


 Editorial

Oxygen, animals and oceanic ventilation: an alternative view

Of all the components of biogeochemical cycles, few attract more attention than the waste product of oxygenic photosynthesis. Chemically unstable and biosynthetically dangerous, diatomic oxygen is the key ingredient in aerobic metabolism, and a prerequisite for the evolution of large complex organisms that define the modern biosphere. Exactly how much they require is only loosely constrained, but Catling *et al.* (2005) suggest something in the order of 10^3 – 10^4 pascals [Pa] (\approx 1–10% atmospheric partial pressure [pO_2]; \approx 5–50% present atmospheric level [PAL]). Moreover, geochemical modelling indicates that pO_2 has fluctuated substantially over the course of the Phanerozoic: up to *c.* 35% in the late Palaeozoic, and down to perhaps 10% in the early Mesozoic (Falkowski *et al.*, 2005; Berner, 2006). Such shifts have been considered instrumental in directing the course of Phanerozoic evolution and extinction (Falkowski *et al.*, 2005; Huey & Ward, 2005; Ward *et al.*, 2006; Berner *et al.*, 2007), including the Ediacaran–Cambrian radiations of macroscopic life (Berkner & Marshall, 1965; Anbar & Knoll, 2002; Catling *et al.*, 2005; Holland, 2006; Canfield *et al.*, 2007). This is certainly a worthy hypothesis, and one that has gained an exceptionally wide following over the past decade – but a popular paradigm still needs to be tested and weighed against competing scenarios. In this editorial, I take critical look at the oxygen–evolution connection and discuss an alternative, biological explanation for geochemical signatures through the terminal Proterozoic.

In the absence of direct measurements, the oxygen content of ancient atmospheres is inferred from a combination of geochemical proxies and modelling. These values, however, are accompanied by substantial error (see Berner *et al.*, 2007: fig. 1; Kump, 2008: fig. 2), and differing modelling assumptions yield conspicuously different results. For example, where Bergman *et al.* (2004) estimate the oxygen content of Mesozoic atmospheres to be continuously at or above PAL, Berner (2006) puts late Triassic/early Jurassic levels close to 50% PAL, followed by an early Cretaceous rise to more or less modern levels. Falkowski *et al.* (2005) also recognize an early Jurassic minimum, but with PAL not reached until the Eocene. All models are of course limited by the runaway wildfire induced at $pO_2 > 35\%$, and lack of fire at $pO_2 < 15\%$ (Belcher & McElwain, 2008), neither of which have obtained for the past 420 million years (with the possible exception of a ‘charcoal gap’ in the late Devonian (Scott & Glasspool, 2006)). Atmospheric oxygen concentrations are more difficult to constrain in the absence of a land plant record, though the

appearance of iron-retaining palaeosols at or around the 2.45 Ga ‘great oxygenation event’ marks the onset of $pO_2 > 0.2\%$ (1% PAL), and the rise of conspicuously macroscopic fossils from *c.* 575 Ma sets a Phanerozoic lower limit of *c.* 1% pO_2 or 5% PAL (Canfield, 2005; Catling *et al.*, 2005; Holland, 2006; Kump, 2008). Deep-sea geochemical proxies and modelling have been used to estimate an upper limit of *c.* 8% pO_2 (40% PAL) for most of the Proterozoic.

OXYGEN AND PHANEROZOIC EVOLUTION

Correlation between modelled pO_2 and macroevolutionary phenomena over the past 500 Myr are widely interpreted as causal (see Berner *et al.*, 2007) though often in the absence of compelling analysis. Falkowski *et al.* (2005), for example, ascribe the Eocene radiation of large placental mammals to their modelled increase in pO_2 , arguing that ‘the density of capillaries per unit muscle scales to the 0.87 power of size in mammals (28); hence, larger animals require high ambient O_2 levels to obtain maximal metabolic rates’. If this were so, then the evolutionary radiation itself provides corroborating evidence for their model, and challenges those indicating either declining pO_2 through the early Tertiary (Bergman *et al.*, 2004) or no statistically significant trend (Berner, 2006).

But there are problems with this physiological argument. In the first instance, it appears to be based on a misreading of the cited literature: the 0.87 scaling relationship discussed in Weibel & Hoppeler (2005) is not between capillary density and body size, but rather *maximum metabolic rate* and body size. Indeed, the conclusion of this particular study was that capillary density is remarkably plastic, and can be ‘simply adjusted to the demand of the mitochondria for O_2 supply (Vock *et al.*, 1996), just as the heart adjusts its frequency to meet the different demands in blood flow’ (p. 1643); the capillary density of dogs, for example, is up to 50% higher than in similarly sized but less athletic goats (Vock *et al.*, 1996). The reason capillary density tends to be so much lower in larger mammals is because larger animals tend to have much lower maximum metabolic rates than smaller ones. In this light, it would have been rapidly metabolizing *small* mammals that were most challenged by low pO_2 . The fact that small, high-oxygen-demand mammals, birds and pterosaurs first appeared in the early Mesozoic – the Phanerozoic pO_2 minimum in most models – argues strongly against any causal connection to atmospheric evolution.

In the Palaeozoic, low pO_2 has been invoked as a driver of late Permian terrestrial extinctions (Huey & Ward, 2005), although this is difficult to relate to the much more substantial terminal Palaeozoic extinctions in the marine realm (see Knoll *et al.*, 2007a). Ward *et al.* (2006) have also correlated 'Romer's Gap' – an early Carboniferous interval preserving anomalously few terrestrial tetrapods – with a modest depletion in modelled pO_2 (14–20% \approx 67–95% PAL). Such hypoxic conditions, however, might just as well be used to explain an *increase* in tetrapod diversification, by driving aquatic forms into oxygen-rich subaerial environments, such as Clack (2007) has argued for the initial tetrapod radiations in the early Devonian. Like the caricatured pan-adaptationism of Gould & Lewontin (1979), hypotheses linking evolutionary phenomena to atmospheric oxygen levels can be frustratingly difficult to disprove.

Gigantism

The most celebrated case of oxygen-driven evolution is undoubtedly the giant 'dragonflies' (Protodonata and Palaeodictyoptera) of the late Palaeozoic, which correlate to significant oxygen maxima in both the Berner (2006) and the Bergman *et al.* (2004) models. In this case, the link between pO_2 and size is thought to derive from fundamental limitations of the tracheal gas-exchange apparatus which – unlike in most lung- and gill-breathing animals – is not coupled to efficient internal or external circulatory systems (Graham *et al.*, 1995; Kaiser *et al.*, 2007). Exceptionally high pO_2 potentially supersedes the constraints of tracheal diffusion and offers a ready explanation for the 71 cm wingspans seen in early Permian protodonates. Indeed, a study on the modern libellulid dragonfly *Erythemis simplicicollis* has shown its rates of flight metabolism to vary directly with pO_2 , suggesting a very low safety margin with respect to maximum metabolic rate (Harrison & Lighton, 1998).

One interpretation of these data is that *E. simplicicollis* is operating close to its maximum size limit (at 21% pO_2), with possible implications for gigantism in its Carboniferous counterparts (Harrison & Lighton, 1998). It is important to appreciate, however, that physiological safety factors represent a selective trade-off between risk and cost (Diamond, 2002), and that the occasional escape of prey items presents no significant risk to an ambush predator. Significantly, the Harrison & Lighton (1998) experiments revealed a much broader tolerance to hypoxia when it came to *E. simplicicollis* simply initiating and maintaining flight, with no qualitative loss of function observed at 10% pO_2 and a residual ability down to 5% pO_2 . In other words, the cost–benefit–risk of *E. simplicicollis* physiology and ecology has been optimized by natural selection to the ambient atmosphere, but this in no way reflects the limits of tracheae-ventilated flight. Certainly its <8 cm wingspan pales beside the 16 cm of *Petalura ingentissima*, the largest living dragonfly (which, by

the same token, can only offer a species-specific measure of tracheal potential).

Kaiser *et al.* (2007) have addressed the issue of insect gigantism by assessing the scaling relationships between tracheal volume and body mass in darkling beetles. A marked positive allometry (mass^{1.29}) presumably reflects a compensatory response to distance effects on oxygen delivery, but the total tracheal volume in even their largest beetle specimens falls well short of that observed in other species. On the other hand, the cross-sectional area of leg orifices – through which tracheae must pass – scales negatively with body mass (^{0.77}), which potentially sets a pO_2 -dependent upper limit on beetle size due to restricted leg ventilation. What it doesn't do, however, is account for the size of *flying* insects, where thoracic tracheae feed directly to thoracic flight muscles, generally assisted by thoracic and/or abdominal pumping (Miller, 1966).

Gigantism is also documented in other fossil arthropods, though the correlation with modelled pO_2 is only weakly circumstantial (Braddy *et al.*, 2008). The Silurian–Devonian radiation of large pterygotid eurypterids, for example, corresponds to a modest peak in the Berner curve (*c.* 25% $pO_2 \approx$ 120% PAL), but fails to account for the relatively diminutive eurypterids that dominated the late Palaeozoic oxygen maximum – or the metre-sized trilobites that thrived during the Ordovician minimum (Rudkin *et al.*, 2003). Perhaps most problematic is the occurrence of Triassic/Jurassic dragonflies with nearly twice the wingspan of extant *Petalura ingentissima*, despite the constraints of a putative 10–15% pO_2 (*c.* 50–70% PAL) atmosphere (see Okajima, 2008). Either arthropod gigantism is not directly related to pO_2 (see Woods *et al.*, 2008) or there is something wrong with the models.

Certainly there is more to organism size than atmospheric permissibility. Modal body size within most extant taxonomic groups, for example, is skewed conspicuously towards smaller, but not smallest, forms, despite the relatively high pO_2 of the modern atmosphere (Brown *et al.*, 1993; Siemann *et al.*, 1996). The presence of larger species identifies the minimal physical/physiological limits on size, but the relative rarity of such forms challenges the assumption that bigger is inherently better. This is particularly well illustrated in natural experiments where populations have become isolated on islands: under conditions of reduced predation and/or competition, lineages characterized by large body sizes (e.g. mammoths, elephants, deer) tend to become miniaturized over evolutionary time, whereas conspicuously small forms tend to enlarge (Lomolino, 2005). This 'island rule' suggests that there is an optimal, relatively small, body size within any particular taxonomic group, and that divergences from this optimum are forced by ecological interactions and evolutionary wedging (Brown *et al.*, 1993; Damuth, 1993). In this light, it is at least possible that dragonflies have become secondarily miniaturized in response to the evolution of birds and bats.

Evolutionary explanations for gigantism clearly need to identify *positive* (as opposed to merely permissive) selective

pressures for large body size. For outsized ‘dragonflies’, this will entail a detailed understanding of aerial ecology in the absence of flying vertebrates, the allometric relationship between insect wingspan and oxygen demand, the allometric relationship between insect wingspan and heat balance (probably a more fundamental problem than gas exchange in large dragonflies (see May, 1982), the *evolutionary* limits of tracheal breathing (as opposed to physiologies optimized for 21% pO_2), and of course the pO_2 of past atmospheres. On present evidence, it is not at all clear that atmospheric oxygen has been a controlling factor.

THE EDIACARAN–CAMBRIAN RADIATIONS

Probably the most significant evolutionary role assigned to oxygen occurs at the beginning of Phanerozoic, where it provides an attractive explanation for the belated appearance of animals and associated phenomena (e.g. Berkner & Marshall, 1965; Catling *et al.*, 2005). Low pO_2 not only has the potential to frustrate the evolution of relatively high oxygen-demand metazoans directly, but also indirectly via the nitrogen crises hypothesized for a sulphidic Proterozoic ocean (Anbar & Knoll, 2002; Fennel *et al.*, 2005). Certainly there is clear geochemical evidence of extensive marine anoxia and stratification through the Proterozoic (Poulton *et al.*, 2004; Brocks *et al.*, 2005; Canfield *et al.*, 2007, 2008; Johnston *et al.*, 2008; McFadden *et al.*, 2008; Scott *et al.*, 2008; Shen *et al.*, 2008; Giddings & Wallace, 2009). On the assumption that ancient oceanic structure was comparable to today’s, these have been used to infer a maximum Proterozoic pO_2 of 8% ($\approx 40\%$ PAL), and a minimum pO_2 of 3% (15% PAL) by the late Ediacaran (Canfield *et al.*, 2007; Kump, 2008).

But is such an assumption valid? Quite apart from whether a 40% PAL atmosphere represents a significant physiological impediment to the evolution of eumetazoans, or the fact that cyanobacteria grown under sulphidic conditions show no significant reduction in N-fixation or growth rate (Zerkle *et al.*, 2006), or indeed whether Neoproterozoic oceans were ferruginous rather than sulphidic (Canfield *et al.*, 2008), it is important to ask whether early ocean-atmosphere dynamics can be usefully modelled on uniformitarian principles (Butterfield in press a). Does deep-water geochemistry invariably reflect the composition of the overlying atmosphere?

Oceanic anoxic events

Palaeontological, sedimentological and geochemical data clearly identify a long-term continuity in the structure of Phanerozoic oceans, but even here there are recurring intervals of marine anoxia/stratification that show no direct relationship to atmospheric pO_2 (Meyer & Kump, 2008). Mid-upper Cretaceous oceanic anoxic events (OAEs), for example, do not register on geochemically modelled oxygen curves, and are accompanied by the ‘mass survival’ of

high-oxygen-demand birds, mammals and aquatic/terrestrial/aerial reptiles. Widespread anoxia/euxinia was also characteristic of the late Devonian (Joachimski *et al.*, 2001), end Permian (Grice *et al.*, 2005) and early Jurassic (Kuypers *et al.*, 2004) oceans, but in none of these instances did atmospheric pO_2 fall to levels that precluded wildfire, giant dragonflies or vertebrates.

The oceanic anoxia/stratification observed in the Proterozoic appears to be more persistent than that observed in Phanerozoic ‘events’, but there are nonetheless some notable similarities. Both, for example, are characterized by at least localized evidence of anoxygenic photosynthesis (Sinninghe Damsté & Köster, 1998; Brocks *et al.*, 2005; Grice *et al.*, 2005), low concentrations of isotopically heavy Mo (Scott *et al.*, 2008; Archer & Vance, 2008; Pearce *et al.*, 2008) and cyanobacteria-dominated export production (Summons *et al.*, 1999; Joachimski *et al.*, 2001; Kuypers *et al.*, 2004; Xie *et al.*, 2005; Dumitrescu & Brassel, 2006). März *et al.* (2008) have also documented intermittent exhaustion of marine sulphate during a late Cretaceous OAE, with pronounced spikes of phosphate and Fe oxides indicating anoxic, but not sulphidic, bottom waters – circumstances broadly comparable to the ferruginous, relatively phosphogenic oceans of the later Neoproterozoic and early Cambrian (cf. Shen *et al.*, 2000; Canfield *et al.*, 2008). None of this, of course, requires that Proterozoic atmospheres were comparable to those in the Mesozoic, but it does mean that the key evidence for linking the terminal Proterozoic appearance of animals to a rise in atmospheric pO_2 is the terminal Proterozoic appearance of animals. . . particularly as geochemical evidence for extensive marine anoxia continues into the early Cambrian (e.g. Goldberg *et al.*, 2007; Lehmann *et al.*, 2007; Schröder & Grotzinger, 2007; Canfield *et al.*, 2008; Wille *et al.*, 2008), well after the evolutionary phenomena that the ‘oxygen threshold hypothesis’ was meant to explain.

Evolutionary controls on the biological pump

The causes of Phanerozoic OAEs are much debated, but are almost universally viewed in terms of physical processes leading to ocean stratification – e.g. restricted circulation, global warming, volcanism – which are thought to have cascaded upwards, inducing the associated ecological and biogeochemical fallout (e.g. Meyer & Kump, 2008; Turgeon & Creaser, 2008). Explanations for marine anoxia in the Proterozoic, however, are much less encumbered by independent proxies, allowing atmospheric pO_2 to be invoked as the first-order control on ocean chemistry. Even so, Logan *et al.* (1995) have presented an intriguing case for a ‘top-down’ biological control on oceanic ventilation based on distinctive $\delta^{13}C$ signatures of Proterozoic versus Phanerozoic hydrocarbons: whereas the former point to extended microbial reworking of primary productivity (phytoplankton) within the water column, thereby depleting dissolved oxygen

and inducing widespread marine anoxia/euxinia, Phanerozoic data point to rapid vertical export with oxygen consumption concentrated in the sediment. The mechanism proposed by Logan *et al.* (1995) for this switch in mode was the early Cambrian introduction of metazoan zooplankton and their rapidly sinking faecal pellets. Unfortunately, the idea floundered on the observation that most export production – at least in the modern oceans – is transferred rapidly to the benthos independently of zooplankton, via physical aggregation or marine snow (see Turner, 2002; Burd & Jackson, 2009).

But this is to ignore the larger-scale impact of animals on plankton dynamics and evolution. Models investigating the adaptive evolution of phytoplankton cell size, suggest that larger sized nano- and microplankton (2–200 µm diameter) – the ‘net-phytoplankton’ that comprise the vast majority of export production in the modern oceans – represent a size-refuge response to grazing zooplankton, and that the ‘optimum’ size for phytoplankton cells lies in the picoplankton (0.2–2.0 µm) range (Jiang *et al.*, 2005). In other words, the early Cambrian expansion of animals into the water column may have been responsible for driving the coevolution of relatively large, export-prone net-phytoplankton, thereby redesigning the structure and function of the biological pump (Fig. 1). Prior to the evolution of planktic metazoans, the oceans would

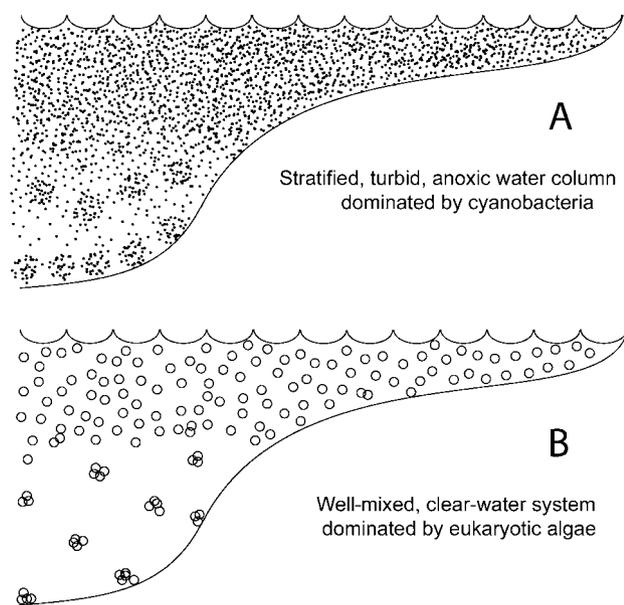


Fig. 1 Schematic diagrams of two alternate stable states for the marine biological pump. (A) Dominance of shade-tolerant and shade-inducing cyanobacterial picoplankton in the absence of top-down selection for large net-phytoplankton, resulting in the stratified, anoxic/euxinic water column typical of pre-Cambrian oceans and Phanerozoic oceanic anoxic events. (B) Dominance of relatively large, export-prone eukaryotic net-phytoplankton in response to zooplankton grazing pressure, leading to increased light penetration and increased water-column ventilation.

have been dominated almost exclusively by picoplankton, which experience fundamentally lower rates of aggregation and sinking than larger forms (see Burd & Jackson, 2009), thereby inducing the widespread euxinia envisaged by Logan *et al.* (1995). Under such nonuniformitarian conditions, deep-sea geochemical signatures cannot be used as a direct proxy for atmospheric pO_2 .

Alternate stable states

Biologically induced marine anoxia and stratification are further supported by the ecological dynamics observed in modern lacustrine systems, which tend to occupy one of two alternate stable states (see Scheffer *et al.*, 1997; Gragnani *et al.*, 1999; Scheffer & Carpenter, 2003): on the one hand, turbid-water conditions dominated by cyanobacteria, low taxonomic diversity, high levels of suspended organic carbon, high nutrient loading and a stratified anoxic water column; and on the other, clear-water conditions dominated by eukaryotic phytoplankton, high diversity, low suspended carbon, low nutrients and an aerated, well-mixed water column. Both states are reinforced by positive feedback effects such that slow-sinking cyanobacterial picoplankton both promote and prefer turbid-water eutrophic conditions, whereas export-prone net-phytoplankton are at a selective advantage under the lower nutrient and higher light conditions that they induce. The resulting hysteresis makes it notoriously difficult to break out of any particular state by manipulating physical conditions. Major reductions in nutrient loading, for example, are necessary but usually not sufficient for the amelioration of stratified eutrophic lakes. The key to tipping these systems back into their alternate clear-water state typically involves suspension-feeding metazoans (Suding *et al.*, 2005; Byers *et al.*, 2006), most famously illustrated by the invasion of dreissenid (zebra) mussels into the lower Great Lakes (Higgins *et al.*, 2008).

One of the curious qualities of sedimentary organic carbon through the Proterozoic and during Phanerozoic ‘anoxic events’ is biomarker evidence for conspicuously elevated export of cyanobacteria (Summons *et al.*, 1999; Joachimski *et al.*, 2001; Kuypers *et al.*, 2004; Xie *et al.*, 2005; Dumitrescu & Brassel, 2006). Although generally interpreted as a response to atmospherically or tectonically driven nitrogen crises (e.g. Anbar & Knoll, 2002; Fennel *et al.*, 2005), the recognition of metazoan-dependent hysteresis in modern lake systems points to a larger-scale ‘top-down’ control (see Scheffer & van Nes, 2004). Prior to the evolution of suspension-feeding eumetazoans, phytoplankton would have been represented almost exclusively by cyanobacterial picoplankton simply because there was nothing to counter the positive feedback loop of small cell-size, low sinking rates, stratification, and physiological advantage of cyanobacteria under the resulting turbid-water conditions. By the same token, the return to cyanobacteria-dominated oceans during Phanerozoic OAEs might be best

explained as a breakdown of the ‘normal’ biological pump (as a consequence of more or less localized extinction and enhanced nutrient fluxes), with the subsequent recovery of clear-water conditions and eukaryote-dominated export reflecting the reestablishment of suspension-feeding zooplankton. Intriguingly, an analysis of Baltic Sea fisheries over the past 30 years has identified two alternate ecosystem configurations based on a cod-herring-zooplankton-phytoplankton trophic cascade (Casini *et al.*, 2009): zooplankton dynamics in the presence of high cod populations (= low herring, high zooplankton) were driven almost entirely by hydroclimatic forces, but switched over to top-down control by zooplanktivorous herring when cod populations fell below a certain threshold abundance – with little likelihood of short-term recovery, regardless of fisheries policy or practice.

At a larger scale, the 100-million-year interval of the Ediacaran and earliest Cambrian witnessed the initial radiation of animals and the establishment of ‘normal’ Phanerozoic-type oceans (Butterfield, 2007) – including increasing contributions of eukaryotic phytoplankton to export production and incremental ventilation of the deep ocean (Fike *et al.*, 2006; Canfield *et al.*, 2007; Knoll *et al.*, 2007b; McFadden *et al.*, 2008; Shen *et al.*, 2008). And although these phenomena have widely been interpreted in terms of increasing concentrations of atmospheric oxygen, they can be alternatively ascribed to the accruing ecological impact of suspension-feeding animals as they began to clear the water column and re-engineer the biological pump (Fig. 1). This process was undoubtedly initiated in the benthos (e.g. Sperling *et al.*, 2007), but a modern-style marine carbon cycle, in which standing biomass, export dynamics and sedimentary recycling are all dominated by animals, was only fully attained with the early Cambrian (Tommotian) appearance of grazing mesozooplankton (Butterfield, 1997, 2007; in press a). More generally, the conspicuous geochemical perturbations that characterize the Neoproterozoic–Palaeozoic transition might be more accurately interpreted in terms of oceanic ventilation than atmospheric oxygenation (see Giddings & Wallace, 2009) – consequences rather than the cause of metazoan evolution.

Evolutionary contingency and convergence

If the stratified anoxic oceans of the Proterozoic are simply an extended OAE-like decoupling of the ocean-atmosphere system, what then accounts for the delayed appearance of animals in putatively well-oxygenated surface waters? Certainly there are other potentially limiting steps to biological evolution than oxygen, not least the assembly of developmental programs necessary to build tissue- and organ-grade multicellular organisms. Indeed, unlike the many quick and easy ways of deriving subtissue-grade multicellularity (Butterfield in press b), the evolution of higher-order complexity is astronomically complex (e.g. Mattick, 2007; Hobert, 2008) – to the extent that it has evolved only twice

on this planet: once in animals and once, some 200 Myr later, in plants. By contrast, environmental threshold or ‘permissive environment’ hypotheses are expected to yield massively polyphyletic radiations once the limiting conditions have been met. Atmospheric pO_2 , for example, does not explain the absence of pre-Ediacaran forests; and the failure of other photosynthetic eukaryotes to converge on this habit in the Silurian argues strongly against alternative physical constraints, such as H_2S poisoning (e.g. Kump *et al.*, 2005). Belated evolutionary singularities such as organ-grade plants and animals are more readily explained by the internal, developmental/informational challenges associated with higher order complexity. Once the requisite gene regulatory networks were compiled, however, the emergent new entities were in a position to revolutionize ecosystem function and its myriad evolutionary and biogeochemical feedbacks.

It is a mistake, of course, to account for all of ecosystem structure in terms of developmental innovation – or indeed to casually model the oceans as large lakes – but so too is the assumption that the only significant evolutionary drivers are external. It is the extraordinary capacity of organ-grade animals and plants to force diversity into coevolutionary niches that wouldn’t otherwise exist – including large placental mammals, gigantic arthropods, arborescent land-plants and large, export-prone net-phytoplankton – that gives the Phanerozoic Earth system its peculiarly dynamic and macroscopic character. Significant levels of free oxygen were undeniably a prerequisite for the evolution of large size and animals, but no more so than liquid water or primary productivity. On present evidence, it is not obvious that atmospheric oxygenation – as opposed to oceanic, sediment and soil ventilation – has played a significant forcing role in biological evolution for the past 1000–2000 million years.

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N. J. BUTTERFIELD

*Department of Earth Sciences, University of Cambridge,
Cambridge, UK, CB2 3EQ
e-mail: njb1005@esc.cam.ac.uk*

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