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Periphytic algal communities are highly influenced by substrate types in small pond, not large floodplain lake

Baogui Liu[a,b], **Wei Wang**[b], **Kuimei Qian**[c], **Jinying Xu**[d], **Xia Liu**[e], **Jiayi Wu**[b], **Yuwei Chen**[f,*], **Guoxiang Wang**[b,*]

[a] School of Geography, Nanjing Normal University, Nanjing 210023 China
[b] School of Environmental, Nanjing Normal University, Nanjing 210023 China
[c] Xuzhou University of Technology, Xuzhou 221000 China
[d] Key Laboratory of Poyang Lake Environment and Resource Utilization of Ministry of Education and School of Resources, Environmental & Chemical Engineering, Nanchang University, Nanchang 330031 China
[e] State Key Laboratory of Lake Science and Environment, Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences, Nanjing 210023 China
[f] Nanchang Institute of Technology, Nanchang 330099 China

*Corresponding authors, e-mail: 976370923@qq.com, wangguoxiang@njnu.edu.cn

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ABSTRACT: Periphyton sampling in hydrologically flexible regions is costly because of diverse substrates and fluctuating inundation time. It remains an open question whether periphytic algae samples in floodplain lakes may be obtained by sampling some representative natural substrates instead. To obtain the answer, algal biomass, richness, diversity, and community compositions were compared on 9 types of substrates in two investigations: in a small concrete pond and in the Poyang Lake, a large floodplain lake. Results in the pond showed that the algal Shannon index and species number on *Potamogeton crispus* and withered *Typha orientalis* were substantially higher than those on *T. orientalis* in March; the algal biomass on *T. orientalis* was considerably lower than that on the other substrates in June. Conversely, no significant differences in periphyton communities were found between substrate types in the Poyang Lake. However, the redundancy analysis revealed that water depth (positively related to the colonization time) plays a key role in shifting the algal community in the Lake. Thus, our results suggest that for a precise estimation of primary production, species richness, community composition, and ecological status assessment in large floodplain ecosystems, periphytic algae must be sampled not only on adequate substrate types but also on different depth gradients.

KEYWORDS: attached algae, community structure, temporal pattern, floodplain

INTRODUCTION

Periphytic algae play an important role in shallow freshwater ecosystems [1] and are recognized as an excellent indicator of water quality changes [2]. Periphytic algal ecology has gained considerable interest among researchers [3], but little is known about the algae in floodplain systems. Given that substrates are diverse and inundation time fluctuates with seasons, periphyton sampling in floodplain lakes is labour-intensive, time-consuming, and expensive. To reduce the cost of sampling, periphytic algal diversity was obtained by sampling some representative natural substrates or artificial substrates with similar shapes. However, this hypothesis is still controversial [4] because determining whether or not values of metrics collected from different substrates can be compared is important [5].

Periphyton abundance, diversity, species richness, and community composition on different substrates have been intensively compared in field studies in the past decades [3, 4, 6]. Biofilms growing on artificial substrates showed that the sampling time and site had significant effects on the abundances of associated bacteria [7]. Studies in one site, or more, within a small water body [6] concluded that substrate specificity affects the periphytic algal community. Conversely, studies in relatively large lakes [8] or between lakes [9] found that substrate characteristics seem to be of minor importance [5, 8]. Besides, colonization by periphytic algae follows a predictable temporal pattern: first by low-profile diatoms, followed by long-stalked and large-rosette diatoms, and finally by filamentous green algae. A large enclosure experiment showed that periphytic biomass and nutrient state were sensitive to incubation time [10]. Similarly, a field experiment demonstrated that the contribution of autotrophic biomass decreased as total biomass increased over time [11]. Few studies, however, have analyzed the effect of substrate types for large floodplain lakes, and the results show that the colonization time of the algae is positively related to the water depth.

The time of colonization was related to disturbances or water level provided by flood pulses in floodplain lakes. For example, submerged macrophytes have the longest colonization time, and emergent macrophytes only inundate periodically during high water level season [12]. In addition, rocks at littoral sites of the river (approximately 0.5 m underwater surface) have the shortest colonization time [5]. The relative importance of substrate types and colonization time, however, has been rarely considered. We

infer that colonization time which is related to water level variation could be more important than substrate types in the development of the periphyton community. Compare with studies conducted in experimental conditions, the relationships between host substrates and associated microalgae in natural freshwater ecosystems are largely unknown [13].

This study compared periphytic algal biomass, diversity, and community composition on different kinds of natural substrates in a concrete pond and a large floodplain lake. We hypothesized that the periphytic algal communities are influenced by the substrate types in the small pond, but water depth (positively related to the colonization time) would play a major role in manipulating the periphytic algal community in the large floodplain lake.

MATERIALS AND METHODS

Sampling process

We performed two investigations: one in a small concrete pond and another in a large floodplain lake (Fig. 1). The pond (length × width × depth = 15 m × 4 m × 3 m) had three cascade slopes and been installed in the Lake Poyang Laboratory for Wetland Ecosystem Research (116.06 E, 29.45 N), and it was designed to imitate the wetland ecosystem of Lake Poyang. The sediments and water in the pond were transported from this lake. During the study period, the incubation time was artificially controlled by fixing the water level. We pumped water into the pond when the water level starts arising (in February 2015) in Lake Poyang; at this time *Potamogeton crispus* and *Typha orientalis* start to germinate and grow; and at the same time withered plants from the last year were being inundated. We sampled periphytic algae with three replicates in the pond firstly in March (2015) (sampled substrates on: PC, *P. crispus*; TO, *T. orientalis*; and TO_d, withered *T. orientalis* with one-month incubation and short colonization time) and then in June (2015) (sampled periphyton on substrates: PC, *P. crispus*; TO, *T. orientalis*; PCs, *P. crispus* var. small leaves; and PW, *P. wrightii* with four-month incubation and long colonization time). The pairwise comparisons of periphytic algal biomass and diversity on different substrates were used to examine the effects of substrate types. The comparison of periphytic algal community on the same substrates but with different colonization times was used to test the effects of colonization time.

We also sampled periphytic algae on four substrates in Lake Poyang (Fig. 1). We sampled algae attached on *Vallisneria* sp. (Va) at sites L1–L4; on *Carex* sp. (Ca) and *Zizania* sp. (Zi) at sites F1, F3, and F4; and on rocks (Ro) at sites R1–R4. Meanwhile, samples for water chemistry analysis were collected. Water depth was measured using a Speedtech SM-5 Portable Depth Sounder (SpeedTech Company, Montana, USA). Water transparency was measured using a Secchi disk. Water temperature, dissolved oxygen, pH, and conductivity were measured in situ with a Hydrolab DataSonda 5 Multiprobe (Hach Company, Loveland, Colorado, USA). Total values of nitrogen, nitrate, ammonia, phosphorus, and orthophosphate were measured according to standard methods by the "American Public Health Association" [14].

Determination of periphyton and data analysis

The "Standard methods for the examination of water and wastewater" [14] and the limnological investigation methods for the periphyton community were used as the basic references. To minimize sampling loss of loosely attached algae, substrates with developed periphyton were always cautiously collected. We bathed whole substrates with periphyton in distilled water and stored them in plastic bags, and the bags were taken to the laboratory in dark coolers. Epiphytes on aquatic plants were sampled from 25 cm apical shoots to 20 cm bottom shoots of submerged macrophytes and vertically mixed together. Periphyton on fragile leaves was removed using soft brushes followed by ultrasonic washing. Periphyton on rocks was removed using brushes and scalpels [15]. Scraped periphytic algae samples were fixed with Lugol's iodine solution (4% v/v). Scrapings were dispersed by vigorous shaking, a suitable volume was then transferred to a thinner version of the Sedgwick-Rafter or Palmer-Maloney cell, and a strip count was made [14]. Any suspensions in the cell that was too dense to count directly was discarded and replaced with a diluted sample. Species identification and cell density of periphytic algae were performed according to the methods of Hu [16]. Algae were counted from aliquots of three replicates of the same sample taken from each substrate using an Olympus BX41 microscope (Olympus Company, Tokyo Japan) at 100/600x magnification; a minimum of 400 cells was counted. The biomass was converted from cell volume, assuming that 1 mg of fresh-weight biomass was equivalent to 1 mm^3 of volume. The mean cell volume was calculated using the appropriate geometric configurations [17]. The degree of dominance of periphytic algal biomass was calculated as follows: $Y = (n_i/N) \times f_i$, where N is the total biomass of all sites; n_i is the biomass of taxa I; f_i is the frequency of species i occurring in each site. If $Y > 0.02$, then the taxa (species) were defined as the dominant taxa. Diversity was calculated from the biomass data according to the Shannon-Wiener (Shannon) index.

Analysis of variance (ANOVA) was conducted to compare the algal biomass, Shannon index and algal richness of the compared substrates. The data of each group were normally distributed and had a common variance (Levene's test). We computed Tukey HSD (Tukey Honest Significant Differences) for performing multiple pairwise-comparison between the means of groups. Non-metric multidimensional scaling

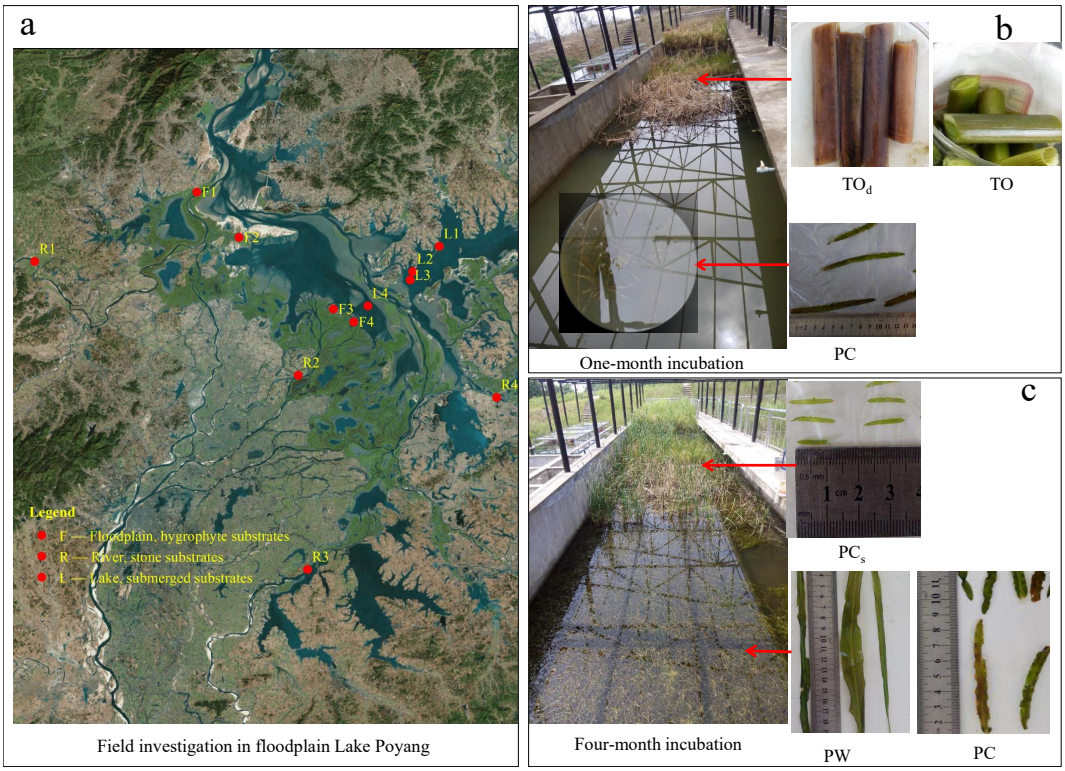

Fig. 1 (a) Sampling sites during the high-water-level season in the Poyang Lake; and (b,c) photographs of the pond and the substrates. (The 9 types of substrates are: PC, *P. crispus*; PCs, *P. crispus* var. small leaves; TO, *T. orientalis*; TO_d, withered *T. orientalis*; PW, *P. wrightii*; Va, *Vallisneria* sp.; Ca, *Carex* sp; Zi, *Zizania* sp.; and Ro, rocks.)

(NMDS) was used to determine whether the composition of periphytic algae differed among substrates; the significance was tested by analysis of similarity (ANOSIM). Redundancy analysis (RDA, because the gradient length on the first axis was lower than 3.0) between the matrix of occurrences of periphytic algal biomass and the most important environmental descriptors selected by forwarding selection was performed in the Poyang Lake. The Shannon index, ANOSIM, NMDS, and RDA were performed in R version 3.4.1 (R Core Team, 2017) with "vegan" package [18]. The relative abundance of the taxon was calculated on the basis of algal biomass.

The periphytic algae were classified into eight functional/ecological groups (Table S1) on the basis of their attachment strategies and growth forms [19]: prostrate or adnate attachment (PM), short stalks (SS), long stalks (LS), rosette or mucilage pads (RMP), filaments (FL), motile (MO), phytoplankton or very loosely attached algae (P), and unknown (U).

RESULTS

Fifty-three periphytic algal taxa were sampled (Table S1), most of which belonged to Chlorophyta (26 taxa), Bacillariophyta (13 taxa), and Cyanobacteria (6 taxa). The percentage of Cyanobacteria biomass was relatively higher in the pond with the long colonization time than in the Poyang Lake; however, no Cyanobacteria was observed with short time colonization. Within the Poyang Lake, the biomass percentage of Bacillariophyta was the highest on *Vallisneria* sp.; Cyanobacteria had the highest biomass percentage on rocks.

The effect of substrates on algal richness, biomass, and Shannon index is significant only in the pond (Fig. 2). With the short colonization time, the algal Shannon index and species number on *P. crispus* and withered *T. orientalis* were substantially higher than those on *T. orientalis*. With the long colonization time, the algal biomass on *T. orientalis* was considerably lower than that on other substrates. RDA analysis, however, showed that water depth (a proxy of colonization times in floodplain) was substantially correlated with periphytic algal community composition in the floodplain lake (Fig. 3).

On the basis of their attachment strategies and growth forms, filament algae were dominant on substrates with long colonization time; whereas adnate or pioneer algae were dominant on substrates with short colonization time (Fig. 4a and Fig. 4b). Compared with those in the pond, the algae in the field

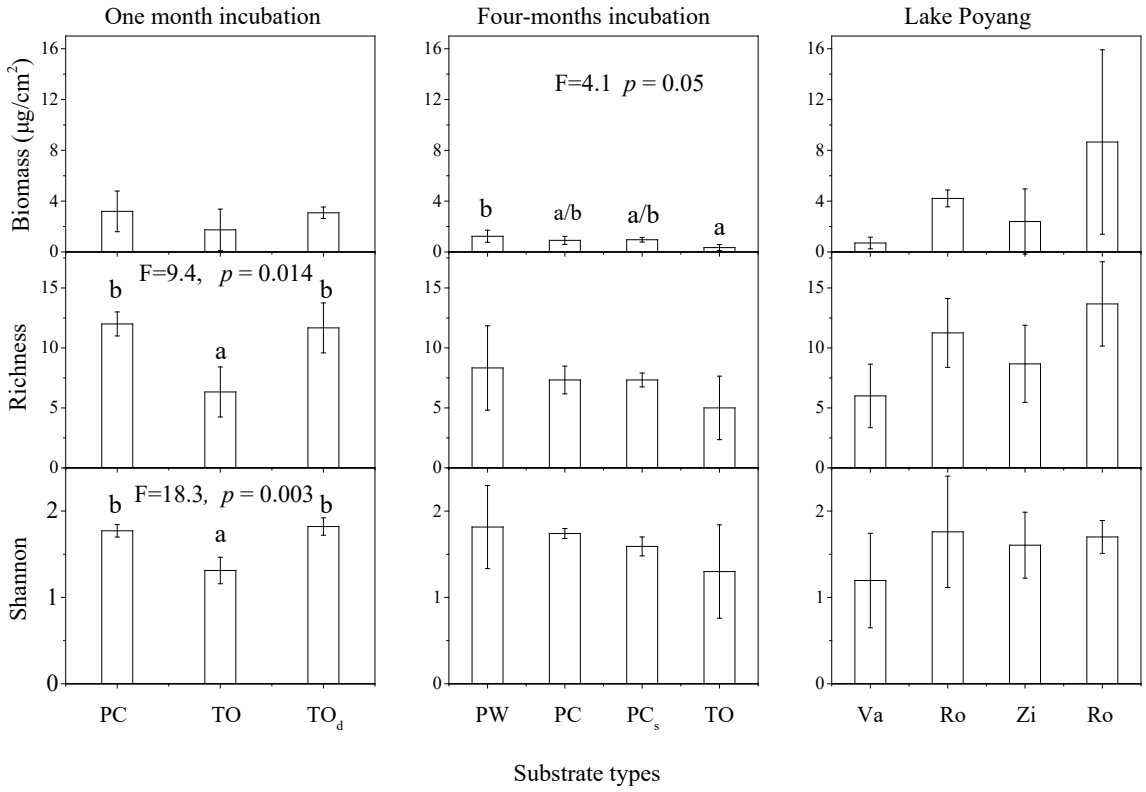

Fig. 2 Comparison of periphytic algal biomass, richness (number of taxon), and Shannon index. (The 9 types of substrates are: PC, *P. crispus*; PCs, *P. crispus* var. small leaves; TO, *T. orientalis*; TO_d, withered *T. orientalis*; PW, *P. wrightii*; Va, *Vallisneria* sp.; Ca, *Carex* sp; Zi, *Zizania* sp.; and Ro, rocks.)

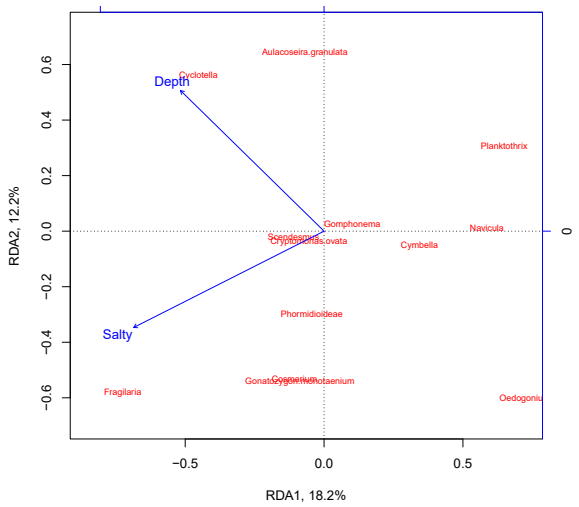

Fig. 3 Redundancy analysis between the matrix of periphytic algal biomass in the Poyang Lake and the two most important environmental descriptors selected by forward selection. Only species occurring more than four times are displayed.

were mostly characterized by communities with strong adhesion abilities (Fig. 4c).

The analysis of NMDS (Fig. 5) showed that substrate types had a remarkable impact on the attached algal taxonomical community only in the pond with long colonization time. Besides, the algal taxonomical community was more similar on substrates with similar architecture, for example, the leaves of *P. crispus* and *P. wrightii*.

DISCUSSION

Our results showed that the substrate's effects on periphytic algal biomass, species number, Shannon diversity, and community structure are highly associated with sampling scale or the colonization time. To our knowledge, few studies have focused on the sampling scale in explaining the effects of substrate types on the periphytic algal community.

In the present study, the results in the pond with long colonization time are consistent with those of previous studies that substrate types have significant effects on periphyton abundance, species richness, and species composition [5, 8, 9]. Live plants may inhibit algal biomass and diversity. In our results, *Typha* spp. may produce volatile oils that can negatively affect the growth of Cyanobacteria *Microcystis aeruginosa* [20] leading to diatoms dominance. Besides,

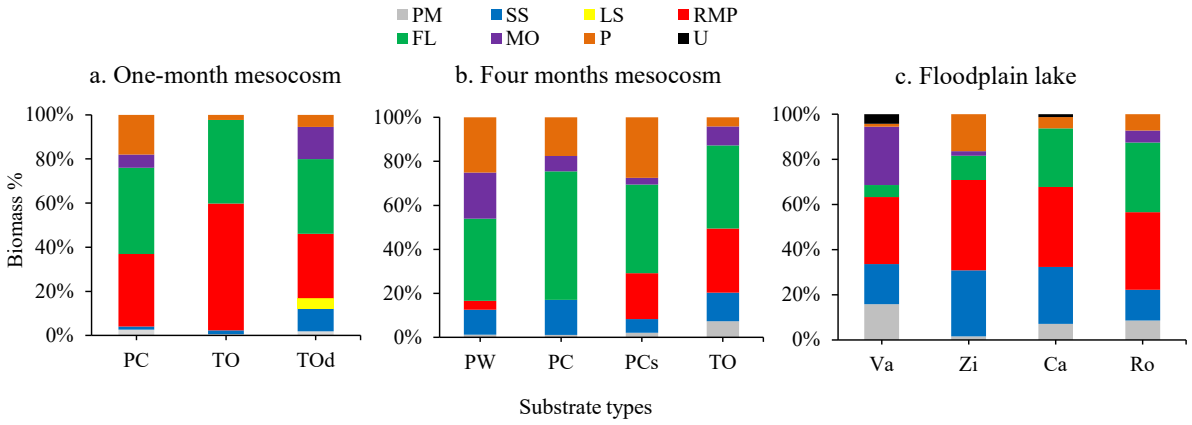

Fig. 4 Ecological groups of periphytic algal community are: PM, prostrate or adnate attachment; SS, short stalks; LS, long stalks; RMP, rosette or mucilage pads; FL, filaments; MO, mobile; P, phytoplankton; and U, unknown. (The 9 types of substrates are: PC, *P. crispus*; PCs, *P. crispus* var. leaves; TO, *T. orientalis*; TO_d, withered *T. orientalis*; PW, *P. wrightii*; Va, *Vallisneria* sp.; Ca, *Carex* sp; Zi, *Zizania* sp.; and Ro, rocks.)

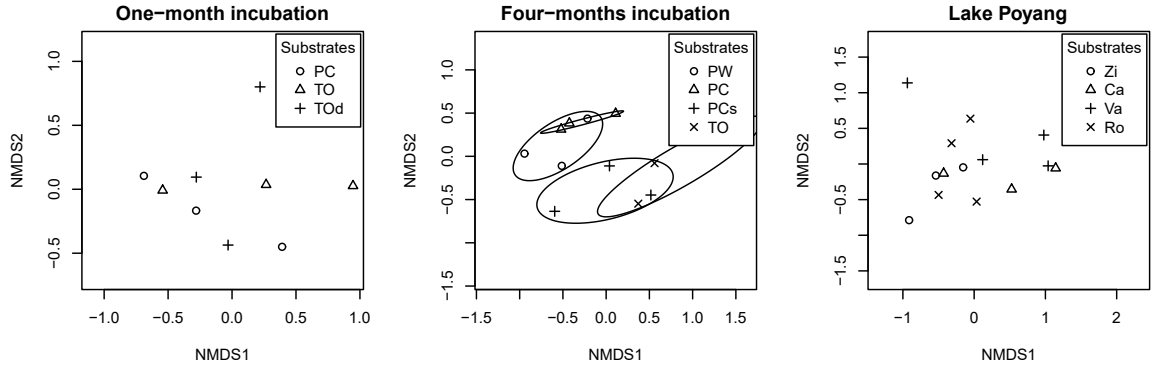

Fig. 5 Non-metric multidimensional scaling analysis of: (a) one-month incubation; (b) four-month incubation; and (c) the Poyang Lake. Ellipses are shown in the figure if the communities between groups are significantly (based on analysis of similarity, Fig. S1) different. (The 9 types of substrates are: PC, *P. crispus*; PCs, *P. crispus* var. small leaves; TO, *T. orientalis*; TO_d, withered *T. orientalis*; PW, *P. wrightii*; Va, *Vallisneria* sp.; Ca, *Carex* sp; Zi, *Zizania* sp.; and Ro, rocks.)

previous studies have revealed that the abundance and composition of periphyton on natural and artificial plants were not statistically different on leaves with a similar morphological architecture [21, 22]. In our study, the algal taxonomical community on the leaves of *P. crispus* and *P. wrightii* were similar, but the biomass and the community structure differed remarkably on different substrates with distinct morphological architectures. However, our results showed that the Shannon diversity and species number of periphytic algae differed remarkably on different substrates only with short colonization time. According to algal attachment strategies [3, 19], pioneer algae with high attachment abilities are the first to colonize the surface of substrates, but most other algae cannot [23]. The differences of attachment ability may explain why the periphytic algal diversity and the number of species showed a considerable difference between substrate types at the preliminary stage. As micro-succession proceeded, the algal diversity and the number of species became more similar to each other, but the host substrates still influenced the algal biomass and community structure [24]. This inference was confirmed by the fact that the biomass ratio of filament algae with long colonization time showed a higher value than that with short colonization time.

Some researchers [6, 25, 26] reported that substrates had a substantial effect on periphyton composition, whereas others reported the opposite [8, 27]. The effects of microhabitats on periphyton are influenced by habitat heterogeneity, thus the interactions between substrate types and the surrounding environments may partly explain the inconsistent conclusions [28]. A probable explanation for this inconsistency is the environmental heterogeneity in the water columns, such as light condition, salinity, and hydrological disturbance [29]. For example, the substrate type effect was diminished by increasing incubation depth [30]. In

general, tightly attached algae constitute over 60% of algal biomass in the Poyang Lake, suggesting that hydrological disturbance had a big effect on the periphyton community in our study. However, distinguishing these factors is difficult because plants and periphyton are intimately tied together [31]. This may explain why there are no remarkable differences that could be found on periphytic algal biomass, richness, or diversity between different substrate types in these types of lakes. Moreover, the RDA analysis indicated that salinity and colonization time (characterized by water depth) are important in shifting the algal community in the Poyang Lake, a result similar to that reported in other lakes [32]. Unlike small pond systems, the pattern of periphytic algae structure can be explained well by colonization time and other surrounding environmental variables instead of substrate types in the Poyang Lake. Floodplain lakes are complex integrated systems with diverse microhabitats and various incubation time for periphyton.

Due to constraints on the steady growth of living natural macrophytes, the length of algae colonization time in this study could not accurately be assessed. Although this limitation didn't affect the conclusions that can be drawn from the findings, more works with artificial substrates, however, are needed to quantitatively assess the effect of substrate type and incubation time on periphyton in the future.

CONCLUSION

The results of this study indicate that periphytic algal communities in the large floodplain lake are influenced by colonization time and the environment of water columns instead of substrate types. Hence, we conclude that to precisely estimate community composition in floodplain ecosystem periphytic algae must be sampled on adequate depth gradients of substrates types.

Appendix A: Supplementary data

Supplementary data associated with this article can be found at http://dx.doi.org/10.2306/scienceasia1513-1874.2022.029.

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Appendix A. Supplementary data

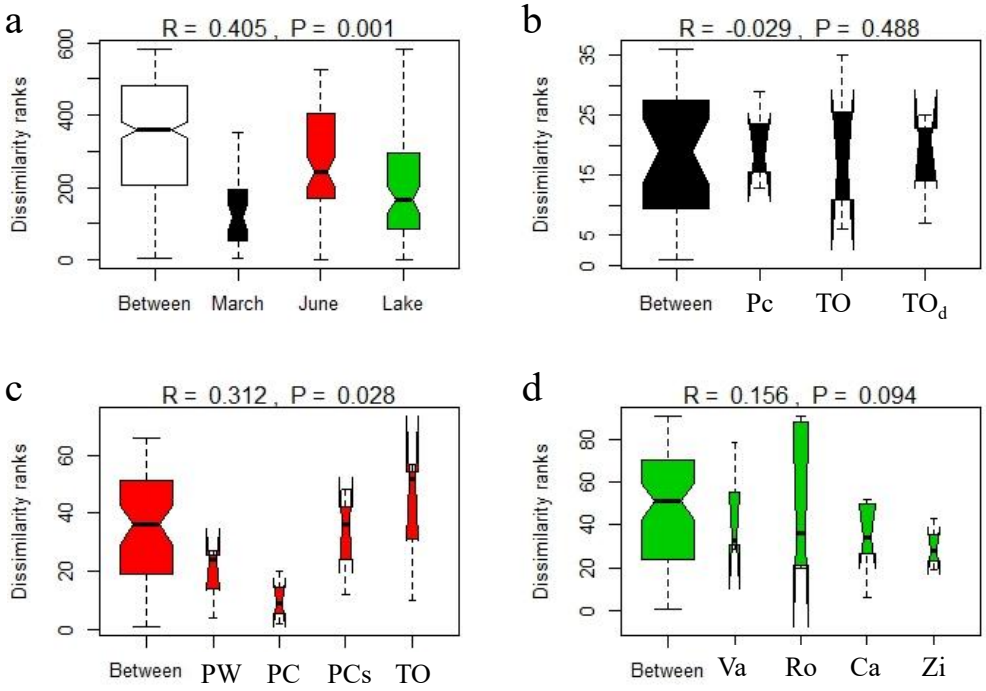

Fig. S1 Analysis of similarity (ANOSIM) between different groups of: (a) all groups; (b) one-month incubation; (c) four-months incubation; (d) Lake Poyang. (The 9 types of substrates are: PC, *P. crispus*; PCs, *P. crispus* var. small leaves; TO, *T. orientalis*; TO_d, withered *T. orientalis*; PW, *P. wrightii*; Va, *Vallisneria* sp.; Ca, *Carex* sp; Zi, *Zizania* sp.; and Ro, rocks.)

Table S1 Algal taxa and their degree of dominance on different substrates. Taxa larger than 0.02 are shown in the table; those lesser than 0.02 are shown by "+". Algal attachment strategies are as follows: PM, prostrate or adnate attachment; SS, short stalks; LS, long stalks; RMP, rosette or mucilage pads; FL, filaments; MO, mobile; P, phytoplankton; and U, unknown. (The 9 types of substrates are: PC, *P. crispus*; PCs, *P. crispus* var. small leaves; TO, *T. orientalis*; TO_d, withered *T. orientalis*; PW, *P. wrightii*; Va, *Vallisneria* sp.; Ca, *Carex* sp; Zi, *Zizania* sp.; and Ro, rocks.)

	One-month incubation			Four-month incubation				Floodplain lake					
Taxa	**PC**	**TO**	**TO_d**	**PW**	**PC**	**PCs**	**TO**	**M**	**Va**	**Zi**	**Ca**	**Ro**	**Colony**
Cyanobacteria													
Anabaena spp.					0.07								FL
Anabaenopsis sp.						0.18	0.08			+	+	+	FL
Oscillatoria spp.										+		+	FL
Planktothrix sp.									0.03	+	+	0.03	FL
Phormidioideae spp.						+				+		+	FL
Microcystis spp.					+								P
Bacillariophyta													
Achnanthes sp.	+	+	0.04	0.07	0.05	0.06	0.13	0.02	+		+		SS
Aulacoseira granulata	+		0.05						0.07	+		+	MO
Aulacoseira granulata var. *angustissima*									+		+		U
Cocconeis sp.									+				PM
Cyclotella spp.			+		+		+		0.06	+	+		PM
Cymbella spp.			0.02		0.04			+	0.05	0.24	0.07	0.12	SS
Eunotia spp.									+		+		PM
Fragilaria spp.	0.33	0.58	0.29	+		0.14	0.10	0.37	0.20	0.40	0.35	0.34	RMP
Gomphonema spp.	+			+					+	0.03	+	+	SS
Gyrosigma sp.	+		+					+				+	PM
Navicula spp.	+	+	+			+		+	+	+	0.05	0.04	PM
Pinnularia spp.	+			+			+	+	+		+		PM
Surirella spp.	0.04												P
Chlorophyta													
Ankistrodesmus spp.	+		+	+	+		+	0.02		+			P
Chlorella spp.				+	+	+		+		+		+	P
Cladophora sp.			+					+			+	0.04	FL
Closterium sp.	+		0.02									+	P
Cosmarium granatum Breb								0.03		+			P
Cosmarium regnellii										+			P
Cosmarium spp.	+	0.02	0.02	0.23	0.13	0.14				0.05	0.03	+	P
Crucigenia spp.										+			P
Eudorina spp.				0.03	0.02								MO
Gonatozygon monotaenium	+	0.02		0.05				+		+	0.03	+	FL
Klebsormidium												+	FL
Mougeotia sp.	0.2	0.16	0.15	0.05	0.16	0.14	0.09			+	0.02		FL
Oedocladium	+	0.02	+										FL
Oedogonium spp.	0.02	0.04	0.02	0.17	0.26	0.07	0.08	0.13	+	0.02	0.07	0.11	FL
Oocystis sp.										+			P
Pandorina spp.												+	MO
Pediastrum duplex										+		+	P
Pediastrum tetras												+	P
Scenedesmus sp.	+						+		+	+		+	P
Schroederia sp.										+		+	P
Spirogyra sp.	0.04	0.03	+		0.04			+		+			FL
Spondylosium sp.	0.03												FL
Staurastrum sp.						0.02		+		+			P
Stigeoclonium sp.			0.06							+	0.02		FL
Tetraedron sp.				+									P
Ulothrix spp.	+							0		+	+	+	FL
Westella spp.			0.03										LS
Zygnema sp.			+										FL
Euglenophyta													
Euglena oxyuris				0.02									MO
Phacus sp.				+				+					SS
Trachelomonas sp.				+									MO
Dinophyta													
Peridinium sp.	+							0.02					P
Cryptophyta													
Cryptomonas ovata	0.03			+		+	0.03	+	0.02	+		+	MO