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Conservation priorities for African Vigna species: Unveiling Angola's diversity hotspots

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ABSTRACT

It is widely recognized that the conservation of the Crop Wild Relatives (CWR) in their wild habitats is fundamental to ensure the continuous supply of novel genetic material, crucial for future crop improvement. *Vigna unguiculata* (cowpea) and *V. subterranea* (bambara groundnut) are amongst the most significant African legumes as sources of food and fodder. In this study we investigated the diversity of *Vigna* species in Angola, to identify hotspot areas for their *in situ* conservation, and thus underpin future food security in Sub-Saharan Africa. Based on four criteria (i.e. potential utilization for crop improvement, threat status, ethnobotanical value, and geographical distribution) we prioritize *Vigna* CWR for conservation actions in Angola. Our results reveal that 28 *Vigna* species occur in Angola, two of which are endemic (*V. mendesii* and *V. ramanniana*). These species are unevenly distributed across the country, with greater dominance in the central-north and western areas, where four hotspot areas (Saurimo, Serra da Chela, N'dalatando, and Huambo) are identified. However, significant gaps in the current *in situ* conservation strategies are highlighted by our results, since the CWR diversity hotspots remain unprotected and only nine of the 28 *Vigna* species are recorded in protected areas. Moreover, in light of the fact that only one accession of *Vigna* collected in Angola exists in genebanks globally at present, we recommend a targeted seed collecting programme to support future management and *ex situ* conservation of plant genetic resources in Angola. Our study calls attention to the fact that Angola, together with Zambia, has the highest *Vigna* species richness in Sub-Saharan Africa, and provides new data and tools for the sustainable use of these species in crop improvement.

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1. Introduction

Legumes (Fabaceae or Leguminosae family) are an important food source in the savanna regions of western and central Africa, where leaves and seeds are used as food and fodder (Carvalho et al., 2017). The genus *Vigna* Savi grows under semi-arid to sub-humid tropical climates and includes some of the most commonly cultivated pulses in Africa (Singh et al., 1997; Timko and Singh, 2008). In particular, *V. unguiculata* (cowpea) and *V. subterranea* (bambara groundnut) are of great social and economic importance across Africa, where many people cannot afford animal protein (Akpapunam and Sefa-Dedeh, 1997; Timko and Singh, 2008). Due to their high tolerance to drought and ability to grow on low fertility soils, *V. unguiculata* and *V. subterranea* are essential agronomic components of sustainability in farming systems of the tropics and, in general, of dry regions worldwide (Carvalho et al., 2017; Ehlers and Hall, 1997; Oyeyinka and Oyeyinka, 2018). Climate change will cause changes in production areas, and in the occurrence of crop pests and diseases (FAO, 2012; Lane and Jarvis, 2007; Vidigal et al., 2019). Moreover, the global population is predicted to reach up to 9 billion people by the middle of the 21st century, thus the world will need 70–100% more food (Godfray et al., 2014; United Nations, 2020). The negative impacts of climate change on food production could be mitigated by the development of novel crop varieties, with more tolerance to high temperatures, drought, low soil fertility, and resistance to pests, and diseases (Easterling et al., 2007; Vidigal et al., 2019).

Since the 20th century, crop wild relatives (CWR), which are taxa with a close genetic relationship to crops, have been used in plant breeding programs to improve the crop nutritional qualities, resilience, and adaptation to a diverse range of habitats (Maxted et al., 2006; Maxted and Kell, 2009). They have been recognized as a critical resource for food security and economic stability, alleviating human poverty and improving ecosystem stability (Hajjar and Hodgkin, 2007; Magos Brehm et al., 2017; Maxted et al., 2012; McCouch et al., 2013).

However, losses of plant diversity, at both taxon and population levels, can lead to a decline in the viability of both CWR and cultivated plant species, and produce unexpected changes in natural ecosystems (Fielder et al., 2015; Kell et al., 2015). Moreover, some CWR species are insufficiently known with respect to their native distribution and ecological variation, as is the case of many of the 63 *Vigna* species recognized in the African continent (Carvalho et al., 2017; Maréchal et al., 1978; POWO, 2020). Thus, there is an urgent need to collate existing geographical and ecological data on these species to support systematic conservation of *Vigna* CWR to ensure their continued availability for sustainable agricultural development and food security worldwide.

The greatest diversity of the genus *Vigna* is found in southern Africa (Singh, 2014). *Vigna* is a morphologically and ecologically variable genus in Africa, growing under different ecological conditions, from dry places to moist habitats (Pope and Polhill, 2001).

Angola is one of the major diversity centres of *Vigna* spp. with 25 native species documented (Figueiredo and Smith, 2008), and is therefore one of the most important sources of *Vigna* germplasm in the world, but the native species have not been studied in detail until now (Maxted et al., 2004). Moreover, the rich flora of Angola, with ca. 6700 native plant species (Figueiredo and Smith, 2008; Goyder and Gonçalves, 2019), includes many taxa with potentially valuable characteristics concerning resistance to biotic and abiotic stress, which could be used to improve cultivated species, including *Vigna* taxa.

Angola faces big challenges to achieve food security for a growing population without compromising the conservation of native biodiversity. Many communities depend on agriculture for food supply and income (INE, 2014; Pröpper et al., 2015), but agricultural expansion, together with wildfires and the harvesting of fuel wood and timber, are the main causes of deforestation in Angola, converting large areas of forest and savanna into extensive grasslands and shrublands (Catarino et al., 2020; Goyder and Gonçalves, 2019; Mendelsohn, 2019). The main losses of natural vegetation were detected around the central plateau and in Northern provinces, such as Cuanza-Norte, Bengo and Uíge (Hansen et al., 2013; Mendelsohn, 2019). The increasing demand for agricultural land is a consequence of population growth, decreasing soil fertility and low-input arable cropping (Chomba et al., 2012), leading to clearing new areas for small-scale crop farming and large-scale commercial agriculture. Desertification and soil erosion are also growing threats for biodiversity, as confirmed by recent studies (Catarino et al., 2019; Romeiras et al., 2014).

The main goal of this study is to contribute new data to support the conservation and sustainable use of *Vigna* CWR in Angola. Specifically we aim to: (i) investigate the diversity of *Vigna* CWR in Angola; (ii) analyse the distribution and main ecological characteristics of the taxa that can provide a valuable resource for *Vigna* breeding programmes; (iii) identify diversity hotspots in Angola and gaps in *in situ* and *ex situ* conservation; (iv) investigate the main uses of these taxa; and (v) identify the priority CWR taxa that should be targeted in future conservation measures. Finally, some guidelines are proposed for the conservation and sustainable management of *Vigna* CWR in Angola.

2. Material and methods

2.1. Study area

The Republic of Angola is the seventh-largest country in Africa and the second-largest one south of the Sahara, covering ca. 1,246,700 km^2 (Huntley, 2019) and comprising 18 provinces. It has a wide climate range due to the vast extent of territory (Santos, 1969). The annual rainfall is about 600 mm in coastal areas, with maximum values in Lunda Norte province (more than 1500 mm), and minimum values in Namibe (about 50 mm) (Huntley, 2019). In general, precipitation decreases from north to south and increases from the coast to the interior of the country. The altitude is also an important factor; it rains more and temperature decreases when the altitude increases. Angola has two well-defined seasons: the rainy season (summer), which is generally wet and hot, running from September to April, and the *cacimbo* season (winter), which is generally characterized by being dry and cold, occurring between May to September (Huntley, 2019). With 15 WWF ecoregions identified (Olson et al., 2001), this country encompasses a great diversity of ecosystems, from tropical rain forests to deserts, and hosts a high richness of endemic species (Figueiredo and Smith, 2008; Frazão et al., 2020). The largest plant family is Fabaceae (Leguminosae), with ca. 160 genera and more than 900 taxa, of which 19% are endemic (Catarino et al., 2019; Soares et al., 2007).

2.2. Data collection

This study is based on a broad definition that considers any taxon in the same genus as a CWR of a cultivated species (for more details see Maxted et al., 2006), which is a widely used definition (e.g. Fielder et al., 2015; Kell et al., 2015; Vincent et al., 2013). According to Maxted et al. (2004), wild and cultivated *Vigna* taxa cross readily. Although taxa more closely related to crops are easier to use in plant breeding programs, there are many examples of more distantly related taxa used to improve crops (Maxted and Kell, 2009; Vincent et al., 2013).

A comprehensive dataset on the native *Vigna* taxa occurring in Angola was gathered from different sources, namely:

i) Herbarium specimens of *Vigna* collected in Angola and stored in the Herbarium of the Instituto de Investigação Científica Tropical, University of Lisbon (LISC); Herbarium of the Museu Nacional de História Natural e da Ciência, University of Lisbon (LISU); Herbarium of the University of Coimbra (COI); and Herbarium of the Royal Botanic Gardens, Kew (K). Outside of Angola, Portuguese Herbaria (LISC, LISU, and COI) hold the largest collections of Angolan plants (Figueiredo and Smith, 2008). The LISC herbarium has ca. 80,000 specimens, which is the largest worldwide collection for Angola, merging duplicate specimens from several expeditions, which are hosted in separate herbaria in Angola (LUBA, LUAI, LUA). Information recorded on the labels allowed us to assess main uses, habitat features, growth form and distribution of each species. More details on the studied specimens are provided in Table S1.

ii) Field research carried out during the last decade by E. Costa, who collected samples of *Vigna* species cultivated in 10 provinces of Angola: Benguela, Bié, Cuando Cubango, Cuanza Norte, Huíla, Luanda, Malanje, Moxico, Namibe, and Uíge. These samples were identified and preserved in the germplasm bank of the Botany Center of the University of Agostinho Neto (Luanda, Angola).

iii) Relevant online databases, namely Plants of the World Online (POWO, 2020) and U.S. National Plant Germplasm System (USDA, 2020) for taxonomic data (subgenus, section, species name and synonyms), gene pool data and native distribution; PROTA - Plant Resources of Tropical Africa (PROTA, 2020) and Useful Tropical Plants Database (UTPD, 2020), for detailed information on uses of many African plants; African Plant Database (APD, 2020) for information on the biology and ecology of each species; the IUCN Red List of Threatened Species (IUCN, 2020) for useful information on extinction risk, threats and conservation actions in place; and the Global Biodiversity Information Facility (GBIF, 2020a) for occurrence data. Finally, we investigated the availability of data on the native *Vigna* of Angola in “The CWR Project platform” (CWR Project, 2020), to know which species have already been identified as CWR of cultivated species and to understand the limitations of knowledge about the wild species under study.

iv) Scientific publications on the Angolan flora (Burkill, 1985; Carvalho et al., 2017; Costa and Pedro, 2013; Costa et al., 2019; Figueiredo and Smith, 2008; Goyder and Gonçalves, 2019; Soares et al., 2007) and particularly concerning *Vigna* (Exell and Mendonça, 1966; Maxted et al., 2004; Moray et al., 2014; Pasquet, 1999; Pope and Polhill, 2001; Singh, 1997; van Zonneveld et al., 2020).

The scientific name of each species follows Plants of the World Online (POWO, 2020), and the subgenus and section follow Maxted et al. (2004) and U.S. National Plant Germplasm System (USDA, 2020). Based on the best currently available knowledge, our dataset includes the scientific and common names, ecological characteristics that can be useful for the improvement of cultivated species, global native distribution, threat status (extinction risk) at species level according to the IUCN Red List (IUCN, 2020), and the main uses of the species (e.g. food, medicinal, forage).

2.3. Diversity hotspots and conservation gap analysis of Vigna CWR in Angola

The geographical distribution of *Vigna* taxa in Angola was estimated based on herbarium specimen data and occurrence data available in the GBIF database (GBIF, 2020b). Herbarium specimens were individually georeferenced based on the description of the collection site, according to the Guide to Good Georeferencing Practices (Chapman et al., 2006). Records with more than 5 km of uncertainty were excluded from the analysis. A total of 1014 records of native *Vigna* species were collected from GBIF with geographical coordinates. Duplicate records (records with the same collector and collection number, i.e., collected from the same plant or population) were excluded and the coordinates of each record were individually confirmed and corrected (if necessary) with Google Earth Pro 7.3.2.5491 (Serea, 2018). The remaining 657 occurrences, belonging to 26 taxa, were used in the analysis.

The geographic boundaries of Angolan protected areas were obtained as GIS shapefiles from the World Database of Protected Areas (WDPA, 2020). The more recent protected areas are unavailable in WDPA and were vectorized based on the Angolan legislation (Diário da República de Angola, law 38/11 December 29th, 2011, p. 6340) using QGIS v.3.4.4 (QGIS Development Team, 2020).

Based on species occurrence records, a species richness map was constructed using QGIS v.3.4.4 (QGIS Development Team, 2020), and the hotspots of *Vigna* species richness (i.e. areas of high diversity in *Vigna* CWR) were identified and compared with the current network of protected areas. This analysis aimed to assess the effectiveness of the current *in situ* conservation coverage and to identify the main gaps, an important step for the development of more effective conservation measures (Magos Brehm et al., 2017; Maxted et al., 2008, 2013).

Finally, the status of *ex situ* conservation of Angola's *Vigna* genetic resources in worldwide genebanks was assessed though the Genesys Database (Genesys, 2020).

2.4. *CWR prioritization*

The establishment of priorities for native CWR is an essential step in conservation planning (Magos Brehm et al., 2017; Maxted et al., 2013). The prioritization of *Vigna* CWR in Angola was based on four criteria: (i) the potential utilization for crop improvement (Kell et al., 2017); (ii) the threat status of the species (Kell et al., 2017); (iii) the ethnobotanical value of the species (Ford-Lloyd et al., 2006; Idohou et al., 2012); and (iv) the geographical distribution (Idohou et al., 2012; Labokas et al., 2016; Ng'uni et al., 2019). Previous studies have used these criteria to prioritize CWR taxa and to develop conservation strategies (e.g. Barazani et al., 2008; Fielder et al., 2013; Kell et al., 2012; Lala et al., 2018; Vincent et al., 2013).

(i) The potential utilization for crop improvement was scored according to the Gene Pool (GP) concept when available and the Taxon Group (TG) concept (more details below): TG1/GP1 (score 4); TG2/GP2 (score 3); TG3/GP3 (score 2); TG4/GP4 (score 1). Given their importance in Africa, we considered the Gene Pool/Taxon Group for both crop species (cowpea and bambara groundnut): *V. unguiculata* subsp. *unguiculata* (subgenus *Vigna*, section *Catiang*) and *V. subterranea* (subgenus *Vigna*, section *Vigna*); the highest score of Gene Pool/Taxon Group was used in the final score.

The potential utilization for crop improvement is related to the degree of affinity between a crop and its CWR. The crop Gene Pool concept (Harlan and de Wet, 1971) considers a primary gene pool (GP1), including the wild species closely related to a particular crop that freely interbreeds with the crop (subdivided into GP1A, the cultivated form, and GP1B, the wild forms); a secondary gene pool (GP2), comprising taxa more remotely related to the crop, but still capable of crossing with it and producing some fertile hybrids; and a tertiary gene pool (GP3) which includes taxa remotely related to the crop and naturally incapable of interbreeding with it, requiring special techniques for gene transfer into a particular crop. For conservation purposes, priority should be given to taxa belonging to GP1, GP2, and also GP3 that include interesting traits and have potential for use as gene donors (Maxted and Kell, 2009). As the knowledge on crossing and genetic diversity is insufficient to apply the Gene Pool concept to all *Vigna* CWR, we applied the Taxon Group concept when the Gene Pool is unknown (Maxted et al., 2006). The Taxon Group concept uses the taxonomic relationship with the crop as a proxy for taxon genetic relatedness and thus potential crossability (for more details see Maxted et al., 2006). TG1 includes the crop or the same species as crop; taxa within same section as the crop are included in TG2; taxa within the same subgenus as the crop are in TG3; and taxa within the same genus as crop are in TG4.

(ii) Threat status (extinction risk) was classified with four scores: Threatened species (score 4); Near Threatened (NT) species (score 3); Not Evaluated (NE) species (score 2 for widely distributed taxa and score 4 for restricted taxa); Least Concern (LC) (score 1). Threat status was based on the global assessments in the IUCN Red List (IUCN, 2020). Threatened species category include Critically Endangered (CR), Endangered (EN) and Vulnerable (VU) species. Taxa classified as NE were individually analysed, and those restricted to Angola and nearby regions were assigned with the highest value (score 4). According to the IUCN (2019) recommendations, NE and Data Deficient (DD) (not present in this study) categories do not imply that a species is not at risk of extinction, thus species classified in such categories should have the same degree of attention as threatened taxa (IUCN, 2019).

(iii) The ethnobotanical value was divided into four categories: used as human food (score 4); two or more uses, but not as human food (score 3); one use, but not as human food (score 2); no identified uses (score 1). The ethnobotanical value of the species is a good indicator of its importance for local communities. Priority should be given to the species that are most valuable to populations (Idohou et al., 2012).

(iv) The geographic distribution was categorized into: taxa endemic to Angola (score 4); taxa restricted to the Zambezian region (i.e., Angola, Democratic Republic of Congo, Malawi, Mozambique, Tanzania, Zambia and Zimbabwe) (score 3); taxa endemic of the African continent (score 2); taxa also present outside Africa (score 1). Thus, species with more restricted distribution have higher priority (Ng'Uni et al., 2019).

For each taxon, a score was assigned for each criterion and the scores were then summed, unweighted. The total scores ranged from 4 to 16. Taxa with scores between 16 and 12 were categorized as of high priority for conservation; medium priority corresponded to scores between 11 and 8, and low priority to those CWR taxa scoring between 7 and 4.

3. Results

3.1. Diversity of Vigna in Angola

Twenty-eight taxa of *Vigna* were identified as native to Angola (Table 1), belonging to 24 different species. Only two endemic species were recognized: *V. mendesii,* which occurs in Cuando-Cubango and Bié provinces, and *V. ramanniana*, only known from the type specimen collected by Hundt, in 1933, in Benguela province. Currently, 105 species of *Vigna* are accepted worldwide (POWO, 2020) and 22% of them (23 species) are native to Angola. Our results differed somewhat from those of Figueiredo and Smith (2008): two species were excluded, *V. adenantha* (G.Mey.) Maréchal, Mascherpa & Stainier, which has been transferred to the genus *Leptospron* (Delgado-Salinas et al., 2011), and *V. lobatifolia* Baker, which is a synonym of *V. vexillata* var. *lobatifolia* (Baker) Pasquet (2001). Moreover, three taxa were added, namely *V. nyangensis* (Mithen and Kibblewhite, 1989), *V. parkeri* subsp. *maranguensis* (Exell and Fernandes, 1966), and *V. unguiculata* subsp. *alba* (Pasquet, 1993).

A high level of infrageneric taxonomic diversity occurs in Angola, with three subgenera (*Haydonia, Plectotropis*, and *Vigna*) and eight sections (*Catiang, Comosae, Glossostylus, Haydonia, Liebrechtsia, Plectotropis, Reticulatae* and *Vigna*) present (Fig. 1, Table S2). The most diverse subgenus is *Vigna*, with 24 taxa; subgenus *Haydonia* has three taxa (*V. nigritia, V. nyangensis* and *V. triphylla*); and subgenus *Plectotropis* has only one taxon (*V. vexillata*). The section *Vigna* is the most diverse, with 10 taxa, followed by sections *Reticulatae* and *Catiang*, with five taxa each. The section *Catiang* comprises five subspecies of *V. unguiculata*, all of them belonging to the "*dekindtiana*" savanna group (Pasquet and Padulosi, 2013). This group includes the domesticated cowpea (*V. unguiculata* subsp. *unguiculata* var. *unguiculata*), and its wild progenitor (var. *spontanea*).

Vigna also displays considerable morphological diversity. Although they are all herbaceous plants, 20 taxa are perennial, three are annual and four can be annual or perennial (the habit of *V. ramanniana* is unknown).

Among the 28 wild taxa, six are cultivated: *V. unguiculata* subsp. *unguiculata* (Fig. 2) and *V. unguiculata* subsp. *dekindtiana* are mainly cultivated for human and livestock consumption; *V. vexillata* is cultivated for pasture and sometimes for its edible tubers; *V. luteola* is cultivated for forage and soil improvement; *V. parkei* subsp. *maranguensis* is used as a pasture legume; and *V. frutescens* is sometimes cultivated as an ornamental in gardens (Table S2).

3.2. Vigna Gene pools

The study of African *Vigna* gene pools remains very incomplete and crossing compatibility is still poorly studied. Only 16 of the 28 taxa native to Angola are reported in USDA (2020). According to this database, *Vigna unguiculata* and four infraspecific taxa (subspecies: *dekindtiana, stenophylla, tenuis*, and *unguiculata*) belong to the primary gene pool of the cultivated populations of this species (GP1-B the former, and GP-1A the latter, corresponding to the spontaneous form of the crop species); *V. unguiculata* subsp. *alba* belongs to GP2, and *V. frutescens* and *V. vexillata* to the tertiary gene pool (GP3) of this crop. Seven species of *Vigna* belong to the tertiary gene pool of *V. subterranea* (bambara groundnut) (*V. gracilis*, *V. heterophylla*, *V. luteola*, *V. multinervis*, *V. oblongifolia*, *V. parkeri* subsp. *maranguensis*, *V. racemosa*). *Vigna unguiculata* also belongs to GP3 of cultivated *Vigna* species of subgenus *Ceratotropis* of Asian origin [*V. angularis* var. *angularis* (azuki-bean), *V. radiata* var. *radiata* (mung bean), *V. umbellata* (rice-bean) and *V. mungo* var. *mungo* (black gram)].

3.3. Ecological preferences of Vigna CWR

Although poorly studied, African wild taxa may have a great potential for genetic improvement of cultivated species due to the great diversity of characteristics they present and the wide range of habitats in which they grow. The native *Vigna* of Angola occur across a wide range of ecosystems with different ecological characteristics. Most taxa (12), including the cultivated *V. luteola* and *V. unguiculata* subsp. *unguiculata,* prefer wet and flooded areas (Table S3). Six taxa (*V. antunesii, V. comosa, V. frutescens*, *V. platyloba, V. radicans* and *V. vexillata*) are mostly found in dry areas, and are well adapted to high temperatures and water scarcity. Half of the taxa (14) are well adapted to sandy soils; *V. luteola* is particularly well adapted to saline soils and *V. parkeri* subsp. *maranguensis* grows well on acidic soils. Four taxa grow mostly in rocky areas (*V. comosa, V. gazensis, V. gracilis* and *V. reticulata*) and six taxa are pyrophytic, growing in recently burned areas (*V. antunesii, V. frutescens, V. procera, V. pygmaea, V. unguiculata* subsp. *dekindtiana* and *V. vexillata*). This characteristic is common to some *Vigna* species that flourish directly from rootstocks following burning (Tomooka et al., 2011).

3.4. Distribution and diversity hotspots in Angola

The distribution of *Vigna* taxa was analysed based on 657 occurrence records, belonging to 26 taxa. The studied taxa are mainly distributed across the central and southern African regions (for detailed distribution of each species see Fig. S5). Only three species have their native range including other continents – *V. luteola* and *V. vexillata*, both distributed worldwide, and

Table 1
Scientific name, common names, ecological preferences, global native distribution, threat status, main uses in Angola, cowpea and bambara groundnut taxonomic groups, scoring of the prioritization criteria and conservation priority level of native *Vigna* taxa in Angola.

Taxon	Common names [a]	Ecological preferences [b]	Native global distribution	IUCN threat status and date [c] (species level)	Main uses	Cowpea taxonomic group [d]	Bambara groundnut taxonomic group [d]	Prioritization criteria				Score (total)	Prioritization level
								Potential utilization for crop	Threat score	Socio-economic value	Geographic distribution		
Vigna antunesii Harms	Elota-kakunde (An)	Dr, Bu, Sd	Angola, Democratic Republic of Congo, Malawi, Mozambique, Tanzania, Zambia, Zimbabwe	LC (2017)	Food	TG3	TG3	2	1	4	3	10	Medium
Vigna comosa Baker	Unknown	Dr, We, Ro, Sd	Tropical Africa	LC (2019)		TG3	TG3	2	1	1	2	6	Low
Vigna frutescens A.Rich.	Wild sweetpea (En)	Dr, Bu	Tropical and southern Africa	LC (2019)	Food, Forage, Fibres	TG3	TG3	2	1	4	2	9	Medium
Vigna gazensis Baker f.	Unknown	Ro	Angola, Madagascar, Malawi, Mozambique, Zimbabwe	LC (2019)		TG3	TG2	3	1	1	3	8	Medium
Vigna gracilis (Guill. & Perr.) Hook.f.	Wild vigna (En)	We, Ro	West Tropical Africa	LC (2019)	Medicinal, Food, Forage	TG3	TG2 (a)	2	1	4	2	9	Medium
Vigna heterophylla A.Rich.	Wild vigna (En)	We, Sd	Tropical Africa	NE	Food	TG3	TG2 (a)	2	2	4	2	10	Medium
Vigna luteola (Jacq.) Benth.	Hairypod cowpea (En)	We, Sd, Sl	Tropics and subtropics (worldwide)	LC (2019)	Medicinal, Food, Forage	TG3	TG2 (a)	2	1	4	1	8	Medium
Vigna mendesii Torre	Unknown	Sd	Angola	NE		TG3	TG2	3	4	1	4	12	High
Vigna multinervis Hutch. & Dalziel	Wild vigna (En)	We, Sd	Tropical Africa	LC (2019)	Medicinal	TG3	TG2 (a)	2	1	2	2	7	Low
Vigna nigritia Hook.f.	Unknown	We	West and central Africa	LC (2019)		TG4	TG4	1	1	1	2	5	Low
Vigna nyangensis R.Mithen & H.Kibblewhite	Unknown	We	Zimbabwe, Angola, Malawi	LC (2020)		TG4	TG4	1	1	1	3	6	Low
Vigna oblongifolia A.Rich.	Unknown	We, Sd	Madagascar, tropical and southern Africa	LC (2019)		TG3	TG2 (a)	2	1	1	2	6	Low
Vigna parkeri Baker subsp. *maranguensis* (Taub.) Verdc.	Creeping vigna (En)	Ac	Angola, Democratic Republic of Congo, Ethiopia, Kenya, Rwanda, Tanzania, Uganda	LC (2019)	Forage	TG3	TG2 (a)	2	1	2	2	7	Low
Vigna platyloba Hiern	Etelendende (An)	Dr, Sd	Angola, Democratic Republic of Congo, Malawi, Mozambique, Tanzania, Zambia	LC (2019)		TG3	TG3	2	1	1	3	7	Low
Vigna procera Hiern	Unknown	Bu, Sd	Angola, Zambia	NT (2019)		TG3	TG3	2	3	1	3	9	Medium
Vigna pygmaea R.E.Fr.	Unknown	Bu	Angola, Botswana, Burundi, Cameroon, Democratic Republic of Congo,	LC (2019)		TG3	TG3	2	1	1	2	6	Low

			Malawi, Mozambique, Tanzania, Zambia, Zimbabwe										
Vigna racemosa (G.Don) Hutch. & Dalziel	Wild vigna (En)	We	Tropical Africa to Namibia	LC (2019)	Medicinal, Forage	TG3	TG2 (a)	2	1	3	2	8	Medium
Vigna radicans Baker	Unknown	Dr, Sd	Angola, Burundi, Central African Republic, Democratic Republic of Congo, Kenya, Malawi, Nigeria, Tanzania, Zambia, Zimbabwe	NE		TG3	TG3	2	4	1	2	9	Medium
Vigna ramanniana Rossberg	Unknown		Angola	NE		TG4[e]	TG4[e]	1	4	1	4	10	Medium
Vigna reticulata Hook.f.	Wild vigna (En); ondangala (An)	We, Ro, Sd	Tropical Africa and Madagascar	LC (2019)	Medicinal, Food, Forage	TG3	TG3	2	1	4	2	9	Medium
Vigna stenophylla Harms	Unknown	Sd	West and central Tropical Africa	NE	Food	TG3	TG2	3	2	4	2	11	Medium
Vigna triphylla (Wilczek) Verdc.	Unknown	We	Tropical Africa	NE		TG4	TG4	1	2	1	2	6	Low
Vigna unguiculata (L.) Walp. subsp. *unguiculata*	Cowpea, black-eye pea (En); feijão-macundi (An)	We	Tropical and southern Africa	NE	Medicinal, Food, Forage, Fibre	TG1	TG1	4	2	4	2	12	High
Vigna unguiculata subsp. *alba* (G.Don) Pasquet	Unknown		Angola, Congo, Democratic Republic of Congo, Gabon, São Tomé	NE		TG1 (b)	TG1	4	4	1	2	11	Medium
Vigna unguiculata subsp. *dekindtiana* (Harms) Verdc.	Blackeyed pea (En); entele-kunde, kakundi-kombambi (An)	Bu	Tropical and southern Africa	NE		TG1 (c)	TG1	2	2	1	2	7	Low
Vigna unguiculata subsp. *stenophylla* (Harv.) Marechal et al.	Cowpea (En)		Tropical and southern Africa	NE		TG1 (d)	TG1	3	2	1	2	8	Low
Vigna unguiculata subsp. *tenuis* (E.Mey.) Marechal et al.	Unknown	Sd	Angola, Malawi, Mozambique, Zambia, Zimbabwe	NE		TG1	TG1	4	4	1	3	12	High
Vigna vexillata (L.) A.Rich.	Zombi-Pea (En); omutunu (An)	Dr, Bu, Sd	Tropics and subtropics (worldwide)	NE	Medicinal, Food, Forage, Fibre	TG4 (e)	TG4	2	2	4	1	9	Medium

Notes.

[a] **Common names**: (**En**) English common name; (**An**) Angolan common name.

[b] **Ecological preferences**: **Dr**, dry areas; **We**, wet or flooded areas; **Ro**, rocky areas; **Bu**, recently burnt; **Sd**, sandy soils; **Sl**, salty soils; **Ac**, acid soils.

[c] **Threat status**: **CR**, Critically Endangered; **EN**, Endangered; **VU**, Vulnerable; **NT**, Near Threatened; **LC**, Least Concern; **DD**, Data Deficient; **NE**, Not Evaluated.

[d] Cowpea taxonomic group and Bambara groundnut taxonomic group are based on the Taxon Group concept developed by Maxted et al. (2006) and is a proxy for taxon genetic relatedness. Some differences were found with the expected gene pool: (a) TG2 of *V. subterranea*, but GP3 according to USDA (2020); (b) TG1 of *V. unguiculata* subsp. *unguiculata*, GP1 according to CWR Project (2020) but GP2 according to USDA (2020); (c) TG1 of *V. unguiculata* subsp. *unguiculata*, GP1 according to USDA (2020) but GP3 according to van Zonneveld et al. (2020); (d) TG1 of *V. unguiculata* subsp. *unguiculata*, GP1 according to USDA (2020) but GP2 according to van Zonneveld et al. (2020); (e) TG4 of *V. unguiculata* subsp. *unguiculata*, but GP3 according to USDA (2020).

[e] Species with unknown section and subgenus was included in TG4 and scored 1.

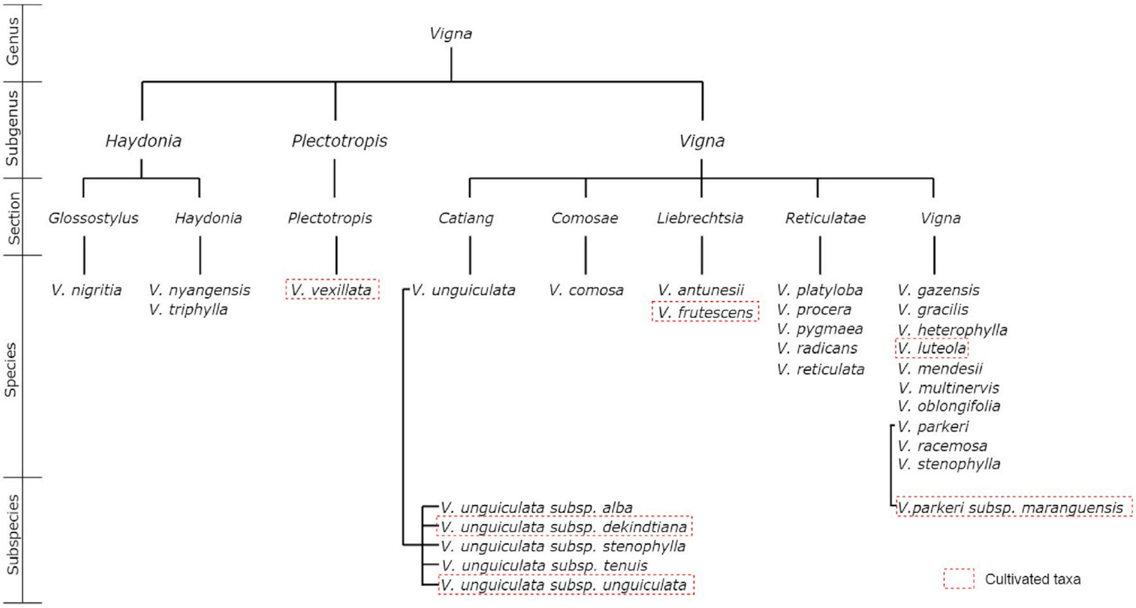


Fig. 1. Infrageneric classification of *Vigna* species and subspecies native to Angola. The endemic *V. ramanniana* was excluded from the diagram due to taxonomic uncertainty at the subgenus and section levels (this taxon is known only from the type collection [Hundt, 557] destroyed and apparently without duplicates).

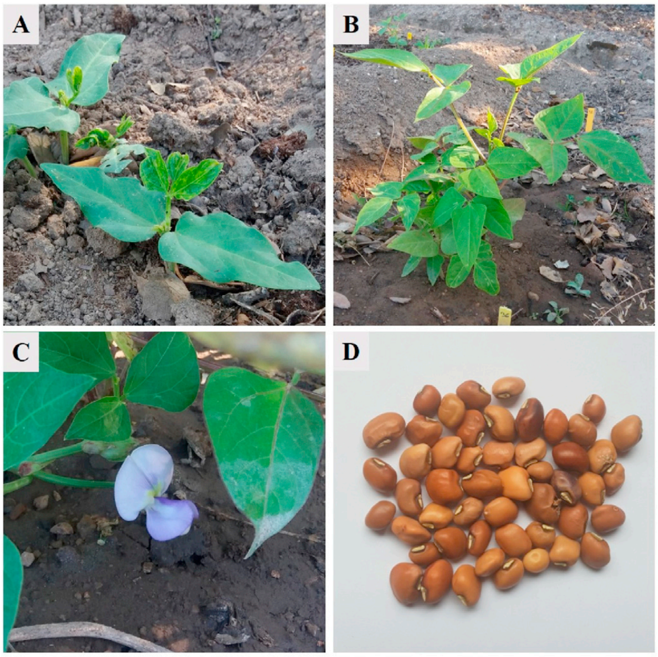


Fig. 2. Details of *Vigna unguiculata* subsp. *unguiculata* cultivated in Angola: A) first leaves; B) developed plant; C) flower; and D) seeds.

V. heterophylla, also present in southwest Arabian Peninsula. *Vigna mendesii* and *V. ramanniana* are endemic to Angola, and *V. procera* is restricted to Angola and Zambia (Table 1).

The species of this genus are distributed across the 18 provinces of Angola, with greater diversity in the central-north and western areas. The most diverse provinces are Malanje, with 14 taxa (50%), Cuanza Norte, with 12 taxa (42.9%), and Huíla, with 11 taxa (39.3%) (Table S2, Fig. 3). Bengo and Moxico, with 3 taxa (10.7%), are the provinces with the lowest diversity. The species richness map (Fig. 4) shows four main centres of diversity, namely Saurimo in Lunda Sul, and Serra da Chela in Huíla,

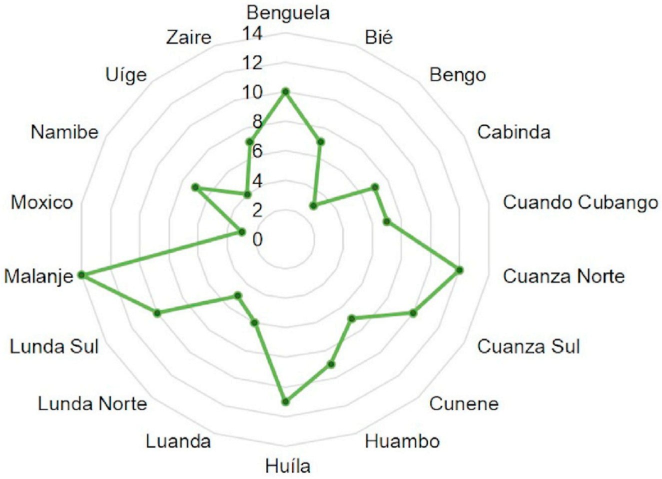


Fig. 3. Number of native *Vigna* taxa identified in each of the 18 provinces of Angola.

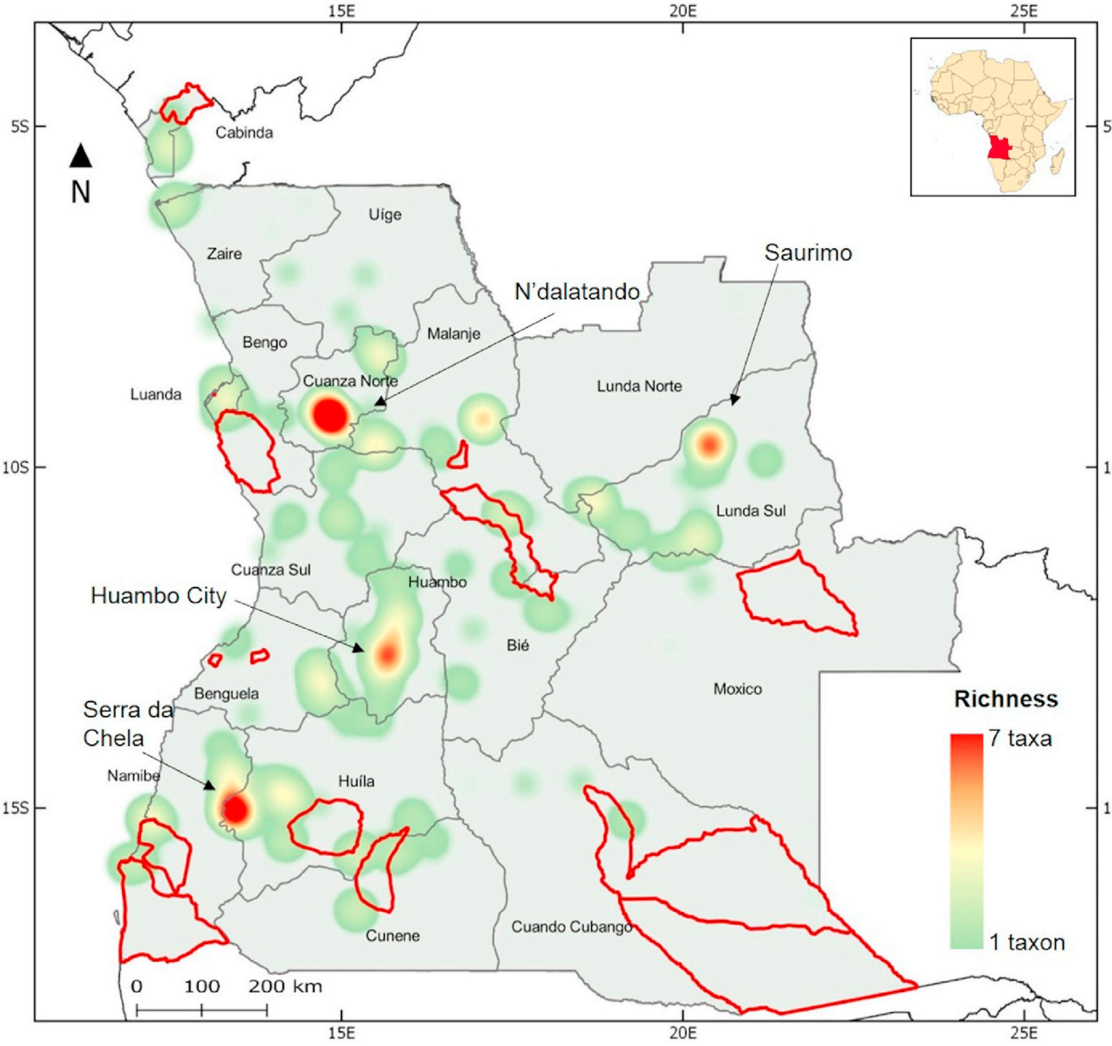


Fig. 4. Species richness of *Vigna* genus in Angola in the provinces and protected areas (red lines). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

reaching a maximum of seven taxa; the area of N'dalatando in Cuanza Norte, with six taxa; and the area of Huambo, with five taxa. *Vigna gazensis* and *V. unguiculata* subsp. *stenophylla* were not included in this analysis due to lack of precise locality data.

3.5. Main uses

At least 12 of the 28 taxa (42.9%) are used by human populations (Table 1). *Vigna unguiculata* subsp. *unguiculata* and *V. vexillata* are the taxa with more uses (e.g. food, forage, fibre, and traditional medicine). Ten taxa are used for food purposes, nine as forage, eight as medicines and two for fibres. *Vigna unguiculata* subsp. *unguiculata* and *V. unguiculata* subsp. *dekindtiana* are mainly used for human and livestock consumption, the young leaves, pods, and seeds being used as vegetables when fresh, and the grains in meal dishes when dried. *Vigna vexillata* is used for pasture, medicine and human food, it is commonly harvested from the wild for local use and is cultivated for its edible tubers.

3.6. Priority taxa for conservation and protected areas

Eight of the 24 studied species (33%) remain unevaluated on the IUCN Red List, including the two endemic species *V. mendesii* and *V. ramanniana,* and none of the others is classified in one of the threat categories at global level. One species is classified as Near Threatened (4%) and 15 species (60%) are classified as Least Concern (Table 1, Fig. 5). In general, the species classified as Least Concern on the IUCN Red List have wide distributions in Africa, while the species with more restricted distributions remain not evaluated.

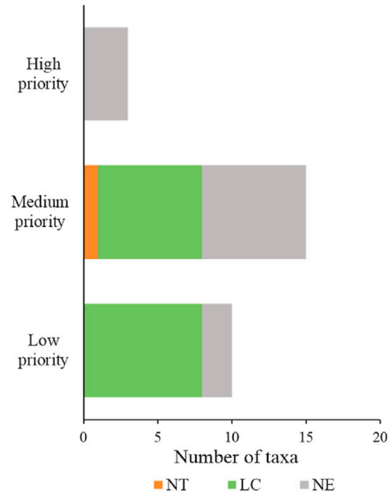
The prioritization of *Vigna* CWR in Angola (Table 1) classified three taxa (10.7%) with high priority, 15 taxa (53.6%) with medium priority and 10 taxa (35.7%) with low priority (Fig. 5).

Taxa with high conservation priority are *V. mendesii, V. unguiculata* subsp. *tenuis,* and *V. unguiculata* subsp. *unguiculata*. None of them have been evaluated in terms of threat status, *V. mendesii* is of special concern because it is a very restricted species, endemic to Angola. This is the only high priority species found in protected areas (Fig. 6).

The medium priority category includes 15 *Vigna* taxa, of which one is classified as NT (*V. procera*), seven as LC, and seven have not yet been evaluated (NE). Five of the medium priority taxa were found in Angola's protected areas (i.e. *V. antunesii; V. frutescens; V. luteola; V. radicans;* and *V. vexillata*).

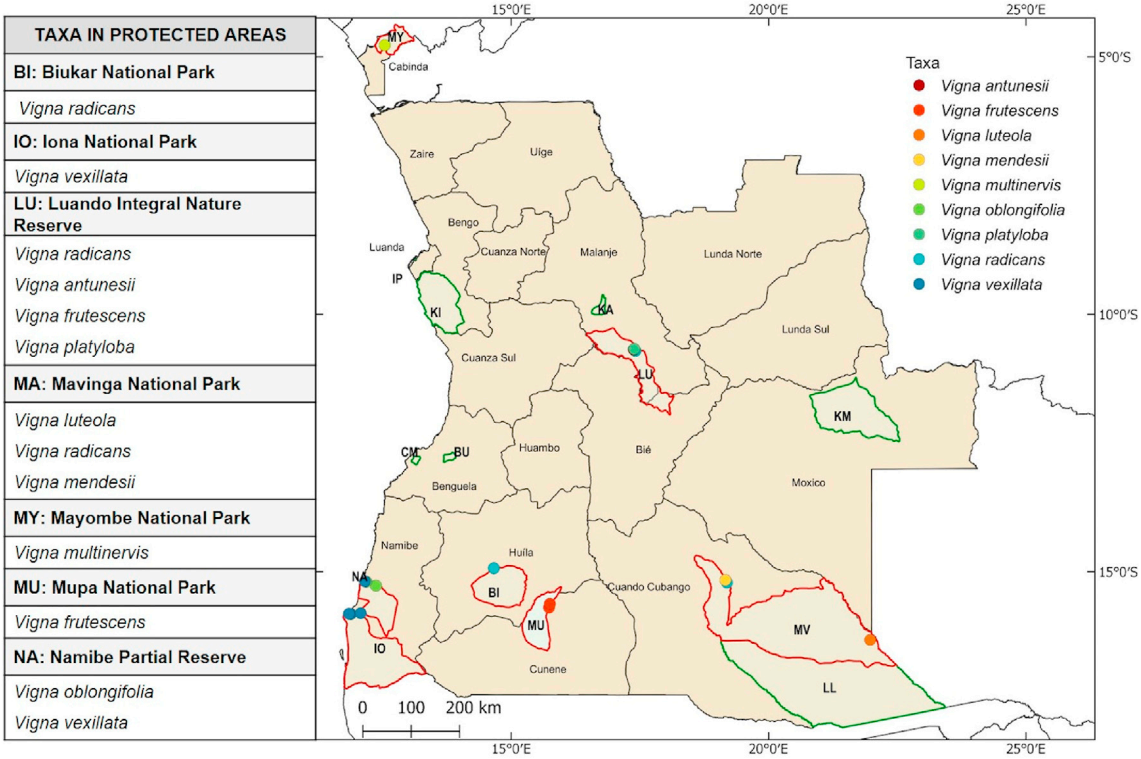
In the low priority category, eight taxa are classified as LC and two are not evaluated (NE); three of them are found in protected areas (i.e. *V. multinervis; V. oblongifolia;* and *V. platyloba*).

Only 6% of the occurrences, corresponding to nine of the 28 taxa studied, were found within the limits of protected areas (Fig. 6). Luando Integral Nature Reserve is the protected area with the most taxa (*V. antunesii*, *V. frutescens, V. platyloba* and *V. radicans*). Three taxa were found in the National Park of Mavinga (*V. luteola, V. radicans,* and the high priority taxa *V. mendesii*), and two taxa were found in Namibe Partial Reserve (*V. oblongifolia* and *V. vexillata*). Bicuar National Park in Huíla, Iona National Park in Namibe, Mupa National Park in Cunene, and Mayombe National Park in Cabinda each include only one species (Fig. 6).



Prioritization level	Score	Species
High	**12**	*V. mendesii; V. unguiculata* subsp. *tenuis; V. unguiculata* subsp. *unguiculata*
Medium	**11**	*V. stenophylla; V. unguiculata* subsp. *alba*
	10	*V. antunesii; V. heterophylla; V. ramanniana*
	9	*V. frutescens; V. gracilis; V. procera; V. radicans; V. reticulata; V. vexillata*
	8	*V. gazensis; V. luteola; V. racemosa; V. unguiculata* subsp. *stenophylla*
Low	**7**	*V. multinervis; V. platyloba; V. parkeri* subsp. *maranguensis;V. unguiculata subsp. dekindtiana*
	6	*V. comosa; V. nyangensis; V. oblongifolia; V. pygmaea; V. triphylla*
	5	*V. nigritia*

Fig. 5. Angolan *Vigna* CWR in high, medium and low priority categories and their threat status according to IUCN Red List (IUCN, 2020). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)



TAXA IN PROTECTED AREAS
BI: Biukar National Park
Vigna radicans
IO: Iona National Park
Vigna vexillata
LU: Luando Integral Nature Reserve
Vigna radicans Vigna antunesii Vigna frutescens Vigna platyloba
MA: Mavinga National Park
Vigna luteola Vigna radicans Vigna mendesii
MY: Mayombe National Park
Vigna multinervis
MU: Mupa National Park
Vigna frutescens
NA: Namibe Partial Reserve
Vigna oblongifolia Vigna vexillata

Fig. 6. Occurrence of *Vigna* taxa within protected areas of Angola. The protected areas with *Vigna* are indicated by red lines and the protected areas without *Vigna* are indicated by green lines. The list of species included in each protected area is presented (left). Protected areas: BI: Bicuar, BU: Búfalo, CG: Cangandala, CM: Chimalavera, IO: Iona, IP: Ilheu dos Pássaros, KM: Kameia, KI: Kissama, LL: Luengue-Luiana, LU: Luando, MV: Mavinga, MU: Mupa, MY: Mayombe; NA: Namibe. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

3.7. Ex situ conservation

The analysis of the extant accessions of *Vigna* spp. in worldwide genebanks (Table S4) revealed that only one species – *V. unguiculata* subsp. *alba* – has accessions collected in Angola, preserved at the Botanic Garden Meise (Belgium). None of the other taxa pertaining to the gene pool of either cowpea or bambara groundnut have accessions from Angola preserved in *ex situ* collections.

Considering all accessions collected globally, 21 species studied (75%) have at least one accession conserved *ex situ*, but with other origins than Angola. *Vigna unguiculata* subsp. *unguiculata* is the taxon with the most accessions (11,613), followed by *V. vexillata* (943). Three taxa (11%) have 200–300 accessions, two taxa (7%) have 100–200, and 13 taxa (46%) have 1–50. Seven taxa (25%), including the high priority taxon *V. mendesii* and the other endemic species, *V. ramanniana*, have no accessions.

4. Discussion

4.1. Diversity and distribution of Vigna CWR in Angola

This study revealed the main hotspots of *Vigna* diversity specifically in Angola for the first time, including some native species that are not included in other studies focused on *Vigna* diversity (e.g. Maxted et al., 2004; Moray et al., 2014; van Zonneveld et al., 2020). We identify 28 native taxa, including two endemics (*V. mendesii* and *V. ramanniana*) and one near-endemic species (*V. procera*) restricted to Angola and Zambia. These two countries have the highest species richness for *Vigna* in southern tropical Africa, with 28 and 30 recognized taxa respectively (Bingham et al., 2020). Malawi has 20 *Vigna* taxa (Hyde et al., 2020a), followed by Mozambique and Zimbabwe, each with 19 taxa (Hyde et al., 2020b, 2020c), and Botswana with 9 taxa (Hyde et al., 2020d).

Native *Vigna* taxa are unevenly distributed across Angola, with greater dominance in the central-north and western areas. The provinces with the highest diversity are Malanje, Cuanza Norte, and Huíla. These results are in accordance with other studies on African plant diversity, namely Linder (2001, 2014) and Frazão et al. (2020). The main centres of diversity were found in Serra da Chela (Huíla), Saurimo (Lunda Sul), N'dalatando (Cuanza Norte), and Huambo (Huambo). The central highlands, including Serra da Chela, are characterized by high fertility soils, resulting in high species richness in most plant groups (Huntley et al., 2019). Serra da Chela is a small area in the Angolan Escarpment Zone, Huíla province, which contains higher *Vigna* diversity than the rest of the Huíla plateau. A succession of scarps and plains, Serra da Chela corresponds to the Angolan Montane Forest-Grassland Mosaic ecoregion (Olson et al., 2001) and is included in the Afromontane archipelago-like regional centre of endemism defined by White (1983). Our results are consistent with other studies (e.g. Clark et al., 2011; Darbyshire et al., 2019; Frazão et al., 2020; Goyder and Gonçalves, 2019; Linder, 2001) that recognize this region as an important centre of diversity and endemism. Saurimo, N'dalatando and Huambo are classified mainly within the Angolan Miombo Woodland ecoregion (Olson et al., 2001). These regions, in Lunda Sul, Cuanza Norte and Huambo provinces respectively, are also recognized as significant areas in terms of plant diversity (Linder, 2014). In contrast, Lunda Norte, Moxico and Cuando Cubango show a low diversity of *Vigna* species; these eastern provinces are covered by Kalahari Sands, mainly composed of quartz grains that hold no mineral nutrients and organic matter, resulting in low water-holding capacity and low fertility soils (Huntley, 2019), and consequently in low species richness in most plant groups. However, the low levels of diversity and endemism recorded in some provinces may be a result of the spatial bias in surveys and collection. Based on modelling techniques, van Zonneveld et al. (2020) reported a greater diversity of *Vigna* species in Angola than is currently represented in herbaria, living collections and germplasm banks; these gaps are located mainly in the northern part the country, which is in line with our findings. According to Figueira and Lages (2019), some regions of Angola, such as Uíge and Zaire provinces, are clearly under-represented in herbarium collections. During the last two centuries, most collectors favoured the western regions of Angola, with the north and east of the country being among the least inventoried regions in continental Africa (Goyder et al., 2018; Stropp et al., 2016). Thus, extensive and exhaustive field surveys have not yet been carried out across the entire country. Most scientific expeditions took place during the 19th and 20th centuries, with a disproportionate number of specimens collected by a small number of botanists, namely F. Welwitsch, J. Gossweiler, A.W. Exell and F.A. Mendonça (Goyder and Gonçalves, 2019). There may be other diversity hotspots for *Vigna* that have not yet been identified, hence new field surveys and explorations, especially in less accessible regions, are urgently required to complement existing information on *Vigna* species distribution and abundance.

4.2. Conservation and prioritization of Vigna CWR in Angola

Angola has an essential role in global CWR conservation due to its high floristic diversity and endemism, resulting from a great diversity of ecogeographical regions. Thus, the effective *in situ* and *ex situ* conservation of Angola CWR is both a national and a global priority.

Only nine of the native species of *Vigna* (i.e., *V. antunesii, V. frutescens, V. luteola, V. mendesii, V. multinervis, V. oblongifolia, V. platyloba, V. radicans* and *V. vexillata*) were recorded in protected areas, and do not include *V. unguiculata* subsp. *tenuis* and *V. unguiculata* subsp. *unguiculata*, two high priority taxa (Fig. 6). Although this result requires further field confirmation, it indicates that the representation of plant species diversity in Angola's Protected Areas network might be poor, which is supported by other studies, namely by Frazão et al. (2020) for the genus *Euphorbia* and Romeiras et al. (2014) for Angolan timber species.

Luando Integral Nature Reserve and Mavinga National Park appear to offer potential protection to the largest number of taxa. However, the main centres of diversity found in this study, namely Serra da Chela, Saurimo, Huambo and N'dalatando areas, remain unprotected and are relatively far from the established protected areas (Fig. 4). Cuanza Norte, Lunda Sul, Huambo and Huíla host a high species diversity but, except for Huíla, these provinces do not have any protected areas. Particular attention should be given to Huíla, previously recognized as an important region for plant groups (Frazão et al., 2020; Goyder and Gonçalves, 2019) and birds (Dean et al., 2019; Sekercioglu and Riley, 2005); this province hosts eight CWR taxa of medium conservation priority (*V. antunesii*, *V. frutescens, V. procera*, *V. radicans*, *V. reticulata*, *V. unguiculata* subsp. *alba*, *V. unguiculata* subsp. *stenophylla*, and *V. vexillata*) and one taxon of high conservation priority (*V. unguiculata* subsp. *unguiculata*). Although Angola's protected areas already cover 13% of the terrestrial territory (MINAMB, 2014), the effective protection of native CWR is not ensured. Most of the protected areas were established with a focus on mammal populations, and many of them have poor management and damaged or inadequate infrastructures (Huntley, 2017; Huntley et al., 2019; MINAMB, 2014; MINUA, 2006). Thus, significant improvements are required in the design and management of extant protected areas to increase the protection of native plant species (Frazão et al., 2020).

The *ex situ* conservation analysis highlights that *Vigna* CWR from Angola are very poorly represented in worldwide genebanks, with only one species (*V. unguiculata* subsp. *alba*), preserved at the Botanic Garden Meise (Belgium) (Genesys, 2020). Therefore, the important genetic diversity of this territory is inaccessible for crop improvement programmes. Seven native taxa were not represented in genebanks. This is of particular concern in the case of the high and medium conservation priority species.

Moreover, 33% of the native *Vigna* species (eight species), especially the most geographically restricted species, have not been assessed for the threat status by the IUCN (2020). Evaluation of the threat status is an important step to establish more effective measures to protect threatened species (Romeiras et al., 2016a, 2016b). To protect wild *Vigna* species, extensive fieldwork should be conducted to better understand their distribution, ecology, and threats, as well as to improve the taxonomical knowledge of this group. The identification of Important Plant Areas (IPAs) could be an effective measure, based on the presence of an exceptional number of species of high conservation importance [criterion B(ii)] and an exceptional number of socially, economically or culturally valuable species [criterion B(iii)] (Darbyshire et al., 2017).

According to Maxted et al. (2013), the process of establishing priorities and the development of national strategic action plans are essential for CWR conservation. Magos Brehm et al. (2017) suggested ten key steps for CWR effective conservation. With this work, we fulfil five of these steps for the genus *Vigna* in Angola: the creation of a national CWR checklist; the prioritization of taxa for active conservation; the collection of taxonomic, ecogeographic and threat data; the identification of the main diversity hotspots; and *in situ* and *ex situ* gap analyses. The next steps should be updated IUCN Red List threat assessments, a climate change analysis of priority CWR; the implementation of complementary conservation recommendations; the monitoring of conserved diversity; and ensuring that the CWR resources are sustainably exploited (Magos Brehm et al., 2017).

Our results should be applied to the development of an *in situ* network of genetic reserves, through improvement of existing protected areas and the establishment of new areas to include the main CWR diversity hotspots. *In situ* conservation is particularly important because it allows species to adapt naturally to changing environmental conditions. *Ex situ* collections of representative genetic diversity of Angolan *Vigna* taxa also need to be developed through collections of seeds, tissues, live plants in botanical gardens and, especially, gene banks, since these are main resources for plant breeding studies (Ramírez-Villegas et al., 2010). A next step should be the analysis of infra-specific diversity within the genus *Vigna* and the corresponding gap analysis, since *in situ* and *ex situ* conservation should be planned for global genetic diversity and not only at the species level. As the information on genetic diversity of this genus is scarce, ecogeographic diversity could be used as a proxy.

4.3. Implications for crop improvement under climate change

Angola hosts a great diversity of plant species, but their potential for crop improvement remains largely unknown. Although some breeding programs have been carried out in Angola in recent decades, they mainly focused on coffee and cotton production (FAO, 1996). In this country, there are many other CWR, such as those of sorghum (*Sorghum bicolor*), pearl millet (*Cenchrus americanus*) and African rice (*Oryza glaberrima*) (FAO, 1996; Figueiredo and Smith, 2008), but more taxonomic and phylogenetic studies are required to correctly identify such CWR and their potential for crop improvement.

The studies on the genetic relationships between *Vigna* species and the composition of their gene pool are incipient, and so in the current study most taxa were classified according to the Taxon Group concept based only on morphological characteristics (Maxted et al., 2004; van Zonneveld et al., 2020). Except for *V. unguiculata*, which has been widely studied worldwide, there are few studies of breeding systems using wild *Vigna* species, and the gene pool of African *Vigna* remains poorly understood (Ng and Padulosi, 1991). The existing data concerning the gene pool, based on crossing and phylogenetic studies, point to some results that would not be expected when the taxon group concept is applied. For instance, *V. unguiculata* subsp. *unguiculata* and *V. unguiculata* subsp. *alba* are TG1 but GP2 according to USDA (2020); *V. unguiculata* subsp. *dekindtiana* is TG1 but GP3 according to van Zonneveld et al. (2020); *V. unguiculata* subsp. *stenophylla* is TG1 but GP2 according to van Zonneveld et al. (2020); and *V. vexillata* is TG4 but GP3 according to USDA (2020). Indeed, the still incomplete knowledge of infrageneric classification poses serious limitations to the use of this concept. That is the case of the position of some sections (e.g. *Catiang* and *Reticulatae*), which is not consensual, with Pasquet and Padulosi (2013) placing them in the subgenus *Plectotropis* rather than subgenus *Vigna*. The close relationships of species belonging to sections *Catiang* and *Reticulatae* with species from subgenus *Plectotropis* is also mentioned by Tomooka et al. (2011), who highlight some cross incompatibility within section *Catiang*. For example, none of the Angolan species included in subgenus *Vigna* is reported as GP of cowpea. Notwithstanding, seven species pertain to the gene pool of bambara groundnut. This debate emphasizes the need to clarify the taxonomic rank of some wild cowpea groups, as already pointed out by Pasquet and Padulosi (2013), as well as a deeper understanding of the phylogenetic relationships in *Vigna*.

The difficulties of using taxon group as a *proxy* for gene pool were already pointed out by Wiersema and León (2016) and Miller and Khoury (2018). Thus, the taxon group proposal, while making an important effort to overcome the limitation set by reliance on hybridization evaluations, does not provide an accurate indicator of interfertility that can be confidently used to establish genetic relationships. This is particularly noticeable in supraspecific categories that, in many cases, do not reflect the genetic relatedness but rather the history of the taxonomic approaches by successive authors.

The study of breeding systems is critical to understand natural crossing rates, gene flows, patterns of genetic diversity and minimum population sizes, all of which are crucial factors to consider in order to take effective conservation measures. Pasquet (1999) suggests that the southern African region houses a considerable genetic and biochemical diversity of *V. unguiculata*, providing a valuable but poorly exploited resource for *Vigna* breeding programmes. Thus, further crossing experiments and molecular studies should be done, especially with the less studied taxa, to clarify the gene pool and the relationships between cultivated and wild species.

A study conducted by van Zonneveld et al. (2020) suggests that *Vigna* species have higher levels of resistance to pests and diseases than to changes in climate and salinization. Of particular importance are Angolan representatives of the section *Catiang*, including subspecies of *V. unguiculata* potentially relevant to pod bug resistance (e.g. subsp. *dekindtiana*, Timko and Singh 2008; Huynh et al., 2013), and aphid resistance (e.g. subsp. *stenophylla*, Badiane et al., 2014); and *V. vexillata*, section *Plectotropis*, a promising species in crop improvement in biotic stress resistance to pests like aphid, bruchid, cowpea mottle carmovirus, flower thrip, pod borer, pod bug and yellow mosaic virus (Boukar et al., 2015; Gomathinayagam et al., 1998; Timko and Singh 2008). This will contribute with new data for an efficient use of germplasm for hybridization in breeding programs, which will allow to develop and improve the quality and yield of *Vigna* crops.

With the acknowledged global value of novel genes to crop resilience, it might be expected that CWR would already be effectively conserved globally. However, genebank collections still have few CWR accessions, representing a small percentage of the global CWR diversity (Maxted and Kell, 2009).

5. Conclusions

Based on *in situ* and *ex situ* conservation analyses, our study highlights the need for significant improvements in the design and management of extant protected areas and for the inclusion of species collected in Angola in global genebanks. The main centres of *Vigna* diversity found in Angola coincide with centres of diversity for other plant groups, but remain unprotected. These areas should be actively protected and should be the focus of future field surveys to gather further conservation-relevant data on plant diversity and ecology. In addition, seven native taxa had no accessions in genebanks globally and, among the studied species, only one has an accession collected in Angola. Thus, in the case of *Vigna* CWR, the genetic diversity of this country remains unprotected and inaccessible for crop improvement. More studies on genetic relationships between *Vigna* species are also required to understand the composition of their gene pool, which remains poorly understood, particularly for African taxa.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2020.e01415.

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