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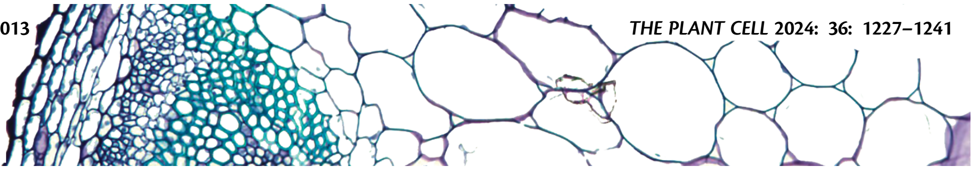

Review

Domestication and the evolution of crops: variable syndromes, complex genetic architectures, and ecological entanglements

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Abstract

Domestication can be considered a specialized mutualism in which a domesticator exerts control over the reproduction or propagation (fitness) of a domesticated species to gain resources or services. The evolution of crops by human-associated selection provides a powerful set of models to study recent evolutionary adaptations and their genetic bases. Moreover, the domestication and dispersal of crops such as rice, maize, and wheat during the Holocene transformed human social and political organization by serving as the key mechanism by which human societies fed themselves. Here we review major themes and identify emerging questions in three fundamental areas of crop domestication research: domestication phenotypes and syndromes, genetic architecture underlying crop evolution, and the ecology of domestication. Current insights on the domestication syndrome in crops largely come from research on cereal crops such as rice and maize, and recent work indicates distinct domestication phenotypes can arise from different domestication histories. While early studies on the genetics of domestication often identified single large-effect loci underlying major domestication traits, emerging evidence supports polygenic bases for many canonical traits such as shattering and plant architecture. Adaptation in human-constructed environments also influenced ecological traits in domesticates such as resource acquisition rates and interactions with other organisms such as root mycorrhizal fungi and pollinators. Understanding the ecological context of domestication will be key to developing resource-efficient crops and implementing more sustainable land management and cultivation practices.

Introduction

Domestication can be considered a specialized mutualism in which a domesticator exerts control over the reproduction or propagation (i.e. fitness) of a domesticated species to gain resources or services, resulting in a unique coevolutionary dynamic (Zeder 2014; Zeder 2015; Purugganan 2022). The process of domestication provides powerful models to study recent evolutionary adaptations and their genetic bases (Ross-Ibarra Morrell and Gaut 2007). Charles Darwin used domesticated crops to understand variation and selection (Darwin 1868), and over the last 150 years, crops have served as models in both genetic and evolutionary studies (Andersson and Purugganan 2022). The domestication and dispersal of crop plant species such as rice, maize, and wheat beginning about 13,000 years ago also helped bring about dramatic changes in human social and political organization (Diamond 2002; Purugganan and Fuller 2009); today, crops are the foundation of modern human societies by providing the majority of food resources—as well as other products—necessary for the survival of the global population.

The nature of domestication has been the subject of intense debate, and over the last two decades our

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understanding of this process has advanced considerably (Abbo et al. 2022; Allaby et al. 2022). Although earlier studies had suggested that domestication could have been a rapid process (Abbo et al. 2011), archaeological evidence increasingly indicates that early domestication was largely a protracted, often landscape-level process characterized by weak, unconscious selection occurring over long time periods (Purugganan and Fuller 2011; Meyer et al. 2012; Arranz-Otaegui et al. 2016; Allaby et al. 2022). Consistent with a protracted transition from wild to domesticated forms, recent genomic studies in multiple domesticated crops have shown a gradual to negligible decline in effective population size during early domestication (Gross et al. 2014; Meyer et al. 2016; Allaby Ware, and Kistler 2019; Trucchi et al. 2021; Zhou et al. 2017) rather than a rapid or instantaneous bottleneck that might be expected if domestication involved sampling from a wild population once or a small number of times followed by strong selection (Purugganan 2019). For example, a recent study on ancient domesticated common beans from South America showed that the beans—with ages ranging from 600 to 2,500 years old—maintained equivalent levels of genetic diversity to modern wild populations, suggesting that the reduced diversity in modern cultivars is a consequence of more recent human cultivation practices rather than processes during the early domestication period (Trucchi et al. 2021).

The discovery of different, independent Neolithic centers of domestication (Vavilov 1994) also provides the opportunity to explore the process of domestication as parallel natural experiments (Gepts 2003). Overall, domestication of crops appears to have occurred in at least 24 different geographic areas, the earliest being in the Fertile Crescent, China, and the Americas (Purugganan and Fuller 2011). Multiple cereal crop species from different domestication centers such as rice, maize, wheat, and sorghum share to varying degrees a set of traits, including non-shattering seeds, increased seed size, reduced seed dormancy, loss of outcrossing, and apical dominance, which are collectively referred to as the domestication syndrome (Hammer 1984; Allaby 2014; Preece et al. 2017). Adaptations such as non-shattering seeds, shoot architecture, and seed dormancy have been shown to at least partially arise from changes in the same underlying genes—*Sh1* (Lin et al. 2012), *Tb1* (Ramsay et al. 2011; Remigereau et al. 2011), and *G* (M. Wang et al. 2018), respectively—in multiple species. Instances of convergent evolution of domestication phenotypes, and sometimes genotypes, are in line with domestication being a distinct evolutionary process among species sometimes leading to shared features and outcomes (Lenser and Theißen 2013). Finally, the process of domestication is also often characterized by gene flow or hybridization between different species or populations, as observed in wheat (Wang et al. 2022), citrus (Wu et al. 2014), maize (Kistler et al. 2020), rice (Choi et al. 2017; Wu et al. 2023), and others. Hexaploid bread wheat, for instance, arose from hybridization between tetraploid emmer wheats—domesticated near the onset of agriculture in the Fertile Crescent more than 10,000 years ago—and wild goatgrass (Dvorak et al. 1998; International Wheat Genome Sequencing Consortium 2014).

Over the last few decades, there have been important strides in our understanding of domestication and crop evolution, although our understanding remains incomplete and multiple issues are unresolved. For this review, we identify and focus on three fundamental areas of crop domestication research that are transforming long-held ideas on the process of domestication. Our first area of focus is on domestication phenotypes and the nature of domestication syndromes. Cereal crop traits heavily inform traditional conceptions of the crop domestication syndrome, but many such traits are not universal across crops (Meyer et al. 2012). In fact, it has been challenging to define a consistent set of domestication phenotypes for other types of crop domesticates such as vegetatively propagated field crops like sugarcane, potato, and cassava (Denham et al. 2020). Understanding variation in domestication traits and syndromes across crops will be key to identifying shared and heterogeneous aspects of the domestication process. Recent comparative analyses have begun to define distinct domestication syndrome traits (Fuller 2018) or reframe the domestication syndrome as more general tendencies (Denham et al. 2020) for specific crop types.

The second area we explore is the genetic architecture underlying domestication and crop evolution. Early studies on genetic loci associated with domestication identified several large-effect mutations associated with phenotypes such as non-shattering seeds and apical dominance (Li et al. 2006; Whipple et al. 2011), which shaped a relatively simple view of the domestication process. It is, however, becoming increasingly clear that many domestication phenotypes have complex and polygenic genetic architectures that often require high-resolution genome-wide association studies (Xue et al. 2016) or observation in a wild genomic background (Ishikawa et al. 2020) to be revealed. In addition, the concept of a domestication locus remains nebulous with regard to when mutations need to have arisen or become selected. Ancient DNA, when available, (Jaenicke-Després et al. 2003; Vallebueno-Estrada et al. 2016) and new methodological advances in dating allele ages and selective sweeps (Speidel et al. 2019; Stern et al. 2019) are likely to be useful in dissecting the evolutionary genetics of the domestication process while distinguishing it from later selection during crop diversification and recent breeding.

Finally, we examine the ecological context of domestication. The milieu and impact of domestication extends beyond the domesticator and domesticated species to their environmental and ecological context. Domestication studies have focused on phenotypic traits that appear to be directly favorable to humans, but there have been relatively fewer studies on selection on ecological traits within human-constructed environments during the protracted domestication period (Chen et al. 2015; Milla 2023). Ecological traits such as growth and resource acquisition rates and interactions with microbes, pollinators, and other organisms have

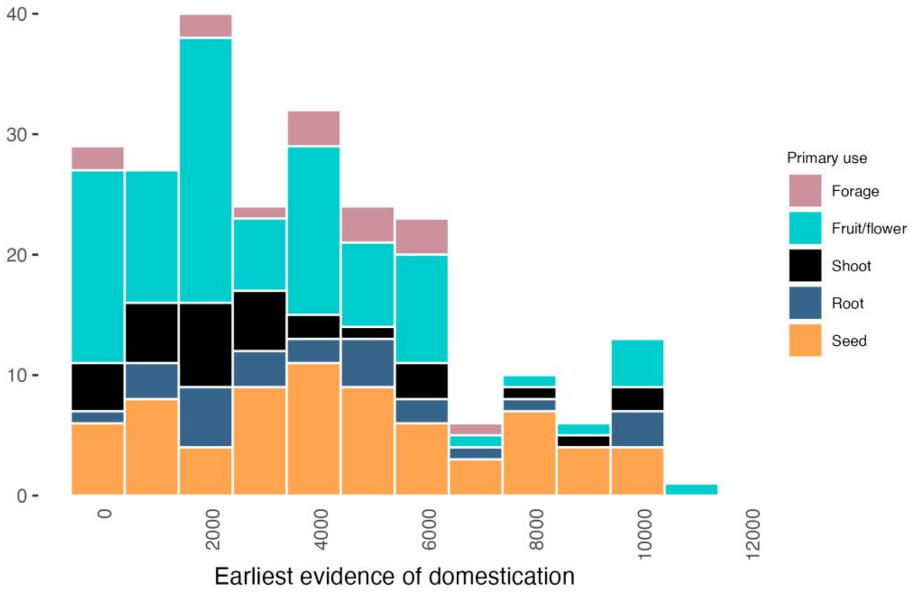

Figure 1. Domestication events through time. Number of domestication events in 1,000-year windows (the label "2000" corresponds to the window between 2,000 and 3,000 years ago). Crops are further grouped by the primary part of the plant used. Based on 235 species with dates for earliest evidence of domestication in the Crop Origins and Phylo Food database reported in Milla 2020.

implications for land management and sustainability of cultivation practices, and a better understanding of the ecology of domestication can help to both raise yield and more sustainably manage local ecosystems.

The domestication syndrome and beyond

Crop plant species evolve under domestication as a direct result of human-associated selection or as adaptations to the human-constructed environments developed for their growth and exploitation. The traditionally defined domestication syndrome in crops comprises a set of common phenotypic traits that were selected across different species during the transition from wild to domesticate, facilitating the mutualistic interaction between crops and humans and allowing for growth in human-constructed agricultural niches (Allaby 2014). For instance, multiple cereal crops including rice, wheat, and sorghum exhibit loss of shattering to facilitate harvesting (Z. Lin et al. 2012), as well as increased grain (Gegas et al. 2010; Zuo and Li 2014; Han et al. 2015) and plant size relative to their respective wild progenitors (Milla et al. 2014; Kluyver et al. 2017; Preece et al. 2018; Allaby et al. 2022).

Analysis of 203 domesticated crop species—including cereals, fruit trees, tubers, and leafy vegetables, among others—revealed that domestication traits vary among crop species depending on biology, the parts of the plant used by humans, and local climates (Meyer et al. 2012). Changes in secondary metabolites linked to changes in flavor, color, and toxicity constituted the most universal domestication-related trait among all the considered species (Meyer et al. 2012). Crops from arid climates such as the Near East tended to undergo changes in seed morphology and shattering during domestication, whereas crops from humid climates such as Near Oceania did not (Meyer et al. 2012). Trees and other perennials tended to be domesticated later than annuals (evident in Fig. 1), while the rate of domestication—measured in terms of the time between first exploitation of wild ancestor and first evidence of domestication for a crop—accelerated with more recently domesticated species, possibly as agriculture became increasingly established (Meyer et al. 2012). In general, the number of domestications attempted increased dramatically starting from about 6,000 to 7,000 years ago (Fig. 1) (Milla 2020).

The degree of completeness of domestication and the number of domestication traits that arise depend on the patterns of human interaction with the domesticate species and their wild ancestors, and these interactions may have prolonged pre-domestication or pre-cultivation histories. Pre-agricultural societies often engaged in some form of ecosystem management, influencing and maintaining the growth of multiple species and foraging what they needed (Rowley-Conwy and Layton 2011). Ecosystems managed for human use, which have been described as domesticated landscapes, can provide the context for greater investment in the care of particularly useful species and include intentional planting and the removal of competitors; these may impose unconscious and conscious selection pressures for domestication even in the absence of cultivation (Levis et al. 2018; Clement et al. 2021). Archaeobotanical studies in the Neotropics have found evidence for incipient or incomplete domestication, occurring as far back as more than 10,000 years ago (Clement et al. 2021). In Amazonia, there is evidence of increasing use and abundance of various palm species starting about 12,000 years ago (Roosevelt et al. 1996; Morcote-Ríos et al. 2021), with species such as the Brazil nut subsequently going on to be domesticated and cultivated (Pärssinen et al. 2021). Major Mesoamerican agricultural crops such as maize and squash had also begun to be domesticated earlier than 9,000 years ago, even though recognizable large-scale food production systems start appearing in the archaeological record only about 4,000 years ago (Clement et al. 2021).

A more nuanced view of domestication traits as continuous (rather than discrete) and possibly unique to the utilization history of individual species is thus emerging. Early landscape management and small-scale cultivation practices pre-dating the origin of agricultural societies likely helped create a continuum of domestication traits rather than a complete domestication syndrome (Clement et al. 2021). Domestication may remain incomplete or incipient for long periods, as has been noted in the amaranth species *Amaranthus caudatus* in South America (Stetter et al. 2017) and fonio millet in West Africa (Abrouk et al. 2020). In addition to weak selection pressures likely experienced in managed ecosystems, genetic constraints such as indirect antagonistic pleiotropy, lack of standing genetic variation, and continuous gene flow from wild populations can impact the rate at which domestication traits are fixed (Stetter 2020).

Understanding variation in domestication traits and syndromes across crops will be key to identifying shared and heterogeneous aspects of the domestication process across groups as divergent as cereals, vegetables, fruit trees, and tubers. Indeed, insights on the domestication syndrome in crops largely come from research on major cereal crops such as rice, wheat, and maize (Meyer et al. 2012), and much less is known about what phenotypes or traits constitute domestication syndrome(s) in other types of crop domesticates. Recently, it has been proposed that specific domesticated crops are associated with seven nonexclusive domestication pathways: (i) palms and nut trees through ecosystem engineering or management, (ii) ruderal plants that initially thrived in human-disturbed environments, (iii) tubers, (iv) grain crops, (v) segetal or former weedy species like oats, (vi) fiber crops, and (vii) fruit trees (Fuller et al. 2023). Such a framework opens up avenues to explore domestication traits and evolutionary dynamics within each pathway and shared across pathways. For instance, grain crops, nut and fruit trees, and tuber crops all tend to show increases in yield of the edible portion, such as through the production of swollen regions along the root system in the root tubers cassava and sweet potato (Denham et al. 2020). On the other hand, non-shattering of seeds or pods to retain seeds for harvesting is more unique to grain crops (cereals and legumes), while fused or bunched vegetative storage organs tend to have evolved in fruit- and nut-bearing trees such as bananas, figs, and breadfruit (Denham et al. 2020). In practice, the domestication pathways defined by Fuller et al. may leave the classification of certain species (for example, agave, tea, and leafy greens such as spinach) ambiguous, and require knowledge of the early domestication or pre-cultivation histories of crops. A cursory look at domestication syndrome traits in crops grouped by the primary part of the plant used—which is correlated with the pathways—reveals different distributions of the traits (Fig. 2).

Similar to the domestication trait continuum (Clement et al. 2021), the idea of domestication tendencies rather than traits

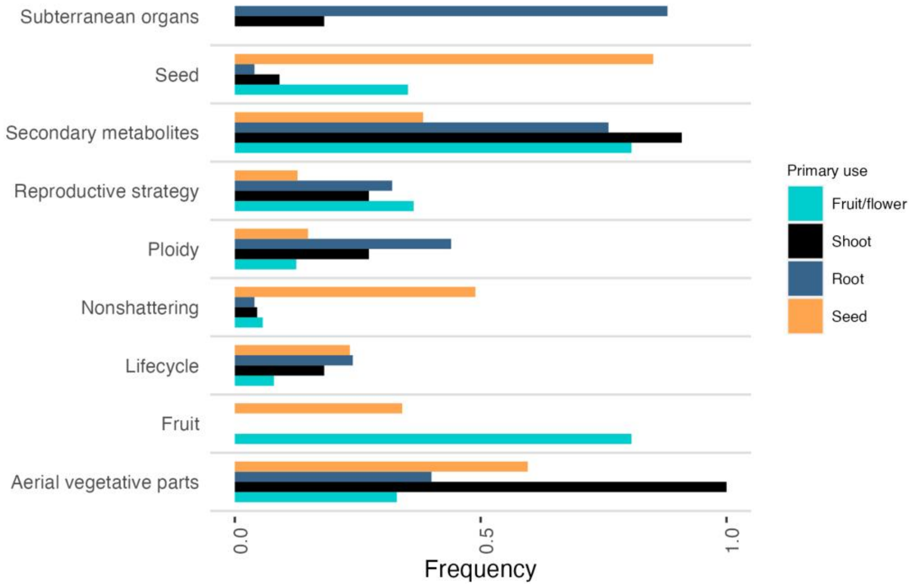

Figure 2. Domestication syndrome traits in crops grouped by the primary part of the plant used. Data on domestication syndrome traits from dataset reported in Meyer et al. 2012 and crop use data from Milla 2020. Based on 182 species identified as either domesticated or semi-domesticated in Meyer et al. 2012 that are present in Milla 2020 and not used primarily as animal feed.

has been invoked for vegetatively propagated field crops such as potato, manioc, and many fruits, as phenotypic signatures of domestication in these species appear more variable than in cereals (Denham et al. 2020; Fuller et al. 2023). More exhaustive study of domestication traits in these crops can help elucidate the process of their domestication. For instance, fewer phenotypic shifts during domestication in perennial fruit trees have been linked to less severe bottleneck effects in the history of perennials compared to annuals; bottleneck effects have a smaller number of generations to accrue in trees, which tend to have longer generation times than cereals (Gaut et al. 2015). Moving forward, evaluating a wider range of possible domestication phenotypes as quantitative traits that differ in distributions or mean values between domesticates and wild progenitors (Casas et al. 2007; Xue et al. 2016) and mapping them along categories like the recently defined domestication pathways (Fuller et al. 2023) may help organize the evident complexity and heterogeneity of crop domestication traits.

Finally, understanding domestication phenotypes in each domesticate is a prerequisite to subsequent exploration of their underlying genetics. The genetic architecture of domestication traits—and perhaps tendencies—as well as the order in which genetic variants associated with the traits arose are key to understanding the dynamics and selective landscape of the domestication process.

In search of domestication loci

A major challenge in plant biology has been the identification of genes associated with crop domestication, especially those that underlie key species-specific traits that distinguish the domesticate from their wild ancestor. Across the major crop species, top-down and bottom-up approaches to understanding the genetic architecture of domestication have yielded differing views of the number of genes involved in crop domestication (Kantar et al. 2017).

Top-down methods seek to identify genetic loci underpinning observed domestication traits by genetic mapping of known domestication phenotypes. The study of the genes and genetic architecture underlying domestication traits have advanced significantly with the advent of genetic mapping, primarily QTL mapping approaches (Paterson 2002; Jantasuriyarat et al. 2004; Li et al. 2006; Liu et al. 2007; Wills and Burke 2007) coupled eventually with genome sequencing (Doebley et al. 2006; Meyer and Purugganan 2013; Andersson and Purugganan 2022). These have led to the identification of canonical domestication loci such as *Sh4* for non-shattering in rice (Li et al. 2006), *Tb1* for plant and inflorescence architectures in maize (Doebley et al. 1995), and *Q* for threshability and other traits in wheat (Kato et al. 2003; Jantasuriyarat et al. 2004). Taking a trait-first view of domestication often revealed a small number of strong-effect alleles driving phenotypes. For instance, a single amino acid substitution in *Sh4* dramatically reduces shattering in domesticated rice (Li et al. 2006).

The few domestication loci that have been identified provide some insight into the type of causative mutations and genes associated with key traits (Doebley et al. 2006; Meyer and Purugganan 2013; Andersson and Purugganan 2022). The causative mutations span all kinds of genetic changes, including single-nucleotide polymorphisms (SNPs), insertion/deletions (including transposable element insertions), and larger structural variants. Interestingly, loss-of-function mutations including premature stop codons and frameshifts constitute the most common type of mutation in domestication genes (Meyer and Purugganan 2013). While coding region mutations are widely observed, several cases of *cis*-regulatory mutations (such as in *Tb1*) (R.-L. Wang et al. 1999) have also been identified.

An alternative, bottom-up approach attempts to detect signatures of selective sweeps or highly differentiated loci in genome-wide assays in domesticated populations compared to the wild ancestor, independent of associated traits (Kantar et al. 2017). Early whole-genome studies used selection scans on SNP data to identify putative domestication loci (Huang et al. 2012; Kantar et al. 2017). These studies often found a larger number of putative domestication loci than top-down methods, ranging from 55 in rice (Huang et al. 2012) to 484 in maize (Hufford et al. 2012). More recently, top-down approaches have been implemented using crop pangenomes, which allow identification of presence-absence variants (PAVs) and large structural variants and thus provide a more accurate reflection of genome-wide diversity (Gong et al. 2023). In a pangenome analysis of rice (Zhao et al. 2018), a selection scan based on comparing nucleotide diversity between wild and domesticated accessions identified similar putative domestication loci to an earlier study that used whole genomes (Huang et al. 2012) but also detected six new domestication loci. A pangenome study on the foxtail millet identified 4,582 domestication-selected PAVs and mapped them to more than 1,400 genes (He et al. 2023). SNP-based selection scans detected only 22.4% of these genes, suggesting that PAV frequencies may be a complementary approach to finding genes under positive selection (He et al. 2023). A major limitation of the bottom-up approach—with pangenomes or otherwise—is that dissection of the functional consequences of genomic regions under selection remains a nontrivial experimental endeavor.

Despite the discovery of several large-effect variants affecting domestication-related traits (Doebley et al. 2006), there is evidence suggesting that domestication may be driven largely by polygenic selection acting on a larger number of loci (Fig. 3, Supplementary Table S1) (Jantasuriyarat et al. 2004; Xue et al. 2016; Kantar et al. 2017; Studer et al. 2017). Even for a trait as well studied as shattering in rice, recent work indicates that there may be more complex, polygenic architecture at play than previously thought (Zhou et al. 2012; Ishikawa et al. 2022). An early study in wheat revealed that multiple genes or loci affected traits such as threshability, spike compactness, and spike length, even though some loci such as *Tg* and *Q* explained large percentages of variation in certain traits (Jantasuriyarat et al. 2004). More recently, a large-scale genome-wide association

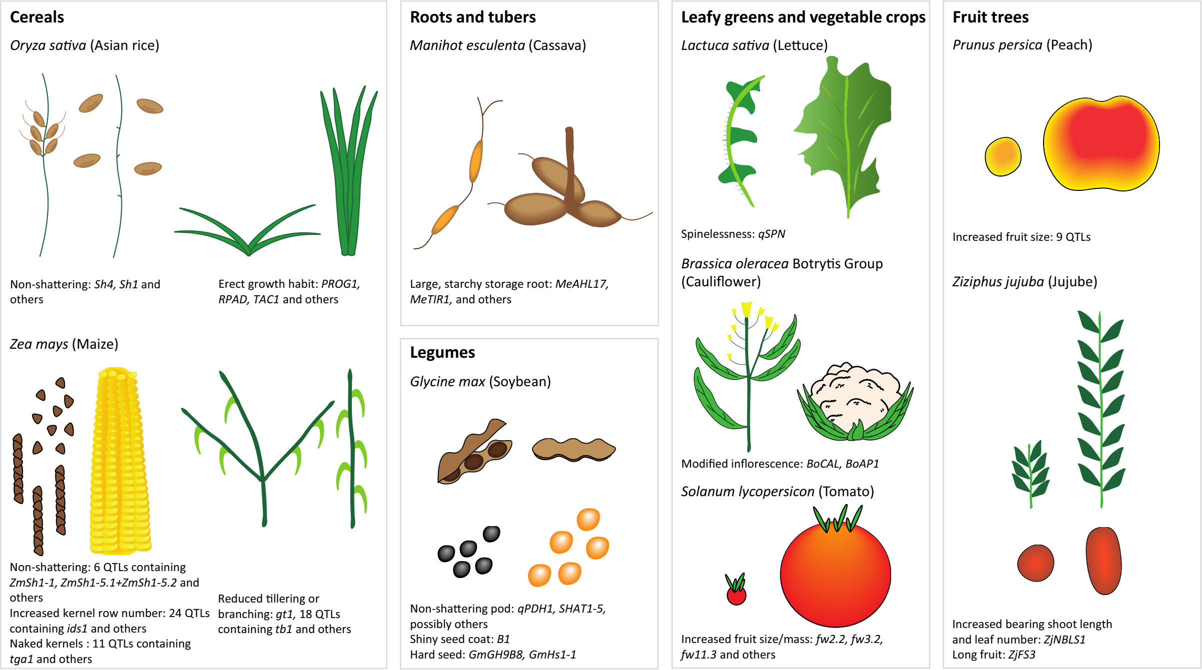

Figure 3. Domestication traits and loci. Examples of domestication traits and associated genes or loci across diverse crop types. A combination of large- and small-effect quantitative trait loci contribute to most domestication-related phenotypes. More information on the loci can be found in Supplementary Table S1.

study (GWAS) analysis of domestication phenotypes such as shank length, cob length, and kernel row number in maize revealed small-effect polygenic variants underlying these traits located in genomic regions that had not been previously linked to domestication (Xue et al. 2016). In rice, 27 years of cultivation of landrace varieties under on-farm conservation conditions led to selection at around 180 loci each in *japonica* and *indica* subspecies, indicating continuous polygenic selection even in a shorter timeframe (Cui et al. 2020).

The number of domestication loci has implications for the strength of selection during domestication and the pace at which domestication occurs. A large number of loci implies weaker selection, as strong selection on many variants would likely lead to excessive loss of competing lineages and population collapse (Allaby et al. 2015). It has been estimated that there is an upper limit of 50 to 100 loci that can be simultaneously under selection without leading to the demise of the population (Allaby et al. 2015). This is lower than the number of putative domestication loci reported based on selective sweep detection in some studies (Hufford et al. 2012; Kantar et al. 2017), but many of these detected sweeps may be false positives or driven by more recent selective pressures. Regardless of the upper limit of the number of domestication loci, weak polygenic selection during domestication is supported by the slow rates of change in domestication phenotypes such as grain size and shattering that are observable in the archaeological record (Purugganan and Fuller 2011).

One key question has been the timing of the origin and selection of mutations associated with crop phenotypic evolution. Domestication studies often draw a distinction between domestication loci that were selected early on as wild crops were brought into cultivation and diversification or improvement loci that arose later as the crops spread to different regions and underwent more conscious selection (Doebley et al. 2006; Meyer and Purugganan 2013; Kantar et al. 2017). To have been involved in domestication, a mutation must not only be experimentally linked to a phenotypic trait or effect, but it must generally also have arisen early during the transition to clearly differentiated domesticated populations. Genetic studies of putative domestication loci can lack temporal resolution to differentiate between domestication versus improvement or diversification loci that may have been selected at different time periods during the evolution of the crop species, although population-specific loci under selection can reveal some diversification loci. Here, the emerging area of ancient DNA studies provides the most direct avenue to investigate the timeline of origin of known domestication alleles. In an early ancient DNA study on maize from Mexico and New Mexico, domestication alleles in *Tb1* and *Pbf*—which is involved in regulating seed storage proteins—were found to be present in maize by 4,400 years ago, while *Su1*—a starch metabolism gene containing variants associated with sweet corn varieties (Tracy et al. 2006)—had not undergone selection at one of its modern-day high frequency alleles by about 2,000 years ago

(Jaenicke-Després et al. 2003). A more recent study reported that the oldest maize cob from San Marcos cave in Tehuacán, Mexico, dated to more than 5,000 years ago, showed genomic signs of incomplete domestication even though it was morphologically indistinguishable from modern landraces (Vallebueno-Estrada et al. 2016). While *Tb1* had undergone strong selection and resembled modern maize across its coding and regulatory regions, *Tga1*, a canonical domestication locus conferring naked kernels in maize (H. Wang et al. 2015), still carried many wild alleles that no longer appear in modern maize, suggesting ongoing selection at the time.

Despite its advantages, ancient DNA sampling is sparse, and it is not yet available for many species including rice. In such cases, population genetic approaches that leverage haplotype reconstructions and gene genealogies can help to temporally constrain allele origins or selection to relative evolutionary timeframes or phases. A recent study, for example, used a panel of interploidy wheat accessions to infer ancestral haplotype blocks, allowing the tracing of histories of genomic loci associated with specific ancestries (Z. Wang et al. 2022). This analysis revealed a stepwise recruitment of domestication alleles, with *TaBtr1-3A/-3B* alleles for brittle rachis becoming fixed in the early domesticated emmer and alleles such as *TaTg-2B* for tenacious glume and *TaQ-5A* (or *Q*) rising to high frequencies later in free-threshing tetraploid wheat and tetraploid durum wheat. Hexaploid wheat subsequently received these domestication loci from its tetraploid contributor. A study in rice reconstructed the genealogies of orthologous genes found in assemblies of wild and domesticated varieties and identified genes under positive selection in early and late phases of domestication (Lu et al. 2022); the late phase followed the emergence of *indica* and *japonica* lineages, and thus represents crop diversification after the initial domestication. Even though this approach used little genome-wide (101 loci) and population-wide information, it was still able to identify canonical loci such as *Sh4*, *PROG1*, and *Hd3a* as under selection during early domestication.

Novel methods that infer and interpret ancestral recombination graphs (ARGs) or their simplified representations (Speidel et al. 2019; Stern Wilton and Nielsen 2019) to date the origin or rise in frequency of specific variants provide powerful possible ways—as yet untapped—to temporally validate domestication loci. An ARG captures the complete coalescent history of every non-recombining block in the genome. In cases where domestication loci have been functionally characterized, ARGs hold promise in resolving the dynamics of the early domestication process and investigating hypotheses such as the sequential recruitment of certain traits and alleles (Ishikawa et al. 2022b). Although ARG-based dating approaches are yet to be applied in domesticates, studies in *Arabidopsis* provide us with a roadmap (Fulgione et al. 2022; Tergemina et al. 2022); in a population of *Arabidopsis* that colonized the base of an active volcano, a mutation in a transporter gene *IRT1* that increased manganese but reduced iron in leaves was shown to have undergone a hard selective sweep about 3,000 years ago, followed by the collective near-fixation of multiple tandem duplicates at NRAMP1 that helped recover iron levels (Tergemina et al. 2022).

Given our evolving understanding of the domestication process, identification of putative domestication loci must incorporate methods to detect multilocus adaptations and estimate timing of allelic origins. This remains a challenge in domesticates that do not yet have the same kind of genomic resources as rice, maize, and wheat.

Domestication and ecological traits

The process of domestication has frequently been viewed through an evolutionary or a genetic lens; less attention has been paid to the ecology of the domestication process. Ecology is often broadly defined as the study of interrelationships among organisms and their environment within an ecosystem (Dice 1955; Friederichs 1958), which in the context of domesticated crops would include canonical domestication traits such as non-shattering seeds that shape interactions between crops and humans. We define ecological traits in domesticated crops in terms of their nonhuman context, including traits such as growth and resource acquisition rates that influence interactions among themselves and their immediate environment, as well as the nature of their interactions with pests, pathogens, and symbionts. For most crops, it remains relatively poorly understood how such ecological traits change during domestication (Chen et al. 2015; Milla 2023); notable exceptions include studies on adaptations to climate (Hung et al. 2012; C. Liu et al. 2018) and photoperiod (Cong Li et al. 2020; C. Liu et al. 2018), and these tend to be linked to diversification and geographical expansion of crops after domestication. Changes in plant density, annual tillage, phenology, fertilization, and irrigation associated with cultivation likely altered the selection landscape for many ecological traits (Chen et al. 2015; Milla 2023), and recent ecological work, as well as genomic studies of interspecies interactions, have begun to investigate the ecology of domestication.

Understanding the nature of selection on ecological traits during cultivation may provide insight into the early stages of domestication in human-constructed niches. A study of several Fertile Crescent crop domesticates including barley, emmer wheat, and chickpea showed that they had, on average, ∼50% higher yield compared to their wild progenitors, driven by increased plant size and seed mass and reduced chaff, and no differences in growth rate and duration, total seed number, and reproductive biomass (Preece et al. 2017); this increased plant size may have arisen from selection for light competition (Milla et al. 2014). A similar pattern was observed for seed traits in a meta-analysis of 49 grain crops that showed an increase in seed mass but no difference in seed number, which may reflect conscious selection for improved nutrition (Garibaldi et al. 2021) or unconscious selection driven, for instance, by light competition as larger seeds are associated with increased plant size (Gómez-Fernández and Milla 2022). Unconscious selection for larger seeds is further supported by the fact that vegetable crops that are not used by humans for their seed also appear to have undergone selection for larger seeds (Kluyver et al. 2017). The magnitude of increase in seed size or mass varies substantially among domesticated crops, suggesting heterogeneity in the nature of selection on the trait during domestication (Preece et al. 2017; Garibaldi et al. 2021).

Domestication also influenced root traits in crops. Maize (Burton et al. 2013), barley (Grando and Ceccarelli 1995), and emmer wheat (Golan et al. 2018) form a higher number of seminal roots—which constitute the initial root system supporting young seedlings—compared to their wild progenitors. This is possibly linked to selection for increased soil nutrient uptake (Perkins and Lynch 2021) or relaxation of selection related to water stress under cultivated conditions (Golan et al. 2018). In wild emmer, for example, two additional suppressed root primordia that do not initially develop into seminal roots can be reactivated after water stress to promote seedling recovery (Golan et al. 2018), a drought adaptation lost in domesticated wheat that could be of use when breeding crops for future climates with increased frequency of drought (Hari et al. 2020). Certain root traits can also reveal fast versus slow resource-acquisitive strategies; for instance, a fast strategy under increased soil fertility is expected to be associated with lower structural investment in roots and reduced root tissue density (Ryser and Lambers 1995). A 2019 study found that while domesticated crops such as wheat, barley, maize, rice, tomato, lentil, and chickpea showed an expected increase in total plant dry mass, root traits such as root thickness and root tissue density evolved modestly and in different directions in different crops during domestication (Martín-Robles et al. 2019). Wild progenitors of domesticated crops had thicker and less dense roots—indicating faster resource acquisition—than other wild herbaceous plants, but similar to what has been observed across a wider range of plant species grown in highly fertile soils (Martín-Robles et al. 2019). This suggests that among wild herbaceous plants, crop progenitors were pre-adapted to growing in agricultural conditions (Martín-Robles et al. 2019).

Comparative growth experiments have been used to explore the question of why only certain wild crop progenitors were selected for subsequent domestication over the last 12,000 years. One study comparing three wild crop progenitors to six wild gathered species found that the crop progenitors have higher seed mass and germinate faster (Cunniff et al. 2014). A later comparison of 13 wild grass species, including progenitors of Fertile Crescent domesticates, showed that while stands of the cereal progenitors do not produce a higher seed yield per ground area than closely related wild species, the progenitors have a higher seed yield per tiller (Preece et al. 2018). This was driven by larger individual seed size with no reduction in seed number per tiller compared to the related wild species, although it should be noted that a subsequent meta-analysis incorporating more progenitor and non-progenitor wild crops did not find a difference in per-seed mass between cereal progenitors and other wild species (Garibaldi et al. 2021). The evidence for progenitor filtering or pre-adaptation thus appears to be inconsistent and may be dependent on the exact wild species being compared. Nevertheless, the ecological traits of wild progenitors of crops domesticates compared to other wild plants remains an underexplored topic. Understanding whether certain types of wild plants are pre-adapted to being domesticated (Preece et al. 2018) can help inform strategies for de novo domestication of crops to tackle food insecurity and climate change; sampling from a wider set of wild crops could lead to more plant services for humans (Molina-Venegas et al. 2021).

Crop-species interactions and the ecology of crop evolution

Domestication also leads to changes in crop traits that alter interactions of crops with other species or organisms (Chen et al. 2015). In squash, for example, domestication led to increased floral attractiveness to pollinators compared to the wild progenitor (Glasser et al. 2023). Selection for increased yield has been hypothesized to have a negative effect on plant defenses against insect herbivory due to reallocation of metabolic resources from defense to growth (Rosenthal and Dirzo 1997). Reduced defenses have been observed in multiple domesticated species (Rosenthal and Dirzo 1997; Rodriguez-Saona et al. 2011; Turcotte et al. 2014; Chen et al. 2015; Soltis et al. 2018; Fernandez et al. 2021). There is some evidence for a negative relationship between growth and defenses reported in a study on wild teosinte and domesticated maize (Rosenthal and Dirzo 1997), although other studies failed to show a consistent effect (Turcotte et al. 2014; Whitehead et al. 2017).

Direct selection against defense-associated metabolites during domestication may also underlie observations of reduced defenses against herbivory (Moreira et al. 2018). Domesticated cabbage has reduced glucosinolates associated with both induced and constitutive defense with no corresponding tradeoff with leaf area, which is a measure of growth (Moreira et al. 2018). Glucosinolates and other secondary metabolites are known to influence flavor and taste (Bell et al. 2018), and selection for palatability can lead to changes in secondary metabolites during domestication (Johns and Alonso 1990; Q. Lin et al. 2023), sometimes with unintended side-effects (Fernández-Marín et al. 2014; Alseekh et al. 2021). Direct defense traits—such as toxic or distasteful secondary metabolites and physical barriers such as trichomes—tend to be reduced in harvested organs as opposed to vegetative tissues, supporting a role for direct selection against the associated metabolites (Whitehead et al. 2017). However, a meta-analysis that additionally incorporated indirect defense traits such as volatile organic compounds that recruit predators of herbivores and induced defenses that are produced in response to herbivore damage found similar reduction of defense traits in both harvested and vegetative tissues (Fernandez et al. 2021). This may suggest greater support for indirect selection via reallocation of resources away from defense, or different selection pressures on direct versus indirect defense traits. Finally, unintended evolutionary phenotypes can also arise through antagonistic pleiotropy, hitchhiking of deleterious alleles, and negative epistasis (Singh and van der Knaap 2022).

Understanding the impact of crop domestication on other interacting species including the domesticator species will help fully contextualize the ecology and coevolutionary dynamics of the process of domestication. There is evidence of genomic adaptations in human populations after domestication, including to high-starch diets composed of millets and/or rice in East Asia (Raj et al. 2019; Landini et al. 2021) and to potato in the Andes (Jorgensen et al. 2023). Crop domesticates that played an important role in the transition from hunter-gatherer to more sedentary, agriculture-based societies are likely to have shaped human evolution by influencing not just diet but also population density and thereby pathogen exposure and dynamics (Mathieson et al. 2015).

Field experiments in regions of origin of crop domesticates where wild diversity is still present can be informative about changes in their ecological context (Chen et al. 2015). One such study showed that *O. sativa* fields contained about half the number of arthropod taxa than ecosystems dominated by *Oryza rufipogon* (Chen et al. 2013). Domestication can also affect patterns of gene flow in insect species; populations of the bean beetle species *Acanthoscelides obvelatus* associated with wild beans show genetic differentiation by geographical distance, but populations associated with cultivated beans do not, possibly as a result of long-distance movement associated with human exchanges (Alvarez et al. 2007).

Domestication affects the relationship between plants and their microbial symbionts (Porter and Sachs 2020). The diversity of seed microbiota has been observed to be higher in cultivated cereals such as bread wheat, einkorn wheat, durum wheat, and barley compared to their wild progenitors, while co-occurrence network analysis suggests a greater number of microbe–microbe interactions in wild progenitors (Abdullaeva et al. 2021). Seed endophytes and host cereals show phylogenetic congruence, suggesting host–microbe coevolution during domestication (Abdullaeva et al. 2021). Studies on the root microbiome of crops have reported contrasting effects of domestication on diversity (Gutierrez and Grillo 2022). The root arbuscular mycorrhizal (AM) symbiosis is of particular interest, as it plays important roles in plant nutrition and growth and could contribute to the development of more sustainable agroecosystems with reduced fertilizer use (Basu et al. 2018). One major analysis of AM symbiosis in domesticates reported that across 14 crops, including spinach, sunflower, and oat, the benefit to plant growth from AM fungal colonization declines compared to wild progenitors in the presence of phosphorus fertilization, but it remains similar under low phosphorus conditions (Martín-Robles et al. 2018). The AM symbiosis involves the fungi providing phosphorus—among other nutrients—to the plant in exchange for carbohydrates, and it is possible that during cultivation in fertilized soil, the fungi no longer provide an essential service (Martín-Robles et al. 2018). This may have selected for reduced responsiveness to mycorrhiza in cultivated crops under high fertilization. Interestingly, wheat landraces exhibit greater responsiveness to AM symbiosis compared to elite cultivars, suggesting an impact of recent cultivation practices (Manske 1990). Among tomato and wild relatives, increase in plant growth in response to the beneficial soil microbe *Trichoderma* decreased through the domestication gradient along wild relatives, landraces, and cultivars (Jaiswal et al. 2020). Cultivars treated with *Trichoderma* exhibited lower suppression of the necrotic fungus *Botrytis cinerea* than wild relatives and landraces, again suggesting an impact of recent breeding practices on host–microbe interactions (Jaiswal et al. 2020).

The distinct environmental context of domesticates in cultivated fields compared to wild progenitors also led to changes in plant species density and diversity (Chen et al. 2015), and thus likely altered plant–plant interactions. Species mixtures often exhibit higher productivity compared to each species in monoculture (Cardinale et al. 2007). However, evolutionary selection for enhanced net facilitative plant interactions is likely more pronounced in mixtures with a mixture coexistence history rather than a history of growth in monoculture (Schöb et al. 2018), suggesting that the benefits of multispecies mixtures may be reduced under sustained monoculture cultivation conditions. In line with this expectation, a study on eight major crops including sunflower, tomato, and sorghum alongside their wild progenitors demonstrated that mixtures of domesticates have reduced enhancement in productivity compared to mixtures of wild progenitors (Chacón-Labella et al. 2019).

Genetics of crop ecological traits

As ecological traits such as resource acquisition and interactions with other species become clearly established as domestication phenotypes, the genetic bases of these traits will be of great interest not only to understand cultivation-mediated selection processes and outcomes during domestication, but also to optimize ecological performance of crops (Thrall et al. 2011; Bargués-Ribera and Gokhale 2020). Studies in non-domesticated plants have established the heritability and genetic bases of ecological traits such as aboveground community productivity (Lojewski et al. 2009; Wuest and Niklaus 2018), and they point the way toward similar investigations in domesticated crops where genetic loci underlying increased productivity from crop rotations and intercropping would be of great interest (Litrico and Violle 2015). While modern crop breeding and cultivation frequently employ monocultures, there is increasing recognition that mixtures of crops may constitute more robust and resilient agroecosystems (Litrico and Violle 2015; McAlvay et al. 2022), for instance, against pathogens (McDonald and Stukenbrock 2016) and future climate challenges such as increased water stress (Natarajan and Willey 1986) under drought conditions. Comparisons with wild progenitors can facilitate reintroduction of traits that were lost during domestication such as water stress–induced seedling recovery in wild emmer (Golan et al. 2018) and increased productivity from species mixtures of wild progenitors (Chacón-Labella et al. 2019).

One example of genetic analysis on a key crop ecological trait is of nitrogen use efficiency, which has been studied in several crop species including rice (Gao et al. 2019), wheat (Shi et al. 2022), and maize (Ertiro et al. 2020). In rice, a variant in the *OsNR2* gene drives increased nitrate reductase activity and nitrogen use efficiency in the *indica* subspecies, with an accompanying increase in grain yield (Gao et al. 2019). Intriguingly, *japonica* rice—the earliest rice domesticate that contributed many domestication alleles to *indica* rice during its later origin—possibly underwent directional selection in the same gene toward reduced nitrogen use efficiency compared to its wild progenitor *Oryza rufipogon* (Gao et al. 2019). Improved resistance to lodging—the flattening of plants by wind or rain due to nitrogen-promoted stem elongation—in rice varieties selected during the Green Revolution is associated with reduced plant height and nitrogen use efficiency, allowing farmers to use large amounts of fertilizer without risk of lodging (Q. Liu et al. 2022). Given that the gene responsible for dwarfism in rice during the Green Revolution, *Sd1*, also underwent selection toward shorter height during *japonica* domestication (Asano et al. 2011), it appears plausible that similar or equivalent selection pressures to those encountered during the Green Revolution—such as highly fertile soils—led to reduced plant height and nitrogen use efficiency during *japonica* domestication. Disentangling the genetic bases of these traits will be key to developing sustainable crops with high nitrogen efficiency without the associated risk of lodging, allowing reduced fertilizer use.

GWAS-based and population genomic approaches have been used to explore evolutionary responses to crop domestication—or to coevolution with domesticates—in interacting species beyond humans. A study in rice found 47 virulence-associated genes in the pathogen *Xanthomonas oryzae* coevolving with 318 rice genes, which included many known resistance genes (Zhang et al. 2021). Several genes in both species showed signatures of positive selection consistent with rapid host–pathogen coevolution. In the agricultural weed *Echinochloa crus-galli* or barnyardgrass, 87 putative plant architecture-related genes have been found to be under selection during the evolution of Vavilovian mimicry to domesticated rice (Ye et al. 2019). The domestication and subsequent dispersal of squash or *Cucurbita* species led to the geographical expansion of the wild pollinator species *Eucera (Peponapis) pruinosa* through the Americas, whose genomes show signatures of selection likely associated with adaptation to novel agricultural niches (López-Uribe et al. 2016; Pope et al. 2023). GWAS studies have identified genetic loci controlling variation in the leaf microbiome in rice (Roman-Reyna et al. 2020) and maize (Wallace et al. 2018) and in the root microbiome in sorghum (Deng et al. 2021), revealing genes involved in plant defense and cell wall function or degradation. These findings invite future investigations of how these loci have evolved in domesticates compared to wild progenitors, and how they may be used to select for microbiome-related outcomes during breeding.

Concluding remarks

Although the study of domestication has a long history that traces back to Darwin, we are beginning to finally get a better understanding of this unique plant evolutionary process, due in part to collaborative efforts by plant biologists, evolutionary geneticists, molecular biologists, archaeologists, and anthropologists. The last few decades have been particularly productive, spurred in part by advances in genomic sciences as well as archaeobotany. Nevertheless, there are still gaps in our understanding of crop domestication. Much of the work in this area has focused on cereal crop species, and this has skewed our knowledge of crop domestication; more efforts are needed to study other crop species, including legumes, vegetable species, and perennial fruit trees. Greater emphasis should be placed on identifying and characterizing more domestication loci, both at the functional and evolutionary genetic levels. A combination of traditional trait-based and selection approaches as well as novel ARG-based dating methods can help reveal more about genomic loci underlying domestication. Some effort should also be made with examining post-domestication evolution, particularly those associated with crop dispersal and adaptation to novel environments.

Domestication may be a process of great evolutionary interest, but crops also underlie our food security, and their study is at the forefront of challenges imposed by climate change (Raza et al. 2019). There has been recent interest in the idea of domesticating new crop species, including through rapid de novo domestication of climate-resilient crops by gene editing, to help human agriculture adapt to future agricultural challenges (Yu et al. 2021; Gutaker et al. 2022). This can also be coupled with more attention to neglected crop species, many of which are confined to local or regional areas, but which may hold promise for future widespread use. In many of these efforts, knowledge of genomic variation associated with desirable domestication-related traits will be key to the success of such approaches, Finally, the ecological context of domestication can not only expand our definition of domestication syndromes in different crops, but also help develop more sustainable agricultural management practices (Milla 2023) to help protect or improve yields in changing environments (Battisti et al. 2018).

Supplementary data

The following materials are available in the online version of this article.

Supplementary Table S1. Details on domestication loci and traits shown in Fig. 3.

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Data availability

The data underlying the figures in this article are cited within the article and in its online supplementary material.

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