RESEARCH

Trans Situ Conservation of Crop Wild Relatives

Erin Coulter Riordan* and Gary Paul Nabhan

ABSTRACT

In the face of unprecedented climatic disasters, social conflict, and political uncertainty, integrating in situ and ex situ strategies may become increasingly necessary to effectively conserve crop wild relatives (CWR). We introduce the concept of trans situ conservation to safeguard CWR genetic diversity and accessibility for crop improvement. Building on initiatives to combine in situ protection with ex situ backup in genebanks, trans situ conservation dynamically integrates multiple in situ and ex situ measures, from conservation to research to education, spanning local to global scales. Two important features emerge from a trans situ approach. First, integrating in situ and ex situ studies of CWR genetic diversity, adaptation, and ecological interactions can lead to advances in crop improvement and in situ management. Second, the complementarity, redundancy, and synergy gained through trans situ conservation buffer climatic, economic, political, and institutional instabilities. Focusing on a case study in the United States–Mexico desert borderlands, we evaluate three components of trans situ conservation: in situ protection on working and public lands; seed and living plant collections in local and regional botanical gardens, arboreta, and nurseries; and genebank accessions in the USDA National Plant Germplasm System. We discuss gaps, tensions, and synergies that emerge when coordinating these three components and offer the conservation of the wild chile [*Capsicum annuum* L. var. *glabriusculum* (Dunal) Heiser & Pickersgill] in southern Arizona as an example of concerted in situ and ex situ research integrated in a trans situ framework

E.C. Riordan and G.P. Nabhan, Desert Lab. on Tumamoc Hill, Univ. of Arizona, Tucson, Arizona 85745; G.P. Nabhan, Univ. of Arizona, Southwest Center, Tucson, Arizona 85721. Received 1 June 2019. Accepted 16 Aug. 2019. *Corresponding author (ecriordan@email.arizona.edu). Assigned to Associate Editor Linghe Zeng.

Abbreviations: CWR, crop wild relative(s); GRIN, Germplasm Resource Information Network; NPGS, National Plant Germplasm System; SEARCH, Southwestern Endangered Aridland Resource Clearing House; USFS, US Forest Service.

With accelerating changes in climatic conditions in agricultural regions deemed globally important for maintaining the food security of humankind, plant breeders have increasingly turned to crop wild relatives (CWR) to address heightened abiotic and biotic stress now affecting food crops (Ceccarelli et al., 2010; Dempewolf et al., 2017; Zhang et al., 2017a). As a subset of plant genetic resources for food and agriculture (PGRFA), a CWR is defined as a "wild plant taxon that has an indirect use derived from its relatively close genetic relationship to a crop" (Ford-Lloyd et al., 2011).

Crop wild relatives can be useful as breeding materials, rootstock, biomimicry analogs to improve crop resistance and tolerance to biotic and abiotic stressors (Dempewolf et al., 2017; Zhang et al., 2017a), or as resilient alternatives to conventional crops (Nabhan and Felger, 1985; Bharucha and Pretty, 2010). Their traits may augment the drought, heat, and salinity tolerance found in land races or cultivars to improve growth and yield in arid landscapes. Some strategies for their use include matching crop phenology to seasonal moisture availability, improving water use efficiency, shifting root/shoot ratios, selecting to escape or avoid stress in critical periods of crop life cycles, and evaluating secondary compounds or morphological features to reduce biotic or abiotic stress (Nabhan, 1979, 1985; Nabhan and Felger, 1985; Bayuelo-Jiménez et al., 2002; Ceccarelli et al., 2010).

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However, just when CWR are gaining consideration for use in adapting crops to climate change, populations and entire species of CWR themselves are threatened by habitat loss from urbanization and agricultural expansion, pollution, overharvesting, invasive species, and climate change (Ford-Lloyd et al., 2011). Jarvis et al. (2008) predict that climate change will fragment or degrade populations of nearly all wild relatives of peanut (*Arachis hypogaea* L.), potato (*Solanum tuberosum* L.), and cowpea [*Vigna unguiculata* (L.) Walp.] worldwide by the year 2055, resulting in range losses by half for most species and outright extinction of 16 to 22% of species. Wild plants across North America face increasing extinction risk from the combination of land use and climate change (Zhang et al., 2017b). In fact, a rare chile pepper endemic to the cloud forests of Guatemala, *Capsicum lanceolatum* (Green ex J.D. Sm.), has already dwindled to just one population over the last century—land use and climate change are among the chief causes. Although rediscovered in a single nature reserve, the Mario D'Arcy Avila Biotopo el Quetzal, its habitat was conserved for reasons other than its specific protection (Bosland and Gonzalez, 2000).

Both nature reserves and genebanks around the world have recently suffered the consequences of climate related disasters, economic crises, political conflicts, and social unrest (Nabhan, unpublished data, 2019). Therefore it is not surprising that several research teams and scientific advisory bodies have argued for a coordinated global approach to CWR conservation, including both in situ and ex situ strategies (Engels et al., 2008; Ford-Lloyd et al., 2011; Maxted et al., 2012; Dempewolf et al., 2014), with priority setting (Vincent et al., 2013; Castañeda-Álvarez et al., 2016) and periodic evaluation of their comprehensiveness of conservation (Khoury et al., 2019).

In a 2018 meeting convened by Colin Khoury of the International Center for Tropical Agriculture (CIAT) and Hannes Dempewolf of the Crop Trust at Oak Springs Farm Foundation in Virginia, participants aptly proposed the term "trans situ conservation" for this integrated approach to safeguard CWR genetic diversity and ensure future access for crop improvement. Trans situ conservation builds on existing initiatives to combine in situ protection with ex situ back-up conservation in genebanks (Dempewolf et al., 2014). We extend this model, proposing a more dynamic integration of multiple in situ and ex situ measures, from conservation to research to education, spanning local to global scales (Fig. 1). Three main components form the foundation of a trans situ safety net: (i) in situ protection, management, and research; (ii) local and regional seed and living plant collections maintained for conservation, research, and education; and (iii) national and global genebanks maintained for plant breeding and crop research.

Trans situ conservation acknowledges that although the conservation and study of CWR genetic diversity are best accomplished in situ in the native environments where species continue to coevolve with their biotic associates (Chen et al., 2017), threats from climate change, land use disruptions, political unrest, and warfare necessitate safeguarding CWR diversity in ex situ collection facilities. These ex situ collections address CWR conservation and use across multiple scales—not just in national and global genebanks, but also in regional seed and living plant collections at botanical gardens, arboreta, biocultural museums, field stations, even hyper-local collections that facilitate direct use by local communities.

Growing and evaluating CWR in controlled ex situ settings where biotic and abiotic stressors are similar to those in nearby in situ populations helps tease apart the complex factors that contribute to CWR adaptation, reproduction, and survival. This interplay of in situ and ex situ research at local to regional scales informs active management to maintain and recover CWR populations in their native habitats. In addition, local and regional ex situ conservation facilities such as botanical gardens, arboreta, and biocultural museums play an important educational role (O'Donnell and Sharrock, 2018) conveying the societal value and distinctive ecological adaptations of regionally relevant CWR. Their seed and living plant collections support research, conservation, and use of locally adapted plant materials that may otherwise be inaccessible from national and global genebanks.

Extra-local national and global genebanks with the capacity for long-term storage and large-scale distribution conserve CWR genetic material and provide access for plant breeding and crop research. With their associated laboratories, greenhouses, and common gardens, these genebanks allow for detailed genetic and horticultural comparisons of CWR taxa with one another and with congeneric domesticated crops. Improving collaboration between national and regional facilities supports efforts to newly domesticate CWR, especially when experiments in the region of origin are needed to understand the environmental adaptations of a new crop. Through this diversity of interacting strategies to safeguard CWR genetic diversity, a trans situ approach bridges gaps in conservation by providing complementarity, redundancy, and synergy.

Given the relatively few long-term efforts in the United States that explicitly integrate in situ and ex situ strategies for CWR conservation, we present a case study of an ongoing trans situ approach initiated over a quarter century ago (Nabhan, 1990a) in the arid borderlands of the United States and Mexico. The United States–Mexico borderlands is an important region for arid-adapted relatives of crops including agave (*Agave* L.), amaranth (*Amaranthus* L.), common bean (*Paseolus vulgaris* L.), pepper (*Capsicum annuum* L.), cotton (*Gossypium* L.), and

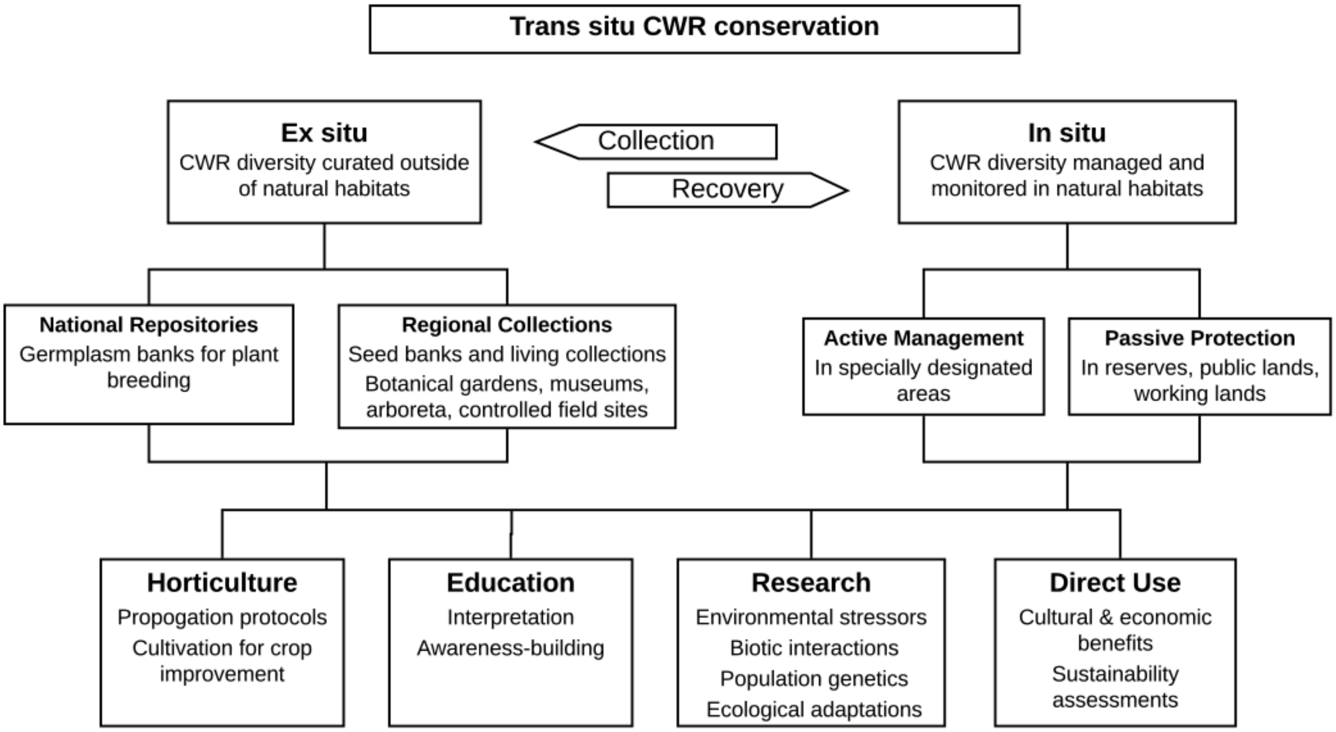

Fig. 1. Tran situ model for integrated in situ and ex situ crop wild relative (CWR) conservation. Adapted from Oldfield and Newton (2012).

squash (*Cucurbita* L.) (Nabhan et al., 1980; Nabhan, 1985; Nabhan and Felger, 1985; Nabhan, 1990b). Of nearly 4600 taxa of CWR and wild utilized species inventoried in the United States (Khoury et al., 2013; Williams and Greene, 2018), >1000 taxa from 50 genera (22%) occur in Arizona (Khoury and Nabhan, 2019). Many wild desert plants have a long history of direct human use. Approximately 540 wild plant taxa of the Sonoran Desert, which spans the United States–Mexico border, are edible or likely edible (Hodgson, 2001).

We evaluate three components of trans situ conservation in the United States–Mexico borderlands: (i) in situ protection on public and working lands; (ii) within-region seed and living plant collections maintained for research, education, and conservation; and (iii) the USDA National Plant Germplasm System (NPGS) genebank network maintained for plant breeding, crop research, and other economic uses. We synthesize over a quarter century of concerted in situ and ex situ research on the wild chile [*Capsicum annuum* L. var. *glabriusculum* (Dunal) Heiser & Pickersgill] in a trans situ framework. We identify gaps, tensions, and synergies that emerge when coordinating the three components of trans situ conservation and discuss how maintaining conservation-oriented complementarity and redundancy functions in the face of climatic, economic, political, and institutional instabilities.

MATERIALS AND METHODS

Arizona Inventory of Crop Wild Relatives

We first created a comprehensive list of wild plant species in Arizona having potential in plant breeding and crop improvement. We compared the Arizona vascular flora (Kearney and Peebles, 1960) and its current digital checklist updates (http://www.canotia.org/vpa_project.html) with recent CWR inventories: the Germplasm Resource Information Network (GRIN) Crop Wild Relative Project (Wiersema and León, 2016) available through GRIN-Global (USDA, 2019b), the United States CWR and wild utilized species inventory (Khoury et al., 2013), and the Mexico CWR inventory (Contreras-Toledo et al., 2018). Our compiled list of CWR genera in Arizona (Table 1) was then distributed at a January 2019 CWR meeting of botanists and crop scientists held at the University of Arizona Desert Laboratory on Tumamoc Hill in Tucson, AZ (Khoury and Nabhan, 2019). We refined the list following feedback from workshop participants.

Borderlands Case Study

Our case study of trans situ conservation documented species from the state-level inventory that occur on two in situ sites: the Wild Chile Botanical Area, a special management area in the US Forest Service (USFS) Coronado National Forest; and the Walnut Gulch Experimental Watershed, a research site of the USDA-ARS (Fig. 2). Established in 1999 to protect and provide opportunities to research the wild chile, the 11.4-km^2 (2836-acre) Wild Chile Botanical Area was the first special botanical area designated for CWR protection in the United States. It is now part of the recently designated Santa Cruz Valley National Heritage Area. The site, which protects wild chile populations at their northernmost range limit, is located in the Rock Corral Canyon subwatershed of the Tumacacori Highlands and consists of oak (*Quercus* spp.) woodland interspersed with semi-desert grassland and riparian vegetation.

As a comparison with the Wild Chile Botanical Area, we surveyed CWR in the Walnut Gulch Experimental Watershed located near Tombstone, AZ. The Walnut Gulch

Experimental Watershed is operated by the Southwest Watershed Research Center and is part of the USDA ARS Long-Term Agroecosystem Research (LTAR) Network. The research site covers 150 km^2 (37,000 acres) of privately owned semiarid rangeland in the transition zone between the Sonoran and Chihuahuan Deserts.

The USDA-ARS staff provided a species checklist, list of herbarium specimens collected within Walnut Gulch Experimental Watershed, vegetation map, and aerial photos of habitats found in and around the site. Our own fieldwork in the spring of 2019 augmented the Walnut Gulch checklist (L. Kennedy, personal communication, 2018) and the Atascosa-Tumacacori

Table 1. Major crop wild relative (CWR) genera in Arizona and their uses.

Genus	Common name	Wild taxa in Arizona	Food use†	Agricultural use ‡
Agave L.	Agave, century plant	11	X	
Allium L.	Onion	15	X	
Amaranthus L.	Amaranth	14	X	
Capsicum L.	Chile pepper	1	X	
Chenopodium L.	Goosefoot, lambsquarters	14	X	
Cucurbita L.	Gourd, squash	3		X
Dasiphora Raf.	Strawberry	1		
Daucus L.	Carrot	1		X
Drymocallis Fourr. ex Rydb.	Strawberry	1		
Dysphania R. Br	Epazote	2	X	
Elymus L.	Wheat, rye	13		X
Fragaria L.	Strawberry	2	X	X
Gossypium L.	Cotton	1		X
Helianthus L.	Sunflower	10		X
Hordeum L.	Barley	4		X
Humulus L.	Hops	1		
Ipomoea L.	Sweetpotato	11		X
Jaltomata Schltdl.	Jaltomato	1	X	
Juglans L.	Walnut	1	X	X
Lactuca L.	Lettuce	4		X
Leymus Hochst.	Wheat	3	X	X
Linum L.	Flax	8		
Lupinus L.	Lupine	20		
Macroptilium (Benth.) Urb.	Siratro	1		
Manihot Mill.	Cassava	2		X
Mentha L.	Mint	1	X	
Morus L.	Mulberry	1	X	
Nicotiana L.	Tobacco	4		
Opuntia Mill.	Prickly pear, cholla	32	X	
Panicum L.	Millet, panicgrass	10		X
Passiflora L.	Passionfruit	5		
Phaseolus L.	Bean, tepary	8	X	X
Physalis L.	Groundcherry, tomatillo	14	X	
Physaria (Nutt. ex Torr. & A. Gray) A. Gray	Bladderpod	1		X
Proboscidea Schmidel	Devil’s claw, unicorn plant	2	X	
Prunus L.	Cherry, plum	4	X	X
Ribes L.	Currant, gooseberry	10	X	X
Rubus L.	Raspberry	5	X	X
Parthenium L.	Guayule	2		
Salvia L.	Chia	16	X	
Sesbania Scop.	Colorado River hemp	1	X	
Simmondsia Nutt.	Goatnut, jojoba	1	X	
Solanum L.	Potato, wonderberry	11	X	X
Stevia Cav.	Stevia, sweetleaf	5	X	X
Tagetes L.	Marigold, Mexican tarragon	7	X	X
Tripsacum L.	Gamagrass	1		X
Vaccinium L.	Blueberry, huckleberry, whortleberry	1	X	X
Vicia L.	Vetch	3		X
Vitis L.	Grape	3	X	X
Yucca L.	Banana yucca, soapweed, Spanish bayonet	11	X	
Ziziphus Mill.	Jujube, lotebush	1		

† Historical direct uses as food by indigenous and other North Americans.

‡ Documented as used in modern plant breeding or as rootstock.

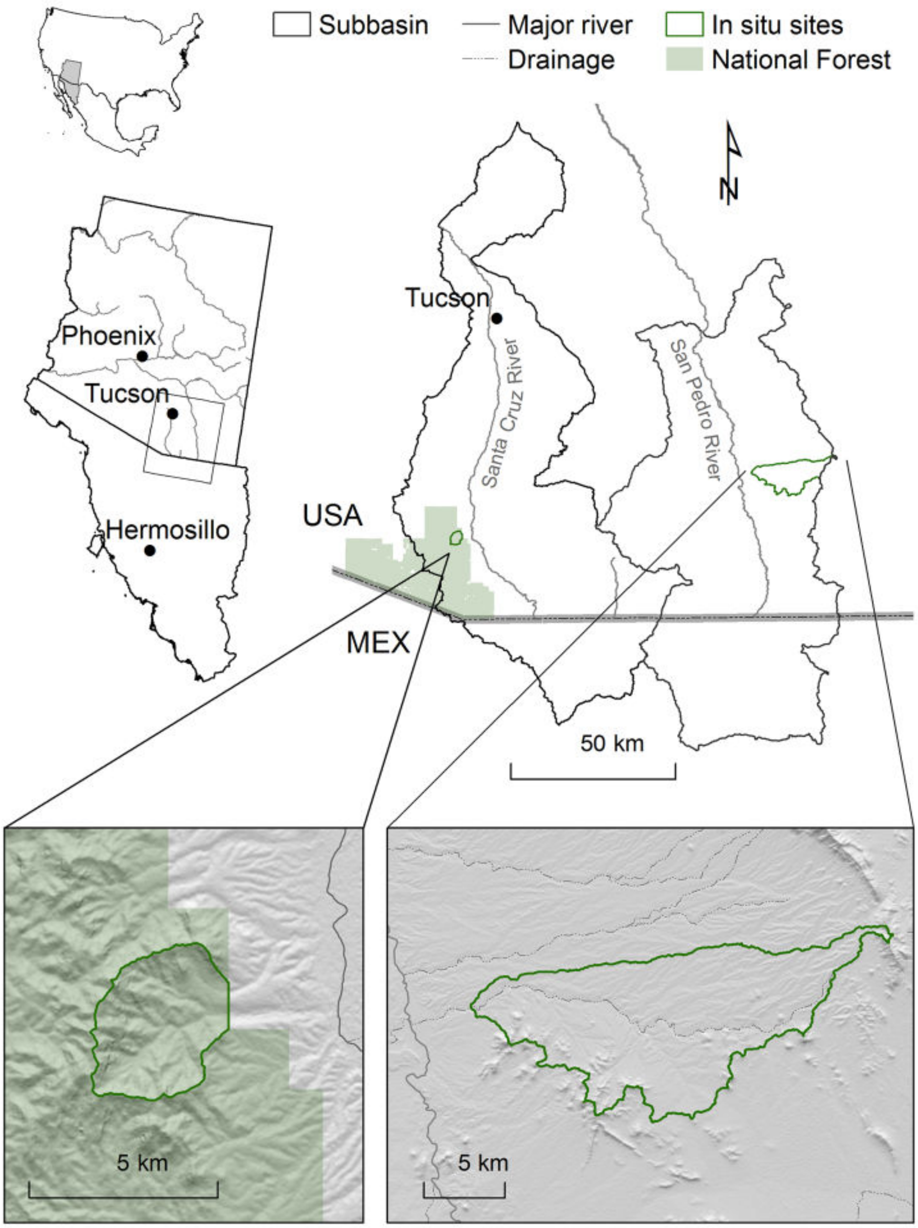

Fig. 2. In situ sites in southern Arizona: Wild Chile Botanical Area (left) and Walnut Gulch Experimental Watershed (right). Hydrologic subbasins of the Upper Santa Cruz River and Upper San Pedro River drainages are provided for reference.

Mountains checklist (J. Dash, personal communication, 2019). To our knowledge, no historical populations of CWR vouchered with herbarium specimens from either site have been locally extirpated. Additional surveys for CWR are planned in historically undersampled seasons.

We compiled a list of CWR present in each in situ site (Table 2) and determined which species were also conserved ex situ in regional collections. We obtained data on seed and living plant collections from the following botanical gardens, nurseries, plant materials centers, genebanks, and museums in close proximity to the in situ sites: the Arizona-Sonora Desert Museum, the Borderlands Restoration Network, the Desert Botanical Garden, the Desert Legume Project of the University of Arizona and Boyce-Thompson Arboretum, Native Seeds/SEARCH (Southwestern Endangered Aridland Resource Clearing House), the Pima County Parks and Recreation Native Plant Nursery, the USDA Natural Resource Conservation Service Tucson Plant Materials Center, and the University of Arizona Campus Arboretum.

We then evaluated the ex situ representation of species in the NPGS (USDA, 2019a), the largest collection of CWR germplasm in the United States (Williams and Greene, 2018). For each species, we summarized the total number of active wild accessions in the NPGS that were collected from the United States and Mexico. We also compiled in situ conservation status rankings for global, national, and state levels from NatureServe (NatureServe, 2019), the List of Threatened Species of the Mexican Norm NOM-059-SEMARNAT-2010 (DOF, 2015), and the Heritage Data Management System of the Arizona Game and Fish Department (AZGFD, 2019).

Finally, we evaluated past land use and management in Arizona potentially affecting the persistence and genetic diversity of CWR. We ranked the two sites—the Wild Chile Botanical Area and Walnut Gulch Experimental Watershed—for active management

Table 2. Case study crop wild relative (CWR) conservation in situ and ex situ in regional collections.

Taxon	Common name	In situ†		Ex situ‡	
		WCBA	WGEW	Seed banks	Live plants
Agave palmeri Engel.	Palmer's agave, lechuguilla	X	X	DBG, NSS	ASDM, DBG, PCNPN, UACA
Agave parviflora Torr.	Santa Cruz striped agave, amole	X		DBG	DBG, PCNPN, UACA
Agave schottii Engelm.	Shindagger, amole	X	E	DBG, PCNPN, TPMC	ASDM, DBG, PCNPN
Allium plummerae S. Watson	Plummer's wild onion	X			
Amaranthus graecizans L.	Mediterranean amaranth		X		
Amaranthus palmeri S. Watson	Palmer's amaranth, bledo, quelite de las aguas	N	X	NSS	
Amaranthus powellii S. Watson	Powell's amaranth, quelite	N			
Capsicum annuum L. var. *glabriusculum* (Dunal) Heiser & Pickersgill	Wild chile, chiltepin	X		NSS, PCNPN	PCNPN, UACA
Chenopodium berlandieri Moq.	Pitseed goosefoot, chual, huazontle silvestre	N	N		
Chenopodium fremontii S. Watson	Fremont's goosefoot, chual	N	X		
Chenopodium neomexicanum Standl.	New Mexico goosefoot	N	N		
Cnidoscolus angustidens Torr.	Mala mujer, ortiguilla, ortija		X		ASDM
Cucurbita digitata A. Gray	Coyote gourd, calabacilla del coyote	N	X	BRN, NSS, PCNPN	PCNPN
Cucurbita foetidissima Kunth	Buffalogourd, calabacilla loca	X	X	BRN, NSS	
Gossypium thurberi Tod.	Wild cotton, algodoncillo	X		BRN, NSS, PCNPN	ASDM, DBG, PCNPN
Helianthus annuus L.	Common sunflower, girasol, mirasol		N		DBG
Helianthus petiolaris Nutt.	Prairie sunflower	N	N		
Hibiscus denudatus Benth.	Rock hibiscus		X	PCNPN, TPMC	DBG
Hopia obtusa (Kunth) Zuloaga & Morrone	Vine mesquite		X		ASDM
Hordeum murinum L. ssp. *glaucum* (Steud.) Tzvelev	Mouse barley	X			
Hordeum pusillum Nutt.	Little barley	N			
Ipomoea costellata Torr.	Crestrib morning-glory, trompillo		X		
Ipomoea pubescens Lam.	Silky morning-glory		X		
Ipomoea ternifolia Cav.	Triple-leaf morning-glory		X		
Juglans major (Torr.) A. Heller	Arizona walnut, Nogal	X	X	PCNPN	DBG, PCNPN, UACA
Linum puberulum (Engelm.) A. Heller	Plains flax	X	X		
Lycium andersonii A. Gray	Desert wolfberry, Salicieso	X	E		DBG, PCNPN
Lycium berlandieri Dunal	Wolfberry, salicieso	X	X	DBG, PCNPN	ASDM
Lycium fremontii A. Gray	Wolfberry, salicieso	N	X	DBG, PCNPN	DBG, PCNPN, UACA
Macroptilium atropurpureum (DC.) Urb.	Purple bushbean, siratro	X			DBG
Manihot angustiloba (Torr.) Müll. Arg.	Desert mountain manihot	X			ASDM
Mentha arvensis L.	Wild mint, yerbabuena		X		
Morus microphylla Buckley	Littleleaf mulberry, Zarza mora	X	N		
Nicotiana obtusifolia M. Martens & Galeotti	Wild tobacco, tabaco del coyote		X	BRN	ASDM
Opuntia macrocentra Engelm.	Long-spine purple prickly pear	X	N	DBG	ASDM, DBG, PCNPN, UACA
Opuntia phaeacantha Engelm.	Engelmann's prickly pear	X	X	DBG	ASDM, DBG, PCNPN
Opuntia santa-rita (Griffiths & Hare) Rose	Pancake prickly pear cactus, Santa Rita prickly pear	N		DBG	ASDM, DBG, PCNPN
Panicum hallii Vasey	Hall's panicgrass		X		
Panicum hirticaule J. Presl	Sonoran/Mexican panicgrass	X	X		ASDM
Passiflora arizonica (Killip) D.H. Goldman (= *Passiflora foetida* var. *arizonica* Killip)	Arizona passionflower, scarlet-fruit passionvine, Tayalote, buli de venado	X			ASDM
Passiflora mexicana Juss.	Mexican passionflower, ojo de venado	X		PCNPN	
Phaseolus acutifolius A. Gray	Tepary bean, frijol tepari	X		BRN, DELEP, NSS	DBG
Phaseolus angustissimus A. Gray	Slimleaf bean, frijolillo	N	X	DELEP	
Phaseolus maculatus Scheele	Metcalfe's bean, cocolmeca	X		DELEP, NSS	
Physalis acutifolia (Miers) Sandwith	Sharpleaf groundcherry	X			
Physalis longifolia Nutt.	Longleaf groundcherry	X			
Portulaca halimoides L.	Dwarf purslane		X		
Portulaca suffrutescens Engelm.	Purslane	N	X		
Portulaca umbraticola Kunth	Purslane	N	X		
Prunus serotina Ehrh.	Southwest black cherry, capulín	X		BRN	

Table 2. Continued.

Taxon	Common name	In situ† WCBA	In situ† WGEW	Ex situ‡ Seed banks	Ex situ‡ Live plants
Solanum douglasii Dunal	Wonderberry, chichiquelite	X			
Solanum elaeagnifolium Cav.	Silverleaf nightshade, trompillo	N	X	PCNPN	DBG
Stevia lemmonii A. Gray	Mt. Lemmon stevia, sweetleaf	N			
Stevia micrantha Lag.	Annual candyleaf, sweetleaf	N			
Stevia serrata Cav.	Sawtooth candyleaf	N			
Tagetes lemmonii A. Gray	Mexican bush marigold, Mt. Lemmon marigold, tangerine scented marigold	X		BRN, DBG	DBG, PCNPN, UACA
Tagetes micrantha Cav.	Mountain marigold, licorice marigold, yerba anís	X			UACA
Vitis arizonica Engelm.	Arizona wild grape, parra Silvestre, uva silvestre	X	N	DBG	ASDM, DBG, PCNPN
Yucca baccata Torr. (= *Y. arizonica* McKelvey)	Banana yucca		X	BRN	
Yucca elata Engelm.	Soaptree yucca		X	BRN, DBG, PCNPN, TPMC	ASDM, DBG, PCNPN
Ziziphus obtusifolia (Hook. ex Torr. & A. Gray) A. Gray	Lotebush	X	N	PCNPN, TPMC	ASDM, DBG, PCNPN

† WCBA, Wild Chile Botanical Area; WGEW, Walnut Gulch Experimental Watershed; X, documented inside site; N, documented nearby in immediately adjacent areas; E, expected to be found with further surveys.

‡ Regional ex situ facilities: ASDM, Arizona-Sonora Desert Museum; BRN, Borderlands Restoration Network; DELEP, Desert Legume Project of the Boyce-Thompson Arboretum and University of Arizona; DBG, Desert Botanical Garden; NSS, Native Seeds/SEARCH; PCNPN, Pima County Native Plant Nursery; TPMC, USDA Natural Resource Conservation Service Tucson Plant Materials Center; UACA, University of Arizona Campus Arboretum. Representation as of April 2019.

practices that may favor or harm the long-term proliferation and maintenance of meta-populations of CWR as recommended by Iriondo et al. (2008) and Maxted and Kell (2009).

Wild Chile Conservation Synthesis

The second portion of this inquiry—what can be learned from CWR conserved, managed, and studied in a trans situ context—integrated wild chile (chiltepin) research in situ at the Wild Chile Botanical Area; ex situ in nearby experimental settings on the grounds of the Arizona-Sonora Desert Museum and Native Seeds/SEARCH Farm in Patagonia, AZ; and ex situ in greenhouse experiments at the New Mexico State University Fabian Garcia Science Center. Over a quarter century of extensive work by various teams involving Nabhan and his colleague Josh Tewksbury has addressed wild chile environmental associations (Tewksbury et al., 1999), biotic interactions (Tewksbury et al., 1999; Tewksbury and Nabhan, 2001; Carlo et al., 2009; Carlo and Tewksbury, 2014), chemical defenses (Luna-Ruiz et al., 2018), and genetic diversity (Votava et al., 2002). We synthesized this work, highlighting the benefits gained from a trans situ conservation approach.

RESULTS

Borderlands Case Study

We documented 61 CWR species inside or immediately adjacent to the in situ sites in southern Arizona (Table 2). Thirty CWR species were documented inside the Wild Chile Botanical Area, and an additional 17 species were documented in areas immediately adjacent. Twenty-eight CWR species were documented inside the Walnut Gulch Experimental Watershed, and an additional eight species were documented in areas immediately adjacent. We expect but have not yet confirmed two additional species in the Walnut Gulch Experimental Watershed. Of the 22 species found in common between the two areas, only seven species were shared strictly inside the sites. We anticipate additional botanical field surveys targeting seasons previously undersampled may confirm as many as 20 shared species.

Only 36 of the 61 CWR species were represented in seed and living plant collections at nearby ex situ facilities (Table 2). Forty-two species were represented in the NPGS by wild accessions collected from the United States or Mexico (Table 3). Most species (50 of 61) were inadequately represented in the NPGS, having <10 wild accessions each. Seven species were represented by a single wild accession each, including Palmer's agave (*Agave palmeri* Engel.), which is used intensively in Mexico and was used historically in Arizona to produce mezcal lechugilla (Table 4). Other species with intensive in situ use but little to no ex situ representation in the NPGS include wolfberry (*Lycium fremontii* A. Gray), Engelmann's prickly pear (*Opuntia phaeacantha* Engelm.), and silverleaf nightshade (*Solanum elaeagnifolium* Cav.). The majority of species we evaluated only had accessions collected from the United States, and just five species had collections from both countries. Moreover, the genetic diversity local to the two in situ sites was very poorly represented in the NPGS—only a single sample of the wild tepary bean (*Phaseolus acutifolius* A. Gray) was collected from the Wild Chile Botanical Area by Nabhan in 1985.

Although many of the CWR in our list are considered globally secure or apparently secure in situ, their conservation status typically has not been ranked at the national or state level in the United States (Table 3). Of the CWR

Table 3. Case study in situ conservation status rankings and ex situ representation in National Plant Germplasm System (NPGS) accessions.

	NatureServe†			NPGS accessions‡	
Taxon	Global	USA	Arizona	USA	Mexico
Agave palmeri	G4?	NNR	SNR	1	0
Agave parviflora	G3§	N3	S3	0	0
Agave schottii	G5	N5	S5	4	0
Allium plummerae	G4	NNR	S3	0	0
Amaranthus graecizans	G4G5	NNR	–	0	0
Amaranthus palmeri	G5	N4N5	SNR	11	0
Amaranthus powellii	G5	N4N5	SNR	8	0
Capsicum annuum var. *glabriusculum*	G5T5	N5	S2¶	1	3
Chenopodium berlandieri	G5	N5	SNR	84	0
Chenopodium fremontii	G5	N5	SNR	18	0
Chenopodium neomexicanum	G4	NNR	SNR	7	0
Cnidoscolus angustidens	G3G5	NNR	SNR	0	0
Cucurbita digitata	G5	NNR	SNR	19	0
Cucurbita foetidissima	G5	N4N5	SNR	6	21
Gossypium thurberi	G4?	NNR	SNR	4	0
Helianthus annuus	G5	N5	SNR	954	10
Helianthus petiolaris	G5	N3N5	SNR	132	0
Hibiscus denudatus	G5	NNR	SNR	1	0
Hopia obtusa	G5	N5	SNR	9	0
Hordeum murinum subsp. *glaucum*	GNRTNR	NNA	SNA	2	0
Hordeum pusillum	G5	N5	SNR	8	0
Ipomoea costellata	G4	NNR	SNR	1	0
Ipomoea pubescens	G3G5	NNR	SNR	0	0
Ipomoea ternifolia	–	–	–	2	0
Juglans major	G4§	N4	S4	30	0
Linum puberulum	G5	NNR	SNR	1	0
Lycium andersonii	G5	NNR	S4	13	0
Lycium berlandieri	G5	NNR	SNR	2	0
Lycium fremontii	G5	NNR	S3S4	1	0
Macroptilium atropurpureum	G5?	NNA	SNA	0	76
Manihot angustiloba	G4G5	NNR	SNR	0	0
Mentha arvensis	G5	N5?	SU	2	0
Morus microphylla	G5?	NNR	SNR	0	0
Nicotiana obtusifolia	G4G5	N4?	S4	8	0
Opuntia macrocentra	G3G4	NNR	S3	0	0
Opuntia phaeacantha	G5	N5	S5	5	0
Opuntia santa-rita	G4	NNR	SNR	0	0
Panicum hallii	G5	NNR	S3S4	2	0
Panicum hirticaule	G5	NNR	S3S4	5	0
Passiflora arizonica	G5T3T5	N4?	S2	0	0
Passiflora mexicana	G3G5	NNR	S3	0	0
Phaseolus acutifolius	G4G5	NNR	SNR	82	58
Phaseolus angustissimus	G4G5	NNR	SNR	4	0
Phaseolus maculatus	G3G5	NNR	SNR	26	14
Physalis acutifolia	G5?	NNR	SNR	2	0
Physalis longifolia	G5	NNR	SNR	0	0
Portulaca halimoides	G5	NNR	SNR	2	0
Portulaca suffrutescens	G4G5	NNR	SNR	1	0
Portulaca umbraticola	G5	N5	SNR	1	0
Prunus serotina	G5	N5	SNR	6	0
Solanum douglasii	G5	NNR	SNR	0	0
Solanum elaeagnifolium	G4G5	N4N5	SNR	0	0
Stevia lemmonii	G3G4	NNR	S2¶	0	0
Stevia micrantha	G4?	NNR	SNR	0	0

Table 3. Continued.

Taxon	NatureServe† Global	NatureServe† USA	NatureServe† Arizona	NPGS accessions‡ USA	NPGS accessions‡ Mexico
Stevia serrata	G5	NNR	SNR	0	0
Tagetes lemmonii	G4	N4	S4	0	0
Tagetes micrantha	G4G5	NNR	SNR	1	0
Vitis arizonica	G5?	NNR	SNR	2	0
Yucca baccata	G5	NNR	SNR	2	0
Yucca elata	G5	NNR	SNR	7	0
Ziziphus obtusifolia	G4G5	NNR	S3S4	0	0

† NatureServe conservation status rankings at global (G-), national (N-, USA), and state (S-, Arizona) levels: critically imperiled (G1, N1, S1), imperiled (G2, N2, S2), vulnerable (G3, N3, S3), apparently secure (G4, N4, S4); secure (G5, N5, S5), rank not yet assigned (GNR, NNR, SNR), unrankable due to lack of information or conflicting information (GU, NU, SU), or rank not applicable (GNA, NNA, SNA); ? denotes inexact numeric rank (NatureServe, 2019).

‡ Number of active wild germplasm accessions in NPGS by country of origin (USDA, 2019b).

§ Threatened taxa in Mexico (DOF, 2015).

¶ US Forest Service sensitive taxa occurring on National Forests in Arizona considered sensitive by the regional forester (AZGFD, 2019).

with state-level rankings, three are imperiled and four are vulnerable in Arizona. Two species are listed as threatened in Mexico (DOF, 2015): Santa Cruz striped agave (*Agave parviflora* Torr.) and Arizona walnut [*Juglans major* (Torr.) A. Heller]. However, neither species had active wild germplasm accessions collected from Mexico in the NPGS. Santa Cruz striped agave, which is ranked vulnerable at global, national (United States), and state (Arizona) levels, did not have a single active germplasm accession. With the exception of the wild chile, none of the species ranked vulnerable or imperiled in the United States had active wild germplasm accessions in the NPGS.

Wild Chile Conservation Synthesis

Turning our focus to the wild chile, we synthesize a quarter century of research and conservation efforts in a trans situ context. Integrating in situ and ex situ research from the Wild Chile Botanical Area and nearby ex situ facilities revealed the importance of biotic interactions for in situ conservation and management. Namely, that wild chile populations cannot be conserved in situ without conserving or restoring the nurse plant guild and the birds that use these plants for roosting, eating, and defecating (Tewksbury et al., 1999). The clumped distribution of wild chile plants under nurse plants results from directed dispersal by frugivorous bird species, most of which are migrating southward after breeding or fledging (Tewksbury et al., 1999; Tewksbury and Nabhan, 2001). The phenological sensitivity of this biotic interaction suggests a potential vulnerability to climate change and has implications for in situ management. Climate-driven shifts in the timing of either wild chile fruiting or bird migration by just 2 to 3 wk could disrupt the directed seed dispersal necessary for successful germination and recruitment (Carlo and Tewksbury, 2014).

Studying the biotic interactions and secondary chemistry of wild chiles in situ and ex situ lent insight into traits with potential use in plant breeding and crop improvement. Studies of bird, micro-moth, and fungal attraction and small mammal aversion to chile fruits demonstrated how secondary compounds such as pyrazines and capsaicinoids favor efficient seed dispersers while repelling seed predators (Tewksbury et al., 2008; Schulze and Spiteller, 2009). Each population of wild chile may be selecting for a different mix and potency of these secondary chemicals, depending on the frequency and intensity of visits by the species they are trying to attract and repel (Tewksbury et al., 2008; Schulze and Spiteller, 2009; Luna-Ruiz et al., 2018). Such knowledge could guide use of wild chiles in not only plant breeding, but also integrated pest management.

Finally, population genetics of the wild chile identified genetic variation relevant for crop improvement, ex situ conservation, and in situ conservation and management. Votava et al. (2002) identified unique alleles found only in populations at the northernmost limit of the species range in the Wild Chile Botanical Area. These alleles could be further investigated for associations with adaptive traits related to climate that may be useful for crop improvement, such as freeze or drought tolerance. Knowledge of the genetic variation found throughout the species range, from Guatemala to southern Arizona (Votava et al., 2002), could guide reserve designation and collecting efforts to improve both in situ and ex situ conservation of wild chile genetic diversity. A history of pre-domestication human management of the wild chile has been associated with reduced genetic diversity (González-Jara et al., 2011), suggesting that in situ conservation should consider past and present human use. In situ sites like the Wild Chile Botanical Area provide an important reference to compare with heavily harvested areas lacking protection or natural resource management plans.

DISCUSSION

Trans Situ Conservation in the Borderlands

Arizona and the United States–Mexico desert borderlands harbor important CWR diversity, including many species significant for food systems from local to continental

Table 4. Artisanal, economic, and agricultural uses of case study crop wild relatives (CWR).

	In situ	Ex situ		
Taxon	Artisanal†	Economic‡	Agricultural§	References
Agave palmeri	Intensive use and sale of thousands of gallons distilled mezcal lechuguilla	Ornamental in xeriscaping (common); bat-friendly pollinator gardens	–	Hodgson, 2001; Nabhan, personal observation
Amaranthus palmeri	Intensive local uses of wild greens as “cooked spinach”	–	–	Hodgson, 2001; Nabhan, personal observation
Capsicum annuum var. *glabriusculum*	Intensive use and sale of tons of green and red fruit for seasoning, salsa, and other artisanal products	Edible landscaping	Backcrossing with domesticates to obtain domesticated chiltepin to provide tons of fruit to binational spice markets	Hodgson, 2001; Nabhan, personal observation
Chenopodium berlandieri	Moderate use and occasional sale of greens for salads or cooking	Potential use of seeds for cooking oil and root for starch; trap crop for diabrotica beetles	–	Metcalf et al., 1982; Hodgson, 2001; Nabhan, personal observation
Cucurbita digitata	Gourds as ornaments and laundry soap	Potential use of seeds for cooking oil and root for starch	–	Nabhan and Felger, 1985; Hodgson, 2001; Nabhan, personal observation
Cucurbita foetidissima	Gourds as ornaments and laundry soap	Sales of painted gourds as crafts; trap crop for cucumber beetles	Hybridization to develop fruit with extra carpels for higher seed yield for oilseed production	Bemis et al., 1978; Metcalf et al., 1982; Nabhan and Felger, 1985; Hodgson, 2001; Nabhan, personal observation
Gossypium thurberi	–	Xeriscaping	Hybridization with domestic cotton to reduce chaffy bracts which cause brown lung disease in cotton ginners	Nabhan, 1985
Helianthus annuus	Eaten as raw seeds or oily seed paste	Bee-attracting plant in pollinator gardens	Screening, selection, and crossing with domestic sunflowers to increase tolerance to soil salinity, broom rape, Verticillium wilt, downy mildew, rusts, and increase oil content of seeds; source of cytoplasmic male sterility and fertility restorer genes	Hodgson, 2001; Seiler and Gulya, 2004; Seiler et al., 2017
Helianthus petiolaris	Eaten as raw seeds or oily seed paste	–	Crossing with domestic sunflowers to increase resilience to Verticillium wilt, rusts, mold; tolerance to sunflower moth, soil salinity, and drought; to increase oil content of seeds	Hodgson, 2001; Seiler et al., 2017
Hopia obtusa	Grass as stabilizing ground cover on charco reservoir banks; seeds historically eaten	Grass as stabilizing ground cover on charco reservoir banks	–	Hodgson, 2001
Juglans major	Rootstock for English walnut scion wood grafts in small orchards; nuts for dark dye	Rootstock for English walnut scion grafts at Hereford, AZ	Rootstock for English walnut scion wood grafts on alkaline soil	Hodgson, 2001; McGranahan and Leslie, 2009; Nabhan, personal observation
Lycium andersonii	Occasional use as fresh berry and for fruit syrup	Xeriscaping (common)	–	Hodgson, 2001
Lycium berlandieri	Occasional use as fresh berry and for fruit syrup	Xeriscaping (common)	–	Hodgson, 2001
Lycium fremontii	Intensive use of fresh or frozen berry as food and for fruit syrup	Xeriscaping (common)	–	Hodgson, 2001; Nabhan, personal observation

Table 4. Continued.

	In situ	Ex situ		
Taxon	Artisanal†	Economic‡	Agricultural§	References
Manihot angustiloba	–	–	Proposed source of drought resistance and higher starch content; bridge in gene transfer	Jennings, 1995; Narina et al., 2011; Contreras-Toledo et al., 2018
Mentha arvensis	–	Emerging use in edible landscaping	–	Nabhan, personal observation
Morus microphylla	Berries as food and for juice	–	–	Hodgson, 2001
Opuntia macrocentra	Fruit as fresh food; fruit for syrup	Xeriscaping (common)	–	Hodgson, 2001; Nabhan, personal observation
Opuntia phaeacantha	Intensive use of fresh or frozen fruit as food; fruit for syrup	Xeriscaping (common)	–	Hodgson, 2001; Nabhan, personal observation
Opuntia santa-rita	–	Xeriscaping (common)	–	Hodgson, 2001
Passiflora spp.	Incidental use as fruit eaten fresh by children	–	–	Hodgson, 2001
Phaseolus acutifolius	Historic harvesting of wild beans for parching or boiling to eat	–	Source of tolerance or resistance to heat, common bacterial blight, Fusarium wilt resistance, ashy stem blight, bean golden mosaic virus, bean rust, bruchids, leafhoppers; bridge in gene transfer	Nabhan, 1979; Thomas et al., 1983; Hodgson, 2001; Singh, 2001; Porch et al., 2013; Contreras-Toledo et al., 2018
Phaseolus angustissimus	–	Emerging use in edible landscaping	Proposed source of frost tolerance	Balasubramanian et al., 2004; Contreras-Toledo et al., 2018
Phaseolus maculatus	Historic harvesting of wild beans for boiling to eat; roots as medicine; foliage as livestock forage	Emerging use in edible landscaping	Source of disease resistance	Nabhan and Felger, 1985; van der Maesen and Somaatmadja, 1989; Hodgson, 2001; Contreras-Toledo et al., 2018
Solanum elaeagnifolium	Intensive use of fruit as vegetal rennet for curdling milk into queso asadero for sales of hundreds of pounds of cheese	Verified as safe as rennet in producing quality cheese with protection from secondary molds	–	Hodgson, 2001; Martínez-Ruiz et., al., 2013; Nabhan, personal observation
Stevia lemmonii	–	Xeriscaping (occasional)	Potential source of breeding for higher diterpene glycosides without bitter aftertaste	Yadav et al., 2011
Tagetes lemmonii	Leaves as culinary herb	Xeriscaping (occasional)	Cover crop for root knot nematode suppression	Suatmadji, 1969
Vitis arizonica	Fruit eaten raw or dried; prehistorically cultivated; fruit for vinegar	Rootstock for merlot and cabernet vineyard in Elgin, AZ	Rootstock for resistance to Pierce's disease bacterium	Hodgson, 2001; Riaz et al., 2006; Nabhan, personal observation
Yucca baccata	Use of roasted fruit by Apache as food and leaves in cordage	Xeriscaping (occasional)	–	Hodgson, 2001; Nabhan, personal observation
Yucca elata	Blossoms in salads, soups; leaves in basketry	Xeriscaping (common)	–	Hodgson, 2001; Nabhan, personal observation
Ziziphus obtusifolia	Minor use of fruit as food	Xeriscaping (occasional)	–	Hodgson 2001

† Local artisanal uses documented in situ.

‡ Economic uses emerging from regional ex situ collections.

§ Plant breeding and rootstock uses emerging from national germplasm collections.

scales (Table 4). The 62 CWR species conserved in situ comprise ~6% of the over 1000 CWR and wild utilized plant taxa in Arizona (Khoury et al., 2013; Khoury and Nabhan, 2019). Notably, some of the in situ populations have been utilized by nearby Native American and Hispanic communities for centuries, with both oral histories and archaeology documenting the use of wild plants like chiltepins at Rock Corral Canyon (Nabhan, 1978).

The low number of CWR species documented in common between the two in situ sites is consistent with the high β diversity found throughout the Sonoran Desert, Chihuahuan Desert, and intervening Sky Island montane landscapes of the United States–Mexico borderlands (McLaughlin, 1986). This high species turnover has implications for planning optimal in situ CWR protection (e.g., reserve size and spacing). We recommend a binational, inter-agency conservation planning effort to improve the in situ protection of CWR diversity and connectivity in the borderlands.

With a few exceptions of common species, most of the CWR we evaluated were inadequately represented in ex situ collections, suggesting conservation gaps and limited availability of genetic resources. Perhaps most disconcerting, the species with the greatest in situ vulnerability had little to no ex situ representation in national genebanks. Although regional seed and living plant collections provide educational and research opportunities for some of these species, the protection these collections offer is likely insufficient given increasing in situ habitat loss and environmental change.

Improving the comprehensiveness of CWR conservation, through both in situ and ex situ measures, is critical given the mounting environmental, social, and political pressures in the United States–Mexico borderlands (Liverman et al., 1999; Peters et al., 2018). We argue that the desert borderlands are disproportionately important relative to their number of CWR species for the following reasons:

1. A number of borderland CWR have high conservation priority in North America due their close relationship to internationally important crops and limited representation in major ex situ collections (Castañeda-Álvarez et al., 2016; Greene et al., 2018). Examples include wild chile, pitseed goosefoot (*Chenopodium berlandieri* Moq.), and desert mountain manihot [*Manihot angustiloba* (Torr.) Müll. Arg.].

2. Compounding effects of climate change and accelerating habitat destruction and fragmentation in the borderlands are increasing in situ extinction risk (Peters et al., 2018). Some borderland CWR already have elevated in situ vulnerability rankings due to their limited distributions, rarity, or threatened status, such as the Santa Cruz striped agave and Arizona passionflower [*Passiflora arizonica* (Killip) D.H. Goldman].

3. Many borderland CWR have adaptations to heat, drought, salinity, or other abiotic and biotic stressors likely to be exacerbated in United States agriculture due to climate change (Table 4). These CWR, such as the common sunflower (*Helianthus annuus* L.), Arizona walnut, and wild tepary bean, hold potential as breeding materials, hardy rootstocks, or new "crops" in and of themselves.

4. Borderland populations of a number of CWR are at their northern range and climatic limits. Of these populations, many contain unique genetic variation or traits not found elsewhere in the species range (Votava et al., 2002). Furthermore, as access to germplasm collected from Mexico decreases, through loss of accession availability from genebanks or increasing restrictions on the movement of plant materials across international borders, these northern populations may become the only sources of genetic material available to plant breeders in the United States.

5. Borderland CWR have direct economic importance at local to regional scales (Table 4). Within the Santa Cruz River watershed, CWR and wild utilized species from 15 genera are being used in 80 different food products from nearly 50 microenterprises (Nabhan et al., 2019). Without proper in situ protection and management, harvesting could erode CWR genetic diversity and negatively affect resources for both direct local use and indirect use in plant breeding and crop improvement.

Trans Situ Conservation at Large

Integrated in situ protection and ex situ collection is increasingly proposed to conserve CWR genetic diversity and safeguard food security in the face of climate change (Dempewolf et al., 2014). Trans situ conservation goes one step further, calling for a more dynamic integration of multiple in situ and ex situ measures, from conservation to research to education, spanning local to global scales. Just what would a trans situ approach to the conservation, evaluation, and use of CWR add to the current mix of conservation strategies being used in the United States? The short answer can be summarized in three words: *complementarity*, *redundancy*, and *synergy* (Becker et al., 1998; Meilleur and Hodgkin, 2004).

Complementarity among in situ and ex situ strategies improves the conservation and availability of CWR genetic diversity for plant breeding and crop research

(Engels et al., 2008). In situ conservation protects not just the target CWR species, but also the native environment within which the species continues to coevolve with its biotic associates. Some aspects of trait selection and crop diversification can only be answered by studying CWR in situ (Chen et al., 2017). Ex situ conservation of CWR genetic diversity in national and global genebanks, such as the NPGS, provide access to genetic materials for use in plant breeding and crop improvement (Byrne et al., 2018). Local and regional ex situ facilities (botanical gardens, arboreta, museums, and nurseries) located near in situ CWR populations offer complementary conservation, research, and education opportunities (O'Donnell and Sharrock, 2018). Their seed and living plant collections support the direct local use of appropriately adapted and regionally relevant CWR.

Trans situ conservation builds *redundancy* across strategies and buffers threats from climatic, political, and economic instabilities. Wild plants face a rising risk of extinction as climate change and human land use accelerate (Zhang et al., 2017b). Ex situ collections serve as an important insurance policy for increasingly threatened in situ CWR populations (Li and Pritchard, 2009). Ex situ sampling should aim to improve the representation of genetic and environmental diversity, and therefore the range of local adaptation, held in national genebanks and regional ex situ collections (Ramírez-Villegas et al., 2010; Hoban and Schlarbaum, 2014; Khoury et al., 2015, 2019). These "backups" require maintenance, however, as ex situ samples themselves are vulnerable to genetic erosion through genetic drift and viability selection (Fu, 2017). Ex situ samples and situ populations are never exact analogs of one another and diverge genetically through time.

Ex situ facilities must also cope with the effects of climate change. As documented in another arid zone, the Bekaa Valley of Lebanon, aquifer depletion and soil salinization are currently threatening years of successful seed regeneration partnerships and impacting germplasm repositories (Daghir, 2012; Duggan, 2017; Nabhan, unpublished data, 2019). Degradation or closure of ex situ facilities is emerging as a secondary effect of the interactions among climate change, social conflict, warfare, and the resulting economic instability of agricultural regions and institutions (Duggan, 2016, 2017). The loss of operations at the International Center for Agricultural Research in the Dry Areas (ICARDA) station near Aleppo, Syria, at the same time that drought and destruction of irrigation infrastructure occurred (Gleick, 2014; Duggan, 2016) produced a negative feedback loop. Increasing the *redundancy* of accessions within and among ex situ collections and facilities will help avert massive losses in CWR genetic diversity.

A number of *synergies* arise when integrating in situ and ex situ components. As illustrated by the wild chile research, integrating in situ and ex situ studies of CWR genetic diversity, adaptation, and ecological interactions can lead to advances in crop improvement and in situ management. Strengthening collaboration between regional ex situ facilities and national genebanks could improve the ex situ conservation and accessibility of CWR genetic resources. National genebanks may not have the resources to adequately regenerate the numerous CWR with potential for crop improvement but do have the infrastructure for large-scale germplasm distribution. Regional ex situ facilities with conditions similar to nearby in situ CWR populations are well positioned to research, regenerate, and regionally distribute locally adapted germplasm but may not be equipped for large-scale distribution. Widely varying infrastructure for genebanking at these facilities underscores a need for training and capacity building to support local and regional ex situ collections (O'Donnell and Sharrock, 2018).

Trans situ conservation must also address the occasional tensions that arise when multiple in situ and ex situ components are simultaneously functioning. For instance, in situ CWR conservation and management have historically received a miniscule proportion of the support provided to ex situ conservation and use initiatives. Our case study illustrates the different, and perhaps at times competing, cultural and economic uses of CWR (Table 4). It is unclear whether formal habitat protection impedes or, alternatively, safeguards traditional stewardship and use. Linking local community livelihoods and other rural development opportunities to local in situ conservation projects (Kux, 1991) may help alleviate some tensions. In the case of the Wild Chile Botanical Area, the right to harvest the wild chile by local families who traditionally used the area as gathering grounds was assured and external commercial extraction was controlled. Studying the effects of human harvest and management on CWR genetic diversity (González-Jara et al., 2011) can guide sustainable in situ use that supports both local economic productivity and crop improvement efforts.

Finally, there is one particular in situ conservation measure that remains understudied and underdeveloped: how can we more actively manage landscapes to favor the persistence and genetic diversity of CWR in situ? Historically, the USFS and USDA-ARS have had neither funds nor mandates to actively manage CWR like the wild chile or its biotic associates. Only recently have the two agencies begun collaborative efforts to support CWR conservation through active in situ management and ex situ conservation (USFS, 2014). Such dynamic management for CWR species has been recommended by Iriondo et al. (2008) and Maxted and Kell (2009), yet in the southern Arizona case study, we know little about which management practices most affect persistence of CWR in situ (Table 5). The presence of two in situ sites with different land use practices overseen by different agencies offers an opportunity

Table 5. Management practices potentially affecting case study crop wild relatives (CWR) in situ following Iriondo et al. (2008).

	History in Arizona		Influence on CWR†	
Management practice	USFS‡	USDA-ARS	WCBA	WGEW
Managed burns	Current, historical	Current, historical	Unlikely due to sheltered microsites	Unlikely
Removal of invasives	Current, historical	Current, historical	Negligible (at present)	Negligible (at present)
Native woody shrub control by herbicides	Historical	Current, historical	Could affect CWR and nurse plants	Could affect CWR and nurse plants
Water catchment in stock tanks	Current, historical	Current, historical	Current minimal impact on water flow could indirectly affect CWR and nurse plant water availability	Current dramatic impact on water flow could affect nurse plant and CWR water availability
Water diversion for roads or pipelines	Historical	Historical	Negligible	Negligible
Rotational grazing	Current	Current	Negligible	Negligible
Mine exploration	Historical	Historical	Unknown	Unknown

† WCBA, Wild Chile Botanical Area; WGEW, Walnut Gulch Experimental Watershed.

‡ USFS, US Forest Service.

to identify which agency is more disposed to actively manage CWR through a trans situ framework.

CONCLUSIONS

We emphasize the importance of dynamically integrating multiple conservation measures through a trans situ framework to safeguard, recover, and utilize CWR genetic resources. Although it is theoretically possible that a single CWR may be simultaneously lost from holdings associated with two or more conservation strategies, the positive synergies that accrue with trans situ coordination offer benefits not provided by in situ or ex situ efforts alone. In particular, local and regional ex situ facilities (botanical gardens, museums, arboreta, and nurseries) play an important role supporting research, conservation, and use of locally adapted plant materials that may be otherwise inaccessible from national and global genebanks.

Two important features emerge from trans situ conservation. First, integrated in situ and ex situ studies of CWR genetic diversity, adaptation, and ecological interactions can lead to advances in crop improvement and in situ management. Second, the complementarity, redundancy, and synergy gained through a trans situ model are essential to weathering the uncertain future ahead. Current conservation gaps in the United States–Mexico borderlands pose opportunities for collaboration to better integrate in situ and ex situ measures. Given the mounting threats from climate change, political and economic uncertainty, habitat fragmentation, and loss of traditional knowledge of desert-adapted resources, effective CWR conservation will depend on cross-border collaboration among agricultural botanists, conservation biologists, land managers, and local communities.

Conflict of Interest

The authors declare that there is no conflict of interest.

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