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Harnessing Knowledge from Maize and Rice Domestication for New Crop Breeding

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ABSTRACT

Crop domestication has fundamentally altered the course of human history, causing a shift from hunter-gatherer to agricultural societies and stimulating the rise of modern civilization. A greater understanding of crop domestication would provide a theoretical basis for how we could improve current crops and develop new crops to deal with environmental challenges in a sustainable manner. Here, we provide a comprehensive summary of the similarities and differences in the domestication processes of maize and rice, two major staple food crops that feed the world. We propose that maize and rice might have evolved distinct genetic solutions toward domestication. Maize and rice domestication appears to be associated with distinct regulatory and evolutionary mechanisms. Rice domestication tended to select *de novo*, loss-of-function, coding variation, while maize domestication more frequently favored standing, gain-of-function, regulatory variation. At the gene network level, distinct genetic paths were used to acquire convergent phenotypes in maize and rice domestication, during which different central genes were utilized, orthologous genes played different evolutionary roles, and unique genes or regulatory modules were acquired for establishing new traits. Finally, we discuss how the knowledge gained from past domestication processes, together with emerging technologies, could be exploited to improve modern crop breeding and domesticate new crops to meet increasing human demands.

Key words: maize, rice, regulatory and evolutionary mechanism, domestication gene network, *de novo* domestication

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INTRODUCTION

Crops arguably represent the most important human inventions, as they have greatly promoted the development of human society. Crop domestication is the process by which wild plants are transformed into useful crops by artificial selection to meet human needs (Doebley et al., 2006). This process was considered a model for natural evolution (Darwin, 1859). Most crops were domesticated within the last 12 000 years (Meyer and Purugganan, 2013), including the most highly productive cereal crops: maize, rice, and wheat. These three crops serve as major staple food crops that have fed and continue to feed the world.

Maize and rice represent two typical mating systems, cross- and self-pollination, respectively. Maize (*Zea mays* ssp. *mays*) was domesticated from its wild progenitor teosinte (*Zea mays* ssp. *parviglumis*) in the central Balsas river valley of southwestern Mexico ~9000 years ago (Matsuoka et al., 2002; Piperno et al., 2009). Unlike maize, cultivated rice includes two species, *Oryza sativa* and *Oryza glaberrima*, which were independently domesticated in Asia and Africa, respectively (Khush, 1997; Vaughan et al., 2008; Agnoun et al., 2012; Wang et al., 2014; Meyer et al., 2016; Wing et al., 2018). Asian cultivated rice (*O. sativa*) was domesticated from *Oryza rufipogon* in Asia ~9000 years ago, and includes two major subspecies, *japonica* and *indica* (Sang and Ge, 2007; Sweeney and McCouch, 2007; Huang et al., 2012; Gross and Zhao, 2014), while African

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cultivated rice (*O. glaberrima*) was domesticated from *Oryza barthii* in West Africa ~3000 years ago (Wang et al., 2014; Meyer et al., 2016).

Although originated from different geographical locations, maize and cultivated rice experienced convergent morphological shifts during domestication, including the loss of seed dispersal, decreased seed dormancy, increased apical dominance, and larger inflorescences and grains (Doebley et al., 2006). These convergent phenotypic changes are collectively known as the domestication syndrome (Hammer, 1984). Extensive research has been performed to understand the genetic basis of maize and rice domestication. Owing to the significant advances in genetic and genomic approaches, a number of key genes controlling maize and rice domestication have been cloned (Olsen and Wendel, 2013; Liu et al., 2020). With the rapid development of sequencing and omics technologies, large-scale population genetic studies have been conducted to uncover systematic changes in the genome, transcriptome, and metabolome associated with maize and rice domestication (Huang et al., 2012; Hufford et al., 2012; Swanson-Wagner et al., 2012; Lemmon et al., 2014; Wang et al., 2018c; Liu et al., 2019; Xu et al., 2019). These advances provided unprecedented insights into the crop domestication process. Despite these substantial progresses, several key evolutionary questions on crop domestication remain unanswered. Are the domestication processes of different crop species controlled by similar regulatory and evolutionary mechanisms? Are the convergent phenotypic changes during crop domestication under convergent genetic control? What kind of genetic and genomic changes have crop species commonly underwent during domestication, and how did these changes shape crop evolutionary history? A systematic comparison of the domestication of maize and rice, two crop species receiving the most extensive genetic and genomic studies, would provide key insights into these questions.

In this article, we summarize the similarities and differences between maize and rice domestication from morphological changes, underlying genes to systematic changes at the molecular level. Based on current insights into maize and rice domestication, we refine the regulatory and evolutionary mechanisms underlying maize and rice domestication and propose a model for the evolution of the domestication gene network. Finally, we discuss how our knowledge of past domestication processes could be exploited to improve modern crop breeding and even domesticate new crops to meet human needs in light of the ever-increasing global population and changing climate conditions.

Crucial Morphological Changes and Major Genes Underlying Maize and Rice Domestication

Phenotype-targeted selection has been the foundation of crop domestication and improvement throughout history. At the onset of domestication, different crops experienced convergent phenotypic changes in domestication syndrome traits (Doebley et al., 2006; Gross and Olsen, 2010; Meyer and Purugganan, 2013; Pickersgill, 2018). These key morphological transformations appear to be largely controlled by a small number of quantitative trait loci (QTLs) with large effects (Paterson et al., 1995; Doebley et al., 2006; Lenser and Theißen, 2013; Meyer and Purugganan, 2013). Here, we summarize the crucial morphological transitions that occurred during maize and rice domestication and the key genes underlying the domestication traits (Figure 1; Supplemental Table 1).

Changes in Plant and Inflorescence Architecture

Plant architecture and inflorescence architecture are major selection targets of crop domestication. Domesticated plants generally have a compact plant architecture, fewer and shorter branches/tillers, and larger inflorescences than their wild ancestors. These characteristics facilitate human cultivation and harvesting, thus achieving higher population yields (Gepts, 2004; Doebley et al., 2006). The most extreme case is maize, which exhibits a profound increase in apical dominance compared with its wild ancestor, teosinte (Doebley, 1992, 2004; Stitzer and Ross-Ibarra, 2018). A typical teosinte plant has multiple long lateral branches that bear many small ears and are terminated by tassels, whereas a typical maize plant has a single stalk with few short branches bearing large ears at their tips. Teosinte ears possess 5 to 12 fruitcase-enveloped kernels that are borne in two ranks of cupules, with one spikelet per cupule. By contrast, maize ears can possess 500 or more naked kernels that are borne in four (or more) ranks of cupules, with two spikelets per cupule.

The dramatic differences in plant and inflorescence architecture between teosinte and maize are mainly controlled by a few genes with large effects. *teosinte branched1* (*tb1*), which encodes a TCP transcription factor (Cubas et al., 1999), plays a crucial role in increasing apical dominance in maize (Doebley et al., 1995, 1997). A *Hopscotch* transposon insertion located ~60 kb upstream of *tb1* functions as an enhancer to upregulate *tb1* expression in maize and thereby represses branch outgrowth (Clark et al., 2006; Studer et al., 2011). *grassy tillers1* (*gt1*), which encodes an HD-ZIP transcription factor (Whipple et al., 2011), regulates ear number or prolificacy. The 2.7-kb causative region upstream of *gt1* controls its specific expression in the nodal plexus in maize, thus suppressing the initiation of multiple ears (Wills et al., 2013). *Zea floricaula leafy2* (*zfl2*), *UNBRANCHED3* (*UB3*), and *Tasselseed6* (*Ts6*)/*indeterminate spikelet1* (*ids1*) may have contributed to the increase in ear rank number during maize domestication (Chuck et al., 1998, 2007, 2014; Bomblies et al., 2003; Bomblies and Doebley, 2006; Liu et al., 2015; Calderón et al., 2016; Chen et al., 2019b; Wang et al., 2019c). *tassels replace upper ears1* (*tru1*) confers sexual conversion of the terminal lateral inflorescence from a tassel (staminate) in teosinte to an ear (pistillate) in maize (Doebley et al., 1995; Dong et al., 2017; Chen et al., 2019b). *ramosa1* (*ra1*) represses inflorescence (the ear and tassel) branching and was targeted by selection during maize domestication (Vollbrecht et al., 2005; Sigmon and Vollbrecht, 2010; Xu et al., 2017; Chen et al., 2019b). Notably, many of these key maize domestication genes function in the same gene network, where *tb1* directly regulates the expression of *gt1*, *tru1*, *ra1*, *UB3*, and *ids1* (Whipple et al., 2011; Dong et al., 2017, 2019b; Studer et al., 2017), highlighting the core role of *tb1* in regulating the domestication of plant and inflorescence architecture in maize.

Like maize, cultivated rice also underwent a remarkable increase in apical dominance during domestication. Wild rice is highly

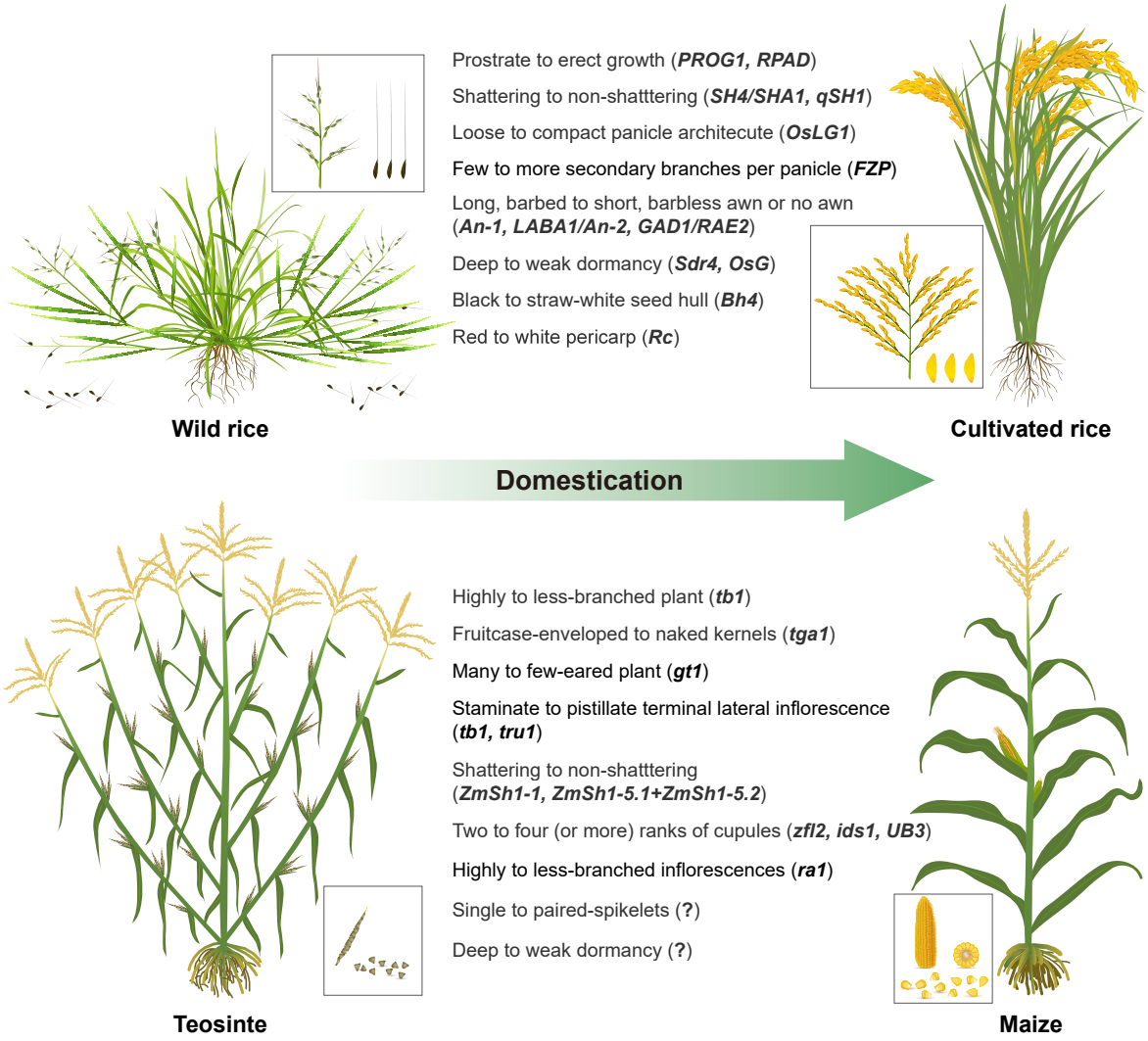

Figure 1. Crucial Morphological Changes during Maize and Rice Domestication and the Underlying Key Genes.
Top, wild rice to cultivated rice; bottom, teosinte to maize.

tillering and shows a prostrate growth habit with a wide tiller angle, which helps it survive in its natural habitat. By contrast, cultivated rice has highly reduced tillering and exhibits an erect growth habit with a narrow tiller angle, allowing for higher density planting and thus greater yields. Cultivated rice has a larger, more compact, highly branched panicle architecture compared with wild rice, making it more amenable to human cultivation.

PROSTRATE GROWTH 1 (*PROG1*), encoding a C2H2 zinc-finger transcription factor, plays a profound role in regulating rice plant architecture, and an amino acid substitution disrupted PROG1 activity in Asian cultivated rice, causing the transition from prostrate to erect growth (Jin et al., 2008; Tan et al., 2008). A 110-kb deletion closely linked to *PROG1*, which harbors a tandem repeat of seven zinc-finger genes, was also involved in the transition from prostrate to erect growth during Asian rice domestication (Wu et al., 2018). A similar but independent 113-kb deletion at the same locus drove the parallel change in plant architecture during the domestication of African cultivated rice (Wu et al., 2018). This locus, plus *PROG1*, is referred to as *RICE PLANT ARCHITECTURE DOMESTICATION* (*RPAD*) (Wu et al., 2018). *OsLIGULELESS1* (*OsLG1*), encoding an SBP transcription factor, regulates panicle architecture, and an SNP located 11 kb upstream of *OsLG1* affects its expression in the panicle pulvinus, leading to the transition from spreading to compact panicles (Ishii et al., 2013; Zhu et al., 2013). *RPAD* also played key roles in increasing inflorescence size during rice domestication (Tan et al., 2008; Wu et al., 2018). *FRIZZY PANICLE* (*FZP*) is another important gene that increased secondary branch number and grains per panicle during rice domestication (Huang et al., 2018).

Loss of Seed Dispersal

The loss of seed dispersal was a key event in the domestication of major cereal crops (Doebley et al., 2006; Meyer and Purugganan, 2013). In wild rice, a complete abscission layer forms between the pedicel and spikelet at the base of the seed, causing the seeds to disperse immediately at maturity. By contrast, cultivated rice forms a partial or no abscission layer, leading to

a non-shattering habit at maturity (Sweeney and McCouch, 2007; Vaughan et al., 2008).

Two major QTLs, *shattering4* (*SH4*)/*Shattering1* (*SHA1*) and *seed shattering in chromosome 1* (*qSH1*), control seed shattering in rice (Li et al., 2006b; Konishi et al., 2006; Lin et al., 2007). An SNP located 12 kb upstream of *qSH1* affects its spatial expression pattern at the abscission layer, leading to loss of seed shattering (Konishi et al., 2006). Notably, two independent causative SNPs in the *SH4* coding region were responsible for the loss of seed shattering during Asian and African rice domestication (Li et al., 2006b; Lin et al., 2007; Wu et al., 2017).

Similar to wild rice, teosinte ears form abscission layers between the fruitcases and disarticulate at maturity, whereas maize ears lack abscission layers and remain intact at maturity for easy harvest (Doebley, 2004). Two major QTLs for ear shattering were detected on chromosomes 1 and 5, respectively (Shannon, 2012; Chen et al., 2019b). Orthologs of the seed-shattering gene *Shattering1* (*Sh1*) from sorghum (*ZmSh1-1* and *ZmSh1-5.1+ZmSh1-5.2*) are the most likely functional genes at these two QTLs (Lin et al., 2012).

Loss of Seed Dormancy

The loss of seed dormancy was an important event in the domestication of cereal crops (Harlan et al., 1973; Gepts, 2004). Seed dormancy in wild species desynchronizes and delays germination, preventing all seeds from germinating under unfavorable conditions. By contrast, the lack of seed dormancy in domesticated species promotes simultaneous germination and ensures a more uniform population and harvest (Finch-Savage and Leubner-Metzger, 2006; Née et al., 2017).

Seed dormancy occurs in teosinte, whereas maize seeds are normally non-dormant (McCarty, 1995; Avendaño López et al., 2011). Wild rice and African cultivated rice exhibit stronger dormancy than Asian cultivated rice (Sarla and Swamy, 2005; Vaughan et al., 2008). Despite the evolutionary importance of seed dormancy, few studies have examined the genetic loci controlling seed dormancy during maize and rice domestication (Cai and Morishima, 2000; Li et al., 2006a; Shu et al., 2015; Liu et al., 2018). Thus far, only two genes controlling seed dormancy during rice domestication have been identified: *Seed dormancy 4* (*Sdr4*) and *OsG* (Sugimoto et al., 2010; Wang et al., 2018a).

Reduced Awns in Rice

The loss of awns or their reduction in size was a critical change during rice domestication. Wild rice typically displays long, barbed awns that contribute to seed dispersal and seed burial and protect the grains from animal predation, whereas cultivated rice bears short or no awns, which facilitates seed harvest, storage, and processing by humans (Sweeney and McCouch, 2007; Agnoun et al., 2012). Three genes associated with the transition from long awns to no or short awns have been cloned: *Awn-1* (*An-1*), *Awn-2* (*An-2*)/*LONG AND BARBED AWN1* (*LABA1*), and *GRAIN NUMBER*, *GRAIN LENGTH AND AWN DEVELOPMENT* (*GAD1*)/*REGULATOR OF AWN ELONGATION 2* (*RAE2*) (Luo et al., 2013; Gu et al., 2015; Hua et al., 2015; Bessho-Uehara et al., 2016; Jin et al., 2016). *An-1* and *An-2* have additive effects on awn length, with *An-1* promoting awn formation and *An-2* enhancing awn elongation (Gu et al., 2015).

Reduced Glumes in Maize

The release of kernels from their protective casing was a specific but critical step in maize domestication (Doebley, 2004; Wang et al., 2005). Teosinte kernels are tightly encased in cupulate fruitcases, whereas maize kernels are uncovered on the surface of the ear and are attached to the cob. Maize contains cupules and glumes, but they are small and do not cover the kernel. *teosinte glume architecture1* (*tga1*), encoding an SBP transcription factor, is the key gene controlling glume architecture, and a single amino acid substitution in maize TGA1 transforms this protein into a transcriptional repressor, resulting in naked grains (Dorweiler et al., 1993; Wang et al., 2005, 2015). *tga1* is also situated in the gene network mediated by *tb1*, where *tb1* directly activates its expression (Studer et al., 2017). In turn, *tga1* directly regulates a set of MADS-box genes that are responsible for glume identity (Wang et al., 2015; Studer et al., 2017).

Regulatory and Evolutionary Mechanisms of Maize and Rice Domestication

A list of additional genes involved in maize and rice domestication is provided in Supplemental Table 1. We particularly note that only those genes that control the critical morphological transformations during the initial domestication of maize and rice are considered domestication genes and included in the following analysis. Of the 29 genes involved in maize and rice domestication, 21 genes (72%) encode transcription factors (Supplemental Table 1), highlighting the prominent roles of transcription factors in controlling the critical morphological transitions associated with maize and rice domestication. Transcription factors usually interact with promoters of many downstream genes, and thus changes at them would produce wide effects, which may help explain why changes at few loci could result in substantial morphological shifts under domestication.

The causative polymorphisms in these QTLs/genes could be classified into regulatory variation, coding variation, and structural variation. Among the 18 rice domestication QTLs with causative variants, 10 (56%) are caused by coding variation, 5 (28%) are caused by regulatory variation, 1 (5%) is caused by both coding and regulatory variations, and 2 (11%) are caused by structural variation (Figure 2A; Supplemental Table 1). Among the five maize domestication QTLs with clear causative variation, three (*tb1*, *gt1*, and *KRN4*/*UB3*) are caused by regulatory variation, one (*tga1*) is caused by a coding variation, and one (*etb1.2*/*ZmSh1-1*) involves both coding and regulatory variation (Figure 2A; Supplemental Table 1). In a recent broader survey of QTLs for traits, including domestication, adaptation, plant architecture, yield component, quality, and abiotic/biotic stress resistance, we found that 57.5% of 143 cloned rice QTLs are caused by coding variation, while 64% of 57 cloned maize QTLs are caused by regulatory variation (Liang et al., 2021). These results suggest that coding variation is more frequently involved in regulating rice traits, whereas regulatory variations play a dominant role in regulating maize traits.

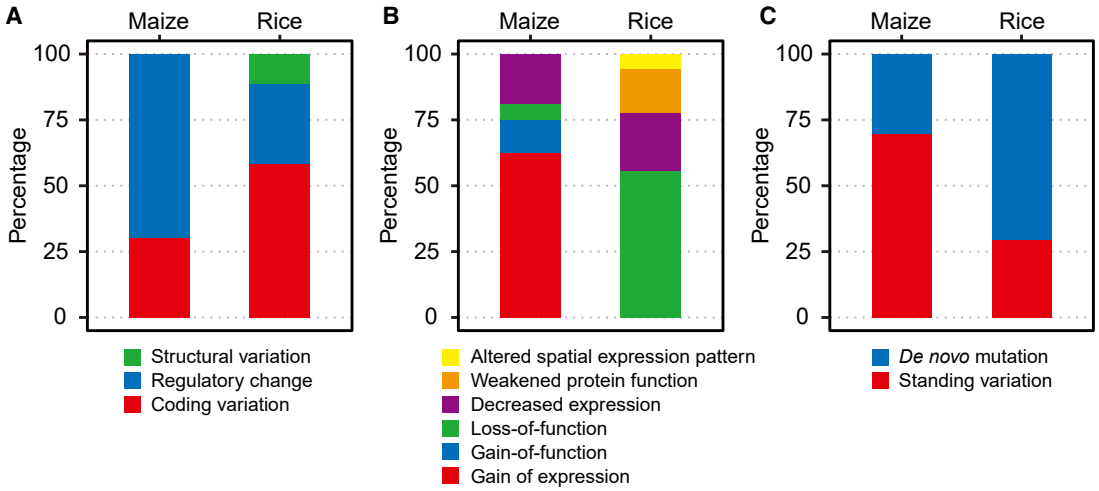

Figure 2. Regulatory and Evolutionary Mechanisms of Maize and Rice Domestication.

(A) Variation types of causative polymorphisms for the key domestication genes cloned in maize and rice (regulatory variation, coding variation, and structural variation).

(B) Functional types of domesticated alleles for the key domestication genes cloned in maize and rice (gain of function, loss of function, weakened protein function, gain of expression, decreased expression, and altered spatial expression pattern).

(C) Origin of selected alleles at the key domestication genes cloned in maize and rice (standing variation and *de novo* mutation). Plotted is the percentage of QTLs/genes involved in each category.

One theory of crop domestication is that the rapid changes from wild plants into domesticated crops principally involve the selection of recessive, loss-of-function alleles (Lester, 1989). Among the eight maize domestication QTLs with clear biological function of the domesticated alleles, six (*tb1*, *tga1*, *gt1*, *tru1*, *ids1*, and *ZmSWEET4c*) involve gain of function (gain of expression or new protein function), one (*KRN4/UB3*) involves reduced expression, while another QTL (*etb1.2/ZmSh1-1*) involves reduced expression or loss of function (Figure 2B; Supplemental Table 1). By contrast, among the 18 QTLs for rice domestication, 10 (56%) involve loss of function (disruption of protein), 3 (17%) involve weakened protein function, 4 (22%) involve decreased expression, and 1 (5%) alters the spatial expression pattern (Figure 2B; Supplemental Table 1). Remarkably, none of the 18 cloned rice QTLs are associated with upregulated gene expression. These contrasting findings suggest that the selection of gain-of-function and loss-of-function alleles might be a general feature of maize and rice domestication, respectively.

The relative importance of standing variation versus *de novo* mutation during domestication has long been debated. Among the five maize domestication QTLs with clear origin of the causative variation, the selected alleles of three QTLs (*tb1*, *gt1*, and *KRN4*) are standing variation, one (*tga1*) is apparently a *de novo* mutation, and one (*etb1.2/ZmSh1-1*) is complicated, involving both standing and *de novo* mutation (Figure 2C; Supplemental Table 1). By contrast, among the 17 rice domestication QTLs with clear origins, the selected alleles at 11 QTLs (65%) are *de novo* mutations, 4 (23%) are standing variation, and 2 (12%) involve both *de novo* mutations and standing variation (Figure 2C; Supplemental Table 1). These results suggest that *de novo* mutations might have played a more important role in rice domestication, whereas standing variation were more frequently used during maize domestication.

Taken together, these findings suggest that rice and maize domestication are associated with distinct regulatory and evolutionary mechanisms, where rice domestication tended to favor the selection of *de novo*, loss-of-function, coding variation, while maize domestication more frequently involved the selection of standing, gain-of-function, regulatory variation. The different mating system of maize and cultivated rice might mainly result in these differences. Domesticated alleles are thought to be strongly deleterious in the wild (Glémin and Bataillon, 2009). In selfing populations, such deleterious alleles are more efficient to be purged, therefore selection would more likely proceed from new mutations (Ohta and Cockerham, 1974; Glémin and Bataillon, 2009). In outcrossing populations, recessive mutations can be selected for only when they are revealed to be homozygotes and accumulated to high frequency. This process will be extremely low. Selection of standing variation or new dominant mutations is thus easier and faster in outcrossing populations (Ohta and Cockerham, 1974; Glémin and Bataillon, 2009; Glémin and Ronfort, 2013).

A Proposed Model for the Evolution of the Domestication Gene Network

Due to similar human needs, maize and rice experienced convergent phenotypic changes during domestication. Taking plant and inflorescence architecture as an example, both maize and rice domestication involved the transformation from highly branched plant architecture with small inflorescences to less-branched plants with large inflorescences. This suppression of tiller or lateral branch growth to enhance apical dominance is a typical shade-avoidance trait (Whipple et al., 2011; Studer et al., 2017). Indeed, the key genes underlying the morphological changes in plant and inflorescence architecture are involved in the shade-avoidance response (Whipple et al., 2011; Studer et al., 2017; Wei et al., 2018). Therefore, maize and rice domestication might

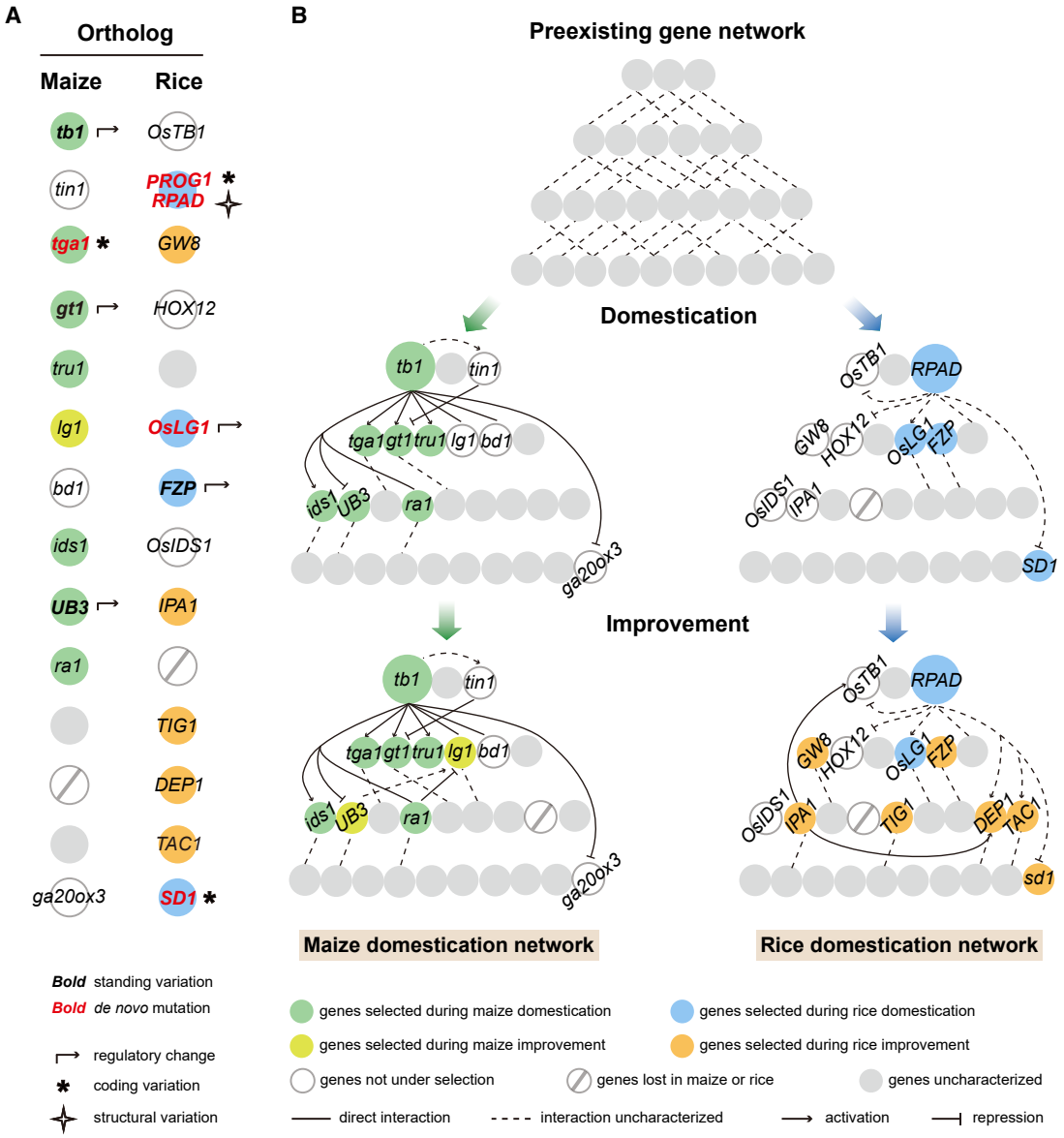

Figure 3. The Evolution of Maize and Rice Domestication Gene Network.

(A) Orthologous genes between maize and rice. The causative variants involving regulatory changes versus coding/structural variation and standing variation versus *de novo* mutation are shown for genes selected during domestication.

(B) Proposed model for the evolution of the domestication gene network. The three layers represent the pre-domestication, early domestication, and present stages, respectively. Each circle represents a gene, and the lines represent regulatory relationships among genes. Starting with a preexisting developmental gene network, maize and cultivated rice appeared to have evolved distinct genetic paths toward domestication: different central genes were utilized, orthologous genes played different evolutionary roles, and unique genes or regulatory modules were acquired for establishing new traits.

have used a preexisting developmental gene network to create plants with constitutive shade-avoidance phenotypes that are adapted to increased planting density under human cultivation. Given this similar developmental requirement, it is natural to ask whether maize and cultivated rice experienced convergent genetic changes to acquire convergent phenotypes during domestication. To address this question, we comprehensively compared the key genes controlling the changes in plant and inflorescence architecture during maize and rice domestication and propose a model for the evolution of the domestication gene network (Figure 3). We highlight four basic features associated with this evolutionary model.

First, different central genes were utilized during maize and rice domestication. *tb1* is the central gene of maize domestication (Studer et al., 2017; Dong et al., 2019a, 2019b). *tb1* is situated at the top of the maize domestication gene network, where it functions as a master regulator that directly regulates the expression of *tga1*, *gt1*, *tru1*, *ids1*, *UB3*, *ra1*, and many other important genes (Studer et al., 2017; Dong et al., 2019b). As a

result, the plant and inflorescence architecture of maize was restructured during domestication. The *RPAD* locus (including *PROG1* and other closely linked functional zinc-finger genes) appears to be the central regulator of rice domestication, given its strong selection signal and dramatic effect on plant and inflorescence architecture. Manipulating *RPAD* substantially altered the rice transcriptome, affecting the expression of many genes important for plant and panicle architecture (Wu et al., 2018), including *LAZY1* (Li et al., 2007), *TAC1* (Yu et al., 2007), *OsTB1* (Guo et al., 2013), *OsMADS57* (Guo et al., 2013), *OsD14* (Arite et al., 2009; Guo et al., 2013), *SD1* (Sasaki et al., 2002; Asano et al., 2011), *OsLG1* (Ishii et al., 2013; Zhu et al., 2013), *DEP1* (Huang et al., 2009; Sun et al., 2014), and *HOX12* (Gao et al., 2016). Therefore, like *tb1*, *RPAD* might also sit at the top of the gene network mediating rice domestication. Although *tb1* and *RPAD* played a crucial role in increasing apical dominance during maize and rice domestication, respectively, they function in different manners. *tb1* functions as a repressor of branching, while *RPAD* acts as a promoter of branching. The selection of a gain-of-function allele of *tb1* represses branching during maize domestication, while the selection of loss of function and deletion of functional zinc-finger genes at *RPAD* reduces branching during rice domestication. These functional differences at initial domestication might have led to the divergent evolutionary directions and strategies used by maize and rice during domestication.

Second, orthologous genes function in the regulatory network but play distinct evolutionary roles during maize and rice evolution. Among the 14 orthologous gene pairs between maize and rice we examined, notably, none of them were simultaneously targeted by selection during initial maize and rice domestication (Figure 3A). They are mostly targeted in only one species or in both species but in different evolutionary stages. For example, *tb1* played a key role in maize domestication, but its ortholog in rice (*OsTB1*), which represses tillering as well, was not targeted by selection during rice domestication or improvement (Xu et al., 2012; Lyu et al., 2020). Perhaps, unlike maize, an enhancer that could enhance *OsTB1* expression was not available for selection at the onset of rice domestication. Instead, a loss-of-function mutation at *PROG1* that reduces tillering and promotes erect growth occurred and was selected during initial rice domestication. Similarly, although *PROG1* played a key role in rice domestication, its ortholog in maize, *tiller number1* (*tin1*), was not selected during maize domestication or improvement, despite the fact that it also affects tillering (Zhang et al., 2019a). *gt1* played a key role in repressing ear prolificacy during maize domestication (Wills et al., 2013), while its rice ortholog *HOX12*, which regulates panicle exsertion (Gao et al., 2016), was not targeted by selection during rice domestication or improvement. In addition, some orthologous genes functioned during different stages of maize and rice evolution. For example, *tga1* was selected at the initial stage of maize domestication, while its rice ortholog *GW8*/*OsSPL16* was selected in modern breeding for improved grain yield and quality (Wang et al., 2012). *IPA1*/*OsSPL14* was selected during rice improvement, while its maize ortholog *UB3* was selected during both maize domestication and improvement (Jiao et al., 2010; Miura et al., 2010; Liu et al., 2015). *OsLG1* was selected at the initial stage of rice domestication, causing the transition in inflorescence architecture from spreading to compact panicles (Ishii et al., 2013; Zhu et al., 2013). However, its maize ortholog *lg1* controls leaf angle and was utilized during modern maize breeding to help maize adapt to high-density planting (Tian et al., 2011).

Third, lineage-specific genes or regulatory modules were selected to establish new traits. Maize and rice inflorescence architectures are very different. It appeared that different genes or regulatory modules were involved in their domestication. For example, *ra1* was crucial for repressing inflorescence branching in maize, but no *ra1* ortholog was found in rice (Vollbrecht et al., 2005; Kellogg, 2007). Conversely, *DEP1* controls panicle architecture in rice, but no *DEP1* ortholog was found in maize (Huang et al., 2009). In other cases, genes function in both maize and rice, but their regulatory networks appear to be different. For instance, *tb1* directly regulates the expression of *UB3* (homolog of *IPA1*) in maize, but *OsTB1* is directly regulated by IPA1 in rice (Lu et al., 2013; Dong et al., 2019b).

Fourth, some genes have been selected multiple times during maize and rice evolution. For example, a 4-bp tandem repeat deletion and an 18-bp tandem duplication in the upstream region of *FZP* were sequentially selected for increased grain number per panicle during the domestication and improvement of rice, respectively (Bai et al., 2017; Huang et al., 2018). The "Green Revolution" gene *SD1* was selected during early rice domestication and again during modern rice breeding (Asano et al., 2011). Two functional SNPs that affect the catalytic activity of SD1 were initially selected during early *japonica* rice domestication because they led to shorter culms (Asano et al., 2011). A second null allele of *SD1* from *indica* rice that resulted in a semi-dwarf phenotype has been extensively used in modern rice breeding, triggering the Green Revolution in the 1960s (Sasaki et al., 2002). This sequential selection of the same gene has been also observed in the flowering time adaptation. Two *cis*-regulatory variants in the promoter region of the maize florigen gene *ZCN8* evolved in a stepwise manner as maize spread from its tropical origin into the Mexican highlands (Guo et al., 2018). Similarly, two independent SNPs in *DHT2*, which controls heading date, were sequentially targeted by selection as *japonica* rice adapted to higher latitudes in northern Asia (Wu et al., 2013).

In summary, starting with a preexisting developmental gene network, maize and cultivated rice appeared to have evolved distinct genetic paths toward domestication: different central genes were utilized, orthologous genes played different evolutionary roles, and unique genes or regulatory modules were acquired for establishing new traits. Consistent with our conclusion, Gaut (2015) comprehensively compared the sets of genes selected during maize and rice domestication and notably found that only a very limited set of genes were selected in parallel in both species. Although a few cases of convergent selection of the same orthologous genes between maize and rice have been reported for a specific domestication trait (Lin et al., 2012; Sosso et al., 2015), at the overall domestication gene network level, the convergent phenotypic changes under maize and rice domestication more likely arose through different genetic routes.

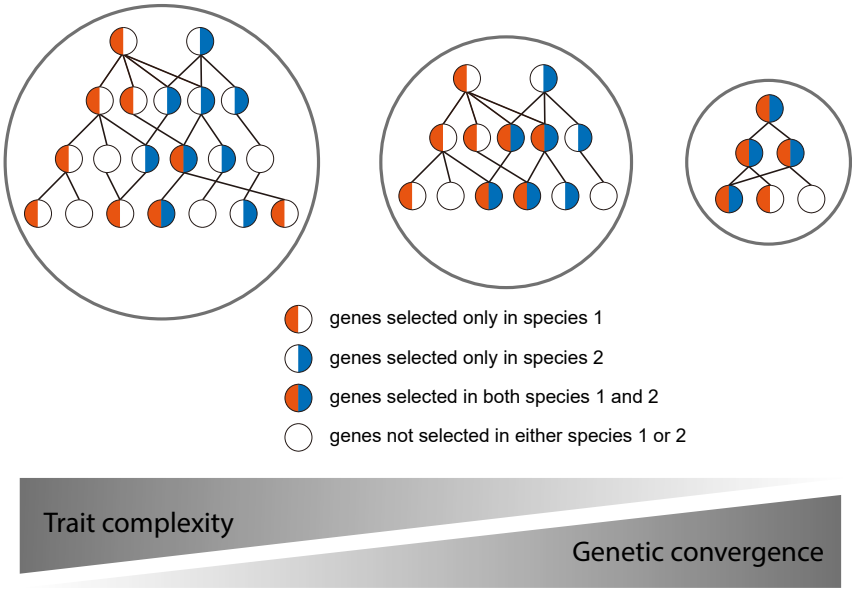

Figure 4. A Model for the Extent to Which Genetic Convergence Underlies Convergent Domestication.

From left to right, the size of the outer circle represents the complexity of the gene network underlying a given domestication trait. Within each circle, each small circle represents a gene, and the lines represent regulatory relationships among genes. The bottom scales indicate the relative degree of trait complexity and genetic convergence. We propose that genetic convergence is related to the conservation and complexity of the gene network underlying domestication traits. The complexity of the regulatory network defines the pool of genes that could be selected during domestication and thus determines the degree of genetic convergence. The leftmost circle represents a highly complex domestication trait involving regulation from many genes, thus which nodes (genes) in the network were actually selected in each crop species is associated with considerable evolutionary flexibility (low genetic convergence). The rightmost circle represents a simple trait with only a few genes involved, thus different crop species very likely repeatedly targeted the same set of orthologous genes to acquire similar phenotypes (high genetic convergence). The middle circle represents a moderately complex trait, and an intermediate genetic convergence is expected to occur.

The extent to which genetic convergence underlies the convergent phenotypic changes during crop domestication has been actively debated (Glémin and Bataillon, 2009; Gaut, 2015; Martínez-Ainsworth and Tenaillon, 2016; Pickersgill, 2018). We argue that the degree of genetic convergence is related to the conservation and complexity of the gene network underlying domestication traits (Figure 4). For domestication traits that possess similar developmental basis between species, the shared regulatory network sets potential constraints in the pool of genes that can be targeted during domestication. The complexity of the regulatory network defines the space of constraints and thus determines the degree of genetic convergence. If the regulatory network is simple with only a few genes involved, different crop species very likely repeatedly targeted the same set of orthologous genes to acquire similar phenotypes. If the pathway is complex involving regulation from many genes, which nodes (genes) in the pathways were actually selected in each crop species is associated with considerable evolutionary flexibility.

Systematic Changes Associated with Maize and Rice Domestication

Reduced Genetic Diversity

Most domesticated crops have experienced a "domestication bottleneck," which reduced genetic diversity throughout the genome (Figure 5A) (Doebley et al., 2006; Meyer and Purugganan, 2013; Olsen and Wendel, 2013). Among cereal crops, maize experienced a mild genetic bottleneck, as domesticated maize retained ~81% of the genetic diversity of its wild ancestor, teosinte (Hufford et al., 2012). Rice experienced a much more severe domestication bottleneck than maize. Asian cultivated rice (*O. sativa*) subspecies *indica* and *japonica* retained ~53% and ~20% of the genetic diversity of the wild ancestor *O. rufipogon*, respectively (Huang et al., 2010, 2012). African cultivated rice species *O. glaberrima* retained ~43%–54% of the diversity of its wild ancestor *O. barthii* (Wang et al., 2014; Cubry et al., 2018).

The genetic diversity of genes targeted by selection is reduced beyond that caused by the domestication bottleneck. Approximately 2%–4% of maize genes (Wright et al., 2005; Hufford et al., 2012) and 6%–8% of rice genes (Huang et al., 2012; Gaut, 2015; Liu et al., 2019) were targeted by selection during domestication and improvement. These genome-level studies potentially indicate that crop domestication and improvement is a gradual and complex evolutionary process involving changes in numerous genes controlling various biological traits or processes. At the onset of domestication, a few large-effect loci controlled the essential morphological transformations that made these plants dependent on humans for propagation (Tian et al., 2009; Stitzer and Ross-Ibarra, 2018). However, the subsequent adaptation to diverse environments and the improvement of various agronomic traits for increased yield and better quality might involve the selection of thousands of genes with small effects (Tian et al., 2009; Stitzer and Ross-Ibarra, 2018).

More Deleterious Mutations

The concept of the "cost of domestication" refers to the accumulation of deleterious genetic variants or increased genetic load in the genomes of domesticated species (Figure 5A) (Lu et al., 2006; Tang and Shi, 2007; Gaut et al., 2018; Moyers et al., 2018). The cost of domestication is primarily due to two factors. First, the reduced effective population size (N_e) during domestication could result in stronger genetic drift and reduced efficacy of selection, allowing deleterious variants to reach high frequency. Second, linked selection can drag deleterious mutations to high frequency through genetic hitchhiking (Lu et al., 2006; Tang and Shi, 2007; Gaut et al., 2018; Moyers et al., 2018). Most crops contain more deleterious variants than their wild relatives (Lu et al., 2006; Tang and Shi, 2007; Nabholz et al., 2014; Renaut and

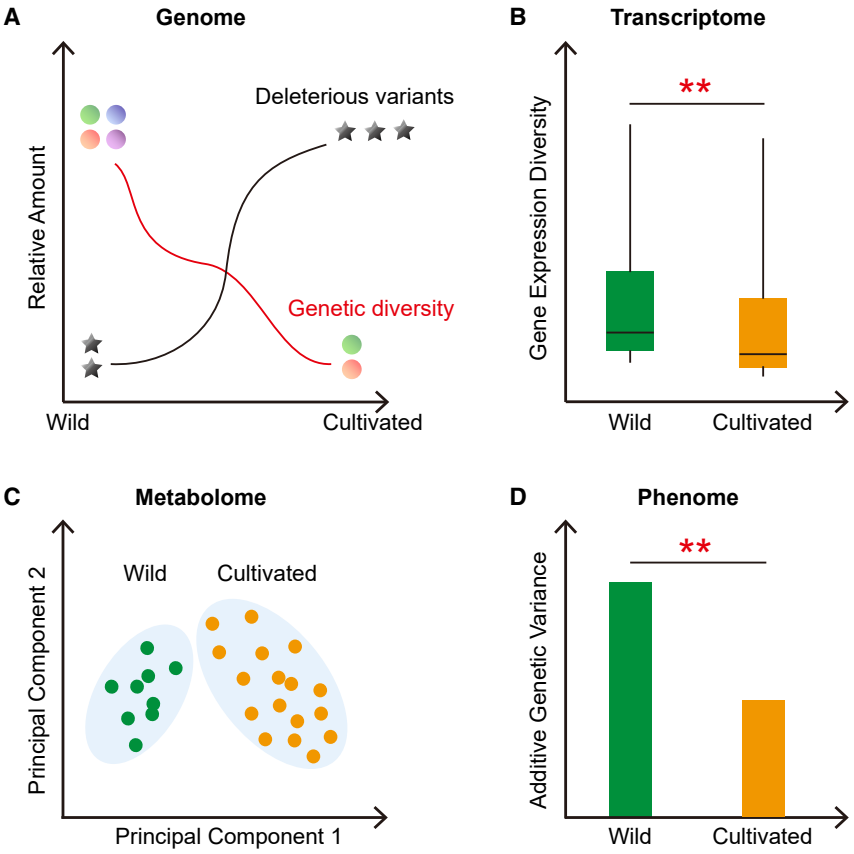

Figure 5. Systematic Changes Associated with Maize and Rice Domestication at the Molecular Level.

(A) Reduced genetic diversity and increased numbers of deleterious mutations in cultivated species.

(B) Reduced gene expression diversity in cultivated species.

(C) Metabolic divergence between wild and cultivated species.

(D) Depleted additive genetic variance in cultivated species (based on maize).

Rieseberg, 2015; Kono et al., 2016; Liu et al., 2017; Ramu et al., 2017; Wang et al., 2017; Zhou et al., 2017; Lian et al., 2019). In rice, domesticated individuals contain 3%–4% more deleterious alleles than wild individuals (Liu et al., 2017). By contrast, domesticated maize contains 10%–30% more deleterious alleles than teosinte (Wang et al., 2017).

Decreased Gene Expression Diversity

Changes in gene expression are central to evolution. Variation in gene expression can arise from both *cis* and *trans* regulatory changes. Like genetic diversity, gene expression diversity is reduced in maize compared with teosinte, primarily due to changes in *cis* rather than *trans* regulation (Hufford et al., 2012; Lemmon et al., 2014; Wang et al., 2018c). An extensive survey of the transcriptomes of domesticated and wild species of representative animals and plants, including maize and rice, revealed that gene expression diversity is generally lower in domesticated species (Figure 5B) (Liu et al., 2019). *Japonica* rice has significantly less expression diversity than *indica* rice (Campbell et al., 2020). Genes that were targeted by selection for regulatory differences have even less expression diversity (Lemmon et al., 2014; Liu et al., 2019).

Metabolic Divergence

Metabolic changes were indispensable to plant domestication. The metabolome is regarded as a bridge between the genome to phenome. Metabolome-based genome-wide association studies are widely performed to examine the natural variation underlying the diversity of plant metabolism (Fang and Luo, 2019). However, only a few studies of evolutionary changes in metabolism during crop domestication have been conducted to date (Beleggia et al., 2016; Zhu et al., 2018; Xu et al., 2019; Szymański et al., 2020).

Wide metabolic restructuring occurred during the domestication of tetraploid wheat due to changes in metabolic correlation networks (Beleggia et al., 2016). The tomato fruit metabolome was rewired during domestication and improvement, as the selection of alleles for larger fruits altered the metabolome due to nearby hitchhiking genes (Zhu et al., 2018).

The maize metabolome was reshaped during domestication and post-domestication adaptation (Figure 5C) (Xu et al., 2019). Distinct sets of metabolites were targeted by selection during the evolution from teosinte to tropical maize to temperate maize, and the recent metabolic divergence between tropical and temperate maize has a simpler genetic architecture than that between teosinte and tropical maize (Xu et al., 2019). Observations from maize, wheat, and tomato indicate that primary metabolites tend to be modified during the earlier stages of crop domestication, while secondary metabolites are more likely to be modified as crops adapt to new environments. Although the metabolic changes that occurred during rice domestication are unclear, the *O. sativa* subspecies *indica* and *japonica* show significant metabolic divergence (Chen et al., 2014; Hu et al., 2014; Deng et al., 2020). Notably, genome-wide association study of natural variation in rice metabolism revealed that most subspecies-specific metabolites are under distinct genetic control (Chen et al., 2014).

Depleted Additive Genetic Variance

Even though many studies on the genetic basis of crop domestication have been performed, the genetic architecture of wild progenitors and how it was altered during domestication remain largely unexplored. A recent evolutionary quantitative genetic study of teosinte and maize landrace populations revealed that additive genetic variance in domestication traits was generally depleted during maize domestication, especially for reproductive traits, whereas the proportion of genetic variance attributable to dominance increased (Figure 5D) (Yang et al., 2019). This notion was further confirmed by a genome-wide QTL analysis showing that maize landrace had significantly fewer QTLs and increased dominance effects compared with teosinte (Chen et al., 2020). Such studies have not yet been performed in rice. Further systematic analyses of the genetic architecture of

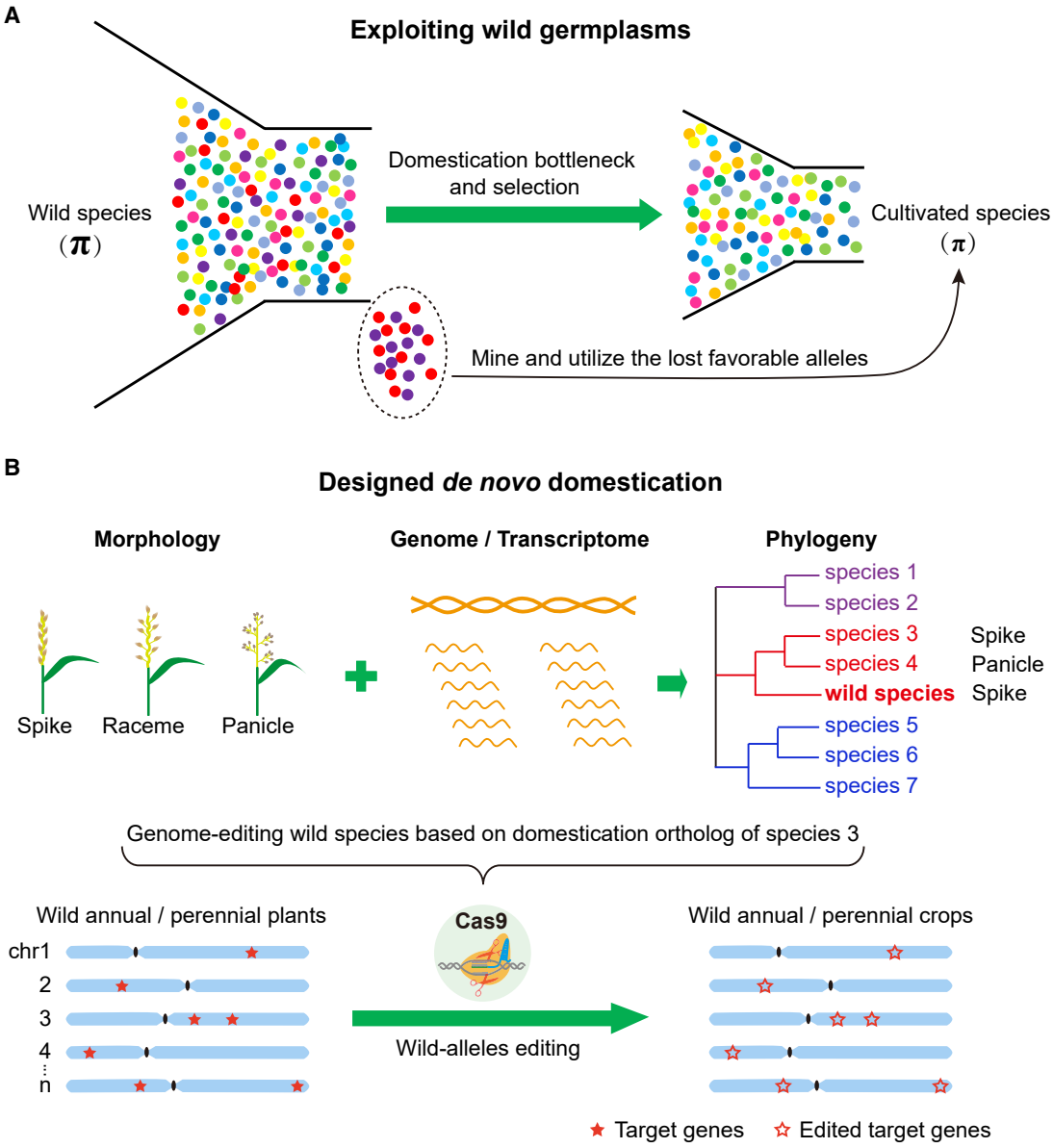

Figure 6. Potential Approaches for New Crop Breeding.

(A) Mining and utilizing favorable alleles from wild species via conventional introgression with marker-assisted selection.

(B) Designed *de novo* domestication of a wild species by genome editing. First, systematically investigate the morphology of the wild species and compare it with domesticated crops. Second, obtain genomic sequences and gene information for the wild species by whole-genome and transcriptome sequencing. Third, perform phylogenetic analysis of the wild species and well-characterized domesticated crops. Fourth, create an efficient tissue culture and transformation system for the wild species. Finally, perform multiplex genome editing of a few domestication orthologs from the ideal crop model and evaluate the performance of the newly created crop.

domestication traits in cultivated crops and their progenitors should shed light on this little-known aspect of crop domestication.

Perspectives and Potential Approaches for New Crop Breeding

Mining and Utilizing Favorable Alleles from Wild Species

Abundant genetic diversity is the basis of crop breeding, as it determines the potential for trait improvement. However, the long domestication and improvement process has led to reduced genetic diversity, which might have excluded many favorable alleles that would be valuable for modern breeding (Figure 6A). Along with reduced genetic diversity, deleterious mutations accumulated in crop genomes over time. These genomic changes caused modern crops to have a narrower genetic basis, thus increasing their vulnerability to climate change and limiting the potential for further improvement. Wild species represent the largest reservoir of genetic diversity for crop improvement (Tanksley and McCouch, 1997). Moreover, wild relatives possess many unique traits, such as abiotic and biotic stress resistance (Zhang and Batley, 2020). Therefore, mining hidden useful

variants from wild species represents an important strategy for modern crop improvement (Hake and Richardson, 2019).

Conventional introgression by marker-assisted selection is the most widely used strategy to mine and utilize favorable alleles from wild species for crop improvement. During this process, an interspecies advanced backcross population in the genetic background of an elite cultivar is constructed, followed by QTL analysis of the traits of interest. QTL-near isogenic lines are then developed to verify the effects of the wild alleles and used as donors in breeding (Tanksley and Nelson, 1996). This type of exotic introgression library was first developed and used for QTL cloning in tomato (Eshed and Zamir, 1995). Similar introgression libraries have been successfully constructed in other crops, including maize and rice, leading to the cloning of a series of domestication QTLs and the discovery of favorable alleles from wild species (Zamir, 2001; Tian et al., 2006; Tan et al., 2007; Ali et al., 2010; Li et al., 2016; Chen et al., 2019b; Shannon et al., 2019).

The QTLs *UPA1* (*Upright Plant Architecture1*) and *UPA2*, conferring upright plant architecture, were identified in a maize-teosinte BC_2S_3 population. The teosinte allele at *UPA2*, which reduces leaf angle, was lost during maize domestication (Tian et al., 2019). Introgressing this allele into modern maize hybrids produced more compact plants and enhanced yields under high planting densities (Tian et al., 2019; Kong et al., 2020). *CHILLING TOLERANCE DIVERGENCE1* (*COLD1*) confers chilling tolerance in rice. The chilling tolerance allele of *COLD1* originated from Chinese *O. rufipogon* and was selected during *japonica* rice domestication, allowing rice to be cultivated in northern areas with lower yearly temperatures (Ma et al., 2015). Favorable alleles that could directly improve the yields of cultivated rice were also identified in wild rice (Xiao et al., 1996; Li et al., 2002; He et al., 2006). In addition to agronomic traits, wild relatives also contain unique alleles that could be used to improve cultivated crops. For example, a wild rice allele of *BROWNING OF CALLUS1* (*BOC1*) that does not exist in cultivated rice could significantly reduce callus browning when introduced into cultivated rice, thereby improving the genetic transformation efficiency (Zhang et al., 2020).

Creating Novel Alleles or New Traits for Crop Breeding

The cloning of QTLs for agronomic traits and our understanding of their regulatory mechanisms provide a basis for rational design breeding (Zeng et al., 2017). To achieve this goal, different favorable QTL alleles for different traits must be pyramided into elite backgrounds. However, this process is challenging, as it involves multiple rounds of crossing and selection via conventional breeding. Linkage drag could become an issue during cross introgression, which would limit the efficiency of this process. Genome-editing technologies, particularly the recently developed clustered regularly interspaced short palindromic repeats (CRISPR)/CRISPR-associated protein (Cas) system (Cong et al., 2013; Mali et al., 2013), allow crop traits to be precisely modified, thus promising to accelerate crop improvement (Song et al., 2016; Zhang et al., 2018b, 2019b; Chen et al., 2019a; Hua et al., 2019; Li et al., 2020b).

Recent studies have demonstrated the great potential of genome editing for rapidly generating and pyramiding novel alleles for both simple and complex traits (Chen et al., 2019a; Hua et al., 2019). Genome editing has been widely used to target specific genes in crops to improve quality (Shan et al., 2015; Sun et al., 2017; Zhang et al., 2018a), stress resistance (Shi et al., 2017; Tang et al., 2017; Oliva et al., 2019), adaptation (Soyk et al., 2017; Cai et al., 2018), and yield-related traits (Li et al., 2016; Xu et al., 2016; Rodríguez-Leal et al., 2017). The newly created novel alleles can behave even better than natural alleles. For instance, due to the elimination of linkage drag, CRISPR/Cas9-edited waxy corn had significantly higher yields than introgressed waxy hybrids in the field (Gao et al., 2020). Replacing the maize *ARGOS8* promoter with the *GOS2* promoter increased yield under drought stress (Shi et al., 2017). The recently developed multiplex genome-editing systems make it possible to simultaneously target multiple genes to achieve the coordinated improvement of multiple traits or creating novel traits (Shen et al., 2017; Wang et al., 2018b; Zhou et al., 2019). For instance, three rice yield-related genes (*Gn1a*, *GW2*, and *GS3*) were simultaneously modified using CRISPR/Cas9 multiplex genome editing, generating triple mutants with significantly better grain yields than the wild type across different genetic backgrounds (Zhou et al., 2019). Simultaneously editing three genes (*TMS5*, *Pi21*, and *Xa13*) generated male sterile rice with enhanced disease resistance (Li et al., 2019). Simultaneously engineering genes controlling meiosis and fertilization led to the establishment of synthetic apomixis, allowing clonal reproduction from F_1 hybrids (Wang et al., 2019b; Khanday et al., 2019).

Genome-editing technologies can be used to rapidly modify crops to make them suitable for new agricultural modes. For instance, by performing one-step targeting of three genes controlling plant architecture and flowering time, Kwon et al. (2020) successfully restructured vine-like tomato plants into compact, early yielding plants suitable for urban vertical farming, a new production mode to help cope with the growing urban population, changing climate, and diminishing availability of resources. Genome-editing techniques have also been coupled with other breeding techniques to achieve rapid breeding. Haploid-Inducer Mediated Genome Editing and Haploid Induction-Edit, which combine haploid induction with CRISPR/Cas9-mediated genome editing, can be used for direct genomic modification of commercial crop varieties, thus bypassing the laborious and lengthy introgression process required in traditional breeding (Wang et al., 2019a; Kelliher et al., 2019).

De novo Domestication of New Crops

Among the >30 000 plant species on Earth, approximately 2500 have undergone some degree of domestication (Meyer et al., 2012), but only ~300 have been fully domesticated (Meyer and Purugganan, 2013; Salman-Minkov et al., 2016). Of these, a dozen crops provide the majority of calories consumed by humans, with maize, rice, and wheat providing more than half of these calories (Ross-Ibarra et al., 2007). Due to rapid, large-scale environmental and social changes, our reliance on a few food species poses challenges for food security and sustainable agriculture. Genome editing and other emerging technologies, together with our unprecedented understanding of the crop domestication process, enable *de novo* domestication of new crops (Figure 6B).

The initial morphological changes that occurred during crop domestication are mainly controlled by a few large-effect loci, providing a theoretical basis for domesticating new crops. Therefore, genetic modifications of a few major genes from "undomesticated" species could bring about rapid evolution. Domestication genes identified from different crops appear to have conserved biological functions, making them primary targets for *de novo* domestication. During crop domestication, changes in plant and inflorescence architecture are the most critical shifts that facilitate human cultivation and harvesting. Therefore, precise editing of the orthologous genes controlling plant and inflorescence architecture could represent the first step in *de novo* domestication. The florigen and gibberellin systems are also important targets for genome editing to rapidly generate beneficial variation (Eshed and Lippman, 2019). Moreover, it would be beneficial to target perennial wild plants, which tend to have longer growing seasons and deeper rooting systems than annual cultivated crops, to achieve sustainable agriculture (Moffat, 1996; Glover et al., 2010; DeHaan et al., 2020).

Significant advances have recently been made in the *de novo* domestication of wild species or ''orphan'' crops by multiplex editing of the orthologs of major domestication genes (Fernie and Yan, 2019). Zsögön et al. (2018) and Li et al. (2018) successfully *de novo* domesticated wild *Solanum pimpinellifolium*, the wild ancestor of the modern tomato, by simultaneously editing a suite of domestication genes involved in fruit traits, plant architecture, and nutritional quality. The engineered *S. pimpinellifolium* plants exhibited significantly improved yield and quality while retaining the stress resistance of the wild species. Lemmon et al. (2018) demonstrated that editing orthologs of tomato domestication genes controlling plant architecture, flower production, and fruit size rapidly improved the productivity of the orphan crop *Physalis pruinosa* (groundcherry), a distant relative of tomato. Ye et al. (2018) successfully re-domesticated potato into a self-compatible diploid by editing the self-incompatibility *S-RNase* gene, opening new avenues for diploid potato breeding.

Through a comprehensive comparison, we demonstrated that domestication of maize and rice is associated with different regulatory and evolutionary mechanism. Rice domestication tended to select *de novo*, loss-of-function, coding variation, while maize domestication more frequently utilized standing, gain-of-function, regulatory variation. These contrasting findings potentially suggest that different engineering strategies might be required when domesticating new outcrossing or selfing species. Simply disrupting the gene coding region can easily create loss-of-function alleles, as performed in many studies (Shan et al., 2015; Li et al., 2016; Cai et al., 2018; Soyk et al., 2017; Sun et al., 2017; Wang et al., 2019b; Khanday et al., 2019; Gao et al., 2020; Kwon et al., 2020). It is relatively challenging to edit variation that affects the expression level and/or tissue specificity of a gene. The increased apical dominance in maize is primarily attributed to the regulatory changes in the branching repressors *tb1* and *gt1*. A *Hopscotch* transposon insertion ~60 kb upstream of *tb1* functions as an enhancer to upregulate *tb1* expression (Studer et al., 2011), while a 2.7-kb upstream regulatory region of *gt1* controls its specific expression in the nodes of the upper branches (Wills et al., 2013). Therefore, precisely upregulating *tb1* and *gt1* would be a key step in re-domesticating teosinte. Newly developed editing techniques, such as base editing, knock-in, and replacement could be used to precisely edit regulatory sequences (Chen et al., 2019a; Hua et al., 2019). Indeed, promoters or *cis*-regulatory regions have been successfully edited using these techniques, including *SlCLV3*, *SlS*, and *SlSP* in tomato, *ARGOS8* in maize, and *Xa13* in rice (Rodríguez-Leal et al., 2017; Shi et al., 2017; Li et al., 2020a).

By comparing the maize and rice domestication gene networks, we showed that maize and cultivated rice used different genetic paths toward acquiring convergent phenotypes during domestication. The gene network controlling domestication traits appears to be relatively conserved, while which genes in the network were targeted during domestication might be associated with considerable flexibility. This evolutionary flexibility under domestication poses challenges but also provides great opportunities in *de novo* domesticating new crops. Given that targeting different sets of genes in the regulatory network might acquire similar phenotypes, it is important to select the appropriate combinations of target genes for engineering. For *de novo* domestication of wild tomato, Zsögön et al. (2018) and Li et al. (2018) selected two common genes and four versus three different genes for precise editing. Both studies generated engineered lines with significantly improved yield and quality. It would be interesting to perform a systematic test to access which combination of genes or alleles behaves the best. Such studies would help us understand and further refine the molecular regulatory network, which in turn would promote new rounds of *de novo* domestication.

Concluding Remarks

The worldwide population is expected to increase by 2 billion in the next 30 years according to the UN's ''World Population Prospects 2019.'' Such an increase will pose a great challenge to food security. Thus, it is crucial to create sustainable agriculture. To achieve this goal, knowledge-driven crop breeding is required. Many genetic and genomic analyses have shed light on the evolutionary processes associated with crop domestication and improvement, providing a theoretical basis for novel crop breeding. Based on our survey, we argue that maize and rice may have evolved distinct genetic solutions toward domestication: domestication of maize and rice is associated with distinct regulatory and evolutionary mechanisms, and distinct genetic paths in the gene network have been used to acquire convergent phenotypes. We provide three potential approaches for new crop breeding, including mining and utilizing favorable alleles from wild species, creating novel alleles or new traits for breeding by genome editing, and *de novo* domestication of new crops via knowledge-driven design. Other cutting-edge techniques, such as synthetic biology and big data-driven machine learning or artificial intelligence, will help achieve the goals of improving old crops and designing new crops to meet the increasing demands for crop production due to the growing population and changing environment.

SUPPLEMENTAL INFORMATION

Supplemental Information is available at *Molecular Plant Online*.

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AUTHOR CONTRIBUTIONS

F.T., L.T., and Q.C. conceived and discussed the ideas for the manuscript. Q.C. drafted the manuscript. F.T., Q.C., L.T., and W.L. revised the manuscript. Q.C. and W.L. prepared the figures and tables.

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