Crop wild relatives of the United States require urgent conservation action

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The contributions of crop wild relatives (CWR) to food security depend on their conservation and accessibility for use. The United States contains a diverse native flora of CWR, including those of important cereal, fruit, nut, oil, pulse, root and tuber, and vegetable crops, which may be threatened in their natural habitats and underrepresented in plant conservation repositories. To determine conservation priorities for these plants, we developed a national inventory, compiled occurrence information, modeled potential distributions, and conducted threat assessments and conservation gap analyses for 600 native taxa. We found that 7.1% of the taxa may be critically endangered in their natural habitats, 50% may be endangered, and 28% may be vulnerable. We categorized 58.8% of the taxa as of urgent priority for further action, 37% as high priority, and 4.2% as medium priority. Major ex situ conservation gaps were identified for 93.3% of the wild relatives (categorized as urgent or high priority), with 83 taxa absent from conservation repositories, while 93.1% of the plants were equivalently prioritized for further habitat protection. Various taxonomic richness hotspots across the US represent focal regions for further conservation action. Related needs include facilitating greater access to and characterization of these cultural-genetic-natural resources and raising public awareness of their existence, value, and plight.

biodiversity conservation | crop diversity | culturally significant plants | food security | plant genetic resources

Wild plants related to domesticated crops provide important genetic resources for plant breeding (1, 2). Owing to their close evolutionary relationships with cultivated species, traits from crop wild relatives (CWR) can be introgressed into domesticates with relative ease (3, 4). These plants are central to research on domestication, evolution, and anthropology (5–8) and may themselves be attractive candidates for de novo domestication (9). Furthermore, many of these species are collected for direct dietary and other cultural uses (10, 11). As populations of some of these taxa are adapted to extreme climates, adverse soil types, and significant pests and diseases, they have been identified as key contributors in breeding for sustainability and climate adaptation (12). As characterization and breeding technologies advance, their use in crop improvement will also become more efficient (1, 13).

Knowledge gaps regarding CWR, including information on their taxonomy, relatedness to pertinent crops, geographic distribution, ecological interactions, agriculturally relevant traits, and degree of representation in conservation systems, constrain their potential use in crop improvement (1). These gaps likewise affect conservation efforts, which are essential to protect vulnerable populations from habitat destruction, climate change, pollution, invasive species, and overharvesting in their natural habitats (in situ), and to ensure that these cultural-genetic-natural resources are safeguarded over the long term and available for research and education in ex situ plant conservation repositories (i.e., gene banks and botanical gardens) (14–16). Previous analyses indicate that many CWR are poorly conserved both in situ and ex situ, highlighting the urgency of addressing fundamental information gaps to support efforts related to their conservation and accessibility for use (16–18).

Here we develop a national inventory of CWR of the United States, wherein taxa are classified based on current knowledge of their relation to agricultural crops and their significance as wild food sources (SI Appendix, Table S1). We use occurrence information combined with climatic and topographic data to model the potential distributions of 600 prioritized native wild taxa, including wild relatives of apples (Malus Mill.); barleys (Hordeum L.); beans (Phaseolus L.), blueberries and cranberries (Vaccinium L.), chile peppers (Capsicum L.), cotton (Gossypium L.), currants (Ribes L.), grapes (Vitis L.), hops (Humulus L.), onions (Allium L.), pears (Pyrus L.), plums (Prunus L.), potatoes (Solanum L.), pumpkins and zucchini (Cucurbita L.), raspberries and blackberries (Rubus L.), strawberries (Fragaria L.), sunflowers (Helianthus L.), sweetpotatoes (Ipocea L.), and other crops (SI Appendix, Table S2). We then use ecogeographic tools to conduct preliminary threat assessments and conservation gap analyses for the CWR. These are based on an approximation of the distribution of species’ genetic diversity, using the extent of geographic and ecological variation in their predicted native ranges as a proxy, which has been

Significance

This study provides conservation assessments for 600 US native plants that are wild relatives of important agricultural crops. We found that more than one-half of the species may be endangered in their natural habitats, and that the great majority require further conservation action, both ex situ (in gene banks and botanical gardens) and in situ (in protected areas). Diversity hotspots across the nation represent focal regions for further collecting for ex situ conservation as well as for enhanced habitat protection. Wider collaborations, as well as greater awareness, access to, and information about these resources are needed to bolster their conservation and use.

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shown to be an effective surrogate (19, 20), facilitating conservation planning despite pervasive gaps in population-level genetic data (20–22). The ecogeographic variation evident in the locations where ex situ conservation samples have been collected and evident in species’ ranges distributed within protected natural areas is measured against the variation found within species’ overall predicted native ranges. Geographic and ecological gaps in current conservation are then identified, providing baseline information for conservation planning, prioritization, and action.

Results

The predicted distributions of the assessed US native CWR ranged from northern Alaska through southern Mexico and the Caribbean and out to Hawaii (Fig. 1). Taxonomic richness across all modeled taxa was concentrated in parts of the Northeast and Midwest, the Pacific Northwest and California, the Mountain West and Southwest, and the Gulf Coast region of the Southeast, with the predicted ranges of up to 91 taxa overlapping in the same ∼5 km² areas.

The assessed crop progenitors and closest wild relatives (1A taxa) displayed the highest predicted richness in the Northeast, Midwest, and Pacific Northwest, with up to 53 taxa overlapping in the same areas (SI Appendix, Fig. S1). Distant relatives (1B) were more evenly dispersed, with concentrations in the Mountain West, Southwest, Pacific Northwest and California, and Midwest and Northeast, with up to 32 taxa overlapping in the same areas. Those taxa with undetermined relation status (1C), which are likely in general to be distant relatives, had the highest predicted richness in the Southwest and Midwest, with up to 29 taxa overlapping. Richness patterns also varied by associated crop and crop type. For instance, the predicted ranges of wild relatives of cereals were concentrated in the western United States; fruits in the temperate regions of the Northeast and Pacific Northwest; vegetables in the Mountain West, Pacific Northwest, and Midwest; nuts in the eastern United States; sugar crops in the Southeast; and pulses, roots and tubers, and fiber crops in the Southwest desert borderlands (SI Appendix, Fig. S2).

Interactive predicted distribution maps for each assessed taxon are provided in Dataset S1 (23).

Preliminary threat assessments, based on extent of occurrence (EOO) and area of occupancy (AOO) analyses (SI Appendix, Table S3) (24), identified 42 taxa (7.1%) as candidates for designation as critically endangered (CR) in their natural habitats, 297 (50%) as endangered (EN), 166 (28%) as vulnerable (VU), 66 (11.1%) as near threatened (NT), and the remaining 23 (3.9%) as of least concern (LC) (SI Appendix, Table S4). AOO was the primary determinant of these designations. Of the 1A taxa, 16 (6.3%) may be considered CR, 121 (47.8%) as EN, 71 (28.1%) as VU, 37 (14.6%) as NT, and 8 (3.2%) as LC.

With regard to ex situ conservation, more than 400 gene banks and botanical gardens worldwide safeguard one or more of the assessed US native CWR. The US Department of Agriculture (USDA) Agricultural Research Service, National Plant Germplasm System; national gene banks in India, Australia, Mexico, Morocco, Brazil, Bulgaria, Canada, Ecuador, Germany, the United Kingdom, Japan, and the Russian Federation; and international agricultural research institutes, including the International Potato Center and the International Center for Tropical Agriculture, hold the greatest numbers of accessions, with 35.9% of the total accessions maintained in the USDA’s system and 79.5% maintained in these repositories collectively (Dataset S2) (23).

Comparing the diversity conserved in these ex situ collections to the predicted native ranges of the plants, we found the great majority of taxa to be significantly underrepresented ex situ. Eighty-three taxa (14% of the total) were entirely absent from the available germplasm and botanical garden databases, and an additional 196 taxa (33%) had fewer than 10 accessions in conservation repositories, thus offering relatively limited genetic variation for research and education (SI Appendix, Table S4). A total of 454 taxa (76.4%) were assessed as urgent priority for further collecting to address gaps in ex situ conservation, with an additional 100 (16.8%) considered high priority, 33 (5.6%) considered medium priority, and only 7 (1.2%) considered low priority (Fig. 2). The mean final ex situ conservation score (FCSex) across taxa was only 13.9 (median, 5.7) on a conservation status scale of 0 (very poor) to 100 (comprehensive), with metrics ranging from 0 to 92.8. The ecological representation of

Fig. 1. Predicted taxonomic richness map for assessed US native CWR, combining 552 potential distribution models. Darker colors indicate greater numbers of taxa potentially overlapping in the same (~5 km²) areas.
Based on their predicted distributions, we found that more than 32,000 protected land areas listed in the World Database of Protected Areas (WDPA) (26) and located in the United States potentially harbor the assessed taxa (SI Appendix, Table S5). Of these, protected areas in the Northeast and East (especially Delaware, Maryland, New Jersey, New York, and Pennsylvania, and Midwest (Illinois and Missouri) potentially provide protection to the greatest numbers of taxa, with a maximum of 89 predicted to occur in a 5-km² area within protected lands. Based directly on occurrence data rather than on modeled distributions, assessed taxa have been sampled from more than 3,800 protected areas in the United States. In this group, the most taxon-rich areas included the Patuxent Research Refuge as well as the Grand Canyon, Kings Canyon, Olympic, Mount Rainier, Indiana Dunes, Gulf Islands, Yellowstone, Rocky Mountain, and other national parks, shores, and wilderness areas.

Despite the large number of protected areas potentially harboring these CWR, the known occurrences and predicted ranges of most of the species were generally poorly represented in protected lands, with a mean final in situ conservation score (FCSin) across all taxa of 35.9 (median, 36.9) (SI Appendix, Table S4). Forty-three taxa (7.2%) were found to have no overlap with protected areas. In total, 66 taxa (11.1%) were designated as urgent priority, 487 (82%) as high priority, 34 (5.7%) as medium priority, and only 7 (1.2%) as low priority for further habitat protection (Fig. 2). Even more pronounced than in the ex situ analysis, ecological representativeness (ERSin) regarding habitat protection (mean, 89.8; median, 95.5) was much higher than geographic (GRSin) (mean, 11.1; median, 8.2), including 245 (41.3%) of the taxa potentially fully represented in protected areas in terms of the diversity of inhabited ecoregions. Of the 1A taxa, 31 (12.3%) were designated as urgent priority, 204 (80.6%) as high priority, 16 (6.3%) as medium priority, and only 2 (0.8%) as low priority for further habitat protection.

Representation of little sunflower in protected areas based on its predicted distribution, as well as the gaps in its potential habitat protection, are depicted in Fig 3C as an example of taxon-level results. The taxon was modeled as occurring in wild areas of the Rocky Mountains. These protected lands collectively occupy a relatively small portion of the species’ predicted range (GRSin of 5.3) but are fairly well distributed and thus represent all five of the ecoregions that it potentially inhabits (ERSin of 100). The most obvious in situ conservation gaps in its predicted range occur in its northern extents in Wyoming and in eastern lower elevation areas. SI Appendix, Figs. S3 and S4 provides additional taxon-level examples, and Dataset S1 (23) provides complete results, including interactive maps, for all taxa.

The major geographic and ecological gaps in ex situ conservation of these wild taxa indicate the need for extensive further collecting throughout most of their predicted ranges. Spatial priorities for collecting thus largely mirror patterns of taxonomic richness, with uncollected populations of up to 89 taxa potentially found in the same ~5 km² areas (SI Appendix, Figs. S5 and S6).

Based on their predicted distributions, we found that more than 32,000 protected land areas listed in the World Database of Protected Areas (WDPA) (26) and located in the United States potentially harbor the assessed taxa (SI Appendix, Table S5). Of these, protected areas in the Northeast and East (especially Delaware, Maryland, New Jersey, New York, and Pennsylvania, and Midwest (Illinois and Missouri) potentially provide protection to the greatest numbers of taxa, with a maximum of 89 predicted to occur in a 5-km² area within protected lands. Based directly on occurrence data rather than on modeled distributions, assessed taxa have been sampled from more than 3,800 protected areas in the United States. In this group, the most taxon-rich areas included the Patuxent Research Refuge as well as the Grand Canyon, Kings Canyon, Olympic, Mount Rainier,
With regard to their combined ex situ and in situ conservation status, which represents an average of the results of the two conservation strategy assessments, individual determinations for taxa ranged from no protection at all (22 taxa; 3.7% of the total, including CWR of beans, blackberries and raspberries, blueberries, grapes, pecans, strawberries, and sunflowers, many of which are natural hybrid taxa) to a moderate level of conservation. For example, the final combined conservation score (FCSc-mean) was 69.3 on a scale of 0 to 100 for Oregon endemic wild strawberry _Fragaria cascadenensis_ K. E. Hummer, 62.9 for a Hawaiian blueberry (_Vaccinium reticulatum_ Sm.), 61.8 for a Santa Cruz Island gooseberry (_Ribes tachetianum_ [Jeps.] Munz) endemic to the Channel Islands, and 58.1 for a recently described wild sunflower (_Helianthus winteri_ J. C. Stebbins) with a narrow range in central California (SI Appendix, Table S4). The FCSc-mean averaged across all taxa was 24.9 (median 23.1). Based on the average of their ex situ and in situ conservation status, 349 taxa (58.8%) were identified as urgent priority for further action, 220 (37%) as high priority, 25 (4.2%) as medium priority, and none as low priority (Fig. 2).

Of the 1A taxa, 135 (53.4%) were classified as urgent priority for further action based on combined ex situ and in situ conservation status, 101 (39.9%) as high priority, and 17 (6.7%) as medium priority, with an average FCSc-mean of 26.8 (median, 24.2) (SI Appendix, Fig. S9). Regarding associated crop types, US native cereal, fruit, nut, root and tuber, sugar, and vegetable CWR had the largest proportions of taxa determined to be urgent priority for further action (SI Appendix, Fig. S10). Regarding associated crops and wild food plants, those of avocado, chestnut, citrus, melon, pecan, potato bean, sugar maple, sugar-cane, vanilla, and wildrice demonstrated the most urgent priorities on average across taxa, whereas relatives of beans, cherimoya, echinacea, sunflower, and zucchini were of somewhat lesser immediate concern (Fig. 4). Comparing the preliminary threat assessment results with the combined conservation gap analysis showed that the most threatened taxa (assessed as CR or EN) were also generally those with the most urgent priorities for conservation action (SI Appendix, Fig. S11).

**Discussion**

Further conservation action for US native CWR is clearly needed, both to safeguard their diversity in ex situ repositories and to facilitate their continued evolution in their natural habitats. Among the taxa assessed to be of urgent conservation priority are wild genetic resources of cereal, fiber, fruit, nut, oil, pulse, root and tuber, spice, sugar, and vegetable crops that collectively generate more than $116 billion in annual US agricultural production value (27). In sunflower alone, whose CWR are exclusively native to North America, the direct annual economic benefits derived from use of the wild taxa have been estimated at $267 to 384 million (28). Here we discuss the critical steps needed to enhance conservation and facilitate use of these cultural-genetic-natural resources, including conducting further field exploration and validation, strengthening collaborative conservation, characterizing and facilitating access to the plants, and raising awareness about their existence, value, and plight.

Species distribution modeling and model-based conservation biogeography are increasingly critical to conservation planning (29), particularly for large-scale prioritization analyses such as this national study, given the increasing numbers of threatened species and decreasing numbers of field botanists (30). Occurrence, ecogeographic predictor, and conservation data deficiencies, as well as modeling method limitations, make field validation of modeling results an essential step before conservation action. (An extended discussion of data and modeling challenges is provided in SI Appendix, Materials and Methods.) Engagement of volunteer botanists, local botanical societies and gardens, students, and other citizen science stakeholders through collaborative initiatives with backstopping from species experts represents a promising approach to accomplishing the discovery, verification, monitoring,
and collection of native CWR populations (31). Meanwhile, further investment by biodiversity, geospatial, and conservation information providers in making these data as complete, correct, and accessible as possible, including incorporating new data from emerging fieldwork, will only improve the potential of conservation biogeographic analyses.

Given the diversity of US native CWR prioritized for action, ambitious collaborative conservation efforts are needed among gene banks, botanical gardens, community conservation initiatives, and organizations focused on habitat conservation (32). Botanical gardens, employing an extensive network of conservation botanists and managing >80,000 acres in North America (33), offer unique opportunities to complement public gene banks in mobilizing field collecting activities and protecting native CWR that do not store well in freezers, in vitro, or in liquid nitrogen, as well as for long-lived, large plants whose propagules may be more easily distributed from adult individuals. Hobby gardeners and other citizen conservationists could be further engaged to curate CWR, especially those with edible fruit, ornamental value, or other attractive traits. Meanwhile, a primary emphasis on in situ conservation is required for taxa that are difficult to maintain outside of their specific natural habitats, such as the federally listed endangered Texas wildrice (Zizania texana Hitchc.).

While extensive field verification, population monitoring, and management planning are needed before a comprehensive national assessment of the in situ status of these taxa is complete, our analyses indicate that expansion of habitat protection in the country, especially within richness hotspots, is needed to safeguard the evolutionary potential of various native CWR over the long term. While the widening of current protected area boundaries or the establishment of new protected spaces may be necessary to accomplish these aims, the challenges to their implementation owing to cost and competing land uses indicate that enhancement of protection on existing open spaces—whether officially protected areas or other effective area-based conservation lands (34)—may be the most feasible approach. Assisted migration of populations into suitable habitats within conservation areas may also be considered. Greater awareness of native CWR by land managers is needed, as the plants are sometimes viewed as weeds or nuisances and may be mistaken for invasive species (18).

Given that the primary justification for conservation of these plants is their usefulness to people—both as genetic resources for research and as direct contributors to human diets and

Fig. 4. Final conservation scores (FCSc-mean) for US native CWR (black circles), grouped by associated crop/wild food plant, with the average score across taxa (red circles). FCSc-mean, the average of the FCSex and FCSin scores, is used to categorize taxa for further action as UP (FCSc-mean < 25), HP (25 ≤ FCSc-mean < 50), MP (50 ≤ FCSc-mean < 75), or LP (FCSc-mean ≥ 75).
culture—it stands to reason that greater awareness of and access to native CWR for use, and more extensive characterizations of their traits, should bolster support for their protection. In turn, conservation of these plants in their natural habitats will also help safeguard ecosystems, other species, and holobionts, providing additional known as well as currently unrecognized benefits to society. Thus, wider awareness of and access to CWR must be integrated into their conservation. For research and education, access via ex situ conservation repositories is related to the degree to which samples are available and have been characterized for their known or potential traits of value. Both aspects can be strengthened through the enhancement of existing online information and ordering systems, including better integration of these platforms so that the overall diversity of taxa across ex situ repositories can be more easily explored. The limited characterization and evaluation of these plants for projected needs represents a major bottleneck in current use of the taxa (1). Access for study of these plants in their natural habitats is also needed (8).

As many native CWR are culturally significant, providing food, spice, and other values to wild harvesters and their communities and markets, ensuring continued access to these resources from their traditionally harvested places is necessary. Consideration and participation in conservation planning of communities who use these plants are essential, given that they are important influencers of the viability of CWR populations and that their exclusion in the name of conservation has been shown to damage this diversity (35, 36).

Achieving CWR’s full potential as conservation champions will require greater public awareness of these plants. While all involved organizations will need to enhance their public outreach around native CWR, botanical gardens, which receive more than 120 million visitors a year in the United States (33), could play a particularly pivotal role in introducing these species to people, communicating their value and plight, and better connecting the concepts of food security, agricultural livelihoods, and services provided by nature for the public (37).

Materials and Methods

We developed a current national inventory of CWR of the United States by verifying taxonomic names (38) listed in a published baseline (11), updating gene pool assignments (39), and ensuring inclusion of all target taxa occurring in the country and its territories (SI Appendix, Table S1). We categorized taxa based on relative crossability with and phylogenetic relation to associated crops, as well as on occurrence status, with category 1A comprising native close relatives of globally important agricultural crops (including the taxa listed as primary or secondary relatives or used as rootstock or putative parents of introduced crops) (38). Category 1B included distant (tertiary) relatives of these crops, while 1C included any other taxa in the same genera but with undetermined relationships. In total, 594 taxa are reported in the main results, including the taxa listed as primary or secondary relatives or used as root/graft of associated crops, as well as on occurrence status, with category 1A comprising the proportion of each taxon’s gene pool assignments and that the exclusion in the name of conservation has been shown to damage this diversity (35, 36).

We produced species distribution models with the MaxEnt algorithm (48) using 26 bioclimatic and topographic predictors (14) and run through the R package “RedList” (52). Taxa were classified as CR when EOO < 100 km² or AOO < 10 km², as EN when 100 km² ≤ EOO < 5,000 km² or 10 km² ≤ AOO < 500 km², as VU when 5,000 km² < EOO < 20,000 km² or 100 km² < AOO < 2,000 km², as NT when 20,000 km² ≤ EOO ≤ 45,000 km² or 10 km² < AOO < 20 km² ≤ AOO < 4,500 km², and as LC when EOO ≥ 45,000 km² and AOO ≥ 5,000 km².

We assessed the degree of representation of each taxon in ex situ and in situ conservation systems, with four scores calculated for each conservation strategy (SI Appendix, Table S3). All scores were bounded between 0 and 100, with 0 representing an extremely poor state of conservation and 100 representing comprehensive protection (10, 17). The sampling representativeness score ex situ (SRSex) calculates the ratio of germplasm accessions (G) available in ex situ repositories to reference (H) records for each taxon, making use of all compiled records irrespective of whether they include coordinate information. The GRSsex uses 50-km-radius buffers created around each G collection coordinate point to estimate geographic areas already well collected within the distribution models of each taxon and then calculates the proportion of the distribution model covered by these buffers. The ERSsex calculates the proportion of terrestrial ecoregions (25) represented within the G buffered areas out of the total number of ecoregions occupied by the distribution model. The FCSex was derived by calculating the average of the three ex situ conservation metrics.

In situ conservation was analyzed based on extent of taxon range representation within protected areas listed in the WDPA (26). The sampling representativeness score in situ (SRSin) calculates the proportion of all occurrences of a taxon within its native range that fall within a protected area. The GRSin compares the area (in km²) of the distribution model located within protected areas versus the total area of the model. The ERSin calculates the proportion of ecoregions encompassed within the range of the taxon located inside protected areas to the ecoregions encompassed within the total area of the distribution model. The FCSex was derived by calculating the average of the three in situ conservation metrics. The FCSex-mean was calculated for each taxon by averaging its final FCSex and FCSin scores. Taxa were then categorized with regard to the two conservation strategies as well as in combination, with UP for further conservation action assigned when FCSEX < 25, HP assigned when 25 ≤ FCSEX < 50, MP when 50 ≤ FCSEX < 75, and LP when FCSEX ≥ 75. An extended description of methods and materials, including references and links to the ecoregographic and spatial input data and code; the US inventory; occurrence data; and further results, including interactive taxon-level models and conservation metrics, are provided in the SI Appendix.

Data Availability. Geographic data and interactive taxon-level models and conservation metrics results have been deposited in the Dataverse repository (https://doi.org/10.7910/DVN/BV4106).

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