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Bacterioplankton community responses to key environmental variables in plateau freshwater lake ecosystems: A structural equation modeling and change point analysis

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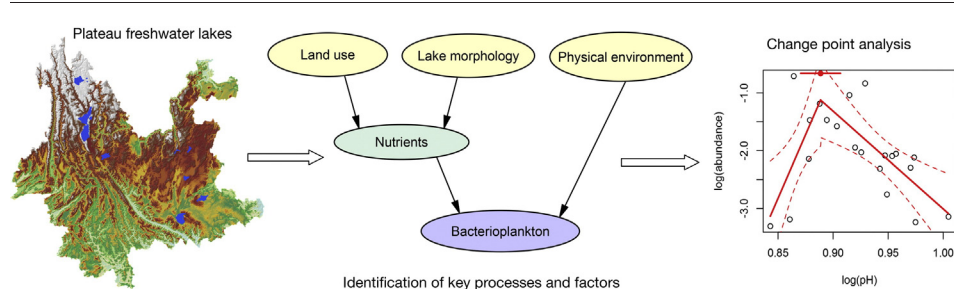
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HIGHLIGHTS

- Two data-driven models between bacterioplankton community structure and environmental variables were developed.
- Significant community thresholds were identified for pH and the percentage of agricultural area.
- An apparent shift in dominance from *Proteobacteria* to *Cyanobacteria* was observed along the gradient of agricultural area.

GRAPHICAL ABSTRACT



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ABSTRACT

Elevated environmental pressures negatively affect the bacterial community structure. However, little knowledge about the nonlinear responses of spatially related environmental variable across multiple plateau lake ecosystems on bacterioplankton communities has been gathered. Here, we used 454 pyrosequencing of 16S rRNA genes to study the associations of bacterial communities in terms of environmental characteristics as well as the potentially ecological threshold-inducing shifts of the bacterial community structure along the key environmental variables based on hypothesized structural equation models and the SEGMENTED method in 21 plateau lakes. Our results showed that water transparency was the major driving force and that total nitrogen was more significant than total phosphorus in determining the taxon composition of the bacterioplankton community. Significant community threshold estimates for bacterioplankton were observed at 7.36 for pH and 25.6% for the percentage of the agricultural area, while the remarkable change point of the cyanobacteria community structure responding to pH was at 7.74. Furthermore, the findings indicated that increasing nutrient loads can induce a distinct shift in dominance from *Proteobacteria* to *Cyanobacteria*, as well as a sharp decrease and adjacent increase when crossing the change point for *Actinobacteria* and *Bacteroidetes* along the gradient of the agricultural area.

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1. Introduction

Bacterioplankton are critical components of aquatic microbial food webs and have central roles in the biogeochemical processes related to nutrient cycling and organic matter transformation in lake ecosystems (Eiler et al., 2011). Therefore, it is particularly critical to unravel the bacterial community structure and succession to comprehensively understand the responses of ecosystems to environmental changes (Lindström et al., 2005; Crump et al., 2007).

Recent efforts have shown spatial and temporal variations in the bacterial community composition of lake ecosystems (Parveen et al., 2012; Jones et al., 2012; Liu et al., 2015b; Ruiz-González et al., 2015b; Niño-García et al., 2016), which is closely related to the physicochemical characteristics (Lindström, 2000; Sodr -Neto and Ara jo, 2008; Fortunato et al., 2012; 2013). The empirical evidence suggests that phosphorus may play an important role in determining the differences in the community structure of bacterioplankton across a wide variety of lakes (Morris and Lewis, 1992). The analysis of the field data also indicated that bacterioplankton can frequently attain maximum growth without sufficient nutrients (Morris and Lewis, 1992). In addition, salinity was found to be one of the predominant environmental factors controlling bacterial community composition in high altitude lakes (Wu et al., 2006), as well as chlorophyll-a (Liu et al., 2013). To make ecosystems more complicated, bacterioplankton with different taxon compositions may have diverse responses to environmental changes (Liu et al., 2015a). For instance, cyanobacteria as a phylum of bacterioplankton are photosynthetic prokaryotes that can form harmful cyanobacteria blooms, which are caused by environmental drivers such as nutrient and temperature factors in freshwater ecosystems (O'Neil et al., 2012; Paerl and Paul, 2012), and many cyanobacteria genera have been known to produce a wide variety of toxins that cause animal and human poisoning or health risks (O'Neil et al., 2012). Furthermore, at the watershed scale, lakes can integrate changes in the surrounding landscape and atmosphere (Pham et al., 2008; Adrian et al., 2009). So some studies indicated that land use affected the bacterial community composition (Liao et al., 2016b), even the dominant freshwater bacterial taxa were mainly recruited from the terrestrial environment (Ruiz-Gonz lez et al., 2015b).

However, to the best of our knowledge, comparatively little is known about how spatially related environmental gradients drive the potentially nonlinear responses of bacterial communities to elevated environmental pressures. Recent studies have reported abrupt changes or threshold responses in biodiversity or index metrics of biotic communities such as phytoplankton (Scheffer and Carpenter, 2003; Scheffer and Jeppesen, 2007; Cao et al., 2016), macroinvertebrate (Evans-White et al., 2009; Baker and King, 2010; Milner et al., 2016), aquatic plants (Vanacker et al., 2016), fish and periphyton (Taylor et al., 2014) along gradients of environmental variables. Nonetheless, little attention has been given to bacterioplankton, even though it is considered one of the most promising indicators of aquatic ecosystem health due to rapid and sensitive responses to environmental changes (Liu et al., 2015a).

In Yunnan province, there are a total of 21 plateau lakes with an area of 1–30 km² located in the second great topographic step of China with the mean elevation ranging from 2000 to 3000 m (Yue et al., 2005). As plateau lakes, they have been shown to be particularly susceptible to environmental change (Battarbee et al., 2002; Liu et al., 2013; Gallina et al., 2013) because of the relatively lower rate of water exchange and resilience (Liao et al., 2016b). Moreover, smaller water bodies are often neglected and not sufficiently studied (Robin et al., 2014). Here, these lakes are distributed across a range of environmental gradients with unique geographical locations and regional characteristics, which can offer insights into the critical environmental conditions and ecological mechanisms that may induce nonlinear changes to bacterioplankton community structures.

In this context, the basic objectives of the present study are (i) to develop data-driven models for determining key environmental factors influencing bacterioplankton community assemblages; (ii) to analyze changes in the community structure across environmental gradients; (iii) to detect the presence of threshold levels for key environmental variables in triggering non-linear responses of community assemblages (i.e., abrupt shifts in community composition). Our results should provide insights into the complex ecological interactions that drive bacterial community dynamics and threshold responses in plateau lake ecosystems.

2. Methodology

2.1. Sampling site and sample collection

The present study was carried out in 21 freshwater lakes- Balonghai (BLH), Bitahai (BTH), Changqiaohu (CQH), Sanjiaohai (SJH), Datunhai (DTH), Haifengshidi (HFSD), Haixihai (HXH), Jianhu (JH), Lashihai (LSH), Napahai (NPH), Puzhehei (PZH), Qinghaihu (QHH), Qingshuihai (QSH), Cibihu (CBH), Shuduhu (SDH), Tianchi (TC), Wenbihai (WBH), Xihu (XH), Yuehu (YH), Changhu (CH), Caohaishidi (CHSD). These lakes are located on the Yunnan plateau (i.e., Yunnan Province) and range from 1273 to 3612 m above sea level in southwestern China (21°8'32"N–29°15'8"N, 97°31'39"E–106°11'47"E) (Fig. 1). This area has a subtropical humid monsoon climate area with distinct dry season (from November to next April) and wet season (from May to October). The mean annual temperature ranges from 14.7 °C to 18.7 °C and annual precipitation is approximately 800–1200 mm (Li et al., 2007; Liu et al., 2012). Over 60% of the Yunnan Province area is covered by forest and grassland, whereas croplands comprise 21.8% of the plateau area (Liu et al., 2012).

Two or three sampling stations per lake were selected according to the lake size and shape in the central and nearshore zones, and sampling was carried out between August and September 2013. All water samples were stored in the dark at 4 °C and were returned to the laboratory for further processing. For the bacterial community analysis, 1000 mL mixed water from two or three samples was filtered through a 0.22 µm pore-sized polycarbonate filter (47 mm diameter, Millipore, Billerica, MA, USA). The filters were stored at –80 °C until they were needed.

2.2. Environmental variables

The water temperature (WT), pH, dissolved oxygen (DO) and salinity were measured in situ with a Hydrolab DS5 multi-parameter water quality sonde (OTT Hydromet, Germany) and Orion Star A 320C-01A (Orion, USA), separately. The water transparency was measured with a 30 cm Secchi disk (SD). The lake volume was obtained from data collection in the literature and from the local authorities. The altitude was measured with a portable GPS during field work. The land use classification and corresponding proportions were derived from the second nationwide land survey database of China in 2012, which was developed using the Digital Orthophoto Maps at a scale of 1:10,000 to identify and assess land use types (Technical specifications for the second nationwide land survey (professional standards), TD/T1014-2007). Here the land use types included agricultural land, forest land, grassland, water bodies, urban land and others.

The total nitrogen (TN), total phosphorus (TP), ammonium nitrogen (NH₄-N), nitrate nitrogen (NO₃-N), chemical oxygen demand (COD_{Mn}) and chlorophyll-a were measured at the Yunnan Key Laboratory of Pollution Process and Management of Plateau Lake-Watershed following the standard methods described by the American Public Health Association (APHA, 1998).

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