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► **To cite this version:**

Kai Feng, Wenbo Deng, Yinzhe Zhang, Kun Tao, Jing Yuan, et al.. Eutrophication induces functional homogenization and traits filtering in Chinese lacustrine fish communities. *Science of the Total Environment*, 2023, 857, pp.159651. 10.1016/j.scitotenv.2022.159651 . hal-04718794

**HAL Id: hal-04718794**

**<https://cnrs.hal.science/hal-04718794v1>**

Submitted on 2 Oct 2024

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1 **Eutrophication induces functional homogenization and traits filtering in Chinese**  
2 **lacustrine fish communities**

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22 **Abstract**

23 Rapid anthropogenic nutrient enrichment has caused widespread ecological problems  
24 in aquatic ecosystems and the resulting eutrophication has dramatically changed fish  
25 communities throughout the world. However, few studies addressed how fish  
26 communities responded to eutrophication in terms of multidimensional functional and  
27 taxonomic structure, especially how eutrophication acted as an environment filter on  
28 functional traits. The aim of the present study was to investigate the effects of  
29 eutrophication on fish species composition, community metrics and species functional  
30 traits in 26 shallow lakes from the middle reaches of Yangtze River basin, China. This  
31 study validated that eutrophication is an important factor shaping the fish community  
32 structure. Regression analyses showed that eutrophication favored higher total  
33 biomass and lower functional diversity of fish communities but had little effect on  
34 species richness. Despite the fact that some pelagic zooplanktivorous species were  
35 more abundant in the most eutrophic lakes, multivariate analyses of the relationships  
36 between species traits and environmental variables revealed weak relationships  
37 between feeding traits and eutrophication. In contrast, species with a benthic life stage  
38 were negatively associated with eutrophication while those with a large body size and  
39 high absolute fecundity showed the opposite trend. Due to demersal habitat  
40 degradation, and to a lesser degree, to changes in trophic resources availability,  
41 eutrophication caused functional simplification of fish communities by increasing  
42 functional traits homogeneity among the most tolerant species. Some relationships  
43 between functional traits and eutrophication well established in the western palearctic

44 have not been observed in this study, emphasizing the importance of biases resulting  
45 from specific evolutionary histories. This work will provide useful insights on  
46 on-going restoration and management of shallow lakes in the Yangtze River basin.

47

48 **Keywords:**

49 Yangtze River, productivity, species richness, life history strategy, trophic ecology,  
50 habitat use.

51 **1. Introduction**

52 Rapid anthropogenic nutrient enrichment (nitrogen or phosphorus) and resulting  
53 eutrophication have caused widespread environmental degradation in natural  
54 ecosystems around the world (Smith and Schindler, 2009). In aquatic systems, high  
55 levels of eutrophication are usually related to harmful algal blooms, bottom water  
56 hypoxia, biodiversity loss, habitat degradation and ecosystem quality deterioration  
57 (Carpenter, 2008; Smith and Schindler, 2009; Eero et al., 2016). Eutrophication can  
58 also cause direct economic losses, including costs of water purification for human use,  
59 reduced fisheries yield, and decreases in the recreational value of water bodies (Pretty  
60 et al. 2003).

61 Not surprisingly, eutrophication has dramatically changed fish communities  
62 throughout the world (Jeppesen et al., 2003) and is one of the major human  
63 perturbations that lacustrine fishes are faced to (Jacobson et al., 2017). An increase in  
64 nutrient loading in lakes results in several environmental changes that can potentially  
65 affect fish community composition, function and dynamics (Jeppesen et al., 2003).

66 The most direct effect of increasing the availability of phosphorous, a nutrient  
67 limiting the phytoplankton growth, is to boost primary productivity of the ecosystem  
68 with potential consequences all along the food chain (Carpenter, 2008; Schindler et al.,  
69 2016). As a result of eutrophication, clear water lakes dominated by macrophytes shift  
70 to turbid ones dominated by phytoplankton, generating changes in both habitat and  
71 trophic resources (Scheffer et al., 1993). At high levels of primary production,  
72 hypoxia events become more frequent because of the decomposition of the organic  
73 matter that accumulates at the bottom and the respiration of phytoplankton at night  
74 (Anderson et al., 2002). Excessive algal growth and biological clogging lead to  
75 hypoxia in the demersal zone, resulting in degradation of the habitat quality for the  
76 benthic communities (Jacobson et al., 2017). As a result, eutrophication leads to the  
77 loss or degradation of habitats where fishes forage, spawn or shelter, such as the loss  
78 of vegetated habitats in shallow lakes and demersal gravel spawning grounds  
79 impaired by hypoxia (Argillier et al., 2013). Eutrophication favors blooms of toxic  
80 cyanobacteria, with detrimental consequences on biodiversity (Smith and Schindler,  
81 2009).

82 The positive impact of rising nutrient loading on fish productivity has been  
83 shown in several lakes worldwide (Olin et al., 2002; Mehner et al., 2008; Hayden et  
84 al., 2017; Yu et al., 2021). However, the effects of nutrient dynamics on fish  
85 productivity could be indirect, not easily anticipated and difficult to assess with  
86 empirical data (Bolle et al., 2021). For some species, as the effects of eutrophication  
87 intensify, fish biomass and density may begin to decline, for example, due to

88 increased food competition and decreased oxygen content in water bodies (Thomas  
89 and Eckmann, 2007). In turn, the diversity of the fish communities could decrease as  
90 well by a combination of lower species richness and higher dominance of a few  
91 species that can thrive in eutrophic waters (Mehner et al., 2005).

92 Nutrient enrichment induced by human activity is likely to act as a set of  
93 environmental filters (Smith and Schindler, 2009) which not only regulate the species  
94 composition of the community, but also affect the functional structure (Petriki et al.,  
95 2017). Assessing the threat of anthropogenic disturbance (e.g., eutrophication) to the  
96 loss of fish diversity in freshwater ecosystems traditionally relied on abundance,  
97 biomass, species richness and taxonomic diversity (Stuart-Smith et al., 2013;  
98 Coleman et al. 2015). However, diversity measurement that takes into account the  
99 functional traits of species could be more sensitive to environmental changes, could  
100 help understanding the underlying mechanistic processes and identifying changes in  
101 ecosystem functioning (Villéger et al., 2010).

102 Identifying indicator species responding to human perturbations is critical to  
103 environmental management (Bal et al., 2018), but this approach can only be applied  
104 where the indicator species occur, which limits its geographical scope. For instance, in  
105 Europe, *Perca fluviatilis* and *Rutilus rutilus* are frequently used as indicator species  
106 for eutrophication, as intolerant and tolerant species respectively (Ritterbusch et al.  
107 2022). In this regard, functional traits are supposed to provide a more general  
108 approach (Villéger et al., 2010; Mouillot et al., 2013). Traits based approaches  
109 assumes that the local habitat acts as a filter, selecting the species having the

110 appropriate combination of traits allowing them to persist given the local  
111 environmental conditions. By revealing traits-environment relationships that are  
112 potentially independent from taxonomic composition, such approaches could help  
113 identifying similar trait-habitat relationships in two different regions having few or no  
114 species in common (Su et al., 2021). However, studies using functional approaches to  
115 assess the effects of eutrophication on lacustrine fish communities are still very rare  
116 and strongly geographically biased toward Europe. In a recent review of fish-based  
117 assessments of ecological status of European lakes, Ritterbusch et al. (2022) pointed  
118 out that fish exhibited an integrated reaction to multiple stressors (including  
119 eutrophication) particularly with regard to their feeding ecology. The relative  
120 contribution of piscivorous fishes tend to decrease with eutrophication, while the  
121 opposite is observed for benthivorous and omnivorous fishes (Ritterbusch et al., 2022).  
122 Those patterns suggest the existence of environmental filtering in which species  
123 sharing the same traits covary along the eutrophication gradient. This trait filtering  
124 process observed for Europe (Jeppesen et al., 2000; Argillier et al., 2013; Petriki et al.  
125 2017) is not necessarily general and could depend on the particular evolutionary  
126 history of this region, the type of lakes encountered or the causes for nutrient  
127 enrichment. In this study we will address the existence of traits-eutrophication  
128 relationships for lacustrine fish communities in a different geographical context (the  
129 Yangtze River floodplain, China) and its consistency with previous studies.

130       The middle and lower reaches of the Yangtze River harbor one of the largest  
131 floodplains in the world in which a great aquatic biodiversity is encountered,

132 particularly with regard to fish, this area accounting for about 3% of known  
133 freshwater fish species of the world (Wang and Dou, 1998). From 1950s to 1970s,  
134 most of the floodplain lakes were disconnected from the Yangtze River by dams or  
135 sluices (Liu and Wang, 2010) and then experienced intensive aquaculture (Le et al.,  
136 2010). This combination of habitat fragmentation and eutrophication resulted in a  
137 significant loss of aquatic biodiversity, especially in fish communities (Liu and Wang,  
138 2018), and environmental management measures have been recently taken to mitigate  
139 this loss and promote ecological restoration. In particular, since the mid-2010s, a  
140 complete prohibition of aquaculture and fishing has been implemented.

141 This study investigated the effects of eutrophication on the taxonomic and  
142 functional structure of fish in 26 shallow lakes along the middle reaches of Yangtze  
143 River basin, China. The aims of this study are to I) uncover the effect of  
144 eutrophication on the taxonomic structure of fish community; II) figure out how  
145 eutrophication correlates with changes in fish community structure apprehended in  
146 terms of a broad array of functional traits related to life history strategy, trophic  
147 ecology and habitat use; III) identify species and traits indicator of eutrophication; IV)  
148 by comparison with studies from other parts of the world, assess whether a general  
149 traits filtering by eutrophication exists. Due to long-term human disturbances (e.g.,  
150 construction of dams and sluices, intensive aquaculture, agricultural expansion and  
151 water pollution), the task of lake management and maintenance of the ecological  
152 resilience of the shallow lake system of the Yangtze River has become more  
153 challenging and pressing (Zhang et al. 2020). This work will provide fresh insight into

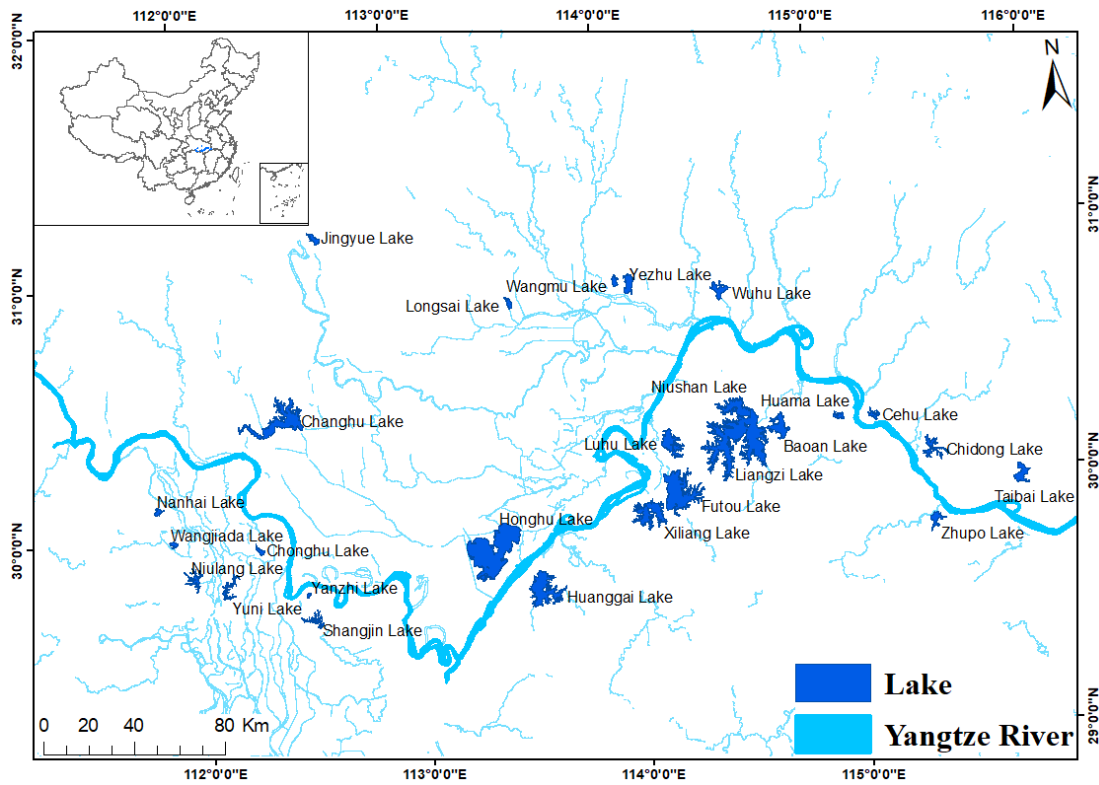


154 water quality restoration and fish resource management of shallow lakes in the  
155 Yangtze River basin.

## 156 **2. Material and methods**

### 157 ***2.1. Study area***

158 The 26 studied lakes are located in the middle reaches of the Yangtze River basin,  
159 China (Figure 1). Different levels of agricultural expansion (Dong et al., 2012) and  
160 fisheries exploitation (Wang et al., 2018) resulted in a gradient of eutrophication (total  
161 phosphorus concentration ranges from 0.01 to 0.77 mg L<sup>-1</sup>) experienced by those  
162 lakes. Lake area ranges from 2.30 km<sup>2</sup> to 274.60 km<sup>2</sup>. Most of these lakes are shallow  
163 with maximum water depth ranging from 0.8 m to 5.7 m (Table S1). The survey of  
164 fish communities was conducted from March to May 2019 in three sampling sites per  
165 lake. The survey of water quality was conducted from October to November 2019, the  
166 location of the sampling sites is the same as those of the fish community sampling  
167 sites. The ranges of variation of all the environmental and biological variables for 26  
168 studied lakes are given in Table S2.



169

170 Figure 1 Map of the study region, the middle Yangtze River, in China, and the  
 171 locations of surveyed lakes.

172 **2.2. Data collection**

173 **2.2.1. Water quality and lake morphology variables**

174 For each sampling site, twelve water quality variables related to characterizing  
 175 physiochemistry and eutrophication were measured: Secchi depth (SD, m), dissolved  
 176 oxygen (DO, mg L<sup>-1</sup>), conductivity (Cond, μS cm<sup>-1</sup>), pH, turbidity (Turb, NTU), total  
 177 phosphorus (TP, mg L<sup>-1</sup>), total nitrogen (TN, mg L<sup>-1</sup>), chlorophyll *a* (Chl<sub>a</sub>, μg L<sup>-1</sup>),  
 178 chemical oxygen demand (COD<sub>Mn</sub>, mg L<sup>-1</sup>), ammonia nitrogen (NH<sub>4</sub><sup>+</sup>-N, mg L<sup>-1</sup>),  
 179 nitrite nitrogen (NO<sub>2</sub><sup>-</sup>-N, mg L<sup>-1</sup>) and nitrate nitrogen (NO<sub>3</sub><sup>-</sup>-N, mg L<sup>-1</sup>). SD was  
 180 measured using Secchi disc. DO, pH, Cond and Turb were measured on site using  
 181 multi-parameter water quality meter (YSI ProDSS, Xylem Analytics). The pooled  
 182 water samples (0.5 m below the surface, middle, and 0.5 m above the bottom) were

183 taken with a modified 1-L Van Dorn water sampler at all sampling sites. TP and TN  
184 concentrations were measured with ascorbic acid method and cadmium reduction  
185 method, respectively, following persulfate digestion.  $\text{NH}_4^+$ -N,  $\text{NO}_2^-$ -N and  $\text{NO}_3^-$ -N  
186 were determined by Nessler's reagent colorimetric, and ultraviolet spectrophotometric  
187 screening methods, respectively. A known volume of pooled water sample was  
188 filtered through WHATMAN GF/C glass-fiber filters for Chl $a$  determination, which  
189 was measured spectrophotometrically following 90% acetone extraction.  $\text{COD}_{\text{Mn}}$  was  
190 determined by potassium permanganate and sodium oxalate titration method (APHA,  
191 1998). Water quality variables were averaged per lake. At the same time, the  
192 maximum water depth (WD, m) and lake area (Area,  $\text{km}^2$ ) were also considered as  
193 factors that may affect the fish community in the lake (Table S1). WD is the  
194 maximum value actually measured in field measurements. Areas are obtained from  
195 satellite maps around the study time (2019). A correlation circle was used to visually  
196 display the correlation between the above 14 variables.

197 Along a eutrophication gradient, it is expected to observe an increase in limiting  
198 nutrients concentration, primary productivity, water turbidity (due mostly to  
199 phytoplankton density), and the frequency of hypoxia events (resulting from the  
200 respiration of primary producers) (Carpenter, 2008). Therefore, in this study, the  
201 following variables will be considered as indicators of eutrophication: TP, TN, Chl $a$ ,  
202 Turbidity, SD, and COD.

### 203 ***2.2.2. Fish sampling***

204 A multi-mesh composite gill net of 30 m in length and 2.0 m in height (modified from

205 European standard methods, CEN, 2015) was used in fish sampling. The composite  
 206 gill net was composed of 12 panels (2.5 x 2 m) with respective mesh sizes of 5, 6.25,  
 207 8, 10, 12.5, 15.5, 19.5, 24, 30, 35, 43 and 55 mm. Mesh sizes are randomly ordered  
 208 within a net, but all gillnets have the same order. A benthic fyke net (15 m in length,  
 209 0.4 m in width and 0.3 m in height) with 5 mm mesh size and 20 entrances on each  
 210 side was also used. The relative abundance of fish during each sampling period at  
 211 each study site was determined using 4 pelagic multi-mesh gill nets, 4 benthic  
 212 multi-mesh gill nets and 4 benthic fyke nets. The nets were exposed for 12h (18:00 to  
 213 6:00 the following day). Catches were registered as number of individuals. The total  
 214 wet weights of all species sampled were obtained from fresh specimens using an  
 215 electronic balance (precision 0.01 g). All collected fish specimens (N = 73056) were  
 216 identified to species level according to Department of Ichthyology, Institute of  
 217 Hydrobiology, CAS (1976). The scientific binomials of the 53 species collected  
 218 (Table 1) were updated according to FishBase (Froese and Pauly, 2020).

219 Table 1 Study Species.

Family	Species	Code	Family	Species	Code
<b>Engraulidae</b>	<i>Coilia nasus</i> *	C.nas	<b>Gobionidae</b>	<i>Sarcocheilichthys nigripinnis</i> *	S.nig
<b>Salangidae</b>	<i>Protosalanx hyalocranius</i>	P.hya	<b>Gobionidae</b>	<i>Squalidus argentatus</i> *	S.arg
<b>Salangidae</b>	<i>Neosalanx tangkahkeii</i>	N.tan	<b>Gobionidae</b>	<i>Saurogobio dabryi</i> *	S.dab
<b>Xenocyprididae</b>	<i>Opsariichthys bidens</i>	O.bid	<b>Gobionidae</b>	<i>Abbottina rivularis</i> *	A.riv
<b>Xenocyprididae</b>	<i>Mylopharyngodon piceus</i> <sup>#</sup>	M.pic	<b>Acheilognathidae</b>	<i>Acheilognathus macropterus</i> *	A.mac
<b>Xenocyprididae</b>	<i>Ctenopharyngodon Idella</i> <sup>*#</sup>	C.ide	<b>Acheilognathidae</b>	<i>Acanthorhodeus chankaensis</i> *	A.cha
<b>Xenocyprididae</b>	<i>Squaliobarbus curriculus</i>	S.cur	<b>Acheilognathidae</b>	<i>Rhodeus ocellatus</i> *	R.oce
<b>Xenocyprididae</b>	<i>Pseudolaubuca sinensis</i> *	P.sin	<b>Acheilognathidae</b>	<i>Rhodeus sinensis</i>	R.sin
<b>Xenocyprididae</b>	<i>Hemiculter leucisculus</i> *	H.leu	<b>Cyprinidae</b>	<i>Cyprinus carpio</i> *	C.car
<b>Xenocyprididae</b>	<i>Hemiculter bleekeri</i> *	H.ble	<b>Cyprinidae</b>	<i>Carassius auratus</i> *	C.aur
<b>Xenocyprididae</b>	<i>Toxabramis swinhonis</i> *	T.swi	<b>Catostomidae</b>	<i>Myxocyprinus asiaticus</i>	M.asi
<b>Xenocyprididae</b>	<i>Culter alburnus</i> *	C.alb	<b>Cobitidae</b>	<i>Misgurnus anguillicaudatus</i> *	M.ang
<b>Xenocyprididae</b>	<i>Chanodichthys erythropterus</i> *	C.ery	<b>Siluridae</b>	<i>Silurus asotus</i> *	S.aso

<b>Xenocyprididae</b>	<i>Chanodichthys mongolicus</i> *	C.mon	<b>Bagridae</b>	<i>Tachysurus fulvidraco</i> *	T.ful
<b>Xenocyprididae</b>	<i>Chanodichthys dabryi</i> *	C.dab	<b>Bagridae</b>	<i>Tachysurus nitidus</i>	T.nit
<b>Xenocyprididae</b>	<i>Parabramis pekinensis</i> *	P.pek	<b>Bagridae</b>	<i>Pelteobagrus eupogon</i>	P.eup
<b>Xenocyprididae</b>	<i>Megalobrama amblycephala</i> *	M.amb	<b>Ictaluridae</b>	<i>Ictalurus punctatus</i> <sup>+</sup>	I.pun
<b>Xenocyprididae</b>	<i>Xenocypris hupeinensis</i> *	X.hup	<b>Hemiramphidae</b>	<i>Hyporhamphus intermedius</i> *	H.int
<b>Xenocyprididae</b>	<i>Xenocypris macrolepis</i>	X.mac	<b>Sinipercidae</b>	<i>Siniperca chuatsi</i> *	S.chu
<b>Xenocyprididae</b>	<i>Xenocypris davidi</i> *	X.dav	<b>Sinipercidae</b>	<i>Siniperca kneri</i>	S.kne
<b>Xenocyprididae</b>	<i>Plagiognathops microlepis</i>	P.mic	<b>Odontobutidae</b>	<i>Odontobutis obscurus</i> *	O.obs
<b>Xenocyprididae</b>	<i>Pseudobrama simoni</i> *	P.sim	<b>Odontobutidae</b>	<i>Micropercops swinhonis</i>	M.swi
<b>Xenocyprididae</b>	<i>Hypophthalmichthys nobilis</i> * <sup>#</sup>	H.nob	<b>Gobiidae</b>	<i>Rhinogobius giurinus</i> *	R.giu
<b>Xenocyprididae</b>	<i>Hypophthalmichthys molitrix</i> * <sup>#</sup>	H.mol	<b>Osphronemidae</b>	<i>Macropodus ocellatus</i>	M.oce
<b>Gobionidae</b>	<i>Hemibrabus maculatus</i> *	H.mac	<b>Channidae</b>	<i>Channa argus</i> *	C.arg
<b>Gobionidae</b>	<i>Paracanthobrama guichenoti</i> *	P.gui	<b>Mastacembelidae</b>	<i>Sinibdella sinensis</i>	S.sin
<b>Gobionidae</b>	<i>Pseudorasbora parva</i> *	P.par			

220 \* Species found in more than 3 lakes. + Introduced species. # Stocked species.

221

222 *Mylopharyngodon piceus*, *Ctenopharyngodon Idella*, *Hypophthalmichthys*

223 *molitrix* and *Hypophthalmichthys nobilis* cannot reproduce in lakes disconnected from

224 the Yangtze River (Zhang et al., 2000). As most of the studied lakes are no more

225 connected to the main river, the presence of those species is likely the result of

226 stocking. Results of analyses including all the species, including the few exotic ones

227 (Table 1), are reported in the main text. However, to take into account the impact of

228 potential stocking, all the analyses were duplicated by excluding the species that

229 might have been stocked (Table 1) and the corresponding results are detailed in the

230 supplementary information (Figure S3-S6, Table S3-S4).

### 231 **2.2.3. Fish species traits**

232 Twenty-two species traits related directly or through well-known ecomorphological

233 relationships to life history strategy, feeding and habitat use were selected for

234 computing functional diversity metrics (Table 2, Table S5). Traits values per species

235 were obtained by consulting published literature, books, scientific reports, expert

236 knowledge, field observations and online databases (Table S6).

Table 2 The functional species traits used in the study. The ecological meanings and references see Table S5.

Traits	Code	Functional category	Type	Units
Maximum standard length	S_SL	Life history strategy	Numeric	Maximum standard body length (cm).
Longevity	S_L	Life history strategy	Numeric	Maximum life span (years).
Growth parameter <i>K</i>	S_K	Life history strategy	Numeric	Parameter <i>K</i> of Von Bertalanffy growth formula (years <sup>-1</sup> )
Vulnerability	S_V	Life history strategy	Numeric	Vulnerability to fishing. Range 10-87.
Resilience	S_R	Life history strategy	Ordinal	Resilience level of fish populations. Range 1-4. Very low, low, medium, high.
Maturity age	S_MA	Life history strategy	Numeric	Mean age at maturation (years).
Absolute fecundity	S_AF	Life history strategy	Numeric	Total number of oocytes per ovary (oocytes).
Maturity standard length	S_ML	Life history strategy	Numeric	Mean standard length at maturation (cm).
Egg diameter	S_ED	Life history strategy	Numeric	Mean diameter of mature (fully yolked) ovarian oocytes (mm).
Egg type	S_ET	Life history strategy	Factor	Drifting (ET1), demersal (ET2), adhesive (ET3), pelagic (ET4).
Parental care index	S_PC	Life history strategy	Ordinal	Parental care level. From low to high. Range 0-4.
Feeding habit	F_FH	Feeding	Factor	Predator sit and wait (FH1), predator active search (FH2), grazer (FH3), scraper (FH4), substrate explorer (FH5), surface feeder (FH6).
Trophic guild	F_TG	Feeding	Factor	Herbivore (TG1), algivore (TG2), detritivore (TG3), omnivore (TG4), zooplanktivore (TG5), zoobenthivore (TG6), piscivore (TG7).
Trophic level	F_TL	Feeding	Numeric	Trophic position in the food chain. Range 2-4.5.
Relative mouth size	F_MS	Feeding	Ordinal	Relative mouth size. From small to large. Range 1-5.
Mouth position	F_MP	Feeding	Factor	Inferior (MP1), inferior-terminal (MP2), terminal (MP3), terminal-superior (MP4), superior (MP5).
Relative eye position	H_EP	Habitat use	Factor	Top (EP1), lateral-top (EP2), lateral (EP3), lateral-bottom (EP4).
Habitat preference	H_HP	Habitat use	Factor	Eurytopic (HP1), rheophilic (HP2), limnophilic (HP3), potamodromous (HP4).
Body shape	H_BS	Habitat use	Factor	Deep (BS1), fusiform (BS2), oval (BS3), flat (BS4), cylindrical (BS5).
Gregariousness	H_G	Habitat use	Factor	Singleton (G1), breeding schools (G2), always schools (G3).

Diel activity pattern	H_DA	Habitat use	Factor	Nocturnal (DA1), diurnal (DA2).
Vertical position	H_VP	Habitat use	Factor	Demersal (VP1), near demersal (VP2), pelagic (VP3).

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238 **2.3. Statistical analyses**

239 **2.3.1. Community metrics**

240 We selected three metrics, species richness (SRic), total biomass (BPUE) and  
241 functional dispersion (FDis) to describe fish community structure. Functional  
242 dispersion is the mean distance of individual species in functional trait space to the  
243 centroid of all species in a community (Laliberté and Legendre, 2010). Note that both  
244 the position of the centroid and the distances to it are weighted by the relative  
245 abundances of the species. The function *dpFD* of package ‘FD’ (Laliberté et al., 2014)  
246 for R version 3.5.2 (R Core Team, 2018) was used to calculate this metrics. For each  
247 sample, total biomass is given per unit effort (g net<sup>-1</sup> h<sup>-1</sup>) and species richness is the  
248 total number of species observed. All metrics were computed for each fish sample site  
249 and then averaged per lake.

250 **2.3.2. Community metrics responses to environmental variables**

251 We analyzed the responses of each community metrics to water quality and lake  
252 morphology with a multiple regression model assuming a gaussian error distribution.  
253 To improve normality of the response variables, SRic was square transformed, BPUE  
254 was square-root transformed. All predictor variables but DO, pH and WD were ln  
255 transformed to obtain more regular environmental gradients. Finally, to improve the  
256 comparability of regression coefficients within and among models, the response and  
257 predictor variables were standardized (zero mean and unit variance).

258 To identify simple but explanatory models, for each response variable, a set of  
259 predictor variables was selected by a stepwise algorithm (backward selection starting

260 with all the 14 predictor variables) using the Akaike Information Criterion (AIC) to  
261 compare models. In this aim the function *stepAIC* of package ‘MASS’ (Venables and  
262 Ripley, 2002) was used. The function *vif* of package ‘car’ (Fox and Weisberg, 2019)  
263 was used to calculate variance inflation factors (VIF) for the models. Predictor  
264 variables with a VIF value greater than 5 were removed to minimize the effect of  
265 multicollinearity in the models. In order to figure out the relative importance of  
266 predictor variables, the function *calc.relimp* of package ‘relaimpo’ (Groemping and  
267 Berlin, 2021) was used to calculate relative importance of predictor variables with  
268 method *lmg*.

### 269 **2.3.3. Community composition response to environmental variables**

270 A Redundancy Analysis (RDA) was used to quantify and visualize the environmental  
271 gradients that contribute the much to community changes in species composition.  
272 (Braak and Verdonschot, 1995). Only species occurring in more than 3 lakes within 26  
273 lakes were retained for analysis (36 species). Abundance data were  $\ln(n+1)$   
274 transformed. The identity of environmental variables and their transformations are as  
275 in the multiple regression analyses. The overall significance of the  
276 community-environment relationship and the contribution of each environmental  
277 variable was assessed with a permutation test (the tested statistic is a “pseudo-F”,  
278 quantifying the contribution of the environmental descriptors to the  
279 among-communities variability) and the effect size of the total model was evaluated  
280 by the adjusted  $R^2$  coefficient. RDA was performed using the R packages “*vegan*”  
281 (Oksanen et al., 2019).

#### 282 **2.3.4. Species traits responses to environmental variables**

283 The relationships between species traits and environmental gradients were analyzed  
284 with RLQ analyses using the R packages “*ade4*” (Dray and Dufour, 2007).

285 The RLQ analysis is a multivariate method allowing quantifying and visualizing  
286 relationships between species traits and environmental descriptors, and in particular  
287 identifying species traits that co-vary along synthetic environmental gradients  
288 described by ordination axes. This analysis relates functional traits of species (Q) to  
289 environmental variables of sites (R) as mediated by species distribution across sites (L)  
290 (Dolédec et al., 1996). To be meaningful, a traits-environment relationship requires  
291 that a) species are not distributed at random with regard to environmental features and  
292 b) species with similar traits covary in space (among sites) more than expected by  
293 chance. Hypothesis a) was already tested with an RDA (see above) and hypothesis b)  
294 by comparing the observed strength of the traits-environment relationship with a null  
295 distribution obtained by permuting the species labels in the traits table (“model4”  
296 permutation type), then run a new RLQ and repeating this operation several times.  
297 (Dray et al., 2014).

298 To help interpreting the traits-environment relationships, three groups of traits  
299 have been considered and used as input for different RLQ analyses: those related to  
300 life history strategy and reproduction, trophic ecology, and habitat use. Environmental  
301 variables and species abundance were transformed as RDA (see above) and numeric  
302 traits were ln transformed.

### 303 **3. Results**

#### 304 ***3.1. Correlations among environmental variables***

305 In the system of lakes considered in this study, the correlations among the variables  
306 supposed to be related to eutrophication (TP, TN, Chl $a$ , Turb, SD, COD) are all of the  
307 expected sign (Figure S1), but could be low (e.g.,  $r = 0.216$  between COD and Turb).  
308 All the other water quality variables but NH $_4^+$ -N display good or moderate positive  
309 correlations with the variables increasing with eutrophication.

#### 310 ***3.2. Community metrics responses to environmental variables***

311 SRic and BPUE are poorly explained by environmental descriptors (Table 3) with R $^2$   
312 values lower than 0.3, while for FDis a better fit has been obtained (near 0.5). In the  
313 model of SRic, TN, COD and NO $_3^-$ -N were removed due to the multicollinearity. For  
314 all metrics but SRic, at least one variable related to eutrophication is among the  
315 significant ones retained in the regression model (Table 3). When selected,  
316 eutrophication related variables were positively correlated with BPUE and negatively  
317 with FDis. Among the other water quality variables, only pH contributed significantly  
318 to one model (FDis), in the opposite direction than eutrophication. One variable  
319 related to lake morphology, WD, was significantly correlated to SRic and FDis,  
320 positively and negatively, respectively.

321 Table 3 Results of multiple regression models explaining community metrics as a  
322 function of the environmental variables selected by a stepwise procedure (see main  
323 text), including regression coefficient estimates and their standard errors (SE),  $p$   
324 values for models and predictor variables, coefficient of determination (R $^2$ ) and

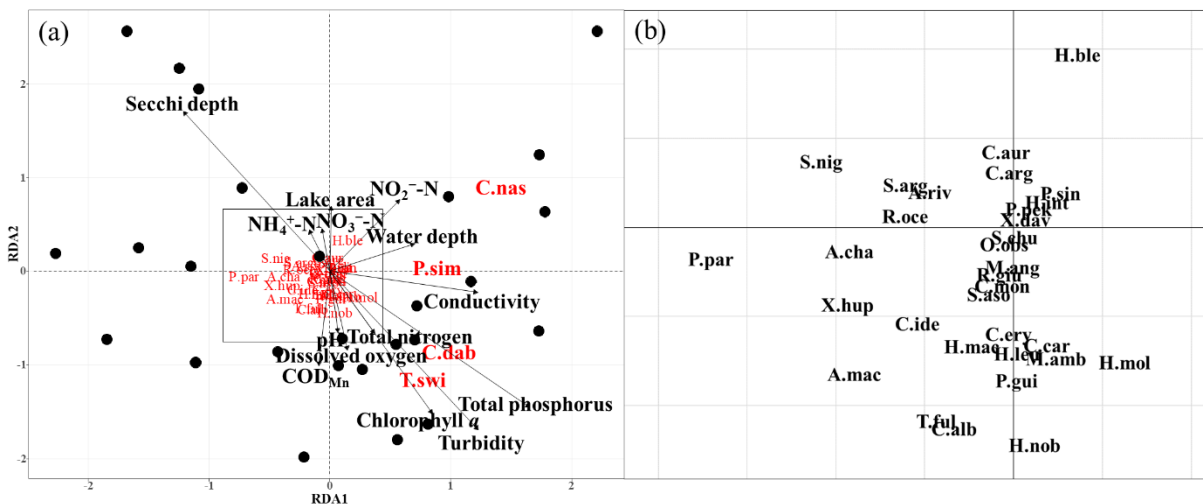
325 relative importance of the predictor variables (%R<sup>2</sup>). Significant ( $p < 0.05$ ) terms are  
 326 highlighted in bold.

Response variable	Coefficient	SE	t	Pr (>  t )	R <sup>2</sup>	% R <sup>2</sup>
Species richness				<b>0.035</b>	0.2572	
Intercept	-2.97E-16	0.17	0.000	1.000		
Water depth	0.50	0.18	2.759	<b>0.012</b>		45.60
Chlorophyll <i>a</i>	0.36	0.18	2.034	0.055		23.43
NO <sub>2</sub> <sup>-</sup> -N	-0.38	0.19	-2.062	0.052		18.28
Lake area	0.25	0.17	1.466	0.158		12.69
Total biomass				<b>0.033</b>	0.2287	
Intercept	9.13E-16	0.17	0.000	1.000		
Total phosphorus	0.52	0.21	2.571	<b>0.017</b>		61.42
Dissolved oxygen	0.63	0.36	1.778	0.089		25.19
pH	-0.60	0.37	-1.597	0.125		13.39
Functional dispersion				<b>0.003</b>	0.4955	
Intercept	-1.16E-16	0.14	0.000	1.000		
Turbidity	-0.71	0.18	-3.900	<b>&lt;0.001</b>		45.97
pH	0.44	0.17	2.594	<b>0.018</b>		17.82
Conductivity	-0.32	0.20	-1.629	0.120		12.95
Water depth	-0.36	0.17	-2.157	<b>0.044</b>		9.97
Lake area	-0.37	0.18	-2.074	0.052		7.55
NO <sub>2</sub> <sup>-</sup> -N	0.30	0.16	1.836	0.082		5.74

### 327 **3.3. Taxonomic composition response to environmental variables**

328 According to the RDA, the species composition of fish communities was significantly  
 329 related to environmental descriptors of the lakes (Figure 2,  $r^2$  adj. = 0.181,  $F_{14,11} =$   
 330 1.39,  $P < 0.05$ ). In particular, two variables related to eutrophication, TP and Chl*a*,  
 331 contributed significantly to community variability ( $P < 0.05$ , Table 4). Note also the  
 332 contribution of NO<sub>3</sub><sup>-</sup>-N. Therefore, the first axis described grossly a eutrophication  
 333 gradient and, according to the permutation test, it explained a significant part of  
 334 community variability. No other axis was significant ( $P < 0.05$ ). Lakes with the  
 335 highest level of eutrophication (with positive coordinates along the first axis, Figure 2)  
 336 were characterized by species with different ecologies. *Toxabramis swinhonis* and

337 *Coilia nasus* are small pelagic zooplanktivores, *Chanodichthys dadryi* is a pelagic  
 338 piscivore, *Pseudobrama simoni* is a detritivore mainly feeding on plant debris and  
 339 periphyton. In the less eutrophicated lakes (along the negative coordinates of the first  
 340 axis) are encountered demersal or near demersal species displaying different degrees  
 341 of parental care (e.g., *Pseudorasbora parva*, *Sarcocheilichthys nigripinnis*,  
 342 *Xenocypris hupeinensis*, *Acheilognathus macropterus*, *Acanthorhodeus chankaensis*,  
 343 *Squalidus argentatus*, *Rhodeus ocellatus*, *Ctenopharyngodon Idella* and *Abbottina*  
 344 *rivularis*, Figure 2) plus a large herbivorous species feeding on macrophytes  
 345 *Ctenopharyngodon idella*, and a species, *Xenocypris hupeinensis*, preferring well  
 346 oxygenated waters.  
 347



348 Figure 2 (a) Redundancy Analysis (RDA) triplot showing the relationships between  
 349 fish communities (dots), environmental variables (arrows) and species (labels). Arrow  
 350 length and direction correspond to the variance that can be explained by each variable.  
 351 The tip of each arrow indicates the loading of each variable on axis 1 and 2. In order  
 352 to better show the relationship between variables and axis, the length of the arrow has

353 been enlarged twice. Species coordinates in black box (a) are enlarged in (b). See  
354 Table 1 for species codes.

355

356 Table 4 Environmental variables scores on the two first axes of the fish  
357 community-environment RDA. The test statistic is a “pseudo- $F$ ”, which is the ratio of  
358 constrained and unconstrained total Inertia. P value is obtained by a permutation test.

359 Significant ( $p < 0.05$ ) terms are highlighted in bold.

Variables	$F$	Pr ( $>F$ )
Total nitrogen	1.50	0.131
Total phosphorus	3.38	<b>0.001</b>
COD <sub>Mn</sub>	1.15	0.328
Chlorophyll $a$	2.12	<b>0.019</b>
Secchi depth	1.07	0.364
Conductivity	1.43	0.150
NO <sub>3</sub> <sup>-</sup> -N	1.77	<b>0.050</b>
NH <sub>4</sub> <sup>+</sup> -N	1.13	0.334
NO <sub>2</sub> <sup>-</sup> -N	1.02	0.408
Turbidity	1.11	0.340
Dissolved oxygen	0.70	0.774
pH	0.68	0.789
Water depth	0.77	0.694
Lake area	1.71	0.069

360

#### 361 ***3.4. Functional traits filtering by environmental variables***

362 In the three RLQ analyses conducted (life history strategy, feeding, habitat use), the  
363 environmental gradients described by the first axis were very similar. For life history  
364 strategy and feeding the first axis opposes small turbid lakes with high TP  
365 concentration and conductivity to large lakes with clearer water and lower TP  
366 concentration and conductivity, the situation is reversed for habitat use (Figure 3).

367 According to those results, the first axis acted as an inverse eutrophication (life

368 history strategy and feeding) or eutrophication (habitat use) gradient in all analyses. It  
369 is worth noting that Area was correlated positively with the first axis in all the RLQ  
370 analyses. Therefore, the relationship of a trait with the first axis of a RLQ plot  
371 provides information about how eutrophication acted as an environmental filter with  
372 respect to this trait.





373

374 Figure 3 Ordinations of RLQ scores of environmental variables (a, c, e) and species

375 traits (b, d, f): (a) and (b) life history strategy, (c) and (d) feeding, (e) and (f) habitat

376 use. See Table 2 for traits codes.

377

378           In the RLQ analysis of the life history strategy traits of community the  
379 cumulative projected inertia obtained by the RLQ analysis is 86% when axis 1 and  
380 axis 2 are combined (Figure S2a), and according to the permutation test, the  
381 relationship between life history traits and lakes environmental descriptors is  
382 significant ( $P = 0.013$ ). Standard body length (S.SL) and absolute fecundity (S.AF)  
383 were positively associated with eutrophication, and the trait “demersal eggs” (S.ET2)  
384 negatively. This result suggests that eutrophication significantly favors species with  
385 large body size and high fecundity over species with demersal eggs and parental care.

386           In the RLQ analysis of the feeding traits of community the cumulative projected  
387 inertia obtained by the RLQ analysis is 84% when axis 1 and axis 2 are combined  
388 (Figure S2c) and, according to the permutation test, the relationship between traits and  
389 environment is not significant ( $P = 0.208$ ). The biological traits the most notably  
390 correlated with the first axis, are inferior mouth position (F.MP1), substrate explorer  
391 (F.FH5), detritivore (F.TG3), scraper (F.FH4), omnivore (F.TG4) (positive  
392 correlations) and terminal-superior mouth position (F.MP4), predator active search  
393 (F.FH2), piscivore (F.TG7), predator sit and wait (F.FH1) (negative correlations).  
394 Although not significant, eutrophication still showed a positive relationship with  
395 piscivory.

396           In the RLQ analysis of the habitat use traits of community the cumulative  
397 projected inertia obtained by the RLQ analysis is 88% when axis 1 and axis 2 are  
398 combined (Figure S2e) and, according to the permutation test, the relationship

399 between traits and environment is significant ( $P = 0.024$ ). The traits “cylindrical body  
400 shape” (H.BS5), “top position of the eye” (H.EP1) and “Rheophilic” (H.HP2) display  
401 the strongest negative response to eutrophication. This result suggests that low  
402 eutrophication lakes favor species with traits adapted to benthic habitats and species  
403 that prefer running, well oxygenated water. Two traits, “Potamodromous” (H.HP4)  
404 and “lateral-bottom relative position of the eye” (H.EP4) are notably correlated with  
405 eutrophication, but those traits are strongly associated with some possibly stocked  
406 species (see Supplementary information, Table S6).

#### 407 **4. Discussion**

##### 408 *4.1. Different roles of eutrophication indicators in fish community changes*

409 Eutrophication is a multifactorial environmental change (Smith and Schindler, 2009),  
410 the effects of which are not necessarily well captured by one variable alone and the  
411 impact of eutrophication on fish communities could result from the action of a limited  
412 number of variables among those that constitute the signature of eutrophication. In  
413 our study the most relevant variables were those related to nutrient concentration (in  
414 particular total phosphorus) and water transparency. As a whole, total phosphorus  
415 appeared to be the better proxy of eutrophication in our study. The critical role of  
416 phosphorus in lake eutrophication has been reported in previous studies (Carpenter,  
417 2008; Schindler et al., 2016). Considering that, for most of the analyses conducted, at  
418 least one variable related to eutrophication is among the significant ones, and that  
419 only one metric, species richness, is better explained by lake morphology, it emerges  
420 that eutrophication is a consistent and major factor shaping fish community structure,

421 based either on taxonomy or functional traits.

#### 422 ***4.2. Increasing productivity affects fish communities of lakes***

423 A signature of eutrophication is an increased primary productivity. The relationship  
424 between ecosystem productivity and biodiversity is a recurrent topic in community  
425 ecology (Dodson et al., 2000; Hayden et al., 2017). For animal communities, the  
426 general pattern is that as productivity increases so does species richness (Cusens et al.  
427 2012) but sometimes a unimodal relationship is observed. For instance, Jeppesen et al.  
428 (2000) observed that fish species richness was unimodally related to TP, and peaked at  
429 0.1-0.4 mg L<sup>-1</sup> among 71 Danish lakes. In our study, there no significant relationship  
430 between TP, or any other variable related to eutrophication, and species richness. This  
431 result suggests that, at highest levels of eutrophication, inter-specific interactions  
432 and/or environmental harshness (e.g., hypoxia, toxic algal bloom) can lead to a  
433 decline in species richness (Thomas and Eckmann, 2007), resulting in the overall flat  
434 relationship we observed in our study. The range of TP concentrations in our lakes is  
435 0.01-0.77 (Table S2), which is similar to the study of Jeppesen et al. (2000) and  
436 covers the peak range they found. This could explain why no linear relationship  
437 between species richness and eutrophication was found but further studies are needed  
438 to assess the generality of this result. Moreover, it is worth remembering that our  
439 study was based on local species richness which is not necessarily a good proxy for  
440 the total number of species inhabiting a lake.

441 Total biomass is frequently used as a proxy of the productivity sustaining a  
442 community, and as such should increase with eutrophication. As expected, total

443 biomass is positively, but weakly, correlated to total phosphorus in our study. This  
444 result is consistent with several other studies that have shown that in lakes  
445 eutrophication correlates positively with total density and biomass (Olin et al., 2002;  
446 Egertson and Downing, 2004; Søndergaard et al., 2005; Mehner et al., 2008; Hayden  
447 et al., 2017; Yu et al., 2021).

#### 448 ***4.3. Changes in trophic availability and resources weakly affects functional*** 449 ***community structure***

450 Some species and traits were expected to increase or decrease with increasing  
451 eutrophication due to accompanying changes in food resources availability (Jeppesen  
452 et al., 2000; Mehner et al., 2005; Yu et al., 2021). In particular, it has been observed in  
453 previous studies that the abundance of zooplanktivorous fishes increases with  
454 eutrophication, probably as a consequence of a higher phytoplankton productivity  
455 sustaining higher zooplankton abundance in eutrophic lakes (Bergstrand, 1990;  
456 Jeppesen et al., 2000). However, in our study chlorophyll a concentration did not  
457 contribute much to the first axis of the RLQ analysis of feeding traits suggesting that  
458 an increase in primary productivity was not a major driver of community change in  
459 this respect. In the same vein, zooplanktivory was only slightly associated with the  
460 first axis. Small zooplanktivorous species (*Toxabramis swinhonis*, *Hemiculter*  
461 *leucisculus*, *Hemiculter bleekeri*, *Coilia nasus* and *Pseudolaubuca sinensis*) are, as a  
462 whole, dominant in the investigated lakes (averaged 64.40% in abundance),  
463 particularly *T. swinhonis* which was found to be the dominant species in many  
464 eutrophic lakes in the Yangtze River (Yu et al., 2021). However only a few of them (*T.*

465 *swinhonis* and *C. nasus*) increased in abundance with eutrophication, suggesting that  
466 zooplanktivory is not systematically associated with eutrophication in our study, and,  
467 as a result, has a weak signature in a RLQ plot. One explanation could be that in  
468 addition to abiotic filters (resource abundance or availability), biotic filters  
469 (competition, predation) are also at play. Some small pelagic zooplanktivorous species  
470 could be prevented from increasing in abundance despite favorable conditions  
471 because of predation from pelagic piscivores or competition with other  
472 zooplanktivores.

#### 473 ***4.4. Habitat degradation affects taxonomy and function of communities***

474 Water clarity declines as eutrophication increases and turbidity has proven to be a  
475 strong factor of fish community structuring in lakes (Rodríguez and Lewis, 1997).  
476 The negative relationship observed between turbidity and functional dispersion (FDis)  
477 suggests that species with particular biological traits are more abundant in turbid lakes,  
478 which is in line with a notable contribution of turbidity and Secchi depth to the RLQ  
479 analysis based on habitat use traits. In other words, fish communities are more  
480 homogeneous (less dispersed) in terms of functional traits in the most eutrophic lakes.  
481 Fish species not strongly depending on vision for foraging, escaping predators or  
482 engaging in intraspecific interactions (e. g. courtship) should be favored in turbid  
483 waters. However, among the traits considered in this study, only one, nocturnal  
484 activity (H.DA1), could confer such a direct advantage in turbid waters, and, indeed,  
485 is correlated positively, but slightly, to eutrophication.

486 Turbidity could have a more indirect and complex action and consequently could

487 act as an environmental filter on traits not necessarily associated with visual  
488 dependency of the species (Smith et al., 2006). For instance, in highly turbid lakes, a  
489 large amount of sediment and organic material could accumulate on demersal eggs  
490 and impair their development by asphyxiating them (Smith et al., 2006). In the same  
491 vein, macrophytes become rare as turbidity increases and fish species (such as  
492 *Carassius auratus*, *Cyprinus carpio*, *Hemibrabus maculatus*, *Paracanthobrama*  
493 *guichenoti*, *Tachysurus fulvidraco*, *Pseudorasbora parva*) that use them for spawning,  
494 sheltering or foraging are expected to decline accordingly.

495 It is well known that eutrophication leads to degradation of the demersal zone by  
496 increasing the frequency of hypoxia events (Argillier et al., 2013) and, indeed, our  
497 results suggest that species foraging or reproducing at the bottom of the lake decrease  
498 in abundance as eutrophication increases. Traits typical of demersal lacustrine fish  
499 species (Department of Ichthyology, Institute of Hydrobiology, CAS, 1976) are  
500 negatively related to eutrophication, such as “cylindrical body shape” (H.BS5), “top  
501 eye position” (H.EP1), “demersal eggs” (S.ET2) and “inferior mouth position”  
502 (F.MP1). In addition, rheophilic species (H.HP2) display the same pattern of low  
503 abundance in eutrophic lakes. Those species that prefer running, well oxygenated,  
504 waters are typically intolerant to hypoxia.

505 A very specific change in habitat likely driven by eutrophication might account  
506 for the rarity of a particular group of fishes in highly eutrophic lakes. The females of  
507 *Sarcocheilichthys nigripinnis*, *Acheilognathus macropterus*, *Acanthorhodeus*  
508 *chankaensis* and *Rhodeus ocellatus* have an ovipositor which is used to deposit eggs

509 inside bivalves and juveniles remain in the host until they can swim (Department of  
510 Ichthyology, Institute of Hydrobiology, CAS, 1976). Those species are negatively  
511 related to eutrophication and this could be explained by a negative relationship  
512 observed in the Yangtze River between the diversity of their hosts and eutrophication  
513 (Zhang et al., 2020). Another interesting pattern is that the periodic type of life history  
514 strategy (Winemiller and Rose, 1992), long living and fecund, seems to be favored in  
515 eutrophic lakes, as exemplified by the positive relationship between body size and  
516 absolute fecundity with eutrophication. If this result is not a by-product of  
517 eutrophication selecting large species for other reasons (e. g. favoring piscivory), this  
518 suggests that eutrophication increases the unpredictability of young stages  
519 survivorship, a factor promoting the evolution of a periodic strategy (Winemiller and  
520 Rose, 1992), a point deserving further investigation.

#### 521 ***4.5. Role of lake morphology***

522 A positive correlation between lake area and fish species richness has been frequently  
523 reported (Dodson et al., 2000; Mehner et al., 2008), as expected for insular habitat in  
524 general. No such pattern has been observed in the present study, which is consistent  
525 with previous research on lakes of Yangtze River basin (Yu et al., 2021). However,  
526 our study is based on local species richness not the total number of species inhabiting  
527 a lake and our results do not exclude the existence of a species-area relationship at the  
528 latter scale. Because the investigated lakes have been disconnected from the main  
529 river for about 50 years (Liu and Wang, 2010), extinction prone species are more  
530 likely to be absent from small lakes because of their small population size. In



531 particular species that cannot reach high densities, such as large or top-predator  
532 species, should be extirpated first from small, isolated habitats (Krauss et al., 2003).  
533 Actually, in our study, it has been observed the opposite trend in which the abundance  
534 of large and piscivorous species tend to be negatively associated with lake area, but  
535 positively with eutrophication. A possible explanation could be that eutrophication,  
536 through increased lake productivity, contributes much more than lake area (ecosystem  
537 size) to population sizes. This result is coherent with the study of Jia et al. (2021)  
538 indicating that productivity was more important than ecosystem size in explaining the  
539 variance in mean trophic level in fish communities in the Yangtze River. Another  
540 important variable for explaining lacustrine fish community patterns is average or  
541 maximum depth of the lake. Despite the fact that all the lakes considered in this study  
542 are shallow (maximum water depth ranges from 0.8 m to 5.7 m), depth was  
543 nevertheless positively correlated to species richness. The effects of depth on  
544 ecosystem processes could be complex, particularly when acting in interaction with  
545 other variables, such as light penetration (Rodríguez and Lewis, 1997). However, it is  
546 generally assumed that habitat diversity increases with depth (Zhao et al., 2006) and  
547 this could explain the observed positive relationship with species richness.

#### 548 ***4.6. Impact of human activities on fish communities responses to eutrophication***

549 One of the most important human activities not accounted for in our analyses and that  
550 could have affected our results is fish stocking (Wang et al., 2018). However, as a  
551 whole, our results are robust to the deletion of the species likely to be present in the  
552 surveyed lakes because of past stocking and the main conclusions are not modified

553 (Figure S3-S6, Table S3-S4). In addition to this, smaller lakes were more likely to  
554 have been fertilized directly for stocking filter-feeding carps, which may be the reason  
555 for the negative correlation between area and eutrophication (Zhang et al., 2020).  
556 Beginning in 2017, various levels of environmental protection and ecological  
557 restoration measures, such as banning aquaculture and fishing (Wang et al., 2018),  
558 have been implemented in the studied lakes. However, the time, extent and modality  
559 of these measures differ among lakes. These differences in lake management patterns  
560 are a possible source of uncontrolled variability in fish community analyses.

#### 561 ***4.7. Geographic constraints on eutrophication induced traits filtering***

562 In this study, we identified several filtering effects of eutrophication on traits related  
563 to habitat use and life history strategies, which adds to the few previous works that  
564 have attempted to link lacustrine fish community metrics or species traits to  
565 anthropogenic disturbances (Jeppesen et al., 2000; Egertson and Downing, 2003;  
566 Jeppesen et al., 2003; Søndergaard et al., 2005; Launois et al., 2011; Sagouis et al.,  
567 2017; Jia et al., 2021; Yu et al., 2021). In Europe, probably the most investigated  
568 region with regard to fish-based assessment of lacustrine ecological status, few  
569 species traits have been successfully tested, most of them related to trophic ecology  
570 (Ritterbusch et al., 2022). In this regard, and despite comparable ranges of  
571 eutrophication, some notable differences occur between China (our study) and Europe.  
572 First in contrast with Europe, eutrophication has a weak effect on trophic structure of  
573 communities in our study. Second, some traits react to eutrophication in opposite  
574 directions in each region. It is the case for instance for large predatory or piscivorous

575 fishes reported to be increasingly disfavored as eutrophication increases in European  
576 lakes (Bergstrand, 1990; Jeppesen et al., 2000; Sandström et al., 2002; Søndergaard et  
577 al., 2005) whereas they display the opposite pattern in the present study. A possible  
578 reason is that, unlike perch, pike, and trout in European lakes, in the Yangtze Basin  
579 some predatory fishes, such as the piscivorous carps (*Culter alburnus*, *Chanodichthys*  
580 *erythropterus*, *Chanodichthys mongolicus*, *Chanodichthys dabryi*), can forage  
581 efficiently at low light intensities in turbid and dim environments (Department of  
582 Ichthyology, Institute of Hydrobiology, CAS, 1976).

583         So far, possible general fish community patterns consistently observed in China  
584 (present study) and other regions (mostly Europe) are as follows. Along a  
585 eutrophication gradient total biomass of the community increases and fish species  
586 having a benthic life stage are disadvantaged and functional homogeneity increases.  
587 Note that the last relationship has been observed in only two studies, ours and Sagouis  
588 et al. (2017), using different metrics, and therefore deserves further investigation. Our  
589 results suggest that in addition to those related to habitat use or trophic ecology, new  
590 metrics based on the life history framework proposed by Winemiller and Rose (1992),  
591 not yet tested in a eutrophication context, are promising. For instance, three  
592 reproductive strategies have been described by these authors (opportunistic, periodic,  
593 equilibrium) and it could be interesting to study how they favor or not the persistence  
594 of species in eutrophic lakes.

595         In the context of environmental protection, informed decision-making criteria  
596 must be based on the biological composition and functional characteristics of the

597 ecosystem (Nandi et al., 2012). Therefore, the identification of sensitive species and  
598 indicative functional traits is critical (Petriki et al., 2017). Our study indicates that  
599 some demersal equilibrium species and their associated functional traits can serve as  
600 indicators of eutrophication-induced habitat degradation in lake management in the  
601 middle reaches of the Yangtze River. And some species increasing with trophic  
602 availability may reflect the extent of eutrophication.

## 603 **5. Conclusion**

604 This study validated that eutrophication is an important factor shaping the  
605 composition and functional structure of fish communities of shallow lakes in the  
606 middle reaches of the Yangtze River. Although eutrophication did not have a  
607 significant effect on fish species richness, the increase in nutrient concentration  
608 promoted fish productivity and especially decreased the functional dispersion of fish  
609 communities. It was also observed a decrease of species diversity with eutrophication,  
610 manifested by the overdominance of a few species. It results that fish communities are  
611 more homogeneous in the most eutrophic lakes, both in terms of species composition  
612 (less diverse) and functional structure (less dispersed). This homogenization of fish  
613 communities is mainly due to the habitat degradation and trophic availability  
614 alternation. Demersal habitat degradation resulted in a reduction in some demersal  
615 equilibrium species and their associated functional traits, while increased trophic  
616 availability resulted in an increase in dominance of several pelagic feeding species.  
617 However, studies assessing the effects of eutrophication on fish communities using  
618 functional approaches are geographically biased (mainly in Europe). Adding an Asian

619 perspective revealed that, because of possible historical contingencies (e. g. absence  
620 of efficient piscivores in turbid waters), using European lacustrine fish communities  
621 as a reference for anticipating eutrophication-related changes (including restoration  
622 measures) in community structure in other parts of the world should be done with  
623 some caution. This study identified a series of species or traits indicators of eutrophic  
624 lakes. These indicators could prove useful to evaluate the effectiveness of prohibition  
625 of aquaculture and fishing and to provide early warning of nutrient loads, points  
626 particularly important in the context of on-going fish resource management and  
627 restoration of shallow lakes in the middle reaches of the Yangtze River basin.

628

### 629 **Acknowledgements**

630 We appreciate the Hubei Provincial Department of Agriculture and Rural Affairs for  
631 providing the convenience and kindly assistance in field sampling. We thank Han Wu,  
632 Fan Li, Jing Wang and for their help in our field work and laboratory analysis. This  
633 work was financially supported by the National Key Research and Development  
634 Program of China (No. 2018YFD0900701), National Natural Science Foundation of  
635 China (No. 32002396), Youth Innovation Promotion Association CAS (No. 2022344).

636

### 637 **Reference**

638 Anderson, D.M., Glibert, P.M., Burkholder, J.M., 2002. Harmful algal blooms and  
639 eutrophication: nutrient sources, composition, and consequences. *Estuaries*, 25(4),  
640 704-726.

641 APHA (American Public Health Association), 1998. *Standard Methods for the*

642 Examination of Water and Wastewater. American Public Health Association,  
643 Washington, DC.

644 Argillier, C., Caussé, S., Gevrey, M., Pédrón, S., De Bortoli, J., Brucet, S., Emmrich  
645 M., Jeppesen E., Lauridsen T., Mehner T., Olin M., Rask M., Volta P., Winfield  
646 I.J., Kelly F., Krause T., Palm A., Holmgren, K., 2013. Development of a  
647 fish-based index to assess the eutrophication status of European lakes.  
648 *Hydrobiologia*, 704(1), 193-211.

649 Bal, P., Tulloch, A.I., Addison, P.F., McDonald- Madden, E., Rhodes, J.R., 2018.  
650 Selecting indicator species for biodiversity management. *Frontiers in Ecology  
651 and the Environment*, 16(10), 589-598.

652 Bergstrand, E., 1990. Changes in the fish and zooplankton communities of Ringsjön,  
653 a Swedish lake undergoing man-made eutrophication. *Hydrobiologia*, 191(1),  
654 57–66.

655 Bolle, L.J., Hoek, R., Pennock, I., Poiesz, S.S.H., van Beusekom, J.E.E., van der Veer,  
656 H.W., Witte, J.I.J., Tulp, I., 2021. No evidence for reduced growth in resident  
657 fish species in the era of de-eutrophication in a coastal area in NW Europe.  
658 *Marine Environmental Research*, 169, 105364.

659 Braak, C., Verdonschot, P., 1995. Canonical correspondence analysis and related  
660 multivariate methods in aquatic ecology. *Aquatic Sciences*, 57(3), 255-289.

661 Carpenter, S.R., 2008. Phosphorus control is critical to mitigating eutrophication.  
662 *Proceedings of the National Academy of Sciences*, 105(32), 11039-11040.

663 CEN. (2015) Water quality – Sampling of fish with multimesh gillnets. European

664 Committee for Standardization. Ref. No. EN 14757: 2015.

665 Coleman, M.A., Bates, A.E., Stuart-Smith, R.D., Malcolm, H.A., Harasti, D., Jordan,  
666 A., Knott, N.A., Edgar, G.J., Kelaher, B.P., 2015. Functional traits reveal early  
667 responses in marine reserves following protection from fishing. *Diversity and*  
668 *Distributions*, 21(8), 876–887.

669 Cusens, J., Wright, S.D., McBride, P.D., Gillman, L.N., 2012. What is the form of the  
670 productivity–animal- species- richness relationship? A critical review and  
671 meta- analysis. *Ecology*, 93(10), 2241-2252.

672 Department of Ichthyology, Institute of Hydrobiology, CAS, 1976. *Fishes of the*  
673 *Yangtze River*. Beijing: Science Press. (In Chinese)

674 Dodson, S.I., Arnott, S.E., Cottingham, K.L., 2000. The relationship in lake  
675 communities between primary productivity and species richness. *Ecology*,  
676 81(10), 2662-2679.

677 Dolédec, S., Chessel, D., ter Braak, C.J.F., Champely, S., 1996. Matching species  
678 traits to environmental variables: a new three-table ordination method.  
679 *Environmental and Ecological Statistics*, 3(2), 143–166.

680 Dong, X.H., Anderson, N.J., Yang, X.D., Chen, X., Shen, J., 2012. Carbon burial by  
681 shallow lakes on the Yangtze floodplain and its relevance to regional carbon  
682 sequestration. *Global Change Biology*. 18, 2205–2217.

683 Dray, S., Choler, P., Dolédec, S., Peres-Neto, P.R., Thuiller, W., Pavoine, S., ter  
684 Braak, C.J.F., 2014. Combining the fourth-corner and the RLQ methods for  
685 assessing trait responses to environmental variation. *Ecology*, 95, 14–21.

686 Dray, S., Dufour, A.B., 2007. The ade4 package: implementing the duality diagram  
687 for ecologists. *Journal of statistical software*, 22, 1-20.

688 Eero, M., Andersson, H.C., Almroth-Rosell, E., MacKenzie, B.R., 2016. Has  
689 eutrophication promoted forage fish production in the Baltic Sea? *Ambio*, 45(6),  
690 649-660.

691 Egertson, C.J., Downing, J.A., 2004. Relationship of fish catch and composition to  
692 water quality in a suite of agriculturally eutrophic lakes. *Canadian Journal of*  
693 *Fisheries and Aquatic Sciences*, 61(9), 1784-1796.

694 Fox, J., Weisberg, S., 2019. *An R Companion to Applied Regression*, Third Edition.  
695 Thousand Oaks CA: Sage. URL:  
696 <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>

697 Froese, R., Pauly, D., 2020. FishBase: World Wide Web electronic publication,  
698 version. <http://www.fishbase.org> (accessed on December 2020).

699 Groemping, U., Berlin, B.H.T., 2021. Relative Importance for Linear Regression in R:  
700 The Package *relaimpo*. R package version 2.2-5.

701 Hayden, B., Myllykangas, J.P., Rolls, R.J., Kahilainen, K.K., 2017. Climate and  
702 productivity shape fish and invertebrate community structure in subarctic lakes.  
703 *Freshwater Biology*, 62(6), 990–1003.

704 Jacobson, P.C., Hansen, G.J., Bethke, B.J., Cross, T.K., 2017. Disentangling the  
705 effects of a century of eutrophication and climate warming on freshwater lake  
706 fish assemblages. *PloS one*, 12(8), e0182667.

707 Jeppesen, E., Jensen, J.P., Jensen, C., Faafeng, B., Hessen, D.O., Søndergaard, M.,



708 Lauridsen, T., Brettum, P., Christoffersen, K., 2003. The impact of nutrient state  
709 and lake depth on top-down control in the pelagic zone of lakes: a study of 466  
710 lakes from the temperate zone to the arctic. *Ecosystems*, 313-325.

711 Jeppesen, E., Jensen, J.P., Søndergaard, M., Lauridsen, T., Landkildehus, F., 2000.  
712 Trophic structure, species richness and biodiversity in Danish lakes: changes  
713 along a phosphorus gradient. *Freshwater biology*, 45(2), 201-218.

714 Jia, Y., Jiang, Y., Liu, Y., Sui, X., Feng, X., Zhu, R., Chen, Y., 2021. Understanding  
715 trophic structure variation in fish assemblages of subtropical shallow lakes:  
716 Combined effects of ecosystem size, productivity, and disturbance. *Ecological*  
717 *Indicators*, 129, 107924.

718 Krauss, J., Steffan-Dewenter, I., Tschardtke, T., 2003. Local species immigration,  
719 extinction, and turnover of butterflies in relation to habitat area and habitat  
720 isolation. *Oecologia*, 137(4), 591-602.

721 Laliberté, E., Legendre, P., 2010. A distance- based framework for measuring  
722 functional diversity from multiple traits. *Ecology*, 91(1), 299-305.

723 Laliberté, E., Legendre, P., Shipley, B., 2014. FD: measuring functional diversity  
724 from multiple traits, and other tools for functional ecology. R package version  
725 1.0-12.

726 Launois, L., Veslot, J., Irz, P., Argillier, C. (2011). Selecting fish- based metrics  
727 responding to human pressures in French natural lakes and reservoirs: towards  
728 the development of a fish- based index (FBI) for French lakes. *Ecology of*  
729 *Freshwater Fish*, 20(1), 120-132.

730 Le, C., Zha, Y., Li, Y., Sun, D., Lu, H., Yin, B., 2010. Eutrophication of lake waters  
731 in China: cost, causes, and control. *Environmental management*, 45(4), 662-668.

732 Liu, X., Wang, H., 2010. Estimation of minimum area requirement of river-connected  
733 lakes for fish diversity conservation in the Yangtze River floodplain. *Diversity*  
734 *and Distributions*, 16(6), 932–940.

735 Liu, X., Wang, H., 2018. Effects of loss of lateral hydrological connectivity on fish  
736 functional diversity. *Conservation Biology*. 32(6), 1336-1345.

737 Mehner, T., Diekmann, M., Bramick, U., Lemcke, R., 2005. Composition of fish  
738 communities in German lakes as related to lake morphology, trophic state, shore  
739 structure and human-use intensity. *Freshwater Biology*, 50(1), 70–85.

740 Mehner, T., Diekmann, M., Gonsiorczyk, T., Kasprzak, P., Koschel, R., Krienitz, L.,  
741 Rumpf, M., Schulz, M., Wauer, G., 2008. Rapid recovery from eutrophication of  
742 a stratified lake by disruption of internal nutrient load. *Ecosystems*, 11(7),  
743 1142-1156.

744 Mouillot, D., Graham, N. A. J., Villéger, S., Mason, N. W. H., Bellwood, D. R., 2013.  
745 A functional approach reveals community responses to disturbances. *Trends in*  
746 *Ecology & Evolution*, 28(3), 167–177.

747 Nandi, S., Aditya, G., Saha, G. K., 2012. Nutrient condition and chironomid  
748 assemblages in Kolkata, India: assessment for biomonitoring and ecological  
749 management. *Journal of limnology*, 71(2), 320-329.

750 Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D.,  
751 Minchin, P.R., O'hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H.,

752 Szoecs, E., Wagner, H., 2019. vegan: Community Ecology Package. R package  
753 version 2.5-6. <https://CRAN.R-project.org/package=vegan>

754 Olin, M., Rask, M., Ruuhjärvi, J., Kurkilahti, M., Ala-Opas, P., Ylönen, O., 2002.  
755 Fish community structure in mesotrophic and eutrophic lakes of southern Finland:  
756 the relative abundances of percids and cyprinids along a trophic gradient. *Journal*  
757 *of Fish Biology*, 60(3), 593–612.

758 Petriki, O., Lazaridou, M., Bobori, D.C., 2017. A fish-based index for the assessment  
759 of the ecological quality of temperate lakes. *Ecological Indicators*, 78, 556-565.

760 Pretty, J.N., Mason, C.F., Nedwell, D.B., Hine, R.E., Leaf, S., Dils, R., 2003.  
761 Environmental costs of freshwater eutrophication in England and Wales.  
762 *Environmental Science & Technology*, 37(2).

763 R Core Team (2018). R: a language and environment for statistical computing,  
764 reference index version 3.5.1. R Foundation for Statistical Computing, Vienna,  
765 Austria. <https://www.R-project.org/>

766 Ritterbusch, D., Blabolil, P., Breine, J., Erős, T., Mehner, T., Olin, M., Peirson, G.,  
767 Volta, P., Poikane, S., 2022. European fish-based assessment reveals high  
768 diversity of systems for determining ecological status of lakes. *Science of the*  
769 *total environment*, 802, 149620.

770 Rodríguez, M.A., Lewis Jr, W.M., 1997. Structure of fish assemblages along  
771 environmental gradients in floodplain lakes of the Orinoco River. *Ecological*  
772 *monographs*, 67(1), 109-128.

773 Sagouis, A., Jabot, F., Argillier, C., 2017. Taxonomic versus functional diversity

774 metrics: how do fish communities respond to anthropogenic stressors in  
775 reservoirs? *Ecology of Freshwater Fish*, 26(4), 621-635.

776 Sandström, A., Karås, P., 2002. Effects of eutrophication on young-of-the-year  
777 freshwater fish communities in coastal areas of the Baltic. *Environmental*  
778 *Biology of Fishes*, 63(1), 89-101.

779 Scheffer, M., Hosper, S.H., Meijer, M.L., Moss, B., Jeppesen, E., 1993. Alternative  
780 equilibria in shallow lakes. *Trends in ecology & evolution*, 8(8), 275-279.

781 Schindler, D.W., Carpenter, S.R., Chapra, S.C., Hecky, R.E., Orihel, D.M., 2016.  
782 Reducing phosphorus to curb lake eutrophication is a success. *Environmental*  
783 *Science & Technology*, 50(17), 8923-8929.

784 Smith, V.H., Joye, S.B., Howarth, R.W., 2006. Eutrophication of freshwater and  
785 marine ecosystems. *Limnology and oceanography*, 51(1part2), 351-355.

786 Smith, V.H., Schindler, D.W., 2009. Eutrophication science: where do we go from  
787 here? *Trends in Ecology & Evolution*, 24(4), 201-207.

788 Søndergaard, M., Jeppesen, E., Jensen, J.P., & Amsinck, S.L., 2005. Water  
789 Framework Directive: Ecological Classification of Danish Lakes. *Journal of*  
790 *Applied Ecology*, 616-629.

791 Stuart-Smith, R.D., Bates, A.E., Lefcheck, J.S., Duffy, J.E., Baker, S.C., Thomson,  
792 R.J., Stuart-Smith, J.F., Hill, N.A., Kininmonth, S.J., Airoidi, L., Becerro, M.A.,  
793 Campbell, S.J., Dawson, T.P., Navarrete, S.A., Soler, G.A., Strain, E.M.A.,  
794 Willis, T.J., Edgar, G. J., 2013. Integrating abundance and functional traits  
795 reveals new global hotspots of fish diversity. *Nature*, 501(7468), 539–542.

796 Su, G., Logez, M., Xu, J., Tao, S., Villéger, S., Brosse, S., 2021. Human impacts on  
797 global freshwater fish biodiversity. *Science*, 371(6531), 835-838.

798 Thomas, G., Eckmann, R., 2007. The influence of eutrophication and population  
799 biomass on common whitefish (*Coregonus lavaretus*) growth—the Lake  
800 Constance example revisited. *Canadian Journal of Fisheries and Aquatic  
801 Sciences*, 64(3), 402-410.

802 Venables, W.N. Ripley, B.D., 2002. *Modern Applied Statistics with S*. Fourth Edition.  
803 Springer, New York. ISBN 0-387-95457-0.

804 Villéger, S., Miranda, J.R., Hernández, D.F., Mouillot, D., 2010. Contrasting changes  
805 in taxonomic vs. functional diversity of tropical fish communities after habitat  
806 degradation. *Ecological Applications*, 20(6), 1512–1522.

807 Wang, Q., Li, Z., Gui, J., Liu, J., Ye, S., Yuan, J., De Silva, S.S., 2018. Paradigm  
808 changes in freshwater aquaculture practices in China: Moving towards achieving  
809 environmental integrity and sustainability. *Ambio*, 47, 410–426.

810 Wang, S., Dou, H., 1998. *Chinese Lake Catalogue*. Science Press, Beijing, p. 1998.  
811 (In Chinese)

812 Winemiller, K.O., Rose, K.A., 1992. Patterns of life-history diversification in North  
813 American fishes: implications for population regulation. *Canadian Journal of  
814 Fisheries and aquatic sciences*, 49(10), 2196-2218.

815 Yu, J., Zhen, W., Kong, L., He, H., Zhang, Y., Yang, X., Chen, F., Zhang, M., Liu, Z.,  
816 Jeppesen, E. ,2021. Changes in Pelagic Fish Community Composition,  
817 Abundance, and Biomass along a Productivity Gradient in Subtropical Lakes.

818 Water, 13(6), 858.

819 Zhang, G., Chang, J., Shu, G., 2000. Applications of factor-criteria system  
820 reconstruction analysis in the reproduction research on grass carp, black carp,  
821 silver carp and bighead in the Yangtze River. *International Journal of General  
822 Systems*, 29(3), 419–428.

823 Zhang, L., Pan, B., Jiang, X., Wang, H., Lu, Y., Lu, Y., Li, R., 2020. Responses of the  
824 macroinvertebrate taxonomic distinctness indices of lake fauna to human  
825 disturbances in the middle and lower reaches of the Yangtze River. *Ecological  
826 Indicators*, 110, 105952.

827 Zhao, S., Fang, J., Peng, C., Tang, Z., Piao, S., 2006. Patterns of fish species richness  
828 in China's lakes. *Global Ecology and Biogeography*, 15(4), 386–394

829