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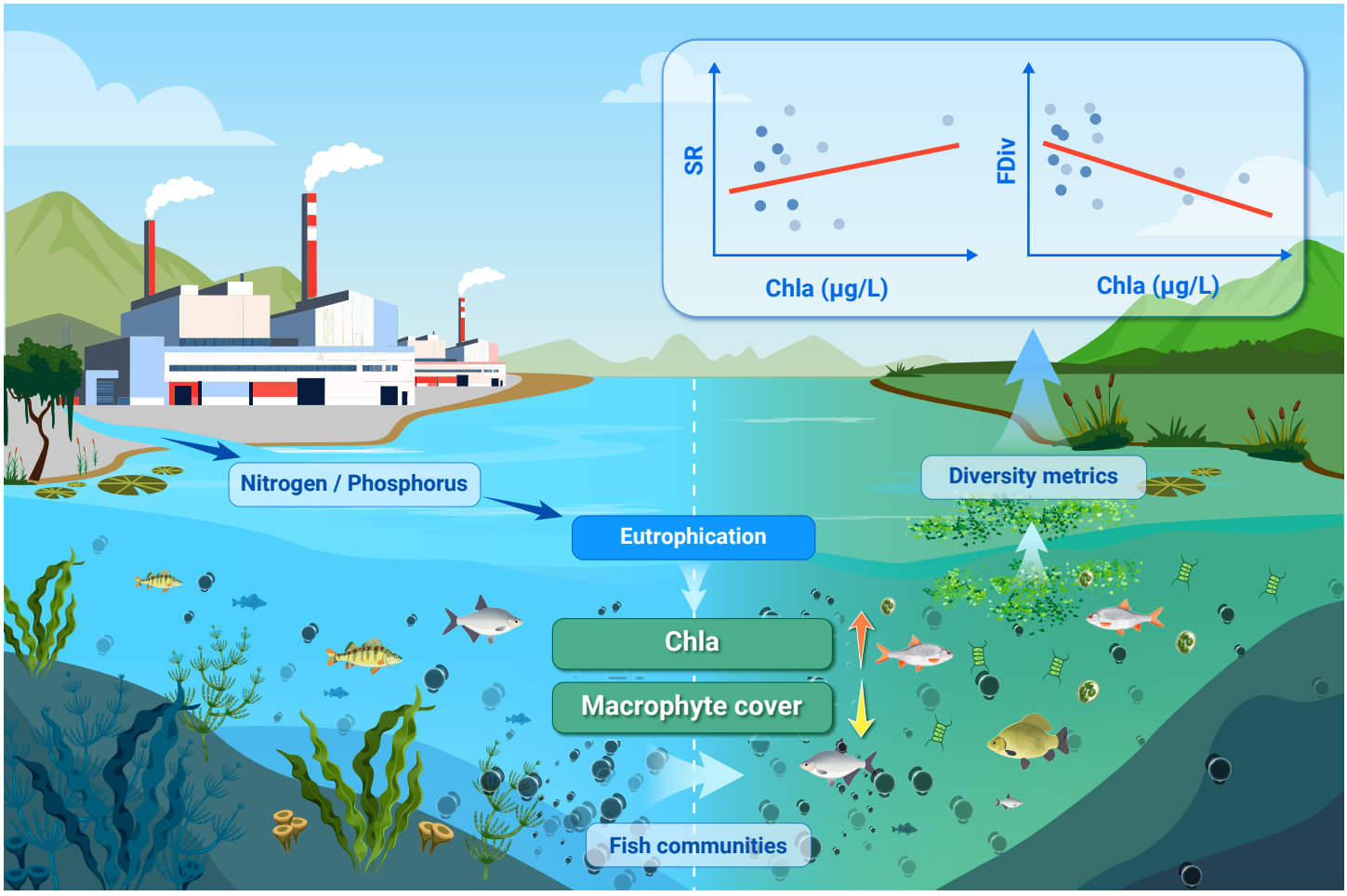
GRAPHICAL ABSTRACT



PUBLIC SUMMARY

- We present fish diversity in 96 Danish shallow lakes that varied greatly in nutrient levels and morphometry.
- Functional divergence fell with lower macrophyte cover and higher chlorophyll *a*, but species richness rose.
- Functional diversity may better detect habitat degradation in lake ecosystems than taxonomic diversity.

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Shallow lakes may shift from a clear state dominated by submerged macrophytes to a turbid state dominated by phytoplankton under increasing nutrient stress. The implications of such an ecosystem state shift for fish taxonomic and functional diversity remain poorly understood. To address this question, we analyzed fish diversity in 96 Danish shallow lakes that varied greatly in nutrient levels and morphometry. We first fit a multiple linear model and used hierarchical variance partitioning to examine the relative importance of multiple environmental variables for changes in fish diversity metrics. Then we used the results to guide the construction of a piecewise structural equation model (pSEM) to quantify the direct and indirect effects of abiotic and biotic variables on fish diversity. Liner regression models demonstrated that the functional divergence of fish communities increased with chlorophyll *a* and decreased with reduced submerged macrophyte cover, whereas species richness and other diversity measures showed the opposite response. Chlorophyll *a* explained more variance in the selected fish diversity metrics than any other predictor. Loss of macrophytes due to eutrophication could lead to habitat homogenization and food resource simplification and, in turn, replacement of species belonging to the functionally diverse benthic and lithophilic species guilds by members of the more species rich but functionally redundant pelagic guild. Our study showed that functional divergence may better detect habitat degradation in lake ecosystems than taxonomic diversity, and it highlights the importance of macrophytes for maintaining the ecosystem functions of shallow lakes.

INTRODUCTION

The majority of ecosystems across the globe are threatened by multiple anthropogenic stressors. Freshwater ecosystems are no exception as they are severely impacted by nutrient pollution, land-use intensification, habitat degradation, morphological alteration, invasive species and climate change.[1] Freshwaters have in fact suffered from a much greater biodiversity loss than terrestrial ecosystems.[2] It is thus important to understand the linkages between biological communities and their environmental conditions.[3] Among the studies examining anthropogenic factors affecting biodiversity in aquatic ecosystems, nitrogen- and phosphorus-driven eutrophication is probably the most common.[4] Eutrophication profoundly influences aquatic ecosystems, often marked by a significant decline in water quality and massive algal blooms, which in turn may cause ecosystems to shift from a clear-water, macrophyte-dominated state to a turbid, phytoplankton-based system.[5,6] However, a growing number of studies also indicate that catastrophic shifts are rare, and that the ecological response of shallow lakes to nutrient enrichment or reduction is typically progressive, not abrupt.[7-9]

Within these fluctuating systems, fish are well-suited for studying diversity. This stems from their status as the most diverse vertebrate group and their performance of numerous key ecological roles.[10] For example, shallow lakes in a clear state usually support a high diversity of fish, in part because submerged macrophytes increase habitat complexity and heterogeneity.[11,12] Macrophytes can provide multiple feeding resources, refugia and foraging areas for fish and in this way facilitate functionally dissimilar species coexistence.[13] Conversely, turbid lakes tend to support lower fish diversity due to habitat homogenisation and low diversity of resources resulting from eutrophication.[14,15] Furthermore, a general pattern of change in fish communities is a shift from percid to cyprinid dominance during this process, especially due to their different foraging strategies.[16] Therefore, an increase in predation and competition because of the niche overlap of species with similar functional traits is expected.[17,18] However, although there is general agreement that positive relations of fish diversity with macrophyte coverage often occur, other forms of responses, including negative, unimodal or hump shaped, are also reported.[19,20] Certainly, in addition to macrophytes and nutrients, fish diversity also depends on lake morphological characteristics such as surface area, water depth, and connectivity.[21,22] For example, Brucet et al. found that larger and deeper European lakes tended to be the most species rich and diverse.[23] Furthermore, hydrological connectivity is widely recognized as a critical attribute of ecological networks and is generally regarded as a positive factor in enhancing fish diversity.[24]

To relate fish biodiversity to the environment, researchers have commonly used taxonomic diversity to characterise communities (e.g., species richness (SR) and diversity indices including information on the presence and abundance of species).[22] However, taxonomic diversity provides an incomplete view of biodiversity as it ignores critical functional and phenotypic distinctions among species.[25] Consequently, the concept of functional diversity (FD) has been developed to measure trait variation that predicts a species' impact on ecosystem functioning.[26] The utility of functional traits lies in their direct link to ecological roles, complementarity, and redundancy, making them powerful for interpreting patterns of community assembly across environmental gradients.[27] In addition, a growing body of research suggests that functional diversity is more sensitive to environmental changes than taxonomic diversity.[3,28,29]

Although studies have documented changes in fish taxonomic diversity between clear and turbid states and/or along nutrient gradients, the concurrent response of taxonomic and functional diversity to such regime shifts or gradual changes has received relatively little attention.[29] Furthermore, most studies focusing upon how fish diversity responds to trophic gradients are case studies or cover only a small geographical region.[20,29] Studies of a wide range of lake types are needed to generalise observations of the relationships between fish communities and environmental changes. In this study, we quantified taxonomic and functional diversity of fish communities in 96 shallow lakes situated along nutrient and morphometrical gradients in Danish lakes, which have been severely impacted by urban expansion and intensive agricultural activities during the last century.[30] Consequently, many lakes have experienced accelerated eutrophication, a decline in habitat heterogeneity, and altered fish community trophic structures.[15] Our study aimed to assess (1) how fish diversity metrics changed along gradients of submerged

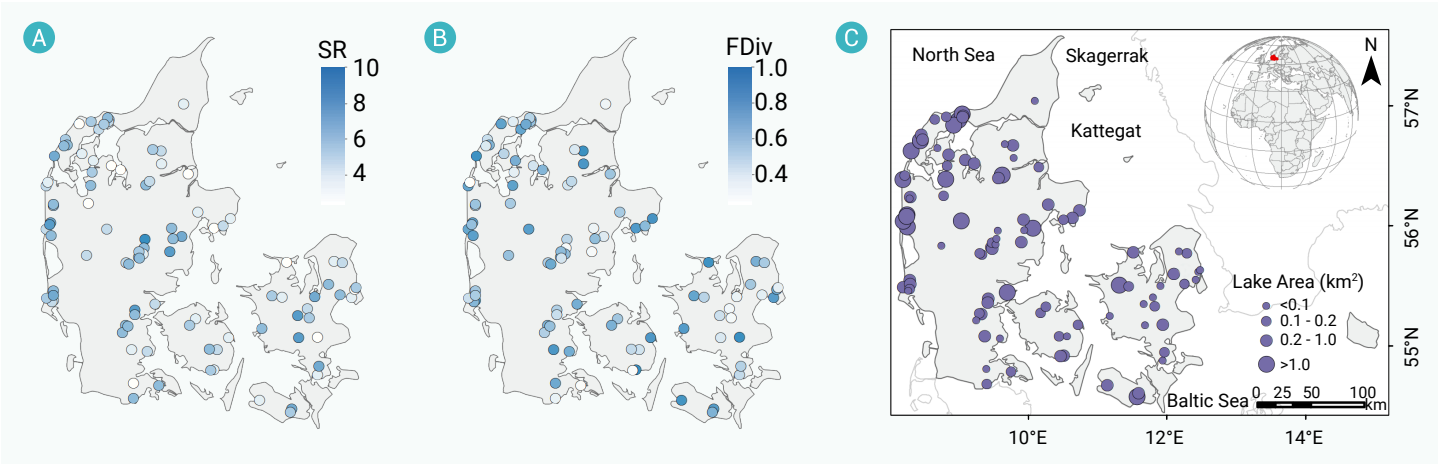

Figure 1. Distribution of (A) species richness (SR), (B) functional divergence (FDiv) and (C) the 96 study lakes included in the analysis across Denmark Colour gradient of (A-B) shows the diversity indices with the lowest to the highest values. Circle size proportional to lake area of (C).

macrophyte cover and productivity (using chlorophyll *a* concentration as a proxy),[31] (2) the key environmental drivers predicting these diversity changes, and (3) the potential divergent responses of taxonomic versus functional diversity metrics to changes in trophic status of lake ecosystems. Our first prediction posited that fish diversity would be elevated in macrophyte-dominated, clear-water conditions, i.e. increase with macrophyte cover and decrease with chlorophyll *a*.[29,32] Secondly, we anticipated that diversity patterns would be primarily shaped by productivity, macrophyte coverage and lake area. Both taxonomic and functional diversity would increase with lake area, though exhibit divergent responses to productivity and macrophyte cover: functional diversity would decline with rising productivity and decreasing macrophyte cover, whereas species taxonomic diversity would tend to increase. Thirdly, we predicted that functional diversity indices might offer better detection of lake habitat degradation than taxonomic diversity since species-environment relationships are assumed to be mediated via functional species traits.[33]

MATERIALS AND METHODS

Study area

Danish lakes are typically small, shallow and highly eutrophic. Denmark has approximately 180,000 lentic and mostly small-sized water bodies (mean area: 4,051 m^2).[34] Over the last hundred years, intensive agricultural practices and urban sprawl have led to a significant surge in nutrient inputs. This has triggered widespread eutrophication and a marked decline in habitat heterogeneity across most Danish lakes.[30,35]

Sampling and processing

Data on biotic and abiotic variables were obtained from the NOVANA program, Denmark's national aquatic environment monitoring initiative running since 1989.[36,37] Selection criteria of a mean depth ≤ 4.5 m and data availability from 2010 to 2020 yielded a final set of 119 lakes for analysis (Figure 1 & Table 1). Then, lakes with ≤ 2 fish species were excluded because at least three species are needed to estimate functional diversity indices.[26] A total of 96 shallow lakes were eventually included in the study. These lakes covered a wide range of nutrient levels and morphometry, but the majority were eutrophic and small.

During the study period (2010-2019), each lake was sampled on a single occasion, with sampling years varying among lakes. As no repeated annual sampling was conducted, the dataset comprises a single temporal snapshot per lake. For each lake, all variables - including physicochemical parameters, macrophyte cover, and fish assemblages - were collected within the same general sampling period for each lake. Specifically, fish sampling was conducted between 14 August and 14 September, macrophyte surveys were performed between 24 June and 15 August, and limnological variables (e.g., water temperature, transparency, and nutrient concentrations) were measured between May and September (see Quirino et al.[38] for detailed methodologies). Although these components were not sampled on the same calendar day, all analytical variables correspond to the same sampling year and comparable seasonal period for each individual lake. Seasonal variability was assumed negligible since almost all data was collected within the summer months. The interannual variability in environmental conditions was also insignificant due to the weak correlations exhibited between sampling years and environmental variables.

Fish were sampled by the same type of multi-mesh New Nordic Norm (NNN) gillnets with EU-standardised dimensions.[39] Each net was 1.5 m deep and 30 m long and consisted of 12 units of 2.5 m length with different mesh sizes (43, 19.5, 6.25, 13, 55, 8, 12.5, 24, 15.5, 5, 35, 29 mm) placed in random order. Gillnetting was conducted both in the littoral and the offshore zones, and all nets were set in late afternoon and retrieved the following morning (about 16 h). More details about the method of setting nets are provided in Jeppesen et al.[40] The number of fish sampling sites in the lakes depended on lake area and shoreline length and ranged from five to 12.[41] For example, lakes with an area of less than 0.5 km^2 usually had six sampling sites, while those with an area of more than 1 km^2 had 10 or more sampling sites. This positive correlation was also well indicated by the Spearman correlations (ρ = 0.71, $p < 0.01$). Catch per unit effort (CPUE, catch per net per night) of fish was calculated as the total number (CPUEn) of individuals per net per night. The resulting data set totaled 657 samples (or communities), capturing 23 taxa belonging to 11 families (Table S1). The CPUEn per lake was the total CPUEn divided by the number of gillnets used in each lake.

We compiled information on nine environmental variables believed to be relevant for fish species occurrence and functional diversity. A suite of physical and chemical parameters was analyzed using standardized methodologies.[36] The physical variables included lake surface area, average water depth, water temperature and Secchi disk depth (Secchi), while the chemical variables included total alkalinity, total nitrogen (TN), total phosphorus (TP) and chlorophyll *a* (Chla). We used the monthly mean values of these measurements derived from samples collected at a mid-lake station during summer (May - September). Submerged macrophytes were surveyed between 24 June and 15 August when the plant community reaches its maximum abundance. Submerged macrophyte species presence and total coverage at each point were evaluated using a water glass and rake. Coverage was estimated according to a seven-point scale ranging from absence to complete cover: 0% (no plants), 0-5%, 6%-25%, 26%-50%, 51%-75%, 76%-95% and 96%-100%. See Quirino et al. for more details.[38]

Data analysis

Species diversity (Hill numbers). Hill numbers were employed to estimate the community taxonomic diversity of each lake, chosen for their recognized advantages over traditional diversity indices.[42] For instance, unlike common metrics used to quantify biodiversity that are sensitive to rare species occurring in low abundances, Hill numbers exhibit the doubling property and provide a continuous framework to estimate the effective number of species. The sensitivity of Hill numbers to species relative abundances is

Table 1. Description, mean and range of fish diversity indices and predictor variables of the 96 study lakes.

Variables	Description	Unit	Mean	SD	Min.	Max.
SR	Species richness	*N*	5.7	1.7	3.0	10.0
Shannon	Shannon diversity	*N*	2.7	0.8	1.1	4.7
Simpson	Simpson diversity	*N*	2.3	0.7	1.0	4.4
FRic	Functional richness	*N*	0.15	0.07	0.01	0.25
FEve	Functional evenness	*N*	0.44	0.29	0.02	0.98
FDiv	Functional divergence	*N*	0.65	0.19	0.22	1.00
SMCover	Submerged macrophyte coverage	%	21.3	25.6	0.0	85.9
Chla	Chlorophyll *a*	μg/L	70.8	71.3	4.4	411.3
TP	Total phosphorus	mg/L	0.17	0.16	0.02	0.81
TN	Total nitrogen	mg/L	1.92	1.00	0.66	5.04
LakeA	Lake surface area	km^2	0.79	2.03	0.01	17.13
AveWD	Average water depth	m	1.35	0.60	0.54	4.10
Secchi	Secchi disk depth	m	0.99	0.56	0.23	2.83
Temp	Water temperature	°C	17.51	1.51	13.34	20.54
Alkalinity	Total alkalinity	meq./L	2.31	1.17	0.05	5.54

controlled by the diversity order q. A low q value produces a diversity index that emphasizes rare species. For example, species richness is recovered when q = 0 (^0D). Higher q values increase the emphasis on common species such as Simpson diversity (q = 2) (^2D). In the limit that q approaches 1, Hill number is equivalent to the exponentiated Shannon index, referred to as Shannon diversity (q –> 1) (^1D).[42,43] The SpadeR package was employed to compute these three Hill numbers.[44]

Functional traits and diversity indices. Functional diversity of fish community for each lake was quantified based on 14 traits related to life history, foraging characteristics, and habitat conditions (Table S2).[24,45] These traits, key to ecosystem functioning, were primarily sourced from FishBase, with supplementary data from the literature[46-48] and expert knowledge of regional fish biologists (Table S3).

For each lake we calculated three primary and independent facets of FD: Functional Richness (FRic), Functional Evenness (FEve) and Functional Divergence (FDiv).[25,26] More detailed explanations of these three indices are provided in Mao et al.[49] In addition, to further describe the functional composition of the fish communities, community-weighted mean (CWM) trait values were calculated for each functional trait. The CWM of a single trait was derived by combining species relative abundance with population-based trait measurements. We computed FD and CWM in R[50] via the dbFD function of the FD package.[51]

Statistical analysis. First, we fitted multivariate linear models to infer the impacts of environmental variables on changes in fish diversity metrics. All nine variables (lake surface area, average water depth, water temperature, Secchi disk depth, total alkalinity, total nitrogen, total phosphorus, chlorophyll *a* and submerged macrophyte coverage) relevant to fish diversity were included as main effects to explain changes in fish diversity indices. Then, hierarchical partitioning (HP)[52] was used to quantify how different environmental variables individually explain the variation in taxonomic and functional diversity metrics. HP quantifies the contribution of a predictor variable by systematically comparing the fit between all possible models containing it and all nested models that exclude it. There is no limit to the kinds of goodness-of-fit measures (e.g., R^2 and rooted mean standard error) that might be used to underlie the variance partitioning, including ordinary least squares, loglinear or logistic regression, and probit analysis. The explanatory power of each predictor was partitioned into independent effects, *I*, and joint effect, *J*. Environmental predictors were randomized many times (1,000 in our case) to produce distributions of *I* for each predictor. Many previous studies have used HP for variance partitioning.[53,54]

We applied piecewise structural equation modeling (pSEM) to evaluate the direct and indirect effects of environmental variables on fish diversity.[55] Since our multivariate linear regression results demonstrated that only SR and FDiv multi-predictor models fitted the data well (Table S5), and the HP models developed for six diversity metrics further indicated that the other metrics responded to the predictors less strongly than SR and FDiv (Table S6), we focused on these two better-explained indices. A conceptual model for the response of fish SR and FDiv to abiotic (e.g., lake surface area and TP) and biotic factors (e.g., macrophyte coverage and Chla) was developed based on the outcomes of the HP models, as well as the hypothesised interaction pathways between fish diversity and environmental characteristics. Model fits were evaluated using the Fisher's C statistic: Models with low Fisher's C statistic values and non-significant *p*-values ($p > 0.05$) were considered acceptable.[56] Standardised coefficients for each path in the model and R^2 for individual paths were also calculated by the piecewise SEM package.

Last, Partial Redundancy Analysis (pRDA) was performed to evaluate the potential associations of the taxonomic and functional structure of fish communities and environmental variables.[57] For this analysis, we classified species into functional groups according to the traits used for calculating FD (Table S2). Statistical significance was tested by a Monte Carlo permutation test with 999 randomisations under the null model of no effect. The fish CPUEn value of each functional group was Hellinger-transformed prior to pRDA. In addition, linear regression models were applied to test how diversity metrics of fish communities may change with Chla concentrations and macrophyte cover. We constructed models incorporating both original and log-transformed terms of the selected variables. The model with the lowest Akaike Information Criterion (AIC) was selected as the best-performing one. This approach was consistently applied to investigate the relationships between fish community composition and Chla concentrations. Spearman's rank correlation coefficient (ρ) was used to measure the correlations between fish community structures and CWM traits and environmental variables. Moran's *I* statistic was applied to assess spatial autocorrelation across the lakes. This metric compares the diversity value at each site against the weighted average of surrounding sites.

All the statistics were performed in R software (version 4.2.0).[50] The HP analysis was performed using the R package "hier.part",[58] the pSEM was calculated using the "piecewise SEM" package,[55] the pRDA analyses were carried out using the "vegan" package,[59] and Moran's *I* was conducted using the package "spdep".[60]

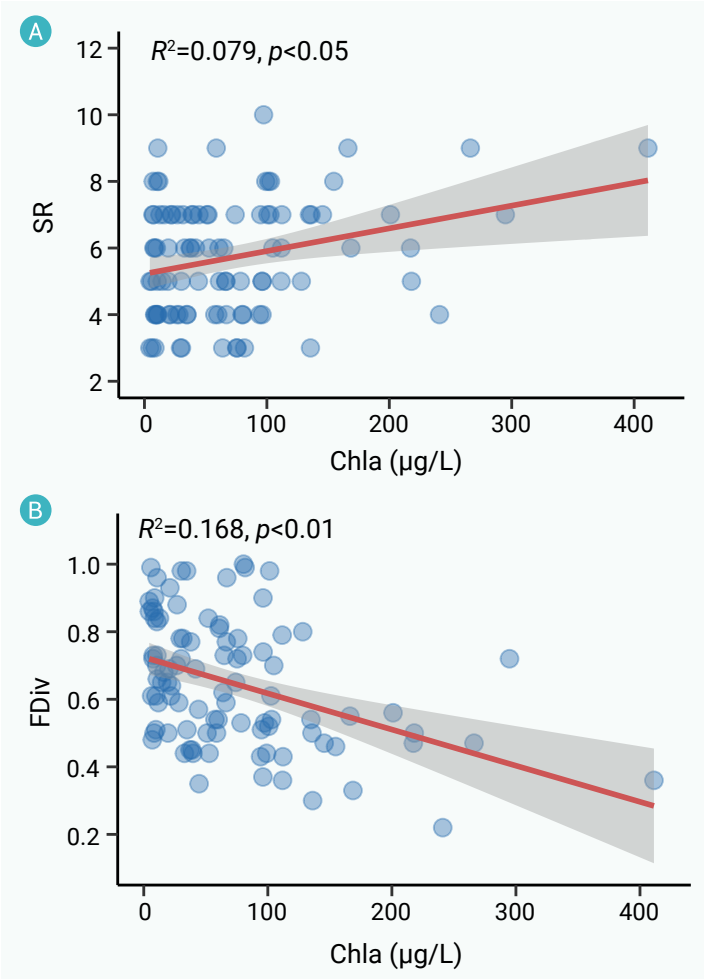

Figure 2. Relationships between chlorophyll *a* (Chla) and (A) species richness (SR) and (B) functional divergence (FDiv) Red solid lines represent the responses of fish diversity indices to changes in Chla concentrations across all sites from linear regression models. Shaded areas are the error bands and denote 95% confidence intervals.

RESULTS

SR was significantly and positively correlated with FRic, ^1D and ^2D but strongly and negatively with FDiv (Figure S1). Similarly, ^1D and ^2D were positively correlated with FRic but weakly and negatively correlated with FDiv. In addition, SR was significantly negatively correlated with the CWM of fish longevity, maximum total body length and diet breadth, while FDiv was highly positively correlated with these CWM traits (Figure S1). These results suggest that species diversity and divergence metrics can provide different information on fish communities. Next, we mapped the SR and FDiv (Figure 1) of fish communities in the Danish lakes at the national scale. The absence of significant Moran's *I* values for any diversity metric (Table S4) indicated that the taxonomic and functional diversities in the lakes were spatially independent.

In our multivariate linear regression results, only SR and FDiv multi-predictor models fitted the data well (R^2_{adj} = 0.144, p = 0.007 and R^2_{adj} = 0.220, p < 0.001, respectively) (Table S5). In the hierarchical variance partitioning, the joint effects of environmental predictors were generally weak (Table S6). We thus focus on the unique effect (*I*-value) from now on. For both response variables, SR and FDiv, HP identified Chla as the most important predictor, followed by TP and Secchi, respectively (Figures 2-3 & Table S6). Submerged macrophyte coverage (SMCover) was ranked the 3rd most important for SR, while lake surface area (LakeA) was ranked 3rd for FDiv. Other variables, such as water temperature and total alkalinity, appeared to have little explanatory power (Figure 3). For other response variables such as Shannon and Simpson diversity, HP ranked LakeA and Secchi as top predictors, followed by nutrient level (Table S6). The HP models developed for FRic and FEve identified almost the same set of key predictors. However, all these diversity metrics responded to the predictors less strongly than FDiv and SR

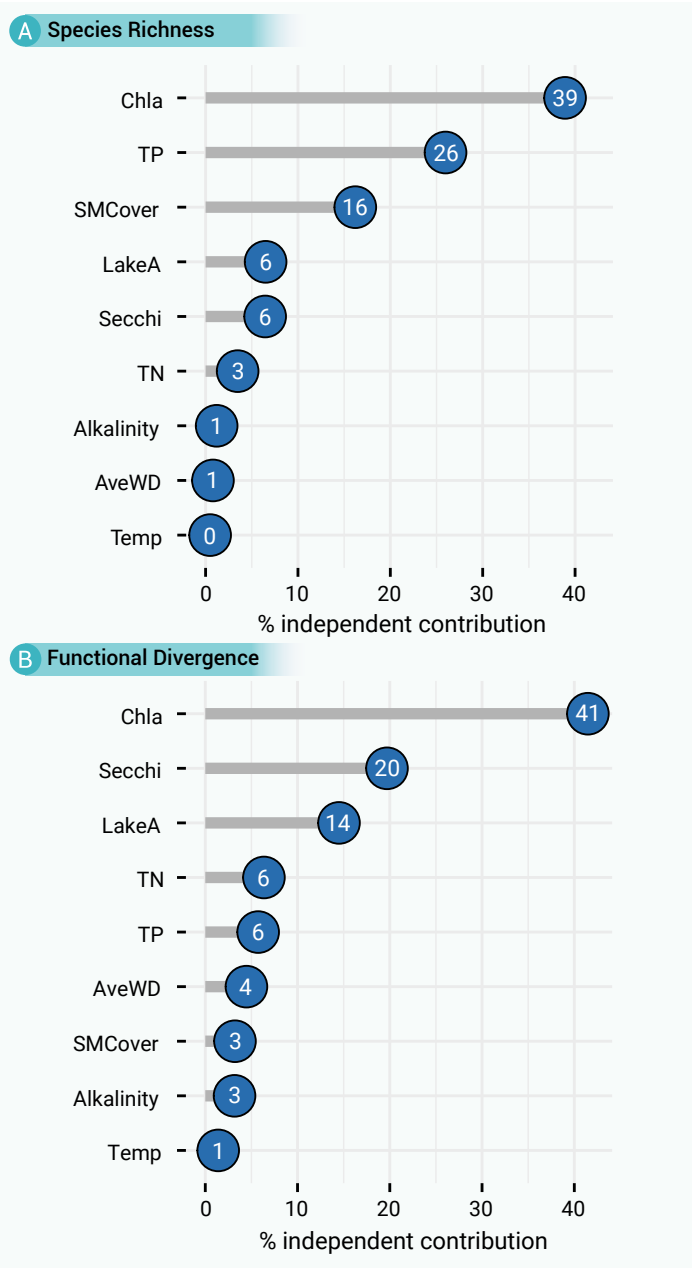

Figure 3. Comparison of predictors explaining the variance of (A) species richness and (B) functional divergence in Danish lakes with % independent contribution (%*I*) The %*I* values were determined through hierarchical partitioning (see full variable description in Table 1).

(Table S6).

Our pSEM fitted the data adequately (Fisher's C = 29.66, d.f. = 22, p = 0.127). The results showed that Chla concentration in the study lakes was mainly boosted by TN, TP, temperature and water depth (Figure 4). The increase in Chla concentration further reduced FDiv and increased the SR of fish communities. The coverage of macrophytes was enhanced by Secchi but reduced by water depth. Macrophyte coverage was negatively related to SR but positively to FDiv, although neither were significant at the 0.05 level (Figure S2). Species richness of fish was directly boosted by lake area. Taken together, the pSEM model results showed that lake nutrient status affected fish functional divergence negatively and positively impacted their species richness indirectly via the concentration changes (Figure 4).

Fish community structures were also strongly correlated with environmental variables. For example, both fish abundance and the species richness of omnivorous and pelagic fish were positively related to Chla (Figures 6A-B). Among the different functional groups, the proportion of piscivorous fish tended to decrease with Chla, while the proportion of omnivores increased

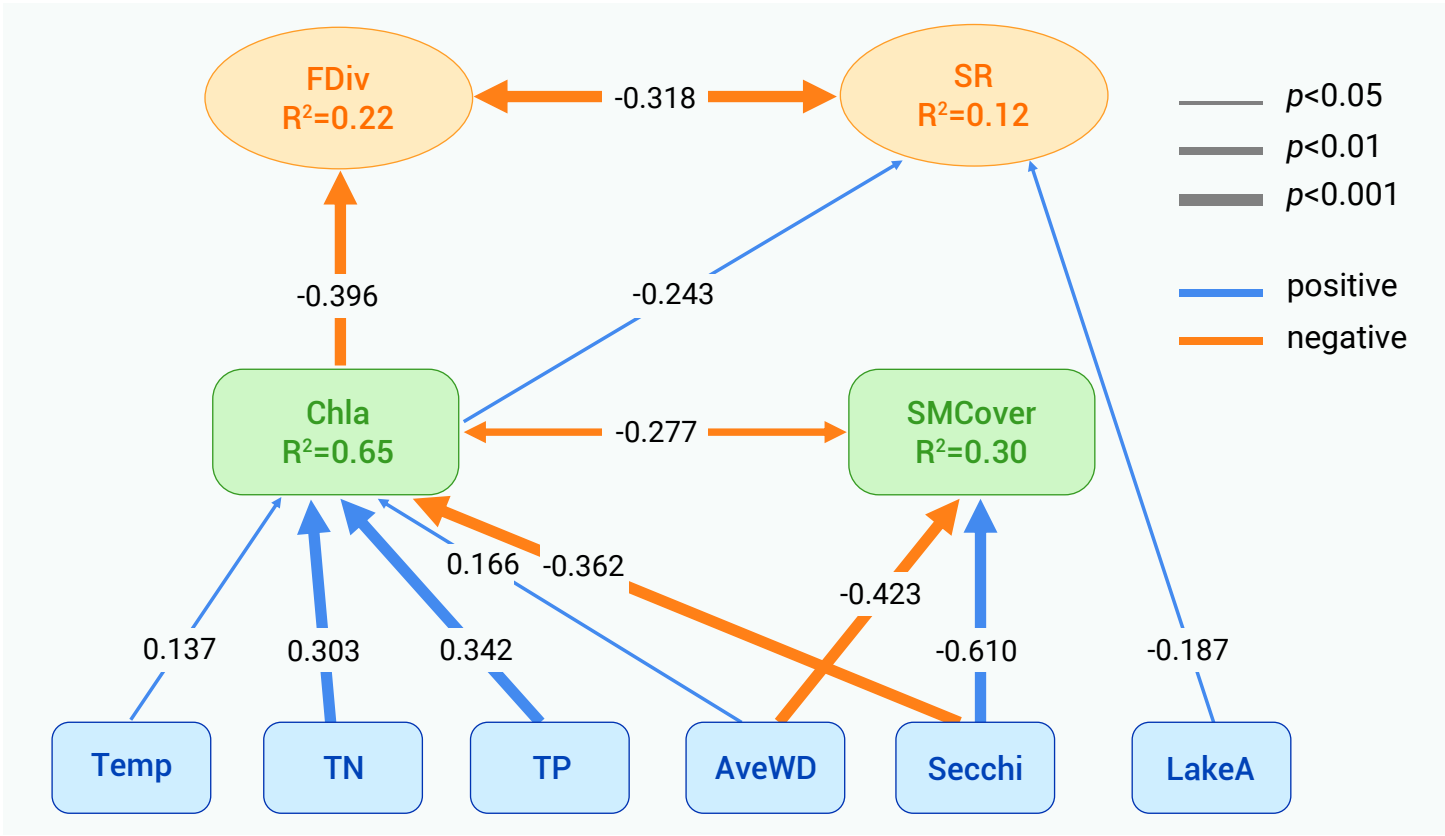

Figure 4. Results of piecewise structural equation modelling (pSEM) showing the effects of abiotic and biotic factors on fish species richness (SR) and functional divergence (FDiv) in the studied 96 Danish lakes Blue arrows indicate positive paths and orange arrows negative paths. For clarity, only the significant paths ($p \leq 0.05$) are shown in the figure (full paths being provided in Figure S2). The thickness of the significant paths reflects the magnitude of the standardized regression coefficients.

slightly (Figures 6C-D). There were also many significant correlations between the CWM of the functional traits and environmental variables. For example, traits related to omnivorous feeding group was positively correlated with Chla and negatively with Secchi (Figure S1). In contrast, traits related to piscivores had strong negative correlations with Chla, TN and TP, while the same traits were positively correlated with Secchi.

Moreover, pRDA analyses showed that a Chla concentration gradient was significantly associated with the taxonomic assemblage structure (permutation test pseudo-$F = 5.74$, $p < 0.05$; Figure 5A; Table S7). Pelagic and omnivorous species such as roach (*Rutilus rutilus*) and the benthic species bream (*Abramis brama*) were positively associated with Chla, while piscivorous fish perch (*Perca fluviatilis*) was positively associated with SMCover and Secchi. Assemblage functional structures were also strongly associated with Chla or SMCover ($p < 0.05$; Figures 5B-D & Table S7). Omnivorous and pelagic species had strong positive associations with Chla and TN (Figure 5B). Piscivores were negatively associated with the Chla gradient but positively associated with SMCover, lake area and water depth. Similarly, species with medium-sized bodies (20-50 cm) tended to be more abundant at higher Chla concentrations (Figure 5C). Large-sized fish (50-100 cm) were positively associated with water depth and SMCover, and small-sized fish (≤ 20 cm) were positively associated with TP and TN. Fish species preferring vegetation substrates were positively associated with SMCover (Figure 5D).

DISCUSSION

Contrasting patterns were observed in the response of fish taxonomic versus functional diversity along a trophic gradient in shallow Danish lakes. Functional divergence (FDiv) decreased with the decline of macrophyte cover and increased chlorophyll *a* concentration, whereas species taxonomic diversity increased. Moreover, other environmental variables, including nutrient conditions and lake area, played an important role in shaping fish diversity. These findings demonstrate how functional divergence can better detect habitat degradation in aquatic ecosystems than taxonomic diversity, thus being a valuable tool for lake monitoring and management.

Different responses of fish diversity to trophic state

Macrophytes play a key role in the functioning of aquatic systems, and most studies have shown that a clear-water macrophyte-dominated state may support a higher taxonomic and functional diversity of aquatic organisms than a turbid state.[11,12] For instance, Law et al. statistically demonstrated that higher macrophyte richness in lakes generally indicates greater mollusk richness.[61] Certainly, the positive relationships between aquatic plants and other organisms' biodiversity are not simply linear, e.g., Kuczyńska-Kippen et al.[62] found that zooplankton diversity in ponds across different trophic gradients exhibits complex nonlinear responses to macrophyte biomass.

Our results showed a positive relationship between submerged macrophyte coverage and fish FDiv, which is consistent with earlier studies.[20,29] This was not surprising considering that macrophytes can increase habitat complexity and heterogeneity by providing greater availability of feeding resources, spawning substrate and refuge against predators than environments free of vegetation, thus facilitating the coexistence of functionally dissimilar species.[13,63] Functional traits such as herbivorous feeding types (in warm lakes) and low predator escape ability are abundant only in the macrophyte-dominated state as reported by Moi et al.[29] In European lakes, many common fish species, including those belonging to Gasterosteidae and Percidae, are aslo phytophils or phytolithophils (obligatory or non-obligatory aquatic plant spawners).[32] Our pRDA results also indicated that fish species preferring vegetation substrates were positively correlated with macrophyte coverage (Figure 5D). Furthermore, macrophytes can provide additional food resources, such as macroinvertebrates living on or among plants.[5] Therefore, macrophytes are not only an important food sources for freshwater fish in temperate lakes but also function as substrates for periphyton and macroinvertebrates that constitute the base of the food web.[64] Overall, our findings highlight the importance of macrophytes as environmental filters in determining the functional traits of fish communities.

Overall, we found a negative relationship between fish SR and macrophyte cover for the 96 lakes. This is inconsistent with some previous studies.[29,32]

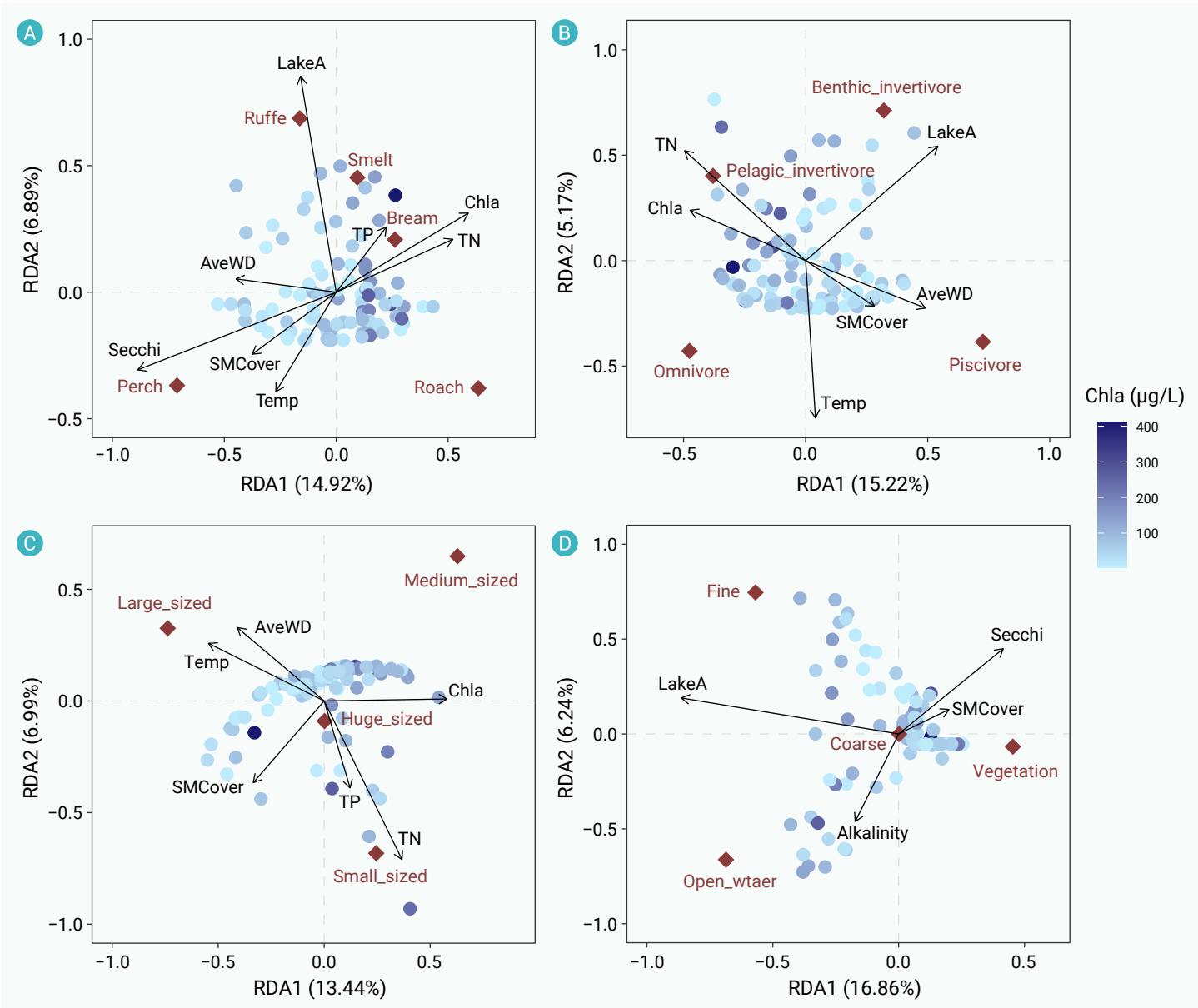

Figure 5. Redundancy analysis (RDA) biplots showing associations of fish communities in terms of (A) taxonomic composition and functional groups of (B) feeding behaviour, (C) body size and (D) substrate preference and statistically significant chlorophyll *a* (Chla) concentrations and environmental variables (arrows) Biplots show RDA scores for the 96 lakes along a Chla gradient ranging from light blue, representing macrophyte-dominated lakes, to midnight blue, representing algal-dominated lakes.

One explanation of this may be that very dense macrophytes by adding visual and movement barriers may make it difficult for the fish to detect and catch their prey.[20] Warfe and Barmuta reasoned that high macrophyte cover may reduce the foraging success for planktivorous and benthic omnivorous fish as these species need sparse plant habitats to move and feed.[65] In contrast, fish SR significantly increased with productivity (using Chla concentration as a proxy) owing to greater nutrient loading (Figure S2). The lakes subject to increase in nutrients and algal biomass may favour species typically occurring in the turbid state, such as small-sized pelagic-foraging fish and species tolerant of poor water quality.[66,67] The pRDA and correlation analysis also showed that omnivorous and pelagic fish had a strong positive association with Chla (Figure 5).

Unlike SR, fish FDiv decreased with increasing nutrient and Chla concentrations, possibly due to the process of biotic homogenisation caused by eutrophication.[14] Various anthropogenic factors, including introduction of non-native species and physical barriers, cause biodiversity loss and homogenisation of fish communities in freshwater ecosystems, but nitrogen- and phosphorus-driven eutrophication may be the most common driver.[4,15] In Denmark, many lakes have also experienced eutrophication and loss of habitat heterogeneity in the past decades due to intensive agriculture and urban expansion.[30,35] Eutrophication-induced macrophyte loss tends to increase the substrate homogeneity, causing the more species-rich but functionally redundant pelagic guild to replace species belonging to the functionally diverse benthic and lithophilic species guilds.[64,68] This may explain why FDiv declined despite an increase in SR.

Furthermore, in Danish and northern European lakes, a general pattern of change in fish communities along the spatial productivity gradient has emerged, i.e. a shift from dominance by percids such as perch to dominance by cyprinids such as roach and bream.[16,31] Roach and bream usually have competitive superiority over perch in highly productive systems. They are able to feed efficiently in the turbid state and at low light intensity, whereas perch depends more on good light conditions.[69] Moreover, their advantage as foragers of zooplankton prey can help roach and bream to limit the recruitment of juvenile planktivorous perch to larger sizes.[31] Consequently, due to competitive advantage and weaker predator control, the abundance of small-sized pelagic and omnivorous species increases with eutrophication (Figures 5-6).[70] Quirino et al. also revealed a positive relationship between Chla and roach and bream abundance based on a dataset from 88 Danish shallow lakes.[38] Therefore, a more probable explanation of functional homogenization is strong dominance by one or a few species (intra-specific homog-

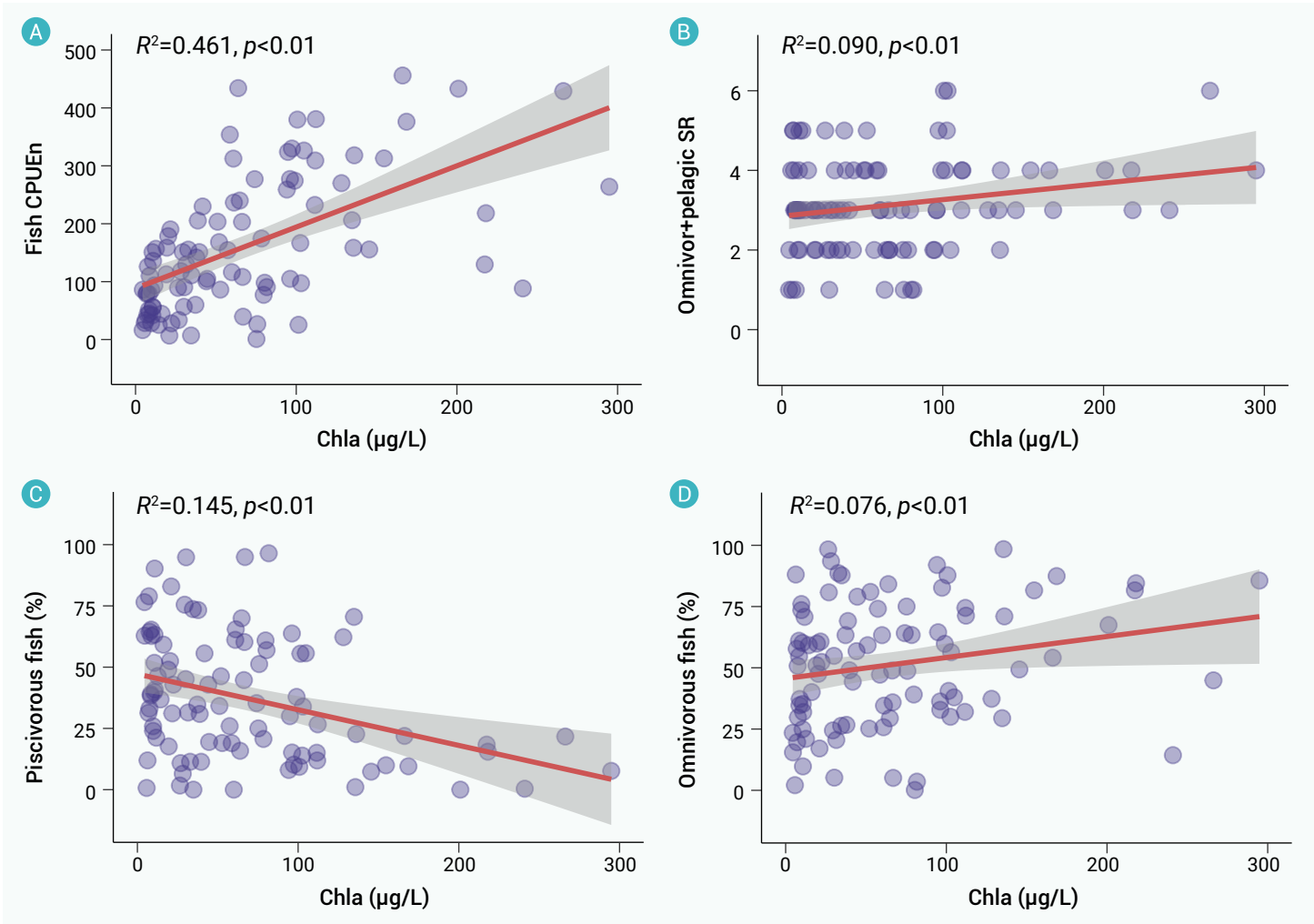

Figure 6. Responses of (A) fish abundance, (B) species richness of omnivorous and pelagic fish, (C) proportion of piscivorous fish and (D) omnivorous fish relative to chlorophyll *a* (Chla) Red solid lines represent the overall responses of fish communities to changes in Chla concentrations across all sites from linear regression models. Shaded areas are the error bands and denote 95% confidence intervals.

enization), followed by a substantial increase in total CPUE (Figure 6). Such functionally redundant communities, particularly with respect to traits related to foraging characteristics, may be highly susceptible to density-dependent regulation.[27] Experimental evidence from tropical stream fish assemblages demonstrates that species sharing similar feeding guilds exhibit high dietary overlap and reduced resource intake, leading to lower growth and intensified antagonistic interactions.[71] In eutrophic lakes, where omnivorous and pelagic species dominate and have high biomasses (Figure 6), such competitive dynamics could be amplified under resource limitation, potentially undermining the long-term stability and resilience of fish communities to environmental fluctuations.[72]

This finding is also largely consistent with the correlations between the CWM of the functional traits and diversity indices (Figure S1). For instance, communities with lower FDiv exhibited significantly reduced CWM for longevity and maximum total body length. This indicates that eutrophication-driven functional homogenization favors species with smaller body size and shorter lifespan, while species possessing larger body size and longer lifespan become progressively rarer (Figure 5C). Therefore, the loss of these trait combinations reduces the overall functional volume and divergence of the community, despite an increase in species richness. Overall, our results support the view that a eutrophication-driven trophic status change likely leads to the replacement of species having unique combinations of functional traits with species with similar sets of traits, producing higher functional redundancy within and between local fish communities.[17,18]

Response of fish diversity to other environmental variables

Taxonomic and functional community structures in the 96 study lakes also depend on lake characteristics such as trophic state and surface area. Firstly, with increasing TP, a significant decline was observed in fish FDiv, whereas SR did not show a clear response pattern. A general unimodal response in SR to increasing TP or trophic state is to be expected as this relationship is well documented in other studies of northern temperate lakes.[16,73] However, Mittelbach et al. reported that although unimodal responses of richness to productivity often occur in nature, other forms of relations, including positive, negative and hump shaped, are also common.[19] A unimodal response appears more frequently in studies of macrophyte vegetation.[73] Conversely, the pattern of fish FDiv response to TP is consistent with its response to productivity and eutrophication, as mentioned above. Homogenisation of fish communities and increased fish abundance have led to higher functional redundancy and enhanced competition for food.[15,16,38]

In addition, as expected, both SR and FDiv, based on species-area relationships,[74] generally increased with lake area (Figure S1). Larger lakes usually provide wider habitat variability and more niche opportunities than smaller lakes.[15,22] For example, larger lakes often have both stony and non-stony substrata, offering multiple habitats for fish, whereas smaller lakes normally have only depositional habitats with fine particulate organic matter.[75]

Finally, our results suggested that lake depth was less important than lake area for fish diversity. Both SR and FDiv were poorly associated with lake depth (Figure S1). The limited impact of depth in our study is probably due to a narrow range of lake depths compared to other studies[15,21] as we excluded all lakes with a mean depth > 4.5 m. Brucet et al. observed a positive relationship between SR and lake depth in a larger set of European lakes with a wider depth gradient range.[23] In short, a combination of nutrient conditions and lake morphology also plays a key role in supporting fish diversity in lake ecosystems.

We noted that a large proportion of the variance could not be explained by either unique or joint effects of the predictors used in the HP models (Table S6). The adjusted R^2 values of our multivariate linear models for SR and FDiv were also low (Table S5). Low explanatory power of ecological models is, however, fairly common.[76] Among the possible reasons is lack of potential important predictors in the models, in our case, e.g., human disturbances not related to nutrients or spatial connectivity to other water bodies. Taking water connectivity as an example, it is recognised as a vital attribute of an ecological network and is widely viewed as a positive factor.[24] However, research by Wilkie et al. further demonstrated that the responses of freshwater biodiversity to landscape connectivity and anthropogenic stress vary across taxonomic groups, frequently transitioning from positive to negative correlations with increasing stress.[77] Future studies should measure, compile and consider those factors in modeling.

Implications for lake ecosystem monitoring

Hill numbers are increasingly used by ecologists due to their statistical advantages over other diversity indices and SR.[42] Sensitivity to the weights of common and rare species is controlled by a parameter, q. Changing q values lead to a family of Hill numbers.[44] However, Shannon and Simpson diversity responded less well to the environmental predictors than SR in the hierarchical partitioning (Table S6). This agrees with the results of Cao and Hawkins who found that these two diversity measures seemingly do not provide additional information on how biological communities respond to human stresses and/or natural environmental changes.[78]

We also showed that FRic and SR were strongly and positively correlated (Figure S1), which is consistent with previous work.[25] In general, the more species there are in the community, the larger is the functional space occupied. However, FDiv and FEve are independent of SR, which allows comparison of communities with different SR without bias.[26] This was confirmed by the values obtained with our dataset (Figure S1). The finding that FDiv appears to more responsive to human disturbances in aquatic ecosystems than SR was confirmed by the patterns observed in Danish lakes.[3] The more rapid decline of FDiv than SR in shallow Danish lakes along a nutrient gradient implies that FDiv can better detect early responses to habitat degradation and loss. We thus agree with Mouillot et al. that a trait-based framework could provide early warning about ecosystem alterations.[3]

Although the response pattern identified aligns with findings from the above studies, we emphasise that it remains debatable to what extent these results can be generalized to other shallow lakes beyond the study area in Denmark. For example, it is well established that fish SR typically shows a unimodal response to increasing trophic state, a pattern repeatedly observed in northern temperate lakes.[16,73] Hence, the observed increase in SR with Chla in the present study may not be sustained across a wider trophic gradient. Therefore, a recommended topic for future research needs to examine whether fish taxonomic and functional diversity continue to exhibit the response patterns observed in Danish lakes on a broader geographical scale.

Another point we want to emphasise is that functional diversity indices can be affected by the traits used and the classification of species for a given trait.[26,27] Furthermore, fish species in European lakes are mainly omnivorous and less specialized than in many other regions of the world.[16] Many are enormously plastic in feeding, habitat use, and life history, and such intraspecific variation may complicate FD estimates and interpretations. For instance, the diet of perch may vary depending on body length and feeding habitat.[79] Particularly during the juvenile stage, perch are omnivorous rather than piscivorous. To address this, we conducted an additional simulation in which we randomly assigned perch individuals as predators only in 25% and 10% of all the lakes. However, the results showed that the original FDiv was strongly and positively correlated with the FDiv values from these simulations (Figure S3). These findings suggest that random variation in perch diet within lakes had a limited impact on functional divergence. The preceding analysis is only a preliminary attempt, and it is therefore recommended that future work incorporates detailed data on the above-mentioned features into FD estimates.

Finally, we would like to point out that although our study primarily adopts the lens of alternative regimes to better understand the relationship between fish biodiversity and lake environmental factors, the findings presented do not rely on this theoretical framework. The existence of alternative state has remained controversial, both in theoretical models and observed natural systems.[5,8] Accumulating evidence from long-term studies suggests that nutrient levels drive predominantly gradual ecological responses, rather than abrupt regime shifts.[7,9] In the present study, fish biodiversity across 96 Danish shallow lakes also exhibited no evidence of catastrophic shifts in relation to gradients of nutrient or chlorophyll *a* concentration. Nonetheless, our findings highlight an urgent management imperative: reducing nutrient loading and preserving considerable levels of macrophyte cover are essential to sustain the resilience of shallow lake ecosystems and their fish communities amid rapid global change.

CONCLUSIONS

Our study showed that the trophic gradients in shallow Danish lakes altered taxonomic and functional diversities of fish communities. Functional diversity decreased with the decline of macrophyte cover and the increase of lake productivity (chlorophyll *a*), whereas the taxonomic diversity increased. Moreover, chlorophyll *a* and nutrients were identified as the main drivers of fish diversity. Eutrophication-caused trophic state changes may lead to replacement of species with unique traits with species of similar traits and/or increased abundance of one or a few common species, ultimately prompting inter-specific and intra-specific functional homogenization. In either case, functional divergence may be more sensitive than taxonomic diversity to habitat degradation in aquatic ecosystems.

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AUTHOR CONTRIBUTIONS

Z.M., B.A.Q., X.G. and E.J. designed the study. B.A.Q., M.S., T.L.L. and L.S.J. collected the data. Z.M. and Y.C. designed the methodology and analysed the data. Z.M. wrote the manuscript with assistance from Y.C., L.Z. and E.J. All authors contributed to the manuscript and approved the final version.

DECLARATION OF INTERESTS

Erik Jeppesen is Steer Committee members of The Innovation Geoscience and is blinded from reviewing or making final decisions on the manuscript. Peer review was handled independently of this member and his research group. The other authors declare no conflicts of interest.

DATA AND CODE AVAILABILITY

Our data are available from Open Science Framework at DOI:10.17605/OSF.IO/BP8AT.

SUPPLEMENTAL INFORMATION

It can be found online at https://doi.org/10.59717/j.xinn-geo.2026.100237.

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