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Anthropogenic drivers shift diatom dominance–diversity relationships and transparent exopolymeric particles production in River Ganga: implication for natural cleaning of river water

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We studied the relationships among diatom biodiversity, transparent exopolymeric particles (TEP) and water quality at the confluences of four tributaries of River Ganga (Yamuna, Assi, Varuna and Gomti) during low flow. Diatom abundance changed with concurrent shifts in water chemistry with dominance–diversity curves markedly skewed from a log-normal pattern. Canonical correspondence analysis segregated chloride-loving and calcifilous species from N- and P-favoured taxa. Despite pollution-induced reduction of diatom diversity, TEP production continued to rise plausibly due to dominance transference of TEP producers. However, with further increase in nutrient pollution, TEP declined. Since TEP enhances sedimentation removal of carbon, nutrients and heavy metals, the present study confirms one of the fundamental mechanisms that underline the self-purification capacity of River Ganga and has relevance from a biodiversity/river conservation perspective.

THE relative positions of species along environmental gradients reflect affinities to resources and modifying influences of stressors and disturbances. Ecosystems with high species diversity are relatively efficient in buffering ecological impacts of, for instance, nutrient pollution[1]. Diatom communities, a diverse group of benthic protists in aquatic ecosystems, are modulated by nutrients as well as ionic composition, pH, light and temperature[2–4]. At the same time, diatoms with unique cell-wall composition and potential to produce transparent exopolymeric particles (TEP) help regulating carbon sequestration and removal of nutrients and heavy metals[5].

The role of biodiversity in improving ecosystem stability and recovery is now well-established[6,7], but the

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specific mechanisms by which biodiversity helps buffering natural ecosystems against anthropogenic perturbations have not been properly identified[1]. Anthropogenic disturbances are known to reduce biodiversity[8], while the existing diversity tends to reduce ecological impacts of such disturbances[1]. Thus, an understanding of how this dual causality balances out to control each other and help maintain ecosystem resilience has great relevance from the conservation perspective. Driven by increasing input of industrial and municipal waste coupled with atmospheric deposition and agricultural run-off causing large changes in its water quality[9], River Ganga may exhibit a shift in diatom community and, consequently, in the concentration of TEP. Preservation of the Ganga is a national priority both in terms of biodiversity conservation and water quality assurance. Since TEP help in C-sequestration and sedimentation removal of nutrients and heavy metals, we studied the aspect of water chemistry–diatom–TEP relationships with possible implications for natural cleaning of river water.

In this study, conducted at the confluence of four tributaries of the Ganga (Yamuna, Assi, Varuna and Gomti; Figure 1), we performed two sets of experiments – first, measurement of relative abundance and diversity of diatoms to understand dominance–diversity links with water quality, and second, determination of TEP and mechanistic links with water chemistry and dominance transference. Limestone bricks (21 cm × 11 cm × 6 cm), fixed with bamboo pole, were deployed (three at each sub-site; before, at and after the confluence; ~100 m upstream and downstream; 10 m reach) at all sites to allow colonization by algae over a period of two months (15 April to 14 June) during low flows (river discharge 372–543 $m^3 s^{-1}$) for four consecutive years (2011–
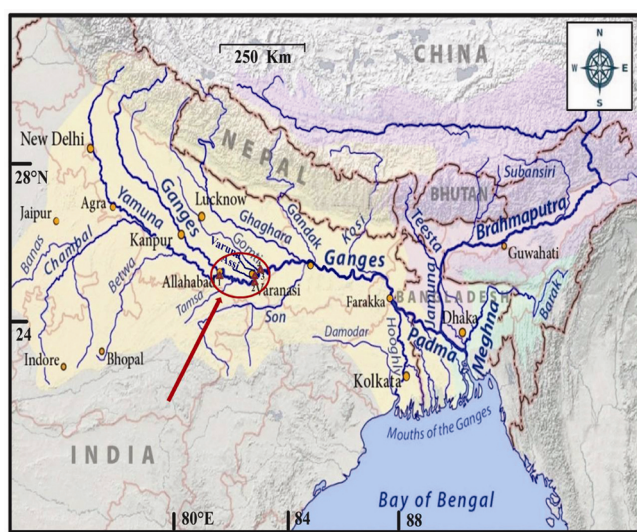

Figure 1. Map showing location of sampling stations. Numbers 1–4 represent confluences of Yamuna, Assi, Varuna and Gomti with River Ganga.

2014)[10]. Bricks (75–85% colonized) were removed after two months; diatoms removed by tooth brushing were digested in hot hydrogen peroxide and valves counted using Nikon trinocular inverted microscope (model TS 100-F) and Metzer light microscope at 1000× following standard protocols[11]. Samples for TEP originating from the same bricks were analysed spectrophotometrically[12]. Six replicate samples were filtered on 0.4 μm polycarbonate filters and stained with Alcian blue. Stained particles were rinsed-off and dissolved in 10 ml 80% H_2SO_4. After 3 h, absorption was measured at 787 nm (ref. 12). Gum xanthan was used for calibration. Three separate sample materials filtered and stained as above were also analysed for TEP abundance using microscopy[12]. Contribution of diatom was validated using autotrophic index and taxonomic biomass as described elsewhere[13]. For analysis of water variables, we collected three composite samples (before, at and after the confluence; ~100 m upstream and downstream) from all sites at the middle of each experimental month, and three composite samples just before the beginning of the first experiment. Samples were collected from directly below the surface (15–25 cm depth) in acid-rinsed BOD bottles and 5 l plastic containers. Variables such as water temperature, pH, total dissolved solids (TDS) and conductivity were measured onsite. Water samples were stored at 4°C (Protocol No. 1060)[14] and analysed for dissolved oxygen (DO), biological oxygen demand (BOD), dissolved organic carbon (DOC), dissolved silica (DSi), biogenic silica (BSi) nutrients and ionic composition following standard methods[14]. Light attenuation in the river was measured onsite using Secchi disk. Differences in water chemistry variables were evaluated using analysis of variance (ANOVA; SPSS, version 16)[15]. A Tukey HSD test was used for comparing TEP at each site. Bilinear regression was used to test relationships between the variables and canonical correspondence analysis (CCA; Past, version 2.00)[16] to verify tendencies in environmental variables and diatom abundance.

Except for water temperature and DSi, the study sites differed significantly with respect to water quality parameters (Table 1), which could be attributed to differences in land use, transportation, atmospheric deposition and urban-industrial release[9]. Diatom abundance (Table 2) and diversity (Table 3) also varied with site. Within-habitat diversity (species evenness, concentration of dominance and Shannon–Wiener index) declined with decreasing N : P stoichiometry and water column light penetration indicating that sites situated downstream, despite being nutrient-enriched, were relatively less favourable for most of the species. The abundance and diversity of diatoms vary with nutrient supply along regional[8] and latitudinal[17] gradients, and the strategy to cope with resource availability/stressors has led to the evolution of diverse life forms[18]. Relatively small difference in Shannon–Wiener index and increases in the index

Table 1. Summary of selected environmental variables measured at different study sites of River Ganga

| | Site | | | | |
Variable	I	II	III	IV	ANOVA
Temperature (°C)	26.40 ± 1.10	26.50 ± 1.15	26.70 ± 0.98	26.70 ± 1.12	NS
pH	7.80 ± 0.38	8.30 ± 0.40	8.70 ± 0.39	8.60 ± 0.43	$P < 0.01$
Transparency (cm)*	86.00 ± 4.90	47.00 ± 2.74	32.00 ± 2.33	37.00 ± 2.18	$P < 0.001$
Total dissolved solids (mg l^{-1})	516.00 ± 32.00	765.00 ± 46.10	826.00 ± 63.54	792.00 ± 60.80	$P < 0.01$
Conductivity (µS cm^{-1})	216.50 ± 17.20	267.90 ± 18.60	307.57 ± 21.67	310.50 ± 21.90	$P < 0.01$
Dissolved oxygen (mg l^{-1})	7.45 ± 0.37	6.30 ± 0.26	4.63 ± 0.24	4.76 ± 0.22	$P < 0.01$
Biological oxygen demand (mg l^{-1})	4.35 ± 0.18	5.70 ± 0.27	7.44 ± 0.32	7.26 ± 0.30	$P < 0.01$
Dissolved organic carbon (mg l^{-1})	5.45 ± 0.30	8.10 ± 0.41	11.67 ± 0.67	11.16 ± 0.71	$P < 0.01$
Chloride (mg l^{-1})	17.25 ± 1.10	27.58 ± 1.60	34.50 ± 2.11	39.00 ± 2.35	$P < 0.001$
Nitrate (µg l^{-1})	386.00 ± 21.50	645.00 ± 37.50	794.50 ± 61.84	724.00 ± 56.70	$P < 0.01$
NH_4^+ (µg l^{-1})	86.20 ± 6.51	122.00 ± 10.94	148.40 ± 11.20	135.46 ± 11.30	$P < 0.01$
Phosphate (µg l^{-1})	76.20 ± 3.56	143.80 ± 7.25	240.70 ± 13.20	200.10 ± 14.58	$P < 0.001$
Sulphate (mg l^{-1})	5.26 ± 0.74	8.15 ± 0.76	10.00 ± 0.81	10.22 ± 0.84	$P < 0.05$
Sodium (mg l^{-1})	8.90 ± 0.66	11.84 ± 0.67	14.05 ± 0.84	14.32 ± 0.78	$P < 0.05$
Potassium (mg l^{-1})	3.56 ± 0.18	5.32 ± 0.27	7.44 ± 0.28	6.08 ± 0.25	$P < 0.01$
Magnesium (mg l^{-1})	1.85 ± 0.06	2.95 ± 0.11	3.86 ± 0.15	3.70 ± 0.21	$P < 0.05$
Calcium (mg l^{-1})	10.50 ± 0.76	11.27 ± 0.75	14.95 ± 0.82	16.10 ± 1.05	$P < 0.05$
Dissolved silica (µg l^{-1})	560.00 ± 37.60	530 ± 38.00	490.70 ± 34.50	509.65 ± 38.00	NS
Biogenic silica (µg l^{-1})	107.00 ± 7.68	129.45 ± 9.60	126.33 ± 10.67	138.40 ± 11.20	$P < 0.05$
Ionic strength (m mol l^{-1})	0.44 ± 0.02	0.58 ± 0.03	0.64 ± 0.03	0.67 ± 0.04	$P < 0.01$

Values are mean ($n = 27$) ± ISE. *Expressed in terms of Secchi depth; NS, not significant.

Table 2. Relative abundance (%) of epilithic diatoms at the four sampling sites of River Ganga

| | | Relative abundance | | | |
Species	Code	I	II	III	IV
Achnanthes exigua Grun.	Aexi	2.20	3.60	2.08	5.20
Achnanthidium minutissimum (Kütz.) Czarn.	Amin	2.41	2.50	4.20	4.26
Asterionella formosa Hassall	Afor	2.10	2.00	1.06	4.88
Aulacoseira granulosa (Ehr.) Simonsen	Agra	2.50	8.50	7.30	2.00
Cocconeis pediculus Ehr.	Cped	6.10	2.60	2.00	2.86
Cocconeis placentula var. *lineata* (Ehr.) van Heurek	Cpla	16.60	3.56	5.50	2.20
Craticula halophila (Grun.) Cleve F. robusta (Hust.) Czarn.	Chal	3.26	2.20	1.20	4.25
Cyclotella meneghiniana Kütz.	Cmen	10.96	3.85	2.50	3.10
Cymbella affinis Kütz.	Caff	10.15	5.77	3.00	3.26
Diatoma vulgaris Bory	Dvul	4.56	15.50	12.32	2.65
Eunotia exigua (Bŕeb. ex Kütz.) Rab.	Eexi	9.00	2.68	3.10	2.10
Eunotia alpine (Naeg.) Hust.	Ealp	1.15	1.25	1.20	1.15
Fragilaria intermedia Grun.	Fint	3.10	10.50	13.00	1.20
Gomphonema parvulum (Kütz.) Kütz.	Gpar	2.26	9.00	10.00	2.50
Gyrosigma acuminatum (Kütz.) Rab.	Gacu	2.20	2.56	2.05	2.60
Melosira varians Agardh	Mvar	1.50	12.50	8.50	2.32
Navicula lanceolata (Ag.) Ehr.	Nlan	2.10	3.68	2.50	7.50
Navicula simplex Krass.	Nsim	2.00	8.25	4.50	10.07
Nitzschia amphibia Grun.	Namp	2.15	3.68	2.50	7.10
Nitzschia palea (Kütz.) W. Smith	Npal	2.20	3.50	1.00	10.40
Pinnularia viridis (Nitzsch) Ehr.	Pvir	1.00	2.50	1.50	10.10
Surirella elegans Ehr.	Sele	2.30	1.50	1.50	2.30
Synedra ulna (Nitzsch) Ehr.	Suln	8.25	4.50	4.90	6.00

of dominance and β-diversity (between-habitat diversity) with increasing levels of nutrient pollution indicate that the system possibly maintained diversity by driving to regulate the proportion of individuals of one or other taxa, including those of TEP producers. Among the water quality variables, DSi did not show significant difference between sites. N : P stoichiometric ratio declined from 11.53 (site I) to 7.31 (site III) with overall ratios <16 : 1 (average required cellular ratio), indicating that P is no more a limiting nutrient in the river. However, significance ($P < 0.05$) between site differences in N : P has relevance to shifting phytoplankton in general[19] and diatoms in particular[20]. Concordant with elevation in P (declining N : P), diatom assemblages also changed from

Table 3. Spatial variation in diversity indices for epilithic diatoms in River Ganga

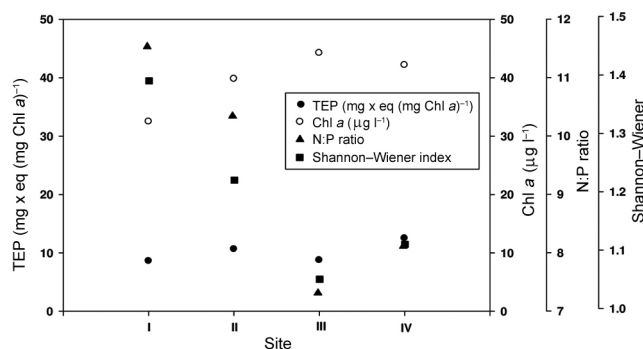|	Site			
Diversity index	I	II	III	IV
Evenness index	1.23	0.99	0.90	0.95
β-Diversity	3.18	3.49	3.96	3.74
Concentration of dominance	0.018	0.013	0.10	0.011
Index of dominance	0.076	0.104	0.125	0.112
Shannon–Wiener index	1.39	1.22	1.05	1.11

Data presented are mean of four low-flow seasons.

Figure 2. Transparent exopolymeric particles (TEP) trends relating chlorophyll *a* (Chl *a*) biomass, N : P stoichiometry and diatom diversity.

sites 1 to IV. As reported elsewhere[21], high profile guild represented by *Gomphonema parvulum* (Kütz.) Kütz., *Diatoma vulgaris* Bory and *Fragilaria intermedia* Grun. was found abundant at high P, whereas low profile guild representing *Cocconeis*, *Cymbella*, *Cyclotella*, *Eunotia* and *Synedra* appeared dominant at site I where P availability was relatively lower; and the motile guild with *Navicula* and *Nitzschia* was abundant at site IV (Table 2).

Particular attention was paid to relate TEP with water chemistry and diatom diversity. The polysaccharides exuded by diatoms result in the formation of TEP that play important role in carbon sequestration and sedimentation removal of nutrients and heavy metals[5,22]. High stickiness of TEP favours formation of aggregates[22], and adsorption of heavy metals and calcium carbonate increases the density and consequently the sinking rates 100-fold[5,23]. Regression analysis showed that BSi explained >71% variability in TEP confirming that diatoms are important predictors of TEP in the Ganga. Diatoms are the major producers of TEP[23] and BSi is a single proxy used as an index of diatom abundance and productivity[24]. Contribution of diatoms was validated using autotrophic index and taxonomic biomass[13]. Concentration of TEP varied between 8.62 and 12.50 mg × eq (mg Chl *a*)$^{-1}$ (Figure 2). TEP was significantly higher (Tukey HSD test, $P < 0.004$) at site IV than at sites I and III. Significant positive correlation ($R^2 = 0.89$; $P < 0.001$) between microscopy-based TEP abundance and spectrophotometrically measured TEP concentration confirmed spatial trends. Relatively small difference in its value between

sites indicates that a decline in its value is partly compensated by dominance transference. As reported elsewhere[22,25], TEP concentration varied with Chl *a*, N : P stoichiomertry and diatom diversity (Figure 2). Furthermore, TEP appeared highest at site IV and showed significant positive correlation ($R^2 = 0.69-0.78$; $P < 0.001$) with ionic strength and concentration of chloride and calcium, indicating that ionic strength and availability of chloride and calcium favour TEP formation[25].

We plotted a dominance–diversity curve using relative abundance and species rank, and found that the curves were skewed from a log-normal pattern (Figure 3). The slipping of the curves towards geometric series appeared more pronounced at downstream sites almost synchronous to changes in water quality, indicating variable affinities to resource supply and to cope with stressors and disturbances[20]. CCA results showed that taxa in the lower right quadrant (Figure 4) were potentially able to capitalize nutrient resources under low light climate. Chloride-loving and calcifilous species like *Navicula simplex* Krass., *N. lanceolata* (Ag.) Ehr., *Nitzschia amphibia* Grun., *Nitzsch palea* (Kütz) W. Smith, *Pinnularia viridis* (Nitzsch) Ehr. and *Achnanthes exigua* Grun. are found in the lower left quadrant, while *Cocconeis placentula* var. lineata (Ehr.) van Heurek, *Cocconeis pediculus* Ehr., *Cyclotella meneghiniana* Kütz and *Cymbella affinis* Kütz appeared in the less impacted zone characterized by poor ionic strength, low nutrients, high transparency, dissolved oxygen and silica[2,26]. Major contributors of TEP appeared to be *Cocconeis placentula* Ehr., *Cyclotella meneghiniana* Kütz. and *Cymbella affinis* Kütz. at site I; *Diatoma vulgaris* Bory, *Fragilaria intermedia* Grun., *Aulacoseira granulata* (Ehr.) Simonsen, *Melosira varians* Agardh and *Navicula simplex* Krass. at site II, *Aulacoseira granulata* (Ehr.) Simonsen, *Diatoma vulgaris* Bory, *Fragilaria intermedia* Grun. and *Melosira varians* Agardh at site III, and *Navicula lanceolata* (Ag.) Ehr. *Navicula simplex* Krass., *Nitzschia amphibia* Grun. and *Nitzschia palea* (Kütz) W. Smith at site IV, also reflecting their ability to withstand variable levels of nutrients and organic pollution[1] recorded at the confluences. These observations indicate that despite increasing levels of stressors and disturbances, TEP production in the river is maintained, at least partly, by dominance shifts. Studies have shown considerable difference in the propensity of TEP production
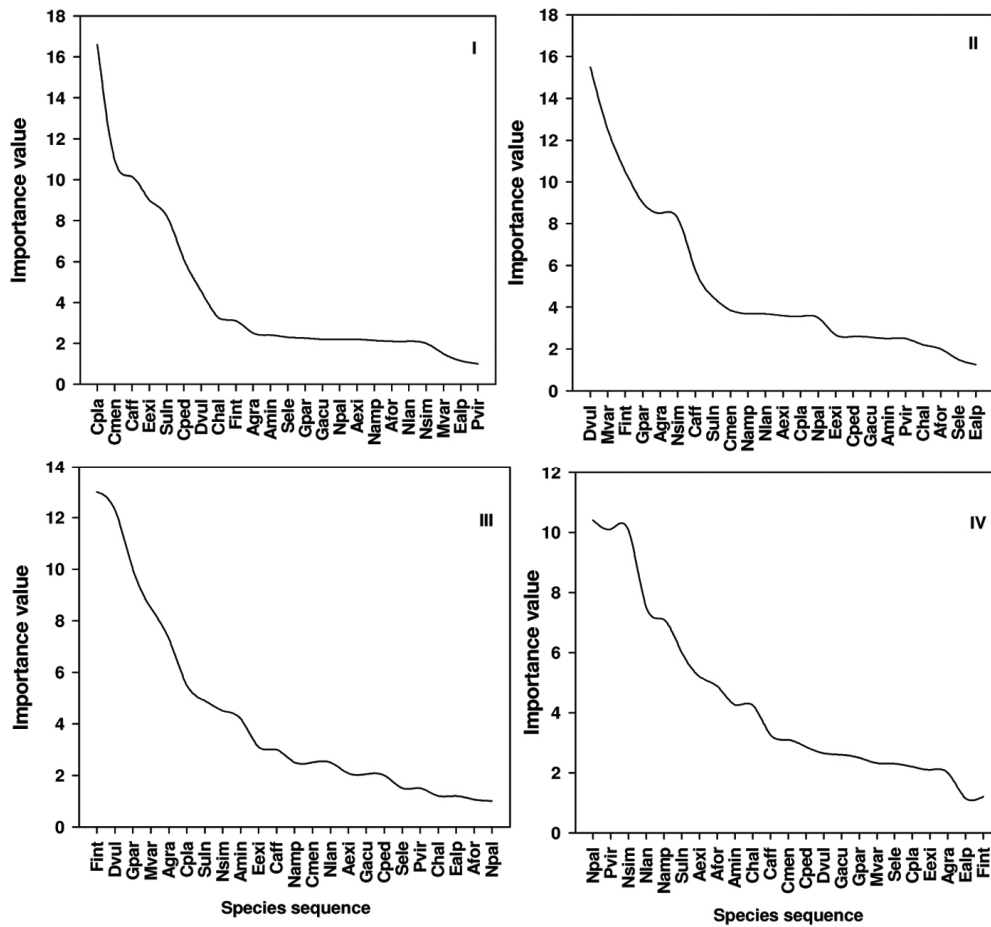
Figure 3. Dominance–diversity curve of epilithic diatoms at different study sites.
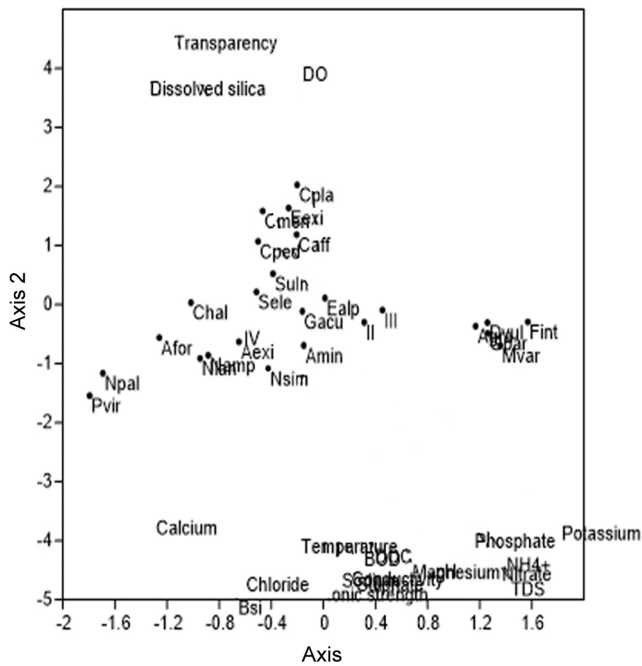

Figure 4. Canonical correspondence analysis bi-plot showing environmental variables and diatom species in the ordination space of the first, third and fourth quadrants. The canonical eigenvalues of axis 1 (horizontal) and axis 2 (vertical) are 0.2135 and 0.1720 respectively.

within taxonomic groups[25]. Further, TEP increased with Chl a, although it showed asynchrony at site III possibly due to increased contribution to Chl a by other microalgae under low-light climate[13] (Table 1). Also, TEP increased with declining N : P from sites I to IV, indicating enhanced carbon excretion for balancing cellular C : N ratio[27]. Diatoms can enhance C consumption or release for maintaining cellular C : N ratio[28]. Further decrease in N : P, as observed for site III, did not support TEP production possibly due to reduced photosynthetic-C fixation and consequently C excretion[28,29]. More importantly, when P is not limiting, at low Si : N (<1), as observed here, less silicified diatoms such as *Aulacoseira granulosa* (Ehr.) Simonsen and *Melosira varians* Agardh, and non-diatom algae with low direct sinking rates may predominate. Under such conditions, diatom–TEP synergy may drive direct sinking[5].

The present study shows that shift in water quality resulting from anthropogenic drivers such as land-use change, transportation, atmospheric deposition and urban-industrial release in River Ganga has altered the patterns of diatom abundance with dominance–diversity curves markedly skewed from a log-normal pattern. The study further shows, under increasing levels of stressors,

nutrient pollution for instance, some species of diatoms, including TEP producers, take greater advantage to potentially capitalize on these resources achieving higher importance relative to others. Since diatom–TEP synergy enhances C-sequestration and sedimentation removal of nutrients and heavy metals, the dominance transference of TEP producers may help in buffering the river against ecological impacts of these pollutants. Although relative contribution of factors controlling TEP production may be evaluated further, this study confirms one of the fundamental mechanisms that underline the self-purification capacity of River Ganga. We postulate a link among water chemistry, diatom diversity and TEP production as an important factor to be considered in the assessment of ecological processes promoting self-purification capacity of the river water. This has relevance from a biodiversity/ river conservation perspective.

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