Research article

How do multidimensional traits of dominant diatom *Aulacoseira* respond to abiotic and biotic factors in a river delta system?

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ABSTRACT

Trait-based approaches are being increasingly applied in ecology, and the influence of individual-level trait variation on communities and species has been demonstrated. However, the responses of individual trait variation to environmental changes remain to be explored. To examine the indicating functions of multidimensional traits, individual-level measurements of the dominant diatom genus Aulacoseira Thwaites in the Pearl River Delta were performed, and corresponding responses of three trait indices (trait richness, trait evenness, and trait dispersion) to abiotic and biotic factors were examined. Our results indicated that the three individual trait diversity indices were regulated by different factors. Trait richness was only significantly affected by abiotic factors (temperature), while trait evenness and trait dispersion were regulated by both abiotic and biotic factors. In addition, the direct influence of abiotic factors was more significant than that of biotic factors, implying that the multidimensional trait variation of Aulacoseira was more responsive to environmental changes than to interspecific interactions. Therefore, the multidimensional trait variation of Aulacoseira could be used as an effective indicator to track environmental changes. Our study elucidated the mechanisms relating individual-level trait variation to phytoplankton community dynamics; this could improve our ability to forecast changes in ecosystem properties across environmental gradients.

1. Introduction

In the context of global change, understanding and predicting biodiversity variation and the corresponding responses to ecosystem processes is becoming imperative (Zakharova et al., 2019). Traits, which are defined as the features of an individual organism's phenotype, have a vital influence on ecological interactions and dynamics, and as such, they can help illuminate the relationship between biodiversity and ecosystem status (Violle et al., 2012). Recently, trait variation has been associated with particular levels of resources, as phenotypic traits often correspond to distinct ecological strategies (Litchman et al., 2007). The trait-based approaches also provide insight into assemblage responses to

environmental changes since morphologically similar species may respond to the environment in the same way, and therefore relationships with environmental factors can be stronger than those with single species (Rimet and Bouchez, 2012; Lange et al., 2016; Zelnik et al., 2018). Consequently, the new wave of interest in traits has been led by the desire to predict the responses of communities and ecosystems to environmental variation (Zakharova et al., 2019). Most research concerning traits has to date largely focused on taxonomic richness as a measure of biodiversity (Cardinale et al., 2011). More recently, the concept of individual-level trait diversity has received increased attention, since previous studies suggest that individual trait diversity is better related to the structure of ecosystem functioning compared to the taxonomic

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diversity that is generally used in traditional research (Reiss et al., 2009; Cardinale et al., 2011). Moreover, many ecological processes such as competition (both interspecific and intraspecific) for resources, predation, and environmental change will affect individual phenotypes and consequently change individual-level trait diversity within and between taxa (Fontana et al., 2017). Although traits of organisms have been studied for decades (Norberg, 2004; Cadotte et al., 2011), the link between individual-level trait diversity and environmental variation has only begun to be explored owing to recent developments in calculating indices that quantify community-level trait diversity using individual-level data (Fontana et al., 2016). In the past, interspecific trait variation was regarded as being more important than intraspecific trait variation (Westoby et al., 2002). As a consequence, interspecific trait variation has received more attention than intraspecific trait variation (Bolnick et al., 2011). However, recent empirical studies have demonstrated that interspecific trait variation does not always override intraspecific variation, and the latter may contribute more significantly to overall trait variation (Violle et al., 2012; Siefert et al., 2015). Empirical evidence for intraspecific trait variation in response to environmental changes is still lacking.

Microalgae are well known as good bioindicators of aquatic environments. For example, phytoplankton trait variation is related to distinct ecological strategies that correspond well to the group distributions along the light availability gradients in lakes (Schwaderer et al., 2011). Another study suggested that phytoplankton traits of cell volume, maximum growth rate, optimum N:P ratio, and P affinity respond strongly to the typical seasonal and trophic status of lakes (Litchman and Klausmeier, 2008). Diatoms are the most ubiquitous group of phytoplankton assemblages in river ecosystems (Reynolds, 2006). Diatoms also have well-established taxon-specific tolerances and preferences for a broad range of environmental factors such as pH, nutrients and salinity (Dixit et al., 1992; Smol and Stoermer, 2010). Because of these characteristics, diatom abundance and traits are used to assess environmental changes in aquatic ecosystems (Lavoie et al., 2006). Diatom traits are increasing studied recently, and several researches suggest that diatom traits are responsive to nutrient (Pásztor et al., 2016; Lavoie et al., 2010), pesticide contamination (Rimet and Bouchez, 2011), organic pollution (Berthon et al., 2011) and changing hydrology (B-Beres et al., 2016). *Aulacoseira* Thwaites (Sinada and Karim, 1984) is a cosmopolitan diatom genus inhabiting freshwaters, and its morphological features are considered as sensitive ecological indicators for both internal population dynamics and external environmental parameters (Denys et al., 2003). For example, size variation in cells and filament dimensions of *Aulacoseira* is closely associated to its population dynamics and life cycle (Jewson and Granin, 2015), and the percentage of curved filaments reflects the nutrient gradient (Wang et al., 2017). Thus, the various traits of *Aulacoseira* and their high sensitivity to environmental changes provide an applicable model system for exploring the responses of individual trait variation to abiotic and biotic factors.

In this study, we aimed to test the following hypothesis: 1) whether individual trait variation of dominant diatoms will be an effective indicator to environmental changes? 2) how do abiotic factors and biotic factors influence the multidimensional trait variation? Our results will help understanding the mechanisms relating individual-level trait variation to phytoplankton community dynamics; this could improve our ability to forecast changes in ecosystem properties across environmental gradients.

2. Methods

2.1. Dataset

2.1.1. Phytoplankton sampling

A total of 16 sampling sites, including Fengkai (FK), Deqing (DQ), Zhaoqing (ZQ), Qingqi (QQ), Zuotan (ZT), Waihai (WH), Xinwei (XW), Xiaolan (XL), Xiaotang (XT), Beijiao (BJ), Lanhe (LH), Hengli (HL),

Chencun (CC), Shiqiao (SQ), Lianhuashan (LHS), and Zhujiangqiao (ZJQ), were set up in the Pearl River, the largest river in southern China (Fig. 1, Table 1). The Pearl River, which consists of West, North and East Rivers, is the third largest river system in China after the Yangtze River and the Yellow River. Before entering the South China Sea, the three rivers, West, North, and East, join together and form the Pearl River Delta (Yang et al., 2010). Fig. 1 showed the general layout of the Pearl River Delta basin: the basin location, the main river sources and tributaries, and the 16 spatial sampling sites. The topography of the Pearl River Delta consisted of an interweaving network of rivers and channels, with shoals and river mouths (gates).

We conducted sampling four times in 2015, in March (MAR), June (JUN), September (SEP), and December (DEC), representing the Spring, Summer, Autumn, and Winter seasons, respectively. At each sampling site, a plankton net with a mesh size of 6 μm was used to collect algae samples that were immediately fixed with Lugol's solution (15‰).

2.1.2. Individual trait measurements for aulacoseira

For each algae sample, 100 individuals of the *Aulacoseira* complex were observed and measured via an inverted microscope (Zeiss Axio Observer A1, Carl Zeiss AG, Germany) equipped with a visual camera (Axio Cam HRc, Carl Zeiss AG, Germany) and computer software (Axio Vision Rel. 4.8, Carl Zeiss AG, Germany). Six traits (numbers of end spines, cell numbers per filament, cell diameter, cell length, filament length, and filament curve degree) were measured. Specifically, the filament curve ratio was calculated as the value of filament height divided by filament width (Wang et al., 2017).

2.1.3. Biotic variables

All algae were identified and enumerated using a 1-mL Sedgewick-Rafte counting frame (Zeiss Axio Observer A1, Carl Zeiss AG, Germany). The systematic grouping of phytoplankton was done following the method of Van den Hoek et al. (1995). In total, 452 species belonging to eight phytoplankton phyla [(Bacillariophyta (diatoms), Chlorophyta (green algae), Cyanophyta (cyanobacteria), Pyrroptata (dinoflagellates), Cryptophyta, Euglenophyta (euglenida), Chrysophyta (golden algae), and Xanthophyta (yellow green algae)] were identified. Their abundances (ind./L, i.e., individual counts per liter of water) were used as biotic factors in further analyses. Note that *Aulacoseira* were excluded when calculating the diatom abundance, and *Aulacoseira* abundance itself was considered as a proxy of competition within the *Aulacoseira* genus. Therefore, nine biotic variables were employed in further analyses.

2.1.4. Abiotic variables

A total of 19 environmental variables were measured at each sampling site. More specifically, the conductivity, pH, water temperature, total dissolved solids (TDS), oxidation-reduction potential (ORP), and dissolved oxygen (DO) were measured in situ with a portable YSI meter (YSI6600V2, YSI Environment Inc., Colorado, USA). Light intensity below the water surface was measured with a hydrophotometer (ZDS-10, Shanghai, China), while transparency was measured with a Secchi disk. 250 mL of water samples was collected and then filtered for determining chemical conditions. Chemical oxygen demand (COD), total phosphorus (TP), phosphate, silicate, total nitrogen (TN), nitrate, nitrite, ammonium nitrogen (NH_4–N) and ammonia were estimated via a water flow injection analyser (Skalar-SA1100, the Netherlands) and a spectrophotometer (Shimadzu UV- 2501PC, China). The TN:TP ratio was also estimated.

2.2. Individual trait index

Individual-level trait measurements were used to estimate two complementary trait diversity measures, i.e., trait richness [trait onion peeling (TOP)] and trait evenness [trait even distribution (TED)] at the individual level according to Fontana et al. (2016). More specifically,
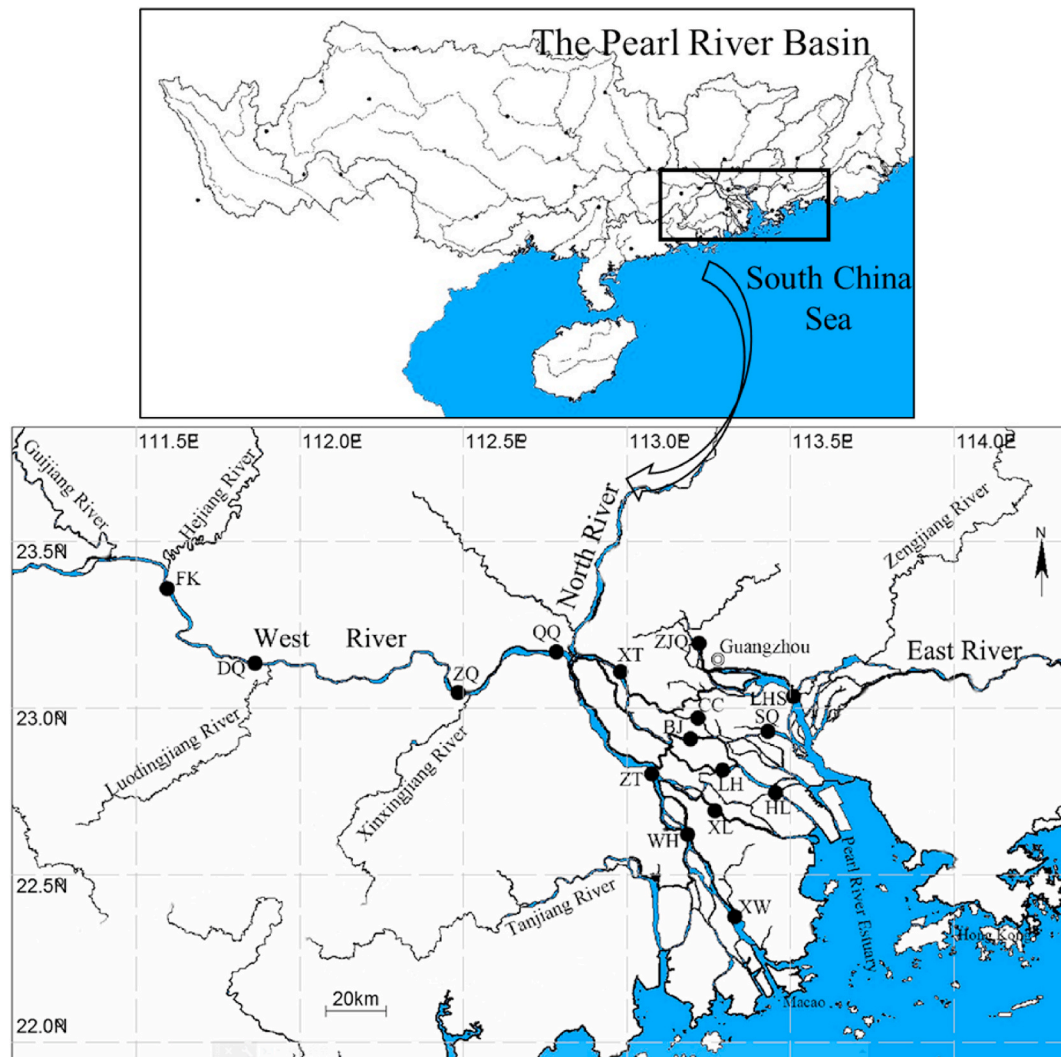
Fig. 1. Sampling sites in the Pearl River Delta.

Table 1
Coordinates of the sampling sites in the Pearl River Delta.

Station	Longitude	Latitude
FK	111°29′30″	23°24′25″
DQ	111°45′18″	23°8′28″
ZQ	112°27′36″	23°2′42″
QQ	112°47′12″	23°10′14″
ZT	113°3′32″	22°48′46″
WH	113°9′17″	22°36′13″
XW	113°16′36″	22°22′31″
XL	113°23′26″	22°36′45″
XT	112°58′10″	23°3′45″
BJ	113°11′47″	22°54′1″
LH	113°19′54″	22°49′15″
HL	113°29′2″	22°44′5″
CC	113°14′56″	22°58′15″
SQ	113°24′49″	22°55′24″
LHS	113°30′19″	22°58′38″
ZJQ	113°13′16″	23°8′12″

TOP represents the sum of all successive convex hull areas touching all individuals within a multidimensional trait distribution, whereas TED measures how evenly individuals are distributed within the multidimensional trait space. Moreover, functional dispersion (fdisp) was also employed to evaluate the degree to which trait values are spread around the community average phenotype. TOP was calculated as follows: after

the first minimum convex hull containing the outermost points has been built and its area has been measured, these points are deleted from the trait distribution and a second convex hull is calculated with the new outermost points (Fontana et al., 2016). TED was calculated as $1 - \log_{10}$ ($KLdiv + 1$), in which $KLdiv$ indicating Kullback-Leibler divergence (Kullback and Leibler, 1951; Kullback, 1959). Fdisp was calculated as the mean distance of individuals to the centroid of trait distribution (Laliberte and Legendre, 2010). Before the calculations, we checked the pairwise correlations between traits in all datasets, and we found that cell number and filament length were highly correlated; cell number was thus excluded. Therefore, five traits, i.e., numbers of end spines, cell diameter, cell length, filament length, and filament curve degree, were retained and used for the estimation. We also z-transformed traits so that they carried equal weight in the calculation (Moretti et al., 2021a,b). For each site at each season, TOP and TED were estimated via R functions provided by Fontana et al. (2016), while fdisp was calculated with the function *fdisp* in the R package FD (Laliberté et al., 2014).

2.3. Data analysis

All data analyses and visualisations were conducted in R (R Core Team, 2020).

To explore the relationships between trait diversity indices and the 28 explanatory variables (nine biotic variables and 19 biotic variables), we first ran linear mixed effects models for each of the pairs between

trait diversity indices and explanatory variables, with sample date as a random effect. Random effects models were performed via the function *lme* in the R package nlme (Pinheiro et al., 2021). Then, for each trait diversity, another mixed effects model was run with all significant explanatory variables identified in the above procedure. For these models, we used the model selection technique of "all possible models" that estimates all potential combinations of predictor variables and ranks them by the Akaike Information Criterion (Barton and Barton, 2020). From this extensive family of models, we selected the most parsimonious model with ΔAIC (Delta Akaike Information Criterion) ≤ 3 and calculated the standardised coefficients (Anderegg et al., 2019). Both response and explanatory variables were log (x+1) transformed to make them more appropriate for linear models. We also z-transformed response and explanatory variables to obtain standardised coefficients that could be compared within/between models (Schielzeth, 2010).

To identify the cascading effects of abiotic factors on each of the three trait diversity indices via affecting biotic variables, structured equation models were implemented with the R package piecewiseSEM (Lefcheck, 2016). We fitted component models of the piecewise SEM as linear mixed effects models with sample date as a random effect, and overall fits of the piecewiseSEM were evaluated using Shipley's test of d-separation. The standardised coefficients for each path from each component model were reported.

3. Results

3.1. Summary of individual trait indices, biotic variables, and abiotic factors

For the three trait indices (Table 2), TOP varied considerably across the sites and seasons, ranging from 57.63 to 521.62, with a mean of 252.03. As for TED and fdisp, compared to TOP, both indices had a much narrower range. TED ranged from 0.56 to 0.98 (average 0.91), whereas fdisp ranged from 0.08 to 0.26 (average 0.18).

For biotic variables, the abundance of main phytoplankton phyla showed substantial variability in the Pearl River (Table 2). Among all the phytoplankton phyla, diatoms (excluding *Aulacoseira*) exhibited the highest abundance, ranging from 3640 ind./L to 2,957,310 ind./L, with a mean value of 170,419 ind./L. *Aulacoseira* was the.

Abiotic variables varied in wide ranges across seasons and sampling sites (Table 2). COD increased gradually from upstream to downstream, ranging from 1.14 mg/L to 15.80 mg/L (average 3.92 mg/L). The value of ORP ranged from 23.10 mV to 187.00 mV and exhibited a distinct seasonal pattern, higher in winter and lower in summer. Water temperature varied between 16.10 °C and 31.20 °C among the four seasons, with a mean temperature of 24.35 °C. TN showed higher values in upstream and lower values in downstream.

3.2. Effects of abiotic and biotic factors on individual trait diversity

Overall, for each of the three individual trait diversity indices, the mixed effects models between pairs of each index and each explanatory variable showed that these diversity measures were affected by different factors (Fig. 2). For TOP, water temperature showed the highest proportion of explained variation (marginal R^2, hereafter $R_m^2 = 35.23\%$) compared to the other two abiotic factors of TDS and salinity. In addition, no biotic factors showed significant effects on TOP. As for TED and fdisp, both biotic and abiotic factors showed significant effects, and the proportion of explained variation varied considerably. Green algae and diatoms were the only two significant biotic factors affecting TED, explaining 11.12% and 9.83% of the total variation, respectively. Among abiotic variables, COD showed the highest percentage of

Table 2
Mean, standard deviation, minimum, and maximum of the individual trait indices, biotic variables (abundance of the main phytoplankton phyla), and abiotic variables (environmental factors).

| Categories	Variables	Abbreviations	Unit	Mean	SD	Min	Max
Individual trait indices	Trait onion peeling	TOP	–	252.03	112.24	57.63	521.62
	Trait evenness	TED	–	0.91	0.08	0.56	0.98
	Functional dispersion	fdisp	–	0.18	0.05	0.08	0.26
Biotic variables	Aulacoseira	Aulacoseira	ind./L	168,947	456,605	560	3,201,800
	Diatom (exclude Aulacoseira)	Diatom	ind./L	170,419	515,038	3640	2,957,310
	Green algae	Green_algae	ind./L	144,007	417,182	840	2,703,380
	Cyanobacteria	Cyanobacteria	ind./L	30,476	64,734	0	392,100
	Dinoflagellates	Dinoflagellates	ind./L	9515	39,718	0	249,750
	Cryptophyta	Cryptophyta	ind./L	2770	12,386	0	81,000
	Euglenida	Euglenida	ind./L	1717	3550	0	19,350
	Golden algae	Golden_algae	ind./L	514	2926	0	22,500
	Yellow green algae	Yelow_green_algae	ind./L	26	96	0	560
Abiotic variables	Chemical oxygen demand	COD	mg/L	3.93	2.90	1.14	15.80
	Conductivity	conductivity	–	1.75	0.78	0.81	3.76
	Dissolved oxygen	DO	mg/L	6.38	1.55	0.30	8.81
	Light intensity	light	lx	5111.87	5509.42	106.98	24,850.00
	Ammonia	NH3	mg/L	0.01	0.01	0.00	0.05
	Ammonia nitrogen	NH4	mg/L	0.22	0.45	0.00	2.10
	Nitrite	NO2	mg/L	0.13	0.19	0.00	1.28
	Nitrate	NO3	mg/L	1.43	0.54	0.22	3.34
	Oxidation Reduction potential	ORP	mV	88.22	37.98	23.10	187.00
	PH	pH	–	7.78	0.36	7.00	8.62
	Phosphate	PO4	mg/L	0.02	0.01	0.00	0.05
	Salinity	salinity	–	0.57	0.41	0.07	1.99
	Silicate	SiO4	mg/L	3.73	0.66	1.78	5.45
	Total dissolved solids	TDS	mg/L	0.65	0.42	0.10	2.44
	Water temperature	temp	°C	24.35	4.99	16.10	31.20
	Total nitrogen	TN	mg/L	2.66	1.58	1.54	9.62
	The ratio between total nitrogen and total phosphorus	TN_TP_ratio	–	28.62	13.88	7.22	76.63
	Total phosphorus	TP	mg/L	0.12	0.11	0.03	0.60
	Transparency	transparency	cm	53.77	28.79	18.00	140.00

Second most abundant taxon in phytoplankton (560–3,201,800 ind./L, averaged 168,947 ind./L), followed by green algae (840–2,703,380 ind./L, averaged 14,407 ind./L) and cyanobacteria (0–392,100 ind./L, averaged 30,476 ind./L). Golden algae and yellow green algae were less abundant in the studied river, with mean values of 512 ind./L and 26 ind./L, respectively.
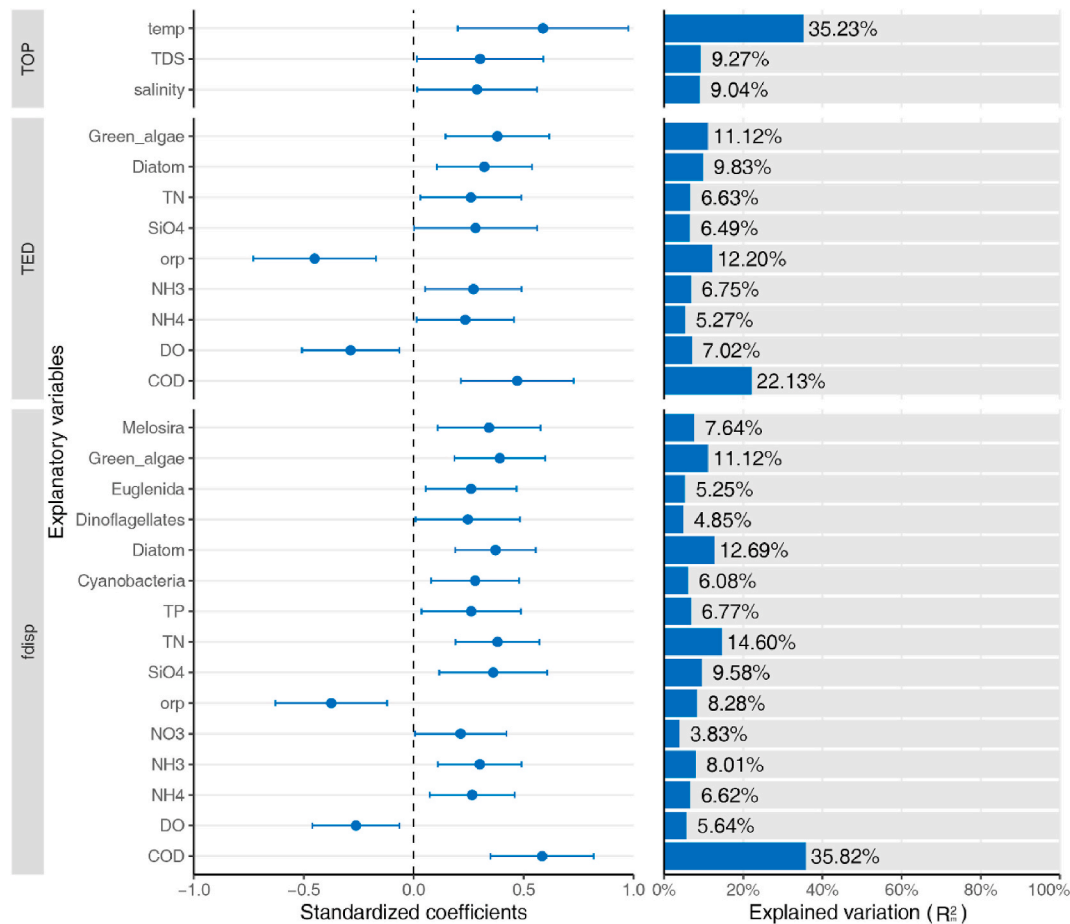
Fig. 2. Standardised coefficients of model predictors and associated 95% confidence intervals for mixed effects models for each pairwise comparison between trait diversity and explanatory variables (with sample date as a random effect). Only significant models are shown here. Proportions of explained variation (estimated as Marginal R square, i.e., R_m^2) by each explanatory variable are shown as bar plots in the right panel. See Table 2 for detailed information on each of the explanatory variables.

explained variation ($R_m^2 = 22.13\%$) on TED, followed by ORP ($R_m^2 = 12.20\%$). Similar to TED, diatoms and green algae were the most significant factors impacting fdisp, explaining 12.69% and 11.12% of the variation, respectively. As for abiotic factors, COD was the strongest predictor ($R_m^2 = 35.82\%$) of fdisp, while TN was the second most important, with the percentage of explained variation at 14.60%.

The best models for each trait index showed that water temperature was positively associated with TOP, whereas COD and dinoflagellates showed positive effects on fdisp (Fig. 3). Other variables had no significant impact on individual trait indices. The percentages of the variation explained by the model for TOP ($R_m^2 = 38.37\%$) and fdisp ($R_m^2 = 32.54\%$) were much higher than that of TED ($R_m^2 = 13.48\%$).
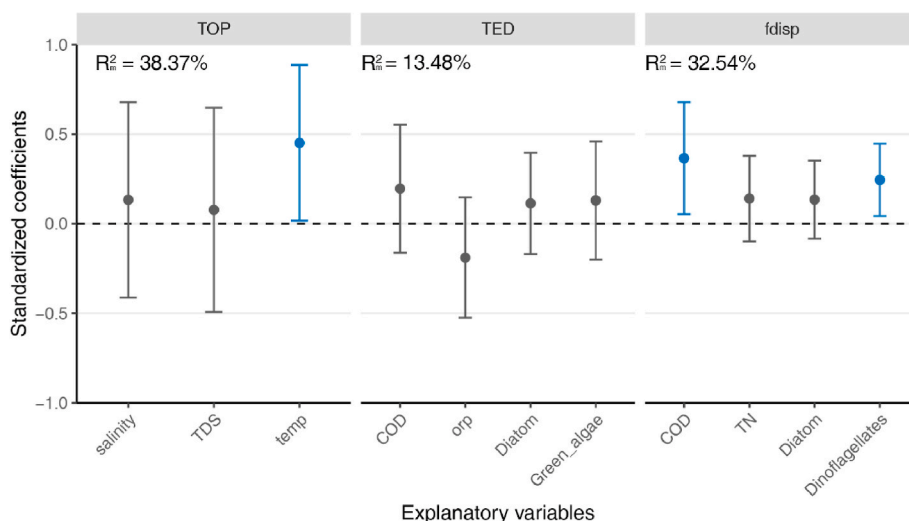
Fig. 3. Standardised coefficients of model predictors and associated 95% confidence intervals for the most parsimonious mixed effect models between trait diversity and explanatory variables. Confidence intervals that do not cross the zero line indicate that the predictors under consideration are associated with a statistically significant change ($P < 0.05$). Proportions of explained variation (estimated as Marginal R square, i.e., R_m^2) for each model are also shown. See Table 2 for detailed information on each of the explanatory variables.

3.3. Effects of abiotic and biotic factors on individual trait diversity

The piecewise structural equation model revealed that green algae were the only biotic factor that had a significant effect on TED (Fig. 4). Additionally, the model for TED showed that COD not only directly affected TED but also showed an indirect effect via the abundance of green algae. Such an indirect pathway was also identified for ORP, as the negative effect on green algae had an indirect negative impact on TED.

The model for fdisp showed that COD was directly positively related to fdisp and that there was an indirect effect via diatoms. In addition, TN had an indirect effect on fdisp via diatoms. The abundances of diatoms and dinoflagellates had direct positive effects on fdisp.

4. Discussion

Although trait-based approaches have been widely applied in ecological studies, most have focused on interspecific trait variation (Fontana et al., 2019; Borics et al., 2020). Few studies have explored how the intraspecific trait space is affected by abiotic and biotic factors. In this study, based on individual-level trait measurements of *Aulacoseira*, a dominant diatom genus in the phytoplankton in the Pearl River Delta, we explored how different aspects of individual trait space, i.e., functional richness (TOP), functional evenness (TED), and functional dispersion (fdisp), responded to abiotic and biotic factors. In this way, we gained insights into the underlying mechanistic regulation by the environment and the community on individual traits that could be applied in aquatic ecosystems.

Specifically, we found that only water temperature had a significant effect according to the multiple regression (Fig. 3), indicating the dominate role of temperature in regulating TOP, although temperature, salinity, and TDS showed positive effects on TOP based on single regression (Fig. 2). Generally, water temperature is a vital factor for regulating algal morphology (e.g., filament length and size variation) and growth (Wang et al., 2015). Within the optimum temperature range (20°C–30 °C), increasing temperature promotes the growth of *Aulacoseira* (Coles and Jones, 2010). The positive correlation between TOP and water temperature in our study could be explained by the specialisation of biotic interactions becoming stronger with increasing temperature, resulting in greater trait richness in warmer environments. Similar to our results, trait richness of terrestrial plants increases with temperature due to the increased biotic interactions and more host specificity at higher temperatures (Sedio et al., 2021). Moreover, only temperature significantly affected TOP, also suggesting TOP's potential application in tracking how temperature affects riverine ecosystems under global warming. For example, the relationship between temperature and TOP could change due to "warmer winter" (winter becoming suitable for *Aulacoseira*) and "hotter summer" (temperature exceeding the optimal value for *Aulacoseira*) under global warming. TOP's function as a bio-indicator of environmental change has also been reported in previous

studies. For example, Cormier et al. (2019) suggested that trait richness was sensitive to variation in community structure, as exhibited by changes in the trait space converging as a consequence of environmental filtering.

TED was affected by both abiotic and biotic factors, and among the abiotic factors, COD and ORP had the strongest effects via affecting green algae (Fig. 4). COD is regarded as a practical measure of organic contamination and is also a positive indicator of the trophic state of water environments (Denys et al., 2003). Higher algal abundance in eutrophic waters with high COD may have led to the positive correlation between COD and TED, since competition for resources in waters with high phytoplankton biomass imposes selection on algae for a more uniform distribution within the viable trait space (Moretti et al., 2021a, b). For example, the higher biomass of other algal groups (for diatoms excluding *Aulacoseira*) resulted in competition with *Aulacoseira* for resources, forcing *Aulacoseira* to adapt via several viable traits (e.g., a higher curved proportion) that could allow them to maintain dominance under such conditions. The negative impact of ORP on the abundance of green algae implied that a higher abundance of green algae would be detected in waters with lower ORP. This pattern was likely due to the freshwater discharge from the Pearl River with high concentrations of nitrogen and phosphorus resulting in eutrophication, thereby contributing to algal proliferation and high concentrations of organic pollutants and lower redox potential (lower ORP) in rivers. Moreover, green algae are more susceptible to ORP than *Aulacoseira* owing to the special electron transport pump in the plasma membrane of green algae (Nimer et al., 2010). As ORP represents the redox capacity driven by electron transfer in waters (Li and Bishop, 2002), this could explain why ORP failed to affect TED of *Aulacoseira* directly but exhibited a negative relationship with the abundance of green algae. Moreover, TED was also determined by the complex interactions between abiotic and biotic factors. For example, variation in environmental factors (COD and ORP) directly affected the abundance of green algae and subsequently influenced the TED of *Aulacoseira* through altering the interspecific interactions between green algae and *Aulacoseira*, as indicated by the indirect effects of COD and ORP on TED via green algae (Fig. 4). Although COD showed both direct and indirect effects on TED, the direct effect of COD on TED was stronger than the indirect effect via green algae. This pattern implied that the trait evenness of *Aulacoseira* was primarily regulated by abiotic factors (COD) rather than by biotic factors. Our results were in accordance with previous findings that phytoplankton communities are vulnerable to environmental variation, especially to water chemical conditions (e.g., COD), while their responses to changing biotic factors (e.g., interspecific competition) are always delayed (Recknagel et al., 2013). Predictive models also confirm that diatom communities are more sensitive to changes in water chemical (Feio et al., 2007).

Similarly, fdisp was also affected by both abiotic and biotic factors, with COD and TN showing indirect effects via regulating the abundance
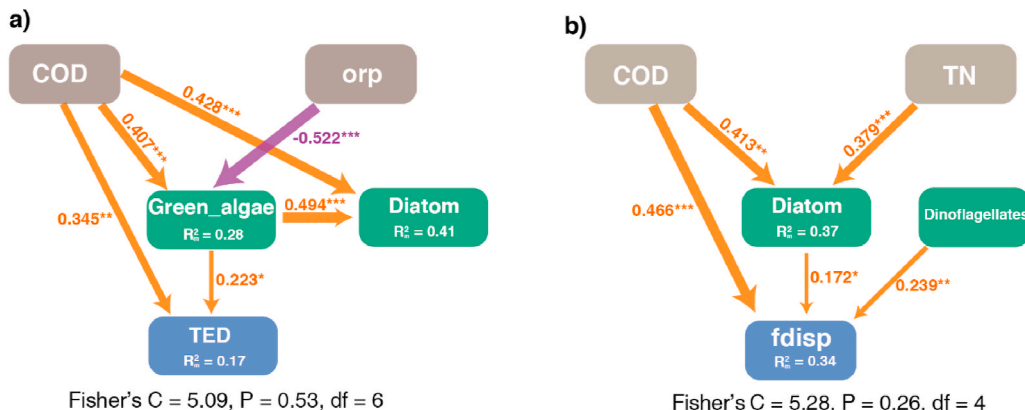
Fig. 4. Structural equation models of abiotic and biotic variables as predictors of individual trait indices. Solid red arrows represent positive paths, while solid blue arrows represent negative paths. Numbers beside arrows are standardised coefficients, with * indicating that the coefficients were significant at a level of 0.1, whereas ** and *** indicate significance at 0.05 and 0.01, respectively. See Table 2 for detailed information on each of the explanatory variables. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

of diatoms, whereas dinoflagellates showed direct effects. COD is regarded as an important index for representing in the degree of organic pollution in waters (Kawabe et al., 1997), while TN represents the trophic status in waters (Saxena and Saksena, 2012). COD and TN are generally high in relatively eutrophic environments with sufficient nutrients and organic substrates (Poleszczuk et al., 2012). The positive effects of COD and TN on fdisp (through diatoms) in our study likely reflected the positive association between fdisp and the eutrophication level of the river. This was in line with the stress-dominance hypothesis that predicts that in the benign ecological conditions with adequate substrates, niche partitioning in phytoplankton communities results in trait divergence and higher fdisp (Coyle et al., 2014; Weiher and Keddy, 1995). By contrast, the direct impact of COD on fdisp was stronger than the indirect effects (Fig. 4), highlighting the dominant effects of organic pollution over those of interspecific interactions on trait divergence of *Aulacoseira*. According to previous studies, the physiology (Smol and Stoermer, 2010) and morphology (Wang et al., 2015) of diatoms are vulnerable to environmental changes. The stronger direct impact on fdisp was probably because environmental variation directly affected the physiology and morphology of *Aulacoseira*, and therefore, the impact was more rapid and more substantial than the impact of diatoms that affected *Aulacoseira* through interspecific interactions. Moreover, the effect of diatoms on fdisp was weaker than that of dinoflagellates (Figs. 4 and 0.172 vs. 0.239), indicating that the interspecific competition between dinoflagellates and *Aulacoseira* was stronger than that between all diatoms and *Aulacoseira*. The study by Marshall (2009) reported similar intense interspecific competition for nutrients between *Aulacoseira* and dinoflagellates. According to the niche differentiation concept, competition for resources would result in greater trait divergence and encourage stable coexistence between community members (Pásztor et al., 2016). Diatoms (excluding *Aulacoseira*), dinoflagellates, and *Aulacoseira* dominated in the phytoplankton in the Pearl River, and their ecological niches partially overlapped. Niche partitioning of *Aulacoseira* occurred when the algal abundance was higher and the niche competition became stronger in order to compel algae to show differences in their niches and weaken interspecific competition. Such depressed competition between diatoms (excluding *Aulacoseira*), dinoflagellates, and *Aulacoseira* led to higher trait divergence (fdisp) of *Aulacoseira*.

Among the three individual trait diversity indices, TOP was only affected by abiotic factors (temperature), while TED and fdisp were regulated by both abiotic and biotic factors. Consistent with our results, previous studies have suggested that TOP was more vulnerable to species distributions that were affected by abiotic conditions (Moretti et al., 2021), while TED (Fontana et al., 2019) and fdisp (Borics et al., 2020) were more sensitive to biotic interactions. For example, trait evenness of phytoplankton increases with light limitation (Fontana et al., 2019), while divergence (Borics et al., 2020) increases with resource supply, since individual organisms adjust their physiological strategies to reduce niche overlap, thereby weakening intra- and interspecific competition and promoting stable coexistence between community members. Although TED and fdisp were affected by both abiotic and biotic factors, the direct influences of abiotic factors (temperature) were more significant, suggesting that the multidimensional trait variation of *Aulacoseira* was more responsive to environmental changes than to interspecific competition. The results suggested that the multidimensional trait variation of *Aulacoseira* could be used as an effective indicator to track environmental changes, especially temperature changes. For example, TOP could be applied as an indicator of temperature changes, while TED and fdisp could be used not only as indicators of varying environmental factors but also as indicators of interactions between algae. Consistent with our study, recent researches show that diatom traits have strong correlations with nutrient and organic matter/turbidity gradients (Tapolczai et al., 2017), and diatom traits could be useful in water quality assessments (Riato et al., 2022).

5. Conclusion

Our study reported that three individual trait diversity indices of *Aulacoseira* were affected by different regulators. The direct influences of abiotic factors on traits were more significant than the indirect impacts of biotic factors, suggesting that the multidimensional trait variation of *Aulacoseira* was more responsive to environmental changes than to interspecific interactions. The results suggested that the multidimensional trait variation of *Aulacoseira* could be used as an effective indicator for tracking environmental changes. In addition, our study manifested that the individual-level traits of *Aulacoseira* could further help us to forecast changes in complex aquatic ecosystem. TOP could be used to forecast temperature changes, while TED and fdisp could predict water chemical conditions.

Credit author statement

CW, WLY collected data; QIANFL, WLY provided the environmental parameters; CQH, KG, CW formulated the idea; KG, NCW, QINGFL performed statistical analysis; CQH, KG and CW wrote the draft version and all authors contributed to corrections substantially. The authors have no conflict of interest to declare.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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