

RESEARCH ARTICLE

Intra-annual fluctuations dominating temporal dynamics of benthic diatom assemblages in a Chinese mountainous river

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Abstract – Understanding temporal dynamics of community may provide insights on biological responses under environmental changes. However, our knowledge on temporal dynamics of river organisms is still limited. In the present study, we employed a multivariate time-series modeling approach with a long-term dataset (*i.e.* 72 consecutive months) to investigate temporal dynamics of benthic diatom communities in four sites located in a Chinese mountainous river network. We hypothesized that: (1) there are multi-scale temporal dynamics within the diatom community; (2) intra-annual fluctuations dominate the community dynamics; (3) diatom species composing the community respond distinctly to environmental changes. We found that intra-annual fluctuations with periodicities <12 months explained 8.1–16.1% of community variation. In contrast, fluctuations with periodicities of 13–36 months and 37–72 months only accounted for 1.1–5.9% and 2.8–9.7% of variance in diatom community dynamics, respectively. Taxa correlating significantly to each significant RDA axis (namely, RDA taxa group) displayed distinct temporal dynamics. Conductivity, total nitrogen, and pH were important to most RDA taxa groups across the four sites while their effects were group-specific. We concluded that intra-annual dynamics dominated temporal variation in diatom communities due to community responses to local environmental fluctuations. We suggest that long-term monitoring data are valuable for identifying multiple-scale temporal dynamics within biological communities.

Keywords: Temporal dynamic / multiple-scale / benthic diatoms / time-series model

1 Introduction

Understanding of temporal dynamics of community composition is essential for interpreting responses of communities to environmental changes and provides basis for predicting biological responses to future scenarios such as climate changes (Peñuelas *et al.*, 2002; Estes *et al.*, 2018; Gotelli *et al.*, 2017). In addition, such research can provide insights on ecological monitoring and environmental management (Blonder *et al.*, 2017; Medrano *et al.*, 2020). Therefore, there has been increased interest in exploring temporal dynamics of community (Rull, 2012; Wolkovich *et al.*, 2014).

As one of main primary producers in low to middle order streams, benthic algae play important roles in lotic ecosystems; therefore, benthic algal ecology is one important aspects of

stream ecology (Lowe and LaLiberte, 2017). Numerous studies have found that seasonal changes in river environments have considerable impacts on temporal dynamics of lotic algal communities (Andrus *et al.*, 2013). Indeed, in-river environmental variables including flow velocity, water depth, turbidity, water temperature, as well as nutrient concentrations are associated with climate seasonality, leading to pulsed disturbances on river organisms such as algae (Mykrä *et al.*, 2019). Therefore, temporal dynamics of algal communities are likely to be dominated by intra-annual dynamics (Paches *et al.*, 2019).

Apart from external environments, temporal dynamics of lotic algal communities also depend on characteristics of component species (Viketoft *et al.*, 2011). According to the fluctuation dependent mechanisms of coexistence (FMC) proposed by Chesson (2000), asynchronous fluctuations among species within communities controlled by characteristics of individual species play a key role in communities

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maintenance (Rodríguez-Verdugo *et al.*, 2019; Shimadzu *et al.*, 2013). Benthic algae are diverse and abundant in lotic ecosystems including species with distinct biological and ecological traits (*e.g.* body shape, attachment ability, growth rate, dispersal ability and sensitivity to environmental changes) (Passy, 2007). Hence, species have distinct responses to the same environmental variables, leading to asynchronous temporal dynamics among different algal species (Lamy *et al.*, 2019).

Most existing studies focusing on temporal dynamics of lotic algal communities used general community metrics such as biomass, species richness and community similarity indices to represent community characteristics (Korhonen *et al.*, 2010; Rosemond *et al.*, 2000). Only a few studies have explored temporal dynamics of algae with an emphasis on changes in the community composition (Thibault *et al.*, 2004). Moreover, variation in temporal dynamics of individual species within the community has not been well addressed (Tang *et al.*, 2016).

In the present study, we aimed to investigate temporal dynamics of lotic benthic diatom communities. We applied a multivariate time-series modeling approach with a long-term dataset collected in a mountainous river network in Central China. The following three hypotheses are to be tested: (1) There are multi-scale temporal dynamics in diatom communities; (2) intra-annual dynamics dominate temporal fluctuations of the diatom communities; (3) diatom species composing the same community respond distinctly to environmental changes.

2 Materials and methods

2.1 Study region

The Xiangxi River is one tributary of the Yangtze River located in the western area of Hubei province of China. The river is 94 km long with three tributaries, Jiuchong River, Gufu River and Gaolan River (Wang *et al.*, 1997). The climate in this mountainous area is subtropical with hot, rainy summers (June to September) and cold, dry winters (December to February) (Tang *et al.*, 2004). Average annual precipitation in this area is 984.0 to 1842.8 mm, and rainfall usually has peaks in July and troughs in January (Yang *et al.*, 2000). Woodland is the dominant land use in the watershed, following with grassland and cultivated land (Wang *et al.*, 2018). Within the basin, rivers run through mountainous area and typically have stony substrates.

2.2 Data collection and preparation

Four sites in the Xiangxi River network were surveyed monthly from January 2011 to December 2016 (Fig. 1). Two sites are located in the upper mainstream, named XX01 and XX02 (following the water flow direction), while the other two, JC01 and JC02, are located in the tributary of Jiuchong River.

Benthic algae were collected from 10 to 15 randomly selected stones (with a diameter range of 6 to 40 cm) at each site. A circle with the radius of 2.7 cm was placed on stones. The area within the circle was scrubbed and flushed with distilled water into the sample bottle. All subsamples from the same site were combined into one composited sample and

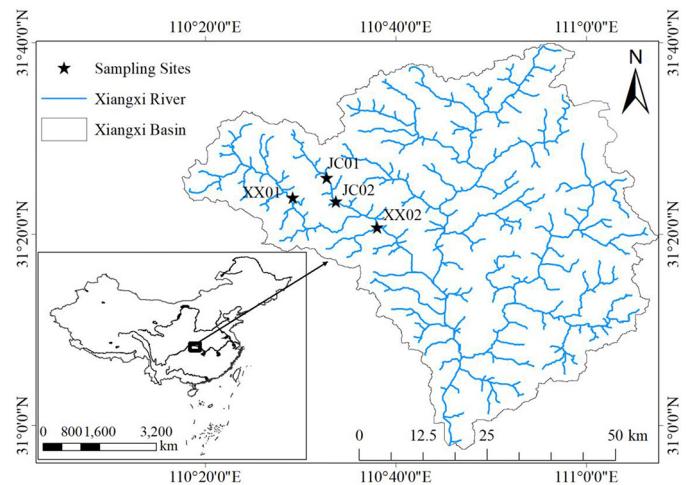


Fig. 1. Location of sampling sites in the Xiangxi River watershed.

the volume was recorded. The algal samples were preserved with 4% formalin for further identification and enumeration (Tang *et al.*, 2016). In the laboratory, permanent diatom slides were prepared after acid digestion. A minimum of 500 valves were identified and counted at 1000 magnification under oil immersion (Olympus CX21, Japan). Most diatom taxa were identified to species level following references Qi *et al.* (1995–2013) and Krammer and Lange-Bertalot (2000). Species names of diatoms were updated according to the AlageBase dataset (<http://www.algaebase.org/>). Finally, relative abundance was calculated for each taxon in each sample.

Physicochemical variables were monitored simultaneously. Wetted width and water depth were measured using a tape meter. Current velocity was measured with a digital water-flow probe (FP211, Global Water Instrumentation, Texas, USA). Discharge (m^3/s) was calculated using the velocity-area method for each cross-section (Gore and Banning, 2017). Water temperature (WT), pH, and conductivity (Cond) were measured using a handheld YSI multiprobe sonde (YSI, Inc. Yellow Springs Ohio, USA). A 355 mL stream water sample was collected and preserved in an acid-proof bottle by adding concentrated sulphuric acid to regulate pH <2 in the field. In the laboratory, total nitrogen (TN), total phosphorus (TP), nitrate ($\text{NO}_3\text{-N}$), phosphate ($\text{PO}_4\text{-P}$), ammonia nitrogen ($\text{NH}_4\text{-N}$) and silica (SiO_2) were measured with a segmented flow analyzer following the user manual (Skalar, The Netherlands).

2.3 Statistical analyses

Separate analyses were conducted for each site in R version 3.0.1 for Windows (R Core Team, 2019).

We first used redundancy analysis (RDA) to examine relationships between algal relative abundance data and time variables. Temporal variables were produced by using the principal coordinate of neighbor matrices (PCNM) approach. Although this method is often used in spatial analysis, it is also competent to disentangle temporal structures within multivariate data (Legendre and Gauthier, 2014). PCNM converted the linear time vector into various frequency sine waves,

representing fine to broad temporal scales (Borcard *et al.*, 2004). In the present study, 35 PCNM variables were obtained by PCNM conversion for the 72-month linear time variables (*i.e.* 1 to 72 months) (Supplementary Fig 1). Redundancy analysis (RDA) was first performed using relative abundance data of diatoms and all the PCNM variables (namely RDA-PCNM) (Borcard *et al.*, 2018) with a forward selection procedure to select important PCNM variables (Blanchet *et al.*, 2008). Then RDA was re-run with selected PCNM variables. Significant RDA axes with a P value <0.05 were identified by the Monte Carlo permutation test (with 9999 times). Therefore, the number of significant RDA axes represents the number of distinct temporal dynamics within the whole community (Angeler and Johnson, 2012). Since RDA axes are orthogonal to each other, temporal dynamics revealed by RDA-PCNM are independent from each other (Angeler *et al.*, 2011). RDA-PCNM was performed with ‘PCNM’ function in package ‘PCNM’ (Legendre *et al.*, 2011). Prior to analysis, relative abundance of diatoms were Hellinger transformed to avoid ‘horseshoe effect’ caused by Euclidean distance (Legendre and Gallagher, 2001). Additionally, non-metric multidimensional scaling (NMDS) was used to identify seasonal patterns of diatom assemblages in Xiangxi River. NMDS aims to represent the original position of data in multidimensional space as accurately as possible using a reduced number of dimensions that can be easily plotted and visualized (like PCA). However, unlike PCA, which uses Euclidian distances, NMDS relies on rank orders (distances) for ordination (*i.e.* non-metric) (Ruokolainen and Salo, 2006). Being based on ranked distances, it tends to linearize the relationship between environmental species distances (just like the Spearman Rank correlation) and can deal with any distance measure, data normalization and transformation, which is very helpful for our research. NMDS was performed with ‘metaMDS’ function in package ‘vegan’ (Oksanen, 2015).

Secondly, associations between diatom taxa and each of significant temporal dynamics were examined using Spearman rank correlation analysis. Correlation coefficient between raw relative abundance of each taxon and linear combination scores (Lc scores) of diatom assemblages along the sampling months were calculated. Lc scores are modeled temporal trends of algal groups that are associated with each significant RDA axis by linear combinations (*i.e.* regression) of selected PCNMs (Legendre and Legendre, 2012). Taxa that displayed significant correlations with a specific significant RDA axes ($P < 0.05$, $|R| > 0.2$) were assigned to the same taxa group (Angeler and Johnson, 2012; Zar, 2005). That is, taxa significantly associated with RDA1 axis were identified and formed RDA1 taxa group; while RDA2 taxa group were composed of taxa significantly correlated with RDA2 axis, and so on. Taxa showing significant correlations with multiple RDA axes were assigned to the group with the highest correlation coefficient.

Next, a generalized additive mixed model (GAMM) was used to examine effects of physical and chemical variables on temporal dynamics of each RDA taxa group. GAMM is effective in modeling relationships between variables using smoothing function, without prerequisite information on the type of relationships (Zuur *et al.*, 2009). In addition, GAMM can handle temporal autocorrelation in model residuals, which was evident for our data (detected by function ‘acf’).

Environmental variables including WT, discharge, Cond, TN, TP, NH₄-N, SiO₂ and pH were used as predictors, with the sum of relative abundance of taxa composing of the RDA group as the response variables. Cubic regression spline function was used in GAMM to fit models while cross validation was used to determine the optimal smoothness. Prior to GAMM fitting, all predictors, except pH, were log10($x+1$) transformed to reduce influence of outliers (Zuur *et al.*, 2010). GAMM was performed with ‘gamm’ function in package ‘mgcv’ (Cibils-Martina *et al.*, 2017).

3 Results

3.1 Temporal variation in environmental variables

Summary for physical and chemical variables was presented in Table 1. Water temperature, SiO₂ and conductivity fluctuated seasonally at all sites, with peaks in summer (June, July, August) and troughs in winter (December, January, February) (Supplementary Fig. 3). TN had the highest concentrations in spring at JC01 and XX01 while it peaked in summer at JC02 and XX02. Seasonal variation in discharge, TP, NH₄-N and pH were not obvious (Supplementary Fig. 3). There was no significant long-term trend in WT and TP at all sites while conductivity decreased significantly in all sites (Supplementary Fig. 4). Besides that, TN showed decreasing trends in JC01, JC02 and XX02 (Supplementary Fig. 4). NH₄-N showed decreasing trend in JC01 and XX01 (Supplementary Fig. 5). Silicate, discharge and pH also showed slight long-term variation in JC01, XX01 and XX02 respectively (Supplementary Fig. 5).

3.2 Multiple temporal dynamics within diatom assemblages

A total of 254 diatom taxa were identified, with the highest taxa number in XX02 (163), followed by XX01 (120), JC01 (118) and JC02 (116). *Cocconeis placentula* Ehrenberg and *Achnanthidium minutissimum* (Kützing) Czarnecki were dominant species with average relative abundance of 36.12% and 24.14%, respectively, followed by *Cocconeis pediculus* Ehrenberg (7.2%) and *Achnanthidium lineare* Smith (5.5%). Additional 14 taxa were observed with an average relative abundance higher than 1% (Tab. 2).

Non-metric Multi-Dimensional scaling (nDMS) analysis revealed seasonal differences in terms of species composition at each site (Fig. 4). The communities was divided into four seasonal groups. There were overlapping and non-overlapping parts among the seasonal groups. According to the relative position of dominant species and communities, the main occurrence seasons of each dominant species can be identified. *Achnanthidium minutissimum* and *Cocconeis placentula* were located in the overlapping part of each seasonal group in all sampling sites which means that they appeared in every season and each site. *Gomphonema intracatum* and *Reimeria sinuate* appeared frequently in different seasons in the tributary sites. *Achnanthidium lineare*, *Cocconeis pediculus* and *Achnanthidium deflexum* also appeared frequently in different seasons at the two mainstream sites. In JC01, *Tetracyclus rubestris* was closer to the summer group. *Gomphonema intracatum*

Table 1. Summary of physical and chemical variables (mean with the range in parentheses) from January 2011 to December 2016 for study sites of the Xiangxi River network.

	JC01	JC02	XX01	XX02
TN (mg/L)	0.90 (0.42–1.52)	0.97 (0.36–1.78)	0.67 (0.32–1.148)	0.97 (0.66–1.79)
NO ₃ -N (mg/L)	0.80 (0.17–1.37)	0.87 (0.22–1.63)	0.56 (0.24–0.92)	0.87 (0.39–1.57)
NH ₄ -N (mg/L)	0.04 (0.01–0.16)	0.04 (0.01–0.16)	0.06 (0.01–0.27)	0.05 (0.01–0.28)
TP (mg/L)	0.01 (0.01–0.04)	0.02 (0.01–0.12)	0.03 (0.01–0.08)	0.03 (0.02–0.11)
PO ₄ -P (mg/L)	0.01 (0.006–0.030)	0.013 (0.002–0.1)	0.027 (0.008–0.110)	0.025 (0.010–0.070)
SiO ₂ (mg/L)	2.45 (1.48–5.08)	3.256 (2.008–9.43)	2.62 (0.97–4.15)	3.09 (2.29–4.54)
WT (°C)	12.26 (2.72–21)	14.49 (6–23.1)	12.63 (4.2–23.70)	14.62 (17.22–22.00)
Cond (us/cm)	208.20 (118.60–267.00)	233.60 (185.60–297.00)	169.20 (120.40–266.00)	203.70 (159.10–288.00)
pH	8.35 (6.93–9.27)	8.54 (7.15–9.54)	8.52 (6.91–9.17)	8.16 (7.11–8.84)
Velocity (m/s)	0.24 (0.03–1.03)	0.35 (0.08–0.7333)	0.33 (0.04–2.48)	0.35 (0.08–0.70)
Discharge (m ³ /s)	0.1853 (0.0002–2.7832)	0.2149 (0.0012–1.1636)	0.5021 (0.0013–3.6790)	1.3684 (0.0148–5.1295)

Table 2. Diatom taxa with mean relative abundance >1% at each site.

Taxon	JC01	JC02	XX01	XX02	Mean
<i>Coccconeis placentula</i> Ehrenberg	40.1	42.5	30.9	31.0	36.1
<i>Achnanthidium minutissimum</i> (Kützing) Czarnecki	26.5	19.2	30.5	20.3	24.1
<i>Coccconeis pediculus</i> Ehrenberg	1.3	13.7	7.9	5.8	7.2
<i>Achnanthidium lineare</i> Smith	1.3	2.8	4.2	13.8	5.5
<i>Reimeria sinuate</i> (Gregory) Kociolek & Stoermer	8.3	2.4	1.2		4.0
<i>Gomphonema intricatum</i> Kützing	2.2	3.6			2.9
<i>Achnanthidium deflexum</i> (Reimer) Kingston	2.2	2.0	3.2	4.3	2.9
<i>Gomphonema parvulum</i> var. <i>subellipticum</i> Cleve	2.1	2.3	4.6	2.1	2.8
<i>Tetracyclus rupestris</i> (Kützing) Grunow	2.6				2.6
<i>Gomphonema intricatum</i> var. <i>pumilum</i> Grunow	2.1	1.4			2.0
<i>Melosira varians</i> Agardh			1.9	2.0	1.9
<i>Diatoma vulgaris</i> Bory				1.9	1.9
<i>Cyclotella meneghiniana</i> Kützing	2.2		1.4		1.8
<i>Gomphonema angustatum</i> (Kützing) Rabenhorst			1.7		1.7
<i>Encyonema silesiacum</i> (Bleisch) Mann				1.4	1.4
<i>Fragilaria capucina</i> Desmazières				1.3	1.3
<i>Amphora pediculus</i> (Kützing) Grunow	1.3				1.3
<i>Aulacoseira granulata</i> (Ehrenberg) Simonsen			1.2	1.0	1.1

var. pumilum was close to the summer and winter groups. *Gomphonema parvulum* var. *subellipticum* was located in the overlapping part of the spring and summer groups. Similarly, *Achnanthidium deflexum* and *Cyclotella meneghiniana* were located in the overlapping part of each seasonal group at the tributary sites. In JC02, *Gomphonema intricatum* was located

in the overlapping part of spring, summer and winter groups. *Achnanthidium lineare* also more frequently appeared in summer and winter. *Achnanthidium deflexum* and *Gomphonema intricatum* var. *pumilum* mostly appeared in summer and *Gomphonema parvulum* var. *subellipticum* usually occurred in summer, autumn and winter. In XX01, *Gomphonema*

Table 3. Proportion of variance explained (adjusted R^2) by significant principal coordinates of neighborhood matrices (PCNM) variables for benthic diatom assemblages from January 2011 to December 2016 at each site.

Name	Period	Site			
		JC01	JC02	XX01	XX02
1	72	2.8	3.0	6.9	1.1
2	51		1.7	2.8	1.9
3	37			1.2	1.1
4	30	1.8	1.7	1.4	
5	25			1.0	
7	18	2.8	2.4	2.4	
8	16			1.1	
10	14		1.7		1.1
11	12	4.5	2.7	1.6	1.3
12	11	2.1	1.8	2.4	2.2
13	10			1.3	
14	10				1.1
15	9			1.8	
16	9				1.1
18	8				1.9
19	7	1.8		1.1	
20	7	1.0		1.1	
21	7				1.1
23	6	1.8			1.1
24	6	1.0		1.0	
27	5		1.2		
28	5	1.1			
29	5			3.1	
31	5		2.4		
32	4	1.8			
35	4	1.0			
1–12 month periodicities	16.1	8.1	13.2	9.7	
13–24 month periodicities	2.8	4.1	3.5	1.1	
25–36 month periodicities	1.8	1.7	2.4	0.0	
37–48 month periodicities	0.0	1.2	0.0	1.1	
49–60 month periodicities	0.0	1.7	2.8	1.9	
61–72 month periodicities	2.8	3.0	6.9	1.1	
Total		23.6	19.9	28.8	14.9

parvulum var. *subellipticum* appeared in all seasons; while, *Aulacoseira granulata* and *Gomphonema angustatum* appeared in spring and autumn. *Cyclotella meneghiniana* only appeared in summer, and *Melosira varians* appeared in spring, autumn and winter. In XX02, *Melosira varians* appeared in all seasons, and *Gomphonema intracatum* var. *pumilum* appeared in all seasons but spring. In contrast, *Encyonema silesiacum*, *Diatoma vulgaris* and *Gomphonema parvulum* var. *subellipticum* only appeared in summer, autumn and winter, respectively.

Nine to fourteen site-specific PCNM variables were selected as significant time variables in RDA, explaining 14.9% (XX02) to 28.8% (XX01) of variance in algal community (Tab. 3). Among selected PCNM variables, PCNM 1, 11, and 12 (with cycle periodicities of 72, 12, and 11 months, respectively) were important at all sites (Tab. 4). Generally, algal dynamics were principally

Table 4. Proportion of variance explained by each significant RDA axis for benthic diatom assemblages from January 2011 to December 2016 at each site.

Site	1	2	3	4	Total
JC01	43.3	18.2	12.8		74.3
JC02	46.7	25.8	11.5		84.0
XX01	38.1	21.9	14.5		74.5
XX02	29.7	19.1	14.3	10.9	74.0

characterized by intra-annual fluctuations that PCNMs with periodicities <12 months totally explained 8.1–16.1% of community variation. By comparisons, PCNM variables having periodicities of 13–24 months, 25–36 months, 37–48 months, 49–60 months and 61–72 months accounted for 1.1–4.1%, 0.0–2.4%, 0.0–1.2%, 0.0–2.8% and 1.1–6.9% of explained variance in diatom community dynamics, respectively.

Three to four site-specific significant RDA axes were detected, which totally accounted for 74% (XX02) to 84% (JC02) of variance in diatom assemblages (Tab. 4, Fig. 2). Among these significant axes, RDA1 accounted for >30% to explained variance in diatom assemblages in all sites, with additional ~20% attributed to RDA2. In contrast, RDA3 and 4 individually contributed ~10%.

Although only 25.9% (XX01) to 31.3% (XX02) of diatom taxa displayed time-related dynamics within whole communities (Supplementary Tab. 2), the identified RDA taxa groups displayed distinct temporal dynamics (Fig. 3, Supplementary Fig. 2). For JC01, RDA1 taxa group had the lowest mean relative abundance in July while RDA2 taxa group was most abundant in this month. Considering JC02, RDA1 and RDA2 taxa groups were more abundant in winter to spring and summer to autumn, respectively. RDA1, RDA2, and RDA3 taxa groups in XX01 were more abundant in winter, spring and summer, respectively. RDA2, RDA3, and RDA4 taxa groups in XX02 also reached their peaks in different seasons (Fig. 3).

3.3 Environmental drivers for temporal dynamics of diatom assemblages

Although different environmental variables were important to temporal dynamics of individual RDA taxa groups in the same site, some variables were more influential than others (Tab. 5). Conductivity, TN, and pH were important to temporal dynamics of RDA taxa groups in 3 sites, and water temperature, discharge and SiO₂ affecting algal dynamics in 2 sites. By contrast, NH₄-N and TP were only important to one taxa group in one site.

Each of important environmental variable displayed various influences on temporal dynamics of RDA groups (Fig. 5, Supplementary Fig. 6). For instance, positive relationships were observed between conductivity and relative abundance of most RDA groups in most sites; while, it displayed a negative influence on RDA4 taxa group in XX02. TN also had positive effects on relative abundance of most RDA taxa groups; however, relative abundance of RDA3

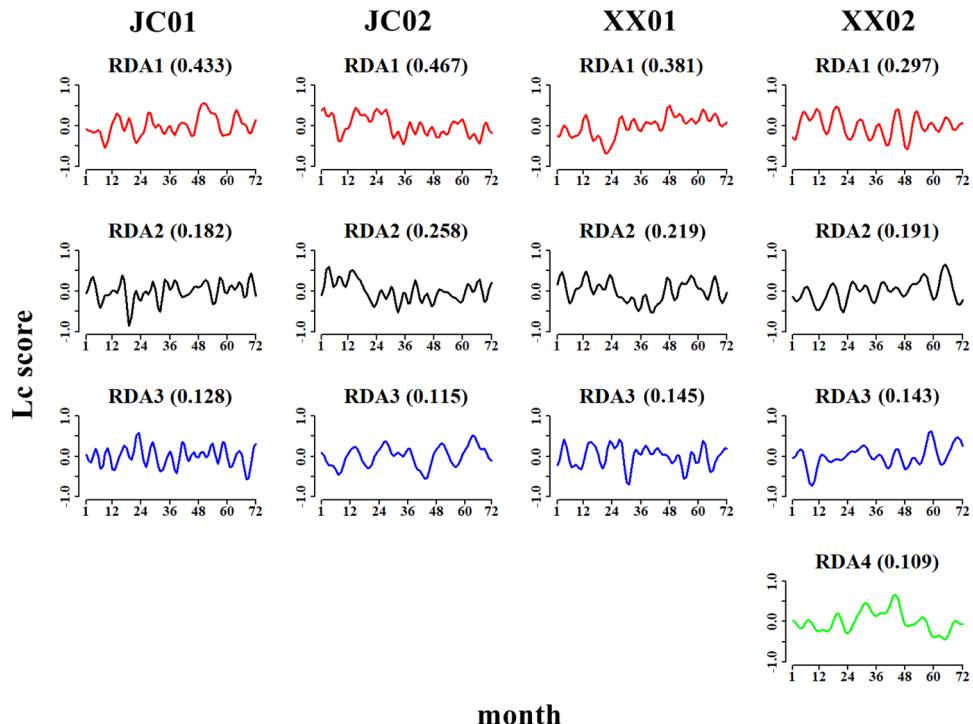


Fig. 2. Linear combination (Lc) score plots summarizing temporal trajectories revealed by individual significant canonical axes in RDA-PCNM models of each site in Xiangxi River (Red-1; Black-2; Blue-3; Green-4).

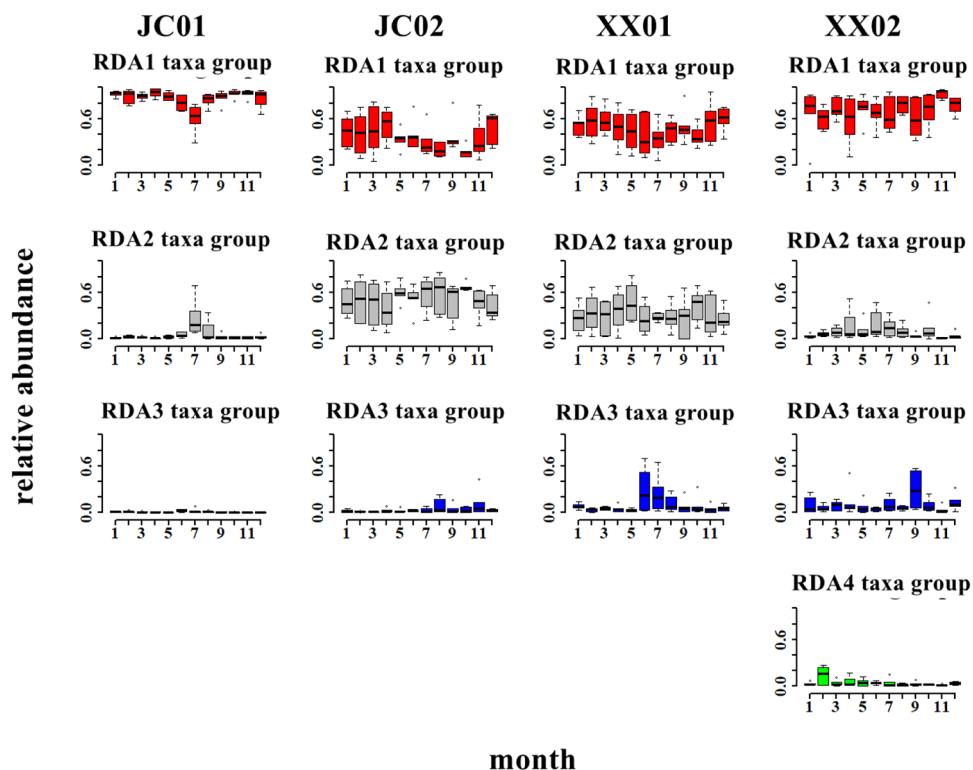


Fig. 3. Intra-annual dynamics of relative abundance of each significant RDA taxa group in each site (Red-1; Black-2, Blue-3, Green-4).

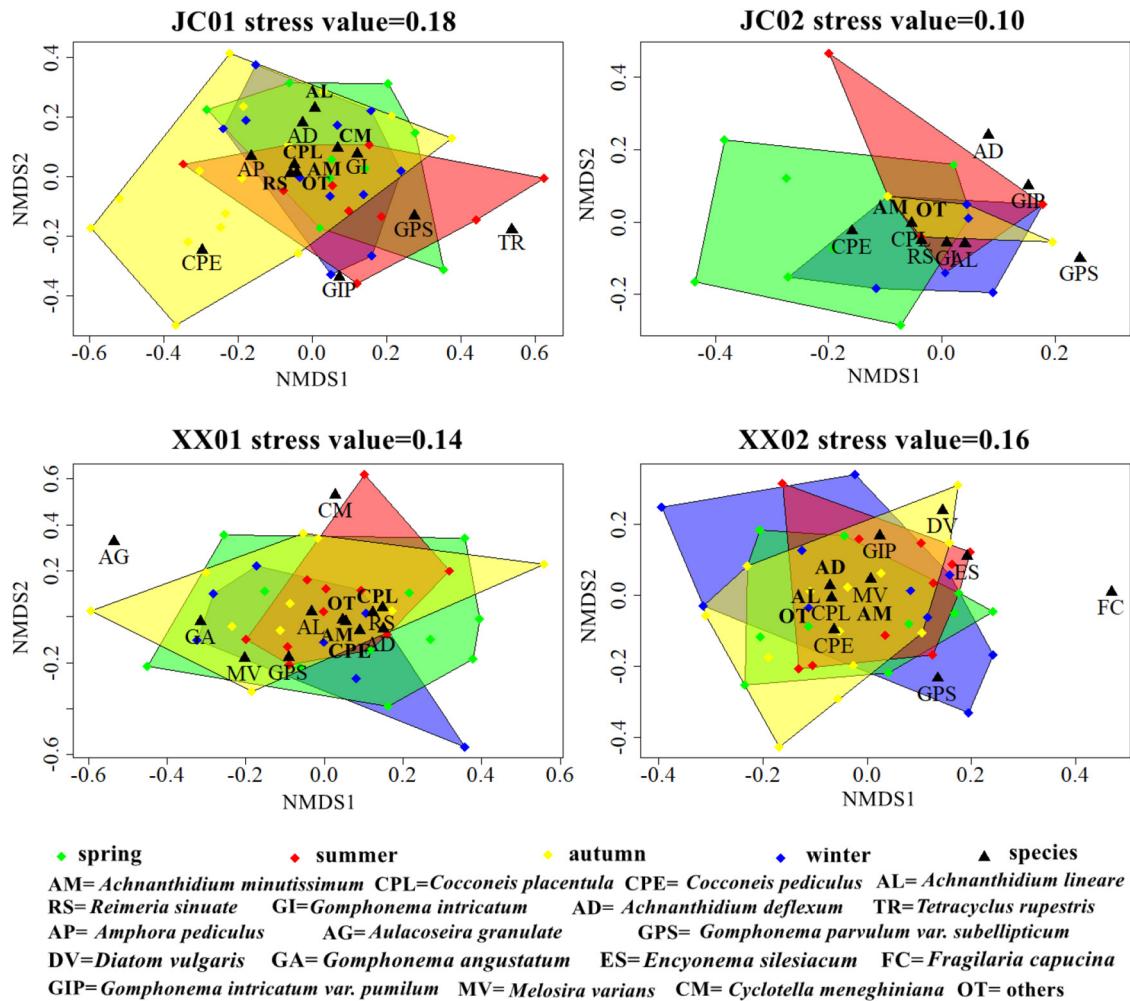


Fig. 4. Nonmetric multidimensional scaling (NMS) ordination of benthic diatom assemblages (presence/absence) of 72 months at 4 sites in Xiangxi River.

taxa group in XX01 decreased along TN gradient. As for pH, more complicated effects were observed that relative abundance of RDA groups monotonically increased, decreased, increased first then decreased or decreased first then increased when pH increased.

4 Discussion

We identified multiple-scale temporal dynamics in the 4 benthic diatom communities from the Xiangxi River network. Three main reasons could have contributed to these patterns: (1) Differences exist in the intrinsic growth rates of species in the same diatom community, as well as in their life cycles (Pouličková et al., 2020). (2) Diatom community is composed of species with various environmental optima; therefore, these species do not respond to environmental fluctuations in the same way (Stevenson, 2014). (3) Temporal dynamics of diatom assemblages may be driven by environmental variables having different fluctuation periodicities. Climate variables usually fluctuate seasonally while water quality variables vary from impulsive fluctuations to long-term periodicities. For instance, SiO₂ and conductivity fluctuated seasonally

while TP, NH₄-N and pH varied impulsively (Labbe and Fausch, 2000).

Intra-annual dynamics dominated temporal variation in benthic diatom communities. This is not surprising as the Xiangxi River watershed has a monsoonal climate, with distinct seasonal changes (Yang et al., 2000). The seasonal changes in environmental conditions including the flow regime, air temperature and riparian vegetation cover, will affect growth and population succession of diatoms, and eventually shape temporal dynamics of diatom communities (Hu and Jiang, 2003; Jia et al., 2008; Tang et al., 2016). Our results of PCNM-RDA also suggested that benthic diatom community in Xiangxi River was a relative stable system that can fluctuate around the equilibrium positions when subjected to environmental perturbations (Ives and Carpenter, 2007). Our results were inconsistent to the findings of Tang et al. (2016), which indicated that relative long-term (12–34 months) fluctuations were more important to diatom communities. The inconsistency is likely due to the difference in data length between the two studies. Tang et al. (2016) used a 42-month long time series, which inferred 10 PCNM variables representing different temporal periodicities. By comparison, a 72-month long time series was used and 35 PCNM variables

Table 5. Important physical and chemical predictors selected by generalized additive mixed models for temporal dynamics of RDA-taxa groups at each site.

Site	RDA-taxa group	Predictors	d.f.	F	P value	R^2_{adj}
JC01	2	pH	2.05	4.20	0.022	0.21
	3	TN	1.00	7.27	0.010	0.31
		Cond	3.00	5.93	0.002	
JC02	1	WT	1.00	8.41	0.005	0.11
		Cond	1.00	4.14	0.047	
	2	WT	1.00	11.65	0.001	0.18
		Cond	1.00	5.54	0.022	
	3	discharge	1.00	10.48	0.002	
		TN	1.00	5.41	0.023	0.13
		discharge	1.00	7.23	0.009	
XX01	1	NH ₄ N	1.00	4.11	0.047	
		TN	3.42	4.66	0.033	0.31
	2	pH	1.00	6.22	0.016	
		TN	1.00	4.25	0.045	0.23
	3	pH	1.00	7.01	0.011	
		SiO ₂	2.34	5.75	0.006	0.57
	4	TN	4.21	12.65	0.000	
		discharge	2.28	3.46	0.036	
XX02	1	pH	2.90	3.08	0.024	0.25
	2	SiO ₂	3.85	2.89	0.021	0.21
	3	Cond	1.80	4.71	0.015	0.56
		TP	1.85	6.14	0.003	
	4	pH	3.93	10.60	0.000	
		WT	4.17	11.28	0.000	0.61
		Cond	1.00	9.93	0.003	
		pH	2.12	4.90	0.010	

were inferred in the present study. It is likely that the longer time series data facilitates modelling intra-annual dynamics in the present study because more replicates in such relative short-time dynamics were involved.

Temporal dynamics differed among species groups, which is the result of different responses of species groups to environmental fluctuations. As for conductivity, different species in the diatom community has unique conductivity optima (Potapova and Charles, 2003). In the present study, most species in RDA1 taxa in JC02 site and RDA3 taxa in XX02 have high optima conductivity while conductivity optima for species of RDA3 taxa in JC01 and RDA4 taxa in XX02 are low. The demand and utilization rate of nutrients as well as the ability to resist high flow disturbance among species are diverse (Passy, 2007), so are their responses to changes in flow and nutrient concentrations. The present study found that the relative abundance of RDA3 taxa in JC01, RDA3 taxa in JC02, RDA1 taxa in XX01 and RDA2 taxa in XX01 increased with changes in total nitrogen concentrations, which means that these groups adapt to the environment with rich nutrition (Rimet and Bouchez, 2012). However, species in RDA3 taxa prefer the environment with low nutrient concentration (Rimet and Bouchez, 2012). The diatom species in the community respond differently to the change of pH (Passy, 2006). This indicates that optimum pH values of different species are different. In JC01, some species of RDA2 taxa are alkalophilic species, such as *Gomphonema* sp.

and *Cyclotella meneghiniana* (Van Dam *et al.*, 1994). Similarly, some species in RDA1 taxa group of XX01 and RDA4 taxa of XX02 are alkalophilic species, such as *Gomphonema* sp., *Amphora pediculus*, *Melosira varians*, *Gyrosigma attenuatum* and *Suriella minuta* (Van Dam *et al.*, 1994). While RDA1 taxa, RDA3 taxa and RDA2 taxa in XX01 are circumneutral or acidophilic (*e.g.*, *Encyonema perforatum*). In JC02, the increase of discharge had negative or positive effects on RDA2 taxa and RDA3 taxa. This means that RDA2 taxa was vulnerable to flood erosion, while species in RDA3 taxa could tolerate relatively high flow and make good use of nutrients brought by flow (Davie and Mitrovic, 2012). Responses of different diatoms species to water temperature fluctuations are distinct for that species have disparate optimum growth temperatures (Singh and Singh, 2015). In addition, changes in other nutrients (NH₄-N and TP) also affected some taxa. Under influences of these environmental factors, different species groups have independent temporal dynamics and various seasonal patterns.

Our results are consistent with the predictions of FMC, that is, asynchronous fluctuations exist in temporal dynamics of species within communities that persist under environmental fluctuation conditions (Shimadzu *et al.*, 2013; Thibaut and Connolly, 2013). This is reasonable for that fluctuations of various environmental factors can provide a competitive advantage period for different species groups, thus generating independent temporal fluctuations among species groups

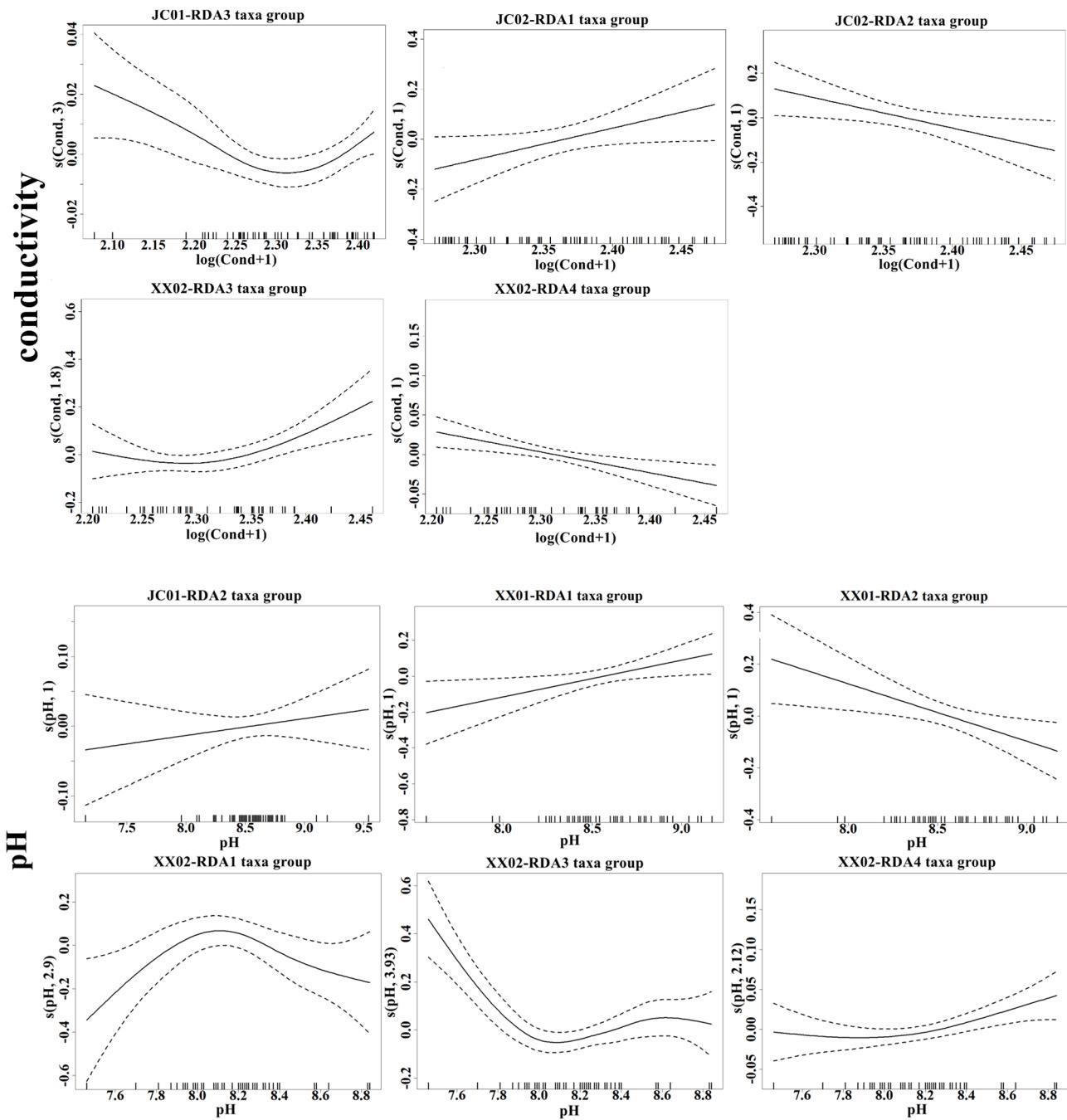


Fig. 5. Generalized additive mixed models showing influences of conductivity, pH and TN on the relative abundance of each RDA taxa group at each site. The area within the dotted lines indicate the approximate 95% confidence intervals for the fitted functions (LOESS). The tick marks inside the panels on the x-axis show the distribution of the observed values for the two covariates. The numbers in brackets on the y-axis are the effective degrees for each smoother. Responses of each RDA taxa group to important predictors were provided in supplementary Figure 6.

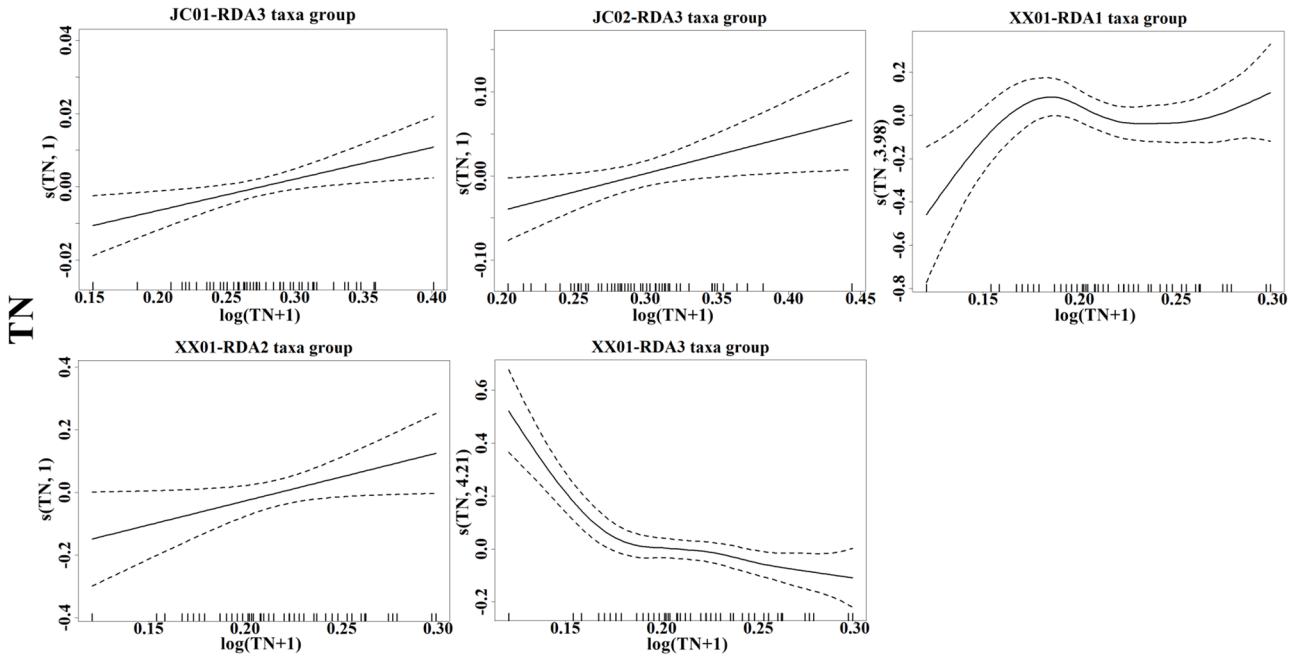


Fig. 5. Continued.

(Chesson, 2000) and independent fluctuations of different species groups buffered fluctuations of the whole community (Thibaut and Connolly, 2013).

In conclusion, intra-annual dynamics dominated temporal variation in benthic diatom communities. This is a result of community's adaptation to seasonal fluctuations in local environmental conditions. Meanwhile, we suggest that long-term monitoring data are greatly valuable in studying multiple-scale temporal dynamics within the biological communities because such dataset can improve the sensitivity and accuracy of the multivariate time series models.

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Supplementary Material

Supplementary Tables S1 and S2.
Supplementary Figures S1 to S6.

The Supplementary Material is available at <https://doi.org/10.1051/limn/2020020>

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