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Planning complementary conservation of crop wild relative diversity in southern Africa

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Abstract

Aim: To identify priority areas for in situ conservation and collection of germplasm for ex situ backup of crop wild relative (CWR) diversity in the Southern African Development Community (SADC) region as part of an action plan for the conservation and use of the region's important CWR diversity.

Location: SADC region.

Methods: Diversity, gap and climate change analyses at species and ecogeographic diversity levels were undertaken for 113 regional priority CWR taxa.

Results: CWR hotspots were identified in Eswatini (former Swaziland), Malawi, Mozambique, South Africa, Tanzania and Zimbabwe. Twenty-one per cent of regionally priority CWR occur exclusively outside existing protected areas (PAs), 50% are not conserved ex situ, and 64% are predicted to be negatively impacted by climate change. A total of 120 existing PAs in 13 countries were identified as containing populations likely to persist in the future for 80% of CWR taxa and about 50% of the ecogeographic diversity of these taxa; remaining diversity can be conserved in an additional 151 complementary sites in 11 countries. Democratic Republic of the Congo, Madagascar, South Africa and Tanzania contain important areas for conserving CWR diversity in situ in which no negative climate change impact is predicted. Priority CWR diversity in the provinces of Bas-Congo (Democratic Republic of the Congo) and Cabinda (Angola) is threatened by climate change and should be collected urgently for ex situ conservation. Other areas rich in ecogeographic diversity that is not conserved ex situ are located in Angola, Democratic Republic of the Congo, Eswatini, Madagascar, Malawi, Mauritius, Mozambique, South Africa, Tanzania and Zimbabwe.

Main conclusions: We identified 120 PAs and 151 complementary sites outside of PAs in 13 SADC countries that could form the basis of the SADC Network for In Situ Conservation of CWR. We also selected priority areas for filling gaps in ex situ collections and for field survey.

KEYWORDS

CAPFITOGEN, climate change analysis, conservation planning, crop wild relatives, diversity analysis, ex situ, gap analysis, genetic conservation, in situ, species distribution modelling

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1 | INTRODUCTION

Crop wild relatives (CWR) are wild plant taxa closely related to crops that have an indirect use as gene donors for crop improvement due to their relatively close genetic relationship to crops (Maxted et al., 2006). They are an important source of novel genetic diversity which is required to maintain food, nutrition and economic security, as amply demonstrated by their use in crop improvement (Dempewolf et al., 2017; Hajjar & Hodgkin, 2007; Maxted & Kell, 2009; USDA, ARS, & NPGS, 2021; Vincent et al., 2013). Yet, CWR diversity is threatened and active conservation of populations in their natural habitats and in genebanks has not received the attention required to ensure no further loss of diversity, as well as access to material for crop improvement.

Climate change is already impacting food security in Africa through increasing temperatures, changing precipitation patterns and greater frequency of extreme weather events which are expected to increase under medium and high CO₂ and greenhouse gas emissions scenarios (IPCC, 2020). Pest, weed and disease pressure on crops and livestock are expected to increase significantly and so are the frequency of wildfires (IPCC, 2020). Further, sub-Saharan Africa has been identified as one of the regions particularly vulnerable to decreases in crop yields which have already been detected in recent years (IPCC, 2020). If current CO₂ and greenhouse gas emissions levels continue, the risks to food security in the region are severe, with limited potential or risk reduction through adaptation (Niang et al., 2014). The Southern African Development Community (SADC), an inter-governmental organization, includes 16 member states (Angola, Botswana, Comoros, the Democratic Republic of the Congo, Lesotho, Madagascar, Malawi, Mauritius, Mozambique, Namibia, Seychelles, South Africa, Eswatini [former Swaziland], Tanzania, Zambia and Zimbabwe) (<http://www.sadc.int/>). The region is important for its diversity of wild relatives of a number of crops of regional and global importance, including coffee, cucurbits, eggplant, lettuce, millets, okra, pulses, rice, sorghum and watermelon (Allen et al., 2019). These wild relatives are likely to possess genes/traits that may help crops adapt to the expected changes in climate and in the environment, but on the other hand, they are also threatened by these same changes, like any other wild plant species. Understanding the expected impacts of climate change on CWR distributions in the SADC region is crucial to plan for their complementary conservation thus contributing to their persistence in the wild, making them available for use in crop improvement.

Combined in situ and ex situ conservation planning is an effective means by which CWR diversity can be conserved in an in situ network of genetic reserves (within existing protected areas, within newly established conservation areas, or in less formally managed in situ locations), with back-up ex situ collections of genetically representative population samples in genebanks (Magos Brehm et al., 2017a). There is no single best method for planning CWR conservation. Nevertheless, CWR conservation planning can be viewed as a series of steps and decisions that follow the same basic pattern: (i) Generation of a CWR checklist; (ii) Prioritization of CWR taxa for

conservation action; (iii) Compilation of the priority CWR inventory; (iv) Diversity analyses of priority CWR (distribution, ecogeographic and genetic diversity analyses); (v) Novel threat assessment of priority CWR; (vi) Gap analysis of priority CWR; (vii) Climate change analysis of priority CWR; (viii) Establishment and implementation of in situ conservation priorities; (ix) Establishment and implementation of ex situ conservation priorities; (x) Monitoring of CWR diversity; and (xi) Promoting the use of CWR (Magos Brehm et al., 2017a; Maxted et al., 1997).

This paper aims at identifying areas in which to establish genetic reserves for active in situ conservation and target areas where collecting germplasm for long-term ex situ conservation should take place. It also presents the results of the first regional assessment of CWR diversity across the SADC region. The results obtained will contribute to the development of a Regional Action Plan for the Conservation and Sustainable Use of CWR, which is a key element to guide national/regional policy development and drive concerted actions throughout the region (Magos Brehm et al., 2019).

The SADC ministers responsible for agriculture, food security, fisheries and aquaculture have approved the white paper for the establishment of the SADC Network for In Situ Conservation of CWR (Dulloo et al., 2020) at their last meeting in May 2021 (J. Shava, SADC secretariat, pers.comm.). Thus, the conservation recommendations presented here will also contribute to the implementation of the SADC Network for In Situ Conservation of CWR, a large step towards regional and global food, nutrition and economic security.

2 | METHODS

2.1 | Occurrence data collation and quality verification

Allen et al. (2017), Allen et al. (2019) identified 113 priority wild relatives (see Table S1.1 in Appendix S1) related to food and beverage crops for immediate conservation action in the SADC region based on two criteria: (i) the value of the related crop for human food and economic security in the region and/or globally, and (ii) the potential or known value of the wild relatives of those crops for crop improvement. Occurrence data for these 113 taxa were then obtained from five sources: Maxted et al. (2004) (*African Vigna*), Nur Fatimah et al. (2012) (*Psophocarpus*), Bioversity International's Collecting Missions Database 1.2 (<https://www.bioversityinternational.org/e-library/databases/collecting-missions/>), GBIF (Global Biodiversity Information Facility) (<http://www.gbif.org/>) and the 'Adapting Agriculture to Climate Change' project's database (version September 2015) (<http://www.cwrdiversity.org/checklist/cwr-occurrences.php>). Occurrence data from all SADC countries, except Comoros, and SADC neighbouring countries (namely Burundi, Central African Republic, Kenya, Republic of Congo, Rwanda, South Sudan, Uganda) were collated. Data from the neighbouring countries to the SADC region were only used for the purpose of species distribution modelling. Occurrence data were merged, standardized

using the 'Occurrence data collation template v.1' (Magos Brehm et al., 2017b), verified, and their quality assessed using GEOQUAL of CAPFITOGEN 2.0 (<http://www.capfitogen.net/en/>; Parra-Quijano et al., 2016) (see Methods S2.1 in Appendix S2). Sampling richness was then mapped at 1 degree resolution (approx. 110 km at the equator) for genebank accessions and for herbarium records, separately.

2.2 | Diversity and gap analyses

Diversity analyses of the priority CWR comprised the identification of regional hotspots based on known occurrences, species distribution models (SDMs) and identification of regional hotspots based on predicted distributions. In situ and ex situ conservation gap analyses were also carried out.

2.2.1 | Species richness and species distribution modelling

Regional taxon hotspots were identified based on SDMs and circular buffers of 50 km (CA50) around each occurrence point as explained next. Twenty-two environmental variables were used to characterize the ecological niche of the 113 priority CWR taxa for which occurrence data were available. These included three geophysical (altitude, aspect, slope) and 19 bioclimatic layers (Table S1.2). Altitude and the 19 bioclimatic variables, representing contemporary baseline climatology (1950–2000), were obtained from the WORLDCLIM 1.4 (Hijmans et al., 2005) at 2.5 arc min (about 4.5 km at the equator) spatial resolution (<https://www.worldclim.org/>), and the derived variables 'aspect' and 'slope' were calculated in ARCGIS 10.4.1 (ESRI, 2016). Species distribution models were obtained using MAXENT 3.4.0 (Phillips et al., 2006) and were considered accurate and stable if they fulfilled the criteria suggested by Ramírez-Villegas et al. (2010) (see Methods S2.2 for more details). For taxa with less than 10 presence records, or whose MaxEnt models did not comply with the validation criteria, potential distributions were estimated by creating a circular buffer of 50 km (CA50) around each occurrence point (Hijmans & Spooner, 2001).

2.2.2 | Conservation gap analyses

CWR observed distributions were overlaid with the existing network of PAs (UNEP-WCMC & IUCN, 2019), and those taxa that did not occur within any existing PAs and those not represented ex situ in genebanks were identified. Additionally, gap analyses at intra-specific level were also carried out based on a generalist Ecogeographic Land Characterization (ELC) map of the SADC region that was created using the ELC mapas tool of CAPFITOGEN (<http://www.capfitogen.net/en/>; Parra-Quijano et al., 2008, 2016). Sixteen ecogeographic variables from three different components (four geophysical variables, seven edaphic and five bioclimatic) were

used to produce the ELC map for the SADC countries at a resolution of 2.5 arc min (approximately 4.5 km at the equator) (Table S1.3); the Calinski and Harabasz (1974) criterion was applied to obtain an objective number of clusters for each bioclimatic, edaphic and geophysical multivariate analysis. By joining the CWR populations (from the occurrence dataset) to the ecogeographic categories of the ELC map (CWR-EC combinations), the representativeness of the ecogeographic diversity of each CWR taxon conserved ex situ in genebanks and passively conserved in situ in the existing network of PAs were assessed using the Representa tool of CAPFITOGEN (<http://www.capfitogen.net/en/>; Parra-Quijano et al., 2008, 2016).

2.3 | Climate change analysis

The impact of climate change on the distributions and richness of the target taxa across the SADC region was assessed using climate projections for 2050 (average 2041–2060) obtained from WORLDCLIM 1.4, (<http://www.worldclim.org>, Hijmans et al., 2005), consisting of downscaled data from General Circulation Models (GCMs) at a spatial resolution of 2.5 arc min (about 4.5 km at the equator). More specifically, median ensembles of 19 GCMs for Representative Concentration Pathway (RCP) 4.5 and RCP 8.5 derived from the fifth assessment of the Intergovernmental Panel on Climate Change (IPCC-AR5) (IPCC, 2014) were developed and used. RCP 4.5 is an intermediate scenario with a likely average increase in annual mean temperature of 2.06°C and range of -1.72 to +4.32°C for 2050, relative to 1960–1990, for the SADC region, and RCP 8.5 is a high greenhouse gas emission scenario with a likely increase of 2.55°C and range of +1.35 to +3.21°C for the same period and region. In order to assess the threat of climate change on suitable habitat for the taxa for which we were able to create stable SDMs (75 taxa), we projected the model results under contemporary baseline conditions (WORLDCLIM v1.4) to future climate scenarios (2050), creating binary layers of suitable versus unsuitable area (Scheldeman & van Zonneveld, 2010).

Maps of change in taxon richness were then obtained where: (i) no species presence is predicted by both current and future climate models; (ii) new potential areas: both future models (RCP 4.5 and RCP 8.5) predict presence in areas where the current model predicts absence; (iii) low impact areas: both future models predict presence in areas where the current model predicts presence; (iv) high impact areas: one future model (RCP 4.5 or RCP 8.5) predicts absence in areas where the current model predicts presence; and (v) very high impact areas: both future models (RCP 4.5 and RCP 8.5) predict absence in areas where the current model predicts presence (based on Scheldeman & van Zonneveld, 2010).

2.4 | In situ and ex situ conservation priorities

The selection of sites where active in situ conservation should take place for the SADC priority CWR was based on the assumption that

CWR in situ conservation should target populations that are as ecogeographically diverse as possible and that are not expected to be negatively affected by climate change (Magos Brehm, Saifan, et al., 2016). On the other hand, it is assumed that CWR ex situ conservation should target areas where species are predicted to occur that are likely to be negatively affected by climate change and areas from diverse ecogeographic conditions (Magos Brehm, Saifan, et al., 2016).

For each taxon for which SDMs were created (75 CWR), information about whether populations occur in new potential areas, low impacted areas, high impacted areas or very high impacted areas by climate change was gathered, as well as in which ecogeographic category (EC) they occur. For each of the remaining 35 taxa for which SDMs were not created (due to the lack of occurrence data or to unstable and underperformed models), only information concerning the EC in which their populations occur was gathered.

The SADC Network for In situ Conservation of CWR would comprise: (i) a network of the existing PAs that include populations of the 75 priority CWR (those for which SDM were developed) that are not predicted to be negatively affected by climate change and that occur in most EC and the most ecogeographic diversity of the remaining 35 taxa, and (ii) a network of complementary sites outside PAs (grids of 50 × 50 km) of the ecogeographic diversity not already included in (i) and also taking account those populations not negatively affected by climate change (only in the case of the 75 taxa for which SDM were created). These complementarity analyses (Rebelo, 1994a, 1994b; Rebelo & Sigfried, 1992) were undertaken using the Complementa tool of CAPFITOGEN (<http://www.capfitogen.net/en/>, Parra-Quijano et al., 2016) to select the minimum number of either PAs or 50 × 50 km grids for the conservation of the 110 priority SADC CWR and their ecogeographic diversity.

The SADC ex situ conservation programme of priority CWR would consist of two different approaches: for taxa with stable SDMs (75 CWR) and for those for which SDMs were not developed (35 CWR). For the 75 CWR, the ecogeographic gaps, that is ecogeographic categories of each taxon that are not represented in genebank, that have already been identified in the ex situ gap analysis, and that correspond to populations that are predicted to be negatively affected by climate change were identified and categorized into two levels of priority. Priority 1 correspond to modelled areas that are exclusive of ecogeographic categories not conserved ex situ and that are negatively affected by climate change, that is occur in high or very high impact areas; and priority 2 correspond to modelled areas that occur in ecogeographic categories not conserved ex situ and that are not negatively affected by climate change (low impact areas). For each CWR taxon, the ELC map was filtered to each of these two priorities and finally the maps of priority 1 and priority 2 modelled taxa richness were created. ArcGIS 10.4.1 (ESRI, 2016) was used to perform these analyses. Regarding those 35 taxa for which SDMs were not created, occurrence records of taxa that are not conserved ex situ

at all as well as those occurrence records of EC not conserved ex situ of partially conserved taxa were compiled and Complementa of the CAPFITOGEN tools (<http://www.capfitogen.net/en/>, Parra-Quijano et al., 2016) was used to identify the minimum number of complementary areas needed to collect and conserve ex situ at least one population from each EC for each taxon.

3 | RESULTS

3.1 | Overview of occurrence data

We collated 14,869 population occurrence records from the SADC region and neighbouring countries, and 12,948 were retained after carrying out data quality checks. A subset of 11,069 occurrences of 110 taxa in this high-quality dataset are from SADC countries only (see Magos Brehm, Gaisberger, et al., 2016). No records were collated for three priority taxa—*Coffea liberica* W. Bull ex Hiern var. *liberica*, *Hibiscus sabdariffa* L. var. *altissimus* Wester, and *Vigna unguiculata* (L.) Walp. subsp. *burundiensis* Pasquet. GenBank accessions are not evenly distributed across the SADC region, with Angola and the western part of the Democratic Republic of the Congo having the least number of genebank accessions. The sampling of herbarium vouchers is more homogeneous, but Angola has again the least number of vouchers, whereas Tanzania and South Africa have the highest number (see Figures S3.1a,b in Appendix S3).

3.2 | Diversity and gap analyses

3.2.1 | Species richness and species distribution models

SDM were obtained for 75 of the priority CWR taxa, and CA50 statistics for 35 taxa (taxa with not enough records to create a SDM or where a SDM was not robust enough) (Table S1.1). Regional hotspots of taxa based on observed species distribution (Figure 1a) and based on predicted distribution (Figure 1b) are mainly located in South Africa, Eswatini, Tanzania, Mozambique, Zimbabwe, and in the Democratic Republic of the Congo. Predicted distributions further locate hotspots in Malawi and Madagascar. Raster files of the SDMs and modelled species richness were made publicly available at Gaisberger (2021) and can be opened in any Geographic Information System.

3.2.2 | Conservation gap analyses

Eighty-seven priority CWR taxa (79%) occur within 443 existing PAs, whereas the remaining 23 do not occur within any existing PAs; the coffee (6 taxa), millet (4) and cowpea (3) crop gene pools present the highest number of priority wild relatives that exist exclusively outside PAs, respectively (Table S1.4). On average, the

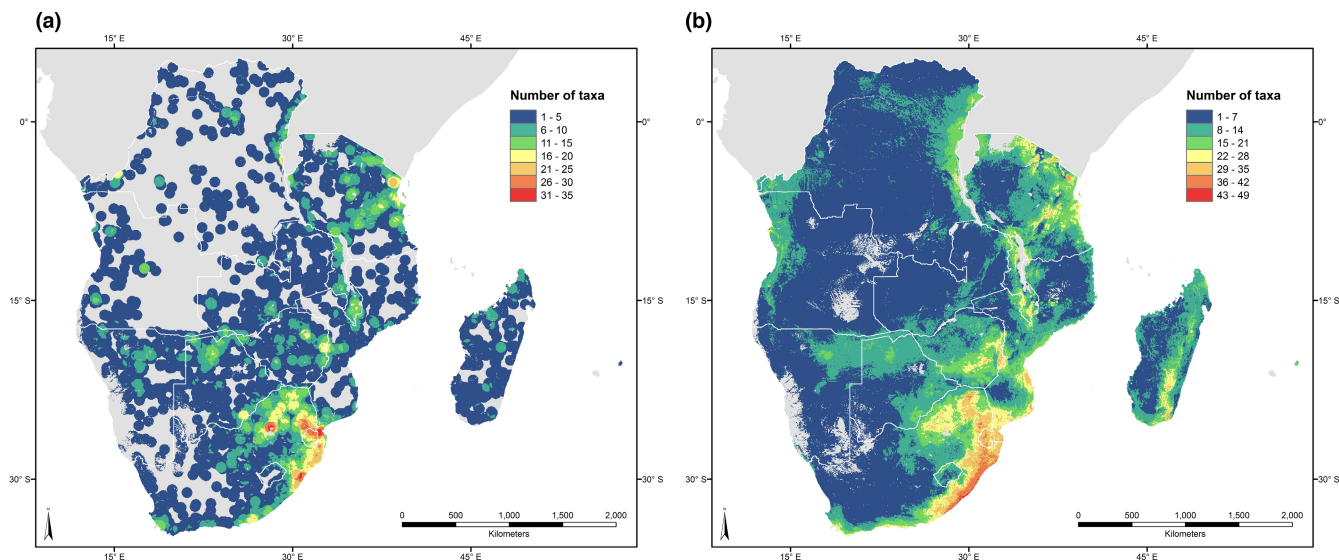


FIGURE 1 Taxon richness based (a) on observed distributions and estimated by creating a circular buffer of 50 km (CA50) around each occurrence point for all 110 priority crop wild relative (CWR) taxa, and (b) on modelled potential distributions of 75 priority CWR taxa combined with CA50 (for the remaining 35 taxa, for which there were not enough records to create species distribution models (SDM) or where SDM were not robust enough)

existing network of PAs passively conserves 60% of the ecogeographic diversity per taxon (considering only those that do occur within PAs), ranging between 9% (*Elaeis guineensis* Jacq.) and 100% (*Abelmoschus ficulneus* (L.) Wight & Arn., *Cichorium intybus* L., *Citrullus rehmii* De Winter, *Coffea bridsoniae* A.P. Davis & Mvungi, *C. kivuensis* Lebrun, *C. mufindiensis* Hutch. ex Bridson subsp. *lundaziensis* Bridson, *C. pocsii* Bridson, *C. racemosa* Lour., *Gossypium anomalum* Wawra subsp. *anomalum*, *G. triphyllum* (Harv.) Hochr., and *Sesamum alatum* Thonn.) of diversity included in these areas (Table S1.5).

The ex situ gap analysis showed that 58 taxa (51%) are not represented in genebank collections; the coffee gene pool encompasses the highest number of priority wild relatives (22 taxa) not conserved ex situ, followed by the *Brassica* complex (4) (Table S1.6). Out of the 55 priority CWR that are conserved ex situ, 89% have less than 50% of known populations conserved ex situ. Additionally, the ex situ gap analysis at ecogeographic diversity level based on the SADC ELC map (Figure S3.2 and Magos Brehm, 2022) revealed that an average of 51% of ecogeographic diversity of SADC priority CWR is not conserved ex situ (Figure S3.3, Table S1.7).

Taking into consideration both in situ and ex situ conservation, there are 18 taxa that do not occur in PAs nor in genebanks, with coffee (6 taxa), cowpea (2) and millet (2) gene pools with the highest number of wild relatives (Table 1). Considering ecogeographic diversity, the taxa with the least amount of diversity conserved are *Solanum umtuma* Voronts. & S. Knapp, *Dioscorea minutiflora* Engl., *D. praehehensis* Benth., *Coffea mayombensis* A. Chev., *D. smilacifolia* De Wild. & T. Durand, *Helianthus debilis* Nutt. subsp. *cucumerifolius* (Torr. & A. Gray) Heiser, *S. aureitomentosum* Bitter, *C. eugenioides* S. Moore, *C. kimboensis* Bridson and *Plectranthus barbatus* Andrews, which are only conserved passively in situ. On the other hand,

Gossypium triphyllum is the only priority CWR that has its full range of ecogeographic diversity conserved both ex situ and passively in situ (Figure S3.3).

3.3 | Climate change analysis

Sixty-four per cent of the target CWR taxa are predicted to lose distribution area in both RCP 4.5 and RCP 8.5 scenarios (44 taxa are predicted to be very highly negatively affected and four highly negatively affected by climate change), whereas 36% (27 taxa) are predicted to be positively affected by climate change under both scenarios (Table S1.8). The cowpeas (8) and millets (7) priority wild relatives are predicted to be the most affected by climate change, whereas the asparagus, date palm, okra, pigeonpea and tamarind wild relatives are predicted to be positively affected. All Brassicas, endive, Hausa potato, Kei apple, lettuce, Natal plum, olive and broad bean wild relatives are predicted to be very highly negatively affected by climate change (Figure S3.4).

Modelled potential distribution richness under RCP 4.5 and RCP 8.5 scenarios show CWR taxon hotspots are mainly located in South Africa, Tanzania and Zimbabwe (Figure S3.5). The impact of climate change on species distribution is, as expected, not homogenous. Particularly the north-western part of South Africa, southwestern parts of Mozambique and Zimbabwe, west Tanzania and south of Madagascar are predicted to suffer the greatest change in both scenarios (RCP 4.5 and RCP 8.5). Other parts of southern Africa are predicted to have an increase in species diversity in both scenarios (e.g. central-west of South Africa, central Democratic Republic of the Congo). The predicted changes under RCP 8.5 seem to be more drastic than under RCP 4.5 (Figure S3.6). Raster files of the SDMs

TABLE 1 Regional priority crop wild relative taxa which are not conserved ex situ nor passively conserved in existing protected areas in the Southern African Development Community region, and their related crops

Related crops	Taxa not conserved ex situ nor passively in situ
Brassica complex	<i>Brassica elongata</i> Ehrh.
Coffee	<i>Coffea brevipes</i> Hiern.
	<i>Coffea congensis</i> A.Froehner
	<i>Coffea kapakata</i> (A.Chev.) Bridson
	<i>Coffea liberica</i> W.Bull ex Hiern var. <i>dewevrei</i> (De Wild. & T. Durand) Lebrun
	<i>Coffea liberica</i> W.Bull ex Hiern var. <i>liberica</i> ^a
	<i>Coffea mufindiensis</i> Hutch. ex Bridson subsp. <i>pawekiana</i> (Bridson) Bridson
Cottonseed	<i>Gossypium longicalyx</i> J.B. Hutch. & B.J.S. Lee
Cowpea	<i>Vigna keraudrenii</i> Du Puy & Labat
	<i>Vigna unguiculata</i> (L.) Walp. subsp. <i>burundiensis</i> Pasquet ^a
Millets	<i>Eleusine tristachya</i> (Lam.) Lam.
	<i>Pennisetum sieberianum</i> (Schltdl.) Stapf & C.E.Hubb.
Okra	<i>Hibiscus sabdariffa</i> L. var. <i>altissimus</i> Wester ^a
Safflower	<i>Carthamus lanatus</i> L.
Shea oil	<i>Vitellaria paradoxa</i> C.F. Gaertn.
Sugarcane	<i>Saccharum spontaneum</i> L. subsp. <i>aegyptium</i> (Willd.) Hack.
Sunflower	<i>Helianthus argophyllus</i> Torr. & A.Gray
Sweet potato	<i>Ipomoea littoralis</i> Blume

^aTaxa for which occurrence records were not obtained.

under the climate change scenarios were made publicly available at Gaisberger (2021).

3.4 | CWR in situ conservation priorities

The results of the ecogeographic diversity and climate change analyses were combined to inform recommendations for the establishment of a network for the in situ conservation of regionally important CWR taxa in the SADC region. The PA complementarity analysis for the 75 taxa for which not only the ecogeographic diversity but also the climate change analyses (only populations predicted not to be negatively affected by climate change) were possible, and the 35 taxa for which only ecogeographic diversity was considered, showed that out of the 570 combinations of CWR–ecogeographic categories (CWR–EC), 87 taxa (79%) and about 50% of their ecogeographic diversity can be actively conserved in 120 existing PAs (Figure 2a, Table S1.9). The 10 highest priority PAs encompass 22% of the CWR–EC combinations and are located in Botswana, Malawi, Namibia, South Africa and Tanzania (Figure 2a), while 97 are needed to conserve 50% of total diversity in situ (Tables S1.9, S1.10). The

number of complementary PAs that form part of the proposed SADC network ranges from 43 in Tanzania and one in Angola and one in Eswatini. The proposed network also includes one transboundary PA: the Parc Maloti-Drakensberg World Heritage Site between Lesotho and South Africa (Figures 2 and 3).

The remaining 21 priority CWR taxa and remaining diversity (257 CWR–EC combinations) not already covered by the proposed PA complementary network are represented in a complementary non-PA network which comprises 151 sites of 50 × 50 km in 11 countries where less formally managed in situ reserves could be established (Figure 2b). The active management of CWR populations in 39 of these sites would be needed to conserve 50% of this remaining diversity, although in situ population management in 10 could conserve 20% of the diversity. The sites in which the greatest amount of diversity could be conserved are situated in northwest Angola, eastern South Africa and southern Tanzania (Table S1.11, Table S1.12). The number of complementary 50 × 50 km sites that could form part of the SADC in situ CWR network ranges between 40 in South Africa and one in Eswatini. The proposed network also includes two transboundary sites that should be protected: one that spans between Mozambique and Eswatini, and another that occurs in Mozambique and Malawi (Figure 3).

3.5 | CWR ex situ conservation priorities

Priority 1 areas were identified for 39% of taxa (29 out of 75 taxa). The provinces of Bas-Congo in the Democratic Republic of the Congo and Cabinda in Angola are the most important areas for conserving CWR ecogeographic diversity predicted to go extinct under climate change scenarios. Other areas include Benguela, Cuanza Norte and Cuanza Sul provinces in Angola, Katanga, Kivu and Orientale in the Democratic Republic of the Congo, Hhohho and Manzini in Eswatini, Antananarivo and Fiaranantsoa in Madagascar, Eastern Cape and KwaZulu-Natal in South Africa, and Kagera and Kigoma in Tanzania (Figure 4). Priority 2 areas were identified in western Angola, eastern Democratic Republic of the Congo, eastern Madagascar, Malawi, Mauritius, Mozambique, south-eastern South Africa, Eswatini, Tanzania, and eastern Zimbabwe. Areas rich in ecogeographic diversity gaps also include Lubombo in Eswatini, Fianarantsoa and Toliara in Madagascar, the Eastern and Western Cape and KwaZulu-Natal in South Africa, and Arusha, Kilimanjaro, Manga, Morogoro and Tanga in Tanzania (Figure 5).

A complementarity analysis of the ecogeographic gaps of the 35 CWR taxa for which SDMs were not developed was also carried out. Out of these 35 taxa, only *Elaeis guineensis*, *Eleusine indica* (L.) Gaertn., *E. kigeziensis* S.M. Phillips, *Oryza schweinfurthiana* Prodoehl and *Secale strictum* (C. Presl) C. Presl subsp. *africanum* (Stapf) K. Hammer have populations conserved ex situ. Four hundred and eighty-one occurrence records were used to identify 97 CWR–EC combinations. Results indicate that germplasm collection in 73 complementary 50 × 50 km sites in 10 countries would be needed to conserve all 97 CWR–EC combinations. This forms a complementary

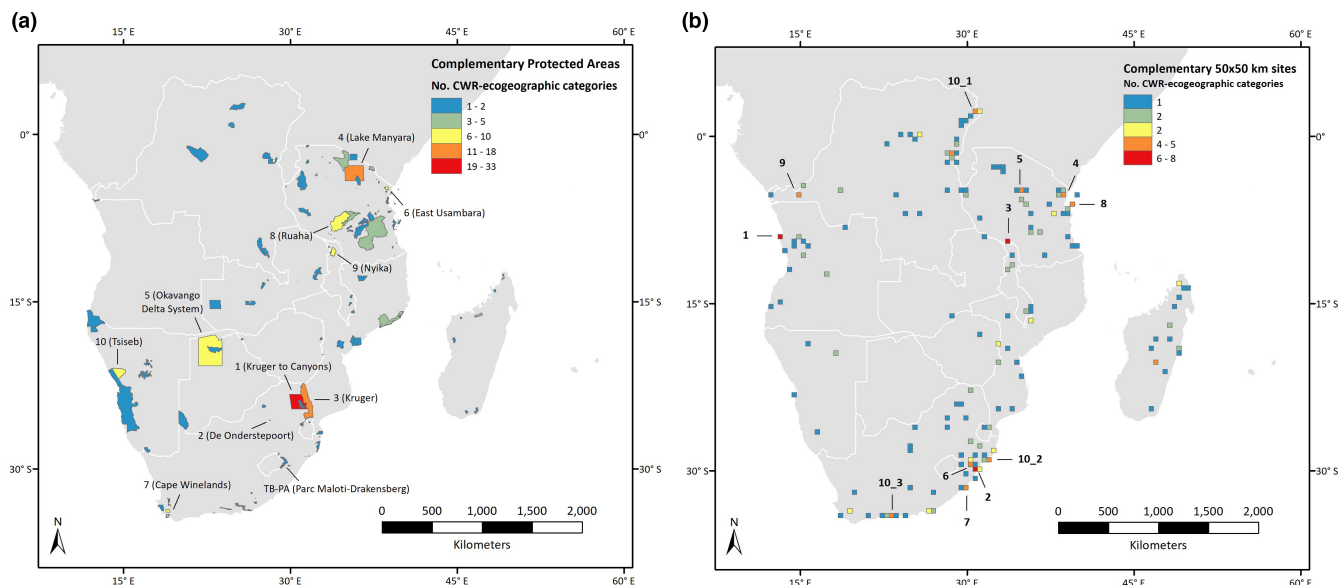


FIGURE 2 Southern African Development Community Network for the In Situ Conservation of Crop Wild Relatives (CWR): (a) Complementary network of the 120 existing protected areas (PAs) where active in situ conservation of 87 regional priority CWR (out of 113) and about 50% of their ecogeographic diversity could be undertaken; (b) Outside-PA in situ complementary network where active in situ conservation of the remaining 21 taxa and their diversity not already covered by the PA complementary network could take place. The numbers on the map indicate the 10 highest priority PA/sites for conservation; rank numbers followed by underscore and 1, 2, etc, correspond to sites with the same priority level (i.e., with the same number of different and complementary CWR–ecogeographic category [EC] combinations, same total number of CWR–EC, the same number of different taxa and the same number of occurrences)

network of sites where collecting for ex situ conservation should be carried out. Twenty-five complementary sites (34% of the total) encompass c. 50% of the CWR–EC combinations (Table S1.13). The four highest priority sites are located in the Free State and KwaZulu-Natal in South Africa, and in Lindi and Tanga provinces in Tanzania. Tanzania, South Africa and the Democratic Republic of the Congo are the countries with the higher number of complementary sites and of CWR–EC gaps (Figure 6).

4 | DISCUSSION

Given the value of CWR for food, nutrition and economic security, the importance of the SADC region to secure regionally and globally important CWR diversity, and that this diversity is not adequately conserved in situ or ex situ, it is important to develop a regional action plan. Such plan raises awareness of the value of CWR diversity, reviews existing policies dedicated to CWR conservation and sustainable use, integrates CWR conservation into existing national, regional and global conservation and sustainable use programmes, and defines the specific actions and resources required to effectively conserve and sustainably utilize regionally important CWR diversity (Magos Brehm et al., 2019). In this paper, we have presented the results of the first analysis of regionally important CWR diversity in the SADC region to inform the establishment of a regional network and action plan for long-term in situ and ex situ conservation and sustainable use of the region's unique CWR diversity. We applied existing methodologies and combined them so that in situ and ex situ

conservation recommendations could be made based on the gaps in the conservation of this diversity and on the impact of climate change in its distribution.

Despite not being identified as one of the major global CWR hotspots, Allen et al. (2019) identified the SADC region as containing important diversity for food and economic security within and outside the region and 68% of the SADC priority CWR taxa have been identified as globally important by Vincent et al. (2013). Further, three sites within PAs in Tanzania and an additional two sites outside PAs in Angola and Tanzania have been identified to conserve globally important CWR diversity (Vincent et al., 2019), whereas Castañeda-Álvarez et al. (2016) recognised southeastern Africa a priority area for further germplasm collecting activities for globally important CWR taxa. Based on the available data, our results show that CWR diversity is mainly concentrated in eastern South Africa, Mozambique, Eswatini, Zimbabwe, eastern Democratic Republic of the Congo, Tanzania, Malawi and Madagascar and that is not adequately conserved either in situ or ex situ. CWR in the SADC region do occur in the existing PA network but they are not actively managed. Nineteen per cent of the regionally important CWR taxa occur exclusively outside PAs and 50% are not found in ex situ collections at all. Our results concur with those of Castañeda-Álvarez et al. (2016), identifying Eswatini and eastern South Africa, but add eastern Democratic Republic of the Congo, Madagascar, and north-eastern Tanzania as important under-collected areas for ex situ conservation of regionally and globally important CWR.

Although the impact of climate change on the distribution of CWR is expected to vary among taxa and ecogeographic conditions

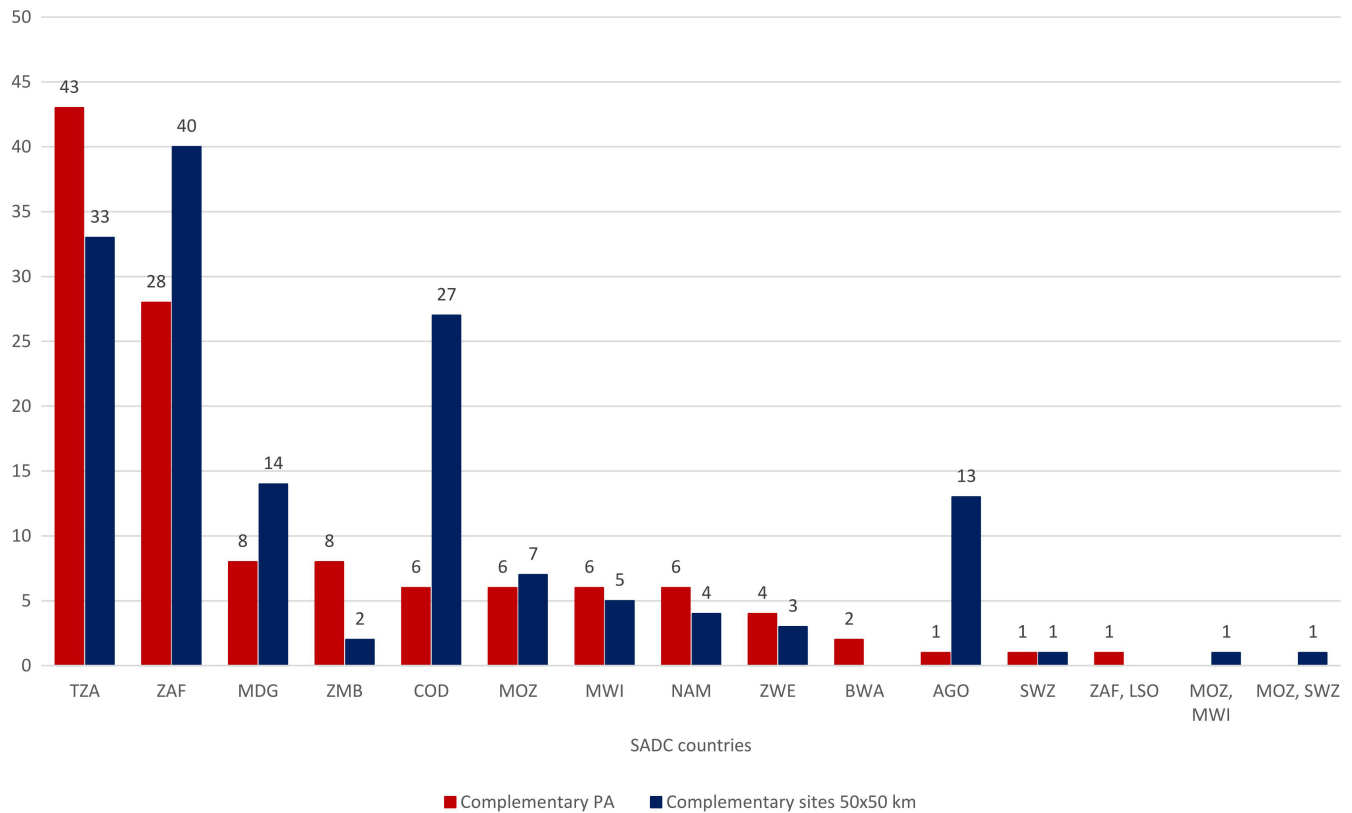


FIGURE 3 Numbers of complementary protected areas (PA) and of complementary 50 × 50 km sites that could form part of the Southern African Development Community regional in situ crop wild relative network per country. AGO, Angola; BWA, Botswana; COD, Democratic Republic of the Congo; LSO, Lesotho; MDG, Madagascar; MOZ, Mozambique; MWI, Malawi; NAM, Namibia; SWZ, Eswatini, TZA, Tanzania, ZAF, South Africa; ZMB, Zambia; ZWE, Zimbabwe

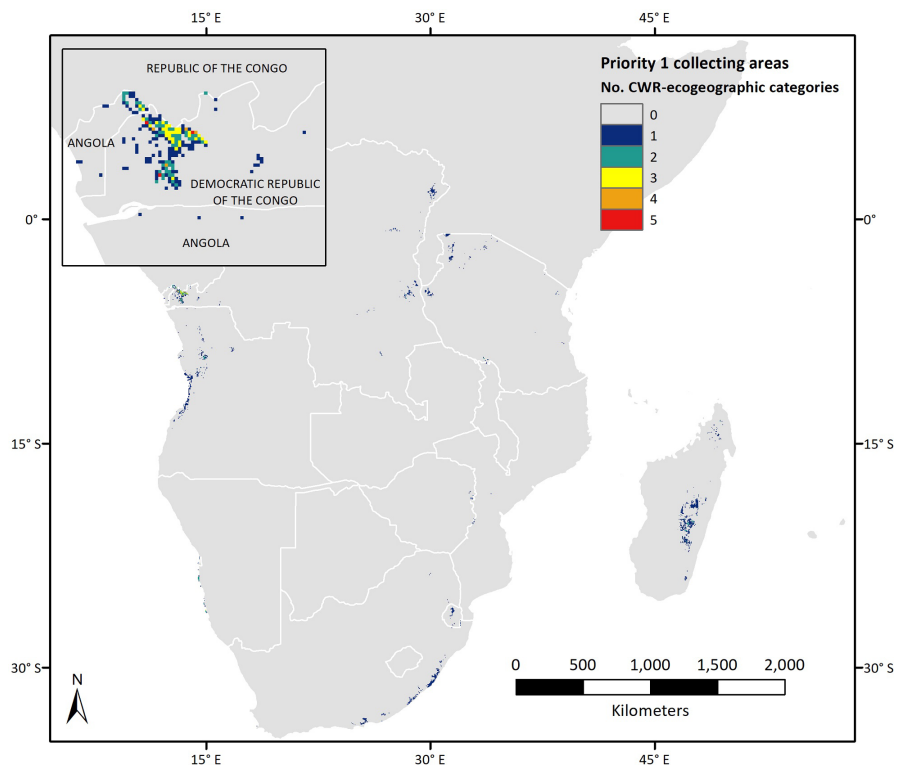


FIGURE 4 Priority 1 areas for germplasm collection of regionally important crop wild relative diversity (i.e., predicted richness areas of ecogeographic diversity not conserved ex situ that is likely to disappear with climate change). In the box, a close-up of Angola and the Democratic Republic of the Congo – the most important priority 1 countries

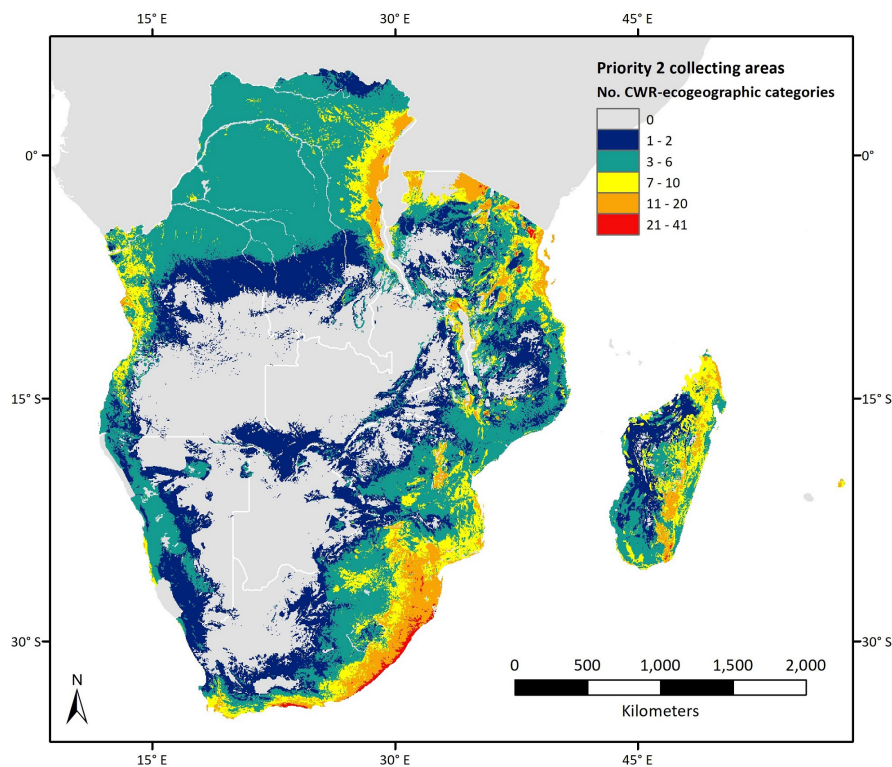


FIGURE 5 Priority 2 areas for germplasm collection (i.e., predicted richness areas of the remaining ecogeographic diversity not conserved ex situ which is not unique to areas negatively impacted by climate change)

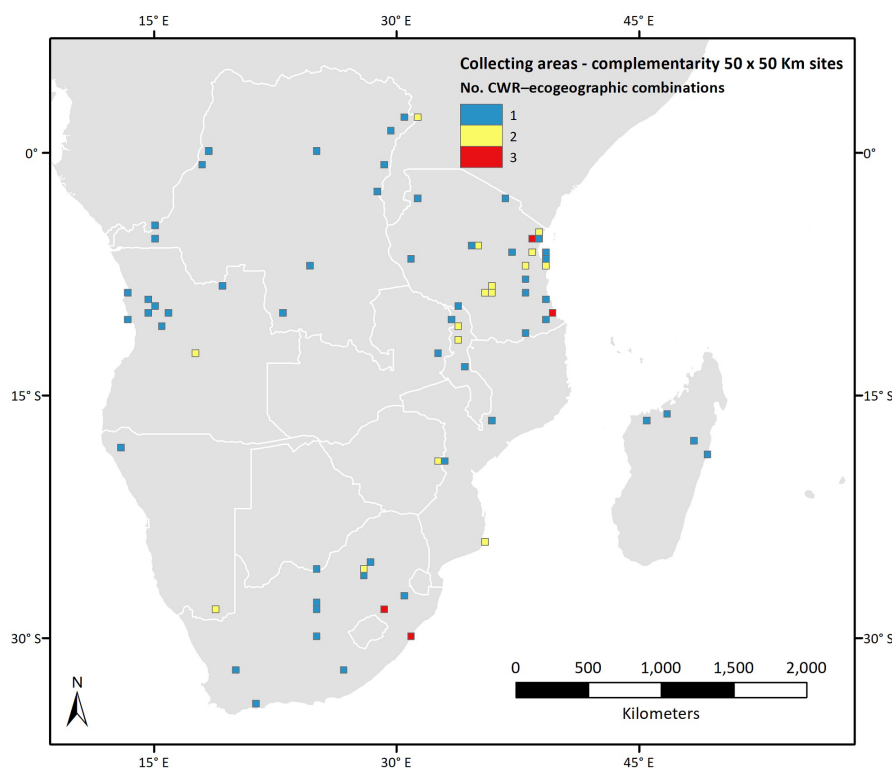


FIGURE 6 Complementarity map of collecting sites for ex situ conservation of the ecogeographic gaps of the 35 taxa for which species distribution models were not developed

(Jarvis et al., 2008; Phillips et al., 2017; van Treuren et al., 2020), it is still predicted to severely impact the distribution and species composition (Gaisberger et al., 2017; Midgley et al., 2001), eventually driving many species to extinction (Thomas et al., 2004). Africa is one of the least studied regions in this respect but climate change is indeed projected to affect negatively all levels of biodiversity (i.e. from genes, to species and biomes—Sintayehu, 2018). Here, we show

that changes in climate are expected to negatively impact on 64% of regionally important CWR taxa. Specifically, the cowpea and millets are the crop gene pools with the largest number of taxa negatively affected by climate change. These are the gene pools, together with coffee, that present the highest number of priority wild relatives not conserved passively in situ or in ex situ in genebanks. Interestingly, some of these taxa have already been used in crop improvement.

For example, *Pennisetum squamulatum* Fresen., a wild relative of millet, that has been used for earliness, long inflorescence, leaf size and male fertility improvement of pearl millet (*P. glaucum* (L.) R. Br.) (Vincent et al., 2013) and that occurs exclusively outside PAs; *Coffea eugenoides* that has been used for flavour improvement of Arabic coffee (*C. arabica* L.) (USDA, ARS, & NPGS, 2021) and that is not conserved *ex situ*; and *C. pseudozanguebariae* that has been used early maturity and caffeine-free arabica (*C. arabica*) and robusta coffee (*C. canephora* Pierre ex A. Froehner) (USDA, ARS, & NPGS, 2021) and that is not conserved *ex situ*. It should be pointed out that microhabitat characteristics (Sedlacek et al., 2015, 2016), small-scale variation in gene flow (Cortés et al., 2014), plasticity in taxa demography (Pichancourt et al., 2019) of target CWR populations, as well as the interactions between target CWR and abiotic (e.g. plant–soil interaction, see Sedlacek et al., 2014) and biotic factors (e.g. plant–plant interaction such as species competition or facilitation, see Bueno & Llambí, 2015; Llambí et al., 2018; Mora et al., 2018; Wheeler et al., 2015) have not been considered in this study. The study of all these additional elements may help clarify and refine our knowledge about how CWR in the SADC region may response to changes in their environments.

Conservation priorities for 113 priority CWR taxa of this region were identified to inform a regional action plan for the conservation and sustainable use of CWR by: (i) establishing genetic reserves in 120 PAs and in 151 sites outside of formally established PAs in 13 SADC countries (contributing to the establishment of the SADC Network for In situ Conservation of CWR); (ii) initiating collecting germplasm collection and an *ex situ* conservation programme for all target taxa which prioritizes collection of population samples of taxa that are not conserved *ex situ*, that present conservation gaps in their ecogeographic diversity range, or for which their diversity is likely to go extinct with climate change; and (iii) undertaking a field survey programme that prioritizes taxa for which records have not been compiled, for which a small number of records exists throughout the region, or for those that are not known to occur within existing PAs (see the details below).

The recommendations for the conservation of the regionally important CWR diversity provided here should also be reviewed in the light of national priorities such as those identified in Malawi (Mponya et al., 2021), Mauritius (Bissessur et al., 2019), South Africa (Holness et al., 2019), Zambia (Ng'Uni et al., 2019), and underway in other several SADC countries (Angola, Democratic Republic of the Congo, Eswatini, Lesotho, Tanzania, Zimbabwe, etc.) in the context of the Darwin Initiative funded project 26–023 'Bridging agriculture and environment: Southern African crop-wild-relative regional network' (<http://www.cropwildrelatives.org/sadc-cwr-net/>). The integration of national and regional priorities (i.e. national sites to conserve national priority CWR and regional sites to conserve regional priority CWR) has already been discussed and recommended for Europe (see Maxted et al., 2015) and it is suggested to follow the same concept in the SADC region.

The foundations of the regional action plan for the conservation and sustainable use of CWR and of the SADC Network for In Situ

Conservation of CWR have been laid with this paper. The network was recently approved by the SADC Ministers responsible for agriculture, food security, fisheries and aquaculture (J. Shava, SADC secretariat, personal communication) and is expected to be implemented soon, thus contributing to the food, nutrition and economic security of the 345.2 million people who live in the region (SADC, 2018) and face the negative impacts of climate change.

4.1 | SADC network for active in situ conservation of regionally important CWR diversity

To effectively conserve the SADC region's important CWR diversity, we suggest the establishment of the SADC Network for the In Situ Conservation of CWR, in which the active management and monitoring of CWR populations would be carried out (see Iriondo et al., 2012, 2021). Based on the results of the current work, this network would include populations that are genetically/ecogeographically diverse and likely to persist in the future under climate change, that is the sites identified act as refugia for the in situ conservation of regionally priority CWR diversity (see Baumgartner et al., 2018; González-Orozco et al., 2021). Our results indicate that Angola, South Africa, Tanzania and Zambia are particularly important countries for this purpose.

Specific recommendations are to:

1. Verify the population occurrences and fitness status (i.e. their ability to survive and reproduce) the recommended areas/sites below, as well as their suitability for the establishment of genetic reserves following the standards of Iriondo et al. (2012).
2. Establish genetic reserves within 120 PAs in 13 countries to actively conserve 87 of the regionally important CWR taxa and 50% of their ecogeographic diversity (see Figure 2a), with priority afforded to the 10 PAs located in Botswana, Malawi, Namibia, Tanzania and South Africa that have particularly high concentrations of regionally important CWR diversity.
3. Establish genetic reserves outside formally established PAs in 151 sites in 11 countries to conserve a further 21 CWR taxa and the remaining ecogeographic diversity (see Figure 2b). Priority afforded to the 10 sites located in Angola, Democratic Republic of the Congo, Tanzania and South Africa.

The conservation of CWR populations in existing PAs is an efficient action as the areas are already allocated for conservation purposes, and these taxa can provide additional value to PAs and the ecosystem services they provide. The management of these areas should be adapted to incorporate the populations of CWR that occur within them (Iriondo et al., 2021). On the other hand, 21% of regionally important CWR diversity found outside PAs has been identified in the SADC region, highlighting the importance of conserving these resources in situ outside formally established PAs. A study carried by Wainwright et al. (2019) concluded that farmers in local communities in Zambia are interested in conserving CWR in their fields and estimated that the incentives needed to achieve this goal would be relatively modest,

ranging from US\$23–91/ha per year. Moreover, a genetic reserve around a farmer's field in currently being established in Malawi (N. Mponya, MPGR, pers. comm.). As such, local communities should be involved in the establishment of genetic reserves and management of the CWR populations to ensure they are efficiently conserved.

4.2 | SADC ex situ conservation programme for regionally important CWR diversity

The ex situ conservation programme for the regionally important CWR diversity in the SADC region recommended here is based on predicted richness areas of ecogeographic diversity not conserved ex situ that is likely to disappear with climate change (Priority 1), and on predicted richness areas of the remaining ecogeographic diversity not conserved ex situ (not unique to areas negatively impacted by climate change) (Priority 2). Our results suggest that Angola and Democratic Republic of the Congo encompass the most important Priority 1 areas, whereas ecogeographic diversity gaps (Priority 2) are concentrated in Angola, Democratic Republic of the Congo, Eswatini, Madagascar, Malawi, Mauritius, Mozambique, South Africa, Tanzania and Zimbabwe.

Germplasm collection based on ENSCONET (2009a) and Guarino et al. (2011) is recommended in order of priority at the following locations:

1. Priority 1: the province of Bas-Congo in the Democratic Republic of the Congo and Cabinda in Angola (Figure 4).
2. Priority 2a: Angola, Democratic Republic of the Congo, Eswatini, Madagascar, Malawi, Mauritius, Mozambique, South Africa, Tanzania, Zimbabwe, with priority assigned to Lubombo in Eswatini, Fianarantsoa and Toliara in Madagascar, the Eastern and Western Cape and KwaZulu-Natal in South Africa, and Arusha, Kilimanjaro, Manga, Morogoro and Tanga in Tanzania, which are the areas rich in ecogeographic diversity gaps (Figure 5).
3. Priority 2b: 73 sites of 50x50 km identified to conserve the ecogeographic gaps of the 35 taxa for which SDMs were not developed (Figure 6), with priority assigned to two sites located in the Free State and KwaZulu-Natal in South Africa, and two sites located in Lindi and Tanga provinces in Tanzania.
4. The 151 sites identified in 11 countries in which to conserve 21 CWR taxa and the ecogeographic diversity not conserved within the complementary network of PAs (see Figure 2b).

Additionally, all CWR diversity conserved in situ should be backed-up in ex situ collections in genebanks as recommended by Ford-Lloyd and Maxted (1993) to avoid the eventual loss of CWR diversity and to facilitate its access and use in crop improvement. Finally, the ex situ accessions should be evaluated for viability, monitored, regenerated and duplicated in national genebanks, in the SADC Plant Genetic Resources Centre, and eventually in another international genebank (e.g. the Svalbard Global Seed Vault) to ensure their long-term conservation following the protocols of ENSCONET (2009b), FAO (2014), and Rao et al. (2006).

4.3 | Other recommendations

1. Immediate search for occurrence data in the known countries of distribution and subsequent field survey of the SADC priority CWR for which records have not been collated (*Coffea liberica* var. *liberica*, *Hibiscus sabdariffa* var. *altissimus* and *Vigna unguiculata* subsp. *burundiensis*).
2. Field survey for the 32 CWR taxa for which data for only 10 or less populations were found (Table S1.1), and in those countries with a low number of recorded populations (Mauritius, Seychelles, Lesotho). Priority should be given to surveys within the network of PAs. It is recommended that the SDMs developed, whenever available, are used to optimize field surveys to areas where target CWR are predicted to occur.
3. Increase the field survey of the taxa that are thought to occur exclusively outside PAs (Table S1.4) to ascertain whether this finding is accurate. Once their occurrence is confirmed then active in situ conservation outside PA and collection for ex situ conservation are recommended.
4. Carry out predictive characterization studies, following the guidelines of Thormann et al. (2014), for identifying SADC populations that may possess important traits, specifically to adapt related crops to changes in climate, and use modern analytical approaches (e.g. machine learning, genomic prediction and multi-trait gene editing) to help increase the use of CWR in pre- and breeding programmes (Cortés & López-Hernández, 2021; Cortés et al., 2020).
5. Undertake more in-depth studies that address microhabitat patterns, CWR intrinsic ecological and genetic characteristics and the interaction of target CWR with other abiotic and biotic factors to have a more clearer understanding of how these taxa are expected to behave in the face of climate change.
6. Use high-resolution downscaled climate projections to evaluate whether these affect the climate envelope model predictions obtained in this study, test new approaches to modelling, such as that applied by Valencia et al. (2020) who coupled climate sensitivity modelling and adaptive potential inferences to assess species climate vulnerability; and test the use of hyperspectral imagery (e.g. Garzon-Lopez & Lasso, 2020) in the identification of CWR taxa in the field thus potentially contributing to monitor demographic changes.
7. Revise and update periodically the recommendations provided in this paper, particularly if priorities or conservation goals change new occurrence data are available, new modelling algorithms are found to perform better or new climatic information is available.

4.4 | Study limitations

Different analytical methodologies were applied in this study in order to provide practical recommendations to the conservation of the priority CWR of the SADC region. However, there are methodological considerations that can be raised.

Species distribution modelling was mainly used to describe and understand the distribution patterns of target CWR due to the heterogeneity nature of their occurrence data in the SADC region. On one side, some SADC countries are under-explored and lack floristic data; on the other side, several priority CWR have a very limited number of occurrence data and their complete distributions are unknown. Additionally, the SDMs developed use bioclimatic, edaphic and geophytic variables and do not account for the presence of microhabitats and microclimates, the intrinsic species ecological and genetic characteristics, the biotic interactions, nor for evolutionary changes.

Climate change analysis was performed to predict changes in CWR's distribution and to incorporate this information in the selection of sites for active in situ conservation and for collecting for ex situ conservation. The future SDMs developed in this study estimate habitat suitability in terms of change in bioclimatic parameters and do not consider potential migration rates and corridors/barriers to geneflow.

Ecogeographic diversity analysis helps understanding the patterns of ecogeographic diversity across the distribution of each CWR taxon; its results were used to identify diverse areas for active in situ conservation and populations suitable for collection and ex situ conservation. Ecogeographic diversity can be used as a proxy for genetic diversity, the premise being that conserving the widest possible ecogeographic range of populations of a species will maximize the overall genetic diversity of the species conserved. This analysis involved the development of an ELC map (Parra-Quijano et al., 2008, 2012) which aimed at identifying various ecogeographic scenarios in which a species occurs, which reflect the adaptations of the studied species that enable it to thrive in that particular set of ecological conditions. In this particular case, a generalist ELC map was created which, rather than reflecting the potential for each species to adapt to different ecogeographic conditions, it characterizes the SADC region from an ecogeographic perspective. Therefore, the variables selected to produce the ELC map are likely to limit or condition plant life in that area and are not so relevant in shaping the distribution of single species.

Despite the limitations identified in this study, the results are considered to provide good guidance on the implementation of the SADC Network for the In Situ Conservation of CWR and the SADC ex situ conservation programme for regionally important CWR diversity. Finally, the methodology used in this paper can be extended to other parts of the world in planning CWR conservation at various geographic scales (sub-national, national, regional and global).

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and implemented through the ACP-EU Co-operation Programme in Science and Technology (S&T II by the ACP Group of States (grant agreement no. FED/2013/330-210), and the Defra/Darwin Initiative funded project 26-023 entitled 'Bridging agriculture and environment: Southern African crop wild relative regional network' (SADC-CWR Network for short) (<http://www.cropwildrelatives.org/sadc-cwr-net/>). We thank our collaborating partners on the research projects mentioned above, including members of the Department of Agriculture, Forestry and Fisheries of South Africa (DAFF), the Malawi Plant Genetic Resources Centre (MPGRC), the National Plant Genetic Resources Centre (NPGRC) of the Tropical Pesticides Research Institute (TPRI) in Tanzania, the Southern African Developing Community Plant Genetic Resources Centre (SPGRC), the University of Mauritius and the Zambia Agricultural Research Institute (ZARI). We are also grateful to Elizabeth Arnaud from the Alliance of Bioversity International and CIAT in Montpellier and Dag Endresen from GBIF-Norway who extracted the GBIF records used in the analyses.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supplementary material of this article as well as in the SADC Crop Wild Relatives Project Dataverse: the occurrence data for SADC priority CWR can be found in Magos Brehm, Gaisberger, et al. (2016) (<https://doi.org/10.7910/DVN/QUOPCB>), the raster files of the diversity and climate change analyses of SADC priority CWR can be found in Gaisberger (2021) (<https://doi.org/10.7910/DVN/7ONUBJ>) and the raster files and statistics of the Ecogeographic Land Characterization map of the SADC region can be found in Magos Brehm (2022) (<https://doi.org/10.7910/DVN/MIYBQE>).

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BIOSKETCH

Our research team has been leading work the conservation and sustainable use of plant genetic resources, in particular on crop wild relatives and crop landraces. Our major research interests include prioritizing of crop wild relatives for conservation, planning for *in situ* and *ex situ* conservation, species distribution modelling, ecogeographic diversity and climate change analyses, and development of plant genetic resources conservation and use strategies. We have led several major collaborative projects, including PGR Secure (<http://www.pgrsecure.org/>), SADC Crop Wild Relatives (<http://www.cropwildrelatives.org/sadc-cwr-project/>), Farmer's Pride (<https://more.bham.ac.uk/farmerspride/>), SADC Crop Wild Relatives Network (<http://www.cropwildrelatives.org/sadc-cwr-net/>).

Author contributions: J.M.B. and H.G. developed the methodologies and conceived the research study with critical inputs from S.K., I.T., M.E.D. and N.M.; J.M.B. and H.G. collected and analysed the data; H.G. performed the species distribution modelling; J.M.B. and M.P.Q. performed the ecogeographic diversity analyses; J.M.B. drafted the manuscript; all authors revised and approved the manuscript; M.E.D. and N.M. obtained the funding.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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