



# Diatom metacommunity structuring in a large lake: geomorphic, water chemistry and dispersal effects on diatom guilds in Lake Ladoga (north-western Russia)

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## Abstract

The relative importance of environmental filtering and dispersal in structuring metacommunities of littoral periphytic diatoms was assessed within a large lake (Lake Ladoga, north-western Russia). We hypothesized that different diatom functional guilds (high-profile, low-profile, motile and planktic) would respond differently to environmental and spatial variables, depending on their mode of attachment and dispersal ability. Guilds showed distinct distributional patterns along a gradient of wave-induced disturbance: low-profile diatoms dominated in exposed shorelines (high disturbance), whereas high-profile and motile diatoms were more abundant in coastal wetlands (low disturbance). Redundancy analysis with variation partitioning of the entire diatom community revealed that environmental variables (littoral geomorphology and water chemistry) outperformed spatial variables, indicating a predominant role of species sorting. When the diatom community was deconstructed into functional groups, benthic guilds (i.e., low-profile, high-profile and motile) showed higher dependence on environmental factors, whereas the planktic guild was primarily predicted by spatial factors. Thus, benthic taxa with lower dispersal abilities were less impacted by mass effects than planktic taxa. Among benthic guilds, motile diatoms were less sensitive to water chemistry compared to low-profile and high-profile diatoms, suggesting that a group-specific habitat preference may interfere with diatom responses to water quality changes. Hence, the response of diatom guilds to water quality parameters was related to their resistance to wave action. Overall, we concluded that the higher importance of environmental filtering than dispersal-related processes in shaping the diatom metacommunity resulted from a combination of a strong environmental gradient in geomorphology/water chemistry and the intermediate spatial scale of our study.

**Keywords** Diatom guilds · Littoral geomorphology · Eutrophication · Dispersal · Mass effects · Lake Ladoga

## Introduction

Mechanisms underlying community structure is one of the main interests in the field of community ecology. Traditionally, a greater emphasis has been placed on environmental

factors that influence community composition through niche differentiation mechanisms (Chase and Leibold 2003). Metacommunity theory, which has emerged in recent decades, considers the composition of local communities to be a result of interplay between environmental filtering and

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dispersal-related processes (Leibold et al. 2004; Cottenie 2005). Therefore, assessing the relative importance of local environmental factors and proxies for dispersal in shaping metacommunity structure has become a central objective of ecological studies (Logue et al. 2011; Heino et al. 2017).

Dispersal limitation and mass effects are basic dispersal processes that influence metacommunity structure by preventing perfect species sorting by environmental factors (Leibold and Chase 2018). Limited dispersal precludes species from reaching sites with optimal environmental conditions (Heino et al. 2015). In contrast, mass effects allow species to persist in suboptimal conditions due to high rates of species supply from source to neighbouring sites (Leibold et al. 2004). Metacommunity theory predicts that the relative role of species sorting and dispersal processes vary depending on spatial scale and connectivity of the environment (Heino et al. 2015). Hence, metacommunities form a continuum where the prevalence of different assembly mechanisms ranges from mass effects (small spatial scales and/or highly connected habitats) to species sorting (intermediate spatial scale) to dispersal limitation (large spatial scales and/or disconnected habitats) (Heino 2011; Heino et al. 2015). In recent years, many studies addressing the issue of the scale dependence of dispersal-driven assembly mechanisms in various aquatic ecosystems have demonstrated an increase in the importance of dispersal limitation with increasing spatial extent of the study (e.g., Soinen et al. 2011; Lebourcier et al. 2019; Rusanov et al. 2022). Regarding habitat connectivity, recent large-scale and middle-scale studies showed that dispersal limitation is an important process shaping metacommunity structure of benthic diatoms of spatially isolated streams (Heino et al. 2010) and lakes (Benito et al. 2018). At the other end of the spectrum, there are highly connected aquatic systems such as large lakes, in which species dispersal rates are high due to lack of obvious dispersal barriers, and therefore metacommunities are thought to be influenced by mass effects (Leibold and Norberg 2004). Indeed, few within-lake studies, conducted at small spatial extents using the metacommunity concept, showed that communities of benthic diatoms and macroinvertebrates were mainly influenced by high dispersal (Vilmi et al. 2016; Cai et al. 2017; Tolonen et al. 2017). However, in the spatially isolated systems, the relative importance of different assembly mechanisms depends on the spatial extent surveyed, with a higher importance of environmental factors versus spatial processes as scale increases from small to intermediate (Heino et al. 2015). Thus, the highly connected systems should also be studied at multiple spatial extents and, especially, at intermediate and large scales, to understand the true importance of environmental filtering and dispersal in structuring metacommunities.

Functional traits are properties of organisms that are related to their environmental response, dispersal and

competitive ability (McGill et al. 2006). Therefore, a deconstructive approach that divides a metacommunity dataset into subsets based on functional traits can help to more clearly understand metacommunity dynamics in response to environmental and spatial factors (Heino et al. 2015). Diatoms are a suitable group of organisms for testing different metacommunity paradigms using this trait-based deconstructive approach because they are represented by a wide range of growth forms linked to resource acquisition, resistance to disturbance and dispersal ability (Soinen and Teittinen 2019). Passy (2007) and Rimet and Bouchez (2012) classified diatom species into four functional guilds (low-profile, high-profile, motile and planktic) that differ in their growth forms and attachment modes to the substrate. According to the classification proposed by Passy (2007) for riverine benthic diatoms, low-profile diatoms are adapted to flow disturbance and can survive under conditions of resource limitation due to their short stature and tight attachment to the substrate. Owing to vertical orientation of attached cells or colonies, high-profile diatoms are more susceptible to disturbance, but are not resource-limited. Motile diatoms can avoid unsuitable microhabitats and are comparatively not disturbance-stressed and resource-limited. A fourth guild proposed by Rimet and Bouchez (2012) is composed of planktic taxa that are adapted to a suspended mode of life and resistance to sedimentation. A recent study showed strong response patterns of diatom guilds along a disturbance gradient: adnate pioneer species (low-profile guild) increased in abundance in highly turbulent lakes with short water renewal time, while high-profile and motile guilds dominated at weak turbulence in lakes with longer renewal time (Rimet et al. 2019). With regard to dispersal abilities, it has been hypothesized that diatom guilds tightly attached to the substratum (low-profile and high-profile) are likely not dispersed as easily as guilds loosely attached to the substratum (motile and planktic) (Wetzel et al. 2012; Vilmi et al. 2017; Benito et al. 2018). These differences in dispersal abilities among diatom guilds likely translate into differences in the spatial and environmental control on these guilds. Recent studies using a trait-based deconstructive approach applied to diatom communities have indeed shown that the relative importance of community assembly mechanisms differs among diatom guilds both in lotic (Göthe et al. 2013; Liu et al. 2013; Jamoneau et al. 2018; Lindholm et al. 2018) and lentic (Vilmi et al. 2017; Benito et al. 2018) environments. For example, some studies focused on diatom distributions along stream watercourses have revealed that the motile guild showed a higher degree of spatial control than the low-profile guild due to their higher dispersal capacity (Liu et al. 2013; Jamoneau et al. 2018). Similar, in a highly connected lake system planktic diatoms exhibited greater spatial control that was attributable to the effect of high dispersal rates (Vilmi et al. 2017). However, it is worth noting

that this study was conducted in a near-pristine lake with an unnoticeable nutrient gradient that could lead to low importance of species sorting processes in structuring the diatom community (Vilmi et al. 2016). Therefore, more research is required in large lakes to find out whether high dispersal rates (i.e., mass effects) would mask the effect of environmental filtering in the case of a strong natural environmental gradient and anthropogenic impacts.

Lake Ladoga, located in north-western Russia (Fig. 1), is the largest lake in Europe and is the 13th largest freshwater lake in the world by surface area. Since the Lake Ladoga catchment extends through north-western Russia and eastern Finland (Fig. S1), the lake serves as a natural accumulation pool for nutrients and different kinds of pollutants (Drabkova et al. 1996). During the late 1960s–the early 1990s, the lake ecosystem changed from an originally oligotrophic to mesotrophic state due to enhanced economic activity in the catchment area (Davydova et al. 1999). In spite of nutrient load reductions in the late 1990s and 2000s, the lake still remains in a mesotrophic state (Letanskaya and Protopopova 2012; Ludikova 2021). Although the pelagic zone of Lake Ladoga is generally mesotrophic, the coastal zone is characterized by high level of spatial heterogeneity in trophic status. The northern part of the coast is mostly oligotrophic, the western part is mesotrophic, and the southern part varies from mesotrophy to eutrophy (Kurashov et al. 2018). Volkhov Bay on the southern coast is the most eutrophic and polluted embayment of Lake Ladoga due to the high influx of nutrients from the Volkhov and Syas rivers, carrying municipal, industrial and agricultural waste (Ignatieva, Susareva 2011). Here, aluminium and chemical production occurs in Volkhov in addition to pulp mills in Syasstroj. High ecological risk areas are also located on the northern coast at Pitkyaranta (an active pulp and paper mill) and Shchuchiy bay (sediments contaminated by pulp mill waste in the past) near Priozersk (Kurashov et al. 2018).

Nowadays, the state of the Lake Ladoga ecosystem is largely determined by a complex interaction of natural and anthropogenic processes occurring both within the lake and in its catchment area. Hydrodynamic processes, associated with shore geomorphology, and nutrients exported from watersheds are the main factors influencing composition and productivity of its littoral communities (Raspopov et al. 1996). Taking into account strong gradients in littoral geomorphology and eutrophication level, Lake Ladoga is a very appropriate large and highly connected aquatic system to test whether metacommunity theory can explain spatial patterns in taxonomic and functional composition of the periphytic diatom community. Here, we assessed the relative role of environmental and spatial variables in structuring the metacommunity of periphytic diatoms in the littoral zone of Lake Ladoga. We hypothesized that different diatom guilds (high-profile, low-profile, motile and planktic) would respond

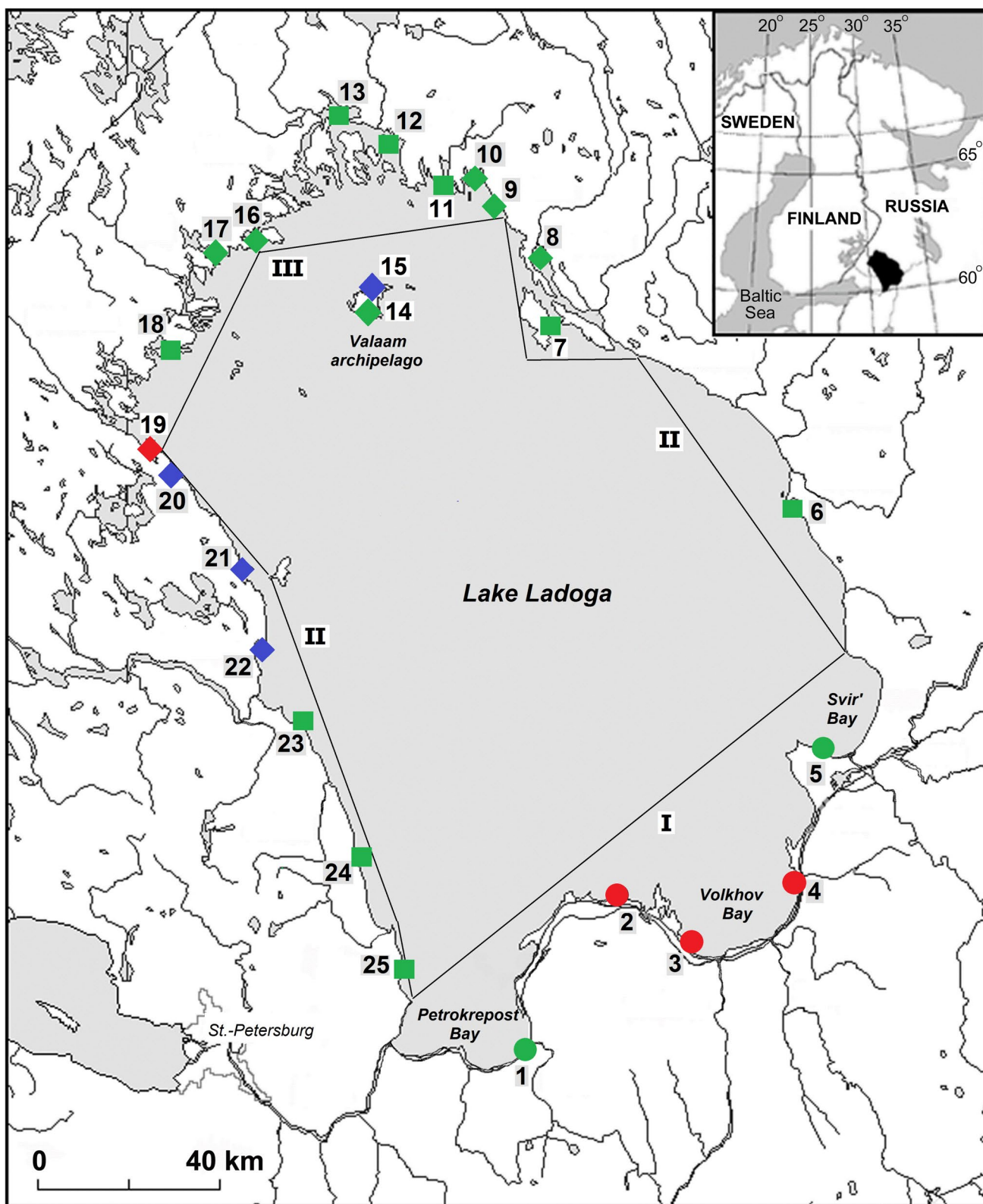
differently to environmental and spatial variables as a surrogate of disturbance sensitivity and dispersal ability due to their different attachment modes. Specifically, we predicted that (H1) diatom taxonomic and functional composition would be significantly influenced by littoral geomorphology due to differences in wave impact regime (Kireta et al. 2007; Rimet et al. 2015; Vilmi et al. 2017). (H2) Due to the intermediate spatial extent of our study and strong environmental gradients of wave-induced disturbance and water chemistry in Lake Ladoga, the diatom metacommunity would show a higher importance of environmental versus spatial control, because species dispersal rates are adequate for efficient species sorting at intermediate spatial scales (Heino et al. 2015). (H3) As dispersal abilities influence metacommunity structuring (De Bie et al. 2012; Heino et al. 2015), diatom guilds loosely attached to the substratum (motile and planktic, which possess higher dispersal abilities) would be more dependent on spatial variables (i.e., mass effects), whereas guilds firmly attached to the substratum (low-profile and high-profile, which possess poorer dispersal abilities) would be more strongly affected by environmental variables (i.e., water chemistry, geomorphology).

## Materials and methods

### Study area

The study area, Lake Ladoga (59°54' to 61°47' N and 29°47' to 32°58' E), is located in north-western Russia. Lake Ladoga is 219 km long and 125 km wide. It has a maximum depth of 230 m and an average depth of 48 m. The lake has a surface area of 17,765 km<sup>2</sup> and a volume of 847.8 km<sup>3</sup>. The mean water retention time is 11 years (Naumenko et al. 1996). Lake Ladoga is a dimictic mesotrophic lake. The Lake Ladoga catchment, with an area of approximately 284,000 km<sup>2</sup>, extends across north-western Russia and eastern Finland, including the large lakes Onega, Ilmen and Saimaa (Fig. S1). The rivers Svir, Volkhov and Vuoksa flowing from these lakes are the main tributaries of Lake Ladoga, which account for 86% of the water inflow into the lake.

Lake Ladoga is situated on the boundary of two geological structures: the crystalline Baltic Shield on the north and the Russian Plain on the south (Subetto et al. 1998). The southern border of the crystalline shield runs approximately along a line running from Vyborg and Priozersk on the west to the mouth of Svir River on the east. Differences in the geological structure of the watershed are reflected in the structure of shores and depression of the lake. According to physical and geomorphic features, the littoral zone of Lake Ladoga can be divided into three main regions (Fig. 1): the southern shallow region (I), the region of open and relatively



**Fig. 1** Schematic map of Lake Ladoga and location of littoral sampling sites. Geomorphological regions: I – southern shallow region, II – region of open shores, and III – northern skerry region. Littoral types: circles – coastal wetlands, rhombs – embayments, and squares

– exposed shorelines. Water quality classes (the IPS values): red – moderate (12–15), blue – good (15–17), and green – high (> 17) quality (Color figure online)



steep shores along the western and eastern coasts (II), and the northern skerry region (III) (Raspopov et al. 1996). Geomorphic characteristics of regions I and II reflect lithological and geomorphological structure of the Russian Plain comprising terrigenous and carbonaceous sedimentary rocks (sandstone, limestone and dolomite). The southern region (I) consists of gently sloping shores composed mainly of sand, gravel and boulders. Owing to moderate wave activity in this region, there exist suitable conditions for the development of aquatic vegetation. The largest beds of reeds (*Phragmites australis* (Cav.) Trin. ex Steud.), with a width of 100 m or more, are located on the southern coast in Petrokrepost and Volkhov bays. The region of open shores (II) is strongly affected by hydrodynamic factors. On the western coast, stone and boulder shores alternate with small sandy beaches and deposited silt. The eastern coast consists of long sandy beaches, with boulder and stone belts fringing the shoreline. The northern skerry region (III) is situated on the crystalline bedrock of the Baltic Shield. The shoreline here is incised with fjord-like bays and defended by numerous rocky islands (skerries). The northern region is characterized by a very narrow littoral zone with steep slopes.

Periphytic diatom and water quality samples were collected from all three geomorphological regions of Lake Ladoga. Sampling stations were classified by littoral geomorphic type according to classification of Kireta et al. (2007): exposed shoreline (ES), embayment (EB) and coastal wetland (CW). ES and EB sites were found in II and III geomorphological regions of Lake Ladoga, whereas CW sites occurred only in I region (Fig. 1).

### Sampling and processing diatoms

Littoral diatoms were sampled at 25 littoral sites of Lake Ladoga in August 2014. At each site, 4–6 fragments of stems approximately 10 cm long were collected in reed stands at a depth of 0.2–0.3 m below the water surface. Diatoms were removed from all the fragments using a toothbrush and preserved in 4% formaldehyde until processing. In the laboratory, to clean diatoms the periphyton samples were treated by cold burning with sulphuric acid and potassium dichromate (Balonov 1975), washed three times in distilled water and centrifuged at 2000 rpm for 10 min for decantation. Diatoms were mounted on permanent slides with Naphrax mounting medium and observed with a light microscope (Zeiss Axio Imager D1) equipped with differential interference contrast (DIC) optics at  $\times 1000$  magnification. To determine the relative abundance of the diatom species, at least 400 valves per sample were counted and identified to the lowest possible taxonomical level. Diatom taxonomy followed Krammer and Lange-Bertalot (1986, 1988, 1991a, 1991b), Lange-Bertalot et al. (2017) and other taxonomical reference works. Taxonomic assignments were not made

for some valves and they were omitted from the analysis. The unidentified diatom valves accounted for 1% on average (ranging from 0 to 5%) of all counted valves in each sample.

We assigned 144 diatom species identified from the 25 samples to four ecological guilds reflecting their growth morphology. The four guilds according to classification of Passy (2007) and Rimet and Bouchez (2012) are low-profile, high-profile, motile and planktic guilds. For the following statistical analyses, we used all 144 species including rare ones with low occurrence (1–2 sites) across the whole dataset.

In order to assess the ecological status of the sampling sites, the Specific Pollution-Sensitivity index (IPS; CEMA-GREF 1982) was calculated using OMNIDIA (ver. 6.1.7) software (Lecoite et al. 1993). The IPS values are classified into the following quality categories: high (IPS > 17), good (IPS 15–17), moderate (IPS 12–15), poor (IPS 9–12) and bad (IPS < 9) quality as adapted from Eloranta and Soinen (2002).

### Explanatory variables

We used three types of explanatory variables including water chemical, physical (Supporting Information Table S1) and spatial variables. At each site, water samples for chemical analysis were collected from a boat approximately 0.5 m from the surface and 5–10 m offshore. Measurements of pH and electrical conductivity (EC) were made in the field using the multiparameter probe Aqua TROLL 500 (In-Situ Inc.). Analysis of inorganic and total phosphorus were performed in the laboratory using national standard methods (Semenov 1977). Inorganic phosphorus (IP) was determined as the sum of dissolved and particulate orthophosphates by a modified molybdenum method of Murphy and Riley (1962), using ascorbic acid as a reducer. Total phosphorus (TP) was determined using the same procedure (Murphy and Riley 1962) after oxidation with  $K_2S_2O_8$  in acidic medium. TP values varied from 16 to  $152 \mu\text{g l}^{-1}$  (Table S1), with a minimum value corresponding to oligotrophic conditions (Dodds et al. 1998), and a maximum value above  $100 \mu\text{g l}^{-1}$  considered to be hypertrophic (OECD 1982).

In addition to water chemical measurements, we used land use data as a proxy for catchment nutrient loads (de Wit et al. 2020). To study land use impacts on periphytic diatoms, we applied a catchment approach (Sliva and Williams 2001). The delineation of the Lake Ladoga catchment and its sub-catchments was based on the global digital elevation model ASTER GDEM. The coverage of the ASTER satellite includes the region between  $83^\circ$  north and south latitude with 30-m spatial resolution (Reuter et al. 2009). The model was subjected to a hydrological correction, which included filtration of closed depressions and selection of the main watercourses. Following this, surface flow paths

were calculated using the Multiple Flow Direction (MFD) algorithm in SAGA GIS software ver. 2.1.4 (Conrad et al. 2015). As a result, the whole catchment of Lake Ladoga (area ~ 284,000 km<sup>2</sup>) was divided into four sub-catchments: Lake Saimaa–Vuoksa River (area ~ 70,000 km<sup>2</sup>), Lake Onega–Svir River (area ~ 82,000 km<sup>2</sup>), Lake Ilmen–Volkhov River (area ~ 82,000 km<sup>2</sup>) and the proper Lake Ladoga (area ~ 48,000 km<sup>2</sup>) (Fig. S1). For land use differentiation within the Lake Ladoga catchment, we used the global dataset ESA WorldCover 10 m v200 (Zanaga et al. 2022). This dataset was developed by the European Space Agency based on satellite data from Sentinel-1 and Sentinel-2. The WorldCover collection has a spatial resolution of 10 m. Land use differentiation in the World Cover dataset has 11 classes, according to the Food and Agriculture Organization of the United Nations (UN-FAO)'s Land Cover Classification System (LCCS), with nine classes located in the Lake Ladoga catchment (Fig. S1). The classification of land use types was based on the Copernicus Global Land Service Collection 3 (CGLS) algorithm (Buchhorn et al. 2020). Sentinel-2 multispectral image data and Sentinel-1 synthetic aperture radar data were used. Individual land use types and their extent in the Lake Ladoga sub-catchments were determined with QGIS software ver. 3.16 “Hannover” (<https://qgis.org/>). In further statistical analysis, six different land use categories were used: (1) forest, (2) grassland, (3) agricultural area, (4) built-up area, (5) water bodies and (6) wetlands (Table S2). Linear correlation analysis was employed to assess relationships between the proportions of agricultural and built-up areas and TP concentration as well as between these land use types and the values of the Specific Pollution-Sensitivity Index (IPS).

Physical variables reflecting the geomorphic parameters of the littoral zone were determined using a 1:25,000-scale topographic map. Three continuous geomorphological variables were included in the analysis: distance from the shore to the 5-m isobath (km), bottom slope at a depth of 5 m (%) and exposure of a site (°) (Table S1). To assess the influence of littoral geomorphic types, we used a categorical (nominal) variable with three levels: ES (exposed shoreline), EB (embayment) and CW (coastal wetland) (Table S3).

Based on coordinates (latitude and longitude) of the sampling sites (Table S3), a matrix of geographical distances was calculated using Euclidean distance. Before a matrix calculation, geographical coordinates were transformed into UTM (zone 36N) coordinates to minimize area distortion using the PAST software ver. 4.13 (Hammer et al. 2001). Spatial variables were derived from the geographical distance matrix using distance-based Moran's eigenvector maps (MEM; Dray et al. 2006). These spatial variables, which are the eigenvectors associated with the positive eigenvalues of the distance matrix, were obtained using principal coordinates of neighbour matrices (PCNM, Borcard and

Legendre 2002). This method has a distinct advantage over using direct geographic coordinates because it is able to detect and quantify spatial patterns over the whole range of scales encompassed by the sampling design (Borcard and Legendre 2002; Dray et al. 2006). The first few PCNM variables exhibit broad-scale spatial patterns with each successive variable resolving finer spatial patterns. Based on our 25 sampling sites, 15 spatial variables showing positive autocorrelation were derived. PCNM variables reflecting various spatial scales could be used for interpretation of dispersal-related processes: broad-scale spatial variables (i.e., those with large eigenvalues) are related to dispersal limitation, while fine-scale spatial variables (i.e., those with small eigenvalues) are related to mass effects (Heino et al. 2015). In this study, we considered PCNM variables 1–4 to reflect broad scale spatial relations, i.e., across the entire lake, variables 5–11 to reflect medium scale relations, and variables 12–15 to reflect fine-scale relations amongst neighbouring sites. PCNM analysis was performed using the function *pcnm* in the ‘vegan’ (ver. 2.6–4) package (Oksanen et al. 2022) written for the R (ver. 4.3.1) statistical programming environment (R Core Team 2023).

## Data analysis

In order to test for significant differences in diatom taxonomic and functional composition among littoral geomorphic types (H1), analysis of similarities (ANOSIM; Clarke 1993) with Bray–Curtis distance and 999 permutations was performed using the function *anosim* in ‘vegan’ (Oksanen et al. 2022). Significant differences in the relative abundance of the four diatom guilds among geomorphic types (ES, EB and CW) were assessed using a Kruskal–Wallis test (nonparametric analogue of one-way ANOVA) with Mann–Whitney tests for pairwise comparison. We identified the best indicator species for each geomorphic type by the indicator value method (IndVal; Dufrene and Legendre 1997; De Cáceres et al. 2010) using the function *multipatt* in ‘indicpecies’ (ver. 1.7.14) package (De Cáceres et al. 2020) written for R (R Core Team 2023). Because indicator species reflect the abiotic state of the environment (Dufrene and Legendre 1997), we expected that indicator species would belong to those diatom guilds that show the highest preferences for one or another geomorphic type. Also, we calculated three site-specific diversity measures: species richness, Shannon's diversity and Pielou's evenness. A Kruskal–Wallis test was used to assess significant differences in these diversity metrics among geomorphic types. Mann–Whitney *U* tests were used for pairwise comparisons with sequential Bonferroni correction. ANOSIM and Kruskal–Wallis tests were used to identify significant changes in diatom community structure associated with littoral geomorphic types, as a prerequisite to making more specific statistical inferences about

differences in community structure (Clarke and Warwick 2001).

Prior to the following analysis, relative abundance data for diatom species were Hellinger-transformed using the function *decostand* in ‘vegan’. This transformation makes the species data more suitable for analysing by linear ordination, downweighting the most abundant species to reduce their influence on the analysis (Legendre and Gallagher 2001). All environmental variables were standardized (mean = 0, variance = 1) to render the variables scale-free and dimensionless before the analysis (Legendre and Legendre 1998).

We analysed spatial patterns in species composition of the whole diatom community as influenced by environmental variables with distance-based redundancy analysis (db-RDA; Legendre and Anderson 1999) using the function *capscale* in ‘vegan’. Bray–Curtis dissimilarity was used as a distance metric. Before db-RDA, we ran Spearman rank correlations between environmental variables and excluded IP and distance to the 5-m isobath, which were highly correlated ( $r_s = 0.81$ ) with TP and slope, respectively. To assess responses of the whole diatom community to chemical (Che), physical (Phy) and spatial (Spa) variables, and to determine the pure and shared fractions of the variation in community composition explained by these predictor groups (H2), we employed partial db-RDA (Borcard et al. 1992), using the function *varpart* in ‘vegan’. Before partial db-RDA, we selected the explanatory variables separately for each predictor group (Che, Phy and Spa) using a forward selection method developed by Blanchet et al. (2008). This method is used to prevent artificially inflated explanatory power of constrained ordination models. The inclusion of variables to the model is based on two stopping criteria: (1) statistical significance of the newly selected variables and (2) comparison of adjusted variation ( $R^2_{adj}$ ) explained by the selected variables to  $R^2_{adj}$  explained by the full model (with all variables). The procedure is stopped when the new variable is not significant ( $p > 0.05$ ) or the  $R^2_{adj}$  of the model including this new variable exceeds the  $R^2_{adj}$  of the full model. The forward selection was carried out using the function *ordiR2step* in ‘vegan’. To compare response of diatom guilds to Che, Phy and Spa variables (H3), we performed partial db-RDA separately for each diatom guild in precisely the same way as for the whole diatom community.

All statistical analyses were carried out in R ver. 4.3.1 (R Core Team 2023).

## Results

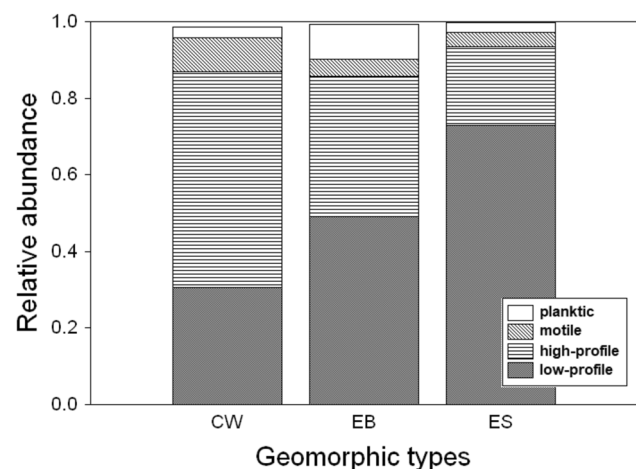
Among 144 diatom species identified from the 25 samples, there were 22 low-profile taxa, 58 high-profile taxa, 50 motile taxa and 14 planktic taxa (Table S4). Based on

relative abundances, 50.1% of all valves belonged to the low-profile guild, 34.8% to the high-profile guild, 5.5% to the motile guild and 5.0% to the planktic guild. The 10 most common taxa were *Achnantheidium minutissimum* (Kütz.) Czarnecki, *Cocconeis placentula* Ehr., *Encyonema minutum* (Hilse in Rabenhorst) D.G. Mann, *Eunotia incisa* W. Smith ex W. Greg., *Gomphonema parvulum* Kützing, *E. silesiacum* (Bleisch) D.G. Mann, *Tabellaria flocculosa* (Roth) Kütz., *T. fenestrata* (Lyngbye) Kütz., *Fragilaria gracilis* Østrup, and *Diatoma tenuis* C. Agardh.

According to the IPS values, water quality varied from high quality mostly on the northern and eastern coasts, to good quality on the western coast and to moderate quality in the Volkhov Bay on the southern coast (Fig. 1, Table S3).

## Geomorphic influence on diatom species and guild compositions and diversity indices

Species composition differed significantly (ANOSIM,  $R = 0.319$ ,  $p < 0.001$ ) between the three geomorphic types. IndVal analysis identified species that were significantly confined to a certain geomorphic type (Table S5). Many motile (*Navicula veneta* Kütz., *Plagiotropis lepidoptera* (W. Greg.) Kuntze, *N. menisculus* Schumann, and *Nitzschia pusilla* Grunow) and high-profile (*Ulnaria ulna* (Nitzsch) Compère, *Gomphonema parvulum* Kütz., *G. angustatum* (Kütz.) Rabenhorst, *Eunotia bilunaris* (Ehr.) Schaarschmidt, and *E. minor* (Kütz.) Grunow) diatoms were specific to CW. High-profile diatoms (*E. minutum* and *D. tenuis*) and a planktonic centric diatom *Aulacoseira subarctica* (O. Müller) E.Y. Haworth were characteristic of EB. A low-profile diatom *A. minutissimum* was an indicator of ES. The three geomorphic types also differed significantly (ANOSIM,  $R = 0.253$ ,  $p < 0.01$ ) in guild composition (Fig. 2). According



**Fig. 2** Relative abundance of diatom guilds in different geomorphic types. Geomorphic types: CW – coastal wetlands, EB – embayments, and ES – exposed shorelines

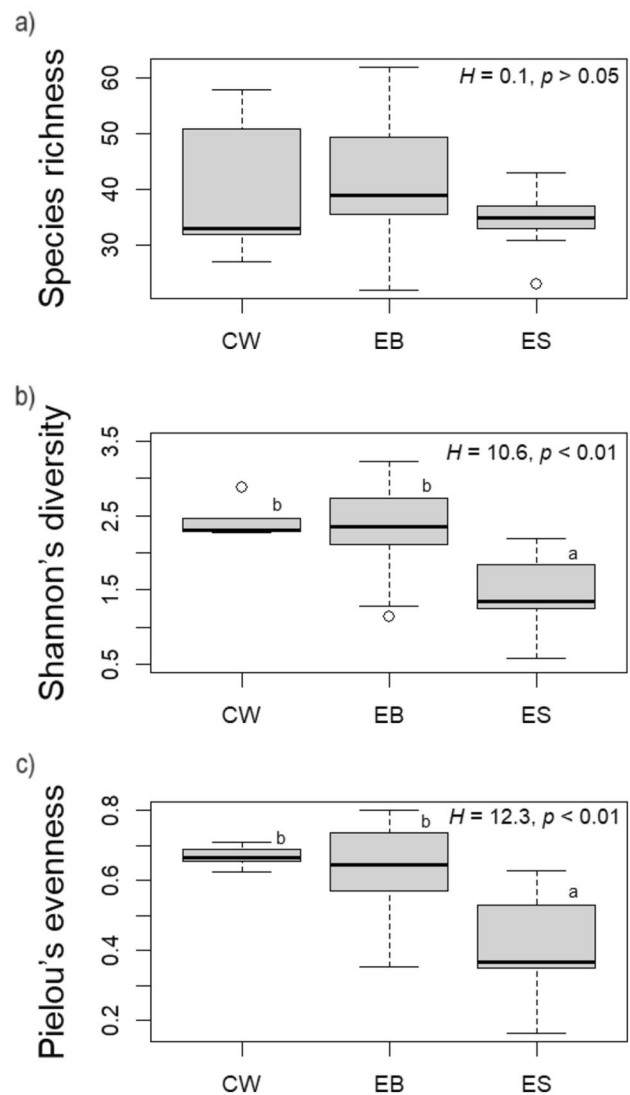
to the Kruskal–Wallis test, three diatom guilds showed significant differences in relative abundance between geomorphic types: low-profile guild ( $H=9.6$ ,  $p < 0.01$ ), high-profile guild ( $H=9.2$ ,  $p < 0.01$ ) and motile guild ( $H=5.9$ ,  $p \leq 0.05$ ) (Fig. S2–4). Mann–Whitney  $U$  tests showed that the low-profile guild had significantly higher abundance in ES than in CW and ES (Table S6), while the high-profile and motile guilds had significantly higher abundance in CW compared with ES (Table S7, S8). No statistically significant differences ( $H=1.7$ ,  $p > 0.05$ ) were evident between geomorphic types for planktic guild (Fig. S5).

Species richness varied from 22 to 62 with no significant differences ( $H=0.1$ ,  $p > 0.05$ ) between geomorphic types (Fig. 3a). In contrast, there were significant differences in Shannon's diversity ( $H=10.6$ ,  $p < 0.01$ ) and Pielou's evenness ( $H=12.3$ ,  $p < 0.01$ ) (Fig. 3b, c). Mann–Whitney  $U$  tests showed that Shannon's diversity and Pielou's evenness in ES were significantly lower compared to those in CW and EB (Table S9, S10).

### Factors driving the structure of the whole diatom community

In the db-RDA for the whole diatom community, chemical (TP and EC) and physical (slope and geomorphic type) variables showed significant ( $p < 0.05$ ) relationships with diatom composition (Table 1; Fig. 4a). Geomorphic types were clearly separated along the first axis (Fig. 4b). CW was on the negative side of the first axis, ES was on the positive side, while EB occupied an intermediate position. Yet EB and ES showed some overlap, indicating that their species compositions were more similar to each other but differed markedly from those of CW. Effect of TP and EC on diatom composition was also evident on the db-RDA biplot, since the most eutrophic sites (2, 3 and 4) in Volkhov Bay, as indicated by the IPS values (Fig. 1, Table S3), were separated from oligotrophic sites (12, 13, 16, 17, 18 and 24) on the northern and western coasts along the first axis (Fig. 4a).

Variation partitioning of the whole diatom community showed that the pure effect (9%) of environmental variables (including chemical and physical) was more important than the pure effect (2%) of spatial variables (Fig. 5a). Chemical variables that explained variation in the structure of the whole community were TP and conductivity (Table 2). Physical variables, such as geomorphic type and bottom slope, explained a somewhat smaller amount of variation in the community structure (4%) than chemical variables (5%) (Fig. 5a; Table 2). Spatial variables described the spatial relations among sites at broad (PCNM1, PCNM2, PCNM3) and medium (PCNM5) scales (Table 2). Shared fractions between chemical, physical and spatial variables jointly accounted for 5% of the variation (Fig. 5a) and indicated spatially structured chemical and physical variables.



**Fig. 3** Variation in diversity measures among littoral geomorphic types. Geomorphic types: CW – coastal wetlands, EB – embayments, and ES – exposed shorelines. Kruskal–Wallis tests were employed for comparing the medians of different diversity metrics between geomorphic types. Mann–Whitney  $U$  tests were used for pairwise comparisons with sequential Bonferroni correction. Different letters indicate significant differences ( $p < 0.05$ )

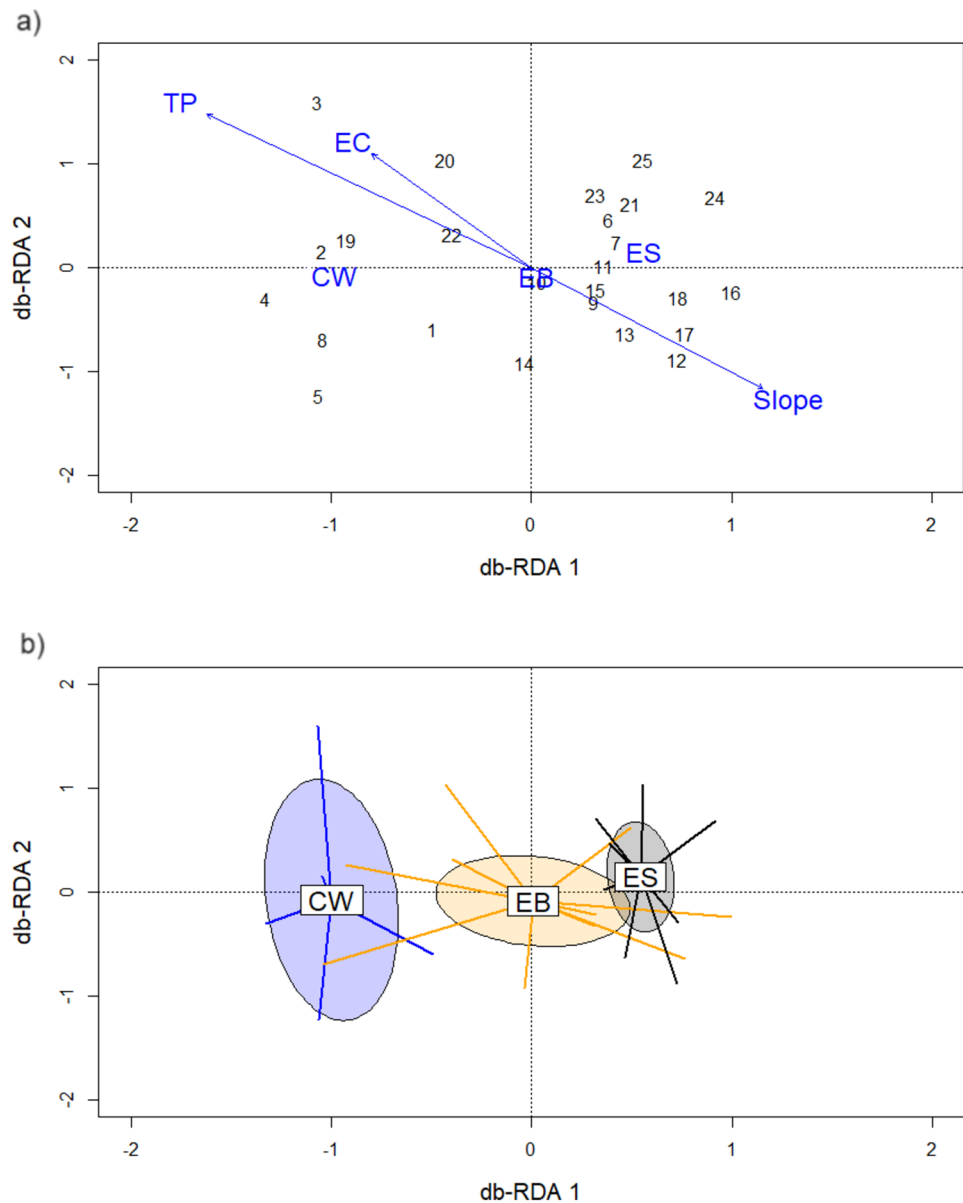
**Table 1** Significant predictors in the distance-based redundancy analysis (db-RDA) model of the whole diatom community

Predictors	$F_{\text{model}}$	$P$
Total phosphorus	4.304	0.001
Electrical conductivity	2.321	0.005
Geomorphic type	2.771	0.001
Slope	1.520	0.046

$P$ -values are based on 999 permutations



**Fig. 4** db-RDA biplot of the whole diatom community, representing sampling sites (1–25), environmental variable vectors and factor centroids (CW, EB and ES) **a**, and groups of sites combined to their class centroids (CW, EB and ES) of geomorphic types **b**. Geomorphic types: CW – coastal wetlands, EB – embayments, and ES – exposed shorelines

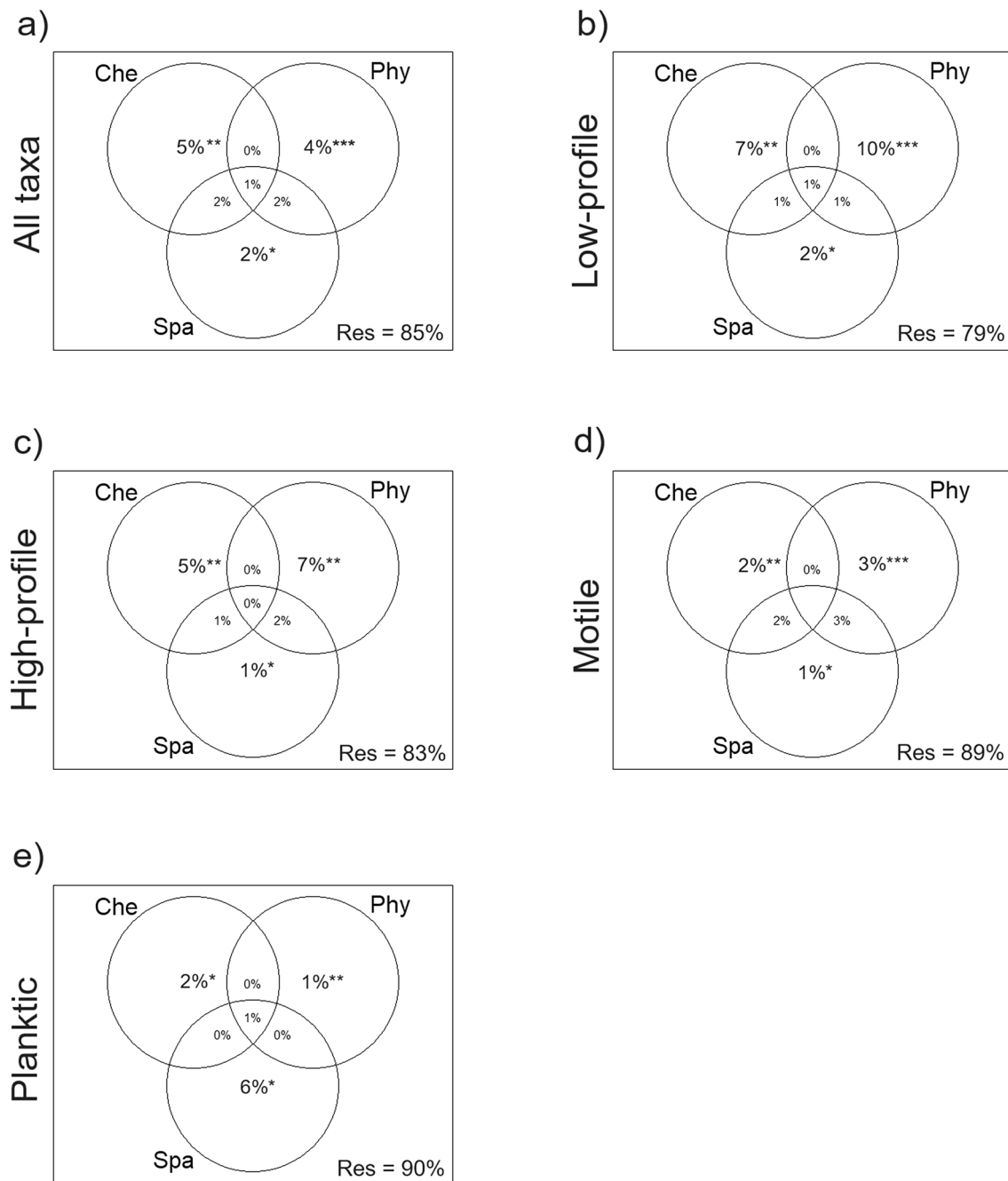


As revealed by db-RDA, land use variables did not show any significant relationships with diatom community structure. However, the IPS was significantly related to the proportion of agricultural ( $r = -0.57$ ,  $p < 0.01$ ) and built-up ( $r = -0.50$ ,  $p < 0.05$ ) area. Likewise, TP concentration correlated significantly with the proportion of agricultural ( $r = 0.40$ ,  $p < 0.05$ ) and built-up ( $r = 0.41$ ,  $p < 0.05$ ) area.

### Factors driving the structure of the four diatom guilds

When variation partitioning was performed separately for each diatom guild, different patterns emerged for the three benthic guilds (low-profile, high-profile and motile) and the planktic guild.

The three benthic guilds were structured more by environmental factors including physical and chemical variables, whereas the planktic guild had a prevailing contribution of spatial factors (Fig. 5b–e). For the three benthic guilds, spatial predictors included broad (PCNM1, PCNM2, PCNM3 and PCNM4) and medium (PCNM5 and PCNM9) scales (Table 2). Contrastingly, for the planktic guild, the spatial predictors included variables of broad (PCNM1) and fine (PCNM13) scales (Table 2). Physical variables that explained variation in the structure of the three benthic guilds were geomorphic variables such as geomorphic type, bottom slope and exposure, whilst temperature was the only physical variable, which explained variation in the structure of the planktic guild (Table 2). Chemical variables such as



**Fig. 5** Results of variation partitioning for the total diatom community structure **a** and taxonomic composition within the diatom guilds **b–e**. The pure and shared fractions of chemical (Che), physical (Phy) and spatial (Spa) variables are based on adjusted  $R^2$  values shown as

percentages of total variation. Statistically significant ( $p \leq 0.05$ ; 999 permutations) pure fractions are indicated by \*. The negative values are not shown. Residuals/unexplained variance (Res) are shown in the lower right corner

TP and conductivity significantly contributed to variation in the structure of the three benthic guilds (Fig. 5b–d; Table 2). In contrast, the proportion of built-up area (as a proxy for nutrient input) had significant relationship to the structure of the planktic guild (Fig. 5e; Table 2). The pure and shared effects of chemical variables were higher for low-profile and high-profile guilds than those

for motile guild (Fig. 5b–d; Table 2). Unexplained variation was somewhat larger for planktic and motile guilds than for low-profile and high-profile guilds (Fig. 5b–e).

**Table 2** Results of the forward selection procedure conducted independently for chemical, physical and spatial variable groups for the whole diatom community and separately the four diatom guilds

Species matrix	Chemical variables	AdjRcum/ <i>p</i> -value	Physical variables	AdjRcum/ <i>p</i> -value	Spatial variables	AdjRcum/ <i>p</i> -value
All species	TP	0.09/0.002	Geomorphic type	0.11/0.002	PCNM1	0.04/0.016
	EC	0.13/0.020	Slope	0.15/0.002	PCNM3	0.08/0.022
Low-profile	TP	0.13/0.006	Geomorphic type	0.21/0.002	PCNM2	0.11/0.038
					PCNM5	0.13/0.048
					PCNM1	0.09/0.018
High-profile	EC	0.20/0.014	Slope	0.07/0.004	PCNM4	0.18/0.042
					PCNM1	0.05/0.014
Motile	TP	0.10/0.002	Geomorphic type	0.11/0.026	PCNM3	0.09/0.008
					PCNM2	0.13/0.038
					PCNM9	0.04/0.016
Planktic	Built-up area	0.04/0.010	Slope	0.11/0.002	PCNM3	0.08/0.034
					PCNM1	0.10/0.042
					PCNM13	0.05/0.040
Planktic	Temperature	0.06/0.006	Temperature	0.06/0.006	PCNM1	0.05/0.040
					PCNM13	0.10/0.036

AdjRcum is the cumulative  $R^2_{\text{adj}}$

## Discussion

### Effect of littoral geomorphology and water chemistry on diatom community structure

In this study, we investigated the influence of geomorphology, water chemistry and spatial factors as proxies for dispersal on species and functional composition of littoral diatoms in Lake Ladoga. Most previous studies on lake diatoms have been devoted to the effect of water quality changes induced by anthropogenic perturbations (e.g., Ács et al. 2005; Gottschalk and Kahlert 2012; Crossetti et al. 2013). However, only a few studies have also examined the effect of natural factors such as littoral geomorphology and related water turbulence regime (Kireta et al. 2007; Rimet et al. 2015; Vilmi et al. 2017). In agreement with our first hypothesis (H1), we found that both species and functional composition were significantly impacted by littoral geomorphic types. These results are consistent with a study from the Great Lakes reporting significant spatial heterogeneity of diatom communities in response to coastal geomorphic variability (Kireta et al. 2007). Moreover, distinct differences in guild composition between various littoral habitat types of Lake Ladoga indicate that wave-induced disturbance was the most important factor behind habitat preferences of littoral diatoms. Our study showed that the most wave-exposed sites (i.e., ES) were dominated by low-profile diatoms, which are favored in habitats with high hydrological disturbance (Passy 2007). In contrast, the least physically disturbed sites (i.e., CW) were characterized by the high-profile guild and an increased relative abundance of the motile guild with lower resistance

to wave action. Diatom assemblages at embayment sites (i.e., EB) were a transitional community comprising mainly low-profile and high-profile diatoms. It is known that emergent vegetation extended several hundred meters into the open water gradually impedes the movement of water towards the shore, thereby decreasing wave energy (Cardinale et al. 1997). Furthermore, the decrease in Shannon's diversity and Pielou's evenness in the ES sites due to reduced abundances of high-profile and motile diatoms with a concomitant increase in dominance of *Achnantheidium minutissimum* is in line with a study on benthic diatoms in Lake Geneva, where the most wave-exposed site was characterized by dominance of pioneer low-profile diatoms such as small *Achnantheidium* and *Amphora* (Rimet et al. 2015).

Apart from geomorphic type, slope was also an important physical variable in determining diatom community structure. The shore slope is a correlate of wave-induced disturbance (Duarte and Kalf 1986), so the steeper the shore slope, the greater the physical stress. Although the gentle slope can be considered as a discriminating parameter for densely vegetated shores (Tolonen et al. 2001), this variable distinguishes the southern shallow region from the northern skerry region and the region of open shores, irrespective of habitat type. Therefore, our CW sites exhibited distinct taxonomic and guild structure in spite of the fact that the width of macrophyte beds ranged from a few tens to several hundred meters. In db-RDA ordination, the CW sites are clearly separated from the EB and SE sites along the first axis correlated with the slope. Hence, the increasing slope is a main cause of the decreased abundance of high-profile and motile guilds in the region of open shores and the northern

skerry region of Lake Ladoga. Similarly, an increase in littoral slope negatively affected richness and diversity of the motile guild in a boreal lake system (Vilmi et al. 2017).

Responses of periphytic diatoms to eutrophication were evident from the significant relationships of community structure with TP and EC concentrations, as shown by db-RDA. Spatial variation in community structure of the whole diatom community was not significantly related to catchment-level land use, as in a study of stream diatoms, where the local chemical variables prevailed in shaping community composition (Stenger-Kovács et al. 2020). However, a significant correlation between TP concentration and the proportions of agricultural and built-up area suggests that these land use types were indirectly responsible for spatial patterns of change in the diatom community. This is indicated by significantly negative relationships between the diatom water quality index (IPS) and the proportions of agricultural and built-up area. It is noteworthy that the IPS values also varied in response to local anthropogenic impacts, as evidenced by the relatively low IPS value in Shchuchiy bay (site 19) (Fig. 1, Table S3), likely due to sediments contaminated by the pulp mill waste in the past (Kurashov et al. 2018).

### Role of environmental and spatial factors

The results of variation partitioning for the whole diatom community supported our second hypothesis (H2), since the effect of environmental variables prevailed over the effect of spatial variables, indicating dominance of species sorting processes in controlling diatom community structure. However, our findings are contrary to the results of a few previous studies demonstrating the higher influence of dispersal processes (i.e., mass effects) over environmental filtering for diatom and macroinvertebrate communities in similar highly connected freshwater lakes (Vilmi et al. 2016; Cai et al. 2017; Tolonen et al. 2017). The steepness of the environmental gradient is likely not a decisive factor of the relative importance of species sorting vs. dispersal processes, because these lakes were characterized as being near-pristine (Vilmi et al. 2016; Tolonen et al. 2017) and anthropogenically impacted (Cai et al. 2017) environments. Rather, differences in the spatial extent of the study area are the most plausible explanation for discrepancies between our and previous results. The previous studies were conducted at smaller spatial scales (i.e.,  $10^2$  to  $10^3$  km<sup>2</sup>) than our study (i.e.,  $10^4$  km<sup>2</sup>). Thus, our results suggest that the importance of environmental factors increases with increasing spatial extent from small to intermediate, while that of spatial factors decreases. Hence, in highly connected lake systems, the pattern of changes in the relative importance of assembly mechanisms is similar to that in spatially isolated water bodies (Heino 2011; Heino et al. 2015).

Wind-driven currents are an important determinant of microalgae distribution in nearshore lake zones (e.g., Cyr 2017). It is noteworthy that directional dispersal of organisms by wind-driven currents may lead to spatial isolation of local assemblages (Moritz et al. 2013), thus decreasing longshore connectivity between local assemblages at the scale of the whole lake. In Lake Ladoga, the decrease in connectivity may be even more substantial in the northern skerry region, which consists of numerous isolated fjord-like bays and narrow straits. The results of our forward selection procedure showed that only large- and medium-scale spatial variables were important in structuring the whole diatom community. The large-scale variables likely reflect the effect of dispersal limitation, which increases with increasing spatial extent (Heino et al. 2015). Thus, considering the spatial extent of our study, we can probably interpret the spatial patterns observed in the whole diatom community as evidence of dispersal limitation. However, the higher importance of environmental factors in shaping diatom community structure indicates that dispersal limitation is not strong, thereby enabling efficient species sorting along environmental gradients at the scale of the entire lake.

### Response of diatom guilds to environmental and spatial factors

According to metacommunity theory, the relative role of environmental filtering and spatial processes varies among taxonomic groups with different dispersal abilities (Heino et al. 2015). The diatom community was deconstructed into groups (i.e., low-profile, high-profile, motile and planktic), which are composed of species with similar traits related to their potential dispersal ability. We found that all benthic guilds including poor dispersers (i.e., low-profile and high-profile) and strong dispersers (i.e., motile) were strongly related to environmental factors, but weakly to spatial factors. Only free-living planktic taxa, that were expectedly effective dispersers, showed stronger spatial compared to environmental signal. Thus, our third hypothesis (H3) regarding different dispersal abilities of diatom guilds and spatial structuring was only partially supported. Also, the planktic guild was more strongly structured by spatial than environmental variables in other studies, in which relatively small spatial scale pointed clearly to mass effects (Vilmi et al. 2017; Lindholm et al. 2018).

A significant pure effect of spatial variables may be attributable to dispersal limitation as well as mass effects (Cottenie 2005). Three lines of evidence let us conclude that mass effects rather than limited dispersal played a dominant role in the spatial distribution of the planktic guild. First, variance in the planktic guild was significantly explained by fine-scale spatial variables, which are generally attributed to mass effects (Heino et al. 2015). Second, when compared



with spatial variables, environmental variables played a negligible role in structuring the planktic guild. Third, the total amount of explained variation was the lowest for the planktic guild. These findings are in accordance with mass effects which can reduce community heterogeneity and thereby mask environmental effects (Leibold et al. 2004; Heino et al. 2015). In contrast, limited dispersal was the more likely process behind the spatial distribution of the three benthic guilds as was evidenced by significant effects of large-scale spatial variables (see above). However, limited dispersal did not strongly interfere with species sorting, since environmental effects overrode those of spatial factors.

It is important to note that planktic species inhabit benthic diatom communities as a result of sedimentation from the water column; therefore, spatial patterns in planktic guild distribution reflect dispersal processes in plankton rather than in benthos. Wetzel et al. (2012) found that the rate of spatial species turnover was lower for phytoplankton than for the benthic diatom community, indicating higher dispersal abilities for phytoplankton taxa. This is in line with our findings demonstrating strong spatial patterns in the planktic guild because of high dispersal rates (i.e., mass effects). Wind-induced water currents have been observed to affect the spatial distribution of lake phytoplankton (e.g., Schernewski et al. 2005). Moreover, a comparison made for phytoplankton and benthic diatom communities in Lake Geneva has shown a higher wind-induced temporal variability in the phytoplankton resulting in a lower correlation with water column nutrients (Rimet et al. 2015). Thus, the higher susceptibility of phytoplankton to wind events could result in a lack of relationship between the structure of the planktic guild and measured TP and EC values in Lake Ladoga during our study. At the same time, the significant effect of the proportion of built-up area suggests that spatial patterns in the phytoplankton community were more driven by impacts of land use change at the catchment level than by local changes in nutrient concentrations.

Our results indicate that environmental factors outperformed spatial ones in shaping the structure of all three benthic guilds (i.e., low-profile, high-profile and motile), irrespective of their potential dispersal ability. When compared to low-profile and high-profile guilds, the motile guild exhibited a similar response to spatial factors, suggesting a lack of strong influence of dispersal processes on this loosely attached guild. However, unlike our research, a previous study of a diatom community in a highly connected lake system revealed that motile taxa showed significant spatial patterns that stemmed from the influence of high dispersal rates (Vilmi et al. 2017). Also, a similar result was reported by Wetzel et al. (2012), who showed a lower rate of spatial species turnover for loosely attached than for firmly attached diatoms in a stream system. A plausible reason for this discrepancy is that in Lake Ladoga the total abundance

of motile species was too low (only 5.5%) to produce mass effects. Our conclusion is supported by a study of benthic diatoms in high mountain streams (Dong et al. 2016) that demonstrated no significant spatial structure for the motile guild with low abundance. Contrastingly, motile diatoms showed the lowest beta diversity (as a measure of species turnover) in downstream reaches, where the guild was the most abundant and, thereby, most strongly influenced by mass effects (Jamoneau et al. 2018). On the other hand, our results showed that the amount of unexplained variation was somewhat larger for the motile guild (89%) than for low-profile and high-profile guilds (79% and 83%, respectively). This may indicate a higher importance of stochastic processes in the spatial dynamics of loosely attached species that are likely more influenced by wind-induced currents than firmly attached species. It is likely, therefore, that some fraction of the unexplained variance in the motile guild was related to unmeasured effects of water currents.

The trait-based deconstructive approach not only accounts for different dispersal abilities of diatom guilds, but also for their environmental adaptability (Passy 2007). We found that the guild sensitivity to changes in water chemistry variables was related to their mode of attachment and resistance to wave-induced disturbance. Motile diatoms, which exhibit greater susceptibility to disturbance because of loose attachment to the substrate, showed weaker relationships with chemical variables than firmly attached guilds (i.e., low-profile and high-profile). IndVal analysis revealed that motile diatoms (such as *Navicula menisculus*, *N. veneta*, *Nitzschia pusilla* and *Plagiotropis lepidoptera*) have strong habitat preferences for coastal wetlands (CW), which are the least hydrologically impaired geomorphic type in Lake Ladoga. Waves decrease diversity and evenness of diatoms in exposed shoreline sites (ES) by detaching loosely attached motile taxa from the substrate. Thus, negative effects of wave-induced disturbance dampen possible positive effects of nutrient enrichment at highly disturbed sites (mainly at ES), decreasing the strength of relationships between motile guild abundance and TP concentration. Furthermore, motile diatoms are more adapted to acquire nutrients within the biofilm matrix (Passy 2007). This might also contribute to reduced responses of the motile guild to nutrient concentration in overlying water. In turn, high-profile taxa respond more to changes in water chemistry variables than do motile diatoms due to their moderate resistance to wave action. Low-profile taxa that tolerate the increased scouring at highly disturbed habitats were the guild that most strongly responded to chemical variables. This is consistent with a study of diatoms in a boreal lake system, demonstrating a strong response of the low-profile guild to a wide array of chemical parameters (Vilmi et al. 2017). Thus, our results indicate that benthic diatoms in a row of guilds arranged in order of increasing tolerance to wave energy (i.e.,

motile—high-profile—low-profile) tend to exhibit increased sensitivity to water chemical parameters. Furthermore, we found that the effect of geomorphology on benthic guilds was somewhat stronger than the effect of chemical variables, after accounting for spatial structure. Also, geomorphology was similar in its importance to chemical factors in structuring the whole diatom community. Hence, shoreline geomorphology and related hydrological conditions seem to be prominent factors structuring littoral diatom communities in large lakes (Brazner et al. 2007; Kireta et al. 2007; Rimet et al. 2015; Vilmi et al. 2017).

It should be noted that the amounts of unexplained variation in our models of the species structure of the whole diatom community and functional guilds are relatively high (79–90%). This may be a result of the relatively small number of sites sampled and difficulties in adequately modeling the spatial dynamics of rare species. Another reason behind the high unexplained variation could be some unmeasured important environmental factors. At the same time, other similar studies also showed a high percentage of unexplained variation (65–91%) (Vilmi et al. 2016, 2017; Lindholm et al. 2018; Stenger-Kovács et al. 2020), which can be explained by the high stochasticity of biological data in general (Velend 2016). Given that in our study the models adequately describe the spatial dynamics of diatom guilds in accordance with their resistance to wave-induced disturbance and ability to disperse, the interpretation of the results of variation partitioning in our data seems to be reasonable.

## Conclusions

Our findings support the results of previous studies (Rimet et al. 2015; Vilmi et al. 2017) showing that trait-based approaches can elucidate disturbance- and dispersal-related mechanisms underlying spatial distribution of diatom communities in the littoral zone of large lake systems. Benthic diatom guilds showed distinct distributional patterns along a gradient of wave-induced disturbance: the low-profile guild dominated in wave-exposed shorelines, whereas high-profile and motile guilds were more abundant in more calm coastal wetland habitats. Environmental factors (i.e., geomorphology and water chemistry) outperformed spatial factors in structuring the whole diatom metacommunity, indicating a predominant role of species sorting processes. However, the planktic guild showed strong dependence upon spatial variables that resulted from mass effect dynamics. Among benthic guilds, low-profile diatoms were the most, and motile diatoms the least, sensitive to chemical variables. This suggested that diatom responses to water quality changes depend on their resistance to wave-induced disturbance. Overall, we conclude that the higher importance of environmental filtering than dispersal-related processes in shaping

diatom community structure resulted from a combination of a strong environmental gradient in geomorphology/water chemistry and the intermediate spatial scale of our study.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s00027-024-01055-0>.

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**Author contributions** AGR – conception and design of the study, collection and preparation of diatom samples, species identification, data analysis and interpretation, visualization, drafting the manuscript; EAK – design of the study, chemical analysis of water samples and critical review; AMR – data analysis and visualization; TB – critical review; EV – critical review; ÉÁ – conception of the study, species identification and data processing, critical review.

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**Data availability** The datasets used and analyzed during the current study are available from the corresponding author on reasonable request.

## Declarations

**Conflict of interest** The authors declare that they have no competing interests.

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