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A prioritized crop wild relative inventory to help underpin global food security

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ABSTRACT

The potentially devastating impacts of climate change on biodiversity and food security, together with the growing world population, means taking action to conserve crop wild relative (CWR) diversity is no longer an option—it is an urgent priority. CWR are species closely related to crops, including their progenitors, which have potential to contribute traits for crop improvement. However, their utilisation is hampered by a lack of systematic conservation which in turn is due to a lack of clarity over their identity. We used gene pool and taxon group concepts to estimate CWR relatedness for 173 priority crops to create the Harlan and de Wet inventory of globally important CWR taxa. Further taxa more remotely related to crops were added if they have historically been found to have useful traits for crop improvement. The inventory contains 1667 taxa, divided between 37 families, 108 genera, 1392 species and 299 sub-specific taxa. The region with the highest number of priority CWR is western Asia with 262 taxa, followed by China with 222 and southeastern Europe with 181. Within the primary gene pool, 242 taxa were found to be under-represented in ex situ collections and the countries identified as the highest priority for further germplasm collection are China, Mexico and Brazil. The inventory database is web-enabled (http://www.cwrdiversity.org/checklist/) and can be used to facilitate in situ and ex situ conservation planning at global, regional and national levels.

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1. Introduction

The human population has recently passed seven billion and is forecast to approach nine billion by 2050 (UN, 2011). Furthermore, in the light of the potentially adverse impacts of climate change on agricultural production (Schmidhuber and Tubiello, 2007; Lobell et al., 2008; Palm et al., 2010), there is a rising awareness of the need to ensure global food security (IPCC, 2007; FAO, 2008). Although there are many approaches to improving food security (FAO, 2012), one option that is currently under-developed, but which could potentially make a significant contribution, is a more systematic and targeted use of crop wild relatives (CWR) in crop improvement programmes. Maxted et al. (2006) define a CWR as: "a wild plant taxon that has an indirect use derived from its relatively close genetic relationship to a crop". CWR have the potential to contribute beneficial traits to crops—such as biotic and abiotic stress resistances—leading to improved yield and production stability (Maxted et al., 2006; Guarino and Lobell, 2011). CWR contain a wealth of genetically important traits due to their adaptation to a diverse range of habitats and the fact that they have not passed through the genetic bottlenecks of domestication (Vollbrecht and Sigmon, 2005; FAO, 2008). Climate change-induced environmental changes are undoubtedly impacting the conditions under which our crops grow. Already, many crop varieties are being replaced with stress tolerant varieties to ensure the agricultural viability of the crop in the same locations (Jones et al., 2003; Duveiller et al., 2007; Deryng et al., 2011; Li et al., 2011; Luck et al., 2011; Yadav et al., 2011). The ability of breeders to increase or even sustain crop yield and quality in the face of dynamic biotic and abiotic threats without greater use of exotic germplasm has been questioned (Feuillet et al., 2008); therefore, CWR are an obvious target to aid crop improvement and food security.

CWR, like other wild plant species, are experiencing widespread genetic erosion and even extinction as a result of direct or indirect human-mediated environmental changes (Jarvis et al., 2008; Bilz

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et al., 2011). A recent study to undertake IUCN Red List assessments of 572 European CWR species in 25 crop gene pools/groups (Bilz et al., 2011; Kell et al., 2012) found that at least 11.5% of the species are threatened—3.3% of them being Critically Endangered, 4.4% Endangered and 3.8% Vulnerable—and that a further 4.5% of the species are classified as Near Threatened. These percentages are likely to increase further following reassessment of the species that are currently classified as Data Deficient (Kell et al., 2012).

With a global estimated value of $115 billion annually for the introduction of new genes from CWR to crops (Pimentel et al., 1997), it might be expected that CWR would already be effectively conserved and readily available for use by breeders. However, conservation of CWR diversity has yet to be addressed systematically. Given that CWR have known value for crop improvement and contain a broad range of genetic diversity, it is surprising that only 2–10% of global gene bank collections comprise CWR accessions and that these samples only represent a very small proportion of global CWR species (Maxted and Kell, 2009). In situ CWR conservation has also been neglected. Most of the world's national parks and other protected areas were established to conserve particular habitats or charismatic animal species (Maxted, 2003); sites targeted at CWR conservation are rare. Although CWR populations are conserved in situ where their inclusion is coincident with other protected area priorities, such as when they are recognized as a nationally rare or threatened species. But their conservation per se and specifically the conservation of their genetic diversity is currently not deemed a priority within the protected area community (Maxted, 2003; Vincent et al., 2012).

The requirement for systematic CWR conservation has been recognised by major bodies such as the Food and Agriculture Organisation of the United Nations in the International Treaty on Plant Genetic Resources for Food and Agriculture (FAO, 2001) and in a number of other international treaties and policy documents. The Convention on Biological Diversity recognizes CWR conservation as a global priority (FAO, 2001, 2011; CBD, 2010a, 2010b). The Global Strategy for Plant Conservation 2011–2020 (CBD, 2010a) states in Target 9 that "70 per cent of the genetic diversity of crops including their wild relatives and other socio-economically valuable plant species [should be] conserved", while the CBD Strategic Plan (CBD, 2010b) Target 13 called for "By 2020, the status of crop and livestock genetic diversity in agricultural ecosystems and of wild relatives [will have] been improved". To address the requirement for systematic CWR conservation, the Global Crop Diversity Trust (GCDT) launched the "Adapting agriculture to climate change: collecting, protecting and preparing crop wild relatives" project (GCDT, 2011) with the objectives of identifying global priority CWR, developing and implementing an ex situ conservation action plan for priority species, and promoting the use of the conserved diversity in crop improvement programmes.

This paper describes the creation of a global priority CWR inventory, including key ancillary data. It also reports on the taxonomic content of the inventory, the geographical distribution of the taxa with particular reference to the Vavilov centres of crop diversity (Vavilov, 1935), their potential use in plant breeding for crop improvement, their current ex situ conservation status, and their seed storage behaviour.

2. Materials and methods

2.1. Creation of the priority CWR inventory

To create the inventory, first it was necessary to produce a list of genera containing the most socio-economically important global food crops. Two sources of the most important food crops are the International Treaty on Plant Genetic Resources for Food and Agriculture Supplementary Annex 1 (FAO, 2001) and the major and minor food crops of the world listed by Groombridge and Jenkins (2002); these were combined to generate a list of genera containing the world's most important crop species. Table 1 lists the 92 genera containing crops which were used to create the initial version of the global priority CWR inventory. Many of the target genera contain multiple crops; for example the genus *Phaseolus* contains Lima bean, tepary bean and common bean. Therefore, it was also necessary to compile a list of all crops included within the target genera; this list was compiled using the list of major and minor food crops (Groombridge and Jenkins, 2002) and Mansfeld's encyclopedia of agricultural and horticultural crops (Hanelt and Institute of Plant Genetics and Crop Plant Research, 2001). A practical decision was made to exclude minor crops with a restricted cultivation range at this stage, but these may be included in future iterations of the CWR inventory.

The next step was to identify the priority CWR within each crop genus. There has been considerable debate over which criteria should be considered when prioritising species for conservation (Fitter and Fitter, 1987) and specifically for prioritising CWR species (Heywood and Dulloo, 2005; Ford-Lloyd et al., 2008; Villard and Jonsson, 2009; Magos Brehm et al., 2010; Hunter and Heywood, 2011). However, most commonly, CWR prioritization is based on three main criteria: (a) relative socio-economical importance of the related crop, (b) potential use for crop improvement (i.e., ease of crossability with the related crop or previously reported known use or potential use in crop improvement programmes), and (c) threatened status. Some or all of these criteria may be used in a variety of combinations, either independently or sequentially (Maxted and Kell, 2009; Magos Brehm et al., 2010; Kell et al., 2012). In developing the global priority CWR

Table 1
Global priority list of 92 crop wild relative (CWR) genera. * = Genera included International Treaty on Plant Genetic Resources for Food and Agriculture (25).

Agropyron Gaertn.*	*Dioscorea* L.	*Panicum* L.
Allium L.	*Diplotaxis* DC. *	*Pennisetum* Rich.
Ananas Mill.	*Echinochloa* P.Beauv.	*Persea* Mill.
Armoracia G. Gaertn., B. Mey & Scherb.*	*Elaeis* Jacq.	*Phaseolus* L.
Arachis L.	*Elettaria* Maton	*Phoenix* L.
Artocarpus J.R. Forst. & G. Forst.*	*Eleusine* Gaertn.	*Pimenta* Lindl.
Asparagus L.*	*Elymus* L. *	*Piper* L.
Avena L.	*Eruca* Mill. *	*Pistacia* L.
Barbarea W.T. Aiton*	*Ficus* L.	*Pisum* L.
Bertholletia Bonpl.	*Fragaria* L.	*Prunus* L.
Beta L.	*Glycine* Willd.	*Pyrus* L.
Brassica L.	*Gossypium* L.	*Raphanus* L. *
Cajanus Adans.	*Helianthus* L.	*Ribes* L.
Camellia L.	*Hordeum* L.	*Rorippa* Scop. *
Capsicum L.	*Ilex* L.	*Saccharum* L.
Carica L.	*Ipomoea* L.	*Secale* L.
Carthamus L.	*Isatis* L. *	*Sesamum* L.
Chenopodium L.	*Juglans* L.	*Setaria* P.Beauv.
Cicer L.	*Lablab* Adans.	*Sinapis* L. *
Citrullus Schrad.	*Lactuca* L.	*Solanum* L.
Citrus L.	*Lathyrus* L. *	*Sorghum* Moench
Cocos L.	*Lens* Mill.	*Spinacia* L.
Coffea L.	*Lepidium* L. *	*Theobroma* L.
Colocasia Schott	*Lupinus* L.	*Triticum* L.
Corylus L.	*Malus* Mill.	*Vicia* L.
Crambe L. *	*Mangifera* L.	*Vigna* Savi
Cucumis L.	*Manihot* Mill.	*Vitellaria* C.F. Gaertn.
Cucurbita L.	*Medicago* L.	*Vitis* L.
Cynara L.	*Musa* L.	*Xanthosoma* Schott
Daucus L.	*Olea* L.	*Zea* L.
Digitaria Haller	*Oryza* L.	

inventory, criteria (a) and (b) were deemed most important as they are directly related to the raison d'etre for defining CWR (i.e., their use for crop improvement).

CWR taxa may be scored for these prioritization criteria by collating information from published crop and CWR crossing experiments and by published concepts of the ease of crossability between a crop and CWR (Maxted et al., 2006). The most commonly used prioritization concept, the gene pool (GP) concept (Harlan and de Wet, 1971), is relatively objective and widely accepted. However, knowledge of whether each CWR is able to cross with its related crop is lacking for many crop complexes and in these cases the taxon group (TG) concept (Maxted et al., 2006) can be used as a proxy. This concept is based on the assumption that the taxonomic classification (including both traditional and phylogenetic methods) is strongly linked to genetic relatedness, and when gene pool and taxon group concepts are compared for known crop complexes, this assumption seems well founded (Maxted et al., 2006). In addition, a third concept was applied in this study: the 'provisional gene pool concept' (PGP). This was used when there was no formally published gene pool concept and when taxonomic treatments lacked subgeneric information, but there was published crossability evidence between the crop and related taxa. Table 2 details the three concepts of potential crossability between the CWR and target crop within a given crop complex.

One of the three prioritization concepts was applied to each crop complex and the priority CWR were identified as those in gene pools or provisional gene pools 1b and 2 (closely related CWR from which gene transfer to the crop is possible and does not require sophisticated techniques) or taxon groups 1b–3 (CWR within the same subgenus as the crop). In addition to those priority taxa identified within the prioritization concepts, more distantly related taxa that are documented to have been previously used for crop improvement or which have shown promise for crop improvement were also given priority status, many of which having recently been identified by Maxted and Kell (2009). Gene pool concepts were obtained from a literature review of published concepts. Taxon group concepts were derived from published taxonomic classifications (primarily phylogenetic taxonomy) for crops where no gene pool concept could be found. A provisional recommendation for which GP, TG or PGP concept was to be used for each crop complex was proposed by the project team, then a panel of experts with specialist knowledge of each crop complex was consulted and agreement reached over which concept should be applied within the inventory.

To manage the CWR data, a web-enabled extendable database was designed which will allow revision and addition as crop/CWR crossability and relatedness data become available and permit interaction with other databases. Once the taxonomic backbone was entered into the database, other data were added for each taxon, including common synonyms and vernacular names, prioritization concepts, countries of occurrence, actual and potential use in plant breeding, other direct uses, seed storage behaviour, and the main herbaria where specimens are expected to be stored (derived from geographical distribution of the taxon). These additional data were compiled from various sources, including literature surveys, online databases (ILDIS, 2011; Tropicos, 2011; USDA, 2011) and the Seed Information Database (Royal Botanic Gardens Kew, 2008). The Plant List (Royal Botanic Gardens Kew, 2011) was used as the nomenclature standard. The database was then made available to crop specific experts to provide feedback and to ensure that the CWR inventory was as accurate as possible. Following review, the database was revised and made available to all users online at http://www.cwrdiversity.org/checklist/. The inventory is named the 'Harlan and de Wet CWR Inventory' in honour of the scientists who originally proposed the crop gene pool concept (Harlan and de Wet, 1971).

2.2. Analysis of the Harlan and de Wet inventory

The GIS program DIVA-GIS (Hijmans et al., 2005) was used to visualise the richness of CWR taxa at species level per country, per geographic region of the world using the TDWG standard (Brummitt, 2001) and per Vavilov centre of diversity (Vavilov, 1935). The Vavilov centres of diversity are geographical areas where domestication of important food crops is thought to have taken place and where the genetic diversity of these crop complexes is still thought to be concentrated. By discovering which countries,

Table 2
Prioritization concepts used in the creation of the global priority crop wild relative (CWR) list.

Prioritization concept	Sublevel description	Prioritization concept description
Gene pool	GP1a: cultivated crop taxa GP1b: (primary GP): wild or weedy forms of the crop that cross easily with the crop	Based upon the Harlan and de Wet gene pool concept (1971), experts assign each CWR to the appropriate sublevel based upon crossability data
	GP2 (secondary GP): less closely related species from which gene transfer to the crop is possible but difficult using conventional breeding techniques GP3 (tertiary GP): species from which gene transfer to the crop is impossible, or if possible, requires sophisticated techniques, such as embryo rescue, somatic fusion or genetic engineering	The highest priority CWR are those in GP1b and GP2, which can be most easily crossed with the crop
Taxon group	TG1a: cultivated crop taxa TG1b: taxa within the same species as the crop TG2: taxa within the same series or section as the crop TG3: taxa within the same subgenus as the crop TG4: taxa within the same genus as the crop	The taxon group concept employs taxonomic hierarchy as a proxy for taxon genetic relatedness and thus crossability (Maxted et al., 2006)
	TG5: taxa within the same tribe as the crop	The highest priority CWR are those in TG1b, TG2 and TG3, which can be most easily crossed with the crop
Provisional gene pool	PGP1a: cultivated crop taxa PGP1b: (primary PGP): wild or weedy forms of the crop that cross easily with the crop PGP2 (secondary PGP): less closely related species from which gene transfer to the crop is possible but difficult using conventional breeding techniques	This concept is used where there is no formally published gene pool concept and where taxonomic treatments lack subgeneric information, but where some crossability evidence between the crop and related taxa was available
	PGP3 (tertiary PGP): species from which gene transfer to the crop is impossible, or if possible, requires sophisticated techniques, such as embryo rescue, somatic fusion or genetic engineering	This approach is the least favoured as it lacked the expert input that exists in published gene pool concepts and taxonomic treatments

regions and centres are the richest in terms of priority CWR, we can more efficiently plan conservation efforts to target them. To gain an insight into the effectiveness of current ex situ conservation efforts for the priority CWR taxa, ex situ holdings data were extracted from the Global Biodiversity Information Facility (GBIF, 2013) and reviewed. Botanical garden records for CWR that have non-orthodox seeds (i.e., seeds that cannot be conserved using conventional drying and freezing techniques) were also included in this analysis.

3. Results

The inventory contains 1667 priority CWR taxa in 173 crop complexes (Supplementary Table S1), 37 families, 108 genera, 1392 species and 299 sub-specific taxa. Families and genera are listed in Table 3 along with the corresponding numbers of priority CWR taxa. The family with the most CWR is Leguminosae (Fabaceae) (253), followed by Rosaceae (194), Poaceae (150), Solanaceae (131) and Rubiaceae (116); while the genera with the most CWR are *Solanum* (124), *Coffea* (116), *Prunus* (102), *Ficus* (59) and *Ribes* (53). Of the 173 crop complexes included, 88 are prioritised using published gene pool concepts, 15 using provisional gene pool concepts and 71 using taxon group concepts. The taxon group concept was applied to a further 16 crop gene pools for which there is no detailed subgeneric classification so in these cases, all taxa in the genus were included. These are the gene pools of: *Agropyron cristatum**, *Elaeis oleifera*, *Armoracia rusticana*, *Elettaria cardamomum*, *Barbarea verna*, *Ensete ventricosum*, *Carica papaya**, *Phoenix dactylifera*, *Colocasia esculenta*, *Pimenta dioica*, *Digitaria exilis*, *Rorippa indica*, *Echinochloa frumentacea*, *Sesamum indicum*, *Elaeis guineensis** and *Xanthosoma sagittifolium* (those marked with * are crops that are documented to have been improved using CWR material).

Table 3
Global priority crop wild relative (CWR) numbers per family and genus.

Family	Number of CWR	Genus	Number of CWR
Amaranthaceae	42	*Beta*	13
		Chenopodium	27
		Spinacia	2
Amaryllidaceae	35	*Allium*	35
Anacardiaceae	61	*Mangifera*	46
		Pistacia	15
Apiaceae	21	*Daucus*	18
		Tornabenea	3
Aquifoliaceae	36	*Ilex*	36
Araceae	2	*Colocasia*	1
		Xanthosoma	1
Arecaceae	4	*Cocos*	1
		Elaeis	2
		Phoenix	1
Asparagaceae	18	*Asparagus*	18
Betulaceae	15	*Corylus*	15
Brassicaceae	70	*Armoracia*	1
		Barbarea	1
		Brassica	28
		Capsella	1
		Coincya	1
		Crambe	2
		Diplotaxis	3
		Eruca	3
		Erucastrum	2
		Isatis	4
		Lepidium	12
		Moricandia	1
		Orychophragmus	1
		Raphanus	5
		Rorippa	1
		Sinapis	3
		Trachystoma	1
Bromeliaceae	5	*Ananas*	5
Caricaceae	4	*Carica*	1
		Vasconcellea	3
Compositae	70	*Carthamus*	10
		Cynara	5
		Helianthus	44
		Lactuca	11
Convolvulaceae	14	*Ipomoea*	14
Cucurbitaceae	48	*Citrullus*	3
		Cucumis	34
		Cucurbita	11
Dioscoreaceae	15	*Dioscorea*	15
Euphorbiaceae	28	*Manihot*	28
Grossulariaceae	53	*Ribes*	53
Juglandaceae	30	*Juglans*	30
Lauraceae	7	*Persea*	7
Lecythidaceae	1	*Bertholletia*	1
Leguminosae	253	*Arachis*	16
		Cajanus	14
		Cicer	5
		Glycine	5
		Lablab	3
		Lathyrus	34
		Lens	4
		Lupinus	29
		Medicago	26
		Phaseolus	36
		Pisum	6
		Vicia	33
		Vigna	42
Malvaceae	29	*Gossypium*	26
		Theobroma	3
Moraceae	71	*Artocarpus*	12
		Ficus	59
Musaceae	46	*Ensete*	1
		Musa	45
Myrtaceae	1	*Pimenta*	1
Oleaceae	8	*Olea*	8
Pedaliaceae	8	*Sesamum*	8
Piperaceae	7	*Piper*	7
Poaceae	150	*Aegilops*	32
		Agropyron	2
		Amblyopyrum	3
		Avena	15
		Digitaria	1
		Echinochloa	1
		Eleusine	7
		Elymus	5
		Hordeum	4
		Oryza	23
		Panicum	8
		Pennisetum	5
		Saccharum	11
		Secale	7
		Setaria	4
		Sorghum	6
		Tripsacum	1
		Triticum	8
		Zea	7
Rosaceae	194	*Amygdalus*	1
		Cydonia	1
		Fragaria	15
		Malus	38
		Potentilla	1
		Prunus	102
		Pyrus	36
Rubiaceae	116	*Coffea*	116
Rutaceae	18	*Atalantia*	1
		Citrus	16
		Clausena	1
Solanaceae	131	*Capsicum*	7
		Solanum	124
Theaceae	34	*Camellia*	34
Vitaceae	21	*Vitis*	21
Zingiberaceae	1	*Elettaria*	1

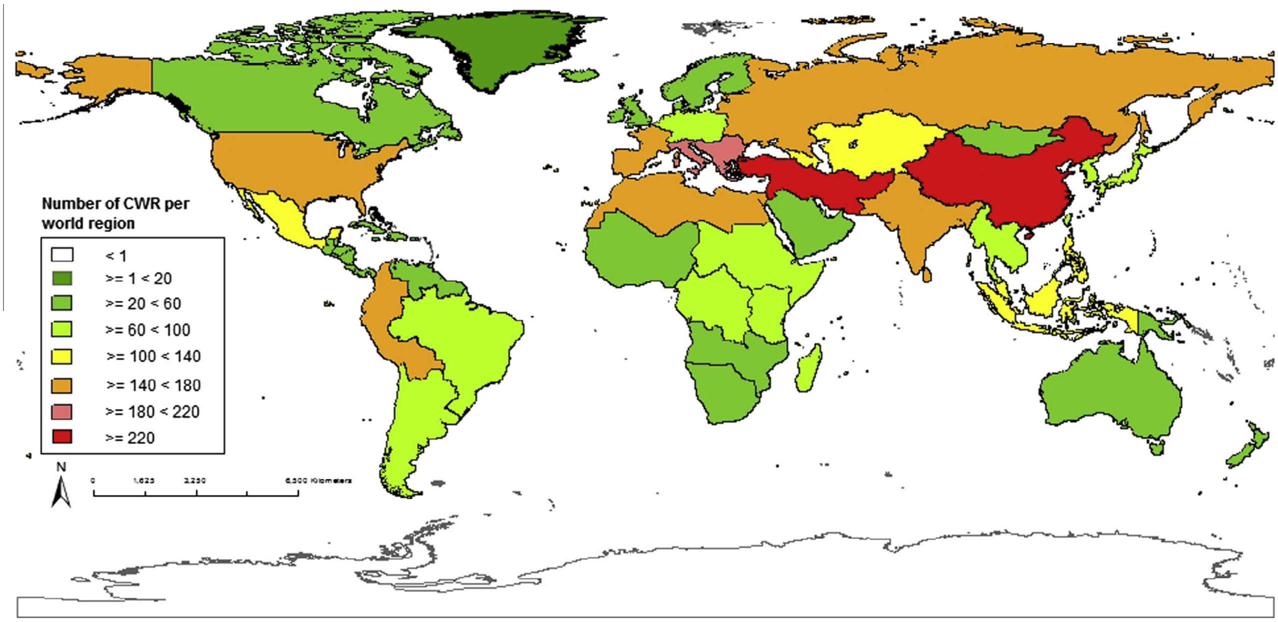

Fig. 1. Number of priority crop wild relatives (CWR) per world region.

Table 4
Concentration and numbers of crop wild relatives (CWR) per country, where total priority CWR is above 80. TG = Taxon Group Concept, GP = Gene Pool Concept, PGP = Provisional Gene Pool Concept.

Country	TG 1A	TG 1B	TG 2	TG 3	GP 1B	GP 2	PGP 1B	PGP 2	Total Priority CWR	Country Area (km^2)	Unit area per CWR
Lebanon	9	0	24	4	17	34	1	1	97	10,452	108
Israel	7	0	24	6	18	30	1	2	98	22,072	225
Albania	8	0	18	6	17	20	0	1	81	28,748	355
Armenia	10	1	11	5	20	22	0	0	81	29,743	367
Azerbaijan	9	1	17	5	22	27	0	0	91	86,600	952
Greece	13	0	28	9	28	33	1	1	134	131,957	985
Portugal	10	0	19	5	19	16	0	3	91	92,090	1012
Bulgaria	11	0	22	8	20	24	0	0	96	110,879	1155
Syria	9	0	28	6	17	41	1	1	112	185,180	1653
Italy	17	0	30	8	25	32	0	1	139	301,336	2168
Spain	16	0	26	7	22	32	0	3	132	505,992	3833
Turkey	17	1	43	8	40	55	1	1	189	783,562	4146
Morocco	8	0	18	6	12	27	2	1	99	446,550	4511
Iraq	8	1	18	5	22	28	0	0	90	435,244	4836
France	15	0	23	6	22	22	0	1	111	640,294	5768
Ukraine	11	0	14	8	19	22	0	0	86	603,500	7017
Iran	13	1	24	9	36	37	0	0	131	1,648,195	12,582
Peru	7	0	2	3	16	56	4	3	96	1,285,216	13,388
Mexico	4	0	9	7	14	55	0	8	109	1,964,375	18,022
Indonesia	4	0	27	38	6	7	1	0	84	1,910,931	22,749
Algeria	9	0	19	4	16	24	1	1	96	2,381,741	24,810
India	9	0	23	19	17	30	6	0	123	3,287,263	26,726
China	11	1	75	21	25	59	0	0	221	9,640,011	43,620
USA	3	0	46	16	8	41	0	7	152	9,629,091	63,349
Russia	12	1	38	11	20	26	0	0	117	17,075,200	145,942

The global priority CWR taxa are native to 39 world regions (Fig. 1). The region with the most CWR taxa present is western Asia with 262, second is China with 222 and third is southeastern Europe with 181. There are 203 countries that have at least one native global priority CWR taxon (see Supplementary Table S2). China has the highest number with 222 taxa, Turkey has 189, the USA has 152, Italy has 139 and Greece has 134. The CWR most likely to be used by breeders are either in GP1b, PGP1b or TG1b, which are the closest wild relatives to the crop where there are no hybridisation barriers. The countries with the highest number of native CWR in GP1b, PGP1b or TG1b are Turkey with 86, Greece with 71, Spain with 66, Italy and Iran with 63 and France with 60. However, the number of CWR per country does not take into account the size of the country, so care should be taken when drawing conclusions about these countries being CWR hotspots. If all countries with over 80 priority CWR are recalculated to indicate the unit area per CWR, then the countries with the highest concentration of all priority CWR are Lebanon, Israel, Greece, Portugal, Azerbaijan, Bulgaria, Syria, Italy, Spain and Turkey (see Table 4). But in absolute terms the countries with the highest concentration of CWR per unit area are all small islands which are likely to contain higher numbers of endemic taxa but whose CWR numbers tend to be inflated by invasive, weedy CWR.

The inventory contains 526 CWR taxa that have a confirmed or documented potential use in crop breeding. 'Confirmed use' means

Table 5
Number of priority crop wild relatives (CWR) per crop and the percentage with less than 50 accessions stored ex situ.

Scientific name	Common name	Number of priority CWR	Percentage of priority CWR with less than 50 ex situ accessions
Agropyron cristatum	Crested wheatgrass	2	0
Allium cepa	Onion	3	100
Allium sativum	Garlic	1	0
Allium chinense	Chinese scallion	23	91
Allium tuberosum	Chinese chives	2	50
Allium schoenoprasum	Chives	23	91
Allium fistulosum	Welsh Onion	5	60
Allium porrum	Leek	8	75
Ananas comosus	Pineapple	5	100
Arachis hypogaea	Peanut	16	94
Armoracia rusticana	Horseradish	1	0
Artocarpus altilis	Breadfruit	12	92
Artocarpus heterophyllus	Jackfruit	12	92
Asparagus officinalis	Asparagus	18	94
Avena sativa	Oat	15	60
Barbarea verna	American cress	1	100
Bertholletia excelsa	Brazil nut	1	100
Beta vulgaris	Sugarbeet	13	54
Brassica juncea	Mustard	9	22
Brassica napus	Rape	24	54
Brassica rapa	Turnip	19	58
Brassica oleracea	Kale	25	72
Brassica carinata	Ethiopian cabbage	3	0
Brassica nigra	Black mustard	7	14
Cajanus cajan	Pigeonpea	14	86
Camellia sinensis	Tea	34	94
Capsicum annuum	Bell pepper	5	20
Capsicum baccatum	Aji	5	40
Capsicum chinense	Bonnet pepper	5	20
Capsicum frutescens	Red chili	5	20
Carica papaya	Papaya	4	75
Carthamus tinctorius	Safflower	10	90
Chenopodium quinoa	Quinoa	27	93
Cicer arietinum	Chickpea	5	20
Citrullus lanatus	Watermelon	3	0
Citrus aurantiifolia	Key lime	13	54
Citrus limon	Lemon	12	50
Citrus sinensis	Sweet orange	16	63
Citrus aurantium	Sour orange	13	54
Citrus paradisi	Grapefruit	12	50
Citrus limetta	Sweet lime	12	50
Citrus reticulata	Mandarin	13	46
Cocos nucifera	Coconut	1	100
Coffea arabica	Arabic coffee	116	99
Coffea canephora	Robusta coffee	116	99
Colocasia esculenta	Taro	1	100
Corylus maxima	Giant filbert	15	60
Corylus avellana	Hazelnut	11	45
Crambe hispanica	Ethiopian kale	2	100
Cucumis sativus	Cucumber	3	33
Cucumis melo	Melon	32	78
Cucurbita ficifolia	Blackseed squash	2	100
Cucurbita pepo	Acorn squash	7	57
Cucurbita argyrosperma	Cushaw	1	0
Cucurbita moschata	Butternut squash	0	0
Cucurbita maxima	Pumpkin	3	67
Cynara cardunculus	Artichoke	5	80
Daucus carota	Carrot	21	95
Digitaria exilis	Fonio millet	1	100
Dioscorea alata	Water yam	8	63
Dioscorea cayennensis	Lagos yam	7	71
Dioscorea bulbifera	Aerial yam	1	0
Dioscorea esculenta	Asiatic yam	1	100
Dioscorea dumetorum	Bitter yam	1	0
Dioscorea rotundata	White Guinea yam	4	50
Diplotaxis tenuifolia	Perennial wall rocket	5	20
Echinochloa frumentacea	White millet	1	0
Elaeis guineensis	African oil palm	2	50
Elaeis oleifera	American oil palm	2	50
Elettaria cardamomum	Cardamom	1	0
Eleusine coracana	Finger millet	7	86
Elymus hispidus	Intermediate wheatgrass	5	40

Table 5 (*continued*)

Scientific name	Common name	Number of priority CWR	Percentage of priority CWR with less than 50 ex situ accessions
Ensete ventricosum	Ethiopian banana	1	100
Eruca versicaria	Salad rocket	7	29
Ficus carica	Fig	59	98
Fragaria × ananassa	Strawberry	16	63
Glycine max	Soybean	5	20
Gossypium hirsutum	Cotton	26	69
Gossypium arboreum	Tree cotton	26	69
Gossypium barbadense	Sea Island cotton	26	69
Gossypium herbaceum	Short-staple cotton	26	69
Helianthus annuus	Sunflower	38	76
Helianthus tuberosus	Jerusalem artichoke	15	60
Hordeum vulgare	Barley	4	0
Ilex paraguariensis	Yerbe maté	36	100
Ipomoea batatas	Sweet potato	14	57
Isatis tinctoria	Woad	4	75
Juglans nigra	Black walnut	14	79
Juglans regia	English walnut	29	86
Juglans ailantifolia	Japanese walnut	6	33
Lablab purpureus	Hyacinth bean	3	67
Lactuca sativa	Lettuce	11	73
Lathyrus cicera	Chickling vetch	30	63
Lathyrus ochrus	Cyprus vetch	3	33
Lathyrus odoratus	Sweetpea	29	66
Lathyrus sativus	Grass pea	4	50
Lens culinaris	Lentil	4	0
Lepidium meyenii	Maca	11	91
Lepidium sativum	Garden cress	1	0
Lupinus albus	White lupin	4	25
Lupinus luteus	Yellow lupin	6	50
Lupinus cosentinii	Sandplain lupin	7	71
Lupinus mutabilis	Andean lupin	15	73
Lupinus angustifolius	Blue lupin	6	50
Malus domestica	Apple	38	55
Mangifera indica	Mango	46	98
Manihot esculenta	Cassava	28	82
Medicago sativa	Alfalfa	15	60
Medicago truncatula	Barrel medic	11	18
Musa acuminata	Banana	40	95
Musa balbisiana	Plantain	40	95
Musa textilis	Manila hemp	6	100
Olea europaea	Olive	8	75
Oryza glaberrima	African rice	23	52
Oryza sativa	Rice	23	52
Panicum miliaceum	Broom millet	8	75
Pennisetum glaucum	Pearl millet	5	40
Persea americana	Avocado	7	86
Phaseolus vulgaris	Common bean	6	50
Phaseolus dumosus	Year bean	3	33
Phaseolus acutifolius	Tepary bean	3	33
Phaseolus lunatus	Lima bean	5	60
Phaseolus coccineus	Scarlet runner bean	25	80
Phoenix dactylifera	Date palm	1	0
Pimenta dioica	Pimenta	1	100
Piper nigrum	Black pepper	7	86
Pistacia vera	Pistachio	15	80
Pisum sativum	Pea	8	38
Prunus avium	Sweet cherry	27	74
Prunus armeniaca	Apricot	15	53
Prunus cerasifera	Myrobalan plum	13	62
Prunus cerasus	Sour cherry	10	50
Prunus domestica	Plum	21	62
Prunus dulcis	Almond	32	78
Prunus persica	Peach	28	64
Prunus salicina	Japanese plum	27	74
Pyrus communis	Pear	32	72
Pyrus pyrifolia	Asian pear	18	72
Raphanus sativus	Radish	5	20
Ribes nigrum	Blackcurrant	19	84
Ribes rubrum	Redcurrant	15	93
Ribes uva-crispa	Gooseberry	22	96
Rorippa indica	Variableleaf yellowcress	1	100
Saccharum officinarum	Sugarcane	11	72
Secale cereale	Rye	7	57

(*continued on next page*)

Table 5 (*continued*)

Scientific name	Common name	Number of priority CWR	Percentage of priority CWR with less than 50 ex situ accessions
Sesamum indicum	Sesame seed	8	88
Setaria italica	Foxtail millet	4	75
Sinapis alba	White mustard	2	50
Solanum lycopersicum	Tomato	12	42
Solanum melongena	Aubergine	18	78
Solanum muricatum	Pepino	6	100
Solanum tuberosum	Potato	88	55
Sorghum bicolor	Sorghum	6	50
Spinacia oleracea	Spinach	2	100
Theobroma cacao	Cacao	3	67
Triticum aestivum	Wheat	47	28
Vicia articulata	Monantha vetch	2	0
Vicia ervilia	Bitter vetch	2	0
Vicia faba	Faba bean	0	0
Vicia narbonensis	Narbon bean	6	67
Vicia pannonica	Hungarian vetch	12	67
Vicia sativa	Common vetch	9	56
Vigna angularis	Adzuki bean	13	77
Vigna mungo	Black gram	21	71
Vigna radiata	Mung bean	24	67
Vigna subterranea	Bambara groundnut	2	100
Vigna umbellata	Rice bean	23	70
Vigna unguiculata	Cowpea	14	86
Vitis amurensis	Amur grape	1	0
Vitis rotundifolia	Muscadine grape	2	0
Vitis vinifera	Wine grape	20	60
Xanthosoma sagittifolium	New cocoyam/Tania	1	0
Zea mays	Maize	8	63

that gene transfer from the CWR to the crop has been successful, while 'potential use' is recorded for CWR taxa that have been found to have important genes or traits for crop improvement, but where breeding has not been totally successful or yet attempted because more sophisticated techniques are required. *Prunus* has the most CWR taxa used in breeding or with breeding potential (68), which is partially due to the large number of CWR taxa that are used in grafting as rootstocks (e.g. *P. persica*, *P. davidiana*, *P. cerasifera* and *P. dulcis*). This is followed by *Solanum* with 32 CWR used in crop breeding (e.g. *S. acaule*, *S. chacoense*, *S. spegazzinii* and *S. vernei*). Note that both genera are large in terms of numbers of taxa included and contain multiple crops, thus boosting the number of CWR. Analysing the inventory in terms of breeding use, the majority of CWR taxa (240) have been used in disease resistance breeding, whilst 170 have been used as graft stock and 103 used in pest resistance breeding.

Brown and Marshall (1995) propose that a minimum of 50 sites are sampled to adequately conserve the genetic diversity of a taxon ex situ. Of the 1667 priority CWR taxa included in the inventory, there are 1247 taxa with 50 or less ex situ accessions (Supplementary Table S1) and of these, 939 taxa have 10 or fewer accessions and 542 have no accessions at all. What is particularly concerning is that 242 of the 422 primary level (GP1b, PGP1b and TG1b) taxa were found to be represented by fewer than 50 ex situ accessions in gene banks (Supplementary Table S3). The ten most important countries for further collecting of under-represented primary level taxa are: China, Mexico, Brazil, USA, Iran, Turkey, Spain, Greece, Indonesia and Guatemala. Of these, China, Mexico and Brazil have 143, 95 and 54 native priority primary level taxa respectively. Table 5 lists the total number of CWR taxa per crop prioritization concept and the percentage of these that have fewer than 50 accessions stored ex situ. The results indicate that all of the priority CWR of 18 crops are represented by fewer than 50 ex situ germplasm accessions, including onion, pineapple, spinach and coconut, and that 80% of the priority CWR of a further 49 crops have fewer than 50 accessions stored ex situ. It should also be noted that a high level of duplicated accessions between genebanks was noted which would tend to, if anything, over emphasise the actual ex situ conservation status of individual CWR. While acknowledging that the data accessible via GBIF may not be complete, it does suggest that the majority of priority CWR taxa are not currently adequately conserved ex situ.

The distributions of the taxa in the inventory were compared to the Vavilov centres of diversity. As the data on geographical distribution are mostly specified at the country level within the inventory, whole countries were used to represent each Vavilov centre. Fig. 2 shows that the Vavilov centres richest in priority CWR are the Chinese centre (centre 1) with 262 native CWR taxa and the Near Eastern centre (centre 4) with 254, representing 15.7% and 15.2% of the total global priority CWR respectively. In total, there are 1,053 CWR found in Vavilov centres, representing 63% of the priority CWR of major and minor crops of the world.

Table 6 ranks the ten most important crops in the world in terms of global net production value according to FAOSTAT (2012) along with the number of priority CWR per crop. With 24 CWR, the rice gene pool has the highest economic value per CWR and apple the lowest economic value per CWR with 31. Potato is ranked 6th in production value but has the highest number of CWR (75), while soybean is economically ranked 3rd but has only one priority CWR. The CWR of these economically important crops were analysed at the species level to identify the most species rich countries. The country with the most native CWR species is Peru with 58, followed by Mexico (39), China (35), Turkey (26) and Bolivia (23).

Information on seed storage behaviour was collated for species from all 108 priority CWR genera in the inventory. Storage behaviour for each genus is recorded as the percentage of CWR that exhibit that behaviour within the genus. The four behaviour categories are orthodox (seed which will survive standard drying and freezing techniques), intermediate (seed that tolerates some drying, but is between orthodox and recalcitrant in behaviour), recalcitrant (seed that cannot withstand standard drying and

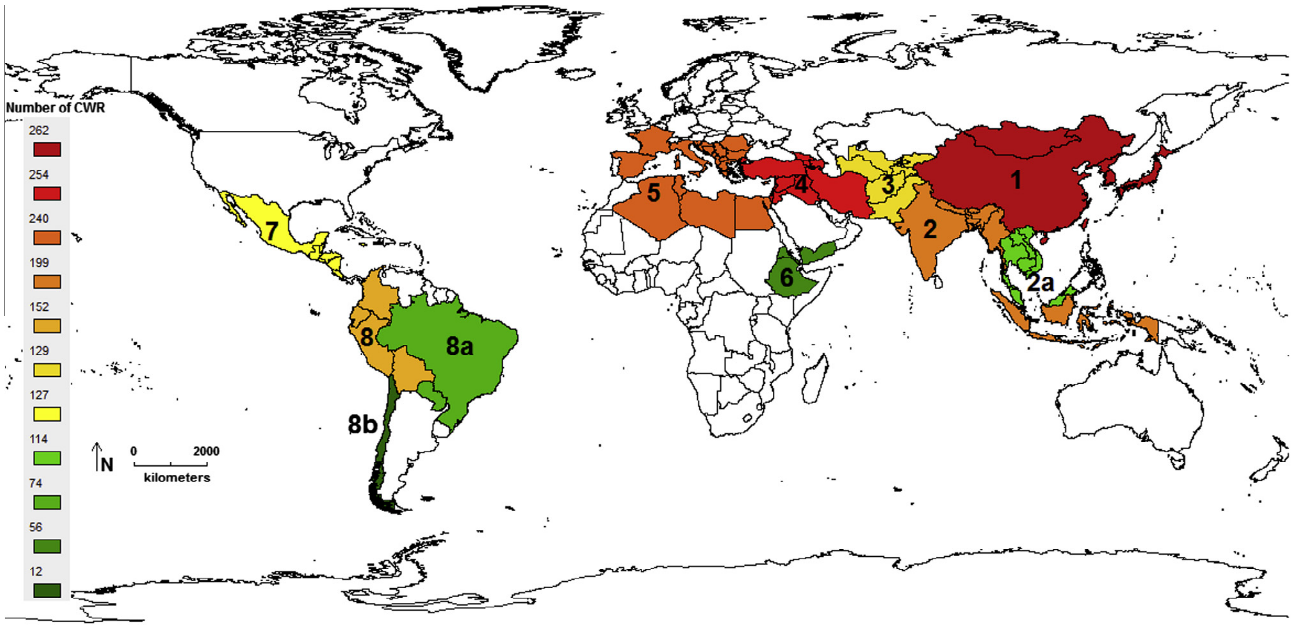

Fig. 2. Number of priority crop wild relatives (CWR) per Vavilov Centre of Diversity.

Table 6
The ten most important crops in the world in terms of global net production value according to FAOSTAT (FAOSTAT, 2012) with numbers of priority CWR per crop.

Crop	Global net production value (1000 Int. $ at the constant 2004–2006 rate)	Number of priority CWR
Rice	178,343,133	24
Wheat	86,720,367	44
Soybean	57,587,844	1
Tomato	55,894,436	12
Sugar cane	52,496,605	12
Maize	51,157,146	7
Potato	44,128,413	75
Grape	38,616,843	6
Cotton	29,936,716	29
Apple	29,919,202	31

freezing and cannot be stored for long periods), and unknown. For this analysis, the category assigned to at least 70% of the total species within a genus was accepted as the storage behaviour of the genus. Of the 108 genera in the inventory, 5.5% (6) are recalcitrant, 8.3% (9) are intermediate, 75.2% (82) are orthodox and 11% are unknown. An understanding of ex situ seed storage behaviour is vital for conservation planning to ensure survival of the seed via the appropriate storage method, and since the majority have orthodox seeds there is no technical reason why they should not be conserved systematically ex situ.

4. Discussion

The Harlan and de Wet CWR Inventory is available at www.cwrdiversity.org/checklist/. The inventory is the first annotated list of priority CWR of the world's most important human and animal food crops. It is already proving to be a significant resource for conservation planning either at the geographic (global, regional and national), or crop complex and multiple crop complex levels. For example, it was used for global ecogeographic studies of the barley (Vincent et al., 2012) and grasspea (Shehadeh et al., 2013) gene pools, and for producing a national CWR inventory for the USA (Khoury et al., 2013). Further national CWR conservation strategy planning utilizing data from the Harlan and de Wet Inventory is underway in Spain, Libya, Jordan and a number of other countries in Europe. The inventory also provides the foundations for the 'Adapting agriculture to climate change: collecting, protecting and preparing crop wild relatives' project (GCDT, 2011), which aims to systematically conserve ex situ the CWR diversity most likely to be of use in underpinning global food security and to use the conserved CWR diversity in novel breeding for crop improvement. The inventory is also being used to inform the planning of the establishment of a global network for in situ CWR conservation (FAO, 2013).

Already including 173 crops and their related 1667 priority CWR taxa, the Harlan and de Wet inventory is comprehensive, but in future the inventory will be expanded to include further crop complexes. The inventory will also have the capacity to include more than one prioritization concept (i.e. gene pool, taxon group or provisional gene pool) per crop. The importance of this can be explained with the example of *Citrus*. Swingle and Reece (1943) recognise 16 species, whereas Tanaka (1977) recognises 162; therefore the online inventory should be able to include multiple prioritization concepts per crop, allowing users to choose a concept or make one aggregated concept from all that are available. Thus, the inventory will act as a global repository for prioritization concepts and will be conceptually and taxonomically neutral as no particular concept will be seen as the preferred concept and problems of disagreements between experts can be avoided.

The geographic analysis of native priority CWR highlighted that south-central Asia is the region with the highest number of taxa, followed by eastern and western Asia. The eastern, south-central and western Asia areas were also highlighted as the most important for priority CWR when the Vavilov centres of diversity concept was applied. This is possibly due to the high number of minor crops originating in the eastern and south-central Asia regions that have no gene pool concept and where the taxon group concept has been applied. For example, tea (*Camellia sinensis*) has 32 priority CWR based on the taxon group concept, which is relatively high compared to most gene pool concepts. It is not known if all of these CWR are actually important in tea breeding, so it may potentially lead to an inflated number of priority CWR present in these regions. Furthermore, these regions have relatively high numbers of fruit trees such as *Prunus*, *Malus*, *Pyrus* and *Ficus* species. Large numbers of these taxa are used in grafting as well as breeding so they are included in the inventory, but their inclusion substantially increases the number of priority CWR found in these regions. Not surprisingly, the major crop complexes and their related CWR have been studied more extensively by the scientific community so the number of priority CWR tends to be fewer because the distinction between close and more distant CWR has been more firmly established (e.g. *Hordeum* – Bothmer et al., 1995; *Pisum* – Maxted and Ambrose, 2001; *Cicer* – Ahmad et al., 2005; *Lens* – Muehlbauer and McPhee, 2005).

The number of CWR per region or country may be somewhat misleading as regions and countries vary considerably in size, so perhaps a more useful view of geographic priorities can be obtained from the unit area per CWR within a country. The countries with the highest CWR concentration per unit area are: Lebanon, Israel, Greece, Portugal, Azerbaijan, Bulgaria, Syria, Italy, Spain and Turkey; six of which are from the Fertile Crescent (Lebanon, Israel, Greece, Azerbaijan, Syria and Turkey) and four from southern Europe (Portugal, Bulgaria, Italy and Spain). Even this does not take into account the distribution of CWR within each country. For example, CWR are found throughout Lebanon and Azerbaijan, but in Greece and Turkey they tend to be concentrated in the south and east, in Israel in the north and in Syria in the western Jebel Al Nusayriyah. In the latter case this is an area of less than 5% of the total area of Syria— an area already indicated to be key for cereal and legume CWR conservation (Maxted et al., 2012a).

The literature concerning breeders' use of CWR diversity is growing rapidly (Maxted et al., 2012b). It is important to note that in this initial version of the inventory the citation for CWR use is not exhaustive—there are likely to be CWR which have been used in crop improvement successfully or have great use potential that are not included, but these will be added as they are identified, further enhancing the resource for the user community.

The numbers of high priority CWR with fewer than 50 accessions highlighted in Supplementary Table S1 is a matter of concern—if CWR remain unconserved ex situ they are unlikely to be used (Maxted and Kell, 2009). Further, a high level of duplicated accessions between genebanks was noted which might also give a false impression of actual taxon conservation ex situ. Both factors lead us to suggest that the level of genetic diversity actually conserved could be much lower than originally thought. However, it should be noted that GBIF does not hold data on all existing ex situ accessions of priority CWR stored in gene banks, so the actual number of accessions may not be as low as portrayed here. Nonethless, the values provided here do act as a preliminary estimate of ex situ conservation effectiveness and are comparable with a similar analysis of priority CWR held ex situ in Europe (Kell et al., 2012). Futhermore, it is important to note that many existing gene bank accessions are only recorded at the species level which may explain the low numbers of ex situ records for subspecific taxa found in Supplementary Table S1. Therefore it is vital for anyone planning conservation of CWR to consult individual gene banks for a more accurate understanding of current conservation efforts before any action is undertaken. Given that 75% of priority CWR taxa were found to be orthodox in terms of their seed storage behaviour it bodes well for the GCDT (2011) project being able to significantly improve this position in the coming years.

Just as the identification of Biodiversity hotspots has facilitated the targeting of conservation action, particularly highlighting the need for more active conservation or restoration in hotspots threatened by habitat destruction (Mittermeier et al., 2004), so we hope that a clearer understanding of the presence and numbers of CWR in individual countries, regions or Vavilov centres of diversity will help promote targeted conservation action. Further, it is also clear that not all Vavilov centres have equal value in terms of the numbers of priority CWR present; for example, there are significant differences between the Chinese centre with 262 and the Chilean centre with 12. However, having made this comparison it is important to understand that numbers of CWR alone are likely to provide relatively crude means of targeting CWR conservation action; the value of the related crop itself should also be considered and high priority CWR taxa may also be found outside of the Vavilov centres. However, it is interesting to note the general agreement between the current distributional analysis and the Vavilov centres as proposed by Vavilov almost a century ago (Vavilov, 1926).

5. Conclusion

To conclude, the Harlan and de Wet CWR inventory provides a resource that will inform future CWR conservation and use, thus underpinning efforts to adapt agriculture to the environmental challenges related to climate change. The first global list of priority CWR species containing 1,667 taxa (1,392 species and 299 subspecific taxa) is already making a significant contribution to targeted conservation action. The inventory is currently being used as a resource for CWR prioritization in several projects other than the Global Crop Diversity Trust project for which it was originally developed, including the creation of national CWR inventories for Wales, Spain, Libya and Jordan, and a regional conservation strategy for Europe. Now that we know which taxa are of highest importance, it will be possible to plan and implement an effective worldwide in situ and ex situ conservation strategy for this critical global resource. The next step will be to collate georeferrenced data points for the priority CWR and compare their distributions with existing in situ and ex situ conservation actions to identify priority areas for further in situ conservation activities and ex situ collection. Plant breeders cannot breed climate change resilient varieties without access to the full range of conserved CWR diversity and more effective CWR use is likely to provide sustainability to conservation actions; as such the Harlan and de Wet CWR inventory will underpin both future CWR conservation and utilisation activities.

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