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The oxygen cycle and a habitable Earth

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Abstract As an important contributor to the habitability of our planet, the oxygen cycle is interconnected with the emergence and evolution of complex life and is also the basis to establish Earth system science. Investigating the global oxygen cycle provides valuable information on the evolution of the Earth system, the habitability of our planet in the geologic past, and the future of human life. Numerous investigations have expanded our knowledge of the oxygen cycle in the fields of geology, geochemistry, geobiology, and atmospheric science. However, these studies were conducted separately, which has led to one-sided understandings of this critical scientific issue and an incomplete synthesis of the interactions between the different spheres of the Earth system. This review presents a five-sphere coupled model of the Earth system and clarifies the core position of the oxygen cycle in Earth system science. Based on previous research, this review comprehensively summarizes the evolution of the oxygen cycle in geological time, with a special focus on the Great Oxidation Event (GOE) and the mass extinctions, as well as the possible connections between the oxygen content and biological evolution. The possible links between the oxygen cycle and biodiversity in geologic history have profound implications for exploring the habitability of Earth in history and guiding the future of humanity. Since the Anthropocene, anthropogenic activities have gradually steered the Earth system away from its established trajectory and had a powerful impact on the oxygen cycle. The human-induced disturbance of the global oxygen cycle, if not controlled, could greatly reduce the habitability of our planet.

Keywords Oxygen cycle, Habitable earth, Mass extinction, Anthropocene

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1. Introduction

Earth is the only planet known to harbor diverse biology and advanced civilizations. Oxygen (O_2) is the most abundant element in Earth's crust and the second most abundant element in Earth's atmosphere. In geologic history, the secular evolution of the atmospheric O_2 level is closely related to the emergence and expansion of complex life (Huey and Ward, 2005; Berner et al., 2007) and is even widely considered the major driver of the evolution of animal life (Nursall, 1959; Reinhard et al., 2016). In the modern Earth system, almost all life ultimately depends on the primary producers responsible for producing and maintaining the O_2 content of the Earth's atmosphere. Thus, an O_2-rich atmosphere has become a ne-

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cessity for the survival of almost all living organisms on Earth.

However, since the dawn of humans on this planet, anthropogenic activities have gradually driven the Earth system away from its established trajectory. Recent dramatic environmental changes on a global scale along with widespread sedimentary evidence indicate that the Earth may have entered a new geological epoch dominated by humans, the Anthropocene (Lewis and Maslin, 2015). Notably, the anthropogenic factors modifying the planetary environment are becoming increasingly pervasive. Although extraordinary achievements in socioeconomic development have occurred worldwide in the past century, the environmental perturbations associated with human activities may have already begun an ongoing mass extinction (Barnosky et al., 2011; Ceballos et al., 2015). Deforestation and emissions from fossil fuels alter the concentration of CO_2 in the atmosphere and destabilize the global climate system, thus jeopardizing global food and water security, causing extinctions of major vertebrate groups (Barnosky et al., 2011; Ceballos et al., 2015, 2017) and even chemically modifying the air we breathe. A decline in atmospheric O_2, albeit nearly negligible, has been detected since the late 1980s (Keeling and Shertz, 1992) and is projected to continue into the future (Huang et al., 2018; Liu et al., 2020).

The silent decline in atmospheric O_2 may potentially pose an additional threat to the survival of human beings and many mammal vertebrates. The principal consequence of a low O_2 level is hypoxemia (a lack of oxygen in the blood). Reducing the ambient O_2 concentration to 15% for 1 hour, as experienced during a commercial flight, can decrease arterial oxygen saturation in healthy subjects from 97±2% to 86±3% (Hobkirk et al., 2013). Hypoxemia can further result in a reduction in O_2 delivery to the tissues (tissue hypoxia), thus affecting human comfort, labor efficiency (Wang et al., 2019), and sleep quality (de Aquino Lemos et al., 2013). Exposure to hypoxic conditions can also lead to the impairment of mental functions and sensory deficits, including loss of color discrimination (Vingrys and Garner, 1987), significant delayed response (Dart et al., 2017), etc.

Due to the physiological importance of free O_2 in the air, considerable research has focused on exploring how biogeochemical cycles in Earth systems have driven the rise of atmospheric O_2 to form a habitable planet in geologic history and how variations in these cycles affect the habitability of the planet in the future under the impact of intensified human activities. In light of the scientific importance surrounding this topic, this review first synthesizes the knowledge of the global oxygen cycle and its connections with other biogeochemical cycles within the Earth system. Subsequently, the long-term evolution of atmospheric oxygen in geologic time is reviewed, focusing on the geologic evolution of atmospheric O_2 and its possible connections with biological evolutions and extinctions. Then, we discuss the recent trend of the oxygen cycle in the modern Earth system, including the global oxygen budget and variations in O_2 at different timescales. In the final section, a synopsis of the existing conclusions and future outlooks for studies of the oxygen cycle are presented.

2. Oxygen cycle in the Earth system

The oxygen cycle is a crucial part of Earth system science and is completed through a cascade of redox reactions (Kasting and Canfield, 2012). As oxygen is in group 6 on the periodic table, it has six electrons in its outer shell. To obtain a stable octet number for electrons in the outermost shell oxygen tends to borrow electrons from any other element or compound. The high electronegativity of oxygen relative to most other elements (a value of 3.44 in Pauling units, compared with 0.7 for francium, 2.20 for hydrogen, and 3.04 for nitrogen) makes oxygen a strong and quintessential oxidizer. Theoretically, any substance on Earth that can be oxidized by O_2 constitutes a sink of the global oxygen cycle (organic carbon, sulfides, reduced minerals, and so on). The oxygen cycle, therefore, is inevitably connected with other biogeochemical cycles within the Earth system and involves the complex interactions among the biosphere, atmosphere, hydrosphere, lithosphere, and the recently proposed anthroposphere (Figure 1a). Understanding the complicated web of chemical, biological, and physical relations among the "spheres" in the Earth system requires a systematic investigation of the global oxygen cycle on different timescales and in different periods.

2.1 The linkage of oxygen with other biogeochemical cycles

In terms of the connections between the oxygen cycle and other biogeochemical cycles, the linkage with the global carbon cycle is the most critical because it is a primary driver of the Earth's climatic and biotic systems (Schimel, 1995). CO_2 is an important greenhouse gas and the raw material required to synthesize organic matter through photosynthesis (which is also a way to produce free O_2), and O_2 is consumed during the oxidation of organic matter (known as respiration or oxidative weathering, the reverse process of photosynthesis). On geologic timescales, the oxygen cycle and carbon cycle are also directly coupled by the burial and weathering of organic matter ('geo'photosynthesis and 'geo'respiration) (Berner, 2004), but are decoupled by other processes, including the burial of carbonates (Hong et al., 2020) and photolysis of water (Catling and Kasting, 2017). The radicals created by water photolysis are important in stabilizing CO_2 on planets like Mars and Venus (Catling and Kasting, 2017). Despite the intimate and strong connection between oxygen

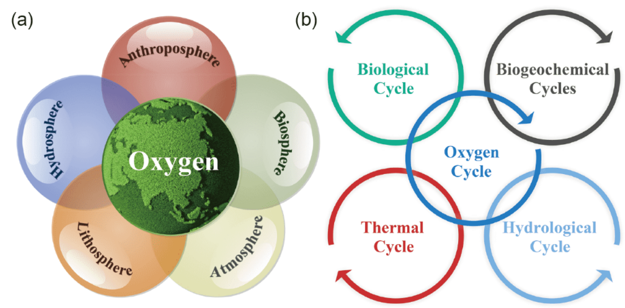

Figure 1 The status of the oxygen cycle in Earth system science (a) and its relationship with other biogeochemical cycles (b)

and carbon cycles, atmospheric O_2 and CO_2 concentrations are found to not always covary with each other. A Pleistocene ice core record showed a declining pO_2 (the partial pressure of O_2) level with no obvious change in pCO_2 (the partial pressure of CO_2) over the past 0.8 Ma, which can be explained by pCO_2 -dependent silicate weathering feedback that stabilizes pCO_2 on million year-time scales (Stolper et al., 2016).

In addition to the carbon cycle, the sulfur cycle is also closely connected with the oxygen cycle (Petsch, 2014a). The cycling of sulfur (with valence varying from –2 to +6) between rocks and the Earth's surface can also significantly influence atmospheric O_2 on geologic timescales. Sulfur from volcanism is commonly in a low valence state as H_2S or SO_2 and becomes the O_2 sink. The oxidative weathering of reduced sulfur will consume O_2 and lead to sulfate accumulation in the ocean. Sulfate-reducing bacteria can produce reduced sulfur (typically as pyrite, FeS_2) by metabolizing organic matter without consuming O_2. If FeS_2 is buried in sediments and remained unreacted, it escapes the reaction with O_2. Thus, the burial of pyrite represents another net O_2 source to the atmosphere. Over long timescales, this process can lead to the accumulation of O_2. The weathering of reduced sulfur will consume O_2 when the sulfur is oxidized in the atmosphere, and conversely, the weathering of oxidized sulfur will lead to a rise in O_2 (Ciborowski and Kerr, 2016). Besides its influences on atmospheric pO_2, the interaction between sulfur, carbon, and oxygen within the sedimentary redox cycle also plays an important role in marine acid-base chemistry (Reinhard and Fischer, 2019).

2.2 Oxygen and Earth system processes

Major processes in the global oxygen cycle are also manifested in other spheres (biotic and abiotic) in the Earth system. Photosynthesis, for instance, is a biological process involving primary producers at the bottom of the food chain (such as plants and algae) that absorb energy from solar light to synthesize carbohydrate molecules and O_2 from CO_2 and water. The process seems simple, but it is related to other essential processes in the hydrological cycle (e.g., water storage) and thermal cycle (e.g., temperature variations), as well as the interactions and feedbacks among these processes. For the thermal cycle, the O_2 production process (i.e. photosynthesis) is usually associated with a cooling effect, and the O_2 consumption process (respiration, combustion, etc.) results in heat release. These relations are easy to interpret because photosynthesis leads to some light energy being stored as chemical energy in the form of carbohydrates as light energy warms the Earth's surface; additionally, in areas with dense vegetation, evapotranspiration by plants can reduce the sensible heat flux and increase the latent heat flux, thus effectively reducing the atmospheric temperature (Huang et al., 2016, 2017). This is also the reason why drylands with sparse vegetation and low water storage capacities have experienced enhanced warming, even though most of the CO_2 emission sources are located in humid regions with dense vegetation and sufficient water resources (Huang et al., 2017). In this process, the bridge between the oxygen cycle and the hydrological cycle is built via evapotranspiration, which can only occur in the presence of vegetation and photosynthesis. Conversely, when O_2 is consumed via respiration and combustion, a certain amount of energy stored in carbohydrates (grains, vegetables, etc.) and fossil fuels (energy consumption) is released back to the atmosphere as heat (Chen et al., 2016), along with CO_2 and other greenhouse gases (GHGs) that cause global warming by influencing the radiation budget. Therefore, it is implied that an increased water storage capacity and the discussed cooling effect are associated with O_2 production, whereas water loss and the "greenhouse" effect are related to O_2 consumption. Throughout geologic time, the changes of pO_2 can also directly alter the radiative budget of the atmosphere as a result of its contribution to the atmospheric mass and density (Poulsen et al., 2015). Increasing atmospheric O_2 can reduce surface shortwave forcing, exerting a cooling effect, and vice versa. However, this does not necessarily lead to a drop in global surface temperature due to a broad range of Earth system feedbacks that are related to changes in atmospheric O_2 level (Poulsen et al., 2015). Under conditions of a pre-industrial Holocene climate state, simulations show an increase in O_2 content can lead to an increase in global-mean surface air temperature. Despite the cooling effect owing to the O_2 increase, a competing warming effect due to an increase in the pressure broadening of greenhouse gas absorption lines dominates the thermal balance. Atmospheric O_2 increase would also initiate a dynamic feedbacks that alter the meridional heat transport of the ocean, which induces warming polar regions and cooling tropical regions (Wade et al., 2019).

Hence, the complex linear and nonlinear interactions among the five cycles in Figure 1b (oxygen cycle, biological cycle, thermal cycle, hydrological cycle, and biogeochemical cycles) can be used to establish a dynamical model to simulate the characteristics of and variations in the Earth system.

3. The rise of atmospheric O_2

3.1 Great Oxidation Event (GOE)

The historical environment of the Earth is quite different from the current environment, especially the oxidation state of the surface. Multiple lines of evidence support an anoxic atmosphere before 2.45 Ga (1 Ga=1×10^9 a) and a significant rise in O_2 in the atmosphere and surface oceans at 2.3–2.4 Ga, popularly known as the Great Oxidation Event (GOE, Figure 2a) (Bekker et al., 2004; Gumsley et al., 2017). Geologic observations, including those of Fe-depleted paleosols older than 2.4 Ga (Rye and Holland, 1998) and preserved redox-sensitive elements such as uraninite (UO_2), pyrite (FeS_2) and siderite ($FeCO_3$), point to an Archean atmosphere devoid of O_2 (Rasmussen and Buick, 1999; Canfield, 2005; Burron et al., 2018). From a geochemical perspective, the most compelling evidence from two major types of sulfur isotope effects (mass-dependent fractionation and mass-independent fractionation) strongly implies low oxygen levels before the GOE (Figure 2a). The mass-independent fractionation of sulfur isotopes (S-MIF) could occur if volcanic sulfur species are photochemically oxidized (Pavlov and Kasting, 2002; Zahnle et al., 2006). The generation and preservation of the S-MIF signal (large anomalies of $\delta^{33}S$ and $\delta^{36}S$) in sedimentary records require an extremely low level of atmospheric O_2 (less than 0.001% of the PAL, Present Atmospheric Level) (Farquhar et al., 2000, 2001). Although there exists controversy about the exact value of increase of atmospheric O_2 during GOE, it is generally believed the disappearance of anomalous sulfur isotope compositions from sedimentary rocks as well as other evidence at approximate 2.33 Ga reflects a marvelous transition that leads to O_2 concentration exceeding 0.1% to 1% of PAL (Figure 2a, Krissansen-Totton et al., 2015; Luo et al., 2016).

Compared to the general consensus about the occurrence of the GOE, the precise causes of what triggered the GOE remains not obvious. Multiple factors ranging from the evolution of ecosystems to deep solid Earth have been suggested to be important (Kasting, 2013; Lyons et al., 2014; Catling and Kasting, 2017). Here we will not try to exhaust all models that have been proposed, but keep our focus and emphasize recent advance about the intrinsic mechanisms of the rise of O_2 level as well as its related processes.

3.2 Photosynthesis as the producer of O_2

Oxygenic producing photosynthesis (namely, $CO_2 + H_2O > CH_2O + O_2$) is widely accepted as the source of essentially all free O_2 on Earth's surface, and thus the ecosystem itself needed to be prepared by the innovation of oxygenic photosynthesis before the rise of O_2. There is currently no consensus about the exact timing of this evolutionary innovation (Cardona, 2019; Kirschvink et al., 2000). Some studies suggested an origin of oxygenic photosynthesis is close in time to the GOE and thus the rise of O_2 was directly driven by the evolution of the ecosystem (Soo et al., 2017). Meanwhile, evidence and arguments from isotopic evidence and trace elements have been accumulated to support whiffs of O_2 much earlier and innovation of oxygenic photosynthesis dated back to at least 3.0 Ga (Rosing and Frei, 2004; Crowe et al., 2013; Planavsky et al., 2014). No matter which case is correct, life on its own cannot change the net redox state of the global environment, because each biological oxidant will be complemented by a reductant (Catling and Zahnle, 2020). Therefore, the reductants must have been consumed or removed/isolated from the surface to begin accumulating O_2 in the atmosphere (Kasting, 2013). In the absence of organic burial, biogenic oxygen merely reoxidizes organic matter during respiration (reversing the equation above) and there is thus no net change in atmospheric oxygen. This is to say, oxygen produced during photosynthesis doesn't constitute a net source of atmospheric oxygen unless it is coupled with organic carbon burial (Krissansen-Totton et al., 2015). In geologic timescale, the organic carbon burial is considered as a net source of atmospheric O_2. Enhanced organic carbon burial would lead to an increase in oxygen source flux, eventually raising the atmospheric O_2 levels. Another category of explanation is associated with the decrease in oxygen sink flux, which includes recycling of carbon and sulfur relative to water (or hydrogen) (Holland, 2009), changes in the redox state of volcanic gases due to mantle redox evolution (Bekker et al., 2010), a switch from submarine to subaerial volcanism (Kump and Barley, 2007), hydrogen escape and continental oxidation (Zahnle et al., 2013), etc.

3.3 Solid Earth and deep oxygen cycle

Since the pioneering works about the GOE, the evolution of the solid Earth has been believed to drive this transition of the atmosphere to some extent, as an important contributor of removing/isolating those reductants (Holland, 1985; Holland et al., 1986; Hayes and Waldbauer, 2006; Kasting, 2013; Eguchi et al., 2020). This is not only because most components of the atmosphere were ultimately derived from degassing of the deep Earth, but also indicated by the coincidence in the evolution history of them (Barley et al., 2005; Kump and Barley, 2007; Campbell and Allen, 2008; Gaillard et al., 2011; Keller and Schoene, 2012; Lee et al., 2016; He et al., 2019). The solid Earth is linked to the at-

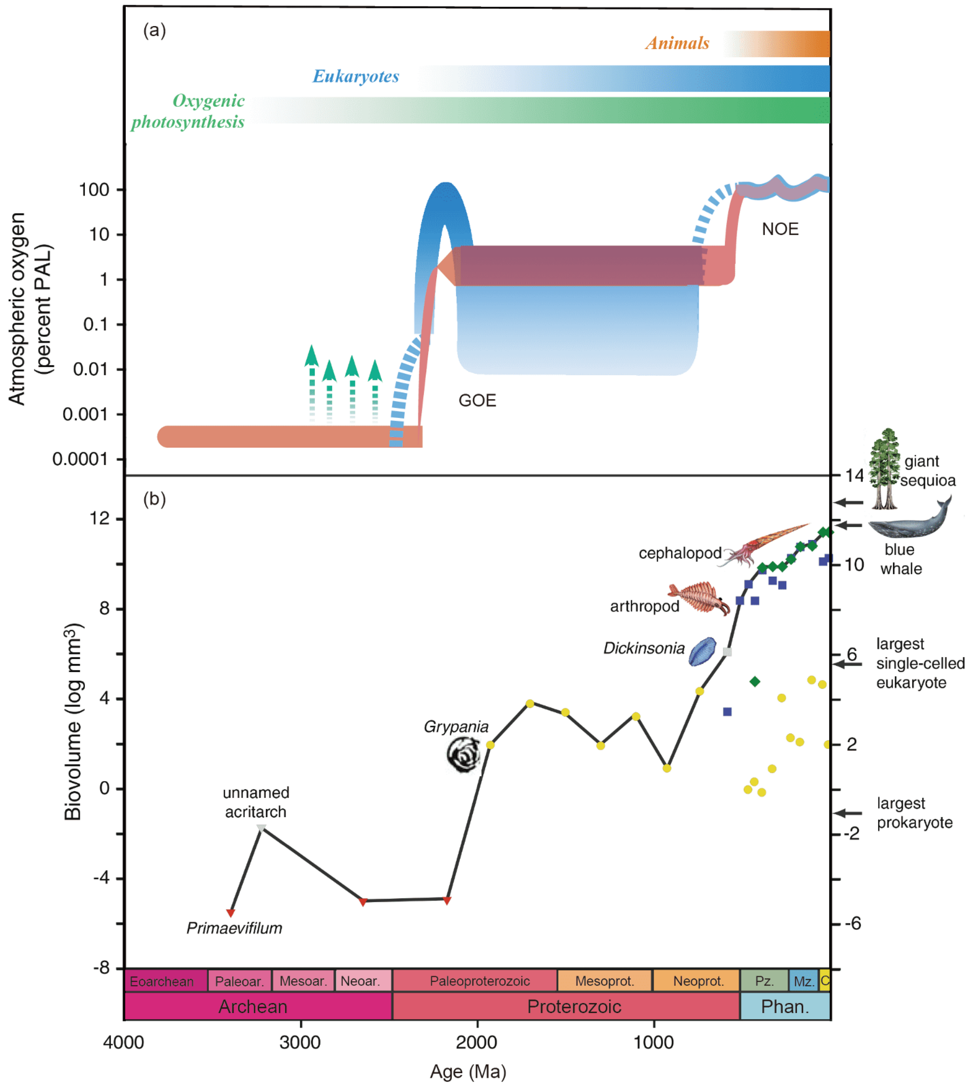

Figure 2 The evolution of atmospheric O_2 (a) and maximum organismal sizes through geological time (b) (Payne et al., 2011; Lyons et al., 2014; He et al., 2019).

mosphere, hydrosphere and biosphere by weathering, alteration and sedimentary processes, magmatism and subduction. It is widely accepted that the buffering effect of the solid Earth will apply only after complex interactions with the surficial abiotic and biotic cycles (Kasting, 2013; Laakso and Schrag, 2014). While if it is true that the atmospheric O_2 level can reach a steady state for a given input in about a couple of million years (Laakso and Schrag, 2014), the impact of the solid Earth on the atmospheric O_2 shall be intrinsically governed by what is input and recovered from the surficial system via volcanism and geological burial (e.g., subduction) as well as their fluxes (Petsch, 2014a). Despite intrinsically driving by processes in deep earth, many studies emphasized the direct effects of evolutionary solid Earth on the surficial cycles buffering the atmospheric O_2. The crustal uplift during the formation of supercontinents has been suggested to enhance nutrient fluxes into the ocean, cause an increase in oxygenic photosynthesis and burial of organic carbon, and ultimately lead to the rise of O_2 (Colman et al., 1997; Campbell and Allen, 2008). The emergence of continents above the sea level, likely at a time close to the Archean-Proterozoic boundary, may have dramatically increased the redox state of volcanic emissions for a decrease in degassing pressure (Gaillard et al., 2011). This transition was also likely accompanied by evolution of the continental crust from an ultramafic to felsic composition, which may also have substantially decreased O_2 sinks during weathering and alteration (Lee et al., 2016; Smit and Mezger, 2017). As consequences of a change in the crustal composition, a decrease in nutrient fluxes key for reductant-producing species (e.g., Ni for methanogenesis) and an increase in nutrient fluxes promoting oxygenic photosynthesis (e.g., P) have been expected (Konhauser et al., 2009; Cox et al., 2018). All these processes tend to help accumulate O_2 in the atmosphere, which makes discrimination of their individual roles difficult unless a quantitative evaluation is possible.

Once the surficial system being considered as a single redox pool, deep oxygen cycles straightforwardly become crucial (Kasting et al., 1993; Evans, 2012; He et al., 2019; Hu et al., 2016; Duncan and Dasgupta, 2017; Mao et al., 2017). Deep oxygen cycles are referred to the cycling of elements with multiple valences that oxygen is bounded with between the solid Earth and its surface through magmatism and subduction (He et al., 2019). The ambient mantle has been believed to be progressively oxygenated through H_2 loss to space, which then promoted oxygenation of the atmosphere (Catling et al., 2001; Kasting et al., 1993). Although controversial (Anser Li and Aeolus Lee, 2004; Aulbach and Viljoen, 2015), this early view is not supported by observations on mantle peridotites and ultramafic to mafic igneous rocks that suggest a constant redox state of the ambient mantle since at least the early Archean (Anser Li and Aeolus Lee, 2004; Dauphas et al., 2009). With mantle cooling, the melting manner of both the mantle and crust has changed across the Archean and Proterozoic boundary (Keller and Schoene, 2012). For example, a decrease in crustal melting depth likely caused a change in residual assemblage from Fe^{3+}-compatible, garnet-pyroxenes-rich to less Fe^{3+}-compatible, olivine-pyroxenes-rich, and thus an increase in the redox state of the relevant melts. This transition has long been argued as an important driving force for oxygenation of the atmosphere (Keller and Schoene, 2012), although a recent study provides evidence on the increase of mantle oxygen fugacity (Nicklas et al., 2019). With the development of the plate tectonics at some time in the Archean (Condie, 2018), exchange of the redox budget between the atmosphere and solid Earth began to be regulated by the balance between magmatic output and subduction input, i.e. the direction and fluxes of deep oxygen cycles (Evans, 2012; Hu et al., 2016; Mao et al., 2017; Duncan and Dasgupta, 2017; He et al., 2019). Recently, three different pathways of deep oxygen cycles have been proposed based on experiments and Fe isotopic evidence of basalts. Experiments under pressures and temperature analogue to deep lower mantle reveal the presence of stable, pyrite-structured FeO_2, which is believed to form by recycling of geothite and/or H_2O downward to depths near the core-mantle boundary (Hu et al., 2016; Mao et al., 2017). With removal of H_2 as the reductant to the space, partial melting of accumulated, FeO_2-rich layers in the deep mantle has been suggested to promote oxygenation of the surface and the GOE (Hu et al., 2016). Another creative experiments recently suggested that a significant proportion of organic carbon can avoid decarbonation in subduction zones and thus be isolated from the surface and buried into the deep mantle, which leads to oxygenation of the atmosphere (Duncan and Dasgupta, 2017). These intriguing experimental advances definitely pilot the future works evaluating the role of deep oxygen cycles in regulating the long-term atmospheric O_2 level. However, it remains largely unknown how much H_2O and organic carbon can survive from de-volatile processes of subducted slabs in the ambient mantle and how these fluxes changed with secular cooling of subduction zones. A nephelinitic magma end-member with heavy Fe isotopic composition has been revealed among Cenozoic basalts from eastern China and been explained by derivation from mantle sources oxidized by recycled carbonates that were partially reduced into diamonds (He et al., 2019). The study has shown the $\delta^{13}C$ composition of diamonds as evidence for subduction of organic matter (Cartigny et al., 2014). The origin of these basalts illustrates a pathway with net transport of oxidizing potential to the surface, that is burial of surface carbonates into deep mantle as diamonds with the oxidizers preferentially release to the surface via oxidizing, alkaline basaltic magmas. The efficiency of this pathway most likely increased at the Archean-Proterozoic boundary and the late Proterozoic with decrease in geotherm of global subduction zones and increase in alkaline magmatism, providing an alternative driving force from the deep Earth for oxygenation of the atmosphere (He et al., 2019).

The evolution of the solid Earth shall have, at least partially, regulated the atmospheric O_2 level through deep oxygen cycles, its effects on key factors of the surficial cycles, or both. The oxygenation of the atmosphere dramatically changed the pathways of weathering, alteration and sedimentary processes in the surface, which in turn has rapidly affected the deep Earth via subduction (Liu et al., 2019). Interactions between the atmosphere and the solid Earth were undoubtedly complex. A better understanding of such interactions and the role of solid Earth in atmosphere oxygenation requires advances in multiple disciplines ranging from experiments with P-T conditions spanning from shallow subduction zones to the core-mantle boundary, observations on geological archives from cell-level to global perspective with billions of years of history, and numerical modeling, being promoted by multiple discipline cooperation and creative techniques.

3.4 Stepwise oxygenation and biological innovations

There have been substantial researches indicating the inextricable relationship between increases of O_2 levels and biological evolutions (Figure 2b). The GOE is of key biological importance, since its timing imposes sharp constraints of the minimum age of oxygenic photosynthesis and diversification of aerobic metabolism (Raymond and Segrè, 2006) and minerals (Hazen et al., 2008). Using a molecular clock approach, the earliest eukaryotes (which require oxygen for biosynthetic reactions) have been dated as early as 2.31 Ga, concurrent with the timing of the GOE (Gold et al., 2017). This finding indicates that the evolution of biosynthesis is closely tied to the first widespread availability of free O_2 in the ocean and atmosphere. Another significant rise in free O_2 in the atmosphere and deep ocean is known as the Neoproterozoic Oxidation Event (NOE, 800~550 Ma, 1 Ma= 1×10^6 a), when near-modern values of atmospheric O_2 were first reached, making it possible to sustain large and complex multicellular organisms (Och and Shields-Zhou, 2012).

The major biological innovations during the NOE include the appearance of new biological and ecological strategies, the appearance of metazoans (Morris, 1993), and the Cambrian Explosion (dramatic diversification of animal body plans and behaviors) (Erwin et al., 2011; Yang et al., 2018; Erwin, 2020). Moreover, two major jumps in the body size of organisms on Earth can be found in fossil records from the middle of the Paleoproterozoic (~1.9 Ga) and during the Neoproterozoic-early Paleozoic (600~450 Ma) (Payne et al., 2009; Smith et al., 2016), which roughly coincide with or shortly followed increases in atmospheric O_2 levels. Dragonflies with 70 cm wingspans and anthropoids as long as 1 m have been found in the fossil records (Clapham and Karr, 2012), and the insect gigantism had already been considered indirect evidence for high O_2 levels during the Carboniferous long before the geochemical modeling of O_2 levels during the Phanerozoic (Rutten, 1966). This result implies that the rise in atmospheric O_2 may have facilitated the biological innovations that led to larger body sizes and further suggests that the two-step increase in atmospheric O_2 served as the pacemakers for biological evolution (Knoll and Nowak, 2017). It should also be noted that some researchers argue for an opposite relationship that the rises in oxygen could have been driven by animals. For example, the metazoans can fundamentally transform the redox balance of modern marine settings by changing the nature of the biological pump (Butterfield, 2018; Cole et al., 2020).

Although the NOE has marked the first oxygenation of the deep ocean, evidence for periodic deep ocean anoxia remains frequent at this time (Sahoo et al., 2016). Until mid-Paleozoic, another major rise in atmospheric O_2, known as the Paleozoic Oxygenation Event (POE) elevated the O_2 levels to present-day levels and a dominantly oxygenated deep ocean is established (Krause et al., 2018; Alcott et al., 2019). It is believed that the appearance and radiation of land plants were responsible for the rise of O_2 via significantly increasing organic carbon burial (Lenton et al., 2016). A number of biogeochemical models argue for a direct relationship between the radiation and diversification of land plants and a major increase in O_2 levels (Kump and Garrels, 1986; Bergman, 2004). However, when exactly the oxygen content of the surface seawater exceeded the minimum requirements for animals to maintain a certain degree of diversity is still unknown (Shu, 2008; Shu et al., 2010; Zhang and Shu, 2014).

3.5 The sources and sinks of atmospheric O_2 in the geologic timescale

Atmospheric O_2 is produced by photosynthesis by plants, algae, and cyanobacteria, while in geological timescale, its accumulation in the atmosphere involves a series of processes. Generally, the long-term sources of atmospheric O_2 are the burial of organic carbon and pyrite. Organic carbon is produced with O_2 during photosynthesis. Thus, when plants are alive and growing, the growth of plants could be equated to oxygen accumulation. However, most of the organic matter would ultimately be decomposed by bacteria and fungi, which consumes the previously accumulated O_2. Only a tiny proportion of the organic carbon is buried as unreactive in marine and freshwater sediments and ultimately solidify into rocks, so that they cannot back-react with O_2 (Petsch, 2014b). The burial of this portion of organic matter represents a net source of O_2 to the atmosphere. Another important source of atmospheric O_2 is pyrite deposition. Generally, pyrite is generated via anaerobic microbial processes, which metabolizes organic matter using sulfate and produces sulfide (usually FeS_2). If pyrite remains unreacted and buried in sediments, the burial of sulfide also serves as an O_2 source for the atmosphere, since pyrite is formed on the utilization of reducing power of organic carbon. The burial of organic carbon has been the main source of atmospheric O_2 in the past few hundred million years, while in the more distant past the pyrite burial may have prevailed as an O_2 source (Olson et al., 2019; Shields et al., 2019).

In the rock cycle, the buried pyrite and organic carbon would be re-oxidized after they are brought back to the Earth's surface via tectonic uplift. The re-oxidation processes thus represent an oxygen sink, which completes the cycle. Another removal pathway for O_2 is the chemically reduced gases (emanated from subaerial volcanos and midocean hydrothermal vents), including H_2, SO_2, and H_2S. The sketch of the modern geologic oxygen budget is shown in Figure 3.

4. Atmospheric O_2 declines and biological extinction

Over time, geological and geochemical records have become more abundant and increasingly informative during the Phanerozoic Eon (541.0±1.0~0 Ma). Since the presence of macrofossils, five major diversity crises, widely known as the "Big Five" extinctions, including the Late Ordovician (~440 Ma), Late Devonian (~367 Ma), end-Permian (~252 Ma), end-Triassic (~200 Ma), and end-Cretaceous (66 Ma) mass extinctions, together with a dozen smaller extinction episodes have been recognized during the Phanerozoic (Bambach, 2006). Two of the most remarkable changes in evolutionary faunas, namely, the end-Permian and end-Cre-

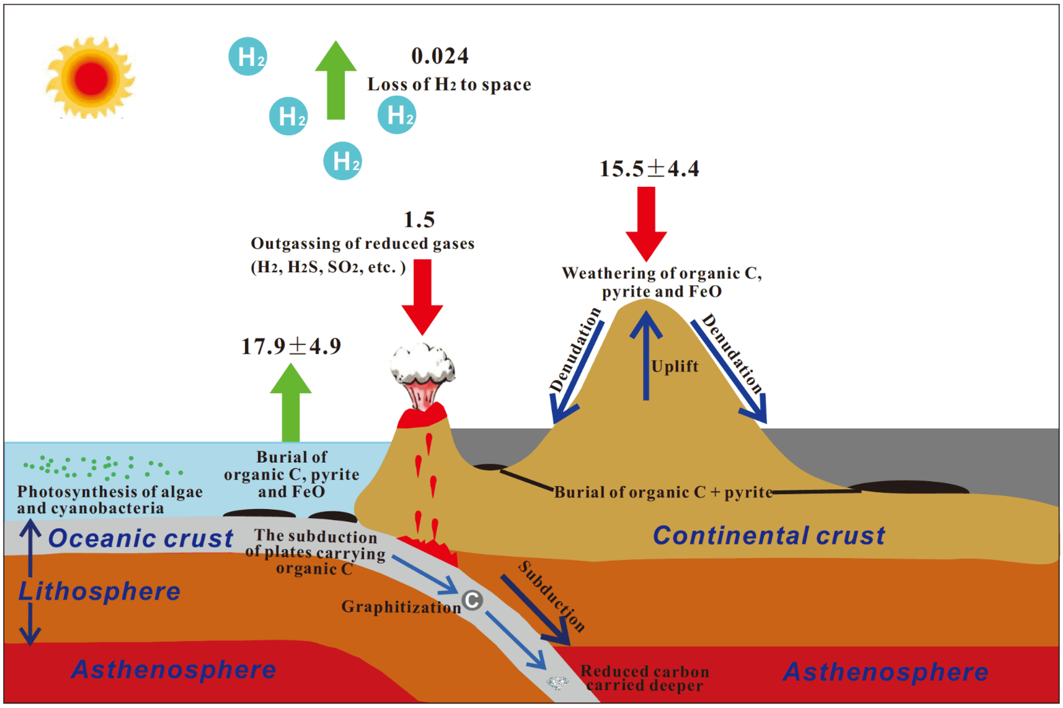

Figure 3 Sketch of the modern geologic oxygen cycle showing the principal sources and sinks. Green and red arrows represent the oxygen source and sink respectively. Revised base on Figure 4 of Duncan and Dasgupta (2017), Figure 2 of Campbell and Allen (2008), and Figure 7 of Canfield (2005). The magnitude of sources and sinks are derived from Kasting and Canfield (2012), with units of 10^{12} mol yr^{-1}.

taceous extinctions, led to the subdivision of the Phanerozoic Eon into the Paleozoic, Mesozoic, and Cenozoic eras (Figure 4).

4.1 The end-Permian mass extinction

The extinction that marks the ending of the Paleozoic Era, the end-Permian mass extinction event (EPME), is considered the most severe biodiversity loss among all the recorded extinctions (Kump, 2014). The latest study suggests that 81% of marine species became extinct (Fan et al., 2020), and the terrestrial ecosystem suffered a similar severity (Shen et al., 2011). In South China, the EPME event was a nearly instantaneous extinction (Bowring et al., 1998; Jin et al., 2000; Shen et al., 2011) that only persisted for a few thousand years (Burgess et al., 2014; Shen et al., 2019). A recent geochronology study suggests that the most plausible trigger, the Siberian Traps (Burgess et al., 2017), which started ~300 kyr before the EPME interval, may have already impaired the resilience and function of ecological systems before the rapid decline in biodiversity (Shen et al., 2019). The eruption would have released substantial amounts of greenhouse gases, leading to an approximately 10°C temperature increase (Joachimski et al., 2012; Chen et al., 2016), the short-term production of acid rain as well as widespread ocean anoxia (Zhang et al., 2018) and acidification (Hinojosa et al., 2012) within the extinction interval. Furthermore, a significant drop in atmospheric O_2 (Berner, 2005), climate warming, and a rising sea level would have substantially reduced the habitats for terrestrial species (Huey and Ward, 2005). Krause et al. (2018) have updated and corrected GEOCARB to better capture the evolution of oxygen. The updated model no longer produces a sharp end-Permian drop in atmospheric oxygen. However, what is certain is that the sudden collapse of terrestrial and marine ecosystems and persistent lethally high temperature in the Early Triassic may have contributed to the delayed recovery until the beginning of the Middle Triassic, 8~9 Ma after the crisis (Sun et al., 2012).

4.2 The end-Cretaceous event

Another major extinction was the end-Cretaceous event, which ended the Mesozoic Era and the age of the dinosaurs; this event is the most intensively investigated among the Big Five during the Phanerozoic (Bambach, 2006; Schulte et al., 2010). Previously, the most convincing trigger for the extinction is the Chicxulub impact event (Alvarez et al., 1980), which was evidenced by the discovery of an anomalously high level of the element iridium at the K-P boundary and widespread distribution of impact materials (Schulte et al., 2009) and a massive Chicxulub crater (180–200 km diameter) beneath the surface of the Yucatan Peninsula (Schulte et al., 2010; Gulick et al., 2019). Asteroid impact models predict massive earthquakes (DePalma et al., 2019) (12.6 magnitudes, the energy of the impact could have supplied the

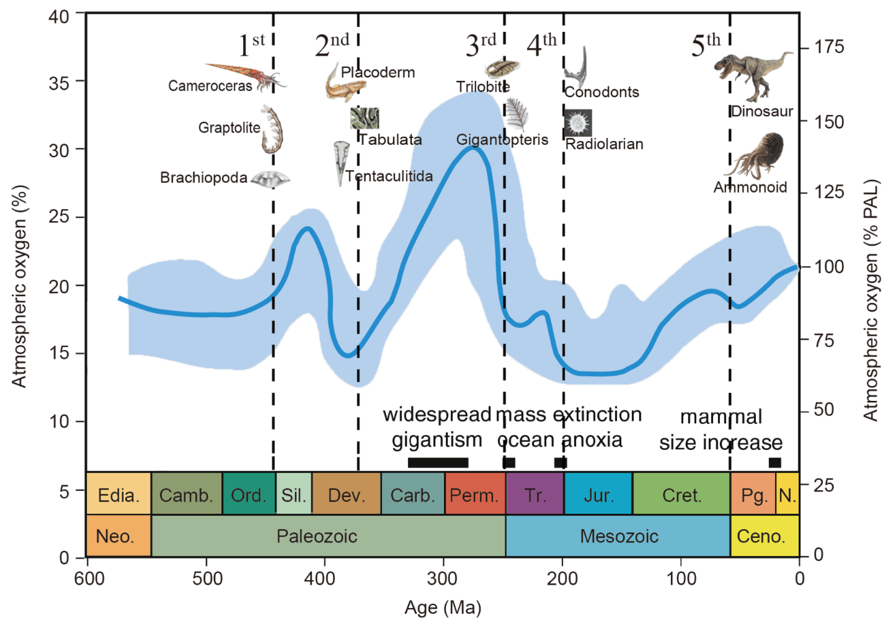

Figure 4 Reconstructed O_2 content during the Phanerozoic Eon with 95% confidence intervals (shaded) obtained from Geocarb simulations (Berner, 2006). The dashed vertical lines show the timing of the five mass extinctions.

US electrical output for 40 years based on 2000 scenario), production of huge globally spreading tsunami waves, and wildfires in the first hours after the impact (Robertson et al., 2004; Shonting and Ezrailson, 2017). Injections of large quantities of dusts and aerosols into the stratosphere would dramatically alter the climate system by blocking the incoming solar radiation for decades, leading to an "impact winter" (Pierazzo et al., 1998). The soot produced during the organic burning absorbed the short-wave radiation, further causing a dark phase with inhibited photosynthesis and the collapse of global food webs in both terrestrial and marine environments (Kring, 2007). The impact is believed to induce the most abrupt climate change in the past 100 Ma (Overpeck and Cole, 2006). Hundreds of years after the impact, a rapid warming occurred. It is estimated that the Chicxulub asteroid impact resulted in an extraordinarily rapid release of over 10^3 Gt CO_2. Significant marine warming reduced gas solubility and ocean ventilation. Increased nutrient inputs may have increased O_2 demand. These factors contributed to a decline in dissolved O_2 and led to shelf hypoxia (Vellekoop et al., 2018). However, recent studies suggest that climate instability during the preceding Maastrichtian stage (Archibald et al., 2010) caused by the voluminous eruption of the Deccan Traps (Renne et al., 2015) becomes a more plausible cause for the extinction (Schoene et al., 2019; Sprain et al., 2019). Studies of diversity patterns across the Cretaceous-Paleogene boundary suggest that dinosaurs and numerous marine foraminifers disappeared in a relatively long-time-interval which cannot be accounted for by an instantaneous impact event. High-precision dating indicates that a distinct temperature rise of ~4°C occurred just before the end-Cretaceous extinction, which was consistent with a peak eruption of the Deccan Traps (Schoene et al., 2019).

4.3 Biological evolution and extinction

Although various triggers and physiological kill mechanisms have been proposed for the extinction events recorded in geological history (Knoll et al., 2007), unfortunately, none of these hypotheses are flawless. An enormous wealth of geological, geochemical, and paleontological information has been only partly deciphered. However, it is certain that almost every mass extinction has been accompanied by abrupt changes in the planetary environment associated with geophysical or astrophysical perturbations. Ever since the two-step increase in atmospheric O_2, aerobic metabolism has diversified and prevailed throughout the Phanerozoic. Thus, the evolution of the atmospheric O_2 level over the past ~550 Ma (Figure 4) is likely intertwined with biological evolution and extinction due to its physiological importance. According to Shen and Zhang (2017), anoxic environments, especially in the ocean, are associated with the four (end-Ordovician, Late Devonian, end-Permian, and end-Cretaceous extinctions) out of the five mass extinctions (Vellekoop et al., 2018; Xiang et al., 2020; Zhang et al., 2020; Zhang et al., 2020).

Theoretically, oxygen availability can limit the size of organisms since the surface area available for diffusion constrains O_2 uptake, whereas the body mass governs the O_2 demand (Bonner, 1988). The existing experiments on the effects of the O_2 content on modern physiology and fossil records indicate a powerful effect on animal development and evolution (Payne et al., 2009, 2011). Under hypoxic conditions, size decreases have been observed to occur in fruit flies, snakes, fish, rats, and even humans, and the effect of hyperoxia associated with increased size was found in only a few studies (Herman and Ingermann, 1996; Berner et al., 2007; Zamudio et al., 2007; Payne et al., 2011). The decline in O_2 levels in oceanic or atmospheric environments may be one of the major kill mechanisms that led to the end-Permian and end-Triassic extinctions. Conversely, it was recently proposed that a series of biological processes, including the emergence of herbivory, had the potential to affect the redox state of the Earth's surface during the Phanerozoic. The evolution and diversification of terrestrial herbivores may have disturbed the global biogeochemical cycles of carbon and phosphorus and led to less organic carbon burial and the subsequent decline in O_2 at the end of the Paleozoic (Laakso et al., 2020).

5. Oxygen cycle in modern Earth system

5.1 Ocean deoxygenation

After a billion years of atmospheric O_2 evolution, the current volume fraction of O_2 in the modern atmosphere has relatively stabilized at 20.95% (Machta and Hughes, 1970). The past decades have witnessed the rapid development of atmospheric CO_2 measurements around the world, and precise measurements of atmospheric O_2 at the part-per-million scale remain a challenge. Since the O_2 background concentration is several orders of magnitude higher than that of CO_2 (210000 ppm (1 ppm=10^{-6} μL/L) for O_2 and 400 ppm for CO_2), detecting relative variations in atmospheric O_2 is challenging (Keeling and Manning, 2014). Therefore, only several organizations in the world are involved in O_2 measurements, including the Scripps Atmospheric Oxygen Program (http://scrippso2.ucsd.edu/). High-precision measurements of O_2 since the late 1980s showed a steady decline in O_2 levels (approximately 4 ppm yr^{-1}) due to the imbalance between the production and consumption fluxes (Figure 5a). Although serious depletion in atmospheric O_2 is unlikely to occur in the near future, ocean deoxygenation since the mid-20th century has posed a serious threat to productivity and biodiversity in marine ecosystems (Figure 5b). Over the past 50 years, a four-fold expansion of oxygen-depleted waters has occurred. In some areas of the ocean, 40% of oxygen has been lost (Schmidtko et al., 2017). The oxygen in the ocean is controlled by both physical and biogeochemical processes. Photosynthesis by autotrophic organisms and O_2 dissolution from the atmosphere in undersaturated waters result in a net gain in oceanic oxygen, and the ocean loses oxygen via oxygen outgassing in oversaturated areas, the respiration of aerobic organisms, and the oxidation of reduced chemicals. The declining oxygen levels in the ocean are mainly attributed to two human-induced causes, the heating of ocean waters and eutrophication. Ocean warming is considered a major driver, both directly (solubility effect) and indirectly (changes in circulation, mixing, and respiration), of this trend (Oschlies et al., 2018). Eutrophication in coastal areas due to increasing anthropogenic inputs of nutrients (nitrogen and phosphorus) from land runoff reflects a large amount of oxygen consumption (Diaz and Rosenberg, 2008). Despite the limited marine oxygen reserve (~0.6% of that in the atmosphere), the ocean is now losing oxygen and has even become a net source for atmospheric O_2. Based on CMIP5 (Coupled Model Intercomparison Project Phase 5) simulations, Li et al. (2020) diagnosed the ocean oxygen budget, revealing the important role of sea-surface oxygen outgassing in marine deoxygenation. Deoxygenation can affect various aspects of marine ecosystem services (Shepherd et al., 2017) and physiology, as well as the behavior and ecology of marine organisms (Prince and Goodyear, 2006; Seibel, 2011). A significant decrease (60~100%) in the vision of marine invertebrates could occur if they are exposed to reduced oxygen availability (McCormick et al., 2019). Slight changes in oceanic oxygen can have a direct effect on the distribution of many major zooplankton who live near their physiological limits (Wishner et al., 2018). Deoxygenation can negatively affect different aspects of fish species, including their growth, survival, reproduction, etc., thus causing perturbations in the population distribution and food web (Pörtner and Peck, 2010). With the effects of global warming and increased nutrient inputs to coastal regions, ocean deoxygenation is predicted to deteriorate in the future (Shaffer et al., 2009). In the 21st century, it is projected in CMIP5 simulations that deoxygenation in the surface and deep ocean will worsen under the RCP2.6 (with a decrease of 1.81±0.31%) and RCP8.5 (3.45±0.44%) scenarios (Bopp et al., 2013). In spite of the potential hazard that O_2 depletion would create, major efforts (Keeling and Shertz, 1992; Keeling et al., 1993; Battle et al., 2006; Manning and Keeling, 2006; Le Quéré et al., 2018) to study the global oxygen cycle have concentrated on optimizing the estimation of the global carbon budget based on the different inorganic reactions of CO_2 and O_2 (carbonate reactions) with seawater. Until now, our understanding of the modern oxygen cycle has been limited. Details of the fluxes involved in O_2 production and consumption processes are too poorly constrained to conclusively establish a modern oxygen cycle.

5.2 Global oxygen budget

In the modern atmosphere, the main source of atmospheric O_2 is primary production from terrestrial and marine ecosystems, and the sinks include autotrophic and heterotrophic

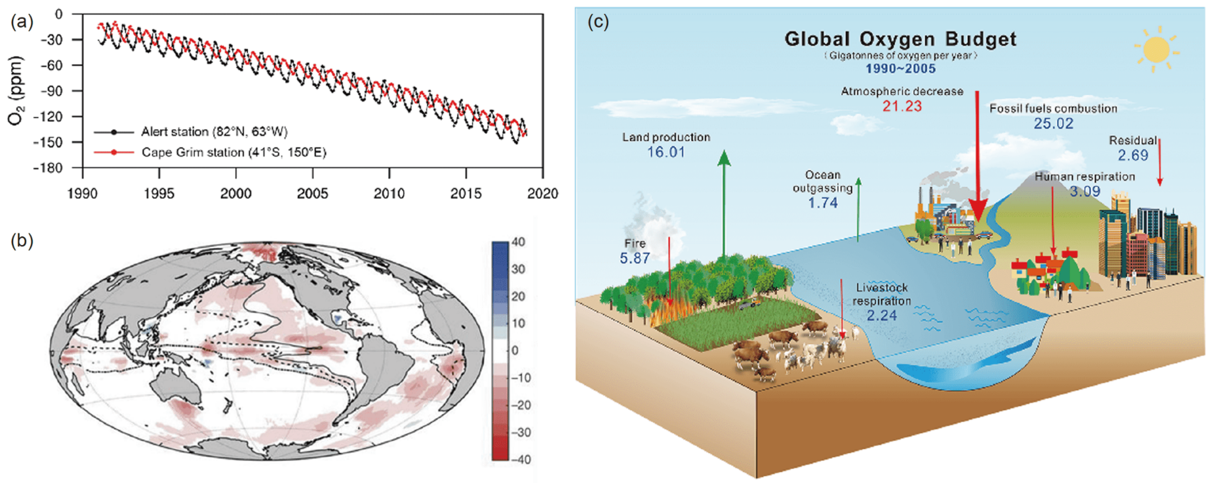

Figure 5 Global oxygen cycle in the modern Earth system. Time series of the O_2 concentration (ppm) at Alert Station and Cape Grim Observatory (a). Changes in the oxygen content of the global ocean in mol O_2 m^{-2} $decade^{-1}$ (Schmidtko et al., 2017) (b). Average global oxygen budget from 1990 to 2005 in 10^{12} mol yr^{-1} (Huang et al., 2018) (c), where the green arrows denote the production from land vegetation and outgassing from oceans and the red arrows represent consumption by fossil fuel combustion, human and livestock respiration, fires, and residual processes.

respiration, wildfires, the weathering of organic matter and minerals, the oxidation of volcanic gases, and most importantly, human activities (combustion of fossil fuels, industrial activities, etc.) (Figure 5). The scientific consensus has been reached that fossil fuel combustion makes the largest contribution to the removal of atmospheric O_2. Keeling et al. (1993) presented a simple conceptual model that shows the short-term sources and long-term sources in the global oxygen cycle and quantified important biological and physical processes that control atmospheric O_2. Huang et al. (2018) quantitatively estimated the global O_2 budget (Figure 5c) based on CMIP5 models and noted that the average O_2 consumption flux from 1990–2005 was 36.22 Gt O_2 yr^{-1} (1131.9×10^{12} mol yr^{-1}) and the average compensation from land and ocean systems over the same period was 17.75 Gt O_2 yr^{-1} (554.7×10^{12} mol yr^{-1}). The imbalance between O_2 production and consumption resulted in a steady decline in O_2 over the past century. Liu et al. (2020) attempted to quantify the land O_2 flux and took the initial step to quantitatively describe the anthropogenic effects on the global O_2 budget on a grid-scale from 1975 to 2018; they found that the burning of fossil fuels led to the largest O_2 fluxes in East Asia, India, North America, and Europe, while wildfires were the main contributor in Central Africa.

In addition to the long-term variability in atmospheric O_2, shorter-term fluctuations (from the diurnal to seasonal scales) in atmospheric O_2 have also been well captured by high-resolution measurements. In both hemispheres, O_2 is observed to increase in spring and summer and decrease in autumn and winter, with opposite changes in CO_2, which reflects the biosphere productivity and air-sea exchange on the equivalent timescale. Minejima et al. (2012) examined the O_2 concentrations during pollution events on Hateruma Island, Japan, and found a decrease in the O_2 content by approximately 10 ppm under the influence of mixed pollutants from China, South Korea, and Japan. Lueker et al. (2001) detected a decline in the O_2 content by 20 ppm associated with wildfires burning 70 km east of the station. Atmospheric measurements of O_2 and CO_2 in a mixed deciduous forest in central Massachusetts, USA, demonstrated strict inverse variations in the diurnal cycles of O_2 and CO_2, with the highest (lowest) daily O_2 concentration at approximately 19:00 (9:30) in autumn of 2006 (Battle et al., 2019). The atmospheric O_2 content is not spatially uniform and displays spatial variations. Shi et al. (2019) collected air samples at different altitudes on the Tibetan Plateau and found that the relative O_2 concentration is not only associated with altitude but is also strongly affected by surface vegetation coverage and weather conditions.

5.3 Future projection of the oxygen cycle

Human impacts on global environments have become increasingly profound and have gradually steered the Earth system away from its natural behaviors (Lenton et al., 2008). Anthropogenic modifications to the planet are extensive enough to affect the long-term geologic processes and have already left worldwide stratigraphic signals. Therefore, the “Anthropocene” was assigned as a new geologic epoch that is both functionally and stratigraphically distinct from the Holocene (Waters et al., 2016). Although the beginning of this new epoch has been widely debated and several thresholds have been invoked to demarcate the onset of the Anthropocene, including (1) the land-use changes and gradual increase in anthropogenic greenhouse gases (CO_2 and CH_4) as early as thousands of years ago (Ruddiman, 2018;

Laurance, 2019), (2) the collision of the old and new worlds, known as the Colombian Exchange in approximately 1610 (Lewis and Maslin, 2015), (3) the Industrial Revolution in the late 18th century (Crutzen, 2002), and (4) the "Great Acceleration" of population growth and energy consumption since the mid-20th century (Steffen et al., 2015), a clear and broad consensus has emerged that human modifications of the global environment are occurring at unprecedented rates, which is progressively drawing us toward the sixth mass extinction. Ceballos et al. (2015) used extremely conservative assumptions to assess whether anthropogenic activities are leading to a mass extinction and concluded that the past few centuries have witnessed an exceptionally rapid loss of biodiversity (for vertebrate species, the current extinction rate is as much as 100 times that of the background rate). Barnosky et al. (2011) found that the rate and extent of current biodiversity loss are close to those of the mass extinctions during the Phanerozoic and distinguished the intervals between them (background values). Collective and immediate human actions are required to avoid a perilous situation, and we may have a chance to reverse the biodiversity decline and subsequent loss of ecosystem functions. However, our chances will become increasingly slim in the future. Studies have shown that positive feedbacks within the Earth system can be a potential trigger, and when a certain threshold is crossed, the Earth system may shift uncontrollably toward an unstable condition, even if anthropogenic emissions are reduced (Lenton et al., 2008; Steffen et al., 2018).

Geological analogs from past climate events provide valuable information for understanding and even predicting anthropogenic impacts on the Earth system. Notwithstanding, scientists find it challenging to match the current climate with a historical analog because the magnitude of perturbations in the Anthropocene is significantly larger than those in the geological past. For example, the Paleocene-Eocene Thermal Maximum (PETM, ~56 Ma), which was associated with 5°C warming and substantial carbon release, is widely regarded as the best analog for future trajectory predictions. However, with a new method, Zeebe et al. (2016) constrained the maximum carbon release rate during the PETM to less than 1.1 Gt C yr^{-1} and concluded that the current carbon release rate (~10 Gt yr^{-1}) was unprecedented during the past 66 Ma and could cause unforeseeable future responses in the Earth system. Foster et al. (2017) suggested that in the 23rd century of a business-as-usual scenario (RCP8.5), radiative forcing will reach an unprecedented level compared to that over the last 420 Ma, and an unpredictable response in the Earth system is anticipated. As an integral part of the Earth system, would the global oxygen cycle experience unprecedented changes in future scenarios? The O_2 concentration is projected to decline throughout the 21st century. Under the Representative Concentration Pathways (RCPs) RCP8.5 scenario, approximately 100 Gt of O_2 would be removed from the atmosphere annually until 2100, and the O_2 concentration will experience a decline from its current level of 20.946% to 20.825% (Huang et al., 2018).

Figure 6 shows different scenarios for future O_2 projections. It is projected that the O_2 concentration will finally stabilize at 20.61%, 20.85%, and 20.90% in RCP8.5, RCP6.0, and RCP4.5, respectively. However, in no-stop RCPs, in which fossil fuel combustion remains unchanged, persistent O_2 decline can occur. In no-stop RCP8.5, the O_2 concentration will drop below 20.0% in the 26th century and reach 19.5% around the beginning of the 29th century, which may lead to potential health-related problems. Based on the available records of atmospheric O_2, Livina et al. (2015) used a tipping point analysis to project the future O_2 concentration and found that the decline in O_2 will lead to health-threatening problems for humans in 5000~10000 years if no measures are taken. Martin et al. (2017) predicted that humans may continue to survive in an unprotected atmosphere for ~3600 years. These projections have demonstrated that the atmospheric O_2 concentration is closely related to the cumulative consumption of fossil fuels over a given timeframe and suggest that persistent anthropogenic modifications to the global oxygen cycle will eventually pose a serious threat to the habitability of our planet. However, it should be noted that fossil fuels are a finite resource. Such resources are not fixed and evolve with time. Estimations of fossil fuel resources on the planet are highly uncertain due to knowledge and boundary limitations (IPCC, 2014; Bauer et al., 2016). Rogner et al. (2012) estimated the total carbon content of fossil fuel resources between 8543~13469 Gt of C. The complete combustion of all the available fossil fuels would consume 28383–47046 Gt of O_2, which would result in a decline in O_2 from the current level of 20.946% to 20.45–20.11%. Of course, we have to find a substitute for fossil fuel (bioenergy, wind energy, solar energy, etc.) before running out of all the resources on our planet, and we still have a chance to stabilize atmospheric O_2 at a relatively healthy level. The future trajectory of the atmospheric O_2 concentration is largely dependent on our mitigation policies.

6. Conclusion and perspective

Studies of the oxygen cycle cover a wide span of timescales from daily to geologic scales (>10^6 yrs). The oxygen cycles of different timescales dominate the control of atmospheric O_2 over the corresponding timescales. However, a distinct boundary that divides the long-term and short-term oxygen cycles has yet to be established, and the complex interactions between the short-term and long-term processes remain unclear. Would the short-term processes in the oxygen cycle trigger sudden changes in the long-term oxygen cycle, or

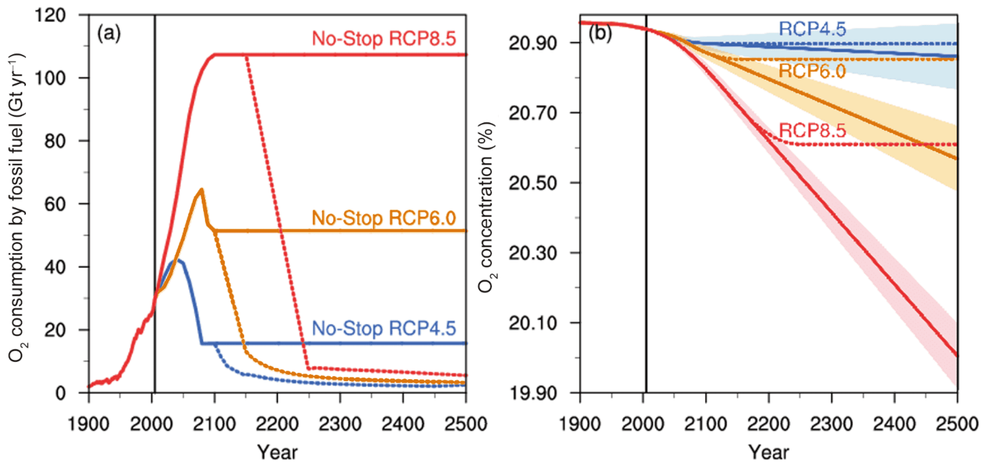

Figure 6 O_2 consumption by fossil fuel in different scenarios (a) and projections of future O_2 concentrations (b). The shading denotes the 95% confidence interval.

would the long-term evolution of the oxygen cycle reach a "tipping point" that can stimulate a cascade of abrupt environmental changes to which the biotic system may not be able to adapt? Knowledge of these processes is essential not only for understanding the history of the Earth system but also for guiding the future of human beings. The Earth system is a highly nonlinear and strongly coupled system in which a minor perturbation can have the potential to cause a series of dramatic changes. Although exaggerating the sensitivity of the initial conditions to the system is not appropriate, the objective existence of nonlinear processes and their complex relations cannot be ignored. To address the abovementioned questions, it is a top priority to connect the short-term and long-term oxygen cycles under a comparable timescale rather than separating them. Furthermore, effective multidisciplinary cooperation among the subdisciplines of Earth sciences (geology, atmospheric sciences, paleobiology, etc.), psychological sciences, and social sciences should be promoted to reveal the hidden mechanisms that control the trajectory of the Earth system and how the trajectory may influence the future of human beings.

Aside from the extensive multidiscipline cooperation in research on the global oxygen cycle, collaborative human action is required to reverse the declining O_2 level before it decreases to a health-threatening level. In Biosphere 2 (an artificial matter-sealed habitat), the sharp O_2 decrease from approximately 21% to 14% in the first 16 months, which was enough to cause health problems, was caused by the imbalance between photosynthesis and respiration; notably, the rate of photosynthesis failed to balance the rate of respiration of organic matter (specifically, the microbial oxidation of organic matter in the soil) (Severinghaus et al., 1994). In a natural environment, human perturbations in the production and consumption of oxygen also have the potential to generate a detectable shift in atmospheric O_2. Thus, the case of Biosphere 2 illustrates that sustaining O_2 levels requires the preservation and promotion of natural O_2 sources as well as the reduction and limitation of anthropogenic O_2 sinks.

Specifically, multiple measures should be implemented to preserve and promote local ecological functions, with principal efforts focused on densely populated urban areas and arid or semiarid regions at high risk of desertification. The common denominators of these areas include sparse vegetation and low biodiversity and therefore a limited ability to capture CO_2 and emit O_2 and a low capacity to reserve and recharge groundwater flow and surface runoff. Increasing vegetation cover and vegetation diversity (in other words, promoting O_2 production) are widely considered an effective measure to avoid soil erosion and restore local ecological services. In urban regions, substantial O_2 production is often cited as a significant benefit of urban forests (Nowak et al., 2007), and the associated byproducts of urban tree management include mitigating urban heat islands, removing air pollutants, carbon sequestration, etc. For regions at high risk of desertification (usually on the edge of desert and dryland areas with almost no ability to produce O_2), large-scale afforestation programs have been conducted to prevent expansion. In China, the Green Great Wall, which was designed to mitigate desertification and expand forests, although disputed, has achieved overall success in past decades (Chen et al., 2019). Recently, the Great Green Wall for the Sahara and the Sahel Initiative have also been proposed as ambitious afforestation programs to enhance ecological resilience (Goffner et al., 2019).

It is also essential to reduce O_2 consumption associated with human activities. The largest sink of atmospheric O_2, as well as the largest source of atmospheric CO_2, is the burning of fossil fuels in the energy sector (Huang et al., 2018; Liu et al., 2020). Therefore, priority should be given to research on and the development of renewable fuels, including carbon-neutral biofuels (with no effect on CO_2 and other GHGs and carbon-negative biofuels (with a net reduction in GHGs) that do not reduce the atmospheric O_2 content. Technical support from developed regions should be offered to other regions to reduce inequalities among and within countries so that effective pollution controls and energy-saving technology can be internationally applied.

We take O_2 for granted because it is just there and we breathe it all the time, yet it took billions of years before there was enough of it to keep animals like us alive (Zimmer, 2013). The future of Earth, the only known habitable planet in the universe (Hu et al., 2011; Hu and Ding, 2011), depends on the actions we take in subsequent decades. If the current trajectories of the biodiversity loss and O_2 decline are allowed to continue, a catastrophic consequence that is essentially irreversible and almost permanent on the timescale of human beings (Ceballos et al., 2015), may occur because it may take millions of years to rehabilitate the Earth, which is too long for humans to wait.

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