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Perspective

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Redox control on rhizosphere priming in wetlands

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Rhizosphere priming describes a positive or negative change in the rate of soil organic matter decomposition caused by root activity and represents an important terrestrial soil–climate feedback. Few studies have investigated rhizosphere priming in wetlands, despite their disproportionate role in the global soil carbon budget. Here we present a literature analysis to show that both positive and negative rhizosphere priming can be much stronger in wetland than upland ecosystems. We argue that differences in plant–soil microbial interactions between dominantly oxic and anoxic soil environments induce the different degrees of rhizosphere priming effects. A conceptual framework is proposed in which wetland plants control soil redox status by acting as sources of both electron donors and acceptors, thereby influencing soil carbon stability through interactions with microbial communities. We identify key uncertainties in the mechanistic and quantitative understanding of wetland rhizosphere priming and demonstrate how priming could govern wetland soil carbon dynamics and ecosystem stability in response to climate change.

Microbial decomposition of soil organic matter (SOM) is a critical component of the climate system because it determines CO_2 and CH_4 fluxes from the vast carbon reserves of Earth's soil organic carbon (SOC) stock to the atmosphere. Climate change-sensitive abiotic factors such as soil moisture and temperature affect SOM decomposition rates and thereby soil–climate feedbacks. However, predictions of soil–climate feedbacks based solely on the abiotic controls of microbial activity are insufficient because they cannot capture the important interactions between primary producers and decomposers in response to abiotic change[1]. In particular, the biotic interactions between plant roots and soil microbes in the rhizosphere can play a strong, sometimes overriding, role in controlling SOM decomposition in response to abiotic change via rhizosphere priming effects (RPEs)[2,3]. Rhizosphere priming describes a change in SOM decomposition rate caused by root activity[4]. Mechanistic and quantitative insight into RPEs has been almost exclusively developed from terrestrial studies on plant–soil interactions in croplands, grasslands and forests[5]. Although there are several hypotheses explaining RPEs in upland soils (Table 1), the release of organic compounds from roots (that is, rhizodeposition) is considered to be a primary factor[4,6].

By comparison, little is known about the relevance and potential drivers of RPEs in the reducing soils of wetlands, despite the fact that they preserve carbon more efficiently and store more carbon per unit area than other ecosystems. Wetlands store about one-third of the global SOC pool on less than 5% of the land area[7,8]. The consequences of RPEs in wetlands for global soil–climate feedbacks may therefore be disproportionate to their area. It is possible that plant-mediated control of SOC stock stability via RPEs is particularly pronounced in wetland ecosystems, because wetland plants not only control the organic carbon (that is, electron donor) supply to microbial communities, but also the availability of terminal electron acceptors by providing oxygen to an otherwise reduced soil environment[9,10]. By regulating the supply of both electron donors and electron acceptors to the rhizosphere, wetland plants exert dual control over soil redox potential, a key regulator of SOC cycling[11].

Direction and strength of wetland priming

We conducted a systematic literature search for quantitative data on RPEs in wetland and upland ecosystems, yielding a total of 470 observations (wetland $n = 26$; upland $n = 444$) from 65 studies. RPE is quantified

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Table 1 | Overview of rhizosphere priming mechanisms proposed for upland soils and their applicability to reducing wetland soils

Upland priming mechanism	Direction	Underlying principle	Wetland applicability	Related references
Substrate-induced activation	Positive	• Root-derived substrates stimulate SOM decomposition for nutrient or energy acquisition from SOM • SOM decomposition stimulated by co-metabolism of SOM through microbial growth	• Limited because wetland SOM is relatively more stable in the absence of oxygen • Bioenergetic constraints and enzymic latch need to be circumvented for substrate inputs to stimulate SOM decomposition	4,12,20
Preferential substrate utilization	Negative	• Preference shift of the microbial community from SOM to root-derived substrates	• Plausible because of the low potential free energy yield of dominant classes of soil organic compounds under anoxia • Possible effect amplification as root-derived substrates increase microbial respiration and oxygen demand	12,19
Inhibiting plant metabolites	Negative	• Reduction of microbial activity through root release of inhibiting allelochemicals	• Plausible and potentially amplified for certain allelochemicals such as phenolics under anoxic conditions	13,38,71
Drying effect	Negative	• Root uptake of water reduces soil moisture below optimum levels for microbial activity	• Unimportant for waterlogged SOM pools but possible in soil environments with variable hydrology • Can act indirectly by phenol oxidase activity and iron-mediated SOC preservation • The opposite effect is possible in surface soils when root water uptake increases soil aeration by reducing waterlogging	71–73
Drying–rewetting	Positive	• Rewetting following root-induced soil drying triggers carbon release from microbial necromass, over-compensating for the drying reduction in SOM decomposition (related to the Birch effect)	• Not applicable to permanently waterlogged SOM pools but possible in soil environments with variable hydrology	4,74,75
Aggregate access and destabilization of mineral bonds	Positive	• Root growth breaks apart soil aggregates, enabling microbial access to previously protected SOM • Root exudates liberate organic compounds from mineral protection, enabling microbial access to previously protected SOM	• Limited in waterlogged soils because aggregation is poorly developed • Liberation of organic compounds from mineral protection may be relevant in mineral-rich wetland soils with fluctuating redox conditions • Root oxygen loss could counteract this process and stabilize SOM into mineral–organic associations (Fig. 3)	6,14,16,50
Nutrient competition and rhizosphere acidification	Negative or positive	• Root uptake of nutrients reduces microbial activity through nutrient limitation (negative) or stimulates microbial nutrient mining from SOM (positive) • Negative priming amplified by reduced microbial activity through rhizosphere acidification	• Nutrient limitation is a possible mechanism in nutrient-poor systems such as ombrotrophic peatlands • Possible because wetland redox chemistry is pH sensitive with indirect effects on decomposition	15,17,76
Plant–animal–microbe interactions	Positive	• Root activity facilitates soil faunal activity stimulating microbial turnover	• Possible because important mutualistic plant–animal interactions have been identified for wetland soils	77,78

here using the standard approach of calculating the relative change in SOM decomposition in relation to an unplanted control, either as percentage change or as log response ratio. It was not possible to standardize SOM decomposition rates to a common absolute flux unit for all observations (details are included in the Methods).

Despite the much lower number of wetland observations, the total RPE range was larger for wetlands than uplands (Fig. 1). Both the strongest positive RPE (+1,242% in wetlands versus 779% in uplands) and the strongest negative RPE (−92% versus −70%) occurred in wetlands (Figs. 1 and 2a,b). The non-unimodal data distribution within the wetland group differs from the unimodal upland distribution, implying that drivers of positive and negative RPEs may differ between ecosystem types (Fig. 1). Separate mixed-effects meta-analytical models of positive and negative priming show a greater potential for both processes in wetland than upland soils (Fig. 2 and Supplementary Table 1). The bidirectional (that is, sign-independent) priming strength is consequently greater in wetlands than uplands by a log response ratio of 0.69 (Fig. 2c), corresponding to an average of about twice as much rhizosphere priming in wetland studies. It is important to note that this higher bidirectional priming sensitivity in wetlands is unlikely to be the result of potentially lower rates of basal respiration, because no relationship exists between relative RPE intensity and absolute decomposition rates in unplanted controls (Supplementary Fig. 1)[5].

The limited data availability for wetlands precludes us from estimating average RPEs with the same precision already achieved for upland ecosystems[5]. Yet, our data do provide the first evidence for greater potential RPE control (both positive and negative) of SOC stability in wetland than upland ecosystems. Given the disproportionate role of wetlands in the global SOC budget, the scarcity of wetland RPE data is a critical knowledge gap in our understanding of biosphere–climate feedbacks.

Applying upland priming mechanisms to wetlands

Several RPE mechanisms have been proposed for upland soils (Table 1), most of which are related to the inputs of root-derived organic compounds (rhizodeposits) to the soil that stimulate, or

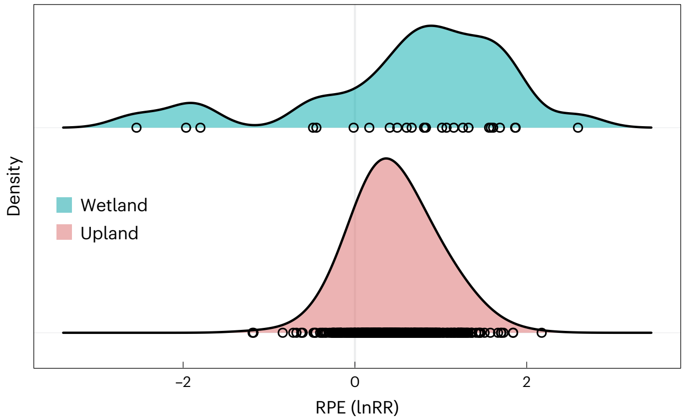

Fig. 1 | Distribution of rhizosphere priming effects. Change in SOM decomposition in planted versus unplanted soils (expressed as a log response ratio), comparing wetland and upland soils. The density distributions show the relative frequency of rhizosphere priming effects within their respective ranges within wetland (top) and upland (bottom) groups.

occasionally suppress, SOM decomposition[6]. Rhizodeposit-induced RPEs are mechanistically diverse and linked to distinct biogeochemical phenomena. Rhizodeposits can serve as microbial substrates[12], microbial inhibitors[13], ligands interacting with reactive minerals to liberate organic matter[14], and acids or bases that alter soil pH[15]. RPE mechanisms that are not directly linked to (but also not necessarily independent of) rhizodeposition include the physical destruction of soil aggregates through root growth[16] or root uptake of water and nutrients[17]. The applicability of these mechanisms to wetland biogeochemistry is uncertain due to the dominant role of redox status in SOM decomposition, which differs markedly between wetland and upland soils[18] (Table 1).

A common concept explaining positive RPEs through rhizodeposition in uplands is that the release of organic substrates from roots stimulates microbial activity and leads to increased SOM decomposition through microbial mining of growth-limiting nutrients from SOM or through the co-metabolism of SOM by the growing microbial community[4,19]. In wetlands, SOM preservation depends foremost on the absence of oxygen[20], although it is increasingly recognized that SOM stabilization in mineral–organic associations also plays a quantitatively important role in mineral-rich wetlands[21,22]. Organic compounds are preserved as SOM because the oxidation of a large fraction of these compounds, depending on their molecular composition and potential free energy yield, is thermodynamically limited without oxygen[11]. In addition to this bioenergetic constraint, phenolic compounds can accumulate in anoxic conditions and suppress the activity of microbial hydrolytic exo-enzymes[23], although, unlike energetic constraints, there is strong evidence both for and against this mechanism, suggesting that it does not operate universally[20,22,24].

When limits to the rate of decomposition are set by the supply of terminal electron acceptors, we can expect SOM decomposition rates to be relatively insensitive to an additional electron donor supply. We therefore argue that our finding of extremely high positive RPEs in wetlands (Fig. 2) is not driven by substrate inputs alone, but is at least enhanced by, if not primarily driven by, other mechanisms specific to wetland plant–microbe interactions. Indeed, several soil incubation studies show that SOM decomposition is insensitive to or decreases in response to substrate additions such as glucose or fresh litter under anoxic or flooded conditions[25–27]. However, there are similarly studies that demonstrate low to moderate rates of positive priming in response to substrate additions in wetland-soil incubations[27–29]. It remains to be evaluated whether these mixed results are caused by differences in SOM composition and age, as suggested for upland soils[30], or if other factors such as the availability of terminal electron acceptors other than oxygen regulate substrate-induced priming in wetlands.

Rhizodeposits can induce positive priming without directly serving as microbial substrates when functioning as ligands that liberate organic matter from protective associations with reactive minerals and thus increase microbial access[14] (Table 1). This mechanism is more complex in wetlands, because SOM preservation in mineral–organic associations is redox-controlled and relies on the availability of reactive metal oxides[31]. Anaerobic microbial metabolism in wetland soils liberates previously bound SOM from reactive mineral surfaces via reductive dissolution of metal oxides and associated pH changes[32,33]. However, mineral-rich wetland soils can contain large amounts of metal-oxide-protected SOM[21], probably facilitated by fluctuating redox conditions[34]. Consequently, rhizodeposit-driven liberation of organic matter from mineral associations is a possible pathway for positive RPEs in mineral-rich wetland soils, but is not sufficient to explain the extreme positive RPEs observed in organic-rich coastal marshes and peatlands (Fig. 2b).

A common hypothesis explaining negative RPEs in upland soils is similarly based on rhizodeposit-induced pathways: preferential microbial utilization of high-quality (that is, relatively nutrient-rich, energy-rich or microbially accessible) root-derived substrates over low-quality SOM leads to lower SOM decomposition in the presence of roots and thus negative priming (Table 1)[4]. Our quantitative survey suggests a greater potential for negative priming in wetland than upland soils (Fig. 2a). Anaerobic microbial communities preferentially utilize soluble compounds with high nominal oxidation states, such as carbohydrates and many amino acids[11,35,36], which are often dominant constituents of rhizodeposition[37]. Other compounds with low nominal oxidation states, which are relatively dominant in SOM, cannot be metabolized without oxygen as the terminal electron acceptor[11]. We therefore predict that preferential substrate utilization may yield even stronger negative priming in wetland than upland soils.

Rhizodeposits are not limited to plant primary metabolites such as sugars, organic acids and amino acids that serve as highly microbially available carbon, nutrient and energy sources[37]. They also include secondary metabolites, such as phenols, that are known to inhibit microbial activity (Table 1) and are capable of inducing negative priming under oxic conditions[13]. Phenol oxidase activity can be suppressed under anoxic conditions, potentially amplifying the inhibition through root-derived phenols on wetland SOM decomposition[23]. Currently, experimental data that could be used to test for the potential of root-derived metabolites to induce diverging or contrasting effects on microbial SOM decomposition under oxic versus anoxic conditions are scarce, representing an important knowledge gap in our understanding of wetland plant–microbe interactions[26,28,38] (Table 2).

Root-driven redox changes drive wetland priming

Established concepts of priming in upland soils do not suffice to explain wetland RPEs, particularly observations of twofold-stronger positive RPEs in wetland versus upland soils (Figs. 1 and 2). Such strong accelerations of SOM decomposition are unlikely to be the sole result of rhizodeposit-induced priming pathways, as proposed for upland systems, given the well-established influence of electron-acceptor limitation on SOM preservation in wetlands. We propose a conceptual framework of wetland priming that considers both positive and negative RPEs that arise from changes in the balance of electron acceptors versus donors, as reflected in soil redox potential (Fig. 3a). Plants can act as both oxidizers or reducers of the soil system, depending on their net effect on the electron acceptor versus donor balance[39], and thereby exert opposing effects on the rate of SOM decomposition. Our framework recognizes two fundamental rhizosphere mechanisms that drive SOC preservation under anoxic conditions in opposing directions: (1) a metabolic pathway in which SOC preservation is governed by the

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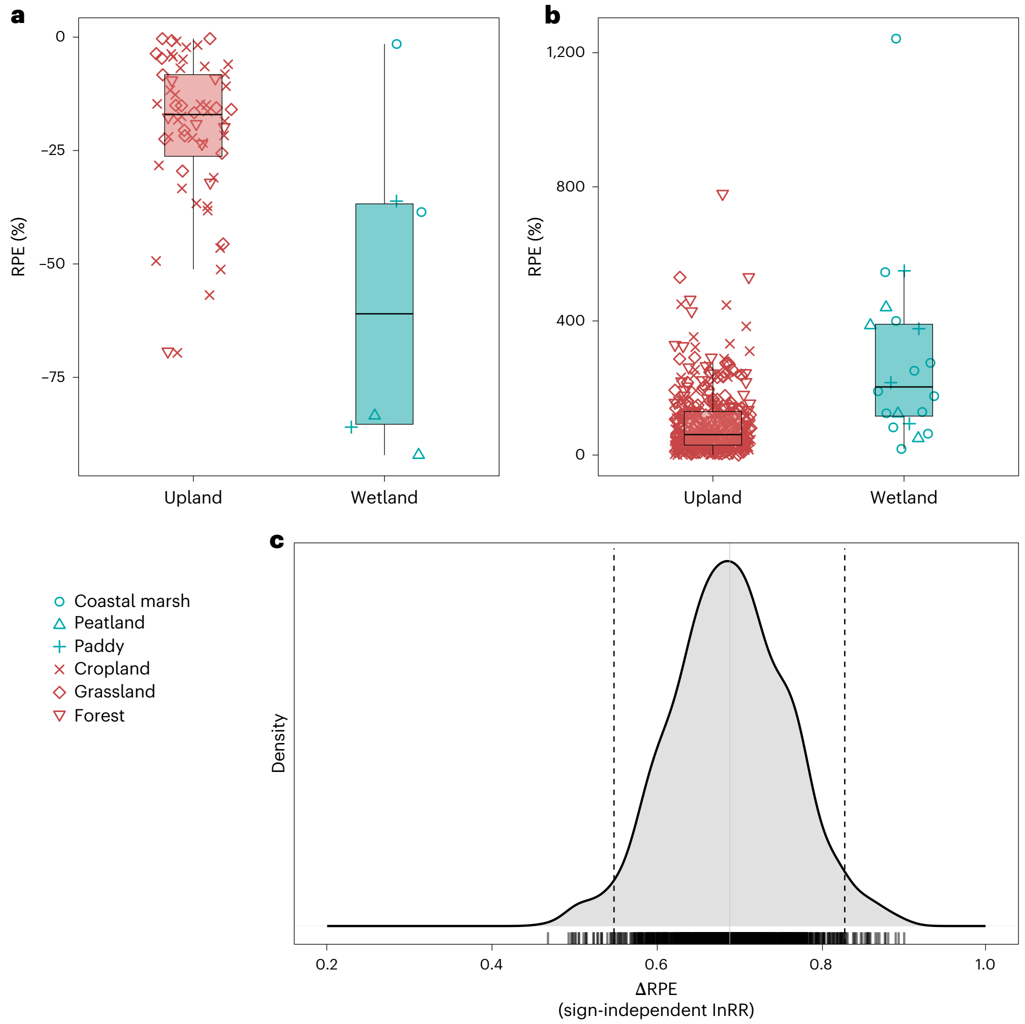

Fig. 2 | Comparison of rhizosphere priming effects. a,**b**, Percentage change in SOM decomposition in planted versus unplanted soils, comparing upland and wetland observations separately for negative RPEs (only RPEs < 0%; **a**) and positive RPEs (only RPEs > 0%; **b**). Notice the difference in *y*-axis scales. The boxplots show the median and interquartile range (IQR), with whiskers based on 1.5 IQR values. Single data points are overlaid. Ecosystem type (upland versus wetland) significantly moderates both negative priming ($P = 0.0056$) and positive priming ($P < 0.0001$) according to mixed-effects meta-analytical models (Supplementary Table 1). **c**, Estimate of the average moderator effect from a mixed-effects meta-analytical model (RPE difference between upland and wetland observations expressed as log response ratio) based on absolute (that is, sign-independent) RPE data determined through Monte Carlo resampling to address imbalanced moderator-group sizes. Shown is the density distribution of 1,000 mixed-effects meta-analytical models based on equal-group-size repeated random subsampling. Dashed vertical lines denote the 0.95 confidence interval. The solid grey vertical line represents the mean estimate. Note that our analysis of RPE distributions is robust against the impact of single potentially influential observations (Methods and Supplementary Table 2).

free energy yield of redox couples (Fig. 3b) and (2) a physicochemical pathway governed by the biogeochemistry of minerals (Fig. 3c).

Our concept predicts for the metabolic pathway of SOC preservation that positive rhizosphere priming occurs when plants act as net oxidizers and negative priming when plants act as net reducers with respect to rhizosphere effects on the soil redox state (Fig. 3b). Wetland plants release oxygen into otherwise anoxic soil systems, thereby directly increasing microbial oxygen availability and indirectly increasing the availability of alternative terminal electron acceptors. These include oxidation products such as nitrate, ferric iron and sulfate, as well as re-oxidized moieties in dissolved organic matter[40]. Oxygen is transported belowground to enable aerobic respiration in plant root and rhizome tissues, some portion of which crosses the rhizodermis into the soil, a process referred to as root (or radial) oxygen loss. Root oxygen loss is a critical plant trait that oxidizes phytotoxins such as hydrogen sulfide and improves plant nutrient uptake[41,42]. From a microbial perspective, root oxygen loss is a process that creates aerobic respiration hot spots and hot moments in which the free energy yield of respiration is dramatically increased and anoxic decomposition constraints on the breakdown of organic polymers are alleviated[42,43]. Thus, variation in root-driven oxygenation of the rhizosphere represents an obvious mechanism to explain large positive RPEs in wetlands. Evidence that net oxidation through root oxygen loss, as opposed to net reduction through organic carbon release, drives positive RPEs in wetlands comes from studies demonstrating a tight association of positive priming with plant-mediated increases in soil redox potential[10,44].

The more pronounced negative RPEs in wetlands than uplands (Figs. 1 and 2) call for a wetland-specific mechanism that either amplifies known upland RPE mechanisms or drives negative priming independently. Rhizosphere processes in wetland soils have the potential to do both. Preferential utilization of rhizodeposits over SOM may be particularly pronounced in wetland soils where anoxia makes decomposition of major SOM components with low nominal oxidation states energetically marginal or impossible[11,45,46]. Furthermore, root-derived substrate inputs that stimulate microbial respiration simultaneously drive electron acceptor depletion and thus likely amplify negative

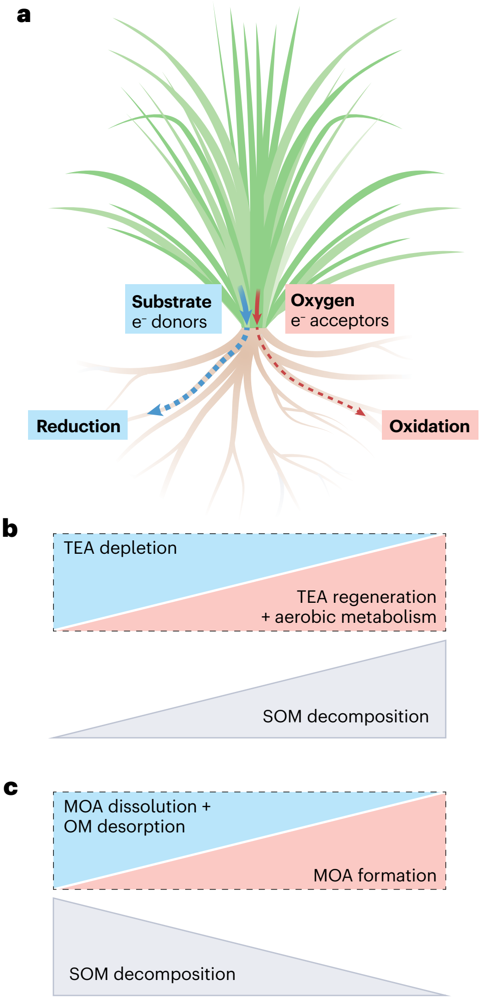

Fig. 3 | Redox mediation of wetland rhizosphere priming. a, Roots influence electron acceptor availability in two ways: directly as sources of electron acceptors (mainly oxygen) and indirectly as sources of electron donors (organic substrate) that deplete acceptors. **b**,**c**, The impact of root-driven redox shifts on SOM decomposition depends on the SOC preservation pathway, distinguished here as metabolic (**b**) and physicochemical (**c**). **b**, The limited availability of terminal electron acceptors (TEAs) constrains microbial respiration, preserving certain SOM components. Root oxygen loss enhances SOM decomposition by supporting aerobic metabolism and regenerating TEAs, whereas electron donor (organic substrate) input from roots via rhizodeposition depletes TEAs, preserving SOC. **c**, Redox changes affect mineral–organic associations (MOAs). Root oxygen loss promotes MOA formation by oxidizing metals that protect organic matter (OM) from decomposition. Conversely, root release of electron donors reduces metal oxides, liberating mineral-protected OM through reductive dissolution and rising pH.

priming (Fig. 3b). Root respiration also depletes electron acceptors by consuming soil oxygen, potentially contributing to redox-driven negative priming and SOC preservation[47,48]. Despite the theoretical importance of these mechanisms for wetland carbon cycling, observations of negative RPEs in wetlands are yet scarce (Fig. 1, $n = 6$), highlighting the need for more experimental, mechanistic research to test the hypotheses outlined here and evaluate the role of negative priming in wetland SOC preservation.

Our conceptual model ties the propensity of plants to drive priming to their propensity to oxidize (positive priming) or reduce (negative priming) the rhizosphere (Fig. 3a) given that anoxic decomposition constraints are the primary driver of SOC preservation in wetlands. However, redox-mediated priming can also respond in the opposite direction when regulated by physicochemical pathways of SOC preservation in mineral-rich wetland soils (Fig. 3c). The formation of mineral–organic associations that physically armour organic matter against microbial decomposition is facilitated by the oxidation of metals (Fig. 3c)[33,34]. In particular, iron-oxide-mediated SOC preservation mechanisms are important in mineral wetlands[21,49]. A recent investigation from a mineral salt marsh provided evidence that root oxygen loss facilitates SOC preservation by favouring oxidized iron precipitates that form strong physical and chemical associations with organic matter[50]. Furthermore, oxidation of ferrous to ferric iron can decrease phenol oxidase activity and thereby preserve wetland SOC[22]. Root oxygen loss in mineral-rich wetland soils is therefore a mechanism for negative priming through metal oxidation (Fig. 3c). Conversely, root inputs of electron donors can stimulate the microbial reduction of iron (and manganese) oxides, a process that liberates organic matter via reductive dissolution of mineral–organic associations and desorption of organic matter from minerals through rising pH, potentially leading to positive priming effects[14,32,33] (Fig. 3c).

Our goal is to contrast RPE mechanisms using the common upland–wetland dichotomy that exists in ecosystem science. Although this is useful for illustrating knowledge gaps, it fails to recognize the wide range of soil conditions in terrestrial ecosystems. Hypoxic and anoxic conditions exist across a continuum of spatial and temporal scales ranging from ephemeral anoxic microsites in dominantly oxic soils, to ephemeral oxic microsites in dominantly anoxic soils, to soils that fluctuate between oxic and anoxic conditions. Rhizosphere processes are at play across the full spectrum, which calls for a conceptual model of redox-driven priming effects as a redox continuum, as illustrated in Fig. 3.

Implications for soil carbon and ecosystem stability

Although our current understanding of the absolute quantitative impact of RPEs on wetland soil carbon budgets is limited, rhizosphere priming potentially exerts control on the stability of wetland ecosystems, because the formation and preservation of SOM are critical processes by which many wetlands generate bio-geomorphic feedbacks[8,51]. Positive priming may enhance nutrient supply to plants, promoting SOM formation, but at the same time stimulate SOM decomposition and thus reduce stability in wetland ecosystems that develop through SOM accumulation[52]. Because negative priming protects SOM from microbial decomposition, it is conceivable that wetland plants have evolved the ability to regulate negative priming to increase soil volume and support the spatial expansion of the ecosystem. This concept finds support in the wetland plant–microbe interaction involving peat mosses (*Sphagnum*), where negative priming-like pathways inhibit soil microbial activity, facilitating *Sphagnum* dominance[53].

RPEs can both amplify and mute climate change effects on wetland SOM decomposition. A number of reports from different wetland types demonstrate a key role for priming in mediating climate change effects on SOC stability. For instance, the climate change-driven encroachment of vascular plants in bryophyte-dominated peat bogs accelerates SOM decomposition[54–56]. In coastal wetlands, plant productivity is a quantitatively significant control on SOM decomposition in response to sea-level rise and elevated atmospheric CO_2 (refs. 10,44). It has consequently been argued that the integration of RPEs into decomposition models would greatly improve predictions on the stability of wetland SOC under climate change[57]. This will require an improved understanding of plant traits and associated rhizosphere processes that control priming and ultimately determine the direction and magnitude of its effect on the overall wetland SOC balance (Table 2).

Conclusions

Rhizosphere priming is an important terrestrial soil–climate feedback mechanism, but few studies have investigated this phenomenon in

Table 2 | Summary of key uncertainties and testable hypotheses regarding plant traits, environmental controls, and ecosystem and carbon-cycle consequences of wetland RPEs

	Uncertainties	Testable hypotheses
Plant traits	• Direction and magnitude of RPEs on wetland SOM decomposition are not predictable because we lack insight into plant eco-physiological processes and traits. • RPEs are driven by complex eco-physiological root traits. Linking these to easily measurable proxy traits or processes is critical to improve the predictability and modelling of wetland RPEs. • The spatio-temporal quantification of rhizodeposition and oxygen dynamics in root zones is highly challenging and necessitates methodological advancements. • Insight into rhizodeposit composition and the variable effects of specific rhizodeposit classes on SOM dynamics is scarce.	• Wetland RPEs are chiefly controlled by plant effects on soil redox through root oxygen loss (electron acceptor input) and root substrate input (electron donor input) (Fig. 3a). • In most wetland plant species, rhizosphere electron acceptor inputs exceed electron donor inputs. These species are net oxidizers with respect to their root-mediated redox control of SOM decomposition, resulting in predominantly positive RPEs (Fig. 3b). • In fewer species, rhizosphere electron donor inputs exceed electron acceptor inputs. These net reducers induce predominantly negative RPEs (Fig. 3b).
Environmental controls	• It is unclear how RPEs differ along environmental gradients and between wetland types characterized by differences in soil mineral and organic content, hydrology and the availability of specific alternative electron acceptors.	• Positive RPEs intensify with lower background soil redox, whereas strong negative RPEs depend on higher background redox conditions favouring the capacity for additional reduction. • As soil mineral content rises, the relevance of mineral-driven SOC stabilization increases. This enhances the likelihood that root oxygen loss will cause negative RPEs and root substrate inputs will cause positive RPEs (Fig. 3c).
Ecosystem and carbon-cycle consequences	• The role of RPEs in overall wetland soil carbon budgets and bio-geomorphic feedbacks is unclear. • We lack predictability of how RPEs mediate the effects of climate change on wetland SOC stock stability.	• Positive RPEs enhance ecosystem stability in wetlands where stabilizing bio-geomorphic feedbacks are limited by productivity and reduce stability in wetlands where decomposition-limiting feedbacks are stabilizing[8]. Negative RPEs exert opposing effects. • Plant community composition and associated traits determine the presence and magnitude of climate change effects on wetland SOC stock stability via positive and negative RPEs. Predictability will improve with a trait-based understanding of the RPE focused on redox chemistry.

the reducing soils of wetlands. Wetland and upland ecosystems share common RPE mechanisms, and the direction and magnitude of priming responses partly overlap (Fig. 1 and Table 1). However, there is evidence that wetland RPEs can be far more extreme, an observation in need of mechanistic explanations (Fig. 2 and Table 2). We propose a conceptual model of wetland priming that emphasizes relatively stronger redox regulation of SOM decomposition in wetland than upland soils, and considers both positive and negative RPEs as the result of variation in the balance of plant-sourced electron acceptors versus donors (Fig. 3). Plants act as oxidizers or reducers of the rhizosphere, thereby exerting opposing effects on the rate of SOM decomposition. We put forward a conceptual model to be tested broadly across diverse wetland types, and call for more mechanistic research on wetland plant–soil interactions.

Methods

Data basis

We conducted a quantitative survey to compare RPEs between wetland and upland soils. For this, we complemented the dataset of Huo and colleagues[5], who conducted the first meta-analysis on RPEs across terrestrial upland ecosystems for the publication years 1900–2016 using the Web of Science search strings (1) TS = rhizosphere AND TS = priming and (2) TS = rhizosphere AND TS = decomposition AND TS = isotope. Studies had to meet three criteria: (1) they report separately on the release of SOM-derived CO_2 and plant-derived CO_2 (which also includes the soil microbial respiration utilizing recent rhizodeposits) from a plant–soil system using a carbon-isotope-partitioning approach; (2) they include unplanted soil controls under the same conditions as the planted treatments; and (3) they were not conducted under wetland settings because of the drastically different soil conditions. Applying these criteria, Huo and colleagues obtained 191 observations from 31 articles. We complemented this dataset by adding the previously excluded wetland studies from the publication years 1900–2016 and by applying the same search strings for the publication years 2017–2022. Some studies did not report the separate values for unplanted and planted SOM decomposition but only reported the RPE based on these values. These studies were also included to enhance data availability. To ensure comprehensive coverage, we extended our search beyond the provided strings to include potential additional studies on wetland rhizosphere priming. We specifically examined the citations of ref. 10, the earliest empirical work on rhizosphere priming in wetlands about which we are aware. In total, the complemented dataset comprises 470 observations from 65 articles.

An observation was classified as a wetland observation when wetland soils were used under wetland-typical hydrological conditions, either in their natural field environment or in laboratory or greenhouse settings. In a few cases, the distinction between wetland or upland group was unclear, and observations were excluded from the analysis. These cases include studies on drained wet meadow soils[58] and drained bog and fen soils[59]. One of the wetland studies included[60] did not report unplanted–planted differences; instead, it compared communities lacking vascular plants (that is, only bryophytes) with those where vascular plants were present. As a result, our study's comparison was not strictly between planted and unplanted conditions, but rather between rhizosphere and non-rhizosphere scenarios, considering that bryophytes lack roots and vascular tissue.

Observations are here defined as averages and associated variances of values for each combination of within-study experimental grouping factors, such as plant species, soil type or nutrient treatment. For each observation we extracted (or calculated), mean effect sizes, log response ratio and percentage change, associated variances, information on ecosystem type, and within-study grouping factor. When data were presented in figures only, they were extracted using WebPlotDigitizer[61]. In cases when only mean effect sizes were reported but variances were missing and could not be calculated based on the information provided, we applied the 'missing cases' procedure following ref. 62.

Wetlands contributed 6% of the observations (26 out of 470), including coastal marshes ($n = 14$, refs. 10,44,63,64), peatlands ($n = 6$, refs. 60,65) and rice paddies ($n = 6$, ref. 66). The vast majority of observations were from upland ecosystems, dominated by croplands ($n = 237$), grasslands ($n = 139$) and forests ($n = 68$).

RPE calculation and reporting

RPEs are typically reported as a relative change in SOM decomposition in relation to an unplanted control, rather than as an absolute flux. We followed this procedure for two reasons: (1) we were unable to standardize SOM decomposition rates to a common absolute flux unit for all observations, as most studies reported rates per mass of soil, some per surface area, and others only as RPE (%); (2) relative (log response ratio-based) approaches enable comparisons across studies with a wide range of absolute baseline (unplanted control) values.

We calculated RPE as the ratio of SOM decomposition rate under planted versus unplanted control conditions as percentage change, RPE (%), or as log response ratio, RPE (lnRR), such that positive values indicate a relative increase in SOM decomposition rate in the presence of plants (that is, positive priming), and negative values a relative decrease (that is, negative priming).

Data analysis

This Perspective aims to describe the range and distribution of wetland RPE observations in relation to upland observations, using density plots and boxplots with single-point overlays (Figs. 1 and 2). These descriptive statistics were complemented with a mixed-effects meta-analytical approach to assess the effect of a two-level categorical moderator (upland versus wetland) on priming effect-size heterogeneity. Positive and negative priming were explored separately, addressing the non-unimodal and pronounced bidirectional distribution of wetland RPE observations and avoiding underestimates of absolute effect sizes (that is, strength independent of direction) owing to the cancellation of positive and negative values[67].

Prior to meta-analytical statistics, we aggregated observations from repeated measures to remove time dependency, resulting in 209 data points. We used mixed-effects meta-analytical models with ecosystem (upland versus wetland) as a moderator. These statistics were performed using the metafor package in R. Models included study ID as random factor. Funnel plots were used to assess potential publication bias[68].

We used Monte Carlo subsampling to complement this statistical approach and to assess the extent to which RPE differences between upland and wetland soils are robust to the imbalance in sample sizes and the relatively small sample size of the wetland group. Specifically, we drew a random subset of 19 observations from the upland group to match the sample size of the wetland group and then ran a mixed-effects meta-analytical model as described above. This process was repeated 1,000 times and outputs were combined (Fig. 2c and Supplementary Table 2)[69,70]. We ran these analyses on sign-independent RPE data to test for differences in RPE sensitivity (or strength) between wetland and upland soils independent of RPE direction (positive versus negative). Our results show that the difference in RPE strength is robust based on 1,000 comparisons of random subsets of equal group sizes (Fig. 2c). We ran an additional sensitivity analysis using the leave-one-out method to recompute the mean and confidence intervals. This approach is akin to the 1,000× resampling mixed-effects model described above (Fig. 2c), but involves systematically leaving out one observation at a time from the wetland group to assess the impact of potentially influential observations within the wetland group on mean effect-size differences. Our results show that the difference in priming strength remains robust (Supplementary Table 2).

Data availability

Data are available from our OSF data repository at https://doi.org/10.17605/OSF.IO/4V73N.

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41561-024-01584-1.

References

1. Bardgett, R. D., Freeman, C. & Ostle, N. J. Microbial contributions to climate change through carbon cycle feedbacks. *ISME J.* **2**, 805–814 (2008).
2. Keuper, F. et al. Carbon loss from northern circumpolar permafrost soils amplified by rhizosphere priming. *Nat. Geosci.* **13**, 560–565 (2020).
3. Hartley, I. P. et al. A potential loss of carbon associated with greater plant growth in the European Arctic. *Nat. Clim. Chang.* **2**, 875–879 (2012).
4. Kuzyakov, Y. Review: factors affecting rhizosphere priming effects. *J. Plant Nutr. Soil Sci.* **165**, 382–396 (2002).
5. Huo, C., Luo, Y. & Cheng, W. Rhizosphere priming effect: a meta-analysis. *Soil Biol. Biochem.* **111**, 78–84 (2017).
6. Dijkstra, F. A., Zhu, B. & Cheng, W. Root effects on soil organic carbon: a double-edged sword. *N. Phytol.* **230**, 60–65 (2021).
7. Gorham, E. Northern peatlands: role in the carbon cycle and probable responses to climatic warming. *Ecol. Appl.* **1**, 182–195 (1991).
8. Temmink, R. J. M. et al. Recovering wetland biogeomorphic feedbacks to restore the world's biotic carbon hotspots. *Science* **376**, 6593 (2022).
9. Armstrong, W. Radial oxygen losses from intact rice roots as affected by distance from the apex, respiration and waterlogging. *Physiol. Plant.* **25**, 192–197 (1971).
10. Wolf, A. A., Drake, B. G., Erickson, J. E. & Megonigal, J. P. An oxygen-mediated positive feedback between elevated carbon dioxide and soil organic matter decomposition in a simulated anaerobic wetland. *Glob. Chang. Biol.* **13**, 2036–2044 (2007).
11. Keiluweit, M., Nico, P. S., Kleber, M. & Fendorf, S. Are oxygen limitations under recognized regulators of organic carbon turnover in upland soils? *Biogeochemistry* **127**, 157–171 (2016).
12. Blagodatskaya, E. & Kuzyakov, Y. Mechanisms of real and apparent priming effects and their dependence on soil microbial biomass and community structure: critical review. *Biol. Fertil. Soils* **45**, 115–131 (2008).
13. Zwetsloot, M. J., Kessler, A. & Bauerle, T. L. Phenolic root exudate and tissue compounds vary widely among temperate forest tree species and have contrasting effects on soil microbial respiration. *N. Phytol.* **218**, 530–541 (2018).
14. Keiluweit, M. et al. Mineral protection of soil carbon counteracted by root exudates. *Nat. Clim. Chang.* **5**, 588–595 (2015).
15. Wang, X., Tang, C., Severi, J., Butterly, C. R. & Baldock, J. A. Rhizosphere priming effect on soil organic carbon decomposition under plant species differing in soil acidification and root exudation. *N. Phytol.* **211**, 864–873 (2016).
16. Lu, J., Dijkstra, F. A., Wang, P. & Cheng, W. Roots of non-woody perennials accelerated long-term soil organic matter decomposition through biological and physical mechanisms. *Soil Biol. Biochem.* **134**, 42–53 (2019).
17. Hodge, A., Stewart, J., Robinson, D., Griffiths, B. S. & Fitter, A. H. Competition between roots and soil micro-organisms for nutrients from nitrogen-rich patches of varying complexity. *J. Ecol.* **88**, 150–164 (2000).
18. Burgin, A. J. & Loecke, T. D. The biogeochemical redox paradox: how can we make a foundational concept more predictive of biogeochemical state changes? *Biogeochemistry* **164**, 349–370 (2023).
19. Dijkstra, F. A., Carrillo, Y., Pendall, E. & Morgan, J. A. Rhizosphere priming: a nutrient perspective. *Front. Microbiol.* **4**, 216 (2013).
20. Neubauer, S. C. & Megonigal, J. P. in *Wetland Carbon and Environmental Management* (eds Krauss, K. W. et al.) Ch. 3 (American Geophysical Union, 2021); https://doi.org/10.1002/9781119639305.ch3

21. Zhu, E. et al. Organic carbon and lignin protection by metal oxides versus silicate clay: comparative study based on wetland and upland soils. *J. Geophys. Res. Biogeosci.* **128**, e2023JG007474 (2023).
22. Wang, Y., Wang, H., He, J. S. & Feng, X. Iron-mediated soil carbon response to water-table decline in an alpine wetland. *Nat. Commun.* **8**, 15972 (2017).
23. Freeman, C., Ostle, N. & Kang, H. An enzymic 'latch' on a global carbon store. *Nature* **409**, 149–150 (2001).
24. Hall, S. J., Treffkorn, J. & Silver, W. L. Breaking the enzymatic latch: impacts of reducing conditions on hydrolytic enzyme activity in tropical forest soils. *Ecology* **95**, 2964–2973 (2014).
25. Agethen, S. & Knorr, K. H. *Juncus effusus* mono-stands in restored cutover peat bogs – analysis of litter quality, controls of anaerobic decomposition, and the risk of secondary carbon loss. *Soil Biol. Biochem.* **117**, 139–152 (2018).
26. Wild, B., Monteux, S., Wendler, B., Hugelius, G. & Keuper, F. Circum-Arctic peat soils resist priming by plant-derived compounds. *Soil Biol. Biochem.* **180**, 109012 (2023).
27. Cui, J. et al. Carbon and nitrogen recycling from microbial necromass to cope with C:N stoichiometric imbalance by priming. *Soil Biol. Biochem.* **142**, 107720 (2020).
28. Liu, L. et al. Carbon stock stability in drained peatland after simulated plant carbon addition: strong dependence on deeper soil. *Sci. Total Environ.* **848**, 157539 (2022).
29. Deroo, H. et al. Effect of organic carbon addition on paddy soil organic carbon decomposition under different irrigation regimes. *Biogeosciences* **18**, 5035–5051 (2021).
30. Zhang, Q. et al. A distinct sensitivity to the priming effect between labile and stable soil organic carbon. *N. Phytol.* **237**, 88–99 (2023).
31. Kramer, M. G. & Chadwick, O. A. Climate-driven thresholds in reactive mineral retention of soil carbon at the global scale. *Nat. Clim. Chang.* **8**, 1104–1108 (2018).
32. Grybos, M., Davranche, M., Gruau, G., Petitjean, P. & Pédrot, M. Increasing pH drives organic matter solubilization from wetland soils under reducing conditions. *Geoderma* **154**, 13–19 (2009).
33. Afsar, M. Z., Vasilas, B. & Jin, Y. Organo-mineral associations and size-fractionated colloidal organic carbon dynamics in a redox-controlled wetland. *Geoderma* **439**, 116667 (2023).
34. Bai, J. et al. Iron-bound carbon increases along a freshwater-oligohaline gradient in a subtropical tidal wetland. *Soil Biol. Biochem.* **154**, 108128 (2021).
35. Lin, Y. et al. Differential effects of redox conditions on the decomposition of litter and soil organic matter. *Biogeochemistry* **154**, 1–15 (2021).
36. Boye, K. et al. Thermodynamically controlled preservation of organic carbon in floodplains. *Nat. Geosci.* **10**, 415–419 (2017).
37. Canarini, A., Kaiser, C., Merchant, A., Richter, A. & Wanek, W. Root exudation of primary metabolites: mechanisms and their roles in plant responses to environmental stimuli. *Front. Plant Sci.* **10**, 157 (2019).
38. Sogin, E. M. et al. Sugars dominate the seagrass rhizosphere. *Nat. Ecol. Evol.* **6**, 866–877 (2022).
39. Mueller, P. et al. Plant species determine tidal wetland methane response to sea level rise. *Nat. Commun.* **11**, 5154 (2020).
40. Agethen, S., Sander, M., Waldemer, C. & Knorr, K. H. Plant rhizosphere oxidation reduces methane production and emission in rewetted peatlands. *Soil Biol. Biochem.* **125**, 125–135 (2018).
41. Bradley, P. M. & Morris, J. T. Influence of oxygen and sulfide concentration on nitrogen uptake kinetics in *Spartina alterniflora*. *Ecology* **71**, 282–287 (1990).
42. Koop-Jakobsen, K., Mueller, P., Meier, R. J., Liebsch, G. & Jensen, K. Plant-sediment interactions in salt marshes – an optode imaging study of O_2, pH and CO_2 gradients in the rhizosphere. *Front. Plant Sci.* **9**, 541 (2018).
43. Zhong, Z. et al. The root tip of submerged plants: an efficient engine for carbon mineralization. *Environ. Sci. Technol. Lett.* **10**, 385–390 (2023).
44. Mueller, P., Jensen, K. & Megonigal, J. P. Plants mediate soil organic matter decomposition in response to sea level rise. *Glob. Chang. Biol.* **22**, 404–414 (2016).
45. Naughton, H. R. et al. Development of energetic and enzymatic limitations on microbial carbon cycling in soils. *Biogeochemistry* **153**, 191–213 (2021).
46. McGivern, B. B. et al. Decrypting bacterial polyphenol metabolism in an anoxic wetland soil. *Nat. Commun.* **12**, 2466 (2021).
47. Ayi, Q. et al. Oxygen absorption by adventitious roots promotes the survival of completely submerged terrestrial plants. *Ann. Bot.* **118**, 674–683 (2016).
48. Maricle, B. R. & Lee, R. W. Root respiration and oxygen flux in salt marsh grasses from different elevational zones. *Mar. Biol.* **151**, 413–423 (2007).
49. Yu, C., Xie, S., Song, Z., Xia, S. & Åström, M. E. Biogeochemical cycling of iron (hydr-)oxides and its impact on organic carbon turnover in coastal wetlands: a global synthesis and perspective. *Earth Sci. Rev.* **218**, 103658 (2021).
50. Hu, D. et al. Increase in iron-bound organic carbon content under simulated sea-level rise: a 'marsh organ' field experiment. *Soil Biol. Biochem.* **187**, 109217 (2023).
51. Kirwan, M. L. & Megonigal, J. P. Tidal wetland stability in the face of human impacts and sea-level rise. *Nature* **504**, 53–60 (2013).
52. Rietl, A. J., Megonigal, J. P., Herbert, E. R. & Kirwan, M. L. Vegetation type and decomposition priming mediate brackish marsh carbon accumulation under interacting facets of global change. *Geophys. Res. Lett.* **48**, e2020GL092051 (2021).
53. van Breemen, N. How *Sphagnum* bogs down other plants. *Trends Ecol. Evol.* **10**, 270–275 (1995).
54. Gavazov, K. et al. Vascular plant-mediated controls on atmospheric carbon assimilation and peat carbon decomposition under climate change. *Glob. Chang. Biol.* **24**, 3911–3921 (2018).
55. Malhotra, A. et al. Peatland warming strongly increases fine-root growth. *Proc. Natl Acad. Sci. USA* **117**, 17627–17634 (2020).
56. Norby, R. J., Childs, J., Hanson, P. J. & Warren, J. M. Rapid loss of an ecosystem engineer: *Sphagnum* decline in an experimentally warmed bog. *Ecol. Evol.* **9**, 12571–12585 (2019).
57. Spivak, A. C., Sanderman, J., Bowen, J. L., Canuel, E. A. & Hopkinson, C. S. Global-change controls on soil-carbon accumulation and loss in coastal vegetated ecosystems. *Nat. Geosci.* **12**, 685–692 (2019).
58. Kaštovská, E., Cardenas-Hernandez, J. & Kuzyakov, Y. Priming effects in the rhizosphere and root detritusphere of two wet-grassland graminoids. *Plant Soil* **472**, 105–126 (2022).
59. Linkosalmi, M. et al. Studying the impact of living roots on the decomposition of soil organic matter in two different forestry-drained peatlands. *Plant Soil* **396**, 59–72 (2015).
60. Walker, T. N. et al. Vascular plants promote ancient peatland carbon loss with climate warming. *Glob. Chang. Biol.* **22**, 1880–1889 (2016).
61. Rohatgi, A. *WebPlotDigitizer* v.4.5 (Automeris, 2021); https://automeris.io/WebPlotDigitizer
62. Nakagawa, S. et al. A robust and readily implementable method for the meta-analysis of response ratios with and without missing standard deviations. *Ecol. Lett.* **26**, 232–244 (2023).
63. Bernal, B., Megonigal, J. P. & Mozdzer, T. J. An invasive wetland grass primes deep soil carbon pools. *Glob. Chang. Biol.* **23**, 2104–2116 (2017).
64. Mozdzer, T. J., Langley, J. A., Mueller, P. & Megonigal, J. P. Deep rooting and global change facilitate spread of invasive grass. *Biol. Invasions* **18**, 2619–2631 (2016).

65. Yan, W., Wang, Y., Ju, P., Huang, X. & Chen, H. Water level regulates the rhizosphere priming effect on SOM decomposition of peatland soil. *Rhizosphere* **21**, 100455 (2022).
66. Zhu, Z. et al. Rice rhizodeposits affect organic matter priming in paddy soil: the role of N fertilization and plant growth for enzyme activities, CO_2 and CH_4 emissions. *Soil Biol. Biochem.* **116**, 369–377 (2018).
67. Tett, R. P., Jackson, D. N., Rothstein, M. & Reddon, J. R. Meta-analysis of bidirectional relations in personality-job performance research. *Hum. Perform.* **12**, 1–29 (1999).
68. Nakagawa, S., Yang, Y., Macartney, E. L., Spake, R. & Lagisz, M. Quantitative evidence synthesis: a practical guide on meta-analysis, meta-regression and publication bias tests for environmental sciences. *Environ. Evid.* **12**, 8 (2023).
69. Leberg, P. L. Estimating allelic richness: effects of sample size and bottlenecks. *Mol. Ecol.* **11**, 2445–2449 (2002).
70. Nipperess, D. A. & Matsen, F. A. The mean and variance of phylogenetic diversity under rarefaction. *Methods Ecol. Evol.* **4**, 566–572 (2013).
71. Wang, H., Richardson, C. J. & Ho, M. Dual controls on carbon loss during drought in peatlands. *Nat. Clim. Chang.* **5**, 584–587 (2015).
72. Reid, J. B. & Goss, M. J. Interactions between soil drying due to plant water use and decreases in aggregate stability caused by maize roots. *J. Soil Sci.* **33**, 47–53 (1982).
73. Dacey, J. W. H. & Howes, B. L. Water uptake by roots controls water table movement and sediment oxidation in short *Spartina* marsh. *Science* **224**, 487–489 (1984).
74. Birch, H. F. The effect of soil drying on humus decomposition and nitrogen availability. *Plant Soil* **10**, 9–31 (1958).
75. Fenner, N. & Freeman, C. Drought-induced carbon loss in peatlands. *Nat. Geosci.* **4**, 895–900 (2011).
76. Wang, X. & Tang, C. The role of rhizosphere pH in regulating the rhizosphere priming effect and implications for the availability of soil-derived nitrogen to plants. *Ann. Bot.* **121**, 143–151 (2018).
77. Clarholm, M. Interactions of bacteria, protozoa and plants leading to mineralization of soil nitrogen. *Soil Biol. Biochem.* **17**, 181–187 (1985).
78. Ren, L., Jensen, K., Porada, P. & Mueller, P. Biota-mediated carbon cycling—a synthesis of biotic-interaction controls on blue carbon. *Ecol. Lett.* **25**, 521–540 (2022).

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Author contributions

P.M. and J.P.M. conceived the study. P.M. conducted the literature survey and meta-analysis. P.M. and J.P.M. wrote the paper in equal shares.

Competing interests

The authors declare no competing interests.

Additional information

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