

Modelled distributions and conservation status of the wild relatives of chile peppers (*Capsicum* L.)

Colin K. Khoury^{1,2,3}  | Daniel Carver⁴ | Derek W. Barchenger⁵ | Gloria E. Barboza^{6,7} | Maarten van Zonneveld⁵  | Robert Jarret⁸ | Lynn Bohs⁹  | Michael Kantar¹⁰ | Mark Uchanski¹¹  | Kristin Mercer¹² | Gary Paul Nabhan¹³ | Paul W. Bosland¹⁴ | Stephanie L. Greene¹

¹National Laboratory for Genetic Resources Preservation, United States Department of Agriculture, Agricultural Research Service, Fort Collins, CO, USA

²International Center for Tropical Agriculture (CIAT), Cali, Colombia

³Department of Biology, Saint Louis University, St. Louis, MO, USA

⁴Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO, USA

⁵World Vegetable Center, Tainan, Taiwan

⁶Instituto Multidisciplinario de Biología Vegetal (IMBIV), CONICET, Córdoba, Argentina

⁷Facultad de Ciencias Químicas, Universidad Nacional de Córdoba, Córdoba, Argentina

⁸Plant Genetic Resources Conservation Unit, United States Department of Agriculture, Agricultural Research Service, Griffin, GA, USA

⁹Biology Department, University of Utah, Salt Lake City, UT, USA

¹⁰Department of Tropical Plant and Soil Science, University of Hawaii at Manoa, Honolulu, HI, USA

¹¹Department of Horticulture and Landscape Architecture, Colorado State University, Fort Collins, CO, USA

¹²Department of Horticulture and Crop Science, The Ohio State University, Columbus, OH, USA

¹³Southwest Center and Institute of the Environment, University of Arizona, Tucson, AZ, USA

¹⁴Department of Plant and Environmental Sciences, New Mexico State University, Las Cruces, NM, USA

Correspondence

Colin K. Khoury, International Center for Tropical Agriculture (CIAT), Km 17, Recta Cali-Palmira, Apartado Aéreo 6713, 763537 Cali, Colombia.

Email: c.khoury@cgiar.org

Funding information

National Science Foundation, Grant/Award Number: DEB-1457366; United States Agency for International Development; Australian Centre for International Agricultural Research

Editor: John Lambrinos

Abstract

Aim: To fill critical knowledge gaps with regard to the distributions and conservation status of the wild relatives of chile peppers (*Capsicum* L.).

Location: The study covered the potential native ranges of currently recognized wild *Capsicum* taxa, throughout the Americas.

Methods: We modelled the potential distributions of 37 wild taxa in the genus, characterized their ecogeographic niches, assessed their ex situ and in situ conservation status, and performed preliminary threat assessments.

Results: We categorize 18 of the taxa as “high priority” for further conservation action as a consequence of a combination of their ex situ and in situ assessments, 17 as “medium priority,” and two as “low priority.” Priorities for resolving gaps in ex situ conservation were determined to be high for 94.6%, and medium or high with regard to increased habitat protection for 64.9% of the taxa. The preliminary threat

*This article has been contributed to by the US Government employees and their work is in the public domain in the USA.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2019 The Authors. *Diversity and Distributions* published by John Wiley & Sons Ltd

assessment indicated that six taxa may be critically endangered, three endangered, ten vulnerable, six near threatened and 12 least concern.

Main conclusions: Taxonomic richness hot spots, especially along the Atlantic coast of Brazil, in Bolivia and Paraguay, and in the highlands of Colombia, Ecuador, Peru and Venezuela, represent particularly high priority regions for further collecting for ex situ conservation as well as for enhanced habitat conservation.

KEYWORDS

biodiversity conservation, *Capsicum*, Chili peppers, crop wild relatives, plant genetic resources

1 | INTRODUCTION

Crop wild relatives—the wild progenitors and closely related species to cultivated plants—have provided many important agronomic and nutritional traits for crop improvement (Dempewolf et al., 2017; Hajjar & Hodgkin, 2007). As populations of some of these taxa are adapted to extreme climates, adverse soil types, and important pests and diseases, they may provide key traits for the adaptation of crop plants to emerging and projected future challenges (Dempewolf et al., 2013).

Knowledge gaps with regard to wild genetic resources, including information on species' taxonomy and relatedness to pertinent crops (i.e., gene pool assignments), geographic distributions, and values for traits of interest, constrain their potential use in plant breeding (Dempewolf et al., 2017; Miller & Khoury, 2018). Such knowledge gaps also affect conservation efforts, which are essential to protect vulnerable populations from habitat destruction, over-harvesting, climate change, pollution, and invasive species (Bellon, Dulloo, Sardos, Thormann, & Burdon, 2017; Díaz et al., 2019; Jarvis, Lane, & Hijmans, 2008), and to ensure that these genetic resources are safeguarded for the long term and available for research in ex situ plant conservation repositories (Castañeda-Álvarez et al., 2016; Gepts, 2006). Global analyses indicate that many crop wild relatives are poorly represented in gene banks (Castañeda-Álvarez et al., 2016) and in protected areas (Khoury et al., 2019a). These reports highlight the urgency of addressing fundamental knowledge gaps to have the information available to guide conservation and crop improvement efforts.

The chile pepper genus (*Capsicum* L.) originated in the Andes Mountains, in north-western South America, and subsequently diversified and dispersed, initially by birds and later also by people, throughout the neotropics and subtropics (Bosland & Votava, 2012; Carrizo Garcia et al., 2016; Noss & Levey, 2014). There is evidence that humans were using wild chile peppers as early as 8,000–10,000 years ago (Davenport, 1970; Heiser, 1969; Pickersgill, 1966). Domesticated forms of chile peppers, as well as human dispersal of the fruits within the Americas, including to parts of the Caribbean, have been documented from at least 6,000 years ago (Jarrett et al., 2019; Perry et al., 2007; Perry & Flannery, 2017; Pickersgill, 1969, 1977; Walsh & Hoot, 2001). Originally used primarily for medicinal

and ceremonial purposes, chile peppers became an important spice and vegetable for diverse Indigenous peoples (Bosland & Votava, 2012; Luna-Ruiz, Nabhan, & Aguilar-Meléndez, 2018; Smith, 1967).

Today, chile peppers are used worldwide as a vegetable, spice, colourant and pharmaceutical (Wall & Bosland, 1998). They are consumed daily by approximately a quarter of the world's population (Halikowski Smith, 2015). Some chile pepper varieties have exceptionally high levels of provitamin A (Guzman, Bosland, & O'Connell, 2011; Kantar et al., 2016) and thus can make a significant contribution to fulfilling that nutritional requirement. Chile peppers are a high value crop (DeWitt & Bosland, 1993), providing economic benefits to both smallholder and larger-scale farmers (Kahane et al., 2013).

Capsicum contains five principle domesticated chile pepper taxa—*Capsicum annuum* L. var. *annuum*, *Capsicum baccatum* L. var. *pendulum* (Willd.) Eshbaugh [incl. syn. *Capsicum baccatum* L. var. *umbilicatum* (Vell.) Hunz. & Barboza], *Capsicum chinense* Jacq., *Capsicum frutescens* L. and *Capsicum pubescens* Ruiz & Pav. (Bosland & Votava, 2012; Walsh & Hoot, 2001)—and ca. 37 wild taxa, some of which are also occasionally cultivated in home gardens (Table 1) (Baral & Bosland, 2002; Zonneveld et al., 2018). Among the domesticated species, *C. annuum* var. *annuum* is the most widely grown and studied. Both *C. annuum* var. *annuum* and *C. baccatum* var. *pendulum* have extant putative progenitors (*Capsicum annuum* var. *glabriusculum* (Dunal) Heiser & Pickersgill and *C. baccatum* L. var. *baccatum*, respectively); the progenitors of the remaining domesticates have not been identified.

Three genetic (species) complexes have been recognized within the genus, based on genetic relatedness and reproductive compatibility with the domesticated taxa (Barchenger & Bosland, 2019; Emboden, 1961; Eshbaugh, 1970; Heiser & Smith, 1948; Pickersgill, 1971, 1980; Scaldaferrro, 2019; Tong & Bosland, 1999). Each of these complexes contains both domesticated and wild taxa. Member species of the *annuum* complex generally have white, greenish, or yellowish flowers, and include the crop species *C. annuum* var. *annuum*, *C. chinense* and *C. frutescens*. Members of the *baccatum* complex typically have white flowers with yellow to green corolla spots. Members of the *pubescens* complex have purple flowers. While comprehensive crossability studies between all species in the genus have yet to be completed (Barchenger & Bosland, 2019), successful

TABLE 1 *Capsicum* L. taxa and their known chromosome numbers, clades, complexes, genetic relative/potential gene pool classifications, and domestication/cultivation status

Taxa	Chromosome (n)	Clade ^a	Complex ^b	Genetic relative/potential gene pool classification ^c	Wild or domesticated ^d
<i>Capsicum annuum</i> L. var. <i>annuum</i>	12	Annuum	Annuum	B2, P3	Domesticated
<i>Capsicum annuum</i> L. var. <i>glabriusculum</i> (Dunal) Heiser & Pickersgill	12	Annuum	Annuum	A1, B2, P3	Wild
<i>Capsicum baccatum</i> L. var. <i>pendulum</i> (Willd.) Eshbaugh [incl. syn <i>Capsicum baccatum</i> L. var. <i>umbilicatum</i> (Vell.) Hunz. & Barboza]	12	Baccatum	Baccatum	A2	Domesticated
<i>Capsicum baccatum</i> L. var. <i>baccatum</i>	12	Baccatum	Baccatum	A2, B1, P3	Wild
<i>Capsicum benoistii</i> Hunz. ex Barboza	Unknown				Wild
<i>Capsicum caatingae</i> Barboza & Agra	12	Caatinga			Wild
<i>Capsicum caballeroi</i> M. Nee	Unknown	Bolivian			Wild
<i>Capsicum campylopodium</i> Sendtn.	13	Atlantic Forest			Wild
<i>Capsicum cardenasii</i> Heiser & P. G. Sm.	12	Purple Corolla	Pubescens	A3, B3, P1	Wild, also cultivated in home gardens
<i>Capsicum ceratocalyx</i> M. Nee	Unknown	Bolivian			Wild
<i>Capsicum chacoense</i> Hunz.	12	Baccatum	Annuum	A2, B2	Wild, also cultivated in home gardens
<i>Capsicum chinense</i> Jacq.	12	Annuum	Annuum	A2, B2, P3	Domesticated; wild status uncertain
<i>Capsicum coccineum</i> (Rusby) Hunz.	Unknown	Bolivian			Wild
<i>Capsicum cornutum</i> (Hiern) Hunz.	13	Atlantic Forest			Wild
<i>Capsicum dimorphum</i> (Miers) Kuntze	Unknown	Andean			Wild
<i>Capsicum eshbaughii</i> Barboza	Unknown	Purple Corolla		P2	Wild
<i>Capsicum eximium</i> Hunz.	12	Purple Corolla	Pubescens	A3, B3, P1	Wild, also cultivated in home gardens
<i>Capsicum flexuosum</i> Sendtn.	12	Flexuosum			Wild
<i>Capsicum friburgense</i> Bianchetti & Barboza	Unknown	Atlantic Forest			Wild
<i>Capsicum frutescens</i> L.	12	Annuum	Annuum	A2, B2, P3	Domesticated; wild status uncertain
<i>Capsicum galapagoense</i> Hunz.	12	Annuum	Annuum	A2, P3	Wild
<i>Capsicum geminifolium</i> (Dammer) Hunz.	13	Andean			Wild
<i>Capsicum hookerianum</i> (Miers) Kuntze	Unknown	Andean			Wild
<i>Capsicum hunzikerianum</i> Barboza & Bianchetti	Unknown	Atlantic Forest			Wild
<i>Capsicum lanceolatum</i> (Greenm.) C. V. Morton & Standl.	13	Andean			Wild
<i>Capsicum longidentatum</i> Agra & Barboza	12	Longidentatum			Wild
<i>Capsicum longifolium</i> Barboza & S. Leiva	13	Andean			Wild
<i>Capsicum lycianthoides</i> Bitter	13	Andean			Wild
<i>Capsicum minutiflorum</i> (Rusby) Hunz.	Unknown	Bolivian			Wild
<i>Capsicum mirabile</i> Mart. ex Sendtn.	13	Atlantic Forest			Wild
<i>Capsicum neei</i> Barboza & X. Reyes	Unknown	Bolivian			Wild
<i>Capsicum parvifolium</i> Sendtn.	12	Caatinga			Wild
<i>Capsicum pereirae</i> Barboza & Bianchetti	13	Atlantic Forest			Wild
<i>Capsicum piuranum</i> Barboza & S. Leiva	13	Andean			Wild

(Continues)

TABLE 1 (Continued)

Taxa	Chromosome (n)	Clade ^a	Complex ^b	Genetic relative/potential gene pool classification ^c	Wild or domesticated ^d
<i>Capsicum praetermissum</i> Heiser & P. G. Sm.	12	Baccatum	Baccatum	A2, B1, P3	Wild
<i>Capsicum pubescens</i> Ruiz & Pav.	12	Pubescens	Pubescens		Domesticated; wild status uncertain
<i>Capsicum recurvatum</i> Witas.	13	Atlantic Forest			Wild
<i>Capsicum rhomboideum</i> (Dunal) Kuntze	13	Andean			Wild
<i>Capsicum schottianum</i> Sendtn.	13	Atlantic Forest			Wild
<i>Capsicum tovarii</i> Eshbaugh et al.	12	Tovarii	Baccatum	B3	Wild
<i>Capsicum villosum</i> Sendtn. (including <i>Capsicum villosum</i> Sendtn. var. <i>muticum</i> Sendtn. and <i>Capsicum villosum</i> Sendtn. var. <i>villosum</i>)	13	Atlantic Forest			Wild

^aProvisional clades of *Capsicum* species based on their positions in strict consensus trees using three molecular markers (Carrizo Garcia et al., 2016).

^bAs outlined in Scaldaferrero (2019).

^cA denotes the crop *C. annuum* var. *annuum*; B for *C. baccatum* var. *pendulum* and P for *C. pubescens*. Taxa are assigned to genetic relative categories for these domesticated species into three groups: 1 for primary (closest relatives), 2 for secondary and 3 for tertiary (most distant relatives in the genus). Assignments as per USDA ARS NPGS (2019), based on crossability, phylogenetic and other evidence. Given assigned complexes, genetic relative classifications for taxa with regard to *C. annuum* var. *annuum* may be assumed equivalent with regard to *C. chinense* and *C. frutescens*.

^dHome garden use as noted in van Zonneveld et al. (2018).

hybridizations are known among species (Scaldaferrero, 2019), including between those belonging to different complexes (Walsh & Hoot, 2001). Provisional clades of *Capsicum* species, based on their positions in phylogenetic trees using sequence-based molecular markers, have also been described (Carrizo Garcia et al., 2016). Genetic relatedness classifications based on interfertility research, supplemented by taxonomic, phylogenetic and ploidy information, provide partial indications of the gene pools of the domesticated species (Table 1; USDA ARS NPGS, 2019).

Unlike tomato (*Solanum lycopersicum* L.; Lin et al., 2014) and potato (*Solanum tuberosum* L.) (Hirsch et al., 2013), other important crops in the Solanaceae, the genetic diversity contained in wild relatives of chile peppers has not been well studied (van Zonneveld et al., 2015) or widely utilized (Mongkolporn & Taylor, 2011), aside from a few reports of disease resistance (Kenyon, Kumar, Tsai, & Hughes, 2014). Tolerance of wild *Capsicum* to abiotic stresses such as salinity, drought, flooding and heat, all recognized challenges in the production of the crop taxa (Aloni, Peet, Pharr, & Karni, 2001; De Pascale, Ruggiero, Barbieri, & Maggio, 2003; Gajanayake, Trader, Reddy, & Harkess, 2011; Han, Li, Wang, & Miao, 1996; Maas & Hoffman, 1977; Rao & Li, 2003), has not been investigated.

A number of wild *Capsicum* taxa are harvested from nearby populations and sold in local and regional markets. For example, fruit of *Capsicum eximium* Hunz. and *C. baccatum* var. *baccatum* are much in demand in Bolivia due to their unique taste profiles, thus providing market opportunities for local communities (van Zonneveld et al., 2015). In Mexico, flavours associated with *C. annuum* var. *glabriusculum* make them highly sought after and consumers are willing to pay a premium for more flavourful fruit (Villalon-Mendoza, Medina-Martinez, Ramirez-Meraz, Solis Urbina, & Maiti, 2014).

Recent conservation assessments are lacking for much of the *Capsicum* genus. The IUCN Red List of Threatened Species lists five taxa—*C. annuum* L. (Least Concern [LC]; Aguilar-Meléndez, Azurdía, Cerén-López, Menjívar, & Contreras, 2019), *Capsicum caatingae* Barboza & Agra (LC; BGCI & IUCN SSC Global Tree Specialist Group, 2019), *Capsicum lanceolatum* (Greenm.) C. V. Morton & Standl. (Endangered [EN], due to agriculture and logging activities; Azurdía, Aguilar-Meléndez, Menjívar, Cerén-López, & Contreras, 2017), *C. frutescens* (LC, although populations decreasing due to agriculture, livestock ranching and wild harvesting; Azurdía, Aguilar-Meléndez, Cerén-López, Contreras, & Menjívar, 2017a) and *Capsicum rhomboideum* (Dunal) Kuntze (LC; Azurdía, Aguilar-Meléndez, Cerén-López, Contreras, & Menjívar, 2017b). The NatureServe Explorer lists conservation assessments only for *C. annuum*, *C. annuum* var. *annuum* and *C. annuum* var. *glabriusculum*, all of which were determined to be secure although the assessments are from the 1990s (NatureServe, 2019).

Here we use taxonomic and geographic occurrence information to model the potential distributions of all 37 currently known wild taxa in the genus *Capsicum*, and to characterize their ecogeographic niches. We assess the conservation status of the taxa, in gene banks and botanic gardens (ex situ), and in protected areas (in situ), and perform preliminary threat assessments.

2 | METHODS

2.1 | Occurrence information

Reference occurrence data were obtained from all records listed within the genus *Capsicum* from the Global Biodiversity Information

Facility (GBIF, 2018), the Global Crop Wild Relative Occurrence Database (Global Crop Diversity Trust, 2018a), scientific literature (Barboza, Agra, Romero, Scaldaferrò, & Moscone, 2011; Barboza & Bianchetti, 2005; Barboza, Carrizo García, Leiva González, Scaldaferrò, & Reyes, 2019) and from the authors' own botanical explorations. Gene bank and botanical garden conservation occurrence as well as reference data were obtained from the Genesys plant genetic resources portal (Global Crop Diversity Trust, 2018b), the USDA National Plant Germplasm System (GRIN Global; USDA ARS NPGS, 2018), 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, 2019). Duplicate records were removed with preference for original/most recently updated data providers (e.g., USDA ARS NPGS dataset instead of equivalent USDA records in Genesys).

Taxonomic names were standardized based on current literature (Barboza & Bianchetti, 2005; Barboza et al., 2011, 2019; Carrizo Garcia et al., 2016; Jarrett et al., 2019) and a monograph on the genus soon to be published (Barboza et al., in prep). Cultivated taxa; records listed in sample status fields as other than wild, weedy or null (e.g., landrace, improved, breeding material and cultivated); fossil specimens in the GBIF dataset; and records listed in collecting/acquisition source fields as sourcing from markets, institutes and home gardens were excluded. In preparation for the conservation analysis, we classified each record according to whether it was a reference observation (labelled H, as most of these records were from herbaria), or a "site where germplasm collected" location of an existing ex situ plant gene bank or botanic garden conservation accession (labelled G, as most records were from gene banks). For GBIF, this classification was accomplished 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. Gene bank/botanic garden (G) occurrences with detailed locality information but lacking coordinates were georeferenced using Google Earth (Google, 2019a) to maximize the comprehensiveness of the ex situ conservation gap analysis.

To review the occurrence data in preparation for distribution modelling, H and G coordinates were uploaded to an interactive mapping platform (Google, 2019b). Occurrences in bodies of water or in clearly incorrect locations were corrected or removed. Refined occurrence data were extracted for use in distribution modelling. The final occurrence dataset is available in Appendix S1, sheet 1 in the Supporting Information.

2.2 | Distribution modelling

The maximum entropy (MaxEnt) algorithm (Phillips, Anderson, Dudik, Schapire, & Blair, 2017) accessed through the R statistical package

"dismo" (Hijmans, Phillips, Leathwick, & Elith, 2017) was used to produce potential ecogeographic (climatic and topographic) suitability models (i.e., potential distribution models) for the taxa, following processes outlined in Khoury et al. (2019a). A total of 26 ecogeographic predictors (Table S2.1 in the Supporting Information) were assembled. These included 19 bioclimatic variables, and solar radiation, water vapour pressure, and wind speed, as derived from WorldClim 2 (Fick & Hijmans, 2017). For the final three variables, we produced annual values by calculating the median across monthly values. Altitude data were obtained from the CGIAR-Consortium for Spatial Information (CSI) dataset based on NASA Shuttle Radar Topography Mission (STRM) data (Jarvis, Reuter, Nelson, & Guevara, 2008). Variables for slope and aspect were also incorporated after having been 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-min (~5 km² at the equator) (values available in Appendix S1, sheet 2 in the Supporting Information; raw data available from Khoury et al., 2019b).

Ecogeographic variables (per taxon) were selected using the R package "VSURF" (Genuer, Poggi, & Tuleau-Malot, 2018). All variables with 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 with a Pearson's correlation coefficient greater than a 0.7 were removed. This process was performed for the top five predictor variables, with the remaining variables employed in the modelling process (Appendix S1, sheet 3 in the Supporting Information).

The number of comparative background points (pseudo-absences) were defined per taxon in proportion to the total area of the spatial background, which was calculated based on pertinent ecoregion boundaries, that is the ecoregions defined in Olson et al. (2001) (available from Khoury et al., 2019b) wherein occurrence data fell, bounded by pertinent country borders, with a maximum of 5,000 pseudo-absences per taxon. Pseudo-absence points that fell within the same cell as a presence point were not included.

For each taxon with at least 10 coordinates, the modelled distribution was calculated as the median of ten 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), the MaxEnt model output was evaluated 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 as per the previous studies required an $AUC \geq 0.7$, $SDAUC < 0.15$, and $ASD15 \leq 10\%$. All models were individually evaluated for quality of fit based on the authors' field experiences. 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 records with coordinates, for all taxa (Appendix S1, sheet 4 in the Supporting Information). These data were used to characterize taxa with regard to their potential 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 analysis described below.

2.4 | Conservation gap analysis

We assessed the degree of representation of each taxon in both ex situ and in situ conservation systems building on methods outlined in Khoury et al. (2019a). For ex situ, four scores were calculated.

The sampling representativeness score ex situ (SRSex) provides a general indication of the completeness of gene bank and botanic garden conservation collections, for each taxon. This compares the total count of germplasm accessions (G) available in ex situ repositories against the total count of reference (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 include geographic coordinates. In this, and in all other metrics, SRSex is bound between 0 and 100, with 0 representing an extremely poor state of conservation and 100 representing comprehensive (complete) conservation.

The geographic 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° (~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. It considers comprehensive conservation to have been accomplished only when every ecoregion potentially inhabited by a taxon is 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, four metrics were calculated based on the extent of representation of the range

of each taxon within officially recognized protected areas. Data were obtained from the World Database of Protected Areas (WDPA) (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 geographic 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. It considers 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 individual in situ conservation metrics.

A final conservation score combined (FCSc-mean) was calculated for each taxon by averaging its final ex situ (FCSex) and in situ (FCSin) scores. Taxa were then categorized, with high priority (HP) for further conservation action assigned when 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 (Khoury et al., 2019a).

To supplement 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 (CR) where EOO < 100 km² or AOO < 10 km², endangered (EN) where 100 km² < EOO < 5,000 km² or 10 km² < AOO < 500 km², vulnerable (VU) where 5,000 km² < EOO < 20,000 km² or 500 km² < AOO < 2000 km², possible near threatened (NT) where 20,000 km² > EOO < 45,000 km² or 2,000 km² < AOO < 4,500 km², and least concern (LC) where EOO ≥ 45,000 km² and AOO ≥ 4,500 km². We did not perform analyses based on rates of change over time due to the limited date information in the occurrence dataset, but provided observations based on our field experiences for some taxa. While the metrics and observations do not provide the full set of criteria needed for Red Listing, they may offer indications of the most probable threat status of the taxa.

3 | RESULTS

3.1 | Distributions of wild *Capsicum*

A total of 6,974 occurrence records for the 37 taxa were compiled, processed and accepted for use for distribution modelling and

TABLE 2 Conservation gap analysis results per wild *Capsicum* L. taxon

Taxon	Total number of records	Total ex situ germplasm (G) records	Total reference (H) records	SRSex	GRSex	ERSex	FCSex	SRSin	GRSin	ERSin	FCSin	FCSc-mean	Priority category	Red List category recommendation
<i>C. annuum</i> var. <i>glabriusculum</i>	1948	37	1911	1.94	2.86	15.15	6.65	15.94	17.39	95.96	43.1	24.87	HP	LC
<i>C. baccatum</i> var. <i>baccatum</i>	326	54	272	19.85	5.5	36	20.45	21.47	13.11	92	42.19	31.32	MP	LC
<i>C. benoistii</i>	3	0	3	0	0	0	0	0	14.23	50	21.41	10.71	HP	CR
<i>C. caatingae</i>	113	0	113	0	0	0	0	2.3	3.75	100	35.35	17.67	HP	LC
<i>C. caballeri</i>	30	0	30	0	0	0	0	44.44	60.55	100	68.33	34.17	MP	VU
<i>C. campylopodium</i>	118	0	118	0	0	0	0	34.78	18	85.71	46.17	23.08	HP	VU
<i>C. cardenasii</i>	19	9	10	90	56.33	100	82.11	16.67	6.06	100	40.91	61.51	LP	EN
<i>C. ceratocalyx</i>	5	0	5	0	0	0	0	20	13.96	100	44.65	22.33	HP	CR
<i>C. chacoense</i>	437	73	364	20.05	7.97	53.33	27.12	9.24	11.99	80	33.74	30.43	MP	LC
<i>C. coccineum</i>	127	0	127	0	0	0	0	31.11	38.64	90.91	53.55	26.78	MP	NT
<i>C. cornutum</i>	29	0	29	0	0	0	0	16.67	54.12	50	40.26	20.13	HP	VU
<i>C. dimorphum</i>	160	0	160	0	0	0	0	37.89	21.2	100	53.03	26.52	MP	LC
<i>C. eshbaughii</i>	5	0	5	0	0	0	0	20	33.3	100	51.1	25.55	MP	CR
<i>C. eximium</i>	132	18	114	15.79	6	50	23.93	8.11	16.92	75	33.34	28.64	MP	LC
<i>C. flexuosum</i>	677	8	669	1.2	3.06	22.22	8.83	21.57	9.43	77.78	36.26	22.54	HP	LC
<i>C. friburgense</i>	8	0	8	0	0	0	0	25	34.41	100	53.14	26.57	MP	CR
<i>C. galapagoense</i>	27	9	18	50	0	0	16.67	85.71	86.57	100	90.76	53.71	LP	EN
<i>C. geminifolium</i>	147	0	147	0	0	0	0	21.88	15.28	100	45.72	22.86	HP	LC
<i>C. hookerianum</i>	46	0	46	0	0	0	0	43.48	15.4	100	52.96	26.48	MP	VU
<i>C. hunzikerianum</i>	20	0	20	0	0	0	0	50	42.28	50	47.43	23.71	HP	EN
<i>C. lanceolatum</i>	152	5	147	3.4	9	40	17.47	32.58	18.85	90	47.14	32.31	MP	NT
<i>C. longidentatum</i>	27	0	27	0	0	0	0	4.35	2.84	75	27.4	13.7	HP	VU
<i>C. longifolium</i>	9	0	9	0	0	0	0	11.11	27.17	100	46.09	23.05	HP	VU
<i>C. lycianthoides</i>	276	1	275	0.36	0	0	0.12	17.45	12.46	72.73	34.21	17.17	HP	LC
<i>C. minutiflorum</i>	23	1	22	4.55	1.48	50	18.68	23.53	25.04	100	49.52	34.1	MP	VU
<i>C. mirabile</i>	153	0	153	0	0	0	0	56.76	34.12	83.33	58.07	29.04	MP	NT
<i>C. neei</i>	14	0	14	0	0	0	0	57.14	36.61	100	64.59	32.29	MP	VU
<i>C. parvifolium</i>	215	0	215	0	0	0	0	9.38	5.77	100	38.38	19.19	HP	LC
<i>C. pereirae</i>	47	0	47	0	0	0	0	25.93	15.3	100	47.07	23.54	HP	VU
<i>C. piuranum</i>	6	0	6	0	0	0	0	0	0	0	0	0	HP	CR
<i>C. praetermissum</i>	207	19	188	10.11	1.86	23.08	11.68	11.84	9.36	92.31	37.84	24.76	HP	LC

(Continues)

TABLE 2 (Continued)

Taxon	Total number of records	Total ex situ germplasm (G) records	Total reference (H) records	SRSex	GRSex	ERSex	FCSex	SRSin	GRSin	ERSin	FCSin	FCSc-mean	Priority category	Red List category recommendation
<i>C. recurvatum</i>	141	0	141	0	0	0	0	46.55	23.43	83.33	51.11	25.55	MP	NT
<i>C. rhomboideum</i>	1,038	8	1,030	0.78	0	0	0.26	25.22	14.12	84.91	41.42	20.84	HP	LC
<i>C. schottianum</i>	120	6	114	5.26	0	0	1.75	50.98	37.13	83.33	57.15	29.45	MP	NT
<i>C. tovarii</i>	15	3	12	25	0	0	8.33	0	5.22	50	18.41	13.37	HP	VU
<i>C. villosum</i> var. <i>muticum</i>	17	0	17	0	0	0	0	100	77.23	100	92.41	46.2	MP	CR
<i>C. villosum</i> var. <i>villosum</i>	137	0	137	0	0	0	0	57.58	25.61	87.5	56.89	28.45	MP	NT
Totals (sums and averages)	6,974	251	6,723	6.71	2.54	10.53	6.60	28.56	24.24	85.13	45.98	26.29		

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 final conservation score combined (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, FCSc-mean < 25), medium priority (MP, 25 ≤ FCSc-mean < 50), low priority (LP, 50 ≤ FCSc-mean < 75), and sufficiently conserved (SC, FCSc-mean ≥ 75). Preliminary Red List recommendation based on extent of occurrence (EOO), area of occupancy (AOO) and field observations. Red List designations: critically endangered (CR), endangered (EN), vulnerable (VU), near threatened (NT) and least concern (LC).

conservation analyses, including 6,723 reference (H) records and 251 living plant conservation repository (G) records (Table 2, Table S2.2 in the Supporting Information). Of these, 3,672 contained coordinates and were thus used as inputs into the species distribution modelling. The total number of records per taxon ranged from three for *Capsicum benoistii* Hunz. ex Barboza to 1,948 for *C. annuum* var. *glabriusculum*—the putative wild progenitor of *C. annuum* var. *annuum* and most widely dispersed and well-studied wild taxon in the genus.

Of the 29 taxa with at least ten distinct occurrences, and thus modelled with ten replicates, all passed the preset distribution modelling evaluation criteria and were therefore considered robust (Table S2.3 in the Supporting Information). The eight taxa with less than ten coordinates were each modelled with three replicates, producing ASD15 scores outside the threshold. Based on our current knowledge, we consider these models to be fair enough representations of their current distributions for use in the conservation analyses. Interactive models and associated evaluation criteria for each taxon are available in Appendix S3 of the Supporting Information.

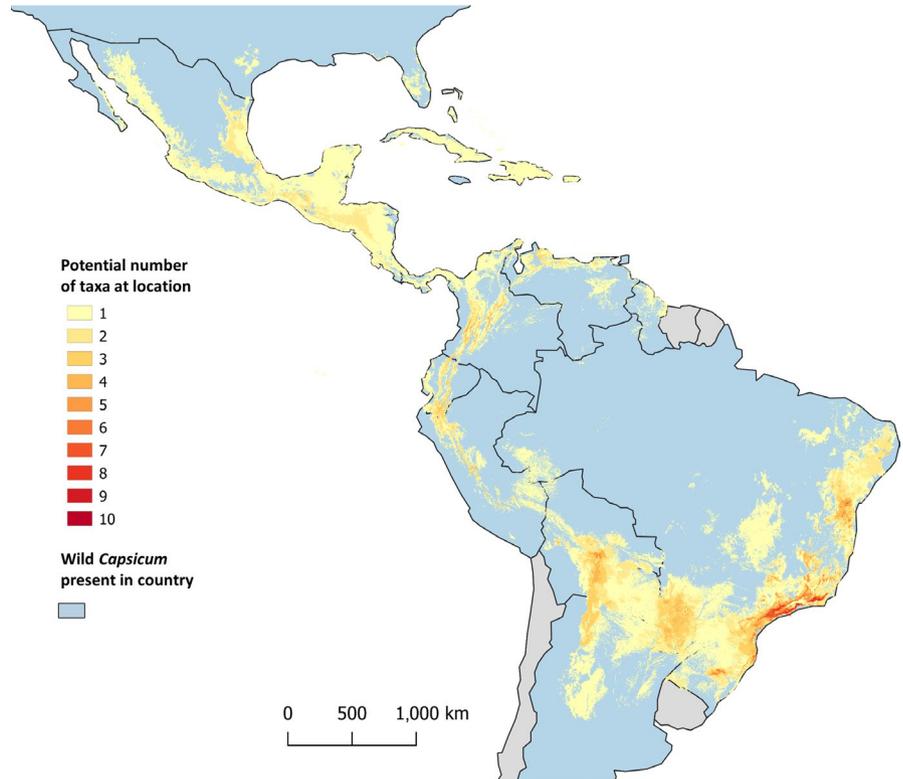
The modelled potential distributions of wild *Capsicum* ranged from the southern United States to northern Argentina, including the Caribbean and on the Galapagos Islands (Figure 1). Predicted taxon richness was highest along the Atlantic coast of Brazil, with up to ten taxa potentially overlapping in the same ca. 5 km² areas. Other taxon-rich regions included areas of Bolivia and Paraguay, and in the highlands of Colombia, Ecuador, Peru and Venezuela. A minority of the taxa (notably *C. annuum* var. *glabriusculum* and *C. rhomboideum* in Mexico, Central, and South America, and *C. baccatum* var. *baccatum* in South America) had relatively widespread models inhabiting a variety of ecoregions.

The majority of the taxa, on the other hand, are endemics or are otherwise restricted to specific environments. These include *Capsicum caatingae* Barboza & Agra, *Capsicum campylopodium* Sendtn., *Capsicum cornutum* (Hiern) Hunz., *Capsicum fr-iburgense* Bianchetti & Barboza, *Capsicum hunzikerianum* Barboza & Bianchetti, *Capsicum longidentatum* Agra & Barboza, *Capsicum mirabile* Mart. ex Sendtn., *Capsicum pereirae* Barboza & Bianchetti, *Capsicum recurvatum* Witas., *Capsicum schottianum* Sendtn., *Capsicum villosum* Sendtn. var. *muticum* Sendtn., and *Capsicum villosum* Sendtn. var. *villosum* in coastal Brazil; *Capsicum caballeroi* M. Nee, *Capsicum cardenasii* Heiser & P. G. Sm., *Capsicum ceratocalyx* M. Nee, *Capsicum eshbaughii* Barboza, *Capsicum minutiflorum* (Rusby) Hunz., and *Capsicum neei* Barboza & X. Reyes in Bolivia; *Capsicum galapagoense* Hunz. in the Galapagos Islands; *C. benoistii*, *Capsicum hookerianum* (Miers) Kuntze, *Capsicum longifolium* Barboza & S. Leiva, and *Capsicum piuranum* Barboza & S. Leiva in mainland Ecuador and/or northern Peru; and *Capsicum tovarii* Eshbaugh et al. in central-southern Peru.

3.2 | Ecogeographic characterization

Substantial variation with regard to ecogeographic niches was found across taxa. For example, the taxa with occurrences in the locations

FIGURE 1 Predicted taxonomic richness map combining the 37 wild *Capsicum* L. taxa potential distribution models. Darker colours indicate greater numbers of taxa potentially overlapping in the same areas



with the highest maximum temperatures in the warmest month of the year included *C. chacoense*, *C. annuum* var. *glabriusculum*, *C. baccatum* var. *baccatum*, *Capsicum coccineum* (Rusby) Hunz. and *C. minutiflorum* (Figure S2.1 in the Supporting Information). Those found in locations with the lowest temperatures in the coldest month measured by median of occurrences included *C. cardenasii*, *C. caballeroi*, *C. eximium*, *C. friburgense* and *Capsicum flexuosum* Sendtn. Those taxa with occurrences in sites with the highest precipitation in the wettest month included *Capsicum lanceolatum* (Greenm.) C. V. Morton & Standl., *Capsicum lycianthoides* Bitter, *C. schottianum* and *C. coccineum*, while those occurring in areas with the lowest precipitation in the driest month included *C. hookerianum*, *C. eximium*, *C. cardenasii*, *C. chacoense*, *C. eshbaughii*, *C. galapagoense*, *C. longidentatum*, *C. neei*, *Capsicum parvifolium* Sendtn., *C. tovarii* and *C. caatingae*.

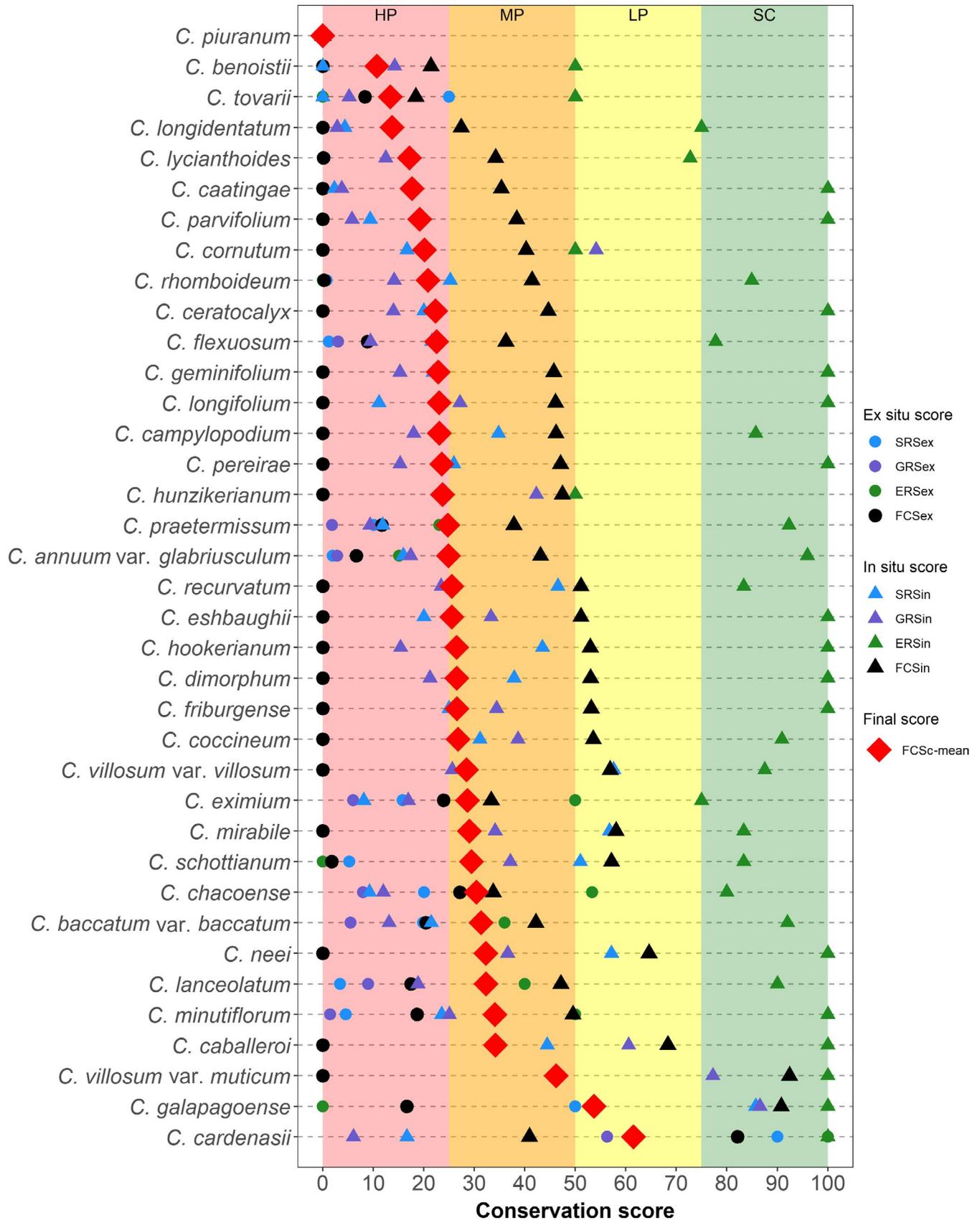
While some of these are distant relatives to the cultivated peppers (with a base chromosome number of 13 rather than 12), a number of the taxa with outstanding potential adaptations are putative progenitors or relatively close relatives, including *C. annuum* var. *glabriusculum*, *C. baccatum* var. *baccatum*, *C. cardenasii*, *C. chacoense*, *C. eshbaughii*, *C. eximium* and *C. galapagoense*. Temperature, precipitation and other ecogeographic variables also varied considerably within the ranges of some of the more widespread taxa, including *C. annuum* var. *glabriusculum*, *C. baccatum* var. *baccatum*, and *C. rhomboideum*, and for the Andean taxa *C. lycianthoides*, *C. geminifolium* (Dammer) Hunz., *Capsicum dimorphum* (Miers) Kuntze, and *C. coccineum*, as well as for *C. lanceolatum*. Thus, populations within these taxa may differ significantly with regard to their ecological adaptations.

3.3 | Conservation status

With regard to the conservation status of wild *Capsicum* in gene banks and botanic gardens, the overwhelming majority of taxa were found to be minimally or completely unrepresented ex situ. Twenty-three taxa (62.2% of the total) were not represented in the available germplasm databases. An additional nine taxa had fewer than ten accessions. A total of 35 taxa were assessed as high priority for further collecting, including the two putative crop progenitors (*C. annuum* var. *glabriusculum*, with an FCSEX of 6.65, and *C. baccatum* var. *baccatum*, FCSEX of 20.45) (Figure 2, Table 2; Table S2.2). *Capsicum chacoense* (FCSEX = 27.1) was assigned medium priority, and *C. cardenasii* (FCSEX = 82.11) was considered sufficiently conserved ex situ. The mean FCSEX across all taxa was 6.60 on the conservation status scale of from 0 to 100.

Due to such a low level of ex situ conservation of these wild taxa, further collecting is needed throughout their distributions. Priorities for collecting largely mirror patterns of taxon richness, thus, uncollected populations of up to ten taxa potentially occur in the same ca. 5 km² areas in coastal Brazil (Figure 3a).

The analysis of representation ex situ of the ecogeographic niches of the taxa indicated that *C. annuum* var. *glabriusculum*, *C. baccatum* var. *baccatum* and *C. chacoense* (i.e., the only taxa with more than 10 germplasm occurrences) are relatively well represented in gene banks and botanic gardens with regard to diverse ecological adaptations (Figure S2.2). The rest of the taxa, with no or very few occurrences, are poorly represented.



As for in situ conservation in the territories included in the World Database of Protected Areas (IUCN, 2019), taxa were generally considerably better protected than with regard to ex situ conservation,

with a mean FCSin across all taxa of 45.98 (Figure 2, Table 2; Table S2.2). One taxon (*C. piuranum*) was determined to have no official habitat protection anywhere within its potential distribution in

FIGURE 2 Conservation gap analysis results per assessed wild *Capsicum* L. taxon. Taxa 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 final conservation score combined (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

northern Peru. Thus, it was categorized as high priority for further action. However, protected areas were detected nearby the modelled distribution of the species. Two other taxa (*C. tovarii* and *C. benoistii*) were also assessed high priority, 21 taxa medium priority (including the two known crop progenitors), 11 low priority and two (*C. galapagoense* and *C. villosum* var. *muticum*) sufficiently conserved in situ.

As with the ex situ analysis, the ERSin scores per taxon were higher than the GRSin, in this case for all taxa but one (*C. cornutum*) and with 16 of the taxa being fully represented in in situ conservation with regard to the diversity of potentially inhabited ecoregions. The most efficient establishment of additional protection for wild *Capsicum* in protected areas with regard to geographic gaps would be concentrated in coastal Brazil, in Bolivia and Paraguay, and in the Andes (Figure 3b).

With regard to combined conservation status (averaging the ex situ and in situ metrics), taxa ranged from no protection at all (*C. piuranum*) to a moderate level of conservation (*C. cardenasii*, with an FCSc-mean of 61.51, and *C. galapagoense*, with an FCSc-mean of 53.71) (Figure 2, Table 2; Table S2.2). The FCSc-mean averaged across all taxa was 26.29. In summary, 18 taxa were determined to be high priorities for further conservation (including *C. annum* var. *glabriusculum*), 17 medium priorities (including *C. baccatum* var. *baccatum*) and two (*C. galapagoense* and *C. cardenasii*) low priorities, with none currently considered sufficiently conserved.

The EOO and AOO Red List analyses, supplemented by our field experience, indicated that *C. benoistii*, *C. ceratocalyx*, *C. eshbaughii*, *C. friburgense*, *C. piuranum* and *C. villosum* var. *muticum* could be candidates for designation as CR; and *C. cardenasii*, *C. galapagoense* and *C. hunzikerianum* as EN (although a number of populations of the last two taxa occur in protected areas). Our results further indicated that *C. caballeroi*, *C. campylopodium*, *C. cornutum*, *C. hookerianum*, *C. longidentatum*, *C. longifolium*, *C. minutiflorum*, *C. neei*, *C. pereirae* and *C. tovarii* could be considered as VU; *C. coccineum*, *C. lanceolatum*, *C. mirabile*, *C. recurvatum*, *C. schottianum* and *C. villosum* var. *villosum* possibly as NT; and the remaining taxa, including the two putative progenitors, as LC (Table 2; Table S2.4).

These results provide further support for the current Red Listings for three LC taxa (*C. annum* var. *glabriusculum*, *C. caatingae* and *C. rhomboideum*) and for designations proposed in previous literature (*C. piuranum* as CR, in Barbosa et al. 2019). They may provide further information for currently Red Listed taxa or taxa discussed in the literature whose designations do not fully align with our results (*C. lanceolatum* on the Red List; *C. benoistii*, *C. longifolium* and *C. neei* in Barboza et al., 2019; and *C. caatingae* and *C. longidentatum* in

Barboza et al., 2011). The results may also provide useful preliminary threat assessment indications for the 28 taxa currently absent from the Red List and previous threat assessment literature.

4 | DISCUSSION

In total, 94.6% of the wild relatives of chile peppers were assessed high priority for further collecting for ex situ conservation, including the two known putative crop progenitors. Among these are 23 taxa with no (zero) reported ex situ representation in the available germplasm databases, and another eight with fewer than ten accessions, and thus very limited genetic diversity accessible for crop breeding and other research. Twenty-four (64.9%) taxa were assessed as medium or high priority for further protection in situ. A total of 48.7% of taxa were determined to be high, and another 46% medium priority for conservation with regard to both ex situ and in situ strategies combined. It is thus clear that further conservation action is needed, both to safeguard these taxa ex situ, and to ensure their continued survival and evolution in their natural habitats.

Across the wild taxa in the genus, the geographic gaps in both ex situ and in situ conservation representation largely aligned with taxonomic richness hot spots. These are especially prevalent along the Atlantic coast of Brazil where the occurrences of multiple taxa overlap. Other hot spots are located in Bolivia and Paraguay, as well as in the highlands of Colombia, Ecuador, Peru, and Venezuela, and to a more limited extent in Mesoamerica. These represent particularly high value regions for further study and collecting of the taxa for ex situ conservation, as well as priority candidate areas for further protection in their natural habitats.

The genus as a whole, as well as at least one of the domesticated taxa (*C. baccatum* var. *pendulum*), have been proposed to have originated in seasonally dry tropical forests (Bosland & Votava, 2012; Scadaferro, Barboza, & Acosta, 2018), and we estimate that at least 19 extant *Capsicum* taxa occur in this highly threatened and often overlooked biome (DRYFLOR et al., 2016). Matching wild *Capsicum* occurrences to spatial information on "Tropical and subtropical dry broadleaf forests" in the Americas (WWF, 2019), we found that over a fifth (22.1%) of all points fell within this major habitat type, including all of the occurrences for *C. eshbaughii*, 70.4% of those of *C. caballeroi*, 60.8% of *C. eximium*, 58.8% of *C. chacoense* and 52.9% of *C. minutiflorum*, among others. We found that only ca. 7% of the total area of these dry broadleaf forests are currently protected within areas included in the WDPA. Alongside geographic prioritizations focused on taxonomic richness, in situ conservation action may

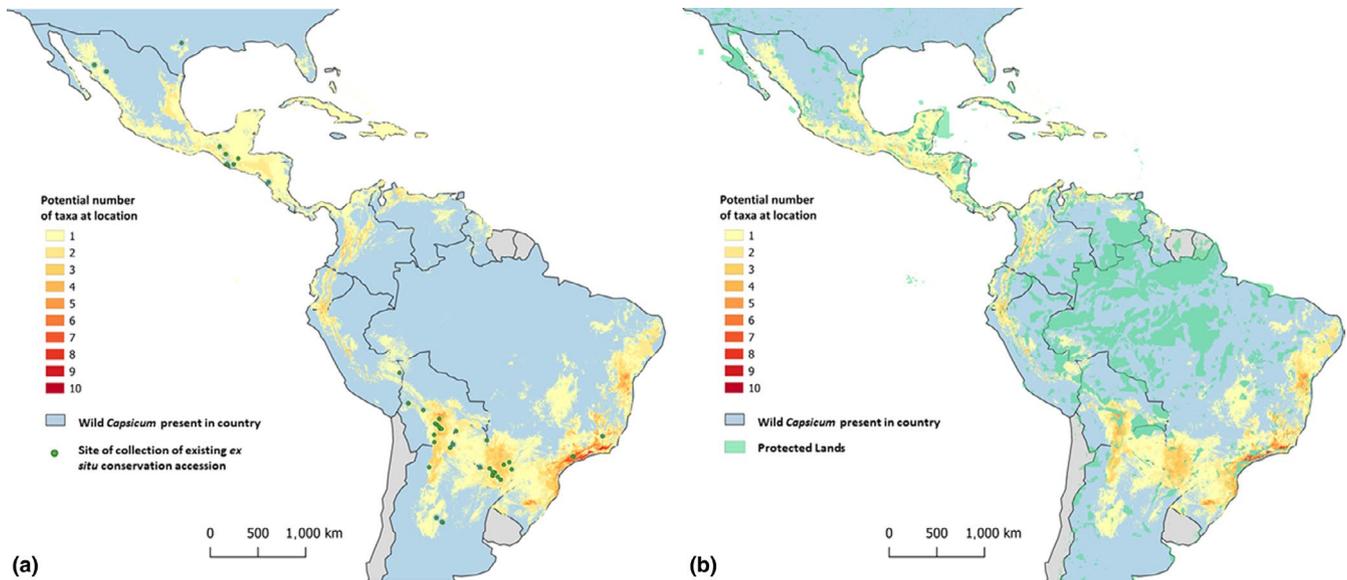


FIGURE 3 (a) Predicted further collecting priorities hot spots map for wild *Capsicum* L. taxa. The map displays richness of areas within the potential distributions of the 37 wild *Capsicum* taxa that have not been previously collected for ex situ conservation, with up to ten taxa in need of further collecting potentially found in the same areas. Sites where existing germplasm of taxa has been collected are overlaid. (b) Predicted further in situ protection priorities map for wild *Capsicum*. The map displays richness of areas within the potential distributions of the 37 wild *Capsicum* taxa that are outside of current protected areas, with up to ten taxa found in the same unprotected areas. Protected areas are displayed in green

thus consider prioritizing such threatened biomes, habitat types and ecoregions (Scaladaferro et al., 2018).

Focusing on the putative crop progenitors and close relatives, that is the taxa most likely to be utilized in crop breeding, which also include the wild taxa sold in local markets or cultivated in home gardens, the high priority taxon *C. annum* var. *glabriusculum* is poorly represented ex situ with regard to geographic coverage of its potential distribution, but fairly well represented with regard to ecogeographic and ecological variation (Table 2; Figure S2.2). This taxon is potentially present in protected areas that are fairly well distributed across its modelled range from the southern United States to northern South America, and was given a preliminary designation of LC in the threat assessment. The majority of the currently recognized secondary relatives of *C. annum* var. *annuum* (and also for *C. chinense* and *C. frutescens*) (i.e., *C. chacoense*, *C. galapagoense*, *C. baccatum* var. *baccatum* and *C. praetermissum*) were assigned high or medium priority for further conservation action, with geographic gaps particularly present in Argentina, Bolivia, Brazil, the Galapagos Islands and Paraguay.

Medium priority putative progenitor taxon *C. baccatum* var. *baccatum* appears to be somewhat better conserved both ex and in situ in comparison with the progenitor of *C. annum* var. *annuum*, but identifiable geographic and ecological gaps remain with regard to both conservation strategies. The other close relatives of *C. baccatum* var. *pendulum*, like those of *C. annum* var. *annuum*, were assigned high or medium priority for further conservation action, with geographic gaps as detailed above.

Among the known close relatives of *C. pubescens*, only *C. cardenasii* is currently fairly well represented ex situ, while *C. eximium* and

especially *C. eshbaughii* are very poorly conserved. These species appear to be comparatively better conserved in situ. Conservation action in Bolivia is necessary to resolve the gaps for these species, one of which was assessed as CR and another as EN, in the preliminary threat assessment.

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

Distributions of wild *Capsicum* are influenced by factors beyond the 26 ecogeographic predictors used here. These may include biotic (e.g., dispersal agents, host plants, mycorrhizae, pathogens and pollinators) and other abiotic (e.g., soil parent material and other edaphic characteristics) factors (Carlo & Tewksbury, 2014; Kraft et al., 2014; Tewksbury et al., 1999, 2008). A number of the taxa, in particular *C. annum* var. *glabriusculum*, but also *C. baccatum* var. *baccatum*, *C. cardenasii*, *C. chacoense*, *C. eximium*, *C. praetermissum* and *C. frutescens* (putative wild/feral populations), are harvested from the wild, with populations exposed to varying levels of human management and impact, which affect their distributions over the long term (Aguilar-Meléndez & Lira Noriega, 2018; van Zonneveld et al., 2015, 2018; Villalon-Mendoza et al., 2014). Furthermore, the current ecogeographic suitability models are unable to fully account for relatively recent extirpation events of populations due to habitat degradation or destruction, for example for *C. lanceolatum*, thought to now be extinct in Mexico (Barchenger & Bosland, 2019). Our results, therefore, should best be considered as planning tools to guide explorations for further confirmation in the field.

Biodiversity occurrence data are often spatially biased, tending to concentrate around roadways and major population centres (Stolar & Nielsen, 2015; Syfert, Smith, & Coomes, 2013). Alongside extensively reviewing the presence coordinate locations for accuracy, to mitigate the potential effect of spatial bias, we generated background points (pseudo-absences) only within the ecoregions in which the presence points were located. This limited the amount of variability present within the range of predictor values in the background dataset (Jarnevich & Young, 2019). For some taxa, it is possible that the current occurrence data did not capture the full ecogeographic range within which the species can be found. As a result, the edges of the predicted distribution models represent particularly important regions for further field exploration (Jarnevich, Stohlgren, Kumar, Morissette, & Holcombe, 2015).

With regard to the conservation analyses, openly available databases on gene bank and botanic garden holdings are not fully representative of all such institutions worldwide. Thus, gaps in information on the ex situ conservation of wild *Capsicum* may yet exist, particularly with regard to gene banks and gardens that are not currently reporting in databases such as Genesys, FAO WIEWS and GBIF (Thomas et al., 2016). Coordinate or other locality information is also presently lacking for a large number of records that are available in online databases. For example, PlantSearch currently does not make locality level information on accessions 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, our review of taxonomic information in these databases for members of the genus indicates that they are in need of improvement. If these constraints were to be remedied, it is possible that the ex situ conservation status of some taxa might be revised in a positive (or even negative) direction. This said, national and institutional policies and other barriers often restrict the distribution of germplasm from the gene banks and botanic gardens for which information is currently not readily available.

Our ecogeographic suitability model-based results did not always align perfectly with our field experience, particularly with regard to presence in protected areas. For example, our models (as well as points) for *C. villosum* var. *muticum* were determined through the analysis to overlap quite well with the protected areas listed in the WDPA. Unfortunately, for the taxon, its observed restricted distribution in fact falls just outside of protected areas, and the quality of its habitat has declined progressively during our field visits over the past six years.

While the lands listed in the WDPA hopefully afford collateral protection to wild *Capsicum* taxa as a result of overall land conservation practices, robust long-term protection of these plants in these areas will likely require the formation of active taxon- and population-specific management plans. Overexploitation of wild populations, particularly those experiencing climate stress, can severely impact their persistence, recovery and genetic diversity (González-Jara, Moreno-Letelier, Fraile, Piñero, & García-Arenal, 2011; Nabhan, 1990). We are aware of only one protected area

worldwide (Rock Corral Canyon, Coronado National Forest), on the Arizona, United States–Sonora, Mexico border, where active monitoring and management plans facilitate the long-term conservation of wild *Capsicum* populations (Nabhan & Riordan, 2019). As a number of the *Capsicum* taxa are wild-harvested and contribute to local cultures, nutrition and economies, it is important to include and to incorporate the priorities of harvesters and local consumers in conservation plans. We note that further domestication of wild *Capsicum* for cultivation could also aid in reducing pressure on natural populations while responding to growing market demands for the edible species.

4.2 | Challenges to utilization of wild *Capsicum* germplasm

While ecogeographic information associated with germplasm accessions can help narrow the potential pool of useful germplasm targeted by plant breeders, these data cannot completely displace the need for phenotypic validation of adaptations, such as for abiotic or biotic stress tolerance. Moreover, ecogeographic data may better predict abiotic than biotic stress tolerance. Phenotypic characterizations of collections under diverse environmental conditions and using manipulative experiments (e.g., imposing moisture stress or inoculating with pathogens) are needed for wild *Capsicum* accessions. To further understanding of the genetics underlying adaptive traits in these wild relatives, associations between particular genetic sequences in wild *Capsicum* and phenotypes of interest could be established through genome-wide association studies (GWAS) or quantitative trait locus (QTL) analyses. Once the function of these candidate loci is established, the phenotypic effects of particular genetic variants can be mobilized for use (Tanksley & McCouch, 1997).

Further, interspecific hybridizations can present challenges for breeding with wild species. For example, crosses made between members of the pubescens complex and other groups have sometimes resulted in unilateral incompatibility (Onus & Pickersgill, 2004; Pickersgill, 1997). Post-fertilization seed abortion or sterility in the offspring has also been reported in several interspecific crosses (Pickersgill, 1991; Smith & Heiser, 1957; Yoon, Yang, Do, & Park, 2006).

These constraints to utilization acknowledged, several successful strategies to overcome barriers to interspecific hybridization do exist in *Capsicum* (Yoon et al., 2006). Furthermore, for more than 20 years, genes from pepper have been moved into tomato using transgenic technologies, increasing resistance to key diseases (Tai et al., 1999). In the emerging era of genome editing, both the 12 and 13 base chromosome number wild *Capsicum* taxa could be useful in the development of more resilient peppers, as well as other crops, although we note that much of the environmental adaptation within wild plants is polygenic and quantitative (Tiffin & Ross-Ibarra, 2014), so there may be limits on the degree to which adaptation can be engineered. Regardless of the breeding methods used, ensuring adequate representation of

these wild relatives in conservation systems, and further characterizing populations with regard to their adaptations to abiotic and biotic stresses, will provide the foundations for their more widespread use.

ACKNOWLEDGEMENTS

The authors thank the botanists, taxonomists, plant collectors, geospatial scientists and genetic resource professionals who compiled and made available through open access repositories the occurrence and ecogeographic information used in this analysis. Funding for World Vegetable Center co-authors was provided in part by the long-term strategic donors to the World Vegetable Center: Republic of China (Taiwan), UK aid from the UK government, United States Agency for International Development (USAID), Australian Centre for International Agricultural Research (ACIAR), Germany, Thailand, Philippines, Korea and Japan. Field explorations by authors G.E.B. and L.B., leading to some of the occurrence data used in this analysis, were supported by NSF DEB-1457366. The USDA is an equal opportunity employer and provider.

ORCID

Colin K. Khoury  <https://orcid.org/0000-0001-7893-5744>

Maarten van Zonneveld  <https://orcid.org/0000-0002-7875-4756>

Lynn Bohs  <https://orcid.org/0000-0003-2803-2656>

Mark Uchanski  <https://orcid.org/0000-0002-8152-4695>

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>.

REFERENCES

- Aguilar-Meléndez, A., Azurdia, C., Cerén-López, J., Menjivar, J., & Contreras, A. (2019). *Capsicum annuum* (amended version of 2017 assessment). The IUCN Red List of Threatened Species 2019: e.T100895534A143826567. <https://doi.org/10.2305/IUCN.UK.2017-3.RLTS.T100895534A143826567.en>
- Aguilar-Meléndez, A., & Lira Noriega, A. (2018). ¿Dónde crecen los chiles en México? In A. Aguilar-Meléndez, M. A. Vasquez-Davila, E. Katz, & M. R. Hernandez Colorado (Eds.), *Los chiles que le dan sabor al mundo* (pp. 75–92). Veracruz, Mexico: Universidad Veracruzana.
- Aloni, B., Peet, M. M., Pharr, M., & Karni, L. (2001). The effect of high temperature and high atmospheric CO₂ on carbohydrate changes in bell pepper (*Capsicum annuum*) pollen in relation to its germination. *Physiologia Plantarum*, 112, 505–512. <https://doi.org/10.1034/j.1399-3054.2001.1120407.x>
- Azurdia, C., Aguilar-Meléndez, A., Cerén-López, J., Contreras, A., & Menjivar, J. (2017a). *Capsicum frutescens*. The IUCN Red List of Threatened Species 2017: e.T110057309A110057536. <https://doi.org/10.2305/IUCN.UK.2017-3.RLTS.T110057309A110057536.en>
- Azurdia, C., Aguilar-Meléndez, A., Cerén-López, J., Contreras, A., & Menjivar, J. (2017b). *Capsicum rhomboideum*. The IUCN Red List of Threatened Species 2017: e.T107659536A107659540. <https://doi.org/10.2305/IUCN.UK.2017-3.RLTS.T107659536A107659540.en>
- Azurdia, C., Aguilar-Meléndez, A., Menjivar, J., Cerén-López, J., & Contreras, A. (2017). *Capsicum lanceolatum* (errata version published in 2018). The IUCN Red List of Threatened Species 2017: e.T107657869A135208239. <https://doi.org/10.2305/IUCN.UK.2017-3.RLTS.T107657869A107657872.en>
- Baral, J. B., & Bosland, P. W. (2002). An updated synthesis of the *Capsicum* genus. *Capsicum Eggplant Newsletter*, 21, 11–21.
- Barboza, G. E., Agra, M. F., Romero, M. V., Scaldaferrero, M. A., & Moscone, E. A. (2011). New endemic species of *Capsicum* (Solanaceae) from the Brazilian Caatinga: Comparison with the re-circumscribed *C. parvifolium*. *Systematic Botany*, 36, 768–781. <https://doi.org/10.1600/036364411X583718>
- Barboza, G. E., & Bianchetti, L. (2005). Three new species of *Capsicum* (Solanaceae) and a key to the wild species from Brazil. *Systematic Botany*, 30, 863–871.
- Barboza, G. E., Carrizo García, C., Leiva González, S., Scaldaferrero, M., & Reyes, X. (2019). Four new species of *Capsicum* (Solanaceae) from the tropical Andes and an update on the phylogeny of the genus. *PLoS ONE*, 14, e0209792. <https://doi.org/10.1371/journal.pone.0209792>
- Barchenger, D. W., & Bosland, P. W. (2019). Wild chile pepper (*Capsicum* spp.) of North America. In S. L. Greene, K. A. Williams, C. K. Khoury, M. B. Kantar, & L. F. Marek (Eds.), *American crop wild relatives, Volume 2: Important species* (pp. 225–242). Cham, Switzerland: Springer International Publishing AG.
- Bellon, M. R., Dulloo, E., Sardos, J., Thormann, I., & Burdon, J. J. (2017). In situ conservation-harnessing natural and human-derived evolutionary forces to ensure future crop adaptation. *Evolutionary Applications*, 10, 965–977. <https://doi.org/10.1111/eva.12521>
- BGCI&IUCNSSCGlobalTreeSpecialistGroup. (2019). *Capsicumcaatingae*. The IUCN Red List of Threatened Species 2019: e.T149211901A149211903. doi:<https://doi.org/10.2305/IUCN.UK.2019-2.RLTS.T149211901A149211903.en>
- BGCI. (2019). PlantSearch. https://www.bgci.org/plant_search.php
- Bosland, P. W., & Votava, E. J. (2012). *Peppers: Vegetable and spice capsicums*, 2nd ed. Oxfordshire, UK: CAB International.
- Carlo, T. A., & Tewksbury, J. J. (2014). Directness and tempo of avian seed dispersal increases emergence of wild chiltepins in desert grasslands. *Journal of Ecology*, 102, 248–255. <https://doi.org/10.1111/1365-2745.12180>
- Carrizo Garcia, C., Barfus, M. H. J., Sehr, E. M., Barboza, G. E., Samuel, R., Moscone, E. A., & Ehrendorfer, F. (2016). Phylogenetic relationships, diversification and expansion of chili peppers (*Capsicum*, Solanaceae). *Annals of Botany*, 118, 35–51.
- Castañeda-Álvarez, N. P., Khoury, C. K., Achicanoy, H. A., Bernau, V., Dempewolf, H., Eastwood, R. J., ... Toll, J. (2016). Global conservation priorities for crop wild relatives. *Nature Plants*, 2, 16022. <https://doi.org/10.1038/nplants.2016.22>
- Davenport, W. A. (1970). Progress report on the domestication of *Capsicum* (Chile peppers). *Proceedings of the Association of the American Geographers*, 2, 46–47.
- De Pascale, S., Ruggiero, C., Barbieri, G., & Maggio, A. (2003). Physiological responses of pepper to salinity and drought. *Journal of the American Society for Horticultural Science*, 128, 48–54. <https://doi.org/10.21273/JASHS.128.1.0048>
- Dempewolf, H., Baute, G., Anderson, J., Kilian, B., Smith, C., & Guarino, L. (2017). Past and future use of wild relatives in crop breeding. *Crop Science*, 57, 1070–1082. <https://doi.org/10.2135/cropsci2016.10.0885>
- Dempewolf, H., Eastwood, R. J., Guarino, L., Khoury, C. K., Müller, J. V., & Toll, J. (2013). Adapting agriculture to climate change: A global initiative to collect, conserve, and use crop wild relatives.

- Agroecology and Sustainable Food Systems, 38, 369–377. <https://doi.org/10.1080/21683565.2013.870629>
- DeWitt, D., & Bosland, P. W. (1993). *The pepper garden*. Berkeley, CA: Ten Speed Press.
- Díaz, S., Settele, J., Brondizio, E., Ngo, H. T., Gueze, M., Agard, J., ... Chan, K. (2019). Global Assessment Report on Biodiversity and Ecosystem Services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. <https://www.ipbes.net/assessment-reports>
- DRYFLOR, Banda-R, K., Delgado-Salinas, A., Dexter, K. G., Linares-Palmino, R., & Oliveira-Filho, A., ... Pennington, R. T. (2016). Plant diversity patterns in Neotropical dry forests and their conservation implications. *Science*, 353, 1383–1387. <https://doi.org/10.1126/science.aaf5080>
- Emboden Jr., W. A. (1961). A preliminary study of the crossing relationships of *Capsicum baccatum*. *Butler University Botanical Studies*, 14, 1–5.
- Eshbaugh, W. H. (1970). A biosystematic and evolutionary study of *Capsicum baccatum* (Solanaceae). *Brittonia*, 22, 31–43. <https://doi.org/10.2307/2805720>
- FAO. (2018). United Nations Food and Agriculture Organization World Information and Early Warning System on Plant Genetic Resources for Food and Agriculture (WIEWS). <http://www.fao.org/wiews/en/>
- Fick, S. E., & Hijmans, R. J. (2017). Worldclim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37, 4302–4315. <https://doi.org/10.1002/joc.5086>
- Gajanayake, B., Trader, B. W., Reddy, K. R., & Harkess, R. L. (2011). Screening ornamental pepper cultivars for temperature tolerance using pollen and physiological parameters. *HortScience*, 46, 878–884. <https://doi.org/10.21273/HORTSCI.46.6.878>
- Genuer, R., Poggi, J. M., & Tuleau-Malot, C. (2018). Package 'VSURF'. <https://github.com/robingenuer/VSURF>
- Gepts, P. (2006). Plant genetic resources conservation and utilization: The accomplishments and future of a societal insurance policy. *Crop Science*, 46, 2278–2292. <https://doi.org/10.2135/cropsci2006.03.0169gas>
- Global Biodiversity Information Facility (GBIF). (2018). GBIF occurrence download. <https://doi.org/10.15468/dl.echmsh>
- Global Crop Diversity Trust. (2018a). Global crop wild relative occurrence database. <https://www.cwrdiversity.org/checklist/cwr-occurrences.php>
- Global Crop Diversity Trust. (2018b). Genesys global portal of plant genetic resources for food and agriculture. <https://www.genesys-pgr.org>
- González-Jara, P., Moreno-Letelier, A., Fraile, A., Piñero, D., & García-Arenal, F. (2011). Impact of human management on the genetic variation of wild pepper, *Capsicum annum* var. *glabriusculum*. *PLoS ONE*, 6, e28715. <https://doi.org/10.1371/journal.pone.0028715>
- Google. (2019a). Google Earth. <https://www.google.com/earth/>
- Google. (2019b). My Maps. <https://www.google.com/maps/about/mymaps/>
- Guzman, I., Bosland, P. W., & O'Connell, M. A. (2011). Heat, color, and flavor compounds in *Capsicum* fruit. In D. R. Gang (Ed.), *The biological activity of phytochemicals* (pp. 109–126). New York, NY: Springer.
- Hajjar, R., & Hodgkin, T. (2007). The use of wild relatives in crop improvement: A survey of developments over the last 20 years. *Euphytica*, 156, 1–13.
- Halikowski Smith, S. (2015). In the shadow of a pepper-centric historiography: Understanding the global diffusion of Capsicums in the sixteenth and seventeenth centuries. *Journal of Ethnopharmacology*, 167, 64–77. <https://doi.org/10.1016/j.jep.2014.10.048>
- Han, X. B., Li, R. Q., Wang, J. B., & Miao, C. (1996). Effect of heat stress on pollen development and pollen viability of pepper. *Acta Horticulturae Sinica*, 23, 359–364.
- Heiser Jr, C. B. (1969). *Nightshades, the paradoxical plants*. San Francisco, CA: WH Freeman.
- Heiser, C. B. Jr, & Smith, P. G. (1948). Observations on another species of cultivated peppers, *Capsicum pubescens* R & P. *Proceedings of the American Society for Horticultural Science*, 52, 331–335.
- Hijmans, R. J. (2017). Raster: Geographic data analysis and modeling. R package version 2.6-7. <https://CRAN.R-project.org/package=raster>
- Hijmans, R. J., Phillips, S., Leathwick, J., & Elith, J. (2017). dismo: Species distribution modeling. R package version 1.1-4. <https://CRAN.R-project.org/package=dismo>
- Hirsch, C. N., Hirsch, C. D., Fletcher, K., Coombs, J., Zarka, D., Van Deynze, A., ... C. R. (2013). Retrospective View of North American potato (*Solanum tuberosum* L.) breeding in the 20th and 21st centuries. *G3*, 3, 1003–1013.
- International Union for Conservation of Nature (IUCN). (2019). World database on protected areas. <https://protectedplanet.net/>
- IUCN Standards and Petitions Committee. (2019). Guidelines for Using the IUCN Red List Categories and Criteria. Version 14. Prepared by the Standards and Petitions Committee. Retrieved from <http://www.iucnredlist.org/documents/RedListGuidelines.pdf>
- Jarnevech, C. S., Stohlgren, T. J., Kumar, S., Morissette, J. T., & Holcombe, T. R. (2015). Caveats for correlative species distribution modeling. *Ecological Informatics*, 29, 6–15. <https://doi.org/10.1016/j.ecoinf.2015.06.007>
- Jarnevech, C. S., & Young, N. E. (2019). Not so normal normals: Species distribution model results are sensitive to choice of climate normals and model type. *Climate*, 7(3), 37. <https://doi.org/10.3390/cli7030037>
- Jarret, R. L., Barboza, G. E., Costa Batista, F. R. D., Berke, T., Chou, Y.-Y., Hulse-Kemp, A., ... Szoke, A. (2019). *Capsicum* - an abbreviated compendium. *Journal of the American Society for Horticultural Science*, 144, 3–22. <https://doi.org/10.21273/JASHS04446-18>
- Jarvis, A., Lane, A., & Hijmans, R. J. (2008). The effect of climate change on crop wild relatives. *Agriculture, Ecosystems, and Environment*, 126, 13–23. <https://doi.org/10.1016/j.agee.2008.01.013>
- Jarvis, A., Reuter, H. I., Nelson, A., & Guevara, E. (2008). Hole-filled seamless SRTM data V4. International Center for Tropical Agriculture (CIAT). <http://srtm.csi.cgiar.org>
- Kahane, R., Hodgkin, T., Jaenicke, H., Hoogendoorn, C., Hermann, M., (Dyno)Keatinge, J. D. H., ... Looney, N. (2013). Agrobiodiversity for food security, health, and income. *Agronomy for Sustainable Development*, 4, 671–693. <https://doi.org/10.1007/s13593-013-0147-8>
- Kantar, M. B., Anderson, J. E., Lucht, S. A., Mercer, K., Bernau, V., Case, K. A., ... Baumler, D. J. (2016). Vitamin variation in *Capsicum* spp. provides opportunities to improve nutritional value of human diets. *PLoS ONE*, 11, e0161464. <https://doi.org/10.1371/journal.pone.0161464>
- Kenyon, L., Kumar, S., Tsai, W. S., & Hughes, J. d'A. (2014). Virus diseases of peppers (*Capsicum* spp.) and their control. In G. Loebenstein, & N. Katis (Eds.), *Advances in virus research* (Vol. 90, pp. 297–354). Burlington, Cambridge, MA: Academic Press.
- Khoury, C. K., Amariles, D., Soto, J. S., Diaz, M. V., Sotelo, S., Sosa, C. C., ... Jarvis, A. (2019a). Comprehensiveness of conservation of useful wild plants: An operational indicator for biodiversity and sustainable development targets. *Ecological Indicators*, 98, 420–429. <https://doi.org/10.1016/j.ecolind.2018.11.016>
- Khoury, C. K., Amariles, D., Soto, J. S., Diaz, M. V., Sotelo, S., Sosa, C. C., ... Wiersema, J. H. (2019b). Data for the calculation of an indicator of the comprehensiveness of conservation of useful wild plants. *Data in Brief*, 22, 90–97. <https://doi.org/10.1016/j.dib.2018.11.125>
- Kraft, K. H., Brown, C. H., Nabhan, G. P., Luedeling, E., Luna Ruiz, J. D. J., Coppens d'Eeckenbrugge, G., ... Gepts, P. (2014). Multiple lines of evidence for the origin of domesticated chili pepper, *Capsicum annum*, in Mexico. *Proceedings of the National Academy of Sciences of the USA*, 111(17), 6165–6170. <https://doi.org/10.1073/pnas.1308933111>

- Lee, C. K. F., Keith, D. A., Nicholson, E., & Murray, N. J. (2019). REDLISTR: Tools for the IUCN Red Lists of ecosystems and threatened species in R. *Ecography*, 42(5), 1050–1055. <https://doi.org/10.1111/ecog.04143>
- Lin, T., Zhu, G., Zhang, J., Xu, X., Yu, Q., Zheng, Z., ... Huang, S. (2014). Genomic analyses provide insights into the history of tomato breeding. *Nature*, 46, 1220–1226.
- Liu, C., Berry, P. M., Dawson, T. P., & Pearson, R. G. (2005). Selecting thresholds of occurrence in the prediction of species distributions. *Ecography*, 28, 385–393. <https://doi.org/10.1111/j.0906-7590.2005.03957.x>
- Liu, C., White, M., & Newell, G. (2013). Selecting thresholds for the prediction of species occurrence with presence-only data. *Journal of Biogeography*, 40, 778–789. <https://doi.org/10.1111/jbi.12058>
- Luna-Ruiz, J. D. J., Nabhan, G. P., & Aguilar-Meléndez, A. (2018). Shifts in plant chemical defenses of chile pepper (*Capsicum annuum* L.) due to domestication in Mesoamerica. *Frontiers in Ecology and Evolution*, 6, 48.
- Maas, E. V., & Hoffman, G. J. (1977). Crop salt tolerance, current assessment. *Journal of Irrigation and Drainage Division*, 103, 115–134.
- Miller, R. E., & Khoury, C. K. (2018). The gene pool concept applied to crop wild relatives: An evolutionary perspective. In S. L. Greene, K. A. Williams, C. K. Khoury, M. B. Kantar, & L. F. Marek, editors, *North American crop wild relatives, Volume 1: Conservation strategies* (pp. 167–188). Cham, Switzerland: Springer International Publishing A.G. https://doi.org/10.1007/978-3-319-95101-0_6
- Mongkolporn, D., & Taylor, P. W. J. (2011). *Capsicum*. In C. Kole (Ed.), *Wild crop relatives: Genomic and breeding resources*. Berlin-Heidelberg, Germany: Springer.
- Nabhan, G. (1990). Conservationists and forest service join forces to save wild chiles. *Diversity*, 6, 47–48.
- Nabhan, G. P., & Riordan, E. C. (2019). Trans-situ conservation of crop wild relatives in Southern Arizona. *Crop Science*, 59. <https://doi.org/10.2135/cropsci2019.06.0356>
- NatureServe. (2019). NatureServe Explorer. <http://explorer.natureserve.org/index.htm>
- Noss, C. F., & Levey, D. J. (2014). Does gut passage affect post-dispersal seed fate in a wild chili, *Capsicum annuum*? *Southeastern Naturalist*, 13, 475–483.
- Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., ... Kassem, K. R. (2001). Terrestrial ecoregions of the world: A new map of life on earth. *BioScience*, 51, 933–938. [https://doi.org/10.1641/0006-3568\(2001\)051\[0933:TEOTWA\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2)
- Onus, A. N., & Pickersgill, B. (2004). Unilateral incompatibility in *Capsicum* (Solanaceae): Occurrence and taxonomic distribution. *Annals of Botany*, 94, 289–295. <https://doi.org/10.1093/aob/mch139>
- Perry, L., Dickau, R., Zarrillo, S., Holst, I., Pearsall, D. M., Piperno, D. R., ... Zeidler, J. A. (2007). Starch fossils and the domestication and dispersal of chili peppers (*Capsicum* spp. L.) in the Americas. *Science*, 315, 986–988. <https://doi.org/10.1126/science.1136914>
- Perry, L., & Flannery, K. V. (2017). Precolumbian use of chili peppers in the valley of Oaxaca, Mexico. *Proceedings of the National Academy of Sciences*, 104, 11905–11909.
- Phillips, S. J., Anderson, R. P., Dudik, M., Schapire, R. E., & Blair, M. E. (2017). Opening the black box: An open-source release of Maxent. *Ecography*, 40, 887–893. <https://doi.org/10.1111/ecog.03049>
- Pickersgill, B. (1966). *The variability and relationships of Capsicum chinense Jacq.* PhD. Dissertation. Bloomington, IN: Indiana University.
- Pickersgill, B. (1969). The archaeological record of chili peppers (*Capsicum* spp.) and the sequence of plant domestication in Peru. *American Antiquity*, 34, 51–64.
- Pickersgill, B. (1971). Relationships between weedy and cultivated forms in some species of chili peppers (genus *Capsicum*). *Evolution*, 25, 683–691.
- Pickersgill, B. (1977). Taxonomy and the origin and evolution of cultivated plants in the New World. *Nature*, 268, 591–595. <https://doi.org/10.1038/268591a0>
- Pickersgill, B. (1980). Some aspects of interspecific hybridization. In: *Capsicum. Unpublished and preliminary report at the IVth Eucarpia Capsicum working group meetings in Wageningen, The Netherlands.*
- Pickersgill, B. (1991). Cytogenetics and evolution of *Capsicum* L. In T. Tsuchiya, & P. K. Gupta (Eds.), *Chromosome engineering in plants: Genetics, breeding, evolution, Part B* (pp. 139–160). Amsterdam, The Netherlands: Elsevier.
- Pickersgill, B. (1997). Genetic resources and breeding of *Capsicum* spp. *Euphytica*, 96, 129–133.
- Ramirez-Villegas, J., Khoury, C. K., Jarvis, A., Deboucq, D. G., & Guarino, L. (2010). A gap analysis methodology for collecting crop gene pools: A case study with *Phaseolus* beans. *PLoS ONE*, 5(10), e13497. <https://doi.org/10.1371/journal.pone.0013497>
- Rao, R., & Li, Y. (2003). Management of flood effects on growth on vegetable and selected field crops. *Horttechnology*, 13, 610–616.
- Scaladaferro, M. A. (2019). Molecular cytogenetic evidence of hybridization in the "purple corolla clade of the genus *Capsicum*" (*C. eximium* × *C. cardenasii*). *Plant Biosystems*, 1–7. <https://doi.org/10.1080/11263504.2019.1674403>
- Scaladaferro, M. A., Barboza, G. E., & Acosta, M. C. (2018). Evolutionary history of the chili pepper *Capsicum baccatum* L. (Solanaceae): Domestication in South America and natural diversification in the seasonally dry tropical forests. *Biological Journal of the Linnean Society*, 124(3), 466–478. <https://doi.org/10.1093/biolinnean/bly062>
- Smith, C. E. (1967). Plant remains. In D. S. Byes (Ed.), *The prehistoric history of the Tehuacan Valley, Vol. 1. Environment and subsistence* (pp. 220–225). Austin, TX: University of Texas Press.
- Smith, P. G., & Heiser, C. B. (1957). Taxonomy of *Capsicum chinense* Jacq. and the geographic distribution of the cultivated *Capsicum* species. *Bulletin of the Torrey Botanical Club*, 84, 413–420.
- Stolar, J., & Nielsen, S. E. (2015). Accounting for spatially biased sampling effort in presence-only species distribution modelling. *Diversity and Distributions*, 21(5), 595–608. <https://doi.org/10.1111/ddi.12279>
- Syfert, M. M., Smith, M. J., & Coomes, D. A. (2013). The effects of sampling bias and model complexity on the predictive performance of MaxEnt species distribution models. *PLoS ONE*, 8(2), e55158.
- Tai, T. H., Dahlbeck, D., Clark, E. T., Gajiwala, P., Pasion, R., Whalen, M. C., ... Staskawicz, B. J. (1999). Expression of the Bs2 pepper gene confers resistance to bacterial spot disease in tomato. *Proceedings of the National Academy of Sciences of the USA*, 96, 14153–14158. <https://doi.org/10.1073/pnas.96.24.14153>
- Tanksley, S. D., & McCouch, S. R. (1997). Seed banks and molecular maps: Unlocking genetic potential from the wild. *Science*, 277, 1063–1066. <https://doi.org/10.1126/science.277.5329.1063>
- Tewksbury, J. J., Nabhan, G. P., Norman, D., Suzan, H., Tuxill, J., & Donovan, J. (1999). In situ conservation of wild chiles and their biotic associates. *Conservation Biology*, 13, 98–107. <https://doi.org/10.1046/j.1523-1739.1999.97399.x>
- Tewksbury, J. J., Reagan, K. M., Machnicki, N. J., Carlo, T. A., Haak, D. C., Penalzoza, A. L. C., & Levey, D. J. (2008). Evolutionary ecology of pungency in wild chilies. *Proceedings of the National Academy of Sciences of the USA*, 105, 11808–11811. <https://doi.org/10.1073/pnas.0802691105>
- Thomas, E., Ramirez, M., van Zonneveld, M., van Etten, J., Alcazar, C., Beltran, M., ... Galluzzi, G. (2016). Assessment of the conservation status of Mesoamerican crop species and their wild relatives in light of climate change. In: N. Maxted et al. (Eds.), *Enhancing crop gene pool use: capturing wild relative and landrace diversity for crop improvement* (pp. 248–270). Oxfordshire (UK): CABI. ISBN: 978-1-78064-613-8.

- Tiffin, P., & Ross-Ibarra, J. (2014). Advances and limits of using population genetics to understand local adaptation. *Trends in Ecology and Evolution*, 29, 673–680. <https://doi.org/10.1016/j.tree.2014.10.004>
- Tong, N., & Bosland, P. W. (1999). *Capsicum tovarii*, a new member of the *Capsicum baccatum* complex. *Euphytica*, 109, 71–77.
- USDA ARS NPGS. (2018). GRIN Global Accessions. <https://npgsweb.ars-grin.gov/gringlobal/search.aspx>
- USDA ARS NPGS. (2019). GRIN Global Taxonomy, Crop Relatives in GRIN-Global Taxonomy. <https://npgsweb.ars-grin.gov/gringlobal/taxon/taxonomysearchcwr.aspx>
- van Zonneveld, M., Larranaga, N., Blonder, B., Coradin, L., Hormaza, J. I., & Hunter, D. (2018). Human diets drive range expansion of mega-fauna-dispersed fruit species. *Proceedings of the National Academy of Sciences*, 115, 3326–3331. <https://doi.org/10.1073/pnas.1718045115>
- van Zonneveld, M., Ramirez, M., Williams, D. E., Petz, M., Meckelmann, S., Avila, T., ... Scheldeman, X. (2015). Screening genetic resources of *Capsicum* peppers in their primary center of diversity in Bolivia and Peru. *PLoS ONE*, 10, e0134663. <https://doi.org/10.1371/journal.pone.0134663>
- Villalon-Mendoza, H., Medina-Martinez, T., Ramirez-Meraz, M., Solis Urbina, S. E., & Maiti, R. (2014). Factors influencing the price of chile piquin wild chili (*Capsicum annuum* L. var. *glabriusculum*) of north-east Mexico. *International Journal of Bio-resource and Stress Management*, 5, 128–131.
- Wall, M. M., & Bosland, P. W. (1998). Analytical methods for color and pungency of chiles (Capsicums). In D. Wetzler, & G. Charalambous (Eds.), *Instrumental methods in food and beverage analysis* (pp. 347–373). Amsterdam, The Netherlands: Elsevier B.V.
- Walsh, B. M., & Hoot, S. B. (2001). Phylogenetic relationships of *Capsicum* (Solanaceae) using DNA sequences from two noncoding regions: The chloroplast atpB-rbcL spacer region and the nuclear waxy introns. *International Journal of Plant Sciences*, 162, 1409–1418.
- World Wildlife Fund (WWF). (2019). Terrestrial Ecoregions. Spatial data Available at https://www.worldwildlife.org/biome-categories/terrestrial-ecoregionshttp://maps.tnc.org/gis_data.html
- Yoon, J. B., Yang, D. C., Do, J. W., & Park, H. G. (2006). Overcoming two post-fertilization genetic barriers in interspecific hybridizations between *Capsicum annuum* and *C. baccatum* for introgression of anthracnose resistance. *Breeding Science*, 56, 31–38.

BIOSKETCH

Colin K. Khoury received his PhD in production ecology and resource conservation from Wageningen University, and works at the USDA Agricultural Research Service, National Laboratory for Genetic Resources Preservation in Colorado, USA, at the International Center for Tropical Agriculture (CIAT), Colombia, and at Saint Louis University in Missouri, USA. His work generally entails bringing together diverse expertise to contribute to conservation strategies for crops and their wild relatives; develop Aichi Biodiversity Target, Sustainable Development Goal, and International Plant Treaty indicators; and support evidence-based decision-making in sustainable food systems. The co-authors on this article comprise biogeographers, genetic resource professionals, *Capsicum* taxonomists, horticulturalists and chile pepper breeders.

Author contributions: C.K.K., D.W.B. and S.L.G. conceived the research; C.K.K., D.C., G.E.B. and M.v.Z. compiled and processed input data, developed the methodologies, and performed the analyses; C.K.K., D.C., D.W.B., G.E.B., M.v.Z., R.J., L.B., M.K., M.U., K.M., G.P.N., P.W.B. and S.L.G. analysed the results; C.K.K. and D.W.B. wrote the article; and C.K.K., D.C., D.W.B., G.E.B., M.v.Z., R.J., L.B., M.K., M.U., K.M., G.P.N., P.W.B. and S.L.G. edited the article.

SUPPORTING INFORMATION

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

How to cite this article: Khoury CK, Carver D, Barchenger DW, et al. Modelled distributions and conservation status of the wild relatives of chile peppers (*Capsicum* L.). *Divers Distrib*. 2019;00:1–17. <https://doi.org/10.1111/ddi.13008>