Tree Genetics & Genomes (2025) 21:36
https://doi.org/10.1007/s11295-025-01721-w

SHORT COMMUNICATION

Mesoamerican origin of European cherimoyas (*Annona cherimola* Mill.)

Jose I. Hormaza[1] · **N. Larranaga**[1]

Received: 18 March 2025 / Revised: 2 September 2025 / Accepted: 23 October 2025 / Published online: 17 November 2025
© The Author(s) 2025

Abstract
Cherimoya (*Annona cherimola*) is a Neotropical fruit tree distributed in subtropical regions of the Americas from Mexico to Chile, typically above 900–1000 m above sea level with the highest diversity found in Mesoamerica. Cherimoya is believed to have arrived to Spain in the 18th century and subsequently spread to other parts of southern Europe. In this study, we analyzed the genetic structure of American and European cherimoyas using highly polymorphic SSR markers to investigate the species' transcontinental history. Our results confirm Central America, particularly Mexico, as the primary source of European cherimoyas and provide new evidence clarifying dispersal routes within Europe (Italy, Portugal, and Spain). These findings extend previous studies by directly testing the origin of the European germplasm and highlight the role of Mexico as the main bridge in the species' introduction to the Old World.

Keywords Annonaceae · *Annona cherimola* · Germplasm exchange · Microsatellites · Diversity · Human-mediated dispersal

Introduction

The cherimoya (*Annona cherimola* Mill.), a fruit tree in the Annonaceae, is characterized by high sugar content and low acidity. It is mainly consumed fresh although it can also be processed into ice creams, smoothies, sorbets, yogurts, or wine (Scheldeman 2002). Secondary metabolites such as isoquinoline alkaloids or acetogenins, which posssess various pharmacological properties, including antitumor and insecticidal activities, have been detected in leaves, stems, bark, and seeds (Alaly et al. 1999; Liaw et al. 2011; Cortes et al. 2014). In fact, traditionally, crushed seeds have been used as insecticides to fight lice and treat skin diseases in different American countries (Scheldeman 2002). The name "cherimoya" derives from the Quechua words "chiri" (cold) and "muya" (seed), likely referring to the relatively cold areas at high altitudes where it is cultivated in the Andean region. The species is distributed from Mexico and Central America to South America at altitudes above 900−1,000 m above sea level.

While early hypotheses considered a South American origin of the cherimoya (Popenoe 1921; van Damme et al. 2000), DNA-based studies have recently demonstrated that *A. cherimola* is of Mesoamerican origin (Larranaga et al. 2017, 2021, 2022). In addition, several of its closest relatives, included in the Atta and other sections of *Annona* (Fries 1959) and with which *A. cherimola* is monophyletic (Larranaga et al. 2019), are naturally distributed in Central America and the Caribbean.

The pollination of *A. cherimola* is mediated mainly by small sap beetles of the family Nitidulidae, although other beetle families such as Staphylinidae, Curculionidae, and Chrysomelidae have been reported as occasional visitors (Peña et al. 2018). Flowers are hermaphroditic and protogynous, opening first in the female stage and later in the male stage, which requires an effective pollinator to ensure successful pollen transfer between individuals. Nitidulid beetles are attracted by floral scents reminiscent of fermenting fruit and feed on the fleshy petals, often visiting multiple flowers and enabling fruit set (Lora et al. 2010, 2011).

Regarding seed dispersal, *A. cherimola* is considered an example of an anachronistic species, whose large fleshy fruits likely evolved for dispersal by extinct megafauna (Barlow 2000; Janzen and Martin 1982). After the

Communicated by S. A. Dev

✉ N. Larranaga
nlarranaga@eelm.csic.es

[1] Instituto de Hortofruticultura Subtropical y Mediterranea La Mayora (IHSM La Mayora – CSIC – UMA), Algarrobo 29750, Spain

extinction of the megafauna around 13,000 years ago, the subsequent dispersal of cherimoya and other large-fruited species would have depended mainly on humans (Van Zonneveld et al. 2018). Several Mesoamerican civilizations may have contributed to the dispersal of the cherimoya throughout Mesoamerica in Precolumbian times (Rovira-Morgado 2007). Thus, cherimoya was collected and cultivated by Mesoamerican people and, at some point, it was dispersed to South America, using maritime trading routes, where cultivation and diversification continued mediated by human activity of the different Andean civilizations (Larranaga et al. 2021). Although phenotypic variation has not yet been studied in detail, it appears lower in Mesoamerica than in northern Peru and southern Ecuador (Scheldeman, pers. comm.), whereas the opposite pattern is observed for genetic diversity (Larranaga et al. 2017, 2021). This suggests a bottleneck event before the formation of the populations in South America, as has already been reported for other species of Mesoamerican origin, such as *Phaseolus vulgaris* (Bitocchi et al. 2012, 2013). The existence of direct routes and exchanges between Ecuador, Peru and Mexico is well-documented in literature, based on shared textiles, metallurgical or mollusk shells (Hosler et al. 1990; Anawalt 1992; Marcos 1994).

After 1492, a unidirectional relationship of exploration and exploitation was established between America and Europe, resulting in numerous, more or less systematic, observations of nature and some deeper chronicles about indigenous knowledge. Although it could also be on a close relative, it is considered that the first known written report on cherimoya was recorded by Jose de Acosta, a sixteenth-century Spanish Jesuit missionary who wrote that "all the flesh inside is soft and tender as butter and white and of an exquisite taste and some believe that it is the best fruit in the Indies" (Acosta 1590). However, little is known about the dispersion of the cherimoya outside the Americas. According to Morton (1987), it was introduced to Spain in 1757, and by the late 18th century it had reached Hawaii, Jamaica and Haiti. It was present in Italy in 1797, particularly in the Province of Reggio Calabria. Seeds from Mexico were planted in California in 1871 and the species was present in Madeira in 1897, and also in the Canary Islands, Algeria, Egypt and, probably via Italy, to Libya, Eritrea and Somalia. At least by 1789–1793, cherimoya trees producing fruits were documented in the province of Malaga in the south of Spain (García de la Leña 1879). Currently, Spain is the world's leading commercial producer of cherimoya, with a planted area of 3,000 hectares and a total production of 44,231 tons of cherimoya in 2021 (Mapa 2021), followed by other countries such as Peru, Ecuador, Portugal (Madeira), and Mexico.

The main objective of this study was to determine the origin of the genetic cluster from which the cherimoya trees present in Europe initially originated. Using a set of highly polymorphic SSR markers, we analysed the genetic structure and relationships of cherimoya trees sourced from natural and managed populations across Latin America, previously characterized in other studies (Van Zonneveld et al. 2012; Larranaga et al. 2017, 2021) alongside newly sampled trees from the *ex situ* germplasm collection of the IHSM La Mayora originated from Spain, Madeira (Portugal), and Italy, and from the Canary Islands.

Methods

Plant material and SSR data

For this study, we used part of the American cherimoya dataset genotyped at nine microsatellite loci, previously analyzed by Larranaga et al. (2021). Most of it is publicly archived in the Dryad Digital Repository (Larranaga et al. 2017; https://doi.org/10.5061/dryad.0p264). This database was resampled to minimize sampling bias using a 2.5-minute raster cell size, with one sample taken randomly per cell, resulting in a new data set of 359 trees across 8 different North, Central and South American countries. In addition, European samples were newly included in this study and amplified with the same 9 loci. These samples included 8 accessions from mainland Spain, 3 from Sicily (Italy) and 24 from Madeira (Portugal) conserved at the cherimoya germplasm bank of the IHSM La Mayora-CSIC-UMA (Spain) and 4 samples from the Canary Islands (Spain) maintained at the Instituto Canario de Investigaciones Agrarias (ICIA). The final dataset consisted of 398 samples collected in both America and Europe.

Genetic distances per individual and populations

To explore relationships among different individuals and populations, we calculated several genetic distance parameters. Pairwise distances between individuals were obtained using Bruvo's distance from the poppr R package (Kamvar et al. 2014, 2015) and visualized in a heatmap using the R stats package (R Core Team 2021). The rows of the heatmap were ordered using the complete clustering method, which groups similar individuals together, facilitating the identification of genetic clusters. At the population level, Nei's distance was calculated between countries and used to construct a Neighbor-Net network using the R packages adegenet (Jombart 2008; Jombart and Ahmed 2011) and phangorn (Schliep 2011; Schliep et al. 2017). This method helps to visualize the relationships and potential reticulations

between different populations, offering insights into historical gene flow and admixture events. Additionally, pairwise Fst distances, which measure genetic differentiation between populations, were also calculated between populations with the adegenet R package (Jombart 2008; Jombart and Ahmed 2011). For each population, only the two lowest pairwise Fst distances were plotted on a map alongside the genetic structure results.

Genetic structure

The genetic structure was calculated using the software STRUCTURE (Pritchard et al. 2000). The program was configured as follows: K (number of populations) ranged from 1 to 10 using the admixed model, with 50 iterations per K. Each run consisted of a burn-in period of 50,000 steps, followed by 500,000 Monte Carlo Markov chain replicates (Pritchard et al. 2009; Martin et al. 2011). To determine the most likely number of populations (K), Delta K, was calculated as described by Evanno et al. (2005), using the Structure Selector server (Li and Liu 2018), which also allowed to align results per population/country for one of the most probable solutions, through clumpack (Kopelman et al. 2015). The selected solution was plotted on a geographical map using the following R packages: rnaturalearth (South 2017), ggplot2 (Wickham 2016), scatterpie (Guangchuang 2022) and ggspatial (Dunnington 2021).

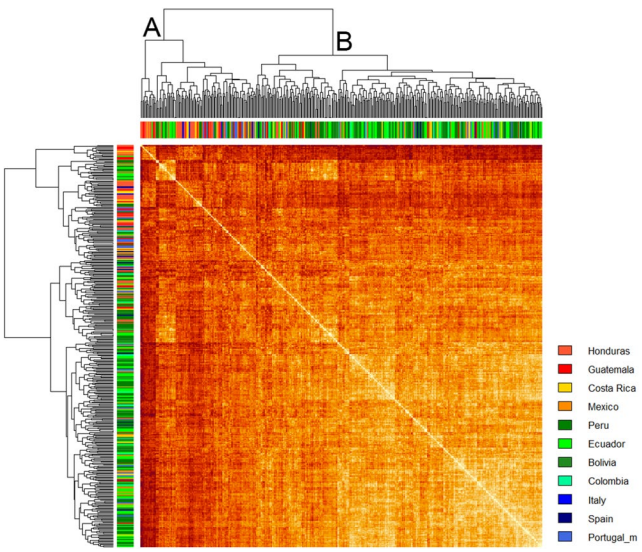


Fig. 1 Heatmap illustrating the pairwise Bruvo distances between individuals, with the arrangement determined by the complete clustering method. To enhance the distinction among groups, a color scheme was applied: Mexico and Central American samples were designated with shades of red and orange tones, South American samples were assigned green tones, and European samples were represented using blue colours

Migration analysis

To identify potential American sources of the three European populations (Italy, Portugal, Spain), we performed a Bayesian structured coalescent analysis in MIGRATE-N (v5.x) (Beerli et al. 2019) using the Brownian stepwise mutation model for microsatellites. Exponential priors were specified for Θ [Exp(0; mean = 3; max = 20)] and directional migration rates M [Exp(0; 0.5; 5)]. We used a custom sparse migration matrix that blocks EU→America routes and most migrations among American populations while allowing all Americas→EU routes and full EU↔EU migration (Italy–Portugal–Spain) to reduce parameters and runtime. MCMC used static heating (temperatures 1.0, 1.5, 3.0, 6.0, 12.0), burn-in = 10,000, long-sample = 100,000 (samples recorded every 100), one long chain, five replicates, and autotuning target 0.44. Putative American origins for each European population were inferred from posterior estimates of M into that population, considering the highest median M values with 95% HPD intervals excluding zero.

Results and discussion

The analyses using 9 SSR loci allowed the characterization of the genetic structure and relationships of cherimoyas from natural and managed populations in different Latin American countries and Europe. Figure 1 provides a comprehensive visualization of genetic relationships among individuals using a heatmap, which portrays a square matrix representing Bruvo genetic distances and ordered by complete WPGMA clustering methodology. The accompanying dendrogram delineates two prominent clusters, each of which undergoes further sub-divisions. Cluster A predominantly groups samples from Central America, Mexico, and Europe. Within this cluster, notable genetic disparities emerge both between subgroups and in comparison to the second cluster. Cluster B predominantly groups samples from South America but also includes a few samples from the other regions, where warmer, more yellowish tones denote smaller genetic distances. Interestingly, the distinct subgroups illustrated in the dendrogram also evidence diminished genetic distances within themselves, showcased as diagonal "squares" with intensified yellow intensity. These findings corroborate previous studies (Larranaga et al. 2021) that identified pronounced genetic divergence between individuals from Mesoamerica and South America using the same markers. Most European samples cluster with those from Central America and Mexico, indicating a shared genetic proximity, although some of them show affiliation with South American branches.

A Neighbor-Net network based on Nei distances (Fig. 2) showed clear divergence of the branches corresponding to Honduras, Costa Rica, and Guatemala from other populations, indicating greater genetic diversity compared to the South American populations. This suggests that these populations may have remained relatively isolated, retaining their original genetic characteristics. The South American cherimoya populations from Colombia, Ecuador, Peru, and Bolivia are closely related genetically, forming a compact group. This implies that they share a common genetic history, which is consistent with the arrival of a limited number of individuals from Central America several thousand years ago. Mexico occupies a unique position, serving as a genetic "bridge" between Central America, South America, and Europe. European populations clustered closely with each other, with the Portuguese cluster positioned close to the Spanish one, although the second shows less genetic distance also with south American groups, reflecting historical introduction of the species during the colonial period.

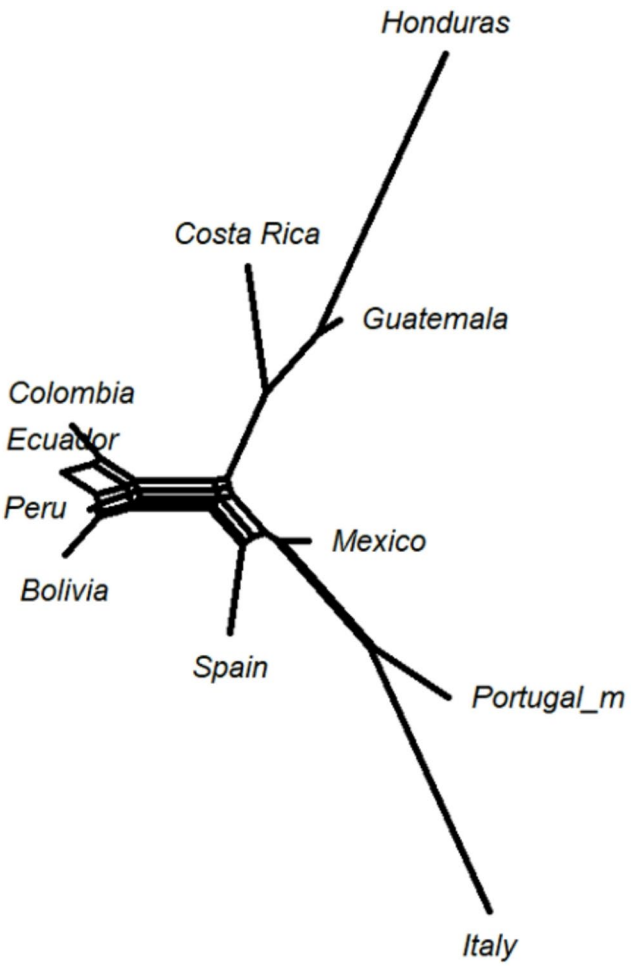


Fig. 2 Neighbor-Net based on NEI distances among populations/countries of origin

Figure 3 presents a map displaying genetic clusters identified by STRUCTURE, represented by pie charts for each population or country of origin. Additionally, for each of these groups, the two smallest FST distances per pairs are depicted (red points). The results from the Delta K analysis indicated prominent values for K2, K3, and, to a lesser extent, for K7. Given that K2 and K3 offered information similar to previous studies (Van Zonneveld et al. 2012; Larranaga et al. 2017, 2021), we opted to showcase the findings corresponding to K7, which shows a high genetic geographical structure. Within this framework, both Central and South American populations are subdivided in an almost geographical manner into distinct clusters, revealing some degree of admixture. Notably, Peruvian samples exhibit membership in a cluster shared with Bolivian samples, as well as a distinct cluster, and with a minor affiliation, with Ecuadorian and Colombian samples. Central American samples are also almost subdivided by country, with Guatemalan population showing admixture between the Honduran and the Costa Rican groups. Mexican samples notably diverge into a predominant separate cluster, with partial affiliation to the Peruvian-Bolivian, and Costa Rican-Guatemalan clusters. Fst values, indicative of genetic differentiation between groups and gene flow, offer substantial insights. Remarkably, the lowest genetic differences are found within the North and South American countries, with the exception of the connection between Mexico and Peru. European samples largely exhibit direct affiliations with the Mexican clusters, excluding the link between Spain and Madeira.

Finally, Bayesian migration estimates using MIGRATE-N consistently pointed to Mexico as the dominant source for all three European populations. For Italy, only Mexico→Italy had a 95% HPD excluding zero (M = 1.06 [0.03–2.55]); all other American to Italy routes had HPDs overlapping zero. For Portugal, again Mexico was the only credible source (Mexico→Portugal M = 0.93 [0.03–2.30]), with other American sources centered near zero. For Spain, multiple American sources showed non-zero support, with Mexico→Spain the strongest (M = 2.15 [0.91–3.03]), followed by Costa Rica→Spain (1.19 [0.14–2.41]) and a weaker but non-zero signal from Bolivia→Spain (0.69 [0.01–1.95]); remaining routes to Spain overlapped zero. Overall, MCMC diagnostics indicated good mixing and precision for these parameters (e.g., acceptance ratios 0.64–0.82 and effective sample sizes > 3.4 × 10^6 for Mexico→Italy/Portugal/Spain), lending confidence to the main inferences, although Italy's small sample size reduced estimate certainty for that population.

In summary, these results are consistent with previous studies that proposed that *A. cherimola* originated in Central America and reached South American in pre-Columbian times. It is interesting to note that the first descriptions of

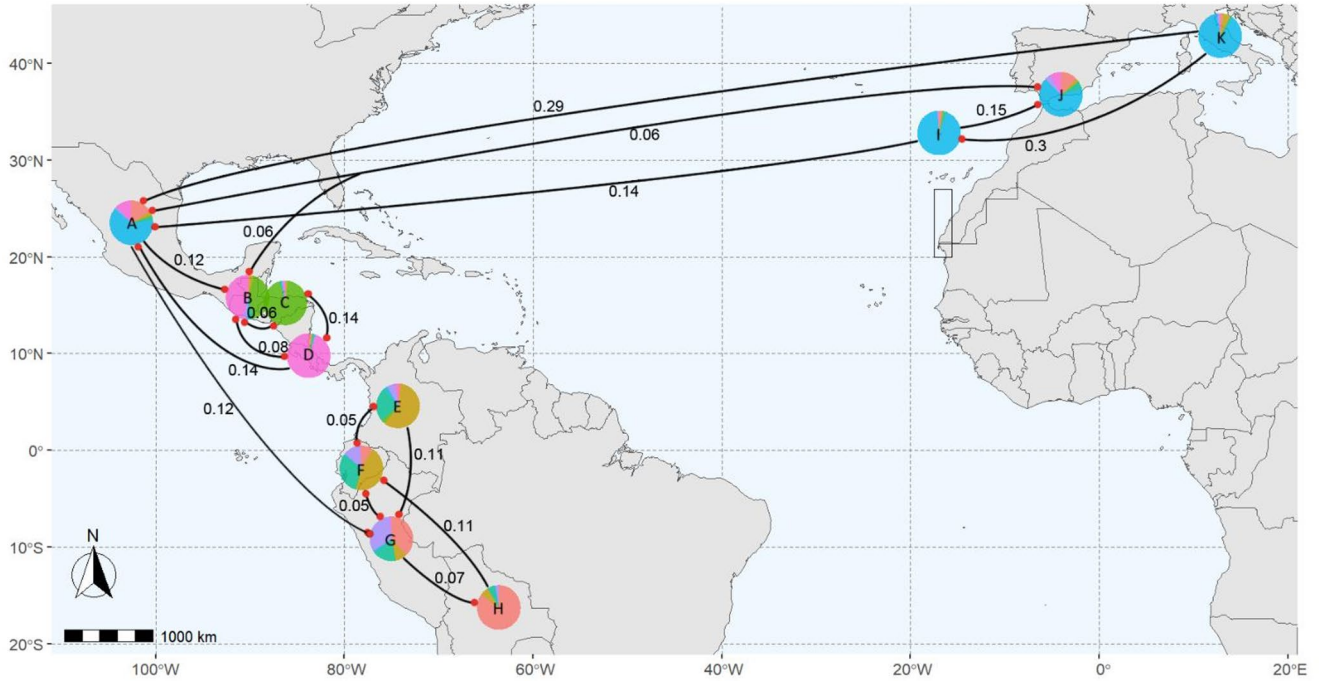


Fig. 3 Genetic clusters represented by pie charts for each population or country of origin obtained by STRUCTURE (K7). Additionally, for each population, the two smallest FST distances showed by each population are depicted (red points). Population/country of origin are shown by letters: A; Mexico, B; Guatemala, C; Honduras, D; Costa Rica, E; Colombia, F; Ecuador, G; Peru, H; Bolivia, I; Portugal (Madeira), J; Spain and K; Italy

cherimoya in the Americas by Spanish chroniclers were based on observations in Central America, where the common word for cherimoya and other closely related species is still "anona", a term that Linnaeus (1737) used to name the genus. The results show that the most probable route for the introduction of *A. cherimola* from the American continent to Europe was through Mexico. These introductions likely reached Spain and Portugal independently, or perhaps travelled from Portugal to Spain, given the importance of the island of Madeira and the Canary Islands over several centuries in the Atlantic trade routes among America, Africa, and Europe (Galan-Sauco and Cubero 2011). In Spain, cherimoya was introduced either to mainland Spain or the Canary Islands, with subsequent transfers between these regions. Some sources suggest that cherimoya was present in the Mediterranean basin as early as the sixteenth century, although most documentary accounts place its introduction and spread in the eighteenth century (Gispert and Garrido 2008). In Spain, its cultivation was documented in various municipalities of Malaga (mainland Spain) such as Almayate, Vélez-Malaga, and Benamocarra between 1789 and 1793 (García de la Leña 1879). Today, Spanish cherimoya production is concentrated in the coastal areas of Malaga and Granada. Regarding Italy, the low number of samples prevents clear conclusions, though these data also suggest an independent introduction. Thus, according to our results, the cherimoya was probably introduced from Mesoamerica to Southern Europe and these findings collectively reinforce the notion of distinct genetic pathways and migrations, supporting the historical dynamics of cherimoya population movements between continents.

Acknowledgements We thank Maria Jose Grajal for providing the Canary samples.

Author contributions NL performed the experiments, analysed the data, and wrote the first version of the manuscript. JIH and NL conceived the article, assisted in its writing, and approved the final version.

Funding Open Access funding provided thanks to the CRUE-CSIC agreement with Springer Nature. This research was funded by the projects PID2022-141851OB-I00 and PID2024-162325OA-I00 supported by MCIN/AEI and ERDF A way to make Europe (MCIN/AEI/10.13039/501100011033). NL is supported by Emergia funding (DGP_EMEC_2023_00196) of Junta de Andalucía, Spain.

Data archiving The primary database used in this study was generated from a resampling of the publicly available dataset of amplicon sizes based on SSRs deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.0p264), together with additional data from Mexico, Colombia, Portugal, Spain, and Italy.

Data accessibility The datasets generated and analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare no conflict of interest.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

References

Acosta J (1590) Historia natural y moral de Las Indias. Casa Juan de Leon, Sevilla, Spain

Alaly FQ, Liu XX, McLaughlin JL (1999) Annonaceous acetogenins: recent progress. J Nat Prod 62:504–540

Anawalt PR (1992) Ancient cultural contacts between Ecuador, West Mexico, and the American southwest: clothing similarities. Latin Am Antiq 3:114–129

Barlow C (2000) The ghosts of evolution: nonsensical fruit, missing partners, and other ecological anachronisms. Basic Books, New York, USA

Beerli P, Mashayekhi S, Sadeghi M, Khodaei M, Shaw K (2019) Population genetic inference with MIGRATE. Curr Protoc Bioinformatics 68:e87

Bitocchi E, Bellucci E, Giardini A, Rau D, Rodriguez M, Biagetti E, Santilocchi R, Spagnoletti Zeuli P, Gioia T, Logozzo G et al (2013) Molecular analysis of the parallel domestication of the common bean (*Phaseolus vulgaris*) in Mesoamerica and the Andes. New Phytol 197:300–313

Bitocchi E, Nanni L, Bellucci E, Rossi M, Giardini A, Zeuli PS, Logozzo G, Stougaard J, McClean P, Attene G et al (2012) Mesoamerican origin of the common bean (*Phaseolus vulgaris* L.) is revealed by sequence data. Proc Natl Acad Sci U S A 109:788–796

Cortes D, Moreno L, Parraga J, Galan A, Cabedo N (2014) Nuevos fármacos inspirados En Annonáceas. Rev Bras Frutic 36:22–31

de la García Leña C (1879) Conversaciones Antiguas Malagueñas, Málaga. https://www.bibliotecavirtualdeandalucia.es/catalogo/es/consulta/registro.do?id=1013396. Accessed May 2024

de la Peña E, Pérez V, Alcaráz L, Lora J, Larranaga N, Hormaza I (2018) Polinizadores y polinización En frutales subtropicales: implicaciones En manejo, conservación y Seguridad alimentaria. Ecosistemas 27:91–101

Dunnington (2021) ggspatial: Spatial Data Framework for ggplot2. R package version 1.1.5. https://CRAN.R-project.org/package=ggspatial

Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Mol Ecol 14:2611–2620

Fries RE (1959) In: Engler A, Prantl K (eds) Annonaceae. Die natürlichen Pflanzenfamilien, 2nd edn. Duncker & Humblot, Berlin, Germany

Galan-Sauco V, Cubero JI (2011) Contribution of Spain and Portugal to the exchange and acclimatization of new and old world crops. Acta Hort 916:71–82

Gispert M, Garrido A (2008) La seducción de los paladares. Junta de Andalucía, Consejería de Agricultura y Pesca, colección El Arado y la Red, Córdoba

Guangchuang Y (2022) scatterpie: Scatter Pie Plot. R package version 0.1.8. https://CRAN.R-project.org/package=scatterpie

Hosler D, Lechtman H, Holm O (1990) Axe-monies and their relatives. Stud Pre-Columbian Art Archaeol 30:1–103

Janzen DH, Martin PS (1982) Neotropical anachronisms: the fruits the gomphotheres ate. Science 215:19–27

Jombart T (2008) Adegenet: a R package for the multivariate analysis of genetic markers. Bioinformatics 24:1403–1405

Jombart T, Ahmed I (2011) Adegenet 1.3-1: new tools for the analysis of genome-wide SNP data. Bioinformatics 21:3070–3071

Kamvar ZN, Brooks JC, Grünwald NJ (2015) Novel R tools for analysis of genome-wide population genetic data with emphasis on clonality. Front Genet 6:208

Kamvar ZN, Tabima JF, Grünwald NJ (2014) Poppr: an R package for genetic analysis of populations with clonal, partially clonal, and/or sexual reproduction. PeerJ 2:e281

Kopelman NM, Mayzel J, Jakobsson M, Rosenberg NA, Mayrose I (2015) Clumpak: a program for identifying clustering modes and packaging population structure inferences across K. Mol Ecol Resour 15:1179–1191

Larranaga N, Albertazzi FJ, Fontecha G, Palmeri M, Rainer H, van Zonneveld M, Hormaza JI (2017) A Mesoamerican origin of Cherimoya (*Annona Cherimola* Mill.). Implications for the conservation of plant genetic resources. Mol Ecol 26:4116–4130

Larranaga N, Albertazzi FJ, Hormaza JI (2019) Phylogenetics of *Annona cherimola* (Annonaceae) and some of its closest relatives. J Syst Evol 57:211–221. https://doi.org/10.1111/jse.12473

Larranaga N, Fontecha G, Albertazzi FJ, Palmieri M, Hormaza JI (2022) Amplification of cherimoya (*Annona cherimola* Mill.) with chloroplast-specific markers: geographical implications on diversity and dispersion studies. Horticulturae 8:807

Larranaga N, van Zonneveld M, Hormaza JI (2021) Holocene land and sea-trade routes explain complex patterns of pre-Columbian crop dispersion. New Phytol 229:1768–1781

Li YL, Liu JX (2018) Structureselector: a web-based software to select and visualize the optimal number of clusters using multiple methods. Mol Ecol Resour 18:176–177

Liaw CC, Wu TY, Chang FR, Wu YC (2011) Historic perspectives on annonaceous acetogenins from the chemical bench to preclinical trials. Planta Med 76:1390–1404

Linnaeus C (1737) Hortus Cliffortianus, Amsterdam, The Netherlands

Lora J, Herrero M, Hormaza JI (2011) Stigmatic receptivity in a dichogamous early-divergent angiosperm species, *Annona cherimola* (Annonaceae): influence of temperature and humidity. Am J Bot 98:265–274

Lora J, Hormaza JI, Herrero M (2010) The progamic phase of an early-divergent angiosperm, *Annona cherimola* (Annonaceae). Ann Bot 105:221–231

Mapa:Ministerio de Agricutura Pesca y Alimentación de España (2021) Available online: https://www.mapa.gob.es/es/estadistica/temas/estadisticas-agrarias/agricultura/superficies-producciones-anuales-cultivos/. Accessed May 2024

Marcos JG (1994) Los pueblos navegantes Del Ecuador prehispanico. Quito, Abya-Yala, Ecuador

Martin C, Herrero M, Hormaza JI (2011) Molecular characterization of apricot germplasm from an old stone collection. PLoS ONE 6:e23979

Morton JF (1987) Fruits of warm climates. Creative Resources Systems, Winterville

Popenoe W (1921) The native home of the Cherimoya. J Hered 12:331–336

Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. Genetics 155:945–959

Pritchard JK, Wen X, Falush D (2009) Documentation for structure software: v.2.3. Accessed January 2024 https://web.stanford.edu/group/pritchardlab/structure_software/release_versions/v2.3.4/structure_doc.pdf

R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rovira-Morgado R (2007) Mesoamérica: Concepto y Realidad de Un espacio cultural. Arqueoweb: Revista Sobre Arqueología En Internet 2007(8):2

Scheldeman X (2002) Distribution and potential of Cherimoya (*Annona Cherimola* Mill.) and highlands Papayas (*Vasconcellea* spp.) in Ecuador. Faculteit Landbouwkundige en Toegepaste Biologische Wetenschappen. Universidad de Gante, Holanda

Schliep KP (2011) Phangorn: phylogenetic analysis in R. Bioinformatics 27:592–593

Schliep KP, Potts AJ, Morrison DA, Grimm GW (2017) Intertwining phylogenetic trees and networks. Methods Ecol Evol 8:1212–1220

South A (2017) rnaturalearth: World Map Data from Natural Earth. R package version 0.1.0. https://CRAN.R-project.org/package=rnaturalearth

van Damme P, van Damme V, Scheldeman X (2000) Ecology and cropping of Cherimoya (*Annona Cherimola* Mill.) in Latin America. New data from Ecuador. Fruits 55:195–206

Van Zonneveld M, Larranaga N, Blonder B, Coradin L, Hormaza JI, Hunter D (2018) Human diets drive range expansion of megafauna-dispersed fruit species. Proc Natl Acad Sci U S A 115:3326–3331

van Zonneveld M, Scheldeman X, Escribano P, Viruel MA, Van Damme P, Garcia W, Tapia C, Romero J, Siguenas M, Hormaza JI (2012) Mapping genetic diversity of cherimoya (*Annona cherimola* Mill.): application of spatial analysis for con-servation and use of plant genetic resources. PLoS ONE 7:e29845

Wickham (2016) ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.