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Diversity and conservation of traditional African vegetables: Priorities for action

Maarten van Zonneveld[1] | Roeland Kindt[2] | Svein Ø. Solberg[3] | Sognigbé N'Danikou[4] | Ian K. Dawson[2]

[1]Genetic Resources and Seed Unit, World Vegetable Center, Headquarters, Shanhua, Taiwan

[2]CIFOR-ICRAF, Nairobi, Kenya

[3]Faculty of Applied Ecology, Applied Ecology, Agricultural Sciences and Biotechnology, Inland Norway University of Applied Sciences, Elverum, Norway

[4]World Vegetable Center, Eastern and Southern Africa office, Arusha, Tanzania

Correspondence
Maarten van Zonneveld, Genetic Resources and Seed Unit, World Vegetable Center, Headquarters, 60 Yi-Min Liao, Shanhua, Tainan 74151, Taiwan.
Email: maarten.vanzonneveld@worldveg.org

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Abstract

Aim: Traditional African vegetables have high potential to contribute to healthy diets and climate resilience in sub-Saharan African food systems. However, their genetic resources are likely at threat because they are underutilized and under the radar of agricultural research. This paper aims to contribute to a conservation agenda for traditional African vegetables by examining the geographical diversity and conservation status of these species.

Location: Sub-Saharan Africa.

Methods: 126 traditional annual and perennial African vegetables were selected for their food and nutrition potential. Food uses and species' areas of origin were recorded from literature. Species' presence records were collected from open-access databases of genebanks and herbaria. These records were used to determine geographical patterns of observed and modelled richness, to distinguish geographical clusters with different compositions of vegetables, to assess species' ex situ and in situ conservation status and to prioritize countries for conservation actions.

Results: Of the 126 species, 79 originated in sub-Saharan Africa. High levels of observed and modelled species richness were found in: (a) West Tropical Africa in Ghana, Togo and Benin; (b) West-Central Tropical Africa in South Cameroon; (c) Northeast and East Tropical Africa in Ethiopia and Tanzania; and (d) Southern Africa in Eswatini. South Sudan, Angola and DR Congo are potential areas of high species richness that require further exploration. In general, ex situ conservation status of the selected species was poor compared to their in situ conservation status.

Main conclusions: Areas of high species richness in West Tropical Africa, South Cameroon and Ethiopia coincide with centres of crop domestication and cultural diversity. Hotspots of diversity in Tanzania and Eswatini are especially rich in wild vegetables. Addressing the conservation of vegetable diversity in West Tropical Africa and South Cameroon is of most urgent concern as vegetable genetic resources from these locations are least represented in ex situ collections.

KEYWORDS

African indigenous vegetables, African leafy vegetables, food security, neglected and underutilized species, nutrition, orphan crops, vegetable genetic resources

1 | INTRODUCTION

Sub-Saharan Africa (SSA) has some of the areas of highest hidden hunger in the world, with these acute nutritional deficiencies exacerbated by climate change (von Grebmer et al., 2014). Governments have highlighted the important role of food production diversification to promote a wider range of healthier foods and support more sustainable production systems (Covic & Hendriks, 2016; von Grebmer et al., 2014). In a revised research and development agenda, traditional African vegetables have high potential to contribute to food production diversification and healthier diets in SSA. These vegetables are naturalized (introduced long ago and now accepted as "traditional") or indigenous to SSA and are adapted to local food and farm systems after generations of interactions with humans and the environment. Many are highly nutritious (Odhav et al., 2007; Yang & Keding, 2009) and are easy to incorporate into farm systems because they require limited space and fit within short rotations (Schreinemachers et al., 2018). Traditional African vegetables therefore potentially help to diversify farm systems and diets with nutritious foods and generate more climate-resilient food production (van Zonneveld, Turmel, et al., 2020). So far, however, the majority of these species have not been considered in climate smart agriculture strategies (e.g. Pironon et al., 2019; Rippke et al., 2016).

Current rural-to-urban migrations in African countries provide opportunities for new urban markets and peri-urban processing of these vegetables, and this may particularly benefit the livelihoods of women (Dinssa et al., 2016; Weinberger & Pichop, 2009). On the other hand, these migrations result in reduced human populations in rural areas and drive the loss of traditional knowledge about these species, as well as the loss of local landraces and populations because of reduced use (Keller et al., 2005; Pilling et al., 2020). These losses are exacerbated by limited research. This means relatively little is known about the origins and distributions of many of these vegetables, and how genetic resources—that can be exploited in crop promotion—are structured within their distribution ranges. It is clear therefore that conserving and documenting the diversity and traditional knowledge of these vegetables is important, before these resources are lost. This is especially relevant within biodiversity-rich food production systems that still exist in Africa but are now threatened by trends to food production homogenization (Dawson, Park, et al., 2019; Khoury et al., 2014).

In this study, we provide insights into the geographical patterns in the diversity and origin of 126 traditional African vegetables in SSA. These vegetables were selected after a review of five renowned species lists of important traditional African vegetables (African Orphan Crops Consortium, 2019; Dinssa et al., 2016; Grubben & Denton, 2004; Guarino, 1995; Maundu et al., 2009).

Second, we prioritize actions to safeguard traditional African vegetables following six conservation principles (Game et al., 2013): (a) Delineation of priorities: we aim to support decision-making in resource allocation to safeguard the genetic resources of traditional African vegetables as a basis for food and nutrition security in SSA; (b) Clear objective functions: our analysis contributes to a conservation agenda to safeguard SSA genetic resources of the 126 selected traditional African vegetables by 2030. We propose ex situ and in situ conservation of a minimum of 50 populations per species (following Brown & Marshall, 1995), while at the same time maintaining diverse ex situ collections of at least 200 genebank accessions and ideally 1,000 or more accessions for those species with high cultivation and breeding potential; (c) Prioritized actions: countries and conservation actions will be prioritized with a focus on multiple-crop germplasm collecting missions for ex situ conservation; (d) Scoring rules: a clear rational is provided for the selection of the 126 species, and we apply a set of indicators to assess and compare the ex situ and in situ conservation status of each species and to prioritize countries for conservation actions; (e) Transparency: scoring is explained in detail and the R coding we use can be requested for verification of our results or to apply to other geographical regions or crop groups; and (f) Risks need to be managed by establishing standard operating procedures to ensure the safety of people when they implement conservation actions, and by establishing germplasm backups, such as at the Global Seed Vault in Svalbard.

2 | METHODS

2.1 | Selection of traditional African vegetables with high potential

We consulted five key species lists on African vegetables to identify which vegetables, according to experts and other stakeholders, have high potential to support food and nutrition in SSA:

- The vegetable volume of the Plant Resources of Tropical Africa (PROTA) (Grubben & Denton, 2004) is the standard reference on vegetables in Africa. We retreived a list of 337 plants from PROTA that were identified as species that are principally used as a vegetable. Our 126 selected species include 110 of these species (33% of the PROTA list).
- In the landmark International Workshop on Genetic Resources of Traditional Vegetables in Africa that was organized in 1994, agricultural scientists from 13 SSA countries identified 171 traditional African vegetables as relevant for food and agriculture (Guarino, 1995). Our 126 selected species include 111 of these species (65% of this list).
- Three renowned scientists in traditional African vegetables identified 64 important vegetables according to country species lists, ethnobotanical surveys in specific communities and the authors' own experiences (Maundu et al., 2009). Our 126 selected species include 60 of these species (94% of this list).
- The African Orphan Crops Consortium (AOCC) (African Orphan Crops Consortium, 2019) species list includes 43 vegetables. These vegetables were selected by a diverse group of stakeholders including experts in the early 2010s as part of a wider set of annual and perennial plants to be considered in regional breeding

research on new and orphan crops. Our 126 selected species include 38 of these species (88% of this list).
- Breeding priorities of the World Vegetable Center (WorldVeg) for traditional African vegetables based on Dinssa et al. (2016) help to define which vegetable genetic resources are used at a regional level. Farmers in Cameroon, Mali, Madagascar and Tanzania selected 15 traditional vegetables during 2008 as promising for crop diversification. Our 126 selected species include all 15 of these species (100% of this list).

In total, these five lists returned an extensive initial list for potential conservation action of 422 species (https://dx.doi.org/10.6084/m9.figshare.11954001). However, limited resources exist to safeguard traditional African vegetables both ex situ and in situ for a sufficient number of populations for conservation and breeding. To avoid the dilution of effort, and to be targeted and pragmatic, we decided to focus only on those species on this initial list that have the most potential for food and nutrition. As most of the species lack suitable metrics on production and consumption that could be used for prioritization purposes, we used a simple consensus-based approach for ranking. This was based on the frequency of each species inclusion in our five species lists. Such an approach, though imperfect, is recognized as sound when detailed information is not available (Romney et al., 1986). In our case, we selected any vegetable mentioned in at least two assessments for more detailed study at regional scale, resulting in a final list of 126 species. The remaining 296 of the 422 species were only mentioned by one of the species lists and were excluded accordingly from this regional assessment.

2.2 | Species' presence records

Taxa names of the 126 vegetables were revised according to the Plant List (The Plantlist, 2013). Species' presence records from SSA used to generate geographical maps of observed and modelled species richness and to develop conservation indicators were obtained from two types of data source:

- Genebank records from the 2017 World Information and Early Warning System on Plant Genetic Resources for Food and Agriculture (WIEWS) (FAO, 2019). The WIEWS database contains information from Genesys—the Global Gateway to Genetic Resources (Crop Trust, 2019)—and additional data. Records were downloaded as batch files and then processed and analysed using R statistical software version 4.0.2 (RC Team, 2020).
- Records from herbaria and inventories stored in the Global Biodiversity Information Facility (GBIF, 2019). These were collected with the "rgbif" package (Chamberlain et al., 2016). The contributing organizations are listed in Text S1.

To detect geographical patterns of species richness, the georeferenced records from WIEWS and GBIF were selected and checked for quality. Presence records with inconsistencies (outside a border buffer zone of 1 arc minute) between geographical coordinates and the given country, as reported in associated passport data, were removed following the procedure of van Zonneveld et al. (2018). Coordinates of presence records located in coastal waters within a 1-arc minute buffer zone to the coastline were relocated to the nearest land point. Presence records with coordinates of country middle points were removed using Coordinate Cleaner (Zizka et al., 2019), as these records likely reflect low georeferenced precision. For each species, duplicate records (i.e. with the same coordinates) were removed to reduce sample bias. Synonyms were checked using the "Taxonstand" package (Cayuela et al., 2012), and presence records were removed when synonyms were rejected by the Plant List.

2.3 | Conservation status

For each vegetable, the number of genebank accessions originating from SSA was recorded from WIEWS to determine to what extent its genetic variation is safeguarded ex situ in genebanks and therefore to what extent it is possible to use their genetic resources for crop improvement programmes. Our threshold number for conservation is 50 accessions: this is the minimum number of populations recommended to be sampled in a region with no prior knowledge of genetic structure (Brown & Marshall, 1995). Our threshold number to start a crop improvement programme is 200 accessions: this is the proximate size of mini-core collections that are used for screening germplasm for crop improvement (Schafleitner et al., 2015; Upadhyaya et al., 2006). Our threshold number to sustain long-term breeding programmes is 1,000 accessions: this follows audit recommendations for the WorldVeg genebank for the minimum size of vegetable crop collections, as part of its Genebank Quality Management System. While these numbers are somewhat arbitrary, they provide an expert-based and practical framework to review, monitor and improve the conservation and coverage of existing genebank collections for conservation and breeding.

To strengthen this framework with details about the geographical and ecological representativeness of the genetic variation safeguarded ex situ, three standard indicators for ex situ conservation were calculated for each species: (a) the amount of all genebank and herbarium records (non-georeferenced and georeferenced) were compared, resulting in the Sampling Representativeness Score (*SRS*); (b) the Geographic Representativeness of georeferenced genebank records (*GRSex*); and (c) the Ecological Representativeness of these records across terrestrial ecoregions (Olson et al., 2001) (*ERSex*). The final conservation score for ex situ conservation (*FCSex*) is the average of *SRS*, *GRSex* and *ERSex*. All indicators were calculated with the "GapAnalysis" package (Carver et al., 2020) following the approach of Khoury et al. (2019).

For each species, standard indicators for in situ conservation status were also calculated following the approach of Khoury et al. (2019) with a focus on conservation in protected areas. First, the Geographical Representativeness Score for in situ conservation (*GRSin*) was calculated as the proportion of the overlap of the modelled distribution range with the World Database of Protected Areas (Bingham et al., 2019). Second, the Ecological Representativeness Score for in situ conservation (*ERSin*) was calculated as the proportion of terrestrial regions of the modelled distribution range covered by the World Database of Protected Areas. The Final Conservation Score for in situ conservation (*FCSin*) is the average of *GRSin* and *ERSin*.

To support decision-making on prioritizing a type of conservation, a *t* test was used to check for differences between the ex situ and in situ conservation scores. An ANOVA was used to assess whether there was a relationship between the potential of species—according to the frequency of their inclusion in the species lists—and their ex situ and in situ conservation status.

Finally, as a measure of sampling representativeness at country level, we compared the number of species and accessions recorded as safeguarded ex situ with the number of species and the number of observations of these species from presence records. All presence records, including non-georeferenced records, were used from the WIEWS and GBIF databases. The larger the number of observed species that is not safeguarded ex situ and the greater the disparity between observations and accessions collected, the greater the urgency to collect germplasm for ex situ conservation in that country.

2.4 | Observed species richness

As a basic initial analysis of geographical patterns to confirm species presence, we mapped the observed richness of traditional African vegetables using our extracted location data. We used the "raster" package and the circular neighbourhood approach to assess these diversity patterns (Hijmans & Etten, 2012; van Zonneveld et al., 2012). In this approach, each cell receives the number of species found within a circle with a specified diameter centred on the cell. Geographical coordinates were transformed to the Mollweide equal area projection to optimize comparison between geographical areas. Cell resolution was set at 50 km and the circular neighbourhood diameter at 300 km; these are scales suitable for a cross-continent analysis.

2.5 | Observed species richness corrected by resampling without replacement

While the observed richness is a good baseline indicator to plan conservation actions, it is limited in detecting biogeographical patterns of plant diversity because the values are biased by the varying densities of observations that occur in most geographical datasets. To account for this, we used a second approach where observed richness estimates were corrected by a common resampling without replacement procedure (Thomas et al., 2012). In our case, a 100-times bootstrap was used to reduce the sampling bias and the minimum sample number was set as the median number of species observed per grid cell.

2.6 | Modelled species richness

We then used a third approach, based on species distribution modelling (SDM), to identify in which agroecological zones people may be growing the selected vegetables or harvesting them from the wild. This approach helps to detect potential areas of high species richness in locations with low sampling density and to confirm areas of observed high species richness. We modelled the distributions of species with the "BiodiversityR" package (version 2.11-2) (Kindt, 2018). Details on the selection of environmental variables, on environmental and spatial thinning, and on model evaluation, are provided in Text S2. After spatial and environmental thinning of presence records, we undertook SDM only on 110 of our 126 species that had sufficient records to qualify for our modelling approach (Text S2). Species suitability maps were created for these species by a consensus modelling method, whereby the ensemble suitability corresponds to the weighted average of suitability values predicted by contributing algorithms that include different machine learning, regression and presence-only approaches (Text S2). Previous studies have shown that consensus methods based on weighted averages can significantly increase the accuracy of SDM (Hao et al., 2019; Kindt, 2018; de Sousa et al., 2019). The 16 remaining vegetables of our 126 species had insufficient records to qualify for our modelling approach. However, we included them in our analysis by mapping a circular area of 50 km radius around each presence record as a surrogate for the potential distribution following the approach of Khoury et al. (2019). Species richness maps based on all 126 species were created by summation of species-specific presence-absence maps obtained via the threshold method of maximizing the sum of sensitivity and specificity (Liu et al., 2013).

2.7 | Vegetable composition structure

As a measure of spatial structure in vegetable diversity, we arranged grid cells in geographical clusters according to their composition of observed species. Parameters for cell resolution and circular neighbourhood diameter were as set out above. Hierarchical clustering was used with Bray–Curtis, Jaccard and Kulczynski dissimilarity indices, to develop distance matrices for dendrograms using the "vegan" package (Oksanen et al., 2019). The Ward linkage method was used to ensure even groups of grid cells to detect geographical patterns of vegetable composition. The final number of clusters was set at five following the Kelley-Gardner-Sutcliffe penalty function, with a maximum number of possible clusters of 25, using the "maptree" package (Grum & Atieno, 2007; White & Gramacy, 2015). Then, each grid cell was assigned to its corresponding cluster. Consensus indicator species were determined per cluster following Dufrêne and Legendre (1997). Indicator values were determined with frequency-only data and calculated with the "indicspecies" package (De Cáceres et al., 2012). Consensus indicator species of a specific cluster returned an average indicator value of higher than 0.3 across the three applied clustering methods.

2.8 | Origin and primary regions of crop diversity

A literature review was carried out for the selected 126 vegetables to identify for each their continent of origin and their primary region(s) of crop diversity (https://dx.doi.org/10.6084/m9.figshare.11954001). Species originating from SSA were identified as indigenous vegetables. Species initially introduced from other continents were classed as naturalized vegetables.

Adjusted from Khoury et al. (2016), "primary regions" of crop diversity are regions that include the locations of the initial domestication of crops, encompassing the primary geographical zones of crops and the genetic variation generated there since initial domestication. These regions are expected to include high levels of allelic richness and crop varieties and may contain wild ancestral populations and those of closely related wild relatives. These regions are of particular interest for safeguarding genetic resources.

The following regions in SSA were identified following level two of the World Geographical Scheme for Recording Plant Distributions (Brummitt et al., 2001): West Tropical Africa, West-Central Tropical Africa, Northeast Tropical Africa, East Tropical Africa, South Tropical Africa, Southern Africa and the Western Indian Ocean.

2.9 | Uses and domestication level

For each selected species, its food uses were recorded from the available literature. Then, for all species, their domestication level was determined from the literature using three categories: wild, semi-domesticated and domesticated. Broadly, the term "wild" is applied when a species is predominantly harvested from natural stands; "semi-domesticated" when a species is both widely harvested from natural stands and is in significant "cultivation"; and "domesticated" when a species is principally cultivated. These are loose definitions because "domesticated" has a specific biological meaning distinct from to be "cultivated," but our applied terms suffice for the current analysis (for further discussion, see Dawson, Powell, et al., 2019).

2.10 | Prioritization of countries to implement conservation actions

We developed eight indicators to score the priority of countries for the implementation of conservation actions.

1. A100: maximum value of observed richness in a country according to the observed richness analysis;
2. A75: upper quartile value of observed richness as an indicator of the extent of the area in a country with a high number of species;
3. Ar100: maximum value of observed richness corrected by resampling without replacement;
4. Ar75: upper quartile value of observed richness corrected by resampling without replacement;
5. Am100: maximum value of modelled richness;
6. Ar75: upper quartile value of modelled richness;
7. ΔAb: difference between the number of observations of the selected species and the number of genebank accessions of these species collected per country; and
8. ΔA: number of selected species that have been observed in a country and for which germplasm is not yet collected in a country for ex situ conservation.

For each cluster of vegetable composition, and for the primary regions of crop diversity, the countries with the highest scores were prioritized for conservation actions.

3 | RESULTS

3.1 | Species summary

The 126 selected vegetables belonged to 31 botanic families. Almost half (44%) belonged to only four families, which in decreasing order of abundance were Cucurbitaceae, Leguminoseae, Amaranthaceae and Malvaceae (https://dx.doi.org/10.6084/m9.figshare.11954001). Of the 126 plants, 77 (61%) were principally reported for use as a leafy vegetable and 24 (19%) as a fruit vegetable. The principal uses of the remaining 25 species (20%) were reported in the following order of frequency: seed, roots and tubers, pods, flowers, bulbs and shoot tips.

Vegetable amaranth (*Amaranthus cruentus*, Amaranthaceae), jute mallow (*Corchorus olitorius*, Malvaceae), roselle (*Hibiscus sabdariffa*, Malvaceae), spider plant (*Cleome gynandra*, Cleomaceae), African eggplant (*Solanum aethiopicum*, Solanaceae) and Ethiopian mustard (*Brassica carinata*, Brassicaceae) were the most-frequently mentioned species; they were included in all five of our species lists (Figure 1; https://dx.doi.org/10.6084/m9.figshare.11954001). These six species can therefore be considered of high potential for food and nutrition. Amaranth is used mainly as a leafy vegetable in SSA and is gaining popularity for its grain use. Spider plant, Ethiopian mustard and jute mallow are popular for their leaves. African eggplant is used primarily for its fruit. Roselle is used primarily for its calyxes that can be consumed directly or used in beverages.

While most of our selected species are annuals, several perennials were included repeatedly in the species lists, most notably baobab (*Adansonia digitata*, Malvaceae), moringa (*Moringa oleifera*, Moringaceae) and eru (*Gnetum africanum*, Gnetaceae). These perennials are primarily consumed as a leafy vegetable (Figure 1; https://dx.doi.org/10.6084/m9.figshare.11954001).

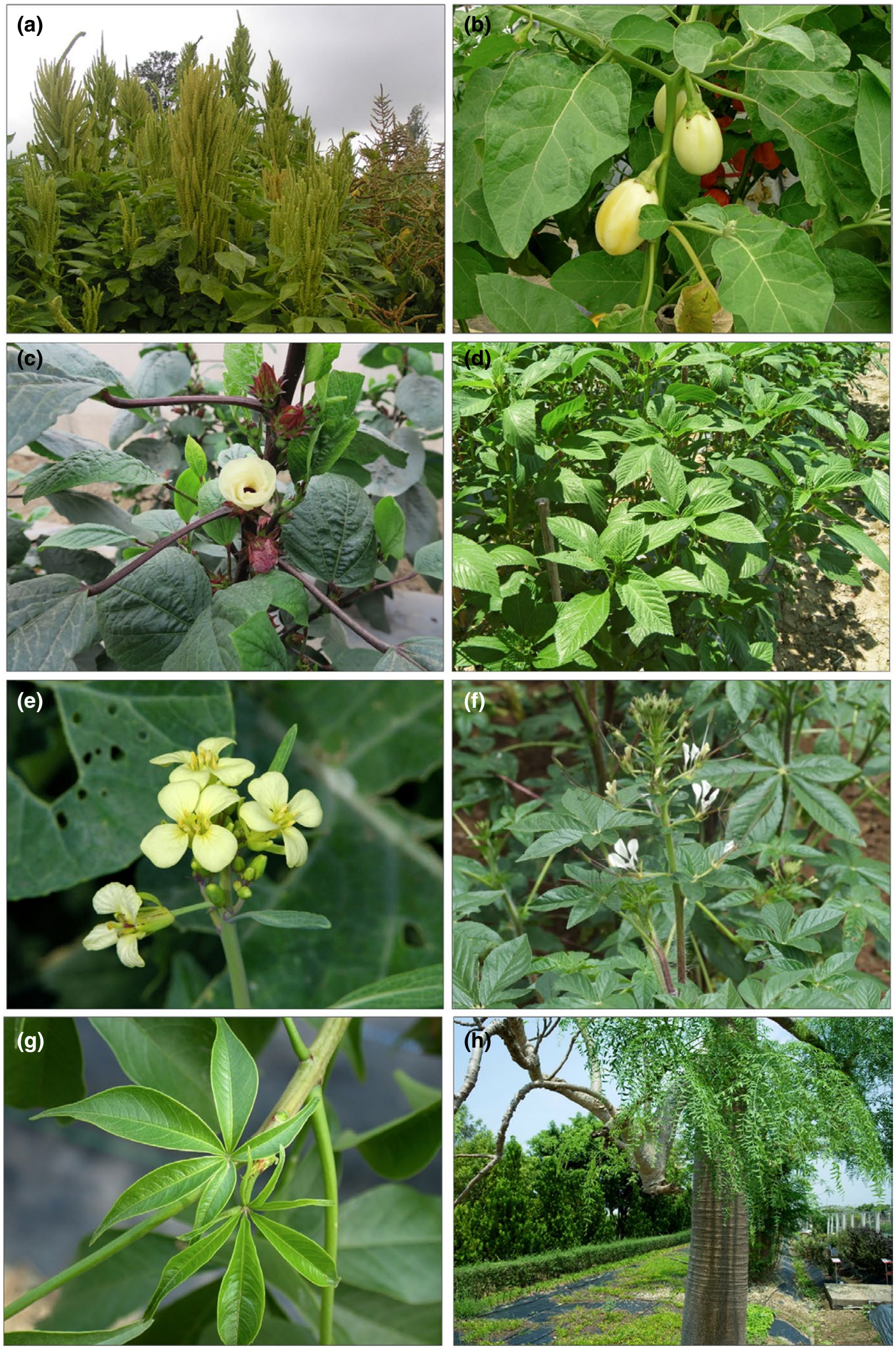

FIGURE 1 Images of eight traditional African vegetables. Panels a–f: the six most-frequently mentioned traditional African vegetables. These species can therefore be considered of high potential. Panels g–h: two frequently mentioned perennial African vegetables in four of the five species lists. Panel a: vegetable amaranth (*Amaranthus cruentus*); panel b: African eggplant (*Solanum aethiopicum*); panel c: roselle (*Hibiscus sabdariffa*); panel d: jute mallow (*Corchorus olitorius*); panel e: Ethiopian mustard (*Brassica carinata*); panel f: spider plant (*Cleome gynandra*); panel g: baobab (*Adansonia digitata*); and panel h: moringa (*Moringa oleifera*). Photos: World Vegetable Center

3.2 | Geographical patterns of species richness

A dataset of 64,463 georeferenced presence records allowed us to detect high levels of observed species richness in: (a) West Tropical Africa in Southeast Ghana, South Togo, South Benin, West Nigeria, and to a lesser degree in South Burkina Faso; (b) West-Central Tropical Africa in South Cameroon, and to a lesser degree in small pockets of DR Congo and Congo; (c) East Tropical Africa in Tanzania; and (d) to a lesser degree, Southern Africa in Eswatini and South Africa (Figure 2a; Table 1).

The following areas with high richness remained after correction of estimates by resampling, which provides a more appropriate comparison: (a) West Tropical Africa in Southeast Ghana, South Benin, South Togo and West Nigeria; (b) West-Central Tropical Africa in South Cameroon, DR Congo and Congo; (c) East Tropical Africa in Tanzania; and (d) to a lesser degree, Southern Africa in Eswatini (Figure 2b; Table 1). The resampling exercise also revealed another hotspot that was not at first evident when considering the uncorrected dataset: (e) Northeast Tropical Africa in the Ethiopian highlands. Additional pockets of diversity were observed in Réunion and Equatorial Guinea.

Our distribution modelling exercise supported the presence of high levels of species richness as identified from georeferenced point data in (a) West Tropical Africa in Ghana, and to a lesser degree in Togo and Benin; (b) West-Central Tropical Africa in DR Congo, and to a lesser degree in South Cameroon; (c) East Tropical Africa

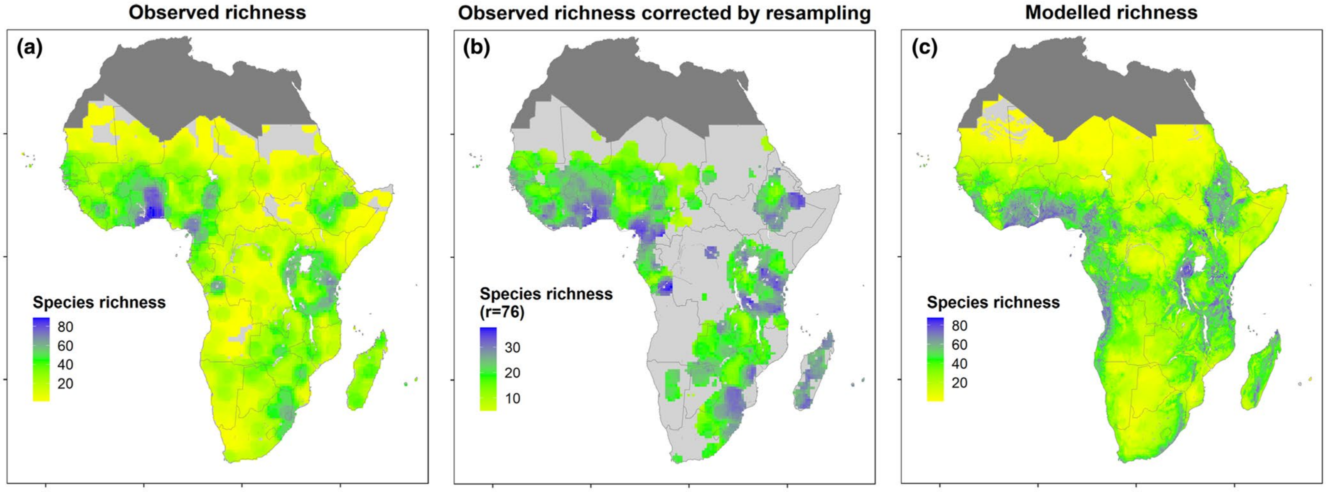

FIGURE 2 Geographical patterns of richness of traditional African vegetables in sub-Saharan Africa. Panel a shows the observed species richness with the use of georeferenced presence records from the WIEWS and GBIF databases; panel b shows the observed species richness corrected by resampling without replacement, using the median number of presence records per cell as the minimum sampling size; and panel c shows the modelled species richness resulting from ensemble species distribution modelling

in Tanzania; and (d) Northeast Tropical Africa in Ethiopia (Figure 2c; Table 1). Modelling further predicted high levels of vegetable diversity in other areas in Northeast and East Tropical Africa: South Sudan, and to a lesser degree in Uganda, Rwanda, Kenya and Burundi. The modelling exercise also revealed potential areas of vegetable richness in the Western Indian Ocean: Madagascar and the Comoros. Finally, small pockets of modelled richness were observed in Côte d'Ivoire and Equatorial Guinea.

3.3 | Vegetable composition structure

The three distance methods (Kulczynski, Bray–Curtis and Jaccard) revealed similar cluster patterns: clustering with the Kulczynski distance method can therefore be considered broadly representative (Figure 3; Figure S1). Here, cluster 1 covered the Sahel zone in West Tropical Africa and Northeast Tropical Africa; and cluster 2 covered large parts of West Tropical Africa, West-Central Tropical Africa and Madagascar. Cluster 3 was consistently located in Northeast Tropical Africa and East Tropical Africa; cluster 4 in Southern Africa; and cluster 5 in South Tropical Africa. Clustering with the Bray–Curtis and Jaccard distance methods diverged from the Kulczynski distance approach in some regards (Figure S1). The Jaccard distance method revealed an additional cluster in West Tropical Africa consisting of Benin, Togo, Ghana, Burkina Faso and Northern Cameroon. Clustering with the Bray–Curtis distance method resulted in broader geographic coverage for the West Tropical African cluster and reduced coverage for the Sahel cluster compared to the Kulczynski method.

Clusters 1 (Sahel) and 5 contained consensus species following our criterion, while the other clusters did not (Table S1). Cluster 1 included one consensus species, the indigenous wild jute mallow (*Corchorus fascicularis*). Cluster 5 included two consensus species, both naturalized and originating from the Americas, winter squash (*Cucurbita maxima*) and crookneck squash (*C. moschata*).

3.4 | Origin and cultivation status

In total, 79 of the 126 selected vegetables were indigenous to SSA. Of these, we were able to identify for 34 species their primary region of crop diversity (Figure 4; https://dx.doi.org/10.6084/m9.figshare.11954001). Our literature review indicated that Northeast Tropical Africa and West Tropical Africa were the two main primary regions of diversity of traditional African vegetables, for at least 16 and 12 vegetables, respectively. Fewer species were reported to originate from other SSA regions, with none reported to originate from Madagascar or other countries from the Western Indian Ocean region.

Forty-three of the 126 selected species (34%) can be considered to be domesticated; another 42 (33%) to be semi-domesticated, while 41 (33%) are indicated as wild. High levels of domesticated vegetables were observed especially in Madagascar and the coastal areas of West Tropical Africa, while semi-domesticated vegetables were most prevalent in West and West-Central Tropical Africa. Wild vegetables were most prevalent in Northeast and East Tropical Africa, and Southern Africa (Figure 5).

3.5 | Conservation status

On average, the final conservation scores for in situ conservation (*FCSin*) were significantly higher than those for ex situ conservation (*FCSex*) ($t = -23.54$, $p < .0001$; Figure 6; Table S2 provides the values per species). In total, 61,644 SSA-sampled genebank accessions of the 126 selected species were reported. Nine species had 1,000

TABLE 1 Prioritization of countries for conservation actions on the basis of eight indicators of species richness, abundance and conservation

Country	priorityScore	A100	A75	Ar100	Ar75	Am100	Am75	ΔAb	ΔA	Cluster	Region of crop diversity
Cameroon	7	**75**	**58.5**	**36.4**	**31.3**	81	**59**	**3,234**	**79**	2	West–Central Tropical Africa
Benin	6	**89**	**79.8**	32	**30.9**	76.9	**63.2**	**5,237**	**78**	2	West Tropical Africa
Togo	6	**89**	**86.5**	**36.3**	**33.2**	80.5	**69.3**	−514	**72**	2	West Tropical Africa
Ghana	6	**83**	**67**	**36.5**	**31.4**	**83.2**	**65.2**	1,533	61	2	West Tropical Africa
Tanzania	6	**71**	**54**	**36.4**	**29.5**	**86.6**	**58.5**	1,302	48	3	East Tropical Africa
DR Congo	6	**64**	20	**37.8**	**29.4**	**82.2**	40.4	**10,530**	**91**	3	West–Central Tropical Africa
Ethiopia	4	60	40	**34.7**	28.1	**85.3**	57	**3,560**	**63**	3	Northeast Tropical Africa
Nigeria	3	**85**	46.3	**34**	22.2	80.2	54.5	**2,078**	60	2	West Tropical Africa
Burkina Faso	3	**71**	**53**	27.7	25.6	66.2	38	**3,616**	30	1	West Tropical Africa
Eswatini	3	**62**	**60.8**	29.1	**28.8**	68.9	55.7	191	22	4	Southern Africa
Rwanda	3	61	**59.5**	18.9	16.8	**84**	**78**	776	46	3	East Tropical Africa
Burundi	3	60	**59**	17.6	16	82	**72.4**	1,119	**65**	3	East Tropical Africa
Kenya	2	**67**	43	31.7	24.5	**84.7**	46	−2,888	15	3	East Tropical Africa
Congo	2	**62**	20	**34.4**	20.4	77.9	50.5	488	47	2	West–Central Tropical Africa
South Africa	2	**62**	33.3	32.5	26.9	75.1	33.9	**6,799**	40	4	Southern Africa
Equatorial Guinea	2	57	44	**34.1**	28.1	77	**65**	545	60	2	West–Central Tropical Africa
Côte d'Ivoire	2	56	47.5	32.3	27.6	82	**64**	1,467	**69**	2	West Tropical Africa
Somalia	2	56	7	**34.7**	**34**	72.3	20.9	310	46	nd	Northeast Tropical Africa
Senegal	2	51	42.3	27	22.1	53.5	27.7	**2,037**	**64**	1	West Tropical Africa
Mozambique	1	61	31	32.6	27.7	74.8	38.6	1,151	**68**	5	South Tropical Africa
Liberia	1	60	**47.5**	32.3	27.6	66.7	40.5	249	51	2	West Tropical Africa
Uganda	1	59	44.3	30.7	25.9	**86.4**	50.9	−710	43	3	East Tropical Africa
Niger	1	57	26	23.4	19.7	34.9	10.7	**2,492**	41	1	West Tropical Africa
Zimbabwe	1	50	35.8	32.6	22.6	72	38.2	**1,996**	48	5	South Tropical Africa
Angola	1	47	14	31.3	22.3	79.3	41.3	1,404	**87**	nd	South Tropical Africa
Reunion	1	45	45	28.7	**28.7**	2	2	454	42	2	Western Indian Ocean
Madagascar	1	44	37	32.9	28.6	**83.5**	50.2	1,737	42	2	Western Indian Ocean
South Sudan	1	37	11	29.6	28.3	**87.8**	33.5	29	18	nd	Northeast Tropical Africa
Eritrea	1	30	26	29.5	**29.5**	67.3	40.4	160	44	3	Northeast Tropical Africa
Comoros	1	10	10	nd	nd	71.9	**63.1**	206	39	2	Western Indian Ocean
Chad	0	60	16	24.2	14.7	64.5	13.6	699	54	3	Northeast Tropical Africa
Guinea	0	58	35.3	29.5	23.2	72	45.4	464	55	1	West Tropical Africa
Zambia	0	53	35	29.5	20.9	74.3	30.6	−638	41	5	South Tropical Africa
Mali	0	52	25.5	27.7	21.7	58.8	19.9	996	35	1	West Tropical Africa
Sierra Leone	0	47	37	26.8	23.1	74.3	57.5	450	56	2	West Tropical Africa
Malawi	0	46	38	23.9	17.8	76.3	54.1	−1,808	40	5	South Tropical Africa
Gabon	0	43	34	30.2	25.2	71.1	54.8	779	56	2	West–Central Tropical Africa

(Continues)

TABLE 1 (Continued)

Country	priorityScore	A100	A75	Ar100	Ar75	Am100	Am75	ΔAb	ΔA	Cluster	Region of crop diversity
Gambia	0	43	42.8	25.8	25.5	40.2	30	40	16	1	West Tropical Africa
Central African Republic	0	41	15	28.5	19.3	75	38.6	542	61	2	West–Central Tropical Africa
Guinea-Bissau	0	41	41	26.1	25.5	52.3	38.8	302	49	2	West–Central Tropical Africa
Botswana	0	41	26	28.4	24	31.3	10.9	−264	33	4	Southern Africa
Namibia	0	40	22	25.5	22.8	67.9	26	0	0	4	Southern Africa
Mauritania	0	39	10	23.2	17.1	25.9	8.9	504	27	1	West Tropical Africa
Lesotho	0	36	26	23.5	20.7	40.1	32.1	65	19	4	Southern Africa
Sudan	0	29	16	25.7	21.8	69.7	13	−2,046	56	3	Northeast Tropical Africa
Mauritius	0	29	29	26.3	26.3	2	2	206	34	2	Western Indian Ocean
Cape Verde	0	26	21.3	20.2	20.2	37.9	34	539	44	2	West Tropical Africa
Djibouti	0	19	17	nd	nd	44.1	28.5	39	13	nd	Northeast Tropical Africa

Note: priorityScore: Count of top-ten rankings per country in the eight indicators of species diversity and conservation. High scores indicate high priority for conservation actions; A100: maximum value of observed richness. Values in bold are the top-ten highest values; A75: upper quartile value of observed richness; Ar100: maximum value of observed richness corrected by resampling without replacement; Ar75: upper quartile value of observed richness corrected by resampling without replacement; Am100: maximum value of modelled richness; Am75: upper quartile value of modelled richness; ΔAb: differences between the number of observations of the selected species and genebank accessions collected per country; ΔA: number of observed species, for which germplasm is not yet collected in a country for ex situ conservation; cluster: the dominant cluster of vegetable composition in a country; region of crop diversity: region of crop diversity where the country is located following level two of the World Geographical Scheme for Recording Plant Distributions. nd: no data available. Mayotte, Sao Tome and Principe, Seychelles and St. Helena are not included because of their small size.

or more accessions of SSA origin maintained in genebanks: cowpea (*Vigna unguiculata*), common bean (*Phaseolus vulgaris*), cassava (*Manihot esculenta*), Bambara groundnut (*Vigna subterranea*), pigeon pea (*Cajanus cajan*), okra (*Abelmoschus esculentus*), sweet potato (*Ipomoea batatas*), watermelon (*Citrullus lanatus*) and Ethiopian mustard (Table S2). Another 20 species had 200 or more accessions with SSA origin, and another 18 species had 50 or more. For 67 species, there were less than 50 accessions, and for 12 species, no accessions of SSA origin were reported.

Species that were included in many species lists had a better ex situ conservation status than those included less frequently ($F = 3.53$, $p = .017$). In contrast, in situ conservation status was not related to the frequency of listing ($F = 0.25$, $p = .86$). The ex situ collections of the six most-mentioned species were all above the minimum threshold for conservation of 50 accessions with SSA origin. Of these species, *Amaranthus cruentus* was the vegetable crop with the poorest conservation status: with 173 accessions, this is below the threshold of 200 accessions considered necessary to sustain a crop improvement programme.

The Kenyan Genetic Resources Research Institute, the South African Genetic Resources Directorate and WorldVeg are the institutions that maintain the collections of most traditional African vegetables. These collections maintain SSA germplasm of, respectively, 83, 38 and 36 of the selected species, and have a Shannon index of, respectively, 2.1, 2.3 and 2.7 (Table S3). In addition, Kew's Millennium Seed Bank maintains 311 accessions from a total of 72 of the selected species (4.3 accessions per species and a Shannon index of 3.9); here, species coverage is therefore good, though the depth of coverage is less than the three aforementioned genebanks (Table S3).

The five countries with the most observed species missing in genebank collections were DR Congo, Angola, Cameroon, Benin and Togo (Figure 7; Table 1). The five countries with the biggest difference in the total number of specimens recorded against the accessions noted in genebanks included DR Congo and Benin that were in common with the nations with the most observed missing species, but with South Africa, Burkina Faso and Ethiopia also featuring (Figure 7; Table 1).

3.6 | Priority countries for conservation actions

Benin, Togo, Ghana and to a lesser degree Burkina Faso are priority countries for conservation representing two vegetable composition clusters in the primary region of vegetable crop diversity in West Tropical Africa (Table 1). Ethiopia is the priority country for conservation in the primary region of vegetable crop diversity of Northeast Tropical Africa. Cameroon is the country with the highest priority score in West-Central Tropical Africa; DR Congo is another country from this region with a high priority score. Tanzania is a priority country for conservation in East Tropical Africa. Eswatini is a priority

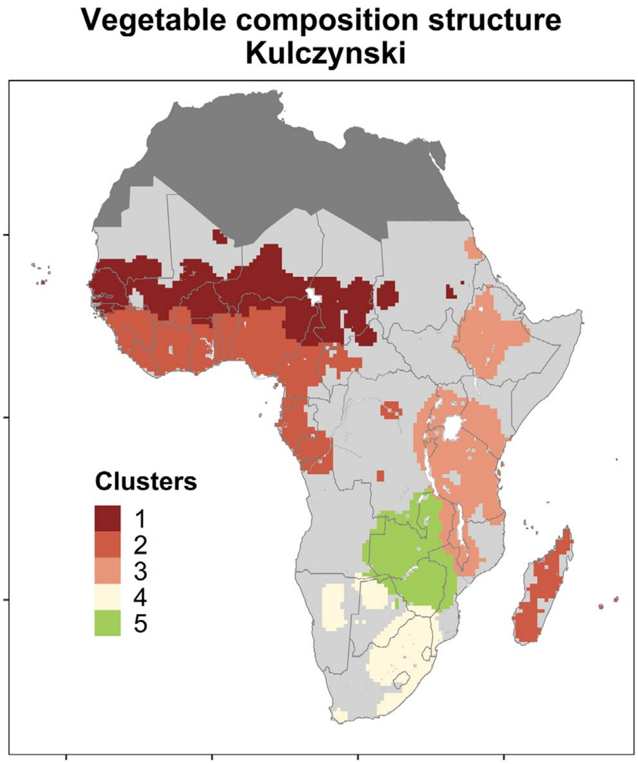

FIGURE 3 Geographical patterns in vegetable composition structure of 126 traditional African vegetables. Hierarchical clustering was applied to generate five clusters using the Kulczynski dissimilarity index and the Ward linkage method

country for conservation in Southern Africa. The countries from the regions of South Tropical Africa and the Western Indian Ocean all returned low priority scores.

4 | DISCUSSION

4.1 | Both human and phytogeographical history explain geographical distribution of traditional African vegetables

Our analysis identifies two hotspots of species diversity in primary regions of diversity of traditional African vegetables: the Dahomey gap covering South Benin, Togo and Ghana; and the Ethiopian highlands. These hotspots overlap with centres of crop domestication in both cases (Larson et al., 2014; Scarcelli et al., 2019). We hypothesize that the relatively dry conditions in the Dahomey gap compared to surrounding upper and lower Guinean rain forests (Salzmann & Hoelzmann, 2005) could have allowed the cultivation of a wide range of vegetables after their initial domestication in the West Tropical African region. The Ethiopian highlands in Northeast Tropical Africa were already a recognized Vavilov centre of diversity for cereals and coffee (Larson et al., 2014; Vavilov, 1992). Our analysis suggests this holds for a wider group of crops that includes vegetables.

Our analysis identifies South Cameroon as another hotspot of species diversity that is especially rich in semi-domesticated vegetables. South Cameroon does not overlap with an historic centre of crop domestication, but does so with a hotspot of cultural diversity (Loh & Harmon, 2005), providing support that the area could be a secondary region of vegetable crop diversity and domestication.

While the Sahel is recognized as a centre of domestication of several vegetables, including roselle, baobab, Bambara groundnut, hyacinth bean (*Lablab purpureus*) and kenaf (*Hibiscus cannabinus*) (Larson et al., 2014), our findings show low levels of species richness in this area. This finding is in contrast with our observed overlap between high species diversity and centres of crop domestication in the coastal areas of West Tropical Africa and the Ethiopian highlands. One possible reason for this contrast is that, for a large number of vegetables, rain-fed production is possible in humid and seasonally dry regions, while their production is constrained in the semi-arid conditions of the Sahel. While the number of vegetables species in the Sahel may be low, the number of landraces and populations of these vegetables is likely to be high in this centre of domestication. These may be of special interest because they are adapted to hot and arid conditions.

The high representation of wild vegetables in East Tropical Africa and Southern Africa indicates that natural vegetation patterns partly explain the geographical patterns of vegetable diversity in SSA. Tanzania and Eswatini, respectively, are hotspots of species richness in these two regions. The high number of coalescing phytogeographical regions in Tanzania (van Breugel et al., 2015; Droissart et al., 2018) could explain the high diversity of the wild vegetables found there. Eswatini is a hotspot of species richness in the Southern African cluster that represents complementary vegetable diversity.

Our analysis shows that Madagascar has a similar vegetable composition to West and West-Central Tropical Africa and is rich in domesticated vegetables, while relatively poor in semi-domesticated and wild vegetables. This pattern could reflect historic crop introductions to Madagascar from the African mainland after the colonization of the island by Bantu people, in combination with historic introductions from Asia (Pierron et al., 2017). We found only one endemic vegetable to Madagascar, the Palmyra palm (*Borassus madagascariensis*), in our longlist of 422 species, and which was not part of the selected 126 vegetables (Grubben & Denton, 2004). In contrast, Madagascar may be rich in endemic wild relatives of our selected vegetables, including *Vigna keraudrenii* that is part of the secondary gene pool of cowpea (van Zonneveld, Rakha, et al., 2020) and three wild relatives of Malabar spinach (*Basella alba*) that have only been observed on this island (data not shown in this paper). A further study on crop wild relatives of traditional African vegetables in Madagascar, as well as in the whole of SSA, would be merited.

That 47 of our 126 traditional vegetables were introduced into Africa from Asia and the Americas confirms the important role of humans in crop dispersal, and the interdependence between countries

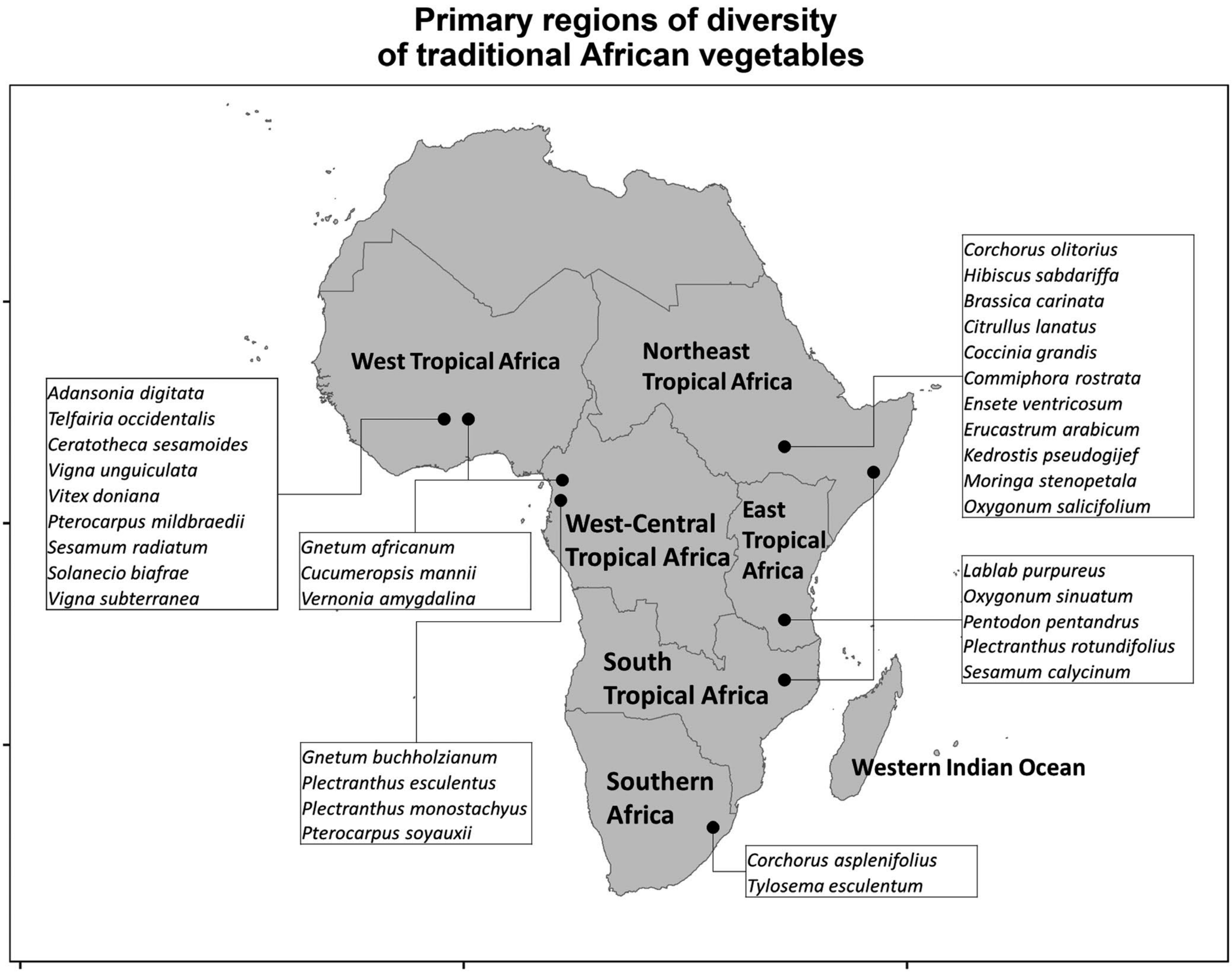

FIGURE 4 Primary regions of diversity of traditional African vegetables. For each region, the species are listed that have been reported in literature to originate from there or have been domesticated there. The division in regions follow the World Geographical Scheme for Recording Plant Distributions

and continents in plant genetic resources for food and agriculture (Khoury et al., 2016).

4.2 | Conservation of traditional African vegetables requires an integrated approach

The conservation indicators show that, in general, the ex situ conservation status of traditional African vegetables is poor compared to their in situ conservation status. Even for most species with high potential, the in situ conservation status is still higher compared to ex situ, and most of these species do not have sufficiently large collections to sustain regional breeding programmes. Our analysis therefore indicates that urgent efforts are needed to strengthen the ex situ conservation status of traditional African vegetables.

Even so, the conservation of traditional African vegetables requires an integrated conservation approach considering both ex situ and in situ. Ex situ conservation refers to storage or planting in external locations such as genebanks and botanic gardens, while in situ conservation refers to safeguarding wild populations in their original habitat or to dynamic conservation with local communities of local varieties or populations in their original areas of cultivation (Frankel et al., 1995). A third form of conservation, *circa situm*, is often used for perennial species in agroforestry systems. This refers to safeguarding planted and/or remnant trees in farmland where natural forest or woodland containing the same trees was once found, but this wild habitat has been lost or modified significantly through agricultural expansion (Dawson et al., 2013).

Our analysis suggests that people collect a high percentage of these vegetables at least in part from the wild, as 66% of the selected vegetables are wild or semi-domesticated. In addition, many of these species play an important role in the diets of wild herbivores, including baobab, *Hibiscus*, *Solanum* and *Cleome* spp. (Barnes et al., 1994; Kartzinel et al., 2015). In situ conservation in protected areas seems therefore to be a suitable measure to safeguard populations of these

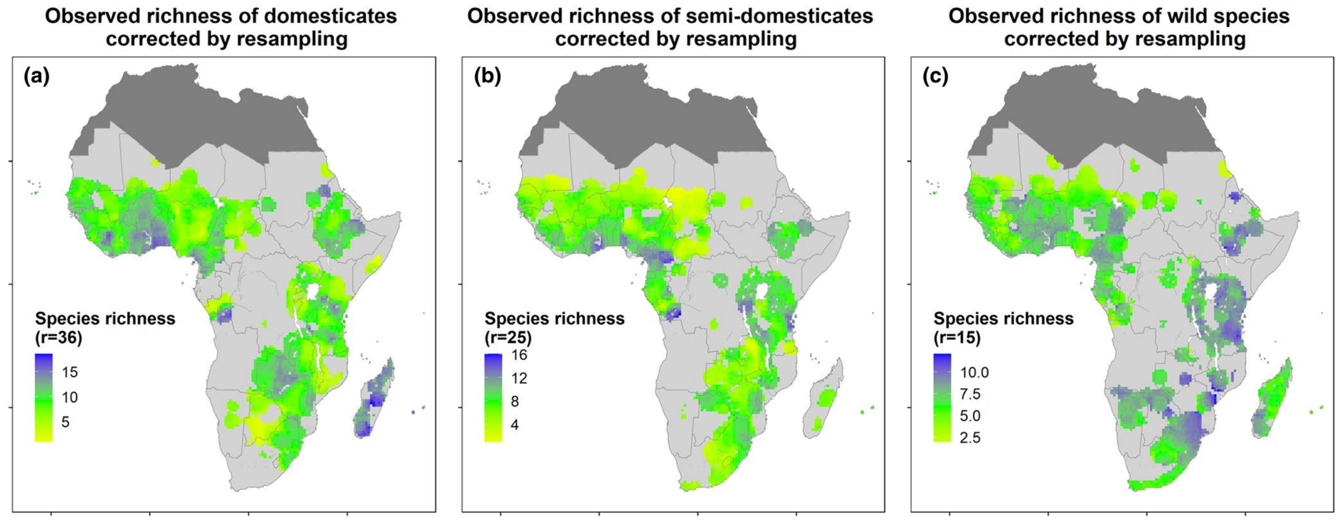

FIGURE 5 Observed richness corrected by resampling without replacement of traditional African vegetables with different domestication levels. Panel a shows the observed species richness corrected by resampling for domesticated vegetables; panel b for semi-domesticated vegetables; and panel c for wild vegetables. Domestication levels were obtained from literature

vegetables. Several of their populations may be threatened in situ by climate change or other factors, which requires periodic monitoring and targeted ex situ conservation actions for populations at risk.

Genetic resources outside protected areas are priority for ex situ conservation, especially local varieties and populations that are vulnerable to extirpation. At the original locations of many herbarium records, people may have abandoned the production and consumption of these species or will do so in the near future because of trends to food production- and consumption-homogenization, and rural-to-urban migrations (Dawson, Park, et al., 2019; Pilling et al., 2020). The promotion of the use of these species in local communities, in combination with capacity building on sustainable cultivation and/or harvesting, can improve their in situ and *circa situm* conservation and complement ex situ conservation of threatened local varieties and populations.

In our analysis, a proviso is that not all African genebanks may have shared comprehensive data with the WIEWS database. Our assessment may thus underestimate the number of ex situ genebank accessions. However, since the absence of such reporting makes this material essentially invisible and therefore inaccessible for researchers, breeders and farmers, these accessions are effectively redundant in analyses of conservation status. At the same time, just because accessions are listed in genebank databases does not mean they are accessible. Poor seed viability or low seed stock may lead to regeneration backlogs and preclude distribution. This may be the case particularly for perennial vegetables that are often hard to regenerate in a timely manner. Unclear international and national biodiversity policies for traditional African vegetables may also hamper access to the germplasm of these species conserved in genebanks. To enhance the access to this germplasm, some genebanks, including the WorldVeg genebank, distribute germplasm of any traditional African vegetable with the Standard Material Transfer Agreement (SMTA) of the International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA).

The high scores for in situ conservation in protected areas of our 126 selected species suggest that this conservation approach could be promising too for many of the remaining 296 of the 422 species that were initially identified in our study. Although these 296 species were not considered further by us in the current study (see Section 2), they could be important to consider in local and/or national conservation plans. Assuming that many of these species are wild or semi-domesticated and that they have high in situ conservation scores, a relatively low investment in resources might safeguard the populations of these wild or semi-domesticated species in protected areas.

Botanic gardens in African countries could play an important role in ex situ conservation of especially wild and semi-domesticated species including many of the remaining 296 species. While genebanks may play a key role in sustainable agricultural development with a focus on safeguarding the genetic variation of the genepools of species with high potential for food and nutrition, botanic gardens especially may play a societal role in safeguarding biocultural heritage with a focus on conserving species diversity (Engelmann & Engels, 2002). In this way, genebanks and botanic gardens can develop complementary ex situ conservation approaches, engaging with different stakeholders (Pearce et al., 2020). Stakeholders for genebanks include researchers and breeders, while for botanic gardens they include the general public as well as researchers.

4.3 | West Tropical Africa and South Cameroon are priority areas for conservation actions

Of the main areas of high vegetable diversity identified above, vegetable varieties from West Tropical Africa and South Cameroon are under-represented in genebank collections. Benin and Cameroon in particular are priority countries for germplasm collecting, because

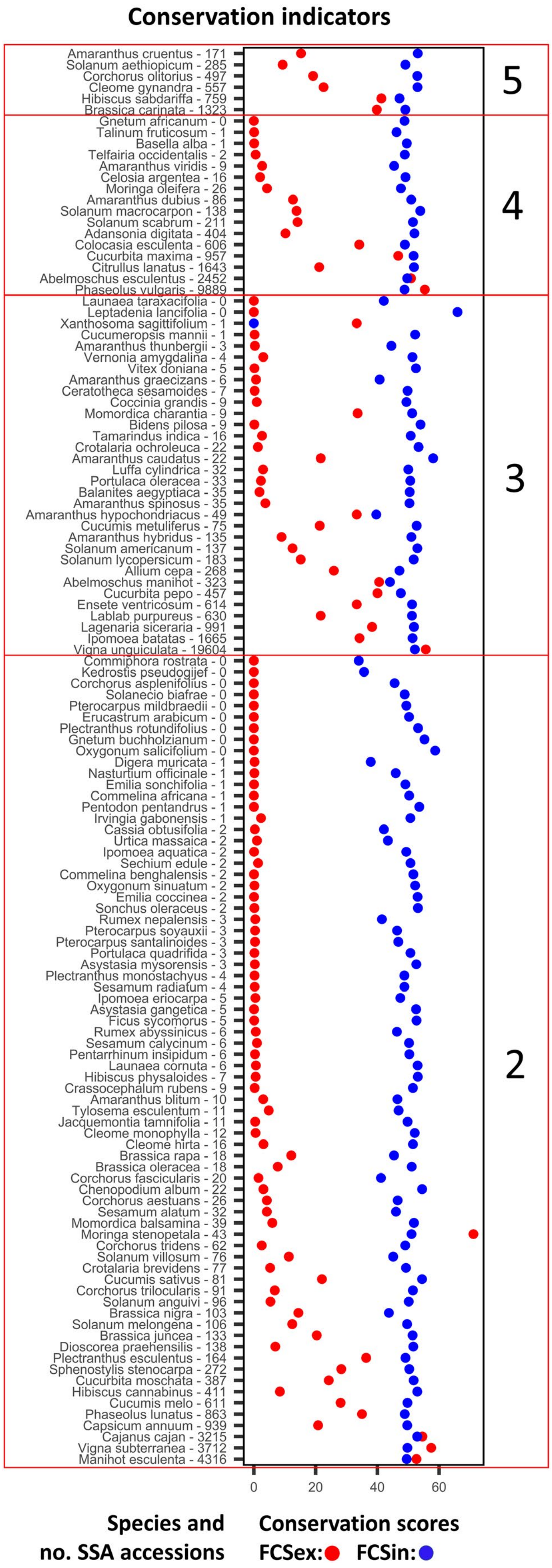

FIGURE 6 Conservation indicators for the status of the genetic resources of the 126 selected traditional African vegetables in sub-Saharan Africa (SSA). For each species, the following three indicators are shown: (i) number of accessions with SSA origin safeguarded; (ii) final conservation score for ex situ conservation (*FCSex*) for the SSA genetic resources; and (iii) final conservation score for in situ conservation (*FCSin*) for the SSA genetic resources. The species are categorized according to the frequency of their inclusion in the five species lists consulted for this study, as a proxy for their potential for food and nutrition. For example, category five refers to the species that were included in all five species lists: accordingly, these species are considered to have most potential. For each category, the species are sorted from low to high numbers of SSA accessions safeguarded, and then from low to high values of the two conservation scores combined. In this way, the species with most urgent conservation needs are listed at the top of each category

of the high levels of vegetable diversity observed in them. Vegetable diversity in Northeast and East Tropical Africa is better represented ex situ. Ethiopia, Tanzania, Kenya, Rwanda and Burundi, identified as having areas with high levels of vegetable diversity, at least have part of this diversity safeguarded already in national and international genebanks.

Among the countries that are covered by the Southern African region and its principal vegetable composition cluster, Eswatini encompasses the highest levels of vegetable diversity according to our analysis. This makes Eswatini another priority country for action to safeguard traditional vegetable diversity that is not represented in the hotspots in West, West-Central, Northeast and East Tropical Africa. Similarly, among the countries that are covered by the vegetable composition cluster in the Sahel, Burkina Faso encompasses the highest levels of vegetable diversity. Burkina Faso is therefore another priority to safeguard traditional vegetable diversity.

Our analysis does not rule out that other SSA countries than those prioritized in this study encompass valuable vegetable diversity. Some of these countries have started conservation efforts and this must continue to complete the geographical and ecogeographical representativeness of all species. However, the countries prioritized in this study for conservation actions can be considered the priorities for SSA as a whole because they encompass the highest levels of richness in combination with low or moderate conservation efforts.

Angola, DR Congo, South Sudan and Sudan are countries with low coverage of georeferenced records. Our species distribution modelling exercise showed that, of these four nations, South Sudan is predicted to encompass the highest level of vegetable diversity for our selected species. This country partly overlaps with the Sudanese centre of crop diversity. Several vegetables are thought to have been domesticated in this centre, including roselle, hyacinth bean and watermelon (Larson et al., 2014; Paris, 2015). Only a few herbarium samples and genebank records for South Sudan were reported in the current study, and it is therefore a priority for germplasm exploration. DR Congo and Angola encompass high levels of non-georeferenced herbarium records and merit further exploration of the vegetable diversity occurring in them.

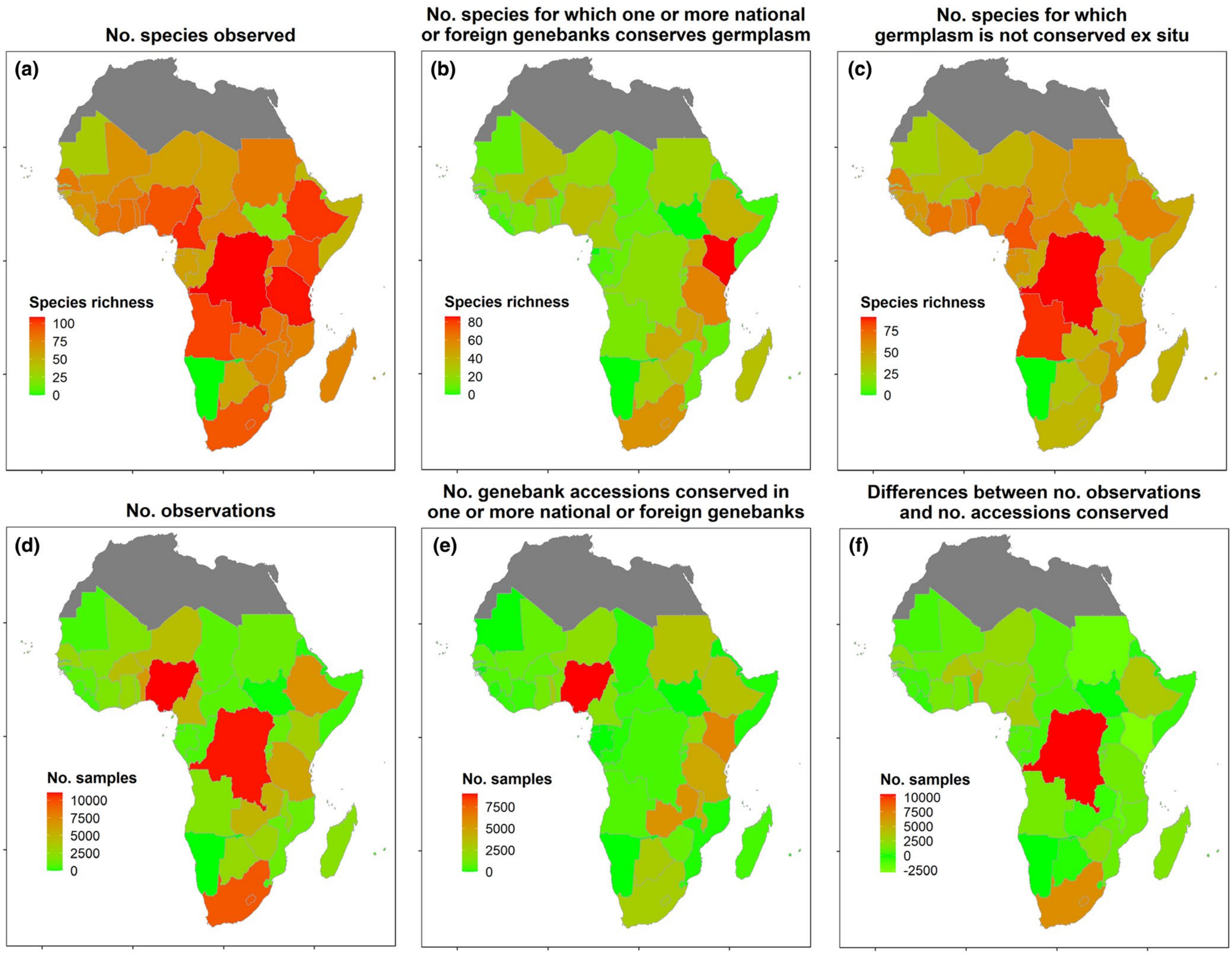

FIGURE 7 Gap analysis of traditional African vegetables at country level in sub-Saharan Africa. Panel a shows per country the number of species observed; panel b shows per country the number of species for which germplasm has been collected and safeguarded in one or more genebanks inside and/or outside the country; panel c shows the number of species for which germplasm has not yet been collected in the country for ex situ conservation. Panel d shows per country the number observations of species; panel e shows per country the number of accessions collected in the country that is safeguarded in one or more genebanks inside and/or outside the country; panel f shows, for each country, the differences between the number of observations of the selected species in that nation and the number of genebank accessions collected

4.4 | Knowledge on intraspecific diversity of traditional African vegetables is incipient

Our literature review indicated that the primary regions of crop diversity are unknown for 45 of the 79 indigenous species selected in our study. Genomic and population genetic studies can provide insights into geographical patterns of diversity and crop dispersal and help identify centres of domestication and origin (Larranaga et al., 2020; Scarcelli et al., 2019). Among the indigenous vegetables on our list, spider plant, African eggplant and jute mallow require the most urgent population genetic studies. This is because they are three of the six most-mentioned traditional African vegetables, yet their centres of domestication and origin are not well understood.

Different parts of SSA may also have developed into important secondary centres of diversity of naturalized vegetables because of wide adoption and adaptation to new environments and food systems, sometimes over periods of centuries. For example, *Amaranthus cruentus*, one of the six most-mentioned traditional African vegetables, originates from the Americas, where it is a popular grain crop. The fact that in Africa it is still used primarily as a leafy vegetable indicates a different domestication trajectory that will have impacted on genetic diversity in the crop over the last 500 years or so since introduction to Africa. Clearly, in such cases, understanding processes of local African adaptation is crucial.

5 | CONCLUSIONS

Even though traditional African vegetables have a high potential for food and nutrition security, and climate change adaptation, they have been relatively little invested in for food production, with limited germplasm conservation to support breeding and cultivation. Developing more effective conservation of these vegetables should consider that SSA encompasses at least three areas of high inter- and intraspecific diversity of traditional African vegetables, where humans have shaped vegetable domestication and cultivation: (a) the West Tropical African coastal region; (b) Northeast Tropical Africa in the Ethiopian highlands; and (c) West-Central Tropical Africa in South Cameroon. Tanzania is a fourth hotspot of vegetable diversity. Vegetable genetic resources in Southern Africa in Eswatini, and the Sahel region of Burkina Faso, complements the above areas with additional high vegetable diversity. South Sudan, Angola and DR Congo potentially encompass high levels of diversity, but are poor on species observations and collected accessions. This makes these countries a priority for further exploration.

Overall, the ex situ conservation status of vegetable diversity in West and West-Central Tropical Africa is poor compared to Northeast and East Tropical Africa, and Southern Africa, arguing for particular action in the first two of these regions. These efforts should include the collection of germplasm as well as corresponding traditional knowledge on use and management. Without these efforts, these genetic resources will be lost, as traditional food production systems in SSA are outcompeted by conventional ones.

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PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13188.

DATA AVAILABILITY STATEMENT

Basic information on the "longlist" of 422 traditional African vegetables and detailed information on our 126 selected vegetables is available at: https://dx.doi.org/10.6084/m9.figshare.11954001. Presence record data and R Scripts can be provided on request.

ORCID

Maarten van Zonneveld https://orcid.org/0000-0002-7875-4756
Roeland Kindt https://orcid.org/0000-0002-7672-0712
Svein Ø. Solberg https://orcid.org/0000-0002-4491-4483
Sognigbé N'Danikou https://orcid.org/0000-0002-4163-8567
Ian K. Dawson https://orcid.org/0000-0003-4245-6973

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BIOSKETCH

Maarten van Zonneveld is responsible for the international genebank of the World Vegetable Center, which safeguards seed of over 65,000 accessions of more than 450 vegetable species and their wild relatives. The genebank studies the diversity of this collection and distributes seed of the accessions maintained to researchers, breeders and farmers around the world to support sustainable agricultural development.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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