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REVIEW ARTICLE

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# Unlocking plant resources to support food security and promote sustainable agriculture

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## Societal Impact Statement

Biodiversity is essential to food security and nutrition locally and globally. By reviewing the global state of edible plants and highlighting key neglected and underutilized species (NUS), we attempt to unlock plant food resources and explore the role of fungi, which along with the wealth of traditional knowledge about their uses and practices, could help support sustainable agriculture while ensuring better protection of the environment and the continued delivery of its ecosystem services. This work will inform a wide range of user communities, including scientists, conservation and development organizations, policymakers, and the public of the importance of biodiversity beyond mainstream crops.

### Summary

As the world's population is increasing, humanity is facing both shortages (hunger) and excesses (obesity) of calorie and nutrient intakes. Biodiversity is fundamental to addressing this double challenge, which involves a far better understanding of the global state of food resources. Current estimates suggest that there are at least 7,039 edible plant species, in a broad taxonomic sense, which includes 7,014 vascular plants. This is in striking contrast to the small handful of food crops that provide the majority of humanity's calorie and nutrient intake. Most of these 7,039 edible species have additional uses, the most common being medicines (70%), materials (59%), and environmental uses (40%). Species of major food crops display centers of diversity, as previously proposed, while the rest of edible plants follow latitudinal distribution patterns similarly to the total plant diversity, with higher species richness at lower latitudes. The International Union for Conservation of Nature Red List includes global conservation assessments for at least 30% of edible plants, with ca. 86% of them conserved

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ex situ. However, at least 11% of those species recorded are threatened. We highlight multipurpose NUS of plants from different regions of the world, which could be key for a more resilient, sustainable, biodiverse, and community participation-driven new "green revolution." Furthermore, we explore how fungi could diversify and increase the nutritional value of our diets. NUS, along with the wealth of traditional knowledge about their uses and practices, offer a largely untapped resource to support food security and sustainable agriculture. However, for these natural resources to be unlocked, enhanced collaboration among stakeholders is vital.

**KEYWORDS**
crops, ex situ conservation, fungi, livelihoods, minor crops, neglected and underutilized species, plant diversity, sustainable agriculture

## 1 | INTRODUCTION

As the world's population is expected to reach 10 billion by 2050, humanity is increasingly facing a double burden of malnutrition, comprising of a shortage of calories (hunger) at one end of the spectrum and excess at the other one (obesity; Abarca-Gómez et al., 2017; Alexandratos & Bruinsma, 2012; FAO, IFAD, UNICEF, WFP, & WHO, 2019). Addressing these challenges will require an increase of food production globally, which cannot be achieved by simply expanding industrial agriculture through land conversion to the detriment of the surrounding environment and already declining biodiversity (Jacobsen, Sørensen, Pedersen, & Weiner, 2013; Padulosi, Heywood, Hunter, & Jarvis, 2011; Sunderland, 2011), and a shift to healthier diets (Abarca-Gómez et al., 2017; FAO, IFAD, UNICEF, WFP, & WHO, 2019). In addition, around 36% (by calorific value) of arable crops such as wheat, maize, and sorghum are consumed by livestock and this requires one-third of the total area currently utilized for arable farming (Cassidy, West, Gerber, & Foley, 2013; Herrero et al., 2013). Overall, 26% (3.4 billion ha) and 4% (0.5 billion ha) of the Earth's ice-free surface is used for livestock grazing and livestock feed production, respectively (Foley et al., 2011). This is a complex situation, as there is a need to ensure the sustainable production of safe and nutritious food, while protecting biodiversity, to allow the delivery of other goods and ecosystem services, which are directly and indirectly critical for human well-being. Furthermore, it is necessary to facilitate societal adaptation to climate-driven environmental changes that can disrupt food production and people's livelihoods (Alae-Carew et al., 2020; FAO, 2019; Jacobsen et al., 2013).

Of the thousands of plant species that have been cultivated since agriculture began around 12,000 years ago, only about 200 have been extensively domesticated, leading to dependence on a narrow range of genetic diversity of crops (Meyer, Duval, & Jensen, 2012; Vaughan, Balazs, & Heslop-Harrison, 2007). Together, wheat, rice, and maize alone provide almost half of the world's food calorie intake, making our food supply extremely vulnerable (Reeves, Thomas, & Ramsay, 2016). Plant-breeding programs narrowed the focus to large-seeded, high-yielding varieties of crops (Gruber, 2017), whose global production intensified (higher yield by unit of land area) during the Green Revolution of the 1960s–1980s. This period of crop intensification was also aided by developments in the use of chemical fertilizers, irrigation techniques, and pesticides (Pingali, 2012). Although the intensification of agriculture led to reduced pressure on natural ecosystems (Godfray et al., 2010; Green, Cornell, Scharlemann, & Balmford, 2005), it created multiple unintended environmental consequences such as water pollution, soil degradation, agrochemical runoff, increased susceptibility to pests and diseases, and biodiversity loss (Pingali, 2012). Crop intensification also decreased dietary diversity along with food cultures, and many traditional crops that were important sources of critical micronutrients (such as iron, provitamin A, and zinc) for poor communities were lost (Webb & Eiselen, 2009). However, there is now increasing recognition given to the importance of biodiversity for food and nutrition security, local livelihoods, and sustainable development (Bala, Hoeschle-Zeledon, Swaminathan, & Frison, 2006; FAO, 2019). Consequently, the benefits of using underutilized traditional crops, and exploring more sustainable production methods to grow mainstream crops, are being widely promoted (FAO & WHO, 2018).

Neglected and underutilized species (NUS) include wild, domesticated, or semi-domesticated plants, whose potential to improve people's livelihoods, as well as food security and sovereignty, is not fully realized because of their limited competitiveness with commodity crops in mainstream agriculture. Nevertheless, they are locally important to people and often adapted to unique climatic and environmental conditions (Padulosi et al., 2011). Bringing NUS into mainstream agriculture could strengthen the resilience and sustainability of food production systems (FAO, 2018; Padulosi, Cawthorn, et al., 2019; Raneri, Padulosi, Meldrum, & King, 2019). In addition, NUS often provide benefits beyond food, by virtue of being multipurpose. For instance, they often yield other useful products such as timber, fibers, or medicines, and contribute to safeguarding biocultural diversity (Cámara-Leret et al., 2019). Increasing the inherent value of wild species as NUS and the ecosystem services that native species can provide to surrounding environments (such as food sources for pollinators and birds, maintenance of water supply and soils, and control of pests and diseases), will support biodiversity protection and provide cultural services (Díaz et al., 2020). Many

NUS are referred to as "minor" or "orphan" crops because of their limited role in larger agricultural production systems and have been "neglected" by agricultural researchers, plant breeders, and policy-makers alike. Some have been major crops in the past, but are now displaced by modern commercial varieties and this is especially the case for many millets (which is a common term for a group of cereals in the Panicodeae and Chlorideae grass subfamilies) and less well-known pulses such as lablab (Reed & Ryan, 2019). Many of these varieties and species, along with a wealth of traditional knowledge about their use and cultivation, are being lost at an alarming rate (Díaz et al., 2020). Access to NUS is also important because domesticated legumes (Fernández-Marín et al., 2014), cereals (Hebelstrup, 2017), other crops that contribute to food security (Tamrat et al., 2020), and fungi (Stojković et al., 2013) can vary in their nutritional, antioxidant, and other chemical content. This has potential implications for human health, which could be positive or negative, as for example on the diversity of the human intestinal microbiome (e.g., Albenberg & Wu, 2014).

As global biodiversity is rapidly declining, limiting our possibilities of finding new food sources (Díaz et al., 2020), and considering that most analyses lack information on the entire spectrum of food resources consumed across the world, an assessment of their current distribution and conservation status to inform science-based policy making has become urgent. In addition, the adverse impacts of climate change on biodiversity, agricultural production, and food security have made the conservation of food diversity and associated traditional knowledge a global priority (Corlett, 2016; Maxted, Ford-Lloyd, Jury, Kell, & Scholten, 2006; Vincent et al., 2013). Finally, as intact habitats come under pressure from the increased demand for cropland worldwide (Tilman et al., 2017), ex situ plant conservation measures need accelerating (Larkin, Jacobi, Hipp, & Kramer, 2016), as promoted in the UN Sustainable Development Goal (SDG) Target 2.5 (https://sustainabledevelopment.un.org/).

In this article, we (a) consider the global state of edible plants, their taxonomic diversity, uses, distribution, and conservation status; and (b) explore untapped plant and fungi resources, by reviewing the role of multipurpose NUS that could be adopted as potential future food crops under a changing climate.

## 2 | THE GLOBAL STATE OF EDIBLE PLANTS AND MAJOR FOOD CROPS

To assess the global diversity of edible plants we used the "World Checklist of Useful Plant Species" data set, produced by the Royal Botanic Gardens, Kew (Diazgranados et al., 2020). This data set includes 40,292 species with at least a documented human use and was redacted by compiling plant uses and reconciling species names using the taxonomic backbone of Kew's Plants of the World Online portal (http://www.plantsoftheworldonline.org/) from 13 large datasets, listed in Diazgranados et al. (2020). Species with "human food" use in this list were extracted and analyzed in this review as "edible plants." Crop wild relatives, although included in the list and analyzed in this review, were not treated separately, as several studies are already available on their richness, global distribution, and conservation, for example in Castañeda-Álvarez et al. (2016) and Milla (2020). Species from Diazgranados et al. (2020) that were also listed in Annex 5 of FAO (2015) were identified as "major food crops" in this review. Plant uses were classified according to the Level 1 of Uses of the Economic Botany Data Collection Standard (Cook, 1995), simplified to 10 categories, as in Diazgranados et al. (2020).

### 2.1 | Taxonomic diversity

Depending on authority, the total number of edible plants in the world varies from 100s (Van Wyk, 2019) to >30,000 plants, including infraspecific taxa (French, 2019). These differences in numbers are based on multiple factors, such as taxonomic rank (e.g., counting infraspecific taxa), accuracy (e.g., using reconciled taxonomy), and precision (e.g., using a unique taxonomic backbone), as well as the types of consumers and their diets. For example, using a conservative approach based on reported uses, RBG Kew has recorded to date 7,039 edible species, in a broad taxonomic sense, from 288 families and 2,319 genera, including 7,030 edible species of Bryophyta, Chlorophyta, Rhodophyta, and Tracheophyta (Diazgranados et al., 2020). Many more edible species are expected to be identified in the future, as under-documented regions, for example, tropical America and New Guinea, are better characterized (Cámara-Leret & Dennehy, 2019; Cámara-Leret, Paniagua-Zambrana, Balslev, & Macía, 2014). Recognizing variation within species (subspecies, landraces, etc.) is equally important. While *Brassica oleracea* is known to cover nine crops, the level of plant diversity in use can be obscured by the widespread use of a common name (e.g., "beans" apply to at least 17 genera, 30 species, and thousands of varieties).

Vascular plants (Tracheophyta) are the most important for human food, encompassing 272 families, 2,300 genera, and 7,014 known species, that is, 2.0% of the total angiosperm species diversity (347,298 accepted species; WCVP, 2020). Sixty percent of the vascular plant families include edible species, covering almost all the major phylogenetic clades (Figure 1). The most diverse orders are Fabales (640 edible species), Malpighiales (550), Sapindales (465), Gentianales (444), and Rosales (395). The richest families (see Figure S1) are Fabaceae (i.e., beans, 625 edible species), Arecaceae (palms, 325), Poaceae (grasses and includes cereals, 314), Malvaceae (mallow family, includes cacao, okra and durian, 257), and Asteraceae (sunflower and lettuce families, 251). With at least 100 edible species, *Ficus* (figs) is the richest genus, followed by *Diospyros* (52), *Solanum* (51), *Garcinia* (48), and *Grewia* (46). Most of the edible plants (97%) correspond to flowering plants, with 245 families, 2,235 genera, and 6,828 species. However, there is substantial variation in the proportion of edible plants among non-flowering plant groups, for example, 0.5% (six species) of Lycopodiopsida, 1.0% (109 species) of Polypodiopsida, 3.9% (13 species) of cycads, 7.5% (47 species) of Pinopsida, 8.9% (10 species) of Gnetopsida, and 100% (one species) of ginkgo.

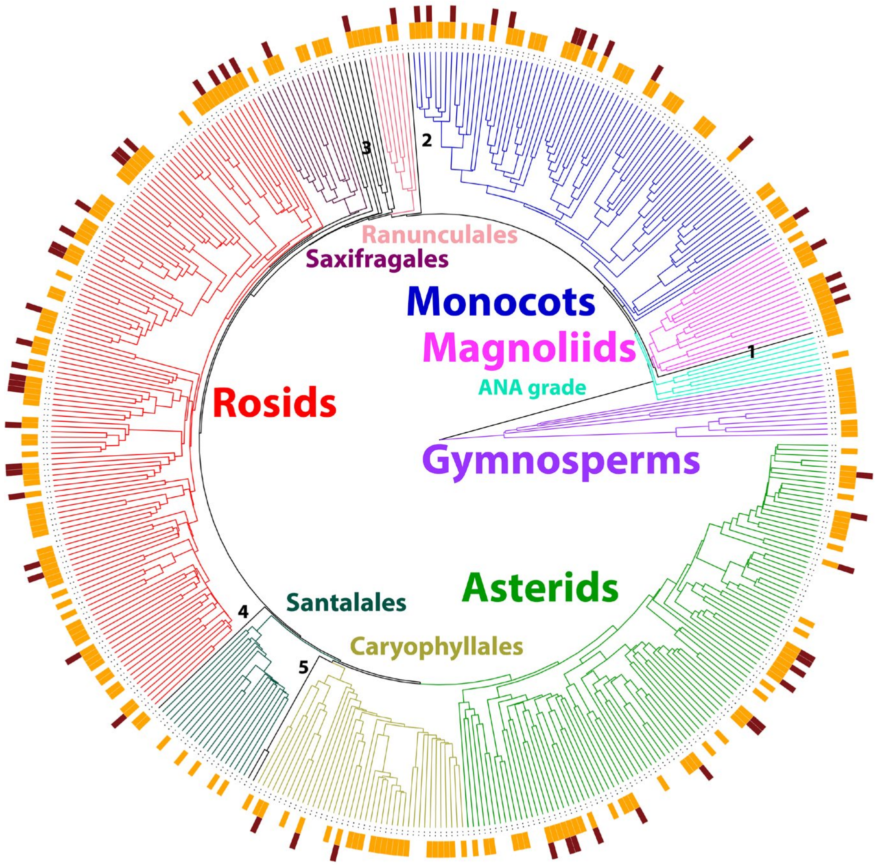


**FIGURE 1** Phylogenetic distribution of edible plants from Diazgranados et al. (2020), and major food crops also listed in FAO (2015). A phylogeny of 448 vascular plant families was derived from the Spermatophyta supertree inferred from sequence data of 79,881 species by Smith and Brown (2018) by keeping one representative species per plant family. Presence/absence of edible plants and major food crops per family was drawn at the tips of the phylogeny using the R-package GGTREE (Yu, Smith, Zhu, Guan, & Lam, 2017). The rectangles at the tips of the phylogeny denote the presence of human food plants (orange) and major food crops (brown) in each family. Major plant clades are color-coded, except for clades with just a few families, indicated with numbers: 1. Chloranthales (1 family); 2. Ceratophyllales (1); 3. Proteales (4), Trochodendrales (1), Buxales (1) and Gunnerales (2); 4. Dilleniales (1 fam.); and 5. Berberidopsidales (2). Please see Figure S1 in the Supporting Information for the detailed tree with the names in the tips for all families

To understand the taxonomic distribution of intensively used food plants, we mapped the major food crop species listed by the FAO (2015) onto the phylogeny (Figure 1). Only 417 (5.9%) of edible plant species from Diazgranados et al. (2020), belonging to 168 (7.2%) genera and 62 (21.5%) families, appear in the FAO (2015) list. The richest families in major crops are Rosaceae (e.g., apples; 51 species/eight genera), Fabaceae (51 species/19 genera), Dioscoreaceae (i.e., yams; 41 species/one genus), Poaceae (27 species/16 genera), and Malvaceae (21 species/eight genera). Interestingly, several edible species-rich families have very few major crops, or none. For example, Arecaceae (325 species) has only six crop species, Apocynaceae (228 spp.) just one, and Phyllanthaceae (101 species) none. The reasons for the low (or absent) domestication rate detected in some families may include: habit (e.g., tall trees/palms from the tropics; parasitic families such as Balanophoraceae or Loranthaceae); high toxicity (e.g., many Apocynaceae bear edible fruits, but all other parts are poisonous); habitat specificity (e.g., plants adapted to harsh weather, making difficult to establish crops); low growth rate (e.g., many woody plants); spatial distribution (e.g., plants from areas where practices of domestication of those species are not known); or simply because it was not needed (e.g., high abundance of mangrove trees in the Rhizophoraceae, which provide food among other uses, may be sufficient for the local demand). Some families, such as Acanthaceae and Phyllanthaceae, have a few species under cultivation but these are not used as food (e.g., as ornamental plants). Lastly, 77 plant families have one or two edible species which are not crops.

## 2.2 | Plant uses

Edible plants often have additional uses, which may differ in the world as part of the existing cultural diversity. The most frequent use is medicines (70% of species), followed by materials (59%), environmental uses (40%), gene sources (i.e., wild relatives of major crops which may possess traits associated to biotic or abiotic resistance and therefore be valuable for breeding programs; Cook, 1995; 32%), and animal food (30%; Figure 2a). The same general trend

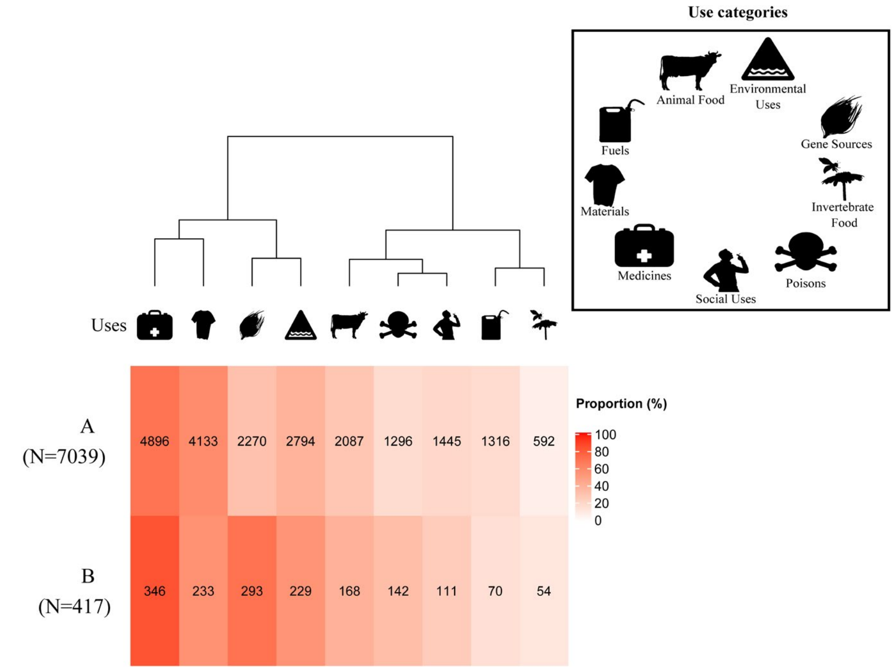


**FIGURE 2** Heat map showing the proportion of plant species in each additional use category for (a) edible plant species from Diazgranados et al. (2020) and (b) species of major food crops also listed in FAO (2015). The dendrogram represents a hierarchical clustering of the uses: clustered uses indicate closer proportion pattern, using the Euclidian distance for building the distance matrix and the "Complete-linkage" method for the hierarchical aggregation of the dendrogram

was identified for species of major crops, with 83% also reported as "medicinal," and with "gene source" having higher weight (70%) than in the full list of edible plants (Figure 2b). The link between food and medicine is well documented (e.g., Iwu, 2016), and already demonstrated for plant-rich diets, such as the traditional Mediterranean diet (Willett et al., 1995). Livestock and wild animals can also make use of the medicinal properties of plants to improve or maintain their health, for example, to control internal parasites (Villalba & Provenza, 2007; Villalba, Provenza, K Clemensen, Larsen, & Juhnke, 2011). Indeed, the boundaries between foods, including functional foods, medicine, and nutraceuticals are often blurred, attributed to certain phytochemicals in edible plants that have mechanistic effects relevant to human health, independent of fundamental nutrition (Howes, 2018b; Howes et al., 2020; Paradee et al., 2019). Certain edible plants and their constituents are associated with a reduced risk of some diseases. For example, there has been interest in the role of cruciferous vegetables and turmeric (*Curcuma longa*) to reduce cancer risk (Howes, 2018a), while *Perilla frutescens* nutlets have been evaluated to provide protection against oxidative stress in some hepatic disorders (Paradee et al., 2019). This concept extends to livestock and there is emerging evidence that the phytochemical composition of animal feed can enhance meat and dairy products, which may reduce the incidence of some diseases in humans (Provenza, Kronberg, & Gregorini, 2019).

## 2.3 | Global distribution

We found the native distribution of the large array of edible plant species documented in Diazgranados et al. (2020) to exhibit a clear latitudinal gradient, with food plant species richness decreasing from low to high latitudes (Figure 3a), similarly to general patterns in total plant diversity (Kier et al., 2009). Although a major hotspot of plant species richness, tropical Americas is under-represented in terms of edible plants. This highlights a likely spatial bias in Diazgranados et al. (2020) toward other tropical, and better investigated, areas of the world, for which information is databased and accessible, such as Africa, which is well represented in the Plant Resources for Tropical Africa (PROTA) database (https://www.prota4u.org/database).

The native distribution of some of the major food crop plant species from FAO (2015; Figure 3b) generally maps over Vavilov's centers of diversity (Vavilov, Vavylov, Vavílov, & Dorofeev, 1992), that is, the Mediterranean, Middle East, and Central Asia (for wheat, lentils, peas, artichokes, apples), Ethiopia/Eritrea highlands (for teff, Arabica coffee, enset), India (for aubergines, pigeon pea, mangoes), East Asia (for soybean, Asian rice, oranges, peaches), Mesoamerica, and the Andes (for maize, chillies, common bean, tomatoes, potatoes). However, there is a relatively low species richness in major food crops from the Malay Archipelago and high edible species richness from parts of Sub-Saharan Africa. Additional centers of origin have been proposed in recent years based on new archaeological evidence, such as West Africa for pearl millet and cowpea and Eastern Sahel for sorghum (Fuller et al., 2014; Harlan, 1971; Purugganan & Fuller, 2009).

There is a geographical spectrum to food plant domestication, with total food plant richness mostly in the tropics and major domestication events more scattered at mid-latitudes, following a global pattern associated with environmental and historical factors (Diamond, 2002). The proportion of highly domesticated species increases from species-rich, forested, warm, and wet areas to drier climates, rugged terrains (i.e., mountainous areas exhibiting high heterogeneity in environmental conditions), and large human settlements developing agriculture (Lev-Yadun, Gopher, & Abbo, 2000; Meyer et al., 2012; Vavilov et al., 1992). In contrast,

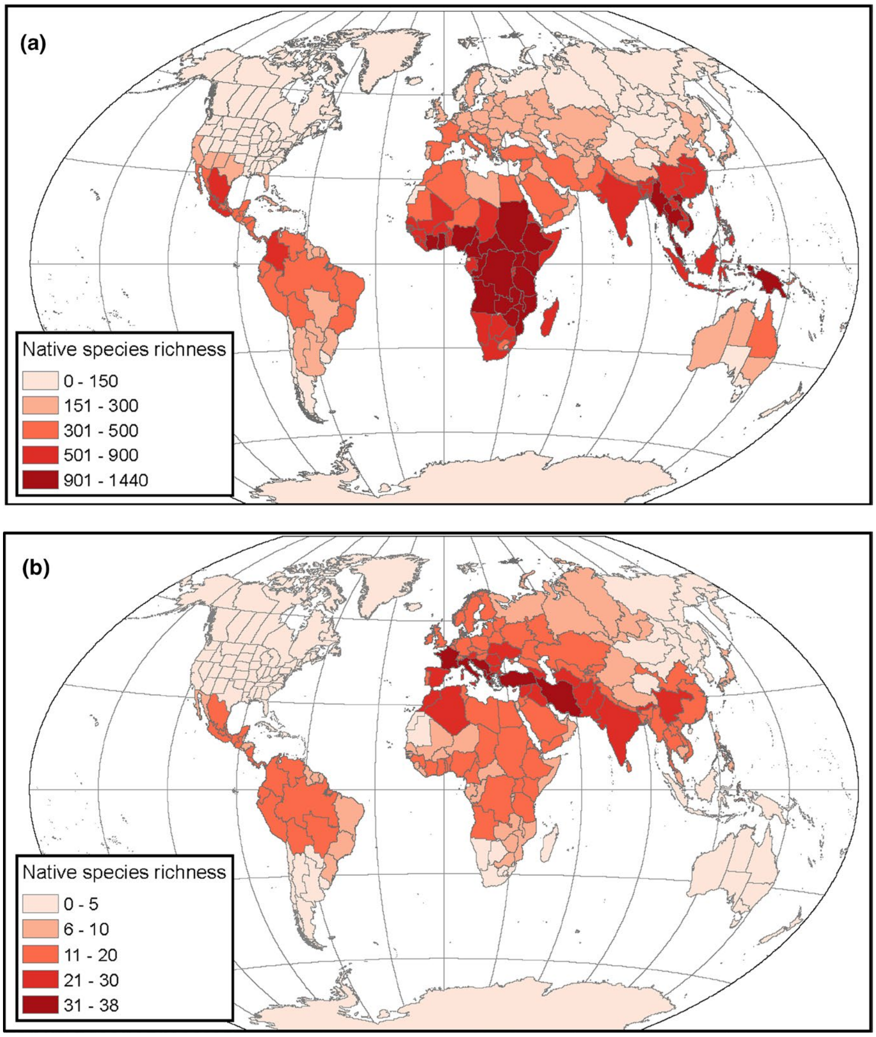


**FIGURE 3** (a) Global species richness per country of 6,959 out of the 7,039 edible species from Diazgranados et al. (2020). (b) Global species richness per country of 171 out of the 417 major food crops also listed in FAO (2015). While edible species richness decreases with increasing latitude, high richness in major food crops is mainly found in centers of domestication at mid-latitudes. Maps include species for which an IPNI ID (https://www.ipni.org/), as well as countries and sub-countries distribution data from the World Checklist of Selected Plant Families (WCVP, 2020), were available

wild, species-poor, cold, and flat areas of high latitudes contain few highly domesticated plants. However, humans are now changing these spatial patterns in food supply, demand, and cultivation by homogenizing the distribution of both agro-biodiversity and biodiversity in general (Baiser, Olden, Record, Lockwood, & McKinney, 2012; Khoury et al., 2014).

Understanding better the global distribution of edible plants offers an opportunity to identify future crops that are better adapted to present and future climatic conditions, and whose plant material is locally accessible. This could improve food security by increasing the cultivation of "climate smart" crops with fit-for-purpose seed lots (Castillo-Lorenzo, Pritchard, Finch-Savage, & Seal, 2019) that will produce food despite changing growing conditions (Borrell et al., 2020; Díaz et al., 2019; Pironon et al., 2019).

## 2.4 | Conservation status and measures in place

Previous studies on the comprehensiveness of the conservation of useful plants have highlighted that they are currently highly underconserved, both ex situ and in situ (Castañeda-Álvarez et al., 2016; Fielder et al., 2015; Khoury et al., 2019). However, when the collections housed in botanic gardens are included, we find a substantial representation of edible plant species conserved ex situ worldwide (Table 1). These results were achieved thanks to the joint efforts of the international CGIAR genebanks (https://www.cgiar.org/), botanic gardens (https://www.bgci.org/), and international plant conservation networks, such as Kew's Millennium Seed Bank Partnership (Liu, Breman, Cossu, & Kenney, 2018). However, some food species might be missing from ex situ collections due to incomplete data sets, geographic rarity, and having recalcitrant (i.e., desiccation sensitive) seeds, such as some tropical fruit trees (Li & Pritchard, 2009) and some priority crops on Annex 1 of the "International Treaty on Plant Genetic Resources for Food and Agriculture" (FAO, 2009). More work is also needed to understand and evaluate the functional and genetic diversity of ex situ collections, their potential for reintroduction efforts (Hay & Probert, 2013) and adaptability to future climate change (Borrell et al., 2020; Fernández-Pascual, Mattana, & Pritchard, 2019).

The International Union for Conservation of Nature (IUCN) Red List (IUCN, 2020) includes species-level global conservation assessments for at least 2,108 (30%) edible species listed in Diazgranados et al. (2020) and 1,811 of these (86%) are conserved ex situ (Table 2). Although most species (78%) are identified as Least Concern, at least

**TABLE 1** Taxonomic representation of food plant species in ex situ conservation facilities worldwide as seeds or/and as living plants

| Taxonomy | Total number in the reference list | Total number conserved ex situ | | | |
|---|---|---|---|---|---|
| | | Seeds[a] | Unspecified | Plants[b] | Overall |
| Class | 8 | 8 | 8 | 6 | 8 (100%) |
| Order | 69 | 62 | 68 | 43 | 69 (100%) |
| Families | 272 | 231 | 254 | 127 | 263 (97%) |
| Genera | 2,300 | 1,573 | 1,834 | 556 | 2,016 (88%) |
| Species | 7,014 | 3,810 | 4,789 | 1,100 | 5,454 (78%) |

[a]As populations/seed lots;

[b]Could be limited to a few individuals.

Sources: RBG Kew's MSB Partnership (https://www.kew.org/science/our-science/projects/banking-the-worlds-seeds), Genesys (https://www.genesys-pgr.org/) and Botanic Gardens Conservation International (https://tools.bgci.org/plant_search.php)

**TABLE 2** Current conservation status and ex situ conservation measures for food plant species

| IUCN category | Total number of species | | |
|---|---|---|---|
| | The IUCN Red List (IUCN, 2020) | Conserved ex situ (*N*) | Conserved ex situ (%) |
| Extinct in the Wild (EW) | 1 | 1 | 100 |
| Critically Endangered (CR) | 23 | 17 | 74 |
| Endangered (EN) | 68 | 53 | 78 |
| Vulnerable (VU) | 142 | 94 | 66 |
| Near Threatened (NT) | 64 | 53 | 83 |
| Lower Risk/conservation dependent (LR/cd) | 5 | 5 | 100 |
| Lower Risk/near threatened (LR/nt) | 35 | 24 | 69 |
| Lower Risk/least concern (LR/lc) | 52 | 42 | 81 |
| Least Concern (LC) | 1,656 | 1,468 | 89 |
| Data Deficient (DD) | 62 | 54 | 87 |
| Total | 2,108 | 1,811 | 86 |

Sources: RBG Kew's MSB Partnership (https://www.kew.org/science/our-science/projects/banking-the-worlds-seeds), Genesys (https://www.genesys-pgr.org/), and Botanic Gardens Conservation International (https://tools.bgci.org/plant_search.php)

234 species (11%) are considered at risk of extinction (i.e., extinct in the wild; critically endangered; endangered; or vulnerable). The Botanic Gardens Conservation International (BGCI) ThreatSearch database (https://tools.bgci.org/threat_search.php) lists conservation assessments at global, regional, and national level for at least 3,893 (55%) of the species in our list, with most species (76%) identified as “Not Threatened” (Figure 4). Many major food crop species are widespread; therefore, it is likely that their extinction risk will be relatively low. Nonetheless, specific plant populations, including landraces, which may have unique climatic and environmental tolerances, and upon which human communities may depend, might still be threatened. Therefore, future conservation priorities should reflect assessments at the global level, and, for narrow distributed species, at the national level (Forest et al., 2018; Liu, Kenney, Breman, & Cossu, 2019).

## 3 | UNTAPPED PLANT FOOD RESOURCES

Beyond habitat destruction, many NUS are at risk of disappearing because of changing cultural views and lack of documentation (National Research Council, 2008). Promoting their role in food security calls for coordinated approaches across plant science and food systems, from local to international levels (Baldermann et al., 2016), as actively promoted since 1988 by the International Centre for Underutilized Crops (Tchoundjeu & Atangana, 2006). However, consolidated attention to NUS has really only emerged in the last decade, as the fight against climate change and the need to make agricultural production systems more diverse and environment resilient has accelerated (see Table S1 for a selection of projects/initiatives). The same trend is also evident for the limited pool of human and animal food crops, for which the challenges of feeding a growing population with a limited pool of crops have been highlighted (Lee, 2018; Lee, Davis, Chagunda, & Manning, 2017).

There are many incentives and subsidies that tie countries into the production of major crops (Hunter et al., 2019; Noorani, Bazile, Diulgheroff, Kahane, & Nono-Womdim, 2015) and which potentially hinder conservation efforts (Kahane et al., 2013). Addressing NUS conservation and their sustainable production is critically important if they are to compete in the marketplaces dominated by a few commodity crops. An integrated conservation approach combines ex situ, in situ and on farm methods and ensures the effective maintenance and use of genetic diversity, the knowledge associated with this diversity and its transmission to future generations (Padulosi, Bergamini, & Lawrence, 2012). The primary challenge is the prioritization of model species for impact, to make the best use of limited resources. Species selection should be driven by shared priorities in terms of nutrition, climate adaptation, income generation, cultural

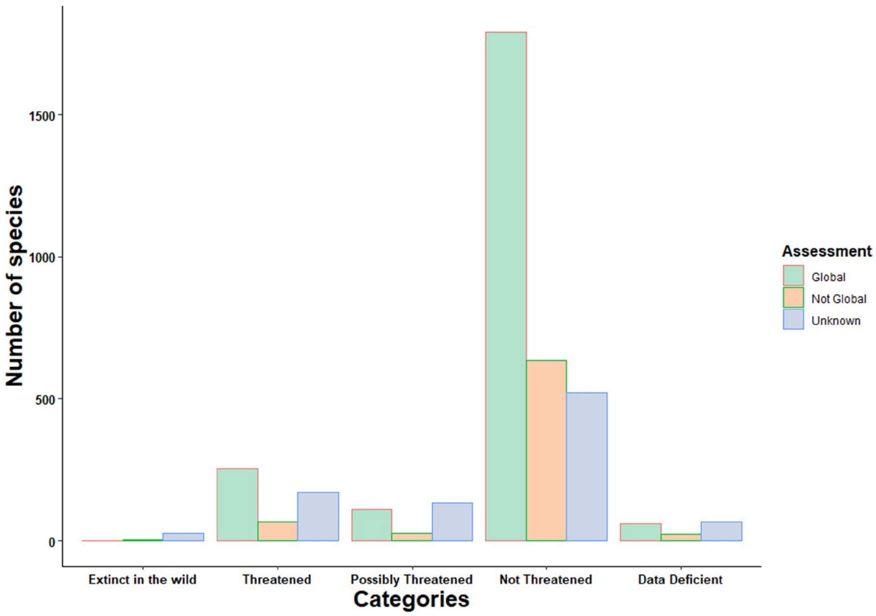


**FIGURE 4** Conservation status for 3,893 edible plant species from Diazgranados et al. (2020), according to the BGCI ThreatSearch database (https://tools.bgci.org/threat_search.php). One assessment per species was selected, giving priority to the most recent assessment with highest risk. Records without an assessment year were excluded

diversity, ecosystem health, and the urgency of the intervention due to ongoing genetic erosion. Women, young people, and indigenous groups must be active participants in all of these exercises, through a participatory bottom-up process (Padulosi, Phrang, Phrang, & Rosado-May, 2019), as carried out by Dansi et al. (2012) in Benin and, more recently, by FAO within its Future Smart Food Initiative in Asia (FAO, 2018). This bottom-up approach will help develop innovative methods and tools of wide applicability that could be applied to other NUS. Success and failures in promoting "new" crops can be found across many regions, for example the effective establishment of lupin cultivation in Australia (Nelson & Hawthorne, 2000), or the negative social and environmental impact in the Andes caused by the quinoa boom (McDonell, 2018). To strengthen the self-sufficiency of food and production systems in terms of climate resilience, agroecological benefits (e.g., soil improvers and species' enhancers), food and nutrition security (e.g., species and varieties that build resilient, more nutritious and healthy diets), and income generation (e.g., diversity to build economic resilience), there is a need for both sustainable promotion and integrated conservation. Sustainable promotion makes diversity a central feature of the food system (at both intra- and inter-specific levels), thereby potentially avoiding what has happened in the Andes with quinoa, where global demand is being met by a few mainstream varieties, while hundreds of others are being marginalized (Zimmerer & Carney, 2019). Low levels of funding for the promotion of NUS, like yams, amaranth, Bambara groundnut, or African leafy vegetables, represents a major challenge for most countries interested in their promotion. Economic incentives and subsidies to private companies for producing local crops or certification schemes to recognize biodiversity-rich products, should be actively pursued and include the establishment of an international "NUS Fund" specifically dedicated to supporting their development (Padulosi, Cawthorn, et al., 2019).

It is with this vision in mind that we provide a selection of highly promising NUS of plants (wild, domesticated, or semi-domesticated) from different regions of the world (Table 3), which have been targeted by major projects, international agencies (Table S1) and researchers (references in Table 3). We highlighted (in bold text in Table 3) those which are not currently listed as major food crops by the FAO (2015), for example, the mesquites in the Americas, morama bean in Africa, Akkoub in Asia, rocket in Europe and Pindan walnut in Oceania (Table 3). In addition, considering the differences in nutritional properties of the organ types (Guil-Guerrero & Torija-Isasa, 2002), we also reported the edible parts of each species. When comparing the taxa listed in Table 3 with those reported by Diazgranados et al. (2020), we found an average of five uses recorded per taxa, and a peak of 24 taxa with seven uses (Figure S2). Examples of NUS with many uses include the baobab in Africa, which is known as the "tree of life," whose leaves, flowers, fruit pulp, and seeds are used as food and to make beverages; the bark, roots, and seeds are medicinal; the bark is used for making rope, roofing material and clothing; and the hard husk of the fruit is used as calabash (Chadare, Linnemann, Hounhouigan, Nout, & Van Boekel, 2008; National Research Council, 2008; Ngwako, Mogotsi, Sacande, Ulian, Davis, et al., 2019). The taro, originally from Asia and also cultivated in Oceania, has edible leaves, flowers, and roots; the roots are also medicinal and used as an additive to render plastics biodegradable (Arora, 2014; Linden, 1996).

Therefore, NUS of plants, as well as many edible species of fungi (see Box 1), represent potentially low-hanging fruit for a more resilient, sustainable, biodiverse, and community participation-driven new "green revolution," equitable and fair to the environment and all members of society.

## 4 | QUALITY OF FOOD RESOURCES IN A CHANGING CLIMATE

In the coming century, major challenges to agriculture and biodiversity will be dominated by increased climate variation. Hence, research needs to increase our knowledge on the biology and ecology of many NUS to be able to synthesize the future impact of climate

**TABLE 3** Selection of neglected and underutilized plants (NUS) that have been recommended in scientific papers or targeted by collaborative projects, networks or international agencies. Species in bold are not listed in FAO (2015). Scientific names are ordered alphabetically and according to Kew's Plants of the World Online portal (http://www.plantsoftheworldonline.org).

| Common name(s) | Scientific name | Source | Plant part(s) used | Region(s) of origin | Main regions of natural occurrence or cultivation | Key reference(s) | Target of projects, included in priority lists or focus of efforts by key international agencies (Table S1) | Number of uses |
|---|---|---|---|---|---|---|---|---|
| **1. Slippery cabbage, bele, abika** | ***Abelmoschus manihot* (L.) Medik.** | **2** | **1** | **Asia, Oceania** | **Oceania, Asia** | Solberg, Seta-Waken, Paul, Palaniappan, and Iramu (2018) | | **7** |
| **2. Baobab** | ***Adansonia digitata* L.** | **1** | **1,2,3,4** | **Africa** | **Africa** | Hall, Rudebjer, and Padulosi (2013), Kahane et al. (2013), National Research Council (2008), Ngwako, Mogotsi, Sacande, Ulian, Davis, et al. (2019) | **3; 9; 12** | **10** |
| **3. Ground elder** | ***Aegopodium podagraria* L.** | **1** | **1** | **Europe** | **Europe** | Łuczaj et al. (2012) | | **0** |
| 4. Candlenut | *Aleurites moluccanus* (L.) Willd | 1 | 5 | Asia, Oceania | Asia, Oceania | | 12 | **10** |
| **5. Amaranth** | ***Amaranthus* L. (incl.: *A. caudatus* L., *A. hybridus* subsp. *quitensis* (Kunth) Costea & Carretero, *A. spinosus* L., *A. retroflexus* L.)** | **3** | **1,4** | **Americas, Asia, Africa, Europe** | **Americas, Asia, Africa, Europe** | Arora (2014), Hall et al. (2013), Hernandez-Bermejo and León (1992), Kahane et al. (2013), Kasolo, Chemining'wa, G., and Temu, A. (2018), Li et al. (2018), National Research Council (1996), Tyagi et al. (2017) | **3; 4; 5; 8; 9;10; 11; 12** | ***A. caudatus* = 7; *A. hybridus* = 7; *A. spinosum* = 7; *A. retroflexus* = 4** |
| **6. Elephant foot yam** | ***Amorphophallus paeoniifolius* (Dennst.) Nicolson** | **2** | **5** | **Asia** | **Asia** | Arora (2014), Raneri et al. (2019), Tyagi et al. (2017) | **2** | **6** |
| **7. Sugar apple** | ***Annona* spp. (incl.: *A. squamosa* L., *A. cherimola* Mill., *A. crassiflora* Mart., *A. muricata* L.).** | **2** | **3** | **Americas, Asia** | **Americas, Asia, Oceania** | Hall et al. (2013), Kasolo et al. (2018), Kour et al. (2018), Hernandez-Bermejo and León (1992), Padulosi et al. (2011), Tyagi et al. (2017) | **3; 12** | **4 (15 species)** |
| **8. Araucarias** | ***Araucaria* Juss. [incl.: *A. angustifolia* (Bertol.) Kuntze, *A. araucana* (Molina) K.Koch, *A. bidwillii* Hook.].** | **1** | **4** | **Americas, Oceania** | **Americas, Oceania** | | **12** | **4 (6 species)** |

(Continues)

**TABLE 3** (Continued)

| Common name(s) | Scientific name | Source | Plant part(s) used | Region(s) of origin | Main regions of natural occurrence or cultivation | Key reference(s) | Target of projects, included in priority lists or focus of efforts by key international agencies (Table S1) | Number of uses |
|---|---|---|---|---|---|---|---|---|
| **9. Estragon** | ***Artemisia dracunculus* L.** | **2** | **1** | **Europe, Asia** | **Europe, Asia** | | **2** | **3** |
| 10. Breadfruit | *Artocarpus altilis* (Parkinson) Fosberg | 2 | 3 | Asia, Oceania | Asia, Oceania | Thomson, Doran, and Clarke (2018), Tyagi et al. (2017) | 3; 9;11; 12 | **10** |
| **11. Jackfruit** | ***Artocarpus heterophyllus* Lam.** | **2** | **3** | **Asia** | **Asia** | Arora (2014), Kour et al. (2018), Li et al. (2018), Tyagi et al. (2017) | **3; 9; 11** | **7** |
| 12. Asparagus | *Asparagus* Tourn. ex L. | 1 | 6 | Europe | Europe | Arora (2014), Łuczaj et al. (2012), Tyagi et al. (2017) | | **4** (19 species) |
| **13. Peach palm** | ***Bactris gasipaes* Kunth** | **3** | **3** | **Americas** | **Americas** | Hernandez-Bermejo and León (1992), Kahane et al. (2013), Raneri et al. (2019), Wickens, Haq, and Day (1989) | **2; 3; 12** | **7** |
| **14. Common bamboo** | ***Bambusa vulgaris* Schrad. ex J.C.Wendl.** | **3** | **6** | **Asia** | **Africa, Asia, Oceania, Americas** | | **14; 15** | **9** |
| **15. Ackee** | ***Blighia sapida* K.D.Koenig** | **3** | **3** | **Africa** | **Africa, Americas** | Dansi et al. (2012), Hall et al. (2013) | **3** | **7** |
| 16. Kale | *Brassica oleracea* L. | 3 | 1 | Asia | Europe, Americas | | 8 | **7** |
| 17. Pigeon pea | *Cajanus cajan* (L.) Huth | 2 | 4 | Asia | Africa, Asia, Americas | FAO (2010) | 3; 10; 12 | **9** |
| **18. Carissa** | ***Carissa spinarum* L.** | **1** | **1,3** | **Africa** | **Africa** | Kour et al. (2018), National Research Council (2006), Omondi et al. (2019) | **3** | **9** |
| **19. Lagos spinach** | ***Celosia argentea* L.** | **1** | **1** | **Africa** | **Africa, Asia** | Hall et al. (2013), National Research Council (2006) | **3; 10; 11** | **8** |
| **20. Bulbous chervil** | ***Chaerophyllum bulbosum* L.** | **1** | **1** | **Europe** | **Europe** | Łuczaj et al. (2012) | | **2** |
| 21. Quinoa, Goosefoots, Cañahua | *Chenopodium* L. [incl.: *Chenopodium quinoa* Willd., *C. pallidicaule* Aellen, *C. giganteum* D.Don, *Blitum bonus-henricus* (L.) Rchb.] | 1 | 4 | Americas | Asia, Americas, Africa, Europe | Kasolo et al. (2018), Arora (2014), Li et al. (2018), Li et al. (2018), Łuczaj et al. (2012), Padulosi et al. (2011), Raneri et al. (2019) | 3; 4; 8; 9 | **4** (5 species) |
| 22. Chicory | *Cichorium intybus* L. | 1 | 1 | Europe | Europe | Łuczaj et al. (2012), National Research Council (1996) | 12 | **6** |

(Continues)

**TABLE 3** (Continued)

| Common name(s) | Scientific name | Source | Plant part(s) used | Region(s) of origin | Main regions of natural occurrence or cultivation | Key reference(s) | Target of projects, included in priority lists or focus of efforts by key international agencies (Table S1) | Number of uses |
|---|---|---|---|---|---|---|---|---|
| **23. Spider plant** | ***Cleome gynandra* L.** | **3** | **1** | **Africa** | **Africa, Asia, Americas** | Dansi et al. (2012), Hall et al. (2013), Kahane et al. (2013), Raneri et al. (2019) | **2; 3; 9; 11; 12** | **7** |
| **24. Chaya** | ***Cnidoscolus aconitifolius* (Mill.) I.M.Johnst.** | **2** | **1** | **Americas** | **Americas** | Raneri et al. (2019) | **4; 9; 10** | **6** |
| **25. Jobs' tears** | ***Coix lacryma-jobi* L.** | **3** | **4** | **Asia** | **Cosmopolitan** | Hall et al. (2013), Li et al. (2018), Sanogo et al. (2019) | **12** | **8** |
| 26. Taro | *Colocasia esculenta* (L.) Schott | 1 | 1,2,5,6 | Asia | Asia, Oceania | Arora (2014), Hall et al. (2013), Kahane et al. (2013) | 3; 11 | **8** |
| 27. Jute mallow | *Corchorus olitorius* L. | 2 | 1,3 | Asia, Africa | Africa, Asia, Americas | Dansi et al. (2012), Padulosi et al. (2011), Raneri et al. (2019) | 4; 11 | **7** |
| 28. Rattlepods | *Crotalaria* L. | 3 | 1 | Africa | Cosmopolitan | | 3; 11; 12 | **4** (23 species) |
| 29. Japanese pie pumpkin | *Cucurbita argyrosperma* C.Huber | 2 | 3 | Americas | Americas | Hernandez-Bermejo and León (1992) | | **3** |
| 30. Squash | *Cucurbita moschata* Duchesne | 2 | 3 | Americas | Americas | Hernandez-Bermejo and León (1992) | | **5** |
| **31. Swamp taro** | ***Cyrtosperma merkusii* (Hassk.) Schott** | **2** | **5** | **Asia** | **Oceania, Asia** | Arora (2014), Kahane et al. (2013), Li et al. (2018), Tyagi et al. (2017) | **3; 8; 9** | **3** |
| 32. Fonio | *Digitaria exilis* (Kippist) Stapf and *D. iburua* Stapf | 2 | 4 | Africa | Africa | FAO (2010), Kahane et al. (2013), National Research Council (1996); Raneri et al. (2019) | 3; 4; 8; 9; 11; 12 | *D. exilis* = **8** *D. iburua* = **3** |
| 33. Yams | *Dioscorea cayenensis* subsp. *rotundata* (Poir.) J.Miège, *D. polystachya* Turcz., *D. dumetorum* (Kunth) Pax, *D. bulbifera* L. | 3 | 5 | Africa | Africa, Asia, Americas, Oceania | Arora (2014), Hall et al. (2013) | 3; 8; 11; 12 | *D. cayenensis* = **05**, *D. polystachya*: **3**, *D. dumetorum* = **6**, *D. bulbifera* = **7** |
| 34. Barnyard grass | *Echinochloa* P.Beauv. | 1 | 4 | Africa, Asia, Americas | Africa, Asia, Americas | Arora (2014), Li et al. (2018), Raneri et al. (2019), Tyagi et al. (2017) | 3 | **5** (10 species) |

(Continues)

**TABLE 3** (Continued)

| Common name(s) | Scientific name | Source | Plant part(s) used | Region(s) of origin | Main regions of natural occurrence or cultivation | Key reference(s) | Target of projects, included in priority lists or focus of efforts by key international agencies (Table S1) | Number of uses |
|---|---|---|---|---|---|---|---|---|
| 35. Finger millet | *Eleusine coracana* (L.) Gaertn. | 2 | 4 | Asia | Asia, Africa | Arora (2014), FAO (2010), Hall et al. (2013), Li et al. (2018), National Research Council (1996), Raneri et al. (2019), Tyagi et al. (2017) | 3; 4; 7; 8; 9; 11; 12 | 7 |
| 36. Teff | *Eragrostis tef* (Zuccagni) Trotter | 2 | 4 | Africa | Africa | Arora (2014), FAO (2010), National Research Council (1996), Wickens et al. (1989) | 2; 3; 8; 9; 11; 12 | 7 |
| 37. Rocket | *Eruca vesicaria* (L.) Cav. | 2 | 1 | Europe, Asia | Europe, Asia, Americas | Arora (2014), Raneri et al. (2019) | 1; 3; 9; | 7 |
| 38. Torch lily | *Etlingera* spp. [incl.: *E. elatior* (Jack) R.M.Sm., *E. hemisphaerica* (Blume) R.M.Sm.]. | 3 | 1,2,3,4 | Asia | Asia, Africa, Americas, Oceania | | 12 | 2 (13 species) |
| 39. Buckwheat | *Fagopyrum esculentum* Moench | 2 | 4 | Asia | Asia, Europe | Arora (2014), Hall et al. (2013), Kasolo et al. (2018), Li et al. (2018), Raneri et al. (2019), Tyagi et al. (2017) | 3; 7; 8; 9; 12 | 9 |
| 40. Sycamore fig | *Ficus sycomorus* L. | 1 | 1 | Africa, Asia | Africa, Asia, Americas | Tyagi et al. (2017) | 3; 12 | 8 |
| 41. Kokum | *Garcinia* L. [incl.: *G. indica* (Thouars) Choisy, *G. parvifolia* (Miq.) Miq., *G. gummi-gutta* (L.) Roxb., *G. morella* (Gaertn.) Desr., *G. binucao* (Blanco) Choisy] | 1 | 3 | Asia | Asia | Arora (2014), Kour et al. (2018), Li et al. (2018), Tyagi et al. (2017) | 3; 6; 12 | 3 (548 species) |
| 42. Ginkgo | *Ginkgo biloba* L. | 1 | 4 | Asia | Asia | Arora (2014) | | 4 |
| 43. Arrowroot | *Goeppertia allouia* (Aubl.) Borchs. & S.Suárez | 2 | 5 | Americas | Americas | Hernandez-Bermejo and León (1992) | 3; 12 | 2 |
| 44. Akkoub | *Gundelia tournefortii* L. | 1 | 6 | Asia | Asia | | 3; 12 | 3 |
| 45. Roselle | *Hibiscus sabdariffa* L. | 2 | 1,2 | Africa | Africa, Asia, Oceania | Arora (2014), Kasolo et al. (2018), Li et al. (2018), Tyagi et al. (2017) | 3; 12 | 8 |

(Continues)

**TABLE 3** (Continued)

| Common name(s) | Scientific name | Source | Plant part(s) used | Region(s) of origin | Main regions of natural occurrence or cultivation | Key reference(s) | Target of projects, included in priority lists or focus of efforts by key international agencies (Table S1) | Number of uses |
|---|---|---|---|---|---|---|---|---|
| **46. Sea buckthorn** | ***Hippophae rhamnoides* L.** | **2** | **3** | **Asia** | **Asia, Europe** | Arora (2014), Łuczaj et al. (2012), Padulosi et al. (2011) | | **0** |
| 47. Hop | *Humulus lupulus* L. | 1 | 1 | Europe | Europe | Łuczaj et al. (2012) | 12 | **5** |
| 48. Lablab | *Lablab purpureus* (L.) Sweet | 2 | 4 | Africa | Africa, Asia | Arora (2014), Kahane et al. (2013), National Research Council (1996), Tyagi et al. (2017) | 3; 9; 11;12 | 7 |
| 49. Lupin | *Lupinus mutabilis* Sweet and *L. albus* L. | 2 | 4 | Americas, Africa, Europe, | Americas, Africa, Europe | Hernandez-Bermejo and León (1992) | 3; 4; 12 | *L. mutabilis* = **7** *L. albus* = **8** |
| **50. Macadamia** | ***Macadamia tetraphylla* L.A.S.Johnson** | **2** | **3** | **Oceania** | **Africa, Asia, Oceania** | Arora (2014), Kasolo et al. (2018), Tyagi et al. (2017) | | **2** |
| **51. Mallow** | ***Malva* Tourn. ex L.** | **1** | **1** | **Europe, Asia** | **Europe, Asia** | Arora (2014), Łuczaj et al. (2012) | **3** | **4** (4 species) |
| **52. Microseris (several common names)** | ***Microseris* D.Don. [incl.: *M. scapigera* Sch.Bip., *M. lanceolata* (Walp.) Sch. Bip.].** | **1** | **1** | **Oceania** | **Oceania** | | **12** | **0** |
| 53. Moringa | *Moringa oleifera* Lam. and *M. stenopetala* (Baker f.) Cufod. | 2 | 1,2,3,4 | Africa, Asia | Asia, Africa, Americas | Arora (2014), Kahane et al. (2013), Kasolo et al. (2018), Kour et al. (2018), Li et al. (2018), National Research Council (2006), Padulosi et al. (2011), Raneri et al. (2019), Tyagi et al. (2017) | 3; 8; 9; 11; 12 | *M. oleifera* = **10** *M. stenopetala* = **7** |
| **54. African Alpine bamboo** | ***Oldeania alpina* (K.Schum.) Stapleton** | **1** | **6** | **Africa** | **Africa** | | **12** | **6** |
| **55. Ostrich fern** | ***Onoclea struthiopteris* Roth** | **1** | **1** | **Europe, Asia, Americas** | **Europe, Asia, Americas** | Łuczaj et al. (2012) | **12** | **2** |
| **56. Oca** | ***Oxalis tuberosa* Molina** | **3** | **5** | **Americas** | **Americas** | Hernandez-Bermejo and León (1992) | **3; 9; 12** | **2** |
| **57. Pandanus, screwpine** | ***Pandanus tectorius* Parkinson ex Du Roi** | **3** | **3** | **Asia, Oceania** | **Asia, Oceania** | Thomson, Cruz-de Hoyos, Cummings, and Schultz (2016) | | **6** |

(Continues)

**TABLE 3** (Continued)

| Common name(s) | Scientific name | Source | Plant part(s) used | Region(s) of origin | Main regions of natural occurrence or cultivation | Key reference(s) | Target of projects, included in priority lists or focus of efforts by key international agencies (Table S1) | Number of uses |
|---|---|---|---|---|---|---|---|---|
| 58. Proso millet | *Panicum miliaceum* L. and *P. decompositum* R.Br. | 2 | 4 | Asia, Europe, Oceania | Asia, Europe, Oceania | Arora (2014), Kahane et al. (2013), Li et al. (2018), Raneri et al. (2019), Tyagi et al. (2017) | 3; 12 | *P. miliaceum* = **5**, *P. decompositum* = **0** |
| 59. Guarana | *Paullinia cupana* Kunth | 1 | 3,4 | Americas | Americas | Hernandez-Bermejo and León (1992) | 3; 12 | **4** |
| **60. Perilla** | ***Perilla frutescens* (L.) Britton** | **2** | **1,4** | **Asia** | **Asia** | Arora (2014), Li et al. (2018), Tyagi et al. (2017) | **3; 12** | **5** |
| 61. Tepary bean | *Phaseolus acutifolius* A.Gray | 2 | 4 | Americas | Americas | Hernandez-Bermejo and León (1992) | 4; 12 | **5** |
| 62. Runner bean | *Phaseolus coccineus* L. | 2 | 4 | Americas | Americas, Asia | Arora (2014), Hernandez-Bermejo and León (1992), Tyagi et al. (2017) | 12 | **6** |
| **63. Moso bamboo** | ***Phyllostachys edulis* (Carrière) J.Houz.** | **1** | **6** | **Asia** | **Asia** | Arora (2014), Li et al. (2018) | | **4** |
| **64. Jaboticaba** | ***Plinia rivularis* (Cambess.) Rotman and *P. cauliflora* (Mart.) Kausel** | **2** | **3** | **Americas** | **Americas** | Hernandez-Bermejo and León (1992) | **3; 12** | *P. rivularis* = **0**, *P. cauliflora* = **2** |
| **65. Zapote** | ***Pouteria sapota* (Jacq.) H.E.Moore & Stearn** | **1** | **3** | **Americas** | **Americas** | Hernandez-Bermejo and León (1992) | **3; 12** | **2** |
| **66. Mesquite** | ***Prosopis* L. [incl.: *P. alba* Griseb., *P. chilensis* (Molina) Stuntz, *P. juliflora* (Sw.) DC.].** | **3** | **4** | **Americas, Africa, Asia** | **Americas, Africa, Asia** | Arora (2014), Wickens et al. (1989) | **3; 12** | **7** (14 species) |
| **67. Bracken** | ***Pteridium aquilinum* L. Kuhn *s.l.*** | **1** | **1** | **Cosmopolitan** | **Cosmopolitan** | Liu, Wujisguleng, and Long (2012) | **12** | **7** |
| **68. Oak** | ***Quercus* L.** | **1** | **3** | **Europe, Asia, Africa** | **Europe, Asia, Africa, Americas** | Łuczaj et al. (2012) | **12** | **4** (9 species) |
| 69. Rasberry | *Rubus* L. [incl.: *R. hawaiensis* A.Gray, *R. macraei* A.Gray, *R. rosifolius* Sm., *R. parvifolius* L.]. | 3 | 3 | Asia, Oceania | Asia, Oceania | Arora (2014), Łuczaj et al. (2012) | 3; 12 | **3** (36 species) |

(Continues)

**TABLE 3** (Continued)

| Common name(s) | Scientific name | Source | Plant part(s) used | Region(s) of origin | Main regions of natural occurrence or cultivation | Key reference(s) | Target of projects, included in priority lists or focus of efforts by key international agencies (Table S1) | Number of uses |
|---|---|---|---|---|---|---|---|---|
| **70. Sorrels** | ***Rumex acetosa* L. and *R. lapponicus* (Hiitonen) Czernov** | **1** | **1** | **Europe, Asia, Americas** | **Europe, Asia, Americas** | Łuczaj et al. (2012) | **12** | *R. acetosa* = **4**, *R. lapponicus* = **0** |
| **71. Arrowhead** | ***Sagittaria* Ruppius ex L.** | **1** | **1** | **Europe** | **Europe, Asia** | Arora (2014) | | **2** (5 species) |
| **72. Elder** | ***Sambucus nigra* L., *S. canadensis* L.** | **1** | **2,3** | **America, Africa, Europe, Americas** | **America, Africa, Europe, Americas** | Łuczaj et al. (2012) | **12** | *S. nigra* = **5**, *S. canadensis* = **5** |
| **73. Quandong** | ***Santalum acuminatum* (R.Br.) A.DC.** | **1** | **3** | **Oceania** | **Oceania** | Arora (2014) | **3; 12** | **6** |
| **74. Marula** | ***Sclerocarya birrea* (A.Rich.) Hochst.** | **1** | **3** | **Africa** | **Africa** | Kahane et al. (2013), National Research Council (2008), Ngwako, Mogotsi, Sacande, Ulian, and Mattana (2019) | **3; 11; 12** | **10** |
| **75. Common golden thistle** | ***Scolymus hispanicus* L.** | **1** | **6** | **Europe** | **Europe** | Łuczaj et al. (2012) | **3; 12** | **2** |
| 76. Black salsify | *Scorzonera hispanica* L. | 2 | 5 | Europe | Europe | | 8; 12 | **4** |
| **77. False sesame** | ***Sesamum sesamoides* (Endl.) Byng & Christenh.** | **1** | **1** | **Africa** | **Africa** | Dansi et al. (2012) | **3** | **6** |
| 78. Foxtail millet | *Setaria italica* (L.) P.Beauv. | 2 | 4 | Asia, Europe | Asia, Europe | Arora (2014), Kahane et al. (2013), Li et al. (2018), Raneri et al. (2019) | 2; 3; 8; 12; | **7** |
| **79. Bladder campion** | ***Silene vulgaris* (Moench) Garcke** | **1** | **1** | **Europe, Americas** | **Europe** | Łuczaj et al. (2012) | | **2** |
| **80. Cardus marianus** | ***Silybum marianum* (L.) Gaertn.** | **1** | **6** | **Europe, Asia** | **Europe, Asia, Africa, Americas** | Łuczaj et al. (2012) | | **4** |
| 81. Mustard | *Sinapis* L. | 1 | 1,4 | Europe | Europe, Asia, Africa, Americas | Arora (2014) | | **7** (*S. alba*) |
| **82. Yacon** | ***Smallanthus sonchifolius* (Poepp.) H.Rob.** | **2** | **5** | **Americas** | **Americas** | Hernandez-Bermejo and León (1992) | **3; 9; 12** | **2** |
| **83. *Greenbriers*** | ***Smilax excelsa* L., *S. glyciphylla* J.White, *S. ferox* Wall. ex Kunth** | **1** | **6** | **Europe, Asa, Oceania** | **Europe, Asa, Oceania** | Tyagi et al. (2017) | **12** | ***S. excelsa* = 0, *S. glyciphylla* = 3, *S. ferox* = 0** |

(Continues)

**TABLE 3** (Continued)

| Common name(s) | Scientific name | Source | Plant part(s) used | Region(s) of origin | Main regions of natural occurrence or cultivation | Key reference(s) | Target of projects, included in priority lists or focus of efforts by key international agencies (Table S1) | Number of uses |
|---|---|---|---|---|---|---|---|---|
| 84. Tomato tree | *Solanum betaceum* Cav. | 1 | 3 | Americas | Americas, Asia, Oceania | Hernandez-Bermejo and León (1992) | 3 | 3 |
| **85. African eggplant and other names** | ***Solanum* L. [incl.: *S. aethiopicum* L., *S. quitoense* Lam., *S. sessiliflorum* Dunal, *S. ellipticum* R.Br., *S. juzepczukii* Bukasov, *S. curtilobum* Juz. & Bukasov, *S. glaucescens* Zucc.]** | **3** | **3** | **Africa, Asia, Americas, Oceania** | **Africa, Asia, Americas, Oceania** | Kahane et al. (2013), National Research Council (2006) | **3; 11; 12** | **4** (51 species) |
| **86. African black nightshade** | ***Solanum scabrum* Mill.** | **3** | **1** | **Africa** | **Cosmopolitan** | | **3; 11** | **6** |
| **87. African yam bean** | ***Sphenostylis stenocarpa* (Hochst. ex A.Rich.) Harms** | **2** | **4,5** | **Africa** | **Africa, Asia** | Arora (2014), Dansi et al. (2012), National Research Council, (1996), Tyagi et al. (2017) | **3; 8; 9; 11** | **5** |
| **88. Jocote** | ***Spondias* spp. (incl.: *S. purpurea* L., *S. mombin* L., *S. dulcis* Parkinson)** | **3** | **3** | **Americas** | **Americas** | Hernandez-Bermejo and León (1992) | **3; 12** | **6** (6 species) |
| **89. Marsh woundwort** | ***Stachys palustris* L., *S. tymphaea*** | **1** | **1** | **Europe, Asia** | **Europe, Asia, Americas** | Arora (2014), Łuczaj et al. (2012), Tyagi et al. (2017) | **12** | **0** |
| **90. Malay apple** | ***Syzygium malaccense* (L.) Merr. & L.M.Perry** | **2** | **3** | **Asia, Oceania,** | **Asia, Oceania** | Thomson et al. (2018) | | **6** |
| **91. Pindan walnut** | ***Terminalia* L. (incl.: *T. cunninghamii* C.A.Gardner)** | **1** | **4** | **Asia, Oceania,** | **Asia, Oceania** | Arora (2014), Tyagi et al. (2017) | **3; 12** | **6** (21 species) |
| 92. Salsify | *Tragopogon* L. | 1 | 6 | Europe, Asia | Europe, Asia, Americas, Oceania | Arora (2014), Tyagi et al. (2017) | | 3 (*T. porrifolius*) |
| **93. Buffalo nut** | ***Trapa* L.(incl.: *T. natans* L., *T. japonica* Flerow)** | **1** | **4** | **Europe, Asia, Africa** | **Europe, Asia, Africa** | Arora (2014), Turner et al. (2011), Tyagi et al. (2017) | **12** | ***T. napans* = 6 *T. japonica* = 0** |
| **94. African breadfruit** | ***Treculia africana* Decne. ex Trécul** | **1** | **3** | **Africa** | **Africa** | Kasolo et al. (2018) | **2; 3; 12** | **7** |
| **95. Snake gourd** | ***Trichosanthes cucumerina* L.** | **2** | **3** | **Asia** | **Asia** | Arora (2014), Li et al. (2018), Tyagi et al. (2017) | | **5** |

(Continues)

**TABLE 3** (Continued)

| Common name(s) | Scientific name | Source | Plant part(s) used | Region(s) of origin | Main regions of natural occurrence or cultivation | Key reference(s) | Target of projects, included in priority lists or focus of efforts by key international agencies (Table S1) | Number of uses |
|---|---|---|---|---|---|---|---|---|
| **96. Morama bean** | ***Tylosema esculentum* (Burch.) A.Schreib.** | **2** | **4** | **Africa** | **Africa** | (Mogotsi, Sacande, et al., 2019) | **8; 12** | **6** |
| **97. Bulrush** | ***Typha orientalis* C.Presl, *T. domingensis* Pers., *T latifolia* L.** | **1** | **6** | **Europe, Asia, Americas** | **Cosmopolitan** | Turner et al. (2011) | **3; 12** | ***T. orientalis* = 5, *T. dominigensis* = 8, *T. latifolia* = 7** |
| **98. Ulluco** | ***Ullucus tuberosus* Caldas** | **2** | **5** | **Americas** | **Americas** | Hernandez-Bermejo and León (1992) | **3; 9; 12** | **2** |
| **99. Nettle** | ***Urtica dioica* L. and *U. massaica* Mildbr.** | **1** | **1** | **Europe, Asia, Africa** | **Europe, Asia, Africa** | (Łuczaj et al., 2012) | **12** | ***U. dioica* = 7, *U. massaica* = 3** |
| 100. Small cranberry | *Vaccinium* spp. (incl.: *V. oxycoccos* L., *V. floribundum* Kunth, *V. praestans* Lamb.) | 1 | 3 | Europe, Asia, Americas | Europe, Asia, Americas | | 12 | **3** (20 species) |
| 101. Bambara groundnut | *Vigna subterranea* (L.) Verdc. | 2 | 4 | Africa | Africa, Asia, Oceania | Arora (2014), Dansi et al. (2012), FAO (2010), Hall et al. (2013), Kahane et al. (2013), National Research Council, (1996), Padulosi et al. (2011), Raneri et al. (2019) | 2; 3; 4; 5; 8; 9; 11; 12 | **5** |
| 102. Shea tree | *Vitellaria paradoxa* C.F.Gaertn. | 1 | 3 | Africa | Africa | National Research Council (2006) | 3; 11; 12 | **10** |

Source: 1, mainly wild; 2, mainly cultivated; 3, wild and cultivated. Edible parts: 1, leaves; 2, inflorescences/flowers; 3, fruits; 4, seeds; 5, roots/tubers; 6, stems/shoots. Number of uses according to Diazgranados et al. (2020); details on the type of uses for each species are reported in Diazgranados et al. (2020); 0, species not listed. When the common name of the NUS corresponds to more than one specific epithet, the number of uses is here reported as an average of the species listed in Diazgranados et al. (2020)

change over the century, including how climate change might impact the quality and nutritional value of edible species (Borrell et al., 2020). Studies in this research area have mainly focused on established domesticated edible crops. For example, under future climate-scenario drought stress conditions, Hummel et al., 2018 reported that iron levels in beans (*Phaseolus vulgaris*) decreased, while levels of protein, zinc, lead, and phytic acid increased. This study also revealed that bean nutritional quality and yields were reduced under future predicted drought conditions, leading the authors to conclude, with supportive data from crop modeling, that current bean growing areas in south-eastern Africa could become unsuitable by 2050. Given the predicted impact of future drought conditions on crops and, as 66% of people live with severe water scarcity for at least one month of the year and humans use 70% of available fresh water for agricultural purposes, the monitoring of water irrigation systems is a recommended strategy to help conserve water (Green et al., 2018).

Although future drought conditions have been suggested to increase protein levels in the legume species *P. vulgaris* (Hummel et al., 2018), in contrast, increased $CO_2$ levels were found to reduce protein levels and increase omega-3 fatty acid levels in mung bean (*Vigna mungo*; Ziska, Epstein, & Schlesinger, 2009). Environmental factors may also impact on the nutritional quality of edible nuts, including almonds, pistachios, and walnuts. For example, in 29 different cultivars, protein, phytosterol, and mineral content were affected, suggesting that climate change may also compromise

**BOX 1 Fungi as food resources**

Beyond the few species that are used in biotechnology for the production of pharmaceuticals, industrial enzymes and plastics (Howes et al., 2020; Prescott et al., 2018), the vast majority of fungi are underutilized. However, those in mainstream agriculture have an estimated annual market value of more than US$62 billion by 2023 (Knowledge Sourcing Intelligence LLP, 2017). As edible fungi are sources of fiber, selenium, potassium, copper, zinc, B group vitamins, and are one of the only non-animal sources of dietary forms of vitamin D, a deficiency of which is a risk factor for rickets in children (World Health Organization, 2019), the potential future use of neglected fungi is considerable. Indeed, during their growth stage and post-harvest, mushrooms exposed to sunlight or controlled levels of UV radiation had increased concentrations of vitamin $D_2$ (Cardwell, Bornman, James, & Black, 2018). The impact of UV radiation on the vitamin D content of mushrooms could be evaluated further as a strategy to enhance availability of dietary vitamin D, especially in regions where rickets or osteomalacia are health risks.

Around 2% of fungi form mutualistic mycorrhizal relationships with plants (Suz et al., 2018). Within these mutualistic relationships, the plant provides sugars in exchange for minerals and nutrients from the fungus. While some mycorrhizal fungi are often the most desirable fungi for consumption, they elude efforts, with a few exceptions, to be cultivated commercially (Boa, 2004). These desirable mycorrhizal species are instead foraged from the wild, based on distinct cultural practices. However, it is unknown if the impact of foraging on wild populations can be sustained into the future, where harvesting is likely to increase. Currently of concern is the Kalahari truffle (*Kalaharituber pfeilii*), which is sold in local markets in southern Africa, with a rapidly increasing commercial harvesting (Mogotsi, Tiroesele, et al. (2019) and references therein). In contrast, saprotrophic fungi are well suited to commercial myco-culture, and up to 200 species are known to be cultivated around the world. Over 85% of cultivated mushroom species belong to just five genera: *Agaricus* (button, portobello, and chestnut mushrooms), *Lentinula* (shiitake), *Pleurotus* (oyster mushrooms), *Auricularia* (jelly and wood ear fungi), and *Flammulina* (Enokitake; Royse, Baars, & Tan, 2017).

The cultivation of fungi represents an opportunity to develop valuable new crops that require low resource inputs, create little waste (SureHarvest, 2017), are sustainable, and can be tailored to local cultural preferences. Cultivation can be at the domestic and community level (Martínez-Carrera et al., 1998) and has the potential to be scaled up commercially (Zhang, Geng, Shen, Wang, & Dai, 2014). Importantly, new species are being brought into cultivation (Rizal et al., 2016; Thongklang, Sysouphanthong, Callac, & Hyde, 2014) and these have economic potential beyond the value of a few internationally grown strains (Hyde et al., 2019). For example, within the genus *Termitomyces*, species such as *T. microcarpus* and *T. clypeatus* are consumed across Africa and Asia (Boa, 2004) and bringing species from this genus into cultivation could be a desirable cash crop for local communities. Myco-agriculture is most diverse in China, with over 100 species of the 1,789 reported edible species already in cultivation and around 60% in commercial production (Fang et al., 2018; Zhang et al., 2014).

Finally, mycorrhizal fungal associations can also improve the nutritional quality of the edible parts of plant crops. For instance, mycorrhizal fungi inoculation of strawberries can increase the levels of anthocyanins and phenolic compounds, and in tomatoes can increase the levels of P, N, and Cu and flavour compounds (Torres, Antolín, & Goicoechea, 2018). More research is needed to understand the promising role that mycorrhizal fungi play in the nutritional value of edible plants, including NUS, particularly in the context of strategies to produce nutritious crops in a changing climate.

nutritional value in this food group (Rabadán, Álvarez-Ortí, & Pardo, 2019). Together, these findings suggest that different climatic factors could mediate contrasting effects on the nutritional value of crops, and this should be considered, separately for each species, with respect to NUS. Although some studies conclude that elevated atmospheric $CO_2$ reduces protein and mineral content in vegetables, $CO_2$ can enhance vegetable yield and concentrations of soluble saccharides, phenolic compounds, including flavonoids, and vitamin C, in addition to the antioxidant capacity (Dong, Gruda, Lam, Li, & Duan, 2018). Furthermore, flavonol and anthocyanin levels in fruits may be increased by changes in expression of hydroxylases in response to environmental conditions, including water deficits and UVB radiation (Martínez-Lüscher et al., 2014).

The impact of emerging environmental stresses on biologically active chemicals of edible plants is important from the perspective of human health. For instance, extreme environmental conditions (late season cultivation) have been shown to increase phenolic and vitamin C content in some broccoli cultivars (Vallejo, Tomas-Barberan, & García-Viguera, 2003). Higher $CO_2$ levels also increased vitamin C and antioxidant capacity in lettuce, celery, and Chinese cabbage, although other nutrients (micro- and macro-) decreased (Leisner, 2020). Thus, certain phytochemicals relevant to health in crop plants may be positively influenced by environmental changes, while levels of some essential macro- and micro-nutrients may be negatively affected. In view of the emerging research that suggests that certain environmental factors could negatively impact on the nutritional quality of food, the potential consequences for human health in the long-term are concerning, particularly against the backdrop of the global scale of malnutrition, which includes protein-energy, vitamin and mineral deficiencies (De Onis, Monteiro, Akré, & Glugston, 1993; Green et al., 2018; https://www.who.int/news-room/fact-sheets/detail/malnutrition). While biofortification could be one approach to mitigate the impact of climatic changes on food nutritional status (Green et al., 2018), more extensive scrutiny of the nutritional quality of crops, including NUS, in the context of predicted environmental challenges, should be aligned with other strategies for food security. In circumstances where saccharide levels increase in edible species in response to climate factors (Dong et al., 2018), the consequences should be considered in the context of providing energy as a source of calories in both undernutrition (such as in wasting and being underweight) and obesity, with the latter associated with increased risk of certain non-communicable diseases (https://www.who.int/news-room/fact-sheets/detail/malnutrition).

Potential strategies to ameliorate the effects of climate change on food security in the future include greater understanding of the global distribution of edible plants and by creating more diverse and climate-resilient agricultural production systems (see Table S1). In addition, improved knowledge of naturally stress-resistant plants and their broader cultivation would enable agriculture, and the human diet, to be diversified as one strategy for global food security in the changing environment (Zhang, Li, & Zhu, 2018), especially when aligned with methods to maintain the genetic diversity of crops (e.g., seed banking; Borrell et al., 2020). More research on elucidating the genes and processes that underlay the mechanisms for climate-resilience of edible species could also underpin future strategies to mitigate environmental challenges that threaten food security (Dhankher & Foyer, 2018). Indeed, a multi-faceted approach integrating physiology, genomics, and climate modeling has been proposed as important to develop a sustainable future food supply considering global climate change (Leisner, 2020).

To address the impact of climate change on nutritional security in the future, a model has been described (Fanzo, Davis, McLaren, & Choufani, 2018) to increase net nutrition in the food chain under climate change. This model encompasses agriculture practices to cultivate improved varieties, and new production locations to minimize loss of biodiversity, through to processing, distribution, marketing (including promotion of food benefits), and consumption strategies to maximize nutrition availability for vulnerable groups. A positive correlation between high agricultural diversity and high nutrient production, irrespective of farm cultivation size, has been suggested from global examination of food commodities (Herrero et al., 2017), indicating that one strategy to protect availability of nutrients may be through promoting agricultural diversity, and therefore, dietary range to support health.

Emerging evidence shows climate change impacts not only on food quality, nutrition, safety (Borrell et al., 2020), and cost, but also on the ability to transport food from "farm to fork," thus, for many communities, restricting their access to an adequate dietary range (Fanzo et al., 2018). These factors combined will limit the availability of nutrients with potentially serious consequences for the health of humanity.

## 5 | CONCLUSIONS

In this article, we provide an overview of the global state of edible plants, highlighting their diversity, and distribution among vascular plant families from around the world. We emphasize that this diversity stands in striking contrast with the few hundred food crops, originating from main domestication centers, that mainstream agriculture currently relies on. By integrating the other uses, we also highlight the additional ecosystem services these plants provide that are important for people's livelihoods and wellbeing (Díaz et al., 2020). While more work is needed to assess the actual conservation status of edible plants, ex situ conservation (and particularly seed banking) is already playing an important role in preserving them. However, information on the functional and genetic diversity of stored seed collections is limited and alternative ex situ conservation approaches, such as cryopreservation, need to be developed for those species with non-bankable seeds (Li & Pritchard, 2009).

We highlight key NUS of edible plants with the potential to improve the quality, resilience, and self-sufficiency of food production, while deploying a more sustainable local food supply. We also consider the importance of fungi, which could enhance the nutritional value of foods, through the provision of beneficial vitamins and minerals, and which have potential to be developed into valuable and sustainable crops.

However, before NUS can become successful crops of the future, many knowledge gaps need to be filled relating to their biology and ecology. In addition, research efforts are needed on understanding the impacts of climate change on NUS, to enable the development of effective and sustainable agricultural practices for future climate conditions (Turner et al., 2011; Ulian, Pritchard, Cockel, & Mattana, 2019). Although methods and tools developed by farmers and researchers for the cultivation of major crops can be easily adapted to improve the cultivation of NUS, these should be integrated with local traditional knowledge on uses and practices to help protect the environment and promote the conservation of biodiversity (Casas et al., 2016; Horlings & Marsden, 2011; Patel, Sharma, & Singh, 2020). To further aid the development of NUS as future crops, research programs need to be strengthened and the necessary research infrastructure put in place, including addressing shortages in relevant fields (FAO, 2019). This will require improved mechanisms for exchanging information rapidly and effectively, as well as increased awareness of the importance of crop diversity among and between stakeholder groups. One way this could be achieved is through participatory decision-making processes (Padulosi et al., 2011) and by putting in place effective legal and policy frameworks (FAO, 2019; Noorani et al., 2015) that are accompanied by economic incentives and subsidies to support the development of NUS (Padulosi, Cawthorn, et al., 2019).

Biodiversity offers a largely untapped resource to support our planet and improve our lives and has the potential to "end hunger, achieve food security and improve nutrition and promote sustainable agriculture," as articulated in the UN SDG 2, through the development of climate-resilient crops and the more widespread use of localized crop species (Antonelli, Smith, & Simmonds, 2019), such as the NUS plants highlighted in this article. However, in order for these natural resources to be unlocked, strengthening, and developing collaborations between producers, researchers, local communities, NGOs, "influencers," media, and governments are key factors for success.

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## AUTHOR CONTRIBUTIONS

T.U. and E.M. conceived and edited the manuscript. M.D., S.Pi., S.Pa., U.L., I.O., O.A.P.-E., S.S., and E.M. analyzed the data. All authors contributed to the writing of the manuscript and approved the final version.

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## SUPPORTING INFORMATION

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

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