

## Opinion

## Anthropogenic Seed Dispersal: Rethinking the Origins of Plant Domestication

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**It is well documented that ancient sickle harvesting led to tough rachises, but the other seed dispersal properties in crop progenitors are rarely discussed. The first steps toward domestication are evolutionary responses for the recruitment of humans as dispersers. Seed dispersal-based mutualism evolved from heavy human herbivory or seed predation. Plants that evolved traits to support human-mediated seed dispersal express greater fitness in increasingly anthropogenic ecosystems. The loss of dormancy, reduction in seed coat thickness, increased seed size, pericarp density, and sugar concentration all led to more-focused seed dispersal through seed saving and sowing. Some of the earliest plants to evolve domestication traits had weak seed dispersal processes in the wild, often due to the extinction of animal dispersers or short-distance mechanical dispersal.**

**The Origins of Agriculture**

The linked questions of why, how, when, and where people first domesticated plants and animals are among the greatest mysteries in the development of human culture. Understanding how and why humans gained the ability to produce grain surpluses is the key to understanding the specialization of artistic and intellectual pursuits, as well as the demographic changes that led to the formation of cities and empires. Over the past century, scientists have made great strides in answering the questions of when and where plants first evolved in response to human selective pressures [1,2]. However, there remains no clear consensus regarding the why and how questions [2,3]. The lack of agreement may be due to the way these two questions have been framed since Darwin presented the concept of 'artificial selection' as opposite to or separate from natural processes [4]. Thinking of domestication as unique from other evolutionary processes effectively makes the why and how questions unanswerable – the greatest trick questions in the sciences. The focus on human agency in the process has left scholars from Pumpelly [5] and Childe [6] to Sauer [7], Cohen [8], Flannery [9], Hayden [10], and hundreds of others searching for rational drivers of human innovation. After 160 years of research into the origins of agriculture, most scholars finally accept that the process was not driven by conscious selection; in accepting this, the scholarly community is poised to reframe the study of evolution under cultivation and focus on the effects of heavy human herbivory on plant communities in the early and mid-Holocene. In this paper, I argue that plant domestication originated through the evolution of those traits which facilitated a stronger mutualistic bond between plants and people, with humans providing seed dispersal services.

Evolutionary studies illustrate that mutualism often evolves from a predatory relationship [11,12]. In some cases, plants evolved sugar-rich fruits in order to recruit dispersers, and in other cases, dispersers were enticed by the green foliage that surrounded small, dry-fruited seeds. The process of plants in the wild evolving new traits in order to change their seed dispersal mechanism is effectively the same process that led to morphological changes in seeds during the first few

**Highlights**

Archaeobotanical and genetic evidence demonstrates that the first morphological changes in all of the earliest domesticated plants were associated with wild seed dispersal strategies that were no longer advantageous under human cultivation.

Domestication was/is a natural response of plants to heavy seed predation by humans. Many plants in the wild have formed a similar seed dispersal-based mutualism with animals as a response to herbivory.

Rather than viewing domestication as an intentional human-driven process, domestication is best modeled as a natural evolutionary response to herbivory. Early domestication traits gave plants a selective advantage through the recruitment of humans as seed dispersers.

Many of the progenitors of our modern domesticated crops relied on animals for seed dispersal. The natural dispersal processes of many of these crop progenitors were weakened by megafaunal extinctions.

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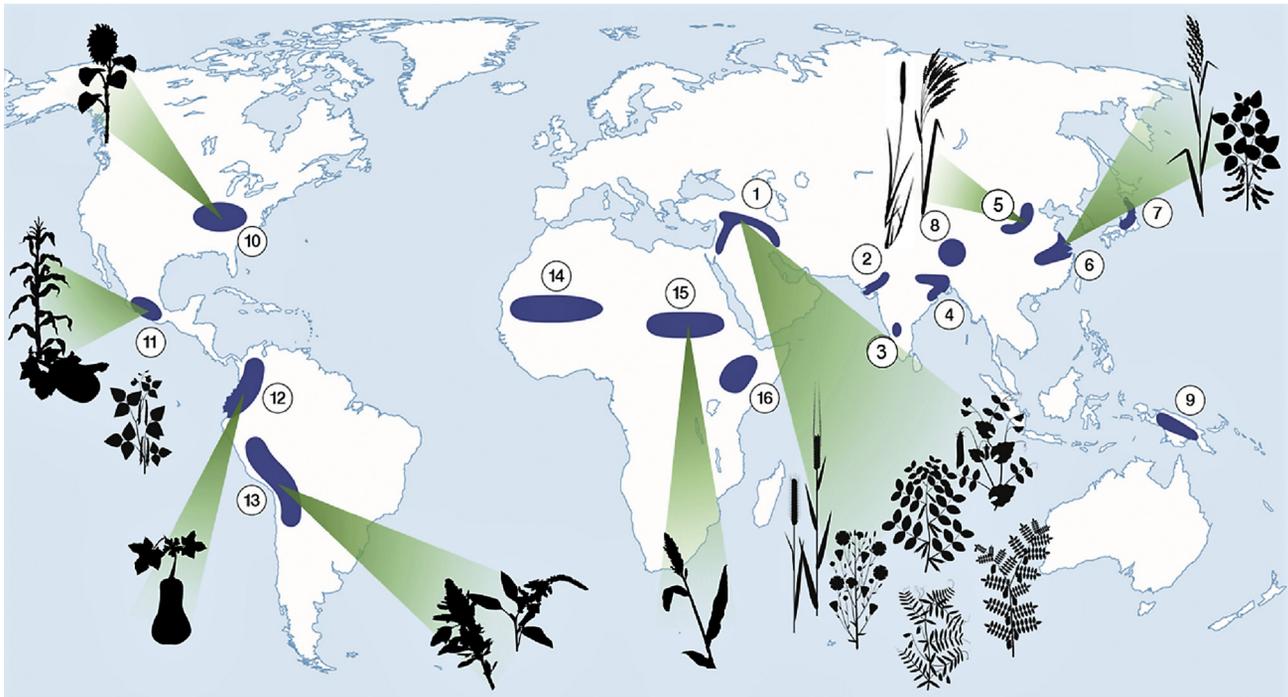
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millennia of human cultivation. As an evolutionary process, domestication is governed by the same drivers as all evolution. Ellstrand [13] recently mused that gene flow, as the incorporation of new alleles between genetically differentiated populations, is one of the strongest evolutionary forces in plants and is facilitated by seed dispersal. Studies show that low levels of gene flow often counteract the effects of mutation, genetic drift, and selection [13]. Gene flow can act to make a population more homogenous, or it can lead to genetic variation [14]. Rates of gene flow vary across space, through time, and between specific individuals [13]. However, it is a necessary process for ensuring a healthy population, promoting diversification, adaptive evolution, and overall fitness [15–17]. In plants, both intra- and interspecies gene flow push evolution forward [18,19]. As part of the gene flow system, seed dispersal allows plants to (i) avoid kin (sibling and parent) competition [20–22], (ii) avoid interspecific competition, (iii) reduce inbreeding [11,12], and (iv) colonize new areas [23–25]. Biotic dispersal can also lead to directed dispersal, targeting prime colonization areas and allowing greater offspring success rates than if dispersal were random [26]. Additionally, germination dormancy is seed dispersal through time [27]. Following the Janzen-Connell hypothesis, low rates of seed dispersal will lead to high rates of density-dependent mortality [28–30]. Many plants possess both biotic and abiotic dispersal strategies or use multiple dispersal systems [31]. However, all plants have evolved ways to move their seeds and spread their genes. Many scholars recognize that these processes are only rarely opportunistic or random, although some scholars see many rapidly growing annuals as having no specific dispersal strategy.

Rindos recognized the significance of seed dispersal in the domestication processes, and he cautiously stated that the ‘evolution of cultivated plants came about by the development of specialized dispersal relationships between humans and numerous previously opportunistically dispersed plants’ ([32], p. 120). Other scholars since then have acknowledged the significance of seed dispersal mechanisms in domestication [33–35]; however, few of these studies looked beyond the role of tough rachises in large-grained cereal domestication or nondehiscent pods in the domestication of some legumes. In this paper, I argue that all evolution of plants under the first steps toward domestication, during the early and mid-Holocene (before ca. 5000 years ago), was linked to a shift in seed dispersal mechanisms (Table S1 in the supplemental information online and Figure 1). Therefore, domestication is the evolution of new traits in order to support a mutualistic relationship with humans, and it was an inevitable evolutionary response in plants to (i) increasingly more complex human harvesting practices, notably sickle harvesting (seed predation), seed saving, seed trading, and sowing (dispersal); (ii) increased human population size (herbivory pressure); and (iii) sedentism (an evolutionarily significant time scale of continual selective pressure). Substantially, evolution under cultivation is no different from the evolution of mutualism or antiherbivory defenses as a response to any heavy herbivory pressure and is simply an example of keeping pace with the Red Queen [36].

### Parallel Evolution of Traits for Seed Dispersal

Scholars recognize the parallel evolution of domestication traits, often called the ‘domestication syndrome’; however, it is not always acknowledged that this parallelism is due to similar selective forces associated with herbivory and seed dispersal [33]. Archaeologists and biologists have studied the switch from the wild to the anthropogenic seed dispersal state in large-seeded cereals and legumes [33,37]. They have studied, in detail, the transition from a brittle rachis to a tough rachis and the role of hygroscopic awns (trypanocarpis) in dispersing and burying large grass seeds [35]. Likewise, studies have illustrated that these cereal crops naturally form dense monodominant fields, which were key for early human harvesting. Greater sibling competition in these dense fields may also have driven evolution of larger seeds with greater offspring provisioning. However, shattering rachises, awns, and dehiscent pods represent only a few of the wild



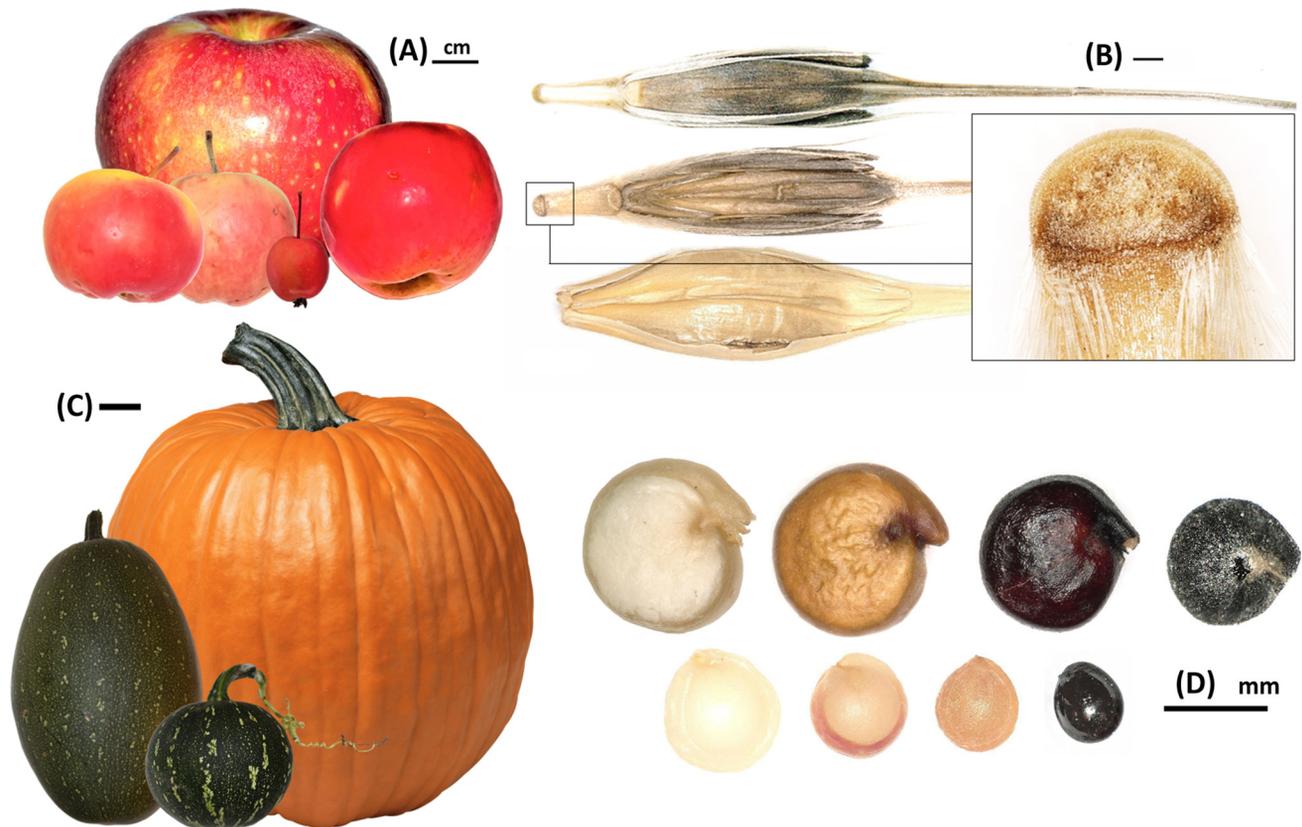
Trends in Plant Science

**Figure 1. Map of the Regions or Centers of Domestication Globally, as Proposed and Discussed by Larson *et al.* [1].** Recognized regions of domestication: 1) Southwest Asia; 2) Savannahs of West India; 3) South India; 4) East Indian Plains; 5) North China Plains; 6) Yangtze Basin; 7) Japanese Islands; 8) Southern Himalaya; 9) New Guinea; 10) Eastern North American Plains; 11) Meso-america; 12) Lowlands of South America; 13) Central/South Andes; 14) West Africa Sahel; 15) East Africa Savannah; 16) Ethiopian Plateau. These centers correlate with the crops presented in Table S1 in the supplemental information online.

dispersal mechanisms employed by crop progenitors (Figure 2B). Notably, the majority of domesticated crops were dispersed through animal vectors, most of which were megafaunal mammals (defined here as any animal larger than 40 kg) [38,39,64]. The effects of the late Pleistocene megafaunal extinctions on these populations have almost completely been overlooked. Janzen and Martin [38] recognized the megafaunal dispersal mechanism as being significant for many of the fruits that we eat today, and Janzen [39] went on to illustrate how megafaunal ruminants spread herbaceous plant seeds.

#### Endozoochoric Fruits and Megafaunal Mammals

The role of seed dispersal in domestication is most evident when looking at the domestication of fruit crops; fleshy fruits are, generally speaking, evolutionary adaptations for dispersing seeds by means of an animal vector. Basic traits of fruiting plant domestication include increases in seed or pit size, pericarp tissue, and concentrations of sugars. In large-fruited wild plants, these traits evolved to recruit megafaunal dispersers, attracted by large sweet fruits. Despite the metabolic consequences for trees, cucurbits, and Solanaceae plants (solanids), these traits clearly increase overall fitness in an anthropogenic niche; they are also maladaptive under natural selective pressures (nonanthropogenic). Large fruits in most ecosystems today rarely disperse far enough from the parent trees or siblings to pay back the metabolic investment in fruit production. A feral apple tree, for example, often has rotting fruit under it in the fall unless it is located in a horse pasture, and it is plausible that the species might either go extinct or evolve smaller fruits (across the population) without humans. Most large-fruited crops are effectively obligate domesticates, without the large animal dispersers of the Pleistocene and earlier. Surveys of the progenitors of these large-fruited trees and cucurbits show that, in most cases, they have small distribution ranges



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**Figure 2. Images of Progenitors and Landraces of Modern Crops That Effectively Illustrate How the Process of Evolution of Seed Dispersal-Based Mutualism Occurred in Crops.** Four distinct pathways toward domestication are illustrated, all of which are tied to a shift in seed dispersal mechanisms. All of the earliest domesticated plants effectively fit into one of these four pathways: (A) arboreal crops with fleshy fruits, (B) mechanically dispersed annuals, (C) cucurbits and herbaceous plants with fleshy fruits, and (D) dry-fruited, small-seeded annuals. (A) A domesticated apple (*Malus pumila/domestica*) with its four wild relatives that collectively contributed to a hybrid complex (*M. sieversii*, *M. sylvestris*, *M. baccata*, and *M. orientalis*). (B) Dorsal and ventral views of a wild barley grain (*Hordeum vulgare* spp. *spontaneum*), with an inset magnification of a brittle, smoothly broken rachis and an example of a modern hulled barley grain below. (C) Wild *Cucurbita texana*, one of the members of the squash hybrid complex and two landraces of *C. pepo*. (D) Wild examples of *Chenopodium album* and *Amaranthus albus* with landraces of quinoa (*C. quinoa*) and amaranth (*A. caudatus*), illustrating the trajectory toward domestication.

and fragmentary populations, characteristic of range loss and reduced ability to colonize. In general, throughout the Holocene, large-fruited species of trees have become increasingly restricted in range due to poor seed dispersal [38,40–45], except in Africa, where large frugivorous dispersers still exist. In some cases, fruits have evolved to be smaller as a response to the loss of large Pleistocene mammalian dispersers [43]. The lineages of these fruit trees that have survived into the Holocene tend to propagate through shoots and natural cloning rather than via seeds (e.g., *Malus sieversii*, *Prunus mira*, *Asimina triloba*, *Maclura pomifera*). Often these dense, clonally reproducing wild stands continue to produce extensive generations with energetically costly fruits, which then decompose under the trees, leading to density-dependent seed death through fungal attack, fermentation, seed predation from small animals, or parent/sibling competition. Large fruits coevolved with megafaunal mammals around the world [12,25], and humans are the most ubiquitous megafaunal mammal to survive the Pleistocene/Holocene boundary. The evolution of even larger fruits and larger seeds under human dispersal is substantially no different from the evolution of large fruits in response to proboscideans (notably gomphotheres), Xenarthra (e.g., *Glyptodon* spp., megalonychids, megatheriids), Perissodactyl (e.g., rhinoceroses, equids), or earlier large primates.

While many mammals coevolved with fruit trees, resulting in seed dispersal-based mutualism, primates are particularly responsible for driving the evolution of larger fruits [46,47]. Primates can consume and carry large-seeded fruits; in some tropical forests, they are the primary factors in determining forest vegetation communities, essentially creating orchards of primate-dispersed fruit trees [48]. High postdigestion germination rates and extensive dispersal distances have been recorded for all great apes, and these megafaunal primates can disperse hundreds of seeds over great distances daily [49]; additionally, they can readily disperse seeds larger than 2.0 cm [50]. The coevolutionary bond between primates and large-fruited angiosperms has been a continuous process since the Eocene [31,47]; humans are just a recent iteration of this mutualism. Therefore, the evolution of agriculture-type seed dispersal-based mutualism in primates has been developing for at least 40 million years.

#### Ruminant Grazers and Millet Domestication

While monogastric species can pass relatively large seeds, ruminant grazers (Bovidae) have a much more effective digestive system. The restricted cecum of most ruminants, combined with double digestion, heavy mastication, and fermentation, constrains the size and the physiomorphological makeup of seeds that can pass through the digestive system and remain viable [51,64]. Ruminant-dispersed plants are mostly herbaceous, contain hard seed coats, and have small seeds, which are often round with smooth surfaces [12,39,51,64]. Most of these plants evolved to display seeds on top of their terminal leaves, often lack mechanical dehiscence, and produce abundant generations [52,53]. The global fossil record shows that annuals diversified and radiated in response to grazing animals during the Miocene, leading to the first grasslands [26,31,53]. Paleogene megafaunal Perissodactyla (including equids, rhinoceroses, and tapirs) were far more likely than true ruminants to disperse large seeds and consume sugary fruits. Artiodactyla (including bison, deer, and their relatives) are responsible for the prominence of small-seeded herbaceous plants that dominate grasslands today [12,54]. In some cases, the evolution of annuals in response to ruminant grazing led to herbivory defenses, such as an increased production of phytoliths or secondary compounds. In other cases, plants evolved mutualistic relationships, such as through seed dispersal. Holocene grasslands are occupied by small herbaceous plants that have phenotypic adaptations to support endozoochoric dispersal.

Studies of seed composition in herbivore dung and seed germination rates postdigestion illustrate that many progenitors were dispersed by mammalian megafaunal grazers [51,64]. Larger seed sizes and greater provisioning allow plants to outcompete their neighbors; however, seed size is often constrained by dispersal mechanisms and seed predation rates [31]. The constraint of the ruminant dispersal mechanism (rarely passing viable seeds larger than 2.0 mm) is one factor explaining why so many of our noncereal grains are small today. Some examples of modern crops that had progenitors with ruminant seed dispersal traits include chenopods (*Chenopodium* spp.), most of our millets, buckwheat (*Fagopyrum* spp.), maize (*Zea mays*), hemp (*Cannabis sativa*), and most of the lost crops of the Eastern Agricultural Complex [55,64]. Switching to anthropogenic dispersal may have allowed a rapid increase in seed size as a response to increased sibling competition in cultivated fields, and it also led to a reduction in seed coat thickness due to the reduced adaptive advantage of dormancy, lack of a need for the protective structure, and the energy expenditures associated with producing it. The role of megafaunal grazers in the dispersal and evolution of the progenitors of many of our small-seeded annual crops has almost completely been overlooked. Recently, Spengler and Mueller [64] illustrated this evolutionary process in early domestication of small-seeded annuals.

### Dormancy as Seed Dispersal through Time

Evolutionary changes can sever more than one function in a plant [18]. For example, dormancy is often closely tied to endozoochoric dispersal [39]. Systematic studies of germination after digestion illustrate how effective the process is at breaking dormancy [39,56]. Paleontological evidence even suggests that the evolution of dormancy was a prerequisite for endozoochoric dispersal and that seed dispersal-based mutualism was the key factor in angiosperm diversification [26,31]. Small-seeded annuals with hard seed coats usually evolve mechanical dormancy, often not germinating until the seed coat is broken and water absorption is permitted. Therefore, the evolution of hard seed coats in species, such as *Chenopodium* spp., would have allowed simultaneous dispersal through time and space. Seeds that are successfully dispersed through space have no need to disperse through time and effectively germinate after defecation. Due to the loss of endozoochoric dispersal and the loss of a need for energetically costly (or neutral) thick seed coats, there was a strong selective pressure against dormancy through sowing and seed saving during early cultivation [34]. These compounding unconscious selective pressures resulted from cultivation and could have rapidly broken dormancy. Still, early farming of high-dormancy plants likely relied, at least in part, on established homogenous vegetation patches and the soil seed bank to avoid high seed loss until dormancy was broken [51,64]. The seeds lying dormant in the seed bank from previous years would have helped cushion losses from seeds not germinating in a given year; over time, the plants in the anthropogenic environment would express less dormancy. The breaking of dormancy was directly tied to a switch from a wild to an anthropogenic dispersal mechanism.

### Domestication: An Evolutionary Response to Human Herbivory

‘Why’ humans domesticated plants and animals has remained one of the most asked questions in both anthropological and biological studies. However, if we accept that domestication is an inevitable consequence of the broader evolutionary process and competition between species, then the question becomes as nonsensical as asking why the rabbit runs fast or why the lion has sharp teeth. Humans did not domesticate the grass, nor did the grass domesticate the human; they coevolved in unison [57]. The grass morphologically evolved in a way that allowed a tighter mutualistic relationship to form from a formerly predatory relationship of heavy seed predation. The new traits of tough rachises, loss of dormancy, thinner seed coats, and nondehiscent pods increased fitness for both the plants and the human seed dispersers. As human cultural practices of the late Pleistocene and early Holocene became increasingly more complex, the selective pressures that people asserted on the organisms around them changed. Likewise, as human populations became larger and they started applying more pressure on one population of organisms (sedentism), the driving forces for evolution increased. Ultimately, those organisms were forced to keep pace or go extinct; a select handful of rapidly reproducing (annual) plants were able to evolve new traits that allowed a more beneficial symbiosis with humans.

The number of centers or regions of plant domestication is still debated; some scholars accept that plants independently evolved domestication traits for the first time (without human knowledge of cultivation prior) in as many as 11 loci globally [1]. In Figure 1 and Table S1 in the supplemental information online, I present each of the crops that appear to be the first crops in these centers, based on archaeobotanical data. These early crops were all brought under cultivation during the early or mid-Holocene. I do not discuss crops that were first cultivated during the past two millennia, because conscious human breeding drove faster evolution and selection for a wide variety of other traits. I am intentionally conservative with the dates in Table S1, and, in many cases, evidence for cultivation predates evidence for morphological change by several millennia. In this paper, I am not attempting to look at the cognitive changes in humans that led to sickle harvesting and seed saving; I am focusing on the biological responses in plants to

human cultural practice. Scholars still know relatively little about the process or domestication in root or stem crops, largely because they do not preserve in the archaeological record. People have clearly been harvesting root and stem crops from the wild since at least the middle Pleistocene and likely much earlier, with some limited evidence for intentional cultivation dating to as early as 7000 to 5000 years ago [58]. Currently, there is limited evidence for evolutionary changes in these plants before the late Holocene (after 5000 years ago), although future research may change this. More importantly, there is no clear mechanism of evolutionary selection among plants that were cultivated for their vegetative parts. Likewise, traditional cultivation practices for vegetative crops, notably root/stem crops, rely on clonal reproduction and low labor investments, ultimately not imposing strong selective forces. Until new data are brought to bear, we should not assume that root crops were morphology domesticated during early human cultivation, although other biological processes may have played a role in changing plant morphology in this group of crops – specifically, developmental plasticity or epigenetic inheritance, which are distinct from the introgression of genes or shifts in allele frequencies.

All of the earliest examples of plants evolving in response to cultivation activities fit into one of four general pathways toward domestication (Figure 2 and Table 1, Key Table). All four of these pathways represent a shift from a wild to an anthropogenic seed dispersal mechanism. The most heavily studied of these systems is the loss of mechanical forms of dehiscence, such as in cereals and legumes (Figure 2B and [37]). However, most crop progenitors (excluding the large-grained cereals, rice, and large-seeded legumes) were dispersed by means of ingestion and transport by animals. In the case of arboreal fruit trees, dispersal relied on either monogastric frugivores or omnivores (Figure 2A and [59]). The same basic process of a shift from wild animal to human dispersal occurred in many small-fruited, often avian-dispersed plants, such as with cherries (*Prunus avium*). Domesticated cherries demonstrate how plants that evolve traits to recruit a new disperser often sever mutualism with previous dispersers, and many varieties of domesticated cherries are too large for birds to swallow. The fact that cherries remained relatively small before human cultivation illustrates how fruit and seed size are often constrained by a dispersal mechanism. Additionally, several herbaceous fruiting plants followed a similar trajectory

## Key Table

Table 1. A Selection of Familiar Examples of Plants That Shifted Their Seed Dispersal Mechanisms under Human Cultivation<sup>a</sup>

Dispersal form		Dispersal animal guild		Associated evolutionary changes	Some familiar examples
Mechanical dispersal				Toughening of the rachises; nondehiscent pods	Wheat, barley, rice, peas, lentils
Endozoochory (animal) dispersal	Herbaceous plants with fleshy fruits	Cucurbits	Megafaunal mammals	Larger fruits; larger seeds; reduced triterpenes	Squashes, melons
		Solanids	Avian	Larger fruits; larger seeds; higher sugar concentration	Peppers, tomatoes
	Arboreal plants with fleshy fruits	Large fruits	Megafaunal mammals	Larger fruits; larger seeds; higher sugar concentration	Avocado, mango, apple, banana
		Small fruits	Avian	Larger fruits; larger seeds; higher sugar concentration	Cherries, small fruits (<2 mm)
Herbaceous plants with small/dry fruits		Megafaunal ruminant grazing mammals		Larger seeds; loss of dormancy; thinning of the seed coat	Quinoa, buckwheat, amaranth, millets

<sup>a</sup>This table displays the four pathways toward domestication in the earliest plants from each area of domestication (see also Figure 2): arboreal plants with fleshy fruits, mechanical dispersal, herbaceous plants with fleshy fruits, and herbaceous plants with small/dry fruits.

from avian dispersal, as seen in the solanids, or megafaunal dispersal, as in cucurbits (likely gomphothere or glyptodonts; Figure 2C and [45]). The last of these categories includes small herbaceous plants with small seeds that evolved for dispersal by ruminant grazers, which inadvertently consume the seeds while eating the vegetation (Figure 2B) [64].

### Concluding Remarks and Future Perspectives

Whether the mammalian dispersers were recruited through sweet, fleshy fruits or green foliage, high gene flow rates and ability to colonize new territory drove adaptation [52,60,64]. In many cases, the loss of megafaunal dispersers during the late Pleistocene extinctions reduced the rates of gene flow in these plant clades [40,43,61] and, in some cases, drove corollary extinctions in obligate plants. Megafauna-dispersed crop progenitors in many areas of the world today have reduced ranges (e.g., *Polygonum erectum* [51,64]), are often endangered or extinct (e.g., for many Cucurbitaceae), and many reproduce clonally through shoots (e.g., *Malus sieversii*). In some cases, megafauna-dispersed plants evolved during the Holocene to recruit new dispersers [43], a process analogous to domestication. These genetically isolated, fragmentary populations with low rates of gene flow had a predisposition toward domestication; that is, they were genetically 'ready' for the recruitment of a new disperser.

Gene flow is one of the strongest forces driving evolution in plants [13]; therefore, evolutionary adaptations selecting for greater rates of seed dispersal can rapidly change allele frequencies. These changes are most visible when plants are brought under cultivation and the seed dispersal mechanism shifts to human dispersal. Conscious human-driven breeding only took place several millennia after the traits relating to the human dispersal syndrome in pioneer plants were fixed. By using nonanthropogenic examples of the evolution of seed dispersal-based mutualism, we can better study how the early processes of domestication took place and address more pressing questions of plant domestication (see Outstanding Questions). For example, understanding how plants evolved to recruit megafaunal dispersers and how they are now evolving to cope with the loss of these dispersers directly influences our understanding of evolution under cultivation [40,43,61]. Likewise, this approach supports discussions of a much deeper time depth for anthropogenic selective pressures [62,63] and ties in to discussion of the evolution of dispersal traits in nonhuman primate-dispersed species. Domestication is part of the evolutionary arms race, whereas plants evolved to recruit humans as seed dispersers in response to heavy human herbivory/seed predation and a need for gene flow.

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### Supplemental Information

Supplemental information associated with this article can be found online at <https://doi.org/10.1016/j.tplants.2020.01.005>.

### References

- Larson, G. et al. (2014) Current perspectives and the future of domestication studies. *Proc. Natl. Acad. Sci. U. S. A.* 111, 6139–6146
- Langlie, B.S. et al. (2014) Agricultural origins from the ground up: archaeological approaches to plant domestication. *Am. J. Bot.* 101, 1601–1617
- Zeder, M.A. and Smith, B.D. (2009) A conversation on agricultural origins: talking past each other in a crowded room. *Curr. Anthropol.* 50, 681–691
- Darwin, C.R. (1859) *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*, John Murray
- Pumpelly, R. (1908) *Explorations in Turkestan: Expedition of 1904 Prehistoric Civilizations of Anau: Origins, Growth, and Influence of Environment*, Carnegie Institution of Washington
- Childe, V.G. (1936) *Man Makes Himself*, Watts
- Sauer, C.O. (1952) *Agricultural Origins and Dispersals*, American Geographical Society
- Cohen, M. (1977) *The Food Crisis in Prehistory: Overpopulation and the Origins of Agriculture*, Yale University Press
- Flannery, K.V. (1973) The origins of agriculture. *Annu. Rev. Anthropol.* 2, 271–310
- Hayden, B. (1990) Nimrods, piscators, pluckers and planters: the emergence of food production. *J. Anthropol. Archaeol.* 9, 31–69

### Outstanding Questions

Researchers have heavily focused on a select handful of domesticated plants, notably large-seeded annual grasses and legumes. These crops are not characteristic of the hundreds of other domesticated species on the planet today. We know little about the evolutionary driving forces in the other crops, notably in long-generation perennials. Future research needs to focus on the evolutionary driving forces that led to morphological changes in the rest of the domesticated plants.

Studies of evolution under cultivation can significantly benefit from an understanding of evolution in the wild, especially fossil evidence for seed dispersal. Collaborations between paleontologists and archaeobotanists/archaeogeneticists are necessary as the field moves forward. Understanding how plants evolved new seed dispersal mechanisms in the wild can inform us about the evolutionary processes under early cultivation.

Scholars studying plant domestication need to let go of concepts of human innovation and to stop looking for rational driving forces for these innovations. The question of 'why' humans domesticated plants has bogged down the entire field in circular discussions for over a century.

The first step in understanding the domestication of any plant should be the study of the progenitor's seed dispersal process. However, we still do not know what the ancient seed dispersers were for many endozoochoric plants and what phenotypic traits allowed for such dispersal mechanisms.

11. Nathan, R. and Muller-Landau, H.C. (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends Ecol. Evol.* 15, 278–285
12. Jara-Guerrero, A. *et al.* (2018) White-tailed deer as the last megafauna dispersing seeds in neotropical dry forests: the role of fruit and seed traits. *Biotropica* 50, 169–179
13. Ellstrand, N.C. (2014) Is gene flow the most important evolutionary force in plants? *Am. J. Bot.* 101, 737–753
14. Mayr, E. (1963) *Animal Species and Evolution*, Harvard University Press
15. Hansson, B. *et al.* (2003) Heritability of dispersal in the great reed warbler. *Ecol. Lett.* 6, 290–294
16. Clobert, J. *et al.* (2001) *Dispersal*, Oxford University Press
17. Pasielli, G. *et al.* (2004) Genetic and environmental influences on natal dispersal distance in a resident bird species. *Am. Nat.* 164, 660–669
18. Feder, J.L. *et al.* (2012) The genomics of speciation-with-gene-flow. *Trends Genet.* 28, 342–350
19. Garant, D. *et al.* (2007) The multifarious effects of dispersal and gene flow on contemporary adaptation. *Funct. Ecol.* 21, 434–443
20. Holt, R.D. *et al.* (2005) Theories of niche conservatism and evolution: could exotic species be potential tests? In *Species Invasions: Insights into Ecology, Evolution, and Biogeography* (Sax, D.F. and Stachowicz, J.J. and Gaines, S.D., eds), pp. 259–290, Sinauer Associates Inc.
21. Hamilton, W.D. and May, R.M. (1977) Dispersal in stable habitats. *Nature* 269, 578–581
22. Ashely, M.V. (2010) Plant parentage, pollination, and dispersal: How DNA microsatellites have altered the landscape. *Crit. Rev. Plant Sci.* 29, 148–169
23. Venable, D.L. and Brown, J.S. (1988) The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. *Am. Nat.* 131, 360–384
24. Howe, H.F. and Smallwood, J. (1982) Ecology of seed dispersal. *Annu. Rev. Ecol. Syst.* 13, 201–228
25. Escribano-Avila, G. *et al.* (2014) Diverse guilds provide complementary dispersal services in a woodland expansion process after land abandonment. *J. Appl. Ecol.* 51, 1701–1711
26. Eriksson, O. (2008) Evolution of seed size and biotic seed dispersal in angiosperms: paleoecological and neoecological evidence. *Int. J. Plant Sci.* 169, 863–870
27. Cohen, D. (1966) Optimizing reproduction in a randomly varying environment. *J. Theor. Biol.* 12, 119–129
28. Kellner, J.R. and Hubbell, S.P. (2018) Density-dependent adult recruitment in a low-density tropical tree. *Proc. Natl. Acad. Sci. U. S. A.* 115, 11268–11273
29. Janzen, D.H. (1970) Herbivores and the number of tree species in tropical forests. *Am. Nat.* 104, 501–528
30. Connell, J.H. (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In *Dynamics of Populations* (den Boer, P.J. and Gradwell, G.R., eds), pp. 298–312, Center for Agricultural Publishing and Documentation
31. Tiffney, B.H. (2004) Vertebrate dispersal of seed plants through time. *Annu. Rev. Ecol. Syst.* 35, 1–29
32. Rindos, D. (1984) *The Origins of Agriculture: An Evolutionary Perspective*, Academic Press
33. Fuller, D.Q. and Allaby, R. (2009) Seed dispersal and crop domestication: shattering, germination and seasonality in evolution under cultivation. *Ann. Plant Rev.* 38, 238–295
34. Ladizinsky, G. (1998) *Plant Evolution under Domestication*, Kluwer Academic Publishers
35. Wood, D. and Lenné, J.M. (2018) A natural adaptive syndrome as a model for the origins of cereal agriculture. *Proc. Biol. Sci.* 285, 20180277
36. Quental, T.B. and Marshall, C.R. (2013) How the Red Queen drives terrestrial mammals to extinction. *Science* 6143, 290–292
37. Li, L.-F. and Olsen, K.M. (2016) To have and to hold: selection for seed and fruit retention during crop domestication. *Curr. Top. Dev. Biol.* 119, 63–109
38. Janzen, D.H. and Martin, P.S. (1982) Neotropical anachronisms: the fruits the gomphotheres ate. *Science* 215, 19–27
39. Janzen, D.H. (1984) Dispersal of small seeds by big herbivores: foliage is the fruit. *Am. Nat.* 123, 338–353
40. Rule, S. *et al.* (2012) The aftermath of megafaunal extinction: ecosystem transformation in Pleistocene Australia. *Science* 335, 1483–1486
41. Pires, M.M. *et al.* (2017) Pleistocene megafaunal extinctions and the functional loss of long-distance seed-dispersal services. *Ecography* 41, 153–163
42. Galetti, M. *et al.* (2017) Ecological and evolutionary legacy of megafauna extinctions. *Biol. Rev.* 93, 845–862
43. Onstein, R.E. *et al.* (2018) To adapt or go extinct? The fate of megafaunal palm fruits under past global change. *Proc. R. Soc. B* 285, 20180882
44. Guimarães, P.R. *et al.* (2008) Seed dispersal anachronisms: rethinking the fruits extinct megafauna ate. *PLOS One* 3, e1745
45. 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
46. Sussman, R.W. (1991) Primate origins and the evolution of angiosperms. *Am. J. Primatol.* 23, 209–223
47. Sussman, R.W. *et al.* (2013) Rethinking primate origins again. *Am. J. Primatol.* 75, 95–106
48. Lambert, J.E. and Graber, P.A. (1998) Evolutionary and ecological impacts of primate seed dispersal. *Am. J. Primatol.* 45, 9–28
49. Lambert, J.E. (1999) Seed handling in chimpanzees (*Pan troglodytes*) and rhesus monkeys (*Cercopithecus aesculani*): implications for understanding hominoid and cercopithecine fruit-processing strategies and seed dispersal. *Am. J. Phys. Anthropol.* 109, 365–386
50. Wrangham, R.W. *et al.* (1994) Seed dispersal by forest chimpanzees in Uganda. *J. Trop. Ecol.* 10, 355–368
51. Mouissie, A.M. *et al.* (2005) Ecological correlates of seed survival after ingestion by fallow white-tailed deer. *Funct. Ecol.* 19, 284–290
52. Pakeman, R.J. *et al.* (2002) Ecological correlates of endozoochory by herbivores. *Funct. Ecol.* 16, 296–304
53. Jacobs, B.F. *et al.* (1999) The origin of grass-dominated ecosystems. *Ann. Mo. Bot. Gard.* 86, 933–950
54. Nathan, R.F.M. *et al.* (2008) Mechanisms of long-distance seed dispersal. *Trends Ecol. Evol.* 23, 638–647
55. Small, E. (2015) Evolution and classification of *Cannabis sativa* (marijuana, hemp) in relation to human utilization. *Bot. Rev.* 81, 189–294
56. Wicklow, D.T. and Zak, J.C. (1983) Viable grass seeds in herbivore dung from a semi-arid grassland. *Grass Forage Sci.* 38, 25–26
57. Zeder, M.A. (2015) Core questions in domestication research. *Proc. Natl. Acad. Sci. U. S. A.* 112, 3191–3198
58. Piperno, D.R. *et al.* (2000) Starch grains reveal early root crop horticulture in the Panamanian tropical forest. *Nature* 407, 894–897
59. Spengler III, R.N. (2019) Origins of the apple: the role of megafaunal mutualism in the domestication of *Malus* and rosaceous trees. *Front. Plant Sci.* 10, 617
60. Campbell, J.E. and Gibson, D.J. (2001) The effect of seeds of exotic species transported via horse dung on vegetation along trail corridors. *Plant Ecol.* 157, 23–35
61. Lundgren, E.J. *et al.* (2018) Introduced megafauna are rewiring the Anthropocene. *Ecography* 41, 857–866
62. 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
63. Allaby, R.G. *et al.* (2017) Geographic mosaics and changing rates of cereal domestication. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 372, 20160429
64. Spengler III, R.N. and Mueller, N. (2019) Grazing animals drove domestication of grain crops. *Nat. Plants* 5, 656–662