



Review

Conservation and Use of Latin American Maize Diversity: Pillar of Nutrition Security and Cultural Heritage of Humanity

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Citation: Guzzon, F.; Arandia Rios, L.W.; Caviedes Cepeda, G.M.; Céspedes Polo, M.; Chavez Cabrera, A.; Muriel Figueroa, J.; Medina Hoyos, A.E.; Jara Calvo, T.W.; Molnar, T.L.; Narro León, L.A.; et al. Conservation and Use of Latin American Maize Diversity: Pillar of Nutrition Security and Cultural Heritage of Humanity. *Agronomy* **2021**, *11*, 172. <https://doi.org/10.3390/agronomy11010172>

Received: 14 December 2020
Accepted: 11 January 2021
Published: 18 January 2021

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Abstract: Latin America is the center of domestication and diversity of maize, the second most cultivated crop worldwide. In this region, maize landraces are fundamental for food security, livelihoods, and culture. Nevertheless, genetic erosion (i.e., the loss of genetic diversity and variation in a crop) threatens the continued cultivation and in situ conservation of landrace diversity that is crucial to climate change adaptation and diverse uses of maize. We provide an overview of maize diversity in Latin America before discussing factors associated with persistence of large in situ maize diversity, causes for maize landrace abandonment by farmers, and strategies to enhance the cultivation of landraces. Among other factors, maize diversity is linked with: (1) small-holder farming, (2) the production of traditional food products, (3) traditional cropping systems, (4) cultivation in marginal areas, and (5) retention of control over the production system by the farmers. On the other hand, genetic erosion is associated with substitution of landraces with hybrid varieties or cash crops, and partial (off-farm labor) or complete migration to urban areas. Continued cultivation, and therefore on-farm conservation of genetic diversity held in maize landraces, can be encouraged by creating or strengthening market opportunities that make the cultivation of landraces and open pollinated varieties (OPVs) more profitable for farmers, supporting breeding programs that prioritize improvement of landraces and their special traits, and increasing the access to quality germplasm of landraces and landrace-derived OPVs.

Keywords: agrobiodiversity; genetic erosion; maize breeding; maize landraces; maize races; open pollinated varieties; on farm conservation; plant genetic resources; value chain

1. Introduction

Maize (*Zea mays* L. subsp. *mays*) is the second most cultivated crop in the world, and together with rice and wheat, is one of the three major cereal crops. For one-third of the world's population, in sub-Saharan Africa, Southeast Asia, and Latin America, maize is the staple crop [1]. Latin America is the center of origin and diversity of maize [2]. Maize landraces, defined as “dynamic populations that have historical origin, distinct identity, lack formal crop improvement, and are often genetically diverse, locally adapted and associated with traditional farming systems” [3], are still widely cultivated in Latin America, mainly by small-holder and subsistence farmers [4]. The cultivation of landraces and open pollinated improved varieties (OPVs) is therefore tightly linked to food security of many Latin American countries, especially in low-and middle-income areas [5].

The conservation of maize landraces is extremely important because they contain the bulk of genetic diversity of this crop [6], and therefore are vital for overcoming current and future challenges to crop production and needs from consumers. There are numerous examples of extensive crop failure in maize in both the archeological record (e.g., the decline of ancient lowland Maya society, influenced by the interaction of the reliance on maize agriculture and extreme dry conditions [7]) and more recent events (e.g., Maize T-Cytoplasm crisis [8]) that underscore the importance of genetic but also cropping system diversity. Latin American maize landraces have been donors of useful traits for maize breeding, especially for enhancing food security, adapting agriculture to climatic changes, and achieving a more resilient and sustainable agricultural system [9,10].

Seed conservation of maize landraces in germplasm banks, storing dry seeds at subzero temperatures, is convenient because it stores many seed accessions in small spaces; seeds stored under those conditions can maintain high viability for the long-term and are available for breeders and farmers worldwide [11]. Nevertheless, ex situ seed conservation in germplasm banks should ideally be complemented with in situ, on farm conservation (i.e., “the sustainable management of genetic diversity of landraces by farmers within traditional agricultural systems” [12]), which allows landraces to evolve in their original area of distribution under selection by farmers and environmental factors; moreover, the populations' genetic diversity is much greater on-farm than in seed bank accessions [13].

Maize landraces are of great heritage value in Latin America, where they are linked to local and traditional products, and are important for food sovereignty and cultural identities [14–17]. Because of their fundamental importance for food security, plant breeding, and cultural identity, strategies are needed to support their sustainable and profitable on-farm cultivation and conservation. To the contrary, however, genetic erosion (i.e., “the loss of genetic diversity and variation in a crop” [18]), due to a plethora of causes, has been observed and raises concerns about the future of maize diversity in Latin America [13,19].

The objective of this review is to provide a current view of the conservation and uses of maize diversity in Latin America, with emphasis on maize for human food uses. After reviewing the diversity and uses of maize in Latin America, we examine literature on maize landraces for human consumption in the study area, highlighting evidence of: (1) current threats to maize diversity, (2) factors associated with large diversity of maize landraces, (3) potential measures to promote the sustainability and on-farm conservation of maize landraces, and (4) research projects, especially breeding programs, aiming at improving and promoting local landraces for human consumption. An overview of conservation of teosintes (maize wild relatives) is also provided.

2. Races of Maize in Latin America

Maize was likely domesticated from the wild teosinte *Zea mays* subsp. *parviglumis* H. H. Iltis and Doebley in the Rio Balsas area in Mexico (currently in the state of Guerrero) around 9000 years B.P. (years before present) [20]. Through human-mediated dispersal, maize traversed Central America by ~7500 years B.P., and spread into South America by ~6500 years B.P. [21]. Germplasm exchanges (also due to human migrations), crosses among different landraces, farmers' selections, adaptation to different climatic conditions,

and gene flow with wild relatives in Mesoamerica shaped the large diversity among maize landraces in Latin America [6,22].

Since the 1940s, efforts have been made to classify Latin American maize populations into different races. A maize race has been defined as “a group of related individuals with enough characteristics in common to permit their recognition as a group” [23]. Crop populations or landraces belonging to the same race show similar history, morphology, geographical distribution, and ecological adaptation, and a certain degree of genetic integrity [24]. The first volume of this series of classification works, *Razas de Maíz en México* [25] was published as a result of a collaboration among the Rockefeller Foundation and the Mexican Ministry of Agriculture. Subsequent books on maize racial classification in different American countries and territories were published by the National Academy of Sciences—National Research Council of the United States (NAS-NRC; see Races of Maize in Colombia [26], Races of Maize in Bolivia [27], Races of Maize in Ecuador [28], and Races of Maize in Venezuela [29]). Recent maize race classification efforts have mainly been led by national institutions in countries that were not fully covered by earlier studies (e.g., Uruguay [30] and Argentina [31]), or to update previous studies (e.g., Bolivia [32], Chile [33], Ecuador [34]).

Maize race classification efforts are based on four types of descriptors: (1) vegetative characters of the plant, (2) characters of the tassel, (3) internal and external characters of the ear, and (4) physiological, genetic and cytological characters [25]. In addition to those that conform to previously described races, many populations clearly result from deliberate or fortuitous crosses and introgression events among races, and more recently with improved cultivars [35]. Several races are thought to result from ancient crosses among more ancient races, for example the Mexican race ‘Chalqueño’ is very likely a cross between the races ‘Conico’ and ‘Tuxpeño’, these two being the result of crossing between ‘Palomero Toluqueño’ and ‘Cacahuacintle’, and ‘Olotillo’ and ‘Tepecintle’, respectively [25].

Some maize races occur in more than one country, for example, ‘Comiteco’, ‘Nal-Tel’, ‘Negro de Chimaltenango’, ‘Quiceño’, ‘Olotón’, ‘Serrano’, ‘Tepecintle’ and ‘Tuxpeño’ were collected both in southern Mexico and in Guatemala [36]. Similarly, in South America, especially in the Andean mountain range, several races are found in two or more countries, e.g., ‘Cuzco’ in Argentina, Bolivia, Ecuador, and Peru; ‘Chullpi’, ‘Chulpi’ or ‘Chuspillu’ in Argentina, Bolivia, Chile, Ecuador, and Peru; and ‘Sabanero’ in Colombia, Ecuador, Venezuela, and Peru [26–29,31,37,38]. Likewise, a few races (i.e., ‘Tusón’, ‘Cuba Yellow Flint’, and ‘Chandelle’) are found in the Caribbean islands and in some South American regions, especially in the coastal areas of Venezuela; it was speculated that those races derive from maize populations cultivated by the Taino-Arawak populations who lived in those regions prior to arrival of Europeans [29,39–41].

A few races with desirable agronomic characteristics were exported to countries outside their native range in recent decades. This is the case, for example, of the Caribbean ‘Tusón’ in Brazil and the Mexican ‘Tuxpeño’ in Ecuador [28,42]. Some races, such as ‘Tuxpeño’ [43], have been subjected to formal crop improvement giving origin to improved cultivars. Figure 1 shows ears of a few of the maize races mentioned in this paper, illustrating diversity for some broadly distributed grain types.

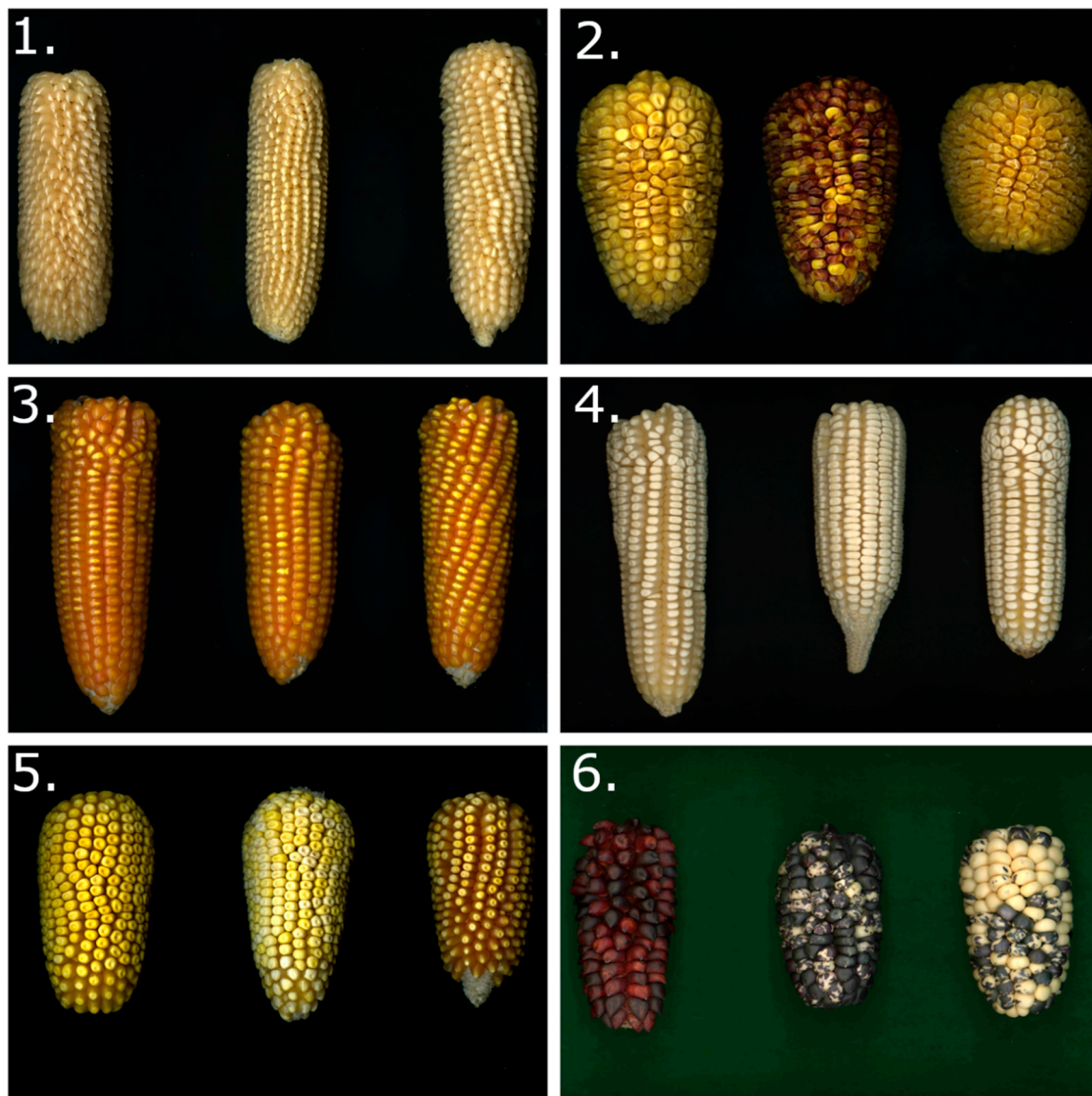


Figure 1. Maize races illustrating grain types: (1). Popcorn of the race ‘Pisingallo’ collected in Argentina (accession number: CIMMYTMA 29717), (2). Sweet corn of the race ‘Chullpi’ collected in Peru (CIMMYTMA 18213), (3). Flint corn of the race ‘Cuban Flint’ collected in Cuba (CIMMYTMA 2424), (4). Dent corn of the race ‘Tuxpeño’ collected in Mexico (CIMMYTMA 679), (5). Dent corn of the race ‘Conico’ collected in Mexico (CIMMYTMA 5645), (6). Floury corn of the race ‘Cuzco’ collected in Peru (CIMMYTMA 32058). These accessions are conserved in the germplasm bank of the International Maize and Wheat Improvement Center (CIMMYT, Mexico). Photo credits: CIMMYT germplasm bank.

Bedoya et al. [41] analyzed the genetic diversity and population structure of 194 native maize populations belonging to 131 distinct races from 23 countries of Latin America and the Caribbean. The races clustered in three main groups: (1) Mexico and Southern Andes (highlighting ancient and modern exchanges of germplasm between North and South America), (2) Mesoamerican lowlands, and (3) Andean (suggesting early introduction of maize in this area, with little mixing since then).

The countries with largest numbers of recognized maize races are Mexico, Peru, Argentina, and Bolivia (Table 1).

Table 1. Number of races of maize described in Latin America per country or region.

Country/Area	Number of Races	Reference
Argentina	43	[31]
Bolivia	40	[32]
Brazil	20	[42]
Chile	23	[33]
Colombia	23	[26]
Cuba	7	[39]
Ecuador	29	[28]
Guatemala	13	[36]
Mexico	64	[44]
Paraguay	10	[45]
Peru	52	[38]
Venezuela	19	[29]
Uruguay	10	[30]
West Indies	7	[40]

3. Uses of Maize Landraces for Human Consumption

Maize is the main staple crop in Latin America and the Caribbean, where almost 30 million tons of grain are annually produced on 10 million hectares [46]. Argentina, Brazil, and Mexico are among the 10 biggest maize producers in the world [47], while Mexico is where the most maize is produced for direct human consumption [48].

Maize landraces have multiple uses, mainly human nutrition and animal feed, but also, for example, maize husks (*totomoxle*) are used in Mesoamerica to steam in *tamales* or to conserve food, stems of particularly tall landraces are used to build fences, seeds and husks are used to create handicrafts, etc. [49,50].

Thousands of food products and recipes are made with maize landraces in Latin America. In Mexico alone, there are more than 700 ways of consuming maize [51]. The hundreds of food products made in Mexico with maize landraces can be grouped in 10 main categories: (1) tortillas, (2) corn on cob, (3) maize flour, (4) biscuits, (5) snacks (*botanas*), (6) soups, (7) *atoles* (maize-based beverages), (8) fermented beverages (such as *pozol* and *tesgüino*), (9) popcorns, and (10) *pinoles* (powders made from roasted corn) [52]. This amazing diversity of maize-based traditional products in Mexico is linked to the great grain diversity of maize landraces which gives particular textures, colors, and qualities to the end products. Grain physical traits, like hardness, size and color, and chemical characteristics like starch, protein or fat content determine the end uses. Races with grains of intermediate size and density are preferred for tortilla-making: these include 'Ancho', 'Apachito', 'Arrocillo', 'Azul', 'Blando', 'Bofo', 'Bolita', 'Conejo', 'Cónico', 'Elotero de Sinaloa', 'Gordo', 'Olotillo', 'Olotón', 'Pepitilla', 'Reventador', 'Tepecintle', 'Tuxpeño', 'Zapalote Chico', 'Zapalote Grande' [52,53]. For the preparation of *pozole*, a traditional soup in Mexico, the most used races are 'Ancho', 'Blando de Sonora', 'Bofo', 'Bolita', 'Cacahuacintle', 'Elotes Occidentales', 'Gordo', 'Harinoso de Ocho', 'Jala', 'Mushito de Michoacán', 'Tabloncillo', and 'Tuxpeño', that have large and soft grains [54]. In Bolivia, the races 'Chuspillu' and 'Kulli' are associated with the production of the famous fermented drink *chicha* [27].

Processing methods also contribute to the diversity of maize food products consumed in Mexico, Central, and South America. The main example of this is nixtamalization, a process originally developed in Mesoamerica and spread across all the Americas [17]. It is estimated that more than 300 food products in Mexico and Mesoamerica are derived from nixtamalization [55]. Nixtamalization consists of soaking and cooking grains in an

alkaline solution, usually calcium hydroxide, and de-hulling the grains prior to a wet milling process. Nixtamalization increases the nutritional value of the grain (especially increasing the availability of vitamins and minerals, ensuring high calcium intake, and reducing antinutrients like phytate), facilitates grinding of the grain, and reduces mycotoxin levels [17,52].

Maize also characterizes the cuisines of South American countries. In the Andean areas, maize landraces are the protagonists of many local recipes and are generally prepared as: (1) *maíz tostado* or *cancha* (toasted maize), (2) *choclo* (fresh maize), (3) *mote* (boiled maize), (4) beverages such as *api* or the fermented *chicha*, (5) popcorn, and (6) maize flour used to prepare several dishes [27,34]. It is noteworthy that several dishes in Mesoamerica and the Andean region are prepared with whole-kernel maize, which contributes to higher nutritional value [56]. In several other areas of South America, maize is used to prepare staple foods, e.g., *arepas* (a maize bread of Colombia and Venezuela) and *angu* (a thick maize porridge typical of Brazil). *Arepas* are consumed by 7 out of 10 Colombians during their breakfast; 75 kinds of *arepas* are recognized in Colombia, often linked with regions of the country, e.g., *arepa boyasence*, *costeña*, or *santanderiana*. Other traditional maize-based foods in Colombia include *champús* (a maize-based beverage), *mazamorra* (soup of cooked maize kernels), and *hojuelas* (sweet, fried maize flour) [57].

4. Genetic Erosion

Genetic erosion has resulted in loss of more than 70% of traditional crop genotypes and landraces in several areas of the world over recent decades [18,58,59]. The factors leading to maize landrace abandonment have been well studied in Mexico. Dyer et al. [13] estimated that the average number of maize varieties cultivated per farm in Mexico dropped from 1.43 to 1.22 in the recent 15 years. Consistently, a field survey in the Mexican state of Morelos, comparing seed collections made in 1967 and 2017 in the same study area, found that of the 66 farmer families originally cultivating 93 maize landraces, only 13 families still conserved a total of 14 landraces directly descended from the 1967 collection [60]. Likewise, while the maize race 'Jala' was historically the dominant maize grown in the valley of Jala in the state of Nayarit, Mexico, today it is grown by fewer than 20% of farmers and on only 5% of the maize cultivation area [61]. The most recent collection of maize races in Mexico [62,63], conducted 60 years after the first collecting mission [62], found only 51 of the 59 races originally reported in Mexico. Of the races still found, only 21 were well represented in the collected material, i.e., the collections of each one of these races represented a percentage of equal or more than 1% of the total collection [62]. In the Sierra region of Ecuador, the cultivation of races 'Canguil', 'Chaucho', and 'Clavito' has been greatly reduced in the last 60 years [19]. Overall, in several countries of Latin America, genetic erosion is perceived as a major threat for the conservation and exploitation of the genetic and cultural wealth of maize landraces [64].

The reasons leading to maize landrace abandonment are often complex and include agronomical, ecological, economic and social factors. One of the major reasons for landrace abandonment is their substitution with modern cultivars, including improved OPVs and hybrids, introduced since the 1950s [60]. Farmers' preference for hybrids over landraces is mainly due to: (1) agronomy, e.g., higher yields or disease resistance; (2) market factors, e.g., uniformity of quality or processing properties; (3) policy, e.g., subsidies for hybrids coupled with agricultural extension; or (4) commercial seed systems that favor the provision of few improved varieties in large quantities, while landraces' seed exchange is based on relations among farmers, friends, families, communities, and markets [60,65,66].

In several areas of Latin America, introduced improved cultivars have been under farmer selection for several generations and are now considered "creolized varieties", often cultivated together with traditional landraces [4,67,68]. Crosses among historically isolated landraces and introgression events between maize landraces and hybrids [69] are variously perceived as a threat or benefit to the genetic wealth of landraces [70,71]. Moreover, concerns have been raised about possible effects of the introduction of transgenic

varieties on the genetic diversity of landraces and wild teosintes in areas of crop origin and diversification, since presence of introgressed transgenic DNA constructs in native maize landraces has been reported in Mesoamerica [72]. Some farmers minimize introgression among maize populations by sowing different maize population at distance or in different periods to avoid simultaneous flowering or selecting ears and kernels with the characteristic features of a particular variety [69,73]. While some farmers maintain the differences among their landraces due to different flowering and maturation times [74], others deliberately seek inter-crossing and enhancement among landraces or between landraces and improved varieties. Farmers in Costa Rica, Honduras, Mexico, and Nicaragua often cross hybrids with landraces to combine the desirable characteristics of both parents [35,73,75]. In this creolization scenario of incorporating and adapting hybrids by the farmers, the distinction between landraces and improved maize varieties could eventually lose its significance and the introduction of hybrid varieties can increase genetic diversity of local maize populations [65]. In this framework, the coexistence of maize hybrids and traditional landraces in the same farming systems in Latin America has been demonstrated, due to their partial different functions in the livelihood strategies of smallholder farmers (i.e., hybrids being mainly planted for the market while landraces for self-consumption) [4]. In Bolivia, several rural communities are substituting their traditional maize landraces, cultivated for own-consumption, with improved varieties intended for the market. Considering that in the rural areas of Bolivia, 60% of the food consumed is self-produced, to improve food security, a coexistence between improved varieties for the market and landraces for self-consumption should be encouraged [76].

In addition to replacement with hybrids and improved OPVs, the abandonment of agriculture due to long-distance migrations, off-farm employment, increased urbanization, and decreasing appeal of farming are influencing the abandonment of maize landraces in many areas. Some of these phenomena have been partially attributed to the opening, in the last decades of the twentieth century, of several Latin American countries to the global markets through macroeconomic policies. While some authors demonstrated that those policies reduced the prevalence of small-holder farming, a great persistence and adaptability of small-holders in heterogeneous and regionally differentiated maize farming systems has also been reported [77]. Another reason for landraces' abandonment is to replace them with cash crops including flowers, fruits (avocado, blackberry, lime, mango, papaya), industrial crops (e.g., sugar cane), and vegetables (e.g., onion) [60,78–81].

Finally, the impact of climate change on maize genetic diversity can be substantial and needs to be further studied, especially in small-scale farms that depend on rainfall for maize cultivation [82]. Acevedo et al. (2020, [83]) recently surveyed literature and identified major determinants for farmers' adoption of climate resilient varieties or crops, i.e., climate-change-related drivers for replacing previously preferred varieties or crops.

5. Conservation

Strategies to conserve maize diversity should include complementary in situ and ex situ measures [9,84]. Ex situ, long-term seed conservation of maize genetic resources is conducted by the germplasm bank of the International Maize and Wheat Improvement Center (CIMMYT), which holds 26,564 accessions of maize from Latin America and the Caribbean. CIMMYT also realizes repatriation of seed accessions to their country of origin (e.g., Guatemala [85]). Several national germplasm banks e.g., the banks of the *Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias* (INIFAP), University of Guadalajara, and University of Chapingo, in Mexico, *Instituto de Ciencia y Tecnología Agrícola* (ICTA) in Guatemala, *Instituto Nacional de Innovación Agraria* (INIA) in Peru, *Instituto Nacional de Tecnología Agropecuaria* (INTA) in Argentina, and National University in Colombia, also conserve seeds of national maize landraces. Additionally, community seed banks (CSB), i.e., small-scale local organizations that conserve seeds of landraces and wild useful plants on a medium-term basis (2–10 years) and serve the needs of local communities, have an

important role in community seed security and seed conservation of maize landraces and wild relatives in several countries of Latin America [86].

As discussed above, *ex situ* conservation must be complemented with *in situ*, on-farm conservation to enable the continued adaptation of landraces and the preservation of traditional knowledge and heritage values of those traditional varieties [12].

5.1. Conservation of Teosintes

The secondary gene pool of maize is represented by eight taxa of wild teosintes found in Mexico and Central America [87]. These comprise three wild subspecies of *Z. mays*: *Z. mays* subsp. *huehuetenangensis* (Iltis and Doebley) Doebley (narrowly endemic in western Guatemala), *Z. mays* subsp. *mexicana* (Schrader) Iltis (endemic in the highlands of central and northern Mexico), and *Z. mays* subsp. *parviglumis* (ancestor of domesticated maize and endemic in western Mexico). The other four species of teosinte are: *Z. diploperennis* Iltis, Doebley and Guzmán (endemic in two locations in the Mexican states of Jalisco and Nayarit), *Z. perennis* (Hitch.) Reeves and Mangelsdorf (endemic in two locations in the Mexican states of Michoacan and Jalisco), *Z. luxurians* (Durieu and Ascherson) Bird (native to southern Mexico, southeastern Guatemala, Honduras, and El Salvador), *Z. nicaraguensis* Iltis and Benz (restricted to few locations in northwestern Nicaragua), and *Z. vespertilio* Gómez-Laurito (restricted to a very small population in the Murcielago Islands in Costa Rica) [88]. Teosinte taxa represent an important resource for maize breeding and have been successfully employed to breed for resistance to biotic stresses, flooding and waterlogging tolerance, and increased yields. Only four germplasm banks hold significant teosinte collections, namely CIMMYT, INIFAP, University of Guadalajara (Mexico), and USDA-ARS (U.S. Department of Agriculture-Agricultural Research Service, USA) [87]. Further collecting missions should collect populations and species underrepresented in current collections, e.g., *Z. diploperennis*, *Z. perennis* and wild *Z. mays* populations from Guatemala and northwest Mexico. Several teosinte populations have already disappeared or are endangered due to overgrazing, use of herbicides, mechanical tilling, or the increasing cultivation of maize or fruit crops in their natural habitats. For these reasons, *in situ* conservation measures are urgently needed, especially for narrowly distributed species. Examples of *in situ* reserves for teosinte conservation are the *Reserva de la Biosfera Sierra de Manantlán*, in Jalisco (Mexico), where *Z. diploperennis* is preserved, and the *Reserva de Recursos Genéticos de Apacunca*, in Nicaragua, where *Z. nicaraguensis* is preserved [88].

5.2. Where to Find Maize Landraces Diversity

The cultivation of maize landraces in Latin America is mostly done by small-holder and subsistence farmers and linked to cultural preferences including traditional food products [4,49]. Smallholder farmers often cultivate more than one landrace of maize [13,89]. Most of the landraces have multiple purposes, however some of them are particularly suited and preferred for specific food products thanks to their organoleptic characteristics [90,91].

Maize landraces are often grown in traditional cropping systems, for example, maize landraces in Mesoamerica are closely associated with *milpa*, a poly-cropping system with maize, beans, and squashes [17,91]. Similarly, in parts of South America, such as the highlands of Ecuador, maize landraces are often cultivated in poly-cropping systems associated with common bean, fava bean, green pea, and fig-leaf gourd. In the highlands of Colombia, maize landraces are cultivated associated with beans and cucurbits. In these systems, the crop residues are often grazed by farm animals [19].

Landraces are common in some marginal areas (e.g., inaccessible areas, low input conditions, low-quality soils), where they may outperform available hybrids [68,92–94], or where investment in hybrid seed is unprofitable. Farmers cultivating in unpredictable environments (as in the case of Yucatecan Mayan farmers in Mexico) often plant a wide diversity of maize landraces with a range of agronomic features, to minimize harvest risk and enhance their food security [89].

Cultivation of landraces is also associated with the interests of some farmers and communities to retain control over their production systems [68], because maize landrace cultivation relies on seed saved from the previous harvests and on farmer-to-farmer seed flow (see e.g., [90] for Mexico; [35] for Central America; [95] for Peru).

5.3. How to Promote On-Farm Landraces Conservation

Crop genetic diversity can be considered a public good due to its importance for food and nutritional security, tradition, and cultural identities. Crop genetic diversity is also the source of crop improvement. Nevertheless, its maintenance is not always profitable for farmers and is not always a priority for the public sector [96]. A recent federal law in Mexico aims to promote the conservation of native maize landraces through both on-farm conservation and community seed banks, and to guarantee the access of every citizen to native maize and its products [97].

Public interventions to support on-farm conservation of maize landraces need to begin by determining whether the genetic erosion in farmers' fields is driven by lack of demand or supply of maize diversity in a specific area [65]. In case of lack of demand for maize landraces, developing market channels for local products, linked with educational and promotional campaigns to expand the demand for landraces, can increase the value of these traditional varieties. Establishing links between landrace cultivation and markets can promote their cultivation and on-farm conservation while improving farmers' livelihoods [79,94]. In some countries, maize landrace cultivation has been recently stimulated by links to traditional food production and niche markets, for example beaked maize for the production of *polenta* in northern Italy [69], 'Millo Corvo' for the production of maize bread in Spain [98], and blue maize from Mexico for national and international restaurants [94]. Maize landraces connected with traditional food products, such as blue maize and maize for *pozole* in Mexico, can command higher prices when sold to specialty markets than maize grain sold to commercial markets, improving livelihoods of small-holder farmers and enhancing on-farm conservation of those landraces [50]. A recent study [99] demonstrated that, in peri-urban areas near Mexico City, consumers were willing to pay more for tortillas made with blue rather than white or yellow maize; consumers reported limited access to blue maize tortillas and insufficient knowledge about product availability, suggesting a considerable demand-side opportunity for expansion of blue maize. This market opportunity, however, is limited by challenges on the supply side, i.e., grain heterogeneity, variable and insufficient production, and lack of farmer aggregation and connectivity to markets.

Maize cobs, grains, and food products derived from Ecuadorian landraces are being exported to other South American countries (e.g., Chile [100]), the United States and Europe [101,102], in these last cases often in connection with demand from migrant communities. Overall, five percent of floury maize produced in the mountains of Peru is exported, 28% as fresh corn (*choclo*) and 72% as dry grains. In 2019, the export of Peruvian floury maize was directed towards Belgium, Canada, Chile, Colombia, France, Germany, Guatemala, Italy, Japan, Spain, United Kingdom, and USA [103]. These examples demonstrate that local and international market opportunities exist for Latin American maize landraces. To date, most such value chain opportunities have evolved without outside investment or stimulus; it is likely that appropriate public and private interventions to provide financial and business opportunities can strengthen value chains connected with maize landraces, produce revenues for local farmers, and consequently enhance on-farm conservation [79]. The creation of collective brands for products derived from maize landraces and the development of quality and origin certificates can benefit their market value [52].

If the abandonment of maize landraces by farmers is due to difficulties in obtaining seed, measures to improve the accessibility of landraces' seeds, such as community seed banks (CSB) could be established or supported [104,105]. Networks of CSBs are active in several areas of Latin America, including Huehuetenango, Guatemala [104], Oaxaca, Mexico [106,107], Nueva Segovia and Madriz, Nicaragua [108], and Honduras [109]. Agro-

biodiversity fairs with seed exchanges among farmers can also increase the availability of maize landraces [65].

In western Guatemala, a scheme of payment for ecosystem service (PES) offered technical support and agricultural supplies to farmers' communities that cultivated maize landraces considered as endangered in the area. A fraction of the seed harvested was stored in community seed banks, while another fraction was left available for seed exchanges among farmers. Cobs of the target landrace were displayed in the local agrobiodiversity fair where seed samples of those landraces were distributed to local farmers [110]. Similar PES schemes were applied in Cotacachi, Ecuador to enhance in situ conservation of maize landraces. These experiences suggest that PES can play an important role in upscaled, on-farm maize conservation programs [111].

The reduction in government policies and programs that subsidize maize hybrid cultivars and incentivize farmers to replace landraces, and increased incentives for landrace cultivation have been proposed as ways to reduce genetic erosion [65,112]. Additionally, the registration of landraces or improved OPVs in national catalogues of crop varieties is essential in many countries for promoting the commercialization of quality-declared or certified seeds, and their accessibility to farmers [113].

Breeding programs can enhance the productivity and cultivation of landraces by local farmers [65]. Participatory breeding (a strategy of breeding in which farmers and researchers work together in the breeding process [114,115]) can encourage the cultivation of locally improved landraces and OPVs enhancing on-farm conservation of maize genetic resources [116]. Participatory breeding or selection approaches have been applied in several Latin American countries, e.g., Brazil [42], Bolivia [117], Cuba [118], Guatemala [119], Honduras [120], Mexico [94,121].

6. Breeding Programs of Maize for Human Consumption in Latin America

The demand for maize in low- and middle-income countries is expected to double by 2050, while the impacts of climate change will cause yield declines on average 10% if actions are not taken. For landraces to remain a viable, attractive option for farmers of many communities in Latin America, improvements for higher yields and resistance to climate-change-driven stresses will be needed, or essential [48,122,123].

Several breeding programs in Latin America have focused on improving traditional maize landraces and developing improved OPV or hybrid varieties from them. The focus of maize improvement has been increased yield. While hybrid varieties often have a yield advantage, up to 50%, compared to landraces and OPVs, their advantage is greatest in high-yielding environments where return on investment in seed and other inputs is most assured. As a rule, a good hybrid will out-yield a good OPV, which will out-yield a good landrace [124,125]; however, in marginal, stressed environments, appropriate hybrids and OPVs may be unavailable and landraces are sometimes competitive or outperform the available hybrids and OPVs [124].

The need to purchase fresh seeds of hybrids for every planting represents a considerable investment for farmers, particularly resource-poor farmers who cannot afford the risk of not recovering this investment in case of a poor harvest or unfavorable market conditions for their harvest. In this scenario some farmers resort to "recycled hybrid seeds" i.e., saving seeds from previous harvest for planting in the next season [126]. The use of recycled seeds leads to inbreeding depression and yield reduction, as high as 35% for single-cross hybrids, but which is negligible for OPVs in the same conditions [124]. Moreover, in some farming systems of low- and middle-income countries, especially where average yields are low (e.g., 1.5 t ha^{-1}) and the prices of hybrid seeds and fertilizers are high relative to the price of grain, highest return on investments may accrue from using improved OPVs seeds, that are cheaper and can be recycled with negligible yield losses [125]. This highlights the importance of OPVs for resources-poor farmers in conditions of highly uncertain yield, e.g., drought-prone areas, or widely fluctuating market price for their harvested grain [124].

Considering the challenges from changing climate, the economic constraints that make hybrids a risky option for some farmers, and our earlier discussion of special characteristics that offer market opportunities for landraces [65], breeding programs focused on developing resilient OPVs (and eventually hybrids) with the preferred quality traits for specific end-use applications can have desirable impacts on farmers' livelihoods and maize diversity conservation [56,127].

The next paragraphs present examples of Latin American breeding programs to improve maize for human consumption, starting mainly from local landraces.

6.1. Bolivia

Few research centers conduct breeding activities on maize for human consumption in Bolivia; the two most active are the National Institute of Agricultural and Forestry Innovation (*Instituto Nacional de Innovación Agropecuaria y Forestal*, INIAF) and the *Centro Fitotécnico y de Semillas Pairumani* (CFSP).

To address the lack of certified seeds available to local farming communities, INIAF, through the National Maize Program (*Programa Nacional de Maíz*), conducts breeding programs to improve native germplasm and provide certified, quality seed of landraces. Approximately 100 accessions of native maize landraces were collected in several areas of the country, especially in the chaco boliviano, Pasorapa-Cochabamba, and the Valley of Tarija, and are currently conserved in the INIAF germplasm bank. Those accessions are the base of INIAF's breeding efforts. Overall, five improved OPVs, selected from native germplasm, were registered in the National Seed Register (*Registro Nacional de Semilla*, RNS). Additionally, the INIAF is characterizing six native races that are particularly valued by local farmers, namely 'Canario', 'Gateado', 'Kulli Criollo', 'Overo', 'Pisankalla', and 'Pistacho'. The aim is to register these as varieties and provide quality seeds to farmers, since there is a lot of demand in the local market for those races, but germplasm with a high level of purity is unavailable. Seeds of some of those varieties, including 'Overo' and 'Pisankalla' are already being produced by farmers' associations in the Valley of Chuquisaca. Seeds of other native landraces that are valued for food production and market are being produced in the chaco de Camiri, Chuquisaca, Yacuiba, and in the Tarija and Cochabamba Valleys.

The CSFP, offers to interested Bolivian farmers, as part of a conservation program, seeds of racial pools of 5 native races. Those pools were created with the best seed collections obtained per each variety in their areas of origin. The three most requested racial pools are 'Hualtaco', 'Huillcaparu', and 'Kulli'; 'Morochó' and 'Blando Cruceño' are also available. Additionally, 72 native landraces were evaluated, 9 of those were selected to breed new disease-resistant and short-season varieties.

6.2. Colombia

Breeding programs of maize for human consumption in the tropical highlands of Colombia focus on different types of maize, according to the needs of local farmers in different geographical areas. The preferred kernel types are mostly floury and flint, white or yellow, with large grains for use as fresh corn.

In the last 40 years, Colombian maize breeding programs registered 23 improved maize cultivars for the tropical highlands in the national inventory of *Instituto Colombiano Agropecuario* (ICA). The breeding methods to develop these cultivars were generally mass selection and recurrent selection, especially by half-sibs. The most widely adopted OPV obtained through these efforts is 'ICA V-508', commonly known as 'Bogotano'. This variety is characterized by semi-conical ears with large, yellow grains; it is cultivated and commercialized in many Departments of Colombia to produce *chocolo* (fresh ears). Another successful OPV, 'ICA V304', is cultivated to produce *arepa santanderiana* or consumed as *chocolo asado* (fresh ears for roasting).

In the tropical lowlands, cultivars for human consumption, especially sweet and biofortified maize, have been selected in the past 10 years. Sweet corn is consumed fresh

(chocolo), and while it covers only 1% of the maize cultivation area in Colombia, it has great economic potential. Several efforts are ongoing to decrease the impact of corn stunt disease, which is the major problem in Colombia's sweet corn producing areas. AGROSAVIA (*Corporación Colombiana de Investigación Agropecuaria*) developed, using inbred families, two sweet corn OPVs, 'CORPOICA V-115' and 'CORPOICA V-116', based on US and national germplasm. 'CORPOICA V-114' and 'CORPOICA V-159' are two other OPVs released by AGROSAVIA with yellow and white kernels, respectively, best suited for consumption as fresh corn, but also good for making *arepas*.

The cultivation of nutritionally-enhanced, or 'biofortified' maize cultivars in Colombia is becoming important in the tropical lowlands, where such cultivars have been recently released. Current biofortified cultivars contain 50% more zinc (Zn) than non-biofortified cultivars. The goal of research and breeding on biofortified maize in Colombia is to produce and commercialize maize cultivars that can help solve the problems of Zn deficiency, which affect 22% of the national population and more than 60% in the Pacific coast and Amazonia regions [128]. Biofortified maize in Colombia is developed by the Harvest Plus project, led by CIMMYT, from where the initial germplasm was introduced. One OPV was selected and registered at ICA as 'BioMZn01' to be cultivated in the Cauca Valley. The biofortified hybrid 'SGBIOH2' was selected for the coffee-producing zone of Colombia (*Eje Cafetero*) from germplasm introduced from CIMMYT, Mexico. Grain of these biofortified cultivars can contain 34 ppm of Zn, which compares to an average of 22 ppm for non-biofortified cultivars.

6.3. Ecuador

Ecuador's National Institute of Agricultural Research (INIAP, *Instituto Nacional de Investigaciones Agropecuarias*) has worked since 1959 on the genetic improvement of maize for human consumption. INIAP's National Maize Program has four research stations (two in the lowlands and two in the highlands) and is supported by other Departments at INIAP. Moreover, some breeding work is conducted in collaboration with universities. Such collaborations have included the development of a purple maize population, led by the *Universidad San Francisco de Quito* [129,130], the evaluation of native maize conducted by the *Universidad Central del Ecuador* [131], and the improvement of the local varieties 'Blanco de Leche' and 'Canguil' by the *Universidad Estatal de Bolívar* and the *Universidad Técnica del Norte*, respectively.

INIAP has released six varieties of maize for human consumption in the last 20 years, most of them adapted to cultivation in the highlands (> 2000 meters above sea level.). Maize breeding for the highlands mainly starts with local germplasm and uses participatory methods with groups of farmers [132]. The breeding process begins by collecting ears of a maize landrace, evaluating and characterizing the morphological and genetic variability [133,134], and making a balanced seed bulk from selected ears to form a population. This population is subjected to several cycles of modified half-sib selection [135], and once the open pollinated population is uniform, stable and distinguishable, it is evaluated for registration with the Intellectual Property National Institute (SENADI, *Servicio Nacional de Derechos Intelectuales*) and the Ministry of Agriculture (MAG, *Ministerio de Agricultura y Ganadería*). The new OPV is released through field days and other technology transfer events. The main breeding goals of the Maize Program in the highlands are to preserve the characteristics of each landrace (type and color of grain), increase yield, and incorporate resistance to diseases, especially ear rot and viral diseases [136,137]. Currently, the Program is breeding landraces of 'Chulpi', 'Blanco de Leche' and 'Canguil' in collaboration with local universities.

The Maize Breeding Program of INIAP in the lowlands develops maize genotypes for human consumption based on OPVs and hybrids introduced from CIMMYT. 'INIAP-543QPM' is an OPV developed for human consumption; it has white dent kernels, enhanced nutritional content (QPM: quality protein maize), and is intended for fresh corn production [138]. This OPV was developed by participatory half-sib selection for at least two years in several locations, and then registered at SENADI and MAG. INIAP has also developed a

white flint hybrid for the food industry (for producing flour and other products), named ‘INIAPH-248’ [139]. After its introduction from CIMMYT’s program in Colombia, the hybrid and parent lines were evaluated at several locations for four years before the new hybrid was registered and released.

6.4. Mexico

In Mexico, INIFAP (*Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias*) and different public governmental institutions and universities like the Antonio Narro University (UAAAN), University of Guadalajara, *Colegio de postgraduados* (COLPOS), and Chapingo University, have contributed to landrace improvement. Using recurrent selection, limited back-crosses, pre-breeding, and participatory breeding, OPVs, hybrids and populations have been selected from landraces. See [140] for a detailed review of landrace improvement in Mexico.

‘Tuxpeño’ is one of the most productive maize races in the world. Tuxpeño Crema 1 and La Posta populations were generated in Mexico in the 1950s by a collaborative program of researchers from the Office of Special Studies and the Rockefeller Foundation. This was done by the recombination of outstanding maize collections or lines derived from ‘Tuxpeño’ [141]. These populations and derived germplasm have been widely distributed throughout the world by CIMMYT.

The varieties ‘V-229 B,’ with white grain, and ‘V-231 A,’ with yellow grain, released in the state of Chiapas, were selected from the recombination of 10 and 9 collections, respectively, of race ‘Comiteco’ [142,143]. Three cycles of half-sib selection were applied during their development. Both varieties promise to increase production in the Comiteca Plateau, in Chiapas.

Several varieties, derived from native maize races by convergent-divergent mass selection, have been released in the state of Guerrero; these include ‘V-236 P,’ from the race ‘Pepitilla,’ with high quality for making nixtamalized foods [144], ‘V-237 AN,’ from the race ‘Ancho,’ with quality for making *pozole* [145] and ‘V-239 AZ,’ characterized by blue kernels with good quality for nixtamalization and making various typical dishes [146]. These varieties offer added market value alternatives for maize in the state of Guerrero.

The variety ‘Jaguan’ was selected from the landrace ‘Jagüey,’ which belongs to the race ‘Cónico Norteño’ [147]. This OPV is recommended for rainfed maize producers in the state of Coahuila.

Pre-breeding efforts in the highlands of Mexico, starting from various accessions of the INIFAP Germplasm Bank, have improved flowering time in the races ‘Bolita,’ ‘Celaya,’ ‘Cónico,’ ‘Cónico Norteño,’ ‘Elotes cónicos,’ and ‘Tuxpeño,’ and various traits for yellow, blue, and white maize [148].

As previously mentioned, CIMMYT has developed several hybrids and OPVs selected from landraces and adapted to the different environments of Mexico (highland, subtropical and tropical) [149]. Moreover, CIMMYT has implemented landrace participatory breeding projects with Mexican farmers and national breeding and researcher institutions (e.g., Chapingo University, COLPOS, INIFAP). Participatory approaches focused on traits prioritized for improvement by the community (e.g., decreased plant lodging, barren plants, or ear rots), without diminishing valued traits, such as grain type. At the same time, these projects worked to connect farmers with high-end markets (e.g., national and international restaurants), and to empower small-scale farmers to create a certification system for native landraces [94].

Various projects with farmers in the Papaloapan (humid tropics), Costa (dry tropics), Valles Centrales (subtropical), and Mixteca Alta (high valleys) regions of the state of Oaxaca have, since 2009, implemented participatory breeding, in situ conservation, and use of the genetic diversity of maize for the benefit of producers [150]. These initiatives included pre-breeding work for OPVs and hybrids at CIMMYT and on farm work led by the University of Chapingo, including collections of landraces, testing of newly developed cultivars, processing and delivering of certified seeds to farmers at reasonable prices. These projects

involved collaborations among public maize research centers, farmers, extension workers, and governmental development agencies. Such integrated efforts are useful examples of projects to enhance the use and conservation of maize diversity.

Started in 2015, CIMMYT's blue maize improvement project is an example of breeding maize for specialty markets. The project is based in Mexico, where blue-grained maize is traditionally used for various food products. Blue maize is perceived by many consumers as better tasting and more nutritious than white maize [51,99]. Although Mexico is the primary target for the improved blue grain varieties, the potential beneficiaries include farmers in Central America and the Andean countries of South America, who have extensive areas where blue maize is also desirable. Blue maize is being developed for three growing environments: (1) winter-planted coastal areas of northwest Mexico, that are 100% irrigated, (2) summer-planted mid-altitude (~900 to 1800 m) areas of central and south-central Mexico, that are mixed irrigated and unirrigated and, (3) highlands of central Mexico, that are ≥ 2000 m in altitude and mostly rainfed.

The objective was to develop a single breeding pipeline to develop two distinct products: (1) inbred lines and hybrid combinations that could be commercialized by small and medium sized national seed companies, and (2) improved OPVs that could be distributed to farmers at low or subsidized cost. The primary objective was grain suitable for production of nixtamalized products such as tortillas. For these products, the deposition of color needs to be in the aleurone so that the color is not quickly leached during the nixtamalization process. Secondary, lesser effort was put into varieties with the deposition of color in the pericarp, which allows quick extraction of the anthocyanin from the grain into water; these materials are for extracting anthocyanins for use as natural colorants or in food products targeting healthy living [151,152].

CIMMYT's primary focus is on developing maize with white grain, because this is the preferred color for food products in most of Latin America and East Africa, followed by a much smaller effort on yellow grain maize. Blue grain maize has not been a target except in a very small project, developing blue varieties for the Mexican highlands. Therefore, seven subtropical and three highland landraces previously identified for having higher than average levels of anthocyanins were used as the initial sources of blue grain color. The subtropical landraces were crossed to elite white grain CIMMYT inbred lines, while the highland landraces were crossed to experimental highland blue inbred lines not yet released by CIMMYT. Additional landraces with blue grain color have been used during the life of the project. The breeding strategy first focuses on developing inbred lines fixed for blue kernel color. During development, the experimental lines are evaluated for yield and agronomic performance in testcross trials. This approach allows fixing of the desired blue color, as many landraces have variation in the shade of blue and kernels with other colors, while identifying and fixing alleles associated with improved agronomy and higher yield potential. Once inbred lines with the desired color, yield potential and agronomic performance have been identified, the best lines are recombined to form experimental OPVs for testing before distributing the best to farmers who do not wish or cannot afford to purchase hybrids. As of the end of 2020, three years of yield trials of blue hybrids have been completed both for the northwest coastal winter environment and the mid-altitude summer environments of Mexico. Second year yield trials for the highland environments will be conducted in summer of 2021. Limited sales of blue grain hybrids by seed companies may begin in the winter of 2021–2022 for the northwest coastal environments and in summer of 2022 for the mid-altitude environments. Highland hybrids will likely be available in summer of 2024. The first OPVs will be available in the summer of 2024.

6.5. Peru

Breeding maize for human consumption in Peru is mainly conducted by La Molina National Agrarian University (UNALM, *Universidad Nacional Agraria La Molina*) and the National Institute of Agrarian Innovation (INIA, *Instituto Nacional de Innovación Agraria*). Floury maize is particularly important for food security in Peru and is cultivated yearly by

310,000 families [153]. Three main types of maize, based on the characteristics and uses of the grains, are subjected to breeding efforts: *maíz choclero*, for consumption as fresh corn or as *mote* (grains processed to eliminate the pericarp, consumed boiled); *maíz canchero*, consumed as toasted grains; and *maíz morocho*, flint corn consumed as *mote*. Other specialty maize considered for breeding programs include purple and black maize (*maíz morado*), with high concentrations of anthocyanins, for the production of *chicha morada* and the race 'Chulpi' for consumption as *cancha* (toasted grains).

Starting from the 1960s, the UNALM has employed mass selection for the improvement of landraces, and half-sib schemes to develop composite varieties and synthetics. INIA started its maize breeding activities in the 70s with half-sib selection to develop six Peruvian maize complexes for use as genetic reservoirs to develop improved varieties. Three types of maize, *choclero*, *canchero*, and *morocho*, and both early- and late-maturity were considered. Recurrent selection methods were used to improve purple and black maize varieties with high levels of anthocyanins, and 'Chulpi'. In the last few years, inbred family selection was also used to develop synthetic and hybrid varieties of *choclero* and of maize with high concentrations of anthocyanins. As a result of these breeding efforts, 30 improved maize cultivars have been registered in the Peruvian Register of Commercial Cultivars (*Registro de Cultivares Comerciales*) since 1983. Overall, 15 cultivars registered by INIA comprised 5 of *maíz choclero*, 6 of *maíz canchero*, 2 of *maíz morocho* and 2 cultivars for production of *chicha morada*. There are plans to promote the cultivation and consumption of the purple variety 'INIA 601' at national and international levels, to improve the livelihoods of Peruvian farmers. This variety, selected by the half-sib method, contains a very high level of anthocyanins, known to have beneficial effects on human health [154]. The other 15 improved cultivars were registered by UNALM: 13 of *choclero*, one of *canchero* and one cultivar for producing *chicha morada*.

These 30 varieties are adapted to altitudes between 2500 and 3600 m.a.s.l. and achieve yields of 3–8 t/ha, much higher than the national average of 1.54 t/ha [153].

7. Conclusions

Latin America is the center of domestication and diversity of maize, the second most cultivated crop species at global scale. Maize landraces of Latin America are of great importance as sources of useful genes for breeding (e.g., to overcome challenges from changing climate), for food and nutritional security in many low- and middle-income areas, and as intrinsic to cultural identities. Maize landraces are pillars of human heritage and future human nutrition security.

Conservation of maize landraces in germplasm banks is crucial to ensuring the preservation and availability of their diversity for future generations. In situ conservation of landraces, however, is also highly desirable because it enables the continued co-evolution of maize with changing climate and farmer preferences. Landrace cultivation, and therefore in situ conservation of maize diversity in Latin America is linked to: (1) small-holder farming, (2) the production of traditional food products, (3) traditional cropping systems, (4) cultivation in marginal areas, and (5) retention of the control over the production system by the farmers.

According to many authors, the main threat to the cultivation and on-farm conservation of maize landraces in Latin America is the substitution by or introgression with hybrid cultivars. Nevertheless, several examples of co-existence of maize landrace and hybrid cultivation signal different functions and value for each. Replacement of landraces with higher-yielding hybrid cultivars, for example, can be an important component of strategies to achieve national food and nutrition security.

Farmers must be offered and must pursue options to improve their livelihoods. Current options include switching to hybrid maize cultivars, cash crops, or seeking off-farm employment. If in situ conservation of landraces and their genetic diversity are valued by society, mechanisms must be implemented to make their cultivation an attractive livelihood option for the farmers who grow them.

Options that enhance the sustainability of landrace cultivation, and therefore their on-farm conservation, include: (1) strengthening market opportunities for landraces (including increase knowledge of nutritional and end use quality of landraces), to make the cultivation of maize landraces and OPVs not only important for subsistence farming, but also profitable for local farmers, (2) strengthening breeding programs that develop improved OPVs starting from local landraces, and make their seed available to resource poor farmers, and (3) increasing the access by local farmers to quality germplasm of maize landraces and OPVs through e.g., community seed banks, agrobiodiversity fairs, and registration of landraces and improved OPVs to national germplasm catalogues. Integration of these strategies, encouraged by public interventions, such as payments for ecological service (PES), and collaboration between different actors and stakeholders (e.g., farmers, consumers, breeding and research centers, policy makers, food manufacturing sector) could enhance the livelihoods of resource-poor farmers who are currently the guardians of in situ maize diversity, and avoid losses of these priceless genetic resources, as well as the agronomic, biological, and cultural diversity that is connected with them.

Author Contributions: Conceptualization, F.G., L.A.N.L., N.P.R., K.V.P.; Writing—Original Draft Preparation, F.G., L.W.A.R., G.M.C.C., M.C.P., A.C.C., J.M.F., A.E.M.H., T.W.J.C., T.L.M., L.A.N.L., T.P.N.L., S.L.M.K., J.G.O.R., G.V., R.E.P.-O., J.L.Z., N.P.R., K.V.P.; Writing—Review and Editing, F.G., N.P.R., K.V.P. All authors have read and agreed to the published version of the manuscript.

Funding: The CGIAR Research Program MAIZE (CRP-MAIZE) provided funding specifically for the CIMMYT's blue maize breeding project. CRP-MAIZE receives support from the Governments of Australia, Belgium, Canada, China, France, India, Japan, Korea, Mexico, Netherlands, New Zealand, Norway, Sweden, Switzerland, United Kingdom, United States, and the World Bank. The blue maize breeding project was implemented by CIMMYT as part of the project “MasAgro”, made possible by the generous support of the Mexican Government through SADER (*Secretaría de Agricultura y Desarrollo Rural*). The work of F.G. was supported by the CGIAR Genebank Platform.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Data sharing not applicable, no new data were created or analyzed in this study. Data sharing is not applicable to this article.

Conflicts of Interest: The authors declare no conflict of interest.

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