

ORIGINAL ARTICLE

Functional and Taxonomic Diversity is Associated With Resource Use Efficiency in Epilithic Algae of Subtropical Qinhuai River, China

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ABSTRACT

1. The effects of biodiversity on ecosystem functioning comprise a central ecological theorem (BEF), because more diverse communities are expected to perform better, for example, in terms of resource use efficiency (RUE). Although biodiversity affects ecosystem functioning, it is seriously constrained by global environmental change. Epilithic algae are a crucial benthic functional group in aquatic food webs, but the effect of their biodiversity on ecosystem functioning is yet to be understood.
2. Here, we compared the capacity of taxonomic versus functional richness and evenness to predict RUE in a dataset on epilithic algae from the Qinhuai River, Nanjing, China. We examined associations between environmental variables and taxonomic and functional diversity (response and ecological indication), and assessed whether taxonomic and functional diversity measures predicted RUE (quantified as total algal biomass standardised by total phosphorus (RUE_{TP}), and total nitrogen (RUE_{TN})).
3. Taxonomic and functional diversity varied more across seasons than space, peaking in spring and summer in association with pronounced environmental changes. Water temperature and nutrient concentrations positively and significantly predicted taxonomic and functional diversity measures. Taxonomic and functional richness positively associated with RUE, while functional evenness negatively associated. However, taxonomic evenness was not related to RUE. Structural equation modelling showed that taxonomic and functional diversity were positively associated with RUE_{TP} and RUE_{TN} . However, taxonomic diversity was more strongly predictive of RUE than functional diversity.
4. Our results suggest that RUE is closely linked to species diversity, and functional diversity provides a complementary approach for better understanding of mechanisms underlying the BEF relationship for benthic algae in large rivers.
5. We suggest using taxonomic and functional approaches in a complementary way to gain a deeper understanding of the interplay among environmental factors, community diversity and ecosystem functioning.

Beryl Ochieng and Ming Chen contributed equally to this study.

1 | Introduction

Epilithic algae form a fundamental benthic functional group in river ecosystems, and are important bioindicators due to their high sensitivity and fast generation time (Stenger-Kovács et al. 2014). Algal species significantly impact ecosystem functions such as primary production and biogeochemical cycling (Velasco et al. 2003). Research on the responses of algal species to global change has focused mainly on phytoplankton (Mei et al. 2022). Less attention has been given to epilithic algae in tropical rivers (Townsend and Gell 2005; Zhang et al. 2020), with studies primarily focused on specific taxonomic groups like diatoms (Mbao et al. 2023). Epilithic algal community composition directly impacts ecological functions and processes, but is subject to spatiotemporal variation related to regional and local variation in the physicochemical environment (DeNicola et al. 2021). A positive algal diversity effect implies that more diverse communities increase ecosystem stability by reducing temporal fluctuations in community biomass (Poikane et al. 2016). In lotic ecosystems, seasonal variability is often more pronounced than spatial variability in algal composition (Wang et al. 2020). For instance, total abundance, biomass and species richness of algae significantly decrease from wet to dry seasons, with markedly different functional compositions (B-Béres et al. 2022).

Taxonomic diversity measures, such as species richness or evenness, have widely been used to evaluate ecological status in aquatic communities (Worischka et al. 2023). Taxonomic diversity, however, does not necessarily reflect ecological processes and functioning directly, limiting our understanding of ecosystem dynamics and services (Cardoso et al. 2014). In contrast, functional diversity measures, such as functional richness or evenness, may provide additional information by more directly linking ecological processes to community diversity via species' traits (Fontana et al. 2018). The use of functional traits to evaluate functional diversity has increased over recent decades (Mammola et al. 2021). In algal ecology, a set of morphological, physiological and behavioural traits has been used to better understand species interactions and their contribution to ecosystem functioning (Litchman et al. 2015). In particular, functional traits, such as biovolume, siliceous structure, flagella or mucilage, are frequently applied to capture how species contribute to overall community fitness and respond to changing environmental conditions (Graco-Roza et al. 2021). Notably, functional diversity can complement taxonomic diversity by quantifying species differences in terms of traits, resource exploitation strategies and mechanisms that support coexistence (Yan et al. 2023). Meanwhile, higher taxonomic diversity can lead to a more stable aquatic ecosystem, while functional diversity helps better understand underlying ecological mechanisms (Gonzalez et al. 2020).

Resource use efficiency (RUE) is one measure of ecosystem functioning, which can be quantified as the ratio between total community biomass and the limiting resource (Hodapp et al. 2019). Biodiversity has been shown to positively affect RUE in natural phytoplankton communities (Ptacnik et al. 2008). Higher species richness and diversity enhance resource use, resulting in greater biomass compared to ecosystems with low diversity (Weis et al. 2008). So far, BEF research

on primary producers has primarily focused on terrestrial ecosystems (Del Río et al. 2017; Duffy et al. 2017). Those few aquatic studies focused mainly on lakes and phytoplankton diversity (Guo et al. 2022; Zhang et al. 2021). Significant knowledge gaps, however, have been reported on how biodiversity influences RUE in fluvial, especially in river benthic algal communities. Additionally, community composition of benthic algae is shaped by hydrological conditions, substrate characteristics and nutrient concentrations in both water and sediment; unlike phytoplankton, which are mainly regulated by mixing and dissolved nutrient availability (DeNicola et al. 2021). Therefore, further in-depth BEF studies on benthic algal communities are necessary to better understand river ecosystem health in terms of diversity and its consequences for ecosystem functioning (Smeti et al. 2019).

Here, we aimed to address: (Q1) how does the variability of taxonomic and functional diversity of epilithic algae respond to seasonal and spatial variation? (Q2) do taxonomic and functional diversity predict epilithic algal RUE in a lotic ecosystem? In 2023, we collected samples across four seasons and 28 sites in the Qinhuai River, a large river basin in Jiangsu Province, China (Figure S1). To address Q1, we analysed the changes in epilithic algal taxonomic and functional diversity across seasons and sites. We hypothesised that (H1) taxonomic and functional diversity of epilithic algae would show greater seasonal than spatial variability due to significant seasonal fluctuations in environmental conditions. To address Q2, we calculated RUE based on the ratio of total epilithic algal biomass to total phosphorus (RUE_{TP}) and total nitrogen (RUE_{TN}), and tested the predictive power of taxonomic and functional diversity for RUE. We expected (H2) a positive correlation of both taxonomic and functional diversity with epilithic algal RUE_{TP} and RUE_{TN} , jointly supporting ecosystem functioning.

2 | Material and Methods

2.1 | Study Area and Sampling Method

The Qinhuai River (118°40'-119°10' E and 31°40'-32°10' N), a major tributary of the lower Yangtze River, is located in the southwest of Jiangsu Province, China. The Qinhuai River basin is about 110 km long, with a catchment area of 2631 km² and an elevation range of 0–417 m. The river basin is located in a subtropical humid climate region with an annual mean precipitation of 1116 mm and an annual mean temperature of 15.4°C. The river flows through Nanjing City, an important economic centre in East China with a population of more than 8 million. Therefore, it has undergone drastic eutrophication over time, primarily due to anthropogenic influences such as land use and urbanisation (Abro et al. 2019).

Sampling was carried out at 28 sites (Figure S1) in spring, summer, autumn and winter 2023. The sites were spaced approximately 4 km apart along the river channel and included upstream, midstream, downstream and intermediate (other) sites. This sampling strategy aimed to ensure good representation of the whole river basin. In situ physical variables such as water temperature (Temp), pH and dissolved oxygen (DO) were measured on site using a multiparameter water

analyser (YSI Pro, YSI, OH, US). Chemical water samples were collected using 500-mL acid-proof bottles, and sulfuric acid was added in the field to regulate the pH < 2 and measure the concentration of chemical oxygen demand (COD), biological oxygen demand (BOD), nitrite nitrogen (NO_2^- -N), nitrate nitrogen (NO_3^- -N), ammonium nitrogen (NH_4^+ -N), total nitrogen (TN), total phosphorus (TP) and phosphate (PO_4^{3-} -P) (Organization WHO 2022). Chemical variables were subsequently measured in the laboratory according to Water and Wastewater Monitoring Methods Chinese (2002) of China.

At each study site, we collected epilithic algal samples by selecting at least five stones (minimum diameter of 10 cm) along a 100-m section of the river. Epilithic algal biofilms were brushed off the stone surfaces (3-cm radius) with a sterile toothbrush, and then rinsed with distilled water. All subsamples were pooled into a composite sample for each site and preserved with Lugol's solution (coloured cognac). Each composite sample was then concentrated to 30 mL using a siphon after 48 h of settling in the sedimentation chamber (Utermöhl 1958). A volume of 0.1 mL of each concentrated sample was analysed in an algal counting chamber using a light microscope (Olympus BX21, Tokyo, Japan) at 40 \times magnification, and taxa were identified to genus and species level (Hu 2006). The epilithic algal biomass (mgL^{-1}) was estimated based on biovolume approximative geometrical forms (Hillebrand et al., 1999). The algal biomass was quantified in biovolume to allow calculation of epilithic algal resource use efficiency with nutrient data.

2.2 | Epilithic Algal Resource Use Efficiency (RUE)

RUE was calculated based on two major limiting nutrients: Total phosphorus (RUE_{TP}) and total nitrogen (RUE_{TN}). The equations for calculating epilithic algal RUE_{TP} and RUE_{TN} are as follows:

$$\text{RUE}_{\text{TP}} = \text{total biomass of epilithic algae} / \text{total phosphorus} \quad (1)$$

$$\text{RUE}_{\text{TN}} = \text{total biomass of epilithic algae} / \text{total nitrogen} \quad (2)$$

2.3 | Epilithic Algal Taxonomic and Functional Diversity

Algal taxonomic diversity is usually quantified as species richness (S) and Pielou's evenness (J) index (Amorim and do Nascimento Moura 2021). Species richness is the total number of unique species within a community, ecosystem or defined area (Fisher et al. 1943), whereas the evenness quantifies the frequency distribution of species within a community (Pielou 1966). Both the species richness and Pielou's evenness indices were calculated using species abundance data in the 'vegan' R package (Oksanen et al. 2019). To calculate functional diversity, we used functional richness (FRic) and functional evenness (FEve) indices. FRic measures trait variety within a community represented by a convex hull volume that species occupy (niche occupation), while FEve is how evenly species abundances are distributed within the functional trait space (Villéger et al. 2008). The epilithic algal functional diversity indices were computed based on 14 functional traits grouped into

morphological, physiological and behavioural characteristics of epilithic algae and were selected according to Litchman and Klausmeier (2008) and Reynolds (2006) (Table S1 and Table S2). Prior to the grouping, each species trait was classified based on presence/absence data. The functional diversity indices were calculated using the *dbFD* function in the R package 'FD' V1.0–12.3 (Laliberté and Legendre 2010).

2.4 | Data Analyses

Firstly, we assessed seasonal and spatial changes in the physicochemical variables using principal component analysis (PCA) and the accuracy of the results was evaluated using variance partitioning analysis (VPA) and linear models for PCA1 and PCA2 (Kherif and Latypova 2020). Then, we used one-way ANOVA to assess seasonal and spatial changes in taxonomic and functional diversity (H1). Pairwise comparisons between means of the diversity indices were calculated using Student's *t*-tests with Benjamini–Hochberg correction (Benjamini and Yekutieli 2001). Furthermore, random forest modelling with 999 permutations was used to predict the relative importance of the physicochemical variables in explaining taxonomic and functional diversity. We performed cross-validation for random forest using 75% of the dataset for training, with the remainder validated at each resampling iteration. Our model used 500 trees and sampled 2 predictors per node to minimise the root-mean-squares error (RMSE) (Zhou et al. 2024). Then, the most significant diversity predictor was regressed against taxonomic and functional diversity using a generalised linear model (GLM).

To test the overall effects of taxonomic and functional diversity on epilithic algal RUE, a generalised linear model was fitted (H2). Prior to the linear analysis, diversity indices were log-transformed to approximate data normality (Knief and Forstmeier 2021). We then used linear mixed models (LMMs) to assess separate seasonal and spatial effects of both taxonomic and functional diversity on epilithic algal RUE_{TP} and RUE_{TN} . In the LMMs, species richness, Pielou's evenness (J), FRic and FEve were included as dependent variables, algal RUE_{TP} and RUE_{TN} as fixed factors, whereas seasons and sites were considered as random factors.

Finally, structural equation modelling (SEM) was used to explore direct and indirect associations between physical variables, chemical variables and taxonomic and functional diversity of epilithic algal RUE. Separate models were fitted for RUE_{TP} and RUE_{TN} , with significance tested using one-way ANOVA. Consistent with past studies (Hu et al. 2020), physical and chemical variables were selected using a stepwise AIC (Akaike's information criteria) method in multiple linear regression models, with models having the lowest AIC values considered. All plausible pathways were included based on residual correlations (Table S4). We adopted the nonsignificant chi-square test ($p > 0.05$), root mean square error of approximation (RMSEA < 0.05 good, 0.05–0.10 moderate, > 0.10 bad) and comparative fit index (CFI > 0.95 great, > 0.90 traditional, 0.80 permissible) to determine final model fitness (Peugh and Feldon 2020).

All statistical analyses were performed in R 4.1.2 using the packages 'FactoMineR' V2.7 (Lê et al. 2008), 'lavaan' V0.6–17

(Oberski 2014), 'randomForest' V4.7–1.1 (Liaw and Wiener 2002), 'lme4' V1.1–35.3 (Kuznetsova et al. 2017) and 'vegan' V2.6–4 (Oksanen et al. 2007).

3 | Results

3.1 | Environmental Characteristics and Species Biomass in Qinhuai River

Physicochemical variables representing the environmental characteristics of the Qinhuai River showed substantial seasonal and spatial changes. The chemical variables including COD, BOD, TN, TP, $\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$, $\text{NO}_2^-\text{-N}$ and $\text{PO}_4^{3-}\text{-P}$ had greater fluctuations over seasons and space than the physical variables (pH, DO and Temp) (Figure 1). Spearman's correlation analysis indicated that the chemical variables showed significant inter-correlations ($p < 0.05$, Figure S2 and Table S3), unlike the physical variables. The epilithic algal community was composed of 206 species and 63 genera throughout the study period. The total biomass of epilithic algae, measured by biovolume, was highest in summer and spring (7.31 mg/L and 6.69 mg/L respectively), and at downstream sites (9.26 mg/L, Figure 2a). Furthermore, the study revealed that RUE_{TP} and RUE_{TN} were positively and significantly correlated with epilithic algal biomass ($R^2 = 0.61$ and $R^2 = 0.52$, $p < 0.001$, Figure S3).

3.2 | Seasonal and Spatial Changes in Taxonomic and Functional Diversity

With few exceptions, the taxonomic and functional diversity indices of epilithic algae showed significant seasonal and

spatial changes. However, the indices had a more significant seasonal than spatial changes supporting our first hypothesis ($p < 0.05$, Figure 2b,c). Based on Student's *t*-tests mean comparisons, species richness peaked in spring and summer, while Pielou's evenness was highest in summer. Significant differences ($p < 0.05$) in species richness and Pielou's evenness were observed across all the four seasons. Regarding functional diversity, the FRic index was highest in spring and summer, with significant differences in spring, autumn and winter ($p < 0.05$). Conversely, the FEve index peaked in winter, with significant difference between spring, autumn and winter ($p < 0.05$). Spatially, species richness was highest in downstream sites and there was a significant difference between upstream and downstream sites. Pielou's evenness was highest in intermediate sites, with no significant spatial differences observed between the four sites. As for functional diversity, the FRic index was highest in downstream and midstream sites, with significant differences between downstream, upstream, and intermediate sites ($p < 0.05$). Finally, the FEve index was highest in upstream sites, with significant differences in downstream, upstream and intermediate sites ($p < 0.05$).

3.3 | Factors Correlated With Epilithic Algal Taxonomic and Functional Diversity

The random forest results showed that water temperature was the most significant predictor for species richness, Pielou's evenness and FRic ($p < 0.05$, Figure 3a–c). Additionally, DO and TP significantly predicted species richness ($p < 0.05$, Figure 3a), while pH, $\text{NO}_3^-\text{-N}$, DO and TP significantly predicted Pielou's evenness ($p < 0.05$, Figure 3b). The FRic index was also significantly predicted by TN, $\text{NO}_3^-\text{-N}$, $\text{NO}_2^-\text{-N}$ and $\text{NH}_4^+\text{-N}$ ($p < 0.05$,

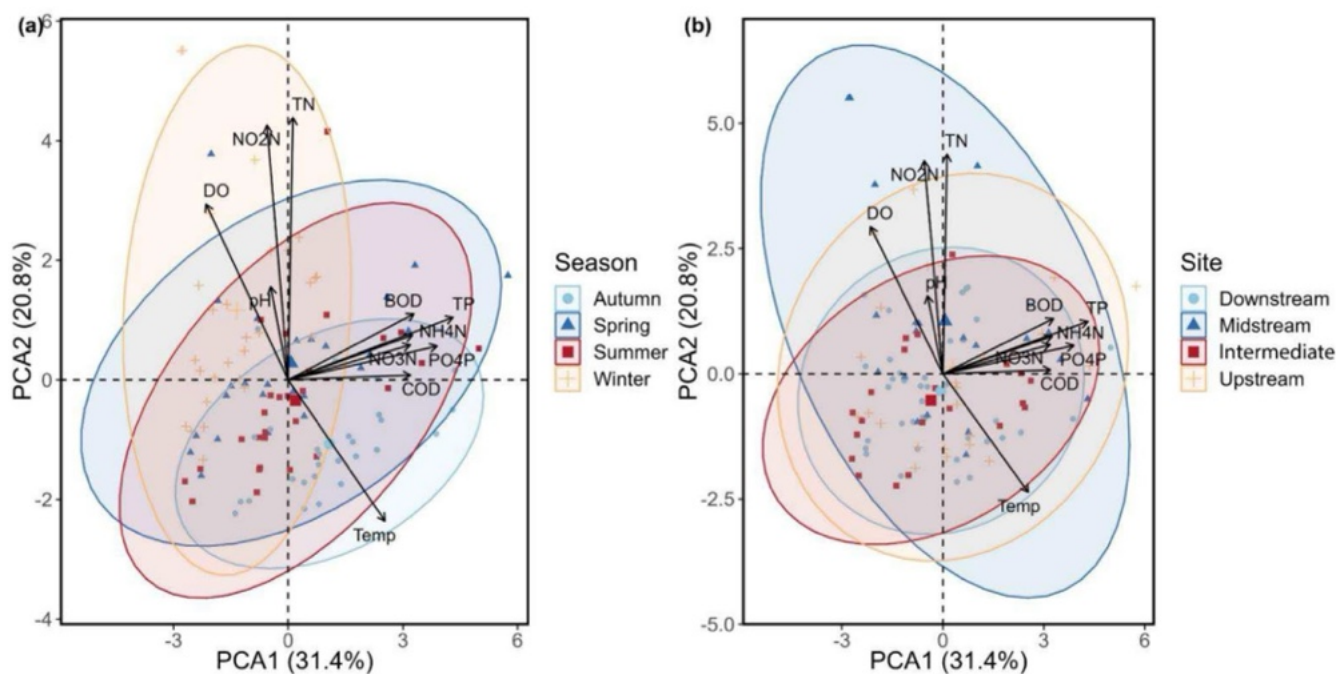


FIGURE 1 | PCA results of physicochemical variables across seasons (a) and sites (b). The first two components explained 31.4% and 20.8% of variances respectively. Ellipses represent variability within groups (seasons or sites), calculated using eigenvalues of covariance matrix, scaled at 95% confidence intervals. Arrows indicate the strength of the changes in physicochemical variables on the first two PCs. The different colour denotes different seasons and sites.

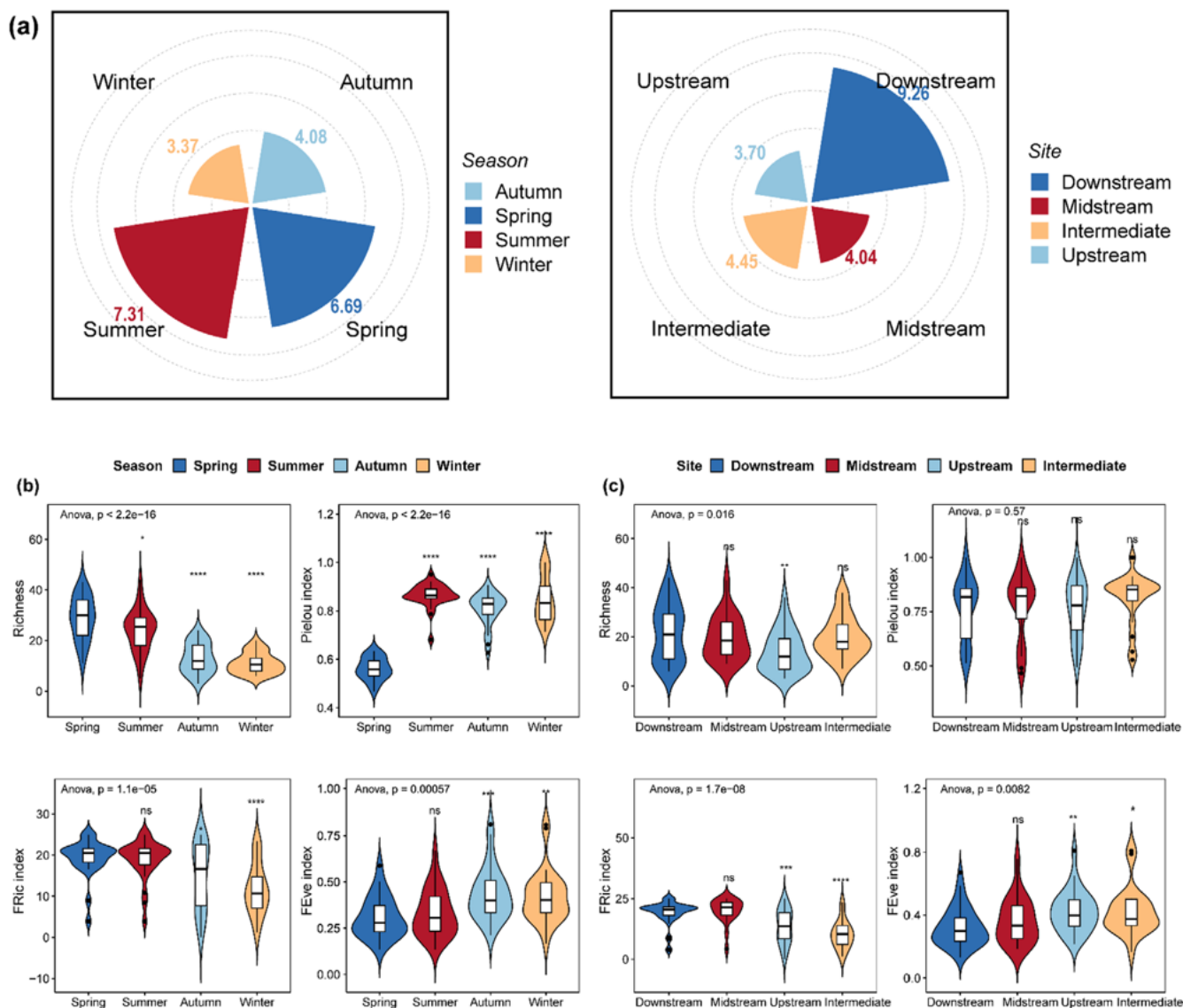


FIGURE 2 | Seasonal and spatial changes in epilithic algal biomass, taxonomic and functional diversity indices. Sunburst plots illustrate the seasonal and spatial changes of the algal biomass for the four seasons and sites (a). Boxplots of one-way ANOVA showing the significant seasonal (b) and spatial (c) variations of taxonomic and functional diversity indices. Significant p -values in Student's t -test are designated with asterisks: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$ and ns as not significant. The different colours denote different seasons and sites.

Figure 3c), while FEve was predicted by TN and TP ($p < 0.05$, Figure 3d). Generalised linear model analysis revealed that the FRic index had a positive significant relationship with temperature ($p < 0.01$, Figure 3g).

3.4 | The Effects of Taxonomic and Functional Diversity on RUE

Overall, our study showed that the taxonomic and functional richness had positive significant effects on RUE_{TP} and RUE_{TN} (Figure 4a,c,e,g), while functional evenness showed a negative significant effects (Figure 4f,h). However, taxonomic evenness had insignificant effects on RUE_{TP} and RUE_{TN} (Figure 4b,d). In particular, there was a seasonal and spatial dependency of RUE_{TP} and RUE_{TN} on taxonomic and functional diversity (Figures S4 and S5). Seasonally, FEve was positively correlated with RUE_{TP} in both summer and winter (Figure S4a), while

species evenness showed positive correlations with RUE_{TN} across spring, summer and winter (Figure S4b). Spatially, the taxonomic and functional indices showed positive linear correlations between FEve and RUE_{TP} in midstream, upstream and intermediate sites (Figure S5a), and the correlation between taxonomic evenness and RUE_{TN} in downstream, upstream and intermediate sites (Figure S5b). Additionally, the taxonomic and functional indices showed high significant linear correlations ($p < 0.05$, Figure S6).

3.5 | Relationships Between Physicochemical Variables, RUE, Taxonomic and Functional Diversity Measures

Across all seasons, physicochemical variables and species diversity showed significant positive effects on epilithic algal RUE_{TP} and RUE_{TN} (Figure 5a,b, Table S4). The chemical variables directly

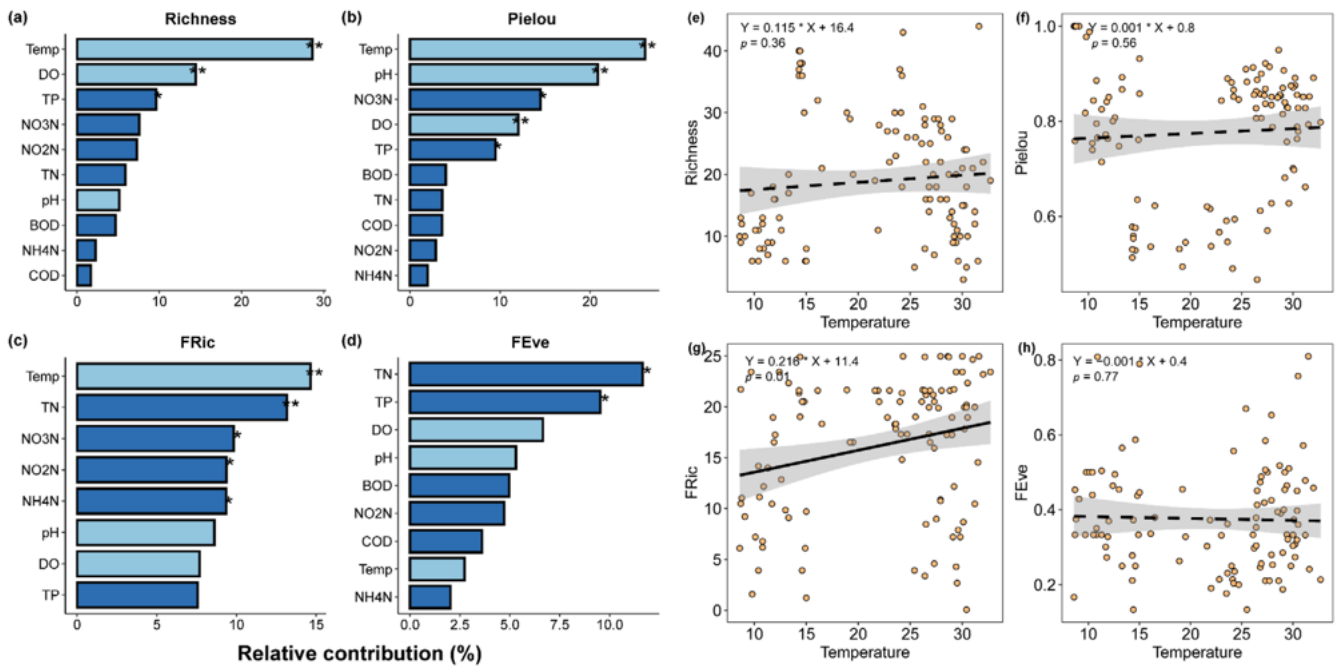


FIGURE 3 | The effects of physicochemical variables on taxonomic (a, b) and functional diversity (c, d) indices. The light blue colours indicate physical variables while the dark blue colours indicate chemical variables. Asterisks signify significance: * $p \leq 0.05$, ** $p < 0.01$, *** $p < 0.001$. The relationship of taxonomic and functional diversity indices with water temperature (e–h). Dark grey shaded areas indicate 95% confidence intervals.

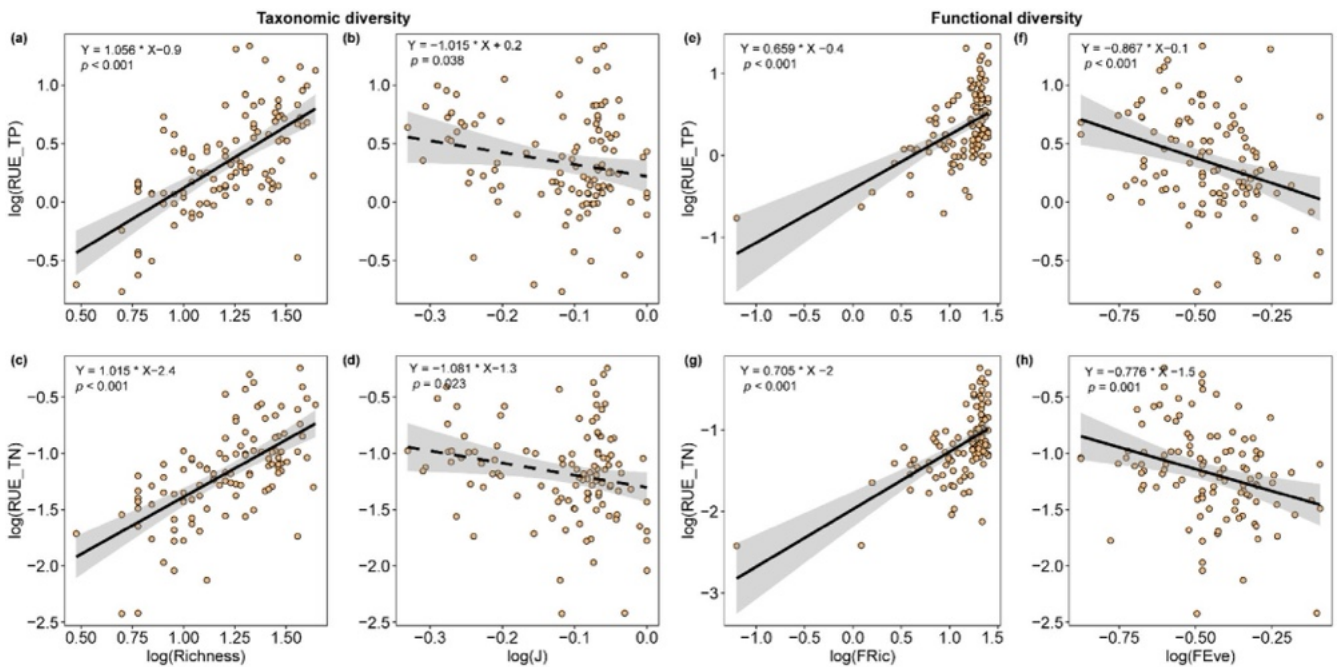


FIGURE 4 | The effects of taxonomic (a–d) and functional diversity (e–h) indices on epilithic algal resource use efficiency (RUE_{TP} and RUE_{TN}). Dark grey shaded areas indicate 95% confidence intervals. Significance levels at $p \leq 0.05$, $p < 0.01$, $p < 0.001$.

affected the taxonomic and functional diversity of epilithic algae and were positively and significantly correlated with both algal RUE_{TP} and RUE_{TN} ($p < 0.001$). The physical variables also showed a positive and significant linear correlation with the algal RUE_{TP} and RUE_{TN} ($p < 0.001$) but had no significant effect on taxonomic and functional diversity. In addition, the taxonomic diversity had

a significant and direct effect on epilithic algal RUE_{TP} ($R^2 = 0.11$, $p < 0.001$) and RUE_{TN} ($R^2 = 0.12$, $p < 0.001$), while functional diversity showed a significant and indirect effect on RUE_{TP} ($R^2 = 0.14$, $p < 0.001$) and RUE_{TN} ($R^2 = 0.21$, $p < 0.001$). Overall, our SEM results explained 47% ($R^2 = 0.47$) of variation in epilithic algal RUE_{TP} and 49% ($R^2 = 0.49$) of variation in RUE_{TN} .

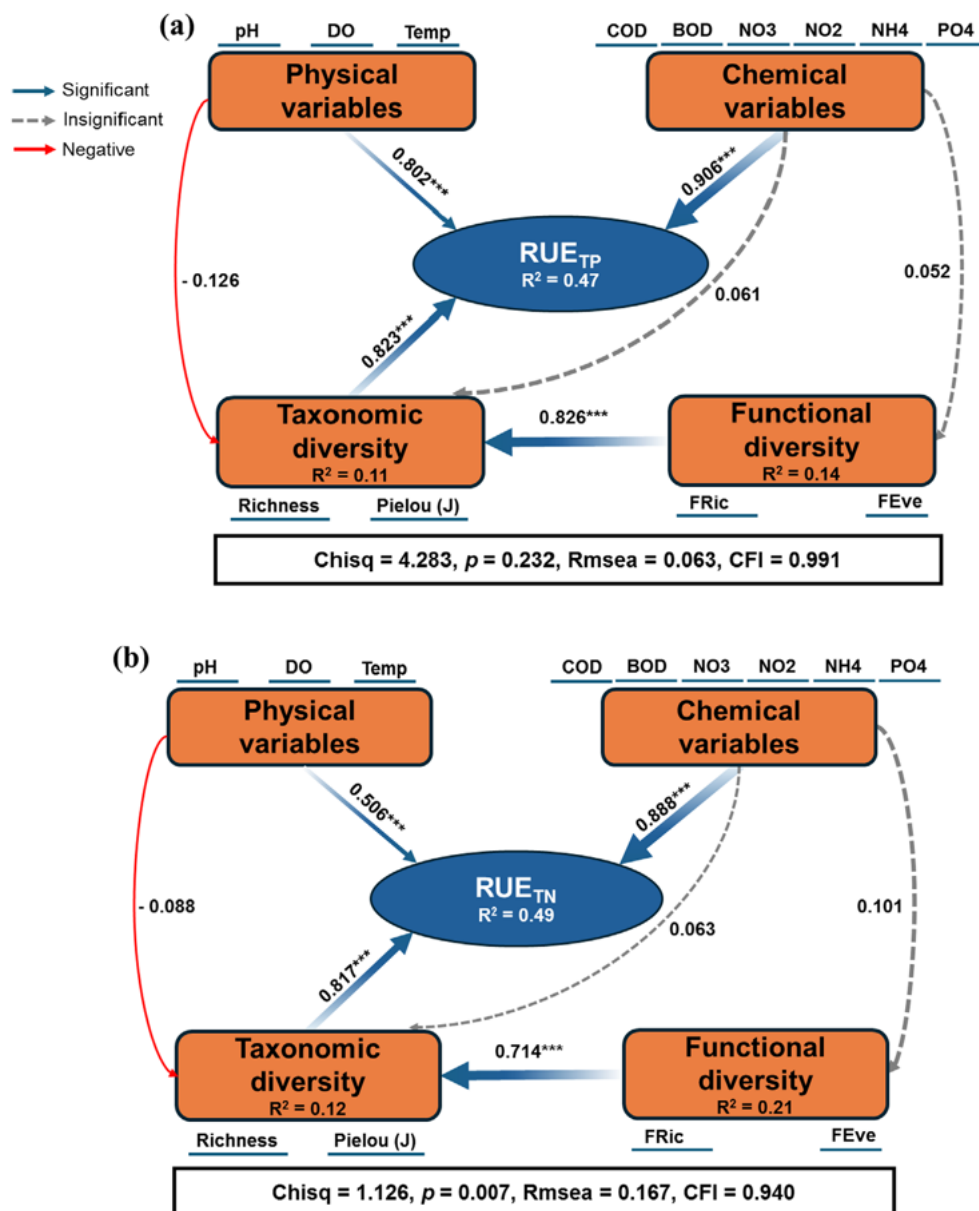


FIGURE 5 | Predictors of epilithic algal RUE_{TP} (a) and RUE_{TN} (b) in the Qinhuai River. Results of Structural equation modelling (SEM) were based on the interactions between physical variables, chemical variables, taxonomic diversity (TD), functional diversity (FD) and resource use efficiency (RUE). The width of a path is proportional to the magnitude of its standardised coefficient. Positive significant paths are in blue, insignificant paths are in grey and negative paths are in red. Significance levels at $*p \leq 0.05$, $**p < 0.01$, $***p < 0.001$. Additional SEM results are in Table S4.

4 | Discussion

4.1 | Seasonal and Spatial Variability of Epilithic Algal Biomass, Taxonomic and Functional Diversity

During the study period, epilithic algal biomass, taxonomic and functional diversity showed significant seasonal and spatial patterns, but seasonal variability was more pronounced than spatial variability. This may potentially reflect seasonal variation in flow rate. River flow influences water mixing and influences the distribution of essential algal nutrients across sites (DeNicola et al. 2021). We found a larger epilithic algal biomass in the growing season, which was expected, as algal biomass in lotic ecosystems is predominantly controlled by flow speed, which promotes nutrient transport required for growth (Bum

and Pick 1996). Additionally, high biomass in spring and summer suggests an increase in nutrient recycling by grazers, potentially driven by increased metabolic rates during warmer months (Iannino et al. 2021). A higher algal biomass was consistently observed at downstream sites, which can be attributed to reduced flow velocity, which lowers shear stress and prevents dislodgement (Wang et al. 2018). In conditions of lower flow velocity, the grazing pressure from herbivores may also be less effective (Peterson and Stevenson 1992). Such seasonal and spatial epilithic algal biomass patterns in the Qinhuai River align with observations on taxonomic groups, like macroinvertebrates in the Mekong River Basin, China (Ding et al. 2017).

The taxonomic diversity of epilithic algae also revealed significant seasonal and spatial variation. Spring had the highest

species richness, which can be attributed to increased photosynthesis from longer daylight (Zhang et al. 2020). On the other hand, summer algal communities showed high evenness values, which likely reflect a more even co-dominance and representation of different epilithic algal taxonomic groups as a result of increased light intensity (McCormick et al. 2019). Similar seasonal dynamics in the taxonomic diversity of benthic algae have been reported in other subtropical rivers such as the 16 rivers in the Chimanimani area of Eastern Highlands, Zimbabwe (Dalu et al. 2022). In contrast to seasonal variability, sites showed minor (but significant) differences in taxonomic diversity, with downstream and intermediate sites having the highest species richness and Pielou's evenness respectively. A previous study indicates that algal richness is higher in downstream sites in lotic ecosystems, primarily because habitat heterogeneity supports species coexistence (Qu et al. 2018). On the other hand, high evenness suggests a balanced representation of different epilithic algal species at intermediate sites, as a result of stable environmental conditions, such as consistent temperature and nutrient availability (Lytle and Poff 2004). Similarly, balanced nutrient availability enhances the growth of several algal species by preventing individual species from resource monopolisation (Hodapp et al. 2019). Potentially, light availability and stable river flow conditions could lead to high algal evenness by preventing disturbances that could favour opportunistic species (Ochieng et al. 2022).

The observed patterns in the algal functional diversity further support the evidence of dynamic seasonal and spatial changes in the Qinhuai River. The FRic and FEve indices were high in summer and winter respectively. The high FRic index in summer suggests the adaptability of epilithic algal communities to the dynamic environmental conditions during summer, such as high nutrients and temperatures, resulting in effective resource use and resilience of the river ecosystem to environmental disturbance (DeNicola et al. 2021). Furthermore, the high FRic index might indicate that epilithic algal communities consist of species with a variety of traits, which favours their coexistence and resistance to invasion (Mason et al. 2005). This, in turn, explains the increased ecosystem productivity during this period. Regarding FEve, the index was highest in winter, suggesting that the epilithic algal functional traits were evenly distributed during this season, allowing effective use of the available resources and increasing the productivity of the entire river ecosystem (Mason et al. 2005). Spatially, our study recorded the highest FRic in downstream and midstream, and the highest FEve in upstream sites. This suggests that the downstream and midstream areas of the Qinhuai river have diverse habitats supporting a wide range of species traits, while high FEve in upstream is an indication of abundant and diverse resources that can support an even distribution of functional traits (Graco-Roza et al. 2021).

4.2 | Taxonomic and Functional Diversity Responses to Environmental Variables

Based on the random forest analysis, epilithic algal taxonomic and functional diversity were positively related to physicochemical variables, such as water temperature, pH, DO and nutrient concentrations. Generally, algal taxonomic diversity, like species

richness, positively correlates with temperature, which has repeatedly been shown to significantly influence algal communities at different spatiotemporal scales by determining species growth rates (Sherman et al. 2016; Zohary et al. 2021). Metabolic theory suggests that algal richness tends to be three times higher in the tropics than at higher latitudes due to temperature differences between the two regions (Righetti et al. 2019). pH and DO also play an important role in predicting the taxonomic diversity of epilithic algae in the Qinhuai River. A previous study on benthic algal communities across 52 river sites throughout Norway indicates that diatom richness reached its maximum at pH 6.9, which could also promote the growth of other taxa, for which diatom assemblage is often considered a proxy (Schneider et al. 2013). Moreover, our result showing the effects of DO on algal diversity is consistent with previous studies showing that the spatial distribution of hypoxia strongly promotes algal blooms (Watson et al. 2016); an important concern for the management of river ecosystems. Besides physical variables, nutrients including TP, TN, NO_3^- -N, NO_2^- -N and NH_4^+ -N positively predicted algal taxonomic and functional diversity measures. The availability and concentrations of nutrients significantly affect algal taxonomic diversity through primary productivity. Furthermore, nutrient availability allows species with distinct physiological and morphological traits to effectively use resources, leading to a more complex and resilient ecosystem (Chase and Leibold 2002).

4.3 | Relationships Among Physicochemical Variables, Taxonomic and Functional Diversity and RUE

The regression analysis and SEM results indicated that physicochemical variables and taxonomic and functional diversity positively and significantly predicted algal RUE_{TP} and RUE_{TN} . However, the extent of taxonomic and functional diversity impacts on RUE varied, supporting our second hypothesis. We found strong positive effects of taxonomic diversity on both RUE_{TP} and RUE_{TN} , which contradict previous studies in which functional diversity outperformed taxonomic diversity in structuring phytoplankton RUE in freshwaters (Abonyi et al. 2018; Graco-Roza et al. 2021). To explain these results, we argue that the functional traits applied were unable to successfully quantify functional differences among species (i.e., to provide additional ecological knowledge on top of taxonomic data). Furthermore, the strong effect of taxonomic diversity on RUE could indicate that the algal species varied functionally, thus species richness best correlated with functional diversity (Yang et al. 2022). It is also noteworthy that the association between functional diversity and RUE via taxonomic diversity indicates that taxonomically diverse communities typically possess a range of functional traits that enable coexistence (Stefani et al. 2020). This consequently contributes to ecosystem stability by enhancing the ability of diverse algal communities to efficiently use available resources, leading to improved ecosystem functioning and resilience (Eisenhauer et al. 2019).

To further explain the relationship between physicochemical variables, species diversity and RUE, two major nonexclusive mechanisms have been proposed. One is the complementarity effect (CE), which supports species coexistence as a result of heterogeneity in resource use, resulting in a productivity increase

in response to a diversity increase (Loreau 2000). A second mechanism is the selection effect (SE), whereby species with the best adapted traits can compete more effectively for resources and thus dominate the community (Tilman 1999). For example, species with small body sizes can more effectively acquire resources than larger ones, leading to the competitive exclusion of small over large-bodied species, especially if nutrients are limiting (Jeppesen et al. 2000).

5 | Conclusions

Understanding complementary between taxonomic and functional diversity approaches in epilithic algal resource use efficiency is imperative, but it is complicated by seasonal and spatial variability in community composition. Our results are consistent with previous ones, showing higher seasonal than spatial variability in the taxonomic and functional diversity of epilithic algae. Our study also provided crucial information on the similarity between the taxonomic and functional diversity indices in predicting epilithic algal RUE in lotic ecosystems. In light of our results, we propose that the taxonomic and functional diversity approaches should jointly be considered for epilithic algal RUE, to further understand species loss effects, for example, in response to global environmental change. Additionally, better linking functional traits of benthic algae to ecosystem functions will help predict how ecosystem functioning may respond to environmental changes and disturbances, a crucial yet unresolved knowledge for the assessment and management of lotic ecosystems.

Author Contributions

J.W.: Conceptualisation. B.O., S.B., J.H., S.Z. and J.W.: Developing methods. B.O. and M.C.: Data analysis. B.O., M.C., A.A. and J.L.: Preparation of figures and tables. B.O., A.A., P.Z., Y.C., J.W.: Conducting the research, data interpretation and writing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.