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The Distribution and Succession of Filamentous Algae in the Southern Taihang Catchment under Different Nutrient Regimes

Bo Yang [1,2,†], Yiguang Zhang [1,2,†], Man Zhang [1,2,*], Xucong Lv [1,2], Yuhua Li [1,2], Jingxiao Zhang [1,2], Xianfeng Wang [1,2], Xiaofei Gao [1,2], Xueqin Zhao [1] and Xiufen Wang [1,2]

[1] College of Fisheries, Henan Normal University, Xinxiang 453007, China; yangbo19981027@163.com (B.Y.); zhangjingxiao@htu.edu.cn (J.Z.); gaoxiaofei@htu.edu.cn (X.G.); zxueqin0708@163.com (X.Z.)
[2] Engineering Technology Research Center of Henan Province for Aquatic Animal Cultivation, Henan Normal University, Xinxiang 453007, China
* Correspondence: zm0378@163.com
† These authors contributed equally to this work.

Abstract: Human activities have resulted in the eutrophication of rivers, leading to heightened concerns regarding the occurrence of filamentous algal blooms. With the increasing utilization of rivers by humans, the occurrence of these nuisance filamentous algae is expected to increase in frequency in the future. Blooms primarily occur due to energy congestion at the trophic level of primary producers, resulting from inefficient energy flow in both the bottom-up and top-down pathways. To investigate the mechanism underlying the outbreak of filamentous algae, two streams in the southern Taihang catchment with different nutrient conditions were selected for this study. The objective of this study was to understand the effects of nutrient levels and other potential factors on the distribution and succession of filamentous algae. Our findings revealed a positive correlation between nutrient conditions and the biomass of filamentous algae. *Cladophora* and *Spirogyra* were identified as the dominant species among filamentous algae, each exhibiting unique distribution patterns in the two streams. *Spirogyra* thrived predominantly in the Baligou stream, where lower nutrient levels and warmer temperatures prevailed. In contrast, *Cladophora* flourished in the nutrient-rich Nanping stream at colder temperatures. Results from the generalized linear model indicated that the biomass of *Cladophora* was influenced by nutrient concentration, water depth, water temperature, and macrobenthic biomass. The biomass of *Spirogyra*, on the other hand, was primarily determined by water temperature, nutrient concentrations, water depth, and velocity. The positive correlation between *Cladophora* and macrobenthos revealed a possible mutually beneficial relationship, suggesting that macrobenthos may promote the growth of *Cladophora* by inhibiting periphytic diatoms. In return, the macrobenthos benefit from a secure refuge and an environment conducive to foraging and reproduction. This study suggested that to alleviate energy flow congestion in the benthic food chain, it is advisable to address this issue by either reducing nutrient loadings in rivers or enhancing the presence of benthivorous fishes in streams.

Keywords: eutrophication; filamentous algae; periphytic diatoms; macrobenthos; interpretation model

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1. Introduction

The muddy substrates commonly observed in rivers and shallow lakes often reveal a prevalent dominance of either macrophytes or phytoplankton, attracting the interest of researchers who are particularly focused on investigating the regime shift dynamics between these two ecological components [1,2]. However, it is worth emphasizing that a distinct contrast arises when considering the rocky and artificial cement substrates within river environments, as these substrates exhibit a higher vulnerability to being overwhelmed by filamentous green algae, which are a diverse group of photosynthetic organisms characterized by long, thread-like structures [3]. The proliferation of filamentous green algae not only significantly diminishes the aesthetic appeal of water bodies but also gives rise to blockage issues in water supply channels, ultimately leading to disruptions in the water distribution network.

Eutrophication refers to the excessive input of nutrients (such as nitrogen and phosphorus) into water bodies due to human activities, leading to the overgrowth of algae [4], which is a significant issue that impacts rivers globally. This phenomenon triggers the overgrowth of nuisance filamentous algae, leading to a shift from well-maintained water bodies to nuisance ones with visible coverage on the water surface [5]. The formation of algal mats not only creates aesthetic and odor problems but also threatens water conservation and recreational value [6]. For example, the explosive growth of *Spirogyra*, a filamentous green alga, in the littoral zone of Lake Baikal is chiefly caused by groundwater contamination stemming from untreated sewage. The excessive growth of *Spirogyra* not only deteriorates water quality but also presents risks to the endemic species inhabiting the lake and endangers the lake's unique ecosystem [7]. Localized blooms of *Cladophora* in the western basin of Lake Erie are mainly driven by nutrient enrichment from agricultural runoff and the presence of invasive dreissenid mussels, resulting in significant ecological degradation and posing risks to recreational activities due to beach fouling and water quality deterioration [8].

Filamentous algae play a vital role in river and stream ecosystems, providing food and habitats for other organisms [9]. Species from the genera *Spirogyra*, *Cladophora*, and *Oedogonium* are common bloom-forming algae. In recent years, the frequency of filamentous algae outbreaks has significantly increased, raising concerns about the negative effects of these blooms on water quality and ecosystem health [10–12]. These algae can grow rapidly and form dense mats, depleting oxygen and blocking sunlight, which adversely affects aquatic organisms and habitats [13]. Researchers have observed that the biomass of *Spirogyra* and *Cladophora* species in filamentous algae tends to increase as nutrient levels increase [12]. However, there is currently a lack of comprehensive understanding of the distribution and succession patterns of filamentous algae communities under different nutrient conditions.

The southern Taihang catchment is a crucial region with abundant streams, multiple conservations, and biodiversity. The impact of human activities on each stream ecosystem varies significantly, resulting in notable differences in water trophic levels across different regions. This discrepancy can be attributed to the distinct management strategies employed in each conservation area. In recent years, frequent outbreaks of filamentous algae have occurred in these regions. Notably, each species of filamentous algae exhibits specific nutrient preferences during the vegetative season [14]. This emphasizes the importance of understanding the influence of trophic levels, such as nitrogen and phosphorus levels, on the growth and proliferation of filamentous algae. These factors can lead to notable changes in the distribution and succession patterns of filamentous algae communities.

Although the trophic level has been recognized as a crucial factor influencing filamentous algae biomass, our study adopted a comprehensive approach by investigating additional ecological variables, such as temperature, water velocity, light availability, and biotic interactions. These variables also significantly influence the distribution of filamentous algae communities [15,16]. Through a comprehensive examination of dense mat composition within aquatic ecosystems and analysis of environmental gradients, our research enhances the fundamental comprehension of filamentous algal blooms and provides practical applications for controlling.

The southern Taihang catchment encompasses several conservation zones, each of which primarily depends on rainfall for its water supply [17]. Nonetheless, the variation in management strategies among these zones renders the area particularly conducive to scientific research. The objective of this study was to explore the distribution and succession patterns of filamentous algae communities under two nutrient regimes within the southern Taihang catchment. By assessing filamentous algae species composition and biomass, we aim to deepen the understanding of their adaptive strategies to different nutrient conditions, as well as their occupation of diverse ecological niches and establishment of succession patterns. Specifically, this study aimed to (i) compare the distribution patterns of filamentous algae in the two regions, (ii) identify the factors influencing the presence of *Cladophora* and *Spirogyra* in the catchment, and (iii) develop effective interpretive models of filamentous algae for water management. In summary, this study significantly contributes to the understanding of the ecological dynamics of filamentous algae while providing valuable insights for the effective management and conservation of water resources.

2. Materials and Methods

2.1. Study Sites

The study sites for this research are two independent conservation areas, Nanping and Baligou, located in the southern Taihang catchment of central China (34°34′–40°43′ N, 110°14′–114°33′ E) (Figure 1). Both streams within these conservation zones primarily rely on rainfall as their water source [17], but their tributary networks are not interconnected. The management strategy in Nanping conservation is relatively lenient, with a local population of approximately 15,000. In contrast, Baligou conservation has a stricter management strategy, with a resident population of less than 500, resulting in distinct and independent water trophic levels. The lengths of the Nanping and Baligou streams are 70 km and 60 km, respectively, and both are punctuated by several waterfalls and deep pools. The dry season spans from October to May, while the wet season spans from June to September and accounts for approximately 70% of the annual precipitation. The catchment area receives an annual precipitation range of 390–750 mm [18]. The average annual temperature is 13 °C, with the lowest (−1.6 °C) and highest (26.3 °C) monthly temperatures occurring in January and July, respectively.

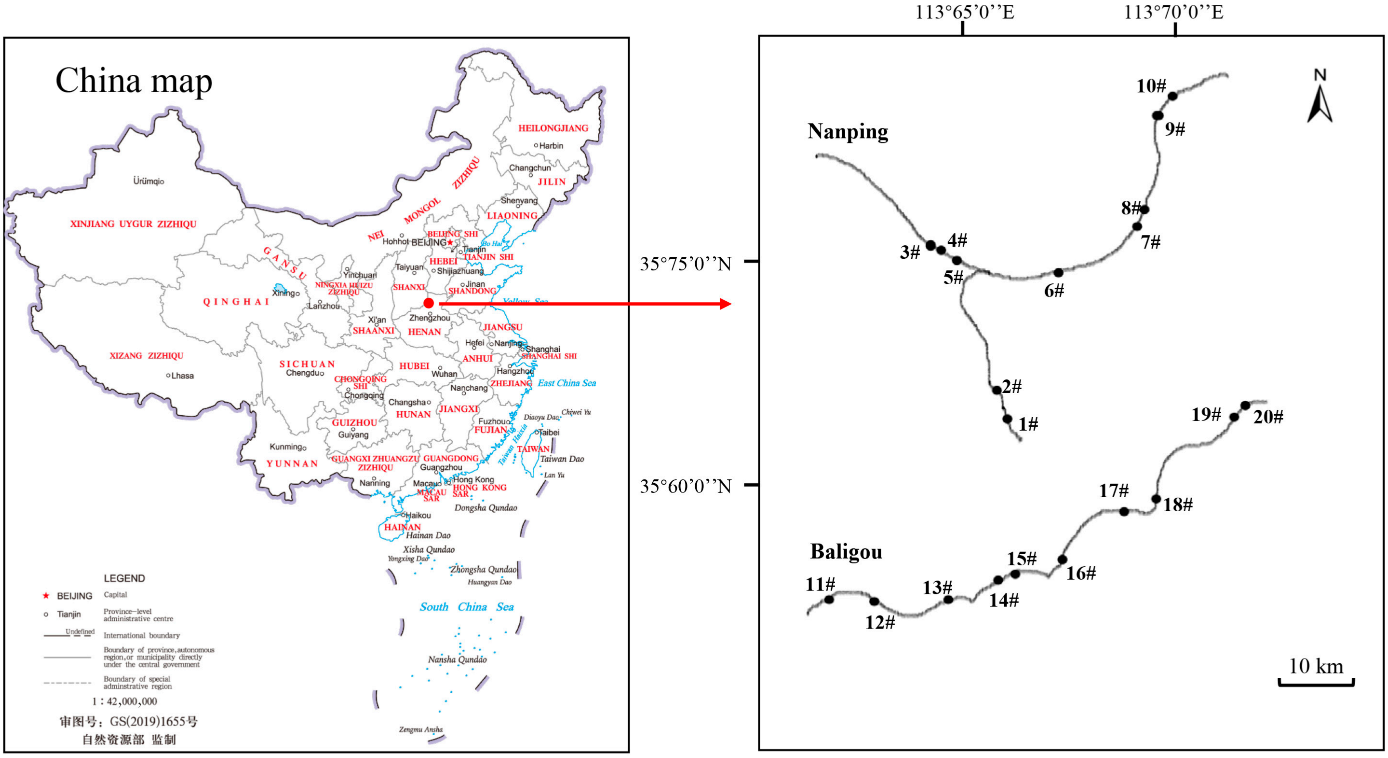

Figure 1. Locations of the Nanping and Baligou streams in the southern Taihang black dots show the sampling sites in the two streams. 1# to 10# are the sampling sites of Nanping; 11# to 20# are the sampling sites of Baligou.

2.2. Filamentous Algae Collection, Identification, and Measurement

Sampling was carried out during the peak growth season from mid-July to mid-September in 2023. Ten designated sites within each stream were sampled once every two weeks

(Figure 1), with a total of five sampling sessions. Filamentous algae samples were collected from the tops of rocks or boulders within the streams using a grab bucket within a defined area of 0.2 m^2. To ensure accuracy, replicate samples ($n = 5$) were collected from the top layer of the rocks, typically within the range of 20 to 50 cm below the water-surfaced depth to assess the filamentous algal biomass. Then, the defined area was scraped with brushes to collect all the filamentous algae on the rocks. The combined samples were then carefully washed using a series of sieves to remove any traces of mud or silt. To remove excess water, the samples were placed between layers of paper towels before their biomass was weighed using an electronic scale [19]. The collected samples were then preserved in polythene bags treated with a 4% formalin solution and transported to the laboratory for further analysis. All the collected algal samples were stored in a refrigerator for future research. In the laboratory, a light microscope (Nikon Ci-L, Tokyo, Japan) with a magnification of ×100 was used to examine the samples, allowing for algae identification and calculation of the relative abundance of each species. The identification of filamentous algae followed the guidelines provided by the Flora Algarum Sinicarum Aquae Dulcis [20]. The spatial and temporal distribution profiles of the filamentous algae samples were analyzed.

2.3. Periphytic Algae Collection, Identification, and Measurement

Periphytic algae were collected simultaneously with filamentous algae samples by using natural substrates such as stones and boulders. The quantitative samples were brushed from the substrate surfaces under 10–30 cm of water using toothbrushes. At each site, samples from three locations were mixed to create a composite sample, which was then rinsed several times with distilled water. The composite sample was placed in a 100 mL plastic bottle and preserved with a 4% formalin solution. The examination of diatom taxa was conducted using an inverted microscope (Nikon ECLIPSE TS2; Tokyo, Japan) and the identification references used were Krammer and Lange-Bertalot and Diatoms of North America (http://diatoms.org/ (accessed on 24 July 2024)) [21,22]. To evaluate the competitive impact of periphytic algae on filamentous algae, the relative abundance of periphytic algae was assessed by counting the number of cells per square centimeter under a microscope [23]. To estimate the periphytic algae biomass, at least 10 individuals for each species were measured and then approximations to geometric solids were applied to calculate individual biovolume [24]. Periphytic algae biomass was estimated from the biovolume, assuming that 10^6 μm^3 corresponds to 1 µg of biomass.

2.4. Macrobenthos Collection, Identification, and Measurement

During the sampling of filamentous algae, macrobenthic samples were simultaneously collected using a Ponar grab. The collection area covered an area of 1 m^2 and focused on substrates predominantly composed of sand, gravel, or cobbles. To ensure effective sampling, riverbank areas containing rocks and boulders were avoided. The grab samples were washed and sieved on-site using a 0.5 mm mesh. The macrobenthos were then extracted using forceps and placed in sampling bottles. The macrobenthic samples were preserved in 70% alcohol, and additional sorting was conducted in the laboratory. The samples were examined under a stereomicroscope (Nikon SMZ645, Tokyo, Japan) at ×100 magnification for identification in accordance with the methods described by Campos et al. [25]. The wet biomass of the macrobenthos was determined using an electronic scale with 10^{-5} g of precision [26].

2.5. Fish Collection, Identification, and Measurement

Fish samples were collected from the two streams using fish traps constructed with 16 steel frames measuring 25 cm × 12 cm × 15 cm and spaced 6 cm apart. The fish entrance had a vertical depth of 15 cm and a mesh size of 4 mm, with a total trap length of 3 m. The traps were set in the evening at 18:00 and retrieved the following morning at 6:00, allowing for a full night of sampling. In the laboratory, the collected fish were carefully identified and classified following the methods described by Joseph S. Nelson [27]. Subsequently, the samples were accurately counted, weighed (using an electronic scale with a precision of 0.1 g), and measured for length (with an accuracy of 0.1 cm). The catch per unit effort (CPUE) of fish was calculated using the formula provided by Harley et al. [28] and Gupta et al. [29]:

$$CPUE = \frac{Total\ catch}{Sum\ of\ efforts}$$

The *sum of effort* was measured in terms of time and the number of traps.

2.6. Abiotic Conditions

Various abiotic conditions were measured to analyze their impacts on filamentous algae. These conditions included water temperature (T), pH, dissolved oxygen (DO), electrical conductivity (EC), water velocity (V), water depth (Dep), light intensity, elevation, hardness, soluble reactive phosphorus (SRP), nitrate (NO_3-N), nitrite (NO_2-N), ammonium (NH_4-N), ferrite (Fe^{2+}), silicate ($SiO_3{}^{2-}$), total carbon (TC), and inorganic carbon (IC) concentrations. We utilized several instruments to collect data for our water quality analysis. A multiparameter water quality monitor (YSI Pro20; Ohio, USA) was used to measure T, pH, DO, EC, and Dep at the water surface. A flowmeter (Xiangruide LS300-A; Weifang, China) was used to measure water velocity. An illuminometer (Spectrum 3415FX LightScout; San Antonio, TX, USA) was used to measure light intensity, and a mobile positioning device (Huawei Pocket; Shenzhen, China) was used to measure elevation. For water sample collection, we employed a 5 L iron sampler. The water was collected at a depth ranging from 0.2 m to 0.5 m.These samples were subsequently analyzed for SRP, NO_3-N, NO_2-N, NH_4-N, hardness, Fe^{2+}, and $SiO_3{}^{2-}$ concentrations in accordance with the Chinese National Standards for Water Quality and the Environmental Protection Agency of the USA [30]. Subsequently, 20 mL of the water samples were filtered through a 0.45-µm membrane filter and subjected to a carbon analyzer (Multi N/C 3100, Jena, Germany) for TC and IC measurements.

2.7. Data Analysis

2.7.1. Patterns in the Filamentous Algae Community and Environmental Contributions

Principal coordinate analysis (PCoA) was performed using the 'VEGAN' package (v2.6-6.1) in R based on Bray-Curtis distance metrics calculated for the species compositions of the filamentous communities [31]. The data points were color-coded and shaped based on two independent streams (Nanping and Baligou). Ellipses with 90% confidence intervals were constructed to indicate differences between the two streams.

A detailed correspondence analysis using the Decorana function was conducted with R's 'VEGAN' package. The results indicated that the first axis had a gradient length of 1.98, suggesting that a linear model was appropriate for further analysis. To identify the key factors influencing filamentous algal species composition, a forward-selection procedure (ordistep function) with Monte Carlo permutation tests (999 permutations) was performed using the ordistep function to select a parsimonious set of factors explaining a statistically significant ($p < 0.05$) amount of variation in the filamentous algae data in each sample [32]. The explanatory variables were sequentially tested using the variance inflation factor (VIF) to eliminate collinearity among the selected factors, employing the VIF function until all the VIF values were less than 20. Finally, a linear model redundancy analysis (RDA) was conducted to examine patterns of interaction between filamentous algae and environmental determinants [33].

To determine the contributions of potential explanatory variables to specific filamentous algae, a variation partitioning analysis (VPA) based on the RDA algorithm was utilized. Prior to conducting the VPA, Hellinger standardization was applied to the filamentous algae biomass data. Furthermore, feature scaling transformation was employed to normalize the environmental explanatory conditions, thereby avoiding differential weighting. VPA was performed using the 'RDACCA.HP' package (v1.1-0) [34].

2.7.2. Generalized Linear Models

To assess the effects of the explanatory variables on filamentous algae biomass, a generalized linear model (GLM) was used to determine the relative contributions of these variables. The 'best' model from the GLMs was selected using a forward stepwise procedure based on the Akaike information criterion (AIC) and Bayesian information criterion (BIC). The model incorporating the set of explanatory factors with the lowest AIC and BIC values was selected [35]. All GLM analyses were performed using the 'GLMULTI' package (v1.0.8) in R.

2.7.3. Association Network between the Filamentous Algae and Macrobenthos

All macrobenthic species and two filamentous algae (*Cladophora glomerata* (Linnaeus) Kützing, 1843 and *Spirogyra communis* (Hassall) Kützing, 1849), were utilized for network analyses aiming to determine the correlations between the filamentous algae and macrobenthos. To simplify the data sets, only species that were present in more than ten samples were included in the construction of networks. Subsequently, all possible pairwise Spearman's rank correlations (r) between these species were calculated using the 'PICANTE' R package. Only correlations that were both effective ($r > 0.4$ or $r < -0.4$) and statistically significant ($p < 0.05$) were used for the network analyses [36]. To visualize the network and perform modular analysis, Gephi 0.9.2 was used. Additionally, node-level topological properties such as degree, betweenness, closeness, and eigenvector were calculated using the 'IGRAPH' R package. Statistical differences in node-level attributes across different taxa were determined using the nonparametric Mann-Whitney U test. Macrobenthos that had a high degree (>100) and low betweenness centrality values (<5000) were considered keystone species for the *C. glomerata* and *S. communis* networks [37].

2.7.4. Other Statistical Analysis

Independent *t*-tests were used to assess differences in abiotic and biotic variables between the two streams.

3. Results

3.1. Characteristics of Nutrients, Other Biotic, and Abiotic Conditions in the Two Streams

During the two-month observation period, there was a peak in the growth of filamentous algae followed by a gradual decrease, marking this sampling period as a significant stage in the succession of filamentous algal communities. Table 1 presents the mean values of nutrients and biotic and abiotic conditions in the Baligou and Nanping streams. All 15 abiotic factors and 9 biotic parameters exhibited wide ranges, demonstrating diverse spatial and temporal disparities.

Independent T-tests revealed significant increases in the SRP and dissolved inorganic nitrogen (DIN, NO_3^{-}-N + NO_2^{-}-N + NH_4^{+}-N) in the Nanping stream compared to those in the Baligou stream (SRP: $p = 0.005$, DIN: $p < 0.001$) (Figure 2a,b). The Baligou stream has a significantly higher water temperature than Nanping ($p = 0.021$) (Figure 2c). No significant differences were found between the two streams in terms of pH, DO, EC, V, Dep, light intensity, elevation, hardness, ferrite, silicate, TC, or IC ($p > 0.05$).

Macrobenthos are grazers of benthic algae [38]. It was found that the abundance and biomass of macrobenthos were significantly higher in Nanping than in the Baligou stream (abundance: $p = 0.003$; biomass: $p = 0.003$) (Table 1, Figure 2d). Fish are the top predators in benthic food chains [39]. The CPUE of total fish was significantly greater in the Baligou stream than in the Nanping stream ($p = 0.001$). A total of five fish species were identified across all sampling sites in the two streams: *Phoxinus oxycephalus* (Sauvage & Dabry de Thiersant, 1874), *Gnathopogon taeniellus* (Nichols, 1925), *Pseudorasbora parva* (Temminck & Schlegel, 1846), *Onychostoma macrolepis* (Bleeker, 1871), and *Rhinogobius giurinus* (Rutter, 1897). Notably, *p. oxycephalus* was the predominant species, and its CPUE was also significantly greater in the Baligou stream than in the Nanping stream ($p = 0.002$). Periphytic diatoms are the most important competitors of filamentous algae [40]. After identification, all periphytic algae were periphytic diatoms. The biomass of periphytic diatoms in Baligou was slightly greater than those in Nanping but the difference was not statistically significant ($p > 0.05$).

Table 1. Environmental factors and biotic parameters (mean values ± standard error, n = 50) in the two streams.

Classification	Environmental Factors and Biotic Parameters	Nanping	Baligou
Environmental factors	T (°C)	19.64 ± 3.34 a	22.82 ± 3.32 b
	pH	8.53 ± 0.26	8.59 ± 0.25
	DO (mg/L)	8.95 ± 1.01	9.03 ± 1.50
	EC (µs/cm)	409.86 ± 24.79	388.76 ± 27.32
	Hardness (mol/L)	0.81 ± 0.04	0.79 ± 0.12
	V (m/s)	0.13 ± 0.19	0.10 ± 0.16
	Dep (m)	0.40 ± 0.44	0.26 ± 0.24
	Light (µmol/m^2·s)	403.16 ± 493.37	641.66 ± 605.37
	Elevation (m)	718.90 ± 101.61	446.20 ± 94.49
	SRP (mg/L)	0.024 ± 0.06 a	0.004 ± 0.00 b
	DIN (mg/L)	7.82 ± 3.00 a	6.60 ± 1.17 b
	Fe^{2+} (mg/L)	0.11 ± 0.03	0.12 ± 0.09
	$SiO_3{}^{2-}$ (mg/L)	216.15 ± 22.69	212.84 ± 27.02
	TC (mg/L)	43.71 ± 5.83	40.39 ± 4.66
	IC (mg/L)	36.64 ± 4.98	34.21 ± 3.67
	Filamentous algae biomass (g/m^2)	49.73 ± 70.47 a	35.95 ± 37.28 b
	S. communis biomass (g/m^2)	4.27 ± 16.85 a	12.48 ± 22.66 b
	C. glomerata biomass (g/m^2)	38.88 ± 68.86 a	11.06 ± 13.46 b
	PDA (cells/cm^2)	51897.45 ± 58567.75	60180.55 ± 68943.36
	PDB (mg/m^2)	603.01 ± 618.43	759.94 ± 918.36
	MBA (cells/m^2)	445.02 ± 514.47 a	198.65 ± 189.86 b
	MBB (g/m^2)	9.35 ± 28.55 a	0.89 ± 1.29 b
	Phoxinus oxycephalus CPUE (g/trap·d)	2171 ± 871.32 a	7794 ± 3913.26 b
	Total fish CPUE (g/ trap·d)	3159 ± 340.74 a	8177 ± 586.73 b

Note(s): a, b: Different letters denote significant differences ($p < 0.05$) between the two streams based on the independent T-tests. T: water temperature, DO: dissolved oxygen, EC: electrical conductivity, V: water velocity, Dep: water depth, Light: light intensity, SRP: soluble reactive phosphorus, DIN: dissolved inorganic nitrogen, Fe^{2+}: ferrite, $SiO_3{}^{2-}$: silicate, TC: total carbon, IC: inorganic carbon, PDA: periphytic diatom abundance, PDB: periphytic diatom biomass, MBA: macrobenthic abundance, MBB: macrobenthic biomass, CPUE: catch per unit effort of fish.

3.2. Distribution Patterns of Filamentous Algae Communities

During the observation period, filamentous algae were highly abundant in both the Nanping and Baligou streams, with average biomasses of 49.73 ± 70.47 g/m^2 and 35.95 ± 37.28 g/m^2, respectively (Table 1). Notably, the total biomass of filamentous algae in the Nanping Reservoir was significantly greater than that in the Baligou River (biomass: $p = 0.036$; biomass: $p = 0.028$). Five taxa were identified across all sampling sites in the two streams, namely, *C. glomerata* (Linnaeus) Kützing, 1843, *S. communis (Hassall)* Kützing, *1849*, *Zygnema* sp. (C. Agardh in Liljeblad, 1816), *Oedogonium* sp. (Link ex Hirn, 1900), and *Tribonema* sp. (Derbes and Solier, 1851). Among these, *C. glomerata* and *S. communis* were the most dominant taxa and were responsible for forming benthic algal blooms (Figure 3). In contrast, the remaining three species collectively accounted for less than 25% in these two areas (Figure 4). Interestingly, the biomass of *S. communis* was significantly greater in the Baligou stream than in the Nanping stream ($p = 0.027$) (Figure 4a), while the biomass of *C. glomerata* was significantly greater in the Nanping stream than in the Baligou stream ($p < 0.001$) (Figure 4b). In the Nanping stream, *C. glomerata* accounted for 78.1% of the total biomass and remained abundant and persistent throughout the observation period. Moreover, *S. communis* contributed 35.4% of the total biomass in the Baligou stream.

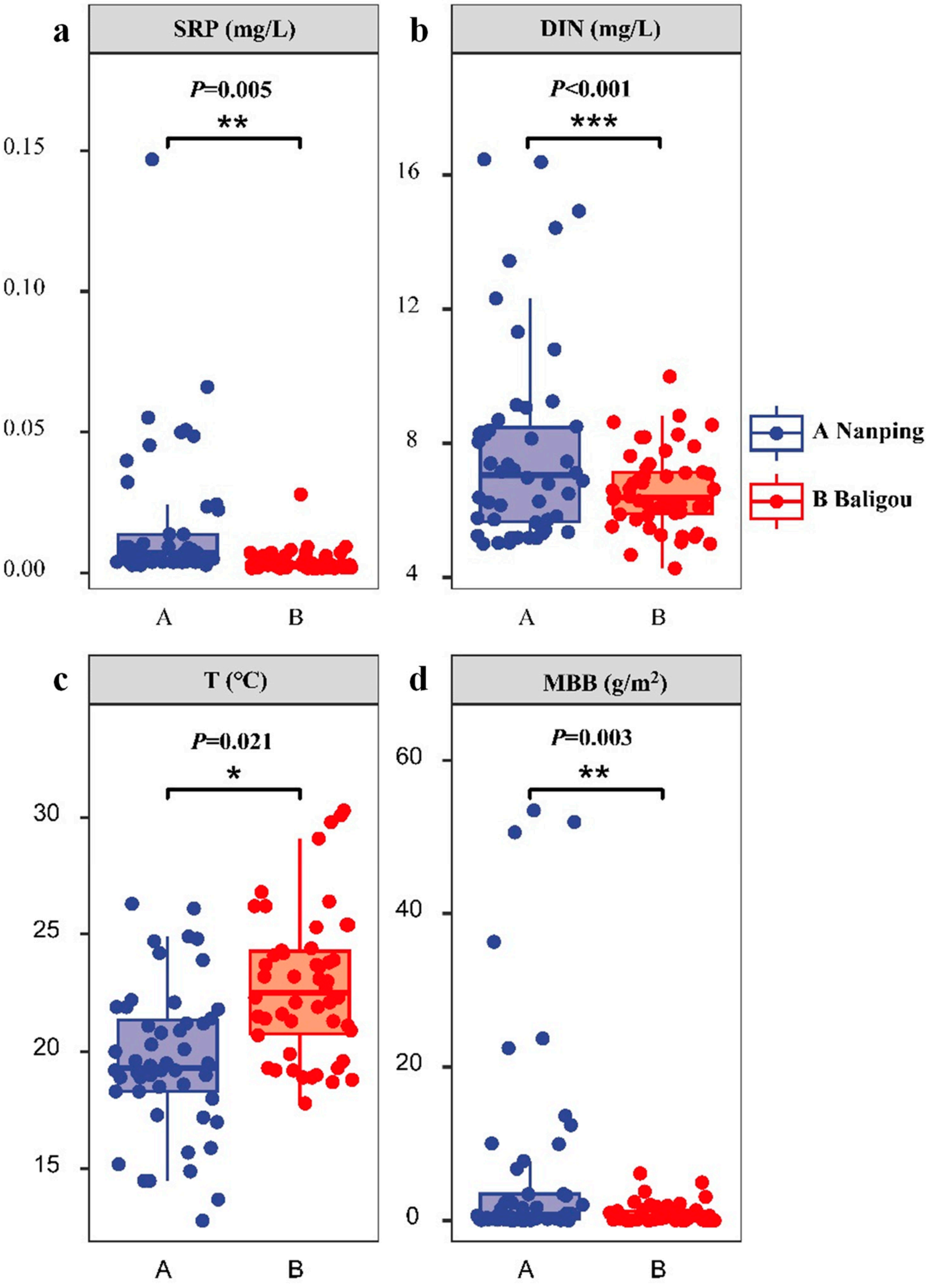

Figure 2. Environmental conditions exhibiting significant differences between the two streams. Boxes represent the interquartile range, central bars represent the median, and solid lines represent the data range. Corresponding letters denote means that do not statistically differ from one another. * Denote that statistically differ from the other ($p \leq 0.05$). ** indicates a significant difference ($p \leq 0.01$). *** indicates an extremely significant difference ($p \leq 0.001$). SRP: soluble reactive phosphorus, DIN: dissolved inorganic nitrogen, T: water temperature, MBB: macrobenthic biomass.

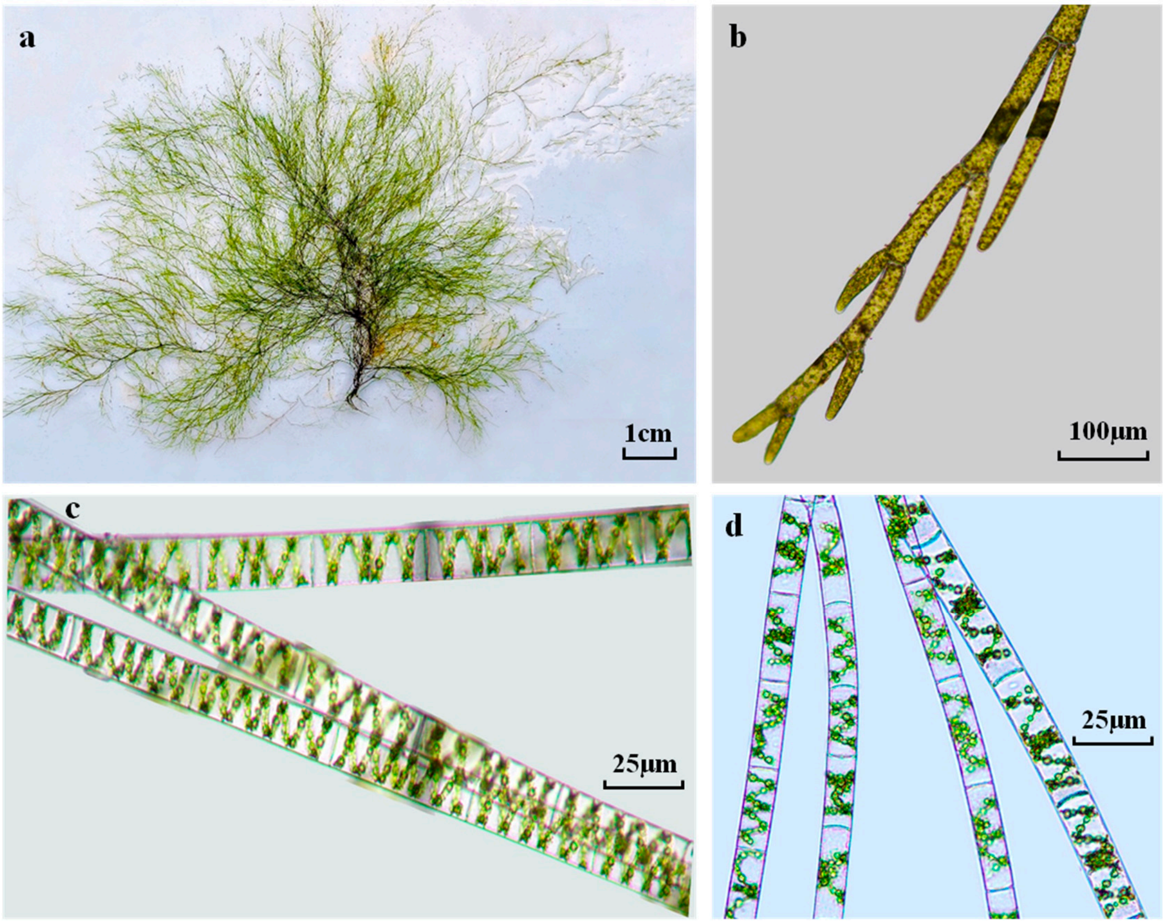

Figure 3. Morphology of the *C. glomerata* (**a**,**b**) and *S. communis* (**c**,**d**).

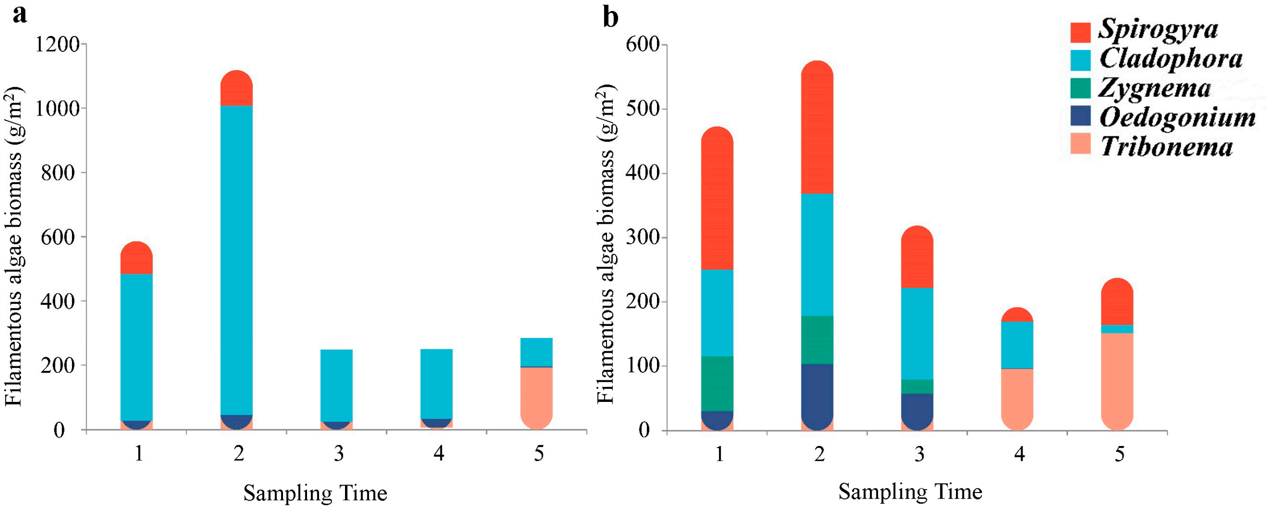

Figure 4. Taxa composition of filamentous algae communities in the Nanping (**a**) and Baligou (**b**) plots.

To assess the difference in community structure for filamentous algae in the two streams, PCoA was conducted, incorporating all temporal and spatial sampling sites. The first two axes explained 32.0% of the variance in the species composition of the filamentous algae. The analysis revealed that the filamentous algal species in the two streams formed distinct communities, indicating a significant difference in community structure ($p = 0.005$) (Figure 5).

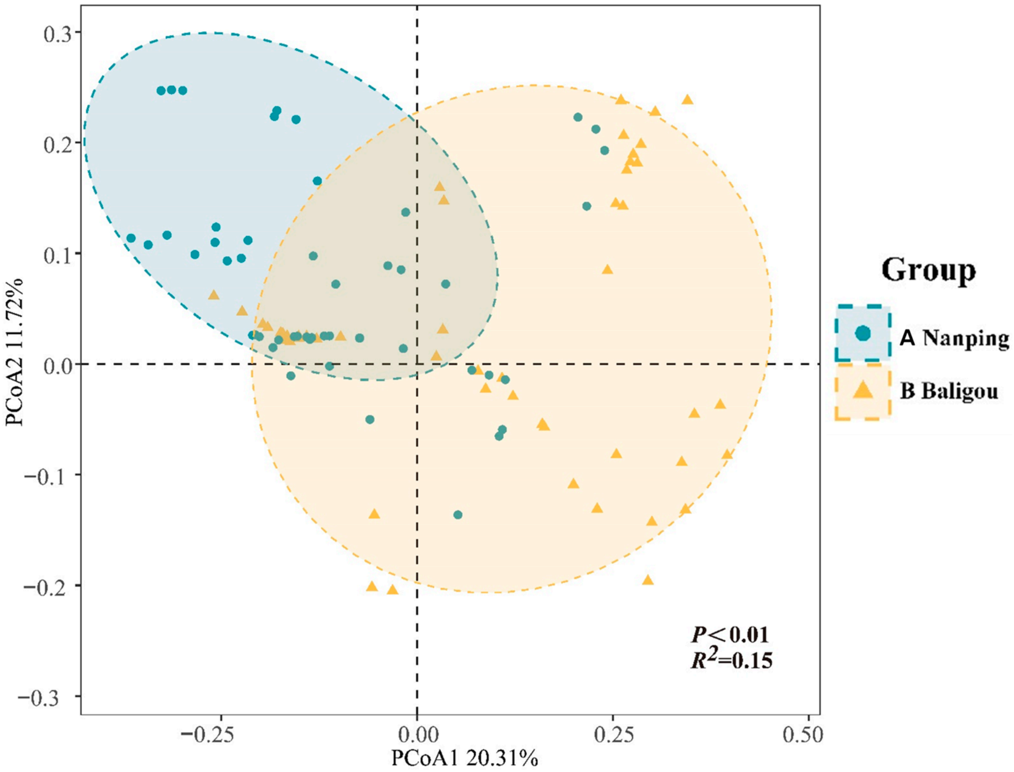

Figure 5. Principal coordinate analysis (PCoA) of filamentous algae communities in the two streams.

3.3. Determinants of the Distribution of Filamentous Algae Communities

RDA was conducted using 17 variables to assess the influence of abiotic and biotic factors on the biomass of filamentous algal species in the two streams. These variables included water temperature, depth, velocity, pH, DO, EC, TC, IC, SRP, DIN, light intensity, elevation, hardness, ferrite, silicate, periphytic diatom biomass, and macrobenthic biomass. The forward selection results revealed that temperature, depth, velocity, DIN, SRP, macrobenthic biomass, and periphytic diatom biomass accounted for 19.46% and 15.18%, respectively, of the variation in environmental variables along the first and second axes (Figure 6, $R^2 = 0.35$, $p = 0.001$). Nutrient levels were identified as key determinants influencing the species composition of filamentous algae. Additionally, abiotic factors such as water depth, velocity, and temperature played significant roles in the distribution of filamentous algae. Biotic factors, including macrobenthic biomass and periphytic diatom biomass, were also found to be important variables.

The VPA results for the 17 explanatory variables indicated that temperature, DIN concentration, SRP concentration, pH, depth, and velocity collectively accounted for more than 70% of the biomass of *S. communis* (Figure 7a). On the other hand, DIN, depth, macrobenthic biomass, SRP, and temperature were identified as determinants of the biomass of *C. glomerata* (Figure 7b). These findings clearly demonstrated the significant contribution of nutrient levels to the presence of both filamentous algal species, highlighting the importance of water trophic status in determining their biomass.

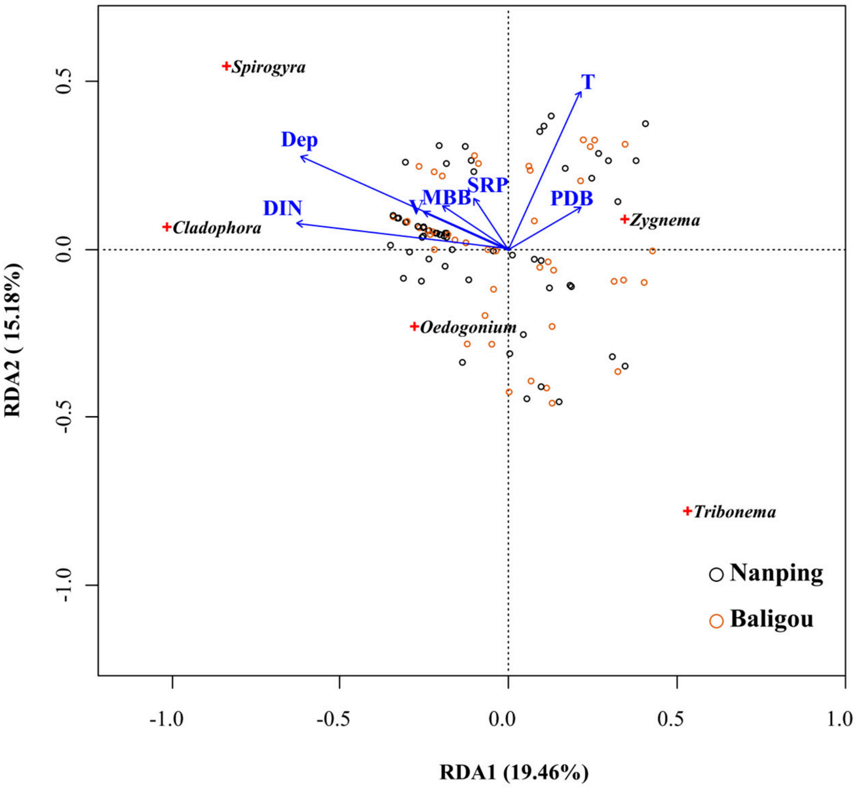

Figure 6. Redundancy analysis (RDA) of filamentous algal species composition and forward-selected environmental factors. T: water temperature, V: water velocity, Dep: water depth, SRP: soluble reactive phosphorus, DIN: dissolved inorganic nitrogen, PDB: periphytic diatom biomass, MBB: macrobenthic biomass.

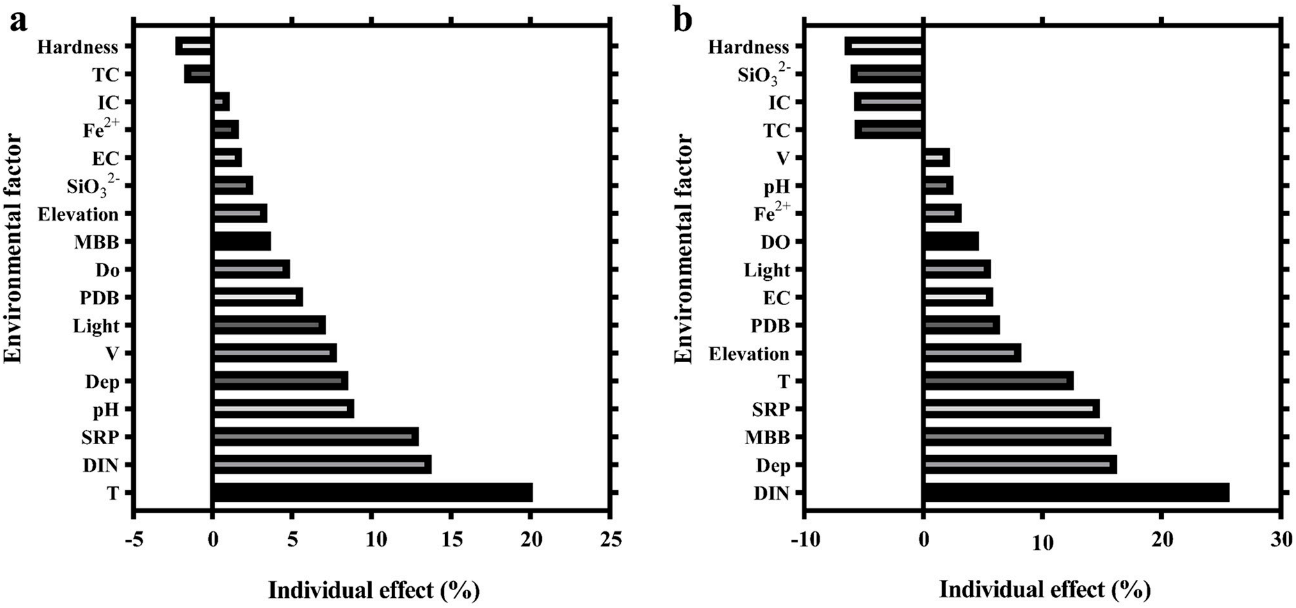

Figure 7. Contributions of the potential variables explaining the biomass of *S. communis* (**a**) and *C. glomerata* (**b**) in the VPA. T: water temperature, DO: dissolved oxygen, EC: electrical conductivity, V: water velocity, Dep: water depth, SRP: soluble reactive phosphorus, DIN: dissolved inorganic nitrogen, Fe^{2+}: ferrite, SiO_3^{2-}: silicate, TC: total carbon, IC: inorganic carbon, PDB: periphytic diatom biomass, MBB: macrobenthic biomass.

The best GLM results from the 17 explanatory variables are presented in Table 2. The determination coefficients (R^2) of 0.37 and 0.27, along with AIC values of 65.88 and 70.12 for *S. communis* and *C. glomerata*, respectively, indicated the valid performance of the GLMs. The Generalized Linear Model (GLM) analysis revealed that both *S. communis* and *C. glomerata* had positive correlations with water temperature, nutrient concentrations, and water depth. Moreover, the models revealed distinct differences for the two species. *S. communis* demonstrated a negative correlation with water velocity (Figure 8a), whereas *C. glomerata* showed a positive correlation with macrobenthic biomass (Figure 8b). A positive correlation observed between macrobenthic biomass and *C. glomerata* biomass suggested a potential mutually beneficial relationship between the two taxa. Notably, *C. glomerata* may serve as an important refuge and habitat for macrobenthos, while macrobenthos may help eliminate competitors for *C. glomerata* in benthic habitats. Macrobenthos increased the availability of light and nutrients for filamentous algae by feeding on periphytic diatoms, thereby promoting the growth of filamentous algae.

Table 2. Best GLMs for explaining the biomass of *S. communis* and *C. glomerata*.

Species	**Adj-R^2**	***AIC***	***BIC***	**Best Model**
S. communis biomass	0.38	65.88	69.92	Y = 0.343T + 0.308SRP + 0.249DIN + 0.22Dep − 0.187V + 0.643
C. glomerata biomass	0.32	70.12	75.38	Y = 0.365DIN + 0.322Dep + 0.238MBB + 0.198T + 0.152SRP + 1.782

Note(s): AIC: Akaike information criterion, BIC: Bayesian information criterion, T: water temperature, V: water velocity, Dep: water depth, SRP: soluble reactive phosphorus, DIN: dissolved inorganic nitrogen, MBB: macrobenthic biomass.

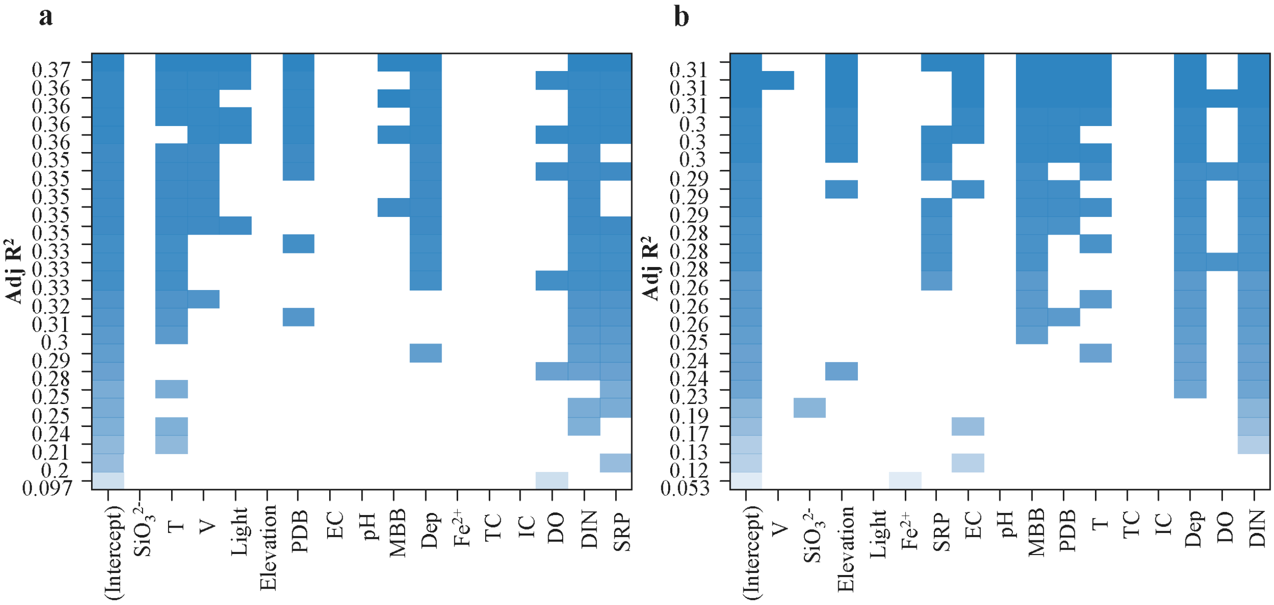

Figure 8. Relative importance of abiotic and biotic factors on *S. communis* (**a**) and *C. glomerata* (**b**). T: water temperature, DO: dissolved oxygen, EC: electrical conductivity, V: water velocity, Dep: water depth, SRP: soluble reactive phosphorus, DIN: dissolved inorganic nitrogen, Fe^{2+}: ferrite, $SiO_3{}^{2-}$: silicate, TC: total carbon, IC: inorganic carbon, PDB: periphytic diatom biomass, MBB: macrobenthic biomass.

The co-occurrence networks between filamentous algae and macrobenthos were further examined. Figure 9 demonstrates that the macrobenthic species associated with *S. communis* and *C. glomerata* were distinctly different. The results demonstrated that macrobenthos species associated with *S. communis* mostly exhibited negative effects, such as *Cordulegastridae* sp., *Polypedilum* sp., *Baetis* sp., and *Hydropsyche* sp., which are common consumers of *Spirogyra* [41]. Conversely, macrobenthic species closely related to *C. glomerata* were primarily herbivores with positive correlations, including *Radix swinhoei* (Adams, 1866), *Hydropsyche* sp. (Pictet, 1834), and *Phryganea* sp. (Linnaeus, 1758). Due to the poor palatability of *Cladophora*, hardly any macrobenthos can feed on it. Competition from periphytic diatoms has become the most significant limiting factor for the growth of *Cladophora*. At sampling sites with abundant herbivorous macrobenthos, periphytic diatoms were rarely observed on *C. glomerata* (Figure 10a). In contrast, at sampling sites lacking herbivorous macrobenthos, a large amount of periphytic diatoms were found attached to *C. glomerata* (Figure 10b). These findings suggested that these herbivores may positively affect the growth of *C. glomerata* by consuming periphytic diatoms attached to filamentous algae.

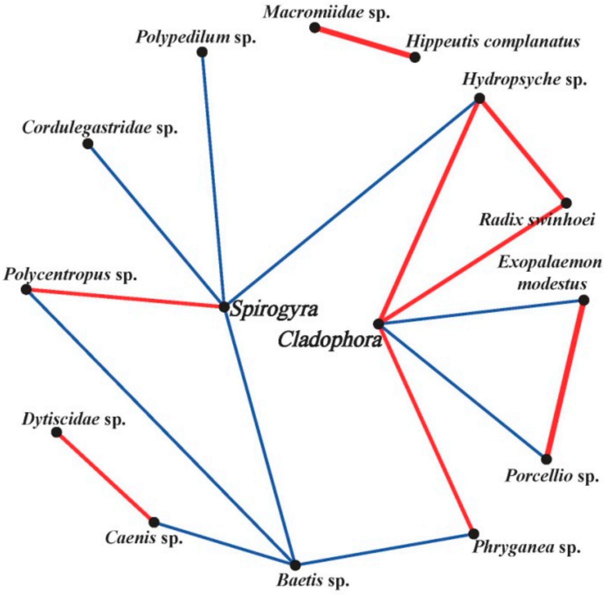

Figure 9. Co-occurrence networks between the filamentous algae and macrobenthic taxa. The red lines represent positive correlations, and the blue lines represent negative correlations.

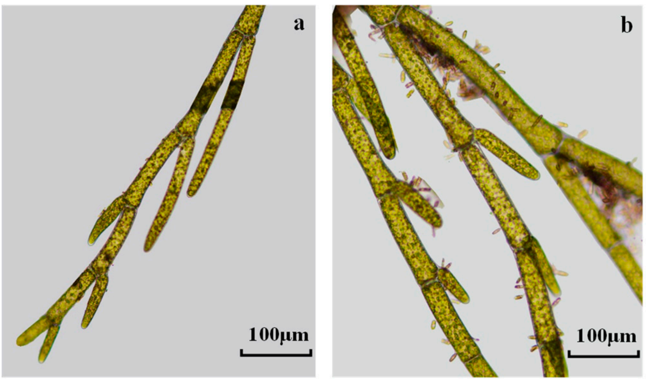

Figure 10. *C. glomerata* at the sites with (**a**) and without macrobenthos (**b**).

4. Discussion

Recent research has identified the frequent bloom of two common filamentous algae, *Cladophora* and *Spirogyra*, in streams [42]. While these streams have exhibited a transition from *Spirogyra* to *Cladophora*, the precise mechanisms underlying this shift remain unclear and lack definitive evidence. During the observed period, we found a low diversity but large biomass of filamentous algae in the southern Taihang catchment. Our study revealed that *S. communis* and *C. glomerata* were the two most prevalent filamentous algal species capable of causing blooms in this area. *C. glomerata* tended to dominate under high-nutrient conditions, while *S. communis* was more likely to thrive at slightly lower nutrient levels, reflecting their different ecological preferences.

Previous studies have shown that the coverage and biomass of filamentous algae generally increase in aquatic ecosystems experiencing eutrophication. For instance, Bosch et al., Higgins et al., and Olsen et al. have indicated this trend [43–45]. Additionally, Page et al. conducted a study in Conesus Lake, New York, and demonstrated a correlation between high filamentous algae coverage and elevated nitrogen and phosphorus loadings in streams [46]. Francoeur et al. [15] investigated the reappearance of filamentous algae blooms in the Great Lakes and found that the growth of filamentous algae was stimulated by mussel nutrient excretion and artificial fertilization with nitrogen and phosphorus. In our study, we observed a significantly greater total biomass of filamentous algae in Nanping compared to Baligou, confirming an increase in filamentous algae coverage with trophic level. Additionally, *C. glomerata* exhibited greater susceptibility to eutrophication than *S. communis* did, consistent with previous findings that *Spirogyra* is tolerant to oligotrophic conditions, while *Cladophora* prefers eutrophic conditions [47,48]. Hawes [49] noted that *Spirogyra* can store nitrogen and phosphorus, even at their low concentrations in water, allowing for the development of a large biomass of this taxon, highlighting its tolerance to nutrient-poor conditions. Han et al. [50] also suggested that internal reserves of inorganic nutrients likely contribute to the initial development of *Spirogyra*, even under low nutrient concentrations. Therefore, as nutrient levels increase, the filamentous algae community may shift from *Spirogyra* to *Cladophora*, which have lower palatability and greater biomass [51].

In addition to nutrient levels, water temperature is also believed to play a significant role in the distribution of filamentous algae, as different taxa have specific temperature preferences that affect their growth and survival [10,12,44,51]. It is thought that the growth of *Cladophora* is favored by relatively high water temperatures [44]. Adams and Stone [52] determined that the optimal temperature range for *Cladophora* was from 25 to 30 °C. Furthermore, Cambra-Sanchez and Aboal [53] reported that the *Spirogyra* typically appears in early spring and is subsequently succeeded by a vigorous growth of *Cladophora* in early summer, suggesting distinct temperature preferences for these two species. However, our findings showed that *S. communis* had a broader distribution in the Baligou, where temperatures were higher, compared to the Nanping stream. The positive effect of water temperature on the distribution of *S. communis*, as indicated in the GLM, also suggested that this species has a broad temperature niche.

Several studies have documented the preferences of these two species for other environmental factors. For instance, Margalef [54] noted that the filamentous algae of *Spirogyra* are replaced by *C. fracta* and *C. glomerata* mats in more permanent waters. *Spirogyra* can survive periodic drought, produce durable zygospores, and become the dominant genus in all types of temporary water [53,55]. Frossard et al. [56] reported that *Cladophora* attached to a solid substrate was more resistant to the effects of wind, waves, and current compared to weakly attached *Spirogyra*. In our study, the GLM results also indicated a preference for *S. communis* for slow flow. Additionally, *C. glomerata* was found to be more sensitive to water depth, confirming its preference for living in permanent waters that do not dry up in the summer.

We observed a positive correlation between *C. glomerata* and macrobenthos, which are larger aquatic organisms that can influence algal growth through grazing and nutrient recycling. It is well documented that grazers can remove periphytic diatoms from the surface of host plants, thus reducing the shading effect on the latter [57,58]. Ye et al. [59] demonstrated that grazing by the shrimp *Neocaridina denticulata sinensis* (Kemp, 1918) removed periphytic diatoms from the submerged plant *Vallisneria denseserrulata* (Makino, 1921), leading to a notable increase in biomass accumulation in the host plants. In spite of these studies have focused primarily on submerged macrophytes as host plants, the ecological effects of these macrobenthos are consistent. Some researchers believe that macrobenthos not only consume periphytic microalgae but also filamentous macroalgae [60]. Notably, a reduction in filamentous algae is often achieved through grazing by large herbivores rather than small species [61]. Pinowska [62] noted out that grazing and nutrient release by the small-sized species *Lymnaea turricula* stimulated the growth of *Cladophora* sp. The macrobenthic species related to *C. glomerata* in our study were mostly small herbivores, indicating that the presence of the macrobenthos may increase the growth of *Cladophora* mainly by reducing the biomass of periphytic diatoms. A high fish density in Baligou has a controlling effect on macrobenthic density, which promotes the development of periphytic diatoms. These diatoms compete strongly with *Cladophora*, ultimately leading to the suppression of *Cladophora* biomass (Figure 11 Left). In contrast, the low fish density in Nanping allows for the flourishing of macrobenthos, which controls periphytic diatoms, ultimately promoting the growth of *Cladophora* (Figure 11 Right).

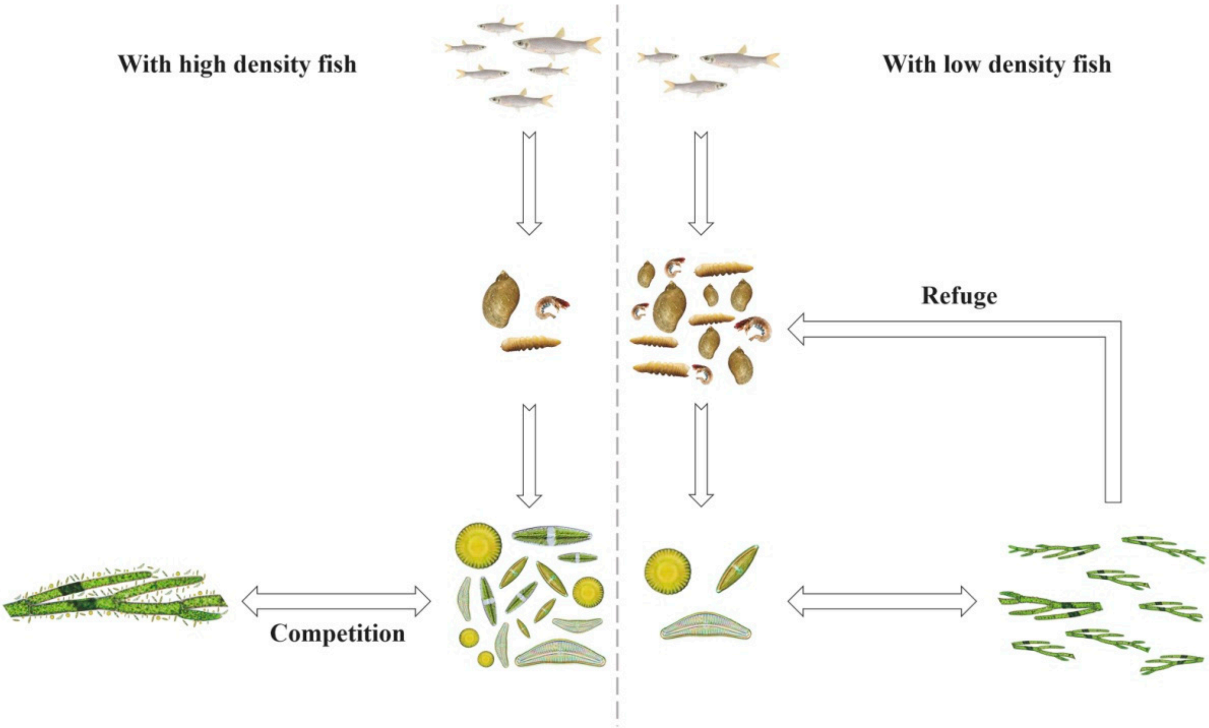

Figure 11. The mechanism diagram illustrating the variations in *Cladophora* biomass under two different fish population density conditions.

5. Conclusions

The findings of our study have important implications for river restoration. As nutrient levels rise, rivers undergo an initial increase in *Spirogyra* density, followed by *Cladophora*, often resulting in a shift from clear water to nuisance water with surface coverage. Many river restoration projects aim to reduce filamentous algal coverage as a primary goal. However, controlling *Cladophora* through biomanipulation is challenging due to its lower palatability to grazers than to other benthic algae [51]. Nevertheless, *Cladophora* provides substrates for periphytic diatom growth, creating the possibility of controlling it by leveraging the competition between *Cladophora* and its periphytic diatoms [63,64]. Food web management is often used to reduce the abundance of macrobenthos, which in turn decreases predation pressure on periphytic diatoms and can be an effective approach. Manipulating the benthic food web to diminish grazing control of periphytic diatoms may prove to be a crucial management tool, as *Cladophora* may be shaded by these periphytic diatoms. Increasing the population of benthivorous fishes, such as the indigenous species *Phoxinus oxycephalus*, in rivers may yield significant improvements with less effort. Nonetheless, managing trophic states in rivers remains the fundamental approach to water management.

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