

The constrictions could propagate from one pericyte to another along the capillary, which could provide a means by which small regions of the vascular system detect and respond to the activity of nearby groups of neurons.

The true impact of pericyte activity in the intact central nervous system still needs to be established. But modifying blood flow through the capillary 'bed' is likely to have a profound impact on overall blood flow. There is *in vivo* evidence from two-photon laser scanning microscopy that capillary blood flow can be dynamically controlled, and even reversed, in some cases^{4,5}. Are these changes at the capillary level due to the actions of pericytes, or do they result from upstream alteration of blood flow in the arterioles? This issue is complicated by the effects of neuronal inputs on blood flow in arteries and arterioles^{6,7}, or of cells called astrocytes, which can also constrict or dilate vessels⁸⁻¹⁰. Furthermore, localized arteriole constrictions have been observed following transient increases in intracellular calcium in astrocytes, but these were due to contractions of the smooth muscle cells, not to pericyte constriction^{8,9}. A future issue is to find out whether pericytes can also induce constrictions of small arterioles.

Ultimately, the goal is to understand the hierarchy of cerebral blood-flow control by the different elements that can alter vascular dilation and constriction. We will then know which levels are indeed important in inducing the changes in flow that underlie functional

imaging techniques. This knowledge is crucial for understanding the link between regional brain activation and blood flow, and for designing therapies for repairing this relationship in brain diseases such as vascular dementia. The known actors in controlling blood flow are endothelial cells, smooth muscle cells, neuronal inputs and astrocytes. Now, thanks to Peppiatt *et al.*, pericytes can be added to the cast. ■

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is preferentially removed from the system. But apart from a transient spike of ¹³C-enriched rocks following the GOE (the cause of which is still being debated⁷), carbonate rocks that formed before and after 2.4 billion years ago show the same isotopic signature. Why didn't things change when oxygen levels went up?

According to Goldblatt and colleagues⁵, once photosynthesis began, the atmosphere became bistable: it could exist in either a low- or a high-oxygen state. This bistability results from variations in the rate of atmospheric oxygen consumption as oxygen levels change. In a low-oxygen atmosphere, oxygen is rapidly consumed in an ultraviolet-catalysed reaction with biogenic methane. But as oxygen levels increase, so does the concentration of ozone, which shields the atmosphere from solar ultraviolet radiation and thus abates oxygen consumption. Therefore, the atmospheric oxygen budget can change even if other sources and sinks of oxygen remain constant. So maybe the atmosphere got stuck in a low-oxygen state for a long time following the start of photosynthesis, even though oxygen levels were poised to go much higher.

To explain why it is curious that the carbon-isotope signature of rocks did not change after the GOE, one must consider how the long-term oxygen cycle works. Photosynthesis by bacteria (and later by algae and plants) produces oxygen, but it is the burial of these organisms in marine sediments that leaves excess oxygen behind in the atmosphere — this excess oxygen would otherwise be used up as the organisms decay. The organic carbon found in living organisms is depleted in ¹³C relative to ¹²C, so increases in the rate of organic-carbon burial should cause changes in the ratio of carbon isotopes dissolved in the ocean. The isotopic signature of carbonate rocks formed from these dissolved substances should mirror the isotopic changes in sea water.

But carbonate rocks are isotopically similar before and after the GOE (apart from the unexplained spike). In other words, the source of atmospheric oxygen — organic-carbon burial — seems to have remained constant with time, even though atmospheric oxygen levels have changed enormously. This led various authors⁸⁻¹⁰ to propose that the GOE was caused by decreases in the sinks for oxygen — that is, by lower emissions of reduced gases from beneath Earth's crust and by lower discharge rates of dissolved ferrous iron from hydrothermal vents. But all such proposals either have internal inconsistencies or violate other constraints provided by the geological record⁵.

Goldblatt *et al.* now suggest that a mere 3% increase in organic-carbon burial would have been enough to trigger the GOE. Such a change is far too small to be detected in the carbon-isotope record. A decrease in reductant input by the same tiny amount could also have prompted the GOE. Such minor fluctuations could have happened for any number of reasons. However, the authors show that a much larger perturbation is required to cause

EARTH SCIENCES

Ups and downs of ancient oxygen

James F. Kasting

The latest models suggest that atmospheric oxygen could have fluctuated between high and low concentrations once photosynthesis had evolved. But does the geological evidence really support this?

The ancient rise of atmospheric oxygen is of great interest because of its close relationship with evolution, but the geological evidence for this is indirect and subject to interpretation. The consensus for more than 30 years has been that atmospheric oxygen first reached appreciable levels around 2 billion to 2.4 billion years ago^{1,2}, an occasion known as the great oxidation event (GOE). But doubters of this event have remained³.

The GOE story was strengthened considerably by the discovery that minerals in ancient rocks had unusual ratios of sulphur isotopes, a phenomenon known as mass-independent fractionation⁴ (MIF). The only known mechanism that can produce this effect is the break-up of sulphur dioxide by ultraviolet light in a low-oxygen atmosphere. The MIF isotopic signature is small or entirely absent in rocks younger than 2.4 billion years, suggesting that

Earth's atmosphere has been oxygen-rich since that time⁴. In this issue, Goldblatt *et al.* (page 683)⁵ extend the oxygen evolution story, and in doing so may have found some common ground for GOE believers and heretics.

Goldblatt and colleagues⁵ do not challenge the conventional wisdom regarding the rise of oxygen. Instead, they present a model that might resolve two problems that have puzzled geochemists for years. First, why did atmospheric oxygen climb to significant levels only around 2.4 billion years ago, when oxygen-producing bacteria apparently evolved 2.7 billion years ago⁶, or earlier? Second, carbonate rocks that form on the sea floor should acquire a distinctive ratio of carbon isotopes, as organic carbon from photosynthesizing organisms gets buried in marine sediments. Increased organic-carbon burial should cause the ratio of ¹³C to ¹²C in carbonates to rise, because ¹²C

a high-oxygen atmosphere to revert back to a low-oxygen state. This wonderful result might explain why oxygen levels stabilized permanently following the GOE.

But there are other unresolved issues in this saga. There is evidence^{11–13} of low sulphur MIF values in rock formations of between 2.76 billion and 2.92 billion years old, suggestive of high atmospheric-oxygen levels preceding the accepted time of the GOE. So far, no high MIF values have been reported in that time interval. How can this be rationalized?

One possible explanation — the so-called ‘yo-yo’ atmosphere theory — was proposed earlier this year¹¹. This theory suggests that oxygen levels first increased about 3.0 billion years ago, decreasing again about 0.2 billion years later, before their final climb to high concentrations 2.4 billion years ago (the GOE). Goldblatt and colleagues’ model⁵ explicitly predicts that the atmosphere was bistable for some time before the GOE, so maybe the yo-yo theory is correct.

But this would still leave some unexplained observations. For example, the Witwatersrand gold deposits in South Africa contain detrital minerals that were washed down streams between 2.8 billion and 3.0 billion years ago¹⁴. In the presence of oxygen, these minerals should have become oxidized and dissolved. So, either the oxygen levels were never high enough for that, or they repeatedly went up and came back down very quickly. Or perhaps oxygen concentrations did not increase at all, and the low-MIF anomaly seen in post-GOE rocks was produced by some entirely anoxic mechanism, such as the shielding of solar ultraviolet rays by an organic haze^{13,15}.

The jury is still out, but all these contradictory observations are stimulating a lot of creative thinking. Let us hope that this will lead to a more unified understanding of a fascinating era in Earth’s history. The ancient atmosphere may have had a more complex evolution than we imagined. ■

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ECOLOGY

Moving to the ideal free home

Douglas W. Morris

Pike move between two basins of a British lake to maximize their evolutionary fitness. This adaptive behaviour suggests that habitat selection is more significant in population dynamics than was thought.

How should animals choose which habitat to live in? An evolutionary biologist is likely to answer that they should maximize their evolutionary fitness — the likelihood that their genes will be passed on to future generations — and live in the habitat that will produce the most descendants. But there is a catch. If all individuals make the same choice, the habitat will become crowded, the probabilities of survival and reproduction will suffer, and fitness will decline. Other habitats with fewer individuals might be a better option. So animals maximizing fitness through habitat selection will disperse among habitats until no individual can improve its fitness by moving.

This ‘ideal free distribution’¹ assumes that an individual can estimate accurately the fitness that can be attained in different habitats, and is free to move and occupy the ideal place that maximizes fitness. Many ecologists have questioned whether the theory is hamstrung by these preconditions. Can such a model really apply to natural populations? Writing in *Proceedings of the Royal Society*, Thronald Haugen and colleagues² provide convincing evidence that it can. They show that, every year, pike in a northern English lake move from a habitat with low fitness (a higher mortality rate) to one with higher fitness, thus eliminating the initial difference. The research tells us that the

spatial distribution of populations may often represent a dynamic equilibrium caused by habitat selection.

To understand the principle of the ideal free distribution, think of queues at airport security. As a passenger, you want to pass through as quickly as possible. If there are several queues, you choose the one that you think will move

the fastest. But everyone with a boarding pass is trying to do the same. So the number of people in each queue is in dynamic equilibrium because, if one line moves more slowly than others, passengers will swap queues. Thus, at any given time, the average wait before passing through the checkpoint is similar for everyone at the end of the lines.

Now apply the same principle to animals choosing their habitat. At equilibrium, the distribution of individuals among habitats is evolutionarily stable³: no individual can improve its fitness by moving to another habitat. But habitats and population sizes change, disturbing that balance. Individuals will track those changes by moving from one habitat to another until their distribution regains its evolutionary stability. The density in every habitat thus depends on the density in others, just as the length

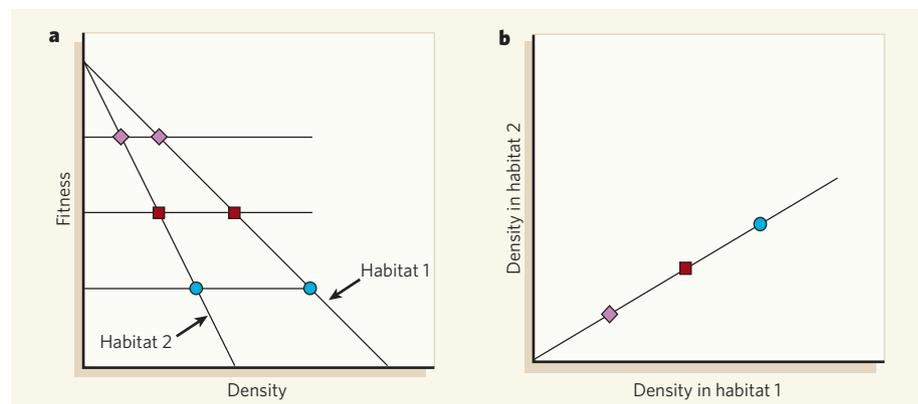


Figure 1 | Testing for an ideal free distribution. **a**, Evolutionary fitness declines more quickly with increasing population density in habitat 2 than it does in habitat 1. Symbols at the intersections with horizontal lines represent densities where fitness is equal in both habitats (an ideal free distribution). **b**, The equilibrium densities can be plotted against each other to yield the expected distribution of individuals in the two habitats (the habitat isodar⁷). Haugen *et al.*² do this for the northern and southern basins of Lake Windermere, and compare these with actual data for pike populations collected since the 1940s. The agreement between the model calculations and the data is astoundingly good.