Grazing animals drove domestication of grain crops

Robert N. Spengler III[1]* and Natalie G. Mueller[2,3]

In addition to large-seeded cereals, humans around the world during the mid-Holocene started to cultivate small-seeded species of herbaceous annuals for grain, including quinoa, amaranth, buckwheat, the millets and several lost crops domesticated in North America. The wild ancestors of these crops have small seeds with indigestible defences and do not germinate readily. Today, these wild plants exist in small fragmentary stands that are not appealing targets for foragers. This combination of traits has led many to argue that they must have been a food of last resort. We propose a new explanation: the domestication of small-seeded annuals involved a switch from endozoochoric dispersal (through animal ingestion) to human dispersal. Humans encountered these plants in dense stands created by grazing megafauna, making them easy to harvest. As humans began to cultivate these plants they took on the functional role of seed dispersers, and traits associated with endozoochory were lost or reduced. The earliest traits of domestication—thinning or loss of indigestible seed protections, loss of dormancy and increased seed size—can all be explained by the loss of the ruminant dispersal process and concomitant human management of wild stands. We demonstrate, by looking at rangeland ecology and herd animal herbivory patterns, that the progenitors of all of these species evolved to be dispersed by megafaunal ruminants and that heavy herbivory leads to dense homogenous clusters of endozoochoric plants. Hence, easily harvested stands on nitrogen hot spots near water sources would have existed in regions where these plants were domesticated. Future experimental and ecological studies could enhance our understanding of the relationships between specific crops and their possible ruminant dispersers.

For decades, scholars have debated how and why humans chose to intensively harvest small-seeded annuals, ultimately leading to their domestication[1–4]. These debates are often framed around discussions of optimal foraging theory or a broad-spectrum revolution, suggesting that humans only turned to these plants due to scarcity of higher yielding resources. The majority of grain crops that evolved domestication traits during the mid-Holocene had small seeds and often contained hard seed or fruit coats, or strongly adhered palea and lemma or glumes. The hard protective structures in all of these species mandate beating, threshing, winnowing and/or grinding before human consumption. High dormancy rates in the wild populations would have hindered or prevented any early attempt at sowing these plants as crops. Additionally, the progenitor populations of these plants today are fragmentary, widely dispersed and, in many cases, endangered. These plants seem to represent a low return on labour. Alternatively, in southwest Asia, large-seeded cereals and legumes provided more obvious candidates for early human harvesting. The cereals of the Fertile Crescent possessed a weak seed dispersal mechanism, awn and brittle-rachis dispersal, which only disperses seeds across a short distance[5]. Hence, sibling competition and unpredictably arid climates likely selected for larger seeds with greater seed provisioning. Hygroscopic burying by awns (trypanocarpy) may have also selected for larger seeds in cereals and rice[6]. As a result of short distance seed dispersal, these cereals naturally cluster into dense monodominant "natural stands almost as dense as a cultivated wheat field"[7]. Hillman[8] demonstrated that these wild homogenous fields can be easily harvested with similar yields as early cultivated fields. Scholars have suggested that these natural monodominant fields were one of the most important factors in large-seeded cereal domestication[6]. In this paper, we propose a model that suggests that small-seeded wild plants evolved for seed dispersal by grazing animals (Figs. 1 and 2; Supplementary Table 1), and, consequently, ecological factors in the past led to different vegetation communities than what exists at present. This realization provides an explanation for: (1) why humans targeted these specific plants; (2) how they first started harvesting them; and (3) why specific traits changed under early cultivation, including how dormancy was broken.

Endozoochory refers to seed dispersal by animal ingestion. It occurs when seeds are able to pass through the digestive tract of an animal while remaining viable, and are thus dispersed away from the parent plant in the animal's dung. Gravity, wind or water dispersal may move the small seeds of many crop progenitors with limited success. However, Janzen's 'foliage as fruit' hypothesis[9] best explains the dispersal mechanism for many grain crop progenitors. Janzen hypothesized that they evolved to take advantage of grazers, who inadvertently consume and disperse the seeds while eating leaves and stems. The progenitors of many small-seeded domesticated grains share a suite of traits that are characteristic of endozoochoric dispersal by ruminants, including: (1) displaying seeds on the top of the plant; (2) high rates of dormancy; (3) synchronistic ripening; (4) lack of lineage-specific compounds or other anti-herbivory defences; (5) rapid annual growth; (6) extremely high numbers of offspring; (7) small seed size (usually <2.0 mm); (8) round seeds; (9) smooth seed surfaces; and, in most cases, (10) lack of or delayed dehiscence[9]. Plants evolve larger seeds with greater provisioning as a way to mitigate sibling and interspecies competition, but constraints of a seed dispersal mechanism or heavy seed predation often force plants to maintain smaller seeds[10–12]. Animal dispersal can direct the spread of seeds to target sites, such as river edges or flood plains, where conditions are ideal for colonization, depositing them in nitrogen-rich packages of dung[10]. Likewise, this dispersal strategy helps plants avoid high density-dependent mortality, as laid out in the Janzen–Connell hypothesis[13–15]. The evolutionary advantage of greater gene flow through seed dispersal, coupled with higher success rates for offspring survival, pushed plants to evolve traits for animal dispersal.

[1]Archaeology Department, Max Planck Institute for the Science of Human History, Jena, Germany. [2]Horticulture Section, School of Integrative Plant Sciences, Cornell University, Ithaca, NY, USA. [3]Department of Anthropology, Washington University in St. Louis, St. Louis, MO, USA.
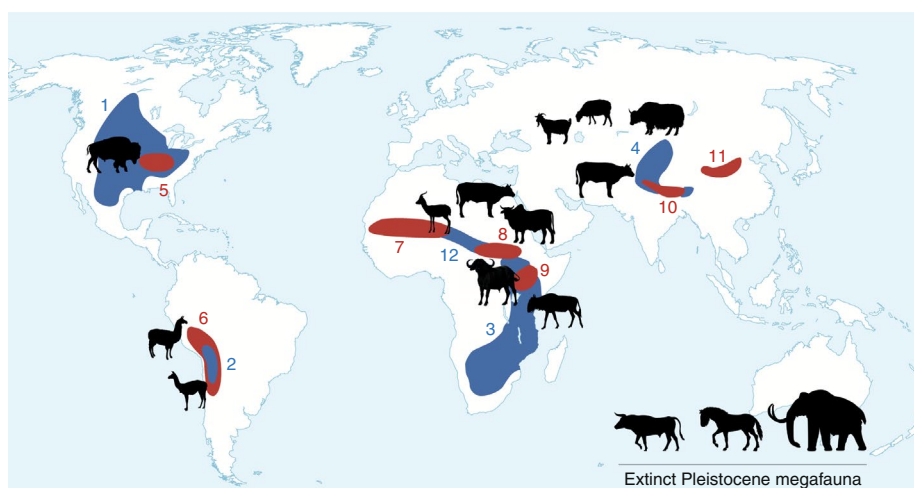*e-mail: Spengler@shh.mpg.de

Fig. 1 | Centres or regions of small-seeded grain domestication in relation to major ranges of extant ungulates. (1) Holocene range of bison; (2) presumed wild range of camalids; (3) presumed wild range of wildebeests; (4) core range of modern herded yaks; (5) centre of domestication of the Eastern Agricultural Complex; (6) domestication range for quinoa; (7) presumed domestication range for pearl millet; (8) presumed domestication range for *sorghum*; (9) presumed domestication range for finger millet; (10) presumed domestication range for buckwheat; (11) domestication range for broomcorn and foxtail millet; and (12) rough central zone for the large grazers of the Sahel. Extinct Pleistocene megafaunal mammals also need to be considered in this model, as these plants were dispersed by them until the Holocene. Paleontological studies better illustrate the ranges for many of these extinct grazers[90].
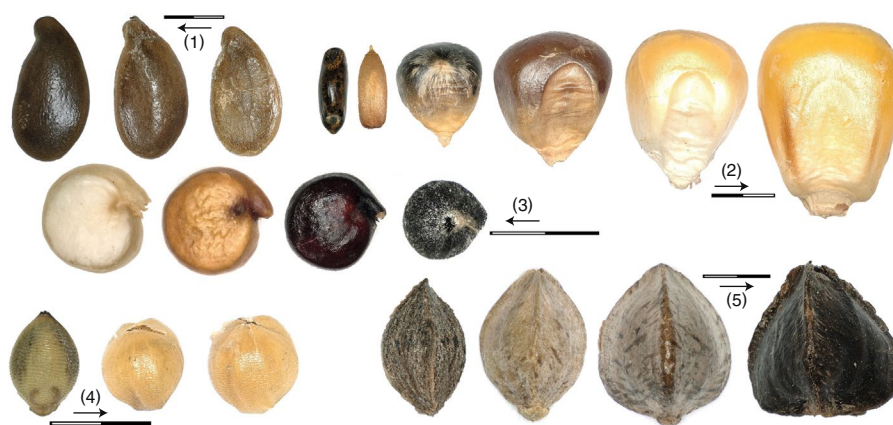

Fig. 2 | Modern seeds simulating the process towards domestication in several globally important economic crops. (1) *Linum bienne* Mill. (USDA accession No. PI 253971), the proposed progenitor of flax, and two landraces of *L. usitatissimum*, collectively illustrating the process towards domestication; (2) teosinte (*Z. mays* ssp. *parviglumis*), and four landraces of maize (*Z. mays* ssp. *mays*) simplistically modelling the domestication pathway; (3) a member of the *C. album* complex (with fruit coat) and three landraces of quinoa (*C. quinoa*), representing the domestication process; (4) *Setaria viridis* (L.) P. Beauv. and two specimens of foxtail millet (*S. italica*); and (5) a seed of buckwheat (*F. esculentum*, either ssp. *ancestralis* or a feral specimen collected from Yunnan, China), and three examples of landraces.

During the Eocene, annual herbaceous angiosperms radiated and diversified, developing new anti-herbivory defences, including high phytolith production[16,17]. In response, herbivores evolved ruminant digestive systems and grinding teeth, allowing them to consume silicone-rich vegetation[11,16,18]. The restrictive caecum of ruminant grazers holds back large plant material, including large seeds, for double digestion and fermentation. Because of this coevolutionary relationship, ruminant-dispersed seeds remain small and retain a hard testa, pericarp or palea and lemma in Panicoids, allowing them to effectively evade digestion[9]. Crops with endozoochoric progenitors include chenopods, notably quinoa (*Chenopodium quinoa* Willd.), huazontle (*Chenopodium nuttalliae* Saff.) and the extinct *Chenopodium berlandieri* ssp. *jonesianum* Smith and Funk; *Amaranthus* spp.; at least two Asteraceae, sunflower (*Helianthus annuus* L.) and sumpweed (*Iva annua* var. *macrocarpa* S.F. Blake);

and a number of small-seeded grasses, many of which are in the Panicoid clade, collectively referred to as millets. Additional examples include *Hordeum pusillum* Nutt.; *Polygonum erectum* ssp. *watsoniae* N.G. Muell.; and the buckwheats (*Fagopyrum* spp.; see also Supplementary Table 1 and Fig. 1). Teosinte (*Zea mays* ssp. *parviglumis* Iltis and Doebley), the wild progenitor of maize, also shares many of these characteristics, although with larger seeds.

Most of these small-seeded grasses and forbs rarely appear naturally in dense stands, and some wild progenitors are rare or endangered today[19–21]. The loss of seed dispersers often leads to reduced gene flow, reduction in genetic diversity, and fragmentary and isolated populations[22,23]. The extinction of a seed disperser can cause corollary extinctions in the plants that it dispersed; in some cases, plants evolve larger or smaller seeds in order to recruit new seed dispersers[24–26]—a process analogous to the recruitment of

humans during domestication. The progenitors for many small-seeded crops, such as *Panicum miliaceum* L. (broomcorn millet), are unknown or extinct[19,27]. Likewise, the progenitor for domesticated erect knotweed is very rare, only existing in fragmentary populations along river floodplains where interspecies competition is reduced by seasonal flooding[28]. Small[29] noted that wild or feral *Cannabis sativa* L. plants thrive in areas of heavy herd animal activity, and he theorized that megafaunal grazers were the natural dispersers for the progenitors. He also theorized that it could have been an easy jump from dense, riverside populations of cannabis deposited by wild ungulates to camp follower plants that eventually adopted humans as their dispersal mechanisms.

The late Pleistocene extinctions had dramatic ramifications on vegetation communities, notably through the loss of seed-dispersal services[23,24,30]. As a response to these megafaunal extinctions, humans became surrogate dispersers for many extant trees with large fleshy fruits[31], and we argue that a similar process occurred in grain crops. As with arboreal communities, herbaceous plant communities were dramatically altered when the large herds of megafaunal grazers became extinct. In some cases, humans or human-maintained herds have shifted vegetation communities back in favour of megafaunal dispersed species[26,32,33]. We define megafauna as any animal that reaches 40 kg at maturity; although, some of the grazers that fit into our discussion fall on the lower end of that scale, including sheep and some gazelle. Small-seeded endozoochoric plants express greater fitness on anthropogenic landscapes and are often found in pastures, agricultural fields or near settlements, hence Anderson's dump-heap hypothesis[34]. Anderson recognized the fact that the progenitors for the small-seeded grain crops thrive in disturbed soils near human occupation and suggested that these plants grew in dense clusters near kitchen middens, where highly fertilized soil was mixed with seeds and other domestic refuse. Some aspects of his theory fit well into the endozoochoric dispersal model. The only natural ecosystems where many crop progenitors grow today are frequently disturbed riverbanks, leading many scholars to hypothesize that floodplain ecology played an important role in domestication[28,35–37]. As Rindos[38] pointed out though, riverside ecologies mimic cultivated fields and weeds, or even non-obligate domesticates, and may be able to persist in these areas long after fields are abandoned. While the seeds of some crop progenitors can be dispersed by floods, many clearly express a syndrome of traits characteristic of ruminant endozoochory, a dispersal strategy that has been largely ignored in domestication studies.

A switch from mechanical dehiscence or senescence to human-mitigated seed dispersal is clearly a factor in the domestication of certain crops, such as large-seeded legumes and grains (wheat, barley, rice, peas and so on). Many small-seeded crops on the other hand have weak shattering mechanisms in their wild state (Fig. 3). Most *Chenopodium* spp., *Amaranthus* spp., non-wind dispersed Asteraceae, *Zea* spp. and *P. erectum* fruits and seeds are non-shattering in their wild state (Supplementary Fig. 1). This lack of dehiscence only results in the separation of the seeds after the plant has senesced and the likelihood of animal-based dispersal is reduced. *Fagopyrum esculentum* Moench fruits have weak pedicels in their wild state; however, they are not directly comparable with shattering inflorescences, as seen in the cereals[39]. Additionally, many Panicoid grasses in temperate zones retain their seeds until well into the winter, long after they reach full ripeness. The exceptions are informative as well; for example, some wild *Setaria* species have a weak shattering trait in the wild[40], but they also have adaptations for exozoochoric dispersal (such as adherence to animal fur), requiring easy separation of the caryopsis from the plant. Many studies have shown that the earliest traits of domestication are linked to a shift from a natural to an anthropogenic seed dispersal strategy[41,42]. Therefore, understanding the natural seed dispersal strategies for small, dry-fruited herbaceous plants is the key to understanding

Fig. 3 | Mature seeds or fruits adhere to senesced wild crop relatives in the manner of domesticated grains that 'wait for the harvester'. Clockwise from top left: *Setaria faberi* R.A.W. Herrm. (foxtail millet relative); *Eleusine indica* (L.) Gaertn. (finger millet relative); *Panicum virgatum* L. (broomcorn millet relative); *P. erectum* L. (domesticated erect knotweed progenitor); *C. album* (domesticated chenopod relative); and *I. annua* L. (domesticated sumpweed progenitor). All photos were taken in late October, 2018, in Ithaca, New York, USA.

how, where and why these specific plants evolved to accommodate human dispersal.

Gene flow and seed dispersal

The success of anthropogenic gene flow, through seed saving, sowing and dispersal, is a prominent driver in evolution under cultivation. Selective pressures were strong enough that plants shifted their dispersal mechanisms from their natural states to anthropogenic dispersal, providing a greater adaptive advantage. We argue that the evolutionary shift between dispersal strategies was facilitated by the fact that: (1) humans are expert seed dispersers; and (2) many of the seed dispersal strategies of our crop progenitors were weakened by megafaunal extinctions at the beginning of the Holocene. Low rates of gene flow or population fragmentation will lead to inbreeding depression and loss of fitness[43]. Some scholars have gone so far as to suggest that gene flow is the main driver of plant evolution writ large[43,44] and that gene flow promotes adaptation, diversification and evolution[45–47]. Lack of seed dispersal increases competition pressures near a plant and makes the colonization of new areas impossible. At the time when many crops recruited humans as their new dispersers, there is evidence that some crop progenitors were already experiencing significant population fragmentation and reduced gene flow—this is most evident when looking at large-fruiting arboreal crops[22,30,31] and squash[23]. Given the demise of so many potential seed dispersers at the end of the Pleistocene, the genetic diversity of ancient crop progenitor populations across this boundary should be a focus of future study.

Even though plant species may appear sedentary, from an evolutionary perspective they can have extreme mobility. Mobility through seed dispersal was important during the interglacial periods of the Pleistocene and in the context of continual aridity or

humidity and thermal climate changes from the Eocene through the Miocene[16,48]. The most impressive migrations in the history of life on Earth are the series of repeated north–south races against the ice[49]. Megafaunal mammals represented effective seed dispersal mechanisms, as is evident from the numerous large-fruiting tree species that still exist today[50]. Biologists have extensively studied fleshy fruits as adaptations for seed dispersal; however, limited research has gone into the study of dry fruit endozoochory by herbivores[50,51]. Scholars have noted that, despite high seed losses, this form of seed dispersal can cause gene flow over great distances and rapid plant migration[51–53]. The time depth of this seed dispersal mechanism in small-seeded annuals is illustrated in Supplementary Table 2 through subfossil evidence.

Evidence for endozoochoric dispersal of crop progenitors

Studies have demonstrated the effectiveness of endozoochoric dispersal of crop progenitors using a variety of methods. Regulated feeding experiments test seed germinability post-digestion. Some of these studies also include control seed batches, which show the effects of passage through a digestive system on germination rates. Another approach is to sample dung from free-ranging animals and then test the germinability of the seeds they contain, thus demonstrating both animal preference and seed viability. Supplementary Table 3 synthesizes studies in which crop progenitors or close relatives were shown to germinate after passing through the digestive systems of ruminants. Close relatives of small-seeded crops frequently remain viable after consumption by both wild and domesticated ruminants. In two case studies, consumption of *Polygonum* by yaks and consumption of *Chenopodium* by either yaks or sheep, the post-digestion germination rate was higher than the control[12]. However, passing through a digestive system does not necessarily need to result in higher germination rates in order for endozoochory to be an evolutionarily successful strategy. Dispersal, especially when directed to an open, nitrogen-rich microenvironment, is an evolutionarily significant benefit that may outweigh the cost of limited seed loss[54], although the dynamics of this trade-off should be explored experimentally. Feeding experiments of wild relatives of small-seeded grains to birds also illustrate catastrophic seed death, clearly eliminating birds as viable dispersers[55].

Germination studies of the dung of free-ranging animals add striking support to our hypothesis. Wicklow and Zac[56] found that of the eight species that germinated from 54 g of pronghorn (*Antilocapra americana*) dung, five of them were close relatives of native small-seeded crops (*Amaranthus*, *Chenopodium* and *Polygonum*). Of the 101 species that Eycott and colleagues[57] observed germinating from four deer species, *Chenopodium album* L. was by far the most abundant, producing 2,627 seedlings out of a total of 9,648, despite the fact that this species has not been recorded in the forest where the study was conducted. A study of six wild ungulates on the Serengeti plains identified *Ergrostis* spp. (tef relatives) and *Digitaria scalarum* (Schweinf.) Chiov. (a fonio relative) to be among the viable seeds in wild ungulate dung[58]. Another study demonstrated that *Pennisetum clandestinum* Hochst. *ex* Chiov. (a relative of pearl millet) can pass through the digestive tract of cattle and remain viable[59]. Free-ranging bison on a tallgrass prairie dispersed the seeds of *H. pusillum* and *I. annua*, two North American crop progenitors[60].

In addition, many studies looking at the presence of seeds in both modern and ancient herd animal dung show how readily the seeds from these progenitor clades were or are spread by grazers. The deeper time depth of this seed dispersal process has been demonstrated by studies of frozen or dessicated animal stomach contents and archaeological remains of dung fuel fires (Supplementary Table 2). Both modern and ancient herbivore dung have consistently yielded abundant dry-fruited seeds[60–64]. In a dung study on the Eurasian steppe, 641 *C. album* seeds were recovered out of

1,291 seeds in total, despite the fact that chenopods were not even observed in the area where the dung was collected[63]. The success of endozoochory in *Chenopodium* spp. is also reflected by fact that it is persistently the most abundant seed in archaeobotanical assemblages, especially in parts of the world where dung is readily used as fuel[64]. Some of these studies have noted specific phenotypic traits among these seeds that make them particularly well adapted to ruminant endozoochory, notably seeds ranging between 1.0–2.0 mm, rounded in shape, have a smooth surface and have hardened testa or glumes[53,60]. The restrictive ruminant caecum only permits small seeds to pass through the digestive system, holding back larger plant material for secondary digestion[65,66]. Therefore, the ruminant digestive system, with secondary digestion and fermentation, is likely the explanation as to why so many of our grain crops have small seeds.

The role of megafaunal hotspots in domestication

Seeds are not dispersed to random locations by endozoochory; they are deposited, through directed dispersal, in open, nitrogen-rich microenvironments, sometimes referred to as 'hotspots'[67–70]. In the Eurasian steppe and foothills, dense stands of *C. album*, *Malva neglecta* Wallr. and *Polygonum* spp. tend to mark seasonally occupied herder camps or areas of heavy herd animal activity[63]. The dense clusters of nettles in European pastures illustrate vegetation homogenization through heavy herbivory. Heavy herbivory removes competitive species, allowing for effective colonization by endozoochoric plants, which also benefit from nutrient-rich dung deposits[71]. Herd animal pens from previous years tend to be dominated by dense homogenous vegetation communities of a single species[63,64]. Herding activity across Eurasia leads to the formation of ecologically rich pockets and applies strong evolutionary forces on plant communities. Ecological studies of the impacts of herd animal grazing in Mongolia also identified areas of greater biomass (or hotspots) near locations where herd animals congregate, notably around water sources[72].

The construction of endozoochoric-dominated vegetation communities by ruminants is not just a phenomenon of the Eurasian steppe. Knapp et al.[71] have documented bison preferentially re-grazing the same areas, preventing the tall grasses from fully rebounding, and creating openings for forbs and annual grasses. Bison could have concentrated communities of crop progenitors (most of which are forbs) in the prairies of eastern North America. Kunzar[20] theorized the role of this coevolutionary process for the domestication of *Chenopodium* and *Amaranthus* in the Andes, linking the process to camelid herding and conducting experimental studies of sheep and goats in the region. He went on to observe the same phenomenon of homogenous and concentrated plant communities among Navaho herders' corals in the North American southwest[73]. Studies of archaeological Bolivian camelid dung found high abundances of seeds, notably from small-seeded Poaceae, Malvaceae, Fabaceae and *Chenopodium*[74]. Lezama-Núñez et al.[75] provide six case studies from across the Americas of herd animal grazing resulting in evolutionary responses by plants, one of which is the ongoing process of domestication among reindeer herders. Andrews et al.[76] studied the ecological impacts of reindeer-constructed vegetation pockets and they were able to date the concentrations of dung in these pastoral hotspots back 5,000 years.

Recent research has demonstrated that eastern African pastoralism also leads to nutrient-rich patches on the landscape. Soil chemistry and microstratigraphy research by Marshall et al.[67] demonstrates that repeated grazing practices by herders in northeast Africa shaped these hotspots. They show that areas of heavy herd animal activity around ancient pastoralist settlements have higher levels of nitrogen and phosphorus, which promote plant growth. These nutrient hotspots support a specific vegetation community that is different from the surrounding matrix vegetation of dry grasslands.

Both wild and domesticated ungulates are known to disperse the viable progenitors of African crops[58,59,77]. Case studies from around the world show that the herding of domesticated ungulates or the grazing of wild ungulate herds concentrates endozoochoric plants in specific pockets on the landscape. We argue that this heavy herbivory also directed evolutionary processes in the plants, and those selective forces changed once humans became the surrogate seed dispersers. Plant communities on these hotspots are often dense and homogenous, containing only one or a few endozoochoric species that could easily have been harvested by foragers (see the 'Breaking Dormancy' section).

Further investigation of these mechanisms is warranted. For example, the last of North Asia's large-scale wild megafaunal herds went extinct or became endangered during the mid to late Holocene, including *Bos primigenius*, *Gazelle* spp. and several wild *Equus*. These herds were largely pushed to extinction as human population increased in response to the domestication and cultivation of *Setaria italica* (L.) P. Beauv. and *P. miliaceum* across the north China grasslands. Likewise, the domestication of the buckwheats in the southern Himalayas appears to have only taken place after the intensification of yak and cow herding. Feeding studies have demonstrated that yaks can disperse the viable seeds of *Polygonum* and *Rumex* species, which are close cousins of buckwheat[12]. Likewise, dense stands of *Polygonum* plants often form in abandoned herding pens in the foothills of the Pamir Mountains. The possibility that many of South Asia's small-seeded grains are linked to large-mammal endozoochory deserves further consideration as well. Teosinte, the wild progenitor of maize, is recognized globally as an excellent fodder crop[78]. Scholars have puzzled over why humans were drawn to the unusually unappealing attributes of teosinte seeds[79]. The dynamics described in our model may help explain how teosinte was first encountered and cultivated by foragers, as well as explaining why the progenitor form has such hard, indigestible seed defences. Scholars have already theorized that alfalfa (*Medicago sativa* L.) and clover (*Melilotus officinalis* (L.) Lam. *Trifolium* spp.) were domesticated through pastoral activities[80].

Breaking dormancy

One of the greatest mysteries of plant domestication is the question of how dormancy was overcome by early cultivators[81,82]. Sowing a field with seeds that express low rates of first-year germination will result in extremely low yields and possibly net losses. Seed dormancy is important in the wild because, in the absence of successful dispersal through space, seeds are all dropped below the parent plant. Without dormancy, a few years of failed dispersal could be devastating to the population, especially if they are also in competition with larger seeded species which are likely to exhibit faster germination and early growth because of their larger energy stores[83]. However, if the seeds can disperse through time (through dormancy), then sibling competition is somewhat mitigated[84]. For species that grow in unpredictable environments, dormancy has been theorized as an alternative to other dispersal strategies[85–87]. However, in the case of endozoochory, dormancy is an inherent component of the dispersal strategy. Chemical digestion can scarify seeds, thus breaking dormancy, while a tough fruit or seed coat is necessary for the seed to avoid being completely digested[88]. Numerous studies have shown that the wild progenitors of small-seeded crops that express high dormancy rates are viable after digestion, and some have higher germination rates post-digestion (Supplementary Table 3). Ruminant endozoochory and dormancy are so well adapted together that they evolved in parallel among a large number of herbaceous annual plant clades. Tiffney and Mazer[11] even suggest that dormancy may have evolved as a prerequisite for angiosperms to adopt seed-dispersal-based mutualism and ultimately diversify and radiate; they also note that, without dormancy, "a trip through a gut may have spelled death".

While dormancy increases fitness in many wild environments, it significantly reduces fitness under cultivation. Ladizinsky[82] suggested that the only possible way early cultivators could have broken dormancy was if they found a naturally occurring population with low dormancy or some naturally non-dormant members, a view that is not altogether satisfying[41]. An alternative explanation for how the original loss of dormancy under cultivation took place is that early plant cultivators relied on seeds stored in the soil seed bank. This means that the earliest cultivation of annuals may have relied on reduced human mobility and maintenance of already dense wild stands of endozoochoric plants. These naturally dense stands of animal-dispersed plants would have been concentrated near water sources where herbivory was highest. High herbivory served to eliminate competition for endozoochoric plants and opened up new disturbed soil for the seeds, which were deposited in a nitrogen-rich package of dung. When humans settled near these water sources, they were already in the vicinity of dense stands of endozoochoric-dispersed plants. Maintaining large dense stands that were located in nutrient-enriched hotspots, which already had well-established seed banks, would have allowed people to temporarily bypass high losses due to dormancy. Then, as maintenance became increasingly more intense, dormancy was gradually lost along with thick seed coats and small seed sizes as a result of selective pressures under cultivation. This process is analogous to how most archaeobotanists envision the loss of brittle rachises in cereals occurring; as Harlan and Zohary[7] demonstrated, large dense wild stands of cereals could easily have been harvested.

We present the following model for how dormancy was broken and seed size increased in small-seeded annuals: as traits of the former dispersal mechanism, neither small size nor dormancy were necessary for survival under cultivation. Both would have been selected against during cultivation by compounding unconscious human selective forces, including: (1) thinning stands[28]; (2) densely planting fields; (3) tilling or overturning fields, whereby seeds are forced deeper into the soil; and (4) sowing or directly burying seeds. Thinning selects for early-germinating and fast-growing seedlings. The deeper the seed is buried, the greater the need for energy stores to reach the surface. When mother plants must allocate their limited resources to seed or fruit coat production, it reduces energy available for nutritive material for the seedling[89]. Hence, thick seed coats were lost under domestication because they represent an energetically costly and maladaptive trait in an anthropogenic niche. Interestingly, the dense stands of these plants that would have existed before human intervention expressed some of the same selective forces as a cultivated field, so the parallel evolution of similar traits as seen under domestication may have begun before human cultivation.

Conclusions

Studying the natural seed dispersal mechanisms of the progenitors of our domesticated crops helps us understand the process of early domestication. The model we present here does not exclude the possibility of other pathways towards domestication, but it does provide a coherent evolutionary model explaining how the process could have unfolded for these small-seeded annuals. Early plant domestication is primarily a switch from a wild to an anthropogenic dispersal mechanism; therefore, the domestication of millets, chenopods, knotweed, amaranth and buckwheat represents a switch from endozoochory to human cultivation. Accompanying this switch, the key characteristics associated with the natural dispersal strategies were lost or reduced, including indigestible seed protections, high levels of dormancy and small seeds. Unlike the large-seeded cereals, the small-seeded grains that mid-Holocene humans targeted often exist today in small fragmentary populations that could not have been effectively harvested due to low plant densities. They also require labour-intensive processing before they can be consumed. In this

paper, we demonstrate that ruminant grazers were likely responsible for concentrating small-seeded plants into homogenous stands that humans could effectively harvest. Ultimately, the switch from a two-part seed dispersal, through time and space, to human-driven seed dispersal rapidly led to the loss of dormancy and a thinning of the seed coat, which was no longer necessary and energetically costly. This model for small-seeded grain domestication attempts to explain: (1) why and how seed coat thickness and dormancy changed under early human cultivation; and (2) why humans selected small-seeded plants that currently exist in fragmentary and dispersed populations.

The experimental and ecological studies cited here were not designed to explore the role of endozoorchory in plant domestication, and thus they provide only strong circumstantial support for our model. Ecologists have studied the evolutionary processes described in this paper, but not with the intention of understanding domestication. Experimental feeding studies should be conducted with crop progenitors and relevant seed dispersers (or their closest extant relatives). Unlike most previous studies, these should include control batches and test germinability to measure the effects on seed viability of passage through the gut. Populations grown from passed seeds in enriched openings should then be compared to an established parent population in terms of subsequent growth and seed production so that the trade-off between seed death during passage through the gut and dispersal to hotspots can be quantified. Additionally, the distribution, density and genetic diversity of crop progenitors on landscapes with and without megafaunal seed dispersers should be rigorously compared.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

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Author contributions

Competing interests

Additional information

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Corresponding author(s):	Robert N. Spengler III
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Study description	This study is composed of a collection of previously published studies of seed germination after digestion and endozoochory analyses.
Research sample	The sample for this research is a comprehensive accumulation of published studies that discuss the viability of endozoochoric seeds from herbaceous plants after ruminant digestion.
Sampling strategy	No statistical methods were preformed, and the studies included in the sample were comprehensive. We did not exclude and studies because they did not support our conclusions. In every case, the study the we reference in the supplementary tables supports the idea that small-seeded herbaceous plants are evolved for endozoochoric seed dispersal.
Data collection	All of the data that we present in this perspectives piece has been previously published in other sources and we collected all relevant publications of endozoochoric studies.
Timing	We have been collecting references and formulating our model for over a year. Any publications published after November of 2018 are not included in this manuscript.
Data exclusions	We did not exclude any data from this study. All known endozoochoric studies illustrate the same conclusions. While some studies demonstrate a greater rate of germination post digestion than prior to digestion, all studies demonstrate that suggest of endozoochory for seed dispersal in the progenitors of our modern crops.
Non-participation	We had no human participants in this study.
Randomization	There were no human participants in this study; the ramifications of our study for understanding domestication processes rely on a greater understanding of the seed dispersal processes in these plant - ultimately leading to a setting that would have facilitated human cultivation.

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