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.), barley (*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.), pecans (*Carya* Nutt.), plums (*Prunus* L.), potatoes (*Solanum* L.), pumpkins and zucchini (*Cucurbita* L.), raspberries and blackberries (*Rubus* L.), strawberries (*Fragaria* L.), sunflowers (*Helianthus* L.), sweetpotatoes (*Ipomoea* 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 km^2 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

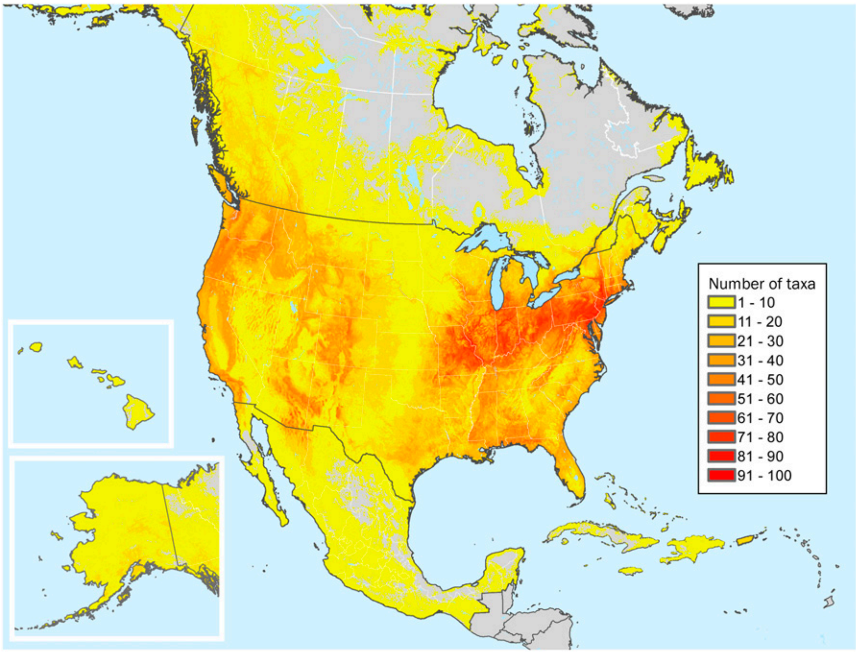

Fig. 1. Predicted taxonomic richness map for assessed US native CWR, combining 552 potential distribution models. Darker colors indicate greater numbers of taxa potentially overlapping in the same (~5 km^2) areas.

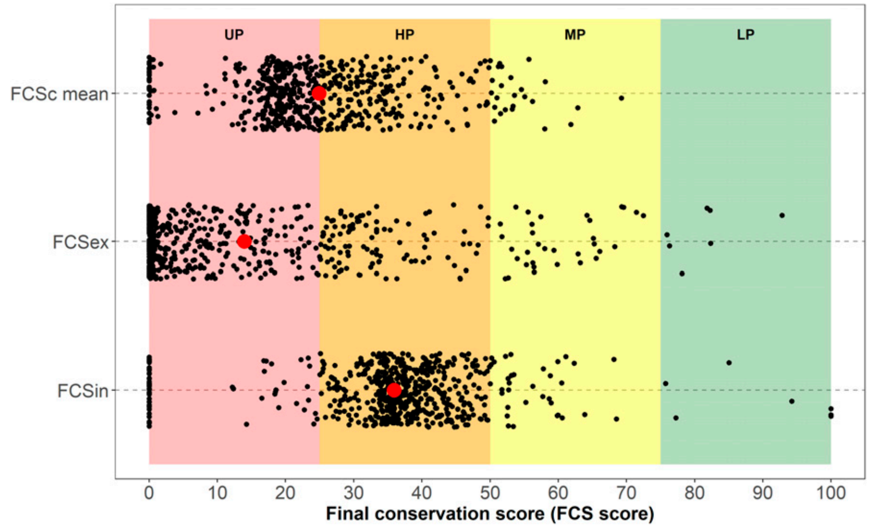

Fig. 2. Conservation scores per US native CWR (black circles), grouped by conservation assessment type—combined FCSc-mean, FCSex, and FCSin—with the average score across taxa displayed as red circles. FCS scores are used to categorize taxa for further conservation action: UP (FCS <25), HP (25 ≤ FCS < 50), MP (50 ≤ FCS < 75), and LP (FCS ≥75).

taxa—based on an analysis of the proportion of potentially inhabited ecoregions (25) in which samples have been collected for conservation repositories—was considerably higher than geographic representation, with a mean ecological representativeness score (ERSex) of 24.9 (median, 7.7), compared with 9.7 (median, 0.5) for the geographic score (GRSex). Of the 1A taxa, 173 (68.4%) were identified as urgent priority for further collecting, 53 (21%) as high priority, 20 (7.9%) as medium priority, and only 7 (2.8%) as low priority.

Visual depictions of the predicted distribution and representation in conservation repositories of little sunflower (*Helianthus pumilus* Nutt.), a CWR of cultivated sunflower native to Colorado and Wyoming, are provided in Fig. 3 *A* and *B* as an example of taxon-level results. The species' ex situ conservation occurrences are well distributed throughout its predicted range (GRSex of 83.2) and provide representation from all five of the ecoregions that it potentially inhabits (ERSex of 100), leaving collecting gaps mainly in the northernmost and other outlying areas of its predicted native range. Two additional taxon-level examples are offered in *SI Appendix*, Figs. S3 and S4, and individual results for all assessed taxa, including interactive maps, are provided in Dataset S1 (23).

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 km^2 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-km^2 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 3*C* as an example of taxon-level results. The taxon was modeled as occurring in wilderness and other protected areas along its north-south gradient in 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 most efficient establishment of additional in situ protection for the maximum number of US native CWR, based on predicted distributions falling outside current WDPA-designated protected areas, would focus on the Northeast and Midwest, the West Coast, and parts of the Mountain West and Southeast (*SI Appendix*, Figs. S7 and S8). Unprotected populations of up to 91 taxa for geographic gaps and up to 33 taxa for ecological gaps could potentially be found in the same ~5-km^2 area.

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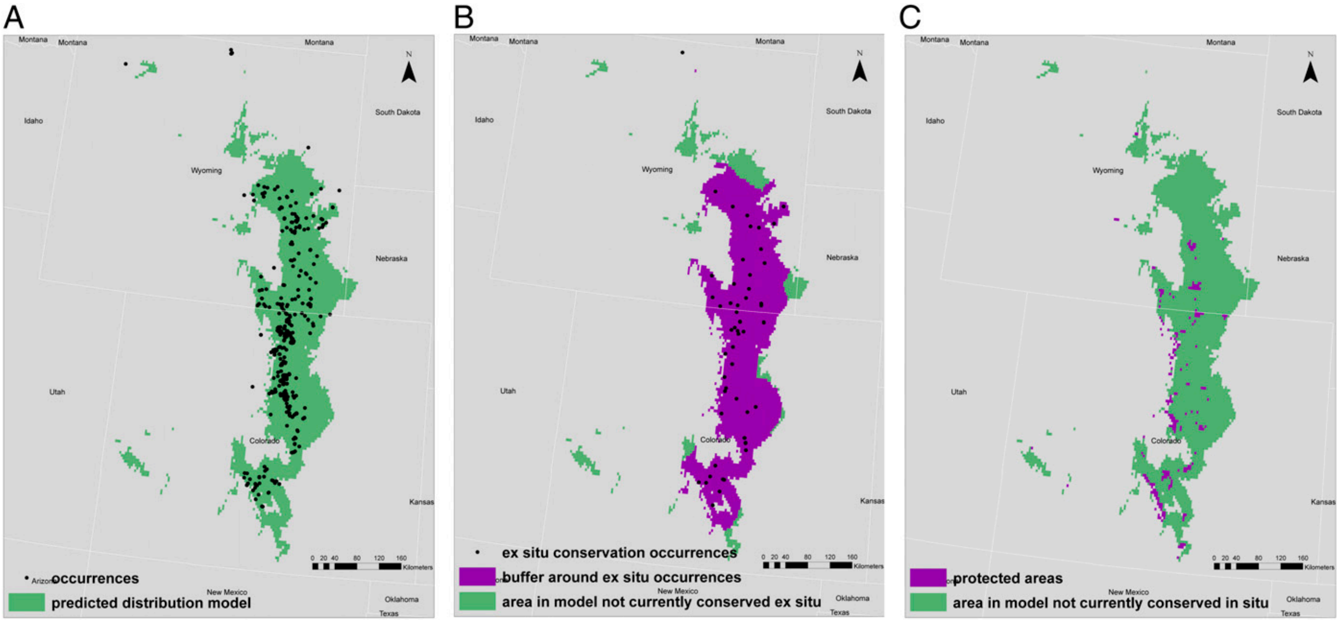

Fig. 3. Predicted distribution, conservation representation, and conservation gaps for little sunflower (*H. pumilus* Nutt.). (*A*) Occurrences and modeled distribution. (*B*) Geographic representation of the taxon in ex situ conservation repositories and gaps. The species' ex situ conservation occurrences are well distributed throughout its predicted range (GRSex of 83.2) and provide representation from all five of the ecoregions that it potentially inhabits (ERSex of 100). (*C*) Geographic representation of the taxon in protected areas and gaps. The taxon was modeled as occurring in protected areas along its north-south gradient in the Rocky Mountains, collectively occupying a relatively small portion of the species' predicted range (GRSin of 5.3) but well distributed and thus representing all ecoregions (ERSin of 100). The FCSex was 64.2 and the FCSin was 38.9, leading to a combined score (FSCc-mean) of 51.5, categorized as medium priority for further conservation action.

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 cascadensis* K. E. Hummer, 62.9 for a Hawaiian blueberry (*Vaccinium reticulatum* Sm.), 61.8 for a Santa Cruz Island gooseberry (*Ribes thacherianum* [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, sugarcane, 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,

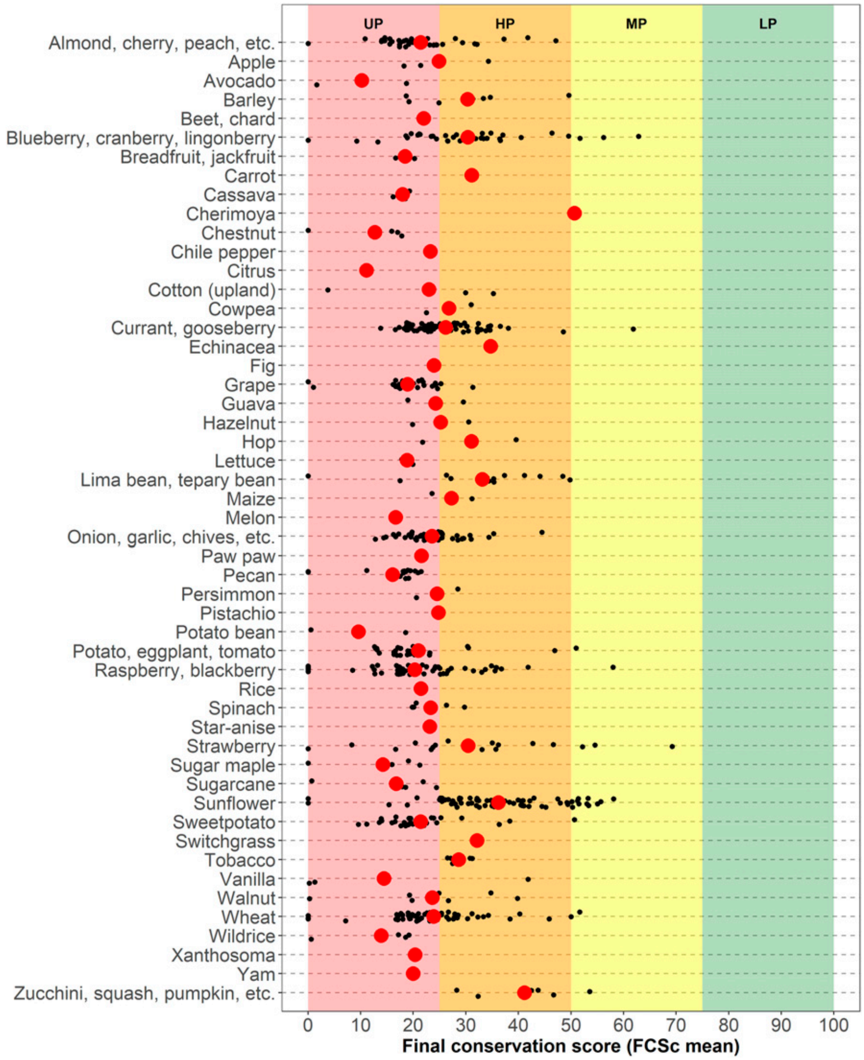

Fig. 4. Final conservation scores (FCSc-mean) for US native CWR (black circles), grouped by associated crop/wild food plant, with the average score across taxa (red circles). FCSc-mean, the average of the FCSex and FCSin scores, is used to categorize taxa for further action as UP (FCSc-mean <25), HP (25 ≤ FCSc-mean < 50), MP (50 ≤ FCSc-mean < 75), or LP (FCSc-mean ≥75).

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 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 root/graft stock), as well as important wild food plants (11, 39). Category 1B included distant (tertiary) native 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 253 in category 1A, 188 in 1B, and 153 in 1C (*SI Appendix*, Tables S2 and S4).

Occurrence data were compiled from biodiversity and conservation repository databases (40–46) and recent literature (17, 18, 47). Identifiable duplicates and nonwild records were removed, and taxonomic names were standardized (38). We classified each record as an existing ex situ accession (labeled "G," because most records were from gene banks) or as a reference observation (labeled "H," because most records were from herbaria) (10). Occurrences were clipped to their native states/provinces (38) within the United States, Canada, and Mexico, as well as to US territories and Caribbean islands. We compiled and processed a total of 834,673 occurrence records for the 594 target taxa, including 32,786 G and 801,887 H (*SI Appendix*, Table S4). Of these, 276,312 (8092 G and 268,220 H) had coordinates located in the target native areas of the taxa and were used for distribution modeling and spatial conservation analyses. The final occurrence dataset is available in Dataset S2 (23).

We produced species distribution models with the MaxEnt algorithm (48) using 26 bioclimatic and topographic predictors (*SI Appendix*, Table S6) (49, 50) at a spatial resolution of 2.5 arc-min, using a subset of variables (51) (*SI Appendix*, Table S7) as well as the number and location of pseudoabsences specific to each taxon. Median models across MaxEnt replicates were evaluated using the area under the receiver operating characteristic curve (AUC), the SD of the AUC across replicates, and the proportion of the potential distribution model with an SD of the replicates >0.15 (17) (*SI Appendix*, Table S4). Interactive models and evaluation metrics for each taxon are available in Dataset S1 (23).

For the preliminary threat assessment, we calculated the EOO and AOO of each taxon (*SI Appendix*, Table S3), adapted from the International Union for Conservation of Nature (IUCN) Red List criteria (AOO cell size 4 km^2) (24) and run through the R package "Redlistr" (52). Taxa were classified as CR when EOO <100 km^2 or AOO <10 km^2, as EN when 100 km^2 < EOO < 5,000 km^2 or 10 km^2 < AOO < 500 km^2, as VU when 5,000 km^2 < EOO < 20,000 km^2 or 500 km^2 < AOO < 2,000 km^2, as NT when 20,000 km^2 > EOO < 45,000 km^2 or 2,000 km^2 < AOO < 4,500 km^2, and as LC when EOO ≥45,000 km^2 and AOO ≥ 4,500 km^2.

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 bound 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 coordinates. The GRSex 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 ERSex 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 km^2) 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 FCSin was derived by calculating the average of the three in situ conservation metrics.

The FCSc-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 FCS <25, HP assigned when 25 ≤ FCS < 50, MP when 50 ≤ FCS < 75, and LP when FCS ≥75. An extended description of methods and materials, including references and links to the ecogeographic 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/BV4I06).

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1. H. Dempewolf *et al*., Past and future use of wild relatives in crop breeding. *Crop Sci.* **57**, 1070–1082 (2017).
2. R. Hajjar, T. Hodgkin, The use of wild relatives in crop improvement: A survey of developments over the last 20 years. *Euphytica* **156**, 1–13 (2007).
3. A. Gur, D. Zamir, Unused natural variation can lift yield barriers in plant breeding. *PLoS Biol.* **2**, e245 (2004).
4. S. D. Tanksley, S. R. McCouch, Seed banks and molecular maps: Unlocking genetic potential from the wild. *Science* **277**, 1063–1066 (1997).

5. J. F. Doebley, B. S. Gaut, B. D. Smith, The molecular genetics of crop domestication. *Cell* **127**, 1309–1321 (2006).
6. G. Larson *et al*., Current perspectives and the future of domestication studies. *Proc. Natl. Acad. Sci. U.S.A.* **111**, 6139–6146 (2014).
7. R. S. Meyer, M. D. Purugganan, Evolution of crop species: Genetics of domestication and diversification. *Nat. Rev. Genet.* **14**, 840–852 (2013).
8. Y. H. Chen, L. R. Shapiro, B. Benrey, A. Cibrián-Jaramillo, Back to the origin: In situ studies are needed to understand selection during crop diversification. *Front. Ecol. Evol.* **5**, 125 (2017).
9. C. Ciotir *et al*., Building a botanical foundation for perennial agriculture: Global inventory of wild, perennial herbaceous Fabaceae species. *Plants People Planet* **1**, 375–386 (2019).
10. C. K. Khoury *et al*., Comprehensiveness of conservation of useful wild plants: An operational indicator for biodiversity and sustainable development targets. *Ecol. Indic.* **98**, 420–429 (2019).
11. C. K. Khoury *et al*., An inventory of crop wild relatives of the United States. *Crop Sci.* **53**, 1496 (2013).
12. H. Dempewolf *et al*., Adapting agriculture to climate change: A global initiative to collect, conserve, and use crop wild relatives. *Agroecol. Sustain. Food Syst.* **38**, 369–377 (2013).
13. I. K. Dawson *et al*., The role of genetics in mainstreaming the production of new and orphan crops to diversify food systems and support human nutrition. *New Phytol.* **224**, 37–54 (2019).
14. Sandra Díaz *et al*., Set ambitious goals for biodiversity and sustainability. *Science* **370**, 411–413 (2020).
15. A. Jarvis, A. Lane, R. J. Hijmans, The effect of climate change on crop wild relatives. *Agric. Ecosyst. Environ.* **126**, 13–23 (2008).
16. N. P. Castañeda-Álvarez *et al*., Global conservation priorities for crop wild relatives. *Nat. Plants* **2**, 16022 (2016).
17. C. K. Khoury *et al*., Modelled distributions and conservation status of the wild relatives of chile peppers (*Capsicum* L.). *Divers. Distrib.* **26**, 209–225 (2019).
18. C. K. Khoury *et al*., Distributions, conservation status, and abiotic stress tolerance potential of wild cucurbits (Cucurbita L.). *Plants, People Planet* **2**, 269–283 (2019).
19. J. O. Hanson, J. R. Rhodes, C. Riginos, R. A. Fuller, Environmental and geographic variables are effective surrogates for genetic variation in conservation planning. *Proc. Natl. Acad. Sci. U.S.A.* **114**, 12755–12760 (2017).
20. S. Hoban, S. Kallow, C. Trivedi, Implementing a new approach to effective conservation of genetic diversity, with ash (Fraxinus excelsior) in the UK as a case study. *Biol. Conserv.* **225**, 10–21 (2018).
21. A. Balmford, P. Crane, A. Dobson, R. E. Green, G. M. Mace, The 2010 challenge: Data availability, information needs and extraterrestrial insights. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **360**, 221–228 (2005).
22. S. Hoban *et al*., Taxonomic similarity does not predict necessary sample size for ex situ conservation: A comparison among five genera. *Proc. R. Soc. B.* **287**, 20200102 (2020).
23. C. K. Khoury, D. Carver, Supplementary datasets for: Crop wild relatives of the United States require urgent conservation action. *Harvard Dataverse*, V1. https://doi.org/10.7910/DVN/BV4I06. Deposited 4 August 2020.
24. IUCN Standards and Petitions Committee, Guidelines for using the IUCN red list categories and criteria (Version 14, Prepared by the Standards and Petitions Committee, 2019). www.iucnredlist.org/documents/RedListGuidelines.pdf. Accessed 30 September 2019.
25. The Nature Conservancy Geospatial Conservation Atlas, Terrestrial ecoregions (2019). https://geospatial.tnc.org/datasets/7b7fb9d945544d41b3e7a91494c42930_0. Accessed 1 October 2019.
26. International Union for Conservation of Nature, World database on protected areas. https://www.protectedplanet.net/en/thematic-areas/wdpa. Accessed 19 April 2019.
27. US Department of Agriculture National Agricultural Statistics Service, Crop values 2019 summary, February 2020. https://www.nass.usda.gov/Publications/Todays_Reports/reports/cpvl0220.pdf. Accessed 10 August 2020.
28. G. J. Seiler, L. L. Qi, L. F. Marek, Utilization of sunflower crop wild relatives for cultivated sunflower improvement. *Crop Sci.* **57**, 1083–1101 (2017).
29. R. J. Whittaker *et al*., Conservation biogeography: Assessment and prospect. *Divers. Distrib.* **11**, 3–23 (2005).
30. D. W. Woodland, Are botanists becoming the dinosaurs of biology in the 21st century? *S. Afr. J. Bot.* **73**, 343–346 (2007).
31. V. Devictor, R. J. Whittaker, C. Beltrame, Beyond scarcity: Citizen science programmes as useful tools for conservation biogeography. *Divers. Distrib.* **16**, 354–362 (2010).
32. C. K. Khoury *et al*., Toward integrated conservation of North America's crop wild relatives. *Nat. Areas J.* **40**, 96–100 (2020).
33. American Public Gardens Association, Benchmarking studies (2020). https://www.publicgardens.org/benchmarking-studies. Accessed 23 June 2020.
34. N. Dudley *et al*., The essential role of other effective area-based conservation measures in achieving big bold conservation targets. *Glob. Ecol. Conserv.* **15**, e00424 (2018).
35. G. P. Nabhan, Destruction of an ancient indigenous cultural landscape: An epitaph from Organ Pipe Cactus National Monument. *Ecol. Restor.* **21**, 290–295 (2003).
36. M. Heiner *et al*., Moving from reactive to proactive development planning to conserve Indigenous community and biodiversity values. *Environ. Impact Assess. Rev.* **74**, 1–13 (2019).
37. S. Krishnan *et al*., Resetting the table for people and plants: Botanic gardens and research organizations collaborate to address food and agricultural plant blindness. *Plants People Planet* **1**, 157–163 (2019).
38. US Department of Agriculture Agricultural Research Service National Plant Germplasm System, GRIN-global taxonomy (2019). https://npgsweb.ars-grin.gov/gringlobal/taxon/taxonomysearch.aspx. Accessed 20 May 2019.
39. US Department of Agriculture Agricultural Research Service National Plant Germplasm System, GRIN-global taxonomy, Crop relatives in GRIN-global taxonomy (2019). https://npgsweb.ars-grin.gov/gringlobal/taxon/taxonomysearchcwr.aspx. Accessed 18 September 2019.
40. Botanic Gardens Conservation International, PlantSearch (2019). https://www.bgci.org/plant_search.php. Accessed 30 May 2019.
41. Consortium of Midwest Herbaria, Specimen search (2019). midwestherbaria.org/portal/collections/index.php. Accessed 28 May 2019.
42. United Nations Food and Agriculture Organization, World information and early warning system on plant genetic resources for food and agriculture (WIEWS) (2019). www.fao.org/wiews/en/. Accessed 24 May 2019.
43. Global Biodiversity Information Facility (GBIF), GBIF occurrence download. https://www.gbif.org/occurrence/download/0006883-191105090559680. 10.15468/dl.rwjrbf. Accessed 14 November 2019.
44. Global Crop Diversity Trust, Genesys global portal of plant genetic resources for food and agriculture (2019). https://www.genesys-pgr.org. Accessed 20 May 2019.
45. Global Crop Diversity Trust, Global crop wild relative occurrence database (2019). https://www.cwrdiversity.org/checklist/cwr-occurrences.php. Accessed 24 May 2019.
46. US Department of Agriculture Agricultural Research Service National Plant Germplasm System, GRIN-global accessions (2019). https://npgsweb.ars-grin.gov/gringlobal/search.aspx. Accessed 17 May 2019.
47. S. L. Greene, K. A. Williams, C. K. Khoury, M. B. Kantar, L. F. Marek, Eds., *North American Crop Wild Relatives, Volume 2: Important Species* (Springer International, 2019).
48. S. J. Phillips, R. P. Anderson, M. Dudik, R. E. Schapire, M. E. Blair, Opening the black box: An open-source release of maxent. *Ecography* **40**, 887–893 (2017).
49. S. E. Fick, R. J. Hijmans, Worldclim 2: New 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* **37**, 4302–4315 (2017).
50. A. Jarvis, H. I. Reuter, A. Nelson, E. Guevara, Hole-filled seamless SRTM data V4, International Center for Tropical Agriculture (CIAT) (2008). srtm.csi.cgiar.org. Accessed 1 July 2018.
51. R. Genuer, J. M. Poggi, C. Tuleau-Malot, Package 'VSURF' (2018). https://github.com/robingenuer/VSURF. Accessed 7 May 2019.
52. C. K. F. Lee, D. A. Keith, E. Nicholson, N. J. Murray, REDLISTR: Tools for the IUCN red lists of ecosystems and threatened species in R. *Ecography* **42**, 1050–1055 (2019).