

As far as mature forests go, this framework of interacting multiple resource limitations makes sense, and it joins a growing number of recent studies that emphasize the influence of nitrogen–phosphorus interactions on ecosystem functioning^{2,3}. However, several important details await incorporation. First, the framework does not attempt to explain the distribution of nitrogen-fixing shrubs and herbs, which can play an important role in ecosystems at all latitudes. Second, the framework only addresses symbiotic nitrogen fixation, but recent studies provide intriguing evidence that nitrogen fixation by free-living soil bacteria^{4,5} and cyanobacteria⁶ may be quantitatively important in some ecosystems. The activity of these free-living nitrogen fixers increases on the addition of phosphorus and in the presence of phosphorus-rich leaf litter^{4,5}, providing more evidence for nitrogen–phosphorus linkages, and also highlighting the need for an improved understanding of competition for phosphorus in soils. Houlton and colleagues

use their model to demonstrate that the advantages of symbiotic nitrogen fixation are lost if all competitors for soil phosphorus benefit from the phosphatase exuded by roots of nitrogen-fixing trees. Given that competition for phosphorus between roots of fixing and non-fixing species, mycorrhizae, free-living nitrogen-fixing bacteria and other soil organisms is poorly understood, we can't yet determine the fate of this phosphorus.

Furthermore, the presence of tree species capable of symbiotic nitrogen fixation is not always a reliable indicator of the presence of nitrogen-fixing nodules; hence the abundance of leguminous trees in some regions of the lowland tropics may not reflect biological nitrogen fixation⁷. Finally, secondary succession (where shrubs and small trees colonize previously disturbed patches of forest) is not completely addressed by this new framework. Nitrogen is often lost from mature forests following disturbance, which should confer a competitive advantage to symbiotic nitrogen-fixing species. But although this often appears to be the case

in temperate zones, it is less clear whether symbiotic nitrogen fixation plays an important role in the secondary succession of boreal and tropical forests^{3,6}.

Frameworks are, of course, meant to be built on. A unified conceptual framework that also encompasses free-living nitrogen fixation, non-tree nitrogen-fixing symbioses, root competition, nodulation and secondary forest succession would provide a more satisfying structure for understanding the distribution of terrestrial nitrogen fixation. But in the meantime, the insights of Houlton and colleagues lay a much needed foundation for future research into the conundrum of terrestrial nitrogen fixation.

References

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GEOMORPHOLOGY

Sculpted by a megaflood



AAAS

Not all canyons are created equal. Steep canyons with amphitheatre-shaped heads are thought to result from the activity of groundwater, on the basis of studies of such features that developed in sand, for example in the Florida Panhandle. In such settings, groundwater emerges in springs and can destabilize slopes. Growth of the canyon is achieved not by surface flow, such as in a river, but by the retreat of canyon heads by periodic toppling of material that could have been softened by groundwater.

But when amphitheatre-headed canyons are carved in hard rock, the

possibility that surface water was involved cannot be discounted. Michael Lamb of the University of California at Berkeley and his colleagues focused on the Box Canyon in Idaho, USA (*Science* **320**, 1067–1070; 2008). The location is ideal to investigate the ways in which water shapes the Earth's surface, because the canyon seemed a perfect example of groundwater-aided carving: a spring originates at its head and provides almost all of the water that flows in this canyon and there is no surface drainage upstream of the canyon head.

But the researchers found heaps of boulders near the canyon head, which are

usually associated with pools of water that assemble under waterfalls, and they discovered scour marks made by surface water extending upstream from the rim of the canyon. In addition, hydraulic calculations suggest that the water flow in the present stream is grossly insufficient to carve a canyon of this size. Something far more powerful would be needed and groundwater-related erosion is not a viable candidate to provide that force.

The most likely process for the formation of Box Canyon is an immense flood. Such a surge would have had to persist for between about a month and six months, eroding the canyon rapidly headward and transporting the resulting debris out of the canyon. Exposure ages of the rocks suggest that the canyon formed tens of thousands of years ago. The flood is unlikely to have resulted from heavy rainfall because precipitation in this area was probably quite low at the time, just as it is now.

Similarly shaped canyons have been found in volcanic terrains on Mars. Landforms like Box Canyon that go back to brief periods of catastrophic flooding may be more suitable terrestrial analogues for these martian canyons than amphitheatre-headed canyons formed by groundwater activity in sand.

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