Diversity and distribution of andean tubers (*Solanum tuberosum, Oxalis tuberosa, Ullusus tuberosus* y *Tropaeolum tuberosum*): an agrogeographic analysis

Diversidad y distribución de tubérculos andinos (*Solanum tuberosum*, *Oxalis tuberosa*, *Ullusus tuberosus* y *Tropaeolum tuberosum*): un análisis agrogeográfico

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Abstract. Andean tubers are a group of basic plants in the security and food sovereignty of Andean community for thousands of years. The conservation of the infra and interspecific diversity of these plants is a strategy for environmental adaptation rooted in the high-Andean cultural identity. *Solanum tuberosum*, *Oxalis tuberosa*, *Tropaeolum tuberosum* and *Ullucus tuberosus*, have in common that they develop edible modified stems with a wide variety of shapes, colors, and flavors, and these are cultivated in the Andean countries. The high diversity of Andean tuberous species is heterogeneously distributed and concentrated in micro-centers of diversification distributed in South American countries. The aim of this work was to determine the general distribution pattern of the four mentioned species and their agrogeographic nodes. With the coordinates of presence of these four species, registered in the GBIF platform (Global Biodiversity Information Facility), biogeographical methods were applied to model the individual traces that show the distribution pattern of each species and through the intersection of these, a generalized trace that makes visible the distribution patterns of Andean tubers, as well as their agro-geographical nodes. The greatest diversity of the four species is concentrated in these intersections, favoring domestication scenarios. Some micro-centers of diversity identified, correspond to those defined in the investigations of morphological or molecular characterizations. The main nodes were found in Peru and Ecuador between the biogeographic provinces of Puno, in the South American Transition Zone and the Yungas, from the southern Brazilian domain. The study of the geographical distribution patterns of cultivated plants allows to identify the patterns of plant exchange of the human groups involved in their management. The study of the geographical distribution patterns of cultivated plants allows to identify the patterns of plant exchange of the human groups involved in their management.

Keywords: biodiversity, domestication, native, geographic information system.

Resumen. Los tubérculos andinos son un grupo de plantas fundamentales para la seguridad y soberanía alimentaria de pueblos andinos desde hace miles de años. La conservación de su diversidad infra e interespecífica es una estrategia de adaptación ambiental arraigada en la identidad cultural alto-andina. *Solanum tuberosum*, *Oxalis tuberosa*, *Tropaeolum tuberosum* y *Ullucus tuberosus,* tienen en común que desarrollan tallos modificados comestibles con una amplia diversidad de formas, colores y sabores, y son cultivados en la cordillera de los Andes. La alta diversidad de las especies tuberosas se distribuye de manera heterogénea y se concentra en microcentros de diversificación distribuidos en los países suramericanos. El objetivo de este trabajo fue determinar el patrón de distribución general de las cuatro especies mencionadas y sus nodos agrogeográficos. Con las coordenadas de presencia de estas cuatro especies, registradas en la Plataforma GBIF (*Global Biodiversity Information Facility*), se aplicaron métodos biogeográficos para modelar los trazos individuales que evidencian el patrón de la distribución de cada especie y mediante la intersección de estos se obtuvo un trazo generalizado que visibiliza los patrones de distribución de los tubérculos andinos, así como sus nodos agrogeográficos. En estas intersecciones se concentra la mayor diversidad de las cuatro especies, propiciando escenarios de domesticación. Algunos microcentros de diversidad identificados corresponden con los definidos en las investigaciones por medio de caracterizaciones morfológicas o moleculares. Los principales nodos se encontraron en Perú y Ecuador entre las provincias biogeográficas de Puno, de la Zona de Transición Suramericana y los Yungas, del dominio Brasilero del Sur. El estudio de los patrones geográficos de distribución de las plantas cultivadas permite identificar los patrones de intercambio vegetal de los grupos humanos involucrados en su manejo. Los resultados soportan la hipótesis de que los tubérculos andinos fueron domesticados inicialmente en la sierra peruana y de ahí se distribuyeron hacia el norte y hacia el sur de los Andes.

Palabras clave: biodiversidad, domesticación, semillas nativas, sistema de información geográfica.

Introduction

A basic group in the security, food sovereignty and cultural identity of the Andean countries is the one made up of tubers, among which are "ibias" or "ocas" (*Oxalis tuberosa* Molina), "cubios", "nabos" or "majuas" (*Tropaeolum tuberosum* Ruiz & Pav.), "chuguas" or "ullucos" (*Ullucus tuberosus* Caldas) and potatoes (*Solanum tuberosum* L.), all with a wide diversity in the inter-Andean valleys (Clavijo-P. et al., 2014; García et al., 2018; Viteri et al., 2020).

Oxalis tuberosa has been used by Andean populations for thousands of years, it has an adaptation to environments where other crops cannot survive, including tolerance to cold climates, thrives in soils with pH of 5.3 to 7.8, resistant to various pests and other phytosanitary problems (Rosero, 2010; Clavijo-P. & Pérez-M., 2014).It is probable that this species or some related ones, have been consumed and perhaps cultivated by the inhabitants of the inter-Andean valleys since the Holocene (Clavijo-P. et al., 2014). Rosero-A. (2010) identified the south of the department of Nariño, especially the municipalities of Cumbal, Guachavéz, El Encano and Puerres, as the area of greatest diversity of this species in the department. Although the species is a material that propagates vegetatively cycle after cycle, there is evidence of variation at the phenotypic and genotypic level that should be conserved and used for the generation of new and better materials that respond to the interests of farmers, producers and consumers (Morillo et al., 2016; Clavijo-P. y Pérez-M., 2014), but conserving native germplasm to avoid its loss.

The *Tropaeolum tuberosum*, like *O. tuberosa* thrives in cold climates and is tolerant of various types of pests and diseases, but its taste is not very liked by the population due to its strong bitter taste caused by the high content of isothiocyanates derived from glucosinolates (Grau et al*.,* 2000) which has decreased its consumption, despite presenting high nutritional and very possibly medicinal value (Leidi et al., 2018). Two possible domestication centers are proposed for this species, the highlands located between Peru and Bolivia and the Cundiboyacense savanna in Colombia, where varieties with dissimilar morphological and physiological characteristics are found (Grau et al., 2003; Tapia & Fries,2007). However, Seminario (2004), considers that the tuberization phenomenon is related to adaptations to areas with prolonged periods of drought, rare phenomena in the Colombian region. Manrique et al*.* (2014) identified the micro-centers of diversity by morphological characterization of 107 accessions; finding that the states of Huancavelica, Junín, Pasco and Cusco represent 62% of all Peruvian accessions (Manrique et al., 2014). In the state of Cusco, Ortega et al. (2007), analyzed the patterns of genetic diversity of cultivated and wild populations of *T. tuberosum*, a wide genetic diversity was found, and it was determined that wild populations are closely related to cultivated ones. These results strengthen the Cusco region as a micro center of diversity of *T. tuberosum*.

Ullucus tuberosus and *T. tuberosum* have been shown to have more than 35% starch, along with high resistance to pests, low temperatures and drought (Campos et al., 2018; Naranjo et al., 2017). Tapia & Fries (2007) consider that one of the domestication centers of *U. tuberosus* is Colombia, since the cultivated morphotypes present wild characteristics such as creeping growth and smaller diameter of the tubers. However, Parra-Q et al. (2012) suggest that the site of origin was in the central Andes, between Peru and Bolivia, from where it was dispersed semi-domesticated towards Colombia and later the erect growth morphotypes were domesticated that had a new wave of dispersal towards the north. In Colombia, in the departments of Boyacá and Cundinamarca, 36 accessions were morphologically and molecularly characterized and it was concluded that the populations of the center of the country correspond to the subspecies in the process of domestication, given its decumbent growth and its genetic distance with the populations of the south of the country (Parra-Q. et al., 2012).

Regarding potatoes, it is widely accepted that one of the main centers of initial domestication of potatoes is in southern Peru on the border with Bolivia 10,000 years ago (Hawkes & Ruel, 1989). From the domesticated species and through hybridization with other species of the genus, the other species of the section would have been obtained *Petota.* Another center for domestication of potatoes is the island of Chiloé in Chile, where wild and domesticated species of *Solanum* have been recorded (Tapia & Fries 2007; Ovchinnikova et al., 2011, Cadima & Terrazas, 2019). According to Gómez et al. (2012), Colombia is the center of origin and domestication of Creole potatoes, *S. phureja*. Navarro et al. (2010) morphologically and molecularly characterized 19 genotypes of *S. tuberosum* and *S. phureja* in Nariño, Colombia; however, it was found that neither morphological nor molecular markers can clearly distinguish the evaluated species and varieties. In fact, Huamán & Spooner (2002) morphologically characterized eight species of potatoes in Latin America and concluded that given the genetic plasticity and continuous hybridization, all the evaluated potatoes could well be classified as a single species, *S. tuberosum*, with eight different cultivars.

As can be seen, the high varietal and intravarietal diversity of these species has been promoted and accumulated after thousands of years of selection and management by traditional Andean farmers. However, factors such as the homogenization of agroecosystems, cultural uprooting and the globalization of the diet, endanger the future maintenance of this diversity (Malice & Baudoin, 2009); in the nineties Stephen Brush (Brush et al, 1992), and those of Karl Zimmerer, carried out several studies where they identified the factors that led to the incorporation of new varieties, but they also highlighted that some groups of peasants sought the conservation of native species, almost thirty years later Velásquez-M et al. (2016). They also point out the need to apply various actions for conservation, including the identification of agrobiodiversity zones at the local, regional and national level, to avoid genetic erosion.

The distribution of the diversity of Andean tubers is not homogeneous but is identified concentrated in micro-centers of diversity and outside of them less interspecific diversity is conserved: various authors have identified as micro centers of diversification of these: Cajamarca, Huancavelica, Huánuco and Cusco in Perú; in Bolivia the Altiplano and La Candelaria territories; in Ecuador the provinces of Carchi and Huaconas and in Colombia in the departments of Boyacá and Nariño (García & Cadima, 2003; Seminario, 2004; Ortega et al., 2007; Parra-Q. et al. 2012; Manrique et al. 2014, Clavijo-P. et al. 2014; Fonseca et al., 2014). These micro-centers of diversification share a high intravarietal diversity, both morphological and genetic, as well as an important cultural roots of these species. The latter is possibly due in part to the fact that they occupy the same agroecological niche and the farmer generally sows them in association or in very close plots with similar management (Tapia, 2000).

Panbiogeography is a geographic approach applied to contribute to the understanding of biodiversity by identifying biotic components, individual traces, generalized traces and panbiogeographic nodes, starting from the distribution of plant and animal species (Morrone, 2004), which was proposed by Leon Croizant in 1952.

Based on the coordinates of the presence of a certain taxon, lines are constructed that connect all the points so that the sum of the segments is the smallest possible (individual trace or minimal laying tree); generalized traces result from the superposition of individual traces of a phylogenetically related group; panbiogeographic nodes are defined as the nodes of the generalized lines and can be interpreted as areas where there is a greater presence of endemisms, greater phylogenetic diversity and geographic limits of taxa (Miguel-T & Escalante, 2013).

These methods have been used to analyze the distribution of wild species (Martínez-G. & Morrone, 2005; Arana et al.,2013; Morrone, 2013), but they have not been used to understand the distribution of cultivated species, considering that the distribution patterns of cultivated plants are not only governed by natural evolutionary dynamics but especially by anthropic dynamics. The objective of this study is to identify for the tuberous species of the Andes, the agrogeographic nodes, thus named to the points that imply the intersection of sociocultural and biogeographic histories, which can have the following interpretations: presence of unique local cultivars, absence of widely distributed varieties, high inter- and infra-specific diversity and agro-ecosystemic affinities between areas. To compare the microcenter nodes reported in the bibliography with the agro-geographic nodes, the generalized line resulting from intersecting the individual lines of the Andean tubers will be estimated (*S. tuberosum, O. tuberosa, U. tuberosus* and *T. tuberosum*). In this way it will be possible to identify potential areas of concentration of the diversity of Andean tubers not previously reported. The identification of these areas will guide research on the conservation and management of Andean tubers. In addition, the agro-geographic nodes shed elements of discussion on the exchange of seeds and knowledges between indigenous peoples.

Materials and Methods

A database was built of the distribution of *O*. tuberosa, *U. tuberosus*, *T. tuberosum* and *S. tuberosum* in: Chile, Argentina, Bolivia, Perú, Ecuador, Colombia, and Venezuela, from the records integrated into the global geographic information platform, *Global Biodiversity Information Facility* (Global Biodiversity Information Facility [GBIF], 2017). Individuals which presented coordinates of complete geographic distribution, latitude, longitude, state and municipality were taken into account.

According to panbiogeographic theory, the distribution coordinates of each species were individually connected in such a way that the distance between the points was minimal, taking into account the curvature of the Earth (Miguel-T. & Escalante, 2013). This procedure was performed with the program PASSaGE 2.14.3 'Essen' (Rosenber & Anderson, 2011) and Quantum-GIS 2. (Sherman et al*.,* 2007), applying the combined method (Liria, 2008), which combines spatial analysis through geodetic distance calculation, creating a connectivity matrix and minimum spanning trees, with layer management and GIS spatial operations of intermediate storage and interception, thus the individual traces obtained from each species intersect each other to obtain the generalized traces and the agro-geographic nodes.

Analogously to the main biogeographic nodes (Morrone, 2015a), the main agro-geographic nodes correspond to the areas where there are more points of intersection of the analyzed species and the secondary ones also represent important areas of diversity but of lesser magnitude. The main nodes, in terms of wild species, identify the areas where speciation phenomena possibly occurred; while for cultivated species they would indicate initial domestication phenomena, from where they would distribute the seeds to other areas where they would continue their domestication.

Results

A number of 8975 records had the required geographic information. The species with the highest abundance is *S. tuberosum* with 6056 records distributed in Peru (3088), Argentina (943), Bolivia (783), Colombia (502), Ecuador (410), Chile (294) and Venezuela (36); regarding infraspecific taxa, it was found that the subspecies *S. tuberosum andigena* (Juz. & Bukasov) Hawkes y Roel (2006) cuenta con mayor número de registros (3758), *Solanum stenotomum* Juz. & Bukasov (456), *Solanum phureja* Juz. & Bukasov (359), *Solanum chaucha* Juz. & Bukasov (352) y los registros restantes corresponden a otras variedades y formas de *S. tuberosum* L (GBIF, c2017).

For its part, *O. tuberosa* had 1400 records distributed in Peru (1056), Bolivia (146), Argentina (111), Ecuador (63), Chile (13) and Colombia (11) (GBIF, c2017).

U. tuberosus presented 1010 records; 736 in Peru, 137 in Ecuador, 83 in Bolivia, 38 in Argentina and 16 in Colombia (GBIF, 2017).

Table 1. Accessions of species in relation to their geographical origin.

	Perú	**Argentina**	**Bolivia**	**Colombia**	**Ecuador**	**Chile**	**Venezuela**	**Total**
S. tuberosum	3088	943	783	502	410	294	36	6056
O. tuberosa	1056	111	146	11	63	13		1400
U. tuberosus	736	38	83	16	137			1010
T. tuberosum	350	6	29	24	100			509
Totales	5230	1098	1041	553	710	307	36	8975

Finally, *T. tuberosum* was registered 509 times, 40 of them correspond to *T. tuberosum silvestre* Sparre and the remaining 469 to *T. tuberosum* Ruiz & Pav.; Regarding the distribution by countries, Peru reports 350, Ecuador 100, Bolivia 29, Colombia 24 and Argentina six (Global Biodiversity Information Facility [GBIF], 2017).

Andean tubers are distributed in the biogeographic regions of the Transition Zone of South America, provinces of Páramo, Puna, Desierto, Monte, Maule, Santiago and Valdivia, and from the Neotropical region in the provinces of Yungas, Rodonia, Ucayali, Cauca, Ecuatorian, Western ecuadorian, Magdalena, Sabana and Chaco. The provinces with the highest number of records are Yungas for S. tuberosum with 2241, while in the province of Puno the highest number of records is reported for *U. tuberosus* (453), *O. tuberosa* (805) and *T. tuberosum* (166); the western Ecuadorian and Sabana provinces are the ones with the fewest records with a single report for *T. tuberosum* and O. tuberosa, respectively (Figure 1).

Current distribution maps and individual traces of each of the species were obtained (Figure 1). These lines converge in a generalized line that runs from the north of Argentina to the center of Colombia, crossing through Bolivia, Peru and Ecuador.

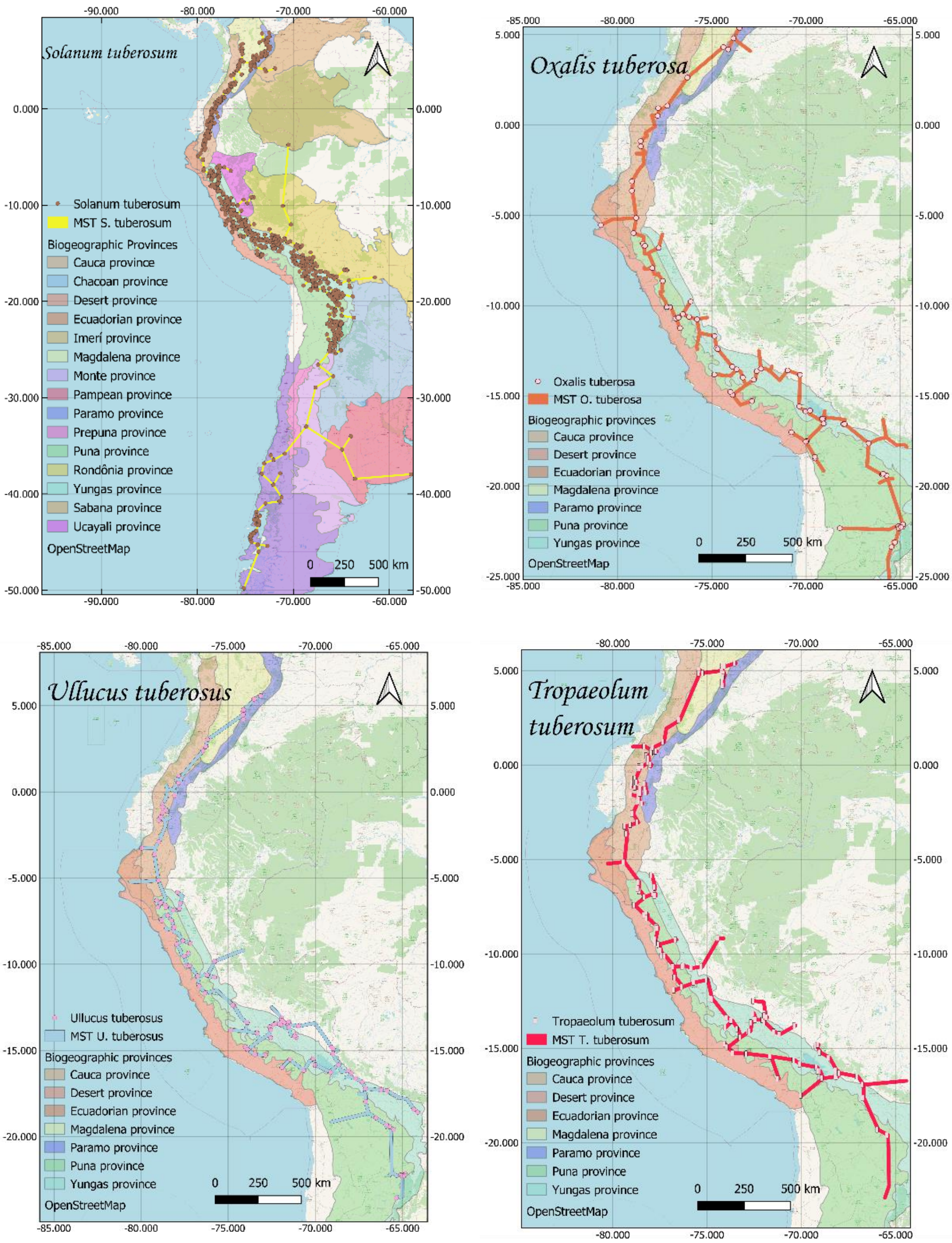

Figure 1. Distribution and minimum laying tree of *S. tuberosum*, *O. tuberosa, U. tuberosus* and *T. tuberosum* on biogeographic provinces (Loöwenberg-Neto, 2014) and Open Street Map.

The main node of this trace, or primary agro-geographic node occurs in southern Peru, a secondary node was identified in the north of this country and several secondary nodes were found in Bolivia, in central Peru, in central Ecuador and on the borders between Colombia and Ecuador (Figure 2). Regarding the biogeographic distribution, the number of nodes is greater in the southern Brazilian domain, followed by the South American Transition Zone and the Pacific domain.

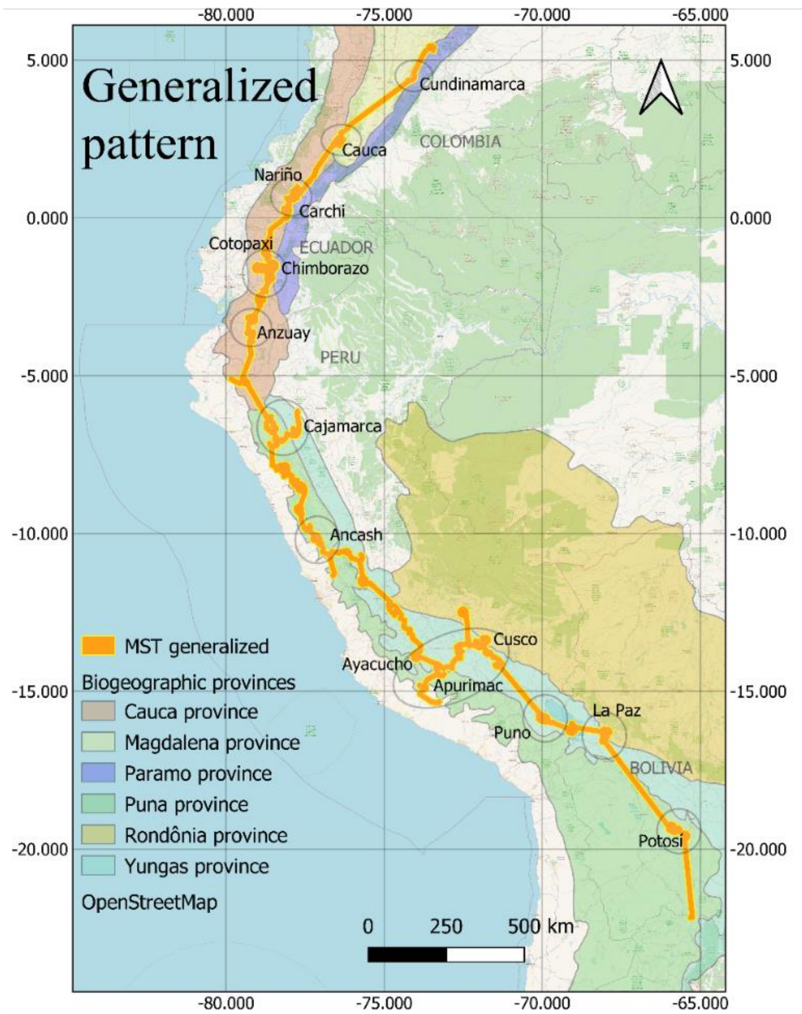

Figure 2. Generalized trace and agrogeographic nodes (in circles) of Andean tubers on Biogeographic Provinces (Löwenberg -Neto, 2014). and Open Street Map.

In Peru, 1,245 of the 2,043 generalized or intersection coordinates were identified (61%). The main node is between the departments of Cusco (277), Apurímac (111) and Ayacucho (89) and in second order are the nodes of Cajamarca (181), Ancash (134) and Puno (103) that stand out for the number of intersection points of individual traces.

In Ecuador, 459 sites with intersection coordinates (22.5%) were found, located mainly in the provinces of Chimborazo (123), Cotopaxi (61), Carchi (51) and Anzuay (42).

In Bolivia there were 204 sites with intersection coordinates (10%), identified in the departments of La Paz (109) and Potosí (95); the municipalities of Tomás Frías (83) Pedro Domingo Murillo (39) and Manco Kapac (34) were the ones that presented the highest abundance of intersection coordinates in the country.

In Colombia, 131 sites with intersection coordinates (6.5%) were identified, in the departments of Cauca (46), Nariño (37), Cundinamarca (28) and Boyacá (19), mainly. In Nariño, the municipalities of Cumbal (16) and Ipiales (6) were the most representative; in Cauca they were Totoró (18) and Silvia (11); in Cundinamarca the municipalities with the highest abundance are Chipaque (11), Bogotá (5), Pasca (5) and Ubaque (4); Finally, in Boyacá, the municipality of Samacá (12) was the one that presented the highest abundance.

Discussion

According to biogeographic theory, panbiogeographic nodes imply the intersection of different ecological and biogeographic histories that can have the following interpretations: presence of local endemisms, absence of widely distributed taxa, high phylogenetic diversity and geographic affinities with other areas and boundaries or geographic or phylogenetic of taxa (Miguel-T & Escalante, 2013; Morrone, 2015b; Grehan, 2020). In this analysis, the identified nodes do not correspond to panbiogeographic nodes but to agro-geographic nodes, understanding that human beings have been decisive in the flow of seeds of cultivated plants, as well as in the selection and adaptation of their varieties (Velásquez et al*.,* 2013).

Molecular studies confirm the highlands of Peru, departments of Huánuco, Pasco, Junín, Huancavelica, Apurímac, Ayacucho, Cusco and Puno as the domestication region of *S. tuberosum*; where, due to temperature fluctuations, the development of plants with growth of underground propagules is favored (Morales-G., 2007). The first presence of potatoes in Peru dates back to 6900 years ago in the department of Lima and towards the beginning of the Formative period (3,800 years ago) in the department of Junín (Morales-G, 2007). Spooner et al. (2005) suggest that the domesticated potato comes from the wild species of the *S. brevicaule* complex from southern Peru, although this complex extends from Huánuco to Puno. Currently in the region of Cusco, Apurímac and Huancavelica it is common to find conservationist farmers for whom biodiversity is their lifestyle and therefore they grow 50, 100 or 300 varieties of potatoes in plots smaller than one hectare (Fonseca et al., 2014).

The Cusco region is also an important area for the conservation of the other Andean tubers. *T. tuberosum* registers a greater genetic and morphological diversity in the agroecosystems of this area than that conserved in the collection of the International Potato Center (Manrique et al., 2014). *O. tuberosa* it also presents a high diversity in the departments described, as well as in Cajamarca, Ancash and Puno (Pissard et al., 2008). Currently, the exchange between Andean tuber seed farmers has been reported between the Peruvian departments of Huánuco, Huancayo, Huancavelica, Ayacucho, Cajamarca and Cusco (Velásquez et al., 2013).

In Bolivia, the departments of La Paz and Cochabamba have been reported as micro-centers of diversity of Andean tubers in this country (García & Cadima 2003). Cochabamba is one of the regions with the greatest morphological and molecular diversity of *O. tuberosa* (Emshwiller & Doyle, 1998), *T. tuberosum* (Grau et al., 2003) and *U. tuberosus* (Parra-Q., 2012).

The Ecuadorian departments of Carchi, Cañar, Bolívar, Chimborazo, Cañar, and Loja, present a wide diversity of potatoes (Morales-G 2007), ullucos (Vimos et al., 1993) and Mashuas (Grau et al., 2003). In Colombia, the use of lithic tools has been reported for more than 5000 years as hoes, the edges of which have residues of starch from tubers (Aceituno-B & Rojas-M, 2012). The southeastern part of the country, mainly the municipality of Cumbal and others in the department of Nariño, are recognized micro-centers of potato diversity (Tinjacá-R. & Rodríguez-M., 2015) and ullucos (Parra-Q., 2012). In the department of Boyacá, the municipality of Ventaquemada has been identified (Clavijo-P. et al., 2014) as one of the Colombian micro-centers. However, in our analysis the municipality of Samacá was also identified as the administrative unit where the intersection coordinates in the department concur with greater abundance. The department of Cauca was also identified, especially the municipalities of Totoro and Silvia, as those with the greatest presence of coordinates where the four species are present in the department; however, studies have not yet been carried out to determine the varietal diversity of these resources. The same occurs in the department of Cundinamarca, where the municipality of Chipaque has the highest abundance of intersection coordinates but does not have associated studies.

Biological diversity is concomitant to areas where there is also a high cultural diversity as a whole, they make up biocultural diversity, a key diversity in the processes of plant domestication in Mesoamerica and the Andes (Casas et al., 2017). In this sense, the identified nodes concur in areas of indigenous predominance: Quechua (Bolivia, Peru, Ecuador, and Colombia), Aimara (Peru and Bolivia), Pastos (Ecuador and Colombia), Nasa, Misak and Coconucos (Colombia); With the exception of the node in central Colombia where only remnants of the Muisca indigenous group remain (Albo et al., 2009).

The panbiographic analysis of Andean tubers offers two benefits, namely: First, it allows the identification of the geographic areas with the greatest agrobiodiversity and this in turn is important to direct protection and recovery strategies for plant genetic resources. On the other hand, it also provides evidence in the reconstruction of the history and diffusion of domestication in America, allowing temporal trans-scalarity, that is, connecting the interpretation of past events with current processes (Casas et al., 2017). The results support the hypothesis that Andean tubers were domesticated in the Peruvian highlands, from where they dispersed to the south and north following the patterns of pre-Columbian human occupations. In this sense, the history of the Andean tubers can be understood as the history and future of the Andean peoples (Viteri et al., 2020; Devaux et al., 2021; Montes et al., 2021).

Author contributions

Conceptualization: R.F.G.-D, E.F.V.-H, L.M.-C. **Experiment design:** R.F.G.-D, E.F.V.-H., L.M.-C., F.J.D.-N., S.A.-S. **Experiment execution:** R.F.G.-D, E.F.V.-H. **Experiment verification:** R.F.G.-D, E.F.V.-H., L.M.-C., F.J.D.-N., S.A.-S. **Data analysis/interpretation:** R.F.G.-D., E.F.V.-H., L.M.-C., F.J.D.N., S.A.-S. **Statistical analysis:** R.F.G.-D, E.F.V.-H., L.M.-C., F.J.D.N., S.A.-S. **Manuscript preparation:** R.F.G.-D, E.F.V.-H., L.M.-C., F.J.D.-N., S.A.-S. **Manuscript editing and revision:** R.F.G.-D, E.F.V.-H., L.M.-C., F.J.D.-N., S.A.-S. **Approval of the final manuscript version:** R.F.G.-D, E.F.V.-H., L.M.-C., F.J.D.-N., S.A.-S.

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