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# The nature of soil blue carbon varies across mangrove geomorphic settings



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Mangrove forests store significant amounts of blue carbon, mainly as soil organic matter. Insights into mangrove organic matter are limited, despite its importance for understanding blue carbon accumulation and vulnerability to global change. Here, we quantified soil organic matter preserved through chemical recalcitrance and association with the mineral phase, as key factors influencing blue carbon persistence. We found that the nature of the soil organic matter varied with mangrove geomorphic settings. Delta settings were dominated by presumably the most persistent soil organic matter associated with minerals, while open coast karstic settings contained mostly particulate soil organic matter, likely preserved due to low microbial activity. Across mangrove soil depths, there was little difference in soil organic matter pools. The soil organic matter pool across mangroves' geomorphic settings exhibited greater variation than that observed across all terrestrial biomes. These findings underscore the need to tailor mangrove conservation and restoration to geomorphic settings.

Mangrove forests, hereafter referred to as mangroves, are among the most carbon-dense ecosystems worldwide<sup>1</sup>. They store up to  $856 \pm 32$  Mg carbon ha<sup>-1</sup> in biomass and soils combined, and they are active carbon sinks<sup>2,3</sup>. Most of their carbon is stored belowground (overall 70%), and this stock is highly persistent, likely due to anaerobic conditions limiting microbial activity<sup>2,4</sup>. Nevertheless, the fraction of carbon stored belowground can vary across distinct coastal geomorphic settings (hereafter referred to as settings). Considerable progress has been made in mapping and quantifying the distribution of soil carbon stocks across global mangroves<sup>5,6</sup>. These studies are important in view of the many mangrove conservation and restoration efforts aiming at mitigating anthropogenic carbon emissions while supporting biodiversity and other ecosystem services<sup>3</sup>. Yet, to evaluate the response of blue carbon to climate change and to optimize conservation and restoration, we need to improve our understanding on the mechanisms that control belowground carbon persistence across distinct coastal typologies (e.g., deltas, estuaries, open coasts, lagoons, and carbonate settings).

The mangrove settings include deltas, open coasts, and estuaries<sup>7</sup>. Delta mangroves occur in settings that are dominated by sediment inputs from

ivers that form a large fan-shaped alluvial plain and comprise 40% of global mangroves<sup>7</sup>. Estuarine mangroves occur in settings that are tide-dominated and receive riverine freshwater inputs<sup>7</sup>. Lagoon mangroves are characterized by sheltered environments with restricted tidal exchange<sup>7</sup>. Open coast mangroves occur in settings that are dominated by wave processes, where the supply of terrestrial sediments is often limited<sup>7</sup>. Additionally, the settings can be terrestrial or karstic depending on their sediment types and underlying geology<sup>7</sup>. Geomorphological classifications have been shown to be important for understanding the heterogeneity of soil carbon content and burial<sup>15,8</sup>, root production<sup>9</sup>, as well as above-ground biomass stock and production<sup>10,11</sup> and have been used to upscale global estimates of mangrove carbon. However, it is still unclear which processes in mangrove soils determine the fate of carbon across these settings, and how these settings influence the vulnerability of the mangrove soil organic matter (SOM) pools to decomposition under anthropogenic activities and global change (e.g., temperature).

Carbon persistence in mangrove soils has been explained by high autochthonous belowground inputs from net primary production coupled

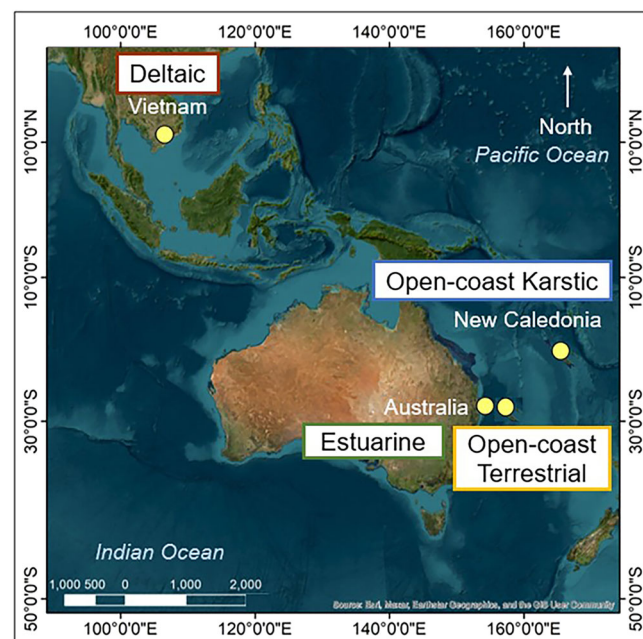
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with anaerobic conditions limiting microbial activity<sup>12,13</sup>. Anaerobic conditions slow the decomposition of organic matter (OM), especially when its lignin content is high<sup>14</sup>. Lignin, an aromatic structural component of plant litter, that requires oxygen for its decomposition, is often used as a tracer of terrestrial plant-derived OM due to its selective preservation under marine conditions<sup>14,15</sup>. Lignin is also an important component of the mangrove SOM pool due to its high contribution from roots<sup>15</sup>. Lignin contents of mangrove soils may therefore be an indicator of recalcitrant OM, underpinning the persistence of the soil carbon pool across different mangroves<sup>16</sup>. Lignin can be characterized by its degree of degradation using the ratio of lignin monomers<sup>15,17–20</sup>. The lignin content of bulk mangrove soil has been reported to be highly variable across mangrove locations (i.e., almost by an order of magnitude), and the lignin molecules under mangroves mostly show a low degree of degradation<sup>15,16,19,21,22</sup>. We hypothesized that elucidating the lignin content, composition, and state of degradation in different settings could contribute to understanding the drivers of SOM recalcitrance, which is pivotal to providing insights into blue carbon persistence under mangroves.

Another potential pathway for carbon preservation in mangrove soil is the association of OM with minerals (i.e., Minerals Associated OM (MAOM))<sup>23</sup>. This process of carbon stabilization has been studied for many years in terrestrial soils and marine sediments but has been rarely studied in mangrove soils<sup>23–26</sup>. MAOM is formed through chemical bonds between OM and mineral surfaces, and occlusion within micropores or small aggregates (of <50–63  $\mu\text{m}$ ) in terrestrial and marine ecosystems<sup>27,28</sup>. The carbon preserved as MAOM is physically and chemically protected and can be stable for decades to millennia in terrestrial soils, unlike the carbon found in particulate OM (POM)<sup>28</sup>. POM in mangrove soils may be composed of incompletely decomposed plant material, microbial-derived and algae compounds. POM could turn over faster than MAOM because its persistence is mostly controlled by chemical recalcitrance and/or microbial and enzymatic inhibition (<10 years to decades-long turnover in terrestrial soils) due to unfavorable environmental conditions<sup>28</sup>. It has been shown that POM is likely to be more vulnerable to global climate-related changes (such as warming) than MAOM because its degradation is controlled solely by microbial activity<sup>28–30</sup>. Therefore, to utilize the climate change mitigation potential of mangroves and guide conservation and restoration efforts of mangroves' blue carbon in various geographic situations, there is a need to characterize OM pools (POM and MAOM) of mangroves with contrasting settings, because they exhibit different biogeochemical and hydrological conditions and geomorphic evolutionary processes that may control the formation and persistence of OM<sup>5,25</sup>.

Similarly, soil depths could control the nature of SOM in mangroves. Deeper mangrove soil layers typically hold older SOM compared to surface soil layers<sup>31,32</sup>. Older SOM might have undergone a longer decomposition process and might be more stable, most likely due to variations of SOM nature<sup>31,32</sup>, as commonly observed in terrestrial soils<sup>33</sup>. Some studies have indicated selective preservation of organic compounds such as lignin and tannin molecules at depth<sup>14,24</sup>, although this phenomenon is not universally observed across all mangroves<sup>15</sup>. Additionally, differences in SOM composition between surface and deep soil layers may be influenced by reduced biota-OM interactions at greater depths<sup>33</sup>. Bioturbation plays a crucial role in SOM dynamics in surface soils, but its impact diminishes with increasing soil depth, potentially leading to a shift towards predominantly anaerobic biogeochemical processes in deeper layers<sup>14,34</sup>. Root systems further contribute to SOM dynamics through the input of fresh organic materials via rhizodeposition (e.g., mucilage, exudates, and litter inputs)<sup>9,14</sup> and radial oxygen loss<sup>23</sup>. Fresh OM inputs are typically more abundant in surface soil layers compared to deeper layers<sup>9</sup>. Consequently, it is likely that the composition and nature of SOM differ between surface and deep mangrove soil layers.

Here, we aimed to determine the nature of mangrove blue carbon in contrasting settings (Fig. 1) and soil depths by assessing two influencing factors of mangrove SOM persistence: chemical recalcitrance and association with the mineral phase. We hypothesized that lignin and MAOM will



**Fig. 1** | Map of the four studied mangrove sites across different settings.

be higher at river-dominated coastlines (delta settings) considering that allochthonous OM generally accounts for an important part of the carbon stocks in these settings. We also posited that depth is a major control on OM nature given that OM turnover time increases with soil depth<sup>31</sup>. Specifically, this study addresses two questions:

1. Is the nature of SOM different among mangroves located in different settings?
2. Is the nature of SOM in mangroves influenced by soil depth?

To tackle these questions, we sampled distinct mangrove coastal typologies spanning 36° in latitude and 45° in longitude across the Indo-West Pacific biogeographic region. We constrained our investigation to *Rhizophora* spp. This genus is known for its ubiquitous occurrence in mangroves throughout the tropical world (Tomlinson 1986). Our findings clarify the mechanisms and patterns of SOM preservation across the world's main mangrove typologies, revealing mangrove settings that might be more susceptible to carbon loss due to climate change effects (e.g., warming, erosion).

## Results

### Mangrove soil carbon content and quantity ranges are highly variable across settings

The carbon content was significantly different among soils from mangroves in different settings ( $\chi^2_{(3)} = 19.61$ ;  $p < 0.001$ ). It was highest in soils from the open coast karstic setting ( $13.4 \pm 0.8\%$ ), amounting to up to 8 times the carbon content of soils of other settings (Table 1). The soils from the delta setting had the second highest carbon content followed by soils from the estuary setting and the open coast terrestrial setting (Table 1). Soil carbon contents from the estuary and the open coast were similar ( $p = 0.4$ ). A similar pattern was observed for N content ranging from  $0.07$  to  $0.40 \pm 0.1\%$  (Table 1), which was significantly different among soils across all settings ( $p < 0.05$ ), except between the estuary and open coast terrestrial settings ( $p = 0.9$ ). The C:N ratios of SOM ranged from  $21 \pm 1$  (delta setting) to  $42 \pm 9$  (open coast karstic setting) (Table 1). They were significantly different in soils from different settings ( $\chi^2_{(3)} = 14.82$ ;  $p < 0.01$ ), but only the delta setting differed from the others ( $p < 0.05$  for all pairwise comparisons). The  $\delta^{13}\text{C}$  of soil was the lowest for the delta setting ( $-31.7 \pm 1.3\text{‰}$ ), while all other settings showed values above  $-30\text{‰}$  (Table 1). The  $\delta^{13}\text{C}$  of soil was significantly different across settings ( $\chi^2_{(3)} = 19.54$ ;  $p < 0.001$ ), except between the estuary and the open coast terrestrial settings (Table 1). Soil carbon and

**Table 1 | Mangrove soil carbon and OM parameters across settings and soil depths**

	Total lignin (mg g <sup>-1</sup> ) n = 25	AcAlv n = 25	AcAls n = 25	C:V n = 25	S:V n = 25	VSC: soil C n = 25	Soil C (%) n = 25	Soil N (%) n = 25	Soil C:N n = 25	Soil δ <sup>13</sup> C (‰) n = 25	MAOM-C (g C kg <sup>-1</sup> ) n = 25	POM-C (g C kg <sup>-1</sup> ) n = 25
<b>Settings</b>												
Delta	1.54	1.09	0.07	0.04	0.3	35	4.2	0.25	21	-31.7	20.6	6.6
Estuary	1.52	0.25	0.13	0.03	0.9	66	2.6	0.09	38	-28.3	9.9	8.0
Open coast karstic	7.09	0.15	0.13	0.04	0.5	49	13.4	0.40	42	-29.9	14.3	55.4
Open coast terrestrial	0.66	0.36	0.13	0.03	0.7	50	1.6	0.07	31	-29.1	1.5	14.9
<b>Soil depth</b>												
Deep	1.37	0.36	0.13	0.03	0.6	54	3.0	0.13	39	-29.2	9.2	2.2
Surface	1.75	0.28	0.11	0.04	0.7	43	4.1	0.22	26	-29.9	18.5	25.5

VSC total lignin as the sum of Vanillyl, Syringyl, and Cinnamyl units, AcAlv Acid to Aldehyde Ratio for Vanillyl units, AcAls Acid to Aldehyde ratio for Syringyl units, C:V cinnamyl to vanillyl, S:V syringyl to vanillyl, VSC soil carbon is total lignin normalized by total soil carbon, soil C total soil carbon, Soil N total soil nitrogen, MAOM-C mineral-associated organic matter in grams of carbon per mass of soil, POM-C particulate organic matter in grams of carbon per mass of soil. All are medians.

N contents, C:N ratios, and δ<sup>13</sup>C were different between surface and deep soils across all mangroves ( $p < 0.05$ ). The surface soil carbon content was  $4.1 \pm 5\%$  with a C:N ratio of  $26 \pm 7$  across all four mangroves, and the deep soil carbon content was  $3 \pm 5\%$  with a C:N ratio of  $39 \pm 15$  (Table 1). The average δ<sup>13</sup>C across settings was  $-29\%$  for the surface and deep soils (Table 1).

#### Plant-derived compound contribution and SOM nature are specific to settings

The total lignin content (VSC) ranged from  $0.7 \pm 0.5$  to  $7 \pm 2$  mg g<sup>-1</sup> soil (Table 1), and was significantly different among settings ( $\chi^2_{(3)} = 17$ ;  $p < 0.001$ ; Fig. 2), except between the delta and estuary settings ( $p = 1$ ). The open coast karstic setting exhibited up to seven times higher total lignin content than the other settings.

In contrast, the total lignin content normalized by the soils' carbon content (VSC:C) decreased in the order: estuary setting ( $66 \pm 20$  mg g<sup>-1</sup> soil C) > open coast terrestrial setting ( $50 \pm 40$  mg g<sup>-1</sup> soil C) > open coast karstic setting ( $49 \pm 10$  mg g<sup>-1</sup> soil C) > delta setting ( $35 \pm 10$  mg g<sup>-1</sup> soil C) (Table 1). However, these differences were not statistically significant ( $\chi^2_{(3)} = 6$ ;  $p = 0.09$ ). The C:V ratios were very similar among settings ( $p = 0.2$ ) ranging from  $0.03 \pm 0.1$  to  $0.04 \pm 0.1$  (Table 1). The S:V ratios were significantly different among settings ( $\chi^2_{(3)} = 20$ ;  $p < 0.001$ ), with the lowest S:V ratio for soils in the delta setting ( $0.3 \pm 0.0$ ), which showed three times lower ratios than observed in soils from the estuary setting ( $0.9 \pm 0.2$ ) (Table 1). All settings were significantly different from each other (all  $p < 0.01$ ) for the S:V ratio, except the open coast ones ( $p = 0.09$ ). The S:V and C:V ratios were the lowest in the delta and the highest in the estuary setting. (Ac:Al)<sub>V</sub> and the (Ac:Al)<sub>S</sub> ratios were different across settings (both  $p < 0.001$ ). The (Ac:Al)<sub>V</sub> was the highest in the delta setting ( $1.09 \pm 0.5$ ) and was at least three times higher than for the other settings. The (Ac:Al)<sub>S</sub> was the lowest for the delta setting ( $0.07 \pm 0.0$ ) and was almost half of the other settings (Table 1). The Ac:Al ratios from soils in the delta settings were significantly different from other settings. There was no significant difference between surface and deep soils for total lignin, total lignin normalized by total carbon, or any of the other lignin ratios, except for the Ac:Al ratio (Fig. 3).

#### Particulate organic matter (POM) and mineral-associated organic matter (MAOM) in mangrove soils vary across settings

MAOM-C content ranged from  $1.5 \pm 3$  to  $20.6 \pm 15$  g carbon kg<sup>-1</sup> soil, while POM-C content ranged from  $2.2 \pm 4$  to  $55.4 \pm 77$  g carbon kg<sup>-1</sup> soil across settings (Table 1). The contribution of POM and MAOM (%) in the soils varied significantly among settings (both  $p < 0.01$ ). All settings showed >85% of carbon in the MAOM fraction (i.e., <15% POM), except for the open coast karstic setting, which was predominantly composed of POM (82%). The MAOM content was significantly different only between the

open coast karstic setting and the other settings, showing a gradient that decreased in the order: delta > estuary > both open coast settings (terrestrial and karstic). This pattern was reversed for POM. Pairwise comparisons of mean values indicated that only the delta setting was significantly different from the other settings for MAOM-C ( $p < 0.01$ ), and only the open coast karstic setting was different from the other settings for POM-C. MAOM-C normalized by total carbon varied significantly among settings ( $p < 0.001$ ), being highest in the delta setting (78%), followed by the estuary setting (66%), the open coast terrestrial setting (17%), and the open coast karstic setting (8%) (Fig. 2). POM-C normalized by total carbon varied significantly among settings ( $p < 0.001$ ) decreasing in the order: open coast karstic (92%), open coast terrestrial (83%), estuary (34%) and delta (22%) settings (Fig. 2).

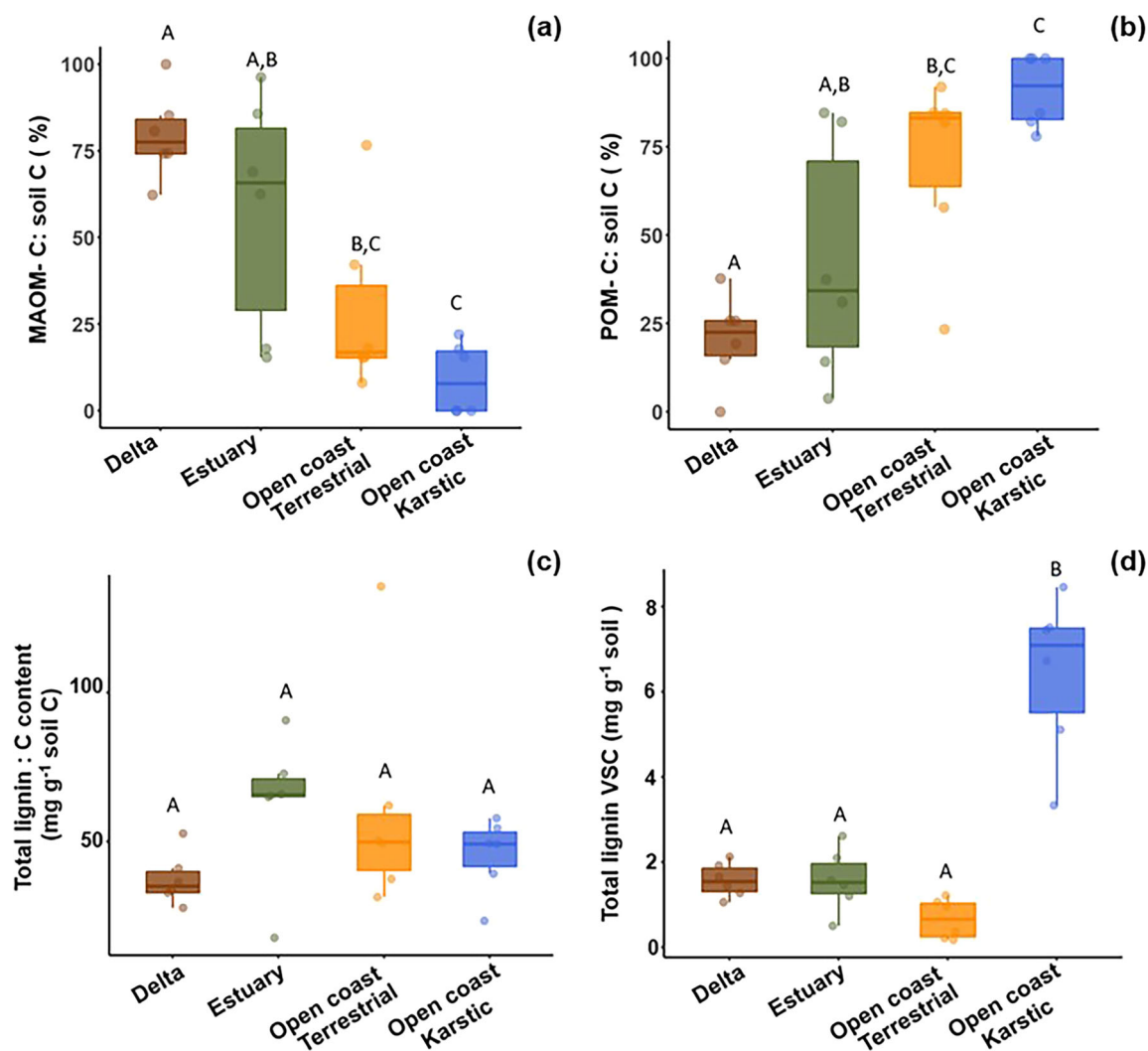
POM-C and MAOM-C were significantly different across soil depths (Fig. 3). There was no significant difference between surface and deep soil for the contribution of POM and MAOM (in %), or for POM-C normalized by total carbon and MAOM-C normalized by total carbon (Fig. 3).

#### Settings influence the nature of mangrove SOM and soil properties

Principal component analysis (PCA) was conducted to determine whether settings could be distinguished by soil parameters. The first two components of the PCA analysis explained ~70% of data variability when all soil parameters were analyzed together (Fig. 4). In the PCA plot, axis 1 differentiated SOM sources and degradation stages, and axis 2 differentiated soil types (mineral vs. organic). The open coast karstic and the delta settings were separated from the other settings along the second axis, correlating negatively with soil parameters related to the MAOM fraction, and positively with POM and total lignin. Both the delta and open coast terrestrial settings exhibited a broad range along axis 1, which was positively correlated with the carbon content of MAOM and the CV/SV ratio, and negatively correlated with δ<sup>13</sup>C. The estuary and open coast karstic settings overlapped and were positioned lower on axis 1; however, soils from the estuary setting were less variable along axis 1 compared to those from the open coast karstic setting.

#### Discussion

We found that the nature of SOM and the mechanisms of carbon preservation vary across settings. In delta settings, soil carbon may be primarily protected by its association with minerals, whereas in open coast karstic settings, the protection may be due to the inhibition of microbial biodegradation activity. The lignin content normalized by soil carbon did not differ across settings, indicating that chemically recalcitrant plant material may not be preferentially preserved in particular mangrove settings. The stage of degradation and the sources of lignin were different for delta mangroves compared to other settings, suggesting important



**Fig. 2 | Variation in the nature of soil organic matter (SOM) across settings.** Mineral-associated organic matter carbon (MAOM-C) as a percentage of total carbon across settings (a), particulate organic matter (POM) as a percentage of total carbon across settings (b), total lignin content (VSC) as a percentage of total carbon across settings (c) and VSC content in soils across settings (d). Different capital letters indicate significant differences between means ( $p < 0.05$ ), same letters indicate no statistical difference. Kruskal–Wallis tests were used. Heavy bars indicate sample medians; box ends indicate upper and lower quartiles; whiskers extend from the hinges to the largest and smallest values, respectively, which is no further from the hinges than 1.5 times the sample interquartile range. Circles indicate individual measurements, with vertical jitter to reduce overwriting.

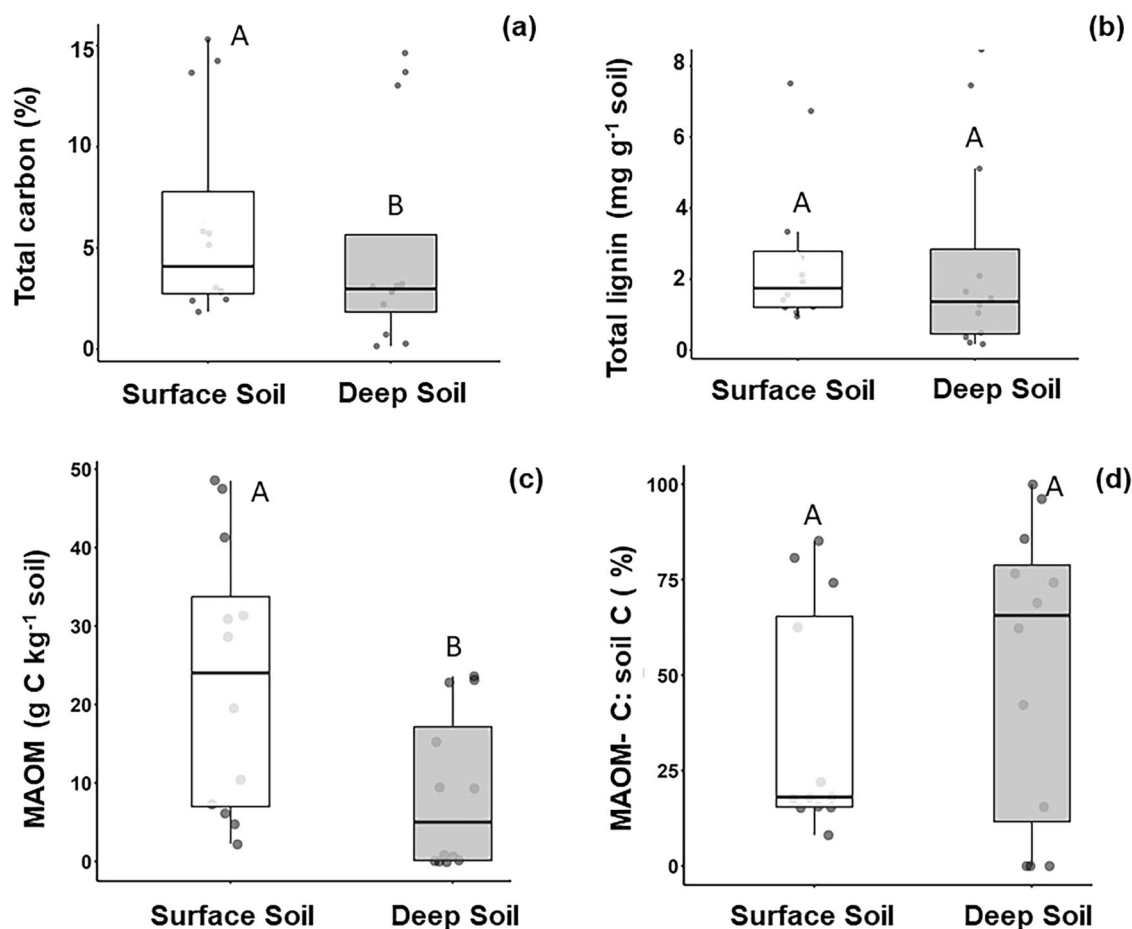
inputs of already degraded lignin from upstream in delta settings<sup>15</sup>. Finally, unlike in terrestrial soils, we did not find an effect of depth on lignin content and decomposition or allocation of SOM to different physical fractions, suggesting the nature of SOC in mangroves may not be influenced by depth.

### The mechanisms of OM preservation in mangrove soils vary across settings

The MAOM pool in mangrove soils under *Rhizophora* spp. shows greater variation than that observed across terrestrial biomes (Fig. 5)<sup>20,35</sup>. The MAOM-C contribution to total soil carbon in open coast karstic and terrestrial mangrove settings was up to ten times lower than that of any other ecosystem, while those of the estuary setting fell within the range of other ecosystems and the delta setting was in the upper range (Fig. 5)<sup>35</sup>. Mangrove soils showed a much higher (up to 4 times) lignin content than most terrestrial soils<sup>20</sup>. This could be explained by the slower degradation of aromatic compounds under anaerobic conditions, which might lead to the preservation of lignin in submerged environments<sup>36</sup>. It may also be related to the higher root inputs in mangrove soils, as roots are often richer in lignin than other plant organs<sup>37,38</sup>.

The heterogeneous nature of SOM in soils under mangroves might be attributed to the properties of mangrove ecosystems, which depend on setting parameters<sup>5</sup>. Mangrove soils in open coast karstic settings are predominantly organic in nature, while mangrove soils in other settings contain higher proportions of mineral matter. This highlights the need to distinguish between organogenic and minerogenic mangrove soils when investigating SOM pools and their dynamics<sup>23</sup>. Indeed, mangrove soil in open coast karstic settings is built mostly from autochthonous OM and is mineral-poor<sup>25</sup>. These organic-rich mangrove soils are composed mainly of fine roots at many sites<sup>39,40</sup>, and can be associated with nutrient limitations and extended flooding<sup>41</sup>. The preservation of POM in open coast karstic settings is not due to preferential preservation of lignin, because the lignin:OC soil ratio was not higher in the open coast karstic environment compared to other settings. This suggests that lignin preservation might occur equally across mangrove settings. Another explanation for high soil carbon in the open coast karstic setting might be related to the geochemical conditions and redox-driven processes, particularly sulfurization and association with pyrite<sup>39</sup>. As observed in other open coast karstic mangroves, sulfurization and pyritization of SOM impede the degradation of OM<sup>42</sup>. Additionally, it was interesting to note that the





**Fig. 3 | Mangrove carbon (C) and the nature of soil organic matter between different soil depths.** Carbon and lignin content (VSC) of the soil (a, b), mineral-associated organic matter (MAOM) in soil (c), and MAOM normalized by soil carbon (d) between soil depths. Different capital letters indicate significant differences ( $p < 0.05$ ), same letters indicate no statistical difference. Kruskal–Wallis tests

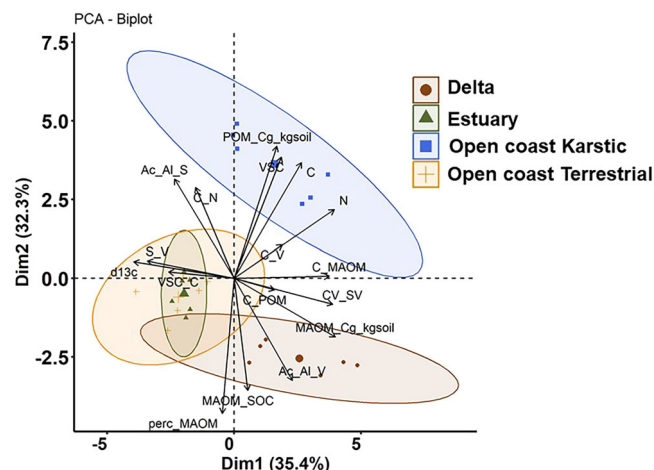
were used. Heavy bars indicate sample medians; box ends indicate upper and lower quartiles; whiskers extend from the hinges to the largest and smallest values, respectively, which is no further from the hinges than 1.5 times the sample inter-quartile range. Circles indicate individual measurements, with vertical jitter to reduce overwriting.

carbon content of MAOM was up to four times higher in surface soil in the open coast karstic setting than in those of the estuary and open coast terrestrial setting. High organic carbon loadings may occur on mineral surfaces in an organic-rich environment because the adsorption of OM onto mineral surfaces occurs in patches and layers, which continue to accumulate on top of each other as long as there are OM inputs from microbial turnover of fresh material<sup>13,44</sup>. The ratio of carbon inputs to the amount of minerals might be the highest in an open coast karstic setting because the soil was mostly peat. This could potentially explain the high carbon loading per unit of mineral. Another possible explanation is that the mineralogy of the sediments<sup>25</sup> in open coast karstic mangroves may be more effective at binding MAOM, although the specific mineral composition and binding capacity of these sediments remain to be determined.

The delta setting showed the highest MAOM-C contribution and the highest level of lignin degradation, revealing contrasting processes compared to the other settings. The high MAOM-C in the delta setting aligns with previous research showing higher MAOM-C in environments receiving large inputs of minerals from upstream<sup>25</sup>. In contrast to the other settings, the sediment texture of the delta setting was largely dominated by clay fractions<sup>45</sup>, which have a higher surface area for OM binding and likely contain minerals (e.g., iron) that are particularly effective at stabilizing organic molecules<sup>18</sup>. Our delta setting had a sediment accretion rate of 2.9 cm year<sup>-1</sup><sup>146</sup>, likely larger than those of the other settings<sup>47</sup> and with likely important allochthonous inputs from upstream.

The lignin in the delta settings likely originated from upstream sources, as suggested by the S:V to C:V ratios of the delta mangrove soils, which indicate contributions from both angiosperms and gymnosperms. This is consistent with previous studies conducted in the downstream water of the Mekong River showing similar lignin sources<sup>48</sup>. Syringyl units are preferentially degraded compared to Vanillyl units, resulting in a decrease of the S:V ratio during lignin degradation<sup>49</sup>. However, the S:V ratio also varies according to lignin plant sources<sup>20</sup>. The depleted  $\delta^{13}\text{C}$  likely also reflects the dominance of terrestrial plant material inputs. Similarly, the Ad:Al ratio was much higher in the delta settings than in the other settings, likely indicating the presence of degraded lignin materials transported from the watershed and deposited in the delta mangrove<sup>15,19</sup>. The relatively high Ad:Al ratio is unlikely due to in-situ decomposition, because most of the mangrove soil is anaerobic, while Ad:Al ratios typically reflect aerobic decomposition<sup>15,19</sup>. Similar processes have been observed in the delta mangroves of French Guiana, where high Ad:Al<sub>v</sub> ratios were linked to allochthonous decayed OM inputs from the Amazon River<sup>15,50</sup>.

The estuary and open coast terrestrial settings had SOM nature that was between those of the open coast karstic and delta settings. This is consistent with findings from Fu et al.<sup>25</sup> as their sediment accretion rates were higher than those in open coast karstic settings, but lower than in delta settings. Rovai et al.<sup>5</sup> found no statistical differences between the estuary and open coast terrestrial settings in terms of carbon content. In agreement with this, we found no statistical difference in MAOM and POM between the



**Fig. 4 | Results of principal components analysis of mangrove soil parameters for the four settings.** MAOM\_SOC is the percentage of mineral-associated organic matter on the total soil carbon; MAOM\_Cg\_kg<sup>-1</sup> soil is the mineral associated with organic matter in grams of carbon per mass of soil; POM\_Cg\_kg<sup>-1</sup> soil is the particulate organic matter, in grams of carbon per kilogram of soil; N is soil nitrogen content in %; C is soil carbon content in %; C:N is the carbon-to-nitrogen ratio of the soil in molar basis; δ<sup>13</sup>C is the stable carbon isotope ratio in ‰; Ac\_AL\_S is syringic acid-to-syringaldehyde ratio; Ac\_AL\_V is vanillic acid-to-vanillin ratio; VSC is total lignin in milligrams per grams of soil; VSC\_C is the total lignin normalized by total soil carbon; C\_MAOM is the carbon content of the mineral-associated organic matter; C\_POM is the carbon content of the particulate organic matter; C:V is the ratio cinnamyl to vanillyl, S:V is the ratio syringyl to vanillyl. The color of the ellipse and the symbols represent each setting, such as the brown color and circles represent the delta, the green color and triangles represent the estuary, the blue color and the squares represent the open coast karstic setting, and the yellow color and crosses represent the open coast terrestrial setting. The colored ellipses represent confidence ellipses (95% confidence interval) around the centroid of each group. These ellipses indicate the dispersion of the data points within each group along the principal components. The central tendency points are displayed as small symbols and are positioned at the centroid means of each group projected onto the PCA space.

estuary and open coast terrestrial settings. Both the estuary and open coast terrestrial settings had similar sediment accretion rates<sup>51</sup> and similar MAOM and POM content. Yet, we observed differences in total lignin and S:V ratio, with the estuary setting having higher values for both. This suggests either different sources of lignin or a higher degree of lignin degradation at the estuarine site<sup>20</sup>.

In summary, the nature of the SOM differs among mangroves from different settings. Carbon pools and lignin content and composition in mangrove soils vary widely, showing even greater variations than those observed across different biomes in terrestrial environments. Both are closely linked to ecosystem properties related to settings. In open coast karstic settings, mangrove soils are mostly organic and characterized by a high proportion of POM, with POM preservation possibly attributed to protection in sulfur and pyrite-rich environments. The delta setting stands out with the highest contribution of MAOM-C and a high degree of lignin degradation, attributed to elevated sedimentation rates and diverse sources of lignin detrital materials. Meanwhile, the estuary and open coast terrestrial settings had similar SOM nature, reflecting intermediate conditions between the more extreme open coast karstic and delta settings. While our study controlled for genus—and thus the range of inundation—it would also be interesting to study the internal variation in SOM nature within each setting, particularly to assess the effects of inundation time and frequency, salinity gradients, or erosion. In addition, to generalize our results further investigations are needed across bioregions (e.g., America, Africa), species, and sediments having a vast range of reactive mineral phases (e.g., carbonates, iron oxides, sulfates) since all of those factors could substantially influence OM binding potential<sup>18</sup>.

## The nature of SOM does not discernibly vary across depths in mangroves

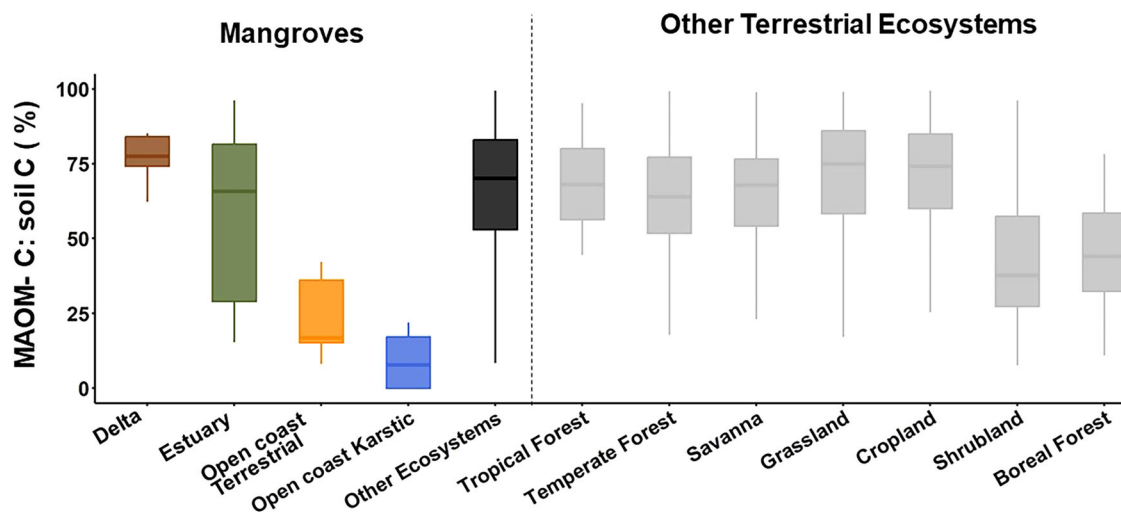
Mangrove lignin did not show a strong degradation pattern with depth, contrasting with most terrestrial ecosystems where deeper soils typically contain more degraded lignin compared to surface soils<sup>20</sup>. In terrestrial soils, lignin degradation is suggested to be linked to limited input of fresh OM in deep soil (i.e., fewer roots) and/or low oxygen contents<sup>50</sup>. However, a few exceptions in terrestrial ecosystems report stable lignin content and composition across soil depths<sup>20</sup>, similar to our observation in mangroves. In terrestrial forests, this preservation at depth is often attributed to lignin preservation mechanisms or vertical transport of lignin<sup>20</sup>. In mangroves, root production can occur at depths greater than 50 cm<sup>9,52</sup> and may contribute to fresh lignin supply. However, the root production often decreases with depth in mangroves, but not the lignin degradation<sup>53</sup>. Therefore, the preservation of lignin at depth in mangroves might rather be due to other processes, such as limited microbial access and efficiency at depth<sup>54</sup>.

The nature of mangrove soil carbon, described as lignin and MAOM content, appeared mostly similar across depths, as previously reported for soil lignin<sup>15,55,56</sup>. There was no indication of higher degradation of materials at depth, as indicated by the lack of change in Ad:Al ratios, and lignin:soil C, C:V, and S:V ratios across depths. This suggests that lignin was relatively stable across depth, as shown for other mangrove soils<sup>15,55,56</sup>. Although the total amount of MAOM-C was higher on the surface compared to deep mangrove soil, as was observed in terrestrial ecosystems<sup>35</sup> and coastal wetlands<sup>25</sup>, this trend was less pronounced when MAOM-C was normalized by total soil carbon, in line with findings from other studies<sup>35,57</sup>. Hamada et al.<sup>57</sup> suggest that the absence of depth-related difference in MAOM-C may be due to high root production in mangroves<sup>9</sup>, notably at depths greater than 80 cm. Yet, at our sites, we observed contrasting root production across depths, at least in the delta setting<sup>53</sup>, where the MAOM-C contribution to soil carbon was similar in surface and subsoils. Another explanation could be that while we defined surface versus deep soil based on soil depth, the age of the deep soils can vary across settings due to differences in vertical accretion and sea level rise history<sup>58</sup>, which might influence the nature of accumulated SOM. For instance, the deep soil in the open coast karstic setting is likely >2000 years old<sup>39</sup>, while the soil of the delta setting is likely ~100 years old<sup>59</sup>. Thus, the nature of SOM in mangroves at different depths is different for some of the soil characteristics, but not for others, which might be due to specific processes in marine environments as compared to terrestrial ones.

## The nature of SOM holds important implications for the conservation and restoration of mangrove blue carbon

We are at a critical time, where nature-based solutions for global change, including those for blue carbon, are gaining attention. Yet, mangroves are highly heterogeneous<sup>5</sup>, and significant knowledge gaps remain in understanding blue carbon preservation amidst ecosystem disturbances and their restoration<sup>60</sup>. Here, we show that the nature of mangrove soil carbon varies across different settings, implying that classifying mangroves based on their settings could facilitate the development of tailored management practices for each environment. In particular, the controls of MAOM versus POM formation in contrasting settings should be considered as a driver of blue carbon accrual under the framework of ecosystem restoration and conservation. For instance, the prominent role of MAOM in delta mangroves underscores the importance of maintaining or restoring upstream detrital and sediment inputs to enhance carbon sequestration in such mangroves.

Additionally, utilizing the POM versus MAOM framework is critical for accurately forecasting the impact of global changes (e.g., temperature) on blue carbon across different settings. POM in mangrove soil systems, such as those in open coast karstic settings, likely persists due to its recalcitrant structure and strongly anaerobic conditions, which hinder microbial decay<sup>2</sup>. Conversely, MAOM in mangrove soils may persist due to adsorption onto mineral and/or organic phases, which prevents enzymatic attack<sup>28</sup>, but may be vulnerable to changes in redox conditions<sup>24</sup>. The response of SOM to disturbances and global change is likely to differ accordingly. For instance,



**Fig. 5 | Mineral-associated organic matter (MAOM) normalized by soil carbon across soil mangrove settings and other ecosystems.** Gray boxplots are all the ecosystems included in the biomes of terrestrial ecosystems. Heavy bars indicate sample medians; box ends indicate upper and lower quartiles; whiskers extend from

the hinges to the largest and smallest values, respectively, which is no further from the hinges than 1.5 times the sample interquartile range. Data are from this article (colored) and Sokol et al.<sup>35</sup> (in gray).

conversion of mangroves and their drainage or warmer climate may increase microbial activity, thereby immediately increasing POM decomposition rates, while MAOM might be less sensitive to microbial decay because MAOM must be destabilized before decomposition can proceed<sup>28</sup>. Therefore, when assessing the effects of human land use and global change on mangrove blue carbon, taking into account the nature of soil carbon is critical.

## Conclusion

- Settings are key determinants of the nature of SOM across mangroves. Soil carbon pools (MAOM and POM) and lignin exhibit substantial variation in mangroves, exceeding the variation observed across all terrestrial biomes. This variation is closely linked to the ecosystem properties specific to different mangrove settings, in particular, if they are connected to an upstream watershed. We call for a more detailed analysis of SOM nature across global mangrove settings to further generalize these results.
- There were no discernible differences in the nature of SOM across depths in mangroves. Lignin content, its degradation stage, and soil carbon pools remain relatively consistent across depths in mangrove soils regardless of their setting.
- Our findings provide fundamental knowledge to grasp the diversity of soil carbon persistence among mangroves and offer valuable insights to guide mangrove conservation and restoration efforts, notably in regards to forecasting changes in blue carbon storage and burial rates in the context of global changes.
- We suggest that distinguishing between mangrove soils of organic and mineral origin is necessary, as the processes governing carbon persistence in these systems are very different.

## Methods

### Site description and sampling

We studied four types of mangrove settings: a delta setting, an estuary setting, a terrestrial open coast setting, and a karstic open coast setting. All were in the Indo-West-Pacific, the most carbon-dense mangrove area in the world. The delta setting (Can Gio mangrove) was located in the south of Vietnam (10°30' N, 106°52' E); the karstic open coast setting (Dumbéa sur mer mangrove) was in the French overseas territories of New Caledonia (22° 8' S, 166° 26' E). The terrestrial estuary and open coast terrestrial settings

(Halloran and North Stradbroke mangroves) were located on the east coast of Australia (27° 31' S, 153° 27' E). At each site, we extracted soil cores from below the *Rhizophora* spp. mangrove, between 1 to 2 m from a *Rhizophora* spp. tree trunk. Our sampling aimed to focus on soils associated with the genus *Rhizophora* spp. only to control for genus and inundation duration, without having detailed inundation data, because *Rhizophora* spp. is known to occur between 150 and 400 min d<sup>-1</sup> inundations<sup>61</sup>.

The soil cores were extracted from 0 to 20 cm (surface soil) after carefully removing the litter (when present) from the soil surface, and from 80 to 100 cm or until the bedrock was reached. This was the case for the karstic open coast mangrove (Dumbéa sur mer), where the deep sample was taken between 60 and 80 cm. In total, we extracted three independent surface soil samples and three independent deep soil samples per site ( $n = 48$ ). The samples were packed wet in vacuum-sealed bags and transported with ice pads. Upon receipt in the laboratory, each sample was immediately freeze-dried. Each freeze-dried sample was then sieved through a 2 mm mesh to remove any large fragments and then ground for further analysis. The sediment texture of the delta setting was dominated by clay<sup>45</sup>, and by sand in the open coast karstic setting<sup>53</sup>.

### Lignin analysis

We analyzed the amount and composition of lignin in bulk soil using the cupric oxide (CuO) oxidation method<sup>18,62</sup> for the surface and deep soils of each setting ( $n = 24$ , 4 sites  $\times$  2 depths  $\times$  3 replicates). We oxidized each sample (500 mg) by mixing it with 250 mg CuO, 50 mg of ammonium iron (II) sulfate hexahydrate, 50 mg of glucose, and 15 ml of NaOH in Teflon-lined bombs. We then flushed all bomb headspace with N<sub>2</sub> and heated them at 172 °C in an oven for 2.5 h. After cooling the bombs to room temperature, we added a standard containing ethylvanillin to estimate the recovery of lignin-derived phenols. We purified the CuO products and removed the humic acid by acidification of the sample at pH 1.8–2.2 with 6 N HCl. We extracted the phenolic monomers with the help of a silica column solid (C18). We transferred the CuO products of lignin to silica columns, eluted them, and derivatized them with BSTFA (bis-(trimethylsilyl)-tri-fluoroacetamide). We then quantified and separated the lignin monomers using an HP GC 6890 gas chromatograph equipped with an SGE BPX-5 column (60 m length  $\times$  0.25 mm internal diameter  $\times$  320  $\mu$ m coating) combined with a flame ionization detector. We injected the samples in split mode (1:10) and used helium as the carrier gas with a flow rate of 1.0 mL min<sup>-1</sup>. We set the oven temperature with an initial temperature at

100 °C for 2 min, with a following increase from 100 to 172 °C at 8 °C min<sup>-1</sup>, from 172 to 184 °C at 4 °C min<sup>-1</sup>, from 184 to 310 °C at 10 °C min<sup>-1</sup>, and a 5 min isothermal at 310 °C. We kept the injector at 280 °C and the detector at 300 °C.

The CuO oxidation releases a suite of lignin-derived phenolic oxidation products that retain the characteristic substitution patterns of different lignin types<sup>17,62,63</sup>. These lignin-derived phenols include characteristic lignin monomer phenols, namely vanillyl (V; vanillin, acetovanillone, and vanillic acid), syringyl (S; syringaldehyde, acetosyringone, and syringic acid), cinnamyl (C; p-coumaric acid and ferulic acid), p-hydroxy benzoic acid, p-hydroxybenzaldehyde, p-hydroxy acetophenone and ethylvanillin monomers. The sum of the contents of the structural units of the V-, S-, and C-types is generally used to represent the lignin quantity in the sample<sup>20</sup>. Total lignin content (VSC) is also reported as the percentage of total carbon by dividing it by the total carbon content of the mangrove soil from each sample. While we did not do the ratio with total organic carbon content, the stable isotope of carbon ( $\delta^{13}\text{C}$ ) of the bulk soils suggests that most of the carbon is from organic origin. The ratios of acid to aldehyde for the vanillyl and the syringyl units ( $\text{Ac:Al}_{\text{V,S}}$ ) are used as indicators of the degree of lignin oxidation during biodegradation<sup>63</sup>. The ratios C:V and S:V are used to quantify the contribution of each plant-derived source to SOM from angiosperms and gymnosperms and as indicators of lignin phenol degradation<sup>20</sup>.

### POM and MAOM analysis

We fractionated the bulk soil into POM (light fraction) and MAOM (heavy fraction) for the surface and deep soils of each setting ( $n = 24$ , 4 sites  $\times$  2 depths  $\times$  3 replicates) based on a slightly modified version of the method proposed by Golchin et al.<sup>64</sup>. We used sodium polytungstate (SPT, TC Tungsten Compounds, Grub am Forst, Germany) with a density of 1.8 g cm<sup>-3</sup> in accordance with previous studies<sup>65,66</sup> to fractionate our samples by density. In short, we mixed 10 g of the soil sample with 80 mL of SPT within a 250 mL centrifuge conical tube and subsequently centrifuged the mixture at 10,000  $\times$  g for 10 min. We then collected the POM materials by carefully removing the floating materials. The MAOM fraction remaining at the bottom of the conical tube has a density >1.8 g cm<sup>-3</sup>. We then washed the POM and MAOM materials to remove any SPT residues. We washed the POM by inserting it into a pre-washed dialysis membrane (Spectra/Por®; 12,000 Dalton) that we placed into a recipient filled with Milli-Q water. We renewed the Milli-Q water 3 times a day for a week to remove as much of the SPT as possible. We then filtered one last time the POM material using glass fiber filters (GF 6, Whatman, Dassel, Germany) until the electrical conductivity of the water recovered after filtration was below 50  $\mu\text{S cm}^{-1}$ . The dialyzed membrane step was necessary as the filters were occluded very rapidly preventing the removal of the SPT from the POM materials. We washed the MAOM by adding 200 mL of Milli-Q water and centrifuged it at 10,000  $\times$  g for 10 min until the electrical conductivity of the supernatant was below 50  $\mu\text{S cm}^{-1}$ . Each fraction was then freeze-dried. We reported the MAOM in grams of carbon per kilogram of soil (g kg<sup>-1</sup>). POM and MAOM are also reported as a percentage of total carbon (MAOM-C and POM-C) by dividing them by the total carbon content of the mangrove soil samples.

### Elemental analysis (carbon and nitrogen) and $\delta^{13}\text{C}$

We determined the total carbon and N contents of the surface and deep bulk soil ( $n = 24$ , 4 sites  $\times$  2 depths  $\times$  3 replicates), as well as their fractions (POM and MAOM,  $n = 48$ , 4 sites  $\times$  2 depths  $\times$  2 fractions  $\times$  3 replicates) using an elemental analyzer (Flash EA 1112 Series, Thermo Electron, Fisher, Netherlands). The  $\delta^{13}\text{C}$  suggests that the total soil carbon is primarily organic carbon or that the contribution of inorganic carbon is negligible (Table 1). We analyzed the  $\delta^{13}\text{C}$  of the bulk soil ( $n = 24$ , 4 sites  $\times$  2 depths  $\times$  3 replicates) using an isotope and gas content analyzer by cavity ring-down spectroscopy (G2131-i, Picarro, USA; precision <0.1‰). We expressed the isotope ratio relative to the conventional standard (Pee Dee Belemnite limestone) as  $\delta$  values. Internal reference materials included IAEA-C6

(sucrose) and IAEA-CH-7 (polyethylene). The standard deviation of  $\delta^{13}\text{C}$  for ten aliquots of the same sample was less than 0.2‰.

### Statistical analysis

We investigated the effects of settings on MAOM, POM, carbon, N, C:N ratio,  $\delta^{13}\text{C}$ , total lignin, and lignin ratio using ANOVAs. We visually inspected the residuals, and when deviations from normality or homoscedasticity were detected from residuals distribution histograms and QQ plots (Supplementary Information S1), using Kruskal–Wallis tests. Only for C:V ratio, and total N, ANOVAs were used. For the other variables, we used Kruskal–Wallis tests. Post hoc pairwise comparisons were conducted using Tukey's HSD tests following the ANOVA tests, and the Wilcoxon test was used after the Kruskal–Wallis tests. We investigated the effects of depths on MAOM, POM, carbon, N, C:N ratio,  $\delta^{13}\text{C}$ , total lignin, and lignin ratio using a linear mixed model with location as a random factor, because both depths were sampled at the same location. Visual inspection of residuals did not reveal any obvious deviations from normality, homoscedasticity, or linearity (Supplementary Information S1). We used PCA to summarize how settings differ in terms of soil properties. The PCA was performed after having removed the variables that were perfectly collinear or linearly dependent (Supplementary Table S1). We also assessed the variation inflation factors (Supplementary Table S2). We also investigated a normalization of our data by soil density (Supplementary Material 1). We used a  $p$  value threshold of <0.05 to determine statistical significance. All statistical analyses, including those performed using the R package stats<sup>67</sup>, and the lme4<sup>68</sup>, car<sup>69</sup> were performed using R<sup>67</sup> (version 4.2.2).

### Data availability

The data that support the findings of this study are available in the Supplementary Data 1 of this article and in a Zenodo repository<sup>70</sup>.

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## Author contributions

M.A., C.R., C.L. and H.D. designed the study and obtained the funding. C.L., S.R., C.M. and H.D. collected samples at the sites. MM performed laboratory analysis with the input of all the co-authors. M.A. led the analysis of the results and the writing of the manuscript with inputs and revisions of C.L., M.M., H.D., S.R., S.A., A.K.M., S.H.F., T.B., A.F., C.M., N.B., T.P.L., A.A.A. and C.R.

## Competing interests

The authors declare no competing interests.

## Additional information

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