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Wetland sulfur isotope signals and dynamic isotope baselines: implications for archaeological research

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Sulfur isotopic composition ($\delta^{34}\text{S}$) is used in archaeological research to reconstruct past mobility patterns and diet using environmental baselines. Human and faunal collagen $\delta^{34}\text{S}$ is generally interpreted as reflecting environmental baselines derived from geological sulfur and marine sulfur near the coast. However, recent studies have highlighted that the $\delta^{34}\text{S}$ of bioavailable sulfur is modified in wetlands and waterlogged environments as a result of microbial sulfate reduction and sulfide oxidation. These processes are driven by fluctuating redox conditions resulting from flooding, and can significantly alter bioavailable $\delta^{34}\text{S}$ baselines in the biosphere, and subsequently in animal tissues, through the food chain. This challenges conventional approaches that assume local geology and coastal proximity alone determine bioavailable baseline $\delta^{34}\text{S}$. This study considers sulfur cycling within terrestrial ecosystems and its implications for archaeological interpretation. We explore how plant $\delta^{34}\text{S}$ is influenced by anoxic soil conditions, hydrological controls and plant waterlogging adaptations, integrating these factors into a theoretical framework and simple numerical models of plant $\delta^{34}\text{S}$ in wetland and waterlogged environments. The models simulate the effect of different hydrological regimes on plant $\delta^{34}\text{S}$ (in flow-through, standing water, drained post-flooding, and simultaneously flooded and drained landscapes). We suggest how $\delta^{34}\text{S}$ could change for crop plants grown using different past water management techniques, and discuss effects of wetland utilization and resource use on animal and human collagen $\delta^{34}\text{S}$. This study demonstrates that different systems can result in multiple “wetland” sulfur isotope signals that can deviate both positively and negatively from local baselines that are driven by geological and marine sulfur. $\delta^{34}\text{S}$ has the potential to be a useful tool for exploring ancient wetland use and water management strategies. Such strategies have long been argued to be critical to early agricultural development and the establishment of complex societies.

KEYWORDS

sulfur isotope baselines, microbial sulfate reduction, wetlands, waterlogging, plant uptake, archaeology, archaeobotany

1 Introduction

Sulfur stable isotopic composition has been used in archaeological research to investigate dietary resource use and mobility of people and animals in the past (e.g., [Czére et al., 2022](#); [Ebert et al., 2021](#); [Paladin et al., 2020](#)). Recent developments in analytical techniques for $\delta^{34}\text{S}$ have significantly reduced the amount of sample material needed for

analysis (Sayle et al., 2019). This has led to an increasingly large number of publications presenting $\delta^{34}\text{S}$ of bioarchaeological material, mostly faunal and human bone collagen, and often including complementary information from carbon, nitrogen, oxygen and strontium isotopes. Such research has been built upon the assumption that human and animal bone and dentine collagen $\delta^{34}\text{S}$ reflects the isotopic composition of bioavailable sulfur at the base of the food chain (plant $\delta^{34}\text{S}$) driven by the local geology. This is because the minimal trophic enrichment during plant and animal uptake of sulfur means that the environmental signals are largely conserved (Krajcarz et al., 2019; Nehlich, 2015; Raoult et al., 2024).

In terrestrial environments underlying bedrock provides sulfur-bearing parent material, while lithology exerts physical and chemical controls which affect the movement of sulfur into soil and on to plants, often via interactions with groundwater and microbiology. Proximity to the ocean (due to sea spray) can mix a marine signal with the bioavailable sulfur in soil derived from the geology (Bataille et al., 2020; Guiry and Szpak, 2020). Estimates of geological baselines of bioavailable sulfur $\delta^{34}\text{S}$ form the basis for archaeological geographic assignment and mobility studies using collagen $\delta^{34}\text{S}$ (Ebert et al., 2021; Lamb et al., 2023; Paladin et al., 2020; Zavodny et al., 2022). While fish consumption may also influence consumer $\delta^{34}\text{S}$ (e.g., Nehlich et al., 2010; Privat et al., 2007), here we focus on sulfur isotope variation in plants, and the implications for sulfur isotopic composition of collagen from terrestrial animals that do not consume fish.

Recent studies indicate that the interpretation of $\delta^{34}\text{S}$ is potentially complex because the $\delta^{34}\text{S}$ of sulfur available to plants can be influenced by microbial sulfate reduction and sulfide oxidation in soil and sediments (Guiry et al., 2021; Lamb et al., 2023; Nitsch et al., 2019; Stevens et al., 2022, 2025). These important processes in the global sulfur cycle are mediated by soil Bacteria and Archaea, and the soil or sediment iron content. Microbial sulfate reduction is a widespread phenomenon in terrestrial (and marine) environments and is stimulated by waterlogged conditions, for example, in wetlands, on poorly drained soils (Canfield, 2001), and in thermokarst environments (Ren et al., 2023), and is often driven by poor permeability in the underlying lithology. In these environments isotope effects from microbial sulfate reduction followed by sulfide oxidation change the $\delta^{34}\text{S}$ of soil sulfur available to plants originally derived from the geology. This modified isotopic signal can be incorporated into plants and passed on to animals to be stored in animal proteins. Sulfur in bioarchaeological material produced in these environments can, therefore, reflect a modified isotopic composition due to the effect of coeval microbial sulfur cycling (Lamb et al., 2023). We refer to environmental $\delta^{34}\text{S}$ baselines of bioavailable sulfur derived from geological and/or marine sources on well-drained land as “dryland” baselines, in order to differentiate them from environmental $\delta^{34}\text{S}$ baselines that have been altered due to waterlogging and sulfur cycling.

Evidence of early human activity has been found in wetland environments, where access to fresh drinking water and fertile soil would have made these locations attractive for resource use and settlement. These environments include marshes, fens, meres, swamps, lagoons, floodplains, lakesides, riverbanks and riparian zones, saltmarshes, estuaries and deltas, as well as land on the margins of these places. Such locations appear to have been used to

provide wild food (e.g., Abu Hureyra, riparian marshland, Hillman et al., 2001), for animal husbandry and to grow crops (e.g., Neolithic Çatalhöyük, Konya plain, Turkey, Ayala et al., 2022; Sherratt, 1980; Must Farm, Cambridgeshire, UK, Ballantyne et al., 2024; Swifterbant, Neolithic wetland creek system, The Netherlands, Huisman and Raemaekers, 2014; Eye, Over, and Langtoft, fenland, Cambridgeshire, UK, Lamb et al., 2023; and Middle Yellow River Valley, China, Wang et al., 2023). Such environments were likely instrumental in the development of farming, with floodplain archaeobotanical assemblages suggesting the presence of crop plants growing alongside wetland plants (e.g., Hillman et al., 2001; Motuzaite-Matuzeviciute et al., 2012).

In archaeological applications, where the sulfur isotopic composition of bioarchaeological material deviates from the local dryland $\delta^{34}\text{S}$ baseline, it may suggest movement of people or animals in the past. However, it could also indicate a wetland $\delta^{34}\text{S}$ baseline signal incorporated via the consumption of crops grown on wetlands and wetland derived resources from the local area (and/or beyond) (Guiry et al., 2021, 2022; Lamb et al., 2023; Nitsch et al., 2019). Such signals in human, animal and plant archaeological material could potentially provide unique insights into ancient wetland resource use and early agriculture. Temporal sequences of such samples may also provide information on natural hydrological changes, seasonal resource use, and human manipulation of local hydrology.

The aim of this study is to explore how different hydrological conditions can impact terrestrial sulfur cycling and overwrite primary dryland $\delta^{34}\text{S}$ baselines derived from parent geology. We use conceptual models to explore wetland sulfur cycling effects. We discuss parameters controlling plant-available sulfur $\delta^{34}\text{S}$, assess the effect of coeval sulfur cycling on biosphere mapping and palaeo-baselines, and explore factors contributing to wetland isotopic signals in plants. We consider how these factors may have interacted with ancient water management practices to affect the $\delta^{34}\text{S}$ of crops and wild plants grown in these environments, and explore the influence of the wetland signal on archaeological collagen $\delta^{34}\text{S}$.

2 Drivers of bioavailable $\delta^{34}\text{S}$ baselines

Almost all biologically incorporated sulfur in terrestrial environments is derived from geological reservoirs in rocks, as bedrock provides parent material from which sulfur is released into soil and groundwater. Therefore, the site specific $\delta^{34}\text{S}$ of geological sulfur is the essential starting point for interpreting $\delta^{34}\text{S}$ in archaeological collagen and plant material from a particular site. There are two broad categories of geological sulfur deposits, sulfate that reflects the $\delta^{34}\text{S}$ of coeval ocean water sulfate with a range of 10‰ to 30‰, and sulfide formed from microbial sulfate reduction, usually with significantly lower $\delta^{34}\text{S}$ values (Bottrell and Newton, 2006; Bottrell and Raiswell, 2000; Claypool et al., 1980; Paytan and Gray, 2012; Pellerin et al., 2019). Together, this results in a very wide range of geological sulfur $\delta^{34}\text{S}$ values spanning c. 70‰, with offshore pyrite sulfide $\delta^{34}\text{S}$ values reported down to −55‰ (Pasquier et al., 2021).

Terrestrial geological sulfur is released from rock into soil via a series of physiochemical processes which weather the rock.

This occurs most commonly with near-surface sedimentary rock when exposed to changes in temperature and moisture at the surface, or via interactions with groundwater in the subsurface. In this way, sulfur bearing the local geological $\delta^{34}\text{S}$ reaches soil and groundwater. It is this weathered, dissolved sulfur that is available to be taken up by plants and animals. Geological weathering product $\delta^{34}\text{S}$ found in these terrestrial reservoirs may reflect a mix of sulfur from different sulfur bearing rocks with varied $\delta^{34}\text{S}$ values. This mix is affected by preferential weathering of some deposits over others due to chemical and structural differences. For example, during weathering, sulfate in evaporites and carbonates readily dissolves in water, often resulting in high concentrations reaching soil, groundwater and rivers, whereas sulfide in pyrite is insoluble, and requires exposure to oxygen to weather, which usually occurs via microbially mediated reactions.

This geological origin sulfur in soil may mix with sulfur from natural atmospheric sources, including wind blown dust, the biogenic gases dimethyl sulfide and hydrogen sulfide (H_2S), as well as ash from forest fires and sulfur dioxide from volcanic eruptions and passive degassing (Aneja, 1990). When two or more inputs of sulfur with different isotopic compositions are mixed, the relative amounts of sulfur and the isotopic difference between each input determine the resulting $\delta^{34}\text{S}$ of the mixture. In near-coast sediments and soils the geological signal is likely to be overwritten by the dominant isotopic signal from sulfate-rich ocean water in sea spray ($\delta^{34}\text{S}$ c. 21‰; Paytan and Gray, 2012), and dimethyl sulfide produced by marine phytoplankton (Aneja, 1990). The distribution of this marine signal is controlled by prevailing weather patterns which affect the continental distribution of sea spray and dimethyl sulfide, and by hydrogeology, which controls the extent of saline intrusion into fresh groundwater in coastal regions.

Archaeological studies may use modern material, (for example from plants), to characterize $\delta^{34}\text{S}$ baselines. However, in modern environments, soil sulfur of geological origin may mix with atmospheric sulfur dioxide from fossil fuel combustion, and sulfur in agricultural fertilizer. Sulfate originating from fossil fuel combustion has an isotopic composition close to 0‰ (e.g., Chung et al., 2019; $\delta^{34}\text{S}$ 2.2 ± 1.6 ‰). Inputs from fossil fuel combustion are likely to be diffuse, dampening the range of soil sulfur derived from geology over the affected area (Stack and Rock, 2011), with a larger effect for geologically derived soil $\delta^{34}\text{S}$ values that are furthest from the value of fossil fuels. Fertilizer $\delta^{34}\text{S}$ values are highly variable (Vitòria et al., 2004) and their effect on soil bioavailable sulfur $\delta^{34}\text{S}$ is likely to be localized and spatially heterogeneous. Sulfur fertilizers may be artificially produced or mined from geological settings far from the locations where they are used. Sulfur from fertilizers can be transported away from the area of application in runoff and groundwater. When anthropogenic sulfur inputs decline or are discontinued, there is likely to be a time lag before their contribution to the bioavailable sulfur pool decreases.

Microbial sulfur cycling can significantly alter $\delta^{34}\text{S}$ values derived from geological sulfur parent material, marine and atmospheric sources, laying down fresh sulfide deposits in soils and sediments (Figure 1), leading to bioavailable $\delta^{34}\text{S}$ values which

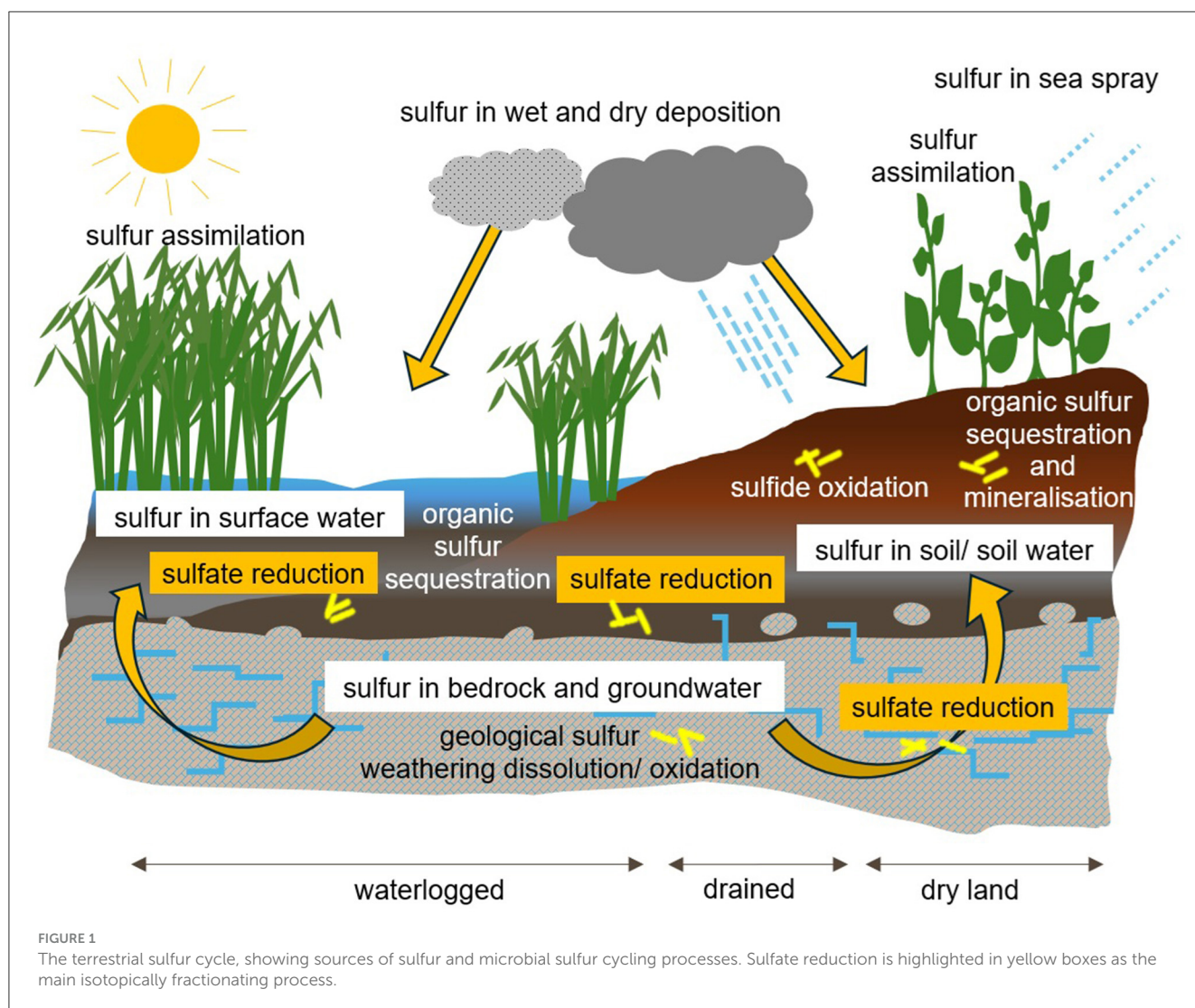
can be lowered or raised. This can occur as a result of poorly draining soils or impervious lithology. Sulfur with $\delta^{34}\text{S}$ values affected by microbial cycling may be taken up by plants and passed up the food chain. Sulfur cycling can occur at local scales and can change over relatively short time periods, for example with alteration in floodplain extent due to dynamic river braiding and meandering, or at vast spatial and temporal scales, for example during continent-wide permafrost thaw during the Late Pleistocene.

Perturbations of geologically derived dryland $\delta^{34}\text{S}$ baselines due to coeval sulfur cycling are relevant to archaeological studies using sulfur isotopic composition of human, animal or plant material. Such perturbations should be considered in archaeological settings to broaden the scope of interpretation and avoid misinterpretation of archaeological $\delta^{34}\text{S}$ values. In particular, where archaeological sites were in wetlands, in periodically waterlogged, poorly draining or low-lying environments, or in thermokarst, saltmarshes or estuaries, dynamic sulfur cycling is likely to have affected bioavailable $\delta^{34}\text{S}$ baselines significantly. However, in order to identify the effects of coeval sulfur cycling, the dryland baseline derived from the local geological parent material, (as well any sea spray influence), should be determined with good spatial resolution and a high degree of confidence. This is particularly important because of the very wide range of possible geological parent material baseline $\delta^{34}\text{S}$ values. Distinguishing the influence of parent material from coeval sulfur cycling can be challenging, as some wetlands form on poorly permeable lithology that has a sulfur isotopic composition strongly affected by sulfate reduction over geological time scales, for example in lowlands underlain by Jurassic mudstones in central England (Lamb et al., 2023).

3 Sulfur cycling affects bioavailable $\delta^{34}\text{S}$ baselines in wetlands and waterlogged environments

3.1 Sulfur cycling in soil

When considering the effects of waterlogging on plant $\delta^{34}\text{S}$, we refer to the partitioning of different amounts of sulfur in organic and inorganic compounds in the soil and their bioavailability to plants (the plant-available fraction), the isotopic composition of these different compounds ($\delta^{34}\text{S}$), and microbial sulfur cycling processes that may incur isotopic fractionations affecting the isotopic composition of the compounds. Around 95% of sulfur in soil is in organic form (Kilham, 1994), derived from biomass of plant, microbial, and animal origin. However, plants are not able to utilize this organic sulfur directly. It is broken down slowly and is only very gradually mineralized and oxidized to sulfate by soil microbes (Chaudhary et al., 2023), with negligible change in $\delta^{34}\text{S}$ (e.g., Norman et al., 2002), to be replenished by organic sulfur in fresh biomass deposits. Breakdown of organic matter is suppressed if the soil is waterlogged (Dušek et al., 2020). Water also limits oxygen diffusion into waterlogged and flooded soils and sediments, which are often formed on poorly permeable lithologies. Under water, there is decreasing oxygen diffusion with depth and distance



from the air-water surface interface. As remaining oxygen is used up by aerobic microbial respirers and plant roots, a steep vertical gradient of oxygen depletion develops, stimulating the activity of different anaerobic microbial communities and progressive electron acceptor depletion (Kilham, 1994). In the anoxic zone, microbial sulfate reducing activity is stimulated where sulfate and organic carbon are available. Within these redox gradients the boundary between well-oxidized conditions near the surface and anoxic conditions at depth can move up or down, for example, in response to water level fluctuations and bioturbation. This can result in dynamic switching between reducing and oxidizing conditions, stimulating rapid microbial cycling of sulfate and sulfide from the soil inorganic sulfur pool through sulfate reduction and sulfide oxidation.

Sulfate reduction in anoxic conditions is associated with a varied and often large isotopic fractionation (c. 3‰ to 68‰, Sim et al., 2011), which results in the production of sulfide with lower $\delta^{34}\text{S}$ values than those of the original sulfate. The isotope effect associated with microbial sulfate reduction occurs via a series of fractionating, reversible enzymatic steps within the sulfate reducing organism. The magnitude of the sulfate reduction isotope effect

in the environment is one of the main controls on wetland plant $\delta^{34}\text{S}$. Large isotope effects from wetland sulfur cycling have been reported, for example from peat wetland environments (11‰ to 51‰, Price and Casagrande, 1991), brackish marshland (c. 33‰, Stribling et al., 1998), and saltmarshes (25‰, Carlson and Forrest, 1982; 50‰, Peterson et al., 1986), although further studies are needed, especially from freshwater environments. At near neutral pH levels, sulfide produced from sulfate reduction can accumulate in the soil as hydrogen sulfide (H_2S). Persistent large isotopic offsets between sulfate in water and sulfide in sediments are brought about via the formation of sulfide precipitates in the sediment which prevent the upward diffusion of dissolved sulfide to the surface where oxygen would enable its oxidation to sulfate. Most sulfide precipitates are formed with iron (Fe^{2+}), as iron sulfide (FeS) and pyrite (FeS_2), thus iron availability is key to the formation of sulfide precipitates and maintaining the large isotopic offsets found between sulfate in water and sulfide in sediments.

Factors causing variation in the isotope effect of sulfate reduction are not fully understood, and include the ratio of sulfate to organic carbon (a larger effect is found when the sulfate to carbon ratio is high), and non-linear effects from differences in

sulfate concentration, temperature, microbial strain, the type of organic carbon, the cell specific sulfate reduction rate, and iron and ammonium availability (Sim et al., 2012, 2023). High groundwater levels, river flooding, heavy rainfall, poor soil permeability and impermeable lithology can cause soil saturation, which stimulates sulfate reduction. Soil waterlogging coupled with sulfate reduction may be a temporary or periodic phenomenon, for example in floodplains and estuaries, or a more permanent phenomenon, for example in marshes and fens. A wide diversity of wetlands are prime sulfate reducing environments, with low $\delta^{34}\text{S}$ sulfide in soil and sediments.

3.2 Pathways for plant sulfur uptake and effects on plant $\delta^{34}\text{S}$

Sulfur is an essential nutrient for plants. It is taken up via sulfate transporter chemicals in roots, and used to make different sulfur containing compounds including the amino acids cysteine and methionine, the protective antioxidant glutathione, as well as many essential metabolites such as vitamins, enzymes, and compounds used for plant defense and stress response (Hill et al., 2022). If plants take up excess sulfate, it can be stored in cell vacuoles until it is needed, and if sulfate uptake is restricted due to low availability sulfur may be recycled within the plant from glucosinolates (secondary plant metabolites) (Maruyama-Nakashita, 2017).

Sulfate reduction results in sulfide with lowered $\delta^{34}\text{S}$. However, most plants are not sulfide tolerant and cannot take up sulfide directly. In order for a lowered $\delta^{34}\text{S}$ from sulfide to be incorporated into plant biomass, sulfide must first be oxidized to sulfate. Here we use the term “lowered plant $\delta^{34}\text{S}$ ” as a relative term to refer to plant $\delta^{34}\text{S}$ values that are lower than those expected from plants grown in non-waterlogged or flooded soil with the same geological parent material. For plants which are not sulfide tolerant, sulfide oxidation to sulfate can occur after waterlogged or flooded soil drains, allowing the ingress of air to oxygenate the soil, for example on seasonally draining floodplains. This enables the oxidizing microbial community to become active resulting in sulfide oxidation to sulfate, utilizing sulfide produced during the preceding period of submergence. Soil sulfide oxidation usually causes negligible isotopic fractionation (Canfield, 2001; Zerkle et al., 2009) so the newly oxidized sulfate retains the lowered $\delta^{34}\text{S}$ from sulfide. This effect is enhanced by differences in the solubility of sulfate and sulfide. Sulfate is highly soluble and some soil sulfate is removed in water as it drains from temporarily waterlogged soil, as a function of soil water retention on draining, which varies with soil type. Sulfide precipitates such as iron sulfide and pyrite are insoluble and remain in the soil when the water drains away, after which they can be oxidized back to sulfate. The relative proportions of plant-available sulfate from soil oxidized sulfide to remaining sulfate in soil water after draining is referred to as the “soil sulfate source ratio” hereafter.

Some plants, primarily those adapted to wetland ecologies (e.g., wetland plants including the crops rice and taro), are sulfide tolerant. They have adapted to root zone (rhizosphere) waterlogging and can oxidize sulfide to sulfate in the root zone

(Lamers et al., 2013; Simkin et al., 2013). This occurs through the development of a barrier along the root length to the tip which protects the plant from absorbing toxic sulfide along the root shaft, but allows leakage of oxygen into the rhizosphere from the root tip (Abiko and Miyasaka, 2020; de la Cruz Jiménez et al., 2021; Nishiuchi et al., 2012; Pan et al., 2021). The oxygen seeping from the root tip into the waterlogged rhizosphere (Ando et al., 1983), leads to localized root zone oxygenation and the development of a symbiotic bacterial community of sulfide oxidizers. This supports *in situ* microbial oxidation of sulfide with lowered $\delta^{34}\text{S}$, forming sulfate which can be then taken up and utilized by the plant. Internal sulfide oxidation by symbiotic bacterial colonies within the roots may also occur (Lamers et al., 2013). Wetland plants can also develop adventitious roots which form laterally at the soil/water interface, allowing uptake of oxygen and sulfate from overlying water (Parent et al., 2008; Steffens and Rasmussen, 2016).

A critical factor determining wetland plant $\delta^{34}\text{S}$ is the relative amounts of sulfur taken up via these two pathways: the uptake ratio of sulfide oxidized in the root zone, to direct uptake of sulfate from overlying water; hereafter referred to as the “plant uptake ratio.” There are limited published data on wetland plant uptake ratios. The few studies that are available show saltmarsh plant uptake ratios ranging from 1.0: 0.0 to 0.6: 0.4 (Carlson and Forrest, 1982; Cornwell et al., 1995; Fry et al., 1982, 2023; Peterson et al., 1986; Price and Casagrande, 1991; Stribling and Cornwell, 1997; Stribling et al., 1998). In these sulfate rich environments sulfate $\delta^{34}\text{S}$ in overlying water is as high as 21‰, but plant $\delta^{34}\text{S}$ ranges from −14‰ to 13‰ due to root zone sulfide oxygenation. Although freshwater wetland plant uptake ratio studies are lacking, the range of $\delta^{34}\text{S}$ from freshwater wetland plants reported recently is similar in magnitude to that of saltmarsh plants, although with lower absolute values (−31‰ to −1‰, Evans et al., 2023; Lamb et al., 2023).

Interestingly, adventitious roots (but not rhizosphere sulfide oxidation), can be induced by waterlogging stress in non-wetland species including the crop plants oats, barley, wheat, maize, and millet (Li et al., 2023; Matsuura et al., 2022; Pan et al., 2021; Yamauchi et al., 2013). This stress response may have enabled early cultivation of crop plants on floodplains and lowlands which would have been at risk of periodic inundation during the growing season.

4 The “wetland” sulfur isotope signal

Archaeologists are rapidly taking on board the concept that lowered $\delta^{34}\text{S}$ is a marker of wetland habitat use. However, it is necessary to highlight that not all wetland and waterlogged environments will produce a distinctive isotopic signal. Whether such a signal is present depends on many variables, including the magnitude of the isotope effect, plant uptake ratios, the nature of the hydrologic system (flow-through, standing water), the duration of waterlogging and progression of sulfate reduction, the extent of drainage and the interplay between microbial sulfur cycling, isotopic fractionation, and plant adaptation. The hydrology of natural wetlands has traditionally been classified according to hydrogeomorphology, combining information about the dominant source of water, position in the landscape and water movement (Shaffer et al., 1999). Wetlands occur where these factors combine

to support a seasonal or permanent high water table, which leads to the development of specific habitat types and wetland soils and sediments, and are often underlain by poorly permeable lithology. Soil waterlogging, while not necessarily leading to wetland development, supports microbial sulfate reduction and changes in $\delta^{34}\text{S}$, and is a function of elevation and/or soil type, with low lying areas, riparian zones and clay soil more likely to be temporarily or permanently waterlogged. Water plays two crucial roles in wetland and waterlogged soil sulfur cycling. First, it provides a barrier that limits oxygen diffusion and leads to soil anoxia, stimulating microbial sulfate reducing activity. Second, water carries dissolved sulfate for microbial sulfate reducers to use. Wetlands receive water directly via precipitation, and lose water via evapotranspiration. However, shallow groundwater is often the most important source of water for these systems, bringing in sulfate and other nutrients to support plant life. Here, we use the term shallow groundwater to include groundwater that originates from deeper circulation but becomes shallow once it has risen to the surface to provide baseflow to rivers and wetlands, and near-surface circulating groundwater that is recharged from surface runoff (Hiscock and Bense, 2021).

Natural and engineered wetland systems span a variety of hydrologic regimes which support sulfate reduction and sulfide oxidation alongside plant life (Figure 2). Here we consider sulfur isotope cycling under four different theoretical hydrological regimes which can support a range of wet environments from permanent wetlands to temporarily waterlogged landscapes in natural and engineered systems; flow-through, standing water, drained post-waterlogging, and simultaneously flooded and drained; and model their potential impact on plant $\delta^{34}\text{S}$ values (models presented in Supplementary Information). Our models represent a first step toward understanding controls on wetland plant $\delta^{34}\text{S}$, by presenting four simple scenarios which, in the real world, are expected to be more complex. For example, wetland landscapes are likely to be supported by heterogeneous hydrology that varies with season and rainfall patterns. Sulfate reduction isotope effects may vary with seasonal temperatures and sulfate and organic carbon availability, and sulfate $\delta^{34}\text{S}$ values may vary with rainfall and hydrology. Furthermore, plant uptake ratios are poorly understood and could vary, for example, with changes in sulfate concentration, temperature, season or phase in the plant's growth cycle, and sulfide adapted and non-adapted plants may grow side by side at wetland margins. These scenarios need to be tested *in situ* to form the foundation for archaeological studies in wetland environments.

Omitted from these scenarios are ombrotrophic, nutrient poor, acid peat bogs, which are usually dominated by sphagnum. Evidence of early crop cultivation in such bogs is lacking and ombrotrophic bogs are unlikely to have been used for early crop cultivation due to their low level of nutrients and low pH. These bogs rely solely on precipitation for their water supply, and are disconnected from groundwater.

4.1 Flow-through hydrology

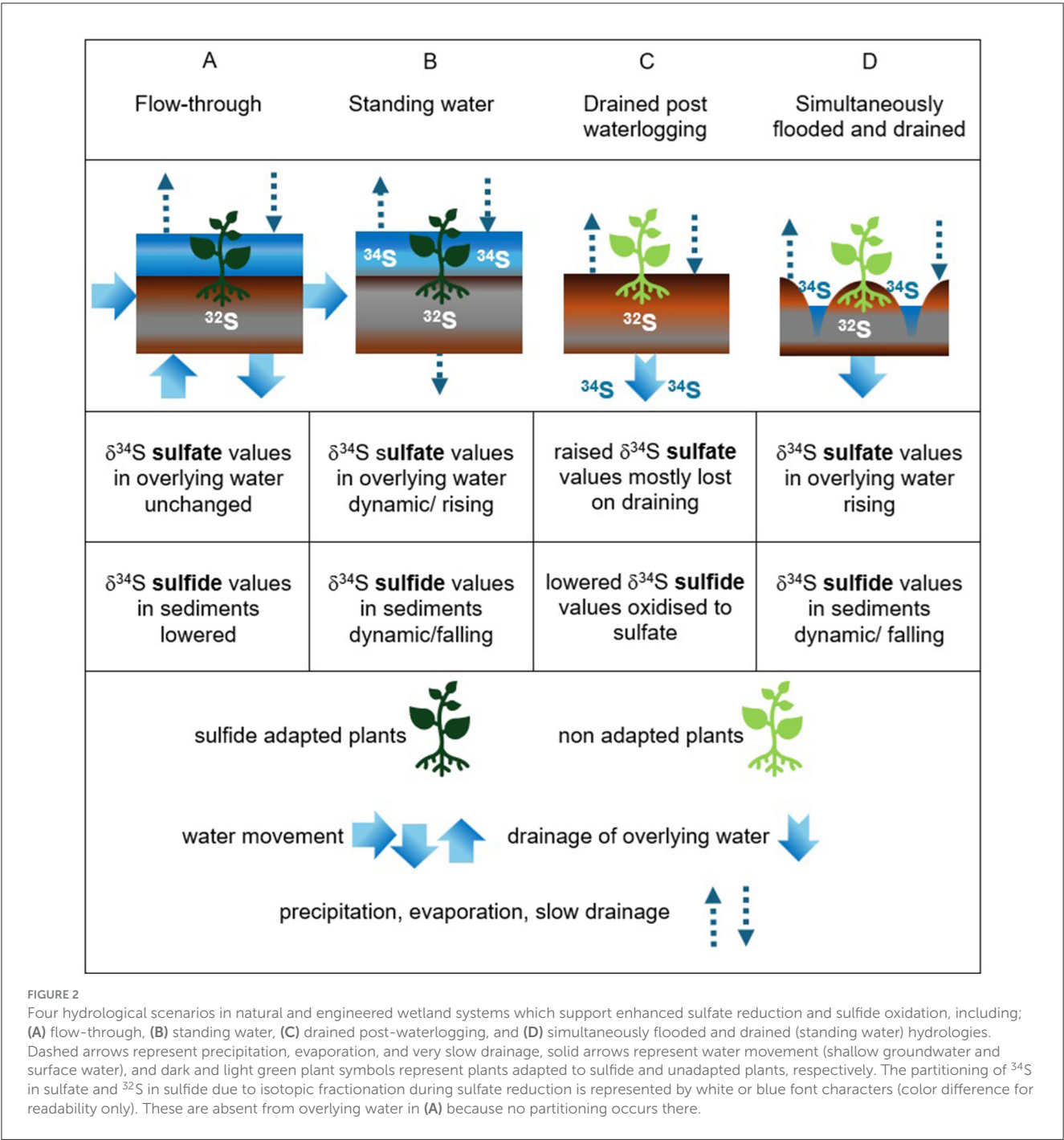
Plants living in wetland systems with flow-through hydrology (including natural wetland plants and the crops rice and taro)

are sulfide adapted. The primary source of water and additional sulfate for many natural wetland environments is continuous lateral and/or vertical shallow groundwater flow (Winter, 1999) which supplies an ongoing input of sulfate derived from geological weathering and atmospheric sources for use by microbial sulfate reducers (Figure 2A). In such flow-through systems, sulfate which is reduced to sulfide in anoxic sediments is replenished with sulfate in the continuously flowing shallow groundwater. Such natural groundwater fed wetlands can be permanently waterlogged if shallow groundwater levels are stable, or temporarily waterlogged if shallow groundwater levels recede, and include riparian wetlands, marshes and fens. A similar hydrology existed where engineered flow-through systems were built, supplied with flowing water channeled from nearby sources such as springs and streams.

Referring to the partitioning of ^{32}S and ^{34}S within different reservoirs of sulfur during isotopic fractionation, flow-through wetlands maintain a near constant sulfate $\delta^{34}\text{S}$ and sulfate concentration in overlying water because the continuous replenishment of sulfate from flowing water erases the effect of preferential removal of ^{32}S by sulfate reduction (Figure 2A). ^{32}S accumulates in sedimentary sulfide resulting in a lowered sulfide $\delta^{34}\text{S}$, which is passed on to plants via rhizosphere oxygenation and sulfide oxidation, resulting in plants with lowered $\delta^{34}\text{S}$. The difference between sulfate $\delta^{34}\text{S}$ in the overlying water and sulfide $\delta^{34}\text{S}$ in the sediment is stable if the magnitude of the isotope effect of sulfate reduction is stable (Högborg, 1997; Kendall and Caldwell, 1998; Mariotti et al., 1981), and is the first control on the lowered $\delta^{34}\text{S}$ of the wetland plants. The magnitude of the isotope effect has been characterized for a limited number of wetlands (e.g., 11‰ to 51‰ Carlson and Forrest, 1982; Peterson et al., 1986; Price and Casagrande, 1991; Stribling et al., 1998). If minor fluctuations in groundwater sulfate $\delta^{34}\text{S}$ occur as a result of changes in the relative proportions of sulfate source contributions, such as after recharge from rainfall or during drought, this could result in fluctuations in sulfate and sulfide $\delta^{34}\text{S}$ values. As plant uptake ratios are not well known (see Section 2) and the sulfate reduction isotope effect is dependent on many factors (see Section 3.1), we use ranges from the literature, modeling plant uptake ratios of 0.6:0.4 to 0.8:0.2 and isotope effects of -10% to -40% (Figure 3A and Supplementary Information). Our models illustrate the effect of sulfate reduction as changes in plant $\delta^{34}\text{S}$ (denoted by $\Delta^{34}\text{S}$) in different systems relative to baseline “initial sulfate,” driven by the geology, and are based on the simplifying assumption that there is no pre-existing sulfate or sulfide in the system. In the real world initial sulfate $\delta^{34}\text{S}$ values could vary significantly depending on the underlying geology, which can encompass values from -20% to 30% (Seal, 2006).

4.2 Standing water hydrology

Most plants growing in persistent standing water hydrology (including natural wetland plants and the crops rice and taro) are also sulfide adapted. Standing water systems receive water containing sulfate from rainfall and include seasonally and ephemerally waterlogged landscapes in low lying areas, and on poorly draining soil. In engineered standing water systems, pulses



of water may have been diverted from local streams, lakes, or seasonal floodwaters, and retained by field edge structures, while poor soil permeability may have been enhanced by soil puddling (tillage under flooded conditions to reduce permeability), to prevent vertical drainage (Figure 2B). In these systems sulfate in overlying water slowly percolates into anoxic sediments to support microbial sulfate reduction. In the overlying water, sulfate $\delta^{34}\text{S}$ and sulfate concentration undergo dynamic changes as sulfate reduction progresses, which in turn affect the $\delta^{34}\text{S}$ of sulfide produced. In standing water systems which receive a single input of water, sulfate is progressively transferred from the overlying

water to sulfide in the sediments where it reacts with iron to form insoluble precipitates. This results in an increase in ^{34}S in the remaining sulfate in overlying water and in ^{32}S in reduced sulfide in sediments as sulfate reduction proceeds. In this system, sulfate concentration in the overlying water decreases over time and the $\delta^{34}\text{S}$ of sulfate rises well above the $\delta^{34}\text{S}$ of the initial sulfate, while the $\delta^{34}\text{S}$ of sulfide in the sediment rises gradually as more sulfide is sequestered, reaching a maximum $\delta^{34}\text{S}$ sulfide value the same as that of initial sulfate. This point is reached when all sulfate from the single input has been reduced to sulfide (Högberg, 1997; Kendall and Caldwell, 1998; Mariotti et al., 1981)

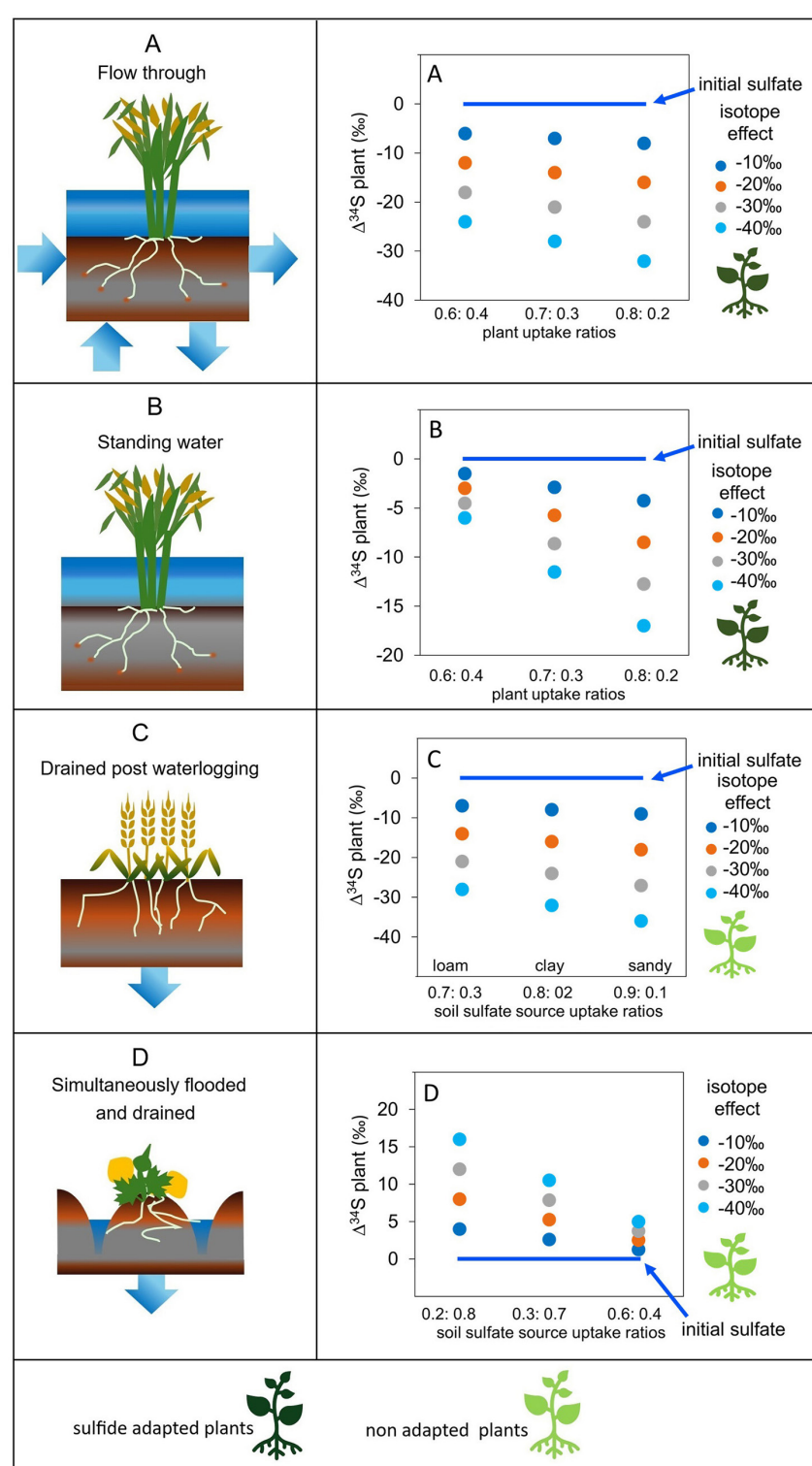


FIGURE 3

Representations of four wetland environments used for crop growing with different hydrologies; (A) flow-through, (B) standing water, (C) drained post flow-through waterlogging, and (D) simultaneously flooded with standing water and drained, with charts presenting ranges of plant $\delta^{34}\text{S}$. The plant changes in sulfur isotopic composition ($\Delta^{34}\text{S}$, where 0‰ refers to no change) relative to initial values were derived by combining modeled effects of sulfur fractionation associated with sulfate reduction (Högberg, 1997; Kendall and Caldwell, 1998; Mariotti et al., 1981), with four isotope effects for sulfate reduction; 10‰, 20‰, 30‰, 40‰, based on reported values from the literature (Carlson and Forrest, 1982; Peterson et al., 1986; Price and Casagrande, 1991; Stribling et al., 1998). These were combined with plant uptake ratios for emergent plants informed from the literature for (A) and (B) (Carlson and Forrest, 1982; Cornwell et al., 1995; Fry et al., 1982, 2023; Peterson et al., 1986; Price and Casagrande, 1991; Stribling and Cornwell, 1997; Stribling et al., 1998), and for soil sulfate source ratios for (C) and (D) using the proportion of sulfate in water remaining on draining based on soil porosity and the maximum available soil moisture on draining across three soil types (Kumar Rai et al., 2017; Marshall and Holmes, 1996). Initial values are not specified as they are controlled by the geological parent material and can span a range of at least 50‰ (e.g., Seal, 2006) (please refer to Supplementary Information for further details).

(Supplementary Information). Due to the fact that sulfide $\delta^{34}\text{S}$ rises as sulfate reduction proceeds, there is a smaller difference between the initial sulfate $\delta^{34}\text{S}$ and that of sulfide than the difference seen from flow-through systems (Figure 3B).

In some standing water systems, periodically repeated inputs of water supply fresh sulfate. Although the $\delta^{34}\text{S}$ of sulfate and sulfide respond dynamically during sulfate reduction (Högberg, 1997; Kendall and Caldwell, 1998; Mariotti et al., 1981), the periodic inputs of sulfate buffer these effects, resulting in a similar effect to that seen from flow through systems. We also modeled plant $\delta^{34}\text{S}$ with standing water hydrology and periodic inputs of “initial” sulfate in water, using sulfate and sulfide $\delta^{34}\text{S}$ over time. The same plant uptake ratios and isotope effects are used as in the flow-through system. However, the range of resulting plant $\delta^{34}\text{S}$ values is slightly smaller (Supplementary Information). Note that the plant uptake ratio is particularly sensitive in the standing water scenario as, if a large proportion of sulfate is taken up from overlying water after significant sulfate reduction, plant $\delta^{34}\text{S}$ values could be raised.

Standing water hydrology and flow-through hydrology can occur on a continuum within the same wetland, often controlled by the seasonality of water inputs. For example, flow-through wetland systems may behave like standing water systems at their margins when water flow is reduced (e.g., Peterson et al., 1986), if they have poorly permeable sediments which restrict water movement, and with sediment depth (e.g., Carlson and Forrest, 1982; Price and Casagrande, 1991). In addition, many standing water systems receive sporadic inputs of water and sulfate from precipitation, flood events, high tides, or temporarily high groundwater levels (Supplementary Information).

4.3 Temporarily flooded and drained post-waterlogging

Plants grown after drainage of flooded soil conditions, (such plants include wild grasses and the crops barley, wheat, sorghum, and barnyard millet), are not able to oxidize sulfide but can tolerate transient flooded conditions. These plants have to take up their sulfur directly as sulfate from the environment. Many flow-through and standing water wetlands are temporarily waterlogged rather than permanently inundated. When flooded soil drains, the water which submerged the soil is mostly lost. This can occur via gradual drainage when flood waters recede and shallow groundwater levels drop, or, in engineered systems, as a result of intentional release (Figure 2C). Due to the high solubility of sulfate, when overlying water drains, much of the sulfate is lost via transport in drainage water. When drainage occurs, oxygen enters the soil triggering sulfide oxidation, creating low $\delta^{34}\text{S}$ sulfate from the sulfide produced during waterlogging and stored in precipitates formed with iron in anoxic sediments (Figure 2C). Plants growing immediately after soils are drained incorporate sulfate primarily from sulfide which has been oxidized in the freshly aerobic soil. Where temporary wetlands are repeatedly flooded and drained, a cumulative effect can occur if conditions promote substantial sulfide oxidation each time the wetland is drained (for example if soils have high porosity, readily allowing oxygen to enter previously waterlogged pore space). Some wetlands, once drained, remain

so permanently, whether as a result of natural processes (e.g., alterations in river courses), environmental change (e.g., lowered shallow groundwater levels as a result of decreases in recharging precipitation), or alteration in land use (e.g., marshland drained to create pasture or rice paddy fields drained to grow different crops). Permanent drainage enables oxygen to remain in the soil, which, as the soil is no longer waterlogged, no longer supports sulfate reduction. Within this drained soil, low $\delta^{34}\text{S}$ sulfide (produced and stored in the soil before it was drained), is gradually oxidized to sulfate and is not replenished. This results in gradually decreasing inputs of low $\delta^{34}\text{S}$ into the plant available sulfate pool from sulfide reserves near the soil surface; a process which may take many years (e.g., Chung et al., 2017). We have modeled $\delta^{34}\text{S}$ for plants grown on drained soils after a flow-through hydrology (Figure 3C). We have estimated the proportion of sulfate lost in water on draining by considering soil water content under saturation and plant-available water on draining, for three soil types with different drainage; sandy, loam and clay soils. The different porosity of these soil types means they hold different proportions of water when saturated, and on draining, these soil properties affect how much of this water is available to plants (Kumar Rai et al., 2017; Marshall and Holmes, 1996) (Supplementary Information). Based on these estimates, we use soil sulfate source ratios (the relative proportions of plant-available sulfate from soil oxidized sulfide to remaining sulfate in soil water after draining), of 0.7:0.3, 0.8:0.2 to 0.9:0.1 for loam, clay and sandy soils, respectively. We use the same isotope effects as in the previous models. This system results in lowered plant $\delta^{34}\text{S}$. If before draining, the system had a standing water hydrology (rather than flow-through modeled here), we expect $\delta^{34}\text{S}$ values of plants grown in drained soil to be lowered, but not lowered to the extent of plants growing in a drained flow-through system, reflecting the smaller signal expected from standing water systems in general (5.2). In landscapes that are repeatedly flooded and drained, we expect $\delta^{34}\text{S}$ of plants grown in drained soil to be lowered by a similar amount as that expected from flow-through systems after draining.

4.4 Simultaneously flooded and drained hydrology

Plants grown in simultaneously flooded and drained systems (including the crops barley, wheat, squash, maize, beans) are not able to oxidize sulfide, but can tolerate partially saturated soil conditions. Such conditions occur through minor variations in elevation in waterlogged and flooded natural landscapes, and in some engineered wetlands (e.g., ridge and furrow, raised fields, floating fields) (Figure 2D). The hydrology in these systems may be standing water or flow-through. Such systems simultaneously support sulfate reduction in the waterlogged soil at depth, producing low $\delta^{34}\text{S}$ sulfide values, and sulfate oxidation in the soil above the water, producing low $\delta^{34}\text{S}$ sulfate (Figure 2D). However, plants grown on unsaturated soil above a high-water table are expected to incorporate sulfate primarily from roots reaching the upper level of saturated soil and the overlying water directly. The sulfate $\delta^{34}\text{S}$ of these sources is controlled by the flow-through or standing water status of the water. We have modeled the plant $\delta^{34}\text{S}$

with standing water hydrology over a range of soil and water sulfate source ratios of 0.4:0.6 to 0.2:0.8, at 50% reduction of sulfate to sulfide (but as discussed above the extent of reduction is dynamic). In simultaneously flooded and drained systems with standing water hydrology, plant $\delta^{34}\text{S}$ could be raised above the initial sulfate $\delta^{34}\text{S}$, as illustrated in Figure 3D. However, if such systems have flow-through hydrology we would expect plant $\delta^{34}\text{S}$ to be slightly below the initial sulfate $\delta^{34}\text{S}$ of the water.

5 Sulfur wetland isotopic signals in archaeology

5.1 Ancient water management practices

These model results suggest that through analysis of archaeological crop $\delta^{34}\text{S}$ we may be able to differentiate different water management practices, many of which played a critical role in subsistence agriculture and its development and intensification. In ancient societies, the ability to access, control and distribute water effectively often determined the success or failure of agricultural production, and increasingly sophisticated techniques often accompanied agricultural intensification (Fuller, 2020). Some of the earliest arable farmers harnessed the natural environment through “least-effort” cultivation on floodplains, as these areas offered fertile soils enriched by seasonal flooding, along with a reliable supply of water (Ma et al., 2016). Later, arable farmers developed infrastructure to manage water supply either to enable cultivation on land that required irrigation, or to utilize waterlogged or frequently flooded land through drainage (Langlie, 2018; Zhuang et al., 2025). This utilization or management of water is argued to have enabled early farmers not only to continue producing food in unpredictable climates but also to create agricultural surpluses that are thought to have underpinned the development of complex societies (Zhuang et al., 2014). While broad patterns of natural and managed water use in prehistoric agriculture are well-documented, the study of past water management regimes primarily relies on indirect evidence such as traces of irrigation infrastructure and weed ecology (Petrie and Bates, 2017; Zhuang et al., 2025). These methods often fall short in accurately reconstructing past water conditions, restricting interpretations to a coarse resolution. Analysis of $\delta^{34}\text{S}$ values of archaeological crop remains may have the potential to elucidate past regimes of water management for cultivation and to determine the hydrological conditions under which agricultural production was taking place (Stevens et al., 2022), particularly if dryland bioavailable sulfur $\delta^{34}\text{S}$ baselines derived from local geological and marine sulfur can be well-characterized.

In addition to supporting early agricultural development and intensification, the human manipulation of natural wet and waterlogged environments and the creation of engineered wetlands for crop production are likely to have resulted in environmental harms to the immediate environment and beyond. Such detrimental effects could have included biodiversity loss, the disruption of sediment cycling, and increases in greenhouse gas emissions (Erickson, 1992; Fuller et al., 2011; Marston and Scott Branting, 2016; Robinson and Lambrick, 1984). By studying archaeological crop $\delta^{34}\text{S}$ we may be able to further our

understanding of the timing and extent of these practices to clarify the likely extent of the environmental damage associated with managing water and wetlands for crop production.

The effects of past water management techniques on archaeological crop $\delta^{34}\text{S}$ depends on the hydrology of the technique involved, and any waterlogging adaptation of the crop grown (Table 1). Here we suggest which model scenario (Section 4.) would best represent a particular past water management technique for specific crops. Rice and taro are probably the only truly flood adapted crops able to oxidize sulfide in the rhizosphere and to thrive when partially submerged (Abiko and Miyasaka, 2020; Nishiuchi et al., 2012). In the natural environment some wild rice and taro species would have grown in permanent wetlands which were likely to have included flow-through and standing water hydrology (Fullagar et al., 2006; Müller et al., 2010; Zheng et al., 2009; Zong et al., 2007) (Figures 3A, B). Under paddy cultivation, flow-through systems and standing water systems were likely used to grow wet rice and taro (Kay et al., 2019; Lee et al., 2014), depending on water source availability, with paddy drainage before harvest. Where such seasonal drainage occurred this would have removed much of the sulfate in overlying water and allowed oxidation of sulfide in the soil, which would then have become available for uptake by catch crops, as in the case of the rice-wheat system (Bates et al., 2017) (Figures 3A, B, followed by Figure 3C). Irrigation techniques which involved temporarily submerging soil, for example by engineered trapping of seasonal flood waters, would have suited cultivation of crops with some waterlogging tolerance such as dry rice, sorghum, and barnyard millet (Bates et al., 2017; Bhinda et al., 2023; Kay et al., 2019; Khalifa and Eltahir, 2023; Dal Corso et al., 2022; Neumann, 2018 (Figure 3C).

Similarly, crops grown after natural drainage of flood waters would have been cultivated in environments with seasonally high groundwater levels such as riverbanks, floodplains, lake margins, river valley lowlands, and ridge and furrow on low lying, poorly draining soil, and were likely to be able to tolerate temporary flooding and high groundwater levels in the root zone (Brechtbühl et al., 2024; Hamerow et al., 2020; Kay et al., 2019; Kingwell-Banham, 2019; Motuzaite-Matuzeviciute et al., 2012; Ortlöff, 2009). Where simultaneous flooding and drainage was engineered, cultivation may also have taken place at elevations above the reach of high groundwater levels, and crop plants may not have required flood tolerance (Figure 3D). Raised fields, floating fields, and sunken gardens, found in the Americas and parts of Africa (Blatrix et al., 2022; Comptour et al., 2018; Erickson, 1987; Frederick, 2007; Ortlöff, 2009), would have enabled a steady supply of water to reach plant roots while protecting crops from waterlogging. It is possible, therefore, that in cases where dryland environmental $\delta^{34}\text{S}$ baselines can be established, and in combination with other contextual information, analysis of $\delta^{34}\text{S}$ in archaeological crop remains could be useful to differentiate between different wetland utilization strategies, as represented in our four modeled scenarios (Figures 3A–D).

5.2 Signals from past climate adaptation

Where changes in $\delta^{34}\text{S}$ values are found in charred archaeological grains from the same site across different phases,

TABLE 1 Past wetland utilization and water management techniques for crop cultivation, showing example crops grown using these techniques, the hydrological type they correspond to (**Figures 3A–D**), and examples of geographical regions and periods associated with techniques were found (examples included in *italics* with references).

Technique	Example crops	Model systems	Geographical examples
Wetland marsh/swamp utilization and cultivation	Rice*/taro*	a–b	Asia/Africa/South East Asia
<i>E.g., rice, China, c. 7000 BP; taro, Papua New Guinea, c. 2500 BP^{1–5}</i>			
Floodplain cultivation	Rice*/taro*	a–b	Asia/Africa/South East Asia
<i>E.g., rice, Northern India c. 4000 BP, Central and Western Africa c. 2500 BP; taro, Hawaii c. 600 BP^{5–7}</i>			
Lake margin utilization and cultivation (flooded)	Rice*/taro*	b	Asia/Africa/South East Asia
<i>E.g., rice, India, c. 1000 BP, China, c. 4000 BP^{8,9}</i>			
Bunded flooded paddy field with flow-through or standing water	Rice*/taro*	a or b	Asia/Africa/South East Asia
<i>E.g., taro, West and Central Africa pre-colonial, rice, Korea c. 3450 BP^{7,10}</i>			
Terraced cultivation with flow-through or standing water	Rice*/taro*	a or b	Asia/Africa/South East Asia
<i>E.g., rice, Korea c. 3450 BP, The Philippines, pre colonia^{10,11}</i>			
Rice-wheat flooded-drained	Rice*/wheat	a–b followed by c	Asia/Africa
<i>E.g., rice followed by wheat or barley, India c.5000 BP¹²</i>			
Seasonally trapped floodwaters in bunded fields	Sorghum	c	Africa
<i>E.g., sorghum, West and Central Africa, pre-colonial⁷</i>			
Riverbank cultivation (drained)	Barley, wheat, oats/rice/maize/pearl millet, sorghum	c	Northern Europe/the Americas/Africa
<i>E.g., rice, Northern India c. 4000 BP⁶</i>			
Lake margin cultivation (drained)	Barley, wheat, oats/maize/pearl millet, sorghum	c	Northern Europe/the Americas/Africa
<i>E.g., wheat and barley, Macedonia, c. 7500 BP¹³</i>			
Floodplain utilization and cultivation (drained)	Barley, wheat, oats/maize/pearl millet, broomcorn millet, sorghum	c	Northern Europe/the Americas/Africa
<i>E.g., broomcorn millet, Eastern Europe, c. 2500 BP¹⁴</i>			
Ridge and furrow	Barley, wheat, oats, rye	c	Northern Europe/Peru
<i>E.g., wheat and barley, Northern Europe, medieval period, maize, beans, squash, Peru, pre-Columbian^{15,16}</i>			
Raised fields on seasonally flooded savannas	Maize, beans, squash	d	Peru, Bolivia, Mesoamerica
<i>E.g., West and Central Africa, pre-colonial, multiple crops, Congo, Zambia historical, Bolivia and French Guiana, pre-Columbian^{7,17–20}</i>			
Sunken gardens intercepting water table	Maize, beans, squash	d	Peru, Bolivia, Mesoamerica
<i>E.g., multiple crops, Peru, pre-Columbian¹⁶</i>			
Floating fields on lakes and marshes	Maize, beans, squash	d	Mexico, Africa
<i>E.g., multiple crops, Mexico, pre-Columbian²¹</i>			

*Wetland adapted plant.

1. Fuller et al., 2010; 2. Zheng et al., 2009; 3. Zong et al., 2007; 4. Fullagar et al., 2006; 5. Müller et al., 2010; 6. Kingwell-Banham, 2019; 7. Kay et al., 2019; 8. Thakur et al., 2018; 9. Fuller and Ling Qin, 2009; 10. Lee et al., 2014; 11. Acabado et al., 2019; 12. Bates et al., 2017; 13. Brechbühl et al., 2024; 14. Motuzaite-Matuzeviciute et al., 2012; 15. Hamerow et al., 2020; 16. Orloff, 2009; 17. Comptour et al., 2018; 18. Blatrix et al., 2022; 19. Renard et al., 2013; 20. Erickson, 1987; 21. Frederick, 2007.

this could suggest different water management practices or environmental change through time, especially if this can be supported by information from weed ecology or weed phytoliths. Since its domestication, rice has been cultivated using wet (flooded) and rainfed (dryland) methods. Switches between cultivation methods, and expansion into higher yielding wet rice cultivation have been linked to changes in climate in Iron

Age North-eastern Thailand and the Lower Yangtze, China between 7000 and 6000 BP (Castillo et al., 2018; Patalano et al., 2015). These studies could be further elucidated by investigating variations in $\delta^{34}\text{S}$ of charred archaeological rice from these sites which may be associated with changes in cultivation method, and to ascertain whether signals correspond in time to changes seen in climate proxies. We would expect significantly

lower $\delta^{34}\text{S}$ values from rice cultivated using wet techniques with flow-through hydrology than from rice grown using the rainfed method.

5.3 Sulfur isotopes in human and animal collagen and wetland resource use

Sulfur in human and animal bone and dentine collagen is derived through diet. At the base of the food chain, sulfur, an essential nutrient for plants, is taken up as sulfate from soil. Once within the plant, sulfur is used to make amino acids cysteine and methionine, and many other compounds (Hill et al., 2022; Li et al., 2022). Sulfur is passed up the food chain with minimal trophic enrichment when plants are eaten, so plant $\delta^{34}\text{S}$ is broadly conserved during the transfer of sulfur from plants to animals (Cavallaro et al., 2022; Krajcarz et al., 2019; Nehlich, 2015; Raoult et al., 2024; Tcherkez and Tea, 2013). Collagen in bones and dentine primarily consists of type 1 collagen, and its sulfur content arises exclusively from methionine (Anné et al., 2019). Therefore, most sulfur preserved in archaeological collagen is derived from the essential amino acid methionine, which is only synthesized by plants. With respect to the transfer of $\delta^{34}\text{S}$ from plants to animals, it is not known whether the overall (bulk) plant $\delta^{34}\text{S}$ is close to, or is significantly different from plant methionine $\delta^{34}\text{S}$. It has been suggested that plant methionine $\delta^{34}\text{S}$ could differ significantly from the $\delta^{34}\text{S}$ of bulk plant material. This is because methionine is produced via a series of reactions which may cause isotopic fractionations in both directions, possibly resulting in an overall isotopic offset (Tcherkez and Tea, 2013). Clarification would require studies using compound-specific measurements of plant methionine $\delta^{34}\text{S}$ in comparison to bulk plant $\delta^{34}\text{S}$ from the same samples. However, until such studies are published, useful information can be found in two controlled animal feeding studies, which compared faunal bone collagen $\delta^{34}\text{S}$ against plant material feed with characterized bulk plant $\delta^{34}\text{S}$ (Tanz and Schmidt, 2010; Webb et al., 2017). These studies found a very small isotopic offset in animal bone collagen $\delta^{34}\text{S}$ (which is primarily from methionine) relative to the bulk $\delta^{34}\text{S}$ of plant-based feed (-0.5‰ , Tanz and Schmidt, 2010; $-1.5 \pm 0.8\text{‰}$; Webb et al., 2017). This suggests bulk plant $\delta^{34}\text{S}$ is similar to plant methionine $\delta^{34}\text{S}$, and that bulk plant $\delta^{34}\text{S}$ can be used to represent “base of the food chain” $\delta^{34}\text{S}$ values in archaeological studies of bone and tooth collagen within a small margin of error. In this way, herbivore bone collagen $\delta^{34}\text{S}$ can be seen as an integrator of environmental signals carried in plant $\delta^{34}\text{S}$ as plant $\delta^{34}\text{S}$ reflects the environment in which the plant grew. See Tanz and Schmidt (2010), and Tcherkez and Tea (2013), for further details on plant sulfur metabolism and isotopic fractionation, Anné et al. (2019) for discussion of collagen synthesis and sulfur preservation in archaeological bones and Devignes et al. (2022), for detailed information on the role of amino acids including methionine in bones.

Some studies also use $\delta^{34}\text{S}$ of archaeological keratin from antlers, horns, hooves and hair. However, sulfur in keratin is mainly in the form of the non-essential amino acid cysteine which can be synthesized by mammals from various dietary sources of sulfur, such that keratin may be a less direct tracer of wetland

environments than collagen $\delta^{34}\text{S}$. Despite this, evidence for a relatively minor effect from isotopic fractionation during sulfur uptake into keratin is also suggested by controlled feeding studies and wild animal tracking (Kabalika et al., 2023; Richards et al., 2003).

The incorporation of a wetland $\delta^{34}\text{S}$ signal into bone and dentine collagen has the potential both to complicate and enhance the interpretation of archaeological human and faunal isotope data. In addition, wetland $\delta^{34}\text{S}$ signals may overlap geologically driven $\delta^{34}\text{S}$ baselines, particularly where geological $\delta^{34}\text{S}$ reflects past large-scale microbial sulfate reduction. The incorporation of a wetland $\delta^{34}\text{S}$ signal by mammals via diet is relevant for studies of hunter gathers, mobile pastoralists, and sedentary agricultural communities. For example, significant wild wetland resources use by hunter gatherers could potentially be seen in human collagen $\delta^{34}\text{S}$ (Rand et al., 2021). Similarly, where a significant proportion of human dietary methionine intake originated from crops cultivated on wetlands and from livestock which grazed on or were foddered from the wetlands, a wetland $\delta^{34}\text{S}$ signal from plants will be reflected in the consumer's collagen $\delta^{34}\text{S}$. This could be used to indicate the cultivation of wetlands by early agricultural communities.

Variations in the magnitude of a wetland signal in human and animal collagen $\delta^{34}\text{S}$ could originate from differences in the proportion of dietary protein from a waterlogged or recently drained environment over time. For example, this could occur with different farming strategies for floodplain use including floodplain grazing, seasonal fodder using floodplain grown plants, and flood recession arable farming (Figures 4A–C).

With well-characterized dryland baseline $\delta^{34}\text{S}$, serial analysis of $\delta^{34}\text{S}$ in dentine collagen from archaeological herbivore teeth could provide high-resolution insights into ancient farming practices, including the movement of animals across regions with different geologies and the use of resources from wetlands or recently drained areas within landscapes. Dentine protein, which comprises c. 90% collagen (Goldberg et al., 2004), records a time series of isotopic inputs from diet which is unchanged after deposition. Dentine growth bands form in hypsodont herbivore teeth every few months (Zazzo et al., 2006), potentially recording seasonal signals in dentine collagen. Thus, incremental $\delta^{34}\text{S}$ analysis of hypsodont tooth dentine collagen, as has been conducted for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Diez-Canseco and Tornero, 2024), could be used to explore different floodplain utilization scenarios (e.g., Figures 4A–C), perhaps with seasonal climate signals constrained by incremental analysis of $\delta^{18}\text{O}$ in enamel bioapatite adjusted for differences in timing and mineralization processes between dentine and enamel (Balasse, 2002).

6 Conclusions

This work highlights the dynamic nature of sulfur isotope baselines affected by sulfur cycling in wet and waterlogged environments, while acknowledging the complexity of establishing local dryland $\delta^{34}\text{S}$ baselines derived from geological and marine sulfur against which to assess potential wetland signals for archaeological applications. Wetland effects on bioavailable sulfur $\delta^{34}\text{S}$ can both confound and

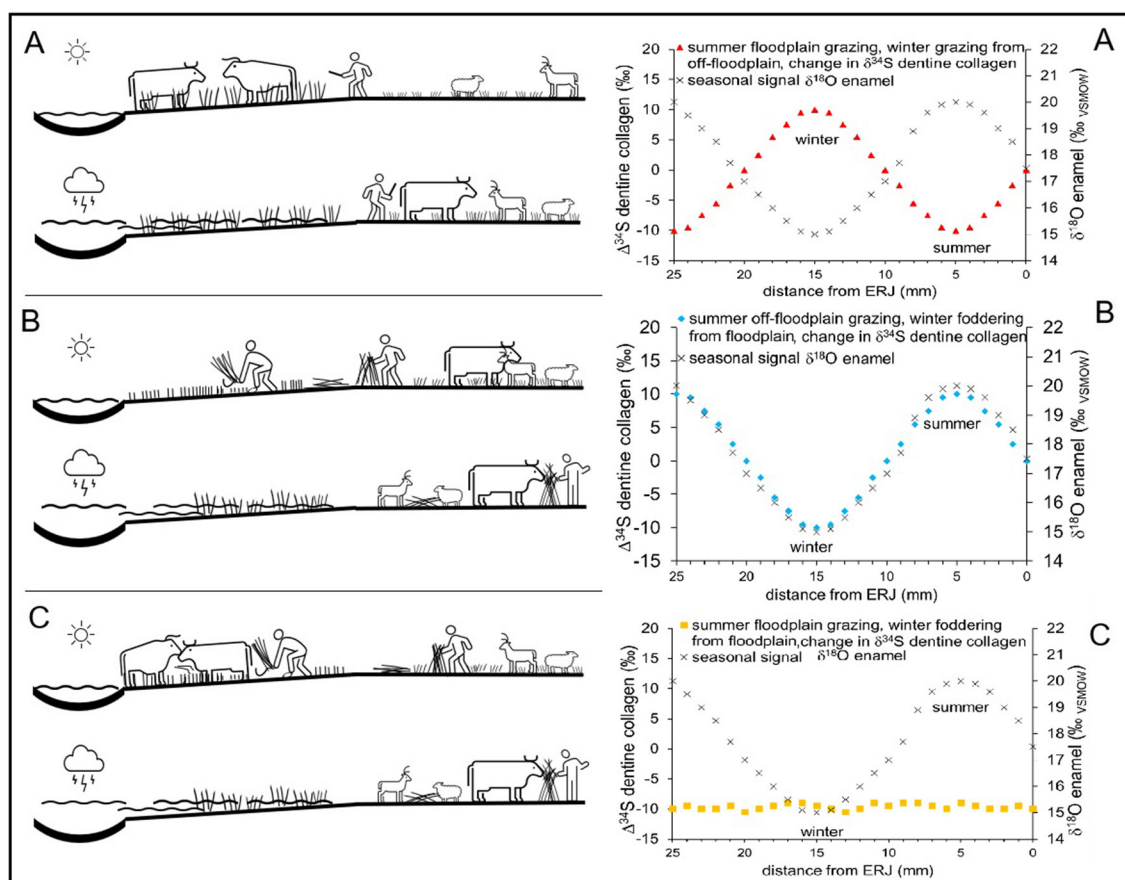


FIGURE 4

Illustrations of three possible floodplain utilization scenarios leading to different incorporation of sulfate reduction signals into cattle dentine collagen $\delta^{34}\text{S}$ [left-hand panels (A–C)], with corresponding patterns of expected changes in sulfur isotopic composition ($\Delta^{34}\text{S}$) where 0‰ on the left hand axis refers to no change, with $\delta^{18}\text{O}$ in millimeter increments of dentine and enamel [right-hand panels (A–C)], which may be revealed by serial analysis.

enrich the interpretation past human and animal movement and crop production, and provide exciting new avenues for archaeological investigation.

This study provides a step toward integrating palaeo sulfur cycling into archaeological isotope studies, but there is much further work to be done. The complex interactions between physiochemical conditions that support isotopically fractionating microbial sulfate reduction and subsequent sulfide oxidation, with varied isotope effects, hydrology and differences in plant sulfate and oxidized sulfide uptake, lead to potentially wide ranges of plant $\delta^{34}\text{S}$. Wetland signals may overlap geological $\delta^{34}\text{S}$ and mimic the effects of movement and diet in faunal and human archaeological collagen $\delta^{34}\text{S}$. Factors affecting the isotope effect of sulfate reduction, plant uptake ratios and soil sulfur source ratios are not well-characterized, yet are key to our understanding of $\delta^{34}\text{S}$ in bioarchaeological material. Further studies are needed to understand these interactions so they can be better resolved for use in archaeological studies in relation to natural and manipulated waterlogged environments. We emphasize the necessity of acknowledging possible effects from coeval sulfur cycling when interpreting $\delta^{34}\text{S}$ values in bioarchaeological material. Where it is possible to resolve a wetland $\delta^{34}\text{S}$ signal in collagen or archaeological crop remains, this could

provide important new information about past resource use, early farming techniques, and animal feeding patterns. Wetlands, both natural and engineered, have long been integral to human subsistence and agricultural innovation, from the fertile floodplains of early farmers to the sophisticated irrigation and drainage systems that sustained complex societies. With further knowledge, $\delta^{34}\text{S}$ analysis of bioarchaeological material could become a powerful tool for directly tracing past wetland use and water management strategies.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding authors.

Author contributions

SKW: Writing – review & editing, Conceptualization, Writing – original draft, Methodology. RES: Writing – review & editing, Writing – original draft, Methodology, Conceptualization.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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References

- Abiko, T., and Miyasaka, S. C. (2020). Aerenchyma and barrier to radial oxygen loss are formed in roots of Taro (*Colocasia esculenta*) propagules under flooded conditions. *J. Plant Res.* 133, 49–56. doi: 10.1007/s10265-019-01150-6
- Acabado, S. B., Koller, J. M., Liu, C., Lauer, A. J., Farahani, A., Barretto-Tesoro, G., et al. (2019). The short history of the Ifugao rice terraces: a local response to the Spanish conquest. *J. Field Arch.* 44, 195–214. doi: 10.1080/00934690.2019.1574159
- Ando, T., Yoshida, S., and Nishiyama, I. (1983). Nature of oxidizing power of rice roots. *Plant Soil* 72, 57–71. doi: 10.1007/BF02185094
- Aneja, V. P. (1990). Natural sulfur emissions into the atmosphere. *J. Air Waste Man. Ass.* 40, 469–476. doi: 10.1080/10473289.1990.10466701
- Anné, J., Edwards, N. P., Brigidi, F., Gueriau, P., Harvey, V. L., Geraki, K., et al. (2019). Advances in bone preservation: identifying possible collagen preservation using sulfur speciation mapping. *Palaeogeog. Palaeoclimatol. Palaeoecol.* 520, 181–187. doi: 10.1016/j.palaeo.2019.01.030
- Ayala, G., Bogaard, A., Charles, M., and Wainwright, J. (2022). Resilience and adaptation of agricultural practice in Neolithic Çatalhöyük, Turkey. *World Archaeol.* 54, 407–428. doi: 10.1080/00438243.2022.2125058
- Balasse, M. (2002). Reconstructing dietary and environmental history from enamel isotopic analysis: time resolution of intra-tooth sequential sampling. *Int. J. Osteoarchaeol.* 12, 155–165. doi: 10.1002/oa.601
- Ballantyne, R., Cooper, A., and Rajkovača, V. (2024). “Food,” in *Must Farm Pile-Dwelling Settlement Volume 1. Landscape, Architecture and Occupation*, eds M. Knight, R. Ballantyne, M. Brudenell, A. Cooper, D. Gibson, and I. Robinson Zeki. (McDonald Institute Monographs, University of Cambridge), 173–204. Available online at: <https://www.repository.cam.ac.uk/handle/1810/365343>
- Bataille, C. P., Chartrand, M. M. G., Raposo, F., and St-Jean, G. (2020). Assessing geographic controls of hair isotopic variability in human populations: a case-study in Canada. *PLoS ONE* 15:e0237105. doi: 10.1371/journal.pone.0237105
- Bates, J., Petrie, C. A., and Singh, R. N. (2017). Approaching rice domestication in South Asia: new evidence from Indus settlements in northern India. *J. Archeol. Sci.* 78, 193–201. doi: 10.1016/j.jas.2016.04.018
- Bhinda, M. S., Joshi, D. C., Parihar, M., Meena, R. P., Joshi, P., Gupta, A., et al. (2023). “Genetics, breeding, and genomics of Indian barnyard millet (*Echinochloa frumentacea*): status and perspectives,” in *Neglected and Underutilized Crops: Future Smart Food*, eds M. Farooq, and K. H. M. Siddique (Amsterdam: Academic Press; Elsevier), 115–135. doi: 10.1016/B978-0-323-90537-4.00017-X
- Blatrix, R., Aramayo, J. L., Zangerlé, A., Roux, B., Jouanne, M., Anselme, B., et al. (2022). Interpreting landscapes of pre-Columbian raised-field agriculture using high-resolution LiDAR topography. *J. Archaeol. Sci. Report* 42:103408. doi: 10.1016/j.jasrep.2022.103408
- Bottrell, S. H., and Newton, R. J. (2006). Reconstruction of changes in global sulphur cycling from marine sulphate isotopes. *Earth-Sci. Rev.* 75, 59–83. doi: 10.1016/j.earscirev.2005.10.004
- Bottrell, S. H., and Raiswell, R. (2000). “Sulphur isotopes and microbial sulphur cycling in sediments,” in *Microbial Sediments*, eds R. E., Riding, and S. M. Awramik (Berlin, Heidelberg: Springer), 96–104. doi: 10.1007/978-3-662-04036-2_12
- Brechbühl, S., van Vugt, L., Gobet, E., Morales-Molino, C., Volery, J., Lotter, A. F., et al. (2024). Vegetation dynamics and land-use change at the Neolithic lakeshore settlement site of Ploča Mičov Grad, Lake Ohrid, North Macedonia. *Veget. Hist. Archaeobot.* 33, 247–267. doi: 10.1007/s00334-023-00931-3
- Canfield, D. E. (2001). Biogeochemistry of sulfur isotopes. *Rev. Min. Geochem.* 43, 607–636. doi: 10.2138/gsrmg.43.1.607
- Carlson, P. R., and Forrest, J. (1982). Uptake of dissolved sulfide by *Spartina alterniflora*: evidence from natural sulfur isotope abundance ratios. *Science* 216, 633–635. doi: 10.1126/science.216.4546.633
- Castillo, C. C., Higham, C. F. W., Miller, K., Chang, N., Douka, K., Higham, T. F. G., et al. (2018). Social responses to climate change in Iron Age north-east Thailand: new archaeobotanical evidence. *Antiquity* 92, 1274–1291. doi: 10.15184/aqy.2018.198
- Cavallaro, V., Maghrebi, M., Caschetto, M., Sacchi, G. A., and Nocito, F. F. (2022). Sulfur stable isotope discrimination in rice: a sulfur isotope mass balance study. *Front. Plant Sci.* 13:837517. doi: 10.3389/fpls.2022.837517
- Chaudhary, S., Singh Sindhu, S., Rinku Dhanker, R., and Anju Kumari, A. (2023). Microbes-mediated sulphur cycling in soil: impact on soil fertility, crop production and environmental sustainability. *Microbiol. Res.* 271:127340. doi: 10.1016/j.micres.2023.127340
- Chung, C. H., You, C. F., Hsu, S. C., and Liang, M. C. (2019). Sulfur isotope analysis for representative regional background atmospheric aerosols collected at Mt. Lulin, Taiwan. *Sci. Rep.* 9:19707. doi: 10.1038/s41598-019-56048-z
- Chung, I. M., Lee, T. J., Oh, Y. T., Kumar Ghimire, B., Jang, I. B., and Kim, S. H. (2017). Ginseng authenticity testing by measuring carbon, nitrogen, and sulfur stable

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fearc.2025.1599779/full#supplementary-material>

isotope compositions that differ based on cultivation land and organic fertilizer type, *J. Ginseng Res.*, 41, 195–200. doi: 10.1016/j.jgr.2016.03.004

Claypool, G. E., Holser, W. T., Kaplan, I. R., Sakai, H., and Israel Zak, I. (1980). The age curves of sulfur and oxygen isotopes in marine sulfate and their mutual interpretation. *Chem. Geol.* 28, 199–260. doi: 10.1016/0009-2541(80)90047-9

Comptour, M., Caillon, S., Rodrigues, L., and McKey, D. (2018). Wetland raised-field agriculture and its contribution to sustainability: ethnoecology of a present-day African system and questions about pre-Columbian systems in the American tropics. *Sustainability* 10:3120. doi: 10.3390/su10093120

Cornwell, J. C., Neill, C., and Stevenson, J. C. (1995). Biogeochemical origin of $\delta^{34}\text{S}$ isotopic signatures in a prairie marsh. *Can. J. Fish. Aquat. Sci.* 52, 1816–1820. doi: 10.1139/B95-174

Czère, O., Lawson, J. A., Müldner, G., Evans, J., Boyle, A., and Britton, K. (2022). The bodies in the 'bog': a multi-isotope investigation of individual life-histories at an unusual 6th/7th AD century group burial from a Roman latrine at Cramond, Scotland. *Archaeol. Anthropol. Sci.* 14:67. doi: 10.1007/s12520-022-01509-2

Dal Corso, M., Pashkevych, G., Filipović, D., Liu, X., Motuzaite-Matuzeviciute, G., Stobbe, A., et al. (2022). Between cereal agriculture and animal husbandry: millet in the early economy of the north Pontic Region. *J. World Prehist.* 35, 321–374. doi: 10.1007/s10963-022-09171-1

de la Cruz Jiménez, J., Pellegrini, E., Pedersen, O., and Nakazono, M. (2021). Radial oxygen loss from plant roots-methods. *Plants* 10:2322. doi: 10.3390/plants10112322

Devignes, C., Carmeliet, G., and Stegen, S. (2022). Amino acid metabolism in skeletal cells. *Bone Rep.* 17:101620. doi: 10.1016/j.bonr.2022.101620

Diez-Canseco, C., and Tornero, C. (2024). New methods for old challenges: a sampling protocol for sequential stable isotope analysis ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of dentine collagen in higher-crowned teeth. *J. Archaeol. Sci.* 162:105923. doi: 10.1016/j.jas.2023.105923

Dušek, J., Darenová, E., Pavelka, M., and Marek, M. V. (2020). "Methane and carbon dioxide release from wetland ecosystems," in *Climate Change and Soil Interactions*, eds M. Narasimha, V. Prasad, and M. Pietrzykowski (Amsterdam: Elsevier), 509–553. doi: 10.1016/B978-0-12-818032-7.00019-9

Ebert, C. E., Rand, A. J., Green-Mink, K., Hoggarth, J. A., Freiwald, C., Awe, J. J., et al. (2021). Sulfur isotopes as a proxy for human diet and mobility from the preclassic through colonial periods in the Eastern Maya lowlands. *PLoS ONE* 16:e0254992. doi: 10.1371/journal.pone.0254992

Erickson, C. L. (1987). "The dating of raised field agriculture in the Lake Titicaca basin of Peru," in *Pre-Hispanic Agricultural Fields in the Andean Region*, eds W. M. Denevan, K. Mathewson, and G. Knapp (Oxford: British Archaeological Reports, International Series, BAR Publishing), 373–383.

Erickson, C. L. (1992). Prehistoric landscape management in the Andean highlands: raised field agriculture and its environmental impact. *Pop. Environ.* 13, 285–300. doi: 10.1007/BF01271028

Evans, J. A., Mee, K., Chenery, C. A., and Marchant, A. P. (2023). Biosphere isotope domains GB (V2): interactive website. *British Geological Survey (Dataset)* (accessed February 10, 2025).

Frederick, C. D. (2007). "Chinampa cultivation in the basin of Mexico," in *Seeking a Richer Harvest. Studies in Human Ecology and Adaptation*, vol 3, eds T. L. Thurston, and C. T. Fisher (Boston, MA: Springer), 107–124. doi: 10.1007/978-0-387-32762-4_5

Fry, B., O'Mara, K., Riekenberg, P. M., Wassenaar, L. I., and Cormier, N. (2023). Flexitraits, natural chemical tracers of plant competition and productivity in pacific mangroves. *Wetlands* 43:31. doi: 10.1007/s13157-023-01672-9

Fry, B., Scanlan, R. S., Winters, K. J., and Parker, P. L. (1982). Sulphur uptake by salt grasses, mangroves, and seagrasses in anaerobic sediments. *Geoch. Cosmochim. Acta* 46, 1121–1124. doi: 10.1016/0016-7037(82)90063-1

Fullagar, R., Field, J., Denham, T., and Lentfer, C. (2006). Early and mid Holocene tool-use and processing of taro (*Colocasia esculenta*), yam (*Dioscorea* sp.) and other plants at Kuk Swamp in the highlands of Papua New Guinea. *J. Archaeol. Sci.* 33, 595–614. doi: 10.1016/j.jas.2005.07.020

Fuller, D. Q. (2020). Transitions in productivity: rice intensification from domestication to urbanisation. *Archaeol. Int.* 23, 88–103. doi: 10.14324/111.444.ai.2020.08

Fuller, D. Q., and Ling Qin, L. (2009). Water management and labour in the origins and dispersal of Asian rice. *World Archaeol.* 41, 88–111. doi: 10.1080/00438240802668321

Fuller, D. Q., Sato, Y. I., Castillo, C., Ling Qin, L., Weisskopf, A. R., Kingwell-Banham, E. J., et al. (2010). Consilience of genetics and archaeobotany in the entangled history of rice. *Archaeol. Anthropol. Sci.* 2, 115–131. doi: 10.1007/s12520-010-0035-y

Fuller, D. Q., van Etten, J., Manning, K., Castillo, C., Kingwell-Banham, E., Weisskopf, A., et al. (2011). The contribution of rice agriculture and livestock pastoralism to prehistoric methane levels: an archaeological assessment. *Holocene* 21, 743–759. doi: 10.1177/0959683611398052

Goldberg, M., Septier, D., Bourd, K., and Menashi, S. (2004). Role of matrix proteins in signalling and in dentin and enamel mineralisation. *Comptes Rendus Palevol* 3, 573–581. doi: 10.1016/j.crpv.2004.07.005

Guiry, E., Noël, S., and Fowler, J. (2021). Archaeological herbivore $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ provide a marker for saltmarsh use and new insights into the process of ^{15}N -enrichment in coastal plants. *J. Archaeol. Sci.* 125:105295. doi: 10.1016/j.jas.2020.105295

Guiry, E. J., Orchard, T. J., Needs-Howarth, S., and Szpak, P. (2022). Freshwater wetland-driven variation in sulfur isotope compositions: implications for human paleodiet and ecological research. *Front. Ecol. Evol.* 10:953042. doi: 10.3389/fevo.2022.953042

Guiry, E. J., and Szpak, P. (2020). Seaweed-eating sheep show that $\delta^{34}\text{S}$ evidence for marine diets can be fully masked by sea spray effects. *RCMS* 34:e8868. doi: 10.1002/rcm.8868

Hamerow, H., Bogaard, A., Charles, M., Forster, E., Holmes, M., McKerracher, M., et al. (2020). An integrated bioarchaeological approach to the Medieval 'Agricultural Revolution': a case study from Stafford, England, c. ad 800–1200. *Europ. J. Archaeol.* 23, 585–609. doi: 10.1017/ea.2020.6

Hill, C. R., Shafaei, A., Balmer, L., Lewis, J. R., Hodgson, J. M., A., et al. (2022). Sulfur compounds: from plants to humans and their role in chronic disease prevention. *Crit. Rev. Food Sci. and Nutr.* 63, 8616–8638. doi: 10.1080/10408398.2022.2057915

Hillman, G., Hedges, R., Moore, A., Colledge, S., and Pettiitt, P. (2001). New evidence of Lateglacial cereal cultivation at Abu Hureyra on the Euphrates. *Holocene* 11, 383–393. doi: 10.1191/095968301678302823

Hiscock, K. M., and Bense, V. (2021). *Hydrogeology: Principles and Practice*, 3rd Edn. New Jersey: Wiley-Blackwell.

Högborg, P. (1997). Tansley review No. 95. ^{15}N natural abundance in soil-plant systems. *New Phytol.* 137, 179–203. doi: 10.1046/j.1469-8137.1997.00808.x

Huisman, D. J., and Raemaekers, D. C. M. (2014). Systematic cultivation of the Swifterbant wetlands (The Netherlands). Evidence from Neolithic tillage marks (c. 4300–4000 cal. BC). *J. Archaeol. Sci.* 49, 572–584. doi: 10.1016/j.jas.2014.05.018

Kabalika, Z., Haydon, D. T., McGill, R. A. R., Morales, J. M., Thomas, A., Morrison, T. A., et al. (2023). Using sulfur stable isotope ratios ($\delta^{34}\text{S}$) for animal geolocation: estimating the delay mechanisms between diet ingestion and isotope incorporation in tail hair. *Rapid Commun. Mass Spectrom.* 38:e9674. doi: 10.1002/rcm.9674

Kay, A. U., Fuller, D. Q., Neumann, K., Eichhorn, B., Höhn, A., Morin-Rivat, J., et al. (2019). Diversification, intensification and specialization: changing land use in western Africa from 1800 BC to AD 1500. *J. World Prehist.* 32, 179–228. doi: 10.1007/s10963-019-09131-2

Kendall, C., and Caldwell, E. A. (1998). "Isotope tracers in catchment hydrology," in *Fundamentals of Isotope Geochemistry*, eds C. Kendall, J. J. McDonnell (Amsterdam: Elsevier), 51–86. doi: 10.1016/B978-0-444-81546-0.50009-4

Khalifa, M., and Eltahir, E. A. B. (2023). Assessment of global sorghum production, tolerance, and climate risk. *Front. Sustain. Food Syst.* 7:1184373. doi: 10.3389/fsufs.2023.1184373

Kilham, K. (1994). *Soil Ecology*. Cambridge: Cambridge University Press. doi: 10.1017/9780511623363

Kingwell-Banham, E. (2019). Dry, rainfed or irrigated? Reevaluating the role and development of rice agriculture in Iron Age-Early Historic South India using archaeobotanical approaches. *Archaeol. Anthropol. Sci.* 11, 6485–6500. doi: 10.1007/s12520-019-00795-7

Krajcarz, M. T., Krajcarz, M., Drucker, D. G., and Bocherens, H. (2019). Prey-to-fox isotopic enrichment of ^{34}S in bone collagen: implications for paleoecological studies. *RCMS* 33, 1311–1317. doi: 10.1002/rcm.8471

Kumar Rai, R., Singh, V. P., and Upadhyay, A. (2017). *Soil Analysis: Planning and Evaluation of Irrigation Projects*. Cambridge, MA: Academic Press, 505–523. doi: 10.1016/B978-0-12-811748-4.00017-0

Lamb, A. L., Chenery, C. A., Madgwick, R., and Evans, J. A. (2023). Wet feet: developing sulfur isotope provenance methods to identify wetland inhabitants. *R. Soc. Open Sci.* 10:230391. doi: 10.1098/rsos.230391

Lamers, L. P., Govers, L. L., Janssen, I. C. J. M., Geurts, J. J. M., Van der Welle, M. E. W., Van Katwijk, M. M., et al. (2013). Sulfide as a soil phytotoxin: a review. *Front. Plant Sci.* 4:268. doi: 10.3389/fpls.2013.00268

Langlie, B. S. (2018). Building ecological resistance: late intermediate period farming in the south-central highland Andes (CE 1100–1450). *J. Anthropol. Archaeol.* 52, 167–179. doi: 10.1016/j.jaa.2018.06.005

Lee, H., French, C., and Macphail, R. I. (2014). Microscopic examination of ancient and modern irrigated paddy soils in South Korea, with special reference to the formation of silty clay concentration features. *Geoarchaeology* 29, 326–348. doi: 10.1002/gea.21478

Li, L., Dong, X., He, M., Huang, M., Cai, J., Zhou, Q., et al. (2023). Unravelling the role of adventitious roots under priming-induced tolerance to waterlogging stress in wheat. *Environ. Exp. Bot.* 216:105516. doi: 10.1016/j.envexpbot.2023.105516

Li, Q., Gao, Y., and Yang, A. (2022). Sulfur homeostasis in plants. *Int. J. Mol. Sci.* 21:8926. doi: 10.3390/ijms21238926

Ma, T., Zheng, Z., Rolett, B. V., Lin, G., Zhang, G., and Yue, Y. (2016). New evidence for Neolithic rice cultivation and Holocene environmental change in the Fuzhou

- Basin, southeast China. *Veget. Hist. Archaeobot.* 25, 375–386. doi: 10.1007/s00334-016-0556-0
- Mariotti, A., Germon, J. C., Hubert, K., Kaiser, P., Letolle, R., and Tardieux, A., Tardieux, P. (1981). Experimental determination of nitrogen kinetic isotope fractionation: some principles; illustration for the denitrification and nitrification processes. *Plant Soil* 62, 413–430. doi: 10.1007/BF02374138
- Marshall, T. J., and Holmes, J. W. (1996). *Soil Physics, 3rd Edn.* CUP. Available online at: <https://doi-org.libproxy.ucl.ac.uk/10.1017/CBO9781139170673> (Accessed April 21, 2025).
- Marston, J. M., and Scott Branting, S. (2016). Agricultural adaptation to highland climate in Iron Age Anatolia. *J. Arch. Sci. Rep.* 9, 25–32. doi: 10.1016/j.jasrep.2016.06.050
- Maruyama-Nakashita, A. (2017). Metabolic changes sustain the plant life in low-sulfur environments. *Curr. Opin. Plant Biol.* 39, 144–151. doi: 10.1016/j.pbi.2017.06.015
- Matsuura, A., Kato, Y., Suzuki, T., Murata, K., and Ping, A. (2022). Hypoxia tolerance of four millet species is attributable to constitutive aerenchyma formation and root hair development of adventitious roots. *Plant Prod. Sci.* 25, 157–171. doi: 10.1080/1343943X.2021.2021092
- Motuzaita-Matuzeviciute, G., Telizhenko, S., and Jones, M. K. (2012). Archaeobotanical investigation of two Scythian-Sarmatian period pits in eastern Ukraine: implications for floodplain cereal cultivation. *J. Field Archaeol.* 37, 51–61. doi: 10.1179/0093469011Z.0000000004
- Müller, J. G., Ogneva-Himmelberger, Y., Lloyd, S., and Reed, J. M. (2010). Predicting prehistoric taro (*Colocasia esculenta* var. *antiquorum*) Lo'i Distribution in Hawaii. *Econ. Bot.* 64, 22–33. doi: 10.1007/s12231-010-9113-4
- Nehlich, O. (2015). The application of sulphur isotope analyses in archaeological research: a review. *Earth Sci. Rev.* 142, 1–17. doi: 10.1016/j.earscirev.2014.12.002
- Nehlich, O., Borić, D., Stefanović, S., and Richards, M. P. (2010). Sulphur isotope evidence for freshwater fish consumption: a case study from the Danube Gorges, SE Europe. *J. Archaeol. Sci.* 37, 1131–1139. doi: 10.1016/j.jas.2009.12.013
- Neumann, K. (2018). Development of plant food production in the West African Savannas: archaeobotanical perspectives. *Oxf. Res. Encycl. Afr. Hist.* doi: 10.1093/acrefore/9780190277734.013.138
- Nishiuchi, S., Yamauchi, T., Takahashi, H., Kotula, L., and Nakazono, M. (2012). Mechanisms for coping with submergence and waterlogging in rice. *Rice* 5:2. doi: 10.1186/1939-8433-5-2
- Nitsch, E. K., Lamb, A. L., Heaton, T. H. E., Vaiglova, P., Fraser, R., Hartman, G., et al. (2019). The Preservation and interpretation of $\delta^{34}\text{S}$ values in charred archaeobotanical remains. *Archaeometry* 61, 161–178. doi: 10.1111/arc.12388
- Norman, A. L., Giesemann, A., Krouse, H. R., and Jager, H. J. (2002). Sulphur isotope fractionation during sulphur mineralization: results of an incubation-extraction experiment with a Black Forest soil. *Soil Biol. Biochem.* 34, 1425–1438. doi: 10.1016/S0038-0717(02)00086-X
- Ortloff, C. R. (2009). *Water Engineering in the Ancient World: Archaeological and Climate Perspectives on Societies of Ancient South America, the Middle East, and South-East Asia.* Oxford. doi: 10.1093/oso/9780199239092.001.0001
- Paladin, A., Moghaddam, N., Stawinoga, A. E., Siebek, I., Depellegrin, V., Tecchiati, U., et al. (2020). Early medieval Italian Alps: reconstructing diet and mobility in the valleys. *Archaeol. Anthropol. Sci.* 12:82. doi: 10.1007/s12520-019-00982-6
- Pan, J., Sharif, R., Xu, X., and Chen, X. (2021). Mechanisms of waterlogging tolerance in plants: research progress and prospects. *Front. Plant Sci.* 11:627331. doi: 10.3389/fpls.2020.627331
- Parent, C., Capelli, N., Berger, A., Crevêcoeur, M., and Dat, J. (2008). An overview of plant responses to soil waterlogging. *Plant Stress* 2, 20–27.
- Pasquier, V., Bryant, R. N., Fike, D. A., and Halevy, I. (2021). Strong local, not global, controls on marine pyrite sulfur isotopes. *Sci. Adv.* 7:eabb7403. doi: 10.1126/sciadv.abb7403
- Patalano, R., Wang, Z., Leng, Q., Liu, W., Zheng, Y., Sun, G., et al. (2015). Hydrological changes facilitated early rice farming in the lower Yangtze River Valley in China: a molecular isotope analysis. *Geology* 43, 639–642. doi: 10.1130/G36783.1
- Paytan, A., and Gray, E. T. (2012). “Sulfur isotope stratigraphy,” in *The Geologic Time Scale*, eds F. M. Gradstein, J. G. Ogg, M. D. Schmitz, and G. M. Ogg (Boston, MA: Elsevier), 167–180. doi: 10.1016/B978-0-444-59425-9.00009-3
- Pellerin, A., Antler, G., Holm, S. A., Findlay, A. J., Crockford, P. W., Turchyn, A. V., et al. (2019). Large sulfur isotope fractionation by bacterial sulfide oxidation. *Sci. Adv.* 5:eaaaw1480. doi: 10.1126/sciadv.aaw1480
- Peterson, B. J., Howarth, R. W., and Garritt, R. H. (1986). Sulfur and carbon isotopes as tracers of salt-marsh organic matter flow. *Ecology* 67, 865–874. doi: 10.2307/1939809
- Petrie, C. A., and Bates, J. (2017). ‘Multi-cropping’, intercropping and adaptation to variable environments in Indus South Asia. *J. World Prehist.* 30, 81–130. doi: 10.1007/s10963-017-9101-z
- Price, F. T., and Casagrande, D. J. (1991). Sulfur distribution and isotopic composition in peats from the Okefenokee Swamp, Georgia and the Everglades, Florida. *Int. J. Coal Geol.* 17, 1–20. doi: 10.1016/0166-5162(91)90002-Z
- Privat, K. L., O’Connell, T. C., and Hedges, R. E. M. (2007). The distinction between freshwater and terrestrial-based diets: methodological concerns and archaeological applications of sulphur stable isotope analysis. *J. Archaeol. Sci.* 34, 1197–1204. doi: 10.1016/j.jas.2006.10.008
- Rand, A. J., Freiwald, C., and Grimes, V. (2021). A multi-isotopic ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$) faunal baseline for Maya subsistence and migration studies. *J. Archaeol. Sci. Rep.* 37:102977. doi: 10.1016/j.jasrep.2021.102977
- Raoult, V., Phillips, A. A., Nelson, J., Niella, Y., Skinner, C., Bell Tilcock, M., et al. (2024). Why aquatic scientists should use sulfur stable isotope ratios ($\delta^{34}\text{S}$) more often. *Chemosphere* 355:141816. doi: 10.1016/j.chemosphere.2024.141816
- Ren, Z., Ma, K., Jia, X., Wang, Q., Zhang, C., and Li, X. (2023). Metagenomics unveils microbial diversity and their biogeochemical roles in water and sediment of thermokarst lakes in the yellow river source area. *Microb. Ecol.* 85, 904–915. doi: 10.1007/s00248-022-02053-1
- Renard, D., Birk, J. J., Zangerlé, A., Lavelle, P., Glaser, B., Blatrix, R., et al. (2013). Ancient human agricultural practices can promote activities of contemporary non-human soil ecosystem engineers: a case study in coastal savannas of French Guiana. *Soil Biol. Biochem.* 62, 46–56. doi: 10.1016/j.soilbio.2013.02.021
- Richards, M. P., Fuller, B. T., Sponheimer, M., Robinson, T., and Ayliffe, L. (2003). Sulphur isotopes in palaeodietary studies: a review and results from a controlled feeding experiment. *Int. J. Osteoarchaeol.* 13, 37–45. doi: 10.1002/OA.654
- Robinson, M., and Lambrick, G. (1984). Holocene alluviation and hydrology in the upper Thames basin. *Nature* 308, 809–814. doi: 10.1038/308809a0
- Sayle, K. L., Brodie, C. R., Cook, G. T., and Hamilton, W. D. (2019). Sequential measurement of $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ values in archaeological bone collagen at the Scottish Universities Environmental Research Centre (SUERC): a new analytical frontier. *RCMS* 33, 1258–1266. doi: 10.1002/rcm.8462
- Seal, R. R. (2006). Sulfur Isotope geochemistry of sulfide minerals. *Rev. Min. Geochem.* 61, 633–677. doi: 10.2138/rmg.2006.61.12
- Shaffer, P. W., Kentula, M. E., and Gwin, S. E. (1999). Characterization of wetland hydrology using hydrogeomorphic classification. *Wetlands* 19:490504. doi: 10.1007/BF03161688
- Sherratt, A. (1980). Water, soil and seasonality in early cereal cultivation. *World Archaeol.* 11, 313–330. doi: 10.1080/00438243.1980.9979770
- Sim, M. S., Bosak, T., and Ono, S. (2011). Large sulfur isotope fractionation does not require disproportionation. *Science* 333, 74–77. doi: 10.1126/science.1205103
- Sim, M. S., Ono, S., and Bosak, T. (2012). Effects of iron and nitrogen limitation on sulfur isotope fractionation during microbial sulfate reduction. *Appl. Environ. Microbiol.* 78, 8368–8376. doi: 10.1128/AEM.01842-12
- Sim, M. S., Woo, D. K., Kim, B., Jeong, H., Joo, Y. J., Hong, Y. W., et al. (2023). What controls the sulfur isotope fractionation during dissimilatory sulfate reduction? *ACS Environ. Au* 3, 76–86. doi: 10.1021/acsenvironau.2c00059
- Simkin, S. M., Bedford, B. L., and Weathers, K. C. (2013). Phytotoxic sulfide more important than nutrients for plants within a groundwater-fed wetland. *Ecosystems* 16, 1118–1129. doi: 10.1007/s10021-013-9671-2
- Stack, P. E., and Rock, L. (2011). A $\delta^{34}\text{S}$ isoscape of total sulphur in soils across Northern Ireland. *Appl. Geochem.* 26, 1478–1487. doi: 10.1016/j.apgeochem.2011.05.021
- Steffens, B., and Rasmussen, A. (2016). The physiology of adventitious roots. *Plant Physiol.* 170, 603–617. doi: 10.1104/pp.15.01360
- Stevens, R. E., Reade, H., Read, D. S., Bottrell, S. H., Frémondeau, D., and Wexler, S. (2022). Iso-Wetlands: unlocking wetland ecologies and agriculture in prehistory through sulfur isotopes. *Archaeol. Int.* 25, 168–176. doi: 10.14324/111.444.ai.2022.11
- Stevens, R. E., Reade, H., Sayle, K., Tripp, J., Frémondeau, D., Lister, A., et al. (2025). Major excursions in sulfur isotopes linked to permafrost change in Eurasia during the last 50,000 Years. *Nat. Geosci.* (in press).
- Stribling, J. M., and Cornwell, J. C. (1997). Identification of important primary producers in a Chesapeake Bay tidal creek system using stable isotopes of carbon and sulfur. *Estuaries* 20, 77–85. doi: 10.2307/1352721
- Stribling, J. M., Cornwell, J. C., and Currin, C. (1998). Variability of stable sulfur isotopic ratios in *Spartina alterniflora*. *Mar. Ecol. Prog. Ser.* 166, 73–81. doi: 10.3354/meps166073
- Tanz, N., and Schmidt, H. L. (2010). $\delta^{34}\text{S}$ -value measurements in food origin assignments and sulfur isotope fractionations in plants and animals. *J. Agric. Food Chem.* 58, 3139–3146. doi: 10.1021/jf903251k
- Tcherkez, G., and Tea, I. (2013). $^{32}\text{S}/^{34}\text{S}$ isotope fractionation in plant sulphur metabolism. *New Phytol.* 200, 44–53. doi: 10.1111/nph.12314
- Thakur, B., Saxena, A., and Singh, I. B. (2018). Paddy cultivation during early Holocene: evidence from diatoms in Lahuradewa lake sediments. *Ganga Plain. Curr. Sci.* 114, 2106–2115. doi: 10.18520/cs/v114/i10/2106-2115

- Vitòria, L., Otero, N., Soler, A., and Canals, À. (2004). Fertilizer characterization: isotopic data (N, S, O, C, and Sr). *Environ. Sci. Tech.* 38, 3254–3262. doi: 10.1021/es0348187
- Wang, J., He, Y., Tang, Y., Liu, L., Li, Y., Chen, X., et al. (2023). An interplay of dryland and wetland: millet and rice cultivation at the Peiligang site (8000–7600 BP) in the middle Yellow River Valley, China. *Agronomy* 13:2130. doi: 10.3390/agronomy13082130
- Webb, E. C., Newton, J., Lewis, J., Stewart, A., Millerd, B., Tarlton, J. F., et al. (2017). Sulphur-isotope compositions of pig tissues from a controlled feeding study. *Star Sci. Tech. Archaeo. Res.* 3, 71–79. doi: 10.1080/20548923.2017.1368821
- Winter, T. C. (1999). Relation of streams, lakes, and wetlands to groundwater flow systems. *Hydrogeol. J.* 7, 28–45. doi: 10.1007/s100400050178
- Yamauchi, T., Shimamura, S., Nakazono, M., and Mochizuki, T. (2013). Aerenchyma formation in crop species: a review. *Field Crops Res.* 152, 8–16. doi: 10.1016/j.fcr.2012.12.008
- Zavodny, E., McClure, S. B., Culleton, B. J., Podrug, E., Balen, J., Drnić, I., et al. (2022). Investigating past livestock mobility using $\delta^{34}\text{S}$ stable isotopes: three preliminary case studies from prehistoric Croatia. *Open Quat.* 8, 1–15. doi: 10.5334/oq.113
- Zazzo, A., Balasse, M., and Patterson, W. P. (2006). The reconstruction of mammal individual history: refining high-resolution isotope record in bovine tooth dentine. *J. Archaeol. Sci.* 33, 1177–1187. doi: 10.1016/j.jas.2005.12.006
- Zerkle, A. L., Farquhar, J., Johnston, D. T., Cox, R. P., and Canfield, D. E. (2009). Fractionation of multiple sulfur isotopes during phototrophic oxidation of sulfide and elemental sulfur by a green sulfur bacterium. *Geochim. Cosmoch. Acta.* 73, 291–306. doi: 10.1016/j.gca.2008.10.027
- Zheng, Y., Sun, G., Qin, L., Li, C., Wu, X., and Chen, X. (2009). Rice fields and modes of rice cultivation between 5000 and 2500 BC in east China. *J. Archaeol. Sci.* 36, 2609–2616. doi: 10.1016/j.jas.2009.09.026
- Zhuang, Y., Ding, P., and French, C. (2014). Water management and agricultural intensification of rice farming at the late-Neolithic site of Maoshan, Lower Yangtze River, China. *Holocene* 24, 531–545. doi: 10.1177/0959683614522310
- Zhuang, Y., Ding, P., Zhuang, L., Wang, Y., Wu, W., Wang, X., et al. (2025). Geoarchaeological study of the evolution of rice farming fields in prehistoric Yangtze Delta and Huai River regions of China. *Quat. Sci. Rev.* 356:109293. doi: 10.1016/j.quascirev.2025.109293
- Zong, Y., Chen, Z., Innes, J. B., Chen, C., Wang, Z., and Wang, H. (2007). Fire and flood management of coastal swamp enabled first rice paddy cultivation in east China. *Nature* 449, 459–462. doi: 10.1038/nature06135