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Multilevel Agrobiodiversity and Conservation of Andean Potatoes in Central Peru

Species, Morphological, Genetic, and Spatial Diversity

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Botanical species and morphological and genetic diversity represent different yet linked units of conservation. These features, and their spatial distribution in the central Peruvian Andean highlands of

Huancavelica, were used as a basis for characterizing and quantifying potato agrobiodiversity at different scales. Results show that individual farm households maintain high levels of cultivar, morphological, and genetic diversity. At the regional level, all cultivated species, with the exception of *Solanum ajanhuiri*, were found to be present. Tetraploid native potatoes

were most abundant, followed by diploids, triploids, and pentaploids. Morphological characterization of 2481 samples belonging to 38 *in situ* collections resulted in the identification of 557 unique cultivars. Genetic fingerprinting of 989 samples belonging to 8 *in situ* collections resulted in the identification of 406 unique cultivars. The principal source of genetic variation is found within rather than between geographically distanced subpopulations. High levels of cultivar diversity are found, particularly at elevations between 3850 and 4150 m.

Keywords: Potato; *in situ* conservation; ploidy; native cultivars; molecular markers; single sequence repeat (SSR) markers; Huancavelica; Peru.

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Introduction

Many of the world's mountainous regions are primary centers of crop origin (Vavilov 1992). The Andes are a center of origin and diversity for numerous crop species (NRC 1989), including the potato (Spooner et al 2005). Of all major crops, the potato is arguably one of the most important species for mountain agriculture, as its present-day genetic diversity is maintained at attitudes well above 3000 m (Zimmerer 1991b). *In situ* conservation of Andean crop genetic diversity, including the on-farm management of native potato cultivars near wild relatives, is important to sustain the ongoing evolution of domesticated plants and nutritious food systems that support mountain livelihoods (Zimmerer 1996; Brush 2004). Contemporary crop evolutionary dynamics stimulated by gene flow, mutations, and human management of varietal mixtures (Johns and Keen 1986; Quiros et al 1992; Scurrah et al 2008) is likely to contribute the novel genetic diversity that will be needed for future global germplasm enhancement.

A major limitation for future monitoring of on-farm conserved potato genetic resources is the lack of systematic baseline data. The combination of species, morphological, and genetic analysis of contemporary *in situ* populations of native potato cultivars in the Andes has only been systematically documented in a few cases

(CIP 2006; Terrazas and Cadima 2008). Documentation of the structure of variability in diversity hotspots is essential, as it constitutes the basis for future comparisons and has the potential to provide a better understanding of the units (alleles, cultivars, and species) and scales (household, community, and region) of conservation.

The department of Huancavelica is a recognized center of potato genetic diversity (Torres 2001; Huamán 2002; de Haan 2009). The region is located within the geographical distribution area of all cultivated potato species, with the exception of *Solanum ajanhuiri* (Hawkes 1990; Ochoa 1999, 2003). Farmers in Huancavelica maintain considerable levels of infraspecific diversity within the potato crop and commonly recognize 3 categories of native potato cultivars that, at the same time, typically coincide with a complex of botanical species: (1) native-floury cultivars (*S. tuberosum* Andigenum group), (2) native-bitter cultivars (*S. juzepczukii* and *S. curtilobum*), and (3) improved cultivars (frequently with *S. tuberosum* Chilotanum group within their pedigree).

A cultivar can be either native (synonymous to ancestral, traditional, or indigenous landrace or variety) or improved (synonymous to modern or high-yielding variety). Native-floury cultivars are generally directly boiled for consumption (Figure 1). They frequently contain high levels of dry matter and are considered to be of high culinary quality by Andean farmers. Native-bitter

FIGURE 1 Sample of native-floury potato cultivars. (Photo by Stef de Haan)



cultivars are freeze-dried into a traditional product called *chuño* (Towle 1961; Burgos et al 2009). Improved cultivars are the product of formal breeding programs that have combined Andean native potatoes, modern European or North American varieties, and few tuber-bearing wild species. They are generally high yielding and resistant to diseases, yet farmers often consider them to be of inferior culinary quality compared to their native counterparts.

The present article quantifies the species and the morphological and genetic diversity of the native potato in Huancavelica, as well as its spatial patterning by altitude and geographical distance. It provides a systems perspective on the planting levels and emergent properties of potato agrobiodiversity in a specific mountain region. Implications for the crop conservation agenda of mountain agrobiodiversity are discussed.

Material and methods

In situ collection for characterization

Between 2003 and 2006, a total of 38 in situ collections (ISCs) of native potato cultivars, belonging to 34 farmer households and 4 communal farmer groups from 8

highland communities, were used as the basis for ploidy counts, botanical species identification, and morphological and genetic characterization (Table 1). Improved cultivars were not included in the collection. The Andean communities where germplasm was collected followed a north–south transect through the department of Huancavelica (latitude 11°59'4"S to 14°7'48"S and longitude –74°16'11"W to –75°48'38"W; Figure 2). All samples from each ISC were labeled, and on-farm trials with a minimum of 5 and a maximum of 10 plants per sample were established for subsequent characterization.

Species and cultivar group identification

Ploidy levels, in combination with morphological keys, were used to determine the taxonomic status of 2097 samples. Taxonomic identification was double-checked in open fields and under greenhouse conditions using the botanical keys developed by Huamán (1983) and the latest taxonomic treatment of the cultivated potato (Spoonier et al 2007). Ploidy was determined through mitotic chromosome counts obtained from root tips by the acetocarmine squash technique (Smith 1974; Watanabe and Orillo 1993; Chen and Hai 2005). We also used flow cytometry with a Partec® ploidy analyzer.

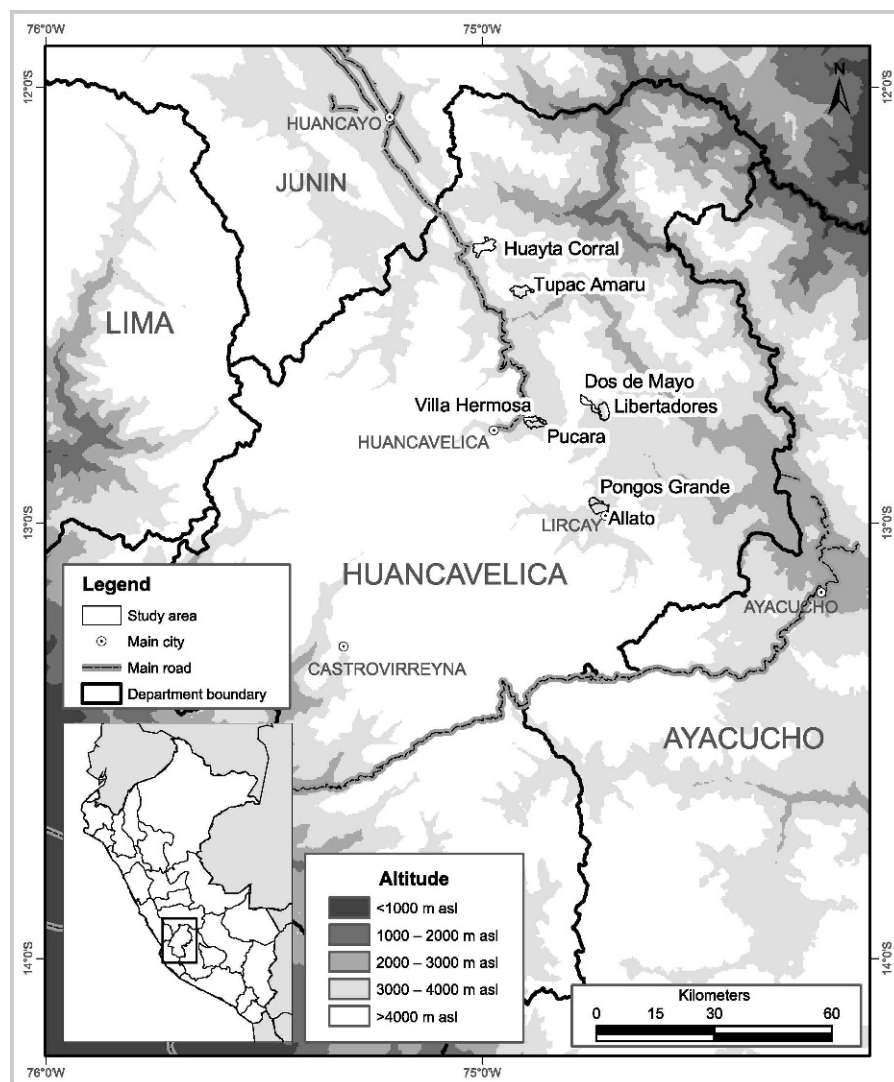
Morphological characterization

The morphological diversity of 2481 samples was characterized using the International Potato Center's (Centro Internacional de la Papa, CIP) descriptor list and color card (Gómez 2000). This list consists of 17 morphological descriptors with a total of 32 morphological character states, 18 of which are considered to be environmentally stable based on long-term experience with CIP's genebank. Similarity analysis, dendrogram construction, cophenetic analysis, and matrix correlation calculations (Mantel tests) were conducted. A standardized similarity analysis with an average taxonomic distance coefficient (DIST), sequential agglomerative hierarchical nested cluster analysis, and unweighted pair group method arithmetic average

TABLE 1 Number of potato accessions installed in on-farm trial and characterized (2003–2006).

Agricultural season	In situ collections (ISCs)	Accessions originally installed	Accessions with ploidy counts	Accessions with species identification	Morphologically characterized accessions	Genetically characterized accessions
2003–2004	1–9	1097	896	772	865	989
2004–2005	10–30	1415	1327	1325	1159	0
2005–2006	31–38	576	0	0	457	0
Total	38	3088	2223	2097	2481	989

FIGURE 2 Location of the Andean communities where research was conducted. (Map by Henry Juárez, CIP)



(UPGMA) clustering method, using the total set of descriptors, was carried out for ISC-01 to ISC-38 with NTSYS-pc 2.1 software (Rohlf 1993). Combined community (8) and regional (sub)population (1) datasets were submitted to the same analysis using only environmentally stable character states.

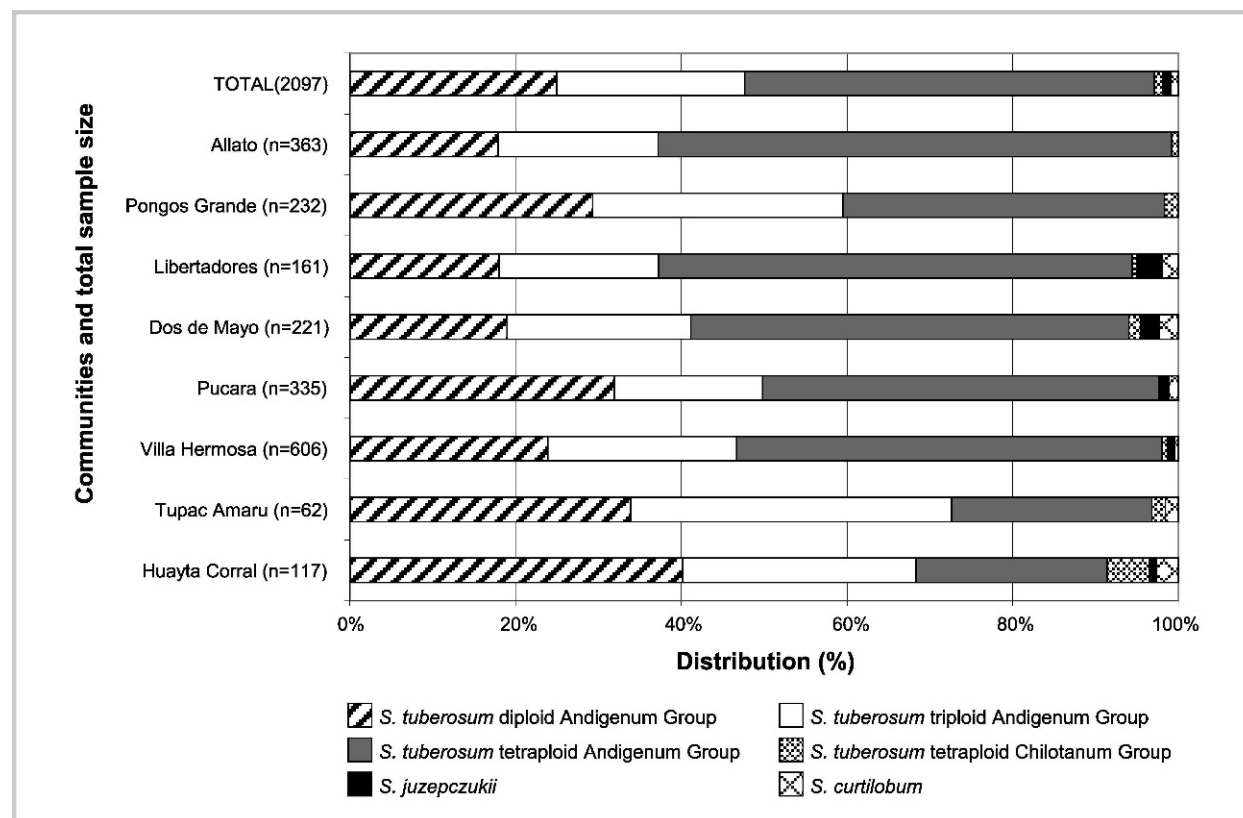
The number of unique cultivars, morphotypes, and pure duplicates within the morphologically characterized populations and subpopulations were determined. Unique cultivars were defined as samples with no pairs at <75.0% similarity for ISC-01 to ISC-38 and community (sub)populations (8) and with no pairs at <66.7% and <58.3% similarity (comparison at 2 defined coefficient limits) for the total regional population (1). Pure duplicates are samples with one or more equal pairs at a

coefficient of 0.00 (100% similarity). Morphotypes are accessions that have no pairs at a coefficient of 0.00 yet belong to a cluster with pairs at >75.0% similarity for ISC-01 to ISC-38 and community (sub)populations (8) and with pairs at >58.3% versus >66.7% similarity for the total regional population (1).

Genetic characterization

A population consisting of 989 samples belonging to 8 farmer households (ISC-01 to ISC-08) was characterized using 18 polymorphic single sequence repeat (SSR; microsatellite) markers covering the whole genome (Ghislain et al 2004). Standard procedures, including DNA extraction with DNeasy 96 plant kits, high-throughput genotyping with a LI-COR 4300 DNA Analysis System,

FIGURE 3 Species and cultivar group distribution for farmer community (sub)populations and the overall regional population.



and SSR allele scoring with SAGA Generation 2 software (LI-COR), were applied. Standardized dissimilarity analysis for ISC-01 to ISC-08 and the regional population (1) were conducted using the Jaccard coefficient and UPGMA clustering method with NTSYS-pc 2.1 software. Dissimilarity trees (dendrograms) were built with the same data using an unweighted neighbor joining clustering method for a dissimilarity matrix calculated with the Jaccard coefficient using DARwin 4.0 and NTSYS-pc 2.1 software.

The number of unique cultivars, morphotypes, and pure duplicates within the genetically characterized (sub)populations was determined. Unique cultivars were defined as accessions with no pairs at >25% dissimilarity, morphotypes as accessions belonging to a cluster at ≤25% dissimilarity, and pure duplicates as accessions with one or more equal pairs at a coefficient of 0.00 (100% similarity).

Spatial diversity

Based on the genetic fingerprinting dataset, the population genetic structures of 2 geographically distanced (sub)populations were compared using analysis

of molecular variance (AMOVA) with Arlequin 3.11 software. The 2 (sub)populations based on geographical distance are (sub)population 1 (P1; $n = 634$; ISC-01 to ISC-04), with all accessions belonging to 4 farmer households from the communities of Villa Hermosa and Pucara (central Huancavelica), and (sub)population 2 (P2; $n = 298$; ISC-05 to ISC-07), with all accessions belonging to 3 farmer households from the communities of Pongos Grande and Allato (southern Huancavelica).

A participatory sampling and field mapping exercise was conducted in each of the 8 communities (2004–2005). All potato fields—independent of their cultivar category (native floury, native bitter, or improved)—belonging to 122 farmer households were mapped using a Garmin GPSMAP76S global positioning system. A total of 601 fields were mapped. Samples of 200 random plants or fields were taken at harvest to quantify the cultivar composition of each field. Samples were taken within each of the rows planted, combining plants at the center and borders of fields. The altitudinal distribution of within-field diversity was characterized using descriptive statistics.

TABLE 2 Results of a similarity analysis using the DIST coefficient and UPGMA clustering method, and consequent identification of unique cultivars, morphotypes, and pure duplicates by community (sub)population.

Community population	Accessions (n)	Coefficient range	Coefficient limit	Mantel test (R)	No. of unique cultivars	No. of morphotypes	No. of pure duplicates
Huayta Corral	146	0.00–1.13	0.28	0.78	127	19	0
Tupac Amaru	243	0.00–1.12	0.28	0.79	195	48	0
Villa Hermosa	588	0.00–1.15	0.29	0.76	425	163	0
Pucara	322	0.00–1.13	0.28	0.73	258	63	1
Dos de Mayo	404	0.00–1.13	0.28	0.75	320	83	1
Libertadores	154	0.00–1.12	0.28	0.80	128	26	0
Pongos Grande	228	0.00–1.10	0.28	0.81	179	48	1
Allato	396	0.00–1.12	0.28	0.76	272	118	6

Results

Species and cultivar group diversity

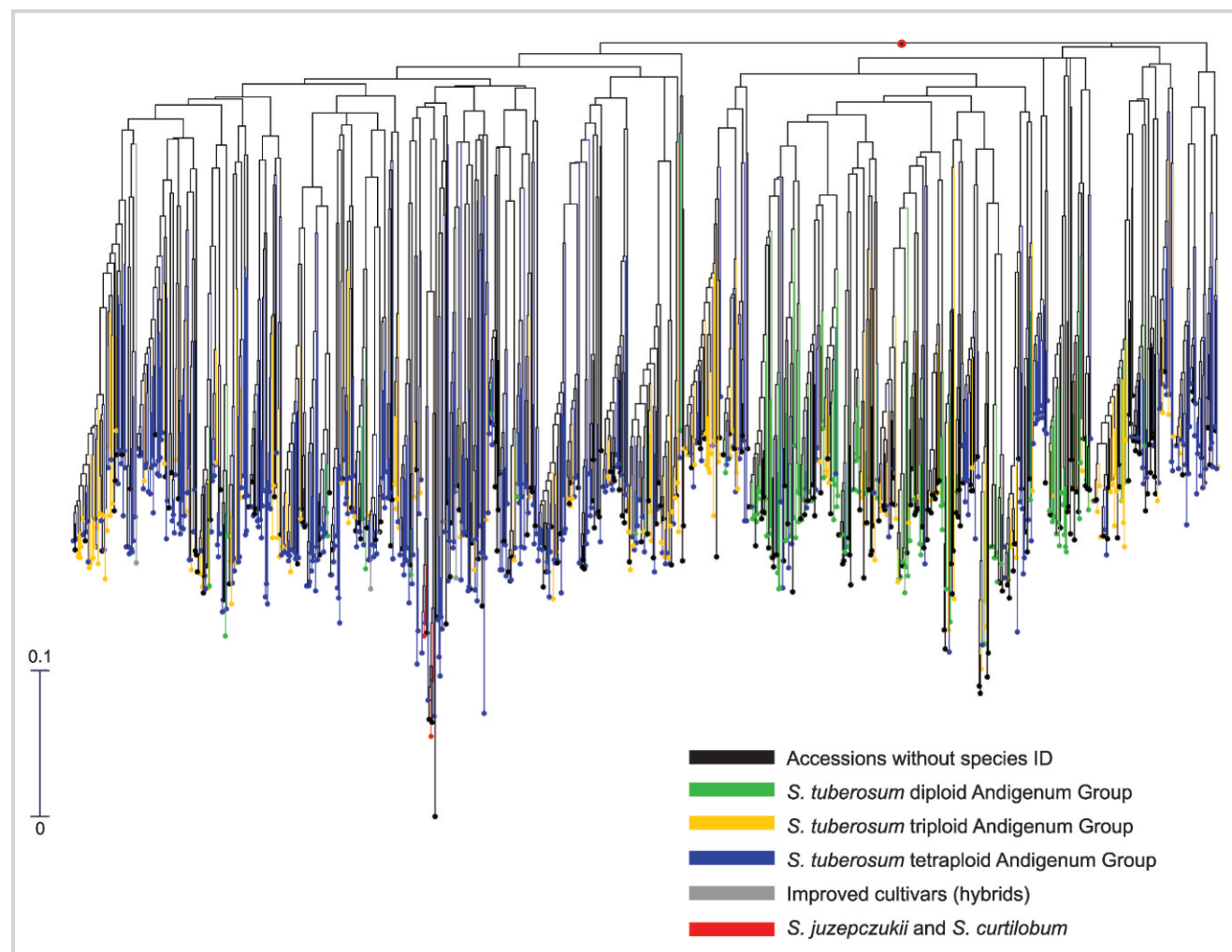
Farmer households managed a minimum of 1 and a maximum of 3 species as part of their potato portfolios, mostly with various ploidy levels being maintained at the household level (diploids, triploids, tetraploids, pentaploids, or a combination of these). The distribution pattern of species and cultivar groups by the farmer community and the overall regional (sub)population provides insights into their relative abundance in terms of infraspecific diversity (Figure 3). The *S. tuberosum* Andigenum group is the most abundant concerning its inherent cultivar diversity, with 97.2% of 2097 samples

belonging to this particular group: 49.5% tetraploids, 25.0% diploids, and 22.7% triploids. Species with the least infraspecific diversity are *S. curtilobum* (0.9%) and *S. juzepczukii* (1.0%). Some improved cultivars from formal breeding programs were encountered, representing 1.0% of the total sample with species identification. These were old, improved potato cultivars that farmers had incorporated into their native cultivar stocks. *S. ajanhuiri* was not encountered in Huancavelica; this is in accordance with previous reports from potato collectors. Accessions belonging to the so-called *Phureja* subgroup (formally *S. phureja*, now part of the *S. tuberosum* diploid Andigenum group) were also not encountered yet were reported to have existed in the past (Ochoa 2003). Older

TABLE 3 Results of a dissimilarity analysis using the Jaccard coefficient and UPGMA clustering method, and consequent identification of unique cultivars, morphotypes, and pure duplicates by population.

Population	Accessions (n)	Coefficient range	Coefficient limit	No. of unique cultivars	No. of morphotypes	No. of pure duplicates
Total	989	0.25–1.00	0.81	406	547	36
ISC-01	175	0.26–1.00	0.82	96	71	8
ISC-02	160	0.29–1.00	0.82	120	39	1
ISC-03	138	0.27–1.00	0.82	90	46	2
ISC-04	161	0.24–1.00	0.81	84	70	7
ISC-05	170	0.33–1.00	0.83	117	49	4
ISC-06	58	0.35–1.00	0.84	52	6	0
ISC-07	70	0.28–1.00	0.82	60	9	1
ISC-08	57	0.25–1.00	0.81	49	8	0

FIGURE 4 Unweighted neighbor joining dissimilarity tree constructed with DARwin 4.0 (Jaccard's coefficient) for 989 samples representing the total fingerprinted population. The scale bar (0–0.1) represents the level of dissimilarity.



farmers reported the past presence of these native potatoes, vernacularly called *chauchas* and recognized for their lack of tuber dormancy, in fields below 3400 m. Cultivars belonging to the *Phureja* subgroup have apparently become scarce.

Morphological diversity

The morphologically characterized (sub)populations ISC-01 to ISC-38 contained a minimum of 13 and a maximum of 160 unique cultivars per (sub)population. No pure duplicates were found within the (sub)populations. Yet 25 of the 38 (sub)populations contained between 1 and 33 accessions classified as morphotypes. This demonstrates that appreciable morphological diversity exists within potato cultivar pools managed by individual households and communal farmer groups.

The total size of unique cultivar pools differs considerably among the 8 farmer communities (Table 2). The highest total number of unique cultivars was identified in the community of Villa Hermosa, affirming the community's regional reputation as a potato diversity hotspot. A lower level of diversity was encountered in the community of Huayta Corral. Yet this community still harbors at least 127 distinct cultivars.

Cophenetic analysis and a comparison of similar and cophenetic matrices for the regional population resulted in a matrix correlation value (R) of 0.76, indicating robustness of the dendrogram constructed with morphological descriptor data of 2481 accessions. Depending on the defined coefficient limit, 0.38 or 0.48 at 66.7% or 58.3% similarity, respectively (coefficient range 0.00–1.15), the regional population

TABLE 4 Summary of relative allele frequencies (%) by population.

	Accessions (<i>n</i>)	Frequent (<i>f</i> ≥ 10%)		Moderately frequent (<i>f</i> < 10%)		Scarce (<i>f</i> < 5%)		Rare (<i>f</i> < 1%)	
		No.	%	No.	%	No.	%	No.	%
ISC-01	175	76	42.0	22	12.2	39	21.5	44	24.3
ISC-02	160	82	45.3	12	6.6	35	19.3	52	28.7
ISC-03	138	79	43.6	20	11.0	25	13.8	57	31.5
ISC-04	161	81	44.8	18	9.9	35	19.3	47	26.0
ISC-05	170	83	45.9	16	8.8	28	15.5	54	29.8
ISC-06	58	87	48.1	15	8.3	23	12.7	56	30.9
ISC-07	70	83	45.9	14	7.7	38	21.0	46	25.4
ISC-08	57	86	47.5	19	10.5	32	17.7	44	24.3
Total	989	81	44.8	19	10.5	40	22.1	41	22.7

consisted of between 764 and 349 unique cultivars. The intermediate value between the two extremes establishes 557 as the total number of morphologically distinct and unique cultivars as regionally maintained by the 8 communities.

Genetic diversity

Table 3 presents the number of unique cultivars, morphotypes, and pure duplicates encountered for each (sub)population (ISC-01 to ISC-08) based on dissimilarity analysis. Analysis based on genetic fingerprinting with SSR markers generally provided a more rigid means of classification, recognizing fewer unique cultivars compared with analysis based on morphological

descriptor data for the same farmer household (sub)populations. The size of genetically distinct cultivar pools ranged between 49 and 120 unique cultivars per farmer household (sub)population. At the household level, each cultivar was recognized with a distinct (folk) name. This reaffirms that households maintain high levels of cultivar diversity.

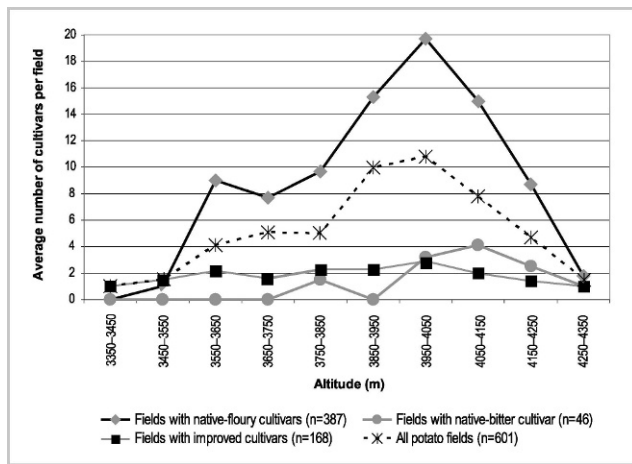
Considerable diversity also exists within the overall regional population (Figure 4). This concerns a single population with all genetically characterized accessions (8 households, 6 communities). Most accessions were genetically distinct, with only 36 pure duplicates encountered within the total population consisting of 989 samples. A total of 406 genetically distinct and unique

TABLE 5 Comparison of geographically distanced (sub)populations P1 and P2 (AMOVA).

Source of variation	df	Sum of squares	Variance components	% of variation
Among (sub)populations P1/P2	1	48.060	0.031 Va	0.19
Among (sub)populations within P1/P2	5	172.902	0.142 Vb	0.87
Within (sub)populations ISC-01 to ISC-07	925	14,935.848	16.147 Vc	98.94
Total	931	15,156.810	16.320	100.00
Fixation indices:		Significance test (1023 permutations):		
F_{sg} : 0.00874		Vc and $F_{st}/P = <0.001$		
F_{st} : 0.01062		Vb and $F_{sg}/P = <0.001$		
F_{gt} : 0.00190		Va and $F_{gt}/P = 0.082$		

F_{sg} , degree of differentiation within a population among groups of demes; F_{st} , degree of differentiation within a population among demes; F_{gt} , degree of differentiation within groups among demes.

FIGURE 5 Average number of cultivars per field by altitudinal ranges (100 m)



cultivars, belonging to clusters showing more than 25% dissimilarity, were identified. No cultivar group or species-specific clusters were observed. A total of 181 alleles were detected within the population. Of these, 22.7% were rare, with a frequency of less than 1.0% (Table 4). Of 8 farmer household (sub)populations, 5 contained alleles unique to these populations at percentages between 0.7% and 4.0%.

Spatial diversity

Cultivar and allelic diversity of geographically distanced (sub)populations: Dissimilarity analysis showed that the 2 geographically distanced (sub)populations contain 250 (P1) and 195 (P2) unique cultivars. The difference of 55 unique cultivars may in part be a consequence of the initial number of accessions considered: 624 (P1) versus 298 (P2). Still, the total size of both cultivar pools, separated geographically by approximately 90 km, is appreciable and suggests that both areas can be considered as diversity hotspots. AMOVA shows that, in the case of the 2 geographically distanced (sub)populations P1 (central Huancavelica) and P2 (southern Huancavelica), the principal source of variation is encountered within the farmer household (sub)populations (ISC-01 to ISC-07) that compose P1 and P2 (Table 5). Molecular variance among (sub)populations P1 and P2 and among (sub)populations within P1 and P2 are limited sources of variation.

Altitudinal distribution of cultivar diversity within fields: High levels of cultivar diversity within fields, particularly for native-floury cultivars, are strongly concentrated at particular altitudes. Fields with native-floury cultivars contained an average of 16.7 distinct cultivars ($SD = 18.4$). This is slightly lower compared to the 20.1 cultivars per field ($SD = 5.1$) reported by Zimmerer (1991b) for the Paucartambo region (Cusco, southern Peru). The highest

levels of infraspecific diversity within fields containing native-floury cultivars were found between 3850 and 4150 m, with an average of 15.0–19.7 cultivars per field (Figure 5). Cultivar diversity within fields containing native-floury cultivars drops sharply at lower and higher altitudes. The highest levels of infraspecific diversity for native-bitter cultivars are concentrated between 4050 and 4150 m, with an average of 4.1 cultivars per field. Native-bitter cultivars only start to appear above 3750 m, and differences concerning infraspecific field diversity by altitudinal range are modest. The levels of cultivar diversity within fields containing improved cultivars fluctuated only modestly, with a minimum of 1.0 (3350–3450 m; 4250–4350 m) and a maximum of 2.9 cultivars per field (3950–4050 m).

Discussion and conclusions

The contemporary species and infraspecific diversity of potato as maintained on farms in Huancavelica, Peru, is high. Farmers maintain all levels of ploidy ($2n = 2x = 24$ to $2n = 5x = 60$) within their cultivar pools, with the *S. tuberosum* Andigenum group being most abundant (49.5% tetraploids, 25.0% diploids, and 22.7% triploids), followed by *S. juzepczukii* and *S. curtilobum*. This is a normal pattern of species and cultivar group distribution when compared with earlier collections in central Peru and CIP's ex situ collections (Huamán et al 1997; Ochoa 1999; Hawkes 2004). The number of diploid accessions belonging to the *S. tuberosum* Andigenum group represented a quarter (25.0%) of the total regional cultivar collection, confirming previous reports that central Peru is an important center of diversity for this particular group. There is no evidence of species or cultivar group loss, with the notable exception of the so-called *Phureja* subgroup. Zimmerer (1991a) also found loss of *Phureja* in the Paucartambo region and relates this phenomenon to temporary migrations and labor shortages. Cultivation of this particular subgroup may also have diminished as a result of direct replacement by improved cultivars, which nowadays predominate in production areas below 3400 m, where *Phureja* cultivars were traditionally grown. Limited tuber dormancy, which farmers report to have led to the loss of seed when they had to temporarily abandon their homes during the years of rural violence, may have been another factor contributing to scarcity.

Morphological characterization suggests the regional cultivar pool consists of 557 unique cultivars. Genetic fingerprinting with 18 polymorphic SSR microsatellite markers suggests the overall regional cultivar pool consists of at least 406 unique cultivars. The difference can be partially explained by the total sample size used. While genetic characterization was done for 8 ISCs from 6 communities ($n = 989$), morphological characterization

was applied to 38 ISCs from 8 communities ($n = 2481$). Yet both results confirm that farm family (sub)populations and the overall regional population are highly diverse in cultivar content. Individual farm households maintain as much as 160 unique cultivars.

The principal source of allelic variation is encountered within the farmer household (sub)populations that compose geographically distanced (sub)populations. This means most alleles are shared among (sub)populations. This confirms findings presented by Zimmerer and Douches (1991), who partially assign weak geographical partitioning of allelic variation to formerly high rates of seed–tuber exchange. High levels of within-field diversity, particularly for native-floury cultivars, are concentrated between 3850 and 4150 m. Different cultivar mixtures are spatially separated by altitude, resulting in the uneven distribution of diversity across the agricultural landscape. This spatial distribution cannot be assigned to a narrow niche adaptation of native potato cultivars (Zimmerer 1998). Differential management and diverse end uses may partially explain this phenomenon. Weather extremes are frequent at the altitudinal range where high levels of cultivar diversity are

concentrated. This suggests the possibility that the spatial arrangement of fields and their level of cultivar diversity may be employed to confront abiotic stress.

On-farm conservation is a historical phenomenon, and Andean households conserve numerous cultivars that are not necessarily present in genebanks. It should also be recognized that in situ conservation of crop genetic resources is dynamic. Final or stable (sub)populations are exceptional, and dynamic management of genetic resources in the hands of farmers, subject to seed exchange, mutation, and possible gene flow, is arguably one of the principal added values that make in situ conservation and a proper understanding of its underlying processes so important. Farmers are active users of cultivar diversity. Cultural value and user options are autonomous drivers of farmer-driven in situ conservation. Farmers typically prefer cultivar mixtures for home consumption, as these are associated with quality traits and long-established culinary preferences. In essence, the indigenous food system is at the heart of farmer-driven conservation. Therefore, food system interventions should try to build on agrobiodiversity.

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