

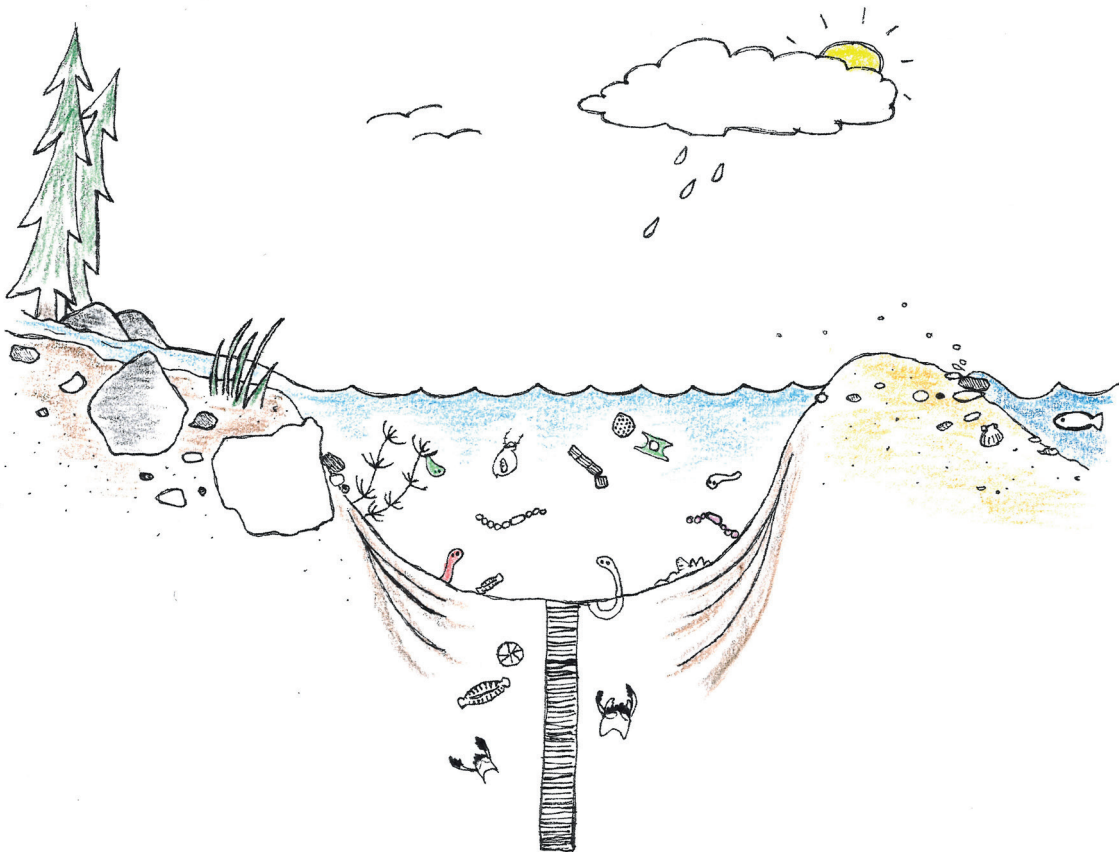
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Henriikka Kivilä

# Functional Paleoecology and Allochthonous Inputs in High Latitude Lake Food Webs

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UNIVERSITY OF JYVÄSKYLÄ  
FACULTY OF MATHEMATICS  
AND SCIENCE

JYU DISSERTATIONS 74

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Henriikka Kivilä

# Functional Paleoecology and Allochthonous Inputs in High Latitude Lake Food Webs

Esitetään Jyväskylän yliopiston matemaattis-luonnontieteellisen tiedekunnan suostumuksella  
julkisesti tarkastettavaksi yliopiston Ambiotica-rakennuksen luentosalissa YAA303  
toukokuun 3. päivänä 2019 kello 12.

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in building Ambiotica, hall YAA303, on May 3, 2019 at 12 o'clock noon.



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## ABSTRACT

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Yhteenveto: Funktionaalinen paleoekologia ja alloktoninen aines pohjoisten järvien ravintoverkoissa

Diss.

Arctic freshwaters are subject to large scale changes triggered by ongoing climate change, including lengthening of the growing season, alterations of thermal regimes and biochemical rearrangements. Better understanding of biological responses to ongoing changes may rise from the past. This paleolimnological work examines functional assemblage structures and their diversity in high latitude lakes from subarctic Finland (spatial dataset of 25 lakes and a core from Lake Loajžejávri) and Arctic Canada (a core from Greiner Lake) in reference to long-term environmental change. Furthermore, responses of benthic functional assemblages to allochthonous inputs (carbon, nutrients), which are predicted to increase along the proceeding climate change, were investigated. In subarctic Finland, chironomid (Diptera: Chironomidae) functional feeding groups (FFG) were found to have different preference for nutrient and carbon based variables, suggesting that they are potential habitat indicators. Resource utilization of chironomids, as revealed by spatial and temporal stable isotope (C and N) modelling, was controlled primarily by availability of resources and secondarily by selective assimilation of different carbon pools, however no strong connection to FFG structure was detected. Regardless, allochthonous carbon input affected resource utilization by increasing allochthony and FFG distribution by habitat changes. External nutrient loads increased productivity in the study lakes, and from the ontogeny of Greiner Lake marine nutrients were found particularly important. This suggests that rising sea level, exposing low-lying coastal lakes to marine influence, may contribute to greening of Arctic from the aquatic perspective. These findings build towards better understanding of past food web functioning and associated responses to environmental change and altered energy flows under influence of multiple stressors.

Keywords: Arctic; Chironomidae; environmental change; nutrients; organic carbon; resource utilization; stable isotopes.

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# TIIVISTELMÄ

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Diss.

Nykyinen ilmastonmuutos aiheuttaa merkittäviä muutoksia arktisissa järvissä, esimerkiksi kasvukauden pidentymistä sekä muutoksia lämpötiloissa, kerrostuneisuudessa ja biokemiallisissa kierroissa. Aiempien muutosten tutkiminen auttaa ymmärtämään myös nykyisiä muutosvasteita. Tässä paleolimnologisessa työssä selvitettiin toiminnallisten yhteisöjen rakennetta ja monimuotoisuutta järvissä Suomen Lapissa (pintasedimenttiaineisto 25 järvestä sekä sedimenttisarja Loazžejävristä) ja arktisessa Kanadassa (sedimenttisarja Greiner Lake -järvestä) suhteessa pitkäaikaiseen ympäristömuutokseen. Tutkimuksessa selvitettiin myös pohjaeläinten toiminnallisten yhteisöjen vasteita alloktoniseen ainekseen (järven ulkopuoliset ravinteet ja hiili), minkä kulkeutumista järviin ilmastonmuutoksen arvioidaan lisäävän. Surviaissäskien (Diptera: Chironomidae) toiminnallisten ravinnonkäyttöryhmien (FFG, functional feeding group) havaittiin suosivan toisistaan poikkeavia ravinne- ja hiilikuormia, mistä johtuen ryhmät voivat toimia elinympäristön ilmentäjinä. Surviaissäskien ravintolähteiden hyödyntämistä tutkittiin niin eri järvien välillä kuin ajassa taaksepäin hiilen ja typen vakaiden isotooppien suhteiden avulla. Ravinnonkäyttöä ohjasi ensisijaisesti ravinnon saatavuus, eikä vahvaa yhteyttä FFG:iden kanssa havaittu. Alloktonista ainesta päätyi ravintoverkkoon enemmän voimakkaan alloktonisen vaikutuksen aikana, ja sen määrä ohjaili myös FFG:iden suhteellisia osuuksia vaikuttamalla elinympäristömuuttujiin. Ravinnekormitus lisäsi järvien tuottavuutta ja Greiner Lake -järven historiassa meriperäisillä ravinteilla oli erityisen suuri merkitys. Aineistosta voidaan päätellä, että merenpinnan nousu saattaa muuntaa laakeilla ranta-alangoilla sijaitsevia arktisia järviä tuottavammiksi. Tutkimuksen tulokset täydentävät käsitystämme ravintoverkkojen toiminnallisuudesta sekä vasteista ympäristön ja energiavirtojen muuttuessa.

Avainsanat: Arktinen; Chironomidae; eloperäinen hiili; ravinteet; ravintolähteiden hyödyntäminen; vakaat isotoopit; ympäristömuutos.

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## LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following original articles, which will be referred to in the text by their Roman numerals I-III.

- I Kivilä E.H., Luoto T.P., Rantala M.V., Kiljunen M., Rautio M. & Nevalainen L. 2019. Environmental controls on benthic food web functions and carbon resource use in subarctic lakes. *Freshwater Biology* 64: 643–658.
- II Kivilä E.H., Luoto T.P., Rantala M.V. & Nevalainen L. 2019. Late-Holocene variability in chironomid functional assemblages and carbon utilization in a tundra lake. Submitted manuscript.
- III Kivilä E.H., Rantala M.V., Antoniadou D., Luoto T.P., Nevalainen L. & Rautio M. 2019. Sea level rise may contribute to Arctic greening of coastal waterbodies, implications from the ontogeny of Greiner Lake, Nunavut, Canada. Submitted manuscript.

Contribution of H. Kivilä and the other authors to preparation of each article (I-III) are presented in Table 1.

TABLE 1 Author contributions to articles I-III. HK = Henriikka Kivilä, TL = Tomi Luoto, LN = Liisa Nevalainen, MVR = Marttiina Rantala, MR = Milla Rautio, MK = Mikko Kiljunen and DA = Dermot Antoniadou.

	I	II	III
Original idea	HK, TL, LN	HK, TL, LN	HK, MR
Data collection	MVR, TL, LN	MVR, TL, LN	HK, MVR, MR
Data analysis	HK, MVR, TL, LN, MK	HK, TL, LN	HK, MVR, MR, DA, TL
Writing	HK, MVR, TL, LN, MK, MR	HK, TL, LN, MVR	HK, MVR, MR, DA, TL, LN



## ABBREVIATIONS

CDOM	Coloured dissolved organic matter
CE	Common Era
C-F	Collector-filterer
C-G	Collector-gatherer
C/N	Carbon to nitrogen mass ratio
DOC	Dissolved organic matter
DW	Dry weight
FA	Fatty acid
FD	Functional diversity
FFG	Functional feeding group
HPLC	High-performance liquid chromatography
LOI	Loss-on-ignition
m a.s.l.	Metres above sea level
MCA	Medieval Climate Anomaly
PCA	Principal components analysis
PERMANOVA	Permutational analysis of variance
PRD	Predator
RDA	Redundancy analysis
SCR	Scraper
SHR	Shredder
SUVA	Specific ultraviolet absorption
TD	Taxonomic diversity

# 1 INTRODUCTION

## 1.1 Arctic lakes in a changing environment

A prominent feature of northern landscapes is abundance of lakes, ponds and temporary freshwater bodies. These northern freshwaters hold many unique qualities considering their biota, interaction with catchment and responses to climatic alterations (Vincent *et al.* 2008, Rautio *et al.* 2011, Smol 2015). Food webs of arctic lakes are often short and simple, frequently composing of only producers and invertebrate consumers. Some lakes host fish, most commonly Arctic char (*Salvelinus alpinus*), which may be landlocked or anadromous. Harsh conditions, including low temperatures, short open water period, extreme seasonality of light and often poor nutrient availability, generate challenges for biological activity in lakes causing the high latitude ecosystems to “live on the edge”. For this reason, high latitude aquatic ecosystems are sensitive and susceptible to change, which makes them a well-suited target for environmental change studies (Smol and Douglas 2007). Furthermore, direct human influence is often minimal on high latitude lakes, allowing for research on natural stressors. Most high latitude lakes are considered pristine to near-pristine, however, indirect human influence is inherently present even at the remotest sites due to atmospheric contamination pathways (Holtgrieve *et al.* 2011).

The ongoing climate change is causing increases in air temperatures and summer precipitation leading to rapid landscape changes especially on permafrost regions and glaciated areas. The thawing permafrost releasing old carbon into the active carbon cycle (Dutta *et al.* 2006, Schuur *et al.* 2015), greening of Arctic landscapes (Pearson *et al.* 2013) and meltwater-derived sea level rise (Meier *et al.* 2007) are examples of critical changes occurring in northern areas. Temperature increase and consequent decrease in ice cover, causing lengthening of the growing season, have resulted in major regime shifts in aquatic communities across the circumpolar Arctic (Smol *et al.* 2005). Arctic warming is considered the main driver of aquatic ecosystem change also in subarctic environments, such as northern Finnish Lapland (Sorvari *et al.* 2002),

which is one of the focal areas of this thesis. In fact, the Northern hemisphere has previously been warming at a similar rate during the Pleistocene–Holocene transition (Stivrins *et al.* 2016), which indisputably is a distinct period of major biotic turnover in many paleoecological records.

Catchment-mediated changes reflected into aquatic environments, such as increased input of carbon and nutrients from surface soils, vegetation and thawing permafrost are considered a major challenge to northern lake ecosystems (Tranvik *et al.* 2009, Vonk *et al.* 2015). Allochthonous components, especially nutrient inputs and concentration of coloured carbon fractions (coloured dissolved organic matter, CDOM), can significantly alter the biochemical, physical and optical characteristics of the receiving lakes (Jansson *et al.* 2007, Karlsson *et al.* 2009, Wauthy *et al.* 2018). Altered balance of light and nutrient availability, as well as changes in thermal regimes, influence primary production, effects of which further cascade into the food web. Increased dissolved organic carbon (DOC) input may enhance heterotrophic production and further alter the energy pathways and nutritional quality of carbon pools available for the lake food webs (Ask *et al.* 2009, Solomon *et al.* 2015). Humic characteristics of lakes are also linked to hypolimnetic oxygen affecting element (incl. carbon) cycling and processing, and recent changes indicate that especially low-humic lakes experience deteriorating oxygen conditions (Luoto *et al.* 2019). Resulting changes may occur in species distribution, community composition and functional arrangements of the ecosystem. Due to the tight connection with active carbon cycle (Battin *et al.* 2009), implications from northern lakes have a global significance, which further highlights the importance of understanding responses to environmental change in these remote ecosystems.

## **1.2 Present as the key to the past – past as the key to the future**

Lake sediments are well known natural archives of environmental change which have provided profound knowledge of past changes in both terrestrial and aquatic ecosystems over a long time (e.g. Smol 2010). Examining long term development of ecosystems from natural archives allows for a remarkably longer observational period than measurements can provide. This applies especially to northern and remote sites, where records of scientific measurement tend to be sparse and short. Natural archives are hence required for understanding long-term changes and for example assessing reference conditions.

However, the long-term perspective is hampered by various factors. All biota does not leave traceable marks into the sediment, taphonomical processes and laboratory pre-treatments may alter the sedimentary signal (e.g. Brodie *et al.* 2011), defining an accurate chronology may be challenging, and the obtained resolution is usually considerably low compared to contemporary ecology. Especially resolving the chronological issues can be a true challenge for

northern lake sediments (Wolfe *et al.* 2004). Despite the multitude of challenges in paleo research, accurate and coherent information within and across sites can be obtained with careful analysis of multiple proxies simultaneously (e.g. Birks and Birks 2006). When methodological limitations are addressed in the study design, sedimentary archives provide an excellent natural laboratory for elucidating questions from climate patterns to ecosystem responses and everything in between. In addition, recent developmental trajectories have brought paleo and contemporary ecology closer to each other, improving our understanding of different scales, patterns and processes of ecosystem change (e.g. Sayer *et al.* 2010, Battarbee *et al.* 2012, Randsalu-Wendrup *et al.* 2016).

While the foundation of paleolimnology builds on the classic idea of uniformitarianism, stating that the present is the key to the past, it has become increasingly evident that the focus of past-orientated research is more often in the future. Understanding systems and mechanisms of nature today and deeper in time provides a constantly improving basis for modelling and estimating future prospects, aiding risk analysis, conservation plans and societal preparing for environmental change (Anderson *et al.* 2006, Dietl *et al.* 2015, Saulnier-Talbot 2016).

### 1.3 Functional ecology in brief

Functional approaches have been developed for improving our understanding on ecosystem dynamics (e.g. Tilman *et al.* 1997, Suding *et al.* 2008). Functional grouping is based on species sharing similar ecological roles, rather than on their taxonomical relationships. In a way, each functional group serves the ecosystem by providing a certain ecosystem function. Accordingly, functional changes in an ecosystem express changes in ecosystem processes, and hence are signs of larger scale, mechanistic changes. As an example from aquatic ecosystems, several non-taxonomic classifications (including functional) have been developed for phytoplankton over past decades and such approaches are widely used to decipher applicable ecological questions (Salmaso *et al.* 2015). Similar functional groupings have been produced also for macroinvertebrates, e.g. chironomids (Cummins and Klug 1979, Merritt *et al.* 2008), which have been especially applied to riverine environments for assessing their biomonitoring value (Heino *et al.* 2004, Statzner *et al.* 2004, Dolédec and Statzner 2008, Heino 2008, Gomes *et al.* 2018). However, functional approaches to date have been rarely used in paleolimnological studies (Gregory-Eaves and Beisner 2011, Luoto and Nevalainen 2015, Nevalainen and Luoto 2017, Luoto and Ojala 2018) and consequently the long-term perspective on ecosystem functioning is still limited.

The current understanding of ecological functionality is challenged by knowledge gaps on species scale, as many taxa (especially benthic-littoral taxa) lack functional and life trait information. While principally the functional grouping does not follow taxonomy, closely related species often share similar

morphological features and traits leading to similar ecological functions. Therefore, in some cases the taxonomical connections may help defining the functional group. For instance, with diatoms the prominent functional characteristics are similar at least up to taxonomical order level (Rimet and Bouchez 2012). Likewise, chironomids often share similar functional characteristics up to subfamily level, as their functional classification is based on feeding method, hence for instance morphology of their mouth parts (Cummins and Klug 1979).

Ecosystem resilience, describing an ecosystem's capacity to resist change and quickly recover after an environmental perturbation (Holling 1973, Hodgson *et al.* 2015), is intimately linked with the functional characteristics of the ecosystem. Resilience is affected by diversity both between and within its functional groups, as larger groups may comprise larger variety of traits and consequently are more likely to be redundant to change (Peterson *et al.* 1998, Oliver *et al.* 2015). Furthermore, reduction in number of functional groups may lead to lowered resilience and reorganization of the ecosystem, causing for example food web changes. Hence, understanding resilience is particularly important for assessing ecosystem's responses to environmental change. Improved understanding of resilience would be valuable concerning today's topical issues of accelerating biodiversity loss and climate change impacts (Loreau *et al.* 2001, Oliver *et al.* 2015).

#### **1.4 Objectives of the study**

The main objective of this thesis was to explore functional food web characteristics of high latitude lakes and their responses to allochthonous inputs and environmental change from a paleolimnological perspective. In a broader context, the new findings may help in assessment of ecosystem responses to future changes that are expected to occur in northern lake ecosystems following the ongoing climate change and associated catchment-mediated biogeochemical shifts.

More specifically, the aim was to define compositional changes in functional assemblages of major organism groups (chironomids, diatoms) in a spatio-temporal setting and to examine these changes in relation to environmental variables, such as catchment-originated carbon-optical variables and nutrient load, as well as climatic factors. It was hypothesised that the allochthonous inputs would affect the functional assemblage composition and that the changes within functional assemblages reflect larger scale mechanistic changes in the lake ecosystem than the taxonomical changes.

Accordingly, the following specific aims were addressed:

1. To relate benthic functional assemblages and their resource utilization with biogeochemical attributes (from the lake sediment, water and catchment) in surface sediments of subarctic lakes across the treeline ecotone in northern Finnish Lapland (I).
2. To explore changes in benthic functional assemblages and their resource utilization in a spatio-temporal setting and evaluate the potential of macrozoobenthic functional groups as bioindicators (I, II).
3. To examine lake ontogeny and explore functional and ecological responses of primary producers and consumers in relation to allochthonous inputs (nutrients, carbon) (II, III).
4. To assess the concept of functional paleoecology as identifying functional responses to environmental change in a long-term context and decipher the character of ecological responses in relation to environmental change (II, III).

## 2 MATERIALS AND METHODS

### 2.1 Study sites

#### 2.1.1 Northern Finland

The regional surface sediment dataset covered in this work (I) originates from 25 small and shallow (max depth 0.5–6.3 m) lakes in the northern Finnish Lapland (Fig. 1a). These sites span over 120 km on a S–N transect and cross the treeline ecotone; featuring a gradient from Scots pine (*Pinus sylvestris*) dominated north boreal mixed pine and birch forest, through mountain birch (*Betula pubescens* spp. *czerepanovii*) woodlands on to the shrub tundra, which is typically vegetated by lichens and dwarf birch (*Betula nana*) among areas of barren ground. In addition to vegetation change, the lakes were chosen to encompass a large gradient in organic carbon concentration and quality. Wetlands, mainly minerotrophic fens, are common in the area and the lakes are located in the region of discontinuous permafrost.

Bedrock in the area is composed of diverse metamorphic Paleoproterozoic rocks including garnet-cordierite gneiss, quartz rich gneisses and diorites. Soil thickness in the area is commonly thin and especially at higher elevations bedrock outcrops are typical. The mineral soils compose mostly of gravel and sand rich glacial tills occurring at different thickness. Organic soils are thin if present, with the exception of peatlands.

Gradient of summer temperature in the study area is short ( $\sim 1$  °C, mean July temperature) considering the geographical extent. The prevailing subarctic climate on the region features mean annual and mean July temperature of  $-2$  °C and  $13$  °C, respectively, with approximately 450 mm of annual precipitation (Finnish Meteorological Institute). The area lies at the fluctuation zone of Eurasian continental air masses and maritime influence from the North Atlantic and Barents Sea, mixing qualities from both climate types. Human activities are a minor factor considering the lake set.

A small and oligotrophic tundra lake, Lake Loazžejávri ( $69^{\circ} 53' N$ ,  $26^{\circ} 55' E$ ) was selected for a down core site for this study (II). This shallow (max depth

1.2 m) lake is located in Utsjoki in the northern Finnish Lapland and lies at an elevation of 255 m a.s.l. above the (mountain birch) treeline (Fig. 1b). The 3.0 ha lake is surrounded by a catchment area covering ca. 2 km<sup>2</sup>, which features mostly subarctic shrub tundra vegetation and some peaty areas. Soil cover is thin and bedrock composing of Proterozoic quartz feldspar and amphibolite outcrops at higher elevations. In addition to precipitation, the lake receives water from surrounding springs and a smaller spring fed lake. One small outlet stream directs the water onward from Lake Loazžejávri. The lake is pristine and situated far from direct human activities.

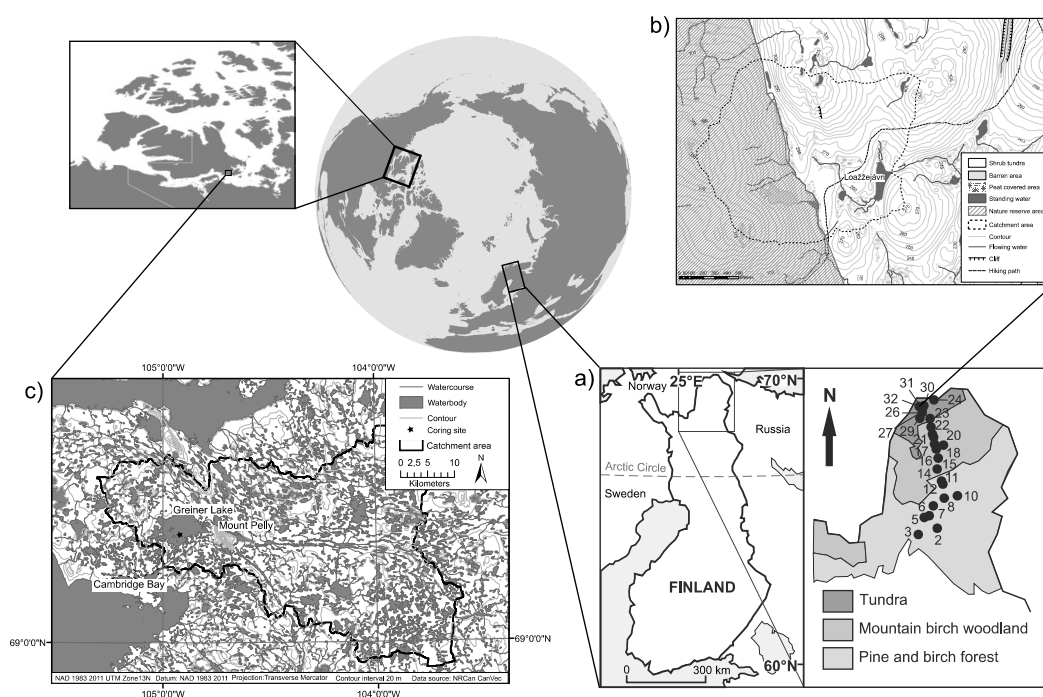


FIGURE 1 Map of the study areas in the northern hemisphere: a) location of the regional lake set of 25 lakes in northern Finland, b) catchment map for a down core site, Lake Loazžejávri, equalling lake number 32 of the regional lake set and c) location of a core site, Greiner Lake, near Cambridge Bay on southern Victoria Island, Nunavut, Canada. Map sources: a) I, b) II, c) III. Spherical index map is by FreeVectorMaps.com.

### 2.1.2 Cambridge Bay area, Arctic Canada

The main site for this study in Cambridge Bay area is Greiner Lake (69° 11' N, 104° 56' W) (III), which is located approximately 7 km away from the settlement of Cambridge Bay on Victoria Island, Nunavut, Canada (Fig. 1c). Greiner Lake is a large (47 km<sup>2</sup>) yet fairly shallow (max. depth 12 m, mostly 3–5 m deep) lake with a 1,580 km<sup>2</sup> catchment area. The lake lies at an elevation of ca. 15 m a.s.l.



and is connected to the sea by a ca. 4 km long outlet river Freshwater Creek. The lowland catchment area hosts a myriad of small lakes and freshwater bodies located between patches of grass and shrub tundra. Bedrock of the catchment area is composed of Ordovician to Silurian limestones and dolomites and covered with thin and discontinuous deposits of glacial origin.

The climate in Cambridge Bay is low arctic with annual mean temperature of  $-14\text{ }^{\circ}\text{C}$  and precipitation of 142 mm. Seasonal variability is high, mean temperature being  $-32\text{ }^{\circ}\text{C}$  in January and  $9\text{ }^{\circ}\text{C}$  in July. Due to the harsh winters ice cover on lakes builds up to approximately two metres and the ice-out does not occur until late June–July, leading to a short open water period of about 2 months. A moat forms around the shore line earlier following the snow melt period.

## 2.2 Sampling and sample handling

Field sampling was carried out in July 2014 for sites in northern Finnish Lapland (I, II), and in June 2015 for northern Canada (III). Sediment sampling was performed with an Aquatic Instruments gravity corer for Greiner Lake (III) and with a Limnos gravity corer for sites in northern Finland (I, II). In addition, limnological data (*in situ* measurements and water samples) were collected from the lakes in northern Finland (I).

Surface sediment samples (0–2 cm) (I) and the 38 cm Late-Holocene series from Lake Loazžejávri (1 cm sample resolution) (II) taken with the Limnos corer were sectioned in the field into zip lock bags and stored in  $+4\text{ }^{\circ}\text{C}$ . The sediment core from Greiner Lake (III) was wrapped into black plastic immediately after retrieval, to prevent light-triggered degradation of sedimentary pigments, and the sediment–water interface was stabilised with sodium polyacrylate (Tomkins *et al.* 2008) to preserve the core as whole. The core was kept in cold and dark until splitting and sectioning (0.5 cm resolution) it in a dark room within two days. The sectioned samples were stored frozen and protected from light until pigment analysis. Subsamples from all sediment samples were treated according to the protocols of following analyses, which are outlined in detail in I–III.

Limnological data (I) were collected from the epilimnetic water of each study lake in northern Finland and represent one time measurements, hence these data do not account for inter-annual nor seasonal variation. The sample bottles were rinsed three times with sample water and the samples were stored in  $+4\text{ }^{\circ}\text{C}$ . For thorough information about handling of water samples and limnological analyses see Rantala *et al.* (2016). As some of the measurements and analyses used in this thesis have been previously published, the original sources are listed in Table 2 for clarification.

TABLE 2 Original sources for data that have been used in making of the articles I-III.

	I	II	III
Limnological & catchment analyses	Rantala et al. 2016, Nevalainen et al. 2015	Rantala et al. 2016	
Sediment geochemistry	Rantala et al. 2016, I	II	III
Chironomid isotopes	I	II	
Chironomid taxonomy	Luoto et al. 2016	Luoto et al. 2017	III
Functional classification	I	II	III
Chronology		Luoto et al. 2017	III
Temperature reconstruction		Matskovsky & Helama 2014	

## 2.3 Laboratory analyses

### 2.3.1 Biological proxies and functional classification

Taxonomic analysis of fossil chironomids (Diptera: Chironomidae) is a well-established paleoecological tool. Chironomids are commonly used in proxy studies of Arctic lake archives, as they often inhabit harsh environments and their chitinous remains preserve well in the sediment. The abundance and taxonomic composition of chironomid communities are controlled by several environmental factors they are sensitive to, such as temperature, water depth, oxygen saturation and nutrients (e.g. Walker 2001, Brodersen and Quinlan 2006, Engels and Cwynar 2011, Luoto 2011, Eggermont and Heiri 2012). Accordingly, chironomid fossils are commonly used to infer qualitative and quantitative trends in environmental attributes, particularly in temperature. In this work, fossil chironomid assemblages were analyzed from a regional surface sediment dataset (I) and two down core sequences (II, III), to assess patterns in their functional composition in relation to environmental variability, particularly for responses to varying quality and quantity of terrestrial carbon (I, II), climatic fluctuations (II) and lake ontogeny (II, III). The taxonomical analyses were performed according to standard methods following Brooks *et al.* (2007) and have been partly published (Luoto *et al.* 2016, 2017). Each taxon was further on assigned a functional feeding group (FFG) following Mandaville (2002) and Merritt *et al.* (2008). In this thesis five FFGs were present, collector-gatherers (C-G), collector-filterers (C-F), shredders (SHR), predators (PRD) and scrapers (SCR) (I-III).

Diatom algae (Bacillariophyceae) are frequently used bioindicators both in modern and paleolimnological studies due to their sensitivity to environmental change and wide distribution (Smol and Cumming 2000, Stevenson *et al.* 2010). Among the most important factors constraining within-lake diatom distribution are light and nutrient availability, pH and availability of suitable physical

habitat. Fossil diatom assemblages were analyzed for their ecological guild composition, reflecting trends in the diatom life strategies linked to nutrient enrichment and resistance to disturbance across different stages of lake ontogeny (III). Preparation of diatom samples followed standard methods (Battarbee *et al.* 2001) and identification was based on Witkowski *et al.* (2000). Ecological guild classification was based on Rimet and Bouchez (2012), and four ecological guilds, treated as functional groups, were identified: low profile (live in the biofilm, tolerate low nutrients and high disturbance), high profile (attached benthic taxa, require high nutrients and low disturbance), motile (fast moving species, tolerate high nutrients and low disturbance) and planktonic (centric taxa, planktonic habitat) groups.

Cladocera (Crustacea: Branchiopoda) are likewise known to be useful indicators of past environmental and climatic conditions. In this study, Cladocera paleoassemblage was used for inferring changes in water depth (II). Samples were produced according to standard procedure (Szeroczyńska and Sarmaja-Korjonen 2007, Rautio and Nevalainen 2013) and cladoceran exoskeletons were identified to planktonic and littoral forms. The planktonic-littoral ratio is closely linked to water depth allowing for reconstruction of former lake level change (Alhonen 1970, Sarmaja-Korjonen 2001).

In addition, when examining biodiversity and ecosystem processes from the mechanistic perspective through functional groups, functional diversity measures should be used instead of taxonomic diversity (Hooper *et al.* 2002). Accordingly, diversity indices were calculated for chironomid and diatom functional (functional diversity, FD) and taxonomic (taxonomic diversity, TD) assemblages (I-III) using the Shannon diversity index  $H'$  (Shannon 1948).

### 2.3.2 Geochemical analyses

Proportion of organic matter (OM) in sediment can be assessed by loss-on-ignition (LOI) technique, where organic components are removed from the sediment by exposing it to temperature of 550 °C (Heiri *et al.* 2001). Elemental composition of carbon and nitrogen can be used for both quantitative and qualitative evaluation of OM. It should be noted that on areas where carbonate minerals occur, the inorganic carbon components are required to be removed from the sediment samples prior to elemental analysis to allow for assessing the organic carbon content. This is implemented by acid fumigation (Ramnarine *et al.* 2011). In this study, LOI (I, II) and elemental composition of OM (I-III) were used to assess between-lake variability in surface sediment composition (I) and long-term trends in OM accumulation (II, III).

The elemental ratio of carbon to nitrogen, the C/N, gives indication on the origin of OM. The ratio is distinctly different between vascular land plants (typical C/N  $\geq 20$ ) and aquatic primary production, especially protein rich algae, which generally range from 4 to 10 (Meyers 2003). In this work, C/N, expressed as a mass ratio, is calculated for all sediment samples (I-III).

Magnetic susceptibility is a method to assess abundance of magnetic minerals in the sediment, and may be used to identify changes in sediment

minerogenic content and environmental perturbances (Oldfield *et al.* 1983). Magnetic susceptibility was analysed for Greiner Lake sediments (III).

### 2.3.3 Stable isotope analyses

Stable isotope ratios of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) were analysed for all sediment samples from the OM (I–III) and from chitinous chironomid remains for the sites in northern Finland (I, II). In sediment approaches, stable isotopic ratios are a useful tool on determining the origin of OM. The  $\delta^{13}\text{C}$  is used to differentiate between allochthonous and autochthonous (benthic and pelagic) sources (e.g. Hecky and Hesslein 1995, Meyers 2003, Finlay and Kendall 2007, Rosén *et al.* 2009). Terrestrial OM ( $\delta^{13}\text{C}$  typically approximately  $-27\text{‰}$ ) and  $^{13}\text{C}$ -depleted phytoplankton may be barely distinguishable from each other, partly because phytoplankton signal is typically inferred from seston, and therefore does not represent a clear phytoplankton signal. However, signs of benthic production, which is usually characterized by less  $^{13}\text{C}$ -depleted values (often below  $-25\text{‰}$ ), may be separated with higher confidence.  $\delta^{15}\text{N}$  is indicative of origin of nitrogen, such as atmospheric fixation of  $\text{N}_2$ , and can bring additional support to analysis of allochthonous–autochthonous dynamics, but due to complexity of aquatic nitrogen cycle and its enrichment in the food web, interpretation of sole  $\delta^{15}\text{N}$  remains often equivocal.

In ecological studies,  $\delta^{13}\text{C}$  indicates the nutrition assimilated by an organism (fractionation  $< 1\text{‰}$ ) and  $\delta^{15}\text{N}$  contains information on both nutrition and trophic position of the organism, as the heavier isotope ( $^{15}\text{N}$ ) enriches in the food web with an average of  $3.4\text{‰}$  per trophic level (Peterson and Fry 1987, Post 2002). These principles were applied to chironomid fossils, which were analysed for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in a spatial (I) and a temporal (II) setting, to elucidate which nutrition pools they have utilized first in varied environments and then in a long-term perspective. Chitinous fossil chironomid remains resemble closely the same isotopic composition as living larvae (van Hardenbroek *et al.* 2018), and hence hold valuable potential for paleoecological food web studies. Furthermore, the approach of stable isotope analysis on invertebrate remains is fairly novel (Perga 2010, Heiri *et al.* 2012, van Hardenbroek *et al.* 2018). For chironomid fossils stable isotopes of carbon have been commonly used for tracing long-term methane emissions (van Hardenbroek *et al.* 2012, 2013, Wooller *et al.* 2012, Belle *et al.* 2016), but they have been increasingly applied to for example disentangling carbon dynamics during lake regime shifts, oxygen depletion and implications for food webs (Frossard *et al.* 2014, 2015, Belle *et al.* 2017a, b, van Hardenbroek *et al.* 2018).

In this research, all sedimentary stable isotope analyses (C and N) were performed on freeze dried sediments with necessary pre-treatments (removal of inorganic carbonates), and standard protocols (Heiri *et al.* 2012) were applied for analyses of chitinous chironomid remains. Chironomid remains were handpicked and represent bulk assemblage due to scarcity of remains in the

sediment and mass requirements for the isotope samples. Throughout the work, isotopic ratios are expressed as delta notations

$$\delta = (R_{\text{sample}}/R_{\text{standard}} - 1) * 1000$$

where R equals the stable isotope ratio ( $^{13}\text{C}/^{14}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$ ) and international reference standards used were Vienna Pee Dee Belemnite (VPDB) for carbon and atmospheric concentration (AIR) for nitrogen.

### 2.3.4 Biomarkers – biochemical traces of past life

While many organisms do not leave behind a fossil record, they may leave identifiable biochemical markers, such as pigments, fatty acids or other molecular components with a specific, well preserving chemical structure. Such biomarkers can be chemically extracted from sediment, and their specific composition and relative abundance may hold valuable ecological information.

Analysis of sedimentary pigments, which evolved after invention of high-performance liquid chromatography (HPLC) techniques, allows for identifying concentrations of different carotenoid and chlorophyll pigments. Mostly the pigments originate from aquatic primary producers, composing of different groups of algae and bacteria. Some particularly common pigments (e.g.  $\beta$ ,  $\beta$ -carotene and chlorophyll-*a*) serve as indicators of whole system production, as they are present in most primary producers, while other pigments may be specific to a certain group (e.g. cyanobacteria), or even to genus (e.g. *Chlorobium*). Pigments are sensitive to light, heat and oxygen, which causes them to easily degrade during falling through water column and early sedimentation, as well as after retrieval when the samples are processed. To prevent post-depositional degradation, the pigment samples are stored frozen and all handling is performed in the dark. In this study, sedimentary pigments were used for detecting patterns in productivity and oxygen conditions from the Greiner Lake core (III). The analysis was performed according to standard protocols (Zapata *et al.* 2000) and identification of the HPLC chromatograms was based on reference spectra (Hurley and Watras 1991, Jeffrey *et al.* 1997). Pigment concentrations were normalized to amount of organic carbon in the samples (%C<sub>org</sub>).

Fatty acids (FA), a type of lipid molecules that are essential for the survival, growth and reproduction of most animals, have become an increasingly common biomarker used in contemporary food web and nutritional studies. Certain types of FAs are produced by certain groups of organisms, for instance, long-chained (more than 20 carbon atoms in a chain) saturated FAs are produced solely by land plants and FAs of unconventional shape (cylindrical or bent) are of bacterial origin. Some of the best known FAs, the omega-3 FAs, originate principally from aquatic primary production, and a ratio between the long ( $\geq 20$  C atoms) and short-chained Omega-3 differs between organism groups and environmental conditions (Galloway and Winder 2015). FAs preserve in sediment but their biomarker potential and

taphonomical processing require further assessment. FAs were analyzed from Greiner Lake sediment sequence to disentangle patterns in productivity, terrestrial input and microbial activity (III). The FAs were extracted from freeze dried sediment samples (stored in  $-80\text{ }^{\circ}\text{C}$  to prevent degradation) in a chloroform-methanol mixture, trans-esterified at  $50\text{ }^{\circ}\text{C}$  and analyzed by gas chromatography mass spectrometry. The resulting fatty acid methyl ester (FAME) concentrations were normalized to the amount of organic carbon in the samples ( $\%C_{\text{org}}$ ).

### 2.3.5 Chronological methods

Temporal context for paleolimnological material is commonly defined by radiometric methods. Fallout radionuclides ( $^{210}\text{Pb}$  and  $^{137}\text{Cs}$ ) are useful for dating recent sediment sequences (Appleby 2001, 2008), whereas older sediments can be dated with radiocarbon ( $^{14}\text{C}$ ). These approaches were applied to the two sediment cores in this study (II, III), however, concentration of  $^{210}\text{Pb}$  and  $^{137}\text{Cs}$  were insufficiently low for constructing an age model in both cases. Therefore the chronology of Lake Loazžejávri (II), which has been first published in Luoto *et al.* (2017), was based on accelerated mass spectrometry (AMS) radiocarbon dates from terrestrial macrofossils, and chronological constrains of Greiner Lake (III) were based on an AMS radiocarbon date (blue mussel) and former knowledge on surrounding landscape evolution, for example land uplift rate. Further details are provided in II and III.

## 2.4 Statistical analyses

### 2.4.1 Stable isotope mixing models

In modern ecological research, Bayesian stable isotope mixing models are common practice in food web studies for inferring relative contribution of different nutritional components to mixed diets. In this work, the method was applied to paleoecological data, using stable isotope measurements of carbon and nitrogen from chironomid fossils as the consumer observations, and literature-based values for the source estimates. The stable isotope mixing model was introduced for a surface sediment dataset to elucidate how environmental variables are linked to resource utilization by chironomids (I) and applied down core to assess these dynamics in a long-term context (II).

The model considered two stable isotope ratios ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) and three potential source end-members: terrestrial (mean  $\pm$  SD  $\delta^{13}\text{C} = -28.3 \pm 1.1$ ,  $\delta^{15}\text{N} = -1.7 \pm 2.9$ ), pelagic ( $\delta^{13}\text{C} = -32.1 \pm 1.6$ ,  $\delta^{15}\text{N} = 3.8 \pm 1.3$ ) and benthic ( $\delta^{13}\text{C} = -21.1 \pm 3.7$ ,  $\delta^{15}\text{N} = 0.7 \pm 1.3$ ) production. End-member values were based on published measurements (I), which allow for considerable variability within the sources and improves robustness of the model. End-member values were corrected for trophic fractionation with a chironomid-specific fractionation

coefficient of  $0.50 \pm 0.56 \text{ ‰}$  and  $1.5 \pm 0.50 \text{ ‰}$  (Goedkoop *et al.* 2006), for carbon and nitrogen, respectively. The model was calculated with *simmr* package (Parnell and Inger 2016) in R. Further details on the model are provided in I.

#### 2.4.2 Multivariate analysis

Multivariate analyses are commonly used in paleoecological studies to disentangle patterns in complex relationships between biological data and multiple environmental drivers. Multi-dimensional ordination methods are one way of exploring relationships for a number of environmental (explanatory) variables with several response variables. The resulting (two dimensional) projections allow for searching relationships and patterns within the data, whereas the axis scores (typically axis 1), which represent major gradients of variability within the data, compress the most prominent changes in a suite of response variables into one variable. A linear unconstrained ordination method, principal component analysis (PCA), was used for summarizing variation in groups of analysed variables (e.g. fatty acids, diatom functional assemblage) to display the strongest gradients within the groups (III). These were used to aid the interpretation of different phases in the Greiner Lake ontogeny.

Redundancy analysis (RDA), a constrained linear ordination method, was applied to the regional dataset (I) and a down core site (II) to unravel relationships for functional groups, isotopic signatures and resource use of chironomids with the environmental attributes in a spatiotemporal setting. Monte Carlo permutations with forward selection were further used to identify significant environmental variables. Selection of environmental variables for the RDA was based on a cut-off value for variation inflation factors ( $< 25$ ). To explore responses between the chironomid functional assemblage and a single environmental variable in the regional dataset, which encompassed large environmental gradients in concentrations of nutrients and dissolved carbon fractions, responses were modelled with generalized linear models (GLM) with quadratic fit and Poisson response distribution (I).

Hierarchical clustering is a method to identify groups of multiple variables based on their similarity with each other. Depth-constrained hierarchical clustering (UPGMA) with Bray-Curtis similarity index was applied to diatom functional assemblages from Greiner Lake to identify functionally different phases during the core evolution (III). Permutational analysis of variance (PERMANOVA), with Bonferroni corrected pair-wise *post hoc* test, was further used to distinguish significant differences between the functionally different phases in Greiner Lake core (III).

## 3 RESULTS AND DISCUSSION

### 3.1 Functional paleoecology

Functional grouping in this study was applied for chironomid fossils (I-III) and fossil diatoms (III), which are both common members of aquatic high latitude ecosystems. The composition and diversity of functional assemblages were explored in reference to environmental change across different levels of ecosystem, both from perspective of primary producers and consumers, in spatial and temporal scales.

#### 3.1.1 Functional groups as habitat indicators

Functional groups of different aquatic organisms are known to show connections with certain habitats. For example, first order grouping of cladoceran functional assemblages divides the groups according to habitat (Nevalainen and Luoto 2017). Also diatom ecological guilds, which can be considered functional groups, are adapted to certain environments associated with particular abiotic factors, such as light availability, nutrient concentrations and physical disturbance (Passy 2007, Rimet and Bouchez 2012). Consequently, they have been used as indicators of changing environmental conditions (III, Stenger-Kovács *et al.* 2013). For chironomids, such habitat preferences have not been properly assessed from a paleoecological perspective. However, contemporary studies highlight local factors as drivers of functional characteristics of macroinvertebrates (Heino 2005, 2008) and also importance of habitat (Johnson and Goedkoop 2002, Johnson *et al.* 2004).

Large environmental variability within the spatial dataset allowed for identifying responses of chironomid functional assemblages to different variables of water and sediment chemistry (I). Responses were tested for four functional feeding groups (FFG): collector-gatherers (C-G), collector-filterers (C-F), shredders (SHR) and predators (PRD) that were present in most of the lakes. Results show that the chironomid FFGs have different preferences for many conditions, especially considering DOC, nutrient concentrations and water



depth (I), which suggests that chironomid FFGs may hold important potential for being habitat indicators (Table 3).

For paleolimnological work on chironomid FFGs, a response to temperature has been suggested previously (Luoto and Nevalainen 2015), especially a low temperature optimum for C-Fs. Other works have suggested connections between nutrients and FFGs; during eutrophication C-Gs tolerate higher concentrations of nutrients than the other FFGs (Luoto and Ojala 2014). Studies on High Arctic ponds reveal that functional assemblages differ between oligotrophic and bird impacted, murkier sites (Luoto and Ojala 2018). C-Fs dominate the oligotrophic sites, whereas C-Gs inhabit the bird impacted sites in absence of C-Fs. Different preferences between these two most common FFGs (C-G and C-F) are also evident in results of this work (I). In agreement with Luoto and Ojala (2018), it was observed that C-Fs had preference for intermediate depth with low sediment organic content and lake water with high transparency and low nutrient content, whereas C-Gs had preference for high organic content in the sediment, and shallow, nutrient rich waters with higher DOC levels.

The other two FFGs occurring in the spatial data set (SHR and PRD) did not show as strong responses to investigated environmental gradients. Partly weak connections may be due to their smaller abundances, but it may also be that these FFGs respond to different factors than what were tested. For instance, presence of SHRs is typically associated with macrophyte containing lake habitats to provide plant material (living or dead) for their food (Merritt *et al.* 2008), hence presence and absence of macrophytes is the likely factor driving distribution of SHRs and consequently water and sediment chemistry exert only a secondary control over SHR distribution. In stream systems SHRs are associated with leaf litter (Cummins *et al.* 1989, Arias-Real *et al.* 2018), however, in lentic environments aquatic macrophytes probably play a more important role than terrestrial plant remains. PRDs are likely controlled by food availability to a large extent, but may also be guided by multiple factors. Luoto and Nevalainen (2015) observed higher occurrence of PRDs in warmer lakes, which are generally also more productive and may feature higher food web complexity and habitat diversity.

Considering temporal patterns, prevalence of C-Gs has been observed during past warmer periods like Holocene Thermal Maximum (Luoto and Nevalainen 2015) and Medieval Climate Anomaly (II), whereas C-Fs have been found to dominate sediment assemblages from the Little Ice Age (II, Luoto and Nevalainen 2015). Responses to recent climate warming do not necessarily show the same pattern, suggesting that instead of direct temperature control, the functional assemblages are directed by long-term climate mediated habitat changes, where changes in catchment load have an important role. In agreement, Luoto and Ojala (2014) showed that eutrophication process controlled midge functional assemblages over climate and Luoto and Ojala (2018) depicted nutrient control over FFG changes in Arctic ponds. One interesting aspect for assessing the habitat indicator potential of FFGs is that some groups may be strictly habitat specific, whereas others have a wider

ecological range. For instance, SHRs require a habitat with vascular plant input, while C-Gs appear to occur in environments where the other FFGs may not thrive (Luoto and Ojala 2014) and have widest tolerance considering many environmental variables (I, II). Current knowledge suggests that the most common FFGs (C-G and C-F) have wider tolerance than the rare groups, but more work is required from different environments to clarify the picture of habitat preference and tolerance width, hence the sensitivity of FFGs as habitat indicators. In addition, it is worth noting that assigning chironomids into a single FFG is somewhat ambiguous, as their feeding modes may incorporate a considerable amount of plasticity and they may employ several feeding modes during their life cycle (Berg 1995, Mihuc 1997, Reuss *et al.* 2013). While drivers of this plasticity are not well known, their effects may be mirrored to the habitat preference and ecological tolerance of FFGs. Adding that current knowledge on chironomid functional traits contains considerable gaps (Heino 2008, Serra *et al.* 2016) there remains much room for future research, however, the current evidence suggests a robust classification into preferred habitats can be constructed. Furthermore, chironomid feeding strategies are not as prone to change along temperature gradient as those of other macroinvertebrates (Gordon *et al.* 2018), which suggests that FFGs of chironomids may be more suitable bioindicators than FFGs of other benthic macroinvertebrates.

TABLE 3 Suggested habitat preferences for chironomid FFGs based on response modelling of environmental variables (I) and temperature preferences from Luoto and Nevalainen (2015), described on a crude three-level (low, medium, high) scale. NS = no significant response in models.

FFG	Depth	Sediment OM content	DOC	Nutrients	Temperature	Tolerance width	Habitat preference
C-G	Low	High	High	High	Low-High	High	Organic rich sediment, shallow, nutrient-rich waters
C-F	Medium	Low	Low	Low	Low	Medium	Oligotrophic, cold, clear waters
SHR	High	Low	Low	NS	Medium	Low	Macrophyte presence
PRD	NS	Medium	NS	NS	High	Low	Complex habitats

### 3.1.2 Functional diversity and sediment composition

Functional diversity (FD) is an essential biodiversity measure when seeking mechanistic understanding of ecosystems and their processes (Hooper *et al.* 2002). In this research, FD ranged between 0.28–1.35 for chironomids and diatoms (Fig. 2a), which both were represented by four functional groups in most cases. On the other hand, taxonomic diversity (TD) for the same group ranged between 0.82–3.60 featuring high variability in number of taxa, diatom samples being generally more diverse than the chironomid samples. In agreement with many former studies (e.g. Micheli and Halpern 2005,

Nevalainen *et al.* 2015, Schmera *et al.* 2017) FD and TD were positively correlated ( $r = 0.71$ ,  $p < 0.0001$ ), although opposing results have also been presented (Cadotte *et al.* 2011).

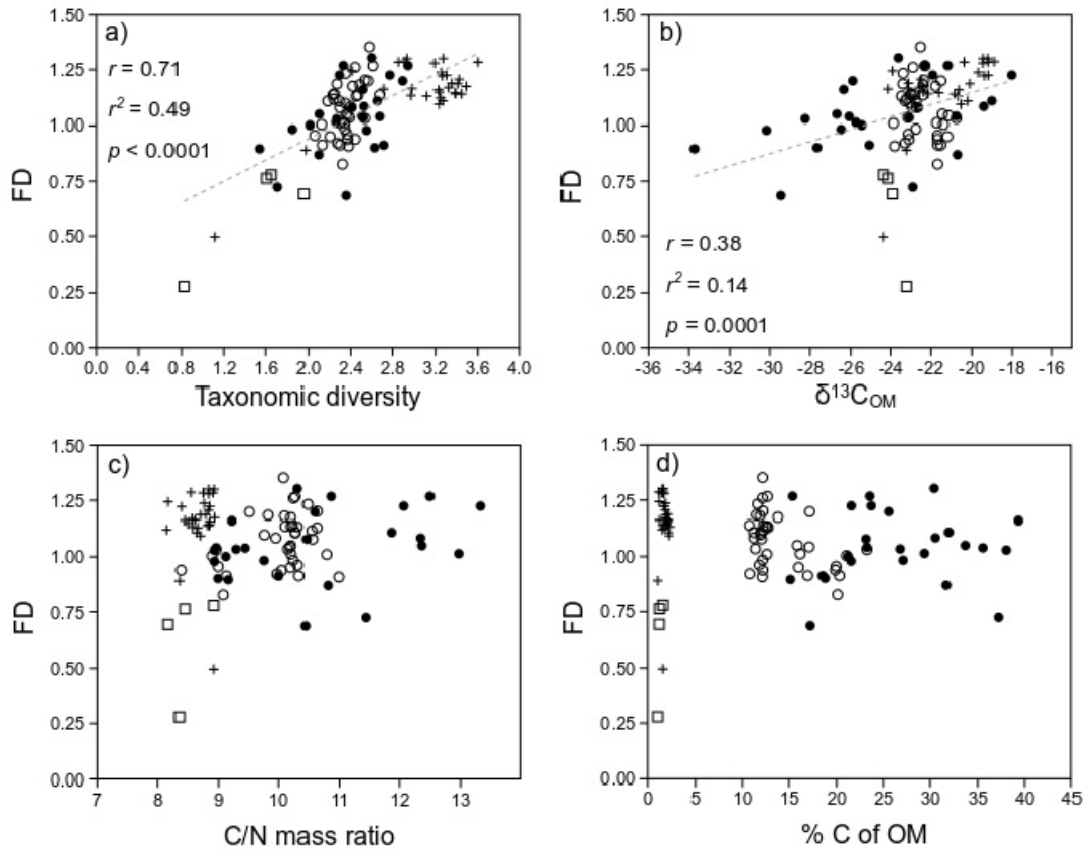


FIGURE 2 Relationships between functional diversity (FD) and a) taxonomic diversity, b)  $\delta^{13}C$  signature of organic matter, c) sedimentary C/N mass ratio and d) percentage of C in sediment organic matter. Black dots: chironomids from a spatial dataset in northern Finland (I), open circles: chironomids from a lake sediment core in northern Finland (II), open squares: chironomids from a sediment core in Arctic Canada (III), crosses: diatoms from a sediment core in Arctic Canada (III). Correlation coefficients ( $r$ ), coefficients of determination ( $r^2$ ) and significances ( $p$ ) are shown where  $p \leq 0.05$ .

For macroinvertebrates, both species richness and FD have been associated with habitat complexity related to physical heterogeneity of lakes (Heino 2008, 2009). From long term records, FD has also been suggested to be higher during intermediate temperatures and generally lower during cold or warm conditions (Luoto and Nevalainen 2015), which may be related to higher habitat variability in intermediate temperature. In agreement with chironomid taxonomical richness patterns in northern Finland (Nyman *et al.* 2005, Luoto *et al.* 2016) this work shows that substrate quality, one crucial component of habitat characterization, is associated with distribution of FFGs (I). Furthermore, a significant, although not very strong, correlation prevails between FD and sedimentary OM  $\delta^{13}C$ , which is an indicator of substrate quality (Fig. 2b). FD

appears to be both highest and most diverse in the  $\delta^{13}\text{C}$  range from  $-20$  to  $-25$  ‰, typical of benthic production, which may be associated with productivity and food availability for the macroinvertebrates, also defined as important factors for the TD (Nyman *et al.* 2005). However, while pelagic food sources are considered to be of high quality (Brett *et al.* 2009), the results of this research do not indicate that pelagic resources would contribute to higher FD, as observations in the pelagic range ( $\delta^{13}\text{C} < -26$  ‰) show slightly lower FD. Alternatively, these samples could hold higher proportion of allochthonous carbon, but as seen from the relationship between FD and sediment C/N (Fig. 2c), the FD was fairly high with high C/N, which again was indicative of terrestrial influence (Meyers and Teranes 2001). The amount of sedimentary organic carbon shows no significant relationship with FD (Fig. 2d), although quantity of sediment OM is associated with FFG distribution (I). These connections suggest that FD is not driven by sediment characteristics in the same way as FFG distribution, but may be more related to for instance habitat richness.

The FD of diatom functional groups (III) included in these analyses does not show noteworthy connections with the sediment quality variables, which most likely owes to them being driven by factors that are not well reflected into sedimentary carbon fractions, such as nutrient concentrations and water turbulence (Passy 2007, Rimet and Bouchez 2012). Instead, diatom FD has been found to be associated with for instance biomass (Vogt *et al.* 2010).

### 3.1.3 Implications for resilience

Ecological resilience derives from distribution of functional groups within and across ecosystem scales (Peterson *et al.* 1998). Ecological resilience is highest, when the functional groups are evenly dispersed (i.e. maintain high FD) and species richness is high, whereas uneven (clumped) distribution of functional groups leads to less resistant ecosystem functions (Oliver *et al.* 2015). In addition, when evenness remains the same (or FD, if equal amount of functional groups are concerned), increased species richness provides higher resistance of ecosystem functions. This view is based on the idea that larger phenotypic diversity within the functional group allows for wider trait diversity, thereby making more diverse functional groups more redundant to environmental change.

In this research (I-III), most functional assemblages composed of four functional groups, where each functional group composed of 0–10 or 1–26 taxa for chironomids and diatoms, respectively (Table 4). In the spatial dataset (I) two lakes (#5 and #30) had a lower FD (below 0.8) and an FFG structure that was clearly dominated by a single group (ca. 80 %). In addition, functional assemblage in lake #8 composes of only three FFGs. These lakes may thus feature lowered resilience compared to the others. However, no geographical gradients were observed in FD that would have provided insight into resilience characteristics among lakes from different areas. A temporal gradient was observed in the core from northern Finland (II), where FD had an overall

declining trend throughout the series, agreeing well with the more even distribution of FFGs in the lower part of the core and higher dominance of C-F and C-G in the upper part (Fig. 3).

TABLE 4 Number of taxa in each functional group, presented as lowest (min), highest (max) and most common (mode) number of taxa included in respective functional group per sample, and as the total number of taxa included in the functional group across the whole dataset (tot taxa). Three studied datasets are presented separately (I-III). Diatom functional groups: P = planktonic, LP = low profile, HP = high profile, M = motile.

	Spatial, Finland (I)				Core, Finland (II)				Core, Canada (III)			
	min	max	mode	tot taxa	min	max	mode	tot taxa	min	max	mode	tot taxa
<u>Chironomids</u>												
C-G	1	10	6	24	4	9	6	17	0	7	4*	8
C-F	2	9	6	15	4	8	5	11	1	3	3	3
SHR	0	3	2	6	0	4	2	7	0	1	0	1
PRD	1	3	2	7	0	3	2	5				
SCR					0	1	0	1				
<u>Diatoms</u>												
P									1	4	3	5
LP									10	24	18	31
HP									4	15	13	24
M									3	26	18	40

\*average, all samples had different number of taxa

In long-term approaches of this research clear evidence of reorganization in both chironomid (II) and diatom (III) functional assemblages was presented. The chironomid FFG assemblage experienced a permanent shift (at 21 cm) from dominance of detritivores (C-G) to suspension feeders (C-F) that was decoupled from geochemical changes in the lake sediment (II). The diatoms on the other hand experienced a prominent, brief dominance (1–2 cm) of the low profile taxa, known to resist disturbance well, while the assemblage afterwards returned to approximately what it used to be relatively consistently before (III). A common factor between both rapid changes seemed to be catchment originating disturbance that is likely linked to hydrological changes and possibly altered precipitation patterns. However, the responses were quite different, as after disturbance diatoms returned to the pre-shift assemblage structure (III) and chironomids remained in the post-shift assemblage (II). In agreement, it has been formerly noted that functional responses of lakes to moisture tend to be more site-specific than responses to temperature due to basin morphology and hydrological connections (Nevalainen *et al.* 2016).

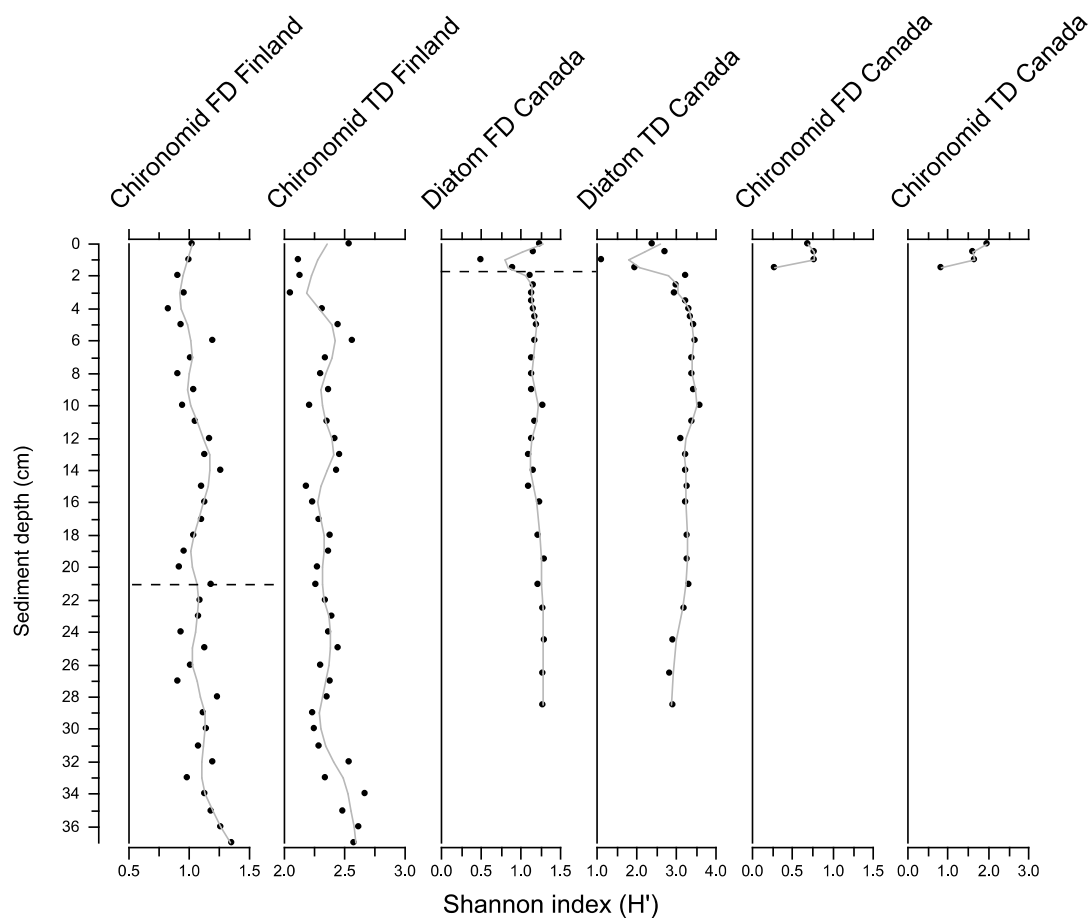


FIGURE 3 Functional diversity (FD) and taxonomic diversity (TD) in the sediment cores from Finland (chironomids) and Canada (diatoms and chironomids) with smoothed trend lines (lowess span 0.2). Dashed horizontal lines represent the horizons where major reorganizations of the functional assemblages occur.

The complete recovery of the diatom functional assemblage (as seen from FD, Fig. 3) suggests that the functional arrangement was resilient in providing the recovery after a major disturbance, whereas the TD did not recover as well. Unfortunately the temporal control of this record does not allow estimation of the duration and pace of the diatom response. In northern Finland, the chironomid FFG assemblage remained somewhat constant since the reorganization despite changes in water level, climate and sediment geochemistry (II), while the reorganization was not much reflected to FD. A steady FD indicates stability of the functional assemblage (i.e. high redundancy), which again would imply fairly constant resilience (Oliver *et al.* 2015) and ecosystem functions (Cadotte *et al.* 2011). Among macroinvertebrates, particularly chironomids have been noted resilient to extreme events (Woodward *et al.* 2015). In addition, paleolimnological records of chironomid FD generally follow climate development (temperature) rather than show abrupt changes (Luoto and Nevalainen 2015, Luoto and Ojala 2018), which may indicate that chironomid functional assemblages are characterized by high resilience.

In cases where FD experiences significant changes, the ecosystem shifts may be related to major thresholds that also alter the resilience patterns (Standish *et al.* 2014). For instance, FD of Cladocera is sensitive to trophic gradients, but FD may not recover during re-oligotrophication after eutrophic conditions (Nevalainen and Luoto 2017, Nevalainen *et al.* 2018). However, the pelagic food web, which cladocerans reflect, may be in general more sensitive to changes in the water column than the benthic food web due to complex food web interactions and fluctuating controls. For example the recovering diatom functional assemblages of Greiner Lake (III) were likely directed by bottom-up controls, enabling recovery once the environmental conditions allow, whereas top-down controls are more common in directing lower level consumers (Leroux and Loreau 2015), contributing to the complexity of interactions.

### 3.1.4 Functional ecosystem responses

With the ongoing fast-paced environmental change, understanding ecosystem responses is of great interest. Functional paleoecology could be an effective tool to explore FD and functional characteristics of past assemblages through different environmental filters reflecting the multiple stressors ecosystems face (Gregory-Eaves and Beisner 2011). Applying the long-term approach may be especially useful in identifying thresholds, periods of functional stability, resilience, ecosystem responses and associated time lags (Dietl *et al.* 2015). Various responses to climatic change have been observed in high latitude lake environments as changing community and food web structure (e.g. Quinlan *et al.* 2005, Wrona *et al.* 2006, Smol and Douglas 2007). Altered resource pools can for instance affect the proportions of specialist and generalist feeders (Thienpont *et al.* 2015a) and the feeding habits of certain taxa (Mariash *et al.* 2018).

In this research, ecosystem responses in two sediment sequences were explored: one reflecting changes in climate and catchment (II) and the other representing a history of marine isolation (III). The ca. 2000 years covering sediment core from northern Finland depicted considerable variability in sediment geochemistry and chironomid FFG assemblages (II). Even though the resource utilization of chironomids and sediment geochemistry were coupled, the FFG structure and sediment geochemistry were decoupled. This suggests that benthic primary producers, which strongly controlled the geochemical shifts, and chironomid functional assemblages responded to different stressors, being functionally decoupled. Decoupling of food web relationships can occur when triggered by environmental controls (Davis *et al.* 2010, McMeans *et al.* 2015), yet the functional connections remain less-studied.

Defining modern analogues from the past ecosystem responses is desirable for assessing future change. The ongoing climate warming and a former warm period, Medieval Climate Anomaly (MCA), were contrasted in the Late-Holocene record from northern Finland (II). These two periods shared relatively little similarity in terms of functional assemblage structure, stable isotope signatures or resource utilization by chironomids, revealing that in this

case the current warming has not analogously resulted in increase of detritivores (C-G) as previously noted from oligotrophic Arctic lakes (Luoto and Ojala 2018). Despite no apparent functional response in the recent sediments, a chironomid response to current warming can be detected from taxonomical changes, even so that chironomid-inferred modern temperatures exceed those of MCA (Luoto *et al.* 2017).

The ecosystem responses to three functionally different isolation phases of Greiner Lake were primarily controlled by nutrient input and altering stratification regimes causing bottom anoxia (III). The diatom functional groups showed primarily response to nutrients and physical disturbance, in accordance with former studies (Passy 2007, Lange *et al.* 2011). Chironomid presence was controlled by oxygen conditions, and the FFG sequence was consequently very short, which hampers the identification of long-term functional responses. An increasing trend in generalist detritivores (C-G) occurred though, which may be related to habitat change or changes in catchment or climate drivers, as in I and II. Overall, the findings support that different levels and components within the ecosystem project complex responses to environmental change, requiring careful assessment of drivers and different scales. While responses appear site-specific, improving knowledge in the future may help to extract trends in responses of aquatic food-webs and ecosystems.

## 3.2 Effects of allochthonous inputs

### 3.2.1 Allochthonous carbon as a resource

Macrobenthic fauna, including chironomids, are commonly considered opportunistic omnivores (Berg 1995, Mihuc 1997, Reuss *et al.* 2013). Accordingly, analyses of gut contents have shown a variety of different ingested food sources independent of primary feeding mode (Henriques-Oliveira *et al.* 2003, Lauridsen *et al.* 2014, Serra *et al.* 2016). In some studies, the diet has been inferred according to the FFG (e.g. Cross *et al.* 2007), however, inferring the diet is more likely to result in biased stoichiometric estimates for the consumer (Lauridsen *et al.* 2014). This suggests that the feeding preferences given to each FFG are indeed preferences. In agreement, no unequivocal relationship between FFG and resource utilization by chironomids was found in this study (I, II). Stable isotopes of C and N have been successfully applied to disentangle nutrition consumption by macroinvertebrates (Zah *et al.* 2001, Grey *et al.* 2004, Bartels *et al.* 2012). Stable isotopes of stream macroinvertebrates also correlate highly with their gut contents (Jardine *et al.* 2005). In this study, resource utilization by chironomid assemblages was examined in a spatio-temporal context from Finnish Lapland using stable isotope modelling (I, II).

Resource utilization was explored by modelling between three sources considered most important in the studied lake systems: pelagic, benthic and terrestrial. Both through space (I) and time (II) the benthic resource was most



utilized, which is in good agreement with both the widespread dominance of benthic production in Arctic lakes (Rautio *et al.* 2011, Rantala *et al.* 2016), and the source proximity implied by basal habitat of chironomid larvae. Pelagic and terrestrial resources were consumed less than benthic (I, II), which may be related to resource availability and quality, respectively. Pelagic algae are high-quality food, containing for instance essential fatty acids, and even small proportions of high-quality algae improve growth rates of detritivores (Crenier *et al.* 2017). However, in Arctic lakes the pelagic production may be limited (Markager *et al.* 1999), and its flow to the benthic food web is weak (Chételat *et al.* 2010), which highlights the importance of benthic pathways in acquiring high-quality nutrition. Terrestrial components are of low nutritional quality and it is debated how much they may support food webs (e.g. Brett *et al.* 2017). However, recent evidence on isopods suggests that they grow better with combined terrestrial and algal sources than just algal nutrition, suggesting synergetic effects between allochthonous and autochthonous resources (Grieve and Lau 2018). Aquatic macrophytes, although their contribution would be interesting, were not assessed in this study as nutrition sources due to their ambiguous stable isotope signatures, which are highly controlled by their growth form and abiotic drivers (Chappuis *et al.* 2017).

From the surface sediment dataset it was observed that terrestrial components were consumed more in lakes with higher allochthonous input and darker water colour (I), in agreement with Solomon *et al.* (2011). However, in lakes where the  $\delta^{13}\text{C}_{\text{OM}}$  indicated high terrestrial load, the chironomid isotopic signatures showed strongest deviation from the sediment ( $\Delta \delta^{13}\text{C}$ ), indicating that they selectively consumed (or assimilated) more other sediment fraction than the terrestrial one, as also shown by Bartels *et al.* (2012) and Belle *et al.* (2017a). Incorporation of allochthonous material seems thus highest when other resources are limited, even if higher quality components were preferred. In the temporal sequence resource utilization featured only subtle changes, however, the lower section of the tundra lake core featured slight increase in utilization of terrestrial components during a time of limited high-quality resources (II). Similar findings were presented in a recent synthesis by Tanentzap *et al.* (2017), who highlighted the effects of catchment size, soil quality and hydrological transport for level of allochthony in the recipient aquatic food webs. Concordantly differences in resource utilization across the coniferous treeline were observed, which can be accounted for differences in quality of allochthonous inputs from coniferous soils and tundra catchments (I). Benthic production highly dominated the tundra lakes, while below the treeline terrestrial and pelagic components played a more important role, associated with the more bioavailable terrestrial carbon input. Despite increased level of uncertainty in modelling paleodata (van Hardenbroek *et al.* 2018), the results suggest that careful application of stable isotope mixing models can provide valuable information about past food web functions.

In relation to the FFG assemblage, allochthonous input exerted a strong control over the concentration of nutrients and chromophoric substances which are important in guiding the distribution of FFGs (I). Yet, no significant

correlation occurred between resource utilization and FFG distribution. Allochthonous effects on FFG distribution are likely habitat-mediated (Luoto and Ojala 2018), whereas importance of terrestrial subsidies for nutrition is dependent on resource availability and selectivity implied by the chironomids (I). Over all, the results of this research suggest that allochthonous inputs affect both defining functional distribution and resource utilization of chironomids.

### 3.2.2 Nutrient enrichment from external sources

Nutrients, nitrogen and most commonly phosphorus are often limiting factors for primary producers of dilute high latitude freshwaters. A commonly addressed phenomenon triggered by climate warming is increased input of nutrients from catchment soils, which alters the biochemistry of the lakes (Jansson *et al.* 2007). Nutrients originating from organic soils are typically accompanied by coloured carbon fractions, which at high enough concentrations counterbalance the advantage of nutrient input for phytoplankton growth by reducing light availability, although the negative impacts are more pronounced in lakes with a higher DOC base level (Seekell *et al.* 2015a, b).

The regional lake set in northern Finland, despite the large variability of wetland-originating nutrients, showed constantly signs of increasing productivity coupled with increasing allochthonous nutrient load (Rantala *et al.* 2016). In a similar manner, in the topmost part (0–2 cm) of the Canadian core (III) a clear increase in terrestrial components and heterotrophic activity was observed from fatty acid (FA) biomarkers, suggesting that the lake biota has been undergoing catchment-mediated changes. In addition to carbon, the terrestrial input has likely brought in nutrients, which agrees well with increases in nutrient tolerant high profile and motile diatom functional groups, as well as planktonic diatoms, as the water column nutrient concentrations are especially affecting pelagic rather than benthic production (Vadeboncoeur *et al.* 2008). This trend fits also together with replacement of C-F with C-G in the chironomid functional assemblage, as C-G prefers higher nutrient concentrations (I, Luoto and Ojala 2014), although climatic and other abiotic stressors cannot be ruled out as drivers of chironomid FFGs.

However, from the Canadian core (Greiner Lake) an alternative view for external nutrient enrichment was obtained (III). The sediment core, featuring a distinct three-phased stratigraphy, represents the isolation history of Greiner Lake containing a gradient from marine to freshwater phase. As the intermediate phase with mixed marine and freshwater input was the most productive, the results suggest that this was due to the marine nutrient enrichment boosting productivity. Furthermore, the predicted sea level rise and increased storminess, triggered by climate change, expose low-lying coastal freshwaters to marine nutrient enrichment. The results suggest that increasing nutrient exposure is prone to boost productivity in such systems and in turn contribute to the Arctic greening from an aquatic perspective. In agreement, recent research on small lakes that have experienced a marine inundation

(storm surge) have shown signs of increased productivity after the saltwater intrusion, such as increased sedimentary chlorophyll-*a* (Deasley *et al.* 2012) and chironomid abundance (Thienpont *et al.* 2015b). Freshwaters are ecologically and economically important features of the Arctic landscape, and changes in their physical and ecological integrity can have ecosystem level implications. While the drastic effects of marine inundation on community change in both terrestrial and aquatic environment (Pisaric *et al.* 2011, Deasley *et al.* 2012, Thienpont *et al.* 2012, 2015b, Smol 2015) have received attention, the aspect of increased productivity is equally consequential for the future trajectories of freshwater systems on low-lying Arctic coasts.

## 4 CONCLUSIONS

This work introduced the concept of functional paleoecology and demonstrated applications of functional approaches in reference to environmental change, particularly investigating effects of allochthonous inputs to functions of high latitude lake food webs in a spatio-temporal setting from subarctic Finland and Arctic Canada. The importance of this work is highlighted by better understanding of rapid environmental change in the high latitudes caused by climate change.

Environmental factors were important in structuring functional assemblages of both chironomids and diatoms, which showed diverse responses to changes in their environment. For the diatoms, nutrient availability and the level of physical disturbance controlled the assemblage composition in the long-term, whereas chironomids likely responded to climate-mediated habitat changes. Responses for specific limnological and sediment variables (depth, nutrients, dissolved and substrate carbon) were modelled for chironomid FFGs. The results indicated different preferences between the FFGs, which together with previous evidence suggest that chironomid FFGs may be useful habitat indicators for paleo-approaches. In agreement, functional diversity increased with habitat heterogeneity.

Stable isotope modelling revealed that resource utilization of chironomid larvae was controlled both by the quantity and quality of available nutrition pools and selective feeding behaviour. In space and time, benthic sources were most important for chironomids. In the regional dataset where resource utilization was contrasted with environmental gradients, it was observed that allochthony was higher in lakes with higher terrestrial input. In addition, a geographical pattern was depicted: resource utilization differed on each side of the coniferous treeline. Consumption of benthic resources dominated the more northerly lakes, while pelagic and terrestrial components exhibited greater importance below the treeline, probably attributable to the higher bioavailability of terrestrial material from coniferous soils. These findings confirm that external carbon loads affect benthic food web functions.

Increasing nutrients from external sources, both from terrestrial and marine environment, were observed to enhance productivity. The inspection of ontogenetic phases of Greiner Lake revealed that productivity was highest during mixed freshwater and marine influence. This can have future implications for lakes on low-lying Arctic coasts, considering predictions of sea level rise and increased storminess triggered by climate change. Numerous freshwater lakes may be exposed to marine nutrients, which would increase their productivity and consequently contribute to the Arctic greening from an aquatic perspective.

Despite the undisputable complexity of multiple drivers affecting lake food webs and their responses, applying approaches such as stable isotope modelling and improving biomarker methods into paleoecological data, in combination with functional and biodiversity perspectives, contribute to a more complete picture of past ecosystem dynamics. The findings of this research suggest that functional approaches are useful paleoecological tools and complement the well-established taxonomy-based approaches with better understanding of ecosystem functions and responses to environmental change.

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## YHTEENVETO (RÉSUMÉ IN FINNISH)

### **Funktionaalinen paleoekologia ja alloktoninen aines pohjoisten järvien ravintoverkoissa**

Ilmastonmuutos aiheuttaa arktisissa ympäristöissä laaja-alaisia muutoksia. Esimerkkejä jo havaituista muutoksista ovat lämpötilan ja sadannan muutosten lisäksi puurajan siirtyminen kohti pohjoista sekä tundrakasvillisuuden lisääntyminen, kasvukauden pidentyminen, lumipeitteen väheneminen, merijään ja jäätiköiden kutistuminen sekä merenpinnan nousu. Yksi merkittävimmistä muutoksista on ikiroudan sulaminen, joka vapauttaa vanhaa eloperäistä ainesta aktiiviseen hiilen kiertoon.

Alloktonisen (järven ulkopuolisen) aineksen, kuten ravinteiden ja hiilen määrien on arvioitu kasvavan merkittävästi arktisissa vesissä sekä ikiroudan sulamisen että tuottavampien tundramaannosten vuoksi. Järviin päätyessään se voi aiheuttaa muutoksia niin vesien biokemiallisissa kuin fysikaalisissakin ominaisuuksissa. Alloktoniset liukoiset hiiliyhdisteet sisältävät usein tummia humusaineita, jotka vaikuttavat veden väriin ja sitä kautta veden lämmönsidontakykyyn, valonläpäisevyyteen ja kerrostuneisuuteen. Alloktoninen aines sisältää useimmiten myös ravinteita, jotka voivat aiheuttaa muutoksia muutoin tyypillisesti ravinneköyhien arktisten järvien tuotannossa ja biologiassa, esimerkiksi tuotannon lisääntymistä ja yhteisömuutoksia.

Monet pohjoisten järvien erityispiirteet, erityisesti lyhyt avovesikausi sekä ympärivuotisesti alhaiset lämpötilat ja ravinnepitoisuudet, ovat muuttumassa, ja nämä muutokset heijastuvat myös järvien biologisiin yhteisöihin. Koska monet arktisten järvien lajit ovat sopeutuneita äärimmäisiin olosuhteisiin, ne ovat myös herkkiä muutoksille. Arktisten järvien ja niiden lajiston muutosherkkyys ilmaston vaihteluille sekä järvien sijainti suoran ihmisvaikutuksen ulottumattomissa tekevät niistä erinomaisia kohteita ympäristönmuutostutkimukselle. Tulevaisuuden muutosten ja ilmastovasteiden arvioiminen pohjoisissa järvi-ekosysteemeissä perustuu nykyisten ja menneiden muutosten pitkäaikaisseurantaan ja -tutkimukseen. Erityisesti arktisilla seuduilla, joilla mittausaineistoa on heikosti saatavilla, pitkäaikaisen ympäristönmuutoksen tutkimiseen tarvitaan luonnon arkistoja, esimerkiksi järvisedimenttejä, puiden vuosilustoja tai muita vastaavia jatkuvia kerrostumia. Paleolimnologia, eli järvisedimenttikerrostumiin perustuva tutkimus, on puutteistaan huolimatta osoittautunut erinomaiseksi työkaluksi arktisten alueiden ilmastohistorian ja ekosysteemimuutoksen tutkimisessa.

Tässä väitöskirjassa tutkittiin paleolimnologisin menetelmin pitkäaikaisen ympäristönmuutoksen ja erityisesti alloktonisen aineksen määrän vaikutusta järven ravintoverkkojen toiminnallisuuteen. Tutkimusaineisto koostui pintasedimenttinäytteistä 25 järvestä Suomen Lapissa sekä kahdesta vertikaalisesta sedimenttiprofiilista: Suomen Lapista (Utsjoki) ja arktisesta Kanadasta (Cambridge Bay, Nunavut). Tutkimuksessa käytettiin monipuolisesti useita menetelmiä, mutta tärkeimmät tutkimusmenetelmät perustuivat surviaissäskien ja

piilevien jäänteiden lajien tunnistamiseen ja toiminnallis-ekologiseen luokitteluun sekä hiilen ja typen vakaiden isotooppien koostumuksen määrittämiseen sedimentistä ja surviaissäskien jäänteistä.

Toiminnallisessa ekologiassa tutkitaan lajiston sijasta eliöiden toiminnallisia ryhmiä. Toiminnalliset ryhmät viittaavat lajien merkitykseen ekosysteemissä, ja siten ryhmien välillä tapahtuvat muutokset kertovat laajemmista, ekosysteemin rakenteellisista muutoksista. Tutkimuksessa todettiin, että surviaissäskien toiminnalliset ryhmät, jotka on luokiteltu ravinnon hankintatavan mukaan (esim. keräilijä, suodattaja, peto), suosivat toisistaan poikkeavia olosuhteita liittyen hiilen ja ravinteiden määrään. Alloktoninen aines, joka sisältää hiiltä ja ravinteita, voi siis vaikuttaa pohjaeläinyhteisöjen toiminnalliseen rakenteeseen. Yleisimpien toiminnallisten ravinnonkäyttöryhmien välillä oli erityisen selkeä ero hiili- ja ravinnepitoisuuksien suosimisessa, sillä suodattajat suosivat keskisyviä, kirkasvetisiä ja ravinneköyhiä ympäristöjä, kun taas keräilijät viihtyivät matalissa ja ravinteikkaissa ympäristöissä sekä sietivät huomattavasti paremmin veden tummempaa väriä. Tulokset siis osoittavat, että toiminnallisia ravinnonkäyttöryhmiä voidaan soveltaa elinympäristön ilmentäjinä sedimenttitutkimuksessa.

Toiminnallisten ryhmien osuukien ohella tutkittiin myös niiden monimuotoisuutta, sillä monimuotoisuus liittyy oleellisesti ekosysteemin resilienssiin, eli kykyyn vastustaa muutosta tai taata nopea palautuminen häiriön jälkeen. Lajiston ja toiminnallisten ryhmien monimuotoisuuksien välillä oli positiivinen yhteys. Lisäksi surviaissäskien toiminnallisten ravinnonkäyttöryhmien monimuotoisuus oli yhteydessä sedimentin orgaanisen aineksen laatuun. Sedimenttiprofiilien aikasarja-aineistoissa havaittiin äkillisiä muutoksia sekä surviaissäskien että piilevien toiminnallisissa ryhmissä. Ajoituksen epätarkkuuden vuoksi muutosten tulkinta resilienssin kannalta oli haastavaa, mutta tulokset viittaavat siihen, että surviaissäskien toiminnalliset ryhmät sietävät hyvin äkillisiä muutoksia ja ryhmien suhteelliset osuudet seurailevat ennemminkin yleisen ilmastokehityksen myötä tapahtuvaa hitaampaa elinympäristön muutosta. Piilevien toiminnalliset yhteisöt reagoivat voimakkaimmin ravinnepitoisuuksien muutoksiin ja mekaanisiin häiriöihin, mutta palautuivat joustavasti ennalleen olosuhteiden niin salliessa.

Lapin sedimenttiprofiilin aikasarja-aineistosta havaittiin myös, etteivät surviaissäskien toiminnalliset yhteisöt olleet kytköksissä sedimentin geokemiallisten ominaisuuksien kanssa, vaikka surviaissäskien ravinnonkäyttö oli. Tämä voi viitata siihen, että benttiset (järven pohjalla elävät) perustuottajat, joiden määrä vahvasti ohjaili sedimentin kemiallista koostumusta, ja surviaissäskien toiminnalliset yhteisöt reagoivat eri ympäristömuuttujiin. Samasta aikasarjasta tutkittiin myös nykyisen lämpenemisen samankaltaisuutta aiemman lämpimän ilmastojakson, Keskiajan lämpökauden, kanssa, eikä vahvaa yhteyttä tässä aineistossa havaittu; sen sijaan vaiheet vaikuttivat varsin erilaisilta niin toiminnallisilta yhteisöiltään kuin kemiallisilta piirteiltään, vaikka nämä piirteet ovat usein yhteydessä ilmastokehitykseen.



Alloktonisen aineksen merkitys ravintolähteenä on herättänyt keskustelua pitkään, erityisesti liittyen sen heikkoon ravinnolliseen laatuun. Tässä tutkimuksessa tutkittiin alloktonisen hiilen sekä järven perustuotannosta peräisin olevan hiilen suhteellisia osuuksia surviaissääskien ravinnonlähteenä Lapissa hyödyntäen surviaissääskien fossiileihin tallentunutta vakaiden isotooppien koostumusta. Benttiset perustuottajat olivat ravinnonlähteistä kaikkein tärkein niin pintasedimentti- kuin aikasarja-aineistossakin. Surviaissääsket hyödynsivät alloktonista lähdettä enemmän silloin, kun sitä päätyi järveen enemmän ja vesi oli tummempaa. Tutkimus osoitti, että vaikka surviaissääsket hyödynsivät alloktonista ravinnonlähdettä enemmän silloin, kun laadukkaampaa ravintoa oli rajoitetusti tarjolla, suosivat ne kuitenkin parempilaatuisia ravinnonlähteitä. Pintasedimenttiaineiston perusteella havaittiin myös maantieteellinen yhteys ravinnonkäytössä: havupuurajan pohjoispuolella benttiset lähteet dominoivat, mutta havupuurajan eteläpuolella alloktonisella ja pelagisella (vesipatsaassa tapahtuvalla) perustuotannolla oli merkittävämpi rooli. Tämän tulkittiin johtuvan alloktonisen aineksen laatueroista, sillä havupuumaannoksista lähtöisin oleva hiili on usein helpommin biologisesti käytettävässä muodossa kuin suoalueilta saapuva hiili, mikä taas dominoi alloktonista ainesta erityisesti puurajan pohjoispuolella.

Järviin päätyvä alloktoninen aines sisältää usein myös ravinteita, jotka voivat lisätä järvien tuottavuutta, kuten tässäkin tutkimuksessa havaittiin. Kanadan sedimenttisarjassa meriperäiset ravinteet vaikuttivat merkittävästi järven tuottavuuteen. Järven kuroutumishistoriaa ilmentävästä sedimenttiprofiilista ilmeni, että tuottavimmillaan vesialue oli meriveden ja makean veden yhteisvaikutuksen aikana, kun alue vaihteittain muuttui meren lahdelmasta järveksi. Merivaikutuksen on osoitettu stimuloivan tuotantoa myös muissa tutkimuksissa. Erityisesti laakeilla ja järvirikkailla arktisilla rannikkoalueilla merivaikutus voi uhata makeanveden ympäristöjä, sillä ilmastonmuutoksesta johtuva meren pinnannousu ja lisääntyvä myrskyisyys lisäävät merivaikutuksen todennäköisyyttä tulevaisuudessa. Meriveden pääsy järviin aiheuttaisi poikkeuksetta muutoksia niiden ekologisissa yhteisöissä ja järvien roolissa tundraekosysteemeissä, mutta muuttuessaan tuottavammiksi merivaikutuksen alaiset järvet myös edesauttaisivat arktisen alueen vihertymistä (Arctic Greening).

Tämän väitöskirjan tutkimustulokset täydentävät nykyistä käsitystämme ravintoverkkojen toiminnallisuudesta ja vasteista ympäristönmuutokseen ja muuttuviin energiavirtoihin. Toiminnallinen paleoekologia on alana vasta lapsenkengissä, mutta se vaikuttaa lupaavalta lisältä muiden paleoekologisten menetelmien rinnalle, erityisesti kun tarkoituksena on tutkia ekosysteemien muutosvasteita.

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## ORIGINAL PAPERS

### I

# ENVIRONMENTAL CONTROLS ON BENTHIC FOOD WEB FUNCTIONS AND CARBON RESOURCE USE IN SUBARCTIC LAKES

by

E. Henriikka Kivilä, Tomi P. Luoto, Marttiina V. Rantala, Mikko Kiljunen, Milla Rautio & Liisa Nevalainen 2019

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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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Key words: organic carbon, Chironomidae, functional ecology, paleolimnology, stable isotopes

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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

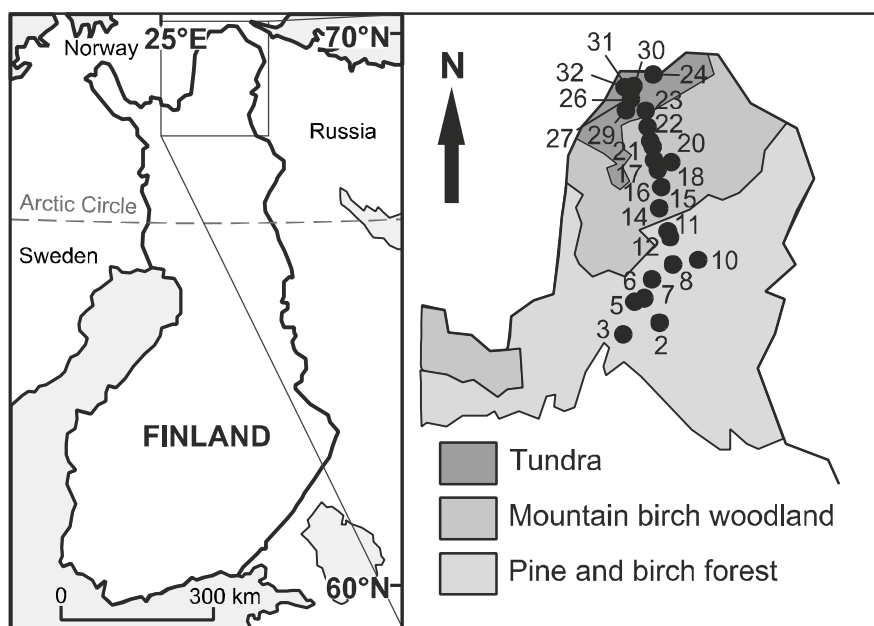


Figure 1. Map of the 25 study lakes located in northern Finland with present vegetation zones.

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	$\text{mg L}^{-1}$	DOC	2.6	9.6	5.0	1.8	12.0	5.2
Water colour	Pt $\text{mg L}^{-1}$	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	$\text{m}^{-1}$	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	$\text{mg DWmg}^{-1}$	Chl-a <sub>s</sub>	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 cm<sup>3</sup> of sediment per sample was extracted three times in 90 % ethanol, filtered (0.2  $\mu\text{m}$ ), 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  $\mu\text{m}$  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  $0.50 \pm 0.56$  ‰ and  $1.5 \pm 0.50$  ‰ 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 ( $\rho$ ) 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<sub>s</sub>, 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.



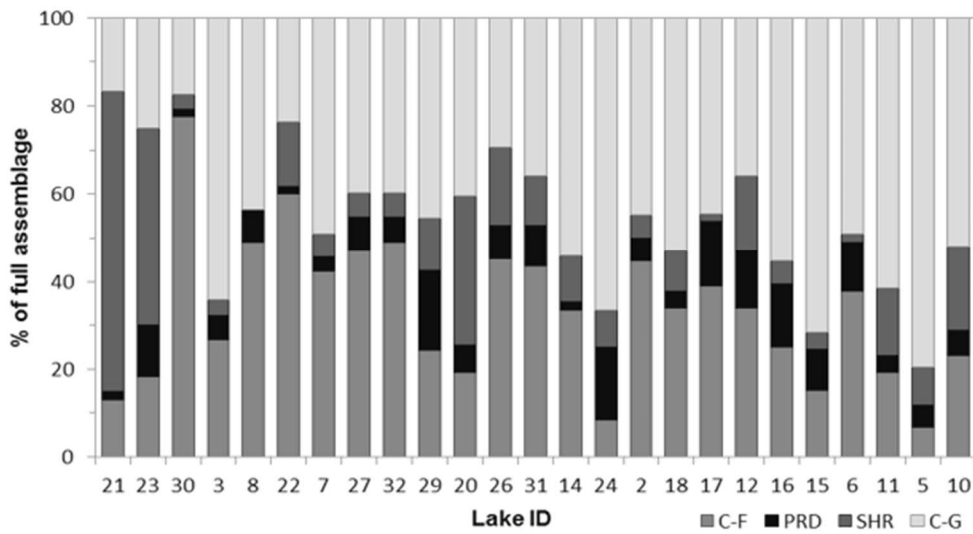


Figure 2. The relative abundance and distribution of functional assemblages in the study lakes, represented by four functional groups: collector-filterers (C-F), predators (PRD), shredders (SHR) and collector-gatherers (C-G). X-axis is scaled along increasing sediment organic matter quantity (LOI).

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  $^{13}\text{C}$ -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 ( $\rho$ ) 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

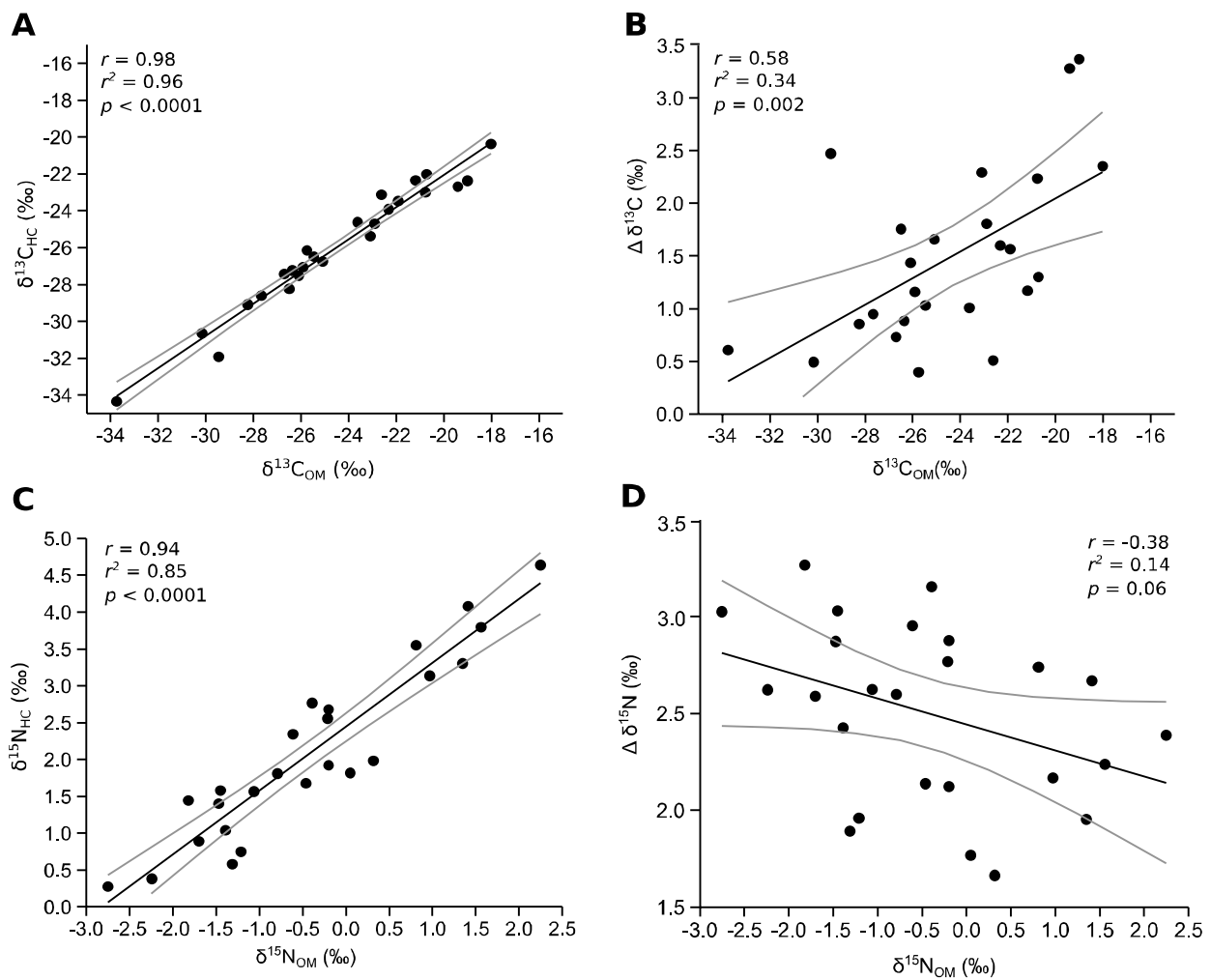


Figure 3. Linear relationships for A) carbon isotopic signature ( $\delta^{13}\text{C}$ ) of sediment organic matter (OM) and chironomid head capsules (HC), B)  $\delta^{13}\text{C}$  of sediment OM and the chironomid-sediment offset ( $\Delta$ ), C) nitrogen isotopic signature ( $\delta^{15}\text{N}$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

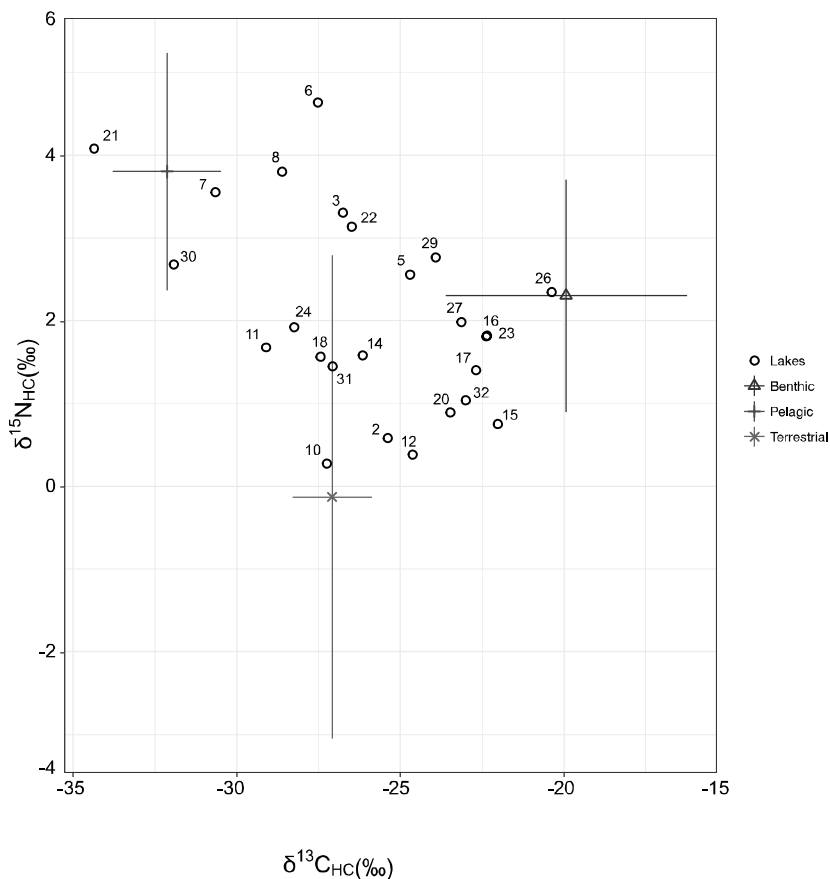


Figure 4. Isospace plot of the stable isotope mixing model. Chironomid assemblage isotope values are marked by lake ID on the plot with benthic, pelagic and terrestrial end-member estimates and their associated variability.

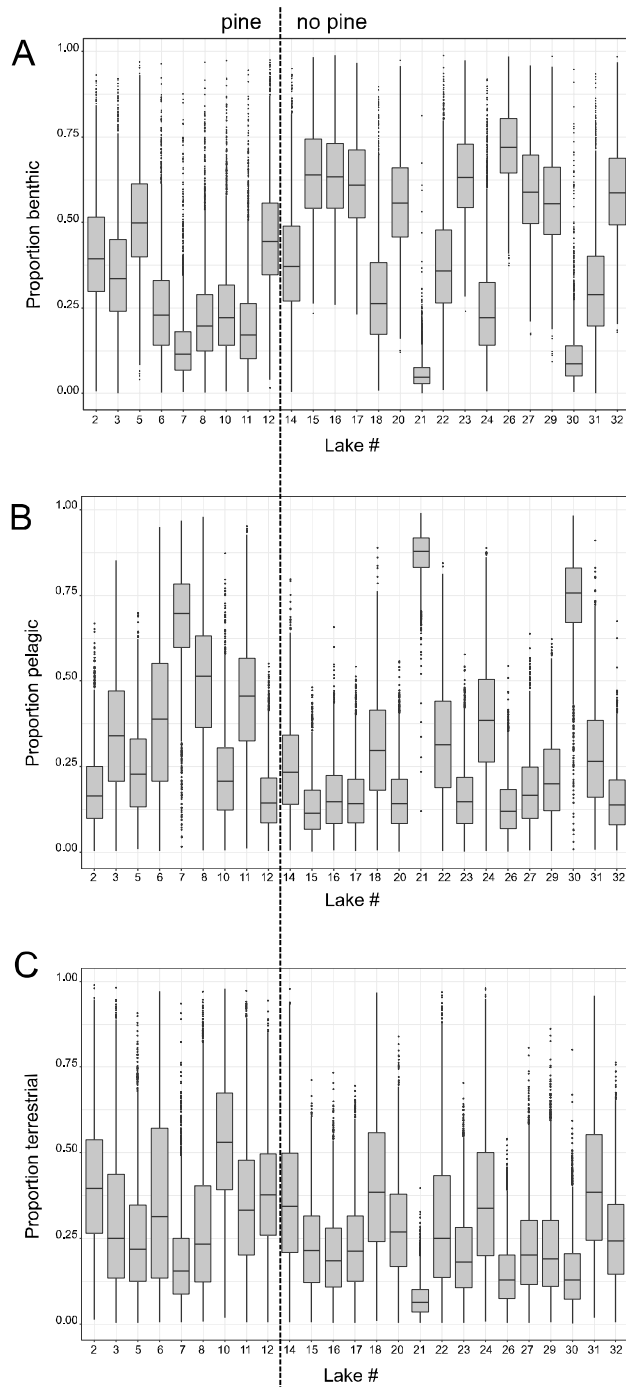


Figure 5. Relative contributions of A) benthic, B) pelagic and C) terrestrial sources for the chironomids according to the stable isotope mixing model. Mean (black line), 50 % range (box) and 100 % range (tails) of distribution results are presented. The vertical dashed line represents the coniferous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

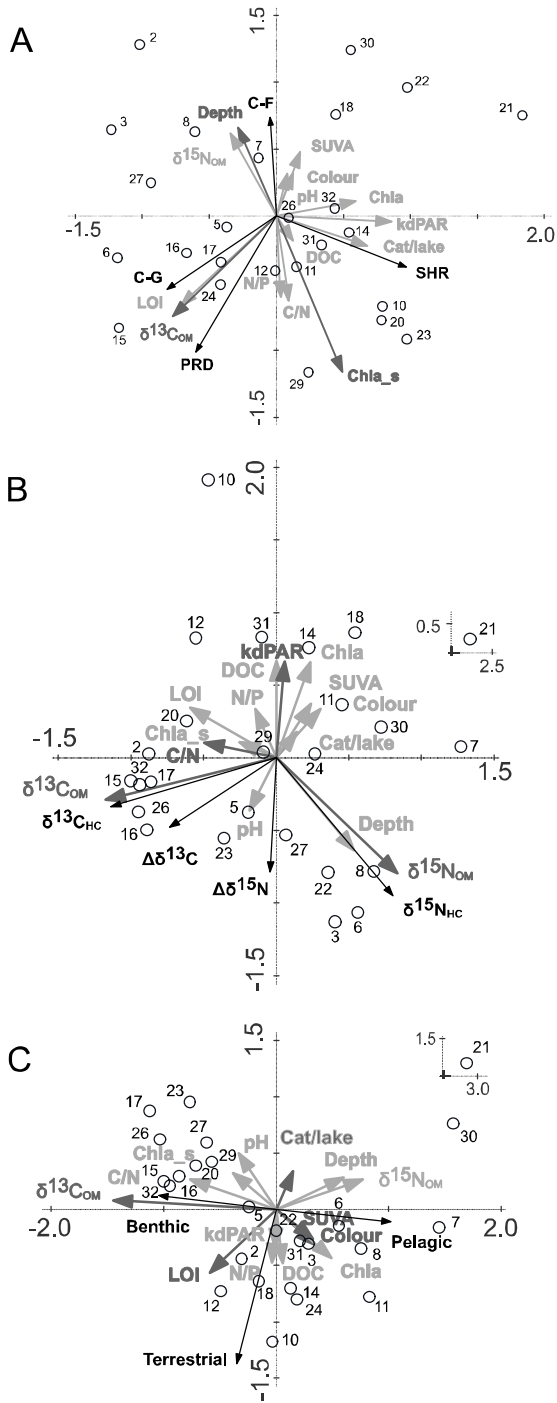


Figure 6. Redundancy analysis of A) functional feeding groups (collector-filterers (C-F), predators (PRD), shredders (SHR) and collector-gatherers (C-G)), B) chironomid stable isotope values ( $\delta^{13}\text{C}_{\text{HC}}$ ,  $\delta^{15}\text{N}_{\text{HC}}$ ) and sediment-chironomid offsets ( $\Delta\delta^{13}\text{C}$ ,  $\Delta\delta^{15}\text{N}$ ), 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.

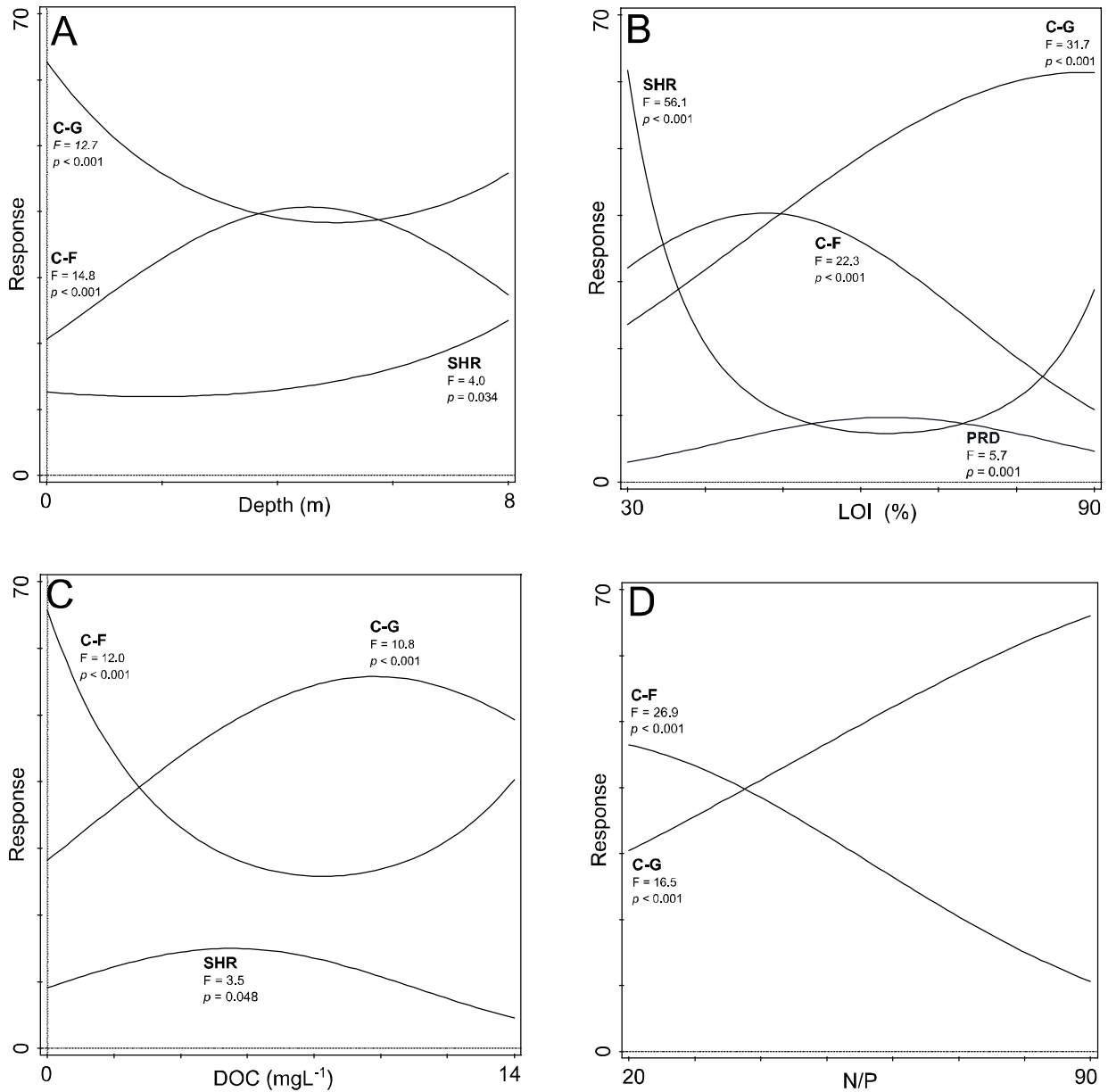


Figure 7. Response models for the functional feeding groups (gatherers C-G, filterers C-F, shredders SHR and predators PRD) and selected extrinsic variables: A) water depth, B) sediment organic matter quantity, C) dissolved organic carbon and D) N/P ratio of lake water. Only statistically significant ( $p < 0.05$ ) 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  $^{13}\text{C}$ -depleted than  $\delta^{13}\text{C}_{\text{OM}}$  ( $-1.48 \pm 0.80$  ‰), 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  $^{15}\text{N}$ -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  $^{13}\text{C}$ -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  $^{13}\text{C}$ -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  $^{15}\text{N}$ -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  $^{13}\text{C}$ -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	Orthoclaadiinae	c-g
Psectrocladius (M#) calcaratus-type	Orthoclaadiinae	c-g
Psectrocladius (M#) septentrionalis-type	Orthoclaadiinae	c-g
Psectrocladius sordidellus-type	Orthoclaadiinae	c-g
Synorthocladus	Orthoclaadiinae	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	Orthoclaadiinae	shr
Cricotopus cylindraceus-type	Orthoclaadiinae	shr
Cricotopus (I#) intersectus-type	Orthoclaadiinae	shr
Cricotopus type P	Orthoclaadiinae	shr
Zalutschia mucronata-type	Orthoclaadiinae	shr
Zalutschia type B	Orthoclaadiinae	shr
Zalutschia zalutschicola	Orthoclaadiinae	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



## II

# LATE-HOLOCENE VARIABILITY IN CHIRONOMID FUNCTIONAL ASSEMBLAGES AND CARBON UTILIZATION IN A TUNDRA LAKE FOOD WEB

by

E. Henriikka Kivilä, Tomi P. Luoto, Marttiina V. Rantala & Liisa Nevalainen 2019

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### III

## SEA LEVEL RISE MAY CONTRIBUTE TO THE ARCTIC GREENING OF COASTAL FRESHWATERS – IMPLICATIONS FROM THE ONTOGENY OF GREINER LAKE, NUNAVUT, CANADA

by

E. Henriikka Kivilä, Marttiina V. Rantala, Dermot Antoniadis, Tomi P. Luoto, Liisa  
Nevalainen & Milla Rautio 2019

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