Potato landraces and their wild relatives in 3 micro-centers of diversity in Ecuador: farmers’ perception and ecogeography

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Abstract Ecuador is one of the centers of diversity for wild and cultivated potatoes. Three micro-centers of diversity were previously identified based on germplasm collecting passport data of potato landraces and their wild relatives. The objective of this study was to understand the potential hybridization dynamic of the genetic diversity present in situ in these micro-centers (provinces of Carchi, Chimborazo and Loja in Ecuador) by means of assessing the possibility of an eventual genetic cross within intercropped potato landraces, or among potato landraces to their wild relatives; besides the mapping of actual geographic location of recent collections of potato landrace and wild potato relatives in the study areas. Information from farmers and eco-geographic data demonstrated that there is no potential crossing between wild and cultivated potato species. Probably the existing genetic variability in Ecuador has been accumulated since the historical movement of potato landraces by American ancestors from the center of origin in Peru and Bolivia and the continuum knowledge and seed sharing besides the conscious and unconscious selection of potato landraces by local farmers for centuries. Additionally, we discuss options to conserve both cultivated and wild potato species in Ecuador due to apparent current genetic erosion processes.

Keywords Traditional knowledge · Genetic diversity crossing · Gene flow

Introduction

At the beginning of the twentieth century, the Russian scientist Nikolai I. Vavilov claimed that crop variation was correlated with global geographic distributions (Vavilov 1927). The Andean region was identified as one of the centers of origin and domestication of various crops, including potatoes. Potato was first domesticated in central South America around Lake Titicaca 10,000 to 6000 years ago (Brush et al. 1995;
CIP 2020; Hawkes 1988; Ames and Spooner 2008; Spooner et al. 2005; Spooner et al. 2018). Ecuador up North is one of the centers of diversity for cultivated and wild potatoes (Hawkes 1988, 1990; Hijmans and Spooner 2001; Hijmans et al. 2002; Pearsall 2008; Monteros-Altamirano 2011; Monteros-Altamirano et al. 2017). The Ecuadorian potato diversity includes three taxa of cultivated tuber-bearing potatoes, known as Solanum tuberosum L. Andigenum group, diploid, triploid and tetraploid, previously classified as (Solanum phureja, S. chacha and S. tuberosum subsp. Andigena) added to 23 wild species related to potato (Spooner et al. 1992, 2007, 2014; Hijmans and Spooner 2001; Hijmans et al. 2002; Monteros-Altamirano et al. 2017). Recently Naranjo et al. (2020) collected 8 wild potato-related species in the Ecuadorian highlands: Solanum albicans (Ochoa) Ochoa, Solanum albormozii Correll, Solanum andreamum Baker, Solanum chilliasense Ochoa, Solanum chomatophilum Bitter, Solanum colombianum Dunal, Solanum minutifoliolum Correll and Solanum olmosense Ochoa.

In Ecuador, agriculture began in the so-called “formative period” (Huerta 1966; Reyes 1984). This period lasted from 4400 to 300 BC and saw the beginning of sedentary village life, agriculture and pottery (Zeidler 2008). The first archaeological record of potatoes in Ecuador was found in Cotocollao (Pichincha province, northern Ecuador) dating from 1500 BC (Zeidler 2008). When the Spanish arrived in South America at the end of the fifteenth century, they discovered what for them were new plant species. Cieza de León was one of the first Europeans to mention the potato in 1553, both in Quito, Ecuador, where he first saw the plant cultivated, and in the highlands of Peru (cited in Hawkes 1947). Native potatoes grown in the Andes have been described under different names: Indian Potatoes (Hawkes 1947), varieties of native potatoes (Brush et al. 1981), potatoes grown in the Andes (Quiros et al. 1990); native potato cultivars (Zimmerer 1991), local potato varieties (Brush et al. 1994) or cultivars (De Haan 2009). The native potatoes growing in the Andes have been described under different names, e.g. Indian potatoes (Hawkes 1947; Spooner et al. 2005), native potato varieties (Brush et al. 1981), Andean cultivated potatoes (Quiros et al. 1990); native potato cultivars (Zimmerer 1991), potato landraces (Brush et al. 1994) or cultivars (De Haan 2009).

Data from collections of cultivated and wild potatoes in Ecuador, carried out in the 1970’s and 1980’s (Database of the International Potato Center, CIP), served to identify 3 micro-centers of genetic diversity by the North, Central and South of the country (Monteros-Altamirano 2011, 2018; Hijmans and Spooner 2001; Hijmans et al. 2002). These 3 micro-centers (provinces of Carchi, Chimborazo and Loja respectively) were chosen, since a high number of cultivated potatoes and their wild relatives coexist. Monteros-Altamirano et al. (2018), studied recently collected local diploid, triploid and tetraploid potato landraces from these three microcenters and found high allelic diversity based on SSR (Simple Sequence Repeat) information; for tetraploid landraces this diversity was comparable to the variation found in a European collection of 892 varieties (Reid et al. 2011; Monteros-Altamirano, 2017). The presence of unique alleles in local Ecuadorian landraces showed that there is untapped variation, as previously reported for Peruvian potatoes by Quiros et al. (1990) and De Haan (2009). Crop genetic resources are known to be the result of collective actions over many generations of farmers and is the result of shared knowledge, seed sharing, and accumulation of valuable traits (selection) in crop populations (Jarvis and Hodkin 1999; Brush 2007). Landrace breeds continue to be produced extensively by smallholder farmers in the center of origin and are a key component of a complex production system that encompasses multiple agro-ecological and production objectives (de Haan & Rodriguez 2016). Farmers decide how to manage crop populations in their fields, which can have an effect on existing genetic diversity: if farmers are aware of hybridization, they could promote or avoid the process between landraces or gene flow with wild relatives (Jarvis et al. 2000). In the era of breeding, the assessment of genetic diversity in tuber-producing Solanaceae and the impact of human selection is essential for the effective use of germplasm (Jansky et al. 2013).

In conventional production systems in Ecuador, potatoes are vegetative propagated by means of “tuber-seeds”, however, true potato seeds (TPS) are the genuine sexual botanical seeds of the potato (Cuesta et al. 2002). These seeds are contained in fruits (berries) of approximately 2–3 cm in diameter that grow from inflorescence; individual sexual potato seeds measure between 1.2 and 2.8 mm and weigh on
average 50–100 mg per 100 seeds that may even present dormancy (FAO 1991; Struik and Wiersema 1999; Upadhya and Cabello 2000; Monteros 2002). In this way, TPS have been generated from cultivated potatoes, landraces and wild relatives to be conserved in genebanks (FAO 1998; CIP 2000; Naranjo et al. 2020).

By selecting the same 3 micro-centers of potato diversity identified for Ecuador by Monteros-Altamirano et al. (2018) and Hijmans and Spooner (2001), the objective of this study was to understand the potential hybridization dynamic of the genetic diversity present in situ by means of: 1. Assessing the possibility of an eventual genetic cross within intercropped potato landraces; 2. Assessing the possibility of potato landraces crossing with their wild relatives; and, 3. Mapping the actual geographic location of recent collections of potato landrace and wild potato relatives in the study areas.

Materials and methods

Study sites

The study locations were the provinces of Carchi, Chimborazo and Loja; these provinces correspond to the three micro-centers of diversity of cultivated and wild potatoes previously identified by Monteros-Altamirano et al. (2018) for Ecuador.

Survey

First, the consent of the farmers was sought previously to carry out with the interviews. With this, 8 questions were asked to understand the potential hybridization dynamic of the genetic diversity present in situ at the microcenters.

Questions A and B tried to answer if there is a possible natural hybridization between local landraces: A. Do you grow potato landraces mixed or separated in rows? B. Do you think that if you plant the potatoes together they will cross? To identify if farmers use the berries of potato plants in a potential natural hybridization, we asked the following question: C. Do you collect potato fruits in the field? To ascertain whether the farmers are aware of the existence of wild potatoes, the following question was asked: D. List the common names of the wild potatoes that you know. After we verified that the farmers know about wild potatoes, it was asked: E. Have you seen wild potatoes near the field where you grow your potato landraces? Later, we inquire about their perception of whether they see a potential cross between the wild relatives and their potato landraces with the following question: F. Do you think that wild potatoes can cross with cultivated potatoes? To inquire a little more about farmers’ knowledge about wild potatoes, we asked about their use: G. Do you know what wild potatoes are used for? Finally, to check if there is another potential source of diversity in the potato fields, the following question was asked: H. Do you exchange potato seed with your neighbors? Finally, the data gathered from these questions were categorized and ordered in a Microsoft Excel® matrix and then analyzed in SPSS to determine frequencies of the responses (IBM Corp. 2011).

Interviewees description

The interviewees were farmers who still grow potato landraces at each of the 3 identified micro-centers, there were 50 representative farmers per micro-center (province) according to Monteros-Altamirano (2011, 2018). Most of the farmers growing potato landraces in the 3 studied areas were over 50 years old, with an average age of 53 years old. The racial distribution (mestizo and indigenous) differed between the provinces, being 100% mestizo in Carchi; 20% mestizo and 80% indigenous in Chimborazo; and 70% mestizo and 30% indigenous in Loja. Native potato growers are mainly farmers with properties of less than 3 ha (48% farmers in Carchi, 76% in Chimborazo and 62% in Loja). The respondents mainly have a high school education level: 90% in Carchi, 94% Chimborazo and 84% in Loja.

Potato flowering assessment

The potato landraces collected in Carchi (25 accesses), Chimborazo (43) and Loja (30), were planted at the Santa Catalina Experimental Station of the National Institute for Agricultural Research (INIAP) in Quito (altitude 3050 masl, latitude 0° 22’ 8” S and longitude 78° 33’ 24” W). Ten plants were planted for each accession; data recorded the number of days from sowing until when the accession presented 50% of
flowering (5 plants). Descriptive statistics were obtained from Infostat (2008).

Geographical location of native potatoes in relation to their wild species

Although the micro-centers (provinces) were identified in the first instance by using available passport data (locality, latitude and longitude,) from Ecuadorian potato collections by CIP and INIAP of the 1970s and 1980s (Monteros-Altamirano 2011), for this study, passport data from more recent collections of native potatoes (98 accessions: 25 Carchi, 43 Chimborazo and 30 Loja) and wild relatives (30 accessions: 4 Carchi, 10 Chimborazo and 16 from Loja) was used (Monteros-Altamirano 2011, 2018; Naranjo et al. 2020). These passport data generated graphs of collection points by provinces in the arcGIS program (ESRI 2011). It is important to mention, that during the collections of potato landraces, if any wild plant potato-like were sighted in a perimeter of 500 m of the farmers’ plots, herbarium samples were prepared to identify them with experts.

Results

Figure 1 includes several histograms with frequencies for the responses to 6 of the 8 questions about farmers’ perception on their cultivated and wild potatoes.

Whether farmers grow varieties together or separately

When asking farmers if they plant their potato varieties together or separate in rows in the field (Fig. 1a), farmers from Carchi, Chimborazo and Loja answered that they mostly plant potato landraces separately (98% in Carchi and Chimborazo; and 92% in Loja). Only one farmer in Carchi, another in Chimborazo and 4 in Loja plant the native potato varieties intermixed within the same row.

Whether native potato varieties are crossed when planted together

Based on Fig. 1b, we can observe that most of the farmers in the 3 provinces do not think that potato landraces cross if they are planted nearby (Carchi 59%, Chimborazo 66% and Loja 76%). Farmers who think that landraces cross are: 16% from Carchi, 20% from Chimborazo and 18% from Loja. A lower percentage (except Carchi with 24%) think that perhaps potato landraces could cross, but they have not seen it, so the answer was they do not know. Some farmers explained a bit more about their answers and we can summarize them by province: in Carchi four farmers (3 men and a woman) think that landraces do interbreed because at harvest they find potatoes that change colors. On the other hand, two other male farmers think that cultivated potatoes do change, but not because they cross, but because they degenerate and change. In Chimborazo, 5 women farmers think that “landraces do interbreed, because if they plant mixed varieties, the product comes out mixed”. Another mentioned that potato landrace Uchurumi changes to Cuchisele (which is a potato that grows as a weed on corn). Another farmer mentioned that potatoes do grow when the fruits “papa lulu” fall; while another farmer mentioned that fruits fall, and plants grow from the seeds. Only one farmer mentioned that they do breed because landraces “get married.” In Loja, two male and six female farmers thought that potatoes do not mixed because “each plant is different, independent and they produce separately.”

Collection of potato fruits (sexual seeds) in the field

Figure 1c shows that the majority of farmers in the province of Carchi, Chimborazo and Loja do not collect potato fruits 74, 72 and 84% respectively, only few of them collect them (24, 22 and 16%). A low percentage 2, 6 and 0% of farmers per province, claimed did not know. In Carchi, 9 male farmers and one female mentioned that the plants are born from the tzimbalo (fruits) naturally and they mention occurring in the following landraces: Violeta, Mampuera, CuriPamba, Leona, Rosa, Curipamba, Ojona, Pamba Rosa, Pamba blanca and some Chauchas (S. tuberosum, diploids). Two farmers mentioned that the fruits do not ripen or that they rot. In this province, two farmers mentioned that they have knowledge of seedlings coming out of potato sexual seeds since a well-known Ecuadorian breeder from the province (Mr. G. Bastidas) created a famous local variety called “Super Chola” using this scheme. In Chimborazo, the fruit of the potato is called “pulo” or “papa lulu”. One
Fig. 1 Frequencies for responses of 150 farmers in three micro-centers of diversity in Ecuador (Carchi, Chimborazo and Loja provinces), in relation to their potato landraces and the potential relationship with their wild relatives in the area: a. Do you cultivate the native potato varieties mixed or separated in rows? b. Do you think that if you plant the potatoes together they will cross? c. Do you collect potato fruits in the field? d. Have you seen wild potatoes near the field where you grow your native potatoes? e. Do you think wild potatoes can be crossed with cultivated potatoes? f. Do you know what wild potatoes are used for?
Fig. 1 continued
farmer noticed that fruit production has decreased in her potatoes. A male and a female farmer mentioned that fruits are “harvested” but no tests have been done to see if they germinate. Two women and a man mentioned that the “fruits are eaten fresh.” There are 3 farmers who have done germination tests and they know that seedlings do come out, one says: “I have tested and they came out well”; another says that: “seedlings come out almost the same as the original”, also mentioning that she has done the test in an improved variety ”Gabriela” but not with the natives; while another mentioned that only rickety plants grow out but they are not used. Two others mentioned that “pulo” is not used in anything, it falls and rots, although they mentioned that they have heard that potatoes come out, but they have not done the test. In Loja farmers mentioned that the fruits are called ”tzimbuslos”, 11 farmers (5 men and 6 women) mentioned that they only fall and rot. Eight farmers (3 women and 5 men) mentioned that these are consumed especially by children since they ”suck fruits”. Seven farmers (3 women and 4 men) mentioned that they do nothing with the fruits, that some fall or they are cut out during crop development, but they do not produce potatoes; fruits are collected, but not sown. Finally, one farmer mentioned that potato fruits are used to feed animals.

Farmers’ knowledge on wild potatoes

In Carchi, farmers (44%) indicate that wild potato species take the name of ”papa de la vieja” ”papa de vieja” “papa de viejas” all of them referring as “old woman potato”. In addition, names such as ”charcheres”, ”Cualla”, ”Juarríos”, ”Cuario”, ”Papa de Monte”, ”Papa Monte” are mentioned and only one farmer do not know about these wild potatoes. In Chimborazo, the most repeated names are “aya papa” (24%), ”urco papa” (10%), ”tzimbalo” (8%) besides other names such as “lobo, chahuara, chavela, papa chavela bejucu, chuco, papa de monte, papa del inca or sacha papa”. In Loja, the most common name is “sacha papa” (10%) and “papa de monte” (6%), followed by “papa de chacra”, although the last one is cultivated (it grows as a weed in corn) it is considered wild by 2 farmers. Other mentioned names are: ”papa de monte”, ”papa chia”, ”papa chiwa”, ”papa de cerro”, ”papa de venado”, ”papa del gentil”, ”tzimbalo”, ”tzimbuslo” and ”ojo de venado” some of them referring to hill or mountain potatoes located far from farming lands.

Whether farmers have seen wild potatoes near the fields where they grow their potato landraces

In Fig. 1d, it is observed that most of the farmers in the provinces of Carchi, Chimborazo and Loja have not seen wild potatoes near their land (51, 80 and 72% respectively); on the other hand, 27, 14 and 26% claimed they have seen those wild potatoes close. Other answers from 22, 6 and 2% (Carchi, Chimborazo and Loja respectively) include: A farmer in Carchi mentioned that he has seen wild potatoes, but away from his crops “he has seen them in the mountains”. In Chimborazo, four male farmers mention that in ancient times the elderly knew ”sacha papas” or wild potatoes, which inhabited the mountains, but nowadays they have not seen them anymore. Others mention seeing wild potatoes in the mountains and streams, but far away from their crops. In Loja, 5 women and 4 men mentioned that these potatoes used to grow far from their cultivation places and refer to them as ”in the mountains”, ”on the hill”, ”on the slopes” and ”the ravines” but they have not seen them anymore. A woman farmer mentioned that wild potatoes still exist, but she mistakes it for the ”papa de chagra” landrace that grows among the corn field.

Whether farmers think that wild potatoes can be crossed with cultivated potatoes.

As can be seen in Fig. 1 E, only 14, 6 and 20% of the farmers believe that wild potatoes could be crossed with potato landraces in Carchi, Chimborazo and Loja respectively; however, the majority (45, 70 and 46% respectively) think that these groups of potatoes cannot be crossed. While 41% of farmers in Carchi, 24% in Chimborazo and 34% in Loja mention that they ”do not know” if these potatoes would cross.

In Carchi, 2 men and 4 women farmers believe that these potatoes could only be crossed if the crossing would be made artificially in a ”laboratory” on purpose; even a male farmer heard that the researchers do so. One farmer mentioned that these groups of potatoes do not interbreed ”because they are not alike at all” while another say that they could interbreed because they are ”related”. In Chimborazo, 3 men and
a woman although stated “they do not know”, mentioned that “the crossing might be possible”, even one farmer said that he would “try” to see if it works. In Loja, a farmer is incredulous that cultivated and wild potatoes can be crossed; another farmer opens the possibility that those potatoes could be crossed and only one farmer affirmed “if they are pollinated, they can be crossed.”

Whether farmers know about the uses of wild potatoes.

In a low percentage 12, 22 and 28% of farmers in Carchi, Chimborazo and Loja know of some use for wild potato species (Fig. 1f), while 38, 32 and 28% answered that wild species have no use. Most of the farmers in the 3 micro-centers studied say they do not know if wild species have any use.

In Carchi several uses for wild potato relatives are reported. A farmer mentions the use of wild species as food “they are eaten as snack”. Other farmers (3 men and 1 woman) mentioned the medicinal properties of wild potatoes: one says that they are crushed with liqueur to be used against “el mal aire” (vomit and diarrhea caused by mystic or climatic conditions); another farmer mentioned medicinal use against “espasmo” (headache and chills that are caused by drastic temperature changes). Another farmer mentioned that these wild potatoes are known to form tiny “tubers”, which grounded in water are used as a remedy for hair growth. Finally, another farmer mentioned: “mashed wild potatoes were rubbed on horses’ geldings to cure them.” In Chimborazo, 4 women and 4 men report various uses as food or medicine e.g. “fruits (tzimbalo or chuco) from a wild potato with a purple flower can be eaten. Another mentioned that “ayapapa” (potato wild relative with blue flowers) is used against dandruff. Two women and a man recognized that the “urco papa” is used to cure back pain with the leaves that are picked, crushed, heated and tied back. One farmer mentioned that the fruits of wild potatoes are used to heal frightened children, and another mentioned the use of wild potatoes as ornamental. In Loja, two women and 4 men mentioned that wild potatoes are eaten, referring to the “tzimbailos” fruits, however, it was done in the past. On the other hand, another farmer indicated that wild potatoes (tubers) are not eaten because they are too hard. As medicine, three male farmers mentioned that the “sacha papa” is used to cure “el mal”, “el viento”, mumps or kidneys.

Exchanging potatoes as a source of potato genetic variability

In Carchi 54% of the interviewed farmers exchange potato tubers and the rest (46%) do not exchange them. In Chimborazo 21% exchange potatoes while 79% do not. In Loja, 62% exchange native potatoes and 38% do not.

Flowering of potato landraces

The different potato landraces have a large variation in terms of days to flowering as follows: in Carchi: mean of 107 days, a minimum of 83 days and a maximum of 125 days and a Coefficient of Variation (CV) 14.85%. For Chimborazo: mean of 11 days, a minimum of 83 days, a maximum of 125 and a CV of 13.38% (Mean: 110); while in Loja: Mean 101, with a minimum of 83 days, a maximum of 133 days and a CV of 16.51% (“Appendix 1”).

Location of native potatoes and their wild relatives in the studied areas

Figures 2, 3 and 4 present maps with the location of potato landraces and wild relatives collected in each of the micro-centers of diversity: Carchi, Chimborazo and Loja respectively. Each map is accompanied with histograms about the relationship between the number of accessions of potato landraces and wild species regarding altitude (meters above sea level, m.a.s.l.) of collection.

In the province of Carchi at the North of Ecuador (Fig. 2a) it is observed that most of the collection records of wild potato relatives are geographically distant from the places where potato landraces are planted. These two groups coincide in the Tulcán canton, but their geographic location is not overlapping. According to Fig. 2b, the altitudes where wild potatoes are grown are different from where potato landraces are grown, only at altitudes between 2900 and 3100 m.a.s.l. cultivated and wild coexist, but are far apart. In this province, wild materials of Solanum andreanum and Solanum colombianum have been collected and among the cultivated materials there are diploid (33%), triploid (4%) and tetraploid (63%) of S.
**Fig. 2**  
(a) Map of the location of potato landraces and wild relatives collected in Ecuador, Carchi microcenter.  
(b) Number of accessions of potato landraces and their wild relatives in relation to the collection altitude (m.a.s.l.) in Carchi-Ecuador.
Fig. 3  

a. Map of the location of collections of cultivated potato landraces and wild relatives in Ecuador, Chimborazo micro-center.  
b. Number of accessions of potato landraces and their wild relatives in relation to the collection altitude (m.a.s.l.) in Chimborazo-Ecuador.
tuberosum. In the province of Chimborazo in central Ecuador (Fig. 3a) we can observe that the collection records of cultivated landraces and wild relatives coincide in the cantons of Guano, Riobamba, Colta
and Guamote. According to Fig. 3 B there are 3 ranges of altitudes where wild potatoes are grown and overlap with native potatoes grown 2761–3900 m.a.s.l.; however, the two collected materials are geographically distant. In this province, wild materials of Solanum albicans and Solanum colombianum have been collected and of the cultivated materials there are S. tuberosum diploid (8%), triploid (8%) and tetraploid (83%). In the province of Loja in the South of Ecuador (Fig. 3a) it is seen that some records of wild and potato landraces coincide in the cantons of Saraguro, Loja and Catamayo. According to Fig. 3b, the altitudes where potato landraces and wild relatives are grown overlap in 2 altitudinal ranges 2101–2500 m.a.s.l. and 2501–2900 m.a.s.l., however, similarly to the other microcenters the collection sites are geographically distant. In this province, wild materials of Solanum albornozii and Solanum olmosense have been collected and of the cultivated materials there are S. tuberosum diploid (21%), triploid (3%) and tetraploid (76%).

Discussion

Potential hybridization of potato landraces

Potato landraces naturally produce fruits (berries) in the field, but most farmers report that fruits fall off and rot, or they are collected and consumed as food, which would indicate that eventual dropping of fruits and seed germination at the site is very difficult. Additionally, it is known that self-pollination is common in potatoes and cross-pollination is very rare, especially in tetraploids that correspond to the majority of cultivated species in Ecuador (Cuesta et al. 2002; Spooner et al. 2014; Monteros-Altamirano et al. 2017; Wang et al. 2019). Additionally, mature TPS have a primary-dormancy period lasting 6 to 18 months after berry extraction (D’Antonio and McHale 1988; Pallais et al. 1989,1991; Pallais 1995; Stuik and Wiersema 1999), which would make it difficult for the seeds that fall from the fruits and germinate under natural conditions. Anyway, if hybridization would occur, seeds wouldn’t be able to survive a process of soil preparation and rotation with other crops, which is common in the study areas according to Monteros-Altamirano et al. (2018). Similarly, farmers mainly planting landraces separated in rows produce a physical barrier that prevents outcrossing.

Another result of this study shows that potato landraces present a variety of flowering stages, which would make an eventual pollen flow and potential natural hybridization between them unlikely. However, it is important to consider that in this study the influence of insects as pollinators was not evaluated as reported by Johns (1986) who identifies insects of the genus Bombus sp. and Anthophora sp. as pollinators of native potatoes and wild species in Bolivia. Parra-Rondinel et al. (2021) mentioned that, in the Andean region of southern Peru, people recognize that cross-breeding occurs between wild and cultivated potatoes, and identify flower visitors and fruit growers as consumers of their berries, situation which is corroborated by Spooner et al. (2010).

Probably the existing genetic variability in Ecuador has been accumulated since the historical movement of potato landraces by American ancestors from the center of origin in Peru and Bolivia (Johns and Keen 1986) and the continuum knowledge and seed sharing of potato landraces by local farmers for centuries (Monteros-Altamirano et al. (2017). Additionally, it is possible that an apparent conscious and unconscious selection of potato landraces by farmers occurs similarly to Peru and Bolivia (Johns and Keen 1986; Jarvis and Hodgkin 1999), since in Ecuador there is an ongoing process of adaptation of potato landraces to particular ecological Andean conditions. Based on our study, there is no evidence of deliberated hybridization among potato landraces unlike Peru where few specific cases of sexual seed management by farmers have been documented for breeding purposes to eliminate diseases, rejuvenate varieties or create new ones (Quiros et al. 1992). Only in Carchi-Ecuador potato hybridization by an outstanding farmer-researcher in the past, produced a new potato variety, however, nowadays there is no indication that farmers have generated new varieties by using this method.

Wild potato species

Based on herbarium identification the only “potato-like species” found close to the cultivated potatoes was Solanum caripense Humb. and Bonpl. ex Dunal which, although looking very similar to wild potato species, belongs to the related section Basarthrum and not to section Petota. This species is a diploid
(2n = 2x = 24), climbing non-tuberizing herb, and sterile when crossed with potato (Nakitandwe et al. 2007). The wild potatoes reported for Ecuador are far away from the potato fields, in the “monte”, a term referring to mountain slopes at the outer limit of the agricultural landscape. This makes crosses between cultivated and wild species not likely to occur.

Most of the farmers growing potato landraces at the studied microcenters do recognize wild potatoes, this is how 31 common names of potato wild relatives were mentioned, these names included both Spanish and Kichwa. Hawkes (1947) registered only three common names of wild potatoes for Ecuador (Aya papa, Papa chio and Sacha papa). It is interesting that in Chimborazo and Loja the “papa del Inca” “papa chia or papa chiwa” is identified as wild, although this could be classified as a “weed species” since this potato coexists in corn fields. In Peru this specific landrace is called “Araq papa” and has been identified as S. tuberosum sbsp. andigena, although it is also considered a weed in corn cultivation (De Haan 2009).

The uses identified by farmers for wild species also determine ancestral knowledge, however, their use is less and less frequent since these species are not geographically accessible.

Relationship between cultivated and wild species

Despite the high diversity of potato landraces (Monteros-Altamirano et al. 2011; Monteros Altamirano et al. 2017; Monteros-Altamirano et al. 2018) and potato wild relatives (Hijmans and Spooner 2001; Hijmans et al. 2002) present in Ecuador; potato landraces collection points do not coincide with their wild relatives neither in geographic space nor in altitude in the 3 micro-centers studied, which support farmers’ observations about the existence of wild potato relatives in places far from their potato crops. In Kenya, a center of diversity for Sorghum sp., Mutegi et al. (2010), found wild relatives in sorghum crops, vacant land, but also many species growing far away from agricultural land; in Ecuador, center of diversity of potatoes, potato landraces and their wild relatives do not match in the vicinity. In Ecuador, altitudinal variation can mean drastic changes in climatic conditions and soil types.

Hypothetically, if a greater sampling were to determine a closeness between the two groups, the species would still have to overcome another limitation, which is that TPS of cultivated and wild potatoes present thermo-dormancy (Monteros 2002; Cunguán 2020); which would make it very difficult that, in a very eventual crossing with the consequent fall of berries in the field, they germinate and produce seedlings. Additionally, wild and cultivated potatoes have different ploidies (Hardigan et al. 2017) and EBN (Endosperm Balance Numbers) that should be sorted out for a potential cross among them. The wild species present in the study areas have the following ploidies and EBN: Solanum albidans (Ochoa) Ochoa, 6x (4EBN); Solanum albormozii Correll, 2x (2EBN); Solanum andreamum Baker, 2x (2EBN); Solanum colombianum Dunal, 4x (2EBN); and Solanum olmosense Ochoa, 2x (2EBN); and, the cultivated species Solanum tuberosum Andigenum group 2x (2EBN), 3x, 4x (4EBN) (Spooner et al. 2004, 2014).

Information from farmers and eco-geographic data from this study did not demonstrate a potential cross between wild and cultivated species, Johns and Keen (1986) and Jarvis and Hodkin (1999) indicate that in the center of origin of the potato (around Lake Titicaca), cultivated potatoes and wild species coexist once the later are rarely removed by farmers from growing areas, then promoting hybridization. This type of behavior has determined the origin of diploid and tetraploid cultivated species by gene flow from wild species or weeds (Ugent 1970). However, this process would be primarily natural and non-farmer-driven process (Spooner et al. 2010).

Although the results of this study do not demonstrate a potential gene flow between local landraces and / or wild relatives, however, intercropping (Thurston 1990; Garret et al. 2001) and intermixing of potatoes (Andrivon et al. 2003; Pilet et al. 2006; Finckh et al. 2007) traditionally used by farmers, are indeed effective for other purposes such as controlling the main disease of the crop: Phytophthora infestans, considering that Ecuadorian native potatoes are mostly susceptible to this disease (Monteros-Altamirano 2011; Monteros-Altamirano and Delgado 2021).

Genetic erosion of native potatoes and wild species

When evaluating the presence of microsatellite alleles in native potato cultivars, in Peru, no erosion was detected based on a comparison of alleles found in the field with alleles found in a central potato collection conserved at CIP (De Haan 2009); similarly in
Ecuador Monteros-Altamirano et al. (2017), determine that high genetic diversity is still maintained in situ in the same locations as this study, however, in this case, a decrease in the frequency of farmers who maintain native potatoes in the fields has been already observed in Ecuador, especially in the province of Carchi (Cañizares and Forbes 1995; Frolich et al. 1999; Cuesta et al. 2005; Monteros-Altamirano et al. 2018). Additionally, local potato landraces in Ecuador are under threat due to the introduction and use of new high-yielding varieties, high pressure of pests and diseases, and the lack of market opportunities (Cuesta et al. 2005). Similarly, in relation to the wild potato relatives, Naranjo et al. (2020) using the IUCN Red List categories preliminarily categorized the wild potatoes collected as follow: Endangered (S. albicans (Ochoa) Ochoa, S. albornozii Correll, S. chilliasense Ochoa, S. chomatophilum Bitter and S. olmosense Ochoa); Vulnerable (S. andreanum Baker and S. minutifolium Correll); and, Near Threatened (Solanum colombianum Dunal).

Strategy for the conservation of cultivated and wild native potatoes in Ecuador

To maintain the diversity of cultivated potatoes and their wild relatives in Ecuador, it is necessary to implement conservation strategies in situ (on farm) and ex situ. The importance of the complementarity of both systems has already been highlighted by authors such as Engels and Visser (2003), Jarvis et al. (2000) or Castañeda-Álvarez et al. (2015), although these two conservation methodologies have inherent advantages and disadvantages (Altieri 1987; Brush 1991; Cohen 1991; Dulloo 2010). Currently, thousands of local varieties and wild relatives of the potato are conserved in gene banks (Bamberg et al. 1996; Pavek and Corsini 2001; CIP 2020; Monteros-Altamirano et al. 2018). In Ecuador, the National Agricultural Research Institute (INIAP) currently conserve the potato landrace genetic diversity by using mainly in vitro techniques, while the potato wild relatives are conserved mainly as sexual seeds in cold storage (Monteros-Altamirano et al. 2018; Naranjo et al. 2020). At the global level only a small part of the total variability has been used for potato breeding e.g. for adaptation and resistance traits, despite the various technologies available for assessment (Pavek and Corsini 2001; Hajjar and Hodgkin 2007). The extensive potato gene pool, rich diversity of landraces and many wild relatives provide options for exploration, pre-breeding, breeding and development of niche markets (de Haan and Rodriguez 2016).

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Authors’ contributions AMA participated in the conception, coordination and design of the study. AMA, FYJ, JC, LCQ, and KC participated in the interpretation of results and drafting the first manuscript. FYJ, RA and JC were involved in the survey data gathering and maintenance of the field experiments. AMA coordinated funding application. All authors read and approved the final manuscript.

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Availability of data Any original data related to this publication will be available to the editors under request.

Declarations

Conflict of interest The authors have declared that no competing interests exist.

Appendix 1

See Table 1.
| Genebank Code | Landraces: Common Name | Ploidy | Country | Province | Days to flowering |
|---------------|------------------------|--------|---------|----------|------------------|
| ECU-18162     | Chaucha Negra          | 2X     | ECU     | Carchi   | 119              |
| ECU-18163     | Mampuera               | 4X     | ECU     | Carchi   | 125              |
| ECU-18164     | Violeta                | 4X     | ECU     | Carchi   | 119              |
| ECU-18165     | Leona Negra            | 4X     | ECU     | Carchi   | 92               |
| ECU-18166     | Rosada                 | 3X     | ECU     | Carchi   | 124              |
| ECU-18167     | Papa botella/Botella (blanca) | 2X | ECU | Carchi | 119 |
| ECU-18170     | Carriza                | 4X     | ECU     | Carchi   | 91               |
| ECU-18171     | Leona del carchi       | 4X     | ECU     | Carchi   | 124              |
| ECU-18172     | Curipamba              | 4X     | ECU     | Carchi   | 102              |
| ECU-18254     | Chaucha botella        | 2X     | ECU     | Carchi   | 119              |
| ECU-18255     | Ratona amarilla        | 2X     | ECU     | Carchi   | 83               |
| ECU-18256     | Ratona amarilla        | 2X     | ECU     | Carchi   | 119              |
| ECU-18323     | Chaucha crespa         | ND     | ECU     | Carchi   | 119              |
| ECU-18348     | Mampuera               | 4X     | ECU     | Carchi   | 92               |
| ECU-18349     | Sulipamba              | 4X     | ECU     | Carchi   | 122              |
| ECU-18351     | Chaucha negra          | 2X     | ECU     | Carchi   | 119              |
| ECU-18353     | Morasurco              | 4X     | ECU     | Carchi   | 83               |
| ECU-18354     | Uva                    | 4X     | ECU     | Carchi   | 122              |
| ECU-18357     | Pamba roja/Tableada roja | 4X | ECU | Carchi | 83 |
| ECU-18358     | Pamba pintada/Tableada pintada | 4X | ECU | Carchi | 100 |
| ECU-18364     | Negra/Morasurco        | 4X     | ECU     | Carchi   | 92               |
| ECU-18366     | Chaucha ratona         | 2X     | ECU     | Carchi   | 100              |
| ECU-18367     | Rosada                 | 4X     | ECU     | Carchi   | 124              |
| ECU-18368     | Roja plancha          | 4X     | ECU     | Carchi   | 100              |
| ECU-18589     | Pura sangre            | 2X     | ECU     | Carchi   | 83               |
| ECU-18209     | Uvilla                 | 4X     | ECU     | Chimborazo | 125 |
| ECU-18215     | Puña                   | ND     | ECU     | Chimborazo | 102 |
| ECU-18217     | Guantiva               | 4X     | ECU     | Chimborazo | 123 |
| ECU-18218     | Puña negra             | 4X     | ECU     | Chimborazo | 120 |
| ECU-18221     | Cacho                  | ND     | ECU     | Chimborazo | 124 |
| ECU-18224     | Uvilla negra           | 4X     | ECU     | Chimborazo | 119 |
| ECU-18225     | Loro papa              | 3X     | ECU     | Chimborazo | 122 |
| ECU-18226     | Leona roja             | 4X     | ECU     | Chimborazo | 124 |
| FMFYRA-011    | Cacho negro            | ND     | ECU     | Chimborazo | 124 |
| ECU-18230     | Huarmi papa            | 4X     | ECU     | Chimborazo | 124 |
| ECU-18233     | Cornos                 | ND     | ECU     | Chimborazo | 124 |
| ECU-18235     | Manuela                | 4X     | ECU     | Chimborazo | 124 |
| FMFY-001      | Mami                   | ND     | ECU     | Chimborazo | 112 |
| ECU-18238     | Mamey                  | 4X     | ECU     | Chimborazo | 110 |
| ECU-18239     | Guancala               | 4X     | ECU     | Chimborazo | 83 |
| ECU-18240     | Uvilla amarilla        | 4X     | ECU     | Chimborazo | 83 |
| ECU-18241     | Alpargate              | 4X     | ECU     | Chimborazo | 124 |
| ECU-18242     | Norte roja             | 3X     | ECU     | Chimborazo | 102 |
| ECU-18317     | Manuela 1              | 4X     | ECU     | Chimborazo | 100 |
| ECU-18318     | Manuela 2              | 4X     | ECU     | Chimborazo | 124 |
| Genebank Code | Landraces: Common Name       | Ploidy | Country | Province        | Days to flowering |
|---------------|------------------------------|--------|---------|-----------------|------------------|
| ECU-18320     | Chuquillinga                 | 3X     | ECU     | Chimborazo      | 100              |
| ECU-18321     | Papa tabla                   | 4X     | ECU     | Chimborazo      | 83               |
| ECU-18330     | Nortena antigua              | 4X     | ECU     | Chimborazo      | 100              |
| ECU-18332     | Chaucha ratona               | 2X     | ECU     | Chimborazo      | 100              |
| ECU-18333     | Frayla                       | ND     | ECU     | Chimborazo      | 100              |
| ECU-18334     | Curiquinga                   | 4X     | ECU     | Chimborazo      | 83               |
| ECU-18335     | Tabaquera colorada           | 2X     | ECU     | Chimborazo      | 124              |
| ECU-18429     | Unknown                      | 4X     | ECU     | Chimborazo      | 124              |
| ECU-18430     | Huagrasinga                  | 4X     | ECU     | Chimborazo      | 120              |
| ECU-18432     | Tanda                        | 4X     | ECU     | Chimborazo      | 124              |
| ECU-18433     | Pera amarilla                | 4X     | ECU     | Chimborazo      | 100              |
| ECU-18434     | Caperucita                   | 4X     | ECU     | Chimborazo      | 124              |
| ECU-18435     | Morosel                      | 4X     | ECU     | Chimborazo      | 122              |
| ECU-18436     | Freila                       | 4X     | ECU     | Chimborazo      | 100              |
| ECU-18440     | Marta                        | 4X     | ECU     | Chimborazo      | 119              |
| ECU-18441     | Marta                        | 4X     | ECU     | Chimborazo      | 83               |
| ECU-18442     | Chaucha manzana              | 4X     | ECU     | Chimborazo      | 103              |
| ECU-18577     | Chaucha colorada             | 4X     | ECU     | Chimborazo      | 124              |
| ECU-18579     | Uvilla original              | 4X     | ECU     | Chimborazo      | 122              |
| ECU-18580     | Puña                         | ND     | ECU     | Chimborazo      | 100              |
| ECU-18592     | Chaucha negra “pera”         | 4X     | ECU     | Chimborazo      | 92               |
| ECU-18595     | Mishi maqui “uña gato”       | 2X     | ECU     | Chimborazo      | 92               |
| ECU-18597     | Curipamba                    | 4X     | ECU     | Chimborazo      | 100              |
| ECU-18372     | Bodeguera blanca (ojo morado)| 4X     | ECU     | Loja            | 124              |
| ECU-18374     | Papa de chacra               | 4X     | ECU     | Loja            | 83               |
| ECU-18377     | Negra ojona                  | ND     | ECU     | Loja            | 92               |
| ECU-18381     | Semibolona 2                 | 4X     | ECU     | Loja            | 100              |
| ECU-18383     | Wicupa amarilla              | 2X     | ECU     | Loja            | 83               |
| ECU-18387     | Chaucha amarilla alargada    | 2X     | ECU     | Loja            | 83               |
| ECU-18388     | Negra, carrizo o catalina    | 4X     | ECU     | Loja            | 92               |
| ECU-18389     | Colorada                     | 4X     | ECU     | Loja            | 83               |
| ECU-18390     | Colorada chaucha             | 4X     | ECU     | Loja            | 103              |
| ECU-18392     | Unknown                      | 4X     | ECU     | Loja            | 122              |
| ECU-18395     | Bodeguera blanca             | 4X     | ECU     | Loja            | 124              |
| ECU-18397     | Guacalá blanca               | 4X     | ECU     | Loja            | 100              |
| ECU-18399     | Guacalá roja                 | 4X     | ECU     | Loja            | 92               |
| ECU-18400     | Bolona                       | 4X     | ECU     | Loja            | 83               |
| ECU-18404     | Bolona amarilla              | 4X     | ECU     | Loja            | 83               |
| ECU-18405     | Carriza                      | 4X     | ECU     | Loja            | 92               |
| ECU-18406     | Papa chacra                  | 2X     | ECU     | Loja            | 124              |
| ECU-18407     | Chaucha amarilla alargada    | 2X     | ECU     | Loja            | 83               |
| ECU-18408     | chaucha roja                 | 2X     | ECU     | Loja            | 119              |
| ECU-18410     | Papa huinga                  | 2X     | ECU     | Loja            | 112              |
| ECU-18413     | Chaucha roja                 | 4X     | ECU     | Loja            | 119              |
| ECU-18415     | Bolona                       | 4X     | ECU     | Loja            | 122              |
Table 1 continued

| Genebank Code | Landraces: Common Name | Ploidy | Country | Province | Days to flowering |
|---------------|------------------------|--------|---------|----------|------------------|
| ECU-18416     | Negra                  | 4X     | ECU     | Loja     | 100              |
| ECU-18419     | Negra ojona            | 4X     | ECU     | Loja     | 100              |
| ECU-18420     | Escalena               | 4X     | ECU     | Loja     | 123              |
| ECU-18423     | Guano de cuchí         | 4X     | ECU     | Loja     | 92               |
| ECU-18584     | Churona rosada         | 4X     | ECU     | Loja     | 83               |
| ECU-18598     | Perra dormida          | 3X     | ECU     | Loja     | 100              |
| ECU-18599     | Cuchicaca “papa de chacra” | 4X   | ECU     | Loja     | 133              |
| ECU-18600     | Roja                   | 4X     | ECU     | Loja     | 83               |

ND: Not determined

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