dynamic vegetation modeling (*15*).

These examples illustrate how topographic change and mountain building are coupled to tectonics, the biosphere, and atmospheric processes. However, process-based models such as those used by Salles *et al.* have their limits. They provide physics-based predictions of how eroded material from mountains is deposited in lowland and marine settings. But, simplifications are needed in the applied geomorphic transport laws to remain computationally feasible. As improved approaches emerge for formulating the physics and chemistry of erosion and deposition under different conditions, they need to be integrated into such models. Consideration of the glacial erosion effects on sediment accumulation is also necessary. These challenges require field and laboratory observations that can be upscaled to more extended time periods.

Understanding weathering, erosion, and deposition; topographic effects on biodiversity; and climate change during mountain building is still in its infancy. Future research efforts should focus on observationally driven parameterizations of these interactions. This will allow questions to be tackled, such as how do temporal and spatial variations in erosion and chemical weathering influence CO_2 drawdown? How did the coevolution of biota and landscapes influence mountain erosion, sediment accumulation, carbon fluxes, and storage? Although Salles *et al.* find that globally averaged sediment accumulation rates have remained somewhat constant over the past 100 million years, answering these questions (and others) requires detailed local and regional studies in which the signal of individual processes can be better understood and is not averaged at the global scale. This will involve advances in process-based landscape evolution models, investigations into the biotic effects on surface processes, and geochemical, stratigraphic, and geochronologic data sets that are suitable for evaluating model predictions. ■

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GENOMICS

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 892 of this issue, Dong *et al.* (*1*) reveal more of this complexity by reporting the unraveling of 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 winemaking, the origin of wine in Western Europe is associated with cross-fertilization (introgression) between Western Europe's 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 (ka), 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 ka (*2*). Increasingly, ecological niche modeling 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 after 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 *sylvestris* into eastern and western ecotypes—distinct and locally adapted varieties—around 500 ka. 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 more than 1000 km, the two domestication processes appear to have occurred contemporane-

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School of Life Sciences, Gibbet Hill Campus, University of Warwick, Warwick, UK. Email: r.g.allaby@warwick.ac.uk

The transition from table grapes (left) to wine grapes (right) by wild introgression resulted in smaller berries with thicker skins, less sugar, and larger seeds.

ously 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 to 20 ka (*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 ka, contemporaneous with the initial emergence of cereals, and the dates of the splits to form four European clusters match tantalizingly closely with 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 and 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 ka. 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 and thick skinned and have lower sugar content. These traits are more similar to those of wild grapes, which also makes them more suited for winemaking 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 were forced by natural selection rather than by humans.

The enormous dataset 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 has suggested that the ancient Muscat flavor is unexpectedly 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. ■

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BIOACOUSTICS

Voices in the ocean

Toothed whales evolved a third way of making sounds similar to that of land mammals and birds

By **Andrea Ravignani**[1,2] *and* **Christian T. Herbst**[3,4,5]

The ability of humans to sing and speak requires precise neural control of the larynx and other organs to produce sounds. This neural control is limited in most mammals (*1*). For animals that create complex sounds, less is known about how peripheral anatomical structures enable vocal feats (*2*). On page 928 of this issue, Madsen *et al.* (*3*) demonstrate that toothed whales, such as dolphins and killer whales, have a distinct nasal structure that produces diverse sounds in a broad frequency range that spans >4 orders of magnitude.

The findings of Madsen *et al.* stem from two long-standing strands of research: cetacean (toothed whales and baleen whales) communication and human voice science. For decades, studies of cetacean communication have relied on evidence from sound recordings complemented by postmortem anatomical investigation. However, cetaceans are large and patchily inhabit the ocean, so sampling sounds from specific individuals can be difficult and the rare postmortem samples cannot elucidate what happens "in action." As a result, finding the mechanism behind the sound production of toothed whales has proved elusive. In parallel, techniques have been developed to measure fine-grained dynamic parameters of the human vocal apparatus and map them to the sounds that are produced. Madsen *et al.* apply the methods used to study human voice to toothed whales to show that they blow air through their nasal passage and finely control it to produce diverse sounds.

This newly described voice production sys-

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[1] Comparative Bioacoustics Group, Max Planck Institute for Psycholinguistics, Nijmegen, Netherlands. [2] Center for Music in the Brain, Department of Clinical Medicine, Aarhus University and The Royal Academy of Music Aarhus/Aalborg, Aarhus, Denmark. [3] Department of Behavioural and Cognitive Biology, University of Vienna, Vienna, Austria. [4] Department of Vocal Studies, Mozarteum University Salzburg, Salzburg, Austria. [5] Janette Ogg Voice Research Center, Shenandoah Conservatory, Winchester, VA, USA. Email: andrea.ravignani@mpi.nl