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Ordered diatom species loss along a total phosphorus gradient in eutrophic lakes of the lower Yangtze River basin, China

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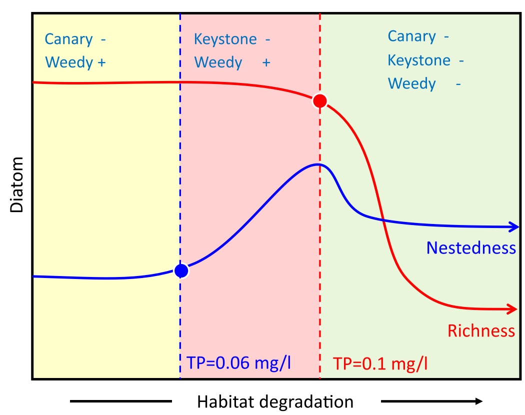
HIGHLIGHTS

- Structural indicators are seldom used to assess ecosystem health.
- Diatom in 76 lakes is used for assessing lakes' health based on nestedness.
- Nestedness reveals a lower total phosphorus threshold than diatom diversity.
- The total phosphorus threshold should be lowered to 60 μg/l for lakes in LYB, China.

GRAPHICAL ABSTRACT



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ABSTRACT

As global changes begin to affect the biosphere profoundly, the impacts on ecosystem health will become more significant. Understanding the sequence of functional species loss along an environmental or ecological gradient remains a research priority for ecosystem conservation. In this paper, nestedness, β-diversity and its components in diatom communities are used as ecological indicators of the dynamic change in functional species along environment gradients in 76 lakes of the lower Yangtze River basin, China. The results indicate that species turnover is typically the dominant component of β-diversity and that the influence of nestedness is generally low. However, changes in nestedness denote a significant threshold of lake eutrophication at a total phosphorus (TP) level of 0.06 mg/l, which is lower than the threshold indicated by diatom diversity. This finding was coupled with theoretical predictions about the successive proportional loss of 'canary' and 'keystone' species, which are replaced by 'weedy' species. These results show that nestedness of diatom communities can provide an additional metric for evaluating lake ecosystem health in this region. As management targets for nutrient control have already been introduced in the region, a revision of the identified critical phosphorus level (i.e., TP = 0.087–0.1 mg/l) to TP = 0.06 mg/l is proposed to keep lakes under low risk.

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1. Introduction

Cultural eutrophication in lakes is defined as an accelerated enrichment in nutrients, such as total phosphorus, in water caused by human activities (Hasler, 1947; Smith, 2006). Many lake ecosystems are experiencing eutrophication accompanied by serious ecological impacts due to global changes and rapid population growth (Qin et al., 2010; Alexander et al., 2017). One of the main consequences of lake eutrophication is the decline of lake ecosystem services, for example, clean water, fishery and biodiversity (Dudgeon et al., 2006; An et al., 2007; Dearing et al., 2012). This environmental issue is particularly serious in developing countries such as China (An et al., 2007; Qin et al., 2010; Le et al., 2010).

The assessment of ecological health is important for lake management. Many biological assessment methods are currently used to assess the ecological status (Birk et al., 2012; European Union, 2000). These assessments are usually based on long term monitoring records, large dataset surveys or palaeolimnological proxies (Bennion et al., 2004; Dong et al., 2008; Leira et al., 2006). Many multiple taxonomic groups, such as macrophytes, phytoplankton and phytobenthos, are used to evaluate lake's ecological health (Schaumburg et al., 2004; Kelly et al., 2016). Among these indicators, diatoms are one of the most widely employed indicators because of their diversity, high sensitivity to environmental change(s) and good preservation in sediments.

In the lower Yangtze River basin (LYB), China, hundreds of shallow lakes provide ecosystem services, such as freshwater products, irrigation, climate regulation, and flooding regulation, for approximately half a billion citizens. The Gross Domestic Product (GDP) in this region contributes to more than a third of China's GPD, and the water quality has greatly declined due to unsustainable development (Le et al., 2010). Althrough improvements have been realized following large investments (in 2006–2015) from both the central and local governments (Zhou et al., 2017), many lakes are still affected by algal blooms every summer, e.g., Taihu Lake and Chaohu Lake. Lake ecosystems in this region need a longer recovery time and more restrictive management policies (An et al., 2007). In the LYB, recovery targets and monitoring criteria for lakes are provided to local governments by scientific groups based on both reference conditions (Dong et al., 2016) and monitoring programs (through the Chinese Research Academy of Environmental Sciences (CRAES) (Liu, 2015). However, independent studies have produced different recovery targets. For example, Dong et al. (2016) specifies that the LYB lake eutrophication nutrient level for total phosphorus (TP) should be set at 0.05–0.06 mg/l based on reference conditions. In contrast, according to CRAES standards, the critical TP value has been set at TP = 0.087 mg/l (Liu, 2015). Both suggestions are well studied and based on observations from multiple lakes. However, such disagreements in criterias are an obvious source of confusion for lake managers.

Both studies consider the composition of algae but ignore spatial or temporal variability in species composition such as β-diversity. Ecological theory predicts that there is an ordered loss of functional species along an environmental or ecological gradient (Atmar and Patterson, 1993; Ulrich and Almeida-Neto, 2012). For example, the slowly replicating and weakly competitive 'canary' species would be replaced by the dominant and competitive but slowly replicating 'keystone' species in the first stage of an environmental forcing (Doncaster et al., 2016). This substitution would result in the eventual collapse of the keystone species as they are replaced by the fast-replicating but weakly competitive 'weedy' species by further forcing. Thus, communities affected by environmental forcing can experience extinctions and replacements of different functional species, which are represented by nestedness components and turnover components in β-diversity (Baselga, 2010; Baselga et al., 2007). Nestedness of species assemblages occurs when the biotas of sites with smaller number of species are subsets of the biotas at richer sites (Wright and Reeves, 1992; Ulrich and Gotelli, 2007), while turnover implies the replacement of some species by others. The portioned approach of β-diversity was first introduced by Baselga (2010) and then successfully implemented to account for species distribution related to dispersal (Viana et al., 2016; Dobrovolski et al., 2012), environmental filtering (Jamoneau et al., 2018) and climate forcing (Dobrovolski et al., 2012; Svenning et al., 2011). β-Diversity and its components may provide a useful measure of regional biodiversity with implications for conservation (Jamoneau et al., 2018; Socolar et al., 2016). It can provide information of how the environment structures metacommunities, which is also quite important for ecosystem stability studies (Loreau et al., 2001; Ives and Carpenter, 2007).

The main purpose of this study is to assess how diatom species respond to environmental forcing(s) in the LYB. We hypothesize that there is an ordered loss of species along an environmental or ecological gradient. To test this hypothesis, we calculate β-diversity in a diatom dataset (76 lakes and 200 species) from the LYB and partitioning of total β-diversity into its components (turnover and nestedness), and then calculate nestedness metrics along the main environmental gradients. We aim to provide a useful framework for assessing the mechanisms underlying metacommunity patterns along the main environmental variables in the LYB.

2. Materials and methods

2.1. Study sites and environmental variables

The diatom dataset for the LYB contains data from 76 lakes (Fig. 1). Details on the lakes and the preparation of diatom samples can be found in Yang et al. (2008) and Yao (2011). In brief, the diatoms were sampled in the deepest part of the lakes, and 1 cm of sediment surface samples were retrieved and kept at 4 °C in a fridge until laboratory analysis. The diatom slides were prepared according to standard procedures (Battarbee et al., 2010). For each sample, around 500 individuals (valves) were counted. The diatom species are expressed as relative abundance (%) in each sample for statistical analysis purposes. The environmental variables in the dataset include total phosphorus (TP), Secchi depth (SD), pH, water depth, Ca^{2+}, SO_4^{2-}, total nitrogen (TN), K^+, Na^+, Cl^- and Mg^{2+}.

2.2. Main environmental gradients in the LYB

The main environmental gradients in the LYB lakes are selected based on the following criteria: 1. the existing literature relating to the status of the lakes in this region; 2. previous studies using the same datasets (Yang et al., 2008 and Yao, 2011); 3. a multivariate constrained ordination technique, i.e., canonical correspondence analysis (CCA) (Ter Braak, 1986). The environmental variables, except pH are log-transformed prior to CCA analysis to reduce the discrepancies between measurement units and the effect of extreme values (Lepš and Šmilauer, 2003). Diatom data are square-root transformed to stabilize variance, with rare species being down-weighted in the analysis. Detrended correspondence analysis (DCA) is used to reduce the dimension of the diatom dataset so that they can be represented by a single indicator. The DCA axis one score (DCA1) represents the variability in the diatom communities.

2.3. Calculation of nestedness, β-diversity and its components

A nestedness metric is calculated based on the overlap and decreasing fill (NODF) of species distributions among sites rather than interspecific interactions within communities (Almeida-Neto et al., 2008). The Sørensen dissimilarity index (Sørensen, 1948; Koleff et al., 2003) is used to represent the total β-diversity; one calculation is based on data from multiple sites (β_{SOR}), while another is based on pairwise sites (β_{sor}) (Baselga, 2010). To partition the contribution of the different components in the β-diversity, the species replacement components (β_{sim} for pairwise sites and β_{SIM} for multiple sites) and the nestedness

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