



Sedimentary, littoral and planktic diatoms show different diversity patterns and assembly mechanisms in mountain lakes of the northern European Alps

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Abstract This study analysed diversity patterns of sedimentary, littoral and planktic diatoms in 43 mountain lakes in the northern European Alps and identified processes that contribute to these patterns. Linear regression models showed a significant increase of sedimentary α -diversity with lake area and conductivity and a negative trend with increasing elevation, whilst the littoral diatom α -diversity increased significantly with conductivity and lake water temperature. Planktic diatom α -diversity significantly decreased with lake area and depth. August water temperature, total phosphorus, conductivity and lake depth explained a significant part of the variation and were significantly correlated with pairwise β -diversities in the data sets, but spatial and shared effects of space

and environment were more important for planktic and littoral diatoms. A null model approach based on assemblages' dissimilarities revealed that the structure of littoral and planktic assemblages was predominantly stochastic. In contrast, sedimentary diatoms were formed by both deterministic and stochastic processes. Abundant and widespread species contributed a large part to the assemblage β -diversity. The results point to a stronger role of niche assembly in sedimentary than for littoral and planktic diatoms. Dispersal limitation, in turn, is likely to contribute to the spatial patterns and stochastic assembly processes observed for littoral and planktic diatoms.

Keywords Diatom diversity · Dispersal · Mountain lakes · β -diversity

We dedicate this publication to our colleague and friend Dr Wolfgang Kuefner, who died in a fatal accident during a ski tour in the mountains shortly after successfully passing his PhD. As a member of our mountain lake team, he actively supported us in our fieldwork and was a valuable discussion partner whom we miss very much.

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Introduction

One of the most important goals of diatom research is to understand the spatial patterns of diatom diversity. The species diversity of a region is composed of α -diversities, i.e. the number and abundance of species in local communities, and β -diversities, i.e. the differences in the composition of local communities (Whittaker, 1972). For diatom α -diversity, especially the role of altitude is controversial. In theory, decreasing α -diversity along the altitudinal gradient can be expected as the number of taxa that can cope with increasingly harsh conditions becomes smaller.

However, a study of subarctic ponds along an elevational gradient from 8 to 887 m a.s.l. (metres above sea level) found no influence of elevation on benthic diatom richness (Heikkinen et al., 2022). Another study of Chinese, Spanish and Norwegian streams found either non-significant, decreasing or unimodal patterns of benthic diatoms along the elevational gradient (Wang et al., 2020). In turn, Blanco et al. (2020) and Taxböck et al. (2020) detected increasing species richness of benthic diatoms with increasing altitude in Mediterranean mountain ponds and Swiss springs, respectively. For lakes in the Alps, elevational α -diversity patterns of diatoms remain unclear.

Another important question in diatom ecology is to what extent spatial and environmental factors influence the β -diversity of diatoms (Heino & Soininen, 2005; Soininen et al., 2007). Long environmental gradients may increase the importance of environmental factors, whilst dispersal limitation is promoted by large spatial extent (Keck et al., 2018) or strong topography (Benito et al., 2018). In general, the likelihood of organisms dispersing in more connected systems such as streams (Vilmi et al., 2017) is less limited compared to ponds or lakes (Heino et al., 2015; Shurin et al., 2009). For lakes in the northern European Alps, an influence of dispersal limitation is likely as elevational differences of mountains between lakes can be more than 2000 m. However, different types of assemblages from a lake may be disparately affected by dispersal processes. For example, dispersal effects are more likely for planktic and benthic assemblages, which are easily attached to water birds or waterborne insects than for sedimentary assemblages. In turn, short-term dispersal processes may be less important for sedimentary diatoms because one sample integrates diatoms from several seasons.

The influence of dispersal related factors has important consequences regarding the use of diatoms as paleolimnological proxies or as bioindicators (Lebourcher et al., 2020). In this context, it is important to understand how the biological community structure responds to changes of environmental conditions and to which extent spatial constraints influence community patterns. In a 468-lake set in the USA, Winegardner et al. (2015) found that environmental and spatial variables explained a similar part of the variance in sedimentary and planktic assemblages and studies from tropical reservoirs are in line with these findings (Bartozek et al., 2019; Zorzal-Almeida et al., 2017).

However, it is less clear, if benthic and planktic diatoms show comparable patterns. Consequently, we aimed to investigate whether α - and β -diversity patterns are congruent amongst sedimentary, littoral and planktic diatoms in the mountain lakes of the northern European Alps using a large altitudinal gradient set (760–2,460 m a.s.l.).

The relative contribution of local environmental variables and spatial predictors was evaluated and the importance of stochastic versus deterministic processes was measured. These complementary approaches were used to disentangle the effects of unmeasured yet important environmental factors and dispersal processes that both may lead to spatial patterns in community structure.

Based on the approaches mentioned, the following hypotheses were tested:

- (1) Along the altitudinal gradient, diatom α -diversity decreases as environmental conditions become harsher at higher altitudes, selecting for a few adapted species.
- (2) The influence of spatial variables on diatom β -diversity is weaker with sedimentary diatoms than with littoral and planktic diatoms due to the integration of introduced diatoms across several seasons and the short-term dispersal of littoral and planktic diatoms by birds and insects.
- (3) Dispersal limitation contributes to spatial patterns in β -diversity amongst littoral and planktic diatoms because most lakes are isolated.

Methods

Study sites

The 43 study lakes are in Bavaria (Germany) and Tyrol (Austria) and span a longitudinal gradient of 220 km and a latitudinal gradient of 50 km (Fig. 1).

Most lakes of this study are located on carbonate bedrock and are well buffered, as reflected by pH values between 8 and 9 (Table S1). The altitudinal gradient comprises the vegetation zones of montane forest (750–1400 m a.s.l.), subalpine forest (1400–1700 m a.s.l.) and alpine meadows (1700–2500 m a.s.l.). In this region, the montane forest is dominated by beech (*Fagus sylvatica* L.),

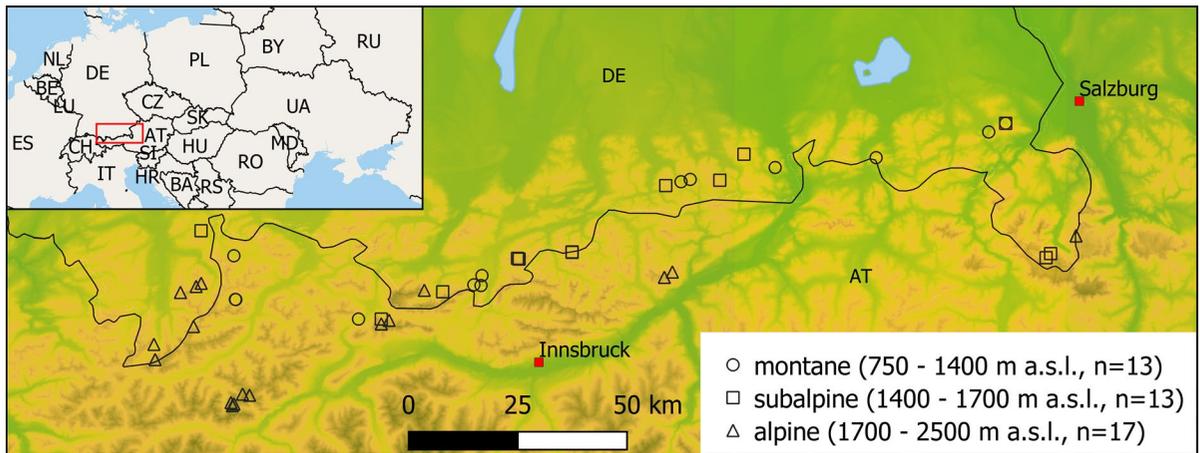


Fig. 1 Geographical and zonal locations of the selected lakes in the northern Alps in Austria and Germany. Background map is based on SRTM and Natural Earth Data

spruce [*Picea abies* (L.) H.Karst] and maple (*Acer pseudoplatanus* L.); the subalpine forest mainly consists of spruce and pine at the ecotone to bare meadows (*Pinus mugo* ssp. *Mugo* Turra). In alpine meadows, shrubs (e.g. *Rhododendron hirsutum* L.), grasslands (e.g. *Carex sempervirens* Elliott) and fell-fields [e.g. *Noccaea rotundifolia* (L.) Moench] mostly predominate.

Most lakes were formed by cirque glaciers and are typically small (<3 ha) and shallow (<10 m) (Table S1) with a single deep zone. Two of the lakes are karstic; they are nearly round and have a higher depth-to-surface ratio than the other lakes. Six of the lakes are polymictic, and macrophytes are found in 26 of the 43 lakes sampled.

Sampling and laboratory procedures

The 43 lakes were sampled twice during the ice-free period: once between June and mid-August and once between August and November. Thirty-six lakes were investigated in 2016 and seven in 2017. On the first sampling date, lake bathymetry was determined with an echo sounder (Lawrence HDS8, Oslo, Norway) and subsequently, a buoy was installed, attached by rope to a stone at the deepest point of each lake. Temperature loggers (Onset Pendant UA-001-64 HOBO, Bourne, USA) were mounted on the rope 0.5 m above the ground and 0.5 m below the water surface. During most of the ice-free period, the loggers in the lakes were exposed to assess the temperature regime

and the lake's mixing type. On both sampling dates, physical variables (temperature, oxygen saturation, pH, and electrical conductivity at 25 °C) were measured with a multiprobe (WTW 350, Weilheim, Germany) in one-metre steps above the deepest point of each lake. After measuring the Secchi depth, 0.5 L of a mixed water sample—comprising the euphotic zone (CEN, 2015)—was collected with a hose sampler. One half of the water sample was filtered (0.45 µm) on-site and stored at 4 °C together with the unfiltered rest until further processing at the laboratory.

Another litre of water was taken from the euphotic zone with the hose sampler and preserved with Lugol's solution to analyse planktic diatom communities (Thronsen, 1978). Planktic samples were taken from every lake on the first sampling date. Periphytic diatom assemblages were assessed by scraping off the diatom communities of five stones at depths of between 20 and 50 cm in the northern littoral zone of each lake with a single-use toothbrush (DIN, 2014). At nine sites there were no stones present in the littoral zone, so no samples were taken there to maintain consistency of the substratum. On the second sampling date, sediment cores were taken from the deepest point of each lake with a gravity corer (Uwitec, Mondsee, Austria) to assess the sedimentary diatom communities (mostly composed of dead individuals) from all 43 lakes according to Küfner et al. (2020a, b, c). Hence, three diatom assemblages could be sampled: planktic diatoms from the open water, periphytic diatoms from the northern littoral zone

and sedimentary diatoms (the uppermost centimetre of each sediment core) from the deepest point of each lake.

All chemical analyses were carried out at the laboratory of the Limnological Research Station Iffeldorf at the Technical University of Munich, Germany. Standard colorimetric methods using a Hitachi 150–200 photometer (Chiyoda, Japan) were applied to determine the concentrations of total phosphorus (Murphy & Riley, 1962), nitrate-N (Navone, 1964), ammonia-N (DIN, 1983) and silica. The concentrations of major ions (calcium, magnesium and sodium) were analysed using a cation chromatograph (Thermo Scientific, ICS-1100, Waltham, USA).

Planktic diatom samples (1 L) were filtered with 0.45- μm syringe filters and the residue on the filters was further processed (Nixdorf et al., 2014). The uppermost centimetre of each sediment core was used to assess the sedimentary diatom assemblages present. The residue on the filters of the planktic samples, the sediment samples and the littoral samples were processed in the same way: preparation of the diatoms was carried out according to van der Werff and Macan (1955). A total of 500 valves were identified in each case using a Leica DNM microscope (Wetzlar, Germany) at $\times 1000$ magnification to analyse the composition of the diatom samples. Eleven of the 43 planktic samples were excluded from the data analysis because they contained an insufficient number of valves. Taxa were counted at the species level and where possible, at the subspecies level. Individuals that could not be identified were given working names. Standard literature was used for identification (Krammer, 2000, 2002; Krammer & Lange-Bertalot, 1991a, b, 1997a, b; Lange-Bertalot, 2001; Lange-Bertalot et al., 2017).

Data analysis

For each sample of the three assemblages, α -diversity was computed as species richness and Shannon diversity. Both measures of α -diversity were included as they are frequently used in the context of conservation (Spellerberg & Fedor, 2003) but may reveal different patterns along environmental gradients (Stirling & Wilsey, 2001). Differences in mean α -diversity amongst the assemblages were assessed with the Wilcoxon Test as diversities were not distributed normally (Wilcoxon, 1945). Relations between

environmental variables and α -diversity measures were investigated using linear regression models and R^2 -values were calculated for significant models. The environmental variables used were selected based on variation inflation factors (see below): altitude (“alt”), lake area (“area”), lake depth (“depth”), nitrate-N (“NO3”), total phosphorous (“TP”), silicate (“Si”), pH, conductivity (“cond”), August bottom temperature (“ABT”) and August surface temperature (“AST”).

The mean and pairwise β -diversity of diatom communities was calculated for sedimentary, littoral and planktic assemblages for abundance and incidence data, based on the method proposed by Baselga and Orme (2012). For the abundance data, the multiple-site Bray–Curtis dissimilarity (β_{tot}) was computed and then partitioned into its “abundance balanced variation” (β_{bal}) and “abundance gradients” (β_{gra}) components (Baselga, 2017). For incidence data, β -diversity was calculated as a Simpson diversity (β_{sim}) and then partitioned into its component for turnover (representing the Sorensen dissimilarity which measures species replacement) (β_{sor}) and nestedness (representing the nestedness component of the Sorensen dissimilarity, reflecting species loss) (β_{sne}) following Baselga (2010). The contribution to abundance and incidence-based β -diversity (SCBD) of each species was assessed according to Legendre and De Cáceres (2013) using Hellinger-transformed data. The relationship between SCBD-values and species abundance and occurrence was modelled using polynomial regression models.

The effect of spatial, environmental and altitudinal distance on total β -diversity (β_{tot} , β_{sim}) and its components (β_{bal} , β_{gra} , β_{sor} , β_{sne}) were investigated with partial Mantel tests (Borcard et al., 1992). Significance levels and r-values were calculated for each combination whilst controlling for the other distance matrices to obtain the exclusive effect values of the factor of interest. Moreover, the decay of assemblage similarity with spatial, altitudinal and environmental distance was assessed by fitting negative exponential functions using the “decay.model” function in the “beta part” package (Baselga & Orme, 2012). This method provides additional information compared to Mantel tests through the shape of the regression line (Dray et al., 2020). Distance decay analysis of the abundance and incidence data were complemented with variation partitioning to investigate the proportion

of variance explained by environmental and spatial variables using Euclidean distances (Borcard et al., 1992).

To select the environmental variables used in distance decay analysis and variation partitioning, separate redundancy analysis (RDA) models for sedimentary, littoral and planktic diatom assemblages were computed based on Hellinger-transformed assemblage data (Legendre & Gallagher, 2001). Only variables with variance inflation factors less than five for all data sets were included in the RDAs. VIF's were calculated and variables were selected with the "vifstep" function in the "usdm" R package (Naimi, 2017). The same ten variables were selected for each dataset and used for all further calculations. Pearson correlations were calculated for these variables, and *P*-values were Bonferroni–Holm corrected. Based on the results, correlation plots were produced using the "corrplot" function (Wei & Simko, 2017). All variables except for altitude and pH were log transformed and the full data set was scaled before RDA using the "scale" function in "vegan". Only variables that were identified by forward selection using the "ordiR2step" function in "vegan" ($P < 0.05$) were incorporated into the final environmental distance matrix (Blanchet et al., 2008). The altitudinal distance matrix used in distance decay analysis and variation partitioning was calculated based on Euclidean distances between sites. Distance-based Moran's eigenvector maps (db MEM) based on the geographical coordinates of the lakes were used in variation partitioning (Dray et al., 2006) to explore spatial effects. Eigenvectors were selected using the "mem.select" function in the "ade4" R package. This function runs a forward selection based on R^2 -values after a global test of significance (Bauman et al., 2018). The significance of each MEM was assessed with the "moran.randtest" function that computes Moran's index and calculates *P*-values using random permutations. To measure the relative strength of stochastic versus deterministic processes, a null model approach was applied using the "tNST" function in the "NST" R package (Ning et al., 2019). Null models were calculated for all three diatom data sets and abundance data using the Bray–Curtis distance and incidence data using the Jaccard index. This function produces results ranging from 0 to 100, with values below 50, indicating a prevalence of deterministic processes and values above 50, denoting stochasticity. The results

for the data sets were compared by ANOVA, PAN-ANOVA and PERMANOVA with 1000 resampling runs. All the analyses were computed using version 3.6.6 of the "R" free statistics software, except for tNST analysis, which was conducted using version 4.1.3 (R Core Team, 2013). Data curation was facilitated using the "dplyr" package (Wickham & François, 2014).

Results

Environmental variables

Variables with VIFs < 5 were altitude ("alt"), lake area ("area"), lake depth ("depth"), nitrate-N ("NO₃"), total phosphorous ("TP"), silicate ("Si"), pH, conductivity ("cond"), August bottom temperature ("ABT") and August surface temperature ("AST"). A significant negative Pearson correlation was found in all data sets between cond and alt ($P_{\text{sed}} = 0.007$, $r_{\text{sed}} = -0.661$, $P_{\text{lit}} = 0.006$, $r_{\text{lit}} = -0.681$, $P_{\text{pla}} = 0.013$, $r_{\text{pla}} = -0.650$), cond and pH ($P_{\text{sed}} = 0.018$, $r_{\text{sed}} = -0.512$, $P_{\text{lit}} = 0.031$, $r_{\text{lit}} = -0.495$, $P_{\text{pla}} = 0.050$, $r_{\text{pla}} = -0.488$) and ABT and depth ($P_{\text{sed}} = 0.041$, $r_{\text{sed}} = -0.597$, $P_{\text{lit}} = 0.034$, $r_{\text{lit}} = -0.625$, $P_{\text{pla}} = 0.024$, $r_{\text{pla}} = -0.651$, Fig. S1).

α -diversity

The mean species richness and Shannon diversity were significantly higher for sedimentary and littoral diatom assemblages than for planktic assemblages (Wilcoxon Test, $P < 0.001$; Fig. 2).

Species richness of sedimentary samples was negatively correlated to altitude ($P = 0.02$, $R^2 = 0.10$) and positively correlated to area ($P < 0.001$, $R^2 = 0.21$), depth ($P = 0.02$, $R^2 = 0.10$) and conductivity ($P = 0.01$, $R^2 = 0.12$). Positive correlations were detected between littoral diatom richness and conductivity ($P = 0.04$, $R^2 = 0.10$), ABT ($P < 0.001$, $R^2 = 0.22$) and AST ($P = 0.01$, $R^2 = 0.18$), whilst a negative correlation was found for planktic diatom richness and depth ($P = 0.01$, $R^2 = 0.17$, Table 1; Fig. S2). The Shannon diversity of sedimentary diatom assemblages was positively correlated with area ($P = 0.04$, $R^2 = 0.08$) and positively correlated with conductivity ($P = 0.04$, $R^2 = 0.10$) for littoral diatoms. The Shannon diversity of planktic diatoms was negatively correlated to area

($P < 0.001$, $R^2 = 0.21$) and depth ($P < 0.001$, $R^2 = 0.24$, Table 1; Fig. S3).

β -diversity and community assembly

The β -diversities amongst the lakes were generally high (β_{tot} : 0.925–0.964; β_{sor} : 0.926–0.954), and the component for the balanced variation (β_{bal}) and turnover (β_{sim}) always accounted for the main part of the total β -diversity (Table 2).

Significant variables of the RDA models chosen by forward selection ($P < 0.05$) were TP, AST and depth

for sedimentary and planktic diatom assemblages. Conductivity and AST had a significant effect on littoral diatoms (Table 3).

Mantel tests and negative exponential regression models produced similar results when comparing species dissimilarity with environmental, geographical and altitudinal distance (bold values in Table 4). For five combinations, either Mantel tests or regression models indicated a significant correlation (italics in Table 4). The abundance- and incidence-based dissimilarity of all assemblages increased significantly with increasing environmental distance except

Fig. 2 Boxplots for species richness and Shannon diversity in sedimentary (“S”, $n = 43$), littoral (“L”, $n = 34$) and planktic (“P”, $n = 32$) diatom assemblages. Asterisks indicate significantly higher mean values for sedimentary and littoral data compared to planktic data (Wilcoxon Test: $P < 0.001$)

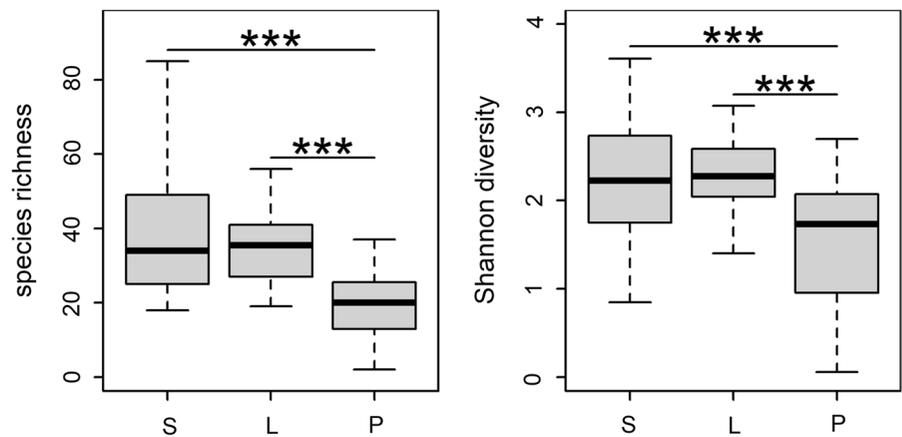


Table 1 Results of linear regression models for species richness and Shannon diversity of sedimentary (“S”), littoral (“L”) and planktic (“P”) diatom assemblages along environmental gradients

Variable	Richness		Variable	Shannon-Index	
	<i>P</i>	<i>R</i> ²		<i>P</i>	<i>R</i> ²
S Altitude	0.02	0.10	S Area	0.04	0.08
S Area	<0.001	0.21	L Conductivity	0.04	0.10
S Depth	0.02	0.10	P Area	<0.001	0.21
S Conductivity	0.01	0.12	P Depth	<0.001	0.24
L Conductivity	0.04	0.10			
L ABT	<0.001	0.22			
L AST	0.01	0.18			
P Depth	0.01	0.17			

Table 2 Mean β -diversity values for abundance and incidence data for sedimentary (“S”), littoral (“L”) and planktic (“P”) diatom assemblages

	β_{tot}	β_{gra}	β_{bal}	β_{sor}	β_{sne}	β_{sim}
S	0.964	0.002	0.962	0.954	0.022	0.932
L	0.925	0.003	0.922	0.926	0.020	0.906
P	0.954	0.007	0.947	0.942	0.033	0.909

Table 3 Percent of explained variance (“Var.”), *F*-values and *P*-values based on Monte Carlo permutation tests for variables selected by forward selection for sedimentary (“S”), littoral (“L”) and planktic (“P”) diatom communities

ANOVA				
	Variable	Var. (%)	<i>F</i>	<i>P</i>
S	depth	2.7	1.83	0.013
	TP	3.7	2.51	0.002
	AST	2.9	1.96	0.006
L	cond	2.1	1.87	0.016
	AST	2.7	2.41	0.005
P	depth	6.1	3.06	0.006
	TP	5.2	2.63	0.006
	AST	4.0	2.04	0.025

Table 4 Model statistics for partial Mantel tests and exponential regression models for the distance decay of β -diversity along with environmental distance, geographical distance and altitudinal distance for sedimentary (“S”), littoral (“L”) and planktic (“P”) assemblages. Statistical tests and regression models were calculated for pairwise β -diversity values derived from incidence data (β_{sor}) and its components for turnover and nestedness (β_{sim} , β_{sne}) as well as for

for planktic assemblages when using incidence data. In turn, planktic assemblages were significantly less similar with increasing lake distance, whilst for littoral diatoms, this was only true for the components representing Simpson diversity and abundance gradients. Dissimilarity of sedimentary incidence data significantly decreased with altitudinal distance (Table 4; Figs. S4–S9).

The contribution of individual species to β -diversity (SCBD) correlated well with species abundance and the number of lakes (N_{lake}) for all data sets using species incidence and abundance data, except for sedimentary and littoral species incidence data (Figs. S10, S11). The most abundant species had above-average SCBD-values, indicating that these

abundance data (β_{tot}) and its components for balanced variation and abundance gradients (β_{bal} , β_{grad}). *P* = *P*-value, *r* = Mantel *r*-value, *ps. R*² = pseudo *R*². Bold font indicates the significance of both the Mantel test and the exponential regression model and italic type indicates the significance of either the Mantel test of the exponential regression model

	S				L				P			
	Mantel test		Regression		Mantel test		Regression		Mantel test		Regression	
	<i>P</i>	<i>r</i>	<i>P</i>	<i>ps. R</i> ²	<i>P</i>	<i>r</i>	<i>P</i>	<i>ps. R</i> ²	<i>P</i>	<i>r</i>	<i>P</i>	<i>ps. R</i> ²
Environmental distance												
β_{sim}	0.001	0.019	0.044	0.010	0.103	0.125	0.200	0.016	0.242	0.041	0.520	0.002
β_{sne}	0.743	0.452	<i>0.002</i>	<i>0.510</i>	0.194	0.082	0.360	0.006	0.342	0.025	0.800	0.001
β_{sor}	<i>0.001</i>	<i>0.091</i>	0.060	0.010	0.007	0.226	0.010	0.052	0.148	0.083	0.340	0.007
β_{bal}	0.007	0.166	0.010	0.027	0.018	0.204	0.020	0.042	0.014	0.170	0.010	0.032
β_{grad}	0.779	– 0.051	0.500	0.003	0.770	– 0.103	0.550	0.008	0.362	0.029	0.750	0.001
β_{tot}	0.005	0.171	0.010	0.029	0.026	0.193	0.030	0.038	0.002	0.215	0.010	0.048
Geographical distance												
β_{sim}	0.324	0.023	0.122	0.009	0.024	0.153	0.043	0.024	0.004	0.173	0.004	0.031
β_{sne}	0.536	– 0.008	0.198	0.005	0.998	– 0.139	<i>0.045</i>	<i>0.019</i>	0.504	– 0.009	0.887	0.001
β_{sor}	0.319	0.024	0.283	0.004	0.089	0.095	0.148	0.009	0.008	0.223	0.008	0.054
β_{bal}	0.320	0.023	0.679	0.001	0.380	0.001	0.765	0.001	0.001	0.287	0.001	0.100
β_{grad}	0.530	– 0.008	0.904	0.001	0.001	0.150	0.001	0.201	0.999	– 0.187	0.037	0.034
β_{tot}	0.320	0.024	0.653	0.001	0.117	0.004	0.218	0.009	0.002	0.230	0.001	0.063
Altitudinal distance												
β_{sim}	0.060	0.095	<i>0.030</i>	<i>0.017</i>	0.297	0.042	0.244	0.008	0.158	0.055	0.276	0.004
β_{sne}	0.408	0.009	0.995	0.001	0.487	– 0.003	0.689	0.001	0.687	– 0.037	0.649	0.001
β_{sor}	0.019	0.138	0.006	0.032	0.234	0.054	<i>0.032</i>	<i>0.021</i>	0.301	0.036	0.496	0.003
β_{bal}	0.131	0.065	0.094	0.009	0.979	– 0.155	0.498	0.003	0.286	0.036	0.322	0.005
β_{grad}	0.972	– 0.103	0.059	0.012	0.926	– 0.129	0.101	0.024	0.494	– 0.008	0.979	0.001
β_{tot}	0.156	0.060	0.116	0.008	0.991	– 0.178	0.337	0.006	0.268	0.039	0.212	0.006

species do not homogenise diatom metacommunities. Selected eigenvectors based on Hellinger-transformed abundance data were MEM 1 (Sed., $P_1=0.008$), MEM 3 and 12 (Lit., $P_3=0.024$, $P_{12}=0.041$) and MEM 1, 2, 6 and 7 (Pla., $P_{1,2,6}=0.006$, $P_7=0.042$) for sedimentary, littoral and planktic assemblages, respectively. Based on incidence data MEM 3 and 5 (Sed., $P_3=0.020$, $P_5=0.009$), MEM 1, 2, 3 and 12 (Lit., $P_1=0.49$, $P_2=0.007$, $P_3=0.022$, $P_{12}=0.009$) and MEM 1, 2 and 9 (Pla., $P_{1,9}=0.005$, $P_2=0.002$) were selected for sedimentary, littoral and planktic assemblages, respectively.

Results for variation partitioning confirmed the principal patterns detected by distance decay analysis. The forward selected variables explained a significant part of variance for all assemblages. The MEMs selected had a greater explanatory power for littoral and planktic assemblages than for sedimentary diatoms. This also accounted for explained variation through shared effects. Unexplained variation was generally lower when using abundance data (Table 5).

Null models based on abundance and incidence data indicate a strong stochastic influence on littoral

and planktic communities. Assembly processes were significantly different for sedimentary diatoms, showing a more balanced deterministic and stochastic influence (Table 6).

Discussion

We compared the patterns of diatom α - and β -diversity for sedimentary, littoral and planktic assemblages within a 43-lake set across the montane, subalpine and alpine region in the northern European Alps. Diatom α -diversity was correlated to altitude, lake depth and area, water temperature and conductivity. The variables explaining a significant portion of community composition were total phosphorus, AST and lake depth for sedimentary and planktic diatoms, as well as AST and conductivity for littoral diatoms. Spatial descriptors and spatial distance were important in explaining littoral and planktic diatom community structure and stochastic community assembly dominated in both groups. In contrast, deterministic and stochastic processes were equally

Table 5 Variation partitioning results for the pure and shared fraction (indicated by “+”) of variance explained by environmental (“E”), spatial (“S”) and altitudinal (“A”) distance as well as unexplained variance (“U”) for abundance and incidence data of sedimentary (“S”), littoral (“L”) and planktic (“P”) diatom assemblages

	Abundance			Incidence		
	S	L	P	S	L	P
E	5	1	7	2	3	4
S	1	2	8	1	4	5
A	0	0	1	1	0	2
E+S	0	3	5	0	0	2
E+A	1	4	0	0	2	0
S+A	0	0	1	0	0	0
E+S+A	0	0	3	1	0	1
U	91	91	78	95	90	87

Table 6 NTS results (“NTS”), standard deviation (“SD”) as well as the F -statistic and P -values for ANOVA, PANOVA and PERMANOVA for pairwise comparison of NTS-values

for sedimentary (“S”), littoral (“L”) and planktic (“P”) assemblages based on Bray–Curtis distance (“BC”) and Jaccard index (“JA”)

Group 1	Group 2	NTS 1	NTS 2	SD 1	SD 2	Δ_{NTS1_NTS2}	F	P_{anova}	P_{panova}	P_{perm}
S _{BC}	L _{BC}	0.492	0.901	0.059	0.039	− 0.409	107,658	<0.001	0.001	<0.001
S _{BC}	P _{BC}	0.492	0.796	0.059	0.074	− 0.304	10,014	0.001	0.004	0.001
L _{BC}	P _{BC}	0.901	0.796	0.039	0.074	0.105	7,063	0.008	0.211	0.453
S _{JA}	L _{JA}	0.606	0.893	0.071	0.049	− 0.287	330,712	<0.001	0.004	<0.001
S _{JA}	P _{JA}	0.606	0.768	0.071	0.079	− 0.162	74,999	<0.001	0.106	0.035
L _{JA}	P _{JA}	0.893	0.768	0.049	0.079	0.125	6,441	<0.001	0.126	0.469

Bold font indicates significance ($P < 0.05$)

important for sedimentary diatoms and spatial patterns were subordinate.

Niche assembly

Our hypothesis that α -diversity decreases with altitude can only be verified for sedimentary diatom richness, but not for littoral or planktic diatoms. This could be due to the fact that sedimentary diatoms integrate climatic conditions over several years, whilst littoral and planktic diatom richness are rather influenced by short-term environmental fluctuations. Other variables additionally explained the variation in α -diversity for all data sets. This underpins the high variability in local diatom diversity patterns along the elevational gradient. For example, in sub-arctic mountain ponds (Heikkinen et al., 2022) and streams (Teittinen et al., 2016), no significant richness elevation pattern was found, whilst a unimodal relationship was detected for a different set of sub-arctic ponds (Teittinen et al., 2017) and a monotonic positive relationship was found for Swiss mountain springs (Taxböck et al., 2020). Combined with these studies, our findings point to the importance of additional mechanisms that act independently of altitude in forming local diatom diversity.

The positive correlation of conductivity with littoral and sedimentary α -diversity probably reflects an influence of alkalinity, which typically correlates with conductivity in mountain lakes (Kamenik et al., 2001). This is in line with the monotonic increase of benthic diatom richness with alkalinity in US streams (Smucker & Vis, 2011), the decrease of diatom richness in fens along a gradient from calcareous to mineral-poor conditions in the western Carpathians (Fránková et al., 2009) and the increase in epilithic diatom richness with conductivity in Swiss mountain springs (Taxböck et al., 2020). Species-specific alkalinity optima (Järvinen et al., 2013) may be coupled to different HCO_3^- uptake efficiencies (Baattrup-Pedersen et al., 2022). Thus, it is likely that alkalinity has a direct effect on diatom α -diversity. However, we do acknowledge that the correlation of conductivity and elevation may mask a direct effect of elevation on sedimentary diatom richness, as suggested by Teittinen et al. (2017).

For sedimentary diatoms, the positive correlation of lake area and depth with α -diversity likely reflects an influence of increasing habitat diversity,

which was correlated to diatom richness in streams and springs (Smucker & Vis, 2011; Taxböck et al., 2020). Sedimentary assemblages integrate diatoms from the whole lake including the pelagic and littoral zone through taphonomic processes and thus reflect the diversity of habitats that is likely to increase with lake size. For planktic diatoms, the negative correlation of α -diversity with lake depth and area probably reflects an effect of lake mixing conditions. This may be through the increased introduction of benthic species under higher mixing frequency in small and shallow lakes. In turn, deep and warm lakes, that tend to be stratified, are frequently dominated by one or only a few taxa (Ossyssek et al., 2020). Our results further show that Shannon diversity and species richness are not interchangeable as a measure of α -diversity, as they are correlated with different environmental variables in some cases. This calls for the application of both measures in diatom studies to assure better comparability. Overall, our results only give a weak indication of the elevational structuring of diatom richness in mountain lakes in the northern European Alps and reveal different processes that control α -diversity amongst sedimentary, littoral and planktic assemblages.

As hypothesised, sedimentary diatom β -diversity was mainly explained by the local environment. The results are in line with previous studies that found environmental filtering effects for sedimentary diatoms in temperate lakes, which may be attributed to the long-term integration of environmental conditions through sedimentary assemblages (Winegardner et al., 2015). The concordance of environmental predictors for sedimentary and planktic assemblage composition reflects the results of previous studies of North American lakes (Winegardner et al., 2015) and tropical reservoirs (Bartozek et al., 2019; Zorzal-Almeida et al., 2017). This indicates that the paleolimnological investigations of diatoms reliably reflect environmental constraints for pelagic diatom assemblages. AST was the sole variable correlating with β -diversity amongst all assemblages, supporting previous paleolimnological studies (Hofmann et al., 2021; Kűfner et al., 2020a, b, c; Kűfner et al., 2020a, b, c). Influence of AST on diatom composition may be through its influence on diatom silicification (Kűfner et al., 2020a, b, c) and due to the coupling of water temperature with lake mixing patterns (Niedrist et al., 2018; Read et al., 2011). In

turn, pure environmental effects were low for littoral diatoms and a shared effect of environment and altitude was more important. This suggests an influence of unmeasured variables intercorrelated with altitude and AST. The significant correlation of TP with the sedimentary and planktic diatom β -diversity reveals a sensitive reaction of the assessed assemblages towards nutrient conditions that ranged from ultra-oligotrophic to mesotrophic. These findings confirm previous results, suggesting an influence of anthropogenic pressure on the share and abundance of Red List species (Ossyssek et al., 2022).

Spatial patterns

The significant correlation between spatial distance and littoral and planktic β -diversity, as well as the explained variation by the selected eigenvector maps reflect either spatial structures amongst unmeasured variables that influence diatom composition or dispersal effects (Leibold & Chase, 2018). The NTS index indicated a strong influence of stochastic processes for littoral and planktic assemblages. These include stochastic birth–death occurrence, i.e. ecological drift, dispersal processes and historical contingency (Ning et al., 2019). Ecological drift may indeed be relevant for diatoms, but this has not yet been directly proven (Remmer et al., 2019). Historical contingencies are known to influence diatom communities, but they ought to influence sedimentary assemblages even stronger than littoral and planktic diatoms (González-Trujillo et al., 2021). Thus, the NTS results suggest that dispersal processes contribute to the observed stochasticity within littoral and planktic diatoms. Dispersal limitation or mass effects can lead to spatial structures of β -diversity and stochasticity (Leibold & Chase, 2018). Evidence for a prevalence of mass effects in planktic and littoral diatom communities remain scarce and even in regions where high migration rates can be expected, only slight indication of mass effects was found (Cottenie, 2005; Michels et al., 2001). In our data set, the contribution of the most abundant species to β -diversity was above average. If mass effects influenced these species, this fact ought to lead to the homogenisation of assemblages, being associated with a lower contribution of these species to overall β -diversity. However, mass effects amongst adjacent lakes cannot be excluded, and they may also influence less abundant species

(Bried & Vilmi, 2022; Lebourcher et al., 2020). In our study, three pairs of lakes were within the same water basin, so they are more likely to be influenced by mass effects than the other lakes were. However, it appears unlikely that this would result in a strong stochastic effect across the whole lake set. More generally, the high overall β -diversity of planktic and littoral diatoms and the significance of the component that represents species loss (β_{Sim}) when using incidence data, further point to dispersal limitation rather than to mass effects. As a result, different evidence suggest a contribution of dispersal limitation to littoral and planktic diatom β -diversity, confirming our initial hypothesis.

Residual variation

Explained variation of variation partitioning for the sedimentary, littoral and planktic abundance data set was relatively low (9%, 9% and 22%, respectively), and it was even lower for incidence data (5%, 10% and 13%, respectively). Such a low amount of explained variation is not unusual in studies investigating diatom metacommunity structure, and it lies within the range of values reported by other studies for diatoms within Europe (6–27%) (Kernan et al., 2009; Szabó et al., 2019, 2018; Teittinen et al., 2017). The inclusion of further environmental variables may increase the explanatory power of the investigated assemblages (Soininen et al., 2021). For sedimentary and planktic diatoms, further important variables may be total organic and inorganic carbon and dissolved organic carbon (DOC) (Vinebrooke & Leavitt, 1999), which are known to be influenced by catchment variables such as land cover (Kamenik et al., 2001) and which may thus vary within our dataset that spans a variety of vegetation zones. Therefore, adding those environmental variables can potentially enhance the explanatory power of pure environmental effects or of shared effects of environment and altitude. For sedimentary diatoms, this is only likely to reinforce the principal pattern detected, namely that environmental gradients are an important driver of diatom metacommunity structure. For planktic and littoral diatoms, the importance of the environmental component may increase and pure spatial effects may decrease if additional environmental variables are spatially structured. An increase in explanatory power can be expected for littoral diatoms if the microhabitat

structure is taken into account (Pla-Rabes & Catalan, 2018). More generally, interspecific interactions do shape diatom community patterns through nutrient competition (Manoylov, 2009), parasitism (Kagami et al., 2007), or grazing (Wigdahl-Perry et al., 2017). Including the composition and density of other biotic groups should also increase the explained variation.

Another factor that may help explain diatom patterns in the study lakes is that of historical legacies (Vyverman et al., 2007). These may lead to priority effects that have already been documented for ostracods (Castillo-Escrivà et al., 2017), aquatic plants (García-Girón et al., 2021) and zooplankton (Leibold et al., 2010; Mergeay et al., 2011). In our dataset, such processes may be caused by the introduction of fish (Chen et al., 2011; Hobbs et al., 2016; Ossyssek et al., 2022) or land-use changes (Martin et al., 2017). Identifying lakes that have been affected by such events and transferring the analytical scheme of this study to downcore assemblages may help interpret historical legacies, yet there are doubts about the completeness and correctness of such information, affecting the ability to track responses of biotic assemblages over time.

A methodological source of residual variation within our study may be that not all samples were collected in the same year. Some seasonal effects such as snow and duration of ice cover or longer-term weather phenomena may have had different effects in the two years of sampling. The impacts on the communities sampled will be greater for littoral and planktic diatoms because sedimentary samples cover several years of sedimentation, levelling out annual patterns. Moreover, previous events may have triggered community-level changes, leading to priority effects (Vass & Langenheder, 2017) that will also increase residual variation.

Conclusion

This study sheds light on the factors controlling diatom metacommunity structure in the mountain lakes of the Northern European Alps. In contrast to our hypothesis, elevation was of minor importance for α -diversity. In turn, alkalinity may be more important for local littoral and sedimentary diatom diversity, whilst habitat diversity and lake stratification may influence sedimentary and planktic diatom

α -diversity, respectively. As expected, sedimentary diatom β -diversity was mainly controlled by environmental factors, whilst planktic and littoral diatom communities also revealed spatial constraints. Dispersal limitation likely contributed to the β -diversity patterns of littoral and planktic diatoms, substantiated by the importance of stochastic effects for both groups. In practice, the minimal spatial impact on sedimentary diatoms suggests that they are reliable bioindicators for total phosphorus, surface water temperature and lake depth, whilst the results for littoral and planktic diatoms may be confounded through stochastic assembly processes. In future studies, the inclusion of water chemical measurements of carbon compounds, the assessment of other biotic groups and historical legacies may explain increased variance.

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Data availability The datasets generated or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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