

Evolutionary Insights into the Nature of Plant Domestication

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Domestication is a co-evolutionary process that occurs when wild plants are brought into cultivation by humans, leading to origin of new species and/or differentiated populations that are critical for human survival. Darwin used domesticated species as early models for evolution, highlighting their variation and the key role of selection in species differentiation. Over the last two decades, a growing synthesis of plant genetics, genomics, and archaeobotany has led to challenges to old orthodoxies and the advent of fresh perspectives on how crop domestication and diversification proceed. I discuss four new insights into plant domestication — that in general domestication is a protracted process, that unconscious (natural) selection plays a prominent role, that interspecific hybridization may be an important mechanism for crop species diversification and range expansion, and that similar genes across multiple species underlies parallel/convergent phenotypic evolution between domesticated taxa. Insights into the evolutionary origin and diversification of crop species can help us in developing new varieties (and possibly even new species) to deal with current and future environmental challenges in a sustainable manner.

Introduction

The domestication of plants and animals has been described as one of the most important developments in the history of *Homo sapiens* [1]. Beginning at the start of the Holocene after the last major glacial period, approximately 12,000 years ago, hunter-gatherer societies began the cultivation of plant species as a major source of food and fiber [1,2], and today we rely on domesticated species for our survival. The transition to agriculture brought about by domestication became associated with sedentary settlements, giving rise to cities that eventually led to many contemporary human cultural features, including writing, state formation and organized religion [1–3]. All this emerged as a result of the dependence of *Homo sapiens* on a wide range of domesticated plant (and animal) species, and the consequent changes in human ecological behavior and global demography [1–3].

Domesticated crop species are the result of an evolutionary process, arising as wild species are exposed to new selective environments associated with human cultivation and use [4]. It is a process of speciation and/or species transformation that occurs when one species (the domesticator) begins to control the reproduction and dispersal of another species (the domesticated) in order to meet the needs of the former, most notably (but not exclusively) for food. Crop domestication is a special case of plant/animal co-evolution in which plant species have adapted to human control and are propagated in human-manipulated environments to enhance the survival and fitness of *Homo sapiens*. The result of this mutualism is not one-sided, as domestication has also resulted in increased fitness in domesticated crop and animal species, leading to dramatic increases in population sizes and expansion of domesticated species ranges outside their original geographic centers of origin [1]. It is estimated that there are 1,000–2,500 semi- and fully domesticated

plant species from about 120–160 taxonomic families [5,6], and all of these species are relatively young, having only originated since the Neolithic, and in some instances possibly existing for just a few centuries.

Domesticated species have been the subject of evolutionary analysis for more than 160 years. Charles Darwin in 1859 devoted the first chapter of his seminal work *Origin of Species* to a discussion of domesticated species, highlighting the variation among breeds, the similarities between offspring and parents, and the transformative role of selection on species differentiation [7]. He subsequently wrote *Variation of Plants and Animals under Domestication* in 1868 to further explore some of the themes he developed in *Origin* [8]. Since Darwin, there has been great interest in the study of domestication and crop evolution, both to advance our understanding of the evolutionary process and to support the breeding of better crops to meet new adaptive challenges. The recent origin of crop species, the wealth of information on their genetics, their human association, and relatively good paleontological (i.e., archaeological) record allows us to use domesticated species as models for the early stages of species formation and population divergence, and to probe the mode and tempo of various evolutionary processes.

We have seen a flowering of domestication research over the last two decades, in particular a growing synthesis of plant genetics, genomics, and archaeology, leading to fresh perspectives on how domestication proceeds [2,4,5,9–14]. Here we discuss four insights on crop domestication that have emerged from new data and analyses over the past few years. None of these insights are strictly new — many had been discussed in the past, some by Darwin himself more than 160 years ago [7]. The last few years have, however, sharpened our focus on these ideas, and in many cases reinforced them with more compelling



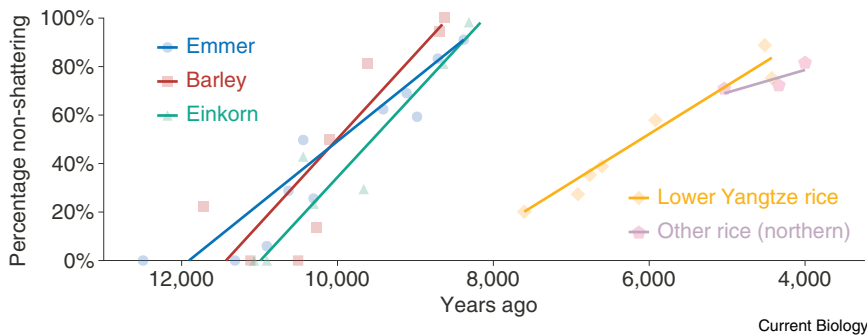


Figure 1. Gradual rise of non-shattering trait in key cereal crops.

The increase in frequency of non-shattering over time as determined from the archaeological record is depicted. Based on [18].

evidence, providing a deeper understanding of domestication as a key co-evolutionary process.

Domestication Is a Protracted Process

The tempo of domestication has been the subject of study and controversy [15–26]. Although Darwin presumed that evolutionary change proceeded gradually, crop species appeared to run counter to this assumption. Early work suggested that domesticated taxa arose rapidly, and that the first plant domestication events were completed in a short span of time at the Pleistocene–Holocene boundary. Indeed, in a compilation of 8 models of the evolution of plant domestication traits [15], six models suggested that evolution could proceed quite rapidly, with one model [27] proposing that the loss of seed dormancy in Near Eastern legumes under intense harvesting of wild stands could evolve in as little as 7 years.

Over the last decade, the idea that domestication was a rapid process began to be seriously questioned. New insights into the pace of domestication arose from two interrelated but conceptually distinct series of observations. The first observations originated from archaeobotanical studies which show the time it takes for domestication phenotypes to arise and fix in evolving domesticated species. In 2006, Tanno and Wilcox showed that it took approximately 3,000 years for the tough rachis phenotype in wheat, an indicator of seed non-shattering and considered a key domestication trait, to predominate in the archaeological record in the Near East [16]. Other workers soon pointed out the relatively slow rise of the non-shattering phenotype for various cereal crops, and a consensus began to emerge that this key domestication trait took 2,000–2,500 years to become fixed in domesticated species, as determined from archaeobotanical remains [17–19] (Figure 1). There seemed to be a few exceptions — pearl millet, for example, may have taken 1,000–2,000 years to domesticate [18]. Nevertheless, this trait associated with loss of natural seed dispersal and the indicator trait of domestication in cereal crops did not achieve fixation in a short period of time, as had been previously thought [15]. Moreover, other major domestication traits in the archaeological record, such as seed size enlargement, also appeared to evolve slowly [17–19].

The second set of observations that lent credence to the protracted model are population genomic analyses that reveal a gradual decline in effective population size (N_e) associated with domestication. These observations began to emerge over the last three years with the application of new computational

data of crop species and their wild relatives, these methods have revealed a gradual decline in crop species N_e over time, rather than the sudden population bottlenecks that would be expected to occur with rapid domestication [24]. This was first observed in *Oryza glaberrima* (African rice), which PSMC analysis showed began to decline in N_e 10,000–15,000 years before present (YBP), reaching a minimum N_e at ~3,500 years ago coincident with the first archaeological evidence of African rice domestication in Mali ~3,000 YBP (Figure 2) [29]. A separate study on *O. glaberrima* confirmed the gradual decline in N_e , although differed from the first study in showing a similar N_e decline in the wild progenitor *O. barthii* [30].

Similar patterns were also observed in other crop species. In grapes, MSMC analysis showed that there was a decline in N_e that began ~22,000 years ago at the divergence of *Vitis vinifera* from wild *Vitis sylvestris*, reaching a minimum N_e at 7,000–11,000 YBP (Figure 2) [31]. The 2- to 3-fold reduction in effective population size in *V. vinifera* is not observed in the wild relative. Around 9,000 years of population decline is also seen in maize, but is not observed in the wild teosinte [32].

The application of these population genomic methods remains at an early stage, and more work may be needed to ensure that these results are robust. It is striking, however, that the patterns observed are found in multiple domesticated species (but in some cases, not the ancestral wild species), and if true these analyses indicate a long and gradual period of effective population size reduction, consistent with the protracted nature of domestication. Interestingly, these analyses also demonstrate that the start of the population size decline begins even before archaeological evidence for the presence of the domesticated taxa. This is certainly evident in grapes, where the reduction in N_e starts well into the Pleistocene [31]. This early start in effective population size reduction may reflect the initial cultivation steps at the start of the domestication process, but may also be due to pre-domestication hunter/gatherer management of wild stands [21–24]. Indeed, archaeologists have shown wild cereal gathering ~23,000 YBP at the Ohalo II site in Israel [33], and there is archaeobotanical evidence for cultivation about 13,000–12,500 years ago during the Younger Dryas period in the Fertile Crescent prior to the rise of domesticated cereals [34]. It should be noted, however, that there is still debate on this topic, with at least one paper suggesting that some of this decline may be due to climatic (and not human-associated) factors [30].

Ancient DNA studies have also provided some support for different aspects of the protracted domestication model.

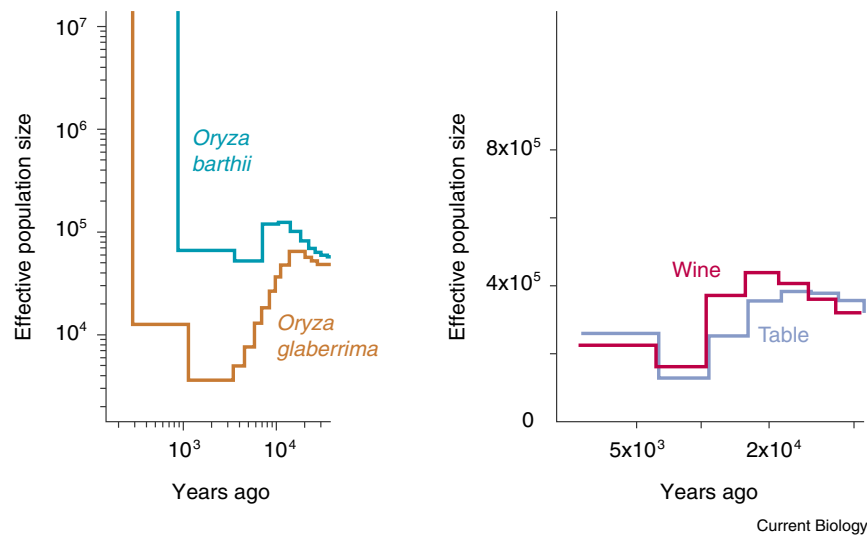


Figure 2. Changes in effective population size using partially or multiple sequentially Markovian coalescent analyses.

(Left) The results show the gradual decline of N_e for African rice *Oryza glaberrima* but not the wild ancestor *O. barthii* [30]. (Right) The gradual decline in grape *Vitis vinifera* beginning in the Pleistocene [31].

Genome sequence of a 5,310-year-old maize cob from Mexico shows that early stages of maize domestication may have involved gradual (and not rapid) incorporation of domestication alleles [35]. Archaeological sorghum samples from Lower Nubia, Egypt that date from 400 to 1,805 years ago show a continued gradual decline in genetic diversity, although this occurs in already domesticated populations [36]. These archaeogenetic studies are still at too early a stage to be conclusive, and some of the interpretation remains debatable, but ancient DNA studies will undoubtedly play a major role in providing understanding of the domestication process.

Why did domestication take longer than previously believed? One possibility is that speciation and/or species differentiation was impeded by recurrent gene flow between incipient domesticates and their wild ancestors [37]. Certainly, it has been shown that cultivation in early agricultural fields occurred in proximity with wild crop ancestors, and there is evidence of gene flow between these populations [34,37–40]. Second, it may be that many of the crop domestication traits have a polygenic basis, with multiple genes of small effect that could take longer to fix in a population [41]. Finally, it may be that much of domestication was not, as generally believed, carried out by deliberate, strong selection, but rather is the result of unconscious (natural) selection of incipient species as they were cultivated by *Homo sapiens* in the novel, managed environments of Neolithic agricultural fields [7,8].

Early Domestication Was Driven in Large Part by Unconscious, Natural Selection

In the co-evolutionary process of domestication, *Homo sapiens* is the animal domesticator, and given its self-aware intelligence there has been some emphasis on selection during domestication being driven by conscious human design. Darwin [7,8] and others [42–45] certainly made a distinction between conscious (or methodical/artificial) vs. unconscious (or automatic/natural) [43] selection. Clearly some traits, such as color and possibly taste, likely were driven by conscious human choice [43]. Other traits, however, such as seed non-shattering, seed size, seed non-dormancy and synchronous germination [42,43,45], may

have occurred largely by unconscious selection, equivalent to natural selection. Indeed, many domestication traits, particularly those that were important early in the process, may simply have been the result of the transition of species from free-living in the wild to managed cultivation.

Although the idea that unconscious selection as a key element in domestication

has a long history [7,8,42–45], the magnitude of selection on domestication traits had never been ascertained. What is new is that over the last decade it has become clear that archaeological remains provide a fossil record that demonstrates slow rates of phenotypic change in early stages of domestication. For seed non-shattering and seed size in cereal crops and some legumes, rates of trait evolution (measured using the evolutionary units *darwins* and *haldanes*), were well within the low end of the distribution for wild plant species [17–19]. More importantly, it was also realized that these standardized measurements of phenotypic change allow us to estimate selection coefficients (s) [17].

For the evolution of non-shattering in cereal crops, estimated s ranged from 3×10^{-4} to 3×10^{-3} [18]. For seed size enlargement, one study in cereal crops [17] gave a range of s from 2×10^{-3} to 3×10^{-4} , while another study [18] gave an s range 2 to 5×10^{-5} . Seed size traits among non-cereal crops give a similar range of selection coefficients [17]. In contrast, estimates of the strength of selection in natural, non-domesticated species show a median selection gradient of ~ 0.16 , although the exponential distribution of selection strength shows that many selection gradients had much smaller values [46]. These results suggest that the evolution of at least two traits — non-shattering and seed size — had selection coefficients that were well within the range of *natural* selection in the wild (Figure 3) [17,46].

Relatively low levels of selection on these traits are concordant with the selection pressures these traits experienced. The rise of cereal non-shattering appears to be linked to cultural use of sickles for harvesting, which selects for plants that did not drop seed upon harvest [45–48]. The early farmers, in this scenario, were not consciously selecting non-shattering plants for propagation, but non-shattering genotypes would presumably be harvested at a higher level and be preferentially represented in planting for the next generation.

For seed size enlargement, the pressure may not have been conscious selection of farmers on larger seeds for consumption; instead, deeper seed burial associated with agriculture would select for larger seeds that would germinate more effectively and produce larger vigorous seedlings with greater fitness [45,49,50]. Indeed, domesticated vegetable crops have

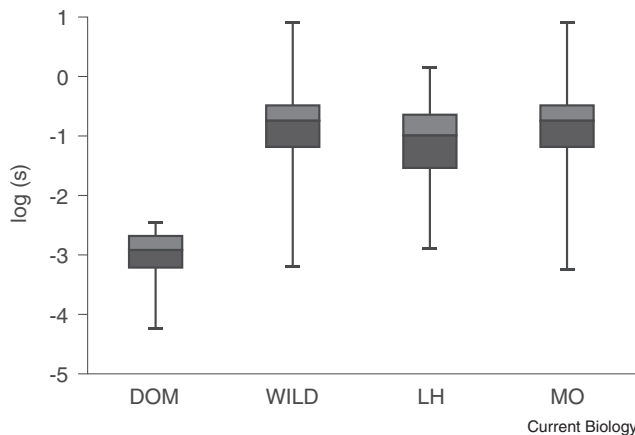


Figure 3. Estimated selection strengths for domesticated vs. wild species.

Dom, domesticated plants; Wild, non-domesticated species in natural populations; LH, life history traits; Mo, morphological traits. Based on [17].

~20–250% larger seeds than their wild ancestors, even though these crops are harvested not for seed but for edible stems, leaves and roots [51]. These vegetable crops are not grown via seed, but by cuttings or tubers, but nevertheless seed enlargement may occur through inadvertent selection for occasional seed germination [51]. There is also a possibility that seed size evolution is a correlated change via indirect selection for larger, more competitive plants [51]. In these cases, seed size is not the direct target of selection.

Estimates of selection during domestication have been refined to account for changing selection strengths over time. Allaby *et al.* [52] demonstrated fluctuating selection on non-shattering in cereal crops, using a method that assumes the genetic architecture of trait variation. In rice, selection coefficient starts at $s \sim 0.001$ at about 7,500 years ago, and peaks at $s \sim 0.0033$ at 6,750 years ago. Einkorn wheat shows an increase in s from about 0.001 to 0.003 after ~10,000 YBP in the Near East. In barley, selection in the Northern Levant starts at $s \sim 0.003$ at about 10,800 YBP, but increases to $s \sim 0.005$ at 9,500 YBP, the peak being associated with introduction of lithic (stone) technologies in the area. In Southern Levant, however, s stays low for barley at < 0.001 from 11,000 YBP to 9,500 YBP. Together, there appears to be a change in the strength of selection for non-shattering after ~10,000 years ago in Near Eastern cereals, and again it is believed that this may be due to the introduction of new harvesting technologies/tools [52].

Several investigators have already previously pointed out that seed shattering and loss of seed dispersal may be one trait under unconscious selection in Near Eastern cereals and legumes [42,43,45,53], but there is reason to believe that other crop traits may also be subject to unconscious selection. These other traits may include lack of dormancy, synchronous germination and perhaps even seasonal flowering time. Other traits, however, are more likely to be under conscious selection by humans, including color, taste and other diversification traits associated with cultural preferences [13,43]. There is also the possibility that unconscious selection may be more predominant in annual seed crops (cereals and legumes) that are

mass-planted [54], while some tuber and vegetable crops as well as perennial crops that are asexually propagated may be domesticated by conscious selection. Unfortunately, many of these other traits (e.g., taste), as well as vegetatively propagated crop species, do not leave the same temporal sequence of archaeological remains that allow us to evaluate rates of phenotypic change and strengths of selection. Nevertheless, the recent application of evolutionary genetic analysis to archaeobotanical data has finally provided measurements that demonstrate that what Darwin called unconscious selection, which is indistinguishable from natural selection in both strength and process, is a key driver of the evolution of early domesticated traits in many key crop species that evolved in the Neolithic.

Interspecific Hybridization with Local Populations Accompanies Range Expansion of Many Crop Species

Hybridization was always thought to be an important component of plant evolution [55–58]. Unlike animals, plants have a higher incidence of interspecific hybridization, and introgressive hybridization has been recognized as an important mechanism for adaptive evolution [55–58]. The role of hybridization in domestication and crop diversification is widely documented [59,60], and there is evidence for hybrid origins of several domesticated crops, including wheat [61], banana [62], and several citrus fruit species [63]. In these cases, the crop species arises from hybridization between two wild relatives, and in some instances accompanied by allopolyploidization [14,61,62].

What is relatively new and now increasingly evident is the role that interspecific hybridization may play in crop diversification and range expansion after domestication, possibly aiding the spread of nascent domesticated species to new agricultural environments, or adapting to new cultural preferences [64]. Perhaps one of the most interesting examples of crop expansion associated with hybridization is Asian rice, *Oryza sativa* (Figure 4) [65–67]. Rice appears to have first been domesticated in the Yangtze Valley in China starting ~9,000 years ago from *Oryza rufipogon*, giving rise to a subspecies or variety group referred to as japonica. In India, local cultures began to harvest the related wild species *Oryza nivara*, and possibly had begun cultivation, but there is no evidence of domestication from these early efforts [68]. Starting about 4,500 YBP, however, japonica rice arrived in South Asia, likely through northwest India via the ancient Silk Road [69,70]. This introduced japonica appears to have hybridized and introduced domestication alleles into either wild *O. nivara* or a proto-domesticated population (i.e., cultivated but not yet domesticated) in the region. This introgression of domestication alleles then led to the evolution of subspecies *indica*, which subsequently spread rapidly and now is the dominant rice group grown in the world (Figure 4). Although this scenario is still debated [71–73], the role of hybridization in the origin of *indica* rice is supported by archaeological evidence [69,70], population genomics analysis [66,67], and genetic studies that show japonica origins of key rice domestication alleles in the non-shattering *sh1*, pericarp color *Rc*, erect growth *Prog1* and barbed awn *LABA1* genes [65,67]. Introgressive hybridization has also been observed for cereal crops such as maize, where it has been shown to be associated with highland adaptation [74,75], and in archaeogenetic samples of 6,000-year-old barley [76].

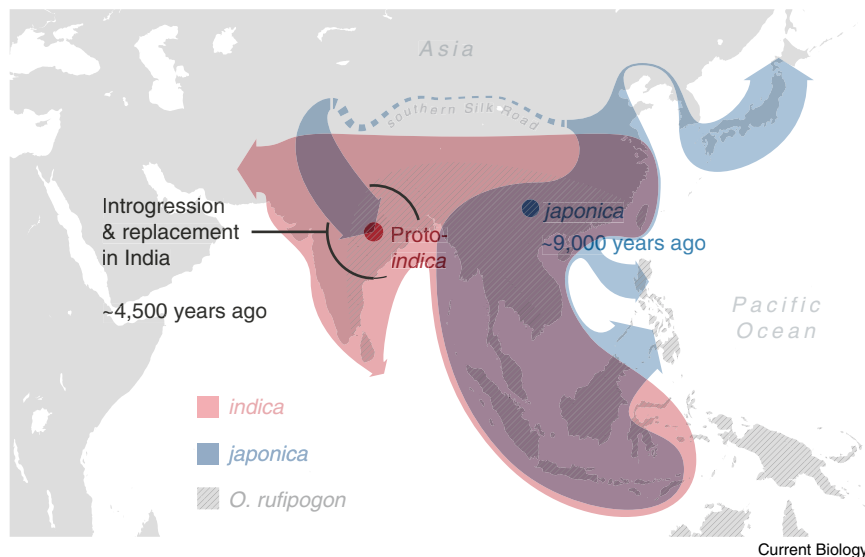


Figure 4. Interspecific hybridization and the origin of indica rice.

In this scenario, japonica rice was domesticated ~9,000 years ago from *O. rufipogon* and a proto-indica possibly started ~8,000 years ago from *O. nivara*. Japonica rice, moving via the Silk Road, is believed to have entered NW India and hybridized with the undomesticated proto-indica, providing domestication alleles and leading to indica.

Parallel Genetic Evolution Is Common

Plant domestication has occurred across the world, with >20 geographic regions serving as cradles for the origins of different crop species [3–5,18]. Across disparate environments, many crops encountered similar selection pressures, both from similarities in agricultural environments, cultivation and processing

practices, and human cultural preferences, resulting in phenotypic convergence of similar traits across multiple species. Some of these comprise the domestication syndrome phenotypes [5,9,86,87], which in cereals includes reduction in seed dispersal and increased seed retention (non-shattering), increased seed size, changes in shoot branching and stature, loss of seed dormancy, and synchronous germination. Moreover, there are also several diversification traits that have been subject to parallel selection in different cultures, including loss of bitterness, enhanced sweetness and fruit color polymorphisms [11–13]. Indeed, the parallel/convergent evolution of traits among domesticated species was noted by N. I. Vavilov, who proposed the genetic law of homologous series of variation among related crop species [88].

Genes underlying domestication and diversification traits in multiple crop species have been identified in an accelerating pace over the last two decades, spurred by increasing genomic and genetic mapping tools and resources [89,90]. It is now becoming clear that in many instances, across multiple species, the same or homologous (i.e., paralogous) genes are used to effect the same phenotypic changes [2,9,12,13,24]. Parallel trait evolution is achieved by the same genes.

There are several examples of this in cereal crop species [14]. The retention of seed in the inflorescence stalk occurs by suppressing abscission as seeds mature. In sorghum, this is regulated by the YABBY transcription factor *Shattering1* (*Sh1*), in which 3 mutations are found that truncate the *Sh1* protein in domesticated *Sorghum bicolor* [91]. Genetic studies have shown that this phenotype evolved independently in maize, where a translocation leads to the fusion of the *Zea mays Sh1* to an unknown gene; this results in the loss of the YABBY domain leading to non-shattering [91]. In rice *Sh1* is not the main gene for non-shattering, but a QTL analysis nevertheless suggests it may be involved as a minor locus [91]. Another example of parallel genetic evolution at the gene level includes selection of *tb1* orthologues in maize [92], pearl millet [93] and barley [94] which are associated with shoot architecture evolution.

Interspecific hybridization between a domesticated species and a wild relative appears to be pervasive among perennial fruit crops. One illustrative example is a recent genomic study in date palms, *Phoenix dactylifera*, an iconic fruit species likely domesticated in the Middle East [77]. As date palms spread to North Africa ~3,000 years ago, they hybridized with wild *Phoenix theophrasti* found in the Eastern Mediterranean, now mostly in Crete and some parts of southwest Turkey (Figure 5), and today the North African *P. dactylifera* genome contains ~5–18% of the *P. theophrasti* genome [77].

Gene flow from crop wild relatives has also accompanied the expansion of domesticated apples [78,79]. The apple *Malus pumila* originated in Central Asia from *Malus sieversii*, but as domesticated apples moved westwards, it hybridized with the European crabapple *Malus sylvestris*, from which modern apples are descended [78,79]. It also has been observed in grapes [80], almonds [81], and apricots [82], and indeed appears to be a key element in perennial crop evolution [83]. In some cases (such as grape, maize and perhaps rice), the wild relative that hybridizes with the domesticated species is a local population of the wild ancestor species, while in others (date palms and apples) the wild relative is a distinct, non-ancestral species.

Interspecific hybridization has also been invoked to explain multiple origins and/or local adaptation of important domesticated animals such as pigs, cattle and chickens [84]. These examples, most of which have come to light over the last decade from evolutionary genetic/genomic analyses, lend support to the idea that hybridization is an important mechanism in the spread of crop species to new geographic areas [64,85], and introgression may provide for sources of novelty, superior quality, and adaptive traits such as those required to survive in new or marginal habitats. It should be noted, however, that while evidence on the prevalence of interspecific hybridization continues to mount, the role of hybridization in facilitating the spread of these crop species remains limited. There is a clear need to go beyond documenting instances of hybridization associated with crop evolution, and investigating the role of adaptive introgression in crop domestication and diversification.

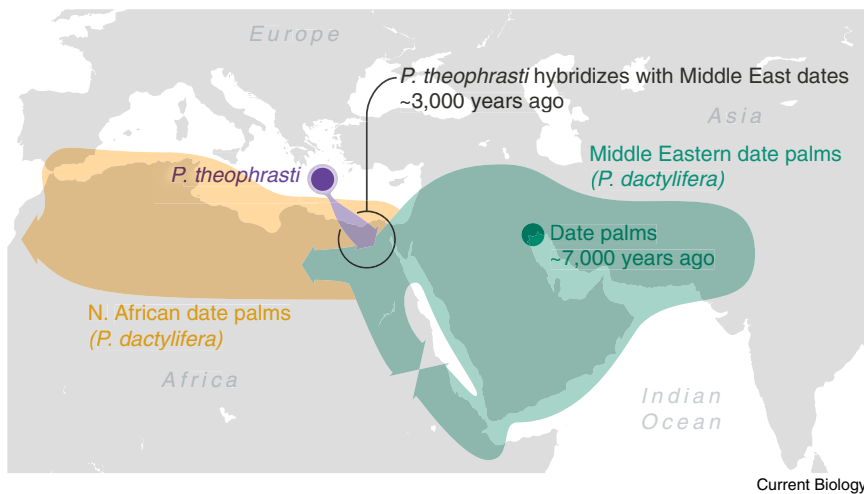


Figure 5. Interspecific hybridization and the origin of North African date palms.

Date palms, *Phoenix dactylifera*, are believed to have originated in the Gulf region ~7,000 years ago, and moved westwards into the Levant and Egypt. Genomic evidence shows that these Middle East date palms hybridized with the wild Cretan palm *P. theophrasti* possibly ~3,000 years ago, leading to North African date palms which subsequently colonized North Africa.

phenotypes are the result of a wider range of genetic changes, including *cis*-regulatory, protein-coding and copy number variation.

All these cases, which have emerged only after nearly 2 decades of molecular genetic studies, suggest that there are genetic constraints in the evolution of parallel

Sh1 and *tb1* are examples of parallel evolution confined to domesticated species within the same taxonomic family, which aligns with Vavilov's law of homologous series [88] that as formulated was limited to variation in related species. However, there are other examples of parallel or convergent evolution that are more widely distributed in the plant kingdom, such as fruit color variation. Various fruits are colored purple by anthocyanins, and across many species suppression of anthocyanins led to light-colored fruits [95]. White grapes evolved from purple grapes by mutations in the *myb*-like transcription factor *VvMYBA2* [96], which normally controls transcription of anthocyanin biosynthetic genes. This locus (or a paralogue) also underlies fruit color variation in various distantly-related species such as apples [97], peaches [98], chocolate [99], date palms [100] and oil palms [101].

Another interesting example is the evolution of glutinous cereals, which are prized by multiple cultures, particularly in North-east Asia. Glutinous rice is common in Japan and Korea, and arises through mutations in the *Waxy* (*Wx*) gene, which encodes an enzyme for amylose biosynthesis [102,103]. Interestingly, other glutinous cereal crops such as barley [104], Job's Tears [105], broomcorn millet [106] and foxtail millet [107], are also used by these cultures, and all have mutations in the *Wx* gene. This parallel genetic evolution is not confined to the grass family; in the New World, the three amaranth pseudocereals are also glutinous as a result of mutations in their *Wx* loci [108].

One final example for widespread parallelism/convergence is the control of flowering time. In the chickpea *Cicer arietinum*, spring flowering arises in landraces through mutations in *CaELF3a*, which regulates gating of light inputs to the circadian clock [109]. This same locus is also seen to control short-day flowering in other legumes such as the pea *Pisum sativum* and lentils *Lens culinaris* [110]. Moreover, the HD17 QTL, which also results in photoperiod response of flowering time in japonica rice, also spans an *ELF3*-like gene that contains a Ser-to-Leu amino acid difference restricted to temperate japonica rice [111]. In other species, such as sunflower [112], tomato [113], soybean [114] and barley [115], the CETS-family gene *FLOWERING TIME* (*FT*) or paralogous duplicates are also involved in flowering time variation; in the case of these genes, the diversity in flowering time

and/or convergent traits in domestication, leading to the same or closely-related genes being evolutionary targets across multiple species in response to similar selection pressures. These examples of widespread parallelisms — fruit color, glutinous seed and flowering time — spanning multiple plant families suggest that Vavilov's law can now be extended and may operate even among distantly related domesticated species [116]. The finding that parallel phenotypic evolution may have parallel genetic underpinnings also highlights the idea of genetic hotspots of variation, which are defined as the repeated occurrence of *de novo* mutations at homologous (orthologous and paralogous) loci directly causing similar phenotypic variation [117]. Moreover, there have been recent efforts to quantify the role of genetic architecture, genotype-to-phenotype mapping and pleiotropy in explaining examples of evolutionary convergence [118]. Why such hotspots exist — they may represent regions of mutational bias or loci with optimal pleiotropy [117] — or which other factors [118] have a role in parallel/convergent evolution remain subject to debate and further exploration, and continued study in domesticated taxa may hopefully unravel the underlying mechanisms that lead to genetic parallelisms. Work in this area is continuing, and there are also indications that several of these traits are polygenic in nature; to what extent these multiple genes also show parallel evolution in different domesticates remains to be seen [41]. Nevertheless, parallel and/or convergent evolution has facilitated functional identification of genes across multiple species, and provides geneticists with a powerful approach to use evolutionary homology in transferring desired crop traits across multiple species.

Summary and Outlook

Domestication continues to provide a rich vein of insights into the evolutionary process, justifying Darwin's early use of domesticated species as models to highlight the nature of variation and the powerful action of selection. Domesticated species — with their recent origins, their wealth of genetic and archaeological information, and our knowledge of their selective environments — provide natural experiments that allow us to dissect the nature of evolutionary change [119].

Over the last few years, convergence of genetic and archaeological research has led to a greater understanding of the mode

and tempo of domestication. We now think, in general, that domestication is a protracted process, that selection strengths in domesticated species are consistent with unconscious (natural) selection, that interspecific hybridization may be an important mechanism for crop species diversification and range expansion, and that parallel genetic evolution underlies parallel phenotypic evolution.

These insights may not be entirely new, but it is clear that new data have solidified these views. This recent rethinking of our ideas on domestication opens up new areas that need further exploration. What governs the rates of domestication across different crop species? Can we estimate the strengths of selection for the full suite of domestication and diversification traits, and what determines their level? Can we identify the adaptive impact of introgressive hybridization on domesticated species? What determines which traits and genes are subject to parallel evolution, and which are not? These and other questions will be (and already are) informing the research agenda in the near future.

Coupled with exciting new developments in archaeogenetics [35,36,76,120,121], which allow us to directly determine genomic composition of crop remains from the archaeological record, and new CRISPR technologies that enable a recapitulation of the genetic steps to domestication [122–124], we can expect more evolutionary insights to emerge in the next few years. These studies continue to demonstrate that crop species are indeed interesting systems to study various evolutionary phenomena, including speciation and/or population differentiation with gene flow, the genetic architecture of adaptation, and sources/causes of pre- and post-mating reproductive isolation and species/population divergence.

Finally, these and other evolutionary insights will become increasingly important as we humans face new environmental challenges. Domestication during the Pleistocene–Holocene boundary occurred in a period of global warming after the last glacial period, first in the Fertile Crescent and in other early centers of agriculture. It is also thought that domestication was triggered in other parts of the world by local climatic change [2,125,126]. As domesticated species moved out of their original ranges and colonized new areas, they had to adapt to local environments and cultures. A greater understanding of the evolutionary processes of adaptation among crop species may thus yield ideas on how we can develop new varieties (and possibly even species) to deal with current and future environmental challenges in a sustainable manner.

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