Temporal variation of rotifer community in three climatic zones and their relationship with environmental factors

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ABSTRACT
Comparative analyses of rotifer community structure in freshwater lakes among different climatic zones are limited. In this study, six freshwater lakes located in warm temperate, subtropical and tropical zones were selected to investigate the annual dynamics of rotifer communities and their major driving factors. The results indicated that rotifer community structure did not exhibit significant seasonal variations. However, significant differences were observed among climatic zones. The species number and total density of rotifers were significantly higher in subtropical lakes than in lakes from other zones (p < .05). Both multidimensional scaling and detrended correspondence analysis revealed significant separation of tropical samplings from warm temperate and subtropical samplings, which was mainly caused by the higher temperature and lower chlorophyll a content in the tropical lakes. Further analyses indicated that rotifer community structure was mainly affected by water temperature, trophic indices and pH in the warm temperate zone but by chlorophyll a content and Secchi depth in subtropical lakes. In addition, only the Simpson index was significantly associated with Secchi depth and pH in tropical lakes. Overall, these results indicated great differences in annual dynamics of rotifer communities and their driving factors among warm temperate, subtropical and tropical zones.

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Introduction
Rotifers are a kind of tiny metazoan with strong dispersal ability and high reproduction rate. They belong to a dominant group of zooplankton (Haberman and Laugaste 2003), accounting for 10–40% of zooplankton biomass (Herzig 1987) that links the macro food web and micro food web in a water body (Arndt 1993; Tadonleke 2004). Therefore, rotifers play a key role in nutrient circulation and energy flow in aquatic ecosystems (Wallace 2002).

The community structure of rotifers is associated with various physical, chemical and biological factors (Duggan et al. 2002; Jeppesen et al. 1997). In a certain range of temperature,
the increase of water temperature (WT) can shorten the main developmental stages of rotifers (Herzig 1987), and weaken the negative impacts of ‘bottom-up’ forces on the rotifer community, thereby driving the spatial variation of rotifer abundance (Wen et al. 2019). The decrease of rotifer abundance and species diversity was always accompanied by increased total phosphorus concentration (TP) but increased inorganic nitrogen level (such as NO$_3^-$/N and NO$_2^-$/N) promoted rotifer density (Castro et al. 2005; Wang et al. 2010). Similarly, investigations on three lakes in Portugal revealed that species abundance decreased but species richness increased with increasing nutrient level (Castro et al. 2005). Khaleqsefat and Malekzadeh-Viayeh (2013) found that the dissolved oxygen (DO) concentration, water conductivity and salinity were the most influential factors driving differences in rotifer species diversity and abundance between two water bodies in Northwest Iran. Similarly, other reports also proved the effects of DO concentration on rotifer community (Armengol et al. 1998; Mikschi 1989). In addition, pH (Bielańska-Grajner 2001) and turbidity (Duggan et al. 2002) were also reported to affect the distribution and abundance of rotifer species. Due to overlap of feeding, the competition pressure of *Moina macrocopa* reduced the survival and reproduction rates of the rotifera *Brachionus calyciflorus* and *Brachionus angularis* (Huang 2014). In addition, predation pressure decreased the maximum population density and maximum population growth rate of rotifers (Sarma et al. 2011).

Climatic zone is a large-scale concept integrating various environmental factors. Division of climatic zones is related to latitude but also is influenced by the differences in altitude, topography, atmospheric circulation and water supply. To explore the spatial differentiation of zooplankton communities, studies have compared the effects of latitude on the structure of zooplankton communities. However, most of these studies investigated locations within the same climatic zone. For example, in the tropical zone, zooplankton biomass decreased and specific diversity increased from 23°S to 18°S at the east-southeast Brazilian continental shelf (Valentin and Monteiro-Ribas 1993). In temperate marine climatic zone, the long-term mean value of zooplankton abundance was higher in south than in north of Iceland. In the south, *Podon leuckarti* and *Cirripede* larvae were relatively more abundant, and changes of zooplankton composition were mainly driven by salinity and nitrogen content. In the north, *Calanus hyperboreus* was more abundant, and WT was a major factor affecting zooplankton community (Gislason et al. 2009). Tavşanoğlu et al. (2017) compared six lakes at different latitudes in the warm zone of Europe and the results showed that rotifer diversity increased, but its total biomass decreased with the increase of temperature. However, water depth and nutrient availability did not significantly affect the community composition and size structure of the zooplankton in these regions.

The spatial heterogeneity of zooplankton community structure is caused by the complex interaction among physical and biological processes (Valentin and Monteiro-Ribas 1993). Thus, comparison of zooplankton communities between different climatic zones might provide more information for understanding the mechanisms underlying differentiation, dynamics and regulation of the zooplankton community than comparisons between latitudes at the same altitude. However, to the best of our knowledge, only a few reports have investigated zooplankton communities spanning two climatic zones. At the western North Pacific, marine zooplankton abundance was the lowest in the South and increased northward from 35°N (subtropics) to 44°N (warm temperate zone) along 155°E (Yamaguchi et al. 2017). Green (1994) covered both temperate and tropical zones, and revealed that differences of zooplankton community between latitudes might be attributed to algal level, size of the lake and salinity. However, neither study compared the factors driving the changes of zooplankton community between temperate and tropical zones.
In addition, from researchers independently exploring the major environmental factors driving the seasonal variation of zooplankton community, one could identify some evidence that the major factors driving the dynamics of zooplankton communities might differ greatly between climatic zones. In the warm temperate zone of the coastal waters of China (34.62°–34.76°N, 119.46°–119.66°E), WT was the primary factor influencing the fluctuations of marine zooplankton abundance and community structure, and high contents of ammonia nitrogen (NH$_4^+$–N) and suspended matter suppressed zooplankton species diversity, evenness and richness indices (Wu et al. 2011). In the subtropical zone of the East China sea, the zooplankton abundance reached the highest level in spring at Xiangshan Bay (29.9°N), but in summer at the Sanmen Bay (29.0°N) and Yueqing Bay (28.0°N). The major factors driving the variations of zooplankton communities in this area included salinity, WT, chlorophyll a (Chl-a), NH$_4^+$–N, soluble reactive phosphate and inorganic nitrogen contents (Sun et al. 2016). Comparison of these two references indicated that Chl-a, representing the algal food level, had a stronger influence on zooplankton community in subtropical than in warm temperate zone.

In both warm temperate and subtropical zones, temperature varies greatly among seasons; thus, it should be an important factor driving the seasonal variation of zooplankton community. Moreover, the subtropical zone has a higher average temperature than the warm temperate zone and can support the growth of more species and a higher density of algae. Thus, algal level might have greater effects in the subtropical zone than in the warm temperate zone. In the tropical zone, the temperature changes little between seasons and the annual average WT is too high to support a broad spectrum of algae species. Thus, both WT and algal level might less have less influence on the zooplankton community in the tropical zone. To test these hypotheses, the annual changes of rotifer communities in six lakes belonging to three temperate zones were investigated in the present study. The parameters of community structure were compared among different climatic zones and the major environmental factors driving these differences were discussed. These results provide more information and insights into the regulatory mechanisms underlying annual changes of rotifer communities in various climatic zones.

**Methods**

**Study sites**

Three pairs of small shallow lakes (average water depth less than 3 m) in eastern China were selected. The pairs were located at Jinan city (Lake Daming and Lake Meili), Nanchang city (Lake Qingshan and Lake Xiang) and Sanya city (Lake Jiuqu and Lake Wuming, Table 1), belonging to warm temperate, subtropical and tropical zones, respectively (Figure 1). The climatic characteristics of these cities are listed in Table 2. The three cities differed greatly in annual average temperature, precipitation and/or daylight hours.

Lake Meili (Warm temperate 1, W1) is located northwest of Jinan City, with a surface area of 30 ha and water depth from 1.7 to 2.2 m. Lake Daming (Warm temperate 2, W2) is located northeast of Jinan City, with an area of 58 ha, mean depth of 2 m and maximum depth of 4.5 m. Lake Meili and Lake Daming both connect to the Yellow river but not directly to each other. Lake Xiang (Subtropical 1, S1) and Lake Qingshan (Subtropical 2, S2) are located southwest and northeast of Nanchang city, with surface areas of 211.1 and 316 ha, and mean depth of 1.8 and 2 m, respectively. Lake Xiang connects to Lake Qingshan through the Yudai river which is approximately 8 km long. They also connect to the Ganjiang river, a branch of the Yangtze river. Lake Jiuqu (Tropical 1, T1) and Lake
Wuming (Tropical 2, T2) are located east of Sanya city, Hainan island. Their areas were 20 and 16 ha and mean depths 2 and 1.4 m, respectively. These two lakes connect through some small rivers. The three pairs of lakes do not link with each other.

### Table 1. Longitude and latitude of sampling locations.

| Sampling lake                  | Longitude and latitude                     | Area (ha) | Depth (m) |
|--------------------------------|--------------------------------------------|-----------|-----------|
| **Warm temperate zone (Jinan City)** |                                           |           |           |
| Lake Meili (W1)                | N36°43'48.17" E116°52'10.78"              | 30        | 1.7–2.2   |
| Lake Daming (W2)               | N36°40'23.34" E117°00'57.90"              | 58        | 2         |
| **Subtropical zone (Nanchang City)** |                                           |           |           |
| Lake Xiang (S1)                | N28°37'51.48" E115°53'37.98"              | 211       | 1.8       |
| Lake Qingshan (S2)             | N28°41'14.95" E115°55'24.74"              | 316       | 2         |
| **Tropical zone (Sanya City)**  |                                           |           |           |
| Lake Jiuqu (T1)                | N18°14'55.73" E109°35'41.03"              | 20        | 2         |
| Lake Wuming (T2)               | N18°15'54.46" E109°36'56.11"              | 16        | 1.4       |

**Figure 1.** Sampling locations for rotifers in the three cities.

**Sample collection, treatment and analysis**

From August 2016 to July 2017, water samples were collected from each lake at the middle of each month. The samplings avoided bad weather, such as strong wind, rain and
snow as much as possible and were conducted between 0900 and 1100. At each site, water samples were collected from 3 depths (0, 0.5 and 1.0 m) using a 2.5 L water sampler. After mixing, the water samples were filtered through a plankton net (pore size 25 μm). Zooplankters were fixed in 5% formalin and then concentrated to 30 mL after 48 h of natural precipitation. Rotifera, Cladocera (Cl), nauplius (Nau), Asplanchna (Aspl) and copepods (Cop) were identified and counted under a microscope. Rotifera were identified to the species level according to Wang (1961) and Zhuge (1997). Cladocera and copepods were identified to the genus level according to Jiang and Du (1979).

**Determination of environmental parameters**

For the mixed water samples, total nitrogen (TN), total phosphorus (TP), ammonium–nitrogen (NH₄⁺–N), and nitrite–nitrogen (NO₂⁻–N) concentrations were measured following Gilcreas (1966). Chlorophyll a (Chl-a) was extracted using acetone and determined spectrophotometrically. Surface water temperature (WT), pH and Secchi’s depth (SD) were measured using a mercury thermometer, a pH meter and a Secchi disk, respectively. Comprehensive trophic state index (TSIc) was calculated using the formula TSIc = Pj(Wj/TSIj), where Wj = rj²/Σrj² to evaluate the nutritional status of lakes, where TSIj means the trophic state indices of Chl-a, TP, TN and SD. Wj means the weight of these indices, rj is the correlation coefficient between each parameter and Chl-a content after normalization. The detailed method has been described in Tang et al. (2019).

**Data analyses**

Based on rotifer species composition and density of each species, the Simpson index (D), Margalef index (d), Shannon–Wiener diversity index (H), Pielou evenness index (E) and Dominance (Y) were calculated as follows:

\[
D = 1 - \sum \left( P_i \times \log_2 P_i^2 \right) \\
d = (S - 1)/\ln N \\
H = -\sum \left[ (N_i/N) \times \log_2 (N_i/N) \right] \\
E = H/H_{\text{max}} \\
Y = (N_i/N)f_i
\]

where \( P_i \) is equal to \( N \) divided by \( N_i \), \( N_i \) is the density of the \( i \)th species, \( N \) is the total density of rotifer, \( S \) is the number of species, \( H_{\text{max}} \) means the \( H \) value of the maximum diversity of the community and \( f_i \) is the frequency of the \( i \)th species. Species with \( Y > 0.02 \) were considered dominant.

Two-way ANOVA was used to compare rotifer community parameters among different seasons and different climatic zones. Stepwise regression analysis was conducted to

| Parameters                          | Jinan | Nanchang | Sanya  |
|------------------------------------|-------|----------|--------|
| The average annual temperature     | 14.7  | 17.7     | 25.7   |
| Extreme high-temperature           | 40.5  | 40.6     | 35.9   |
| Extreme low-temperature            | -14.9 | -9.7     | 5.1    |
| The coldest month and mean temperature | January, -0.4 | January, 5.5 | January, 21.4 |
| The hottest month/mean monthly temperature | July, 27.5 | July, 29.5 | June, 28.7 |
| Mean annual precipitation          | 671.1 | 1613.6   | 1347.5 |
| Mean annual sunshine hours         | 2546.8| 1832.9   | 2534   |

Table 2. The climatic features of the three sampling zones.
identify the dominant environmental factors affecting $S, N, E, H, D$ and $d$. These analyses were performed using SPSS 19.0 software.

The similarity coefficient matrix of rotifer community structure was constructed based on Bray Curtis distance. The spatio-temporal influences on rotifer community structure were tested using the two-way ANOSIM analysis. Significance and community separation degree were assessed using the $p$ value and $R$ value ($R > 0.75$, complete separation; $0.5 < R \leq 0.75$, obvious separation with slight overlap; $0.25 < R \leq 0.5$, obvious overlap with partial separation; $R \leq 0.25$, obvious overlap and almost inseparable). A two-dimensional biplot map of rotifer community structure was constructed using the multidimensional scaling (MDS) method. The similarity percentage (SIMPER) was used to identify the important species contributing to the similarity and dissimilarity between rotifer communities. In order to reduce the impacts of extreme data, the data were converted into $\log_{10}(aX + b)$ for analysis. ANOSIM, MDS and SIMPER were conducted using the primer 5.0 software.

The gradient analysis of rotifer community and environmental factors was carried out using CANOCO 5.10. Firstly, the species composition data were analyzed using the detrended correspondence analysis (DCA), and the corresponding models and methods were selected according to the gradient length of the longest axis (Leps and Smilauer 2003). For DCA, the data of species composition were $\log(x + 1)$ transformed. The measured environmental factors were also $\log(x + 1)$ transformed to remove skew and then standardized to zero mean and unit variance to remove the influence of differing scales of measurement (Duggan et al. 2002). Because occasional rotifers with densities of less than 0.1% could provide little information to the overall community structure (Eti[99]é et al. 2009), only species with densities higher than 0.1% were included in the analysis. DCA revealed that the gradient (3.08) was about 3 standard deviation units in the regional study. Therefore, unimodal ordination techniques would be more appropriate (ter Braak and Smilauer 2002). Hence, the redundancy analysis (RDA) was used to investigate the relationship between the rotifer community structure and all predicted environmental variables (ter Braak and Verdonchot 1995). Before the analysis, the contribution rate and significance of each environmental factor were calculated using the forward selection procedure. Combined with Monte Carlo replacement test, variables with expansion coefficient less than 10 (VIF < 10) and $p < .05$ were selected into the model for ordination.

**Results**

**Environmental parameters**

During the sampling period, the annual average water temperature of the six lakes ranged from 16.4 to 25.6°C. The lowest water temperature appeared in January for all three zones, equal to 4.4, 7.8 and 22.9°C in Jinan, Nanchang and Sanya City, respectively. The highest water temperature was observed in July at Jinan (29.5°C) and Nanchang (30.7°C) City, but in August at Sanya City (28.4°C, Figure S1).

The highest TP content was observed in subtropical lakes and the lowest was observed in warm temperate lakes ($p < .05$, Table S1). SD of the two lakes in subtropical zone was significantly lower than other climatic zones ($p < .05$, Table S1). The Chl-$a$ concentration of the two lakes in tropical zone was significantly lower than subtropical and warm temperate zones ($p < .05$, Table S1). TSIc of the two lakes in subtropical zone was significantly higher than the other climatic zones ($p < .05$, Table S1). However, no significant
differences in $\text{NH}_4^+ - \text{N}$, $\text{NO}_2^- - \text{N}$ and pH were observed among the three climatic zones (Table S1).

**Species composition and dominance**

A total of 76 species of Rotifera belonging to 22 genera and 15 families were observed in the six lakes, of which 36, 42, 47, 39, 29 and 22 species were identified in Lake Meili (W1), Lake Daming (W2), Lake Xiang (S1), Lake Qingshan (S2), Lake Jiuqu (T1) and Lake Wuming (T2), respectively (Table 3). Obviously, subtropical and warm temperate lakes showed more species than tropical lakes. Twelve species were shared by the six lakes, of which *Polyarthra dolichpotera*, *Trichocerca rousseleti* and *Anuiaeopsis fissa* displayed higher abundance than other species (Table 3). Rotifer species identified in the lakes were consistent with those found in other shallow lakes in China (Wen et al. 2017).

The changes of rotifer total density in the six lakes showed similar trends with water temperature. In the two warm temperate lakes (Lake Daming and Meili), the highest rotifer density appeared in August with the lowest in March. In the two subtropical lakes (Lake Qingshan and Xiang), the highest rotifer density appeared in September with the lowest in February. In the two tropical lakes (Lake Jiuqu and Wuming), the highest rotifer density appeared in June with the lowest in May (Figure 2). Analysis of ANOVA showed that the average density of rotifers in the two subtropical lakes (Lake Qingshan and Xiang) was significantly higher than those in warm temperate (Lake Daming and Meili) and tropical (Lake Jiuqu and Wuming) lakes ($p < .05$, Table S2).

In Lake Meili, Daming, Xiang, Qingshan, Jiuqu and Wuming, 7, 6, 8, 8, 7 and 9 species were identified as dominant species ($Y > 0.02$), respectively. Among them, *A. fissa* and *Trichocerca pusilla* were shared by the six lakes, and the relative abundance of *A. fissa* was higher than 15% in all lakes (Tables 3 and 4). *Keratella cochlearis*, *T. rousseleti* and *P. dolichpotera* were dominant species in one or two lakes at each climatic zones. Moreover, *Brachionus forficula*, *Keratella tropica* and *Polyarthra major* were dominant only in the tropical lakes (Table 4).

**Comparisons of community structure indices**

The two subtropical lakes showed significantly higher rotifer total density ($N$) than warm temperate and tropical lakes. The annual average Shannon–Weiner diversity index ($H$) of the rotifer community in Lake Xiang (subtropical zone) was significantly higher than those in other lakes ($p < .05$, Table S2). No significant differences were detected in species number ($S$), Pielou evenness index ($E$), Margelef index ($d$) and Simpson index ($D$) between the six lakes (Table S2).

The annual average densities of potential competitors and predators to herbivorous rotifers in the six lakes are shown in Table S3. The densities of nauplius (Nau) and *Asplanchna* (Aspl) were significantly higher in the two subtropical lakes (Lake Qingshan and Xiang) than other lakes ($p < .05$). The densities of Cladocera (Cla) and Copepoda (Cop) in Lake Jiuqu (tropical zone) were significantly higher than other lakes ($p < .05$, Table S3).

Correlation analysis showed that number of species ($S$), total density of rotifer ($N$) and Margelef index ($d$) were significantly positively correlated with Chl-$a$ content, TSIc, *Asplanchna* density (Aspl) and Cladocera density (Cla). Shannon–Weiner diversity index ($H$) was significantly positively associated with Aspl (Table 5). Two-way ANOVA showed that $S$, $N$ and $d$ were significantly affected by climatic zone and season independently.
Table 3. Species composition and their relative abundance in the sampling lakes.

| Species            | Abbre. | W1 | W2 | S1 | S2 | T1 | T2 |
|--------------------|--------|----|----|----|----|----|----|
| Brachionus         |        |    |    |    |    |    |    |
| B. calyciflorus    | Brcl   | 2  | 3  | 2  | 3  | 2  | 2  |
| B. forficula       | Bfrf   | N  | N  | 1  | 1  | 2  | 2  |
| B. leydigi         | Brld   | N  | N  | 0  | 0  | N  | N  |
| B. angularis       | Brag   | 2  | 1  | 2  | 3  | 2  | 2  |
| B. caudatus        | Brca   | N  | N  | 0  | N  | N  | N  |
| B. variabilis      | Bvr    | N  | N  | N  | 1  | N  | N  |
| B. budapestiensis  | Brp    | N  | N  | N  | 1  | N  | N  |
| B. urceolarius     | Bru    | N  | N  | N  | 1  | N  | N  |
| B. quadridentatus  | Brq    | 0  | 2  | 1  | 2  | 1  | N  |
| B. diversicornis    | Brd    | 3  | 3  | 3  | 4  | 2  | 2  |
| B. caudatus        | Brca   | N  | N  | N  | 1  | N  | N  |
| B. forcatus        | Bro    | N  | N  | N  | N  | 1  | 1  |
| Keratella          |        |    |    |    |    |    |    |
| K. cochlearis      | Kec    | 1  | 1  | 2  | 1  | 3  | 3  |
| K. vaigavarga      | Kev    | N  | N  | 2  | 1  | 1  | N  |
| K. tropica         | Ket    | N  | N  | N  | N  | 1  | 3  |
| Anuraeopsis        |        |    |    |    |    |    |    |
| A. cfissa          | Anf    | 6  | 5  | 5  | 6  | 5  | 5  |
| A. coelata         | Anc    | N  | 1  | N  | N  | N  | N  |
| Lepadella          |        |    |    |    |    |    |    |
| L. quinquecostata  | Leq    | N  | 1  | N  | N  | N  | N  |
| Lecane             |        |    |    |    |    |    |    |
| L. luna            | Leh    | N  | N  | 1  | N  | N  | N  |
| L. (M.) ornata     | Lmo    | N  | N  | N  | 1  | N  | N  |
| L. (M.) lulla      | Lml    | N  | N  | 1  | 0  | N  | N  |
| L. tenuiseta       | Let    | N  | 1  | N  | N  | N  | N  |
| L. (M.) decipens   | Lmd    | N  | N  | N  | N  | 1  | N  |
| Asplanchna         |        |    |    |    |    |    |    |
| A. brightwelli     | Asb    | N  | 2  | 1  | 2  | N  | N  |
| A. priodontia      | Asp    | 1  | 1  | 2  | 1  | 1  | 1  |
| A. sieboldi        | Ass    | N  | N  | 1  | 1  | 1  | N  |
| A. girodii         | Asg    | 2  | 2  | 1  | 2  | 1  | N  |
| Synchaeta          |        |    |    |    |    |    |    |
| S. tremula         | Syt    | 1  | 1  | 2  | 1  | N  | N  |
| S. pectinata       | Syp    | 2  | 2  | 1  | 0  | N  | N  |
| S. styloata        | Sys    | 2  | 1  | 2  | N  | N  | N  |
| S. monostyla       | Sym    | N  | N  | N  | 0  | N  | N  |
| S. oblonga         | Syo    | 1  | 0  | N  | N  | N  | N  |
| Trichocerca        |        |    |    |    |    |    |    |
| T. pusilla         | Trp    | 3  | 4  | 3  | 2  | 2  | 2  |
| T. chattoni        | Tc     | N  | 1  | 2  | 1  | 1  | N  |
| T. elongata        | Tre    | N  | N  | 1  | N  | N  | N  |
| T. tenuior         | Ttr    | 1  | 2  | 2  | N  | N  | N  |
| T. rousseleti      | Trr    | 3  | 4  | 3  | 4  | 2  | 3  |
| T. tattas          | Tra    | N  | 1  | 1  | 2  | N  | N  |
| T. gracilis        | Trg    | N  | 1  | 1  | 0  | 1  | 2  |
| T. cylindrica      | Try    | N  | N  | 1  | N  | N  | N  |
| T. vargai          | Trv    | 1  | 1  | 2  | 1  | N  | N  |
| T. capucina        | Tru    | 0  | 1  | N  | N  | N  | N  |
| T. stylata         | Trs    | N  | 1  | N  | N  | N  | N  |
| Filinia            |        |    |    |    |    |    |    |
| F. longiseta       | Fil    | 3  | 1  | 2  | 2  | 5  | 2  |
| F. camasecla       | Fic    | N  | N  | 1  | N  | N  | 2  |
| F. oponensis       | Fio    | N  | N  | 0  | N  | N  | N  |
| F. saltator        | Fis    | 1  | N  | 0  | N  | 3  | 2  |
| F. brachiata       | Fib    | N  | N  | 1  | N  | N  | 0  |
| F. major           | Fim    | 1  | 1  | N  | N  | 2  | N  |
| F. cornuta         | Fic    | N  | N  | N  | N  | 1  | N  |
| Polyarthra         |        |    |    |    |    |    |    |

(continued)
(p < .05). In addition, interaction of season × climatic zone only significantly affected N (p < .01; Table S4).

Two-way ANOSIM revealed that rotifer communities significantly overlapped between summer and winter (R = 0.322, p = .01) and between autumn and winter (R = 0.264, p = .01). The MDS results indicated that all samples were obviously overlapped and almost inseparable among seasons (global R = 0.138; Figure 3(a)). In contrast, the rotifer communities from three climatic zones were significantly separated (global R = 0.369, p = .01). The rotifer communities from subtropical and warm temperate zones partially overlapped but still retained some significant differences (R = 0.156, p = .01). However, they were significantly separated from the tropical zone (subtropical zone: R = 0.462, p = .01; warm temperate zone: R = 0.525, p = .01; Figure 3(b)).

The similarity percentage analysis (SIMPER) identified 14, 14 and 10 species contributing to the similarity in warm temperate, subtropical and tropical zones, respectively.
Among them, *A. fissa*, *T. rousseleti*, *T. pusilla*, *P. dolichpotera*, *Brachionus diversicornis* and *Filinia longiseta* were the most important, and their accumulative contribution rates were 56.59%, 51.43% and 65.82% in warm temperate, subtropical and tropical zones, respectively (Table S5). Moreover, 9, 8 and 2 important species mainly contributed to the dissimilarity between warm temperate and tropical zones, tropical and subtropical zones, warm temperate and subtropical zones, respectively. Compared with tropical zone, the relative abundances of *Anuiaeopsis cfissa*, *B. diversicornis*, *T. rousseleti*, *Ascomorpha saltans* and *T. pusilla* were higher, but those of *P. dolichpotera*, *F. longiseta*, *K. cochlearis* and *P. major* were lower in warm temperate zone. The relative abundances of *A. cfissa*, *B. diversicornis*, *B. calyciflorus*, *B. angularis* and *A. saltans* were higher, but that of *P. major* was lower in subtropical zone. In addition, *B. calyciflorus* showed higher abundance in warm temperate and subtropical zones than in tropical zone, and *P. dolichpotera* showed higher abundance in tropical and subtropical zones than in warm temperate zone (Table S6).

Stepwise regression analysis showed that *S* was significantly associated with TP and WT in the warm temperate zone, but with Chl-*a* in subtropical zone (*p* < .05). *N* was significantly correlated with WT, NH$_4^+$–N and NO$_2^-$–N in the warm temperate zone, but with SD and Chl-*a* in the subtropical zone (*p* < .01). In addition, *d*, *H* and *E* were significantly associated with TP, WT and pH in the warm temperate zone, respectively. *D* was significantly associated with pH and SD in the tropical zone (*p* < .05; Table 6).
Multivariate analysis

RDA showed that the first two ordination axes explained 73.55% of species–environment variability. Only six environmental variables showed significant effects after forward selection, including TN, WT, SD, Chl-a, Cla and Aspl. These results indicated that trophic state, algal food resource, water temperature and top-down effect might be major factors affecting rotifer community. All 72 samples were clearly divided into two parts on the plot (Figure 4). Samples from the tropical zone (numbers: 49–72) were clearly separated from subtropical and warm temperate zones (numbers 1–48). The division of these two parts was along axis 2. TN, WT and Chl-a were the major influential factors on axis 2, which might be the major factors driving this separation (Figure 4).

Discussion

Throughout the year, warm temperate and subtropical zones revealed more species number (S) than tropical zone, and total rotifer density (N) was higher in subtropical lakes that other lakes. First, eight species (including Synchaeta tremula, Synchaeta pectinate, Synchaeta stydata, Trichocerca tenuior, Trichocerca vargai, Pompholyx sulcata and Euchlanis triquetra) were detected in warm temperate and subtropical zones but not in tropical zones, suggesting that these species might be unable to tolerate high WT. As reported, S. tremula, S. pectinate, and S. stydata were spring to early summer species (Elliott 1977). P. sulcate was considered a thermophile but not thermobiont (Rogozin et al. 2015). Second, rotifers feed on phytoplankton, bacteria and detritus, and green algae are the most important food to herbivorous rotifers (Bërziç and Pejler 1989; Sládeček 1983). Warm temperate and subtropical lakes showed significantly higher Chl-a content than tropical lakes (Table S1), suggesting a higher algal food level, which could support more species and a higher density of rotifers (Hofmann 1977). Third, warm temperate and subtropical zones revealed greater temperature changes over seasons than the tropical zone, which might sustain more algal species. Different rotifers have different or differentiated preference for food resources (Gilbert and Bogdan 1984). Thus, a higher food diversity could support a higher rotifer diversity. Overall, variation of temperature and abundant food resource could explain the higher species number and total rotifer density in the subtropical zone.

The highest Shannon-Weiner diversity index (H) of the rotifer community in Lake Xiang (subtropical zone) (P < 0.05) may be due to its high trophic state, which was

| Table 4. Dominant species and their relative dominance in the six lakes. |
|-----------------------------|------|-------|------|-------|------|------|
| Species                     | W1   | W2    | S1   | S2    | T1   | T2   |
| B. calyciflorus             | –    | 0.0402| 0.0346| 0.0739| –    | –    |
| B. forcifica                | –    | –     | –    | –     | –    | –    |
| B. angularis                | –    | –     | –    | 0.0523| 0.0363| –    |
| B. diversicornis            | –    | 0.0293| 0.0411| 0.0755| –    | –    |
| K. cochlearis               | 0.0744| –    | 0.0337| –     | 0.0393| 0.0664|
| K. tropic                   | –    | –     | –    | –     | –    | 0.0201|
| A. fissa                    | 0.2044| 0.1096| 0.1326| 0.2189| 0.1811| 0.1434|
| T. pusilla                  | 0.052 | 0.0943| 0.0406| 0.0621| 0.0419| 0.026 |
| T. rousselet                | 0.0804| 0.0677| 0.0557| 0.1008| –    | –    |
| F. longistoma               | 0.0389| –    | –     | 0.028 | 0.1385| 0.0304|
| P. dolichopota              | 0.0514| –    | 0.0868| 0.2008| 0.0311| 0.2286|
| P. major                    | –    | –     | –    | –     | 0.1599| 0.0408|
| A. saltans                  | 0.1112| 0.0509| 0.0705| –    | –    | –    |

W1, Lake Meili; W2, Lake Daming; S1, Lake Xiang; S2, Lake Qingshan; T1, Lake Jiuqu; T2, Lake Wuming. – means that this species is not dominant in the lake (Y < 0.02).
consistent with the report that higher rotifer diversity was observed in eutrophic lakes (Demetraκi-Paleolog and Sender 2013). Dodson (1992) found that species diversity was negatively associated with trophic state, while Kuczyńska-Kippen and Joniak (2016) reported that the Shannon-Weiner index of rotifers was highest in eutrophic waters but lowest in hyper-eutrophic waters. Thus, from low to moderate trophic levels, higher trophic state in subtropical lakes promotes more food resources for diverse rotifers to survive, thereby explaining the increase in rotifer diversity.

Both MDS and RDA plots demonstrated that samplings from the tropical zone were obviously separated from warm temperate and subtropical zones (Figures 3 and 4). In contrast, Fernández de Puelles et al. (2019) reported no differences in zooplankton abundance and component between tropical and subtropical oceans. Zooplankton have a high capacity for dispersal. The ocean current, waves, and tides greatly strengthen the exchange of seawater across different latitudes, which may then disperse rotifers. In the present study, lakes in the warm temperate and subtropical zones belong to the Yellow river and Yangtze river systems, respectively, and lakes in the tropical zone are located at an isolated island. Thus, the exchange of water between them could be ignored, which might promote the differentiation of zooplankton community between tropical and the other two climatic zones in the present study. Two species, *A. saltans* and *P. major*, were identified as important contributors to the dissimilarity between tropical and subtropical/warm temperate zones, but not between subtropical and warm temperate zones (Table S5). The relative abundance of *A. saltans* decreased from warm temperate to subtropical and then to tropical zone (Table 3), and *P. major* was dominant in tropical but not in warm temperate and subtropical zones (Table 4). These results were consistent with the previous field investigations that *A. saltans* was a dominant species in cooler seasons (Liu et al. 2014) and *P. major* dominated in summer (Özçalkap and Temel 2011). Thus, these two species might be major characteristic species between tropical zone and the other two climatic zones.

The RDA analysis revealed that the separation between tropical and other climatic zones was mainly consistent with the changes in WT, TN and Chl-*a* (Figure 4). In addition, WT was significantly higher but Chl-*a* was significantly lower in the tropical zone than in the other climatic zones (Table S1). These results suggested that WT and Chl-*a* content might be the major factors driving the differentiation of rotifer community between tropical and subtropical/warm temperate zones. WT preference is a main factor regulating the occurrence of rotifer species. Some species are strict stenotherms, showing a definite range of temperature preference, outside which they are unable to maintain a population. For example, *T. pusilla* is a warm stenothermal species present at temperatures above 10 °C (May 1983), while *B. angularis* prefers temperatures from 12 °C to

### Table 5. Pearson moment correlation between biological factors and parameters of rotifer community structure.

|       | Chl-*a* | TSlc | AspL | Nau | Cla | Cop |
|-------|---------|------|------|-----|-----|-----|
| *S*   | 0.394** | 0.413** | 0.516** | −0.023 | 0.380** | −0.163 |
| *N*   | 0.415** | 0.584** | 0.672** | 0.09 | 0.491** | −0.094 |
| *D*   | 0.293* | 0.256* | 0.334** | −0.084 | 0.248* | −0.189 |
| *H*   | 0.201 | 0.225 | 0.349** | −0.104 | 0.164 | −0.166 |
| *E*   | −0.063 | −0.147 | −0.014 | −0.104 | −0.129 | −0.081 |
| *D*   | 0.114 | 0.105 | 0.218 | −0.095 | 0.002 | −0.087 |

Chl-*a*, content of chlorophyll *a*; TSlc, trophic state indexs; AspL, density of *Asplachna*; Nau, density of Nauplius; Cla, density of Cladocera; Cop, Copepoda; *S*, number of species; *N*, total density of rotifer; *d*, Margelef index; *H*, Shannon-Winner diversity index; *E*, Pielou evenness; *D*, Simpson index.

* *p < .05.
** *p < .01.
24°C (Bërzinš and Pejler 1989). Similarly, in the present study, *T. pusilla* was a common dominant species in all three climatic zones, but *B. angularis* was not a dominant species in warm temperate lakes. These results were consistent with the seasonal dynamics in temperate lakes (Castro et al. 2005). Taken together, WT directly affected the difference in rotifer species composition between tropical and other climatic zones. Chl-α content represents the abundance of algal food resources, and also partially reflects the trophic state of lakes (Matsushita et al. 2015), which intimately influences rotifer fecundity (Devetter and Sed’a 2003) and diversity. Overall, WT and Chl-α content were the major

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**Figure 3.** Multidimensional scaling (MDS) analysis plots of rotifer community based on different seasons (a) and different climatic zones.
factors driving the separation of samplings between tropical and subtropical/warm temperate zones.

In the present study, species number (S), rotifer density (N) and Margalef index (d) were significantly affected by season, climatic zone and/or their interaction, but Shannon–Weiner diversity index (H), Pielou evenness (E) and Simpson index (D) were not significantly affected by any of them, suggesting that the S, N and d might be better indices to describe the differences among climatic zones. In each climatic zone, stepwise regression analyses revealed different driving factors affecting the seasonal changes of rotifer community structure, indicating different regulatory mechanisms underlying seasonal variation between climatic zones.

In the warm temperate zone, S and N were significantly correlated with TP, WT, \( \text{NH}_4^+ - \text{N} \) and/or \( \text{NO}_2^- - \text{N} \), and d was significantly correlated with TP. Similarly, in North Island of New Zealand (temperate zone), rotifer assembly was most strongly associated with WT and trophic indices (Duggan et al. 2002). In addition, our findings were consistent with the established results that rotifer diversity in warm temperate lakes is positively correlated with TP (Wen et al. 2017; Spoljar et al. 2018). Among the three climatic zones, the warm temperate zone showed the greatest variation throughout the year. Thus, WT displayed stronger effects on warm temperate lakes than subtropical and tropical lakes. TP, \( \text{NH}_4^+ - \text{N} \) and \( \text{NO}_2^- - \text{N} \) are indices of trophic state. All of them affect algae and bacterial growth and subsequently mediate food availability to rotifers (Steinberg and Hartmann 1988). Among them, TP may be the most important indicator of trophic state (Jeppesen et al. 1990; OECD 1982). In the present study, TP in the two warm temperate lakes was significantly lower than in subtropical lakes, suggesting that TP might be a limiting factor in warm temperate lakes. Under the P-limited conditions, increase of TP would promote phytoplankton growth (Steinberg and Hartmann 1988) and thus increases rotifer abundance and diversity, which reflected in the present study as the significant association between S, d and TP in warm temperate lakes.

In subtropical zone, S and N were significantly associated with Chl-a content and SD. Consistently, Segers and De Smet (2008) reported that S and N showed significant spatial variations (\( p < .05 \)) and were significantly affected by the content of Chl-a and SD in subtropical lakes. Wang et al. (2010) also revealed a strong association between rotifer species

| Table 6. Stepwise regression analysis between environmental factors and the species diversity indices in different climatic zones. |
|---------------------------------------------------------------|
| **Index** | **Variables** | **Regression equation** | **\( R^2 \)** | **p** |
|----------|---------------|------------------------|----------------|------|
| **Warm temperate zone** | | | | |
| S | TP | \( Y = 6.70 + 62.50TP + 0.160WT \) | 0.613 | .02 |
| N | WT | \( Y = 10.818WT + 148.984\text{NH}_4^+ - \text{N} + 164.584\text{NO}_2^- - \text{N} - 31.501 \) | 0.864 | <.01 |
| d | TP | \( Y = 1.690 + 1.330TP \) | 0.229 | .018 |
| H | WT | \( Y = 2.483 + 0.028WT \) | 0.18 | .039 |
| E | pH | \( Y = 2.460 - 0.210pH \) | 0.209 | .025 |
| **Subtropical zone** | | | | |
| S | Chl-a | \( Y = 10.991 + 1.30 \text{Chl-a} \) | 0.305 | .021 |
| N | SD | \( Y = 1032.738 - 14.786SD + 4.404 \text{Chl-a} \) | 0.886 | <.01 |
| E | pH | \( Y = 2.460 - 0.210pH \) | 0.209 | .025 |
| **Tropical zone** | | | | |
| D | pH | \( Y = 3.225 - 0.288pH - 0.003SD \) | 0.327 | .004 |
| SD | | | 0.49 |

Chl-a, content of chlorophyll a; SD, Secchi’s depth; TP, total phosphorus; WT, water temperature; S, number of species; N, total density of rotifer; d, Margalef index; H, Shannon-Weiner diversity index; E, Pielou evenness; D, Simpson index.
distribution and Chl-a content in subtropical lakes. As discussed above, Chl-a content reflects algal abundance in water and is an indicator of food availability to rotifers. SD is closely related to suspended particle matters, mainly affected by organic matters (concentration and composition) and phytoplankton biomass (Zhou et al. 2019). In general, there is a negative correlation between SD and Chl-a content in water body (Yoshida et al. 2003). In the present study, warm temperate lakes showed higher SD but lower Chl-a than subtropical lakes ($p < .05$), also demonstrating a negative relationship between these two indices. Overall, we suggested that Chl-a content, an indicator of algae level, greatly affected rotifer species component in subtropical zone.

In addition, the Simpson index was significantly negatively associated with pH and SD in tropical zone. Horvath and Hummon (1980) indicated that low pH reduced rotifer species number, abundance and diversity. In a water body, pH is mainly influenced by the concentration of dissolved CO$_2$, which is a net result of photosynthesis and aerobic respiration. In the tropical zone, Chl-a content was relatively low, implying the CO$_2$ fixation was less active, which might be a reason for the lower pH value. Meanwhile, in the tropical zone, the green algal food supply might be insufficient and rotifers might switch to feed on bacteria and other insoluble organic matter, which is an important factor affecting SD. Thus, variation of bacteria abundance might explain why the Simpson index of the rotifer community was significantly associated with SD but not with Chl-a in the tropical zone. Clearly, more investigations are required to validate this hypothesis.

Figure 4. RDA ordination biplots of site scores and environmental variables. SD, Secchi's disk depth; TN, total nitrogen content; WT, water temperature; Cla, Cladocera density; AspL, Asplanchna density.
In summary, the seasonal variation of rotifer community structure was not obvious, but there were significant differences in environmental factors and rotifer community structures among three climatic zones. Samplings from the tropical zone were significantly separated from warm temperate and subtropical zones, which might be due to the great difference in water temperature and chlorophyll $a$ content. Subtropical lakes showed higher species number, density and diversity of rotifer than warm temperate and tropical zones. The seasonal variation of rotifer diversity was mainly driven by water temperature and trophic indices in warm temperate zone, by chlorophyll $a$ content and transparency in subtropical zone. Only the Simpson index was significantly associated with pH and transparency in the tropical zone.

**Disclosure statement**

The authors have no conflict of interest to declare.

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**Data availability statement**

All data have been included in this manuscript and supplementary materials.

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