

Multi-scale temporal dynamics of epilithic algal assemblages: evidence from a Chinese subtropical mountain river network

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Abstract Research on multi-scale temporal dynamics of lotic algal assemblages remains scarce. In this study, we analyzed epilithic algae sampled monthly from a Chinese subtropical mountain river network from 2004 to 2007, by using a multivariate time series modeling approach. We hypothesized that (1) multi-scale temporal dynamics exist within algal communities; (2) physical and chemical conditions drive algal temporal dynamics; and (3) tributary sites differ in algal temporal changes. This study revealed 2–4 site-specific algal temporal dynamics, contributed by 23–45% component taxa. Among the time-related taxa, percentages of high profile guild taxa were higher than both the low profile and the motile guild

taxa. Several algal temporal dynamics were found to be driven by water temperature, conductivity, or current velocity, within which influences of conductivity at two sites resulted in directional changes in algal communities. Furthermore, tributary sites differed in algal temporal changes when compared to the two mainstream sites. Our findings imply that natural fluctuations and agricultural disturbance together shaped algal temporal dynamics in the studied river network. In conclusion, for accurately tracking algal temporal dynamics, we recommend that long-term and high-frequency biomonitoring protocols are developed. Moreover, both the mainstream and tributary sites should be monitored simultaneously.

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Introduction

Temporal dynamics of algal assemblages are frequently addressed in stream ecology (Kennen et al., 2012; Miller et al., 2012) because such studies form an important foundation for answering other complex questions, such as ecological stability mechanisms, succession trends, or disturbance responses of lotic algal assemblages (Angeler, 2009; Angeler et al., 2010; Virtanen et al., 2011; Baho et al., 2012; Schneck

& Melo, 2013). Numerous studies have revealed that temporal variability of lotic algal assemblages is the results of interactions among biological traits (e.g., resistance, resilience, reproductivity ability, etc.) and environmental factors (e.g., nutrients, irradiance, hydrodynamic regimes, predatory pressures, etc.) (Rosemond et al., 2000; Soininen & Eloranta, 2004; Yang et al., 2009; Graba et al., 2013). Algal short-term dynamics usually involve two phases: the first, accrual phase, which is driven by immigration/colonization and exponential growth, and the second, loss phase, which is dominated by processes of death, emigration, sloughing, and grazing (Biggs, 1996). During short-term dynamics, algal structures are controlled primarily by nutrients supply (Passy & Larson, 2011). Considering intra-annual and inter-annual dynamics, algal biomass and biodiversity display distinct seasonal cycles, and community composition changes among seasons and years (Miller et al., 2012; Tan et al., 2014). Long-term fluctuation tendencies of algal assemblages are synchronous with temporal nutrient dynamics and hydrological and climatic regimes (Reid et al., 2006; Korhonen et al., 2013).

Hitherto, most studies on temporal dynamics of algal assemblages focus on community metrics such as biomass, richness, or biodiversity indices (Rosemond et al., 2000). Temporal patterns of community composition (represented by taxa abundance data) or temporal turnover (represented by similarity/dissimilarity matrices of community compositions across different sampling times) is also frequently addressed by treating algal community as a single metric (Passy, 2006; Korhonen et al., 2010, 2013). However, algal assemblages are composed of species possessing diverse biological characteristics and distinct environmental optima (Stevenson, 2014). These species differ in body size, attachment ability, growth rate, dispersal ability, population abundance, and sensitivity/tolerance to disturbances (Virtanen et al., 2011). Therefore, it is reasonable to expect that different temporal dynamics among algal species will exist within the whole community. That is, some species will exhibit short temporal fluctuation dynamics, and some species will have relatively long fluctuation periodicities. In contrast, some species within the same community will display stochastic, time-unrelated dynamics. Species-specific temporal dynamics are essential for sustaining a dynamically stable algal community because asynchronously temporal variability among

species can buffer environmental stress and fluctuation effectively. Disentangling multiple temporal scales of variability patterns within a community, namely multi-scale temporal dynamics (Legendre & Gauthier, 2014), can provide especially useful information on temporal changes of an algal assemblage. Such process-oriented research can elucidate temporal dynamics of algal communities more comprehensively than previous studies, which is especially important if we are curious about the stability mechanisms of lotic algal communities under changing environments or determining contributions of component species to temporal dynamics of the whole algal community. However, research on multi-scale temporal dynamics within lotic algal assemblages remains scarce.

In the present study, we applied a multivariate time series modeling approach to research multi-scale temporal dynamics within epilithic algal assemblages, which were sampled monthly from five sites of one Chinese subtropical mountain river network from 2004 to 2007. Three hypotheses are to be tested: (1) Multi-scale temporal dynamics exist within algal communities, and contributions of ecological guilds to algal dynamics will differ. (2) Several physical and chemical variables are important driving forces for algal temporal dynamics. (3) Algal assemblages from different tributaries will differ in temporal evolution.

Materials and methods

Study region

The Xiangxi River is a tributary of the Three Gorges Reservoir in Hubei Province of China. The river is 94 km long with three main tributaries, the Jiuchong, Gufu, and Gaolan River (Wang et al., 1997). This mountain watershed is located in a subtropical climate region characterized by hot and rainy summers and cold and dry winters, with a mean annual air temperature of 16.9°C (range: 5.5–27.7°C) and precipitation of 900–1,200 mm (Tang, 2003). Woodland is the dominant land use in the catchment, with a few towns and farmland distributed along the riverside (Seeber et al., 2010).

Five sites were selected within the whole river network, with two sites located in the mainstream (xx1 and xx2, following the water flow direction) and one

site in each of the three tributaries (named jc, gf, and gl, respectively) (Fig. 1). For these sites, there was no visible human disturbance in the stream or riparian zone of the sample reaches during the study duration. However, stream water quality of these sites might be influenced by agricultural activities in upstream catchments, especially in rainy seasons.

Algal data

Epilithic algae were sampled monthly from September 2004 to June 2007. Three to five moveable stones (with a diameter range of 15–60 cm) were randomly selected at each site during each sampling occasion. The sampling area was confined using a circular lid (radius: 2.7 cm). For each stone, the surface within the lid was vigorously scrubbed using a nylon brush and rinsed 3–4 times with distilled water. All subsamples from each site were combined into one composited sample and its volume was recorded. The algal sample was preserved with 4% formalin for further identification and enumeration.

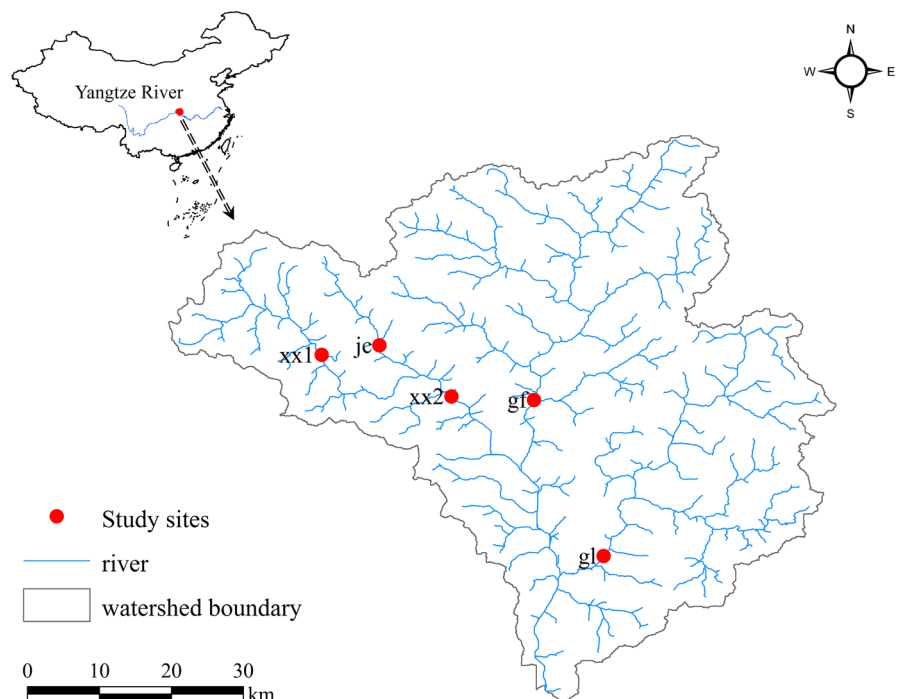
In the laboratory, soft algae were first identified to the lowest possible taxonomic level (most to genus) and counted, using a 0.1-ml counting chamber at 400× magnification under a compound microscope

(Olympus CX21: Olympus Optical Co., Japan). All diatoms were grouped into one category during this process. Subsequently, species-level identification and enumeration of diatoms were conducted, after the sample was acid cleaned and slide mounted at 1,000× magnification with an oil immersion objective (Hu & Wei, 2006). At least 500 valves were counted for each sample, and relative abundance was calculated for each taxon. Algal identification was based on Patrick & Reimer (1966, 1975), Jao (1988), Qi (1995), Li & Bi (1998), Shi (2004), and Zhu (2007).

Physical and chemical variables

At each site, conductivity and water temperature (WT) were measured by using an Environmental Monitoring System (HORIBA W23: Horiba Co., Japan). Wetted width and water depth were measured using a tape measure and current velocity with a current flow meter (LJD type, Chongqing hydrological instruments factory, China). A 600 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, the acidified water sample was partitioned into two parts. One part was used to measure concentrations of TN, TP, and SiO₂

Fig. 1 Locations of the study sites in the Xiangxi River network



on a Skalar segmented flow analyzer (Skalar Analytical B.V., The Netherlands) following the user manual. The other part was used to measure alkalinity using the titration method following the national water monitoring protocol (Chinese NEPA, 2002). Summary for physical and chemical variables is presented in Table 1.

Statistical analyses

To make the results comparable among the five sites, data collected in November 2006 and April and May 2007 were excluded from analysis because several sites were not sampled in these months. Therefore, the time vector is composed of 31 months (i.e., 34 continuous sampling months from September 2004 to June 2007, in which data for three discrete months were excluded).

All analyses were performed with R software (version 3.0). Each site was analyzed separately. Time variables were firstly produced by using the principal coordinate of neighbor matrices (PCNM) approach, which converts the linear time vector (31 months) into various frequency sine waves representing nonlinear and independent fine to broad temporal scales (Borcard & Legendre, 2002; Borcard et al., 2004; Angeler et al., 2009). Although this method is more frequently used in spatial analysis, it is also competent to disentangle temporal structures within multivariate data (Angeler et al., 2011; Legendre & Gauthier, 2014). Ten PCNM variables were obtained in the case of our study. Redundancy analysis (RDA) was then applied to detect relationships between algal relative abundance and PCNM variables (RDA-PCNM) (Borcard et al., 2011), accompanied by forward selection procedures for selecting important PCNM variables (Blanchet et al., 2008; Tang et al., 2013b). RDA was re-run with selected PCNM variables, and significant RDA axes were identified by the Monte Carlo permutation test (with 9,999 times). The linear combination scores (lc scores) on each significant RDA axis are the coordinates of the algal community on each sampling occasion in the space of selected PCNM variables (Borcard et al., 2011), representing a special temporal trend. Therefore, the number of significant RDA axes represents the number of distinct temporal dynamics within the whole community (Angeler & Johnson, 2012). Since RDA axes are orthogonal to each other, temporal dynamics revealed

Table 1 Summary of physical and chemical variables (mean with the range in parentheses) from September 2004 to June 2007 for study sites of the Xiangxi River network

	xx1	xx2	jc	gf	gl
Wetted width (m)	9.1 (2.6–38.0)	15.3 (3.6–36.0)	7.1 (4.3–11.2)	17.9 (4.6–70.0)	19.2 (9.4–35.0)
Water depth (m)	0.24 (0.13–0.56)	0.30 (0.10–0.78)	0.35 (0.12–0.73)	0.32 (0.15–0.57)	0.43 (0.13–0.80)
Velocity (m s ⁻¹)	0.52 (0.19–1.21)	0.67 (0.22–1.41)	0.48 (0.12–1.17)	0.86 (0.19–1.66)	0.71 (0.12–1.79)
WT (°C)	13.82 (3.90–24.33)	14.84 (5.50–25.50)	13.25 (3.80–22.40)	15.59 (9.00–21.10)	15.70 (8.14–25.71)
TN (mg l ⁻¹)	0.80 (0.32–1.55)	0.90 (0.42–2.04)	0.78 (0.24–1.68)	1.22 (0.40–2.29)	1.10 (0.34–2.71)
TP (mg l ⁻¹)	0.04 (0.02–0.06)	0.03 (0.01–0.15)	0.03 (0.01–0.33)	0.03 (0.01–0.07)	0.04 (0.01–0.10)
SiO ₂ -Si (mg l ⁻¹)	3.94 (0.04–7.66)	3.59 (0.36–7.76)	3.42 (0.33–5.96)	3.82 (0.44–6.35)	5.37 (0.53–8.33)
Conductivity (μS cm ⁻¹)	233.5 (25.5–383.0)	239.0 (16.0–414.0)	253.8 (22.9–498.0)	311.2 (26.8–470.0)	293.6 (25.4–538.0)
Alkalinity (mg l ⁻¹)	123.12 (90.09–160.16)	144.31 (90.09–240.24)	151.99 (60.06–190.19)	173.67 (90.09–210.21)	154.62 (120.12–252.25)

WT water temperature

by RDA-PCNM are independent from each other (Angeler & Johnson, 2012). RDA-PCNM was performed with function ‘quick PCNM’ in PCNM package (Legendre et al., 2010a). Algal relative abundance data were Hellinger transformed prior to analysis to avoid problems caused by Euclidean distance (Legendre & Gallagher, 2001).

Correlation between raw relative abundances of each taxon and modeled temporal trends (lc scores of algal assemblages on each significant RDA axis) was analyzed by using Spearman rank correlation with a test of significance. Taxa that significantly correlated with a specific temporal trend composed of one distinct taxa group.

Generalized additive mixed model (GAMM) was applied to examine the relationship between physical and chemical variables and each temporal dynamic of algal communities for each site. GAMM is competent to model relationships by using smooth function, where the shape of the relationship between response and predictor is not known a priori (Zuur et al., 2009). In addition, GAMM can account for temporal autocorrelation of model residuals, which is evident in our data (detected by function ‘acf’). Water temperature, current velocity, TN, TP, SiO₂, conductivity, and alkalinity were predictor variables, with a response variable of lc scores of the algal community on specific significant RDA axis. Cubic regression spline was used to fit fixed effect for each predictor, with cross-validation determining the optimal amount of smoothing. Temporal autocorrelation structure in residuals was fitted with the auto-regressive model of order 1 (Zuur et al., 2009). Because *P* values for each smoother estimated from GAMM are approximate, only predictors with *P* < 0.001 were selected as significant ones. Prior to fitting, all the predictor variables were examined for extreme values and collinearity following the steps suggested by Zuur et al. (2010). Variables were log₁₀ (*x* + 1) transformed when extreme values were detected. GAMM was fitted using function ‘gamm’ in package ‘mgcv’ (Wood, 2014).

We further detect correlations between ecological guilds and physical and chemical variables to confirm algae–environment relationships. That is, algal taxa were assigned to one of the three ecological guilds: high profile guild, low profile guild and motile guild following Passy (2007) and Passy & Larson (2011). Spearman correlations between percentage of each

ecological guild and physical and chemical variables that used in GAMM were analyzed for each site, and significance of correlations was tested. Moreover, we compared difference in percentages among ecological guilds for time-related taxa that appeared in the taxa groups. Considering that number of taxa groups differed among sites and many taxa appeared in more than one group at each site, we combined all the time-related taxa for each site and then calculated percentages for each ecological guild. Differences between percentages of the three guilds across all the sites were compared using one-way ANOVA.

Finally, a two-way ANOVA model was applied to compare the differences of time series of algal relative abundance data among the 5 sites. Because there is no replication for individual sites on each sampling occasion, our dataset belongs to an un-replicated (each site) repeated-measures (sampling time) design. Following classical statistical theory, a test of the space–time (S–T) interaction is impossible due to lacking of degree of freedom (Zar, 1999). Legendre et al. (2010b) proposed a new method that codes space or time using PCNM variables to economize on the degree of freedom, which makes tests on the effects of S, T, and S–T interactions all possible. We adopted this method to our data by using PCNM variables representing time factor. This analysis was conducted with TSI models in ‘PCNM’ package, in which ANOVA Model 5 was selected due to its accurate assessment of Type I error and powerful detection of S–T interactions compared with other models (Legendre et al., 2010b). Since this method only provides general results when more than two sites are included, pairwise comparisons were then performed given that significant S–T interactions among all the five sites existed.

Results

A total of 219 algal taxa, comprising 190 Bacillariophyceae, 16 Chlorophyceae, 13 Cyanophyceae, and 1 Xanthophyceae, were identified during the study. The number of taxa ranged from 144 (jc) to 163 (xx1 and gf), with mean value of 157. *Rossithidium linearis* (Smith) Round & Bukhtiyarova and *Cocconeis placentula* Ehrenberg were predominant species, occurring in all sites and all months, with mean relative abundance of 43.9 and 14.0%, respectively. The other

8 frequently occurring taxa (with mean relative abundance >1%) included *Achnanthes lanceolata* (Brébisson ex Kützing) Grunow (6.2%), *Oscillatoria* sp. (3.9%), *Stephanodiscus minutulus* (Kützing) Cleve & Möller (3.3%), *Achnantheidium minutissimum* (Kützing) Czarnecki (2.5%), *Eunotia* sp. 1 (2.0%), *Diatoma vulgare* Bory (1.8%), *Navicula cryptocephala* Kützing (1.2%), and *Synedra ulna* (Nitzsch) Ehrenberg (1.1%).

Three to six site-specific PCNM variables were selected as significant time variables in RDA (Table 2). Algal dynamics in most sites were related to PCNM1–5 in which PCNM1 and 5 were important to the all sites. PCNM1 represented a nearly finished fluctuation during the study duration (34 months) (Supplementary Fig. 1). PCNM2 displayed unimodal dynamic with an approximate 24-month periodicity. PCNM3–5 had periodicities of approximately 18, 16, and 12 months, respectively. In contrast, PCNM6 and 7, with fluctuation periodicities of ~10 months, only contributed to algal dynamics in 1–2 sites. These significant PCNM variables totally explained 10% (xx1) to 32% (gl) of variation in algal abundance (Table 2).

RDA-PCNM detected 2–4 significant RDA axes, indicating site-specific number of time-related taxa groups (Fig. 2). The dynamics associated with the first two taxa groups were most important for all the sites, which contributed on average 53 and 21% of explained variation in algal community compositions, respectively. The patterns associated with the third and

fourth taxa groups each explained approximately 12 and 10% of the explained variation in the algal community compositions (Table 3). Additional analysis detected significant S–T interactions among study sites ($R^2 = 0.21$, $F = 1.587$, $P < 0.001$). Pairwise comparisons further showed that algal communities differed in temporal changes among tributaries, while the difference between xx1 and xx2 was not significant (Supplementary Table 1).

Among all observed algal taxa, 23% (xx1) to 45% (gl) contributed significantly to temporal dynamics of the whole community (Supplementary Table 2). Each time-related taxon associated with one or more taxa groups, in which more than half of the taxa were associated with the first taxa group (Supplementary Table 3). Water temperature was the unique significant predictor for four temporal dynamics of algal assemblages in site xx2, jc and gl. Conductivity was important to the first temporal dynamic of xx1. The third temporal dynamic of site gf was highly related to both conductivity and current velocity (Table 4).

Similar to GAMM results, temporal dynamics of ecological guilds were also significantly correlated to WT, conductivity, or current velocity (Supplementary Table 4). Considering time-related taxa, the percentages of high profile guild taxa (with the mean value of 46.0% for the all sites) was significantly higher than that of the low profile (mean: 29.3%) and the motile guild taxa (mean: 24.7%) ($F_{2,12} = 10.38$, $P = 0.002$).

Discussion

Multi-scale temporal dynamics of algal communities and driving forces

Multi-scale temporal dynamics within lotic epilithic algal communities were observed in our study. For xx1 and xx2, algal dynamics were dominated by relatively long temporal trends (with periodicities >12 months); in contrast, relative short temporal trends (with periodicities <12 months) were also important to jc, gf, and gl. This result indicates that temporal trends of algal assemblages differed among mainstream and tributaries sites. Curves displaying lc scores of algal communities along time axis on significant RDA axes fluctuated in amplitudes and frequencies (Fig. 2); therefore, it is difficult to draw distinct fluctuation cycles. Additionally, we did not find directional trends

Table 2 Percentage of variance explained (adjusted R^2) by significant principal coordinates of neighborhood matrices (PCNM) variables for epilithic algal relative abundance data from September 2004 to June 2007 at each study site of the Xiangxi River network

PCNM variable	Site				
	xx1	xx2	jc	gf	gl
1	3.3	9.7	2.7	8.5	10.7
2		4.0	9.1	3.6	7.8
3	3.3	3.3	2.9		
4		2.8	6.0	2.5	4.3
5	3.8	7.4	2.9	5.5	4.8
6					4.7
7			2.5	3.4	
Total	10.4	27.3	26.1	23.5	32.4

Fig. 2 The linear combination scores (lc scores) of algal communities on the space of significant principal coordinates of neighborhood matrices (PCNM) variables along the temporal axis for each study site of Xiangxi River network (the red dotted line represents the equilibrium line where the lc score = 0)

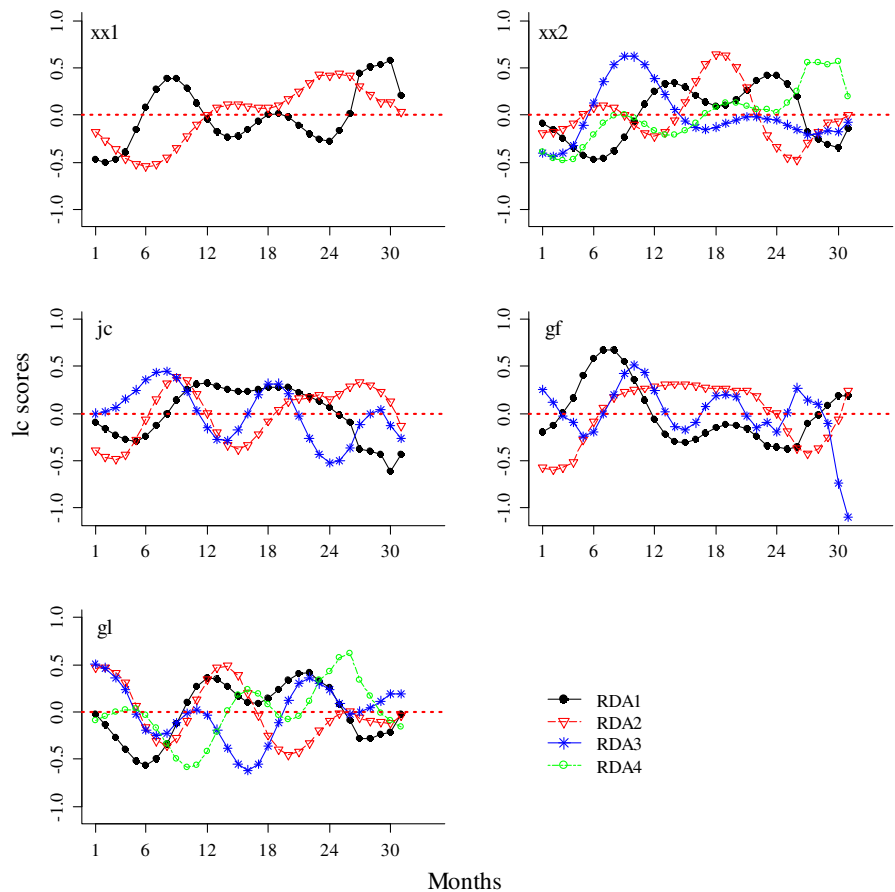


Table 3 Proportion of variance explained by each significant RDA axis for epilithic algal relative abundance from September 2004 to June 2007 at each site of the Xiangxi River network

Site	Proportion of variance explained			
	RDA1	RDA2	RDA3	RDA4
xx1	52.1	36.8		
xx2	53.1	20.0	12.3	10.8
jc	51.8	16.3	11.2	
gf	45.2	21.4	15.1	
gl	62.4	12.7	10.8	9.0

in most curves. It implies that temporal dynamics of algal assemblages in Xiangxi River network were not dominated by any single periodic factor or external process during the study duration. Since PCNM1 was important to all sites, some observed temporal patterns may be parts of long-term periodic dynamics.

Less than 50% of taxa were found to contribute to temporal dynamics of algal assemblages, and the ten dominant taxa (with mean relative abundance >1%) all appeared in time-related taxa groups of more than three sites (Supplementary Table 3). This finding indicates that only small part of taxa within algal assemblages had time-related dynamics, and abundant taxa were highly possible to contribute to such dynamics. Owing to inadequate autecological information, it is difficult to interpret why these taxa displayed time-related dynamics. However, when they were categorized into ecological guild groups, a clearer trend was discovered. We found that nearly half of time-related taxa belonged to the high profile guild, indicating that this ecological guild was an important intrinsic trait in shaping temporal dynamics of algal assemblages. This can be attributed to the fact that the high profile taxa have relatively low growth rates, lower dispersal, and smaller population size due to their tall stature, compared to the low profile guild

Table 4 Important physical and chemical predictors for temporal dynamics of algal assemblages (represented by linear combination scores on each significant RDA axis) for each study site of the Xiangxi River network selected by generalized additive mixed models

Site	RDA	Predictor(s)	df	<i>F</i>	<i>P</i> value	R_{adj}^2
xx1	1	s(conductivity ^a)	1.00	14.127	0.0014	0.212
xx2	1	s(WT)	1.00	18.176	0.0003	0.018
jc	3	s(WT)	1.00	14.552	0.0009	0.332
gf	3	s(conductivity ^a)	3.17	26.008	0.0001	0.894
		s(velocity)	1.00	31.542	0.0007	
gl	1	s(WT)	1.00	35.557	<0.0001	0.198
	3	s(WT)	1.00	14.725	0.0009	0.139

^a $\text{Log}_{10}(x + 1)$ transformed

(Passy, 2008; Virtanen et al., 2011). The high profile taxa consequently are more susceptible to flow-related disturbances and prefer relative nutrient-rich conditions, resulting in more distinct temporal patterns than those of the low profile guild taxa. The motile guild taxa can escape from unfavorable environments owing to their mobility (Stevenson & Bahls, 1999), and therefore had the lowest proportion in time-related taxa groups. Our results imply that ecological guilds are good indicators for algal temporal dynamics. Stenger-Kovács et al. (2013) also drew similar conclusions in research on Hungarian streams (but see Virtanen et al., 2011).

Multi-scale temporal dynamics of algal communities in the present study were mainly determined by WT, conductivity, and current velocity. Water temperature is an essential driving force for most algal autecological traits such as enzymic activities, photosynthetic processes, growth rates, interactions among species, etc. (DeNicola, 1996; Allan & Castillo, 2007). Periodical fluctuations of solar radiation induce temporal variability of stream water temperatures. Correspondingly, taxa-specific temperature optima cause different temporal dynamics within the entire algal community. In addition to WT, conductivity also was another influential environmental factor. Conductivity, indicating total ionic concentrations in river water, influences algal physiologic and biochemical processes. Also, each algal taxon has specific optimum for conductivity (Potapova & Charles, 2003; Philibert et al., 2006). Therefore, algal responses to temporal changes in conductivity concentration of stream water were also taxa specific, resulting in different temporal dynamics among algal communities. Lastly, current

velocity also showed significant influence on algal temporal dynamics. Algal taxa with different morphological forms and attaching capabilities prefer or tolerate specific current velocity conditions (Tornés et al., 2015). Temporal changes in hydrodynamic conditions induce different algal temporal dynamics.

These important physical and chemical variables, however, only had an influence on six within the 16 observed algal temporal dynamics. This finding can be explained in two ways. First, we set a conservative *P* value of 0.001 in GAMM analysis following the suggestion of Zuur et al. (2010) because this method only provides an approximate estimation for the significance of each independent variable. This borderline excluded several variables with margin *P* values between 0.05 and 0.001. Second, several likely important environmental variables have been omitted due to procedural limitations. For example, climatic and water flow fluctuations may affect temporal patterns of algae (Hering et al., 2010; Tang et al., 2013a). However, such variables are difficult to characterize for each site in this remote mountain river network with only one gauge station and one meteorological station. Simulated values from watershed modeling technique may be an appropriate remedy for these parameters. Moreover, pH is also an important environmental variable for algal pattern (Andrén & Jarlman, 2008; Smucker & Vis, 2011), but this variable was excluded in our analysis due to insufficient data. Obviously, the development of more robust and flexible approaches to analysis that can handle missing values is needed in the future for more accurate modeling of temporal monitoring data.

Potential implications in stream biomonitoring

Our findings have several applied implications. First, variations in *lc* scores of algal communities on each RDA axis can be used to identify whether the assemblages have been impacted by anthropogenic disturbances when the information on influential environmental variables is also considered. Directional changes of *lc* scores along a time axis indicate that variations in community composition are mainly driven by human disturbance. Conversely, if there is no directional change of *lc* scores, the data suggest that environmental effects are minor (Angeler & Johnson, 2012). In our study, most *lc* scores fluctuated around the equilibrium line (*lc* score = 0), implying that algal assemblages were mainly influenced by natural variation. However, the difference between the beginning and ending *lc* scores of *xx1* on RDA1 and of *gf* on RDA3 is relatively large. Subsequent GAMM analysis suggests that conductivity had a significant influence on these *lc* scores. Because agricultural activities in the watershed often increase conductivity of stream water (Potapova & Charles, 2003), this parameter is commonly used as an indicator of agricultural disturbance. We hence infer that agricultural activities in the watershed had partly changed algal temporal dynamics of *xx1* and *gf*. We can therefore see that RDA-PCNM, accompanied with other statistical techniques (GAMM in our study), can be used to determine which environmental forces have driven directional changes of algal assemblages, which is unobtainable when using other temporal analysis methods, such as time-lag analysis (Collins et al., 2000; Kampichler & van der Jeugd, 2013).

Furthermore, important PCNM variables with distinct fluctuation frequencies can be detected by using RDA-PCNM, which can be used to quantify monitoring duration and frequency (Angeler et al., 2009). For example, PCNM1 indicated that our study duration of 34 months was inadequate for detecting algal temporal dynamics completely, and a longer monitoring period should be employed in future studies. In addition, PCNM6 and 7 suggested the shortest fluctuation frequency (~10 months) of algal assemblages in the three tributary sites, which is informative for setting sampling frequency. To capture the complete process of the shortest fluctuation, the minimum sampling frequency should be every ~3 months (at the beginning, middle and ending time of the

frequency). To obtain algal temporal dynamics more accurately, the sampling frequency may less than 3 months. A more frequent sampling schedule, such as monthly in our study, is even better for characterizing fluctuation processes of algal communities with greater accuracy.

Finally, results of RDA-PCNM and S–T interaction tests are helpful for selecting locations of monitoring sites. We found that algal assemblages at the mainstream sites (*xx1* and *xx2*) had similar fluctuation dynamics in the study duration. However, algal assemblages from the three tributary sites changed distinctly. We thereby suggest simultaneous sampling of both mainstream and tributary sites in algae-based stream monitoring.

In conclusion, time series modeling is an effective approach for disentangling multi-scale temporal dynamics within lotic epilithic algal assemblage. The discovered temporal dynamics imply that the algal assemblages of the Xiangxi River network were influenced by both natural fluctuations and directional changes driven by agricultural disturbance. To effectively track variation processes of algal assemblages from fine to broad scales, we recommend a long-term monitoring duration (3 years minimum) with a high monitoring frequency (i.e., monthly). Moreover, both the mainstream and tributaries sites should be monitored simultaneously.

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