



## RESEARCH ARTICLE

# Functional diversity promotes phytoplankton resource use efficiency

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**Abstract**

1. Understanding the relationship between biodiversity and ecosystem functioning (BEF) is a central topic in ecology. Multi-trait-based functional diversity has been proposed to improve mechanistic understanding of the BEF relationship; however, how trait-based functional diversity affects ecosystem functioning and processes has rarely been addressed in aquatic ecosystems.
2. Here, we examined the causal relationships between three phytoplankton functional diversity indices (FAD2, functional diversity based on dendrograms [FDc], FRic) and Shannon diversity index versus resource use efficiency for nitrogen ( $RUE_N$ ), phosphorus ( $RUE_P$ ) and silicate ( $RUE_{Si}$ ), with monthly long-term datasets from the marine (Western English Channel, 2000–2014) and freshwater (Lake Kasumigaura, 1984–2012) ecosystems.
3. We employed Convergent Cross Mapping (CCM), a novel method developed for identifying causality for nonlinear dynamical systems; this is in contrast to linear approaches that cannot distinguish causality from correlation. CCM found that FDc is the most robust functional diversity index among the selected functional diversity indices (FAD2, FDc, FRic) in predicting phytoplankton resource use efficiency and exhibited a much stronger causal effect than the Shannon index.
4. Furthermore, scenario exploration analysis indicates that most causal effects from phytoplankton diversity indices on resource use efficiency ( $RUE_N$ ,  $RUE_P$  and  $RUE_{Si}$ ) are on average positive, and FDc exhibited the most consistent positive causal effects on phytoplankton resource efficiency in both marine and freshwater ecosystems. Thus, increasing FDc can enhance phytoplankton resource use efficiency in aquatic ecosystems.
5. *Synthesis.* Our results show significant causal effects of functional diversity on phytoplankton resource use efficiency in both marine and freshwater ecosystems. Among all selected functional diversity indices, functional diversity based on dendrogram is the most robust functional diversity index in promoting phytoplankton resource efficiency. Our study provides empirical evidences in natural aquatic systems that trait-based functional diversity represents better species niche partitioning than the Shannon index and thereafter enhances resource use efficiency.

This finding can improve our understanding on trophic transfer and nutrient cycling in aquatic ecosystems.

#### KEYWORDS

biodiversity–ecosystem functioning, causality test, functional diversity, nonlinear dynamical system, resource use efficiency, trait-based approach

## 1 | INTRODUCTION

Understanding the relationship between biodiversity and ecosystem functioning (BEF) is a central topic in ecology (Allhoff & Drossel, 2016; Brophy et al., 2017; Cardinale et al., 2012; Hooper et al., 2005; Tilman, Isbell, & Cowles, 2014). BEF relationships have been intensely investigated in the past decades, due to concerns on potential impacts of globally increasing species loss on ecosystem functioning and services (Cardinale et al., 2012; Tilman et al., 2014). A general consensus of BEF is that species diversity is a major determinant of ecosystem productivity, stability, invasibility and nutrient dynamics (Tilman et al., 2014).

While traditional BEF research mainly focused on species diversity that includes only information of species richness and relative abundance, increasing number of studies have shown that influences of diversity on ecosystem functions depends largely on the traits and functional roles of species (Cadotte, Carscadden, & Microtchnick, 2011; Diaz & Cabido, 2001; Gagic et al., 2015; Klais, Norros, Lehtinen, Tamminen, & Olli, 2017; Petchey & Gaston, 2006). Thus, functional diversity, measuring the functional differences among species based on their traits, has been proposed to improve mechanistic understandings of BEF (Abonyi, Horváth, & Ptacnik, 2018; Cadotte et al., 2011; Gagic et al., 2015; Petchey & Gaston, 2006). Indeed, several studies have shown that trait-based functional diversity predicts ecosystem functioning better than species diversity (Abonyi et al., 2018; Gagic et al., 2015; Ye, Chang, García-Comas, Gong, & Hsieh, 2013). Therefore, functional diversity has been suggested as a principal concept for revealing mechanisms linking diversity with ecosystem functioning and processes (Nathan, Osem, Shachak, & Meron, 2016).

Another challenge for understanding BEF in natural systems is the methodological concern. Existing studies using observational long-term monitoring data to analyse BEF have largely relied on linear approaches (e.g. correlation, regression and structural equation modelling). However, correlation does not always imply causation (Sugihara et al., 2012); for instance, significant correlation between diversity and ecosystem functioning can be a consequence of sharing determinants (i.e. affected by the same environmental factor) instead of causality. Moreover, lack of correlation does not always imply lack of causation, either (Sugihara et al., 2012). In fact, correlation may appear to change in magnitude and sign through time (known as mirage correlation), even though the causal relationship remains unchanged; this is a hallmark of nonlinear dynamical systems (Deyle et al., 2013; Ye, Beamish, et al., 2015a). Mirage correlations

as well as spurious correlations render difficulty to identify causal relationship between diversity and ecosystem functioning based on linear analyses. To overcome these issues, we employ novel approaches, convergent cross mapping (CCM; Sugihara et al., 2012) and S-map (Deyle, Maher, Hernandez, Basu, & Sugihara, 2016) that are designed for analysing nonlinear dynamical systems, to quantify the cause–effect of BEF using time-series data collected from natural systems.

Among ecosystem functions, resource use efficiency is a very important one, determining nutrient cycling and trophic transfer processes (Filstrup, Hillebrand, Heathcote, Harpole, & Downing, 2014; Funk & Vitousek, 2007; Nathan et al., 2016; Olli, Klais, & Tamminen, 2015; Ptacnik et al., 2008). The Niche Diversification Hypothesis suggests that ecosystems of higher diversity could take greater advantage of the niche opportunities in an environment, and this allows a diverse ecosystem to capture a greater proportion of resource (Connell, 1978). Following this reasoning, one may expect that functional diversity, as measured by the functional traits that determine how an organism extracts resources from its environment, should play an important role in determining resource use (McGill, Enquist, Weiher, & Westoby, 2006). Thus, a community with higher functional diversity is expected to have a greater resource niche partitioning and thus resource use efficiency (García-Comas et al., 2016; Gross et al., 2017; Ye et al., 2013). Here, we hypothesize that phytoplankton functional diversity has a stronger effect on resource use efficiency than species diversity.

Most of current knowledge on BEF has come from terrestrial ecosystems, including grasslands and forests (Forrester, Benneter, Bouriaud, & Bauhus, 2017; Hautier et al., 2015; Tilman, Wedin, & Knops, 1996). Studies on the BEF relationship in aquatic ecosystems, especially those focusing on how functional diversity affects functions of aquatic ecosystems remain understudied. In this study, we aim to examine the effects of phytoplankton diversity on resource use efficiency in both marine and freshwater ecosystems. We focus on phytoplankton because phytoplankton represent the base of aquatic ecosystems and consist ~ 50% of global net primary production (Behrenfeld et al., 2001). Although resource use efficiency has previously been shown to increase with phytoplankton species richness (Ptacnik et al., 2008) but decrease with phytoplankton evenness (Filstrup et al., 2014) in natural communities, the effects of functional diversity on phytoplankton resource efficiency remain unclear in natural aquatic ecosystems. Specifically, we test the hypotheses that (a) phytoplankton species diversity and functional diversity enhance resource use efficiency in aquatic

ecosystems, and (b) phytoplankton functional diversity has a stronger causal effect on resource use efficiency than species diversity.

## 2 | MATERIALS AND METHODS

### 2.1 | Data

Two long-term monthly time-series datasets representing the marine (Station L4 in the Western English Channel, UK) and freshwater (Station ST9 in the Lake Kasumigaura, Japan) ecosystems were used to test our hypotheses addressing whether phytoplankton diversity determines resource use efficiency. We chose these two datasets because the long-term monthly records of these two sites are long enough for examining coupling of phytoplankton and nutrient dynamics. In addition, both datasets are publicly available and well managed which can assure the accuracy of data. The Western English Channel data were collected by the Western Channel Observatory ([www.westernchannelobservatory.org.uk](http://www.westernchannelobservatory.org.uk)). For the L4 long-term dataset (50°15.00'N, 4°13.02'E in the Western English Channel), most data were collected weekly. We selected only the data from 2000 to 2014 to keep the consistency of phytoplankton and water chemistry data and avoid the substantial amount of missing data in the earlier period. The data sampled around the middle of each month were chosen to comprise a monthly dataset for further analyses. Finally, we used monthly observations for phytoplankton taxonomic abundance and biomass (used to calculate the functional and Shannon diversity), chlorophyll *a* (Chl<sub>a</sub>), dissolved inorganic nitrogen (DIN as sum of nitrite, nitrate and ammonia), dissolved phosphate (PO<sub>4</sub>P) and dissolved silicate (DSi) to calculate phytoplankton diversity indices and resource use efficiency. The Lake Kasumigaura data were collected by the Japan National Institute for Environmental Studies (<http://db.cger.nies.go.jp/gem/moni-e/inter/GEMS/database/kasumi/index.html>). Monthly data of station ST9 (36°02.14'N, 140°24.22'E) from 1984 to 2012, including phytoplankton taxonomic abundance and biomass, the concentration of Chl<sub>a</sub>, DIN and PO<sub>4</sub>P, were used in this study. Note that the DSi was not measured in Lake Kasumigaura; therefore, phytoplankton resource use efficiency for dissolved silicate was not calculated. Note that, a small amount of missing data still exists in both datasets; these missing data are ignored in the following analyses. The detail information for phytoplankton composition and nutrient dynamics in the Western English Channel L4 and Lake Kasumigaura ST9 could be found in the aforementioned websites and the literature (Smyth et al., 2015; Takamura & Nakagawa, 2012; Widdicombe, Eloire, Harbour, Harris, & Somerfield, 2010).

### 2.2 | Phytoplankton taxonomic and functional diversity

The species diversity of phytoplankton is measured as the Shannon diversity index (H), which is one of the most widely used species

diversity indices in ecological researches (Heumann, Hackett, & Monfils, 2015; Peet, 1975). We examined three widely used functional diversity indices, which are based on different theoretical frameworks: the second generation functional attribute diversity (FAD2) (Walker, Kinzig, & Langridge, 1999), the community-based functional diversity based on dendrograms (FDc) (Petchey & Gaston, 2002, 2006) and the multidimensional functional diversity index of the functional richness (FRic) (Villegger, Mason, & Mouillot, 2008). The theories and equations for calculating these functional diversity indices could be found in FDiversity user manual (Casanoves, Pla, Rienzo, & Díaz, 2011).

To calculate the functional diversity indices, six functional traits associated with the net growth and population performance of phytoplankton were selected (Weithoff, 2003), including (a) nitrogen fixation, (b) silica demand, (c) capacity for mixotrophy, (4) tendency to form chains or colonies, (5) motility, (6) size. These traits are related to resource acquisition, predator avoidance and reproduction of phytoplankton. Specifically, the functional traits i–iv were binary variables (0, 1). Motility was classified as: 0, non-motile; 0.5, buoyancy regulation through gas vacuoles; and 1 (high motility) for flagellated species capable of moving in three-dimensional space and adapting their behaviour according to environmental conditions (Weithoff, Rocha, & Gaedke, 2015). Cell size was classified into 10 different logarithmically scaled categories of size from 0.1 to 1.0 (Weithoff et al., 2015). With the matrix of phytoplankton functional traits, the functional diversity indices were calculated using the software of FDiversity (Casanoves et al., 2011). Time-series variations of the diversity indices are presented in the Figures S1 and S2 and the online deposited data (Ye et al., 2019).

### 2.3 | Phytoplankton resource use efficiency

The natural logarithm of the ratio of phytoplankton biomass (estimated as chlorophyll *a*) to nutrient concentration was used as the proxy for phytoplankton resource use efficiency (Olli et al., 2015; Ptacnik et al., 2008). Note that the estimated phytoplankton resource use efficiency from water chemical parameters (Chl<sub>a</sub>, DIN, PO<sub>4</sub>P and DSi) is methodologically independent from the phytoplankton taxonomical and functional diversity indices. The equations for calculating phytoplankton resource use efficiency of dissolved inorganic nitrogen (RUE<sub>N</sub>), dissolved phosphate (RUE<sub>P</sub>) and dissolved silicate (RUE<sub>Si</sub>) follow:

$$RUE_N = \text{LN}(\text{Chl}_a:\text{DIN}) \quad (1)$$

$$RUE_P = \text{LN}(\text{Chl}_a:\text{PO}_4\text{P}) \quad (2)$$

$$RUE_{Si} = \text{LN}(\text{Chl}_a:\text{DSi}) \quad (3)$$

### 2.4 | Statistical analyses

We used the CCM technique (Chang, Ushio, & Hsieh, 2017; Clark et al., 2015; Sugihara et al., 2012) to examine the causal effects

of phytoplankton Shannon diversity and functional diversity on resource use efficiency ( $RUE_N$ ,  $RUE_P$  and  $RUE_{Si}$ ). CCM is a recently developed analytical method and has been demonstrated as a great utility in identifying causal relationships between two time-series variables in nonlinear complex ecosystems (Clark et al., 2015; Frossard, Rimet, & Perga, 2018; Sugihara et al., 2012). In simple terms, CCM is based on Takens' embedding theorem (Takens, 1981), which states that generically the attractor of a dynamical system can be reconstructed using time series of a single observational variable of the system through lagged coordinate embedding (Chang et al., 2017). CCM tests for causation by measuring the extent, to which the historical record of the effect variable can reliably estimate states of the cause variable inferred from attractor reconstruction. CCM is a quite rapidly developing analytical method; more theoretical details about CCM could be found in Sugihara et al. (2012) and Chang et al. (2017).

We note that spurious results of CCM may occur if there is a shared forcing variable (e.g. seasonality) in cause and effect variables (Deyle et al., 2016). Thus, to account for a possible shared seasonality of diversity indices and resource use efficiency variables in CCM tests, we generated 500 seasonal surrogates for both diversity indices and phytoplankton resource use efficiency, following Deyle's method (Deyle et al., 2016). That is, causal forcing is deemed significant only when CCM prediction based on observed data is significantly better than that based on the seasonal surrogates (Deyle et al., 2016). Furthermore, considering that the phytoplankton diversity may exhibit time-delayed effects on resource use efficiency, we carried out 0- to 6-month time-lagged CCM analyses (Ye, Deyle, Gilarranz, & Sugihara, 2015b), considering the relevant time-scale in this study. In the main text, we focus on the best result (highest  $\rho$ ) among the 0- to 6-month time-lagged CCM analyses, while we report the details in the Supporting Information.

Furthermore, we tested whether the causal effects identified by CCM are positive or negative by the scenario exploration (Deyle et al., 2016). Specifically, for each historical time point ( $t$ ), we predict phytoplankton resource use efficiency at time  $t + 1$  with a small increase ( $+\Delta Z/2$ ) and a small decrease ( $-\Delta Z/2$ ) of the diversity index at time  $t$ ,  $Z(t)$ . The difference in predicted resource use efficiency is  $\Delta RUE = RUE_{t+1}[Z = Z(t) + \Delta Z/2] - RUE_{t+1}[Z = Z(t) - \Delta Z/2]$ , and the ratio of  $\Delta RUE/\Delta Z$  indicates the sensitivity of phytoplankton resource use efficiency to the driver  $Z$  at time  $t$ . Specifically, a higher positive value of  $\Delta RUE/\Delta Z$  indicates a more sensitive positive causal effect of the diversity index on phytoplankton resource use efficiency and vice versa. This calculation was done for each time point, and then, the averaged value from the whole series was used as indicative of system-level sign of causal effect. Here, following Deyle et al. (2016), we use 5% of the standard deviation of the observed values of the phytoplankton diversity indices  $Z(t)$  as  $\Delta Z$ .

Scenario forecasts were carried out using S-map (Sugihara & May, 1990). In S-map, the tuning parameter theta ( $\theta$ ) indicates non-linearity of the dynamical system, where  $\theta = 0$  gives a linear map, and increasing values of  $\theta$  give increasingly nonlinear maps (Tsonis,

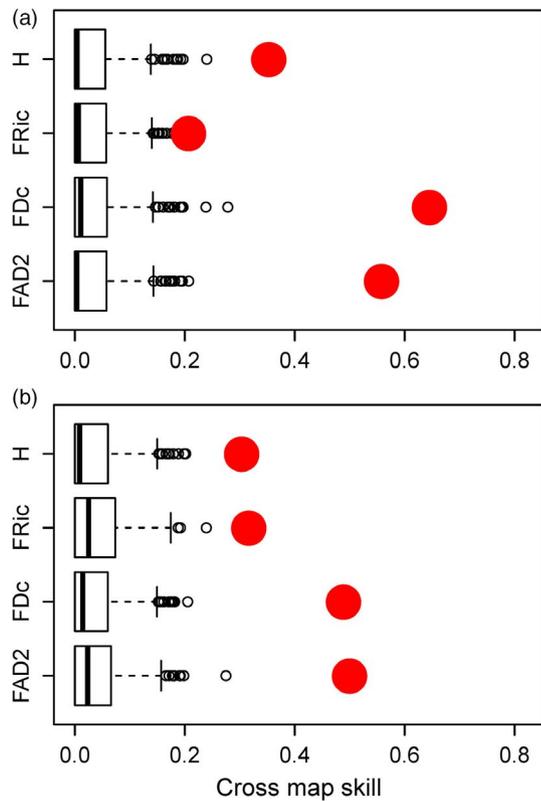
Deyle, Ye, & Sugihara, 2018). When  $\theta = 0$ , the S-map is equivalent to an autoregressive model (Chang et al., 2017). The best  $\theta$  was searched from 0 to 10 with an increment of 0.1. To compare the values of  $\Delta RUE/\Delta Z$  on the same level, the diversity indices and resource use efficiency variables were normalized to z-scores prior to analyses.

The appropriate embedding dimension ( $E$ ) for both CCM and S-map were determined by the false nearest neighbour method (Kennel, Brown, & Abarbanel, 1992; Shalizi, 2006). The main idea of this method is that if the current embedding dimension  $k$  is sufficient to resolve the dynamics,  $k + 1$  would be too, and the reconstructed state space will not change much (Shalizi, 2006). The detailed processes in determining embedding dimension could be found in the Figure S3. Throughout the analyses, we used  $\tau = 1$  (month) for embedding. CCM analyses and S-map forecasting were carried out using the R package of rEDM (Ye, Clark, Deyle, Keyes, & Sugihara, 2016). Moreover, the false nearest neighbour analyses were performed using the R package of fractal (Constantine & Percival, 2017).

### 3 | RESULTS

Results of CCMs show significant causal forcing from all selected functional diversity indices to phytoplankton resource use efficiency ( $RUE_N$ ,  $RUE_P$ ) in the freshwater ecosystem (Figure 1). Furthermore, the causal strength from functional diversity FAD2 and FDC on  $RUE_N$  and  $RUE_P$  is much stronger than FRic and Shannon indices. FRic and Shannon indices have a similar causal strength on  $RUE_P$ , whereas the causal strength from FRic on  $RUE_N$  is much weaker than the Shannon index in the freshwater ecosystem (Figure 1). The conclusions remain qualitatively the same (Figure S4) when we used a shorter time series (subsampling the time-series length to be the same as the length of L4 data). In the marine ecosystem, results of CCMs indicate that not all selected functional diversity indices exhibit significant causal effects on phytoplankton resource use efficiency (Figure 2). Specifically, CCMs find that none of the analysed functional or taxonomical diversity indices has causal effects on  $RUE_N$ . FRic has a significant causal effect on both  $RUE_P$  and  $RUE_{Si}$  ( $p \leq 0.05$ ). FDC has a significant causal effect on  $RUE_P$  ( $p \leq 0.05$ ) and a marginally significant causal effect on  $RUE_{Si}$  ( $p = 0.08$ ). Meanwhile, FAD2 and Shannon diversity index only exhibit a marginal causal effect on  $RUE_{Si}$  ( $p = 0.06$ ) and  $RUE_P$  ( $p = 0.06$ ) respectively.

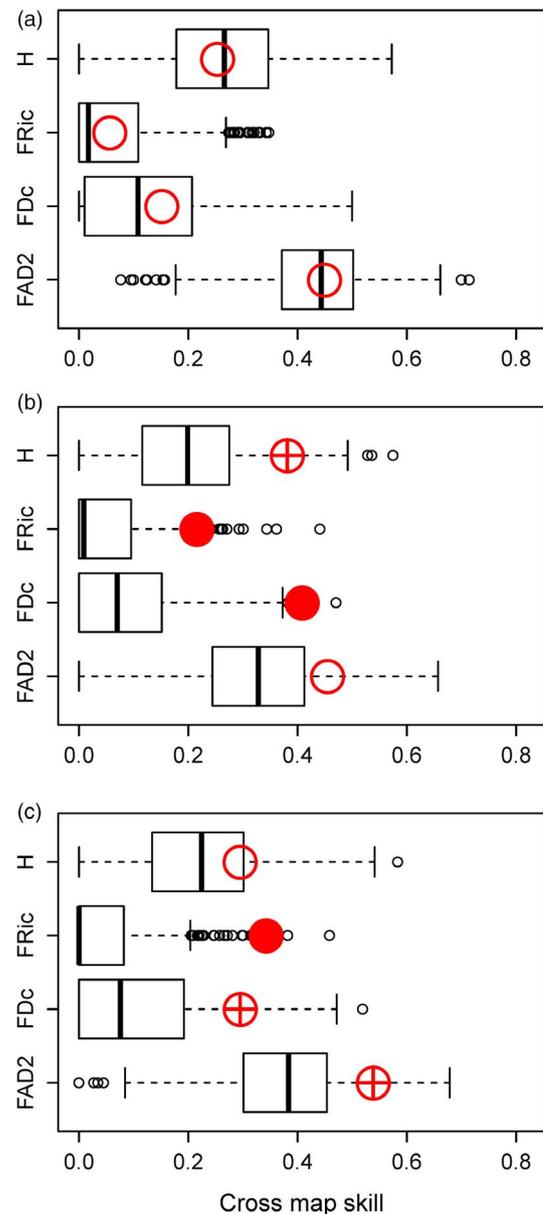
We further examined the sign of causal effect by testing the response of phytoplankton resource use efficiency to a small perturbation in the phytoplankton diversity indices (Figures 3 and 4). The results of scenario exploration show that most significant causal effects from phytoplankton diversity indices on resource use efficiency identified by CCM are on average positive, supporting our hypothesis that functional diversity enhances its resource use efficiency in aquatic ecosystem. Specifically, the causal forcing from FDC on  $RUE_N$  in the Lake Kasumigaura (Figure 3b), with an averaged  $\Delta RUE_N/\Delta Z$  value of 0.172, was identified as the strongest positive



**FIGURE 1** Results of best convergent cross mappings (CCMs) selected from 0- to 6-month lagged CCM analyses (Table S1) showing significant causal effects of phytoplankton diversity on resource use efficiency beyond shared seasonality for dissolved inorganic nitrogen (a) and dissolved phosphate (b) in the Lake Kasumigaura. Red circles show the cross map skill ( $\rho$ ) for phytoplankton resource use efficiency in observations. Box-and-whisker plots show the null distributions for  $\rho$  expected from 500 seasonal surrogates. Filled circle indicates that the measured  $\rho$  is significantly better than the null expectation ( $p \leq 0.05$ ). The meanings of H, FRic, FDC and FAD2 are explained in methods

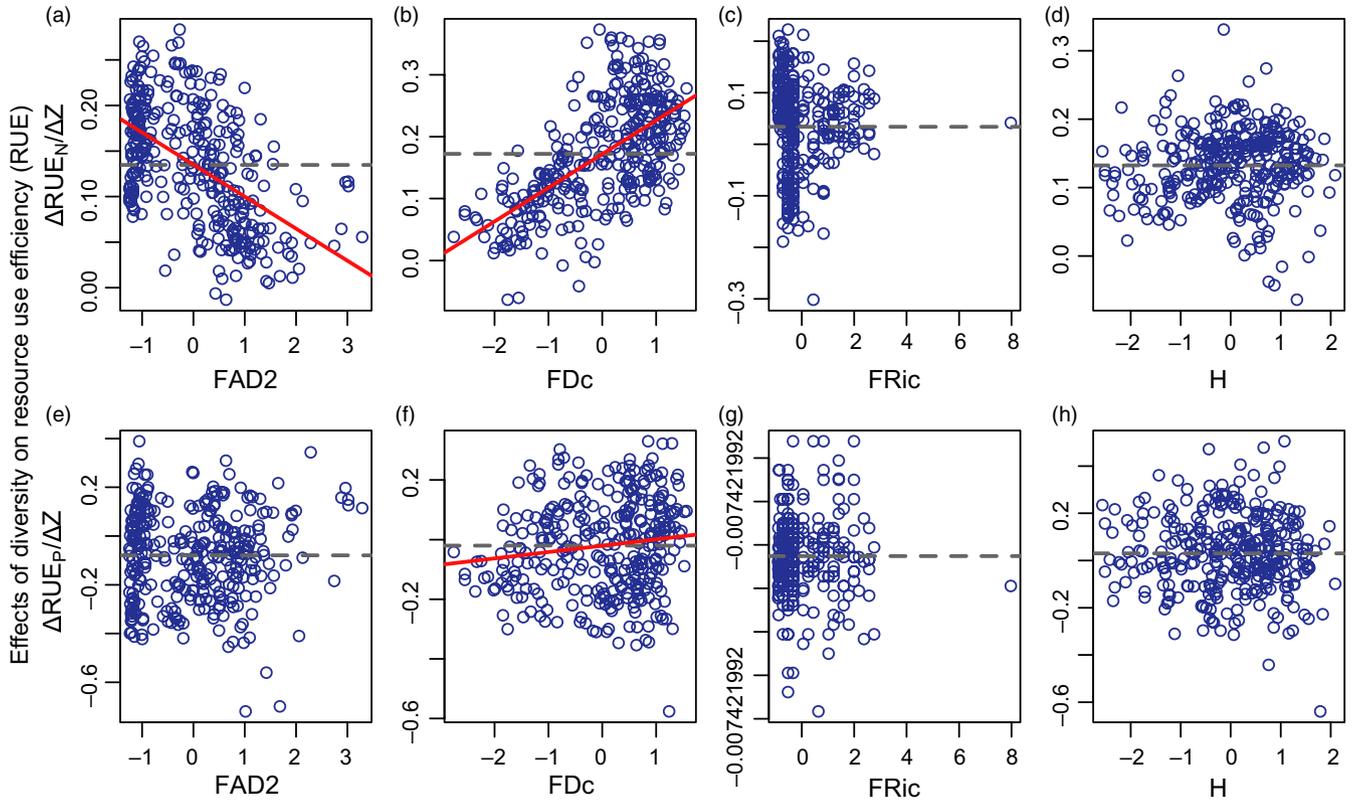
effect from phytoplankton diversity on resource use efficiency in all tested cases. In addition, except for  $RUE_p$  in the Lake Kasumigaura where no evident positive forcing was found from all selected diversity indices (mean  $\Delta RUE_p / \Delta Z \leq 0.03$ ), FDC showed strong average positive effects (mean  $\Delta RUE_p / \Delta Z \geq 0.08$ ) on  $RUE_N$ ,  $RUE_p$  and  $RUE_{Si}$  in all other cases. Furthermore, the positive effects from FDC in these cases were significantly stronger than those from FAD2, FRic and Shannon diversity index (paired Mann-Whitney  $U$  test,  $p < 0.001$ ). This suggests that FDC is the most strong and reliable diversity index among the selected diversity indices (FAD2, FDC, FRic and H) in enhancing phytoplankton resource use efficiency.

Through examining the effect of changes in diversity on resource use efficiency ( $\Delta RUE / \Delta Z$ ), we found that the values of  $\Delta RUE / \Delta Z$  varied significantly with the values of diversity indices in most cases (Figures 3 and 4). This indicated a nonlinear relationship between the selected diversity indices and phytoplankton resource use efficiency. Specifically, FDC have a consistent positive linear relationship with  $\Delta RUE / \Delta Z$  in all scenarios (Figures 3b,

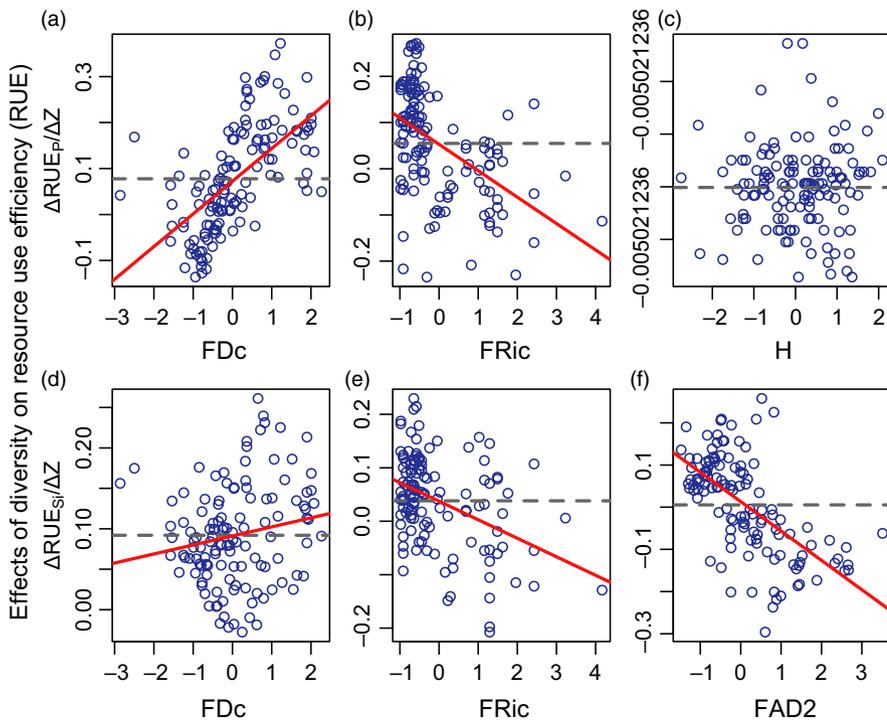


**FIGURE 2** Results of best convergent cross mappings (CCMs) selected from 0- to 6-month lagged CCM analyses (Table S2) showing significant causal effects of phytoplankton diversity on resource use efficiency beyond shared seasonality for dissolved inorganic nitrogen (a), dissolved phosphate (b) and dissolved silicate (c) in the Western English Channel. Red circles show the cross map skill ( $\rho$ ) for phytoplankton resource use efficiency in observations. Box-and-whisker plots show the null distributions for  $\rho$  expected from 500 seasonal surrogates. Filled circle indicates that the measured  $\rho$  is significantly better than the null expectation ( $p \leq 0.05$ ), circle plus indicates that the measured  $\rho$  is marginally significant better than the null expectation ( $0.05 < p \leq 0.10$ )

3f, 4a, and 4d), indicating that stronger positive causal effects on resource use efficiency were usually observed in the phytoplankton community with higher FDC values. Conversely, for FAD2 and FRic, stronger positive causal effects on resource use efficiency were observed with lower values of FAD2 and FRic, while negative effects were generally accompanied by higher value of FAD2



**FIGURE 3** Results of scenario exploration showing the effect of changes in diversity indices ( $\Delta Z$ ) on resource use efficiency ( $\Delta RUE$ ) in the Lake Kasumigaura ST9. Panels a-d show the effect of changes in FAD2, FDc, FRic, and H on  $RUE_N$ ; panels e-h show the effect of changes in FAD2, FDc, FRic, and H on  $RUE_P$ . Dashed grey line represents the mean value of  $\Delta RUE/\Delta Z$ , and the solid red line indicates a significant ( $p < 0.05$ ) regression. Note that, to compare the magnitude of the effects of changing diversity on RUE, all diversity and RUE variables were normalized prior to analysis. Only the diversity indices showing significant causal effects on RUE in convergent cross mapping analyses (Figure 1) were selected for scenario exploration analysis



**FIGURE 4** Results of scenario exploration showing the effect of changes in diversity indices ( $\Delta Z$ ) on resource use efficiency ( $\Delta RUE$ ) in the Western English Channel L4. Panels a-d show the effect of changes in FAD2, FDc, FRic, and H on  $RUE_N$ ; panels e-h show the effect of changes in FAD2, FDc, FRic, and H on  $RUE_P$ . Dashed grey line represents the mean value of  $\Delta RUE/\Delta Z$ , and the solid red line indicates a significant ( $p < 0.05$ ) regression. Note that, to compare the magnitude of the effects of changing diversity on RUE, all diversity and RUE variables were normalized prior to analysis. Only the diversity indices showing significant causal effects on RUE in convergent cross mapping analyses (Figure 2) were selected for scenario exploration analysis

and FRic (e.g. Figure 4b, 4e and 4f). No significant relationship between Shannon diversity index and  $\Delta\text{RUE}/\Delta Z$  was found in our study (Figures 3a, 3h, and 4c), suggesting that changes in Shannon diversity index can either have a positive or a negative effect on resource use efficiency at the same value of Shannon diversity index. Finally, worthy noting that the values of selected best  $\theta$  in the S-maps are larger than 0 in most cases (Table 1), indicating that the relationships between the diversity indices and the phytoplankton resource use efficiency are generally nonlinear and dynamical in aquatic ecosystems.

## 4 | DISCUSSION

### 4.1 | Functional diversity promotes phytoplankton resource use efficiency

We find that functional diversity (FDc) is an important causal factor in enhancing phytoplankton resource use efficiency in both marine and freshwater ecosystems (Figures 1 and 2). To the best of our knowledge, this is the first field study reporting unambiguous causal relationships between multi-trait-based functional diversity and phytoplankton resource use efficiency in natural aquatic ecosystems. We find that FDc has the strongest causal effect on phytoplankton resource use efficiency in most cases (Figures 1 and 2). More importantly, scenario exploration analysis indicated that FDc exhibited the strongest and most consistent on average positive causal effects on phytoplankton resource efficiency in both marine and freshwater ecosystems. (Figures 3 and 4). These results support our hypothesis that functional diversity can enhance phytoplankton resource use efficiency. Among the selected functional diversity indices, FDc appears to be the most robust functional

**TABLE 1** Best theta ( $\theta$ ) selected in the S-map scenario exploration in marine (L4) and freshwater (ST9) ecosystems, where  $\theta = 0$  indicates a linear map, and increasing values of  $\theta$  indicates increasing nonlinearity in S-map

Site	Cause	Effect	$\theta$
ST9	FAD2	RUE <sub>N</sub>	1.3
ST9	FDc	RUE <sub>N</sub>	1.6
ST9	FRic	RUE <sub>N</sub>	1.6
ST9	H	RUE <sub>N</sub>	1.4
ST9	FAD2	RUE <sub>P</sub>	2.7
ST9	FDc	RUE <sub>P</sub>	2.5
ST9	FRic	RUE <sub>P</sub>	0.0
ST9	H	RUE <sub>P</sub>	2.9
L4	FAD2	RUE <sub>Si</sub>	1.2
L4	FDc	RUE <sub>Si</sub>	0.8
L4	FRic	RUE <sub>Si</sub>	1.2
L4	FDc	RUE <sub>P</sub>	1.0
L4	FRic	RUE <sub>P</sub>	1.0
L4	H	RUE <sub>P</sub>	0.0

diversity index in enhancing phytoplankton resource use efficiency. In addition, results of S-map reveal significant nonlinear and dynamical relationships between most of the functional diversity indices and phytoplankton resource use efficiency (RUE<sub>N</sub>, RUE<sub>P</sub> and RUE<sub>Si</sub>), suggesting that nonlinear BEF relationships are common in natural aquatic ecosystems.

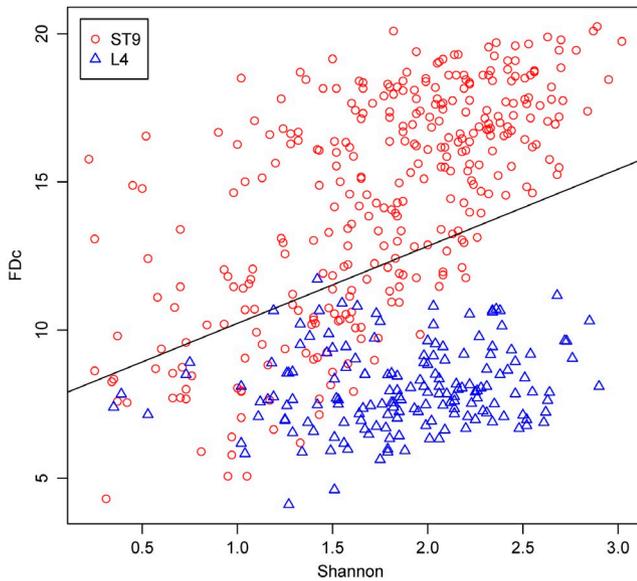
### 4.2 | Functional diversity performs better than species diversity

Results of CCM indicate that FDc has a much stronger causal strength on phytoplankton resource use efficiency than Shannon index in either marine or freshwater ecosystem (Figures 1 and 2). This finding supported our hypothesis that the functional diversity reflects a better niche differentiation in a phytoplankton community than species diversity. Along the similar line of investigation, previous studies in zooplankton-phytoplankton systems reported that single trait-based functional diversity (size diversity) performs better than taxonomic diversity in elucidating a stronger strength of zooplankton predation efficiency on phytoplankton through better niche partitioning with higher size diversity (García-Comas et al., 2016; Ye et al., 2013).

Why does functional diversity perform better than taxonomic diversity in analysing BEF? Theoretically, for a given community, species may have strong niche overlap, and thus adding or losing species with the same functional niche has negligible effect on ecological functions (Carmona, Bello, Mason, & Lepš, 2016; Diaz & Cabido, 2001). Therefore, trait-based functional diversity, which represents better species niche partitioning or functions (Cadotte et al., 2011; Gagic et al., 2015; Gross et al., 2017), can perform better. In our case, although FDc and Shannon indices are correlated ( $r = 0.34$ ,  $p < 0.001$ ), the corresponding values of Shannon index for a given value of FDc have a wide range of variation (Figure 5), suggesting that Shannon diversity does not encompass the overall variability of FDc, likely because of the strong species niche overlap. In contrast, trait-based FDc may represent a better niche segregation and thereafter enhances resource use efficiency. Our study highlights the importance of functional diversity in mechanistic understanding of trophic transfer, and suggests that the phytoplankton community with higher functional diversity would have a higher biomass yield, due to more effective use of nutrients.

### 4.3 | Choosing the proper phytoplankton functional diversity index

Among different functional diversity indices, we found that FDc is the most reliable index in predicting phytoplankton resource use efficiency (Figures 1 and 2). This finding is in accordance with another research in the terrestrial ecosystem, which reported that FDc provides a better explanation of grass biomass than the functional attribute diversity and functional richness (Petchey, Hector, & Gaston, 2004). To explain why FDc performs better than FAD2 and FRic, we ought to consider theory and algorithm underlying these



**FIGURE 5** Scatter plot illustrating the linear relationship between functional diversity FDC and Shannon index in the Lake Kasumigaura (ST9) and Western English Channel (L4). The solid line represents the best-fit regression line ( $p < 0.05$ ) from the pooled data

functional indices. FDC is defined as the extent of complementarity among species' trait values by calculating the total branch length of the dendrogram based on the functional traits (Petchey & Gaston, 2002). Mathematically, FDC is only dependent on trait differences among species rather than species richness. Specifically, adding a novel species (the traits of the species have some differences from the existing species) to a community will increase the value of FDC, yet adding a non-unique species (the traits is identical to one already existed) will leave FDC unchanged. This notable property of FDC matches well the theoretical expectation of functional diversity; that is, a community with higher trait differentiation has a higher value of functional diversity (Petchey & Gaston, 2006).

In contrast, both FAD2 and FRic have some limitations, which might lead to an unreliable estimation of the functional diversity in some cases. Firstly, FAD2 is estimated by the sum of the distances between species in trait space (Walker et al., 1999). In brief, FAD2 is a function of both trait difference among species and the species richness. Consequently, FAD2 might misestimate the real value of the functional diversity in some situations. For example, when adding a new species whose traits information has no difference from the existing species in a community, the estimated value of FAD2 will decrease although the functional diversity should remain unchanged (Petchey & Gaston, 2006). Secondly, FRic is defined as the convex hull volume filled by a community (Villegger et al., 2008). Mathematically, for a community with  $T$  functional traits, at least  $2^T$  species are required to constitute the  $T$ -dimensional hull. This means that for communities with  $T$  functional traits, the estimated value of FRic may be unreliable if the species richness is below  $2^T$  (Villegger et al., 2008). Thus, in our study, to estimate a reliable value of FRic, a minimum requirement of the species number in each sample is

64 because a total of six functional traits were selected in calculating functional diversity. However, the species number for each phytoplankton sample in the Western English Channel and Lake Kasumigaura is far below the minimum species number of 64 (Figure S5). This implies that the estimated values of FRic may be unreliable because the existing species number is not enough to constitute the six-dimensional hull. As such, FRic is not reliable in predicting phytoplankton resource use efficiency in our study.

Furthermore, scenarios exploration suggests that most significant causal effects from phytoplankton diversity indices on resource use efficiency are on average positive (Figures 3 and 4). Yet, the detail values of  $\Delta\text{RUE}/\Delta Z$  exhibit substantial variation, with both positive and negative values in most cases. This may be because the environmental context might affect the BEF relationships (Ratcliffe et al., 2017). However, the most consistent effects of FDC on phytoplankton resource use efficiency suggest that FDC is more robust to the environmental context. This result further reinforces the conclusion that FDC is a robust functional diversity index in enhancing phytoplankton resource use efficiency in aquatic ecosystem.

Our comparison of different functional diversity indices highlights the challenge of selecting the ideal index, considering the conceptual complexity of those indices. As shown in our study, the causal strength on phytoplankton resource use efficiency by different functional diversity indices varied widely (Figures 1 and 2). For example, CCM found that FDC and FAD2 have much stronger causal strength on  $\text{RUE}_N$  and  $\text{RUE}_P$  than FRic in the freshwater ecosystem. However, FAD2 has no causal effects on neither  $\text{RUE}_N$  nor  $\text{RUE}_P$  in the marine ecosystem. Undoubtedly, different performances of functional diversity indices will cause uncertainty in understanding BEF relationships. We are aware of existence of a suite of functional diversity indices in the literature (Carmona et al., 2016); however, comprehensive exploration of those indices is beyond the scope of this study. Developing unified and robust methods for estimating functional diversity emerges as an important topic for future functional diversity-related researches.

Another challenge in estimating functional diversity is to decide which traits should be included in the calculation. Generally, the traits related with the function are selected based on experts' knowledge (Petchey & Gaston, 2006). To remove the subjectivity, researchers also try to choose optimal traits by maximizing the explanatory power of the interested functions (Petchey et al., 2004). This method can select traits quantitatively, especially for the case with numerous candidate traits; however, at the same time, some functionally important traits might be missed, and seemingly functional less important traits might be selected simply owing to statistical reasons (e.g. by chance, the explanatory power is higher).

For phytoplankton, as far as our knowledge, there is still no research addressing the quantitative selection of traits because of the limited candidate functional traits. The six functional traits selected in our study, reflecting the resource acquisition and growth of phytoplankton, are the most widely used traits in phytoplankton functional diversity-related researches (e.g. Abonyi et al., 2018, Weithoff, 2003, Weithoff et al., 2015). Nevertheless, we should add a caveat

that we have not examined the optimal phytoplankton traits matrix for each functional diversity index, and our finding that FDc is the most reliability functional diversity index in predicting phytoplankton resource use efficiency is based on the most widely accepted six functional traits.

#### 4.4 | Ecological and management implications

Functional diversity-driven increase of phytoplankton biomass can bring us some deeper considerations on the eutrophication management and algal bloom problems in aquatic ecosystems. Eutrophication and algal bloom, generally owing to the enrichment of nutrients (e.g. nitrogen, phosphorus), present as one of the most serious environmental and ecological concerns of aquatic ecosystems worldwide (Conley et al., 2009). Our study found that increasing functional difference stimulates the phytoplankton resource use efficiency, leading to a higher level of phytoplankton biomass per unit nutrient. This suggests that the community with higher functional diversity can improve the water quality and reduce the eutrophication because of the higher resource use efficiency. However, at the same time, the consumed nutrients were transformed into the algal biomass, which might lead to the problem of algal bloom if the transformed algal biomass cannot be transferred to higher trophic levels efficiently. However, we found a former study reported that single trait-based phytoplankton functional diversity (size diversity) hinders biomass trophic transfer from phytoplankton to zooplankton (García-Comas et al., 2016). If the findings of García-Comas et al. (2016) are generally applicable in aquatic systems when multi-trait-based functional diversity is considered, aquatic ecosystems with higher phytoplankton functional diversity might actually bear a higher risk of phytoplankton blooms; this is because the enhanced phytoplankton biomass cannot be transferred to higher trophic level effectively. From this perspective, our study suggests that further researches should evaluate the ecological consequence of phytoplankton functional diversity on eutrophication and algal blooms in aquatic ecosystems and should consider multiple trophic levels (García-Comas et al., 2016; Yang et al., 2018).

## 5 | CONCLUSIONS

Using long-term high-frequency datasets from the Western English Channel and Lake Kasumigaura, we found significant causal effects of functional diversity on phytoplankton resource use efficiency in both marine and freshwater ecosystems. Our results based on CCM clearly identified causality. Specifically, we found that FDc is the most robust functional diversity index in predicting phytoplankton resource efficiency, and FDc has a much stronger causal strength on phytoplankton resource use efficiency than the Shannon index in both marine and freshwater ecosystem. Moreover, scenario exploration suggests that FDc has the most consistent on average positive causal effects on phytoplankton resource efficiency in both marine and freshwater ecosystems.

These findings support our hypotheses that phytoplankton functional diversity enhances its resource efficiency and has a stronger causal effect on resource use efficiency than species diversity in aquatic ecosystems. Our study reveals the importance of functional diversity in determining trophic transfer efficiency and nutrient cycling in aquatic ecosystems.

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#### AUTHORS' CONTRIBUTIONS

C.-h.H., C.-W.C. and L.Y. designed the project; S.-i.S.M., N.T. and C.E.W. provided data; L.Y. analysed the data with assists from C.-h.H. and C.-W.C.; L.Y. and C.-h.H. wrote the manuscript with comments from co-authors. All authors have approved the final article.

#### DATA ACCESSIBILITY

The data for L4 can be found: [www.westernchannelobservatory.org.uk](http://www.westernchannelobservatory.org.uk). The data for Lake Kasumigaura can be found: <http://db.cger.nies.go.jp/gem/moni-e/inter/GEMS/database/kasumi/index.html>. Processed data, trait data and R-scripts for computation are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.271k5k0>.

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