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Environmental and spatial drivers of diatom biodiversity in Baltic Sea coastal rock pools

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Abstract

Aquatic biodiversity is largely affected by spatiotemporal variation in environmental stressors. Following global climatic change, understanding the roles and consequences of abiotic variability and dispersal limitation on coastal communities has become increasingly important.

The primary aims of this thesis were to investigate (1) the covariation and drivers of taxonomic and functional diatom spatial alpha diversity; (2) the relative roles of environmental and spatial variables as drivers of diatom taxonomic spatial beta diversity; and (3) patterns and drivers of taxonomic and functional diatom temporal beta diversity in rock pool communities on the Baltic Sea coast. A combination of taxonomic and trait-based diversity indices, regression models, redundancy analyses, Mantel tests and variation partitioning were applied to examine these biodiversity patterns within and across benthic diatom communities in space and time.

The results showed that alpha and beta diversity were structured by pool location, and spatial and temporal variation in the abiotic environment. Overall, taxonomic alpha and beta diversity had a stronger link with spatial variables; functional diversity metrics showed a slight tendency toward environmental variation but were also related to spatial variables. The most influential factors for diatom community composition were consistently water conductivity and pool location. The studied pools were taxonomically diverse but functionally divergent, referring to trait redundancy. Taxonomic and functional alpha diversity followed a rather similar temporal trend and were principally collinear but partly driven by different explanatory factors. Spatial beta diversity was high, indicated by strong distance decay of community similarity along both spatial and environmental distance, the relative influence of the latter increasing with time. Taxonomic temporal beta diversity was higher than functional temporal beta diversity. Some of the pools were characterized by significant temporal turnover, but this change in community composition did not follow clear temporal pattern. While functional temporal beta diversity was explained by several abiotic variables, temporal environmental variability was significantly related to taxonomic temporal beta diversity only.

The results suggested that diatom communities were structured by high spatial and temporal variability in abiotic resources, accompanied by random stochastic processes typical of highly disturbed habitats. As a result, the studied communities were taxonomically heterogeneous yet functionally redundant both in space and time. The results thus highlight the importance of simultaneous application of taxonomic and functional diversity metrics, and the significance of rapid environmental alterations in shaping biodiversity within dynamic coastal diatom communities.

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In Helsinki, 17th April 2026

Sonja Aarnio

Contents

Publications I–III

List of original publications

This thesis is based on the following publications:

I **Aarnio, S.**, Soininen, J. 2021. Taxonomic and functional diversity covary in rock pool microalgal communities despite their different drivers. *Ecology and Evolution* 11, 11852–11873.

II **Aarnio, S.**, Teittinen, A., Soininen, J. 2019. High diatom species turnover in a Baltic Sea rock pool metacommunity. *Marine Biodiversity* 49, 2887–2899.

III **Aarnio, S.**, Soininen, J. 2024. Environmental and stochastic processes drive diatom taxonomic and functional temporal beta diversity. *Marine Ecology Progress Series* 742, 59–71.

The publications are referred to in the text by their roman numerals.

Authors' contributions to the publications

	Paper **I**	Paper **II**	Paper **III**
Original idea and study design	JS, SA	JS, AT, SA	JS, SA
Field and laboratory work	SA	SA, AT	SA
Data analysis	SA	SA	SA
Manuscript preparation	SA, JS	SA, AT, JS	SA, JS
Overall responsibility	SA	SA	SA

SA = Sonja Aarnio[a], AT = Anette Teittinen[a], JS = Janne Soininen[a]. [a]) Department of Geosciences and Geography, University of Helsinki, Finland.

Abbreviations

AIC	Akaike’s information criterion
dbRDA	Distance-based redundancy analysis
FDiv	Functional divergence
FEve	Functional evenness
FRic	Functional richness
GLM	Generalized linear model
GLMM	Generalized linear mixed model
H	Shannon’s diversity
J	Pielou’s evenness
PCoA	Principal component analysis
RDA	Redundancy analysis
S	Species richness
TBI	Temporal beta diversity index

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1 Introduction

Studying community diversity and species distribution patterns along environmental, biotic, spatial and temporal gradients is central to ecology (Leibold *et al.*, 2004). Species distribution into local communities is regulated by scaled habitat features such as dispersal barriers, abiotic environmental conditions and biotic interactions such as competition and herbivory (Soininen, 2007). Dispersal-related processes largely act on a regional scale while abiotic environmental factors are mainly local yet fluctuate also on a temporal gradient (Begon *et al.*, 2006). Quantification of community dynamics requires determining the extent to which communities are regulated by either environmental or spatial factors.

Local biodiversity has traditionally been assessed by taxonomic diversity metrics, largely ignoring variation in species ecological traits such as body size or life-form (Mouchet *et al.*, 2010; Roswell *et al.*, 2021). Furthermore, while many community-level biodiversity studies concentrate on spatial beta diversity (Whittaker, 1960), temporal beta diversity is less studied (Magurran *et al.*, 2019). However, studying all these aspects of biodiversity enhances understanding of the roles of environmental factors and dispersal limitation in structuring communities (Green *et al.*, 2004).

The ongoing global climatic change has increased the need to understand the consequences of climate-driven shifts on spatial and temporal community dynamics particularly in coastal ecosystems that are naturally prone to frequent abiotic disturbance (Crabot *et al.*, 2020; Buckley *et al.*, 2021). Microorganisms are responsible for a variety of biogeochemical processes vital for ecosystem functioning and biodiversity. However, studies of spatiotemporal variation in microbial eukaryotic communities are still rare compared to macroorganisms (Martiny *et al.*, 2006). Especially, less is known about small-scale microalgal community dynamics at coastal areas at a marine-freshwater transition zone (Vanschoenwinkel *et al.*, 2008a).

Separating the effects of environmental stressors from other underlying drivers of microalgal diversity is vital, widening the knowledge of responses of primary producers to environmental perturbations.

1.1 Alpha and beta diversity

Local biodiversity within a community, defined as alpha diversity, is often quantified as taxonomic species richness referring to the total number of species in a community. Yet not only does it ignore species identities and relative abundances (i.e. species evenness) in a community, but the variety of species ecological traits, or functional diversity, as well (Mouchet *et al.*, 2010; Roswell *et al.*, 2021). These inherited physiological, morphological and metabolic traits are shared by polyphyletic groups of species and are commonly related more strongly to environmental variation, whereas the classic taxonomic diversity metrics usually respond more to species dispersal processes (Reynolds *et al.*, 2002; Graco-Roza *et al.*, 2022). Although variation in ecological traits may well outweigh the variation in taxonomic diversity due to intraspecific variation in traits (Green *et al.*, 2008), functional diversity in aquatic microbial communities is still understudied (Schmera *et al.*, 2016; Alahuhta *et al.*, 2019).

Spatial beta diversity, defined as the variation in species composition between sites (Whittaker, 1960), is often quantified as species turnover describing the rate of change in community composition due to species replacement (Baselga, 2010). Distance decay (Nekola and White, 1999) describes this change in community similarity between sites along environmental or spatial distance due to species-specific variation in ecological niche and dispersal ability, respectively (Condit *et al.*, 2002; Chave, 2004). High turnover is characterized by fast reduction in community similarity with distance, while low turnover rates indicate slower change in community composition along environmental or spatial distance due to fewer species replacements (Soininen *et al.*, 2007; Wetzel *et al.*, 2012).

Natural communities are, however, not static but vary on their taxonomic and functional composition also in time. Temporal beta diversity, defined as the unidirectional increase or decrease in community similarity over time, is attributed to species gained and lost from a community between two separate points in time (Buckley *et al.*, 2021; Schmera *et al.*, 2022). Although less studied in aquatic ecosystems (Cook *et al.*, 2018), measuring the degree to which communities are differentiated from each other on a temporal gradient is vital to better understand microbial community dynamics both across space and in time (Dornelas *et al.*, 2013; Buckley *et al.*, 2021).

1.2 Coastal rock pools

Granitic rock pools are small, geologically old formations on rocky outcrops typically surrounded by sea (Figure 1). Their hydrology is simple, regulated by seasonal changes in rainfall, evaporation and wind conditions (Jocque *et al.*, 2010). Pool water salinity decreases gradually with increasing vertical and horizontal distance to sea due to reduced seawater influence, changing the habitat type from marine toward mostly rainfall-fed freshwater pools (Underwood and Skilleter, 1996).

Rock pools are generally shallow, typically less than 100 cm deep (Brendonck *et al.*, 2010). Low water volume reduces pool buffering capacity against periodic abiotic disturbances such as desiccation or alterations in water physicochemistry, resulting in high spatial and temporal heterogeneity in pool environmental characteristics (Metaxas and Scheibling, 1996). Despite their small size, coastal rock pools have diverse biota, consisting primarily of a mixture of freshwater, brackish and marine species of bacteria, phytoplankton, zooplankton and aquatic invertebrates (Blaustein and Schwartz, 2001; Brendonck *et al.*, 2016). Most pool species are ecological specialists with a high tolerance toward environmental stress and habitat ephemerality (Dethier, 1984).

Figure 1. a) View from the study area on the western Pihlajasaari island, Helsinki, toward Southwest. b)–d) Some of the sampled rock pools on the study area on the Baltic Sea coast. Pools b) and c) have clear water and visible bottom sediment; pool d) is located at an immediate proximity to the sea and has an exceptionally large coverage of macroalgae. Photos: Sonja Aarnio.

Despite sporadic overflows between adjacent pools, rock pools are spatially isolated from each other. However, discrete pools are interconnected to form a metacommunity, a set of interacting communities linked by species dispersal (Blaustein and Schwartz, 2001; Leibold *et al.*, 2004). Within these interacting communities, sampling and quantification of community dynamics is usually simpler compared to larger aquatic habitats (Srivastava *et al.*, 2004; De Meester *et al.*, 2005).

1.3 Benthic diatoms

Microalgal diatoms (Bacillariophyceae) are abundant and diverse eukaryotes, constituting a large proportion of benthic biomass and biodiversity in aquatic ecosystems (Martiny *et al.*, 2006; Soininen, 2007).

Unicellular diatoms are classified taxonomically by morphological differences in their siliceous cell wall (Round *et al.*, 1990). Along with morphology, diatoms are categorized after their physiological and metabolic features such as cell size, growth form or acid-tolerance into polyphyletic functional groups reflecting their functional role in a community (Mason *et al.*, 2005; Rimet and Bouchez, 2012).

As autotrophs responsible for primary production, diatoms are important players in biomass production

(Soininen, 2007). Their population growth is largely limited by several abiotic factors such as water physicochemistry (e.g. conductivity, nutrient concentrations) and environmental disturbances (e.g. water turbulence, desiccation), affecting their local diversity and community composition. Due to this sensitivity to environmental alterations and fast reactions to water quality, diatoms represent well local habitat variability (Soininen, 2007). Small habitat size facilitates biotic interactions within and across trophic levels, as interspecific competition and grazing by invertebrates also shape diatom communities (Jocque *et al.*, 2010).

Despite the lack of flagella or active swimming capabilities, diatoms are efficient in dispersing passively via different dispersal vectors such as wind, water and animals (Soininen, 2007; Vanormelingen *et al.*, 2008). Hence, diatoms were long considered to have wide distribution ranges limited primarily by their often narrow environmental preferences (Finlay, 2002). Later, this view has been challenged by numerous studies indicating strong spatial control over diatom communities especially at broader spatial scales (Verleyen *et al.*, 2009).

Due to their high diversity, limited environmental preferences, short generation times and often geographically wide distribution, diatoms have proven to be useful model taxa in community-related ecological studies over different timescales and spatial extents (Smucker and Vis, 2011).

1.4 Study objectives

This thesis investigates the environmental and spatial drivers of diatom biodiversity on the Baltic Sea coast, specifically examining alpha diversity as well as spatial and temporal beta diversity. These patterns are examined by taxonomic and trait-based approaches among a set of natural rock pool communities.

The study consists of three main objectives:

O_1 To examine the covariation and drivers of diatom taxonomic and functional spatial alpha diversity by three taxonomic and three trait-based diversity metrics in 30 coastal rock pools (**I**).

O_2 To investigate the relative roles of environmental and spatial variables as drivers of diatom taxonomic spatial beta diversity among 30 coastal rock pools in a metacommunity context (**II**).

O_3 To explore patterns and drivers of diatom taxonomic and functional temporal beta diversity among nine coastal rock pools throughout the growing season (**III**).

2 Material and methods

2.1 Study area

All three studies (**I**–**III**) were conducted on the same granitic outcrop on the western Pihlajasaari island (60°08’ N, 24°54’ E), ca. two km south of Helsinki, Finland (Figure 2). The coast of the northern Baltic Sea lacks notable tidal influence, and changes in sea level are mainly mediated by wind and differences in air pressure (Pajunen and Pajunen, 2007).

Two datasets consisting partially of the same brackish-water rock pools were sampled from an area of ca. 1,200 m^2 during two separate summer seasons (Table 1). For the first dataset (**I**, **II**), 30 pools were sampled once a month (90 samples in total) in May-July 2016 (Data 1 in Table 1); for the second dataset (**III**), nine pools were sampled 12 times (108 samples in total) at roughly 10-day intervals in May-September 2019 (Data 2 in Table 1).

The sampled pools were isolated from each other and mainly rainfall-fed, yet the pools closest to the sea were influenced by direct inflows and splashes of seawater. All pools were unshaded by vegetation and most of them were covered by a thin sediment layer; decaying organism remains, and faunal excretions e.g. from birds were the likely sources of nutrient enrichment (Methratta, 2004; Brendonck *et al.*, 2016).

2.2 Environmental data

To minimize diurnal variation in water physicochemistry, the pools were sampled roughly at the same time of the day. For both datasets (**I**–**III**), water pH, conductivity, and temperature were measured in situ with a YSI Professional Plus field meter. Pool morphometrics (i.e. maximum depth, length and width) were measured with a meter stick, and pool area was approximated by multiplying pool length by pool width. A 0.5 l water sample was collected from each pool and preserved at 4°C for the determination of total P (following SFS-EN ISO 6878) and total N (following SFS-EN ISO 11905-1) concentrations. For Data 2 (**III)**, nutrient supply (i.e. N:P) ratio was also determined.

For Data 1 (**I**, **II**), pool X and Y coordinates, mean isolation (the mean Euclidean distance to five closest pools; Vanschoenwinkel *et al.*, 2007), and distance to the sea were determined from a drawn grid map of the study area showing pool relative location to each other and to the coastline. For Data 2 (**III**), pool location was determined by latitude and longitude with a GPS, and distance to the sea and mean isolation were measured on an aerial photograph.

2.3 Diatom analyses

Benthic diatoms were sampled following standard BS EN 13946:2003 by collecting 10 subsamples (ca. 25 cm^2) from each pool with a toothbrush into a plastic container filled with pool water and combining the accumulated diatom suspension as a single composite sample in a plastic test tube in the field (**I**–**III**). Between each sampling, the toothbrush was rinsed in pool water to remove attached cells and reduce contamination between the samples (Kelly *et al.*, 1998).

The samples were stored at 4°C until treatment with 30% H_2O_2 to remove organic material and mounting on slides with Naphrax. A minimum of 500 valves per slide were counted and identified to the lowest taxonomic level possible (mostly species level) with a phase contrast light microscope (Olympus BX40, Melville, NY; 1000-fold magnification) following Krammer and Lange-Bertalot (1986, 1988, 1991a,b), Snoeijs (1993), Snoeijs and Vilbaste (1994), Snoeijs and Potapova (1995), and Snoeijs and Kasperovicienè (1996).

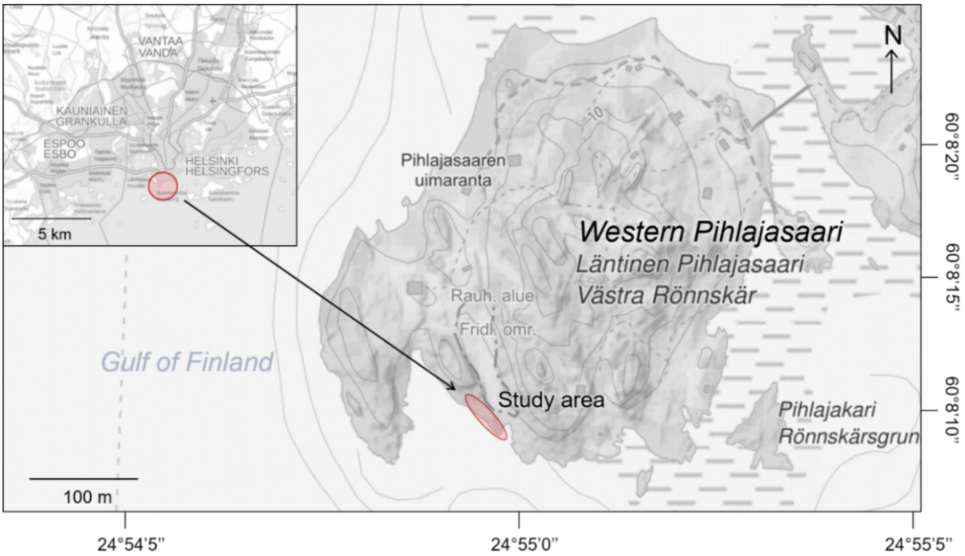

Figure 2. Map of the study area. The study area is located on the western Pihlajasaari island ca. 2 km off the coast of Helsinki (the red circle on the index map), on a rocky outcrop on the southwestern part of the island (the red oval on the larger map). Map: National Land Survey of Finland (2018).

Table 1. Data attributes of the two datasets collected from Pihlajasaari island, Helsinki. For both datasets 1 (used in **I**, **III**) and 2 (used in **III**), given are the number of study sites (i.e. rock pools) and subsequent sampling occasions, the total number of samples (study sites × sampling occasions), as well as the approximated time interval between subsequent sampling occasions, and the temporal range of the whole sampling period in days.

	Data 1	Data 2
Study sites	30	9
Sampling occasions	3	12
Samples	90	108
Sampling interval (d)	30	10
Temporal range (d)	67	119

2.4 Taxonomic and functional diatom data

Taxonomic diatom data constituted of site-species matrices based on species relative abundances (**I**, **II**), and a binomial site–species matrix based on species presence–absence after the count abundances (**I**, **III**).

For the functional data (**I**, **III**), the diatom species were classified into 21 functional groups. The species were first divided into five size classes by their biovolume (based on cell length, width, thickness, and shape) and 14 life-form categories by their morphological adaptations to physical and chemical disturbance. Any taxon with successive life forms was classified into multiple life-form categories (Berthon *et al*., 2011; Rimet and Bouchez, 2012).

The species were further divided into four ecological guilds according to their preferences for nutrient concentration and physical disturbance: high profile, low profile, motile, and planktic guild (Passy, 2007; Rimet and Bouchez, 2012). Lastly, a few genera were classified after their metabolism into acid-tolerant (Van Dam *et al.*, 1994) and nitrogen-fixing species (Soininen *et al.*, 2016). Based on these functional species data, binomial site–trait matrices were created (**I**, **III**).

2.5 Statistical analyses

Prior to statistical analyses (Table 2), the data were pretreated following mainly Zuur *et al.* (2010; see **I**–**III** for more detailed descriptions). All statistical analyses were conducted in R (versions 3.4.3 and 3.6.2; R Core Team, 2022) primarily by utilizing R source code provided in Zuur *et al.* (2009; **I**, **III**). All regression models (**I**, **III**) were validated following the protocol proposed in Zuur *et al.* (2010).

2.5.1 Taxonomic and functional alpha diversity (I)

To account for spatial taxonomic and functional alpha diversity among the diatom communities (**I**), species richness *S*, Pielou's evenness *J* (Pielou, 1966), and Shannon's diversity *H* (Shannon, 1948) were quantified for the taxonomic abundance data (function *diversity* in the R package vegan; Oksanen *et al.*, 2019), and functional richness (*FRic*), functional evenness (*FEve*), and functional divergence (*FDiv*) for the functional presence-absence data (function *dbFD* in the R package FD; Laliberté *et al.*, 2014), respectively. The functional indices were calculated using the first two ordination axes of principal coordinate analysis (PCoA; Gower, 1966) for the square root corrected species–species distance matrix; *FEve* and *FDiv* were further weighted with species relative abundances (Villéger *et al.*, 2008).

To examine the most influential factors explaining variation in taxonomic and functional diversity, generalized linear mixed models (GLMMs; Zuur *et al.*, 2013) with a Gaussian error distribution were applied for all diversity indices (function *glmmTMB* in the R package glmmTMB, Brooks *et al.*, 2017) except *S*, for which the model was run with Poisson and refitted with a negative binomial error distribution due to overdispersion in the residuals. The covariates were removed from the full models by a backward stepwise method, considering the model with the lowest AIC value (Akaike information criterion; Akaike, 1973) the best.

2.5.2 Taxonomic spatial beta diversity (II)

To explore spatial beta diversity among the diatom communities (**II**), the most influential explanatory variables affecting diatom community composition were first examined with redundancy analyses (RDA; ter Braak, 1994) with the Hellinger-transformed species data (function *rda* in the R package vegan; Oksanen *et al.*, 2019).

Halving distance of community similarity was then calculated with a formula $(\beta - \alpha)/2\beta$, and an initial similarity at a 1-m distance with a formula $\beta \times 1 + \alpha$, where β is the regression coefficient and α the intercept (Soininen *et al.*, 2007).

Mantel tests (Mantel, 1967) were performed with function *mantel* in the R package vegan (Oksanen *et al.*, 2019) to reveal the roles of spatial and environmental distance on community similarity (expressed with the Bray-Curtis similarity index; Bray and Curtis, 1957). A partial Mantel test (Legendre and Legendre, 2012) was further conducted with function *mantel.partial* in the R package vegan (Oksanen *et al.*, 2019) for examining the roles of pure environmental and pure spatial variables on community similarity, while controlling for the effects of the other variable set.

Finally, the variation in diatom community composition was shared to fractions explained by pure spatial, pure environmental, and pure temporal variables, as well as their joint effect by variation partitioning (Borcard *et al.*, 1992) using function *varpart* in the R package vegan (Oksanen *et al.*, 2019).

2.5.3 Taxonomic and functional temporal beta diversity (III)

To measure temporal taxonomic and functional beta diversity within the diatom communities (**III**), temporal beta diversity index (TBI; Legendre, 2019) was quantified by applying Sørensen dissimilarity coefficient for taxonomic and functional presence–absence data, respectively (function *TBI* in the R package adespatial; Dray *et al.*, 2021). TBI measures the degree to which communities are differentiated from each other in time and is constrained between 0 (no temporal differentiation) and 1 (complete temporal differentiation; Legendre, 2019).

The resulting site-specific taxonomic and functional dissimilarities were decomposed into loss and gain components according to species or traits gained and lost over time, respectively, to assess the direction and significance of temporal community change (Schmera *et al.*, 2022). TBI was further assessed for standardized environmental data to examine whether a significant change in taxonomic or functional composition coincided with significant changes in environmental conditions.

Table 2. Main statistical methods, response and explanatory variables, and datasets used in I-III. dbRDA = Distance-based redundancy analysis; GLM = Generalized linear model; GLMM = Generalized linear mixed model; RDA = Redundancy analysis; TBI = Temporal beta diversity index.

Paper	Data	Statistical method	Response variable(s)	Explanatory variables
I	1	GLMM	taxonomic diversity indices, functional diversity indices	pool location, environmental variables, sampling month
II	1	RDA	taxonomic community composition	pool location, environmental variables, sampling month
		Mantel and partial Mantel tests	taxonomic community composition	pool location, environmental variables
		Variation partitioning	taxonomic community composition	environmental variables, pool location, sampling month
III	2	GLM	taxonomic TBI, functional TBI	pool location, environmental variables
		GLMM	taxonomic TBI, functional TBI	environmental TBI
		dbRDA	taxonomic community composition, functional community composition	sampling day

The factors best explaining variation in taxonomic and functional TBI were then examined with generalized linear models (GLMs; McCullagh and Nelder, 1983) with function *betareg* in the R package betareg (Cribari-Neto and Zeileis, 2010); a GLMM (function *glmmTMB* in the R package glmmTMB; Brooks *et al.*, 2017) was further used to test whether variation in taxonomic and functional TBI could be explained by variation in environmental TBI. All regression models were run with a beta error distribution (Ferrari and Cribari-Neto, 2004), and the full models reduced by a backward stepwise method, considering the model with the lowest AIC value the best.

Lastly, distance-based redundancy analysis (dbRDA; Legendre and Anderson, 1999) was applied to partition variation in the taxonomic and functional community composition according to sampling day (function *dbrda* in the R package vegan; Oksanen *et al.*, 2019). PCoA was applied for a square-rooted Sørensen dissimilarity matrix, and the resulting matrix was then used as a response variable in dbRDA, constrained by a factor representing the 12 consecutive sampling days.

3 Results and discussion

3.1 Taxonomic and functional spatial alpha diversity (I)

Three taxonomic and three functional diversity indices were used to examine diatom spatial alpha diversity within 30 coastal rock pool communities. Taxonomic diversity declined steadily toward the end of the sampling period; functional divergence was high, whereas functional richness and evenness stayed moderate. The taxonomic and functional diversity indices were significantly collinear with each other ($r_s \geq |0.4|$) except functional evenness, which merely correlated with taxonomic evenness ($r_s = -0.2$) (Figure 3 in **I**).

As the covariance would suggest functional redundancy, the moderately low *FEve* more refers to trait complementarity in functionally divergent communities (Cadotte *et al.*, 2011). Possibly, the pool exposure to seawater intrusions is infrequent enough to limit permanent establishment of marine species, reducing functional evenness and redundancy in the communities (Mouchet *et al.*, 2010; Mazzei *et al.*, 2018). The observed patterns thus agree with the notion that strong environmental filtering usually limits trait diversity in highly disturbed habitats such as the studied rock pools, leading to ecologically specialized biota dominated by only a few functional guilds (Cadotte *et al.*, 2011; Mazzei *et al.*, 2018).

In the GLMMs, all six diversity indices were explained significantly by water conductivity either by an interaction with sampling month (functional evenness) or directly (all the other indices), and an interaction between water temperature and sampling month (Tables 2–3 in **I**). Variation in taxonomic diversity was also consistently significantly explained by pool distance to the sea and sampling month, while functional diversity was linked to varying physicochemical variables and pool location (i.e. isolation or distance to the sea). Water temperature and conductivity are important factors regulating diatom communities in coastal rock pools (Soininen, 2007). Inversely related to pool distance to the sea ($r_s = -0.5$), the conductivity gradient serves as a key environmental constraint shaping species composition in coastal pools. At the marine-freshwater transition zone, pool exposure to seawater intrusions may promote functional redundancy by limiting the persistence of species with very narrow salinity preferences (Mouchet *et al.*, 2010; Mazzei *et al.*, 2018).

There was no notable difference in the amount of explained variation between the taxonomic ($R_c^2 = 0.45–0.57$) and functional regression models ($R_c^2 = 0.33–0.52$). Regardless of the covariance between the two sets of diversity indices, different factors were responsible for their variation. Rather unexpectedly, all diversity indices were related to water physicochemistry and pool spatial location, the latter finding contradicting the general view of functional diversity responding primarily to environmental variability (Graco-Roza *et al.*, 2022). Thus, rather than supporting the superiority of either set of diversity indices in measuring alpha diversity, the results emphasize the importance of considering both taxonomic and functional aspects of biodiversity, as individual diversity metrics may be driven by different factors and their patterns thus show probably high context-dependency depending on specific environmental gradients in the study area.

3.2 Taxonomic spatial beta diversity (II)

The most influential environmental and spatial factors and their relative roles for diatom spatial beta diversity were examined across 30 rock pool communities. In the RDAs, the taxonomic community composition was significantly explained by pool distance from the sea and several physicochemical variables such as water conductivity (Figure 3, Table 3 in **II**). As with alpha diversity, water conductivity was negatively linked to increasing pool distance from the sea ($-0.65 \leq r_s \leq -0.43$) throughout the study period, emphasizing the importance of seawater influence for the studied communities.

Considering the whole sampling period, variation partitioning showed that the amount of variation in community composition explained by pure environmental and pure spatial factors was nearly equal (6.8% and 6.5%, respectively), whereas 3.7% of the variation was explained by temporal gradient (Figure 6 in **II**). The monthly percentage in species composition explained by spatial factors decreased during the summer from 8.2% to 2.8%, while the monthly proportion explained by pure environmental factors stayed rather comparable (5.5%–6.9%) (Figure 5 in **II**). Overall, the values explained by environmental and spatial variables were relatively low compared to many other study taxa and settings (Soininen, 2014, 2016). This probably reflects the high levels of physical disturbances (caused e.g. by wind, rain or waves) faced by the diatom communities.

According to the Mantel and partial Mantel tests, community similarity decreased along both environmental and spatial distance even when the other variable group was controlled for (Table 4 in **II**). At the end of the study period, decrease in community similarity along environmental distance accelerated, exceeding the rate of decay along spatial distance (Figure 4 in **II**). The halving distance of diatom community similarity decreased during the summer below 60 meters, which is extremely short in comparison with a global average of several hundred kilometers (Soininen, 2007) (Table 4 in **II**).

Such a high turnover rate and the intensifying environmental control over the communities with time likely resulted from an interplay between environmental heterogeneity and pool distance from the sea. Temporal variation in local weather conditions was reflected in pool water physicochemistry and indirectly in species dispersal rate, as higher precipitation and stronger winds likely promoted passive dispersal, especially later in the summer (Vanschoenwinkel *et al*., 2008a). These heterogeneous abiotic conditions triggered by random environmental perturbations likely acted as a strong abiotic selecting force for a specialized biota, while effective passive dispersal between the isolated but relatively closely located pools maintained viable species assemblages in environmentally less suitable pools as well, shaping community composition between the sites (Vanschoenwinkel *et al*., 2008b; O'Neill, 2016).

3.3 Taxonomic and functional temporal beta diversity (III)

Temporal differentiation in taxonomic and functional community composition, and abiotic environmental variability were examined within nine rock pool communities. On average, taxonomic and functional TBI and their components (i.e. losses and gains) followed rather similar temporal trend (Figure 1 in **III**). Taxonomic TBI was substantially high and exceeded functional TBI throughout the study period. Recently, strikingly fast temporal turnover rates have been discovered for other coastal microbial communities as well (Wu *et al*., 2016; Martin-Platero *et al*., 2018). Instead, comparably low functional diversity is a typical feature in environmentally disturbed habitats, where frequent taxa replacements largely cover few functionally redundant, temporally dominant traits best suited for the abiotic variability (Villéger *et al*., 2012; Crabot *et al*., 2020).

In the GLMs, variation in both taxonomic and functional TBI was explained by pool isolation and distance to the sea. Functional TBI was further related to water conductivity, temperature, N:P ratio, and pool area (Figure 2, Table 1 in **III**). Generally, functional diversity is thought to respond more strongly to environmental gradients and taxonomic diversity to local dispersal processes (Graco-Roza *et al*., 2022). Although functional TBI showed sensitivity toward several physicochemical variables, its linkage with pool spatial location does not fully support this view.

The pools with significant change in taxonomic or functional TBI were characterized by moderate, non-significant changes in environmental TBI; contrastingly, significant variation in environmental TBI did not coincide with the pools with significant change in either taxonomic or functional TBI at any point in time. According to GLMMs, environmental TBI further had a negative relationship with taxonomic TBI, and no significant relationship with functional TBI (Figure 3, Table 2 in **III**). Rather, the taxonomic community composition seemed to converge over time in the dbRDA, regardless of the high environmental heterogeneity (Figure 4 in **III**).

Such a lack of relationship between environmental heterogeneity and taxonomic beta diversity is an interesting finding as abiotic variability maintains spatiotemporal divergence in species composition between local communities. Thus, higher beta diversity is commonly encountered in habitats of high environmental heterogeneity (Astorga *et al.*, 2014). Recent studies, however, have found signs of similar independence, or even a negative relationship between the level of aquatic temporal beta diversity and abiotic variability (Lopes *et al.*, 2017; Lindholm *et al.*, 2021; Galvanese *et al.*, 2022). This has been attributed to severe environmental disturbances that homogenize communities not only in abiotic resources but in species composition as well. As a result, beta diversity is reduced, as communities are inhabited by species with similar ecological preferences (Hawkins *et al.*, 2015).

4 Conclusions

This thesis examined patterns and drivers of diatom biodiversity in coastal rock pools by taxonomic and trait-based approaches. More specifically, the study concentrated on alpha and beta diversity of the pool communities both in space and time.

The study revealed significant spatial and temporal heterogeneity in species composition within and among the diatom communities linked to high environmental variability and pool spatial location (Figure 3). Sharp transitions in local abiotic conditions were largely driven by short-term microclimatic variations, maintaining spatial and temporal instability in pool water physicochemistry. Especially, the conductivity gradient played a key role in determining species taxonomic and trait composition at this marine-freshwater transition zone. Accompanied by random stochastic events and efficient passive species dispersal over the relatively short among-pool distances, these environmental oscillations shaped the studied communities both in space and time. However, while the spatial differences in community composition increased with time, temporal beta diversity did not follow a consistent pattern.

Both taxonomic and functional diversity indices performed successfully in explaining alpha and beta diversity. The results supported the view of strong

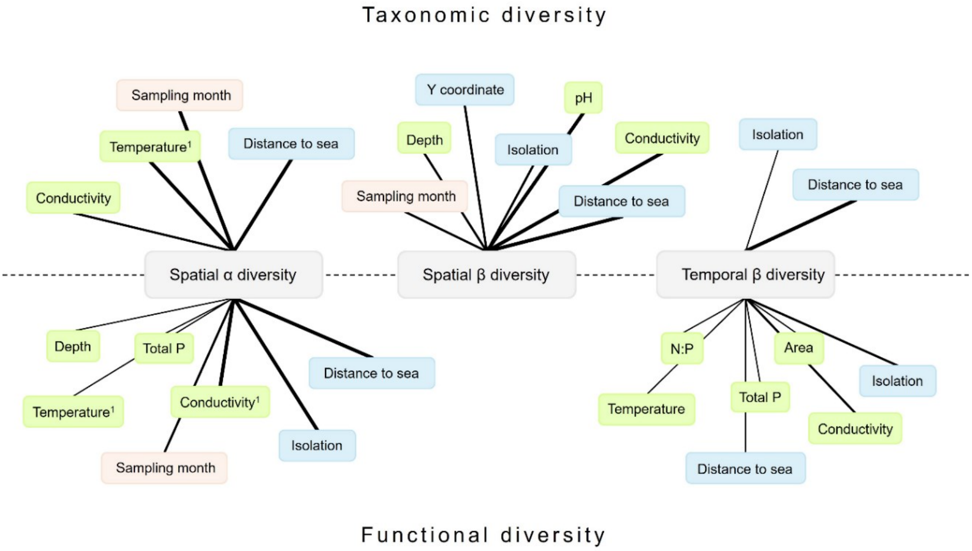

Figure 3. Factors affecting taxonomic and functional (separated by the horizontal dashed line) diatom biodiversity in the studied rock pools, according to the results of regression models (spatial alpha diversity; I, and temporal beta diversity; III) and redundancy analysis (spatial beta diversity; II). Shown are all statistically significant ($p \leq 0.05$) explanatory variables; for spatial alpha and beta diversity, these variables are combined from multiple regression models. Environmental variables are colored green and spatial variables blue; the temporal variable (sampling month) is colored red. The width of the arrows refers to the significance of the explanatory variables based on the model-specific p-values. Note that for spatial beta diversity, only taxonomic diversity was considered. Note also that not all models included the same set of explanatory variables. [1] Direct effect or an interaction with sampling month.

relatedness of taxonomic diversity with spatial processes. Contrary to the general assumption, functional diversity was related not only to environmental variability but to spatial factors as well, which may reflect the covariation of spatial and environmental (including environmental variables not measured in the field) factors in the study area. The taxonomic indices also failed to reflect functional diversity due to redundant traits. As the results do not fully support the superiority of functional indices over the taxonomic ones in explaining coastal microalgal diversity, the greatest advantage in assessing diatom biodiversity is likely achieved with a combination of taxonomic and trait-based methods.

Partly due to practical challenges in field sampling, most temporal community research still relies on relatively short time series with a few temporal replicates. Especially in highly dynamic habitats such as rock pools studied here, future microbial studies should preferably consider finer temporal scales and longer time series to track for the effects of rapid environmental alterations and stochastic processes. The results also highlight the suitability of rock pools for modeling coastal community dynamics along steep environmental gradients over small spatial extent.

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