

in heterosis (5). These breakthroughs in understanding a fundamental phenomenon of plant biology are leading the way to identifying the underlying genes or small RNAs with the prospect of improving heterosis in maize and other crops.

The full potential of a genome sequence for elucidating complex agronomically important traits (such as yield, quality, and stress tolerance) can be achieved only if there is sufficient resolution in genetic mapping and phenotyping of the target traits. In maize, this has been accomplished with the recent development of a nested association mapping (NAM) population (11) that is based on B73 (5000 recombinant inbred lines generated by crossing B73 with 25 diverse maize lines) and captures ~136,000 chromosomal crossover events. This powerful resource has revealed already the genetic basis of flowering time in maize, which is driven by numerous (50 to 100) small-effect QTL (12). Using knowledge from the B73 genome sequence features, Gore *et al.* (4) targeted the gene fraction of the maize genome for resequencing in the founder inbred lines of the NAM population. Two data sets comprising 3.3 million

single-nucleotide polymorphisms (DNA sequence variations) were used to produce a first haplotype map (“HapMap”) and analyze the recombination and diversity distribution along the maize chromosomes. The relative distance along a chromosome arm and the repeat density were identified as the two major drivers of recombination distribution, while 21% of the genic fraction was found in low-recombination pericentromeric regions. Moreover, Gore *et al.* established the relation between low recombination and the residual heterozygosity found in the pericentromeric regions that likely underpins heterosis. This maize HapMap and comparative genome hybridization experiments (5) permitted the identification of more than 100 low-diversity regions that are possibly associated with domestication and geographic differentiation of maize. These analyses set up the next goals for maize, including overcoming recombination constraints that limit the full exploitation of the genetic diversity present in the maize gene pool.

The results reported around the maize genome sequence will have a broad impact on plant breeding and provide far-reaching

benefits for humans and animals. Years of hard work by the maize community to accumulate resources, populations, phenotypic data, and agronomic knowledge can now be integrated with sequence information to accelerate crop improvement. Moreover, this will open the floodgates for genome sequencing and genome-enabled breeding of other economically important crops such as wheat, barley, or pine whose larger and more complex genomes have long been viewed as making these plants “unapproachable.”

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PALEONTOLOGY

Megafaunal Decline and Fall

Christopher Johnson

One of the most dramatic environmental changes in recent Earth history has been the disappearance of very big animals—mammoths, mastodons, ground sloths, giant kangaroos, moa and hundreds of others—from most of the land area of the globe. What caused these extinctions? And how did they affect the world’s ecosystems? The first question has generated such intense debate that few scientists have got past it to confront the second. On page 1100 of this issue, Gill *et al.* (1) give answers to both questions.

Twenty thousand years ago, North America had a more impressive array of big mammals than Africa does today; by 10,000 years ago, 34 genera of these mammals were gone, including the 10 species that weighed more than a ton. Many other drastic changes occurred in this interval, all of which have

been advocated as possible causes of megafaunal extinction. The climate flipped from cold to warm, then back to cold in a 1000-year chill (the Younger Dryas), before rapidly rewarming. There were more, larger fires (2), and the structure and species composition of vegetation changed drastically. People arrived, and the Clovis culture—with a characteristic style of beautifully crafted stone spear points—flourished for less than 1000 years (3). Some scientists have argued that an extraterrestrial object struck Earth ~13,000 years ago, triggering the Younger Dryas, starting fires, killing the megafauna, and putting an end to the Clovis culture (4).

The power of the new study (1) comes from the use of a tiny organism to reconstruct the decline of the very biggest animals. *Sporormiella* is a fungus that produces spores in the dung of large herbivorous vertebrates. Lots of dung means lots of spores, so *Sporormiella* gives an index of the biomass of large herbivores. The spores accumulate in sediments along with pollen and charcoal,

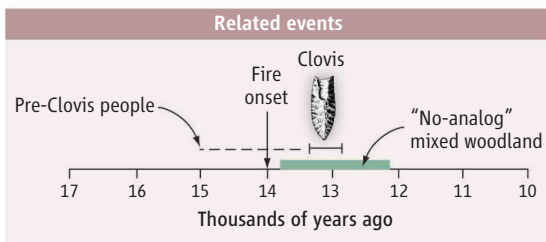
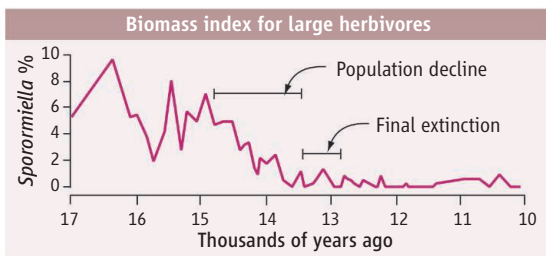
Declines in North American megafauna populations began before the Clovis period and were the cause, not the result, of vegetation changes and increased fires.

allowing changes in biomass of large herbivores to be matched exactly to sediment records of vegetation and fire, which can in turn be dated and aligned with other archaeological and environmental records.

Gill *et al.* analyzed sediments from a lake in Indiana in this way, and found that megafaunal decline began ~14,800 years ago and took more than a thousand years (see the figure). Large vegetation changes and an increase in fire followed this decline. All this happened long before the proposed extraterrestrial impact. This rules out vegetation change, fire, and cosmic disaster as primary causes of megafaunal extinction. Climate change as a cause also looks implausible: Climate would most likely have affected megafauna by changing vegetation, but vegetation changes followed megafaunal decline.

What about people? It has long been argued that Clovis artifacts signal the first arrival of people in North America south of the boreal ice sheets and that the Clovis people were specialized big-mammal hunters

School of Marine and Tropical Biology, James Cook University, Townsville, Queensland 4811, Australia. E-mail: christopher.johnson@jcu.edu.au



Pushed to the brink. Megafauna such as mastodons (**top**) lived in North America until about 13,300 to 12,900 years ago and maintained open savanna-like vegetation. Gill *et al.* have now used the abundance of the dung fungus *Sporormiella* as an indicator of megafaunal populations to study the pattern of megafaunal decline around Appleman Lake in Indiana. They show that this decline began about 14,800 years ago (**middle**). The decline of the megafauna was followed by an increase of fire and development of novel plant communities; although the megafaunal extinction coincides with the presence of the Clovis people, earlier human communities may have been responsible for the initial decline (**bottom**).

of the endgame, possibly reflecting an intensified hunting strategy that developed once megafauna had become rare, possibly wary, and harder to hunt.

The results of Gill *et al.* thus help to elucidate the cause of megafaunal extinction in North America and raise new questions on how people and megafauna interacted. But they also show that this extinction caused a major ecological transformation. Before 14,800 years ago, the environment around the site studied by Gill *et al.* was an open savanna or parkland, probably with scattered spruce and rare broad-leaved trees growing over a short grass-dominated pasture, and almost no fire. As the megafauna declined, woody biomass increased, mainly by growth of broad-leaved trees that had presumably been suppressed by the large herbivores. The result was a transitory spruce/broadleaf woodland, the like of which does not exist today. Big fires broke out ~14,000 years ago, and for the next few thousand years, major fires returned every few centuries. These changes were widespread (7): Fire increased throughout North America ~14,000 years ago (2), and the transitory "no-analog" woodland extended over a vast area (8).

None of this should surprise us. The interactions of mega-herbivores with vegetation and fire can still be seen at work in Africa (9). Megafaunal extinctions elsewhere should have had similarly dramatic consequences (10). The world's ecosystems must have been profoundly restructured as megafaunal extinctions stepped around the globe. Describing these ecological transformations, and understanding the development of today's ecosystems in light of them, is the next big challenge for ecologists.

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who caused a crash of megafaunal populations from prehuman abundance to extinction within a few hundred years. This "blitzkrieg" scenario is supported by the fact that terminal dates on megafaunal fossils range from 13,300 to 12,900 years ago (5), which coincides almost exactly with the Clovis period (3). But the new data show that the megafaunal decline had begun more than a thousand years earlier. If people were responsible for that decline, they must have been pre-Clovis settlers. The existence of such people has been controversial, but archaeological evidence is slowly coming to light (6) and is consistent with their arrival around the beginning of the megafaunal decline (1). It is beginning to look as if the greater part of that decline was driven by hunters who were neither numerous nor highly specialized for big-game hunting. Clovis technology may have been a feature

of the endgame, possibly reflecting an intensified hunting strategy that developed once megafauna had become rare, possibly wary, and harder to hunt. The results of Gill *et al.* thus help to elucidate the cause of megafaunal extinction in North America and raise new questions on how people and megafauna interacted. But they also show that this extinction caused a major ecological transformation. Before 14,800 years ago, the environment around the site studied by Gill *et al.* was an open savanna or parkland, probably with scattered spruce and rare broad-leaved trees growing over a short grass-dominated pasture, and almost no fire. As the megafauna declined, woody biomass increased, mainly by growth of broad-leaved trees that had presumably been suppressed by the large herbivores. The result was a transitory spruce/broadleaf woodland, the like of which does not exist today. Big fires broke out ~14,000 years ago, and for the next few thousand years, major fires returned every few centuries. These changes were widespread (7): Fire increased throughout North America ~14,000 years ago (2), and the transitory "no-analog" woodland extended over a vast area (8).

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