



# Diatom species assemblages and their environmental drivers in the major biogeographic provinces of India

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## Abstract

The present study was carried out in three distinct biogeographic provinces of India: the Himalaya, the Northeastern region, and the Deccan Plateau. The investigations aimed to understanding the association between physicochemical characteristics of water bodies and their influence on diatom assemblages. The majority of water quality parameters and diatom assemblages exhibited significant variations across the biogeographic regions. Canonical Correspondence Analysis (CCA) revealed that water quality parameters, including turbidity, iron, and potassium, significantly influenced diatom assemblages at the local scale (within rivers). Generalized Linear Model (GLM) analysis revealed that water temperature significantly impacted the abundance of diatom communities in the Himalayas and the Northeastern region, whereas dissolved oxygen influenced diatom abundance in the Deccan Plateau. The ecoregional differences in climatic and geological features influenced overall water quality, which, in turn affected the diatom communities at regional scales. A total of 21 common taxa were recorded across all biogeographic provinces. Among these taxa, *Ulnaria ulna*, *Achnantheidium affine*, *Achnantheidium lineare*, *Cocconeis placentula* var. *euglypta*, *Fragilaria pinnata*, *Navicula radiosa*, *Cymbella affinis*, and *Gomphonema olivaceum* indicated their broad tolerance to environmental variables, which was confirmed by their abundance and frequency distribution. The Himalayan waters were more conducive to inhabiting *Achnanthes*, *Navicula*, and *Cymbella* species, while the Deccan Plateau supported a relatively higher diversity of *Nitzschia* spp. Our study suggests that diatom assemblages and abundance respond not only to water quality but also to overall ecoregional differences.

**Keywords** Benthic diatom · Biogeography · Himalaya · Northeast India · Deccan Plateau · Environment

## Introduction

India is divided into 10 biogeographic provinces based on physiographic, climatic, and biotic features (Rodgers and Pawar 1988). Despite the richness of habitats and biodiversity, biogeographic studies in India have primarily focused

on terrestrial biodiversity, while aquatic biodiversity—except for fish fauna—has largely been overlooked (Bhatt et al. 2012; Singh and Chaturvedi 2017; Kotov and Taylor 2019). This trend may be true globally, as evidenced by the fewer macroecological studies on aquatic ecosystems and biodiversity worldwide (Heino 2011). Specifically, riverine ecosystems have received limited attention from ecologists and biogeographers, resulting in a lack of comprehensive understanding of the diversity and distribution of aquatic life across the Indian region. Nevertheless, the significance of aquatic ecosystems and their biodiversity cannot be overstated, given their crucial role in regulating biogeochemical cycles and primary productivity (Benoiston et al. 2017). Diatoms, in particular, are valuable indicators for evaluating the quality of aquatic ecosystems (Benoiston et al. 2017; Leira and Sabater 2005).

Diatom assemblages primarily respond to the physical and chemical characteristics of water, as well as to physiographic features such as the slopes and gradients of aquatic

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ecosystems (Stevenson and Pan 1999). Numerous studies have demonstrated the relationship between diatom assemblages and variables such as the physical and chemical properties of water, river morphology, and river size (Hughes et al. 2011; Lu et al. 2022; Lindholm et al. 2018; Wang et al. 2021). These environmental drivers significantly influence the community structure of diatoms at the local scale. However, very few comparative studies focus on diatoms inhabiting two or more distinct geographical regions with vastly different climatic, physiographic, and geomorphological characteristics (e.g., Cantonati et al. 2001; Nautiyal and Verma 2009). Such comparative studies can help address how diatom species composition and richness vary, as well as identify the drivers influencing diatom community structure at a regional scale (Charles et al. 2006).

This study investigated the variation in diatom community structure and its environmental drivers across three biogeographic regions in India: the Eastern Himalaya, North-east India, and the Deccan Plateau. These regions exhibit considerable diversity in physiographic and climatic features, supporting a wide range of fauna and flora. Given the limited studies on diatom biogeography in India (e.g. Nautiyal and Verma 2009; Verma et al. 2016) Given the limited

studies on diatom biogeography in India (e.g., Nautiyal and Verma, 2009), this research contributes to advancing the understanding of diatom biogeography. The findings of this comparative study will be valuable for understanding diatom assemblages in the context of ecoregional differences.

## Materials and methods

### Study area

The study was conducted between 2014 and 2018 in three distinct biogeographic regions: the Eastern Himalaya (Dibang, Kuri-Gongri, and Siang rivers), Northeast India (Umiew, Kopli, and Dikhu rivers), and the Deccan Plateau (Sileru, Krishna, and Godavari rivers) (Fig. 1). The Eastern Himalayan rivers are glacier-fed, flow through steep elevational gradients, and have riverbeds abundant in boulders. The predominant land use category surrounding the sampling sites is forest. In contrast, the rivers of the Deccan Plateau are rain-fed, with lower gradients and predominantly muddy riverbeds. The area is influenced by the anthropogenic activities, such as agriculture. The rivers of Northeast

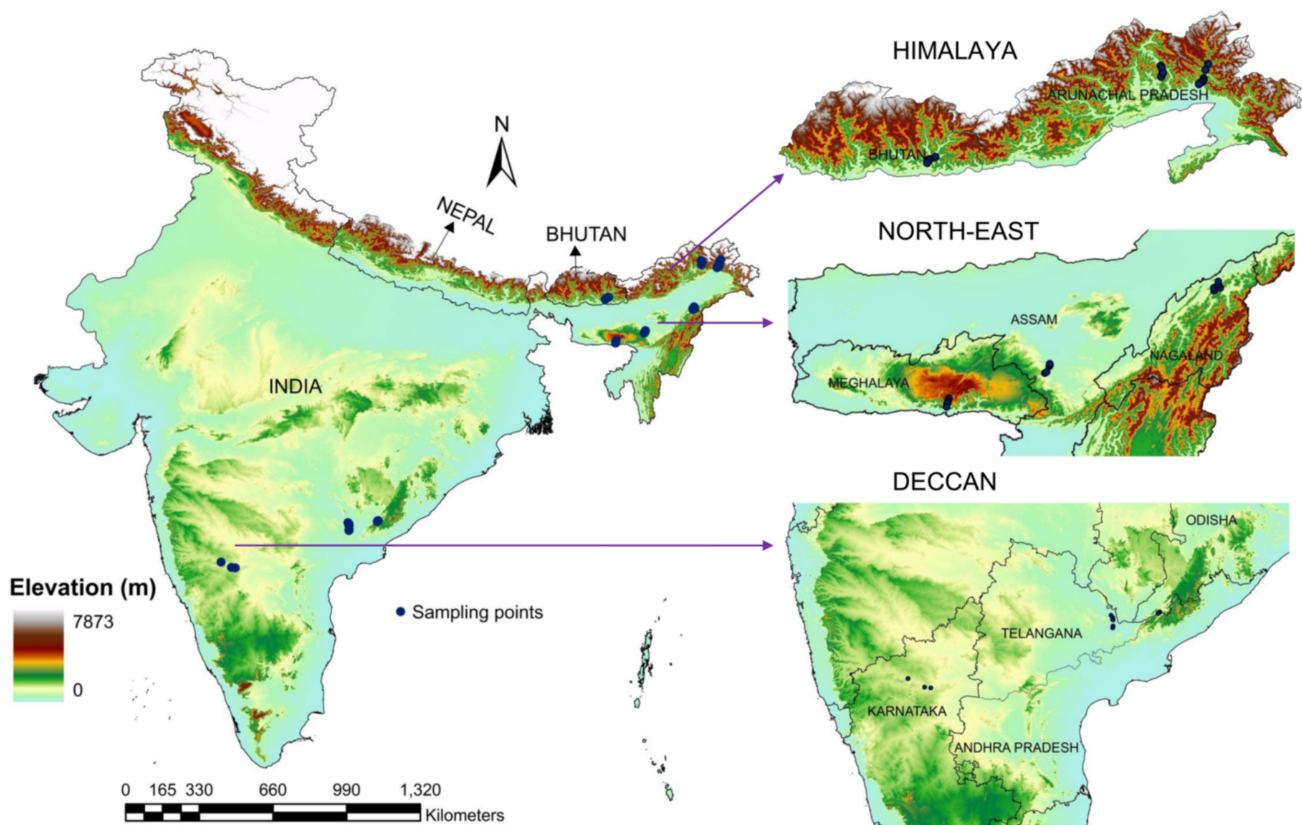


**Fig. 1** The location of different biogeographic provinces and sampling points. Upper right: Eastern Himalaya (Bhutan and Indian Himalaya). Middle right: Northeast India. Lower right; Deccan Plateau

India, which are also rain-fed, have moderate gradients, and their riverbeds are primarily characterized by sand and mud intermixed with boulders. The predominant land use category surrounding the sampling sites is forest. To conduct the Environmental Impact Assessment (EIA) study, we collected diatom and water quality samples from various regions of India across different seasons between 2014 and 2018. For this specific analysis, however, we selected these regions due to the similarity in sampling periods (winter season from November to February), which allowed for meaningful comparisons. Additionally, the winter season is considered to exhibit the highest richness in diatom flora.

## Environmental variables

A total of 21 physico-chemical environmental variables of river waters were measured from 49 sites in three biogeographic provinces (Eastern Himalaya, Northeast Region and Deccan Plateau). Water temperature was assessed using a graduated thermometer, while the float method was employed to measure the water current velocity (Bhatt et al. 2012). The pH measurements were recorded using a pHtestr 30 (Eutech). Electrical conductivity, total dissolved solids, and salinity were recorded using the TDSscan 3/ECtestr

11 + (Eutech), TDSscan 1/TDSest 11 + (Eutech), and Salttestr (Eutech), respectively. Three replicate samples were taken from each site and an average value was calculated for each site to obtain the final result. For other parameters, water samples were collected in sampling bottles (1000 ml) at each site and brought to the laboratory for further analysis. Water turbidity was measured using a digital turbidity meter (TN 100; Eutech). The remaining parameters listed in Table 1 were measured following the methods described by APHA (2005) and Adoni (1985). The physicochemical investigations thus carried out were grouped into three biogeographic provinces.

## Diatom assemblages

Benthic diatom samples were collected from all the sampling sites by scraping rock, boulder (from Himalaya), or mud and sand surfaces (Northeast Region and Deccan Plateau) covering a 5 cm<sup>2</sup> area with the help of a hard toothbrush, following the method described by Bhatt et al. (2008). Three replicates at each sampling site were collected, pooled, and preserved in Lugol's solution. The samples were brought to the laboratory for further analysis. For quantitative analysis, each sample was diluted to a volume of 100 ml using

**Table 1** Average values of physical and chemical variables recorded from different rivers of Himalaya Northeast and Deccan biogeographic provinces of India. The table also depicts the 'F' values (obtained One way 'ANOVA')

| Parameters                                            | Himalaya     | Northeast    | Deccan        | 'F' Value |
|-------------------------------------------------------|--------------|--------------|---------------|-----------|
| Water Temperature (°C)                                | 13.24±2.89   | 22.00±3.76   | 30.50±2.30    | 161.11    |
| Turbidity (NTU)                                       | 3.35±3.65    | 0.96±0.63    | 5.12±3.96     | 7.71      |
| Water current velocity (m s <sup>-1</sup> )           | 0.99±0.23    | 0.67±0.42    | 0.12±0.08     | 51.44     |
| pH                                                    | 8.14±0.18    | 7.23±1.17    | 8.04±0.87     | 6.34*     |
| Electrical Conductivity (µS cm <sup>-2</sup> )        | 152.82±69.14 | 107.73±68.07 | 314.78±232.26 | 10.06     |
| TDS (mg L <sup>-1</sup> )                             | 98.86±44.49  | 73.34±44.82  | 206.41±145.21 | 10.73     |
| Salinity (mg L <sup>-1</sup> )                        | 0.06±0.05    | 0.04±0.05    | 0.14±0.14     | 6.16*     |
| Dissolved Oxygen (mg L <sup>-1</sup> )                | 7.98±0.81    | 6.70±0.69    | 6.05±0.44     | 42.76     |
| Total Alkalinity (mg L <sup>-1</sup> )                | 60.53±32.77  | 34.82±15.40  | 90.67±59.77   | 8.42      |
| Total hardness mg L <sup>-1</sup> )                   | 105.05±48.84 | 78.71±35.06  | 121.50±109.72 | NS        |
| Calcium hardness (mg L <sup>-1</sup> )                | 80.96±37.91  | 39.49±16.18  | 65.17±60.95   | NS        |
| Ca <sup>++</sup> (mg L <sup>-1</sup> )                | 32.41±15.16  | 15.81±6.49   | 26.09±24.42   | NS        |
| Magnesium hardness (mg L <sup>-1</sup> )              | 24.09±13.23  | 39.22±25.60  | 54.24±50.31   | NS        |
| Mg <sup>++</sup> (mg L <sup>-1</sup> )                | 5.85±3.21    | 9.52±6.23    | 13.73±12.40   | NS        |
| Chloride (mg L <sup>-1</sup> )                        | 24.16±4.19   | 21.41±3.55   | 43.44±27.63   | 9.72      |
| Nitrate as NO <sub>3</sub> -N (mg L <sup>-1</sup> )   | 0.24±0.36    | 0.20±0.13    | 0.46±0.23     | 5.49†     |
| Phosphate as PO <sub>4</sub> -P (mg L <sup>-1</sup> ) | 0.27±0.15    | 0.16±0.09    | 0.10±0.07     | 12.14     |
| Sodium (mg L <sup>-1</sup> )                          | 5.51±2.81    | 9.43±5.42    | 10.91±1.64    | 6.31*     |
| Potassium (mg L <sup>-1</sup> )                       | 2.72±1.98    | 4.30±1.82    | 3.04±0.21     | 5.25†     |
| Iron (mg L <sup>-1</sup> )                            | 0.29±0.19    | 0.67±0.60    | 1.70±1.61     | 9.88      |
| Silicate (mg L <sup>-1</sup> )                        | 7.82±4.86    | 7.08±2.35    | 3.95±2.23     | NS        |

\* (P<0.005); † (P<0.01); For all values other than marked as \*, † (P<0.001); NS = Non-significant; Degree of freedom for Nitrate as NO<sub>3</sub>-N=2,39; Degree of freedom for silicate=2,15; Degree of freedom for other=2,53



distilled water and mixed thoroughly. Subsequently, a drop of 0.1 ml volume of each sample was transferred to a micro slide, and all diatom cells were counted under a microscope (Adoni 1985).

For the identification of diatom taxa, permanent slides were prepared. A portion of each benthic sample was centrifuged and treated with an equal volume of nitric acid. A few grains of potassium dichromate were added to the centrifuged residue, and the samples were left overnight. The samples were thoroughly washed the next day with distilled water to remove all traces of acid. A drop of the cleaned sample was placed on a micro slide and smeared using Mayer's egg albumin. The micro slide was allowed to air dry, after which the sample was dehydrated for 3 min in 95% alcohol, followed by absolute alcohol. It was then washed twice with xylol, following the method described by Bhatt et al. (2008). Permanent slides were prepared by mounting the material in Canada Balsam or Euparal. These slides were examined under a phase-contrast microscope using oil immersion (100 X 10× magnification). The identification of diatom taxa was conducted with the assistance of standard taxonomic literature, including Hustedt and Jensen (1985), Krammer and Lange-Bertalot (1986), and Sarode and Kamat (1984). The taxonomic validity of each diatom species was checked using the DiatomBase database (<https://www.diatombase.org/>) and the synonyms were removed from further analysis. After identifying the diatom species, we performed various statistical tests to determine the distinctiveness of diatom species assemblages and their associated environmental drivers in the three biogeographic zones.

## Diversity indices

We used three different diversity indices (species richness, Simpson diversity index, and Shannon diversity index) to compare the diatom diversity across the three biogeographic regions following standard methodologies (Simpson 1949; Shannon and Wiener 1963). We used PAST 4.02 software (Hammer et al. 2001) to calculate the species richness, the Simpson diversity index, and the Shannon diversity index for each biogeographic region.

In addition to the diversity indices, we used the measures of relative abundance (RA) and frequency (F) to identify the dominant and common diatom taxa in each biogeographic region using the following formulas:

$$RA = \frac{\text{density of } i\text{th taxon}}{\text{total density}} \times 100$$

where, RA = relative abundance (in %). The taxon that contributed 10% or more than 10% of the total density was

categorized as a dominant taxon in a particular biogeographic region.

$$F = \frac{\text{number of sites in which } i\text{th taxon occur}}{\text{total number of the sites studied in a river}} \times 100$$

where, F = frequency (%). The taxon that recorded 100% frequency was categorized as a common taxon of a particular biogeographic province.

## Statistical analyses: ordination analyses

To identify species assemblages and their environmental drivers, we used two statistical techniques: ordination and regression analyses. Canonical Correspondence Analysis (CCA) was applied to explore the relationship between diatom species distributions and environmental gradients in each biogeographic region, following the methodology of Ter Braak (1986). For each region, we averaged the abundance data of diatom species and environmental variables from the various rivers belonging to that biogeographic region.

In CCA, only diatom species present in at least 20% of the sampling sites within a region were selected for analysis. We used only environmental variables that were normally distributed (tested with Shapiro–Wilk tests) and had a Variance Inflation Factor (VIF) of less than 10. Variables that failed the normality test after log transformation were excluded from the analysis.

For each biogeographic region, we performed CCA on the selected diatom species and environmental variables using the following settings in CANOCO version 4.5 software (Ter Braak and Šmilauer 2002): biplot scaling, focused scaling on inter-species distances, correlation matrix, and automatic forward selection of environmental variables. The significance of the CCA and its axes was tested using Monte Carlo permutation tests (999 permutations,  $p = 0.05$ ).

## Statistical analyses: regression analyses

To quantify the strength and significance of the relationship between diatom species abundance and various environmental variables, we used the Generalized Linear Modelling (GLM) regression technique with Poisson error distribution and a logarithmic link using the broad methodology of Bhatt et al. (2012) and Manish et al. (2017). Before performing the GLM exercise, we used the averaged abundance data for different diatom species and environmental variables from different rivers belonging to a single biogeographic region. GLM modelling exercise first involved stepwise regression analyses using forward selection and backward elimination

procedures with the environmental variables in their linear and quadratic forms for each biogeographic region. It was followed by the selection of the environmental driver that best explained the diatom species abundance based on Akaike's information criterion (AIC) and Residual Deviance (RD). The variable with the least AIC and RD values, in either its linear or quadratic terms in the GLM, was considered the best environmental driver of diatom species abundance in a particular biogeographic region. In addition, the significance of the models ( $p < 0.05$ ) was also tested for each GLM of every environmental variable in its linear and quadratic form using z-tests. All GLM analyses were performed using R version 4.2.2 software (R Foundation for Statistical Computing, 2022).

## Results

### Environmental variables

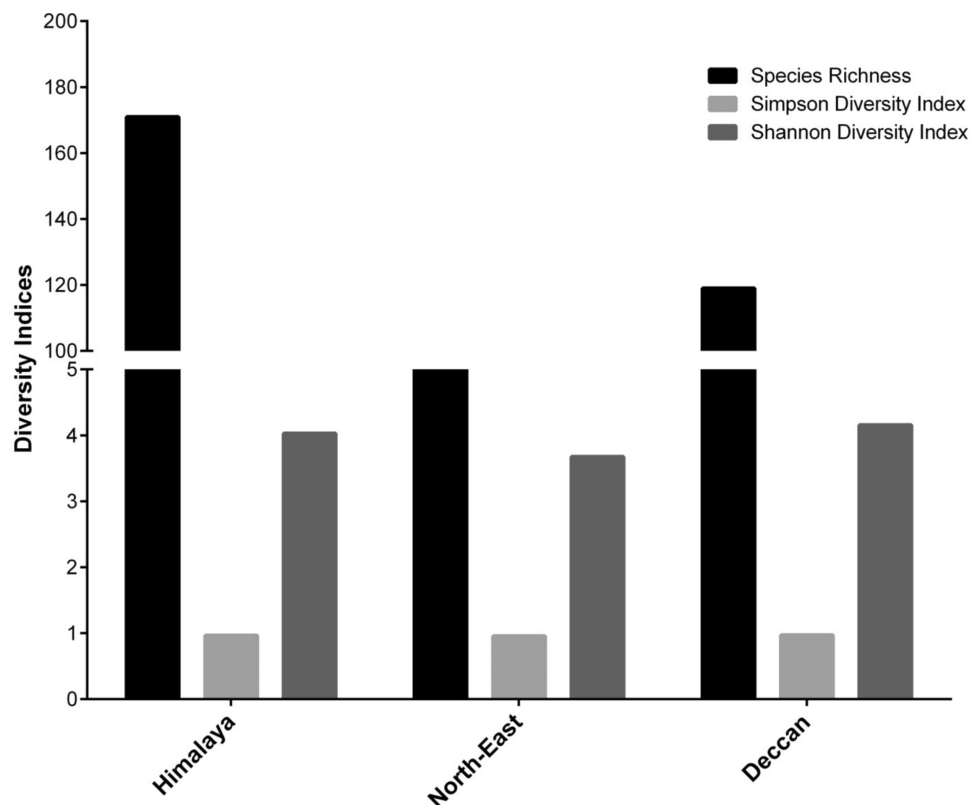
Table 1 presents the average values and standard deviations of each water quality parameter observed in three biogeographic provinces. Except for hardness, calcium, magnesium contents, and silicates, all the physical and chemical characteristics exhibited significant variations among the three biogeographic provinces. The details of the critical 'F' values and corresponding levels of significance are provided

in Table 1. Notably, water temperature ( $F_{2,53} = 161.11$ ;  $P < 0.001$ ), water current velocity ( $F_{2,53} = 51.44$ ;  $P < 0.001$ ), and dissolved oxygen ( $F_{2,53} = 42.76$ ;  $P < 0.001$ ) showed the most significant variations between the biogeographic provinces.

### Diversity indices and richness

The densities of benthic diatom taxa ranged from  $679.28 \pm 20.94$  to  $1655.71 \pm 47.58 \text{ cm}^{-2}$  in the Eastern Himalaya, from  $122.20 \pm 2.22$  to  $976.00 \pm 56.78 \text{ cm}^{-2}$  in Northeast region, and from  $809.00 \pm 13.82$  to  $2047.16 \pm 67.44 \text{ cm}^{-2}$  in Deccan region. The diversity indices indicated that the Eastern Himalayan region had the highest diatom species richness (153 species from 26 genera), followed by the Deccan region (114 species from 26 genera) and the Northeast region (85 from 24 genera) biogeographic regions (Fig. 2). A list of diatom taxa present in three different biogeographic provinces is given in Supplementary Information S1. Maximum values of species diversity were recorded in the rivers of the Eastern Himalayan region (Shannon diversity index = 4.36; Simpson diversity index = 0.96) followed by Deccan biogeographic region (Shannon diversity index = 4.12; Simpson diversity

**Fig. 2** The species richness and diversity indices used to explain the biodiversity attributes in the various biogeographic provinces



index = 0.97) and the Northeast region (Shannon diversity index = 4.03; Simpson diversity index = 0.95) (Fig. 2).

## Relative abundance

A list of taxa that accounted for more than 10% of the total density (dominant) and/or recorded 100% frequency (common) in one of the rivers of biogeographic regions is provided in Supplementary Information S2. A total of 8 dominant taxa, viz., *Ulnaria ulna*, *Achnantheidium affine*, *Achnantheidium lineare*, *Cocconeis placentula* var. *euglypta*, *Fragilaria pinnata*, *Navicula radiosa*, *Cymbella affinis*, and *Gomphonema olivaceum*, were cosmopolitan in distribution, recorded from all biogeographic provinces. These taxa were recorded with either more than 10% abundance, 100% frequency, or both in at least one of the rivers within each biogeographic province. The other taxa recorded from all biogeographic provinces included *Cocconeis placentula*, *Fragilaria capucina*, *Achnantheidium minutissimum*, *Planothidium lanceolatum*, *Navicula cryptocephala*, *Navicula halophila*, *Navicula rhynchocephala*, *Navicula pupula*, *Cymbella amphi-cephala*, *Cymbella ventricosa*, *Cymbella rupicola*, *Gomphonema bohemicum*, and *Gomphonema parvulum*. However, they did not meet the criteria for abundance and frequency as mentioned above. Greater similarity was observed in genera-richness compared to the species richness. Of the 37 genera, 17 (47%) were common across all biogeographic provinces.

The diatom taxa accounting for more than 1% of the total density that was unique to the Eastern Himalayan rivers included *Cymbella reinhardtii* and *Reimeria sinuata*. The taxa (> 1% of the total density) observed only from the Northeast region comprised *Navicula turgida*, *Navicula zebra*, and *Epithemia zebra* var. *saxonica*. The

diatom taxa accounted for > 1% of the total density and recorded exclusively from Deccan region comprised *Cymbella kolbei*, *Nitzschia fonticola*, *Nitzschia frustulum*, and *Nitzschia tryblionella* var. *calida*. There were a few species, such as *Didymosphenia geminata* *Rhopalodia gibberula* (Kurio-Gongri River), *Rossithidium nodosum* (Siang River), *Melosira granulata* (Umiew River), and *Stauroneis phoenicenteron* (Sileru River, which were rarely observed (less than 1% of the total density and specific to a particular river). The genera *Achnanthes/Achnantheidium* and *Fragilaria*, *Epithemia*, and *Nitzschia* exhibited relatively high diversity in the Himalayan, Northeastern, and Deccan regions, respectively (Supporting Information S1). The genera exclusive to the Himalaya included *Cymatopleura*, *Didymosphenia*, *Hannaea*, *Rhopalodia*, *Rossithidium*, and *Tetracyclus*. Similarly, the genera such as *Denticula* and *Licmophora* were found exclusively in the Northeast region. In contrast, the genera unique Deccan region were *Cymbopleura*, *Geissleria*, *Luticola*, *Mastogloia*, *Pleurosigma*, and *Stauroneis*.

## Species assemblages and the environmental drivers

The results of CCA analyses revealed distinct environmental gradients and unique diatom species assemblages across different rivers in biogeographic regions (Fig. 3). In the Eastern Himalayan region, three distinct clusters of diatom species assemblages were identified. The first cluster corresponded to the Kuri Gongri River (indicated by sampling site numbers 1–7). The second cluster to the Dibang River (sampling site numbers 9–14), and third cluster to the Siang River (sampling site numbers 15–19) (Fig. 3). Turbidity, Potassium (K), and Iron appeared to influence the diatom

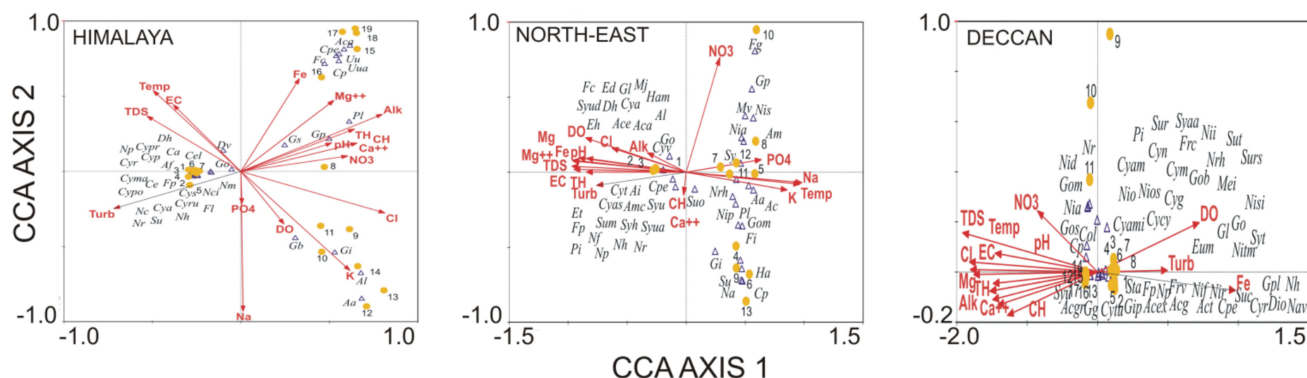


**Fig. 3** CCA analysis depicting the relationship between physicochemical variables and diatom assemblage in the Himalaya, the Northeast, and the Deccan biogeographic provinces. A list of diatom species and

their abbreviations used in the data analysis and manuscript can be found in the Supplementary Information S4

assemblages in three rivers of the Himalaya (Fig. 3). For the Northeast biogeographic region, the CCA results revealed two distinct clusters: the first cluster corresponded to the Dikhu River (indicated by the sampling site numbers 1–3), while the second, more diffused cluster, was formed by the Kopli and Umiew Rivers (sampling site numbers 4–13) (Fig. 3). The CCA results for the Deccan biogeographic region did not show any cluster (Fig. 3).

The results of GLM analysis, viewed from an overall regional perspective, revealed that water temperature was the primary environmental variable driving diatom species abundance in the Eastern Himalaya and Northeast biogeographic regions while dissolved oxygen (DO) was the main driver in the Deccan Plateau biogeographic region (Fig. 4). This result is based on the least AIC and RD values for water temperature in the Eastern Himalaya (AIC=105.4; RD=187.7) and the Northeast regions (AIC=42.9; RD=13.01) as well as for DO in the Deccan regions (AIC=96.77; RD=207.4) (Supplementary Information S3). When diatom species abundance was modelled as a function of the best predictor (environmental variable), the results indicated a hump-shaped relationship between diatom

abundance and water temperature in the Eastern Himalayan region (Fig. 4). Maximum diatom abundance was observed in water with temperatures ranging from 13<sup>0</sup> to 15<sup>0</sup> C in the Eastern Himalayan region (Fig. 4). In the Northeast region, diatom species abundance showed a uniform decline with the increasing water temperature levels (Fig. 4). Maximum diatom abundance in the Northeast region correlated with waters having temperatures of 16<sup>0</sup> C to 17.5<sup>0</sup> C. (Fig. 4).

## Discussion

India's biogeographic regions exhibit a wide range of variations in terms of topography, geology, and climate (Rodgers and Pawar 1988). The variations in topography and climate affect the physical and chemical characteristics of river waters as reflected in the present study and reported previously (Subramaniam 2004). These variations are also known to influence the diatom assemblages in the rivers (Pan et al. 2000; Szczerba et al. 2023; Potapova and Charles 2002). Compared to higher taxa, diatom assemblages are significantly influenced by the physical and chemical variables of

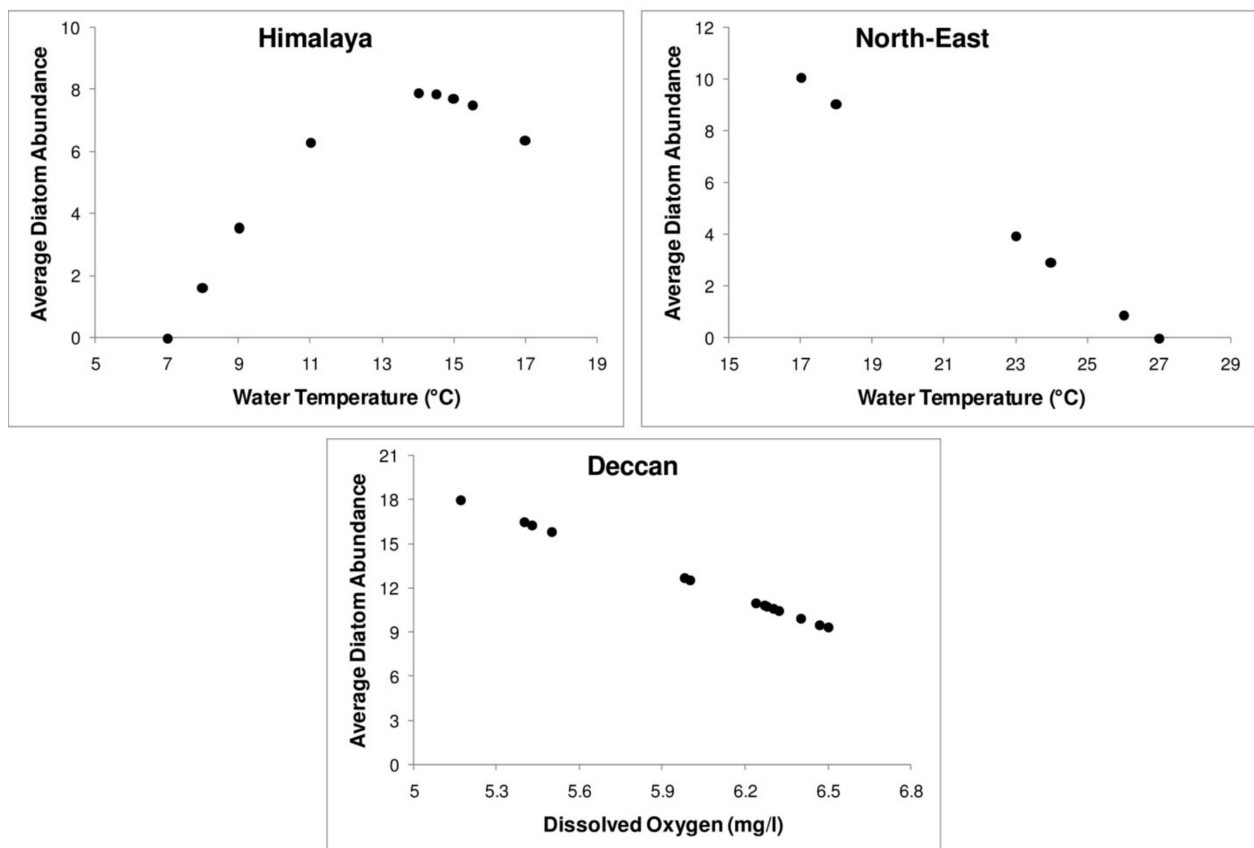


**Fig. 4** A Generalized Linear Model (GLM) depicting the relationship between species abundance and water quality parameters. Water temperature emerged as the most important determining factor shaping

diatom abundance in the Himalaya and the Northeast region, while dissolved oxygen shaped diatom abundance in the Deccan Plateau



river waters due to their short life cycles and high sensitivity to environmental factors (Lobo et al. 2016). In the present study, certain specific physical and chemical characteristics of water bodies appeared to affect the diatom assemblages at a local scale (within a river and within a region) but did not indicate any specific effects on the diatom assemblages at a regional scale (Charles et al. 2006; Shibabaw et al. 2021). However, the cumulative impact of these parameters may explain the variation in the density, diversity, and richness of diatom species. This inference is based on the fact that the majority of physical and chemical characteristics showed significant variations between the Eastern Himalaya, Northeast and Deccan biogeographic regions (Charles et al. 2006).

Different water quality parameters (turbidity, K,  $\text{PO}_4$ , and iron) affected diatom assemblages differently in the rivers of the same biogeographic province. Water temperature seemed to affect the diatom abundances within a region, especially in the Eastern Himalayan and Northeast biogeographic provinces, as suggested by GLM results in the present study. Conversely, the Dissolved Oxygen in the Deccan rivers appeared to be the important environmental driver of diatom species assemblages (see Tan et al. 2017). The analyses indicated that temperatures in the Himalayan and the Northeast region rivers, ranging from  $14^\circ\text{C}$  to  $17.5^\circ\text{C}$ , were optimal for the growth of diatom communities. This result is supported by earlier studies that suggested water temperatures  $\leq 25^\circ\text{C}$  are relatively favourable for the growth of benthic diatom communities (Delgado et al. 2020). These findings are also supported by the studies of Jüttner et al. (2003) carried out in the rivers of Nepal. Their results revealed that electrical conductivity and concentrations of  $\text{NO}_3$ ,  $\text{PO}_4$ , Si, Na, and Cl were critical factors in shaping diatom assemblages within a region.

The drivers of diatom species composition may vary at the regional scale when comparing different regions. Variation in the land use, land cover, geological characteristics, and physiographic features are key factors influencing diatom assemblages at the regional scale (Jüttner et al. 2003; Soininen 2007; Baker et al. 2022). In the Himalaya, the high richness of diatoms can be attributed to their predominantly epilithic nature, as opposed to the epipsammic and epipelagic nature observed in the northeastern and Deccan regions (e.g. Townsend and Gell 2005). In addition, the steep gradients of Himalayan rivers, along with the presence of boulders, create numerous microhabitats that support epilithic diatoms, contributing to their high richness and diversity (Taxböck et al. 2020; Baker et al. 2022).

Investigation of the diatom community composition revealed that there was a high degree of dissimilarity at the species level across the three regions investigated. For instance, of more than 265 diatom species/varieties in the three regions, only 21 species/varieties were common to all the regions whereas maximum 38 species (about 18%) were common in

any two biogeographic regions (the Himalaya and Northeast India). In contrast, community composition at the genera level exhibited greater similarity (as compared to the species level), with approximately 47% genera being common. Similar findings were reported by Verma et al. (2016) in their study on diatom assemblages across three distinct biogeographic provinces: the Central Highlands, the Eastern Ghats, and the Western Himalaya. Similarly, Borrego-Ramos et al. (2023) showed that similarity in genera richness exhibits stronger phylogenetic signals than species richness. Our results, i.e. high similarity in community composition at the genera level and high dissimilarity at the species level, point out that the different biogeographic regions have become centres of speciation and species diversification. This can be due to a high level of habitat and environmental heterogeneity within the aquatic ecosystems of the Himalaya, Northeast India and Deccan region (Pandit 2017). The movement of the landmasses, especially in the Himalaya and Northeast India has shaped the evolution of drainage patterns that have resulted in high genera similarity (e.g., Verma et al. 2016). In the Himalaya, periodic episodes of geophysical and climatic upheavals have repeatedly created new conditions for speciation and diversification (Manish and Pandit 2018).

One of the significant findings in this study was the spatial structuring exhibited by diatom assemblages. The CCA results revealed that spatial structuring in the diatom flora was more predominant in the Eastern Himalaya, followed by the Northeast region. Both are mountainous landscapes, with the Himalaya characterized by deep, steep, undulating, and rugged topography in contrast to the Northeast region. On the other hand, the sampling area in the Deccan plateau biogeographic region is relatively flat in its topographic features.

Diatoms are suitable indicators of water quality due to their specific ecological preferences, which are shaped by the physico-chemical properties of water (Cantonati et al. 2001). A total of 21 taxa mentioned above exhibit a wide range of distribution across various environmental variables, as confirmed in other studies (see Hoagland et al. 1982; Caglar et al. 2017). Some of them, such as *Cocconeis euglypta*, *Ulnaria ulna*, *Navicula rhynchocephala*, *Cymbella affinis*, *Gomphonema olivaceum*, *Gomphonema parvulum*, etc., not only exhibit a cosmopolitan distribution but are also known as the indicators of nutrient rich-water (Hoagland et al. 1982; Patrick and Palavage 1994). Based on the abundance and frequency, these diatom species can be designated as highly tolerant of environmental variables in the present study.

In the current study, *Achnanthes*, *Achnanthidium*, *Fragilaria*, and *Cymbella* emerged as notable diverse genera in the Himalayan waters, characterized by low temperatures, a high concentration of dissolved oxygen, and swift water currents. These genera typically align with the Himalayan

conditions, with exceptions such as *Achnantheidium affine*, *Achnantheidium lineare*, and *Fragilaria virescens* f. *subsalina* (Patrick and Palavage 1994). In the Northeast region, the genus *Epithemia* exhibits relatively high diversity, thriving in environments characterized by low pH and low concentrations of  $\text{NO}_3\text{-N}$ . *Epithemia* has been identified as an indicator of microhabitats with limited fixed nitrogen (Lowe 2003). Conversely, *Nitzschia* demonstrated a higher diversity in Deccan rivers compared to the Himalayan and Northeastern rivers. The Deccan river waters were characterized by higher temperature, turbidity, electrical conductivity, total dissolved solids (TDS), total alkalinity, and hardness. These habitats appeared conducive to the growth of *Nitzschia*, an indicator of deteriorated water quality (Whitton and Rott 1996). Some genera were unique to specific biogeographic regions. For example, *Cymatopleura* and *Hannaea*, which are considered highly sensitive to pollution, were reported from Himalayan waters. Similarly, *Denticula*, recorded exclusively from rivers in the Northeastern region, is intolerant of organic pollution. In contrast, genera such as *Luticola*, *Mastogloia*, and *Pleurosigma* are known for their tolerance to stressed waters. These genera were observed only in the Deccan rivers, which are characterized by high nutrient concentrations, hardness, alkalinity, elevated temperatures, and low dissolved oxygen levels (Muscio 2002).

Many rare species of diatoms are specific to particular rivers and account for less than 1% of the total population density. Among these, two species are particularly notable for their ecological significance. *Melosira* sp., a centric diatom, is rarely found in freshwater environments but has been identified in sediments with a historical record exceeding 10,000 years (Kilham 1990). *Didymosphenia geminata*, on the other hand, is a highly invasive species that inhabits freshwater ecosystems in some European rivers and the Southern Hemisphere. In India, it has been recorded exclusively in Himalayan rivers under oligotrophic conditions and is dominant at high elevations in certain river systems (Bhatt et al. 2008). However, it was not invasive in any Himalayan rivers.

## Conclusion

This study investigates the ecological dynamics affecting the distribution of diatom flora across the biogeographic provinces of India. Understanding diatom assemblages across biogeographic regions requires consideration of complex ecological processes, including the interaction of diatom flora with overall water quality, substrate structure, geological, and climatic features (e.g. Le Reun et al. 2022). Our findings revealed that the richness and abundance of diatom species can be influenced by various physical and chemical characteristics, either individually or in combination, such

as temperature, pH, K, conductivity, dissolved oxygen, nutrients, etc., at a local scale (within a river). Two parameters, temperature and dissolved oxygen appeared to influence the diatom assemblages within a region. The spatial structuring of diatoms was largely shaped by specific features of biogeographic provinces like Geology (nature of substrata), and physiography (gradients) (Soininen 2007) at regional scale. The substantial differences in substratum types, gradient-driven current velocity across these regions appear to influence diatom assemblages, particularly their species composition (Baker et al. 2022; Le Reun et al. 2022; Passy 2001).

Although brief, this study provides valuable insights into the evolutionary pattern in the diatoms. Our findings also highlight the indicator value of diatoms in assessing habitat quality (Jüttner et al. 2003). The diatom assemblages suggest that genera such as *Achnanthes*, *Achnantheidium*, and *Fragilaria* thrive in highly oxygenated water with low temperatures, high current velocity, and epilithic substrates. In contrast, *Nitzschia* flourishes in stressed water conditions. Understanding diatom assemblages and their response to various water quality parameters can play a crucial role in water quality monitoring.

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**Data availability** The data has been provided in supplementary information.

## Declarations

**Conflict of interest** The author declares no competing interest.

## References

- Adoni, A.D.: Work Book on Limnology. Bandna Printing Service, New Delhi (1985)
- APHA: Standard Methods for the Examination of Water and Wastewater. American Public Health Association, New York (2005)
- Baker, L.A., Biron, D.G., Millan, F., Voldoire, O., Breton, V., Allain, E., Wetzel, C.E., Ector, L., Beauger, A.: The substrate, a key factor or not, to explain the species diversity of diatom communities in mineral springs. *Bot. Lett.* **169**, 155–165 (2022). <https://doi.org/10.1080/23818107.2022.2028186>
- Benoiston, A.-S., Ibarbalz, F.M., Bittner, L., Guidi, L., Jahn, O., Dutkiewicz, S., Bowler, C.: The evolution of diatoms and their biogeochemical functions. *Phil. Trans. Roy. Soc.* **372**, 20160397 (2017). <https://doi.org/10.1098/rstb.2016.0397>



- Bhatt, J.P., Bhaskar, A., Pandit, M.K.: Biology, distribution and ecology of *Didymosphenia geminata* (Lyngbye) Schmidt an abundant diatom from the Indian Himalayan rivers. *Aquat. Ecol.* **42**, 347–353 (2008). <https://doi.org/10.1007/s10452-007-9106-2>
- Bhatt, J.P., Manish, K., Pandit, M.K.: Elevational gradients in fish diversity in the Himalaya: water discharge is the key driver of distribution patterns. *PLoS ONE* (2012). <https://doi.org/10.1371/journal.pone.0046237>
- Borrego-Ramos, M., Rimet, F., Becares, E., Blanco, S.: Environmental drivers of genetic variability in common diatom genera: Implications for shallow lake biomonitoring. *Ecol. Indic.* **154**, 110898. <https://doi.org/10.1016/j.ecolind.2023.110898>
- Caglar, M., Pala, G., Selamoglu, Z.: Study on epilithic diatoms in the Balikli Tohma Creek (Darende/Malatya in Turkey). *Iran J. Fish. Sci.* **16**, 858–868 (2017)
- Cantonati, M., Corradini, G., Jüttner, I., Cox, E.J.: Diatom assemblages in high mountain streams of the Alps and the Himalaya. *Nova Hedwig. Beih.* **123**, 37–61 (2001)
- Charles, D.F., Acker, F.W., Hart, D.D., Reimer, C.W., Cotter, P.B.: Large-scale regional variation in diatom-water chemistry relationships: rivers of the eastern United States. *Hydrobiologia* **561**, 27–57 (2006). <https://doi.org/10.1007/s10750-005-1603>
- Delgado, C., Feio, M.J., Pardo, I., Almeida, S.F.P.: Effects of water temperature over benthic diatom communities: insights from thermal springs. *Plant Ecol. Divers.* **13**, 325–337 (2020). <https://doi.org/10.1080/17550874.2020.1762133>
- Hammer, Ø., Harper, D.A., Ryan, P.D.: PAST: paleontological statistics software package for education and data analysis. *Palaeontol Electron* **9** (2001)
- Heino, A.: A macroecological perspective of diversity patterns in the freshwater realm. *Freshwat. Biol.* **56**, 1703–1722 (2011). <https://doi.org/10.1111/j.1365-2427.2011.02610.x>
- Hoagland, K.D., Roemer, S.C., Rosowski, J.R.: Colonization and community structure of two periphyton assemblages with emphasis on the diatoms (Bacillariophyceae). *Am. J. Bot.* **69**, 188–213 (1982)
- Hughes, R.M., Kaufmann, P.R., Weber, M.H.: National and regional comparisons between Strahler order and stream size. *J. n. Am. Benthol. Soc.* **30**, 103–121 (2011)
- Hustedt, F., Jensen, N.G.: *The Pennate Diatoms*. Koeltz Scientific Books, Koenigstein (1985)
- Jüttner, I., Sharma, S., Dahal, B.M., Ormerod, S.J., Chimonides, P.J., Cox, E.J.: Diatoms as indicators of stream quality in the Kathmandu Valley and Middle Hills of Nepal and India. *Freshwat. Biol.* **48**, 2065–2084 (2003)
- Kotov, A.A., Taylor, D.J.: Contrasting endemism in pond-dwelling cyclic parthenogens: the *Daphnia curvirostris* species group (Crustacea: Cladocera). *Sci. Rep.* **9**, 6812 (2019). <https://doi.org/10.1038/s41598-019-43281-9>
- Krammer, K., Lange-Bertalot, H.: *Bacillariophyceae, Süßwasserflora von Mitteleuropa*, 2 (1–4). Fischer Verlag, Jena, VEB G (1986)
- Le Reun, N., Bramucci, A., O'Brien, J., et al.: Diatom biogeography, temporal dynamics, and links to bacterioplankton across seven oceanographic time-series sites spanning the Australian continent. *Microorganisms* **10**, 338 (2022). <https://doi.org/10.3390/microorganisms10020338>
- Leira, M., Sabater, S.: Diatom assemblages distribution in Catalan rivers, NE Spain, in relation to chemical and physiographical factors. *Wat. Res.* **39**, 73–82 (2005). <https://doi.org/10.1016/j.watres.2004.08.034>
- Lindholm, M., Gronroos, M., Hjort, J., Karjalainen, S.M., Tokola, L., Heino, J.: Different species trait groups of stream diatoms show divergent responses to spatial and environmental factors in a sub-arctic drainage basin. *Hydrobiologia* **816**, 213–230 (2018). <https://doi.org/10.1007/s10750-018-3585-0>
- Lobo, E.A., Heinrich, C.G., Schuch, M., Wetzel, C.F., Ector, L.: Diatoms as bioindicators in rivers. In: Necchi, J.R. (ed.) *River algae*, pp. 245–271. Springer, Cham, (2016). [https://doi.org/10.1007/978-3-319-31984-1\\_11](https://doi.org/10.1007/978-3-319-31984-1_11)
- Lowe, R.L.: Keeled and canalised raphid diatoms. In: Wehr, J.D., Sheath, R.G., Kociolek, J.P. (eds.) *Freshwater algae of North America: ecology and classification*, pp. 669–684. Academic Press, (2003)
- Lu, X., Zhang, Y., Liu, Y., Fan, Y.: Differences in planktonic and benthic diatoms reflect water quality during a rainstorm event in the Songhua River basin of Northeast China. *Ecol. Indic.* **144**, 109547 (2022). <https://doi.org/10.1016/j.ecolind.2022.109547>
- Manish, K., Pandit, M.K.: Geophysical upheavals and evolutionary diversification of plant species in the Himalaya. *Peer J* **6**, e5919 (2018). <https://doi.org/10.7717/peerj.5919>
- Manish, K., Pandit, M.K., Telwala, Y., Nautiyal, D.C., Koh, L.P., Tiwari, S.: Elevational plant species richness patterns and their drivers across non-endemics, endemics and growth forms in the Eastern Himalaya. *J. Plant Res.* **130**, 829–844 (2017). <https://doi.org/10.1007/s10265-017-0946-0>
- Muscio, C.: The diatom pollution tolerance index: Assigning tolerance values. city of Austin - Watershed Protection and Development Review Department, 17 pp (2002).
- Nautiyal, P., Verma, J.: Taxonomic richness and diversity of the epilithic diatom flora of the two biogeographic regions of the Indian subcontinent. *Bull. Nat. Inst. Ecol.* **20**, 15–21 (2017)
- Pan, Y., Stevenson, R.J., Hill, B.H., Herlihy, A.T.: Ecoregions and benthic diatom assemblages in Mid-Atlantic Highlands streams. *USA. J. n. Am. Benthol. Soc.* **19**, 518–540 (2000)
- Pandit, M.K.: *Life in the Himalaya: An ecosystem at risk*. Harvard University Press, (2017)
- Passy, S.I.: Spatial paradigms of lotic diatom distribution: a landscape ecology perspective. *J. Phycol.* **37**, 370–378 (2001). <https://doi.org/10.1046/j.1529-8817.2001.037003370.x>
- Patrick, R., Palavage, D.M.: The value of species as indicators of water quality. *Proc. Acad. Nat. Sci. Philad.* **145**, 55–92 (1994)
- Potapova, M.G., Charles, D.F.: Benthic diatoms in USA rivers: distributions along spatial and environmental gradients. *J. Biogeogr.* **29**, 167–187 (2002). <https://doi.org/10.1046/j.1365-2699.2002.00668.x>
- Rodgers, W.A., Panwar, H.S.: Planning a wildlife protected area network in India. 2 vol. Project FO: IND/82/003, FAO, Dehradun, 339, 267 (1988)
- Sarode, P.T., Kamat, N.D.: *Freshwater Diatoms of Maharashtra*. Sainkripa Publication, Aurangabad (1984)
- Shannon, C.E., Weaver, W.: *The Mathematical Theory of Communication*. University of Illinois Press, Urbana (1949)
- Shibabaw, T., Beyene, A., Awoke, A., Tirfie, M., Azage, M., Triest, L.: Diatom community structure in relation to environmental factors in human influenced rivers and streams in tropical Africa. *PLoS ONE* **16**, e0246043 (2021). <https://doi.org/10.1371/journal.pone.0246043>
- Simpson, E.H.: Measurement of diversity. *Nature* **163**, 688 (1949). <https://doi.org/10.1038/163688a0>
- Singh, J.S., Chaturvedi, R.K.: Diversity of ecosystem types in India a review. *Proc. Indian. Nat. Sci. Acad.* **83**, 569–594 (2017)
- Soininen, J.: Environmental and spatial control of freshwater diatoms - a review. *Diatom Res.* **2**, 473–490 (2007). <https://doi.org/10.1080/0269249X.2007.9705724>
- Stevenson, R.J., Pan, Y.: Assessing conditions in rivers and streams with diatoms. In: Stoermer, E.F., Smol, J.P. (eds.) *The diatoms: applications for the environmental and earth sciences*, pp. 11–40. Cambridge University Press (1999)
- Subramaniam, V.: Water quality in South Asia. *As. J. Wat. Environ. Poll.* **1**, 41–54 (2004)
- Szczerba, A., Rzedkiewicz, M., Tylmann, W.: Modern diatom assemblages and their association with meteorological conditions in

- two lakes in northeastern Poland. *Ecol. Indic.* **47**, 110028 (2023). <https://doi.org/10.1016/j.ecolind.2023.110028>
  - Tan, X., Zhang, Q., Burford, M.A., Sheldon, F., Bunn, S.E.: Benthic diatom based indices for water quality assessment in two subtropical streams. *Aquat. Microbiol.* (2017). <https://doi.org/10.3389/fmicb.2017.00601>
  - Taxböck, L., Karger, D.N., Kessler, M., Spitale, D., Cantonati, M.: Diatom species richness in Swiss springs increases with habitat complexity and elevation. *Water* **12**, 449 (2020). <https://doi.org/10.3390/w12020449>
  - Ter Braak, C.J.F.: Canonical correspondence analysis: A new eigenvector technique for multivariate direct gradient analysis. *Ecology* **67**, 1167–1179 (1986)
  - Ter Braak, C.J.F., Smilauer, P.: CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (version 4.5). Biometris, Wageningen (2002)
  - Townsend, S., Gell, P.A.: The role of substrate type on benthic diatom assemblages in the Daly and Roper rivers of the Australian wet/dry tropics. *Hydrobiologia* **548**, 101–115 (2005). <https://doi.org/10.1007/s10750-005-0828-7>
  - Verma, J., Gopesh, A., Nautiyal, P.: Biogeography and distribution of bacillariophyceae in the highland rivers of India. *Int. J. Appl. Res.* **2**, 356–359.
  - Wang, X., Zhang, Y., Tan, X., Zheng, Y., Zhang, Q.: Do water quality, land use, or benthic diatoms drive macroinvertebrate functional feeding groups in a subtropical mountain stream? *Inland Wat.* **11**, 67–77 (2021). <https://doi.org/10.1080/20442041.2020.1816111>
  - Whitton, B.A., Rott, E. (eds.): Use of algae for monitoring rivers II. University of Innsbruck, Innsbruck, Austria, Institute of Botany (1996)
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