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RESEARCH ARTICLE

Effects of human-induced eutrophication on macroinvertebrate spatiotemporal dynamics in Lake Dianchi, a large shallow plateau lake in China

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Abstract

The Yungui Plateau lakes, which are characterized by a highly endemic biodiversity, have been suffering severely from anthropogenic intervention in the recent decades. Studies on the response of these biodiversity to human-mediated effects are still limited. Here, we selected the typical Lake Dianchi to investigate the correlation between macroinvertebrate spatiotemporal dynamics and human-induced eutrophication across a 2-year span (2009–2010). A total of 26 taxa were recorded, and the assemblage pattern of the macroinvertebrate community was mainly controlled by the spatiotemporal (region, season, and year) density fluctuations of some pollution-tolerant species (*Limnodrilus hoffmeisteri*, *Tubifex tubifex*, *Branchiura sowerbyi*, and *Chironomus plumosus*). Taxon richness, total density, biomass, and the abundance of Oligochaeta and Chironomidae decreased from the north to the south of the lake but were much higher in 2009 than in 2010. Moreover, the high densities of total assemblages and oligochaete occurred during spring and/or autumn, whereas that of chironomids was only high during summer. The contributions of important factors varied in different seasons, but the community variations were mainly shaped by eutrophication-related factors (e.g., Chla, N, and P). Variance partitioning analyses showed that aquatic factors were able to explain more community variations than sediment (6.9–36.6 vs. 5.3–14.7%) across seasons, but their interactive effects were negligible. The results of this study will be beneficial for restoring and managing hypereutrophic lakes in the Yungui Plateau and imply the necessity of long-term monitoring in bioassessment projects involving intensively disturbed lakes.

Keywords Macroinvertebrate assemblages · Eutrophication · Yungui Plateau · Lake Dianchi · Spatiotemporal variation

Introduction

Accelerating lake eutrophication has become one of the most serious environmental problems worldwide (Liu et al. 2012a; Søndergaard et al. 2007; Ye et al. 2015), resulting in consequences, such as deterioration of water quality, loss of biodiversity, and destruction of ecosystem structure and multifunctions (Gong et al. 2009; Levin 1992; Wang et al. 2011). As for biota, for example, human-induced eutrophication has profoundly altered the richness and composition of local assemblages from sensitive and indigenous species to pollution-tolerant or invasive species in many lakes, leading to species extinction and biotic homogenization (Cai et al. 2011; Olden and Poff 2004; Rahel 2000; Strayer 2006; Toussaint et al. 2014; Villéger et al. 2011).

Benthic macroinvertebrates are taxonomically and functionally diverse and play crucial roles in the lake–ecosystem structure and functions (Covich et al. 1999; Fontanarrosa et al. 2013). These macroinvertebrates are also good bioindicators

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for ecological monitoring and assessment due to their sensitivities to different environmental conditions (Bazzanti et al. 2012; Donohue et al. 2009; Li et al. 2016). However, based on their short-term life history and complicated population behavior in the aquatic ecosystems, the macroinvertebrates' spatiotemporal variation is quite elusive in nature and in human-induced conditions (Levin 1992). Therefore, systematically clarifying the response of macroinvertebrate assemblages to eutrophications at spatiotemporal scales can enhance our understanding of the driving mechanisms of macroinvertebrate communities under anthropogenic disturbances and contribute to environmental monitoring and ecological restoration. The spatial dynamics in eutrophic lakes are community-specific across different lake types and mainly affected by environmental filtering (Zhong et al. 2008; Takamura et al. 2009; Cai et al. 2011) and biotic inter-reactions (Cai et al. 2016; Céréghino et al. 2008; Żbikowski and Kobak 2007; Żbikowski et al. 2010). At the temporal scales, numerous previous studies have focused on successions and interannual community variations in coarse scale (Burlakova et al. 2014; Cai et al. 2015; French et al. 2009; Jimenez et al. 2011). Carefully examining the spatiotemporal response of macroinvertebrate assemblages to eutrophication in the fine scales (daily, seasonally, or annually) is warranted to provide detailed information for generalizing the dynamics between macroinvertebrates and environment conditions. The information should be imperative to restore and manage degenerated lake ecosystems (Jackson and Füreder 2006). However, detailed information about macroinvertebrates in eutrophic lakes is still limited.

The patterns of macroinvertebrates in plain eutrophic lakes have been extensively investigated in China, but such studies have seldom been carried out in plateau lakes (Cai et al. 2016; Meng et al. 2016). As one global hotspot for biodiversity conservation, plateau lake ecosystems breed some special and important species, such as *Margarya melanioides*, *Margarya mansuyi*, and *Cipangopaludina dianchiensis* (Kang et al. 2010; Olson and Dinerstein 1998; Zhang et al. 2012; Wang et al. 2013). The Yunnan Plateau lakes are situated in southwestern China and listed as one of the Palearctic Lake ecosystems of the Global 200 Priority Ecoregions due to its highlighted biodiversity (Olson and Dinerstein 1998; Ye et al. 2015). More than 30 lakes were located in this region, and most of them were tectonic lakes formed by faultage sinking with no connection with each other. The unique formation supports numerous endemic species. However, most of these lakes have been suffering from severe anthropogenic intervention in recent decades, resulting in extensive loss of endemic biodiversity (Ding et al. 2017; Liu et al. 2012a; Song et al. 2013; Wang et al. 2013; Yang et al. 2004; Ye et al. 2015).

Lake Dianchi is typical of these lakes. It has been experiencing strong ecosystem degeneration due to high nutrient level and grievous blue–green algal bloom (Gray and Wang 1999; Wang et al. 2012; Wu et al. 2016). However, the mechanism of how human-induced eutrophication drives the macroinvertebrate assemblages in this lake remains to be elucidated (Wang 1985; Wang et al. 2007). In the present study, this lake was chosen to carefully examine the spatiotemporal dynamics of macroinvertebrate assemblages under eutrophication stress for two years (from 2009 to 2010) and understand the response mechanism of macroinvertebrates to human activities (e.g., eutrophication). The specific objectives were (1) to portray the seasonal, yearly, and cross-region variations of macroinvertebrate community and (2) to detect how environmental variables drive these patterns, especially the eutrophication-related ones.

Materials and methods

Study area

Lake Dianchi (24° 23′–26° 22′ N, 102° 10′–103° 40′ E), which is located in the southwestern outskirts of Kunming City, the capital of Yunnan Province, is the sixth largest freshwater lake in China and the most polluted plateau lake. This lake experiences a characteristic tropical plateau monsoon climate and hydrological condition and is separated into three distinct regions, namely, northern (NR), middle (MR), and southern (SR) regions, by their abiotic and biotic conditions (Liu et al. 2013). The lake mainly accommodates the surface runoffs of 22 river flows, with the rivers of the Panlong, Baoxiang, and Baiyu being the largest ones. The lake's water discharges into the Tanglangchuan River via its only outlet in the southwest. The hydrologic residence time is approximately 2–4 years (Liu et al. 2013; Wang et al. 2004). The annual average water temperature is approximately 16.0 °C (ranging from 10 to 27 °C), and the mean annual precipitation is approximately 1070 mm (Wang et al. 2010).

Sampling sites and data collection

Benthic macroinvertebrate data were collected quarterly (April, July, October, and January) from April 2009 to January 2011. A total of 24 sampling sites were established in the whole lake, and NR, MR, and SR had 9, 8, and 7 sampling sites, respectively (Fig. 1). At each site, three quantitative bottom samples were collected using a modified Petersen grab (0.0625 m^2 in area) and sieved using a 500-μm sieve in the field. Each site was positioned accurately by the Garmin GPS-76 system. Specimens were manually sorted from sediment on a white porcelain plate and preserved in 10% formalin. The animals were identified to the lowest feasible taxonomic taxa in accordance with related references (Brinkhurst 1986; Epler 2001; Liu et al. 1979; Morse et al.

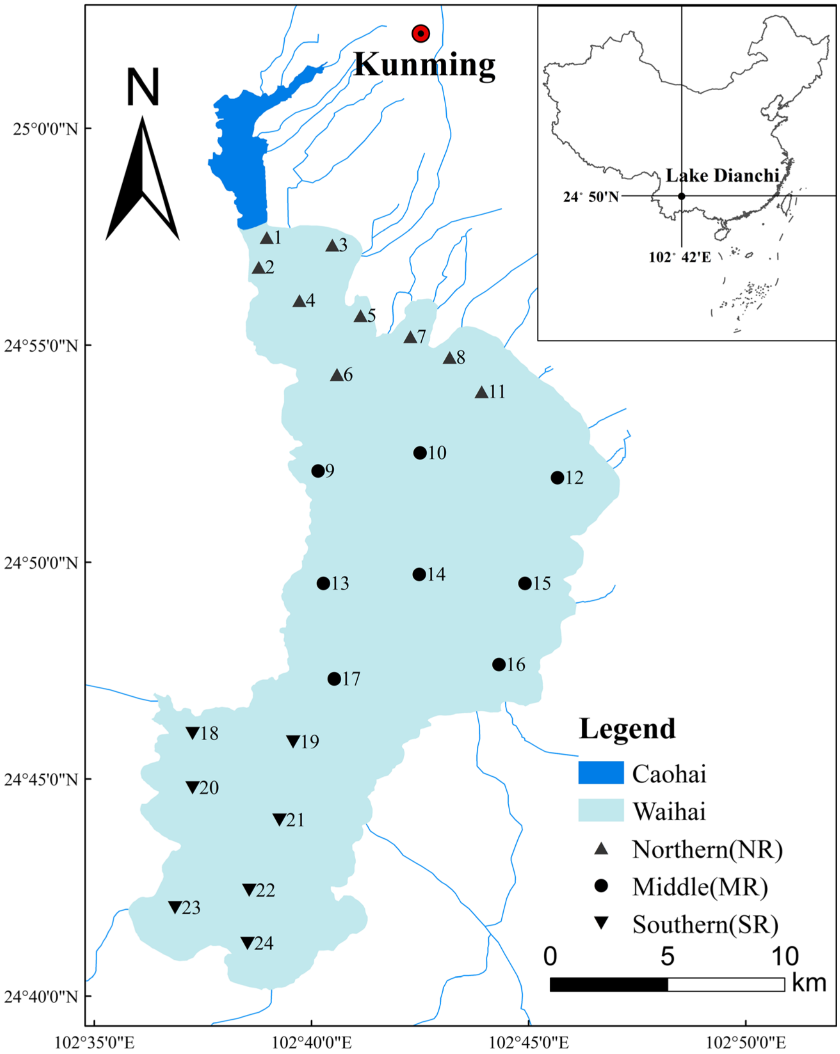

Fig. 1 Locations of 24 sampling sites in Lake Dianchi (black triangle, NR; black circle, MR; black inverted triangle, SR)

1994), counted, and weighed (wet weight) using an electronic balance (accuracy of 0.0001 g).

Environmental data were also collected quarterly, but only for six seasons (from April 2009 to July 2010). On each sampling occasion, 18 environmental variables, namely, water temperature (WT), dissolved oxygen (DO), wind speed, water depth (WD), pH, Secchi depth (SD), total phosphorus (TP), total nitrogen (TN), ammonia nitrogen (NH_4^+–N), nitrate nitrogen (NO_3^-–N), nitrite nitrogen (NO_2^-–N), chlorophyll a (Chla), sediment pH (Sed pH), sediment oxidation–reduction potential (Sed Eh), total sediment nitrogen (Sed TN), total sediment phosphorus (Sed TP), sediment organic matter (Sed OM), and sediment oxidation–reduction capacity (Sed Ca), were measured. WT, DO, pH, Sed Eh, and Sed pH were measured in the field using the YSI Environmental Monitoring Systems 6600. SD, WS, and WD were measured at each site using the Secchi disc, anemoscope, and sounding lead, respectively. TN, NH_4^+–N, NO_2^-–N, NO_3^-–N, TP, Chla, Sed TN, Sed TP, Sed OM, and Sed Ca were determined in the laboratory in accordance with the Chinese Water Analysis Methods Standards (Huang et al. 1999).

Data analysis

The Kruskal–Wallis tests were used to detect the significance of region vs. season for all measured environmental variables. The differences in community parameters (total density, biomass, richness, Shannon–Wiener diversity, and abundance of dominant groups) among regions, seasons, and years were analyzed by one-way repeated measure analysis of variance (ANOVA). The repeated measure analysis was selected due to the temporally nonindependent data generated by the same sampling sites on eight subsequent occasions. When the assumption of data revealed a violation of the Mauchly's test of sphericity, the Greenhouse–Geisser correction was used to correct the results of the within-subject analysis (Quinn and Keough 2002). When the between-subject effects of the ANOVA were significant, pairwise comparisons between regions were carried out using the Tukey's honestly significant difference (HSD) multiple comparison analysis. In cases of nonhomogeneity (significant results of Levene's test), the Games–Howell tests were applied for post hoc comparisons (Beckmann et al. 2005). When the within-subject effects of the ANOVA were significant, the Helmert contrasts were used to compare the two sampling seasons and the two years. Before executing the ANOVA, the macroinvertebrate assemblages' data were tested for normality and transformed when needed. Nonmetric multidimensional scaling (NMDS) was performed using density data to examine the community compositional differences between regions, seasons, and years. Prior to NMDS analysis, the density data were subjected to $\log(x+1)$ transformation. Then, the similarity matrix was calculated using the Bray–Curtis similarity coefficients. The similarity percentage analysis (SIMPER) was used to estimate the contribution of responsible species to the divergence of communities between groups identified from the NMDS and permutational analysis of variance (PERMANOVA). PERMANOVA was conducted to determine the spatial and temporal community variances based on the similarity matrix. The Kruskal–Wallis tests and ANOVA were run in the SPSS software (version 19.0), and NMDS, SIMPER, and PERMANOVA were performed in the PRIMER (version 6.1.16) and the PERMANOVA+ for PRIMER package (Anderson et al. 2008).

Constrained and partial canonical ordinations were used to assess the influence of environmental variables on macroinvertebrate variations. The detrended correspondence analysis (DCA) was used to classify the data and determine the appropriate type of model for direct gradient analysis (Ter Braak and Verdonschot 1995). DCA indicated that a linear model (gradient lengths < 3 standard units) would best fit the data. As such, redundancy analysis (RDA) was used. Prior to RDA, the fauna data were subjected to $\log(x+1)$ transformation, and the down weighting option was used to reduce the influence of rare species. Environmental variables that did not fit the normality assumption (Shapiro–Wilk test, $P < 0.05$) were subjected to logarithm transformation. The environmental variables that had variance inflation factors > 20 were removed from the analysis to avoid high collinearity. The forward selection with Monte Carlo permutation tests (9999 permutations) was used to select a parsimonious set of explanatory variables under the cutoff point of 0.05. Finally, six RDAs were computed for six quarters to evaluate the key environmental variables affecting the macroinvertebrate assemblages. Variation partitioning analyses (Borcard et al. 1992; Legendre and Legendre 1998) were implemented to quantify the relative importance of aquatic and sediment factors in the community structure. The 12 aquatic variables were WT, wind speed, DO, WD, pH, SD, TP, TN, NH_4^+–N, NO_2^-–N, NO_3^-–N, and Chla. The sediment factors included Sed pH, Sed Eh, Sed TN, Sed TP, Sed OM, and Sed Ca. The "Varpart" function (R, vegan package) was used to partition the variations in the two sets of environmental variables (i.e., aquatic and sediment variables). The adjusted R^2 values ("RsquareAdj" function) were calculated to determine the explanatory power of the final RDA models because these values were unbiased and had been recommended previously (Peres-Neto et al. 2006). DCA and RDA analyses were performed using the R version 3.3.1 (R Development Core Team 2016).

Results

Environmental parameters

Almost all water parameters (TN, TP, NH_4^+–N, NO_2^-–N, NO_3^-–N, and Chla) in the NR were significantly higher than those in the MR and SR, whereas the opposite was observed in terms of SD (Table 1, ESM Appendix A). However, most sediment parameters except pH and TP were not obviously different. All water factors except WD showed significant season differences (Table 1). Sed pH and Eh were high during summer and autumn, whereas Sed TN was low during spring (Table 1).

Table 1 Kruskal–Wallis results of determining the significance of factors among regions and seasons for all environmental variables

Environmental parameters	Region			season		
	X^2	*df*	*P*	X^2	*df*	*P*
WD	33.133	2	0.000	5.006	3	0.171
WT	1.138	2	0.566	113.420	3	0.000
SD	7.995	2	0.018	52.764	3	0.000
TN	36.394	2	0.000	11.984	3	0.007
TP	53.629	2	0.000	14.142	3	0.003
DO	0.831	2	0.660	49.404	3	0.000
PH	0.019	2	0.991	95.548	3	0.000
NH_4^+–N	19.665	2	0.000	18.864	3	0.000
NO_2^-–N	33.769	2	0.000	61.210	3	0.000
NO_3^-–N	10.653	2	0.005	93.529	3	0.000
Wind speed	2.280	2	0.320	34.964	3	0.000
Chla	56.374	2	0.000	20.128	3	0.000
Sed pH	6.899	2	0.032	58.742	3	0.000
Sed Eh	0.333	2	0.846	22.644	3	0.000
Sed TN	0.579	2	0.748	13.707	3	0.003
Sed TP	18.906	2	0.000	3.588	3	0.310
Sed OM	3.551	2	0.169	5.126	3	0.163
Sed Ca	3.686	2	0.158	50.122	3	0.000

Spatial and temporal variation in macroinvertebrate assemblages

A total of 26 taxa (9 oligochaetes, 14 chironomids, 2 gastropods, and 1 leech), which belonged to 5 families of 4 classes of 3 phyla, were recorded in the 576 samples. Oligochaetes, which controlled the community structure, represented 96.36% of the total individuals due to its predominant members, namely, *Limnodrilus hoffmeisteri* (83.90%), *Tubifex tubifex* (8.44%), and *Branchiura sowerbyi* (2.07%). Chironomids (3.58%) were also common and mainly attributed to frequently occurring *Chironomus plumosus* (1.73%).

Repeated measure ANOVA indicated that the community parameters (total density, biomass, Oligochaeta density, and density and percentage of Chironomidae) in NR were significantly higher than those in MR and SR. In addition, the MR biomass was significantly higher than the SR biomass, and the richness and the percentage of Oligochaeta in NR were higher than those in SR (Table 2, Fig. 2). The richness and the abovementioned parameters were higher in 2009 than in 2010 (Table 2, Fig. 2). The high oligochaete density occurred during spring and/or autumn, and high chironomid density occurred during summer (Fig. 2). The interaction of season × region was significant for taxon richness, Shannon diversity, and biomass, whereas that of year × region was negligible (Table 2). Finally, the percentage of Oligochaeta had no significant difference among the three regions in different temporal scales (seasons or years) (Table 2).

PERMANOVA indicated that the region ($F = 23.587$, $P = 0.0001$), season ($F = 6.4593$, $P = 0.0001$), and year ($F = 16.961$, $P = 0.0001$) were the key explanatory variables for community variations. The interactions of region × year ($F = 1.9391$, $P = 0.049$) and season × year ($F = 1.7774$, $P = 0.033$) were also the sources of variation (Table 3). Detailed pairwise comparisons showed the significant interaction of region × year ($P < 0.01$ in all comparisons), and the assemblages in 2009 varied significantly across all three regions (Table 3, ESM Appendix B). Pairwise tests revealed that the assemblages during the seasons of 2009 were significantly different from those during the seasons of 2010 ($P < 0.01$ in all comparisons). Within the year, only the winter in 2009 evidently differed from spring and summer ($P < 0.05$), whereas all seasons in 2010 were distinct from each other ($P < 0.05$ in all comparisons) (Table 3, ESM Appendix B).

The variations in sampling sites among different regions, seasons, and years were distinct (Fig. 3). SIMPER analysis showed that the regional community variations were due to *L. hoffmeisteri* and *T. tubifex*, which accounted for 61.43% in NR, 77.40% in MR, and 87.96% in SR (Fig. 4a). Additional amounts were due to *B. sowerbyi* (13.01% in NR and 16.42% in MR), *C. plumosus* (12.92% in NR), and *L. grandisetosus* (4.40% in SR) (Fig. 4a). The seasonal differences were caused by *T. tubifex* (43.29%) during winter, *L. hoffmeisteri* (50.38 to 51.80%) and *B. sowerbyi* (10.67% to 15.52%) in other seasons, and *C. plumosus* (9.44%) during summer (Fig. 4b). Moreover, the annual variations were attributed to *T. tubifex* (34.59%) in 2009 and *L. hoffmeisteri* (51.80%) and *B. sowerbyi* (15.31%) in 2010 (Fig. 4c).

Relationships between macroinvertebrate and environmental variables

Among the 18 environmental variables detected, season-based RDAs retained 11 (Chla, pH, NO_2^-–N, NO_3^-–N, NH_4^+–N, wind speed, WD and TN, Sed TN, Sed TP, and Sed pH) for community variations, even though they were quite different across seasons (Table 4, Fig. 5). These retained variables were almost related to eutrophication. The final RDA models accounted for 22.0 to 46.0% of community variations in different seasons (Table 4).

The pure contributions of water and sediment variables to community variations, which ranged from 6.9 to 36.6% and from 5.3 to 14.7%, respectively, remarkably differed among seasons (Table 5). The conditions in the water environments, which were on the average three times higher (from 0.5 to 6.9) in value than those in the sedimentary environments, played important roles in regulating the community structures. However, their interactive effects were insignificant. Some variations (54.0 to 78.0%) remained unexplained by the RDA models.

Discussion

Characteristics of macroinvertebrate assemblages

Some pollution-tolerant species, i.e., oligochaetes and chironomids, dominated the benthic assemblages in Lake Dianchi, resulting in its low biodiversity and simple structure. Previous studies have shown that the lake's benthic community has been experiencing a continuous diversity decline in recent decades (Wang 1985; Wang et al. 2007, 2011). For example, about 24 and 19 mollusk species, including a high endemic diversity (such as *Cobicula fenouilliana*, *Radix yunnanensis*, *Margarya melanioides*, *M. mondi*, *M. elongata*, and *M. tropidophora*) (Wang et al. 2011; Zhang et al. 2015), were recorded in the 1970s (Zhang and Wu 1983) and the 1980s (Wang 1985), respectively, but only two species, including the only endemic species (*M. melanioides*), which was rated as endangered (EN) by the IUCN in 2009 (http://www.iucnredlist.org), were occasionally collected during our investigation. Thus, the long-term eutrophication has destroyed the lake's benthic diversity and structure through a series of processes, such as deterioration of water and sediment quality, the trophic shift, the disappearance of aquatic macrophytes, and extensive algal bloom (Cai et al. 2012a;

Table 2 Repeated measures ANOVA of effects of regions (NR, MR, and SR) in four seasons on taxon richness, Shannon diversity, total density, biomass, and density and percentage of Oligochaeta and Chironomidae

	F	*P* value	Ranking (post hoc test or contrasts)
Taxon richness			
Between subjects (region)	5.160	*0.015*	NR > SR
Within subjects			
Season	0.726	0.495	
Season × region	3.685	*0.010*	Summer vs. autumn
Year	30.033	*< 0.001*	2009 vs. 2010
Year × region	2.437	0.112	
Season × year	0.409	0.747	
Season × year × region	1.418	0.222	
Shannon diversity (*H′*)			
Between subjects (region)	0.563	0.578	
Within subjects			
Season	2.511	0.067	
Season × region	4.621	*0.001*	All four seasons vs. each other
Year	0.001	0.973	
Year × region	4.534	*0.023*	2009 vs. 2010
Season × year	1.941	0.132	
Season × year × region	4.528	*0.001*	
Total density			
Between subjects (region)	19.117	*< 0.001*	NR > MR and SR
Within subjects			
Season	37.935	*< 0.001*	Spring and summer vs. autumn vs. winter
Season × region	2.154	0.059	
Year	77.203	*< 0.001*	2009 vs. 2010
Year × region	0.834	0.448	
Season × year	4.016	*0.021*	
Season × year × region	1.191	0.328	
Biomass			
Between subjects (region)	24.189	*< 0.001*	NR > MR > SR
Within subjects			
Season	43.007	*< 0.001*	All four seasons vs. each other
Season × region	3.067	*0.011*	Summer vs. autumn and winter
Year	78.991	*< 0.001*	2009 vs. 2010
Year × region	0.907	0.419	
Season × year	3.547	*0.019*	
Season × year × region	0.613	0.719	
Oligochaeta density			
Between subjects (region)	18.469	*< 0.001*	NR > MR and SR
Within subjects			
Season	37.810	*< 0.001*	Spring and summer vs. autumn vs. winter
Season × region	2.105	0.065	
Year	65.562	*< 0.001*	2009 vs. 2010
Year × region	0.795	0.465	
Season × year	3.749	*0.015*	
Season × year × region	1.371	0.240	
% Oligochaeta			
Between subjects (region)	2.424	*< 0.001*	NR > SR
Within subjects			
Season	1.731	0.197	

Table 2 (continued)

	F	*P* value	Ranking (post hoc test or contrasts)
Season × region	1.274	0.300	
Year	5.501	*0.029*	2009 vs. 2010
Year × region	3.036	0.069	
Season × year	1.542	0.229	
Season × year × region	1.199	0.326	
Chironomidae density			
Between subjects (region)	16.076	< *0.001*	NR > MR and SR
Within subjects			
Season	5.821	*0.001*	Summer vs. autumn and winter
Season × region	0.330	0.919	
Year	36.477	< *0.001*	2009 vs. 2010
Year × region	0.049	0.952	
Season × year	1.617	0.194	
Season × year × region	0.125	0.993	
% Chironomidae			
Between subjects (region)	5.985	< *0.001*	NR > MR and SR
Within subjects			
Season	3.568	*0.019*	Summer vs. autumn
Season × region	0.728	0.629	
Year	15.925	*0.001*	2009 vs. 2010
Year × region	0.485	0.622	
Season × year	1.328	0.273	
Season × year × region	1.042	0.407	

P values < 0.05 are in italics

Du et al. 2011; Erman and Erman 1984; Pan and Gao 2010; Tews et al. 2004). Therefore, the protection of these remnant benthic animals is a tremendous challenge for conservationists and stakeholders. Our results revealed that the dominant species of macroinvertebrates in Lake Dianchi (plateau lake) were similar to those of Lake Taihu (plain lake) (Cai et al. 2012a), suggesting that although the hydrological and climatic characteristics in the plateau lakes are different from the eastern plain lakes in China, human-induced eutrophication has promoted macroinvertebrate taxonomic and functional homogenization at broad spatial scales.

Spatial and seasonal patterns

Although extreme habitat homogenization occurred across the lake (e.g., the decline of aquatic macrophytes and fine silt–clay sediment), the remnant benthos showed a distinct spatial pattern (Du et al. 2011). This pattern can be attributed mainly to the predominant pollution-tolerant species. These species, which are good indicators of eutrophication, generally indicate positive correlation to environmental nutrient concentrations to some extent (Cai et al. 2015; Gong and Xie 2001; Lang 1978). Consequently, high water nutrients in NR produced high densities of oligochaetes and chironomids. Nevertheless, the low level of abundance and biodiversity in SR may be determined by the high level of Sed TP level in this region due to the undisposed wastewater discharge by nearby rich phosphorus mineral resources and phosphorus fertilizer factories (Gao et al. 2005; Liu et al. 2012b). The phosphorus level may exceed the tolerable thresholds of most benthic species in this region (Correll 1998). In the last two seasons of our investigation, the negative effects of high phosphorus on chironomids were further confirmed because of the disappearance of chironomids in the last two seasons. Cai et al. (2015) also found that chironomids had lower tolerance to phosphorus pollution than *L. hoffmeisteri*. Moreover, our RDA models indicated that Sed TP was significantly negatively correlated with macroinvertebrate variations. However, the extent of harm of these ultrahigh Sed TP levels to macroinvertebrate remains to be identified and needs further study.

Our study also demonstrated significant seasonal and interannual macroinvertebrate fluctuations. Natural community fluctuation is controlled by extrinsic (abiotic and biotic) and intrinsic (life history) factors (Cai et al. 2015, 2017; Hao et al. 1995; Pan et al. 2016; Talbot and Ward 1987). Since the environmental homogenization across the lake, the benthic community seasonal dynamics were mainly regulated by the community behavior. Such dynamics were determined by the

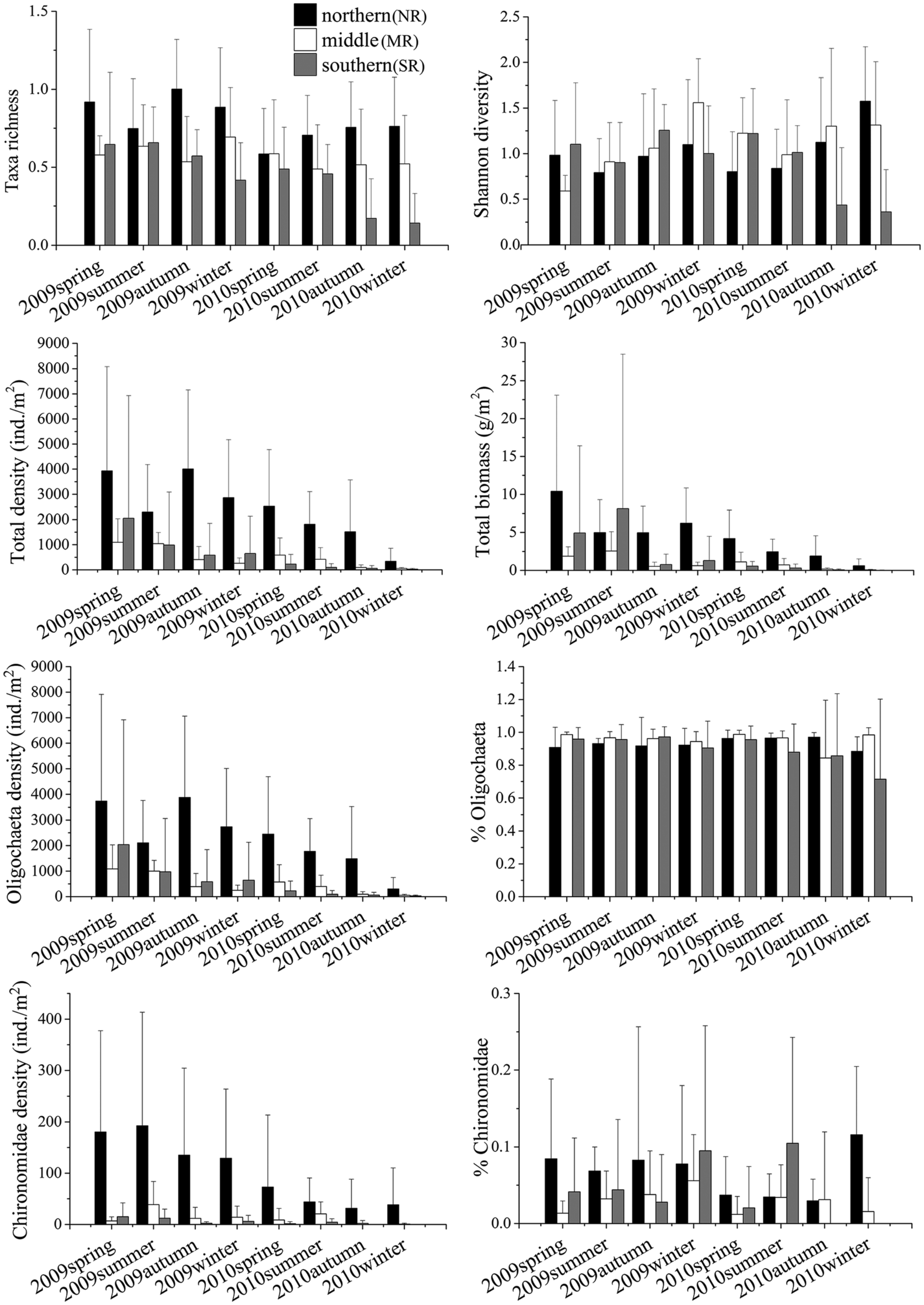

Fig. 2 Taxa richness, Shannon diversity, total macroinvertebrate density and biomass, Oligochaeta density and percentage, and Chironomidae density and percentage across the NR, MR, and SR of the lake in two years (mean ± standard deviation)

Table 3 Permutational MANOVA results of macroinvertebrate communities

Source	*df*	SS	MS	Pseudo-*F*	*P* (perm)
Region	2	44,181	22,091	23.587	*0.001*
Season	3	18,149	6049.6	6.4593	*0.001*
Year	1	15,885	15,885	16.961	*0.001*
Region × season	6	5434.3	905.72	0.96706	0.502
Region × year	2	3632.2	1816.1	1.9391	*0.049*
Season × year	3	4994.1	1664.7	1.7774	*0.033*
Region × season × year	6	8356.9	1392.8	1.4872	0.056
Residual	164	15,360	936.57		
Total	187	25,157			

P values < 0.05 are in italics

df degrees of freedom, *SS* square sum, *MS* mean sum, *P* (*perm*) *P* values using permutation of residuals under a reduced model

fluctuations in four dominant pollution-tolerant species (*L. hoffmeisteri*, *T. tubifex*, *B. sowerbyi*, and *C. plumosus*), indicating high abundance during spring and/or autumn. These oligochaetes mainly complete their life cycles within 1 year, and their reproduction time is during spring and/or autumn (Wang et al. 2007). In addition, the high summer densities of chironomids should be related to the large-scale eclosion of chironomids larva during autumn. However, the cross-year abundance dynamics, which had a remarkable decline from 2009 to 2010 was also distinct. The abundance in 2009 was in the same level as that in 2002 (Wang et al. 2007, 2011), possibly indicating a turning point, in which the deteriorative benthic assemblage turned to a moderate condition. Our updated investigation (2014–2015) also indicated this trend (unpublished data). Thus, ongoing multiple restoration projects for Lake Dianchi (such as the control of point and nonpoint wastewater and the in-lake restoration act) may be effective in improving the environmental condition for benthic animals (Wang et al. 2012).

Community–environment relationships in different seasons

Eutrophication-mediated environmental factors drove the lake benthic assemblage variation across time despite their varying relative contributions in different seasons. These filters were mostly related to Chla, nutrients (nitrogen and phosphorus), pH, and transparency.

Chla played a strong role in regulating benthic assemblage during winter and spring. Cyanobacterial blooms persisted in Lake Dianchi all year round due to the high temperature during winter but with different dominant species through time (Zhang et al. 2012). *Aphanizomenon flos-aquae* dominated during the cold seasons (spring and winter), whereas *Microcystis* spp. were noted during the warm seasons (summer and autumn) (Wu et al. 2016). Massive blooming activity can consume the DO in water due to algal respiration and decomposition, leading to exasperated DO condition for benthos survival, especially during the cold season (Cai et al. 2016). Moreover, the cyanobacterial toxic metabolites (e.g., cyanotoxins) can be harmful to benthic animals (Nogueira et al. 2004; Zhang et al. 2012). For example, *A. flos-aquae* can synthesize one type of neurotoxin (paralytic shellfish poisons), which was regarded as one of the most hazardous toxins in cyanotoxins, and has been confirmed to lead to the malformation and mortality of aquatic organisms (Lefebvre et al. 2004; Liu et al. 2006; Mahmood and Carmichael 1986; Zhang et al. 2013). Nevertheless, Chla was not detected by the RDA model to affect significantly the benthos community in most serious cyanobacterial bloom seasons (summer and

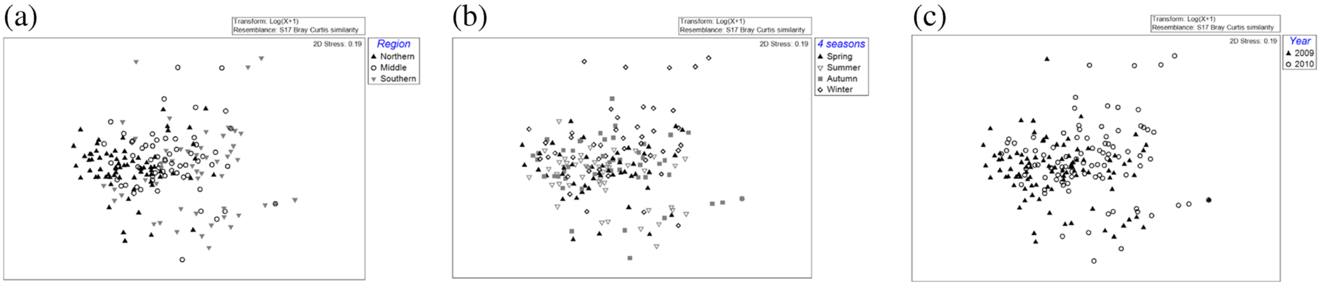

Fig. 3 Nonmetric multidimensional scaling (NMDS) of macroinvertebrates collected from three regions (NR, MR, and SR), four seasons (spring, summer, autumn, and winter), and two years (2009 and 2010)

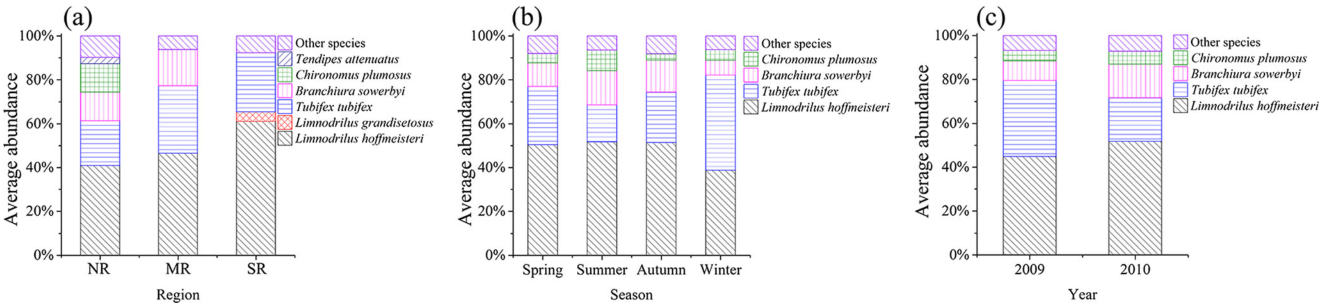

Fig. 4 Average abundance of dominant species represented at the **a** three regions (NR, MR, and SR), **b** four seasons (spring, summer, autumn, and winter), and **c** two years (2009 and 2010)

autumn). This situation can be attributed to other environmental factors (e.g., nitrogen and phosphorus) possibly outcompeting the other parameters in regulating the variations in these seasons (Qu et al. 2019). In addition, the lake's algal growing time is during warm seasons, whereas moribund algae occur during the cold seasons, indicating that the high DO produced by algal photosynthesis should benefit animal survivals during summer and autumn (Wang et al. 2012).

Table 4 Results of redundancy analyses (RDA), giving the relative influence of significant environmental variables on community composition in different seasons

Variable	Adj. R^2	Pseudo-*F*	*P*
April 2009			
Chla	0.182	6.115	0.001
pH	0.263	3.419	0.005
Sed TN	0.320	2.755	0.011
NO_2	0.368	2.509	0.022
NH_3	0.398	1.950	0.047
July 2009			
Sed pH	0.151	5.092	0.002
Wind speed	0.220	2.935	0.009
October 2009			
NO_2	0.202	6.812	0.001
NH_3	0.325	5.009	0.001
Sed TP	0.371	2.552	0.025
WD	0.405	2.131	0.046
January 2010			
Chla	0.162	5.455	0.001
Sed pH	0.229	2.902	0.018
April 2010			
Chla	0.188	6.311	0.001
pH	0.243	2.624	0.033
Sed TP	0.318	3.281	0.004
TN	0.401	3.781	0.003
WD	0.460	3.078	0.006
July 2010			
SD	0.213	7.230	0.001
Sed TP	0.282	3.108	0.010
NO_3	0.325	2.331	0.019

Different forms of nitrogen had remarkable negative correlations with the assemblages across seasons. In recent decades, human-induced nitrogen inputs into this lake have sharply increased (Gao et al. 2015). These increased nitrogen concentrations caused by high sedimentation rates destroyed the benthic composition and structure through a battery of physical mechanisms of siltation, habitat modification, and oxygen depletion (Grall and Chauvaud 2002; Li et al. 2012; Pearson and Rosenberg 1978). The pollution-tolerant species, especially *L. hoffmeisteri*, have actively responded to the increase in the black layer and increase in the organic sedimentation in similar fashions (Lang and Hutter 1981; Zhong et al. 2008). This condition is beneficial for these species in terms of nutrient availability. The decomposition of organic matter led to oxygen depletion in the sediment and, in turn, to its enrichment with nutrients. This enrichment is known to generate an increase in the levels of NO_3^-–N and NH_4^+–N in the interstitial water through nitrification and denitrification (Hansen et al. 1998; Shang et al. 2014; Svensson et al. 2001). Their toxicities at high concentrations are considered key factors in the succession of benthic macroinvertebrates (Frazier et al. 1996; Sparks and Sandusky 1981; Wilson et al. 1995).

Sediment TP significantly affected the benthos assemblage dynamics. Phosphorus is a fundamental nutrient for invertebrate growth and metabolism (Elser et al. 2000), but a stoichiometric balance of carbon and phosphorus in the tissues is necessary (Elser 2005). Thus, a possible mechanism for the TP effect is that the very low carbon–phosphorus values in the lake's animal tissue caused by highly phosphorus-enriched sediments can be harmful (Song et al. 2013).

Investigators have argued that pH, especially Sed pH, is an important factor regulating the benthos community (Shaw and Mackie 1989). Weakly acidic sediment is deleterious to molluscan fecundity, hatching survival, and formation of calcareous shells and can lead to high mortality of embryos and low recruitment (Echeverría et al. 2010). Thus, the weakly acidic sediment conditions in Lake Dianchi (ESM Appendix A) should play key roles in eradicating most of the molluscan biodiversity across the lake scale.

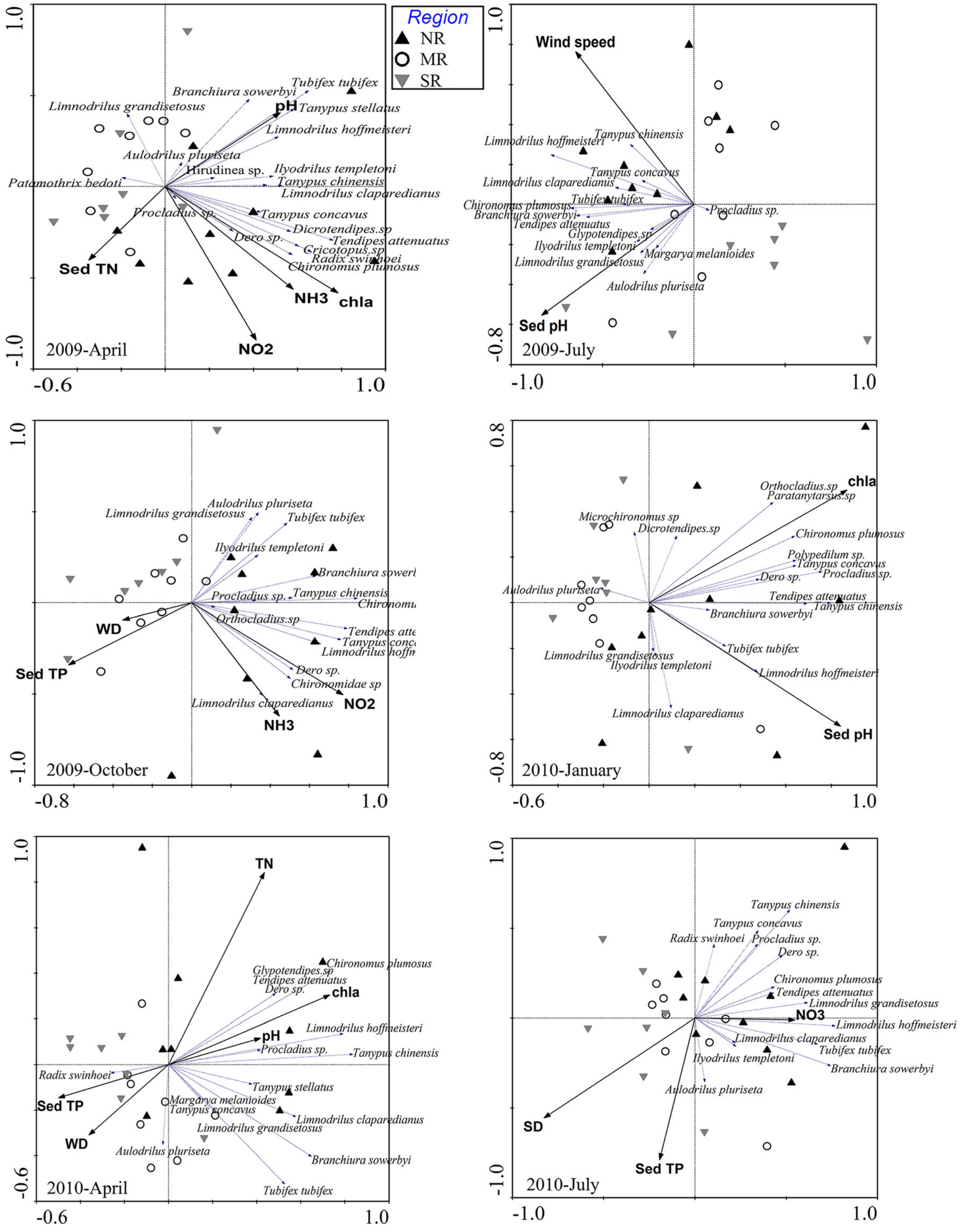

Fig. 5 RDA triplot of macroinvertebrates, environmental variables, and sampling sites based on the first two axes in different seasons (April 2009, July 2009, October 2009, January 2010, April 2010, and July 2010)

Naturally induced physical disturbance by wind and related factor (SD) had certain effects on the community dynamics during summer. From May onwards, the southwestern and southeastern monsoons can take shape in the Yunnan plateau (Yang et al. 2004). The south-directed long wind can historically cause severe water waves in the lake oriented in the north–south, accompanied by the low SD. These naturally caused activities, combined with the severe cyanobacterial bloom and high nutrient levels (Wang et al. 2010; Zhang et al. 2012), can aggravate the conditions for benthic survivals and other biological activities, especially in NR, where the moribund algae were heavily stacked due to the wind.

Table 5 Percentage variations in macroinvertebrate community structure in four seasons attributed to aquatic parameters (Aqua), shared fraction (Shared), sediment parameters (Sed), and unexplained variation (Unexplained). *explanations of the sets of variables are testable and the level of significant at <0.05

	Aqua	Shared	Sed	Unexplained
April 2009	0.366*	− 0.022	0.053*	0.603
July 2009	0.069*	0.017	0.134*	0.780
October 2009	0.280*	0.067	0.059*	0.594
January 2010	0.077*	0.086	0.067*	0.770
April 2010	0.364*	− 0.051	0.147*	0.540
July 2010	0.312*	− 0.104	0.117*	0.675

To our knowledge, few studies have assessed the effects of different environmental types (water and sediments) on macroinvertebrate community in the hypereutrophication plateau lakes. Inconsistent with previous studies (Cai et al. 2011, 2012b; Pan et al. 2015), the present study found that the water condition plays a fundamental role in the determination of macroinvertebrate structure compared with sediments in the lake studied. The wind-induced disturbance of the water/sediment interface in the large shallow lake is beneficial for nutrient exchange on the interface between the water and sediment, probably causing eutrophication-related aquatic factors affecting the benthic community in appearance (Cai et al. 2012a, 2016; Scheifhacken et al. 2007). Only a few sediment factors have been determined in our study. In general, only one factor in this phase became a significant driver in regulating the benthic assemblage. Nevertheless, a few sediment factors still showed quite important influences on the macroinvertebrate communities, implying that monitoring and protecting the sedimentary environment are essential for the restoration of eutrophic lakes and conservation of biodiversity.

Some unexplained variance of community variation across seasons was observed due to the failure to include key extrinsic and intrinsic variables. The extrinsic variables may include key environmental filters (e.g., human-induced habitat fragmentation and breakwater construction) and biotic reactions (e.g., alteration of algal resources available and exotic introduction). The intrinsic variables include community traits, such as the demographic characteristics (e.g., natality, fatality, and fecundity), and dispersal ability.

Conclusion and implications for conservation

The spatiotemporal dynamics of macroinvertebrate linking to ambient factors were carefully examined across two years in a once-fascinating plateau lake (Lake Dianchi). To date, this lake's benthic members were severely destroyed, as demonstrated by the indications of the massive biodiversity loss (especially its endemism) and oversimple structure. The predominant members were all pollution-tolerant and widespread taxa (oligochaetes and chironomids), which governed the community composition and structure throughout the year. This homogenization had been driven strongly by human-induced eutrophication in recent decades. The eutrophication-related water and sediment factors independently played pivotal roles in the remnant benthos patterns across seasons, with the former being important. In addition, the information of a remarkable interannual fluctuation suggested that a long-term monitoring project be conducted to provide in-depth information for macroinvertebrates in lakes in this plateau. These findings can provide detailed information for the local government and environmental agency to restore and manage these eutrophic Yun-Gui Plateau lakes.

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