

ECOGEOGRAPHY OF PLOIDY VARIATION IN CULTIVATED POTATO (*SOLANUM* SECT. *PETOTA*)¹

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- *Premise of the study:* The taxonomy of cultivated potatoes has been highly controversial, with estimates of species numbers ranging from 3 to 17. Ploidy level has been one of the most important taxonomic characters to recognize cultivated potato species, containing diploid ($2n = 2x = 24$), triploid ($2n = 3x = 36$), tetraploid ($2n = 4x = 48$), and pentaploid ($2n = 5x = 60$) cultivars. We tested the environmental associations of different ploidy levels in cultivated potato species that traditionally have been recognized as Linnaean taxa to see whether, in combination with prior morphological, molecular, and crossing data, some of the ploidy variants can be recognized as distinct taxa.
- *Methods:* We summarize 2780 chromosome counts of landrace cultivated potatoes, provide georeferences to 2048 of them, and analyze these data for 20 environmental variables at 10-min resolution using the randomForest algorithm to explore associations with taxa and ploidy variants.
- *Key results:* Except for the *S. tuberosum* Chilotanum Group and extreme northern and southern range extensions of the Andigenum Group, it is impossible to find distinct habitats for the ploidy variants of the *S. tuberosum* Andigenum Group.
- *Conclusions:* Our distributional and ecological data, in combination with prior results from morphology, microsatellites, and crossing data, provide yet additional data to support a major reclassification of cultivated potato species. A rational, stable, and universally accepted taxonomy of this major crop plant will greatly aid all users of wild and cultivated potatoes from breeders to gene bank managers to ecologists and evolutionary biologists.

Key words: climate; geographic distribution; GIS; ploidy; potato; sect. *Petota*; Solanaceae; *Solanum*.

The occurrence of polyploid series in plants has long held interest to plant systematists and evolutionists. A wide range of effects has been attributed to polyploids relative to their diploid progenitors (Stebbins, 1971; Grant, 1981; Levin, 2002; Soltis et al., 2004). Polyploids are thought to possess transgressive physiological characters such as higher stress and disease tolerances, allowing them to occupy new ecological niches and expand their geographic ranges (Wu et al., 2006). Stebbins (1971) conceived polyploids to be “general-purpose genotypes”. They often possess increased size of certain organs; for example, large seeds from polyploids often produce vigorous seedlings, which aids in establishment and stabilization in new habitats. Hijmans et al. (2007) determined the geographical and environmental correlates of ploidy for the wild taxa of *Solanum* sect. *Petota*, containing wild and cultivated potato. They found multiple cytotypes to exist in 21 wild species. Diploids occupy a larger geographical area than polyploids, but diploid and tetraploid

species have similar range sizes, and the two species with by far the largest range of sizes are tetraploids.

Polyploidy is asymmetrically distributed in the genus *Solanum*, which contains ca. 1500 species (Bohs, 2007) and is mostly confined to the sects. *Petota* and *Solanum*, with scattered polyploids in subgenus *Leptostemonum* and a few other scattered *Solanum* (Hunziker, 2001). The taxonomy of wild and cultivated potatoes (*Solanum* sect. *Petota*) is complicated by sexual compatibility among many species, interspecific hybridization, introgression, a mixture of sexual and asexual reproduction, auto- and allopolyploidy, possible recent species divergence, phenotypic plasticity, and consequent great morphological similarity and difficulty in defining and distinguishing species (Spooner and van den Berg, 1992; Spooner, 2009). These many complicating biological factors have led to great differences among taxonomic treatments of both the wild and the cultivated species. The latest taxonomic estimate in sect. *Petota* is ca. 100 wild species (Spooner, 2009) and four cultivated species (Spooner et al., 2007) divided into three clades (Spooner et al., 2008; Rodríguez et al., 2009; Rodríguez and Spooner, 2009). This differs from the widely used taxonomy of Hawkes (1994), in which 228 wild species and seven cultivated species are divided into 19 tuber-bearing taxonomic series.

Using known crossing data, morphological analyses of Huamán and Spooner (2002), and microsatellite data, Spooner et al. (2007) provided a reclassification of the cultivated potatoes into four species, with two groups defined using the *International Code of Nomenclature for Cultivated Plants*

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(Bricknell et al., 2009): (1) *S. tuberosum*, with the Andigenum Group of upland Andean genotypes containing diploids, triploids, and tetraploids and the Chilotanum Group of lowland tetraploid Chilean landraces, from which our modern cultivars were selected (Ames and Spooner, 2008), (2) diploid *S. ajanhuiri*, formed by hybridization between diploid cultivars of the *S. tuberosum* Andigenum Group and the diploid wild species *S. boliviense* (= *S. megistacrolobum*), (3) triploid *S. juzepczukii*, formed by hybridization between diploid cultivars of *S. tuberosum* Andigenum Group and the tetraploid wild species *S. acaule*, and (4) pentaploid *S. curtilobum*, likely formed by hybridization between tetraploid forms of *S. tuberosum* Andigenum Group and *S. juzepczukii*.

These hybrid origins received further support from GBSSI sequencing data (Rodríguez et al., 2010) and from morphological and microsatellite data (Gavrilenko et al., in press), except *S. ajanhuiri* was not supported in the latter study, possibly due to misidentifications of a few accessions of *S. ajanhuiri* used in that study. *Solanum acaule* and *S. boliviense* are frost-resistant wild species (Hijmans et al., 2003, in which *S. boliviense* is listed as *S. megistacrolobum*) and are thought to be responsible for frost resistance in *S. ajanhuiri*, *S. curtilobum*, and *S. juzepczukii*, allowing them to be grown at presumably higher altitude extremes than *S. tuberosum* (Hawkes, 1990; Ochoa, 1990).

All of the landrace cultivated potato species are indigenous to the South American Andes except the *S. tuberosum* Chilotanum Group that is indigenous to the lowlands of south central Chile. The diploid, triploid, and tetraploid cultivars of the *S. tuberosum* Andigenum Group are widespread throughout northern Colombia to central Bolivia. Tetraploid populations of this group extend slightly more north into western Venezuela and farther south into northern Argentina. In addition, tetraploid landraces of *S. tuberosum* have been cultivated by indigenous peoples in Mexico and Central America. These have been considered to be post-Colombian introductions of the *S. tuberosum* Andigenum Group (Ugent, 1968). However, Zhang et al. (2010) found that seven of 20 landrace accessions of *S. tuberosum* from Mexico and Central America possessed the 241-bp plastid DNA deletion in the *trnV-UAC/ndhC* intergenic region which is absent in 94% (or 95%) of the *S. tuberosum* Andigenum Group and present in 86% (or 81%) of the *S. tuberosum* Chilotanum Group Chilean landraces, depending on the studies of Hosaka (2004) or Spooner et al. (2007), suggesting that landraces from Mexico and Central America had multiple introductions from both the Andes and from lowland Chile.

Polyploidy has had tremendous significance in the taxonomy and systematics of cultivated potatoes. Prior taxonomic systems of cultivated potatoes by Lekhnovich (1971), Bukasov (1978), Hawkes (1990), and Ochoa (1990, 1999) recognized from 7 to 17 cultivated species as distinct Linnaean taxa (McNeill et al., 2006). Dodds (1962), in contrast, recognized three cultivated species with five Groups in *S. tuberosum* (see table 2 of Huamán and Spooner [2002] for a summary of alternative taxonomic systems and Table 1 here for names recognized in the most widely used taxonomic system of Hawkes [1990]). Each former cultivated species name within these traditional taxonomies was partially defined by its ploidal level. It often is impossible to use morphology alone to consistently identify these former taxa (Huamán and Spooner, 2002; Ghislain et al., 2006; Gavrilenko et al., in press), and identifications are frequently changed in gene bank collections when chromosome counts do not match expectations (Spooner et al., 2005; Ghislain et al., 2006; Gavrilenko et al., in press).

Soltis et al. (2007) argued that autopolyploid cytotypes within a species should be formally named and considered to represent species distinct from the diploid progenitor if they fulfilled a range of biological, taxonomic, diagnostic, apomorphic, and evolutionary criteria. Compared to the diploid parent, such recognized autopolyploid species should possess distinct geographic ranges, be distinguished morphologically, and be largely reproductively isolated (via a diversity of mechanisms that could include reproductive or ecological isolation). Cytologically, tetraploid landraces of *S. tuberosum* are autopolyploids (Irikura, 1976; Gavrilenko, 2007), so these criteria should be applicable here, although segmental allopolyploidy has been proposed for other cultivated polyploids: *S. chaucha* (= triploid cytotypes of *S. tuberosum* Andigenum Group), *S. curtilobum*, and *S. juzepczukii* (Matsubayashi, 1991).

The purpose of our study is to provide a geographical and ecological analysis of ploidy variants of cultivated potato and to use these results, in combination with prior morphological, crossing, and molecular data, to test alternative taxonomies of cultivated potato species. Potato is the fourth most important food crop worldwide (FAO, 2009), and these results have tremendous importance for the efficient organization of gene bank accessions, for biogeographical and evolutionary studies, and for the use of genetic resources in breeding.

MATERIALS AND METHODS

Reports of chromosome numbers were obtained by searching the standard cytological indices (Darlington and Janaki Ammal, 1945; Delay, 1951; Darlington and Wylie, 1955, 1961; Cave, 1958a, b, 1959a, b, 1960, 1961, 1962, 1963, 1964, 1965; Ornduff, 1967, 1968, 1969; Federov, 1969; Roitman et al., 1969; Moore, 1970, 1971, 1972, 1973, 1974, 1977; Goldblatt, 1981, 1984, 1985, 1988; Goldblatt and Johnson, 1990, 1991, 1994, 1996, 1998, 2000, 2003, 2006). We discovered other reports through cross referencing (Table 1). Each report was verified by checking the original publications cited therein. We obtained data for *S. acaule* and *S. boliviense*, two species involved in the hybrid origins of the cultivated species *S. ajanhuiri*, *S. curtilobum*, and *S. juzepczukii* from Hijmans et al. (2007). We omitted reports from abstracts of oral presentations, reports involving colchicine-induced polyploids and interspecific hybrids, and reports of accessions maintained at experimental stations. We also excluded reports of modern cultivars, so that only apparent landraces collected in Central or South America (not modern cultivars of potato) were considered in the analysis.

For each report, we summarized the species name recorded in the paper, the current name following the taxonomy of Spooner et al. (2007), the reference for the count, collector and number, collection date, country, state, region, locality, altitude, and latitude and longitude. In total, we analyzed seven classes: (1) *S. ajanhuiri*, (2) *S. juzepczukii*, (3) *S. curtilobum*, (4) *S. tuberosum* Andigenum Group 2x, (5) *S. tuberosum* Andigenum Group 3x, (6) *S. tuberosum* Andigenum Group 4x, (7) *S. tuberosum* Chilotanum Group, all are 4x. For the latter, we mapped only the cultivars, not the apparent escapes from cultivation in the Chonos Archipelago (Contreras et al., 1993). When latitude and longitude were not provided, we determined these data when possible using maps and digital gazetteers. Geographical coordinates were checked by overlay techniques as described in Hijmans et al. (1999), by inspecting distribution maps for each species, and by looking for climatic outliers using DIVA-GIS (Hijmans et al., 2004). Our database is deposited online as Appendix S1 (see Supplemental Data online at <http://www.amjbot.org/cgi/content/full/ajb.1000277/DC1>).

Environmental data preparation—The records were annotated using global grids of 20 variables at 10-min resolution from the world climate database (Hijmans et al., 2005). We assessed mean values for 19 bioclimatic “niche variables”: annual temperature, monthly temperature range, isothermality (mean diurnal range/temperature annual range, which quantifies “hot” vs. “cold” regions), temperature seasonality (the difference between winter and summer temperature, measured as the coefficient of variance, $CV \times 100$), maximum temperature of warmest month, minimum temperature of coldest month, temperature annual

TABLE 1. Reports of ploidy determination in cultivated potatoes. Numbers in parentheses are the actual total counts used in analysis. The numbers in boldface below Data sources for species *S. tuberosum* indicate chromosome counts of 24, 36, or 48.

Species	2n chromosome number				Data sources
	24	36	48	60	
<i>Solanum ajanhuiri</i>	28 (18)				Juzepczuk and Bukasov, 1929; Rybin 1933; Ochoa 1958, 1964; Gavrilenko et al., in press
<i>S. juzepczukii</i>		83 (73)			Juzepczuk and Bukasov, 1929; Rybin, 1933; Ochoa, 1958, 1964; Gavrilenko et al., in press
<i>S. curtilobum</i>				51 (42)	Juzepczuk and Bukasov, 1929; Rybin, 1933; Lamm, 1941; Ochoa, 1958, 1964; Gavrilenko et al., in press
<i>S. tuberosum</i> Andigenum Group ^a	562 (380)	227 (176)	2437 (1784)		24: Juzepczuk and Bukasov, 1929; Rybin, 1929, 1933; Bukasov, 1937; Sidorov, 1937; Choudhuri, 1943, 1944; Hawkes, 1944; Lamm, 1945; Ochoa, 1958, 1964; Matsubayashi, 1962; Jackson et al., 1980; Bamberg et al., 1996; Gavrilenko et al. in press; NRSP-6 website ^b 36: Juzepczuk and Bukasov, 1929; Rybin, 1929, 1933; Vavilov, 1935; Hawkes, 1944; Lamm, 1945; Ochoa, 1958, 1964; Brücher, 1960; Jackson et al., 1980; Gavrilenko et al., in press 48: Juzepczuk and Bukasov, 1929; Rybin, 1929, 1933; Juzepczuk, 1937; Sidorov, 1937; Ratera, 1942, 1944; Hawkes, 1944; Lamm, 1945; Ochoa, 1958, 1964; Brücher, 1969; Jackson et al., 1980; Spooner et al., 1994; Bamberg et al., 1996; Castillo and Spooner, 1997; Salas et al., 2001; Gavrilenko et al. in press; NRSP-6 website ^b 48: Rybin, 1929, 1933; Juzepczuk, 1937; Sidorov, 1937; Ratera, 1942; Avanzi, 1949; Brücher, 1966; Lekhnovich, 1978; Bamberg et al., 1996; Gavrilenko et al., in press; NRSP-6 website ^b 96 (one count): Ratera, 1942
<i>S. tuberosum</i> Chilotanum Group ^a			181 (131)		

^a Hawkes (1990) recognized the following names (indented), which Spooner et al. (2007) and we recognize as synonyms.

S. tuberosum Andigenum Group diploids

S. phureja Juz. and Bukasov subsp. *phureja*

S. stenotomum Juz. and Bukasov subsp. *stenotomum*

S. stenotomum subsp. *goniocalyx* (Juz. and Bukasov) Hawkes

S. tuberosum Andigenum Group triploids

S. chaucha Juz. and Bukasov

S. tuberosum Andigenum Group tetraploids

S. phureja subsp. *estradae* (L. López) J. G. Hawkes

S. phureja subsp. *hygrothermicum* (Ochoa) J. G. Hawkes

S. tuberosum subsp. *andigenum* Hawkes

S. tuberosum Chilotanum Group (all tetraploids)

S. tuberosum subsp. *tuberosum*.

^b See counts listed on the website of the United States Potato Genebank (USDA, 2010).

range, temperature of wettest quarter, temperature of driest quarter, temperature of warmest quarter, temperature of coldest quarter, annual precipitation, precipitation of wettest month, precipitation of driest month, precipitation seasonality (CV), precipitation of wettest quarter, precipitation of driest quarter, precipitation of warmest quarter, and precipitation of coldest quarter; we also assessed the absolute values of latitude as a 20th variable. The absolute value of latitude is an indicator of daylength seasonality.

Environmental modeling: Do the environmental variables form niches corresponding to the species?—One common view of the ecological niche developed by Grinnell (1917; cited after Morrison and Hall, 2002) is a set or range of environmental features that enable individuals to survive and reproduce. This idea was generalized by Hutchinson (1957) to the concept that a set of environmental factors describes the distribution of a species (Morrison and Hall, 2002). Thus, environmental factors may be used to “profile” a species. We used the randomForest library (Liaw and Wiener, 2002) (in R; R Development Core Team, 2010) to examine association of our seven classes to the 20 variables. The randomForest builds a set of regression trees. Each regression tree is used to predict the response variable. Using sampling with replacement, hundreds of trees are built, and a final overall result is calculated. The algorithm calculates how reliably the distribution of a species can be predicted based on the variables, using a simple error rate.

Intermediate habitats for three cultivated hybrid species—We tested case (a) whether *S. ajanhuiri* occupies an intermediate habitat of *S. boliviense* and

diploid populations of the *S. tuberosum* Andigenum Group, case (b) whether *S. juzepczukii* occupies an intermediate habitat of *S. acaule* and diploid populations of the *S. tuberosum* Andigenum Group, and case (c) whether *S. curtilobum* occupies an intermediate habitat of *S. juzepczukii* and tetraploid populations of the *S. tuberosum* Andigenum Group. To this end, all accessions for each test were restricted to the latitude range of the hybrid: for case (a), *S. ajanhuiri* (18), *S. boliviense* (36), diploid Andigenum Group (144); for case (b), *S. acaule* (381), *S. juzepczukii* (73), diploid Andigenum Group (221); for case (c), *S. curtilobum* (42), *S. juzepczukii* (73), tetraploid Andigenum Group (1138). The randomForest results indicate whether the hybrid habitats can be predicted without error.

Altitude range—We tested whether *S. ajanhuiri*, *S. curtilobum*, and *S. juzepczukii* (group 1) occurred at significantly higher altitude ranges than the *S. tuberosum* Andigenum Group (all ploidy variants together), using only accessions in the same overlapping latitude ranges, using the one-sided Kolmogorov–Smirnov test (in R). This nonparametric test compares both the location of a probability distribution and the shape. We used the violin plot (Hintze and Nelson, 1998) to visualize the results. A violin plot shows the density distribution of data. It is related to the box plot in that it provides a summary overview but gives more information about the distribution.

Northern and southern range extension of the tetraploid populations of the *S. tuberosum* Andigenum Group—We used the function importance in the randomForest algorithm to assess the relative importance of 20 variables that are

associated with the northern and southern range extension of the tetraploid populations of the *S. tuberosum* Andigenum Group north and south of the area where diploids and triploids occur. For this, we divided the tetraploid populations into three geographic areas: (1) Mexico and Central America, Venezuela; (2) Colombia to central Bolivia; (3) southern Bolivia to northern Argentina.

Comparison of ecological niches of (1) different *S. tuberosum* Andigenum Group ploidy levels and (2) tetraploid populations of *S. tuberosum* Andigenum vs. *Chilotanum* Group—Similar to the previous assessment, we used the randomForest algorithm to examine possible ecological niches associated with the three ploidy levels of *S. tuberosum* Andigenum Group from South America (excluding the populations from Mexico and Central America). As before, the relative importance of variables was assessed using results from the randomForest library.

Richness analysis—We examined the richness of taxonomic and ploidal levels by (1) using MaxEnt (Phillips et al., 2006) to calculate the probability at each geographic unit or pixel, (2) using the p -value of the threshold “maximum training sensitivity and specificity” to include only geographic units for each taxonomic and ploidy class where the probability of presence was significant, (3) summing up these values for all classes, and (4) the sum was also adjusted for the different areas of each unit area at different latitudes. This analysis results in a high-resolution richness map based on the probable predicted geographic distribution. Maps were constructed using the software packages maps (Brownrigg et al., 2007), RColorBrewer (Neuwirth, 2007) and maptools (Lewin-Koh et al., 2008) in R.

Extent of geographic coverage of taxonomic groups—The area of the distribution of each species and the ploidy levels within the *S. tuberosum* Andigenum Group were calculated using the presence probabilities calculated by MaxEnt for each geographic unit or pixel and again only counting areas with a significant probability of presence as determined by a significance threshold calculated by MaxEnt (see *Richness analysis*). To ease comparison, we used relative area amounts; to this end, the taxonomic and ploidy classes with the smallest area were set to 1, and the expected areas covered by other classes were expressed as multiples.

RESULTS

General distributional data—The final database of the landraces (excluding *S. acaule* and *S. boliviense*) included 2780 records; of these, 2048 had existing latitude and longitude data or had sufficient locality information for us to determine these data (Table 1). The tetraploids extend their range to the north in Venezuela and Central America and Mexico, and to the south in southern Bolivia and northern Argentina (Fig. 1A–C). The *S. tuberosum* Chilotanum Group is exclusive to central and south central Chile, with a break in distribution of 560 km from the southernmost record of the Argentinean populations of the Andigenum Group (Fig. 1D). The hybrid potatoes *S. ajanhuiri*, *S. curtilobum*, and *S. juzepczukii* have much smaller distributions and are restricted to central Peru and Bolivia (Fig. 1E–G, 2A).

Environmental modeling—The results from the randomForest analysis show a very high average error rate of 27% for the seven classes. *Solanum ajanhuiri* has a classification error rate of 100%; four classes (*S. curtilobum*, *S. juzepczukii*, *S. tuberosum* Andigenum Group diploid, *S. tuberosum* Andigenum Group triploid) have error rates over 50%, the tetraploid *S. tuberosum* Andigenum Group an error rate of 11%, but the *S. tuberosum* Chilotanum Group had 0%. This indicates that *S. tuberosum* Chilotanum Group, but not the other six classes, can be well distinguished by environmental variables.

Intermediate habitats for three cultivated hybrids—(Case a) Only two of the 18 populations of *S. ajanhuiri* were predicted by the randomForest method as *S. ajanhuiri*; one is predicted as *S. boliviense* and 15 as diploid populations of *S. tuberosum* Andigenum Group (an 88.8% error rate).

(Case b) Of 74 populations of *S. juzepczukii*, nine are predicted as *S. acaule*, 33 as *S. juzepczukii*, and 32 as diploid *S. tuberosum* Andigenum Group (55.4% error rate). (Case c) Of the 44 populations of *S. curtilobum*, only four are classified as *S. curtilobum*, five as *S. juzepczukii*, and 35 as tetraploid populations of *S. tuberosum* Andigenum Group (90.9% error rate). In summary, all results show both the hybrid potatoes and their parents to have similar habitats.

Altitude range—There is no significant difference in altitude among six of the seven cultivated potato classes; only the *S. tuberosum* Chilotanum Group grows at a significantly lower altitude (Fig. 2B).

Southern and northern range extensions of tetraploid populations of the *S. tuberosum* Andigenum Group—The subset of tetraploid populations of the *S. tuberosum* Andigenum Group growing south of diploid populations (central Bolivia into northern Argentina) can be clearly predicted; the predicted set has only one accession out of 87 that is misclassified as a diploid population of the Andigenum Group (error rate of 1.1%). The most important predictive variable is temperature seasonality (standard deviation $\times 100$). The median value for tetraploid populations of the Andigenum Group is 414 (4.14°C) vs. 185 for the diploid Andigenum Group. High values of temperature seasonality indicate high variability of temperatures, and low values indicate low variability or a more uniform climate. Thus, diploid cultivars of the *S. tuberosum* Andigenum Group are present in more uniform climates than the tetraploid cultivars. The northern range expansion of the tetraploids into Venezuela and Mexico and Central America can be clearly classified but with a slightly higher error rate (9%). For this expansion, the most important environmental variable to distinguish both geographic subsets is the precipitation seasonality. Whereas diploid members of the Andigenum Group have a median value of 79 for precipitation seasonality, tetraploid populations north of the diploid populations have a median of 101.

Comparison of *S. tuberosum* Andigenum Group (all ploidy levels) and *Chilotanum* Group—These two groups can be clearly classified without any error based on the niche variables. The most important distinguishing variable is the absolute value of latitude (Fig. 3); the Andigenum Group has a median of 14° latitude and the Chilotanum Group a median of 42° latitude. The niche variable isothermality is the second most important, monthly mean temperature range third, and altitude fourth (Fig. 2B).

Comparison of ecological niches of different *S. tuberosum* Andigenum Group ploidy levels—Within the overlapping latitudinal range of the Andigenum Group, the overall prediction error rate is 27.4%. For diploid members of the Andigenum Group, the misclassification reaches 54%, for triploid 71% and for tetraploid 11%. This indicates that the three ploidy levels cannot be reliably distinguished by ecological criteria within their area of sympatry. However, the tetraploids have been successful in extending their ranges north and south of the main diploid distribution.

Richness analysis, coverage—The results show that the highest diversity of the seven cultivated classes is north and south of Lake Titicaca in the Bolivia–Peru border; a wider range of diversity is between 8° and 20° southern latitude (Fig. 3). The smallest coverage is occupied by *S. ajanhuiri*, *S. juzepczukii*,

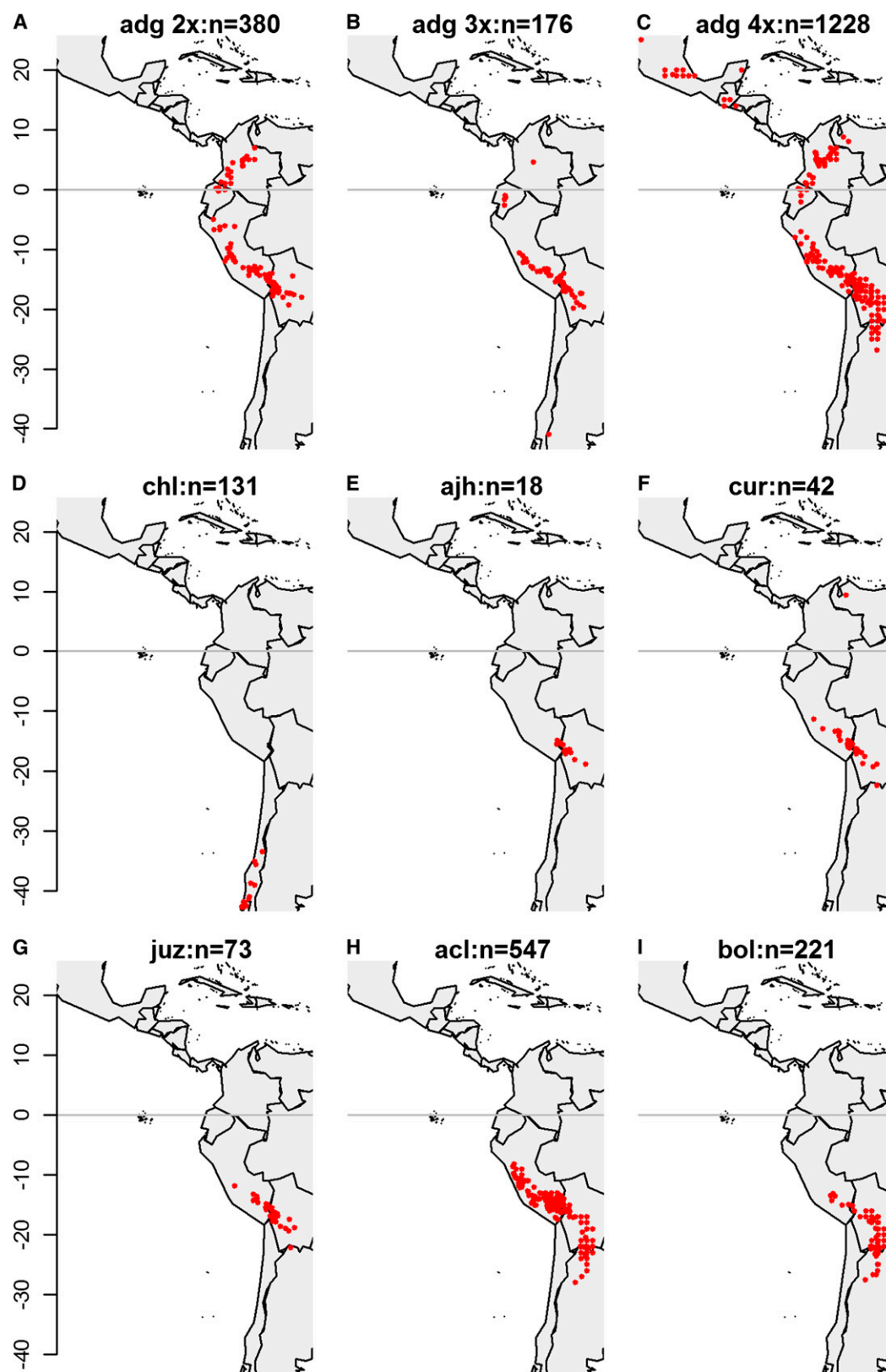


Fig. 1. Geographic distribution of ploidy accessions of the three ploidy levels of (A–C) *S. tuberosum* Andigenum Group (adg), (D) *S. tuberosum* Chilotanum Group (chl), (E) *S. ajanhuiri* (ajh), (F) *S. curtilobum* (cur), (G) *S. juzepczukii* (juz), and the wild species (H) *S. acaule* (acl, involved in the hybrid origin of *S. curtilobum* and *S. juzepczukii*) and (I) *S. boliviense* (bol, involved in the hybrid origin of *S. ajanhuiri*). The maps are labeled by the abbreviated codes listed plus the number of mapped accessions.

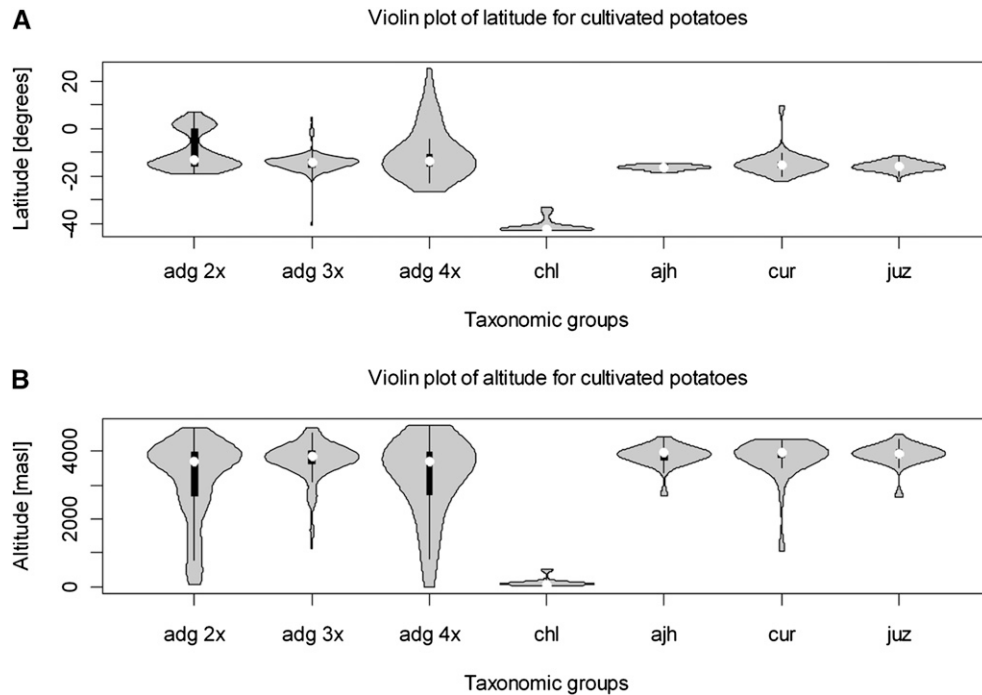


Fig. 2. Violin plots showing the density distribution of all seven classes of cultivated potatoes along the variables (A) latitude and (B) altitude. Abbreviations: *S. tuberosum* Andigenum Group (adg), *S. tuberosum* Chilotanum Group (chl), *S. ajanhuiri* (ajh), *S. curtilobum* (cur), and *S. juzepczukii* (juz).

and the *S. tuberosum* Chilotanum Group. About double the geographic area of the preceding three taxa is occupied by triploid *S. tuberosum* Andigenum Group and *S. curtilobum*. The largest area of landraces is clearly occupied by the diploid and tetraploid populations of *S. tuberosum* Andigenum Group (Fig. 1).

DISCUSSION

Summary of geographical and ecological analyses—This is the first geographic analysis of ploidy variation in the landrace cultivated potatoes. It documents that landrace potato populations are widely distributed in the uplands of the Andes from Venezuela south to northern Argentina, with a break in distribution of 560 km to the lowlands of central to south-central Chile. Post-Colombian landrace introductions continue to be cultivated in Mexico and Central America (Ugent, 1968), as they are elsewhere in the Canary Islands (Ríos et al., 2007) and India (Spooner et al., 2005). The majority of the range of *S. tuberosum* and most of its ploidy variation occur from northern Peru to central Bolivia (Fig. 4). The *S. tuberosum* Andigenum Group dominates the geographical coverage of the landraces, with the tetraploids most widespread, followed by diploid and triploid ploidy levels. Except for the *S. tuberosum* Chilotanum Group and the extreme northern and southern range extensions of the tetraploid populations of the Andigenum Group, it is difficult to define distinct habitats for the ploidy variants of the *S. tuberosum* Andigenum Group that are recognized as distinct Linnaean taxa by the taxonomic systems of Bukasov (1978), Ochoa (1990, 1999), or Hawkes (1990) (Table 1, footnote 1). Such distinct habitats also do not occur for *S. ajanhuiri*, *S. curtilobum*, and *S. juzepczukii*, species we recognize, but that are clearly distinguished by morphological (Huamán and Spooner, 2002) and microsatellite data (Spooner et al., 2007;

Gavrilenko et al., in press) and have distinct allopolyploid origins (Rodríguez et al., 2010).

Crossability data—Two considerations bear on the question of whether cultivated landraces are to be considered a single biological species. First, are the groups sexually compatible and thus capable of genetic exchange? If so, are they actually undergoing recombination in their natural environment, resulting in a single biological species? Because the cultivated landraces exist in a polyploid series, both intraploidy and interploidy crosses must be considered. Artificial intraploidy crosses within both diploid and tetraploid cultivated potatoes can be made without difficulty (Glendinning, 1969; Haynes et al., 1995). Thus, in natural conditions, hybrid swarms of weedy *S. ajanhuiri* have been found in potato fields containing both *S. ajanhuiri* as a crop and diploid *S. tuberosum* (as *S. stenotomum*, Johns and Keen, 1986; Johns et al., 1987). Within the diploids, *S. stenotomum* is readily crossable with *S. phureja* reciprocally (Matsubayashi, 1991). In addition, regular bivalent chromosome pairing has been observed in diploid hybrids of cultivated potato, such as between diploid members of the *S. tuberosum* Andigenum Group (= *S. stenotomum* and *S. phureja*; Matsubayashi, 1991).

Among ploidy levels, frequent genetic exchange is not only well documented, but it is considered to be important in the evolution of *Solanum* species (Carpato et al., 2003; Den Nijs and Peloquin, 1977). Endosperm failure typically prevents the formation of triploid hybrids from crosses between cultivated diploids and tetraploids (Marks, 1966b). Endosperm balance number (EBN) provides a system to predict endosperm failure (Hanneman, 1994). *Solanum* species have been assigned EBN values such that inter-EBN crosses typically fail, while intra-EBN crosses are successful, barring other incompatibility mechanisms. However, the widespread occurrence of $2n$ gametes (gametes with the

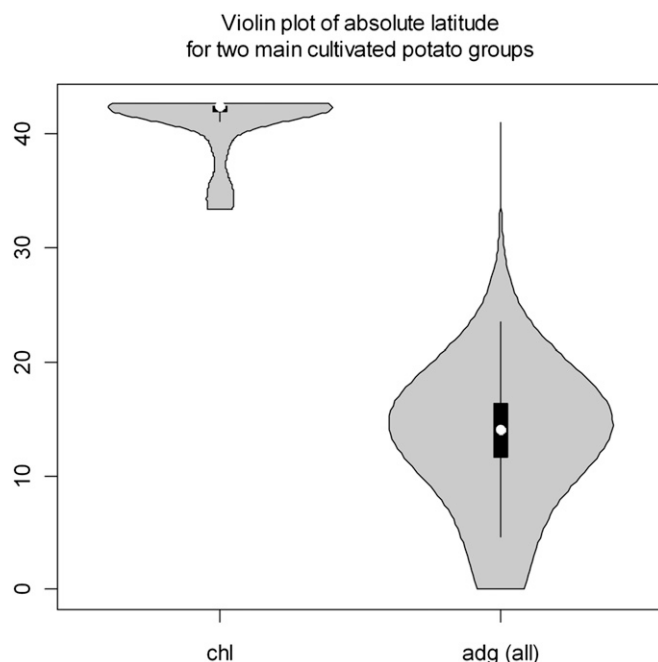


Fig. 3. Violin plots showing the density distribution of *S. tuberosum* Chilotanum Group (chl) vs. all ploidy levels of the *S. tuberosum* Andigenum Group (adg) along the variable absolute degrees of latitude.

somatic chromosome number) in diploid potatoes allows for genetic exchange with tetraploids (Quinn et al., 1974; Den Nijs and Peloquin, 1977; Jackson and Hanneman, 1999). Tetraploid offspring are produced following the hybridization of $2n$ -gamete-producing diploids. In addition to $2n$ -gamete-mediated genetic exchange between diploids and tetraploids, some sexual offspring are produced in the absence of $2n$ gametes.

The triploid block is not complete in cultivated potato, and it seems to be weaker in *S. tuberosum* Andigenum Group than in the Chilotanum Group (Marks, 1966a). Consequently, crosses between tetraploid and diploid populations of the *S. tuberosum* Andigenum Group have been reported to produce triploid offspring (Jackson et al., 1977, 1978). The widespread occurrence of $2n$ gametes in diploid potatoes also leads to formation of autotriploid forms (cytotypes) (Bukasov 1978). That's why triploid populations of the Andigenum Group are highly polymorphic and widespread in Andean production regions (Marks, 1966a; Bukasov, 1978; Gavrilenko et al., in press). Because of their diversity, it is likely that they are produced regularly in nature and that they continue to hybridize with *Solanum* relatives.

Gene flow from tetraploids to diploids can occur through triploids. Therefore, while $2n$ gametes allow for gene flow from diploids to tetraploids, triploids permit gene flow back to the diploid level because allotriploids might produce haploid gametes in $3x \times 2x$ crosses (Marks, 1966a).

Triploids carrying genes for $2n$ gamete production can regularly produce balanced 36 chromosome gametes. For example, triploid hybrids were created from crosses between the Mexican $4x$ (2EBN) species *S. stoloniferum* and $2x$ (2EBN) cultivated diploids (Brown, 1988). Both parents were selected for $2n$ pollen production, which is a recessive trait. Consequently, fertile $2n$ pollen was formed by their triploid offspring, allowing them to be crossed with $4x$ potato breeding cultivars (of hybrid origin with *S. demissum*) (Brown and Adiwilaga, 1990).

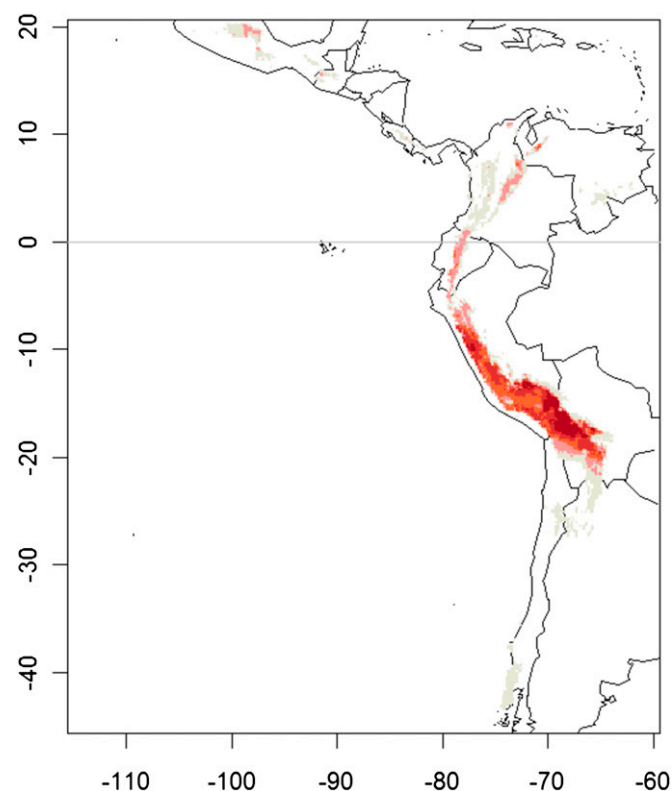


Fig. 4. Richness map of cultivated potato. The darker the shades of red the higher the total probability of cultivated potatoes summed over seven taxonomic and ploidy classes. Probabilities were calculated using MaxEnt.

Adiwilaga and Brown (1991) extended the triploid technique to $4x$ (2EBN) North and Central American species in the series *Longipedicellata* to include *S. stoloniferum*. The species were crossed as females to $2x$ (2EBN) cultivated species in *S. tuberosum* Andigenum Group plants selected for $2n$ pollen production. Several of the resulting triploids produced $2n$ pollen and were successfully crossed as males to $4x$ (4EBN) cultivars. When crossed with tetraploids, pentaploid offspring were produced. The pentaploid *S. curtilobum* was likely produced from the union of $2n$ gametes from triploid *S. juzepczukii* and normal gametes from tetraploid *S. tuberosum* Andigenum Group. This hybrid has been recreated artificially using this scheme (Schmiediche et al., 1980, 1982; Hawkes, 1990). Pentaploid *S. curtilobum* is fertile and able to hybridize with *S. tuberosum* (Hawkes, 1990). Pentaploid landraces, therefore, are not genetically isolated from the remainder of the cultivated gene pool. Consequently, some level of genetic recombination is likely to occur in hybrids among landraces. With every generation of sexual reproduction among the Groups, this recombination blurs genetic boundaries.

Andean farmers actively pursue genetic diversity among landrace cultivars (Quiros et al., 1990). Gene exchange among diverse genotypes is thought to be important for crop sustainability because it results in increased genetic diversity, disease resistance, and adaptability to climate change (Ugent, 1970). Each potato field typically contains a diversity of cultivars and ploidy levels (Jackson et al., 1980; Brush et al., 1981; Quiros et al., 1990; Zimmerer, 1991). In southern Peru, up to five tubers are placed into a single hole when the crop is planted. These tubers are often from different cultivars and ploidy levels (Quiros et al., 1990). This planting strategy serves at least three purposes

(Quiros et al., 1992): (1) it allows the farmer to produce a food crop that is variable for flavor and appearance, (2) it provides a buffer against pest and disease damage, (3) it allows the farmer to produce tubers for different culinary purposes.

The potato production system in the Andean highlands allows for the introduction of new genotypes via sexual reproduction. In the Peruvian Andes, a potato crop is typically followed in the next production year by another tuber crop (Jackson et al., 1980; Brush et al., 1981). During the potato crop year, sexual hybridization among cultivars in the same field will produce berries containing seeds. Some of those seeds will germinate during the following year. Tubers from those potato seedlings will be harvested along with the second tuber crop, separated from the crop, and saved for propagation (Jackson et al., 1980). In western Bolivia, the potato crop is often followed by a non-tuber crop derived from seedlings. However, in that second year of production, volunteer potatoes from the previous year are harvested. Consequently, tubers from seedlings would also be collected, allowing new genotypes to be introduced (Johns and Keen, 1986). In addition, farmers are known to collect open-pollinated true seed from their fields and select among seedling transplants for desirable phenotypes (Quiros et al., 1992). In any case, sexual hybrids have the opportunity to enter the complex array of landrace cultivars. These sexual hybrids could be from intraploidy crosses or, as discussed already, from interploidy crosses.

Self-pollination is common in polyploid potato, both cultivated and wild (Krantz and Hutchins, 1929; Camadro and Peloquin, 1982). Consequently, some naturally formed seeds in farmers' fields are likely products of selfing. However, as long as cultivars overlap in their flowering periods and bees move among cultivars, cross pollination is expected to occur as well. At the diploid level, a self-incompatibility system prevents the formation of self-pollinated seed. Consequently, open-pollinated seed are likely to be hybrids. In fact, 95% of seedlings from open-pollinated berries were found to be hybrids when *S. brevicaulle* (as *S. sparsipilum*) and diploid members of *S. tuberosum* Andigenum Group were grown near each other in experimental plots in Peru (Rabinowitz et al., 1990).

Hybridization in landrace cultivars is probably not only likely, but also necessary for the vitality of the potato crop in the long term. According to Grun (1990, p. 46), tetraploid members of the *S. tuberosum* Andigenum Group act like a "genetic sponge, absorbing genes via introgression from closely wild species, or other cultivated populations with which it hybridize[s]." This has allowed the Andigenum Group to expand to include countless variants through the processes of hybridization, recombination, and segregation. This massive variation is reflected in the more than 400 synonyms for *S. tuberosum* (Ovchinnikova et al., in press). Quiros et al. (1992, p. 112) suggested, "The Andean potato is a large and plastic gene pool being increased and renovated by outcrossing."

In conclusion, many simultaneous lines of evolution have likely contributed to the development of primitive diploid and polyploid potato cultivars (Ugent, 1970). The cultivated potatoes have frequent genetic exchange among ploidy levels, a high incidence of interspecific hybridization, a low degree of genomic differentiation, and a high level of diversity among cultivars (Ugent, 1970). Even if polyploids arise by independent events, gene flow from interbreeding homogenizes differences due to their evolutionary origins (Soltis et al., 2007). Some results (the southern and northern range expansions described) indicate that tetraploids occur over a wider range

of habitats (temperature seasonality for example) coinciding with the general idea of broader adaptability of polyploids (Ehrendorfer, 1980; Grant, 1981; Levin, 1983). However, in the case of cultivated plants, this is being confounded by human impact. Humans may have selected tetraploids over diploids if they were linked to useful traits such as appearance, taste, or yield. For cultivated plants, one could argue that utility is one more dimension of their niche. But there is also an element of chance in history and selection for varieties that are actually selected and where they are grown. Thus, the question of broader inherent adaptation capacity of polyploids is difficult to resolve in cultivated potatoes.

Taxonomic conclusions—Our present ploidy and ecological analysis follows prior morphological analyses of Huamán and Spooner (2002) and Gavrilenko et al. (in press), microsatellite analyses by Raker and Spooner (2002) and Ghislain et al. (2006), and morphological and microsatellite analyses by Gavrilenko et al. (in press). All these recent studies fail to support the cultivated potato taxonomies of Bukasov (1978), Hawkes (1990), and Ochoa (1990, 1999), all of which fail to provide repeatable, reliable, and phylogenetically supportable classifications. These previous systems have all relied on ploidal level as one of a major set of discriminating factors, together with morphology and geography, for the names that Spooner et al. (2007) place in synonymy under the *S. tuberosum* Andigenum Group (Table 1, footnote 1).

Soltis et al. (2007) argued that an autopolyploid cytotype should be formally named and considered to represent a species distinct from its diploid progenitor if it fulfilled a range of biological, taxonomic, diagnosability, apomorphic, and evolutionary criteria. They applied this concept to wild species, but for taxonomic considerations, the concept should apply to cultivated species as well. We agree with this view, and our study was stimulated by an examination of geographical and ecological factors that may provide support for formal taxonomic recognition of ploidy variants within the *S. tuberosum* Andigenum Group. *Solanum ajanhuiri*, *S. curtilobum*, and *S. juzepczukii* are all the result of hybridization at either the diploid level or are allopolyploids and are recognizable by morphological and molecular criteria; we recognize them at the species level here. The *S. tuberosum* Chilotanum Group can be distinguished by its geographical range alone, and only with difficulty, by morphological, molecular, or crossing data; we circumscribe it as a group according to the ICNCP (Bricknell et al., 2009), but not using the ICBN (McNeill et al., 2006). The failure of taxonomic, diagnostic, apomorphic, and evolutionary species concepts to provide that support justifies placing all ploidy variants of the *S. tuberosum* Andigenum Group in synonymy. This circumscription is supported by studies of Huamán and Spooner (2002), Ghislain et al. (2006), and Gavrilenko et al. (in press). We have summarized the lack of biological barriers among the ploidy variants of the *S. tuberosum* Andigenum Group. The present analysis documents extensive geographical overlap and indistinguishable habitats throughout the majority of the range of the names we now recognize as synonyms. We consider our revised four-species taxonomy of cultivated potato now to be upheld by every major criterion used to define species.

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