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# Dynamics and drivers of phytoplankton richness and composition along productivity gradient



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#### HIGHLIGHTS

#### GRAPHICAL ABSTRACT

- A unimodal PRR for phytoplankton in 71 lakes along the Yangtze River was observed.
- Temperature and light mainly affected phytoplankton richness and composition.
- At low productivity, competition and regulation jointly affected the dynamics.
- At high productivity, negative feedback of productivity affected the dynamics.
- Phytoplankton composition gradually became similar with increasing productivity.

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#### ABSTRACT

The shape of the productivity–richness relationship (PRR) for phytoplankton has been suggested to be unimodal, that is, the richness peaks at intermediate productivity levels. However, the mechanistic understanding for this pattern is still widely debated. In this study, we observed a unimodal PRR within 71 lakes along the Yangtze River encompassing an altitude range of 0–2700 m, and an over 2200 km distance from the upper reaches to the lower reaches. At low productivity, the competition for resources and regulatory processes jointly affected phytoplankton richness and composition, and their explanatory power depend on the gradient scale of driving factors. The variation of temperature attributing to altitudinal difference explained the majority of the variations of phytoplankton. If the altitude variation in temperature was eliminated, the explanatory power of temperature decreased from 31.7 to 7.6, and the independent effect of each resource and regulatory variable were limited and not decisive. At high productivity, the negative feedback of increased productivity (light limitation) affected the phytoplankton species richness and composition. The light-sensitive species disappeared, low-light-adapted species was retained and the phytoplankton composition gradually became similar with an increase in productivity. The findings contribute to an increased understanding of the mechanisms resulting in a hump-shaped PRR for phytoplankton.

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#### 1. Introduction

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Recently, the productivity-richness relationship (PRR) has received increasing attention due to the global diversity crisis. The relationship is of fundamental importance for the management and preservation of biodiversity and ecosystem functioning, and various PRRs, such as positive monotonic, negative monotonic, hump-shaped, and U-shaped have been documented (Reviewed by Adler et al., 2011; Fraser et al., 2015; Mittelbach et al., 2001; Waide et al., 1999). The relationship patterns and the exact mechanistic explaining these patterns are still widely debated during the last few decades (Korhonen et al., 2011; Strong, 2010). One way forward is to better understand the mechanistic processes based on the dynamics of species richness and community composition along the productivity gradients.

The PRRs depended on the scale, organism and environment (Graham and Duda, 2011; Mittelbach et al., 2001). From the perspective of scale, diversity generally was a hump-shaped function of productivity on a local scale, but monotonically increased with productivity at a regional scale (Chase and Leibold, 2002; Chase and Ryberg, 2004; Mittelbach et al., 2001; Waide et al., 1999). Positive, negative, and hump-shaped patterns were commonly found for animals at most geographical scales, and no single pattern predominated. Hump-shaped patterns were especially common (65%) in plant diversity studies with plant biomass as a productivity parameter and in studies in aquatic systems (Mittelbach et al., 2001). Resource gradients (e.g., nutrients) and regulatory gradients (e.g., temperature) can often generate a unimodal relationship (Graham and Duda, 2011).

Two of the more common PRRs are a monotonically increasing relationship, where diversity increases across all productivity levels, and a "hump – shaped" (i.e., unimodal) relationship. Where diversity is the highest at an intermediate productivity level (Dodson et al., 2000; Graham and Duda, 2011; Huston, 1994; Leibold, 1999; Mittelbach et al., 2001; Rosenzweig and Abramsky, 1993; Tilman et al., 1997). Due to the complexity of PRRs, the mechanism(s) that lead to a positive or unimodal PRR remains highly elusive (Korhonen et al., 2011). The debate about PRR mechanisms is very closely related to the debate about species coexistence mechanisms since the maintenance of species diversity is a necessary condition for a PRR (Palmer, 1994). Recent research suggests that more than one underlying mechanism can generate variability in PRR patterns in disturbed environments. Theoretical studies have suggested many productivity-diversity hypotheses (Palmer, 1994) including the intermediate disturbance hypothesis (Connell, 1978; Huston, 1979); the species-energy theory (Wright, 1983); the resource-supply ratios hypothesis (Tilman, 1982; Tilman, 1985); the combined multivariate hypothesis (Cardinale et al., 2009); and the keystone-predation hypothesis (Leibold, 1996). These hypotheses, except for the species-energy theory (which predicts a positive relationship), can predict a unimodal productivity-diversity relationship. They all address different and complementary aspects of the productivity-diversity relationship but their applicability is probably limited to special organisms and environments (i.e., plankton in an aquatic ecosystem) (Vallina et al., 2014).

Notwithstanding the debate about PRR patterns or their theoretical mechanisms, obtaining a better understanding of the processes that explain the patterns is one way to promote the understanding of the patterns themselves (Adler et al., 2011), including the dynamics of community composition along the productivity gradient. Rosenzweig and Abramsky (1993) suggested the following process to generate a unimodal species richness-productivity curve. At low productivity, resources are unable to support the rarest species, and species richness is low. As productivity increases, more species can coexist, up to a point where the number of species begins to decrease because of competition. At high productivity, a few highly competitive species monopolize all of the resources. From this perspective, competition drives both sides of the function - competition for scarce resources at low productivity and competition with competitively dominant species for abundant resources at high productivity. However, Vallina et al. (2014) suggested that selective predation may cause low diversity at low productivity while transient competitive exclusion may result in low diversity at high productivity in a marine ecosystem. This inconsistent argument indicated that there might be different mechanistic processes that generate unimodal patterns in different ecosystems. However, the underlying mechanistic processes in various ecosystems is still poorly understood, especially for often highly abundant small organisms.

In this study, we analyzed the dynamics of the community composition and richness of freshwater phytoplankton along the production gradient in 71 lakes located in the Yangtze River catchment. First, a specific PRR pattern was identified based on the average richness and the chlorophyll *a* concentration (as a measure of productivity) in each lake, and a significant unimodal curve was found. Second, the primary driving factors for the variation in richness were screened by generalized additive model (GAM) and boosted regression tree (BRT). Third, the composition dynamics of the phytoplankton along productivity were analyzed by calculating the beta diversity and species shifts along the productivity gradient. Finally, we analyzed the primary driving factors of the variation of the phytoplankton composition at the low and high ends of the PRR curve using ordination method. Based on these analysis, we address three following questions: (1) What is the PRR pattern for phytoplankton in the regional scale? Which types of phytoplankton appear or disappear along the productivity gradients? (2) Which factors drive the variation of composition and richness in phytoplankton along the productivity gradients? (3) What are the driving mechanisms for the PRR, source competition, regulatory processes or others?

#### 2. Methods

#### 2.1. Study lakes

This study investigated 71 lakes (all areas >1 km<sup>2</sup>, median/interquartile range of lake area: 31.1/65.1 km<sup>2</sup>) along the Yangtze River encompassing an altitude range of 0–2700 m, and a chlorophyll *a* range of 0.65–258.70  $\mu$ g/L from the upper reaches to the lower reaches (over 2200 km) in China (Table S1, Fig. 1). Most of these lakes are shallow and polymictic, but Fuxian Lake, Yangzonghai Lake and Chenghai Lake are monomictic. The lakes are all freshwater.

#### 2.2. Sampling and analyses

Sampling was carried out during the summer of 2008 and 2012, from June to August. Three to fourteen sampling sites in each lake were established based on the area and the nutrient gradient of the lake. A total of 223 samples were collected.

Vertical profiles of physical and chemical parameters (temperature, dissolved oxygen (DO), pH and conductivity) were measured at every sampling site to calculate the mean values and determine the depth of the mixed layer using a multiparameter meter (model 6600 V2; Yellow Springs Instruments, Yellow Springs, OH, USA). Transparency (SD) was measured with a Secchi disk. Five liters of water were collected for laboratory analyses. Ammonium (NH<sub>4</sub><sup>+</sup>), nitrate (NO<sub>3</sub><sup>-</sup>), nitrite (NO<sub>2</sub><sup>-</sup>) and dissolved inorganic phosphorus (PO<sub>4</sub><sup>-</sup>) were measured using a continuous flow analyzer (Skalar SA 1000, Breda, The Netherlands). Dissolved anions (Cl<sup>-</sup>, SO<sub>4</sub><sup>2-</sup>, K<sup>+</sup>, Na<sup>+</sup>, Ca<sup>2+</sup>, Mg<sup>2+</sup>) were analyzed by ion chromatography, inductively coupled plasma atomic emission spectroscopy or inductively coupled plasma mass spectrometry. Total nitrogen (TN) and total phosphorus (TP) were analyzed by peroxodisulfate oxidation and spectrophotometric methods (APHA, 1985). Chlorophyll *a* was extracted and measured using methods developed by Yan et al. (2004).

Integrated 500-mL phytoplankton samples were collected at each site and fixed with acid Lugol. Identification and counts were performed at the species level or genus level (some species, such as some diatoms, are difficult to identify to the species level via optical microscopy) using the most recent literature (Hu and Wei, 2006). The biovolume was calculated from the measurements of 30 organisms of each species at each site. The biomass was determined as the algal volume for each lake and converted to fresh weight assuming a specific gravity of 1 g•cm<sup>-3</sup>

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