

RESEARCH ARTICLE

Prioritising crop wild relatives to enhance agricultural resilience in sub-Saharan Africa under climate change

David Satori^{1,2}  | Carolina Tovar¹  | Aisyah Faruk³  | Eleanor Hammond Hunt¹ | Gemma Muller¹ | Christopher Cockel³ | Nicola Kühn⁴ | Ilia J. Leitch¹ | Ermias Lulekal⁵ | Laura Pereira⁶ | Philippa Ryan¹ | Katherine J. Willis^{1,4} | Samuel Pironon¹ 

¹Jodrell Laboratory, Royal Botanic Gardens, Kew, Richmond, UK

²School of Biological and Chemical Sciences, Queen Mary University of London, London, UK

³Millennium Seed Bank Building, Royal Botanic Gardens, Kew, Wakehurst Place, Sussex, UK

⁴Oxford Long-Term Ecology Laboratory, Department of Zoology, University of Oxford, Oxford, UK

⁵Department of Plant Biology and Biodiversity Management, Addis Ababa University, College of Natural Sciences, Addis Ababa, Ethiopia

⁶Global Change Institute, University of the Witwatersrand, Johannesburg, South Africa

Correspondence

Samuel Pironon, Jodrell Laboratory, Royal Botanic Gardens, Kew, Richmond, UK.
Email: s.pironon@kew.org

Funding information

UK Natural Environment Research Council (NERC), Grant/Award Number: NE/M021351/1; Global Crop Diversity Trust; Norwegian Ministry of Foreign Affairs

Social Impact Statement

Climate change is expected to disproportionately affect sub-Saharan Africa in the next century, posing a threat to the livelihoods of smallholder farmers and deepening food insecurity. To adapt to this threat, more climate-resilient crops need to be brought into the food system; these may be developed through breeding with crop wild relatives with key traits to cope with climate change. Here, we assess the level of open-access trait documentation of crop wild relatives of 29 important crops, their resilience, how threatened they are in situ, how well they are preserved ex situ and we provide priorities for their conservation and use in breeding programmes.

Summary

- Climate change is projected to adversely affect smallholder agriculture in sub-Saharan Africa (SSA) over the next century, with many areas becoming unsuitable for growing crops. Breeding programmes using crop wild relatives (CWRs) that are pre-adapted to projected future climatic conditions may lead to more resilient crops, but their traits have not been screened across a large diversity of CWRs. Furthermore, many are threatened and require greater protection in situ and ex situ to prevent the loss of an important adaptive solution to climate change.
- A previous ecogeographical study found that 303 out of 836 CWRs of 29 major crops cultivated across SSA may represent priorities for future crop resilience. Here, we assessed the availability of trait information and compared traits between resilient and non-resilient CWRs. Subsequently, we analysed the conservation status of CWRs in situ and ex situ to set new global priorities for protection.
- Our findings show that the traits of many CWRs are poorly described, but for those species with better coverage, key differences between resilient and non-resilient CWRs were identified, including lower plant height amongst resilient CWRs of tree crops (arabica and robusta coffee, mango and cacao) and a higher likelihood of invasive CWRs to be resilient. We found that 14% and 36% of resilient CWRs are threatened in situ and absent from seed collections, respectively.

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2021 The Authors. *Plants, People, Planet* published by John Wiley & Sons Ltd on behalf of New Phytologist Foundation.

- Our study highlights CWR priorities for conservation based on resilience. A concerted international effort is recommended to conserve CWRs and improve agricultural resilience in a changing climate.

Il est prédit que le changement climatique affectera l'Afrique Sub-Saharienne de manière disproportionnée d'ici à la fin du siècle, menaçant la subsistance des petits exploitants agricoles et renforçant l'insécurité alimentaire. L'apport de nouvelles cultures résistantes au climat futur représente une stratégie adaptative majeure; celles-ci pouvant être développées lors de programmes de sélection à partir de l'usage d'espèces sauvages apparentées aux plantes cultivées possédant des traits fonctionnels associés à la résilience climatique. Dans cette étude, nous évaluons la disponibilité d'information de traits fonctionnels des parents sauvages de 29 cultures importantes, leur niveau de résilience au changement climatique, leur menace in situ, leur état de conservation ex situ, and nous proposons de nouvelles priorités pour leur préservation et usage.

El cambio climático afectará de manera desproporcionada a la región sub-Sahariana de África en los siguientes cien años, poniendo en riesgo la subsistencia de los pequeños agricultores y agudizando el problema de la inseguridad alimentaria. Una estrategia adaptativa es el uso de cultivos fitomejorados con parientes silvestres que poseen rasgos funcionales que los hacen resilientes al cambio climático. En este trabajo evaluamos la disponibilidad de información de rasgos funcionales de parientes silvestres de 29 cultivos importantes, su nivel de resiliencia al cambio climático, que tan amenazados se encuentran in situ, que tan bien representados están en colecciones ex situ y proponemos prioridades para su conservación y uso en programas de fitomejoramiento.

KEYWORDS

conservation, food security, functional traits, nature-based solutions, plant pre-breeding, seed banks

1 | INTRODUCTION

Agriculture is set to face great challenges globally in the coming century, as climate change places pressure on crop productivity (Schlenker & Lobell, 2010). The world's population has become increasingly dependent on a small number of crops where over half the world's plant-derived calories come from just three species: rice, wheat and maize (Gennari et al., 2015; Ulian et al., 2020), further increasing the fragility of food systems. The pressure from climate change is compounded particularly in sub-Saharan Africa (SSA), where a predicted increase in higher mean annual temperatures and altered precipitation regimes over the next century pose major risks to small-holder agriculture (Kurukulasuriya et al., 2006; Morton, 2007; Müller et al., 2011). SSA accounts for only 1.7% of global agricultural exports (Schmieg, 2016), but the contribution of agriculture to a country's gross domestic product (GDP) can be as high as 50% (OECD/

FAO, 2016). Despite the importance of agriculture in SSA, many crops cultivated in this region may be adversely affected by climate change (Pironon et al., 2019), weakening public health, food and nutrition security, and livelihoods (Ziervogel & Ericksen, 2010). Adapting agriculture to climate change will therefore be a paramount task for meeting the 2030 Agenda for Sustainable Development (United Nations, 2015), and one nature-based solution for achieving these goals is through crop improvement programmes using the wild relatives of domesticated crops (Dempewolf et al., 2014; Pironon & Soto Gomez, 2021).

Previous studies have demonstrated the important role of climate as an environmental and evolutionary driver of plant functional traits (Blonder et al., 2018). By understanding the traits of CWRs that are pre-adapted to climatic conditions predicted for SSA, we can prioritise further pre-breeding and breeding efforts to maximise crop resilience to climate change (Warschefsky et al., 2014). Crop wild relatives

(CWRs) have been used to improve crops by conferring adaptive traits (Dempewolf et al., 2014; Prohens et al., 2017). Through their uses, studies have shown that crop yields can still be maintained (Hodgkin & Hajar, 2007; Tanksley & McCouch, 1997). Pironon et al. (2019) showed that 303 out of 836 wild relatives of 29 major crops in SSA already inhabit climatic conditions that are expected to become widespread across SSA in the next century, providing an opportunity to screen for traits associated with resilience.

Crop improvement using CWRs could be important for addressing global food security, yet they are currently underutilised. One reason is the unavailability of suitable CWR material for targeted breeding programmes (Ford-Lloyd et al., 2011). The opportunity to understand and utilise CWRs is diminishing, as wild populations are under increasing threat from extinction (Nic Lughadha et al., 2020). With each extinction or population decline, the overall genetic diversity of CWRs also decreases (Maxted et al., 2006). Many CWRs are also found to be underrepresented in ex situ collections (Khouri et al., 2019). Given these challenges, efforts to reach the UN Sustainable Development Goals need concurrent initiatives, which protect the habitats where CWRs are found and ensure sufficient ex situ collections are accessible for future breeding programmes. Such initiatives would allow farmers in SSA to adapt their agricultural practices without switching to new production systems (Castañeda-Álvarez et al., 2016).

Here, we build on the findings of Pironon et al. (2019), using data of 836 CWRs belonging to 29 major crops cultivated in SSA to (i) assess the availability of life-history, functional and genetic trait data for CWRs; (ii) identify traits that are associated with resilience to future climate conditions predicted to occur in SSA, including invasiveness as a proxy trait; (iii) determine whether the in situ conservation status of resilient CWRs have been assessed; and finally, (iv) determine how well represented resilient CWRs are in global seed banks. Our study sets priorities for future trait documentation, and in situ and ex situ conservation of CWRs as key steps towards adapting agriculture to climate change in SSA.

2 | MATERIALS AND METHODS

2.1 | Species selection and resilience

We studied a total of 778 CWR species of 29 crops widely cultivated in SSA (Dataset S1, Table 1). The 29 selected crops are key to subsistence and the economy across the continent given they provided around 2000 kcal per capita per day and a total production value of more than US\$108 billion in 2013 and 2016, respectively (Pironon et al., 2019). The 'degree of resilience' of each CWR species was previously estimated in Pironon et al. (2019) as the percentage of overlap between the current global climatic niche of the CWR and the novel climatic conditions predicted in the future (2050 and 2070) for its associated crop grown in SSA. Niche estimates were based on occurrence records retrieved for each CWR species across their global distribution and eight bioclimatic variables (mean, seasonal, low and high

extreme temperature and precipitation) and land slope. CWRs that had no overlap (i.e., those whose current climatic niche did not overlap with that predicted for its corresponding crop in SSA in the future) were identified as 'non-resilient' whereas those with positive overlap values were classed as 'resilient' (Table 1). The 'degree of resilience' for each crop was taken as the aggregate value of the degrees of resilience for each of its CWR species. Using these data, we created a Resilience Score (RS) for each crop for both 2050 and 2070 using the following formula:

$$\text{Resilience Score} = \frac{(\text{degree of resilience of crop}) \times (\text{number of resilient CWR of crop})}{R_{\max}}$$

where R_{\max} denotes the maximum value of the numerator when carried out across all 29 crops. It is important to note that this score is likely to be an underestimate given that the degree of resilience of 189 additional CWR species was not assessed in previous analyses from Pironon et al. (2019) due to a lack of geographic information.

2.2 | Trait data and analysis

We selected a set of traits that are (i) not only known to be associated with overall plant development, survival and reproduction (Díaz et al., 2016) but also with climate resilience and/or importance for agriculture (e.g., yield and breeding; Table 2) and (ii) the most widely collected and available traits in online databases, allowing the retrieval of data for many CWR species (Dataset S4). This selection included adult plant height, stem specific density (SSD), leaf area, leaf mass per area (LMA), nitrogen content per unit leaf mass, seed mass, lifespan, photosynthetic pathway, C-value (genome size) and ploidy level (Table 2). Given that invasive species are known to exhibit traits related to a greater environmental tolerance (Higgins & Richardson, 2014), we also assessed whether CWRs have been documented to be invasive to an area within SSA as well as being potentially invasive, which we refer to as 'invasive' herein. Species-level trait data, including invasiveness, were recovered from online databases and measurements were standardised (Supporting Information Methods S1).

A single value for each trait was calculated per CWR as a geometric mean of all the entries present for that species (Dataset S1). For each of the 29 crops, two mean values and two standard errors were calculated, representing the trait values of its resilient and non-resilient CWRs (Dataset S2). For each crop, we also measured the number of CWR values used to calculate trait means and the proportion of CWRs with available data. Categorical traits (lifespan, photosynthetic pathway and ploidy level) were treated as binary (Table 2) to conduct a chi-square test of independence, but, due to low sample sizes, crops were grouped according to their botanical family for analysis. For invasiveness, the proportion of resilient species classed as invasive were compared with those not documented as invasive, for which we also conducted a chi-square test of independence.

TABLE 1 Summary of the 29 crops and associated crop wild relative (CWR) species considered in this study

Crop name	Crop type	Geographic origin	Number of CWRs	Number of resilient CWRs
Peanut (<i>Arachis hypogaea</i>)	Leguminous crop	Southern America	72	1
Pigeon pea (<i>Cajanus cajan</i>)	Leguminous crop	Tropical Asia	17	15
Watermelon (<i>Citrullus lanatus</i>)	Vegetable	Africa	3	1
Arabica coffee (<i>Coffea arabica</i>)	Beverage crop	Africa	62	25
Robusta coffee (<i>Coffea canephora</i>)	Beverage crop	Africa	58	16
Taro (<i>Colocasia esculenta</i>)	Root/tuber crop	Tropical Asia	4	0
Squash (<i>Cucurbita moschata</i>)	Vegetable	Northern and Southern America	11	7
Winged yam (<i>Dioscorea alata</i>)	Root/tuber crop	Tropical Asia	11	9
Guinea yam (<i>Dioscorea rotundata-cayennensis</i>)	Root/tuber crop	Africa	5	2
Oil palm (<i>Elaeis guineensis</i>)	Oilseed crop	Africa	1	0
Finger millet (<i>Eleusine coracana</i>)	Cereal	Africa	9	3
Enset (<i>Ensete ventricosum</i>)	Root/tuber crop	Africa	4	2
Soybean (<i>Glycine max</i>)	Oilseed crop	Temperate Asia	27	16
Cotton (<i>Gossypium hirsutum</i>)	Fibre crop	Northern and Southern America	40	16
Sweet potato (<i>Ipomoea batatas</i>)	Root/tuber crop	Northern and Southern America	13	8
Tomato (<i>Lycopersicon esculentum</i>)	Vegetable	Southern America	16	11
Mango (<i>Mangifera indica</i>)	Fruit	Tropical Asia	23	3
Cassava (<i>Manihot esculenta</i>)	Root/tuber crop	Southern America	90	8
Rice (<i>Oryza sativa</i>)	Cereal	Temperate Asia	20	9
Pearl millet (<i>Pennisetum glaucum</i>)	Cereal	Africa	3	2
Common bean (<i>Phaseolus vulgaris</i>)	Leguminous crop	Northern and Southern America	10	7
Pea (<i>Pisum sativum</i>)	Leguminous crop	Europe, Temperate Asia, Africa	3	2
Sugarcane (<i>Saccharum officinarum</i>)	Sugar crop	Tropical Asia	30	7
Potato (<i>Solanum tuberosum</i>)	Root/tuber crop	Southern America	94	59
Sorghum (<i>Sorghum bicolor</i>)	Cereal	Africa	21	7
Cacao (<i>Theobroma cacao</i>)	Beverage crop	Northern and Southern America	18	5
Wheat (<i>Triticum aestivum</i>)	Cereal	Temperate Asia	152	53
Bambara groundnut (<i>Vigna subterranea</i>)	Leguminous crop	Africa	1	1
Maize (<i>Zea mays</i>)	Cereal	Northern and Southern America	18	8

Note: Some CWR species are shared between crop species, namely, the two species of coffee (*Coffea* sp.) and yam (*Dioscorea* sp.), with the number of unique CWRs totalling to 778. Only species with sufficient geographic records to calculate their degree of resilience in Pironon et al. (2019) were considered in this study. Geographic origins were retrieved from Plants of the World Online (<http://www.plantsoftheworldonline.org/>) and Khoury et al. (2016) and follow the resolution of TDWG Level 1 regions (i.e., continents) of the World Geographical Scheme for Recording Plant Distributions (WGSRPD; Brummitt et al., 2001). Resilient CWRs refer to 2050 data; see Table S1 for 2070 values.

2.3 | Conservation data and analysis

The most recent 'Interpreted conservation status' data were compiled from Botanic Gardens Conservation International (BGCI) ThreatSearch (https://tools.bgci.org/threat_search.php—accessed April 9, 2020), and we extracted (1) which species were assessed versus not (or Data Deficient) and (2) which species were considered Threatened or Possibly Threatened. Seed accession data were compiled from the Millennium Seed Bank Partnership (MSPB) Data Warehouse (<http://brahmsonline.kew.org/msbp/SeedData/DW>—accessed April 10, 2020) and Genesys (<https://www.genesys-pgr.org/>—accessed April 13, 2020). In

total, 2,040 seed accessions for 146 unique species were matched from the MSBP Data Warehouse, along with 33,112 accessions for 297 unique species from Genesys.

We calculated two indices for each crop: the Assessment Score and the Threat Score, which represent how extensively the conservation status of resilient CWRs have been assessed, and what proportion of those CWRs are Threatened or Possibly Threatened with extinction in situ, respectively. The following formulae were used:

$$\text{Assessment Score} = \frac{\text{number of resilient CWRs not assessed or 'Data Deficient'}}{\text{total number of resilient CWRs}}$$

TABLE 2 Trait definitions and justifications for use

Trait	Definition	Justification for selection
Plant height (m)	The maximum stature of a typical mature individual of a species (Pérez-Harguindeguy et al., 2016). Equivalent to the plant length of vine species.	Associated with competitive vigour and whole-plant fecundity (Pérez-Harguindeguy et al., 2016). Taller plants seem to be more tolerant to increasing temperatures, but taller (particularly in grassland species) and shorter plants (forest tree species) seem more resilient under drought conditions (Kühn et al., 2021, and references therein).
Stem specific density (SSD) (mg·mm ⁻³)	The dry mass of a section of the main stem of a plant divided by the volume of the same section, when still fresh (Pérez-Harguindeguy et al., 2016).	Important for the stability, defence, architecture, hydraulics, carbon gain and growth potential of plants (Pérez-Harguindeguy et al., 2016). Higher wood density is associated with increased tolerance to drought in moist forests (Ouedraogo et al., 2013), mixed forest and the Mediterranean biome amongst others (Kühn et al., 2021).
Leaf area (mm ²)	The one-sided area of an individual leaf (Pérez-Harguindeguy et al., 2016).	Stress from heat, cold, drought, nutrient availability and high radiation tends to select for smaller leaves (Pérez-Harguindeguy et al., 2016) and is found to be a dominant trait, for example, of African grasses in regions of lower rainfall (Pasturel et al., 2016).
Leaf mass per area (LMA) (g·m ⁻²)	The dry mass of an individual leaf divided by the one-sided area of the leaf when fresh (Pérez-Harguindeguy et al., 2016).	Promotes conservative leaf water economy. LMA shows a predominantly positive relationship with drought (Chirino et al., 2017; Ribeiro et al., 2016), and both positive (Soudzilovskaia et al., 2013) and negative (Guittar et al., 2016) correlations with increased temperature.
Leaf nitrogen (mg·g ⁻¹)	The total amount of nitrogen per unit of dry leaf mass (Pérez-Harguindeguy et al., 2016).	It has been shown that high leaf nitrogen is a significant predictor of higher plant biomass response to increasing temperatures (Gornish & Prather, 2014).
Seed mass (g)	The average dry mass of 1000 seeds of a species.	Heavier seeds have been associated with enhanced germination and seedling survival under warmer and drier conditions in Mediterranean plant species (Hallett et al., 2011). It is also useful in predicting the ability of a plant to be suitable for ex situ storage (Wyse & Dickie, 2017).
Lifespan (annual/perennial)	The time period from establishment of the plant until no live part remains (Pérez-Harguindeguy et al., 2016).	Longer lifespans have been associated with high environmental stress regimes but tend to be short-lived in seed banks (Pérez-Harguindeguy et al., 2016). Other research indicates that for grass species, as temperature increases, the proportion of perennial species can decline in relation to annuals (Sandel & Dangremond, 2012).
Photosynthetic pathway (C ₃ /C ₄ /CAM)	Biochemical pathways for photosynthesis of terrestrial plants: C ₃ , C ₄ or CAM (Pérez-Harguindeguy et al., 2016).	Affects optimum temperatures of photosynthesis, water- and nutrient-use efficiencies and response to elevated CO ₂ . C ₄ plants perform better in warmer and drier environments compared with C ₃ , whereas CAM plants have higher water-use efficiency and occur predominantly in dry, warm ecosystems (Pérez-Harguindeguy et al., 2016). However, increases in CO ₂ have been postulated to reduce the physiological advantages of C ₄ strategy common in grasses and favour C ₃ trees in South African savannas (Bond & Midgley, 2012).
C-value (pg)	Measurement of genome size. The amount of DNA in an unreplicated haploid nuclear genome.	Smaller genome sizes have been shown to be associated with higher photosynthetic rates (and hence biomass production), and water- and nutrient-use efficiency (Faizullah et al., 2021; Roddy et al., 2020). Such traits impact a plant's resilience and ability to grow, adapt and survive.

(Continues)

TABLE 2 (Continued)

Trait	Definition	Justification for selection
Ploidy level (diploid/polyploid)	Number of sets of chromosomes in a cell.	Changes induced by polyploidy may be associated with adaptation by generating individuals with the potential to exploit new niches (van de Peer et al., 2021), which also has implications for plant breeding for desirable traits such as increased plant organ size, buffering deleterious mutations and hybrid vigour (Sattler et al., 2016).
Invasiveness (invasive/not documented as invasive)	Species that have escaped from areas of introduction, such as gardens, cultivation or both (Randall, 2017).	Invasive species have been shown to possess different traits and higher environmental tolerance than non-invasive species (Higgins & Richardson, 2014).

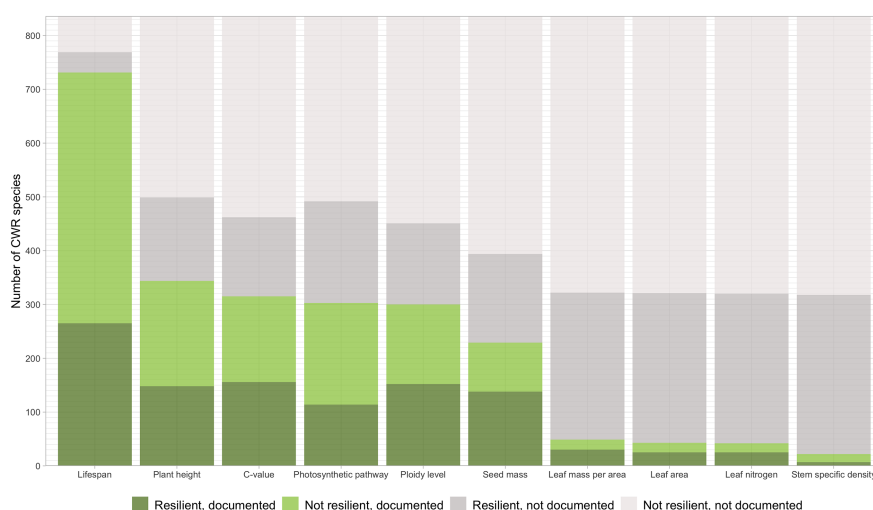


FIGURE 1 Trait documentation for 836 crop wild relative (CWR) species classed as resilient and not resilient to the novel climate predicted for 2050 across the sub-Saharan range of 29 crops. ‘Resilient’ CWR species are those whose current climatic niche resembles the novel climatic conditions predicted in the future for its associated crop grown in sub-Saharan Africa, whereas ‘not resilient’ CWR species are those whose current climatic niche does not resemble that predicted for its corresponding crop in this region. ‘Documented’ refers to taxa that have known values for a particular trait in online databases, whereas ‘not documented’ represents taxa for which no trait information was present. See Figure S1 for the same analysis but with the novel climate predicted for 2070, and Dataset S5 for a breakdown of trait documentation per CWR

$$\text{Threat Score} = \frac{\text{number of resilient CWRs 'Possibly Threatened' or 'Threatened'}}{\text{number of resilient CWRs assessed}}$$

A Conservation Priority Score (CPS) was calculated for each crop as an average of the Assessment Score and Threat Score, which represented the degree of prioritisation needed for the CWRs of their associated crops. The CPS is measured between 0 and 1, with 0 denoting all CWRs for a particular crop are assessed and none of them are Possibly Threatened or Threatened, whereas a value of 1 denotes the converse scenario. For ex situ conservation prioritisation, a gap analysis of seed accession data was used to identify which CWRs are currently present or absent in seed banks across the world and matched with their degree of resilience.

A Crop Importance Score (CIS) was calculated that ranked each crop in order of socio-economic and nutritional importance based on FAOSTAT data (<http://www.fao.org/faostat/en/#data/QC>—accessed June 15, 2020). The CIS was calculated using the methodology of Castañeda-Álvarez et al. (2016) (Supporting Information Methods S1). Crop information and indices used in the analysis can be found in Dataset S3.

3 | RESULTS

3.1 | Traits

Of the 10 traits studied, nine covered <50% of the CWR species in our study. LMA, leaf area, leaf nitrogen and SSD had missing values for over 90% of CWR species. The most extensive trait coverage was that of lifespan (87.4%) and plant height (41.1%) (Figure 1). We found that seven crops have zero CWR trait information for five or more traits (peanut, taro, enset, sweet potato, pea, potato and Bambara groundnut), whereas an additional 10 have <10% of CWR trait information for five or more traits (pigeon pea, arabica and robusta coffee, squash, winged yam, soybean, cotton, tomato, mango and cassava) (Dataset S5).

For crops with the most documented traits, we determined whether there was a difference in the mean trait values of resilient versus non-resilient CWRs (Figure 2 for the year 2050). For example, the mean plant height of sweet potato's resilient CWRs was 48% higher, the height of maize's resilient CWRs was 40% higher and the height of winged yam's resilient CWRs was 54% higher than

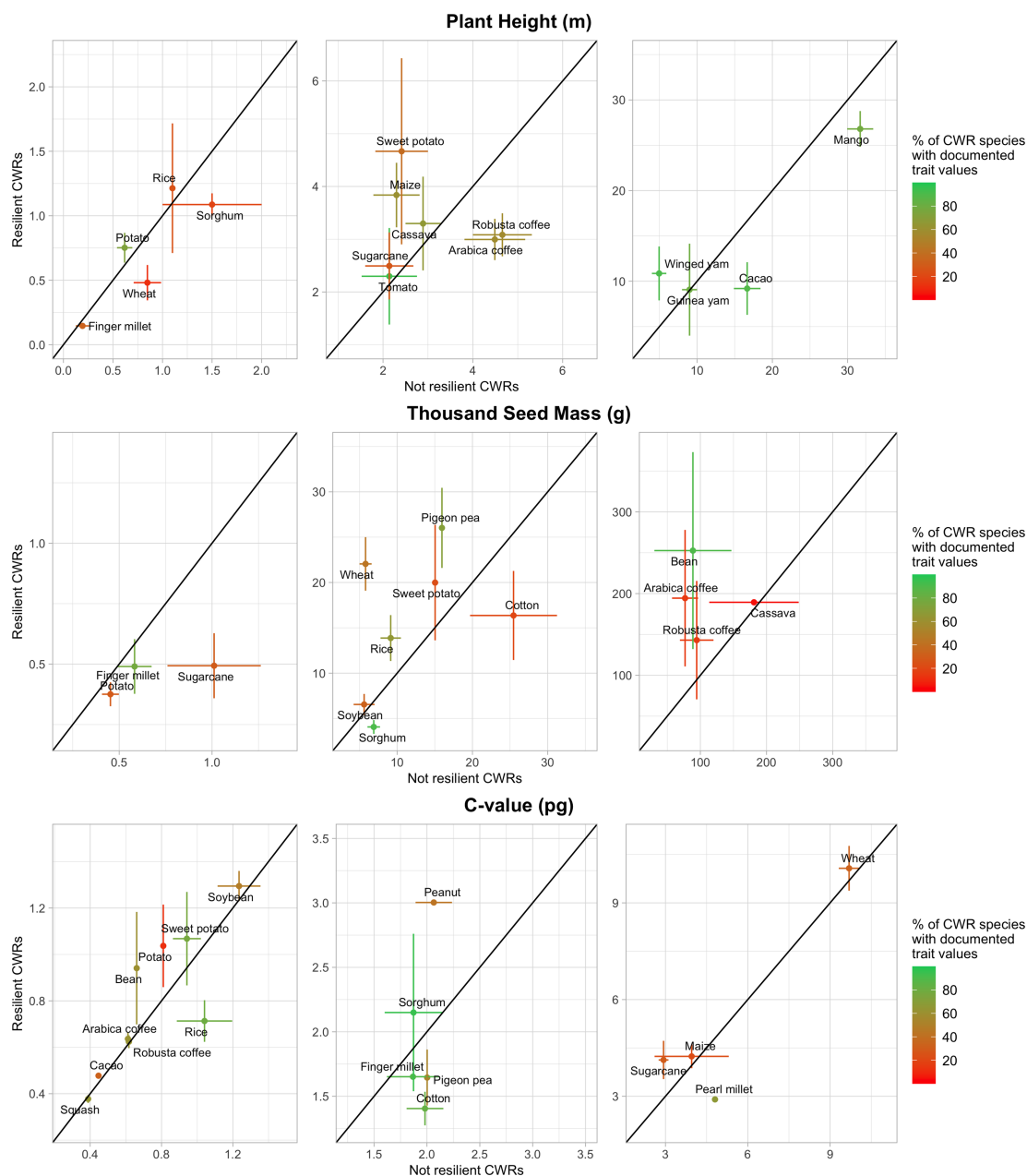


FIGURE 2 Comparison of the mean plant height, thousand seed mass and C-value (i.e., genome size) values for resilient (y-axis) versus non-resilient (x-axis) crop wild relative (CWR) species for the year 2050. Each trait has three graphs in ascending order (left to right) to improve visibility. The diagonal represents the line at which mean trait values of resilient and not resilient CWRs are equal; thus, any value above the line indicates higher mean values for resilient species, and vice versa. No statistical test was conducted to compare the two groups due to low sample sizes. However, we provide error bars that represent standard error, and the colour scale denotes the proportion of CWRs with documented trait values out of the total CWRs per crop. Some crops are omitted due to the available trait data covering only their resilient or non-resilient CWRs, leaving no opportunity for comparison between these two categories. See Figure S2a for repeated analysis for 2070, and Figure S2b for stem specific density, leaf area, leaf nitrogen and leaf mass per area

their non-resilient CWRs. In contrast, wheat's resilient CWRs had a 43% lower mean height. Plant height is relatively well documented for the tree crops: arabica coffee and robusta coffee, cacao and mango (Figure 2), all of which showed lower mean heights amongst their resilient species by 33%, 34%, 45% and 15%, respectively. Resilient CWRs of rice, wheat and common bean had 34%, 74% and 65% heavier seeds, respectively. Resilient CWRs of sweet potato

and sorghum had 12% and 13% larger genomes, respectively, whereas resilient CWRs of rice and cotton had 31% and 29% smaller genomes, respectively. Similar patterns were found for comparisons made using the 2070 data (Figure S2a). The documented trait values of CWRs for SSD, leaf area, LMA and leaf nitrogen are insufficient (i.e., <10%) for comparison of resilient and non-resilient CWRs (Figure S2b).

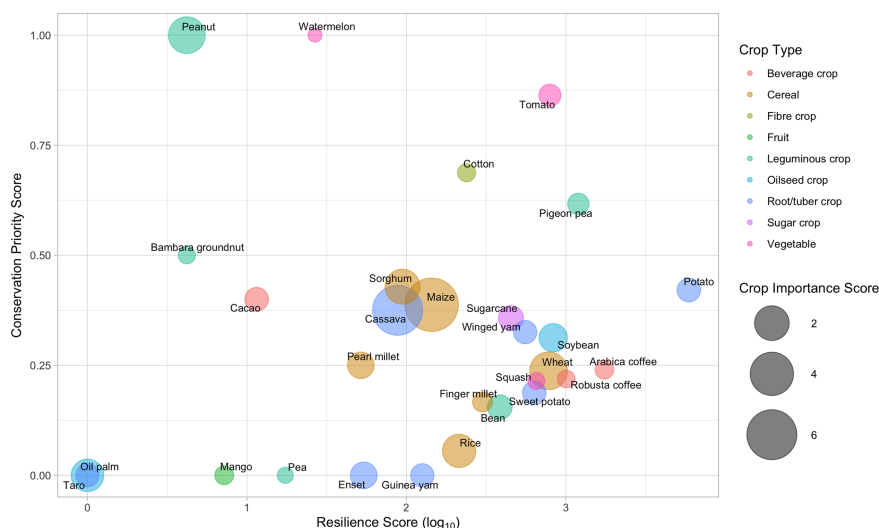


FIGURE 3 Conservation Priority Score (CPS) against Resilience Score (RS) for the year 2050. The CPS is a measure of how much priority should be given to the wild relatives of each crop based on the proportion of species assessed for their conservation status and the number of species threatened in situ. CPS provides a measure between zero and one, with one indicating high priority. The RS aggregates the resilience of each CWR per crop, weighted by the number of resilient CWR species per crop. Circle size represents the Crop Importance Score, which ranks each crop according to its socio-economic and nutritional value in sub-Saharan Africa. See Figure S3b for repeated analysis for 2070

For analysis of lifespan and photosynthetic pathway, significant differences between resilient and not resilient CWRs were only found for grasses (Poaceae). The positive relationship between lifespan and resilience was significant for 2050 ($X^2 [1, N = 238] = 30.1, p = 4.01 \times 10^{-8}$), suggesting that annuals are likely to be more resilient than perennials. Additionally, for 2070, a C_4 photosynthetic pathway was associated with resilience ($X^2 [1, N = 247] = 32.9, p = 9.62 \times 10^{-9}$), though this pattern was not observed for 2050. No significant differences were found for ploidy level for any of the comparisons.

The proportion of resilient CWRs was higher amongst potentially invasive species than those that were not documented as invasive, with 37 out of 61 (61%) invasive CWRs being resilient for 2050 and only 266 out of 775 (34%) of CWRs not documented as invasive being resilient (Figure S2c). For 2070, 20 out of 61 (33%) invasive CWRs are resilient, whereas 190 out of 775 (25%) of CWRs not documented as invasive are resilient (Figure S2d). These results are statistically significant for 2050 ($X^2 [1, N = 836] = 15.849, p = 6.859 \times 10^{-5}$), but not for 2070 ($X^2 [1, N = 836] = 1.6403, p = .2003$). However, these proportions vary drastically when analysed per crop, partly due to the large variation in the number of CWR species documented for each crop (Figure S2e).

3.2 | Conservation in situ

We found that the conservation status of 39% ($n = 119$) of resilient CWRs in our study have not been assessed or are data deficient, and of those that have been assessed 19% ($n = 59$) are threatened or possibly threatened in situ (Figure S3a). The comparison between the RS and CPS shows that CWRs of tomato, cotton and pigeon pea each have high resilience and high conservation priority for 2050 (Figure 3; Dataset S3). CWRs of wheat, soybean, winged yam, sugarcane, squash, sweet potato, arabica and robusta coffee, finger millet and common bean (lower right-hand quadrant in Figure 3) have a relatively high RS but low CPS, signifying better conservation coverage or lower

threat levels. CWRs with low resilience and low conservation priority also have low numbers of CWRs in our study, namely, oil palm ($n = 1$), taro ($n = 4$), Bambara groundnut ($n = 1$) and pea ($n = 3$).

3.3 | Conservation ex situ

Seed bank accession analysis revealed large disparities in the relative representation of CWRs amongst crops. Seven of the 29 crops have no CWR seed accession, comprising arabica coffee ($n = 62$), robusta coffee ($n = 58$), taro ($n = 4$), oil palm ($n = 1$), mango ($n = 23$), cacao ($n = 18$) and Bambara groundnut ($n = 1$) (Figure S4a).

We found that 64% of resilient CWRs have documented seed bank accessions. The three most important crops (maize, cassava and wheat) based on the CIS (see Methods) have 7 (88%), 3 (38%) and 40 (75%) of their resilient CWRs in seed collections, respectively, though their maximum degrees of resilience fall below that of many CWRs of other crops that rank lower in the CIS (Figure 4). Crops with medium CISs such as potato, pigeon pea and common bean show higher degrees of resilience with considerably more CWRs preserved in seed banks compared with maize, cassava and wheat. Crops with a low CIS, namely, arabica coffee, robusta coffee and cotton, have low numbers of resilient CWRs in seed banks but show higher resilience than CWRs of maize, cassava and wheat.

4 | DISCUSSION

4.1 | Trait documentation and comparisons

Knowledge of plant traits is vital for improving crop resilience through breeding; however, we found strikingly poor trait documentation for wild relatives of crops grown in SSA from widely accessible databases, which can be seen in the low CWR coverage per trait, and low CWR trait coverage per crop for the majority of crops studied here. Thus, trait information for many CWRs of key crops such as enset and

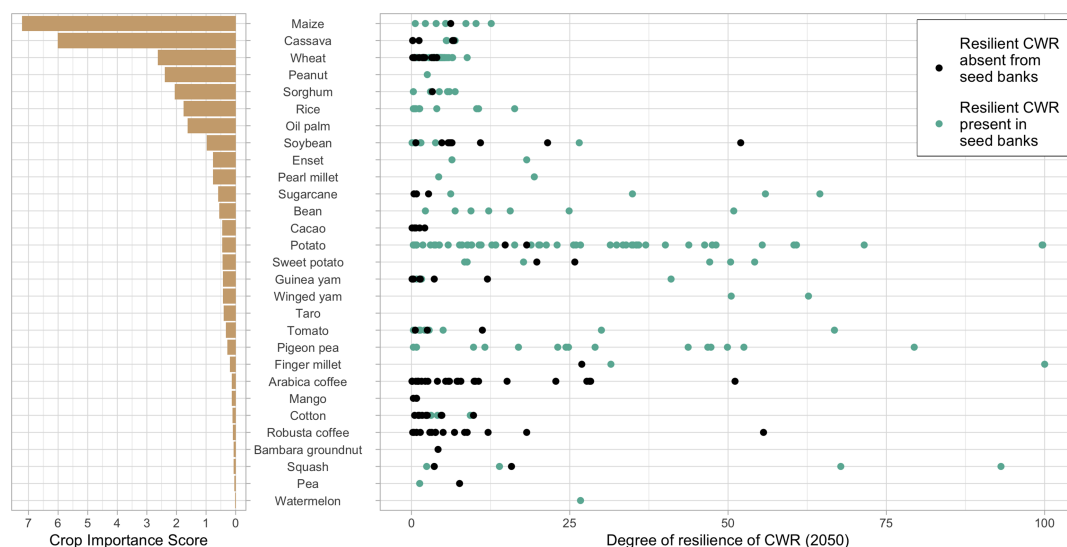


FIGURE 4 Seed accession status of resilient crop wild relatives (CWRs) for 2050 ranked in order of Crop Importance Score. The scale on the right-hand graph represents the degree of resilience of each CWR species, coloured green if present in seed banks or black if absent. A value of 100 represents a complete overlap between the climatic niche of the CWR species with the novel climate predicted for its respective crop in sub-Saharan Africa in 2050. See Figure S4b for 2070

cassava remain critically under-represented despite their high ranks in the CIS. More data may exist, for example, in localised crop breeding organisations and/or research institutions; therefore, making trait data more widely available could greatly improve the effective use of CWRs in (pre-)breeding programmes. International collaborative efforts to collate and distribute trait data could begin with the analysis of pre-existing plant material found within herbaria and botanical gardens (Perez et al., 2020), as shown in the ‘Adapting Agriculture to Climate Change’ project (Dempewolf et al., 2014) or the Australian *Vigna* species project (Lawn, 2015).

Despite small sample sizes (Supporting Information S1), our analysis revealed differences in traits between resilient and non-resilient CWRs. Whilst these differences could be due to other factors such as phylogenetic signal (i.e., more closely related CWRs may exhibit more similar traits), we discuss them here in the context of climate change adaptation in the hope that future studies will disentangle causes and mechanisms from correlations. A key finding was the association between resilience and shorter height amongst CWRs of tree crops (arabica and robusta coffee, cacao and mango), possibly because shorter trees may maintain higher water conductance with increasing vapour pressure deficit, thus making them less susceptible to drought stress under elevated temperatures (McDowell & Allen, 2015; Zhou et al., 2013). This pattern for tree crops remains consistent for 2070, with the exception of mango. Given the additional time needed to breed tree crops (or perennial species in general), the 2070 results would be of greater significance to breeders. Conversely, we found associations between resilience and taller plants amongst herbaceous CWRs of sweet potato, winged yam and maize, in 2050 and 2070, indicating a possible competitive advantage due to increased light-capturing ability (Sandel & Dangremond, 2012). This trait would arguably be more relevant to herbaceous species than trees, as tree height

can be modified via grafting and pruning, though the effects of these practices on tree resilience are uncertain.

Higher seed mass amongst resilient CWRs was found in wheat, rice, pigeon pea, soybean, common bean, arabica coffee and robusta coffee. A study of the seed mass of soybean relatives in Australia concluded that the increasing rate of metabolic reactions at higher temperatures and the improved availability of photosynthates from increased solar radiation results in heavier seeds (Murray et al., 2004). Heavier seeds can also enhance germination and seedling survival under warmer and drier conditions by providing larger nutrient reserves and subsequently allowing the development of other key traits such as longer roots (Haeuser et al., 2017; Hallett et al., 2011). Whilst the link between seed mass and other traits needs to be further studied in a wider range of CWRs, our results indicate that the introduction of resilience traits may not necessarily induce major decreases in yields of seed crops.

A higher proportion of annual CWRs was resilient than perennials for the year 2050, which may reflect their ability to adapt to elevated temperatures and altered precipitation regimes through dormancy and shorter generation times (Franks et al., 2007). This ‘drought escape strategy’ allows plants to complete reproduction at a faster time or wait for the right conditions to germinate, thus, avoiding dry conditions (Norton et al., 2016). Shorter generation times also allow for shorter breeding experiments to be carried out. However, for 2070 this analysis did not yield significant results. A C_4 photosynthetic pathway in grasses has been linked to improved fitness in a warming climate compared with C_3 species (Lattanzi, 2010). This is supported in our study where we found that the CWRs of grasses identified as resilient for 2070 climates, but not 2050, had C_4 photosynthetic pathways.

As genomic trait data (ploidy levels and genome size) were insufficient, we could not conclude a link to resilience within this study.

More research into CWR ploidy levels is needed given that they determine the feasibility of crossbreeding between different species and would have to be accounted for if there were differences in ploidy level between the CWR and the crop (Dempewolf et al., 2017).

The higher proportion of invasive CWRs being classed as resilient could indicate the presence of traits that may improve survival and productivity in future predicted climatic conditions of SSA. Invasiveness is higher in resilient CWRs than non-resilient CWRs, but proportions are still low, with only 7.3% of all CWRs being invasive, indicating its rarity in CWRs and hence the limited number of relatives with this trait available for crossing (Figure S2e).

4.2 | Conservation in situ and ex situ

Agricultural expansion, overexploitation, pollution and extractive industries pose major threats to wild plant diversity, including CWRs (Brummitt et al., 2015; Nic Lughadha et al., 2020). Future climate change is also expected to affect the distribution of CWR diversity (Aguirre-Gutiérrez et al., 2017). Failure to take action to stem this potential loss can have devastating effects on food security (Maxted et al., 2010); therefore, conservation priority should be afforded to CWRs that have high potential to provide resistant genes to crops facing environmental change (e.g., potato, pigeon pea and tomato). Crops such as coffee and cotton make substantial contributions to the overall GDP of SSA (Gilbert et al., 2013; Roger & Thigpen, 1993); therefore, efforts towards their CWR preservation should not be diminished despite their low nutritional importance. Our results support the CWR prioritisation system of Vincent et al. (2013), which we build upon by incorporating a metric for resilience. CWR prioritisation can be a useful tool for conservationists and crop breeders. Enset, for example, should be highlighted as a conservation priority due to its high potential for future food security potential (Borrell, Goodwin, et al., 2020) and for crop breeding priority as its resilient wild relatives are in seed banks. CWRs offer an important long-term solution to climate change adaptation in the food system, but a concerted interdisciplinary research effort must be undertaken to develop this potential.

Whilst our CPS highlights where to target conservation resources, future refinements should account for the presence or absence of CWRs within protected areas (Khouri et al., 2019). Networks dedicated to CWR protection should monitor and manage protected areas to ensure predicted range shifts can be accounted for and appropriate conservation actions taken (Meilleur & Hodgkin, 2004). Protecting CWRs in their natural habitats is an essential strategy to prevent extinctions, especially where ex situ conservation of sufficient genetic diversity is practically or economically unfeasible (León-Lobos et al., 2012).

Overall, we found an under-representation of CWRs within global seed repositories. We acknowledge that our study does not represent an exhaustive list of all available conservation efforts, as some CWRs that are missing from seed banks (e.g., coffee, mango and taro) are

absent because typically they are unable to survive the drying process necessary for long-term preservation (i.e., intermediate/recalcitrant) (Wyse et al., 2018). Such exceptional species may be represented within alternative conservation efforts, such as in living collections or within cryobanks (Acker et al., 2017). Of notable example is the Robusta living collection held in the Yangambi Research Station of the Institut National pour l'Etude Agronomique du Congo Belge (INEAC), Democratic Republic of Congo. However, the majority of these efforts are focused on main crop plants rather than their CWRs, which highlights the need for a global concerted effort of conserving wild relatives with recalcitrant seeds. Key challenges to achieving this require access to appropriate land to maintain genetically diverse living collections, establishment and maintenance of cryopreservation units, and extensive research to develop species-specific protocols, posing further challenges for countries that have limited ex situ conservation capacity. Our analysis also revealed a shortfall in conserving key taxa with orthodox seeds, including wheat, soybean, sugarcane and cotton, with 50% or less of their wild relatives banked (Vincent et al., 2013). Our finding justifies the need to include CWRs of these crops in priority lists and immediately target these CWRs for further collection.

4.3 | Accelerating CWR breeding

Previous ecogeographic studies have highlighted a potential role for the global diversity of CWRs in building more resilient food systems (Khouri et al., 2015; Pironon et al., 2019); however, our study shows that the functional potential of this wide diversity of species remains poorly documented and understood. More projects focused on collecting CWR trait information that feed into accessible databases are needed, as well as increased sharing of pre-existing trait information. A better general characterisation of the global diversity of CWRs would then inform the selection of the most relevant candidate species for further exploration in pre-breeding and breeding efforts. Long-term preservation and accessibility are also key for an efficient and sustainable breeding process; thus, major collection gaps identified in our study are of particular concern. Fortunately, projects aimed at both trait documentation and conservation of useful wild plants are already in place in some countries in SSA. For instance, the national seed collection programme of Zambia targets species based on utility, conservation concern, endemism and economic value (<http://brahmsonline.kew.org/msbp/Where/Africa>—accessed August 26, 2020), and the Bean Evaluation Project aims to determine traits associated with increased heat tolerance to generate new bean varieties in Mozambique (<https://www.cwrdiversity.org/partnership/bean-evaluation-project/>—accessed August 26, 2020).

After identifying the most promising candidate species for resilience to future climate change and guaranteeing in situ and ex situ conservation and access to plant material, the next step towards implementation would involve agronomists and geneticists to further discover, characterise and evaluate CWRs' traits and genes. This step is particularly important given many traits of interest (including some

presented in our study) are not controlled by a single gene but through the interaction between many genes (Dempewolf et al., 2017). Moreover, it is important to understand genetic correlations amongst traits to ensure that any gain in climatic stress resistance is not made at the expense of other traits (e.g., reduced nutrition, yield and/or pest resistance) (Dinesh et al., 2011). Based on such information, pre-breeders and breeders would develop new crop varieties that could then end up in agricultural fields and consequently the market. This last step would not be without obstacles; for instance, farmers and markets will need to adapt trade and management systems, and so too will consumers need to adopt novel cultivars (Morris & Heisey, 2003). In this context, enhancing participatory breeding in close collaboration with local and indigenous communities would also be necessary for a more demand-driven process (Kline et al., 2020).

All in all, delivering new resilient crop varieties through breeding with CWRs is a long and costly procedure (Beddow et al., 2015). Documenting CWR environmental niches and functional traits and preserving them in the wild and in ex situ collections are fundamental first steps towards informed, accelerated and expanded CWR breeding. Adapting agriculture to future climate change can be achieved through different strategies involving the sustainable use of agrobiodiversity (Borrell, Dodsworth, et al., 2020; Pironon & Soto Gomez, 2021). Further delays in characterising and preserving CWRs could cause the loss of a major adaptation option and ultimately affect the most vulnerable populations dramatically.

ACKNOWLEDGEMENTS

We acknowledge the financial support of the UK Natural Environment Research Council (NERC) for the Belmont Forum project FICESSA (Food Security Impacts of Industrial Crop Expansion in Sub-Saharan Africa) NE/M021351/1, as well as the Norwegian Ministry of Foreign Affairs and the Global Crop Diversity Trust for the 'Adapting Agriculture to Climate Change: Collecting, Protecting and preparing Crop Wild Relatives' project. We thank Paul Wilkin, Justin Moat, Jack Plummer, Steven Bachman and Serene Hargreaves for their help with extracting data and insightful discussions.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

D.S., S.P., C.T., A.F., E.H.H. and K.J.W. designed the study; D.S., S.P., E.H.H., I.L., G.M., N.K. and P.R. collected data; D.S. analysed the data with help from S.P., C.T. and A.F.; D.S., S.P., C.T. and A.F. wrote the manuscript with substantial help from C.C., N.K., I.L., E.L., L.P. and P.R.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supporting information of this article, in public domain resources cited in the Methods and supporting information sections of this article and from a previous publication (Pironon et al., 2019).

ORCID

David Satori  <https://orcid.org/0000-0002-9077-8996>

Carolina Tovar  <https://orcid.org/0000-0002-8256-9174>

Aisyah Faruk  <https://orcid.org/0000-0003-0463-5495>

Samuel Pironon  <https://orcid.org/0000-0002-8937-7626>

REFERENCES

- Acker, J. P., Adkins, S., Alves, A., Horna, D. & Toll, J. (2017). Feasibility study for a safety back-up cropreservation facility. <http://www.croptrust.org>
- Aguirre-Gutiérrez, J., van Treuren, R., Hoekstra, R., & van Hintum, T. J. L. (2017). Crop wild relatives range shifts and conservation in Europe under climate change. *Diversity and Distributions*, 23(7), 739–750. <https://doi.org/10.1111/ddi.12573>
- Beddow, J. M., Pardey, P. G., Chai, Y., Hurley, T. M., Kriticos, D. J., Braun, H.-J., Park, R. F., Cuddy, W. S., & Yonow, T. (2015). Research investment implications of shifts in the global geography of wheat stripe rust. *Nature Plants*, 1(10), 1–5. <https://doi.org/10.1038/nplants.2015.132>
- Blonder, B., Enquist, B. J., Graae, B. J., Kattge, J., Maitner, B. S., Morueta-Holme, N., Ordóñez, A., Šímová, I., Singarayer, J., Svenning, J. C., Valdes, P. J., & Violle, C. (2018). Late Quaternary climate legacies in contemporary plant functional composition. *Global Change Biology*, 24(10), 4827–4840. <https://doi.org/10.1111/gcb.14375>
- Bond, W. J., & Midgley, G. F. (2012). Carbon dioxide and the uneasy interactions of trees and savannah grasses. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 367(1588), 601–612. <https://doi.org/10.1098/RSTB.2011.0182>
- Borrell, J., Dodsworth, S., Forest, F., Pérez-Escobar, O., Lee, M., Mattana, E., Stevenson, P., Howes, M., Pritchard, H., Ballesteros, D., Kusumoto, B., Ondo, I., Moat, J., Milliken, W., Ryan, P., Ulian, T., & Pironon, S. (2020). The climatic challenge: Which plants will people use in the next century? *Environmental and Experimental Botany*, 170(103), 872. <https://doi.org/10.1016/j.envexpbot.2019.103872>
- Borrell, J., Goodwin, M., Blomme, G., Jacobsen, K., Wendawek, A. M., Gashu, D., Lulekal, E., Asfaw, Z., Demissew, S., & Wilkin, P. (2020). Enset-based agricultural systems in Ethiopia: A systematic review of production trends, agronomy, processing and the wider food security applications of a neglected banana relative. *Plants, People, Planet*, 2(3), 212–228. <https://doi.org/10.1002/ppp3.10084>
- Brummitt, N. A., Bachman, S. P., Griffiths-Lee, J., Lutz, M., Moat, J. F., Farjon, A., Donaldson, J. S., Hilton-Taylor, C., Meagher, T. R., Albuquerque, S., Aletrari, E., Andrews, A. K., Atchison, G., Baloch, E., Barlozzini, B., Brunazzi, A., Carretero, J., Celesti, M., Chadburn, H., ... Nic Lughadha, E. M. (2015). Green plants in the red: A baseline global assessment for the IUCN sampled red list index for plants. *PLoS ONE*, 10(8), e0135152. <https://doi.org/10.1371/journal.pone.0135152>
- Brummitt, R. K., Pando, F., Hollis, S., & Brummitt, N. A. (2001). World geographical scheme for recording plant distributions. *International Working Group on Taxonomic Databases for Plant Sciences (TDWG)*.
- Castañeda-Álvarez, N. P., Khoury, C. K., Achicanoy, H. A., Bernau, V., Dempewolf, H., Eastwood, R. J., Guarino, L., Harker, R. H., Jarvis, A., Maxted, N., Müller, J. V., Ramirez-Villegas, J., Sosa, C. C., Struik, P. C., Vincent, H., & Toll, J. (2016). Global conservation priorities for crop wild relatives. *Nature Plants*, 2(4), 1–6. <https://doi.org/10.1038/NPLANTS.2016.22>
- Chirino, E., Ruiz-Yanetti, S., Vilagrosa, A., Mera, X., Espinoza, M., & Lozano, P. (2017). Morpho-functional traits and plant response to drought conditions in seedlings of six native species of Ecuadorian ecosystems. *Flora*, 233, 58–67. <https://doi.org/10.1016/J.FLORA.2017.05.012>
- Dempewolf, H., Baute, G., Anderson, J., Kilian, B., Smith, C., & Guarino, L. (2017). Past and future use of wild relatives in crop breeding. *Crop*

- Science*, 57(3), 1070–1082. <https://doi.org/10.2135/cropsci2016.10.0885>
- Dempewolf, H., Eastwood, R. J., Guarino, L., Khoury, C. K., Müller, J. V., & Toll, J. (2014). Adapting agriculture to climate change: A global initiative to collect, conserve, and use crop wild relatives. *Agroecology and Sustainable Food Systems*, 38(4), 369–377. <https://doi.org/10.1080/21683565.2013.870629>
- Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P. B., Moles, A. T., Dickie, J., Gillison, A. N., Zanne, A. E., ... Gorné, L. D. (2016). The global spectrum of plant form and function. *Nature*, 529(7585), 167–171. <https://doi.org/10.1038/nature16489>
- Dinesh, M. R., Vasugi, C., & Ravishankar, K. V. (2011). Morphological, molecular characterization and breeding for biotic and abiotic stress in mango (*Mangifera indica* L.). *Acta Horticulturae*, 1(066), 37–46. <https://doi.org/10.17660/ACTAHORTIC.2015.1066.3>
- Faizullah, L., Morton, J. A., Hersch-Green, E. I., Walczyk, A. M., Leitch, A. R., & Leitch, I. J. (2021). Exploring environmental selection on genome size in angiosperms. *Trends in Plant Science*, 26(10), 1039–1049. <https://doi.org/10.1016/J.TPLANTS.2021.06.001>
- Ford-Lloyd, B. V., Schmidt, M., Armstrong, S. J., Barazani, O., Engels, J., Hadas, R., Hammer, K., Kell, S. P., Kang, D., Khoshbakht, K., Li, Y., Long, C., Lu, B. R., Ma, K., Nguyen, V. T., Qiu, L., Ge, S., Wei, W., Zhang, Z., & Maxted, N. (2011). Crop wild relatives—Undervalued, underutilized and under threat? *BioScience*, 61(7), 559–565. <https://doi.org/10.1525/bio.2011.61.7.10>
- Franks, S. J., Sim, S., & Weis, A. E. (2007). Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *Proceedings of the National Academy of Sciences of the United States of America*, 104(4), 1278–1282. <https://doi.org/10.1073/pnas.0608379104>
- Gennari, P., Heyman, A., & Kainu, M. (2015). *FAO Statistical Pocketbook*. <http://www.fao.org/3/a-i4691e.pdf>
- Gilbert, N. A., Linyong, S. G., & Divine, G. M. (2013). Impact of agricultural export on economic growth in Cameroon: Case of banana, coffee and cocoa. *International Journal of Business and Management Review*, 1(1), 44–71.
- Gornish, E. S., & Prather, C. M. (2014). Foliar functional traits that predict plant biomass response to warming. *Journal of Vegetation Science*, 25(4), 919–927. <https://doi.org/10.1111/jvs.12150>
- Guittar, J., Goldberg, D., Klanderud, K., Telford, R. J., & Vandvik, V. (2016). Can trait patterns along gradients predict plant community responses to climate change? *Ecology*, 97(10), 2791–2801.
- Haeuser, E., Dawson, W., & van Kleunen, M. (2017). The effects of climate warming and disturbance on the colonization potential of ornamental alien plant species. *Journal of Ecology*, 105(6), 1698–1708. <https://doi.org/10.1111/1365-2745.12798>
- Hallett, L. M., Standish, R. J., & Hobbs, R. J. (2011). Seed mass and summer drought survival in a Mediterranean-climate ecosystem. *Plant Ecology*, 212(9), 1479–1489. <https://doi.org/10.1007/s11258-011-9922-2>
- Higgins, S. I., & Richardson, D. M. (2014). Invasive plants have broader physiological niches. *Proceedings of the National Academy of Sciences of the United States of America*, 111(29), 10610–10614. <https://doi.org/10.1073/pnas.1406075111>
- Hodgkin, T., & Hajjar, R. (2007). Using crop wild relatives for crop improvement: Trends and perspectives. *Euphytica*, 156, 1–13. <https://doi.org/10.1007/s10681-007-9363-0>
- Khoury, C. K., Achicanoy, H. A., Bjorkman, A. D., Navarro-Racines, C., Guarino, L., Flores-Palacios, X., Engels, J. M. M., Wiersema, J. H., Dempewolf, H., Sotelo, S., Ramírez-Villegas, J., Castañeda-Álvarez, N. P., Fowler, C., Jarvis, A., Rieseberg, L. H., & Struik, P. C. (2016). Origins of food crops connect countries worldwide. *Proceedings of the Royal Society B: Biological Sciences*, 283(1832), 20160792. <https://doi.org/10.1098/RSPB.2016.0792>
- Khoury, C. K., Amariles, D., Soto, J. S., Díaz, M. V., Sotelo, S., Sosa, C. C., Ramírez-Villegas, J., Achicanoy, H. A., Velásquez-Tibatá, J., Guarino, L., León, B., Navarro-Racines, C., Castañeda-Álvarez, N. P., Dempewolf, H., Wiersema, J. H., & Jarvis, A. (2019). Comprehensiveness of conservation of useful wild plants: An operational indicator for biodiversity and sustainable development targets. *Ecological Indicators*, 98, 420–429. <https://doi.org/10.1016/j.ecolind.2018.11.016>
- Khoury, C. K., Castañeda-Álvarez, N. P., Achicanoy, H. A., Sosa, C. C., Bernau, V., Kassa, M. T., Norton, S. L., van der Maesen, L. J. G., Upadhyaya, H. D., Ramírez-Villegas, J., Jarvis, A., & Struik, P. C. (2015). Crop wild relatives of pigeonpea [*Cajanus cajan* (L.) Millsp.]: Distributions, ex situ conservation status, and potential genetic resources for abiotic stress tolerance. *Biological Conservation*, 184, 259–270. <https://doi.org/10.1016/J.BIOCON.2015.01.032>
- Kline, K. L., Ramirez, L. F., Sum, C., Lopez-Ridaura, S., & Dale, V. H. (2020). Enhance indigenous agricultural systems to reduce migration. *Nature Sustainability*, 3(2), 74–76. <https://doi.org/10.1038/s41893-020-0473-1>
- Kühn, N., Tovar, C., Carretero, J., Vandvik, V., Enquist, B. J., & Willis, K. J. (2021). Globally important plant functional traits for coping with climate change. *Frontiers of Biogeography*. <https://doi.org/10.21425/F5FBG53774>
- Kurukulasuriya, P., Mendelsohn, R., Hassan, R., Benhin, J., Deressa, T., Diop, M., Mohamed Eid, H., Yefri Fosu, K., Gbetibouo, G., Jain, S., Mahamadou, A., Mano, R., Kabubo-Mariara, J., El-Marsafawy, S., Molua, E., Ouda, S., Ouedraogo, M., Séne, I., Maddison, D., ... Dinar, A. (2006). Will African agriculture survive climate change? *The World Bank Economic Review*, 20(3), 367–388. <https://doi.org/10.1093/wber/lhl004>
- Lattanzi, F. A. (2010). C3/C4 grasslands and climate change. In *Grassland science in Europe* (pp. 3–13).
- Lawn, R. J. (2015). The Australian Vigna species: A case study in the collection and conservation of crop wild relatives. In *Crop wild relatives and climate change* (pp. 318–335). John Wiley & Sons. 10.1002/9781118854396.ch18
- León-Lobos, P., Way, M., Aranda, P. D., & Lima-Junior, M. (2012). The role of ex situ seed banks in the conservation of plant diversity and in ecological restoration in Latin America. *Plant Ecology and Diversity*, 5(2), 245–258. <https://doi.org/10.1080/17550874.2012.713402>
- Maxted, N., Ford-Lloyd, B. V., Jury, S., Kell, S., & Scholten, M. (2006). Towards a definition of a crop wild relative. *Biodiversity and Conservation*, 15(8), 2673–2685. <https://doi.org/10.1007/s10531-005-5409-6>
- Maxted, N., Kell, S., Toledo, Á., Dulloo, E., Heywood, V., Hodgkin, T., Hunter, D., Guarino, L., Jarvis, A., & Ford-Lloyd, B. (2010). A global approach to crop wild relative conservation: Securing the gene pool for food and agriculture. *Kew Bulletin*, 65(4), 561–576. <https://doi.org/10.1007/s12225-011-9253-4>
- McDowell, N. G., & Allen, C. D. (2015). Darcy's law predicts widespread forest mortality under climate warming. *Nature Climate Change*, 5(7), 669–672. <https://doi.org/10.1038/nclimate2641>
- Meilleur, B. A., & Hodgkin, T. (2004). In situ conservation of crop wild relatives: Status and trends. In *Biodiversity and conservation* (Vol. 13, Issue 4) (pp. 663–684). Springer. 10.1023/B:BIOC.0000011719.03230.17
- Morris, M. L., & Heisey, P. W. (2003). Estimating the benefits of plant breeding research: Methodological issues and practical challenges. *Agricultural Economics*, 29(3), 241–252. <https://doi.org/10.1111/J.1574-0862.2003.TB00161.X>
- Morton, J. (2007). The impact of climate change on smallholder and subsistence agriculture. *Proceedings of the National Academy of Sciences of*

- the United States of America, 104(50), 19680–19685. <https://doi.org/10.1073/pnas.0701855104>
- Müller, C., Cramer, W., Hare, W. L., & Lotze-Campen, H. (2011). Climate change risks for African agriculture. *Proceedings of the National Academy of Sciences of the United States of America*, 108(11), 4313–4315. <https://doi.org/10.1073/pnas.1015078108>
- Murray, B. R., Brown, A. H. D., Dickman, C. R., & Crowther, M. S. (2004). Geographical gradients in seed mass in relation to climate. *Journal of Biogeography*, 31(3), 379–388. <https://doi.org/10.1046/j.0305-0270.2003.00993.x>
- Nic Lughadha, E., Bachman, S. P., Leão, T. C. C., Forest, F., Halley, J. M., Moat, J., Acedo, C., Bacon, K. L., Brewer, R. F. A., Gâteblé, G., Gonçalves, S. C., Govaerts, R., Hollingsworth, P. M., Krisai-Greilhuber, I., Lirio, E. J., Moore, P. G. P., Negrão, R., Onana, J. M., Rajaovelona, L. R., ... Walker, B. E. (2020). Extinction risk and threats to plants and fungi. *Plants, People, Planet*, 2(5), 389–408. <https://doi.org/10.1002/ppp3.10146>
- Norton, M. R., Malinowski, D. P., & Voltaire, F. (2016). Plant drought survival under climate change and strategies to improve perennial grasses. A review. *Agronomy for Sustainable Development*, 36(2), 1–15. <https://doi.org/10.1007/s13593-016-0362-1>
- OECD/FAO. (2016). Agriculture in Sub-Saharan Africa: Prospects and challenges for the next decade. In *OECD-FAO agricultural outlook 2016–2025* (pp. 59–95). https://doi.org/10.1787/agr_outlook-2016-5-en
- Ouédraogo, D.-Y., Mortier, F., Gourlet-Fleury, S., Freycon, V., & Picard, N. (2013). Slow-growing species cope best with drought: Evidence from long-term measurements in a tropical semi-deciduous moist forest of Central Africa. *Journal of Ecology*, 101(6), 1459–1470. <https://doi.org/10.1111/1365-2745.12165>
- Pasturel, M., Alexandre, A., Novello, A., Dièye, A. M., Wélé, A., Paradis, L., Cordova, C., & Hély, C. (2016). Grass physiognomic trait variation in African herbaceous biomes. *Biotropica*, 48(3), 311–320. <https://doi.org/10.1111/BTP.12282>
- Perez, T. M., Rodriguez, J., & Mason Heberling, J. (2020). Herbarium-based measurements reliably estimate three functional traits. *American Journal of Botany*, 107(10), 1457–1464. <https://doi.org/10.1002/ajb2.1535>
- Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., de Vos, A. C., ... Cornelissen, C. J. H. (2016). Corrigendum: New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, 64, 715–716. https://doi.org/10.1071/BT12225_CO
- Pironon, S., Etherington, T. R., Borrell, J. S., Kühn, N., Macias-Fauria, M., Ondo, I., Tovar, C., Wilkin, P., & Willis, K. J. (2019). Potential adaptive strategies for 29 sub-Saharan crops under future climate change. *Nature Climate Change*, 9(10), 758–763. <https://doi.org/10.1038/s41558-019-0585-7>
- Pironon, S., & Soto Gomez, M. (2021). Plant agrobiodiversity to the rescue. *Nature Climate Change*, 11(1), 6–8. <https://doi.org/10.1038/s41558-020-00925-3>
- Prohens, J., Gramazio, P., Plazas, M., Dempewolf, H., Kilian, B., Díez, M. J., Fita, A., Herraiz, F. J., Rodríguez-Burruezo, A., Soler, S., Knapp, S., & Vilanova, S. (2017). Introgressomics: A new approach for using crop wild relatives in breeding for adaptation to climate change. *Euphytica*, 213(7), 158. <https://doi.org/10.1007/s10681-017-1938-9>
- Randall, R. P. (2017). A global compendium of weeds. *A Global Compendium of Weeds*, Ed.3.
- Ribeiro, P. C., Souza, M. L., Muller, L. A. C., Ellis, V. A., Heuertz, M., Lemos-Filho, J. P., & Lovato, M. B. (2016). Climatic drivers of leaf traits and genetic divergence in the tree *Annona crassiflora*: A broad spatial survey in the Brazilian savannas. *Global Change Biology*, 22(11), 3789–3803. <https://doi.org/10.1111/GCB.13312>
- Roddy, A. B., Thérout-Rancourt, G., Abbo, T., Benedetti, J. W., Brodersen, C. R., Castro, M., Castro, S., Gilbride, A. B., Jensen, B., Jiang, G.-F., Perkins, J. A., Perkins, S. D., Loureiro, J., Syed, Z., Thompson, R. A., Kuebbing, S. E., & Simonin, K. A. (2020). The scaling of genome size and cell size limits maximum rates of photosynthesis with implications for ecological strategies. *International Journal of Plant Sciences*, 181(1), 75–87. <https://doi.org/10.1086/706186>
- Roger, J., & Thigpen, M. E. (1993). *Should Sub-Saharan Africa Expand Cotton Exports?* World Bank Publications. https://books.google.co.uk/books?hl=en&lr=%26id=Br1IVdFegjYC%26oi=fnd%26pg=PA1%26dq=cotton+gdp+sub+saharan+africa%26ots=jOvaJVYIH%26sig=qAb81jI8PeGeKw4HzmyXkVjAv4%26redir_esc=y#v=onepage%26q=cotton+gdp+sub+saharan+africa&f=false
- Sandel, B., & Dangremond, E. M. (2012). Climate change and the invasion of California by grasses. *Global Change Biology*, 18(1), 277–289. <https://doi.org/10.1111/j.1365-2486.2011.02480.x>
- Sattler, M. C., Carvalho, C. R., & Clarindo, W. R. (2016). The polyploidy and its key role in plant breeding. *Planta*, 243(2), 281–296. <https://doi.org/10.1007/s00425-015-2450-x>
- Schlenker, W., & Lobell, D. B. (2010). Robust negative impacts of climate change on African agriculture. *Environmental Research Letters*, 5(1), 8. <https://doi.org/10.1088/1748-9326/5/1/014010>
- Schmieg, E. (2016). *Africa's Position in Global Trade—Free Trade Agreements, WTO and Regional Integration*. <http://data.worldbank.org/indicator/NE.TRD.GNFS.ZS>
- Soudzilovskaia, N. A., Elumeeva, T. G., Onipchenko, V. G., Shidakov, I. I., Salpagarova, F. S., Khubiev, A. B., Tekeev, D. K., & Cornelissen, J. H. C. (2013). Functional traits predict relationship between plant abundance dynamic and long-term climate warming. *Proceedings of the National Academy of Sciences*, 110(45), 18180–18184. <https://doi.org/10.1073/pnas.1310700110>
- Tanksley, S. D., & McCouch, S. R. (1997). Seed banks and molecular maps: Unlocking genetic potential from the wild. *Science*, 277(5329), 1063–1066. <https://doi.org/10.1126/science.277.5329.1063>
- Ulian, T., Diazgranados, M., Pironon, S., Padulosi, S., Liu, U., Davies, L., Howes, M. R., Borrell, J. S., Ondo, I., Pérez-Escobar, O. A., Sharrock, S., Ryan, P., Hunter, D., Lee, M. A., Barstow, C., Łuczaj, Ł., Pieroni, A., Cámara-Leret, R., Noorani, A., ... Mattana, E. (2020). Unlocking plant resources to support food security and promote sustainable agriculture. *Plants, People, Planet*, 2(5), 421–445. <https://doi.org/10.1002/ppp3.10145>
- United Nations. (2015). Transforming our world: The 2030 Agenda for Sustainable Development.
- van de Peer, Y., Ashman, T. L., Soltis, P. S., & Soltis, D. E. (2021). Polyploidy: An evolutionary and ecological force in stressful times. *The Plant Cell*, 33(1), 11–26. <https://doi.org/10.1093/plcell/koaa015>
- Vincent, H., Wiersema, J., Kell, S., Fielder, H., Dobbie, S., Castañeda-Álvarez, N. P., Guarino, L., Eastwood, R., Lén, B., & Maxted, N. (2013). A prioritized crop wild relative inventory to help underpin global food security. *Biological Conservation*, 167, 265–275. <https://doi.org/10.1016/j.biocon.2013.08.011>
- Warschefsky, E., Varma Penmetza, R., Cook, D. R., & von Wettberg, E. J. B. (2014). Back to the wilds: Tapping evolutionary adaptations for resilient crops through systematic hybridization with crop wild relatives. *American Journal of Botany*, 101(10), 1791–1800. <https://doi.org/10.3732/ajb.1400116>
- Wyse, S. V., & Dickie, J. B. (2017). Predicting the global incidence of seed desiccation sensitivity. *Journal of Ecology*, 105(4), 1082–1093. <https://doi.org/10.1111/1365-2745.12725>
- Wyse, S. V., Dickie, J. B., & Willis, K. J. (2018). Seed banking not an option for many threatened plants. *Nature Plants*, 4(11), 848–850. <https://doi.org/10.1038/s41477-018-0298-3>

- Zhou, G., Peng, C., Li, Y., Liu, S., Zhang, Q., Tang, X., Liu, J., Yan, J., Zhang, D., & Chu, G. (2013). A climate change-induced threat to the ecological resilience of a subtropical monsoon evergreen broad-leaved forest in Southern China. *Global Change Biology*, 19(4), 1197–1210. <https://doi.org/10.1111/gcb.12128>
- Ziervogel, G., & Ericksen, P. J. (2010). Adapting to climate change to sustain food security. *Wiley Interdisciplinary Reviews: Climate Change*, 1(4), 525–540. <https://doi.org/10.1002/wcc.56>

SUPPORTING INFORMATION

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

How to cite this article: Satori, D., Tovar, C., Faruk, A., Hammond Hunt, E., Muller, G., Cockel, C., Kühn, N., Leitch, I. J., Lulekal, E., Pereira, L., Ryan, P., Willis, K. J., & Pironon, S. (2022). Prioritising crop wild relatives to enhance agricultural resilience in sub-Saharan Africa under climate change. *Plants, People, Planet*, 4(3), 269–282. <https://doi.org/10.1002/ppp3.10247>