


## Review

## Emerging evidence of plant domestication as a landscape-level process

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The evidence from ancient crops over the past decade challenges some of our most basic assumptions about the process of domestication. The emergence of crops has been viewed as a technologically progressive process in which single or multiple localized populations adapt to human environments in response to cultivation. By contrast, new genetic and archaeological evidence reveals a slow process that involved large populations over wide areas with unexpectedly sustained cultural connections in deep time. We review evidence that calls for a new landscape framework of crop origins. Evolutionary processes operate across vast distances of landscape and time, and the origins of domesticates are complex. The domestication bottleneck is a redundant concept and the progressive nature of domestication is in doubt.

## A re-evaluation of the assumptions of plant domestication

The evolution of **domesticated** (see [Glossary](#)) plants underpinning the rise of agriculture is often seen as a pivotal moment in human progress, but the process was also associated with the initial costs of malnutrition [1], disease [2], and **labor traps** that lock humans into dependency on agriculture [3]. Consequently, the mechanisms and motivations that drove the process remain unclear, and it is likely that aspects of the domestication paradigm framework require some revision to accommodate the accumulation of paradoxes. In this context, culture and biology are closely entwined – as research breakthroughs occur in one field, the ramifications can run like shockwaves through the other to expose unconscious underlying assumptions.

We are increasingly appreciating the complexities involved in the evolution of domestication [4,5]. A decade ago saw a shift in thinking from simple single-localized crop origins to more complex origins [6]. Recently, increasingly diverse disciplines have contributed evidence highlighting the complexity of domestication. In parallel cases, domestication occurred over vast but culturally connected distances, over long periods of time, and initially in periods long before early agriculture. This evidence resets the frame of the debate as emerging data reveal that domestication does not fit with conventional visualizations of the process ([Figure 1](#)). The consequences for the interpretation of cultural shifts are potentially profound, and will require rethinking of how human societies evolved with so far underappreciated levels of long-distance social interaction that allowed exchange of plant germplasm and knowledge.

We detail below aspects of the plant domestication process that have come under revision through emerging **archaeogenomic** and archaeobotanical evidence. We conclude that a landscape perspective will be necessary, as visualized in [Figure 2](#), to frame domestication research in a way that incorporates current anomalies to the conventional view.

## Highlights

Current theories of plant domestication are based on localized founder models in which single or multiple domestications occur as a progressive result of adaptation processes, but anomalies that do not fit within this perspective have been accumulating.

We describe developments in archaeology and genetics over the past decade in which cultural connections between groups stretch back much further in time than was previously realized, and over wide geographic distances. Weak selection for domestication substantially pre-dates domestication and/or cultivation practices, large populations appear to have been maintained throughout the emergence of domesticates, and the resulting forms were not necessarily an improvement in terms of yield.

We present a framework in which the process of domestication evolved as a landscape-level process involving large populations connected through sustained long-term human contact over large distances from which domesticate forms emerged in a complex manner as an adaptive reaction to long-term exploitation that did not necessarily provide immediate benefits.

The landscape framework addresses several anomalies and radically changes the dynamic visualization of the evolution of domestication. It also opens up a list of new questions regarding the mechanisms of selection and the assembly of domestication syndrome alleles, and obliges a profound rethink of the progressive nature of domestication and human cultural evolution.

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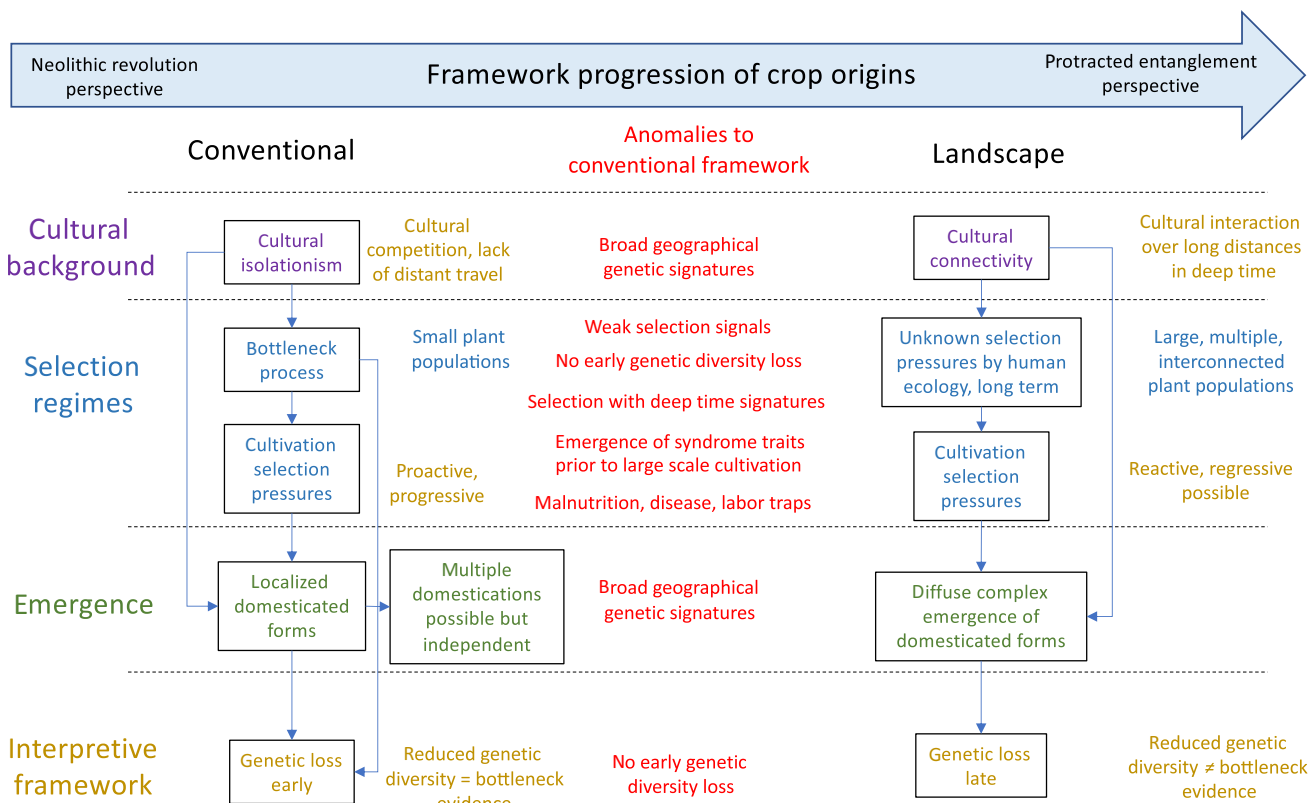
### The vast temporal window of selection for the domestication syndrome

The progression of domestication can be tracked from the archaeological record through observation of changes in the key visible traits of the **domestication syndrome**. These traits include seed size and dispersal (shattering) in crops such as cereals. In many species seeds transition to larger dimensions with the rise of domesticated forms [1,7]. Seed-shattering changes are evident in abscission scar morphology where jagged forms indicate the threshing of Southwestern Asiatic cereals (einkorn, *Triticum monococcum*; emmer, *Triticum dicoccum*; and barley, *Hordeum vulgare*) and rice (*Oryza sativa*) in the Lower Yangtze [7–9], and fruit body remodeling in maize (*Zea mays*) [10] and pearl millet (*Pennisetum glaucum*) [11]. The continuum of wild and derived morphological characters that are underpinned genetically can be used to define the state of the domestication process, and can indicate forms that are visibly domesticated.

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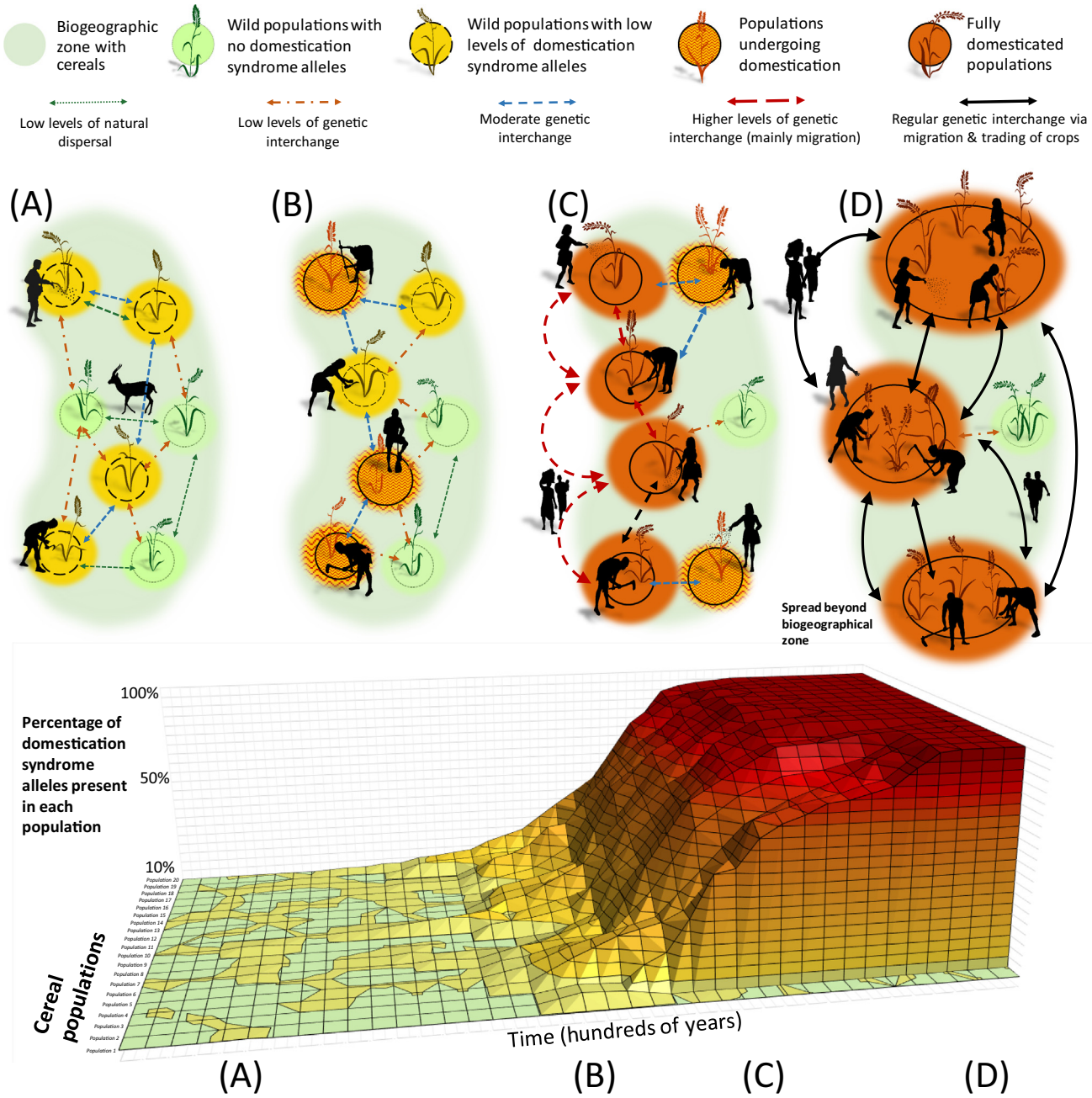
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Despite early expectations and views of domestication as a rapid process that involved strong forces of artificial selection, the past 15 years have demonstrated a gradual transition to domesticated forms over timeframes spanning millennia in a range of species. Archaeological remains of Southwest Asian cereals document a transition of over 2000 years in decreased seed-shattering and increasing seed size [7, 12–14], with similar observations for rice in East Asia [8]. This same pattern was observed for numerous crops in other world regions; these include sorghum (*Sorghum bicolor*), common millet (*Panicum miliaceum*), pearl millet, pea (*Pisum sativum*), lentil



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Figure 1. The landscape framework of crop origins. The landscape framework differs from the conventional framework by operating at a larger temporal and geographical scale into deep time through previously unappreciated pervasive cultural connections that greatly pre-date the onset of cultivation practices. The process that leads to domestication is driven by so far unidentified selection pressures in deep time, resulting in resource changes that could necessitate reactive measures such as cultivation to maintain food security.



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**Figure 2. Visualization of a landscape-level process of domestication.** The upper diagram shows the interaction between the changing distribution of domestication syndrome alleles within for any given cereal population (A) under low-level exploitation and management, (B) at beginnings of domestication (pre-domestication cultivation), (C) at the end of domestication (pre-domestication cultivation), and (D) in fully domesticated populations. The arrows indicate genetic transfer between cereal populations in which increasing transfer of domestication syndrome alleles between populations through time takes place predominately through human movement and exchange. The lower diagram shows the accumulation and interchange of domestication syndrome alleles for several hypothetical populations over the time-period for the four stages above. The diagram shows variable speeds of accumulation of domestication syndrome alleles through both internal selection and acquisition via genetic transfer between populations. Note the different starting points to domestication and end points for any given population. For the cereals for which such periods has been measured using genetic and archaeobotanical data, time-frames may be place on these divisions in terms of approximate start dates. For Western Asia, barley and wheat: (A) 25–20 kyr BP, (B) 12.5–11.5 kyr BP, (C) 10–9.5 kyr BP, and (D) 9.4–8 kyr BP. For Lower Yangtze rice: (A) ~14 kyr BP, (B) 9–6 kyr BP, (C) 7–6 kyr BP, and (D) 6–5.5 kyr BP.

(*Lens culinaris*), soybean (*Glycine max*), chickpea (*Cicer arietinum*), Indian horsegram (*Macrotyloma uniflorum*), sumpweed (*Iva annua*), sunflower (*Helianthus annuus*), squash (*Cucurbita pepo*), and pitseed goosefoot (*Chenopodium berlanderi*) [11,15–19]. It has therefore become apparent that the slow pace of the rise of domesticated morphologies is a general rather than an anomalous observation. This raises a question of why strong selection does not generally appear to have been involved in the evolution of domestication.

In addition to the inferred slow rise of domesticated forms, expansion of the archaeological evidence allowed a second observation – that early domesticated forms were widely dispersed and had no single epicenter for their emergence. This phenomenon is seen for all early crops in the Fertile Crescent [12,15,20] and East Asia [21,22]. The slow evolution of domestication and diffuse distribution of early forms highlights the importance of crop movement in which gene flow between plant populations is a consequence of cultural interactions across the landscape. To better understand this process at both the biological and cultural levels, we need to understand the length of time over which domestication and the emergence of domesticated forms occurred, and how wide a region was involved.

The strength of selection can be directly assessed from the archaeobotanical record by measuring the change over time in the frequency of shattering and variance in seed size using the statistical approaches of **Haldane units** and **Darwin units**. It was first established that, for the cereals of Southwest Asia (einkorn, emmer, barley) and East Asia (rice), the **selection coefficients** for both traits were very low, and, crucially, were comparable to those involved in natural selection [23,24]. This observation was similarly found in a wider range of crops, including lentils, goosefoot, mung-bean, sunflower, soybean, pea, and squash [15]. Such findings question the notion that strong artificial selection associated with early domestication was a general principle, and this has implications for the modes and mechanisms of selection involved.

Further dissection of the strength of selection established that selection pressures changed over time [25]. Notably in the case of Southwest Asian cereals (einkorn, emmer, barley) a strong increase in selection is associated with the development and increasing dominance of stone sickle technologies [26]. Before the rise of sickles, selection for non-shattering was very weak, but domestication syndrome traits were already at substantial frequencies in the range of 20–30% before investment in sickle tools increased. This suggests that a weak source of selection pressure pre-dated clear agricultural activities by many millennia. Backward extrapolation with genetic models suggests that the onset of such weak selection pressures dates to as early as 20–25 thousand years ago (kyr BP) in Southwest Asia, and 14 kyr BP in East Asia for rice [25]. This evidence indicates that processes other than pre-agricultural cultivation played a role in the initiation of the domestication trajectory which is likely rooted in changing human ecologies impacting on wild plant populations during the late Pleistocene.

The late Pleistocene is increasingly recognized as a time of human transformation of ecosystems through vegetation burning and the hunting of megafauna [27]. The period following the Last Glacial Maximum, ~20 kyr BP, is associated with intensified foraging in China [28] and Southwest Asia [29], possibly driven by overhunting and climatic amelioration [30–33]. During the **Epipalaeolithic** in the Near East (24–11 kyr BP), increasingly complex microlithic toolkits emerged, along with increased social communication revealed by long-distance exchange of obsidian and seashells, and increased investment in settlement structures [34–36]. Similarly, central places became established in the landscape in East Asia and new ceramic and microlithic technologies arose during this same period [28,37]. A clear trend of increased exploitation of wild grasses and cereals occurred throughout this period, occasionally culminating in aborted

## Glossary

**Archaeogenomics:** the study of genomic evolution in real time through the reconstruction of genomes of archaeological samples from ancient DNA.

**Competitive selection:** a form of frequency-dependent selection in which the selective disadvantage of the wild type is a function of the frequency of the adaptive mutant such that selection can be initially weak but becomes increasingly intense over time.

**Darwin unit:** a measure of rate of phenotypic change defined as the logarithmic change in the mean value of a trait per million years.

**Domestication:** the process of adaptation of plants and animals to the human environment, usually to the mutual benefit of both.

**Domestication syndrome:** a set of traits that are often associated with domestication, although not all are always present. These include changes in seed size, seed dispersal, plant architecture, seasonal habit, dormancy, environmental sensitivity such as vernalization, and toxin content.

**Environmental selection:** a class of selection model in which the selective disadvantage of the wild type is determined by a change in the environment, leading to a genetic load.

**Epipalaeolithic:** an archaeological period of hunter-gatherer-fisher economies at the end of the Pleistocene, characterized by microlithic stone tools and wood and bone points, and that is inferred to represent innovations including harpoons and bow and arrow. In Southwest Asia this is placed between 24 kyr BP and 11.5 kyr BP.

**Genetic drift:** the random change in allele frequency taking place in each generation, the strength and rate of which is inversely related to population size.

**Genetic load:** the general reduction in fitness in a population relative to an adapted type. Genetic load can be generated in multiple ways including through mutation load or a general change in environmental conditions.

**Haldane unit:** a measure of rate of phenotypic change, defined as the fraction of a standard deviation change per generation.

**Labor trap:** an activity that, once undertaken, commits an individual to that activity to the exclusion of others. The onset of agriculture is associated

cultivation regimes [38,39]. How those activities relate to mechanisms of selection is currently a matter of conjecture, but they may account for persistent, weak selection for traits that later were adaptive for domestication.

### Agency and the mode and strength of selection – was it necessarily 'progress'?

Two key aspects of domestication concern the role of human agency and the adaptive potential of plants undergoing domestication. A disparity has developed here between the biological and archaeological sciences. Domestication theories in archaeology have evolved over the past century from a standpoint of a high degree of consciousness and human agency [40,41] to one of unconsciousness as archaeologists increasingly viewed domestication as an emergent ecological process in which plants adapted to the human environment [4,42]. In this instance, consciousness pertains to selective breeding carried out by proto-agriculturalists that led to the rise of domesticated forms, a view that is still supported in some biological quarters [43]. Most domestication researchers now recognize the teleological paradox that conscious initial domestication engenders: proto-agriculturalists would need to recognize traits and predict the complex consequences of breeding before having ever achieved it. It further requires an ability to identify very low frequencies of extremely subtle differences between plants, a scenario that most find unconvincing. However, the notion of selective breeding has deep roots in biological thought. Darwin first used it to demonstrate the principal of natural selection [44], although he attributed the domestication process itself to unintentional selection biases [45]. Later it was invoked in the guise of **truncation selection** as a possible general mode of selection [46]. The latter was identified as a highly efficient mechanism of selection that largely avoids the selection costs caused by **genetic load** under conventional **environmental selection** models (Box 1) [48,49]. Although truncation selection operates in selective breeding, it is questionable whether the ranking and truncation it requires (Box 1) could occur in nature [48], and, given the lack of natural empirical examples, it is likely to be vanishingly rare if it exists at all.

An assumption of a selective breeding approach by incipient farmers brings with it a suite of cultural assumptions about the intentionality and mode of selection [43]. These include conscious ranking of plants by trait value so as to apply the selective truncation process because no known cultivation mechanism could achieve this unconsciously. These assumptions run contrary to half a

with labor traps of increased labor expenditure on crop processing and soil maintenance, in particular as crops themselves adapt to the tillage environment and become dependent on human intervention for survival.

**Mutation load:** that part of the genetic load which is described by deleterious mutations which purifying selection removes over time. However, under conditions of small population size in which genetic drift becomes more powerful than selection, mutation load accumulates as new deleterious mutations become randomly incorporated into the population.

**Selection coefficient:** the difference in fitness between the ideal adapted type and the type to which selection is being applied.

**Substitution load:** that part of the genetic load which is described by the difference in fitness between an ideal adapted state and the current state. The consequence of the substitution load is that not all individuals will be reproductively successful, consequently population declines are associated with selective episodes owing to the substitution load.

**Truncation selection:** a process by which all individuals below a given threshold value of a trait are eliminated from further reproduction.

#### Box 1. Models of selection

Selection models are invoked to describe mechanisms of selection that remove less-fit individuals. Many models apply Haldane's original approach [47] of environmental degradation (Figure 1A) in which an environmental factor challenges the population such that the majority is suddenly at a selective disadvantage, and a genetic load is therefore imposed. Mutations that overcome the challenge rise in frequency while wild types have a probability of extinction that is expressed by the magnitude of the selection coefficient ( $S$  in Figure 1). The resulting reduction in population size during selection is the substitution load. Strong selection can rapidly lead to the demise of the population, and numerous simultaneous adaptive challenges rapidly bring maximum possible selection strengths to nearly neutral levels [54] even when multiple adaptive solutions are available, an initial criticism of Haldane's approach [55–57]. The standard stabilizing selection model is a subset of environmental selection that is often applied to complex traits [65]. This model accounts for the increasing fitness of individuals as numerous loci involved in a single adaptive challenge gain adaptive alleles. Here the strength of selection necessarily diminishes as individuals approach the fitness threshold, and hence will always behave as stabilizing selection.

Selective breeding works through the alternative mechanism of truncation selection (Figure 1B) in which individuals are ranked by fitness with respect to a particular trait, and again a fitness threshold is imposed [46]. In contrast to Haldane's selection, all individuals below the threshold are removed, and all individuals above are retained. Because the fitness threshold can be placed in a way that predictably splits the population, such as retaining the top half while discarding the lower half, the extent to which the population is reduced can be controlled and the problem of the substitution load becoming excessive is overcome [48].

A third class of selection model differs from Haldane's original system in that the strength of selection is a dynamic function of individuals of the population rather than the environment. These often work by frequency- or density-dependency. One such example is competitive selection [68] (Figure 1C). Here an advantage is gained by a mutant in resource acquisition. This increase in resource acquisition elicits a burden shared by the remainder of the population. As more advantaged individuals appear, resource becomes rarer for the wild type, thus intensifying their selective removal, and the excess resource diminishes with increasing competition between advantaged individuals until the population returns to its original state.

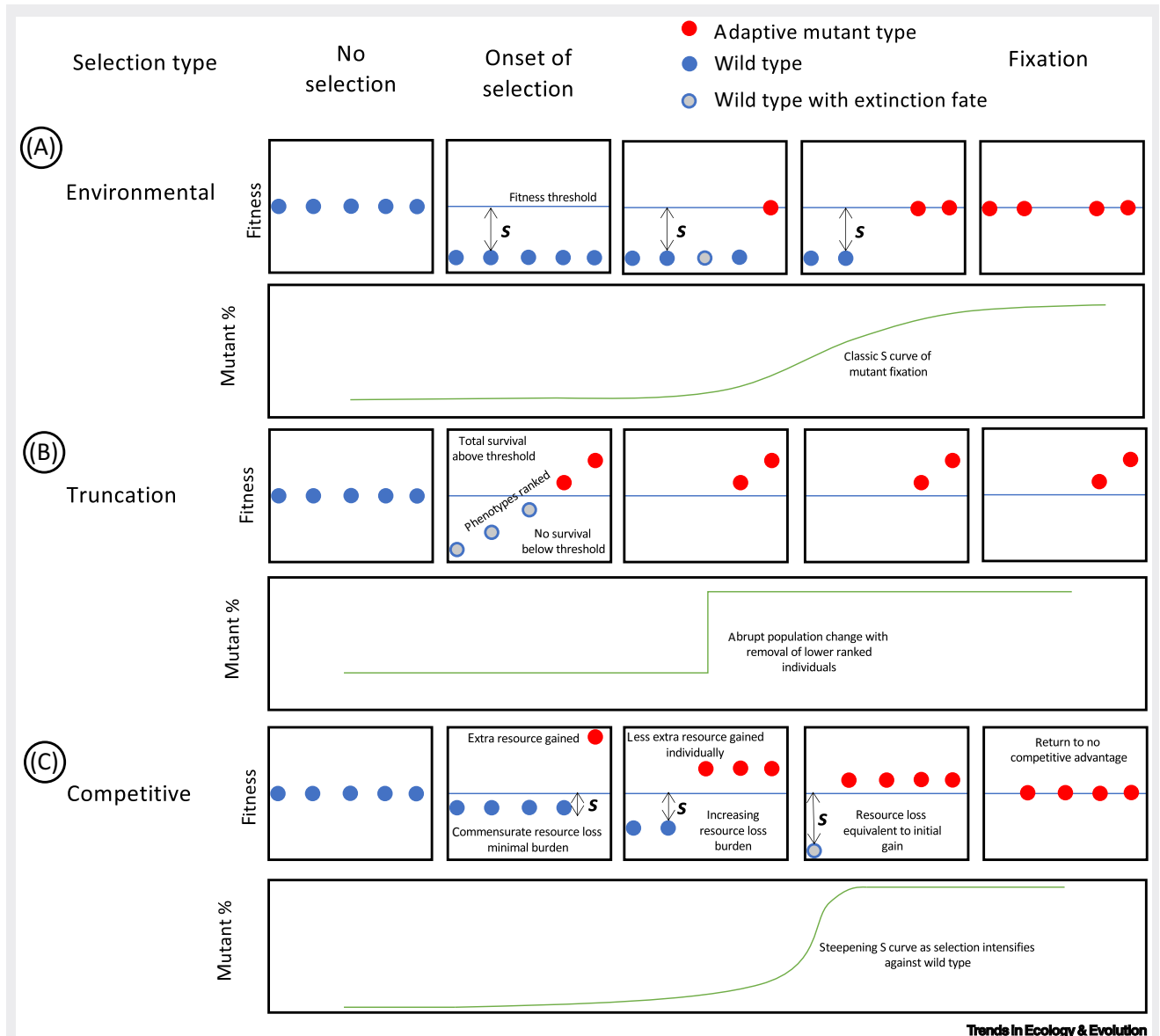


Figure I. Mechanisms of selection models.

century of archaeological thought, and do not appear to be borne out by the direct evidence of slow, weak selection over millennia that is apparent in the archaeological record [7,9,15,24]. A scenario in which plants adapted to the human environment without a truncation selection-based mechanism opens up several questions about the mechanism, the number of adaptations, and the loci involved [50,51], as well as the selection limits, the associated strength of selection, and the general detectability of soft versus hard selective sweeps [52,53]. Simple application of Haldanian environmental selection suggest that load restrictions under mounting adaptive challenges lead to weak selection [54]. This is in agreement with models that do not account for selection cost, but account for the additive effects of quantitative trait loci [58,59]. Such models describe relatively simply controlled

phenotypes, such as shattering loss, and also have been found to describe the short-term dynamics of directional selection in more complex systems sufficiently well to be usefully informative [60]. This use of models to test the stress of the **substitution load** on populations is informative about the possible causes of repeated agricultural collapse where environmental selective challenges could have been too numerous during agricultural expansion [61–64].

Many crop traits are under complex control following a pattern of stabilizing selection [65] (Box 1). Such models focus on indirect selection at loci through additive effects on the phenotype, leading to a general expectation that alleles of small effect react to shifts in environmental conditions [58,59,66]. These are broadly in agreement with the theoretical expectation of weak selection at the locus level, and it has been noted that strong selection over numerous adaptive challenges induces inhibitive population bottlenecks at levels comparable to the simple Haldanian models [67].

In the absence of selective breeding mechanisms of truncation selection, theoretical biological expectations of selection and archaeological data are largely reconciled to a scenario of weak selection over long time-periods. This opens up the debate about the mechanisms of selection involved. Archaeological data indicate that different selective mechanisms were likely in play over time in the case of shattering loss [25]. Conversely, the complex trait of seed size shows trends that would be unexpected under the standard stabilizing selection model. Instead of the expected reduction in selection intensity over time as size shifts to new optima and the trait becomes restabilized, an anomalous intensification of selection is observed. This observation could possibly be explained by competition. Seedling competition has been suggested as a mechanism for increases in seed size based on archaeological data [17,69,70], and a similar conclusion was recently reached from examining competition between seedlings of different wild progenitor species in disturbed human environments [71]. One intuitive expectation of competition is that, as more effective competitors prevail, diminishing resource availability will intensify the removal of the less competitive. A novel class of selection model that works by **competitive selection** between plants (Box 1) confirms this expectation of periods of intensification of selection, and these appear to explain well the observed archaeological trends [68]. Crucially, larger-seeded crops do not necessarily translate to a higher yield [72], casting doubt on the general interpretation that the rise of increased seed size represents a progressive beneficial trait for humans. Together, this leads to a picture in which plant groups adapt to the human environment independently of humans, and these groups do not necessarily represent the most nutritionally important plants for humans.

Increasingly, the first opportunity for adaptation is ascribed to plants in the niches produced by human activity. Translated to the cultural landscape, the conventional view of a progression that is beneficial in terms of improving food security is questionable. The current evidence is beginning to suggest an exploited resource that changes slowly over long time-periods in response to exploitation and other disturbance in ways that may not always have been welcome or immediately beneficial.

### The redundancy of a domestication bottleneck concept

The domestication bottleneck involves a contraction and recovery in census population size that both reduces genetic diversity and causes an increase in **mutation load** through the strong effects of **genetic drift** [73]. It has been a fundamental component of paradigms of domesticated species origins which envisage proto-farmers retrieving wild plants for cultivation which ultimately evolved into domesticated forms.

The emerging picture of the evolution of domestication as a very slow process that was initiated long before the rise of cultivation makes the notion of a classical bottleneck at the onset of

domestication both unnecessary and unlikely. A reduction in population size that is sufficient to raise the strength of drift sufficiently to override purifying selection and increase the mutation load would similarly be expected to override weak selection. Consequently, the domestication bottleneck concept appears to be incompatible with the observed weak selection in the archaeological record. Direct archaeogenomic examination of genetic diversity during domestication (barley, maize, wheat, sorghum, and beans [74–82]) consistently do not show a loss of genetic diversity associated with the domestication bottleneck. Mutation load was found to be attributable mostly to processes after the domestication bottleneck [75,81]. These findings from archaeogenomics reverberate with observations of einkorn [83] and barley [84] in which heterozygosity differs little between wild and domesticated forms. Alternative approaches using coalescent models to reconstruct past population histories [85,86] have shown trends consistent with very long-term declines in population size over tens of thousands of years, and that vastly pre-date the rise of domesticated forms or the presence of humans [87,88]. Bottlenecks inferred from troughs in population size have both coincided [88] and missed [87] the expected time of domestication. These long-term trends could possibly reflect unknown ecological processes, but have also been demonstrated to be an artefactual product of subdivided wild metapopulation structures [89].

Taken together, these data have led to the suggestion that large populations were likely to have been involved in the process of domestication [90]. Importantly, a general reduction of genetic diversity of domesticate relative to wild progenitor species is not sufficient to infer a domestication bottleneck without knowing the diversity of the wild population substructure, the relative contributions of subpopulations to the domestication gene pool, and the timing of diversity reduction [90]. The domestication bottleneck concept is still often held as an obvious necessity to explain how proto-farmers subsumed a fraction of wild species into their regimes of cultivation, and debate is likely to continue for some time on this topic. Over the past decade the severity of the bottleneck invoked has been progressively downgraded [91], and is an increasingly redundant concept in a framework in which crops bear the signatures of emergence from large meta-populations under long-term weak selection.

### The slow and complex emergence of domesticates

Conventionally, crop origins have been sought in terms of specific places in a localized visualization of the process. This fits comfortably within the rapid transition model where a fast rise of domesticates occurred in response to artificial selection pressures under a high degree of localized human agency (e.g., [92]). This scenario implies a lack of human communication between regional centers and associated geneflow. Persistent expectations of a place for human agency in the evolution of domestication under a protracted model [93] are met by evidence in archaeological data which runs counter to the localized model. Regular trade millennia before agriculture, extending back into the Epipalaeolithic (>20 kyr BP), has been revealed in commodities such as obsidian and seashells that demonstrate sophisticated long-range networks capable of facilitating geneflow [34,37,94]. Reflecting this, crops such as barley [95] and emmer wheat [96] show genetic affiliation across the wild biogeographic range, including similarities to divergent wild ecotypes.

Several crops clearly show independent domestication trajectories in different regions, including beans in the Andes and Meso-America [97], *Chenopodium* in the Andes, Mesoamerica, and eastern North America [98], and squashes (*Cucurbita* spp.) from several localities throughout the American continents [99]. Even within regions parallel domestications for beans [100], chili peppers [101], and, over a wider geographical range, emmer wheat [102] have occurred. To fit such patterns of genetic diversity within the conventional framework requires attribution to



post-domestication introgression [92,103], but still requires strong selection signals and lowered genetic diversity during domestication which are not borne out by the data [15,25]. However, it is also the case that introgressive processes underlie post-domestication adaptation to altitude [104] and latitude [105].

A key issue is whether domestication syndrome alleles were assembled centrally before dispersal, or alternatively emerged during extensive geneflow across the wild progenitor range. This is a challenging knot to unravel under a system of decentralized long-term extensive geneflow and weak selection. In the case of maize, analysis of the soft selection of domestication syndrome alleles from wild standing variation demonstrates that different waves of semi-domesticated maize dispersed from the Mesoamerican range, and show different biases in teosinte background, and thus variant processes of syndrome fixation [75]. In this case maize origins resulted from multiple extractions over time from the region of origin against a background of extensive geneflow across wild teosinte populations.

Overall a picture is emerging for the slow emergence of crops at a regional scale in which extensive processes of geneflow occurred. As genomic tools improve, more of these subtle and complex trajectories are likely to be uncovered.

### Concluding remarks

The strands explored here, that are represented in the framework progression of Figure 1, bring together the emergent evidence of the past decade of a protracted time-frame of domestication involving complex processes and weak selection pressures that stretch beyond a direct progressive switch to domesticated forms. The landscape framework visualized in Figure 2 is a fundamentally different model in both mechanism and interpretation of the evolution of domestication than has been discussed across disciplines in the past. The involvement of large populations over wide areas actively connected through human agency mediated geneflow, from which a spectrum of development of domesticated forms emerged pluralistically, frames a model that operates at the landscape level. The framework outlined in Figure 1 erases paradoxes that have accumulated in the domestication paradigm, and presents a series of new avenues of investigation (see Outstanding questions). Radically, a general assumption that the evolutionary changes seen in plants in response to their exploitation were universally beneficial or welcome to humans is no longer necessary in all cases. This is a fundamental departure from the notion of attributing origins to a specific locality and advantaged cultural group, and the implications may be far-reaching and make a fruitful area of investigation in the coming decade. The high level of crop diversity involved will encourage a rethink about the plasticity and adaptability of crops and their robustness to adaptive challenges [61,62,64,69]. The framework supports a potential range of mechanisms to be explored to understand the role of agricultural weeds and their entry into the food chain as a part of the same extended system rather than as exceptional oddities [70,106]. Establishing the extent to which human communication across landscapes elevated geneflow between crops above wild levels, in unison with the growing recognition of early human cultural connectedness that stretches to the Epipalaeolithic, has the potential to profoundly impact on our understanding of early cultures, the role of human agency, and the mechanisms by which the process of domestication arises.

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### Outstanding questions

What were the mechanisms that actually initiated selection for domestication syndrome traits?

How widespread is the lack of the hallmarks of the domestication bottleneck among crops?

Were domestication syndrome alleles assembled before or after dispersal of early cultivars?

What is the relationship between deep-time human networks and wild crop progenitor gene flow?

Are weeds that transitioned into food sources part of the same framework?

Could domestication have evolved in the absence of long-term human contact between groups?

How does long-term sustained contact revise our understanding of human cultural evolution?

### Declaration of interests

No interests are declared.

### References

- Larsen, C.S. (1995) Biological changes in human populations with agriculture. *Annu. Rev. Anthropol.* 24, 185–213
- Wolfe, N.D. *et al.* (2007) Origins of major human infectious diseases. *Nature* 447, 279–283
- Fuller, D.Q. *et al.* (2010) Domestication as innovation: the entanglement of techniques, technology and chance in the domestication of cereal crops. *World Archaeol.* 42, 13–28
- Larson, G. *et al.* (2014) Current perspectives and the future of domestication studies. *Proc. Natl. Acad. Sci. U. S. A.* 111, 6139–6146
- Purugganan, M. (2019) Evolutionary insights into the nature of plant domestication. *Curr. Biol.* 29, R705–R714
- Brown, T.A. *et al.* (2009) The complex origins of domesticated crops. *Trends Ecol. Evol.* 24, 103–109
- Fuller, D. (2007) Contrasting patterns in crop domestication and domestication rates: recent archaeobotanical insights from the Old World. *Ann. Bot.* 100, 903–924
- Fuller, D.Q. *et al.* (2009) The domestication process and domestication rate in rice: spikelet bases from the Lower Yangtze. *Science* 323, 1607–1610
- Tanno, K.-I. and Willcox, G. (2012) Distinguishing wild and domestic wheat and barley spikelets from early Holocene sites in the Near East. *Veg. Hist. Archaeobot.* 21, 107–115
- Benz, B.F. (2001) Archaeological evidence of teosinte domestication from Guilá Naquitz, Oaxaca. *Proc. Natl. Acad. Sci. U. S. A.* 98, 2104–2106
- Fuller, D.Q. *et al.* (2021) Transition from wild to domesticated pearl millet (*Pennisetum glaucum*) revealed in ceramic temper at three Middle Holocene Sites in Northern Mali. *Afr. Archaeol. Rev.* 38, 211–230
- Arranz-Otaegui, A. *et al.* (2016) Regional diversity on the timing for the initial appearance of cereal cultivation and domestication in southwest Asia. *Proc. Natl. Acad. Sci. U. S. A.* 113, 14001–14006
- Fuller, D. *et al.* (2018) From intermediate economies to agriculture: trends in wild food use, domestication and cultivation among early villages in southwest Asia. *Paleorient* 44, 61–76
- Tanno, K.-I. and Willcox, G. (2006) How fast was wild wheat domesticated? *Science* 311, 1886
- Fuller, D.Q. *et al.* (2014) Convergent evolution and parallelism in plant domestication revealed by an expanding archaeological record. *Proc. Natl. Acad. Sci. U. S. A.* 111, 6147–6152
- Winchell, F. *et al.* (2018) On the origins and dissemination of domesticated sorghum and pearl millet across Africa and into India: a view from the Butana Group of the Far Eastern Sahel. *Afr. Archaeol. Rev.* 35, 483–505
- Stevens, C.J. *et al.* (2020) A model for the domestication of *Panicum milliaecum* (common, proso or broomcorn millet) in China. *Veg. Hist. Archaeobotany* 30, 21–33
- Murphy, C. and Fuller, D.Q. (2017) Seed coat thinning during horsegram (*Macrotyloma uniflorum*) domestication documented through synchrotron tomography of archaeological seeds. *Sci. Rep.* 7, 5369
- Barron, A. *et al.* (2020) Snapshots in time: microCT scanning of pottery sherds determines early domestication of sorghum (*Sorghum bicolor*) in East Africa. *J. Archaeol. Sci.* 123, 105259
- Fuller, D.Q. *et al.* (2011) Cultivation and domestication had multiple origins: arguments against the core area hypothesis for the origins of agriculture in the Near East. *World Archaeol.* 43, 628–652
- Ren, X. *et al.* (2016) Foothills and intermountain basins: does China's Fertile Arc have 'Hilly Flanks'? *Quat. Int.* 426, 86–96
- Stevens, C.J. and Fuller, D.Q. (2017) The spread of agriculture in eastern Asia: archaeological bases for hypothetical farmer/language dispersals. *Lang. Dyn. Change* 7, 152–186
- Purugganan, M.D. and Fuller, D.Q. (2009) The nature of selection during plant domestication. *Nature* 457, 843–848
- Purugganan, M.D. and Fuller, D.Q. (2011) Archaeological data reveal slow rates of evolution during plant domestication. *Evolution* 65, 171–183
- Allaby, R.G. *et al.* (2017) Geographic mosaics and changing rates of cereal domestication. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 2, 20160429
- Maeda, O. *et al.* (2016) Narrowing the harvest: increasing sickle investment and the rise of domesticated cereal agriculture in the Fertile Crescent. *Quat. Sci. Rev.* 145, 226–237
- Boivin, N.L. *et al.* (2016) Ecological consequences of human niche construction: examining long-term anthropogenic shaping of global species distributions. *Proc. Natl. Acad. Sci.* 113, 6388–6396
- Chen, S. and Yu, P.L. (2017) Intensified foraging and the roots of farming in China. *J. Anthropol. Res.* 73, 381–412
- Roberts, N. *et al.* (2018) Human responses and non-responses to climatic variations during the last Glacial–Interglacial transition in the eastern Mediterranean. *Quat. Sci. Rev.* 184, 47–67
- Stiner, M.C. (2001) Thirty years on the 'Broad Spectrum Revolution' and paleolithic demography. *Proc. Natl. Acad. Sci.* 98, 6993–6996
- Zeder, M.A. (2012) The broad spectrum revolution at 40: resource diversity, intensification, and an alternative to optimal foraging explanations. *J. Anthropol. Archaeol.* 31, 241–264
- Weiss, E. *et al.* (2004) The broad spectrum revisited: evidence from plant remains. *Proc. Natl. Acad. Sci.* 101, 9551–9555
- Ramsey, M.N. *et al.* (2016) Risk, reliability and resilience: phytolith evidence for alternative 'Neolithization' pathways at Kharaneh IV in the Azraq Basin, Jordan. *PLoS One* 11, e0164081
- Maher, L.A. *et al.* (2012) The pre-Natufian Epipaleolithic: long-term behavioral trends in the Levant. *Evol. Anthropol.* 21, 69–81
- Maher, L.A. (2019) Persistent place-making in prehistory: the creation, maintenance, and transformation of an Epipaleolithic landscape. *J. Archaeol. Method Theory* 26, 998–1083
- Frahm, E. and Tryon, C.A. (2018) Origins of Epipaleolithic obsidian artifacts from Garrod's excavations at Zarzi cave in the Zagros foothills of Iraq. *J. Archaeol. Sci. Rep.* 21, 472–485
- Liu, L. *et al.* (2013) Paleolithic human exploitation of plant foods during the last glacial maximum in North China. *Proc. Natl. Acad. Sci.* 110, 5380–5385
- Snir, A. *et al.* (2015) The origin of cultivation and proto-weeds, long before Neolithic farming. *PLoS One* 10, e0131422
- Asouti, E. and Fuller, D.Q. (2012) From foraging to farming in the southern Levant: the development of Epipaleolithic and Pre-pottery Neolithic plant management strategies. *Veget. Hist. Archaeobot.* 21, 149–162
- Childe, V.G. (1928) *The Most Ancient East: The Oriental Prelude to European Prehistory*, Kegan Paul
- Levi-Strauss, C. (1962) *La Pensée Sauvage*, Plon
- Rindos, D. (1984) *The Origins of Agriculture: An Evolutionary Perspective*, Academic Press
- Abbo, S. *et al.* (2011) Origin of Near Eastern plant domestication: homage to Claude Levi-Strauss and 'La Pensée Sauvage'. *Genet. Resour. Crop. Evol.* 58, 175–179
- Darwin, C. (1859) Variation under domestication. In *Origin of Species*, pp. 7–43, Murray
- Darwin, C. (1869) *Variation of Plants and Animals under Domestication*, Murray, p. 114
- Sved, J.A. (1968) Possible rates of gene substitution in evolution. *Am. Nat.* 102, 283–293
- Haldane, J.B.S. (1957) The cost of selection. *J. Genet.* 55, 511–524
- Crow, J.F. and Kimura, M. (1979) Efficiency of truncation selection. *Proc. Natl. Acad. Sci. U. S. A.* 76, 396–399
- Barton, N.H. (1995) Linkage and the limits to natural selection. *Genetics* 140, 821–841
- Milla, R. *et al.* (2013) Shifts in stomatal traits following the domestication of plant species. *J. Exp. Bot.* 64, 3137–3146

51. Milla, R. *et al.* (2015) Plant domestication through an ecological lens. *Trends Ecol. Evol.* 30, 463–469
52. Jensen, J.D. (2014) On the unfounded enthusiasm for soft selective sweeps. *Nat. Commun.* 5, 5281
53. Innan, H. and Kim, Y. (2004) Pattern of polymorphism after strong artificial selection. *Proc. Natl. Acad. Sci. U. S. A.* 101, 10667–10672
54. Allaby, R.G. *et al.* (2015) Surprisingly low limits of selection in plant domestication. *Evol. Bioinforma.* 11, 41–51
55. Maynard-Smith, J. (1968) 'Haldane's dilemma' and the rate of evolution. *Nature* 219, 1114–1116
56. Felsenstein, J. (1971) On the biological significance of the cost of gene substitution. *Am. Nat.* 105, 1–11
57. Barton, N. and Partridge, L. (2000) Limits to natural selection. *Bioessays* 22, 1075–1084
58. Chevillon, L.M. and Hospital, F. (2008) Selective sweep at a quantitative trait locus in the presence of background genetic variation. *Genetics* 180, 1645–1660
59. De Vladar, H.P. and Barton, N. (2014) Stability and response of polygenic traits to stabilizing selection and mutation. *Genetics* 197, 749–767
60. Jain, K. and Stephan, W. (2017) Rapid adaptation of a polygenic trait after a sudden environmental shift. *Genetics* 206, 389–406
61. Shennan, S. *et al.* (2013) Regional population collapse followed initial agricultural booms in mid-Holocene Europe. *Nat. Commun.* 4, 2486
62. Stevens, C.J. and Fuller, D.Q. (2012) Did Neolithic farming fail? The case for a Bronze Age agricultural revolution in the British Isles. *Antiquity* 86, 707–722
63. Stevens, C. and Fuller, D. (2015) Alternative strategies to agriculture: the evidence for climatic shocks and cereal declines during the British Neolithic and Bronze Age (a reply to Bishop). *World Archaeol.* 47, 856–875
64. Timpson, A. *et al.* (2014) Reconstructing regional population fluctuations in the European Neolithic using radiocarbon dates: a new case-study using an improved method. *J. Archaeol. Sci.* 52, 549–557
65. Barton, N.H. (1986) The maintenance of polygenic variation through a balance between mutation and stabilizing selection. *Genet. Res. Camb.* 47, 209–216
66. Thornton, K. (2019) Polygenic adaptation to an environmental shift: temporal dynamics of variation under Gaussian stabilizing selection and additive effects on a single trait. *Genetics* 213, 1513–1530
67. Stetter, M.G. *et al.* (2018) Genetic architecture and selective sweeps after polygenic adaptation to distant trait optima. *PLoS Genet.* 14, e1007794
68. Allaby, R.G. *et al.* (2020) A novel cost framework reveals evidence for competitive selection in the evolution of complex traits during plant domestication. *BioRxiv* Published online October 31, 2020. <https://doi.org/10.1101/2020.10.30.362236>
69. Fuller, D.Q. and Stevens, C.J. (2017) Open for competition: domesticates, parasitic domesticoids and the agricultural niche. *Archaeol. Int.* 20, 110–121
70. Fuller, D.Q. and Stevens, C.J. (2019) The making of the botanical battleground: domestication and the origins of the World's weed floras. In *Far from the Hearth: Essays in Honour of Martin K. Jones* (Lightfoot, E. *et al.*, eds), pp. 9–21, McDonald Institute of Archaeology
71. Preece, C. *et al.* (2021) Fertile Crescent crop progenitors gained a competitive advantage from large seedlings. *Ecol. Evol.* 11, 3300–3312
72. Preece, C. *et al.* (2018) Cereal progenitors differ in stand harvest characteristics from related wild grasses. *J. Ecol.* 106, 1286–1297
73. Moyers, B.T. *et al.* (2018) Genetic costs of domestication and improvement. *J. Hered.* 109, 103–116
74. Mascher, M. *et al.* (2016) Genomic analysis of 6,000-year-old cultivated grain illuminates the domestication history of barley. *Nat. Genet.* 48, 1089–1093
75. Kistler, L. *et al.* (2018) Multiproxy evidence highlights a complex evolutionary legacy of maize in South America. *Science* 362, 1309–1313
76. da Fonseca, R.R. *et al.* (2015) The origin and evolution of maize in the Southwestern United States. *Nat. Plants* 1, 14003
77. Vallebuena-Estrada, M. *et al.* (2016) The earliest maize from San Marcos Tehuacán is a partial domesticate with genomic evidence of inbreeding. *Proc. Natl. Acad. Sci. U. S. A.* 113, 14151–14156
78. Swarts, K. *et al.* (2017) Genomic estimation of complex traits reveals ancient maize adaptation to temperate North America. *Science* 357, 512–515
79. Ramos-Madriral, J. *et al.* (2016) Genome sequence of a 5,310-year-old maize cob provides insights into the early stages of maize domestication. *Curr. Biol.* 26, 3195–3201
80. Scott, M.F. *et al.* (2019) A 3300 year old Egyptian emmer wheat genome reveals dispersal and domestication history. *Nat. Plants* 5, 1120–1128
81. Smith, O. *et al.* (2019) A domestication history of dynamic adaptation and genomic deterioration in *Sorghum*. *Nat. Plants* 5, 369–379
82. Emilliano, T. *et al.* (2019) Ancient genomes reveal early Andean farmers selected common beans while preserving diversity. *Nat. Plants* 7, 123–128
83. Kilian, B. *et al.* (2007) Molecular diversity at 18 loci in 321 wild and 92 domesticate lines reveal no reduction of nucleotide diversity during *Triticum monococcum* (einkorn) domestication: implications for the origin of agriculture. *Mol. Biol. Evol.* 24, 2657–2668
84. Russell, J. *et al.* (2016) Exome sequencing of geographically diverse barley landraces and wild relatives gives insights into environmental adaptation. *Nat. Genet.* 48, 1024–1030
85. Li, H. and Durbin, R. (2011) Inference of human population history from individual whole-genome sequences. *Nature* 475, 493–496
86. Schiffels, S. and Durbin, R. (2014) Inferring human population size and separation history from multiple genome sequences. *Nat. Genet.* 46, 919–925
87. Meyer, R.S. *et al.* (2016) Domestication history and geographical adaptation inferred from a SNP map of African rice. *Nat. Genet.* 48, 1083–1088
88. Wang, L. *et al.* (2017) The interplay of demography and selection during maize domestication and expansion. *Genome Biol.* 18, 215
89. Mazet, O. *et al.* (2016) On the importance of being structured: instantaneous coalescence rates and human evolution – lessons for ancestral population size inference. *Heredity* 116, 362–371
90. Allaby, R.G. *et al.* (2018) A re-evaluation of the domestication bottleneck from archaeogenomic evidence. *Evol. Appl.* 12, 29–37
91. Glemin, S. and Bataillon, T. (2009) A comparative view of the evolution of grasses under domestication. *New Phytol.* 183, 273–290
92. Hufford, M.B. *et al.* (2019) Crop biodiversity: an unfinished magnum opus of nature. *Annu. Rev. Plant Biol.* 70, 727–751
93. Brown, T.A. (2018) The role of humans in a protracted transition from hunter-gatherer to plant domestication in the Fertile Crescent. *Front. Plant Sci.* 9, 1287
94. Frahm, E. and Hauck, T.C. (2017) Origin of an obsidian scraper at Yabroud Rockshelter II (Syria): implications for Near Eastern social networks in the early Upper Palaeolithic. *J. Archaeol. Sci. Rep.* 13, 415–427
95. Poets, A.M. *et al.* (2015) Barley landraces are characterized by geographically heterogeneous genomic origins. *Genome Biol.* 16, 173
96. Cíván, P. *et al.* (2013) Reticulated origin of domesticated emmer wheat supports a dynamic model for the emergence of agriculture in the Fertile Crescent. *PLoS One* 8, e81955
97. Schmutz, J. *et al.* (2014) A reference genome for common bean and genome-wide analysis of dual domestications. *Nat. Genet.* 7, 707–713
98. Fritz, G.J. *et al.* (2017) Cultigen chenopods in the Americas: a hemispherical perspective. In *Social Perspectives from Environmental Archaeology: Food, Place, and People* (Sayre, M.P. and Bruno, M.C., eds), pp. 55–75, Springer
99. Kistler, L. *et al.* (2015) Gourds and squashes (*Cucurbita* spp.) adapted to megafaunal extinction and ecological anachronism through domestication. *Proc. Natl. Acad. Sci. U. S. A.* 112, 15107–15112

100. Rodríguez, M. *et al.* (2016) Landscape genetics, adaptive diversity and population structure in *Phaseolus vulgaris*. *New Phytol.* 209, 1781–1794
101. Kraft, K.H. *et al.* (2014) Multiple lines of evidence for the origin of domesticated chili pepper, *Capsicum annuum*, in Mexico. *Proc. Natl. Acad. Sci. U. S. A.* 111, 6165–6170
102. Riehl, S. *et al.* (2013) Emergence of agriculture in the foothills of the Zagros Mountains of Iran. *Science* 341, 65–67
103. Huang, X. and Han, B. (2015) Rice domestication occurred through single origin and multiple introgressions. *Nat. Plants* 2, 15207
104. Calfee, E. *et al.* (2021) Selective sorting of ancestral introgression in maize and teosinte along an elevational cline. *PLoS Genet.* 17, e1009810
105. Gutaker, R.M. *et al.* (2019) Flax latitudinal adaptation at LuTFL1 altered architecture and promoted fibre production. *Sci. Rep.* 9, 976
106. Bogaard, A. *et al.* (2018) Arable weeds as a case study in plant–human relationships beyond domestication. In *Hybrid Communities. Biosocial Approaches to Domestication and Other Trans-Species Relationships* (Stepanoff, C. and Vigne, J.-D., eds), pp. 97–112, Routledge