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ORIGINAL ARTICLE

Strong and weak trait-environment associations in subarctic stream diatoms

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Abstract

- 1. Ecological traits are functional characteristics measurable at the species level and provide valuable insights into how organisms respond to environmental constraints. Here, we investigated how diatom trait-groups and individual species respond to environmental variables, and identified indicator species that are particularly sensitive to environmental variation.
- 2. Diatoms were sampled at 129 sites in the subarctic streams of Norwegian islands and mainland, and were categorised into three trait groups: high-profile species that live in an erect position, low-profile species living in low position along the surface, and motile diatoms. Data were analysed using a recently developed method known as Hierarchical Modelling of Species Communities, which is a flexible framework for joint species distribution modelling.
- 3. We found that diatom trait-groups responded relatively weakly to measured environmental variables but showed positive or negative relationships with major ion levels of the water (e.g., conductivity, calcium [Ca²⁺], sodium [Na⁺] or chlorine [Cl⁻]). Variance partitioning showed a similar, important contribution of the chemical variables for all of the trait groups, while the contributions of physical variables and especially random (spatial) factors were notably lower for all trait groups.
- 4. Our findings also highlighted considerable among-species variation in their relation to environmental variables within the trait groups. Notably, we identified a high number of indicator species within each trait group that were explained by specific environmental factors, mostly chemical variables (conductivity, pH, total nitrogen and phosphorus, Ca²⁺, Na⁺, Cl[−]).
- 5. Our study suggests that certain diatom species can be considered as useful environmental indicators but the variability in species preferences within the trait group may in some circumstances hamper the use of ecological traits in environmental assessments. Thus, we suggest using species-level ecology combined with trait information to better track environmental change when using diatoms as indicators.

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algae, diatoms, joint species distribution modelling, subarctic streams, traits

INTRODUCTION Diatoms are typically representative of benthic algal communities as they often form a large proportion of the algal diversity in fresh waters (Kelly et al., 2008). Their remarkable diversity, widespread distribution across geographical gradients and high sensitivity to changes in water quality facilitate their use for ecological assessment (Soininen et al., 2016; Stenger-Kovács et al., 2013). Diatom indices

KEYWORDS

widely used in current freshwater monitoring practices rely on taxonomic inventories of species present at sampling sites. However, the conventional method of identifying diatoms based on morphological characteristics is often challenging and time-consuming (Alers-García et al., 2021). As an alternative, trait-based diatom analyses provide a promising approach circumventing the mere reliance on morphological species-based indices (Kahlert et al., 2021).

Traits encompass observable characteristics, such as morphology, physiology or phenology that can be measured at species and individual levels, and are linked to ecological functions (Tapolczai et al., 2016). Traits offer potential ecological insights into how organisms respond to environmental constraints (Graco-Roza et al., 2022; Statzner & Bêche, 2010). In the case of diatoms, Passy (2007) introduces a classification system based on ecological guilds distinguishing three groups: (1) the high-profile guild, encompassing larger diatom species or those that tend to form colonies (e.g., tube-forming, filamentous and branched diatoms such as *Eunotia* and *Fragilaria*), which are less resistant to turbulence but thrive in nutrient-enriched environments; (2) the low-profile guild, comprising diatom species with a compact structure (e.g., prostrate, adnate, and erect diatoms such as Achnanthes and Cymbella), which exhibit resilience to physical disturbances such as water turbulence but show limited tolerance to nutrient enrichment; and (3) the motile guild, consisting of diatom species known for their mobility (e.g., Navicula and Nitzschia), proposed to be adapted to habitats characterised by turbulence and high nutrient concentrations. Since this seminal paper, multiple studies have highlighted the value of diatom traits, including ecological guild, size and life-form, among others, as indicators of nutrient availability, organic pollution, shear stress resulting from water flow, and grazing pressure (Berthon et al., 2011; Passy, 2007).

The presence and abundance of taxa having certain traits serve as indicators of particular environmental conditions (Tapolczai et al., 2017). For instance, previous studies focused on developing a trait-based framework for diatom assessment in environmental studies have recognised the influence of nutrients, conductivity, pH, connectivity and physical disturbance as key factors shaping the composition of diatom traits (Liu et al., 2023; Rimet & Bouchez, 2012; Zorzal-Almeida et al., 2017). Kahlert et al. (2021) observe that the presence of low-profile and high-profile guilds does not align closely with nutrient gradients, suggesting the involvement of other factors

such as physical disturbance in driving the distribution of these traits. There is still a pressing need to deepen our understanding of how environmental factors shape the distribution of diatom traits in different types of freshwater environments (Tapolczai et al., 2016). This is important since recently the reliability of diatom species as environmental indicators has been questioned, especially because diatom species may be locally adapted, and the same index values of species cannot be perhaps directly used in different geographical regions (Soininen et al., 2019). Consequently, metrics based on these traits have potential for the purposes of water quality assessment by overcoming the limitations of taxonomy-based methods (Tapolczai et al., 2017). Moreover, they offer a more efficient response of the community to environmental factors (stressors) (Bailet, 2021).

In this study, we examined diatom communities from the subarctic Norwegian islands and mainland streams aiming to investigate how similarly diatom trait-groups and individual diatom species within the trait groups respond to environmental variables. Such trait-environment relationships are poorly studied for diatoms in arctic and subarctic cold environments. Moreover, we identified indicator species that were most sensitive to environmental variation. We used a recent joint species distribution model Hierarchical Modelling of Species Communities (HMSC; Ovaskainen et al., 2017), to investigate how different trait groups and individual diatom species are associated with environmental variables.

MATERIALS AND METHODS 2

2.1 Study region and sample collection

The study region comprised streams in mainland and islands in northern Norway. The geomorphology of this region is rather complex as the coastlines exhibit a striking pattern of extensive indentations featuring large promontories and enclosed bays. These coastal landscapes also have deep, narrow muddy bays and cliffs of solid rock (Jenkins et al., 2008) (Figure 1). Being a subarctic region, most of the streams in the study area are characterised as oligotrophic and cold environments for the biota.

In August 2013, we obtained diatom samples at 129 sites. Of these, 18 sites were in mainland and 111 sites in 18 islands with at least six sites per island (Figure 1). Following established protocols outlined in Wang et al. (2011), each study site was divided into either five or 10 cross-sections, depending on the width of the stream. Within these sections, we randomly selected 10 stones from riffle or run habitats. Using a toothbrush, we gently scraped off the biofilms covering the stones to obtain subsamples from a predefined area of approximately 9 cm². These subsamples were then combined to create a composite sample representing each specific site.

FIGURE 1 Sampling sites in Norway.



At each location, we assessed various environmental features (Figures S1 and S2) using established methods outlined in Wang et al. (2017) simultaneously to diatom sampling. Using a GPS device (Garmin Etrex 10), we recorded the latitude, longitude and elevation of each site. Additionally, we quantified water conductivity, pH, slope and distance to the sea in metres. We also approximated visually the level of human impact/land cover of each site by assigning semi-qualitative scores ranging from 0 to 1. We assessed if there was agricultural land use (1) or not (0), and whether the land cover around the streams was trees/bushes (92 sites), grass (34 sites) or both (three sites).

Ion concentrations (in mg/L) (chlorine [Cl⁻], fluorine [F⁻], nitrite $[NO_2^-]$, nitrate $[NO_3^-]$, bromine $[Br^-]$, phosphate $[PO_4^{3-}]$ and sulfate $[SO_4^{2-}]$) were measured with a Shodex IC-50 4E column for suppressor method anion chromatography. Major metal ions (potassium [K⁺], sodium $[Na^+]$, magnesium $[Mg^{2+}]$ and calcium $[Ca^{2+}]$) were analysed with inductively coupled atomic emission or mass spectrometry (ICP-AES/MS) by following previous literature (Wang et al., 2011). Total nitrogen (TN) and total phosphorus (TP) were analysed by peroxidesulphate oxidation and the spectrophotometric method (Wang et al., 2011).

In a laboratory, the diatom samples were thoroughly cleaned from organic matter through a wet combustion process employing hydrogen peroxide. Subsequently, diatoms were affixed to Naphrax slides and subjected to identification and quantification, with 500 frustules analysed per sample, utilising phase-contrast light microscopy at a magnification of \times 1,000. All identified diatoms were classified at the species level, following established references from standard European and North American references (Krammer & Lange-Bertalot, 1986–1991; Lange-Bertalot & Metzeltin, 1996).

2.2 | Trait database

Diatom species were classified into one of four guilds, hereafter trait groups (high-profile, low-profile, motile and planktonic) based on the information provided by Passy (2007), Rimet and Bouchez (2012)

and Riato et al. (2017). Approximately 5% of the species could not be assigned to a specific trait group owing to insufficient information. Additionally, we excluded planktonic diatoms from the analysis as they comprised only five species.

2.3 | Statistical analyses

In order to avoid multicollinearity, we removed variables that exhibited a correlation higher than 0.7 with each other (Legendre & Legendre, 2012). We used non-metric multidimensional scaling to visualise the community composition in islands and mainland. Redundancy analysis (RDA) was used to test which of the environmental variables were significantly related to diatom community composition and used in further analyses. Permutational multivariate ANOVA (function "Adonis" with presence-absence data) and a linear mixed effect model were used to test for possible significant differences in community composition and species richness, respectively, between islands and mainland. In the mixed model, island or mainland were used as fixed effects and island name (or mainland) as a random effect.

In order to investigate how diatom trait-groups and individual species within different trait groups respond to environmental variables, we applied HMSC using the R package *Hmsc* (Tikhonov et al., 2022), a recently developed hierarchical joint species distribution modelling (JSDM) method (Ovaskainen et al., 2017). We used a binomial distribution (probit link function) fitted with the following environmental variables pH, elevation, conductivity, slope and distance to the sea. Response variables included diatom presence-absence data. Taxa with fewer than four occurrences were excluded to improve model performance. To account for any spatial autocorrelation of the study sites, we included a spatially explicit random effect on the level of individual sites using spatial coordinates and the full Gaussian process spatial technique as a default method in HMSC.

For the model performed, posterior distribution was sampled with four Markov chain Monte Carlo (MCMC) chains, each run for 15,000 iterations. The first 5,000 iterations were removed as

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burn-in, and the remaining were thinned by 2 to yield 5,000 posterior samples per chain.

Model convergence was assessed by analysing Gelman and Rubin's convergence diagnostic (potential scale reduction factor; Gelman & Rubin, 1992). To evaluate explanatory power of models, we used taxon-specific Tjur R^2 (Tjur, 2009) and area under the curve (AUC) (Pearce & Ferrier, 2000) within the HMSC framework, with default prior distributions (Ovaskainen & Abrego, 2020). In line with Ovaskainen et al. (2017), we conducted variance partitioning to discern the contributions of environmental variables and random effects in shaping diatom communities. This analysis involved examining the respective R^2 variance components attributed to the fixed and random effects of the HMSC models.

Finally, we assessed the influence of each diatom trait on species' responses to environmental gradients by analysing the gamma parameters collected from the model. These parameters measure the relationships between traits and niches (Ovaskainen & Abrego, 2020). Specifically, we examined the signs of gamma parameters—whether they were positive, negative or indicated no response, meaning no significant impact—with \geq 60% posterior probability. Moreover, we examined the beta parameters to see the individual response of species to environmental variables.

3 | RESULTS

According to the mixed model, there was not a statistically significant (p=0.56) difference in species richness between islands (median 17) and mainland (median 18) (Figure S3). Community compositions also overlapped between islands and mainland, but they were significantly (p < 0.05) different (Figure S4).

The Gelman and Rubin potential scale reduction factor for the HMSC model was <1.1, indicating good conversion for the model. With a mean explanatory power of Tjur R^2 =0.21 across species, the model provided valuable insights regarding the relationships

between different trait groups and environmental variables. However, the responses of the different traits were weak (with statistical support of 0.60). In particular, on the one hand, the highprofile trait group exhibited a negative relationship with Ca^{2+} . On the other, the low-profile group demonstrated a positive relationship with conductivity and Ca^{2+} , but a negative relationship with distance to the sea. Finally, motile showed a positive response to Na⁺ and a negative response with Cl^- (Figure 2). These trait responses align with some of the responses that we observed at species level. For example, we observed that at the individual level of the low-profile trait group, all the significant responses of species to conductivity and Ca^{2+} were positive. However, there were other variables such as Ca^{2+} in the high-profile or pH for all three trait groups that had both positive and negative responses at the species level (Figure S5).

The variance partition showed a similar, important contribution of the chemical variables for all of the traits, whereas the contributions of physical variables and especially random factors were notably lower for all traits (Figure 3).

Within the chemical variables, Ca^{2+} , Cl^- , Mg^{2+} and conductivity showed a higher contribution to trait variation than the others (Figure 4). For the physical variables, the stream length and slope showed slightly higher contribution than the other variables. Of individual variables, random variables (spatial location of sites) had overall the largest contribution to the three traits.

The variance partitioning analysis of the chemical variables revealed significant among-species differences in environmental associations within the trait groups, indicating distinct occurrences of specific species along environmental gradients. Notably, we identified a high number of indicator species within each trait group that were explained by particular environmental factors, in this case chemical variables. For example, among high-profile species, the occurrence of species such as *Eunotia bilunaris* (EBIL) and *Eunotia rhynchocephala* (ERHY) were best explained by pH, *Eunotia implicata* (EIMP) by conductivity, *Fragilaria capucina* var. *vaucheriae* (FCVA) by TN, *Gomphonema olivaceum* (GOLI) by Cl⁻, and *Eunotia tenella* (ETEN)

Motile Low-profile High-profile FIGURE 2 Heat map illustrating the gamma (γ) parameters, which depict the impact of traits on species responses to Intercept environmental characteristics. The colour of each cell indicates the direction of Stream length Area Slope – Sea distance – TN – F⁻– Cl⁻– B^r– Cl⁻– SO⁴²– N^a[†]– Ca²⁺– N^a[†]– the response (red for positive, blue for - pH -Elevation -Conductivity Intercept negative and white for no response). Note that only associations with statistical support of ≥60% posterior probability are represented by blue or red fills.

0



FIGURE 3 Variance partition results from the Hierarchical Modelling of Species Communities showing the mean relative contributions of different variable groups on diatom traits. The contributions of individual chemical and physical variables are all grouped into chemical or physical groups. Also, the contribution by random factor (spatial location of sites) on traits is shown.



by Ca²⁺ (Figure 5a). Among low-profile species, the occurrence of *Cocconeis placentula* (CPLA) was best explained by conductivity and *Eucocconeis laevis* (EULA) by TP, *Fragilaria arcus* (FARC) by Cl⁻ and *Rossithidium pusillum* (RPUS) by Ca²⁺ (Figure 5b). Among motile group species, the occurrence of *Navicula cryptotenella* (NCTE) was best explained by conductivity, *Navicula cocconeiformis* (NCOC) by TP, *Nitzschia alpina* (NZAL) by Cl⁻, *Navicula cryptocephala* (NCRY) and *Nitzschia hantzschiana* (NHAN) by Na⁺ (Figure 5c).

4 | DISCUSSION

We found that the motile and high- and low-profile diatom species as trait groups were overall relatively weakly associated with measured environmental variables. However, we found that the trait groups showed either positive or negative relationships with main anions or cations, for example Ca²⁺, Na⁺ or Cl⁻, or indicated the overall level of dissolved matter in the water (conductivity or sea distance). This was highlighted in the overall higher importance of chemical variables in determining communities compared with physical or

random factors. Moreover, we found that within a trait group, there was some among-species variation in species responses to environmental variables, which is important to consider when using diatom traits in ecological research and biomonitoring. Note, however, that responses were typically either negative or positive among those species that showed significant responses.

Our results showed that high-profile diatoms were favoured by lower Ca²⁺ concentrations, suggesting that they preferred soft waters, agreeing with Marcel et al. (2017) and Stenger-Kovács et al. (2013). By contrast, low-profile diatoms responded positively to Ca²⁺ and conductivity levels, which was also seen as their preference for being closer to the sea where conductivities are typically higher. Other studies have also found a preference of low-profile diatoms for higher conductivity levels in Finland (Soininen et al., 2016). However, it must be noted that the conductivity levels in our study area ranged from 15 to only 246 μ S/cm. Therefore, our study area might not cover a conductivity gradient notably high for suggesting very strong conclusions about trait preferences for conductivity.

The motile guild was likewise relatively weakly related to the environmental variables but like the low-profile diatoms, they showed FIGURE 5 Variance partition results from the Hierarchical Modelling of Species Communities showing the explained variance of diatom species to most important chemical variables: (a) High-profile; (b) low-profile; and (c) motile diatoms. The species codes can be found in Table S1.



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a negative relationship with Cl⁻ but a positive relationship with Na⁺. Other studies have shown more notable species-environment associations for motile species as they were shown to be positively associated with conductivity and nutrients (Bailet, 2021; Marcel et al., 2017; Stenger-Kovács et al., 2013), and negatively with water flow (Guo et al., 2020), for example. Note that Jamoneau et al. (2018) showed that motile species might be influenced by both local environmental conditions and dispersal mechanisms as these species could be more susceptible to mass effects hiding the impact of the local conditions (see also Heino et al., 2015). Such strong dispersal effects within stream networks may explain the weak species-environment relationships for this guild in our study.

Overall, our results support the earlier findings that chemical factors are typically more important for diatoms than physical or spatial factors (Soininen et al., 2004). This emphasises the usefulness of diatoms as indicators of water chemistry. However, water pH typically belongs to the most important local environmental factors that determine the diatom distribution and community composition in fresh waters (Soininen, 2007; Soininen et al., 2016). In this study, as in that by Teittinen et al. (2018), the effect of pH was surprisingly weak. The reason for such a finding is speculative at present but it could be linked to the fact that 94% of the sample sites had pH between 7.0 and 8.3, a not particularly extensive range. In addition, a clear variation was found in the response to pH in the three traits (i.e., species in the same trait showed different signs of response). Moreover, snapshot water pH measurements in the field are less reliable than conductivity measurements, which may decrease its importance in the models (Soininen et al., 2004). Likewise, we found that nutrients did not show strong importance on diatoms even if they are repeatedly considered as key drivers of stream diatoms (Soininen, 2007). This may be explained at least partly by the relatively low variability in nutrient levels among the study sites, all being oligotrophic with low human impact. Finally, it is likely that land cover type may have influenced diatom communities somewhat (Mutinova et al., 2020), even though it was found to be an insignificant factor in our analysis.

Despite the found trait-environment associations, our study indicated that environmental preferences may vary broadly within the diatom trait-groups. This variability of species preferences within the trait group may somewhat hinder in some circumstances (i.e., when communities comprise species that have similar traits but vary notably in their ecological preferences towards the key environmental factors) the use of ecological traits to describe the diatom community for ecological research or environmental assessment using diatoms. Furthermore, as some authors have suggested, these results highlight the need for creating subdivisions within the current guilds to enhance their suitability for evaluating environmental conditions (B-Béres et al., 2014). Note, however, that it is also possible that under some environmental conditions the response at the trait level may remain relatively conserved owing to the dominance of certain species, even though species may often vary in their dominance patterns. Moreover, adding traits other than those related to growth form will likely improve the use of traits in environmental assessments.

Our results highlight that there are certain indicator genera for water chemistry within the trait groups: such as Eunotia in the high-profile group, Achnanthes, in the low-profile group; and Navicula in the motile group. However, we also found some differences in their responses for the most important environmental variables within the genera. For instance, for the high-profile E.implicata species, conductivity emerged as the most important environmental variable, whereas E. bilunaris was more closely associated with water pH and E. tenella with Ca²⁺. In the low-profile group, conductivity was the most important explanatory variable for A. nodosa, whereas Ca²⁺ was the most important for A. minutissima. Conductivity was the most important driver of Navicula cryptotenella, whereas N. cryptocephala was best explained by Na⁺. Moreover, there were also some species that were not associated with measured environmental variables and their variance was best explained by spatial factors (Lindholm et al., 2018) or some environmental variables that were not measured in the study. For example, other physicochemical variables potentially important for freshwater diatoms and not considered here are substrate composition and colour (Castro et al., 2019; Kahlert et al., 2021; Passy, 2007; Soininen et al., 2004).

5 | CONCLUSIONS

Our results showed that diatom trait-groups were overall relatively weakly associated with measured environmental variables. However, we found that the trait groups indicated best the overall level of major ions in the water. This was highlighted in the high importance of chemical variables in determining communities compared with physical or random factors. We also found somewhat surprisingly that diatoms had very weak relationships with water pH or nutrients, highlighting that diatom species from geographically separated regions may not share the same environmental preferences owing to local adaptations. Moreover, the lack of certain environmental data and the overall oligotrophic stream water chemistry in our study area may contribute to different findings among studies. Furthermore, we propose that relying solely on ecological traits may not be sufficient to describe the relationships between diatoms and environmental variables, as there typically is some variation in species-level environmental preferences within each diatom trait-group. Ultimately, this suggests that biomonitoring campaigns should perhaps combine species-level taxonomic inventories with information about ecological traits.

AUTHOR CONTRIBUTIONS

Conceptualisation, data analysis and data interpretation: LC, JP, JS. Preparation of figures and tables: LC. Developing methods and conducting the research: JW, VP, MS. Writing: LC, JP, JS, JW, VP, MS.

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CONFLICT OF INTEREST STATEMENT

The authors of this manuscript do not have any conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data is available from the authors upon reasonable request.

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SUPPORTING INFORMATION

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

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