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Original Research

Can Turbidity-Tolerant Submerged Macrophytes Improve Water Quality in Subtropical Lakes?

Jun Wang[1 #], Chunlei Yue[1 #], Bo Wang[2 #], Hepeng Li[1], Xinyu Miao[2], Yaoyao Fang[1], Xiaomian Zhang[1], Delin Xu[3*]

[1]Zhejiang Academy of Forestry, Hangzhou 310023, China
[2]School of Life Sciences, Nanjing University, Nanjing 210023, China
[3]Nanjing Institute of Environmental Science, Ministry of Ecology and Environment of the People's Republic of China, Xuanwu District, Nanjing 210042, China

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Abstract

The existence of alternative stable states and hysteresis underpinned by positive feedback mechanisms explains why it is often difficult to restore submerged macrophytes in shallow lakes. It is especially difficult to restore water quality of turbid tropical lakes. It has been speculated that transplanting macrophytes tolerant of high turbidity may help the system escape from the turbid state, but systematic assessments are so far largely lacking. Here we conducted a mesocosm transplanting experiment in a shallow lake of subtropical China to mimic macrophyte restoration. We transplanted three common native turbidity-tolerant submerged macrophyte species in shallow-water mesocosms and monitored water quality within one growing season. Our experiment demonstrated that following artificial recolonization, the submerged macrophytes could indeed persist in turbid shallow water. However, the persistence of submerged macrophytes cannot significantly improve water quality, and cannot reverse the ecosystem state of tropical shallow lakes within one growing season. Our results thus provide useful implications to the current lake restoration practices. In real-world situations, it may not be realistic to anticipate rapid restoration through macrophyte transplantation only. Monitoring the long-term effects of macrophyte transplantation is imperative for lake restoration. Our work highlights the need to harness the nuanced hidden complexity for tropical lake restoration and calls for attention to alternative stable states among practitioners of lake management.

Keywords: alternative stable states, ecological restoration, hysteresis, mesocosm experiment, shallow lake

#Authors contributed equally to this paper
*e-mail: xudelin11@163.com

Introduction

Excessive nutrient loading induced by human activities has produced profound impacts on the composition, structure, and functioning of freshwater ecosystems worldwide [1-4]. Eutrophication often leads to massive loss of macrophytes, resulting in a series of cascading effects on biotic and abiotic components of the ecosystems, such as bloom of phytoplankton, loss of zooplankton and carnivore fish, and enhanced sediment resuspension [5-9]. Importantly, these changes may create positive feedback loops that can further amplify the loss of macrophytes. For example, increased phytoplankton biomass and enhanced sediment resuspension can elevate water turbidity, in turn reducing light availability for submerged macrophytes [10-13]. These feedbacks are often sufficiently strong to trap the ecosystems in unwanted degraded states, typically characterized by low biodiversity and poor water qualities [14-17].

Mounting evidence has suggested that alternative stable states underpin the degradation processes of many freshwater ecosystems [18-21]. Along with gradually increasing nutrient loading, freshwater ecosystems such as shallow lakes are likely to undergo abrupt shifts from one stable state (often referred to as "clear water state") to another (often referred to as "turbid water state") when a certain tipping point is crossed. The degraded turbid-water ecosystem states are often difficult to reverse because of the existence of "hysteresis" between the two distinct stable states [22-25]. Mathematically, the existence of alternative stable states is grounded on saddle-node bifurcation, a dynamical system behavior that two equilibria collide and merge to one equilibrium (the bifurcation point) with changing control parameters [26]. During the past decades, the theory of alternative stable states has been becoming increasingly influential, generating many important implications to restoration practices of freshwater ecosystems [27-30].

The existence of alternative stable states and hysteresis underpinned by positive feedback mechanisms explains why it is often difficult to restore the clear water state from the turbid water state of shallow lakes [31]. Much effort seeks to break such "vicious cycles", characterized by positive feedback loops that trap the aquatic ecosystems in a turbid-water state. It has been shown that "shock therapy" based on bio-manipulation through temporarily removing fish from the shallow lakes could amplify restoration success, as in this way sediment resuspension agitated by benthivorous fish can be largely weakened, consequently facilitating the recolonization of macrophytes. The effectiveness of this bio-manipulation approach has been validated mostly for temperate lakes, but it remains uncertain for subtropical and tropical lakes where the turbidity is mainly caused by high algae concentrations. Alternatively, it has been speculated that transplanting macrophytes tolerant of high turbidity may help the system to escape from the turbid state, in the sense that the macrophytes can effectively reduce sediment resuspension, outcompete the phytoplankton, and provide shelters for zooplankton species to avoid fish predation [32, 33]. This approach is expected to work for the restoration of lakes in tropical and subtropical regions, as it has been observed in the field that submerged macrophyte vegetation can often persist in relatively turbid waters with low light availability [34, 35]. However, so far, systematic assessments are largely lacking, hampering our understanding if and to what extent the persistent macrophytes can improve water quality and restore the turbid-water state to the clear-water state in tropical lakes.

To address this gap, here we conducted a mesocosm transplanting experiment in a subtropical shallow lake to mimic macrophyte restoration. We selected three common native turbidity-tolerant submerged macrophyte species and transplanted them in the separated shallow enclosures built in the lake. We monitored water quality on a bi-weekly basis after transplantation. As the first growing season is often the crucial stage of macrophyte restoration, we focused on the effects of macrophyte transplantation on the trajectories of water quality within one growing season. We expect to provide useful implications to large-scale lake restoration practices for the purpose of counteracting the degradation of aquatic ecosystems in tropical regions.

Materials and Mehods

Study Site

Our transplanting experiment was conducted in the Xianshan Lake, Zhejiang Province, Eastern China (119.60°E, 30.89°N), with a surface area of 3.19 km^2. The study site is located in a national wetland park where human disturbances are strictly controlled. The water depth of the study site is 1 m. The mean annual temperature is 16.4ºC, and the mean annual precipitation is 1,045 mm. The dominant native submerged plants include *Vallisneria natans*, *Ceratophyllum demersum*, and *Myriophyllum spicatum*. The studied lake represents a typical subtropical lake in Eastern China that has undergone eutrophication at moderate to high levels. The annual average water clarity (Secchi disk depth) reached a minimum of 0.16 m [36].

Experiment Setup and Data Collection

We designed a mesocosm transplanting experiment in a bay area of the Xianshan Lake, using three submerged macrophyte species as the experimental materials, i.e., *Vallisneria natans*, *Ceratophyllum demersum*, and *Myriophyllum spicatum*. These species have been frequently used as "tool species" for macrophyte restoration in shallow lakes and rivers in southern China, due to their high turbidity tolerance [37-39]. On 4 June 2018, we transplanted the macrophytes in 5 m × 5 m enclosures (small ponds) enclosed by waterproofed polypropylene (i.e., closed-bottom mesocosms) in the water at a density of 100 shoots per m^2. The enclosures were built one month before transplanting. Fish and plants were removed before the experiment. The shoot lengths are controlled at 30 cm. The water depths of 1 m are consistent across all the enclosures. We set up 6 replicates for each treatment (species) and control (without transplantation).

Post transplantation, we collected the water samples on an approximately bi-weekly basis until 5 September 2018, representing an experiment period of 3 months. To avoid the potential influences of precipitation, we collected the water samples on precipitation-free days. We measured the water quality indicators, including pH, dissolved oxygen (DO), Total Nitrogen (TN), Total Phosphate (TP), Chemical Oxygen Demand (COD), and chlorophyll-a (Chla). The water quality indicators were measured using standard methods [40]. pH was measured using a portable pH meter (Leici, PHB-4, Shanghai, China). DO was measured using a portable dissolved oxygen meter (Leici, JPB-607A, Shanghai, China). Total nitrate (TN) and orthophosphate (TP) were measured after digestion with K2S2O8 at 120ºC for 30 minutes. COD was measured by titration with ferrous ammonium sulfate solution after being fully oxidized by potassium dichromate. Chla was measured with a spectrophotometer after extraction from the residue using 90% acetone at 4ºC.

We weighed the biomass of the macrophytes for each treatment at the start and end of the experiment. At the end of the experiment, macrophytes were collected at each pond using a rotatable reaping hook. All macrophytes were cleaned by removing the adhered attachments. We used bibulous paper to dry the plant individuals and then measured their fresh biomass. We also collected the mean daily temperature and precipitation across the experiment period from a nearby weather station with a distance of 10 km to the study site.

Statistical Analyses

We plotted the temporal trajectories of the six water quality indicators across the three-month experiment period for the treatments and control. We used one-way ANOVA with post hoc Tukey HSD to test the differences between the group means. We then fit the temporal trends of the indicators as well as the between-replicate variations using linear models with Theil-Sen estimator. The Theil-Sen estimator is one of the most widely used nonparametric approaches for estimating a linear trend [41]. It has many advantages over non-robust simple linear regression based on least-square methods (for instance, it is insensitive to outliers and is accurate for skewed or heteroskedastic data). The data analyses were conducted with R 4.1.0 [42].

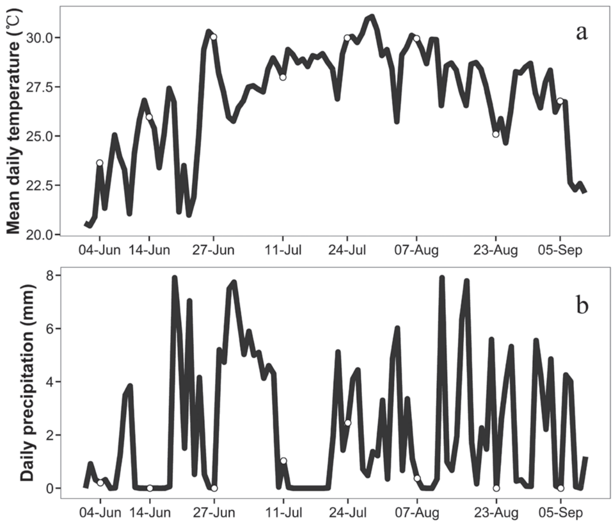

Fig. 1. Mean daily temperature a) and precipitation b) at the study site during the experiment period (between 4 June and 5 September, 2018).

Results

Our transplantation experiment covered the majority of the growing season of 2018, with the peak season included. The mean daily temperature showed a humped pattern, ranging between 22ºC and 30ºC, and the mean precipitation was 5.8 mm per day between 4 June and 5 September (Fig. 1). No severe drought or extreme weather events occurred during the experiment period. Thus, the weather conditions have been very suitable for the growth of macrophytes.

The transplanted submerged macrophytes had fresh biomass densities of around 400 g/m^2 on average at the start of the experiment. After the three-month experiment, the mean fresh biomass density was 389 g/m^2 (Fig. 2). The mean biomass is reduced slightly,

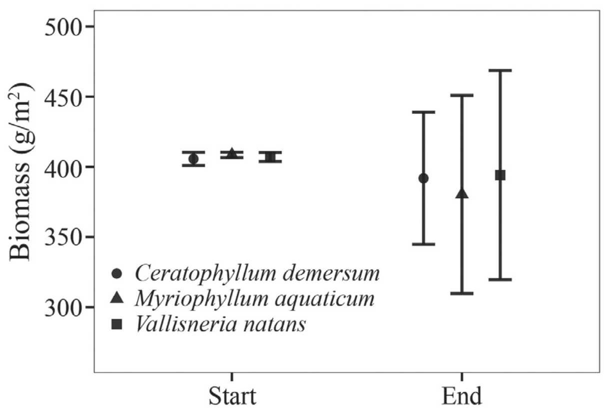

Fig. 2. Fresh biomass (mean ± standard deviation) of the three macrophyte species at the start and end of the transplanting experiment. One-way ANOVA shows that there are no significant differences between group means.

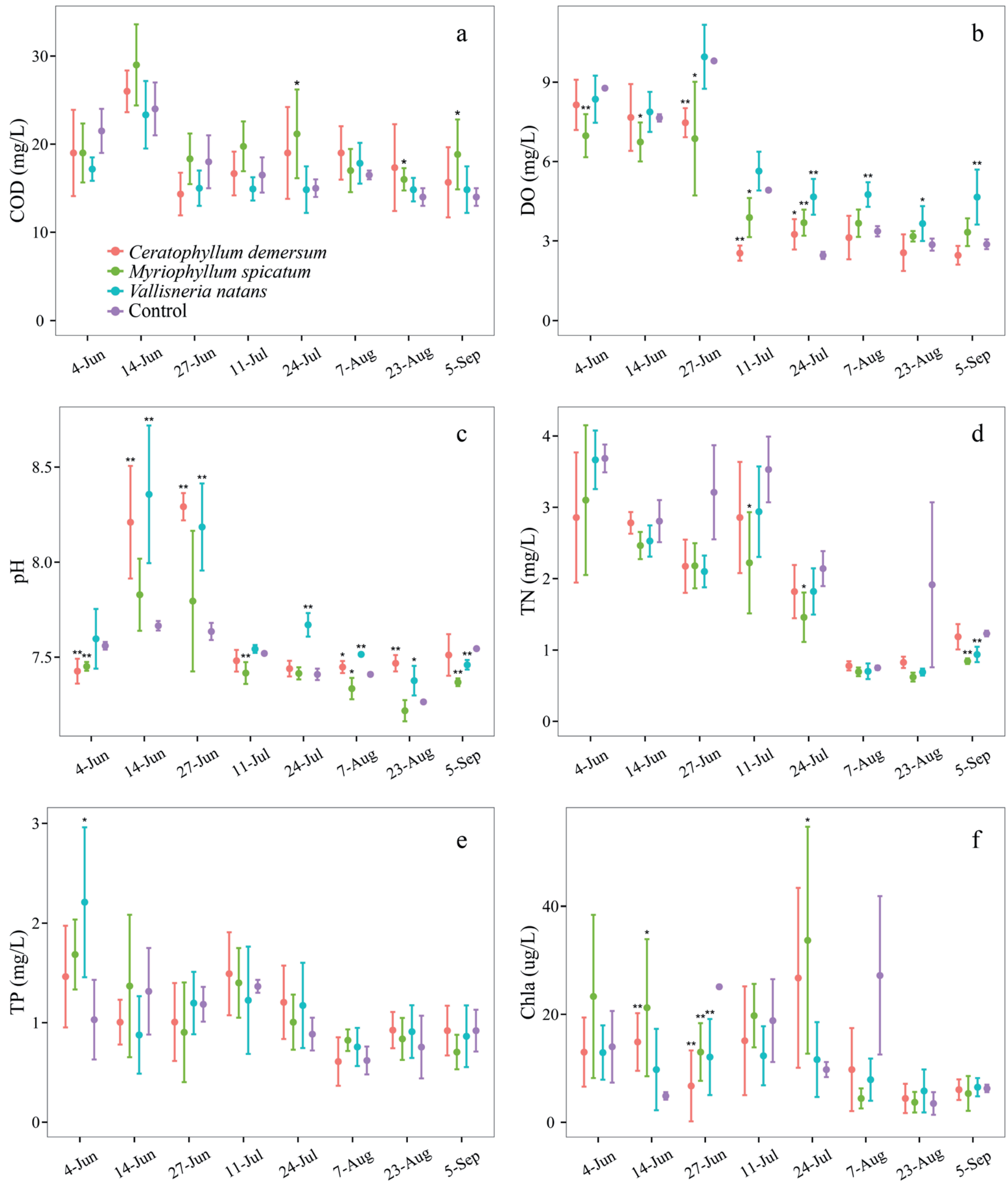

Fig. 3. Water quality indicators (mean ± standard deviation) during the experiment period. Significant ($p < 0.05$) and extremely significant ($p < 0.01$) differences between each treatment and control were marked with * and **.

and nearly half of the enclosures showed an increasing biomass, indicating that the transplanted submerged macrophytes can indeed persist under turbidity. However, we did not observe a significant expansion of the macrophytes during the three months.

The water quality indicators showed fluctuated patterns across the experiment period of 3 months. In general, COD, DO and pH showed a rising trend at the early stage before the end of June, and then a declining pattern towards September (Fig. 3 (a-c)). By contrast, there seemed a declining trend of TN and TP across the study period (Fig. 3 (d-e)). A close scrutiny to the difference between the 3 transplanted species showed that *Vallisneria natans* tended to present lower COD and higher DO than the other two species. However, we did not observe significant differences between the treatments and control in TN, TP and Chla. In addition, the extent of temporal variation appeared to be larger than that of treatment variation in all water quality indicators.

We then used the trend fitting model with the Theil-Sen estimator to further check if the water quality indicators exhibited specific temporal trends (Fig. 4 (a-f)). The result showed that all 6 water quality indicators consistently presented a declining trend across the 3 months. Interestingly, all three treatments as well as the control (without macrophyte transplantation) showed highly similar temporal (linear) trends, suggesting that the transplanted macrophytes generally have not exerted significant effects on water

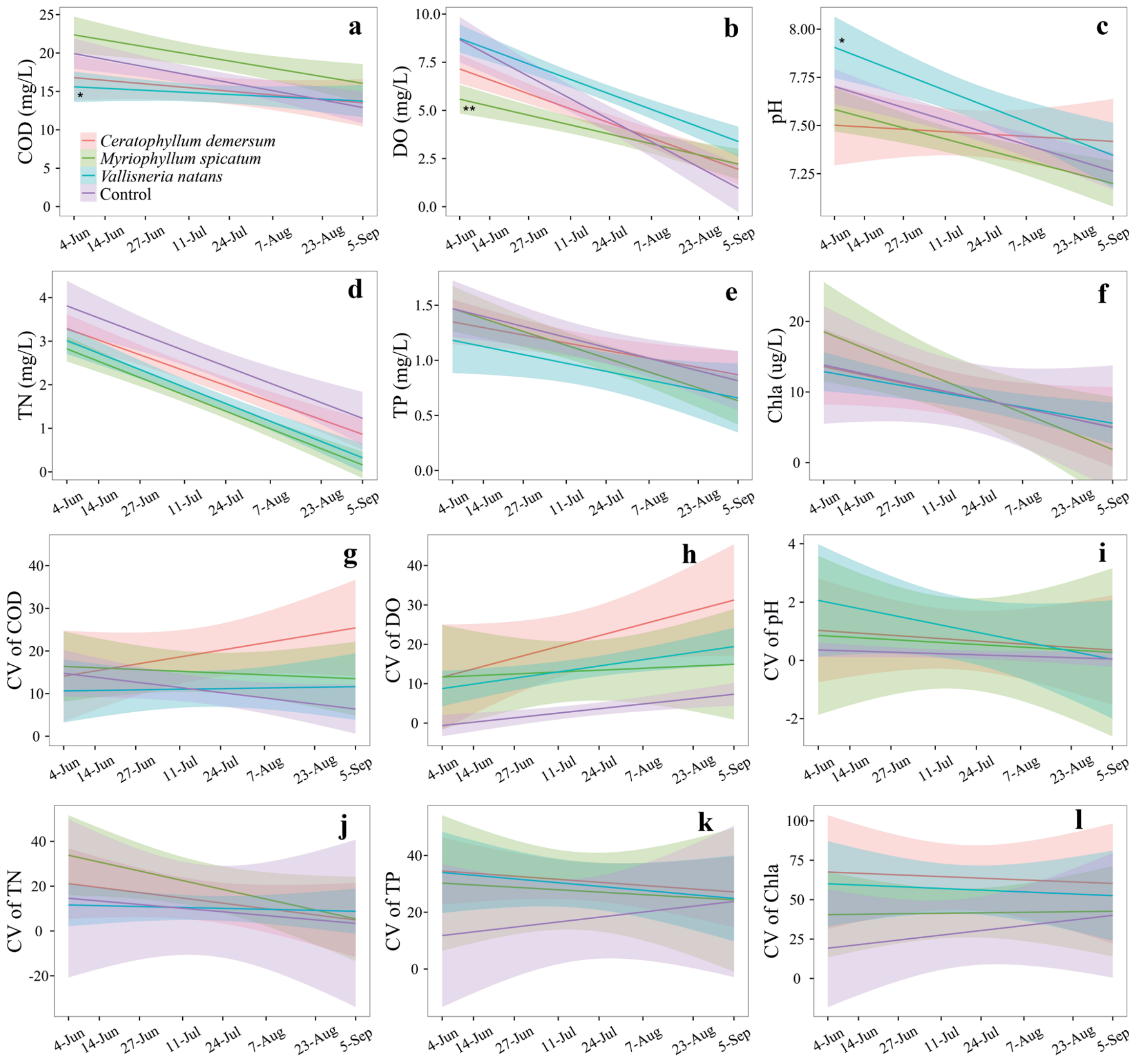

Fig. 4. Trends of water quality indicators (a - f) and their CV (coefficient of variation, g - l) with the 95% confidence intervals. Significant ($p < 0.05$) and extremely significant ($p < 0.01$) differences between each treatment and control were marked with * and **.

quality in terms of temporal trend of mean values across 3 months. However, we observed clear declining trends of variability measured by the coefficient of variation (CV) (Fig. 4 (g-l)).

Discussion

Our transplanting experiment clearly demonstrated that the artificial recolonization of the three submerged macrophyte species could indeed persist in the turbid shallow water of the Xianshan Lake across one growing season. Previous studies on temperate lakes have demonstrated that submerged macrophytes will experience rapid loss once the water shifts from a clear to a turbid state due to reduced light availability [43-45]. However, our results reinforce the suggestion that many submerged macrophyte species can survive under shading stressed environments in warmer subtropical regions. Indeed, tropical and subtropical water bodies are usually rich in algae with much higher turbidity than their temperate counterparts. In adaptation to such environmental conditions, submerged macrophyte species may become more shade-tolerant [46, 47]. However, our results suggest that the persistence of submerged macrophytes may not significantly improve water quality, and may not reverse the ecosystem state of tropical shallow lakes within one growing season.

During the past decades, increasing studies have repeatedly shown that temperate shallow lakes can present alternative stable states separated by tipping points [21, 48, 49]. Based on the theoretical predictions, bio-manipulations through temporarily removing fish (and thus breaking the positive feedback between sediment resuspension induced by disturbances of benthivorous fish and macrophyte loss) have yielded conspicuous success for restoring degraded European shallow lakes [50-52]. However, this bio-manipulation approach may not work well for tropical lakes [53-55], implying that major differences between geographic conditions may underlie the ecosystem processes. While a handful of studies have suggested that Chinese tropical shallow lakes can also have alternative stable states, the underlying feedbacks could be different and more complex than the temperate counterparts [48, 56]. An important difference is that removing fish may not increase water clarity because of the growth of algae. In the meantime, submerged macrophytes could be highly persistent in low-light conditions, promoting the coexistence of algae and macrophytes in tropical lakes. Such shade-tolerant attribute of submerged macrophytes has been used as an empirical basis for the increasingly applied measure of macrophyte restoration for the purpose of counteracting lake eutrophication and biodiversity loss [32, 33, 57].

It is especially the case in southern China, as increasing attention is being paid to the restoration of eutrophic aquatic ecosystems in terms of environmental policies [58-61]. Freshwater lakes and rivers in relatively developed regions have become a major focus for implementing ecological restoration projects, where nature-based solutions have been adopted as the main approach [62-64]. Concerning the widespread macrophyte loss, most of these projects set macrophyte restoration as the major goal [65-67]. However, the effectiveness of these restoration practices have been unclear. While the transplanted macrophytes may survive and grow well in the turbid, eutrophicated waters, it remains uncertain if and to what extent they could contribute to water purification, as expected by the designed restoration projects.

Macrophyte restoration is also facing challenges from climate change. Increasing water temperature will enhance the fitness of the algae and make the survival and expansion of the transplanted macrophytes more arduous [68]. Attributed to the disruption of the balance of nutrient exchange at the sediment-water interface, water temperature change will trigger a more intense eutrophication [69]. In addition, climate change will induce more extreme weather events. Extreme precipitation or droughts can raise the instability of lake water storage and rapid precipitation can also directly cause resuspension of sediments, ultimately leading to the failure of restoration practices [70].

In this context, our mesocosm experiment conveys a clear message that in real-world situations, the transplantation of submerged macrophytes may not fulfill the expectation of water purification. Although the survival rates appeared to reach relatively high levels, our results suggested that at least in one growing season, the macrophytes could not yield sufficient accumulation of biomass and could not expand their distribution ranges to a substantial degree. The low performance of macrophyte growth and expansion could explain why they had minor influence on water quality levels. However, we observed a declining pattern of water quality variability across the experiment period, suggesting that the macrophytes may serve as an effective stabilizer, that could reduce sediment resuspension, and thereby reducing internal nutrient loading from the sediments [71, 72].

Our experiment over one growing season cannot translate to the evaluation of the long-term effect of macrophyte restoration. It is possible that the short time period could act as the bottleneck stage of the re-establishment of macrophyte vegetation. Once this bottleneck phase is passed, the submerged macrophyte may expand extensively and rapidly, unfolding the positive feedback to reinforce vegetation cover and reduce algae concentration as well as water turbidity. On the other hand, it could well be that the persistence of the submerged macrophyte, despite their shade tolerance, will be prone to further nutrient loading and algae bloom [73]. In this sense, the early stage of macrophyte recolonization would be a vulnerable phase of restoration and should not be expected to contribute to water quality improvement.

Future studies may be conducted to better understand the underlying mechanisms of our observations. Particularly, in order to amplify restoration efficiency, we need to understand what causes the poor growing trends in this study by investigating a range candidate factors such as length of growing season, potential effects of plant density (density-dependent mechanisms), nutrient release potential from sediment, potential effects of plant tissue decay and nutrient release, as well as potential effects of growth form of macrophytes.

Our work provides valuable implications for the current lake restoration practices. First, while some microcosm studies have suggested that submerged macrophytes can improve water quality in relatively short terms, our results suggested that in real-world situations (e.g. open waters), it may not be realistic to anticipate rapid restoration purely through macrophyte transplantation, and monitoring the long-term effects of macrophyte transplantation is imperative for lake restoration. Second, While the alternative stable states theory has been gaining momentum in the community of researchers, much less attention has been paid among practitioners. Apart from macrophyte transplantation, other measures such as the introduction of fish that feed on algae may help to break the vicious circle [74-76] and eventually amplify restoration success. Our work highlights the need to harness the nuanced hidden complexity for tropical lake restoration.

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Conflict of Interest

The authors declare no conflict of interest.

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