NEWS & VIEWS


Ritual centres: the imposing remains of Tikal (left) and Angkor Wat.

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ARCHAEOLOGY

Maya, Khmer and Inca

Jared Diamond

Past societies have struggled against environmental problems similar to those that beset us today. Three publications illuminate the outcomes for three different tropical civilizations during the period AD 700–1600.

From time to time, separate archaeological projects on different societies end up by suggesting common themes to events in the ancient world. Thus, two new studies[1,2] point to parallels between the collapse of cities on opposite sides of the globe — the southern lowland Maya cities in Central America, and Angkor, the centre of the Khmer empire in what is now Cambodia. These parallels include the effects of climate change, which hurt both the Maya and the Khmer. By contrast, as a third report[3] indicates, climate change seems to have benefited another ancient civilization, the Incas of South America.

The Maya of Central America, famous for their architecture and writing, abandoned most cities in their southern lowlands between AD 800 and 950 (ref. 4). Lentz and Hockaday[1] have now contributed to our understanding of this collapse by identifying the wood used in 135 support beams from all six major temples and two palaces at the Maya city of Tikal, spanning the century of its peak population (AD 700–810). Although the surrounding forests are rich in tree species, only two species — sapodilla and logwood — accounted for all of the beams. Both share the advantages of being composed of strong, durable wood. Sapodilla is slower growing but superior because it grows much larger; logwood has the drawbacks of thorns, of gnarling with age and of growing in poorly accessible thickets.

Use of these two species shifted with time. All beams sampled from buildings erected early in the eighth century were from sapodilla, often from big trees found only in old-growth forest. During the mid-eighth century, logwood supplanted sapodilla. In the early ninth century, just before temple construction ceased at Tikal, builders resumed using sapodilla, but as smaller beams, presumably from younger trees in secondary forest. These shifts are as expected if builders first used the best and biggest trees, then shifted to suboptimal or smaller trees as preferred trees became depleted.

This study[1] expands on other evidence for deforestation's role in the decline of the southern-lowland Maya. But it seems significant that some old forests with big sapodilla trees were still standing around Tikal in AD 700, nearly two centuries after Tikal's population began to soar. As Lentz and Hockaday note[1], this implies that the Maya practised some forest conservation, perhaps by designating sacred groves or royal forests. Nevertheless, those efforts were ultimately overwhelmed by the demand for timber and farmland.

For the next study[2], we move halfway around the world, to the Khmer empire's capital of Angkor in modern Cambodia[5], where a collaboration directed by Roland Fletcher, Michael Barbetti and Daniel Penny has been studying another famous abandonment[2,6]. Data gathered by NASA radar imaging, ultra-light airplane overflights and ground surveys have transformed our understanding of Angkor. Early archaeologists could easily recognize Maya and Khmer ritual centres, because Tikal's temples soar to heights of 70 metres, and Angkor Wat is the world's largest religious monument. But the households surrounding these centres did not leave impressive ruins, producing the mistaken view that the centres stood in isolation. The new surveys[2] show that, at its peak (about AD 1100–1300), Angkor was probably the world's most extensive low-density city, covering 1,000 square kilometres and with half a million or more inhabitants.

Other parallels between Tikal and Angkor include the multifactorial causes of their declines. Both involved population growth and deforestation for timber and agriculture, resulting in erosion and siltation, droughts and fighting. Still another parallel is the slowness of both declines. Whereas Norse Greenland's Western Settlement disappeared in a single winter[7], the declines at Angkor and the Maya cities stretched over at least a century. But the end result was the same in both the latter cases: populous cities reduced to uninhabited, jungle-covered ruins.

Along with those parallels were big differences between Angkor and the Maya realm. Foremost was the unification of the whole Angkor region into a Khmer empire, whereas the Maya remained splintered into dozens of warring city states. Was that because the Khmer area's higher agricultural productivity, domestic animals for transport and abundant fish and other protein sources enabled the Khmer — but not the Maya — to control large domains and feed standing armies of conquest? Related to that political difference, the Khmer practised water management on a scale dwarfing that of the Maya and most other regions of the world. Angkor's surrounds were converted into an artificial landscape criss-crossed with canals, embankments, reservoirs, dams and other massive engineering works to redirect river flows, store water for the dry season and avert floods by disposing of excess water during monsoons. The Khmer struggled for centuries to maintain their hydraulic landscape until it became overwhelmed by climate change, producing floods that broke embankments and canals filled with sediments from eroded terrains[6].

For the third study[3], a success story, we return to the New World. Why did the Inca empire of the Andes expand to become the largest Native American empire, only a few centuries after the Wari and Tiwanaku empires of the same region collapsed? Chepstow-Lusty and colleagues[3] have analysed a mud core from Lake Marcacocha near the Inca capital of Cuzco, representing 4,200 years of accumulated sediments. By sampling every centimetre over the core's top 1.9 metres, they obtained a temporal resolution of about 6 years. They measured the concentrations of pollen and other plant parts, and of charcoal, and $^{13}C/^{12}C$ and C/N ratios, as proxies for local climate, human activity and plant communities.

It turned out that after AD 880 there was increasing drought, which may thus have contributed to the Wari and Tiwanaku collapses, as well as to the earlier and later collapses of the Maya and Khmer. But after AD 1100, during the Northern Hemisphere's Medieval Warm Period, temperatures rose, enabling the Incas to extend agriculture to higher elevations, increase their arable-land area, exploit increased glacial meltwater for irrigation, store more food for their armies, and grow alder trees for nitrogen fixation and timber. Thus, although the Incas' military and administrative organization was essential to their conquests, climate amelioration played a part.

This reminds us that climate can change in either direction, and that in the past such change has variously helped or hurt human societies. But human overexploitation of environmental resources never helps. As Lentz and Hockaday note[1], "Tikal's inhabitants became trapped in a positive feedback loop wherein increasing demands on a shrinking resource base ultimately exceeded the carrying capacity of their immediate environs. The ecological lessons learned from the Late Classic Maya, with their meteoric population increase accompanied by environmental overstretch, serve as a distant mirror for our own cultural trajectory." Amen. ■

Jared Diamond is in the Geography Department, University of California, Los Angeles, California 90095-1524, USA.
e-mail: jdiamond@geog.ucla.edu

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DEVELOPMENTAL BIOLOGY

Rise of the source–sink model

Alexander F. Schier and Daniel Needleman

Gradients of signalling molecules dictate where specific cell types form in developing tissues, but how these gradients are set up is much debated. A model proposed 40 years ago by Francis Crick may provide an answer.

How do the thousands of different cell types in an animal arise time and again at particular locations during embryonic development? The answer lies partly in the distribution of signalling molecules called morphogens[1], which are released from local sources and form concentration gradients in target tissues. Cells that are close to the source of the morphogen are exposed to high signal concentrations and activate developmental programs that differ from those in cells that are farther away and exposed to lower levels of morphogen. This powerful strategy means that the same signalling molecule can be used in the formation of different cell types. But how are morphogen gradients established? On page 533 of this issue, Yu *et al.*[2] describe one mechanism. They propose that, during the development of the zebrafish embryo, the morphogen fibroblast growth factor 8 (FGF8) spreads rapidly by diffusion from a local source and is then taken up by target tissues. This implies that the combination of free random motion and cellular uptake generates a signalling gradient that endows cells with different developmental fates.

Yu and colleagues' findings[2] support a model proposed almost 40 years ago by Francis Crick, dubbed the source–sink model. Crick put forward a mechanism[3] to explain how morphogen gradients could be set up in a developing tissue. He calculated that a stable gradient can be generated by the local production of a signal at one end of a tissue (the source), its spread into surrounding cells, and its local removal at the other end (the sink). Crick argued as part of the source–sink model that the spreading of the morphogen occurs through Brownian motion — the random thermal motion of molecules — akin to the spreading of a drop of ink in a glass of water. If correct, this would imply that simple diffusion was a plausible mechanism for patterning embryonic tissues. But is there evidence for the source–sink mechanism *in vivo*?

The authors[2] used fluorescent correlation spectroscopy (FCS) to analyse the properties of the FGF8 morphogen in zebrafish embryos. FCS is a powerful technology that was introduced in 1972, when it was shown[4] that measuring fluctuations in fluorescence in a small volume can determine the diffusion properties of labelled molecules in solution. In its modern incarnation, FCS is sufficiently sensitive to probe the dynamics of single molecules. The technique is widely used by biophysicists to measure the behaviours and interactions of proteins, but its use has largely been limited to *in vitro* systems, single-celled organisms and cells in tissue culture.

By contrast, Yu and colleagues[2] apply FCS to measure the distribution, diffusion and clearance of FGF8 in zebrafish embryos. These embryos are translucent and are therefore ideal for the visualization of the movements of molecules and cells. Yu *et al.* observed that a stable FGF8 gradient forms within 3 hours after production of fluorescently tagged FGF8 in a local region of the early zebrafish embryo. They obtained a diffusion coefficient for FGF8 in the extracellular space of $\sim 50\ \mu m^2\ s^{-1}$, which is strikingly similar to that obtained for molecules of the same size diffusing in water. Therefore, FGF8 seems to move freely and randomly through extracellular space.

But how can such rapidly moving molecules form stable concentration gradients? Yu *et al.* find that extracellular FGF8 has a half-life of only 10–20 minutes. The authors propose that it is the interplay between fast diffusion and the rapid uptake of FGF8 by target-cell endocytosis that creates the gradient. Indeed, green fluorescent protein (GFP), a molecule with similar diffusion properties to FGF8 but much slower clearance, also spreads rapidly but does not form a stable gradient. As predicted by source–sink models, manipulations that increase FGF8 removal, for instance by increasing cellular endocytosis, decrease the range of the FGF8 gradient. By contrast, decreasing endocytosis