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Relationship between cladoceran (Crustacea) functional diversity and lake trophic gradients

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Summary

1. Functional diversity (FD) as a biodiversity measure has an explicit role in ecosystem functioning because the effects of environmental changes in ecosystems are determined by biological functions, such as feeding type and trophic position, of particular species.

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- Accepted Article
2. We evaluated the usability of functional characterization and FD of an aquatic keystone group (Crustacea: Cladocera) for enhancing the understanding of long-term lake functional responses to environmental changes. The aims were to separate ecologically significant functional groups, investigate succession of such functional groups during nutrient enrichment process, and determine the relationship between FD and lake productivity using a paleolimnological approach.
 3. We selected two eutrophicated study lakes from southern Finland for down-core investigations, one with a centennial (past ~350 years) and the other with a decadal (past ~70 years) nutrient enrichment record. Cladoceran microfossils in the sediment cores were used to determine the taxonomic structure of the past communities. Ecologically relevant functional characteristics were determined to separate functional groups by utilizing a functional dendrogram and a weighted community-based FD index together with a set of multidimensional FD indices. The indices were applied to the down-core assemblages.
 4. The functional dendrogram separated cladocerans into functional groups where habitat type principally separated open-water filterers and predators from epibenthic scrapers and detritivores. Further separation in the pelagic branch was based on body size and feeding and among the benthic branch body shape.
 5. Functional assemblages changed markedly during the nutrient enrichment process. In the early stage of eutrophication, the largest functional changes were caused by small planktonic filterers and predators. Small filterers and epibenthos responded strongest during the eutrophic– hypereutrophic succession. FD had a positive long-term relationship with lake trophic status until eutrophic conditions that was likely caused by diversifying resources and versatile food webs. Under hypereutrophic conditions,

and especially at a decadal temporal resolution, alternating predation regimes caused variance to FD.

6. In the current records, cladoceran FD was positively related to lake productivity and bottom-up controls during the early stages of eutrophication in the long-term record but top-down controls apparently were more important at a decadal scale and under hypereutrophic conditions.

Key-words Aquatic ecology, Biodiversity, Environmental change, Food web functioning, Nutrient enrichment, Paleolimnology

Introduction

Community has been the main unit for paleoecological research on fossil assemblages of aquatic taxa (e.g. diatom algae, crustaceans, and insect larvae) preserved in lake sediment archives (Frey 1988). Ecological communities of sedimentary fossils have been reconstructed by their taxonomic structure (e.g. Smol et al. 2005), i.e. species composition and accordingly, biodiversity of the communities have equaled species richness and diversity. Taxonomically structured fossil communities have also been the basis to infer long-term changes in ecosystem processes, such as predation regimes and lake primary production (Jeppesen et al. 2001). Despite the fact that taxonomic classification is essential in ecological research, ecosystem functions are not completely dependent on taxonomic identity but rather the functional characters. Therefore, functional diversity (FD), focusing on functional traits of species in ecological communities may enable the assessment of ecosystem functioning and stability more comprehensively than traditional taxonomic identification (Hooper et al. 2002; Barnett, Finlay & Beisner 2007; Cadotte, Carscadden & Mirotnick 2011). Functional traits

define species for their specific ecological roles; how species interact with other species and with their living environment for example via habitats, movement, feeding, or reproduction.

Spatial and temporal biodiversity patterns have gained attention under recent degradation of freshwater lakes. The paleolimnological approach and biological surface sediment assemblages of various aquatic organisms have been used in detecting spatial biodiversity patterns over environmental gradients (Nyman, Korhola & Brooks 2005; Laird, Kingsbury & Cumming 2010; Nevalainen 2010; Pla-Rabes et al. 2011). Furthermore, biodiversity indices for determining species richness and diversity have been used to track long-term biodiversity dynamics of aquatic communities under environmental changes (Korosi & Smol 2012; Thienpont et al. 2013; Ilyashuk et al. 2015). Some studies have investigated biodiversity patterns from sedimentary archives along different spatial and temporal gradients utilizing information extracted from both surface sediments and sediment cores (Richard Albert et al. 2010; Velghe, Vermaine & Gregory-Eaves 2012). Recent literature has emphasized the importance of integrating paleolimnological approaches with biodiversity science, highlighting the possibilities of a long-term perspective on issues in biodiversity and conservation (Froyd & Willis 2008; Gregory-Eaves & Beisner 2011).

FD as a biodiversity measure has a more explicit role in ecosystem functioning than the measures based on taxonomic classification (Barnett et al. 2007), since the effects of environmental changes in the ecosystem are determined by the biological processes of particular species present in the community. Within paleolimnology, which has still quite rarely focused on functional classification of aquatic communities, crustacean Cladocera provide an excellent opportunity to examine ecosystem and food web functioning and environmental changes since their fossils are preserved and well identifiable in lake sediments (Korhola & Rautio 2001; Rautio & Nevalainen 2013). In addition, cladocerans

inhabit open-water and littoral-benthic habitats and occupy different feeding preferences being extremely diverse both morphologically and functionally (Flössner 1972). For example, in earlier paleolimnological studies, cladoceran taxa associated with specific habitats in the form of the planktonic-littoral ratio has been used to examine long-term water-level fluctuations in lakes (Alhonen 1970; Hofmann 1998; Sarmaja-Korjonen 2001). The more recent sediment studies have investigated relationships between cladoceran community functioning and ecosystem changes related to nutrients and climate (Chen, Dalton & Taylor 2010; Nevalainen & Luoto 2013; Nevalainen et al. 2015; Thienpont et al. 2015). This has been an aspect of interest also for modern biodiversity investigations (Barnett & Beisner 2007).

The general objective of this study is to evaluate the usability of FD in paleolimnological studies for enhancing the knowledge of long-term lake ecosystem responses to environmental changes. The specific aims are to separate ecologically significant functional groups within cladocerans, investigate the succession of such functional groups during a nutrient enrichment process, and determine the relationship between FD and lake productivity. We hypothesized that cladoceran functional diversity is connected with lake productivity through bottom-up controls (i.e. changes in resource type) in a way that FD reduces under progressive nutrient enrichment due to domination of planktonic primary production and associated changes in food type and habitat structure that reduce the success of benthic animals. We selected two study lakes from southern Finland for down-core investigations of FD, both with a documented history of severe eutrophication during the past centuries after a pre-disturbance reference state. The lakes are located close to each other and are similar in their catchment features having clay soils and strong agricultural land use but differ with the past rate of nutrient enrichment and recent fish status. Cladoceran microfossils

in the sediment cores were used to determine the taxonomic structure of the past communities. Ecologically relevant characteristics indicating the functioning of cladoceran taxa in lake ecosystems were determined to separate functional groups and FD indices were applied on the down-core functional assemblages.

Materials and methods

STUDY SITES AND SAMPLING

The study sites, lakes Mallusjärvi (Orimattila) and Tiiläänjärvi (Askola), are located in the south boreal zone of Finland approximately 20 km apart and 30–40 km north of the Baltic Sea coastline (Table 1). Both of the lakes are naturally clay-turbid basins being located partly on clay soils. The catchments consist of mosaics of agricultural land and forest. According to previous paleolimnological investigations, the lakes have experienced a severe nutrient enrichment process during the past centuries (Luoto & Raunio 2011; Luoto & Ojala 2014) culminating with current hypereutrophic conditions (Table 1). The cause of this eutrophication is intensive agriculture on the catchments. Lakes' current fish stocks mainly consist of roach (*Rutilus rutilus*) and pike perch (*Sander lucioperca*), which during the hypereutrophic period have increased in Mallusjärvi but decreased in Tiiläänjärvi (Nevalainen & Luoto 2013; Luoto & Ojala 2014).

Sediment cores were sampled with Limnos (Mallusjärvi, 28 cm core) and Kajak (Tiiläänjärvi, 41 cm) gravity corers in 2009 and 2012, respectively. Both cores were split into 1-cm slices in the field and stored in plastic bags in a cold room. The Mallusjärvi core has been previously examined for fossil Chironomidae to quantitatively infer eutrophication (Luoto & Nevalainen 2011; Luoto & Raunio 2011) and Cladocera for investigating community and phenotypic (sexual reproduction, body size) responses during the

eutrophication (Nevalainen & Luoto 2013). The Tiiläänjärvi core has been previously examined for fossil Chironomidae and to infer total phosphorus (TP) (Luoto & Ojala 2014).

In the current study, chironomid-inferred TP from both cores (Luoto & Rautio 2011; Luoto & Ojala 2014) is used to indicate nutrient enrichment. We separated the down-core samples of the two sediment sequences into three different periods of nutrient enrichment according to their TP concentrations (Table 1) by applying the Finnish lake trophic classification (meso-, eu-, and hypereutrophic). The separation includes reference ($TP < 30\text{-}40\mu\text{g L}^{-1}$), eutrophic ($\sim 40\text{-}80\mu\text{g L}^{-1}$), and hypereutrophic ($>80\text{-}100\mu\text{g L}^{-1}$) periods that are mostly consistent in their reconstructed TP concentrations and trends. The use of "pre-disturbance" reference conditions in the cores acts as a pseudo-control for pre-eutrophication conditions. In addition to TP, indirect proxy-data of bottom-up and top-down controlling environmental factors were utilized. Sediment magnetic susceptibility was used as an indicator for erosion and lake-water turbidity (related to habitat structure) and relative abundance of predatory fossil midges (Chironomidae and Chaoboridae) was utilized to indicate food web structure (related to predation regimes). These data are derived from the original publications referred above.

CLADOCERA AND STATISTICAL ANALYSES

The sediment subsamples (1-cm slices) were each treated separately with standard methods for fossil Cladocera analysis by heating and stirring in 10% KOH for 15-20 min and sieving through a 51- μm mesh (Szeroczyńska & Sarmaja-Korjonen 2007). The residues were mounted in glycerin jelly, stained pink with safranin, on preparation slides and analyzed with a light microscope (100–400x). The most commonly encountered body part (e.g. carapace, head shield, post-abdomen, post-abdominal claw, ephippium) of each cladoceran taxa was used to calculate the number of individuals. The identification of fossil specimens

followed Szeroczyńska & Sarmaja-Korjonen (2007). *Chydorus sphaericus*-type specimens were considered as *Chydorus cf. sphaericus*.

Qualitative functional characters of body size (small <500 μm , intermediate 500-1000 μm , large >1000 μm), body shape (elongated, oval, globular), feeding type (filterer, scraper-detritivore, predator), and microhabitat (pelagial, bottom substrate, vegetation) were determined for all the encountered cladoceran taxa from the sediment cores to separate functional traits based on Flössner (1972; 2000). All the functional properties were inserted as binary codes (1 = functional character present, 0 = functional character absent), because detailed information for the ordinal (e.g. exact body size as micrometers) traits and for all taxa is highly variable in the literature. A functional dendrogram was generated using hierarchical clustering analysis with average linkage clustering, unweighted pair grouping, and Euclidean distances, following Barnett et al. (2007). The clustering was performed with the Paleontological Statistics (PAST) Software (Hammer, Harper & Ryan, 2001). A community-based weighted FD index (wFDc, Pla et al. 2008) was applied on the sediment core cladoceran communities. The index is based on the total branch length of the functional dendrogram. It takes into account the species community pool with weights of species relative abundances and calculates a weighted distance matrix. In addition, multidimensional FD indices (Villéger, Mason & Mouillot, 2008) including functional evenness (FEve) and functional divergence (FDiv) were used as supplementary measures. The FD indices were generated with the Statistical Software for the Analysis of Functional Diversity (FDiversity) (Casanoves et al. 2011).

Similarity percentage analysis (SIMPER) was performed for the functional groups to detect which of the groups mostly contributed to the changes between the three periods of nutrient enrichment. Multiple linear regressions were performed to investigate relationships between FD scores (wFDc) and chironomid-inferred TP, sediment magnetic susceptibility, and abundance of predatory midges firstly during the core succession (all samples included), secondly during the reference–eutrophic phase, and thirdly during the eutrophic–hypereutrophic sample succession. Further regression model (i.e. 3rd order polynomial regression) was applied on the wFDc scores and chironomid-inferred TP to examine their bivariate relationships throughout the cores. Polynomial regression was chosen based on the nonlinear relationship between the variables and highest coefficient of determination (R^2). These analyses were performed with PAST software (Hammer et al. 2001).

Results

Thirty-six cladoceran taxa occurred in the Mallusjärvi and Tiiläänjärvi cores (Table 2). Inferred TP during the three phases of nutrient enrichment process fluctuated in Mallusjärvi from the mean of 11 (pre-disturbance) to 108 $\mu\text{g L}^{-1}$ (hypereutrophic) and in Tiiläänjärvi from 30 to 100 $\mu\text{g L}^{-1}$ (Table 2). The most common species in Mallusjärvi were *Eubosmina coregoni* (mean relative abundance 40.5%, number of occurrences 28), *Bosmina longirostris* (16.5 %, 25), *Chydorus cf. sphaericus* (12.9 %, 24), and *Leptodora kindti* (9.5%, 28). In Tiiläänjärvi, the same taxa were the most common; *B. longirostris* (28.9%, 41), *E. coregoni* (14.9%, 41), *L. kindti* (15.9%, 41), and *C. cf. sphaericus* (11.8%, 40). The dendrogram separated cladocerans into five functional groups having Euclidean distance >1.75 (Fig. 1). Habitat type principally separated open-water filterers and predators (groups 1–3) from the benthic scrapers and detritivores (groups 4–5). In the pelagic branch, further separation was

based on body size and feeding to predators (group 1), large filterers (group 2) and small and intermediate filterers (group 3, small filterers hereafter). Among the benthic branch, where several taxa could not be characterized strictly to sediment or vegetation associated, body shape separated taxa into globular (group 4, globular epibenthos) and oval (group 5, oval epibenthos).

Relative abundances of the actual prevalence of each functional group varied during the nutrient enrichment process in the Mallusjärvi core, where small filterers were most abundant (Fig. 2a). Predators, large filterers, and oval epibenthos occurred at ~10–20% abundance during the pre-disturbance and eutrophication periods, but decreased and disappeared during the hypereutrophic conditions when globular epibenthos increased to ~30% (Fig. 2a). According to SIMPER, groups that mainly contributed to the changes between reference and eutrophic periods were small filterers (29.0%) and predators (24.6%). Largest changes between eutrophic and hypereutrophic conditions were due to globular (35.8%) and oval epibenthos (18.5%).

In the Tiiläänjärvi core (Fig. 2b), predators, large filterers, and oval epibenthos increased during eutrophic and hypereutrophic periods (to 10–30%). Small filterers were most abundant during the reference period (60–70%), fluctuated during the eutrophic period, and occurred at ~30% abundance during the hypereutrophic conditions. Globular epibenthos had an increasing trend during the nutrient enrichment process and it occurred at 20% abundance under hypereutrophic conditions (Fig. 2b). SIMPER showed that largest contribution in the changes between reference status and eutrophic period were due to small filterers (44.7%) and predators (15.7%), whereas small filterers (32.4%) and globular

epibenthos (23.9%) had the highest contribution in the changes between eutrophic and hypereutrophic conditions.

FD index (wFDc) was low (mean 12.3) in Mallusjärvi during the pre-disturbance period, increased through the eutrophic period (15.5) and decreased to lowest values (9.2) during hypereutrophic conditions (Fig. 2a, Fig. 3). Functional evenness index (FEve) and divergence (FDiv) decreased during the hypereutrophic periods. In Tiiläänjärvi, FD was lower during the pre-disturbance conditions (mean wFDc 13.8), increased during eutrophication (18.1), and slightly decreased (17.3) during the hypereutrophic period (Fig. 2b). FEve showed corresponding changes with wFDc, being lower during the pre-disturbance phase and increasing during eutrophications (Fig. 2b). FDiv index stayed steady throughout the core (Fig. 2b).

In the Mallusjärvi core, multiple linear regressions indicated significant relationships between wFDc and magnetic susceptibility throughout the core and during eutrophic–hypereutrophic phases. In addition, TP was significant during reference–eutrophic and eutrophic–hypereutrophic successions (Table 3). The only significant explanatory variable for wFDc in Tiiläänjärvi was the abundance of predatory midges during reference–eutrophic period (Table 3). The polynomial regression fitted to the Mallusjärvi data (wFDc and chironomid-inferred TP) had coefficient of determination (R^2) of 0.36 ($p = 0.013$), but no significant relationship ($R^2 = 0.05$, $p = 0.564$) was observed in the Tiiläänjärvi core (Fig. 3).

Discussion

FUNCTIONAL GROUPING

The species pool (Table 1) and the selected functional traits resulted in a functional dendrogram separating the taxa primarily into pelagic filterers and predators and epibenthic scrapers and detritivores (Fig. 1). The functional dendrogram, such as the current one, is always dependent on the number and quality of the characters included (Barnett et al. 2007) and the current classification can be considered as an example of a general local dendrogram based on the communities of the two lakes. In addition, the use of presence-absence data instead of quantitative information (e.g. actual size of fossil remains as micrometers) has likely simplified the current functional classification. However, the resulting first-order grouping to planktonic and littoral-benthic functional groups is in accordance with the traditional separation of cladocerans according to their habitat (planktonic vs. littoral), used also widely in sediment studies (Kattel et al. 2007; Nevalainen 2011), and it mainly follows the taxonomic genus-based separation (Fig. 1; Flössner 1972). As stated by Barnett et al. (2007), the result is not surprising because taxonomic identity still has a relationship with species' functioning. The current dendrogram provides a very general and simplified example of functional classification (Fig. 1). However, it contains information about the community that is highly relevant to the functioning of lake food webs and even littoral-pelagic coupling (Carpenter et al. 1987; Perga et al. 2010; Adamczuk 2014), since, for example, the abundance and size of zooplankters are related to the presence of planktivorous fish and the littoral-benthic taxa are an important food resource for pelagic fish.

In the pelagic branch of the functional dendrogram, further separation to large predators and filterers and smaller sized filterers was based on body size and feeding habits (Fig. 1). The predatory cladocerans *Leptodora kindti* and *Polyphemus pediculus* formed a

clearly distinct branch (group 1, Fig. 1). Functional differences between them arise from their body shape and habitat, since *Leptodora* is more elongated and *Polyphemus* tends to prey also in the littoral zone (Flössner 1972). These taxa have specific roles in the food web, consuming smaller invertebrates for food and being food items for fish and larger zooplankton, e.g. copepods, and their occurrence in the community provides information on structure of the food web (Hertzog 1995; Packard 2001; Vogt et al. 2013). Dynamics of predatory cladocerans have been used previously in examining long-term functioning of aquatic food webs with respect to, for example, eutrophication (Nevalainen & Luoto 2013) and biomanipulation (Nykänen et al. 2010), where the abundance and size structure of zooplankters changed significantly during these processes.

In the branch of large filterers (group 2, Fig. 1), the genus *Daphnia* can be considered as a keystone taxon in aquatic food webs since it acts a herbivorous grazer of phytoplankton (Sarnelle 2005) and energy mobilizer from microbial loop (Jürgens 1994). *Sida*, *Limnosida*, and *Latona* are mostly restricted to vegetation (two former) or bottom substrata from where they filter food particles (Flössner 1972) but again provide implications on the food web structure due to their more or less specialized feeding habits and large size (e.g. Fairchild 1983; Leclerc et al. 2011) The functional group of small sized filterers (group 3) contained genera *Bosmina* and *Ceriodaphnia* and plays a significant functional role in lakes as their occurrence is controlled by bottom-up and top-down processes (Zaret & Kerfoot 1975; Geller & Müller 1981; DeMott 1982). Among the planktonic filterers, especially *Bosmina* (all chitinous body parts preserved in lake sediments) and *Daphnia* (ephippia and post-abdomina claws) have been used in paleolimnology to infer food web processes and productivity (Sweetman & Finney 2003; Nevalainen et al. 2014a). In addition, their morphological attributes, e.g. body size and antennule and mucro length, have been

utilized in explaining past food web changes (Korosi et al. 2008; Korosi, Kurek & Smol 2013).

Among the benthic branch of the dendrogram, body shape separated the taxa into globular and oval epibenthic functional entities (groups 4 and 5, Fig. 1). Lateral body shape, here considered as the general shape of the cladoceran carapace, is a significant feature in functional morphology and ecology in all crustaceans since it participates in protection and movement (Olesen 2013). Carapace shape and their many micro-morphological features, including marginal setae and structure and shape of the ventral margin, contain much information on the feeding preferences and moving abilities of benthic cladoceran taxa on different substrates (Fryer 1968). The general carapace shape (i.e. globular or oval) is linked with habitat and food resource type and can therefore be a significant functional trait across the trophic gradient. For example, globular body shape allows movement through mud and detritus and better protects against predators, whereas bilaterally compressed oval body shape permits the utilization of cracks in vegetation (Fryer 1968). Most of the epibenthic taxa in groups 4–5 could not be characterized as strictly associated with vegetation or sediment (Flössner 1972) making these functional traits less significant in the current dendrogram (Fig. 1). For example, common chydorid species in boreal lakes *Alona affinis* and *Alonella nana* (Nevalainen et al. 2013) were here considered as epibenthic generalists, occurring on both sediment surfaces and among vegetation. Despite the lack of detailed autecological information on most of the chydorid taxa, they have been used in previous paleolimnological studies to indicate specific habitats and catchment-lake processes, since they seem to be especially sensitive in responding to changes through their littoral habitats (López-Blanco, Miracle & Vicente 2011; Nevalainen 2012; Zawiska et al. 2013).

In the benthic branch and among globular epibenthos, *Chydorus cf. sphaericus* has gained special attention in sediment studies due to its ubiquitous nature (Belyaeva & Taylor 2009). Its functional characters here included a globular body shape and affiliation to open-water and vegetative habitats (Fig. 1). The taxon's bilateral body shape is spherical, affording better protection against predators, and it contains some less specialized features of the carapace than other globular (but not spherical) chydorid taxa (Fryer 1968). *C. sphaericus*-type fossil specimens has been recorded in many different regions, including extreme systems in high arctic and alpine lakes (Bigler et al. 2006; Luoto et al. 2011; Nevalainen et al. 2014b), but it has been assigned as an indicator for eutrophication process in paleolimnological studies (Szeroczyńska 1998; Manca et al. 2007). Its feeding and locomotion, in addition to its body shape and size, are advantageous under nutrient enrichment process as it easily escapes predators, consumes fine and attached particles (bacterial and small algae), and is able to utilize open-water habitats by attaching to filamentous algae (Fryer 1968; Geller & Müller 1981; de Bernardi et al. 1990).

FUNCTIONAL DIVERSITY AND LAKE PRODUCTIVITY

Functional characterization of species is justifiable, since many of the environmental changes occurring in aquatic ecosystems are mediated by organisms' functionality (Hooper et al. 2002) and functional diversity may better capture the reason for the response to these changes than community composition. Functional diversity of a community may also add information on niche and resource diversity and utilization, and food web complexity. Indeed, functional characters of cladocerans, e.g. trophic position and microhabitat (Fig. 1) are also significant for the functioning of food web and biogeochemical cycling characterizing lakes' trophic status (Jeppesen et al. 2000). If functional properties of a community can be linked with ecosystems functions, for example lake productivity, then functional characterization of fossil

biological assemblages and FD may provide additional insights into processes that occur in aquatic ecosystems in a long-term perspective. The general connection between FD of aquatic organisms and lake productivity is previously shown to be negative. For example, benthic macroinvertebrates and lake productivity is negative, FD of benthic macroinvertebrates reduces under increasing nutrients and is largely controlled by bottom-up forces, i.e. changes in habitat and food type (Heino 2008; Luoto & Ojala, 2014). Barnett & Beisner (2007) showed similar results with zooplankton, as FD of crustacean communities declined linearly over a TP gradient.

The current results of down-core functional assemblages in lakes Mallusjärvi and Tiiläänjärvi showed some coherent responses among the lakes during eutrophication process (Fig. 2). In both lakes, small filterers and globular epibenthos (Fig. 1) were most abundant throughout the cores due to dominance of bosminids and *Chydorus cf. sphaericus* (Fig. 2, Table 2) and major changes in functional assemblages occurred in both lakes during the nutrient enrichment process. According to SIMPER, largest changes between the reference and eutrophic phases were caused by small filterers and predators (both lakes, Fig. 2). Under increasing nutrient status from eutrophic to hypereutrophic, epibenthos (Mallusjärvi) together with small filterers (Tiiläänjärvi) accounted most for the shifts in functional groups (Fig. 2). These functional groups among Cladocera may thus serve as indicators for nutrient enrichment driven changes in food webs and habitats.

When the relationships between FD and environmental factors related to nutrient enrichment process were examined with multiple regression analyses, there appeared to be differential responses and short-term patterns among the lakes (Table 3). In Mallusjärvi, magnetic susceptibility seemed to have the strongest connection with FD when the entire

sediment sequence was used and over the eutrophic–hypereutrophic succession. Magnetic susceptibility was inserted as an environmental factor as an indicator for turbidity of the aquatic environment since it may provide information on catchment erosion and lake-water turbidity (Thompson et al. 1975). TP was significant during reference–eutrophic ($R^2 = 0.62$, $p = 0.001$) and eutrophic–hypereutrophic ($R^2 = 0.39$, $p = 0.017$) periods but not throughout the core succession (Table 3). This suggests that nutrient status is not straightforwardly related to cladoceran FD during eutrophication process (Fig. 3) and it cannot explicitly account for long-term changes in FD. Instead, general changes in the physical characters of aquatic environment due to catchment disturbances, such as reduced water transparency and its negative effects on submerged vegetation and phytoplankton distribution (i.e. habitat structure and food resources), may be important in explaining the shifts in FD and functional assemblages. Barnett & Beisner (2007) showed that zooplankton FD and TP have a clear negative relationship in a spatial data set and attributed this to changes in spatial distribution and type of phytoplankton resource, in specifically decreasingly heterogeneous distribution on algae. A similar negative relationship was observed between FD and TP in the Mallusjärvi record during the hypereutrophic period when FD declined (Fig. 3).

The Mallusjärvi core extended back in time for several centuries and it recorded the oligotrophic ($TP < 20 \mu\text{g L}^{-1}$) reference status before the lake was more heavily impacted by historic agriculture and nutrient enrichment (Luoto & Raunio 2011). The location of Lake Mallusjärvi in Porvoonjoki River Valley with fertile soils has attracted humans and agricultural activities since the 14th–16th centuries. Eutrophic lake status was recorded between ca. 1700–1850 C.E. after which TP increased to $> 80 \mu\text{g L}^{-1}$ (Fig. 2a; Luoto & Raunio 2011). This succession was shown in the record as an even distribution of different functional groups (high FEve) and as a steady increase in FD (Fig. 2a) likely due to

diversifying resources and stable and versatile food web structure. After the lake became hypereutrophic during the 20th century, predators, large filterers, and oval epibenthos decreased and even disappeared, whereas small filterers and globular epibenthos dominated the community and FD and FEve reduced dramatically (Fig. 2a). The reduced success of oval epibenthos over the hypereutrophic period likely relates to their niche preferences among aquatic vegetation, which was negatively affected by increasing lake-water turbidity and phytoplankton blooms. On the other hand, large filterers and predators were negatively affected by increasing abundance of cyprinid fish, which hunt them (Nevalainen & Luoto 2013), and planktonic habitats were occupied by smaller filterers, which are not affected by fish predation. The success of small filterers is also likely due changes in phytoplankton communities during nutrient enrichment (cf. Barnett & Beisner 2007). Significant relationships between FD and TP occurred during the reference–eutrophic and eutrophic–hypereutrophic phases, when also magnetic susceptibility was significant (Table 3), but not during the core succession. This suggests that the relationship is not linear through long time scales and over the eutrophication process (Fig. 3).

Whereas FD in the Mallusjärvi core was significantly related to turbidity and nutrient status, such associations could not be found from the Tiilään järvi core, where the only statistically significant explanatory variable was the abundance of predatory midges ($R^2 = 0.22$, $p = 0.039$) over the reference–eutrophic phase (Table 3). Invertebrate predation may substantially alter cladoceran communities (de Bernardi et al. 1987). For example, the phantom midge *Chaoborus flavicans*, which was the most abundance predatory midge in Tiiläänjärvi (Luoto & Ojala 2014), is known to feed preferably on smaller planktonic cladocerans such as *Bosmina longirostris* and *B. coregoni* (Jäger et al. 2011). The functional group "small filterers" included the both *Bosmina* taxa (Table 2), which also accounted for

largest variability in the Tiiläänjärvi core (Fig. 2b). Therefore, it is possible that the observed relationship between FD and predatory midges during the early nutrient enrichment process actually reflects an ecological phenomenon, where cladocera FD is controlled by predation regimes (Table 3).

In Tiiläänjärvi (Fig. 2b), the relative abundance of functional groups exhibited more fluctuation than in Mallusjärvi. The core extended back in time until ~1940 C.E., recording the nutrient enrichment process from the oligo-mesotrophic state but not the actual reference status of the lake (Luoto & Ojala 2014). A marked shift in functional assemblages and FD occurred around 1950–1960 C.E. when TP increased to $>40 \mu\text{g L}^{-1}$ (over reference-eutrophic phases, Fig. 2b). All functional groups showed more even distribution when small filterers decreased, as indicated by increased FEeve, and also FD increased (Fig. 2b). This response was similar to the relationship between FD and TP in Mallusjärvi during the early eutrophication (Fig. 3) suggesting that FD increases under moderate nutrient enrichment. Yet, FD and TP did not exhibit statistically significant relationship in Tiiläänjärvi but multiple regressions indicated that predatory midges partly control cladoceran FD (Table 3). Predation could have impacted cladoceran FD by restricting the dominance of small filterers and allowing more a more even distribution of other functional groups (predators, large filterers) to thrive (Fig. 2). The FD succession in Tiiläänjärvi differed from Mallusjärvi over the hypereutrophic period, when FD did not reduce but stayed mostly in the same high level irrespective of high TP (Figs. 3). The lake has experienced anoxic conditions since 2000 C.E. and has seen reductions in fish catches during the past decades (Luoto & Ojala 2014). This has had a negative impact on the macrobenthic midge larval communities, severely reducing their functional diversity (Luoto & Ojala 2014). Predatory midges reduced and disappeared from the record (Luoto & Ojala 2014) and functional assemblages exhibited short-term

variability with no major trends (Fig. 2b). The reason why anoxia and high TP did not reduce cladoceran FD is likely related to cladoceran habitats outside the anoxic profundal zone.

Cladocerans utilize epilimnetic waters (planktonic filterers) and shallow benthic habitats (epibenthic groups) with available oxygen, whereas midge larvae inhabit deep bottoms suffering from anoxia. In addition, it is likely that the recently reduced fish and midge predation allowed predatory cladocerans and large filterers to occur and succeed in the pelagial zone during the hypereutrophic period (Fig. 2b).

FD indices have potential to unravel ecological phenomena behind the structure of biological communities and utilize tools to examine interactions of biodiversity and ecosystem processes (Mouchet et al. 2010). The main FD index (wFDc, Fig. 2) of the current study is based on the branch-length of the functional dendrogram (Fig. 1) and takes into account the relative abundances of taxa in the species pool (Pla et al. 2008). It was selected here as the primary FD index, others (FEve and FDiv) being supplementary, because it summarizes the multi-trait approach with species relative abundances into a single measure. There has arisen criticism against approaches utilizing the hierarchical classification due to bias it may cause, including loss of information and modification of interspecific functional distances (Podani & Schemara 2007). A set of multidimensional indices, including FEve and FDiv used here, have been suggested to allow for a more comprehensive picture of functional diversity (Villéger et al. 2008; Mouchet et al. 2010). The development of these indices during the nutrient enrichment process in the two lakes of the current study indicated that functional evenness (FEve) seemed to correspond with trends in wFDc, depicting the evenness of abundance distribution in niche space (Mason et al. 2005). FEve index then is indicative for the utilization efficiency of resources available within the niche space and it seemed to reduce in Mallusjärvi and slightly increase in Tiiläänjärvi during the nutrient enrichment (Fig. 2).

FDiv was steadier, experiencing only slight decrease in Mallusjärvi, suggesting high niche differentiation (i.e. low resource competition) and efficient resource use (Mason et al. 2005).

Concluding remarks

The use of downcore paleolimnological data in answering ecological questions in a temporal perspective is well justified, and should also be applied widely in biodiversity and FD investigations to unravel long-term trends and natural fluctuations. Although mostly valuable and reliable, it is also "noisy" and always dependent on the individual characters of the study site, its history, and time coverage and resolution of the core. In the current study, in the absence of a non-eutrophicated control lake with similar environmental settings (e.g. clay-turbidity), historical pre-disturbance conditions in the early cores were considered as references. Since both study lakes have individual succession of anthropogenic impacts and the sediments cores cover different time periods, the number of observations (i.e. sediment subsamples) between the progressive phases of eutrophication process varied and was lower during reference period. This may have an effect on the observed relationships between FD and nutrient enrichment, and makes it difficult to completely ascertain pre-disturbance succession of functional groups and FD. To tackle the question of FD variability under pristine conditions and its change under increasing nutrient status, a spatial surface sediment data set along a TP gradient should be examined in the future. In addition, the observed non-linear FD–TP relationships were partly obscured by the different time span and resolution of the cores, Mallusjärvi providing long-term trends of FD during the past centuries and Tiiläänjärvi allowing to see short-term, decadal variability.

The relationships between FD and TP exhibited some comparable features among the lakes, as FD was low during the reference period and increased with increasing nutrient enrichment until TP was $\sim 40\text{--}60 \mu\text{g L}^{-1}$ when highest FD was observed.

Accordingly, meso-eutrophic conditions induced cladoceran FD, and this was apparently due to the establishment, availability, and utilization of diverse niches in both pelagic and littoral zones of lakes emphasizing the role of bottom-up controls (habitat and food type) on FD.

Increasing primary production during the early nutrient enrichment likely provided food for different types of planktonic filterers and also predators flourished due to high number of prey items of different size. In addition, at the early stage of nutrient enrichment process aquatic macrophytes likely benefited from increasing TP providing diversity of niches for the littoral-benthic taxa. However, different responses were observed between the lakes under hypereutrophic conditions when FD decreased dramatically in Mallujärvi, but remained high irrespective of high TP in Tiiläänjärvi. This variation may have been caused by differing fish status among the lakes during the hypereutrophic phases, since fish likely controlled large planktonic cladocerans in Mallusjärvi, but were reduced along with invertebrate midge predators due to anoxia in Tiiläänjärvi allowing these functional groups to succeed and utilize the available niche space.

Based on the results, it can be suggested that in naturally mesotrophic lakes cladoceran FD is related with lake productivity and bottom-up controls during early stages of eutrophication. Under hypereutrophic conditions, top-down controls become more important in shaping the functionality of the communities and FD. FD and its connections to lake productivity and food web structure make it a promising concept in examining ecosystem functioning under long-term environmental changes in lakes.

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Data accessibility

Data (cladoceran functional assemblages and functional diversity indices from the sediment cores of lakes Mallusjärvi and Tiiläänjärvi) are deposited in the PANGAEA data publisher of Earth and Environmental Sciences (doi:10.1594/PANGAEA.863605).

References

- Adamczuk, M. (2014) Niche separation by littoral-benthic Chydoridae (Cladocera, Crustacea) in a deep lake - potential drivers of their distribution and role in littoral-pelagic coupling. *Journal of Limnology*, **73**, 490-501.
- Alhonen, P. (1970) On the significance of the planktonic/littoral ratio in the cladoceran stratigraphy of lake sediments. *Commentationes Biologicae*, **35**, 1-9.
- Bernett, A.J. & Beisner, B.E. (2007) Zooplankton biodiversity and lake trophic state: explanations invoking resource abundance and distribution. *Ecology*, **88**, 1675-1686.
- Barnett, A.J., Finlay, K., Beisner, B.E. (2007) Functional diversity of crustacean zooplankton communities: towards a trait-based classification. *Freshwater Biology*, **52**, 796-813.

- Belyaeva, M. & Taylor, D.J. (2009) Cryptic species within the *Chydorus sphaericus* species complex (Crustacea: Cladocera) revealed by molecular markers and sexual stage morphology. *Molecular Phylogenetics and Evolution*, **50**, 534-546.
- Bigler, C., Heiri, O., Krskova, R., Lotter, A.F. & Sturm, M. (2006) Distribution of diatoms, chironomids and cladocera in surface sediments of thirty mountain lakes in south-eastern Switzerland. *Aquatic Sciences*, **68**, 154-171.
- Cadotte, M.V., Carscadden, K. & Mirotnik, N. (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, **48**, 1079-1087.
- Carpenter, S.R., Kitchell, J.F., Hodgson, J.R., Cochran, P.A., Elser, J.J., Elser, M.M., Lodge, D.M., Kretchmer, D., He, X. & von Ende, C.N. (1987) Regulation of lake primary productivity by food web structure. *Ecology*, **68**, 1860-1876.
- Casanoves, F., Pla, L., Di Rienzo, J.A. & Díaz, S. (2011) FDiversity: a software package for the integrated analysis of functional diversity. *Methods in Ecology and Evolution*, **2**, 233–237.
- Chen, G., Dalton, C. & Taylor, D. (2010) Cladocera as indicators of trophic state in Irish lakes. *Journal of Paleolimnology*, **44**, 465-481.
- de Bernardi, R., Giussani, G., & Manca, M. (1987). Cladocera: predators and prey. *Hydrobiologia*, **145**, 225-243.
- de Bernardi, R., Giussani, G., Manca, M. & Ruggiu, D. (1990) Trophic status and the pelagic system in Lago Maggiore. *Hydrobiologia*, **191**, 1-8.
- DeMott, W.R. (1982) Feeding selectivities and relative ingestion rates of *Daphnia* and *Bosmina*. *Limnology and Oceanography*, **27**, 518-527.

- Fairchild, G.F. (1983) Birth and death rates of a littoral filter feeding microcrustacean, *Sida crystallina* (Cladocera), in Cochran Lake, Michigan. *Internationale Revue der gesamten Hydrobiologie und Hydrographie*, **68**, 339-350.
- Flössner, D. (1972) *Krebstiere, Crustacea. Kiemen- und Blattfüßer, Branchiopoda. Fisschläuse, Branciura*. Gustav Fischer Verlag, Jena.
- Flössner, D. (2000) *Die Haplopoda und Cladocera Mitteleuropas*. Backhuys Publishers, Leiden.
- Frey, D.G. (1988) Littoral and offshore communities of diatoms, cladocerans and dipterous larvae, and their interpretation in paleolimnology. *Journal of Paleolimnology*, **3**, 179-191.
- Froyd, C.A. & Willis, K.A. (2008) Emerging issues in biodiversity & conservation management: The need for a palaeoecological perspective. *Quaternary Science Reviews*, **27**, 1723-1732.
- Fryer, G. (1968) Evolution and adaptive radiation in the Chydoridae (Crustacea: Cladocera): A study in comparative functional morphology and ecology. *Philosophical Transactions of the Royal Society of London B*, **254**, 221-385.
- Geller, W. & Müller, H. (1981) The filtration apparatus of Cladocera: filter mesh-sizes and their implications on food selectivity. *Oecologia*, **49**, 316-321.
- Gregory-Eaves, I. & Beisner, B.E. (2011) Palaeolimnological insights for biodiversity science: an emerging field. *Freshwater Biology*, **56**, 2653-2661.
- Hammer, Ø., Harper, D.A.T. & Ryan, P.D. (2001) *PAST: Paleontological Statistics Software Package for Education and Data Analysis*. *Palaeontologica Electronica* 4 (1), 9, http://palaeo-electronica.org/2001_1/past/issue1_01.htm.
- Heino, J. (2008) Patterns of functional biodiversity and function-environment relationships in lake littoral macroinvertebrates. *Limnology and Oceanography*, **53**, 1446-1455.

Herzig, A. (1995) *Leptodora kindti* : efficient predator and preferred prey item in Neusiedler See, Austria. *Hydrobiologia*, **307**, 273-282.

Hooper, D.U., Solan, M., Symstad, A., Díaz, S., Gessner, M.O., Buchmann, N., Degrande, V., Grime, P., Hulot, F., Mermillod-Blondin, F., Roy, J., Spehn, E. & Van Peer, L. (2002) Species diversity, functional diversity, and ecosystem functioning. In: *Biodiversity and ecosystem functioning. Synthesis and perspectives* (Eds M.Loreau, S. Naeem & P. Inchausti, pp: 195–281. Oxford University Press, Oxford.

Ilyashuk, E.A., Ilyashuk, B.P., Tylmann, W., Koinig, K.A. & Psenner, R. (2015) Biodiversity dynamics of chironomid midges in high-altitude lakes of the Alps over the past two millennia. *Insect Conservation and Diversity*, doi: 10.1111/icad.12137.

Jeppesen, E., Jensen, J.P., Søndergaard, M., Lauridsen, T. & Landkildehus, F. (2000) Trophic structure, species richness and biodiversity in Danish lakes: changes along a phosphorus gradient. *Freshwater Biology*, **45**, 201-218.

Jeppesen, E., Leavitt, P., De Meester, L. & Jensen, J.P. (2001) Functional ecology and palaeolimnology: using cladoceran remains to reconstruct anthropogenic impact. *Trends in Ecology & Evolution*, **16**, 191-198.

Jürgens, K. (1994) Impact of *Daphnia* on planktonic microbial food webs - a review. *Marine Microbial Food Webs*, **8**, 295-324.

Jäger, I. S., Hölker, F., Flöder, S., & Walz, N. (2011) Impact of *Chaoborus flavicans*-predation on the zooplankton in a mesotrophic lake—a three year study. *International Review of Hydrobiology*, **96**, 191-208.

Kattel, G.R., Battarbee, R.W., Mackay, A. & Birks, H.J.B. (2007) Are cladoceran fossils in lake sediment samples a biased reflection of the communities from which they are derived? *Journal of Paleolimnology*, **38**, 157-181.

- Korhola, A. & Rautio, M. (2001) Cladocera and other Branchiopod Crustaceans. In: *Tracking environmental change using lake sediments, vol 4: Zoological Indicators* (Eds Smol J. P., Birks H.J.B. & Last W.M., pp: 5–41. Kluwer Academic Publishers, Dordrecht.
- Korosi, J. & Smol, J.P. (2012) Contrasts between dystrophic and clearwater lakes in the long-term effects of acidification on cladoceran assemblages. *Freshwater Biology*, **57**, 2449-2464.
- Korosi, J.B., Kurek, J. & Smol, J.P. (2013) A review on utilizing *Bosmina* size structure archived in lake sediments to infer historic shifts in predation regimes. *Journal of Plankton Research*, **35**, 444-460.
- Korosi, J.B., Paterson, A.M., DeSellas, A.M. & Smol, J.P. (2008) Linking mean body size of pelagic Cladocera to environmental variables in Precambrian Shield lakes: a paleolimnological approach. *Journal of Limnology*, **67**, 22-34.
- Laird, K.R., Kingbury, M.V. & Cumming, B. (2010) Diatom habitats, species diversity and water-depth inference models across surface-sediment transects in Worth Lake, northwest Ontario, Canada. *Journal of Paleolimnology*, **44**, 1009-1024.
- Leclerc, V., Sirois, P., Planas, D. & Bérubé, P. (2011) Diet and feeding success of fast-growing yellow perch larvae and juveniles in perturbed boreal lakes. *Transactions of the American Fisheries Society*, **140**, 1193-1205.
- López-Blanco, C., Miracle, M.R. & Vicente, E. (2011) Cladoceran assemblages in a karstic lake as indicators of hydrological alterations. *Hydrobiologia*, **676**, 249-261.
- Luoto, T.P. & Nevalainen, L. (2015) Climate-forced patterns in midge feeding guilds. *Hydrobiologia*, **742**, 141-152.
- Luoto, T.P. & Nevalainen, L. (2011) Inferring reference conditions of hypolimnetic oxygen for deteriorated Lake Mallusjärvi in the cultural landscape of Mallusjoki,

southern Finland using fossil midge assemblages. *Water, Air, & Soil Pollution*, **217**, 663-675.

Luoto, T.P. & Raunio, J. (2011) A comparison of chironomid-based total phosphorus training sets developed from contemporary pupal exuviae and sedimentary larval head capsules to infer lake trophic history. *Fundamental and Applied Limnology*, **179**, 93-102.

Luoto, T.P. & Ojala, A.E.K. (2014) Paleolimnological assessment of ecological integrity and eutrophication history for Lake Tiiläänjärvi (Askola, Finland). *Journal of Paleolimnology*, **51**, 455-468.

Luoto, T.P., Nevalainen, L., Kubischta, F., Kultti, S., Knudsen, K.L. & Salonen, V.-P. (2011) Late Quaternary ecological turnover in High Arctic Lake Einstaken, Nordaustlandet, Svalbard (80 °N). *Geografiska Annaler, Series A: Physical Geography*, **93**, 337-354.

Manca, M., Torretta, B., Comoli, P., Amsinck, S.L. & Jeppesen, E. (2007) Major changes in trophic dynamics in large, deep, sub-alpine Lake Maggiore from 1940s to 2002: a high resolution comparative palaeo-neolimnological study. *Freshwater Biology*, **52**, 2256-2269.

Mason, N.W.H., Mouillot, D., Lee, W.G. & Wilson, J.B. (2005) Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos*, **111**, 112-118.

Mouchet, M.A., Villéger, S., Mason, N.W.H. & Mouillot, D. (2010) Functional diversity measures: an overview and their ability to discriminate community assembly rules. *Functional Ecology*, **24**, 867-876.

Nevalainen, L. (2010) Evaluation of microcrustacean (Cladocera, Chydoridae) biodiversity based on sweep net and surface sediment samples. *Écoscience*, **17**, 356-364.

- Nevalainen, L. (2011) Intra-lake heterogeneity of sedimentary cladoceran (Crustacea) assemblages forced by local hydrology. *Hydrobiologia*, **676**, 9-22.
- Nevalainen, L. (2012) Distribution of benthic microcrustaceans along a water depth gradient in an Austrian Alpine lake – Sedimentary evidence for niche separation. *Limnologica*, **42**, 65-71.
- Nevalainen, L. & Luoto, T.P. (2013) Limnological deterioration forces community and phenotypic changes in Cladocera: Tracking eutrophication Mallusjärvi, a lake in southern Finland. *Boreal Environment Research*, **18**, 209-222.
- Nevalainen, L., Luoto, T.P., Kultti, S. & Sarmaja-Korjonen, K. (2013) Spatio-temporal distribution of sedimentary Cladocera (Crustacea: Branchiopoda) in relation to climate. *Journal of Biogeography*, **40**, 1548-1559.
- Nevalainen, L., Lami, A., Luoto, T.P. & Manca, M. (2014b) Fossil cladoceran record from Lake Piramide Inferiore (5067 m a.s.l.) in the Nepalese Himalayas – biogeographical and paleoecological implications. *Journal of Limnology*, **73**, 156-166.
- Nevalainen, L., Ketola, M., Korosi, J.B., Manca, M., Kurmayer, R., Koinig, K., Psenner, R. & Luoto, T.P. (2014a) Zooplankton (Cladocera) species turnover and long-term decline of *Daphnia* in two high mountain lakes in the Austrian Alps. *Hydrobiologia*, **722**, 75-91.
- Nevalainen, L., Luoto, T.P., Manca, M. & Weisse, T. (2015a) A paleolimnological perspective on aquatic biodiversity in Austrian mountain lakes. *Aquatic Sciences*, **77**, 59-69.
- Nykänen, M., Malinen, T., Vakkilainen, K., Liukkonen, M. & Kairesalo, T. (2010) Cladoceran community responses to biomanipulation and re-oligotrophication

in Lake Vesijärvi, Finland, as inferred from remains in annually laminated sediment. *Freshwater Biology*, **55**, 1164-1181.

Nyman, M., Korhola, A. & Brooks, S.J. (2005). The distribution and diversity of Chironomidae (Insecta: Diptera) in western Finnish Lapland, with special emphasis on shallow lakes. *Global Ecology and Biogeography*, **14**, 137-153.

Olesen, J. (2013) The crustacean carapace: morphology, function, development, and phylogenetic history. In: *Functional morphology and diversity* (Eds Watling L. & Thiel M.), pp: 103-139. Oxford University Press, Oxford.

Packard, A.T. (2001) Clearance rates and prey selectivity of the predaceous cladoceran *Polyphemus pediculus*. *Hydrobiologia*, **442**, 177-184.

Perga, M.-E., Desmet, M., Enters, D. & Reyss, J.-L. (2010) A century of bottom-up- and top-down-driven changes on a lake planktonic food web: A paleoecological and paleoisotopic study of Lake Annecy, France. *Limnology and Oceanography*, **55**, 803-816.

Pla, L., Casanoves, F., Di Rienzo, J., Fernandez, F., & Finegan, B. (2008) Confidence intervals for functional diversity indices considering species abundance. XXIV International Biometric Conference, Dublin.

Pla-Rabes, S., Flower, R.J., Shilland, E.M. & Kreiser, A.M. (2011) Assessing microbial diversity using recent lake sediments and estimations of spatio-temporal diversity. *Journal of Biogeography*, **38**, 2033-2040.

Podani, J. & Schmera, D. (2006) On dendrogram-based measures of functional diversity. *Oikos*, **115**, 179-185.

Rautio, M. & Nevalainen, L. (2013) Cladocera. In: *Encyclopedia of Quaternary Science* (Ed Elias S.A.), pp: 271–280. Elsevier, Amsterdam.

- Richard Albert, M., Chen, G., MacDonald, G.K., Vermaire, J.C., Bennett, E.M. & Gregory-Eaves, I. (2010) Phosphorus and land-use changes are significant drivers of cladoceran community composition and diversity: an analysis over spatial and temporal scales. *Canadian Journal of Fisheries and Aquatic Sciences*, **67**, 1262-1273.
- Sarmaja-Korjonen, K. (2001) Correlation of fluctuations in cladoceran planktonic:littoral ratio between three cores from a small lake in southern Finland: Holocene water-level changes. *The Holocene*, **11**, 53-63.
- Sarnell, O. (2005) *Daphnia* as keystone predators: effects on phytoplankton diversity and grazing resistance. *Journal of Plankton Research*, **27**, 1229-1238.
- Smol, J.P., Wolfe, A.P., Birks, H.J.B., Douglas, M.S.V., Jones, V.J., Korhola, A., Pienitz, R., Rühland, K., Sorvari, S., Antoniades, D., Brooks, S.J., Fallu, M.-A., Hughes, M., Keatley, B.E., Laing, T.E., Michelutti, N., Nazarova, L., Nyman M., Paterson, A.M., Perren, B., Quinlan, R., Rautio, M., Saulnier-Talbot, É., Siitonen, S., Solovieva, N. & Weckström, J. (2005) Climate-driven regime shifts in the biological communities of arctic lakes. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 4397–4402.
- Sweetman, J.P. & Finney, B.P. (2003) Differential responses of zooplankton populations (*Bosmina longirostris*) to fish predation and nutrient-loading in an introduced and a natural sockeye salmon nursery lake on Kodiak Island, Alaska, USA. *Journal of Paleolimnology*, **30**, 183-193.
- Szeroczyńska, K. (1998) Anthropogenic transformation of nine lakes in Central Poland from Mesolithic to modern times in the light of Cladocera analysis. *Studia Geologica Polonica*, **112**, 123-165.

Szeroczyńska, K. & Sarmaja-Korjonen, K. (2007) *Atlas of Subfossil Cladocera from Central and Northern Europe*. Friends of the Lower Vistula Society, Świecie.

Thienpont, J.R., Rühland, K., Pisari, M.F.J., Kokelj, S.V., Kimpe, L.E., Blais, J.M. & Smol, J.P. (2013) Biological responses to permafrost thaw slumping in Canadian Arctic lakes. *Freshwater Biology*, **58**, 337-353.

Thienpont, J.R., Korosi, J.B., Cheng, E.S., Deasley, K., Pisaric, M. & Smol, J.P. (2015) Recent climate warming favours more specialized cladoceran taxa in western Canadian Arctic lakes. *Journal of Biogeography*, **42**, 1553-1565.

Thompson, R., Battarbee, R. W., O'Sullivan, P. E., & Oldfield, F. (1975) Magnetic susceptibility of lake sediments. *Limnology and Oceanography*, **20**, 687-698.

Villéger, S., Mason, N.W.H. & Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaced framework in functional ecology. *Ecology*, **89**, 2290-2301.

Velghe, K., Vermaire, J.C. & Gregory-Eaves, I. (2012) Declines in littoral species richness across both spatial and temporal nutrient gradients: a palaeolimnological study of two taxonomic groups *Freshwater Biology*, **57**, 2378-2389.

Vogt, R.J., Matthews, B., Cobb, T.P, Graham, M.D. & Leavitt, P.R. (2013) Food web consequences of size-based predation and vertical migration of an invertebrate predator (*Leptodora kindtii*). *Limnology and Oceanography*, **58**, 1790-1801.

Zaret, T.M. & Kerfoot, W.C. (1975) Fish predation on *Bosmina longirostris*: body-size selection versus visibility selection. *Ecology*, **56**, 232-237.

Zawiska, I., Zawisza, E., Woszczyk, M., Szeroczyńska, K., Spychalski, W. & Correa-Metrio, A. (2013) Cladocera and geochemical evidence from sediment cores show trophic changes in Polish dystrophic lakes. *Hydrobiologia*, **715**, 181-193.

Tables

Table 1. Geographical and limnological parameters (measured from the water column at the year of sampling) of lakes Mallusjärvi and Tiiläänjärvi and total phosphorus (TP) inferences (mean values, number of samples included in brackets) for the three periods of nutrient enrichment (hypereutrophic, eutrophic, and reference).

	Mallusjärvi	Tiiläänjärvi
Location (N)	60°44' N	60°54' N
Location (E)	25°38' E	25°70' E
Altitude (m a.s.l.)	46.1	17.1
Catchment (km ²)	88	38
Size (km ²)	5.4	2.1
Maximum depth (m)	8.8	10.5
pH (units)	7.3	7.4
Total nitrogen (µg L ⁻¹)	960	1300
Total phosphorus (µg L ⁻¹)	103	102
Inferred TP: hypereutrophic (µg L ⁻¹)	108 (N= 12)	100 (N = 10)
Inferred TP: eutrophic (µg L ⁻¹)	60 (N = 11)	43 (N = 24)
Inferred TP: reference (µg L ⁻¹)	11 (N = 5)	30 (N = 7)

Table 2. Cladoceran taxa and their occurrence (mean relative abundance, minimum–maximum, and Hill’s N2) in the Mallusjärvi and Tiiläänjärvi cores.

	Mallusjärvi			Tiiläänjärvi		
	N	Mean	N2	N	Mean	N2
<i>Leptodora kindti</i>	28	9.5	19.3	41	15.9	34.3
<i>Sida crystallina</i>	13	0.5	11.1	36	1.6	24.0
<i>Limnospira frontosa</i>	7	0.1	6.1	36	2.7	22.3
<i>Latona setifera</i>	12	1.0	8.3	12	0.4	10.6
<i>Daphnia</i> spp.	26	3.6	15.5	41	5.8	28.3
<i>Ceriodaphnia</i> spp.				5	0.1	4.1
<i>Bosmina longispina</i>				4	0.0	3.4
<i>Bosmina coregoni</i>	28	40.5	25.4	41	14.9	20.7
<i>Bosmina longirostris</i>	25	16.5	16.1	41	28.9	33.7
<i>Eurycercus</i> spp.	1	0.0	1.0	5	0.1	4.4
<i>Chydorus</i> cf. <i>sphaericus</i>	24	12.9	13.4	40	11.8	29.5
<i>Paralona pigra</i>	1	0.0	1.0	5	0.1	4.4
<i>Peracantha truncata</i>	2	0.0	1.7	3	0.1	2.6
<i>Pleuroxus uncinatus</i>	14	0.4	10.3	26	0.8	17.0
<i>Pleuroxus laevis</i>	2	0.0	1.9	3	0.1	2.3
<i>Pseudochydorus globosus</i>				2	0.0	1.9
<i>Alonella nana</i>	11	0.4	8.8	35	1.6	28.2
<i>Alonella excisa</i>	3	0.1	2.7	15	0.3	10.9
<i>Alonella exigua</i>				2	0.0	1.4
<i>Disparalona rostrata</i>	21	1.2	14.3	33	1.5	24.9
<i>Alona quadranguaris</i>	28	5.3	22.5	38	3.2	27.5
<i>Alona affinis</i>	28	3.1	19.8	34	1.8	25.0
<i>Alona rectangula</i>	2	0.0	2.0	16	0.4	12.9
<i>Alona intermedia</i>	13	0.4	11.3	25	0.9	20.5
<i>Alona guttata</i>	3	0.1	2.5	7	0.2	6.2
<i>Alona guttata</i> f. <i>tuberculata</i>	5	0.2	4.6	12	0.3	9.8
<i>Alona costata</i>	11	0.5	9.5	3	0.1	2.5
<i>Camptocercus rectirostris</i>	4	0.2	3.4	21	0.5	14.7
<i>Alonopsis elongata</i>	4	0.2	3.8	9	0.2	6.8
<i>Acroperus harpae</i>	19	0.8	13.5	38	1.8	25.8
<i>Graptoleberis testudinaria</i>	5	0.1	4.1	28	0.9	20.9
<i>Leydigia leydigi</i>	12	0.7	8.3	37	1.8	23.6
<i>Leydigia acanthocercoides</i>	2	0.1	2.0			
<i>Rhynchotalona falcata</i>	9	0.3	7.7	9	0.2	8.6
<i>Monospilus dispar</i>	23	1.2	13.3	21	0.8	16.4
<i>Polyphemus pediculus</i>				1	0.0	1.0

Table 3. Multiple linear regressions with coefficient of determination R^2 (and statistical significance, p) between functional diversity (wFDc index) and total phosphorus (TP), relative abundance of predatory midges (PRD), and magnetic susceptibility (MS) in Mallusjärvi and Tiiläänjärvi during the core succession, and over reference–eutrophic and eutrophic–hypereutrophic phases. Statistical significance ($p < 0.05$) is highlighted by bold type.

	Core succession	Reference – eutrophic	Eutrophic – hypereutrophic
Mallusjärvi	N = 28	N = 16	N = 23
TP	0.11 (0.933)	0.62 (0.001)	0.39 (0.017)
PRD	0.00 (0.509)	0.01 (0.905)	0.01 (0.054)
MS	0.49 (<0.001)	0.09 (0.594)	0.59 (<0.001)
Multiple	0.50 (<0.001)	0.63 (0.006)	0.72 (<0.001)
Tiiläänjärvi	N = 41	N = 31	N = 34
TP	0.02 (0.218)	0.08 (0.698)	0.01 (0.846)
PRD	0.06 (0.124)	0.22 (0.039)	0.02 (0.723)
MS	0.00 (0.596)	0.01 (0.264)	0.02 (0.604)
Multiple	0.11 (0.224)	0.26 (0.043)	0.03 (0.837)

Figure legends

Fig. 1 Functional dendrogram of cladoceran taxa encountered from the sediment cores of lakes Mallusjärvi and Tiiläänjärvi. The dendrogram separates the down-core species pool into functional groups, where group 1 = predators, group 2 = large filterers, group 3 = small filterers, group 4 = globular epibenthos, group 5 = oval epibenthos.

Fig. 2 Relative abundance of functional groups (see Fig. 1) and functional diversity (wFDc index), functional evenness (FEve index), and functional divergence (FDiv index) of the cladoceran assemblages in a) Mallusjärvi and b) Tiiläänjärvi sediment cores. The Cladocera data is compared with magnetic susceptibility (white dots, x-axis scale under the Mallusjärvi

diagram), relative abundance of predatory midges (black dots, x-axis scale under the Tiiläänjärvi diagram), and chironomid-inferred total phosphorus (Luoto & Raunio, 2011;

Luoto & Ojala, 2014). A LOESS smooth (span 0.4) is applied to the diversity indices.

Eutrophication succession is indicated by different shades of gray: light gray = reference period (oldest samples), mid gray = eutrophic period, and dark gray = hypereutrophic period (youngest samples).

Fig. 3. Relationship between functional diversity (wFDc index) and estimated (chironomid-inferred) total phosphorus (TP) in the Mallusjärvi (black) and Tiiläänjärvi (gray) cores. The dots represent down-core samples and lines are 3rd order polynomial regressions. The coefficient of determination (R^2) for the models was 0.36 ($p = 0.013$) in Mallusjärvi and 0.05 ($p = 0.564$) in Tiiläänjärvi.



