

RESEARCH ARTICLE

Ex Situ Conservation Priorities for the Wild Relatives of Potato (*Solanum* L. Section *Petota*)

Nora P. Castañeda-Álvarez^{1,2*}, Stef de Haan³, Henry Juárez³, Colin K. Khoury^{1,4}, Harold A. Achicanoy¹, Chrystian C. Sosa¹, Vivian Bernau¹, Alberto Salas³, Bettina Heider³, Reinhard Simon⁵, Nigel Maxted², David M. Spooner⁶

1 Decision and Policy Analysis Program, International Center for Tropical Agriculture (CIAT), Cali, Colombia, **2** School of Biosciences, University of Birmingham, Birmingham, United Kingdom, **3** Global Program Genetic Resources, International Potato Center (CIP), Lima, Peru, **4** Centre for Crop Systems Analysis, Wageningen University, Wageningen, The Netherlands, **5** Integrated IT and Computational Research Unit, International Potato Center (CIP), Lima, Peru, **6** USDA-ARS, Vegetable Crop Research Unit, Department of Horticulture, University of Wisconsin, Madison, Wisconsin, United States of America

* n.p.castaneda@cgiar.org



OPEN ACCESS

Citation: Castañeda-Álvarez NP, de Haan S, Juárez H, Khoury CK, Achicanoy HA, Sosa CC, et al. (2015) *Ex Situ* Conservation Priorities for the Wild Relatives of Potato (*Solanum* L. Section *Petota*). PLoS ONE 10(4): e0122599. doi:10.1371/journal.pone.0122599

Received: October 24, 2014

Accepted: February 11, 2015

Published: April 29, 2015

Copyright: This is an open access article, free of all copyright, and may be freely reproduced, distributed, transmitted, modified, built upon, or otherwise used by anyone for any lawful purpose. The work is made available under the [Creative Commons CC0](https://creativecommons.org/licenses/by/4.0/) public domain dedication.

Data Availability Statement: Data are available within the paper and its Supporting Information files. The associated records with coordinates used as inputs for the analysis and in [Fig 2A](#) are available on Figshare: <http://dx.doi.org/10.6084/m9.figshare.1284187>.

Funding: This work was undertaken as part of the initiative "Adapting Agriculture to Climate Change: Conserving, Protecting and Preparing Crop Wild Relatives," which is supported by the Government of Norway. The project is managed by the Global Crop Diversity Trust with the Millennium Seed Bank of the Royal Botanic Gardens, Kew UK and implemented in partnership with national and international genebanks and plant breeding institutes around the world. For

Abstract

Crop wild relatives have a long history of use in potato breeding, particularly for pest and disease resistance, and are expected to be increasingly used in the search for tolerance to biotic and abiotic stresses. Their current and future use in crop improvement depends on their availability in *ex situ* germplasm collections. As these plants are impacted in the wild by habitat destruction and climate change, actions to ensure their conservation *ex situ* become ever more urgent. We analyzed the state of *ex situ* conservation of 73 of the closest wild relatives of potato (*Solanum* section *Petota*) with the aim of establishing priorities for further collecting to fill important gaps in germplasm collections. A total of 32 species (43.8%), were assigned high priority for further collecting due to severe gaps in their *ex situ* collections. Such gaps are most pronounced in the geographic center of diversity of the wild relatives in Peru. A total of 20 and 18 species were assessed as medium and low priority for further collecting, respectively, with only three species determined to be sufficiently represented currently. Priorities for further collecting include: (i) species completely lacking representation in germplasm collections; (ii) other high priority taxa, with geographic emphasis on the center of species diversity; (iii) medium priority species. Such collecting efforts combined with further emphasis on improving *ex situ* conservation technologies and methods, performing genotypic and phenotypic characterization of wild relative diversity, monitoring wild populations *in situ*, and making conserved wild relatives and their associated data accessible to the global research community, represent key steps in ensuring the long-term availability of the wild genetic resources of this important crop.

further information, go to the project website: <http://www.cwrdiversity.org/>. Funding was provided by the aforementioned initiative; the CGIAR Research Program on Roots, Tubers and Bananas; and the CGIAR Research Program on Climate Change, Agriculture, and Food Security in Cali, Colombia. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

Introduction

Potato (*Solanum tuberosum* L.) is the most important tuber crop worldwide, continuing to gain significance in temperate and tropical regions as a source of carbohydrates, vitamins, and minerals [1] as well as for industrial purposes [2]. The crop is susceptible to a wide range of biotic stresses, in particular fungal diseases and pests [3,4]. A relatively low historical influx of variation has led to a genetic bottleneck within potato cultivars [5–7], thus the development of potato varieties with novel genetic diversity is expected to improve resistance to biotic and abiotic constraints [8].

As one source of such variation, potato breeding programs have looked to related wild species [8–10]. Widely used and well documented sources of valuable traits such as frost and late blight (*Phytophthora infestans* (Mont.) de Bary) resistance include *S. acaule*, *S. bulbocastanum*, *S. chacoense*, *S. demissum* and *S. stoloniferum*. The search for late blight resistance has been a center point in the evaluation and use of wild relatives in potato breeding [11–15]. In addition, *S. commersonii* and *S. berthaultii* have been evaluated for bacterial wilt (*Ralstonia solanacearum* Smith) and verticillium wilt (*Verticillium* spp.) resistances, respectively [16–18]. Other species have been proposed as valuable sources of resistance, e.g., *S. acroglossum* for Colorado potato beetle (*Leptinotarsa decemlineata* Say), and *S. albicans* for cold sweetening [19,20] (Table 1).

Despite the extensive history of use of the wild relatives of potato in breeding, most species have not yet been evaluated for their potential for utilization. These include species from the eastern Andean slopes where resistance to late blight is particularly key for survival (e.g. *S. laxissimum* and *S. rhomboideilanceolatum*), as well as more distant relatives that may display drought resistance due to their adaptation to dry habitats (e.g. *S. immite* and *S. mochiquense*). Enhanced understanding of species reproductive biologies, advances in pre-breeding technologies to bypass reproductive barriers, improvements in cisgenic techniques, and the evolution of new genotyping and phenotyping platforms are likely make the use of wild relatives more attractive and efficient [45–49].

Table 1. Crop wild relatives that have been evaluated and/or used in potato breeding.

Genepool	Species	Resistance trait(s)	Reference
Primary	<i>S. acaule</i>	Biotic: <i>Nacobbus aberrans</i> . Abiotic: frost	[21–24]
	<i>S. berthaultii</i>	Biotic: <i>Erwinia carotovora</i> , <i>E. atroseptica</i> ; <i>Verticillium</i> wilt. Other: cold induced sweetening	[25–28]
	<i>S. brevicaulis</i>	Biotic: <i>Globodera</i> sp., <i>G. pallida</i> , virus	[22,29–31]
	<i>S. candolleianum</i>	Biotic: <i>Globodera</i> sp., <i>G. pallida</i> , <i>Erwinia carotovora</i> , <i>E. atroseptica</i>	[25,26,31]
	<i>S. vernei</i>	Biotic: virus, pest and nematode	[22,31,32]
Secondary	<i>S. boliviense</i>	Abiotic: frost	[33,34]
	<i>S. cajamarquense</i>	Biotic: <i>Phytophthora infestans</i>	[35]
	<i>S. chacoense</i>	Biotic: virus, pest, <i>Verticillium</i> wilt Other: cold induced sweetening	[27,28,30,36,37]
	<i>S. demissum</i>	Biotic: <i>Phytophthora infestans</i>	[36,38]
	<i>S. kurtzianum</i>	Biotic: <i>Globodera</i> sp.	[31]
	<i>S. paucisectum</i>	Biotic: <i>Phytophthora infestans</i>	[39]
	<i>S. raphanifolium</i>	Other: cold induced sweetening	[28]
	<i>S. stoloniferum</i>	Biotic: <i>Phytophthora infestans</i> , PVY	[32,36]
Tertiary	<i>S. bulbocastanum</i>	Biotic: <i>Phytophthora infestans</i>	[12,40,41]
	<i>S. commersonii</i>	Biotic: <i>Ralstonia solanacearum</i> . Abiotic: frost	[16,18,42]
	<i>S. palustre</i>	Biotic: PLRV	[43]
	<i>S. tarnii</i>	Biotic: PVY, <i>Leptinotarsa decemlineata</i> , <i>Phytophthora infestans</i>	[44]

doi:10.1371/journal.pone.0122599.t001

Species designations within the section *Petota*, where potato resides, have recently been revised on the basis of new molecular findings in combination with morphological studies [50–55]. The wild related species of potato have been organized into primary, secondary and tertiary gene pools according to the ease of crossability with the cultivated species [56,57]. These wild relatives constitute a morphologically and genetically diverse group of plants distributed from central Chile and Argentina to the southwestern United States. They occupy a variety of habitats within deserts, forests and mountainous regions [58] (Fig 1). Mexico, Bolivia, Argentina, and especially Peru are considered to possess the greatest total diversity of potato wild relatives, although high levels of endemism are reflected in unique species occurring in most of the total 16 countries where these wild relatives grow [58].

While CWR are likely to play a role in climate change adaptation of novel potato cultivars [59], a number of the wild relatives of cultivated potato are threatened due to habitat destruction and climate change [60–62]. It is therefore becoming more important to address gaps in the *ex situ* conservation of these plants, particularly for species that are currently underrepresented in genebanks and are most impacted in their native habitats.

Gap analysis is a systematic methodology for assessing the comprehensiveness of *ex situ* conservation of plant species, and for assigning taxonomic and geographic priorities for further collecting [63,64]. Gap analysis has been applied to the wild relatives of a wide range of crops, including grains, forages and legumes [57,64,65]. The analysis can also contribute to the identification of species and habitat priorities for complementary *in situ* conservation.

Here we assessed the current state of *ex situ* conservation of the wild relatives of potato through a gap analysis, in order to identify those species and geographic areas in need of conservation in order to assure their long-term availability for plant breeding efforts.

Materials and Methods

Wild relative species and geographic area of study

We assessed the closely related wild relatives of potato (i.e. primary and secondary gene pool wild relatives [66]), as well as any distant relatives in the third gene pool that have been reported with confirmed or potential uses in crop breeding (Table 2). We followed the most recent taxonomic revision of *Solanum* L. section *Petota* [55] (see also Solanaceae Source, <http://solanaceaesource.org/>), henceforth “Solanaceae Source taxonomy”. A complementary analysis was also performed following the taxonomy of Ochoa [67–69] (henceforth “CIP taxonomy”), in order to provide a gap analysis for the potato wild relative collection conserved as the International Potato Center (CIP), based on its current taxonomic classification (S1 Table). Our study focused on the native distributions of potato wild relatives, which occur in Argentina, Bolivia, Brazil, Chile, Colombia, Costa Rica, Ecuador, Guatemala, Honduras, Mexico, Panama, Paraguay, Peru, Uruguay, USA, and Venezuela [55].

Germplasm data were obtained from repositories that provide straightforward access to genetic resources and associated data to the global research community through online information systems (i.e. EURISCO -<http://eurisco.ipk-gatersleben.de/>, GRIN -<http://www.ars-grin.gov/> and CIP’s biomart portal -<http://germplasmdb.cip.cgiar.org/>-). Species presence records and additional germplasm accessions passport data were gathered from online databases and via communications with data managers (i.e. GBIF -<http://www.gbif.org/>-, CRIA -<http://smlink.cria.org.br/>-, SINGER, CPNWH -<http://www.pnwhherbaria.org/>-, the Atlas of Guatemalan Crop Wild Relatives [72], “PBI Solanum—a worldwide treatment”, “LAC biosafety”, CAS, F, FSU, H and MANCH), extracted from the literature [55], and through visits to herbaria (i.e. E, K, L, NY, MA, PH, RB and US). The occurrence data utilized in this analysis is available on <http://dx.doi.org/10.6084/m9.figshare.1284187>.



Fig 1. Flowers, plants and habitats of six potato wild relatives. A) *Solanum acaule*, B) *S. candolleianum*, C) *S. laxissimum*, D) *S. rhomboideilanceolatum*, E) *S. simplicissimum* and F) *S. wittmackii*. Photographs by S. de Haan. The author of the photographs has given written consent to publish them.

doi:10.1371/journal.pone.0122599.g001

Table 2. List of 73 species analyzed and their corresponding prioritization category, genepool, ploidy level, native areas and count of data retrieved for this study.

Species scientific name	Countries	Ploidy [70] and (EBN)[71]	Genepool	No. of reference samples (georeferenced)	No. of germplasm accessions (georeferenced)	SRS	GRS	ERS	FPS	FPCAT
<i>S. acaule</i> Bitter	ARG; BOL; PER; CHL	4x (2EBN), 6x	Primary	3058 (864)	1762 (521)	3.66	10.00	10.00	7.89	NFCR
<i>S. acroglossum</i> Juz.	PER	2x (2EBN)	Secondary	92 (23)	4 (4)	0.42	0.61	3.00	0.00	HPS
<i>S. acroscopicum</i> Ochoa	PER	2x	Secondary	93 (38)	11 (7)	1.06	0.90	6.36	2.77	HPS
<i>S. agrimonifolium</i> Rydberg	GTM; HND; MEX	4x (2EBN)	Secondary	345 (118)	40 (14)	1.04	6.48	4.21	3.91	MPS
<i>S. albicans</i> (Ochoa) Ochoa	ECU; PER	6x (4EBN)	Secondary	288 (73)	132 (40)	3.14	5.20	10.00	6.11	LPS
<i>S. albornozii</i> Correll	ECU	2x (2EBN)	Secondary	25 (7)	13 (8)	3.42	5.06	7.50	5.33	LPS
<i>S. andreanum</i> Baker	COL; ECU	2x (2EBN); 4x (4EBN)	Secondary	448 (234)	111 (71)	1.99	5.06	6.47	4.51	MPS
<i>S. ayacuchense</i> Ochoa	PER	2x (2EBN)	Secondary	10 (7)	0 (0)	0.00	0.00	0.00	0.00	HPS
<i>S. berthaultii</i> J. G. Hawkes	ARG; BOL	2x (2EBN), 3x	Primary	836 (292)	323 (116)	2.79	7.68	10.00	6.82	LPS
<i>S. boliviense</i> M. F. Dunal in DC.	BOL; PER; ARG	2x (2EBN)	Secondary	1724 (657)	388 (185)	1.84	8.00	10.00	6.61	LPS
<i>S. bombycinum</i> C. M. Ochoa	BOL	4x	Secondary	8 (6)	1 (1)	1.11	1.62	5.00	0.00	HPS
<i>S. brevicaule</i> Bitter	ARG; BOL; PER	2x (2EBN); 4x (4EBN); 6x (4EBN)	Primary	4428 (1477)	1159 (457)	2.07	10.00	10.00	7.36	LPS
<i>S. buesii</i> Vargas	PER	2x (2EBN)	Secondary	63 (32)	6 (4)	0.87	0.24	2.73	0.00	HPS
<i>S. bulbocastanum</i> Dunal in Poiret	GTM; MEX	2x (1EBN), 3x	Tertiary	970 (399)	175 (47)	1.53	6.20	10.00	5.91	LPS
<i>S. burkartii</i> Ochoa	PER	2x	Secondary	88 (18)	7 (5)	0.74	6.09	8.33	0.00	HPS
<i>S. cajamarquense</i> Ochoa	PER	2x (1EBN)	Secondary	223 (39)	16 (8)	0.67	1.06	6.00	2.58	HPS
<i>S. candolleianum</i> Berthault	PER; BOL	2x (2EBN), 3x	Primary	2910 (1245)	739 (349)	2.03	10.00	9.17	7.06	LPS
<i>S. cantense</i> Ochoa	PER	2x (2EBN)	Secondary	155 (68)	3 (3)	0.19	0.93	3.75	0.00	HPS
<i>S. chacoense</i> Bitter	ARG; BOL; PRY; PER; URY; BRA	2x (2EBN), 3x	Secondary	2527 (1004)	710 (119)	2.19	1.94	5.52	3.22	MPS
<i>S. chilliasense</i> Ochoa	ECU	2x (2EBN)	Secondary	15 (7)	5 (4)	2.50	10.00	10.00	0.00	HPS
<i>S. chiquidenum</i> Ochoa	PER	2x (2EBN)	Secondary	360 (148)	17 (11)	0.45	3.27	7.00	3.57	MPS
<i>S. chomatophilum</i> Bitter	PER; ECU	2x (2EBN)	Secondary	967 (378)	124 (55)	1.14	6.54	8.33	5.34	LPS
<i>S. clarum</i> D. S. Correll	GTM; MEX	2x	Secondary	244 (92)	6 (4)	0.24	3.69	2.78	0.00	HPS
<i>S. colombianum</i> Dunal	COL; ECU; PAN; VEN	4x (2EBN)	Secondary	1116 (444)	214 (105)	1.61	6.47	9.14	5.74	LPS
<i>S. commersonii</i> M. F. Dunal	ARG; BRA; URY	2x (1EBN), 3x	Tertiary	692 (272)	112 (30)	1.39	2.14	5.83	3.12	MPS
<i>S. contumazaense</i> Ochoa	PER	2x (2EBN)	Secondary	21 (13)	2 (2)	0.87	5.26	6.67	0.00	HPS
<i>S. demissum</i> Lindley	GTM; MEX	6x (4EBN)	Secondary	1669 (513)	613 (85)	2.69	8.30	10.00	6.99	LPS

(Continued)

Table 2. (Continued)

Species scientific name	Countries	Ploidy [70] and (EBN)[71]	Genepool	No. of reference samples (georeferenced)	No. of germplasm accessions (georeferenced)	SRS	GRS	ERS	FPS	FPCAT
<i>S. flahaultii</i> Bitter	COL	4x	Secondary	99 (37)	39 (10)	2.83	2.66	3.75	3.08	MPS
<i>S. gandarrillasii</i> H. M. Cárdenas	BOL	2x (2EBN)	Secondary	48 (28)	21 (7)	3.04	3.72	7.14	4.64	MPS
<i>S. garcia-barrigae</i> Ochoa	COL	4x	Secondary	21 (10)	3 (2)	1.25	0.52	1.90	0.00	HPS
<i>S. gracilifrons</i> Bitter	PER	2x	Secondary	19 (8)	1 (1)	0.50	1.47	3.75	0.00	HPS
<i>S. guerreroense</i> D. S. Correll	MEX	6x (4EBN)	Secondary	4 (2)	20 (2)	8.33	10.00	10.00	9.44	NFCR
<i>S. hastiforme</i> Correll	PER	2x (2EBN)	Secondary	49 (32)	2 (2)	0.39	0.38	4.00	0.00	HPS
<i>S. hintonii</i> D. S. Correll	MEX	2x	Secondary	39 (18)	0 (0)	0.00	0.00	0.00	0.00	HPS
<i>S. hjertingii</i> J. G. Hawkes	MEX	4x (2EBN)	Secondary	155 (62)	54 (10)	2.58	1.93	4.00	2.84	HPS
<i>S. hougasii</i> D. S. Correll	MEX	6x (4EBN)	Secondary	186 (79)	39 (10)	1.73	2.12	3.68	2.51	HPS
<i>S. huancabambense</i> Ochoa	PER	2x (2EBN)	Secondary	111 (28)	29 (10)	2.07	2.07	5.56	3.23	MPS
<i>S. incasicum</i> Ochoa	PER	2x (2EBN)	Secondary	9 (5)	2 (2)	1.82	10.00	5.00	0.00	HPS
<i>S. infundibuliforme</i> R. A. Philippi	ARG; BOL	2x (2EBN)	Primary	836 (277)	234 (116)	2.19	4.71	7.78	4.89	MPS
<i>S. iopetalum</i> (Bitter) J. G. Hawkes	MEX	6x (4EBN)	Secondary	626 (313)	93 (51)	1.29	5.23	7.50	4.67	MPS
<i>S. kurtzianum</i> Bitter & L. Wittmack	ARG	2x (2EBN)	Secondary	764 (253)	276 (32)	2.65	4.02	8.75	5.14	LPS
<i>S. laxissimum</i> Bitter	PER	2x (2EBN)	Secondary	139 (91)	19 (10)	1.20	1.73	5.00	2.64	HPS
<i>S. lesteri</i> J. G. Hawkes & Hjerting	MEX	2x	Secondary	23 (12)	12 (4)	3.43	4.22	4.44	4.03	MPS
<i>S. limbaniense</i> Ochoa	PER	2x (2EBN)	Secondary	56 (28)	12 (7)	1.76	1.18	5.00	2.65	HPS
<i>S. lobbianum</i> Bitter	COL	4x (2EBN)	Secondary	1 (1)	4 (1)	8.00	NA	NA	0.00	HPS
<i>S. longiconicum</i> Bitter	CRI; PAN	4x	Secondary	546 (198)	25 (12)	0.44	10.00	10.00	6.81	LPS
<i>S. maglia</i> D. F. L. von Schlechtendal	CHL; ARG	2x, 3x	Secondary	190 (51)	15 (4)	0.73	0.14	1.33	0.74	HPS
<i>S. medians</i> Bitter	PER; CHL	2x (2EBN), 3x	Secondary	849 (305)	98 (35)	1.03	4.32	4.44	3.27	MPS
<i>S. microdontum</i> Bitter	ARG; BOL	2x (2EBN), 3x	Secondary	1178 (349)	422 (94)	2.64	6.25	9.09	5.99	LPS
<i>S. morelliforme</i> Bitter & Muench	GTM; MEX; HND	2x	Secondary	364 (140)	45 (18)	1.10	4.74	6.55	4.13	MPS
<i>S. multiinterruptum</i> Bitter	PER	2x (2EBN), 3x	Secondary	496 (204)	95 (45)	1.61	7.33	8.75	5.90	LPS
<i>S. neocardenasii</i> J. G. Hawkes & J. P. Hjerting	BOL	2x	Secondary	25 (17)	17 (5)	4.05	0.56	3.64	2.75	HPS
<i>S. neorossii</i> J. G. Hawkes & J. P. Hjerting	ARG	2x	Secondary	76 (35)	45 (14)	3.72	4.17	10.00	5.96	LPS
<i>S. neovavilovii</i> Ochoa	BOL	2x (2EBN)	Secondary	26 (13)	0 (0)	0.00	0.00	0.00	0.00	HPS
<i>S. nubicola</i> Ochoa	PER	4x (2EBN)	Secondary	36 (20)	2 (2)	0.53	0.70	5.45	0.00	HPS
<i>S. okadae</i> J. G. Hawkes & J. P. Hjerting	BOL	2x	Primary	139 (55)	75 (19)	3.50	1.08	7.14	3.91	MPS
<i>S. olmosense</i> Ochoa	ECU; PER	2x (2EBN)	Secondary	26 (15)	0 (0)	0.00	0.00	0.00	0.00	HPS
<i>S. oxycarpum</i> Schiede in D. F. L. von Schlechtendal	MEX	4x (2EBN)	Secondary	203 (77)	58 (20)	2.22	2.45	7.93	4.20	MPS

(Continued)

Table 2. (Continued)

Species scientific name	Countries	Ploidy [70] and (EBN)[71]	Genepool	No. of reference samples (georeferenced)	No. of germplasm accessions (georeferenced)	SRS	GRS	ERS	FPS	FPCAT
<i>S. paucissectum</i> Ochoa	PER	2x (2EBN)	Secondary	182 (20)	20 (10)	0.99	10.00	10.00	7.00	LPS
<i>S. pillahuatense</i> Vargas	PER	2x (2EBN)	Secondary	15 (11)	1 (1)	0.63	10.00	10.00	0.00	HPS
<i>S. piurae</i> Bitter	PER	2x (2EBN)	Secondary	226 (38)	17 (7)	0.70	0.47	3.00	1.39	HPS
<i>S. polyadenium</i> Greenman	MEX	2x	Secondary	286 (97)	99 (14)	2.57	3.52	8.13	4.74	MPS
<i>S. raphanifolium</i> Cárdenas & Hawkes	PER	2x (2EBN)	Secondary	597 (206)	220 (69)	2.69	6.52	8.57	5.93	LPS
<i>S. rhomboideilanceolatum</i> Ochoa	PER	2x (2EBN)	Secondary	99 (46)	7 (3)	0.66	1.04	6.67	0.00	HPS
<i>S. salasianum</i> Ochoa	PER	2x	Secondary	13 (7)	0 (0)	0.00	0.00	0.00	0.00	HPS
<i>S. schenckii</i> Bitter	MEX	6x (4EBN)	Secondary	105 (37)	49 (13)	3.18	2.45	6.80	4.14	MPS
<i>S. sogarandinum</i> Ochoa	PER	2x (2EBN), 3x	Secondary	157 (81)	27 (13)	1.47	3.22	6.67	3.79	MPS
<i>S. stoloniferum</i> D. F. L. von Schlechtendal	MEX; USA	4x (2EBN)	Secondary	3807 (1464)	1582 (314)	2.94	10.00	10.00	7.65	NFCR
<i>S. tarnii</i> J. G. Hawkes & Hjerting	MEX	2x	Tertiary	68 (31)	45 (10)	3.98	2.58	4.62	3.73	MPS
<i>S. venturii</i> J. G. Hawkes & J. P. Hjerting	ARG	2x (2EBN)	Secondary	165 (62)	39 (6)	1.91	0.47	4.44	2.28	HPS
<i>S. vernei</i> Bitter & L. Wittmack	ARG	2x (2EBN)	Primary	429 (122)	261 (47)	3.78	2.46	8.89	5.04	LPS
<i>S. verrucosum</i> D. F. L. von Schlechtendal	MEX	2x (2EBN), 3x, 4x	Secondary	968 (378)	222 (36)	1.87	6.56	5.91	4.78	MPS
<i>S. violaceimarmoratum</i> Bitter	BOL; PER	2x (2EBN)	Secondary	234 (104)	61 (16)	2.07	0.98	2.86	1.97	HPS

SRS: Sampling Representativeness Score., GRS: Geographical Representativeness Score., ERS: Environmental Representativeness Score., FPS: Final priority score., FPCAT: Final priority category., HPS = high priority species, MPS = medium priority species, LPS = low priority species, and NFCR = 'no further collecting required' (NFCR). ARG: Argentina, BOL: Bolivia, BRA: Brazil, CHL: Chile, COL: Colombia, CRI: Costa Rica, ECU: Ecuador, GTM: Guatemala, HND: Honduras, MEX: Mexico, PAN: Panama, PER: Peru, PRY: Paraguay, URY: Uruguay, USA: United States of America and VEN: Venezuela.

doi:10.1371/journal.pone.0122599.t002

Environmental niche modelling

Environmental niche modelling (ENM) techniques were used to estimate the potential geographic distribution of each wild potato species. MaxEnt [73] was selected as the modelling algorithm due to its performance when compared with other modelling approaches, and to its wide use in conservation analyses [74–76]. Ten thousand random points were used as background records across Central and South America, the native range of the wild relatives. A five-fold cross-validation option (k = 5) was implemented to maximize the use of small sets of georeferenced records in the modelling, producing five replicates per species, subsequently summarized into a single ensemble model by estimating the mean values across the replicates. The models were restricted to their known native countries per species as reported in the literature [55], and further refined using a species-specific threshold corresponding to the shortest distance to the upper left corner of the Receiver Operating Characteristic (ROC) curve [77].

For environmental drivers, we used 19 bioclimatic variables (S2 Table) derived from the WorldClim database [78] at a resolution of 2.5 arc-minutes (approx. 5 km at the equator).

The performance of each ENM was assessed to determine its suitability for use in the gap analysis. Three parameters were checked: (i) the 5-fold average Area Under the Test ROC Curve (ATAUC), (ii) the standard deviation of the ATAUC for the 5 different folds, and (iii) the proportion of potential distribution where the standard deviation is greater than 0.15 (ASD15). A suitable model had to meet these conditions: $ATAUC > 0.7$, $STAUC < 0.15$ and $ASD15 < 10\%$ [64]. In those cases where a suitable niche model was not produced (either due to lack of data or low performance of the ensemble model), a convex hull (polygon surrounding the outermost georeferenced points) was prepared.

Gap analysis

We used a gap analysis methodology [63,64] including three metrics to determine the urgency of collecting wild relatives for conservation *ex situ*. A Sampling Representativeness Score (SRS) compared the number of germplasm accessions to the total number of samples (germplasm plus species presence records, with or without geographic coordinates), giving a general overview of the sufficiency of accessions per species. A Geographic Representativeness Score (GRS) compared the ENMs of the species to the geographic distribution of existing germplasm accession collecting sites, estimated by creating circular buffers of 50 km (CA50) around each site where the accession was collected [79], in order to assess the geographic coverage of germplasm collections. An Ecosystem Representativeness Score (ERS) assessed the number of ecosystems currently represented in *ex situ* collections (CA50 of germplasm collections), in comparison to the total number of ecosystems distributed within the ENMs of species. For this, a world terrestrial ecoregions map was used to determine the ecosystem units [80]. The three gap analysis metrics were given equal weight and an average was calculated to obtain a Final Priority Score (FPS). Four categories were employed to assign priority for further collecting for *ex situ* conservation: high priority species (HPS) when $FPS \leq 3$, or when ten or less accessions were recorded in germplasm collections; medium-priority species (MPS) when $3 < FPS \leq 5$; low priority species (LPS) when $5 < FPS \leq 7.5$; and 'no further collecting of germplasm required' (NFCR) when $7.5 < FPS \leq 10$.

The gap analysis was performed using R v2.15.1 [81], and the packages *maptools* [82], *rgdal* [83], *SDMTools* [84], *raster* [85], *sp* [86,87], *dismo* [88] and *ggplot2* [89].

Identification of geographic areas of priority for further collecting

Maps highlighting areas identified as priorities for further collecting (collecting gaps) were prepared for each species by subtracting the existing germplasm CA50 buffers from the ENMs. For those species where a niche model was not produced, CA50 buffers were prepared around all presence records, with germplasm CA50 buffers subtracted from these representations of the distribution of species. Collecting gap maps for all high priority species were analyzed using the "Zonal Statistics" tool in ArcMap 10.1 to produce a count of species in need of further collecting per country.

Results

Wild relative species and geographic area of study

Seventy-three species were included in the analysis as relatively close relatives of potato (i.e. members of the primary and secondary genepools [66] or due to published actual or potential use in breeding efforts). These included seven species from the primary genepool of potato, 63

from the secondary gene pool, and three tertiary gene pool species with reported use in crop improvement (Table 2). Almost half of the species analyzed are diploids with an endosperm balance number of 2 (2 EBN), followed by tetraploids (2 EBN and 4 EBN) and hexaploids (4 EBN) [71]. For the complementary gap analysis, following the CIP taxonomy, a total of 187 putative species were analyzed, equivalent to the 73 Solanaceae Source taxonomy species [55] (S1 Table). A total of 49,164 records for the 73 potato wild relatives were gathered (75.76% with coordinates), with 11,100 germplasm accessions and 37,251 presence records, including herbarium references, inactive germplasm accessions, and field sighting recordings (Fig 2A).

Environmental niche modelling

The environmental niche models of 75 species (89%) met the parameters used to consider an ENM suitable for use in the gap analysis. For the remaining eight species (*S. chilliasense*, *S. guerreroense*, *S. incasicum*, *S. lobbianum*, *S. neovavilovii*, *S. olmosense*, *S. paucisectum*, and *S. pillahuatense*), convex hulls were prepared and used in the gap analysis, as the ENM replicates produced were highly variable and did not comply with the ASD15 condition. Potato crop wild relative species richness was found to be highest in Peru, followed by Mexico and Argentina (Fig 2B, S1 File).

Occurrence data, ENMs and the collecting priorities maps for the species analyzed, following the Solanaceae Source taxonomy, are available in an interactive format at <http://www.cwrdiversity.org/distribution-map/>.

Gap analysis

The gap analysis for the 73 species resulted in the assignment of 32 HPS, 20 MPS, 18 LPS and 3 NCFR (Table 2). There are no germplasm accessions currently available for *S. ayacuchense*, *S. neovavilovii*, *S. olmosense* and *S. salasianum*, and these species therefore represent the greatest urgency for further collecting. All HPS belong to the secondary gene pool (Fig 3).

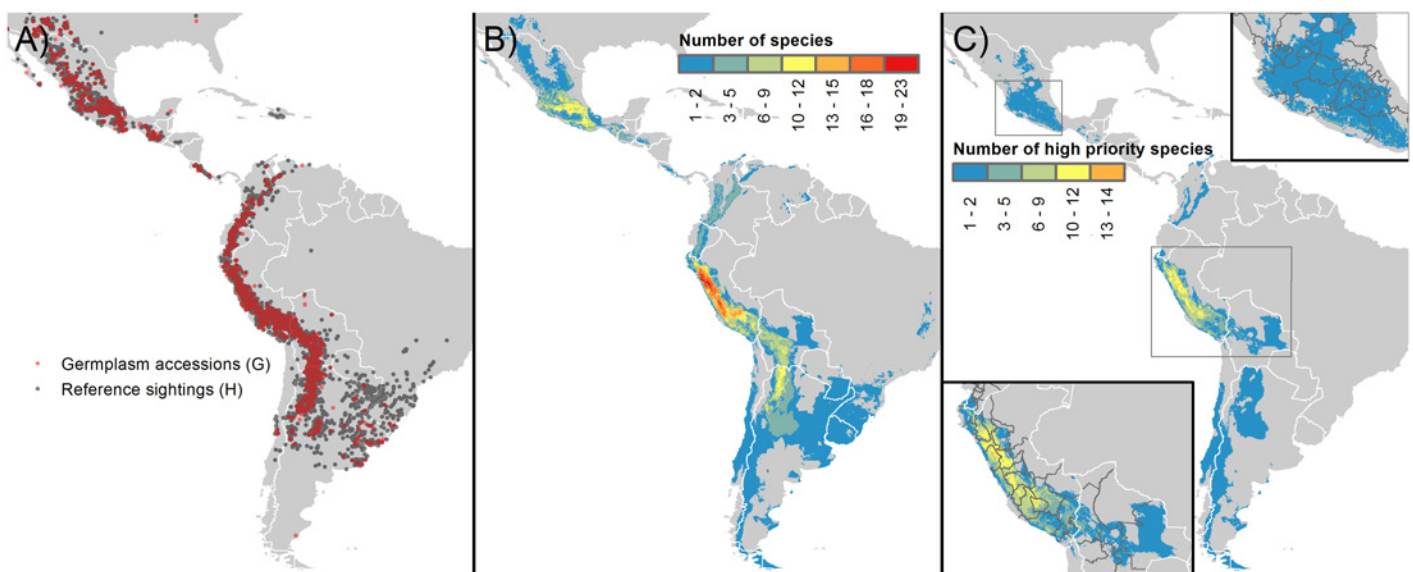


Fig 2. Distribution of the wild relatives of potato and hotspots for collecting. A) Distribution of germplasm and herbarium records included in the analysis. Red dots represent germplasm accessions (G) and dark gray dots herbarium/presence records (H). B) Species richness based upon environmental niche models, and C) Potential hotspots for further collecting of high priority species (HPS).

doi:10.1371/journal.pone.0122599.g002

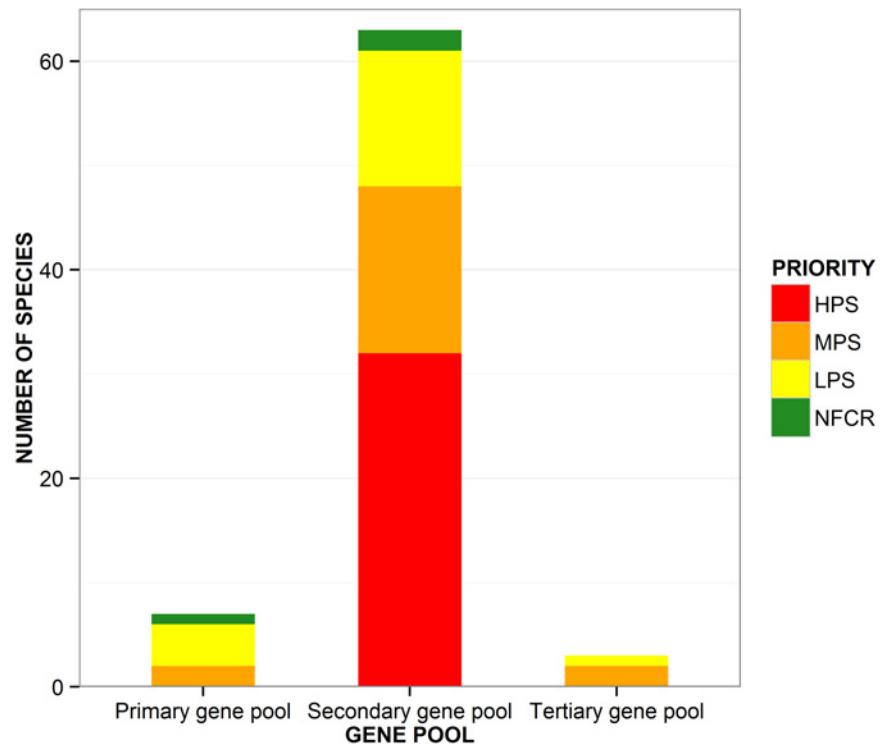


Fig 3. Potato wild relatives' priorities for further collecting by gene pool. Categories are: high priority species (HPS), medium priority species (LPS), low priority species (LPS), and 'no further collecting required' (NFCR).

doi:10.1371/journal.pone.0122599.g003

Solanum neocardenasii and *S. lobbianum* possessed a single dominant factor contributing to their priority category assignment for further collecting. All other species possessed two (40.6% of the species), three (28.1%) or four (28.1%) factors contributing importantly to their FPS status (S3 Table). Ninety-four percent of the species classified as HPS had a low SRS (SRS equal or less than 3) [median (mean) = 0.73 (1.22)] (Fig 4A, S1 Fig). Likewise, 78.1% of HPS exhibited a low GRS [0.930 (2.07)] (S1 Fig), with five species well represented (*S. candolleianum*, *S. brevicaulis*, *S. stoloniferum* and *S. acaule*), as shown in Fig 4B, where the dashed line is the complete representativeness line, and the continuous line is the average representativeness line, the former showing an ideal scenario where the potential geographic extension of the gene pool is completely represented at genebank collections and the latter showing the extent of representativeness compared to the potential extent of the gene pool. On the other hand, the ERS contributed less to the FPS of high priority species, with less than half (37.5%) of the HPS exhibiting an ERS ≤ 3 [median value 3.75 (4.01)] (Fig 4, S1 Fig). A total of 65.6% of the species ranked as high priority had less than ten active accessions and consequently very limited representativeness in terms of absolute numbers of accessions available in germplasm collections.

A total of 31 HPS were mapped together for targeting of geographic hotspots for further collecting (Fig 2C, S2 File). Peru contained the highest count of HPS for further collecting (21 species), followed by Mexico (4); Bolivia (3); Colombia (2), Ecuador (2) and Argentina, Chile and Guatemala (each with 1 species) (Fig 2C). Twenty-eight species (out of 32) were found to be endemic to a single country (Fig 5). The greatest concentrations of species requiring further collecting were predicted to occur in the Peruvian Departments of Cajamarca, La Libertad, Ancash and Huánuco. S4 Table provides an overview of sites recommended for further collecting of high priority species based on their presence points.

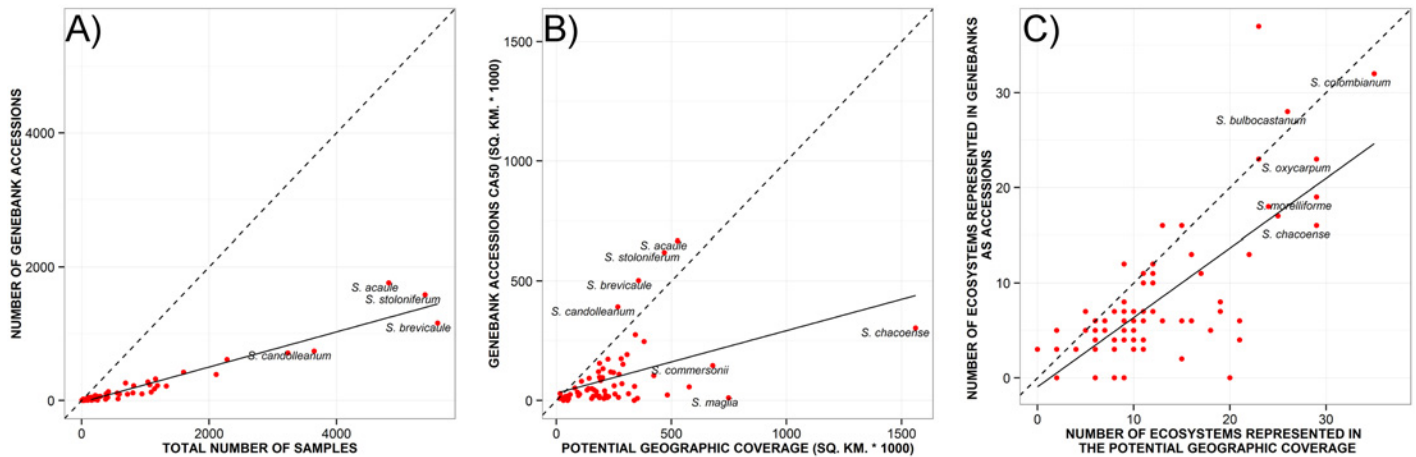


Fig 4. Gap analysis metrics. A) Sampling Representativeness Score (SRS), B) Geographic Representativeness Score (GRS), and C) Ecosystem Representativeness Score (ERS) gap analysis metrics for potato wild relatives. Red dots represent results per species. Dashed lines represent complete representativeness in *ex situ* conservation systems. A linear regression (continuous lines) depicts the mean trend for the genepool.

doi:10.1371/journal.pone.0122599.g004

A total of 18 species were assessed as MPS for further collecting, and are distributed in: Argentina (1 species), Bolivia (2), Colombia (1), Ecuador (2), Guatemala (2), Mexico (8), Peru (5), Honduras (2), Paraguay (1), Uruguay (1) and Brazil (1) (Fig 6).

The restricted range and endemic nature of many of the insufficiently collected taxa implies that targeted collecting trips to specific regions outside the gap richness areas are needed in order to form comprehensive germplasm collections for potato wild relatives. Some of the HPS species are known to occur in threatened habits, requiring urgent attention; e.g. *S. rhomboideilanceolatum* (Fig 1D) and *S. piurae*. Other species, such as *S. laxissimum* (Fig 1C) and *S. neovavilovii*, occur in relatively intact natural areas or within the boundaries of national parks and can thus be expected to be more secure. Active monitoring of these species in the wild can provide greater assurance of continued conservation in these areas.

Discussion

With 32 species classified as high priority and another 20 as medium priority for collecting, it is evident that further conservation action is needed to safeguard the wild genetic resources of this globally important crop. We propose three levels of priority for further collecting: first for the four HPS species that are completely lacking from internationally available genebank collections (*S. ayacuchense*, *S. neovavilovii*, *S. olmosense* and *S. salasianum*); second for the other 28 HPS species occurring in a total of eight countries; and third for the MPS.

In addition to gap filling for *ex situ* collections, the results can help establish priorities for the establishment of genetic reserves for the *in situ* conservation of potato wild relatives. Such reserves may most effectively be established at sites where several HPS and/or MPS overlap, especially if coinciding with existing protected areas. Habitats undergoing significant disturbance may also represent high priorities for consideration for *in situ* conservation efforts.

Some of the HPS display very restricted distributions and are considered to be threatened *in situ*. The limited habitat of *S. rhomboideilanceolatum* in Peru is increasingly exposed to road building and overgrazing by livestock (field observation by the authors, 2013). Yet other HPS with restricted distributions, such as *S. bombycinum* in Bolivia, are reported to grow in habitats that are not presently highly exposed to threats [62], while additional species with relatively extensive ranges such as *S. laxissimum* in Peru show considerable spatial overlap with protected

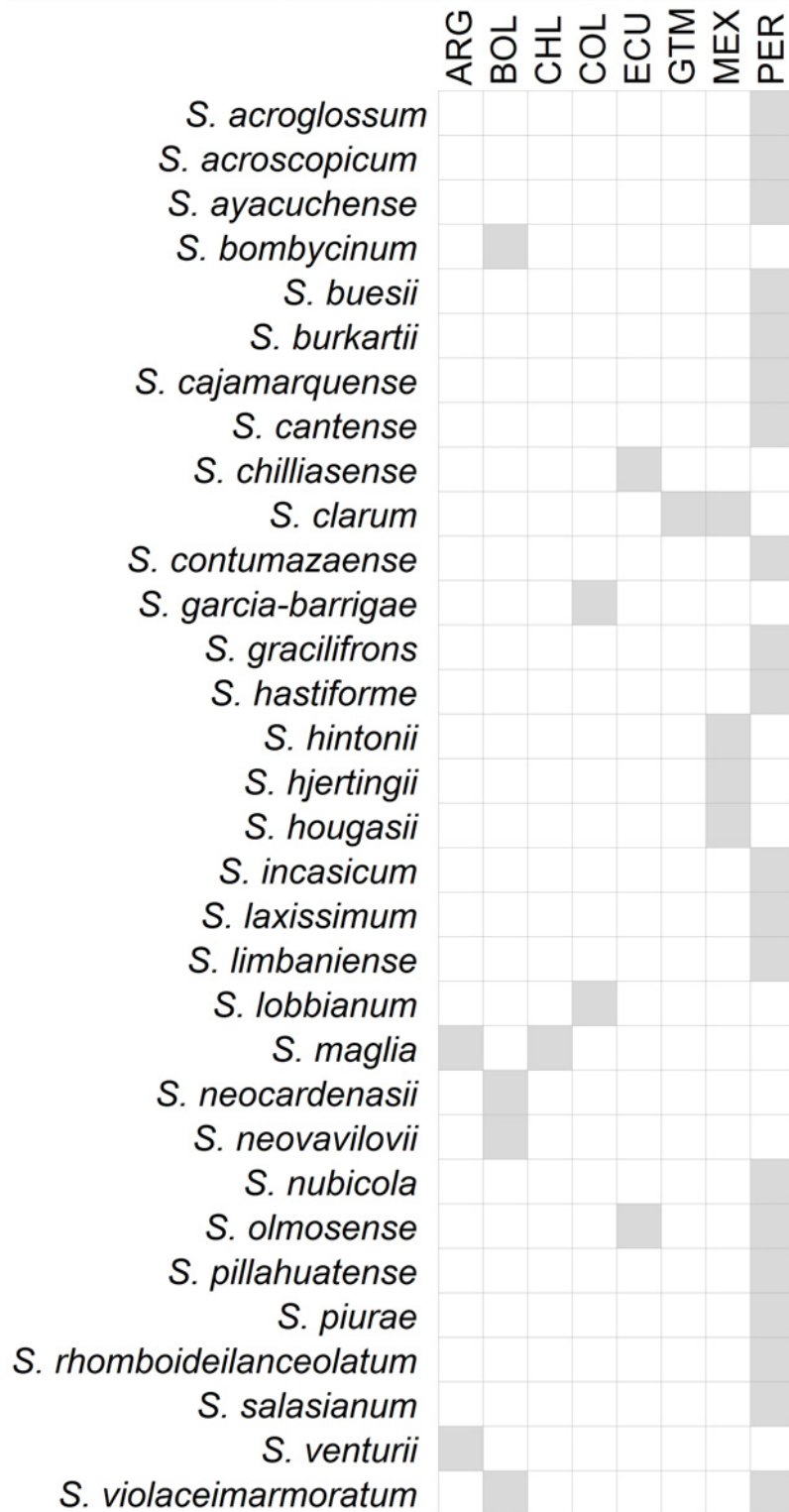


Fig 5. Countries identified for potential further collecting per high priority crop wild relative species.
 ARG: Argentina, BOL: Bolivia, CHL: Chile, COL: Colombia, ECU: Ecuador, GTM: Guatemala, MEX: Mexico, PER: Peru.

doi:10.1371/journal.pone.0122599.g005

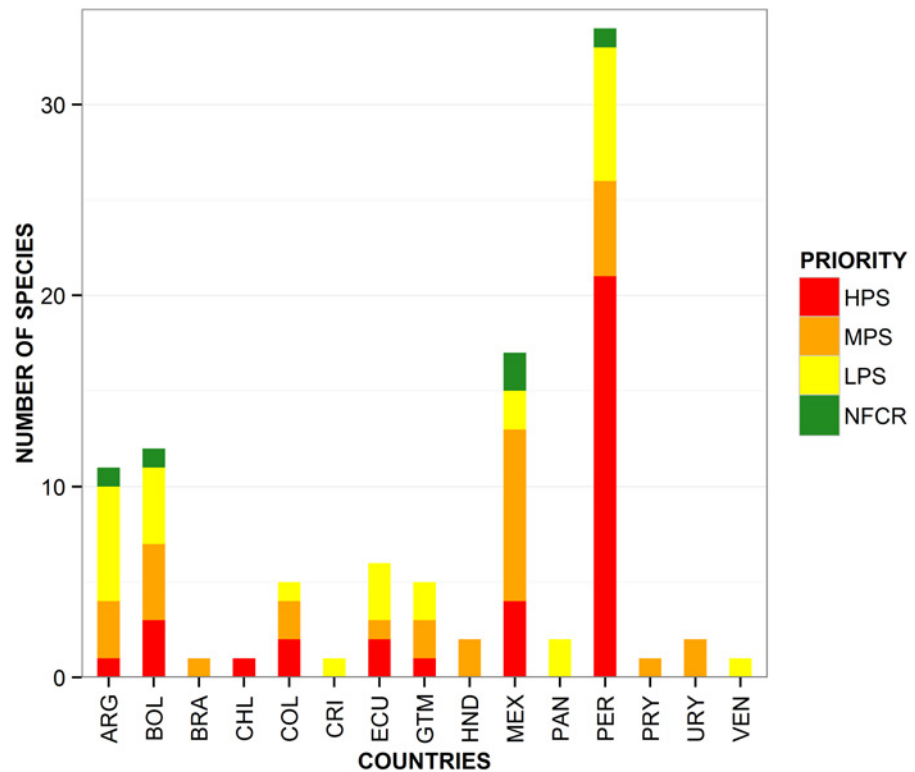


Fig 6. Number of CWR species prioritized for further collecting per country. HPS = high priority species, MPS = medium priority species, LPS = low priority species, and NFCR = 'no further collecting required' (NFCR). ARG: Argentina, BOL: Bolivia, BRA: Brazil, CHL: Chile, COL: Colombia, CRI: Costa Rica, ECU: Ecuador, GTM: Guatemala, HND: Honduras, MEX: Mexico, PAN: Panama, PER: Peru, PRY: Paraguay, URY: Uruguay and VEN: Venezuela.

doi:10.1371/journal.pone.0122599.g006

areas. Factors such as threats to the *in situ* conservation of wild populations, overlap with protected areas, and degree of endemism can further refine collecting priorities. Monitoring the population dynamics, ecology and genetics of selected species to corroborate the effect of climate change and other threats to wild relatives also represent useful contributions to conservation planning [90]. Such studies can help to ground-truth climate change forecasts and to enhance the understanding of the adaptive capacity of wild relatives.

Many of the taxa classified as generally well conserved (LPS and NFCR) are those that are widely used in breeding programs, such as *S. bulbocastanum* and *S. stoloniferum*. This is a logical consequence of demand from such programs. It is anticipated that demand for as yet underutilized species will increase as potato breeding efforts expand the use of wide diversity in order to confront emerging biotic and abiotic stresses.

Our results assign a relatively large number of species from Peru to the category of high priority for further collecting. This may seem surprising given the long history of collecting missions in the center of species diversity. Sampling biases relative to road systems, time limitations of collecting missions and the tendency of collectors to sample in areas of previous expeditions have been reported [58,91]. The high levels of endemism, and difficult access to some of the areas where HPS potato wild relatives occur provide further insight into the low level of representation of a number of these species in genebanks. New roads in Peru in previously isolated and remote habitats will soon make these populations increasingly accessible for collecting but at the same time more vulnerable to habitat destruction.

Long-term conservation of the genetic diversity of wild relatives of potato will also require further research in population genetics and reproductive biology of the species [92]. Gap filling of the taxa identified here as critically under-represented in germplasm collections will provide an important step in making germplasm available for such analyses. Future studies should incorporate morphological and molecular analyses in order to elucidate the diversity and genetic distances within and between populations of wild relatives as well as between genebank collections and *in situ* reserves [93–95]. Genetic variability encountered within natural populations of CWR has been described in few cases [96,97] but has not generally been taken into account when planning collecting expeditions for wild relatives [98]. Further taxonomic research may also be useful. The complementary gap analysis following the CIP taxonomy displayed differences in resulting priorities for further collecting (S2 Fig), and may reveal potentially useful infraspecific variation for further exploration, as some of the species in CIP taxonomy may represent unique subpopulations within the Solanaceae Source taxonomy.

The collecting priorities identified here, combined with further emphasis on improving *ex situ* conservation technologies and associated data management, performing genotypic and phenotypic characterization of wild relative diversity, monitoring wild populations *in situ*, and making conserved wild relatives and their associated data accessible to the global research community, represent key steps in ensuring the long-term availability of the wild genetic resources of this critically important crop.

Supporting Information

S1 Fig. Boxplots showing the values obtained for the Gap Analysis metrics. Sampling Representativeness Score (SRS), Geographic Representativeness Score (GRS) and Ecosystem Representativeness Score (ERS), ordered by high priority species (HPS), medium priority species (MPS), low priority species (LPS), and ‘no further collecting required’ (NFCR). (TIFF)

S2 Fig. Share of species per prioritization category by taxonomic classification system. High priority species (HPS), medium priority species (LPS), low priority species (LPS), and ‘no further collecting required’ (NFCR). (TIFF)

S1 File. Species richness map for further exploration in Google Earth. (ZIP)

S2 File. Potential hotspots for further collecting of high priority species (HPS) for further exploration in Google Earth. (ZIP)

S1 Table. List of 172 species following CIP taxonomy, its equivalences in Solanaceae Source Taxonomy [55] and the prioritization category obtained through the gap analysis. SRS: Sampling Representativeness Score, GRS: Geographical Representativeness Score, ERS: Environmental Representativeness Score, FPCAT: Final priority category. (DOCX)

S2 Table. List of bioclimatic variables [99] used as environmental drivers to produce environmental niche models. C.V.: coefficient of variation (DOCX)

S3 Table. High priority species for further collecting and the main factors contributing to insufficient representation in germplasm collections.

(DOCX)

S4 Table. List of regions and localities where further collecting may be targeted per species.

(DOCX)

Acknowledgments

We thank the institutions and researchers that provided taxonomic and geographic inputs that made this analysis possible, María Andrea Orjuela Restrepo, Tiina Särkinen and Sandy Knapp for providing occurrence records, Julián Ramírez-Villegas for facilitating occurrence records and providing methodological advice, the curators from E, K, L, NY, MA, PH, RB and US for allowing the consultation of herbaria specimens, and Shirley Calderón, Alex Castañeda, Ovidio Rivera, and Ingrid Vanegas, for gathering and organizing occurrence data.

Author Contributions

Conceived and designed the experiments: NPC-A SdH CKK HJ NM. Performed the experiments: NPC-A HJ CKK HAA CCS VB. Analyzed the data: NPC-A SdH HJ CKK HAA CCS VB AS BH RS NM DMS. Wrote the paper: NPC-A SdH. Edited the manuscript: NPC-A SdH HJ CKK AS BH RS NM DMS.

References

1. Khoury CK, Bjorkman AD, Dempewolf H, Ramirez-Villegas J, Guarino L, Jarvis A, et al. Increasing homogeneity in global food supplies and the implications for food security. *Proc Natl Acad Sci*. 2014; 111: 4001–4006. doi: [10.1073/pnas.1313490111](https://doi.org/10.1073/pnas.1313490111) PMID: [24591623](https://pubmed.ncbi.nlm.nih.gov/24591623/)
2. Kraak A. Industrial applications of potato starch products. *Ind Crops Prod*. 1992; 1: 107–112.
3. Stevenson W, Loria R, Franc GD, Weingartner DP. *Compendium of potato diseases*. 2nd ed. St Paul, USA: American Phytopathological Society Press; 2001.
4. Wale SJ, Platt HW, Cattlin ND. *Diseases, Pests and Disorders of Potatoes: A Color Handbook*. Florida: Elsevier; 2008.
5. Mendoza HA, Haynes FL. Genetic relationship among potato cultivars grown in the United States. *HortScience*. 1974; 9: 328–330.
6. Hawkes JG. Genetic poverty of the potato in Europe. In: van Harten AM, Zeven AC, editors. *Broadening the genetic base of crops*. Wageningen: Centre for Agricultural Publishing and Documentation; 1979. pp. 19–27.
7. Wang F, Li F, Wang J, Zhou Y, Sun H. Genetic Diversity of the Selected 64 Potato Germplasms Revealed by AFLP Markers. *Mol Plant Breed*. 2011; 2: 22–29.
8. Jansky SH, Dempewolf H, Camadro EL, Simon R, Zimnoch-Guzowska E, Bisognin DA, et al. A case for crop wild relative preservation and use in potato. *Crop Sci*. 2013; 53: 746–754.
9. Rudorf W. The significance of wild species for potato breeding. *Eur Potato J*. 1958; 1: 10–20.
10. Pavék JJ, Corsini DL. Utilization of potato genetic resources in variety development. *Am J Potato Res*. 2001; 78: 433–441.
11. Mattheij WM, Eijlander R, de Koning JR, Louwes KM. Interspecific hybridization between the cultivated potato *Solanum tuberosum* subspecies *tuberosum* L. and the wild species *S. circaefolium* subsp. *circaefolium* Bitter exhibiting resistance to *Phytophthora infestans* (Mont.) de Bary and *Globodera pallida*. *Theor Appl Genet*. 1992; 83: 459–66. doi: [10.1007/BF00226534](https://doi.org/10.1007/BF00226534) PMID: [24202592](https://pubmed.ncbi.nlm.nih.gov/24202592/)
12. Van der Vossen E, Sikkema A, Hekkert Bt, Gros J, Stevens P, Muskens M, et al. An ancient R gene from the wild potato species *Solanum bulbocastanum* confers broad-spectrum resistance to *Phytophthora infestans* in cultivated potato and tomato. *Plant J*. 2003; 36: 867–82. PMID: [14675451](https://pubmed.ncbi.nlm.nih.gov/14675451/)
13. Liu Z, Halterman D. Different genetic mechanisms control foliar and tuber resistance to *Phytophthora infestans* in wild potato *Solanum verrucosum*. *Am J Potato Res*. 2009; 86: 476–480.
14. Smyda P, Jakuczun H, Dębski K, Sliwka J, Thieme R, Nachtigall M, et al. Development of somatic hybrids *Solanum* × *michoacanum* Bitter. (Rydb.) (+) *S. tuberosum* L. and autofused 4x *S. x michoacanum*

- plants as potential sources of late blight resistance for potato breeding. *Plant Cell Rep.* 2013; 32: 1231–41. doi: [10.1007/s00299-013-1422-5](https://doi.org/10.1007/s00299-013-1422-5) PMID: [23525760](https://pubmed.ncbi.nlm.nih.gov/23525760/)
15. Jones JDG, Witek K, Verweij W, Jupe F, Cooke D, Dorling S, et al. Elevating crop disease resistance with cloned genes. *Philos Trans R Soc B.* 2014; 369: 20130087. doi: [10.1098/rstb.2013.0087](https://doi.org/10.1098/rstb.2013.0087) PMID: [24535396](https://pubmed.ncbi.nlm.nih.gov/24535396/)
 16. Laferriere LT, Helgeson JP, Allen C. Fertile *Solanum tuberosum* + *S. commersonii* somatic hybrids as sources of resistance to bacterial wilt caused by *Ralstonia solanacearum*. *Theor Appl Genet.* 1999; 98: 1272–1278. doi: [10.1007/s001220051193](https://doi.org/10.1007/s001220051193)
 17. Hijmans RJ, Jacobs M, Bamberg JB, Spooner DM. Frost tolerance in wild potato species: Assessing the predictivity of taxonomic, geographic, and ecological factors. *Euphytica.* 2003; 130: 47–59.
 18. González M, Galván G, Siri MI, Borges A, Vilaró F. Resistencia a la marchitez bacteriana de la papa en *Solanum commersonii*. *Agrociencia Uruguay.* 2013; 7: 45–54.
 19. Pelletier Y. Level and genetic variability of resistance to the colorado potato beetle (*Leptinotarsa decemlineata* (Say)) in wild *Solanum* species. *Am J Potato Res.* 2007; 84: 143–148.
 20. Luthra SK, Gopal J, Kumar D, Singh BP, Pandey SK. *Solanum* wild and cultivated species as source of resistance to cold induced sweetening. *Potato J.* 2009; 36: 115–120.
 21. Estrada RN. Frost resistant potato hybrids via *Solanum acaule*, Bitt. Diploid—Tetraploid crosses. *Am Potato J.* 1980; 57: 609–619.
 22. Ross H. Potato breeding—Problems and perspectives. In: Parey P, editor. *Fortschritte der Pflanzenzüchtung* 13; 1986.
 23. Suárez S, Chaves E, Clausen A, Franco J. *Solanum* tuber-bearing species resistance behavior against *Nacobbus aberrans*. *J Nematol.* 2009; 41: 5–10. PMID: [22661771](https://pubmed.ncbi.nlm.nih.gov/22661771/)
 24. Watanabe K, Orrillo M, Vega S, Masuelli R, Ishiki K. Potato germ plasm enhancement with disomic tetraploid *Solanum acaule*. II. Assessment of breeding value of tetraploid F1 hybrids between tetrasomic tetraploid *S. tuberosum* and *S. acaule*. *Theor Appl Genet.* 1994; 88: 135–140. doi: [10.1007/BF00225888](https://doi.org/10.1007/BF00225888) PMID: [24185917](https://pubmed.ncbi.nlm.nih.gov/24185917/)
 25. Carputo D, Speggorin M, Garrefa P, Raio A, Monti L. Screening for resistance to tuber soft rot and blackleg in diploid *Solanum* species and *S. tuberosum* haploids. *J Genet Breed.* 1996; 50: 221–226.
 26. Carputo D, Cardi T, Speggorin M, Zoina A, Frusciante L. Resistance to blackleg and tuber soft rot in sexual and somatic interespecific hybrids with different genetic background. *Am Potato J.* 1997; 74: 161–172.
 27. Frost KE, Jansky SH, Rouse DI. Transmission of *Verticillium* wilt resistance to tetraploid potato via unilateral sexual polyploidization. *Euphytica.* 2006; 149: 281–287.
 28. Jansky SH, Hamernik A, Bethke PPC. Germplasm release: Tetraploid clones with resistance to cold-induced sweetening. *Am J Potato Res.* 2011; 88: 218–225.
 29. Uhrig H, Wenzel G. *Solanum gourlayi* Hawkes as a source of resistance against the white potato cyst nematode *Globodera pallida* Stone. *Plant Breed.* 1981; 86: 148–157.
 30. Santini M, Camadro EL, Marcellan ON, Erazzu LU. Agronomic characterization of diploid hybrid families derived from crosses between haploids of the common potato and three wild Argentinian tuber-bearing species. *Am J Potato Res.* 2000; 77: 211–218.
 31. Bradshaw JE, Ramsay G. Utilisation of the Commonwealth Potato Collection in potato breeding. *Euphytica.* 2005; 146: 9–19.
 32. Ross H. Wild species and primitive cultivars as ancestors of potato varieties. In: Zeven A, van Harten A, editors. *Broadening the genetic base of crops.* Wageningen, The Netherlands: Centre for Agricultural Publishing and Documentation; 1979. pp. 237–245.
 33. Tucci M, Carputo D, Bile G, Frusciante F. Male fertility and freezing tolerance of hybrids involving *Solanum tuberosum* haploids and diploid *Solanum* species. *Potato Res.* 1996; 39: 345–353.
 34. Hawkes JG, Maxted N, Ford-Lloyd BV. *The ex situ* conservation of plant genetic resources. Dordrecht, The Netherlands: Kluwer Academic Publishers; 2000.
 35. Lindqvist-Kreuzer H, Carbajulca D, González-Escobedo J, Pérez W, Bonierbale M. Comparison of transcript profiles in late blight-challenged *Solanum cajamarquense* and B3C1 potato clones. *Mol Plant Pathol.* 2010; 11: 513–530. doi: [10.1111/j.1364-3703.2010.00622.x](https://doi.org/10.1111/j.1364-3703.2010.00622.x) PMID: [20618709](https://pubmed.ncbi.nlm.nih.gov/20618709/)
 36. Bradshaw JE, Bryan GJ, Ramsay G. Genetic Resources (Including Wild and Cultivated *Solanum* Species) and Progress in their Utilisation in Potato Breeding. *Potato Res.* 2006; 49: 49–65.
 37. Narancio R, Zorrilla P, Robello C, Gonzalez M, Vilaró F, Pritsch C, et al. Insights on gene expression response of a characterized resistant genotype of *Solanum commersonii* Dun. against *Ralstonia solanacearum*. *Eur J Plant Pathol.* 2013; 136: 823–835.

38. Jo K-R, Arens M, Kim O-Y, Jongsma MA, Visser RGF, Jacobsen E, et al. Mapping of the *S. demissum* late blight resistance gene *R8* to a new locus on chromosome IX. *Theor Appl Genet.* 2011; 123: 1331–1340. doi: [10.1007/s00122-011-1670-0](https://doi.org/10.1007/s00122-011-1670-0) PMID: [21877150](https://pubmed.ncbi.nlm.nih.gov/21877150/)
39. Villamon F, Spooner D, Orrillo M, Mihovilovich E, Pérez W, Bonierbale M. Late blight resistance linkages in a novel cross of the wild potato species *Solanum paucissectum* (series *Piurana*). *Theor Appl Genet.* 2005; 111: 1201–1214. PMID: [16133311](https://pubmed.ncbi.nlm.nih.gov/16133311/)
40. Naess SK, Bradeen JM, Wielgus SM, Haberland GT, McGrath JM, Helgeson JP. Resistance to late blight in *Solanum bulbocastanum* is mapped to chromosome 8. *Theor Appl Genet.* 2000; 101: 697–704.
41. Hodgkin T, Hajjar R. Using crop wild relatives for crop improvement: trends and perspectives. In: Maxted N, Ford-Lloyd BV, Kell SP, Iriondo J, Dulloo E, Turok J, editors. *Crop wild relatives conservation and use.* Wallingford: CABI Publishing; 2008. pp. 535–548. doi: [10.1186/1471-2105-9-116](https://doi.org/10.1186/1471-2105-9-116) PMID: [18298814](https://pubmed.ncbi.nlm.nih.gov/18298814/)
42. Cardi T, D'Ambrosio E, Consoli D, Puite KJ, Ramulu KS. Production of somatic hybrids between frost-tolerant *Solanum commersonii* and *S. tuberosum*: characterization of hybrid plants. *Theor Appl Genet.* 1993; 87: 193–200. doi: [10.1007/BF00223764](https://doi.org/10.1007/BF00223764) PMID: [24190212](https://pubmed.ncbi.nlm.nih.gov/24190212/)
43. Estrada N. Utilization of *Solanum brevidens* to transfer PLRV resistance into the cultivated potato, *Solanum tuberosum*. In: Hawkes JG, Lester RN, Nee M, Estrada N, editors. *Solanaceae III: Taxonomy, Chemistry and Evolution.* London: Royal Botanical Gardens, Kew; 1991.
44. Thieme R, Rakosy-Tican E, Gavrilenko T, Antonova O, Schubert J, Nachtigall M, et al. Novel somatic hybrids (*Solanum tuberosum* L.+*Solanum tarnii*) and their fertile BC1 progenies express extreme resistance to potato virus Y and late blight. *TAG Theor Appl Genet.* 2008; 116: 691–700. doi: [10.1007/s00122-007-0702-2](https://doi.org/10.1007/s00122-007-0702-2) PMID: [18202839](https://pubmed.ncbi.nlm.nih.gov/18202839/)
45. Watanabe K, Orrillo M, Vega S, Valkonen J, Pehu E, Hurtado A, et al. Overcoming crossing barriers between non tuber-bearing and tuber-bearing *Solanum* species: towards potato germplasm enhancement with a broad spectrum of solanaceous genetic resources. *Genome.* 1995; 38: 27–35. PMID: [18470149](https://pubmed.ncbi.nlm.nih.gov/18470149/)
46. Hanneman RE. The reproductive biology of potato and its implications for breeding. *Potato Res.* 1999; 42: 283–312.
47. Camadro EL, Carputo D, Peloquin SJ. Substitutes for genome differentiation in tuber-bearing *Solanum*: interspecific pollen-pistil incompatibility, nuclear-cytoplasmic male sterility, and endosperm. *Theor Appl Genet.* 2004; 109: 1369–1379. PMID: [15278199](https://pubmed.ncbi.nlm.nih.gov/15278199/)
48. Jansky SH, Simon R, Spooner DM. A test of taxonomic predictivity: resistance to white mold in wild relatives of cultivated potato. *Crop Sci.* 2006; 46: 2561–2570.
49. Uitdewillgen J, Wolters A, D'Hoop B, Borm T, Visser R, van Eck H. A next-generation sequencing method for genotyping-by-sequencing of highly heterozygous autotetraploid potato. *PLOS ONE.* 2013; 8: 1–14.
50. Rodriguez F, Wu F, Ané C, Tanksley S, Spooner DM. Do potatoes and tomatoes have a single evolutionary history, and what proportion of the genome supports this history? *BMC Evol Biol.*
51. Spooner DM. Single copy nuclear gene analysis of polyploidy in wild potatoes (*Solanum* section *Petota*). *Am J Bot.* 2009; 96: 1177–1189. doi: [10.3732/ajb.0800246](https://doi.org/10.3732/ajb.0800246) PMID: [21628268](https://pubmed.ncbi.nlm.nih.gov/21628268/)
52. Ames M, Spooner DM. Phylogeny of *Solanum* series *Piurana* and related species in *Solanum* section *Petota* based on five conserved ortholog sequences. *Taxon.* 2010; 59: 1091–1101.
53. Fajardo D, Spooner DM. Phylogenetic relationships of *Solanum* series *Conicibaccata* and related species in *Solanum* section *Petota* inferred from five conserved ortholog sequences. *Syst Bot.* 2011; 36: 163–170.
54. Cai D, Rodríguez F, Teng Y, Ané C, Bonierbale M, Mueller LA, et al. Single copy nuclear gene analysis of polyploidy in wild potatoes (*Solanum* section *Petota*). *BMC Evol Biol.* 2012; 12: 70. doi: [10.1186/1471-2148-12-70](https://doi.org/10.1186/1471-2148-12-70) PMID: [22624678](https://pubmed.ncbi.nlm.nih.gov/22624678/)
55. Spooner DM, Ghislain M, Simon R, Jansky SH, Gavrilenko T. Systematics, diversity, genetics, and evolution of wild and cultivated potatoes. *Bot Rev.* 2014; 80: 283–383.
56. Wiersema JH, León B, Garvey EJ. Identifying Wild Relatives of Subtropical and Temperate Fruit and Nut Crops. In: Aradhya MK, Kluepfel DA, editors. *ISHS Acta Horticulturae 948: I International Symposium on Wild Relatives of Subtropical and Temperate Fruit and Nut Crops.* ISHS; 2012. pp. 285–288.
57. Vincent H, Wiersema J, Kell S, Fielder H, Dobbie S, Castañeda-Álvarez NP, et al. A prioritized crop wild relative inventory to help underpin global food security. *Biol Conserv.* 2013; 167: 265–275.
58. Hijmans RJ, Spooner DM, Salas AR, Guarino L, de la Cruz J. *Atlas of Wild Potatoes.* Rome: International Plant Genetic Resources Institute (IPGRI); 2002. p. 143.
59. Guarino L, Lobell DB. A walk on the wild side. *Nat Clim Chang.* 2011; 1: 374–375.

60. Jarvis A, Lane A, Hijmans RJ. The effect of climate change on crop wild relatives. *Agric Ecosyst Environ.* 2008; 126: 13–23.
61. Vice-ministry for the environment biodiversity and climate change (VMABCC), Bioversity International. Red book of crop wild relatives in Bolivia. La Paz, Bolivia: Plural Editores; 2009. p. 340.
62. Cadima X, van Zonneveld M, Scheldeman X, Castañeda N, Patiño F, Beltran M, et al. Endemic wild potato (*Solanum* spp.) biodiversity status in Bolivia: Reasons for conservation concerns. *J Nat Conserv.* Elsevier GmbH.; 2014; 22: 113–131.
63. Maxted N, Dulloo E, Ford-Lloyd BV, Iriondo JM, Jarvis A. Gap analysis: a tool for complementary genetic conservation assessment. *Divers Distrib.* 2008; 14: 1018–1030.
64. Ramírez-Villegas J, Khoury C, Jarvis A, Debouck DG, Guarino L. A gap analysis methodology for collecting crop gene pools: a case study with *Phaseolus* beans. *PLOS ONE.* 2010; 5: e13497. doi: [10.1371/journal.pone.0013497](https://doi.org/10.1371/journal.pone.0013497) PMID: [20976009](https://pubmed.ncbi.nlm.nih.gov/20976009/)
65. Maxted N, Hargreaves S, Kell SP, Amri A, Street K, Shehadeh A, et al. Temperate forage and pulse legume genetic gap analysis. *Bocconea.* 2012; 115–146.
66. Harlan JR, de Wet MJM. *Toward a Rational Classification of Cultivated Plants.* *Taxon.* 1971; 20: 509–517.
67. Ochoa C. *The potatoes of South America: Bolivia.* Cambridge: Cambridge University Press; 1990.
68. Ochoa C. *Las papas de Sudamerica: Perú.* Lawrence, KS: Allen Press; 1999. p. 1036.
69. Ochoa C. *Las papas del Perú: base de datos 1947–1997.* Lima, Perú: Universidad Nacional Agraria La Molina (UNALM), Agencia Suiza para el Desarrollo y la Cooperación (COSUDE), Centro Internacional de la Papa (CIP); 2003.
70. Hijmans RJ, Gavrilenko T, Stephenson S, Bamberg J, Salas A, Spooner DM. Geographical and environmental range expansion through polyploidy in wild potatoes (*Solanum* section *Petota*). *Glob Ecol Biogeogr.* 2007; 16: 485–495.
71. Spooner DM, Hijmans RJ. Potato systematics and germplasm collecting, 1989–2000. *Am J Potato Res.* 2001; 78: 237–268.
72. Azurdia C, Williams KA, Williams DE, Van Damme V, Jarvis A, Castaño SE. Atlas Guatemalteco de Parientes Silvestres de las Plantas Cultivadas. 2011. Available: <http://www.ars.usda.gov/Services/docs.htm?docid=22225>.
73. Phillips S, Anderson R, Schapire R. Maximum entropy modeling of species geographic distributions. *Ecol Modell.* 2006; 190: 231–259.
74. Elith J, Graham CH, Anderson RP, Dudík M, Ferrier S, Guisan A, et al. Novel methods improve prediction of species' distributions from occurrence data. *Ecography.* 2006; 29: 129–151. PMID: [16622301](https://pubmed.ncbi.nlm.nih.gov/16622301/)
75. Simon R, Xie CH, Clausen A, Jansky SH, Halterman D, Conner T, et al. Wild and cultivated potato (*Solanum* sect. *Petota*) escaped and persistent outside of its natural range. *Invasive Plant Sci Manag.* 2010; 3: 286–293.
76. Simon R, Fuentes AF, Spooner DM. Biogeographic implications of the striking discovery of a 4,000 kilometer disjunct population of the wild potato *Solanum morelliforme* in South America. *Syst Bot.* 2011; 36: 1062–1067. doi: [10.1600/036364411X605065](https://doi.org/10.1600/036364411X605065)
77. Liu C, Berry PM, Dawson TP, Pearson RG. Selecting thresholds of occurrence in the prediction of species distributions. *Ecography.* 2005; 28: 385–393.
78. Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. Very high resolution interpolated climate surfaces for global land areas. *Int J Climatol.* 2005; 25: 1965–1978.
79. Hijmans RJ, Spooner DM. Geographic distribution of wild potato species. *Am J Bot.* 2001; 88: 2101–2112. PMID: [21669641](https://pubmed.ncbi.nlm.nih.gov/21669641/)
80. Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC, et al. Terrestrial Ecoregions of the World: a New Map of Life on Earth. *Bioscience.* 2001; 51: 933–938.
81. R Core Team. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing; 2014. Available: <http://www.r-project.org/>. doi: [10.1016/j.jneumeth.2014.06.019](https://doi.org/10.1016/j.jneumeth.2014.06.019) PMID: [24970579](https://pubmed.ncbi.nlm.nih.gov/24970579/)
82. Bivand R, Lewin-Koh N. mapproj: Tools for reading and handling spatial objects. 2014. Available: <http://cran.r-project.org/package=mapproj>.
83. Bivand R, Keitt T, Rowlingson B. rgeos: Bindings for the Geospatial Data Abstraction Library. 2014. Available: <http://cran.r-project.org/package=rgeos>.
84. VanDerWal J, Falconi L, Januchowski S, Shoo L, Storlie C. SDMTTools: Species Distribution Modelling Tools: Tools for processing data associated with species distribution modelling exercises; 2014. Available: <http://cran.r-project.org/package=SDMTTools>.

85. Hijmans RJ. raster: raster: Geographic data analysis and modeling; 2014. Available: <http://cran.r-project.org/package=raster>.
86. Bivand RS, Pebesma E, Gomez-Rubio V. Applied Spatial Data Analysis with R, 2nd ed. Berlin: Springer; 2013. p. 405.
87. Pebesma EJ, Bivand RS. Classes and methods for spatial data in R. R News 5 (2). 2005. Available: <http://cran.r-project.org/doc/Rnews/>.
88. Hijmans RJ, Phillips S, Leathwick J, Elith J. dismo: Species distribution modeling. 2014. Available: <http://cran.r-project.org/package=dismo>.
89. Wickham H. ggplot2: elegant graphics for data analysis. New York: Springer; 2009.
90. Iriondo JM, Maxted N, Kell SP, Ford-Lloyd BV, Lara-Romero C, Labokas J, et al. Quality standards for genetic reserve conservation of crop wild relatives. In: Maxted N, Dulloo ME, Ford-Lloyd BV, Frese L, Iriondo J, Pinheiro de Carvalho MAA, editors. Agrobiodiversity conservation: securing the diversity of crop wild relatives and landraces. Wallingford: CABI; 2012. pp. 72–77.
91. Hijmans RJ, Garrett KA, Huamán Z, Zhang DP, Schreuder M, Bonierbale M. Assessing the Geographic Representativeness of Genebank Collections: the Case of Bolivian Wild Potatoes. Conserv Biol. 2000; 14: 1755–1765.
92. Ovchinnikova A, Krylova E, Gavrilenko T, Smekalova T, Zhuk M, Knapp S, et al. Taxonomy of cultivated potatoes (*Solanum* section *Petota*: Solanaceae). Bot J Linn Soc. 2011; 165: 107–155.
93. Camadro EL. Is the genetic integrity of natural plant populations ex situ preserved with the current sampling, conservation and regeneration approaches? J Basic Appl Genet. 2014; 25: 41–44.
94. Del Rio AH, Bamberg JB, Huaman Z. Assessing changes in the genetic diversity of potato gene banks. 1. Effects of seed increase. Theor Appl Genet. 1997; 95: 191–198.
95. Del Rio AH, Bamberg JB, Huaman Z, Salas A, Vega SE. Assessing changes in the genetic diversity of potato gene banks. 2. In situ vs ex situ. Theor Appl Genet. 1997; 95: 199–204.
96. Shan F, Clarke HC, Plummer JA, Yan G, Siddique KHM. Geographical patterns of genetic variation in the world collections of wild annual *Cicer* characterized by amplified fragment length polymorphisms. Theor Appl Genet. 2005; 110: 381–91. PMID: [15551033](https://pubmed.ncbi.nlm.nih.gov/15551033/)
97. Wang MX, Zhang HL, Zhang DL, Qi YW, Fan ZL, Li DY, et al. Genetic structure of *Oryza rufipogon* Griff. in China. Heredity (Edinb). 2008; 101: 527–535. doi: [10.1038/hdy.2008.61](https://doi.org/10.1038/hdy.2008.61) PMID: [18827837](https://pubmed.ncbi.nlm.nih.gov/18827837/)
98. Camadro EL. Relevance of the genetic structure of natural populations, and sampling and classification approaches for conservation and use of wild crop relatives: potato as an example. Botany. 2012; 11: 1065–1072.
99. Nix HA. A biogeographic analysis of Australian elapid snakes. In: Longmore R, editor. Atlas of Elapid Snakes of Australia. Canberra: Australian Government Publishing Service; 1986. pp. 4–15.