



# Diversity of benthic diatoms in the Baltic Sea: alpha and beta diversity, environmental drivers, and diversity–biomass relationships

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**ABSTRACT:** Benthic diatoms are crucial for the functioning of ecosystems, but their diversity patterns along large gradients are poorly studied. By using 3 self-collected data sets along large environmental gradients in the Baltic Sea, represented over spatial scales of 60, 1300, and 2300 km, I investigated whether different aspects of diversity follow general patterns or are context- and region-specific. General diversity patterns along different gradients would likely indicate high resilience of benthic diatoms against differences and changes in the environment, whereas context-dependent patterns would possibly suggest that environmental change is likely to modify diatom communities and that region-specific differences should be considered when designing ecosystem management. I investigated the effect of environmental conditions on taxonomic and functional diatom diversity with distance-based redundancy analyses, variability of taxonomic diversity with species accumulation curves, taxonomic and functional aspects of spatial beta diversity with pairwise Bray-Curtis dissimilarity indices and Mantel tests, and diversity–biomass relationships with generalized linear models. The effect of environment on diatom communities was context-dependent, and different factors controlled communities along different gradients. Diversity varied along gradients and correlated with salinity in a U-shaped way. Beta diversity followed a general pattern of high taxonomic but low functional beta diversity along all gradients. Relationships between diatom diversity and ecosystem biomass were weak along all gradients. These results suggest that although the regional diversity of diatoms seems resilient, environmental change is likely to modify the local diversity of diatom communities. Finding out how these changes will affect ecosystem functioning requires further investigation.

**KEY WORDS:** Benthic diatoms · Baltic Sea · Brackish · Taxonomic · Functional · Salinity · Biomass

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## 1. INTRODUCTION

Benthic diatoms, i.e. photosynthesizing microalgae growing on all illuminated submerged surfaces, are crucial for the functioning of aquatic ecosystems. They are the basis for benthic food webs (Lebreton et al. 2011), recycle elements (Merikhi et al. 2021), and stabilize the sediment (Hope et al. 2020). They are major primary producers in non-vegetated sediments (Hope et al. 2020) and strongly contribute to the pro-

ductivity of vegetated ecosystems. It has been suggested that it is production by benthic diatoms that converts seagrass meadows and mangrove forests, i.e. classical Blue Carbon habitats that are among the most productive ecosystems on Earth, from carbon sources to carbon sinks (Chen et al. 2019, Cox et al. 2020). Hence, benthic diatoms have a crucial role in mitigating ongoing climate change. However, despite all evidence of their important ecological roles, the diversity patterns of marine benthic diatoms and

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the effect of their diversity on ecosystem functioning are understudied and poorly known. Here, I used 3 different self-collected data sets from 3 environmental gradients in the Baltic Sea, to resolve whether different aspects of benthic diatom diversity follow general or context-dependent patterns along gradients and whether the diversity of diatoms is connected to ecosystem biomass. General diversity patterns along different environmental gradients would suggest that benthic diatoms are resilient against differences in the environment and, hence, possibly also resilient against environmental change. Context-dependent diversity patterns, on the other hand, would suggest that the ongoing environmental change will likely modify the diversity of benthic diatom communities and that region-specific differences in the environment should be considered when designing environmental management.

Biodiversity is one of the most important aspects of ecology because it has been shown to affect several ecosystem functions, such as productivity (Tilman et al. 2001), stability (Ives & Carpenter 2007), and nutrient cycling (Semchenko et al. 2017) as well as services that ecosystems provide to humans, such as food production (Renard & Tilman 2019). However, biodiversity is currently severely threatened by human-induced changes in the global environment. This has led to increased interest in studying different aspects of biodiversity and its effect on ecosystem functioning; however, due to the immense complexity of natural systems, much is still unknown, and the knowledge gaps compromise the effective management of ecosystems. A good example of an ecosystem in need of effective management and protection is the Baltic Sea. It is a semi-enclosed estuary that is vulnerable to environmental change because it is located in high northern latitudes where the effects of climate change have been and are predicted to continue to be among the strongest (Cohen et al. 2020). The vulnerability of the Baltic Sea is further increased by low species richness caused by a challenging salinity gradient from freshwater to brackish and marine water (Bonsdorff 2006).

Biodiversity patterns in nature are often related to different environmental, spatial, or temporal gradients (Condamine et al. 2012). Gradients have been understudied in community ecology (McGill et al. 2006), but studies conducted along gradients can facilitate dimensions of ecology that would otherwise remain undiscovered, such as consideration of natural heterogeneity and environmental change as drivers of biodiversity patterns (Hewitt et al. 2007). Gradients also allow us to study different perspectives of

diversity, such as alpha and beta diversity. Alpha diversity, i.e. the diversity of single sites, has been frequently studied, and the alpha diversity of many different organisms has been shown to affect ecosystem functioning (Cardinale et al. 2002). Beta diversity, i.e. differences in diversity and composition of communities between sites, has been studied more rarely, and differences and drivers of the beta diversity patterns of different organism groups are still understudied (Antiqueira et al. 2018). However, beta diversity can be as important as alpha diversity for variability in ecosystem functioning, the stability and resilience of ecosystems, and, thus, ecosystem conservation and management (Mori et al. 2018). This is due to the close connection between beta diversity and the connectivity of communities (Thrush et al. 2009). Ecosystems with low beta diversity, i.e. quite similar communities along the gradient, often consist of closely connected sites and are likely resilient against environmental change because the local loss of a species or a function can be replaced from the regional species pool. Ecosystems with high beta diversity, on the other hand, are often less resilient against environmental change because the species or trait composition of a single site is so different from the composition of adjacent sites that replacing a disappeared species or function is difficult.

Biodiversity, such as alpha and beta diversity, can be described using different proxies. Taxonomic species richness is still the most used proxy for the diversity of a community (Torma et al. 2019), but the connection between diversity and ecosystem functioning can often be more effectively resolved using the diversity of traits, i.e. functions of organisms that influence ecosystem properties or species' responses to the surrounding environment (Hooper et al. 2005). The relationship between biodiversity and ecosystem functions has been studied widely, but because of the differences between organisms and geographic regions, no consensus on the biodiversity–ecosystem functioning relationship has been reached (Hagan et al. 2021). Aquatic microorganisms, such as benthic diatoms, have been among the organisms whose diversity–ecosystem functioning relationships have produced the most controversial patterns (Smith 2007). Thus, more research is needed to understand how the diversity of benthic diatoms affects the surrounding ecosystem.

Here, I used 3 self-collected data sets from different environmental gradients and spatial scales (60–2300 km) to study different aspects of benthic diatom diversity because (1) large environmental gradients facilitate a better understanding of the

connection between diversity and environment, (2) using several different environmental gradients simultaneously facilitates resolving the generality or context-dependency of diversity patterns, and (3) a large part of the diversity–ecosystem functioning studies of marine ecosystems have, so far, been experiments (Gamfeldt et al. 2015). Field studies are necessary because they can demonstrate the effect of heterogeneity and complexity of natural ecosystems and, thus, shed light on the connection between diversity and ecosystem functions in the real world. My specific hypotheses were ( $H_1$ ) environmental factors controlling the diversity of communities are context-dependent and vary between regions and spatial scales; ( $H_2$ ) the diversity of diatoms is generally high but variable along environmental gradients; ( $H_3$ ) spatial beta diversity shows a general pattern, i.e. high taxonomic but low functional beta diversity along environmental gradients; and ( $H_4$ ) diversity–ecosystem functioning relationships of different spatial scales show a general significantly positive pattern.

## 2. MATERIALS AND METHODS

### 2.1. Study area and sampling

Samples were collected from 3 different spatial scales in the Baltic Sea (Fig. 1). On all spatial scales, study sites were chosen to represent varying habitats, from sheltered to more exposed sites. On the smallest scale (Spatial scale I; ~60 km), samples were collected from littoral stones in southern Finland, along a gradient from river Karjaanjoki through its estuary, Pojo Bay, to the archipelago of Hanko, and finally to the open sea of the Gulf of Finland. On the second smallest spatial scale (Spatial scale II; ~1300 km), samples were collected from littoral stones along the entire Finnish coastline. On the largest spatial scale (Spatial scale III; 2300 km), samples were collected from the entire Swedish coastline that extends from the northern Baltic Sea to the transition zone from the Baltic Sea to the North Sea. On Spatial scales I and II, salinity changed from ~0 to ~6 along the gradients, which led to biotic communities

changing from freshwater species to brackish species. On Spatial Scale III, the salinity gradient was large (~1–27), and the biotic communities changed completely along the gradient, from freshwater to brackish and, finally, fully marine species.

On Spatial scale I, 51 samples from as many sites were collected in June–July 2017; on Spatial scale II, 37 samples from as many sites were collected in July 2013; and on Spatial scale III, 52 samples from as many sites were collected in August 2018. All data sets were collected in the summer months to avoid confounding seasonal variation in diversity between years. Any annual variation should be minimal based on a previous investigation of alpha diversity through time (Virta et al. 2020a). On all spatial scales, samples were collected from littoral stones following the modified recommendations of Kelly et al. (1998). In total, 5 (Spatial scale II), 10 (Spatial scale I), or 20 (Spatial scale III) stones were collected along the shoreline from depths of 20–50 cm at each site, and diatom samples were collected by scraping the surface (25 cm<sup>2</sup>) of each stone with a toothbrush or

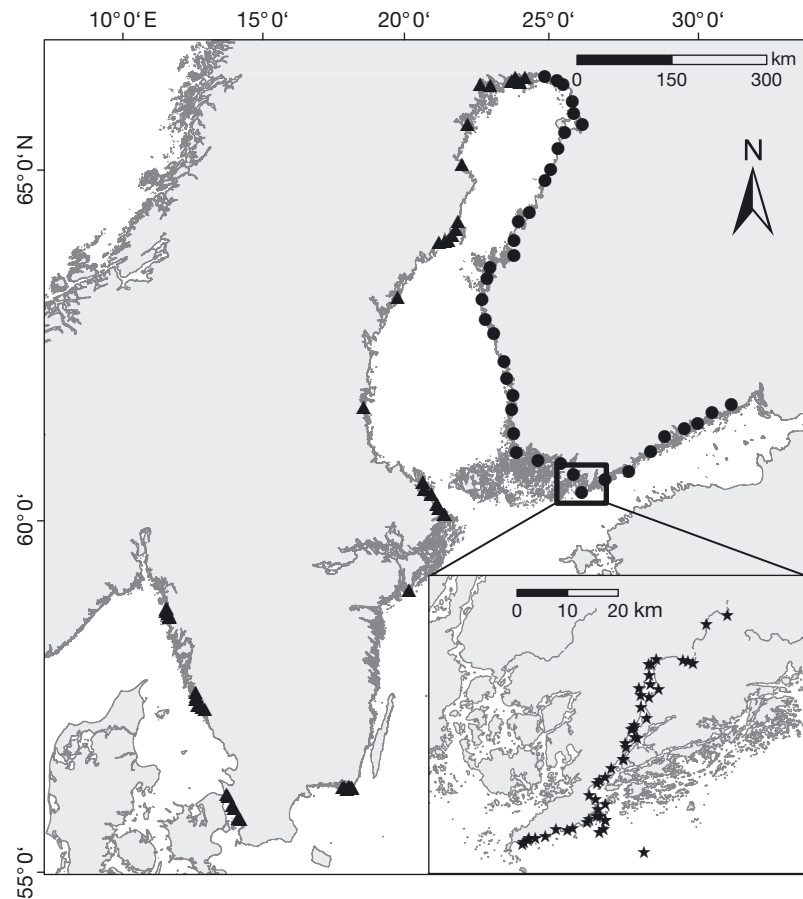


Fig. 1. Sampling sites of Spatial scales I (★), II (●), and III (▲) in the Baltic Sea, Northern Europe

sponge. The accumulated suspension was pooled into a composite sample and stored in cold (+4°C) and dark conditions until further processing. Water temperature, salinity, pH, and dimensions of each sampling stone (length × width × height; except on Spatial scale II) were measured *in situ*, and water samples were collected for further nutrient analyses. On Spatial scales I and III, chlorophyll *a* (chl *a*) samples were also collected at each site by scraping the surface (25 cm<sup>2</sup>) of 2 sampling stones. The accumulated material was pooled into a composite sample and stored in brown bottles and dark conditions until further processing. On Spatial scale III, habitat characteristics were evaluated by classifying the bottom type according to the amount of sediment (classes 1–3) and the amount of macroalgae or vegetation on stones (classes 1–3).

## 2.2. Diatom species and trait characterization, laboratory analyses, and calculations of wind exposure and climatic variables

I analyzed the taxonomic composition of diatoms by boiling the samples collected from littoral stones with hydrogen peroxide (30% H<sub>2</sub>O<sub>2</sub>) to remove organic material, mounting the cleaned diatoms on slides using Naphrax (Brunel Microscopes), and identifying 300 (Spatial scale II) or 500 (Spatial scales I and III) frustules per sample to the lowest possible taxonomic level (typically species level) using a phase contrast light microscope with 1000× magnification. Diatom identification followed Krammer & Lange-Bertalot (1986, 1988, 1991a,b), Snoeijs (1993), Snoeijs & Vilbaste (1994), Snoeijs & Potapova (1995), Snoeijs & Kasperovicienė (1996), and Witkowski (2000). I transformed species counts into relative abundances and verified taxonomic names according to AlgaeBase (Guiry & Guiry 2022).

To study the functional composition of communities, I classified all diatom species according to the following traits: size (biovolume classes: large [ $>1000 \mu\text{m}^3$ ] or small [ $<1000 \mu\text{m}^3$ ]), mobility (mobile [species with raphe] or non-mobile [species without raphe]), attachment (non-attached or adnate or pedunculate, which was further divided to pad-attached or stalk-attached), colonization (colonial or non-colonial), guild (low-profile or high-profile or motile or planktonic; Rimet & Bouchez 2012), and nitrogen-fixing abilities (nitrogen-fixer or non-nitrogen-fixer; Passy 2007). I did this with the above-mentioned species literature as well as Spaulding et al. (2022) and Snoeijs et al. (2002).

In the laboratory, the water samples of Spatial scale I were used for the analyses of total P, NO<sub>2</sub><sup>-</sup> + NO<sub>3</sub><sup>-</sup>, PO<sub>4</sub><sup>3-</sup>, and Si (analyzed with a Thermo Scientific Aquakem 250 automated photometric analyzer), and total N and NH<sub>4</sub><sup>+</sup> (analyzed manually). Water samples of Spatial scale II were used for analyses of total P (analyzed following standard SFS-EN 1189). On Spatial scale II, values of total N, Si, and chl *a* were also extracted from data provided by the Finnish Environment Institute and interpolated to sites using ArcGIS (ESRI 2014). Water samples of Spatial scale III were used for the analyses of NO<sub>2</sub><sup>-</sup> + NO<sub>3</sub><sup>-</sup>, PO<sub>4</sub><sup>3-</sup>, and Si (analyzed with a Thermo Scientific Aquakem 250 automated photometric analyzer), and NH<sub>4</sub><sup>+</sup> (analyzed manually). Chl *a* samples collected on Spatial scales I and III were filtered on Whatman GF/F filters and analyzed with a fluorescence spectrophotometer.

Wind and waves constitute a major disturbance to biotic communities in the sea. Thus, on Spatial scales I and III, I analyzed the wind exposure of each study site by calculating fetch, i.e. the distance over which wind can travel over open water. I measured fetch as the average of distances from the exact study site to the closest shore, island, or islet along 36 (Spatial scale III) or 40 (Spatial scale I) lines that were 9 or 10° apart from each other (Mason et al. 2018). I conducted the calculations using a transparent circular disc and sea charts and the ruler tool in Google Earth.

In studies conducted on large spatial scales, climate can affect the composition of biotic communities. Thus, on the largest spatial scales (II and III), I analyzed the climatic variables of each study site by calculating values of July air temperature and July precipitation (Spatial scale II; Pirinen et al. 2012) or average annual temperature and precipitation (Spatial scale III; WorldClim global climate data) using ArcGIS (ESRI 2014, 2018).

All environmental variables that I used in this study to explain the variation in diatom communities are commonly used explanatory variables and have repeatedly been shown to affect the distribution of benthic diatoms. However, the combination of environmental variables differs somewhat between spatial scales. This is because I gained experience during the study and learned which environmental variables might most effectively explain the variation of diatom communities in my study area and, thus, would be worth including in the study. The means and ranges of all environmental variables measured on each spatial scale are shown in Table S1 in the Supplement at [www.int-res.com/articles/suppl/](http://www.int-res.com/articles/suppl/)

[m712p035\\_supp.pdf](#). Sampling sites and procedures used in sampling and laboratory analyses are more thoroughly described in Virta et al. (2021; Spatial scale I), Virta & Soininen (2017; Spatial scale II), and Virta et al. (2020b; Spatial scale III).

### 2.3. Statistical analyses

Before statistical analyses, I  $\log_{10}$  transformed most of the environmental variables (Spatial scale I: total P, total N,  $\text{NO}_2^- + \text{NO}_3^-$ ,  $\text{NH}_4^+$ ,  $\text{PO}_4^{3-}$ , Si, salinity, fetch; Spatial scale II: total P, total N; Spatial scale III:  $\text{NO}_2^- + \text{NO}_3^-$ ,  $\text{NH}_4^+$ ,  $\text{PO}_4^{3-}$ , Si, salinity, stone volume, fetch, chl *a*) to reduce their skewed distributions. I assessed the statistical dependence between environmental variables on all spatial scales using Spearman's rank correlations ( $r_s$ ), and excluded highly correlated ( $r_s > 0.7$ ) variables from further analyses (Spatial scale II: longitude that correlated with pH and air temperature, and Si that correlated with pH; Spatial scale III: Si, air temperature, precipitation, latitude and longitude that correlated with salinity).

I studied the effect of environmental factors on the species and trait composition of communities on each spatial scale using distance-based redundancy analysis (dbRDA). I constructed the dbRDA using Hellinger-transformed data and Bray-Curtis distance for species composition and Gower's distance for trait composition (Legendre & Anderson 1999). I considered environmental factors with  $p < 0.05$  statistically significant. I used the R package 'vegan' for the dbRDA (Oksanen et al. 2020).

To study diversity patterns along spatial scales, I divided the study sites of each spatial scale into groups according to either the most significant environmental variable (Spatial scales II and III) or all significant variables (Spatial scale I; dividing according to the most significant individual variable failed to effectively divide the study sites into groups) indicated by the dbRDA conducted on species composition. For this, I used hierarchical clustering in the R package 'dendextend' (Galili 2015). I continued by applying species accumulation curves that show the observed species richness of the entire data and the groups formed by hierarchical clustering on each spatial scale. Because the groups contained different numbers of sites, I constructed the species accumulation curves with randomly sampled sites. I used the R package 'vegan' (Oksanen et al. 2020) with the function 'specaccum' and method 'random' with 999 permutations.

I studied the spatial beta diversity of communities on each spatial scale by calculating all pairwise dissimilarities in species and trait community composition. I used abundance data and the Bray-Curtis dissimilarity index (Bray & Curtis 1957). I continued by constructing linear models to illustrate the relationships between dissimilarities and the gradients of the most significant environmental variables indicated by the dbRDA on each spatial scale. I determined the significance of the relationships using Mantel tests with Pearson's correlation and 999 permutations and considered relationships with  $p < 0.05$  statistically significant.

Finally, I studied the relationships between biodiversity and ecosystem biomass of Spatial scales I and III using generalized linear models (GLMs) with linear and quadratic terms and Gamma distribution that does not assume normally distributed errors. To analyze the relationship from different perspectives, I used several different measures for biodiversity. As the measure of taxonomic diversity, I used species richness, Shannon's diversity index (Shannon & Weaver 1962), Simpson's diversity index (Simpson 1949), and Pielou's evenness (Pielou 1966), and as the measure of functional diversity, I used Shannon's diversity index, Simpson's diversity index, and Pielou's evenness. As the measure of benthic biomass, I used chl *a* concentration. I evaluated the deviance explained by each GLM using  $D^2$  values, and considered relationships with  $p < 0.05$  statistically significant.

All statistical analyses were conducted using R version 4.1.2 (R Core Team 2021).

## 3. RESULTS

The observed species richness was 408, 230, and 522 on Spatial scales I, II, and III, respectively, and the average species richness per sample was 55, 34, and 54 on Spatial scales I, II, and III, respectively.

According to the dbRDA models, the taxonomic and functional composition of communities was controlled by different environmental variables on different spatial scales (Table 1, Fig. S1). Water temperature was the most important environmental variable controlling the taxonomic and functional composition on Spatial scale I and the functional composition on Spatial scale II. Salinity was the most important environmental variable controlling the taxonomic composition on Spatial scale II and the taxonomic and functional composition on Spatial scale III. The dbRDA models of different spatial scales explained

Table 1. Distance-based redundancy analyses investigating the effect of environmental variables on the taxonomic and functional community composition on Spatial scale I (60 km), Spatial scale II (1300 km), and Spatial scale III (2300 km). *F* is a measure of how much the response variable is related to the explanatory variable. \*\*\**p* < 0.001; \*\**p* < 0.01; \**p* < 0.05

	Species			Traits	
	<i>F</i>	<i>p</i>		<i>F</i>	<i>p</i>
<b>Spatial scale I</b>					
Water temperature	15.259	0.001***	Water temperature	5.947	0.001***
NH <sub>4</sub> <sup>+</sup>	5.111	0.001***	NO <sub>2</sub> <sup>-</sup> + NO <sub>3</sub> <sup>-</sup>	3.159	0.022*
NO <sub>2</sub> <sup>-</sup> + NO <sub>3</sub> <sup>-</sup>	4.066	0.002**	NH <sub>4</sub> <sup>+</sup>	2.379	0.060
Fetch	3.308	0.001***	Total P	1.546	0.153
Stone volume	2.501	0.013*	Stone volume	1.097	0.337
PO <sub>4</sub> <sup>3-</sup>	2.402	0.014*	Salinity	1.005	0.360
Total N	2.304	0.020*	Total N	0.869	0.449
Salinity	2.177	0.029*	Si	0.800	0.517
Total P	1.837	0.055	PO <sub>4</sub> <sup>3-</sup>	0.782	0.540
Si	0.693	0.721	Fetch	0.699	0.596
pH	0.685	0.782	pH	0.453	0.802
Explained variation: 50.9%			Explained variation: 32.5%		
<b>Spatial scale II</b>					
Salinity	4.725	0.001***	Water temperature	7.482	0.002**
Water temperature	3.916	0.001***	Salinity	4.080	0.015*
Total N	1.928	0.014*	Total P	1.805	0.145
Latitude	1.827	0.033*	Latitude	1.232	0.267
Precipitation	1.154	0.266	Precipitation	0.678	0.574
Air temperature	1.026	0.364	Air temperature	0.516	0.707
Total P	0.920	0.558	pH	0.477	0.765
pH	0.777	0.747	Total N	0.431	0.795
Explained variation: 36.8%			Explained variation: 37.4%		
<b>Spatial scale III</b>					
Salinity	13.477	0.001***	Salinity	14.892	0.001***
NH <sub>4</sub> <sup>+</sup>	4.844	0.001***	Water temperature	7.270	0.002**
Sediment amount	3.424	0.003**	PO <sub>4</sub> <sup>3-</sup>	7.201	0.002**
Water temperature	3.284	0.001***	NH <sub>4</sub> <sup>+</sup>	4.737	0.009**
PO <sub>4</sub> <sup>3-</sup>	3.216	0.001***	Sediment amount	2.277	0.072
Fetch	3.065	0.001***	Fetch	2.036	0.100
Vegetation amount	2.893	0.005**	pH	1.962	0.116
NO <sub>2</sub> <sup>-</sup> + NO <sub>3</sub> <sup>-</sup>	2.451	0.008**	Vegetation amount	1.711	0.140
pH	1.790	0.064	NO <sub>2</sub> <sup>-</sup> + NO <sub>3</sub> <sup>-</sup>	1.468	0.177
Stone volume	0.948	0.485	Stone volume	0.822	0.457
Explained variation: 49.0%			Explained variation: 52.0%		

32.5–52.0% of the variation in taxonomic or functional community composition.

Hierarchical clustering effectively divided the samples of each spatial scale into 3 groups (Fig. S2). On Spatial scale I, the groups included 27, 16, and 8 samples on the gradient of all significant environmental variables. On Spatial scale II, the groups included 9, 11, and 17 samples on the salinity gradient from low to high salinity, respectively. On Spatial scale III, the groups included 14, 21, and 17 samples on the salinity gradient from low to high salinity, respectively.

Species accumulation curves showed that on each spatial scale, the taxonomic diversity varied between groups that were formed by hierarchical clustering (Fig. 2). On Spatial scale I, where groups were

formed using all significant environmental variables indicated by the dbrDA, diversity was low in group 1 and high in groups 2 and 3. On Spatial scale II, where salinity varied between 0.1 and 6.1, diversity decreased along the salinity gradient. On Spatial scale III, where salinity varied between 1.2 and 27.6, samples with low and high salinity had high diversity, whereas samples with medium salinity had low diversity.

On all spatial scales, the pairwise taxonomic dissimilarities between communities were high along the environmental gradient (Fig. 3). The pairwise mean (minimum; maximum) taxonomic dissimilarities were 0.675 (0.236; 0.983), 0.721 (0.213; 0.940), and 0.732 (0.206; 0.990) on Spatial scales I to III, respectively. The pairwise functional dissimilarities

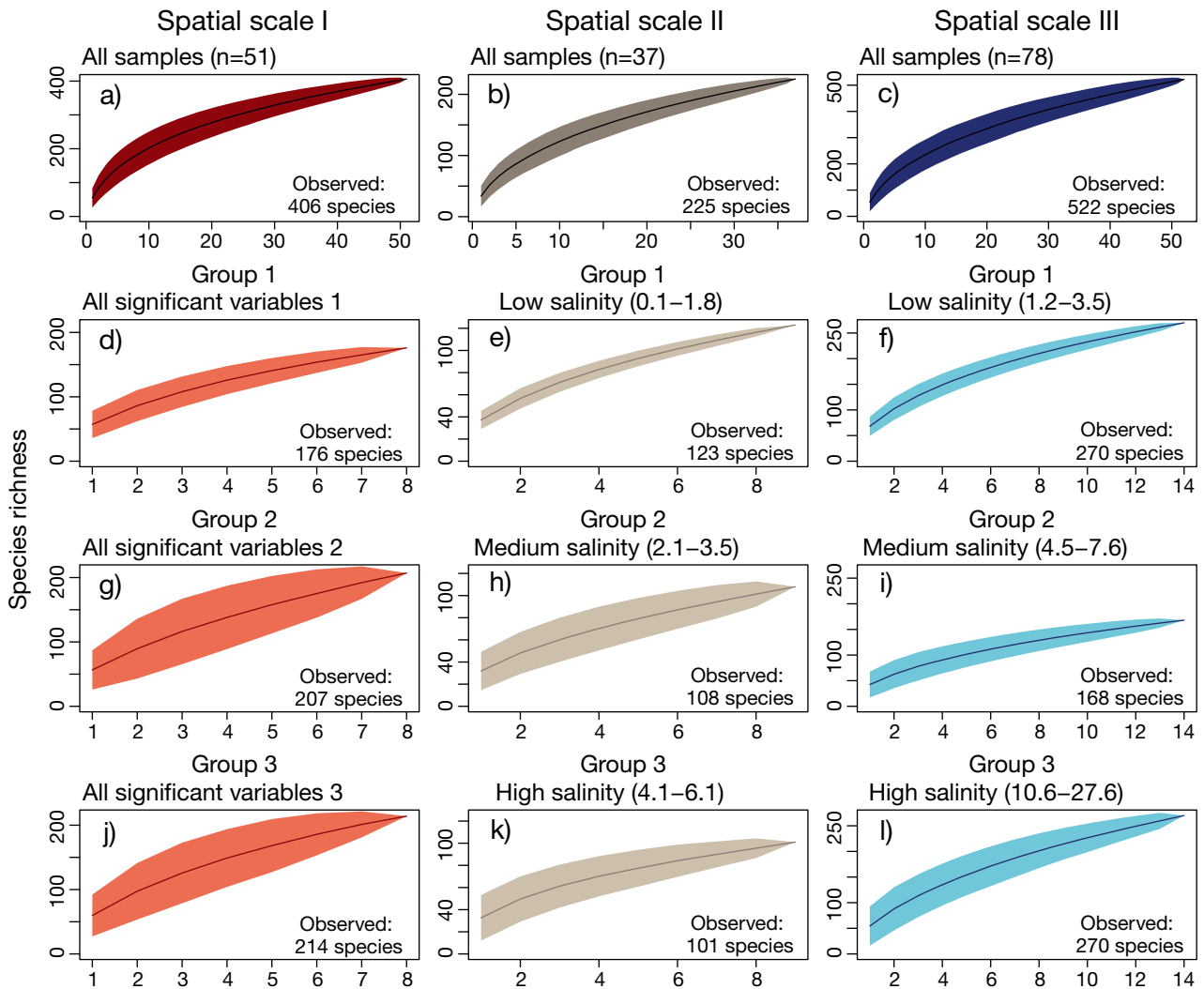


Fig. 2. Species accumulation curves of all samples on (a) Spatial scale I (60 km), (b) Spatial scale II (1300 km), and (c) Spatial scale III (2300 km) and (d–l) samples of groups formed by hierarchical clustering

between communities were considerably lower. The pairwise mean (minimum; maximum) functional dissimilarities were 0.196 (0.023; 0.486), 0.289 (0.007; 0.630), and 0.230 (0.032; 0.577) on Spatial scales I to III, respectively. On all spatial scales, the relationship between environmental gradient and the taxonomic and functional dissimilarity between communities was statistically significant.

The GLMs showed that on Spatial scale I, none of the linear or quadratic terms of taxonomic or functional diversity measures significantly explained ecosystem biomass, and the models including both the linear and quadratic term of each diversity measure explained <5% of ecosystem biomass (Table 2). On Spatial scale III, only taxonomic Shannon's diversity significantly ( $p < 0.05$ ) explained ecosystem biomass, and the models including the linear and quadratic

terms of species richness and Shannon's diversity explained >10% of ecosystem biomass.

#### 4. DISCUSSION

I investigated the biodiversity patterns of benthic diatoms on 3 different spatial scales (60–2300 km) in the Baltic Sea. My aim was to resolve whether different aspects of diatom diversity followed a general pattern across gradients and regions that would make it easier to predict the effects of environmental change on diversity and to manage the environment, or if the diversity patterns were context-dependent and variable between spatial scales and regions. Several aspects considered here, such as the use of different spatial scales and environmental gradients

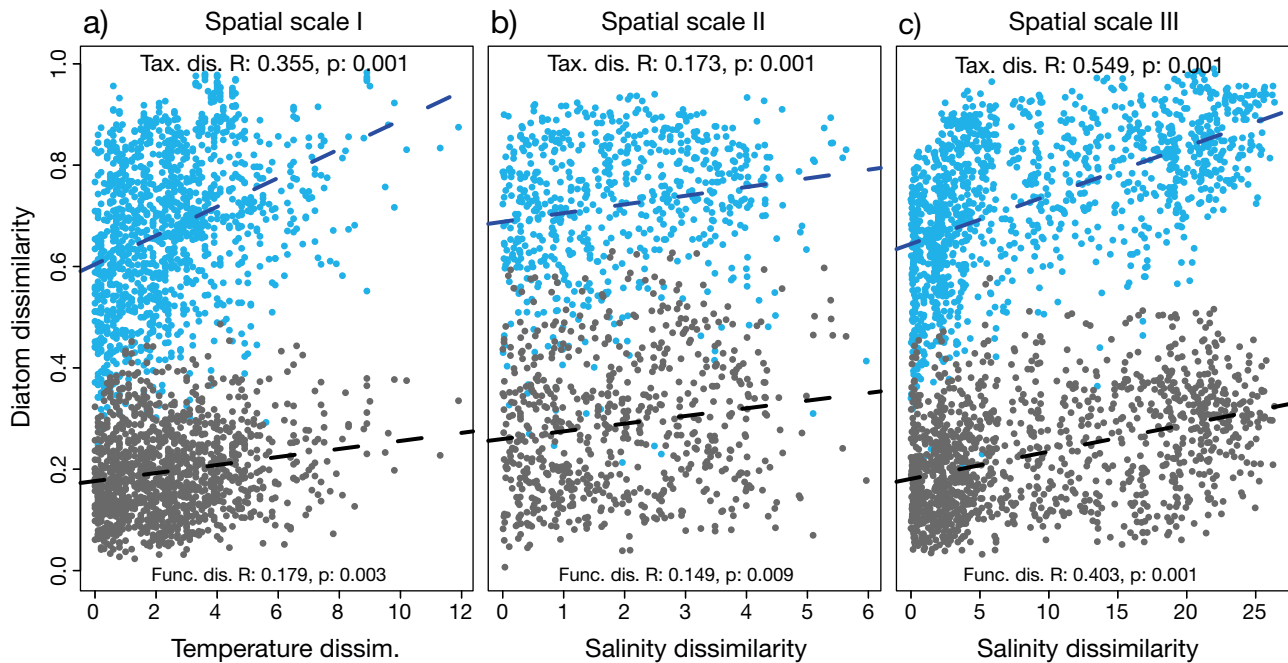


Fig. 3. Relationships between environmental gradient and pairwise taxonomic/functional dissimilarity (Bray-Curtis dissimilarity index) of communities on (a) Spatial scale I (60 km), (b) Spatial scale II (1300 km), and (c) Spatial scale III (2300 km). Dashed lines: linear models fitted to data; blue dots and lines: taxonomic dissimilarity; gray dots and lines: functional dissimilarity

Table 2. Generalized linear models investigating the effect of taxonomic and functional diversity of communities on ecosystem productivity on Spatial scale I (60 km) and Spatial scale III (2300 km).  $D^2$ : proportion of deviance explained by each model. \*\*\* $p < 0.001$ ; \*\* $p < 0.01$ ; \* $p < 0.05$

	Spatial scale I			Spatial scale III		
	p (linear term)	p (quadratic term)	Model $D^2$ (%)	p (linear term)	p (quadratic term)	Model $D^2$ (%)
<b>Taxonomic diversity</b>						
Species richness	0.490	0.543	1.15	0.068	0.062	11.59
Shannon's diversity	0.751	0.747	0.21	0.024*	0.022*	15.39
Simpson's diversity	0.288	0.293	2.63	0.139	0.140	6.56
Pielou's evenness	0.379	0.387	1.80	0.063	0.058	9.67
<b>Functional diversity</b>						
Shannon's diversity	0.269	0.274	2.97	0.564	0.581	2.28
Simpson's diversity	0.242	0.246	4.25	0.728	0.735	2.30
Pielou's evenness	0.350	0.361	2.76	0.456	0.474	2.85

to find general patterns and the functional diversity of diatom communities, have previously been understudied.

#### 4.1. Environmental variables controlling the diversity of diatom communities ( $H_1$ )

As hypothesized, environmental variables that controlled the taxonomic and functional composition

of diatom communities were context-dependent and varied among spatial scales (Table 1, Fig. S1). This indicates that considering region-specific differences is important when trying to predict the effects of environmental change on biotic communities or when planning environmental management strategies. However, general patterns were also found:

**4.1.1. Nutrients.** Nutrients, i.e. different forms of phosphorus and nitrogen, significantly explained community composition on all spatial scales. This



was expected because nutrients have repeatedly been reported to be important drivers for microphytobenthic communities (Thornton et al. 2002, Donato-R et al. 2022). Based on previous studies that have shown P to be the main limiting nutrient in freshwaters (Passy et al. 2018) and N to be the main limiting nutrient in marine waters (Cotiyane-Pondo et al. 2021), I expected the significance of P to be high on Spatial scales I and II, where large parts of samples were collected from sites with low salinity, and the significance of N to be high on Spatial scale III, where most of the samples were collected from sites with high salinity. However, such a pattern could not be detected, as both P and N were among the significant environmental variables on almost all spatial scales. I assume that this is due to the combination of freshwater, brackish, and marine communities on each spatial scale. The result may have been different if parts of gradients with different salinities would have been analyzed separately.

**4.1.2. Salinity and water temperature.** Salinity and water temperature were among the most significant variables for the composition of communities on all spatial scales. The strong effect of salinity on diatom diversity was expected due to similar results in previous large-scale studies on benthic diatoms in the Baltic Sea (Snoeijs 1995, Ulanova et al. 2009). The effect of salinity grew stronger along the size of the salinity gradient from Spatial scales I and II, where salinity varied between ~0 and ~6, to Spatial scale III, where salinity varied between 1.2 and 27.6. This was expected because the intermediate salinities of 5–8 are the tipping point for the diversity of aquatic communities (Remane 1934, Olli et al. 2019) and, thus, a gradient that reaches beyond the tipping point is likely to lead to large salinity-driven changes in the composition of communities. The pronounced effect of water temperature was more surprising, as other studies have shown contradictory results on the effect of temperature on diatom communities (e.g. Soininen 2007, Passy et al. 2018). While temperature may have a direct effect on diatom communities in controlling growth, other factors often override the temperature effect (Anderson 2000). Hence, I assume that the high significance of temperature in this study may stem from the high correlation of temperature with some unmeasured variables, such as biotic interactions or water flow.

**4.1.3. Habitat characteristics.** On Spatial scale III where habitat characteristics (i.e. the amount of sediment and vegetation on the bottom) were considered, they had a high significance on the composition

of communities. Reasons for the significance of such habitat characteristics are diverse. For example, a high amount of vegetation on the bottom can modify the benthic diatom communities by providing microhabitats and by stabilizing sediment (Cox et al. 2020). The importance of habitat characteristics for aquatic communities has been reported before for different organisms, such as benthic macrofauna (Bernard et al. 2014, Gammal et al. 2019), but habitat characteristics have rarely been included in studies concerning microphytobenthic communities (but see Dalu et al. 2020). Based on the findings of this study and some previous studies conducted on Baltic Sea benthic diatoms (Ulanova & Snoeijs 2006, Svensson et al. 2014), including habitat characteristics as explanatory environmental factors allows a better understanding of the diversity patterns of microphytobenthic communities.

**4.1.4. Disturbances.** Disturbances have often been ignored in benthic diatom studies, possibly because they are complex and difficult to measure. However, this study showed that they should be considered when trying to understand the diversity patterns and functions of benthic diatom communities. Disturbance by wind exposure significantly affected the taxonomic composition of communities on both spatial scales where it was included in the models, i.e. Spatial scales I and III. This was expected because wind-induced waves and currents have strong and versatile effects on sessile coastal organisms, especially in practically tideless environments such as the Baltic Sea. The effects of wind on the diversity of communities are both negative and positive because wind-induced waves detach organisms from the substratum (Lunt et al. 2017), but wind-induced currents facilitate distribution (Demmer et al. 2022). Surprisingly, the effect of wind exposure on the functional composition of communities was nonsignificant. This finding disagrees with the results of some previous diatom studies conducted in the Baltic Sea, where functionally different species responded differently to wind and wave disturbance (Ulanova & Snoeijs 2006) and wave action affected the functional composition of diatom communities by increasing the number of attached species compared to mobile species (Svensson et al. 2014).

**4.1.5. Spatial gradient.** On Spatial scale II, the latitudinal gradient significantly explained the taxonomic composition of communities. This agrees with some other studies that have found a strong effect of large-scale variables on diatom communities (Pajunen et al. 2016). However, the spatial effect is typically difficult to distinguish from the environmental

effect, especially in an environment with a strong environmental gradient such as the Baltic Sea, where environmental variables, mainly salinity and temperature, follow a north–south gradient. Moreover, in the marine ecosystem, the importance of spatial gradients may be decreased by the unrestricted water flow between sites and consequent free dispersal of organisms. Hence, I assume that the significance of the latitudinal gradient on Spatial scale II at least partly reflects the environmental gradient of some unmeasured variables.

#### 4.2. High but patchy diversity ( $H_2$ )

As I hypothesized, the taxonomic diversity of diatoms was high on all spatial scales, as the total observed species richness per spatial scale varied between 230 and 522. Such a high diversity is typical for benthic diatoms (Ulanova & Snoeijs 2006, Jamoneau et al. 2022) but it is astonishing in the Baltic Sea, where the challenging brackish water salinity generally results in low species richness of different organisms. Thus, diatoms seem to effectively tolerate different—even challenging—environmental conditions.

However, as hypothesized, diversity varied along the environmental gradient, namely the gradient of salinity (Figs. 2 & S2). Communities were most diverse in low salinity (0–3.5) and high salinity (>10), and least diverse in medium salinity (4–8). This finding agrees with some previous studies on Baltic Sea benthic diatoms that have shown a clear change in taxonomic composition of communities in a salinity range of 5–6 (Snoeijs 1995, Ulanova et al. 2009). It also perfectly agrees with the Artenminimum, i.e. the so-called Remane curve (Remane 1934). Remane's theory suggests that the species richness of different organisms along the salinity gradient from freshwater to marine water is lowest in brackish water of ca. 5–8 because tolerating such salinity is difficult for both freshwater and marine species, and because the global brackish water areas are so small and isolated from each other that the number of species specialized to brackish waters is too small to compensate the absence of freshwater and marine species. However, Remane's concept was designed to apply to macrobenthic organisms, and it has been argued that the theory fails to apply to microorganisms (Pavlouli et al. 2017). My data sets suggest that, for benthic diatoms, Remane's Artenminimum is a perfect match.

#### 4.3. Taxonomic and functional spatial beta diversity ( $H_3$ )

As I hypothesized, beta diversity along environmental gradients followed a general pattern of high taxonomic but low functional beta diversity on all spatial scales (Fig. 3). Thus, species were replaced by taxonomically highly different but functionally similar species along the gradients. It seems that the selection of traits needed for the effective functioning of the diatom community is similar in different environments and that diatom communities are able to maintain that trait selection despite differences in environmental stressors. This might indicate that the functioning of benthic diatom communities is resilient against environmental change.

To date, studies examining the combination of taxonomic and functional beta diversity have been rare. However, quantifying both of these diversity aspects simultaneously can reveal surprising and even contrasting patterns and provide indications on community assembly processes (Villéger et al. 2012).

#### 4.4. Biodiversity–ecosystem biomass relationships ( $H_4$ )

Contrary to my hypothesis, most of the diversity–biomass relationships on Spatial scales I and III were non-significant, and the proportion of biomass explained by the linear and quadratic terms of taxonomic or functional diversity was low (Table 2). The only significant diversity–biomass relationship was found on Spatial scale III, where taxonomic Shannon's diversity explained 15.4 % of the biomass.

Due to the current consensus that diversity determines variation in ecosystem functioning (Hooper et al. 2012, Tilman et al. 2012), the weak impact of diatom diversity on ecosystem biomass in my study was surprising. However, the assumption of positive diversity–ecosystem functioning relationships is strongly based on experimental studies (e.g. van der Heijden et al. 1998, Tilman et al. 2001) and ecological theory, whereas observational field studies have shown variable relationships (Hagan et al. 2021). Moreover, the relationship between microbial diversity and biomass in aquatic ecosystems has been reported to be context-dependent and variable (Smith 2007). I suspect that there are several possible reasons for the non-significant diversity–biomass relationships that I found. For example (1) the range of biomasses at my sampling sites may have been too narrow for clear and statistically convincing diversity–biomass rela-

tionships (Smith 2007); (2) the direct and indirect effects of environment on biomass overrode the effect of diatom diversity; (3) benthic biomass is the result of several different organisms, and the contribution of other organisms, mainly cyanobacteria, may have been strong (Abe et al. 2007); (4) biomass was more strongly related to the dominance of certain highly productive species than to the diversity of the entire communities (Isbell et al. 2013); or (5) finding clear patterns in diversity–biomass relationships may have required different statistical approaches, such as quantile regression models that can reveal trends that remain hidden with mean regression models (Virta et al. 2019).

Even though my results revealed a small effect of diatom diversity on benthic biomass, there is strong evidence that benthic diatoms are crucial for different functions in aquatic ecosystems (Forster et al. 2006, Karsten et al. 2021, Riley & Seekell 2021, Virta & Teittinen 2022). Thus, it would be important to resolve how the current environmental change modifies benthic diatom communities and how these community changes affect the functioning of aquatic ecosystems (Newbold et al. 2020).

## 5. CONCLUSIONS

Benthic diatoms are, in many regions, the most abundant organism group of microphytobenthos and, thus, strong contributors to ecosystem functioning and aquatic food webs. However, the diversity patterns of benthic diatoms are poorly studied in marine and brackish waters. My results from 3 different environmental gradients in the Baltic Sea revealed that some of the patterns of diatom diversity are general and independent of the region, whereas other diversity patterns are context- and region-specific. It seems that environmental change will likely modify the local diversity of diatom communities but regional diversity may be more resilient. This gives hope that benthic diatoms may be able to provide resilience to the functioning of benthic ecosystems during the ongoing environmental change. However, it also indicates that region-specific characteristics should be considered when designing the management of the Baltic Sea and other estuarine areas.

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