Capsicum pubescens Ruiz & Pav.: evolutionary history, genetic resources and future opportunities for an overlooked Andean chile

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Abstract

Growing concerns over food security, agrobiodiversity loss, and climate change are driving renewed interest in neglected and underutilized crops with high agronomic, nutritional, and adaptive potential. *Capsicum pubescens* Ruiz & Pav. is one of the five domesticated chile pepper species and a distinctive crop of Andean agriculture. Adapted to cool mountain environments and characterized by its conspicuous pubescence, purple flowers, and dark seeds, the species has long played important culinary, cultural, and economic roles across the Central Andes. Despite its uniqueness, *C. pubescens* remains comparatively understudied relative to other cultivated chiles. Here, we review current knowledge on its evolutionary history, diversity, domestication, genetic resources, and prospects for conservation and crop improvement. Available evidence supports a Central Andean origin and identifies the inter-Andean valleys of the Bolivian Yungas as the primary center of diversity and the most plausible center of domestication, although the direct wild progenitor of the species remains unknown. Recent genomic studies reveal substantial genetic variation, with the highest diversity concentrated in Bolivia and distinct northern and southern lineages shaped by human-mediated dispersal across the Americas. We also highlight important gaps in germplasm conservation, particularly the underrepresentation of Bolivian diversity and the limited *ex situ* coverage of the three wild relatives of *C. pubescens* in public collections. The growing availability of genomic resources creates new opportunities for evolutionary research, conservation planning, and crop improvement. We argue that *C. pubescens* represents a valuable yet overlooked biocultural, agricultural, and genetic resource deserving greater scientific and conservation attention.

Keywords

agrobiodiversity; Andean crops; crop wild relatives; chile peppers, plant domestication; plant genetic resources

Introduction

Crop domestication has profoundly shaped human societies and terrestrial ecosystems, leading to a wide variety of cultivated plants that underpin global food systems. However, despite the dominance of a few major crops in modern agriculture, many domesticated species remain locally important but globally underrepresented in scientific research. These so-called “neglected”, “overlooked” or “underutilized” crops often harbor significant genetic variation, unique evolutionary trajectories, and valuable traits for agricultural sustainability in the face of changing environmental conditions (Mabhaudhi et al. 2019; Ulian et al. 2020). Understanding their origins, diversity and adaptive potential is therefore increasingly relevant both for developing effective conservation strategies of genetic resources and for meeting the increasing global demand for improved yield and food quality (Ross-Ibarra et al. 2007; Meyer and Purugganan 2013; Khoury et al. 2022; Alavez et al. 2026).

Sweet and hot chile peppers (*Capsicum* L., Solanaceae) are among the most culturally and economically important horticultural crops worldwide. Five species of *Capsicum* have been independently domesticated in the Americas: *C. annuum* L., *C. baccatum* L., *C. chinense* Jacq., *C. frutescens* L., and *C. pubescens* Ruiz & Pav. (Jarret et al. 2019; Barboza et al. 2022). Together, these species encompass a remarkable variety of fruit colors, shapes, aromas, pungency, and agricultural uses, reflecting long histories of human selection under different ecological and cultural contexts. Among them, *C. pubescens*, commonly known as “rocoto”, remains particularly distinctive and understudied. Adapted to relatively cool environments where other domesticated chiles fails, the species is cultivated primarily in mid- to high-elevation regions of Central and South America. It is further distinguished by conspicuous pubescence, purple flowers and brownish-black seeds, while its fruits are widely used fresh, cooked, or processed as condiments and remain integral to culinary traditions across the Central Andes (**Fig. 1**; Bosland and Votava 2012; Barboza et al. 2022).

Beyond its biocultural value, *C. pubescens* has gained a renewed economic and nutritional importance. Its fruits are a significant source of bioactive compounds relevant to human health, including ascorbic acid (vitamin C), flavonoids, phenolics, carotenoids and a distinctive capsaicinoids profile, the latter comprising pungency-associated alkaloids that are largely unique to the genus *Capsicum* (Meckelman et al. 2015; Caballero Gutiérrez et al. 2017; de Sá Mendes et al. 2020). While its presence is expanding in international markets, production still relies heavily on traditional landraces with limited agronomic improvement, driving demand for cultivars with enhanced performance and functional values (Salas-Zeta et al. 2026, and references herein). Recent explorations of its genetic and morpho-functional diversity have begun to uncover the hidden value of *C. pubescens* (e.g., Palombo and Carrizo García 2022; Salas-Zeta et al. 2026), highlighting its significance for both conservation and crop improvement.

Fig. 1 Distribution, morphology, and uses of *Capsicum pubescens*: **a** cultivation range of the species across the Americas, outlined in yellow, according to Barboza et al. (2022), **b** adult plants growing in a family garden, **c** flower, **d** characteristic pubescence, **e** mature fruit in longitudinal section showing the distinctive brownish-black seeds (arrow), **f** diversity of fruit forms and colors, **g** fresh fruits sold in a local market in Bolivia, **h** *C. pubescens*-based sauces**, i** the traditional dish "rocoto relleno"**, j** dried fruit powders. Scale bar (**c**-**f**) = 1 cm. Photos by C. Carrizo García and N. Palombo.

Despite this growing interest, the evolutionary history of *C. pubescens* remains unusually unresolved. No unequivocal wild population or direct progenitor is known, leaving a critical gap in our understanding of its origin and the extent of its diversity. Moreover, the species remains comparatively underrepresented in global crop research relative to other domesticated chiles. To illustrate this neglect, a recent search conducted on Google Scholar revealed that the species accounts for merely 0.62% of the global *Capsicum* literature, yielding only 4,390 *C. pubescens* articles compared to the 715,000 articles retrieved for the broader genus. Current knowledge on the species is also fragmented across different disciplines, including taxonomy, ethnobotany, agronomy and phytochemistry. To date, no comprehensive synthesis has integrated these perspectives into a unified framework. Here, we review the current state of knowledge on *C. pubescens*, with emphasis on its biological distinctiveness, diversity patterns, and evolutionary and domestication history. We further identify major research gaps and propose future directions to advance the understanding and conservation of this overlooked Andean crop.

Biology, distribution and uses

Geographic distribution and growth conditions

Capsicum pubescens is primarily associated with mid- to high elevation regions in the Americas, where it is grown from (800–)1,200 to 3,500 m, spanning a broad latitudinal range from north-western Argentina to central Mexico (**Fig. 1a**; Eshbaugh 1979; Tapia and Campos 2016; Aguilar-Meléndez and Lira Noriega 2018; Barboza et al. 2022). Across this range, it is cultivated under diverse production systems, from backyard gardens (**Fig. 1b**) and smallholder mixed farms to more intensive commercial plantings. Its strongest cultural and economic significance is concentrated in the Central Andes, particularly in Bolivia and Peru, where *C. pubescens* remains deeply embedded in local food systems and markets (Jäger et al. 2013a, b; Rodríguez et al. 2016; Barboza et al. 2022). In recent decades, its cultivation and commercial relevance have also expanded in Mexico (Xingú-López et al. 2025). Cultivation of *C. pubescens* outside the Americas remains limited, likely because of specific environmental constraints combined with the perishability of its fleshy fruits (Eshbaugh 1993). Nevertheless, successful introductions have been documented; the species has been cultivated in montane environments of Indonesia for more than a century (Yamamoto et al. 2013, 2016), and additional records exist from north-western China, the Tibetan mountains (Djian-Caporalino et al. 2006), and in Nagano, Japan (Matsushima et al. 2010).

The species occupies a distinctive ecological niche among domesticated chiles, characterized by its unique adaptation to mid- to high-altitude, cool montane environments, where it thrives under frost-free conditions and marked thermal amplitudes (Bosland and Votava 2012). Optimal growth occurs between 16 and 24ºC at elevations around 2,400 m, with a sharp decline in physiological performance above 30°C, and requirement for well-drained soils with annual rainfall ranging from 600 to 1,250 mm, although the species tolerate levels between 500 and 2,000 mm (Villagómez et al. 1999; Tapia and Campos 2016; Aguilar-Meléndez and Lira Noriega 2018; Yapo-Cárdenas and Pacheco-Lizárraga 2023). Owing to its particular growing conditions, *C. pubescens* has received growing attention as a rootstock for other chile species. High-altitude accessions have demonstrated superior vigor and cold tolerance compared to commercial rootstocks, offering a promising avenue for chile pepper production under usually suboptimal temperature regimes (Agnello et al. 2024).

The phenology and reproductive biology of *C. pubescens* also presents several distinctive features. The species is perennial and can remain productive for 10 or more years. Fruit maturation is notably slow compared to other cultivated chiles, requiring approximately 90 to 120 days from pollination to full ripeness (Pérez Grajales et al. 2014; Yapo-Cárdenas and Pacheco-Lizárraga 2023). Although *C. pubescens* is generally regarded as self-compatible, the documentation of varying degrees of self-incompatibility (Yaqub and Smith 1971; Saborío and Da Costa 1992; Bo et al. 2011; Bosland and Votava 2012) suggests that natural outcrossing rates may be higher than traditionally assumed. Furthermore, characterizations of pollen morphology and performance indicate that while studied individuals were male fertile with high *in vitro* pollen germination rates, significant inter-individual variation in pollen viability and germinability exists (Bo and Carrizo García 2015). Such heterogeneity likely carries significant agronomic implications for fruit set under variable field conditions.

Uses, value chains and socioeconomic importance

Although formally described in the late 18th century by Hipólito Ruiz and José Pavón after their botanical expeditions to Peru (Ruiz and Pavón 1799), *C. pubescens* remained comparatively overlooked in the scientific literature until the mid-20th century. Landmark studies of Heiser and Smith (1948) and Rick (1950) finally brought broader attention to its distinctive ecology, morphology, and ethnobotanical significance. However, the cultural importance of *C. pubescens* in the Central Andes predates European contact. Historical sources suggest it was among the most significant plants utilized by pre-Columbian societies in Peru (Yacovleff and Herrera 1934). Its common names also reflect deep linguistic roots. The name "rocoto" derives from the Quechua *rukutu* as is mostly known in Peru and Ecuador, whereas "locoto" originates from the Aymara *luqutu* and is widely used in Bolivia and also in Argentina and Chile (Barboza et al. 2022). In Mesoamerica, where the species arrived in the early 20th century, it is known by Spanish descriptive names such as "chile manzano", "perón", "canario", "caballo", "morrón", or "siete caldos", referencing fruit shape, color, pungency, or culinary use (Long Towell 2009; Aguilar-Meléndez et al. 2023).

The species remains central to modern Andean gastronomy, holding a foundational role in the everyday culinary traditions of the region. Household surveys indicate that *C. pubescens* is consumed on a daily basis by 67% of families in Bolivia and 62% in Peru (Jäger et al. 2013a, b), either fresh, cooked, or processed into a variety of traditional dishes (**Fig. 1g-j**). The fruits are the primary ingredient in “llajwa”, the emblematic spicy sauce of the Southern-Central Andes. Their thick and fleshy pericarp also makes them suitable for stuffed preparations such as “rocoto relleno”, one of the signature dishes of Peruvian cuisine (Jäger et al. 2013c). Both immature and mature fruits are also used as vegetables and spices in Indonesia (Yamamoto et al. 2013). Beyond culinary use, the fruits are highly valued for their distinctive phytochemical profile, dominated by dihydrocapsaicin and high concentrations of ascorbic acid and flavonoids (Salas-Zeta et al. 2026). These compounds underpin traditional ethnomedical applications documented (Barboza et al. 2022), and experimental studies also suggest anti-inflammatory, antioxidant and gastroprotective properties (Oboh and Rocha 2008; Castañeda and Salazar 2014; Rivas et al. 2014), highlighting the potential of this Andean crop for the functional food and nutraceutical industries (de Sá Mendes et al. 2020).

The species is commercialized commonly as fresh fruit and, to a lesser extent, processed products such as sauces, pastes or powders. Commercialization occurs mainly through local and wholesale markets, from which fruits are distributed to lower-elevation regions and exported to other countries (Jäger et al. 2013a, b; Rodríguez Pastor 2016). In Argentina, for example, although minor local cultivation exists in the northwest, the domestic market is largely supplied by imports from neighboring Bolivia (Pochettino et al. 2012; Petrucci et al. 2022). Demand has also increased in Europe and North America, driven by migrant communities, the internalization of Andean cuisine, and growing interest in distinctive chile products (Jäger et al. 2013c).

Systematics and closest wild relatives

Phylogenetic relationships and genomic divergence

Capsicum pubescens is a member of the genus *Capsicum*, which currently encompasses 43 species distributed across tropical to temperate regions of the Americas, from central Argentina to southern United States (Barboza et al. 2022). The most comprehensive phylogenetic framework for the genus to date, based on genome-wide SNP data, has provided a robust basis for understanding interspecific relationships (Carrizo García et al. 2022). Within this framework, two main lineages can be distinguished in the genus: an early-diverging Andean clade comprising species from Central America to north-western South America, and a second lineage encompassing the remaining species, where domesticated taxa and their closest wild relatives are grouped into three well-supported clades: Annuum, Baccatum and Pubescens (**Fig. 2a**; Carrizo García et al. 2022).

The Pubescens clade comprises *C. pubescens* and a sister lineage formed by *C. cardenasii* Heiser & P.G.Sm., *C. eximium* Hunz. and *C. eshbaughii* Barboza, which represent its closest wild relatives but not its direct ancestors (**Fig. 2b**; Carrizo García et al. 2022). The clade is phylogenetically distinct from the other domesticated chiles due to its earlier divergence (Carrizo García et al. 2022).

While absolute dating of these evolutionary events varies depending on genomic datasets and molecular clock calibrations used, all current evidence points to a prolonged period of isolation. For instance, whole-genome analyses estimate the divergence between *C. pubescens* and the other domesticated chiles around 1.8 Ma (Zhang et al. 2025), whereas comprehensive genome-wide SNP phylogenies propose an even older divergence around 4 Ma (Carrizo García et al. 2022). This prolonged period of evolutionary isolation from the other domesticated chiles has likely facilitated the strong genomic differentiation and unique morphological attributes observed in *C. pubescens*.

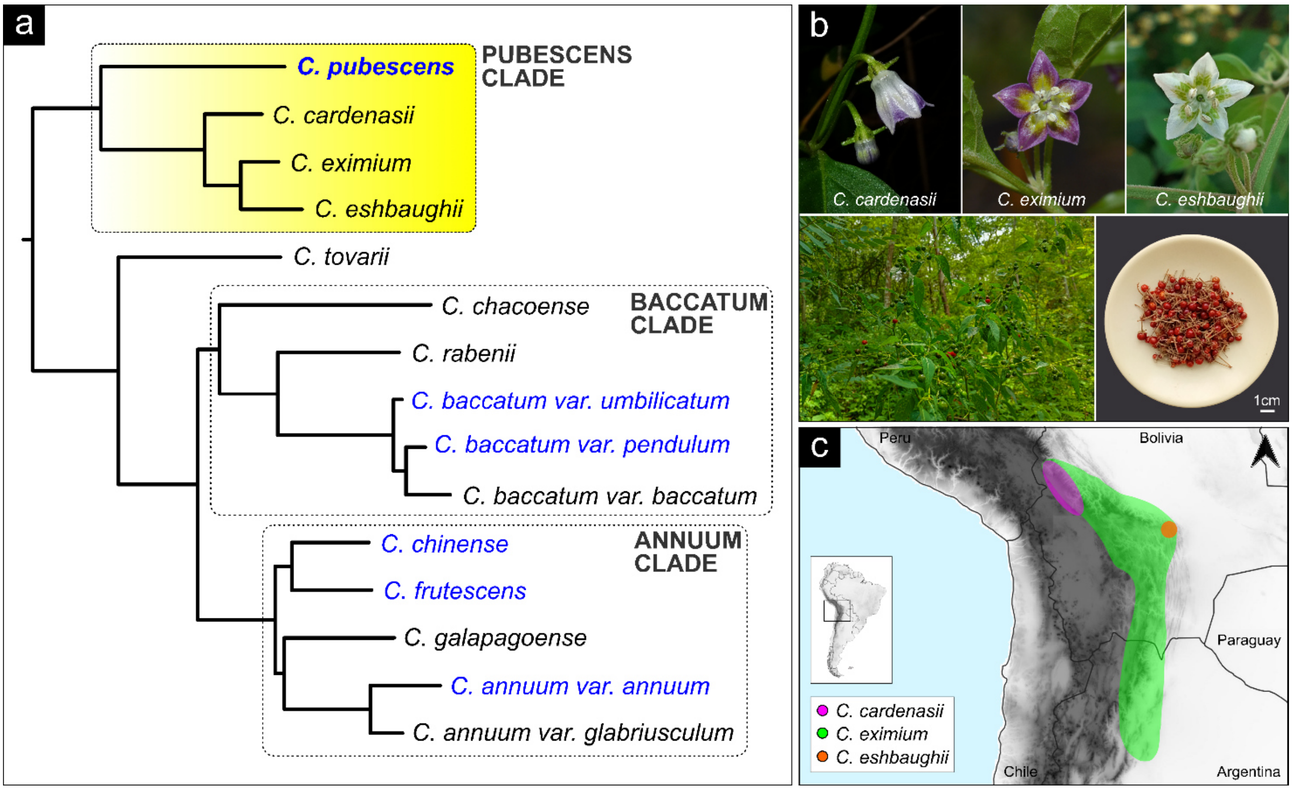

Fig. 2 Interspecific relationships and wild relatives of *Capsicum pubescens*: **a** simplified phylogeny of *Capsicum* based on Carrizo García et al. (2022), showing the phylogenetic placement of *C. pubescens* within the Pubescens clade. Domesticated taxa are colored in blue, and *C. pubescens* is shown in bold, **b** representative photos of the closest wild relatives of *C. pubescens* (*C. cardenasii*, *C. eximium*, *C. eshbaughii*), **c** native geographic ranges of these species according to Barboza et al. (2022); South America is depicted in the inset. Photos by C. Carrizo García and N. Palombo.

Cytogenetic evidence further supports the Pubescens clade: all four species share the same chromosome number ($2n = 2x = 24$) and similar karyotype formulas, while genome size estimates available for *C. cardenasii*, *C. eximium*, and *C. pubescens* indicate comparable values among these taxa (Scaldaferro and Moscone 2019). This circumscription is also consistent with the traditional grouping of these four species as the “purple-flowered group” or “Pubescens complex”, a hypothesis historically sustained by morphological, chemical, and crossing data (Heiser and Smith 1958; Ballard et al. 1970; Eshbaugh and Smith 1971; Eshbaugh 1975; Jensen et al. 1979).

Diversity and conservation status of the wild relatives

The wild sister taxa of *C. pubescens* are commonly known as "ulupicas". Their highly pungent fruits are widely used as spices or in pickles in Bolivia and Argentina, where the species are native; they are traditionally harvested from the wild or cultivated in home gardens and small farms for family consumption and local trade (Hilgert 1999; Jäger et al. 2013a; Barboza et al. 2022; Morandini et al. 2024). The distribution of ulupicas extends from central-western Bolivia to north-western Argentina across diverse environmental conditions (**Fig. 2c**; Eshbaugh 1982; Barboza et al. 2022), partially overlapping with the native cultivation range of *C. pubescens*.

The conservation status of the ulupicas is of particular concern. *Capsicum cardenasii* is a narrowly endemic species restricted to the dry valleys of Luribay (Loayza Prov., La Paz Dept., Bolivia) at 2,400–3,000 m elevation and is currently classified as Endangered due to its limited extent of occurrence and few known localities where it is found (Barboza et al. 2022). Similarly, *C. eshbaughii* is endemic to central Bolivia (Florida Prov., Santa Cruz Dept.), where it inhabits mid elevation dry deciduous and marginal forests, and also is considered as Endangered due to its highly restricted distribution and ongoing habitat degradation. In contrast, *C. eximium* is the most widespread and variable ulupica, with an eco-geographical range extending from the Yungas of northern Argentina and Bolivia to the dry valleys of central Bolivia (8,00–2,600 m). While currently classified as Least Concern (LC), its substantial phenotype and genetic variation has not been comprehensively analyzed (Eshbaugh 1982; Carrizo García et al. 2020; Barboza et al. 2022). Given its extensive geographical distribution across contrasting ecosystems, this broad range may harbor distinct lineages that would require local-level assessment.

Collectively, these three wild species constitute the primary gene pool of *C. pubescens* (van Zonneveld et al. 2015), as they exhibit high reproductive compatibility and the ability to produce fertile hybrids under controlled conditions (Eshbaugh and Smith 1971; Eshbaugh 1975; Tong and Bosland 1999; Onus and Pickersgill 2004), making them valuable genetic resources for crop improvement. In breeding contexts, artificial hybrids between *C. pubescens* and either *C. cardenasii* or *C. eximium* are colloquially termed "rocopica" (rocoto + ulupica). Putative natural hybrids have been documented in areas of sympatry where rocoto and cultivated or wild ulupica individuals co-occur (Eshbaugh 1979, 1982; Barboza et al. 2022; Palombo et al. 2024). A notable example is found under the name *C. arachnoideum* (M. Nee unpublished), long associated with specimens that may represent natural hybrids between *C. pubescens* and *C. eshbaughii* in central Bolivia (Palombo pers. obs.).

Intraspecific diversity in *Capsicum pubescens*

Phenotypic variation and local landraces

Capsicum pubescens is readily distinguishable from other domesticated *Capsicum* species by a combination of vegetative and reproductive characters: dense general pubescence, purple violet flowers and large brownish-black seeds (**Fig. 1c-e**; Barboza et al. 2022). Floral morphology is relatively conserved, with rotate, 5–8-merous corollas ranging from deep purple to pale lilac tones (Eshbaugh 1979; Barboza et al. 2022), although white-flowered mutants have also been registered (e.g., Yamamoto et al. 2013; Xingú-López et al. 2025). As the primary product of agronomic interest and the main target of artificial selection, the greatest phenotype variation is found in fruit characteristics. These fleshy, pungent berries show a broad range of size, shape (round, oblong or elongated), and glossy mature colors, spanning red, orange and yellow (**Fig. 1f**; Barboza et al. 2022). Early studies documented the extent of this variation across the species cultivation range. Rick (1950) recorded up to 14 distinct fruit types in markets from Ecuador and Peru, while Eshbaugh (1979), examining material from southern Bolivia to Colombia, found that larger fruits predominated in Colombia and Ecuador, greater color diversity was concentrated in Bolivia and Peru, and the smallest fruits were restricted to Bolivia.

Until recently, no varieties or cultivars had been formally described for this species, yet a rich diversity of landraces and ecotypes have been recognized across its range (Villagómez et al. 1999; Bosland and Votava 2012; Xingú-López et al. 2025). In Peru, farmers and traders distinguish two broad ecotypes: forest rocoto ("rocoto de selva" or "de monte"), growing in the central forest, characterized by larger fruits and commonly used for stuffed preparations, and orchard rocoto ("rocoto de huerta" o "serrano"), cultivated across Andean valleys, with smallest, more pungent fruits predominantly used for sauces (Jäger et al. 2013c; Hernández-Amasifuen et al. 2021). Systematic characterizations of Peruvian germplasm have catalogued over two hundred accessions from the highland departments of Arequipa and Huánuco alone (García-Serquén et al. 2022). Similarly, morpho-agronomic studies in Mexico have consistently identified fruit traits as the most informative characters for differentiation among local races (Leyva-Ovalle et al. 2018; Escalera-Ordaz et al. 2019).

Building upon this diversity, recent breeding efforts have led to the official description and registration of the first formal Mexican cultivars, including 'Mayito' and 'Reynolito' (Hernández-Hernández et al. 2024, 2025). At the same time, a variety of genotypes is currently exchanged or commercialized by chile pepper enthusiasts worldwide (e.g., Samuels 2014) though the geographic origin, breeding history, and genetic identity of most of these materials remain unknown. Whether any correspondence exists between the morphological and genetic variation of the species remains an open question, as the latter has only recently begun to be characterized.

Geographical patterns of genetic diversity

The intraspecific genetic diversity of *C. pubescens* has remained largely unexplored until recently. Early phylogenetic studies using plastid and nuclear markers provided virtually no resolution at the intraspecific level, as the markers employed and the number of accessions analyzed proved nearly invariant within the species (e.g., Ince et al. 2010; Ibarra-Torres et al. 2015; Carrizo García et al. 2016; Grabiele et al. 2021). The first molecular insights into its genetic structure came from two studies based on a limited set of DNA markers: amplified fragment length polymorphisms (AFLPs; Ibiza et al. 2012) and simple sequence repeats (SSRs; Silvar and García González 2016). Both studies identified a geographic pattern of genetic differentiation associated with country of origin, primarily across germplasm from Bolivia, Peru and Ecuador. However, the scope of these studies was insufficient to evaluate the evolutionary significance of the inferred clusters nor to characterize genetic diversity across the entire American cultivation range.

The first genomic-scale assessment of genetic diversity was achieved through RAD-seq applied to 67 geographically representative accessions (Palombo and Carrizo García 2022). These data revealed three major genetic groups with high levels of admixture and reticulation, alongside a significant south-to-north gradient of decreasing genetic diversity. Although the drivers of these reticulate patterns remain to be formally evaluated, they are consistent with the decentralized cultivation and farmer-managed seed exchange systems that characterize much of the species' production range. The highest levels of diversity are concentrated in central-western Bolivian accessions and the lowest in those from Central America and Mexico. These findings provided the first genetic evidence supporting central-western Bolivia as a primary center of diversity for the species, consistent with earlier morphological observations (Eshbaugh 1979), and established a baseline for interpreting the domestication history of *C. pubescens*. Nevertheless, the identified genetic groups warrant further investigation to assess their ecological correlates and relevance for agronomic use, especially regarding the germplasm maintained by smallholder farmers across Peru and Bolivia, which remains insufficiently sampled.

Linking phenotypic and genomic variation

Recent phenomics and nutraceutical characterizations are finally linking morphological traits with genomic population structure, directly addressing a longstanding question of morpho-genetic correspondence. Hierarchical clustering of Peruvian germplasm has distinguished three primary morpho-functional clusters with weak geographic structure, as accessions from disparate regions intermingle within the same phenotypic groups (Salas-Zeta et al. 2026). This lack of strict provenance-based partitioning aligns with the high admixture and moderate population differentiation previously observed (Palombo and Carrizo García 2022). From a breeding perspective, the fact that desirable traits (e.g., high fruit size, high phytochemical content, attractive colors) are not confined to specific regions suggests that diverse geographic source populations can contribute equally superior alleles for crop improvement (Salas-Zeta et al. 2026).

The unresolved origin and domestication history

Archaeobotanical evidence

The species is widely considered to have originated and undergone domestication in the Central Andes, specifically within present-day Bolivia and Peru (**Fig. 3**; Barboza et al. 2022). It has been proposed that its domestication occurred in this region approximately 6,000 years ago (DeWitt and Bosland 2009), followed by human-mediated dispersal across the continent; however, direct archaeobotanical evidence supporting this timeline remains elusive. Unlike other domesticated *Capsicum* species recovered from the arid Peruvian coast or dry Mexican caves (Chiou et al. 2014; Kraft et al. 2014), the presumed center of diversity of *C. pubescens* lies mainly within humid inter-Andean valleys where taphonomic conditions may be substantially less favorable for long-term preservation of plant remains. Furthermore, the fruits of *C. pubescens* possess an unusually thick and fleshy pericarp with high moisture content, attributes that may promote rapid decay rather than the desiccation or carbonization process required for archaeobotanical persistence. Consequently, although *Capsicum* macro-remains (seeds) dated between 7,600 and 6,000 BP have been recovered from coastal sites such as Huaca Prieta and Paredones in northeastern Peru (**Fig. 3a**; Dillehay et al. 2017), these materials cannot be assigned unequivocally to *C. pubescens*. Microfossil analyses have provided more promising, though still limited, evidence. Perry et al. (2007) identified starch granules resembling those of *C. pubescens* on archaeological tools from the Waynuna site in southeast Peru (**Fig. 3a**), dated to approximately 4,000 BP. Their study demonstrated that starch granules of *C. pubescens* can be distinguished from those of other domesticated chiles. Nevertheless, species-level identification remains challenging because diagnostic morphotypes occur at low frequency and may partially overlap morphometrically with those of *C. baccatum*. Notably, to our knowledge, no confirmed archaeological remains attributable to *C. pubescens* have yet been identified in Bolivia, leaving a major geographical gap that necessitates the integration of historical, phenotypic and molecular evidence to reconstruct its domestication history.

Hypothesis on domestication and the missing progenitor

The evolutionary history of *C. pubescens* has been investigated through a variety of approaches over several decades (e.g., Eshbaugh 1979; McLeod et al. 1983; Perry et al. 2007; Moscone et al. 2007; Carrizo García et al. 2016, 2022), yet both geographic origin of the species and the specific location of its domestication center(s) remain incompletely resolved. The central challenge lies in the fact that *C. pubescens* is not known from the wild: no unambiguous wild populations have been documented, and the identity of its direct wild progenitor has not been conclusively established.

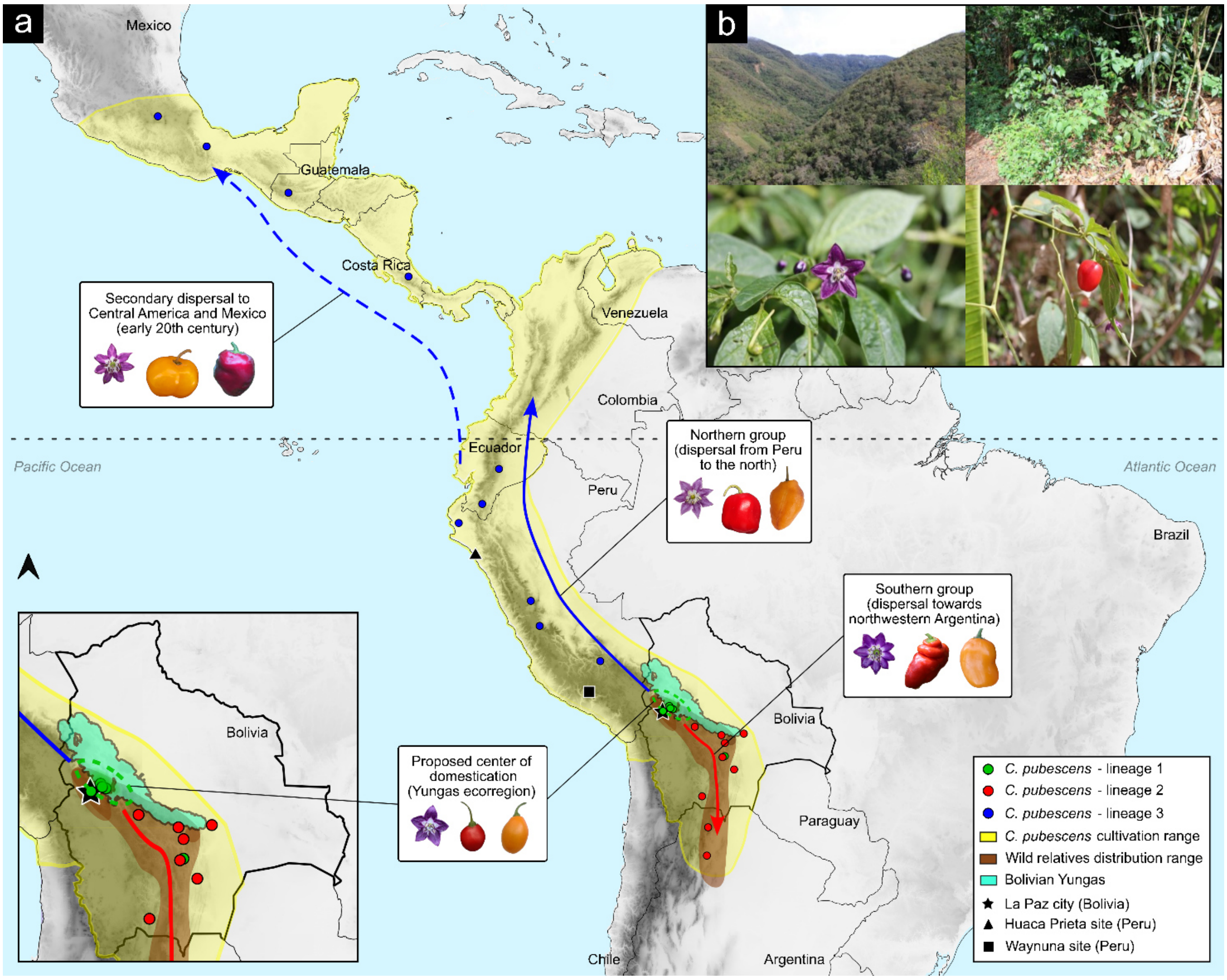

Fig. 3 Integrative hypothesis of the origin, domestication, and dispersal history of *Capsicum pubescens*: **a** geographic synthesis of current evidence supporting a putative center of diversity and domestication in the inter-Andean valleys of the Bolivian Yungas (dashed green oval) and subsequent human-mediated dispersal throughout the Americas (arrows). Colored circles represent the main genomic lineages identified by RAD-seq analyses (Palombo et al., 2024). The inset highlights the proposed center of diversity and domestication in central-western Bolivia, **b** representative habitat and morphology of individuals from the surroundings of Apa Apa (Bolivia). Photos by C. Carrizo García and N. Palombo.

Traditionally, *C. pubescens* has been considered a species native to the Central Andes, with its origin rooted in the territories of present-day Bolivia and Peru (Bosland and Votava 2012; Barboza et al. 2022). Although robust archaeological evidence still remains elusive, the central highlands of Bolivia were identified as the most plausible domestication center on three grounds: the distributions of *C. cardenasii* and *C. eximium* overlap with the Bolivian cultivation range of *C. pubescens*; the three species are interfertile; and the greatest morphological diversity of *C. pubescens* (including the smallest fruits, interpreted as a more ancestral character state) was documented in Bolivian material (**Fig. 3a**). Based on morphological, chemical and crossing data (Heiser and Smith 1958; Ballard et al. 1970; Eshbaugh and Smith 1971; Eshbaugh 1975; Jensen et al. 1979), it was early proposed that *C. cardenasii* and/or *C. eximium* were the wild progenitors of *C. pubescens*, a hypothesis widely accepted despite lacking rigorous testing.

The introduction of molecular markers brought new data to bear these questions, but also generated discordant hypotheses (Ince et al. 2010; Ibiza et al. 2012; Silvar and García González 2016; Walsh and Hoot 2001; Carrizo García et al. 2016). A decisive advance came with the application of genome-wide SNP data, which firmly circumscribed the Pubescens clade as a well-supported lineage comprising *C. pubescens* as sister to a clade formed by *C. cardenasii*, *C. eximium*, and *C. eshbaughii* (Carrizo García et al. 2022). This phylogenomic framework established that none of the three wild species is the direct ancestor of *C. pubescens* and revealed a striking temporal gap between the origin of the domesticated lineage and the diversification of its extant wild sister clade, estimated at approximately 1.5 Ma. This deep divergence reinforces the notion that *C. pubescens* did not originate directly from any currently known wild relative (Carrizo García et al. 2022). The species likely represents an ancient, independent lineage whose direct wild progenitor may have gone extinct or been genetically eroded through millennia of domestication. Since the cultivation of *C. pubescens* is primarily limited to specific environmental conditions, Rick (1950) suggested that the original wild populations might have occupied narrow niches subsequently overtaken by human cultivation, facilitating hybridization that progressively blurred the distinction between wild and domesticated forms.

Genomic insights into geographic origin, domestication and dispersal

Recent extended genomic assessments using RAD-seq data have pinpointed central-western Bolivia as the primary center of diversity and origin of *C. pubescens* (**Fig. 3a**; Palombo and Carrizo García 2022; Palombo et al. 2024). This region, specifically the inter-Andean valleys of the Bolivian Yungas near La Paz, hosts the highest levels of genetic diversity and early-diverging lineages within the species. Significantly, individuals collected *in situ* in this area (e.g., surroundings of Apa Apa, Huancané, and Coroico) exhibits a "semi-domesticated" syndrome: sparse pubescence, smaller and mostly pentamerous flowers and small, globose, but persistent fruits (**Fig. 3b**). These features suggest that these populations represent less-domesticated landraces, feral forms, or the closest extant link to the ancestral gene pool. From this core, the species appears to have diversified via human-mediated dispersal into two main geographic lineages: a southern group reaching Argentina and a northern group extending through Peru into Mesoamerica (Palombo et al. 2024). Consistent with the historical records (Bukasov 1965; Heiser and Smith 1953), the introduction into Central America and Mexico likely represents secondary dispersal bottleneck (*sensu* Louwaars 2018) occurring in the early 20th century, an interpretation supported by the significant reduced genetic diversity and the lack of indigenous names for the crop in the region.

Genetic resources and conservation gaps

Ex situ conservation status and geographical representation

Access to broad genetic variability is essential for the long-term conservation and improvement of *C. pubescens*, particularly for traits related to fruit quality, nutraceutical value, and cold-climate adaptation (Barchenger and Khoury 2022). A recent search in the Genesys plant genetic resources portal (Global Crop Diversity Trust 2026) revealed that although *Capsicum* germplasm is conserved in several international and national repositories, collections of *C. pubescens* are notably modest relative to those of *C. annuum* and other globally dominant chiles (**Fig. 4a**). The current 523 publicly accessible *C. pubescens* accessions are concentrated in a limited number of international and national germplasm banks, with major collections held at the National Agricultural Innovation Institute (Peru) and the USDA Plant Genetic Resources Conservation Unit (USA).

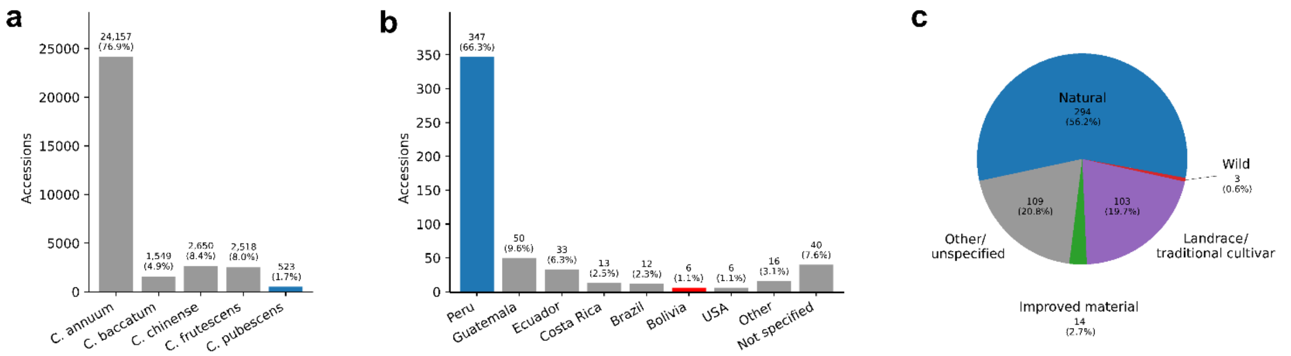

Fig. 4 *Ex situ* conservation status of *Capsicum pubescens* on publicly accessible germplasm repositories according to the Genesys Plant Genetic Resources Portal (Global Crop Diversity Trust, 2026): **a** representation of *C. pubescens* collections relative to the other four *Capsicum* domesticated species **b** country of origin of conserved *C. pubescen*s germplasm, highlighting the predominance of Peruvian accessions (blue) and the limited representation of Bolivian material (red) **c** biological status of *C. pubescens* accessions as recorded in passport data. Data retrieved in June 2026.

These holdings are heavily biased towards Peruvian material (**Fig. 4b**) and suggest that they capture only a fraction of the species' known diversity. This underrepresentation is particularly striking for Bolivia (the primary center of diversity) as farmer-maintained landraces and locally adapted populations from Bolivian agroecosystems are largely absent from public *ex situ* collections, leaving much of this biocultural and genetic diversity inaccessible for global research and at risk of erosion (Barchenger and Khoury 2022). However, the active collection maintained by the Bolivian National Institute of Agricultural and Forestry Innovation safeguards hundreds of local accessions (van Zonneveld et al. 2015), although this invaluable germplasm remains largely siloed from global integrated platforms. Wild relatives of the Pubescens clade are even more poorly represented. While *C. cardenasii* has comparatively better *ex situ* coverage, it is still classified as high priority due to limited representation; *C. eximium* and especially the endemic *C. eshbaughii* have been designated as requiring urgent conservation efforts (Khoury et al. 2020).

Documentation challenges and collection priorities

In addition to geographic gaps, many *C. pubescens* accessions remain incompletely passported or ambiguously characterized, although important advances have recently been made in the phenotypic documentation of Peruvian germplasm (Barchenger and Khoury 2022; García-Serquén et al. 2022). Current global gene bank databases also classify accessions according to standardized biological categories, such as "natural/wild" or "advanced/improved cultivars" (**Fig. 4c**). However, the application of this framework to *C. pubescens* is conceptually problematic, as no unequivocal wild or weedy populations are currently known and formal advanced breeding materials remain scarce. Consequently, many accessions are difficult to place within conventional domestication categories. This discrepancy highlights a broader knowledge gap and underscores the need to systematically re-evaluate, standardize, and curate existing passport data.

A systematic gap analysis evaluating the extent to which existing collections capture the genetic and morpho-functional diversity documented in recent studies (Palombo et al. 2024; Salas-Zeta et al. 2026) remains lacking and represents a critical next step. Such an analysis would provide a quantitative baseline for targeted collection missions and help maximize the conservation value of new accessions. Addressing these gaps will require coordinated efforts to document, collect, and conserve Pubescens clade diversity through complementary *ex situ*, on-farm, and participatory approaches, ensuring that these invaluable genetic resources are safeguarded and remain accessible for future research and crop improvement.

Future research prospects

Despite growing attention in *C. pubescens* during the last decades, major gaps remain in our understanding of its origin, diversification, genetic resources, and improvement potential. The expanding availability of genomic resources and renewed interest in underutilized, climate-resilient crops create new avenues for advancing both basic and applied research. The priorities outlined below prioritize an integrative framework to address the gaps identified in this review and harness the opportunities opened by recent scientific advances.

Origin and domestication history

One of the most important priorities concerns reconstructing the domestication trajectory of the species through expanded geographic and genomic sampling. Current datasets, while informative, still rely on geographically incomplete sampling of cultivated materials. Intensive surveys in Bolivia and Peru should be prioritized; specifically, the humid inter-Andean valleys of central-western Bolivia remain particularly unexplored and may harbor populations with a reduced domestication syndrome or transitional phenotypes that could illuminate the early stages of domestication. Intensive field surveys integrating population genomics, demographic modelling, archaeobotanical investigations, and morpho-functional characterization could help rigorously test alternative domestication scenarios. Simultaneously, the wild species of the Pubescens clade (i.e., *C. cardenasii*, *C. eximium*, and especially the geographically restricted *C. eshbaughii*) constitute an additional priority. Their diversity, population structure, ecological distribution and conservation status remain incompletely documented. Expanded fieldwork and genomic analyses are needed to assess patterns of diversification and natural hybridization within the clade. This represents the most promising avenue for finally addressing the unresolved question of the wild progenitor of *C. pubescens*.

Intraspecific diversity and domestication genomics

Improved characterization of local landraces and farmer-recognized ecotypes represents another major opportunity. Much of the evolutionary and phenotypic diversity of *C. pubescens* has been maintained not by formal breeding institutions, but by generations of Andean farmers through seed exchange and continuous cultivation in heterogeneous mountain agroecosystems. Integrating genomics with ecological information would improve our understanding of local selection and diversification across these complex landscapes. Furthermore, genomic characterization alongside standardized morpho-agronomic evaluations, following the approach of Salas-Zeta et al. (2026), should be extended across the full cultivation range to establish whether the morpho-functional clusters identified in Peruvian germplasm replicate at a continental scale.

Identifying the genomic regions subjected to selection during domestication is another major unaddressed frontier. While pangenomic approaches and selection sweep analyses have identified candidate loci associated with fruit traits, pungency, and adaptation in the Annuum and Baccatum clades (e.g., Ou et al. 2018; Cao et al. 2022; Lee et al. 2022), equivalent analyses in *C. pubescens* have lagged. The recent publication of the *C. pubescens* reference genome (Liu et al. 2023) and population-level genomic data (Palombo and Carrizo García 2022; Palombo et al. 2024) provide a solid foundation. Comparing the genome of *C. pubescens* with those of its wild relatives, alongside selective sweep analyses contrasting the less-domesticated Bolivian material with fully domesticated accessions, would allow identification of candidate genes underlying the domestication syndrome and shed light on the genomic basis of the species' distinctive traits.

Functional genomics and molecular breeding

Modern genomics offers unprecedented opportunities to accelerate crop improvement. Genome-wide association studies (GWAS) linking morpho-functional variation to specific genomic regions represent a natural next step toward marker-assisted selection in *C. pubescens*. The multivariate architecture of phenotypic variation suggests that targeted improvement of fruit quality, nutritional composition, and agronomic performance may be feasible without major trade-offs. The interfertility of *C. pubescens* with its closest relatives further expands the possibilities for crop improvement. Wild taxa may harbor genetic variation associated with disease resistance, abiotic stress tolerance, and other adaptive traits that have yet to be systematically evaluated (e.g., Silvar and García González 2020; Parisi et al. 2020). Genomics-assisted introgression and pre-breeding programs could therefore facilitate the incorporation of valuable alleles from these largely underexplored resources.

Multi-omics approaches incorporating transcriptomics, metabolomics, and comparative genomic data could substantially advance our understanding of the molecular mechanisms underlying the species' distinctive features. In particular, *C. pubescens* constitutes an attractive model for investigating adaptation to cool montane environments. Identifying the genes and regulatory pathways associated with cold tolerance and growth under suboptimal temperatures could provide valuable targets for breeding climate-resilient cultivars. Functional genomics may also support the enhancement of traits associated with nutritional and nutraceutical quality. Integrating genomic and metabolomic analyses could help identify the genetic determinants of bioactive compounds, enabling the development of cultivars with improved nutritional profiles and greater value for functional food markets.

Value addition, agrobiodiversity and cultural heritage

Beyond crop improvement, *C. pubescens* possesses considerable potential for value addition and rural development. Its adaptation to cool montane environments, high nutritional value, and strong culinary identity position the crop as a promising component of diversified mountain agriculture under changing climatic conditions. Recent evidence also suggests that *C. pubescens* may contribute to more sustainable production systems: a life-cycle assessment showed that cultivation systems incorporating biochar can simultaneously reduce environmental impacts and maintain high fruit quality, highlighting opportunities to integrate productivity, nutraceutical value, and sustainability value chains (Salgado et al. 2026). Opportunities exist for the development of differentiated products and locally based value chains linked to regional food traditions.

Ultimately, the future of *C. pubescens* research lies in bridging biological and cultural perspectives. Because much of the species' diversity persists within farmer-managed seed systems, future initiatives should recognize the central role of local communities in maintaining and generating genetic resources. Understanding how human management, seed systems, culinary traditions, and environmental heterogeneity have shaped the diversity of this crop will be essential for ensuring its conservation and sustainable use. As global interest in resilient, nutritious, and culturally significant crops continues to grow, this overlooked Andean chile represents an exceptional model for integrating crop evolution, agrobiodiversity conservation, and sustainable food-system development.

Conclusions

This work synthesizes current knowledge and critical gaps regarding the domesticated chile *C. pubescens*. Over the last decade, scientific advances have delivered a first population-genomic base (Palombo and Carrizo García 2022; Palombo et al. 2024), a reference genome (Liu et al. 2023), and the first comprehensive morpho-functional characterization of Peruvian germplasm (Salas-Zeta et al. 2026). In contrast, major conservation and agronomic gaps persist: the primary center of diversity in central-western Bolivia remains undersampled in global germplasm banks, wild relatives of the Pubescens clade are highly underrepresented in *ex situ* collections, and advanced breeding programs have yet to exploit the functional diversity maintained by Andean smallholders. Ultimately, the Pubescens clade as a whole represents a singular evolutionary and biocultural asset that warrants comprehensive exploration. This synthesis offers a baseline to guide future research, conservation, and breeding efforts centered on these singular Andean genetic resources.

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Author contributions

All authors developed the conceptual framework of the study. N.E.P. conducted the research and wrote the first draft of the manuscript. C.C.G. and M.A.S. commented on previous versions of the manuscript. All authors reviewed and approved the final manuscript.

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