

Laying the groundwork for crop wild relative conservation in the United States

Emily J. Warschefsky^{a,b} and Loren H. Rieseberg^{c,1}

The wild relatives of crop species have long been deemed important genetic resources for breeding and improvement programs (1). Because crop wild relatives (CWR) are typically adapted to different environmental conditions than their domesticated relatives, genetic material from these wild species has the potential to play an important role in breeding for greater abiotic and biotic stress tolerance (2). Indeed, CWR have been used to overcome potentially detrimental pest and disease outbreaks in the past—as when Phylloxera nearly decimated the French wine industry until resistance was identified in North American grape species (3). As climate change and human population expansion threaten global food security (4), CWR are poised to play a critical role in facing these imminent challenges. Although the advent of marker- and genomic-assisted breeding has facilitated the use of CWR for numerous crops, their diversity remains underutilized (5) and global efforts to collect and conserve CWR diversity remain a priority. In PNAS, Khoury et al. (6) provide a foundational assessment of the conservation status of native CWR taxa in the United States.

Wild relatives of some 37 crops are represented in the US flora, including those of squash, pumpkin, sunflower, persimmon, grape, and cranberry (Fig. 1) (7). In addition, some species in North America persist as wild-harvested and/or managed populations with important cultural and culinary legacies, such as wild rice (Ziziphus) (7). Khoury et al. (6) compiled a list of 600 CWR taxa native to the United States (including its territories), assigning each taxon to one of three gene pool groups (1A = wild progenitors, primary and secondary gene pools, rootstocks, and wild food sources; 1B = tertiary gene pool; and 1C = taxa in the same genus with undetermined relationships to the crop). Using locality data from over 800,000 herbarium records and 30,000 Gen-Bank collections, Khoury et al. (6) modeled the distribution of each of these 600 taxa across North America. The composite distribution map highlights important CWR hotspots within the United States, including a large and taxonomically rich region stretching across the Midwest and Mid-Atlantic.

Over the past few decades, CWR have received increasing attention from global conservation efforts, and crop genetic resources are specifically targeted in the Convention on Biological Diversity's Global Strategy for Plant Conservation (8). Alongside a global network of seed banks and germplasm repositories, the opening of the Svalbard Global Seed Vault in 2008 demonstrates the progress being made toward longterm preservation of crop diversity ex situ. Nevertheless, ex situ collections of CWR are often limited in number as well as geographic and ecological scope, and CWR taxa are rarely the focus of in situ conservation efforts. Using the distribution models for US CWR, Khoury et al. (6) assessed each taxon's in situ and ex situ conservation status, factoring in ecological, geographical, and population-level representation (Box 1). The conservation scores calculated by Khoury et al. (6) indicate that the vast majority of CWR taxa in the United States are poorly represented both in situ, in conservation areas, and ex situ, in germplasm collections, and are in urgent need of protection.

Among the taxa that Khoury et al. (6) analyze, we suggest that three partially overlapping sets merit particular attention for conservation. Of the 600 taxa examined, 253 were placed in group 1A—the germplasm that is most readily used for breeding programs and therefore represents the most vital CWR diversity. While 1A taxa have the greatest agricultural potential of the three CWR groups, more than half are categorized as urgent priority for conservation, and average conservation scores among groups show 1A taxa are only slightly better conserved than more distantly related taxa. Given these results, future research and conservation should begin by

The authors declare no competing interest.

PNAS 2021 Vol. 118 No. 4 e2024375118

Published under the PNAS license.

See companion article, "Crop wild relatives of the United States require urgent conservation action," 10.1073/pnas.2007029117.

¹To whom correspondence may be addressed. Email: Iriesebe@mail.ubc.ca.

Published January 7, 2021.

^aDepartment of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO 80309; ^bWilliam L. Brown Center, Missouri Botanical Garden, St. Louis, MO 63110; and ^cDepartment of Botany, University of British Columbia, Vancouver, BC V6T 1Z4, Canada Author contributions: E.J.W. and L.H.R. wrote the paper.



Fig. 1. Photos of four native CWR from the United States: Cucurbita palmata [Top Left image credit: Heather Rose Kates (photographer)], wild Helianthus annuus [Top Right image credit: Jason Rick (photographer)], Vaccinium oxycoccos [Bottom Left image credit: Lorraine Rodriguez Bonilla (photographer)], and Diospyros virginiana [Bottom Right image credit: Emily Warschefsky (photographer)].

targeting 1A taxa, particularly in their geographical hotspots of the Midwest to Mid-Atlantic and northwest coast.

In addition to focusing on the closest relatives of crops, special attention should be paid to wild relatives of crops that were domesticated in North America and those that are still used as wild food sources today. Sunflower, domesticated in the eastern United States, is an oilseed crop of increasing importance around the world, which has a history of using wild germplasm in breeding programs (9). Furthermore, some of the most recently commercialized crops have originated in the United States, including blueberry (1910s), cranberry (1810s), and pecan (1700s) (10), making the wild progenitors and relatives of these species particularly important for continued improvement. Also, while overall relatively few globally important crops originated in North America, the ones that exist as wild food sources represent an important cultural and biological legacy that deserves preservation.

Khoury et al. (6) demonstrate some variation in the conservation status of CWR taxa that fall under particular product categories (e.g., sugars, fruits, pulses, etc.); however, it may be that the more critical factors to consider are growth habit and longevity (e.g., herbaceous, woody, vine, annual, biennial, or perennial). Examining conservation scores through this lens of life history, a third group of taxa come into focus: woody perennial species. Although roughly half of the 37 crops with CWR in the United States are woody species, their wild relatives make up nearly three-quarters of 1A taxa and 87% of the 1A taxa that are found to be of urgent priority for conservation. The disproportionate representation of woody species within the group of 1A taxa might reflect the inclusion of CWR used as rootstocks, which broadens the range of CWR that can be of direct use for crop improvement. Woody species may represent relatively easy targets for domestication, as some of the world's most recently domesticated species are woody (e.g., kiwifruit, blueberry, macadamia, grapefruit, and pecan) (10), and desirable individuals can easily be cultivated and clonally propagated via grafting. Unfortunately, many woody perennials have recalcitrant seeds that cannot be stored in seed banks and must therefore be maintained in living collections, which are resource-intensive (time, space, and labor). Because of the unique challenges in conserving woody perennial species, we propose the formation of a working group aimed at the conservation of North American woody CWR taxa.

As a whole, Khoury et al. (6) provide a framework for the conservation of CWR in the United States; further work is now needed to refine conservation assessments for individual taxa and, more importantly, to act on these assessments. Given the large number of CWR taxa that exist in the United States and the limited resources. available for CWR ex situ conservation and in situ management, effective and efficient conservation of these taxa is critical. One important next step is to incorporate more detailed information on the ecology, life history, and genetic diversity of CWR taxa, which will help to inform collection priorities and practices (as in refs. 11 and 12). The conservation of CWR in the United States requires the expertise and support of many sectors: Botanic gardens, government agencies, germplasm repositories, universities, users of wild species, landowners, small-scale and hobbyist farmers, and the general public must all come together to ensure that the invaluable resources of CWR are protected for coming generations.

Box 1. Conservation Scores in Khoury et al. (6)

Scores range from 0 to 100 with higher numbers indicating more comprehensive conservation of germplasm

Ex Situ Conservation Scores

- Sampling Representativeness Score (SRSex): ratio of germplasm accessions to herbarium records
- Geographical Representativeness Score (GRSex): proportion of modeled distribution that has been sampled for germplasm collections (using 50-km radius around each collection point)
- Ecological Representativeness Score (ERSex): the proportion of terrestrial ecoregions within the modeled distribution that have been sampled for germplasm collections
- Final Conservation Score ex situ (FCSex): Average of SRSex, GRSex, and ERSex

In Situ Conservation Scores

- Sampling Representativeness Score (SRSin): proportion of records and collections that fall within a protected area
- Geographical Representativeness Score (GRSin): proportion of the total distribution that falls within a protected area
- Ecological Representativeness Score (ERSin): the proportion of terrestrial ecoregions within the modeled distribution that are within protected areas
- Final Conservation Score in situ (FCSin): Average of SRSin, GRSin, and ERSin

Final Conservation Score (FCSc-mean): average of FCSex and FCSin



- 1 N. I. Vavilov, Origin and Geography of Cultivated Plants (Cambridge University Press, 1987).
- 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 P. This, T. Lacombe, M. R. Thomas, Historical origins and genetic diversity of wine grapes. Trends Genet. 22, 511–519 (2006).
- 4 C. Mbow et al., "Food security" in Climate Change and Land: An IPCC Special Report on Climate Change, Desertification, Land Degradation, Sustainable Land Management, Food Security, and Greenhouse Gas Fluxes in Terrestrial Ecosystems, P. R. Shukla et al., Eds. (Intergovernmental Panel on Climate Change, 2019), pp. 437–550.
- 5 B. V. Ford-Lloyd et al., Crop wild relatives—Undervalued, underutilized and under threat? Bioscience 61, 559-565 (2011).
- 6 C. K. Khoury et al., Crop wild relatives of the United States require urgent conservation action. Proc. Natl. Acad. Sci. U.S.A., 10.1073/pnas.2007029117 (2020).
- 7 C. K. Khoury et al., An inventory of crop wild relatives of the United States. Crop Sci. 53, 1496–1508 (2013).
- 8 Convention on Biological Diversity, Updated Global Strategy for Plant Conservation 2011-2020. https://www.cbd.int/gspc/.
- 9 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).
- 10 R. S. Meyer, A. E. DuVal, H. R. Jensen, Patterns and processes in crop domestication: An historical review and quantitative analysis of 203 global food crops. New Phytol. 196, 29–48 (2012).
- 11 S. Hoban, G. Volk, K. J. Routson, C. Walters, C. Richards, "Sampling wild species to conserve genetic diversity" in North American Crop Wild Relatives, S. Greene, K. Williams, C. Khoury, M. Kantar, L. Marek, Eds. (Springer, 2018), vol. 1, pp. 209–228.
- 12 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).