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# Identifying priority sites for the on-farm conservation of landraces and systematic diversity monitoring through an integrated multi-level hotspot analysis: the case of potatoes in Peru

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**Introduction:** Effective monitoring of the *in situ* conservation status and change dynamics of landrace populations in their centers of origin ideally requires the identification of sites that are complementary in terms of the richness, uniqueness and coverage of genetic diversity.

**Methods:** We applied a 4-step approach to identify sites of high potato landrace diversity which will guide the set-up of a network of complementary prospective conservation observatories in Peru, the potato center of origin. A GIS mapping approach was used to determine which combination of sites would provide the most comprehensive and complementary genepool coverage. A landrace inventory was developed from 49 sources, comprising 47,272 landrace records, 97.1% with coordinates, which was used to derive landrace, cultivated species, and cultivar group richness. Data on known indicators of agrobiodiversity, including potato wild relative concurrence, cultivated area, ecogeographic diversity, and ethnolinguistic diversity were included in the spatial overlay analysis, which was used in conjunction with expert opinion data to provide further insight to hotspot selection.

**Results:** Thirteen hotspots with high, unique, and complementary levels of landrace diversity were identified. We recommend that robust baselines are established, documenting current diversity in these sites using semi-standardized methods and metrics for future tracking.

**Discussion:** Our results, while being the most robust of their kind to date, were inevitably affected by data gaps, infrastructure and hotspot biases. New documentation efforts should record landrace diversity in uncovered regions, as well as explore complementary mechanisms to track the conservation status of unique endemic landraces that occur in coldspots.

#### KEYWORDS

Andes, complementary reserve analysis, genetic resources, GIS, *in situ* conservation, multilevel indicators, observatories

## Introduction

A large reservoir of crop genetic diversity continues to be conserved on-farm with the most widely utilized diversity by farmers and breeders being landrace populations (Dreisigacker et al., 2005; Veteläinen et al., 2009; Oliveira et al., 2016). These locally adapted traditional, ancestral, farmer or indigenous varieties have developed - and continue to evolve - through an intricate process of human selection and diversification in response to dynamic socioecological environments (Camacho Villa et al., 2005; Tiranti and Negri, 2007; Choudhury et al., 2013). Intraspecific diversity provides an essential means for households and rural communities to achieve yield stability, adaptive capacity and food security while retaining their cultural identity. Landraces also offer a key reservoir of characters providing farmers with the flexibility to adapt to diverse environmental or biological conditions, as well as being an essential source of traits for the development of new resilient and nutritious crop varieties (Frankel and Bennett, 1970; Esquinas-Alcazar, 1993; Gibson, 2009; Zabel et al., 2021). Importantly, landraces are also biocultural resources carrying local identity, prestige and heritage (Nazarea, 1998; Ellen and Simon Platten, 2011).

Potato is the fourth most important staple in the world in terms of production and the most important non-grain crop for human food intake (Ezekiel et al., 2013). Its domestication is characterized by a complex evolutionary history (Hawkes, 1990; Hardigan et al., 2017; Denham et al., 2020). The Andes are its center of origin where, 8,000 to 10,000 years after its initial domestication, a large pool of landraces continue to be managed and nurtured by smallholder and indigenous farmers (De Haan et al., 2010; Monteros, 2011; CIP et al., 2021). International missions to collect and safeguard diversity *ex situ* started in the 1930s in response to the early needs of formal breeding programs and perceived threat of diversity loss (Hawkes, 1973; Ochoa, 1975). The International Potato Centre (CIP) was established in Peru in 1971 with the mission to securely conserve potato genetic resources. Soon after its establishment, CIP scientists recognized the unique role of on-farm conservation and started researching the ongoing conservation dynamics and human ecology of the crop in its natural habitat (Jackson et al., 1980; Brush et al., 1981).

The complementary nature of integrated crop genetic resources approaches, or efforts aiming to effectively link *ex situ* and *in situ* approaches, is receiving increased recognition (Maxted et al., 1997; Dulloo, 2010; Nagel et al., 2022). In the case of potato in Peru it has resulted in multidirectional germplasm exchange and the emergence of diverse conservation approaches ranging from agrobiodiversity zones and annual biodiversity seed fairs to Payments for Agrobiodiversity Conservation Services schemes. However, processes of regular monitoring and tracking remain relatively underdeveloped within integrated conservation contexts, hindering the wider understanding of processes of varietal and genetic change. The need for such a framework is arguably more urgent than ever. The high Andes are characterized by accelerated change which is likely to affect intraspecific diversity. The climate crisis is affecting these high altitude rainfed cropping systems through increased temperatures and pest-disease pressure as well as more frequent extreme out-of-season weather events such as hails, frosts and droughts (Hijmans, 2003; Quiroz et al., 2018; Raymundo et al., 2018; Klein et al., 2019; Narouei-Khandan et al., 2020; Poveda et al., 2020). The bulk of landrace diversity is concentrated in a narrow altitudinal range with intense levels of abiotic stress (De Haan and Juarez, 2010; Arce et al., 2019). Rapidly changing socioeconomic drivers such as markets, migration and food policies also affect Andean agriculture (Remy, 2014; Antiportia et al., 2016; Bedoya-Perales et al., 2020).

Historically, it is likely that landrace populations in the Andes have been affected by numerous extreme events. These would have included the little ice age (1300-1800), the demographic collapse following the Conquista (1520-1620) and more recently from 1980 to 1995 a period of rural violence in Peru (Smith et al., 1970; Rabatel et al., 2008). The current reality for potato diversity in the Andes suggests a complex dynamic with processes of loss, enrichment and conservation occurring in parallel (De Haan et al., 2010; Monteros, 2011). Even for a relatively well-studied crop like potato, a knowledge gap persists when it comes to the conservation status of landraces in the centre of origin (Veteläinen et al., 2009). Robust country-wide inventories of landraces do not yet exist in any country (Veteläinen et al., 2009). However, a rough estimate of 3,000-4,000 landraces is often mentioned for Peru based on genebank inventories (De Haan and Rodriguez, 2016;

Lüttringhaus et al., 2021; Parra-Rondinel et al., 2021). The volume of detailed baseline inventories at the subnational level continues to grow (e.g., De Haan et al., 2016b; CIP et al., 2021).

The crop genetic resources community remains a late adopter of *in situ* monitoring approaches compared to communities of practice working with wild flora and fauna where *in situ* application is the norm and *ex situ* is only used as a backup for *in situ* (Maxted et al., 1997). An underlying factor relates to the comparatively complex nature of documenting landraces as compared to species and that for agrobiodiversity *ex situ* provides the means of supplying the germplasm to potential users. Systematic inventorying and monitoring of agrobiodiversity is the foundational approach for tracking the actual conservation status and dynamics of biodiversity (Maxted et al., 2007; Bruford et al., 2017). A range of semi-standard protocols and complementary methodologies have been developed for potato landraces (De Haan et al., 2016a). The establishment of multilevel baselines covering time- and geotagged genetic, ploidy, species, nutritional, traditional knowledge, red lists and spatial assessments is still a relatively costly effort. Yet, it is essential as *in situ* conservation in centers of crop origin sustains ongoing evolution and *ex situ* conservation gaps persist (Ramirez-Villegas et al., 2022). A resource-efficient starting point for conservation monitoring could involve baseline documentation and regular resampling in those regions with the highest complementary landrace diversity.

To maximize the efficiency, genepool coverage and comparability of monitoring efforts, one approach is to set-up a network of complementary sites or observatories. Here we report on an integrated multilevel hotspot analysis for potato landraces in Peru, the largest of its kind to date, designed to inform ongoing and future efforts to build a network of complementary sites or observatories for the systematic monitoring of the conservation status and change dynamics of intraspecific diversity. Like other monitoring efforts for flora, fauna and ecosystems (e.g., Baker et al., 2021; Rhea et al., 2023), we hypothesize that long-term and regular monitoring can provide researchers, policymakers and local communities with valuable information. Here, we provide an exhaustive analysis of possible complementary hotspots for potato landraces in Peru to guide investment in and the gradual expansion of a network and community of practice focused on systematic monitoring. This in turn will further our understanding of the actual conservation status of potato landrace diversity and inform the need to take conservation action.

## Materials and methods

A 4-step approach was followed to identify complementary conservation sites for systematic potato landrace diversity monitoring (Figure 1). Step 1: inventory all potato landrace collection and occurrence data we could access. Step 2: weighted overlay analysis involving different spatially explicit layers that together combine the best possible conditions for landrace diversity to thrive and evolve. Step 3: complementary reserve analysis to assure the highest level of complementary diversity is captured between

conservation sites. Step 4: final prioritization combining steps 1, 2 and 3, adding the results of a key expert survey.

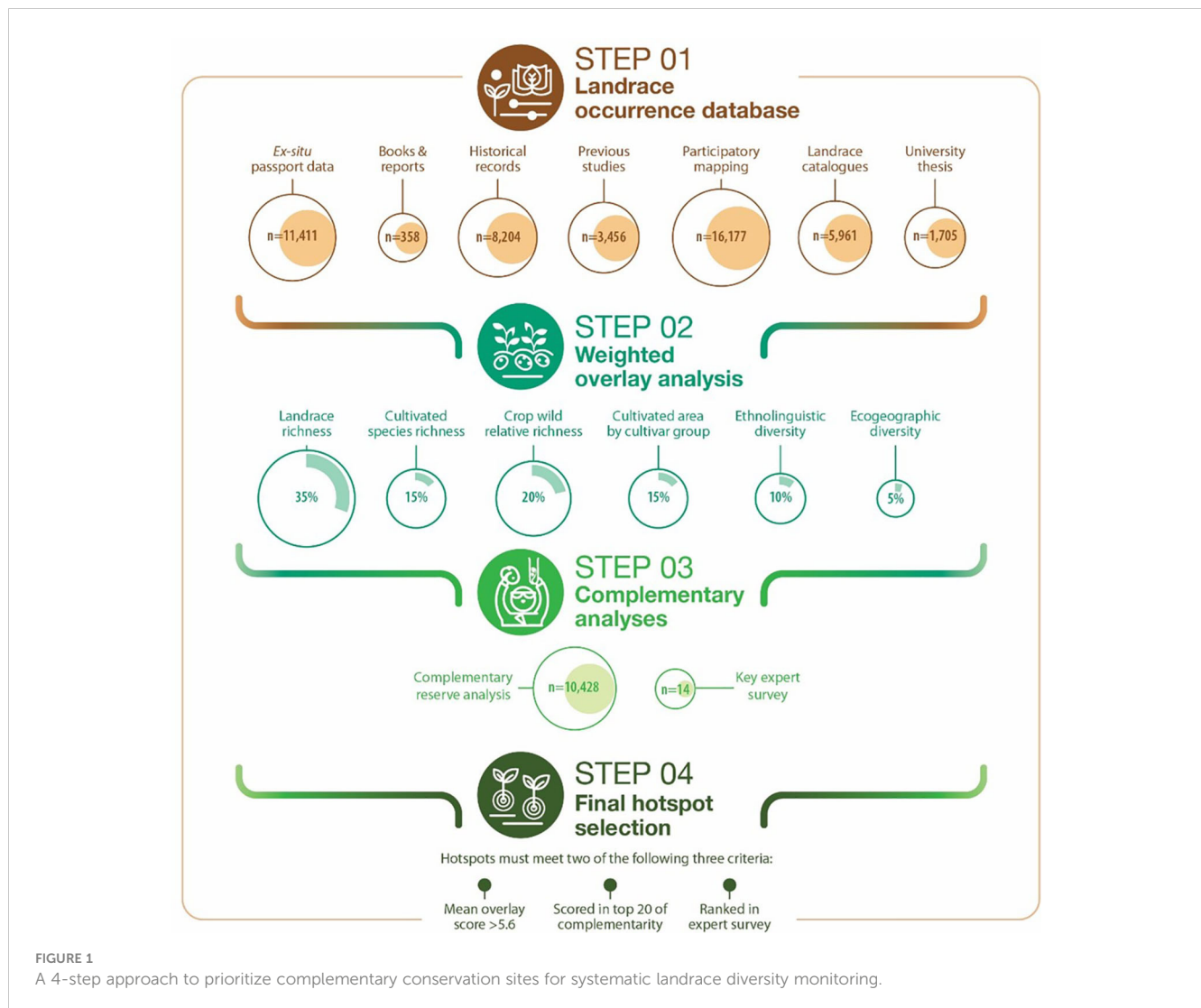
### Step 1: build a landrace occurrence database

All accessible occurrence data for Peruvian potato landraces were compiled and documented into a single inventory. Collection mission reports, genebank passport data, in depth location-specific catalogues, university theses, varietal adoption impact assessments, participatory mapping baseline assessments and grey literature were included (Table 1). In total 47,722 landrace occurrences from 49 sources were assimilated (see: S1 Supplementary Materials). The following variables (where present) were compiled: (i) landrace name and synonym (ii) location data (community, district, province, and department), (iii) geographic coordinates, (iv) cultivated species, (v) main cultivar group, and (vi) farmer information (converted to unique anonymized IDs). Where possible, missing variables were derived and added. This mostly involved geographic coordinates based on location data or for taxonomic equivalents (Table 2). Non-recoverable variables were simply maintained as missing data.

Due to the oral nature of indigenous Andean languages, there were different spellings of the same landrace across different sources. To avoid synonyms being classed as different landraces, all spellings were standardized with uniform homologs assigned for a total of 1305 terms, predominantly following the panandean alphabet (DIGEIBIR, 2013). The determination and sorting of homologs involved standardizing written spelling in Aymara, Quechua and Spanish based on the principles of indigenous biosystematics (De Haan et al., 2007). Homologs were used in the distinct landrace counts with the original names also being left in the dataset for reference. Apostrophes, numbers, and any other punctuation were removed, as well as landrace records that only had codes and records of modern varieties.

Analysis was done using both coordinates and district (ADM3) locations. Many sources had coordinates along with community names. To define coordinates where they were not provided with the source data, community, district, and province names were matched with those in the Gazetteer (INEI, 2012). Spatial data was converted to UTM Zone 18S projection. After data cleaning, georeferencing and standardization a useable database with 45,884 records remained for analysis. The resulting database covers a 1913 - 2018 timeframe and contains 10,426 distinct landrace names (Table 1; Supplementary Material).

Species data and cultivar group data was determined for 9,550 and 25,806 records respectively. These are key variables to assure taxonomic groups are adequately covered. Several taxonomies exist for the cultivated potato and there is no uniform system among the genebank community (Hawkes, 1990; Ochoa, 1990; Ochoa, 1999; Huamán and Spooner, 2002; Spooner et al., 2007; Ovchinnikova et al., 2011). We used the taxonomy of (Ochoa, 1990; Ochoa, 1999) which is also used by the CIP genebank and reclassified records accordingly where possible. The cultivar group is a taxon in between



the landrace and species level, recognizing three basic taxa: (i) floury landraces, (ii) bitter landraces, (iii) modern varieties. The later was not included in this study as we only considered landraces.

## Step 2: weighted overlay analysis

Multiple complementary spatially explicit data sources and key indicators were used as an input for analysis to determine landrace hotspots. A key layer involves the large national dataset of potato landrace collection and occurrence data, including species richness and cultivar groups derived from Step 1. Additional layers used for the spatially explicit weighted overlay analysis included data on: (i) crop wild relative concurrence, (ii) area cultivated with landraces, (iii) ethnolinguistic diversity, and (iv) ecogeographical diversity. The 6 key variables, each treated as a layer, were combined as rasters in Arcmap 10.7 and classified using the Reclassify tool to be combined in the weighted overlay analysis (Figure 1). The relative weight given to each indicator is also shown in Figure 1.

## Landrace richness

Areas of high landrace richness were evaluated at the district (ADM 3) and raster (25km cell) level. The district is a subunit of the province level, which in turn is a subunit of a department or region. Most landrace registers were originally collected at the community or village (district) level. A total of 591 Andean districts where potato landraces are grown were included in the assessment. The complete dataset for this study can be accessed using the following link: <https://doi.org/10.21223/68RQFJ>. Sampling intensity was identified using the point to raster tool in ArcMap 10.7 via the count function. Landrace richness was determined using the Richness point to grid tool in DIVA GIS version 7.5 (Hijmans et al., 2012). A simple point to grid procedure was used and data was exported as an ASCII file to be processed in ArcMap 10.7.

## Cultivated species richness

Based on the taxonomy of Ochoa (1990, 1999) a range of 8 species were examined, involving: (i) *Solanum goniocalyx*, (ii) *S. stenotomum*, (iii) *S. phureja*, (iv) *S. ajanhuiri*, (v) *S. chaucha*,

TABLE 1 Sources of Landrace data.

Data Source	# Land-race	# Records	# Sources	Sources
Genebank databases	4,625	11,411	3	CIP (2021); GRIN (2020); CGN (2020); Genesys (2021)
Catalogues	2,237	5,961	18	See S1 Supplementary Materials
Theses	1,125	1,705	11	See S1 Supplementary Materials
Participatory mapping	771	16,177	6	Juarez et al., (2017a); Juarez et al., (2017b); Juarez et al., (2017c); Juarez et al., (2017d); Juarez et al., (2017e); Polreich et al. (2018)
Other Studies	277	3,456	3	Zimmerer (1991b); Pradel et al. (2018); Pacheco et al. (2023)
Grey literature	1,035	358	2	Pérez Baca (1996); Meza Valasco (2011)
Historical	3,868	8,204	6	Cook (1925); Hawkes (1944); Vargas (1949); Vargas (1956); Hawkes (1997); Ochoa (1999)

(vi) *S. juzepczukii*, (vii) *S. tuberosum* subsp. *andigena*, and (viii) *S. curtilobum* (Table 2). All these species have landraces populations in Peru, including diploids ( $2n=2x=24$ ), triploids ( $2n=3x=36$ ), tetraploids ( $2n=4x=48$ ) and pentaploids ( $2n=5x=60$ ). The subspecies *S. tuberosum* subsp. *tuberosum* was not included as true landrace populations are restricted to central and southern Chile.

### Crop wild relative richness

Crop wild relatives (CWR) are defined in Maxted et al. (2006) as wild plant taxa that have an indirect use derived from their relatively close genetic relationship to a crop. Gene flow between the potato CWR and landraces has been well documented and can potentially contribute to ongoing evolution (Johns and Keen, 1986; Jackson and

Hanneman, 1999; Scurrah et al., 2008). Location data for the closest wild relatives of the potato - sorted for primary, secondary and tertiary gene pool status - were taken from Castañeda-Álvarez et al. (2015) and Särkinen et al., (2015) (available at: [https://figshare.com/articles/dataset/Gap\\_analysis\\_potatoes\\_occurrences/1284187a](https://figshare.com/articles/dataset/Gap_analysis_potatoes_occurrences/1284187a)). This compiled database contains location data from multiple repositories, including EURISCO, GRIN and CIP. Concurrent distribution of these species is essential as an enabler of gene flow and possible evolutionary processes. The analysis included 3, 32 and 13 species of the primary, secondary and tertiary gene pools respectively which have known occurrence in Peru (De Haan and Rodriguez, 2016). In total, 43 out of the 48 species are endemic to Peru (Spooner et al., 2014).

TABLE 2 Taxonomical species equivalents, cultivar groups and number of records.

Ploidy	Taxonomic equivalents				Cultivar group	# Records
	Ochoa (1990, 1999)	Human and Spooner (2002)	Spooner et al. (2007) Ovchinnikova et al. (2011)	Hawkes (1990)		
$2n=2x=24$	<i>S. goniocalyx</i>	<i>S. tuberosum</i> Stenotomum Group	<i>S. tuberosum</i> diploid Andigenum Group	<i>S. stenotomum</i>	Floury landrace	800
	<i>S. stenotomum</i>	<i>S. tuberosum</i> Stenotomum Group	<i>S. tuberosum</i> diploid Andigenum Group	<i>S. stenotomum</i>	Floury landrace	1085
	<i>S. phureja</i>	<i>S. tuberosum</i> Phureja Group	<i>S. tuberosum</i> diploid Andigenum Group	<i>S. phureja</i>	Floury landrace	350
	<i>S. ajanhuiri</i>	<i>S. tuberosum</i> Ajanhuiri Group	<i>S. ajanhuiri</i>	<i>S. ajanhuiri</i>	Bitter landrace	13
$2n=3x=36$	<i>S. chaucha</i>	<i>S. tuberosum</i> Chaucha Group	<i>S. tuberosum</i> triploid Andigenum Group	<i>S. chaucha</i>	Floury landrace	1195
	<i>S. juzepczukii</i>	<i>S. tuberosum</i> Juzepczukii Group	<i>S. juzepczukii</i>	<i>S. juzepczukii</i>	Floury landrace	338
$2n=4x=48$	<i>S. tuberosum</i> subsp. <i>andigena</i>	<i>S. tuberosum</i> Andigenum Group	<i>S. tuberosum</i> tetraploid Andigenum Group	<i>S. tuberosum</i> subsp. <i>andigenum</i>	Floury landrace	5479
	<i>S. tuberosum</i> subsp. <i>tuberosum</i>	<i>S. tuberosum</i> Chilotanum Group	<i>S. tuberosum</i> tetraploid Chilotanum Group	<i>S. tuberosum</i> subsp. <i>tuberosum</i>	Floury landrace	N/A
$2n=5x=60$	<i>S. curtilobum</i>	Curtilobum Group	<i>S. curtilobum</i>	<i>S. curtilobum</i>	Bitter landrace	290

N/A, Not applicable.

## Cultivated area

This indicator is identified in [Brown and Brubaker \(2001\)](#) as an indicator for sustainable management of plant genetic resources. The greater the coverage of landraces, the more likely that endogenous management practices and evolutionary processes are in place. Data was taken from the 2012 Agricultural census (INEI, 2012) and filtered for native and bitter potatoes. This resulted in 295,829 data points for native potato cultivation area: 266,268 and 29,561 for flourey and bitter landraces respectively. Districts cultivating less than 1ha of potatoes were discarded due to the possibility of outliers.

## Ecogeographic diversity

The potato in Peru is grown in a diverse array of mountain environments and cropping systems ([Zimmerer, 1991a](#)). Crops subject to more varying environmental factors potentially have a greater adaptive genetic diversity ([Brown and Brubaker, 2001](#)). The SelecVar tool ([Parra-Quijano, 2020](#)) and literature search were used to determine the following bioclimatic variables suitable for potato for ecogeographic land characterization: (i) mean annual temperature, (ii) maximum temperature of hottest month, (iii) minimum temperature of coldest month, (iv) elevation, (v) solar radiation, (vi) longitude. Ecogeographic data was obtained from WorldClim ([Fick and Hijmans, 2017](#)). Ecogeographic zones were identified using the ELCMapas tool at 5km cells ([Parra-Quijano et al., 2012](#)). These cells were aggregated to 25km cell using the point to grid richness tool in DIVA GIS 7.5 ([Hijmans et al., 2012](#)) to identify cells of high ecogeographic diversity.

## Ethnolinguistic diversity

Ethnolinguistic diversity is a solid proxy of biocultural diversity associated with landrace conservation ([Benz et al., 2007](#); [Naino Jika et al., 2017](#)). Traditional potato farmers in the Peruvian Andes speak Quechua, Aymara, Jaqaru and/or Spanish. Biocultural diversity in turn has great predictive power for landrace richness and is therefore a valuable variable to consider when evaluating potential hotspots ([Perales et al., 2005](#); [Ureta et al., 2013](#)), with higher proportions of indigenous farmers being associated with greater landrace diversity ([Spirito et al., 2022](#)). Geospatial data on the proportion of indigenous languages spoken was taken from agricultural census data and applied exclusively to farmers cultivating potato landraces ([INEI, 2012](#)). This was aggregated to the 25km cells by calculating the percentage of farmers speaking an indigenous language compared to solely Spanish.

## Step 3: complementary analyses

A complementary reserve analysis was conducted in grid cells at 25 km<sup>2</sup>. The number of unique landraces per cell was identified using the Reserve Selection tool in DIVA GIS described by [Rebelo \(1994\)](#). A key feature of the procedure is the use of the principle of complementarity. It ensures that areas chosen for inclusion in a network of monitoring sites that complement each other based on their unique added value ([Justus and Sarkar, 2002](#); [Kati et al., 2004](#)). In our in-depth analysis, the principle of complementarity specifically involved identifying those hotspots

or complementary conservation sites with the highest proportion of unique landraces not covered in other sites. Standardized vernacular nomenclature was used as a proxy for unique landrace presence based on our current knowledge of the indigenous biosystematics of potato landraces ([De Haan et al., 2007](#)). A total of 100 cells covered 89.1% of unique names captured. We used the threshold of 20 cells covering more than 50% of unique landrace names.

An online expert survey was conducted using Microsoft Forms. Confirmation by 14 Peruvian experts in potato landrace diversity without prior knowledge of the results of steps 1, 2 and 3 was used as an additional criterion prior to the final selection of sites. These were senior experts from public genetic resources conservation programs and civil society organizations with cumulative experience of over 400 years. The experts were asked to identify hotspots with the highest unique potato landrace diversity (community to province level).

## Step 4: final hotspot selection

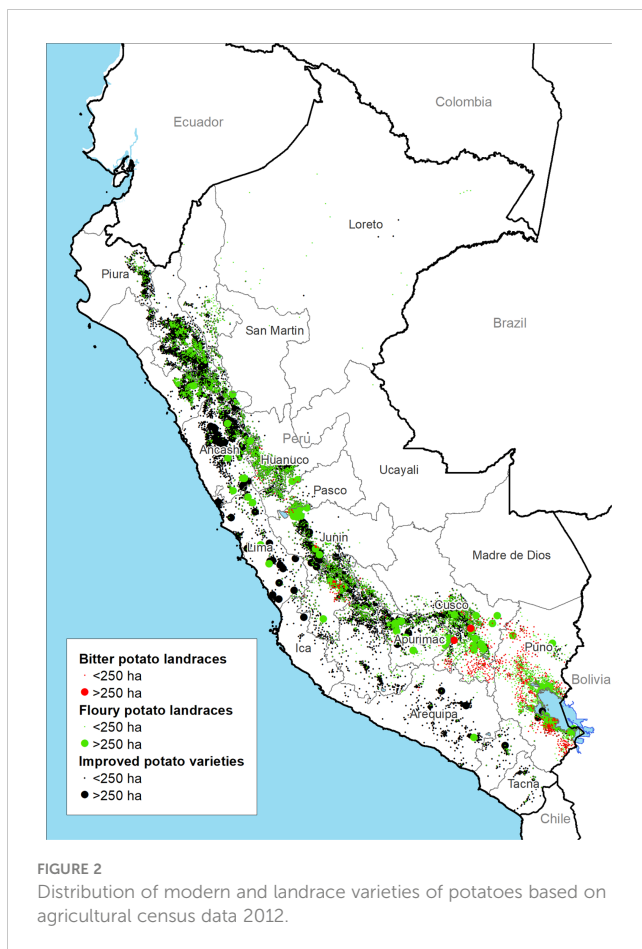
A final prioritization was done combining the previous steps. The hotspots selected were required to meet two out of three criteria. First, correspond to a cell with a mean overlay score value of 5.6 or higher. Second, be scored in a cell corresponding to the top 20 complementary reserve sites. Third, be ranked as a hotspot by key experts.

## Results

### Weighted overlay analysis

The total potato cropping area covers 367,692 ha with 142,429 ha and 9,254 ha dedicated to flourey and bitter landraces respectively ([Figure 2](#)). The regions with the largest cultivated areas of landraces include Puno, Cusco and Huánuco ([Figure 3C](#)). Flourey landraces occur in the whole of the country's highland region from 16.6° south in Puno to 4.3° degrees south latitude in Piura covering altitudes from 3,200 to 4,300 m (86% of the records fall in this range). In most of Peru, flourey landraces concur with modern varieties. Bitter landraces on the other hand have a more restricted distribution range compared to flourey landraces, occurring from the central to southern Andes between 10.2° and 4.3° degrees south latitude with the bulk of the cropping area concentrated in the regions of Cusco and Puno. Bitter landraces occur in a restricted altitudinal belt between 4,000 and 4,300 m (80% of the records fall in this range) with limited concurrence with modern varieties.

[Figure 3](#) shows the results of six different spatial layers considered in the weighted overlay analysis. Clearly the areas richest in potato landraces and cultivated species are concentrated in central and southern Peru ([Figures 3A, B](#)). Central Cusco represents a large continuous region rich in landrace diversity. Other regions with large, connected areas with comparatively high levels of landrace richness include Apurímac, Ayacucho, Huancavelica, Junín, Pasco and Huánuco. Areas containing 6 to 7



out of the 8 potato species are not uncommon but spatially scattered. Regions with patchy concentrations of landrace richness are Puno, Lima, Ancash, La Libertad, and Cajamarca.

The wild relatives of the potato are widely distributed throughout the country with many having a restricted distributed range. Certain regions stand out for their CWR species richness (Figure 3D). Notably central Cusco, the highlands of Lima, Ancash, Huánuco and La Libertad where the concurrence of multiple wild relatives with potato landraces can facilitate gene flow and evolutionary processes. The regions with the highest concentration of indigenous languages and associated culture are distributed and concentrated from the region of Huancavelica in central Peru up to Puno bordering with Bolivia and Chile (Figure 3E). The largest cropping area of potato landraces overlaps with regions where indigenous languages are spoken. It is in these regions that the indigenous knowledge system is most intrinsically linked to landrace diversity. On the other hand, the ecogeographic diversity is highest towards the eastern slopes of the Andes where the highlands transition towards the Amazon (Figure 3F). The maximum variation present per grid cell is three ecogeographic zones, with most cells having only one type of zone.

All combined layers were assessed using a scoring system with relative weight factors. All cells with a value of 5.6 (1 standard deviation) or higher are considered key landrace hotspots (Figure 4A). All cells with a value between 3.6 and 5.5 are considered of intermediate interest while cells with values of 3.5

and lower are currently considered of low interest. A total of 94 cells classify as hotspots. These cover a total of 15 single cells and 11 clusters covering 13 highland regions. Clearly, hotspots are scattered throughout the Peruvian Andes with a notable absence in the most northern (Piura, Amazonas) and southwestern (Arequipa, Moquegua, Tacna) regions of Peru. This absence may in part be attributable to sampling gaps, though it is well-known that landrace richness declines towards northern Peru.

## Complementary analyses

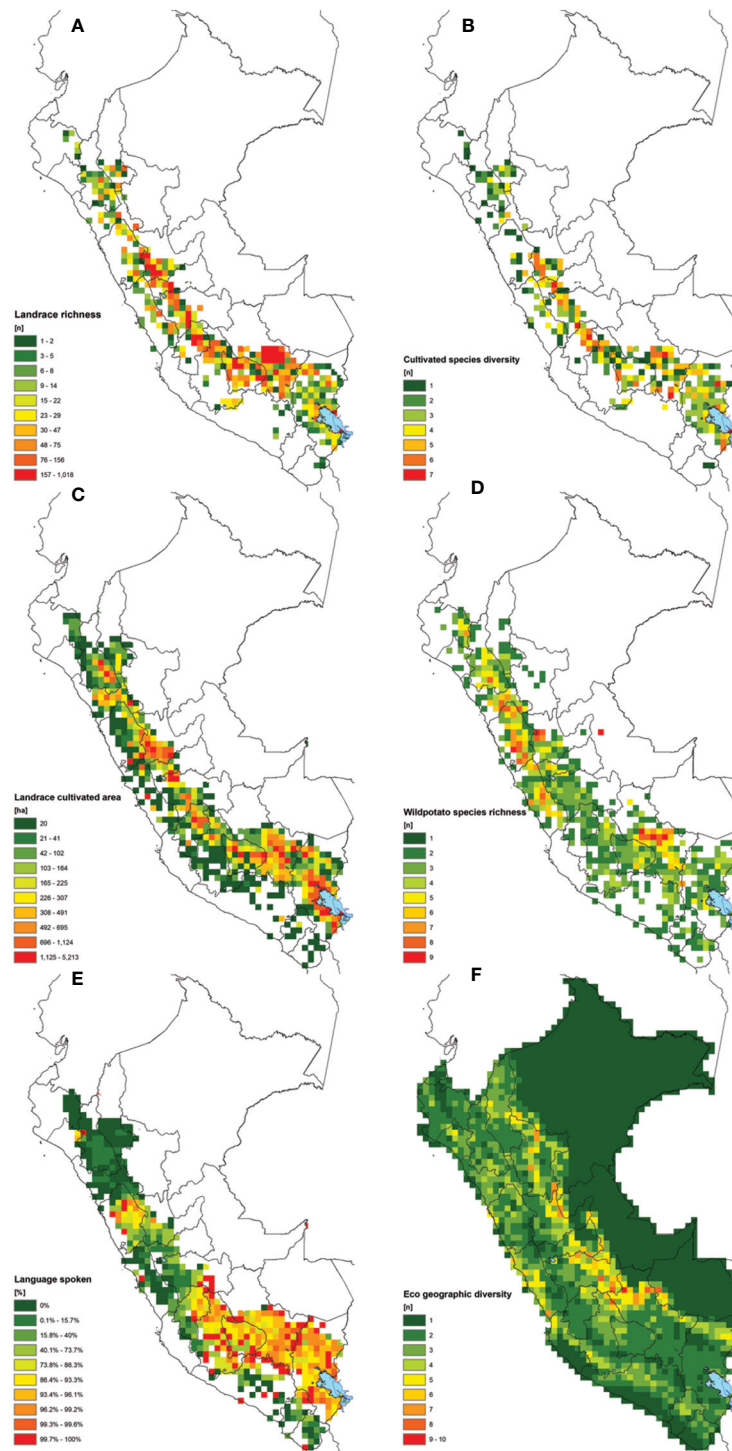
The complementary reserve analysis shows that the first 20 cells (25 x 25 km<sup>2</sup>) conserve 52.1% of the total nomenclatural diversity (see: S2 Supplementary Materials). The number in the cell indicates the sequence in which order cells were selected (Figure 4B). Combined they cover 11 spatially distanced areas: 3 clusters of connected cells and 8 single cells. Together, these areas conserve the maximum diversity of unique landraces within the least space based on unique nomenclature. They cover eight regions: Puno, Cusco, Apurímac, Huancavelica, Junín, Huánuco, Pasco, and La Libertad. 100 cells conserve 89.1% of total diversity of landraces based on nomenclature. The matrix in S2 Supplementary Materials provides an overview of each of the reserves or cells, the unique potato landrace contained within and the combined cumulative of potato landrace diversity that is not present in any of the previously selected reserves.

The expert survey shows a consistent high level of agreement with the weighted overlay and complementary reserve analysis (Figure 4C). Results point to 87 districts (41 connected clusters) from 48 provinces and 14 regions as priority landrace hotspots. Importantly, the expert survey highlights some specific sites within the regions of Arequipa and Amazonas that were not captured in the other analyses. These departments and sites are characterized by known sampling gaps, suggesting they may indeed be underappreciated hotspots. Four districts were noted as hotspots of by three different experts. These were the three districts of Paucará, Yauli and Lircay in the region of Huancavelica and the single district of Comas in the region of Junín.

## Final hotspot selection

Based on the weighted overlay analysis and the complementary analyses a total of 13 hotspots emerged (Figure 5). These represent complementary conservation sites with the highest value for systematic *in situ* diversity conservation and monitoring. Each of the hotspots met at least two of the following criteria: (i) a mean overlay score >5.6, (ii) scored in top 20 of complementarity, (iii) ranked in the expert survey. The sites cover a total of 107 district, 34 provinces and 11 regions (S3 Supplementary Materials). Except for hotspot 9, all others coincide with at least 2 out of 3 of Peru's CWR from the primary genepool present in their territories: *S. candolleianum*, *S. acaule* and/or *S. brevicaulis*. The southernmost hotspots - 1, 5, 6, 7 and 8 - have all 3 species from the potato's primary crop wild relative genepool present in their territory.



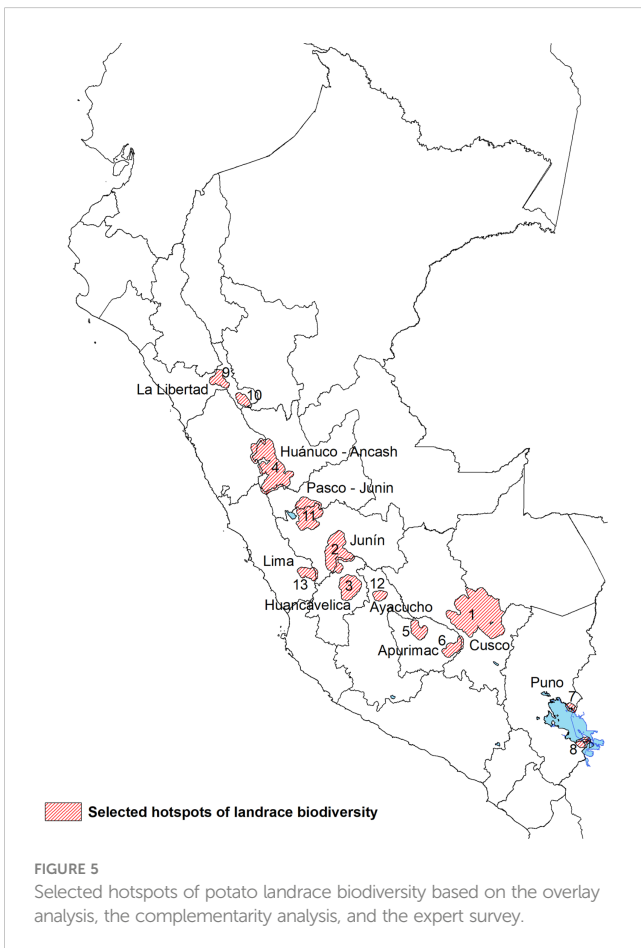
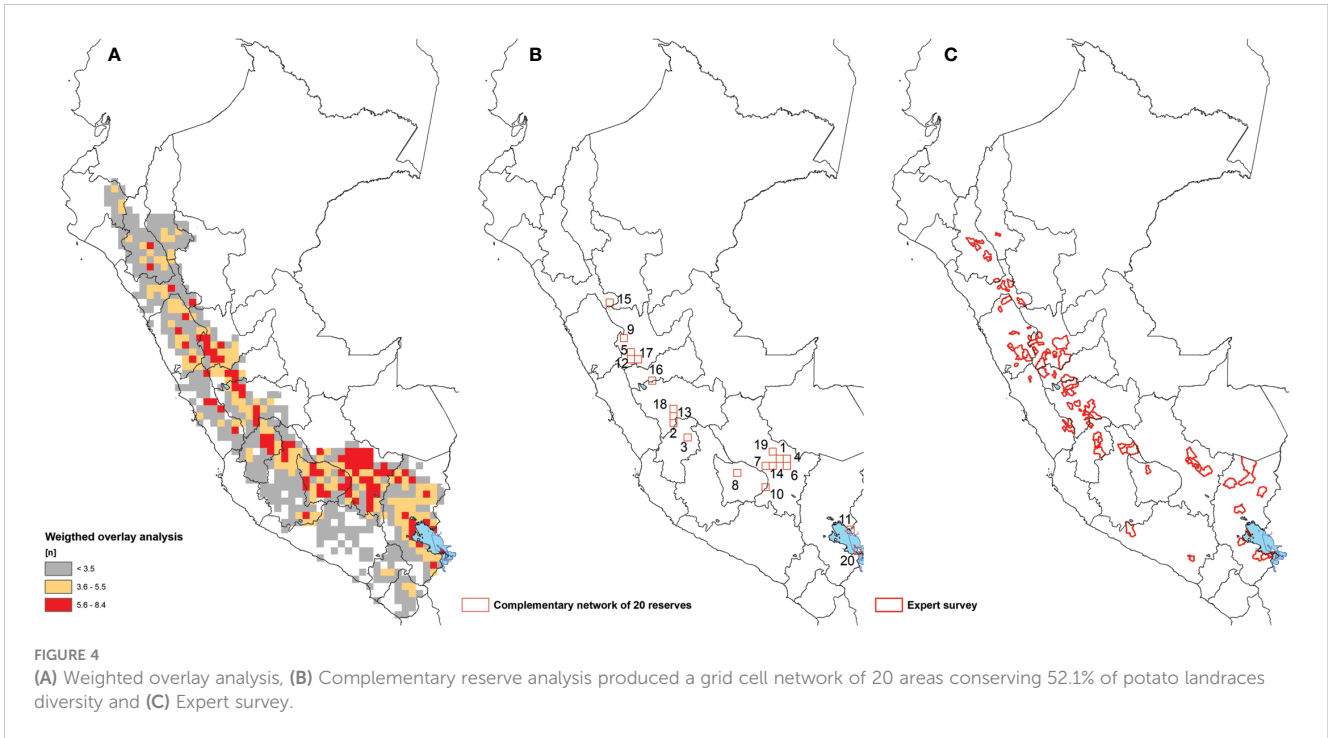


**FIGURE 3** Combined set of maps used in the study for the overlay analysis considering: (A) potato landrace richness, (B) landrace species richness, (C) potato landrace cultivated area in Ha (including floury and bitter varieties), (D) wild potatoes species richness, (E) percentage of native languages spoken by farmers (different than Spanish), and (F) eco geographic diversity.

### Hotspot 1: Cusco

This is the largest continuous complementary conservation site and covers a total of 10,115 km<sup>2</sup>, 7 provinces and 32 districts. This vast landscape contains landrace richness levels of 2,622, and most farmers are primarily Quechua speaking. Well-known landrace groups include *maqtilu*, *boli*, *kusi*, *qompis*, *pitikiña*. Historically, it has been one of the

best documented sites because of early collection missions, international research, and national conservation efforts. Farmer communities between 3,700-4,300 m of altitude tend to maintain unique and high levels of floury and bitter landrace diversity with certain communities belonging to districts like Lares, Pisac, Colquepata and Paucartambo having a reputation as potato diversity stewards.



### Hotspot 2: South Junin and North Huancavelica

This complementary conservation site covers a large area of 2,989.1 km<sup>2</sup> across the border of two regions with 5 provinces and 25 districts. The site is characterized by highly commercial potato production on flat land combined with diverse landraces being grown in the upper belts in so-called *chaqru* mixtures in high-altitude fallowing systems. Landrace richness levels in the hotspot are 484. Well-known landrace groups include *huayro*, *amarilla*, *camotillo*, *winku*, *duraznillo*. Farmers in the site are both Quechua and Spanish speaking. Specific communities belonging to districts like Comas, Quilcas Pasos and Huasahuasi have a reputation as potato diversity stewards.

### Hotspot 3: Central Huancavelica

This relatively isolated complementary conservation site is characterized by small-scale mixed subsistence and market-oriented potato cropping systems. The site covers 1,730 km<sup>2</sup>, 4 provinces, 8 districts and includes the ethnically unique Chopcca group. Landrace richness is recorded at 525 in the hotspot. Potato farmers primarily speak Quechua and well-known landrace groups include *puqya*, *suytu*, *manua*, *gaspar* and *pasña*.

### Hotspot 4: Huanuco and Ancash

This is the second largest complementary site covering 4,606.6 km<sup>2</sup>, 6 provinces and 21 districts. This is the heartland of diploid yellow potato landraces belonging to *S. goniocalyx* and the unique ancestral practice of anaerobic fermentation of tubers into *tocosh*. Landrace richness in the hotspot is 1,051. Well-known landrace groups, often grown in so-called wachuy mixtures, include *walas*,

*tumbay, pishgosh, warmi, coletto*. Farmer speak a distinct Quechua dialect with most of the population being bilingual. Wild potatoes from the primary genepool with very large tubers occur in this region (*S. ambosinum* according to Ochoa, 1999, reclassified as *S. candolleianum* by Spooner et al., 2014).

### Hotspots 5 and 6: North and South Apurimac

These two sites are each comparatively small and show striking differences. The North Apurimac site cover 683 km<sup>2</sup>, 2 provinces and 2 districts. It represents a well-connected commercial potato production site where both landraces and modern varieties are produced. The Southern Apurimac site is largely subsistence oriented with land dedicated to landraces. It covers 676 km<sup>2</sup>, 1 province and 2 districts that have recently been affected by mining. Potato farmers in both sites are primarily Quechua speaking. Between the two sites, landrace richness is 306 for hotspot 5 and 157 in hotspot 6. Well-known landrace groups from the North and South site include *qeqorani, putis, huancaína, millco* and *wallata, susu, linli, tikachi, isakaña* respectively. The so-called *waña* group is common in both sites and used for freeze-drying *chuño*.

### Hotspot 7 and 8: North and South Titicaca Lake

These two sites are the most southern hotspots and unique as they are in what is frequently considered the birthplace of potato domestication. Also, both sites are characterized by considerable diversity of bitter landraces belonging to the species *S. ajanhuiri, S. juzepczukii* and *S. curtilobum*. The North Titicaca Lake site covers 120.3 km<sup>2</sup> (1 province, 2 district) while the South Titicaca Lake site covers 239.8 km<sup>2</sup> (1 province, 5 districts). Aymara is the primary language of farmers and cross border seed exchange with Bolivia is common. Between the two sites, landrace richness is 210 for hotspot 7 and 168 in hotspot 8. Well-known landrace groups include *imilla, piñaza, keta, ruki, locka*.

### Hotspot 9 and 10: Central and Southeast Libertad

These two sites are the most northern hotspots with a relatively small surface area of 515.9 and 338.2 km<sup>2</sup> each. They are relatively isolated – particularly the Southeast Libertad site – and cover 1 district in a separate province. This secluded location may in part have contributed to the relatively high levels of diversity grown in mixtures known as *papa embrosada*. Farmers in these sites do not speak an indigenous Andean language and this is reflected in the predominantly Spanish varietal nomenclature. Landrace richness is 134 for hotspot 9 and 156 in hotspot 10. Well-known landrace groups from the Central and Southeast site include *lampina, huevo de indio, ñata, bretaña* and *jovera, escalera, kaywa, tarantina* respectively.

### Hotspot 11: North Junín and South Pasco

This intermediate size hotspot of 2,878.3 km<sup>2</sup> comprises the most northern point where the sporadically distributed bitter landraces are still grown. The site covers four districts, each belonging to a different province, with a regional reputation as tuber seed sources for landraces. Farmers are predominantly Spanish speaking. Landrace richness is 430. Well-known landrace groups from this complementary site include *chaulina, galleta, camotillo, huayro*.

### Hotspot 12: La Mar Ayacucho

This complementary site is relatively isolated and well-known in the Ayacucho region for its high levels of potato landrace diversity. The site covers 310.0 km<sup>2</sup> with only the district of Tambo in the province of La Mar qualifying as a hotspot in our analysis. Potato farmers are predominantly Quechua speaking. Landrace richness is 153. Well-known landrace groups from this complementary site include *wira pasña, llumchuy waqachi, millqus, sisa, waña*.

### Hotspot 13: Nor-Yauyos

This is the most western hotspot and in a part of the Lima highlands where small-scale terrace agriculture persists. The site covers 532.3 km<sup>2</sup>. Farmers in the site are monolingual Spanish speaking though pockets of the Andean Quechua and Jaqaru languages persist in the wider Yauyos province. Districts of Laraos and Carania are qualified as a hotspot in our analysis, but the districts of Miraflores and Huancachi are also well-known for their landrace diversity. Landrace richness is 59. Common landrace groups include *bauchi, cuchi ismay, cachito, huayro, piña*.

## Discussion

The landrace inventory developed is substantial and the most comprehensive available for potatoes in their Andean center of origin. However, it is not an infallible source for determining complementary conservation sites. Our assessment and results are inevitably affected by data gaps and other limitations. Not all landrace growing areas have adequate occurrence data. This includes some remote and inaccessible regions, but also the source of occurrence data directly affects representativeness. Typically, genebank collection missions have followed road systems and aimed to cover comparatively large distances in the least amount of time. This infrastructure bias is strong even for wild species (Hijmans et al., 2000). Therefore, genebank passport data are often only representative of landrace distribution pattern at the subspecies and ploidy levels, rather than fine-grained ecogeography of intraspecific or landrace level diversity (e.g., Hawkes, 1990; Spooner et al., 2010). To avoid redundancy, genebanks routinely remove accessions of so-called duplicates with the same genetic identity but from different locations if they are already conserved. Consequently, spatially and temporally explicit occurrence data for the same landrace is typically absent in genebank databases. *In situ* catalogues and multi-household assessment surveys on the other hand are often much more representative of the varietal diversity in a particular locality.

The hotspot bias involves the disproportionate sampling of landraces in perceived hotspots relative to the total distribution area in which intraspecific diversity occurs. This has inevitably affected our results and is evidenced by the fact that 27.7% of all occurrence data corresponds to the Cusco region. The fact that some of Peru's well-known potato experts like Cesar Vargas and Carlos Ochoa were from Cusco, in combination with the region's numerous attractions, will likely have contributed to the bias. While potato

is undoubtedly among Peru's most intensely researched crop genetic resources, there are still many localities that are under-represented in terms of their intraspecific landrace diversity. Both the infrastructure and hotspot bias may make identification of hotspots more opaque. Importantly, it also poses the question, how the conservation status of unique landraces in coldspots can be systemically monitored. Crop diversity is more than just the number of landraces in a region, and like wild flora and fauna (Marchese, 2015; Thompson et al., 2021), it is doubtful that a holistic *in situ* conservation strategy can be exclusively based on the number of taxa present in a particular geography. Therefore, we included a range of additional criteria in our hotspot assessment to provide greater insight to the true level of potato diversity. Given the current shortage of systematic monitoring efforts for *in situ* landrace diversity in centers of crop origin, it makes sense to initially prioritize complementary hotspots. Monitoring unique and highly endemic varietal diversity outside of hotspots will need complementary approaches in the future.

Another limitation relates to the use of vernacular nomenclature or landrace names as a proxy for a unique landrace. We assume that areas with high levels of recorded landraces indicate higher levels of richness (Brown and Brubaker, 2001; Maxted et al., 2009; Porfiri et al., 2009; Pacicco et al., 2018). This is partially supported by research suggesting that the folk taxonomy of the potato is consistent and robust (Hawkes, 1947; Brush, 1980), and as concluded by Maxted et al. (2009) this is a common practical assumption applied through necessity. Yet, only cosmopolitan and commercial landraces receive names that are consistent at geographical scales beyond the region. And rare or scarce landraces that are of particular interest for conservation tend to receive numerous names (De Haan et al., 2007). Using vernacular names can lead to either under- and over-representation of diversity (Quiros et al., 1990; Monteros-Altamirano et al., 2017). Despite extensive written standardization of landrace names, our inventory consists of over 10,000 different names, when there are estimated to be only 3,000 to 4,000 genetically distinct landraces in Peru (De Haan and Rodriguez, 2016). However, trust in folk taxonomy is our most practical option to initially assess landrace richness at the national and hotspot scale. Over time this assumption can be tested with more time-consuming and costly tools such as genetic fingerprinting, ploidy counts and morphological descriptions.

Despite limitations, our integrated multi-level hotspot analysis, and the resulting identification of thirteen complementary conservation sites for systematic landrace diversity monitoring in Peru, provides a key step forward to anchor *in situ* conservation and monitoring efforts in locations that jointly provide robust socioecological coverage. Specifically, it will facilitate the targeting of the most representative gene pool coverage possible in terms of richness and complementarity of cultivated species and landraces, as well as biocultural drivers that enable evolution. The *in situ* management of landraces is by definition dynamic, individual landraces will go extinct and new landraces form over time (Veteläinen et al., 2009). Yet a knowledge gap exists concerning the conservation dynamics of farmer-managed landrace diversity, particularly in centers of origin, which affects our ability to generate

timeline monitoring series and evidence underlying genetic erosion, cultivar loss and/or incorporation of new cultivars (Veteläinen et al., 2009; FAO, 2019; Khoury et al., 2021). Systematic diversity monitoring requires science-based site selection and prioritization to establish long-term population monitoring, in combination with the application of semi-standardized tools to establish multilevel baselines and assess natural and deleterious population changes.

A range of semi-standard tools currently exists to establish multilevel baselines from the gene to the landscape level. These include (i) genetic fingerprinting, (ii) rapid agrobiodiversity assessments, (iii) farmer field trials and morphological description, (iv) photographic documentation, (v) quantitative red listing, (vi) qualitative red listing, (vii) cataloging, (viii) threat assessment and (ix) participatory cartography (Veteläinen et al., 2009; De Haan et al., 2016a; Dulloo et al., 2017; Poets et al., 2020). Furthermore, participatory approaches have been developed that involve teachers, students and parents from local communities in the documentation of the indigenous knowledge associated with varietal diversity (e.g., Hilares, 2021). Many of these tools can be applied separately yet, their combined use helps to build a holistic assessment of the genetic, varietal, spatial and cultural conservation status of crop diversity.

In addition to sites and shared monitoring tools, an active community of practice is needed to systematically measure and track the landrace diversity in each site. Network approaches, institutional and technological innovations are needed to build an agile knowledge base. Many of the location-specific *in situ* baseline catalogues used in our analysis are examples of diversity assessments for a single point in time (e.g., Cosío Cuentas et al., 2006; Egúsqüiza Bayona et al., 2018; CIP et al., 2021). While these inventories with detailed morphological, genetic and ethnobotanical details offer a solid register, they often lack temporal occurrence data per landrace. To increase the number of observations in space and time, citizen science and crowdsourcing approaches hold great promise to underpin long-term diversity monitoring (Johnston et al., 2022; Suter et al., 2023). An example of such a pilot-level effort is the WikiPapa Platform ([www.wikipapa.org](http://www.wikipapa.org)). Both action research approaches and participation incentive systems for custodian farmer organizations, civil society organizations, schools, students, teachers, and parents can contribute to intergenerational conservation knowledge exchange and raise awareness of the true value of agrobiodiversity conservation and use.

## Data availability statement

The datasets used in this study can be found in the following online repositories: <https://doi.org/10.21223/68RQFJ> and <https://doi.org/10.21223/1RBTV>.

## Author contributions

SH designed the study. SH, TD and HJ performed collections of landrace occurrence and observation data. SH, TD and HJ cleaned

the dataset. TD and HJ performed the spatial analysis. SH, TD, NM and HJ performed analyses and interpreted results. SH and NM supervised the study and acquired funding. SH, TD, HJ and NM wrote the manuscript collaboratively. All authors approved the final manuscript.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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## Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fcosc.2023.1130138/full#supplementary-material>

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