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Review

A Five-stage Evolution of Earth's Phosphorus Cycle

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Abstract: Phosphorus (P) is a key biological nutrient and probably the ultimate limiter of marine productivity during Earth history. In recent years, a wealth of new knowledge has revolutionized our understanding of the global P cycle, yet its long-term evolution remains incompletely documented. In this paper, we review the effects of three major controlling factors on the long-term evolution of the global P cycle, i.e., tectonics, marine redox conditions, and bio-evolution, on the basis of which a five-stage model is proposed: Stage I (>~2.4 Ga), tectonic-lithogenic-controlled P cycling; Stage II (~2.4 Ga to 635 Ma), low-efficiency biotic P cycling; Stage III (~635 Ma to 380 Ma), transitional biotic P cycling; Stage IV (~380 Ma to near-modern), high-efficiency biotic P cycling; and Stage V (Anthropocene), human-influenced P cycling. This model implies that the earlier-proposed Ediacaran reorganization of the marine P cycle may represent only the start of a ~250-Myr -long transition of the Earth's P cycle (Stage III) between the low-efficiency biotic mode of the Proterozoic (Stage II) and the high-efficiency biotic mode of the Phanerozoic (Stage IV). The development of biologically-driven, high-efficiency P cycling may have been a key factor for the increasing frequency and volume of phosphorite deposits since the late Neoproterozoic.

Key words: tectonics, marine redox, life evolution, phosphorite, Ediacaran, Anthropocene

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1 Introduction

Phosphorus (P) is an essential macronutrient required by all organisms for generation of DNA, membrane lipids, and the compounds that shuttle energy in cells (Westheimer, 1987; Bowler et al., 2010). Therefore, P availability determines the population dynamics and overall biological productivity of ecological systems such as oceans, lakes, and rainforests (Lomas et al., 2014; Cunha et al., 2022; Wu et al., 2022), thus affecting biodiversity, nutrient cycling, and climate (Elser, 2012; Peñuelas and Sardans, 2022; Wu et al., 2022). P is also generally considered to be the ultimate limiting nutrient for marine primary productivity on geological timescales (Tyrrell, 1999), and the evolution of the P cycle may have played a critical role in enabling Earth's development of a persistently oxygenated atmosphere (Papineau et al., 2013; Alcott et al., 2022; Dodd et al., 2023).

In recent years, a wealth of new knowledge has revolutionized our understanding of the modern and ancient global P cycle. Application of modern tools, particularly sensitive geochemical techniques and computer quantitative models, has illuminated a complex, dynamic, microbially-mediated modern P cycle that is intimately integrated with marine and terrestrial ecosystems as well as the climate system (Ruttenberg, 2014; Duhamel et al., 2021; Inomura et al., 2022; Tanioka et al., 2022). In contrast, Precambrian oceans potentially had a smaller P reservoir (Reinhard et al., 2017; Laakso et al., 2020; Dodd et al., 2023; Walton et al., 2023a) that was controlled mainly by external factors such as continental weathering (Dodd et al., 2023), and the Archean P cycle may have been simpler and less efficient than its modern counterpart (Hao et al., 2020a, b; Walton et al., 2023b). A recent hypothesis proposed that a "fundamental shift" or "reorganization" of the marine P cycle occurred during the Late Neoproterozoic (Kipp and Stüeken, 2017; Reinhard et al., 2017; Laakso et al., 2020), coincident with major changes in atmospheric-oceanic redox conditions and bio-evolutionary events. Despite these advances, the pattern of

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the long-term evolution of Earth's P cycle is still unclear, impeding an understanding of the coevolution of the P cycle with life and environments on Earth.

In this paper, we consider three important controlling factors on the long-term evolution of Earth's P cycle, i.e., tectonics, marine redox conditions, and bio-evolution. Our analysis leads us to propose a five-stage model of evolution of the P cycle through Earth history. The stages in this evolutionary model can be related to major geological events, including changes in plate-tectonic style, the Great Oxidation Event (GOE), and bioevolutionary events such as the emergence of eukaryotes, plant terrestrialization, and human activity. In particular, this evolutionary model provides new insight into the significance of the late Neoproterozoic "reorganization" of the marine P cycle and the increasing frequency of phosphorite deposits since that time.

2 Major Factors Controlling P Cycling in Earth History

Many influences on the Earth's P cycle have been identified, including the intensities of subaerial (Reinhard et al., 2017; Ma et al., 2022a) and submarine weathering (Filippelli, 2022; Sharoni and Halevy, 2023), igneous activity (Horton, 2015; Cox et al., 2018) and orogenic events (Ma et al., 2022a; Nance, 2022), the solubility of P minerals under variable redox conditions (Syverson et al., 2021; Brady et al., 2022) and P bioavailability (Cole et al., 2022; Walton et al., 2023b), and uptake and release of P by (micro)organisms (Lumas et al., 2021; Lambers, 2022). These influences operate within three nested P subcycles, each with a unique set of transformations, that represent a range of temporal and spatial scales (Fig. 1): (1) the tectonic-lithogenic P cycle, (2) the oceanic P cycle, and (3) the marine biotic P cycle. Here, we examine how the influences of tectonics, marine redox conditions, and life evolution have substantially influenced the long-term evolution of the Earth's P cycle.

2.1 Tectonics

P cycling on a global scale between the surface and deep Earth is likely mediated by tectonics (Ma et al., 2022a, b), including the transport of P from the Earth's interior to its surface through volcanic arc, ocean ridge, and mantle plume emissions, and its return to the interior through plate subduction (Fig. 2a). Due to the siderophilic affinity of phosphorus, over 80% of Earth's total P inventory resides in the iron-rich core in the form of reduced (metal-bound) P (Righter et al., 2010, 2018). Of phosphorus in the bulk-silicate Earth (BSE), the mantle contains the largest share, although P concentrations are higher in oceanic and continental crust, which together account for >30% of BSE phosphorus (Rudnick and Gao, 2014; Cox et al., 2018; Walton et al., 2021). In continental crust, the most important P-hosting phase is apatite ($Ca_5[PO_4]_3F$), which accounts for >95% of all continental crustal P, thus providing a P-rich weatherable crustal source. Crustal rocks together with marine sediments

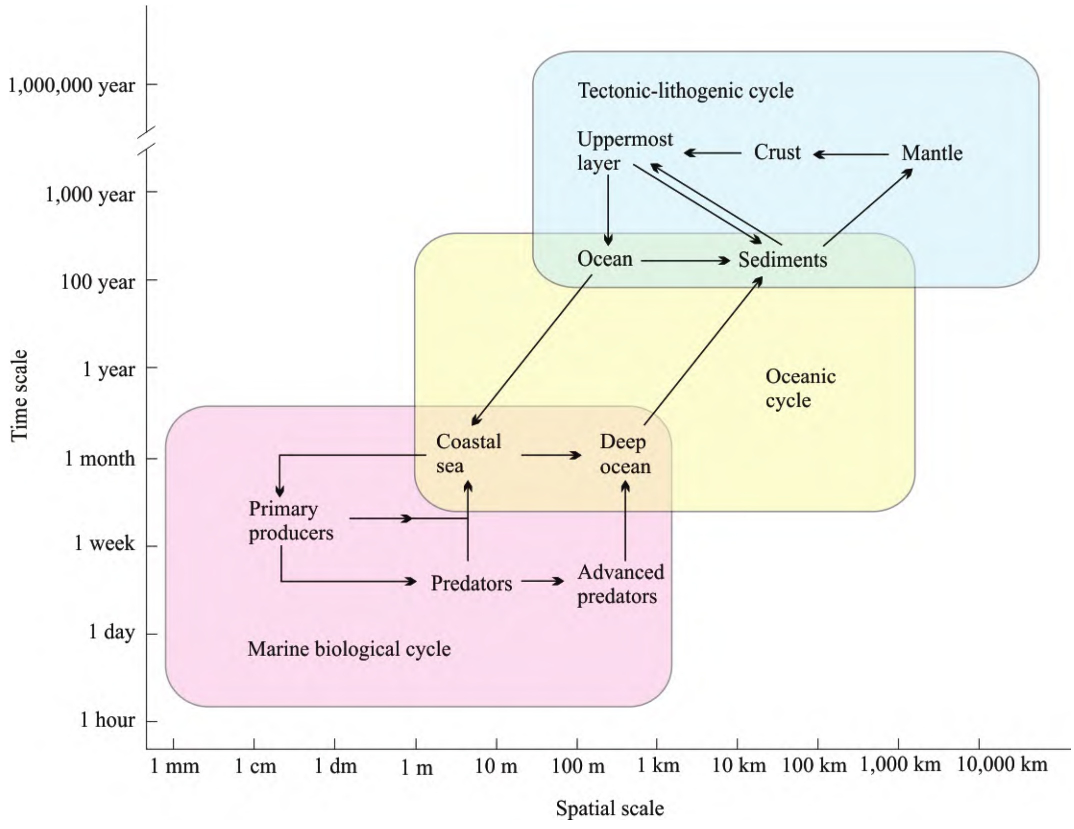

Fig. 1. Schematic diagram of the three subcycles of the global phosphorus (P) cycle, representing a range of temporal and spatial scales, modified from Karl (2014).

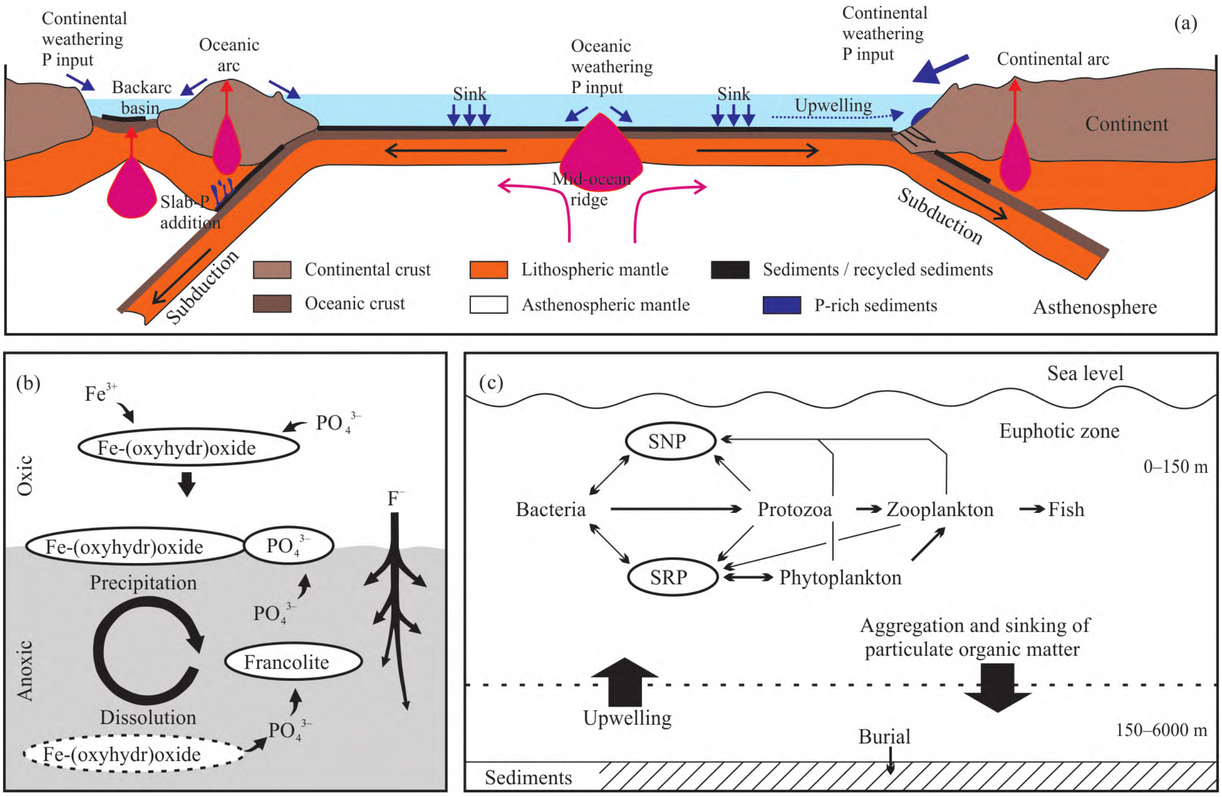

Fig. 2. Phosphorus (P) cycling processes related to (a) tectonic, (b) redox, and (c) biotic influences on the global P cycle.
The long-term P cycle between Earth's interior and exterior is modified from Ma et al. (2022) and Zheng (2023); precipitation and dissolution of francolite near the redox boundary are based on Nelson et al. (2010), and biologically-driven marine P cycling is modified from Benitez-Nelson (2000). SNP = soluble non-reactive phosphorus; SRP = soluble reactive phosphorus.

make up the largest P reservoir on surface Earth (Fig. 3a).

The global-scale P cycle is driven by plate tectonics, however, the definition and timing of global plate tectonic onset are still debated (Windley et al., 2021; Ren et al., 2022). There is much discussion over when it may have become the dominant regime on Earth, with conclusions ranging from the early Hadean (before ~4.0 Ga) to 700 Ma. It is generally suggested that around ~3.0 Ga the global tectonic attributes may have changed (Dhuime et al., 2012, 2015, 2017; Palin and Santosh, 2021; Windley et al., 2021; Fig. 4a). Before ~3.0 Ga, it is characterized by relatively high net rates of continental growth (Fig. 4a), forming mafic, dense, relatively thin (<20 km) crust. After ~3.0 Ga, the continental crust gradually became more intermediate in composition, buoyant and thicker, accompanied by increasing rates of crustal reworking and increasing input of sediment to the ocean and its final subduction into the deep Earth (Fig. 4b). Thus, the onset of global rapid cratonization and large-scale subduction at ~3.0 Ga may have established the long-term tectonic-lithogenic P cycle between the interior and exterior Earth which continues throughout subsequent Earth history to this day.

Weathering is the key step and the only pathway in releasing P locked up in insoluble P-hosting minerals into the biosphere to form bioavailable dissolved P in both marine and terrestrial ecosystems (Ruttenberg, 2014; Cox et al., 2018; Dzombak and Sheldon, 2020; Syverson et al., 2021; Walton et al., 2021, 2023a, b; Dodd et al., 2023), i.e., physical and chemical interactions, sometimes biologically involved, between the weatherable uppermost layer of crust and the surface environment. On this assumption, the P concentration of weatherable crust and weathering intensity dominate the P flux of the source, thus affecting the marine P reservoir (Reinhard et al., 2017; Cox et al., 2018; Peters et al., 2021; Walton et al., 2023a). The supercontinent cycle, a consequence of plate tectonics, exhibits a close relationship to the igneous P_2O_5 content curve (red curve in Fig. 4b). According to statistics of Cox et al. (2018), the igneous P_2O_5 content reached about 0.5 wt% during the assembly of Rodinia, and over 0.3 wt% during the breakup of Rodinia and assembly of Gondwana. It may have been due to variation in the volumes of different igneous rock types (mafic, intermediate, felsic) exposed during each supercontinent cycle (Cox et al., 2018). However, the simulated long-term P weathering flux (black curve in Fig. 4b) by Walton et al. (2023a) shows no obvious relationship with the supercontinent cycle but may have been affected more by crustal P content (blue curve in Fig. 4b), which was controlled mainly by P-rich sedimentary rock volume (Walton et al., 2023a).

2.2 Marine redox conditions

The marine redox state is a key controlling factor of phosphate bioavailability, due to the differing geochemical behavior of P under a range of redox conditions (Fig. 2b). Generally, under oxygenated bottom waters, P becomes trapped in the sediment by a variety of pathways, including uptake by Fe-(oxyhydr)oxides, biological sequestration of polyphosphates, or precipitation of authigenic phosphate minerals (e.g., francolite; Algeo and Ingall, 2007; Filippelli, 2008; Ruttenberg, 2014), preventing the return of P to the oceans. Under anoxic bottom waters, a proportion of the P can diffuse out of sediments due to the reduction of Fe-(oxyhydr)oxides (Nelson et al., 2010), thus are particularly conducive to sedimentary P release and limiting P sequestration by iron minerals (Filippelli, 2008; Ruttenberg, 2014). However, studies also suggest that under ferruginous waters, P can be captured by Fe(II)-phosphate precipitation as vivianite (Derry, 2015; Hao et al., 2020b) or reduction to Fe(II) and formation of ferric phosphites (Herschy et al., 2018). Experiments and models have shown that Fe^{2+} can significantly increase the solubility of all phosphate minerals in anoxic systems (Brady et al., 2022), which may have set the stage for development of a phosphate-rich ferruginous ocean.

Oxygenation of Earth's surface environment is thought to have occurred mainly in three broad stages (Fig. 4c). The Great Oxygenation Event (GOE) at ~2.4 Ga saw atmospheric O_2 rise to more than 10^{-5} of the present atmospheric level (PAL) and likely sustained at levels of ~10^{-3} to 10^{-1} PAL in the following ~1 billion years (Farquhar et al., 2000; Planavsky et al., 2014), which may have resulted in partial oxygenation of the surface ocean throughout the Proterozoic (Hardisty et al., 2011). The deeper waters, however, remained dominantly anoxic and ferruginous until the late Neoproterozoic (Canfield et al., 2008; Poulton and Canfield, 2011). The Neoproterozoic Oxygenation Event (NOE) occurred between ~720 and ~510 Ma and is believed to have resulted in atmospheric O_2 levels of >10%–25% PAL (Och and Shields-Zhou, 2012; Lyons et al., 2014), as well as the first oxygenation of the deep ocean (Canfield et al., 2007; Och and Shields-Zhou, 2012). However, there was considerable variability in the temporal and spatial extent of oxygenation at this time, including the possibility of pulsed deep-oceanic oxygenation events (Sahoo et al., 2012, 2016), or dynamic marine shelf oxygenation (Li et al., 2018, 2020). Periodic deep-water anoxia may have remained frequent up until the Paleozoic Oxygenation Event (POE) around 450 to 400 Ma, which appears to have elevated atmospheric O_2 to present-day levels and established a dominantly oxygenated deep ocean (Krause et al., 2018; Stolper and Keller, 2018). Considering the different behavior of P under different redox conditions, marine redox can possibly determine the size of P sinks and P availability, and thus may have substantially affected the marine P cycle pattern in Earth history.

2.3 Bio-evolution

In the sea, microorganisms are primarily responsible for P assimilation and remineralization (Fig. 2c), including P reduction-oxidation bioenergetic processes discovered in past years, which add new complexity to the marine microbial P cycle (Benitez-Nelson, 2000; Ruttenberg, 2014; Karl, 2014). The key factor is the different residence times of P in organisms and their living environments (Fig. 1). The residence time of P in the deep ocean can be thousands of years, but only weeks (even hours) in oceanic biota (Ruttenberg, 2014; Karl, 2014). Efficient uptake and fast release of P by marine organisms can accelerate the transfer of dissolved P from the watermass to the sediment (Benitez-Nelson, 2000), leading to P-deleted surface waters (Fig. 3b) and a variable carbon-nitrogen-phosphorus (C:N:P) stoichiometry in marine plankton (Duhamel et al., 2021; Lomas et al., 2021; Inomura et al., 2022; Tanioka et al., 2022). Therefore, variation in the abundances of taxonomic groups with different phosphorus storage capacities can generate regional variation in P concentrations within the ocean (Fig. 3b; Sharoni and Halevy, 2023; Duhamel et al., 2021; Inomura et al., 2022). In terrestrial ecosystems, P exchange between plants and soils also plays a key role in the modern biotic P cycle (Ruttenberg, 2014; Du et al., 2020). The residence time of P in land biota (13–48 years) is much shorter than in the soil (425–2311 years) and terrestrial sediments (4–20 Myr), greatly enhancing the efficiency of the terrestrial P cycle (Fig. 3a), thus providing more net available P to the ocean at short timescales (Ruttenberg, 2014). Therefore, tracing the evolutionary development of marine eukaryote and land plant ecosystems is crucial to understanding patterns of P cycling through Earth history.

Secular variations in P source and sink fluxes can be reconstructed by various methods, allowing testing of the effects of tectonic and marine redox influences, but changes in the efficiency of biotic P cycling at geological timescales are difficult to quantify. Considering that efficient biotic cycling by organisms can result in rapid transfer of large amounts of P to the sediment, this process has the potential to generate P-rich sediments such as phosphorites. Significantly, marine sedimentary phosphorite deposits have become more frequent in the geologic record since the Ediacaran (Fig. 4b; Cook and Shergold, 1984; Drummond et al., 2015; Reinhard et al., 2017; Jiao et al., 2022), a time interval corresponding to the emergence and rapid radiation of metazoans and plants (Fig. 4d–e). Despite the poorly understood connection between global phosphogenesis episodes and the evolution of life, the abundance of marine phosphorite deposits has the potential to serve as a proxy for the efficiency of biotic P cycling.

3 A Five-stage Model of the Evolution of Earth's P Cycle

Based on our discussion in Section 2, here we propose a five-stage evolution model for the Earth's P cycle (Fig. 5): Stage I, tectonic-lithogenic-controlled P cycling (>~2.4 Ga); Stage II, low-efficiency biotic P cycling (~2.4 Ga to 635 Ma); Stage III, transitional biotic P cycling (~635 Ma to 380 Ma); Stage IV, high-efficiency biotic P cycling (~380 Ma to near-modern); and Stage V, human-influenced P cycling (Anthropocene). All three major factors outlined above for the long-term evolution of the Earth's P cycle, tectonics, marine redox conditions, and bio-evolution, may have played roles during each stage but with varying degrees of influence.

3.1 Stage I: Tectonic-lithogenic-controlled P cycling (>~2.4 Ga)

Stage I, representing a tectonic-lithogenic-controlled P cycle (Fig. 5a), spans early Earth history up to the Early

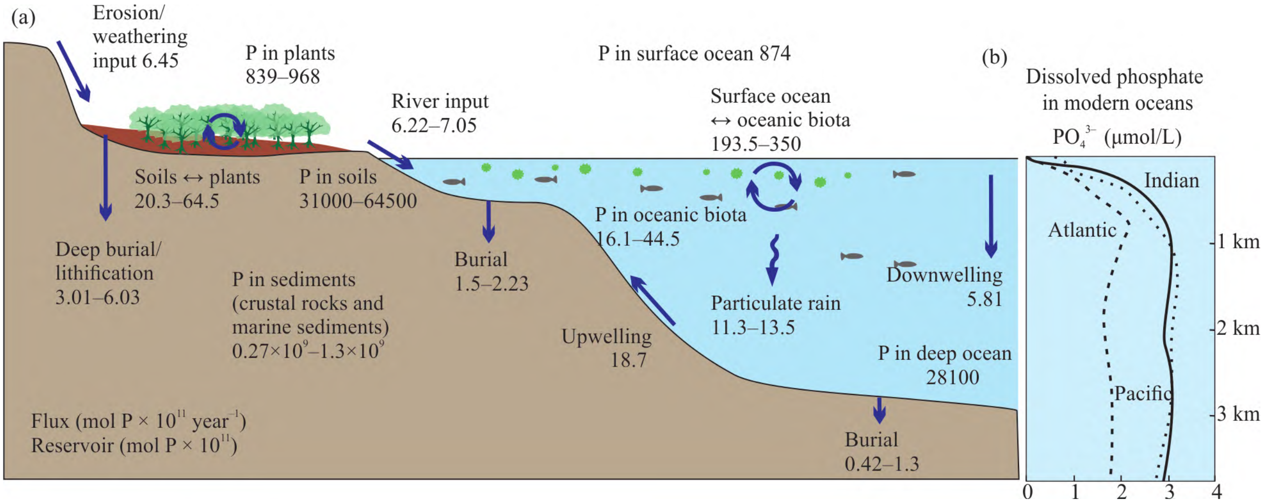

Fig. 3. The modern P cycle (a) and P depth gradients (b) in modern oceans.
Flux data (units of 10^{11} mol/yr) and reservoir data (units of 10^{11} mol) are from Ruttenberg (2014).

Paleoproterozoic (>~2.4 Ga). The early Earth was tectonically characterized by mass formation of a thin (<20 km) bimodal TTG (tonalite-trondhjemite-granodiorite)-greenstone crust before the onset of rapid cratonization and large-scale subduction. After that, the accretion of multiple thick cratons and resulting supercontinent cycles have been present throughout Earth's history since then. This transition is thought to occur at ~3.0 Ga (Dhuime et al., 2012, 2015, 2017), or during a longer transitional period (3.2 to 2.5 Ga, Cawood et al., 2018; Cawood, 2020; Windley et al., 2021). The marine redox and ecosystem may have been quite simple in Stage I, marked by uniformly ferruginous conditions (Poulton and Canfield, 2011) and a possibly cyanobacterially dominated biosphere (Sánchez-Baracaldo et al., 2022).

Anoxic seafloor alteration may have enhanced P input fluxes (Syverson et al., 2021; Brady et al., 2022) and served as the principal source of oceanic P during this stage (Walton et al., 2023a). Despite the potential gradual increase of continental P weathering due to the increasing rates of crustal reworking after 3.0 Ga, the total P weathering flux from continental and seafloor weathering is speculated to have remained stable (Walton et al., 2023a; Fig. 4b). Meteorite impacts during this time may also have provided P to the biosphere through weathering and photochemical reactions (Ritson et al., 2020; Farr et al., 2023; Walton et al., 2023b), although whether the P flux of the Late Heavy Bombardment was sufficiently great to affect the global P cycle is uncertain.

The influence of marine redox conditions on P sinks in this stage is uncertain. Considering experimental evidence for enhanced P input fluxes from anoxic seafloor alteration (Syverson et al., 2021), it is suggested that phosphate-rich oceans may have persisted through this period (Brady et al., 2022). However, it is also thought that Fe(II)-phosphate precipitation (vivianite) and reduction by Fe(II) (forming ferric phosphite) from ferruginous oceans could have been a major P sink and thus limit the P availability on early Earth (Herschy et al., 2018; Hao et al., 2020b; Walton et al., 2023b). Whichever scenario is correct, the role of redox conditions in P cycling during Stage I is not important because of the nearly invariant ferruginous conditions in early Earth oceans (Poulton and Canfield, 2011). The contribution of organisms to both P sources and sinks was probably limited due to the small size of the biosphere during this stage. In summary, Stage I was dominantly characterized by a tectonic-lithogenic-controlled P cycle, setting the stage for later development of a biotically modulated P cycle.

3.2 Stage II: Low-efficiency biotic P cycling (~2.4 Ga to 635 Ma)

Stage II, representing a low-efficiency biotic P cycle (Fig. 5b), spans most of the Proterozoic Eon, extended from the GOE to the Ediacaran (i.e., ~2.4 Ga to 635 Ma). This stage witnessed the breakup-convergence cycles of the Columbia and Rodina supercontinents (Palin and Santosh, 2021; Fig. 4a). Due to enhanced oxygenation of Earth's surface after the GOE, the surface ocean became at least partially oxic, although the deep ocean remained ferruginous (Hardisty et al., 2011; Poulton and Canfield, 2011). Sulfate weathering may have triggered development of dynamic euxinic wedges on continental shelves at this time, altering the previously nearly stable redox conditions of the global ocean (Hardisty et al., 2011; Poulton and Canfield, 2011). Major cyanobacterial clades radiated into many diverse forms after the GOE (Sánchez-Baracaldo et al., 2022), building stromatolites in shallow-water areas (Papineau, 2010).

In this stage, the most important P source was continental weathering, which was influenced by collisional orogeny during the process of supercontinent assembly and by magmatic activity during supercontinent breakup (Fig. 4d; Cox et al., 2018; Williams et al., 2019; Peters et al., 2021; Ma et al., 2022a). P released from oceanic organisms might have been a minor secondary source (Fig. 5b). The major P sinks in this stage were sediments deposited near the redox boundary between oxic and anoxic watermasses, often in shallow-water coastal environments (Nelson et al., 2010), and

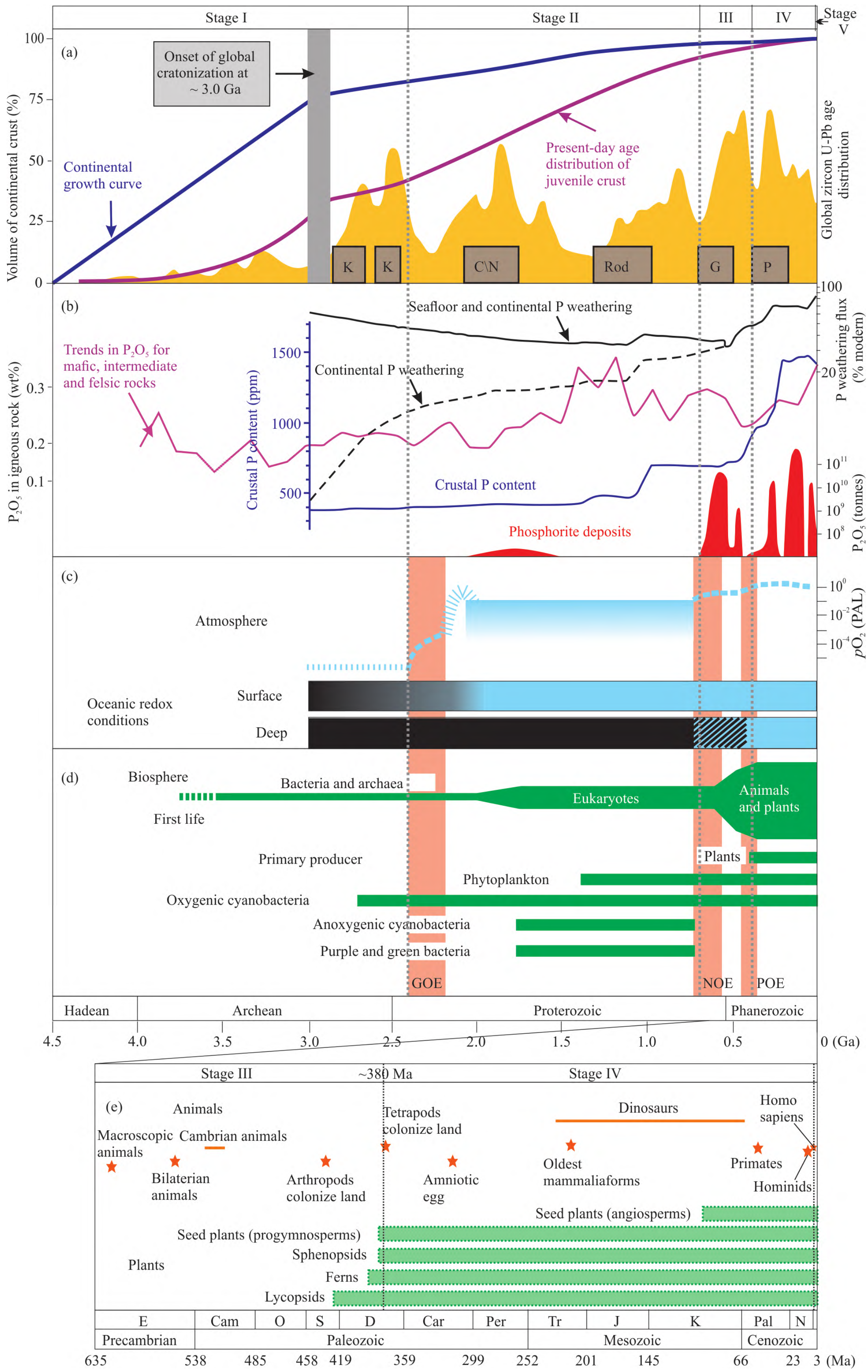

Fig. 4. Co-evolutionary relationships between the phosphorus (P) cycle and global tectonics, P reservoir masses and

fluxes, atmospheric and marine redox conditions, and biotic evolution.

(a) Tectonic influences; continental crustal growth curves from Dhuime et al. (2017), supercontinent cycle from Palin and Santosh (2021), where brown boxes denote supercontinents: P = Pangea; G = Gondwana; Rod = Rodinia; C/N = Columbia/Nuna; K = Kenorland. (b) Secular changes in P reservoirs; igneous P content from Cox et al. (2018), crustal P content and weathering from Walton et al. (2023a), and the temporal distribution of phosphorite deposits from Drummond et al. (2015). (c) Redox history of the Earth, modified from Lyons et al. (2014). (e) Biotic ranges from Cawood (2020), with primary producer data from Pufahl and Hiatt (2012). (e) Biotic ranges and events for the Ediacaran-Phanerozoic, with animal data from Knoll and Nowak (2017) and plant data from Boyce and Lee (2017). GOE = Great Oxygenation Event; NOE = Neoproterozoic Oxygenation Event; POE = Paleozoic Oxygenation Event.

precipitation of P-rich minerals or incorporation of P into other minerals, such as shallow-water carbonates (Dodd et al., 2021) and phosphatic stromatolites (Papineau, 2010) and shales in the deep ocean (Reinhard et al., 2017).

In the oceans at this time, oxic conditions and biological activity were mainly restricted to shallow-water areas (Fig. 5b). Laakso and Schrag (2020) argued that P was delivered mainly by rivers, which may have led to a concentration of marine life in coastal areas. Reinhard et al. (2017) and Laakso et al. (2020) also inferred that the marine P reservoir was small at this time based on relatively low P concentrations in marine shales. Under such conditions, according to quantitative modeling by Dodd et al. (2023), increasing oceanic sulfate from weathering may have increased oceanic P and atmospheric O_2, leading to a contraction of oceanic anoxia (i.e., an oceanic oxygenation event) and a corresponding increase in sedimentary P burial in shelf areas. Based on these studies, most P cycling would have occurred in coastal settings to which P was delivered by weathering fluxes, thus concentrating the biosphere in shallow-water areas during this stage. Due to the simplicity of prokaryotic ecosystems (Sánchez-Baracaldo et al., 2022), P cycling in shallow-water areas would have operated slowly during Stage II, and, thus, P-rich deposits would have formed only intermittently (Papineau, 2010). In summary, Stage II is characterized by low-efficiency biotic cycling of P, marked by a small oceanic P reservoir, slow P cycling, and active areas limited mainly to coastal environments to which continental weathering delivered P (Fig. 5b).

3.3 Stage III: Transitional biotic P cycling (~635 Ma to 380 Ma)

Stage III, which represents a transitional interval from the low-efficiency biotic P cycle of Stage II to the high-efficiency biotic P cycle of Stage IV, extended from ~635 Ma to 380 Ma (Fig. 5c–d; also see Section 3.4). Changes in P cycling during Stage III were driven by several developments. First, initial oxygenation of the deep ocean to have occurred at the beginning of this stage (Sahoo et al., 2012), and to have gone more-or-less to completion by the end of the stage (Krause et al., 2018). Second, the macrobenthic ecosystem is thought to have become established around the beginning of this stage (Yuan et al., 2011, Brocks et al., 2017; Yang et al., 2022), and other major events in biological evolution such as the Cambrian Explosion and Ordovician radiation also occurred early in this stage (Knoll and Nowak, 2017). Third, a recent long-term simulation identified a threefold increase in average crustal P concentrations during this period, suggesting that preferential biomass burial on shelves acted to progressively concentrate P in the continental crust (Walton et al., 2023a). Fourth, global phosphogenesis episodes became increasingly common during this period (Pufahl and Hiatt, 2012; Jiao et al., 2022), implying an increase in the efficiency of oceanic P cycling.

The major P sources and sinks were the same as in Stage II, but the influence of marine redox conditions and biological activities gradually came to dominate during Stage III. As discussed in Section 2, vivianite and ferric phosphite may have been major P sinks under anoxic ferruginous conditions. Therefore, gradual oceanic oxygenation during Stage III decreased the size of marine P sinks, and the flourishing of the oceanic biota increased the rate of biotic P cycling, leading to more frequent global phosphogenesis episodes (Fig. 4b). Increases of P concentrations in coastal sediments (i.e., phosphorite deposits) in turn increased the P source flux through weathering of exposed P-rich deposits (Walton et al., 2023a). Another key event was the terrestrialization of plants toward the end of Stage III, which greatly increased the efficiency of terrestrial P cycling. Vascular land plants first recorded appeared during the Silurian, followed by a major radiation during the Devonian encompassing all of the major vascular plant lineages (Boyce and Lee, 2017; Fig. 4e). In the Early Devonian, land plants were no more than a few centimeters in axial diameter and under a meter in height, and they lacked leaves, wood, and deep root systems (Boyce, 2008). Trees and forests were present in the Middle Devonian but increased greatly in abundance during the Late Devonian (~380 Ma; Algeo and Scheckler, 1998, 2010), marking the point in time when land plants began to substantially alter the surface roughness of continents (Boyce and Lee, 2017). This represents the establishment of modern-like terrestrial plant ecosystems, which may have profoundly changed continental weathering regimes. In summary, Stage III was a transitional stage that witnessed a shift from low-efficiency biotic P cycling of the Proterozoic to high-efficiency biotic P cycling of the Phanerozoic.

3.4 Stage IV: High-efficiency biotic P cycling (~ 380 Ma to near-modern)

Stage IV, representing the establishment of a high-efficiency biotic P cycle, spans the Middle Phanerozoic (~380 Ma) to the near-modern. This stage broadly shares boundary conditions (i.e., related to atmospheric composition, marine redox state, land plant ecosystem, and a marine ecosystem dominated by complex eukaryotes; Fig. 5d) with the modern era in which anthropogenic influences have become dominant (Stage V; see Section 3.5).

In this stage, the initial P source is still continental weathering, and the final P sink is still the sediments. Organisms can also act as P sources and sinks. Although its P flux is much smaller than that of weathering and deposition (Ruttenberg, 2014), the rate of P cycling in

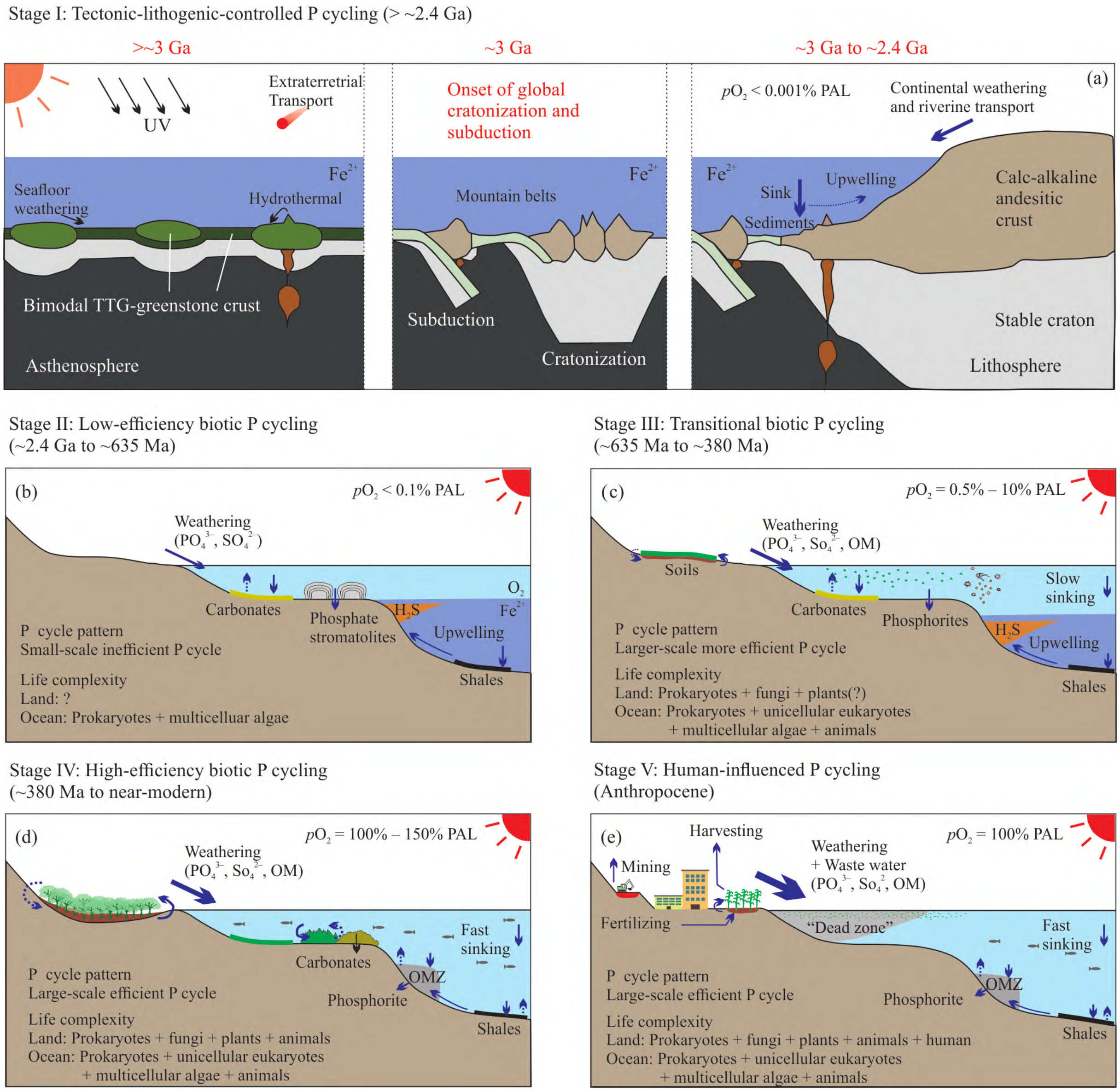

Fig. 5. Five-stage evolution of Earth's P cycle.
(a) Stage I (>~2.4 Ga), tectonic-lithogenic-controlled P cycling, with only weak biological and redox influence; (b) Stage II (~2.4 Ga to 635 Ma), low-efficiency biotic P cycling, which occurred mainly in coastal seas and was controlled by external stimuli; (c) Stage III (~635 Ma to 380 Ma), transitional biotic P cycling, characterized by a gradual shift from the Precambrian mode (Stage II) to the Phanerozoic mode (Stage IV); (d) Stage IV (~380 Ma to near-modern), high-efficiency biotic P cycling. (e) Stage V (Anthropocene), human-influenced P cycling. OMZ = Oxygen Minimum Zone; OM = Organic Matter. See text for details.

both terrestrial and oceanic systems was greatly accelerated by the involvement of biological activities, resulting in a much larger P reservoir (Benitez-Nelson, 2000; Karl, 2014). The fully oxidized ocean in Stage IV (Fig. 4c) greatly reduced the P sinks by ferruginous waters and also increased the marine P reservoir (Laakso et al., 2020). At the same time, a fully oxidized ocean provided a wider living environment for complex eukaryotic life, thus extending the P cycling from the Precambrian coastal environments into deep ocean (Nelson et al., 2010; Ruttenberg, 2014). In addition, we note that considering the much shorter residence time of P in organisms, especially in ocean biota (Ruttenberg, 2014; Karl, 2014), long-term geological activities are difficult to directly affect the fast biotic P cycling in ecosystems although during the mass extinctions when previous ecosystems broke, the long-term regulation of tectonic and marine redox on Earth's P cycle could be re-highlighted (Schobben et al., 2020; Reershemius and Planavsky, 2021; Ma et al., 2022b).

High-efficiency biotic cycling of P is the key feature of Stage IV (Fig. 5d). Fast uptake of P by tall trees from soil and land increases the net weathering flux of P. Such bioavailable P is used by oceanic phytoplankton and rapidly transferred to the deep ocean in the form of necromass. Upwelling returns a fraction of this organic P to shelf and upper slope settings where it can accumulate as phosphorite deposits in oxygen minimum zones

(OMZ). Uplift and weathering of such deposits allow a fraction to be recycled back to land and taken up again by terrestrial plants. While P reservoirs may not have changed much in size, the flux of P was significantly accelerated, except, perhaps, for slowing during major biocrises when ecosystem collapse slowed the rate of P cycling.

3.5 Stage V: Human-influenced P cycling (Anthropocene)

In Stage V, the P cycle is affected by human activities compared to Stage IV (Fig. 5e). Human-induced enhancement of the global P cycling via mining, and agriculture will likely influence the pace of P-cycle dynamics, especially in lake and coastal marine habitats (Vaccari, 2009; Elser and Bennett, 2011; Elser, 2012; Karl 2014; Waston, 2017; Duhamel et al., 2021; Yan et al., 2021). Crop harvesting removes P from the land, and meanwhile limits our ability to return nutrients to the land (Vaccari, 2009; Elser and Bennett, 2011; Elser, 2012). At the same time, too much P from eroded soil, mining and human waste ends up in lakes and oceans, resulting in uncontrolled blooms of cyanobacteria (also known as blue -green algae) and algae. Once these primary producers die and fall to the bottom, their decay starves other organisms of oxygen, creating "dead zones" (Vaccari, 2009; Elser and Bennett, 2011; Duhamel et al., 2021). Similar human effects also produce a huge effect on the C and N cycles (Sutton et al., 2011; Liu and Zhang, 2023), contributing hugely to the "broken biogeochemical cycle" of our modern world (Elser and Bennett, 2011).

4 Implications

4.1 Ediacaran reorganization of the P cycle

Although an Ediacaran P cycle transition was proposed in recent studies (Reinhard et al., 2017; Kipp and Stüeken, 2017; Laakso and Schrag, 2020), it has long been recognized that, due to the widespread occurrence of phosphorite deposits, the P cycle in this period may have been different from that of earlier periods. Such a "reorganization" or "fundamental shift" is inferred from the change of P sources and/or sinks, which can be tracked by methods such as P/Fe ratios in iron formations (Bjerrum and Canfield, 2002; Planavsky et al., 2010), phosphorus speciation (Thompson et al., 2019; Guilbaud et al., 2020), and bulk-rock phosphorus concentrations (Reinhard et al., 2017; Laakso et al., 2020). However, a recent study of carbonate-associated phosphate (CAP) argued that the Ediacaran P cycle may have remained similar to that of earlier times (Dodd et al., 2023). A long-term simulation of crustal P concentrations and weathering fluxes also suggested that the increase of P concentrations in the uppermost crust continued to ~400 Ma (Walton et al., 2023a).

Considering the key role of biological activity in the control of the modern P cycle (Benitez-Nelson, 2000; Ruttenberg, 2014; Duhamel et al., 2021), we emphasize the effect of biotic evolution on the ancient P cycle in addition to changes in P sources and sinks. On this basis, we propose a five-stage model of P cycle evolution, in which the previously hypothesized Ediacaran reorganization of the P cycle was actually part of an extended process lasting nearly 250 million years (i.e., the Stage III from ~635 Ma to 380 Ma). This process did not go to completion until ferruginous watermasses had almost completely disappeared from the oceans, atmospheric O_2 concentrations had approached their modern levels, and plant-based ecosystems had become established on land. In this context, changes in the P cycle during the Ediacaran Period noted in earlier studies were in fact just the beginning of a long-term reorganization of Earth's P cycle. This transitional period (i.e., Stage III, ~635 Ma to 380 Ma) witnessed significant changes in several major controls on the P cycle, including gradual oxygenation of the deep ocean (Sahoo et al., 2012; Krause et al., 2018), increasing complexity of marine and terrestrial ecosystems (Yang et al., 2022; Knoll and Nowak, 2017), a threefold rise in average uppermost crustal P concentrations (Walton et al., 2023a), and a greatly increased frequency of global phosphogenesis episodes (Pufahl and Hiatt, 2012; Jiao et al., 2022). The ~250 Myr-long transition, which spanned the Ediacaran and Early Paleozoic, was characterized by enhanced P source fluxes, decreased P sink fluxes, and significant innovations in the Earth's biosphere, resulting in gradual replacement of the low-efficiency Precambrian P cycle by a high-efficiency modern-like P cycle.

4.2 Ediacaran–Phanerozoic phosphogenesis episodes

Major global phosphogenesis episodes (Fig. 4b) occurred during the Neoproterozoic–Cambrian (Cook and Shergold, 1984; Cook, 1992), the Permian–Triassic (Larina et al., 2019), the Cretaceous–Eocene, and the late Cenozoic (Schöllhorn et al., 2019). In addition, relatively smaller phosphorite deposits accumulated during other Phanerozoic periods, such as the Ordovician phosphorites of Sweden (Ilyin and Heinsalu, 1990), the Devonian phosphorites of northern Iran (Salama et al., 2018) and Brazil (Abram and Holz, 2020), and the Jurassic phosphorites of North America (Poulton and Aiken, 1989) and the Russian Platform (Kholodov and Paul, 2001). In our model, the development of phosphorite deposits is suggested to have been the result of highly efficient, rapid biologically-driven P cycling, which led to large amounts of P being transferred to the sedimentary reservoir over short periods of time. However, no obvious correspondence is observed between specific bio-evolutionary events and these phosphogenesis episodes (Fig. 4b, d), suggesting that long-term changes in the global P cycle occurred in response to myriad, mutually reinforcing biotic developments, possibly in combination with a long-term increase in biosphere mass. Therefore, the exact connection between phosphorite abundance and P cycling efficiency remains unclear, and further study of the mechanisms of phosphorite formation is needed.

5 Conclusions

Tectonics, marine redox conditions, and bio-evolution are three key influences on the modern and ancient global P cycle, which have shaped the long-term evolution of the

Earth's P cycle by influencing P sources and sinks as well as P cycle efficiency. Based on the review of the evolution of these three key factors, a five-stage model of the global P cycle evolution in Earth history is proposed: Stage I (>~2.4 Ga), tectonic-lithogenic-controlled P cycling; Stage II (~2.4 Ga to 635 Ma), low-efficiency biotic P cycle; Stage III (~635 Ma to 380 Ma), a transitional biotic P cycle; Stage IV (~380 Ma to near-modern), a high-efficiency biotic P cycle; Stage V (Anthropocene), the human-influenced P cycle. This five-stage evolution model implies that the previously proposed Ediacaran reorganization of the marine P cycle may only represent the beginning of a transition lasting ~250 Myr, representing a long-term shift of the Earth's P cycle from a low-efficiency Precambrian mode to a high-efficiency Phanerozoic mode. The high efficiency of the biologically-driven Phanerozoic-mode P cycle has likely played a key role in increasing phosphorite deposition since the late Neoproterozoic.

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