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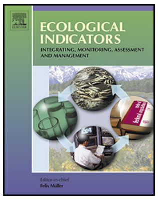

Deterministic diversity changes in freshwater phytoplankton in the Yunnan–Guizhou Plateau lakes in China

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ABSTRACT

Diversity measures reflect different aspects of a community, which are determined by different ecological processes. However, information is still limited on the ecological processes that are represented by different measures of species diversity. In this study, the primary driving factors for richness and diversity indices were tested. The possible ecological processes represented by each index were analyzed. First, the type of ecological process that governed the phytoplankton community in the Yunnan–Guizhou Plateau lakes, either deterministic or stochastic, was identified by Caswell's neutral model. The results indicate that a deterministic process governs the phytoplankton community. Second, the driving factors of richness and diversity indices were screened with mixed models. The results suggest that the variation of phytoplankton richness in different lakes or sites was primarily related to bottom-up factors. The variations in evenness and other measures based on the relative abundance were driven by both top-down and bottom-up factors, such as zooplankton biomass, and pH and mean light, respectively. Finally, although the different measures of diversity may respond to specific bottom-up or top-down processes, the responses to the two processes were not independent of each other. These findings will increase our understanding of the relationships between ecological processes and diversity measures for freshwater phytoplankton.

1. Introduction

Biodiversity represents the complexity of life and includes phenotypic, genotypic, taxonomic and ecological diversity (Wilsey et al., 2005). These characteristics are represented by important conceptual components of species diversity, such as richness, evenness, species dominance and proportional abundance. These measures were used with different frequencies in both basic and applied research. It is important to select appropriate measures to reflect ecological status and processes.

Although many measures were used to estimate diversity, they provide different information about community and even have different sensitivity to environmental changes. Species richness is largely used as the only measurement of species diversity in many studies (Ptacnik et al., 2008; Tilman, 1996; Willig, 2009). When the pattern of species diversity in communities is described simply by the number of species, important aspects of the quantitative structure of the communities are overlooked, such as which species are rare and which species are common (Ma, 2005). Many ecologists realize that species richness alone is inadequate as a diversity measure (e.g., Wilsey et al., 2005), and evenness and other measures based on relative abundance provide a significant amount of information on the variation in species diversity (Soininen et al., 2012; Wilsey et al., 2005). Therefore, ecologists use methods to include information regarding the relative species abundance in their studies (Altieri et al., 2009; Bock et al., 2007), which provides meaningful information in the functional analyses of diversity variations along environmental gradients (Huston, 1997; Skácelová and Lepš, 2014; Wilsey and Potvin, 2000). Moreover, studies that included the relative abundance obtained inconsistent results as to whether the richness, evenness or diversity indices were more sensitive to changes in the environment. For example, studies of terrestrial plants (Bowman et al., 2006) and phytoplankton (Cottingham and Carpenter, 1998) reported that evenness or diversity indices were more sensitive measures of environmental gradients than richness, whereas studies of aquatic invertebrates (García-Criado et al., 1999) and fish (Magurran and Phillip, 2001) determined that richness was more sensitive than the diversity indices that contained

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the relative species abundance. These inconsistencies might may have been observed because of differences across taxa (Cottingham and Carpenter, 1998; Stirling and Wilsey, 2001). Furthermore, a number of studies showed that there are either no relationships or only weak ones between species richness and evenness, particularly in aquatic systems; therefore, and the diversity indices of relative species abundance might represent different and independent ecological processes (Ma, 2005; Soininen et al., 2012; Stirling and Wilsey, 2001).

Diversity is a community attribute that responds to different ecological processes, and different diversity measures may measure the effect of different ecological processes on the community. Stirling and Wilsey (2001) synthesized published data and proposed that richness is related to the direct effect of migration and that evenness is related to the direct effects of biotic and abiotic interactions on diversity according to the partial regression coefficients of the Shannon–Wiener's index. Specifically, different factors affect the diversity components in different taxonomic groups because of the differences in their relationships with richness, evenness, and proportional diversity (e.g., Bock et al., 2007; McArt et al., 2012; Willig et al., 2003). For example, numerous studies found that evenness and richness responded differently to grazing (Alados et al., 2003; Altesor et al., 1998; Wilsey and Polley, 2003), predator control (e.g., Schmitz, 2003, 2008), and latitude and longitude (e.g., Stevens and Willig, 2002; Stomp et al., 2011). These studies led to important insights on the relationships between diversity measures and ecological processes and indicated that different driving forces may be affecting the variations among diversity measures. Though some studies describe ecological processes that govern both richness and evenness (Symonds and Johnson, 2008), much remains to be learned about the ecological processes reflected by different components of the species diversity.

In this study, the objective is to identify the ecological processes reflected by the values of different diversity measures, including richness (S), evenness (Pielou, J'), the Shannon–Wiener's index (H'), the Simpson's index (D_s) and the Berger–Parker's index (D_b), which covered the full range of the scale parameter of the Rényi's diversity formula and were used frequently (Magurran, 1988). The ecological processes were divided into two large separate groups, deterministic and stochastic, which included many specific processes according to the niche and neutral theory (Ellwood et al., 2009; Wang et al., 2013). First, the type of ecological process that governed the phytoplankton community in the Yunnan–Guizhou Plateau lakes, either deterministic or stochastic, was identified. The results of Caswell's neutral model (Caswell, 1976) (The model was originally developed in population genetics. It can predict the pattern of distribution in abundances and the values of species diversity.) were used as a benchmark to generate the null relationships (null models) between the richness, evenness and proportional diversity, and the predictions of the null models were tested against the empirical relationships derived from the data (Caswell, 1976). The results showed deterministic process govern the community. Second, we screened the primary driving factors of different diversity measures in the phytoplankton communities of theYunnan–Guizhou Plateau lakes using mixed models. In aquatic ecosystems, phytoplankton communities are influenced by a variety of factors that affect the species composition and diversity, which include bottom-up factors, such as nutrient availability, and top-down factors, such as grazing (Larson and Belovsky, 2013). Therefore, we subsequently divided the primary factors into the two types and discuss ecological processes related to different diversity measures. Additionally, we analyzed the independence of the top-down and bottom-up effects on the variations of the diversity measures.

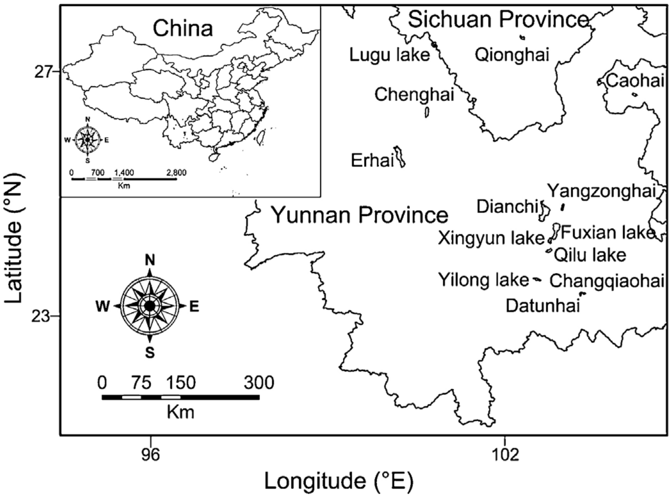

Fig. 1. Locations of the lakes on the Yunnan–Guizhou Plateau.

2. Materials and methods

2.1. Study lakes

Thirteen lakes (area >10 km^2) on the Yunnan–Guizhou Plateau, China were investigated (Table 1, Fig. 1). The climate of the Yunnan–Guizhou Plateau was controlled by the southwest monsoon from the Indian Ocean. Therefore, these lakes had similar meteorological conditions and relatively weak seasonal variations in climate. The majority of the lakes were fault lakes, with low catchment to lake ratios and different mixing regimes, and they were also polymictic, except Lake Fuxian, Lake Lugu, Lake Yangzonghai and Lake Chenghai, which were monomictic. The lakes were all freshwater and spanned a trophic gradient from oligotrophy to hypereutrophy due to different levels of human activities (Zhang et al., 2012). Within the lakes, the study sites were located at the pelagic zone of the different lake regions, where submerged vegetation was scarce. Because of the relatively large lake areas, the sites at each lake were expected to represent the different lake regions.

2.2. Sampling and analyses

Sampling was performed during the summer of 2008 from June to August. In each lake, three to seven sampling sites were established based on the area (>100 km^2, with 5–7 sites and 10–100 km^2 with 3–4 sites) and nutrient gradient of the lake. In the polymictic lakes, water samples collected with a Ruttner sampler were integrated by mixing the surface (50 cm below the surface), middle and bottom (50 cm above the bottom) samples. In the monomictic lakes, the upper, middle and lower samples from the mixed layer were mixed to obtain an integrated water samples. The mixed layer depth was determined from the vertical temperature profiles. A total of 5 L of samples were collected.

The vertical profiles of the physical and chemical parameters, including the temperature, pH and conductivity, were measured at each sample site to calculate the mean values and to determine the depth of the mixed layer using a multiparameter meter (model 6600V2; Yellow Springs Instruments, Yellow Springs, OH, USA). The transparency (SD) was measured with a Secchi disk. Five liters of water was collected for the laboratory analyses. The ammonium (NH_4^+), nitrate (NO_3^-), nitrite (NO_2^-) and dissolved inorganic phosphorus (PO_4^-) were measured using a continuous flow analyser (Skalar SA 1000, Breda, The Netherlands). The total nitrogen (TN) and total phosphorus (TP) were analyzed by peroxodisulfate