

RESEARCH ARTICLE

Distributions, conservation status, and abiotic stress tolerance potential of wild cucurbits (*Cucurbita* L.)

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Societal Impact Statement

Crop wild relatives—wild species closely related to cultivated plants—are valuable genetic resources for crop improvement, but gaps in knowledge constrain their conservation and limit their further use. We develop new information on the distributions, potential breeding value, and conservation status of the 16 known wild relatives of cultivated pumpkins, squashes, zucchini, and gourds (*Cucurbita* L.). The taxa occur from the central USA to Central America, plus two South American species, with the greatest richness in central Mexico and the western borderlands between Mexico and the USA. We determine the majority of species are of medium priority for conservation, both with regard to collecting for ex situ maintenance, and for enhanced habitat protection.

Summary

- Crop wild relatives are valuable genetic resources for crop improvement. Knowledge gaps, including with regard to taxonomy, distributions, and characterization for traits of interest constrain their use in plant breeding. These deficiencies also affect conservation planning, both with regard to in situ habitat protection, and further collection of novel diversity for ex situ maintenance.
- Here we model the potential ranges of all 16 known wild cucurbit taxa (*Cucurbita* L.), use ecogeographic information to infer their potential adaptations to abiotic stresses, and assess their ex situ and in situ conservation status.
- The taxa occur from the central USA to Central America, plus two South American species. Predicted taxon richness was highest in central Mexico and in the western borderlands between Mexico and the USA. We find substantial ecogeographic variation both across taxa and among populations within taxa, with regard to low temperatures, high and low precipitation, and other adaptations of potential interest for crop breeding.
- We categorize 13 of the taxa medium priority for further conservation as a combination of the ex situ and in situ assessments, two low priority, and one sufficiently

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conserved. Further action across the distributions of the taxa, with emphasis on taxonomic richness hotspots, is needed to comprehensively conserve wild *Cucurbita* populations.

KEYWORDS

biodiversity conservation, crop wild relatives, *Cucurbita*, ex situ conservation, gap analysis, in situ conservation, plant genetic resources

1 | INTRODUCTION

Crop wild relatives—the wild progenitors and closely related species to cultivated plants—have provided many beneficial agronomic, nutritional, and breeding efficiency traits for crop improvement (Dempewolf et al., 2017; Hajjar & Hodgkin, 2007). As some populations of these wild plants are adapted to extreme climates and deficient soils, and to challenging pests and diseases, they may offer particularly valuable traits for crop adaptation to emerging and to projected future agricultural challenges (Dempewolf et al., 2013).

Gaps in knowledge with regard to these genetic resources, including information on species' taxonomy and crossability with crops (i.e., genepool and taxon group concepts), distributions, and characterization for traits of interest, constrain their potential for use in plant breeding (Dempewolf et al., 2017; Miller & Khoury, 2018). Such foundational knowledge gaps also affect conservation efforts for the taxa. These are necessary to protect vulnerable populations from habitat destruction and degradation, over-harvesting, climate change, and invasive species so that they may continue to evolve (Bellon, Dulloo, Sardos, Thormann, & Burdon, 2017; Brummitt et al., 2015; Díaz et al., 2019; Jarvis, Lane, & Hijmans, 2008), and to ensure that genetic resources are safeguarded for the long term and available for use in living plant conservation repositories (Castañeda-Álvarez et al., 2016; Gepts, 2006). Global analyses indicate that wild relatives are poorly represented in genebanks (Castañeda-Álvarez et al., 2016) and in protected areas (Khoury et al., 2019a), highlighting the urgency of addressing these information gaps to guide future conservation and to support crop improvement efforts.

The genus *Cucurbita* L. includes a number of globally as well as regionally important crops with outstanding fruit morphological diversity (Naudin, 1856) and adaptations to a wide range of agro-ecosystems (Table 1). Three crop taxa are native to North America (including Mexico): the widely cultivated and economically significant *Cucurbita pepo* L. subsp. *pepo* (cocozele, pumpkin, vegetable marrow, zucchini), *C. pepo* L. subsp. *ovifera* (L.) D. S. Decker (acorn, crookneck, scallop, straightneck), and finally *C. argyrosperma* C. Huber subsp. *argyrosperma* (calabaza pipiana, green-striped cushaw, silver-seed gourd), a less widely cultivated taxon but which remains important in traditional Mesoamerican agriculture (Montes-Hernandez & Eguiarte, 2002). The three taxa likely domesticated in Central or South America include the widely cultivated *C. maxima* Duchesne subsp. *maxima* (buttercup squash, giant pumpkin, Hubbard squash, kabocha squash) and *C. moschata* Duchesne (butternut squash), as

well as *C. ficifolia* Bouché (figleaf gourd), which is cultivated only in Latin America and in some regions of Asia.

The wild taxa in the genus *Cucurbita* include seven mesophytic annual species and six perennial xerophytic species, which occupy diverse habitats from the Midwestern United States to southern Argentina (Table 2). The greatest species diversity occurs in Mexico, although phylogenetic data suggest that the genus likely originated in Central or South America (Schaefer, Heibl, & Renner, 2009). Once dispersed by megafauna, wild *Cucurbita* appear to have declined with the extirpation of these animals (Kistler et al., 2015).

The domesticated taxa originated from at least six different wild species in North, Central, and South America as early as ~ 10,000 years ago (Smith, 2006). Phylogenetic studies have identified the wild progenitors for only three of the six crop taxa (Figure S1) (Kates, Soltis, & Soltis, 2017): *C. argyrosperma* subsp. *sororia* (L. H. Bailey) L. Merrick & D. M. Bates is considered to be the wild ancestor of cushaw (Merrick, 1995), *C. maxima* Duchesne subsp. *andreaana* (Naudin) Filov the wild ancestor of buttercup squash (Decker-Walters & Walters, 2000), and the wild varieties of *C. pepo* L. subsp. *ovifera* (L.) D. S. Decker [var. *ozarkana* D. S. Decker and var. *texana* (Scheele) Filov] are likely ancestral to acorn squash. A third lineage of wild *C. pepo*, *C. pepo* (L.) subsp. *fraterna* (L.H. Bailey) Lira et al. is also a primary (i.e., very close) relative, although it is not considered ancestral to any extant *Cucurbita* crop taxon (Kates et al., 2017). The wild progenitors of the remaining crop taxa are most likely extinct but possibly rare and uncollected (Kistler et al., 2015).

All six domesticated taxa originated from mesophytic species, which form a clade and are apparently the result of a very recent radiation (~7 mya) from a common ancestor in Central or South America (Schaefer et al., 2009). The xerophytic perennials occur in deserts and dry scrub of Mexico and the southwestern USA (Nee, 1990), and may represent the ancestral habit of the genus (Kates et al., 2017).

Archaeological evidence points to widespread movement of some *Cucurbita* species by humans in the Americas prior to European contact (Lira-Saade & Montes-Hernandez, 1994), and genetic and archaeological studies suggest that for at least one species (*C. maxima*), wild and semi-domesticated forms were used concurrently with the domesticate for thousands of years (Lema, 2011; H.R. Kates, pers. comm.). Gene flow is common between wild and domesticated *Cucurbita* and can occur between different species. Wild *Cucurbita* are still commonly utilized by rural people in Latin America living in proximity to wild populations.

TABLE 1 Cultivated *Cucurbita* and their geographic origins, current extent of cultivation, and common uses

Taxon	Main cultivar groups	Origin	Current cultivation	Most common uses
<i>Cucurbita argyrosperma</i> C. Huber subsp. <i>argyrosperma</i> (cushaw)	Silver-seed gourd; green-stripe cushaw; Calabaza pipiana ^a	Southern Mexico ~ 7,000 years B.P. ^b	Limited. Mexico, U.S.A., Central America	Seeds (snack food, oil, meal); Fruit (usually mature)
<i>C. ficifolia</i> Bouché (figleaf gourd)	Not well understood; local cultivars are documented	Unknown (highland regions of Mexico, Central America, or South America) >4,000 years B.P. ^{a,c}	Limited. Latin America, Asia, Spain, Portugal	Greens; Fruit (immature, mature); Seeds; Root stock
<i>C. maxima</i> Duchesne subsp. <i>maxima</i> (buttercup squash)	Banana squash; Delicious squash; Buttercup squash; Hubbard squash; Show pumpkins; Turban squash; Kabocha ^d	South America ~ 4,000 years B.P. ^b	Worldwide esp. Africa and Asia	Fruit (immature, mature, canned, decorative)
<i>C. moschata</i> Duchesne (butternut squash)	Cheese; Crookneck; Bell ^e	Unknown (Mexico, Central America, or South America) >5,000 years B.P. ^{c,f}	Worldwide esp. Africa and Asia	Fruit (immature, mature, canned)
<i>C. pepo</i> L. subsp. <i>ovifera</i> (L.) D. S. Decker (ovifera pumpkin and squash)	Scallop, Acorn, Crookneck, Straightneck, oviform ornamental gourds ^g	Eastern North America ~ 5,000 years B.P. ^b	Worldwide	Fruit (immature, mature, canned, decorative)
<i>C. pepo</i> L. subsp. <i>pepo</i> (pepo pumpkin and squash)	Pumpkin, Vegetable Marrow, Cocozelle, Zucchini, round ornamental gourds ^g	Mexico ~ 10,000 years B.P. ^b	Worldwide	Fruit (immature, mature, canned, decorative)

^aLira-Saade and Montes-Hernandez (1994).

^bSmith (2006).

^cCohen (1978).

^dDecker-Walters and Walters (2000).

^eRobinson and Decker-Walters (1997).

^fTowle (1961).

^gParis, Lebeda, Kristkova, Andres, and Nee (2012).

Genomic resources and genetic transformation protocols have recently become available in *Cucurbita* (Montero-Pau et al., 2018, 2017; Nanasato, Okuzaki, & Tabei, 2013; Sun et al., 2017). Alongside improvements in the characterization of genetic diversity within the crop wild relatives, these resources are facilitating breeding and genetic research (e.g., Holdsworth, LaPlant, Bell, Jahn, & Mazourek, 2016).

Virus resistance is one of the most sought after traits for *Cucurbita* crop improvement (Paris, 2016). Wild *Cucurbita* exhibit higher resistance to viral diseases than do domesticated taxa and have been successfully used to increase resistance in some cultivars (Table 2). *C. lundelliana* L. H. Bailey has been notably important as a genetic bridge species for introgressing disease resistance from wild species into cultivars. Important abiotic stresses for the *Cucurbita* crops include low temperatures (Lira-Saade & Montes-Hernandez, 1994; Sharma & Tarsem, 1998), low precipitation (in rainfed production systems) (Daniello, 2003), and high precipitation (causing fruit rot) (Kennedy, 2015).

IUCN Red List assessments have recently been published for the majority of wild *Cucurbita*, at least at the species level, although five of the determinations concluded that more information was needed (Data Deficient) (Table 2). Seven taxa were assessed Least Concern, while *C. ecuadorensis* H. C. Cutler & Whitaker was assessed Vulnerable, and *C. radicans* Endangered (with a decreasing population trend due to urbanization, agriculture, pollution, and climate change impacts). The NatureServe Explorer lists conservation assessments for six wild *Cucurbita* (NatureServe, 2019). Of these, only *C. okeechobeensis* (Small) L. H. Bailey subsp. *okeechobeensis* was listed as a conservation concern (G1, Critically Imperiled); this taxon is also Listed Endangered under the US Endangered Species Act (USFWS, 2019).

The distributions of wild *Cucurbita* may decrease substantially in the coming decades due to climate change (Lira, Téllez, & Dávila, 2009), although potential habitat for some taxa may expand (Thomas et al., 2016). The specialized pollinators of wild *Cucurbita*, including *Xenoglossa* and *Peponapis* (squash bees), are known to be affected

TABLE 2 Wild *Cucurbita* and their gene pool assignments, habitats and longevity, native ranges, published breeding research, and conservation designations

Taxon	Gene pool (A; B; C; D; E) ^a	Habitat and longevity	Native range	Breeding research ^b	Current conservation designation ^c
<i>Cucurbita argyrosperma</i> C. Huber subsp. <i>sororia</i> (L. H. Bailey) L. Merrick & D. M. Bates	2; 1; 2; 3; 3	Mesophytic annual	Pacific and gulf coasts from Sonora in Mexico south to Nicaragua	Resistant to BYMV and TmRSV	RL- Least Concern (assessed at species level)
<i>C. cordata</i> S. Watson	3; 3; 3; 3; 3	Xerophytic perennial	Baja California (Mexico)	Drought-tolerant; resistant to CMV, TRSV, BYMV	RL- Data Deficient
<i>C. digitata</i> A. Gray	3; 3; 3; 3; 3	Xerophytic perennial	Southwestern United States and northwestern Mexico	Drought-tolerant; resistant to CMV, TmRSV	RL- Least Concern; NS- G5
<i>C. ecuadorensis</i> H. C. Cutler & Whitaker	3; 3; 3; 2; 3	Mesophytic annual	Ecuador	Resistant to papaya ringspot virus, WMV, powdery mildew, downy mildew	RL- Vulnerable
<i>C. foetidissima</i> Kunth	3; 3; 3; 3; 3	Xerophytic perennial	Southwestern United States and northern Mexico	Drought-tolerant; resistant to CMV, TRSV, BYMV, WMV, and squash vine borer	RL- Least Concern; NS- G5
<i>C. lundelliana</i> L. H. Bailey	2; 3; 2; 2; 2	Mesophytic annual	Southern Mexico (Tabasco to Yucatan) (and northern Central America)	Resistant to SqLCV, CMV, powdery mildew; used as a genetic bridge for breeding nonin-terfertile species	RL- Least Concern
<i>C. maxima</i> Duchesne subsp. <i>andreaea</i> (Naudin) Filov	3; 3; 3; 1; 3	Mesophytic annual	Eastern Argentina, possibly Bolivia	Precocious yellow fruit pigmentation (Bicolor)	
<i>C. okeechobeensis</i> (Small) L. H. Bailey subsp. <i>martinezii</i> (L. H. Bailey) T. C. Andres & Nabhan ex T. W. Walters & D. S. Decker	2; 3; 2; 3; 3	Mesophytic annual	Southern Mexico (gulf coast)	Resistant to CMV, BYMV, TRSV, bacterial leaf spot, powdery mildew, downy mildew	RL- Data Deficient (assessed at species level)
<i>C. okeechobeensis</i> (Small) L. H. Bailey subsp. <i>okeechobeensis</i>	2; 3; 2; 3; 3	Mesophytic annual	Southern Florida (United States)	Resistant to CMV, BYMV, TRSV, bacterial leaf spot, powdery mildew, downy mildew	RL- Data Deficient (assessed at species level); NS- G1 (assessed at species level but indicated to be this taxon); US ESA- LE
<i>C. palmata</i> S. Watson	3; 3; 3; 3; 3	Xerophytic perennial	Southwestern United States and Baja California and Sonora, Mexico	Drought-tolerant; resistant to CMV, TRSV, BYMV, TmRSV	RL- Data Deficient; NS- G4–5
<i>C. pedatifolia</i> L. H. Bailey	3; 3; 3; 2	Xerophytic perennial	North-central to southern Mexico	Drought-tolerant; disease resistance unstudied; potential as bridge species between xerophytic and mesophytic species	RL- Data Deficient
<i>C. pepo</i> L. subsp. <i>fraterna</i> (L. H. Bailey) Lira et al.	1; 2; 2; 3; 3	Mesophytic annual	Northern gulf coast of Mexico	Unknown	RL- Least Concern (assessed at species level)
<i>C. pepo</i> L. subsp. <i>ovifera</i> (L.) D. S. Decker var. <i>ozarkana</i> D. S. Decker	1; 2; 2; 3; 3	Mesophytic annual	Central United States	Unknown	RL- Least Concern (assessed at species level); NS- G4–5 (assessed at species level)

(Continues)

TABLE 2 (Continued)

Taxon	Genepool (A; B; C; D; E) ^a	Habitat and longevity	Native range	Breeding research ^b	Current conservation designation ^c
<i>C. pepo</i> L. subsp. <i>ovifera</i> (L.) D. S. Decker var. <i>texana</i> (Scheele) Filov	1; 2; 2; 3; 3	Mesophytic annual	Texas (United States)	Light coloration of the fruit	RL- Least Concern (assessed at species level); NS- G4-5 (species level, with infraspecific taxon estimated at G4)
<i>C. radicans</i> Naudin	3; unknown; 2; 3; unknown	Xerophytic perennial	North-central to southern Mexico	Drought-tolerant; resistant to CMV, TmRSV; BYMV; production of potato-sized tubers	RL- Endangered, with populations decreasing
<i>C. x scabridifolia</i> L. H. Bailey ^d	3; 3; 3; 2 or 3	Xerophytic perennial	Central Mexico	Drought-tolerant	

^aGenepool designations from OECD (2016); Esquinas-Alcazar and Gulich (1983); Whitaker and Bemis (1964); Metwally, Haroun, and El-Fadly (1996).

^bPotential and documented use in breeding from Paris and Kabelka (2009); Paris and Brown (2005); Behera, Sureja, Islam, Munshi, and Sidhu (2012); Herrington, Byth, Teakle, & Brown (1989).

^cConservation designations as per the IUCN Red List of Threatened Species (RL) (Aragón Cuevas, Sánchez de la Vega, Castellanos Morales, Contreras, & Lira Saade, 2019b, 2019c; Contreras, 2016; Sánchez de la Vega, Castellanos Morales, Contreras, & Lira Saade, 2019a, 2019b, 2019c; Contreras, 2016; Sánchez de la Vega, Castellanos Morales, Contreras, Aragón Cuevas, Contreras, & Lira Saade, 2019a, 2019b; Sánchez de la Vega, Contreras, Aragón Cuevas, Contreras, Aragón Cuevas, & Lira Saade, 2019; Santiana & Pitman, 2004), NatureServe (NS) (G1 = Critically Imperiled; G4 = Apparently Secure; G5 = Secure) (NatureServe, 2019), and the US Endangered Species Act (US ESA) (LE = Listed Endangered) (USFWS, 2019).

^d*C. x scabridifolia* is likely a naturally occurring hybrid between *C. foetidissima* and *C. pedatifolia* (Andres, 1987) and its genepool designations were inferred from these species.

by climate change and the widespread use of agricultural pesticides (Watanabe, 2013). Finally, the potential deregulation of transgenic zucchini (*C. pepo* L. subsp. *pepo* var. *cylindrica*) in Mexico has raised concerns with regard to the preservation of genetic variation in the genus in its primary region of diversity (Cruz-Reyes, Avila-Sakar, Sanchez-Montoya, & Quesada, 2015), although transgenic x wild hybrids do not appear to have a competitive advantage over wild taxa (Arriaga, Huerta, Lira-Saade, Moreno, & Alarcon, 2006; Cruz-Reyes et al., 2015; Sasu, Ferrari, Du, Winsor, & Stephenson, 2009).

Here we model the potential distributions of all 16 currently known wild taxa in the genus *Cucurbita* (Table 2). We use ecogeographic information to infer the potential adaptations of the crop wild relatives to abiotic stresses significant in *Cucurbita* crop production. We then assess their conservation status, both in genebanks and botanic garden collections (ex situ), and in protected areas (in situ).

2 | MATERIALS AND METHODS

2.1 | Occurrence information

We gathered reference occurrence data for all records listed as within the genus *Cucurbita* L. from the Global Biodiversity Information Facility (GBIF, 2018), the Global Crop Wild Relative Occurrence Database (Global Crop Diversity Trust, 2018), and from the authors' own botanical explorations. We compiled genebank and botanical garden conservation occurrence as well as reference occurrence data from the Genesys plant genetic resources portal (Global Crop Diversity Trust, 2018), the USDA National Plant Germplasm System (GRIN Global) (USDA ARS NPGS, 2018a), the United Nations Food and Agriculture Organization World Information and Early Warning System on Plant Genetic Resources for Food and Agriculture (WIEWS) (FAO, 2018), and from the Botanic Gardens Conservation International PlantSearch database (BGCI, 2018). Duplicates in the databases were removed with preference for original/most recently updated data providers (e.g., USDA NPGS dataset instead of equivalent USDA records in Genesys).

Taxonomic names were standardized against USDA GRIN Global Taxonomy (USDA ARS NPGS, 2018b). Cultivated taxa; records listed in sample status fields as other than wild, weedy, or null (e.g., landrace, improved, breeding material, or cultivated); fossil specimens in the GBIF dataset; and records listed in collecting/acquisition source fields as from markets, institutes, and home gardens were removed. In preparation for the conservation analysis, we classified each record according to whether it was a field observation (labeled H, as most of these records are from herbaria), or a "site where germplasm collected" location of an existing plant genebank or botanic garden conservation accession (labeled G, as most records are from genebanks). For GBIF, this classification was performed by filtering the "Basis of Record" field, assigning "living specimen" records as G, with the other categories (observation, literature, preserved specimen, human observation, machine

observation, material sample, and unknown) assigned as H. All records in Genesys, WIEWS, and PlantSearch were assigned G, while GRIN Global records were assigned G when their status field was listed as active and H when inactive. Records from the Global Crop Wild Relative Database had already been categorized accordingly. To maximize the comprehensiveness of the ex situ conservation gap analysis, we georeferenced the (49) G occurrences in the dataset that had detailed locality information but lacked coordinates, using Google (2019a).

To review the occurrence data in preparation for distribution modeling, we uploaded all H and G coordinates to an interactive mapping platform (Google, 2019b), and corrected or removed points occurring in bodies of water or in clearly incorrect locations. Due to the large number of occurrences for *C. foetidissima*, points for this species were proportionally thinned by country to less than a total of 2,000, to facilitate distribution modeling (Khoury et al., 2019a). Refined occurrence data were extracted from the interactive mapping platform. The final occurrence dataset is available in Dataset S1, sheet 1.

2.2 | Distribution modeling

We used the Maximum Entropy (MaxEnt) algorithm (Phillips, Anderson, Dudik, Schapire, & Blair, 2017) accessed through the R statistical package *dismo* (Hijmans, Phillips, Leathwick, & Elith, 2017) to model the potential distributions of the taxa, following processes outlined in Khoury et al. (2019a). We assembled a total of 26 ecogeographic predictors (Table S1). These included 19 bioclimatic variables, plus solar radiation, water vapor pressure, and wind speed, derived from WorldClim 2 (Fick & Hijmans, 2017). For the final three variables, we produced annual values by calculating the median across monthly values. Altitude was compiled from the CGIAR-CSI dataset based on the NASA Shuttle Radar Topography Mission data (Jarvis, Reuter, Nelson, & Guevara, 2008). Variables for slope and aspect were also incorporated, calculated from the altitude dataset using the terrain function in R package *raster* (Hijmans, 2017). All ecogeographic predictors were processed at a spatial resolution of 2.5 arc-minutes (approximately 5 km² at the equator) (results available in Dataset S1, sheet 2; raw data available from Khoury et al., 2019b).

Ecogeographic variables were selected per taxon using the R package *VSURF* (Genuer, Poggi, & Tuleau-Malot, 2018). All variables that made no measurable impact on model performance were removed and the remaining variables were ranked in order of importance. Starting with the most important predictor, variables that were correlated with greater than a 0.7 Pearson correlation coefficient were removed. This process was performed for the top five predictor variables, with the remaining variables selected for use in the modeling process (Dataset S1, sheet 3).

The number of comparative background points ("pseudo-absences") were determined per taxon in proportion to the total number of pixels within the spatial background, which was calculated based on pertinent ecoregion boundaries, i.e., the ecoregions

defined in Olson et al. (2001) (available from Khoury et al., 2019b) wherein occurrence data fell, bounded by the borders of the countries wherein occurrence data fell, with a maximum of 5,000 pseudo-absences per taxon. Pseudo-absence points that fell within the same cell as a presence point were removed.

For each taxon with at least 10 coordinates, the modeled distribution was calculated as the median of 10 MaxEnt model replicates ($K = 10$), using linear, quadratic, hinge and product features, with a regularization parameter $\beta = 1.0$. For taxa with less than ten coordinates, the median of three replicates ($K = 3$) was calculated. Following previous gap analysis studies (Castañeda-Álvarez et al., 2016; Ramirez-Villegas, Khoury, Jarvis, Debouck, & Guarino, 2010), we evaluated the MaxEnt model output using the area under the receiver operating characteristic curve (AUC), the standard deviation of the AUC across replicates (SDAUC), and the proportion of the potential distribution model with a standard deviation of the replicates above 0.15 (ASD15). A robust model required an AUC mean ≥ 0.7 ; SDAUC < 0.15 ; and ASD15 $\leq 10\%$. Distribution models were thresholded using the maximum sum of sensitivity and specificity (Liu, Berry, Dawson, & Pearson, 2005; Liu, White, & Newell, 2013) and clipped to the extent of the native country–ecoregion boundaries (Olson et al., 2001).

2.3 | Ecogeographic characterization

Ecogeographic predictor information at a resolution of 30 arc-seconds (approximately 1 km² at the equator) for 23 pertinent variables (slope and aspect variables were not included as they do not provide meaningful ranges with which to distinguish variation among taxa) from the WorldClim 2 and CGIAR-CSI datasets were extracted for all occurrence data with coordinates for all taxa (Dataset S1, sheet 4). These data were used to characterize taxa with regard to their ecogeographic niches for each variable. We also used these data to assess the representation of these niches in ex situ conservation by comparing the distributions of G points for each taxon within the full spread of its occurrences, as supplement to the conservation gap analysis assessment detailed below.

2.4 | Conservation gap analysis

We assessed the degree of representation of each taxon in conservation systems, both ex situ and in situ, building on methods outlined in Khoury et al. (2019a). For ex situ, three scores were calculated. The Sampling Representativeness Score ex situ (SRSex) provides a general indication of the completeness of genebank and botanic garden conservation collections for each taxon, comparing the total counts of G records against H records, with an ideal ratio of 1:1. Unique among the conservation metrics, this score makes use of all compiled reference and germplasm records, regardless of whether they possess geographical coordinates. In this and all other metrics, SRSex was bound between 0 and 100, with 0 representing

an extremely poor state of conservation, and 100 a comprehensive (complete) state of conservation.

The Geographical Representativeness Score *ex situ* (GRSex) is a geographic measurement of the proportion of the range of the taxon conserved *ex situ*. Buffers (“CA50”) of 0.5 degrees (approximately 50 km radius) were created around each G collection point in order to estimate geographic areas already collected within the distribution models. Comprehensive conservation under this metric was considered to have been accomplished when the buffered areas covered the entire distribution model.

The Ecological Representativeness Score *ex situ* (ERSex) is an ecological measurement of the proportion of the range of the taxon conserved in *ex situ* repositories. The ERSex compares the ecoregional diversity encompassed in *ex situ* conservation repositories to the diversity throughout the distribution models, considering comprehensive conservation to have been accomplished only when every ecoregion potentially inhabited by a taxon was included at least once within the set of CA50 buffered areas. The layer used for estimating the ERSex contained 867 distinct terrestrial ecoregions worldwide (Olson et al., 2001) (available from Khoury et al., 2019b). A Final Conservation Score for *ex situ* (FCSex) was derived by calculating the average of the three individual *ex situ* conservation metrics.

For the analysis of the state of *in situ* conservation, three metrics were calculated based on the extent of representation of the range of each taxon within officially recognized protected areas. We used the World Database of Protected Areas (IUCN, 2019), selecting terrestrial and coastal reserves marked as designated, inscribed, or established. The Sampling Representativeness Score *in situ* (SRSin) calculates the proportion of occurrences of a taxon that fall within a protected area.

The Geographical Representativeness Score *in situ* (GRSin) compares the area (in km²) of the distribution model located within protected areas versus the total area of the distribution model, considering comprehensive conservation to have been accomplished only when the entire distribution occurs within protected areas.

The Ecological Representativeness Score *in situ* (ERSin) compares the ecological variation encompassed within the range located inside protected areas to the ecological variation encompassed within the total area of the distribution model, considering comprehensive conservation to have been accomplished only when every ecoregion potentially inhabited by a taxon is included within the distribution of the species located within a protected area. A Final Conservation Score for *in situ* (FCSin) was derived by calculating the average of the three *in situ* conservation metrics.

A combined Final Conservation Score (FCSc-mean) was calculated for each taxon by averaging its *ex situ* (FCSex) and *in situ* (FCSin) scores. Taxa were then categorized, with High Priority (HP) for further conservation action for species where FCSc-mean < 25; Medium Priority (MP) where 25 ≤ FCSc-mean < 50; Low Priority (LP) where 50 ≤ FCSc-mean < 75; and Sufficiently Conserved (SC) for taxa whose FCSc-mean ≥ 75.

In supplement to the conservation gap analysis, we used the occurrence information to calculate the Extent of Occurrence (EOO) and Area of Occupancy (AOO) of each taxon, adapted from the IUCN Red List criteria (IUCN Standards & Petitions Committee, 2019) and run through the R package Redlistr (Lee, Keith, Nicholson, & Murray, 2019). Taxa were classified per each metric and in combination, as Critically Endangered where EOO < 100 km² or AOO < 10 km²; Endangered where 100 km² < EOO < 5,000 km² or 10 km² < AOO < 500 km²; Vulnerable where 5,000 km² < EOO < 20,000 km² or 500 km² < AOO < 2,000 km²; Possible Near Threatened where 20,000 km² > EOO < 45,000 km² or 2,000 km² < AOO < 4,500 km²; and Least Concern where EOO ≥ 45,000 km² and AOO ≥ 4,500 km². We did not perform rates of change over time analyses due to the limited date information in the occurrence dataset. While the metrics do not provide the full set of criteria needed for Red Listing, they may offer indications of the probable threat status of the taxa.

3 | RESULTS

3.1 | Distributions of wild *Cucurbita*

A total of 7,595 occurrence records were compiled and processed for the 16 taxa for distribution modeling and conservation analyses, including 7,142 reference (H) records and 453 living plant conservation repository (G) records (Tables 3 and S2). Of these, 4,784 (4,514 H, 270 G) contained coordinates and were thus used as inputs into the species distribution modeling. The total number of records per taxon ranged from eleven (*C. pepo* subsp. *fraterna*) to 3,203 (*C. foetidissima*).

Models for 15 of the taxa passed our evaluation criteria (Table S3). Due to the very few occurrence points for *C. pepo* subsp. *fraterna*, we modeled the taxon with a limited set of replicates ($K = 3$). Based on current knowledge of the taxa, we consider all 16 models sufficiently robust for use in the conservation gap analysis. Interactive models and associated evaluation criteria for each taxon are available in Dataset S2.

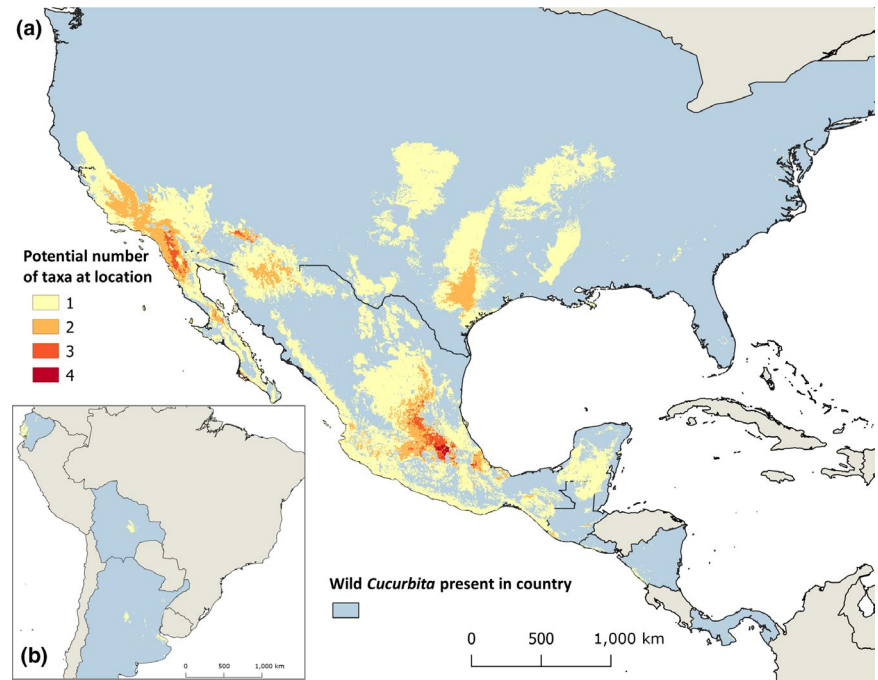
Predicted potential distributions of wild *Cucurbita* occur from the central, southwestern, and far southeastern (i.e., southern Florida) USA south to Central America (sparsely in Nicaragua and Panama), with two additional species occurring in South America (*C. ecuadorensis*, endemic to Ecuador, and *C. maxima* subsp. *andreaana*, from limited areas of Argentina and potentially Bolivia) (Figure 1). The modeled potential ranges of the taxa varied from relatively widespread (e.g., *C. foetidissima* and *C. palmata* S. Watson in the arid southwestern USA and northwestern Mexico, and *C. argyrosperma* subsp. *sororia* as well as *C. radicans* in the Sierra Madre Occidental or transverse ranges of Mexico) to narrowly endemic (*C. okeechobeensis* subsp. *okeechobeensis* around Lake Okeechobee in southern Florida, USA; *C. pepo* subsp. *fraterna* in the Sierra Madre Oriental in Northeast Mexico; *C. cordata* S. Watson in southern and central Baja California, Mexico;

TABLE 3 Conservation gap analysis results per taxon

Taxon	Total number of records	Total reference (H) records	Total germplasm (G) records	SRSex	GRSex	ERSex	FCSex	SRSin	GRSin	ERSin	FCSin	FCSc mean	Priority category
<i>Cucurbita argyrosperma</i> subsp. <i>sororia</i>	818	720	98	13.61	44.95	81.48	46.68	8.45	9.05	77.78	31.76	39.22	MP
<i>C. cordata</i>	210	207	3	1.45	10.88	25	12.44	68.35	57.86	100	75.4	43.92	MP
<i>C. digitata</i>	547	522	25	4.79	27.22	50	27.34	7.11	8.69	100	38.6	32.97	MP
<i>C. ecuadorensis</i>	72	56	16	28.57	65.98	83.33	59.3	8.11	4.27	50	20.79	40.05	MP
<i>C. foetidissima</i>	3,203	3,118	85	2.73	11.16	66.67	26.85	10.71	7.67	90	36.13	31.49	MP
<i>C. lundelliana</i>	308	279	29	10.39	40.82	71.43	40.88	22.79	22.78	71.43	39	39.94	MP
<i>C. maxima</i> subsp. <i>andreaana</i>	71	51	20	39.22	23.55	66.67	43.14	0	9.81	100	36.6	39.87	MP
<i>C. okeechobeensis</i> subsp. <i>martinezii</i>	287	255	32	12.55	64.6	72.22	49.79	12.05	9.63	83.33	35	42.4	MP
<i>C. okeechobeensis</i> subsp. <i>okeechobeensis</i>	112	98	14	14.29	97.05	100	70.44	0	2.94	100	34.31	52.38	LP
<i>C. palmata</i>	1,295	1,249	46	3.68	31.89	53.85	29.81	42.54	30.06	84.62	52.41	41.11	MP
<i>C. pedatifolia</i>	197	189	8	4.23	25.82	61.54	30.53	12.93	12.66	69.23	31.6	31.07	MP
<i>C. pepo</i> subsp. <i>fraterna</i>	11	0	11	100	68.93	100	89.64	75	31.84	100	68.95	79.29	SC
<i>C. pepo</i> subsp. <i>ovifera</i> var. <i>ozarkana</i>	72	29	43	100	43.29	100	81.1	5	7.07	100	37.36	59.23	LP
<i>C. pepo</i> subsp. <i>ovifera</i> var. <i>texana</i>	75	58	17	29.31	61.6	83.33	58.08	0	2.01	66.67	22.89	40.49	MP
<i>C. radicans</i>	278	274	4	1.46	20.86	54.55	25.62	8.87	10.25	72.73	30.61	28.12	MP
<i>C. x scabridifolia</i>	39	37	2	5.41	15.52	50	23.64	6.67	11.07	100	39.25	31.44	MP
Totals (sums or averages)	7,595	7,142	453	23.23	40.88	70.00	44.71	18.04	14.85	85.36	39.42	42.06	

Note: Results of the conservation assessments within each strategy (sampling representativeness score ex situ [SRSex], geographic representativeness score ex situ [GRSex], and ecological representativeness score ex situ [ERSex] for ex situ; and sampling representativeness score in situ [SRSin], geographic representativeness score in situ [GRSin] and ecological representativeness score in situ [ERSin] for in situ) are displayed. The combined Final Conservation Score (FCSc-mean) is the average of the final ex situ (FCSex) and in situ (FCSin) scores. The FCSc-mean is used to categorize taxa for further conservation action: High Priority (HP); Medium Priority (MP); Low Priority (LP); and Sufficiently Conserved (SC).

FIGURE 1 Predicted taxonomic richness map combining the 16 wild *Cucurbita* potential distribution models in (a) Central and North America; and (b) South America. Darker colors indicate greater numbers of taxa potentially overlapping in the same areas



and *C. maxima* subsp. *andreaana* and *C. ecuadorensis*), as described above.

Predicted taxon richness was the highest in central Mexico and the western borderlands between Mexico and the USA, with up to four taxa potentially overlapping in the same ca. 5 km² areas. These centers of richness align with described ecological divisions in the genus between the mesophytic and the arid-adapted species.

3.2 | Ecogeographic characterization

Throughout their ranges, substantial variation with regard to abiotic adaptations of potential interest in crop breeding was found across taxa, e.g., with occurrences in the highest maximum temperatures in the warmest month of the year for *C. palmata*, *C. digitata* A. Gray, *C. pepo* subsp. *ovifera* var. *texana*, and *C. cordata*, and the lowest temperatures in the coldest month for *C. pepo* subsp. *ovifera* var. *ozarkana*. Outstanding taxa with regard to adaptation to the highest precipitation in the wettest month included *C. okechobeensis* subsp. *martinezii* (L. H. Bailey) T. C. Andres & Nabhan ex T. W. Walters & D. S. Decker, *C. argyrosperma* subsp. *sororia*, and *C. lundelliana*, while those adapted to the lowest rainfall in the driest month included *C. cordata*, *C. palmata*, and *C. ecuadorensis*. While many of these are distant relatives to the crops, a number of the taxa with outstanding potential adaptations are putative progenitors or close relatives, including *C. argyrosperma* subsp. *sororia* and *C. pepo* subsp. *ovifera* var. *ozarkana* and var. *texana*. Considerable variation was also evident between populations within taxa, particularly in *C. foetidissima*, *C. palmata*, and *C. argyrosperma* subsp. *sororia* with regard to temperature variables, and *C. lundelliana*, *C. argyrosperma* subsp. *sororia*, *C. foetidissima*, *C. pepo* subsp. *ovifera* var. *ozarkana*, and *C. ecuadorensis* for precipitation (Figure S2).

3.3 | Conservation status

With regard to the status of conservation of wild *Cucurbita* in genebanks and botanic gardens, taxa ranged from very few germplasm accessions (two of *C. x scabridifolia* L. H. Bailey, three of *C. cordata*, four of *C. radicans*, and eight of *C. pedatifolia*) and corresponding low ex situ conservation scores, to fairly comprehensive representation, both for restricted distribution taxa (*C. pepo* subsp. *fraterna*, with 11 accessions and an FCSex of 89.64; and *C. okechobeensis* subsp. *okechobeensis*, with 14 accessions and an FCSex of 70.44) and more widespread species (*C. pepo* subsp. *ovifera* var. *ozarkana* with an FCSex of 81.1) (Figure 2, Tables 3 and S2). The ERSex was higher than the GRSex for all taxa, with three species fully represented in conservation repositories with regard to diversity of ecoregions potentially inhabited. The mean FCSex across all taxa was 44.71.

In total, with regard to the current state of ex situ conservation, two taxa (*C. cordata* and *C. x scabridifolia*) were assessed as high priority for further collecting, nine medium priority (including two putative progenitors), three low priority, and two sufficiently conserved. Geographic priorities for further collecting parallel predicted taxonomic richness patterns, with uncollected populations of up to four taxa potentially occurring in the same ca. 5 km² areas in central Mexico and in the western borderlands between Mexico and the USA (Figure 3a,b).

The analysis of representation ex situ of ecogeographic variation in the target taxa indicated that, in general, taxa with restricted ranges and numerous existing germplasm collections (i.e., *C. pepo* subsp. *fraterna*, *C. okechobeensis* subsp. *okechobeensis*, and *C. ecuadorensis*) as well as a number of wider ranging taxa (*C. argyrosperma* subsp. *sororia*, *C. digitata*, *C. lundelliana*, *C. okechobeensis* subsp. *martinezii*, *C. palmata*, *C. pepo* subsp. *ovifera* var. *ozarkana*, and *C. pepo* subsp. *ovifera* var. *texana*) are fairly well represented

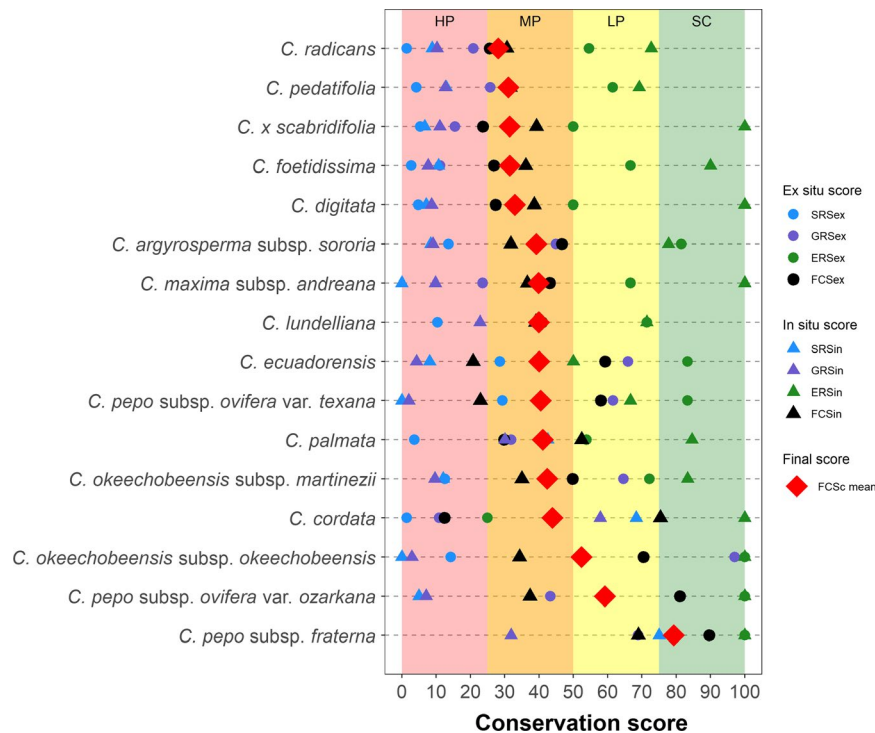


FIGURE 2 Conservation gap analysis results per taxon. Wild *Cucurbita* are listed by descending priority for further conservation action by priority categories (High Priority [HP] [red]; Medium Priority [MP] [orange]; Low Priority [LP] [yellow]; and Sufficiently Conserved [SC] [green]). The red diamond represents the combined Final Conservation Score (FCSc-mean) for the taxon, which is the average of the final ex situ (FCSEX) (black circle) and in situ (FCSin) (black triangle) scores. Results of the conservation assessments within each strategy [sampling representativeness score ex situ (SRSex), geographic representativeness score ex situ (GRSex), and ecological representativeness score ex situ (ERSex) for ex situ; and sampling representativeness score in situ (SRSin), geographic representativeness score in situ (GRSin) and ecological representativeness score in situ (ERSin) for in situ] are also displayed

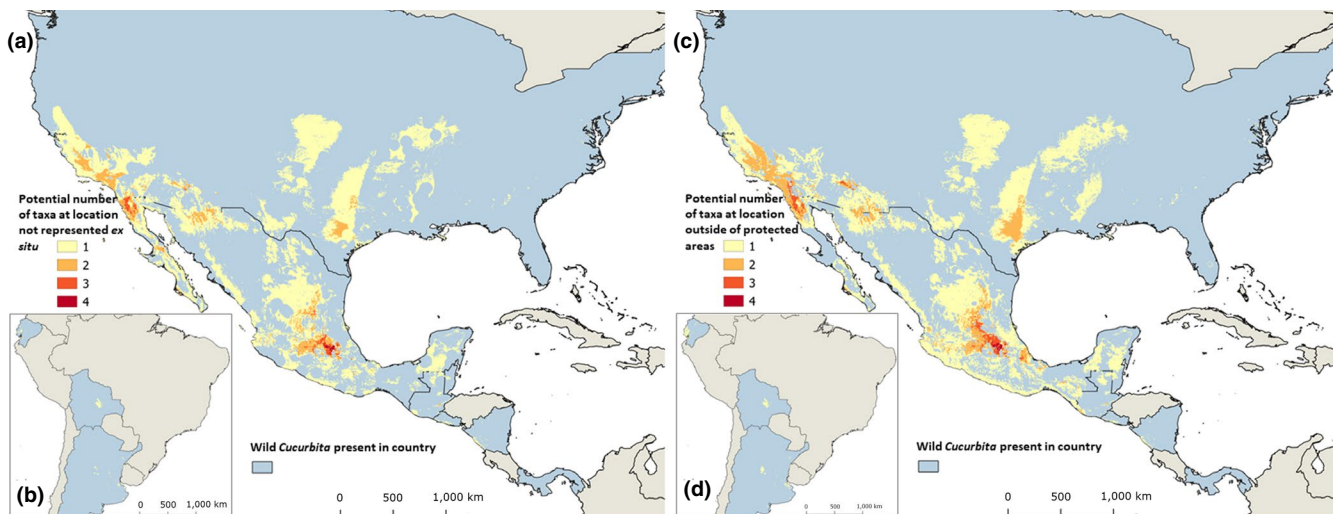


FIGURE 3 Further conservation priorities maps for wild *Cucurbita*. Predicted further collecting priorities hotspots map displaying richness of areas within the potential distributions of the 16 taxa that have not been previously collected for ex situ conservation, with up to four taxa in need of further collecting potentially found in the same areas, in (a) Central and North America, and (b) South America. Predicted further in situ protection priorities map, displaying richness of areas within the 16 potential distributions of taxa that are outside of current protected areas, with up to four taxa found in the same unprotected areas, in (c) Central and North America, and (d) South America

in genebanks and botanic gardens with regard to temperature, precipitation, and other measured variables (Figures 4 and S3). Other species, especially *C. cordata*, *C. pedatifolia*, *C. radicans*, and *C. x*

scabridifolia are sparsely and unevenly represented. *C. maxima* subsp. *andreana* in particular, and also *C. digitata* and *C. argyrosperma* subsp. *sororia*, to some degree, appear to be relatively well

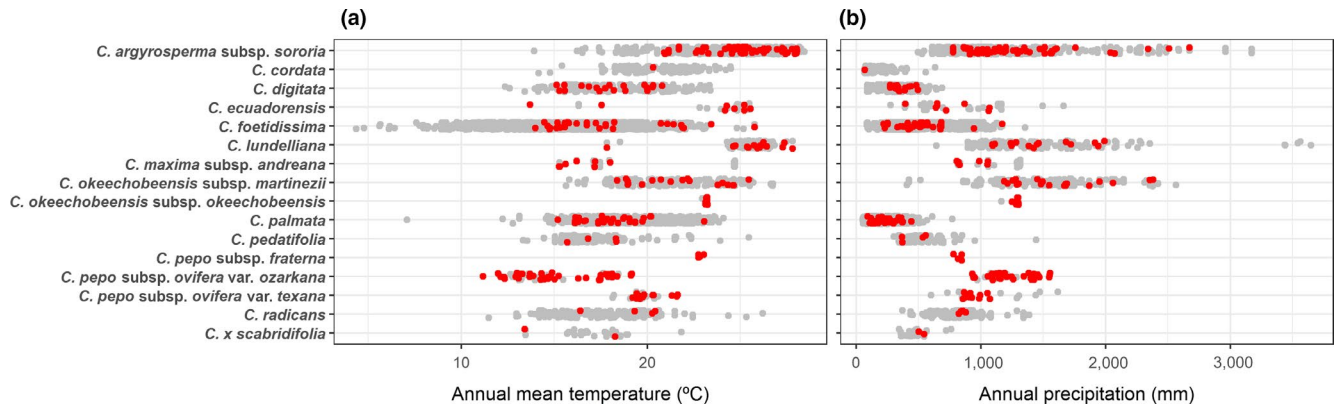


FIGURE 4 Ecogeographic niches of wild *Cucurbita* for a) annual mean temperature and b) precipitation, and an indication of their degree of representation in ex situ conservation. Reference (H) records in gray; germplasm (G) records in red. For niches per all ecogeographic variables per taxon, see Figures S2 and S3

represented in the majority of their ranges, but with important outlying ecogeographic niches not well conserved (e.g., the Argentine distributions of *C. maxima* subsp. *andreana* represented, but the possible Bolivian populations not).

With regard to in situ conservation in officially recognized protected areas, taxa ranged from a low-moderate level of representation (*C. ecuadorensis*, [FCSin = 20.79] and 12 other taxa with FCSin scores below 50, including all of the putative crop progenitors), to a fairly high level of representation (*C. cordata*, FCSin = 75.4 and *C. pepo* subsp. *fraterna*, FCSin = 68.95) (Figure 2, Tables 3 and S2). As with the ex situ analysis, the ERSin was higher than the GRSin for all taxa, with seven of the taxa being fully represented in protected areas with regard to diversity of ecoregions potentially inhabited. On average across all taxa, in situ conservation was estimated to be marginally less well established than ex situ, with a mean FCSin = 39.42 versus FCSex = 44.71.

In total, with regard to the state of conservation of wild *Cucurbita* in protected areas, two taxa (*C. ecuadorensis* and *C. pepo* subsp. *ovifera* var. *texana*) were assessed high priority for further in situ conservation, eleven taxa medium priority, two low priority, and one sufficiently conserved. The most important geographic areas for establishment of additional protection for these crop wild relatives in protected areas, in terms of further coverage of the greatest amount of populations of the largest number of taxa, include central Mexico and the western Mexico–USA borderlands (Figure 3c,d).

With regard to combined conservation status (assessing both ex situ and in situ together), taxa ranged from fairly poorly conserved (*C. radicans*, FCSc-mean = 28.12) to well conserved (*C. pepo* subsp. *fraterna*, FCSc-mean = 79.30) (Figure 2, Tables 3 and S2). The FCSc-mean averaged across all taxa was 42.06. In combination, no taxon was assessed high priority for further conservation action, 13 taxa including three putative crop progenitors medium priority, two low priority and one sufficiently conserved.

The EOO and AOO Red List analyses indicated that *C. okeechobeensis* subsp. *okeechobeensis* and *C. pepo* subsp. *fraterna* could be listed Endangered; *C. x scabridifolia* and *C. maxima*

subsp. *andreana* as Vulnerable; *C. ecuadorensis* and *C. pepo* subsp. *ovifera* var. *texana* possibly as Near Threatened; and the remaining taxa as Least Concern (Table S4). These results provide further support for the current listings for three Least Concern taxa (*C. digitata*, *C. foetidissima*, and *C. lundelliana*), while they may facilitate Least Concern listing for an additional six taxa currently listed as Data Deficient and/or only assessed at the species level (*C. argyrosperma* subsp. *sororia*, *C. cordata*, *C. okeechobeensis* subsp. *martinezii*, *C. palmata*, *C. pedatifolia*, and *C. pepo* subsp. *ovifera* var. *ozarkana*). The results may also provide useful preliminary conservation concern indications for taxa currently absent from the Red List (*C. maxima* subsp. *andreana* and *C. x scabridifolia*) or lacking information at the taxon level (*C. okeechobeensis* subsp. *okeechobeensis*, *C. pepo* subsp. *fraterna*, and *C. pepo* subsp. *ovifera* var. *texana*), while also highlighting one taxon potentially in need of further revision (due to discord between our results and current Red List categorizations) (*C. radicans*).

4 | DISCUSSION

With 68.8% of wild *Cucurbita* assessed as high or medium priority for further collecting for ex situ conservation, including two of the putative crop progenitors; 81.3% as high or medium priority for further protection in situ, including all of the progenitors; and 81.3% as medium priority for conservation with regard to the strategies in combination, it is clear that further conservation action is needed to safeguard these wild relatives. Included in this list of priorities are taxa with very few germplasm accessions conserved in genebanks and botanic gardens, and thus very limited genetic diversity accessible for crop breeding and other research (especially *C. x scabridifolia*, *C. cordata*, *C. radicans*, and *C. pedatifolia*).

As the geographic gaps with regard to both ex situ and in situ conservation largely align with taxonomic richness geography, hotspots in central Mexico and on the western Mexico–USA border represent particularly high value regions for efficient further

collecting of the taxa for living plant repository conservation as well as priority candidate areas for further habitat protection. Additional collecting across the ranges of the taxa will be needed to form germplasm collections that are comprehensive at the population level, and additional protected areas will also be needed to sufficiently conserve the taxa so that they can continue to evolve in their natural habitats.

4.1 | Challenges and limitations to distribution modeling and conservation gap analysis

A challenge inherent to the modeling analysis is that distributions of taxa are driven by factors beyond the 26 ecogeographic predictors used here. These include biotic (e.g., pollinators, mycorrhizae, and dispersal agents) and other abiotic (e.g., soil types), as well as stochastic factors. Furthermore, the current habitat suitability models are unable to fully account for extirpation processes due to habitat degradation or destruction like those recorded by the authors during fieldwork along the shores of the St. John's River in Florida, one of only two habitats where the endangered *C. okeechobeensis* subsp. *okeechobeensis* is known to occur. Our results, therefore, should best be considered as planning tools to guide explorations for confirmation in the field.

With regard to the conservation analyses, openly available databases on genebank and botanic garden holdings are not fully representative of all holdings in all such institutions worldwide, and thus important gaps in information may exist, particularly with regard to Latin American national genebanks that are not currently reporting in databases such as Genesys and FAO WIEWS (Thomas et al., 2016). Coordinate and/or other locality information is also presently lacking for a substantial number of records that are available in online databases. For instance, the PlantSearch database currently does not make locality and coordinate-level information available, and the presence of a taxon in a botanic garden as listed in the database indicates at least one accession (but no information on the actual number). Furthermore, taxonomic information in germplasm databases for members of the plant family has been recognized to be in need of improvement (Guzzon & Ardenghi, 2018). If these information constraints were to be remedied, it is possible that the ex situ conservation status of the taxa could be revised. This said, national and institutional policies and other barriers often restrict the distribution of germplasm from genebanks and botanic gardens for which information is currently not easily available online.

Moreover, while the lands listed in the World Database on Protected Areas hopefully afford collateral protection to wild *Cucurbita* taxa because of overall land conservation practices, robust long-term protection of these taxa in these areas will likely require the formation of active taxon- and population-specific management plans. We are not aware of any active management plans for wild *Cucurbita*, even for the USA Federally listed Endangered Okeechobee gourd (*C. okeechobeensis* subsp. *okeechobeensis*) (Kates, 2019).

4.2 | General challenges to conservation and utilization of wild *Cucurbita*

Most wild *Cucurbita* are considered to be reducing in range due both to the extinction of their original wildlife dispersers and to more recent habitat degradation, and current taxon-specific conservation efforts are minimal or nonexistent. Wild *Cucurbita* populations may be locally vigorous and viewed as weedy and as an agricultural nuisance (Nabhan, 1985), which can limit local interest in in situ conservation. The lack of public awareness of the nearly extinct Okeechobee gourd highlights this issue. Many landowners along St. John's River are unaware that a Federally listed Endangered plant occurs in this area, and local accounts that the vine is regarded as a weed suggests some populations may be at risk of removal (H.R. Kates, pers. comm.). Likewise, farmers in Mexico who grow cushaw often remove nearby populations of wild *C. argyrosperma* subsp. *sororia*, which commonly grows near agricultural fields, because gene flow between the two subspecies can introduce bitterness into the fruit of the crop (Montes-Hernandez & Eguiarte, 2002; Nabhan, 1985).

Policy and phytosanitary regulation constraints to germplasm collection and exchange have limited international collaborations on wild *Cucurbita* over recent decades. Although most countries rich in native wild *Cucurbita* are Parties to the International Treaty on Plant Genetic Resources for Food and Agriculture, with the notable exception of Mexico, the genus is not currently listed in Annex 1 under the Multilateral System of Access and Benefit Sharing (FAO, 2002). Within genebanks, the large vining habit, outcrossing reproductive strategy, photoperiod sensitivity, and relatively short shelf life in orthodox freezer conditions of wild *Cucurbita* lead to high conservation costs (Paris, 2016). International collaborations, for example to regenerate tropical materials in suitable habitats in their countries of origin are constrained by the lack of aforementioned policy facilitation. Thus, many ex situ germplasm accessions of wild *Cucurbita* are not currently available for distribution, including those within the U.S. National Plant Germplasm System (Kates, 2019). Enhanced partnerships on conservation and exchange of *Cucurbita* will be needed to resolve many of the challenges to safeguarding and making greater use of wild *Cucurbita*.

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AUTHOR CONTRIBUTIONS

CKK, DC, HRK, HAA, MvZ, and ET compiled and processed input data, developed the methodologies, and/or performed the analyses. CKK, DC, HRK, MvZ, ET, CH, RJ, JAL, KR, GPN, and SLG analyzed the results. CKK, DC, and HRK wrote the article. CKK, DC, HRK, HAA, MvZ, ET, CH, RJ, JAL, KR, GPN, and SLG edited the article.

DATA AVAILABILITY STATEMENT

Occurrence data, processed ecogeographic data, and interactive taxon-level modeling and conservation status results and metrics are provided in the Supporting Information. Associated ecogeographic and spatial input data are available through open access repositories (Khoury et al., 2019b). All code implemented in the analysis is available at: <https://github.com/dcarver1/cwrSDM>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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