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Crop wild relatives of pigeonpea [*Cajanus cajan* (L.) Millsp.]: Distributions, ex situ conservation status, and potential genetic resources for abiotic stress tolerance

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ABSTRACT

Pigeonpea [*Cajanus cajan* (L.) Millsp.] is a versatile, stress-tolerant, and nutritious grain legume, possessing traits of value for enhancing the sustainability of dry sub-tropical and tropical agricultural systems. The use of crop wild relatives (CWR) in pigeonpea breeding has been successful in providing important resistance, quality, and breeding efficiency traits to the crop. Current breeding objectives for pigeonpea include increasing its tolerance to abiotic stresses, including heat, cold, drought, and waterlogging. Here we assess the potential for pigeonpea CWR to be further employed in crop improvement by compiling wild species occurrence and ex situ conservation information, producing geographic distribution models for the species, identifying gaps in the comprehensiveness of current germplasm collections, and using ecogeographic information to identify CWR populations with the potential to contribute agronomic traits of priority to breeders. The fifteen prioritized relatives of pigeonpea generally occur in South and Southeast Asia to Australia, with the highest concentrations of species in southern India and northern Australia. These taxa differ considerably among themselves and in comparison to the crop in their adaptations to temperature, precipitation and edaphic conditions. We find that these wild genetic resources are broadly under-represented in ex situ conservation systems, with 80% of species assessed as high priority for further collecting, thus their availability to plant breeders is insufficient. We identify species and highlight geographic locations for further collecting in order to improve the completeness of pigeonpea CWR germplasm collections, with particular emphasis on potential traits for abiotic stress tolerance.

1. Introduction

Challenges to global food production are compounding. Our growing population and dietary expectations are projected to increase demand on food systems for at least the next four decades, outpacing current yield trends (Ray et al., 2013). Limitations in land, water, and natural resource inputs, competition for arable soils with non-food crops and other land uses, the need to minimize harmful impacts on biodiversity and other ecosystem

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services, and greater climatic variability further constrain production potential (Cordell et al., 2009; Rosenzweig et al., 2013; Lobell et al., 2008). Although gains in food availability may partially be obtained through dietary change and waste reduction (Tilman and Clark, 2014; West et al., 2014), a transition toward more sustainable, yet highly productive, agricultural systems is necessary. This transformation must be achieved through improved agronomic practices combined with the use of varieties of crops with reliable yields under more adverse conditions (Foley et al., 2011).

One such crop is pigeonpea [*Cajanus cajan* (L.) Millsp.], a sub-tropical and tropical grain legume that originated in the northern region of the Indian sub-continent, spreading to East Africa at least 4000 years BCE, and then to Southeast Asia, West Africa, Latin America, and the Caribbean. The seed is eaten as a green vegetable and dry pulse and is an important source of protein, vitamin B, carotene, and ascorbic acid (Odeny, 2007; Choudhary et al., 2013). The pods and foliage of the plant are used as livestock forage and fodder, the crop is cultivated as a green manure, and its woody stem is used as fuel and construction material (Mallikarjuna et al., 2011). Pigeonpea is an important income generator, particularly in Tanzania, Malawi, and Myanmar as an export crop to India (Odeny, 2007).

Pigeonpea is generally planted by smallholder farmers in low input, rain-fed conditions. The crop is well suited to a wide range of agricultural systems, including intercropping and no-till. Cultivation improves soil fertility through biological nitrogen fixation as well as through the solubilization of soil-bound phosphorus (Mallikarjuna et al., 2011; Choudhary et al., 2013), increasing the yield of intercropped cereals, other pulses, and vegetables (Saxena, 2005; Odeny, 2007), and has been shown to enhance the control of *Striga* (Odeny, 2007). Pigeonpea is more heat tolerant than the majority of grain legume crops (Fig. 1) and is regarded as drought-resistant. These traits are associated with the ability to maintain or regulate transpiration under high temperatures and/or low soil moisture, for example through adjustment of leaf osmotic pressure (Subbarao et al., 2000), maintenance of photosynthetic function under stress (Lopez et al., 1987), and deep root systems (Flower and Ludlow, 1987).

Due to its high nutritive value and agronomic traits, pigeonpea can play an increasing role in low input production systems in India, East Africa, and elsewhere in the dry sub-tropics and tropics (Saxena, 2005; Odeny, 2007). Concerted breeding efforts for this purpose have resulted in a number of promising advances, particularly the creation of early maturing varieties, and developments toward diverse high yielding hybrids (Saxena, 2005; Saxena et al., 2013; Saxena and Sawargaonkar, 2014). However, crop yield in most production regions is well below its potential and has been stagnant for a number of decades, with increased production during this time largely due to an expansion of harvested area (Saxena, 2005; Odeny, 2007; Jones et al., 2002). In order to increase pigeonpea yield and adaptability, current breeding priorities include photoperiod insensitivity, resistance to biotic pressures, and tolerance to abiotic stresses, notably waterlogged and mineral deficient soils, cold and heat stress, salinity, and drought (Saxena, 2005; Odeny, 2007; Mligo and Craufurd, 2005; Choudhary et al., 2011; Upadhyaya et al., 2007).

The long-term viability of major food crops, particularly in light of the increasing need for sustainable production techniques, is dependent upon the use of diverse genetic resources to maintain productivity and adapt to changing climatic conditions and emerging pest and disease pressures (McCouch et al., 2013; Guarino and Lobell, 2011; Xiao et al., 1996). Due to the genetic bottleneck effect caused by domestication and crop improvement, pigeonpea cultivars possess only a small portion of the overall genetic diversity present within the genepool (Kassa et al., 2012), which also includes traditional farmer varieties and wild related species (Vincent et al., 2013). Crop wild relatives (CWR) of pigeonpea have contributed valuable genetic resources for pest and disease resistance, improved nutritional quality, desirable plant architecture, and breeding efficiency. They are considered to possess superior levels of resistance to diseases such as *Fusarium* wilt and *Phytophthora* blight, insect pests such as pod borer, pod fly, and pod wasp, and tolerance to abiotic stress, in comparison to the cultivated species (Table 1).

Increasing awareness of the extent of habitat destruction, invasive species, and other threats to the habitats of the CWR of major crops has given urgency to efforts to identify important species, determine their distributions, and to ensure their conservation for the long term and thus their availability to plant breeders (Jarvis et al., 2008; FAO, 2010b; Khoury et al., 2010). Genetic resource conservation planning efforts have benefitted from advancements in geographic information systems technologies, which have enabled high resolution species distribution modeling in order to inform collecting priorities (Jarvis et al., 2005), recognition of important gaps in ex situ collections (Ramírez-Villegas

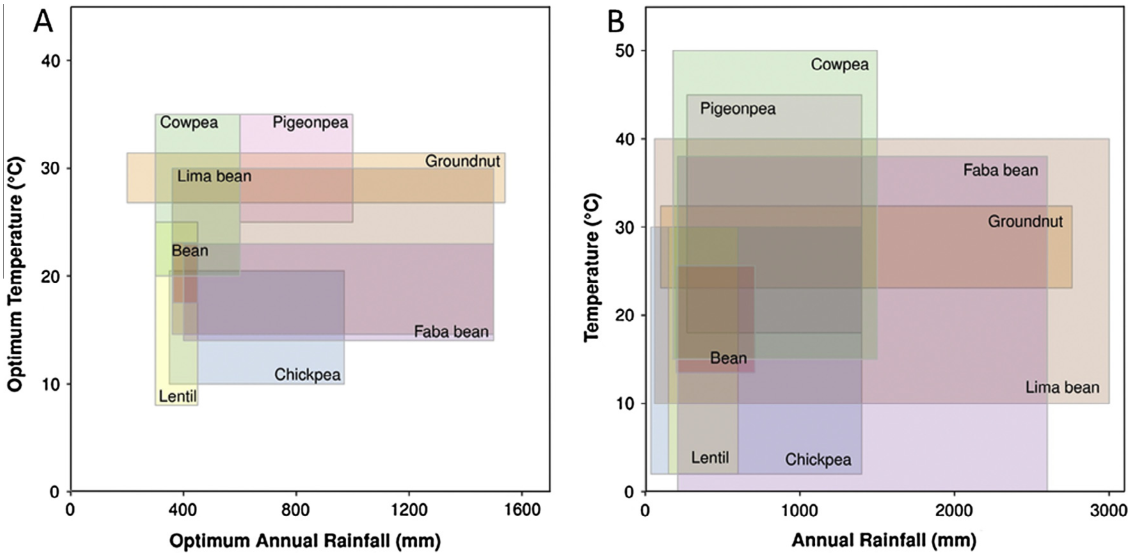

Fig. 1. Climatic niches for temperature and precipitation for major grain legumes. (A) Optimal range and (B) minimum and maximum observed range (Bogdan, 1977; FAO, 2010a; Odeny, 2007; Sardana et al., 2010; Saxena et al., 2010; Valenzuela and Smith, 2002; van der Maesen, 1989).

Table 1
Published confirmed (C) and potential (P) uses of pigeonpea CWR in crop improvement.

Taxon	Trait
C. acutifolius	Cytoplasmic male sterility (C[a]), Pod borer resistance (C[b]), High seed weight (C[c]), Sterility mosaic disease resistance (P[c]), Pod fly resistance (P[d])
C. albicans	High seed protein (C[c],P[e]), Pod borer resistance (P[b]), Pod fly resistance (P[d]), Pod wasp resistance (P[d]), Broad pods (P[e]), More seeds per pod (P[e]), Good forage source (P[e]), Sterility mosaic disease resistance (P[f]), Salt tolerance (P[g])
C. cajanifolius	Nuclear male sterility (C[a]), Cytoplasmic male sterility (C[h]), High seed protein (P[e])
C. cinereus	More seeds per pod (P[e])
C. crassus	High seed protein (P[e]), Good forage source (P[e]), Sterility mosaic disease resistance (P[f])
C. lineatus	Cleistogamy (C[i]), Cytoplasmic male sterility (C[j]), Pod fly resistance (P[d]), Sterility mosaic disease resistance (P[f])
C. mollis	More seeds per pod (P[e]), High seed protein (P[e]), Good forage source (P[e])
C. platycarpus	*Phytophthora* blight resistance (C[f,k]), Sterility mosaic disease resistance (P[c]), Pod borer resistance (P[c]), Early flowering (P[e]), High seed protein (P[e]), Cyst nematode resistance (p[f]), Salt tolerance (P[g,l]), Aluminum toxicity resistance (P[g]), Annuality (P[m]), Photoperiod insensitivity (p[n]), High flower and pod setting (P[n])
C. scarabaeoides	Pod borer resistance (C[b,f]), Sterility Mosaic Disease Resistance (C[c]), Protein improvement (C[o]), Dwarfism (C[p]), Cytoplasmic male sterility (C[q]), Pod fly resistance (P[d]), Pod wasp resistance (P[d]), Early flowering (P[e,r]), Salt tolerance (P[g]), Aluminum toxicity resistance (P[g]), Drought tolerance (P[r])
C. sericeus	High seed protein (C[c]), Cytoplasmic male sterility (C[s]), Pod borer resistance (P[b]), Pod fly resistance (P[d]), Salt tolerance (P[g]), Sterility mosaic virus resistance (P[m,f]), *Phytophthora* blight resistance (P[m])

[a] Mallikarjuna and Saxena (2005).
[b] Mallikarjuna et al. (2007).
[c] Mallikarjuna et al. (2011).
[d] Sharma et al. (2003).
[e] Upadhyaya et al. (2013b).
[f] Saxena (2005).
[g] Choudhary et al. (2011).
[h] Saxena et al. (2005).
[i] Saxena et al. (1998).
[j] Saxena et al. (2010).
[k] Mallikarjuna et al. (2005).
[l] Subbarao et al. (1990).
[m] Observation by authors.
[n] Mudaraddi et al. (2013).
[o] Reddy et al. (1979).
[p] Reddy (1990).
[q] Saxena and Kumar (2003).
[r] Upadhyaya (2006).
[s] Ariyanayagam et al. (1995).

et al., 2010), and the identification of populations that may possess particularly valuable traits for crop improvement (Tapia et al., 2014).

Given the importance of pigeonpea in low input production systems in regions facing food and nutritional insecurity and the capacity for enhancement of the crop through breeding, the aim of this research is to contribute to ensuring the conservation and availability of a broad range of diversity of CWR genetic resources of potential value to present and future crop improvement objectives. Therefore, we analyzed the comprehensiveness of ex situ conservation of pigeonpea CWR through a series of questions: (a) what constitutes a potentially useful wild relative of pigeonpea?; (b) where are these species encountered in the wild?; (c) what is the state of conservation and availability of these species to plant breeders? If suboptimal, what are the highest taxonomic and ecogeographic priorities for further collecting? And finally; (e) what CWR resources possess high potential for contribution of traits of value for crop breeding objectives?

2. Materials and methods

2.1. Identification of target CWR species and occurrence data compilation

We identified potentially useful CWR at the species level based upon a genepool concept (Harlan and de Wet, 1971) for pigeonpea, which focused on those wild species capable of hybridization with the crop (i.e., members of the primary or secondary genepools), as these species possess the greatest potential for successful introgression of traits (Vincent et al., 2013). Taxa in the tertiary genepool with published evidence of confirmed or potential use in crop improvement (Table 1) were also included.

Occurrence records for pigeonpea CWR were acquired from online biodiversity, herbarium, and germplasm databases; via communications with herbarium and genebank managers, and other crop researchers; and through direct recording of provenance data during visits to selected herbaria (Supplemental Table 1). 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. Occurrence data were compiled in a standardized format and taxonomically verified following GRIN Taxonomy for Plants (2012) and The Plant List (2010) as references. Existing coordinates were cross-checked to country and verified as occurring on land (Hijmans et al., 1999), and records with locality information but no coordinates were geo-referenced using the Google Maps Geocoder (2013) application programming interface. Occurrence data were mapped, iteratively evaluated for correctness with pigeonpea CWR experts, and subsequently further processed in order to form a final dataset of maximized taxonomic and spatial accuracy.

2.2. Species potential distribution modeling

A potential distribution model for each species was calculated using the maximum entropy (Maxent) algorithm (Phillips et al., 2006), with a set of ecogeographic variables and unique species presence records as inputs. We chose Maxent due to its wide application in predicting species distributions (Elith et al., 2006; Costa et al., 2010; Phillips and Dudik, 2008). We performed modeling at a resolution of 2.5 arc-minutes (∼5 km × 5 km cell size at the equator), employing 10,000 background points for model training over the combined distributional range of the pigeonpea CWR. Ecogeographic inputs included altitude and nineteen bioclimatic variables from the WorldClim database (Hijmans et al., 2005), and seven major edaphic drivers of plant species distributions with consistent data coverage throughout the range of the pigeonpea CWR species, obtained from ISRIC- World Soil Information (Hengl et al., 2014) (Supplemental Table 2). For the edaphic variables we calculated a weighted mean across 0–5, 5–15, 15–30, 30–60, and 60–100 cm soil depth values in order to derive a single data value for 0–100 cm. We then resampled the 1 km resolution data to form 2.5 arc-minutes resolution inputs aligned with the WorldClim datasets.

In order to refine and test the stability of the distribution models for each species, we analyzed Maxent results across three ecogeographic input variations: (a) the full set of nineteen bioclimatic variables (Ramírez-Villegas et al., 2010); (b) the bioclimatic variables, altitude, and the additional set of seven edaphic variables, totaling 27 input variables; and (c) a species-specific derivation of the most important drivers of distribution based upon presence data, further refined by removing highly correlated variables. For the ecogeographic variables in the species-specific method, we utilized a non-linear iterative partial least squares (NIPALS) algorithm to perform a principal-component analysis (PCA), as NIPALS can handle data arrays in which the number of observations is less than the number of input variables, and identified those variables with the greatest contribution (>0.7 or <-0.7) to the first two principal components per species based upon occurrence data points. We then used a variance inflation factor (VIF) to identify the variables with a low degree of collinearity (see Supplemental Table 3 for a list of variables utilized per species). A calibrated area under the ROC curve (cAUC) was obtained to assess the predictive performance of each model (Hijmans, 2012). The three modeling methods were evaluated with a correlation coefficient against a null model, and the species-specific variables method showed the least spatial sorting bias among methods (spearman's rho for the 19 variables was 0.53; for 27 variables was 0.56; and for the species-specific method was 0.37), and the differences in median AUC distributions across species for each method were found to be statistically significant ($p = 0.0002$) through a Kruskal-Wallis non-parametric analysis of variance test. Potential distribution models based upon the species-specific variables method were therefore utilized in subsequent analyses.

Potential distribution models were constrained per species by a native range defined at the country level as listed in GRIN (2012) and van der Maesen (1986), and were clipped by measuring the shortest distance between the receiver operating characteristic curve (ROC-curve) and the top-left corner of the plot (Liu et al., 2005). We limited the spatial analysis to the native distributions of taxa in order to focus prioritization recommendations on those regions with species with long-term adaptation to specific ecogeographic conditions.

Adapted from Ramírez-Villegas et al. (2010), Maxent models were produced using the cross-validation option ($k = 5$) and were subjected to a four-fold assessment process including: (a) the 5-fold average area under the ROC curve of test data (ATAUC), (b) the standard deviation of the test AUC of the 5 different folds (STAUC), (c) the proportion of the potential distribution coverage with standard deviation above 0.15 (ASD15), and (d) the cAUC value. Models with ATAUC above 0.7, STAUC below 0.15, ASD15 below 10%, and cAUC exceeding 0.40 were considered accurate and stable. For species where the Maxent model did not pass the cross-validation, potential distributions were mapped with a circular buffer of 50 km (CA50) surrounding each geo-referenced record (Hijmans et al., 2001).

2.3. Analysis of current ex situ conservation and further collecting needs for CWR

We adapted a gap analysis methodology proposed by Ramírez-Villegas et al. (2010), combining three metrics used to assess the urgency of further collecting in order to fill gaps in ex situ conservation of CWR. The total sample representation of each species in genebank collections was estimated via a sampling representativeness score (SRS), calculated as the number of germplasm samples (G) divided by the total number of samples (G + herbarium samples (H)) (i.e., all other records aside from available genebank accessions).

The sufficiency of geographic coverage of germplasm collections of each species was estimated through a geographic representativeness score (GRS), calculated as the share of the combined total area of CA50 placed around each existing germplasm collection point compared to the overall potential geographic distribution of the species.

The comprehensiveness of ecological coverage of germplasm collections of each species was estimated through an ecological representativeness score (ERS), calculated by estimating the distinct ecosystem classifications (Olson et al., 2001) represented in the CA50 of existing germplasm collection points compared to the diversity of ecosystems in which the overall potential geographic distribution model of the species occurs.

A final priority score (FPS) for further collecting for ex situ conservation was assigned to each species by averaging the three gap analysis metrics (SRS, GRS, and ERS). FPS scores were further classified into four categories of urgency for collecting: high priority species (HPS) for taxa whose $0 < \text{FPS} \leqslant 2.5$ or when no germplasm accessions currently exist; medium priority species (MPS) when $2.5 < \text{FPS} \leqslant 5$; low priority species (LPS) when $5 < \text{FPS} \leqslant 7.5$; and 'no further collecting recommended' (NFCR) when $7.5 < \text{FPS} \leqslant 10$. We produced collecting priorities maps for all species, displaying the geographic areas that have not yet been collected from within the potential distributions of taxa.

The ecogeographic data preparation, species distribution modeling, and gap analysis were written and performed in R v2.15.1 (R Core Team, 2013), utilizing packages maptools (Bivand and Lewin-Koh, 2014), rgdal (Bivand et al., 2014), SDMTools (van der Wal et al., 2014), raster (Hijmans, 2014), sp (Bivand et al., 2013; Pebesma and Bivand, 2005), dismo (Hijmans et al., 2013), and plsdepot (Sanchez, 2012). Resulting spatial files were mapped in ArcMap v.10 (ESRI, 2011). Collecting priorities spatial files were analyzed using the Zonal Statistics tool in ArcMap to list the countries prioritized for further collecting for ex situ conservation.

In order to validate and/or expose deficiencies in our findings, we subjected the gap analysis numerical and spatial results to an evaluation performed by four crop experts with experience in the distribution and/or conservation status of CWR of pigeonpea: Mulualem Kassa, Cereal Research Centre, Agriculture and Agri-Food Canada; Sally Norton, Australian Grains Genebank, Australia; Hari Upadhyaya, International Crops Research Institute for the Semi-Arid Tropics (ICRISAT); and Jos van der Maesen, Naturalis Biodiversity Center, the Netherlands). These experts were first asked to provide an evaluation of the sufficiency of germplasm collections per species based only upon their knowledge of total accessions, and geographic and environmental gaps. Such an assessment [comparable expert priority score (EPS)] was considered directly comparable to the FPS of the gap analysis results. A second evaluation score (contextual EPS) based on the entirety of expert knowledge, including threats to species in situ and prioritization by usefulness in crop improvement, was collected in order to provide additional information to collecting prioritization efforts. In both cases, an EPS between 0 and 10, aligned with the gap analysis results prioritization scale, was requested. After these steps, experts were shown the gap analysis results and asked to comment on assessed quantitative results, occurrence data, potential distribution models, and maps of collecting priorities. Following these contributions by experts, input occurrence data were further refined by eliminating clearly incorrect points and adjusting country-level native areas, and the potential distribution modeling and gap analyses were re-run in order to improve the quantitative and spatial outputs. Expert metrics displayed in the results pertain to the final evaluation of improved gap analysis outputs.

A multiple factor analysis (MFA) was used in order to compare the various forms of expert evaluation inputs with the gap analysis results, and an expert evaluation index was created, which estimated the degree of accord between all experts and the gap analysis results for each species, with a scale from 0 (disagreement) to 100 (agreement). Analyses were performed using R package FactoMineR (Husson et al., 2009).

2.4. Identification of CWR with potential traits of use in breeding for abiotic stress tolerance

We utilized ecogeographic information in combination with species presence data in order to identify populations of species with outstanding adaptations to climatic and/or edaphic conditions of interest to pigeonpea breeding objectives. We assessed the relative importance of the 27 ecogeographic variables (Supplemental Table 2) in explaining the total variation among pigeonpea CWR through a PCA, utilizing all occurrence data points found within the native areas of the species. We created a hierarchical cluster of principal components (HCPC) in order to identify ecogeographic clusters for the species using R package FactoMineR.

Boxplots for each of the 27 ecogeographic variables were created based upon CWR species occurrence data points, displaying the median and variance parameters per species per variable. Comparable ecogeographic variable data for the pigeonpea crop was extracted from area of cultivation maps (Monfreda et al., 2008) at a resolution of 5 arc-minutes, with a random sample of 1000 points weighted by harvested area, taken from the major cultivation areas in Asia, Africa, and Latin America. As both the CWR and the crop displayed outlier occurrence points that could potentially contribute to an overinflated ecogeographic niche concept, for further comparative analyses focused on breeding objectives for the crop we restricted the ecogeographic niche per species to the central 90% of variation (i.e., 10% outliers were excluded). Ecogeographic niches for CWR and the pigeonpea crop were mapped in R package ggplot2 (Wickham, 2009).

3. Results

3.1. Wild relatives of pigeonpea

The genus *Cajanus* Adans. is composed of 32-34 taxa divided into three clades: Indian, Australian, and *Scarabaeoides* (Kassa et al., 2012; van der Maesen, 1986). No wild conspecific to the cultivated species exists, and thus there are no wild taxa falling within the primary genepool of pigeonpea as defined by Harlan and de Wet (1971). The secondary genepool is comprised of *Cajanus cajanifolius* (Haines) Maesen, in the Indian clade, the putative progenitor of the crop (Kassa et al., 2012), *C. acutifolius* (F.Muell.) Maesen, *C. albicans* (Wight & Arn.) Maesen, *C. cinereus* (F.Muell.) F.Muell., *C. confertiflorus* F.Muell., *C. lanceolatus* (W.Fitzg.) Maesen, *C. latisepalus* (Reynolds & Pedley) Maesen, *C. lineatus* (Wight & Arn.) Maesen, *C. reticulatus* (Dryand) F.Muell., *C. scarabaeoides* (L.) Thouars, *C. sericeus* (Baker) Maesen, and *C. trinervius* (DC.) Maesen (Mallikarjuna et al., 2011; Saxena et al., 2005). Three additional species from the tertiary gene pool [*C. crassus* (King) Maesen, *C. mollis* (Benth.) Maesen, and *C. platycarpus* (Benth.) Maesen] have been the subject of publications of confirmed or potential uses in crop improvement and were therefore also included in the analysis (Table 1, Supplemental Table 3). *Cajanus volubilis* (Blanco) Blanco was recorded in Wanjari et al. (1999) as contributing sterility traits, but we believe that the material studied in this reference was actually *C. crassus*, therefore *C. volubilis* was not included in this analysis.

A total of 3171 occurrence records for the fifteen CWR were gathered for use in potential distribution modeling and in the gap analysis, including 377 germplasm accession records sourced from six genebanks, and 2794 herbarium and other occurrence reference records sourced from 17 providers (Supplemental Table 1). Records per species ranged from 15 (*C. mollis*) to 594 (*C. acutifolius*). Of these, 1068 records containing distinct cross-checked coordinates were used to model species potential distributions and to locate the original collecting site of existing germplasm accessions (Supplemental Table 3).

3.2. CWR species distributions

Potential distribution models performed in Maxent passed the four-fold cross-validation for eleven out of the fifteen CWR. Models for *C. albicans*, *C. cajanifolius*, *C. mollis* and *C. platycarpus* failed the cross-validation due generally to insufficient and dispersed presence records, and were instead mapped by creating CA50 buffers around their occurrences. Native distributions of pigeonpea CWR occur from South Asia through Southeast Asia into northern Australia, as well as on the eastern coast of Madagascar. Species diversity is richest in southern India and in northern Australia, with up to six modeled potential species distributions overlapping in a single area (Fig. 2).

3.3. Analysis of current ex situ conservation and further collecting needs for CWR

Twelve out of fifteen species were assigned high priority for further collecting due to the average of total samples, geographic, and ecological gaps in their ex situ germplasm collections (Fig. 3, Supplemental Table 3 and Fig. 1). These high priority species included taxa with narrow distributions (*C. cajanifolius*) as well as those with large ranges (e.g., *C. cinereus*, *C. crassus*, and *C. scarabaeoides*). *Cajanus albicans* was assessed as medium priority due to being modeled as relatively well represented ex situ in regard to ecosystem coverage, and *C. mollis* and *C. platycarpus* as low priority for the same reason, plus high sampling representativeness scores due to having a disproportionately large number of germplasm samples in comparison to herbarium records. The failure of cross-validation of the Maxent models for these species as well as for *C. cajanifolius* resulted in CA50 buffer potential distributions that are likely to be underestimates of the full range of the taxa, especially given the relatively dispersed distributions of available presence records. Thus, the gap analysis assessments for these species likely overestimated the comprehensiveness of their coverage in ex situ repositories. The mean final priority score across all CWR was 2.05 ± 1.94.

Further collecting priorities for the pigeonpea CWR were identified in 20 countries, all of which contained gaps for high priority species (Supplemental Fig. 2 and Table 4). As with species richness, the regions identified for further collecting of the greatest number of species occurred in southern India and in northern Australia (Fig. 4). Occurrence data, potential distribution models, and collecting priorities maps for all species are available in an interactive map format at http://www.cwrdiversity.org/distribution-map/.

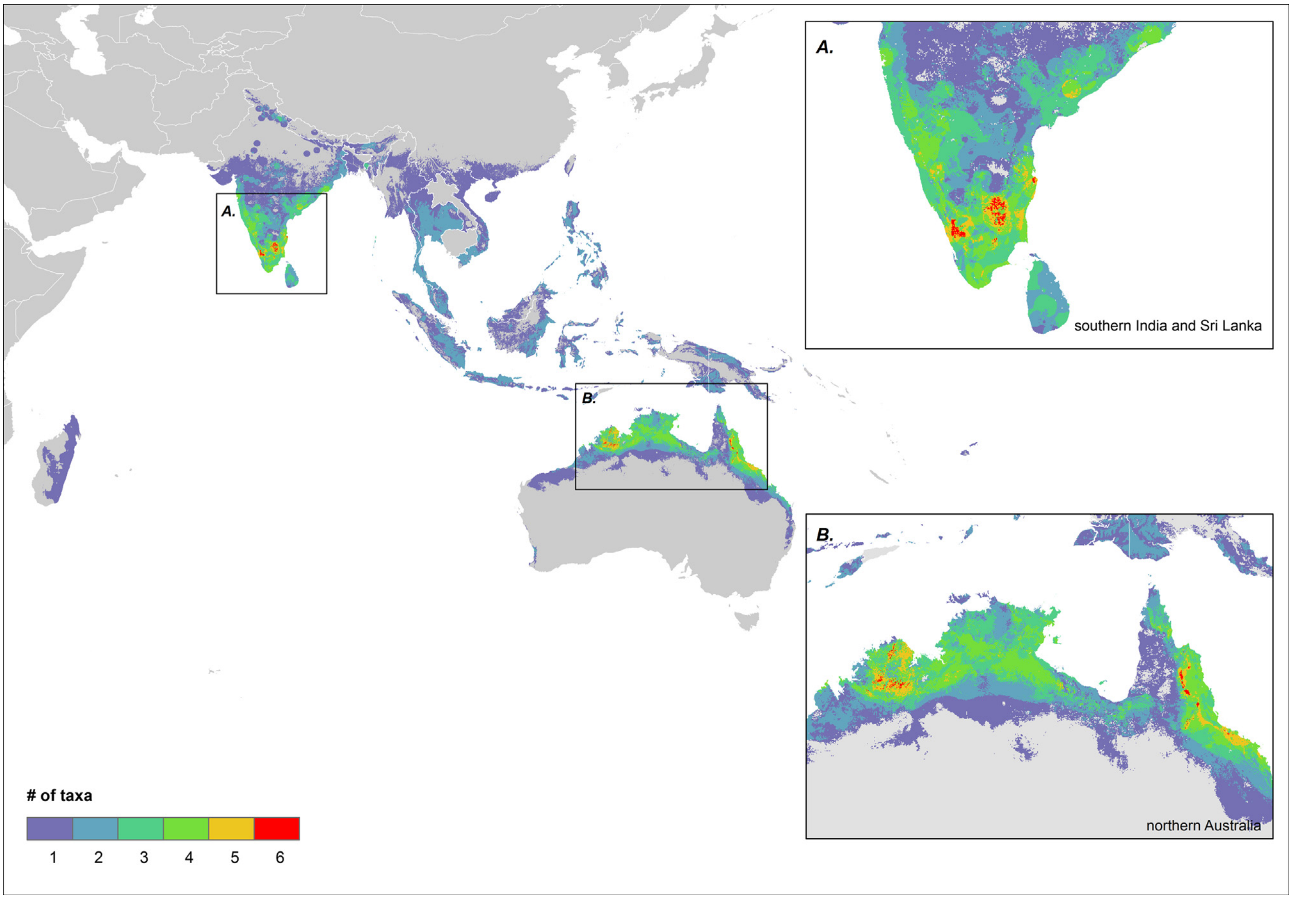

Fig. 2. Richness map for assessed pigeonpea CWR potential distribution models, including high species richness areas in (A) southern India and (B) northern Australia.

The average of the directly comparable expert evaluation priority scores (EPS) across the four experts correlated with the gap analysis results for pigeonpea CWR, with a mean EPS across all experts and all CWR of 2.67 ± 0.9. The assignment of lower priority for further collecting in the mean score across experts in comparison to the gap analysis, with seven species assigned as HPS and eight as MPS, was highly influenced by one expert's determination of species at a lower priority level than the other three experts. This trend was consistent across species (Fig. 3; Supplemental Fig. 3A and Table 3). The contextual expert priority score per species did not vary widely from the comparable score, with a mean across all experts and species of 2.3 ± 0.89. The mean contextual score gave slightly higher priority to species for further collecting than did the comparable score, due to knowledge of threats to taxa in situ and/or to the generally high value given to pigeonpea CWR in regard to their potential contributions to crop improvement (Supplemental Fig. 3B).

The multiple factor analysis revealed relatively strong agreement among the experts and the quantitative and spatial evaluation variables and thus confidence in the expert evaluation index (Supplemental Fig. 3C). Those taxa with the highest accord between all experts and variables and the gap analysis results included Indian species *C. trinervius* and *C. sericeus*, and most of the Australian species (*C. cinereus*, *C. acutifolius*, *C. confertiflorus*, *C. lanceolatus*, and *C. latisepalus*). *Cajanus scarabaeoides* was given a very low index score, and assigned least priority of all species for further collecting by the experts, due to the relatively large total number of ex situ germplasm accessions held for the species, whereas the gap analysis assessed the species as high priority due to large geographic and ecological gaps in ex situ collections in comparison to the total potential distribution. The taxa with relatively few and dispersed occurrence records and resulting CA50 potential distribution models (*C. albicans*, *C. cajanifolius*, *C. mollis* and *C. platycarpus*) were also among those species receiving the lowest index scores (Supplemental Fig. 3D). The evaluations thus served to highlight those species with greatest need of further investigation in regard to their distributions, and at the same time confirmed the robustness of the Maxent models in creating valid depictions of the general range of those CWR with sufficient data availability. Furthermore, the evaluations were useful in identifying erroneous occurrence records for the species, and in highlighting factors contributing to sampling bias in existing collections (e.g., proximity to roads or to research sites), which may affect species distribution modeling.

3.4. Identification of CWR with potential traits of use in breeding for abiotic stress tolerance

Strong linear relationships were found between ecogeographic variables within the study area, justifying the application of the PCA, with 70.3% of variance explained through the first three principal components. The first component (37.9% of variation) was generally positively correlated with high and variable temperatures, soil bulk density and pH, and negatively with precipitation and soil organic carbon. The second component (20.8% of variation) was determined by extreme temperature variables. The third component (11.6% of variation), was positively related with precipitation and finer soils (Supplemental Fig. 4A and Table 2).

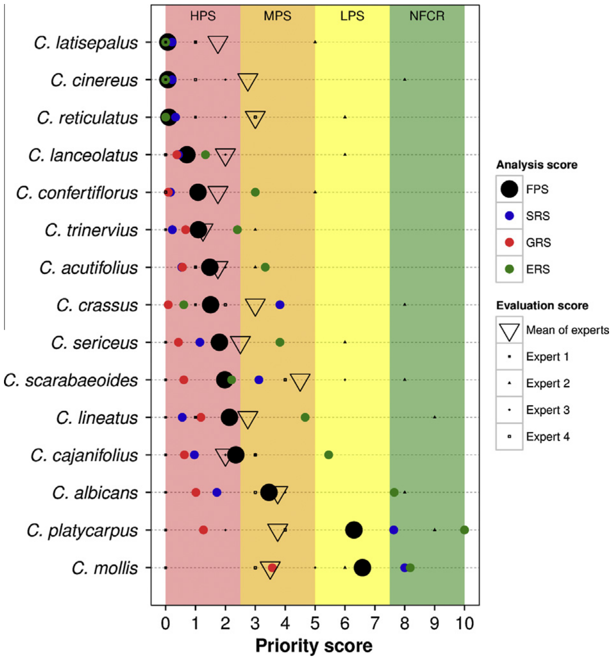

Fig. 3. Gap analysis results and comparable expert assessments per species. CWR are listed by descending priority for further collecting by priority categories [high priority species, HPS (red); medium priority species, MPS (orange); low priority species, LPS (yellow); and no further collecting recommended, NFCR (green)]. The black circle represents the final priority score (FPS) for the species, which is the mean of the sampling representativeness score (SRS), geographic representativeness score (GRS), and ecological representativeness score (ERS). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Occurrence data were segregated into three ecogeographic clusters. The first cluster, corresponding to lowland areas of Southeast Asia and southern India, was characterized generally by highly variable temperatures and finer soils. The second cluster corresponded to more temperate and/or highland regions in South Asia as well as the eastern coast of Australia, and was characterized by dry conditions and colder temperatures. The third cluster, corresponding more generally to India, the Mekong region, and northern Australia, was characterized by low precipitation and low soil carbon (Supplemental Fig. 4B). The exploration of germplasm through the lens of ecogeographic clusters may facilitate the identification of populations of species with valuable traits, in this case for temperature stress resistance and waterlogging tolerance; cold tolerance; and tolerance to drought and low soil fertility, respectively. The great majority of presence records of Australian species *C. acutifolius*, *C. cinereus*, *C. latisepalus*, and *C. lanceolatus*, fell within one cluster, while the South and Southeast Asian species generally contained populations falling into two or three clusters (Table 2, Supplemental Fig. 4C).

The assessment of climatic and edaphic niches of CWR species based upon occurrence data points revealed large differences in adaptation to temperature, precipitation, and soil characteristics variables (Supplemental Fig. 5), including populations of species tolerant of low and high temperatures, as well as very low and very high rainfall. Such variables for many species fell well outside the ecogeographic niche of the cultivated taxon, particularly for low temperatures and high precipitation (Fig. 5A).

For adaptation to high temperatures, populations of northern Australian species such as *C. latisepalus*, *C. cinereus*, *C. acutifolius*, and *C. lanceolatus* stood out, as did *C. platycarpus* and *C. cajanifolius* (Table 2, Supplemental Fig. 5B, F and K). Taxa with large spreads in their adaptation to temperature generally were those more relatively widespread species such as *C. scarabaeoides*, *C. crassus*, and potentially *C. platycarpus*. Species with populations of notable adaptation to low temperatures included *C. mollis*, *C. trinervius*, *C. confertiflorus*, and again *C. platycarpus* (Supplemental Fig. 5B, G and L). Scant occurrence information was available for a number of these species and further exploration is needed to determine the full range of the taxa, which may result in the identification of populations with even greater tolerance to extreme temperatures, e.g. from populations at higher elevations.

Pigeonpea CWR occurring in areas of notably high annual and/or seasonal precipitation included the central and southern Indian species *C. lineatus*, *C. sericeus*, and *C. trinervius*, as well as *C. crassus* (Table 2, Supplemental Fig. 5M, N and Q). As populations of most of these species are adapted to soils with relatively high clay content, these may also represent candidates for traits for waterlogging tolerance (Fig. 5B, Supplemental Fig. 5W).

Populations of CWR encountered in regions of very low annual and/or seasonal precipitation included those from Australian species *C. latisepalus*, *C. cinereus*, *C. acutifolius*, and *C. lanceolatus*, as well as *C. sericeus* and *C. lineatus*, among others (Table 2, Supplemental Fig. 5M, O and R). The pigeonpea crop was also modeled as being tolerant to very low rainfall regions. Despite such tolerance in pigeonpea, we identified eleven CWR species with distributions occurring in regions with less annual precipitation than the driest areas modeled within the middle 90% of occurrence data inputs in regard to the area of cultivation of the crop (i.e.,<500 mm). Maps of potential distributions for a selected number of these CWR that are not currently represented in ex situ genebanks are displayed in Fig. 6, and the differentiation of the occurrence data of these species in the PCA is shown in Supplemental Fig. 4D.

4. Discussion

With 80% of the CWR of pigeonpea in this study assessed as high priority for further collecting for ex situ conservation, agreement from expert evaluators of medium to high importance for all species, and with significant geographic gaps in ex situ collections for virtually all species, it is clear that further conservation action is needed to safeguard the wild genetic resources of this important grain legume. Included in this list of priorities are species with very few germplasm accessions accessible to the global community in genebank information systems, including *C. confertiflorus*, *C. trinervius*, *C. latisepalus*, and the putative progenitor *C. cajanifolius*. Such taxa represent the highest level of priority for further collecting to fill gaps in germplasm collections at the species level. As the species diversity gaps in genebank collections largely align with the geographic distribution of species richness of pigeonpea CWR, hotspots in India and in northern Australia represent particularly high value regions for efficient collecting of the taxa (Fig. 4). These areas may also be of interest for encountering genetic variation created through hybridization between CWR species.

Additional unrepresented distributions of high priority species such as *C. crassus* and *C. scarabaeoides* occur outside these regions, thus targeted collecting throughout the geographic distributions of the species is necessary in order to form germplasm collections that are comprehensive at the population level. Non-native distributions of widespread species, particularly *C. scarabaeoides*, may also be considered for further collecting in the search for useful traits for crop improvement. As techniques for the efficient utilization of wide diversity of plant genetic resources improve, the collection, conservation, and availability of more distant relatives of the crop may also become more worthwhile. We assessed the representation of the other 17–19 species within genus *Cajanus* in ex

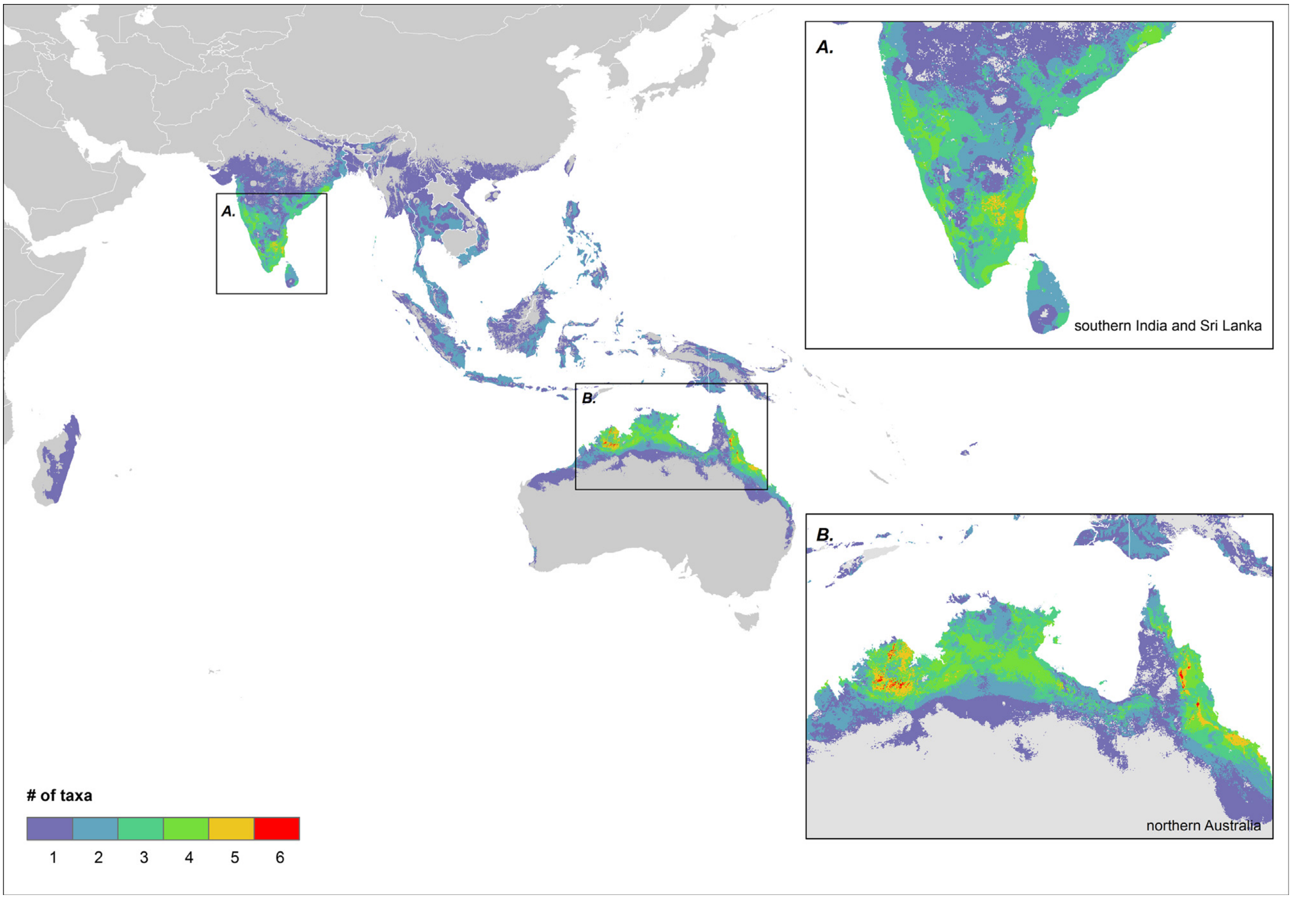

Fig. 4. Further collecting priorities hotspots map for high priority (HPS) pigeonpea CWR. The map displays areas within the potential distributions of HPS species that have not been previously collected for *ex situ* conservation, including areas of high species richness in (A) southern India and (B) northern Australia.

Table 2
Agronomic traits prioritized in pigeonpea breeding objectives potentially associated with ecogeographic niches of CWR.

Taxon	Gene pool	Gap analysis priority	Mean expert priority	Eco geographic cluster	Potential traits of value for major breeding objectives for abiotic stress tolerance in pigeonpea
C. acutifolius	2	HPS	HPS	3	Heat, drought
C. albicans	2	MPS	MPS	1,3,2	
C. cajanifolius	2	HPS	HPS	3,2	Heat
C. cinereus	2	HPS	MPS	3	Heat, drought
C. confertiflorus	2	HPS	HPS	2,3	Cold
C. crassus	3	HPS	MPS	1,3	Temperature variation/seasonality, high precipitation, waterlogging
C. lanceolatus	2	HPS	HPS	3	Heat, drought
C. latisepalus	2	HPS	HPS	3	Heat, drought
C. lineatus	2	HPS	MPS	1,3	High precipitation, waterlogging, drought
C. mollis	3	LPS	MPS	2	Cold
C. platycarpus	3	LPS	MPS	3,2	Heat, temperature variation/seasonality, cold
C. reticulatus	2	HPS	MPS	3,2	
C. scarabaeoides	2	HPS	MPS	1,3,2	Heat, temperature variation/seasonality
C. sericeus	2	HPS	HPS	3,1,2	High precipitation, waterlogging, drought
C. trinervius	2	HPS	HPS	2,1	Cold, high precipitation

Genepool 2 refers to the secondary genepool, and 3 to the tertiary. Priority categories for the CWR of pigeonpea included high (HPS), medium (MPS), and low priority species (LPS) for further collecting for ex situ conservation.

situ conservation as currently minimal, with only 41 accessions from 7 species listed in germplasm repositories.

Cajanus scarabaeoides and *C. platycarpus* were identified as exhibiting potential adaptation to climatic extremes, and are represented by some diversity of accessions conserved ex situ. Existing collections should therefore be further screened for adaptive traits. Other species identified as having potentially useful adaptations in contribution to major abiotic stress tolerance breeding objectives for pigeonpea are represented by very few germplasm accessions, especially *C. confertiflorus*, *C. trinervius*, *C. cajanifolius*, *C. latisepalus*, *C. lanceolatus*, and *C. cinereus*. The climatic extremes of potential distribution models, such as those displayed in Fig. 6, may represent particular areas of interest for exploration. As Maxent models are based upon known presence points for species and

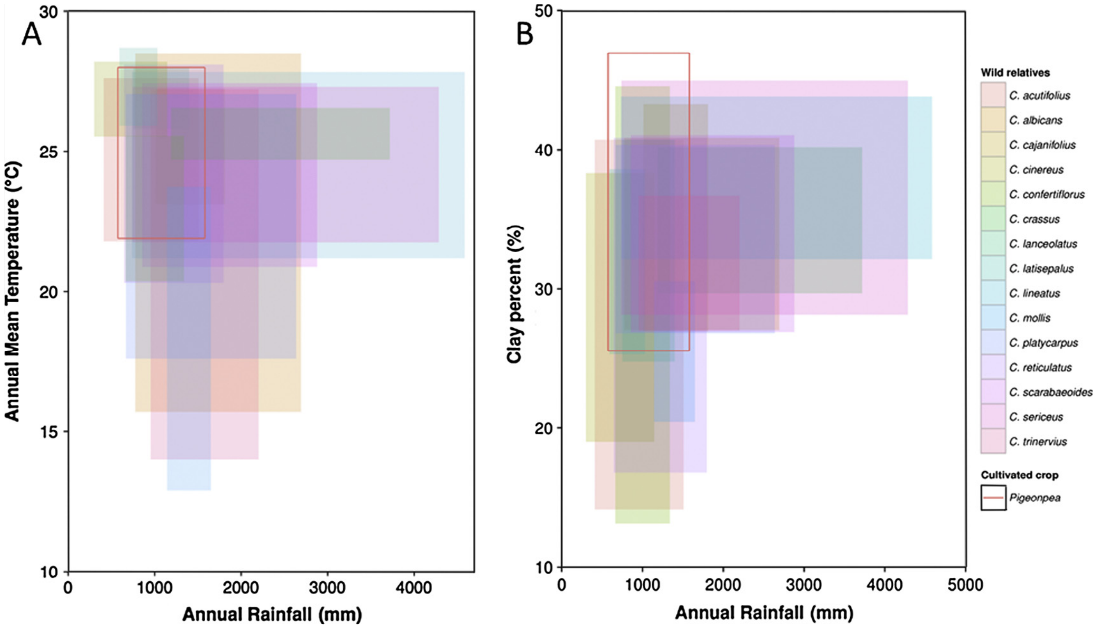

Fig. 5. Ecogeographic niches of pigeonpea CWR for (A) annual mean temperature and precipitation and (B) percent clay and annual precipitation. Niches per species represent the middle 90% of occurrence points, i.e., 10% outliers were excluded. For niches per ecogeographic variable per species, see Supplemental Fig. 5.

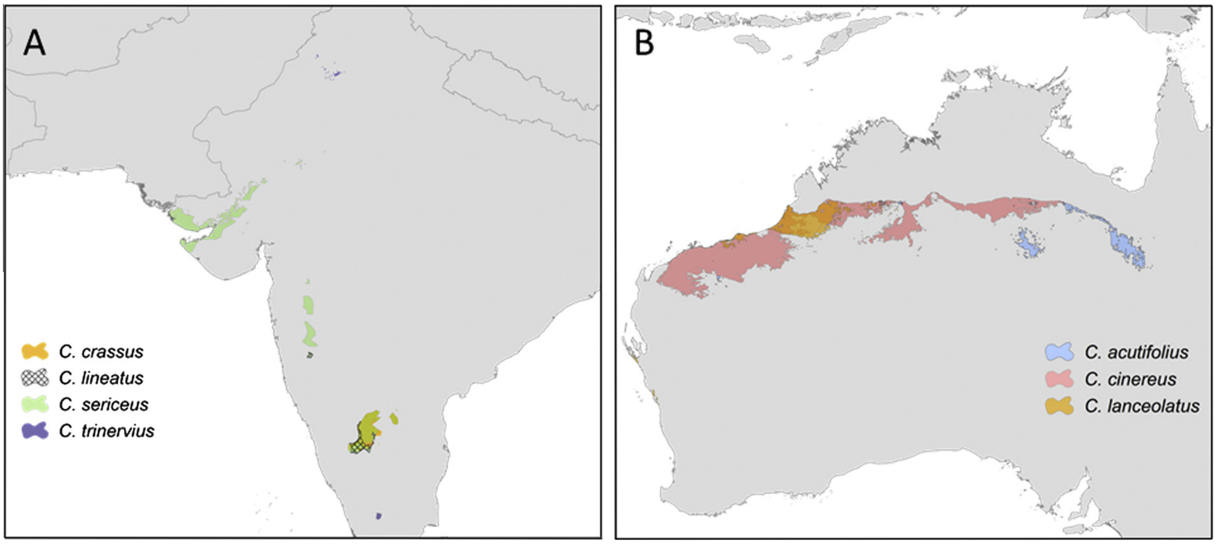

Fig. 6. Potential distributions of selected CWR in (A) south Asia and (B) Australia that are not currently represented in germplasm collections and which occur in regions with <500 mm annual precipitation.

are thus subject to sampling bias, they may not fully capture the possibility of occurrence of populations of CWR species in unique climates (Araújo and Guisan, 2006; Kramer-Schadt et al., 2013; Loiselle et al., 2007). Further field exploration of climatic extremes beyond the edges of the distributions created through these methods may therefore lead to the discovery of new populations with particularly valuable adaptations to abiotic stress (Williams et al., 2009).

Despite sizable existing germplasm collections, species such as *C. scarabaeoides* and *C. albicans* were categorized as medium or high priority for further collecting due to geographic and ecological gaps in the collections. As the cost of conserving and investigating germplasm ex situ is significant, particularly for CWR, a further assessment informed by genotypic diversity analyses of what constitutes sufficient germplasm collections for pigeonpea CWR is warranted. Given adequate resources, further collecting should be considered for these species, as extremely valuable traits sourced from CWR of native Southeast Asian crops such as rice have been found in only a few populations despite screening of a large number of accessions (Brar and Khush, 1997), and accessions of individual CWR species of pigeonpea have been shown to possess notable variation in traits such as resistance to insect pests (Sharma et al., 2003), seed protein content, and days to maturity (Upadhyaya et al., 2013a).

The regions of distribution of pigeonpea CWR species occur in areas undergoing habitat change due to conversion to agriculture, logging, urbanization, mining, invasive species, and climate change, among other factors (Sahai and Rawat, 2014; Sodhi et al., 2004, 2009; Upadhyaya et al., 2013a). It is clear that the window of opportunity for comprehensive collecting for ex situ conservation of pigeonpea CWR will not exist indefinitely.

5. Conclusions

Pigeonpea cultivation is still largely limited to its origins in South Asia and in East Africa. Due to its high nutritive value, agronomic versatility, stress-tolerance, and multiple uses, increasing yield in existing production lands as well as expanding the crop into other areas of Asia and Africa, as well as the Americas, can contribute toward greater agricultural sustainability and improved human nutrition in sub-tropical and tropical regions. While pigeonpea already possesses very favorable agronomic characteristics compared to other major grain legumes, its productivity can be improved via breeding, and its wild relatives show promise in providing critical adaptive traits for major breeding objectives, including heat and cold tolerance, high precipitation, waterlogging, and drought tolerance. Further collecting for ex situ conservation of this diversity, securing long-term funding for this conservation and associated research, ensuring safety duplication of unique germplasm, and sharing of this diversity with the global research community are critical to this process (FAO, 2002; Esquinas-Alcázar, 2005). Greater investment in genotypic and phenotypic characterization and evaluation for traits of interest (Mallikarjuna et al., 2011; Upadhyaya et al., 2013a; Varshney et al., 2011) and in breeding programs using CWR, represent equally urgent steps (Henry, 2014; Tester and Langridge, 2010; Guarino and Lobell, 2011). Through such actions the crop research community will contribute to ensuring the long term viability of this important crop, and be better prepared to adapt to the challenges facing present and future grain legume production.

Author contributions

C.K.K., N.P.C.-A., and A.J. conceived and designed the study. C.K.K., N.P.C.-A., H.A., C.C.S., and V.B. gathered data and performed the analyses. C.K.K., N.P.C.-A., H.A., C.C.S., V.B., M.K., S.L.N., L.J.G.v.d.M., H.D.U., J.R.-V., and P.C.S. analyzed the results. C.K.K., N.P.C.-A., and V.B. wrote the manuscript. C.K.K., N.P.C.-A., H.A., C.C.S., V.B., M.K., S.L.N., L.J.G.v.d.M., H.D.U., J.R.-V., A.J., and P.C.S. edited the manuscript.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2015.01.032. These data include Google maps of the most important areas described in this article.

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