image caption: a, Geographic ranges of wild *Oryza* species and the outgroup species *L. perrieri* sequenced in this study. Dashed red lines show the limits of rice cultivation. Mapped ranges are adapted from IRRI’s Knowledge Bank (see URLs). b: Most frequently estimated species phylogeny in supermatrix and MP-EST analyses of each chromosome (inferred in 10 of 12 chromosomes and 11 of 12 chromosomes, respectively). Bootstrap proportions were obtained from 400 supermatrix bootstrap replicates, and MP-EST support values were obtained as described in the Methods. All clades were supported by both methods at 100%, except as indicated. Divergence times within the *Oryza* genus were estimated by PATHd8, assuming an age of 15 million years for the *Oryza* crown group. Bars on nodes represent the range of PATHd8 age estimates across all 12 chromosomes. Mya, million years ago (Adopted from Stein et al., 2018)

2.2 Fossil evidence and early records

Fossil evidence and early records of rice cultivation provide insights into the ancient origins of *Oryza* species. The cultivation of African rice (*Oryza glaberrima*) dates back more than 3 000 years, with evidence suggesting that it was domesticated in a single region along the Niger River (Wang et al., 2014). In contrast, the domestication of Asian rice (*Oryza sativa*) has been traced back to China, where it is believed to have originated from the wild species *Oryza rufipogon* (Huang et al., 2012; Wei et al., 2012). The genetic diversity center of *O. rufipogon* is located in Southern China, particularly around the Pearl River basin, which is also considered the domestication center of *O. sativa* (Huang et al., 2012; Wei et al., 2012).

2.3 Genetic ancestry and lineage

The genetic ancestry and lineage of *Oryza* species have been extensively studied through population genomics and multilocus analyses. *Oryza sativa*, the most widely cultivated rice species, has two subspecies: indica and japonica. These subspecies were domesticated independently from different populations of *O. rufipogon*, with gene flow occurring later from japonica to indica (Wei et al., 2012). The domestication of *O. sativa japonica* rice is believed to have occurred around the middle area of the Pearl River in southern China, while *O. sativa indica* rice was subsequently developed from crosses between japonica rice and local wild rice as the initial cultivars spread into South East and South Asia (Huang et al., 2012).

The population genetic structure of *Oryza rufipogon* and *Oryza nivara*, two closely related wild species, has also been studied to understand their evolutionary history. *O. rufipogon* exhibits a complex population genetic structure shaped by repeated extinction and colonization events due to glacial-interglacial cycles during the Quaternary period. *O. nivara*, on the other hand, is believed to have independently originated multiple times from different *O. rufipogon* populations, highlighting the role of climatic factors in its adaptation and expansion (Liu et al., 2015).

3 Geographical Distribution of Wild *Oryza* Species

3.1 Global distribution patterns

Wild *Oryza* species exhibit a broad geographical distribution, spanning various continents and ecological zones. For instance, *Oryza rufipogon*, a significant wild relative of cultivated rice, is found extensively across Asia, including India, China, and Vietnam (Singh et al., 2018). In India, *O. rufipogon* populations are distributed across diverse agro-climatic zones, indicating a wide ecological adaptability (Singh et al., 2018). Similarly, in China, *O. rufipogon* populations are concentrated in regions such as Guangdong, Hainan, and Guangxi, which are identified as centers of genetic diversity (Wang et al., 2020; Zhang et al., 2022). The Mekong Delta in Vietnam also serves as a crucial habitat for *O. rufipogon*, showcasing significant genetic diversity (Lam et al., 2019).

3.2 Ecological niches and habitats

Wild *Oryza* species occupy a variety of ecological niches, ranging from riverine systems to wetlands and upland areas. In India, *O. rufipogon* is found in diverse habitats, including marshes, swamps, and riverbanks, reflecting its adaptability to different environmental conditions (Singh et al., 2018). In China, *O. meyeriana* populations are distributed across various administrative regions, river systems, and climatic zones, each exhibiting different levels of resistance to bacterial blight, which is influenced by their specific habitats (A et al., 2020). The Mekong Delta's channels and rivers provide a unique ecological niche for *O. rufipogon*, where it thrives in both upstream and downstream areas, showing vigorous vegetative growth in specific channels (Lam et al., 2019).

3.3 Factors influencing distribution

Several factors influence the distribution of wild *Oryza* species, including climatic conditions, geographical barriers, and human activities. In Yunnan, China, the resistance of *O. meyeriana* to bacterial blight varies significantly with latitude and altitude, indicating that climatic factors such as temperature and humidity play a crucial role in shaping its distribution (Mokodongan et al., 2018). Human activities, such as habitat fragmentation and agricultural expansion, have also impacted the distribution and genetic diversity of wild rice populations. For example, in China, the genetic structure of *O. rufipogon* populations has been affected by habitat fragmentation, necessitating conservation efforts to preserve its genetic diversity (Wang et al., 2020). Additionally, the genetic diversity of *O. rufipogon* in the Mekong Delta is influenced by both nuclear and maternal lineages, suggesting that historical migration and local adaptation have played significant roles in its current distribution (Lam et al., 2019).

4 Migration Pathways of *Oryza* Species

4.1 historical migration routes

The historical migration routes of *Oryza* species, particularly *Oryza sativa* and *Oryza glaberrima*, have been extensively studied to understand their domestication and spread. *Oryza sativa*, commonly known as Asian rice, is believed to have originated from the wild species *Oryza rufipogon*. Genetic evidence suggests that the domestication of *O. sativa* occurred in multiple regions across Asia, with subsequent migration and diversification leading to the widespread cultivation of rice across the continent (Stein et al., 2018; Chen et al., 2019). On the other hand, *Oryza glaberrima*, or African rice, is thought to have been domesticated independently from its wild progenitor *Oryza barthii* in West Africa. The domestication and migration of *O. glaberrima* are characterized by a non-centric or polycentric origin, with multiple regions contributing to its domestication traits (Choi et al., 2019; Veltman et al., 2019).

4.2 Biogeographical barriers and facilitators

The migration of *Oryza* species was influenced by various biogeographical barriers and facilitators. For instance, the geographical isolation of different regions in Africa and Asia played a significant role in the independent domestication events of *O. sativa* and *O. glaberrima*. In Asia, the diverse climatic and geographical conditions facilitated the spread and adaptation of *O. sativa* to different environments, leading to the development of various rice ecotypes (Stein et al., 2018; Chen et al., 2019). In Africa, the presence of distinct genetic clusters and isolation by distance in coastal populations of *O. glaberrima* suggests that geographical barriers such as rivers and mountains influenced the migration and diversification of this species (Veltman et al., 2019). Additionally, human activities, such as trade and agriculture, acted as facilitators for the spread of domesticated rice species across different regions (Choi et al., 2019).

4.3 Genetic evidence of migration

Genetic studies have provided substantial evidence for the migration and domestication pathways of *Oryza* species. Genome sequencing and analysis of wild and domesticated rice accessions have revealed genome-wide signatures of domestication and migration. For example, the analysis of genome variations in *O. sativa* and *O. rufipogon* has identified specific genetic markers associated with domestication traits, supporting the theory of multiple domestication events in Asia (Stein et al., 2018; Chen et al., 2019).

Similarly, whole genome sequencing of *O. glaberrima* and *O. barthii* has shown genetic structure and phylogeographic patterns that indicate a non-centric domestication origin in Africa (Choi et al., 2019; Veltman et al., 2019). These genetic insights have been crucial in tracing the roots and migration pathways of *Oryza* species, providing a deeper understanding of their evolutionary history and domestication processes.

5 Domestication Centers and Processes

5.1 Primary domestication centers

South Asia is recognized as one of the primary centers for the domestication of *Oryza* species, particularly *Oryza sativa*. Genetic and genomic studies have revealed that the domestication of Asian rice involved significant genetic diversity and complex evolutionary processes. The division of *Oryza sativa* into subgroups such as indica and japonica, and further into aus, tropical japonica, and aromatic, highlights the intricate domestication history in this region. The emergence of these subgroups is believed to have occurred over the last 4-5 millennia, with aus diverging from indica earlier than tropical japonica from japonica (Lu, 2023).

East Asia also played a crucial role in the domestication of *Oryza* species. The genomic analysis of numerous wild and cultivated rice accessions has provided insights into the origin and domestication of Asian rice. The identification of genome-wide signatures of domestication in *Oryza sativa* underscores the importance of this region in the evolutionary history of rice. The release of a complete long-read assembly of IR 8 ‘Miracle Rice’ further emphasizes the significance of East Asia in modern rice research and breeding (Stein et al., 2018; Chen et al., 2019).

In Africa, the domestication of *Oryza glaberrima*, the African rice, presents a different narrative. Unlike the centric domestication observed in Asian rice, African rice is believed to have undergone a non-centric, multiregional domestication process. Genetic analyses of *Oryza glaberrima* and its progenitor *Oryza barthii* suggest that domestication traits such as seed non-shattering were selected from multiple genotypes across different geographical regions in West and Central Africa. This multiregional origin hypothesis is supported by the genetic structure and phylogeographic analysis of domestication-related genes (Lu, 2023).

5.2 Archaeological evidence of domestication

Archaeological evidence plays a pivotal role in tracing the domestication history of *Oryza* species. Excavations and studies of ancient rice remains have provided crucial data on the early cultivation and domestication practices. For instance, the presence of domesticated rice grains in ancient archaeological sites across South and East Asia corroborates the genetic findings and helps establish a timeline for the domestication events. These findings are essential for understanding the transition from wild to cultivated rice and the spread of domesticated varieties across different regions (Chen et al., 2019; Choi et al., 2019).

5.3 Genetic markers of domestication

Genetic markers have been instrumental in identifying the domestication signatures in *Oryza* species. Genome sequencing and analysis have revealed specific mutations and genetic variations associated with domestication traits such as seed shattering, plant architecture, and flowering time.

For example, the study of genome-wide variations in *Oryza sativa* and *Oryza glaberrima* has identified key domestication genes and their evolutionary trajectories. These genetic markers not only provide insights into the domestication processes but also offer potential targets for future rice breeding programs aimed at improving crop resilience and yield (Stein et al., 2018; Chen et al., 2019; Choi et al., 2019; Lu, 2023).

6 Evolution of Cultivated *Oryza* Species

6.1 Key domestication traits

The domestication of *Oryza* species, particularly *Oryza sativa*, has been marked by the selection of key traits that distinguish cultivated varieties from their wild counterparts. These traits include reduced shattering, increased grain size, and changes in plant architecture. The analysis of 3 010 diverse Asian cultivated rice genomes revealed significant genetic variation and identified numerous single nucleotide polymorphisms (SNPs) and structural variations that contribute to these domestication traits (Figure 2) (Wang et al., 2018).

The genome-wide analysis presented in Figure 2 offers valuable insights into the genetic diversity and domestication history of *Oryza sativa*, highlighting the complexity of its genomic composition in relation to geographical distribution and environmental adaptation.

This analysis reveals over 10 000 new full-length protein-coding genes and a wide range of presence/absence variations (PAVs), which are crucial for the adaptation and survival of rice in diverse environments. Additionally, it demonstrates the complex structural variations within the rice species and evidence of multiple independent domestication events, indicating that the domestication and evolution of rice are diverse and region-specific processes.

The presence of selfish genetic elements, such as the toxin-antidote system, has been shown to play a role in reproductive isolation and the maintenance of domestication traits by preventing gene flow from wild to cultivated varieties (Yu et al., 2018).

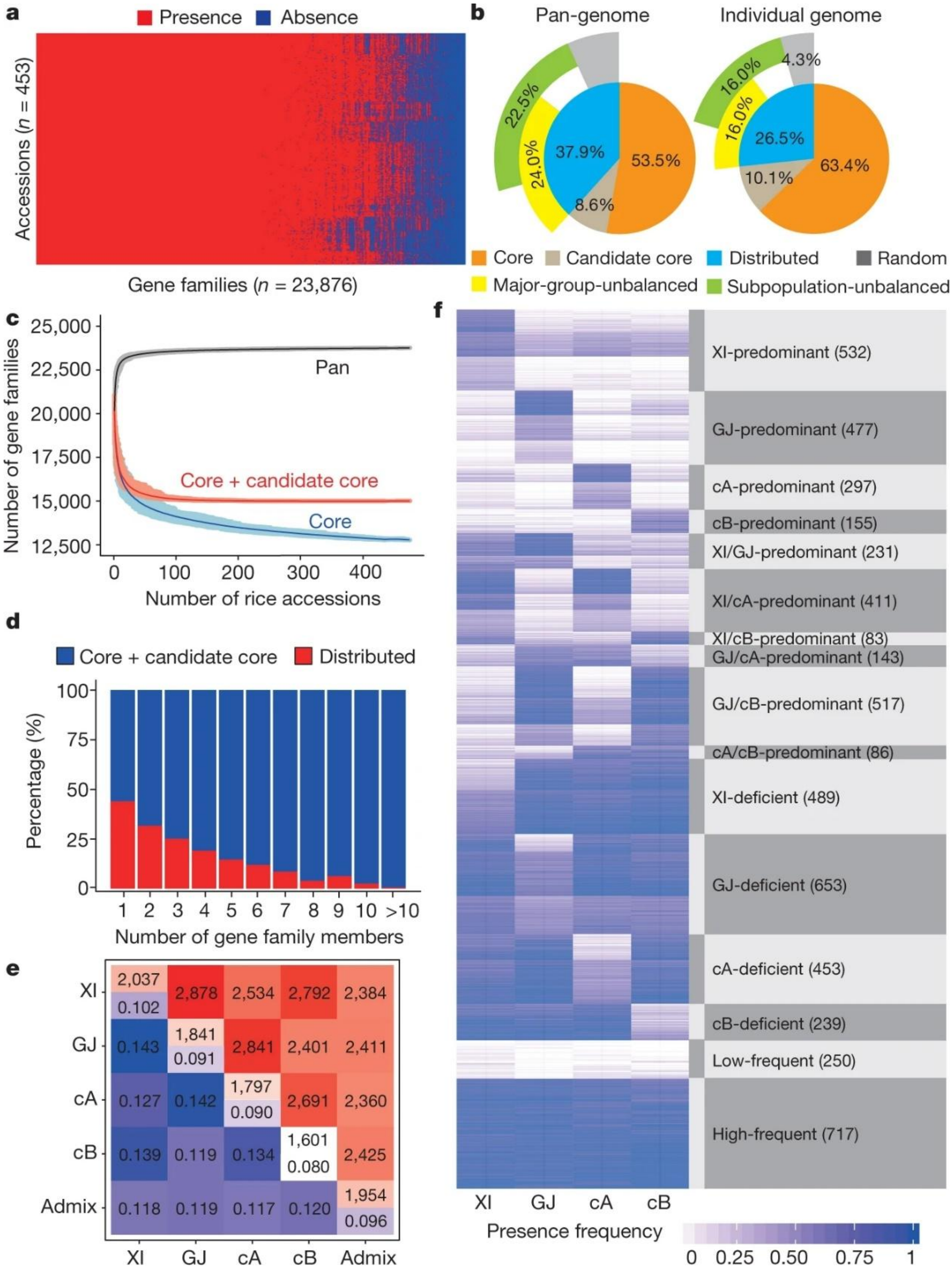

Figure 2 Pan-genome of *O. sativa* (Adopted from Wang et al., 2018)

Image caption: a: Landscape of gene-family PAVs; Gene families were sorted by their occurrence and rice accessions were clustered with k-means method (k = 10); b: Compositions of the pan-genome and an individual genome; c: Simulation of the pan-genome and core genome based on 500 randomizations of rice genome orders. d: Proportions of the core and distributed gene families binned by gene family sizes; e: The average number of gene families that are different between two accessions; f: Characterization of 5 733 major-group-unbalanced gene families detected by two-sided Fisher’s exact tests (Adopted from Wang et al., 2018)

6.2 Differentiation of cultivated varieties

The differentiation of cultivated rice varieties is a complex process influenced by both natural and artificial selection. The genomic analysis of 13 domesticated and wild rice relatives highlighted the rapid species diversification and the emergence of novel genetic elements, including transposons, which contribute to the differentiation of rice varieties (Stein et al., 2018). Furthermore, the study of evolutionary relationships among *Oryza* species has provided insights into the phylogenetic and evolutionary dynamics that underlie the differentiation of cultivated rice (Wambugu et al., 2018). Interspecific hybridization and introgression have also played a crucial role in the origin and diversification of Asian cultivated rice, leading to the development of various subgroups such as indica, aus, and basmati, which are adapted to different ecological and climatic conditions (Zhou et al., 2022).

6.3 Hybridization and gene flow

Hybridization and gene flow have been significant driving forces in the evolution and domestication of *Oryza* species. Natural hybridization-introgression events have contributed to the genetic diversity and adaptation of *Oryza sativa*, facilitating the development of subgroups that are well-suited to diverse environments. The complex patterns of introgression observed in domestication genes suggest multiple independent domestication events, further highlighting the role of hybridization in the evolution of cultivated rice (Wang et al., 2018). Additionally, artificial interspecific hybridization has led to significant breakthroughs in rice breeding, such as the development of three-line hybrid rice and the introduction of important pest and disease resistance genes (Zhou et al., 2022). These efforts have been instrumental in enhancing rice production and ensuring food security.

7 Impact of Human Activity on *Oryza* Migration and Domestication

7.1 Agricultural practices and expansion

Human agricultural practices have significantly influenced the migration and domestication of *Oryza* species. The domestication of rice (*Oryza sativa*) from its wild progenitor, *O. rufipogon*, in tropical and subtropical regions of Asia, required adaptations to various local environments, including changes in daylight sensitivity, thermal tolerance, and resistance to biotic stresses (Zheng et al., 2021). The introduction of rice cultivation to new regions, such as Madagascar, involved migration bottlenecks and genetic recombination, which resulted in unique genetic diversity patterns among local rice populations (Ahmadi et al., 2020). The selection for traits such as non-shattering seeds and erect plant architecture facilitated dense planting and high yield, which were crucial for the success of rice as a staple crop (Huang et al., 2020).

7.2 Trade routes and cultural exchange

Trade routes and cultural exchanges have played a pivotal role in the spread of *Oryza* species. The movement of rice along trade routes facilitated the exchange of genetic material and the introduction of rice to new regions. For instance, the genetic diversity of African rice (*Oryza glaberrima*) suggests a non-centric domestication origin, with multiple regions contributing key alleles for different domestication traits (Choi et al., 2019; Veltman et al., 2019). The spread of rice cultivation to Madagascar was associated with the arrival of Austronesians, who introduced new rice varieties and cultivation practices, leading to the emergence of unique rice groups specific to the island (Ahmadi et al., 2020). These exchanges not only expanded the geographical range of rice but also contributed to the genetic diversity and adaptation of rice to different environments.

7.3 Modern breeding and genetic modification

Modern breeding and genetic modification have further shaped the domestication and migration of *Oryza* species. Advances in genomics have enabled the identification of genome-wide signatures of rice domestication and the unlocking of genetic diversity among *Oryza* species. The development of hybrid rice varieties has leveraged heterotic loci to enhance yield and stress resistance, contributing to the global spread and success of rice cultivation (Chen et al., 2019). The release of complete genome assemblies, such as that of IR 8 ‘Miracle Rice’, has provided valuable resources for future crop protection and breeding efforts (Stein et al., 2018). These modern techniques have not only improved rice productivity but also facilitated the conservation and utilization of genetic resources from wild and domesticated rice relatives (Labroo et al., 2023).

8 Case Studies of Geographical Migration and Domestication

8.1 *Oryza sativa* in Asia

The migration of *Oryza sativa* within Asia is a complex process that has been extensively studied. The domestication of *O. sativa* is believed to have occurred in multiple regions within Asia, with significant centers of origin identified in China and India. The first known center of rice cultivation in China generated the *O. sativa* subspecies japonica, while the indica subspecies arose from the second center of domestication in the Ganges River plains of India (Chatterjee et al., 2020). This dual-origin hypothesis is supported by genetic evidence showing that Asian rice originated from multiple wild progenitor subpopulations, although de novo domestication appears to have occurred only once, with domestication alleles being transferred between rice subpopulations through introgression (Lam et al., 2019).

The domestication of *Oryza sativa* involved a series of genetic changes that were selected for their advantageous traits. Comparative analysis of domestication genes between Asian and African rice has revealed that the two species underwent independent but convergent evolution processes (Thierry et al., 2022). Key domestication traits such as non-shattering seeds, erect plant architecture, and increased yield were selected during the domestication process. For instance, the gene PROG1, associated with an erect plant architecture phenotype, showed convergent selection in both *O. sativa* and *O. glaberrima* (Chatterjee et al., 2020). The domestication of *O. sativa* was a complex process influenced by both natural and human selection, leading to the development of high-yielding and adaptable rice varieties.

8.2 *Oryza glaberrima* in Africa

The migration patterns of *Oryza glaberrima*, the African rice, are less well understood compared to its Asian counterpart. However, recent genomic studies have provided insights into its geographical diversification. Population structure analysis revealed five genetic clusters localizing to different geographic regions, suggesting a non-centric or polycentric origin of African rice domestication (Veltman et al., 2019). The inner Niger delta has been suggested as a significant center of origin, but molecular data to support this hypothesis is still emerging. The genetic structure within *O. glaberrima* shows a geographical association, indicating that different regions contributed key alleles for various domestication traits (Singh et al., 2018).

The domestication of *Oryza glaberrima* is characterized by a severe bottleneck caused by domestication, with signatures of recent and strong positive selection not unequivocally pointing to candidate domestication genes (Veltman et al., 2019). This suggests that domestication proceeded differently than in Asian rice, either by selection on different alleles or different modes of selection. The domestication of African rice was influenced by significant climatic changes, such as the drying of the Sahara, which triggered the domestication process (Zhang et al., 2022). The genetic and developmental basis of some domestication traits are conserved between Asian and African rice, indicating a convergent evolution process (Thierry et al., 2022). Despite the challenges in identifying the exact domestication center, it is clear that African rice underwent a complex domestication process influenced by both environmental and human factors.

9 Challenges and Future Directions in Research

9.1 Gaps in current knowledge

Despite significant advancements in understanding the domestication and migration of *Oryza* species, several gaps remain. One major gap is the incomplete understanding of the genetic basis of domestication traits across different *Oryza* species. For instance, while the domestication of Asian rice (*Oryza sativa*) has been extensively studied, the evolutionary history of African rice (*Oryza glaberrima*) is less clear, with evidence suggesting a multiregional origin rather than a single centric domestication event (Fujino et al., 2019). Additionally, the role of introgression from wild relatives into domesticated species, such as the introgression of the Pi-cd locus from *Oryza* meridionalis into *O. sativa*, is not fully understood. There is also a need for more comprehensive phylogenetic analyses to resolve the complex history of introgression and diversification within the *Oryza* genus (Stein et al., 2018).

9.2 Technological advances in studying migration and domestication

Recent technological advances have significantly enhanced our ability to study the migration and domestication of *Oryza* species. High-throughput genome sequencing and comparative genomic analyses have provided deeper insights into the genetic diversity and evolutionary history of these species. For example, the use of long-read sequencing technologies has enabled the assembly of complete genomes, such as the IR 8 ‘Miracle Rice’, which has been pivotal in understanding the genetic innovations and conservation across the *Oryza* genus (Stein et al., 2018). Additionally, integrated genomic approaches have been instrumental in identifying heterotic loci in hybrid rice, thereby revealing the genomic architecture underlying yield heterosis (Chen et al., 2019). These technological advancements are crucial for dissecting the genetic basis of domestication traits and for facilitating the development of improved rice varieties.

9.3 Implications for conservation and breeding

The insights gained from studying the migration and domestication of *Oryza* species have significant implications for conservation and breeding programs. Understanding the genetic diversity and evolutionary history of wild and domesticated rice can inform strategies for conserving genetic resources and for breeding resilient rice varieties. For instance, the identification of novel resistance loci from wild species, such as the bacterial blight resistance locus from *Oryza latifolia*, can be leveraged to enhance disease resistance in cultivated rice (Angeles-Shim et al., 2020). Moreover, the evidence of multiregional domestication in African rice suggests that conservation efforts should focus on preserving the genetic diversity across different geographical regions (Choi et al., 2019). Future research should aim to bridge the existing knowledge gaps and harness the potential of advanced genomic technologies to drive sustainable rice breeding and conservation efforts.

10 Concluding Remarks

The study of the geographical migration and domestication of *Oryza* species has revealed significant insights into the genetic diversity, evolutionary history, and domestication processes of both Asian and African rice. The analysis of 13 reference genomes across the *Oryza* species tree has highlighted rapid species diversification and the emergence of novel genetic elements, including transposons and new coding and noncoding genes. The genomic studies have also provided evidence for multiple independent domestication events in both Asian and African rice, with distinct genetic signatures and population structures correlating with geographic locations.

In particular, the domestication of African rice (*Oryza glaberrima*) has been shown to involve a severe genetic bottleneck and strong positive selection, with evidence supporting both centric and non-centric origins of domestication. Comparative genomic analyses have revealed that Asian and African rice underwent independent but convergent evolutionary processes, with conserved genetic and developmental bases for domestication traits. Additionally, the study of de novo gene origination in *Oryza* species has demonstrated the rapid evolution of protein diversity, contributing to the adaptive potential of rice.

Continued research into the geographical migration and domestication of *Oryza* species is crucial for several reasons. Understanding the genetic basis of domestication and adaptation can inform rice breeding programs aimed at improving crop resilience and productivity. The identification of novel haplotypes and functionally coupled disease resistance genes provides valuable resources for future crop protection and enhancement. The study of genetic diversity and population structure in rice can help identify key loci associated with important agronomic traits, such as yield heterosis and stress tolerance, thereby facilitating the development of high-yielding and stress-resistant rice varieties.

The reconstruction of rice dispersal history and its climatic correlates can shed light on the genetic adaptations associated with the spread of rice, offering insights into how rice can be cultivated in diverse environmental conditions. The preservation of genetic diversity in rice and its wild relatives is also essential for maintaining the adaptive potential of rice in the face of changing climates and emerging biotic stresses. Overall, continued research in this field will contribute to global food security by ensuring the sustainable production of one of the world's most important staple crops.

The study of the geographical migration and domestication of *Oryza* species has provided a comprehensive understanding of the genetic and evolutionary processes underlying rice domestication. The findings underscore the complexity and diversity of domestication events, highlighting the importance of both historical and contemporary genetic analyses in unraveling the domestication history of rice. As we move forward, integrating genomic, environmental, and archaeological data will be key to further elucidating the intricate patterns of rice domestication and adaptation.

The insights gained from these studies not only enhance our knowledge of plant domestication but also have practical implications for rice breeding and conservation. By leveraging the genetic diversity and adaptive potential of rice and its wild relatives, we can develop resilient and high-yielding rice varieties that can meet the growing demands of the global population. Continued research and collaboration in this field will be essential to harnessing the full potential of rice as a cornerstone of global food security.

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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.

References

A X.X., Qin F.L., Tang C.F., Zhang F.F., Dong C., Yang Y.Y., Zhang D.P., and Dai L.Y., 2021, Diversity of resistance to bacterial blight and geographical distribution of 29 populations of wild rice (*Oryza meyeriana* (Zoll., and Moritzi) Baill.) in Yunnan China, Genetic Resources and Crop Evolution, 68: 513-527.
https://doi.org/10.1007/s10722-020-01001-7

Ahmadi N., Ramanantsoanirina A., Santos J., Frouin J., and Radanielina T., 2020, Evolutionary processes involved in the emergence and expansion of an atypical *O. sativa* group in Madagascar, Rice, 14(1): 44.
https://doi.org/10.1186/s12284-021-00479-8

Angeles-Shim R., Shim J., Vinarao R., Lapis R., and Singleton J., 2020, A novel locus from the wild allotetraploid rice species *Oryza latifolia* Desv. confers bacterial blight (*Xanthomonas oryza*e pv. *oryzae*) resistance in rice (*O. sativa*), PLoS One, 15(2): e0229155.
https://doi.org/10.1371/journal.pone.0229155

Chatterjee J., Thakur V., Nepomuceno R., Coe R., Dionora J., Elmido-Mabilangan A., Llave A., Reyes A., Monroy A., Canicosa I., Bandyopadhyay A., Jena K., Brar D., and Quick W., 2020, Natural diversity in stomatal features of cultivated and wild *Oryza* species, Rice, 13: 1-20.
https://doi.org/10.1186/s12284-020-00417-0

Chen E., Huang X., Tian Z., Wing R., and Han B., 2019, The genomics of *Oryza* species provides insights into rice domestication and heterosis, Annual Review of Plant Biology, 70(1): 639-665.
https://doi.org/10.1146/annurev-arplant-050718-100320

Choi J., and Purugganan M., 2018, Multiple origin but single domestication led to *Oryza sativa*, G3: Genes Genomes Genetics, 8(3): 797-803.
https://doi.org/10.1534/g3.117.300334

Choi J., Zaidem M., Gutaker R., Dorph K., Singh R., and Purugganan M., 2019, The complex geography of domestication of the African rice *Oryza glaberrima*, PLoS Genetics, 15(3): e1007414.
https://doi.org/10.1371/journal.pge N.,1007414

Civáň P., Craig H., Cox C., and Brown T., 2015, Three geographically separate domestications of Asian rice, Nature Plants, 1(11): 1-5.
https://doi.org/10.1038/nplants.2015.164

Cubry P., Tranchant-Dubreuil C., Thuillet A., Monat C., Ndjiondjop M., Labadie K., Cruaud C., Engelen S., Scarcelli N., Rhoné B., Burgarella C., Dupuy C., Larmande P., Wincker P., François O., Sabot F., and Vigouroux Y., 2018, The rise and fall of African rice cultivation revealed by analysis of 246 new genomes, Current Biology, 28(14): 2274-2282.
https://doi.org/10.1016/j.cub.2018.05.066

Fujino K., Hirayama Y., Obara M., and Ikegaya T., 2019, Introgression of the chromosomal region with the Pi-cd locus from *Oryza meridionalis* into *O. sativa* L. during rice domestication, Theoretical and Applied Genetics, 132: 1981-1990.
https://doi.org/10.1007/s00122-019-03332-1

Guo Y., and Ge S., 2005, Molecular phylogeny of *Oryzeae* (Poaceae) based on DNA sequences from chloroplast mitochondrial and nuclear genomes, American Journal of Botany, 92(9): 1548-1558.
https://doi.org/10.3732/ajb.92.9.1548

Huang L., Liu H., Wu J., Zhao R., Li Y., Melaku G., Zhang S., Huang G., Bao Y., Ning M., Chen B., Gong Y., Hu Q., Zhang J., and Zhang Y., 2020, Evolution of plant architecture in *Oryza* driven by the *PROG1* locus, Frontiers in Plant Science, 11: 876.
https://doi.org/10.3389/fpls.2020.00876

Huang X., Kurata N., Wei X., Wang Z., Wang A., Zhao Q., Zhao Y., Liu K., Lu H., Li W., Guo Y., Lu Y., Zhou C., Fan D., Weng Q., Zhu C., Huang T., Zhang L., Wang Y., Feng L., Furuumi H., Kubo T., Miyabayashi T., Yuan X., Xu Q., Dong G., Zhan Q., Li C., Fujiyama A., Toyoda A., Lu T., Feng Q., Qian Q., Li J., and Han B., 2012, A map of rice genome variation reveals the origin of cultivated rice, Nature, 490(7421): 497-501.
https://doi.org/10.1038/nature11532

Labroo M., Clark L., Zhang S., Hu F., Tao D., Hamilton R., and Sacks E., 2023, Solving the mystery of Obake rice in Africa: population structure analyses of *Oryza longistaminata* reveal three genetic groups and evidence of both recent and ancient introgression with *O. sativa*, Frontiers in Plant Science, 14: 1278196.
https://doi.org/10.3389/fpls.2023.1278196

Lacchini E., Kiegle E., Castellani M., Adam H., Jouannic S., Gregis V., and Kater M., 2020, CRISPR-mediated accelerated domestication of African rice landraces, PLoS One, 15(3): e0229782.
https://doi.org/10.1371/journal.pone.0229782

Lam D., Buu B., Lang N., Toriyama K., Nakamura I., and Ishikawa R., 2019, Genetic diversity among perennial wild rice *Oryza rufipogon* Griff., in the Mekong Delta, Ecology and Evolution, 9(5): 2964-2977.
https://doi.org/10.1002/ece3.4978

Liu R., Zheng X., Zhou L., Zhou H., and Ge S., 2015, Population genetic structure of *Oryza rufipogon* and *Oryza nivara*: implications for the origin of *O. nivara*, Molecular Ecology, 24(20): 5211-5228.
https://doi.org/10.1111/mec.13375

Londo J., Chiang Y., Hung K., Chiang T., and Schaal B., 2006, Phylogeography of Asian wild rice *Oryza rufipogon* reveals multiple independent domestications of cultivated rice *Oryza sativa*, Proceedings of the National Academy of Sciences of the United States of America, 103(25): 9578-9583.
https://doi.org/10.1073/PNAS.0603152103

Lu Y., 2023, Gene genealogy-based mutation analysis reveals emergence of aus, tropical japonica, and aromatic of *Oryza sativa* during the later stage of rice domestication, Genes, 14(7): 1412.
https://doi.org/10.3390/genes14071412

Mokodongan D., Montenegro J., Mochida K., Fujimoto S., Ishikawa A., Kakioka R., Yong L., Yong L., Mulis, Hadiaty R., Mandagi I., Masengi K., Wachi N., Hashiguchi Y., Kitano J., and Yamahira K., 2018, Phylogenomics reveals habitat-associated body shape divergence in *Oryzias woworae* species group (Teleostei: Adrianichthyidae), Molecular Phylogenetics and Evolution, 118: 194-203.
https://doi.org/10.1016/j.ympev.2017.10.005

Nabholz B., Sarah G., Sabot F., Ruiz M., Adam H., Nidelet S., Ghesquière A., Santoni S., David J., and Glémin S., 2014, Transcriptome population genomics reveals severe bottleneck and domestication cost in the African rice (*Oryza glaberrima*), Molecular Ecology, 23(9): 2210-2227.
https://doi.org/10.1111/mec.12738

Roma-Burgos N., Sudo M., Olsen K., Werle I., and Song B., 2021, Weedy rice (*Oryza* spp.): what’s in a name, Weed Science, 69(5): 505-513.
https://doi.org/10.1017/wsc.2021.22

Singh B., Singh N., Mishra S., Tripathi K., Singh B., Rai V., Singh A., and Singh N., 2018, Morphological and molecular data reveal three distinct populations of Indian wild rice *Oryza rufipogon* Griff., species complex, Frontiers in Plant Science, 9: 123.
https://doi.org/10.3389/fpls.2018.00123

Stein J., Yu Y., Copetti D., Zwickl D., Zhang L., Zhang C., Chougule K., Gao D., Iwata A., Goicoechea J., Wei S., Wang J., Liao Y., Wang M., Jacquemin J., Becker C., Kudrna D., Zhang J., Londono C., Song X., Lee S., Sanchez P., Zuccolo A., Ammiraju J., Talag J., Danowitz A., Rivera L., Gschwend A., Noutsos C., Wu C., Kao S., Zeng J., Wei F., Zhao Q., Feng Q., Baidouri M., Carpentier M., Lasserre E., Cooke R., Farias D., Maia L., Santos R., Nyberg K., McNally K., Mauleon R., Alexandrov N., Schmutz J., Flowers D., Fan C., Weigel D., Jena K., Wicker T., Chen M., Han B., Henry R., Hsing Y., Kurata N., Oliveira A., Panaud O., Jackson S., Machado C., Sanderson M., Long M., Ware D., and Wing R., 2018, Genomes of 13 domesticated and wild rice relatives highlight genetic conservation turnover and innovation across the genus *Oryza*, Nature Genetics, 50(2): 285-296.
https://doi.org/10.1038/s41588-018-0040-0

Thierry M., Charriat F., Milazzo J., Adreit H., Ravel S., Cros-Arteil S., Borron S., Sella V., Kroj T., Ioos R., Fournier E., Tharreau D., and Gladieux P., 2022, Maintenance of divergent lineages of the rice blast fungus *Pyricularia oryza*e through niche separation loss of sex and post-mating genetic incompatibilities, PLoS Pathogens, 18(7): e1010687.
https://doi.org/10.1371/journal.ppat.1010687

Veltman M., Flowers J., Andel T., and Schranz M., 2019, Origins and geographic diversification of African rice (*Oryza glaberrima*), PLoS One, 14(3): e0203508.
https://doi.org/10.1371/journal.pone.0203508

Wambugu P., Ndjiondjop M., and Henry R., 2021, Genetics and genomics of African rice (*Oryza glaberrima* Steud) domestication, Rice, 14(1): 6.
https://doi.org/10.1186/s12284-020-00449-6

Wambugu P., Nyamongo D., Ndjiondjop M., and Henry R., 2018, Evolutionary relationships among the *Oryza* species, 2018: 41-54.
https://doi.org/10.1007/978-3-319-71997-9_3

Wang J., Shi J., Liu S., Sun X., Huang J., Qiao W., Cheng Y., Zhang L., Zheng X., and Yang Q., 2020, Conservation recommendations for *Oryza rufipogon* Griff., in China based on genetic diversity analysis, Scientific Reports, 10(1): 14375.
https://doi.org/10.1038/s41598-020-70989-w

Wang M., Yu Y., Haberer G., Marri P., Fan C., Goicoechea J., Zuccolo A., Song X., Kudrna D., Ammiraju J., Cossu R., Maldonado C., Chen J., Lee S., Sisneros N., Baynast K., Golser W., Wissotski M., Kim W., Sanchez P., Ndjiondjop M., Sanni K., Long M., Carney J., Panaud O., Wicker T., Machado C., Chen M., Mayer K., Rounsley S., and Wing R., 2014, The genome sequence of African rice (*Oryza glaberrima*) and evidence for independent domestication, Nature Genetics, 46(9): 982-988.
https://doi.org/10.1038/ng.3044

Wang W., Mauleon R., Hu Z., Chebotarov D., Tai S., Wu Z., Li M., Zheng T., Fuentes R., Zhang F., Mansueto L., Copetti D., Sanciangco M., Palis K., Xu J., Sun C., Fu B., Zhang H., Gao Y., Zhao X., Shen F., Cui X., Yu H., Li Z., Chen M., Detras J., Zhou Y., Zhang X., Zhao Y., Kudrna D., Wang C., Li R., Jia B., Lu J., He X., Dong Z., Xu J., Li Y., Wang M., Shi J., Li J., Zhang D., Lee S., Hu W., Poliakov A., Dubchak I., Ulat V., Borja F., Mendoza J., Ali J., Gao Q., Niu Y., Yue Z., Naredo M., Talag J., Wang X., Li J., Fang X., Yin Y., Glaszmann J., Zhang J., Li J., Hamilton R., Wing R., Ruan J., Zhang G., Wei C., Alexandrov N., McNally K., Li Z., and Leung H., 2018, Genomic variation in 3 010 diverse accessions of Asian cultivated rice, Nature, 557(7703): 43-49.
https://doi.org/10.1038/s41586-018-0063-9

Watarai N., Yamamoto N., Sawada K., and Yamada T., 2019, Evolution of aspergillus *Oryza*e before and after domestication inferred by large-scale comparative genomic analysis, DNA Research, 26(6): 465-472.
https://doi.org/10.1093/dnares/dsz024

Wei X., Qiao W., Chen Y., Wang R., Cao L., Zhang W., Yuan N., Li Z., Zeng H., and Yang Q., 2012, Domestication and geographic origin of *Oryza sativa* in China: insights from multilocus analysis of nucleotide variation of *O. sativa* and *O. rufipogo*, Molecular Ecology, 21(20): 5073-5087.
https://doi.org/10.1111/j.1365-294X.2012.05748.x

Yu X., Zhao Z., Zheng X., Zhou J., Kong W., Wang P., Bai W., Zheng H., Zhang H., Li J., Liu J., Wang Q., Zhang L., Liu K., Yu Y., Guo X., Wang J., Lin Q., Wu F., Ren Y., Zhu S., Zhang X., Cheng Z., Lei C., Liu S., Liu X., Tian Y., Jiang L., Ge S., Wu C., Tao D., Wang H., and Wan J., 2018, A selfish genetic element confers non-mendelian inheritance in rice, Science, 360(6393): 1130-1132.
https://doi.org/10.1126/science.aar4279

Zhang J., Pan D., Fan Z., Yu H., Jiang L., Lv S., Sun B., Chen W., Mao X., Liu Q., and Li C., 2022, Genetic diversity of wild rice accessions (*Oryza rufipogon* Griff.) in Guangdong and Hainan provinces, China, and construction of a wild rice core collection, Frontiers in Plant Science, 13: 999454.
https://doi.org/10.3389/fpls.2022.999454

Zheng X., Pang H., Wang J., Yao X., Song Y., Li F., Lou D., Ge J., Zhao Z., Qiao W., Kim S., Ye G., Olsen K., Liu C., and Yang Q., 2021, Genomic signatures of domestication and adaptation during geographical expansions of rice cultivation, Plant Biotechnology Journal, 20(1): 16.
https://doi.org/10.1111/pbi.13730

Zhou J., Yang Y., Lv Y., Pu Q., Li J., Zhang Y., Deng X., Wang M., Wang J., and Tao D., 2022, Interspecific hybridization is an important driving force for origin and diversification of Asian cultivated rice *Oryza sativa* L., Frontiers in Plant Science, 13: 932737.
https://doi.org/10.3389/fpls.2022.932737