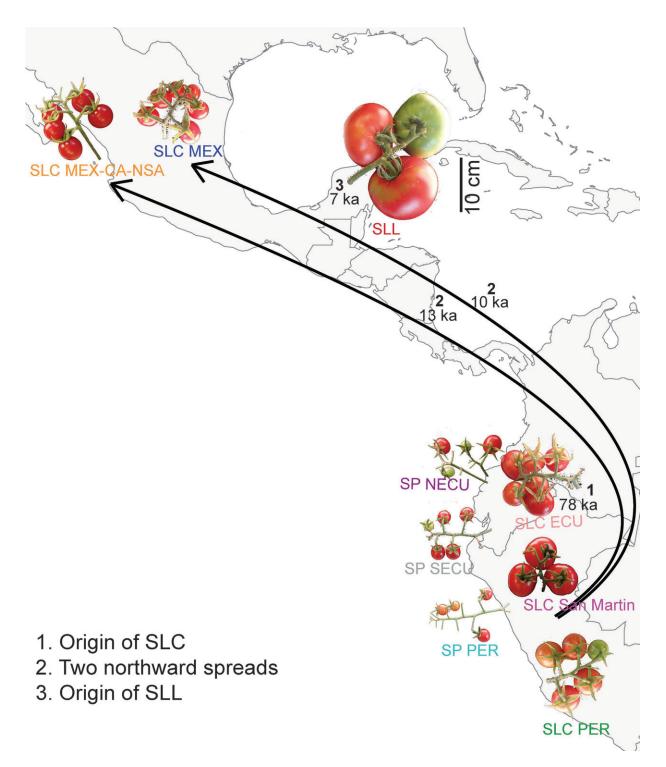


## **Evolution on the vine: A history of tomato domestication in Latin America**

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Tomato domestication history is generally depicted as a "two-step" process with an increase in fruit size from blueberry-sized SP to generally cherry-sized SLC, and then to the very large-fruited common tomatoes (SLL) consumed around the world. All the signs from the study analyses pointed to the intermediate group



(SLC) emerging in Ecuador---far earlier than human domestication--- then spreading out northward over time, suggesting that human use of SLC came much later. They reconstructed a putative domestication history of tomato groups, focusing especially on the under-explored intermediate stage represented by SLC. They found that SLC originated in Ecuador probably as a wild species over 78 KYA, likely as a vicariance event that separated more coastal SP populations from inland emerging SLC. Credit: Hamid Razifard, University of Massachusetts, Amherst

The common cultivated tomato (*Solanum lycopersicum L. var. lycopersicum*; or (SLL)) is among the world's most widely grown vegetable crops, from big agricultural farms to heirloom grown varieties.

In 2012, the domesticated 'Heinz 1706' tomato, an SLL, became the very first tomato to have its whole genome sequenced in an effort to better understand the world's highest value vegetable crop.

Since then, scientists from around the world have been adding to our rich understanding of the evolutionary variation responsible for the changes within the tomato's 12 chromosomes.

The ultimate origin traces the lineage of the modern tomato to South America. Previous studies have proposed that wild red-fruited S. pimpinellifolium L. (SP) was domesticated in South America to give rise to *S. lycopersicum L. var. cerasiforme* (SLC), and SLC later gave rise to SLL in Mesoamerica through subsequent improvement for SLL's around the world.

Now, a new study funded by the US National Science Foundation, published in the Advance Access edition of *Molecular Biology and Evolution*, has revealed and confirmed the history of tomatoes from South America, from once blue-berry sized to the large fruits of today.



"Tomato <u>domestication</u> history is generally depicted as a "two-step" process with an increase in fruit size from blueberry-sized SP to generally cherry-sized SLC, and then to the very large-fruited common tomatoes (SLL) consumed around the world," said the study authors.

In particular, the authors attempted to shed light on the evolutionary history of the first ancient split, between SP and SLC, and the subsequent evolution of SLC, whose status as the intermediate group in tomato domestication has historically been hotly debated.

What they found in all the signs from their analyses pointed to the intermediate group (SLC) emerging in Ecuador—-far earlier than human domestication—- then spreading out northward over time, suggesting that human use of SLC came much later.

"We have reconstructed a putative domestication history of tomato groups, focusing especially on the under-explored intermediate stage represented by SLC. We found that SLC originated in Ecuador probably as a <u>wild species</u> over 78 KYA, likely as a vicariance event that separated more coastal SP populations from inland emerging SLC," said the authors.

In the study, the scientific team performed whole-genome sequencing, and population genomics analyses from a sampling of SLL, SLC, and SP tomatoes to reconstruct tomato domestication history. In total, the team generated new whole-genome sequences for 166 samples, representing SP across its native range in South America and SLC across its native range in South America and Mesoamerica, along with SLL landraces from Mesoamerica, which previously have been under-represented. A total of 23,797,503 single nucleotide polymorphisms (SNPs) were identified by aligning sequences to the SLL reference genome. They also performed extensive phenotyping to determine the traits that most differentiate cultivated from wild tomatoes.



"It is evident that the common cultivated tomato accessions (SLL) have experienced radical changes compared to wild tomato (SP) phenotypes, with fruits that on average have thicker pericarps, more locules, lower dry weight, lower levels of beta-carotene, soluble solids, and citric acid, and higher levels of malic acid," said the authors.

Further surprising details of the tomato history could be gleaned on what happened after the initial ancient split of SLC from SP. The authors found that although SLC groups in South America contain many characteristics that would seem consistent with human domestication, these traits were lost when SLC spread north to Mesoamerica. Intriguingly, these "wild-like" northern SLC groups are the closest relatives of modern tomato.

"Although SLC accessions that feature traits consistent with domestication are persistent in South America, remarkably, these traits were reduced once SLC populations spread northward. SLC populations in northern South America, Central America, and Mexico on average have smaller fruits, with fewer locules, thinner pericarps, and higher levels of beta-carotene and citric acid compared with South American SLC populations, ", said the authors.

The authors estimate that the timeframe of SLC moving northwards allows for human influence, but the reason for the reduction of domestication-like traits is unknown. With SLC in Mexico the most likely ancestors of SLL, the authors point out that re-selection of domestication traits may have occurred.

"Thus, the origin of the common cultivated tomato, SLL, about 7 KYA in Mexico, probably entailed re-selection of domestication traits (or a redomestication) from an SLC population that was phenotypically more wild-like than previously thought."



In addition to estimating the timing of the emergence of different tomato groups, the genomic survey also identified many known or novel plausible candidate genes responsible for changes in tomato physical traits.

"With our strict sweep filtering criteria, we found sweeps associated with our results of genome wide association studies, or GWAS peaks, for dry weight, locule number, soluble solids, and citric acid," said the authors.

These included Lin5, which has previously been implicated in changes in sugar content in tomato domestication, and malic acid, which was associated with an insertion or deletion event upstream of Solyc06g072840, which codes for a hydrogen peroxide-induced protein 1, a gene highly expressed in tomato fruits and seeds and part of a co-expression network involved in the Krebs cycle and <u>citric acid</u> production.

There were additional surprises in their analyses. The origin of SLC seems to have involved a much higher number of putative selective sweeps (133) compared to any other group (origin of northern SLC: 54 and 91, and origin of SLL: 55). This suggests that the origin of SLC involved selection on either more traits or traits with more underlying genes than any other main event in the evolutionary history of domesticated tomato.

What the scientists have now learned from reconstructing the domestication history of the cultivated tomato in Latin America could help tomato growers today identify beneficial genes to re-introduce to modern tomato varieties to improve its agricultural and consumer desirable traits.

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