



1 **Deglacial records of terrigenous organic matter accumulation off the**  
2 **Yukon and Amur rivers based on lignin phenols and long-chain *n*-**  
3 **alkanes**

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**Abstract:**

14 Arctic warming and sea level change will lead to widespread permafrost thaw  
15 and subsequent mobilization. Sedimentary records of past warming events during the  
16 last glacial–interglacial transition can be used to study the conditions under which  
17 permafrost mobilization occurs. Long-chain *n*-alkyl lipids and lignin phenols are two  
18 types of biomarkers excellently suited for the reconstruction of terrestrial higher plant  
19 vegetation, as they are derived from epicuticular waxes and from the major rigidifying  
20 material of higher plants. For the Okhotsk and Bering Seas off the mouths of the  
21 Amur and Yukon rivers, respectively, published records reported the temporal  
22 variations of *n*-alkyl lipid accumulation recording mostly erosive processes. Surface  
23 runoff, vegetation type, and degree of organic matter degradation as reflected by  
24 lignin have not been investigated so far.

25 Here, we present new lignin phenol records from marine sediment cores and  
26 compare them with previously published lipid biomarker data from these two  
27 subarctic marginal seas. We find that in the Yukon Basin, vegetation change and  
28 wetland expansion began already in the early deglaciation (ED, 14.6–19 ka BP). This  
29 timing is different from observed changes in the Okhotsk Sea reflecting input from  
30 the Amur Basin, where wetland expansion and vegetation change occurred later in the  
31 Preboreal (PB). In the two basins, angiosperms contribution and wetland extent all  
32 reached maxima during the PB, both decreasing and stabilizing after the PB. We also  
33 find that the permafrost of the Amur Basin began to become remobilized in the PB.  
34 Retreat of sea-ice coupled with increased sea-surface temperatures in the Bering Sea



35 during the ED might have promoted early permafrost mobilization. In both records,  
36 accumulation rates of lignin phenols and lipids are similar, suggesting that under  
37 conditions of rapid sea-level rise and shelf flooding, both types of terrestrial  
38 biomarkers are delivered by the same transport pathway.

## 1. Introduction

39 Climate warming caused by anthropogenic perturbation affects the Arctic more  
40 strongly than other regions of the world. Warming climate induces environmental  
41 changes that accelerate degradation of organic matter (OM) stored in permafrost and  
42 promote greenhouse gas release (Schuur et al., 2015). Permafrost, or permanently  
43 frozen ground, is soil, sediment, or rock that remains at or below 0 °C for at least two  
44 consecutive years. It occurs both on land and beneath offshore arctic continental  
45 shelves, and underlies about 22 % of the Earth's land surface (Brown et al., 2002).  
46 Most of today's circum-arctic permafrost deposits in the Yedoma region of Siberia  
47 and Alaska developed under continental cold climate conditions in unglaciated  
48 regions during the late Pleistocene (Strauss et al., 2021). Across the northern circum-  
49 polar permafrost regions, Yedoma deposits, 0–3 m soils and deltas contain about twice  
50 as much carbon as the pre-industrial atmospheric carbon pool (Hugelius et al., 2014).

51 During the deglacial and Holocene warming ground ice melted, causing the land  
52 surface to collapse into space previously occupied by ice wedges, a process called  
53 thermokarst. This led to the formation of thermokarst lakes and thermo-erosional  
54 valleys as well as rivers, and also likely the release of carbon from thawed deposits  
55 (Walter et al., 2006; Walter Anthony et al., 2014). Around 70 % of the Yedoma region  
56 thawed beneath thermokarst lakes and streams since 14.7 ka BP (Walter Anthony et  
57 al., 2014). Based on a carbon cycle model, Köhler et al. (2014) suggested that  
58 deglacial thawing of permafrost in the Northern Hemisphere at the onset of the  
59 Bølling/Allerød (B/A) may have caused an abrupt CO<sub>2</sub> rise and a drop in atmospheric  
60  $\Delta^{14}\text{C}$ , with a possible contribution from flooding of the Siberian continental shelf  
61 during melt water pulse 1A (MWP-1A).

62 During millennia following the formation of thermokarst lakes, mosses and other  
63 plants grew in and around them, which may in part have offset permafrost carbon  
64 release (Walter Anthony et al., 2014; Schuur et al., 2015; Turetsky et al., 2020). *Alnus*  
65 is a common genus in Yukon Holocene pollen records but far less common in  
66 interglacials, because *Alnus* groves frequently develop along newly formed local



67 drainage features linked to permafrost degradation (Schweger et al., 2011). Several  
68 studies suggested major deglacial changes in the vegetation of permafrost-affected  
69 areas during the last deglaciation, including the Yukon Territory (Fritz et al., 2012),  
70 Sakhalin peninsula and Hokkaido (Igarashi and Zharov, 2011), the Lena River basin  
71 (Tesi et al., 2016), and the Amur River basin (Seki et al., 2012).

72 Biomarker compositions, distributions and contents in marine sediments can help  
73 to elucidate the processes responsible for terrestrial OM export from land and the fate  
74 of this OM in the ocean. Long-chain *n*-alkyl lipids and lignin phenols are two types of  
75 biomarkers commonly used to reconstruct supply of terrigenous OM to the ocean.  
76 While long-chain *n*-alkyl lipids with a strong predominance of the odd carbon number  
77 homologues derive from the epicuticular waxes of vascular and aquatic plants  
78 (Eglinton and Hamilton, 1967), the latter are constituents of the lignin polymer, which  
79 constitutes up to one third of all woody material of living plants (Erdtman, 1971). The  
80 *n*-alkanes (Alk) likely trace terrigenous OM which has been mobilized from thawing  
81 permafrost deposits (Feng et al., 2013) and may be transported into the marine  
82 sediment primarily following coastal erosion during shelf flooding (Winterfeld et al.,  
83 2018). In contrast, lignin is transported from land to sea via different conduits than *n*-  
84 alkane biomarkers (Feng et al., 2013) and has the potential to provide information on  
85 surface runoff processes and wetland extent (Tesi et al., 2016; Feng et al., 2015). In  
86 addition, lignin reflects the type of vegetation and the degree of OM degradation  
87 (Hedges and Mann, 1979; Hedges et al., 1988). According to lignin phenols and the  
88 so-called branched and isoprenoid tetraether index (BIT), Seki et al. (2014) found that  
89 terrestrial OM from the Amur River is a major source of OM in the North Pacific  
90 Ocean at present and that terrestrial OM in surface sediments is dominated by  
91 gymnosperms in the Okhotsk Sea. So far, no records exist that combine both types of  
92 terrigenous biomarker data to explore the potentially different transport histories of  
93 terrestrial OM archived in them.

94 In this study, we present downcore records of lignin phenols from the early  
95 deglaciation to the early Holocene from two contrasting river-dominated continental  
96 margin sites in the North Pacific area. We interpret the lignin phenol records in  
97 context of vegetation and wetland development and investigate the temporal evolution  
98 of the different pathways of terrigenous OM export to the ocean by comparing the two  
99 types of terrigenous biomarkers, i.e., Alk and lignin phenols.



## 2. Study area

100 The Bering Sea is located in the north of the Pacific Ocean. The Yukon River is the  
101 fourth largest river in North America in terms of annual discharge, and drains into the  
102 Bering Sea (Holmes et al., 2012). The deglacial sediments from the Bering Sea  
103 contain records both of sea-level rise-induced erosion of the vast Bering Shelf, and of  
104 runoff from the Yukon River (Kennedy et al., 2010; Meyer et al., 2019). The Yukon  
105 Basin was mostly unglaciated during the LGM, featuring permafrost (Schirrmeister et  
106 al., 2013; Meyer et al., 2019), and remains mostly so until today. Arctic coasts today  
107 often are eroded at high rates of up to several meters per year (Lantuit et al., 2011;  
108 Couture et al., 2018), suggesting that during past periods of sea-level rise, similar or  
109 even stronger erosive forces were at play supplying vast amounts of terrigenous  
110 materials to marine sediments. Today the catchment of the Yukon River is covered by  
111 spruce forest (20 %), grassland (40 %), shrubland (20 %), and open water and  
112 wetlands associated with the lowland areas (8 %) (Amon et al., 2012). Pollen records  
113 indicate there were no significant changes in vegetation pattern from the LGM to  
114 about 16 ka BP, but after about 16 ka BP, birch pollen became significantly more  
115 abundant from western Alaska to the Mackenzie River (Bigelow, 2013). In the early  
116 Holocene, significant *Populus-Salix* woodland development occurred in interior  
117 Alaska and in the Yukon Territory (Bigelow, 2013).

118 The Okhotsk Sea, a semi-enclosed marginal sea located in the west of the North  
119 Pacific, is known as the southernmost region of seasonal sea ice in the Northern  
120 Hemisphere today. The continental slope off Sakhalin Island in the Okhotsk Sea  
121 receives runoff from the Amur river, which is one of the largest rivers in the world in  
122 terms of the annual total output of dissolved OM (Nakatsuka et al., 2004) and  
123 substantially influences the formation of seasonal sea ice (Nakatsuka et al., 2004).  
124 The catchment of the Amur transitioned from complete permafrost coverage during  
125 the LGM to almost entirely permafrost-free conditions at present (Vandenberghé et al.,  
126 2012). The climate of the Amur Basin is largely determined by continental patterns  
127 from Asia, while monsoon influences from the Pacific transport precipitation to this  
128 region during the summer. Previous studies found that herbaceous plants were the  
129 predominant vegetation in the last glacial periods in the Amur Basin, and were  
130 replaced by gymnosperms during the deglaciation and Holocene (Bazarova et al.,  
131 2008; Seki et al., 2012). The vegetation of the Amur Basin belongs mostly to the



132 Taiga zone, with larch as the most common species in the area. The upper reaches of  
133 the Amur Basin belong to the coniferous continental taiga at present. The central areas  
134 are dominated by mixed coniferous and broad-leaved forests and the coniferous larch  
135 forests are the predominant vegetation in the lower Amur Basin.

### 3. Material and methods

#### 3.1. Sampling and age control

136 Piston core SO202-18-3 (60.13° N, 179.44° W, water depth: 1111 m) and neighboring  
137 Kasten core SO202-18-6 (60.13° N, 179.44° W, water depth: 1107 m) were recovered  
138 from the northeastern continental slope of the Bering Sea in 2009 during R/V Sonne  
139 cruise SO202-INOPEX (Gersonde, 2012). The two cores can be treated as one  
140 composite record according to their ultrahigh-resolution micro-X-ray-fluorescence  
141 data, sediment facies analysis of laminae and radiocarbon dating results (Kuehn et al.,  
142 2014). It represents an apparently continuous sedimentary sequence dated back to the  
143 Last Glacial (~25 ka BP) (Kuehn et al., 2014). Selected samples from core SO202-18-  
144 6 ( $n = 20$ , 10–589 cm core depth, 6.23–12.65 ka BP) and from core SO202-18-3 ( $n =$   
145 29, 447–1423 cm core depth, 12.99–24.1 ka BP) with an average temporal resolution  
146 of ~510 years were analyzed for lignin-derived phenol contents.

147 The 23.7 m-long piston core SO178-13-6 (52.73° N, 144.71° E) was collected  
148 from the Sakhalin margin in the Okhotsk Sea during the expedition SO178-KOMEX  
149 with R/V Sonne (Dullo et al., 2004) (Fig. 1) with the lowermost interval  
150 corresponding to ~17.5 ka (Max et al., 2014). Selected samples ( $n = 51$ , 100–2340 cm  
151 core depth, 1.11–17.27 ka BP) from core SO178-13-6 were analyzed for lignin-  
152 derived phenol contents with an average temporal resolution of ~340 years.

153 Radiocarbon-based age models for the two cores are from Kuehn et al. (2014) for  
154 core SO202-18-3/6 and Lembke-Jene et al. (2017) for core SO178-13-6. The time  
155 interval covered by the records will be subdivided into five intervals, the early  
156 deglaciation (ED; 19–14.6 ka BP), the B/A (14.6–12.9 ka BP), the Younger Dryas  
157 (YD; 12.9–11.5 ka BP), the Pre-Boreal (PB, 11.5–9 ka BP) and the Holocene (<9 ka  
158 BP).

#### 3.2. Laboratory analyses

159 The extraction of lignin phenols was carried out based on the method of Goñi and  
160 Montgomery (2000a) and as described in Sun et al. (2017). Dried samples were  
161 oxidized with CuO (~500 mg) and ~50 mg ferrous ammonium sulfate in 12.5 ml 2N



162 NaOH under anoxic conditions. The oxidation was conducted with a CEM MARS5  
163 microwave accelerated reaction system at 150 °C for 90 min. After oxidation, known  
164 amounts of recovery standards (ethyl vanillin and trans-cinnamic acid) were added to  
165 the oxidation products. The alkaline supernatant was acidified to pH 1 with 37 % HCl.  
166 The reaction products were subsequently recovered by two successive extractions  
167 with ethyl acetate. The combined ethyl acetate extracts were evaporated under a  
168 stream of nitrogen, then re-dissolved in 400 µl pyridine. Prior to injection into the gas  
169 chromatograph-mass spectrometer (GC-MS), an aliquot (30 µl) was derivatized with  
170 30 µl bis-trimethylsilyl-trifluoroacetamide (BSTFA) + 1 % trimethylchlorosilane  
171 (TMCS) (55 °C, 30 min). An Agilent 6850 GC coupled to an Agilent 5975C VL MSD  
172 quadrupole MS operating in electron impact ionization (70 eV) and full-scan ( $m/z$  50–  
173 600) mode was used for analysis. The source temperature of the MS was set to 230 °C  
174 and the quadrupole to 150 °C. The GC was equipped with a DB-1 MS column (30 m  
175 × 0.25 mm i.d., film thickness 0.25 µm). Helium was used as carrier gas at a constant  
176 flow rate of 1.2 ml min<sup>-1</sup>. Samples were injected in splitless mode in a split/splitless  
177 injector (S/SL) held at 280 °C. The temperature of the GC-MS column was  
178 programmed from 100 °C (initially held for 8 min.), ramped by 4 °C min<sup>-1</sup> to 220 °C,  
179 then by 10 °C min<sup>-1</sup> to 300°C with a final hold time of 5 min.

180 Eight lignin-derived phenols were analyzed in this study. They can be classified  
181 into three groups according to their plant sources and structures:

182 1. Vanillyl phenols (V) consisting of vanillin (VI), acetovanillone (Vn) and  
183 vanillic acid (Vd).

184 2. Syringyl phenols (S), comprising syringaldehyde (SI), acetosyringone (Sn)  
185 and syringic acid (Sd).

186 3. Cinnamyl phenols (C) that include *p*-coumaric acid (*p*-Cd) and ferulic acid  
187 (Fd). Besides, we also included some other oxidation products that do not necessarily  
188 originate from lignin, such as 3,5-dihydroxybenzoic acid (3,5Bd) and para-  
189 hydroxybenzenes (P) like *p*-hydroxybenzaldehyde (PI), *p*-hydroxybenzophenone (Pn),  
190 and *p*-hydroxybenzoic acid (Pd).

191 These compounds were identified based on retention time and mass spectra.  
192 Quantification was achieved by peak areas of the respective compounds and using  
193 individual 5-point response factor equations obtained from mixtures of commercially  
194 available standards analyzed periodically. The yields of PI, VI and SI were corrected



195 by the recovery rate of ethyl vanillin and the recovery rate of trans-cinnamic acid was  
196 applied to correct the yield of other lignin-derived compounds and 3,5Bd (Goñi et al.,  
197 2000a, b). The standard deviation was determined from repeated measurements of a  
198 laboratory internal standard sediment extract ( $n = 12$ ) and for the carbon-normalized  
199 concentration of the sum of 8 lignin phenols ( $\Sigma 8$ ,  $\text{mg } 100\text{mg}^{-1} \text{ OC}$ ) equals 0.31.

200 Mass accumulation rates (MAR) of vascular plant-derived lignin phenols were  
201 calculated as follows:

202 sediment MAR expressed in  $\text{g cm}^{-2} \text{ a}^{-1} = \text{sedimentation rate (cm a}^{-1}) \times \text{dry bulk}$   
203  $\text{density (g cm}^{-3})$

204 lignin MAR expressed in  $\mu\text{g cm}^{-2} \text{ a}^{-1} = (\text{sediment MAR} \times \Sigma 8) \div 100$

205  $\Sigma 8$  represents the lignin content in  $\text{mg } 10\text{g}^{-1}$  dry sediment.

206 Lignin MAR were compared to published Alk MAR from the Okhotsk Sea  
207 (Winterfeld et al., 2018) and the Bering Sea (Meyer et al., 2019). The high molecular  
208 weight (HMW) Alk quantified for the Okhotsk Sea sediment core are  $C_{27}$ ,  $C_{29}$ ,  $C_{31}$  and  
209  $C_{33}$  (Winterfeld et al., 2018). In the Bering Sea sediment core are,  $C_{23}$ ,  $C_{25}$ ,  $C_{27}$ ,  $C_{29}$ ,  
210  $C_{31}$  and  $C_{33}$  Alk were quantified (Meyer et al., 2019).

211 Alkanes also have been shown to provide a second marker for wetland extent via  
212 the Paq index (Ficken et al., 2000). It represents the relative proportion of mid-chain  
213 length Alk ( $C_{23}$  and  $C_{25}$ ) to long-chain Alk ( $C_{29}$  and  $C_{31}$ ):

214  $\text{Paq} = (C_{23} + C_{25}) / (C_{23} + C_{25} + C_{29} + C_{31})$

215 From the polar fractions of the lipid extracts used by Meyer et al. (2019) for the  
216 Alk analyses, the abundances of isoprenoid glycerol dialkyl glycerol tetraethers  
217 (isoGDGTs) were determined using the methodology described in Meyer et al. (2016).  
218 The average temporal resolution is approximately 390 years. Briefly, 5 g freeze-dried  
219 sediment samples and 10  $\mu\text{g } C_{46}\text{-GDGT}$  (internal standard) were extracted with an  
220 accelerated solvent extractor using 22 ml cells and dichloromethane:methanol = 9:1  
221 (vol/vol) as solvent at 100 °C and 6.895E+6 Pa with 3 cycles of 5 min each. Then the  
222 extracts were dried by a rotary evaporator. After being dried, the extracts were  
223 hydrolyzed with 0.1 N potassium hydroxide in methanol:H<sub>2</sub>O = 9:1 (vol/vol) and the  
224 neutral compounds were extracted with *n*-hexane. Different compound classes were  
225 separated by deactivated SiO<sub>2</sub> column chromatography. Polar compounds (including  
226 GDGTs) were eluted with methanol:dichloromethane = 1:1 (vol/vol). Afterward they  
227 were dissolved in hexane:isopropanol = 99:1 (vol/vol) and filtered with a



228 polytetrafluoroethylene filter (0.45  $\mu\text{m}$  pore size). Samples were brought to a  
229 concentration of 2  $\mu\text{g } \mu\text{l}^{-1}$  prior to GDGT analysis. GDGTs were analyzed by high-  
230 performance liquid chromatography and a single quadrupole mass spectrometer (see  
231 Meyer et al. (2017) for more details). The relative abundances of isoGDGTs can be  
232 expressed as the  $\text{TEX}_{86}^{\text{L}}$  index (Tetra Ether index) which quantifies the relative  
233 abundance of isoGDGTs consisting of 86 C-atoms and can be used as a sea surface  
234 temperature (SST) proxy in settings where SST is below 15  $^{\circ}\text{C}$  (Kim et al. 2010). The  
235 regional calibration of SST and  $\text{TEX}_{86}^{\text{L}}$  is based on Seki et al. (2014).

$$\text{TEX}_{86}^{\text{L}} = \log(\text{GDGT-2}/(\text{GDGT-1}+\text{GDGT-2}+\text{GDGT-3}))$$
$$\text{SST}/^{\circ}\text{C} = 27.2 \times \text{TEX}_{86}^{\text{L}} + 21.8$$

## 4. Results

### 4.1. Lignin concentrations and MARs

238 Lignin phenol concentrations were 0.19–1.43  $\text{mg } 100\text{mg}^{-1} \text{ OC}$  (A8) or 0.20–1.07  $\text{mg}$   
239  $10\text{g}^{-1}$  sediment ( $\Sigma 8$ ) in the Bering Sea sediments and 0.32–1.29  $\text{mg } 100\text{mg}^{-1} \text{ OC}$  or  
240 0.40–2.16  $\text{mg } 10\text{g}^{-1}$  sediment in the Okhotsk Sea record. Overall, the MAR of lignin  
241 is lower in the Bering Sea than in the Okhotsk Sea (Fig. 2c, d). During the ED, the  
242 lignin MAR began to increase in the Bering Sea sediment and kept increasing until it  
243 reached a maximum (17.70  $\mu\text{g cm}^{-2} \text{ a}^{-1}$ ) at the B/A-YD transition (Fig. 2c). After the  
244 B/A, the lignin MAR started to decrease in the Bering Sea until the onset of the YD.  
245 The lignin MAR in the Bering Sea reached a more pronounced but short maximum  
246 (20.61  $\mu\text{g cm}^{-2} \text{ a}^{-1}$ ) at the YD-PB transition, followed by a decrease to the Holocene.  
247 The lignin MAR in the Okhotsk Sea is more variable than in the Bering Sea record  
248 (Fig. 2d). The lignin MAR shows an initial maximum in the B/A, but reaches a more  
249 pronounced second peak (31.16  $\mu\text{g cm}^{-2} \text{ a}^{-1}$ ) in the early PB. Similar to the Bering Sea,  
250 the lignin MAR decreased after about 11 3ka BP and into the Holocene, however, the  
251 lignin MAR in the Okhotsk Sea sediment featured a rather broad maximum between  
252 B/A and early Holocene.

253 Deglacial changes in the MARs of long-chain Alk have previously been reported  
254 for the same cores (Meyer et al., 2019; Winterfeld et al., 2018). The MAR of lignin  
255 and Alk changed mostly synchronously in the Bering Sea, but in the Okhotsk Sea, the  
256 increase in lignin MAR occurred later than in Alk MAR, and notably also later than in  
257 the Bering Sea (Fig. 2c, d). Alk MAR in the Okhotsk Sea featured two similar  
258 maxima in the B/A and during the YD-PB transition, while the lignin MAR maximum



259 in the B/A is less pronounced than that at the YD-PB transition. Lignin MAR are  
260 more variable than Alk MARs between 10 and 7.8 ka BP.

#### 4.2. Lignin source and degradation indicators

261 The S/V and C/V ratios yielded values of 0.36–0.86 and 0.11–0.46 in the Bering Sea  
262 (Fig. 3, Ia, b), while slightly higher ratios of 0.41–0.92 and 0.19–0.70 were obtained  
263 in the Okhotsk Sea (Fig. 3, IIa, b). The standard deviations for S/V and C/V are 0.08  
264 and 0.10, respectively. In the Bering Sea, the S/V ratios began to increase from 18 ka  
265 BP and kept increasing until it reached a maximum in the transition of the YD to the  
266 PB. The change of C/V values was not as obvious as S/V values, but it also reached  
267 its maximum at YD-PB transition. Subsequently, S/V and C/V ratios decreased during  
268 the Holocene and reached minima at the top of the core.

269 In the Okhotsk Sea, the S/V values increase slowly from the ED to PB, but the  
270 C/V ratios do not display an obvious increase over the same time, except for a  
271 maximum in C/V ratios around 15 ka BP. Minimum values were found in the ED and  
272 values remained rather low before the YD-PB transition. After reaching maxima in  
273 the PB, S/V and C/V ratios decreased during the Holocene, stabilizing at a higher  
274 level than during the ED.

275 In the Bering Sea, the 3,5Bd/V ratio ranged from 0.09 to 0.20 (Fig. 3, Id)  
276 (standard deviation: 0.02). From the end of LGM to the YD, the 3,5Bd/V ratio  
277 decreased slowly, but began to increase and reached a small local maximum at the  
278 YD-PB transition. During the Holocene, the 3,5Bd/V ratio decreased again and  
279 reached the lowest values near the top of the core.

280 The 3,5Bd/V ratios in the core from the Okhotsk Sea range from 0.10 to 0.23  
281 (Fig. 3, IIId) (standard deviation: 0.02). The values were rather uniform throughout the  
282 record, with the exception of a maximum during the PB, and the ratio remained rather  
283 stable afterwards.

284 The (Ad/Al)<sub>s</sub> and (Ad/Al)<sub>v</sub> ratios ranged from 0.19 to 0.80 (standard deviation:  
285 0.24) and 0.51 to 1.04 (standard deviation: 0.26), respectively, in the Bering Sea (Fig.  
286 3, Ie, f). Maxima in (Ad/Al)<sub>s</sub> and (Ad/Al)<sub>v</sub> were reached in the Holocene and YD. The  
287 Ad/Al ratio in the Bering Sea showed low values during the PB and increased towards  
288 the early Holocene, when highest values of Ad/Al were obtained.

289 In the Okhotsk Sea, the (Ad/Al)<sub>s</sub> and (Ad/Al)<sub>v</sub> ratios are overall similar and  
290 range from 0.30 to 0.79 (standard deviation: 0.24) and from 0.22 to 0.89 (standard  
291 deviation: 0.26), respectively (Fig 3, IIe, f). The (Ad/Al)<sub>v</sub> ratio decreased slowly until



292 10.5 ka BP when the biomarker MARs reached maxima. All minima and maxima in  
293 both indices occurred in the PB. Throughout the rest of the Holocene, Ad/Al values  
294 remained rather constant.

#### 4.3. Sea surface temperature in the Bering Sea ( $TEX_{86}^L$ )

295 The SST estimates derived from the  $TEX_{86}^L$  index are shown in Fig. 4, Ic. The  
296 deglacial evolution of the  $TEX_{86}^L$ -derived SST ranging from 4.48 to 10.81 °C. The SST  
297 in the Bering Sea remained rather constant during the LGM and the ED. The onset of  
298 the B/A is characterized by an abrupt temperature increase of ~2 °C, followed by a  
299 decrease at the end of the B/A. At the end of the YD, the SST abruptly increased by  
300 ~2 °C, while staying rather constant from 11.5 ka BP to 10 ka BP. At the end of PB,  
301 the SST progressively dropped by ~1 °C. During the Holocene, the SST ranged  
302 between 8.0 °C and 9.7 °C.

### 5. Discussion

#### 5.1. Vegetation changes in the two river basins

##### 5.1.1. Yukon River Basin

303 As the climate warmed during the transition from the LGM to the ED, moisture  
304 increased and an increasing number of thermokarst lakes developed in Alaska,  
305 especially after about 16–14 ka BP (Bigelow, 2013; Walter et al., 2007). We observe a  
306 increase in S/V ratios from the ED to the B/A, indicating increasing contributions of  
307 angiosperms around this time, extending into the B/A (Fig. 3, Ia). The S/V and C/V  
308 ratios are also influenced by degradation of lignin, with increasing ratios suggesting a  
309 lower degradation state (Hedges et al., 1988), but there is no parallel decrease in the  
310 more commonly used degradation indicator, i.e., the Ad/Al ratios, at the same time  
311 (Fig. 3, Ie, f). Anderson et al. (2003) also found birch pollen becoming significantly  
312 more prevalent after about 16 ka BP from western Alaska to the Mackenzie River.  
313 Coevally, the Paq index (Fig. 3, Ic, from Meyer et al., 2019) shows an increase,  
314 indicating wetland expansion.

315 There is evidence that herb-dominated tundra was replaced by *Betula-Salix* shrub  
316 tundra around Trout Lake (the northern Yukon) during the B/A (Fritz et al., 2012) as  
317 the climate warmed and became more humid than during the ED. In line with these  
318 observations, our C/V ratios indicate that the contribution of non-woody plant tissues  
319 was lower in the B/A than in the ED (Fig. 3, Ib).



320 After the B/A, the summer temperatures during the YD dropped by  $\sim 1.5$  °C  
321 (Fritz et al., 2012), thus cold-adapted non-arboreal plants briefly increased in  
322 abundance (Fritz et al., 2012). The S/V ratios indicate that the non-woody angiosperm  
323 plants' contribution reached a maximum in the Yukon Basin during the YD-PB  
324 transition (Fig. 3, Ia). Since the opening of the Bering Strait ( $\sim 11$  ka BP, Jakobsson et  
325 al., 2017), a trend of increase in *Betula* was observed in eastern Beringia (Fritz et al.,  
326 2012; Kaufman et al., 2015) which indicates a progressively more maritime climate  
327 developing in response to changes in the marine environment (Igarashi and Zharov,  
328 2011). Since vegetation responds to changes in both temperature and moisture,  
329 significant *Populus/Salix* woodland development occurred in interior Alaska and in  
330 the Yukon Territory during the early Holocene (Anderson et al., 2003). However, the  
331 expansion of these angiosperm plants is not reflected in our S/V record (Fig. 3, Ia), the  
332 interpretation of S/V ratios may be complicated by the influence of degradation  
333 processes during the early Holocene. Pollen assemblages from northern Siberian soils  
334 have shown that woody plants occurred only after the onset of the Holocene (Binney  
335 et al., 2009), which agrees with a decrease in the C/V ratios since the early PB into the  
336 early Holocene (Fig. 3, Ib).

337 We compare our S/V and C/V ratios with published values from sediment cores,  
338 surface sediments and suspended materials in the Arctic and subarctic (Fig. 5). Such  
339 plots can help to identify the main types of plant tissues the lignin phenols are derived  
340 from, and enable the detection of potential degradation effects.

341 The S/V and C/V ratios from our Bering Sea core compare favorably with those  
342 from a core recovered from the Chukchi shelf covering parts of the B/A and the YD as  
343 well as the late Holocene (Martens et al., 2019) (Fig. 5). This may suggest that a  
344 similar type of vegetation prevailed across much of Beringia. After the opening of the  
345 Bering Strait, Pacific waters flowed into the Chukchi Sea, and it is conceivable that  
346 the terrestrial material transported to the Bering Sea by the Yukon River may have  
347 been in part be transported into the Chukchi Sea. The top of our core dates to the early  
348 Holocene, a period that was characterized by more wide-spread broad-leaf  
349 angiosperm vegetation than today, which might explain the offset between our early  
350 Holocene S/V and C/V ratios and those reported for Yukon River surface sediment  
351 (S/V: 0.28, C/V: 0.14) (Feng et al., 2015) and dissolved organic carbon in the Yukon  
352 (S/V: 0.47, C/V: 0.14) (Amon et al., 2012) at present. Degradation of lignin in  
353 sediments may explain some of the discrepancy between sediment data and S/V and



354 C/V ratios reported from suspended materials collected in the modern Lena River (Fig.  
355 5). As the Amur River catchment is dominated by gymnosperms at present (Seki et al.  
356 2014), the S/V ratios of the Amur River and Okhotsk Sea surface sediments (Seki et  
357 al., 2014) are lower than in the Bering Sea core (Fig. 5).

358 The highest values of the 3,5Bd/V ratio correlate with the enhanced degradation  
359 of lignin phenols around 17.5 ka BP (Fig. 3, Id). This suggests that degraded OM is  
360 the dominant source for the lignin phenols at this time, in agreement with previous  
361 studies (Meyer et al., 2016, 2019). Global melt water pulses according to Lambeck et  
362 al. (2014) occurred during the following time periods: MWP-1A from 14.6 to 14.0 ka  
363 BP and the MWP-1B from 11.5 to 10.5 ka BP. The 3,5Bd/V and (Ad/Al)<sub>s</sub> ratios  
364 decreased slowly from the ED to the MWP-1A, which indicates that the change  
365 3,5Bd/V values from the LGM to the early B/A reflects a variable degree of OM  
366 degradation, rather than expansion of wetlands or peatlands. The 3,5Bd/V also  
367 featured a short maximum during the late YD and early PB when the 3,5Bd/V signal  
368 is likely dominantly ascribed to increases in wetland or peatland sources, as there is  
369 no parallel maximum in Ad/Al ratios (Fig. 3, Id, e, f).

370 This pattern of 3,5 Bd/V change is not in agreement with the Paq ratio  
371 determined for the same core earlier (Meyer et al., 2019), although both proxies may  
372 reflect wetland expansion (Goñi et al., 2000b; Amon et al., 2012). The temporal  
373 evolution of Paq is similar to that of S/V and C/V, where Paq began to increase in the  
374 ED and reached its maximum in the YD-PB transition (Fig. 3, Ic), indicating that the  
375 proxies are influenced to some extent by degradation.

376 Notably, a lower degree of OM degradation is indicated for periods with high  
377 MAR of terrigenous OM, indicating that rapid transport and burial might contribute to  
378 better preservation of lignin. This better preservation, in particular during the early PB  
379 (Fig. 3e, f), is in agreement with previous studies (Anderson et al., 2003; Meyer et al.,  
380 2019). Kuehn et al. (2014) found that increases in biological export production and  
381 remineralization of OM in the Bering Sea during the B/A and PB, reduced oxygen  
382 concentration to below 0.1 ml L<sup>-1</sup> and caused the occurrence of laminated sediments  
383 (Fig. 2c). This anoxic condition in the Bering Sea during the B/A and PB also slowed  
384 down rates of OM decomposition and increased the accumulation of OM.

385 With progressive sea-level rise through the early Holocene, the distance between  
386 the Yukon River mouth and the core-site increased, leading to longer transport  
387 distance and stronger degradation of lignin. In the East Siberian Arctic Shelf, Tesi et



388 al. (2014) found that lignin concentrations exhibit a marked decrease by three orders  
389 of magnitude with increasing distance from the coast.

390 In summary, our data together with published evidence indicate that in the Yukon  
391 Basin, vegetation change and wetland expansion began in the ED. Angiosperm plant  
392 contribution and wetland extent all reached their maxima during the PB, both  
393 decreasing and stabilizing at lower levels after the PB. During the PB, terrigenous  
394 OM appeared least degraded, suggesting rapid supply and burial of rather well-  
395 preserved terrigenous OM.

### 5.1.2. Amur River Basin

396 The lowest contribution of non-woody angiosperms as indicated by low S/V and C/V  
397 ratios occurred at 16.6 ka BP (Fig. 3, IIa, b). Subsequently, both ratios increased and  
398 reached maxima during the PB, suggesting expansion of angiosperms and non-woody  
399 tissues contributing substantially to lignin. After the PB, the S/V decreased rapidly  
400 and remained stable during the Holocene, while the C/V ratio showed a second  
401 maximum at 9.2 ka BP suggesting an increasing contribution of non-woody  
402 angiosperms in the PB (Fig. 3, IIa, b). In agreement with our data, published lipid  
403 records provide evidence that the vegetation in the Amur Basin did not change  
404 significantly in the ED (Seki et al., 2012). Winterfeld et al. (2018) found a general  
405 synchronicity of Amur River discharge and northward extent of monsoon  
406 precipitation in the early Holocene. Climate warming associated with high moisture  
407 supply allowed the expansion of birch-alder forests in the Amur Basin in the PB  
408 (Bazarova et al., 2008; Igarashi and Zharov, 2011).

409 C/V and S/V ratios indicate that the contribution of non-woody gymnosperm  
410 tissue was higher in the early than in the later deglaciation (Fig. 6), similar to what has  
411 been reported from East Siberian Shelf records (Keskitalo et al., 2017). Apparently, the  
412 YD caused only minor vegetation changes in the East Asian hinterland (Igarashi and  
413 Zharov, 2011). Our lignin records for this period are in agreement with previous  
414 studies that indicated that the Lower Amur River basin mainly featured shrub birch-  
415 alder forests and rare *Pinus* (Bazarova et al., 2008; Seki et al., 2012).

416 Non-woody angiosperm plant contributions to the Okhotsk Sea sediment  
417 strongly increased during the PB (Fig. 3, IIa, b), when the summer insolation and  
418 regional temperatures reached the highest values since the LGM. Significant  
419 vegetation changes in the Amur Basin thus started in the PB period, temporally offset  
420 from the Yukon Basin, and the contribution of angiosperms from 14.6 ka BP to 9 ka



421 BP appears to be higher than during the ED (Fig. 6). Bazarova et al. (2008) reported  
422 based on pollen analyses that a turning point in vegetation development in the Amur  
423 Basin occurred at a boundary of 10 ka BP. The Middle Amur depression registered the  
424 first appearance of broad-leaved species pollen and a prevalence of spores over  
425 arboreal pollen at that time (Bazarova et al., 2008). The C/V ratio did not decrease as  
426 rapidly as the S/V ratio after the peak and showed a second maximum at ~9 ka BP.  
427 Some pollen of *Picea* (such as *P. glauca* and *P. mariana*) yield exceptionally high  
428 amounts of cinnamyl phenols (Hu et al., 1999), which may have affected the C/V ratio  
429 as the end member of woody/non-woody tissues. An et al. (2000) concluded that  
430 lakes were deepest and most extensive around 10 ka BP in northeastern China (the  
431 upper Amur basin), and 3,5Bd/V and Paq values reached maxima at the same time  
432 (Fig. 3, IId, c) suggesting wetland extent peaked during the PB. Therefore, wetland  
433 plants which have broad leaves, such as sedges, may also have a positive influence on  
434 the C/V ratio.

435 The S/V and C/V data from the Holocene part of our core do not agree with  
436 published values for the Okhotsk Sea and Amur River surface sediments (Fig. 6).  
437 During the past 250 years, vegetation was marked by significant rises of  
438 gymnosperms, such as pines, combined with the reduction in the swamp area and a  
439 large increase in fire activity (Seki et al., 2014), likely resulting in higher  
440 contributions of gymnosperm to the surface sediment while these changes are not  
441 resolved in the samples analysed for our record.

442 The 3,5Bd/V and Paq ratios of the Okhotsk Sea both display relatively high  
443 values during the PB (Fig. 3, IId, c). Seki et al. (2012) found high Paq values during  
444 the PB in a nearby sediment core XP07-C9, and the values in their core were higher  
445 than in ours (Fig. 3, IIc). Spores of *Sphagnum* show a distinct peak during the PB  
446 (Morley et al., 1991), reflecting an expansion of mesic and boggy habitats. Our  
447 records together with published evidence thus suggest that permafrost destabilization  
448 and wetland expansion in the Amur Basin occurred only at the beginning of the PB,  
449 while those processes were initiated much earlier in the Yukon basin.

450 The Ad/Al values were decreasing until 10.5 ka BP and reached minima during  
451 the PB (Fig. 3e, f), indicating that low temperatures on land on the one hand, and  
452 rapid burial in marine sediments during shelf flooding and coastal erosion during  
453 MWP-1B on the other hand, contributed to the Ad/Al signals. In the course of climate  
454 amelioration from around 11.6 ka BP (Tarasov et al, 2009), the rates of vegetation



455 development, wetland expansion and Amur River discharge (Fig. 2f) all displayed  
456 maxima in the PB. Generally higher Ad/Al values in the later part of the PB suggest  
457 that fluvial runoff supplied more degraded lignin. Aerobic degradation of OM in soils  
458 by fungi has also been shown to increase Ad/Al values (Goñi et al., 1993). Reports  
459 that the degradation degree of Lena River-derived OM and surface sediments of Buor  
460 Khaya Bay are similar (Winterfeld et al., 2015), suggest that the oxidative degradation  
461 occurred mainly on land. The Okhotsk Sea shelf is narrower than the Bering Shelf and  
462 Siberian shelves, the lateral shelf transport times (i.e., the cumulative time a particle  
463 spends in sedimentation-resuspension cycles) of the Okhotsk shelf are therefore likely  
464 to be much shorter than what has been reported for the Laptev Shelf (Bröder et al.,  
465 2018), further supporting our interpretation.

466 In summary, our records indicate that in the Amur Basin vegetation change and  
467 wetland expansion began during the PB and in the early Holocene, in agreement with  
468 previous paleo-vegetation studies. This timing is different from observed changes in  
469 the Yukon Basin. However, similar to the Yukon Basin, the wetland extent and non-  
470 woody angiosperm contribution were reduced and stabilized after the PB in the Amur  
471 Basin. The increased vegetation and wetland indices, as well as increased degradation  
472 of lignin in the Okhotsk Sea sediment at the end of the PB, may be related to changes  
473 in the source of OM (shelf and coastal erosion vs river transported material).

### 5.2. Terrigenous OM mobilization during the deglaciation

474 Permafrost remobilization has a strong impact on local topography, vegetation, and  
475 OM fate (Feng et al., 2013; Walter Anthony et al., 2014). We observed distinct MAR  
476 peaks of terrigenous biomarkers in both sediment cores, but the temporal evolution of  
477 MARs and the relative magnitude of change differ between the sites.

478 In the Bering Sea, lignin MAR began to increase at 17.5 ka BP (Fig. 2c), but  
479 evidence for change in vegetation in the Yukon Basin was only found near 15 ka BP  
480 and the Yukon River discharge did not increase until 16.5 ka BP (Wang et al., 2021).  
481 Therefore, the increased lignin MAR may correspond to the mobilization of terrestrial  
482 OM from surface sources, like permafrost soils. Previous studies indicated that Ice  
483 Complex Deposit (ICD) samples yield relatively high S/V and C/V ratios, indicating  
484 the OM likely to stem from grass-like material typical of tundra or steppe biome  
485 (Schirrneister et al., 2013; Tesi et al., 2014; Winterfeld et al., 2015). Thus, the  
486 increased S/V, C/V, and Paq values near 17.5 ka BP (Fig. 3, Ia–c) lend support to the



487 notion that permafrost of the Yukon Basin may have begun to be remobilized in the  
488 ED.

489 Vaks et al. (2020) found that Siberian permafrost is vulnerable to warming when  
490 Arctic sea-ice is absent. Retreat of sea ice will increase the SST, and open waters  
491 increase the moisture content of the atmosphere, so the transport of heat from the  
492 ocean via atmospheric pathways to continental interiors increases (Ballantyne et al.,  
493 2013; Vaks et al., 2020). Praetorius et al. (2015) found that SST warming commenced  
494 around 16.5 ka BP (core 85JC, Fig. 4, If) in the northern Gulf of Alaska, and Méheust  
495 et al. (2018) observed rising SST of the northeast Pacific by ~1.5 °C near 16 ka BP  
496 (core SO202-27-6, Fig. 4, Ie) which agrees with our SST record (core SO202-18-3/6,  
497 Fig. 4, Ic). The same authors reconstructed sea-ice extent based on the IP<sub>25</sub> proxy to  
498 decrease from around 16 ka BP in the Northeast Pacific (Fig. 4, Ie). Jones et al. (2020)  
499 reported that the sea ice in the Bering Sea is highly sensitive to small changes in  
500 winter insolation and atmospheric CO<sub>2</sub>. Further evidence for regional climate  
501 warming in the hinterland of Alaska is provided by the Brooks Range glacial melting  
502 during a time of widespread cooling on the Northern Hemisphere (Dyke, 2004; Wang  
503 et al., 2021). The permafrost of the Yukon Basin may thus have begun to be  
504 remobilized at ~16 ka BP. Examining the records in more detail reveals that the lipid  
505 MAR increase lags behind lignin MAR in the ED, lipid MAR increase at a similar  
506 time to when the rate of sea-level change began to increase (Fig. 2c). This suggests  
507 that lipid flux can reflect permafrost mobilization via coastal erosion (Meyer et al.,  
508 2019).

509 In the B/A, all biomarker fluxes increased and reached short maxima (Fig. 2c, d).  
510 Warming may have caused widespread permafrost thaw in the Yukon Basin. At this  
511 time, SST increased, sea-ice cover decreased (Méheust et al., 2018), and an increase  
512 in river discharge was reconstructed (Wang et al., 2021), which may have fostered  
513 diatom bloom events.

514 Little degraded lignin may also have been derived from ice-rich ICD deposits  
515 rapidly eroding during warming phases and sea-level rise induced mobilization of  
516 permafrost deposits. The degree of lignin degradation was lower than before, and  
517 combined with S/V and C/V ratios (Fig. 5), we suggest that the OM deposited in the  
518 Bering Sea during the B/A may have been derived from ICD OM. Similar to our  
519 findings, Martens et al. (2019) found relatively high lignin fluxes in the Chukchi Sea  
520 during the B/A (Fig. 2e) and showed that lignin deposited during this period was



521 poorly degraded. The authors interpreted this degradation state as permafrost OM  
522 from ICD being the dominant source. The relative contribution of ICD and the main  
523 pathway of transportation (abrupt thaw or gradual thaw on land) cannot be deduced  
524 from our data alone. Further analyses may reveal possible ICD contributions to lignin  
525 exported to the marine realm during this interval.

526 During the YD-PB transition, the Northern Hemisphere experienced an abrupt  
527 temperature increase, the maxima of biomarker MAR (Fig. 2c) and wetland indices  
528 (Fig. 3I) indicate that the permafrost remobilization in the Yukon Basin reached a  
529 peak at this time. The Yukon River discharge increased during the PB (Wang et al.,  
530 2021) which can also promote lignin flux. Evidence for widespread permafrost  
531 decomposition and wetland expansion at the same time has been reported from the  
532 Bering Sea (Meyer et al., 2019), the Siberian-Arctic (Tesi et al., 2016; Martens et al.,  
533 2020), and eastern Beringia (Kaufman et al., 2015). Bering Sea sediments deposited  
534 during the time intervals of lignin MAR peaks were laminated (Fig. 2c), indicating  
535 increased export productivity and terrigenous OM supply may have promoted anoxic  
536 conditions during the YD-PB transition.

537 Different from the Bering Sea records, lignin MAR did not yet increase in the  
538 Okhotsk Sea during the ED (Fig. 2d), except for a short peak at the transition from the  
539 ED to the B/A. SSTs were higher in the Northeast Pacific and the Bering Sea than in  
540 the Northwest Pacific and Okhotsk Sea during the ED, and the IP<sub>25</sub> value was  
541 relatively high in the Okhotsk Sea (Fig. 4, IIc), indicating the sea ice of the Okhotsk  
542 Sea did not begin to retreat in the ED (Lo et al., 2018). Caissie et al. (2010) found that  
543 the first detectable concentration of alkenones in the Bering Sea sediment at 16.7 ka  
544 BP occurred earlier than in the Okhotsk Sea, although the Bering Sea is located  
545 further north than the Okhotsk Sea. In addition, the discharge of the Amur River  
546 began to increase at ~16 ka BP, and the vegetation of the Amur Basin had not begun  
547 to change during the ED. As a consequence, the permafrost of the Amur Basin may  
548 have not yet been remobilized in the ED (Vaks et al., 2013, 2020; Winterfeld et al.,  
549 2018; Meyer et al., 2019).

550 Biomarker MARs increased and lignin degradation decreased slightly during the  
551 B/A warm interval. The rate of sea-level change reached a peak during MWP-1A (Fig.  
552 2d) which likely also caused an increase in the rate of coastal erosion. Thus, the  
553 increased biomarker MAR during the B/A may be attributed largely to coastal erosion,  
554 and high rates of sedimentation promoted burial and reduced degradation of OM.



555 Therefore, this suggests that both types of biomarkers are supplied via the same  
556 erosive process, in contrast to findings from the modern-day Arctic.

557 From the YD to the PB, the Northern Hemisphere experienced an abrupt  
558 temperature increase and the SST of the North Pacific increased significantly (Max et  
559 al., 2012; Riethdorf et al., 2013; Méheust et al., 2016, 2018; Meyer et al., 2016, 2017).  
560 All biomarker MARs in the Okhotsk Sea increased and reached maxima in the YD-  
561 PB transition. The permafrost of the Amur Basin may have begun to be remobilized  
562 coevally with previously reported periods of stalagmite growth starting after the PB in  
563 the south of Siberia, which indicates the decay of permafrost and opening of water  
564 conduits into the caves (Vaks et al. 2013, 2020). A pronounced lignin flux maximum  
565 occurred during MWP-1B, coinciding with a period of enhanced discharge from the  
566 Amur River. This implies that hinterland permafrost thawing played a more important  
567 role in the land-ocean OM transport during the later deglaciation. The Ad/Al ratios  
568 decreased when the biomarker MAR peaked in the MWP-1B which may correspond  
569 to better preservation during rapid burial, or higher contribution of ICD OM and fresh  
570 angiosperm debris. Conversely, Martens et al. (2019) found that the degradation  
571 degree of lignin in the Chukchi Sea sediment increased during rapid sea-level rise  
572 between 13 and 11 ka BP, which might be attributed to ongoing degradation during  
573 transport to the core site during times of increasing distance from the shoreline.

574 MARs decrease drastically after maxima in both the Okhotsk and Bering Seas  
575 (Fig. 2c, d). The Amur Basin was completely covered with permafrost during the  
576 LGM and almost all of the permafrost was lost as a result of permafrost mobilization  
577 (Vaks et al., 2013; Vandenberghe et al., 2014). Thus, the contribution of permafrost  
578 OM from the Amur Basin to the marine sediment began to decrease in the early  
579 Holocene in agreement with the results of Seki et al. (2012).

580 In summary, the permafrost of the Amur Basin began to be remobilized in the PB  
581 later than in the Yukon Basin. We suggest that this is caused by decreased sea ice or  
582 increased SST in the Bering Sea during the ED, while the Okhotsk Sea remained ice-  
583 covered.

### Conclusions:

584 By analyzing mass accumulation rates of terrigenous biomarkers in sediments from  
585 the Bering and Okhotsk Seas, we provide the first downcore records of lignin from  
586 the Yukon and Amur Basins covering the early deglaciation to the Holocene. We find  
587 that vegetation changed earlier in the Yukon than in the Amur Basin. Although S/V,



588 C/V and 3,5Bd/V ratios can reflect vegetation change and wetland development, the  
589 degradation state of lignin strongly overprints these proxy signals and should be  
590 considered as a function of temperature, transport distance and burial rate. Similar to  
591 changes in vegetation, we observe that degradation and remobilization of permafrost  
592 of the Yukon Basin also occurred earlier than in the Amur Basin. Sea-ice extent and  
593 SSTs of adjacent ocean areas might have had a strong influence on the timing of  
594 hinterland permafrost mobilization. Our study reveals that lignin transported by  
595 surface runoff may account for significant proportions of lignin during inland  
596 warming, but export of lignin and lipids do not always occur via different pathways,  
597 as both biomarker groups can be contributed from rapidly eroding deep deposits  
598 during phases of rapid permafrost thaw. In contrast to modern day evidence  
599 suggesting different pathways for lipid and lignin biomarker transport, our records  
600 imply that during glacial peaks of permafrost decomposition, lipids and lignin might  
601 have been delivered to the ocean by identical processes, i.e., runoff and erosion.

#### 602 **Authors' contributions**

603 MC measured and compiled lignin data, and wrote the manuscript with the help of all  
604 co-authors. JH was responsible for all biomarker analyses. LLJ and RT provided  
605 samples. VM carried out sea surface temperature measurements of SO202-18-3/6.  
606 GM designed the study. All authors participated in the discussion of results and  
607 conclusions and contributed to the final version of the paper.

#### 608 **Competing interests**

609 The authors declare that they have no conflict of interest.

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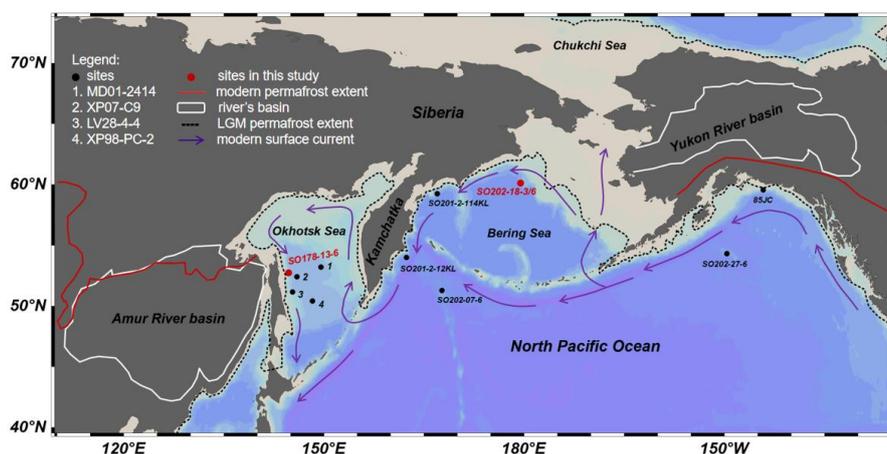
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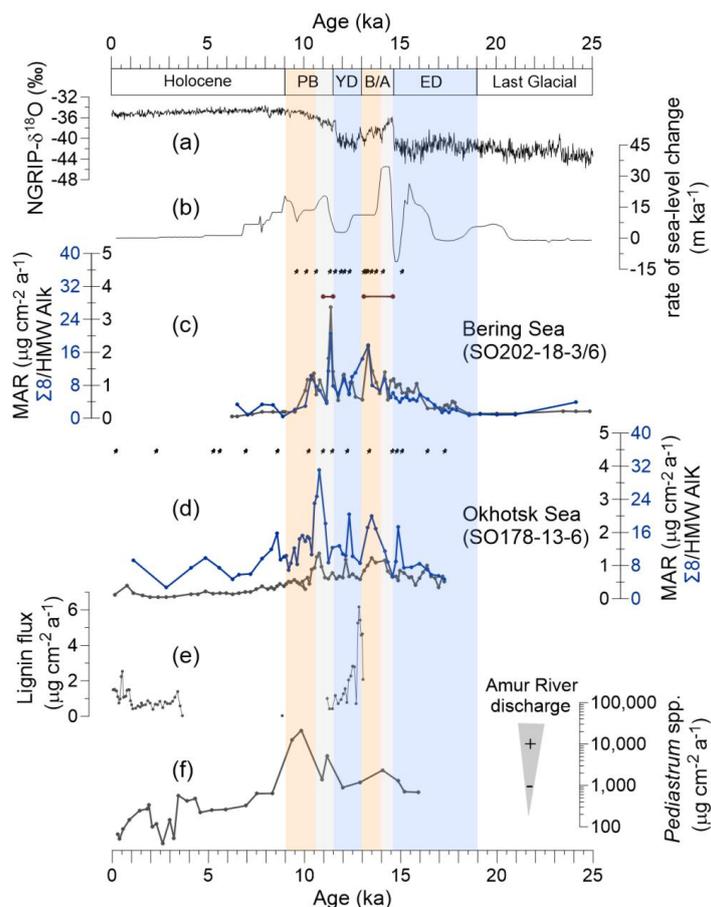
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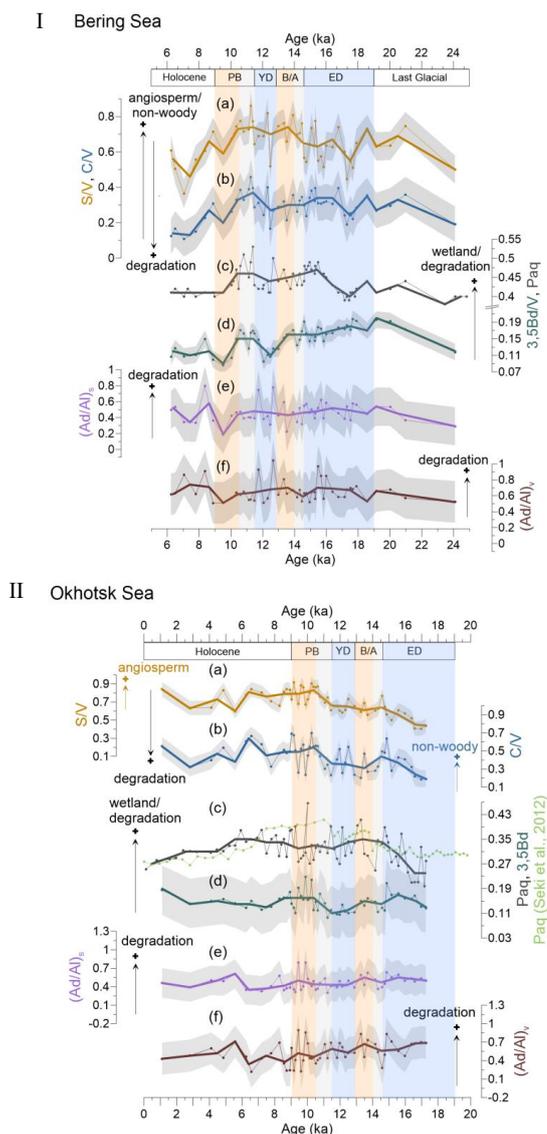
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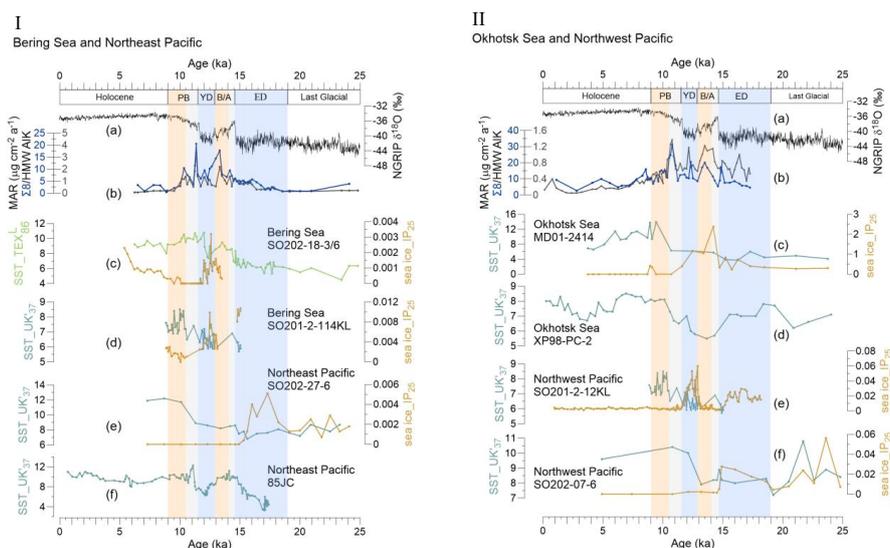
906 **Figure 1.** Study area. Red dots indicate locations of sediment cores investigated in this study;  
907 black dots denote cores described in previous studies. 1: site MD01-2414 (Lattaud et al., 2019;  
908 Lo et al., 2018). 2: site XP07-C9 (Seki et al., 2012). 3: site LV28-4-4 (Winterfeld et al., 2018).  
909 4: site XP98-PC-2 (Seki et al., 2014).



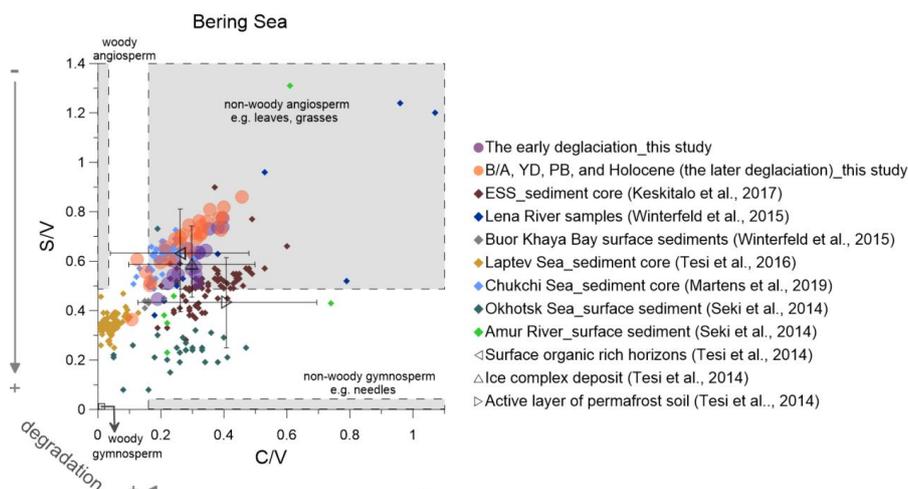
910 **Figure 2.** Proxy records of terrestrial organic matter supply and environmental records of  
 911 deglacial changes. (a) Greenland NGRIP  $\delta^{18}\text{O}$  (Rasmussen et al., 2008). (b) Global rate of  
 912 sea-level change (Lambeck et al., 2014). (c) MAR of lignin phenols (blue) and HMW Alk  
 913 (black; Meyer et al., 2019) from core SO202-18-3/6. (d) MAR of lignin phenols (blue) and  
 914 HMW Alk (black; Winterfeld et al., 2018) from core SO178-13-6. Pin marks at the top of (c)  
 915 and (d) show age control points, the accelerator mass spectrometry  $^{14}\text{C}$  dates for SO202-18-  
 916 3/6 (Kuehn et al., 2014) and SO178-13-6 (Max et al., 2012). Brown bars in panel c indicate  
 917 laminated/layered (anoxic) core sections (Kuehn et al., 2014). (e) Lignin flux from core 4-  
 918 PC1 (Chukchi Sea, Martens et al., 2019). (f) Accumulation rate of chlorophycean freshwater  
 919 algae *Pediastrum* spp. from core LV28-4-4 (Winterfeld et al., 2018). Blue boxes represent the  
 920 cold spells the early deglaciation (ED) and Younger Dryas (YD), orange boxes are for the  
 921 warm phases Bølling-Allerød (B/A) and Pre-Boreal (PB). Gray boxes highlight the periods of  
 922 melt water pulse 1A (MWP-1A) and 1B (MWP-1B).



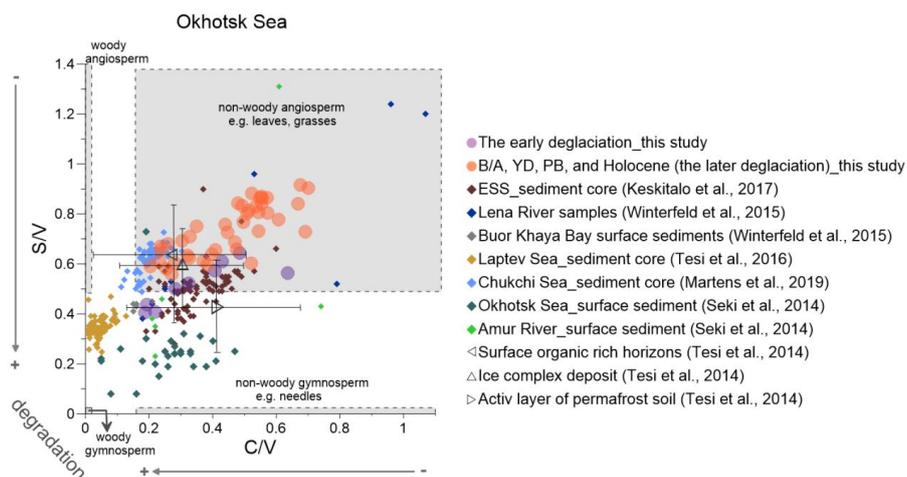
923 **Figure 3.** Records of lignin indices compared with the HMW Alk and Paq index in Bering  
 924 and Okhotsk Sea sediments. (a and b): S/V and C/V ratios reflect the vegetation change  
 925 and/or degree of lignin degradation in the respective river basins. (c and d): 3,5Bd/V and Paq  
 926 ratios represent the wetland extent or degree of degradation in the respective catchments. In  
 927 the Okhotsk Sea record, the light green line represents the Paq of a nearby core, XP07-C9  
 928 (Seki et al., 2012). (e and f): The Ad/Al can reflect the degradation of lignin phenols. Grey  
 929 shaded areas illustrate the uncertainty of these indices. Bold lines are the 1 ka averages of the  
 930 corresponding indices. Blue boxes represent the cold spells the early deglaciation (ED) and  
 931 Younger Dryas (YD), orange boxes are for the warm phases Bølling-Allerød (B/A) and Pre-  
 932 Boreal (PB). Gray boxes highlight the periods of melt water pulse 1A (MWP-1A) and 1B  
 933 (MWP-1B).



934 **Figure 4.** Records of sea surface temperature (SST) and sea ice (IP<sub>25</sub>) in the Bering Sea and  
 935 Northeast Pacific, and Okhotsk Sea and Northwest Pacific during the past 25 ka. (a) The  
 936 NGRIP- $\delta^{18}\text{O}$  of the Greenland (Rasmussen et al., 2008). (b) The MAR of biomarkers.  
 937 I: (c) Light green line is the SST (TEX<sub>86</sub><sup>L</sup>) of this study, SO202-18-3/6. The brown line is the  
 938 IP<sub>25</sub> of this core (Méheust et al., 2018). (d) SST and IP<sub>25</sub> of the core SO202-2-114KL (Max et  
 939 al., 2012; Méheust et al., 2016). (e) SST and IP<sub>25</sub> of the core SO202-27-6 in the Northeast  
 940 Pacific (Méheust et al., 2018). (f) SST of the core 85JC (Praetorius et al., 2015).  
 941 II: (c) SST and IP<sub>25</sub> of the core MD01-2414 in the Okhotsk Sea (Lattaud et al., 2019; Lo et al.,  
 942 2018). (d) SST of the core XP98-PC-2 (Seki et al., 2014). (e) SST and IP<sub>25</sub> of the core SO201-  
 943 2-12KL in the Northwest Pacific (Max et al., 2012; Méheust et al., 2016). (f) SST and IP<sub>25</sub>  
 944 of the core SO202-07-6 (Méheust et al., 2018). The units of the SST and IP<sub>25</sub> are  $^{\circ}\text{C}$  and  $\mu\text{g g}^{-1}$   
 945 sediment, respectively. Blue boxes represent the colder conditions during the early  
 946 deglaciation (ED) and Younger Dryas (YD) cold spell, orange boxes are for the warm phases  
 947 Bølling-Allerød (B/A) and Preboreal (PB). Gray boxes highlight the periods of melt water  
 948 pulse 1A (MWP-1A) and 1B (MWP-1B).



949 **Figure 5.** Lignin indicators of terrigenous material in the Bering sediment (solid circles)  
 950 compared with previously studied (Martens et al., 2019; Keskitalo et al., 2017; Tesi et al.,  
 951 2016; Seki et al., 2014; Winterfeld et al., 2015). The early deglaciation is from 19 to 14.6 ka  
 952 BP and after the early deglaciation is the later deglaciation. The dark triangles represent the  
 953 ratio of S/V and C/V from surface soils, Ice Complex deposits and active layer permafrost  
 954 (Tesi et al., 2014). ESS is short for the East Siberian Shelf.



955 **Figure 6.** Lignin indicators of terrigenous material in the Okhotsk Sea sediment (solid circles)  
956 compared with previously studied (Martens et al., 2019; Keskitalo et al., 2017; Tesi et al.,  
957 2016; Seki et al., 2014; Winterfeld et al., 2015). The early deglaciation is from 19 to 14.6 ka  
958 BP and after the early deglaciation is the later deglaciation. The dark triangles represent the  
959 ratio of S/V and C/V from surface soils, Ice Complex deposits and active layer permafrost  
960 (Tesi et al., 2014). ESS is short for the East Siberian Shelf.