Trends in Plant Science

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Feature Review

Near Eastern Plant Domestication: A History of Thought

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The Agricultural Revolution and plant domestication in the Near East (among its components) have fascinated generations of scholars. Here, we narrate the history of ideas underlying plant domestication research since the late 19th century. Biological and cultural perspectives are presented through two prevailing models: one views plant domestication as a protracted, unconscious evolutionary mutualistic (noncentric) process. The second advocates a punctuated, knowledge-based human initiative (centric). We scrutinize the research landscape while assessing the underlying evolutionary and cultural mechanisms. A parsimony measure indicates that the punctuated-centric view better accords with archaeological records, and the geobotany and biology of the species, and requires fewer assumptions. The protracted alternative requires many assumptions, does not account for legume biology, fails to distinguish domestication from postdomestication changes, and, therefore, is less parsimonious.

Trends

Ever since Darwin, plant domestication has been conceptualized as an evolutionary continuum in various frameworks.

Genome-wide sequence polymorphism data are being used in plant domestication studies to: analyze domestication selection signatures; estimate the number of plant domestication and crop evolution selective sweeps; assess the number of domestication events and putative locations; and evaluate the relative role of reproductive isolation from wild progenitors versus introgressive hybridization with wild relatives during crop evolution.

In attempts to corroborate theoretical scenarios, archaeologists tend to incorporate ethnographic data in their plant domestication models.

The current incorporation of biological and cultural niche-construction theoretical considerations in plant domestication models is being used mostly to redress previous coevolutionary domestication models that rely on unconscious prey–predator relations, thereby minimizing the role of human consciousness and agency.

The Expulsion from Eden

Here, we survey the history of thought and ideas behind plant domestication research in the Near East. We treat the Near East only, despite the fact that plant domestication and the beginning of agriculture are worldwide phenomena (e.g., [1,2]), and assume that understanding the dynamics in one **primary domestication center** (see Glossary) may reflect on other plant domestication centers.

The domestication of plants (and animals) as part of the overarching Neolithic or Agricultural Revolution brought humanity across a socioeconomic Rubicon leading to the modern human condition. The Biblical story of the expulsion of Adam and Eve from their (hunter-gatherer) Garden of Eden to the laborious farming life ' . . . cursed is the ground for your sake; in sorrow shall you eat of it all the days of your life. Thorns also and thistles shall it bring forth to you; and you shall eat the herb of the field. In the sweat of your face shall you eat bread, till you return to the ground' (Genesis 3: 17–19) echoes a starting point in history, in retrospect, a point of no return. Socially and culturally, this revolution involved all aspects of human existence, ending millions of years of the hunting-gathering way of life, and beginning an era of food production. This change generally reflected a shift from what can be stereotypically viewed as egalitarian, small, mobile, socially flexible bands of humans to large, sedentary, more rigid social entities and, later, ranked and stratified urban state societies; from low demographic to intensive demographic growth; from a local, community-centered primordial cosmology of sharing to a competitive household-based society; and most importantly, from a positive world view based on trust to one based on domination, that is, from an economy based on naturally available resources to one based on manipulative expansion (e.g., [3,4]).

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Plant domestication research involves several fundamental questions: When [the time frame of Near Eastern plant domestication (NEPD)]? Where (was NEPD a geographically diffuse or centered phenomenon? If it was centered, where did it occur?) How [by what biological and cultural mechanisms did NEPD unfold? Do crop plants have mono- or polyphyletic origins? Was plant domestication a circumstantial (unconscious) development or was it a knowledge-based move? What was the role of predomestication cultivation (resource management)]? And the elusive Why question, usually relating to the wider scope of the Agricultural Revolution. Beyond offering a critical review of NEPD scholarly traditions, ideas, and history of research, we also highlight the interrelatedness of these fundamental questions and evaluate their role in plant domestication studies.

Two worldviews and their respective NEPD models have been debated in recent years. One holds that plant domestication is a form of evolutionary mutualism that emerged from deep-time human liaisons with plants [5–9], unfolded slowly [10–14], occurred autonomously in subcenters across the Near East (e.g., [15,16]), was mostly unconscious [11,13,17], involved many cases of lost lineages [18] or failures altogether [16,19,20], and often involved one crop at a time [21]. The opposing model views plant domestication as a punctuated, knowledge-based human initiative [22–25] that was rapid [26], geographically localized [27,28], fully conscious [29,30], mostly monophyletic [e.g., 31–34]), and gave rise to a nutritionally–agronomically balanced crop package. The various aspects of the two models are intricately interrelated to the extent that deciding on one issue, for example, geographically diffused domestication, will inevitably tip the balance across other debated aspects.

We chose the ‘How’ question as the axis for this review since it best exposes implicit and explicit ideas and frameworks of thought on NEPD. The evolutionary ‘How’ is relevant to modern plant science since the crops domesticated in antiquity remain central to the global economy, and crop improvement has been, and will always be, crucial to the future of humanity as we know it. The ingenuity of our ancestors in species selection for domestication is admirable, and no major additions have been made by modern science to the crop repertoire. To elucidate the complex landscapes of thought involved in plant domestication research, we outline two narratives (biological and sociocultural) and then assess the parsimony of the two, above-mentioned, models.

The Biological Narrative

Darwin [35,36] provided one of the earliest accounts of animal and plant domestication. As evident from the title of his book *Variation of Animals and Plants under Domestication*, Darwin [36] dealt with evolutionary processes that create and sustain phenotypic variation under domestication. These are in fact crop evolutionary processes [29] that do not represent pristine domestication episodes [37]. Referring to the adoption of plants from the wild, Darwin suggested that ‘Savages’ ([36], p. 326) were acquainted with nutritious plants in their homelands and harvested them (a hunting-gathering era); gradually, humans began cultivating some of these plants near their dwellings and ‘ . . . as the soil near the hovels of the natives would often be in some degree manured, improved varieties would sooner or later arise.’ ([36], p. 327). While Darwin did not suggest that cereals with domesticated phenotypes existed in nature, he did mention the possibility of adopting naturally occurring variants, namely ‘ . . . unusually good variety of a native plant might attract the attention of some wise old savage; and he would transplant it, or sow its seeds’ ([36], p. 327).

Darwin [36] was also aware of the uneven geobotanical pattern of crop plants, an issue addressed during the late 19th century by the Swiss botanist de Candolle [38], who pioneered a multidisciplinary methodology for inferring the geographic origins of crops and noted their ‘unequal’ geographic distribution ([38], p. 449). Following the rediscovery of Mendel’s laws, and

Glossary

Archaeological recovery techniques: refers to field methods used to recover finds from archaeological sites. It relates to the spatial and horizontal resolution of the excavation (the size and depth of excavated units) and to the resolution of the sieving (i.e., size of mesh used). For archeobotanical remains, a series of field techniques and devices (washing, floating etc.) is used that may be critical for the rate of recovery.

Early Epipaleolithic: the Epipaleolithic period in the Levant precedes the Neolithic period and covers a range of time starting some 23 000 ago and ending ca. 12 000 ago or later. It includes a series of local cultural entities (e.g., Mazraqan, Kebaran, Hamran, Mushabian, Ramonian, and more), of which the Natufian culture that started some 15 000 ago is the latest. Early Epipaleolithic is referred to here mainly because of the rich and well-preserved archeobotanical assemblage recovered at the site of Ohalo II by the Lake of Tiberias.

Human agency: in the context of archaeological and anthropological thought, this emphasizes the role of the human individual as an active actor within their cultural context (community or society) and their capability to make decisions and choices based on their ideology and/or beliefs and bring about change in accordance with their intentions (see also Box 1, main text). This is a reaction to views that see the individual and community as well as culture as means of adapting to the environment.

Husbandry operations: in terms of crop plants, this denotes the entire spectrum of activities exercised by farmers to facilitate the healthy growth of their crop plants, and their timely development to ensure their yield. These operations include, but are not limited to, selective harvest of special seed stocks for sowing, threshing, cleaning, and storing of the seed corn, working the soil (tillage, plowing, harrowing, etc.), timely sowing, removal of weeds, manuring, protection from pests and diseases, and so on.

Material culture dynamics: the changes in materials, technologies, and typology of material finds in archaeological sites over time. This being aware of de Candolle's work, the Russian geneticist Vavilov aspired to modernize agriculture in his country. Recognizing that an array of allelic variation is an imperative for systematic breeding, Vavilov [39] conducted expeditions across five continents between 1916 and 1940 [40] and assembled a large collection of crop varieties. After documenting the geographical pattern of crop diversity, he proposed 'eight independent centers of origin of the world's most important cultivated plants' ([39], p. 20), defining these centers as having the maximal genetic diversity for their respective crop complexes.

Engelbrecht [41] was probably the first to address the evolutionary mechanism by which crop plants emerged and suggested that plant parts (e.g., seeds, bulbs, tubers, or fruits) collected as food stuffs were brought to human dwellings for processing and consumption. Such parts that were either discarded or lost later developed on sites or near refuse heaps (hence, the 'Dump-Heap' hypothesis). It was assumed that soil fertility was higher in such areas and, hence, prolific volunteer (i.e., camp followers or weedy) plants attracted human attention. This reasoning was endorsed by Darlington [42] and the geographer Sauer (e.g., [43]), who argued that 'attractive volunteers' that thrived in manmade disturbed habitats were adopted as crops, and by Anderson [44], based on ecological considerations. Hawkes [45,46] argued that manmade disturbed habitats created optimal conditions for the weedy ancestors of crop plants. Harlan and de Wet [47] discussed the possible role of weeds in plant domestication and crop evolution, but concluded that, although in some cases weeds were progenitors of crops [e.g., oats (*Avena sativa*) or rye (*Secale cereale*)], in many cases this assumption was erroneous. This long-lived tradition of thought forms the basis of all plant domestication circumstantial explanations to this very day, although see [48] concerning its inapplicability to NEPD.

Multidisciplinary research projects aimed at understanding agriculture origins in the Near East were a post-World War II development. Prominent expressions of this approach were the joint work of the botanist Helbaek and the anthropologist Braidwood (e.g., [49]), and later of Zohary and the archeobotanist Hopf [50]. Three major contributions emerged from the coalescence of geobotanical and archaeological data: (i) the recognition that NEPD occurred within the oak-pistachio woodland belt of the Fertile Crescent, within the native range of the wild ancestors (e.g., [49,51]); (ii) the crop assemblage notion [49], a package of species that provides balanced nutrition and fibers [50]. Recently, the yield compensation ability of the Near Eastern crop assemblage was highlighted by Abbo *et al.* [24]; and (iii) an agroecological scenario for the emergence of domesticated plants [49], namely that **husbandry operations** provided the required selection pressures for the emergence of morphologically domesticated plants. This evolved into the concept of 'automatic selection' expressing the view that the emergence of morphologically domesticated genotypes was an inevitable, unconscious (thereby unintended) outcome of human activities in the nascent cultivated fields [52–54]. A school of thought that considers predomestication cultivation as a necessary stage (or a precondition) for plant domestication emerged in parallel (e.g., [17,54]; see Supplement A in the supplemental information online). To us, the element of unconsciousness is incompatible with the notion of husbandry operations that, by definition, need to be fully intentional and require high awareness of the outcome [30,55].

Comparative evolutionary analyses of cereals [52] and studies incorporating cereals, legumes, and vegetables have shown convergent evolutionary trends among domesticated plants compared with their wild progenitors, including: increase in size of the economically important organ(s), loss of seed dispersal mechanisms, change in growth habit, and reduced seed dormancy [56]. Accordingly, Hammer [57] coined the 'Domestication Syndrome' concept, a term denoting the multitude of morphophysiological differences between crops and their wild progenitors, but without differentiating between domestication traits and phenotypes that evolved under domestication. Addressing the adaptations of crop plants to cultivation (i.e.,

may include any material manifestation of human behavior, such as stone tools, pottery vessels, architectural features, or symbolic imagery items.

Parsimony: in the context of hypotheses testing or evaluation of several possible explanations, the adoption of the simplest alternative (that requires the fewest assumptions), in the spirit of Ockham's razor.

Primary domestication center: a world region where local plants (and animals) were independently domesticated, with no external cultural influence. Several such centers are known, including Meso-America or China. The Near East is an important such center and among the best studied.

Quantitative trait locus (QTL): a chromosomal region carrying (or linked to) a DNA sequence variant that modulates the phenotype of a metric trait. Many agronomically important traits are attributed to the cumulative and interaction effects of many quantitative loci (hence, polygenic traits). The identification of genomic regions affecting such traits is done via statistical methods that associate polymorphic genotypic data with the measurement of the value of the respective phenotype (e.g., plant height, grain protein content,or fruit yield) among a segregating hybrid population or array of genotypes.

Relative chronology: as opposed to absolute chronology providing calendaric dates based on radiometric methods (such as ^{14}C), this is an indirect dating method based on stratigraphy, for example, and/or associations of material culture elements (types of find). These can be seriated in a simple manner based on the presence–absence of artifact types (i.e., contextual seriation) or in a quantitative manner based on the frequency of the different artifact types (i.e., frequency seriation). Eventually, relative and absolute dating methods are used in tandem.

Sedentism: used in Near East archaeology to describe a settled way of life in which communities were living in a site for many rather than seasonally. Compared with the classical nomadic way of life of hunter-gatherers, this is an adoption of a less mobile way of life.

a husbandry regimen), Harlan *et al.* [52] claimed that an automatic selection regimen driven by perpetual cultivation would likely select for linked adaptive gene complexes. Indeed, **quantitative trait loci** (QTL) analyses confirmed the existence of gene clusters associated with domesticated phenotypes (e.g., [58–63]).

Accepting the cultivation-dependent automatic selection scenario, Hillman and Davies [64,65] sought to understand plant domestication dynamics via experimental cultivation of wild Near Eastern cereals. It was argued that following a sowing–harvesting–stocking–sowing regimen and with natural mutation rates, a nonbrittle spike (domesticated phenotype) mutation could establish among the original wild-type population within a few years, and the managed (cultivated) crop population could become fully domesticated within decades or up to two centuries even without conscious selection by the cultivators [64–66]. Accordingly, Hillman attempted to identify archeobotanical signatures of the presumed predomestication cultivation (see Supplement A in the supplemental information online and below).

While most researchers assume that the first fields cultivated by humans were sown to morphologically wild types (e.g., [12,17,36,52,64–68]), relying on the seed dormancy of wild lentil, Ladizinsky [22] introduced the unorthodox notion of 'Domestication before Cultivation', thereby rendering the predomestication cultivation concept altogether redundant. This controversial suggestion, that the identification of a naturally occurring free-germinating stock was imperative for successful lentil cultivation, sparked a debate (e.g., [53,69–71]), but only later did field experiments [26] validate and confirm the futility of the predomestication cultivation notion of Near Eastern legumes.

During the 1970s, a view emerged that plant domestication resulted from coevolutionary processes (a form of specialized mutualism between humans and their crops), equating plant domestication with other presumably similar natural phenomena, such as ant–fungus relationships (e.g., [8,9]). Consequently, the evolution of 'nonhuman agriculture' became a model for plant domestication and human agriculture was viewed as an individual case of this wider evolutionary phenomenon. Ant–fungus and other mutualistic relationships in nature most probably evolved gradually by step-wise accumulation of mutually adaptive mutations and selection (in partner organisms) over evolutionary timescales (e.g., [72]). Such processes advanced via numerous intermediate stages because it is difficult to see how macromutations, conferring suites of concerted mutually adaptive mutations, could occur simultaneously in two unrelated lineages. For his hypothesis, Rindos [8] relied on the supposed weedy tendencies of crops, the role of land disturbance in creating suitable niches for 'would-be' crops, the role of discarded plant organs in rich niches in giving rise to attractive plants, and the crowding of target plants around human dwellings, all prominent features of Engelbrecht's 1916 Dump-Heap hypothesis. The fact that the biology of Near Eastern grain crops does not accord with that scenario [47,48] notwithstanding, Rindos' idea became prominent during the 1990s and 2000s within the 'protracted domestication scenario' and its long predomestication cultivation stage. It is also intimately associated with the recently applied Niche Construction Theory (NCT) vis à vis agricultural origins in various world regions, the Near East included (e.g., [73–80]).

This view is based on the recognition that most organisms actively intervene in their environment, and modify their own evolution as well as that of their niche companions. Examples include nest building by birds, dam and pond creation by beavers, or changes in soil chemistry and texture caused by earthworms, all termed 'niche construction' phenomena [81], or likewise, resource management by humans (e.g., [77,82,83]) and Cultural Niche Construction [75]. Indeed, the application of NCT to plant domestication studies also relies heavily on human-caused ecological disturbances [76,79] associated with the Dump-Heap hypothesis.

The cereals paradigm: after Harlan *et al.* [52] and Zohary [53], a view of grain crop evolution that considers the breakdown of the seed dispersal mode as the most important phenotypic change underlying domestication, including the claim that domestication syndrome traits (e.g., reduced seed dormancy, nonshattering, or large grains) evolved as a result of an automatic selection regimen soon after humans adopted wild taxa and subjected them to perpetual cultivation cycles. This view does not account for the unique biological features of grain legumes [26,29,151].

The legumes paradigm: after Ladizinsky [22] and Abbo *et al.* [151], a view that considers free germination as the crucial domestication syndrome trait, and suggests that pod indehiscence evolved under (post) domestication. Consequently, neither automatic selection nor predomestication cultivation can account for Near Eastern grain legume domestication.

Three stages domestication model: a model presenting a continuum of ways of life starting with wild-food gathering (stage I), moving through minimal intervention in the wild flora through to predomestication cultivation (stage II), and, consequently, to fully fledged agriculture based on crop plants (i.e., having domesticated morphology, stage III).

Younger Dryas (YD): a global climatic event represented by a cool (decline in annual average temperature) and dry stadial in the European glacial sequence that started 12 900 years ago or even a little later, and ended ca. 11 700 years ago (or somewhat later) when the warmer Holocene started. The main effect attributed to the YD in the Near East, based on various scientific lines of evidence, is drought (viewed by some as a climatic crisis), which resulted in resource depletion. This has been linked in various cases to the beginning of agriculture in the region.

The advent of DNA-based markers facilitated the identification of the wild stocks closely related to extant domesticated germplasms and their ecogeographic origin. Heun *et al.* [31] flagged Mt Karaçadag, in the vicinity of important Neolithic sites with early dated domesticated cereals remains in southeastern Turkey, as the likely origin of domesticated einkorn. This approach enabled researchers to readdress whether the crop was mono- or polyphyletic in origin [84] as well as to answer the (Where) question of domestication within the range of the wild progenitors [33,85]. Following Heun *et al.* [31] and based on geobotanic, archeobotanic, and archaeological data, Lev-Yadun *et al.* [27] presented their core area hypothesis, claiming that NEPD occurred within a distinct cultural context, over a relatively short time span, in a well-defined area in southeastern Turkey and north Syria, and involved all (if not most) of the founder crop package species [27,28,86].

Throughout the early 2000s to the present day, there has been a growing tendency among biologists to see NEPD as a geographically diffused (e.g., [15]), polyphyletic [87] millennia-long process [11,88,89] that relied mostly on unconscious selection exerted by predomestication cultivation activities [11,17]. This is also echoed in archaeologists' and archeobotanists' views on the subject (e.g., [10,13,16,19,21,90–93], and see the 'Archaeology' section below), including the idea of 'false starts' or plant domestication failures ([16,18–20], but see [55]).

Genetic mapping (e.g., [59,61,63,94]) and gene cloning (e.g., [95,96]) have enabled researchers to dissect the genetic basis of many domestication syndrome traits (e.g., [97–99]). Genome-wide screening and resequencing of wide germplasm arrays highlighted differences between genomic domestication changes and traits that occurred post domestication (e.g., [100–102]). The distinction between domestication and postdomestication changes stemmed from a refinement of the domestication syndrome concept and enabled Abbo *et al.* [37] to provide genetic and agronomic guidelines for differentiating between the two trait categories.

The Archaeological–Archeobotanical Narrative

The recovery of botanical finds from relevant archaeological sites and their analyses are basic aspects of plant domestication research by archaeologists and archeobotanists.

Archaeology

Archaeologists studying agricultural origins initially made statements about the Agricultural Revolution based on material culture data sets as well as on faunal and floral remains retrieved from archaeological sites. They eventually focused on addressing the 'When' and 'Where' questions so fundamental for archaeological statements (Boxes 1 and 2) and, concomitantly, on answering the 'Why' question, looking for (prime) movers of the Agricultural Revolution. At the same time, most archaeologists distanced themselves from discussing practical 'How' details of major components of this revolution (e.g., plant domestication), investing only limited efforts in testing statements about the biological, agronomic, and dietary features of the plants.

Statements relating to how were plants domesticated may benefit from advances in **archaeological recovery techniques** and improved absolute dating methods. One would expect a similar influence of developments in archaeological thought (Box 1).

Initial research on agricultural origins and plant domestication by archaeologists of the Culture History School began during the late 19th century and focused on locating areas of suitable potential (i.e., centers), suggesting prime movers for plant domestication, and describing its diffusion to other regions [38,103,104]. This historical 'Core Area' modeling continued into the 1960s and 1970s, with work by Braidwood [105,106], and later Garrard [107], Lev-Yadun *et al.* [27], and others (e.g., [108–111]).

Box 1. On Archaeological Thought

Archaeology was established as a systematic discipline during the late 19th century and developed into what was later called the 'Culture History' school. This way of thinking was based on inductive scientific dynamics and characterized by a normative view of culture (i.e., norms of behavior are transmitted from generation to generation, father to son, and can be recognized by their material manifestations). Thus, it focused on particularistic (local) historical reconstruction and usually explained change as a reaction to external (diffusing) developments.

Well established by the mid-20th century, this 'old' way of thinking was severely attacked by a 'new' archaeology lead by Neo-Darwinian evolutionary thinking, and based on extreme (Poperian) hypothetico-deductive scientific logic. Archaeology was now viewed as anthropology (synchronic) and not as history (diachronic), and culture was now viewed as an 'extrasomatic' means of adaptation. Society was viewed as a functioning (organic) system and cultural change was viewed as an eventual attempt to sustain systems equilibrium and was explained by adaptations to the environment (rather than by diffusion) and by internal social dynamics and reorganization. One of the most successful aspects of 'New (also called Processual) Archaeology' was its Middle Range theory, involved in basic archaeological questions, such as the formation of, and postdepositional processes in, archaeological sites. These aspects were mediated by a plethora of experimental, ethnographic, and ethnoarchaeological studies, some of which also became part and parcel of plant domestication studies (e.g., [64–66,158,159,176,177]).

Negative reactions to 'New Archaeology' began during the 1970s and accelerated during the 1980s and 1990s. ('Post-Processual') 'Contextual Archaeology', which was presented as an alternative, emphasized the ideological landscape and its central role in human behavior and decision-making and returned to particularistic, historical ways of thinking. Human agency has become central in explaining culture change as well as the diffusion or external influence. A radical wing of this school of thought advocates an interpretive view that relates to material culture as a text and emphasizes both the active agents of past societies as well as the agendas of present-day researchers.

As the New/Processual Archaeology of the 1960s gained in popularity, environmental and demographic aspects of agricultural origins gained in importance, while the historical aspect dwindled. Within this framework, social institutions and behavior were viewed through adaptive neo-Darwinian lenses (e.g., [73–75,78,112]). In the spirit of New Archaeology, Binford [113] suggested an overarching (global) explanation for agricultural origins. He envisaged agricultural origins (both animal and plant domestication) as an end result of post-Pleistocene (new) adaptations, that is, a multi-staged reaction to environmental change. He claimed that the changing post-Pleistocene environment, **sedentism** (decreased mobility), and demographic growth, coupled with social dynamics, eventually created marginal zone populations that, due to resource shortages, opted to intensify food availability and became engaged in plant domestication. Another interpretation in the spirit of New Archaeology by Hayden [114,115] provided a socioeconomic explanation: the 'competitive feasting' model focusing on the role of social dynamics and emphasizing competition as a major mover that generated intensified production through domestication [114–116].

The 'Where, When and Why' of the Agricultural Revolution (including animal and plant domestication) were also assessed by scholars residing between historical particularistic (Culture History) 'old' approaches and New Archaeology. For example, Bar-Yosef consistently argued that the Agricultural Revolution and plant domestication originated in a core area within the Near East and then diffused outwards. The movers emphasized were climate change (mainly the **Younger Dryas**; see Supplement B in the supplemental information online) and resource depletion triggering a cultural and/or behavioral change best expressed by embarking on predomestication cultivation [108,117].

Explanations for the Agricultural Revolution (including plant domestication) in the spirit of Post-Processual/Contextual archaeology gained popularity from the 1980s through to the 1990s, represented by figures such as Cauvin and Hodder. These authors emphasized aspects of ideology (e.g., as reflected in imagery symbolic items), social dynamics, and the emerging role of the supernatural (towards established religions). In a pioneering study based on long field experience in Neolithic sites in the Levant and a crystalized view on human cognition, Cauvin

Box 2. Archaeological Scale, Chronology, Resolution, and Context in Near Eastern Plant Domestication Studies

Space/Scale

J. Cauvin's early Neolithic 'koine' or 'interaction sphere' [178] viewed the Levant as a whole, with evidence for contacts, either economic and/or wider cultural contacts expressed by the exchange of materials, technologies, artifacts, and ideas. The various levels of contact intensity led Cauvin to discuss aspects of acculturation and migrations within the Levantine koine, from southeastern Turkey and Iran in the north to the Sinai desert in the south and from the Mediterranean in the west to the desert stripe in the east, throughout the Pre-pottery Neolithic period (11 750–8500 calendar years BP). This scale calls for caution from archeobotanists (and geneticists) who, on the one hand, interpret archeobotanical data in terms of meta population gene flow [11] and, on the other hand, suggest autonomous plant domestication subcenters in the Levant while ignoring that both biogeographic and cultural isolation are needed for such a claim [21,19], which is an inherent contradiction of this approach (Table 1, main text).

Time Chronology and Resolution

Beyond **relative chronology** based on stratigraphy and **material culture dynamics** of change, and beyond absolute chronology based on calibrated ^{14}C dates, there is a question of resolution in NEPD archaeological research. Being 'splitters' in spirit, as opposed to 'lumpers', we see major advantages in an as high a resolution as possible for the successful reconstruction of any past story, plant domestication included. Praising blurred chronological borders (e.g., [163,179]) appears to us to be both an obstacle to using archaeological data sets and redundant, given the efforts invested to improve resolution. Surprisingly, archaeologists also lower the resolution and use large blocks of time and culture (e.g., [14,164,180–182]), which is instinctively counterproductive.

Archaeological Context Is Not Contextual Archaeology

While 'Contextual Archaeology' is a well-known school of thought (Box 1), it should not be confused with 'archaeological context', which refers to places on-site in which various activities occur, for example a building or rooms within it, a courtyard, an installation or a burial. Identifying archaeological contexts is important for reconstructing and interpreting relevant aspects of plant domestication, yet this does not necessarily indicate one's archaeological way of thought. For example, Asouti and Fuller's interpretation [14] of a context on-site as a domesticating context or a public facility, and their use of a series of such contexts to reconstruct site scale and organization, is not contextual archaeology if not done in the spirit of this school, which is clearly the case here (see [183]). With no full application of a robust theoretical framework to plant domestication studies, neither cultural nor social, contextual thinking and described contexts eventually become mixed. Cooperation between archaeologists and archeobotanists directed towards reconstructions integrating sociocultural (ideological) aspects and botanical finds have recently gained momentum (e.g., [68,90,164]), yet some of the archeobotanists engaged do not view human agency as being central to plant domestication and, thus, their sociocultural, ideological, or contextual interpretations are likely to be futile.

[118,119] discussed the involvement of humans in plant domestication within his 'Revolution of Symbols' and the 'Birth of the Gods'. He argued that the Agricultural Revolution was influenced by changes in thinking, perception, and ideology that brought about socioeconomic reorganization (of which plant domestication was one component), eventually changing all aspects of human life. Whether changes in the symbolic array preceded economic change or vice versa or whether they were simultaneous, is still debated. Cauvin's view, encapsulated in 'symbols before economy' [118,119], stands in opposition to economic–environmental explanations (e.g., [108,113,120]) and was not welcomed by other researchers (e.g., [121–123], p. 231). Both earlier and recent statements based on Post-Processual/Contextual/Interpretive archaeology (e.g., [124–126]) remain remote from the biological and agronomic practicalities of how plants (and animals) were domesticated and are problematic in themselves when misapplied (see the final section of Box 2).

The Archeobotanical Sphere

Since the mid-20th century, archeobotanists have concentrated on producing detailed reports on plant remains from relevant sites. Their 'When' and 'Where' are derivatives of the fact that their samples are extracted from excavated archaeological sites, in many cases ^{14}C dated. They also invested efforts via experimental programs and ethnoarcheobotany to answer how plants were domesticated. However, their statements on the 'Why' question are casual and usually remote from sociocultural aspects of the relevant communities (e.g., [49,50,127–129]).

The concept of cultivation (including predomestication cultivation) encompasses the fundamental 'How' question of plant domestication. The view of cultivation as a route to domestication was shaped by Helbaek [49,130]. What was called 'proto-agricultural' practices or 'incipient agriculture' gradually assumed the status of an imperative step on the way to domestication and agriculture (e.g., [12,67,68,90,128,131,132], but see [133] on cultivation and predomestication cultivation as intellectual constructs; Supplement A in the supplemental information online). It became widely accepted by archeobotanists that plants underwent selection processes (and eventual domestication) in human-made arenas, with either local or displaced plant stocks. Significant efforts were recently invested in reconstructing this man-made arena as a field plot in which plants were grown, for example, by presenting archaeobotanical remains of plants species identified as weeds as a testimony for cultivation (e.g., [19,20,68,134,135]). Cultural remains (storage facilities, the presence of commensal animals, harvesting and processing tools, chaff in construction materials, etc.) were also recruited to support cultivation.

Recently, predomestication cultivation was viewed as a (1–4) millennia-long stage (e.g., [6,10,11,129]). Based on the evolutionary continuum of Harris [133,136], this trend culminated in advocating predomestication cultivation over 12 millennia before NEPD, based on finds from the 23 000-year-old **Early Epipaleolithic** site of Ohalo II [12,20]. This is contrary to experiments and claims that plant domestication in a cultivation context could have been rapid (two decades to two centuries) under the appropriate husbandry regimen [64–66,137]. A somewhat 'median' suggestion for the pace of cereal domestication was advocated by Kislev [128] and recently, for various reasons, Weiss and Zohary [129] and Willcox [68,90] suggested cultivation over one millennium only.

Associated with cultivation are the concepts of experimentation ('auditioning of candidate species'), failed cultivation attempts, lost crops, and lost lineages (e.g., [16,18,19,20,76]), although no adequate evidence of these was presented [55].

Since Halbaek's idea of automatic selection and its adoption [67,52], it is widely accepted that one need not assume human intention for plant domestication (selection) processes to mature (e.g., [6,19,64,65,129,137]), surprisingly, an issue that was almost never disputed. Moreover, in recent years, the capabilities of Neolithic humans to carry out knowledge-based plant domestication were questioned [11,91] and archaeologists, who generally 'represent' culture and **human agency**, made few protests against this unconsciousness claim.

Although opinions vary, archeobotanical research since the 1960s followed a geographically diffused plant domestication model. For example, van Zeist [137] argued for geographically diffused domestications in the Near East, as did others [16,19,21,129]. Note that, except for barley, genetic studies mostly suggest monophyletic origins for Near Eastern crops [31,33,34,138–142]. Interestingly, the genetic data were rejected by archeobotanists and geneticists alike (e.g., [6,18]) and also by some archaeologists (e.g., [143–145]) who preferred polyphyletic reconstructions based on simulations ([6,88,89], but see [146,147]). However, it should be noted that a polyphyletic origin of crops might be a valid reconstruction under a core area framework when both genetic and cultural independence are taken into consideration ([28], p. 321).

Although the crop complex concept [49] is used also for other plant domestication centers [148], the question of the coalescence of crop complexes is missing from the archaeological and archeobotanical literature and is taken for granted despite being basic for understanding the domesticators' choices. It is fundamental for appreciating the depth of the knowledge involved in assembling biologically viable, agronomically sustainable, and dietary-compensating packages [24]. The case of chickpea is an outstanding example of a special investment made to maintain the balanced package, albeit with major agronomic difficulties [23,149].

Conservative versus Innovative Plant Domestication Research

Many plant domestication concepts were developed some time ago {e.g., Darwin's **three stages domestication model** ([36] pp. 326–327), also proposed by Merrill [150]} and, while redressed by each scholarly generation (e.g., [133]), and jargonized anew, innovation in fundamental perceptions was rare [6,12]. A prominent example is the thread running for over a century through ecological reconstructions based on biological and/or cultural circumstantial approaches. Conceptualizing plant domestication as an evolutionary continuum arising from human ecological disturbances, or from indigenous resource management [8,9,36,41,46,93,133] has much in common with Smiths' [83] low-level food production continuum, or with Hillman's predomestication cultivation concept, and heavily relies on the 'good old' Dump-Heap hypothesis (Box 3). Phrased differently, within the metaphoric 'middle ground' continuum of low-level food production strategies, humans constructed niches (e.g., created land disturbances and dump-heaps, burned vegetation, and broadcasted seeds of wild annuals, [82]), thereby providing the arena for the phenotypic changes within the manipulated ('candidate') plant populations without any need for conscious selection [11,52,54].

A different, isolated, view was voiced by Ladizinsky following his work on legume domestication and his unorthodox 'domestication before cultivation' scenario (Box 4). Working with wild and domesticated lentils, Ladizinsky [22,69,70] noted that: (i) there is no profitable option for

Box 3. From Circumstantial to Mutualistic Explanations of Domestication

During the early 20th century, Engelbrecht, and followers (e.g., Sauer, Darlington, and Anderson) of his Dump-Heap hypothesis, were free of any archaeological or archeobotanical agenda. Yet, their circumstantial model is intimately related to the existence of a human cultural niche as the 'stage' on which the 'play' unfolds. Namely, domestication was 'initiated' by the plants that presented themselves to humans in human-made or -affected contexts in a way that was hard to ignore (e.g., prolific plants or large fruiting organs), or in other words, until their potential was eventually acknowledged by a 'wise old savage' (Darwin's 19th-century wording). Humans are involved in two ways: first, they unintentionally create the circumstances that provide the suitable arena for plant domestication and, second, they notice what happened once plant phenotypes become conspicuous.

As the 'Culture History' of the early 20th century was giving way to a Neo-Darwinian 'New Archaeology', scholars such as Rindos resumed the investigation of the 'How' questions of plant domestication, based on biological logic. As so typical for 'New Archaeology' (Box 1), he chose to use a radical mutualistic model to explain plant domestication. Accepting Rindos' (Dump-Heap hypothesis-based) mutualistic model (seemingly following general evolutionary principles) immediately provokes the question 'who domesticated whom?', thereby lowering or denying the role of human agency. Interesting derivatives of this school of thought are, for example, studies entitled 'The evolution of agriculture in ants' [184], 'Do lichens domesticate photobions like farmers domesticate crops?' [185], 'Primitive agriculture in a social amoeba' [186], or 'Small molecules mediate bacterial farming by social amoeba' [187]. As evident from the citations used in such papers (e.g., [72,75,186,187]), the use of terms such as 'agriculture', 'farming', and 'domestication' was not at all metaphoric. In our view, there is an apparent scholarly mutualism between entomologists, botanists, zoologists, and anthropologists all using a similar reasoning in what can be viewed as a multidisciplinary feast. However, as we note in the main text, much of this (too) generalized overarching modeling of Agriculture Origins has become possible via a departure from the biology of the concerned species (e.g., [48,147,151]), dissociation from archeobotanical databases [77,83], or a 'flexible' use of data [134,172,188].

Rindos' mutualistic suggestions in the spirit of the Dump-Heap hypothesis [8,9] have also set the stage for reconstructions such as Smith's 'Low Level Food Production' [83]. These reconstructions later took the shape of ecosystem engineering [76] in the spirit of Niche Construction Theory and were eventually incorporated into a wide-arching model in the framework of a larger scale battle between macroevolutionary thinking and Neo Darwinian 'traditional' theory ([73,75,78], but see [189,190]). Yet, as far as plant domestication is concerned, this circumstantial attitude, based on a mutualistic biological plant–human relationship, remains distant from human cultural agency as such.

Box 4. Lentil Domestication before Cultivation

The distribution of wild lentils (*Lens* sp.) includes the Mediterranean basin, Asia Minor through to Central Asia and eastward to Tajikistan [191]. In nature, wild lentils are mostly confined to primary habitats with shallow soil pockets, where they are free from competition from species with a more aggressive growth habit (e.g., wild cereals). Across this range, wild lentil populations are patchy (disjunct), with each local spot hosting a sparse stand, often containing few individuals [191].

Wild lentils are characterized by low seed yield and strong seed dormancy resulting from the impermeability of their seed coat to water [22,70]. Under natural conditions, only approximately 10% of the seeds will germinate in the following autumn, although the germinating individuals do not represent genetic variation in this trait of seed dormancy because their seeds (their next generation) germinate at the same rate. Lentil seed dormancy and low seed yield (approximately ten seeds per plant) have a clear adaptive value in the wild habitats characterized by shallow stony soil. Experimental evidence showed that, by sowing 100 wild lentil seeds, only ten germinated, each of which produced on average ten seeds, the same amount that was planted. This is not an incentive to continue sowing any further ([22,70] and illustrations in [37,151]).

Domesticated lentil seeds are nondormant, a trait controlled by one dominant gene [22,70]. The mutation rate in this gene is unknown but even at a rate as high as 10^{-5}, a nondormant seed (mutant) is likely to appear in one out of 10^5 individuals following the sowing of 10^6 seeds. Selection in favor of such a mutant under cultivation would require hundreds of years of perpetual sowing without any yield gain. In wild stands, such a mutant is ill adapted for two reasons; (i) it will multiply annually by factor of ten until the poor habitat is no longer able to support the population; and (ii) the mutant genotypes will be quickly eliminated if a long dry period follows the first effective rain, a common feature of the semiarid habitats of lentils across the Mediterranean and eastwards to Central Asia.

Ladizinsky suggested that the dilemma as to how nondormant lentil seed variants evolved could be solved by assuming that affluent (high-density) nondormant wild lentil populations may have attracted the attention of hunter-gatherers who regularly visited those spots for seed collection (e.g., data on lentil seeds from the Kabara cave some 60 000–50 000 years BP [192]). Such repeated harvests have the capacity to prevent local population explosion [22,70]. When seeds from such populations were used for sowing, the yield was satisfactory and encouraged further sowing. Consequently, according to Ladizinsky's model, lentil domestication (i.e., the emergence of an ill-adapted mutant in wild populations) most probably preceded lentil cultivation.

predomestication cultivation without free-germinating genotypes; (ii) the yield of wild lentil is meager and, therefore, it is unlikely that lentil had a prominent role in the diet of hunter-gatherers; (iii) lentil domestication did not involve any significant advance in terms of grain yield; and (iv) wild lentils have no weedy tendencies and are sensitive to anthropogenic disturbances. In so doing, Ladizinsky slashed the Gordian knot between the following canonic pairs: cultivation of wild plants and morphological domestication; selection of plant candidates and productivity; deep-time human–food source liaison and domestication; and weediness of would-be crops and domestication. However, most members of the research community rejected Ladizinsky's postulations and adhered to the **cereals paradigm** (e.g., [53,65]).

At the inception of ideas on convergent crop evolution and the domestication syndrome, it was recognized that different crop groups are characterized by different suites of domestication syndrome traits (i.e., while many similar evolutionary trends were recognized among vegetables, among fruit trees, and among grain crops, each of these crop groups evolved along its own idiosyncratic trajectory [56,57]). However, following Ladizinsky's work [22], it became apparent that even within the superficially similar grain crops [56], there are significant differences. A comparative assessment of ecology, reproductive biology, and yield physiology shows prominent differences between domestication syndrome traits of cereals and legumes [151]. These biological differences must have necessitated a different approach by Neolithic domesticators and optimal use of their capabilities and naturalistic knowledge. Moreover, grain legume domestication must have involved a higher perceptual leap than cereals, being physically distinct from their wild counterparts [151]. The differences in developmental and yield physiology between legumes and cereals exposed the yield compensation ability and agronomic rationale underlying the Near Eastern crop package, elements missing altogether from various plant domestication models based on the auditioning of numerous candidates [16,20,76], let alone single species domestication (e.g., [21]), thereby reducing the **parsimony** of these models.

Additional ramification of the '**legume paradigm**' was the need (and ability) to refine the domestication syndrome concept to a degree that enabled one to distinguish between pristine selection events associated with plant domestication episodes and later crop evolution processes that occurred under domestication [29,37,55,100,101]. The plant domestication versus crop evolution distinction emerges as a powerful key for reconstructing the biological (including agronomic) and cultural (including human preferences) aspects that underlined the adoption of wild species for domestication. This distinction helps one to draw an evidence-based picture of domestication episodes sensu stricto by focusing on the crucial domestication traits [37]. No less important is the problem-solving power of the plant domestication–crop evolution distinction.

For example, claims for millennia-long wheat domestication processes [10,11] and counter-claims have both been published [147,152,153]. However, experimental processing of domesticated and wild emmer [63,154] confirmed that traits showing a clear domesticated–wild dimorphism (e.g., spike brittleness) are more appropriate to describe the pristine domestication episode, whereas traits showing a phenotypic continuum (e.g., grain size or spike threshability) between wild and domesticated gene pools mostly reflect postdomestication improvements [37]. Consequently, it appears that the protracted plant domestication model is mixing genuine plant domestication episodes with long-lasting crop evolutionary changes [29,37].

Likewise, we suggest that adopting the plant domestication–crop evolution distinction will help resolve the debate on the role of conscious versus unconscious selection in plant domestication, a key for granting parsimony to either of the two models evaluated herein. Zohary [54] suggested that domestication of grain crops and clonally propagated plants was mostly based on unconscious selection; however, McKey *et al.* [155,156] claimed that Zohary's approach [54] does not fit some tropical clonally propagated crops. In this context, we point out that such disagreements can be settled easily by using the plant domestication–crop evolution distinction [157]. In fact, Zohary [54] mostly addressed evolutionary processes 'under domestication', 'under cultivation', 'under traditional farming', or in other words, crop evolutionary processes [29,37], as did McKey *et al.* ([156], pp. 385, 391, 399). Hence, the fruit trees example as seen from a plant domestication–crop evolution perspective indicates both a conscious and rapid domestication [157] tipping the balance in favor of the knowledge-based model.

A Parsimony Measure

Similar to researchers in geology, paleontology (including paleoanthropology), and evolution, agricultural origins and plant domestication researchers are engaged in answering the 'What happened in the past and How' questions. The basic practice of these disciplines is the accumulation of observations forming multitude lines of evidence, converging into a coherent pattern vis à vis the issue discussed, assuming that this supports and strengthens the validity of the suggested reconstruction. Plant domestication research followed (implicitly or explicitly) this path from its very beginning [38,103] and, while interdisciplinary in nature and approached by a range of professionals (archaeologists, geneticists, agronomists, and botanists) and respective scientific procedures, it remains a historical science in many ways. Over the past two decades, with the advent of DNA markers and a series of studies (experimental work included) on legumes [26,158–160] and cereals [154], a somewhat deeper scrutiny of the prevailing ideas and models via detailed hypotheses testing emerged.

Recent cooperation of archaeologists and geneticists yielded the protracted (and geographically diffused) domestication model via the incorporation of population genetic models and archeobotanical databases. This necessitated assumptions concerning the flow of information and seed stocks among human populations and, likewise, the gene flow among wild and domesticated plant populations [7,11,16,87–89]. Our own experience based on the cooperation between archaeologists, botanists, and agronomists, and genetic studies of the relevant plant species suggests a core area–one-event domestication model that, in our view, is a better alternative and a more parsimonious reconstruction of NEPD (see below). The major components of this model include, but are not limited to: an experimental approach embracing the ecology of the Near Eastern wild progenitors and their potential as a resource for hunter-gatherers [22,48,55,158–160]; recognition of the fundamental differences between legumes and cereals biology [151]; distinction between plant domestication and crop evolution under domestication; nutritional aspects of the domesticated species [23]; agronomic considerations [24,26,161]; postharvest processing work load [154]; floral biology of the relevant taxa and population genetic principles [147]; archaeological evidence indicating major cultural dynamics of change in southeastern Turkey and northern Syria (the suggested core area) during the early Neolithic (Pre-Pottery Neolithic A, PPNA); the flow of innovations from this area to other parts of the Levant; and the fact that the first appearance of domesticated plants known to date is in this region during the EPPNB, some 10 500 calendar years before present (BP) [27,86]; using the best available archaeological (cultural) resolution without lumping together the PPNA and EPPNB periods and their respective cultural entities since they show a multitude of cultural differences that may be most significant for plant domestication; accurate use of the available archeobotanical data and its dating; rejecting claims for unconscious automatic processes; and emphasizing the major role of human knowledge-based action and social awareness [30,86,162].

In our view, ignoring the unique biology of grain legumes and the absence of agronomic considerations are two major features of the protracted domestication model and, therefore, detract significantly from its explanatory power. In addition, it is hard to accommodate a claim for cultural independence of multiple putative domestication centers (e.g., [16]) with a suggestion to view the entire cereal population across the Fertile Crescent as a metapopulation [11], both part and parcel of the protracted geographically diffused domestication model. Likewise, a claim for experimentation and auditioning of candidate species for domestication (e.g., [76]) is contradictory to the unconscious (automatic) dynamics. This is because by their very definition, experiments in specific wild species and their evaluation as potential crops would have necessitated premeditation, a careful selection of experimental species candidate, particular attention to results, and a process of inference. Thus, in our view, any model that incorporates such ideas is logically flawed.

It appears that, in recent years, and despite all the abovementioned developments, NEPD research shows an imbalance between hard and detailed archaeological, archeobotanical, genetic, and ecological databases, and intellectual constructs, including speculative ones (e.g., [13,18,88]). Consequently, current NEPD research is swamped by low-parsimony models (e.g., [11,13,19,129]) that fail to reach safe conclusions. Admittedly, the circumstantial (mutualistic when looked at through ecological and/or genetic eyes), protracted, autonomous (noncentered) NEPD model prevails in the current literature, while a reconstruction based on centered, rapid, knowledge-based selection of a package of plant species for domestication (based on the human capability to identify suitable genotypes among standing genetic variation) is a minority view.

Testing the parsimony of the two abovementioned plant domestication models based on the data they rely on and their accompanying assumptions (Table 1, Key Table) suggests that the

Key Table

Table 1. A Parsimony Measure of the Two Alternative Plant Domestication Models Expressed as a List of the Assumptions Underlying Each Model[a]

The protracted-autonomous model assumptions	Validity of the protracted-autonomous assumptions	The core area-one event model assumptions
Genetic considerations		
It is impossible (or nearly so) to domesticate plants in the presence of the wild progenitors because of introgression of wild-type alleles (e.g., [6]).	See [102,170] showing the opposite for maize in Mexico	Not needed
Preemptive D is not accounted for	See [1] pp. 179–180	Preemptive D is a valuable concept, biologically and culturally
PD was polyphyletic per species [88,89]. The simulations supporting this scenario rely on a protracted assumption embedded in the model	A polyphyletic signal is not seen without an embedded protracted component [33,147], as confirmed by Allaby *et al.* [87] (also see [146])	PD was monophyletic per species and per package
The population of wild species (progenitors) and the autonomous (multiple) cultivated islands behave as a meta population in which alleles conditioning the domesticated phenotypes flow freely across the entire range of the respective species	In self-pollinating species (wheat, barley, pea, lentil, and chickpea), the entire range of the species cannot be seen as a panmictic population with free gene flow. Moreover, how does free exchange of domesticated alleles accord with the autonomy of the different D foci (e.g., [21])? Would this assumption not negate the autonomous aspect of the model [147]?	Not needed
Domesticated morphotypes could not be identified by Epiplaleolithic and Neolithic foragers and cultivators in nature or in their cultivated plots (e.g., [11])	Domesticated phenotypes are available as part of the standing genetic variation (see [171]). The knowledge and attentiveness of hunter-gatherers to their environment (e.g., [25,82]) makes relying on protracted cultivation for their appearance redundant	Neolithic humans were fully capable of identifying useful phenotypes in the wild
Behavioral and cultural aspects		
A long stage of cultivation (predomestication cultivation) is a prerequisite conditioning D (e.g., [12,17])	There is a biological option for rapid D of package cereals [64–66]. There is no option for the protracted cultivation of Near East grain legumes [26,69]	Not needed
The context of PD was circumstantial. Humans have adopted ‘camp-following’ plants or species that thrive in disturbed habitats and on refuse heaps [9,41,45,76,79]	Under meticulous botanical scrutiny, weedy and/or ruderal tendencies do not conform to the biology of most species that were domesticated in the Near East [48].	Not needed
The process was characterized by numerous ‘false starts’ and failures as well as some successful starts, from which the package of founder crops emerged. Under this reasoning, the Near East crops do not represent a selected package but rather remains of an erratic process (e.g., [16,18])	The appearance of an agronomically and nutritionally balanced crop assemblage [24,49] is not in line with this assumption. In addition, see [55]) concerning the alleged ‘evidence’ for the ‘lost crops’ claim	Not needed
Weeds increase as a consequence of cultivation; hence, weed remains increase with the protracted timeline of PD (e.g., [134])	The data fail to demonstrate this claim (see discussion in [29]). For example, Riehl *et al.*'s data [134] do not conform to their interpretation [172]	Not needed
Plant remains of no use to humans are likely to represent weeds of cultivation (e.g., [68,134])	Given that, in many cases, the identification is only to the genus level (in genera including many nonweedy species), such a claim is weak. In addition, would it then mean that weeds were not used if available?	Not needed
Cereal processing after D is a ‘labor trap’ lowering D incentives and resulting in selection pressure in favor of the wild-type phenotype	Experiments demonstrate the opposite (see [154])	Not needed

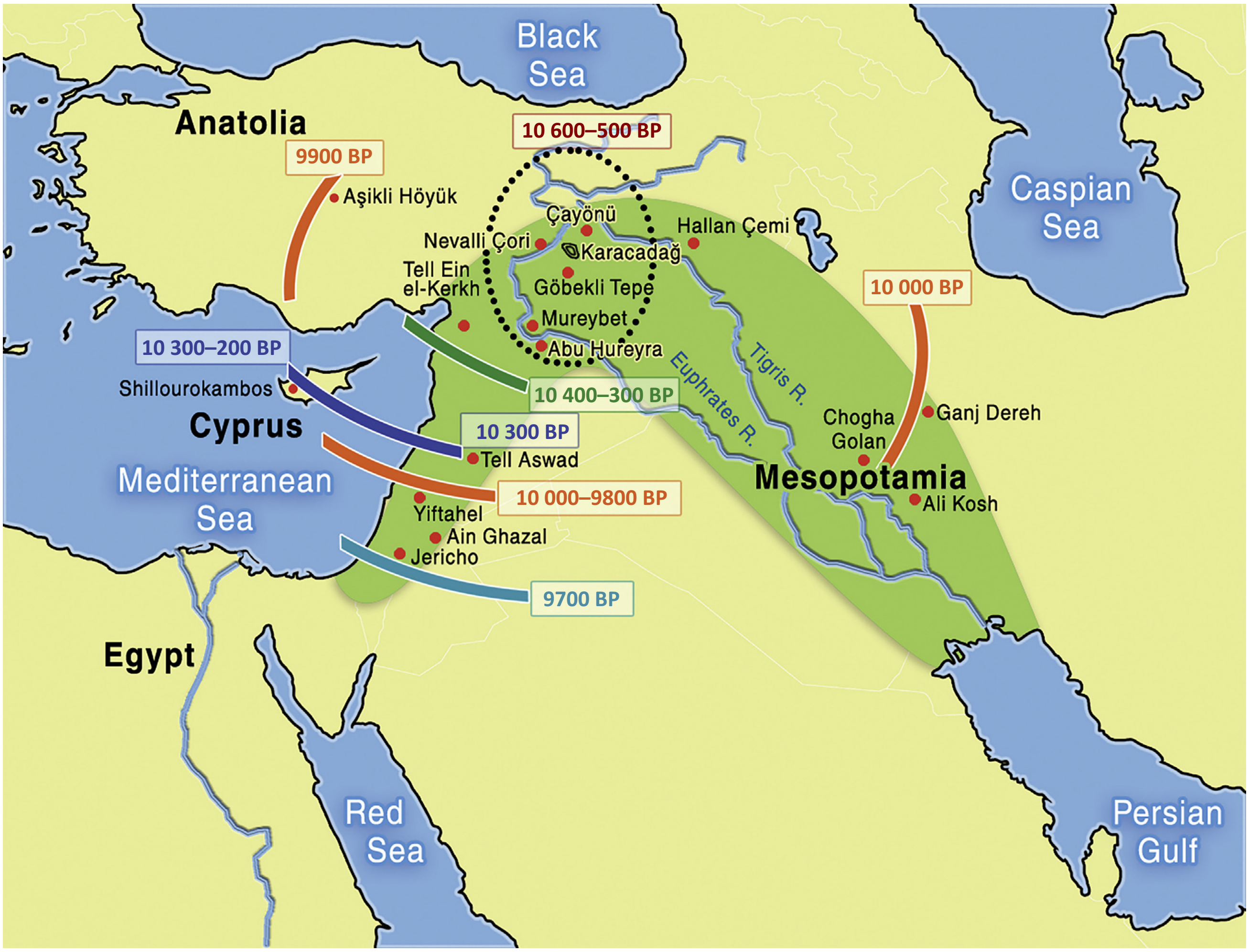
Table 1. (continued)

The protracted-autonomous model assumptions	Validity of the protracted-autonomous assumptions	The core area-one event model assumptions
Storage installations attest to cultivation (e.g., [14,68,90,164,173])	Natufian or PPNA installations provide no direct evidence of stored grains. The use of such installations for foraged wild plants or for entirely other uses cannot be excluded	Not relevant
The use of plant material for construction attests to cultivation [164]	Foraged wild cereals required processing to extract the grains. The remains could have later been used for various purposes	Not relevant
Rodent droppings attest to cultivation [68,164]	Why would this be the sole explanation for the presence of mice or other rodents in the sites?	Not relevant
There will, by definition, be no spread of domesticates for as long as the alleged (sub) centers remain independent	The arrival of *Cicer* to EPPNB Tel Ein el-Kerkh (located in Syria nearby the suggested core area) considering its wild progenitor distribution and the case of Cyprus indicate a fast spread of domesticates already in the EPPNB	Spread of domesticates is correlated with spatiogeographical dynamics of other cultural elements (e.g., [174,175], Figure 1 in the main text).
Resolution can be lowered; cultural change is not in direct correlation with cultivation and PD. Thus, Epipaleolithic communities may be included and the PPNA and EPPNB can be lumped at need and viewed as a single unit	This is a 'waste' of resolution earned by hard field and laboratory work, for example, the PPNA and EPPNB show a multitude of differences in settlement patterns and nature, architecture, burial customs, material culture and technology, symbolic behavior and economy (PD included), and, thus, should remain distinct	Cultural change is major and directly correlated with PD. Using the highest resolution available may help a refined historical and evolutionary reconstruction of PD in the Near East [25,27,30,86]

[a]Abbreviations: D, domestication; EPPNB, Early Pre-Pottery Neolithic B (generally ca. 10 500–10 000 years before present); PD, plant domestication; PPNA, Pre-Pottery Neolithic A (generally ca. 12 000–10 500 years before present).

'core area–one event' model of NEPD [27,28,86] is highly parsimonious (Figure 1).This is because: (i) it accords well with multiple lines of evidence and data sets; and (ii) since it requires fewer assumptions than the protracted, geographically diffused (autonomous), the unconscious model that must lean on a longer series of assumptions, some of which require further, secondary assumptions that partly turn problematic when closely scrutinized. Table 1 briefly summarizes the sets of assumptions needed for the two models.

One possible explanation of this imbalance may relate to the theoretical background (scholarly milieu) of the researchers involved. It may also relate to the gaps between the different disciplines involved in plant domestication research, that is, the remoteness of some of the biologists (and archeobotanists) from the sociocultural dimension (the 'Why' question), and archaeologists distancing themselves from the biological (especially agronomic) details and rationale ('How' aspects). A prominent, surprising, expression of this situation is the fact that (for all scientists involved, including archaeologists), human agency in its full sense became marginal and one may explicitly or implicitly view humans as (almost) passive (nearly equal to the plant) partners in plant domestication (e.g., as indicated by Zeder [75]). This divorce from human agency and intention, especially by archaeologists, needs a thoughtful explanation since the arena was left open for ethnography (e.g., [76,77,83,93]) thereby, in our case, departing from the 'deep', relevant, Near Eastern Neolithic archaeological data. It is no wonder that this occurs in conjunction with extensive blurring of the picture and a lowering of the resolution [68,163,164] (Box 2), both in terms of the genetic (e.g., [88]) and archeobotanical (e.g., [10,11]) records. Moreover, the lowered archaeological resolution results in reconstructions built of large blocks of time [giving up much of the resolution power provided by both archaeology and radiometric (^{14}C) dating] and an amalgamation of distinct cultural entities. This means that we are likely to lose the higher explanatory potential residing in the cultural



Trends in Plant Science

Figure 1. Charting the spread of Near East Domesticated Plants. The Levant as a primary center of plant domestication is a good arena for a detailed look into the intraregional spread of domesticated plants because of rich data sets resulting from many years of intensive archaeological, geobotanical, archeobotanical, and genetic research. The spatial pattern emerging for the spread of domesticated plants in the Near East supports a centered core area (in southeastern Turkey and northern Syria) model revealing a radiating pattern of spread outward from this region (e.g., [10,152,193]), mainly towards the west, and the south. Based on archeobotanical data, the (genetic-based) 'ripple-waves of advance' pattern [193] accords well with chronological (^{14}C-based) and geographical data available regarding Levantine plant domestication (see map). The map shows the spread of domesticated plants throughout the greater Levant and into Cyprus within a few centuries. Archaeological evidence indicates that the suggested core area was a major active cultural center from which Neolithic innovations (and materials) spread to other parts of the Levant ([86] and references therein). This hypothesis is also supported by ^{14}C dates recording the flow of Pre-pottery Neolithic cultural elements from a core area in the northern Levant to the west and the south. This spread of cultural phenomena shows movement in geography in the form of a 'ripples-wave of advance' pattern. Thus, the spread of domesticated plants within the Levant is in line with the spread of other cultural elements, as reported by other studies, notwithstanding the domestication model they endorse (e.g., [10,21,134]).

array. This is yet another indication of how the seemingly cooperative plant domestication research milieu has distanced itself from past human agency.

For example, a recent vivid discussion on theoretical frameworks in agricultural origins and domestication research [75,78,112] exposes a puzzling situation especially vis à vis evolutionary models and the role of human agency. While human agency is presented as central, both Gremillion *et al.* [164] and Zeder [75], in our view, may be considered as being dismissive of human agency and intent. Gremillion *et al.*'s Neo-Darwinian approach [112] clearly suggests that (human) agency has no explanatory power despite later reservations [165,166]. By contrast, Zeder [75] endorses human agency and accuses Gremillion *et al.* [112] of nullifying the role of human agency and consciousness in agricultural origins and plant domestication. Yet, she herself underestimates human agency, as indicated by the very fact that she adheres to Niche Construction Theory, which implies a coevolutionary (mutualistic in nature) scenario of domestication in which little room is left for human agents' intention, initiative, and consciousness. Although both views do not claim that humans were not involved (an impossible claim), they leave little space for human cultural context (in its historical sense) and for human knowledge-based decisions.

In a Levi-Straussian spirit, we acknowledge our Neolithic ancestors' ability to identify plant species as food sources (and for many other uses) and argue in favor of a major conscious component leading human action that resulted in plant domestication [24,28,151,162]. Surely such action was based on an immense floristic knowledge and deep insight into biotic and abiotic environmental and seasonal phenomena (e.g., [25]). We strongly adopt Levi-Strauss' view that the emergence of agriculture could not have been either incidental or 'automatic', or in his words a 'fortuitous accumulation of a series of chance discoveries outside the faculty of man'. Instead, it emerged through initiatives of individuals and/or communities who were blessed by amazing 'concrete scientific', social, and practical ingenuity. Portraying Near Eastern Neolithic cultivators as unable to selectively propagate useful and/or desired stocks is based on linear thinking and exposes a derogatory attitude [29,167]. Despite the efforts invested in distancing oneself from linearity [93,133], nobody fails to 'read' this linearity [11,168]. Plant domestication was one of the most successful ingenuities of humankind, and still maintains its major economic and cultural role in our modern world. Why is human agency so difficult to acknowledge in this context? We have no answer.

Concluding Remarks and Future Perspectives

Circumstantial (linear) thinking cuts through over a century of plant domestication research even when simple biological and archaeological data suggest the opposite, as in the case of the Dump-Heap hypothesis and the Near Eastern crops [48], or the biology of Near Eastern grain legumes [26].

While a convergent view concerning plant domestication at the global scale, with independent domestication centers (see [1,2]) is acceptable, for the regional level in the Near East, we adopt a centric 'core area–one event' (Figure 1) model, especially given the required cultural and genetic isolation (independence) for the presumed subcenters [147] and in light of the pre-emptive domestication principle [1].

Counterintuitively, in recent years, there has been a tendency to compromise resolution both in terms of the biological aspect of plant domestication (e.g., lumping crop evolutionary processes under the domestication umbrella or attributing similar Domestication Syndrome traits and their relative importance to both cereals and legumes) and of the archaeological–archeobotanical aspects (e.g., lumping together the PPNA–EPPNB, which together span almost a millennium and a half). Apart from stressing the involved scientific losses, we ask the following: why give up so many useful and well-established databases that were assembled by the collective efforts of so many scientists over so many years?

From modern plant science and breeding perspectives, the plant domestication versus crop evolution distinction provides a powerful conceptual and practical tool. For example, chromosomal 'Domestication Syndrome charting' with the respective selective sweeps associated with domestication episodes [101] is fundamental for effective 'allele-mining' attempts to introduce agronomically important phenotypes into modern crop cultivars [169]. Indeed, in

Outstanding Questions

Can the plant domestication research community overcome the classical 'cereals paradigm' bias in favor of a more balanced view that accommodates the unique biological features of different crops (e.g., grain legumes, vegetables, or clonally propagated crops)?

Is the plant domestication (PD)–crop evolution (CE) distinction a private case of a limited number of crops or a true to life, wider-scale phenomenon?

Can genomic approaches help resolve the protracted domestication (a domestication–improvement–breeding continuum) versus episodic domestication (clear PD–CE distinction) dilemma?

What should be the role of experimental biological data relative to ethnographic data in cultural and biological reconstructions of PD episodes?

Can scholars (naturalists and humanists alike) agree on a prominent role for genuine human agency (including knowledge-based species targeting, consciousness, intentionality, and choice making) in plant (and animal) domestication models?

the postgenomic era and with ever-increasing understanding of the genetic basis of plant phenotypes, crop evolution researchers are adopting the distinction between domestication and improvement (postdomestication) traits (e.g., [37,62,98,100,101,161]).

Explaining (cultural) change takes freedom of thought and the ability to go beyond one's own context and agenda, no doubt, a complex task (see Outstanding Questions). Yet, plant domestication studies in the Near East, as well as other research fields of the social sciences and the humanities, are in need of such freedom, given that they are heavily masked by modern history.

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