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Crop Biodiversity: An Unfinished Magnum Opus of Nature

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Journal

Annual Review of Plant Biology, 70(1)

ISSN

1543-5008

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Publication Date

2019-04-29

DOI

10.1146/annurev-arplant-042817-040240

Peer reviewed

*Annual Review of Plant Biology***Crop Biodiversity: An
Unfinished Magnum
Opus of Nature****Matthew B. Hufford,¹ Jorge C. Berny Mier y Teran,²
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Annu. Rev. Plant Biol. 2019. 70:727–51

The *Annual Review of Plant Biology* is online at
plant.annualreviews.org<https://doi.org/10.1146/annurev-arplant-042817-040240>Copyright © 2019 by Annual Reviews.
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farmer selection, gene flow, genetic diversity, parallel and convergent evolution, phenotypic plasticity, seed systems

Abstract

Crop biodiversity is one of the major inventions of humanity through the process of domestication. It is also an essential resource for crop improvement to adapt agriculture to ever-changing conditions like global climate change and consumer preferences. Domestication and the subsequent evolution under cultivation have profoundly shaped the genetic architecture of this biodiversity. In this review, we highlight recent advances in our understanding of crop biodiversity. Topics include the reduction of genetic diversity during domestication and counteracting factors, a discussion of the relationship between parallel phenotypic and genotypic evolution, the role of plasticity in genotype × environment interactions, and the important role subsistence farmers play in actively maintaining crop biodiversity and in participatory breeding. Linking genotype and phenotype remains the holy grail of crop biodiversity studies.

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1. INTRODUCTION

Some of the most colorful sights around the world are vegetable markets and the stalls of grocery stores. The grains, vegetables, fruits, and spices of innumerable colors, sizes, shapes, and aromas offer a kaleidoscopic view of—mostly domesticated—crop biodiversity (**Figure 1**).



Figure 1

The kaleidoscope of fruits and vegetables sold in this market are the result of millennia of farmer selection during and after domestication around the world. Crop biodiversity is represented by both different crops and varieties within crops. From <https://www.publicdomainpictures.net>, license CC0 Public Domain.

Underlying these everyday, down-to-earth sights are important considerations about diversity. First, what qualifies as crop biodiversity, and which species fit this definition? We define crop plants here as any plant being cultivated, mainly those that have been or are being domesticated. Of the 390,000 to 420,000 plant species that are estimated to exist (76, 126), some 2,500 species may have been domesticated (30, 59). This is a fairly generous estimate, which encompasses not only domesticated species but also wild species that are cultivated in some way. We must consider the nature and degree of domestication of these species (28), the extensiveness of their distribution, and the level of their production. For example, some 80% of plant-derived foods originate in just 17 botanical families (of a total of 416 families); several of these are major contributors of domesticated species, including the Poaceae, Fabaceae, Apiaceae, Brassicaceae, Rosaceae, Arecaceae, and Zingiberaceae. About 100 species contribute 90% of all calories in the human diet (76); however, other domesticated species fulfill important functions as sources of essential nutrients, such as proteins, vitamins, and minerals and as medicines. This collective crop biodiversity can be considered at several levels: (a) populations or lines within species, (b) assemblages of crops in time and space (i.e., agroecosystems), and (c) several agroecosystems composing an agricultural landscape. All organisms populating agroecosystems and agricultural landscapes can be considered components of agrobiodiversity, including crop and noncrop plants, insects, and microorganisms, both beneficial and detrimental (22, 68). In this review, we specifically focus on domesticated crop species, regardless of their degree of domestication, and their wild relatives, especially their progenitors. Genetic diversity within these species is not only the raw material for plant breeding, but also a key factor in assuring the productivity and stability of agriculture (e.g., 8, 89, 133, 136).

Second, how is crop biodiversity produced? Crop biodiversity is the result of a triad of interacting factors, which include the plant itself, its environment, and the actions of humans, as illustrated by the domestication triangle (**Figure 2**). Whereas natural evolution is confined to organismal characteristics and interactions with the environment, crop evolution involves the all-important contributions of humans, who are responsible for selection and dissemination of crop plants, not only in the first stages of transition from gathering to cultivation but in all subsequent stages as well. Today, this process includes both modern plant breeding and management of seed stocks by subsistence farmers, activities that continue to adapt crops to the needs of their respective users. Thus, our domesticated crop plants should be considered not merely as biological organisms, each with their genetic, life history, and production characteristics, but more significantly as biocultural artifacts. We use the word artifact in the anthropological sense, namely as a product of human ingenuity and skill within their cultural contexts. Crops are one of the most important inventions of humanity, and humans and crops are now symbiotically related because of their mutual dependence for survival. Seven billion humans cannot be fed without agriculture because plants contribute 80% of our food; conversely, humans assure the survival of some of our major crops, given that domestication has eliminated their ability to survive on their own. Thus, crop cultivation represents a case of mutually assured survival of two classes of organisms further underscoring the need to understand selection during domestication and contemporary plant breeding and the continued involvement of farmers in shaping crop biodiversity to fit their own uses.

Third, to what extent has evolution during domestication shaped crop biodiversity? The evolutionary processes that shaped diversity, regardless of their nature and origin (see the previous paragraph), have operated from before the initiation of cultivation of wild progenitors some 10,000–12,000 years ago, through the initial selection for adaptation to cultivation and subsequent worldwide dissemination (77), up until today. For example, the general reduction in diversity of crops, especially observable at the molecular level, traces back to the domestication process, or in some cases even before this process. Understanding the contemporary biodiversity of crops, therefore, requires an analysis of its evolutionary history (50, 46, 47, 74, 85, 98, 106–108, 115, 132). Studies

Domestication: the process of heritable genetic adaptation to human cultivation and consumption conditions

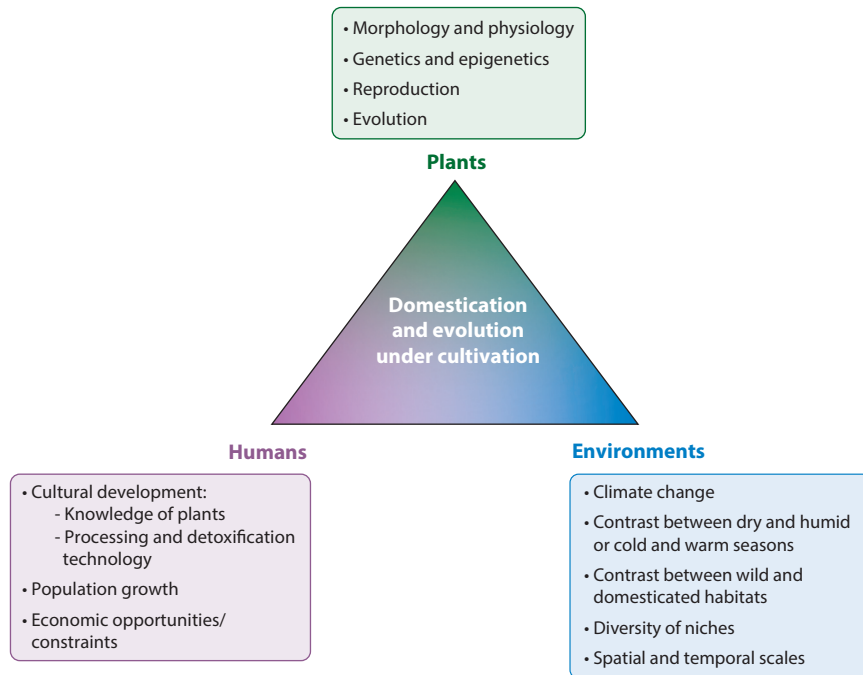


Figure 2

Domestication and subsequent crop evolution involve interactions of plant, environmental, and human factors. All three factors are required for domestication to generally take place, but specifics vary among domestication regions. The figure lists examples of specific factors that have been implicated in domestication. Modified from Reference 43 with permission.

of crop evolution are very active not only because the transition from hunting-gathering lifestyles to those of farming is one of the most important evolutionary steps of humanity but also because wild relatives represent a significant aspect of sound conservation due to their utility in breeding by cross hybridization.

The importance of crop biodiversity will rise in the near future because of additional qualitative or quantitative demands on agricultural production. The human population is expected to increase from 7.5 billion in 2017 to 9.8 billion in 2050 and 11.2 billion in 2100 (166). The increase in demand for agricultural products due to a larger population will be compounded by increased consumption accompanying greater affluence. Because expecting a sharp reduction in the human population is illusory (15), humanity is faced with a long-term need for increased agricultural production. There is no single magical solution that will achieve this goal (79). However, genetic crop improvement has been responsible for about half of on-farm yield increases (154); the other has been contributed by cultivation practices. Furthermore, there is increasing pressure for agricultural production to evolve to a more sustainable model that is resource efficient and reduces environmental impact (e.g., 35, 123). There is no doubt that other factors like education, infrastructure, and policy, among others, also play a role, but these are topics beyond the scope of this review.

Biodiversity in general and crop biodiversity, in particular, are threatened. Paradoxically, agricultural activity is the second most prevalent threat in this regard (104). Agricultural biodiversity is harmed by habitat destruction through agricultural conversion (174); urbanization (80); road

construction (86); increasing global cultural homogenization (77); and introduction of modern, elite varieties with limited conservation of traditional varieties (i.e., genetic erosion) (168, 169).

Although the existence of human-induced global climate change is not in doubt, the future intensity of this change remains uncertain given various emission profiles of greenhouse gases. Uncertainties relate mainly to the political will, both nationally and internationally, to control emissions. What is certain is that global average temperatures will increase, and rainfall will become more unpredictable and erratic. What is uncertain are the magnitude and interactions of these changes and their effects on Earth and its biota. Climate change leads to shifts in climate zones and biome distributions (140, 145). In this regard, changes in crop distribution to higher altitudes or latitudes are likely (54, 152). Mitigation of these changes requires a multifaceted response in which crop biodiversity will play a role by, for example, providing variety or crop substitution or an earlier phenology (73, 93, 119). Not surprisingly, a current emphasis in biodiversity utilization includes screening for heat and drought tolerance to identify new sources of adaptive genetic diversity to mitigate yield reductions caused by global climate change (e.g., 39).

Additional pressures on crop biodiversity are the current diversification of human diet and crop nutritional quality to improve human well-being, especially that of children (2, 72). Although this is a complex issue involving mainly sociopolitical and economic factors affecting food security, agricultural biodiversity plays roles through crop species diversification in agroecosystems and biofortification of crops (e.g., 56, 112).

In this review, we focus on the genetic diversity of domesticated plants from the perspective of crop evolution and domestication. Understanding this diversity, including how it has been shaped and maintained, is fundamental to all steps of genetic conservation (whether in gene banks or in situ) and the utilization of genetic resources in plant breeding. We concentrate on specific issues that have recently been studied, spanning the full range of genomic studies of crop diversity and gene flow to parallel and convergent evolution to plasticity and ending with the farmers' ongoing roles in shaping their seed stocks. We end with a series of future issues or recommendations regarding the study, management, and utilization of crop biodiversity.

2. ORIGIN OF VARIATION AND THE COST OF DOMESTICATION

2.1. Origin of Variation

During domestication and after domestication, crop biodiversity was shaped by both genome-wide demographic effects and locus-specific selection on favorable alleles (**Figure 3**). In most crop-wild relative pairs evaluated to date, reduced genetic diversity is observed in the crop due to what is known as a domestication bottleneck. Ancient cultivators likely focused their efforts on particular wild subpopulations and, through both unconscious and conscious selection on specific alleles, increased the prevalence of desirable traits such as reduced branching and shattering that facilitated harvest (31). A focus on a few wild relative subpopulations would result in a subset of genome-wide diversity being passed to domesticates. Continued selection on loci underlying domestication traits would further reduce diversity in these specific chromosomal regions relative to the genomic background. For example, maize retains approximately 83% of genome-wide diversity found in its wild relative teosinte (66), whereas near domestication loci, such as *teosinte branched1* (*tb1*), essentially all diversity in maize has been lost (160). The same general trend has been observed in many of the world's major crops, including rice (18), wheat (58), soybean (84), and common bean (11), with weaker bottlenecks typically observed in perennials relative to annual crops (41).

Exceptions to this general pattern have been found. Domesticated carrot, for instance, shows no reduction in overall diversity compared to wild populations potentially due to its outcrossing

Plasticity: the capacity of a genotype to produce different phenotypes under different environmental conditions

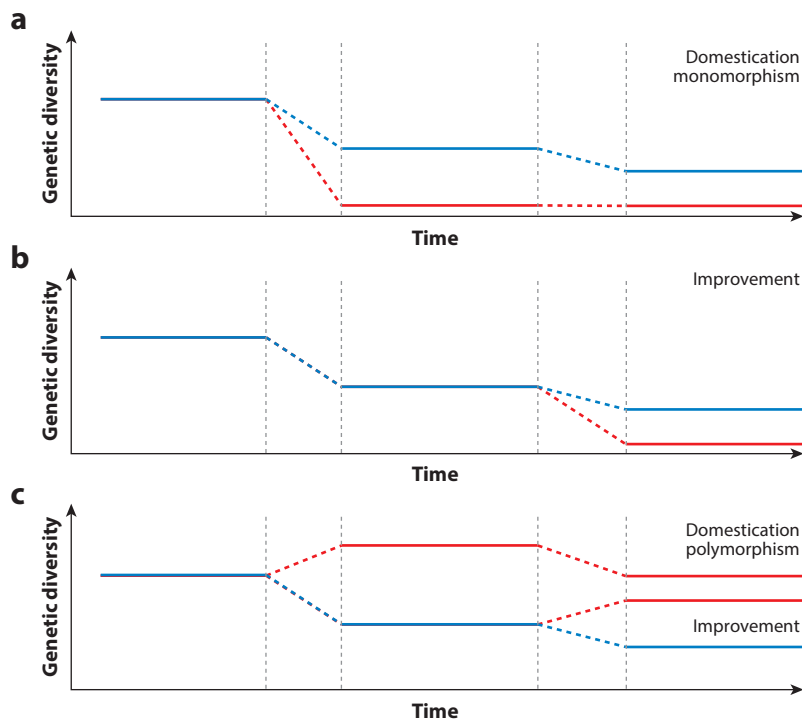


Figure 3

Fate of genetic diversity during and after domestication. The blue line indicates neutrally evolving loci subject to genetic drift. The red line depicts loci subject to selection, leading to either reduction of diversity (or even monomorphism) during (a) the initial domestication step and (b) subsequent steps. (c) An increase of diversity may occur during the domestication process or subsequently during dissemination or breeding for certain genes involved in agronomic adaptation or consumer preference. Adapted from Reference 47.

mating system and ongoing history of gene flow with wild relatives (69). Likewise, high diversity is found at the *PvTFL1y* locus in common bean, which underlies the determinacy domestication phenotype (82). Determinacy in common bean is achieved through loss of function of *PvTFL1y*, a factor that may explain the diversity of putatively causal alleles because a greater proportion of mutations will break a gene than will create a novel function (see more about the *PvTFL1y* locus in Section 4). A more general analysis of genic sequences in common bean identified a higher diversity in nonsynonymous mutations in domesticated types, suggesting an increase in functional diversity selected during and after domestication (12) (although an alternative explanation is provided by an insufficient purging of deleterious mutations). Traits that were particularly affected include tolerance of abiotic stress, flowering time, and morphology (11, 12).

An additional, important factor determining diversity levels at domestication loci is whether causal alleles are sourced from standing variation in the wild or de novo mutations in protodomes-ticates. Many domesticated traits are deleterious in the wild. For example, decreased shattering and reduced dormancy are appealing to cultivators, but these characteristics would dramatically reduce survival and reproduction in the wild. Given the loss of fitness conferred by domestication traits, some have speculated that their causal mutations must have occurred de novo in cultivated crops. Others have countered, however, that standing variation has likely played an important role given the long waiting time for novel beneficial mutations and the fact that many domestication

Standing variation: preexisting genetic variation acted upon domestication or selection postdomestication

De novo mutation: change in DNA sequence appearing during or after the domestication process (in contrast with standing variation)

traits are polygenic, which would require multiple de novo mutations per trait (158). Given the relatively rapid time frame of domestication, it is likely that standing variation has been a source of adaptation (9). In fact, the causal polymorphism at *tb1*, for example, which leads to an unbranched phenotype in maize has been shown as a transposon insertion that is segregating in teosinte (160). Because standing variation is older and has had more opportunity to recombine onto multiple genomic backgrounds, the selection signature of reduced diversity can be more attenuated (i.e., a soft sweep) than selection on de novo mutations (9). Selection scans based on sweep detection in domesticates or increased differentiation between domesticated types and wild relatives may therefore be biased toward identification of selection on de novo mutations. However, methods have recently been developed using approximate Bayesian computation (121) and machine learning frameworks (144, 147), which appear to be capable of detecting soft sweeps and distinguishing these from hard sweeps. Future application of these methods may help clarify the extent to which domestication relied on standing variation versus de novo mutations.

Cost of domestication:
accumulation of deleterious mutants during and subsequent to domestication due to demographic effects and strong selection limiting recombination

2.2. Cost of Domestication

The general decline in crop diversity due to demographic bottlenecks and targeted selection during domestication also has implications for the prevalence of deleterious alleles in crop genomes. The reduction in effective population size that is associated with declines in diversity lowers the efficiency of purifying selection, permitting the accumulation of deleterious alleles. In the context of crops, this phenomenon has been termed the cost of domestication (reviewed in 110) and was first proposed by Lu and colleagues (95) as an explanation for the excess of deleterious alleles in domesticated rice. The trend of increased genetic load in crops has since been observed in maize (176), cassava (135), grape (182), sunflower (137), and other species, suggesting this is a general phenomenon tied to domestication. Several computational methods have been developed to identify deleterious alleles, primarily based on constraint across a phylogeny (e.g., 25, 159). In the future, detection of particularly damaging alleles in genes of agronomic importance could facilitate the amelioration of load in crop germplasm through recombination or targeted gene editing.

3. POSTDOMESTICATION EXPANSION, GENE FLOW, AND ADAPTATION

Following domestication, many crops spread beyond their initial centers of origin to near-global distributions. During this period of expansion, crops often encounter new populations of their progenitor and closely related wild species. In multiple instances, hybridization between crops and these newly sympatric wild relatives has been documented. At times, this hybridization provided crops with adaptations to local conditions. In other new environments where wild relatives did not occur, crops have acquired adaptations de novo as they colonized these new regions. As we describe below, the processes of expansion, gene flow, and adaptation postdomestication have each meaningfully shaped crop biodiversity (**Figure 4**).

Patterns of diversity and genetic similarity of crops to specific populations of extant wild relatives suggest that, in many instances, crops have arisen from one or a few centers of origin. For example, Matsuoka and colleagues (103) determined that maize was likely domesticated a single time in the Balsas River basin of southwest Mexico, a finding that has been corroborated by additional genetic analyses (170) and archaeological data (128). The number of domestication events for other crops like Asian rice remains in question, with some investigations suggesting a single origin potentially in the Pearl River valley of southern China (64), and others suggesting

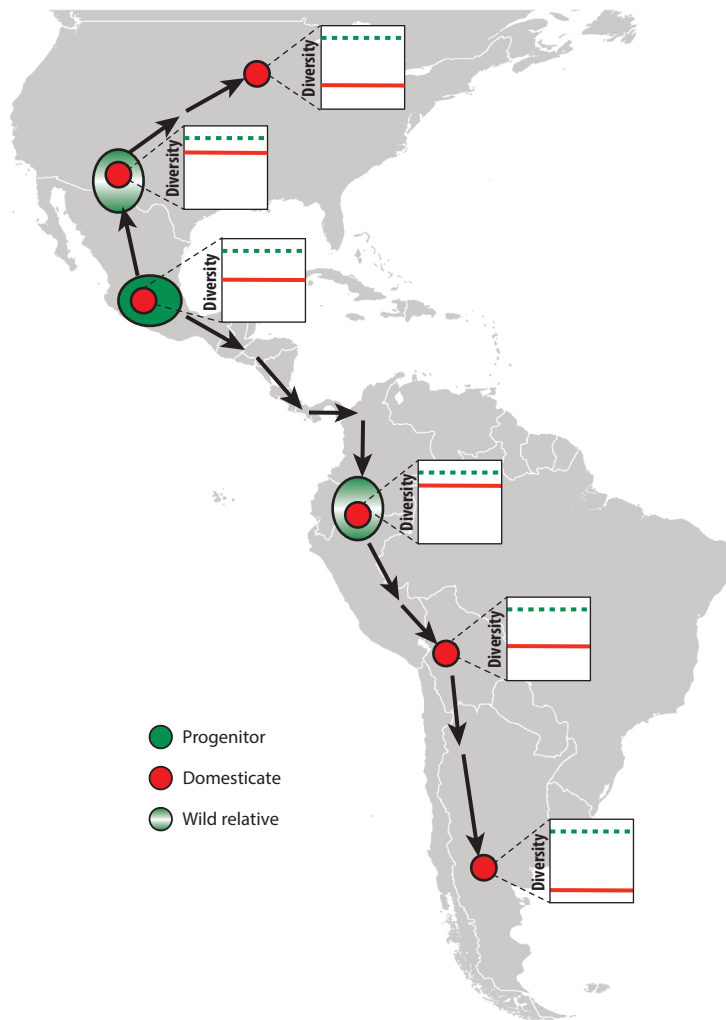


Figure 4

Migration and gene flow history of a fictional domesticate originating in central Mexico. Plots to the right of each population place diversity of the local domesticated population (*red solid line*) in the context of the ancestral diversity of the crop's progenitor (*green dashed line*). Black arrows represent repeated migration and founding events. Although gene flow with wild relatives outside the crop's center of origin can help restore diversity lost during the domestication bottleneck, repeated founding events further erode diversity. Original figure by M. Hufford.

multiple origins in both China and south Asia (21). In still other cases, such as the clear independent domestications of common bean in the Lerma River valley of Mexico and the southern Andean highlands of South America (48, 82), multiple domestication events are clearly supported. However, few examples of diffuse, noncentric domestications have been conclusively proven, and most crops likely share a history of local domestication followed by expansion.

Geographic expansion of a species is known to affect patterns of genetic diversity. For example, as humans migrated out of Africa, diversity was subsampled repeatedly through a series of

colonization and/or founder events. In fact, a survey of genetic diversity in modern human populations has demonstrated the effects of this subsampling persist even today, with decreasing diversity observed in humans with increasing distance from Africa (134). Given their similar history of expansion, it is not surprising to find the same geographic trend in the genetic diversity of crops. For example, Wang and colleagues (176) recently demonstrated a decline in genetic diversity in modern maize landraces with increasing distance from the Balsas River valley. Although not extensively studied, this pattern is likely repeated in many of the world's crops, particularly those such as rice, wheat, common bean, and barley, which experienced sustained, postdomestication expansion over several millennia. Additionally, serial founder effects during expansion have likely shaped patterns in the local prevalence of deleterious alleles. Similar to the cost of domestication described above, declining effective population size due to repeated expansion bottlenecks has likely increased the prevalence of deleterious alleles as crops spread away from their site of origin. This has been clearly demonstrated in maize (176) and may well be a more common trend.

In some crops, gene flow with newly encountered populations of wild relatives has likely been an important countervailing force to genetic erosion experienced due to expansion. A recent review (70), for example, summarized evidence for substantial wild-to-crop gene flow during postdomestication expansion of many of the world's most important crops including potato, barley, and maize. Gene flow has been so substantial between domesticated potato and several wild relative species, for instance, that it long obscured the identity of the initial progenitor and likely contributed to the high level of diversity currently found in this domesticate (55). In crops such as barley, postdomestication introgression from wild relatives has not remained geographically constrained because it was carried by the crop throughout its period of expansion, leading to an ever-widening genetic base of the crop (130). However, in other cases like common bean (117, 118), gene flow has predominantly occurred from domesticate to wild relative, doing little to ameliorate the diversity lost in the crop owing to expansion. In fact, substantial crop-to-wild gene flow has the potential to rapidly diminish wild diversity or even genetically swamp wild relatives to extinction (60, 164).

Beyond the neutral, demographic effects of serial founding events and gene flow, the process of adaptation required when colonizing new environments has shaped crop diversity. Some common adaptive challenges for crops during expansion include abiotic gradients of elevation, precipitation, temperature, and latitude, as well as exposure to novel biotic stressors (65, 97). Sources of adaptive variants for crops encountering new environments include the standing variation with which they arrived, gene flow from locally adapted wild relatives, and *de novo* mutations. Although the former two sources of variation allow for rapid adaptation, the latter requires a waiting time until an adaptive mutation randomly occurs. Perhaps, for this reason, the few studies that have investigated the source of adaptation in expanding crops suggest standing variation and gene flow from wild relatives predominate (161). In fact, some have hypothesized that, given the constraints associated with *de novo* mutations, adaptation may commonly occur across a broad range of species through standing variation and hybridization (9, 122). Importantly, the winnowing effects of selection on diversity during adaptation would not be as pronounced if adaptation were to occur from standing variation (9) or repeated introgression rather than from *de novo* mutations.

Most recently, modern plant breeding, with its awareness of crop biodiversity, has added to the genetic diversity through a thorough mixing of available germplasm, including introgression from wild types and landraces (e.g., tomato) (93), interspecific crosses (e.g., cotton) (181), and reconstruction of polyploids (e.g., strawberry) (96).

4. PARALLEL EVOLUTION AND CONVERGENCE

Vavilov (172) observed that phenotypic variation tended to show parallelism among closely related species, as stated in his article “The Law of Homologous Series in Variation.” He even used this observation to predict the occurrence of specific phenotypes in related species. Many of the traits observed by Vavilov were domestication traits, contrasting wild and domesticated types of the same species. The existence of these domestication syndrome traits (53, 57) supposes a common set of selection pressures that has acted during and after domestication, leading to parallel phenotypic variation as illustrated by Reference 124 for domesticates of the Americas. This group of crops provides an excellent model to illustrate the concept of homologous series of phenotypic variation because several genera show multiple domestications within the Americas, notably *Capsicum* and *Phaseolus*, which both contain five domesticated species. In addition, two of the domesticated *Phaseolus* species have been domesticated twice, in Mesoamerica and the Andes (48, 81).

The determinacy phenotype—a diversification trait, which appeared after domestication—is present in three of the domesticated *Phaseolus*: *P. vulgaris* (common bean), *P. lunatus* (lima bean), and *P. coccineus* (runner bean). In the former two species, the determinacy trait appears in both the Andean and Mesoamerican gene pools. In *Capsicum*, loss of pungency is observed in three domesticated species: *C. annuum*, *C. frutescens*, and *C. chinense* (156). In addition to domestication (40, 92, 124), other examples of repeated selection are high-altitude selection (see Section 3), edaphic conditions (10, 165), and host-plant adaptation (42, 52, 114).

To what extent does parallel phenotypic evolution reflect changes at the same or different loci, and are these structural or, more often, regulatory? An answer to these questions would reveal how natural selection shapes the form and function of living organisms. Moreover, the assumption of convergence is part of the justification of model systems like *Arabidopsis* and rice, which rely on the widespread distribution of shared molecular and genetic mechanisms. It is also of practical importance because it helps identify candidate genes that can be used for gene isolation and marker-assisted selection (e.g., 91, 113).

Two important factors affecting the relationship of phenotypic and molecular convergence are the homology of the trait and the phylogenetic relationships among the species being studied. There are two extreme situations: homologous traits in closely related species (same genus or family) versus heterologous traits in distantly related species (different families). In between, all combinations are possible to a degree. In the former situation, the same or similar genes or gene networks are presumably involved; in the latter, different genes or pathways are more likely implicated. These two situations are called, respectively, parallel and convergent (or collateral) evolution (124, 157).

It has been suggested, however, that data did not support a role of phylogenetic distance in distinguishing between parallelism and convergence (5). The common bean provides a case in point. Wild types of this crop show a viny growth habit, allowing them to compete for resources with native vegetation. By contrast, domesticated types display a range of growth habits, from indeterminate, climbing, to determinate, bush. With determinate plants, main stem and branches end in a terminal inflorescence, whereas with indeterminate types the terminal meristems remain vegetative. Thus, the determinacy trait fundamentally changes the growth pattern of bean plants in that it stops its modular growth (82, 162). Determinacy is controlled by a single recessive allele at the *PvTFL1y* locus, a homolog of the *Arabidopsis* *TERMINALFLOWER1* (*TFL1*) gene (83, 138). A sequence analysis of variation at the *PvTFL1y* locus showed that indeterminate types—wild or domesticated—showed only synonymous nucleotide substitutions. Different de novo mutations leading to loss of function of the gene (i.e., a determinate phenotype) were only present among domesticated types and not among wild types, consistent with field observations. Among these

Convergence:

independent evolution of the same phenotype in phylogenetically distinct lineages (phenotypic convergence), determined by homologous genes (genotypic convergence) or not

mutations, the most abundant one was a retrotransposon insertion in the fourth exon; others included nonsynonymous substitutions, indels, a putative intron-splicing failure, and a deletion of the entire locus. The multiple mutations leading to the same determinate phenotype provide evidence of parallel evolution under human selection (82). Farmers in distinct locations of the centers of origin of the species have selected for a dwarf and early plant type controlled by this determinate phenotype.

Equally remarkable is that other plants, whether they also belong to the Fabaceae family [e.g., soybean (163); pea (37); pigeon pea (142); and others (151)] or more distant botanical families, also show phenotypic variation attributable to homologs of *TFL1*. Among these are the Scrophulariaceae (snapdragon, *CENTRORADIALIS*) (26), Solanaceae (tomato, *SELF-PRUNING*) (129), and Vitaceae (grape, *VvTFL1*) (14) in dicots and Poaceae (barley, *HvCEN*) (23). Similarities exist also for the seed color gene *P* with both another legume, pea, and a Brassicaceae, *Arabidopsis*) (105). Another example of phenotypic variation among closely and distantly related taxa caused by homologous genes are mutations in *replumless* orthologs, affecting fruit opening and seed shattering in the Brassicaceae (*Arabidopsis* and *Brassica*) and in rice (*Sb1* gene), despite their very different phylogenetic position and fruit or seed anatomy (6).

Are there features that increase the occurrence of molecular convergence? Lenser & Theißen (90) suggest that a nodal position in gene regulatory networks, such as occupied by the *FT/TFL1* genes, could be more prone to convergence because they collect regulatory signals from several upstream sources and control several downstream targets. Relatively simple pathways like the anthocyanin pathway could also be a target, especially for a gene situated at the beginning of the pathway such as the *P* color gene in common bean. White seed color controlled by recessive alleles at the *P* locus appeared repeatedly in the Andean and Mesoamerican domesticated gene pools through distinct de novo mutations at the same *P* locus, controlled by a basic helix-loop-helix transcription factor (105).

In summary, the determinacy case is one of the most extensive examples to date of phenotypic variation attributable to a homologous gene that is widely distributed phylogenetically. This case provides a counterexample of the prevailing concept of parallel versus convergent evolution. One could also argue that initial identification based on homology between phylogenetically distant species favors molecular convergence in unrelated species. Thus, to date, there is an insufficient number of cases that have been described to quantify the factors involved in molecular convergence. More information is needed from comparisons involving homologous organs or biochemical pathways among a range of species of varying phylogenetic distances.

5. PLASTICITY AND GENOTYPE × ENVIRONMENT INTERACTIONS

Due to the sessile nature of plants, the environment plays an outsized, compelling role in adaptation in these species under both natural and agricultural settings (36). Although phenotypic plasticity is the ability of a genotype to express phenotypic variation in different environments, genotype × environment interaction (G×E) can be interpreted as differences in plasticity (29, 36, 125). For plasticity to be under selection, there needs to be environmental variation, genetic differentiation between competing individuals, transgenerational inheritance, and adaptiveness (101). Although these four conditions are often met in a natural landscape, they may be less prominent under cultivation, particularly under intensive modern production, which strives to limit genotypic (through monocropping) and environmental variation (through cultivation practices). By contrast, range expansion of domesticated forms, as compared with wild ancestors, has exposed domesticates to novel environments (57, 173) where plasticity could be adaptive as it may provide general adaptation.

Parallel evolution: the development of the same trait in two separate lineages descending from phylogenetically related individuals

Genotype × environment interaction (G×E): the nonlinear response of genotypes to environmental conditions affecting the stability of genotypes

Quantitative trait locus (QTL):

gene controlling the expression of a trait specifying a quantity or number, which is usually subject to genetic and environmental effects

The detection and study of variation in plasticity can be difficult because environmental variation can encompass both biotic and abiotic factors, agricultural management (for crops), the interactions between these factors, and different temporal and spatial scales. Variation is also found in the degree of plasticity across phenotypic traits (1, 29). A meta-analysis (29) found that natural species are more plastic than domesticates for an array of traits. In addition, more quantitative trait loci (QTLs) per environment were found for wild species compared with crops. Moreover, although the existence of QTLs by environmental interactions is common, differential sensitivity to environmental conditions (change in magnitude of plasticity) is the most frequent type of interaction. A comparison of productivity traits between domesticated types and their wild forms in six herbaceous species found that, even though the domesticates performed better under favorable conditions, plasticity in the wild forms led to higher productivity under water limitation (102). Similarly, wild maize (teosinte), when exposed in environmental chambers to simulated early Holocene conditions similar to those at the time of domestication (low carbon dioxide and temperature), showed significant plasticity in its morphology, resembling the morphology of its domesticated descendant (127). A higher plasticity was also observed in teosinte relative to maize when comparing gene expression levels under modern and simulated early Holocene conditions (94).

By contrast, when considering association with arbuscular mycorrhizae under high and low phosphorus availability, wild plants benefited from the association across environmental conditions (low plasticity), and domesticated forms could modulate the symbiosis based on phosphorus availability (99). Modern breeding, although usually evaluated in more stable and uniform conditions, does employ multienvironment testing, which allows the detection and selection of beneficial responses to an array of biotic and abiotic stresses, and when recombined improves the overall productivity and plasticity of crops, as has been found in maize (34) and wheat (51).

There are different molecular mechanisms associated with plasticity and its variation among genotypes. Although relatively few $G \times E$ genetic factors have been cloned, emerging research suggests that loss-of-function mutations and nonsynonymous changes in receptors play important roles in plasticity (29). Polyploidy and epigenetics are increasingly active areas for plasticity research. Domesticated species are more likely to originate from polyploid than diploid wild species (141), perhaps because polyploidy can lead to phenotypic novelty and plasticity due to gene dosage effects (32). Allopolyploids may show increased plasticity relative to autopolyploids due to their allelic diversity (171). Furthermore, allopolyploidy allows gene expression to resemble each of its genome progenitors depending on environmental conditions (149). Epigenetics, the heritable change in gene and phenotype expression that is not coded in DNA, is controlled by mechanisms such as DNA methylation, histone modification, small RNA, and enhanced homologous recombination (63). The epigenetic profile can be shaped by standing and de novo epimutations and may be environmentally induced, with this latter property having special importance during range expansion or under rapidly changing environments (139). The lability of epigenetic profiles may have facilitated plastic changes during crop domestication and adaptation. Although the variation explained by the epigenetic profile might be small compared with the genetic factors (3), epigenomic signatures during domestication have been found, for example, in cotton (155).

6. FARMER MANAGEMENT OF CROP BIODIVERSITY

It was Darwin (27) who remarked that domesticated plants showed more diversity in their harvested organs than in the nonharvested parts, compared to their wild relatives. Numerous examples illustrate Darwin's observation from the multicolored seeds of *Phaseolus* beans to the astonishing diversity among domesticated cabbage (*Brassica* sp.) species. Although several factors can

account for this variation, including gene flow (see Section 3), human selection plays a major role in the generation and maintenance of this diversity. This is especially the case in the context of smallholder farming systems in which plants are a primary resource and seeds or vegetative plant materials are part of the capital—instead of being inputs—of the farming enterprises. It is in these systems—often in centers of agricultural origins and domestication (173)—that crop evolution and landrace development have taken place for millennia.

6.1. Sociocultural Factors Influencing Crop Biodiversity

Crop biodiversity should be placed in the broader context of plant management of both domesticated and wild or weedy plants, which are managed in parallel. Blancas and colleagues (13) studied the way the Náhuatl-speaking people of the village of Coyomeapan managed 122 plant species (including some 35 domesticated species) in different ways and with different intensities within a subsistence system based on the multipurpose use of plant resources and ecosystems. The intensity of plant management appeared to be related to the cultural and economic importance of the plant, its ease of propagation, and a perception of scarcity. On average, some two-thirds of the variation in management intensity could be accounted for by sociocultural factors (e.g., frequency of consumption, number of uses, medicinal use, commercialization), and the remaining variation included 21% by ecological factors (e.g., temporal distribution of harvestable parts, life cycle, ecological dominance) and 12% by the intersection of ecological and sociocultural factors. More intensely managed species are likely subjected to greater selection pressures. Conversely, species that are merely gathered may not be strongly affected unless the gathering involves a selection *per se* for specific traits (e.g., 87).

The sociocultural organization of farmers plays a role in the structure of crop genetic diversity at the local level. This role is enhanced when crops play an important symbolic role in societies, such as maize in Mesoamerica and pearl millet in Africa. A clear relationship was observed between the spatial limits of genetic groups of pearl millet and boundaries among three ethnolinguistic groups west of Lake Chad (71). The authors attributed this situation to limited circulation of pearl millet, a crop that is generally inherited from fathers to sons, whose seeds are obtained generally from relatives and neighbors. Similar patterns were observed in African sorghum populations (177). At the level of the African continent, the molecular analysis identified three large geographic sorghum populations (each with their own ecogeographic races) that largely overlapped with local language families. These distributions reflect at least two past farming-language expansions, i.e., the Bantu and Nilo-Saharan expansions.

Although several factors could promote seed exchange across ethnolinguistic boundaries (such as the antiquity of pearl millet or sorghum cultivation, the mixing of landraces and fields, and the ever-increasing density of cultivation), barriers to seed circulation among ethnic groups in these regions seem to have the upper hand (e.g., 116). Correlations between genetic diversity and ethnolinguistic distributions are tied to accumulated local traditional knowledge (TK) and preferences concerning morphological and adaptive characteristics of plants and their use (16, 183). The importance of such knowledge cannot be overstated. For example, local communities in the Tehuacán valley of Mexico know of nearly 2,000 plant species, including their useful properties, distribution, year-to-year abundance, and interactions with other plants and animals (167). Agroforestry systems, such as coffee and cocoa plantations, are probably some of the oldest forms of agriculture. They can be particularly rich in biodiversity and TK associated with each biological and genetic resource they contain (89). In turn, this information can be the basis for intensification of new crops, such as indigenous fruit and nut trees (88). TK is, therefore, an integral part of crop

Traditional knowledge (TK): information, knowledge, and practices obtained and inherited by local or indigenous communities, generation after generation

biodiversity. Not surprisingly, recent international treaties on biodiversity have included TK as part of their purview.

Within ethnic groups, gender can sometimes be an important factor for farmer preferences. In Ethiopia, both genders ranked earliness as their top priority, most likely because this trait is crucial in assuring food security when faced with depletion of harvests from previous growing seasons. Additional shared preferences, with slightly different rankings, included yield, drought tolerance, and marketability. Women were more preoccupied with addressing fast cooking and taste, whereas men focused more on field problems, including germination and specific adaptation, and market demand (7). By contrast, a different study (179) did not observe gender differences regarding preferences for high grain yield, earliness, short heads, low kernel weight, and short plants. However, in this study, no postharvest traits like cooking and taste were reported. The diversity of household mixtures of food crops is, therefore, the outcome of a complex set of constraints, which vary across gender preferences and involvement in production, crop location, and time.

6.2. Farmer Practices and Crop Biodiversity

Farmers must make difficult decisions about farming practices that integrate a complex series of biological, climatic, and socioeconomic variables, over some of which they have little control. The practice of planting mixtures is widespread in subsistence agriculture, which is in contrast with industrial agriculture where genetic monocultures are the norm. Farmers in Eritrea and the neighboring province of Tigray in Ethiopia engage in the practice of planting mixtures of barley and wheat, called *hanfets* in the local Tigrigna language, as a means of dealing with the unpredictability of rainfall (179). In wet years, the higher yield potential of wheat is favored, whereas in dry years the higher drought tolerance of barley is advantageous. On average across locations and years, the yield of *hanfets* is like that of barley monoculture but markedly higher than that of wheat. Not all *hanfets* mixtures were more stable than pure crops, but generally, they showed fewer or no interactions with location or year within location, unlike pure barley or wheat.

Farmers use several approaches to conserve or enhance crop diversity in their fields. In Santa María Jaltianguis (Oaxaca, Mexico), farmers use three taxa of *Phaseolus* beans in their plantings, including two ecogeographic races of common bean (*P. vulgaris*, races Nueva Granada and Mesoamerica) and runner bean (*P. coccineus*), with distinct altitudinal adaptation (180). Farmers consider the altitude of each field to adjust the mixtures planted to increase the proportion of the most adapted component. For example, the most recent introduction of beans—small, black beans—constituted an attempt to introduce marketable beans; it required opening new fields at lower altitudes. Furthermore, farmers adapt these introduced beans to their local environmental conditions by unilateral introgressive hybridization with traditional beans, a process called creolization. Elsewhere, in the state of Guanajuato, Mexico, farmers maintain genetic diversity in the field at a level comparable to those observed in wild beans. They include existing landraces and an improved variety, and tolerate wild beans in their fields (184).

The practice of planting mixtures has several potential motivations. It is a risk-mitigating strategy when faced with a variable and uncertain biotic and abiotic environment; it is also a way of dealing with diverse topography spanning a range of microenvironments. Diverse plantings also cater to various postharvest needs, including different cooking characteristics and consumer tastes. Both bananas and beans in smallholder farms of Uganda showed high richness and evenness in frequency of traditional varieties (111). In locations with higher disease incidence of anthracnose (*Colletotrichum lindemuthianum*) and angular leaf spot (*Pseudocercospora griseola*), a negative correlation between richness and the disease index was observed, suggesting that increased within-field bean diversity can act as a partial disease control measure. In the Mulumba et al. (111) study, richness was determined on the basis of the number of traditional varieties

regardless of the genetic relatedness of the varieties. However, traditional bean varieties grown by households in Uganda include both Andean and Mesoamerican domesticates of *Phaseolus vulgaris* (178). For both diseases, there is a parallel organization of genetic diversity with Andean and Mesoamerican strains, which are more virulent on Andean and Mesoamerican hosts (52, 150), respectively. A household or community mixture consisting of both Andean and Mesoamerican varieties is inherently more resistant to diseases than varietal portfolios consisting of one or the other gene pool. Furthermore, a greater evenness in frequencies is more conducive to disease epidemic control, as is planting variety mixtures in spatial patterns within fields (111).

During the crop cycle, weeding plays an important role in maintaining the yield potential by removing damaging competition with crop plants. Cassava farmers practice selective weeding of volunteer plants resulting from outcrossing among clonal plants. Because there is a positive correlation between plant size and multilocus heterozygosity, the resulting volunteer population after weeding had a lower level of inbreeding (131). This example illustrates how farming practices exert an action on the genetic diversity of crops since domestication and up to today.

Farmers express preferences for certain agronomic, culinary, and consumption traits with varying degrees of heritability. These traits are important because they provide the basis for local adaptation addressing the needs of farmers and local consumers. In two Ethiopian communities, the inheritance of farmer preferences in their durum wheat crops was investigated (78). They combined quantitative evaluations of farmer preferences (for flowering time, spike morphology, tilling capacity, and overall quality) and measurements by researchers of agronomic and phenology traits in a collection of 400 Ethiopian wheat varieties, genotyped with single-nucleotide polymorphisms. For farmer traits, 124 putative QTLs were identified, whereas 30 putative QTLs were identified for researcher traits. Twenty of these were shared. This research showed that farmer evaluations were highly correlated across environments and, thus, reproducible and heritable.

6.3. Seed Systems

The previous examples illustrate that farmers in a subsistence context, i.e., often in centers of crop domestication, play an active role in managing their seed stocks, including their biodiversity, in their respective households. These farmer seed systems are often called informal in contrast with the commercial or state-led formal seed sector. Farmer seed networks can be described as systems through which plant materials may come from a range of sources, including farmers' saved seeds, other farmers, markets, nongovernmental organizations, national and international research institutions, and commercial seed suppliers (24, 178). These farmer networks disseminate not only seeds of wild plants but also new crops and new varieties created by on-farm management, including creolized varieties, increasing crop diversity and providing an avenue for resiliency in the case of biotic, abiotic, or economic shocks. Furthermore, informal systems may be the only system for crops overlooked by commercial systems and research, such as vegetables and grain legumes. An important part of crop biodiversity is, therefore, maintained by these informal networks. Maintaining this biodiversity requires further research and a legal and political system that supports both formal and informal seed systems (120).

6.4. Application to Participatory Breeding

The results of Kidane and coauthors (78), mentioned in Section 6.2, suggest that farmer knowledge can be integrated into modern plant breeding, using QTL mapping, marker-assisted selection, and genomic selection. However, can farmers themselves be engaged in plant breeding? This is a question that has been asked repeatedly in participatory research focusing on variety selection or breeding (reviewed in 20, 67, 148) in the hope of obtaining improved varieties that satisfy the

Seed system: a set of biological, social, and economic conditions that affect the production, storage, and distribution of cultivar seeds

Participatory research: collaborative research between scientists and farmers (or users) leading to the development of a research product or outcome

needs and preferences of farmers and consumers who live in diverse and variable environments. The example of beans in Honduras provides a strong confirmation of the success of participatory variety breeding (67) and reflects the use of local crop biodiversity, combined with advanced breeding lines in the development of locally released improved varieties. Additional examples of decentralized selection activities using local crop biodiversity are the on-farm stratified recurrent mass selection experiments conducted in maize. In these experiments, heterogeneous local maize populations planted in the field are divided into plots; in each plot, the best individuals are selected, and their seeds are pooled for the next generation. This process is then repeated several times until the necessary breeding objectives are achieved (4, 109, 153).

SUMMARY POINTS

1. Crop biodiversity is both one of the most important inventions of humanity and a crucial resource for plant breeding to develop crop varieties.
2. The overall evolutionary pattern of genetic diversity is one of gradual reduction due to demographic (genome-wide) and selective (gene-specific) causes from the initial domestication process until today. This reduction is tempered, however, by several factors including gene flow in wild \times domesticated and domesticated \times domesticated hybridizations, selection for functional diversity and broader adaptation, and, more recently and to a certain extent, modern plant breeding.
3. There is a cost to domestication owing to the accumulation of deleterious mutations in domesticated populations caused by limited recombination in populations with reduced effective size. A future focus of plant breeding will be the elimination of these deleterious alleles through recombination or targeted genome editing.
4. It remains to be determined to what extent the domestication syndrome and homologous series of crop variations are caused by genetic variation in similar (parallel evolution) or different genes or gene networks (convergent evolution). An answer to this question would help quantify the role of model systems and predictability across the taxa of candidate genes.
5. Plasticity is a form of genotype \times environment interaction. Its magnitude relative to total genetic variation, its inheritance and heritability, and its evolution remain to be fully understood.
6. Farmers are active agents of the conservation and development of genetic diversity, reflecting their membership in different ethnic and socioeconomic groups, their gender, and their farming practices. Their abilities to select and conserve genetic diversity are being utilized in participatory breeding, leading to the release of locally adapted varieties.

FUTURE ISSUES

1. To promote their utilization, gene banks will need in-depth characterization, including systematic DNA sequencing (e.g., 175), high-throughput phenotyping (146), and biochemical (19) and physiological observations (49), while maintaining current activities aimed at maintenance of the viability and disease-free status of collections (38).

2. Historical demography coupled with selection during domestication and adaptation have shaped crop diversity over millennia (176). We must therefore better understand how modern in situ diversity and the evolutionary potential of a crop have been determined by historical diversity in its progenitor, the strength of its domestication and expansion bottlenecks, and the historical opportunities for gene flow with locally adapted wild relatives.
3. A full accounting of temporal and spatial patterns of crop biodiversity require an understanding of how plants function at different levels from the genome to the whole-plant levels so that the effects of genes and gene networks can be translated into a population genetic perspective (e.g., 47, 75).
4. There is a need to assess the variation of plastic responses among wild ancestors to determine whether this variation was lost during domestication and whether it is advantageous in a domesticated genetic background and under agricultural conditions (29, 102).
5. The current emphasis on individual plants or crops should be complemented with a more comprehensive view of the crop's interactions with other plants, animals, and microorganisms in its (agro)ecosystem with potential benefits for plant breeding, integrated pest management, and crop husbandry (17, 61, 143).
6. The focus on crop wild relatives must be maintained, as these relatives have proven to be a source of additional genetic diversity, especially considering the overall reduction in genetic diversity of the domesticated gene pool and changes in pest and disease pressures, global climatic conditions, and market and consumer demands (28).
7. Local informal seed systems and participatory breeding involving farmers and scientists are crucial to promote utilization of crop biodiversity and maximize local adaptation, including consumer preference (67, 100).
8. Genetic conservation efforts, including gene banks, are chronically underfunded and deserve better support commensurate with their importance as stewards of biodiversity as an insurance policy for the adaptability and resilience of agro- and managed ecosystems (45, 62).
9. Because efforts such as the international Convention on Biological Diversity (and its agreements like the Nagoya Protocol), as well as the national Intellectual Property Law, have had counterproductive effects, limiting the use and conservation of this diversity (33, 44), a significant legal effort needs to be developed to promote research and education in biodiversity conservation.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

Recent research by M.B.H. in this area has been supported by National Science Foundation (NSF) grant IOS-1546719. P.G. received recent funding from the US Department of Agriculture, National Institute of Food and Agriculture (2013–67013–21224 and 2016–67013–24460)

and NSF ERA-CAPS (European Research Area Network for Coordinating Action in Plant Sciences) (1539848). We thank J. Dubcovsky for a helpful discussion of the parallel and convergent evolution and genetic diversity of wheat.

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178. Illustrates how farmer management and participatory research affect seed stock genetic diversity, based on genotypic information.

180. Shows farmers' awareness of adaptation of species-level adaptation and the directed adaptation to local conditions (creolization) by introgressive hybridization.

RELATED RESOURCES

Crop Trust. <https://www.croptrust.org/>

Crop Wild Relatives. <https://www.cwrdiversity.org/>

Food Agric. Organ. United Nations. *What Is Agrobiodiversity?* <http://www.fao.org/docrep/007/y5609e/y5609e01.htm#TopOfPage>

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Errata

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