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The next era of crop domestication starts now

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Current food systems are challenged by relying on a few input-intensive, staple crops. The prioritization of yield and the loss of diversity during the recent history of domestication has created contemporary crops and cropping systems that are ecologically unsustainable, vulnerable to climate change, nutrient poor, and socially inequitable. For decades, scientists have proposed diversity as a solution to address these challenges to global food security. Here, we outline the possibilities for a new era of crop domestication, focused on broadening the palette of crop diversity, that engages and benefits the three elements of domestication: crops, ecosystems, and humans. We explore how the suite of tools and technologies at hand can be applied to renew diversity in existing crops, improve underutilized crops, and domesticate new crops to bolster genetic, agroecosystem, and food system diversity. Implementing the new era of domestication requires that researchers, funders, and policymakers boldly invest in basic and translational research. Humans need more diverse food systems in the Anthropocene—the process of domestication can help build them.

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Why is Domestication Critical to Address the Agricultural Challenges of the Anthropocene?

The Process of Domestication Shapes Diversity. Crop domestication is an ongoing process of building and sustaining dynamic, coevolutionary relationships between plants and humans (1). The degree of interdependence in such relationships varies over time and across human practices and cycles of selection, ranging from use of wild harvested species to human cultivation to selective breeding programs, with crops shifting across a spectrum of "wild," "semi-domesticated," "domesticated," and "improved"/"elite" (*SI Appendix*, Table S1). The domestication triangle [sensu (2, 3)], which comprises (i) the genetic and phenotypic particularities of crop plants, (ii) human agronomic and cultural practices, and (iii) ecological and geographical factors, illustrates the complexity of ongoing crop domestication processes across scales [(4); Fig. 1]. Together, the three elements of domestication (i.e., crops, humans, and ecosystems) help explain how the beginnings of agriculture resulted in major transitions in human history, facilitating the rise of dominant contemporary societies and food systems (5, 6). Yet while crop domestication enabled intensified production regimes that could sustain large populations, it has also contributed to the depletion of genetic, agroecosystem, and dietary diversity, and subsequent negative ecological and social impacts, as summarized below.

Crop diversity—from genetic diversity within crops, to diversity within fields and agroecosystems, to diversity of foods within diets and across regions—has frequently been proposed as an answer, even a panacea, to the problems faced by modern agricultural and food systems (3, 7–15). There is a general agreement that we do not have enough—or the right kinds of—crop diversity in current agricultural systems to drive the adaptation necessary to sustain yields under changing climates (3, 9). And, although crop diversity is linked to improved nutrition (13, 15) as well as economic resilience (16), current major crops are the foundation of agricultural and food systems that diminish, rather than enhance, diversity at the landscape scale (17).

Given the scientific consensus that increased crop diversity is an important solution to many, though not all, of the challenges facing our global food systems, it is now time to shift the conversation to key processes through which we can realize this goal. Food systems encompass the full suite of people and actions that produce, process, distribute, market, and consume foods. Narrowing in on agricultural crop production systems, two primary pathways for change are evident: agronomic management and crop domestication. Cropping system diversity will play a critical role in the future success of agriculture and agronomic management practices have become increasingly rich—including polyculture and crop rotation alongside organic, no till, hydroponic, vertical, and biodynamic farming (4, 18, 19). However, in this perspective, we focus on the second pathway, outlining the possibilities for broadening the palette of food crop diversity through a new era of crop domestication that engages and benefits the three elements of domestication: crops, ecosystems, and humans.

Current and Future Food Systems Are Challenged by Relying on a Few Input-Intensive, Staple Crops. In 1983, the preeminent American agronomist Norman Borlaug wrote, "I am convinced that the eight billion people projected to be living

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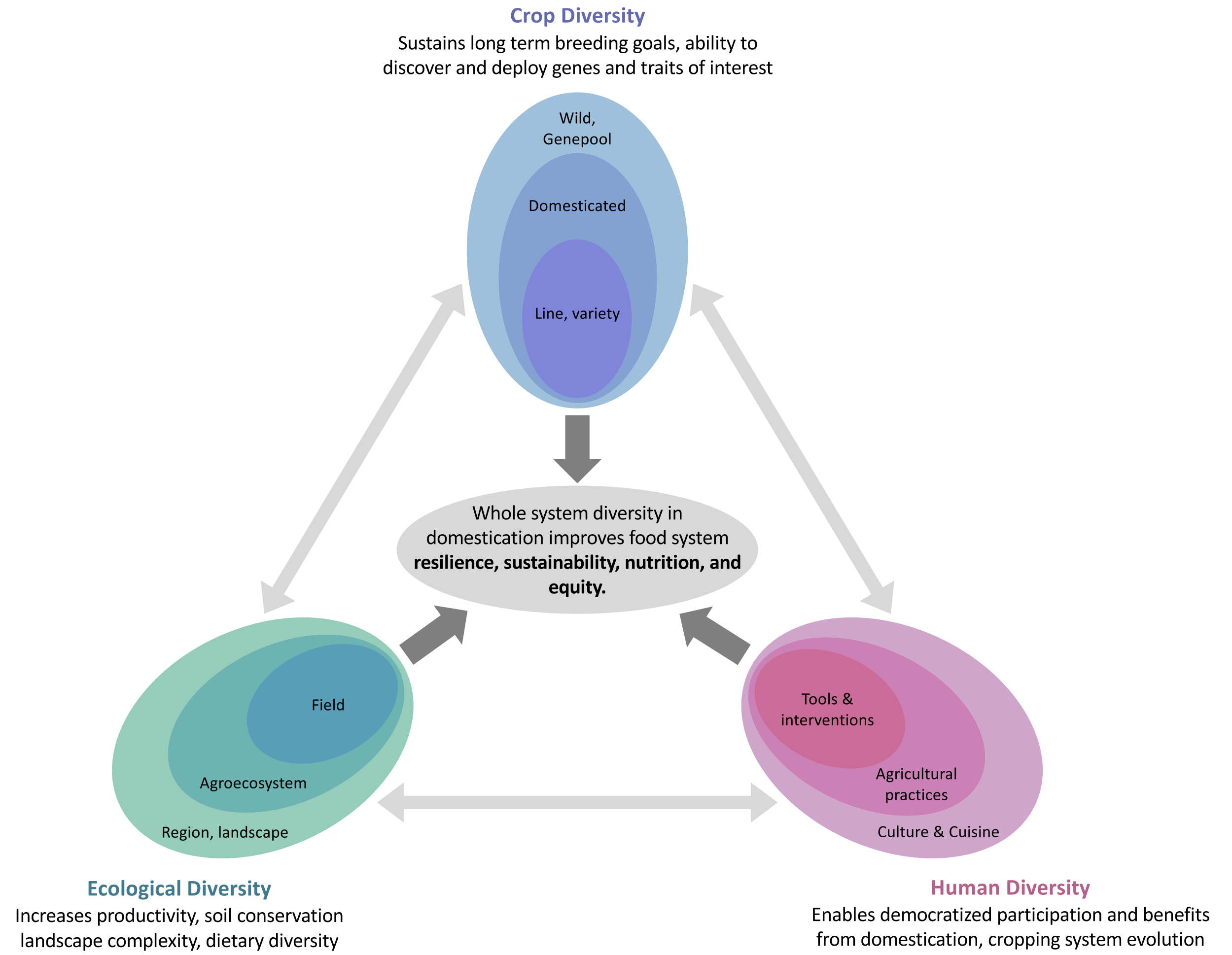

Fig. 1. The domestication triangle [sensu (2, 3)] provides a framework for describing the diversity of factors present within the process of domestication. The triangle is comprised of the genetic particularities of crop plants, ecological and geographical factors, human agronomic and cultural practices, and the interrelations between these three elements. Diversity within the domestication process is hierarchical (4). Crop diversity encompasses diversity within lines/varieties, within the crop as a whole, and across the entire crop genepool, which includes crop wild relatives. Ecological diversity spans from the level of a single field, to agroecosystems, which incorporate multiple fields and their surrounding areas, to regions and landscapes. Human diversity includes the tools and interventions used in domestication, agricultural practices and forms of labor, and culture and cuisine that drive domestication. The domestication triangle acknowledges that genetic diversity and biodiversity at the species level interacts with diversity in human systems to shape diversity in domesticates and agroecosystems. For example, the agricultural practice of polyculture increases ecological diversity within a field and can drive the demand for new crop diversity that maximizes yield under this cultivation scheme. Alternatively, cultural demands for specific nutrient content in food such as "complete proteins" or vitamin A can drive breeding programs for underutilized crops that fill these gaps, thereby increasing the species richness of ecological systems. This depiction of domestication makes it clear that the challenges facing modern food systems–creating crops that are resilient, sustainable, nutritional, and equitable–lie at the intersection of the three elements of domestication, and can only be overcome by engaging factors from across each of these elements to improve whole system diversity in domestication.

40 to 50 years from now will continue to find most of their sustenance from the same plant species that supply most of our food needs now" (20). Not only was Borlaug's prediction correct, but in the past five decades, our reliance on these staple crop species has intensified: Human diets have become 36% more similar across the globe (21). As of 2019, the global population relied on rice, wheat, and maize for more than 40% of its calories, with a handful of crops—annual cereals, legumes, sugarcane, and roots/tubers—making up more than 75% of plant-based calories (22). Furthermore, the increased cultivation of and reliance on just a few crops has contributed to the loss and imperilment of critical agrobiodiversity (23) and accompanying biocultural knowledge (24).

For millennia, crop domestication was primarily directed by small-scale farmers. However, in the twentieth century, centralized agricultural programs sought to improve global food security. These programs prioritized yield gains through intensive breeding practices, the development of hybrid crops, investments in irrigation schemes, the invention and subsidization of synthetic fertilizers, mechanized crop management, and the release of "Green Revolution" wheat and rice cultivars bred to take advantage of these modern inputs (25–27). Such efforts, which focused on a handful of staple crop species, were, by some numbers, wildly successful: between 1940 and 1980, production of major crops in the United States increased 242% while using only 3% more cropland (20). Since that time, a feedback loop of funding, research, breeding, and markets and trade has developed that promotes and preserves production of these crops at the global scale (25). However, over the past three decades, yield plateaus have been observed in many staple crops, including rice, wheat, and maize (28). These plateaus are predicted to be exacerbated by climatic changes (29), and current projections indicate that production will not keep pace with rising demand in the coming years (30, 31).

Furthermore, yield improvements for staple crops have often come at the expense of genetic diversity underlying beneficial traits, including abiotic stress tolerance, nutritive value, and pest or disease resistance (7, 26, 32). Today, we face many unanticipated challenges resulting from the history of domestication, including but not limited to: 1) high energetic input costs of agricultural and food systems and unsustainable ecological impacts on the land, water, air, and biodiversity of a limited planet; 2) vulnerability of existing crops and agricultural systems to climate change; 3) lack of adequate nutrition in our food systems; and 4) social inequities arising from the interactions of the first three factors; all of which contribute to the need to change agriculture (33).

1. Unsustainable. Food systems are key contributors to the loss of biodiversity, including agrobiodiversity, seen around the globe (3, 27, 31, 34–38). Agriculture acts as a primary sink for water, nitrogen, and pesticides, and is a leading cause of eutrophication, soil degradation, and land cover and land use change (37, 39–41). The construction of agricultural niche space (42) has led to the simplification of ecosystems and loss of ecosystem functions (17, 19, 43, 44). Globally, agriculture represents a major driver of environmental change, contributing 23% of greenhouse gas emissions (40, 45, 46).

2. Climate vulnerable. Agricultural systems are extremely vulnerable to changes in climate, including increasing temperatures and declining precipitation (47–49), which can affect the intensity and distribution of pest and disease outbreaks (50–52). Collectively, these impacts are expected to reduce yields for a number of primary crops in the next two decades, particularly in semi-arid regions (53, 54). Although individual crops may be more or less vulnerable to changes in climate, dependence on a small number of crops (with limited genetic diversity) and the need for increased investment in reactive adaptation of those species may limit society's ability to explore and develop alternatives (9).

3. Nutrient poor. The lack of diversity in food systems has a negative impact on diet quality and nutrient adequacy (55). We have not made adequate progress toward the UN's Sustainable Development Goal 2, "Zero Hunger" (56). In 2020, some 768 million people faced hunger; this includes 21% of the human population in Africa, 9% of the populations of Asia and Latin America and the Caribbean (57), and 40% of people living in the world's mountainous regions (58). Beyond sheer caloric content, the displacement of nutrient-dense crops with calorie-dense starches has left billions of people lacking adequate nutrients, from protein to critical micronutrients such as iron and vitamin A (26, 38, 59). Malnutrition due to overconsumption of high-calorie foods is also increasingly common, particularly in populations with low socioeconomic status, and the number of countries facing both types of malnutrition is on the rise (31, 38).

4. Inequitable. The benefits of agriculture and threats that impact agriculture are not equally distributed. Many parts of the world, particularly in the tropics and subtropics, have been underserved by modern agriculture: Cultivars bred for high-input and mechanized regimes perform poorly under low-input conditions and suitable lines are not widely accessible (20, 26). Climate change is already impacting geographic regions unequally (60). Agricultural systems in developing regions of Africa, Southeast Asia, Central America, the Pacific, and the Caribbean are predicted to be most severely affected (9) because of their reliance on low-input, rain-fed cropping systems which are contingent upon regular weather patterns (61). These regions are among those facing the fastest growth in both population size and affluence, placing greater pressure on agricultural production and increasing food security risks (57).

The next era of crop domestication must engage the reality of our current social-ecological crisis. Humans need to sustain and accelerate the domestication of new and better crops while remembering past insights and avoiding past mistakes. The livability of the earth, home or "domus" to humans and many other forms of life, including an array of plant species, critically depends on the choices humans make about how we live, including how we eat. As Boivin et al. remind us, "Highlighting a long-term human role in shaping biodiversity does not absolve present day populations of taking responsibility for Earth's environments. Instead, it ... suggests that we should own up to our role in transforming ecosystems and embrace responsible policies befitting a species that has engaged in millennia of ecological modification" (36). Crop domestication has contributed to the challenges food systems now face—yet going forward, it may serve as an important process to build solutions.

How Can Domestication Increase Diversity to Enable Agricultural Change? What Might the Next Era of Crop Domestication Look Like?

Crop Domestication Can (and Must) Be Done Differently to Build Diverse Future Food Systems. Starting now, our food systems must face the demands of the future, shifting focus from maximizing caloric production to maximizing nutrient density, sustainability, climate resilience, and equity (Fig. 1), with the ultimate goal of global nutritional resilience (26, 59, 62). Meeting this goal requires a new era of domestication that will build more diverse food systems. Crop domestication efforts, such as leveraging plant microbiomes and the development of perennial cereals and agroforestry systems, are among the important research goals laid out for this decade that will support long-term resilience (8, 33–35, 63, 64).

Creating crops that support global nutritional resilience requires that we engage in different—meaning at once novel and alternative—methods that benefit interdependent ecological and human systems. We can utilize different technological interventions and breeding approaches across different levels of crop diversity, target different types of crop species and traits that provide ecosystem services, and engage different human systems in diverse geographic locations.

We can utilize different tools and interventions across multiple levels of crop diversity. Diversity within a crop, both genetic and phenotypic, is hierarchical: There is diversity among individuals, among crop lines or varieties, and across the entire genepool, which includes landraces and wild relatives of the same or closely related species (Fig. 1). The tools and technologies that we have available (*SI Appendix*, Table S2) can be used to identify, utilize, and foster diversity across these levels.

Rapid developments in next-generation sequencing (NGS) and third-generation sequencing (TGS) technologies over the past decade have permitted the proliferation of genetic and genomic datasets for a growing number of plant species (65). While sequencing costs and/or the assembly of a reference genome remain a barrier in some cases (particularly for underutilized crops), the limiting factor for other crops is now the collection of phenotypic data. High-throughput phenotyping ("phenomics") represents an important advance (66–70), utilizing sensors on autonomous ground or aerial vehicles to impute plant traits including height and yield in the field, or to complement (or perhaps replace) DNA "fingerprints" with multidimensional phenomic profiles to enable rapid, prediction-based breeding.

The availability of inexpensive sequence data and high-density marker sets has revolutionized our understanding of genotype–phenotype associations and the genetic architecture of agronomically important traits, which is critical for plant breeding (3, 71, 72). Genomic data increase efficiency and mapping resolution in genome-wide association studies [GWAS (73, 74)]. Additionally, examining selective sweeps and population subdivision can also reveal genes underlying less obvious morphological, physiological, and biochemical traits, particularly those with polygenic underpinnings (74, 75), while genome–environment associations (or "environmental GWAS") identify loci correlated with environmental factors, such as precipitation, soil type, or temperature (76, 77). To date, many of these analyses have focused on single-nucleotide polymorphisms (SNPs), but as resequencing and the production of pangenomes has increased in prevalence, so has recognition that structural variants (e.g., inversions, copy number variation, and transposable elements) play an important role in plant adaptation and evolution, including in crop species (78–81).

Genomics-assisted breeding (e.g., marker-assisted selection, genomic selection) enables the prediction of phenotypic performance in genotyped individuals and accelerates crop domestication and improvement (65, 66, 82–85). Genome editing technologies, including CRISPR/Cas9, also have the potential to fast-track both the domestication of new crops and the improvement of existing ones (65, 86–89) through precise alterations to genes underlying traits of interest. For example, de novo domestication might be facilitated via the editing of loci known to be associated with desired domestication traits in nondomesticated plants (86, 90). For existing crops, a new era of "breeding by editing" has been envisioned (91) where novel diversity is introduced into elite lines without transgenesis, deleterious mutations are purged, and novel beneficial variants are created using editing technologies. However, many important traits of interest for breeding (e.g., aspects of yield and quality) are polygenic, while editing approaches are limited to traits controlled by only one or a few loci, and further complexities may arise due to editing-imposed genetic bottlenecks, epistasis, gene-by-environment interactions, and polyploidy (discussed in ref. 90). Practical limitations include the requirement for tissue culture regeneration and transformation protocols (not yet available even for all major crops) and regulatory hurdles. While genome editing techniques represent a boon for research (e.g., for gene discovery and to elucidate genotype–phenotype associations), they provide neither a simple nor complete solution for current breeding challenges.

New technology could also reduce the number of traits to alter genetically in new domesticates and semi-domesticates, focusing breeding attention on yield and quality traits and accelerating the adoption of latecomer crops. For example, many grain crops were bred to be harvested en masse by scythe or by machine, necessitating architectural uniformity and phenological synchronicity. Innovations in small autonomous machines (92) may someday allow asynchronous harvesting (and weeding and planting), thereby reducing the soil compaction and fuel use associated with heavy machinery. Machine vision-based "smart" harvesting (e.g., of individual heads or fruits as they ripen) (93) would allow the design of modern cropping systems that feature greater plasticity of individual plants, genetic variation within crops, and multispecies intercropping: All features of traditional cropping systems with higher habitat complexity than today's simplified agroecosystems.

Of course, to take advantage of agrobiodiversity, we must also heed the urgent calls to conserve it, both in and ex situ (94, 95). While progress toward comprehensive conservation of crop genetic resources is essential, curation and characterization of these genetic resources is also needed to facilitate informed selection of individuals for breeding pipelines (96–98).

We can prioritize different types of crop diversity. The species that make up our current food systems are remarkably homogeneous. While it is estimated that tens of thousands of plant species are edible to humans, only around 2,500 species from 170 taxonomic families have undergone some degree of domestication, with fewer than 300 considered "fully domesticated" (99, 100). To build our future food systems, we must leverage the diversity of plant forms, life histories, and functional traits to support ecosystem services (14, 17, 101, 102).

Our current food systems are dominated by annual crop species. However, with roots that develop over multiple years, perennial plants provide an array of ecosystem services that have the potential to benefit agricultural systems, including carbon sequestration, stabilization of soil, water conservation, and the development of soil microbiomes (40, 103–107). For herbaceous species, efforts toward the perennialization of annual species and the domestication of new perennial crops are in progress (106, 108), and numerous species have been suggested as candidates (see "We Can Domesticate New Species" below). In addition to their ecological benefits, woody crops have been targeted for improvement because of their important role in small-scale and subsistence agriculture, particularly in tropical regions (107, 109).

Root systems, which have the potential to improve yield, decrease fertilizer and irrigation needs, and mitigate the impacts of pathogens and soil conditions (e.g., drought or salinity), are coming into focus as targets for crop improvement (110–113). Grafting, a practice already widely employed for many cucurbit, solanaceous, and woody perennial crops, enables independent selection of traits within root and shoot systems, and can expedite root system breeding (110, 111, 113). The recent advance of grafting in monocots (114), once thought to be biologically impossible, suggests it may soon be applied in important staple crops, including wheat, rice, and bananas (114).

We can work with diverse human systems in different geographic locations. Humans are a critical component of and reason for crop domestication, and our choices have important implications for diversity. There are a range of available choices with regard to the domestication and breeding locations for crops and suites of crops; the sociocultural and agronomic contexts for which crop domesticates are targeted; and the methods for engaging diverse human systems in domestication processes.

Over the past century, public and private plant breeding have been the driving force behind crop domestication (24). Green Revolution rice and wheat cultivars have been rolled out across many locations, but there have been geographic disparities, namely in Africa, and marginal environments in particular have not been effectively served by modern varieties that were bred for favorable conditions (25). Perhaps, this is because programs to revolutionize crop yield have focused on annual cereals that are not able to thrive (despite breeding efforts) on depleted, fragile, or degraded soils—soils in some cases degraded by millennia of raising annual cereals. The next era of domestication can better serve Africa and farmers with limited access to or limited interest in commercial fertilizers by investing in multifunctional agricultural systems that include food crops with a broader range of lifespans, rooting depths, nitrogen acquisition strategies, mycorrhizal associations, and other functional traits. New domestication could lead to a richer set of agroecological options that would allow better matching between crops and cropping systems and diverse geographies, farm sizes, economic systems, and nutritional needs (55, 110).

Meanwhile, domestication performed informally and at the local scale by farmers continues (115). Home gardens also continue to be sites where agrobiodiversity is stewarded (3, 116). Across locations and scales, human systems have traditions of culturally valuing particular plants, and therefore knowledge of these plants, that can contribute to catalyzing and sustaining domestication processes (90). The diversity of humans' plant knowledge can make a difference for domestication. For example, in Africa, many wild fruit and nut trees and herbaceous orphan crops are already known by humans and have great potential for further domestication (27, 107).

Different methods can support work with diverse human systems in both localized and decentralized geographies. Integrative research and education efforts can be led by, or codesigned with, the specific human communities who hold relevant plant knowledge and tend key wild and domesticated landscapes. Participatory modeling approaches may support agrobiodiversity through building stakeholders' understanding and ideas about management (117), and participatory plant breeding may support agrobiodiversity through engaging many agronomic environments (118). Citizen science can be used to collaboratively collect crop and ecology data and to invite social learning, all of which may be useful for studying and advancing domestication (90, 119, 120), though agricultural citizen science efforts need to consider low-income contexts and the Global South (121).

Nutrition, resilience, sustainability, and equity are at the intersections of the elements of domestication. Asking questions about geographies and locations—i.e., asking "where" questions—can be a way to investigate the intersections of the genetic, ecological, and human diversity elements of domestication (Fig. 1). To guide different choices in domestication that advance nutrition, resilience, sustainability, and equity, domesticators and funders can consider:

- Assets: Where are hotspots of plant biodiversity, agrobiodiversity, and landscape diversity? Where are human communities with sustained, revitalizing, or emergent food cultures? Where are past centers of domestication, regional assemblages, and domesticated landscapes? Where are human systems with knowledge and resources to motivate and maintain domestication now?
- Needs: Where are ecologically threatened and degraded landscapes? Where are human communities most vulnerable to climate injustice? Where are regional food systems with low nutritional densities? Where is early stage or ongoing domestication possible or already happening with limited resources?

The Next Era of Domestication Can Feature Existing, Underutilized, and New Crops. Transformation of our food systems depends on engagement with each of the three elements of domestication—crops, ecosystems, and humans—to diversify the palette of species, we grow and consume. Below, we describe how efforts targeting species across the domestication continuum (e.g., domesticated, semi-domesticated, and wild) can begin to realize such change.

We can introduce new diversity into major and minor crops. The classic "domestication syndrome," or suite of phenotypic traits associated with domestication, varies among crops, but often includes larger seed size and loss of seed shattering, reduction of lateral branching, and modification of reproductive timing (122, 123); collectively, these traits enhance yield and facilitate harvest. However, domestication has also resulted in undesirable changes in many of our major crops, such as the loss of genetic diversity (124, 125) and accumulation of deleterious mutations (i.e., the "cost of domestication") (81, 126, 127), as well as altered metabolomic profiles and decreased nutritional content (32, 86, 122, 128). The challenge ahead is to introduce new diversity, reduce the mutation load, and increase overall crop resilience (e.g., improving photosynthetic capacity, water use efficiency, nutrient retention, and disease resistance), while maintaining important agronomic traits acquired during domestication.

Traits associated with stress adaptation, including pest and pathogen resistance and tolerance to drought, heat, salinity, and flooding, are often present in crop wild relatives and landraces, and can be introduced into elite lines via introgressive hybridization (11, 20, 129, 130). However, introgressed segments are typically large and may include undesirable traits and deleterious alleles alongside beneficial targets, a phenomenon known as "linkage drag." To diminish these effects, complex breeding and backcrossing schemes are utilized in combination with marker-assisted selection and genomic selection (130, 131). However, introgression breeding has proven challenging and expensive, even for singular, known targets, and the types of traits that are introgressed from wild species tend to be limited (132).

As the complex interactions between genome, transcriptome, and proteome [i.e., the interactome sensu (133)] become more apparent, there is a growing realization that the introgression of a single or even a few genomic regions from a wild species may not be sufficient to overcome the challenges facing our crops. Rather than moving wild diversity into cultivated lines, some authors have proposed a reversal of this gene flow, transferring genes from cultivated lines into crop wild relatives to explore the potential role of genetic background effects and epistasis in agronomic trait variation (86, 134). This method may also serve to counteract the accumulation of deleterious mutations in our crops, as wild species are expected to carry lower genetic loads (129).

New methods show promise for improving the efficiency of introgression breeding. For example, genome–environment associations can facilitate selection of the most environmentally appropriate wild materials to use in breeding programs (76, 77). Feralized populations of crops and landraces may also serve as important genetic resources for locally adaptive traits, as well as potential targets for "de novo redomestication" (135). Similarly, screening cultivated material, especially landraces, for wild introgressions can identify admixed populations that have reduced linkage drag (129).

We can improve underutilized crop species. Humans have developed agricultural relationships with many crop species that are not considered major crops and have not received organized, concerted breeding and improvement efforts (59, 136). Individually, these species make up a relatively small portion of global agricultural production, but collectively, they play an important role as cash crops and/or subsistence or famine foods in many of the world's poorest regions, which are underserved by major crops (38, 136). These species, often considered "semi-domesticated," are referred to as "neglected," "orphan," or "promising" crops (8, 59). Additionally, harm to indigenous human communities and the erosion of biocultural knowledge and agrobiodiversity has contributed to the loss of entire agricultural systems and their traditional food plants, termed "lost crops" (32, 137). Here, we use the term "underutilized crops" to collectively refer to both of these categories of plants.

Underutilized crops are recognized as an important resource for agricultural diversification that supports food security, nutrition, and sustainable practices (8, 10, 38, 59). While major crops require an infusion of diversity (see above), underutilized crops have plenty to choose from, with forms ranging from trees, vines, shrubs, and herbs; annual and perennial life histories; and products that include sweet and starchy fruits, nuts, oilseeds, grains, legumes, vegetables, leafy greens, succulents, woody perennials, roots and tubers, and more (reviewed in ref. 138). Many underutilized crops contain high levels of both macro- and micronutrients, and may therefore offer an avenue toward combating malnutrition (32, 38, 59). Because underutilized crops are primarily grown using low-input traditional practices, often in harsh conditions and in food-insecure regions, many of these species are well suited for sustainable, climate-resilient systems (8, 32, 136, 139). Other underutilized crops and traditional foods, such as macroalgae and seagrasses, can expand our ideas of agriculture to include new cultivation schemes (140, 141).

The majority of resources directed toward crop improvement focus on major and minor crop species, and underutilized crops suffer from a lack of genomic resources (86). However, having already undergone some level of human selection, underutilized crops have the potential for great gains with only modest investments of time and resources (38). Therefore, the first step for many of these species is the collection of genotypic and phenotypic data, including critical data on reproductive habits (32), and the creation of genetic maps and reference genomes that can facilitate genome-wide association studies (GWAS), genomic selection, and phenomic selection (8). As the costs of sequencing continue to drop, advanced tools and resources like machine learning, population genomic datasets, and pan-genomes, and in some cases even genetic modification, will also become more readily available for underutilized crops (8, 142).

For underutilized species, breeding targets will likely include traits that are important to scaling up cultivation, such as productivity, reproductive synchronicity, palatability, harvestability, and durability/storage capacity (143). But, in order to ensure we do not repeat the missteps of past domestication efforts, we must be more intentional. For example, domestication via natural selection, in which humans played the role of seed dispersers, led to the evolution of both larger fruits and seeds but also, in some cases, an intraspecific arms-race leading to excessive height (144). Preference for more palatable seeds may have led to a loss of defense compounds in both seeds and stems, and the practice of shifting cultivation and seasonal nomadism may have selected against plant investments in belowground structures and longevity (144). We now have the opportunity to domesticate species with the benefit of evolutionary genetics. We can practice artificial selection, in which plants lose individual fitness (e.g., semi-dwarf stature) in favor of greater collective yield. Importantly, we can also monitor and select against negative genetic correlations to avoid unintended alterations in plant defenses or ecosystem services.

Bringing underutilized species to a broader audience will require coordinated efforts between local farmers, researchers, and national food systems, as well as acknowledgment of the biocultural context in which they were domesticated (59, 90). There are lessons to be learned from other underutilized species such as avocado, quinoa, and açaí, which, marketed as "superfoods," have seen a rapid rise in global importance (145–147). Supporting the agricultural and social infrastructure required to increase crop production is critical, as are efforts to mitigate environmental impacts of agricultural expansion, and ensuring equity of monetary and dietary benefits within the areas of traditional cultivation (145–149).

We can domesticate new species. Due to economic investment in improving and tailoring major staple crops, which most people around the world rely upon for the majority of their calories, the "domestication of new crops has nearly stopped" (86). Alternatively, and as a result of limited support of the needed basic research (39), we propose that domestication of new crops has barely started.

Domestication of new plant species in the twenty-first century has been initiated despite resource constraints, and these efforts span plant families and types: bioenergy crops (150), cacti (151), ferns (152), halophytes (153–160), tree fruits and nuts (161, 162), macroalgae (163–166), marine grasses

(141, 167), microalgae (168), palms (169, 170), perennial grasses (171–173), perennial groundcovers (174), perennial oilseeds (90, 175, 176), and perennial tree and grain legumes (177–179).

Wild species targeted for domestication typically face many of the same challenges as underutilized crops: A lack of essential genetic and phenotypic data, including reference genomes. Exceptions are the wild relatives of major crops, which can leverage genomic resources to enable advanced techniques such as gene editing (180). In such cases, genes of major effect that underlie the primary domestication traits of the major crop may be modified. However, this method does not account for the effects of minor alleles and genetic interactions (epistasis), which, while poorly understood at the mechanistic level, are known to impact agriculturally relevant traits. While gene editing may in some cases yield important advances, domestication processes that will help realize diversity still require engagement with all the three elements of crops, ecosystems, and humans (90).

Selection on new domesticates can target novel uses and innovative cultivation schemes, but it must also consider downstream needs, such as harvestability, storage capacity, and nutrient retention (143). Furthermore, breeding programs must select for limited tradeoffs between stress tolerance and yield, a goal that may be best accomplished by domesticating species that are already adapted to the environmental/climatic conditions in which they will be cultivated (143). Careful attention should also be paid to maintaining genetic diversity, including cryptic variation (i.e., not observed/expressed in domesticates) and that of important polygenic traits such as pest and pathogen resistance (181). The use of genomic selection and breeding strategies, including introgression breeding with wild relatives, and independent selection in multiple breeding populations may help achieve these goals. While the timeframe for neo-domestication is often portrayed as a drawback, new methods like speed breeding may facilitate more rapid domestication and improvement of new crop species (182, 183).

Ecologically, new crop domestication could be targeted for functions in addition to human use and consumption, such as the restoration of degraded and threatened ecosystems and for the provision of ecosystem services (73). New crop domestication for human food and to meet additional ecological sustainability goals may be compatible with simultaneous efforts to restore biodiverse landscapes. Because domestication of new species involves the sustained cultivation and production of large supplies of seeds, a domestication-based approach can generate the scientific knowledge, agronomic practices, and cultural valuation for seed harvest, processing, and storage that are also needed to accelerate restoration and rewilding. An example of this approach has been envisioned for domesticated seagrass (184).

Socially, new crop domestication could prioritize “identifying new plant sources for nutritional improvement” (35), particularly in regions and cultures vulnerable to climate change. New crop domestication could also advance equity. Communities with plant knowledge can grow that knowledge and their food cultures as they steward landscapes and pursue culturally appropriate domestication projects—and they may choose to collaborate with, and utilize knowledge and resources from, scientific and transdisciplinary research institutions and organizations around the world. However, additional hurdles besides funding of basic research include the time, labor, and skill involved in making strategic and collective decisions about new crop domestication, particularly the work involved in spanning and integrating disciplines, human behaviors, and diverse communities.

Discussion: What Will It Take to Advance the Next Era of Crop Domestication?

Which crop domestication strategies will make the most impact on building the diverse food systems needed in the Anthropocene? A multifaceted approach is recommended depending on the type of crop and geographic region, as explored above. In all cases, there is a need to accelerate crop domestication and/or improvement in the face of climate change while maintaining genetic diversity during the breeding process.

While some traits desired in our future crops will certainly be species specific, others should be universally sought after. Unmet needs and examples of related traits that could be addressed in domestication pipeline strategies (108, 143) include:

- increased ecological benefits such as for soil health, by targeting carbon sequestration and perenniality, and for biodiversity, by targeting pollinator services and habitat stability and complexity;
- decreased reliance on inputs, by targeting nitrogen production and efficiency and pest and pathogen resistance;
- hardiness in the face of climate variability and weather extremes, by targeting water use efficiency and cold and heat tolerance;
- adaptation for degraded, detrimental, and novel environments, by targeting carbon sequestration, length of life, and/or salt tolerance;
- fit of the crop into innovative and valuable cropping systems and rotations (with other plants, microorganisms, etc.), by targeting growth habit for harvestability, resource partitioning traits, micronutrient and high protein content for human use, and multipurpose uses along with human food, such as fiber, lumber, forage, medicine, or fuel;
- fit of the crop into more resilient and sustainable supply chains and food economies, by targeting storability and durability of the harvested crop, including nutrient content and retention.

If the next era of crop domestication is to start now, we must recognize barriers to change in the form of currently dominant systems and landscapes. Sustaining the domestication and widespread cultivation of a few input-intensive staple crops requires effort. For humans to gain access to edible energy (in the form of plants powered by the sun and fed by soils and fossil fuels), our societies deploy energy—particularly fossil fuel energy—in activities ranging from scientific research and development, to plowing and fertilizing and harvesting, to trading and storing and cooking foods.

Despite being vulnerable to climate change and other environmental crises, currently dominant annual grain crops and cropping systems are also resilient in the sense that they are relatively resistant to change; this is due to the investments they have already received, and the investments that they continue to receive, of both biophysical and sociocultural energetic resources (103, 185). As overall relative investment in agriculture is decreasing (186), there is increasing competition for research and development resources simply to maintain current crops and yields (34).

Yet we must grow investments in basic and translational research to enable bold advances in crop domestication that support diversity. Some effort and energy will need to be reallocated and repurposed. In addition to basic knowledge such as scientific tools and reference genomes (39), investments are needed to develop the context in which domestication emerges (123), including physical infrastructure, social networks, and cultural interest. Translational research–i.e., applying basic knowledge to pursue practical results, often through interdisciplinary and international collaboration–is needed across the elements of domestication, including to advance crop genetic improvement (187). Because domestication relationships have to be not just started but sustained, we recommend strategically targeting investments based on assets and needs, while simultaneously building a network across which social learning can be accelerated and maintained over time.

Many of the dramatic yield gains in major crops in the twentieth century were made possible by foundational public investments in innovative technologies and institutions—including land-grant universities and agricultural extensions, plant material centers, research stations, and international research centers and global partnerships—that transformed landscapes as well as agricultural and food systems. The next generation of crop domestication will similarly require materials and mechanisms for agricultural transformations that increase diversity (34, 36). It is now possible to do crop domestication differently, combining new genomic and geospatial technologies, interdisciplinary approaches (188), the rediscovery of place-based public agronomy and selective breeding, and innovative public–private partnerships. Humans need more diverse food systems in the Anthropocene—the process of domestication can help build them.

Data, Materials, and Software Availability. No data was collected or analyzed for this perspective.

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