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Environmental controls on benthic food web functions and carbon resource use in subarctic lakes

Short title: Benthic feeding functionality and resources

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Summary

1. Climate warming and consequent greening of subarctic landscapes increase the availability of organic carbon to the detrital food webs in aquatic ecosystems. This may cause important shifts in ecosystem functioning through the functional feeding patterns of benthic organisms that rely differently on climatically altered carbon resources.
2. 25 subarctic lakes in Finnish Lapland across a tree line ecotone were analysed for limnological and optical variables, carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope (SI) composition of surface sediment organic matter (OM) and fossil Chironomidae (Diptera) remains to examine environmental controls behind chironomid functional feeding group (FFG) structure and their isotopic associations for assessing ecosystem functioning and carbon utilization. We hypothesize that the chironomid SI signatures reflect increased allochthony with increasing allochthonous input, but the resource use may be altered by the functional characteristics of the assemblage.
3. Multivariate analyses indicated that carbon geochemistry in the sediments ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, C/N), nutrients, indices of productivity (Chlorophyll-a) and lake water optical properties, related to increasing presence of OM, played a key role in defining the chironomid FFG composition and isotopic signatures.
4. Response modelling was used to examine how individual FFGs respond to environmental gradients. They showed divergent responses for OM quantity, dissolved organic carbon (DOC) and nutrients between feeding strategies, suggesting that detritivores and filter feeders prefer contrasting carbon and nutrient conditions, and may thus hold paleoecological indicator potential to identify changes between different carbon fluxes.
5. Benthic production was the primary carbon source for the chironomid assemblages according to a three-source stable isotope mixing model, whereas pelagic and terrestrial components contributed less. Between-lake variability in source utilization was high and controlled primarily by allochthonous OM inputs.

6. Combination of biogeochemical modelling and functional classification is useful to widen our understanding of subarctic lake ecosystem functions and responses to climate-driven changes in limnology and catchment characteristics for long-term environmental change assessments and functional paleoecology.

Introduction

Increasing inputs of terrestrial carbon into freshwaters from catchment surface soils, vegetation (Tranvik et al. 2009) and thawing permafrost (Vonk et al. 2015) are considered a major challenge to Arctic lake ecosystems. Consequent increases in levels of dissolved organic carbon (DOC), coloured dissolved organic matter (CDOM) and nutrient loads have a high potential to alter many biochemical and physical lake characteristics (Jansson et al. 2007; Karlsson et al. 2009). These characteristics include changes in light climate, UV attenuation and thermal regimes, which control primary production and affect the balance between pelagic and benthic producers. DOC input may also enhance heterotrophic production (e.g. Karlsson et al. 2009). As a result, altered carbon pools might affect the amount of energy and quality of nutrition available for lake fauna, which may have consequences for species distribution and eventually for the whole food web structure and its functions (Solomon et al. 2011). Changes in Arctic freshwater systems have global implication through their tight connections to the active carbon cycle, as they play a key role in sequestering and conveying carbon from the terrestrial environment into the atmosphere (Battin et al. 2009). Therefore, it is important to understand how small and shallow Arctic lakes function under natural environmental variability and anthropogenic environmental stresses, such as climate warming.

The benthic zone is often the most productive part of shallow Arctic lakes (Bonilla, Villeneuve & Vincent 2005) and benthos has been recognized as an integrated part of the aquatic food web (Karlsson et al. 2009; Vadeboncoeur, Vander Zanden & Lodge 2002; Rautio & Vincent 2006). In Arctic lakes chironomids (Diptera: Chironomidae) are a crucial component of the benthic fauna, playing a key role in processing OM and

recycling nutrients (Wallace & Webster 1996; Vanni 2002). Chironomid fossils preserve well in lake sediments, and their communities are sensitive to various environmental factors, such as temperature, oxygen saturation, lake depth and nutrients, which control their abundance and taxonomic distribution, consequently making them a useful tool for paleoecological studies (Walker 2001; Luoto 2011; Eggermont & Heiri 2012). However, environmental controls affecting their feeding behaviour and its plasticity are less known. The ability to adjust feeding to the availability of carbon sources would make chironomids sensitive to increasing OM inputs, and leave traces of such changes in the paleolimnological archives.

Functionality of taxa (e.g. feeding habits), rather than just their taxonomic composition, may better define ecosystem functions and responses to environmental changes. Recently, functional aspects have been increasingly incorporated into ecological research, including studies of macrozoobenthos especially in riverine systems (Johnson, Goedkoop & Sandin 2004; Heino 2008; Dolédec & Statzner 2010). However, our knowledge of chironomid functional traits still includes considerable gaps (Heino 2008; Serra et al. 2016). Chironomid larvae can be divided into several different functional feeding groups (FFGs), from detritivores to predators. The explanatory factors governing feeding mode are considered to be larval body size, food quality and sediment composition (Berg 1995; Merritt, Cummins & Berg 2008). Chironomids are also often considered opportunistic omnivores due to high levels of plasticity in their feeding mode, which may change according to larval stage and external conditions (Berg 1995; Mihuc 1997; Reuss et al. 2013). Although the functional approach may give essential information about ecosystem functions (Gregory-Eaves & Beisner 2011), it has been rarely applied to paleoecology. As an example, it has been used to examine connections between climate fluctuations and large scale patterns of midge functional assemblage composition and diversity (Luoto & Nevalainen 2015). Increased understanding of changes in functional ecology of the benthic community, triggered by extrinsic environmental variables, would improve our understanding of how lakes and their biota may face global change, including temperature increase and altered carbon fluxes.

Stable isotopes (SI) are a well-established tool for food web studies and widely used in ecology to disentangle trophic relationships and significance of different nutritional sources consumed by organisms (Peterson & Fry 1987; Post 2002). SI analytics are increasingly applied in paleolimnological studies by analysing chitinous remains of aquatic invertebrates (Perga 2010; van Hardenbroek et al. 2010, 2012, 2016). For chironomid fossils, the focus has been on carbon isotopes directly associated with food sources, and the method has been used especially for tracing changes in methane emissions over long time periods (van Hardenbroek et al. 2012, 2013; Belle et al. 2016). A growing number of applications reflecting carbon dynamics during lake trophic regime shifts, oxygen depletion and implications for feeding behaviour have emerged (Frossard et al. 2014; Belle et al. 2017a b). Investigation of fossil food webs greatly benefit from incorporating other SIs, such as those of nitrogen, and functional approaches to the carbon SI analysis, leading to more detailed insight on nutrition consumption and trophic interactions in space and time.

Changes in balance between carbon sources, carbon assimilation, and their environmental controls can alter ecosystem functioning and consequently the role of freshwaters in carbon sequestration (e.g. Seekell et al. 2015; Solomon et al. 2015). Hence, identifying contributions of allochthonous and autochthonous carbon is a key question in aquatic feeding ecology (Tanentzap et al. 2017). The quantity and quality of allochthonous carbon input is largely dependent on catchment vegetation and associated variability in soil chemistry (Michalzik et al. 2001; Aitkenhead-Peterson, McDowell & Neff 2003). Therefore, it is particularly important to compare ecotonal lakes that encompass large eco-climatic gradients. In this study, we aim to improve understanding of carbon incorporation from different sources into the benthic food web, and how the process is related to extrinsic (environmental) and intrinsic (functional) attributes. Our specific aims are, firstly, to determine SI signatures of fossil chironomid assemblages and elucidate potential source contribution of pelagic, benthic and terrestrial carbon pools with linkages to environmental variables and vegetation zones in 25 ecotonal lakes across the northern tree line in Finnish Lapland. Secondly, we aim to determine the FFG composition of chironomid assemblages to decipher their relations with carbon source contributions and environmental controls between lakes. We hypothesize that the chironomid SI values

reveal increased allochthony with increasing allochthonous input reflected as higher proportion of DOC and chromophoric substances, but the functional characteristics of chironomids may alter resource use. We also presume that the FFGs respond uniquely to environmental gradients across the tree line and that the functional classification may retain paleoecological indicator potential.

Methods

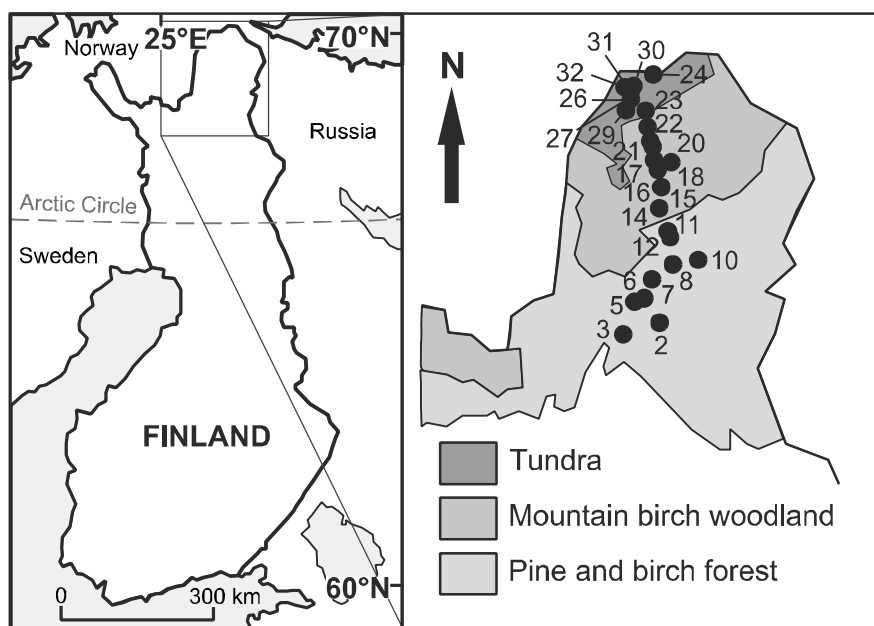


Figure 1. Map of the 25 study lakes located in northern Finland with present vegetation zones.

A surface sediment data set comprising 25 small and shallow (max depth 0.5-6.3 m, Table 1.) ecotonal lakes was collected from northern Finland (68-70°N) in late summer 2014 (Fig. 1). The sites form a geographical S-N transect and were chosen to represent large environmental gradients, including varying humic content and catchment vegetation change across the northern tree line from pine dominated forest to barren tundra. Wetlands are also common in the region. The study area features subarctic climate (mean annual air temperature -2°C, precipitation 450 mm/y), with a ~1°C gradient in temperature.

Table 1. Summary of limnological and sedimentary variables with units and abbreviations. Minimum, maximum and mean values are shown separately for lakes below and above the coniferous tree line.

	Unit	Abbreviation	Below pine tree line (n= 9)			Above pine tree line (n=16)		
			Min	Max	Mean	Min	Max	Mean
Limnological variables								
Lake area	ha	Area	0.5	9.3	4.5	0.7	13.2	3.9
Sampling depth (max water depth)	m	Depth	0.5	7.5	3.8	0.5	6.3	2.6
pH		pH	5.1	8.2	6.6	6.4	8.4	7.5
Chlorophyll a	$\mu\text{g L}^{-1}$	Chl-a	1.0	5.2	2.2	0.3	3.8	1.7
Total phosphorus	$\mu\text{g L}^{-1}$	TP	5.9	14.1	8.3	5.1	24.1	9.8
Total nitrogen	$\mu\text{g L}^{-1}$	TN	225.0	806.3	460.4	137.5	762.5	430.1
Nitrogen to phosphorus ratio	ratio	N/P	32.5	84.6	53.4	23.5	66.7	45.0
Dissolved Organic Carbon	mg L^{-1}	DOC	2.6	9.6	5.0	1.8	12.0	5.2
Water colour	Pt mg L^{-1}	Colour	0.0	20.0	9.4	0.0	70.0	18.1
Specific UV-absorbance	$\text{mg C L}^{-1} \text{m}^{-1}$	SUVA	0.8	3.2	1.8	0.7	3.2	1.9
Attenuation coefficient for photoactive radiation	m^{-1}	kdPAR	0.3	2.0	0.8	0.2	4.3	1.3
Coloured dissolved organic matter	R.U.	CDOM	1.7	14.1	7.4	1.0	35.1	10.0
Drainage ratio	ratio	Cat/Lake	0.0	0.2	0.1	0.0	2.8	0.4
Sedimentary variables								
Carbon SI composition (sediment OM)	‰	$\delta^{13}\text{C}_{\text{OM}}$	-30.2	-22.9	-25.9	-33.8	-18.0	-23.7
Nitrogen SI composition (sediment OM)	‰	$\delta^{15}\text{N}_{\text{OM}}$	-2.8	2.3	-0.1	-1.8	1.4	-0.6
Loss-on-ignition (550°)	%	LOI	40.9	82.8	64.3	32.7	69.4	53.5
Carbon to nitrogen ratio	ratio	C/N	8.9	11.4	9.6	9.0	13.3	11.1
Sedimentary chlorophyll-a	mg DWmg^{-1}	Chl-a _s	0.1	0.8	0.4	0.0	0.7	0.4
Carbon SI composition (chironomid remains)	‰	$\delta^{13}\text{C}_{\text{HC}}$	-30.7	-24.6	-27.2	-34.4	-20.4	-25.3
Nitrogen SI composition (chironomid remains)	‰	$\delta^{15}\text{N}_{\text{HC}}$	0.3	4.6	2.3	0.7	4.1	1.9

A Limnos gravity corer was used to sample sediments (0–2 cm) from central lake basins. To determine OM quantity and carbon source mixture for the sediments (Meyers & Teranes 2001), we analysed the amount (Loss-on-ignition at 550°, LOI), elemental (C, N) and isotopic ($\delta^{13}\text{C}_{\text{OM}}$ and $\delta^{15}\text{N}_{\text{OM}}$) composition of the sediment organic matter as described in Rantala et al. (2016b). Chl-a concentration of sediment was measured following Nusch (1980). 1-3 cm³ of sediment per sample was extracted three times in 90 % ethanol, filtered (0.2 μm), and analysed spectrophotometrically. The results were normalized with the sediment dry weight.

Stable isotope analysis (SIA) of carbon and nitrogen from chironomid head capsules ($\delta^{13}\text{C}_{\text{HC}}$ and $\delta^{15}\text{N}_{\text{HC}}$) was performed following previously established methodology (van Hardenbroek et al. 2010; Heiri, Schilder & Hardenbroek 2012). Mild acid and base pre-treatments were omitted as both sediment deflocculation and carbonate removal (detected with negligible LOI 950°) were considered unnecessary, hence, the chironomid SI signatures represent natural decay. Subsamples of the surface sediments were sieved through a 100 μm mesh, thoroughly rinsed with ultrapure water, and chironomid head capsules were handpicked with forceps from the residue under a stereo microscope (x40) into a drop of ultrapure water on an aluminium dish. The head capsules were picked as bulk assemblages due to low concentration and high diversity of morphotypes, which did not favour higher taxonomic specificity in the current analysis. Samples were then dried in an oven (40°C) to remove excess moisture and transferred into pre-weighed tin cups for SIA. The capsules were dried in an oven (40°C) overnight to remove all residue moisture, re-weighed, closed and stored in a desiccator until analysis. Samples composed of 200-550 individual remains to reach required dry sample mass (0.2 - 0.4 mg). SIA was performed with a FlashEA 1112 elemental analyser coupled with a Thermo Finnigan DELTA plus Advantage mass spectrometer (Thermo Electron Corporation, Waltham, MA, USA). The SI values are expressed as delta notations $\delta = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$, where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$ and standardised to VPDB for carbon and atmospheric concentration for nitrogen. Also, the differences between chironomid and sediment OM isotopic values (e.g. for carbon $\Delta \delta^{13}\text{C} = \delta^{13}\text{C}_{\text{HC}} - \delta^{13}\text{C}_{\text{OM}}$), were calculated for each sample and are later referred to as isotopic offsets ($\Delta \delta^{13}\text{C}$ and $\Delta \delta^{15}\text{N}$). They show chironomid discrimination from the bulk OM and indicate level of selectivity between sedimentary carbon pools. As selectivity indices, we use the absolute value of $\Delta \delta^{13}\text{C}$ and $\Delta \delta^{15}\text{N}$, to focus on the level of discrimination.

Results for taxonomic analysis of fossil chironomid assemblages from the same sediment samples are presented and discussed in Luoto et al. (2016). In this study, each taxon was assigned a FFG (Mandaville 2002; Merritt, Cummins & Berg 2008). Four groups were present in the data: collector-gatherers (C-G), collector-filterers (C-F), shredders (SHR) and predators (PRD) and a list of taxa grouped into each FFG is

available in Appendix 1. Relative abundance (%) of each FFG of the total assemblages was calculated for each study lake.

Water samples were collected from the epilimnion for analysis of total nitrogen (TN), total phosphorus (TP), chlorophyll-a (Chl-a), DOC and CDOM concentrations. CDOM concentration is a combination of humic components (1-5, 6) from PARAFAC analysis. In situ field measurements involved pH and photosynthetically active radiation (PAR) profiling, which gives indication on the level of primary production. These analyses are thoroughly described in Rantala et al. (2016b) and Nevalainen et al. (2015). A summary of selected limnological and sediment biochemical variables is presented in Table 1.

A three-source (pelagic, benthic and terrestrial) SI mixing model was calculated with package `simmr` (Parnell & Inger 2016) in R 3.4.0 (R Core Team 2017). Values for end-member estimates were collected from literature (Appendix 2) with preference for measurements from lakes in the same region. We used benthic mat and biofilm values to detect the benthic signal (mean \pm SD: $\delta^{13}\text{C} = -21.1\pm 3.7$, $\delta^{15}\text{N} = 0.7\pm 1.3$), zooplankton values to trace pelagic signal (mean $\delta^{13}\text{C} = -32.1\pm 1.6$, $\delta^{15}\text{N} = 3.8\pm 1.3$), and a mixture of terrestrial leaves, litter and soil for determining terrestrial signal (mean $\delta^{13}\text{C} = -28.3\pm 1.1$, $\delta^{15}\text{N} = -1.7\pm 2.9$). Fractionation correction coefficients (\pm SD) of 0.50 ± 0.56 ‰ and 1.5 ± 0.50 ‰ for carbon and nitrogen, respectively, were applied to benthic and terrestrial sources to account for trophic enrichment (Goedkoop, Åkerblom & Demandt 2006).

To explore bivariate relationships within the data, Spearman's rank correlations (ρ) were calculated. Linear models (ordinary least squares) were used for further investigation of the isotopic relationships and variance analyses (ANOVA, Kruskal-Wallis) were used for comparing mean source contribution groups between vegetation zones (shown in Fig. 1.). These analyses were performed with PAST 3.0 (Hammer, Harper & Ryan 2001). For multivariate analyses, we used $\delta^{13}\text{C}_{\text{OM}}$, $\delta^{15}\text{N}_{\text{OM}}$, depth, pH, C/N, Chl-a_s, LOI, DOC, KdPAR, N/P, Chl-a, Colour, SUVA and Cat/Lake (see Table 1 for abbreviations) as the set of environmental

variables (inflation factor < 25). Redundancy analysis (RDA) was used for exploring relationships between environmental variables (Table 1) and (1) chironomid SI values ($\delta^{13}\text{C}_{\text{HC}}$, $\delta^{15}\text{N}_{\text{HC}}$) and isotopic offsets ($\Delta \delta^{13}\text{C}$, $\Delta \delta^{15}\text{N}$), (2) chironomid FFGs, and (3) potential carbon sources. The data were \log_{10} transformed for standardization and a constant was added to variables with negative values prior to transformation. A suite of ecologically meaningful environmental variables with inflation factor < 25 were chosen for the analysis and further identification of significant variables was based on forward selection with 999 Monte Carlo permutations. FFG response models for selected ecologically relevant environmental variables (LOI, DOC, depth and N/P -ratio) were calculated as RDA based generalized linear models (GLM) with predictor form set to quadratic fit and response distribution to Poisson. Response data were \log_{10} transformed prior to analysis. All multivariate analyses were produced with Canoco 5 (ter Braak & Šmilauer 2012).

Results

High between-lake diversity was observed in FFG distribution (Fig. 2.). Collector-gatherers (C-G) were the most common feeding group with a mean abundance of 46 %, followed by collector-filterers (C-F, 33 %), shredders (SHR, 13 %) and predators (PRD, 8 %). Highest variability was observed within SHR, ranging 0-69% between lakes, and lowest within PRD constituting 2-18 % of assemblages. Of the 25 lakes, 15 lakes were dominated by C-G and 8 lakes by C-F groups. Two lakes (#21, 23) were dominated by SHR, while PRD occurred in all lakes in small quantities. All lakes but one (#8) featured all four FFGs and their relative proportions varied markedly between lakes.

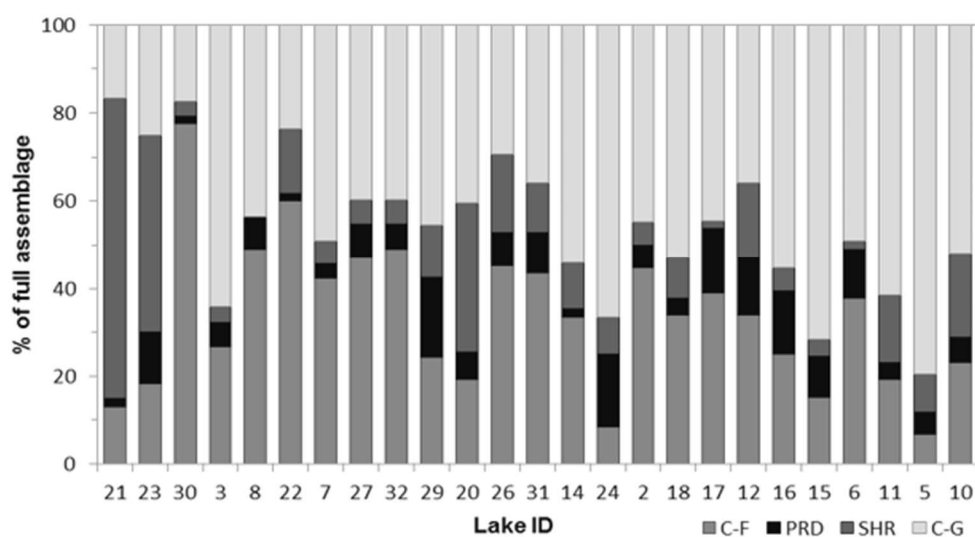


Figure 2. The relative abundance and distribution of functional assemblages in the study lakes, represented by four functional groups: collector-filterers (C-F), predators (PRD), shredders (SHR) and collector-gatherers (C-G). X-axis is scaled along increasing sediment organic matter quantity (LOI).

The SI values of fossil chironomid assemblages showed variation ranging between -20.4 ‰ and -34.4 ‰ for $\delta^{13}\text{C}$ and between 4.6 ‰ and 0.3 ‰ for $\delta^{15}\text{N}$ (Table 1, Fig. 3A, C). The $\delta^{13}\text{C}_{\text{HC}}$ values were consistently more ^{13}C -depleted than $\delta^{13}\text{C}_{\text{OM}}$, while $\delta^{15}\text{N}_{\text{HC}}$ were more positive than $\delta^{15}\text{N}_{\text{OM}}$, however, the difference showed considerable variation between lakes. As the direction within each offset is the same ($\Delta \delta^{13}\text{C}$ negative and $\Delta \delta^{15}\text{N}$ positive), we concentrate only on the level of offset in the following, and hence use the absolute values of isotopic offsets. Accordingly, absolute values of $\Delta \delta^{13}\text{C}$ and $\Delta \delta^{15}\text{N}$ varied between 0.4 - 3.4 ‰ and 1.7 - 3.3 ‰ respectively (Fig. 3B, D).

Spearman's correlations (ρ) between the chironomid SI signatures and environmental variables revealed strong relationships with limnological and sediment quality variables (Table 2). Sediment and chironomid SI values were strongly positively correlated (Table 2., Fig. 3A, C). The offset - sediment OM relationships were much weaker with divergent directions for C and N (Fig. 3B, D), showing a positive and negative correlation, respectively, and lower coefficients of determination.

Table 2. Spearman correlation coefficients for chironomid isotopic signatures ($\delta^{13}\text{C}_{\text{HC}}$, $\delta^{15}\text{N}_{\text{HC}}$), sediment-chironomid offsets ($\Delta \delta^{13}\text{C}$, $\Delta \delta^{15}\text{N}$) and source contributions (benthic, pelagic, terrestrial) with environmental variables. For abbreviations, see Table 1. Significant ($p < 0.05$) values are marked with bold and highly significant ($p < 0.01$) with bold italic.

	Chironomid SI		SI offset		Source contribution		
	$\delta^{13}\text{C}_{\text{HC}}$	$\delta^{15}\text{N}_{\text{HC}}$	$\Delta \delta^{13}\text{C}$	$\Delta \delta^{15}\text{N}$	Benthic	Pelagic	Terrestrial
Depth	-0.30	0.71	-0.10	-0.35	-0.28	0.48	-0.35
pH	0.51	0.00	0.21	-0.15	0.52	-0.41	-0.37
Chl-a	-0.44	-0.29	-0.28	0.29	-0.47	0.27	0.39
TP	0.08	-0.56	-0.28	0.18	0.07	-0.21	0.34
TN	0.01	-0.55	-0.41	0.05	-0.02	-0.14	0.45
N/P	0.01	-0.48	-0.12	0.00	-0.02	-0.14	0.37
DOC	-0.24	-0.50	-0.32	0.22	-0.26	0.06	0.48
Colour	-0.25	-0.26	-0.17	0.13	-0.22	0.12	0.33
SUVA	-0.26	-0.14	-0.29	-0.05	-0.24	0.15	0.32
kdPAR	-0.11	-0.53	-0.37	0.21	-0.15	-0.08	0.48
CDOM	-0.31	-0.39	-0.36	0.14	-0.33	0.14	0.51
Cat/Lake	0.05	-0.12	-0.09	-0.03	0.03	-0.14	-0.22
$\delta^{13}\text{C}_{\text{OM}}$	0.98	-0.38	0.56	-0.10	0.99	-0.95	-0.22
$\delta^{15}\text{N}_{\text{OM}}$	-0.40	0.92	-0.13	-0.40	-0.38	0.65	-0.47
LOI	0.16	-0.51	0.11	0.15	0.16	-0.27	0.48
C/N	0.55	-0.25	0.25	0.34	0.58	-0.50	-0.09
Chl-a_s	0.24	-0.43	-0.12	0.09	0.18	-0.38	-0.03

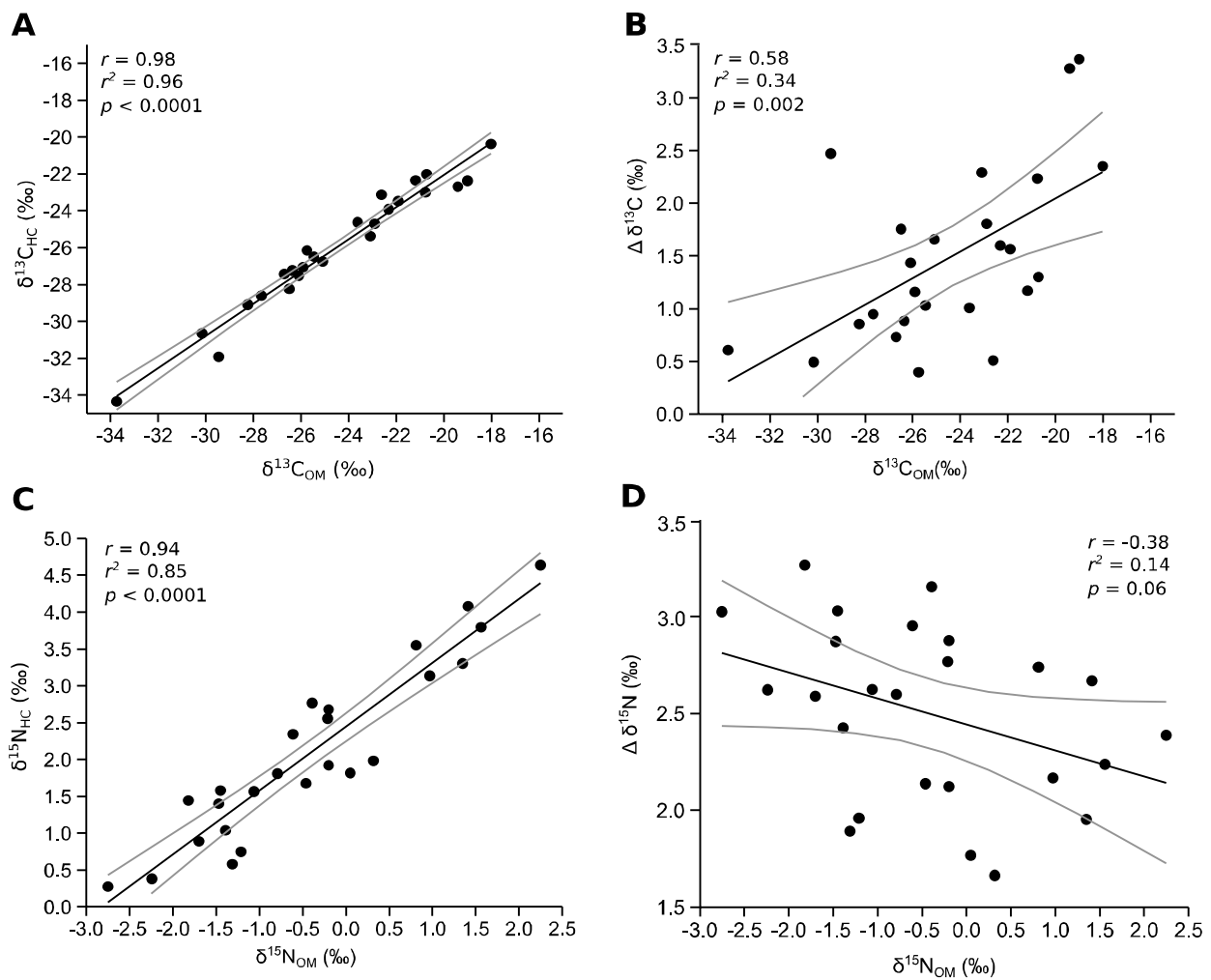


Figure 3. Linear relationships for A) carbon isotopic signature ($\delta^{13}\text{C}$) of sediment organic matter (OM) and chironomid head capsules (HC), B) $\delta^{13}\text{C}$ of sediment OM and the chironomid-sediment offset (Δ), C) nitrogen isotopic signature ($\delta^{15}\text{N}$) of sediment OM and chironomid HC and D) $\delta^{15}\text{N}$ sediment OM and $\Delta \delta^{15}\text{N}$.

The SI mixing model showed that samples were distributed within the area defined by the source estimates on isospace plot (Fig. 4.) For the whole lake set, SI mixing model showed the benthic source dominant (mean = 44 %, SD = 0.075), followed by pelagic (29 %, 0.062) and terrestrial (27 %, 0.072) components, with high between-lake variability (Fig. 5.). When comparing the mean source contributions between ecoregions (Fig. 1.), there were no significant differences between the tundra and mountain birch woodland for any source, however, there were significant differences between lakes below (# 2-12, n = 9) and above (# 14-34, n = 16) the pine limit (Fig. 5.) when tundra and mountain birch woodland were pooled. The benthic

carbon contribution was relatively more dominant in lakes north of the pine limit than south of it (Kruskal-Wallis $\chi^2 = 4.04$, $p = 0.044$), whereas pelagic component had marginally higher importance in the north boreal type lakes south of the pine limit. Terrestrial component differed significantly across the pine limit (anova $F_{1,23} = 4.59$, $p = 0.043$), although its contribution had less variability than the others (Fig. 5C), and was strongly linked to wetland coverage through significant ($p < 0.05$) correlations with the carbon optical variables (Table 2, Fig. 6C) and sediment composition (C %, $\rho = 0.50$; N %, $\rho = 0.56$). Other significant correlations showed that pelagic component is favoured in deeper lakes, and that C/N ratio has fairly strong, convergent trends with benthic and pelagic sources (Table 2).

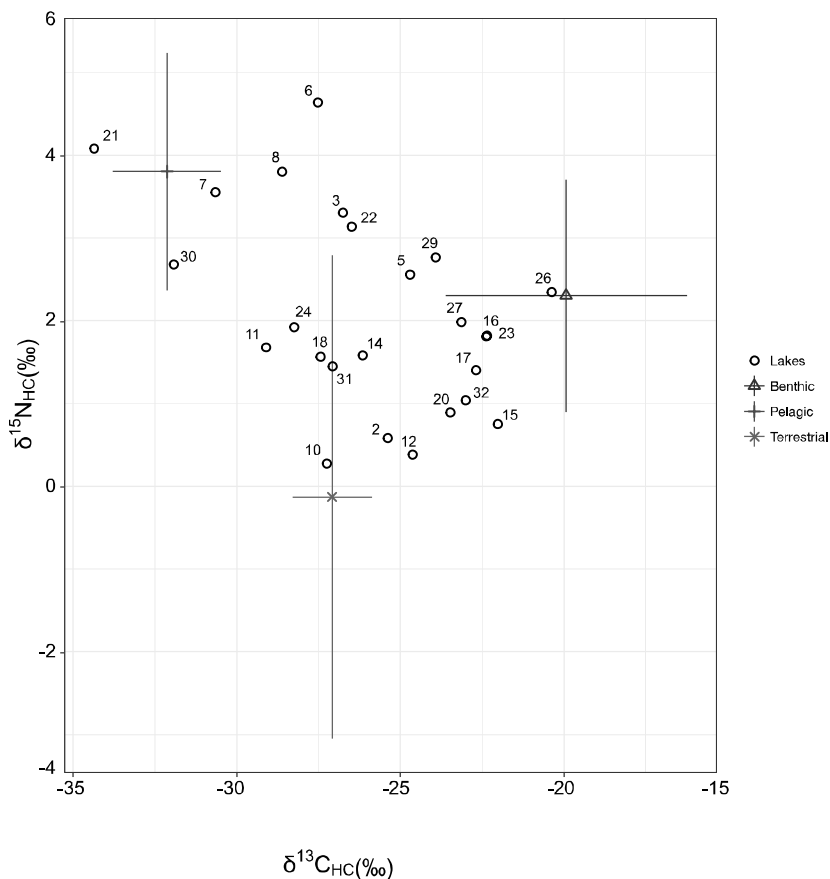


Figure 4. Isospace plot of the stable isotope mixing model. Chironomid assemblage isotope values are marked by lake ID on the plot with benthic, pelagic and terrestrial end-member estimates and their associated variability.

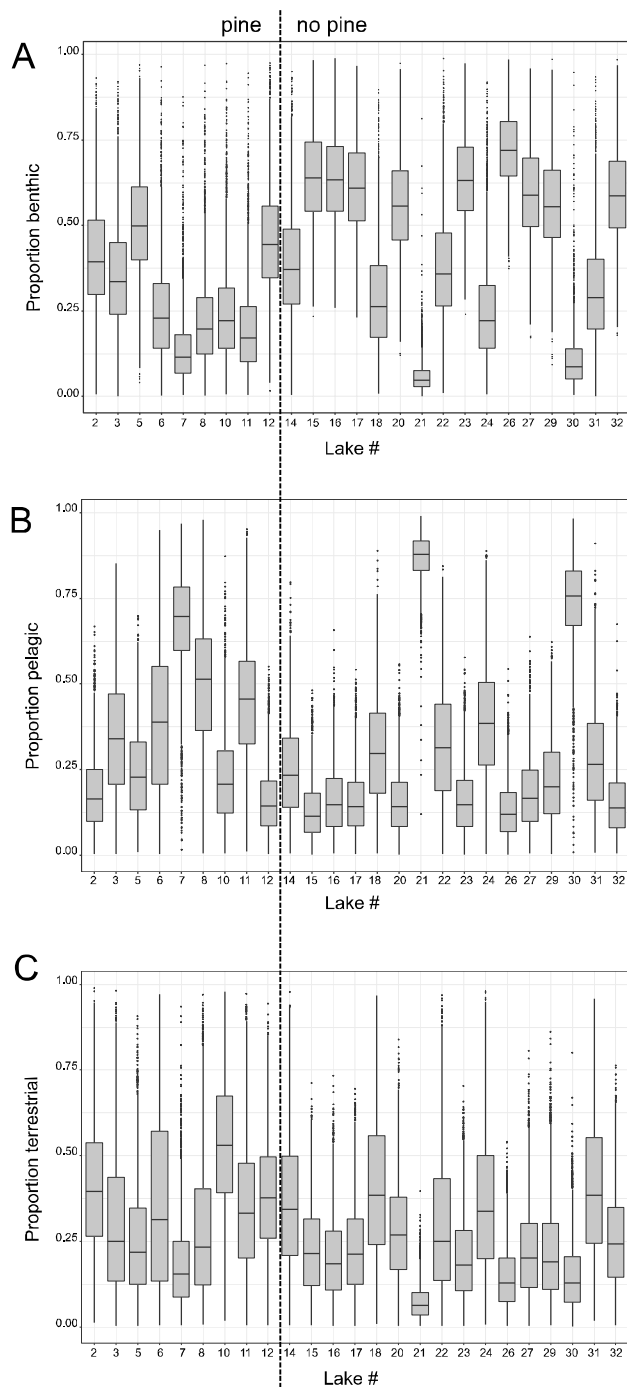


Figure 5. Relative contributions of A) benthic, B) pelagic and C) terrestrial sources for the chironomids according to the stable isotope mixing model. Mean (black line), 50 % range (box) and 100 % range (tails) of distribution results are presented. The vertical dashed line represents the coniferous tree line, lakes on the left are below and lakes on the right are above the tree line.

Full RDA model for FFG–environment relationships ($\lambda_1 = 0.37$, $\lambda_2 = 0.20$) explained 69.5 % of variance (Fig. 6A). Significant ($p < 0.05$) environmental variables identified with forward selection were Chl-a_s (14.2 %), $\delta^{13}\text{C}_{\text{OM}}$ (11.1 %) and depth (8.9 %), which together explained 34.2 % (adjusted 24.8 %; $\lambda_1 = 0.18$, $\lambda_2 = 0.13$). RDA model for examining chironomid SI signatures and offsets with a full set of sedimentary and limnological parameters ($\lambda_1 = 0.39$, $\lambda_2 = 0.21$) explained 83.7 % of the variance (Fig. 6B). Based on forward selection, the significant explanatory variables were $\delta^{13}\text{C}_{\text{OM}}$ (35.1 %), $\delta^{15}\text{N}_{\text{OM}}$ (21.8 %), C/N (6.9 %) and kdPAR (4.9 %), which together accounted for 68.7 % (adj. 62.4 %; $\lambda_1 = 0.38$, $\lambda_2 = 0.20$) of variance. The full RDA model explaining carbon sources with environmental variables ($\lambda_1 = 0.77$, $\lambda_2 = 0.15$) explained 94.6 %, while forward selection picked out $\delta^{13}\text{C}_{\text{OM}}$ (73.9 %), LOI (6.6 %), SUVA (3.7 %) Cat/Lake (2.2 %) and Colour (1.7 %), altogether explaining 88.1 % (adj. 85.0 %; $\lambda_1 = 0.75$, $\lambda_2 = 0.15$) (Fig 6C). The strength of ecological relevance of each environmental variable was explored with single variable constrained RDAs, which indicate that the most relevant ($\lambda_1/\lambda_2 > 0.8$) relationships for chironomid SI signatures are $\delta^{13}\text{C}_{\text{OM}}$ and $\delta^{15}\text{N}_{\text{OM}}$, while for the sources $\delta^{13}\text{C}_{\text{OM}}$ is most relevant.

FFG response curves for carbon quantity (substrate and dissolved), nutrients and depth (Fig. 7) revealed that there were divergent preferences between the major feeding strategies (C-G and C-F) and selected limnological variables. Detritivores (C-G) preferred shallowest lakes with highly organic substrate and tolerated better higher DOC and N load, whereas filter feeders (C-F) preferred lakes 4-5 m deep and LOI of ca. 50 %. They preferred a lower N/P ratio and had a positive response to both ends of DOC concentration. SHR preferred low (<40 %) and weakly very high (>80 %) sediment OM quantity and preferred deeper water. For PRD there were no clear relationships.

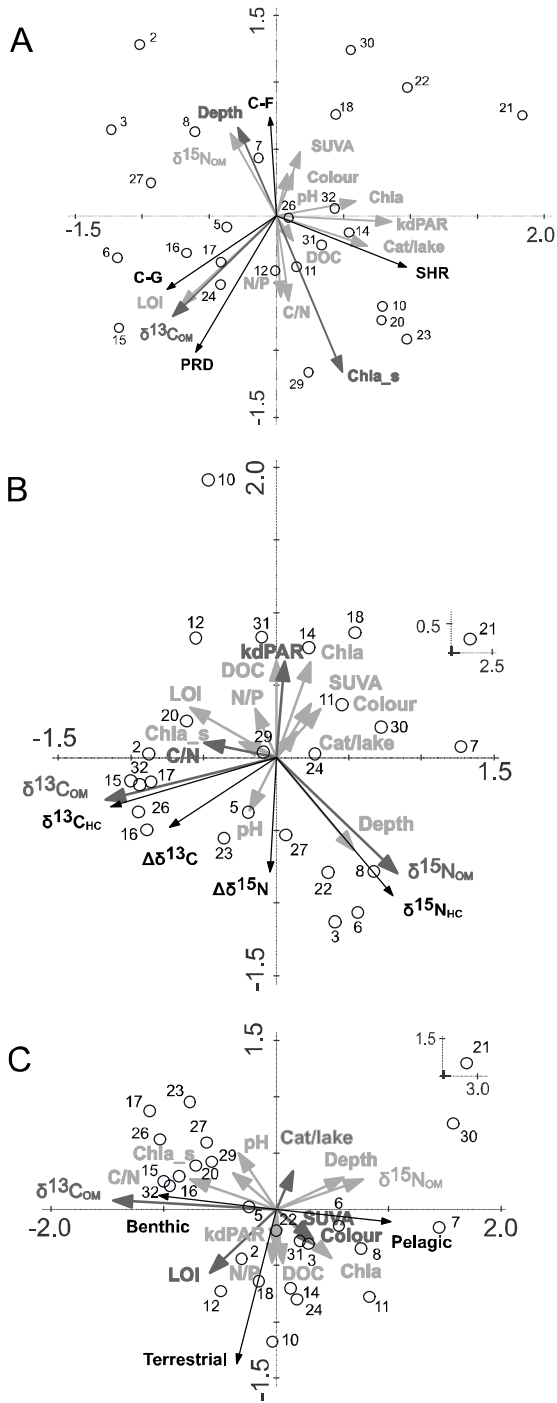


Figure 6. Redundancy analysis of A) functional feeding groups (collector-filterers (C-F), predators (PRD), shredders (SHR) and collector-gatherers (C-G)), B) chironomid stable isotope values ($\delta^{13}\text{C}_{\text{HC}}$, $\delta^{15}\text{N}_{\text{HC}}$) and sediment-chironomid offsets ($\Delta\delta^{13}\text{C}$, $\Delta\delta^{15}\text{N}$), and C) mean stable isotope mixing model source contributions (benthic, pelagic, terrestrial) explained with a suite of environmental variables. Lakes are represented as circles, black arrows represent the response variables, and grey the environmental variables. Dark grey arrows are variables identified significant with forward selection. For abbreviations, see table 1.

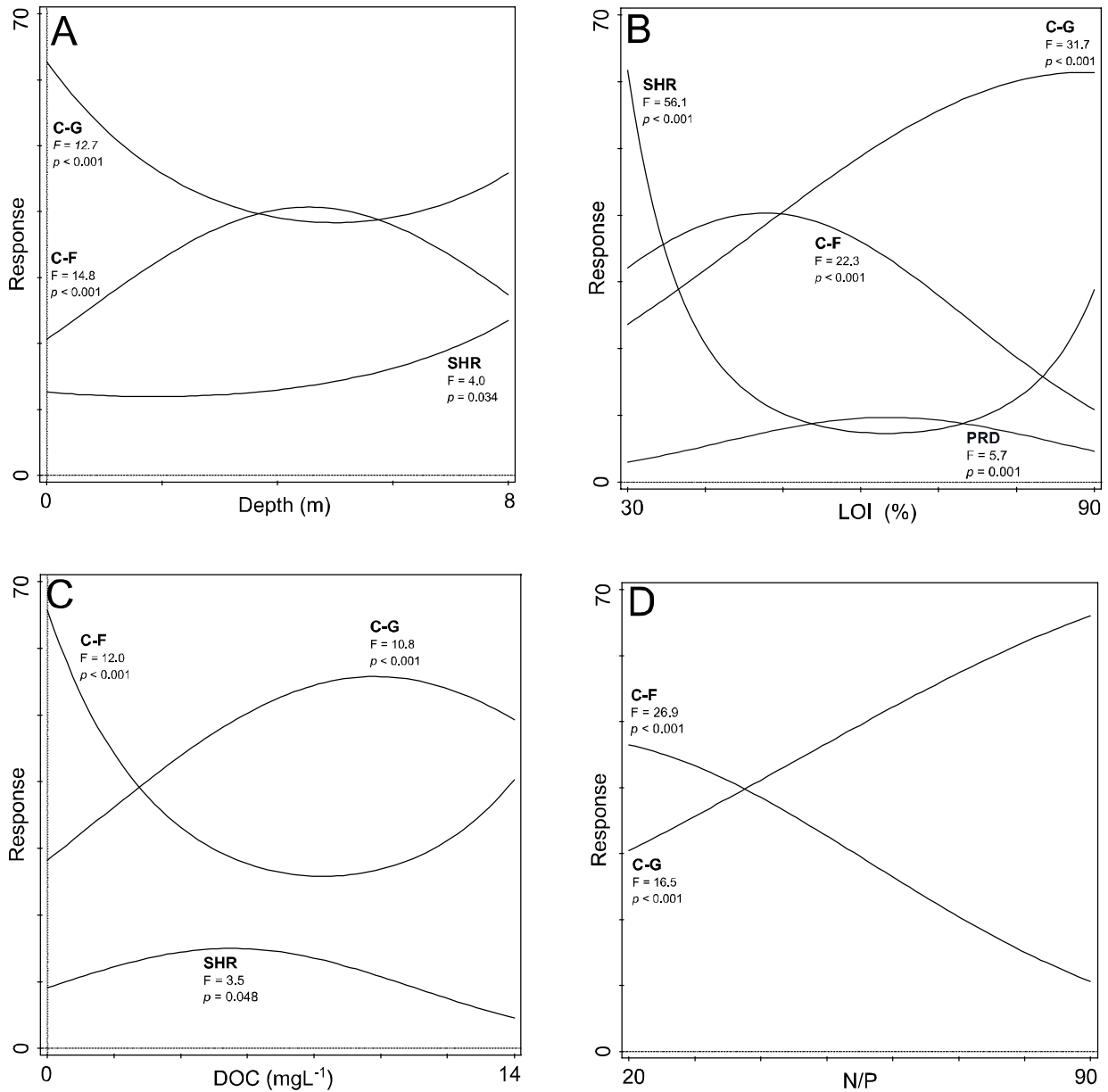


Figure 7. Response models for the functional feeding groups (gatherers C-G, filterers C-F, shredders SHR and predators PRD) and selected extrinsic variables: A) water depth, B) sediment organic matter quantity, C) dissolved organic carbon and D) N/P ratio of lake water. Only statistically significant ($p < 0.05$) responses are shown.

Discussion

Functional feeding behaviour and its relation to environmental variables

The subarctic lakes in Finnish Lapland feature dominance of benthic over pelagic production (Rantala et al. 2016b) and retain diverse communities of benthic invertebrates, including chironomids (Luoto et al. 2016). Our results show that generalist feeding strategies amongst chironomids were beneficial for survival in the lakes, as collectors (C-G and C-F) were dominant, while specialized FFGs (PRD and SHR) were less abundant. This is typical of high-latitude lake food webs with low biocomplexity (Christoffersen et al. 2008). As exceptions, two lakes (#21 & #23) featured a high dominance of shredders (SHR), reflecting the availability of adequate nutrition sources and habitats likely associated with aquatic macrophytes. Collectors tend to be omnivorous, consuming all suitable sized particles (Cummins & Klug 1979), which allows them to adapt to various food sources. The relative distribution of filter-feeders (C-F) and detritivores (C-G) was associated with the sediment OM quantity (LOI), C-F being more abundant in low organic content and C-G preferring high organic content. This agrees with previous studies stating that substrate quality or LOI is one of the driving factors of taxonomic chironomid diversity in lakes (Nyman, Korhola & Brooks 2005; Heino 2008; Luoto et al. 2016). This relationship was clear also in our FFG response models, where C-G preferred shallow systems with organic rich substrate (high benthic production), while C-F opted for medium depth and OM quantity in the sediment. High abundance of C-Fs is likely associated with increased pelagic production as food source, which is also supported by their preference for low DOC and N/P ratio, as phytoplankton is typically phosphorus limited. Instead, mat-forming benthic communities are less dependent on dissolved phosphorus, as they circulate nutrients internally (Bonilla et al. 2005). C-Gs on the other hand preferred higher DOC, as well as higher N/P ratio, where increased nitrogen was most likely associated with increased terrestrial input (Rantala et al. 2016b). The FFG response models suggests that C-Fs and C-Gs respond strongly and in a different manner to carbon and nutrient gradients and thus have specific but opposing habitat preferences. Accordingly, different habitat preferences may be useful

indicators for paleolimnological studies, as C-Fs prefer oligotrophic clear water conditions and C-Gs organic rich substrates tolerating dark water colour better.

A multitude of environmental factors shapes the taxonomic and functional diversity, distribution and composition of macrobenthic fauna on various scales. Luoto & Nevalainen (2015) concluded that both spatial and temporal changes in midge FFG distribution are driven by climatic controls, primarily temperature, on local-scale factors. Luoto et al. (2016) identified LOI, TN, pH and water depth as the significant environmental variables driving taxonomic chironomid distribution in northern Finland, while we found $\delta^{13}\text{C}_{\text{OM}}$, depth and Chl-a_s significant for FFG distributio. Both taxonomic and functional approaches thus identified factors related to productivity among the most influential, yet divergent forcings prevailed for taxonomic versus functional groups. Interestingly, LOI was not a significant variable in our RDAs. However, significant for the FFGs were $\delta^{13}\text{C}_{\text{OM}}$, indicating the origin of OM (Meyers & Teranes 2001), and sedimentary Chl-a, representing a combination of pelagic and benthic production and likely reflecting the latter more closely due to source proximity. This suggests that OM quality plays an important role for FFG composition. Water depth is a well-known indirect factor affecting taxonomic chironomid diversity (Korhola, Olander & Blom 2000) and its effects on chironomid functionality are related to different habitats and altered substrate quality along a depth gradient.

Isotopic signatures of chironomids

Several studies have previously noted that chironomid carbon SI signatures are closely associated with those of sediment OM (e.g. Wooller, Wang & Axford 2008; van Hardenbroek et al. 2013; Belle et al. 2017a), which is evident also in our data. Chironomid nitrogen SIs have been widely applied in ecological studies of living larvae (e.g. Grey, Kelly & Jones 2004; Chételat, Cloutier & Amyot 2010; Bartels et al. 2012a; Reuss et al. 2013), but rarely in paleolimnological approaches (Griffiths et al. 2010). Typically, our $\delta^{15}\text{N}_{\text{HC}}$ enrichment relative to $\delta^{15}\text{N}_{\text{OM}}$ values (mean \pm SD 2.50 \pm 0.45 ‰) reflect trophic fractionation (Vander Zanden &

Rasmussen 2001), whereas $\delta^{13}\text{C}_{\text{HC}}$ values were more ^{13}C -depleted than $\delta^{13}\text{C}_{\text{OM}}$ (-1.48 ± 0.80 ‰), likely due to selective ingestion or assimilation of preferred components rather than bulk OM (Doi, Katano & Kikuchi 2006; Solomon et al. 2008). The $\delta^{13}\text{C}_{\text{HC}}$ values showed variation of over 14 ‰ (from -34.36 to -20.38 ‰), covering a range of typical allochthonous and autochthonous production (France 1995; Meyers & Teranes 2001), and had a strong positive relationship with $\delta^{13}\text{C}_{\text{OM}}$. This indicates significance of sedimentary carbon in the chironomid diet and agrees with the observed FFG patterns, where detritus feeding strategies were dominant. The $\delta^{15}\text{N}_{\text{HC}}$ (ranging over 4.36 ‰) had a relationship with $\delta^{15}\text{N}_{\text{OM}}$ nearly as high as for carbon, suggesting a strong dependence on the variation within isotopic base level of the nutrition, and a weaker connection to the trophic dynamics for the $\delta^{15}\text{N}_{\text{HC}}$. Lake depth also had a strong relationship with $\delta^{15}\text{N}_{\text{HC}}$, likely through the connection between $\delta^{15}\text{N}_{\text{HC}}$ and $\delta^{15}\text{N}_{\text{OM}}$. Rantala et al. (2016b) suggested that reduction of benthic production in deeper waters may partially explain the ^{15}N -enriched $\delta^{15}\text{N}_{\text{OM}}$. Accordingly, $\delta^{13}\text{C}_{\text{HC}}$ is affected through similar changes in carbon composition along a depth gradient becoming more ^{13}C -depleted in deeper waters (Solomon et al. 2008).

The isotopic carbon offset $\Delta \delta^{13}\text{C}$ between the lakes varied over almost 3 ‰, indicating differences in the level of selectivity of chironomid feeding between sites. It has been previously shown that chironomids (Bartels et al. 2012a; Belle et al. 2017a) and aquatic insects in general (Marcarelli et al. 2011) select for higher quality nutrition. In our results $\Delta \delta^{13}\text{C}$ tended to be higher when the $\delta^{13}\text{C}_{\text{OM}}$ was less ^{13}C -depleted, suggesting that feeding selectivity is higher in conditions with higher proportion of carbon from terrestrial sources or benthic production in the sediment. This may be related to discriminating against allochthonous or poor quality organic components either in ingestion or assimilation. It may also be connected to the presence of rich benthic algal and bacterial production, where a variety of autochthonous resources of different nutritional quality is easily available, thus creating a situation where highly selective foraging strategy is easy and cost-efficient.

For the $\Delta \delta^{15}\text{N}$ and $\delta^{15}\text{N}_{\text{OM}}$, a weaker inverse relationship was observed. Although the relationship was less clear than for carbon, the pattern where higher $\Delta \delta^{15}\text{N}$ is associated with lower $\delta^{15}\text{N}_{\text{OM}}$ support feeding preference for the isotopically more ^{15}N -enriched autochthonous sediment fraction, such as benthic algae, over poorer quality nutrition, such as bacteria or terrestrial resources. Besides diet quality (Post 2002; McCutchan et al. 2003; Vanderklift & Ponsard 2003), nitrogen isotopes discrimination can also increase, for instance, by starvation of the fauna (Hobson, Alisauskas & Clark 1993) or nitrogen limitation of the algae (Vander Zanden & Rasmussen 2001) they feed on. The trophic N enrichment for chironomids is smaller (ca 1.5 ‰, Goedkoop et al. 2006) than 3.4 ‰ generally considered a standard in food web studies (Minagawa & Wada 1984; Vander Zanden & Rasmussen 2001; Post 2002). The combination of our bulk assemblage approach and low numbers of predatory chironomids may result in challenges distinguishing positive relationships between higher $\Delta \delta^{15}\text{N}$ values and assemblages with larger proportion of predators, even though our $\Delta \delta^{15}\text{N}$ range is wide enough to accommodate several trophic levels. Partly for the same reason, all isotopic relationships directly with the FFGs are difficult to interpret and impossible to quantify, as our isotopic signatures represent the bulk assemblage while the FFG analysis was performed with a finer resolution. Accordingly, such relationships should be viewed cautiously acknowledging the discrepancy in resolution.

Carbon sources and contributions

SI mixing models may provide valuable information on potential carbon sources for paleoecological studies. Assigning the fractionation coefficient is a challenge for mixing models, as fairly small changes may significantly alter the model outcome (Caut, Angulo & Courchamp 2009; Bond & Diamond 2011). Our model appears robust in this regard, as we used a chironomid-specific average for fractionation (Goedkoop et al. 2006) and tested others applicable for aquatic food webs (Vander Zanden & Rasmussen 2001; McCutchan et al. 2003), which all yielded similar between-lake patterns. Also, the literature-based end-member SI value estimates provide sensible spatio-temporal variability, excluding the problem with site-

specific isotope ‘snapshot’ of the end-members. They also define a clear area where the observations are located within the isospace plot (e.g. Phillips et al. 2014). It has been shown that Bayesian models are relatively insensitive to variation in the source values if isotopic differences between the end-members are large (Tanentzap et al. 2017). Accordingly, the model is used only for relative across-lake comparisons.

In the study lakes autochthonous material was composed primarily by benthic production (Rantala et al. 2016b), typical of shallow subarctic lakes (Vadeboncoeur et al. 2002; Rautio et al. 2011). Benthic algal and bacterial mats were observed in several of the lakes during sampling while the chl-a values from the water column remained low indicating low planktonic production (Rantala et al. 2016b). This agrees with our SI mixing model, which identified benthic sources generally most dominant (mean benthic > 50 % in 10 lakes), especially above the pine tree line. Mean pelagic contribution was less than 25 % in more than half of the lakes, and accordingly, pelagic coupling to the zoobenthos has been previously reported weak in Arctic lakes (Hershey et al. 2006; Chételat et al. 2010). However, the pelagic component appeared highly important in some lakes (mean pelagic > 50 % in 4 lakes). The most ^{13}C -depleted $\delta^{13}\text{C}$ values ($\delta^{13}\text{C}_{\text{HC}}$ -34.4 ‰ and $\delta^{13}\text{C}_{\text{OM}}$ -33.8 ‰) possibly representing mixed methanogenic signal (e.g. Jones & Grey 2011) instead of sole high pelagic dominance were found in lake #21, which is a deeper funnel shaped basin likely experiencing bottom anoxia at least part of the year. Although the $\delta^{13}\text{C}_{\text{HC}}$ and $\delta^{13}\text{C}_{\text{OM}}$ values were in the range of pelagic production (Finlay & Kendall 2007), even lower $\delta^{13}\text{C}$ values (-39.8 ‰) from fossil cladocerans from the same site (Rantala, Luoto & Nevalainen 2016a) support incorporation of methane oxidizing bacteria into the food web.

We observed a geographical pattern within the source contributions where benthic and terrestrial components differed below and above the coniferous (pine) tree line. A similar pattern can be seen in the pelagic component. Benthic resources are generally dominant in lakes above the pine tree line, whereas pelagic and terrestrial components have higher relative importance below it. While vegetation zones are often identified as significant drivers of lake and sediment chemistry (e.g. Korhola, Weckström & Blom

2002), Rantala et al. (2016b) found that vegetation zones did not significantly explain the variability of limnology or sediment geochemistry in the study lakes owing to overriding influence of wetland cover. Wetland-related environmental parameters such as CDOM, DOC, and nutrient concentrations do not show clear differences above versus below the pine tree line. However, higher N/P ratio and lower pH below the tree line suggests that the differences in resource use across the tree line may be associated with the quality of allochthonous input. Allochthonous substances originating from cool coniferous forest soils are more acidic (Aitkenhead-Peterson et al. 2003) and bioavailable (Berggren, Laudon & Jansson 2007) than those from wetlands, which may boost pelagic production in small concentrations and increase heterotrophic production, consequently leading to the higher importance of pelagic and terrestrial source contributions.

Depth of the water column was positively linked with the pelagic source contribution, indicating that pelagic food components are preferred when available in deeper lakes. Benthic and pelagic mean source contributions correlated with the C/N ratio of OM, suggesting that the relative availability of these resources is reflected in the surface sediment chemistry. The C/N relationship to terrestrial source utilization was small and non-significant, which could be an indication that most of the terrestrial carbon is in the dissolved form as DOM (dissolved organic matter) instead of sedimentary forms which would be more available for foraging chironomids. This would highlight the importance of heterotrophic pathways over direct ingestion of allochthonous OM.

Allochthonous input to the study lakes is variable and linked to catchment wetland coverage, which is mirrored at the lakes as higher nutrient loading and increased concentrations of DOC and chromophoric substances (Rantala et al. 2016b). Mean terrestrial source contribution in our mixing model varied from 7 to 53 % between lakes, and was clearly associated with the N/P, DOC and kdPAR as seen by similar ordination directions. Positive correlations of terrestrial contribution with DOC, CDOM and kdPAR showed that allochthony is higher in lakes with higher terrestrial input and lower water transparency as also

observed by Solomon et al. (2011). The question of how much allochthonous carbon is capable of supporting the aquatic food webs has been debated (e.g. Cole et al. 2011; Brett et al. 2012, 2017). However, a recent study by Tanenzap et al. (2017) linking allochthony to lake and catchment parameters showed that terrestrially derived resources for lake food webs are important, constituting a minimum of 42 % in half of the consumer (zooplankton) observations. Our study suggested more modest importance of terrestrial resources in chironomid diet, which is in accordance with experimental studies noting that omnivores are less likely to incorporate terrestrial subsidies (Bartels et al. 2012b), and that while there is a large variability between allochthony amongst benthic organisms, chironomids especially have a low reliance on terrestrial OM (Bartels et al. 2012a). These differences are likely linked to the different feeding strategies, which diverge even among detritivores. For instance, during high terrestrial load detritivores feeding directly on the sediment surface incorporate more terrestrial resources, while burrowing chironomids can consume sediment OM from different depths and hence can easily select for better quality nutrition, as suggested by experiments (Bartels et al. 2012a).

Terrestrial carbon is known as poor quality nutrition (Brett et al. 2009) and, while becoming more available through processing by heterotrophic bacteria (Jansson et al. 2000), both the mechanisms and conditions where allochthonous resources serve as an important source supporting the aquatic food web require further investigations. With the RDA, we identified extrinsic variables related to substrate quality and quantity in addition to carbon optical measures to be most significant for determining directly the $\delta^{13}\text{C}_{\text{HC}}$ and $\delta^{15}\text{N}_{\text{HC}}$, as well as the relative SI resource contributions. RDA identified water colour and SUVA, which are directly linked to the extent of terrestrial input in the lakes (Weishaar et al. 2003; Rantala et al. 2016b), important for source contributions and kdPAR for the $\delta^{13}\text{C}_{\text{HC}}$ and $\delta^{15}\text{N}_{\text{HC}}$, indicating that light availability and consequent effects on productivity (Ask et al. 2009; Karlsson et al. 2009; Seekell et al. 2015) affect resource consumption by chironomids. In addition, the drainage ratio (Cat/Lake) was identified significant for the source contributions, likely due to its association with the quality and quantity of catchment inputs through hydrological features.

The tight coupling between primary production (pelagic and benthic) and terrestrial OM through nutrient input and light limitation controls the relative availability of resource pools (Seekell et al. 2015), which is important in guiding consumer resource use in lakes. Allochthonous input can supplement autochthonous resources (Solomon et al. 2008), while it may not be capable of superseding autochthonous components due to weaker nutritional quality (Kelly et al. 2014; Carpenter et al. 2016). It has become evident that the time (e.g. seasonality) or space (e.g. habitat) limited availability of these different resources is directly related to their usage within and between lakes (Tanentzap et al. 2017). Our results suggest that resource availability is controlled by environmental attributes, but resource consumption is guided by preference for higher quality nutrition when available.

Conclusions

Controls over chironomid isotopic signatures, FFGs and nutrition pools used by chironomids appear to be related to the quantity and quality of OM, nutrient load and light climate in the study lakes. Allochthonous input from the catchment exerted a strong control over the levels of nutrients and chromophoric substances, which together with water depth, guided the distribution of FFGs in the lakes. The use of different carbon pools as nutrition sources was dependent on resource availability and quality. The environmental parameters related to carbon, bio-optics and nutrients, controlled resource availability and were crucial in defining the framework where functional differences occur. Chironomids appeared to feed selectively as isotopic discrimination was higher in excess of poor quality food suggesting that different feeding strategies should be considered in studies of macrozoobenthos. Resource use is thus linked to the proportion of available carbon pools in different habitats, but also feeding strategies and level of selectivity implied by the fauna, highlighting the importance of understanding the functional ecology of different food web components, especially among the lower levels of secondary production as the effects are further cascaded in the food web. By applying the functional approach into a paleolimnological context, we open

doors for a wider understanding of organic carbon processing by macrobenthic fauna, and its consequent effects for the aquatic ecosystem functions in space and time. Accordingly, functional paleoecology, as defined and applied in the current study by a combination of chironomid functional classification, SIA and mixing models, has potential to disentangle ecosystem functions beyond taxonomic information, and will be particularly interesting when applied to longer timescales covering lake ontogeny and biological adaptations to changing climate.

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Appendix 1. A list of Chironomid morphotypes assigned to different functional feeding groups (FFG)

Morphotype	Subfamily	FFG
Collector-filterer		
Cladotanytarsus mancus-type	Chironominae	c-f
Corynocera ambigua	Chironominae	c-f
Corynocera oliveri-type	Chironominae	c-f
Micropsectra contracta-type	Chironominae	c-f
Micropsectra insignilobus-type	Chironominae	c-f
Micropsectra radialis-type	Chironominae	c-f
Paratanytarsus	Chironominae	c-f
Paratanytarsus austriacus-type	Chironominae	c-f
Paratanytarsus penicillatus-type	Chironominae	c-f
Rheotanytarsus	Chironominae	c-f
Tanytarsus glabrescens-type	Chironominae	c-f
Tanytarsus lactescens-type	Chironominae	c-f
Tanytarsus lugens-type	Chironominae	c-f
Tanytarsus mendax-type	Chironominae	c-f
Tanytarsus pallidicornis-type	Chironominae	c-f
Microtendipes pedellus-type	Chironominae	c-f
Collector-gatherer		
Constempellina	Chironominae	c-g
Pseudochironomus	Chironominae	c-g
Chironomus anthracinus-type	Chironominae	c-g
Cladopelma lateralis-type	Chironominae	c-g
Demicryptochironomus	Chironominae	c-g
Dicrotendipes nervosus-type	Chironominae	c-g
Pagastiella	Chironominae	c-g
Paratendipes nudisquama-type	Chironominae	c-g
Sergentia coracina-type	Chironominae	c-g
Stictochironomus rosenschoeldi-type	Chironominae	c-g
Corynoneura arctica-type	Orthoclaadiinae	c-g
Heterotanytarsus	Orthoclaadiinae	c-g
Heterotrissocladius grimshawi-type	Orthoclaadiinae	c-g
Heterotrissocladius maeaeri-type	Orthoclaadiinae	c-g
Heterotrissocladius marcidus-type	Orthoclaadiinae	c-g
Hydrobaenus conformis-type	Orthoclaadiinae	c-g
Hydrobaenus johannseni-type	Orthoclaadiinae	c-g
Limnophyes	Orthoclaadiinae	c-g
Metriocnemus fuscipes-type	Orthoclaadiinae	c-g
Parakiefferiella bathophila-type	Orthoclaadiinae	c-g
Prosilocerus type N	Orthoclaadiinae	c-g
Psectrocladius (A#) flavus-type	Orthoclaadiinae	c-g

Psectrocladius (M#) barbatipes-type	Orthocladiinae	c-g
Psectrocladius (M#) calcaratus-type	Orthocladiinae	c-g
Psectrocladius (M#) septentrionalis-type	Orthocladiinae	c-g
Psectrocladius sordidellus-type	Orthocladiinae	c-g
Synorthocladius	Orthocladiinae	c-g
Monodiamesa	Diamesinae	c-g
Predator		
Ablabesmyia longistyla-type	Tanypodinae	prd
Ablabesmyia monillis-type	Tanypodinae	prd
Derotanypus	Tanypodinae	prd
Procladius	Tanypodinae	prd
Thienemannimyia	Tanypodinae	prd
Cryptochironomus	Chironominae	prd
Protanypus	Diamesinae	prd
Shredder		
Polypedilum nubeculosum-type	Chironominae	shr
Brillia	Orthocladiinae	shr
Cricotopus cylindraceus-type	Orthocladiinae	shr
Cricotopus (I#) intersectus-type	Orthocladiinae	shr
Cricotopus type P	Orthocladiinae	shr
Zalutschia mucronata-type	Orthocladiinae	shr
Zalutschia type B	Orthocladiinae	shr
Zalutschia zalutschicola	Orthocladiinae	shr

Appendix 2. Values and literature references that are used for defining end-member estimates for the stable isotope mixing model.

d13C ‰	SD	d15N ‰	SD	Material	Location	Literature source
Pelagic endmember						
-32.8	1.9	4.8	1.9	CLAD	Saanajärvi	Eloranta, Kahilainen & Jones 2010
-31	0.5			CLAD	Saanajärvi	Rautio, Mariash & Forsström 2011
-29.5	0.8	4.8	0.8	ZPL	Lake Fyresvatnet	Jensen, Kiljunen & Amundsen 2012
-31	0.7	3.5	0.8	ZPL	Inarijärvi	Thomas et al. 2016
-33.3	4.5	4.5	1.6	ZPL	Saanajärvi	Eloranta, Kahilainen & Jones 2010
-31	0.7	1.1	0.6	ZPL	Lake Fyresvatnet	Jensen et al. 2017
-31	1	3.8	0.7	ZPL	Inarijärvi	Eloranta, Nieminen & Kahilainen 2014
-30.9	0.2	3.1	0.3	ZPL	Inarijärvi	Kahilainen et al. 2017
-31.5	0.4	3.9	0.9	ZPL	Muddusjärvi	Kahilainen et al. 2017
-32.5	0.1	3.8	0.1	ZPL	Paadarjärvi	Kahilainen et al. 2017
-31.6	0.1	4.3	0.1	ZPL	Kilpisjärvi	Kahilainen et al. 2017
-33.6	0.03	3.4	0.1	ZPL	Kuohkima	Kahilainen et al. 2017
-32.4	0.3	3.8	0.2	ZPL	Siilasjärvi	Kahilainen et al. 2017
-31.8	1.2	4.5	1.4	ZPL	Kilpisjärvi	Hayden, Harrod & Kahilainen 2014
-31	1.5	3.7	0.7	ZPL	Tuulisjärvi	Eloranta et al. 2015
-31	2	2	1	ZPL	Gæsjavri	Eloranta et al. 2015
-31.5	0.7	2	0.2	ZPL	Lille Rostavatn	Eloranta et al. 2015
-32	0.5	3.5	0.2	ZPL	Muddusjärvi	Eloranta et al. 2015
-32	2	3	1	ZPL	Saanajärvi	Eloranta et al. 2015
-37	2	7.5	2	ZPL	Sagelvatn	Eloranta et al. 2015
-32	2	3	1	ZPL	Takvatn	Eloranta et al. 2015
-31	0.7	4	0.2	ZPL	Inarijärvi	Eloranta et al. 2015
-32	0.2	3	0.2	ZPL	Vuolit spielgjavri	Eloranta et al. 2015
-32.5	2	4	0.7	ZPL	Biggijavri	Eloranta et al. 2015
-32	2	3.5	0.7	ZPL	Ukonjärvi	Eloranta et al.

-37	2	8	1	ZPL	Josefvatn	2015 Eloranta et al.
-34	2	2.5	0.7	ZPL	Fjellfrøsvatn	2015 Eloranta et al.
-32	0.7	4	0.2	ZPL	Rahajärvi	2015 Eloranta et al.
-32	0.2	3	0.7	ZPL	Datkujvari	2015 Eloranta et al.
-31	1	4	1	ZPL	Pulmankijärvi	2015 Eloranta et al.
-32	0.7	4	0.2	ZPL	Kilpisjärvi	2015 Eloranta et al.
-32.1	1.1	3.8	0.7	MEAN		
1.6	0.9	1.3	0.5	STD		
Benthic endmember						
-24.4	1	2.5	1	B. MAT	Masi	Mariash et al. 2011
-24.2	0.5	-0.8	0.1	B. MAT	Boat	Mariash et al. 2011
-27	0.2	-0.2	0.4	B. MAT	Big rock	Mariash et al. 2011
-23	0.5	-0.1	0.1	B. MAT	Happy	Mariash et al. 2011
-19.5	2.7	0.5	0.4	B. MAT	North Malla	Mariash et al. 2011
-15.7	1.5	0.3	0.5	B. MAT	South Malla	Mariash et al. 2011
-16.4	1.3	-1.1	0.1	B. MAT	Reindeer	Mariash et al. 2011
-19	1	0.8	0.8	B. MAT	Lampo	Mariash et al. 2011
-21.4	2	-1.4	1	B. MAT	Tuono	Mariash et al. 2011
-17	1.5	1	1	B. MAT	Straca	Mariash et al. 2011
-21.6	4.3	1.1	0.6	BIOFILM	Saanajärvi	Eloranta, Kahilainen & Jones 2010
-28		3.7		BIOFILM	Inarijärvi	Kahilainen et al 2017
-17.5		1.3		BIOFILM	Muddusjärvi	Kahilainen et al 2017
-20.8	2.5	2	0.6	BIOFILM	Paadarjärvi	Kahilainen et al 2017
-18	0.2	1.8	1	BIOFILM	Kilpisjärvi	Kahilainen et al 2017
-17.7		-0.4		BIOFILM	Kuohkima	Kahilainen et al 2017
-24.4	0.3	0.9	0.3	BIOFILM	Siilasjärvi	Kahilainen et al 2017
-24.7				EPILITHOS	Lake Almerga	Karlsson, Ask & Jansson 2008
-21.1	1.4	0.7	0.6	MEAN		
3.7	1.1	1.3	0.3	STD		
Terrestrial endmember						
-27				C3 plant	Global	Marshall, Brooks & Lajtha 2007
-28	0.8			SOIL	Njakajaure	Rosen et al. 2009

-26.5	0.6			SOIL	Ohio	Weber et al. 2017
-29.73	2.31	0.99	2.11	LITTER	Västerbotten	Jonsson & Stenroth 2016
-29	0.8	-0.5	0.4	LITTER	Gollinsee	Syväranta et al. 2016
-29.5	1.2	-1.3	0.3	LITTER	Schultzensee	Syväranta et al. 2016
-28.5	1	0.3	1	LITTER	Hudson river	Cole & Solomon 2012
		-3	0.5	LEAF	Toolik	Nadelhoffer et al. 1996
		-6	0.5	LEAF	Toolik	Nadelhoffer et al. 1996
		2	0.5	LEAF	Toolik	Nadelhoffer et al. 1996
		2	0.3	LEAF	Sag River	Nadelhoffer et al. 1996
		-5	0.5	LEAF	Sag River	Nadelhoffer et al. 1996
		-6	0.5	LEAF	Sag River	Nadelhoffer et al. 1996
-28	1.25	-2.5	3	LEAF	W Greenland	Reuss et al. 2013
-28.3	1.1	-1.7	0.9	MEAN		
1.1	0.5	2.9	0.8	STD		

Abbreviations: CLAD = cladoceran, ZPL = zooplankton (bulk), B. MAT = benthic bacterial mat, BIOFILM = benthic biofilm, EPILITHOS = epilithic algae, SOIL = organic soil C, LITTER = aged leaf litter, LEAF = alive vegetation