



Spatio-temporal cladoceran (Branchiopoda) responses to climate change and UV radiation in subarctic ecotonal lakes

Liisa Nevalainen¹  | Marttiina V. Rantala² | Milla Rautio³ | Tomi P. Luoto¹

¹Faculty of Biological and Environmental Sciences, Ecosystems and Environment Research Programme, University of Helsinki, Lahti, Finland

²Faculty of Biological and Environmental Sciences, Ecosystems and Environment Research Programme, Environmental Change Research Unit (ECRU), University of Helsinki, Helsinki, Finland

³Département des Sciences Fondamentales, Centre for Northern Studies (CEN) & Group for Interuniversity Research in Limnology and Aquatic Environment (GRIL), Université du Québec à Chicoutimi, 555 boulevard de l'Université Chicoutimi, Québec, Canada

Correspondence

Liisa Nevalainen, Faculty of Biological and Environmental Sciences, Ecosystems and Environment Research Programme, University of Helsinki, Niemenkatu 73, 15140 Lahti, Finland.
Email: liisa.nevalainen@helsinki.fi

Funding information

Luonnontieteiden ja Tekniikan Tutkimuksen Toimikunta, Grant/Award Number: 287547; Biotieteiden ja Ympäristön Tutkimuksen Toimikunta, Grant/Award Number: 308954, 314107

Editor: Jani Heino

Abstract

Aim: To understand modern and past aquatic community responses to climate-induced shifts in productivity and ultraviolet radiation (UV) exposure.

Location: Tree line ecotone from north boreal forest to subarctic tundra in north-eastern Finnish Lapland.

Taxon: Cladocera (Crustacea: Branchiopoda).

Methods: Thirty-one small and shallow lakes were examined for summer epilimnetic communities (SEC) and surface sediment fossil integrative communities (FIC) of Cladocera for species distribution and their environmental correlations. A 700-year down-core sediment sequence from a tree line lake (Námmájávri) was analysed for FICs and cladoceran-inferred UV absorbance (ABS_{UV} , indicative of melanin pigmentation) for evidence of long-term community and photoprotective responses and compared with records of palaeotemperature, solar intensity, and composite sediment biogeochemistry by variance partitioning analysis.

Results: The SECs were primarily correlated with specific UV absorbance (indicative of UV exposure) and total phosphorus and FICs by mean July air temperature and total nitrogen. The Námmájávri FICs showed subtle changes with a directional shift between the 19th and 21st centuries and were mostly explained by solar intensity. ABS_{UV} exhibited increases during the 18th and 20th centuries, being related to variation in sediment biogeochemistry, which was indicative of changes in auto- versus allochthonous production.

Main conclusions: The ecotonal distribution of cladocerans is sensitive to temperature, nutrients, and allochthonous carbon, which is closely linked with UV exposure. The long-term community shifts and photoprotection have been governed by solar intensity and biogeochemical shifts through lake water optics, attributable to direct UV impact or climate-mediated intensification in photodegradation of allochthonous carbon. Estimations of the dual effects and mechanisms of increasing temperatures and UV on subarctic lakes and their biota remain challenging as their individual impacts on key species were partly contradictory.

KEYWORDS

biodiversity, Cladocera, global change, Lapland, microbenthos, palaeolimnology, space-for-time substitution, zooplankton

1 | INTRODUCTION

Holarctic landscapes of glacial and periglacial origin are typically characterized by numerous lakes and ponds (Downing et al., 2006). These ecosystems have become subjected to new environmental regimes under the 20th–21st centuries' global change (ACIA, 2005). Among other threats, warming climate and increased solar ultraviolet (UV) irradiance cause multiple biotic responses, including changes in habitat structure, resource pool, and species distribution that are significant for ecosystem functioning (Häder et al., 2015; Williamson et al., 2014). High latitude aquatic systems, being often small, shallow and closely connected to the terrestrial and atmospheric realms, are susceptible to even slight changes in external forcing such as climate (Rautio et al., 2011). For example, they respond physically to climate warming by changes in ice-cover and lake-water thermal structure that significantly influence the distribution of aquatic organisms.

Solar forcing can affect species' distribution in arctic aquatic systems because they are exposed to consistent sun exposure during their active season and are usually low in UV-attenuating dissolved organic carbon (DOC) and chlorophyll-a (Chl-a). These factors increase UV exposure necessitating adaptive photoprotection by organisms (Rautio & Korhola, 2002). In conjunction, solar irradiation has a significant role in photodegradation of DOC in the arctic waters (Cory, Ward, Crump, & Kling, 2014) further increasing water column UV transparency. In addition to arctic waters, shallow and transparent subarctic lakes and their biota are susceptible to UV and even slight fluctuations of DOC that can be mediated through climate-induced catchment vegetation transition spatially or temporally (Leavitt et al., 2003). Lake water bio-optics, including DOC and associated UV gradients across vegetation change at the subarctic tree line impact the photoprotection of aquatic biota (Nevalainen, Luoto, Rantala, Galkin, & Rautio, 2015) and acts as significant biogeographical driver for aquatic organisms (Rautio, Bonilla, & Vincent, 2009).

Elucidating high latitude lake functioning and aquatic responses across the circumpolar regions under global change are significant as these ecosystems are sentinels for environmental changes (Smol, 2016) and globally significant in the sequestration of organic carbon (Tranvik et al., 2009). They are additionally ecologically important in acting as one of the final refugia for cold-water biodiversity, which is at high risk of being extirpated through rapidly increasing temperatures (Rühland, Paterson, Keller, Michelutti, & Smol, 2013). Due to their remoteness and lack of appropriate long-term monitoring data, palaeolimnological approaches have been successfully utilized in examining biodiversity, species distribution, and aquatic responses to environmental changes during the Anthropocene. Previous studies have recorded significant aquatic responses in northern lakes, including, for example, increases in organic carbon burial (Heathcote, Anderson, Prairie, Engstrom, & del Giorgio, 2015; Rantala, Luoto, & Nevalainen, 2016), changes in organisms' UV responses (Nevalainen, Rantala, Luoto, Ojala, & Rautio, 2016), and community reorganizations in different trophic levels (Luoto, Oksman, & Ojala, 2015; Smol et al., 2005).

In this study, we focused on the distribution and environmental forcing of a keystone microcrustacean group (Cladocera, Branchiopoda) along spatial and temporal gradients with the main aim to understand cladoceran responses in the tree line ecotone lakes to solar forcing and climate-induced shifts in aquatic production and UV regimes at different time-scales. We examined the composition of contemporary (seasonal) and surface sediment (long-term) cladoceran communities with respect to temperature and limnological parameters in 31 subarctic lakes in northern Finland in order to clarify environmental determinants of their ecotonal distribution at the subarctic landscape and evaluate their sensitivity to climate warming and its limnological consequences, such as changes in bio-optical characters including DOC and UV transparency. To put the modern spatial ecological patterns into a long-term temporal context, we further investigated the past community dynamics and UV exposure of cladocerans in a sediment core from a tree line lake. We approached our data sets with assumptions that climate-driven bio-optical characters (e.g., DOC through vegetation change) impose significant controls on cladoceran distribution in subarctic lakes and lakes' underwater UV exposure through time is partly controlled by solar radiation intensity due to consistent diurnal sun light during the open water season and naturally low abundance of UV-attenuating compounds.

2 | MATERIALS AND METHODS

2.1 | Sampling and sample analyses

Thirty-one lakes located in northern Finnish Lapland along a catchment vegetation gradient from north boreal coniferous forest to treeless subarctic tundra were selected for the study (Figure 1). The lakes were examined for limnological, geographical, and temperature variability (details in Rantala, Nevalainen, Rautio, Galkin, & Luoto, 2016) and categorized as forest, tundra or wetland lakes according to the dominant vegetation features on their catchments (Appendix S1). The lakes were sampled for Cladocera community composition using two comparative sampling methods during late July 2014. First, qualitative sweep net samples were taken from the littoral open-waters for summer epilimnetic communities (SECs) with a 63- μ m plankton net to estimate community composition of Cladocera during the peak production in the lakes. For each sample, the net was swept back and forth over about 1.5 m of lake shore from three different littoral locations around the basin to collect animals from different locations and habitats if such appeared (e.g., vegetation, rocks, sand). The sampling was done from the shoreline. The samples were preserved in ethanol in small plastic jars and analysed for their cladoceran species composition under an inverted microscope. Second, single surface sediment samples (topmost 0–2 cm) were collected from the mid basins (aiming for the deepest part) for fossil integrative communities (FICs) with a Limnos gravity corer from a small boat to estimate cladoceran community composition during the recent past (from years to decades depending on sedi-

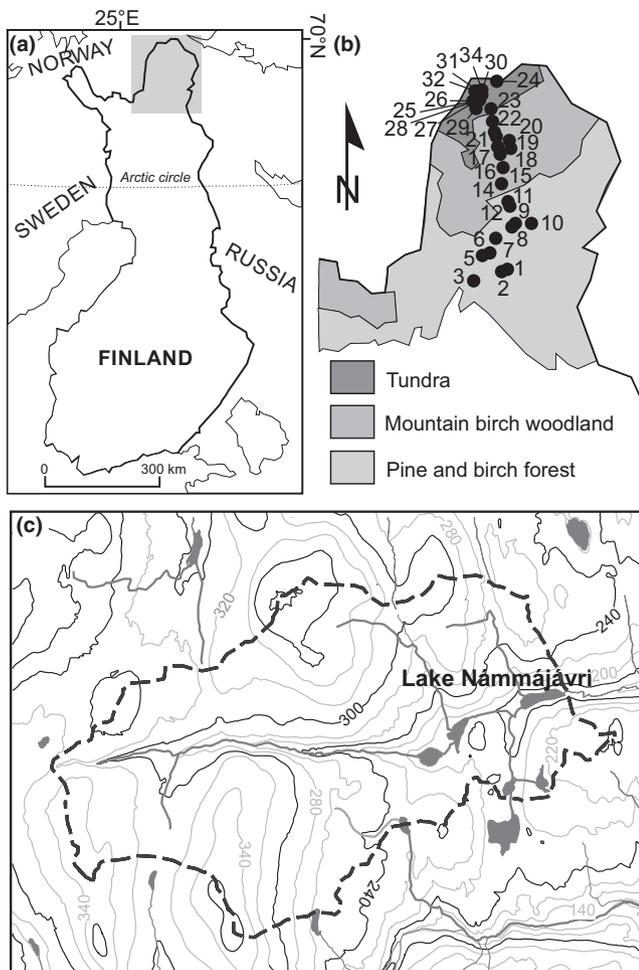


FIGURE 1 (a) Location of the study region in Finland indicated with a grey index box, (b) location of the 31 study lakes in Finnish Lapland indicated with black dots and numbers (according to their lake identification code) along the vegetation gradient from pine and birch forest to subarctic tundra, and (c) catchment (dashed line) of the sediment core study site Lake Námájávri (lake number 29) with detailed topographic features (contours and altitudes as metres above sea level) and lakes and streams (dark grey shading)

mentation rate). The sediment samples were prepared for fossil Cladocera analysis according to standard protocol by Szeroczyńska and Sarmaja-Korjonen (2007), including pretreatment in hot 10% KOH, sieving through a 51- μm mesh, and centrifugation at 4,000 rpm for 10 min. The samples were analysed for fossil cladoceran exoskeletal remains (e.g., carapaces, headshields, postabdomens) and the number of the most abundant body part was chosen to represent the number of individuals.

Lake Námájávri (Figure 1, Table 1) was selected as a down-core case study site due to its location in a tree line ecotone between mountain birch woodland and tundra. It was hence expected to have experienced past variation in lake-water bio-optical properties (e.g., DOC) due to climate-driven changes in catchment vegetation. The lake is located in a steeply sloped valley covered by mountain birches and the higher fells to the north and south of the lake consist of tundra vegetation. A 42-cm sediment core was

TABLE 1 Geographical and limnological variability in Lake Námájávri, northern Finland, in relation to the mean (M), minimum (Min.), and maximum (Max.) values of the 31 study lakes

	M	Min.	Max.	Námájávri
Altitude (m a.s.l.)	186	71	289	169
Catchment slope (m)	65	6	211	211
Lake area (ha)	3.6	0.3	13.2	3.2
Catchment area (ha)	78	2	901	901
Depth (m)	2.7	0.3	7.5	1.7
Dissolved organic carbon (mg L^{-1})	5.2	1.7	16.6	1.8
Specific UV absorbance ($\text{mg C L}^{-1} \text{m}^{-1}$)	1.9	0.7	3.2	2.4
Total phosphorus ($\mu\text{g L}^{-1}$)	9.3	4.7	24.1	5.9
Total nitrogen ($\mu\text{g L}^{-1}$)	416	138	806	138
Chlorophyll-a ($\mu\text{g L}^{-1}$)	1.8	0.2	6.1	0.6
pH (unit)	7.1	5.1	8.4	7.8

sampled from the mid basin with the Limnos gravity corer from a small boat. The core was divided into 1-cm subsamples that were analysed for past changes in FICs following the above described methods (Szeroczyńska & Sarmaja-Korjonen, 2007). Relative content of UV-protective melanin pigments (UV absorbance) was measured from fossil cladoceran (*Alona affinis*) carapaces (Nevalainen & Rautio, 2014) as established by Rantala, Luoto, et al. (2016). This included sieving of the sediment through a 100- μm mesh, extracting the *A. affinis* carapaces under a binocular microscope, and measuring UV absorbance of the remains using a specifically designed adapter in a UV-VIS spectrophotometer (UV-1800, Shimadzu Corporation, Kyoto, Japan). Seven carapaces were measured under UV radiation at 305 and 340 nm from each subsample and their average (ABS_{UV}) was used after highest and lowest absorbance values were omitted to reduce the influence on any sudden background disturbance on the absorbance measurements. The ~700-year chronology of the core is based on an age-depth model from ^{14}C of two terrestrial macrofossils (leaf fragments) and ^{137}Cs activity from the upper part of the core. ^{210}Pb dating method was used, but these measurement did not provide any reliable age estimates because of very low Pb activities in the sediment core (Rantala, Luoto, et al., 2016). All the analyses are based on single samples in the SEC, FIC, and down-core data sets as replicate samples were not taken and replicate analyses from individual samples were not performed.

2.2 | Numerical analyses

Multivariate statistics were used to analyse the main environmental drivers behind the cladoceran species distribution in the SEC and FIC samples. Redundancy analysis (RDA) was chosen based on the length of the first compositional gradients of the SEC (2.7 SD units) and FIC (2.6 SD units) species data (square root transformed) (Šmilauer & Lepš, 2014). In the RDAs, forward selection with permutation tests (999 permutations) were performed for both data sets to indicate statistically significant ($p < 0.05$) environmental variables.

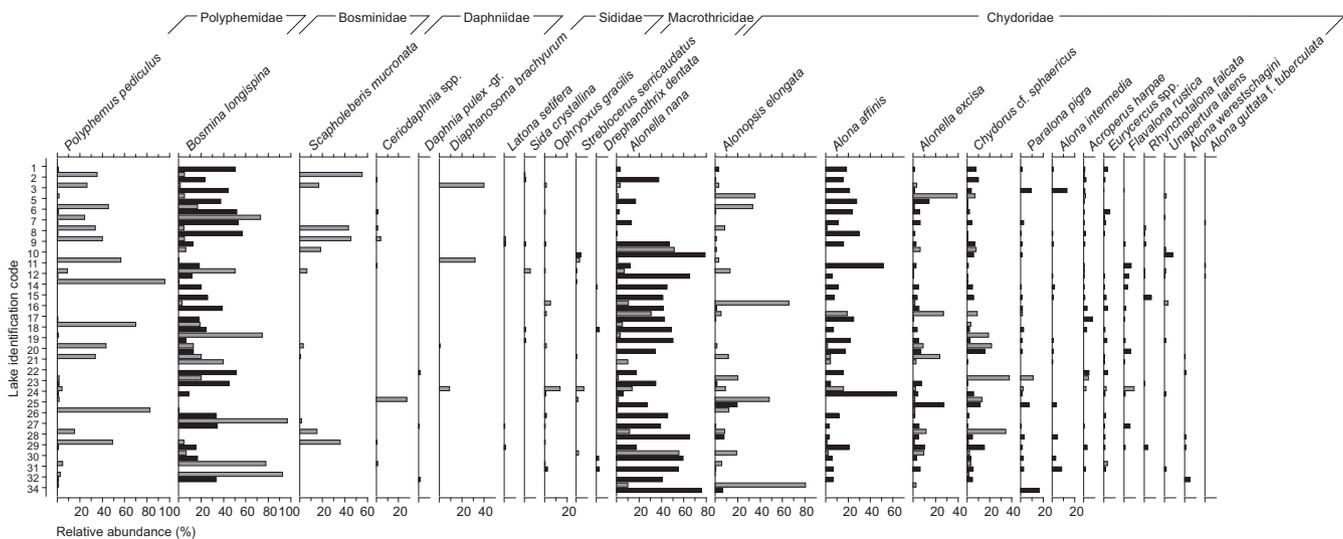


FIGURE 2 Relative abundance of the most common Cladocera taxa (Hill's effective number of occurrence $N_2 > 2.5$) in summer epilimnetic communities from sweep net samples (grey bars) and fossil integrative communities from surface sediment samples (black bars) in the study lakes in northern Finland (see Figure 1 for locations). Detailed information on all encountered taxa and their occurrences is available in Appendix S2

Limnological and climate variables without major intercorrelations (variance inflation factors < 20) were selected to be included in the RDAs as explanatory environmental variables: DOC, Chl-a, specific UV absorbance (SUVA), humification index (HI-index), fluorescence index (FI-index), diffuse attenuation coefficient of UV radiation at 305 nm (K_dUV) and photosynthetically active radiation (K_dPAR), pH, total phosphorus (TP), total nitrogen (TN), and mean July air temperature (T_{jul}) (Appendix S1).

For the down-core FICs in the Námajávri core, principal component analysis (PCA) was performed with square root transformed species data and PCA axis 1 scores were used to summarize the long-term variation in the fossil assemblages. Variance partitioning analysis (VPA), which analyses explanatory power of different explanatory variables on a response variable, was used to examine the contribution of palaeoenvironmental factors (composite sediment biogeochemistry, climate, and solar intensity) on temporal FIC and ABS_{UV} development. Here, previously available sediment biogeochemical data, including sediment organic matter (OM, as loss-on-ignition, LOI), $\delta^{13}C_{OM}$, $\delta^{15}N_{OM}$, carbon (as C%), nitrogen (as N%), and C/N ratio (from Rantala, Luoto, et al., 2016) were integrated into a single variable through PCA axis 1 scores, and used as a composite sediment biogeochemical variable. A previously available Chironomidae-based July air temperature reconstruction from Lake Námajávri core (Rantala, Luoto, et al., 2016), was used as an indicator for long-term climate variability, and a record of sun spot numbers (Solanki, Usoskin, Kromer, Schüssler, & Beer, 2004) as a proxy for solar intensity. RDAs and VPAs were performed with the Canoco5 software (Šmilauer & Lepš, 2014). Hill's effective number of occurrences (N_2) and locally weighted scatterplot smoothing were calculated with C2 software (Juggins, 2007). A lower smoothing span (0.13) from the original publication (Rantala, Luoto, et al., 2016: span 0.4) was used for ABS_{UV} to illustrate multidecadal fluctuations in melanization.

3 | RESULTS

3.1 | Sweep net and surface sediment samples

In sweep net samples, cladocerans were encountered in adequate numbers in 28 of the studied lakes (Figure 2) and *Bosmina (Eubosmina) longispina* and *Polyphemus pediculus* were the most abundant (Hill's $N_2 = 9.4$ and 12.6) and frequent ($N = 23$ for both) euplanktonic species in the SECs. Of the littoral-benthic taxa, *Alonopsis elongata* (Hill's $N_2 = 9.1$, $N = 21$), *Alonella nana* (6.4, 17), *Chydorus cf. sphaericus* (7.3, 16) and *Alonella excisa* (6.7, 16) were dominant. Surface sediment FICs were recovered from all of the lakes (Figure 2). Dominant fossil taxa were *B. longispina* (20.9, 26), and chydorids *A. nana* (22.1, 31) *Alona affinis* (16.4, 27), *A. excisa* (14.1, 26), *C. cf. sphaericus* (16.5, 27), and *Acroperus harpae* (11.5, 19). All encountered taxa and their occurrences among the two data sets are presented in Appendix S2 for detailed comparison.

The full RDA model with the 11 explanatory variables on SECs resulted in eigenvalues of 0.191 and 0.110 for RDA axes 1 and 2. The RDA axes 1 and 2 together explained 30.1% of species data. Forward selection of environmental variables identified SUVA ($F = 3.3$, $p = 0.003$) and TP ($F = 2.4$, $p = 0.022$) as the most significant explanatory factors (Figure 3a) as they explained 11.3 and 7.7%, respectively, of the total variation. In this model (Figure 3a), *Bosmina longispina* had a positive association with both TP and SUVA and *P. pediculus*, *Scapholeberis mucronata*, and *Eurycerus spp.* were associated with SUVA. *Alonella excisa*, *A. elongata*, and *A. nana* were, on the opposite, associated with more negative RDA axis 1 values. Wetland lakes had mainly positive RDA axis 1 values (Figure 3a).

The full RDA model on FICs resulted in eigenvalues of 0.261 and 0.083 for RDA axes 1 and 2 and the first two RDA axes together explained 34.4% of species data. Forward selection of explanatory

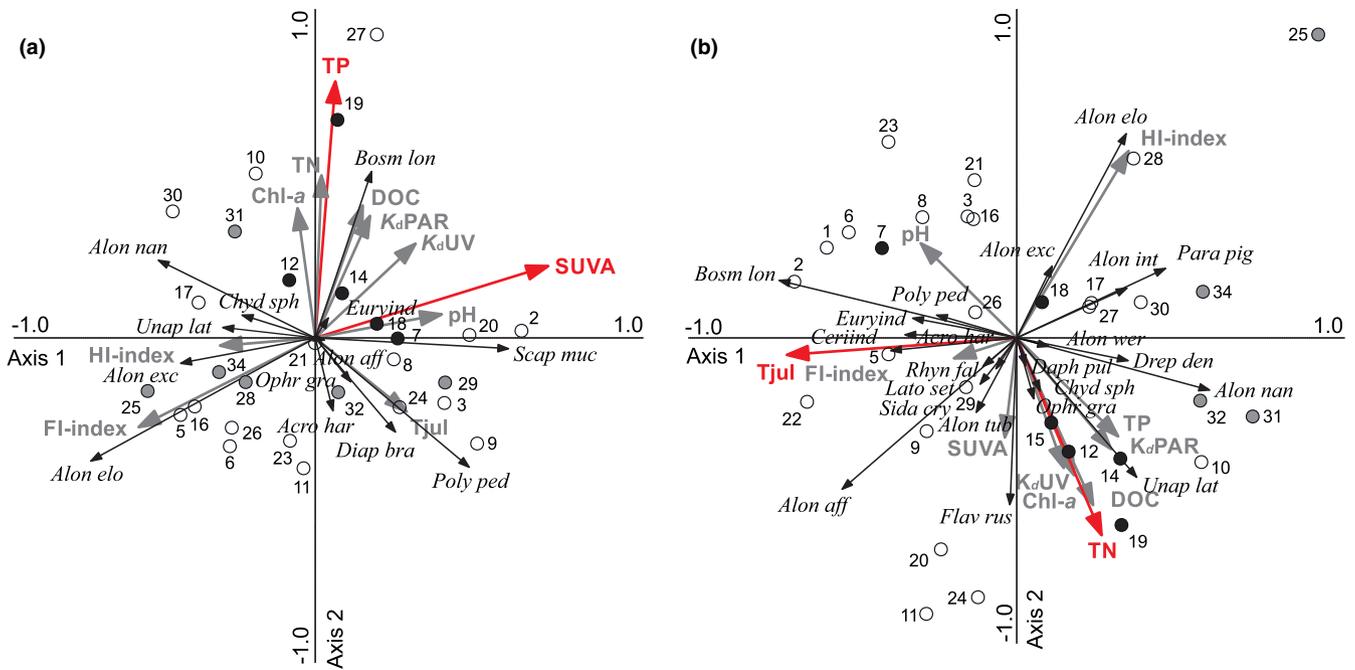


FIGURE 3 Redundancy analysis (RDA) ordination diagrams along RDA axes 1 and 2 of the relative abundance of most abundant cladoceran taxa (Hill's $N2 > 2.5$) as black arrows and environmental variables as grey arrows (significant environmental variables as red arrows) in the 31 study lakes in northern Finland for (a) summer epilimnetic communities and (b) fossil integrative communities. White dots indicate forest lakes, black dots wetland lakes, and grey dots tundra lakes (numbered according to their lake identification code) and species names are abbreviated (four letters from the genus and three from species name, details in Appendix S2). Abbreviations for environmental variables: DOC (dissolved organic carbon, mg L^{-1}), Chl-a (chlorophyll-a, $\mu\text{g L}^{-1}$), SUVA (specific UV absorbance, $\text{mg C L}^{-1} \text{m}^{-1}$), HI (humification index, ratio), FI (fluorescence index, ratio), $K_d\text{UV}$ (diffuse attenuation coefficient for UV at 305 nm, m^{-1}), $K_d\text{PAR}$ (diffuse attenuation coefficient for photosynthetically active radiation at 400–700 nm, m^{-1}), pH (pH units), TP (total phosphorus, $\mu\text{g L}^{-1}$), TN (total nitrogen, $\mu\text{g L}^{-1}$), and T_{jul} (mean July air temperature, $^{\circ}\text{C}$)

variables identified T_{jul} ($F = 4.81$, $p = 0.002$) and TN ($F = 2.98$, $p = 0.006$) as the most significant explanatory variables (Figure 3b), explaining 14.2 and 8.3% of the variation respectively. *Alona affinis*, *A. harpae*, and *B. longispina* were associated with positive RDA axis 1 values and high T_{jul} , whereas *Paralona pigra*, *Alona werestschagini*, *A. elongata*, and *A. nana* scored in the opposite direction in the ordination model (Figure 3b). *Flavalona rustica* and *Unapertura latens* were positively associated with increasing TN. Wetland lakes were located along the TN gradient and tundra lakes at the most negative end of T_{jul} gradient in the ordination model (Figure 3b).

3.2 | Lake Námajávri core

The down-core FICs were dominated by *B. longispina* (Hill's $N2 = 40.0$, $N = 42$), *A. affinis* (39.5, 42), *A. nana* (39.0, 42), and *A. excisa* (32.4, 42) (Figure 4). In the early core, *A. nana* decreased gradually from ~40 to 20% until 1400 C.E. and *B. longispina* exhibited periodic increases along with minor increases of several chydorids (Figure 4). A distinct assemblage shift occurred between 1700 and 1850 C.E. with reductions in *B. longispina*, *A. nana*, and *A. affinis* and increases in *C. cf. sphaericus* and *R. falcata*. This period was followed by a gradual shift with decreasing *B. longispina* and *A. nana* and increasing *A. affinis*, *C. cf. sphaericus*, *A. excisa*, and *P. pediculus* abundances since ~1850 C.E. until the present.

PCA of the down-core FICs resulted in eigenvalues 0.222 and 0.138 for PCA axes 1 and 2 respectively. Cumulative variance of species data explained by axes 1 and 2 was 36% (Appendix S3a). PCA for sediment biogeochemical variables (OM, $\delta^{13}\text{C}_{\text{OM}}$, $\delta^{15}\text{N}_{\text{OM}}$, C%, N%, and C/N) resulted in eigenvalues 0.520 and 0.206 for the axes 1 and 2 and cumulative variance explained by the two first axes was 72.6% (Appendix S3b). Long-term trends in PCA axis 1 scores of down-core communities and composite sediment biogeochemistry showed increasing values through the stratigraphy, whereas a stable period of more negative scores occurred between 1400 and 1700 C.E. in the FICs (Figure 5a) and around 1400 C.E. in sediment biogeochemistry (Figure 5e).

UV absorbance of fossil carapaces varied between 0.8 and 1.7 absorbance units (AU) with standard deviations between 0.07 and 1.02. Lowest absorbance values were measured in the early part of the core before 1400 C.E. (Figure 5b). Carapace absorbance showed an increasing trend after 1700 C.E. until the 20th century with a short decline at ~1850 C.E. and in the topmost sample.

According to the explained variation (60.5%) in the VPA (Figure 5), solar intensity (Figure 5d) and composite sediment biogeochemistry (PCA axis 1 scores, Figure 5e) uniquely explained 23.2 ($F = 14.9$, $p = 0.001$) and 6.1% ($F = 4.7$, $p = 0.052$) of variation in long-term community changes (i.e., PCA axis 1 scores). In the VPA, climate (T_{jul} , Figure 5c) did not significantly explain variation in the

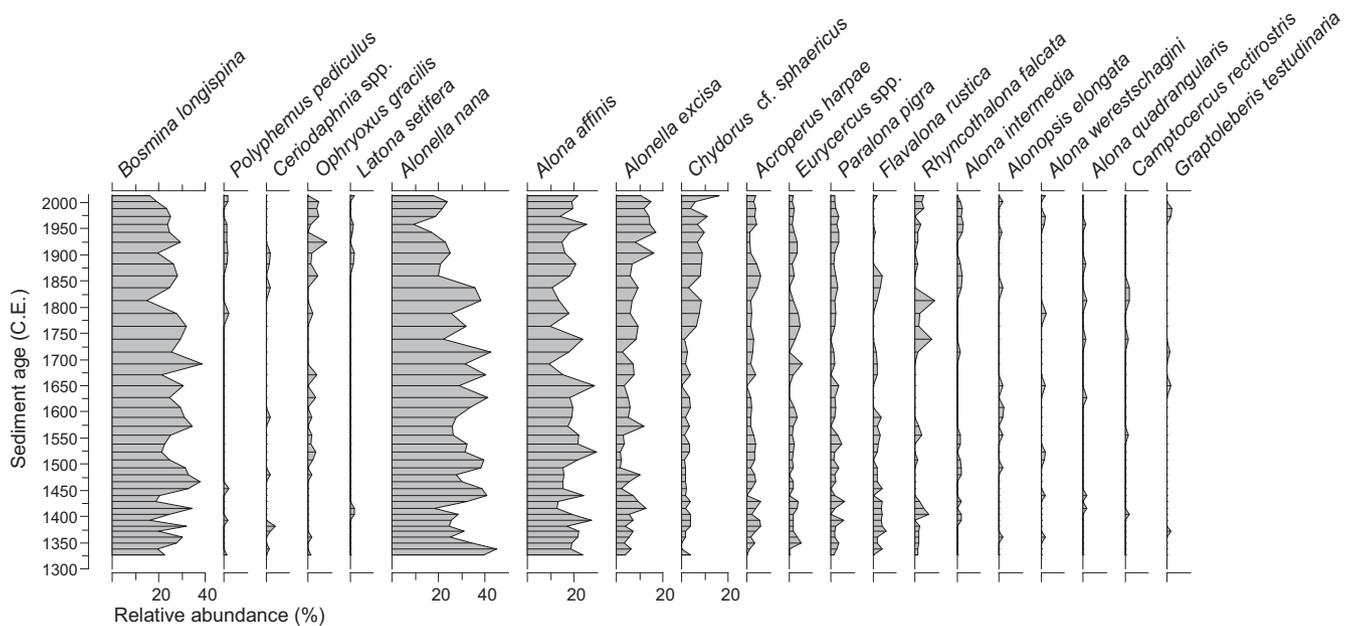


FIGURE 4 Relative abundance of the most abundant (Hill's $N_2 > 2.5$) fossil cladoceran taxa in Lake Námajávri sediment core during the past 700 years until ~1350 Current Era (C.E.). Horizontal bars indicate down-core sediment subsamples and the black lines with grey silhouette connect sediment subsamples in the stratigraphy

communities ($F = 1.0$, $p = 0.341$). The VPA on the ABS_{UV} record (Figure 5b) resulted in 32.6% of variation explained (Figure 5). Of this percentage, solar intensity (nonsignificant, $F = 1.9$, $p = 0.163$) and limnological factors ($F = 4.5$, $p = 0.047$) uniquely explained 4.9 and 18.8% with a nonsignificant contribution of climate ($F = 0.5$, $p = 0.484$).

4 | DISCUSSION

4.1 | Environmental forcing on ecotonal distribution

As cladocerans have high dispersal ability (Havel & Medley, 2006), the study region in question covers only approximately a 100 km geographical transect, and most taxa have generally widespread occurrences (Figure 2, Sweetman, Rühland, & Smol, 2010), dispersal is not likely a limiting factor for their distribution in the subarctic tree line. Rather, cladoceran distribution is regulated by local environments. The integrative results based on both the SECs and surface sediment FICs indicated that the distribution of Cladocera was principally related to underwater UV exposure (SUVA, i.e., DOC normalized absorbance at UV-wavelength 254 nm), nutrients (TP, TN), and climate (T_{jul}) (Figure 3). These environmental constraints on cladoceran communities were comparable to those across the Canadian subarctic ecotone (water temperature, DOC, and TP) with a similar type of vegetation transition (boreal forest–tundra) (Sweetman et al., 2010) suggesting, in combination with the current results, that nutrients, climate, and UV exposure act as major biogeographical drivers for microcrustacean communities across the subarctic tree line in the Holarctic. Previous studies from northern Finnish Lapland have indicated that lake depth, sediment organic content, climate (temperature, altitude), and pH are important factors in shaping

cladoceran communities (Korhola, 1999; Rautio, 1998). In this study, lake depth was not included in the RDA analyses because the study focus was set on limno-climatic factors and all the sampled lakes were shallow (<7.5 m, Table 1). In addition to lake depth, fish presence and abundance have been deemed important in structuring cladoceran communities (Jeppesen, Madsen, Jensen, & Anderson, 1996) but fish were not included in the current analyses due to the lack of information on fish distribution and abundance in the sampled remote lakes. The relatively low individual explanatory power of SUVA and TP (11 and 8% respectively) on SECs and TN and T_{jul} (14 and 8%) on FICs is likely partly explained by the confounding effects of biotic interactions (e.g., fish predation) (Figure 3).

Seasonal distribution of cladocerans (SECs) were mostly explained by the SUVA and TP gradients (Figure 3a). The role of TP is widely observed in acting as a bottom-up controller of cladoceran community structure (Chen, Dalton, & Taylor, 2010) because food (e.g., abundance and quality of phytoplankton and periphyton) and habitat (e.g., aquatic macrophytes) resources are dependent on available nutrients. The nutrient gradient in the current data set comprised ultraoligotrophic and mesotrophic waters with TP from 4.6 to 24.1 $\mu\text{g L}^{-1}$ where the highest TP concentrations were observed in wetland lakes and lowest in tundra lakes (Rantala, Nevalainen, et al., 2016). The pattern was evident in cladoceran SECs, as the RDA separated the mesotrophic wetland lakes from the oligotrophic tundra lakes in the ordination space (Figure 3a) suggesting that the trophic gradient is significant for cladoceran distribution during their peak season in the subarctic landscapes with wetlands. In combination, SUVA separated the current wetland lakes according to their SECs indicating that water colour and terrestrial organic carbon influence cladoceran community composition at the subarctic tree line (Figure 3b). Previously, DOC has been deemed as an important factor in

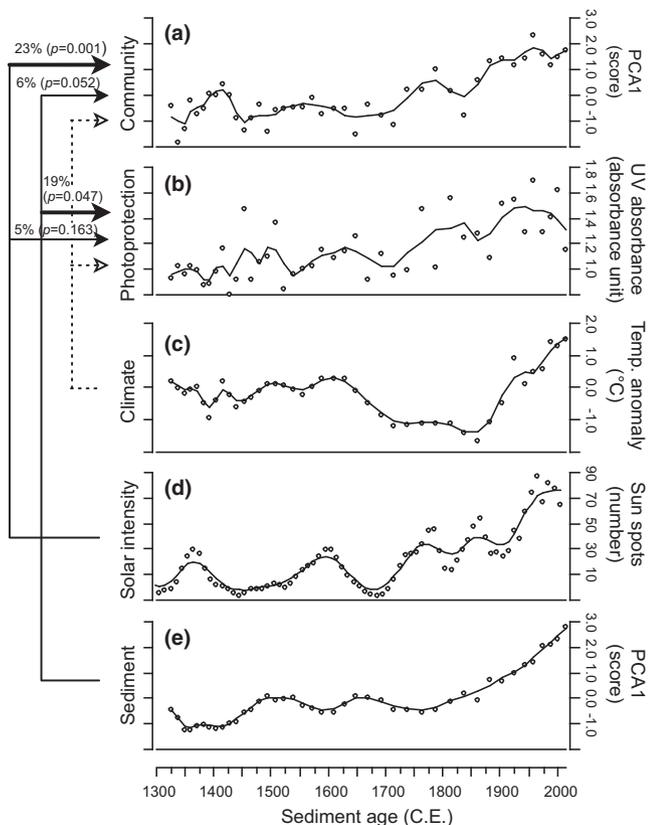


FIGURE 5 (a) Cladoceran community shifts as principal component analysis (PCA) axis 1 scores (community PCA1, see Appendix S3a for the PCA ordination diagram) and (b) cladoceran melanization as mean carapace UV absorbance (Rantala, Luoto, et al., 2016) in Lake Námájávri sediment core during the past 700 years. The cladoceran-based indices (a, b) are plotted against (c) Chironomidae-inferred mean July air temperature reconstruction (Rantala, Luoto, et al., 2016), (d) sun spot reconstruction (Solanki et al., 2004), and (e) PCA axis 1 scores from composite sediment biogeochemistry (sediment PCA1, see Appendix S3b for the PCA ordination diagram). The arrows (insignificant as dashed lines) indicate variance partitioning analysis results with the amount (%) of variance explained with significance (p -value) in brackets. The dots represent values for each respective variable (a–e) and black lines indicate long-term trends generated with locally weighted scatterplot smoothing (span 0.13)

cladoceran distribution across tree line gradients in Lapland and the Alps (Bigler, Heiri, Krskova, Lotter, & Sturm, 2006; Rautio & Korhola, 2002). The current results give further support on the role of terrestrial DOC, which is significant in aquatic UV attenuation, in shaping cladoceran community structure in high latitude lakes.

The observed SUVA–SEC relationships may contain a sign of direct UV impacts in shaping cladoceran communities of the subarctic tree line lakes through the vegetation induced DOC gradient (Figure 3a). Many of the current study lakes contained $\text{DOC} > 4 \mu\text{g L}^{-1}$, a threshold under which aquatic UV exposure increases (Laurion, Vincent, & Lean, 1997), and were deep enough to provide UV protection for Cladocera through depth refugia (Sommaruga, 2010). Accordingly, the observed SUVA (and DOC)–SEC relationship was likely not solely a result of direct UV impact but contained diverse

forcing mechanisms including, for example, DOC fuelling the microbial loop or inducing lower visibility for decreased the predation risk from fish (Berggren, Bergström, & Karlsson, 2015; Wissel, Boeing, & Ramcharan, 2003). Although the current results suggested a community level response to UV exposure, interspecies differences in UV protection (Hylander & Hansson, 2010) causing differences in UV susceptibility of species, have likely contributed in the observed patterns as some taxa are more tolerant to UV.

The SECs were mostly dominated by the euplanktonic taxa (filter-feeder) *B. longispina* and (predaceous) *P. pediculus* and by the benthic *A. elongata* and *A. nana*. The dominance of *B. longispina* in fossil assemblages in north-western Lapland is well documented, where it occurs widely in clear-water and cold deep lakes (Korhola, 1999). In the current SEC data set it seemed to be associated with nutrient-rich and dark waters, that is, high TP and SUVA (Figure 3a), which contradicts the previous knowledge on its preferences for clear-water sites. The current connection is likely related to wetland lakes being more nutrient-rich environments providing suitable food particles for consumption. *Bosmina* is able to utilize both phytoplankton and heterotrophic food particles and has a “dual mode” in food particle collection allowing it to utilize different sized particles for food (DeMott, 1982). Stable isotopic composition ($\delta^{13}\text{C}$) of *Bosmina* has indicated that it relies largely on phytoplankton as a food source in subarctic lakes (Rantala, Luoto, et al., 2016). *Polyphemus pediculus* had an association to lakes with high SUVA together with some other large-bodied (*Eurycercus* spp.) or highly visible (neustonic and melanistic *Scapholeberis*) cladocerans (Figure 3a). The high abundance of *Polyphemus*, and the other highly visible taxa in dark-water lakes may be caused by the fact that such lakes were often very shallow and likely not suitable for fish due to, for example, complete winter-time freezing to the bottom or low oxygen availability. However, lower visibility for fish predation may also have been causing the observed association of SUVA and the high visibility taxa (Wissel et al., 2003). The opposite distribution towards low-productive and transparent lakes was observed in common chydorids *A. elongata*, *Alonella excisa*, and *A. nana* (Figure 3a) due to their association in grazing on periphyton at the benthic substrata or aquatic vegetation (Fryer, 1968; Rantala, Luoto, et al., 2016).

The SECs were clearly different from the FICs (Figure 2), and diverse environmental factors were significant in explaining the distribution of the FICs in the RDA (Figure 3b), where T_{Jul} and TN were most powerful. This contradiction between the SEC and FIC forcing is logical, as the sampling strategies and sample types (sweep net vs. surface sediment) collect animals differently. Surface sediment samples collect animals from both littoral and pelagic habitats and during different seasons into a single integrative whole lake samples over longer time scales, that is, several years or even decades depending on sedimentation rates in individual lakes (Frey, 1988). On the other hand, sweep net samples are representative of more habitat specific and short term (seasonal) communities (Nevalainen, 2010). These two sampling procedures may per se lead to inherent differences in community composition and their environmental relationships. For example, SUVA had a significant relationship with the SECs but did

not contribute as a driver for the FICs (Figure 3) that likely caused by seasonal changes in SUVA, it being highest during the peak season of SEC sampling due to increased autochthonous production and allochthonous carbon inputs from the nonfrozen soils. Accordingly, examining environmental determinants behind short (SEC) versus long-term (FIC) community structures may allow a more comprehensive understanding on the mechanisms and response times of the communities to diverse environmental changes, for example, climate change.

Climate is known to impact cladoceran biogeography over wide spatial temperature gradients and over the course of Holocene interglacial (Bigler et al., 2006; Sweetman et al., 2010; Nevalainen, Luoto, Kultti, & Sarmaja-Korjonen, 2013). The current data covered a 1°C (T_{jul}) temperature gradient along the latitudinal and altitudinal transect (Figure 1; Rantala, Nevalainen, et al., 2016). Despite the relatively short climate transect, T_{jul} was shown to be the most significant factor in explaining cladoceran FIC distribution (Figure 3b). This indicates that temperature acts as an important biogeographical forcer in cladoceran communities across the northern tree line at a time scale beyond seasons as the surface sediment FICs are integrative communities from several years to even decades. The climate forcing on the distribution and structure of cladoceran communities originates from its indirect impacts on for example, habitat quality and length of the open-water season that favour or restrict species occurrences. However, temperature as a climate parameter also has a direct influence on cladoceran metabolism and reproduction (de Eyto & Irvine, 2001; Vandekerckhove et al., 2005). With respect to temperature, *B. longispina*, *Acroperus harpae* and *Eurycerus* spp. clearly had high-temperature preferences, whereas *A. nana*, *Paralona pigra*, *A. elongata*, *A. intermedia*, and *Alona werestschagini* were associated with cold tundra lakes (Figure 3b). According to Thienpont et al. (2015), climate warming may impact high latitude cladoceran communities by increasing specialized taxa (in feeding and habitats) such as filter-feeding *Bosmina* and macrophyte-associated *Acroperus* and *Eurycerus*, and reducing generalists. This suggestion is in agreement with the taxon–temperature relationships in the spatial FIC data (Figure 3b) basing on the assumption that taxa with high-temperature preferences will increase under climate warming and vice versa. As subarctic–arctic regions acts a “final refugium” for cold stenothermic species, for example, for the rare cold-adapted glacial relict *Alona werestschagini* (Sarmaja-Korjonen & Sinev, 2008), there may occur extinctions that reflect through the food web up to ecosystem functions.

In addition to temperature, TN had a secondary, yet a significant relationship with the FICs (Figure 3b). The important role of TN as an explanatory variable in the current analysis may be due to its close connection to allochthonous nutrient inputs and primary production (Rantala, Nevalainen, et al., 2016) that were highest in the wetland lakes which contained unique surface sediment cladoceran assemblages (Figure 3b). Lakes with high nutrient status were inhabited by specific communities of primary producers, for example, periphyton (Rantala, Luoto, Weckström, Rautio, & Nevalainen, 2017), and provide abundant food for grazing cladocerans shaping their communities through food web interactions. In addition, the ecologically

relevant connection of TN with cladocerans may be related to presence of microbial benthic mats (including N-fixing benthic cyanobacteria) that may provide unique habitats and food resources. A similar pattern on the impact of TN on aquatic invertebrate communities (Chironomidae) has been observed in the same lakes (Luoto, Rantala, Galkin, Rautio, & Nevalainen, 2016) suggesting that nitrogen is a significant driver of aquatic communities in the subarctic region.

4.2 | Community succession and UV response through time

Long-term climate changes of the Holocene are known to impact cladoceran biogeography through the influence of lake ontogenic processes (Nevalainen et al., 2013; Zawiska et al., 2015) on habitat quality and resources. Although the Námájávri cladoceran assemblage shifts were visually subtle (Figure 4), there occurred major community changes in the history of the lake according to the PCA axis 1 scores (Figure 5a, S3a). For example, the coldest period of the Little Ice Age (LIA, ~1700–1850 C.E.) was displayed by decreasing abundance of the planktonic grazer *B. longispina* and increases in *A. nana* and *Rhyncotalona falcata*, which were associated with cold lakes in the spatial data (Figure 3b). According to the VPA, the long-term changes were mainly explained by the variation in solar intensity and composite sediment biogeochemistry rather than climate (Figure 5). The VPA included two sediment-derived explanatory factors (composite biogeochemistry and fossil Chironomidae-inferred T_{jul}) that may have impacted the VPA results potentially causing closer correlation within the sediment-derived variables. Despite this, the VPA suggested that long-term community changes were mostly explained by solar intensity (Figure 5). Such a connection has been established to exist earlier in pristine high alpine lakes, mediated through limnology and light environment (Luoto & Nevalainen, 2016), possibly associated with the damaging impacts of UV in aquatic ecosystems (Bancroft, Baker, & Blaustein, 2007; Rautio & Korhola, 2002). High solar activity is expected to reduce biologically damaging UV at the Earth's surface by inducing thicker ozone layer (Rozema, van Geel, Björn, Lean, & Madronich, 2002) but it should also cause increased photochemical degradation of UV-absorbing DOC in aquatic systems thus increasing aquatic UV exposure (Cory et al., 2014).

Previous studies on Lake Námájávri suggested that climate exerted a control on limnological characters (primary production, pH) that were most pronounced during the 20th–21st centuries (Rantala, Luoto, et al., 2016, 2017) in conjunction with cladoceran community changes (Figure 5a, Appendix S3a). At that time benthic autotrophic production increased as a result of warming climate and reduced ice-cover period, which also likely contributed to higher degradation of terrestrial organic matter inducing more transparent water column. It is possible that the long-term development of Námájávri cladoceran assemblages was regulated by the superimposed influence of solar intensity directly (Figure 5) and temperature indirectly (reduced ice-cover period exposing water column to longer period of solar radiation). This would have caused more intense photochemical DOC degradation and UV exposure of the lake through more transparent



lake water. In agreement, the RDA results on the spatial short-term communities showed that SUVA had a strong relationship with SECs (Figure 3a) and T_{jul} with surface sediment FICs (Figure 3b) suggesting that both UV and climate impacts cladoceran distribution. Taxon specific responses to UV that were evident in the spatial SEC data occurred also in the Námajávri record possibly as a result of increased UV exposure, as, for example, *B. longispina*, associated with high SUVA (i.e., low UV exposure, Figure 3a), decreased markedly since the early 20th century, whereas *Alonella excisa*, related to low SUVA (high UV), increased. UV sensitivity of *Bosmina* may be due to the lack of melanin and other photoprotective pigments, for example, mycosporine-like amino acids (Tartarotti, Laurion, & Sommaruga, 2001) although it is suggested that it may utilize melanization under high UV exposure (Hansson & Hylander, 2009). Despite, *Bosmina* seems to be vulnerable to high underwater UV doses (Williamson et al., 2001).

Aquatic UV exposure is dependent on the geographical location defining the angle and seasonality of solar radiation and intrinsic limnological properties, such as amount and quality of UV-attenuating compounds (Rautio & Tartarotti, 2010). In addition, lake depth is relevant for underwater UV exposure of mobile organisms, which can mitigate UV through horizontal or vertical migration to search for deep-water UV refugia (Sommaruga, 2010). In previous high arctic Holocene and late Holocene records, solar activity has been shown to be positively related to lakes' UV exposure (Nevalainen, Rantala, et al., 2015; Nevalainen et al., 2016) suggesting that solar forcing has an important role in aquatic UV exposure of such regions. Although the long-term trends of Námajávri's ABS_{UV} and solar intensity were synchronous, exhibiting gradual increases from 1700 C.E. towards the 20th century, the VPA results displayed a clearly stronger control of composite sediment biogeochemistry over solar intensity on the current ABS_{UV} record (Figure 5). In fact, the contribution of solar intensity in explaining variation in ABS_{UV} was low implying that intrinsic lake-water properties are more important in controlling underwater UV in subarctic lakes, even in those with low DOC such as Námajávri (Table 1). This observed contradiction in UV forcing between subarctic and high arctic lakes is most likely related to catchment characteristics, as subarctic lakes are mostly impacted by vegetation cover and wetlands as a source of coloured carbon compounds, whereas the high arctic landscape is barren (Rantala, Nevalainen, et al., 2016; Rose, Williamson, Saros, Sommaruga, & Fischer, 2009).

SUVA of lake waters, indicating underwater UV exposure and terrestrially-derived UV-attenuating DOC, is the main determinant for photoprotection of benthic cladocerans in subarctic tree line lakes (Nevalainen, Luoto, Rantala, Galkin, & Rautio, 2015). Therefore, it was reasonable to assume that long-term changes in catchment originated DOC concentrations have contributed in ABS_{UV} variability in the Námajávri core. The ABS_{UV} record suggests that the lake-water was higher in UV-attenuating compounds (i.e., darker) in the early record until 1400 CE and exhibited periods of higher UV transparency around 1500 and 1600 CE. The most distinctive feature in the record is the increase in ABS_{UV} since 1700 CE onward indicating higher UV transparency. In agreement, previous palaeolimnological studies from the lake suggest that benthic autotrophic production,

rather than allochthonous carbon inputs, increased due to increasing temperatures and longer open-water season (Rantala, Luoto, et al., 2016, 2017). This is in accordance with the increase of littoral-benthic taxa in the topmost sequence, likely associated with diversifying benthic resources through benthic primary production and negative UV impacts on the dominant planktonic species *B. longispina* (Figure 4). Alternatively, decreasing lake depth could have caused higher UV absorbance values by subjecting cladocerans to more intensive UV in a shallow water column and the increased proportion of littoral taxa (and reductions in *Bosmina*) in the record, although the previous studies (Rantala, Luoto, et al., 2016, 2017) do not give any indications on such changes.

In conclusion, the modern distribution of cladocerans along the subarctic tree line ecotone is sensitive to temperature, nutrient status, and UV transparency with associated allochthonous carbon inputs. Temporal patterns in cladoceran community succession through the past millennium were principally driven by solar intensity impacting lake water optical properties and primary production, yet the drastic 20th century community shift was concurrent and superimposed on progressively increasing temperatures suggesting codirectional climate forcing on the long-term distribution patterns. The comparison of community–environment relationships among the three data sets (i.e., SECs, surface sediment FICs, and down-core FICs) summarizes the partly local limnological (lake water optics, primary production) and partly external (UV, climate) drivers to regulate cladoceran spatio-temporal distribution. It further suggests that the main environmental drivers behind the observed distribution patterns have prevailed somewhat similar during the past millennium. Even though biogeographical patterns are temporally dynamic and dependent on the time-scale (Fisher, Frank, & Leggett, 2010), space-for-time substitution in evaluating major environmental constraints in cladoceran distribution at the current geographical range and time-scale seems to remain valid. Climate change with increasing temperatures and terrestrial organic matter inputs will likely alter cladoceran community structures with increases in planktonic filter-feeding *Bosmina* and benthic specialized taxa (cf. Thienpont et al., 2015) causing large functional changes in the lakes. The long-term record on cladoceran photoprotection indicated clearly increased UV exposure during the LIA and the 20th century due to higher lake water transparency through increased photodegradation of UV-attenuating compounds. If future aquatic UV exposure still increases, impacted indirectly by longer open-water seasons and associated increases in DOC photodegradation, UV-sensitive cladocerans (e.g., key species *Bosmina*) may be threatened in shallow subarctic lakes without UV refugia causing cascading effects on the food web. Accordingly, estimations on the dual effects and mechanisms of increasing temperatures and UV on subarctic lakes and their biota should gain further attention, as their individual impacts on, for example, planktonic taxa may be diverse.

ACKNOWLEDGEMENTS

This study was funded by the Academy of Finland (#287547, 308954), Doctoral Program in Geosciences of University of Helsinki,

Natural Sciences and Engineering Research Council of Canada, the Canada Foundation for Innovation, and Emil Aaltonen Foundation (#160156). Metsähallitus provided permits (#MH1127/2014) for sampling in the Kaldoaivi Wilderness Area. We thank Annukka Galkin and personnel of the Kevo Subarctic Research Station for their assistance during the fieldwork and John Smol for constructive comments on a previous version of the manuscript. Comments of three anonymous reviewers are acknowledged.

DATA ACCESSIBILITY

Data (Cladocera assemblages) are deposited in the PANGAEA data publisher of Earth and Environmental Sciences (<https://doi.org/10.1594/PANGAEA.890563>).

ORCID

Liisa Nevalainen  <http://orcid.org/0000-0001-6837-8753>

REFERENCES

- ACIA Arctic Climate Impact Assessment (2005). Cambridge, UK: Cambridge University Press.
- Bancroft, B. A., Baker, N. J., & Blaustein, A. R. (2007). Effects of UVB radiation on marine and freshwater organisms: A synthesis through meta-analysis. *Ecology Letters*, 10, 332–345. <https://doi.org/10.1111/j.1461-0248.2007.01022.x>
- Berggren, M., Bergström, A. K., & Karlsson, J. (2015). Intraspecific autochthonous and allochthonous resource use by zooplankton in a humic lake during the transitions between winter, summer and fall. *PLoS ONE*, 10(3), e0120575. <https://doi.org/10.1371/journal.pone.0120575>
- 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. <https://doi.org/10.1007/s00027-006-0813-x>
- Chen, G., Dalton, C., & Taylor, D. (2010). Cladocera as indicators of trophic state in Irish lakes. *Journal of Paleolimnology*, 44, 465–481. <https://doi.org/10.1007/s10933-010-9428-2>
- Cory, R. M., Ward, C. P., Crump, B. C., & Kling, G. W. (2014). Sunlight controls water column processing of carbon in arctic fresh waters. *Science*, 345, 925–928. <https://doi.org/10.1126/science.1253119>
- de Eyto, E., & Irvine, K. (2001). The response of three chydorid species to temperature, pH and food. *Hydrobiologia*, 459, 165–172. <https://doi.org/10.1023/A:1012585217667>
- DeMott, W. R. (1982). Feeding selectivities and relative ingestion rates of *Daphnia* and *Bosmina*. *Limnology and Oceanography*, 27, 518–527. <https://doi.org/10.4319/lo.1982.27.3.0518>
- Downing, J. A., Prairie, Y. T., Cole, J. J., Duarte, C. M., Trankvik, L. J., Strigl, R. G., ... Middelburg, J. J. (2006). The global abundance and size distribution of lakes, ponds, and impoundments. *Limnology and Oceanography*, 51, 2388–2397. <https://doi.org/10.4319/lo.2006.51.5.2388>
- Fisher, J. A., Frank, K. T., & Leggett, W. C. (2010). Dynamic macroecology on ecological time-scales. *Global Ecology and Biogeography*, 19, 1–5. <https://doi.org/10.1111/j.1466-8238.2009.00482.x>
- Frey, D. G. (1988). Littoral and offshore communities of diatoms, cladocerans and dipterous larvae, and their interpretation in paleolimnology. *Journal of Paleolimnology*, 1, 179–191.
- 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. <https://doi.org/10.1098/rstb.1968.0017>
- Häder, D. P., Williamson, C. E., Wängberg, S. Å., Rautio, M., Rose, K. C., Gao, K., ... Worrest, R. (2015). Effects of UV radiation on aquatic ecosystems and interactions with other environmental factors. *Photochemical & Photobiological Sciences*, 14, 108–126. <https://doi.org/10.1039/C4PP90035A>
- Hansson, L. A., & Hylander, S. (2009). Effects of ultraviolet radiation on pigmentation, photoenzymatic repair, behavior, and community ecology of zooplankton. *Photochemical & Photobiological Sciences*, 8, 1266–1275. <https://doi.org/10.1039/b908825c>
- Havel, J. E., & Medley, K. A. (2006). Biological invasions across spatial scales: Intercontinental, regional, and local dispersal of cladoceran zooplankton. *Biological Invasions*, 8, 459–473. <https://doi.org/10.1007/s10530-005-6410-4>
- Heathcote, A. J., Anderson, N. J., Prairie, Y. T., Engstrom, D. R., & del Giorgio, P. A. (2015). Large increases in carbon burial in northern lakes during the Anthropocene. *Nature Communications*, 6, 10016. <https://doi.org/10.1038/ncomms10016>
- Hylander, S., & Hansson, L. A. (2010). Vertical migration mitigates UV effects on zooplankton community composition. *Journal of Plankton Research*, 32, 971–980. <https://doi.org/10.1093/plankt/fbq037>
- Jeppesen, E., Madsen, E. A., Jensen, J. P., & Anderson, N. (1996). Reconstructing the past density of planktivorous fish and trophic structure from sedimentary zooplankton fossils: A surface sediment calibration data set from shallow lakes. *Freshwater Biology*, 36, 115–127. <https://doi.org/10.1046/j.1365-2427.1996.00085.x>
- Juggins, S. (2007). *C2 Version 1.5 User guide. Software for ecological and palaeoecological data analysis and visualisation*. Newcastle upon Tyne, UK: Newcastle University.
- Korhola, A. (1999). Distribution patterns of Cladocera in subarctic Fennoscandian lakes and their potential in environmental reconstruction. *Ecography*, 22, 357–373. <https://doi.org/10.1111/j.1600-0587.1999.tb00573.x>
- Laurion, I., Vincent, W. F., & Lean, D. R. (1997). Underwater ultraviolet radiation: Development of spectral models for northern high latitude lakes. *Photochemistry and Photobiology*, 65, 107–114.
- Leavitt, P. R., Cumming, B. F., Smol, J. P., Reasoner, M., Pienitz, R., & Hodgson, D. A. (2003). Climatic control of ultraviolet radiation effects on lakes. *Limnology and Oceanography*, 48, 2062–2069. <https://doi.org/10.4319/lo.2003.48.5.2062>
- Luoto, T. P., & Nevalainen, L. (2016). Solar and atmospheric forcing on mountain lakes. *Science of the Total Environment*, 566–567, 168–174. <https://doi.org/10.1016/j.scitotenv.2016.05.079>
- Luoto, T. P., Oksman, M., & Ojala, A. E. K. (2015). Climate change and bird impact as drivers of High Arctic pond deterioration. *Polar Biology*, 38, 357–368. <https://doi.org/10.1007/s00300-014-1592-9>
- Luoto, T. P., Rantala, M. V., Galkin, A., Rautio, M., & Nevalainen, L. (2016). Environmental determinants of chironomid communities in remote northern lakes across the treeline—Implications for climate change assessments. *Ecological Indicators*, 61, 991–999. <https://doi.org/10.1016/j.ecolind.2015.10.057>
- Nevalainen, L. (2010). Evaluation of microcrustacean (Cladocera, Chydoridae) biodiversity based on sweep net and surface sediment samples. *Écoscience*, 17, 356–364. <https://doi.org/10.2980/17-4-3364>
- 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. <https://doi.org/10.1111/jbi.12101>
- Nevalainen, L., Luoto, T. P., Rantala, M. V., Galkin, A., & Rautio, M. (2015). Role of terrestrial carbon in aquatic UV exposure and photo-protective pigmentation of meiofauna in subarctic lakes. *Freshwater Biology*, 60, 2435–2444. <https://doi.org/10.1111/fwb.12670>
- Nevalainen, L., Rantala, M. V., Luoto, T. P., Ojala, A. E. K., & Rautio, M. (2016). Long-term changes in pigmentation of arctic *Daphnia* provide



- potential for reconstructing aquatic UV exposure. *Quaternary Science Reviews*, 144, 44–50. <https://doi.org/10.1016/j.quascirev.2016.05.022>
- Nevalainen, L., Rantala, M. V., Luoto, T. P., Rautio, M., & Ojala, A. E. K. (2015). Ultraviolet radiation exposure of a high arctic lake in Svalbard during the Holocene. *Boreas*, 44, 401–412. <https://doi.org/10.1111/bor.12108>
- Nevalainen, L., & Rautio, M. (2014). Spectral absorbance of benthic cladoceran carapaces as a new method for inferring past UV exposure of aquatic biota. *Quaternary Science Reviews*, 84, 109–115. <https://doi.org/10.1016/j.quascirev.2013.11.020>
- Rantala, M. V., Luoto, T. P., & Nevalainen, L. (2016). Temperature controls on organic carbon sequestration in a subarctic lake. *Scientific Reports*, 6, 34780. <https://doi.org/10.1038/srep34780>
- Rantala, M. V., Luoto, T. P., Weckström, J., Rautio, M., & Nevalainen, L. (2017). Climate drivers of diatom distribution in shallow subarctic lakes. *Freshwater Biology*, 62, 1971–1985. <https://doi.org/10.1111/fwb.13042>
- Rantala, M. V., Nevalainen, L., Rautio, M., Galkin, A., & Luoto, T. P. (2016). Sources and controls of organic carbon in lakes across the subarctic treeline. *Biogeochemistry*, 129, 235–253. <https://doi.org/10.1007/s10533-016-0229-1>
- Rautio, M. (1998). Community structure of crustacean zooplankton in subarctic ponds—Effects of altitude and physical heterogeneity. *Ecography*, 21, 327–335. <https://doi.org/10.1111/j.1600-0587.1998.tb00570.x>
- Rautio, M., Bonilla, S., & Vincent, W. F. (2009). UV photoprotectants in arctic zooplankton. *Aquatic Biology*, 7, 93–105. <https://doi.org/10.3354/ab00184>
- Rautio, M., Dufresne, F., Laurion, I., Bonilla, S., Vincent, W. F., & Christoffersen, K. S. (2011). Shallow freshwater ecosystems of the circumpolar Arctic. *Écoscience*, 18, 204–222. <https://doi.org/10.2980/18-3-3463>
- Rautio, M., & Korhola, A. (2002). UV-induced pigmentation in subarctic *Daphnia*. *Limnology and Oceanography*, 47, 295–299. <https://doi.org/10.4319/lo.2002.47.1.0295>
- Rautio, M., & Tartarotti, B. (2010). UV radiation and freshwater zooplankton: Damage, protection and recovery. *Freshwater Reviews*, 3, 105–131.
- Rose, K. C., Williamson, C. E., Saros, J. E., Sommaruga, R., & Fischer, J. M. (2009). Differences in UV transparency and thermal structure between alpine and subalpine lakes: Implications for organisms. *Photochemical & Photobiological Sciences*, 8, 1244–1256. <https://doi.org/10.1039/b905616e>
- Rozema, J., van Geel, B., Björn, L. A., Lean, J., & Madronich, S. (2002). Toward solving the UV puzzle. *Science*, 296, 1621–1622. <https://doi.org/10.1126/science.1070024>
- Rühland, K., Paterson, A. M., Keller, W., Michelutti, N., & Smol, J. P. (2013). Global warming triggers the loss of a key Arctic refugium. *Proceedings of the Royal Society B*, 280, 20131887. <https://doi.org/10.1098/rspb.2013.1887>
- Sarmaja-Korjonen, K., & Sinev, A. Y. (2008). First records of *Alona werestschagini* Sinev in Finland-subfossil remains from subarctic lakes. *Studia Quaternaria*, 25, 43–46.
- Šmilauer, P., & Lepš, J. (2014). *Multivariate analysis of ecological data using Canoco 5*. Cambridge, UK: Cambridge University Press. <https://doi.org/10.1017/CBO9781139627061>
- Smol, J. P. (2016). Arctic and Sub-Arctic shallow lakes in a multiple-stressor world: A paleoecological perspective. *Hydrobiologia*, 778, 1–20.
- Smol, J. P., Wolfe, A. P., Birks, H. J. B., Douglas, M. S. V., Jones, V. J., Korhola, A., ... Weckstrom, J. (2005). Climate-driven regime shifts in the biological communities of arctic lakes. *Proceedings of the National Academy of Sciences USA*, 102, 4397–4402. <https://doi.org/10.1073/pnas.0500245102>
- Solanki, S. K., Usoskin, I. G., Kromer, B., Schüssler, M., & Beer, J. (2004). An unusually active Sun during recent decades compared to the previous 11,000 years. *Nature*, 431, 1084–1087. <https://doi.org/10.1038/nature02995>
- Sommaruga, R. (2010). Preferential accumulation of carotenoids rather than of mycosporine-like amino acids in copepods from high altitude Himalayan lakes. *Hydrobiologia*, 648, 143–156. <https://doi.org/10.1007/s10750-010-0141-y>
- Sweetman, J. N., Rühland, K. M., & Smol, J. P. (2010). Environmental and spatial factors influencing the distribution of cladocerans in lakes across the central Canadian Arctic treeline region. *Journal of Limnology*, 69, 76–87.
- Szeroczyńska, K., & Sarmaja-Korjonen, K. (2007). *Atlas of subfossil Cladocera from Central and Northern Europe*. Świecie, Poland: Friends of the Lower Vistula Society.
- Tartarotti, B., Laurion, I., & Sommaruga, R. (2001). Large variability in the concentration of mycosporine-like amino acids among zooplankton from lakes located across an altitude gradient. *Limnology and Oceanography*, 46, 1546–1552. <https://doi.org/10.4319/lo.2001.46.6.1546>
- Thienpont, J. R., Korosi, J. B., Cheng, E. S., Deasley, K., Pisaric, M. F., & Smol, J. P. (2015). Recent climate warming favours more specialized cladoceran taxa in western Canadian Arctic lakes. *Journal of Biogeography*, 42, 1553–1565. <https://doi.org/10.1111/jbi.12519>
- Tranvik, L. J., Downing, J. A., Cotner, J. B., Loiselle, S. A., Strigl, R. G., Ballatore, T. J., ... Weyhenmeyer, G. A. (2009). Lakes and reservoirs as regulators of carbon cycling and climate. *Limnology and Oceanography*, 54, 2298–2314. https://doi.org/10.4319/lo.2009.54.6_part_2.2298
- Vandekerckhove, J., Declerck, S., Brendonck, L., Conde-Percuna, J. M., Jeppesen, E., & De Meester, L. (2005). Hatching of cladoceran resting eggs: Temperature and photoperiod. *Freshwater Biology*, 50, 96–104. <https://doi.org/10.1111/j.1365-2427.2004.01312.x>
- Williamson, C. E., Olson, O. G., Lott, S. E., Walker, N. D., Engstrom, D. R., & Hargreaves, B. R. (2001). Ultraviolet radiation and zooplankton community structure following deglaciation in Glacier Bay, Alaska. *Ecology*, 82, 1748–1760. [https://doi.org/10.1890/0012-9658\(2001\)082\[1748:URAZCS\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[1748:URAZCS]2.0.CO;2)
- Williamson, C. E., Zepp, R. G., Lucas, R. M., Madronich, S., Austin, A. T., Ballaré, C. L., ... Bornman, J. F. (2014). Solar ultraviolet radiation in a changing climate. *Nature Climate Change*, 4, 434–441. <https://doi.org/10.1038/nclimate2225>
- Wissel, B., Boeing, W. J., & Ramcharan, C. W. (2003). Effects of water color on predation regimes and zooplankton assemblages in freshwater lakes. *Limnology and Oceanography*, 48, 1965–1976. <https://doi.org/10.4319/lo.2003.48.5.1965>
- Zawiska, I., Stowiński, M., Correa-Metrio, A., Obremaska, M., Luoto, T., Nevalainen, L., ... Milecka, K. (2015). The response of a shallow lake and its catchment to Late Glacial climate changes—A case study from eastern Poland. *Catena*, 126, 1–10. <https://doi.org/10.1016/j.catena.2014.10.007>

BIOSKETCH

Liisa Nevalainen is a palaeolimnologist and her research focuses on long-term lake ecosystem dynamics and aquatic biodiversity patterns with an emphasis on the impacts and interconnections of UV radiation and auto-allochthonous production.

Author contributions: L.N. conceived the ideas; L.N., M.V.R., and T.P.L. conducted the field work and collected the materials; L.N. analysed the data (Cladocera) and M.V.R., M.R., and T.P.L. provided the supporting data (previously published sediment biogeochemistry and palaeotemperature); L.N. led the writing with assistance from M.V.R., M.R., and T.P.L.



SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Nevalainen L, Rantala MV, Rautio M, Luoto TP. Spatio-temporal cladoceran (Branchiopoda) responses to climate change and UV radiation in subarctic ecotonal lakes. *J Biogeogr.* 2018;00:1–12. <https://doi.org/10.1111/jbi.13371>