



Tracing terrestrial organic matter dynamics in the subarctic North Pacific using sedimentary ancient DNA metabarcoding

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Abstract. The subarctic North Pacific receives and preserves substantial amounts of terrestrial organic matter, yet the limited taxonomic resolution of traditional isotope and biomarker proxies constrains our ability to identify its source taxa and source regions, leaving its provenance and transport dynamics poorly understood. Here we use land-plant sedimentary ancient DNA (sedaDNA) metabarcoding to trace terrestrial plant organic matter in marine sediment cores from off-Kamchatka and the Bering Sea. We achieved unprecedented taxonomic resolution for marine sedaDNA records, identifying 328 terrestrial plant taxa, including 173 resolved to species level, across the two marine cores. Comparison with Siberian and Alaskan lake sedaDNA records showed that terrestrial plant assemblages recovered from the marine cores broadly reflected regional vegetation patterns and their temporal changes, while contrasts in relative taxon abundances indicated taphonomic filtering in marine sedaDNA records. Compositional relationships between the marine and lacustrine records, together with Siberian- and Alaskan-associated indicator taxa (e.g., *Spiraea salicifolia* and *Shepherdia canadensis*), provided taxonomic evidence for regional source attribution. Across the glacial–interglacial transition, the two marine records preserved distinct regional vegetation histories. Diversity patterns differed between the sites, with the Bering Sea record more strongly influenced by deglacial terrigenous delivery and the off-Kamchatka record more closely associated with postglacial warming. Our results demonstrate the potential of targeted sedaDNA metabarcoding as a high-resolution tool for tracing terrestrial organic matter in high-latitude oceans and highlight the need for expanded DNA reference databases and improved understanding of marine sedaDNA taphonomy.



1 Introduction

The burial of terrestrial organic matter in marine sediments represents an important pathway in the long-term carbon cycle and contributes to the regulation of atmospheric CO₂ on geological timescales (Burdige, 2007). Terrestrial organic matter transported by rivers constitutes a substantial proportion of this marine sedimentary carbon (Ludwig et al., 1996), particularly on continental shelves, where it represents a primary mechanism for the net sequestration of atmospheric carbon by the biosphere (Berner, 1982). Specifically, land plants (embryophytes) account for the majority of the biomass of the terrestrial biosphere (Bar-On et al., 2018), contributing a large proportion of the global terrestrial organic matter flux. In the context of global warming caused by carbon emissions, tracing the source and fate of land plant matter in marine sediments has become a focal point in carbon cycle research, with profound implications for predicting the response of carbon sinks to ongoing climate change (Dai et al., 2022; Regnier et al., 2022).

In high-latitude regions, these land-ocean carbon linkages are exceptionally sensitive to environmental change (Vonk et al., 2025). The subarctic North Pacific receives substantial inputs of terrigenous organic matter from surrounding continents on glacial–interglacial timescales (e.g., Cao et al., 2023; Meyer et al., 2019). Here, the unglaciated landscapes of Eastern Siberia and Alaska (Beringia) supported extensive steppe-tundra vegetation during the last glacial period (Wang et al., 2021b), maintaining a large terrestrial carbon pool (Ciais et al., 2012). The subsequent large-scale warming during the last deglaciation (~19–11 ka) (Clark et al., 2012) triggered a profound reorganization of this carbon pool. This transition was characterized by a highly sensitive ecological response, as deciduous erect shrubs and trees increasingly colonized the Beringian region, particularly with the onset of the Holocene (e.g., Clarke et al., 2024; Huang et al., 2021), leading to the establishment of modern-day boreal forests and tundra (Edwards et al., 2000) and fundamentally altering the taxonomic composition of terrestrial organic carbon inputs. Simultaneously, deglacial warming destabilized the landscape, transforming permafrost stability (Winterfeld et al., 2018), meltwater regimes (Dyke, 2004), and fluvial discharge patterns (Tesi et al., 2016). Together, these biological and physical shifts reshaped the source-to-sink transfer of terrestrial organic carbon by altering both vegetation composition and transport pathways. Deciphering these coupled biological and physical responses is essential for understanding how terrestrial organic carbon is transferred, transformed, and ultimately buried and sequestered in North Pacific marine sediments.

However, directly tracing the taxonomic composition and provenance of terrestrial plant matter in marine sediments remains challenging. Traditionally, this has been achieved using biomarkers (e.g., lignin phenols, *n*-alkanoic acids, and *n*-alkanes), and stable isotopes, which are effective for estimating bulk fluxes and distinguishing between terrestrial and marine sources of organic matter (Prah et al., 1994; Yunker et al., 1995). Although state-of-the-art biomarker methods can distinguish fossil from contemporary carbon (Meyer et al., 2019; Winterfeld et al., 2018), they provide only rough taxonomic information on plant matter sources—such as C₃ and C₄ vegetation (Smith and Epstein, 1970), gymnosperms and angiosperms



(Pempkowiak, 2020), and different aquatic plants (Diefendorf and Freimuth, 2017; Sikes et al., 2009)—making it difficult to trace specific plant taxa. Furthermore, pollen taphonomy in marine sediments differs markedly from that of most other plant material, which is primarily transported via rivers (Galy et al., 2015; Regnier et al., 2022). In contrast, pollen is at least partly transported by air, especially in offshore regions away from estuaries (e.g., Faye et al., 2020; Zheng et al., 2013), and thus reflects land–ocean carbon linkages only indirectly. Consequently, a proxy capable of directly resolving the composition and contribution of terrestrial plants is needed to connect terrestrial carbon sources with marine carbon sinks.

Sedimentary ancient DNA (sedaDNA) offers the potential for species-level taxonomic resolution and has consequently been recognized as a promising tool for tracing the sources and transport dynamics of organic matter in marine sediments (Geraldini et al., 2019; Herzschuh et al., 2025b; Zimmermann et al., 2017). Herzschuh et al. (2025b) applied shotgun metagenomics—analyses of the total environmental DNA preserved in sediments—to marine sediment records, providing information on source vegetation taxa at the family level. Nevertheless, this approach remains challenging compared to plant DNA metabarcoding, due to the limited taxonomic resolution resulting from incomplete reference databases and the greater sequencing depth often required to recover sufficient DNA signals (Heintzman et al., 2023; Strandberg et al., 2026). In contrast, plant metabarcoding targeting the short and variable P6 loop of the chloroplast *trnL* (UAA) intron is a robust approach that has been widely applied in sedaDNA studies (e.g., Alsos et al., 2016; Liu et al., 2025; Parducci et al., 2017), as large numbers of samples can be processed with comparatively low effort and cost, and bioinformatic workflows are easier to handle (Capo et al., 2021; Taberlet et al., 2007). Moreover, relatively complete public reference databases are available for chloroplast *trnL* P6 loop sequences, including ArctBorBryo (Soininen et al., 2015; Sønstebo et al., 2010; Willerslev et al., 2014), EMBL (Kanz et al., 2005) and PhyloNorway (Alsos et al., 2020), enabling more accurate taxonomic assignments compared to shotgun metagenomics (Strandberg et al., 2026).

In this study, we investigate the temporal and spatial dynamics of terrestrial plant DNA signals preserved in two marine sediment cores from off-Kamchatka and the Bering Sea over the last ~26 ka (cores SO201-2-12KL and SO202-18-3/6; see Materials and Methods for site descriptions). We use land-plant DNA metabarcoding data as a high-resolution proxy to trace the taxonomic composition and continental source regions of terrestrial organic matter, performing a comparison between marine sediment cores and lacustrine records from Siberia and Alaska. As a preliminary exploration, we identify taxa indicative of Siberian-side and Alaskan-side sources in the marine records to demonstrate the feasibility of our approach to trace the land-to-ocean carbon transfer. We evaluate the composition and temporal dynamics of terrestrial plant DNA signals preserved in the two marine sediment cores, including differences in regional source signatures and their responses to glacial–interglacial environmental change. We further assess how land–ocean taphonomic processes shape patterns of plant-derived organic matter burial in marine sediments. Finally, we discuss the potential of metabarcoding-based sedaDNA in marine sediments as a proxy linking terrestrial ecosystems and the marine carbon sink.



90 2 Materials and Methods

2.1 Materials

Two marine sediment cores from the subarctic North Pacific were analyzed for this study (Fig. 1). The off-Kamchatka core (SO201-2-12KL) was retrieved from the western continental slope of Kamchatka about 70 km from the coast of Kamchatka (53.99° N, 162.37° E; water depth: 2145 m) during cruise SO201 in 2009 (Max et al., 2012). We applied the age–depth
95 model established by Max et al. (2012). The Bering Sea sediment record (SO202-18-3/6) consists of a composite core constructed from piston core SO202-18-3 (60.13° N, 179.44° W; water depth: 1111 m) and kasten core SO202-18-6 (60.13° N, 179.44° W; water depth: 1107 m), which were retrieved from the continental slope off the northern Bering Sea during cruise SO202 in 2009 (Kuehn et al., 2014). The age–depth model of this composite core is based on radiocarbon dating and was adopted from previous studies (Kuehn et al., 2014; Meyer et al., 2019). Inter-core correlation and splicing, based on
100 elemental scanning data, sediment facies analysis, and radiocarbon dating (Kuehn et al., 2014), produced a continuous sedimentary sequence extending back to the last glacial period (~26 ka).

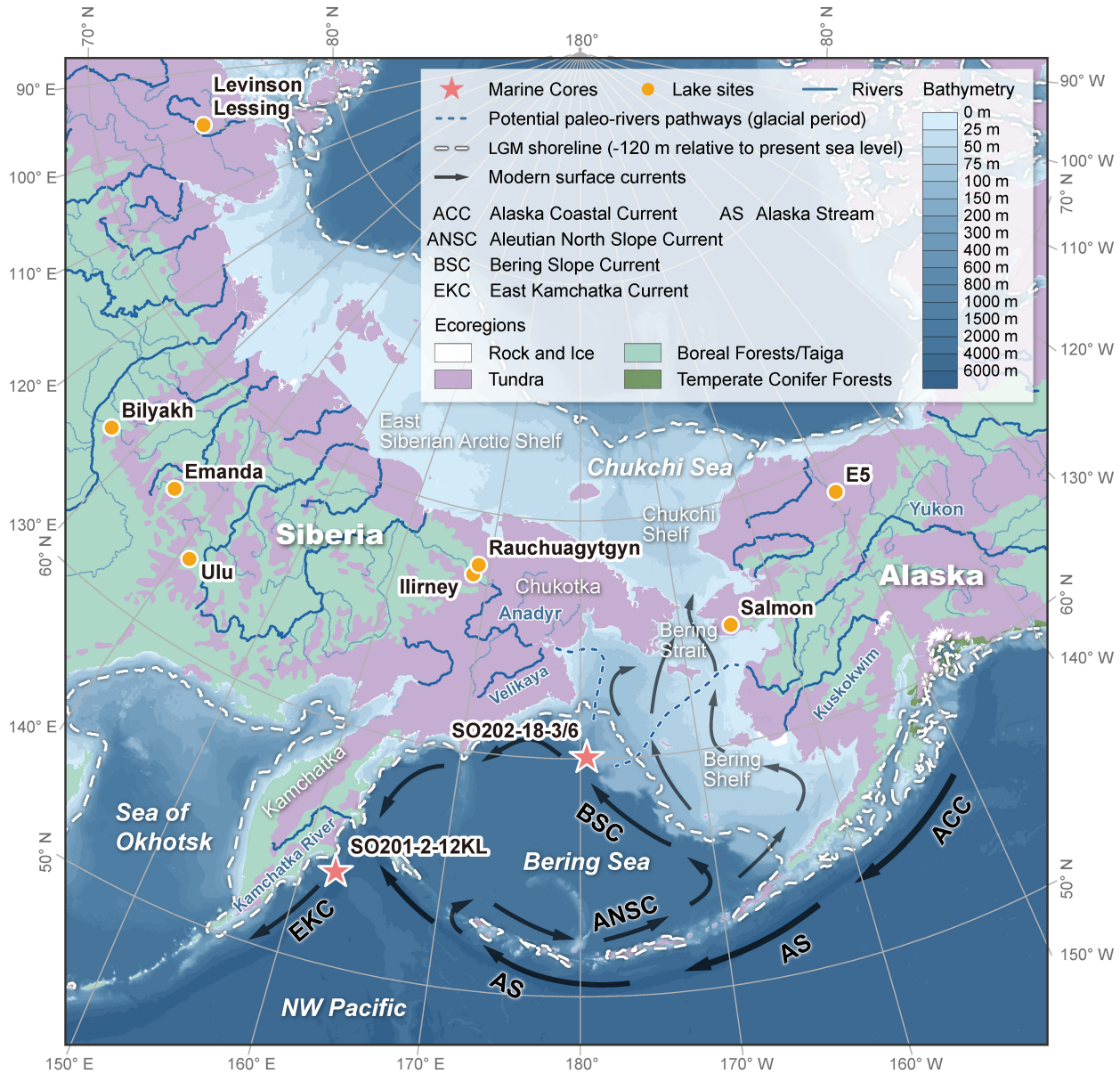
The two marine cores were subsampled in a subsampling room far away from any molecular biology laboratories at the GEOMAR Helmholtz Center for Ocean Research (Kiel, Germany). All subsequent working steps were performed in a dedicated ancient DNA laboratory at Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research (AWI) in
105 Potsdam to avoid contamination from modern DNA and followed the procedures from Zimmermann et al. (2021). In total, DNA from 89 sediment samples (Table A1) was extracted using the DNeasy PowerMax Soil Kit (Qiagen). Each extraction batch contained nine samples and one blank control. The extracted DNA and blanks were purified and concentrated using the GeneJET PCR Purification Kit (Thermo Fisher Scientific) and quantified using the dsDNA BR Assay Kit with a Qubit 2.0 fluorometer (Invitrogen). Finally, the DNA solution was diluted to 3 ng μL^{-1} for PCR reactions.

110 The PCR reactions were performed using the *trnL* g–h primers (Taberlet et al., 2007). The reactions contained Platinum Taq High Fidelity DNA Polymerase (Invitrogen), HiFi buffer, MgSO_4 , dNTPs (Life Technology), Bovine Serum Albumin (VWR), primers and DNA. PCRs were carried out in a Professional Basic Thermocycler (Biometra) with initial denaturation at 94 °C for 5 min, followed by 50 cycles consisting of 94 °C for 30 s, 50 °C for 30 s, 68 °C for 30 s, and a final extension at 72 °C for 10 min. For each extraction sample, three PCR replicates with differently tagged primers were performed. The
115 extraction blanks and no template controls (NTC) were also included in each PCR to identify possible contamination during extraction and PCR set-up. After PCR reactions, PCR success was checked with gel-electrophoresis on 2 % agarose gels (Carl Roth GmbH & Co. KG). The PCR products were then purified using the MinElute PCR Purification Kit (Qiagen) and quantified using the dsDNA BR Assay Kit with a Qubit 2.0 fluorometer (Invitrogen) for sequencing. All extraction blanks and NTCs were included in the sequencing run, even though they were negative in the PCRs. The PCR pool from core
120 SO202-18-3/6 was sequenced in paired-end mode (2×100 bp) on the AVITI Exclusive 500M. The PCR pool of core



SO201-2-12KL was sequenced in paired-end mode (2×150 bp) on the Illumina NextSeq. Both sequencing runs and PCR-free library preparation were performed by Genesupport Lifescience (Fasteris) in Switzerland.

125 To investigate the extent to which terrestrial plant DNA preserved in marine sediments reflects continental vegetation compositions and changes, we compared the two marine sediment cores with metabarcoding data from nine lacustrine cores derived from eight lakes (six in Siberia and two in Alaska), each covering at least the last 26,000 years (Fig. 1, Table A2). Metabarcoding data from these lacustrine cores were generated using similar laboratory workflows (Courtin et al., 2025; Herzschuh et al., 2025a; Huang et al., 2021; Jia et al., 2024). For direct marine–lacustrine comparisons, lacustrine samples were restricted to 0–26 ka to match the temporal coverage of the marine cores.



130 **Figure 1: Map of the study area showing the locations of the two marine sediment cores (red stars) and reference lake sites (yellow**
135 **circles) across Siberia and Alaska. River systems are based on the HydroRIVERS database (Lehner and Grill, 2013). Potential**
paleo-river pathways during glacial low sea-level conditions are simplified after previous Beringian paleodrainage reconstructions
(Bond, 2019). Major ocean currents, including the Alaska Coastal Current (ACC), Alaska Stream (AS), Aleutian North Slope
Current (ANSC), Bering Slope Current (BSC), and East Kamchatka Current (EKC) are shown. Bathymetry is based on the
GEBCO global elevation model (GEBCO Bathymetric Compilation Group, 2026). Terrestrial ecoregions are simplified from the
WWF Terrestrial Ecoregions of the World classification (Olson et al., 2001).



2.2 Bioinformatics analysis

Both marine and lacustrine sedaDNA metabarcoding datasets were analysed individually using OBITOOLS (version 3; Boyer et al., 2016). Overlapping paired reads were merged using the command *obi alignpairedend*. The unmerged reads were removed with *obi grep -a mode:alignment*. The command *obi ngsfilter* assigned each sequence to its corresponding sample according to the tag combination. Reads were dereplicated with the command *obi uniq --merge sample* and cleaned from PCR and sequencing errors using *obi clean -s MERGED_sample -r 0.05 -H*, which keeps head sequences (-H) that lack variants with a count greater than 5 % of their own count (-r 0.05).

To ensure reliable taxonomic assignments of the amplicon sequence variants (ASVs), we used a customized *SibAla_2023* reference database (Courtin et al., 2025; Herzsuh et al., 2025a) developed for Siberia and Alaska (55–90° N, 50–150° E; 40–90° N, 150° E–140° W) for both marine and lacustrine sedaDNA metabarcoding datasets. This regional plant DNA metabarcoding reference database comprises 4939 entries representing 3398 species, 947 genera and 223 families, collapses into 2371 unique P6 loop sequence types, and achieves taxonomic coverage of 95.7 % at the family level, 89.4 % at the genus level and 70.1 % at the species level relative to Global Biodiversity Information Facility (GBIF) occurrence records (Courtin et al., 2025). Taxonomic assignments were performed using *obi ecotag* with the use of the customized *SibAla_2023* database.

Data quality was assessed by investigating the replicability of the PCR replicates and their compositional patterns by non-metric multidimensional scaling (NMDS) analyses. The analysis was done core-wise and only assigned ASVs that have a 100 % identity match to the reference database were used. Analyses were conducted in R (version 4.2.2; R Core Team, 2022). The ASV compositional data were Hellinger-transformed using the function *decostand* and ordination was performed with *metaMDS* in the R package *vegan* (version 2.6-8; Oksanen et al., 2024). If replicates of the same sample did not form a cluster but showed that one replicate was distant from the others (indicating a different compositional signal), we checked read count and composition of the replicate. If the total read count of the affected replicate was below 100 counts and/or the sample was composed of fewer (less than three) and different plant sequence types as compared to the remaining replicates of the sample, replicates were excluded from the dataset. After replicate evaluation, the replicate removal was done on the raw data (Obitools3 output). The remaining high-quality replicates were merged per sample by summarizing the replicate read counts. Sequencing depths (reads per sample) for each marine core are summarized in Table A1.

2.3 Data analysis

We collapsed ASVs to taxa based on their assigned scientific names (i.e., the lowest taxonomic rank to which each ASV could be resolved); thus, multiple ASVs could map to the same plant taxon. All downstream summaries and analyses were performed at the taxon level, which may lead to an underestimation of richness when distinct ASVs share the same higher-



level taxonomic assignment and are therefore merged into a single taxon. We applied a sample-level low-information filter to ensure comparability across marine and lacustrine samples in downstream analyses. Samples with extremely low read counts (< 1000 reads) and low observed taxon richness per sample (< 10 taxa) were excluded (11 of 519 samples; 2.12 %).

170 To provide an overview of the taxonomic inventory and identification resolution of plant taxa recovered from marine sediments, taxa were summarized across the entire record of each marine core without temporal stratification. We reported the numbers of taxa identified at the species level, at ranks between species and family (e.g. genus, tribe, or subfamily), and at the family level, and summarized core-wise overlap between the two marine records.

For α -diversity, inventory comparison, and Sørensen-based β -diversity analyses between marine and lacustrine records, 175 sequencing depth was standardized using the Scaling with Ranked Subsampling (SRS) algorithm in R (package SRS, version 0.2.3; Heidrich et al., 2021), as these analyses are sensitive to uneven sequencing depth due to differential detection of rare taxa. SRS preserves relative abundance structure and retains more rare taxa through deterministic scaling rather than stochastic rarefaction (Beule and Karlovsky, 2020). To ensure comparability between marine and lacustrine samples, all samples were standardized to 34 515 reads, the minimum sequencing depth among marine samples retained after the low- 180 information filter. Four lacustrine samples with lower read counts were consequently excluded.

To assess terrestrial plant DNA α -diversity in the two marine cores, we calculated Hill numbers (Hill, 1973; Jost, 2006) at the sample level using the hillR package (version 0.5.2; Li, 2018) in R, based on SRS-standardized counts. Hill numbers are expressed as the effective number of taxa and parameterized by the order q , where $q = 0, 1$, and 2 correspond to richness (N_0), Shannon diversity (N_1 ; the exponential of Shannon index), and Simpson diversity (N_2 ; the inverse Simpson index), 185 respectively. Temporal trends in α -diversity were analysed using generalized additive models (GAM) fitted with the R package mgcv (version 1.9-1; Wood, 2017). Correlations between cores were tested at an 800-year resolution, matching the mean sampling density of the lower-resolution record (off-Kamchatka) to prevent over-interpolation and ensure robust p -values. Taxon contributions to α -diversity were assessed using a leave-one-taxon-out jackknife on Simpson diversity, quantified as the change in N_2 following taxon removal.

190 Taxonomic inventory comparisons between marine and lacustrine cores were performed to evaluate the overlap of plant DNA assemblages between marine and terrestrial records. Analyses were first conducted at the core scale within the analysed age intervals (off-Kamchatka core: 20–0 ka; Bering Sea core: 26–6 ka), comparing each marine core with (i) a pooled lacustrine inventory including nine cores and (ii) individual lake cores. Differences in sample numbers among sediment cores were controlled using bootstrap resampling of samples ($n = 1000$). In each iteration, 18 samples were 195 randomly drawn from each core, corresponding to the minimum sample number among the cores. For comparisons with the pooled lacustrine dataset, the 18 samples drawn from each lake core were combined to form the pooled inventory. We



calculated bootstrap medians and 95 % confidence intervals for taxon inventory size, numbers of shared and unique taxa, proportion of shared taxa in the marine cores, and Sørensen similarity (Sørensen, 1948), all based on the resampled inventories. These metrics were first used to compare each marine core with the pooled lacustrine inventory, then to compare each marine core with individual lake cores by plotting the proportion of shared taxa versus Sørensen similarity. Shared-taxa proportion and Sørensen similarity were evaluated in relation to the taxon inventory size of individual lake cores to assess whether observed overlap was influenced by lacustrine inventory size. To further assess temporal consistency, comparisons of Sørensen similarity between each marine core and individual lake cores were additionally performed using 2000-yr sliding time windows. This analysis was also based on bootstrap resampling of samples ($n = 1000$). In each iteration, one sample (corresponding to the minimum sample number among time bins) was randomly drawn from samples within each time bin.

For abundance-based analyses (proportional time series, percentage comparisons), relative read abundances were calculated from raw read counts and SRS standardization was not applied. Stratigraphic diagrams of plant DNA relative abundance at the scientific-name level were plotted for the two marine cores, and zonation was performed using CONISS clustering (constrained incremental sum-of-squares clustering; Grimm, 1987) implemented in the R package rioja (version 1.0-7; Juggins, 2024). Period-averaged relative abundances were calculated for major late-glacial and Holocene intervals for each marine core (off-Kamchatka: deglacial period [19–11.7 ka], Early to Mid Holocene [11.7–6 ka], Mid to Late Holocene [6–0 ka]; Bering Sea: Last Glacial Maximum [26–19 ka], deglaciation [19–11.7 ka], Early to Mid Holocene [11.7–6 ka]). For each interval, mean relative abundances of taxa were calculated for the marine core and for the pooled lacustrine dataset. Taxa were compared using scatter plots of marine versus lacustrine mean relative abundances, and relationships were evaluated using Spearman's rank correlation.

Community dissimilarity among samples was calculated using Bray–Curtis dissimilarity based on relative abundances derived from non-SRS-standardized read counts after excluding rare taxa (maximum abundance <0.1 % or occurrence in fewer than three samples). Non-metric multidimensional scaling (NMDS) ordination based on Bray–Curtis dissimilarities was used to visualize temporal changes and overall patterns of community composition while retaining information on relative taxon abundances. Analyses were performed using the R package vegan. First, NMDS was performed using only marine samples to examine compositional differences between the two marine sediment cores and to visualize taxa associated with the main gradients in community composition. Temporal trajectories of community change were visualized by fitting GAM smoothers to NMDS scores using the R package mgcv. Second, a joint NMDS including both marine and lacustrine samples was performed to compare marine and lake plant DNA assemblages within a common Bray–Curtis compositional space. This allows the compositional variability of marine assemblages to be interpreted relative to that observed in lake records. Because NMDS does not provide a projection framework, Procrustes analysis was used to assess



whether the inclusion of the relatively few marine samples altered the ordination structure of the much larger lacustrine dataset. Procrustes analysis was performed using the function `procrustes` in the R package `vegan`. To identify taxa contributing most strongly to Bray–Curtis dissimilarity between marine and lacustrine assemblages, similarity percentage (SIMPER) analysis was performed using the function `simper` in the R package `vegan`.

To assess whether taxon-specific temporal trends were consistent between the two marine cores and between marine and lacustrine records, we calculated the correlations based on relative abundance changes. CLR transformation (centered log-ratio) was applied to relative abundances derived from raw read counts to account for compositionality. Samples were grouped into 2000-year time bins, and CLR-transformed values within each bin were summarized by their mean values to generate taxon-specific time series. Spearman rank correlations (r_s) were then calculated based on these time-series. For each taxon, correlations were first computed between each marine core and individual lake cores, and the resulting correlation coefficients were then summarized by their median value across lake cores. To focus on dominant contributors to community structure, analyses were restricted to the 30 taxa contributing most to Simpson diversity (Hill N_2).

Candidate regional indicator taxa were identified among taxa detected in the two marine cores based on their modern geographic distributions. Modern occurrence records were obtained from the Global Biodiversity Information Facility (GBIF.org, 2025) to evaluate present geographic distributions and assess whether taxa were restricted to either the Siberian or Alaskan side of the study region. Taxa confined to one side were considered candidate regional indicators. To test the regional specificity of these candidates in the *sedaDNA* dataset, a cross-region comparison with the lacustrine *sedaDNA* dataset was conducted. Candidate taxa were excluded if their corresponding ASVs were detected in lake records from the opposite region, indicating a lack of regional exclusivity within the *sedaDNA* dataset. Candidate taxa assigned only at genus or tribe level were generally excluded when the corresponding higher taxa showed broad circumpolar distributions, because such assignments lacked sufficient regional specificity for robust provenance inference. However, exceptions were made for taxa whose broader biogeographic patterns still supported regional exclusivity within the Siberia–Alaska framework. Potential assignment ambiguity associated with short *trnL* P6 ASVs and low interspecific sequence divergence within certain taxonomic groups was conservatively considered when evaluating indicator confidence. Further details are provided in Appendix C.

3 Results

3.1 DNA composition in marine cores

In the marine sediment samples, a total of 430 amplicon sequence variants (ASVs), corresponding to 328 plant taxa (hereafter, taxa) were matched at 100 % identity to the *SibAla_2023* reference database, a regional plant DNA



metabarcoding reference dataset covering Siberian and Alaskan taxa (see Materials and Methods; Courtin et al., 2025; Herzschuh et al., 2025a). Of these, 173 taxa (~52.7 %) were identified to species level and 113 taxa (~34.5 %) to genus level. The remaining taxa were assigned to other taxonomic ranks between species and family (28 taxa; ~8.5 %; including section, subtribe, tribe, and subfamily) or to the family level (14 taxa; ~4.3 %) (Fig. 2a). The identified taxa comprised 90 plant families, with a few families (e.g., Ericaceae, Poaceae, Ranunculaceae, Orobanchaceae, Asteraceae, Rosaceae) exhibiting high taxonomic diversity, whereas most contributed only a few taxa (Fig. 2b). Across the two marine cores, the observed taxon inventories (without controlling for sequencing depth or sample number) overlapped substantially (156 taxa, ~47.6 %). The Bering Sea core (SO202-18-3/6) contains more core-specific taxa (123 taxa, ~37.5 %) than the off-Kamchatka core (49 taxa, ~14.9 %) (Fig. 2a), consistent with its higher sequencing depth and larger number of samples (Table A1). After controlling for sequencing depth by applying Scaling with Ranked Subsampling (SRS; 34 515 reads per sample), richness (Hill N_0) shows distinct peaks in both cores, occurring at ~16–15 ka in the Bering Sea core and ~11–10 ka in the off-Kamchatka core, with comparable peak magnitudes (Fig. 3). Shannon and Simpson diversity (Hill N_1 and N_2) increase across the Holocene in the off-Kamchatka core, whereas the Bering Sea core remains relatively constant through the Holocene (Fig. 3). In terms of magnitude, Shannon diversity is consistently higher in the off-Kamchatka core, while Simpson diversity is broadly comparable between cores during the Pleistocene but higher in the off-Kamchatka core during the Holocene (Fig. 3), consistent with greater evenness and weaker dominance by a few taxa relative to the Bering Sea core.

The major taxa—defined as the top 30 contributors to Simpson diversity in the marine sediments—tend to exhibit relatively high occurrence frequencies and abundances through time (Fig. 4). Taxon-specific temporal trends recorded in the two marine cores are moderately correlated (median $r_s \approx 0.5$; Fig. 5). Most of the top 30 taxa show positive Spearman correlations between the two records, with several showing moderate to strong correlations (e.g., *Dryas*, *Betula*, $r_s > 0.5$), indicating a consistent signal between the sites. Notably, this pattern is not driven by the most abundant taxa, as dominant taxon Saliceae do not consistently exhibit a strong positive correlation.

The land-plant DNA composition of both marine cores is dominated by woody and dwarf shrub taxa, driven mainly by Saliceae (the willow tribe within Salicaceae)—which has a median relative abundance of 71.2 % in the Bering Sea core and 48.4 % in the off-Kamchatka core—followed by the dwarf shrub *Dryas* as the second most abundant taxon. Jackknife decomposition of α -diversity reveals a negative contribution of Saliceae to Simpson diversity (Fig. B1), indicating that its dominance reduced the evenness of the assemblages. In the off-Kamchatka core, recurrent subdominant taxa include the arboreal taxa *Alnus* and *Betula* and the ferns *Athyrium* and *Matteuccia struthiopteris*, most notably in the Holocene. In contrast, the Bering Sea core tends to feature a mix of shrubs and herbs among the non-dominant taxa, including Papaveraceae, Ericaceae (e.g., *Arctous*), Polygonaceae, and Asteraceae, whereas *Alnus* and *Athyrium* are not consistently prominent.



Both cores exhibit a marked shift in terrestrial plant composition across the glacial–deglacial–Holocene transition, as revealed by CONISS age-constrained cluster analysis that divides both cores into 4 zones (Fig. 4). NMDS ordination reveals a clear temporal structuring of DNA composition, with samples ordered along the age gradient on the first axis and separation between the two cores along the second axis, indicating that temporal differences in both cores are greater than compositional differences between cores (Fig. 6).

During the Pleistocene, the inferred vegetation composition of the adjacent land areas recorded by the two marine cores was relatively similar (Fig. 6), with only minor differences in the relative abundance of individual taxa, smaller than those observed during the Holocene (Fig. 4). Around the Last Glacial Maximum (LGM, 26–19 ka), assemblages were dominated by Saliceae and *Dryas*, while herbaceous taxa (e.g., Papaveraceae, Polygonaceae and Asteraceae) were also present and more abundant than in later periods (Fig. 4). During the deglacial period (19–11.7 ka), the abundance of *Dryas* increased substantially, whereas herbaceous taxa declined (Fig. 4). Richness increased, while Shannon and Simpson diversity decreased in both marine cores (Fig. 3), indicating that the dominance of a few abundant taxa became more pronounced. CONISS clustering further divides this period into two stages (Fig. 4), corresponding approximately to an early (~19–14 ka) and a late deglacial (~14–11.7 ka) phase. The early deglacial was characterized by the persistence of herbaceous taxa at abundances lower than during the LGM but higher than in the late deglacial and the Holocene. The late deglacial displayed a widespread emergence and expansion of *Betula* and various (dwarf-) shrubs across adjacent subarctic land areas, including *Arctous rubra*, *Empetrum nigrum*, *Rhododendron tomentosum*, and *Vaccinium*.

In the Holocene, both marine cores recorded a major turnover in terrestrial vegetation composition, especially in the off-Kamchatka record, characterized by the expansion of trees, ferns, and aquatic taxa (Fig. 4). Meanwhile, the compositions of the two marine cores diverged significantly in this period (Fig. 6), indicating that the vegetation sources of the two sites evolved differently. In the off-Kamchatka core, richness decreased by approximately 50 %, whereas Shannon and Simpson diversity roughly doubled (Fig. 3), indicating the reduction in the dominance of previously abundant taxa. This dramatic change was accompanied by the significant increase in the relative abundance of *Alnus*, *Alnus alnobetula*, *Populus*, and ferns (e.g., *Athyrium* sect. *Athyrium*, *Matteuccia struthiopteris*, *Phegopteris connectilis*, and *Pseudathyrium alpestre*). In contrast, changes in the Bering Sea core were less pronounced (Fig. 6), with Saliceae and *Dryas* remaining dominant and only minor increases in *Picea*, *Alnus*, and *Athyrium*. Consequently, richness and Shannon and Simpson diversity showed only slight shifts, and both diversity metrics remained relatively low (Fig. 3).

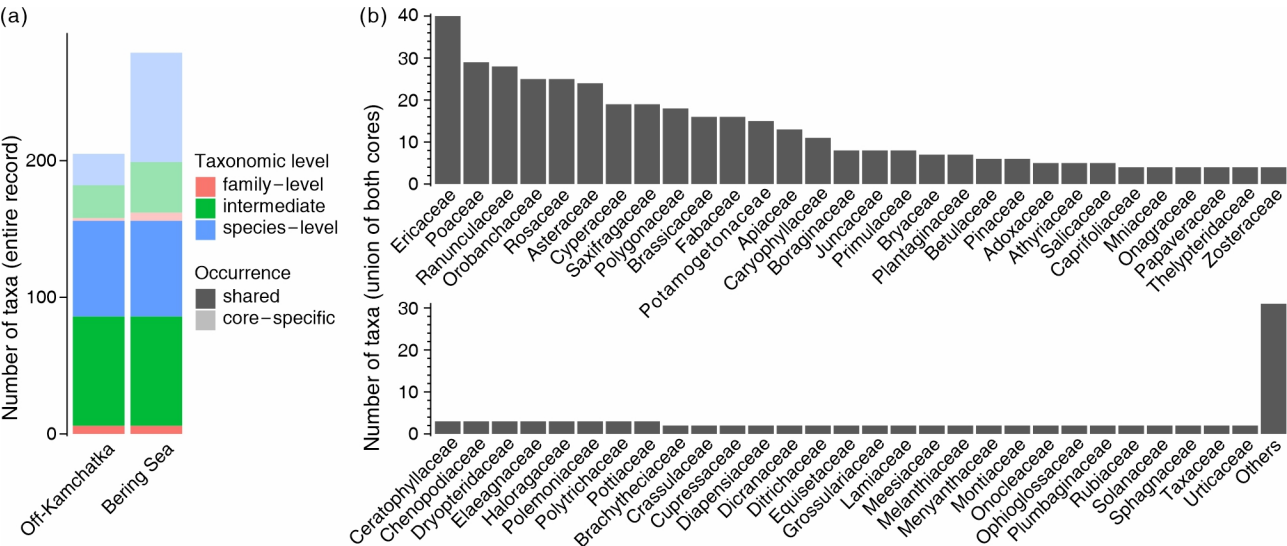


Figure 2: Overview of taxonomic resolution of terrestrial plant sedaDNA in the two marine sediment cores, summarized as unique assigned taxa. (a) Taxonomic resolution and overlap of plant taxa across the two marine cores, summarized across their entire stratigraphic records. Bar height indicates the total number of taxa detected per core. Colours represent taxonomic resolution (species-level, intermediate ranks, and family-level). Fully saturated colours indicate taxa shared between the two cores, whereas semi-transparent colours indicate core-specific taxa. (b) Family-level distribution of detected plant taxa across both cores combined. Bars represent the number of taxa assigned to each plant family. “Others” includes all families represented by only one taxon.

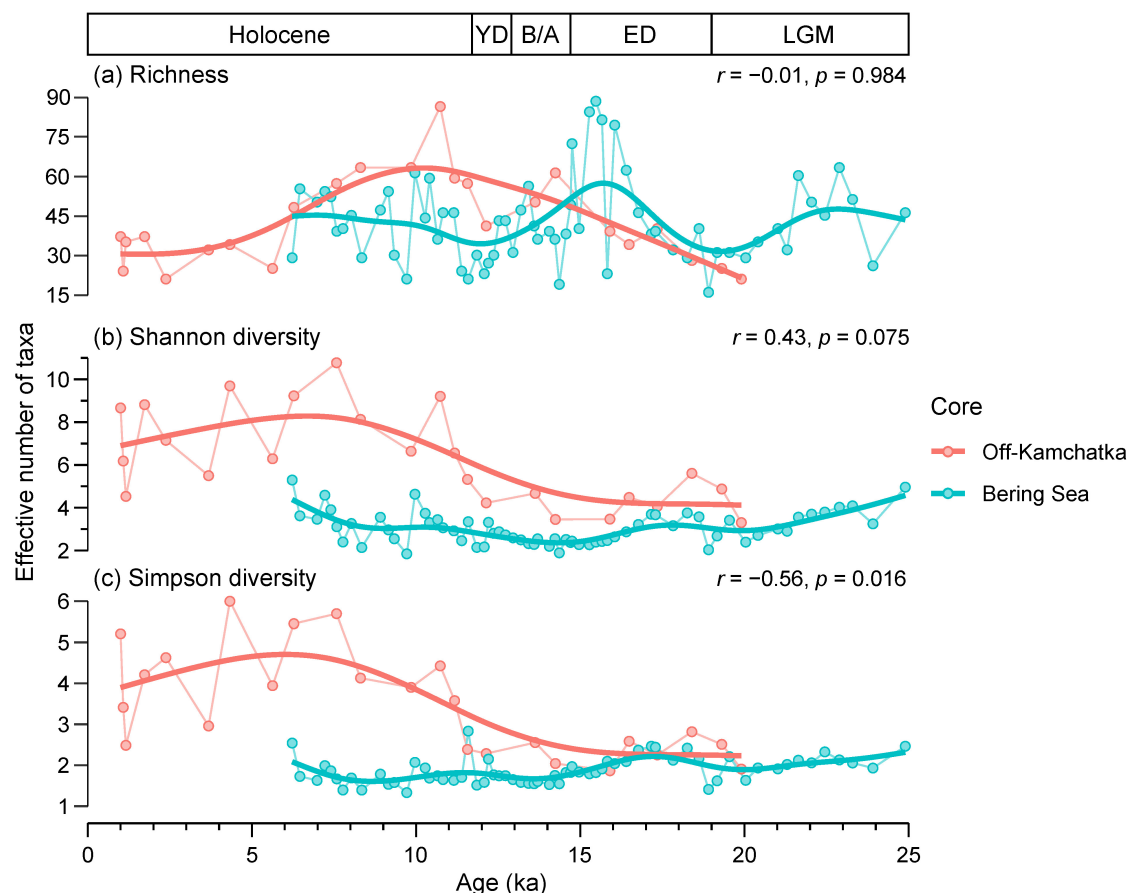


Figure 3: Hill α -diversity of marine samples. (a) Richness (N_0); (b) Shannon diversity (N_1); (c) Simpson diversity (N_2). To standardise sequencing depth, Scaling with Ranked Subsampling (SRS) was applied to each marine sample at 34 515 reads, corresponding to the minimum sequencing depth among all marine samples. Points represent the individual sample values of Hill α -diversity indices, interconnected by thin faint lines. Thick lines denote the generalized additive model (GAM) fit. The r and p -values indicate Spearman correlations and their significance of α -diversity time series between the overlapping intervals of the two cores, calculated based on GAM-fitted curves resampled at an 800-year resolution to align sample ages. The Holocene (< 11.7 ka), Younger Dryas (YD: 12.9–11.7 ka), Bolling–Allerød (B/A: 14.7–12.9 ka), early deglacial (ED: 19–14.7 ka), and Last Glacial Maximum (LGM: > 19 ka) are indicated above the panels.

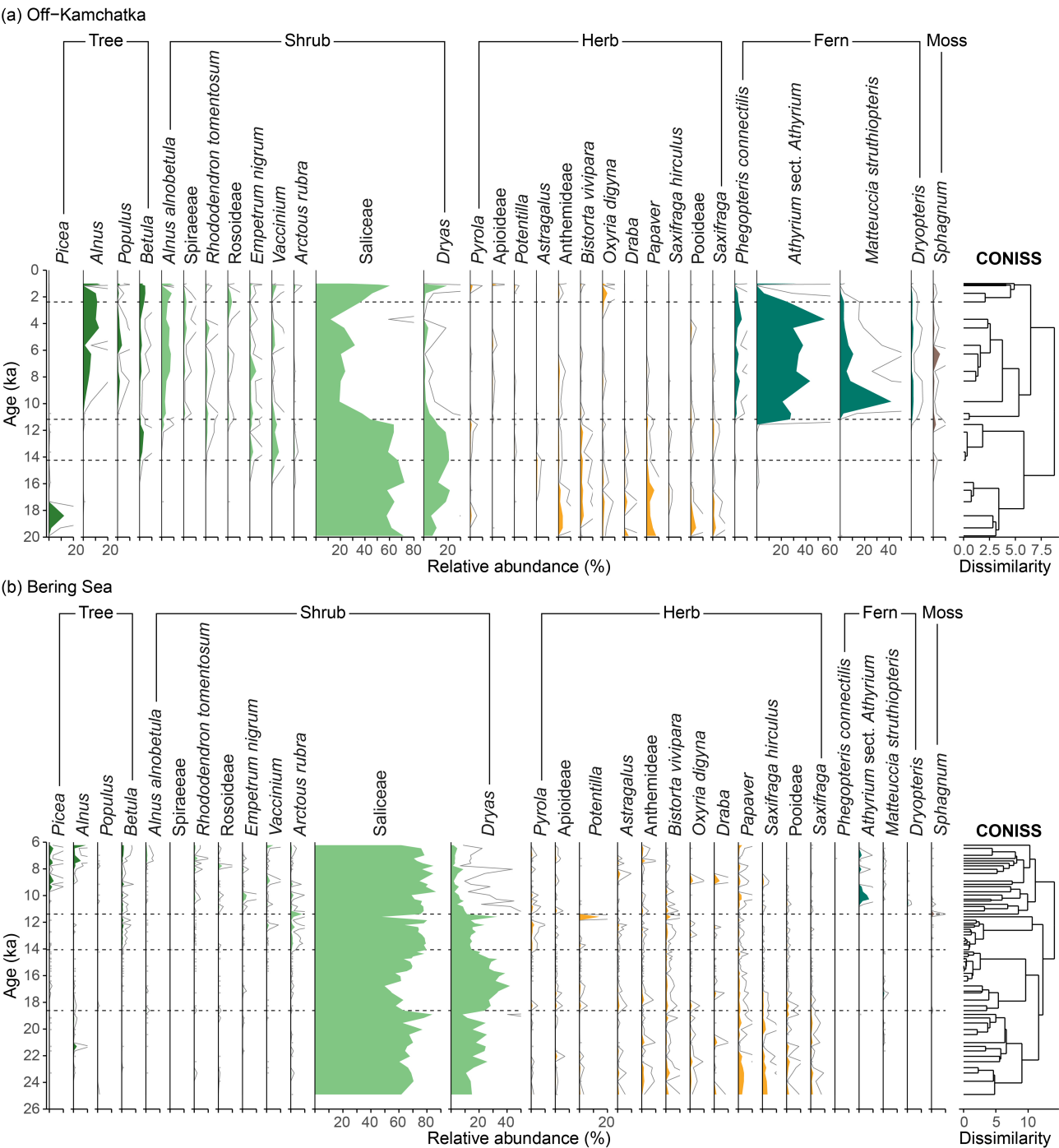


Figure 4: Stratigraphic diagrams of land-plant DNA composition with CONISS clustering in the two marine cores. (a) off-Kamchatka core; (b) Bering Sea core. Stratigraphic plots on the left show the top 30 taxa contributing most to Simpson diversity (N_2). Each panel represents an individual taxon, ordered by weighted mean age within the overlapping interval and grouped into



functional types (Tree, Shrub, Herb, Fern, Moss). Colored areas indicate relative abundance. Grey lines are 5 times exaggeration of scale. Grey points indicate very low but non-zero abundances ($< 0.2\%$), plotted at 1% for visibility and representing presence only (not actual values). Dendrograms on the right show CONISS hierarchical clustering based on compositional dissimilarity. Dashed horizontal lines mark CONISS zonation boundaries.

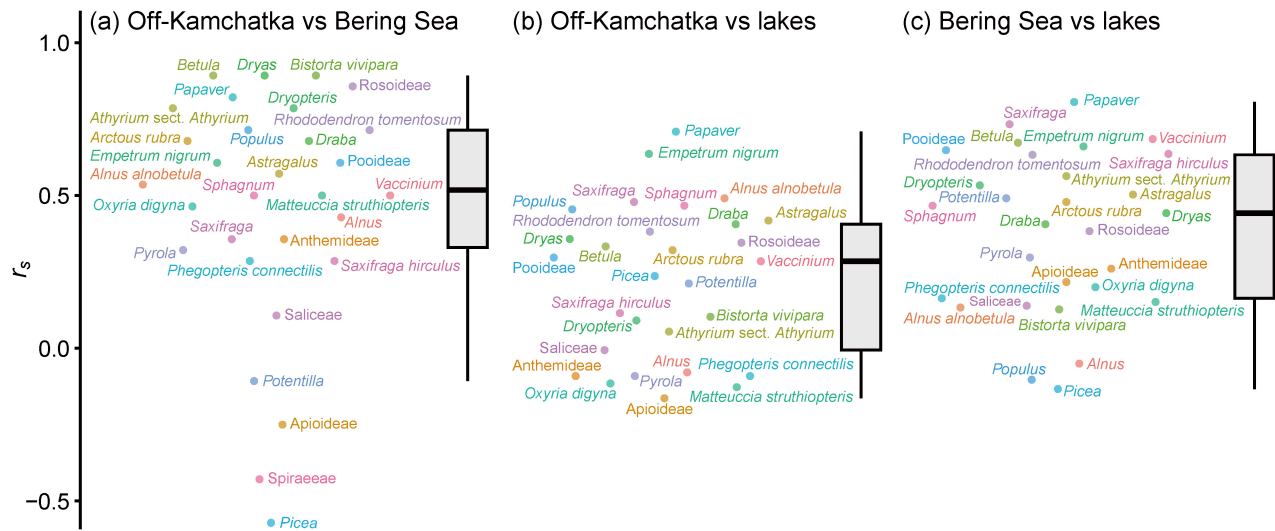


Figure 5: Spearman correlations of taxon-specific temporal trends between the two marine cores and lake records, with boxplots summarizing taxon-specific correlations. (a) off-Kamchatka core vs. Bering Sea core; (b) Off-Kamchatka core vs. lake records (median correlation across lake sites for each taxon); (c) Bering Sea core vs. lake records (median correlation across lake sites for each taxon). Spearman correlations were calculated on centered log-ratio (CLR)-transformed percentage data using 2000-year sliding windows. For each taxon, correlations were first calculated between each marine core and individual lake records and subsequently summarized by the median r_s across lake records. Results are shown for the top 30 taxa contributing most to Simpson diversity, as determined using a jackknife approach. Colored points indicate taxon-specific Spearman correlation coefficients, with taxa labels shown next to each point. Summary boxplots are displayed with a slight horizontal offset for visual clarity.

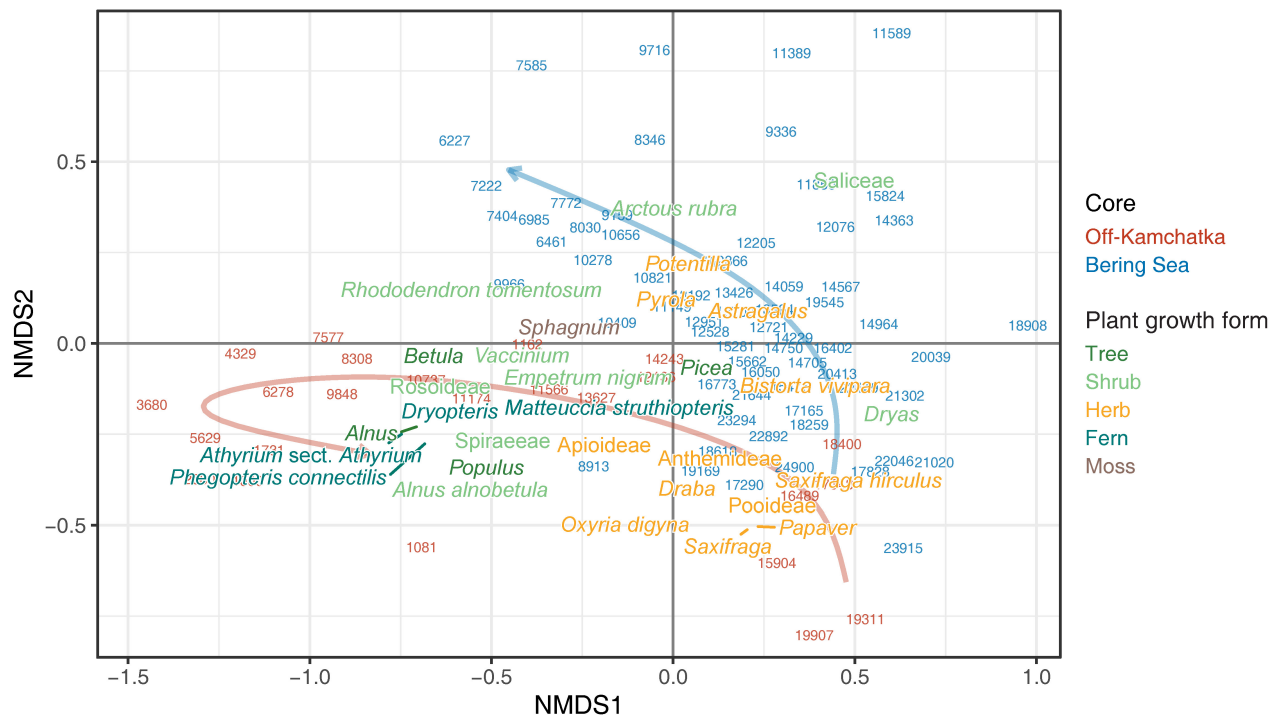


Figure 6: NMDS ordination of land-plant DNA assemblages from the two marine cores based on Bray-Curtis distances. Taxon labels represent plant taxa and are coloured by growth form (tree, shrub, fern, herb, and moss). Sample labels (numbers) are coloured by core. Arrows represent GAM-smoothed trajectories showing the direction of community turnover from the oldest (arrow tail) to the youngest (arrow head) samples. The ordination stress value is 0.184. Rare taxa (max abundance < 0.1 % or occurrence < 3 samples) were excluded prior to analysis to reduce noise.

3.2 DNA composition comparison between marine cores and lake records

Based on effort-controlled inventories (SRS standardisation for sequencing depth and bootstrap resampling across samples), both marine records share a large fraction of their taxa with the pooled lacustrine inventory within the analysed intervals (off-Kamchatka: 20–0 ka; Bering Sea: 26–6 ka; Table 1). Median taxon inventory size was ~170 taxa in each marine core versus ~400 taxa in the pooled lake dataset, with ~154 taxa shared in both marine cores, representing 88–89 % of the marine inventory (Table 1). Pairwise comparisons against individual lake cores revealed substantial heterogeneity in marine–lacustrine taxon overlap. The percentage of taxa detected in the marine core that were also detected in a given lake core was generally moderate to high, ranging from ~40 % to ~80 % across lake cores, corresponding to moderate Sørensen similarity (~0.50–0.67; Fig. 7). Notably, Salmon Lake (eastern Alaska) and Ulu Lake (Oymyakon Upland, Siberia) showed the highest overlap with both marine records: >70 % of the taxa detected in each marine core were shared with Salmon Lake and Ulu Lake, and both lakes also exhibited among the highest Sørensen similarity values (Fig. 7). Across lake cores, the proportion of taxa detected in the marine record that were also recovered in a given lake core, as well as Sørensen similarity, tend to



increase with lacustrine taxon inventory size (Fig. B2). This suggests that lakes with larger inventories provide more complete reference inventories.

370 Relative-abundance patterns indicate consistent divergence between marine and lacustrine records. Across all time slices (Fig. 8, Fig. B3), power-transformed mean relative abundances in each marine core show moderate rank-order correspondence with the lake-averaged assemblage (Spearman $r_s \approx 0.30$ – 0.46 ; $p < 0.001$). However, asymmetry (i.e., departures from the 1:1 line) differs by site and period: the off-Kamchatka core is predominantly lake-skewed during the deglacial interval but shows more pronounced two-sided departures in the Holocene, whereas the Bering Sea core remains
375 largely lake-skewed throughout, with outliers enriched towards the marine record only slightly more prominent in the Holocene. These site- and period-specific shifts are driven by changes in which taxa deviate most strongly from the 1:1 relationship. *Larix*, an important regional woodland taxon, is consistently lake-enriched, showing higher mean abundances in the lake-averaged dataset but near-zero values and occasional non-detection in the marine cores. Aquatic macrophytes (e.g., *Potamogeton*, *Stuckenia*, *Myriophyllum*, *Hippuris*, *Ceratophyllum*, *Callitriche*) are repeatedly highlighted among the top
380 taxa and also tend to be lake-enriched, in some cases exceeding the $2\times$ envelope. In contrast, Saliceae is consistently among the most abundant taxa in both marine cores across the Holocene and Pleistocene, generally plotting close to the 1:1 line (and in several panels slightly below), indicating broadly comparable dominance—and occasional relative enrichment—in the marine records. A smaller subset of taxa is strongly marine-enriched, including several ferns (e.g., *Athyrium sect. Athyrium*, *Matteuccia struthiopteris*), wetland/shoreline-associated taxa (e.g., *Argentina anserina*, *Sium suave*), and Spiraeae,
385 particularly in the off-Kamchatka core during the Holocene. *Zostera* (seagrass), a characteristic coastal marine macrophyte, was detected in both marine cores but is absent from the lake records, indicating input from coastal environments. Despite these differences, joint NMDS ordination based on Bray–Curtis distance places the marine samples near the centre of the lacustrine point cloud, indicating that marine assemblage composition falls within the multivariate compositional space spanned by the lake samples (Fig. B4a).

390 We assessed the correspondence between marine and lacustrine records by correlating temporal abundance trends of individual plant taxa between each marine core and individual lake records, and summarizing these correlations as the median r value across lake records for each marine core (Fig. 5). Summary plots indicate that, overall, the temporal abundance trends of the top 30 taxa contributing most to Simpson diversity in marine sediments are positively correlated with those in the lakes (median $r_s \approx 0.25$). While some taxa show relatively strong positive correlations (e.g., *Papaver*, *Dryas*,
395 *Betula*, median $r_s > 0.5$), a substantial proportion of major taxa show weak or even opposing trends. Taxon temporal trend correlations varied widely across individual marine–lacustrine pairwise comparisons (spanning positive, near-zero, and negative values; Fig. B5), indicating strong lake-specific heterogeneity.

Across 2000-year time-bin comparisons, Salmon Lake and Ulu Lake consistently rank among the closest matches to both marine records in terms of inventory overlap (Fig. B6a) and Sørensen similarity (Fig. B6b), showing that the whole-core pattern identified in Fig. 7 is temporally robust.

Table 1: Comparative taxon inventory statistics between marine records and pooled lacustrine dataset based on bootstrap resampling (n=1000). Values represent median [95 % bootstrap confidence interval]. Shared taxa (%) is calculated as the percentage of taxa detected in the marine core that are also detected in the pooled lacustrine dataset.

Marine core	Interval	Marine core taxon inventory size	Pooled lake taxon inventory size	Shared taxa	Marine unique taxa	Shared taxa in marine core (%)	Sørensen similarity
Off-Kamchatka	0–20 ka	177 [166–186]	401 [386–412]	154 [145–163]	23 [18–28]	87.2 [84.6–89.7]	0.535 [0.509–0.558]
Bering Sea	6–26 ka	173 [156–191]	410 [397–421]	155 [140–170]	19 [13–25]	89.3 [85.9–92.6]	0.531 [0.492–0.569]

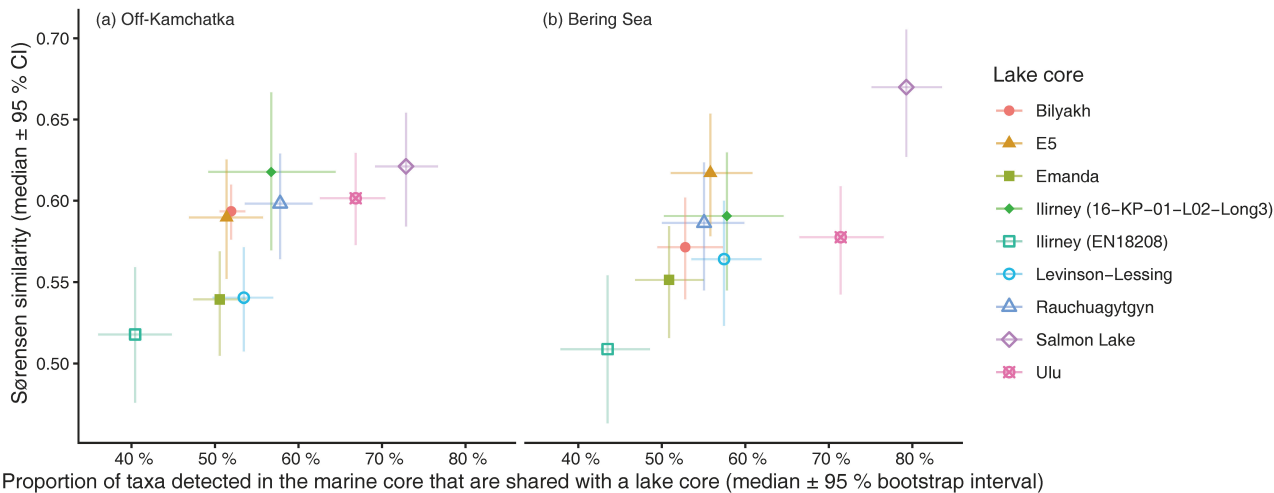


Figure 7: Marine-lacustrine overlap in shared taxa and Sørensen similarity at core-wide scale, showing overall taxonomic overlap between marine and lacustrine records. (a) off-Kamchatka core; (b) Bering Sea core. Points represent median values from bootstrap resampling, and error bars indicate 95 % confidence intervals, accounting for unequal sampling effort among cores. The x-axis shows the proportion of taxa in each marine core that are shared with individual lake cores, and the y-axis shows the corresponding Sørensen similarity between marine and lake cores.

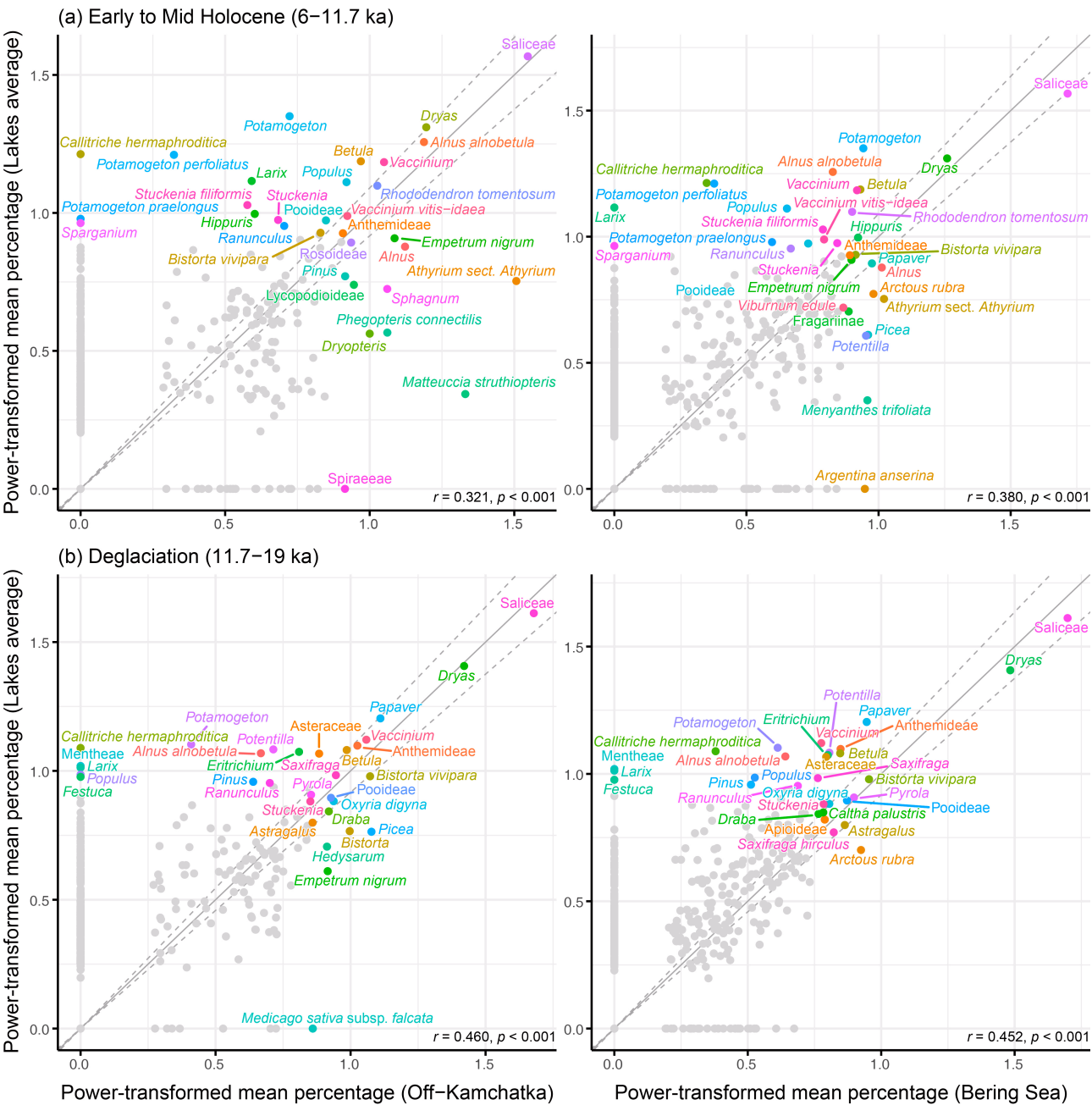


Figure 8: Comparison of period-averaged relative abundances between marine cores and lake records during the (a) Early to Mid Holocene (11.7–6 ka) and (b) deglacial period (11.7–19 ka). Each panel compares marine cores with lake records, with the Off-Kamchatka core shown on the left and the Bering Sea core on the right. Each point represents one taxon, plotted by its power-transformed mean percentage (exponent = 0.125) in the marine core (x-axis) and in the lake dataset (y-axis) for the corresponding period. The top 20 taxa (by period-mean relative abundance) are highlighted for each core, while all other taxa are shown in grey; since these lists differ between cores, the total number of highlighted taxa can exceed 20. Correlation statistics (Spearman's r and



420 *p*-value) are reported on the panel. The solid grey line indicates the 1:1 relationship (equal mean relative abundance in marine and lake records), and the dashed grey lines indicate twofold departures ($y = 2x$ and $y = x/2$). Time intervals without overlap between marine cores (i.e., the Mid to Late Holocene for the off-Kamchatka core and the LGM for the Bering Sea core) are shown in Supplementary Fig. B3.

3.3 Terrestrial source indicators in marine sedimentary archives

Candidate regional indicators with modern distributions restricted to either the Siberian or Alaskan side were identified among all taxa detected in the two marine sediment cores. Among the 328 taxa identified, 33 taxa were initially classified as
425 Siberia-side candidates and 18 as Alaska-side candidates based on GBIF-derived modern distributions (Table C1). After applying the cross-region lake comparison filter, we excluded 22 candidate Siberia-side indicator taxa and 9 candidate Alaska-side indicator taxa, as their corresponding ASVs were detected in lakes from the opposite region, indicating a lack of regional specificity (Table C1).

We furthermore excluded candidate indicators that could only be assigned to genera or tribes (e.g., *Aconitum*, *Cicuta*, *Rosa*,
430 *Vicia*, and *Inulinae*) when the corresponding higher taxa were broadly distributed across both Siberia and Alaska, because such assignments lacked sufficient regional specificity to serve as reliable indicators (Table C1). However, *Phacelia* and *Tsuga* were retained despite genus-level annotations because broader biogeographic patterns still supported regional exclusivity within the Siberia–Alaska framework (see Appendix C). Potential assignment ambiguity associated with short ASV lengths and low interspecific sequence divergence within certain taxonomic groups was conservatively considered
435 when evaluating indicator confidence (Appendix C). Following these filtering and conservative evaluation steps, three Siberia-side and seven Alaska-side taxa were retained as the most reliable regional indicators. Specifically, *Diplazium sibiricum*, *Spiraea salicifolia* and *Filipendula camtschatica* were identified as the most reliable Siberia-side indicators, whereas *Anticlea elegans*, *Astragalus nutzotinensis*, *Boykinia richardsonii*, *Eriogonum flavum*, *Phacelia*, *Shepherdia canadensis*, and *Tsuga* were identified as the most reliable Alaska-side indicators (Table C2).

440 These validated regional indicator taxa generally occurred at low abundances and were detected intermittently throughout the marine sediment records (Fig. 9), limiting direct comparisons of their abundances and temporal patterns between the two sites. Nevertheless, Alaska-side indicators were detected more frequently in the Bering Sea core than in the off-Kamchatka core, whereas the clearest Siberia-side signals (e.g., *Spiraea salicifolia* and *Filipendula camtschatica*) occurred only in the off-Kamchatka core. A notable exception was the Alaska-side indicator *Shepherdia canadensis*, which occurred
445 synchronously at ~7 ka BP in both marine cores.

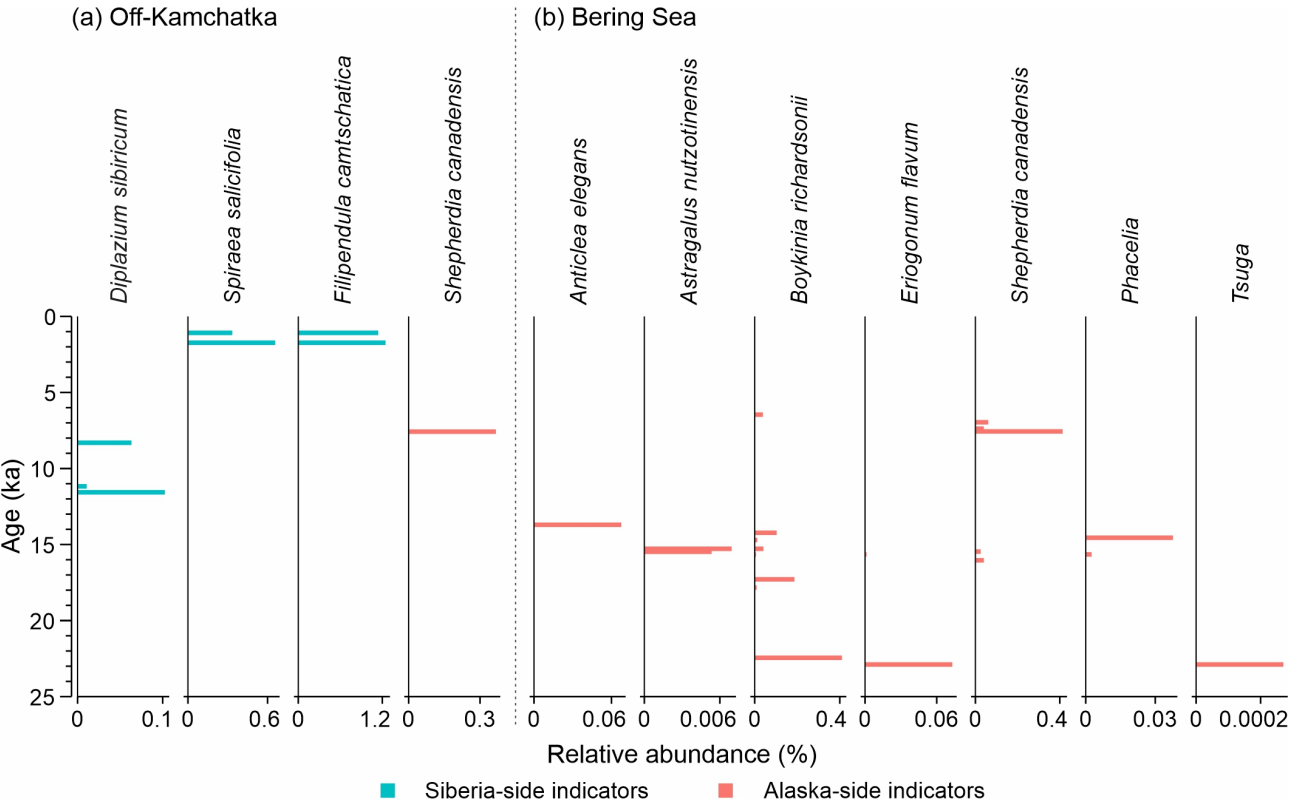


Figure 9: Relative abundances of validated regional indicator taxa in the (a) off-Kamchatka and (b) Bering Sea marine sediment cores. Blue bars indicate Siberia-side indicators and red bars indicate Alaska-side indicators. Taxa not detected in a given marine core are not shown.

450 **4 Discussion**

4.1 Terrestrial source signals of plant-derived organic matter and their temporal dynamics recorded in marine sedaDNA

We observe clear connections between plant DNA signals in marine sediments and vegetation patterns in adjacent Siberia and Alaska. This linkage is reflected by the 88–89 % taxa overlap between each marine core and the pooled lake dataset (Table 1), as well as by a moderate correlation between taxon abundances in the marine and lacustrine cores (Fig. 8). The placement of marine samples within the lacustrine Bray–Curtis cloud (Fig. B4a) further supports this connection. In contrast, taxonomic overlap with individual lake records is substantially lower than with the pooled lacustrine dataset (Fig. 7), indicating that the marine record reflects a broad regional taxon pool rather than the vegetation represented by any single lake record. This finding is consistent with a previous sedaDNA study assessing shotgun data showing strong correspondence between terrestrial plant DNA signals in marine sediments and pollen-derived vegetation patterns across



adjacent continental regions (Herzschuh et al., 2025b), and more generally with interpretations based on other terrestrial proxies in marine sediments (e.g., Cao et al., 2023; Meyer et al., 2019). A small fraction of taxa detected in marine sediments is absent from the lacustrine dataset (Table 1), likely reflecting the incomplete spatial coverage of the available lake records and the much larger effective catchment represented by the marine archive. This interpretation is further supported by
465 geographic gaps in the lacustrine dataset, such as the absence of lake records from the Kamchatka region, whereas the off-Kamchatka marine core integrates signals from this area. Minor contributions from taxonomic misassignments or database limitations cannot be excluded, but our 100 % similarity threshold for using taxonomic assignments kept this contribution likely very low.

The clearest source signal is the persistent dominance of Saliceae (willow tribe), pointing to strong coupling between
470 riparian vegetation and fluvial export pathways. Saliceae account on average for ~70 % of the Bering Sea assemblage and ~50 % of the off-Kamchatka assemblage (Fig. 4). A similar pattern has been reported from sedaDNA shotgun data in the North Pacific (Herzschuh et al., 2025b), indicating that it does not simply reflect a metabarcoding marker bias. Although Saliceae are widespread across Beringian shrub tundra, willow shrublands are particularly prominent components of riparian vegetation along river corridors and floodplains in arctic landscapes (Schickhoff et al., 2002). Their overrepresentation in
475 marine sedaDNA assemblages therefore likely reflects preferential coupling to fluvial transport pathways rather than regional vegetation abundance alone. Although the physical form of transported sedaDNA remains uncertain (Parducci et al., 2017), both plant tissues containing chloroplasts and extracellular chloroplast DNA are likely more readily transferred into aquatic systems from riparian vegetation growing in close proximity to rivers (Alsos et al., 2018). This interpretation is consistent with riparian zones disproportionately contributing terrestrial organic matter to aquatic systems by concentrating
480 biomass at the land–water interface and facilitating direct transfer of plant material into rivers (Regnier et al., 2022; Wohl et al., 2017). Our results therefore suggest that terrestrial plant inputs to marine sedimentary archives are not evenly derived from all vegetation types across Beringia, but are biased toward taxa most strongly connected to riverine transport pathways.

The two marine cores register different continental sectors of Beringia. Alaska-side indicators such as *Shepherdia canadensis*, *Phacelia* and *Tsuga* are more frequent and persistent in the Bering Sea core, whereas robust Northeast Asian
485 indicators such as *Spiraea salicifolia* and *Filipendula camtschatica* are restricted to the off-Kamchatka core (Fig. 9). Whole-core and time-slice comparisons further show that Salmon Lake on the Seward Peninsula provides the closest lacustrine analogue to the Bering Sea terrestrial plant assemblage (Fig. 7; Figs. B7a–c), suggesting terrestrial inputs from ecosystems similar to those represented in western Alaska. Although Salmon Lake is also the closest available analogue for the off-Kamchatka core, its similarity and taxonomic overlap are consistently lower than those observed for the Bering Sea core.
490 This contrast suggests a weaker influence of Alaska-like source regions on the off-Kamchatka assemblage, although lacustrine records from Kamchatka are currently not represented in the available sedaDNA dataset.



The Holocene off-Kamchatka assemblage closely matches independent evidence for local forest and wet understory development on Kamchatka. The increase in *Alnus*, *Betula* as well as mesic understory taxa like *Athyrium*, *Matteuccia* together with higher evenness (Figs. 3–4), is consistent with pollen records indicating Holocene expansion of birch
495 woodland, shrub alder, and fern-rich understories under relatively warm and moist conditions (Dirksen et al., 2013). This agreement indicates that the off-Kamchatka record primarily reflects vegetation changes on the Kamchatka peninsula during the Holocene, rather than a broadly homogenized regional signal.

By contrast, the Bering Sea core retained a more open, tundra-rich source signature for longer. Saliceae and *Dryas* remain dominant through most of the record, and arboreal expansion is weaker than in the marine sediment core off-Kamchatka (Fig.
500 4), implying that the source area continued to integrate a broad western/interior Alaskan landscape in which open shrub tundra and steppe-tundra legacies persisted alongside later woodland development. This is in line with records from eastern Beringia showing late-glacial *Dryas*-rich open vegetation followed by shrub expansion and only later, spatially heterogeneous tree spread (Bigelow et al., 2019; Clarke et al., 2024; Cocker et al., 2026). The result is a weaker Holocene increase in evenness, as reflected by lower Shannon and Simpson diversity, compared to off-Kamchatka (Fig. 3).

505 Within this spatial provenance framework, the validated indicator taxa are most informative as provenance constraints rather than dominant flux tracers. Their low abundances and intermittent occurrence (Fig. 9) mean that they cannot carry the whole source interpretation alone. However, when placed against the broader compositional structure of Figs. 4–7, they reinforce a coherent picture: the Bering Sea core mainly registers Alaska-linked source regions, while the off-Kamchatka core mainly registers Kamchatka/Northeast Asian source regions. The indicators matter because they provide direct taxonomic anchors
510 inside a signal otherwise dominated by widespread Beringian taxa such as Saliceae, *Dryas*, and *Betula*.

Temporal turnover is the primary organizing gradient of the marine sedaDNA data. In the NMDS, samples separate mainly by age rather than by site (Fig. 6), and the top 30 taxa show overall positive between-core temporal correlations (median $r \approx 0.5$), even though the cores diverge in the Holocene (Fig. 5). This pattern fits wider Beringian syntheses: LGM vegetation was dominated by open steppe-tundra or tundra across much of the region (Wang et al., 2021b), whereas the deglaciation
515 and Early Holocene brought shrub expansion, floristic reorganization, and the establishment of structurally novel woody biomes (Clarke et al., 2024; Edwards et al., 2005; Monteath et al., 2025). In our cores, that regional trajectory is expressed by declining herbs after the LGM, expansion of *Betula* and Ericaceae in the late deglaciation, and the strongest spatial divergence after 11.7 ka (Fig. 4).

Temporal patterns of terrestrial DNA inputs in the off-Kamchatka core are broadly consistent with deglacial climate changes.
520 Taxon richness from metabarcoding data and Embryophyta relative abundance from shotgun data (Herzschuh et al., 2025b) both increase during the Bølling–Allerød and Early Holocene (Fig. 10). This pattern is consistent with regional vegetation



expansion and increasing plant productivity in Kamchatka under warmer conditions (Dirksen et al., 2013; Pendea et al., 2017), although both proxies are influenced by vegetation production and transport efficiency. The mass accumulation rate (MAR) of high molecular weight *n*-alkanes further indicates an increased flux of terrestrial plant-derived organic matter to the marine sediments, suggesting increased terrestrial carbon mobilization during these intervals (Fig. 10; Meyer et al., 2019). Together, these observations suggest that terrestrial DNA inputs respond to large-scale environmental changes during the deglacial and Early Holocene.

Assemblages from the two cores are more similar during the glacial period compared with the Holocene (Fig. 6). This glacial convergence of terrestrial plant DNA assemblages is consistent with lacustrine records indicating higher ecological connectivity across Beringia during the glacial period (Herzschuh et al., 2025a). In contrast, Holocene samples show stronger separation between the two marine cores, indicating more distinct vegetation sources contributing to terrestrial organic matter burial. Together, these patterns suggest that changes in vegetation connectivity influenced the composition of terrestrial carbon inputs to the marine system, with more similar source contributions during the glacial and more distinct, regionally differentiated inputs in the Holocene.

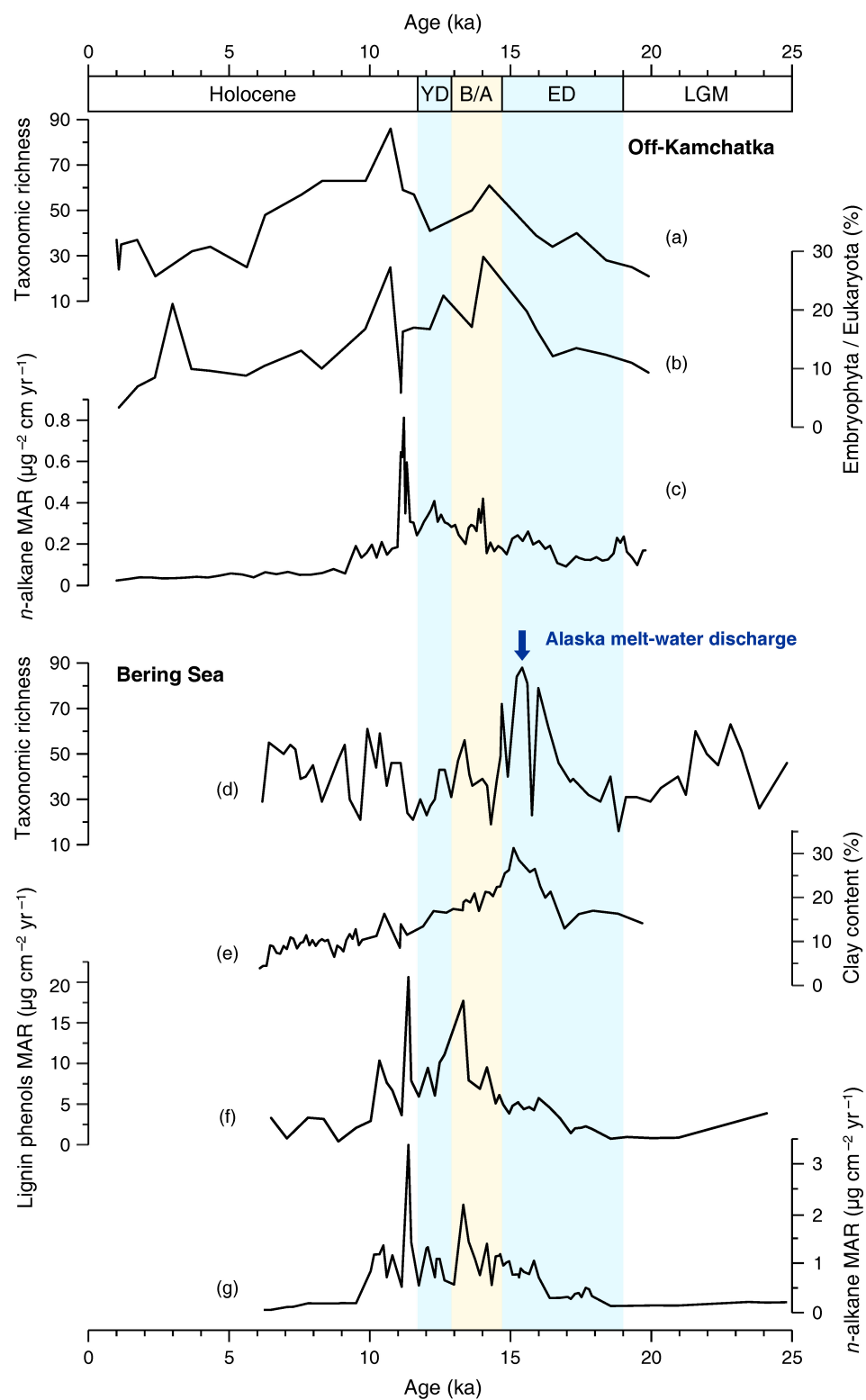




Figure 10: Multi-proxy comparison of plant DNA signals and terrestrial input in the off-Kamchatka core (a–c) and the Bering Sea core (d–g) since the Late Glacial. (a, d) Land-plant DNA taxonomic richness based on metabarcoding data in this study. (b) Relative abundance of Embryophyta reads (% of total Eukaryota) from shotgun sequencing in the off-Kamchatka core (Herzschuh et al., 2025b). (c, g) Mass accumulation rates (MAR) of long-chain n-alkanes (Meyer et al., 2019). (e) Clay content (%) in the Bering Sea core (Wang et al., 2021a). (f) MAR of lignin phenols (Bering Sea only; Cao et al., 2023). Shaded vertical bands indicate major climatic intervals: Younger Dryas (YD: 12.9–11.7 ka), Bølling–Allerød (B/A: 14.7–12.9 ka), and early deglacial (ED: 19–14.7 ka). The Holocene (< 11.7 ka) and Last Glacial Maximum (LGM: > 19 ka) are indicated above the panels. The blue arrow marks the timing of the glaciofluvial melt-water pulse in Alaska (Wang et al., 2021a).

4.2 Regional patterns of terrestrial organic matter burial related to land-ocean taphonomic dynamics

The two marine sites exhibit distinct diversity patterns across the deglacial and Early to Mid Holocene, suggesting that different controls influence terrestrial organic matter delivery. In the Bering Sea core, the taxon richness maximum at ~16–15 ka BP coincides with a peak in clay-rich terrigenous input during deglacial meltwater discharge (Wang et al., 2021a), as illustrated in Fig. 10. Previous work interpreted this clay pulse as reflecting enhanced terrigenous input from glacially influenced Alaskan drainage systems (Wang et al., 2021a). This strongest diversity response is therefore centered on an early deglacial pulse of terrigenous input, implying a strong role for meltwater-driven sediment transfer. In the Bering Sea, this effect may have been enhanced by lowered sea level during glacial lowstands, which displaced major paleo-river systems, including the high-discharge paleo-Yukon system, far across the exposed shelf (Knebel and Creager, 1973; Fig. 1) and increased the efficiency of terrigenous sediment delivery to the slope environments (Nagashima et al., 2012; VanLaningham et al., 2009). The association with clay-rich input is also consistent with studies showing preferential preservation of DNA and organic matter in clay-rich fine sediment fractions, likely related to their greater specific surface area and retention capacity relative to coarser sediments (Kanbar et al., 2020; Levy-Booth et al., 2007). In contrast, richness peaks later during warmer periods in the Early Holocene (~10 ka), and effective diversity increases progressively through the Holocene in the off-Kamchatka core (Fig. 3). This pattern better matches progressive warming, forest expansion, and local habitat diversification on Kamchatka than a single pulse of terrigenous input. The contrast of the two sites suggests that the Bering Sea archive is strongly influenced by deglacial sediment-routing changes, whereas the off-Kamchatka archive more directly reflects postglacial ecological reorganization of a nearby source landscape.

Marine sedaDNA records preserve signals of ecological turnover in source vegetation in addition to sedimentological transport signals. The strong early deglacial rise of *Dryas* in both marine cores (Fig. 4), particularly in the Bering Sea record where it begins prior to the maximum clay-rich terrigenous input (Fig. 10), suggests that vegetation turnover and peak sediment mobilization were not synchronous. Because *Dryas* is a classic pioneer of cold, disturbed, and freshly deglaciated substrates (Chapin et al., 1994; Lawrence et al., 1967), this sedaDNA signal reflects real plant expansion on fresh surfaces, not only remobilization of older deposits. The synchronous expansion of *Dryas* is also observed in Siberian and Alaskan lake cores, resulting in a strong positive correlation between marine and lacustrine temporal abundance trends (Fig. 5). This represents an important advantage of the DNA proxy: it may capture signals of ecological turnover in source vegetation that



570 are less directly resolved by bulk terrigenous biomarkers, although disentangling these from sedimentological remobilization remains challenging.

Shelf flooding reduced transport efficiency but did not terminate synchronous terrestrial signaling. After postglacial inundation and shoreline retreat, terrigenous biomarker accumulation in the Bering Sea declined (Cao et al., 2023; Meyer et al., 2019), accompanied by a decrease in terrestrial plant DNA richness relative to deglacial levels (Fig. 3). However, 575 vegetation composition inferred from the DNA record continues to track shifts in terrestrial ecosystems, with increases in *Betula*, *Alnus*, and ferns and declines in herbs (Fig. 4). Arctic-margin geochemical studies similarly show that river-derived terrigenous organic matter remains traceable across shelves and upper slopes after entering the ocean, although substantial attenuation and reworking occur during transport (Bröder et al., 2016; Goñi et al., 2013).

Long-distance transport between Alaska and Kamchatka appears to have been rare. Robust Alaska-side indicators are largely 580 absent from the off-Kamchatka record, and robust Kamchatka-side indicators are absent from the Bering Sea record (Fig. 9). The synchronous occurrence of *Shepherdia canadensis* around 7 ka in both cores is intriguing and may reflect occasional long-distance transport facilitated by circulation pathways linking the eastern and western Bering Sea margins, including the Bering Slope Current and East Kamchatka Current. However, based on the presently available evidence, this signal should be framed as a tentative, low-frequency exception rather than evidence for sustained inter-basin sedimentary exchange or 585 mixing.

The marine records are filtered archives, not neutral mirrors of regional vegetation. Even though most taxa detected in the marine cores are recovered in the pooled lake inventory, the composition is dominated by a limited set of taxa (Fig. 8). Saliceae, *Alnus*, and ferns are relatively enriched in marine sediments, while *Larix* and several herbaceous taxa are depleted (Fig. 8). This pattern is consistent with hydrological transport processes preferentially representing vegetation growing in 590 close proximity to aquatic systems, while progressively filtering taxa from hydrologically disconnected environments (Alsos et al., 2018; Ataman et al., 2025). Lake-enriched aquatic macrophytes such as *Potamogeton* and *Myriophyllum* (Fig. 8) primarily reflect strong in-lake production and extremely short transport distances, which is why they behave as archive-specific taxa rather than as reliable tracers of regional source vegetation. In contrast, the occurrence of the seagrass *Zostera* in marine sediments reflects production in shallow coastal waters and represent a marine-specific component absent from the 595 lake records. These taxon-specific abundance asymmetries are therefore mechanistically informative, with part of this filtering likely reflecting habitat differences and hydrological transport biases.

Additional filtering arises from taphonomic and preservational processes. DNA preservation in sediments is influenced by sediment composition and depositional conditions (Jia et al., 2022; Kanbar et al., 2020; Sand et al., 2024), as well as post-depositional degradation processes, including degradation mediated by microbial activity (Strickler et al., 2015; Torti et al.,



2015). Consequently, sedaDNA signals may be amplified or attenuated independently of source abundance, meaning that abundance contrasts between marine and lake sedaDNA metabarcoding records cannot be interpreted as direct measures of differences in source vegetation composition or relative carbon contribution.

4.3 Metabarcoding as a proxy to track the composition of terrestrial plant-derived organic matter

Metabarcoding provides high taxonomic resolution for tracing terrestrial organic matter from land to ocean. We obtained diverse plant DNA metabarcoding data from high-latitude marine sediment cores using chloroplast *trnL* g–h primers, which are among the most widely applied markers for plant DNA (Taberlet et al., 2007). Our metabarcoding data provide taxonomically detailed insights into tracing terrestrial organic matter from terrestrial sources to marine sinks, overcoming limitations inherent in currently-used biomarker, isotopic, and palynological approaches. In our metabarcoding data, 53 % of taxa were identified at the species level (Fig. 2a). Taxa resolved to these finer taxonomic ranks typically exhibit narrower geographic distributions, thereby providing clearer and more specific source signals of organic carbon. However, sedaDNA signals were not always fully coupled with other terrestrial biomarkers (Fig. 10; Cao et al., 2023; Meyer et al., 2019), suggesting that different proxies may capture partially distinct aspects of terrestrial organic matter dynamics.

Metabarcoding improves detection efficiency in degraded samples by targeting short loci. Compared with shotgun metagenomic approaches, metabarcoding often yields higher detection rates and more confident taxonomic assignments for the focal plant group in sedaDNA studies, albeit with known PCR- and primer-related biases (Strandberg et al., 2026). From a practical standpoint, metabarcoding concentrates sequencing effort on targeted plant markers, whereas shotgun metagenomics often requires substantially deeper sequencing to recover comparable terrestrial plant signals (Heintzman et al., 2023).

Direct comparison with lake records demonstrates consistent source–sink linkages. Tracing terrestrial organic carbon in marine sediments from source to sink requires establishing a robust link between marine records and their potential source vegetation on land. Here, we directly compare plant DNA metabarcoding data from marine sediments (off-Kamchatka and the Bering Sea) with lake records from Siberia and Alaska, all based on the *SibAla_2023* reference database (Courtin et al., 2025; Herzsuh et al., 2025a). We demonstrated an overall compositional consistency between marine and lacustrine plant DNA archives, as supported by the subset relationship and positive temporal trends of major taxa. This finding is consistent with previous biomarker research (e.g., Cao et al., 2023; Meyer et al., 2019), together indicating substantial delivery of continental material to the subarctic North Pacific. Furthermore, our synchronized comparison of sedaDNA archives provides an improved understanding of the spatio-temporal patterns of correspondence between terrestrial sources and marine sinks, reflecting both geographical structuring and temporal variation across glacial–postglacial transitions.



Interpretation remains limited by reference database gaps and taphonomic uncertainty. While our metabarcoding data offer
valuable insights into terrestrial carbon transfer from source to sink, their interpretation remains limited by several
methodological uncertainties, including the incompleteness of reference DNA databases and the instability of DNA
taphonomic processes. The *SibAla_2023* database we used in this study represents approximately 70 % species coverage and
89.4 % genus coverage of the GBIF database (Courtin et al., 2025). This incompleteness of the reference database may lead
to both false negatives—i.e., DNA sequences that cannot be assigned to any taxon—and false positives—i.e., DNA
sequences that are assigned to only one of several taxa sharing the same sequence (Heintzman et al., 2023). Our indicator
analysis further suggests that indicators of Siberia or Alaska, based on modern vegetation distribution, are not always
restricted to lake sedaDNA records within their expected regions, likely reflecting false-positive assignments arising from
identical sequences shared among multiple species distributed in different areas. Furthermore, transport- and degradation-
related biases may selectively reduce the preservation and detectability of certain taxa during source-to-sink transfer. As our
results show, at limited sequencing depth, relatively rare indicator species are often masked by the signals of dominant taxa
and usually cannot appear continuously, which limits our ability to analyse the source of organic matter more quantitatively.
Nevertheless, with the ongoing expansion and curation of reference databases, the refinement of bioinformatic pipelines
(Capo et al., 2021), and increasing efforts to elucidate the taphonomic processes that terrestrial plant DNA undergoes from
source to sink (e.g., Giguët-Covex et al., 2019; Jia et al., 2022), the potential and reliability of metabarcoding as a proxy for
organic carbon sources in future studies are expected to improve substantially.

5 Conclusion

Our study provides a high-resolution terrestrial plant sedaDNA record from two marine sediment cores in the subarctic
North Pacific using chloroplast *trnL* g–h metabarcoding. The dataset achieved exceptionally high taxonomic resolution for
marine sedaDNA records, including extensive species-level identifications. Comparison with Siberian and Alaskan lake
sedaDNA records showed that most terrestrial plant taxa recovered from the marine cores reflected regional vegetation
composition. Major taxa exhibited coherent temporal trends between marine and lacustrine records. Compositional
relationships between marine and lacustrine records, together with regionally informative indicator taxa, provided taxonomic
evidence for terrestrial organic matter sourcing from northeastern Asia and Alaska.

Temporal patterns differed markedly between the off-Kamchatka and Bering Sea records across the glacial–deglacial–
interglacial transition, indicating contrasting source-to-sink dynamics between the two regions. The two records preserved
distinct regional vegetation histories, while diversity dynamics reflected different controlling factors: the Bering Sea record
was more strongly influenced by deglacial terrigenous sediment delivery, whereas the off-Kamchatka record more closely
tracked postglacial warming and vegetation development. Marine sedaDNA records continued to preserve regional



660 vegetation signals after postglacial shelf flooding, indicating continued land-to-ocean signal transfer. However, regional indicator taxa remained largely basin-specific, suggesting limited long-distance transport of terrestrial plant DNA across basins. Systematic abundance differences between marine and lacustrine records further indicate strong taphonomic filtering during transport and deposition.

665 These findings highlight the potential of targeted sedaDNA metabarcoding as a high-resolution tool for tracing terrestrial organic matter in marine sediment archives over millennial timescales. Future expansion of regional DNA reference libraries and improved understanding of marine sedaDNA taphonomy will further strengthen the application of sedaDNA for investigating terrestrial organic matter transport and source-to-sink dynamics in high-latitude ocean systems.

Appendix A

Table A1: Summary of sample numbers and sequencing depths for the two marine cores analyzed in this study

Location	Core ID	Number of samples	Reads per sample (median)	Reads per sample (range)
Off-Kamchatka	SO201-2-12KL	24	268 591	120 433–796 560
Bering Sea	SO202-18-3/6	65	639 161	34 515–2 324 405

670 **Table A2: Summary of previously published lake sediment datasets used in the marine–terrestrial comparison**

Lake	Core ID	Latitude	Longitude	Collection year	Length (cm)	Number of samples	Age range (ka BP)	Age model references	sedaDNA studies references
Bilyakh	PG1755	65.28° N	126.78° E	2005	936	57	50	Müller et al., 2010	Courtin et al., 2025
Emanda	Co1412	65.28° N	135.75° E	2017	610	45	57	Baumer et al., 2021	Courtin et al., 2025
Iirney	EN18208	67.35° N	168.32° E	2018	1055	82	52	Vyse et al., 2020	Courtin et al., 2025
Iirney	16-KP-01-L02	67.35° N	168.32° E	2016	235	58	28	Andreev et al., 2021	Huang et al., 2021
Levinson-Lessing	Co1401	74.45° N	98.65° E	2017	4600	88	62	Lenz et al., 2022	Courtin et al., 2025
Rauchuag-ytgyn	EN18218	67.78° N	168.73° E	2016	653	66	29	Vyse et al., 2021	Courtin et al., 2025
Ulu	EN21103	63.34° N	141.05° E	2021	1100	72	43	Jia et al., 2024	Jia et al., 2024
E5	E5	68.63° N	149.45° W	2014	500	61	35	Vachula et al., 2019	Courtin et al., 2025



Salmon	EN22502	64.90° N	165.00° W	2022	1700	56	30	Kaufman, 2025	Herzschuh et al., 2025a
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Appendix B

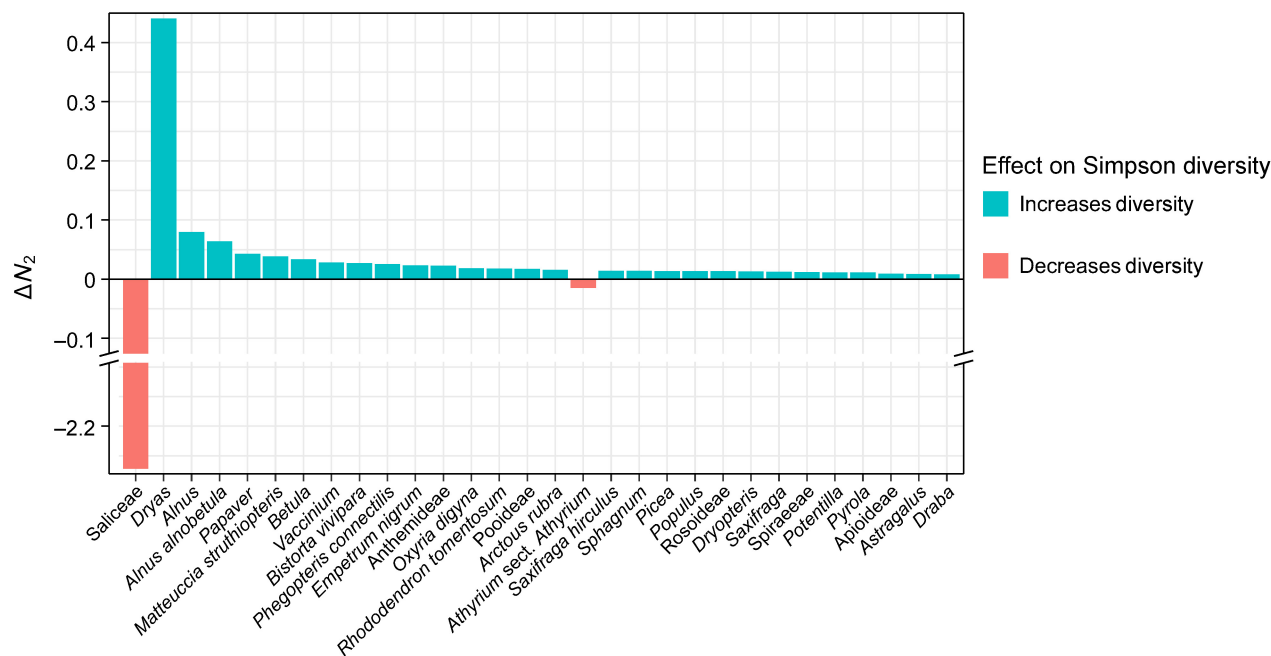


Figure B1: Jackknife decomposition on Simpson diversity (Hill N_2). ΔN_2 represents the change in Simpson diversity (Hill N_2) after removing each taxon. Positive values indicate taxa that increase overall diversity, whereas negative values indicate taxa whose removal increases diversity. Taxa are ranked by effect size.

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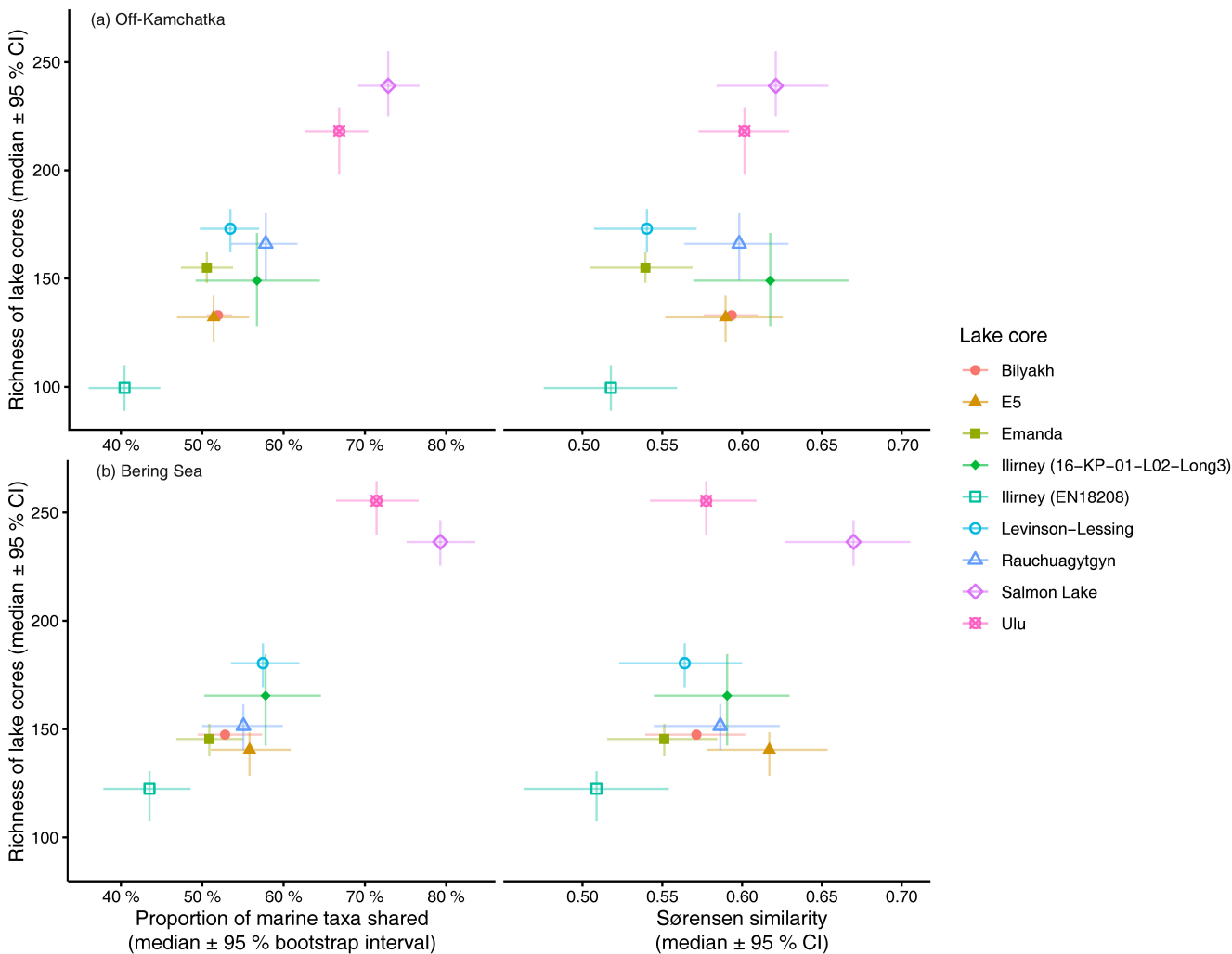


Figure B2: Relationship between lacustrine taxon inventory size and taxonomic overlap with marine sediment cores at core-wide scale. (a) off-Kamchatka core; (b) Bering Sea core. For each marine core, the left panel shows the proportion of marine taxa shared with individual lake cores and the right panel shows the corresponding Sørensen similarity. Points represent median values from bootstrap resampling, and error bars indicate 95 % confidence intervals, accounting for unequal sampling effort among cores.

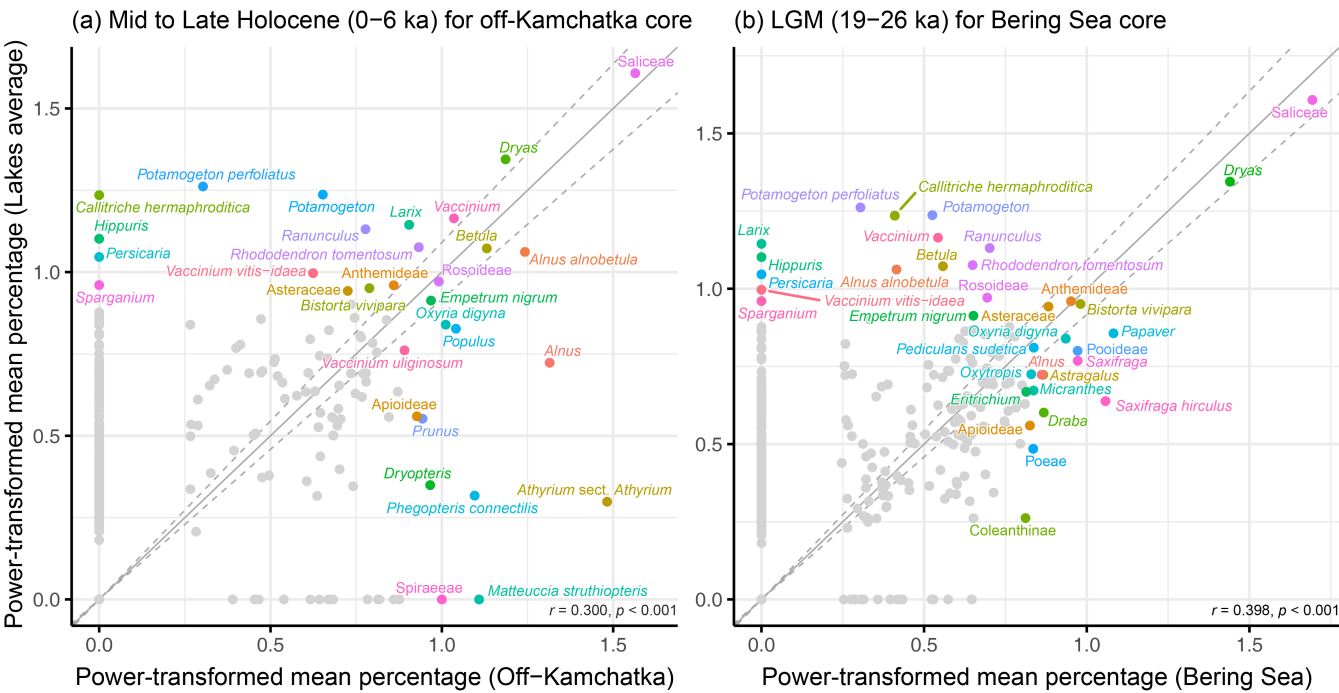
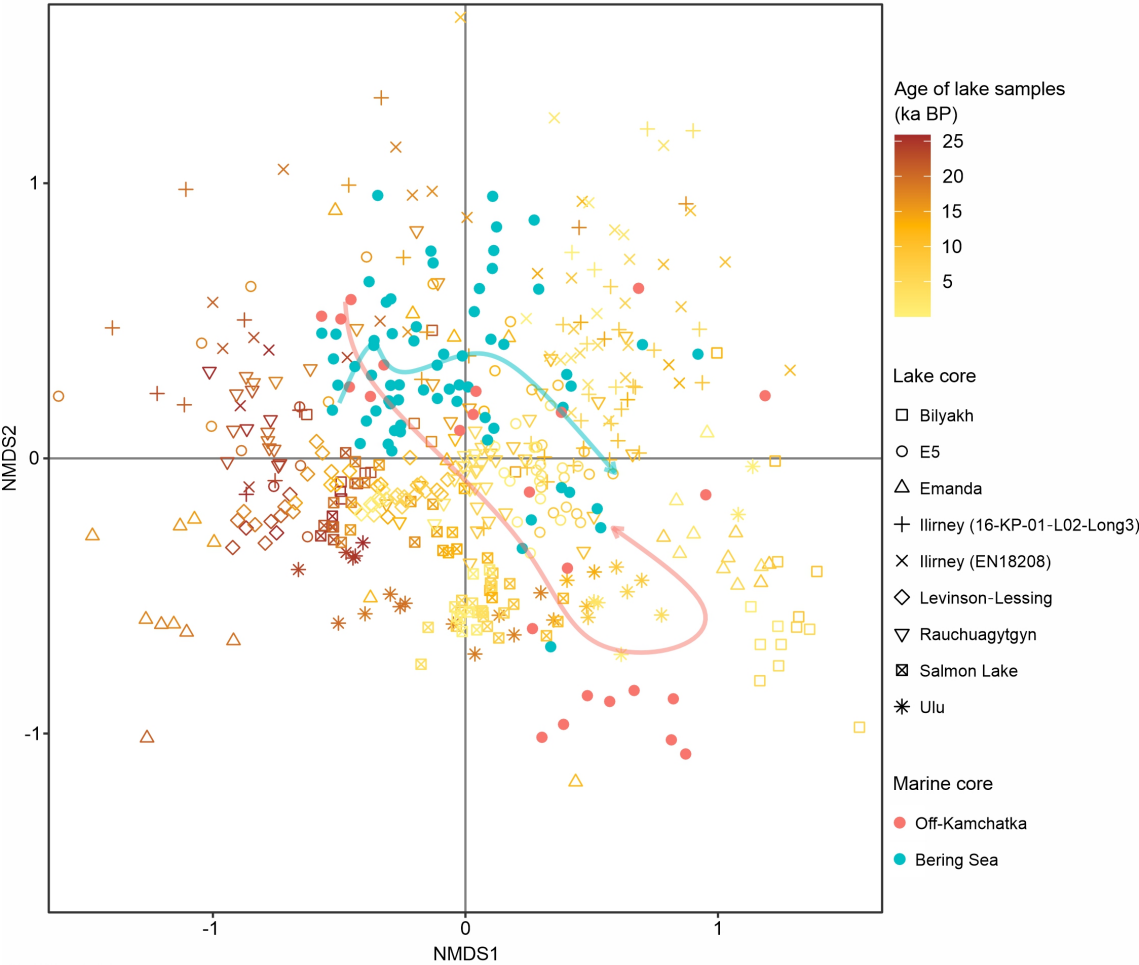


Figure B3: Comparison of period-averaged relative abundances between marine cores and lake records during (a) Mid to Late Holocene (0–6 ka) in the Off-Kamchatka core and (b) LGM (19–26 ka) in the Bering Sea core. Each point represents one taxon, plotted by its power-transformed mean percentage (exponent = 0.125) in the marine core (x-axis) and in the lake dataset (y-axis) for the corresponding period. The top 20 taxa (by period-mean relative abundance) were highlighted for each core, while all other taxa are shown in grey; since these lists differ between cores, the total number of highlighted taxa can exceed 20. Correlation statistics (Spearman's r , p) are reported on the panel. The solid grey line indicates the 1:1 relationship (equal mean relative abundance in marine and lake records), and the dashed grey lines indicate twofold departures ($y = 2x$ and $y = x/2$).



(a) NMDS ordination



(b) SIMPER

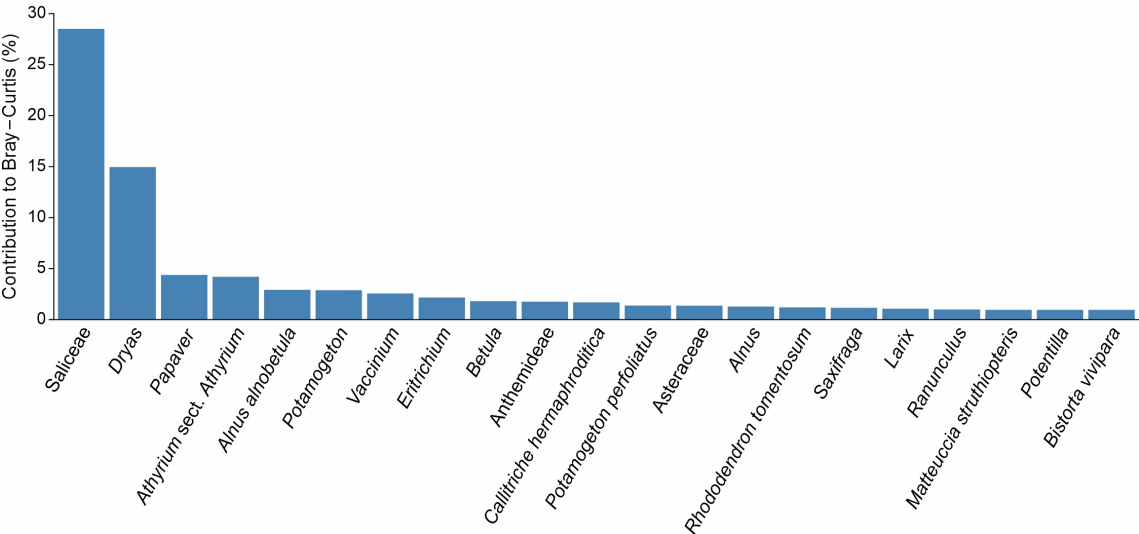


Figure B4: NMDS ordination of land-plant sedaDNA assemblages from marine and lacustrine samples based on Bray–Curtis dissimilarity, and species contributions to marine–lacustrine dissimilarity (SIMPER). (a) NMDS ordination. Open symbols represent samples from nine lake sediment cores, with colours indicating sample age (ka BP). Filled circles represent marine sediment samples, coloured by core. Arrows show GAM-smoothed temporal trajectories, indicating community turnover from older (tail) to younger (head) marine samples. For visual clarity, the plotting window is limited to NMDS1 and NMDS2 values between -1.5 and 1.5 ; a small number of lake-sample outliers fall outside the displayed range. Stress = 0.199 . Inclusion of marine samples had negligible effects on lake-sample positions in the NMDS space (Procrustes $r = 0.995$). (b) Mean contributions of individual taxa to Bray–Curtis dissimilarity between marine and lacustrine assemblages, calculated using SIMPER analysis. The dissimilarity was primarily driven by Saliceae and *Dryas*, whereas all remaining taxa contributed individually less than 5 %.

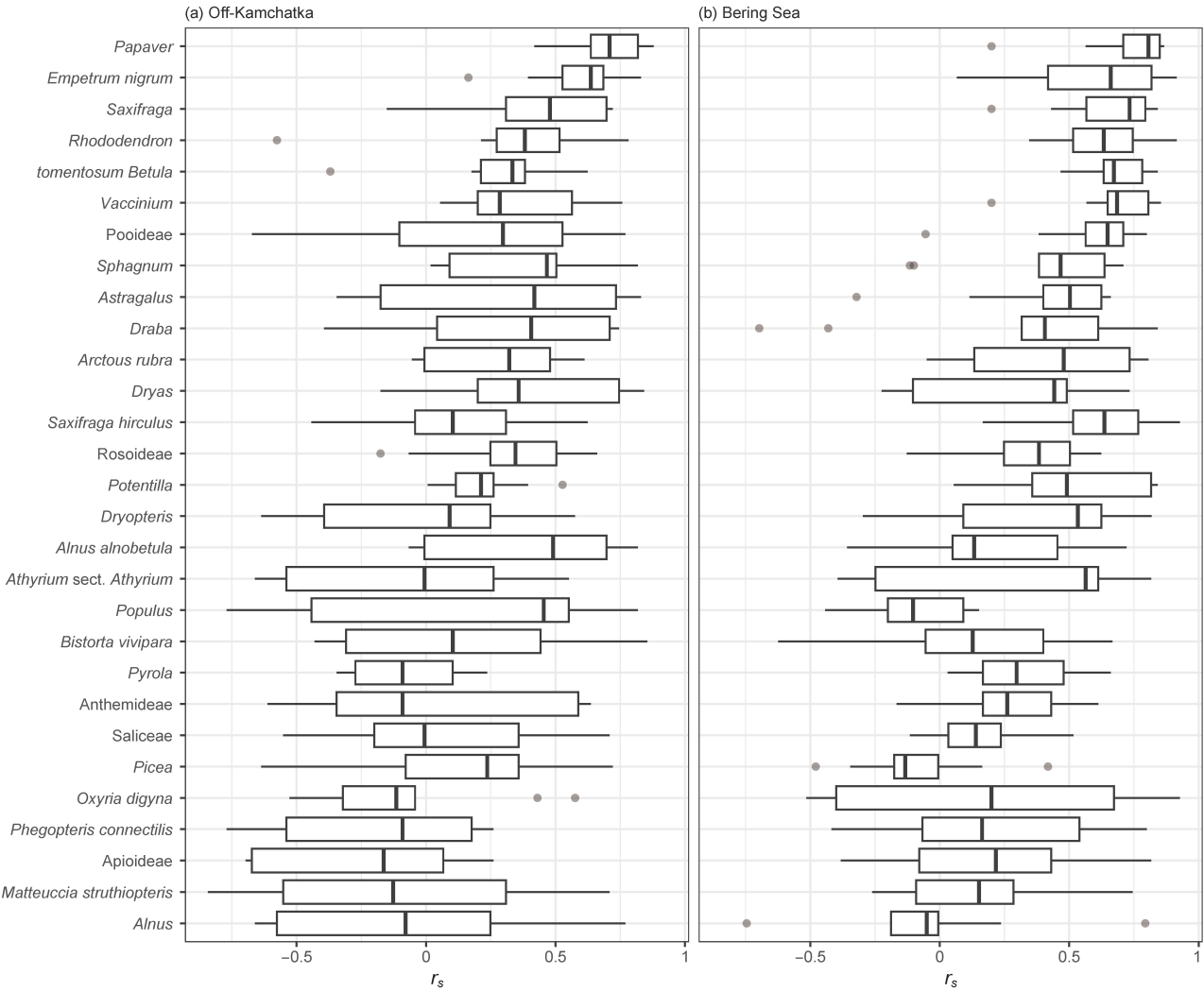
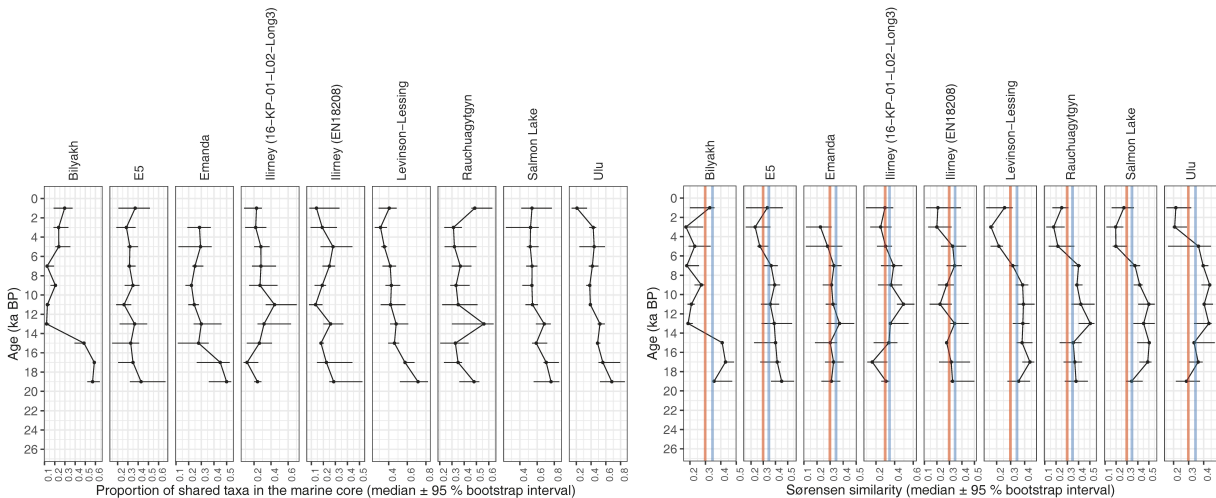


Figure B5: Distribution of taxon-specific trend correlations between marine and lacustrine records. (a) off-Kamchatka core; (b) Bering Sea core. Boxplots show the distribution of Spearman's correlations (r_s) between CLR-transformed relative abundance trends in marine and lacustrine records for the top 30 taxa contributing most to Simpson diversity. For each taxon, the boxplots summarize correlations across all marine–lake comparisons, with centre lines indicating medians, boxes representing interquartile

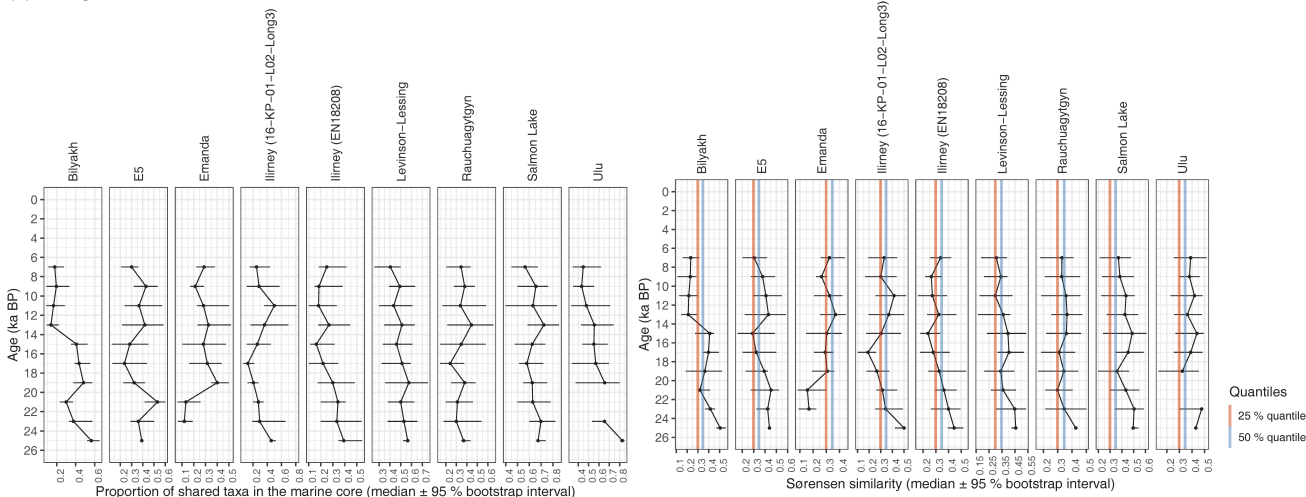


705 ranges, whiskers extending to $1.5 \times \text{IQR}$, and points denoting outliers. Correlations were calculated using 2000-year sliding windows.

(a) Off-Kamchatka



(b) Bering Sea



710 **Figure B6: Temporal variation in shared taxa proportion and Sørensen similarity between marine and lacustrine sedaDNA assemblages. (a) off-Kamchatka core; (b) Bering Sea core.** The left column shows the proportion of taxa detected in the marine core that are shared with each lake core, and the right column shows Sørensen similarity. Points represent median values from 1000 bootstrap resamples after standardizing sample numbers within each time bin, and horizontal bars indicate 95 % bootstrap intervals. The blue and red lines indicate the 50% and 25% quantiles of the reference distribution of Bray-Curtis distances among all lakes, respectively.



Appendix C

715 C1 Evaluation of candidate indicator taxa based on GBIF occurrences, lake sedaDNA data, and manual assessment

To identify candidate regional indicator taxa, all ASVs detected in the marine sediment cores were examined individually. For each marine ASV, the complete list of species associated with that ASV in the *SibAla_2023* reference database (Courtin et al., 2025) was extracted. Species names were matched against the GBIF backbone taxonomy using the GBIF species-matching API to obtain taxonomic identifiers. Returned matches were manually inspected and corrected where necessary.

720 Geographic distribution evaluations were performed at the ASV level. Because a single OBITools taxonomic assignment could correspond to one or multiple ASVs, each ASV was evaluated independently based on the geographic distributions of its associated species. Results were subsequently linked back to the taxonomic assignments reported by OBITools and summarized at the taxonomic assignment level for presentation and interpretation. Candidate indicator taxa were queried against the Siberian and Alaskan lake sedaDNA datasets and classified as detected in Siberia only, Alaska only, both regions, or neither (Table C1). Additional evidence considered during manual evaluation included ASV length and taxonomic resolution (Table C1).

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Blitum asiaticum, *Knorringia sibirica*, and *Polytrichum pallidisetum* were classified as ambiguous because their assignments were based on exceptionally short ASVs (17–32 bp, Table C1). Given the limited species-level resolution associated with very short *trnL* sequences (Taberlet et al., 2007), confidence in species-level assignment was considered insufficient for

730 robust provenance inference.

The 56 bp ASV annotated as *Salix triandra* differed by only a single nucleotide from a broadly distributed Saliceae ASV. This minor sequence difference was considered insufficient to support a robust species-level provenance assignment.

Modern distributions may not fully reflect the late Pleistocene range of *Ephedra*. The genus is characteristic of arid and semi-arid environments (González-Juárez et al., 2020), whereas glacial Beringia is generally reconstructed as substantially drier than at present (Elias and Crocker, 2008). However, no *Ephedra* DNA was detected in either the Siberian or Alaskan lake sedaDNA datasets used in this study, and therefore its value as a regional provenance indicator remains uncertain.

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Although *Phacelia* occurs in modern Asia as an introduced taxon, the genus is native to North America and therefore retains strong biogeographic relevance within the Siberia–Alaska framework (Plants of the World Online, 2026). Similarly, although *Tsuga* exhibits a disjunct distribution between eastern Asia and North America, it is naturally absent from Siberia (Plants of the World Online, 2026). Consequently, both taxa were retained as genus-level exceptions because their broader

740 biogeographic patterns remain informative for provenance inference within the study region.



Table C1: Assessment and classification of candidate Siberia–Alaska indicator taxa based on modern distributions, lake sedaDNA occurrence, and manual assessment.

Scientific Name	Taxonomic level	ASV length (bp)	Modern distribution	Lake occurrence	Assessment	Note
<i>Aconitum</i>	Genus	62	Siberia	Siberia only	Excluded	Genus-level assignment lacking regional specificity
<i>Anemone amurensis</i>	Species	50	Siberia	Alaska only	Excluded	Contradicted by lake occurrence data
<i>Anemone sylvestris</i>	Species	68	Siberia	Both regions	Excluded	Contradicted by lake occurrence data
<i>Artemisia austriaca</i>	Species	53	Siberia	Both regions	Excluded	Contradicted by lake occurrence data
<i>Artemisia gmelinii</i>	Species	51	Siberia	Both regions	Excluded	Contradicted by lake occurrence data
<i>Blitum asiaticum</i>	Species	32	Siberia	Siberia only	Ambiguous	Short sequence, assignment uncertain
<i>Ceratophyllum submersum</i>	Species	44	Siberia	Alaska only	Excluded	Contradicted by lake occurrence data
<i>Diplazium sibiricum</i>	Species	39	Siberia	Siberia only	Retained	
<i>Ephedra</i>	Genus	35	Siberia	Not detected	Ambiguous	Modern distribution may not reflect glacial distribution
<i>Filipendula camtschatica</i>	Species	56	Siberia	Not detected	Retained	
Inulinae	Tribe	50	Siberia	Both regions	Excluded	Contradicted by lake occurrence data
<i>Knorringia sibirica</i>	Species	32	Siberia	Not detected	Ambiguous	Short sequence, assignment uncertain
<i>Papaver paucistaminum</i>	Species	54	Siberia	Both regions	Excluded	Contradicted by lake occurrence data
<i>Pedicularis elata</i>	Species	44	Siberia	Both regions	Excluded	Contradicted by lake occurrence data
<i>Pedicularis palustris</i>	Species	45	Siberia	Both regions	Excluded	Contradicted by lake occurrence data
<i>Pedicularis palustris</i>	Species	46	Siberia	Both regions	Excluded	Contradicted by lake occurrence data
<i>Pedicularis sceptrum-carolinum</i>	Species	45	Siberia	Both regions	Excluded	Contradicted by lake occurrence data
<i>Pedicularis tristis</i>	Species	47	Siberia	Both regions	Excluded	Contradicted by lake occurrence data
<i>Pinus</i>	Genus	45	Siberia	Both regions	Excluded	Contradicted by lake occurrence data
<i>Polytrichum pallidisetum</i>	Species	17	Siberia	Not detected	Ambiguous	Short sequence, assignment uncertain
<i>Potamogeton crispus</i>	Species	85	Siberia	Alaska only	Excluded	Contradicted by lake occurrence data
<i>Pulsatilla dahurica</i>	Species	51	Siberia	Both regions	Excluded	Contradicted by lake occurrence data
<i>Ranunculus cassubicus</i>	Species	52	Siberia	Both regions	Excluded	Contradicted by lake occurrence data
<i>Rhododendron aureum</i>	Species	46	Siberia	Alaska only	Excluded	Contradicted by lake occurrence data



<i>Rhododendron redowskianum</i>	Species	47	Siberia	Both regions	Excluded	Contradicted by lake occurrence data
<i>Rosa</i>	Genus	51	Siberia	Siberia only	Excluded	Genus-level assignment lacking regional specificity
<i>Salix triandra</i>	Species	56	Siberia	Siberia only	Ambiguous	Closely related to a broadly distributed Saliceae ASV
<i>Spiraea salicifolia</i>	Species	60	Siberia	Siberia only	Retained	
<i>Thelypteris palustris</i>	Species	39	Siberia	Both regions	Excluded	Contradicted by lake occurrence data
<i>Ulmus</i>	Genus	46	Siberia	Both regions	Excluded	Contradicted by lake occurrence data
<i>Viburnum lantana</i>	Species	42	Siberia	Alaska only	Excluded	Contradicted by lake occurrence data
<i>Vicia</i>	Genus	55	Siberia	Siberia only	Excluded	Genus-level assignment lacking regional specificity
<i>Anticlea elegans</i>	Species	64	Alaska	Alaska only	Retained	
<i>Astragalus nutzotinensis</i>	Species	49	Alaska	Alaska only	Retained	
<i>Boykinia richardsonii</i>	Species	55	Alaska	Alaska only	Retained	
<i>Carex filifolia</i>	Species	81	Alaska	Both regions	Excluded	Contradicted by lake occurrence data
<i>Cicuta</i>	Genus	45	Alaska	Not detected	Excluded	Genus-level assignment lacking regional specificity
<i>Eriogonum flavum</i>	Species	41	Alaska	Not detected	Retained	
<i>Micranthes razshivinii</i>	Species	27	Alaska	Both regions	Excluded	Contradicted by lake occurrence data
<i>Micranthes reflexa</i>	Species	25	Alaska	Both regions	Excluded	Contradicted by lake occurrence data
<i>Phacelia</i>	Genus	45	Alaska	Alaska only	Retained	Native to North America
<i>Phlox hoodii</i>	Species	68	Alaska	Both regions	Excluded	Contradicted by lake occurrence data
<i>Phlox hoodii</i>	Species	64	Alaska	Both regions	Excluded	Contradicted by lake occurrence data
<i>Phlox hoodii</i>	Species	70	Alaska	Both regions	Excluded	Contradicted by lake occurrence data
<i>Ranunculus abortivus</i>	Species	50	Alaska	Both regions	Excluded	Contradicted by lake occurrence data
<i>Saxifraga tricuspidata</i>	Species	50	Alaska	Both regions	Excluded	Contradicted by lake occurrence data
<i>Shepherdia canadensis</i>	Species	52	Alaska	Alaska only	Retained	
<i>Stellaria borealis</i>	Species	53	Alaska	Both regions	Excluded	Contradicted by lake occurrence data
<i>Tsuga</i>	Genus	45	Alaska	Alaska only	Retained	East Asian–North American disjunct distribution



C2 Characteristics of retained indicator taxa

The retained Siberia-side indicators include *Diplazium sibiricum* (fern), *Filipendula camtschatica* (tall forb) and *Spiraea salicifolia* (shrub). The retained Alaska-side indicators include *Anticlea elegans* (herb), *Astragalus nutzotinensis* (herb), *Boykinia richardsonii* (herb), *Eriogonum flavum* (herb), *Shepherdia canadensis* (shrub), *Phacelia* (herb), and *Tsuga* (coniferous tree). Additional information on taxonomy, growth form, habitat, and modern distribution is provided in Table C2.

Table C2: Ecological and biogeographic characteristics of retained Siberia–Alaska indicator taxa

Scientific Name	Common Name	Family	Life form	Modern distribution region	Habitat
<i>Diplazium sibiricum</i>	Mole-ladder	Athyriaceae	Fern	Native to: N. & NE. Europe to N. & NE Asia.	Mixed broad-leaved coniferous forests and broad-leaved forests (Flora of China, 2026)
<i>Filipendula camtschatica</i>	Giant meadowsweet	Rosaceae	Tall perennial forb	Native to: Japan, Kamchatka, Korea. Introduced into: W. & N. Europe, Czechia-Slovakia.	Stream valleys and river floodplains, wet mountain slopes, forest edges; on nutrient-rich soils (Korznikov et al., 2024).
<i>Spiraea salicifolia</i>	Bridewort, willow-leaved spirea	Rosaceae	Deciduous shrub	Native to: E. Central Europe, N. & Central Asia, and NE. Asia. Introduced into: W. & N. Europe, NW. & Central European Russia, and N. America.	Moist and well-aerated environments, including river valleys, humid depressions associated with river networks, and other habitats with flowing moisture (Poliakova, 2022).
<i>Anticlea elegans</i>	Mountain deathcamas	Melanthiaceae	Perennial herb	Native to: Subarctic America to Mexico.	Moist grasslands, river and lake shores, bogs in coniferous forests (Flora of North America, 2026).
<i>Astragalus nutzotinensis</i>	Nutzotin milkvetch	Fabaceae	Perennial herb	Native to: Alaska to W. Canada.	Gravelly glacial outwash and braided glacial stream habitats in Alaska and the Yukon Territory (Viereck, 1966).
<i>Boykinia richardsonii</i>	Bear flower	Saxifragaceae	Perennial herb	Native to: Subarctic America.	Stream-side gullies, snowbed grasslands and meadows, often in open habitats or partial shade of <i>Salix</i> thickets (Flora of North America, 2026).
<i>Eriogonum flavum</i>	Yukon Buckwheat	Polygonaceae	Perennial herb	Native to: Alaska to Central U.S.A.	Dry, talus slopes and overdrained rocky soils in open sparse vegetation of subarctic interior Alaska (Flora of North America, 2026).
<i>Shepherdia canadensis</i>	Canada buffaloberry	Elaeagnaceae	Deciduous shrub	Native to: Subarctic America to W., Central & N. U.S.A.	Woods, open rocky slopes, sandy-gravelly shores, granitic sands (Flora of North America, 2026).
<i>Phacelia</i>	Scorpionweed	Hydrophyllaceae	Perennial herb	Native to: N. America to Guatemala, Peru to S. South America. Introduced into: Europe, N. Africa, and N. Asia.	Inland dry rubble slopes in subarctic Alaska (Lloyd et al., 1994).



<i>Tsuga</i>	Hemlock	Pinaceae	Evergreen coniferous tree	Native to: Himalaya to Temp. E. Asia, Alaska to Canada and U.S.A. Introduced into: Europe.	Moist to wet temperate and boreal forests, commonly in cool maritime or montane environments (Flora of North America, 2026).
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Code and data availability

755 The raw DNA sequencing data of the plant metabarcoding approach for the marine cores (SO201-2-12KL and SO202-18-3/6)
are deposited in the European Nucleotide Archive (ENA), with the accession number to be provided upon acceptance of the
manuscript. The re-used plant metabarcoding datasets and related references are listed in the Appendix Table A2. The
analysis code is available on GitHub under the link [https://github.com/hongyulu21/Tracing-terrestrial-OM-dynamics-in-the-](https://github.com/hongyulu21/Tracing-terrestrial-OM-dynamics-in-the-subarctic-North-Pacific-using-sedaDNA-metabarcoding)
760 [subarctic-North-Pacific-using-sedaDNA-metabarcoding](https://github.com/hongyulu21/Tracing-terrestrial-OM-dynamics-in-the-subarctic-North-Pacific-using-sedaDNA-metabarcoding) (Zenodo DOI will be provided after the acceptance of the
manuscript).

Author contributions

U.H. conceived the study. L.L.-J. provided sediment core material. K.R.S.-L., and U.H. supervised the lab work. H.L., J.F.W.
and H.H.Z. performed the lab work. H.L., K.S.L performed bioinformatic analyses. H.L. performed the statistical data
analyses under supervision of UH. H.L. wrote the first draft of the manuscript under supervision of UH. All authors
765 contributed to the final manuscript.

Competing interests

The authors declare that they have no conflict of interest.

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