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## Coastal permafrost was massively eroded during the Bølling-Allerød warm period

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The Bølling-Allerød interstadial (14,700–12,900 years before present), during the last deglaciation, was characterized by rapid warming and sea level rise. Yet, the response of the Arctic terrestrial cryosphere during this abrupt climate change remains thus far elusive. Here we present a multi-proxy analysis of a sediment record from the northern Svalbard continental margin, an area strongly influenced by sea ice export from the Arctic, to elucidate sea level - permafrost erosion connections. We show that permafrost-derived material rich in biospheric carbon became the dominant source of sediments at the onset of the Bølling-Allerød, despite the lack of direct connections with permafrost deposits. Our results suggest that the abrupt temperature and sea level rise triggered massive erosion of coastal ice-rich Yedoma permafrost, possibly from Siberian and Alaskan coasts, followed by long-range sea ice transport towards the Fram Strait and the Arctic Ocean gateway. Overall, we show how coastal permafrost is susceptible to large-scale remobilization in a scenario of rapid climate variability.

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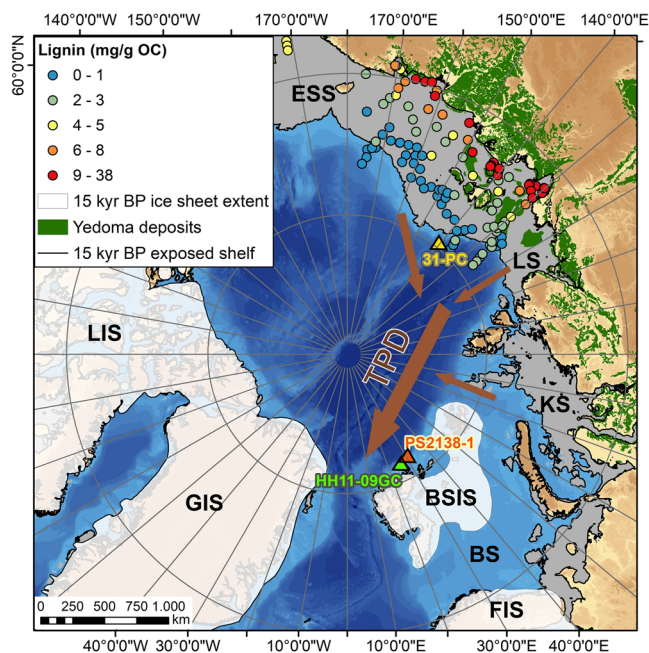
The last deglaciation (ca. 21–11 kiloyears before 1950 AD, hereafter reported as kyr BP) represents the transition from the Last Glacial Maximum (LGM) to the current Holocene interglacial. The general reorganization of global climate during this period affected atmospheric and oceanic temperature, sea level and biogeochemical cycles<sup>1,2</sup>, particularly in the polar regions<sup>3</sup>. This transition is characterised by a series of abrupt climate changes, including the Bølling-Allerød interstadial (B-A; ca. 14.7–12.9 kyr BP<sup>4</sup>), the onset of which coincided with a period of enhanced sea level rise known as Meltwater Pulse 1A (MWP-1A; ca. 14.7–14.3 kyr BP<sup>5,6</sup>). The B-A period is also characterised by a rapid warming of the North Atlantic region<sup>7,8</sup>, and there is now a consensus that this climate transition was triggered by significant strengthening of the Atlantic Meridional Overturning Circulation (AMOC)<sup>8–10</sup>. During MWP-1A, sea level rose by approximately 18 m in less than 500 years ( $\sim 4 \text{ cm yr}^{-1}$ ) as a result of the retreat of the Laurentide and Eurasian Ice Sheets (LIS and EIS) as well as the Antarctic Ice Sheet<sup>5,6,11</sup>.

During the B-A, the northern hemisphere climate experienced important modifications that share similarities with the anticipated Polar Amplification<sup>12–14</sup>. Indeed, the destabilization of key elements of the cryosphere such as permafrost deposits and ice sheets is considered a threat to Earth's future climate because of their potential to further increase the concentrations of atmospheric Green House Gases (GHGs) and sea level rise<sup>15–18</sup>, respectively. Thus, the study of past abrupt warming events offers the opportunity to understand the behaviour of permafrost in a scenario of rapid cryosphere retreat, as well as place the modern anthropogenically-induced permafrost-climate feedbacks into a broader context of natural centennial-scale climate variability.

Recent estimates indicate that the vast majority of carbon in permafrost regions during the LGM was found in loess and ice-rich deposits, while in modern times, considering the same areal extent, peatlands have become the dominant reservoir for organic carbon (OC)<sup>19</sup>. Overall, this indicates that a complete reorganization of OC reservoirs in Circumpolar Arctic soils must have taken place at some point during the last 20 kyr.

Between Marine Isotopic Stage (MIS) 5 and MIS 2 (ca. 120–18 kyr BP), the large sea level drop and the subsequent exposure of large portions of the Laptev Sea, East Siberian Sea and Chukchi Sea continental shelves caused the expansion of Ice Complex deposits<sup>20–22</sup>, also referred to as Yedoma deposits, formed by fine-grained material with high amounts of OC and ice (up to 5% and 80%, respectively<sup>23</sup>). Today, the Yedoma domain represents approximately one third of the total OC stored in the Circumpolar Arctic permafrost region (327–466 Pg C), with Yedoma deposits accounting for 83–129 Pg C<sup>17,24</sup>. During the last glacial period, Yedoma deposits were a relatively large carbon pool, mainly because of the exposed land on Circumpolar Arctic shelves, with recent estimates indicating a potential carbon stock of  $657 \pm 97 \text{ Pg}^{24}$ , suggesting that a significant portion of the permafrost OC loss, within the reorganization of OC reservoirs happened during the last 20 kyr, likely involved these deposits. In fact, previous modelling studies and records from coral reefs<sup>25,26</sup> also highlighted the potential contribution of Yedoma destabilization to deglacial atmospheric CO<sub>2</sub> increase.

In contrast, a recent study has suggested that Yedoma deposits remained relatively unaltered during the last deglaciation, with negligible changes to their extension and storage capabilities<sup>19</sup>. However, during post-glacial sea level rise, when the continental shelves were flooded, Yedoma deposits possibly became vulnerable to mechanical erosion and thermal degradation<sup>24,27,28</sup>. In any case, a survey of the recent literature clearly reveals how the exact processes and feedbacks regarding Yedoma permafrost erosion during the last deglaciation are still a matter of debate,

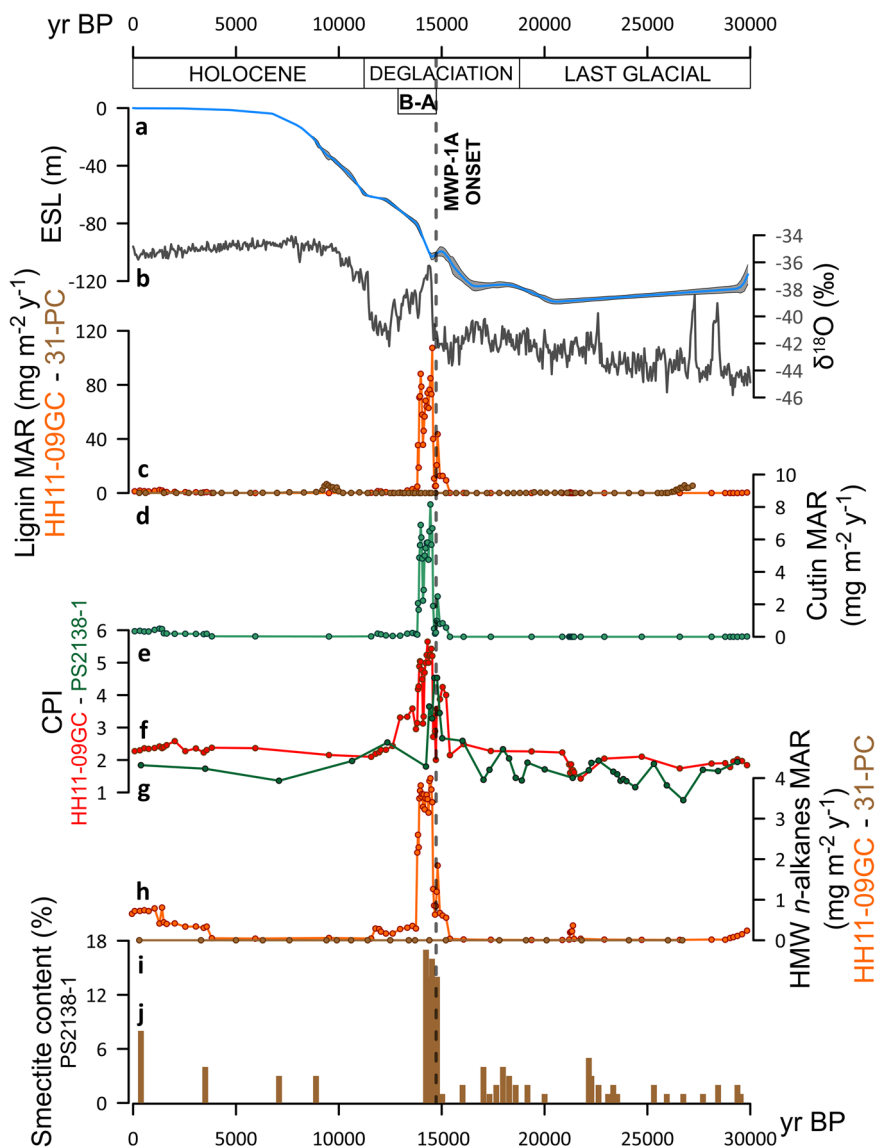


**Fig. 1** Location of sediment cores and main geomorphological features.

Base map represents bathymetry and morphology of the Arctic region (IBCAO V4<sup>17</sup>), with major Eurasian coastal seas indicated by their acronyms (BS Barents Sea, KS Kara Sea, LS Laptev Sea, ESS East Siberian Sea). Sediment cores HH11-09GC (this study), PS2138-1<sup>33</sup> and 31-PC<sup>22</sup> are shown as green, orange and yellow triangles, respectively. The extent of the major ice sheets of the northern hemisphere at ca. 15 kyr BP<sup>46,118</sup> (LIS Laurentide Ice Sheet, GIS Greenland Ice Sheet, BSIS Barents Sea Ice Sheet, FIS Fennoscandian Ice Sheet) is shown as partially transparent white areas. The grey area indicates the approximate extent of the exposed shelves at the onset of the B-A (without accounting for glacial isostatic adjustment). Green areas represent the current Yedoma deposit distribution<sup>24</sup>, also showing its remnants on the shelf. Blue, green, yellow, orange and red dots on the continental shelves and slopes represent OC-normalized lignin content of surface sediment from the Circumpolar Arctic Sediment Carbon DatabasE (CASCADE)<sup>69</sup>. Brown arrows indicate the main directions of sea ice transport out from the continental shelves and their merging towards the TPD.

mainly because of the lack of past observational evidence and continuous records<sup>29</sup>.

In this study, we present a multi-proxy analysis of a sediment gravity core (HH11-09GC) collected in the upper slope north of Nordaustlandet continental margin, Svalbard (Fig. 1 and Supplementary Fig. 1; 81°16'N, 26°13'E; core length 4.66 m; 488 m water depth<sup>30,31</sup>). This area is characterized by an exceptionally high sedimentation rate during the last deglaciation<sup>30,32,33</sup>, which allows high-resolution paleoenvironmental reconstructions in a region where expanded, continuous records of the last Termination are rare. We combined a suite of terrestrial, marine and sea ice biomarkers (lignin phenols, cutin acids, *n*-alkanes, alkenones, highly branched isoprenoids and sterols) at high resolution, together with Compound Specific Radiocarbon Analyses (CSRAs) performed on individual high-molecular weight (HMW) *n*-alkanoic fatty acid methyl esters (FAMES), to characterise the land-ocean connections during the last 30 kyr in response to natural climate change. Despite the lack of any direct riverine input proximal to the study area, we found an exceptionally high terrestrial biospheric contribution, starting when sea level rise was getting close to its maximum rate during the deglaciation (MWP-1A; Fig. 2a) and the climate signal from Greenland  $\delta^{18}\text{O}$  was rapidly changing (Fig. 2b). To explain these findings, we



**Fig. 2** Sedimentary record of abrupt terrestrial carbon deposition at the onset of the B-A. Main data plotted against calibrated age. **a** Estimated sea level curve (ESL, blue line), showing  $1\sigma$  error bars as shaded area<sup>102</sup>. **b** Oxygen isotopes ( $\delta^{18}\text{O}$ ) from Greenland ice cores<sup>119</sup>. **c** Lignin phenols Mass Accumulation Rate (MAR) from core HH11-09GC (orange line and dots) and **(d)** from core 31-PC (brown line and dots)<sup>22</sup>. **e** Cutin-derived products MAR (green line and dots) from core PS2138-1<sup>33</sup>. **f** CPI of *n*-alkanes from core HH11-09GC (red line and dots) and **(g)** from core PS2138-1<sup>33</sup> (green line and dots). **h** High molecular weight (HMW) *n*-alkanes MAR from core HH11-09GC (orange line and dots) and **(i)** from core 31-PC (brown line and dots)<sup>22</sup>. **j** Relative content of smectite in the clay fraction of core PS2138-1<sup>33</sup> (brown bars). The vertical dashed line displays the onset of MWP-1A.

considered four possible mechanisms: (A) a local source from Svalbard; (B) a pulse of freshwater discharge from the western Eurasian margin; (C) a transport process associated with the retreat of the Barents Sea Ice Sheet (BSIS); and (D) sea ice transport via the Transpolar Drift (TPD).

We used the gateway to the Arctic Ocean as a strategic region due to its relevance for sea ice export via the TPD (Fig. 1). Our final objective was to elucidate permafrost carbon reactivation mechanisms driven by abrupt climate warming and rapid sea level rise during MWP-1A. We also compared our dataset with other previously obtained records from the Eurasian Arctic, most notably from cores PS2138-1<sup>33</sup> and 31-PC<sup>22</sup> (Fig. 1). Specifically, the former, retrieved in the deeper part of the slope 80 km east of HH11-09GC, allows us to demonstrate that our record is not confined to a local effect, while the latter represents a valuable record from the Eurasian Arctic that covers the entirety of the last

Termination and for which terrestrial biomarkers have also been analysed at high resolution.

## Results

**HH11-09GC age-depth model and sedimentation rates.** We developed a Bayesian age-depth model (Supplementary Fig. 2) with OxCal v4.4.4<sup>34</sup> based on 14 AMS radiocarbon dates calibrated using Marine20<sup>35</sup>. The radiocarbon dates include 13 foraminiferal tests and one bivalve shell (Supplementary Table 1), of which 5 have been analysed in the current study and 9 published previously by Chauhan et al.<sup>30</sup>. The near surface  $\Delta R$  values used here for reservoir correction were obtained from the work of Brendryen et al.<sup>5</sup> (see section “Radiocarbon dating and age-depth model” in Materials and Methods for details) in the Norwegian Sea, which affects surface waters entering the Arctic Ocean

(an analogous approach was used by Keigwin et al. for the Beaufort Sea<sup>36</sup>). Here we focused on the uppermost section of the core (3.35 m), which spans from ca. 31.5 kyr BP to the present day. Our age-depth model suggests that, during the glacial period (30.0–19.0 kyr BP), sedimentation rates were relatively low ( $\sim 0.01\text{--}0.02\text{ cm yr}^{-1}$ ; Supplementary Fig. 3b), apart from a short period coinciding with the LGM (up to  $0.08\text{ cm yr}^{-1}$ ). The onset of the deglaciation was also characterized by low sedimentation rates followed by a rapid increase to  $\sim 0.1\text{ cm yr}^{-1}$  in the interval between 14.8 and 13.8 kyr BP (almost one third of the considered core section in length). After 13.8 kyr BP, sedimentation rates decreased again featuring low values ( $\sim 0.01\text{--}0.02\text{ cm yr}^{-1}$ ), consistent with those found typically in the study region over the Holocene<sup>33,37</sup>.

**Biospheric deposition at the B-A transition.** We quantified lignin phenols and cutin acids, a suite of biopolymer-derived monomers, which are found, respectively, in the main structure of vascular plants and in leaf waxes of soft plant tissues (i.e., needles and leaves), and can thus be used as tracers of the input of terrestrial biospheric material<sup>38,39</sup>. Between 30.0 and 15.2 kyr BP both biomarkers display extremely low mass accumulation rates (MARs) (Fig. 2c–e), indicating the virtual absence of biospheric input from land, likely due to the absence of widespread vegetation across the Svalbard archipelago<sup>40,41</sup> and the large distances from river outlets. The MAR of HMW *n*-alkanes (C<sub>23</sub>–C<sub>33</sub>), another proxy of terrestrial biospheric contribution, shows consistent results (Fig. 2h). Similar background values for lignin and *n*-alkanes, during the LGM, are also found on the Laptev Sea lower slope on the Lomonosov Ridge (sediment core 31-PC; Figs. 1 and 2d–i)<sup>22</sup>. Between 30.0 and 15.2 kyr BP, the Carbon Preference Index (CPI; Eq. 1 in Supplementary Material), an index based on the ratio of odd-over-even *n*-alkanes, shows low values (ca. 1.8; Fig. 2f) consistent with modern sediments from Svalbard's fjords<sup>42</sup> and with the widespread presence of fossil OC-rich units in Svalbard<sup>43</sup>. In fact, low CPI values are usually distinctive of old reworked OC and bedrock-derived material with thermally mature organic material (OM)<sup>44</sup> (i.e., CPI close to 1). Alternatively, this could be evidence of highly degraded terrestrial material that experienced long-range transport, not least since the study region is disconnected from any direct river input. The only noteworthy event registered in the core before 15 kyr BP is the deposition of a 40 cm thick sandy interval<sup>30</sup> around 22 kyr BP with low terrestrial biomarker and OC content (Fig. 2; Supplementary Fig. 3c). This likely corresponds to the maximum advance of the BSIS on the continental shelf<sup>45–47</sup> and to the subsequent remobilization of material that accumulated on the upper slope. Overall, before 15 kyr BP, the depositional environment is characteristic of polar continental margins<sup>48</sup>, with a strong influence of the BSIS that resulted in the deposition of mainly glacially-eroded material. After this interval, the impact of the BSIS on the site gradually weakened as the grounding line retreated more inland.

After several millennia of relatively small changes in OC deposition, the content of terrestrial biospheric material increased substantially around 15 kyr BP, notably within the B-A unit (Fig. 2c–h). Specifically, lignin, cutin and HMW *n*-alkane MARs increased by two orders of magnitude, along with an increase in CPI values (ranging from 3 to 6). A comparison with data obtained from other Arctic continental margins reveals that these terrestrial-derived biomarkers reached concentrations (4–10 mg g<sup>-1</sup> OC for lignin; Fig. 3c) commonly observed in inner shelf areas of the river-dominated Siberian margin<sup>39,49</sup> (Fig. 1). A similar event was also found in a previous study from core PS2138-1<sup>33</sup> located proximal to our record (Fig. 1). Despite the lower resolution, the authors

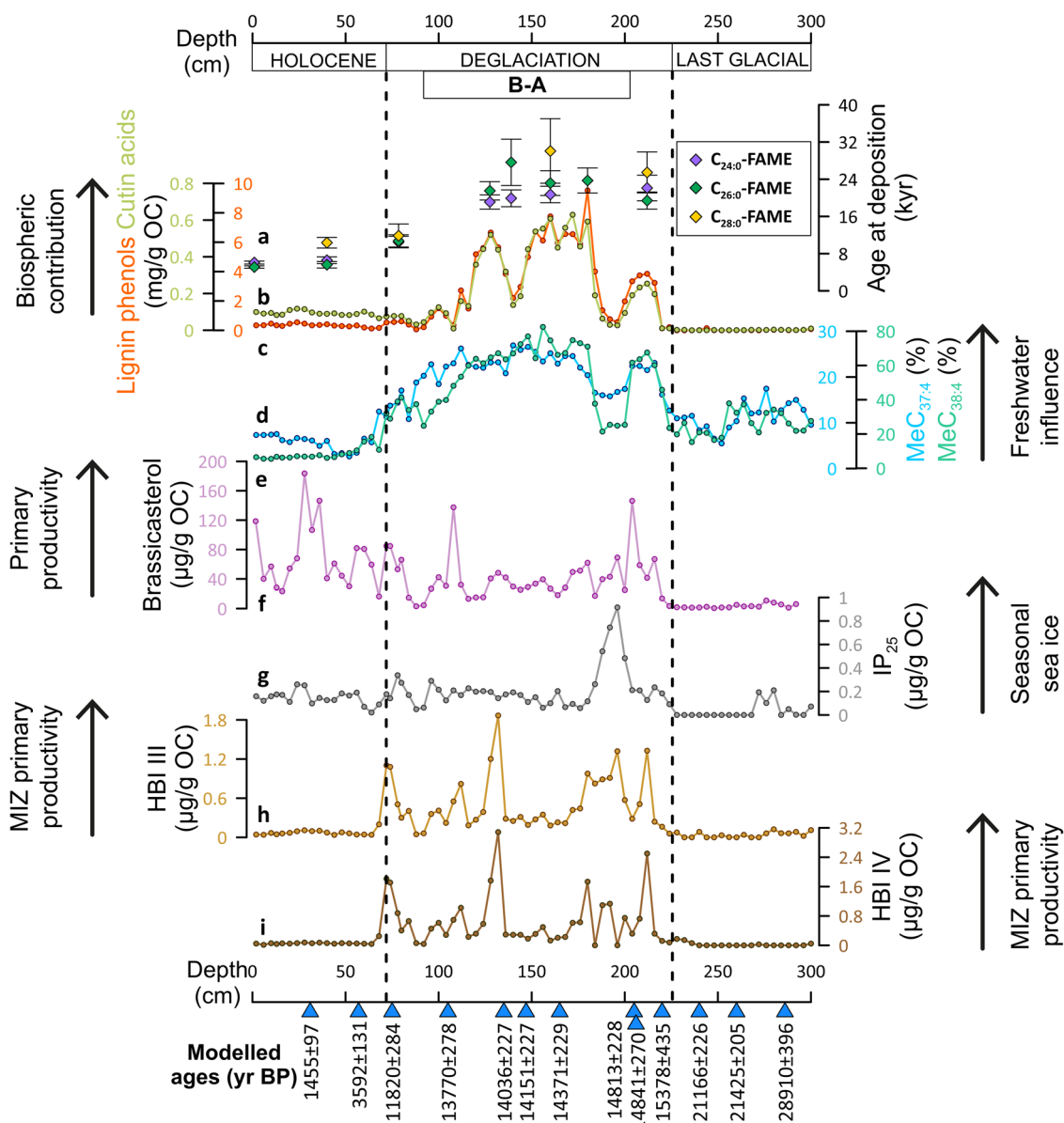
were able to identify a clear peak in the CPI (values between 3 and 4) during the deglaciation (Fig. 2g). By recalibrating the <sup>14</sup>C ages (see section “Radiocarbon dating and age-depth model” in Materials and Methods) for core PS2138-1 reported in Matthiessen et al.<sup>37</sup>, the terrestrial biospheric input occurred coeval among the two cores (Fig. 2f, g). A follow-up study on PS2138-1<sup>32</sup> focused on the clay mineral assemblages to better define the origin of this exotic material, and an increase in smectite content during the same time span was identified (Fig. 2j). Smectite is an uncommon clay mineral around the Svalbard archipelago, with potentially significant sources further east<sup>50–52</sup>, indicating that this material likely travelled several thousands of kilometres prior to its deposition at the gateway to the Arctic Ocean. Interestingly, lignin and HMW *n*-alkanes MARs recorded in core 31-PC show, in contrast, much lower values (by 2–3 orders of magnitude) for the entire deglaciation (Fig. 2d–i).

Finally, following the relatively short period of intense terrestrial OC deposition identified in HH11-09GC (ca. 15.2–13.8 kyr BP), the late deglaciation and the entire Holocene were characterised by a low accumulation of biospheric carbon, as expected for a core site far from any direct river input. Lignin concentration (on average  $0.35\text{ mg g}^{-1}\text{ OC}$ ) and CPI (on average 2.3) display values slightly higher than during the glacial period, suggesting a small contribution from Holocene vegetation, noticeably degraded, mixing with the locally sourced bedrock material.

#### Organic carbon characteristics and environmental parameters.

Alkenones are unusual algal lipids biosynthesized by certain phytoplanktonic microorganisms, whose distribution is traditionally used for paleo sea surface temperature reconstructions<sup>53,54</sup>. In the polar regions, the concentration of the MeC<sub>37:4</sub> alkenone relative to those of MeC<sub>37:2</sub> and MeC<sub>37:3</sub> (Eq. 3 in Supplementary Material) has also been used as a proxy for paleo salinity to infer freshening episodes driven by changes in the cryosphere<sup>53,55</sup>. More recently, the MeC<sub>37:4</sub> alkenone has also been identified in Isochrysidales algae associated with sea ice<sup>56</sup>, while the Arctic strain of *Gephyrocapsa huxleyi* produces large amounts of MeC<sub>37:4</sub> in nutrient-rich conditions<sup>57</sup>. In our HH11-09GC record, the relative concentrations of MeC<sub>37:4</sub> and other tetra-unsaturated alkenones (i.e., EtC<sub>38:4</sub> and MeC<sub>38:4</sub>) follow the same general trend observed with lignin and cutin content (Fig. 3b–e), implying that a common mechanism could explain both sets of biomarkers. In general, EtC<sub>38:4</sub> and MeC<sub>38:4</sub> alkenones are more typical of freshwater systems<sup>53,58,59</sup> and were not observed in Isochrysidales algae. Indeed, MeC<sub>38:4</sub> (Eq. 4 in Supplementary Material), which is relatively abundant in the B-A section compared to the Holocene (Fig. 3e), is dominant in freshwater organisms<sup>60</sup>. To investigate this further, we quantified IP<sub>25</sub>, a mono-unsaturated Highly Branched Isoprenoid (HBI) biomarker derived from some Arctic sea ice algae<sup>61</sup> and HBIs III and IV, which are produced by different diatoms that inhabit the open waters of the Marginal Ice Zone (MIZ)<sup>62,63</sup>. Between ca. 30 and 15 kyr BP, IP<sub>25</sub> and HBIs III and IV are virtually absent (Fig. 3g–i), indicating that the core site was likely under a perennial ice cover<sup>62</sup>. This conclusion is corroborated by the observation of exceptionally low concentrations of brassicasterol (Fig. 3f), a ubiquitous biomarker produced by marine phytoplankton<sup>64</sup>.

Overall, IP<sub>25</sub> concentrations do not exhibit any clear correlation with terrestrial biomarkers (Supplementary Fig. 4) or with the relative abundance of the MeC<sub>37:4</sub> alkenone, further suggesting that tetra-unsaturated alkenones in HH11-09GC were not derived from a sea ice source. IP<sub>25</sub> values started to increase around 15.5 kyr BP before reaching a peak at 14.8 kyr BP (Fig. 3g), which corresponds to a minimum in the terrestrial influence. Following a period of lower IP<sub>25</sub> content, values increased again towards the Holocene,



**Fig. 3 Biomarker fingerprint of the exotic organic material.** Main data from core HH11-09GC plotted against the core depth to ensure a better visualization of the extended deglaciation record. **a** Compound specific radiocarbon pre-depositional ages for terrestrial  $C_{24:0}$ ,  $C_{26:0}$ ,  $C_{28:0}$  FAMES (purple, green and yellow dots respectively) with  $1\sigma$  error bars; OC-normalized concentration of **(b)** cutin acids (green line and dots) and **(c)** lignin phenols (orange line and dots); relative abundances of **(d)**  $MeC_{37:4}$  (light blue line and dots) and **(e)**  $MeC_{38:4}$  alkenone (aqua green line and dots) referred to  $MeC_{37}$  and  $MeC_{38}$  groups respectively. **f** OC-normalized concentration of brassicasterol (light purple line and dots); OC-normalized concentration of **(g)**  $IP_{25}$  (grey line and dots), **(h)** HBI III (light brown line and dots) and **(i)** HBI IV (brown line and dots). The vertical dashed lines highlight the temporal division between Holocene, deglaciation and the last glacial period. Blue triangles and numbers at the bottom represent median values of 13 modelled dating points with  $1\sigma$  uncertainty (for visualization purposes, the lowest age is not displayed in this plot because its core depth exceeds 300 cm). Black arrows and texts on both sides of the graph indicate what each corresponding biomarker is associated with.

probably reflecting the establishment of modern sea ice conditions<sup>65,66</sup>. HBIs III and IV display somewhat variable values throughout the deglaciation (Fig. 3h, i), likely reflecting changes in sea ice dynamics (cf.  $IP_{25}$ ) and/or in the contributions from in situ production and laterally advected material.

To further characterize the source of terrestrial OC, CSRA were carried out on individual isolated long-chain FAMES of terrestrial origin (i.e.,  $C_{24:0}$ ,  $C_{26:0}$  and  $C_{28:0}$ ) deposited during the deglaciation and the Holocene. For the LGM unit, the concentration of FAMES was too low to obtain reliable age estimates. Figure 3a shows the compound specific radiocarbon pre-depositional ages in kyr,

obtained from the absolute radiocarbon ages corrected for the age at deposition (see Supplementary methods). The oldest pre-depositional ages (>25 kyr) were measured during the deglaciation, primarily in correspondence with the high terrigenous OC flux during the B-A. These ages imply the deposition of heavily pre-aged terrestrial OC or, alternatively, a mixture of relatively young terrestrial pools with ancient terrestrial OC sources. During the Holocene, pre-depositional ages of FAMES become younger, showing an average value of ca. 7 kyr, which is closer to values observed along Arctic margins (ca. 4 kyr in the Northern Pacific sectors<sup>67</sup> and in the major Russian Arctic rivers<sup>68</sup>).

## Discussion

Collectively, our multi-biomarker analysis provides compelling evidence for an unprecedented input of pre-aged terrestrial carbon and, more specifically, biospheric material at the gateway to the Arctic Ocean during the B-A warm period, consistent with the onset of MWPI-A. Indeed, both the composition and concentration of this material show characteristics more commonly associated with inner-shelf sediments of terrigenous-rich, river-dominated Arctic margins<sup>39,69</sup>, which do not correspond to the expected depositional settings of the core site, located in the high Arctic. Such a finding, therefore, raises questions about the mechanisms behind the release of this pre-aged terrestrial OC and whether the high terrigenous deposition can be attributed to rapid climate change and sea level rise during the B-A.

Given the different pathways for land-to-ocean transport in the Eurasian Arctic during the B-A, we considered four possible mechanisms to explain the delivery of ultra-high terrigenous OC to the core location: (A) local Arctic material from the Svalbard archipelago, remobilized and transported by the BSIS ice streams; (B) freshwater discharge from the western Eurasian margin in response to the ice sheet retreat; (C) transport of land-derived material via a meltwater outburst involving the BSIS collapse; and (D) advection and melting of sediment-laden sea ice via the TPD. To evaluate each of these, we interpreted our combined biomarker findings alongside sediment properties and previous literature data.

Firstly, hypothesis A, regarding local sources of OM driven by the BSIS, can be easily discarded as an explanation, owing to the Svalbard archipelago being extremely devoid of vegetation prior to the deglaciation. Even in modern times, in a warm interglacial, the dominant bioclimatic subzones in Svalbard include tundra, moss-dominated tundra and polar desert<sup>70,71</sup>. In fact, the modern vascular plant contribution to our study region, estimated as lignin contents in the archipelago soils (average value ca. 0.4 mg g<sup>-1</sup> OC, which declines to ca. 0.1 mg g<sup>-1</sup> OC in surface sediment of fjord coasts<sup>40,41</sup>), is well below the lignin concentration measured in the B-A unit (4–10 mg g<sup>-1</sup> OC). The high CPI of *n*-alkanes in the B-A unit also argues against a significant contribution from metamorphic local bedrock units<sup>43</sup> (CPI values around 172) and glacier erosion-derived supply. This is further supported by CSRAs, which exclude the presence of primarily radiocarbon dead material - despite it being highly pre-aged - that would be the major fingerprint of bedrock-derived material. Finally, the absence of a well-developed trough mouth fan system in the Albertini Trough<sup>73</sup> where the core was retrieved, as well as the presence of coarse IRDs limited to around 14.7–14.6 kyr BP during the terrigenous OC minimum, are not consistent with a significant influence from ice sheet dynamics (Supplementary Fig. 5).

The rejection of a locally-sourced terrestrial OC pool to HH11-09GC during the B-A implies a long-range transport from a distal source. Hypothesis B, regarding supply by Eurasian rivers and redistribution through sediment transport processes, seems unlikely, because more than 1500 km separate the core location from the closest Eurasian coastline. In fact, upon release into the coastal system, lignin and cutin experience intense degradation during sediment transport over the Arctic margins until final burial in sediments<sup>49,74</sup> (e.g., Siberian margin; Fig. 1). Such degradation is believed to be a consequence of the protracted oxygen exposure during transport<sup>49,74</sup>. For the B-A unit, our data suggest an opposite scenario, with rapid burial of land-derived material and minimal degradation, as corroborated by lignin-based degradation proxies, indicating that samples with higher lignin concentration show minimal signs of degradation (Supplementary Fig. 6). In addition, the sediment transport pathway is unlikely, given the bathymetry, as the material would have needed to bypass major troughs (e.g., St. Anna trough, with

a maximum depth of more than 600 m) to reach the core location. Furthermore, the pre-depositional age of the FAMES within the B-A unit is much older than the material supplied by modern Arctic rivers (up to ca. 8 kyr), including those located in continuous permafrost<sup>68</sup>.

Thirdly, one might potentially envisage temporary storage in a proglacial basin inland (e.g., around the White Sea area) for at least 20 kyr, followed by a large meltwater discharge as the BSIS was retreating at the onset of the B-A (hypothesis C). However, in addition to the presence of major troughs and the labile nature of terrigenous biomarkers described previously, the terrestrial material is significantly older than the maximum extent of the BSIS towards the LGM<sup>45,46,75</sup>, when the entrapment of land-derived material would have presumably occurred. In fact, the absolute age of FAMES, without correcting for the time of deposition, reaches up to ca. 45–35 <sup>14</sup>C kyr (Supplementary Table 2), when the continental shelf was mostly ice free<sup>46,76,77</sup>.

Along with the hypothesis C, a scenario involving a subglacial transport associated with the rapid retreat of the BSIS during the B-A<sup>5</sup> could certainly explain the extremely high sedimentation rate given the short distance from the BSIS edge. However, this would require the formation of a proglacial lake along the southern margin of the BSIS and the subsequent subglacial accumulation of riverine and lacustrine material from inland beneath the ice sheet, followed by subglacial transport across the entire BSIS from south to north. From a purely mechanical perspective, however, previously published hydraulic gradient maps<sup>78</sup> and past subglacial flow direction indicators<sup>79</sup> are inconsistent with a land-to-ocean connection across the ice sheet<sup>78</sup>, not least since, to achieve this, the material would need to overcome the ice divide of the BSIS and move against the hydraulic gradient to reach northern Svalbard.

Finally, we evaluated hypothesis D, concerning the transport of biospheric OM to HH11-09GC via sediment-laden sea ice, which stands as our preferred explanation. This scenario implies an active advection via the TPD, as seen in modern times, that projects sea ice from the Siberian shelves and regions further east towards the Fram Strait<sup>32,80–83</sup> (Fig. 1). The presence of sea ice is especially evident from the continuous presence of IP<sub>25</sub> after ca. 15 kyr BP (Fig. 3g), following virtual absence during the LGM. It is also well-known that sea ice forming along the Arctic coastline can incorporate heterogeneous particles, including riverine material containing plant remnants, terrigenous-rich sediments and freshwater algae<sup>83,84</sup>, depending on the environment and physiography of the area<sup>83,85</sup>. For example, Wegner et al.<sup>83</sup> showed that about 20% of the diatom assemblages in sea ice collected within the TPD derived from freshwater systems, and this provides a plausible explanation for the relatively high tetra-unsaturated alkenone fingerprint in the terrigenous-rich B-A unit (Fig. 3d, e), that follows the general lignin and cutin trend. In addition, the relatively fine-grained sediment texture and the paucity of coarse IRDs<sup>30</sup> (Supplementary Fig. 5) corroborate hypothesis D, especially considering the silty-type sediments most commonly transported by sea ice<sup>86,87</sup>. Transport via sea ice also explains the absence of significant degradation of the terrestrial OM found in the B-A unit (Supplementary Fig. 6). Assuming suspension freezing could be, as today<sup>88</sup>, the main process for the entrapment of particles inside sea ice, this implies the partial isolation of OM from oxygen exposure, which is the main driver of degradation in the marine environment<sup>39,49</sup>. Further, this transport mechanism is relatively rapid (only a few years are necessary for sea ice to travel from Siberian shelves towards the Fram Strait<sup>89</sup>) and does not entail intermediate deposition sites, where the material could undergo degradation.

Under this sea ice transport and melting scenario, the development of a MIZ-like environment for a large part of the

deglaciation<sup>63</sup> likely explains the increase in the open water biomarkers brassicasterol and HBIs III and IV, as a consequence of higher marine primary productivity stimulated by nutrients released from melting sea ice<sup>90,91</sup>, which could also promote the synthesis of larger amounts of the MeC<sub>37:4</sub> alkenone in the Arctic strain of *Gephyrocapsa huxleyi*<sup>57</sup>. Lastly, the relatively high percentage of smectite in the clay fraction measured in the nearby core PS2138-1 is a clear indication of the sediment provenance, which rules out a local source from Svalbard<sup>52</sup>, instead pointing to sources further east including the Kara and Laptev Sea shelves<sup>32,50</sup>. We also believe that the lack of a clear increase in the sea ice proxy IP<sub>25</sub> within the terrigenous OC-rich unit indicates that this event was characterised by a significant increase in the number of sediment particles bound to sea ice during this time (i.e., sediment-laden sea ice), rather than by an increase in the sea ice export per se. In fact, several previous studies that focused on sea ice reconstructions of glacial and deglacial periods around the Fram Strait and the Northern Barents Sea<sup>66,92,93</sup> do not point to particularly high sea ice presence and export at the onset of the B-A.

Recent estimates<sup>94,95</sup> show that the modern average annual sea ice export through the Fram Strait is on the order of 2500 km<sup>3</sup>, with a total annual sediment export of ~160 Tg<sup>86</sup>. This corresponds to an average sediment particle concentration of ~60 g m<sup>-3</sup>, which falls within the lower range found in discrete sea ice samples documented in the literature (between 10 and 56000 g m<sup>-3</sup>)<sup>85</sup>. Consequently, if the higher limit for sediment concentrations in sea ice were replicated, or even exceeded, during the B-A, it becomes reasonable to propose that sediment-laden sea ice export from the Eurasian Arctic could readily have been responsible for generating the observed deposit.

Despite several lines of evidence pointing towards a sediment-laden sea ice transport mechanism, two aspects remain to be explained, namely (a) the reason why sea ice entrained so much sediment during the B-A and (b) the source of the material. Our hypothesis is that, during MWP-1A, sea level rise massively enhanced coastal erosion<sup>96–98</sup> resulting in the entrainment of large volumes of coastal deposits within newly formed sea ice. CSRA of the terrestrial biomarkers indicate that the material was pre-aged at deposition with an overall age of formation consistent with MIS 3. The coastal Yedoma deposits documented around the Siberian and Alaskan margins<sup>17,99</sup> (Fig. 1) display radiocarbon ages that align very closely with the ages measured in the B-A unit<sup>24,100</sup>. In addition, lignin-based proxies enable us to discriminate between different sources (i.e., woody vs non woody material and angiosperm vs gymnosperm tissues) based on the ratios of syringyl and cinnamyl phenols over vanillyl phenols<sup>39,101</sup> and the fingerprint of the B-A unit is compatible with a Yedoma signature (Supplementary Fig. 7). Coastal Yedoma deposits are known to be highly susceptible to instability due to their high ice content, with modern erosion rates reaching several meters per year<sup>27,28</sup>. We could therefore propose that MWP1-A (with a sea level rise of almost 18 m in less than 500 y<sup>6,102</sup>) corresponded to a period of exceptional Yedoma erosion. Furthermore, the B-A is also known for the general reorganization of the AMOC, which resulted in an enhanced transport of heat towards the northern Hemisphere<sup>8,103</sup>, including the Arctic Ocean. We therefore propose that sea ice melting, sustained by the warm Atlantic inflow, promoted the deposition of sea ice-advected sediments at the boundary between the Atlantic and Arctic domains.

Prior to the current study, none of the previous Arctic reconstructions dealing with permafrost remobilisation during past warming events have documented the massive erosion of Yedoma during MWP-1A. For example, sediment core 31-PC from the Lomonosov Ridge<sup>22</sup> (Fig. 1) failed to capture this event

in both magnitude and timing. Specifically, fluxes of terrestrial biomarkers measured in the 31-PC record are, if compared to our B-A unit, 2 to 3 orders of magnitude lower (Fig. 2d–i) (see also Supplementary Material in Martens et al.<sup>22</sup>, Fig. S2c). The reason behind the weak influence of sea ice-driven sediment deposition in 31-PC could be that the core site was positioned north of the sea ice edge during the sea ice minima, as seen in the modern satellite record (1979–2010) prior to the recent retreat further north<sup>104</sup>. In fact, most of the modern sea ice melting occurs further west within the Fram Strait, which accounts for 90% of Arctic sea ice outflow<sup>95</sup>. The resulting heat loss driven by sea ice melt in the Fram Strait and Nordic Sea region is around 115 TW, compared to 16 TW in the entire Arctic Ocean<sup>105</sup>, further confirming the different impact of sea ice dynamics between regions. The 31-PC sediment core location was also probably too deep (1120 m water depth) to be directly influenced by coastal erosion and sediment transport mechanisms (Fig. 1) and the material deposited in HH11-09GC was potentially sourced from locations further east or west. In any case, a survey of the recent literature describing past permafrost dynamics in the Arctic Ocean clearly indicates that previous reconstructions are partially discontinuous and, in several cases, only start after the B-A period, and, therefore, do not document past changes to Yedoma stability during MWP1-A<sup>106,107</sup>.

## Conclusions

The role of sea level rise in coastal permafrost erosion during the last deglaciation was first documented in the North Pacific by Winterfeld et al. in 2018<sup>15</sup>. However, while in this region the source of coastal permafrost was proximal to the sediment core location, our study area is located far from any direct land-to-ocean conduit. Thus, this highlights the severe impact that MWP-1A must have had on the Yedoma stability along the flooded Arctic margin. Today, coastal erosion of Yedoma-like ice-rich permafrost in the Arctic Ocean is a widespread phenomenon<sup>27,28</sup>, with average erosion rates on the order of 0.5–0.7 m yr<sup>-1</sup> and extremes >25 m yr<sup>-1</sup><sup>127,108,109</sup>. However, the magnitude of sediment-laden sea ice export documented in this study is far from that described in modern studies. We therefore infer a scenario of unprecedented coastal erosion during MWP1-A, capable of producing a Yedoma-rich unit at the gateway to the Arctic Ocean through the export of sediment-laden sea ice within the TPD.

Previous modelling studies and indirect evidence from coral records<sup>25,26</sup> have suggested that flooding of the Siberian margin and erosion of coastal permafrost deposits could have affected deglacial atmospheric CO<sub>2</sub> increase. Yedoma deposits, including the exposed Arctic continental shelves during the last glacial period, potentially accounted for 657 ± 97 Pg C susceptible to mechanical and thermal destabilization<sup>24</sup>. In particular, MWP1-A has been proposed as a key period for the release of CO<sub>2</sub> from collapsing permafrost, with atmospheric CO<sub>2</sub> concentration increasing by 12 ± 1 ppm<sup>2</sup>, despite the absence of empirical evidence of sea level-Yedoma interactions<sup>25</sup>. Other studies, dealing with the reorganization of permafrost-carbon soils during the LGM-Holocene transition, have instead assumed virtually stable Yedoma domains over the shelf despite the post-glacial sea level rise<sup>19</sup>. Our reconstruction, in this respect, represents a fundamental benchmark as it provides a mechanistic understanding of the processes driving permafrost release during rapid sea level rise and, thus, it offers new conceptual frameworks for future models and permafrost carbon budgets. In particular, we provide compelling evidence from the Arctic Ocean about the interaction between sea level rise and coastal Yedoma erosion, accurately constraining its timing during MWP1-A<sup>2</sup>. Further investigations



from the Greenland Sea, Fram Strait and Nordic Seas are needed to corroborate the large-scale nature of this event and, ultimately, elucidate the response of permafrost to rapid sea level rise and warming.

## Methods

**Subsampling and pretreatment.** Sediment core HH11-09GC was subsampled at 2-cm resolution and a total of 149 samples were collected from the upper 300 cm of the core. Chauhan et al.<sup>30,31</sup> subsampled at 2-cm resolution for grain size analyses, at 5-cm resolution for bulk geochemical analyses and at 5-, 2- and 1-cm resolution, depending on the core section, for micro-paleontological and IRD analyses (115 samples in total over the entire 466 cm core).

Sediments for the current study were freeze-dried, ground for homogenization and stored in glass vials prior to geochemical analyses at the Institute of Polar Sciences of the National Research Council in Bologna, Italy.

**Radiocarbon dating and age-depth model.** A total of 14 radiocarbon dates on calcareous marine organisms were used in this study (Supplementary Table 1), of which 9 were retrieved from the literature<sup>30</sup>. 5 radiocarbon dates were measured at the AWI-MICADAS facility<sup>110</sup> in Bremerhaven, Germany (4 samples) and at the US-NSF NOSAMS facility in Woods Hole, USA (1 sample). Radiocarbon dates were calibrated using the Marine20 calibration curve<sup>35</sup> and the age-depth model was generated using a *P Sequence* model in OxCal v4.4.4<sup>34</sup>. We applied a variable regional marine reservoir correction ( $\Delta R$ ) to each <sup>14</sup>C date following the marine radiocarbon reconstruction for the Norwegian Sea published in Brendryen et al.<sup>5</sup>. The  $\Delta R$  value for each <sup>14</sup>C determination was estimated as the difference between the Normarine18 radiocarbon age<sup>5</sup> and its counterpart on Marine20<sup>35</sup> using linear interpolation. Beyond the Normarine18 calibration period (i.e., before 21 kyr BP), we applied the lower-most assessable  $\Delta R$  correction, that is ca. 170 years.

We employed the same approach to recalibrate and construct an age-depth model for the radiocarbon dates of sediment core PS2138-1<sup>37</sup>. For both sediment sequences, the age output shows a robust and coherent age model as indicated by high agreement indices, with values higher than 98% (i.e., well above the critical threshold of 60%<sup>34</sup>).

**Bulk data and biomarkers.** Bulk data, in the form of total organic carbon (TOC) and total nitrogen (TN) content, were measured in all 149 samples via EA-IRMS (Elemental Analyzer-Isotope Ratio Mass Spectrometry). Around 20 mg of grounded sediment was acidified with diluted HCl (1.5 N) in silver capsules to remove inorganic carbonates. Analyses were then performed by a Finnigan Delta Plus XP mass spectrometer coupled with a Thermo Fischer Scientific FLASH 2000 Elemental Analyzer as described by Tesi et al.<sup>111</sup>.

Out of the total 149 samples, 77 were then analyzed for specific biomarkers (4-cm resolution).

Lignin phenols and cutin acids were analyzed via CuO oxidation following the method published by Goñi and Montgomery<sup>112</sup>. Around 250–300 mg of sediment were oxidized in a 2 M NaOH aqueous solution under oxygen-free conditions in Teflon vessels using CEM Mars6 Microwave Digestion System (150 °C for 90 min). After the oxidation, the samples were transferred into Falcon tubes and a known amount of internal standard (ethylvanillin) was added to each sample to estimate recovery rates. Samples were centrifuged and then the liquid phase was transferred into pre-combusted glass tubes. The solution was acidified (pH=1) with concentrated HCl and

extracted twice with ethyl acetate. The extracts were filtered with anhydrous Na<sub>2</sub>SO<sub>4</sub> to remove excess water, dried under N<sub>2</sub> stream and redissolved in pyridine. Samples, prior to the analysis, were derivatized at 50 °C for about 30 min with N,O-Bis(trimethylsilyl)trifluoroacetamide (BTSFA) with 1% trimethylchlorosilane (TMCS). The quantification of CuO oxidation products was performed via gas chromatography-mass spectrometry (GC-MS), using an Agilent 7820 A Gas Chromatograph coupled with a 5977B Mass Selective Detector in single ion monitoring (SIM), equipped with a Trajan SGE 30 m × 320 μm (0.25 μm-thick film) PB-1 capillary column. The oven temperature ramp was set from 95 °C to 300 °C at a rate of 4 °C/min with a hold time of 10 min.

CuO oxidation products analyzed include (a) 3,5-dihydroxybenzoic acid, (b) 8 lignin phenols: vanillyl (V) (vanillin, acetovanillone, vanillic acid), syringyl (S) (syringaldehyde, acetosyringone, syringic acid) and cinnamyl (C) phenols (p-coumaric acid, ferulic acid) and (c) 8 cutin acids: 16-hydroxyhexadecanoic acid, hexadecan-1,16-dioic acid, 18-hydroxyoctadec-9-enoic acid, 7 or 8-dihydroxy C<sub>16</sub> α,ω-dioic acid and 8, 9 or 10 16-dihydroxy C<sub>16</sub> acids<sup>38,112</sup>. Quantification of lignin phenols was achieved through calibration curves obtained from commercially available standards (Sigma-Aldrich). Cutin acids were quantified against the concentration of the internal standard. We reported the total lignin concentration as the sum of the 8 lignin-derived phenols and the total cutin concentration as the sum of the 8 cutin acids.

Hydrocarbons (HBIs and *n*-alkanes) and algal lipids (sterols, alkenones) were extracted following a slightly modified method from Tesi et al.<sup>113</sup>. A known amount of internal standards (7-hexylnonadecane, 9-octylheptadec-8-ene, docosane, 5α-Androstan-3β-ol) was added to ~1.5 g of sediments. Samples were left in a 5 wt% KOH, MeOH:H<sub>2</sub>O (9:1 v/v) solution at 70 °C for 1 h to complete saponification. The neutral fraction was then extracted from the aqueous solution three times, after centrifugation, with pure hexane (HEX). Extracts were dried under N<sub>2</sub> stream and redissolved in HEX:DCM (3:2 v/v). Purification was performed using silica gel (60–200 μm) column chromatography. The apolar fraction (containing HBIs, *n*-alkanes and alkenones) was eluted with HEX:DCM (3:2 v/v) and the polar fraction (containing sterols) with MeOH:DCM (1:1 v/v). The polar fraction was then redissolved in DCM and, prior to GC-MS analysis, subsampled and derivatized with BTSFA with 1% TMCS.

We then followed the method developed by Rontani et al.<sup>114</sup> to quantify alkenones in small concentrations via GC-MS. The apolar fraction was redissolved in MTBE:MeOH (3:1 v/v) with an excess NaBD<sub>4</sub> and left at room temperature for an hour to transform alkenones into alkenols. Excess NaBD<sub>4</sub> was then neutralized by adding NH<sub>4</sub>Cl-saturated ultrapure water. The aqueous solution was subsequently acidified with concentrated HCl and extracted with HEX:DCM (4:1 v/v). Reduced extracts were dried under N<sub>2</sub> stream, redissolved in pyridine and derivatized with BTSFA with 1% TMCS for GC-MS analysis.

The analyses of both apolar and polar fractions were performed via GC-MS, using an Agilent 7820 A Gas Chromatograph coupled with a 5977B Mass Selective Detector in SIM, equipped with a Trajan SGE 30 m × 320 μm (0.25 μm-thick film) PB-1 capillary column. For the analyses of the entire apolar fraction, the oven temperature ramp was set from 60 °C to 250 °C at a rate of 10 °C/min, and then up to 300 °C at a rate of 4 °C/min, with a final hold time of 25 min. For the analyses of the polar fraction, the oven temperature ramp was set from 70 °C to 200 °C at a rate of 8 °C/min, and then up to 300 °C at a rate of 4 °C/min, with a final hold time of 10 min.

The analyzed compounds included (a) IP<sub>25</sub>, HBI II, III and IV, (b) C<sub>15</sub> to C<sub>35</sub> *n*-alkanes, (c) brassicasterol, cholesterol, sitosterol and campesterol, and (d) MeC<sub>37:2</sub>, MeC<sub>37:3</sub>, MeC<sub>37:4</sub>, MeC<sub>38:2</sub>,

MeC<sub>38:3</sub>, MeC<sub>38:4</sub>, EtC<sub>38:2</sub>, EtC<sub>38:3</sub>, EtC<sub>38:4</sub>, EtC<sub>39:2</sub>, EtC<sub>39:3</sub> alkenone-derived alkenols. HBIs were quantified with the method presented in Belt et al.<sup>61</sup> for the IP<sub>25</sub>, applying it also for HBI III and IV. The SIM peak areas of the individual HBIs were correlated with the SIM peak areas of the internal standard and a response factor was applied to account for the differences in mass spectral responses. Alkanes were quantified using commercially available external standards after correcting for the internal standard. Alkenones were quantified by converting the SIM results to total ion chromatogram (TIC) results using a correction factor (obtained by the analysis of concentrated samples over different concentrations) and comparing them to the response of the internal standard. Relative abundances of methyl C<sub>38</sub> and ethyl alkenones, due to co-elution problems impeding the conversion of their SIM peak areas into TIC, have been calculated based on the integrated peak areas from SIM mode only. Results of the quantified compounds are shown as both MARs (Mass Accumulation Rates) and OC-normalized data.

**Compound specific radiocarbon analyses (CSRA).** CSRA data were obtained from specific high molecular weight *n*-alkanoic acids. We integrated different ranges of sediment depths (Supplementary Table 2) in order to collect a sufficient amount of material for the analysis (at least 100 µg of the selected compounds are necessary for radiocarbon dating). The different integrated depth for each sample corresponds, on average, to a period of 75 years according to our age-depth model. Taking into account that the analytical uncertainty on the <sup>14</sup>C age of the individual compounds is on average ca. 2000 years, we thus considered the uncertainty caused by the sediment depth integration as negligible.

Around 100 g of sediment was extracted for 48 h with a Soxhlet system using a DCM:MeOH (9:1 v/v) mixture. Extracts went through saponification with a 0.1 M KOH solution (MeOH:H<sub>2</sub>O, 9:1 v/v) for 2 h at 80 °C. The aqueous solution was acidified to pH = 1 with concentrated HCl and extracted 3 times with HEX. Samples were dried under N<sub>2</sub> stream and methylated at 80 °C overnight with HCl and MeOH (with a known <sup>14</sup>C signature). The resulting FAMES were extracted 3 times using HEX and separated from the polar fraction via silica gel column chromatography. Specific FAMES were isolated and purified via Preparative Capillary Gas Chromatography (PC-GC)<sup>115</sup> with an Agilent HP6890N GC coupled with a Gerstel Preparative Fraction Collector and a Restek Rxi-1ms fused silica capillary column (30 m, 0.53 mm diameter, 1.5 µm film thickness). The purity and recovery of each FAME fraction were then checked via Gas Chromatography – Flame Ionization Detection (GC-FID).

Purified FAMES were subsequently transferred into 25 µL tin capsules using a minimum amount of DCM as solvent. After thorough drying, capsules were packed, and combusted using an Elementar Vario ISOTOPE EA (Elemental Analyzer), and the isotopic ratios (<sup>14</sup>C/<sup>12</sup>C) of produced CO<sub>2</sub> were determined via the directly connected AMS, the MICADAS system, which is equipped with a gas-ion source. Radiocarbon contents of the samples were analyzed along with reference standards (oxalic acid II; NIST SRM 4990 C) and blanks (phthalic anhydride; Sigma-Aldrich 320064)<sup>110</sup>. Background correction and standard normalization were performed via the BATS software. Corrections for the procedural blank were made using the approach described in Sun et al.<sup>116</sup>. Briefly, several aliquots of differently sized FAMES were extracted from two in-house reference materials with known radiocarbon content, namely a modern apple peel with Fraction Modern relative to the reference standard (F<sup>14</sup>C<sub>OC</sub>) = 1.029 ± 0.001 and <sup>14</sup>C-free Eocene Messel shale with F<sup>14</sup>C<sub>OC</sub> = 0, using the same procedures applied for the samples

studied here. Assuming constant blank contribution, mass and radiocarbon signature of the blank were determined, and F<sup>14</sup>C values of unknown FAME samples were corrected for its contribution, with full propagation of uncertainties. An additional correction was implemented for the addition of the methyl group<sup>15,116</sup>, since it affects the slope of the regression lines. In order to remove its contribution from the blank assessment, the F<sup>14</sup>C values the unprocessed fatty acids would have if they were methylated have to be calculated. This was achieved by combining the F<sup>14</sup>C of the bulk apple peel and the FAs with the F<sup>14</sup>C<sub>methyl</sub> through isotopic mass balance<sup>15</sup>.

### Data availability

All data needed to evaluate the conclusions are available in the main text and/or in the supplementary materials. The Excel spreadsheet containing the complete dataset used in this work can be accessed at <https://zenodo.org/record/8305777>. The Excel spreadsheet containing the Supplementary Tables can be accessed at <https://zenodo.org/record/8305694>. Additional information related to this paper may be requested from the authors.

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## Author contributions

A.N. and T.T. planned the research project and activities. R.N. and T.C. provided the sediment and foraminifera samples. F.M. developed the age-depth model. L.C. and C.P. helped with the radiocarbon dating on foraminifera. A.N. carried out the biogeochemical analysis of all samples. H.G. and J.H. carried out the analysis and quantification of CSRA. A.N. drafted the figures. A.N., T.T., S.B., G.M. and F.C. interpreted the data. All authors contributed to the final manuscript.

## Competing interests

The authors declare no competing interests.

## Additional information

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