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Opinion

‘Domesticability’: were some species predisposed for domestication?

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Crop domestication arises from a coevolutionary process between plants and humans, resulting in predictable and improved resources for humans. Of the thousands of edible species, many were collected or cultivated for food, but only a few became domesticated and even fewer supply the bulk of the plant-based calories consumed by humans. Why so few species became fully domesticated is not understood. Here we propose three aspects of plant genomes and phenotypes that could have promoted the domestication of only a few wild species, namely differences in plasticity, trait linkage, and mutation rates. We can use contemporary biological knowledge to identify factors underlying why only some species are amenable to domestication. Such studies will facilitate future domestication and improvement efforts.

Highlights

Only a small number of the species originally collected and cultivated by humans have become domesticated, but the reasons for this are not well understood.

Crop progenitors could differ from never-domesticated relatives in traits that enhance their ‘domesticability’, for example, plasticity, trait integration, and mutation supply.

Identifying these features will develop our understanding of the relationship between human choices and the genetic or physiological constrains that gave rise to early agriculture and this will help identify species for future domestication to combat food insecurity.

Domestication and its use as a model for evolution

Crop domestication is a mutualistic relationship between plants and humans. Humans gain a more predictable and improved resource from the plants, usually by taking control over the plants’ reproduction, and in parallel the plants become adapted to the environment of the domesticator [1,2]. Tens of thousands of plant species are edible, yet just a few hundred have been domesticated and a mere 15 provide 90% of our calories [3]. Hundreds of wild plants were collected and cultivated during the Neolithic, but later abandoned as food sources [4]. This extreme bottleneck in the adaptation of wild plants to a cultivated environment, resulting in the domestication of only a few, raises an important question – are there genomic and phenotypic features that facilitated or constrained the domestication of certain wild species under human management or cultivation? This knowledge would have consequences for understanding how future food security can be ensured.

Domestication has been used as a model for evolutionary processes since Darwin’s original work [5], due to the rapidity and recency of adaptive changes, the parallel diversification events, and the socio-economic importance of crops, which means a wealth of genomic data is available [6,7]. However, if crop progenitors possess traits that increase their domesticability, then domesticated species are a biased sample not representative of natural selection in the wild. If so, domestication could instead be a model for understanding the rapid evolution of highly evolvable species.

Domestication and ‘domesticability’

We adopt the term ‘domesticability’ [8] to describe the ability of a species to generate and/or maintain heritable, adaptive variation that can be targeted, directly or indirectly, in the domestication process [9]. Variation in domesticability posits that some wild species have greater domestication potential than others. The term is then akin to evolvability (i.e., some inherent flexibility of organismal form that facilitates evolutionary change [10]). Whether domesticability has a role

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that spans specific temporal, spatial, and societal contexts, requires building a comparable evidence base. Our review focusses on plant domestication, but the hypotheses could equally be important for animal domestication.

Direct archaeological evidence of the nature of the interactions of people and plants during the domestication process provides us with a list of the plant taxa available, including progenitor species, their domestication status and potential use, as well as their growing conditions and a window on morphological evolution. Indirect evidence comes from comparisons between crops and their wild relatives. Care needs to be taken when using the terms ‘crop progenitors’ and ‘crop wild relatives’, however. No contemporary crop wild relative is ‘the progenitor’, as they too have evolved since the divergence of the crop, and in some instances their genetic makeup is affected by the backflow of alleles from crops [11,12]. Here, we use the term ‘progenitor species’ as a proxy term when describing the extant wild species that have evolved from the actual progenitor.

We thus build on the work by Diamond [8], who focused on the phenotypes of domesticated mammals, and a few indirect suggestions as to what plant traits could affect domesticability of a species: for example, ploidy levels [13] or life history traits [14]. Our intention in this opinion is to coalesce a range of findings, mostly unrelated to studies of domestication, surrounding traits and processes that could affect domesticability around a series of hypotheses and raise the question ‘were/are crop progenitors intrinsically different from never-domesticated relatives when cultivated?’. We then identify gaps in the literature and pathways to solve these interesting and important questions.

Plasticity – novel traits from existing variation

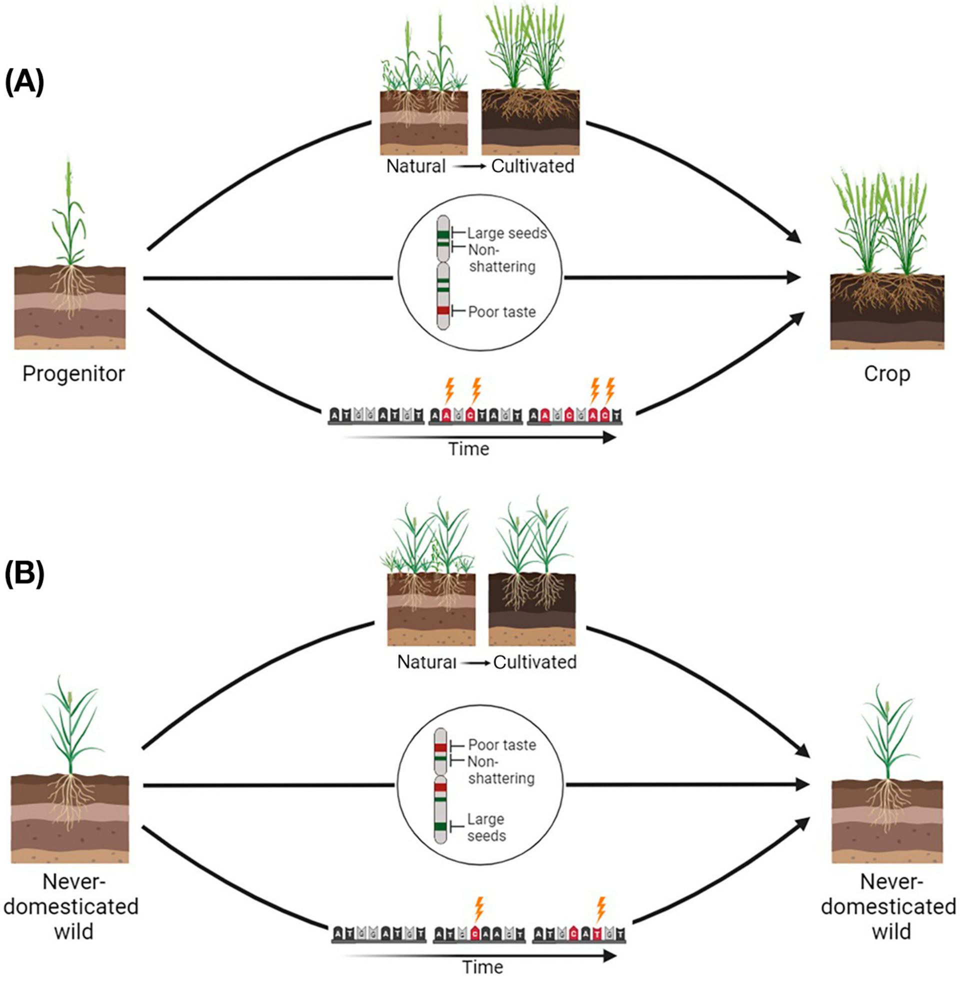
Hypothesis 1. phenotypes that were selected during domestication are more plastic in crop progenitors than other wild species and were induced by climate change and/or human management.

Plasticity is an adaptive mechanism that can result in multiple phenotypes from a single genotype and is driven by transcriptomic changes in response to environment [15]. This is a rapid way of introducing new phenotypes into the population with pre-existing genetic variation [16]. Several studies have suggested a plastic response to novel environments can lead to local adaptation via subsequent genetic assimilation [17–19]. Genotypes with high plasticity may be able to acquire resources quicker and increase growth under optimal conditions [20]. Plasticity could therefore ‘push’ crop progenitors in the right direction when brought into cultivation, accelerating adaptation to the cultivated environment and producing traits that humans would benefit from, as opposed to waiting for the relevant genetic mutation.

Based on analysis of the functional ecology of wild plants collected alongside crop wild progenitors, pre-domestication management involved human activity designed to encourage or maintain/protect dense wild plant stands suitable for harvesting [21]. In these scenarios, new plant characteristics became important instead of, or in combination with, ‘traditional’ attributes of the domestication syndrome (e.g., seed size and dispersal). Research into these characteristics offers a way to understand the selective pressures involved that led to a small subset of species becoming domesticated out of a pool of closely related species and genera. Two aspects may be particularly important: (i) climate change around the time of domestication, and (ii) local changes in nutrients and pests upon cultivation.

The increase in atmospheric CO_2 and temperature prior to ca. 12–10 KYBP [22] (the time of crop domestication in the Fertile Crescent) could have induced or increased traits through plasticity that humans selected (directly or indirectly). For example, in most species, CO_2-fertilisation can increase yield [23,24]. However, different genotypes may vary significantly in their yield response to the same CO_2 increase, such that CO_2-fertilisation is a heritable environmental response [25,26]. Empirical work in teosinte (*Zea mays* subsp. *parviglumis*), the progenitor of maize (*Z. mays* subsp. *mays*), suggests that climate change leading into the Early Holocene could have induced maize-like phenotypes [27,28].

Around the same time, the transition from foraging to cultivation took wild plants from their natural environment to human-modified fields, where people ensured the availability of water and nutrients (e.g., manure [29]), reduced interspecific competition through weeding, potentially increased intraspecific competition by growing at high density, and protected plants from herbivory (Figure 1, top of each panel). These environmental changes can induce phenotypic plasticity in



Trends in Ecology & Evolution

Figure 1. Schematic diagrams describing the key hypotheses identified in this article that could influence domesticability. (A) The transition from a progenitor to a domesticated crop; (B) the parallel for a wild species that does not become domesticated. The differences between (A) and (B) represent how progenitors and never-domesticated species respond differently to a cultivated environment (i.e., plasticity) (top of each panel), have different traits linked in the genome (with positive traits in green and negative traits in red) (middle of each panel), and have a different mutation rate (bottom of each panel).

contemporary species [30,31]; roots and leaves are sensitive to growing conditions [32] and root traits are known to be highly plastic [33]. As an example, when wild erect knotweed (*Polygonum erectum* L., the progenitor of a now extinct early domesticate) is grown with fewer neighbouring plants, a shift in plant architecture is observed, from a herb with minimal branching to a branched shrub with more seeds as a response to light availability [34]. Crop progenitors may also be more resilient to disturbance; defoliation of crop progenitors led to a 31% decrease in tillering and seed production, but a 61% reduction in never-domesticated relatives [35].

These examples highlight how plasticity may have resulted in certain wild species being better adapted than others to a cultivated environment and increased yield through the exposure of cryptic genetic variation for selection [36]. Plasticity can facilitate adaptive evolution through non-genetic inheritance [37], for instance, the stable maintenance of human-modified fields in cultivation can lead to the fixation of adaptive plastic response, resulting in the reduction of plasticity [38], known as genetic assimilation [39]. As discussed earlier, teosinte has high phenotypic plasticity [27], and gene expression plasticity is greater in teosinte than in maize, supporting the hypothesis of genetic assimilation during domestication [40]. Hence, plasticity could have played an important role in the early stages of domestication, such that species varying in the plasticity of relevant traits would have different domesticability potential.

The genetic architecture and linkage of domestication traits

Hypothesis 2. domestication traits are linked to a greater extent in crop progenitors than in other wild species.

The number of loci responsible for selected traits, their dominance/recessiveness, and their arrangement in the genome (i.e., linkage), determines how fast species can adapt/evolve under selection, which together could have favoured some species over others. Selection from standing variation can fix small numbers of alleles with large effects faster than a large number of alleles with small effects [41].

In studying the genetic basis of domestication traits in most crops, small numbers of quantitative trait loci (QTL) with large effect are typically uncovered [42–45]. In maize, most variation between domesticated and wild forms are explained by as few as five major QTL [46]. We have yet to discover if these traits are controlled by a similarly small number of large-effect QTL in the never-domesticated relatives. If not, then the genetic basis of domestication traits may have played a major role in their domesticability.

Further, the linkage between QTLs will affect the speed and efficacy of selection [47]. Two beneficial QTLs (e.g., larger seeds and loss of shattering) in linkage disequilibrium are likely to be co-inherited and therefore speed up domestication [48,49] (Figure 1A, centre). Conversely, linkage between a beneficial and a negative trait (e.g., loss of shattering and poor taste; Figure 1B, centre) could prevent specific combinations of desirable alleles from arising. Non-random co-localization of QTL for domestication traits is seen in wheat progenitors (*Triticum dicoccoides*), rice (*Oryza rufipogon*), and certain legumes (e.g., *Vigna vexillata*) [50–52]. Relatedly, it could be that greater pleiotropy (i.e., a small number of genetic loci that influence many traits, e.g., transcription factors), for selection to act upon, plays a role in the speed or efficacy of selection. In black gram (*Vigna mungo*), a highly pleiotropic QTL for gigantism of multiple organs has been reported [53], whereas in other examples, what was originally described as a single highly pleiotropic QTL has been shown to comprise multiple tightly linked QTL of moderate effect (e.g., [54]). Regardless of which, if the crop progenitors have linkage relationships between beneficial traits, or extensive pleiotropy, that allow (or speed up) selection, and never-domesticated relatives do not (or had QTL for desirable and undesirable traits linked), then the former would be domesticated, and the latter abandoned, again suggesting that species vary in domesticability.

Non-genetic linkage (i.e., phenotypic integration) is also relevant here. Stronger covariations facilitate rapid diversification down a single line of least resistance but provide less scope for evolutionary change in other directions [47]; weaker correlations provide more variation that natural selection could act on and that might be effectively targeted in the domestication process. All traits covary to some extent; for example, seed mass determines variation in yield amongst 18 annual herbaceous crops and their progenitors, producing crops with heavier seeds and higher yields despite domesticated variants not growing faster or for longer than their wild progenitors [55]. Here, variation facilitates trait changes in multiple axes that are beneficial for domestication. If wild species differ in their trait integration, extent of pleiotropy and/or genetic linkage, different species would have different domesticability.

The role of mutation in generating variation

Hypothesis 3. mutation rates are faster in crop progenitors than other wild species, generating more variation for selection to act on during domestication.

Several domestication or diversification traits were a result of new mutations [i.e., not present as standing genetic variation (SGV) in the wild] [56]. During domestication, these mutations arise, are selected, and become fixed. Faster mutation rates can lead to faster adaptation (e.g., [57]), which could influence domesticability (Figure 1, bottom of each panel). Beneficial mutations are expected to be very rare [58], and so a faster mutation rate means the faster production of deleterious mutations; however, a human-modulated environment with reduced competition and greater nutrients would be expected to relax purifying selection, thereby permitting populations to persist despite their increasing mutation load {as shown for sorghum (*Sorghum bicolor*) [59], sunflower (*Helianthus annuus*) [60], and chickens (*Gallus gallus*) [61]}.

Estimates of the number of loci under artificial selection during crop domestication vary greatly. At the high end, Hufford *et al*. [62] estimate >1600 genes in maize experienced artificial selection during domestication, whereas theoretical estimates suggest that artificial selection on no more than ca. 100 loci is sustainable [63]. However, even if only a subset of these arose as *de novo* mutations (as opposed to SGV) this represents tens to hundreds of new mutations required for domestication. Could progenitors have gained an evolutionary advantage over never-domesticated relatives through a higher mutation rate, resulting in novel traits arising more often to promote faster domestication?

Another source of genetic diversity is the activity of transposable elements (TEs); these are mobile DNA elements able to move or copy within the genome [64] and can have a significant effect on gene function and expression [65]. TEs are therefore a mutagen and can result in phenotypic change. TE insertions have been linked to a variety of domestication traits [66–69]. TEs also drive genome plasticity [70], and a change in the environment can induce TE activation, increasing the ability of the genome to respond flexibly to novel conditions [71], as one might expect when a wild species is moved into cultivation. Rates of mutation, including TE activity, can enable an increase in adaptation and diversification across a range of species [72] and therefore may play a role in domesticability of only some plant species.

Why is domesticability important?

First, if domesticability exists as a composite trait, it means that our crops today are a biased sample of edible plants. If so, domesticated species are a non-random set of species to study evolutionary processes, enriched for certain phenomena. If progenitors have greater plasticity, beneficial trait linkage relationships, and/or an increased mutation rate, then the domestication transition is not representative of evolutionary divergence more broadly. However, if progenitors differ from related wild congeners in their domesticability, then this may mean comparing these is the ideal scenario to study evolvability.

Second, not only could domesticability be the cause of our current reliance on only a small number of staple crops, but pivotal factors present (or even necessary) at the time of domestication (e.g., plasticity and mutation) may have since been bred out. Increasing the flexibility of existing crops to adjust to seasonal weather events could help ensure modern agriculture will cope with future environmental change and extreme weather events.

Beyond coping with rapid anthropogenic climate change in staple crops, there is a need to diversify contemporary food systems, particularly in the most affected regions [73]. Domesticability might have limited our options thousands of years ago, but what was important to our prehistoric ancestors may have little significance today. This is particularly important because environmental conditions, needs, and preferences have changed drastically. This neodomestication is a novel way of increasing agrobiodiversity through the accelerated domestication of wild and underutilised food plants for a vast range of environments and human needs [74]. Domesticability may explain why some underutilised crops have not been fully domesticated. Understanding the limits that were dictated by domesticability will help us understand which gaps we should fill in our crop portfolio. For example, in the Neolithic, nearly all cereals were domesticated from annual

Box 1. What do we need to know? And how can we find it out?

Diamond [8] proposed several factors that play a role in whether a species can be domesticated, including the resources needed, growth rate/generation time, number of genes controlling adaptive traits, as well as several animal-specific factors. Twenty years later there have still been limited quantitative comparative analyses of progenitors and never-domesticated relatives. Some important work has revealed how crop progenitors may have been pre-adapted to cultivation [35,75–77]. For example, barley (*Hordeum vulgare* subsp. *spontaneum*) and wheat progenitors have larger spikes and seeds than never-domesticated relatives [77], traits that humans could have consciously or unconsciously selected and which correlate with greater and more rapid seed germination. Similarly, herbaceous crop progenitors tend to be tall with high leaf N [76] and photosynthesis [75], and have thicker, less dense roots [78], suggesting they are pre-adapted to the competitive and fertile environments, respectively, expected under cultivation.

These studies suggest that some progenitor phenotypes represent pre-adaptations to cultivation and/or that plasticity could reveal adaptive phenotypes under the novel environment of the early Holocene and under cultivation. However, we know little about the relative plasticity of progenitors and never-domesticated relatives, except for the work detailed earlier. We lack studies that compare crop progenitors to never-domesticated relatives for other characteristics that could influence domesticability; we are not aware of any studies that compare the size and linkage of QTL in crop progenitors and never-domesticated relatives. Similarly, there is a lack of genome-wide comparisons of polymorphism and mutation between crop progenitors and never-domesticated relatives.

There are reasons why we lack this information. For example, experimenting with the role of plasticity and generating QTL populations is only possible with extant species and populations which, as we state earlier, are only proxies for the progenitor. For other questions about domesticability it may be that archaeological samples and ancient DNA can help provide clues; however, this is challenging due to poor preservation and availability of samples.

A technical consideration is whether enough germplasm is available, inevitably limiting research that relies on it. Many seedbanks have a disproportionate collection of domesticated plant species compared with wild relatives, with accessions of crop progenitors being more numerous than accessions of never-domesticated relatives. Based on the Genesys-PGR database (accessed June 2023), there are 11–84 times more seed accessions for barley, rye (*Secale cereale*), lentil (*Lens culinaris*), chickpea (*Cicer arietinum*), and field pea (*Pisum sativum*) than their progenitors and, for four of these five, progenitors are the most numerous of the wild species (up to 17-fold for barley wild relatives). And, finally, many wild species are harder to grow, have enhanced dormancy, and may be perennial, relative to their related crops, therefore have typically been overlooked in QTL analyses or studies requiring flowering and seed set.

grasses, but today perennial cereals are touted for carbon sequestration and reducing fertiliser applications [14].

There are several gaps in our overall knowledge that, if filled, would reveal whether domesticability played a role in the species we rely on for food (Box 1).

Concluding remarks

We currently lack the data to determine whether crop progenitors possess traits that increased their domesticability. A small number of important studies suggest that crop progenitors may differ genetically and phenotypically from their never-domesticated relatives, however, the species studied vary and the methods are not standardised. Our understanding of evolutionary processes points towards promising research avenues (see Outstanding questions). Given the important ramifications of domesticability on using domestication as an evolutionary model and on crop climate resilience, we encourage the incorporation of never-domesticated crop congeners into any investigation of domestication.

More broadly, domestication is the result of directional selection on wild taxa. Establishing the rules that govern the species that do and do not respond to this can be used to inform investigations of which wild species will respond to rapid climate change. Understanding the fundamental mechanisms via our lessons on domestication therefore has implications for biodiversity conservation.

Outstanding questions

Are domestication traits more plastic in crop progenitors than never-domesticated wild species? A positive response to this question would suggest that plasticity in traits that humans saw as relevant (yield, loss of shattering and so on) could have promoted the domestication of some species over others. A related question is whether climate change and/or human management can induce or modify these traits.

Are the linkage relationships of domestication traits different between crop progenitors and their never-domesticated wild relatives? If domestication traits are controlled by a smaller number of large effect loci than in never-domesticated species, and tend to be linked in progenitors, this would suggest that domestication would proceed more efficiently and therefore rapidly.

Is mutation rate (including the movement of transposable elements) more rapid in crop progenitors? If so, it is plausible that novel traits arise more rapidly in some species than others, resulting in an increase in domesticability.

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Declaration of interests

The authors declare no competing interests.

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