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Two domestications for grapes

Glacial cycles and wild adaptations shaped grape domestication and the rise of wine

By Robin G. Allaby

The domestication of plants that underpin the rise of human civilization is increasingly recognized as a complex interplay of processes across a culturally connected landscape. On page XXX of this issue, Dong *et al.* (1) reveal more of this complexity by unravelling the evolutionary events that led to grape (*Vitis vinifera* ssp. *vinifera*) domestication. By incorporating the effects of glacial oscillations on biogeographical distributions of the wild progenitor (*Vitis vinifera* ssp. *sylvestris*) across Eurasia, they resolved two separate domestication processes from two distinct populations of *sylvestris* in the Near East and South Caucasus that were separated during the last glacial advance. They found that although the South Caucasus domestication is associated with early wine making, the origin of wine in Western Europe is associated with cross-fertilization (introgression) between Western Europe wild populations and domesticated grapes originating from the Near East that were initially used as food sources.

The roots of domestication are frequently to be found deep in the Pleistocene, ending 11.5 thousand years ago (Kya), where climate played a crucial role in determining human population densities and underlies the mosaic rates at which Neolithization occurred in the early Holocene beginning 11.5 Kya (2). Increasingly, ecological niche modelling is being used to track the past distributions of wild forms across these climatic shifts to help identify likely progenitor populations, for example in *Brassica* (3), as well the formation of subspecies post domestication, such as in rice (4). Incorporating this approach and using a titanic set of 2448 genomes from grapevine samples collected in 23 institutions across 16 nations around the world, Dong *et al.* establish that glacial episodes split *V. sylvestris* into Eastern and Western ecotypes, distinct and locally adapted varieties, around 500 Kya. The last glacial advance saw the split of the Eastern ecotype into two groups that each gave rise to a domestication process. It is this split of the Eastern ecotypes that has not been previously resolved into two different domestications (5, 6).

Despite being separated by over 1000 km, the two domestication processes appear to have occurred contemporaneously with a high degree of shared signatures of selection on the same genes. Recent evidence demonstrates that long distance networks of human communication and exchange over this distance occurred in the Epipalaeolithic, 10-20 Kya (7, 8). The findings of Dong *et al.* appear to show multiple emergences of domesticated forms occurring at a landscape level in which human communication would likely have been a key factor in promoting gene flow (9). To what extent the same domestication alleles might have been transported between different populations by humans or were present in the wild populations is a question that remains, and the answers will illuminate the role of human agency in grapevine domestication.

The South Caucasus domestication had limited spread and very little further influence, but the Near Eastern domestication came to dominate, establishing four major European cultivated grape clusters. Domestication is estimated to have occurred 11.5 Kya, contemporaneous with the initial emergence of cereals, and the dates of the splits to form four European clusters match tantalizingly closely to the initial spread of the Neolithic into Europe. These dates are much earlier by several thousand years for both origin and spread than is expected from the archaeological evidence from domesticated seed morphology, which is distinct from wild seeds. The processes of selection that led to plant domestication can greatly predate the rise of morphological forms (10), so these earlier-than-expected dates may indicate exploitation of wild forms. Alternatively, although Dong *et al.* attempted to account for it, the long history of vegetative propagation (asexual reproduction) in grape cultivation (11) may be a confounding factor in divergence estimates by inflating generation time, which could explain the discrepancy with the archaeological record. To test between these alternatives will require direct investigation of the archaeological record using ancient DNA (archaeogenomics), as the authors also conclude.

The spread of domesticated plants from the Near East into new European environments is associated with a requirement for adaptation (12, 13). Unlike cereals, grapes had wild populations in Europe from which they could obtain local adaptations. Gene flow from wild populations into domesticated forms can be hard to avoid and supplies both locally adapted variation as well as a resurgence of wild traits. Such adaptive introgression has also been noted in previous grape studies (5, 6) and was recently reported in flax, which also originates from the Near East and has wild populations distributed throughout Europe (14). In both cases, the adaptive introgression is associated with a change in use. In flax, wild flowering time genes introgressed and enabled adaptation to changes in daylength at higher latitudes. This was at the cost of seed size and oil content, but also generated an architecture that was suitable for fiber production and may well have driven the textile revolution in central Europe, around 6 Kya. In grapes, adaptations to the environment have been acquired that are associated with water stress and disease resistance (1, 5). However, such introgressions also carried wild traits that compromise edibility. Compared with table grapes, wine grapes are smaller, thick skinned and have lower sugar content. These traits are more similar to wild grapes, which also make them more suited for wine making and less appealing for eating. That natural environmental adaptations underly the transition to wine raises key questions about the drivers behind such usage changes and to what extent they are forced by natural selection rather than by humans.

The enormous data set produced by Dong *et al.* will provide insight into the finer points of grape evolution for some time to come. The increased resolution has pinpointed the lightening of berry color to some unknown genes close to the previously implicated *MybA* locus (15), and that the ancient Muscat flavor is surprisingly rare, possibly because of a pleiotropic constraint that prevents fixation. This study does not stray into the effects of structural variation in the genome, whereby many regions have been lost across various cultivar lineages. This has been shown to be key to the functional changes seen in domesticated grapes relative to their wild ancestors (15). The next big step will be to integrate these data into a structural landscape.

REFERENCES AND NOTES

1. Y. Dong *et al.*, *Science* **379**, XXX (2023).
2. A. Palmisano *et al.*, *Quat. Sci. Rev.* **252**, 106739 (2021).
3. M. E. Mabry *et al.*, *Mol. Biol. Evol.* **38**, 4419 (2021).
4. R. M. Gutaker *et al.*, *Nat. Plants* **6**, 492 (2020).
5. G. Magris *et al.*, *Nat. Comm.* **12**, 7240 (2021).

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6. S. Freitas *et al.*, *Sci. Adv.* **7**, eabi8584 (2021).
7. E. Frahm, C. A. Tryon, *J. Archaeol. Sci. Rep.* **21**, 472 (2018).
8. L. A. Maher, *J. Archaeol. Method Theory* **26**, 998 (2019).
9. R. G. Allaby *et al.*, *Trends Ecol. Evol.* **37**, 268 (2021).
10. R. G. Allaby *et al.*, *Phil. Trans. Roy. Soc. B.* **372**, 20160429 (2017).
11. J. Ramos-Madriral *et al.* *Nat. Plants* **5**, 595-603 (2019).
12. A. Timpson *et al.*, *J. Archaeol. Sci.* **52**, 549 (2014).
13. S. Shennan *et al.*, *Nat. Comm.* **4**, 2486 (2013).
14. R. M. Gutaker *et al.*, *Sci. Rep.* **9**, 976 (2019).
15. Y. Zhou *et al.*, *Nat. Plants* **5**, 965 (2019).